Need for split: integrative taxonomy reveals unnoticed diversity in the subaquatic species of *Pseudohygrohypnum* (Pylaisiaceae, Bryophyta)

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We present an integrative molecular and morphological study of subaquatic representatives of the genus *Pseudohygrohypnum* (Pylaisiaceae, Bryophyta), supplemented by distribution modelling of the revealed phylogenetic lineages. Phylogenetic analyses of nuclear and plastid datasets combined with the ASAP algorithm revealed eight distinct species within the traditionally circumscribed *P. eugyrium* and *P. subeugyrium*. These species are therefore yet another example of seemingly widely distributed taxa that harbour molecularly well-differentiated lineages with narrower distribution ranges. Studied accessions that were previously assigned to *P. eugyrium* form three clearly allopatric lineages, associated with temperate regions of Europe, eastern North America and eastern Asia. Remarkably, accessions falling under the current morphological concept of *P. subeugyrium* were shown to be even more diverse, containing five phylogenetic lineages. Three of these lineages occur under harsh Asian continental climates from cool-temperate to Arctic regions, while the remaining two, referred to *P. subeugyrium* s.str. and *P. purpurascens*, have more oceanic North Atlantic and East Asian distributions. Niche identity and similarity tests suggested no similarity in the distributions of the phylogenetically related lineages but revealed the identity of two East Asian species and the similarity of two pairs of unrelated species. A morphological survey confirmed the distinctness of all eight phylogenetic lineages, requiring the description of five new species. *Pseudohygrohypnum appalachianum* and *P. orientale* are described for North American and East Asian plants of *P. eugyrium* s.l., while *P. sibiricum*, *P. subarcticum* and *P. neglectum* are described for the three continental, predominantly Asian lineages of *P.*

subeugyrium s.l. Our results highlight the importance of nontropical Asia as a center of bryophyte diversity. Phylogenic dating suggests that the diversification of subaquatic *Pseudohygrohypnum* lineages appeared in late Miocene, while mesophilous species of the genus split before Miocene cooling, in climatic conditions close to those where the ancestor of *Pseudohygrohypnum* appeared. We speculate that radiation of the *P. subeugyrium* complex in temperate Asia might have been driven by progressive cooling, aridification, and increases in seasonality, temperature and humidity gradients. Our results parallel those of several integrative taxonomic studies of North Asian mosses, which have resulted in a number of newly revealed species. These include various endemics from continental areas of Asia suggesting that the so-called Rapoport's rule of low diversity and wide distribution range in subpolar regions might not be applicable to bryophytes. Rather, the strong climatic oscillations in these regions may have served as a driving force of speciation and niche divergence.

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Abstract

21 We present an integrative molecular and morphological study of subaquatic representatives of
22 the genus *Pseudohygrohypnum* (Pylaisiaceae, Bryophyta), supplemented by distribution
23 modelling of the revealed phylogenetic lineages. Phylogenetic analyses of nuclear and plastid
24 datasets combined with the ASAP algorithm revealed eight distinct species within the
25 traditionally circumscribed *P. eugyrium* and *P. subeugyrium*. These species are therefore yet
26 another example of seemingly widely distributed taxa that harbour molecularly well-
27 differentiated lineages with narrower distribution ranges. Studied accessions that were previously
28 assigned to *P. eugyrium* form three clearly allopatric lineages, associated with temperate regions
29 of Europe, eastern North America and eastern Asia. Remarkably, accessions falling under the
30 current morphological concept of *P. subeugyrium* were shown to be even more diverse,
31 containing five phylogenetic lineages. Three of these lineages occur under harsh Asian
32 continental climates from cool-temperate to Arctic regions, while the remaining two, referred to
33 *P. subeugyrium* s.str. and *P. purpurascens*, have more oceanic North Atlantic and East Asian
34 distributions. Niche identity and similarity tests suggested no similarity in the distributions of the
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36 similarity of two pairs of unrelated species. A morphological survey confirmed the distinctness
37 of all eight phylogenetic lineages, requiring the description of five new species.
38 *Pseudohygrohypnum appalachianum* and *P. orientale* are described for North American and East
39 Asian plants of *P. eugyrium* s.l., while *P. sibiricum*, *P. subarcticum* and *P. neglectum* are

40 described for the three continental, predominantly Asian lineages of *P. subeugyrium* s.l. Our
41 results highlight the importance of nontropical Asia as a center of bryophyte diversity.
42 Phylogenic dating suggests that the diversification of subaquatic *Pseudohygrohypnum* lineages
43 appeared in late Miocene, while mesophilous species of the genus split before Miocene cooling,
44 in climatic conditions close to those where the ancestor of *Pseudohygrohypnum* appeared. We
45 speculate that radiation of the *P. subeugyrium* complex in temperate Asia might have been
46 driven by progressive cooling, aridification, and increases in seasonality, temperature and
47 humidity gradients. Our results parallel those of several integrative taxonomic studies of North
48 Asian mosses, which have resulted in a number of newly revealed species. These include various
49 endemics from continental areas of Asia suggesting that the so-called Rapoport's rule of low
50 diversity and wide distribution range in subpolar regions might not be applicable to bryophytes.
51 Rather, the strong climatic oscillations in these regions may have served as a driving force of
52 speciation and niche divergence.

Introduction

55 The genus *Pseudohygrohypnum* was introduced by Kanda (1977) to accommodate two autoicous
56 species of subaquatic pleurocarpous mosses, previously placed in the genus *Hygrohypnum*, that
57 have serrulate leaf apices and well-differentiated, coloured and often excavate alar cells.
58 However, this novelty was not broadly accepted until molecular phylogenetic data for
59 *Hygrohypnum/Pseudohygrohypnum eugyrium* first appeared. According to the phylogenetic
60 reconstruction by Gardiner et al. (2005), the generitype of *Hygrohypnum*, *H. luridum* (Hedw.)
61 Jenn. clearly belongs to Amblystegiaceae, while *H. eugyrium* appears in a clade assigned to
62 Pylaisiaceae. A similar result was published by Oliván et al. (2007), that also showed the close
63 relationship between *H. eugyrium* and *H. subeugyrium*. Based on molecular data later published
64 by Gardiner et al. (2005), Ignatov & Ignatova (2004) accepted the genus *Pseudohygrohypnum*
65 and transferred *H. subeugyrium* Renauld & Cardot to it. Kučera et al. (2019) in their morpho-
66 molecular revision of the genus *Hypnum* suggested broadening of the concept of
67 *Pseudohygrohypnum* by placing a suite of non-aquatic species from sect. *Fertilia* (*H. calcicola*,
68 *H. fauriei, H. fertile*, etc.) within it. Currently, according to the Tropicos online database
69 (http://www.tropicos.org/name/35001387, accessed 28 Oct 2021) and The Bryophyte
70 Nomenclator (https://www.bryonames.org/nomenclator?group=Pseudohygrohypnum, Brinda &
71 Atwood, 2021), the genus includes ten accepted species and one species in synonymy.
72 Although the diversity of *Pseudohygrohypnum* in its current delimitation is largely concentrated
73 in temperate East Asia, subaquatic or hygrophytic species of the genus in the region remain
74 insufficiently known and have generally been treated as synonymous with the species from
75 Europe and Eastern North America, i.e., *P. eugyrium* and *P. subeugyrium* (Jamieson, 1976;
76 2014; Czernyadjeva, 2003; Hu et al., 2008; Blockeel, Kiebacher & Long, 2019). Japanese
77 authors have also accepted two additional taxa for eastern Asia, *Hygrohypnum purpurascens*
78 Broth. (Kanda, 1977; Iwatsuki, 1991; Noguchi, 1991) and *H. subeugyrium* var. *japonicum*
79 Cardot (Iwatsuki, 1991; Noguchi, 1991), but these have not become more widely accepted.

80   Potentially unnoticed diversity was suspected due to conflicts between the descriptions and
81   illustrations of *P. eugyrium* and *P. subeugyrium* based on plants from different areas of their
82   distribution. While Lüth (2019) and Blockeel et al. (2019) illustrated European *P. subeugyrium*
83   as lacking a central strand, and the same is true for the illustration of North Siberian plants by
84   Czernyadjeva (2003), Ignatov & Ignatova (2004) depicted a well-developed central strand based
85   on a specimen from Bashkiria (south Ural Mountains). In addition, the latter plants are
86   substantially smaller, with leaves shorter than 1 mm and denser branching, reminiscent of non-
87   aquatic species of the genus. Similar discrepancies exist in descriptions of *P. eugyrium*: while
88   Jamieson (1976) emphasized coloration of the alar cells as quite distinctive for the species,
89   Kanda (1977) did not mention this for Japanese plants, which agrees with plants from the
90   Russian Far East that have hyaline or greenish, rarely partly brownish but never reddish alar
91   groups. In addition to differences in the morphological descriptions of the plants, the unusual
92   distribution pattern of *P. subeugyrium* s.l. also raised doubts about its integrity; in Europe and
93   North America, it is associated with areas of rather mild oceanic and suboceanic climates, very
94   different from the climatic conditions under which the species occurs in north Siberia
95   (Czernyadjeva, 2003; Fedosov & Ignatova, 2005; Ivanov et al., 2017) or Transbaikalia (Afonina,
96   2009; Ivanov et al., 2017). Considering recent treatments of species with seemingly disjunct
97   distributions (e.g., Vigalondo et al., 2019), we decided to check the identity of Asian subaquatic
98   *Pseudohygrohypnum* species using molecular data, which were so far only available for plants
99   from subatlantic populations. We also decided to verify the somewhat arguable monophyly of
100 *Pseudohygrohypnum* as defined by Kučera et al. (2019) with respect to the different topologies
101 obtained by Câmara et al. (2018) and Schlesak et al. (2018) using additional plastid markers. To
102 account for differences in the ecology of subaquatic *Pseudohygrohypnum* species in different
103 areas of their distribution, we attempted to employ species distribution modelling within an
104 integrative taxonomic framework.
105
106 ## Materials & Methods
107
108 *Molecular phylogenetic methods*
109 The study is based on the analysis of plants currently referrable to *Pseudohygrohypnum*
110 *eugyrium* and *P. subeugyrium*, for which 59 accessions were included that cover their known
111 distribution area. To place our data in a broader phylogenetic context, we added a selection of
112 non-aquatic representatives of the genus and outgroup Pylaisiaceae taxa identified using the
113 dataset of Kučera et al. (2019). In total, 104 accessions were included in our study, of which 70
114 represent seven currently recognized species of the genus *Pseudohygrohypnum*: *P. eugyrium*
115 (16), *P. subeugyrium* (43), *P. calcicola* (2), *P. densirameum* (2), *P. fauriei* (3), *P. fertile* (2), and
116 *P. skottsbergii* (2). Molecular sampling included the nuclear internal transcribed spacers 1, 2 and
117 5.8S rRNA gene as well as the plastid *trnL–trnF* region and *atpB–rbcL* spacer that were used by
118 Kučera et al. (2019; see also Stech & Quandt, 2010 for details). In addition, we added newly
119 sampled sequences for the *rps4–trnS* region, *rbcL* gene and *trnK–psbA* region; the two latter

120   regions were obtained only for selected accessions from each lineage that were later identified as
121   species. Specimen vouchers and GenBank accession numbers are provided in the Supplemental
122   materials 1.
123   The laboratory protocols followed our previous studies (Gardiner et al., 2005; Fedosov et al.,
124   2016b and Kučera et al., 2019). For the *rbcL* gene and *trnK–psbA* region, we designed new
125   primers based on published sequences for other hypnalean chloroplast genomes (see
126   Supplemental materials 2). The length of the *trnK–psbA* region (ca. 2600 bp) necessitated
127   amplification and sequencing in 4 parts; similarly, the *rbcL* gene (1428 bp) was amplified and
128   sequenced in two parts. Sequences were aligned using the online interface of MAFFT v. 7.487
129   (Katoh & Standley, 2013), applying the E-INS-i strategy and otherwise default settings before
130   manual fine-tuning in BioEdit (Hall, 1999). Indels were scored using the simple indel coding
131   approach (Simmons & Ochoterena, 2000) in SeqState 1.4.1 (Müller, 2005). One of two
132   alternative states of a highly homoplastic inversion in the *trnL–trnF* spacer, missing in
133   subaquatic species of *Pseudohygrohypnum* and within the genus present only in *P. fauriei* was
134   inserted as a reverse complement and coded as a deletion. that enables considering this state as
135   binary code by SeqState and keeping further changes in the alternative state available for
136   analysis. In the single gene analyses, the ITS matrix (113 terminals, 930 positions, 161 indels)
137   was divided into three partitions, which corresponded to ITS1, 5.8S rRNA gene and ITS2;
138   plastid markers were divided into three partitions, one for cds, one for coding tRNAs, and one
139   for non-coding parts (spacers and introns), except for *atpB–rbcL* which was coded as a single
140   partition. In the combined cp dataset plastid data (*atpB–rbcL*, *trnL–trnF*, *rps4*, *trnK–psbA*, *rbcL*,
141   named cpATRKR dataset hereafter, with 112 terminals, 5995 positions, 112 indels), the matrix
142   was divided into two partitions, one for *trnK–psbA* plus *rbcL* where a significant part of data was
143   absent, and one for *atpB–rbcL* plus *trnL-trnF* plus *rps4 trnS*, as suggested by Partitionfinder
144   2.1.1 (Lanfear et al., 2017). Phylogenetic analyses were performed using Bayesian Inference (BI)
145   estimated by MrBayes 3.2.7a (Ronquist et al., 2012) and Maximum Likelihood (ML) analysis
146   calculated in RAxML 8.2.12 (Stamatakis, 2014). BI was run in two parallel analyses, each
147   consisting of six Markov chains, 10 000 000 generations with the default number of swaps and a
148   sampling frequency of one tree each 2000 generations, the chain temperature was set at 0.02. The
149   GTR+G+I substitution model was selected for nuclear and combined plastid dataset based on the
150   Akaike information criterion assessed by MegaX (Kumar et al. 2018). The convergence between
151   runs assessed as an average split deviation frequency lower than 0.01 was reached after 0.5 – 1
152   million generations. Additionally, PSRF values were checked to be close to 1.000 and ESS
153   values were checked to be higher than 200 using Tracer v.1.7.2 (Rambaut et al. 2018).
154   Consensus trees were calculated after omitting the first 25% trees as burn-in. In ML analysis,
155   robustness of the nodes was assessed using the thorough bootstrapping algorithm (Felsenstein,
156   1985) with bootstopping based on the extended majority rule consensus tree criterion. Analyses
157   were performed on the Cipres Science Gateway (http://www.phylo.org/portal2) on XSEDE
158   (Miller, Pfeiffer & Schwartz, 2010) and MetaCentrum VO computing infrastructure
159   (https://metavo.metacentrum.cz/). Trees were rooted by two accessions of *Stereodon*, based on

160 the topology published by Kučera et al. (2019), and visualized using FigTree 1.4.3 (Rambaut,
161 2009).
162 Since the ingroup topologies inferred from the nuclear and plastid markers differed in their
163 topology at multiple well-supported nodes, the combined nr & cp dataset was not analysed. As
164 the incongruence between nr and cp-based topologies might imply reticulate evolution or
165 incomplete lineage sorting, we used the Neighbour Net method implemented in SplitsTree
166 v.4.16.2 (Huson & Bryant, 2006) to visualize affinities between lineages within the crown
167 Pylaisiaceae clade (i.e. the clade remaining after the *Aquilonium* clade split). The split trees were
168 built based on nr ITS and cp *atpB–rbcL*, *trnL–trnF*, *rps4* (cp ATR hereafter) datasets with 1000
169 bootstrap iterations. Testing for best schemes of assembling species by automatic partitioning of
170 lineages to account for lumping vs. splitting hypotheses in *Pseudohygrohypnum* was performed
171 for 64 *Pseudohygrohypnum* accessions for which all-four markers were available with unscored
172 indels using the online interface of ASAP (https://bioinfo.mnhn.fr/abi/public/asap/, Puillandre,
173 Brouillet & Achaz, 2020) with the default parameters. Statistics for ITS and cp ATR
174 *Pseudohygrohypnum* alignments were as follows: alignment length 930 and 1835 bp
175 respectively; 92 and 114 sites were variable, 79 and 108 were parsimony informative. Since the
176 cp and ITS datasets resulted in different topologies, we ran the ASAP test for the nuclear and cp
177 data separately, searching for a scheme of dividing the dataset into species which (1) would not
178 challenge accepted species concepts outside the two subaquatic *Pseudohygrohypnum* species,
179 under consideration in the present study; (2) could be assigned to both the plastid and nuclear
180 datasets; (3) would not contradict the topologies of the phylogenetic trees (since ASAP uses
181 similarity of pairwise genetic distances rather than phylogenetic inferences), (4) would have
182 threshold distance values of at least 0.005 for the ITS dataset (minimal barcode gap considered
183 as default by ASAP) and 0.001 for the less variable cpATR dataset; (5) would have a high
184 probability rank and all the suggested species also with a high probability rank, and (6) would
185 have the lowest summarized ASAP score among all proposed schemes which meet criteria 1–5.
186 In addition, within and between group nucleotide uncorrected p-distances in the ITS and cp ATR
187 datasets were estimated within the genus *Pseudohygrohypnum* using Mega X (Kumar et al.,
188 2018). Analyses were conducted using the Maximum Composite Likelihood model (Tamura, Nei
189 & Kumar, 2004) for the 64 *Pseudohygrohypnum* accessions in both the nr ITS and cp ATR
190 datasets.
191 Divergence time estimates were calculated in BEAST 1.10.4 (Suchard et al., 2018) based on a
192 specially designed exATRKRN dataset (73 accessions, 6819 sites without indel coding), which
193 added the mitochondrial *nad5* gene intron to the ATRKR dataset. In this dataset, Pylaisiaceae
194 was represented by 29 accessions (with a single accession of Pylaisiaceae per species/molecular
195 lineage) and were supplemented by representatives of Leskeaceae, Amblystegiaceae,
196 Brachytheciaceae, and other lineages of crown Hypnale for which fossil records were available
197 (Laenen et al., 2014). Accessions of *Enrothia polyclada* (Müll. Hal.) Ignatov & Fedosov,
198 *Homalia trichomanoides* (Hedw.) Brid. and *Leptodon smithii* (Dicks. ex Hedw.) F. Weber & D.
199 Mohr were included as outgroup, used for rooting. The analysis was run for 100 million of

200 generations and the Yule model was set as the tree prior. The uncorrelated lognormal relaxed
201 clocks were set for all partitions individually. Calibration points of five fossil records from Baltic
202 and Dominican amber are shown in Table 3 in the Appendix (See Huttunen et al., 2008 for
203 discussion). We checked the convergence of the runs and that the effective sample sizes were all
204 above 200 by exploring the likelihood plots using Tracer v1.5 (Rambaut et al., 2018). The initial
205 10% of trees were discarded as burn-in. A lineage through time plot was generated in Tracer
206 using log and tree outputs from BEAST.
207
208 *Morphological methods*
209 The molecular phylogenetic study was complemented by a morphological revision of subaquatic
210 *Pseudohygrohypnum* species in MW, MHA, LE, NSK, CBFS, and MO. In addition to standard
211 microscopic observations, peristomes of selected specimens were studied by the Scanning
212 Electron Microscope Jeol 6380, coated by gold without any additional preparation. Light
213 microscope observations were made under a Zeiss Axioplan Imaging microscope, images were
214 prepared using the 3D digital microscope Hirox RH-2000.
215
216 *Distribution modelling methods*
217 To account for heterogeneity/differences in species distribution in terms of their ecology and
218 formalize it within the integrative taxonomic framework, we employed species distribution
219 modelling using the MaxEnt 3.4.1 software package (Phillips, Anderson & Schapire, 2006;
220 Phillips & Dudik 2008), followed by niche identity, similarity and divergence tests.
221 Revised georeferenced specimens from MW, MHA, LE, NSK, and MO supplemented by
222 occurrences with coordinates with precision better than 0.01° downloaded from GBIF, the Moss
223 Flora of Russia (Ivanov et al., 2017) database and literature data were used as an input for
224 distribution modelling. Species distribution models (SDMs) were obtained for each lineage,
225 revealed by phylogenetic analyses with more than 15 available occurrences. Based on the
226 revealed distribution pattern of the molecularly defined lineages, GBIF occurrences were used
227 only for three molecular lineages, "*eugyrium* 1", "*eugyrium* 2" and "*subeugyrium* 1" (see Results
228 section), which are well differentiated from other lineages geographically, for their European and
229 East North American localities, since occurrences from other areas were assumed to represent
230 different lineages. In this way, accessions of *P. eugyrium* from Europe were automatically
231 referred to the lineage A, while those from North America were referred to lineage B.
232 Theoretically, misidentifications between *P. subeugyrium* s.str. and *P. eugyrium* lineage A in
233 Europe and lineage B in North America may influence the results of modelling, but their
234 confusion is not very common except for older American specimens of *P. subeugyrium*, which
235 are often kept under the name *P. eugyrium*. To account for this possibility, we excluded *P.*
236 *eugyrium* specimens collected before 1970.
237 Seven non-correlated bioclimatic layers were chosen as variables for modelling (Table 4 in the
238 Appendix). The input bioclimatic layers were downscaled to 2.5 arc second resolution and
239 restricted to North America and Eurasia in QGIS 3.16.1 (QGIS.org 2021 m) and ArcGIS 10.3

240 (ESRI Inc.) software. Since herbarium data are often spatially biased, we created a bias
241 correcting file using the biased prior method to estimate the relative search effort through
242 modelling in MaxEnt of all moss herbarium occurrences from the GBIF and Moss Flora of
243 Russia databases as a single target group (Phillips et al., 2009; Merow et al., 2013; Fourcade et
244 al., 2014; El-Gabbas & Dormann, 2018a,b). The resulting output layer can be considered to
245 reflect sampling effort and was used for non-uniform weighting of background points during
246 modelling. The spatial k-fold cross-validation approach (Shcheglovitova & Anderson, 2013;
247 Radosavljevic & Anderson, 2014) implemented in SDMtoolbox 2.4 (Brown, Bennett & French,
248 2017) for ArcGis was used to choose feature classes and B-regularization. It allowed us to
249 choose 10 models from among the 30 with the lowest omission error rate and with maximum
250 AUC. The final models were selected from this set by both Akaike and Bayesian information
251 criteria (Warren & Seifert 2011; Warren et al., 2014) implemented in ENMTools 1.4.4 (Warren,
252 Glor & Turelli, 2010).
253 To compare the environmental niches of the revealed *Pseudohygrohypnum* lineages we used the
254 identity and similarity tests based on Schoener's D and the Hellinger's I metrics (Warren, Glor &
255 Turelli, 2008) in ENMTools 1.4.4. At first, we tested pairs of revealed lineages for niche
256 identity. This test is used to ask whether the models generated from two or more species are
257 more different than would be expected if they were drawn from the same underlying distribution
258 (Warren, Glor & Turelli, 2008). For pairs with non-identical niches, we performed the niche
259 similarity background test to determine whether the models drawn from populations with
260 partially or entirely non-overlapping distributions are more different from one another than
261 expected by random chance (Warren, Glor & Turelli, 2008). During both tests, 100 iterations of
262 random points (pseudoreplicates) were assigned in two directions for each of the species pairs.
263 To visualize the environmental niche similarity/difference, box-plots of nine selected bioclimatic
264 variables, in which the divergence was most remarkable, were drawn in GraphPad Prism 8.4.3
265 (GraphPad software, LLC). Distributions of 8 revealed lineages along these variables were
266 checked for significance of the median difference using the Mann-Whitney U Test in Past v4
267 (Hammer, Harper & Ryan, 2001). Values of 7 bioclimatic variables used for modelling in
268 observed localities assigned to the revealed phylogenetic lineages of subaquatic
269 *Pseudohygrohypnum* were then used as an input for PCA in the pca3d package for R (R Core
270 Team, 2021).
271
272 The electronic version of this article in Portable Document Format (PDF) will represent a
273 published work according to the International Code of Nomenclature for algae, fungi, and plants
274 (ICN), and hence the new names contained in the electronic version are effectively published
275 under that Code from the electronic edition alone. In addition, new names contained in this work
276 which have been issued with identifiers by IPNI will eventually be made available to the Global
277 Names Index. The IPNI LSIDs can be resolved and the associated information viewed through
278 any standard web browser by appending the LSID contained in this publication to the prefix

279 "http://ipni.org/". The online version of this work is archived and available from the following
280 digital repositories: PeerJ, PubMed Central SCIE, and CLOCKSS.
281
282

283 **Results**

284

285 *Molecular phylogenetic analyses*
286 The topology obtained from the concatenated plastid data matrix differs at several nodes from
287 the topology inferred from nuclear ITS data (Fig. 1). Plastid data support the monophyly of
288 *Pseudohygrohypnum* as defined by Kučera et al. 2019 (PP1/0.99, BS73/58, see caption to Fig. 1),
289 while ITS data render *Pseudohygrohypnum* paraphyletic, forming a grade of lineages basal to the
290 crown Pylaisiaceae, containing accessions of *Pylaisia*, *Homomallium*, *Buckia*, *Calohypnum*,
291 *Ectropothecium,* and *Vesicularia*. Subaquatic representatives of *Pseudohygrohypnum* appear in
292 eight lineages interspersed among non-aquatic species; the relationships among these lineages
293 also differ between the plastid and nuclear datasets. Plants with a differentiated stem epidermis
294 (hitherto named *P. eugyrium*) appear in three fully supported lineages, with the European
295 (lineage A) and eastern North American (lineage B) lineages forming together a fully supported
296 monophyletic clade of amphi-Atlantic plants, while the Far Eastern lineage C occurs well outside
297 of this clade and instead among other clades composed of subaquatic *Pseudohygrohypnum*
298 species. Plants without a differentiated epidermis (hitherto named *P. subeugyrium* and *P.*
299 *purpurascens* if recognized from the former) form a fully supported monophyletic clade based
300 on plastid data with five recognizable internal lineages which mostly also receive full support,
301 however, based on ITS data, one of these internal lineages (lineage E) appears outside of the
302 clade containing the rest of *P. subeugyrium* s.lat. lineages.
303 Four *P. subeugyrium* s.l. accessions have different clade assignments in the nr- and cp-based
304 topologies (marked x in the tree in Fig. 1). One accession of *P. subeugyrium* clade C in the ITS
305 tree appears in clade B of the cp-based tree, and three accessions of clade E based on ITS data
306 occur in clade D of the plastid tree.
307 NN split networks (Fig. 2) reveal the same entities within the subaquatic *Pseudohygrohypnum*
308 species. Although they are less divergent than the currently accepted mesophytic
309 *Pseudohygrohypnum* species included in the analysis, these entities are nearly identical in
310 composition in the networks constructed from nuclear and plastid markers (excepting the four
311 aforementioned specimens), and have reliable support inferred from both the plastid and nuclear
312 datasets or only from the nuclear dataset. Mean nucleotide p-distances between identified
313 lineages in most cases are much higher than the mean within-group p-distances. The latter are
314 mostly below 0.001 in the cp dataset and 0.005 in the ITS dataset, while between-group distances
315 exceed 0.003 in the the cp dataset and 0.010 in the ITS dataset (Supplemental Table 5). The
316 smallest between-group distances are observed between *P. eugyrium* lineages A and B; and *P.*
317 *subeugyrium* lineages A, B, C, and in the cp dataset also D and E. Although the mean distances

318   between *P. eugyrium* lineages A and B and *P subeugyrium* lineages D and E are low according
319   to cp data, they are rather high in the ITS dataset.
320   Among the 10 best schemes proposed by ASAP for dividing the plastid dataset into species, the
321   13 species scheme which recognizes all letter-named lineages as separate species in addition to
322   the already existing ones (Fig. 1, 2 in online Appendix) has the second-best score after an
323   unrealistically oversplitting 22-species scheme. Two other schemes, which agree with most
324   criteria specified in the Methods section, a 12-species scheme (with *subeugyrium* lineage D and
325   E merged) and an 8-species scheme (*subeugyrium* lineage A-E merged) have worse scores and
326   contradict the topology of the ITS based phylogenetic trees, where *subeugyrium* lineage E is
327   found well outside of the *P. subeugyrium* clade. Among the 10 best schemes proposed for the
328   ITS dataset, only the 13-species scheme was shared with the best-scoring schemes based on cp
329   data. Although the 13-species scheme was not proposed as an optimal one for the ITS dataset,
330   the similar 12 species scheme with *P. subeugyrium* C and D merged has a high score among
331   schemes proposed for ITS. However, the topology of the phylogenetic trees precludes further
332   consideration of this 12-species scheme. Thus, a 13-species scheme is the only one, which meets
333   the criteria specified in the methods section and is justified as a working hypothesis supporting
334   specific status for *P. purpurascens* and further splitting of the traditional concepts of *P. eugyrium*
335   and *P. subeugyrium* into 7 species based on molecular data.
336   The topology of the tree, inferred from the expanded dataset, designed for dating
337   *Pseudohygrohypnum* diversification, is well resolved and statistically supported excepting a few
338   deep nodes (Fig. 3). Topology within the Pylaisiaceae clade is congruent with the one, obtained
339   from the plastid dataset (Fig. 1b), but demonstrates higher support for the clades within the genus
340   *Pseudohygrohypnum*. The *Pseudohygrohypnum* clade splits into two weakly supported clades,
341   first of which accommodates *P. fauriei*, *P. fertile*, *P. skottsbergii*, *P. eugyrium* A and B while the
342   second one comprises *P. eugyrium* C, *P. calcicola*, and *P. subeugyrium* s.l. According to the
343   divergence dates, inferred based on the expanded dataset, the split of two major clades of
344   *Pseudohygrohypnum* is estimated at 28.96 (23.93-34.44) Ma. Splitting of the *P. eugyrium* C
345   lineage from its closest relative, *P. calcicola* is estimated at 21.26 (15.58-26.8) Ma. Average
346   estimates for splits of the mesophilous *Pseudohygrohypnum* lineages vary and are 26.78 Ma for
347   *P. fauriei* (the rather closely related *P. densirameum* was not included in this dataset), 25.58 for
348   *P. fertile* and 23.85 Ma for *P. skottsbergii*. Splitting of the two Atlantic lineages of *P. eugyrium*
349   is estimated to have occurred 10.56 (6.25-15.5) Ma, and the basal radiation of *P. subeugyrium* at
350   10.63 (7.22-14.75) Ma.
351
352   *Morphological analyses*
353   The overall morphology and leaf anatomy of subaquatic mosses is often strongly affected by the
354   hydrological regime of their habitat and this is especially true for *Pseudohygrohypnum*.
355   However, our morphological survey has shown that the eight above-described molecularly
356   defined lineages are also reasonably distinct morphologically (see Table 1 and Figs. 4-7) and
357   therefore ought to be recognized as distinct species. In addition to diagnostic characters, plants

358   previously referred to *P. subeugyrium* differ in their habit (Fig. 4). *Pseudohygrohypnum*
359   *subeugyrium* lineages A and C also differ in plant coloration: lineage A (*P. subeugyrium* s.str.) is
360   typically represented by olivaceus to brownish plants, while plants of lineage C are typically
361   purplish to vinaceous. With its typically complanate shoots and weakly falcate, nearly plane and
362   acute leaves, plants from lineage B resemble *Hygrohypnum luridum* (Hedw.) Jenn., Asiatic
363   morphotypes of *Calliergonella lindbergii* (Mitt.) Hedenäs, or *Stereodon pratensis* (W.D.J. Koch
364   ex Spruce) Warnst. At the same time, specimens of lineage B from Primorsky Territory resemble
365   plants from the lineages C and D in habit, although differing in having a well-developed central
366   strand and different alar group shape. Plants of the molecularly closely related lineages D and E
367   are quite dissimilar morphologically. While lineage E resembles *Campylium bambergeri*
368   (Schimp.) Hedenäs, Schlesak & D. Quandt in habit having narrow and strongly falcate leaves
369   and differing from it and all other *Pseudohygrohypnum* species in its much smaller size, plants of
370   lineage D are rather large and resemble *Calliergonellopsis dieckii* (Renauld & Cardot) Jan
371   Kučera & Ignatov. In most cases, microscopic examination allows identification of the newly
372   recognized species, although we observed problematic specimens which we discuss in the
373   Taxonomy section below.
374
375   *Distribution modelling analyses*
376   Phylogenetic lineages of subaquatic *Pseudohygrohypnum* as revealed by our analyses are quite
377   distinct geographically (Fig. 8). Results of the pairwise comparison using Mann-Whitney U Test
378   (Appendix 7) suggest significant differences in their distribution along the nine analysed
379   bioclimatic variables. Only for one pair of lineages (*eugyrium* C and *subeugyrium* C) no
380   significant difference of medians was revealed, while in all other pairs significant median
381   difference was suggested for least four variables. All three lineages previously assigned to *P.*
382   *eugyrium* occur exclusively in mild climatic conditions influenced by oceanic air masses.
383   Observed occurrences of these species originate exclusively from the areas with BiO1 above 0°C
384   (Fig. 9). The same is true for two species of the *P. subeugyrium* complex, so far referred to as
385   lineages A and C. Contrary to these five, three lineages recognized within *P. subeugyrium* s.l.
386   generally occur in colder environments, largely associated with a mean annual temperature
387   below 0°C. Plants with markers combining ITS and cp loci characteristics for different lineages
388   of *P. subeugyrium* largely occur in areas with conditions suitable for both lineages. BiO2 can be
389   considered as a proxy for air moisture; occurrences of "continental" lineages B and D of *P.*
390   *subeugyrium* generally are associated with higher BiO2 values, but it is rather low in continental
391   lineage E and high in *P. eugyrium* lineage B. Likewise, BiO7 indicates temperature seasonality;
392   occurrences of *P. subeugyrium* lineages B, D and E are confined to areas with rather high
393   temperature seasonality, while *Pseudohygrohypnum eugyrium* as well as *P. subeugyrium*
394   lineages A and C inhabit areas with lower BiO7 values; European and American lineages of *P.*
395   *eugyrium* are noticeably different in their relation to BiO7.
396   The same two groups, "suboceanic" (*eugyrium* A-C, *subeugyrium* A, C) and "continental"
397   (*subeugyrium* B, D, E) appeared in relating the 8 subaquatic *Pseudohygrohypnum* lineages to the

398   annual rate of precipitation (BiO12), but the distribution of *P. subeugyrium* lineage D along this
399   gradient overlaps with *P. subeugyrium* lineage A, rather than with lineage E. Two East Asian
400   lineages, *P. eugyrium* C and *P. subeugyrium* C occur in areas with higher precipitation rates than
401   the Atlantic suboceanic lineages (Fig. 9). The three Atlantic lineages are confined to areas with
402   low seasonality of precipitations (BiO15); north Siberian and two East Asian lineages occur
403   under much higher precipitation seasonality, and *P. subeugyrium* clades B and D, which occur in
404   inland boreal areas of Asia, grow under even higher BiO15 values. Precipitation of the driest
405   quarter (BiO17) in inland north Asian areas inhabited by *P. subeugyrium* B, D and E is
406   significantly lower than in the areas where other lineages of subaquatic *Pseudohygrohypnum*
407   occur. At the same time, precipitation of the warmest quarter (BiO18) in the ranges of East Asian
408   species *P. eugyrium* C and *P. subeugyrium* C exceeds areas where the other lineages occur while
409   subarctic *P. subeugyrium* lineage E survives in the driest summer conditions. Mean monthly
410   precipitation in the coldest quarter (BiO19) is rather high in the areas where suboceanic *P.*
411   *eugyrium* A-C and *P. subeugyrium* A, C lineages occur, and much lower within the ranges of
412   continental *P. subeugyrium* lineages B, D and E. Noteworthy, according to an aridity index,
413   lineage B is associated with even drier areas than subarctic lineage E, but at the same time may
414   occur in the same areas where two East Asian subaquatic *Pseudohygrohypnum* occur (Fig. 9).
415   Statistics of SDMs obtained for seven of the eight phylogenetic lineages of *Pseudohygrohypnum*
416   are summarized in Table 6 in Appendix. Models obtained for these seven lineages have reliable
417   quality and largely meet the criteria for bronze-silver standards, introduced by Araujo et al.
418   (2019). The final SDMs for these species demonstrate a "good" quality with AUC >0.960 (only
419   for *P. subeugyrium* lineage B model AUC = 0.915) and with a training omission rate under
420   maximum sensitivity and specificity thresholds from 0.00 to 0.056. Although identical sets of
421   predictors were used for modelling, SDMs of the individual lineages differ in the contributions
422   of these predictors. Both metrics (i.e. contribution and permutation importance) indicate BiO7 is
423   the most important for distribution of European *P. eugyrium* (lineage A) and its values are least
424   in this lineage among all subaquatic *Pseudohygrohypnum* species. At the same time, SDM of
425   North American *P. eugyrium* (lineage B) is affected by precipitation seasonality and it is
426   associated with the areas where this predictor has lower values compared to all other lineages.
427   The second-best predictor for this lineage, BiO17 (precipitation in the driest quarter) also has
428   somewhat higher values than in other lineages. SDMs obtained for East Asian lineages of *P.*
429   *eugyrium* and *P. subeugyrium* are largely controlled by BiO18, which is higher in areas inhabited
430   by these lineages, than in areas where other lineages of subaquatic *Pseudohygrohypnum* occur.
431   SDMs obtained for *P. subeugyrium* lineages A and B do not reveal clearly dominant climatic
432   variables, but in the case of lineage B, the significant variables are those associated with
433   precipitation. Finally, the SDM obtained for *P. subeugyrium* lineage E indicates BiO1 is the most
434   important variable, and its value is much lower in areas inhabited by this lineage compared with
435   other lineages of subaquatic *Pseudohygrohypnum*.
436   PCA suggested clear delimitation of environments where the three lineages so far assigned to *P.*
437   *eugyrium* occur (Fig. 10). For the five lineages of *P. subeugyrium*, distributions of suboceanic

438   lineages (A and C) and continental lineages (B, D, E) partly overlap. According to results of
439   identity tests via I and D metrics, nearly all species pairs have non-identical niches (p<0.01),
440   excluding the *P. eugyrium* lineage C — *P. subeugyrium* lineage C pair; both tests found their
441   distributions identical (p below 0.01).
442   Niche similarity tests (Table 2) revealed significant similarity (see MM section for details) for
443   the species pairs *P. eugyrium* B and *P. eugyrium* C (I=0.54, D=0.25), *P. eugyrium* B and *P.*
444   *subeugyrium* C (I=0.52, D=0.24), *P. eugyrium* B and *P. subeugyrium* A (I=0.72, D=0.46), *P.*
445   *eugyrium* C and *P. subeugyrium* C (I=0.52, D=0.24). Contradicting results of "direct" and
446   "reverse" pairwise comparisons were obtained for species pairs of *P. eugyrium* A and *P.*
447   *subeugyrium* A, *P. eugyrium* C vs. *P. subeugyrium* A, *P. eugyrium* C vs. *P. subeugyrium* B, P.
448   *subeugyrium* A vs. C, *P. subeugyrium* C vs. E which might be assessed as rather similar. For the
449   rest (more than half) of the species pairs, significant niche divergence was suggested.
450

451   **Discussion**
452   Taxonomic implications of the molecular phylogenetic results
453   Topologies of the phylogenetic trees, obtained during the present study generally do not
454   contradict previously published large-scale phylogenies (Gardiner et al., 2005, Cox et al., 2010,
455   Huttunen et al., 2012, Câmara et al., 2018, Schlesak et al., 2018, Kučera et al., 2019). As an
456   exception, in the trees by Gardiner et al. (2005) inferred from combined ITS and trnL-trnF
457   sequences, *Buckia vaucheri* (Lesq.) D. Ríos, M.T. Gallego & J. Guerra groups with
458   *Pseudohygrohypnum eugyrium* not with *Pylaisia polyantha* (Hedw.) Schimp., although with a
459   low support. The highly supported grouping of *Roaldia revoluta* (Mitt.) P.E.A.S. Câmara &
460   Carv.-Silva and *Pseudostereodon procerrimus* (Molendo) M. Fleisch. in the same tree likely
461   originates from misidentification.
462   Molecular data retrieved from specimens traditionally assigned to *Pseudohygrohypnum*
463   *eugyrium* and *P. subeugyrium* as reported above were found to be congruent with the
464   morphological heterogeneity observed in our initial morphological studies. The three
465   molecularly suported lineages of *P. eugyrium* and five lineages of *P. subeugyrium*, recognized
466   also by means of automatic partitioning based on genetic distances, can be characterized
467   morphologically and their distribution patterns were found to be distinct in occupying mostly
468   non-overlapping climatically defined niches. We therefore propose recognizing these lineages as
469   eight species, five of which are newly described in the Taxonomy section. The need for
470   description of a new species for the East Asian *P. eugyrium* lineage C is obvious on both
471   molecular and morphological grounds, while the degree of niche overlap and metrics of niche
472   similarity are nearly the same between the morphologically and molecularly closer *P. eugyrium*
473   lineages A and B, as between the less similar and phylogenetically rather distant lineages A vs.
474   C, and B vs. C. On the other hand, it would be theoretically possible to merge the European and
475   North American lineages of *P. eugyrium*, which form a well-supported monophyletic unit, and
476   likewise the topology inferred from the plastid dataset would allow for preserving *P.*
477   *subeugyrium* s.l. including *P. purpurascens*, i.e. *P. subeugyrium* lineages A-E. However, *P.*

478 *eugyrium* lineages A and B differ in both morphology and occupied niches, and molecular data
479 suggest a sufficient divergence of these lineages, corroborated by the results from the ASAP
480 analysis. Similarly, a broad circumscription of *P. subeugyrium* as including lineages A-E would
481 become vague due to high variability of diagnostic traits, strongly disjunctive range and obvious
482 niche divergence among them. Since European and North American populations of *P.*
483 *subeugyrium* s.str. (lineage A) are identical morphologically and have identical sequences they
484 must be maintained as a single species, however the four other lineages are better recognized as
485 separate species. In particular, the presence of a central strand, short leaves, thin-walled alar cells
486 and growth under continental climatic conditions suggest a rather clear exclusion of lineage B
487 from the broadly circumscribed *P. subeugyrium.* Similarly, lineage C, despite sharing with
488 lineage A the lack of a central strand, canaliculate leaves, cell areolation in the basal leaf portion,
489 and occupying somewhat similar climatic regions, their ranges have been isolated for a long time
490 and tests of niche identity suggest their divergence. Plants of these lineages differ in habit,
491 especially in their coloration. Although *P. subeugyrium* lineages D and E are closely related
492 according to cp data and recombinant plants between these two occur, the ITS-based topology,
493 clear-cut difference in size, coloration and structure of alar group and allopatric distributions
494 support considering them as separate species.
495 The name *Pseudohygrohypnum eugyrium* is based on a type from Central Europe (northern
496 Black Forest, Germany) where no other lineage of subaquatic *P. eugyrium* except lineage A
497 occurs. The name *P. subeugyrium* is based on a type from North America (Newfoundland,
498 Canada), which we verified as corresponding to our *P. subeugyrium* lineage A (see Taxonomy
499 Section). The type specimen of *P. purpurascens* illustrated by Kanda (1977) perfectly
500 corresponds to several of our specimens assignable to *P. subeugyrium* clade C, and plants from
501 Japan are (nearly) identical with several specimens used for our molecular study. We are
502 therefore reasonably certain of the identification of this lineage with the type of *P. purpurascens.*
503 The type of another name, *Hygrohypnum poecilophyllum* Dixon, was synonymized with *P.*
504 *purpurascens* by Kanda (1977). According to the protologue, it differs from the latter in the more
505 slender plants which excludes identity with *P. subeugyrium* lineage D, which consists of rather
506 robust plants in combination with purplish coloration. These plants also do not possess the
507 strongly concave ovate broadly acute to subobtuse leaves that are mentioned in the protologue of
508 *H. poecilophyllum* (Dixon, 1934). The other recognized lineages of *P. subeugyrium* occurring in
509 East Asia even more strongly conflict with the protologue of this species. Therefore, this name
510 most likely applies to the continental morphotype of *P. purpurascens* (see the Taxonomy
511 section).
512 According to the description of *Hygrohypnum subeugyrium* var. *japonicum* Cardot by Noguchi
513 (1991), this variety resembles *P. eugyrium* lineage C, in occasionally lacking a hyalodermis, but
514 the reported shorter leaf cells and smaller spores seem to preclude the identity of *P. eugyrium*
515 lineage C with *P. subeugyrium* var. *japonicum*. The epithet "*japonicum*" has never been applied
516 to a taxon at the rank of species within *Pseudohygrohypnum*. However, a combination with this
517 epithet already exists in the genus *Hygrohypnum* (*H. molle* var. *japonicum* Sakurai), where

Pseudohygrohypnum species were considered for a long time. For these reasons we prefer not to
apply this epithet to our *H. eugyrium* lineage C despite the possibility of their identity.
Hygrohypnum mackayi (Schimp.) Loeske, described from Ireland, was suggested by Jamieson
(1976), who studied the type specimens of this taxon, to be identical with *P. eugyrium*, and we
have no reason to doubt this opinion. Presumeably, the type would belong to our lineage A as no
other lineage of *P. eugyrium* s.lat. is known to occur on the British Isles. In sum, *P. eugyrium*
lineages B and C as well as *P. subeugyrium* lineages B, D and E do not have any available names
and consequently are described as new species in the Taxonomy section.

Since molecular phylogenetic studies became a common tool within the framework of integrative
taxonomy, a large number of taxonomic concepts that were previously accepted have been
challenged. In particular, Patiño & Vanderpoorten (2018) suggested that "apparently widely
distributed bryophyte species actually correspond to complexes of multiple species with much
narrower distribution ranges" and indeed, an abrupt increase in narrowly circumscribed species
with overlapping morphological characters can be observed in the last decade. The specific
concepts have been often challenged in taxa with the disjunct distributions, where isolation and
different climatic conditions in different parts of the species range could trigger allopatric
speciation. In such cases, acceptance of the geographically circumscribed, genetically distinct
species is a common practice (for discussion see Heinrichs et al., 2009) even if they are hardly
distinguishable morphologically. For instance, *Rhynchostegium shawii* Hutsemékers & Vanderp.
was described for a distinct lineage within *R. riparioides* (Hedw.) Cardot s.l., which however
hardly differs morphologically from the European plants considered as *R. riparioides* s.str.
(Hutsemékers et al., 2012). Similarly, allopatric and phylogenetically distinct populations of
Bryoxiphium, despite the lack of morphological differentiation between some of them, are still
considered separate species (Patiño et al., 2016, Fedosov et al., 2016a). On the contrary, disjunct
genetically distinctive European and North American populations of *Claopodium whippleanum*
(Sull.) Renauld & Cardot and *Dicranoweisia cirrata* (Hedw.) Lindb. ex Milde were considered
conspecific by Shaw, Werner & Ros (2003), as no morphological differentiation between them
could be discerned.
Our results which quadrupled the number of accepted semiaquatic species of
Pseudohygrohypnum compared to the earlier monograph of Jamieson (1976) and further
treatments based on this study, has underlined the importance of cool-temperate and boreal Asia
as one of the overlooked centers of bryophyte diversification. For a long time, diversity in this
region has been underestimated due to poor bryological exploration and in general, northern Asia
has been assumed to house a limited number of endemic mosses. Rapoport's rule (Rapoport,
1982; Stevens, 1989) enhanced by their rather slow evolution and high migration rate was
thought to lead to large ranges for Holarctic mosses (cf. Patiño & Vanderpoorten, 2018) until
molecular phylogenetic studies started to suggest differently. Recent studies of both mosses and
liverworts based on the integrative taxonomic approach (Sofronova, Mamontov & Potemkin,
2013; Vilnet, Borovichev & Bakalin, 2014; Bakalin & Vilnet, 2014; 2018; Ignatova et al., 2016;

558   2017; 2019; Fedosov et al., 2017; Ignatova, Kuznetsova & Ignatov, 2017; Bakalin et al., 2020;
559   Hedenäs, Kuznetsova & Ignatov, 2020; Ignatov et al., 2020) have revealed a number of
560   overlooked or previously unknown species that are endemic to the Asian sector of the Holarctic.
561   In many cases these have for a long time been considered conspecific with European or North
562   American species but are in fact remarkably distinct. These studies focused on northern Asia
563   thus corroborate patterns seen in other recent studies on bryophyte species with disjunct
564   distributions (Medina et al., 2013; Draper et al., 2015; Ignatova et al., 2015; Patiño et al., 2016;
565   Vigalondo et al., 2019, etc.).

566   ## Species distribution modelling, the missing piece of integrative taxonomy

567   Our results indicate remarkable niche divergence between two related lineages of *P. eugyrium*
568   (lineages A and B) and four related lineages of *P. subeugyrium* (lineages A, B, C and E). On the
569   other hand, we confirmed niche identity for a pair of species that are not related to each other but
570   are distributed in the same area (*P. eugyrium* C and *P. subeugyrium* C), although the equivalency
571   tests tend to reject the null hypothesis of excessive niche identity (Peterson, 2011; Broennimann
572   et al., 2012). Likewise, a niche similarity higher than random was found for two pairs of
573   unrelated suboceanic lineages, (1) American *P. eugyrium* (B) and amphiatlantic *P. subeugyrium*
574   s.str. (A), as well as (2) American *P. eugyrium* (B) and *P. purpurascens* (*P. subeugyrium* C),
575   which are clearly allopatric. At the same time, the niches of (1) two suboceanic lineages of *P.*
576   *eugyrium* (A, C), (2) two suboceanic lineages of *P. subeugyrium* (A, C), and (3) two continental
577   lineages of *P. subeugyrium* (B, E) are less similar. This is especially interesting since no
578   evidences of niche divergence have been obtained in bryophytes by environmental niche
579   modelling (for discussion see Collart et al., 2021).
580   Although the integrative taxonomy approach implies combining different data sources helpful in
581   species delimitation, most studies which claim to employ this approach are based on only two
582   sources: a molecular phylogenetic study and a morphological examination of the revealed
583   entities. The ecological and distributional data rarely enjoy formal consideration, and formal
584   methodologies such as SDMs, which have undergone an explosive development recently, are not
585   typically used to explore the niche divergence among the studied lineages. This is unfortunate
586   since niche divergence and/or allopatric distributions might typically present the final pieces of
587   evidence supporting the taxonomic conclusions (Van Valen, 1976; Mayr, 1982; De Queiroz,
588   2007). Moreover, niche differentiation likely reflects a primary physiological differentiation (in
589   our case probably increasing tolerance to dessiccattion in continental lineages), which is as
590   significant as a morphological differentiation, although harder to assess.
591   The few exceptional studies (Gama, Aguirre-Gutiérrez & Stech, 2017; Moroni, O'Leary, &
592   Sassone, 2019; Nie et al., 2020; Collart et al., 2021, etc.) usually consider only limited areas and
593   therefore do not deal with intercontinental disjunctions. With their effective dispersal (Shaw,
594   2001; Huttunen et al., 2008; Patiño & Vanderpoorten, 2018), bryophytes are suitable model
595   organisms for considering niche similarity/ divergence hypotheses on wider areas, covering
596   whole species distribution ranges.

597 The congruence of the molecular results, morphological evidence and niche divergence of
598 individual lineages, all obtained from independent lines of evidence, justifies the need to split the
599 two traditionally recognized subaquatic *Pseudohygrohypnum* species into eight species as
600 proposed in the Taxonomy Section. We believe that complementing the standard morpho-
601 molecular toolkit of integrative taxonomic studies with species distribution modelling should
602 become recommended common practice.
603

Origin and early radiation of *Pseudohygrohypnum*

605 According to our topology, inferred from plastid markers (Figs 1, 2, 3), the genus
606 *Pseudohygrohypnum* represents a well-established and remarkably diverse lineage, distributed
607 mostly in the Holarctic, with its centre of species diversity occurring in temperate East Asia. An
608 East Asian centre of distribution is characteristic of earlier diverging species in both major clades
609 identified within *Pseudohygrohypnum* (Fig. 3)*, P. fauriei* (which also occurs in Eastern North
610 America), *P. densirameum*, *P. calcicola* and *P. eugyrium* C, and three poorly known species
611 assigned to the genus by Kučera at al. (2019), *P. perspicuum* (Mitt.) Jan Kučera & Ignatov, *P.*
612 *submolluscum* (Besch.) Jan Kučera & Ignatov and *P. emodifertile* (Broth. ex Ando) Jan Kučera
613 & Ignatov, have a Sino-Himalayan distribution. East Asian representatives also prevail among
614 the closely related genera of Pylaisiaceae, *Calohypnum*, *Pylaisia* and *Homomallium*. In the case
615 of *Pylaisia*, the East Asian representatives also prevail among the early diverging species
616 according to the topology of the ITS-IGS-*trnL* tree published by Ignatova et al. (2020). This
617 strengthens the hypothesis that the radiation of core Pylaisiaceae including the basal radiation of
618 the genus *Pseudohygrohypnum* occurred in East Asia while the Atlantic region was colonized
619 later and independently by several lineages of the family. According to our estimate (Fig. 3), the
620 genus *Pseudohygrohypnum* originated in the Oligocene; and the common ancestor of current
621 *Pseudohygrohypnum* species likely was an element of the Arcto-Tertiary flora. The East Asian –
622 East North American disjunction, shown by the earliest diverging extant *Pseudohygrohypnum*
623 species, *P. fauriei*, is believed to be typical of Arcto-Tertiary species (Schofield & Crum, 1973;
624 Schofield, 1988).
625 The two main lineages of the genus (Fig. 3) are somewhat distinct morphologically, since within
626 clade 1 most of the species have a well-developed hyalodermis (weakly developed in *P. fertile*
627 and *P. skottsbergii*), while species of clade 2 have no hyalodermis except for *P. eugyrium* C
628 where it is irregularly differentiated. The phylogenetic reconstructions suggest that the
629 mesophilous species of *Pseudohygrohypnum* originated in the late Oligocene and warmer early
630 Miocene before the cooling of the climate; the same is true for *P. eugyrium* C, which remains
631 associated with temperate climates in Asia where it mostly occurs south of the 43th parallel
632 (Ivanov et al., 2017).
633

634   Diversification of the "atlantic" *Pseudohygrohypnum* clade

635   Diversification of the *P. eugyrium* A plus B and *P. subeugyrium* A–E lineages occurred much
636   later, after Miocene cooling (14 Ma), and apparently nearly simultaneously in different areas.
637   Since the earliest diverging lineage of *Pseudohygrohypnum* clade 1 (*P. fauriei*, cf. Fig. 3) is
638   distributed in both East Asia and eastern North America and the remaining species of this clade
639   (except *P. densirameum*, which likely originated from an Asian population of *P. fauriei*) occur
640   either in the amphiatlantic region (*P. eugyrium* A & B, *P. fertile*), or in South America (*P.*
641   *skottsbergii*), we assume that diversification of the *P. eugyrium* A plus B clade was associated
642   with the Atlantic region, and an example of allopatric speciation. Although our sampling is
643   sparse, we discovered a notable divergence within North American populations of *P. eugyrium*
644   B, as compared to the low nucleotide diversity in European *P. eugyrium* A, despite sampled
645   plants originating from quite distant areas (Alps, Scandinavia, UK). Schofield (1988) proposed
646   pre-Pliocene isolation of relict groups of southern amphiatlantic bryophytes, to which he
647   assigned *P. eugyrium* and indeed, it seems plausible that the amphiatlantic *P. eugyrium* (A+B)
648   lineage originated in North America and colonized Europe as a result of a single dispersal event
649   or several such events within a short period of time. Our dating provides a median age of 10.56
650   Ma for the *P. eugyrium* A/B node. This was a period of an abrupt late Miocene cooling and
651   drastic changes in atmospheric circulation, which resulted in the formation of modern biomes
652   (Pound et al., 2012). Nearly at the same time (8-10 Ma), migration of several tree species across
653   the north Atlantic land bridge occurred (Grímsson & Denk, 2005; Denk, Grímsson & Zetter,
654   2010). For other groups of plants with amphiatlantic disjunctions, more recent divergence times
655   between European and North American taxa have been suggested (Milne, 2004). The
656   phylogeographic study of the moss genus *Homalothecium* by Huttunen et al. (2008) provides an
657   estimate of the divergence between the American and Eurasiatic clades at 5.69 Ma and this
658   estimate might rather refer to the origin of the European – western North American disjunction
659   of the genus *Homalothecium*, while the amphiatlantic disjunction of *H. sericeum* (Hedw.)
660   Schimp. originated later, likely as a result of recent colonization of eastern North America from
661   Europe (see reconstruction by Huttunen et al., 2008). Likewise, the molecular phylogenetic study
662   of the genus *Antitrichia* Brid., showed no differentiation between European and eastern North
663   American populations of *A. curtipendula*. This also is the case of *Pseudohygrohypnum*
664   *subeugyrium* s.str., for which no molecular differentiation of European and eastern North
665   American populations was found, but not the case of *P. eugyrium* A & B, which are remarkably
666   distinct phylogenetically. The diversification of these lineages might thus represent the first
667   evidence of the pre-quaternary isolation of eastern North American and European populations of
668   an amphiatlantic lineage in mosses.
669   Heat transfer associated with the Gulf Stream which supports the mild climatic conditions of the
670   northern amphiatlantic region likely contributes to the present distribution of *P. eugyrium* A in
671   Europe and *P. eugyrium* B in North America. Moreover, the stability of these climatic conditions
672   since the Pliocene (see Denk, Grímsson & Zetter, 2010; Denk et al., 2013; Utescher, Bondarenko

673   & Mosbrugger, 2015) may be responsible for the lack of further diversification within the
674   European *P. eugyrium* clade, as contrasted with *P. subeugyrium* s.lat.
675

676   Diversification of *P. subeugyrium* s.l.

677   Along with the two early diverging East Asian species, *P. eugyrium* C and *P. calcicola*, the
678   second major clade of *Pseudohygrohypnum* (Fig. 3) includes the remarkably diverse *P.*
679   *subeugyrium* complex. In contrast to the Atlantic clade of the genus (cf. Fig. 3), diversification of
680   this clade apparently was associated with temperate East Asia, which has experienced cooler
681   climatic conditions than temperate Europe since the mid-Oligocene (Utescher, Bondarenko &
682   Mosbrugger, 2015). The *P. subeugyrium* complex underwent a remarkable shift in ecology and
683   spread across the continental areas of North Asia. According to obtained estimates, the two
684   clades, containing the "continental" lineages D & E and B split 10.63 and 5.97 Ma, in the period
685   that likely was associated with two stages of late Miocene cooling, at 14 and 7 Ma. Along with
686   the decreasing annual temperatures, this period was characterised by a dramatic aridification of
687   continental Asia, increased seasonality in temperature and precipitation, and a stronger
688   latitudinal temperature gradient. Xeric environments appeared in the continental part of North
689   Asia due to intensification of the Siberian zone of high pressure and the establishment of the East
690   Asian summer monsoon pattern (Liu et al., 2009; Pound et al., 2012; Utescher, Bondarenko &
691   Mosbrugger, 2015; Holbourn at al., 2018). This resulted in the formation of modern biomes
692   (Herbert at al., 2016) and no significant glacial events followed in continental Asia during the
693   Pleistocene (Sheinkman et al., 2017). The ancestor of the *P. subeugyrium* complex, which
694   apparently faced these changes in East Asia, radiated and formed several lineages adapted to
695   different climatic conditions (monsoon/oceanic versus continental). In the latter case, the
696   adaptation may have included increasing tolerance to desiccation, since small watercourses,
697   where such mosses typically grow in continental North Asia, usually dry out in mid-summer.
698   Thus, the monsoon-related west to east moisture gradient may have been a driver of speciation in
699   both *P. subeugyrium* subclades. Further climate oscillations during the Pliocene might have
700   resulted in expansion northwards in warmer and moister periods and the subsequent isolation of
701   northern populations in cooler and drier periods, causing bottlenecks and subsequent gene drift.
702   Such effects might be inferred from the remarkable divergence of the continental *P. subeugyrium*
703   lineages B, D and E and their low within group genetic diversity as compared to the "oceanic"
704   lineage C.
705   One of the two major lineages of *P. subeugyrium* s.l. spread northwards and differentiated into
706   the *P. subeugyrium* lineage D which is locally common in a restricted area with a cool-temperate
707   climate, and the subarctic *P. subeugyrium* lineage E. Lineage D also colonized North America,
708   where it occurs sympatrically with *P. eugyrium* B and *P. subeugyrium* A, while lineage E has
709   adapted to harsh subarctic environments that was associated by undergoing remarkable
710   miniaturization. Interestingly, traces of gene flow between lineages D and E persist as
711   recombinant plants occurring sympatrically in the same ecotopes throughout its range in Asia.

712   All small plants from southern Siberia, Yakutia and Khabarovsk Territory tested using molecular
713   markers appeared recombinant and thus the identity of a specimen from Altai, referred to lineage
714   E on morphological grounds, remains unclear. Apparently, the origin of these recombinant
715   haplotypes is associated with milder climatic periods when the distributions of lineages D and E
716   may have overlapped.
717   *Pseudohygrohypnum subeugyrium* lineage B, which occupies continental areas with a dry
718   climate and strong temperature seasonality, has spread throughout southern Siberia and reached
719   the Ural Mountains. Although the range of this species appears spotty, this might be the result of
720   poor bryological exploration of southern Siberia.
721   The clade sister to *P. subeugyrium* lineage B (Fig. 3) is formed by two morphologically similar
722   allopatrically distributed species which have remarkably diverged from each other. Unlike the
723   quite homogeneous Atlantic *P. eugyrium,* the East Asian *P. purpurascens* (*P. subeugyrium* C) is
724   represented by several separate lineages which might even be worthy of recognition as separate
725   taxa. This diversity may have originated from the strong climate gradients between insular East
726   Asia, the continental Russian Far East and the Sino-Himalayan region, where different lineages
727   of *P. subeugyrium* C occur, in contrast the range of *P. subeugyrium* A is rather uniform
728   climatically. On the other hand, *P. subeugyrium* A may have originated from a long-distance
729   dispersal event or its haplotype structure may be the result of bottleneck effects associated with
730   survival during glaciation in the Atlantic sector. Traces of the wider distribution of *P.*
731   *purpurascens* persist in recombinant plants from the Khamar-Daban Range (Baikal Region,
732   south Siberia), suggesting past expansions of its range during milder climatic periods. Several
733   disjunct species/populations of vascular plants considered as tertiary relicts with their closest
734   relatives in East Asia have survived in this mountain range due to locally mild climatic
735   conditions resulting from the influence of Lake Baikal (Chepinoga, Protopopova & Pavlichenko
736   et al., 2017). It is noteworthy that our SDM obtained for *P. purpurascens* predicts its presence
737   exactly in this isolated area.
738   There are numerous examples of species with East Asian–eastern North American disjunct
739   ranges, including those in the genus *Pseudohygrohypnum*. In this case, we suggest that the
740   ancestor of *P. subeugyrium* lineage A first inhabited North America and after diverging from
741   lineage C it then colonized Europe, repeating the path travelled by the "Atlantic" clade. Higher
742   haplotype diversity of *P. subeugyrium* lineage A in North America, according to both plastid and
743   ITS data, with plesiomorphic character states revealed in sequences obtained from specimen
744   P2274, supports this suggestion.
745

746   Has late Cenozoic climate cooling increased bryophyte diversity?

747   Milankovitch climatic oscillations, which are considered to be responsible for low diversity and
748   larger species ranges in higher latitudes (Dynesius & Jansson, 2000; 2002), have apparently not
749   affected the overall diversity of bryophytes since the latitudinal diversity gradient is weakly
750   expressed in this group (Hillebrand & Azovsky 2001; Dynesius & Jansson, 2002; Shaw,

751 Szövényi & & Shaw, 2011; Mateo et al., 2016). Because of this, bryophyte diversification has
752 been proposed to have been associated with cooler climatic conditions (Romdal et al., 2012).
753 Massive extinctions suggested to have taken place in bryophytes (Laenen et al., 2014) likely
754 have been balanced by the diversification of new lineages, such as those described above for
755 *Pseudohygrohypnum*, or previously for other genera such as *Hedwigia* (Ignatova et al., 2016)*,*
756 *Orthotrichum* (Fedosov, Fedorova & Ignatova, 2017), *Orthothecium* (Ignatov et al., 2020)*,*
757 *Schistidium* (Ignatova et al., 2010), *Tomentypnum* (Hedenäs, Kuznetsova & Ignatov, 2020), and
758 many other groups of bryophytes common at middle and high latitudes in Asia. Indeed, the
759 diversification rate within the *P. subeugyrium* clade (0.38-0.7 new lineages per million years) is
760 comparable with the one found by Huttunen et al. (2008) for *Homalothecium* and considered by
761 those authors as fairly high. At the same time, within the amphiatlantic *P. eugyrium* clade, which
762 arose around the same time, no significant radiation has followed.
763 According to Jonsgard & Birks (1996), Ellis & Tallis (2000) and Patiño & Vanderpoorten
764 (2018), ecotopes appearing due to the change of climatic phase likely have been colonized by
765 bryophytes as soon as they developed and became available. However, we suggest that such
766 changes affecting simultaneously huge areas of North Asia, have resulted in a high local
767 proportion of open ecological niches (so called "dark diversity", see Pärtel, Szava-Kovats &
768 Zobel, 2011) even for easily dispersable bryophytes. For instance, Carter (2021) concluded that
769 substantial areas of climate suitable for North American endemic mosses exist (and likely existed
770 before) outside of North America. Weakly saturated local species pools with the constant
771 presence of open niches have favoured niche divergence in populations which have survived
772 these changes *in situ* and thus may have been a driver of speciation followed by divergence along
773 climatic gradients. Such mechanisms might have contributed significantly to the diversification
774 burst proposed by Laenen et al. (2014) and lead to the formation of the inverse latitudinal
775 gradient of species diversity, revealed in Europe by Mateo et al. (2016).
776

Conclusions

778 Our integrative taxonomic study, which combined molecular evidence, morphological revision
779 of specimens and species distribution modelling revealed eight lineages within two traditionally
780 circumscribed subaquatic species of the genus *Pseudohygrohypnum*. These lineages were found
781 in three clades, the subatlantic *P. eugyrium* clade (with two lineages), *P. subeugyrium* clade
782 (with five lineages), and the clade containing East Asian specimens, previously assigned to *P.*
783 *eugyrium*. The former two clades originated rather recently, following the 14 Ma Miocene
784 cooling, while the mesophilous species of the genus originated earlier, during a warmer climatic
785 period. Within the main *P. eugyrium* clade, two species diverged allopatrically in mild
786 suboceanic areas of Europe and Eastern North America. The distributions of several lineages
787 within the *P. subeugyrium* clade partly overlap. At the same time, species distribution modelling
788 and consequent niche similarity tests showed that closely related species occupy distinct niches.
789 Within the *P. subeugyrium* clade where diversification was largely associated with Asia, three
790 lineages underwent significant shifts in ecology that allowed them to colonize continental areas

791 of northern Asia. Thus, we propose that Milankovitch climatic oscillations may have induced
792 speciation, through the cooling and aridification of climates in the late Miocene and Pliocene.
793 We propose that in northern Asia this has enhanced climate gradients and served as a driver of
794 recent diversification of bryophytes.
795

796 **Taxonomic treatment**

797 Key to identification of aquatic species of *Pseudohygrohypnum*

798

799 1.   Stems with distinct central strand; leaves ovate, rarely ovate-lanceolate, with length/width
800 ratio 1.5–2.5, straight to distinctly falcate, acuminate; costae extending to ¼–½ of leaf length;
801 reddish coloration rare   2
802 -   Stems without or with weak central strand; leaves ovate-lanceolate to lanceolate, with
803 length/width ratio (2–)2.5–4.5, acuminate or attenuate at apex, distinctly to strongly falcate,
804 rarely leaves shorter, ovate, but then plants have distinct red coloration; costae typically shorter
805 than ¼ of leaf length   5
806 2.   Stem hyalodermis not differentiated or differentiated in several patches; alar cells not
807 sharply delimited; Asia and Ural Mountains 3
808 -   Stem hyalodermis differentiated throughout the cross section; alar cells sharply delimited;
809 Western Europe, Caucasus and Eastern North America   4
810 3.   Leaves strongly concave, with involute margins, apiculate distally; median leaf cells
811 elongate to short linear, 30–50(–65) μm long*P. orientale* (*P. eugyrium* C)
812 -   Leaves weakly concave, with plane margins. acuminate; median leaf cells linear or
813 vermiculate, 35–70(–85) μm long   *P. sibiricum* (*P. subeugyrium* B)
814 4.   Leaves 1.2–1.6(–1.8) mm long; alar group composed of thick-, rarely thin- walled, red- or
815 brownish coloured cells; upper leaf cells 30–62 μm long; endostome with three, free, typically
816 short cilia, ca. 1/2–2/3 of segment length; Europe   *P. eugyrium* (*P. eugyrium* A)
817 -   Leaves 1.6–1.8 mm long; alar group with thin-walled, hyaline cells or firm-walled
818 hyaline cells forming the outer parts and reddish-colored, somewhat thicker-walled cells forming
819 the inner parts; upper leaf cells 45–75 μm long; endostome with cilia adherent to each other,
820 typically longer than or equal to segments; North America   *P. appalachianum* (*P. eugyrium* B)
821 5.   Plants small; stems usually densely pinnately branched; leaves 0.6–1(–1.2) mm long,
822 lanceolate to linear-lanceolate; alar cells not inflated; North Siberia 6
823 -   Plants medium-sized; stems irregularly branched; leaves usually longer than 1.2 mm,
824 ovate-lanceolate to lanceolate; alar cells distinctly differentiated; cool temperate, humid areas of
825 Holarctic   7
826 6.   Plants with remarkable golden sheen; alar groups indistinct, composed of few small,
827 quadrate, thick-walled cells   *P. subarcticum* (*P. subeugyrium* E)
828 -   Plants purplish or brownish; alar group distinct, composed of subquadrate, thick-walled
829 cells with reddish to brownish cell walls   *P. neglectum* × *P. subarcticum*

830   7.   Leaves slightly concave; alar groups round, inflated, composed of thin-walled cells; leaf
831   base from alar region to costae occupied by not excavated, concolorous cells with thick, strongly
832   porose walls   *P. neglectum* (*P. subeugyrium* D)
833   -   Leaves concave, in upper part canaliculate; alar groups transversely elongate, composed
834   of thin- or moderately thick-walled cells; leaf base from alar region to costae occupied by one
835   row of excavated, brownish cells with thick, not or slightly porose walls   8
836   8.   Plants with reddish coloration, typically deeply wine red, rarely variegate to green; spores
837   15–30 μm; East Asia   *P. purpurascens* (*P. subeugyrium* C)
838   -   Plants bronze to brownish, typically without or with slight reddish coloration; spores 12–
839   20 μm; north Europe and Atlantic North America   *P. subeugyrium* (*P. subeugyrium* A)
840

841   ***Pseudohygrohypnum appalachianum*** Brinda, Fedosov & Ignatova, sp. nov. (Fig. 4-7, 11, 12)
842   **Type:** USA, North Carolina, McDowell County, Pisgah National Forest, along Newberry Creek
843   and Forest Road 482A, 35.6977N, 82.2397W, 872 m. alt., eastern deciduous forest with
844   *Rhododendron*, on rock in stream; 28.V.2018, Brinda 11916 (Holotype MO-6967804!, Isotype
845   MW!).
846   **Diagnosis.** Similar to *P. eugyrium* in its stem with central strand and weak hyalodermis, and
847   leaves with well-marked, usually excavate alar regions of inflated, rectangular cells, but differing
848   from that species in: (1) somewhat longer laminal cells, 45–75 μm vs. 30–62 μm; (2) alar groups
849   composed of thin-walled, hyaline cells excepting the innermost rows with slightly thicker walls
850   vs. uniformly thick-walled, reddish to brownish cells in *P. eugyrium*; (3) more closely set, often
851   adherent endostome cilia vs. free ones in *P. eugyrium*; and (4) spores, which are on average
852   larger, (14–)15–20(–23) μm vs. 13–20 μm in *P. eugyrium*.
853   **Etymology:** The species is named after the Appalachian Mountain Range, which spans the
854   length of eastern North America where the species is especially frequent.
855   **Description.** Plants medium-sized, yellowish-green to reddish-brown, generally with a satin-like
856   sheen. Stems prostrate or ascending, irregularly branched, to 4 cm long, yellow, becoming
857   reddish-brown with age; epidermal cells somewhat larger, with thin outer walls, forming a weak
858   hyalodermis; sclerodermis composed of 3–5 layers of smaller, thick-walled cells; central strand
859   distinct. Stem leaves 1.3–1.8 × 0.6–0.9 mm, straight to, more commonly, falcate-secund, ovate,
860   oblong-ovate or ovate-lanceolate, concave, narrowed to the insertion, widest at ca. 1/3 of leaf
861   length, apex acuminate or more commonly with apiculus formed due to incurved upper leaf
862   margins; costa usually short and double but sometimes reaching mid-leaf, or rarely single and/or
863   spurred; margins erect and entire below, becoming increasingly denticulate and broadly incurved
864   above, especially in the apiculus where they are consistently serrulate or eroded; upper laminal
865   cells firm-walled, fusiform to linear, flexuose, (32–)45–75(–80) × 4–5(–6) μm, somewhat shorter
866   toward the apices; basal juxtacostal cells concolorous or reddish, thicker-walled, frequently
867   porose; alar group clearly delimited, enlarged to inflated, usually excavate, composed of several
868   thin-walled, hyaline cells at margins which are surrounded by more firm-walled, usually reddish-
869   colored cells in the interior but not reaching the costa; short-rectangular supra-alar cells usually

870 present in one to several rows. Autoicous. Perichaetial leaves lanceolate, acute or acuminate,
871 plicate, up to 3.5 mm long. Setae yellowish-brown to reddish-brown, 1.5–2.5 cm, smooth.
872 Capsules horizontal, 1–2 mm long, oblong-cylindrical, strongly curved, contracted below mouth,
873 yellowish-brown, mostly smooth. Exothecial cells at the capsule mouth small, oblate or rounded
874 in 1–3 rows, the rest elongate, firm-walled. Opercula conic-apiculate. Annuli well differentiated,
875 composed of 2–4 rows of inflated cells. Exostome teeth up to 500 μm, yellowish-brown to
876 orange-brown, cross-striolate proximally, papillose distally; endostome nearly of the same
877 length, weakly papillose, basal membrane ca. 200 μm; segments keeled, narrowly perforate
878 along the median line; cilia 2–3, closely set or occasionally fused for part of their length,
879 filiform, nodose. Spores (14–)15–20(–23) μm, smooth to finely papillose.
880 **Variation.** Coloration of the plants naturally varies from yellowish-green to reddish-brown with
881 age and exposure. The alar cells also become better differrentiated with age, so observations are
882 best made along mature stems. The longer laminal cells of North American plants as compared
883 to *P. eugyrium* s.str. were already pointed by Jamieson (1976) in his revision of *Hygrohypnum*.
884 Therefore, the given ranges for laminal cell size follow that treatment.
885 **Differentiation.** The unique structure of the alar groups of *P. appalachianum* is fairly
886 diagnostic: they are composed of thin-walled, hyaline cells ringed by firm-walled, reddish-
887 colored cells that abruptly transition into the thick-walled, and often porose juxtacostal basal
888 cells. In both *P. eugyrium* s.str. and *P. subeugyrium,* the firm-walled cells generally extend all
889 the way to the leaf margin. In addition, the cilia of the endostome of *P. appalachianum* are
890 longer than in *P. eugyrium,* the same length as the segments vs. half of the segment length, more
891 closely set and partially joined (free in *P. eugyrium*); finally, spores of *P. appalachianum* are
892 somewhat larger (rarely less than 15 μm in *P. appalachianum* but frequently less than 15 μm in
893 *P. eugyrium*). Differentiation from *P. neglectum* is perhaps more difficult, since both species
894 have at least partly thin-walled, hyaline alar cells. However, the distinct stem central strand,
895 hyalodermis, and strongly concave leaves of *P. appalachianum* with coloured interior basal cells
896 should serve to separate it from that species.
897 **Ecology:** The species grows on acidic rocks both in and along watercourses, usually in the
898 mountains. In the southern Appalachian Mountains the species reaches more southerly latitudes
899 than are generally experienced in this group. Therefore, it seems reasonable to hypothesize that
900 these habitats could have served as refugia for this species through past climatic oscillations as
901 was considered for other species (Billings & Anderson 1966, Anderson & Zander 1973).
902 **Distribution.** *Pseudohygrohypnum appalachianum* is apparently a common member of the
903 genus from the southern Appalachian Mountains of North Carolina, Georgia, and Tennessee
904 (Crum & Anderson 1981) north to Maine (Allen 2014) and eastern Canada (Jamieson 1976,
905 2014). In the north-eastern portion of its range, it may be confused with *P. subeugyrium, P.
906 neglectum*, or *P. eugyrium* s.str., and a revision of herbarium material is needed to outline the
907 true limits of its distribution.
908 **Other specimens examined (Paratypes):** Canada: Nova Scotia, Kings County, creek in mixed
909 forest, 16.VII.1974, R.R. Ireland 17459 (LE); Quebec, Terrebonne County, On wet rocks at edge

910 of brook, 17.VII.1959, H. Crum & H. Williams 10333 (LE); USA: Maine, Oxford County,
911 Batchelders Grant, White Mountain National Forest, along Route 113, Stony Brook, on boulder
912 in stream, 17.VI.2007, B. Allen 28268 (MO); Knox County, Camden Township, Mount
913 Megunticook, Maiden Cliff trail, Camden State Park, on boulders in stream, 25.VII.1997, B.
914 Allen 20038 (MO); the same place, 2.VII.1993, B. Allen 14642 (DUKE); North Carolina, Kanati
915 Fork, Great Smoky Mts. Natl. Park, Swain County, wet boulders of stream, 11.VII.1959, W.B.
916 Schofield 10332 (LE); the same area, over boulders in streamlet, 13.VII.1959, W.B. Schofield
917 10075 (LE, MO); the same area, wet rocks in stream, hemlock cove, 22.X.1969, L.E. Anderson
918 20994 (LE); Clay County, rocks at the edge of stream, 13.VIII.1948, L.E. Anderson 8004 (LE);
919 McDowell County, locality same as the type (both collected during the 2018 Crum Workshop),
920 on streamside rock; 28.V.2018, Brinda 11911 (MO, MW); Pennsylvania, Centre County, ca. 2.5
921 mi. ESE of Millheim, 5.VI.1975, R.A. Pursell 10322 (MO); Tennessee, Rainbow Falls, Great
922 Smoky Mts. Natl. Park, wet cliff slope near waterfall, 28.VII.1959, W.B. Schofield 10656 (LE).
923 **Affinity.** *P. appalachianum* is closely related to European *P. eugyrium*, but since their
924 divergence, has gained both molecular synapomorphies and morphological differences, which
925 substantiate recognition of *P. appalachianum* at the species level.
926
927 ***Pseudohygrohypnum eugyrium*** (Schimp.) Kanda, J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot.
928 16: 106. 1976[1977]. – *Limnobium eugyrium* Schimp., Bryol. Eur. 6: 73. pl. 579. 1855. –
929 *Hypnum eugyrium* (Schimp.) Sull., Manual (ed. 2) 671. 1856. – *Amblystegium eugyrium*
930 (Schimp.) Lindb., Musci Scand. 33. 1879. – *Calliergon eugyrium* (Schimp.) Kindb., Eur. N.
931 Amer. Bryin. 1: 83. 1897. – *Hygrohypnum eugyrium* (Schimp.) Loeske, Verh. Bot. Vereins Prov.
932 Brandenburg 46: 198. 1905. = *Hypnum eugyrium* var. *mackayi* Schimp., Syn. Musc. Eur. (ed. 2)
933 782. 1876. (Fig. 4-7, 13).
934 **Description.** For species description see Smith (2004).
935 **Differentiation.** For differentiation of *P. eugyrium* s.str. from North American *P.*
936 *appalachianum* and from East Asian *P. orientale* see comments under those species.
937 **Distribution.** *P. eugyrium* has a subatlantic distribution, largely restricted to Europe. But since
938 we have assigned nearly all studied North American specimens previously referred to *P.*
939 *eugyrium* to the newly described *P. appalachianum,* its distribution outside Europe is poorly
940 understood. A single specimen from Newfoundland, which however lacks sporophytes and for
941 which we failed to obtain molecular data, in the structure of the alar group rather resembles
942 European *P. eugyrium*. A revision of all American specimens previously referred to *P. eugyrium*
943 is needed to clarify if this species occurs in North America. *Pseudohygrohypnum eugyrium* is
944 reported from Georgia, Adzharia based on a single specimen (Zündorf, 2011), but we have not
945 been able to examine those plants. According to the model produced based on European
946 localities of *P. eugyrium*, this species is expected to occur both in humid coastal areas of the
947 western Caucasus and in eastern North America, although its predicted distribution there is
948 shifted northward, compared to the model based on north American occurrences, which largely
949 represent *P. appalachianum*.

950 **Specimens examined:** Sweden, 28.VII.1902. T. Gustafson (LE); 19.VII.1896, A. Arven (LE);
951 24.VII.1879, O.L. Sillen (LE); 12.VI.1883, O.L. Sillen (LE); 20.VI.1916, P.A. Larsson (LE);
952 Belgium, V.1921, Fr. Toussaint. Austria, 16.10.2005. G. Schlüsslmayr (CBFS, MW); Poland,
953 24.IV.1956, S. Lisowski (LE); Faroes, 8.V.1896, C. Jensen (LE); 23.V.1896, C. Jensen (LE);
954 UK, 7.VII.1919 (LE); Scotland, 6.7.2003, J. Kučera (CBFS). ?Canada, Newfoundland, Avalon
955 Peninsula, 12.V.1981, G.R. Brassard 13562 (LE).
956
957 *Pseudohygrohypnum orientale* **Fedosov & Ignatova, sp. nov.** (Figs. 4-7, 12, 14).
958 Type: Russia. Primorsky Territory, Partizansk Distr., Ol'khovaya Mt., Kamenystyj Creek valley,
959 43.33N, 133.65E, ca. 530 m alt., on boulder near the creek, 4.IX.2006, M.S. Ignatov 06-2399,
960 MW9060444* (Holotype), MHA9046084, LE (Isotypes).
961 **Diagnosis**. This species is similar to *P. eugyrium* in presence of stem central strand, ovate,
962 strongly concave, apiculate leaves with distally serrulate margins, and rather short leaf cells, but
963 differs from it in (1) lack of dark coloration in older parts of shoots, while in *P. eugyrium* older
964 parts of plants are typically brownish to blackish or reddish; (2) weakly developed hyalodermis,
965 which is present only as fragments or may be absent; (3) weakly delimited alar groups; (4) larger
966 spores, 19–23 μm vs. 13–20 μm in *P. eugyrium,* and (5) distribution in Eastern Asia, whereas *P.*
967 *eugyrium* occurs mainly in Europe.
968 **Etymology.** The species name is given due to its East Asian distribution.
969 **Description.** Plants medium-sized, light yellowish to bright green, pale brownish proximally,
970 moderately turgid, not or weakly glossy. Stems prostrate, yellow, brownish or reddish, to 5 cm,
971 irregularly branched; hyalodermis well differentiated in several areas of the cross section and not
972 or weakly differentiated in other places, rarely weakly differentiated throughout cross section;
973 sclerodermis 3–4 layered; central strand well differentiated. Stem leaves (0.9–)1–1.6(–2) × (0.3–
974)0.55–0.8(–0.85) mm, falcate-secund, ovate to ovate-lanceolate, acuminate, typically with
975 slightly attenuate tips, strongly concave; margins broadly and gently incurved below apices;
976 longer leaves canaliculate to tubulose distally to nearly cucullate, slightly and gently or abruptly
977 narrowed toward insertion, widest at ca. (1/5–)1/3–1/2 of leaf length; costa double, rather strong,
978 typically reaching 1/4–1/3(–1/2)of leaf length; margins serrulate distally; upper laminal cells 30–
979 50(–65) × 3–5(–6) μm, linear, thin- to moderately thick-walled, not porose, near leaf tip shorter,
980 elongate to rhomboid, with thicker walls; basal cells usually thick-walled, concolorous, often
981 with porose walls; alar groups distinctly delimited, inflated, ovate to trapezoidal, rarely
982 transversely elongate, composed of wide, inflated, hyaline or thick-walled, short rectangular
983 cells, in the later case usually with brownish cell walls, not reaching costa, bordered by small
984 subquadrate supra-alar cells. Cells between alar groups linear, very thick-walled, porose.
985 Autoicous. Perichaetial leaves lanceolate, acuminate, plicate, up to 3.6 mm long. Setae red, 1.5–
986 2.3 cm. Capsules 1.5–2 mm long, horizontal, curved, not contracted below mouth (but abruptly
987 widened to operculum when young), pale-brown, smooth. Exothecial cells moderately thick-
988 walled, elongate, below mouth in few rows rounded. Opercula conic. Annuli differentiated,
989 composed of large, inflated cells. Exostome teeth up to 400 μm, reddish-brown, cross-striolate

990   proximally, papillose distally; endostome longer, up to 550 μm, basal membrane ca. 250 μm,

991   papillose on the inner surface; segments carinate, perforated along a median line, papillose on the

992   inner surface; cilia 2, filiform, nodulose. Spores 19–23 μm. This species was also illustrated and

993   described by Czernyadjeva (2003) based on the specimen from Primorsky Territory as *P.*

994   *eugyrium*.

995   **Variation.** *Pseudohygrohypnum orientale* is rather variable morphologically and the spectrum of

996   its morphotypes largely corresponds to that described by Jamieson for *P. eugyrium.* Leaf length

997   and shape is among the most variable traits; typically leaves in this species are ovate to short

998   ovate (all Russian specimens and nearly half of the Japanese ones), but in several samples the

999   leaves are longer and then resembling *P. purpurascens* in their canaliculate distal portion. The

1000   alar groups are also extremely variable in shape and areolation; typically, they are round or

1001   round-trapezoidal (i.e. resembling those of *Calliergon giganteum* in shape) and stop far from

1002   reaching the costae, but in a few Japanese specimens they are transverse-elongate. In a few other

1003   specimens (mostly also from Japan) the alar groups are composed of thick-walled cells with

1004   brownish walls. Although based on stem cross sections such specimens can be assigned to *P.*

1005   *orientale,* they may actually represent a different haplotype than the continental plants. The

1006   hyalodermis in *P. orientale* is less developed than in *P. appalachianum* and *P. eugyrium*, and in

1007   several specimens it is nearly absent, but other morphological traits and molecular data suggest

1008   their assignment to *P. orientale*. Most likely *P. subeugyrium* var. *japonicum* Cardot was

1009   described based on such specimens, at least the description provided by Noguchi (1991) in most

1010   points corresponds to *P. orientale* except for the shorter laminal cells, 25–30 μm vs. 30–50 μm,

1011   and smaller spores, 12–20 μm vs. 19–23 μm. Thus, synonymization of *P. subeugyrium* var.

1012   *japonicum* with *P. orientale* at the moment seems premature, although it seems there is no other

1013   possibility of what *P. subeugyrium* var. *japonicum* might be. In general, insular specimens are

1014   more variable than those from Primorsky Territory, but this variability does not have an obvious

1015   geographical pattern; at least, the description provided by Kanda (1977) for Japanese *P.*

1016   *eugyrium* (which actually represents *P. orientale*) clearly fits plants from Primorsky Territory

1017   and Shikotan Island.

1018   **Differentiation.** Although morphologically *P. orientale* is reminiscent of *P. eugyrium*, the origin

1019   of the material (East Asian vs. Atlantic) clearly indicates if the specimen represents one or the

1020   other. Differentiation of them is considered in the diagnosis; among other useful traits coloration

1021   is worth mentioning. According to Kanda and our observation, *P. orientale* never has dark,

1022   especially brownish or blackish coloration, and just a single specimen has a pinkish color.

1023   Typically, living plants are light to bright green throughout, while in *P. eugyrium* older parts of

1024   the plants are usually darker or have a red coloration. Two other species of *Pseudohygrohypnum*,

1025   *P. sibiricum* and *P. purpurascens*, occur sympatrically with *P. orientale* and may be similar

1026   morphologically. From *P. sibiricum* the latter species usually differs in its differentiated

1027   hyalodermis and strongly concave, apiculate leaves, that are canaliculate distally. In a few cases,

1028   the hyalodermis may be misleading since it may be absent in *P. orientale* and present in *P.*

1029   *sibiricum*. In such cases the shorter upper leaf cells, typically 30–50 μm vs. 35–70 μm in *P.*

1030 *sibiricum,* are helpful. Due to their canaliculate, falcate leaves, long leaved morphotypes of *P.*
1031 *orientale* (such collections occur in Japan) may resemble *P. purpurascens*, which is especially
1032 likely to be confused with *P. orientale*, since these two species occur in the same areas and
1033 habitats. Absence of the red coloration and the presence of a stem hyalodermis and central strand
1034 differentiate *P. orientale* from *P. purpurascens*. In addition, *P. orientale* has shorter laminal cells
1035 than most species of *P. subeugyrium* affinity, excepting one of the continental morphotypes of *P.*
1036 *purpurascens*, described under that species.
1037 **Ecology.** In Primorsky Territory and Shikotan Island *P. orientale* grows on wet siliceous rocks in
1038 and near creeks and in the spray zone of waterfalls at lower elevations; according to our field
1039 observations and specimens in herbaria, near waterfalls this species may be very abundant. All
1040 studied collections are restricted to an elevation range of 0–100 m on Shikotan Island and 200–
1041 400 m in Primorsky Territory; however, according to Kanda (1977), in Japan this species reaches
1042 an elevation of 1400 m.
1043 **Distribution.** Distribution of this species is restricted to temperate East Asia and remains
1044 insufficiently known. In the Russian Far East it occurs in the southern part of Primorsky
1045 Territory, southward to the 43th parallel and on Shikotan Island between the 43th and 44th
1046 parallels, but according to the SDM, it also may also occur in the middle and northern parts of
1047 the Sikhote-Alin Range (Primorsky Territory), which remain insufficiently studied for
1048 bryophytes. In addition, it also occurs nearly throughout Japan, but so far has not been found on
1049 Sakhalin and the Islands of Greater Kuril Ridge, even though at least Kunashir is well studied for
1050 mosses. Although we have not seen the specimens, we would propose that records of *P.*
1051 *eugyrium* from Korea (Kim, Higuchi & Yamaguchi, 2020) and in SE China and the Sino-
1052 Himalayan Region actually represent *P. orientale*, since our SDM predicts its presence there.
1053 According to the Maxent SDM, the species distribution is strongly dependant on precipitation of
1054 the Warmest quarter (BiO18), which should be above 300–350 mm, that likely limits the species'
1055 distribution westward.
1056 **Other specimens examined (Paratypes)**: Russia. Primorsky Territory, Ussurijsky State
1057 Reserve, Suputinka River upper course, Mironov Klyuch, on basalt rock, 23.X.1934, A.S.
1058 Lazarenko (LE); Shkotovsky Distr., vicinity of Anisimovka village, 21.IX.1977, L.V. Bardunov
1059 (MW9060447, LE); Olsky Distr., waterfall on Milogradovka Creek, 43.458N, 134.322N, wet
1060 cliffs, 310-370 m alt., wet cliffs and temporary flooded cliffs, rocks near waterfall, 21.VIII.2007,
1061 M.S. Ignatov 07-316, 07-318, 07-332 (MHA9046081*, 9046082, 9046083, MW9060445,
1062 9060446, 9060448*, LE); Lazovsky Distr., Elomovskyj Klyuch Creek on the path to Benevskie
1063 Waterfalls, 43.232N, 133.751E, 290 m. alt., on boulders near stream; 6.IX.2019, V.E. Fedosov
1064 19-2-296 (MW9116124), the same place, Kučera (CBFS:21474*), the same place, 5.IX.2013,
1065 M.S. Ignatov, E.A. Ignatova & E. Malashkina, Pr-5-12-13 (MHA9046080*). Sakhalin Province,
1066 Shikotan Island, vicinity of Dimitrova Bay, 26.VIII.2021, V.E. Fedosov & A.V. Shkurko
1067 (MW9116127*, 9116128*, 9116130, 9116131); the same area, vicinity of Malokuril'skoe Settl.,
1068 8.VIII.2021, V.E. Fedosov & A.V. Shkurko (MW9116126*, 9116134*). Japan, Hokkaido,
1069 21.VIII.1951, A. Noguchi (MHA9056558 ex NICH), Honshu, 14.VIII.1909, Ishiba

1070 (MHA9056557 ex NICH), 6.VI.1951 (MHA9056561 ex NICH), 3.VIII.1954, A. Noguchi
1071 (MHA9056559, 9056560 ex NICH), 16.VI.1959, K. Nosoi (MHA9056562 ex NICH), Kyushu,
1072 pref. Fukuoka, Mts. Sebui, 4.V.1968, J. Amakana 6110 (MHA9056556 ex NICH). China,
1073 Sichuan, Markham County. ca 20 km E of Markham along Dai Dou river, 2675-2760 m. alt.,
1074 steep NE facing slope, 30.VIII.1988, Allen 6926 (MO 90066605).
1075 **Affinities.** Despite the morphological similarity of *P. orientale* and *P. eugyrium*, molecular data
1076 suggest that these species are not particularly close phylogenetically; according to the
1077 reconstruction inferred from plastid data, among known *Pseudohygrohypnum* species *P.*
1078 *orientale* is rather close to *P. calcicola*, which has a similar structure of alar groups, strongly
1079 concave leaves with rather short cells, and long perichaetial leaves. The similarity of *P. orientale*
1080 and *P. eugyrium* is likely caused by environmentally induced convergence.
1081
1082 ***Pseudohygrohypnum subeugyrium*** (Renauld & Cardot) Ignatov & Ignatova, Arctoa 11
1083 (Supplement 2): 845. 2004. – *Hypnum subeugyrium* Renauld & Cardot, Bot. Gaz. 22(1): 52, pl.
1084 5, f. B. 1896; Type: Newfoundland: Exploits (Rev. A. C. Waghorne, 1893), syntype: !MO-
1085 406297, http://legacy.tropicos.org/Specimen/90207675 – *Calliergon subeugyrium* (Renauld &
1086 Cardot) Kindb., Ottawa Naturalist 14: 80. 1900. – *Limnobium subeugyrium* (Renauld & Cardot)
1087 G. Roth., Eur. Laubm. 2: 648. 1905. *Hygrohypnum subeugyrium* (Renauld & Cardot) Broth, Nat.
1088 Pflanzenfam. 231[I,3]: 1039. 1908. (Fig. 4-7, 15).
1089 **Description.** For species description see Blockeel, Kiebacher & Long (2019).
1090 **Comments on morphology.** For a long time, *P. subeugyrium* was considered to be a subspecies
1091 of *P. eugyrium* and therefore it is absent from key European Checklists, manuals and floras
1092 published in 20th century (Podpěra, 1954; Nyholm, 1965; Smith, 2004; etc.). This species was
1093 revived in the monographic treatment of the genus *Hygrohypnum* by Jamieson (1976), which
1094 was accepted by Crum & Anderson (1981) and Corley & Crundwell (1991). The protologue of
1095 *Hypnum subeugyrium* is not very informative so its circumscription was further clarified by
1096 Jamieson (1976). This treatment was subsequently followed by Czernyadjeva (2003) Ignatov &
1097 Ignatova (2004), Flora of North America editorial committee (2014), and finally Blockeel,
1098 Kiebacher & Long (2019). However, Jamieson's description also included the taxon recognized
1099 below as *P. neglectum*. The descriptions by Czernyadjeva (2003) and Ignatov & Ignatova (2004)
1100 which are based on Russian specimens do not actually represent *P. subeugyrium* s.str. The
1101 description by Blockeel, Kiebacher & Long was based on plants from the United Kingdom,
1102 which were partly included in the present study. We are able to confirm the identity of type
1103 material of *P. subeugyrium* (duplicate at MO) with plants illustrated by Blockeel, Kiebacher &
1104 Long (2019).
1105 **Variation.** Unlike *P. eugyrium*, European and North American populations of *P. subeugyrium*
1106 have identical sequences for all studied markers, indicating either presence of gene flow between
1107 them or recent colonization of the European or North American range. The amount of studied
1108 material is not sufficient to fully assess its morphological variation; but at first glance, although
1109 the specimens studied by us originate from all parts of species' range, they look quite uniform.

Differentiation. *P. subeugyrium* differs from related species in the combination of brownish coloration with weak purplish tint, lack of a differentiated stem central strand and hyalodermis, leaves canaliculate distally, which is especially evident in falcate leaves, and transversely elongate alar groups, composed of thick-walled cells and typically extending to the costa. In addition, this species occurs in northern Europe, where we failed to find any other *Pseudohygrohypnum* species except *P. eugyrium*, despite this area being likely the most thoroughly studied worldwide. In eastern North America the ranges of *P. subeugyrium* s.str. and *P. neglectum* (see description below) overlap, and these species may be confused. Small, round alar groups typically composed of thin-walled cells and less strongly incrassate sclerodermis are the best traits to differentiate *P. neglectum* from *P. subeugyrium*, since canaliculate leaves, typical for *P. subeugyrium*, occasionally occur in the former species. Differentiation of *P. subeugyrium* and *P. purpurascens* is considered under the latter species.

Distribution. *Pseudohygrohypnum subeugyrium* s.str. is an oceanic or even hyperoceanic north Atlantic species, which occurs in areas with a mild climate: SW Norway, S Sweden, UK (mostly in the NW), and eastern North America – Newfoundland (locus classicus), and the eastern states of Canada and the USA, from Quebec to Tennessee (Jamieson, 2014).

Specimens examined: Canada: Newfoundland, ca. 49.525N 55.070W, 14.XI.1893, A.C. Waghorne 26 (MO, syntype); Spruce Brook, George's Lake, St. George's, 8-9.VII.1949, R. Tuomikoski 2791 (LE, as *P. eugyrium*). USA, Maine, Waldo County, Lincolnville Town, Camden Hills State Park, 44.263N, 69.045W, 337 m alt., on rocks and roots in small stream, 4.VII.2002, Bruce Allen 24431 (MO*); New York, Essex County, Town of Keene, Adirondack Park, cliffs and valley SW of Chapel Pond, 44.141N, 73.747W, 460 m alt., on boulder in stream, 19.IX.2004, Bruce Allen 27202 (MO*). Virginia, Nelson County. Shamokin Springs Nature Preserve, Large rock in stream, mostly above water. H. Hamilton 742, 13.8.2017, as *P. eugyrium* (DUKE*); Sweden, Närke, Tysslinge, 10.X.1992, N. Hakelier (MHA9056564* ex NICH). UK, Scotland, Allt Donachain Dalmally, 88 m alt., on rock in large burn, 25.XI.2018, G.P. Rothero 2018176 (MW* ex Herbarium GP Rothero); Corarsik Burn, Coval, 210 m alt., on rocks in burn, 20. I.2019, G.P. Rothero 2019001 (MW* ex Herbarium GP Rothero); Leacann, Water north of Furnace, 300 m alt., on rock in burn, 8.VI.2019, G.P. Rothero 2019029 (MW* ex Herbarium GP Rothero).

Discussion. Identity of *P. subeugyrium* var. *japonicum* Cardot is discussed under *P. orientale*.

Pseudohygrohypnum purpurascens (Broth.) Kanda, (J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 6: 109. 1976[1977]. – *Hygrohypnum purpurascens* Broth., Öfvers. Finska Vetensk.-Soc. Förh. 62A(9): 36. 1921. = *Hygrohypnum poecilophyllum* Dixon, Rev. Bryol. Lichénol. 7: 113. 1934. (Fig. 4-7, 12, 16).

Description. For description and illustration based on the holotype see Kanda (1976 [1977]).

Differentiation. *Pseudohygrohypnum purpurascens* differs from other species of the genus in having a combination of (1) purplish to deep vine-red color; (2) absence of stem central strand; (3) leaves canaliculate distally, and (4) transversely elongate alar groups (nearly) reaching the

1150   costa. Somewhat similar combinations occur in its two closest relatives, *P. subeugyrium* and *P.*
1151   *neglectum*. *P. subeugyrium* resembles *P. purpurascens* in all essential traits (Jamieson, 1976)
1152   like absence of stem central strand and hyalodermis, strongly incrassate sclerodermal cell walls,
1153   transversely elongate groups of elongate, thick-walled, brownish cells reaching the costae at leaf
1154   base, thick-walled upper leaf cells, and canaliculate upper leaf portion. The few differences
1155   between them include much weaker red coloration in *P. subeugyrium,* which is often absent,
1156   somewhat smaller spores, 12–20 µm vs. 15–30 µm, and amphiatlantic vs. East Asian
1157   distribution. The latter is the most obvious way to differentiate these species. Although Jamieson
1158   (1976) considered coloration to be an unreliable trait for maintaining *P. purpurascens* as a
1159   separate species, molecular data indicate their divergence and here we propose its use only for
1160   distinguishing these separate lineages. Although Jamieson noticed that similar coloration occurs
1161   in numerous specimens of North American and Scandinavian plants, this observation may be
1162   based on specimens of *P. neglectum*, which occur in North America; actually only one of eight
1163   *P. subeugyrium* s.str. specimens studied in the course of the present study had a slight pinkish
1164   coloration. At the same time, shape and denticulation of leaf apex, which was noticed by
1165   Jamieson (1976) as possibly a suitable trait for differentiating Atlantic (i.e. *P. subeugyrium*) and
1166   Japanese (i.e. *P. purpurascens*) plants, does not work for continental East Asian plants which
1167   often have serrulation descending up to 1/3 of the leaf length. *P. neglectum* differs from *P.*
1168   *purpurascens* (which often can be variegate) in somewhat larger plant size, weakly concave, not
1169   canaliculate or tubulose in upper part leaves, and round alar groups, restricted to lateral portion
1170   of the base and sharply delimited from sublinear thick-walled and porose cells of the middle
1171   basal portion. Recombinant *P. neglectum* × *P. subarcticum* specimens may look very similar to
1172   *P. purpurascens* in size, lack of central strand, leaf shape, coloration, and brown cells of alar
1173   groups. They differ in their smaller alar groups, not reaching costae, and the presence of well
1174   delimited, strongly porose cells located between the alar groups. Differentiation of *P.*
1175   *purpurascens* and *P. orientale* is considered under the latter species.
1176   **Variation.** Remarkably, the description of the same species provided by Noguchi (1991) is quite
1177   different. According to Kanda's description, it has "median laminal cells 70–80 × 3–4 µm, …
1178   alar cells usually very incrassate, sometimes arranged in a single row extending to costa in leaf
1179   base; the detailed description sporophytes is provided". This description does not contradict
1180   Brotherus (1921) and generally fits well for plants from our clade C, especially the specimen
1181   from Shikotan Island; however, according to our experience, *P. purpurascens* never has a central
1182   strand, while in the description provided by Kanda "central strand small" is written; since this
1183   trait is sometimes hard to define clearly, we do not consider this controversy as problematic.
1184   According to the description provided by Noguchi (1991), it has "median laminal cells 85–100 ×
1185   3–4 µm, … alar cells bulging, thin-walled; sporophytes unknown".
1186   Among eleven Japanese specimens available for our study nearly half have hyaline, thin-walled
1187   lateral alar cells, which correspond to the description of Noguchi and our plants from the
1188   southern Kuril Islands, while the remaining Japanese specimens have thick-walled, brownish alar
1189   cells that correspond to the description by Kanda and several plants from the continental part of

1190 the Russian Far East. In other respects these two groups are identical. In other words, insular
1191 plants of *P. purpurascens* often have alar groups composed of thin-walled, hyaline cells, while
1192 all continental specimens have alar groups composed of thick-walled cells. Two insular
1193 specimens with thin-walled hyaline alar cells do not form a group in the tree inferred from the cp
1194 markers, although they share specific ITS haplotype; at the moment we would prefer to consider
1195 this trait to be variable without further taxonomic recognition. Three continental specimens from
1196 Primorsky Territory have a very remarkable combination of thick-walled alar cells and wide and
1197 rather short median leaf cells, ca. 40–60 × 6-7 µm (vs. 60-85 × 3–5 µm in insular and other
1198 continental specimens), which are distinctly prorate ventrally. In addition, serrulation of the
1199 upper leaf portions descends in these plants well below the leaf apices, while, according to
1200 Jamieson (1976) and our own observation, the "insular" morphotype is typically characterized by
1201 only a few teeth near the extreme apex. These specimens have a nearly identical ITS haplotype
1202 (shared also by a "recombinant" specimen from Irkutsk Province), are basalmost within the *P.*
1203 *purpurascens* clade and form a strongly divergent clade on the tree inferred from cp markers.
1204 The revision of available specimens of *P. purpurascens* revealed no additional specimens from
1205 continental Asia, which share the aforementioned combination of traits and the remaining
1206 specimens from Primorsky Territory are nearly identical to insular plants, although they have
1207 thicker cell walls. In our opinion, the three specimens from Primorsky Territory discussed above
1208 may deserve taxonomic recognition at the infraspecific level. Comparison with the type of *P.*
1209 *poecilophyllum* is needed first, although its protologue does not agree with plants from the
1210 southern part of Primorsky Territory. Finally, two specimens from the Sino-Himalaya region are
1211 found in a distinct clade and share variegate to greenish coloration that differentiates them from
1212 all other examined specimens of *P. purpurascens*. These plants rather resemble *P. subeugyrium*
1213 s.str., although molecular data and their distribution suggest placement in *P. purpurascens*.
1214 **Ecology.** This species grows on rocks and boulders composed of acidic rocks in or near
1215 mountain creeks, often together with *P. orientale, Entodon luridus*, etc. According to our
1216 collections, this species is rather common in the southern part of the Sikhote-Alin Mountains in
1217 the forest belt, up to 1100 m alt. However, places where it was collected (Elomovsky Klyuch
1218 Creek, Pidan Mountain, Ol'khovaya Mountain) are also the best studied places, since these areas
1219 are known to house the highest amount of temperate East Asian species, which apparently
1220 survived there due to the absence of massive fire events, and thus our impression of its frequency
1221 may be false. In the Kuril Islands this species occurs in the *Betula lanata* & *Sasa* or *Botryoides,*
1222 *Sasa, Spiraea* etc. dominated belt. In the southern part of its range this is a strictly montane
1223 species, which occurs at an altitudinal range of 2510 – 4090 m (Blockeel, Kiebacher & Long,
1224 2019).
1225 **Distribution.** *Pseudohygrohypnum purpurascens* occurs in East Asia: in Russia (southern Kuril
1226 Islands and the southern part of the Sikhote-Alin Mountains), throughout Japan, in South Korea,
1227 a few montane localities in China (Manchuria, Yunnan) and India (Sikkim) (Kanda, 1976
1228 [1977]; Blockeel Kiebacher & Long, 2019; Kim et al., 2020 supplied by our data).

1229 **Specimens examined:** Russia. Primorsky Territory, Lazovsky Distr., Elomovskyj Klyuch Creek
1230 on the path to Benevskie Waterfalls, 43.237N, 133.725E, 400 m. alt., on boulders near stream;
1231 9.IX.2019, V.E. Fedosov 301 (MW9116122), the same area, 43.217N, 133.767E, ca. 250 m. alt.,
1232 6.IX.2013, E.V. Malashkina & O.V. Ivanov Pr-6-15-13 (MHA9046092); the same area, 43.245,
1233 133.719, 670 m alt., rock outcrops near stream; 6.IX.2013, M.S. Ignatov & E.A. Ignatova 13-
1234 1388 (MHA9046091); the same area, Lazovsky State Reserve, middle course of Perekatnaya
1235 River, on boulders near stream, 21.IX.1974, L.V. Bardunov (LE); Shkotovsky Distr., Khalaza
1236 Mt., near stream, partly submerged, 18.X.1933, A.S. Lazarenko (LE); Livadijskaya Mt.,
1237 43.083N, 132.683E, ca. 700 m alt., on boulders near stream, 25.IX.2006, M.S. Ignatov &
1238 E.A.Ignatova 06-2197 (MW9060473*, MHA9046109, 9046110); Partizansk Distr., Ol'khovaya
1239 Mt., Kamenystyj Creek upper course, 43.345N, 133.675E, ca. 1100 m alt., on boulder with
1240 oozing water, 13.IX.2014, V.E. Fedosov (MW9116129); Sakhalin Province, South Kuril Islands,
1241 Iturup Island, vicinity of Circ Bay, Circ Creek, 45.35N, 148,6E, ca. 50 m. alt, on boulder in
1242 stream bed; 10.IX.2015, V.E. Fedosov 15-2-047 (MW9060477*); Shikotan Island, Notoro Mt.,
1243 43.776N, 146.739E, ca. 250 m alt., wet bank of temporary stream, 25.VIII.2007, V.A. Bakalin
1244 K-42-44-07 (MW9060475*, MHA9036958). Japan. Honshu, V.1931, Y. Koyama
1245 (MHA9056574 ex NICH); 10.VII.1932 (MHA9056569 ex NICH); 18.V.1948, M. Mizutani 541
1246 (MHA9056575, LE ex NICH); 3.VIII.1948, N. Takaki 5013 (MHA9056566 ex NICH);
1247 16.X.1948, M. Mizutani 525 (MHA9056571, LE ex NICH); 28.VIII.1952, T. Nakajima 3057
1248 (MHA9056572 ex NICH); 3.VIII.1954, A. Noguchi (MHA9056568 ex NICH); 22.VIII.1954, T.
1249 Nakajima 6120 (MHA9056570 ex NICH); 24.XIII.1976, Z. Iwatsukii 12052 (MHA9056567, LE
1250 ex NICH); Shikoku, 27.VII.1940, S. Hattori 124, 160 (MHA9056565, 9056573 ex NICH).
1251 China. Liaoning, Feng-cheng Co., Feng-huang Shan Mt., 8.IX.1988, X-Y Jia 686 (MO
1252 90103637). Yunnan, Fu Gong County, Salween River watershed, 27.175N, 98.757E, 2675 m alt.,
1253 on granitic boulders in river; 3.V.2004, J.R. Shevock 25337 (MO*); Gong Shan County, Cikai
1254 Xiang, QiQi He River, 27.713N, 98.502E, 2820 m alt., on granitic boulders seasonally
1255 submerged; 28.IX.2007, J.R. Shevock 30900 (MO*).
1256 **Taxonomic comments.** Following Jamieson's (1976) revision, *P. purpurascens* has largely been
1257 synonymised with *P. subeugyrium*, although in both the Japanese and Chinese floras (Noguchi,
1258 1991, Hu et al, 2008) the name *P. purpurascens* is used along with or instead of *P. subeugyrium*.
1259 Actually, among the revealed species, *P. purpurascens* is most similar to *P. subeugyrium* and
1260 also the most closely related according to the cp data. However, our results indicate significant
1261 divergence of these two clearly allopatric lineages (for comments on *P. subeugyrium* var.
1262 *japonicum* see under *P. subeugyrium*).
1263 Since our data suggest rather strong segregation of at least three molecular lineages within *P.*
1264 *purpurascens*, the name *P. poecilophyllum* with a Manchurian type, which was placed into
1265 synonymy with *P. purpurascens* by Kanda (1976), could be used for one of the two continental
1266 lineages, but since ASAP has not suggested segregation of these lineages at the species level and
1267 the amount of material available for morphological and molecular study is quite limited, we

1268 would prefer keeping these lineage within one species, within which three varieties or subspecies
1269 might be delimited.
1270
1271 ***Pseudohygrohypnum sibiricum* Fedosov & Ignatova, sp. nov. (**Fig. 4-7, 12, 17).
1272 **Type:** Kalarsky Distr., Kodar Mts, Srednij Sakukan River, 56.906N, 117.809E, ca. 1060 m alt.,
1273 3.VII.2013, I.V. Czernyadjeva 13-13 (LE – Holotype; MW9077400*, MHA9046093 – Isotypes);
1274 **Diagnosis.** This species is similar to *P. orientale* in its well-developed stem central strand, ovate
1275 leaves and well differentiated, compact alar groups composed of thin to moderately thick-walled
1276 cells, but differs in its lack of a stem hyalodermis, less concave leaves that are not apiculate,
1277 longer leaf cells, and weakly inflated alar groups**.**
1278 **Etymology.** The species epithet originates from the area where the range of the newly described
1279 species largely lies.
1280 **Description.** Plants medium-sized, light- or yellowish-green to purplish-brown, not glossy or
1281 with bronze sheen, reminiscent of *Pohlia cruda*. Stems prostrate, green, brownish or reddish, to 2
1282 cm, complanate, with leaves curved downward, with weakly differentiated epidermal cells (i.e.
1283 with thinner walls than the inner sclerodermis cells), moderately thick, 3–4 layered sclerodermis
1284 and well differentiated central strand, irregularly to nearly pinnately branched, typically
1285 distinctly complanate. Leaves (1.2–)1.3–1.6(–1.8) × (0.5–)0.6–0.9 mm, straight or slightly
1286 falcate-secund, ovate to ovate-lanceolate, acuminate or apiculate, often blunt at tip, slightly
1287 concave to nearly plain, notably narrowed toward insertion, widest at ca. 1/5–1/3 of leaf length;
1288 costa double, rather strong, typically reaching 1/4–1/2 of leaf length, rarely (in narrower leaves)
1289 shorter; margins plane, serrulate in upper half or only near leaf apex; upper laminal cells 35–70(–
1290 85) × 4–5 μm, vermicular, thin- to moderately thick–walled, not porose, at leaf tip shorter,
1291 elongate to rhomboid; basal cells usually thick-walled, concolorous, along margin indistinctly
1292 bordered by a row of a few shorter and wider, lightly colored cells; alar groups well delimited,
1293 ovate to triangular, with base of triangle facing upward, not reaching costae, more or less
1294 inflated, composed of (1–)2–3 rows of inflated, more or less thin-walled, hyaline cells, more
1295 rarely alar groups composed of thick-walled cells with brown walls, or inflated, thin-walled cells
1296 may have slight brownish coloration; subquadrate supra-alar cells usually present. Autoicous.
1297 Perichaetial leaves lanceolate, acuminate, plicate. Setae reddish-brown, 1.5–2 cm. Capsules 1.5–
1298 2 mm long, inclined to horizontal, arch-like curved when young, contracted below mouth,
1299 brownish, usually longitudinally plicate. Exothecial cells moderately thick-walled, elongate,
1300 below mouth in few rows round. Opercula conic. Annuli well differentiated, composed of 2 rows
1301 of large cells. Exostome teeth ca. 400 μm, yellowish-brown, cross-striolate proximally, strongly
1302 serrate, papillose distally; endostome of the same length or a little longer, basal membrane ca.
1303 180 μm, papillose on the inner surface; segments carinate, perforated along a median line; cilia
1304 2–3, filiform. Spores 13–20 μm, papillose.
1305 **Variation.** Most specimens which represent *P. sibiricum* resemble each other although they vary
1306 in the density of branching, shape and areolation of alar cells – typically they are thin- to
1307 moderately thick-walled and in latter case brownish. However, two specimens, one from

1308 Transbaikalia and one from Badzhal Mountains (Khabarovsk Territory) have longer leaves
1309 which are more strongly falcate; alar groups in these specimens are strongly differentiated,
1310 inflated, brown, composed of thick-walled cells (that resemble *P. subeugyrium* s.str., *P.*
1311 *purpurascens* and "*P. neglectum × P. subarcticum*") that do not reach base of costae; however,
1312 sequences, obtained from both specimens are identical to "typical *P. sibiricum*" therefore, we
1313 consider these specimens as representing an unusual morphotype of *P. sibiricum,* likely
1314 ecologically induced. Most Siberian specimens and plants from Bashkortostan lack purplish
1315 coloration and have weakly falcate leaves, while several specimens from Primorsky Territory are
1316 variegate to purple, and their leaves are more falcate; at the same time, the sequences from these
1317 specimens are identical to Siberian ones and no sufficient evidence of gene flow between them
1318 were revealed excepting a single recombinant specimen from the Khamar-Daban Mountains. In
1319 one specimen of *P. sibiricum* the upper branch leaves are tubulose, forming an acute branch
1320 apices which resembles *Calliergonella cuspidata.*
1321 **Differentiation.** Typically, *P. sibiricum* can be recognized and differentiated from other species
1322 of *P. subeugyrium* affinity due to its complanate, yellowish- or brownish-green shoots and rather
1323 short and wide, weakly falcate leaves; it rather resembles such riparian mosses as *Hygrohypnum*
1324 *luridum, Stereodon pratensis* or complanate morphotypes of *Calliergonella lindbergii.* Unlike
1325 the former species, *P. sibiricum* grows on acidic rocks, while *H. luridum* usually settles on basic
1326 ones; forked costae typically reaching midleaf differentiate *H. luridum* from *P. sibiricum.* Both
1327 *Stereodon pratensis* and *Calliergonella lindbergii* differ from *P. sibiricum* in having a
1328 hyalodermis well developed throughout the stem and dioicous sexual condition. Long-leaved
1329 morphotypes of *P. sibiricum* may resemble *P. neglectum*, but they differ in having alar groups
1330 composed of thick-walled cells with brown walls. Such alar cells never occur in *P. neglectum*,
1331 but are characteristic of "recombinant *P. neglectum × P. subarcticum*" specimens, which,
1332 however lack any trace of central strand, are somewhat smaller and have strongly porose basal
1333 leaf cells. Differentiation from *P. orientale* is considered under that species.
1334 **Ecology.** *Pseudohygrohypnum sibiricum* occurs on wet boulders composed of acidic siliceous
1335 rocks along streams or on wet cliffs, at middle elevations (all specimens are restricted to the
1336 forest belt). Most specimens comprise pure mats, usually encrusted by alluvium, which rarely
1337 occurs in other species of the genus. Compared with the other subaquatic *Pseudohygrohypnum*,
1338 *P. sibiricum* occupies lower parts of watercourses where the stream is slower, and this apparently
1339 results in more deposition of sandy alluvium.
1340 **Distribution.** So far, *P. sibiricum* is known as an endemic of Russia, although its occurrence in
1341 Mongolia and Manchuria is quite likely. Its localities are scattered in montane areas with
1342 continental climatic conditions, predominantly along the southern border of Asiatic Russia
1343 eastward to Primorsky Territory with a single locality in European Russia (Bashkortostan) and
1344 two isolated localities in subarctic Anabar Plateau and Magadan Province. This species is locally
1345 abundant in the areas where rather xeric/continental climatic conditions with high temperature
1346 and precipitation seasonality are combined with very acidic rocks (granites or quartzites).
1347 Moreover, among all considered subaquatic species, only *P. sibiricum* demonstrates an affinity

1348   for continental areas with a rather xeric climate (including remarkably xeric Transbaikalia, where
1349   this species is rather frequent). It is hard to imagine hyperoceanic *P. subeugyrium* s.str. being
1350   able to survive in these areas. In more humid areas *P. sibiricum* becomes rarer, being partially
1351   replaced by *P. neglectum* or *P. neglectum* × *P. subarcticum* (i.e. in the Altai and Badzhal Mts.),
1352   *P. purpurascens* and *P. orientale* (Primorsky Territory) or "*P. sibiricum* × *P. purpurascens*" in
1353   Khamar-Daban. The locality in Bashkortostan is somewhat outstanding climatically and
1354   modeling does not predict the presence of *P. sibiricum* there.
1355   **Other specimens examined (Paratypes):** Russia. Bashkortostan Republic, Beloretzkiy Distr.,
1356   South Uralian State Reserve, 54.183 N, 57.617 E, montane creek, on quartzite; 27.VII.1996, E.Z.
1357   Baisheva s.n. (MW9060449, 9060450*, LE). Altay Republic, Altaisky State Reserve, Teletskoe
1358   Lake shore, 51.667N, 87.667 E, ca. 440 m alt., on wet cliffs near waterfall; 11.VII.1989, N.
1359   Zolotukhin (MHA9046105); Ulagan Distr., Chulcha River (Chulyshman River tributary)
1360   51.117N, 88.100E, ca. 800 m. alt., boulder near creek; 14.VIII.2012. M.S. Ignatov & Ignatova
1361   12-854 (MW9060471*, MHA9046107); Kurkure Range, Kayakkatuyarykski, Creek basin, on
1362   wet cliffs near waterfall, 2.VI.1991, M.S. Ignatov (LE). Krasnoyarsk Territory, Taimyr
1363   Autonomous District, Anabar Plateau, Kotuykan River valley, 70.721 N, 105.584 E, on wet
1364   quartzite sandstone rock; 27.VII.2007, V.E. Fedosov 07-380 (MW9060459). Buryatia Republic,
1365   Kabansky Distr., Baikalsky State Reserve, Pereemnaya River valley, 51.425N, 105.294E, ca.
1366   1000 m alt., rock outcrop, near water, 17.VIII.1989, S.G. Kazanovsky (LE); the same area,
1367   valley of Osinovka Creek, 51.504N, 105.133E, ca. 600 m alt., on rocks near waterfall,
1368   29.VII.2016, O.M. Afonina 0116/1 (LE); the same area, Mishikha River valley, 51.623N,
1369   105.535E, ca. 480 m alt., on boulder near stream, 08.VIII.2016, O.M. Afonina 40716/4a (LE).
1370   Zabaikalsky Territory, Kalarsky Distr., Kodar Mts, Srednij Sakukan River, 56.906N, 117.809E,
1371   ca. 1060 m alt., 3.VII.2013 I.V. Czernyadjeva (MHA9046093*, LE); the same area, 56.907N,
1372   117.809E, ca. 1160 m. alt., 7.VII.2013, O.M. Afonina (LE*); the same area, Levyi Syulban River
1373   basin, 56.862N, 117.288E, ca.1460 m. alt.; 11.VI.2015, O.M. Afonina (LE*); Kyrinsky Distr.,
1374   Sokhondinsky State Reserve, Agutsa River valley, Zolotoy Klyuch Spring, 49.753 N, 111.253 E,
1375   ca. 1330 m alt., boulders in stream; 13.VII.2013, I.V. Czernyadjeva (LE*); the same area, near
1376   field station on Enda River, 49.450N, 110.850E, ca. 1070 m alt., 09.VII.2010 & 12.VII.2010,
1377   Czernyadjeva (LE*); the same area, ca. 30 km northward Kyra settl., 49.883 N, 112.050 E, ca.
1378   1310 m. alt., 16.VIII.2006 O.M. Afonina (LE11606, 11707, MHA9046095). Magadan Province,
1379   Yagodinsky Distr., vicinity of Sybit-Tyellakh abandoned settlement, Olen' Creek, ca. 61.94N,
1380   149,57E, 23.VII.1976, L.S. Blagodatskikh (LE). Khabarovsk Territory, Khabarovsk Distr.,
1381   Mountain ridge between Yarap River and its tributary, 50.285 N 134.710 E ca. 600 m. alt.,
1382   stream bank; 30.VII.2016 V.E. Fedosov s.n. (MW*). Primorsky Territory, Sikhote-Alin Mts,
1383   Dalnegorsk Distr., vicinity of Vysokogorsk – Dalnegorsk Pass, 44.494 N, 135.4 E, ca. 700 m alt.,
1384   rocks in creek; 17.IX.2019, Fedosov, s.n. (MW9116123); Olsky Distr., vicinity of Milogradovo
1385   village, irrigated creek bed, 12.VIII.1977, L.V. Bardunov & V.Ya. Cherdantseva (LE);
1386   Skotovsky Distr., Livadijskaya Mt., 43.108 N, 132.693 E, ca. 400 m alt., on boulders near creek;
1387   11.IX.2019, Fedosov, s.n. (MW*); the same area, 43.09 N, 132.693 E, ca. 570 m alt., on boulders

1388 near creek, 13.IX.2019, Fedosov, s.n. (MW9130407); the same place and date, Kučera.
1389 (CBFS21701*, 21737*); Lazovsky Distr., Elomovskyj Klyuch Creek on the path to Benevskie
1390 Waterfalls, 43.237N, 133.725E, 400 m. alt., on boulders near stream; 9.IX.2019, Kučera
1391 (CBFS21434*, 21478*).
1392 **Note:** One specimen tested using molecular markers combines an ITS sequence characteristic of
1393 the northern continental lineage of *P. purpurascens* with plastid markers identical to those of *P.*
1394 *sibiricum*. Morphologically it largely corresponds to *P. sibiricum* and has purplish coloration,
1395 which is not characteristic of this species. The northern slope of the Khamar-Daban Range,
1396 where it was collected, although situated in the central part of southern Siberia, has rather mild
1397 and humid climatic conditions due to the influence of Lake Baikal.
1398 Irkutsk Province, Slyudyanka District, Khamar-Daban Range, valley of Snezhnaya River 5.31
1399 km SSE of the road bridge over Snezhnaya at Vydrino, 51.394N, 104.654E, ca. 500 m alt.,
1400 inundated siliceous boulder at the riverbank, 31.VIII.2018, J. Kučera 20629 (CBFS
1401 Interestingly, the northern slope of the Khamar-Daban Range is the only area in Siberia where
1402 the presence of *P. purpurascens* was predicted by SDM, well isolated from the East Asian Range
1403 of this species. Its penetration there may be dated from nearly the same time as "relict"
1404 populations of nemoral vascular plants concentrated in Khamar-Daban (Chepinoga et al., 2017),
1405 i.e. in the late Pliocene. Since that time, isolated due to further climate cooling, populations of *P.*
1406 *purpurascens* in Khamar-Daban may have been assimilated by *P. sibiricum*, which currently
1407 occurs sympatrically, but the continental *P. purpurascens* ITS haplotype still persists there.
1408
1409 ***Pseudohygrohypnum subarcticum*** Fedosov & Ignatova, sp. nov. (Fig. 4-7, 12, 18).
1410 **Type:** Krasnoyarsk Territory, Taimyrky Autonomous District, Anabar Plateau, Kotuykan River
1411 upper course, slope of Merkyu River valley, 70.446N, 106.464E, ca. 250 m. alt., dolerite rock
1412 outcrops, on fine soil; 19.VII.2011, V.E. Fedosov 11-1237 (Holotype MW9060458*).
1413 **Diagnosis.** This species is similar to *P. subeugyrium* in its lack of purplish coloration, absence of
1414 stem central strand and hyalodermis and falcate leaves, but differs from it by its smaller size,
1415 weakly differentiated alar groups and rostrate opercula.
1416 **Etymology.** The species name is given due to its distribution in northern Siberia, mostly
1417 restricted to Putorana and Anabarskoe Plateau, which are situated near the northern limit of larch
1418 forests in the subarctic climatic zone.
1419 **Description.** Plants small, golden-brownish, more rarely light- or yellowish-green to brownish,
1420 usually with very remarkable golden sheen. Stems prostrate, yellow, brownish or reddish, to 1.5
1421 cm, with undifferentiated epidermal cells, thick 2–4 layered sclerodermis and no central strand,
1422 densely pinnately or, more rarely, irregularly branched. Leaves (0.65–)0.7–0.9(–1.0) × 0.2–0.35
1423 mm, strongly falcate-secund, lanceolate, rarely ovate-lanceolate, acuminate, with blunt tips,
1424 rarely short apiculate, concave to slightly canaliculate, rarely nearly plain, not narrowed or
1425 slightly and gently or abruptly narrowed toward insertion, widest at ca. 1/9–1/5 of leaf length;
1426 costa double, very weak, typically reaching 1/10–1/7 of leaf length; margins plane, denticulate in
1427 upper half or throughout; upper laminal cells 50–80 × 3–4.5 μm, linear, not flexuose, thin- to

moderately thick-walled, not porose, at leaf tip shorter, elongate to rhomboid, with thicker walls; basal cells usually thick-walled, concolorous, often with porose cell walls; alar groups indistinctly delimited, not inflated, composed of few large, brown, thick-walled, short rectangular or elliptic cells, among which the marginal cell is usually thinner-walled, not reaching the costa; an excavated row of thick-walled brownish cells along insertion usually present; few small subquadrate supra-alar cells usually present. Autoicous. Perichaetial leaves lanceolate, acuminate, plicate, up to 1.6 mm long. Setae red, 1–1.5 cm. Capsules 1.5–2 mm long, inclined to horizontal, curved, contracted below mouth, yellowish-brown, smooth. Exothecial cells moderately thick-walled, elongate, below mouth rounded in few rows. Opercula conic-rostrate. Annuli well differentiated, composed of large, inflated cells. Exostome teeth up to 450 μm, yellowish-brown, cross-striolate proximally, papillose distally; endostome of the same length or a little longer, basal membrane ca. 200 μm, weakly papillose on the inner surface; segments carinate, perforated along a median line, papillose on the inner surface; cilia 2, filiform. Spores 15–19 μm, weakly papillose. This species was also illustrated and described by Czernyadjeva (2003) as *P. subeugyrium.*

Variation. Although all studied specimens of *P. subarcticum* and two "recombinant *P. subarcticum* × *P. neglectum* specimens" have identical ITS haplotypes, sequences from the cp markers in *P. subarcticum* are different even though all the *P. subarcticum* s.str. specimens sampled for molecular study came from a rather small area (Taimyrsky District). Studied specimens from Anabar Plateau, SE Taimyr bear apomorphic characters that result in their grouping, while specimens from Byrranga and Putorana occupy a basal position within the *P. subarcticum* clade. Morphological variation is rather insignificant within this species. Plants from shaded environments typically have greener coloration, thinner and less porose cell walls. Of the variability that is apparently not induced environmentally, the leaf apices are worth mentioning. Typically, *P. subarcticum* has blunt leaf tips; however, a few specimens have fairly acuminate leaf tips, which hardly agree with the traditional morphological concept of the genus *Pseudohygrohypnum.*

Differentiation. In having rather long, typically strongly falcate leaves, pinnate branching, golden sheen, thick-walled brown alar cells, and growth on moist rocks often not associated with watercourses, *P. subarcticum* resembles *Campylium bambergeri* rather than any other *Pseudohygrohypnum* species, and a collection of this species made by L.V. Bardunov indeed was referred by him to *C. bambergeri.* From this species *P. subarcticum* differs in its smaller size (leaves shorter than 1 mm vs. 1.2–2 mm), strongly denticulate leaf apices and autoicous sexual condition. The combination of small plants, weakly differentiated alar cells, well-developed annulus, lack of purplish pigmentation, and no stem central strand or hyalodermis differentiate *P. subarcticum* from all other *Pseudohygrohypnum* species.

Ecology. Unlike the other species of *P. subeugyrium* affinity, *P. subarcticum* often occurs on moist bases of cliffs and boulders, in shady niches in rock fields and montane rocky tundra throughout its altitudinal range. Moreover, it is not rare in plateau summit areas and near snowfields where vegetation is nearly absent due to severe environments. When growing along

1468   streams, it inhabits acidic rocks, like other related species, but in other ecotopes it prefers basic

1469   siliceous rocks, *i.e.* basalts, dolerites, ijolites, *etc.*, often growing with species of the genera

1470   *Schistidium, Grimmia, Andreaea, Hymenoloma, Isopterygiopsis, Bryoerythrophyllum,*

1471   *Encalypta, Distichium*, and saxicolous hepatics.

1472   **Distribution.** The distribution of *P. subarcticum* looks quite intriguing. This species mostly

1473   occurs in continental subarctic and Arctic mountains in Northern Siberia; it is very frequent on

1474   Putorana and Anabarskoe Plateaus, as well as in the central part of the Byrranga Range, the

1475   northernmost continental mountain system. Just a few localities were found in the Altai

1476   mountains and in Yakutia; moreover, although plants from these localities fit well the

1477   morphological concept of *P. subarcticum*, they may represent "recombinant haplotypes" which

1478   combine the ITS of *P. subarcticum* with cp markers characteristic of *P. neglectum*. Despite the

1479   first author's special search, this species has been not been found either in the Dixon area or in

1480   Polar Ural, despite environments seemingly quite similar to those where it occurs in central

1481   Byrranga, Putorana and Anabar Plateau. It is also hard to imagine that this remarkable species

1482   could be overlooked in well studied subarctic areas such as the Kola Peninsula, Yakutia and

1483   Alaska; therefore we assume that this species does not occur there despite the model predicting

1484   its presence. Somewhat similar overall distributions have been found for several recently

1485   discovered species such as *Orthotrichum hyperboreum* Fedosov & Ignatova*, Orthothecium*

1486   *remotifolium* Ignatov & Ignatova, *etc.*, but they still differ in details.

1487   **Other specimens examined (Paratypes):** Russia. ?Altai Republic: Shebalino Distr.,

1488   Karakolskie Lakes, 51.483N, 86.433N, ca. 1900 m. alt., subalpine belt, moist rock outcrops;

1489   3.VIII.1991, M.S. Ignatov 28/74 (MHA9046106). Krasnoyarsk Territory, Taimyrky

1490   Autonomous District: Byrranga Range on the northern shore of Taimyr Lake, Ledyanaya Bay,

1491   74.481N, 99.770E, ca. 150 m alt., moist niche of dolerite cliff; 30.VII.2004, V.E. Fedosov

1492   (MW9060465*), the same area, ca. 180 m alt., moist niche of dolerite cliff near the top of rocky

1493   ridge; 12.VIII.2004, V.E. Fedosov (MW9060469). Putorana Plateau, northern shore of Ajan

1494   Lake, 69.267N, 93.483E, ca. 400 m. alt.; forest belt, in water of stream, 4.VIII.1983, I.V.

1495   Czernyadjeva (LE, MHA9046094, MW9060468, 9060451); the same area, 19.VII.1983, I.V.

1496   Czernyadjeva 65 (LE); the same area, 8.VII.1983, I.V. Czernyadjeva 15 (LE); Ajan Lake

1497   southern shore, I.V. Czernyadjeva, 28.VII.1984-15.VIII.1984, ##46, 50, 58, 61, 82, 85, 89, 102,

1498   103 (LE); vicinity of Kapchuk Lake, subalpine belt, on moist rock, VIII.1978, R. Vilde (LE);

1499   Glubokoe Lake, northern shore, 69.307N, 90.101E, ca. 200 m. alt, on fine soil at cliff base;

1500   30.VII.20015, V.E. Fedosov 15-0763 (MW9060452*); Kotuyskoe Plateau, Kogotok Creek lower

1501   course, 70.810N, 100.961E, ca. 100 m alt., shaded crevice of dry andesite cliff; 2.VII.009, V.E.

1502   Fedosov 09-281 (MW9060462), same area, Maymecha River valley 11 km upstream Chopko

1503   River Mouth, 70.723N, 101.234E, ca. 150 m. alt., on boulder near creek; 23.VI.2009 09-381

1504   (MW9060463); middle course of Kotuy River near Medvezhja River mouth, Plateau with

1505   altitudinal mark 347 m, 71.119N, 102.657E, ca. 300 m. alt., moist cliff crevice; 13.VII.2005,

1506   V.E. Fedosov 05-485 (MW9060467), same area, Odikhincha Mt., 70.930N, 103.039E, ca. 620 m

1507   alt., rocky montane tundra, on soil; 13.VIII.2011, V.E. Fedosov 11-983 (MW9060453); same

1508 area, vicinity of Kotuykan River mouth, 70.570N, 103.563E, ca. 120 m alt., onboulder near
1509 stream, 9.VIII.2011, V.E. Fedosov 11-1437 (MW9060454*); lower course of Kotuy River near
1510 Kayak settl., 71.522N, 103.007E, ca. 30 m. alt, moist cliff niche; 23.VIII.2007, V.E. Fedosov,
1511 07-813 (MW9074994); Khara-Tas Range in NW periphery of Anabar Plateau, Longdoko Mt.
1512 71.688N, 104.887E, ca. 500 m. alt., rockfield on the top surface of plateau, on
1513 finesoil;13.VIII.2006, V.E. Fedosov, 06-654, 06-673, 06-699, 06-722, 06-720 (MHA9046089,
1514 9046087, 9046088, MW9060470*, 9075168), the same area, vicinity of Fomich River mouth,
1515 plateau with altitudinal mark 386 m, 72.062N, 110.19E, ca. 350 m alt., rockfield on the top of
1516 Plateau, on moist shaded surface of boulder, 13.VII.2008, V.E. Fedosov 08-8, 08-469
1517 (MW9060464*, MHA9046086); Anabar Plateau, Kotuykan River valley upstream Merkyu River
1518 mouth, 70.527N, 105.909E, ca. 250 m alt., on boulders near water; 14.VII.2007 V.E. Fedosov
1519 07-383 (MW9060460), the same place, 20.VII.2007, V.E. Fedosov 07-362 (MW9060461), the
1520 same area, Burdur Creek lower course, 70.541N, 105.854E, ca. 240 m alt., shaded base of
1521 sandstone boulder; 17.VII.2007, V.E. Fedosov 07-405 (MW9060455); Kotuykan River upper
1522 course, 70.471, 106.383, ca. 250 m alt, 16.VII.2011, V.E. Fedosov 11-690, 11-741
1523 (MW9060456, 9060457), 19.VII.2011, V.E. Fedosov 11-1237 (MW9060458*). Evenkiya Distr:
1524 Southern periphery of Putorana Plateau, vicinity of Beldunchana Lake, ca. 67.89N, 95.74E, ca.
1525 330 m alt., on boulders near lake; 27.VII.1971, L.V. Bardunov s.n. (LE). Yakutia Republic:
1526 Tomponsky Distr., Suntar-Khayata Range, At-Moole Creek, 63.11N, 138.62E, ca. 770 m. alt.,
1527 wet cliffs; 22.VII.2003, E.I. Ivanova & V.I. Zolotov s.n. (MHA9020464).
1528
1529 ***Pseudohygrohypnum neglectum* Fedosov & Ignatova, sp. nov. (**Fig. 4-7, 19).
1530 **Type:** Khabarovsk Territory, southern spoors of Badzhal'sky Range, Yarap River in its upper
1531 course; 50.285 N 134.713 E, 580 m alt., on wet and submerged boulders along a stream.
1532 2.VIII.2016 V.E. Fedosov & O.Yu. Pisarenko (Mosses Of The Russian Far East Exsiccatae Fasc.
1533 II. № 62), MW9077401 (Holotype), MHA, LE, NSK?, VGBI?, KRAM?, MO?, CAS? (see
1534 Differentiation) (Isotypes).
1535 **Diagnosis.** This species is similar to *P. purpurascens* in its weakly developed to absent stem
1536 central strand and epidermis, falcate leaves and variegate, pink to purplish coloration, but differs
1537 by (1) larger size of plants; (2) slightly concave, not tubulose distally, narrowed toward insertion
1538 leaves; (3) alar groups composed of inflated, hyaline, thin-walled cells; (4) not excavated
1539 basalmost cells between alar groups; and (5) somewhat larger spores.
1540 **Etymology.** This epithet is chosen since this species actually occurs in eastern North America
1541 but has not yet been separated from *P. subeugyrium* s.str. despite rather clear morphological
1542 differentiation. It no doubt would have remained neglected had the molecular data presented here
1543 not suggested it be recognized.
1544 **Description.** Plants medium-sized to large, green yellowish-green or often variegate, purplish-
1545 green with light green leaf bases and pink to dark purplish distal leaf portions. Stems prostrate,
1546 green, brownish or reddish, to 4 cm, weakly complanate, with weakly differentiated epidermal
1547 cells (*i.e.,* with thinner walls than the inner sclerodermis cells), moderately thick 2–3(–4)-layered

1548   sclerodermis and a poorly or undifferentiated central strand, weakly and irregularly branched.
1549   Leaves (1.3–)1.4–1.8(–2.0) × 0.45–0.7 mm, falcate-secund, ovate-lanceolate, acuminate,
1550   moderately concave to nearly plain, notably narrowed toward insertion widest at ca. 1/7–1/3 of
1551   leaf length; costa double, weak, 1/7–1/5 of leaf length, rarely reaching 1/3 of leaf length; margins
1552   plane, denticulate in upper half; upper laminal cells 40–75 × 4–5 μm, vermicular, moderately to
1553   strongly thick-walled, subporose, at leaf tips shorter, elongate; basal cells usually strongly
1554   porose, concolorous, along margin indistinctly bordered by a row of a few shorter and wider,
1555   cells; alar groups well delimited, rounded, more or less inflated, composed of 2–3 rows of
1556   inflated, more or less thin-walled, hyaline to concolorous cells, not reaching costa; subquadrate
1557   supra-alar cells usually present. Autoicous. Perichaetial leaves lanceolate, acuminate, plicate.
1558   Setae reddish-brown, 1–1.5 cm. Capsules 1.5–2 mm long, inclined to horizontal, curved,
1559   contracted below mouth, brownish, usually longitudinally plicate. Exothecial cells moderately
1560   thick-walled, elongate, below mouth rounded in a few rows. Opercula conic-apiculate. Annuli
1561   differentiated, composed of large, inflated cells. Exostome teeth up to 450 μm, yellowish-brown,
1562   cross-striolate proximally, papillose distally; endostome of the same length or a little longer,
1563   basal membrane ca. 150 μm, papillose on the inner surface; segments carinate, perforated along a
1564   median line; cilia 2, filiform, appendiculate. Spores 12–18 μm, papillose.
1565   **Variation.** Asian plants of *P. neglectum* look quite uniform, varying only in coloration: a
1566   specimen from the Altai Mountains and one of the specimens from Khabarovsk Territory have
1567   bronze rather than pink or purplish coloration and somewhat longer leaves; a single North
1568   American specimen also has a rather poorly expressed pinkish aspect, although in other respects
1569   it fits well the morphological concept of *P. neglectum*. The alar region varies even on a single
1570   stem, in a few leaves a purplish to light brownish alar group may occur; in a few specimens it is
1571   more poorly delimited, concolorous, composed of cells with thicker walls. The stem central
1572   strand in the type specimen is absent, while the specimens from Dusse-Alyn Range (Khabarovsk
1573   Territory), Maine and the Altai Mountains (South Siberia) have an indistinctly differentiated
1574   central strand.
1575   **Differentiation.** *P. neglectum* typically differs from all other species of *Pseudohygrohypnum* in
1576   the combination of pink to purplish coloration, weakly concave leaves and inflated, round alar
1577   group, which does not reach the costa, composed of thin-walled hyaline cells. This combination,
1578   together with the rather large size of the plants, indistinct stem central strand, falcate leaves with
1579   denticulate margins, and thick-walled, porose basal laminal cells makes *P. neglectum* remarkably
1580   similar to *Calliergonellopsis dieckii,* which differs from *P. neglectum* in having a well
1581   differentiated stem hyalodermis and dioicous sexual condition. According to the phylogenetic
1582   tree inferred from the cp data, *P. neglectum* is close to *P. subarcticum*. However, these two
1583   species are quite easy to distinguish since the plant sizes are very different and their leaf length
1584   ranges do not overlap; alar groups in *P. neglectum* are well differentiated, composed of thin-
1585   walled cells, while in *P. subarcticum* they are weakly differentiated, composed of few thick-
1586   walled cells; in addition, *P. subarcticum* has a quite specific golden sheen, while plants of *P.*
1587   *neglectum* are not glossy, but usually have pink to purplish coloration. Its rounded alar group

composed of thin-walled hyaline cells, not reaching costa and well delimited from the cells of the medial portion of the insertion, lack of canaliculate aspect of the upper portion of the leaf as well as its larger plant size and less incrassate sclerodermis differentiate *P. neglectum* from *P. purpurascens* and *P. subeugyrium*, which may occur in the same areas. *Pseudohygrohypnum neglectum* may be hard to differentiate from *P. sibiricum*, which also may have an inflated alar group composed of hyaline cells but usually has shorter, less falcate leaves with shorter upper leaf cells and only seldomly has a purplish tint. In addition, the central strand in *P. sibiricum* is typically well differentiated, while in *P. neglectum* it is absent or weak, and most Siberian specimens of *P. sibiricum* possess a more or less distinctly complanate habit that is not characteristic of *P. neglectum*. It may also resemble *Calliergonella lindbergii*, although it usually differs from it by having a pink tint. In the field, the somewhat larger plants of *P. neglectum* should help separate it from other species of the *P. subeugyrium* group. Together with *P. neglectum* recombinant plants which bear ITS sequences characteristic of *P. subarcticum* and cp markers of *P. neglectum* occur, and several duplicates of «Mosses of the Russian Far East Exsiccatae» №62 actually comprise such plants instead of *P. neglectum*. One such specimen kept in CBFS was demonstrated using molecular data. These recombinant plants are much smaller than *P. neglectum*, with leaves up to 1.2 mm long; they also differ from *P. neglectum* by having a more weakly delimited alar group, composed of quadrate cells with brownish cell walls that are not inflated.

Ecology. *Pseudohygrohypnum neglectum* occurs on wet boulders composed of acidic siliceous rocks along streams at middle elevations reaching the subalpine birch krummholz zone. Typically, it forms pure mats, or grows admixtured with *Hygrohypnella polaris* (Lindb.) Ignatov & Ignatova, *Sciuro-hypnum plumosum* (Hedw.) Ignatov & Huttunen and *Codriophorus* spp., often encrusted by sandy alluvium and diatoms.

Distribution. *P. neglectum* has a disjunctive "east-eastern" cool temperate distribution, which is still insufficiently known since quite a limited amount of material is available for study. At the same time, with ca. 10 specimens collected in NE part of Khabarovsk Territory in two rather well studied areas, we may assume that this species is rather common there; two isolated localities are known from the vicinity of Teletskoe Lake in the Altai Mts, and in Maine, USA. Limited distribution in North Asia with remote occurrence of *P. neglectum* in eastern North America and its plesiomophic position in the tree inferred from ITS suggest that *P. neglectum* is rather close to the ancestor of this clade and may be considered relictual. The east Asian early diversification of the genus *Pseudohygrohypnum* and most likely of the *P. subeugyrium* clade, supports this view. In addition, the areas where *P. neglectum* occurs in Khabarovsk Territory are home to several remarkable relict species like *Apotreubia hortonae* R.M. Schust. & Konstant., *Cryphaea amurensis* Ignatov, *Actinothuidium hookeri* (Mitt.) Broth., etc (Ignatov et al., 2000; Bakalin, pers. comm.). Although, quite a limited number of specimens was available for study during the MS preparation, further records of *P. neglectum* in North America are expected, especially in the western part of the North American range of *P. subeugyrium* s.l.

Other species examined (Paratypes): Russia. Altay Republic, vicinity of Telezkoe Lake, Bolshoe Istyube Creek, ca. 51.783N, 87.450E, ca. 570 m. alt., wet cliffs; 22.VII.1991. M.S. Ignatov (MHA9046107). Khabarovsk Territory, Khabarovsk Distr., Mountain ridge between Yarap River and its tributary, 50.338 N 134.656 E ca. 1300 m. alt., stream bank; 9.VIII.2016 V.E. Fedosov s.n. (MW9112895); the same area, Yarap River valley, 50.285N 134.710 E ca. 600 m. alt., on wet boulder near stream, 30.VII.2016, V.E. Fedosov 16-27 (MW9112894), the same place and date, O.Yu Pisarenko (NSK2006566); Verknebureinsky Distr., Bureinsky State Reserve, Dusse-Alin Range, Medvezh'e Lake, 52.083N 135.016 E ca. 1700 m alt., on wet W-facing cliff; 10. VIII.1997 M.S. Ignatov 97-571 (MHA9046090, 9046102, 9046103), Ignatov 97-575 (MHA9046098); the same area, Lednikovyj Klyuch Creek basin, 52.117N, 134.416E, ca. 1420 m alt., on moist boulder on the bottom of temporary stream; 24.VIII.1987, Petelin D.A. (MHA9046104). USA. Maine. Franklin County, Town of Eustis; along Tim Brook near Tim Pond; 5.VII.2008, B. Allen 29078 (MO).

P. neglectum × *P. subarcticum* **(**Fig. 4, 6, 20).

Although only three specimens which combine ITS sequences characteristic of *P. subarcticum* and plastid sequences of *P. neglectum* were detected using molecular data, they are quite distinct morphologically due to a combination of (1) small plant size (although somewhat larger than in *P. subarcticum*); (2) brownish, pinkish to purplish coloration; (3) strongly falcate leaves; (4) distinct alar groups composed of quadrate cells with thick, brownish walls which ascend along leaf margins, and thus have a triangular shape; (5) linear cells with thick and typically strongly porose walls between alar groups; (6) often pinnate branching resembling that of *P. subarcticum*. The revision of herbarium collections revealed at least five additional specimens.

Specimens examined: Zabaikalsky Territory, Kalarsky Distr., Kyrinsky Distr., Sokhondinsky State Reserve, upper course of the Larionov Klyuch Creek, 49.784N, 111.242E, ca. 1440 m alt., rocky outcrops; 14.VII.2013 O.M. Afonina 4713 (LE). Yakutia, Tomponsky Distr., Kyurbelyakh Creek valley, 63.117N, 139.033E, ca. 900 m alt., in creek, 9.VII.2011, M.S. Ignatov & E.A. Ignatova 11-2242 (MW9060472*, MHA9046085); Khabarovsk Territory, Khabarovsk Distr., Yarap River valley, 50.303N 134.739 E ca. 600 m. alt., stream bank; 12.VIII.2016, O.Yu. Pisarenko s.n. (NSK2006568); the same area, 50.296N 134.718 E ca. 580 m. alt., stream bank; 2.VIII.2016, O.Yu. Pisarenko s.n. (NSK2006567); Verknebureinsky Distr., Bureinsky State Reserve, Dusse-Alin Range, Kuraigagna Creek, 52.067N, 134.867E, 1540 m. alt., rocky slope; 4.VIII.1992, B. Borisov (MW9060476*); the same place, 1050 m. alt., rocks near waterfall, 14.VIII.1997 M.S. Ignatov 97-576 (MHA9046099); the same area, Medvezh'e Lake, 52.083N 135.016 E ca. 1700 m alt., wet cliff crevice; 9.VIII.1997 M.S. Ignatov s.n. (MHA9046096). Thus, these "recombinant" specimens occur in NE Asia in the same areas as *P. neglectum* or between the ranges of *P. neglectum* and *P. subarcticum*. Most likely, these plants originated as a result of hybridization/introgression until climate oscillation, and further speciation divided the ranges of these species by a large area, apparently not populated by *Pseudohygrohypnum* at all.

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1675

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Morphological differentiation of the revealed subaquatic *Pseudohygrohypnum* lineages

Trait	Eugyrium A (P. eugyrium s.str.)	Eugyrium B (P. appalachianum)	Eugyrium C (P. orientale)	Subeugyrium A (P. subeugyrium s.str.)	Subeugyrium B (P. sibiricum)	Subeugyrium C (P. purpurascens)	Subeugyrium D (P. neglectum)	Subeugyrium E (P. subarcticum)
Coloration	Bright green, pinkish to reddish or blackish	Bright green	Light green	Olivaceous green, brownish rarely reddish	Green, dirty yellow to brownish or reddish	Variegated, green / purple to deep vinaceous	Variegated, green / pinkish to purple	Bronze with golden sheen
Stem central strand	present	present	present	absent	present	absent	absent or indistinct	absent
Stem hyalodermis	Differentiated (nearly) throughout	Differentiated throughout or in patches	Differentiated in patches to not differentiated	Not differentiated	Not differentiated, rarely differentiated in patches	Not differentiated	Not differentiated	Not differentiated
Leaf shape	Ovate to ovate-lanceolate, acute to apiculate	Ovate to ovate-lanceolate, apiculate	Ovate to ovate-lanceolate, apiculate	Ovate-lanceolate, acute rarely blunt	Ovate to ovate-lanceolate, blunt, acute to short acuminate	Ovate-lanceolate, rarely ovate, blunt, rarely acute	Ovate-lanceolate, acute to short acuminate	Lanceolate, rarely ovate-lanceolate, blunt
Leaf falcateness	Not or slightly falcate	Not or slightly falcate	Distinctly falcate	Slightly to strongly falcate	Not or slightly falcate	Slightly to strongly falcate	Distinctly falcate	Strongly falcate
Leaf size (mm)	1.2-1.6(-1.8)	(1.3-)1.5-1.8	(0.9)1-1.6(-2) x (0.3-)0.55-0.8 (-0.85)	1.2-1.75	(1.2-)1.3-1.6(-1.8) x (0.5-)0.6-0.9	1.2-1.8(-2)	(1.3-)1.4-1.8(2.0) x 0.45-0.7	(0.65-)0.7-0.9(-1) x 0.2-0.35
Leaves widest at	1/5-1/2	1/5-1/2	(1/5-)1/3-1/2	1/7 – 1/5(-1/3)	1/5-1/3	1/7 – 1/5(-1/3)	1/7-1/3	1/9-1/5
Leaf concavity	Strongly concave	Strongly concave	Strongly concave	Concave, canaliculate distally	Weakly concave	Concave, canaliculate distally	Slightly to moderately concave	Concave, canaliculate distally
Costa extension	¼-1/2	¼-1/2	¼-1/2	1/5	¼-1/2	1/5	1/7-1/5 (-1/3)	1/10-1/7
Margin serrulation	At tip	Nearly entire or at tip	At tip to upper 1/3	At tip to upper 1/3	At tip to upper 1/2	At tip to upper 1/3	1/2	Nearly to the base
Leaf cells	30-62 µm flexuose	45-75 µm flexuose	30-50(-65) x 3-5(-6) µm, not flexuose	40-105 µm flexuose	35-70 x 4-5 µm, slightly flexuose	40-105 x 3-7 µm flexuose	40-75 x 4-5 flexuose	50-80 x 3-4.5 not flexuose
Alar group differentiation	Strongly differentiated, Rounded, or transverse elongate, usually not reaching costa, inflated	Strongly differentiated, Rounded, not reaching costa, strongly inflated	Moderately differentiated, rounded, or transverse elongate, usually not reaching costa, weakly inflated,	Moderately to strongly differentiated, transverse elongate, weakly delimited proximally, usually reaching costa, inflated	Moderately differentiated, rounded, or transverse elongate, usually not reaching costa, inflated or not	Moderately to strongly differentiated, transverse elongate, weakly delimited proximally, reaching costa, inflated	Strongly differentiated, rounded, not reaching costa, inflated	Small, weakly delimited, not inflated
Alar cells shape	Large, thick-walled brown, rarely hyaline	Large, thin-walled, hyaline to slightly colored	Large, thin-walled, hyaline to thick walled, brownish	Large, thick-walled with brown walls	Large, Thin-walled, hyaline to thick walled, brownish	Large, thick-walled with brown walls or hyaline	Large, thin-walled, hyaline to slightly colored	Small, quadrate, thick walled, brownish
Operculum	conic	conic	conic	conic	conic	conic	conic	conic-rostrate
Spore size (µm)	12-20	14–23	17-25	12-20	13-20	15-30	12-18	15-19
Distribution	Europe,	East North	East Asia	North Europe, East North	South Ural, Central & East	East Asia	NE Asia & E	North Siberia

Caucasus?	America		America	Asia	North America

Results of niche similarity tests

Black values - similarity lower than random Red values - similarity higher than random Orange values - in one direction similarity is higher than random, while in second lower. "D" and "I" columns indicate Schoener's D and Hellinger's I metrics

Species Pair	I	D
EUGYRIUM GROUP		
eu A – eu B	0.51	0.18
eu B – eu C	0.54	0.25
eu A – eu C	0.30	0.08
SUBEUGYRIUM GROUP		
seu A - seu B	0.05	<0.01
seu A - seu C	0.47	0.22
seu A - seu E	<0.01	<0.01
seu B - seu C	0.68	0.40
seu B - seu E	0.66	0.35
seu C - seu E	0.35*	0.12
EUGYRIUM – SUBEUGYRUM		
eu A - seu C	0.34	0.09
eu A - seu B	<0.01	<0.01
eu A - seu E	<0.01	<0.01
eu A - seu A	0.70	0.36
eu B – seu C	0.52	0.24
eu B - seu B	0.10	<0.01
eu B - seu E	0.04	<0.01
eu B - seu A	0.72	0.46
eu C - seu C	**0.98**	**0.83**
eu C - seu B	0.60	0.34
eu C - seu E	0.26	0.07
eu C - seu A	0.46	0.21

1 *Black values - similarity lower than random*
2 *Red values - similarity higher than random*
3 *Orange values - in one direction similarity is higher than random, while in second lower*

Figure 1

Bayesian trees inferred from cp ATRKR (left side) and nr ITS (right side) datasets

Statistical support indicating Bayesian posterior probabilities (PP) and maximum-likelihood bootstrap support (BS) inferred from matrices without (1) and with (2) indel coding is provided at the branches in the order PP1/PP2/BS1/BS2; a dash (-) indicates no support (PP < 0.7 and BP < 50). Dashed line indicates not or weakly supported clades

Figure 2

Split trees of the crown clade of Pylaisiaceae, originated from the cp ATR (a) and nr ITS (b) datasets

Colors indicate revealed lineages of subaquatic *Pseudohygrohypnum*. Bootstrap values are indicated at branches corresponding to genus- and/ or species level. The bootstrap values appeared from 1000 iterations of the bootstrap analysis in Splitstree 4

A

Ectropothecium + Vesicularia

Calohypnum sakuraii

Calohypnum plumiforme

Calohypnum amabile

100

99

100

P. eugyrium A

HyF39
HyF38 H_eu
Hh2275 HyF31
HyF16
HyF15

P. eugyrium B

P. skottsbergii

Hy1538 Hy1539

87 94

Buckia vaucheri

100

100 100

P. subeugyrium A

HyF41
H_sub HyF35
HyF40 P2274
HyF36 HyF37

99

P. subeugyrium B

Hh2513 HyF25 HyF12
HyF18 HyF20 HyF50, HyF19
HyF46 HyF47
HyF7 Hh1896 Hh2514
HyF4, HyF60, Hh1900

99

Hh1585
HyF52
HyF29 HyF61
HyF45 HyF6
HyF44 HyF28

Pylaisia + Homomallium

100

100

P. calcicola

HyF51 Hy657

P. densirameum

Hy1481
Hy858

HyF17
HyF27
HyF43
HyF58

P. subeugyrium D

99

Hy1480
Hy17 Hy990

90

P. subeugyrium C

99 *P. fauriei*

Hh1898 HyF1
HyF62 HyF2
HyF63
HyF64
HyF53, HyF49
HyF65

HyF55
Hh2520
HyF23 HyF24
HyF21
HyF54 HyF56
HyF5
HyF3

P. eugyrium C

100

P. subeugyrium E

0.001

Hy1038

P. fertile Hy655

B

Hy655
Hy1038

P. fertile

0.001

P. eugyrium B

HyF39
HyF38
Hh2275

P. eugyrium C

HyF53
HyF2, HyF49
HyF64 HyF1
HyF62 Hh1898
HyF65
HyF63

P. calcicola

HyF51

Hy657

100

Calohypnum plumiforme

P. eugyrium A

HyF31
HyF16
eu_H
HyF15

100

98

Calohypnum sakuraii

Calohypnum amabile

P. subeugyrium D

89

91

91

96

92

Calohypnum oldhamii

x_HyF5
x_HyF55
HyF43
HyF17, HyF58
HyF27

P. subeugyrium E

91

HyF56
HyF54 HyF21
HyF3
HyF23
HyF24

96

*Ectropothecium
+ Vesicularia*

P. subeugyrium B

HyF12 HyF50
x_Hh1585 HyF60 HyF18
Hh1896 HyF47 HyF19
HyF25 HyF46
HyF7 HyF4

100

Buckia vaucheri

HyF40
HyF37 HyF36
HyF41 Hh2274
su_H
HyF35

P. subeugyrium A

HyF45
HyF28 HyF44
HyF29
HyF61

HyF6
HyF52
HyF20

P. subeugyrium C

100 100 100

*Pylaisia +
Homomallium*

Hy858 Hy990
Hy1481
Hy1480, Hy17

P. densirameum *P. fauriei*

Hy1539
Hy1538

P. skottsbergii

Figure 3

Bayesian tree inferred from expanded cp & mt dataset for Pylaisiaceae with nodes dated by Beast

Temperature course is indicated by black curve and also by colour filling above according to Westerhold et al. (2020). Coloured bars in the temperature curve indicates estimated periods of basal radiation of the genus *Pseudohygrohypnum* (a), origin of mesophilous species of the genus (b), basal radiation of subaquatic lineages of the genus (c), further radiation of *P. subeugyrium* complex (d) in relation to temperature
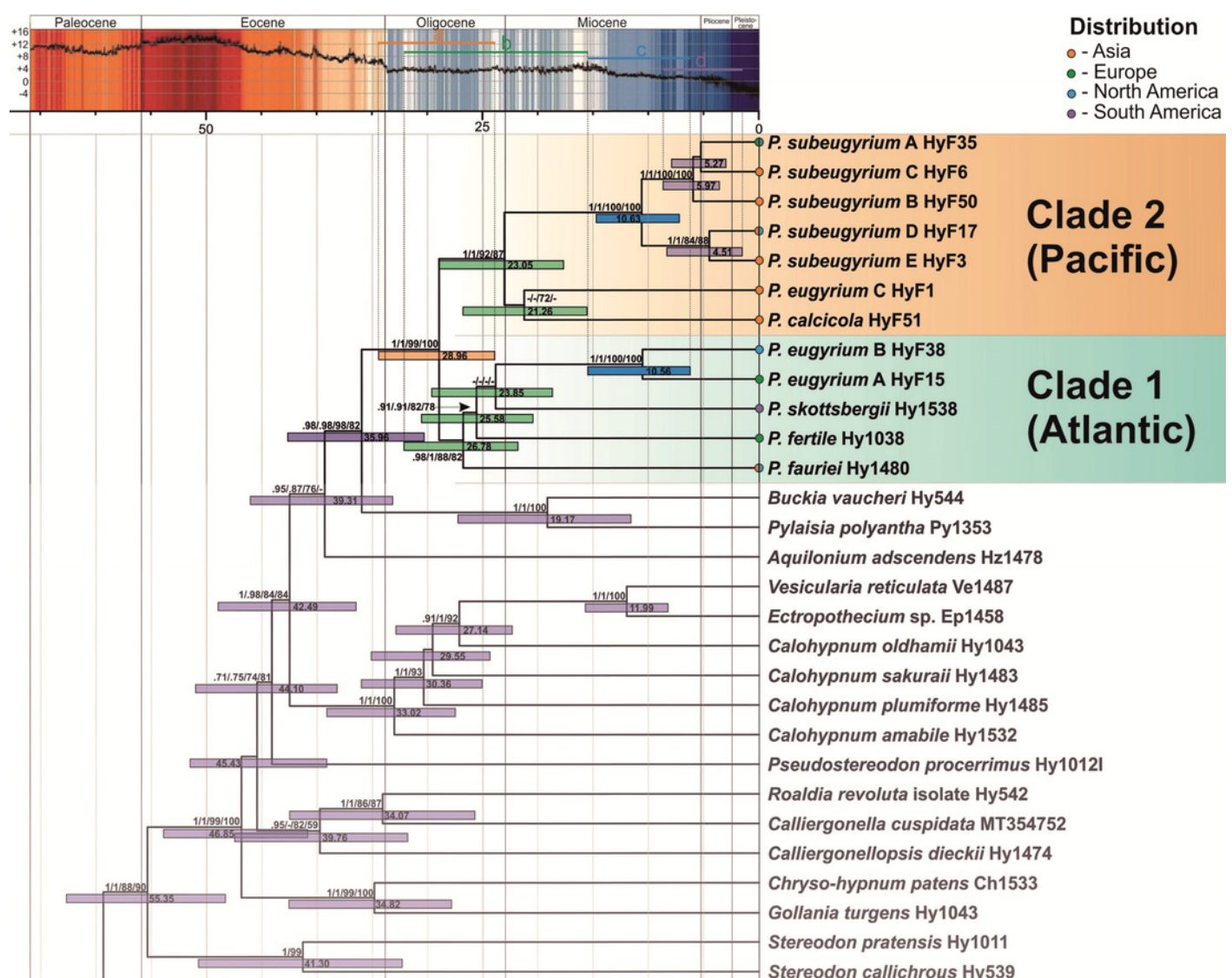
Figure 4

Habit of plants from the revealed lineages of subaquatic *Pseudohygrohypnum*

A-C – *P. eugyrium* lineages A-C correspondingly, D-G – *P. subeugyrium* lineages A-D correspondingly, H – recombinant plant *P. subeugyrium* D x *P. subeugyrium* E, I – *P. subeugyrium* lineage E Fig. 4. Stem leaves in plants from the revealed lineages of subaquatic *Pseudohygrohypnum*: A-C – *P. eugyrium* lineages A-C correspondingly, D-H – *P. subeugyrium* lineages A-E correspondingly
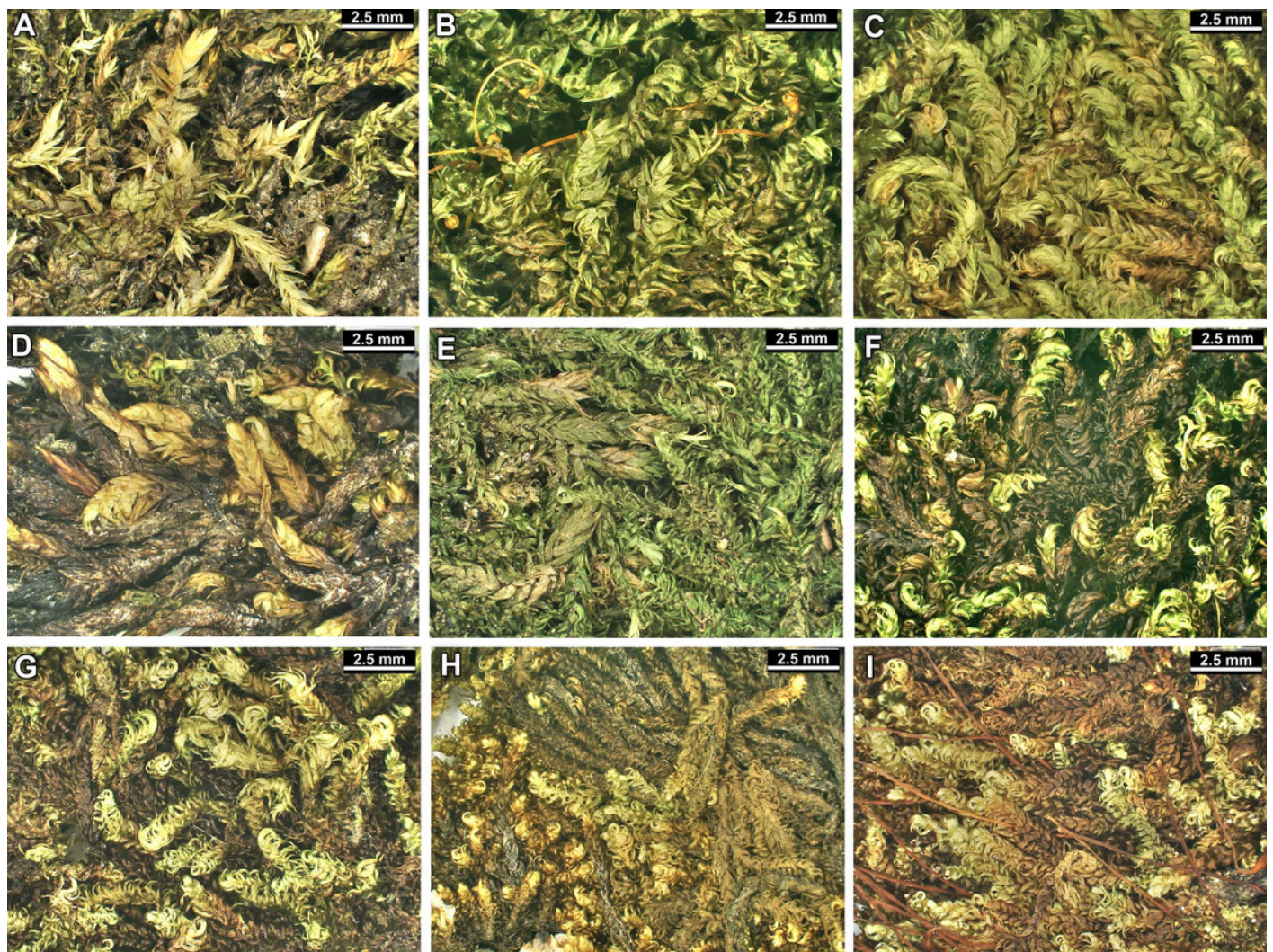
Figure 5

Stem leaves in plants from the revealed lineages of subaquatic *Pseudohygrohypnum*

A-C – *P. eugyrium* lineages A-C correspondingly, D-H – *P. subeugyrium* lineages A-E correspondingly

0.5 mm
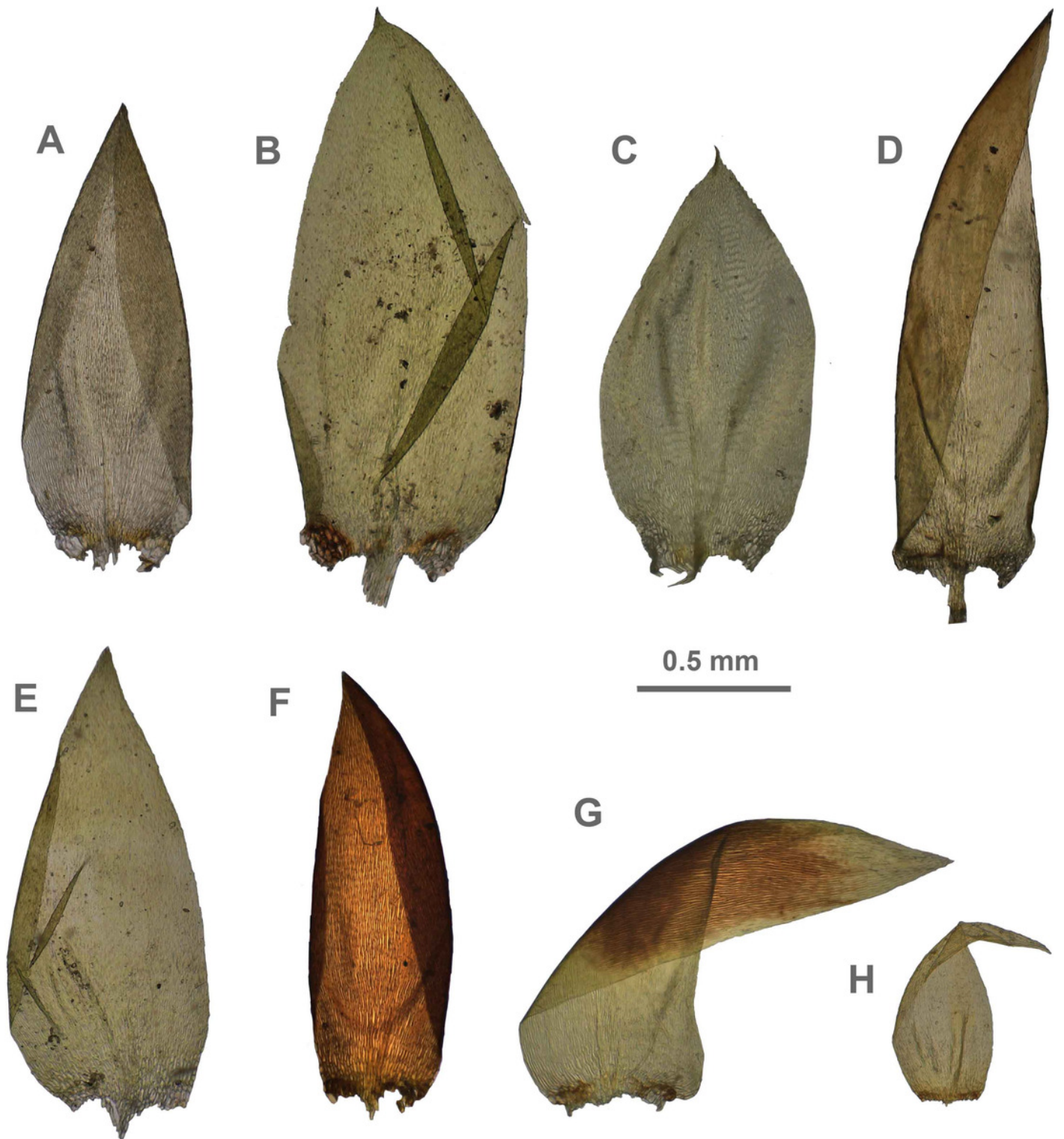
Figure 6

Stem leaf tips in plants from the revealed lineages of subaquatic *Pseudohygrohypnum*

A-C – *P. eugyrium* lineages A-C correspondingly, D-H – *P. subeugyrium* lineages A-E correspondingly
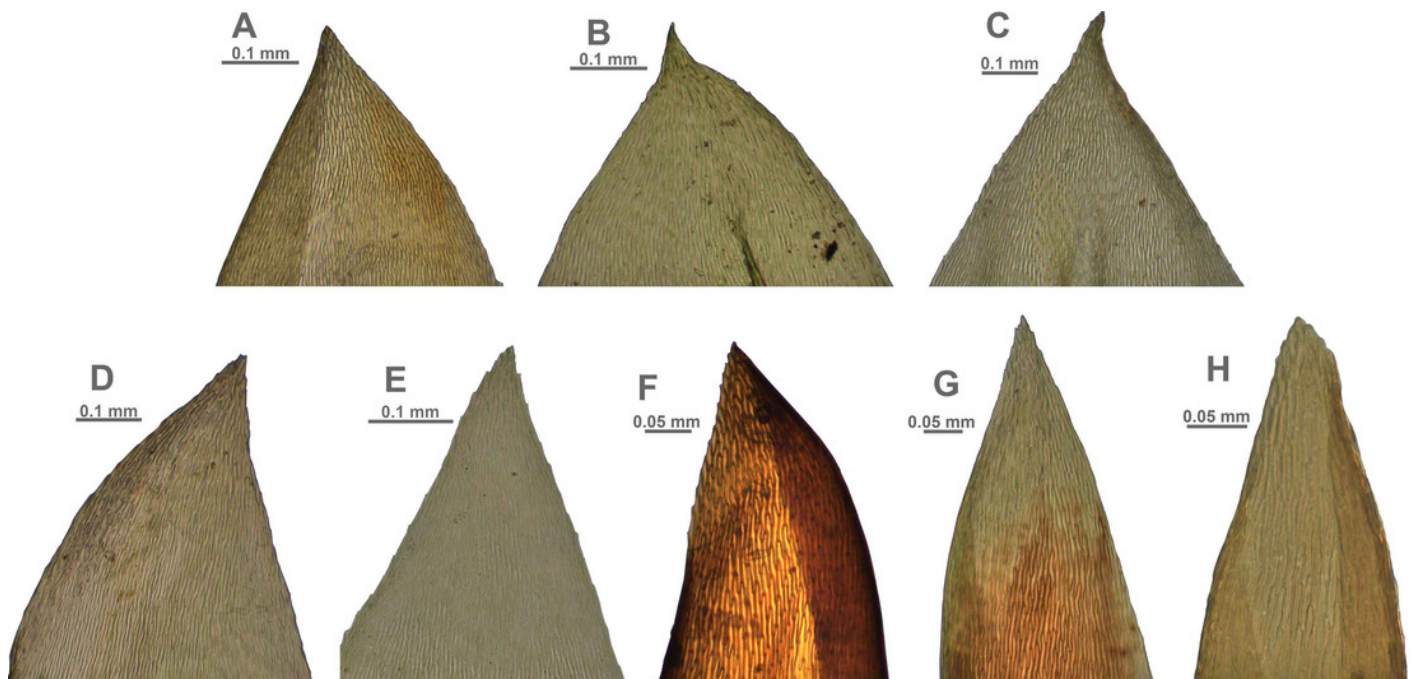
Figure 7

Stem leaf base in plants from the revealed lineages of subaquatic *Pseudohygrohypnum*

A-C – *P. eugyrium* lineages A-C correspondingly, D-G – *P. subeugyrium* lineages A-D correspondingly, H – recombinant plant *P. subeugyrium* D x *P. subeugyrium* E, I – *P. subeugyrium* lineage E
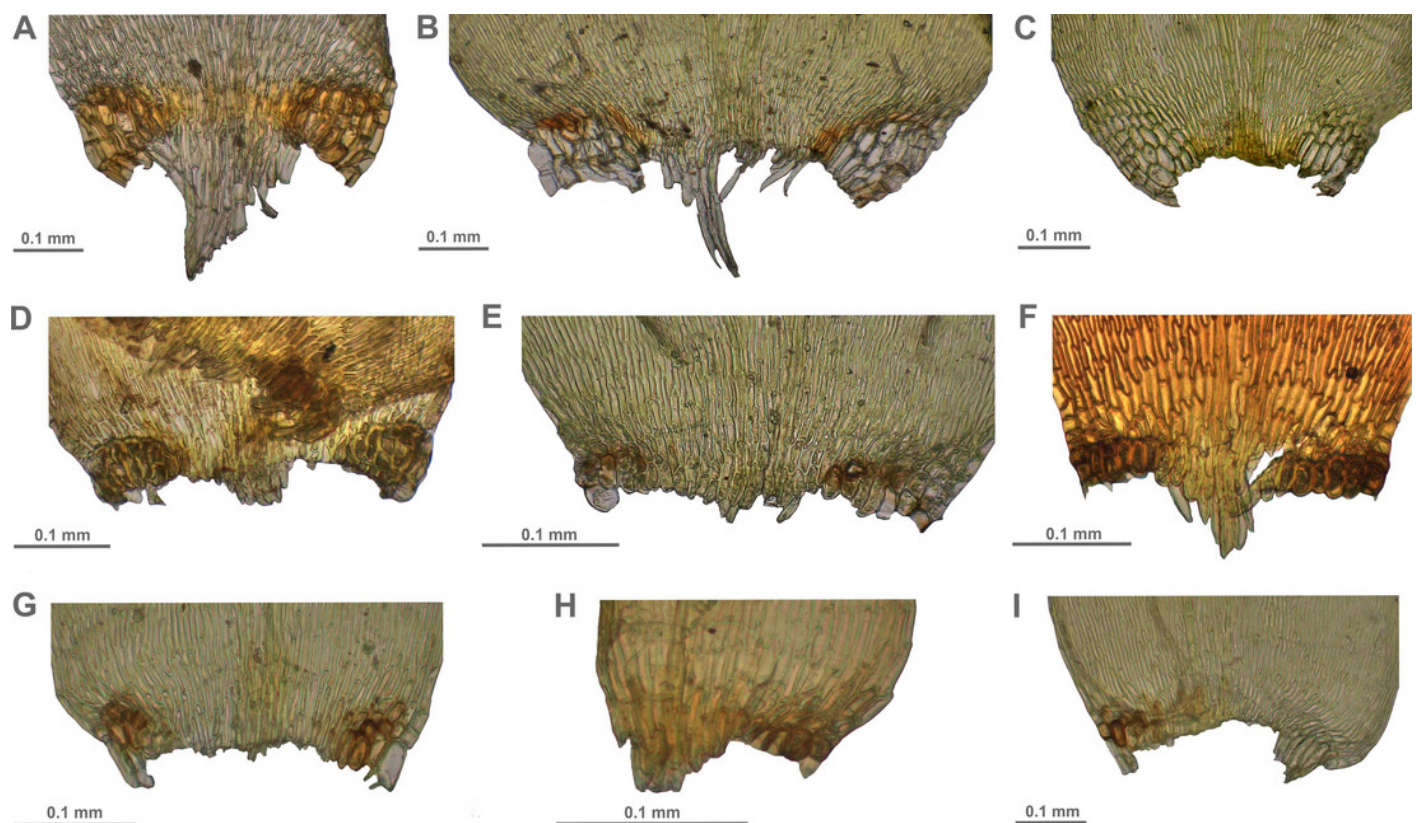
Figure 8

Distribution of the revealed lineages of subaquatic *Pseudohygrohypnum*

upper map – *P. eugyrium* A (blue squares), B (violet squares) and C (green squares); lower map – *P. subeugyrium* A (lemon circles), B (orange circles), C (red circles), D (dark blue circles), E (pale blue circles) and recombinant specimens *P. subeugyrium* BxC (orange stars) and DxE (pale blue stars). Colour shades indicate distribution of the lineage with concolorous symbols obtained from SDMs
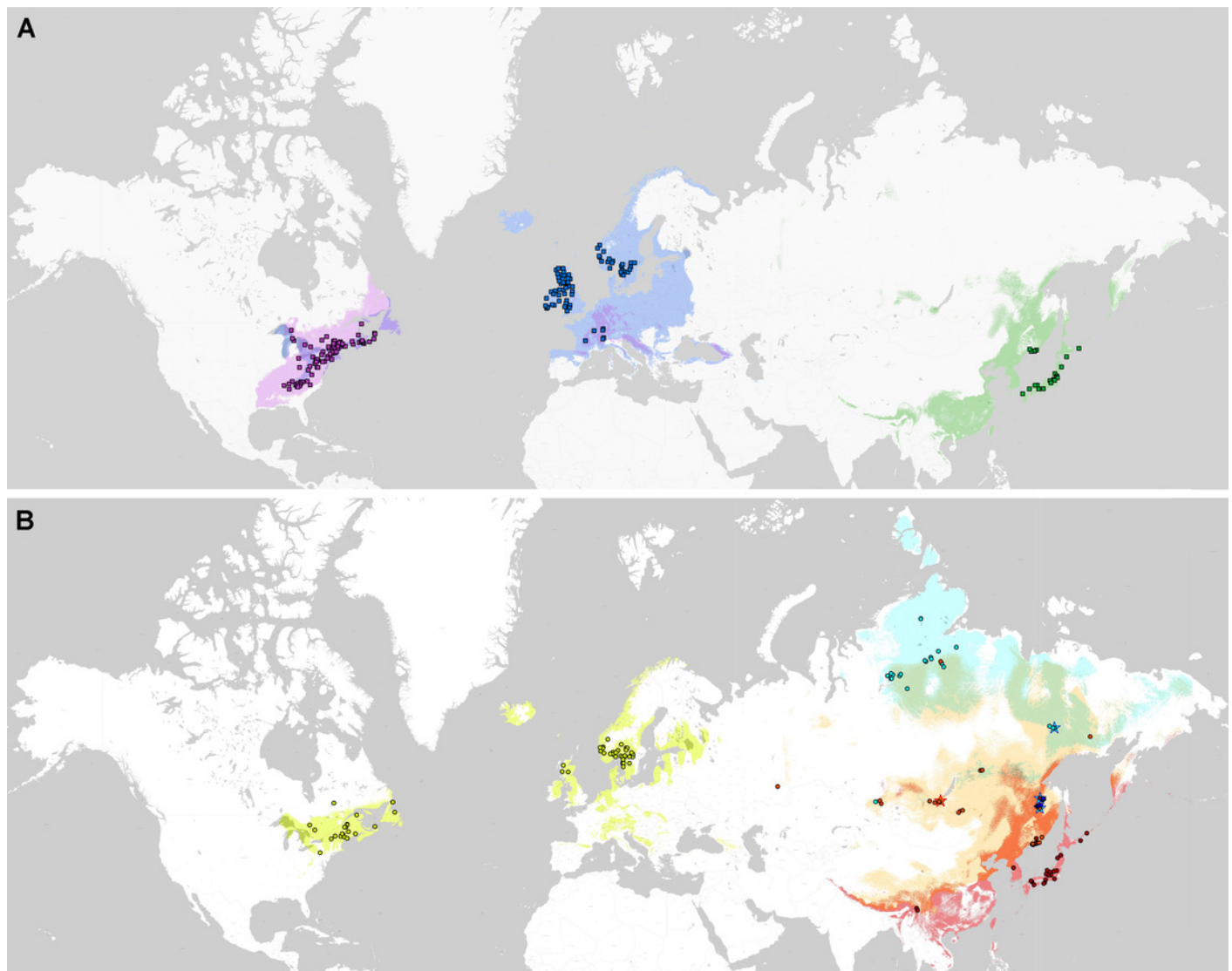
Figure 9

Distribution of the revealed lineages of subaquatic *Pseudohygrohypnum* along nine selected CHELSA bioclimatic variables based on observed occurrences

Colour legend for the lineages under consideration follows the one in Fig. 8
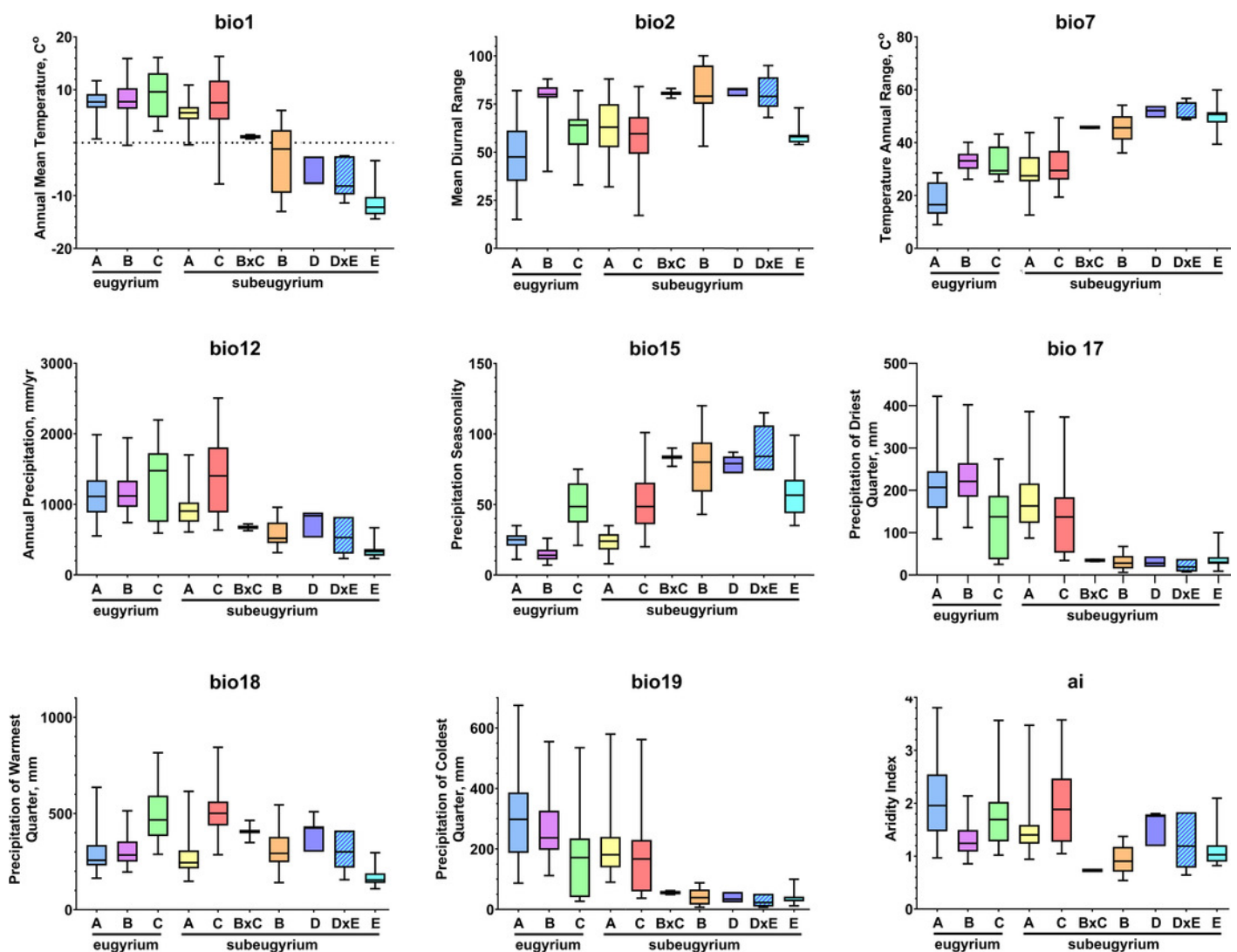
Figure 10

3-D PCA scatterplots of the observed occurrences (small symbols) and those predicted by model under 80% threshold (clouds) based on their distribution along the CHELSA bioclimatic variables used for modelling for *P. eugyrium* A-C (a) and [i]P. subeug
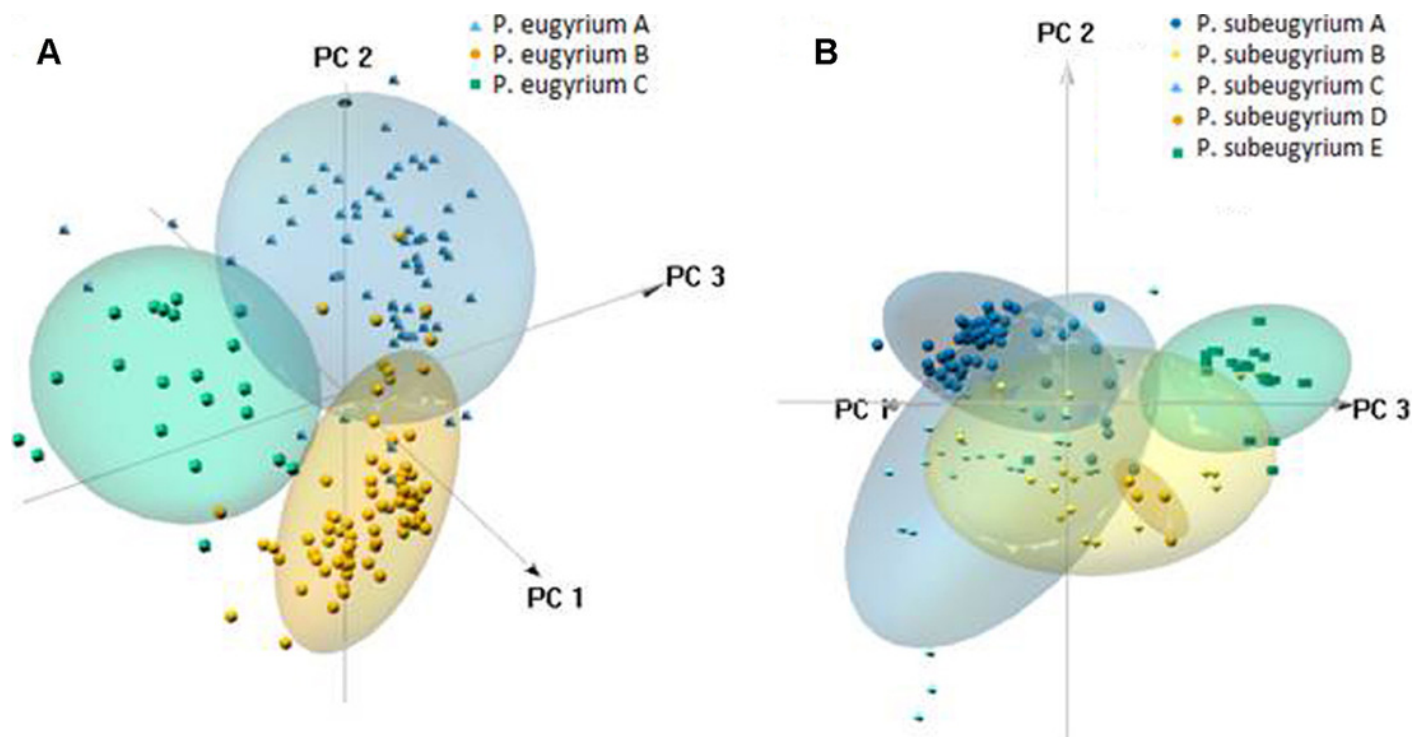
Figure 11

Pseudohygrohypnum appalachianum (from Holotype)

(A, B, J) Habit. (C) Stem transverse section. (D) Capsule. (E, G) Mid-leaf cells. (F) Upper leaf cells. (H, I, K) Leaves. (L) Basal leaf cells. Scale bars: 5 mm for B; 2 mm for A, D; 1 mm for H, I, K; 100 μm for C, E-G, L

A

B

C

D

E

F

G

H

I

J

K

L

2 mm

5 mm

100 μm

1 cm

1 mm
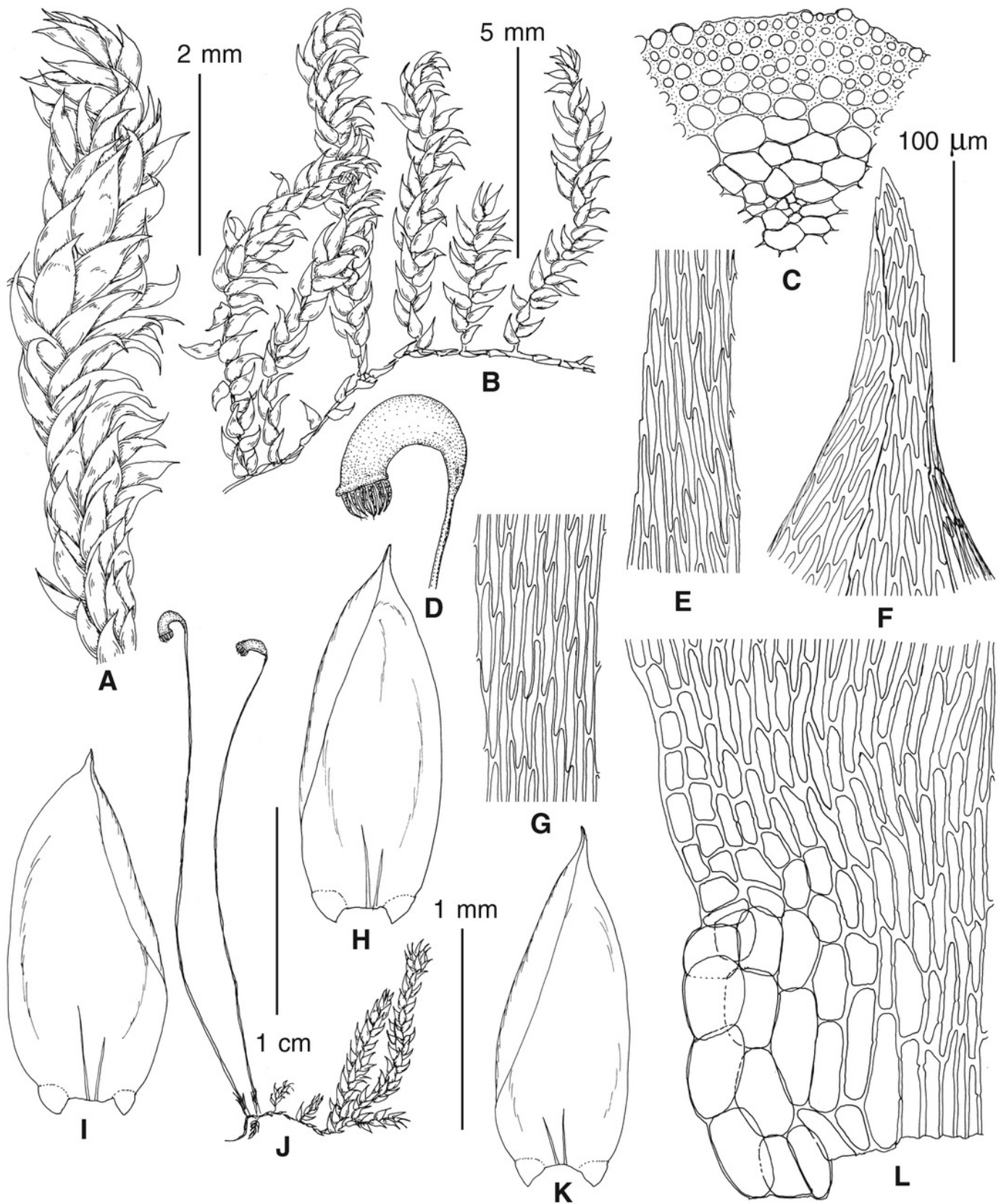
Figure 12

SEM images of peristome and spores of selected subaquatic species of the genus *Pseudohygrohupnum*

Peristome (A) *Pseudohygrohypnum appalachianum* (from Holotype). (B) *P. orientale* (from Holotype). (C) *P. sibiricum* (from Holotype). (D) *P. subarcticum* (from Holotype). (E) *P. neglectum* (from Holotype). Distal portion of tooth from the outside (F) *Pseudohygrohypnum appalachianum* (from Holotype). (G) *P. orientale* (from Holotype). (H) *P. sibiricum* (from Holotype). (I) *P. purpurascens* (from Russia, Primorsky Territory, Ignatov & Ignatova 13-1388, HyF52). (J) *P. neglectum* (from Holotype). Fragments of peristome with outer endostome surface (K) *P. orientale* (from Holotype). (L) *P. sibiricum* (from Holotype). (M) *P. subarcticum* (from Holotype). Spore (N) *P. sibiricum* (from Holotype). (O) *P. neglectum* (from Holotype).
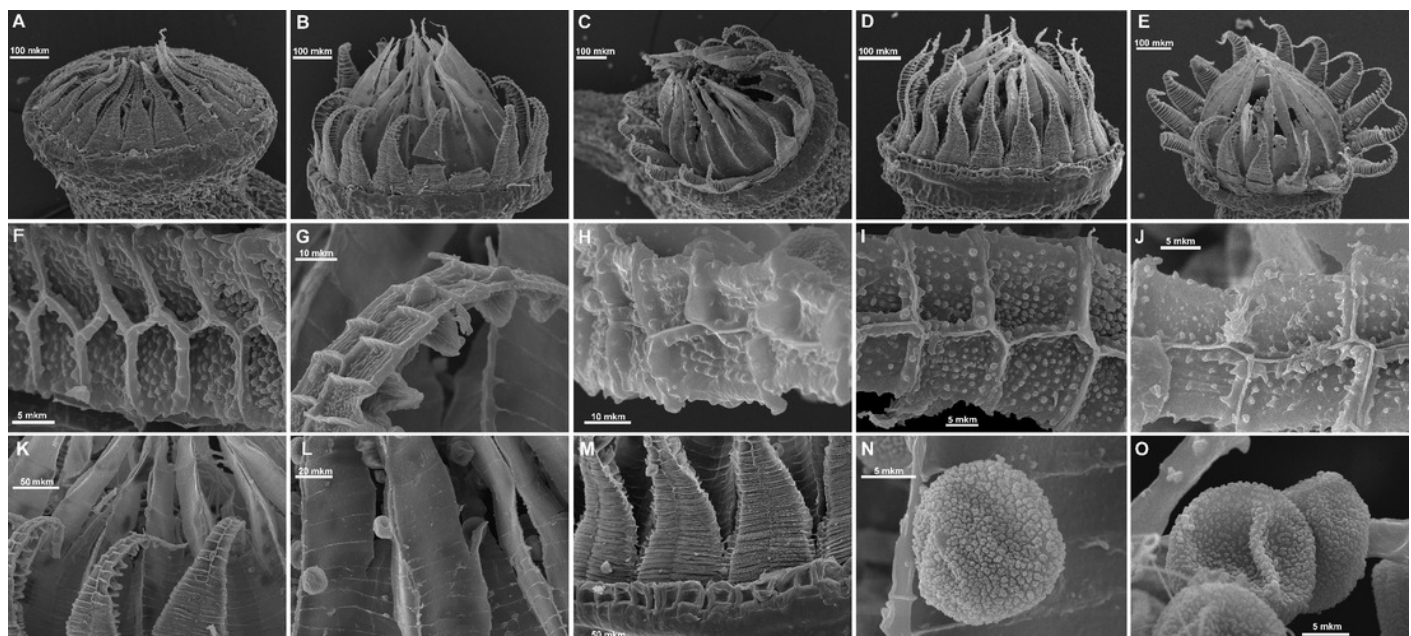
Figure 13

Pseudohygrohypnum eugyrium (from Austria, 16.10.2005. G. Schlüsslmayr, HyF15)

(A, B) Habit. (C) Stem transverse section. (D) Upper leaf cells. (E, G) Mid-leaf cells. (F–I) Leaves. (K) Basal leaf cells. Scale bars: 5 mm for B; 2 mm for A; 1 mm for F–I; 100 μm for C–E, G–K

100 μm

5 mm

2 mm

C

D

A

B

E

F

1 mm

G

H

I

J

K
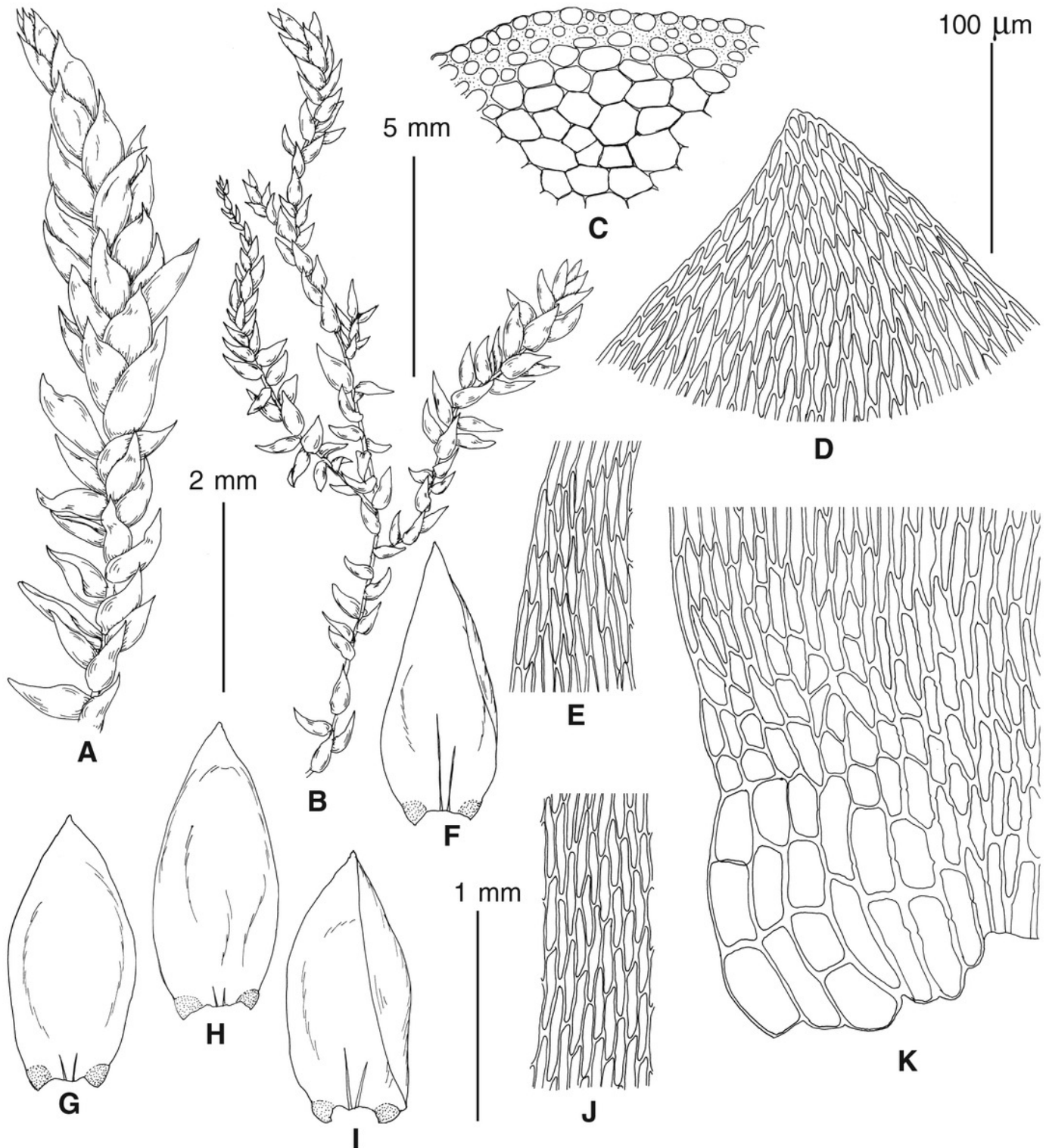
Figure 14

Pseudohygrohypnum orientale (from Holotype)

(A) Capsule. (B–D) Habit. (E–G, J) Leaves. (H) Mid-leaf cells. (I) Upper leaf cells. (K) Stem transverse section. (L) Basal leaf cells. Scale bars: 5 mm for B, C; 2 mm for A, D; 1 mm for E–G, J; 100 μm for H, I, K, L
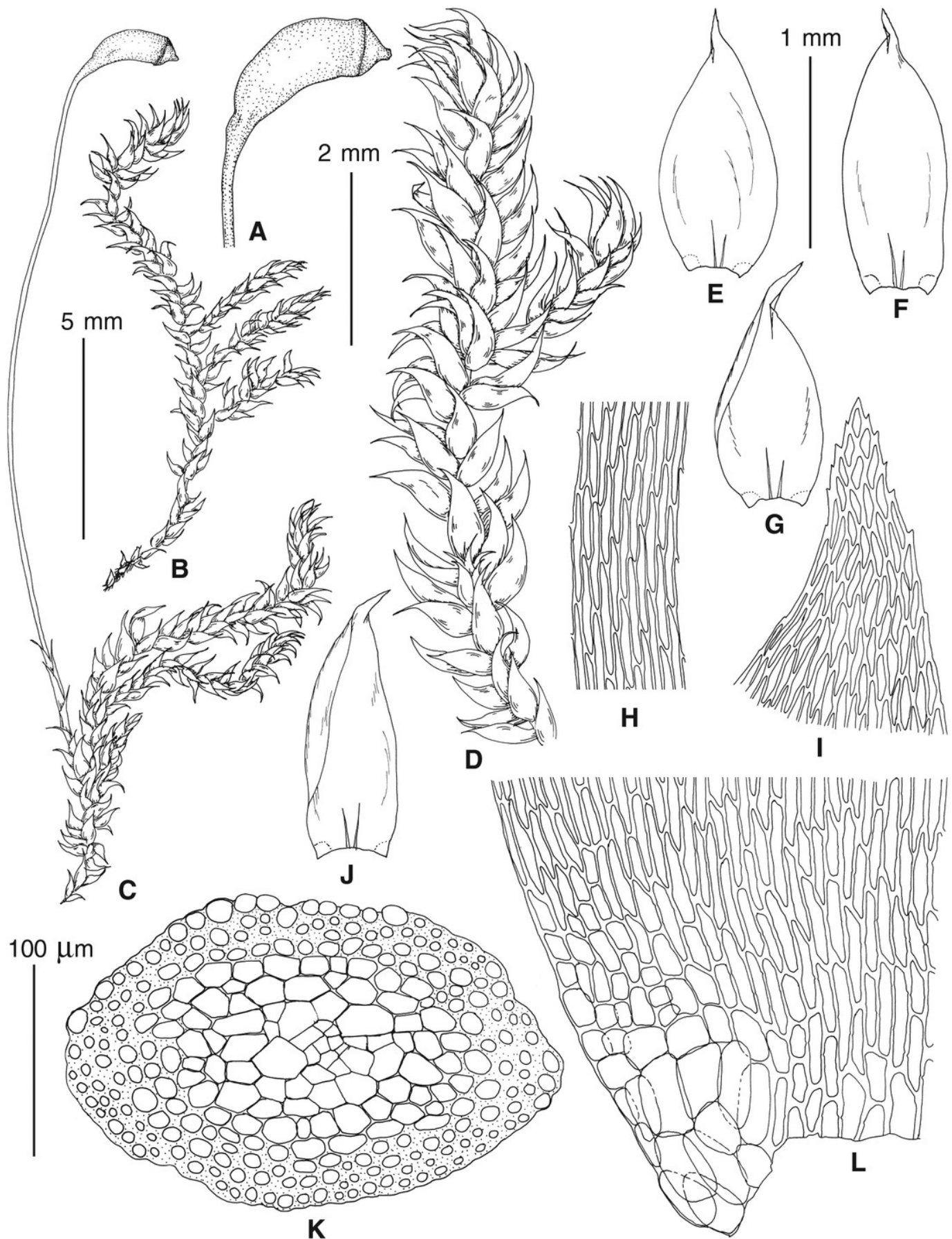
Figure 15

Pseudohygrohypnum subeugyrium (from UK, Scotland, Rothero, 2019001, dupla in MW, HyF35)

(A, B) Habit. (C) Stem transverse section. (D) Upper leaf cells. (E, I) Mid-leaf cells. (F–H) Leaves. (J) Basal leaf cells. Scale bars: 5 mm for B; 2 mm for A; 1 mm for F–H; 100 μm for C–E, I, J
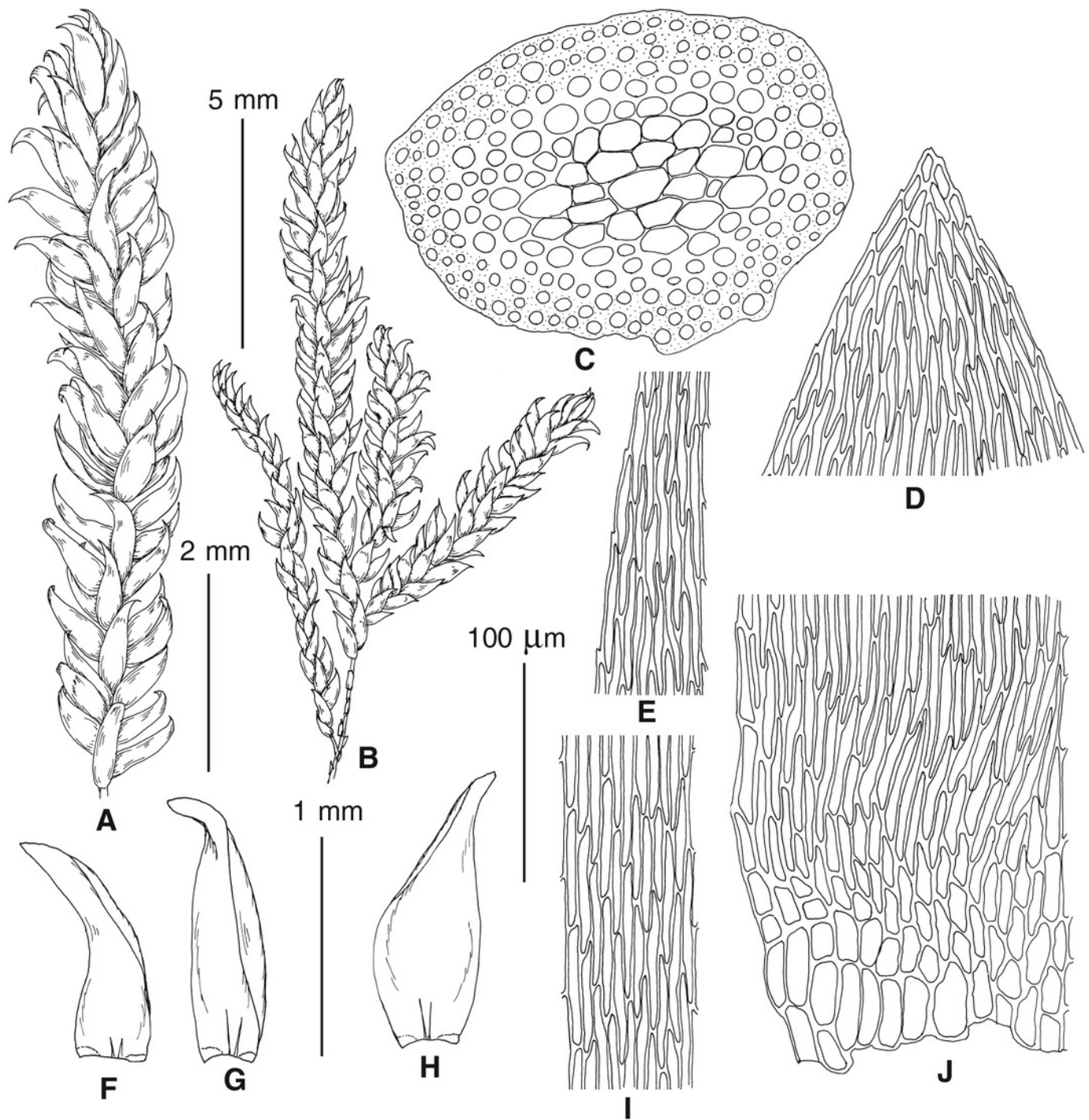
Figure 16

Pseudohygrohypnum purpurascens (from Primorsky Territory, Pidan Peak, Ignatov & Ignatova 06-2197 MW, HyF61)

(A, B, J) Habit. (C) Stem transverse section. (D) Upper leaf cells. (E–H) Leaves. (I) Mid-leaf cells. (K) Basal leaf cells. Scale bars: 5 mm for A, J; 2 mm for B; 1 mm for E–H; 100 μm for C, D, I, K

2 mm

C

D

1 mm

F

G

I

B

A

E

H

J

5 mm

100 μm

K
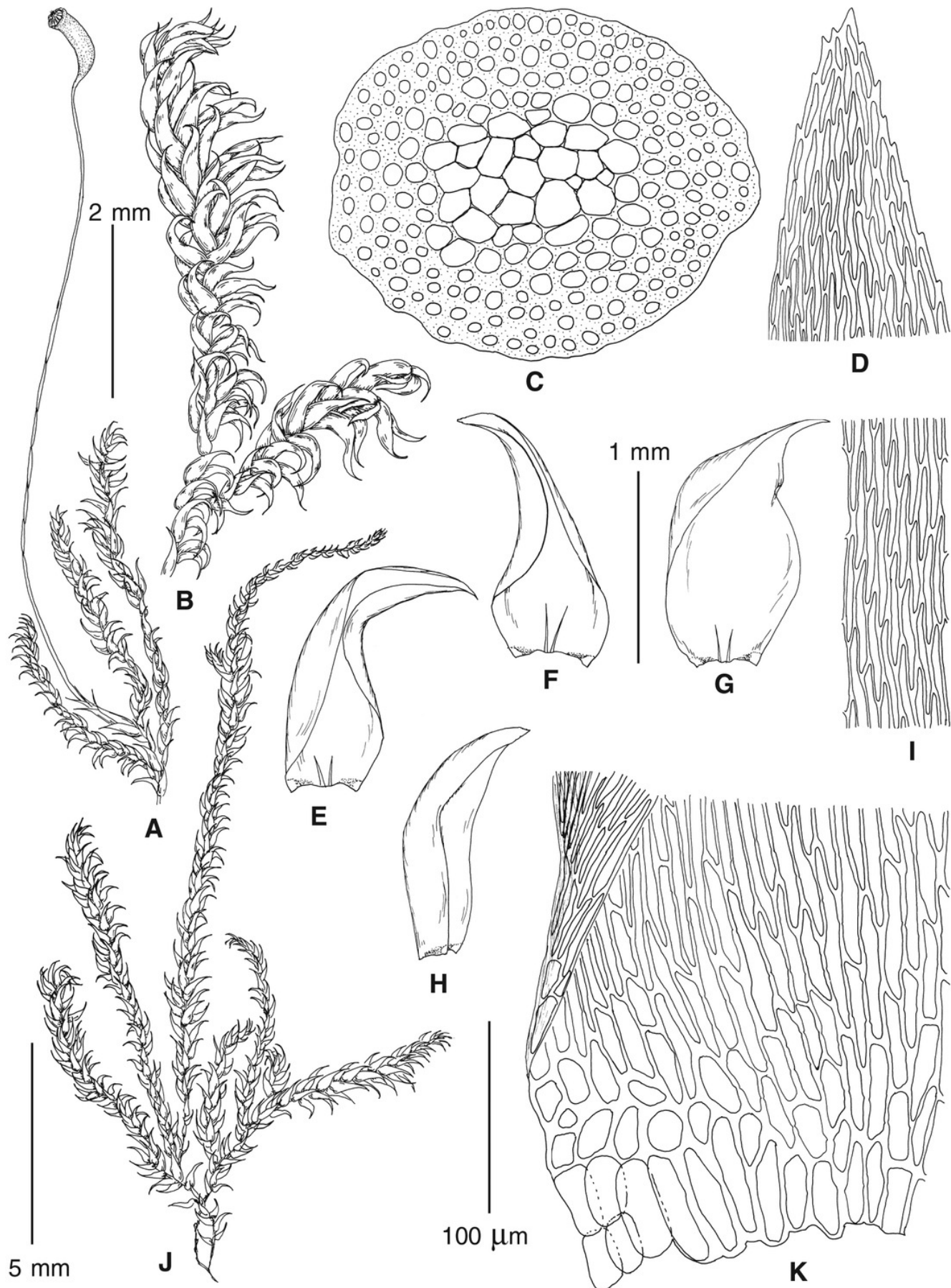
Figure 17

Pseudohygrohypnum sibiricum (from Isotype MW9077400)

(A) Stem transverse section. (B) Upper leaf cells. (C, H) Mid-leaf cells. (D, F, G, I) Leaves. (E) Habit. (J, K) Basal leaf cells. Scale bars: 2 mm for E; 1 mm for D, F, G, I; 100 μm for A–C, H, J, K
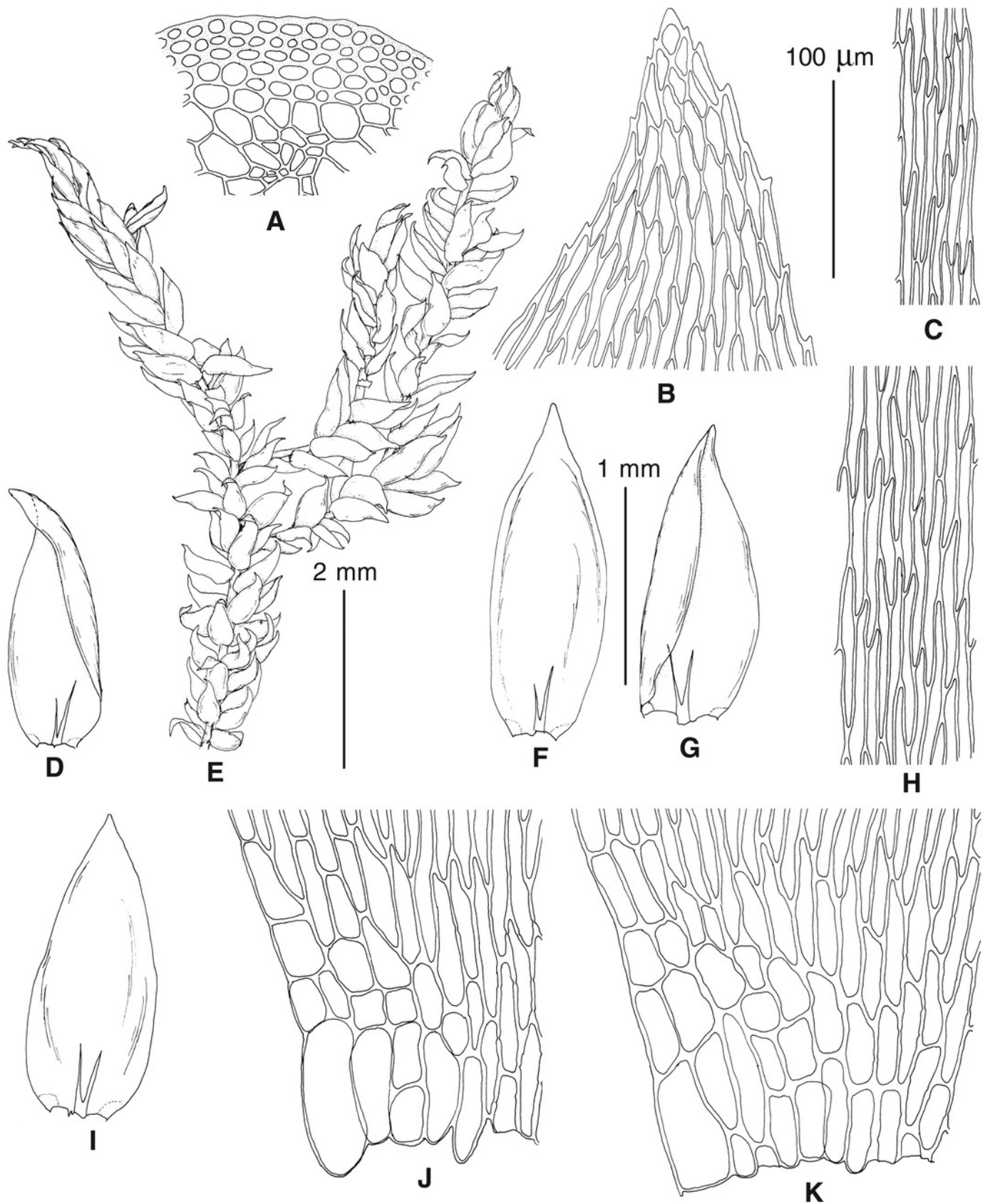
Figure 18

Pseudohygrohypnum subarcticum (from Holotype)

(A, C, M) Habit. (B) Capsule. (D) Stem transverse section. (E, I–L) Leaves. (F) Mid-leaf cells. (H) Upper leaf cells. (N) Basal leaf cells. Scale bars: 5 mm for A, M; 2 mm for B, C; 1 mm for E, I–L; 100 μm for D, F–H, N

A

B

C

D

E

F

G

H

I

J

K

L

M

N

100 μm

2 mm

1 mm

5 mm
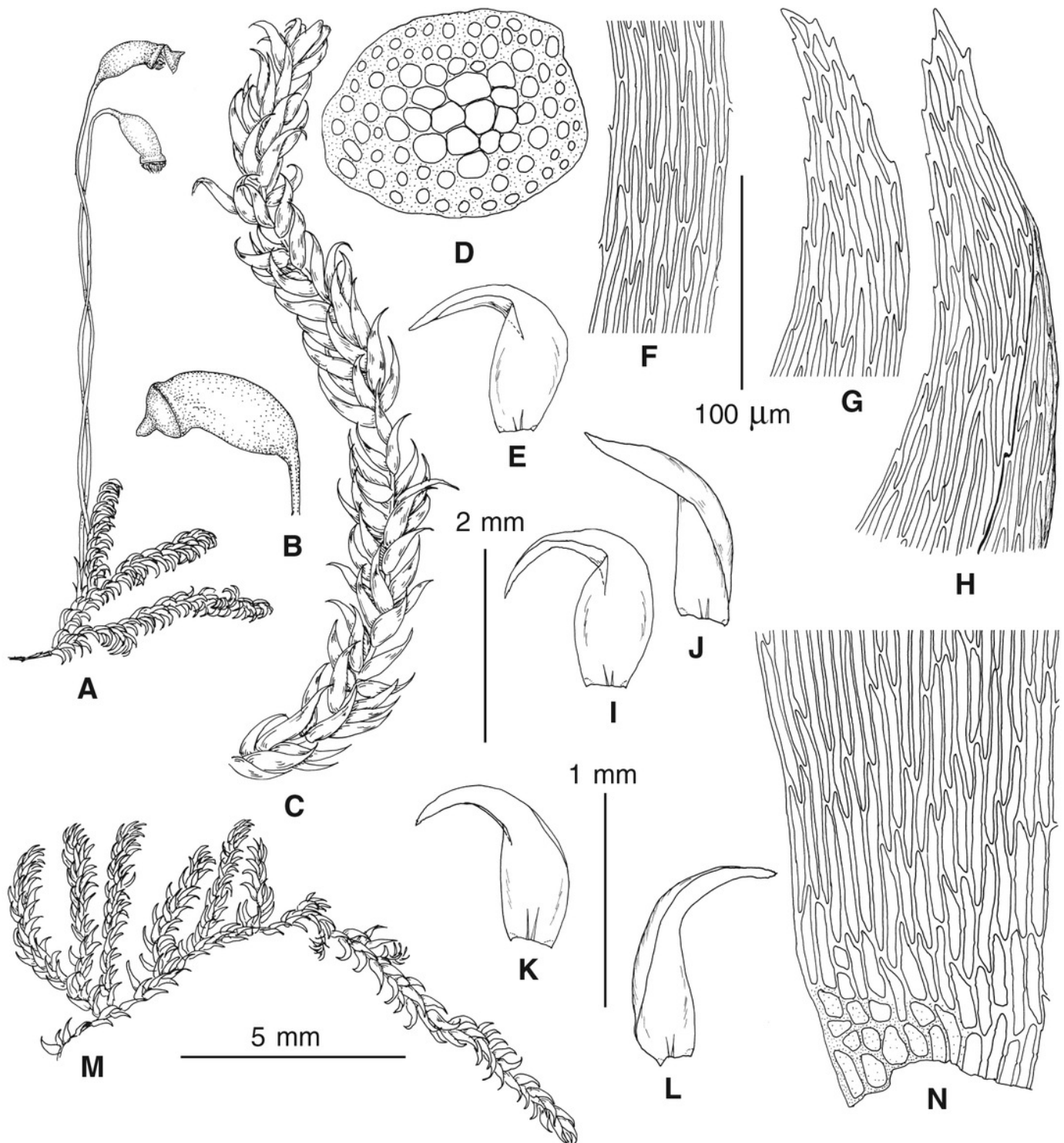
Figure 19

Pseudohygrohypnum neglectum (from Holotype)

(A) Stem transverse section. (B) Upper leaf cells. (C, D) Habit. (E, G–I) Leaves. (F) Mid-leaf cells. (J) Basal leaf cells. Scale bars: 5 mm for D; 2 mm for C; 1 mm for E, G–I; 100 μm for A, B, F, J

J
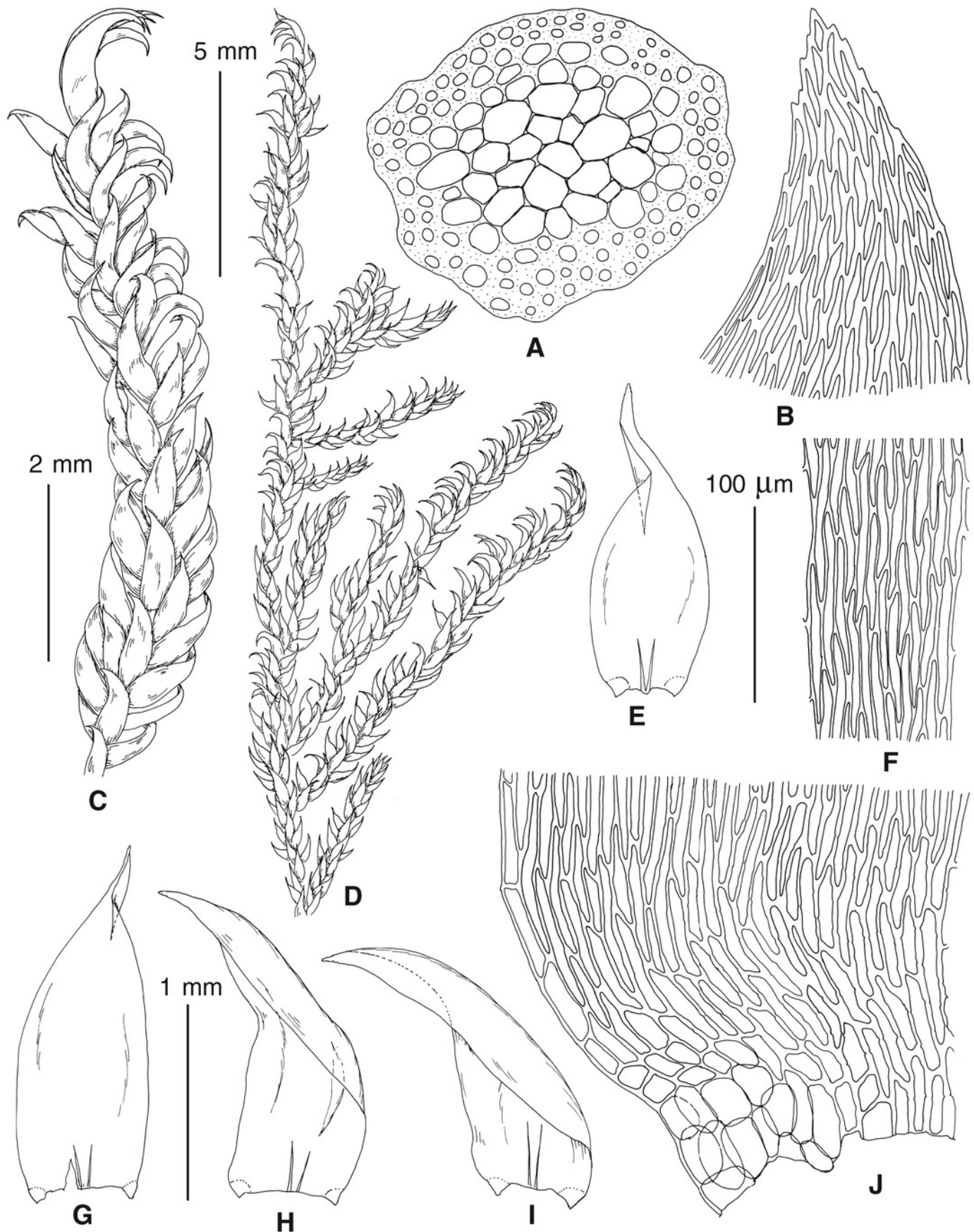
Figure 20

Pseudohygrohypnum subarcticum X *P. neglectum* (from HyF5 Yakutia, Kyurbelyakh, Ignatov & Ignatova 11-2242 MW, HyF5)

(A, B) Habit. (C) Upper leaf cells. (D) Mid-leaf cells. (E) Stem transverse section. (F–H) Leaves.

(I) Basal leaf cells. Scale bars: 5 mm for B; 2 mm for A; 1 mm for F–H; 100 μm for C–E, I