A review of the genus Glyphomitrium Brid. (Rhabdoweisiaceae, Bryophyta) in the Russian Far East

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Introduction

The genus Glyphomitrium Brid. includes about 10 species that occur mostly in South, Southeast and East Asia, together with a single rare hyperoceanic species found in Europe. The reported ‘North American’ species, G. canadense Mitt, does not differ from G. daviesii (Dicks.) Brid., according to Crum (1972), and moreover was probably described from a British collection. Reese (2008) thus excluded the genus Glyphomitrium from the North American flora. Noguchi (1988) and Iwatsuki (2004) accepted three species in Japan. Suzuki (2015) revised the genus for Japan and added two more species. Wang (2011) reported nine Glyphomitrium species for China.

In Russia, the genus Glyphomitrium occurs in the southern part of the Far East, where it is rather widespread in hemiboreal forests. The first record of Glyphomitrium in Russia was published by Lazarenko (1933), who referred his specimen to G. humillimum (Mitt.) Card., a species described from Japan. Later, Abramova and Abramov (1955) revised several Russian specimens and assigned them to the Chinese G. warburgii (Broth.) Card., because the long-acuminate inner perichaetial leaves in Russian collections do not fit the protologue of G. humillimum (as Aulacomitrium humillimum, Mitten 1891). Subsequent publications used one or other of these two names (e.g. G. warburgii in Bardunov and Cherdantseva 1982, and G. humillimum in Ignatov et al. 2006 and Cherdantseva et al. 2018).

In the course of our study of the genus for the Moss Flora of Russia, however, we found it difficult to assign names based on recently published keys because the combinations of characters in Russian specimens did not precisely fit species descriptions in these taxonomic treatments. Some specimens have bistrose patches in the distal portions of their leaves and costae ending below the leaf apex, thus resembling the Japanese Glyphomitrium crispifolium Nog. as described by Noguchi (1968, 1988) but not in every character. Other specimens, that is, those having unistratose laminae (rarely partly bistrose along the margin only) and excurrent costae, appeared to not fully correspond with any described species, excepting a few specimens with acute to obtuse perichaetal leaves that could be referred to G. humillimum.

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Therefore, a molecular phylogenetic study was carried out to determine whether these morphotypes differ genetically and to clarify their distributions. Hereafter, for ease of discussion, we apply the names Glyphomitrium crispifolium, Glyphomitrium sp. and Glyphomitrium cf. humillimum to these groups, respectively. To achieve a more comprehensive and integrative taxonomic assessment, we supplemented standard morphological and molecular phylogenetic approaches with species distribution modelling and ecological niche similarity/divergence estimates. The latter approach allows an explicit assessment of niche differences and potential ranges among species, thus addressing geographical and ecological criteria within an integrative taxonomic framework. Additionally, due to nomenclatural issues, we aimed to check the environmental suitability of areas where several species of Glyphomitrium have been described from.

**Materials and methods**

**DNA sequencing**

To provide comparative data for the molecular phylogenetic study, the morphology of the herbarium specimens from MW and MHA was re-examined. For the molecular phylogenetic study itself, we used the plastid trnS–trnF region following the protocol described by Hernández-Maqueda et al. (2008). It includes a portion of the trnA-Ser gene, the trnS–rps4 spacer, the rps4 gene, the rps4–trnT spacer, the tRNA-Thr gene, the trnT–tRNA-Leu gene, the trnL–trnF spacer, and part of the tRNA-Phe gene. The sequences of the trnS–trnF region and the rps4 and trnL–trnF sequences used by Fedosov et al. (2021) were then included, and the missing portion of the trnS–trnF region considered as missing data for these accessions. To provide additional phylogenetic data, we used the highly variable nuclear ITS region, obtained according to the protocol described in detail by Gardiner et al. (2005).

Seventeen Glyphomitrium accessions were included in the analysis. Five accessions from the dataset of Fedosov et al. (2021) (one of G. daviesii, one of G. humillimum, and three of G. crispifolium) were supplemented by 12 additional specimens (five of G. crispifolium, three Glyphomitrium sp. and four of Glyphomitrium cf. humillimum). Thus, the ingroup, representing the Asian clade of Glyphomitrium, contained 13 accessions from the Russian Far East and three Japanese accessions of G. humillimum. PCR products were sequenced using the ABI PRISM BigDye Terminator v. 3.1 (ThermoFisher Scientific, Waltham, MA, USA) and further analysed on an Applied Biosystems 3730 DNA Analyzer automated sequencer (ThermoFisher Scientific).

Accessions of Rhabdoweisia Bruch & Schimp., Cnestrum Hagen, Oncophorus (Brid.) Brid., Oreas Brid., Pseudodinia Fedosov, M.Stech & Ignatov and Symblepharis Mont. from the analysis of Fedosov et al. (2021) were used as outgroups for the trnS–trnF dataset, and three accessions of Oncophorus and Symblepharis were used as outgroups for the ITS dataset. Trees were rooted on Rhabdoweisia (trnS–trnF dataset) and Symblepharis accessions (ITS dataset), according to the topology of Fedosov et al. (2021). Specimen vouchers and GenBank accession numbers are provided in Appendix Table A1.

**Molecular phylogenetic analyses**

Sequences were aligned using MAFFT v. 7.487 (Katoh and Standley, 2013) and then edited manually in Bioedit (Hall 1999). The two datasets used for phylogenetic inferences corresponded to the trnS–trnF region (26 terminals, 1943 positions) and the nrITS region (17 terminals, 896 positions). Alignment quality was tested using T-Coffee v. 11.00 on a web server (Di Tommaso et al. 2011). Indel data in all analyses were scored using the simple indel-coding approach (Simmons and Ochoterena 2000) in SeqState 1.4.1 (Müller 2005) after checking indels within the ingroup for reliability using Relindel v. 1.0 (Ashkenazy et al. 2014).

Phylogenetic analysis was carried out using Bayesian inference by running two parallel analyses in MrBayes 3.2.7a (Ronquist et al. 2012), with each run consisting of six Markov chains and 5,000,000 generations, because the convergence between runs (assessed as a standard deviation of split frequencies lower than 0.01) was reached after 0.5–1 million generations in the analyses of both datasets. Trees were sampled every 1000 generations, with the chain temperature set at 0.03 in all analyses and with sampling across the GTR model space (model setting ‘Nst = mixed’).

Consensus trees were calculated after omitting the first 25% of the trees as burn-in. Convergence of analyses was assessed based on average PSRF values approaching 1.000 in both analyses with effective sample sizes greater than 200, as determined by Tracer v. 1.7.2. (Rambaut et al. 2018).

**Morphological observations**

In addition to standard microscopic observations, peristomes of members of the revealed clades were studied by scanning electron microscopy (SEM) using a Jeol 6380 scanning electron microscope (Jeol, Tokyo, Japan), with specimens sputter-coated with gold without any additional preparation. Light microscope observations were made under a Zeiss Axioplan imaging microscope (Zeiss, Jena, Germany), and the
images prepared using a Hirox RH-2000 3D digital microscope (Tokyo, Japan).

Species distribution modelling

After the molecular and morphological studies confirmed the hypothesis that distinct taxa are present in Russia, species distributions were assessed in terms of environmental variables and then compared. Species distribution modelling is a method of estimating the relationships between species records at sites and the environmental characteristics (environmental variables) of those sites to infer spatially explicit habitat suitability (Elith et al. 2011; El-Gabbas and Dormann 2017).

Because our species occur in an area that is incompletely surveyed for bryophytes (the Russian Far East), no true absences may be assumed, and the presence-only modelling approach is most suitable. The maximum entropy method, which allows the use of presence-only data and is implemented using the MaxEnt v. 3.4.4 software package (Phillips et al. 2006; Phillips and Dudik 2008), is one of the best-performing and most popular methods for species distribution and niche modelling. This is due to its predictive accuracy and simplicity of use (Elith et al. 2011; Merow et al. 2013; El-Gabbas and Dormann 2018), and its advantages over other modelling algorithms used for presence-only data, especially at smaller sample sizes (Pearson et al. 2006; Wisz et al. 2008; El-Gabbas and Dormann 2017). However, because we had a relatively small number of presence points, we also used Ensembles of Small Models (ESM), which was designed for modelling small datasets (Lombeta et al. 2010; Breiner et al. 2015, 2018). ESM produces a set of simple bivariate models in all possible combinations, which are then filtered and averaged into one ‘ensemble’.

Examples of the revised specimens in MW and MHA (21 occurrences for Glyphomitrium crispifolium and 15 for Glyphomitrium sp.) were used as input for distribution modelling. Distribution modelling for Glyphomitrium cf. humillimum was not carried out due to an insufficient number of available records (fewer than 10). Because the size of the considered area is critical for modelling, especially for presence-only methods (Pearce and Boyce 2006), the study area was outlined using a rectangular bounding box with a 1000 km buffer based on all presence points of the two taxa in QGIS 3.16.1 (QGIS Development Team 2021). The resulting model area was restricted within the coordinates 107.27–155.51 longitude and 24.90–59.08 latitude of the EPSG:4326–WGS 84 coordinate system. Ten environmental layers with a spatial resolution of 30 arc-seconds (~1 km per pixel at the equator) were chosen as variables, including five bioclimatic layers (CHELSA 2.1, Karger et al. 2017; 2021) with a correlation coefficient less than 0.7 and variance inflation factor less than 10, calculated in GRASS 7.8.4 and 5 land-cover layers (EarthEnv, Tuanmu and Jetz 2014, see Section I in Supplemental Material).

Because herbarium data are typically spatially biased, especially in the case of under-explored territories, various approaches were used for bias correction. We tested models with two different bias-correction layers based on a biased prior approach with non-equal weighting of background points (Dudik et al. 2005; Phillips et al. 2009; Merow et al. 2013; El-Gabbas and Dormann 2018), created in accordance with researcher activity and without bias correction (see Section II in Supplemental Material for details). Because MaxEnt modelling settings such as feature classes and the β-regularisation multiplier strongly affect resulting models (Merow et al. 2013; Shcheglovitova and Anderson 2013; Radosavljević and Anderson 2014), we tested different combinations of parameters through three rounds of modelling and estimation for two bias-correction layers and without bias correction. This allowed us to choose the best combination of model parameters and bias-correction manipulation (see Supplemental Material for details).

To test different combinations of parameters, SDMtoolbox 2.4 (Brown et al. 2017) for ArcGis (ESRI 2011) was used in the first round of modelling. The spatial 3-fold cross-validation approach was applied, which allows both avoidance of overfitting of the resulting models (Shcheglovitova and Anderson 2013; Radosavljević and Anderson 2014) and assessment of their predictive accuracy. The output consisted of 30 combinations of parameters ranked by the highest values of area under the curve (AUC) and lowest omission error for each of three bias-correction approaches for each species. The first 10 combinations (Supplemental Tables 2 and 3 in Supplemental Material) were used for the second round of modelling. In the second round, we applied MaxEnt v. 3.4.4 to create 30 replications with each of 10 model settings. During modelling, we used 10,000 background points selected randomly, which differed between the replicates.

To calibrate the models, we used 3-fold spatial-block cross-validation, with checkerboard blocks of 1 × 1 degree size (Fithian et al. 2015; El-Gabbas and Dormann 2018). The resulting AUC and true skill statistics (TSS) for the test data were computed manually from the MaxEnt outputs and averaged for 30 replicates. The Boyce index was calculated for the resulting raster layers averaged for 30 replicates using the ecospat package (Di Cola et al. 2016) for R (R Core Team 2020). According to the highest sum of all three metrics, we chose three model settings (four for Glyphomitrium crispifolium b2) for each of the three bias-correction approaches (Supplemental Tables 4 and 5 in Supplemental Material) for use in the third round of modelling. The final round of
modelling was carried out with 100 replications for each of 9 or 10 model configurations per species. During modelling, 10,000 background points that differed between the replicates were randomly selected.

Bootstrap testing was carried out, in which 80% of the presence points were used for training and 20% for testing. We used the ‘pooling approach’ for estimating model quality, as recommended by Collart et al. (2021). The resulting suitability values of the ‘test’ presence points were averaged across the replicates; this set of values was then combined with the background data, sampled from the resulting models averaged for 100 replicates and used for evaluating each modelling combination through the AUC, TSS and Boyce index, using the ROCr (Sing et al. 2005), biomod2 (Thuiller et al. 2019) and ecospat packages for R respectively (Supplemental Tables 6 and 7 in Supplemental Material). Thus, a single model per species with the best sum of evaluates was chosen to produce the final species distribution models (SDMs) trained on all the occurrence data.

For the ESM modelling technique, we used an ecospat package for R to generate ESM separately based on two modelling techniques under the default settings: Gradient Boosting Machine (GBM, Friedman 2001) and MaxEnt. Following the methods of Collart et al. (2021), the ESM modelling for each of the two Glyphomitrium species was carried out for 10 replicates, using 80% of the occurrence data for training and 20% for evaluation. The same sets of pseudo-absence points for GBM-based ESM and background points for MaxEnt-based ESM were randomly selected using the biomod2 package for R, the sets differing between the species. All the resulting bivariates were weighted by Somers’ D metric (rescaled AUC, which is equal to AUC^2-1), and only bivariates with Somers’ D > 0 were used to generate the ensemble model. The generated models were evaluated through AUC, maxTSS and Boyce index, using the ‘pooling approach’ mentioned above.

Among the models obtained for Glyphomitrium crispifolium, the evaluations of the standard MaxEnt model were better than the ESM ones (Supplemental Table 8 in Supplemental Material). Thus, we chose the SDMs obtained through standard MaxEnt modelling, with bias correction by non-equal weighting of background points in accordance with researcher activity models, as the final ones (Supplemental Table 9 in Supplemental Material).

Finally, to check that the chosen models’ predictions reliably differed from random ones, we compared them with null models generated from the sets of background points, which were used as occurrence data (van Proosdij et al. 2016; Collart et al. 2021). The sets of 100 null models were obtained using the same number of occurrence points and model settings/bias-correction approach as used in the final models of respective species. The null models were evaluated through AUC, maxTSS and Boyce index, and compared with the evaluations of respective SDMs. If 95% of the evaluations of the null models were lower than the evaluations of respective SDMs, the latter were considered reliable. The evaluations of the final models and the corresponding null models are shown in Supplemental Figure 1 in Supplemental Material and suggest that the final models obtained were of reliable quality.

To visualise the final SDM maps, we restricted the pixels by maxTSS threshold, using QGIS 3.16.1. To compare the environmental niches of Glyphomitrium crispifolium and Glyphomitrium sp., we carried out a niche equivalency test based on Schoener’s D and the I statistics (Warren et al. 2008), using ‘ranges overlap’ and ‘identity test’ provided by ENMTools v. 1.4.4 (Warren et al. 2010). The niche equivalency test assesses whether the habitat suitability scores generated by ENM models for two species exhibit statistically significant ecological differences by pooling empirical occurrence points and randomising their identities to produce two new samples with the same numbers of observations as the empirical data. During the tests, 100 iterations of SDM pseudoreplicates generated from random points were created and compared automatically using ‘ranges overlap’. We then compared these results with the range overlap statistics of our final models for the two species.

To visualise the distribution of the three species along the variables used for modelling, box plots for each of 10 environmental variables were built in GraphPad Prism 8.4.3 (GraphPad software, San Diego, CA, USA). Distributions of two lineages, Glyphomitrium crispifolium and Glyphomitrium sp., along these variables were checked for significance of the median difference using the Mann–Whitney U test in Past v. 4 (Hammer et al. 2001). The values of 10 environmental variables in the observed localities assigned to each species were then used as input for PCA analysis carried out in a pca3d package for R (R Core Team 2021).

Results

Molecular phylogenetic study

Although no supported conflict of topologies was observed and the results for both datasets appeared to delimit the same lineages, the topologies of the deeper nodes within the ingroup were different (Figure 1). Both analyses showed the genus Glyphomitrium to be monophyletic (posterior probability = 1). In the plastid trnS–trnF dataset, which included more accessions, G. daviesii occurred in a sister position to
the unsupported clade representing East Asian specimens of the genus. The latter comprised three clades ranging from unsupported to maximally supported. These clades correspond well to the main morphotypes defined by the characters outlined in the Introduction and include specimens from various regions of the Russian Far East.

Two Japanese accessions were found in the clade labelled as Glyphomitrium cf. humillimum in Figure 1. This clade is well supported in the topology inferred from the trnS–trnF dataset, and it also comprises two saxicolous specimens from the continental part of the Russian Far East (GF12, GF13), which form a separate nested grouping. The well supported clade, corresponding to Glyphomitrium sp. (G. ambiguum in Figure 1), includes three accessions from the Russian Far East, namely GF9, GF14 and GF15; it is represented by specimens that combine excragen costae on the stem leaves with perichaetial leaves that are contracted to a short, narrow acumen. The combined clade of Glyphomitrium cf. humillimum and Glyphomitrium sp. is sister to the G. crispifolium clade. The clade that combines all Asian Glyphomitrium specimens received no support.

In the tree inferred from the nuclear ITS region, the composition of the three main lineages of East Asian Glyphomitrium is the same, but the Glyphomitrium cf. humillimum and Glyphomitrium sp. lineages do not form a clade; instead, the Glyphomitrium cf. humillimum lineage was found in an unsupported clade with G. crispifolium.

Further morphological studies and revision of specimens kept in MHA and MW allowed assessment of the morphological variability of the revealed molecular lineages, including peristome structure (see the Taxonomy section), clarified their distributions (Figure 2), and provided input for species distribution modelling carried out for two of the three lineages.

**Distribution modelling**

The final models show high AUC values and reliable values for the Boyce index (0.968 and 0.884, respectively, for Glyphomitrium sp.; 0.968 and 0.867, respectively, for G. crispifolium). For G. humillimum, SDMs were not produced because fewer than 10 sample points were available, and they probably represent a heterogeneous taxon (at least in terms of distribution) awaiting further revision. To visualise the species distributions, the maximum sensitivity and specificity threshold was applied (Figure 3). The resulting plots of both models are available in Section V in Supplemental Material.

The resulting SDM of Glyphomitrium crispifolium shows a rather small predicted area, mostly situated in the coastal and mountainous parts of...
the southeast of Khabarovsk Territory and Sikhote-Alin within the Primorsky Territory, nearly throughout Sakhalin, the South Kuril Islands, and Hokkaido, with few locally suitable areas to the south in the mountains of Honshu and North China. By contrast, the area predicted as suitable for *Glyphomitrium* sp. is mostly restricted to lowland continental areas and spans further southwestwards, whereas at its northern extent it is largely restricted to the Amur River valley and lowland areas surrounding it.
Mean annual air temperature (bio1) is one of the leading predictors in the distribution models of both *Glyphomitrium crispifolium* and *Glyphomitrium* sp.; however, the combinations of other important predictors differ (see Supplemental Table 9 in Supplemental Material). The SDM obtained for *G. crispifolium* largely depends on isothermality (bio3 – ratio of diurnal variation to annual variation of temperatures) and aridity index (ai), whereas the SDM of *Glyphomitrium* sp. is affected by the coverage of mixed trees (lc_class4), as well as cultivated and managed vegetation variable (lc_class7, Figure 4, see Supplemental Table 9 in Supplemental Material). Lower aridity and annual temperature favour *G. crispifolium*; by contrast, the areas with higher temperature and more seasonal precipitation are probably more suitable for

**Figure 4.** Distribution of observed occurrences along various bioclimatic variables. A = * Glyphomitrium humillimum* s.l., B = *G. crispifolium*, C = *G. ambiguum* (= *Glyphomitrium* sp.).
Glyphomitrium sp. This inference was confirmed by the results of the Mann–Whitney U test, which revealed a significant median difference of two distributions (probability above 99%) for two of five tested predictors, aridity index and precipitation seasonality (Supplemental Table 10 in Supplemental Material).

Annual precipitation is lower and precipitation seasonality higher in the areas where Glyphomitrium sp. grows than in those where G. crispifolium occurs (see Figure 4). Glyphomitrium crispifolium typically occurs in cooler environments than those of Glyphomitrium humillimum and Glyphomitrium sp. Overall, Glyphomitrium humillimum s.l. largely inhabits rather warm and humid environments, although this is true only for insular ‘G. humillimum s.s.;’ the continental localities of Glyphomitrium cf. humillimum not conforming to this pattern. Despite the weak contribution of variables reflecting the coverage of coniferous forests to the obtained SDMs, the species distributions along this gradient differ. Glyphomitrium sp. shows the lowest association with areas dominated by conifers, this being well reflected in the curve of its response to this variable (Supplemental Figure 3 in Supplemental Material), whereas G. crispifolium is associated with areas where coniferous or mixed forests occur in sufficient quantities. The wide distribution of G. humillimum s.l. along the gradients of annual temperature and precipitation probably reflects the ecological heterogeneity of this clade.

According to the results of the equivalency test, obtained using ENMTools, the niches of the two species with niche overlap values of \( D = 0.678 \) and \( I = 0.902 \) have no statistically significant differences compared with the niche overlaps of the random background points \( (P > 0.05) \), and the hypothesis of the niche equivalency cannot be rejected. At the same time, the scatter plots of occurrences based on the observed values of environmental variables (Figure 5) show remarkable differences in the distinct environmental factors associated with Glyphomitrium crispifolium and Glyphomitrium sp. presence points, and the spatial overlap of the predicted distribution ranges is rather low (0.257).

**Discussion**

The topology of the Glyphomitrium clade obtained from the plastid data in the present study is similar to that described by Fedosov et al. (2021). Notably, in the tree based on trnS–trnF data, from the present study, the accessions of Glyphomitrium form a well-supported clade that is sister to the well-supported clade formed by the remaining accessions of the R2 Rhabdoweisiaceae clade (cf Fedosov et al. 2021) included in the analysis, whereas in the results presented by Fedosov et al. (2021), the topology of the R2 clade remained unresolved. Because of the reliable support for the three revealed East Asian Glyphomitrium lineages and their morphological distinctness, together with the incongruence of the trees based on the plastid and nuclear data regarding their relationships to each other, we consider these lineages to represent three separate species.

At the same time, the results of our niche comparison analyses rather confirm niche similarity/conservation despite the low degree of overlap of the predicted ranges of the two Glyphomitrium species compared. This finding agrees with the results obtained by Collart et al. (2021) for eight complexes of cryptic species/ infraspecific lineages in Sweden, although in that study another modelling technique was used. However, according to the voucher data of the studied specimens, the distribution of Glyphomitrium crispifolium and Glyphomitrium sp. in the southern part of the Primorsky Territory differs in the altitudinal ranges they occupy. This is also likely to be due to the existence of several cryptic species/ infraspecific lineages, as revealed by Hedenäs (2019) and considered by Collart et al. (2021). Similarly, results indicating strong phylogenetic signal associated with altitudinal gradient and climatic variables were obtained for infraspecific variation within two cosmopolitan moss species in the Sierra Nevada Mountains, Spain (Pisa et al. 2013; Magdy et al. 2016).

In light of these findings, we propose that for sympatrically distributed species, computed niche similarity/divergence metrics based on models estimated on a limited number of occurrences fail to confirm trends that are revealed in specially focused studies, due to methodological limitations. One possible reason for this is that the 1 km² resolution of the climatic variables may be too coarse to properly reflect
climatic effects associated with the altitudinal gradient. On a larger scale, and with allopatrically distributed species, Fedosov et al. (2022) confirmed niche divergence even with a limited number of available occurrences. Peterson (2011) suggested that the results of niche comparisons should be considered reliable only if the area under consideration is accessible to both species. This constraint may affect results obtained for invasive species (Guisan et al. 2014; Qiao et al. 2017; etc.) or heavily allopatric cases, whereas in cases of effectively dispersing bryophytes with non-partitioned and partly overlapping ranges (as in our case), both predicted species ranges can be considered accessible for the other species.

Although our analysis did not reveal niche divergence, it showed rather weak overlap between the ranges of Glyphomitrium crispifolium and Glyphomitrium sp. and a significant difference in their distribution along bioclimatic variables as partially confirmed by the Mann–Whitney U test. In our case, this differentiation may be considered meaningful because we are working with whole species distribution ranges (as they are currently known). In our opinion, this simple independent test may usefully complement niche similarity/divergence metrics, because the results obtained from the latter are often hard to interpret and not informative (Peterson 2011). Insofar as our results indicated differences in relation to several climatic variables, we have no reason not to consider the revealed phylogenetic lineages to be separate species, thus supporting the original hypothesis of the presence of more than one species of Glyphomitrium in the Russian Far East.

To ensure application of the correct names to the multiple species identified in our results, we considered the available names and associated information.

**Glyphomitrium humillimum** (Mitt.) Card. According to the protologue (Mitten 1891), this species has mucronate leaves, obtuse perichaetial leaves, and reflexed and paired peristome teeth. The term ‘obtusa’ used by Mitten (1891), or even ‘obtussissima’, used by Brotherus (1929), seems only moderately appropriate because the perichaetial leaves are broadly acute and abruptly contracted to a very short acumen, as seen from his drawings accompanying the type specimens in NY (http://sweetgum.nybg.org/science/vh/specimen-details/?irn=708872). Noguchi (1988) illustrates considerable variation in the upper part of the leaf, ranging from apiculate to short acuminate with a short and narrow, sometimes almost piliferous acumen in the perichaetial leaves but always shorter that in other species from Russia.

**Glyphomitrium crispifolium** Nog. Comparison of the Russian specimens of Glyphomitrium crispifolium with photographs made from its type (https://hattorilab.org/pdf/species/Glyphomitrium-crispifolium.pdf) leaves little doubt that this name fits Russian specimens, especially because of the presence of peculiar bistratose strips on the lamina (see Figure 9) and crispate leaves. Previous difficulty in identification can partly be explained by the treatment of Noguchi (1968, 1988), in which the species is described as having ovate-lanceolate leaves, distinctly mammillose cells, and rather short setae such that the inner perichaetal leaves reach the capsule base. The leaf shape seems to be inadequately described, because in the type illustrations all leaves are narrowly lanceolate. Cell mammilosity is at best low in the type illustrations as well as in Russian specimens. Because this species was described based on a single specimen, its variation was not fully observed, and some Russian specimens have nearly smooth laminal cells. The perichaetal leaves mostly cover the seta in the type specimen, which contrasts with most Russian collections; however, this character is highly variable, thus we do not consider that it contradicts the placement of the Russian specimens with partly bistratose laminae in G. crispifolium. Finally, the predicted probability coverage obtained for G. crispifolium based on the Russian occurrences (see Figure 3) found the *locus classicus* of this species in the Nagano area to be the most plausible within Honshu. There are even more suitable places in Hokkaido, but the species may not have been reported from there due to fewer bryophyte inventories. With this additional biogeographical evidence, we suggest using this name for one of the Russian species as proposed in the Introduction.

**Glyphomitrium formosanum** Z.Iwats. Larger Russian specimens resemble this species in having crissed leaves, percurrent costae and reflexed peristome teeth according to the key in Wang (2011), and these could be assigned to this taxon. Differences between Russian specimens and the description in the account by Wang (2011) include capsule size, ca 1 mm vs 1.4–1.8 mm in the Russian specimens, short and straight peristome teeth ca 160 μm long vs 280–350 μm long and reflexed in the Russian specimens, spore size, 28–40 μm vs (40–)50–60(–70) μm in the Russian specimens. Finally, the unistratose lamina composed of thick-walled cells, seen in photographs of the types of *Glyphomitrium formosanum* and *G. formosanum var. serratum* Z.Iwats. (https://hattorilab.org/pdf/species/Glyphomitrium-formosum-v.-serratum.pdf), is very different from that of Russian specimens referred to *G. crispifolium*.

**Glyphomitrium warburgii** (Broth.) Card. According to the protologue of *Aulacomitrium warburgii* (Brotherus 1899) and its description in the account by Wang
(2011), this taxon resembles our Russian *Glyphomitrium* sp. in having leaves with excurrent leaf costae, but it differs in that it includes rather large specimens (stems up to 1.5 cm, setae ~ 4 mm), with serrulate leaf margins, finely papillose leaf cells, acuminate-subulate perichaetal leaves, and peristome teeth arranged in pairs that are densely articulate, longitudinally striolate, and minutely papillose. We know of no published illustrations or detailed description of this species, and the type in H was on loan and unavailable for our study (in 2012 and 2018). We examined one of the specimens, studied by Abramova and Abramov (1955), who reported *G. warburgii* from Russia and found no difference from *G. crispifolium*, as it was understood here. We found no specimens from Russia that agree with available descriptions of *G. warburgii*.

*Glyphomitrium acuminatum* Broth. This was described from Yunnan, at ca 2000 m elevation. The name was used by Fedosov et al. (2021) for three Russian specimens based on the key and description of Wang (2011). However, comparing these Russian specimens with syntypes of *Glyphomitrium acuminatum* kept in KRAM and LE revealed that the latter have smaller spores (38–46 (~65) µm vs 50–60 (~70) µm) than *Glyphomitrium* sp., and different exothecial cells: in *G. acuminatum* they are thick-walled, variable in shape, mostly less than 20 µm wide and irregularly arranged, whereas in *Glyphomitrium* sp. they are thin-walled, mostly 20-38 µm wide, and arranged in rather regular longitudinal rows. Moreover, the peristome structure in the syntype specimen in LE has orange-brownish, upward-directed teeth in mature capsules. Thus, this name does not fit any of the Russian *Glyphomitrium* species. Brotherus (1929) and Wang (2011) characterised perichaetal leaves of *G. acuminatum* as very long, up to 7 mm, which does not fit *Glyphomitrium* sp. and disagrees with the examined syntype specimens as well.

*Glyphomitrium calycinum* (Mitt.) Card. was described from Sri Lanka, and reported from China by Wang (2011) and Suzuki (2015). It deserves discussion because our specimens of *Glyphomitrium* sp. are similar in having an excurrent costa and perichaetal leaves reaching the capsules. However, Wang and Suzuki described *G. calycinum* as having densely papillose peristome teeth, which have not been observed in any Russian species of the genus. The protologue of *Macromitrium calycinum* (Mitten 1859) lacks data on peristome texture. Otherwise, according to its description, this species has short and broad peristome teeth, unlike our *Glyphomitrium* sp. specimens. Moreover, according to Mitten’s description, the stems of this species are densely branched.

*Glyphomitrium elatum* Takaki. This species was considered by Iwatsuki (2004) to be a synonym of *Glyphomitrium humillimum*; according to the protologue, it has papillose peristome teeth and thus differs from all *Glyphomitrium* species from the Russian Far East.

There are several differences in DNA sequences between (i) two continental Russian specimens of *Glyphomitrium cf. humillimum*; (ii) the GenBank rps4 sequence of *G. humillimum* from Japan, Kyoto (EU246851); and (iii) two Japanese specimens, originally studied here. Moreover, occurrences of *G. humillimum* s.l. are widely spread along climatic gradients. The Japanese specimens originate from moister conditions with lower seasonality in temperature and precipitation, whereas the continental occurrences are associated with stronger seasonality and lower humidity. Assuming the need for a further improvement in the taxonomy of the *G. humillimum* complex, at the moment we see no better option than to assign our continental specimens to *G. humillimum* s.l., based on both morphology and the topologies of the trees obtained.

The Russian specimens of *Glyphomitrium* sp. appear to be the most difficult to interpret. Owing to their longer perichaetal leaf acumens and remarkably larger size, they differ from *G. humillimum* s.l. and the other species, which do not fit these specimens, as discussed above. The predicted probability coverage obtained for *Glyphomitrium* sp. (see Figure 3) shows low prediction probability in the vicinity of Beijing, from where *G. warburgii* was described; Heilongjiang (47°50′ N, 127°46′ E), where the second known specimen of *G. warburgii* was collected (http://legacy.tropicos.org/Name/35146150?tab=specimens); and throughout Japan. Therefore, we may reject the ecological suitability of the *loci classici* of *G. warburgii* and *G. humillimum*. Because we failed to find an appropriate name for *Glyphomitrium* sp., we propose describing it as a new species.

**Taxonomic treatment**

*Glyphomitrium* Brod., Muscol. Recent. Suppl. 4: 30. 1819 (1818).

Plants small to medium-sized, in loose tufts, green to brownish green. Stems ascending or erect, not or weakly fasciculate-branched, with distinct central strand, usually brown-tomentose below. Leaves curved, flexuose, contorted, crisped or spirally twisted when dry, erect-spread when moist, lanceolate to linear, keeled distally, acute to shortly acuminate, slightly narrowed to insertion; margins entire, minutely crenulate, plane or recurved below, uni- or bistratose; costa single, ending below apex, percurrent or shortly excurrent, with dorsal and sometimes also ventral stereid bands, 3 or 4 guide cells, ventral and
dorsal epidermis; lamina unistratose or bistratose distally and with bistratose strips in mid-leaf; median laminal cells isodiametric, rounded-square to transverse short rectangular, moderately thick-walled, smooth or indistinctly bulging; basal cells rectangular, as wide as laminal cells, in one row along margins or nearly throughout with incrassate transverse walls. Autoicous, perigonia in leaf axils well below perichaetia. Inner perichaetial leaves tubulose, tightly clasping seta to halfway or throughout, oblong-lanceolate, broadly or moderately broadly tapered above and then ± abruptly contracted to apiculus or narrow acumen of 0.10–0.30 times the leaf length; costa single, slender, subpercurrent to shortly excurrent. Setae yellow to brownish. Capsules short-exserted or emergent, erect, symmetrical, ovoid, short cylindrical or cup-shaped, pale, smooth or indistinctly furrowed, narrowly red rimmed; exothecial cells elongate or rectangular, moderately thick-walled, thick-walled subquadrat to oblade below the mouth. Annuulus not differentiated. Operculum low-conical and with narrow erect or oblique beak. Peristome haplolepideous, composed of remnants of cells of the inner peristomial layer (IPL) and primary peristomial layer (PPL), deeply inserted, teeth 16, sometimes distinctly or indistinctly pairwise arranged, reflexed and appressed to the outer capsule wall when dry, narrowly triangular, entire, strongly trabeculate dorsally, smooth and glossy ventrally, bright orange, red or red brown. Spores large, multicellular, densely papillose, green to brownish. Calyptra completely covering capsule, campanulate, lobed at base, pale to yellowish, longitudinally plicate.

Key to species of *Glyphomitrium* in Russia

1. Leaves narrow lanceolate to linear, usually contorted to crisped, gradually tapered to apex; costa ending below apex to percurrent; mid-lamina with bistratose strips not only along margins but also in middle part.......................... *G. crispifolium*

1. Leaves ovate-lanceolate to lanceolate, flexuose to crisped; abruptly tapered to apex; costa short excurrent, rarely percurrent; mid-lamina unistratose, sometimes with bistratose margins ......................... 2

2. Leaves (1–)1.2–1.8 mm long, inner perichaetial leaves 1.8–2.2 mm long, distally contracted to apiculus or narrow acumen of 0.05–0.10(–0.15) times the leaf length .................. *G. humilimum*

2. Leaves (1.2–)1.8–2.4(–2.5) mm long, inner perichaetal leaves 2.4–4.0 mm long, distally contracted to narrow acumen of 0.1–0.2 times the leaf length...... ................................................................. *G. ambiguuum*

*Glyphomitrium crispifolium* Nog., J. Hattori Bot. Lab. 31: 313. f. 1: 7–15. 1968 (Figures 6, 9, 10). Type: Japan. Honshu: Nagano Pref., Mt Ontake, about 2200 m alt., August 1953, *K. Manago* (Herb. Nog. 43068), holotype, NIC. (Photographs of the type are available at the NICH website, https://hattorilab.org/pdf/species/Glyphomitrium-crispifolium.pdf).

Plants small to medium-sized, green. Stems 0.5–1.5(–2.0) cm long. Leaves flexuose, contorted to crisped, rarely spirally twisted when dry, 1.6–2.5(–3.2) × 0.3–4.5(–0.55) mm, narrow-lanceolate to linear, widest just above the base and very gradually narrowed towards the tip, acuminate; margins entire, minutely crenulate, recurved in the lower half, bistratose in the upper part; costa ending below apex or percurrent; lamina bistratose distally and with bistratose strips in mid-leaf; median laminal cells 7–8(–10) × 5–8(–10) μm; basal cells short rectangular, 12–24(–29) × 6–10 μm, narrower in one row along margin, with slightly incrassate transverse walls. Inner perichaetial leaves 2.4–3.5 mm long, not reaching base of capsule, broadly to moderately broadly tapered above, abruptly contracted to narrow acumen of 0.15–0.30 times the leaf length. Setae 2.5–3.5 mm. Capsules ovoid to short cylindrical, (0.8–)1.0–1.8 × 0.4–0.7 mm, pale yellowish, smooth or irregularly furrowed, exothecial cells elongate to rectangular, in more or less regular rows, moderately thick-walled. Operculum long rostrate or conical-rostrate. Peristome teeth not in pairs or pairwise arranged, 280–350 μm long, deep red, rarely orange or brownish, with one column of PPL cells. Spores (40–)50–60(–70) μm. Calyptra 1.5–2 mm.

**Differentiation and variation.** The contorted to crisped leaves with costae ending below the apex or percurrent help with species identification in the field. Conclusive identification requires transverse leaf sections – no other species of the genus in Russia has partly bistratose upper leaf laminae.

**Distribution.** In Russia, this species occurs in humid areas of the southern part of the Russian Far East – in the Khabarovsk Territory, the Primorsky Territory, the southern part of Sakhalin, and the South Kuril Islands (Kunashir and Shikotan).

**Ecology.** *Glyphomitrium crispifolium* occurs on trunks of spruce, fir, birch, and alder shrubs, etc. in humid montane forests. In the southern part of the Primorsky Territory, it occurs at (350–)600–1600 m, whereas in more northern continental regions, such as in the south of the Khabarovsk Territory and in humid island climates, it grows just above sea level.

**Specimens examined.** RUSSIA. Khabarovsk Territory: Bereisky State Reserve, Ignatov 97-47 (MHA9120772); Khabarovsk Dist., Yarap River upper course, Badzhal Mts, Fedosov 16-23 (MW, dupla ex
Figure 6. Glyphomitrium crispifolium (from: Russia, Primorsky Territory, 14 September 2014, Fedosov s.n., MW). (A) Habit, dry. (B) Part of the peristome. (C) Exothelial cells. (D) Habit, wet. (E, F) Perichaetal leaves. (G–I, M) Leaf transverse sections. (J) Median leaf cells. (K) Upper leaf cells. (L) Stem transverse section. (N–R) Stem leaves. (S) Basal leaf cells. Scale bars: 2 mm (A, D); 1 mm (E, F, N–R); 200 μm (B, C); 100 μm (G–M, S). Drawn by Elena A. Ignatova.
Chuguyevsky District, Puzikov Pass area, 14 September 2014, Fedosov s.n. (MW, MHA); Verkhne-Ussuriysky Scientific Station of Far Eastern branch of Russian Academy of Sciences, Ignatov 07-606 (MHA9120762); ibid., Ignatov 07-565 (MHA9120762); Olkhovaya Mt, Ignatov, Ignatova & Cherdantseva 06-2631 (MHA9120765); ibid., Ignatov, Ignatova & Cherdantseva 06-2850 (MHA9120768); Terneisky Distr., vicinity of Terney, 1 October 2019, M.A. Kolesnikova 19-85 (MHA); Isakov Creek, 3 September 2007, Ignatov, Ignatova & Malashkina 13-1831 (MHA); Shkotovskiy Distr., Pidan (Livadiyskaya) Mt, Ignatov & Ignatova 06-2114 (MHA9120766); Kavalerovo Distr., vicinity of Lud’e sett., 29 November 1971, Bardunov s.n. (MHA9120770).

Sakhalinskaya Province: Sakhalin Island, Korsakovskiy Distr., O.Yu. Pisarenko 03700 (MHA9120763 dupla ex NSK); Kuril Islands; Kunashir Island, outer slope of caldera of Golovina Volcano, Ignatov 06-1001 (MHA9120752); ibid., vicinity of Saratovka River Mouth, Ignatov 06-1351 (MHA9120755); ibid., Mendeleeva Volcano, Ignatov 06-1695 (MHA9120753); ibid., 30 September 1978, Bardunov (MW9111795); ibid., Ignatov 06-3103 (MHA9120756); vicinity of Tret’yakovskoye setti., T.I. Koroteeva 15-10/5-4 (MHA9101386); ibid., T.I. Koroteeva 15-10/8-3 (MHA9101403, + G. ambiguum); ibid., T.I. Koroteeva 15-10/4-11 (MHA9101389); Shikotan Island, vicinity of Kraboazvodsksoe vellage, Bakalin K-45-30-07 (MHA9120757, dupla ex VLA); ibid., 9–25 August 2021, Fedosov & Shkurko s.n. (MW9116136, 9116141, 9116142); vicinity of Malokuril’skoe village, 6 August 2021, Fedosov & Shkurko s.n. (MW9116137-9116140).

Glyphomitrium humillimum (Mitt.) Cardot, Rev. Bryol. 40: 42. 1913.

(Figure 7)

Type. Japan, leg. Maingay (NY, scans of the specimen and supplementary Mitten drawings available at http://sweetgum.nybg.org/science/vh/specimen-details/?irm=708872).

Description. Plants small, green to brownish green. Stems 0.4–0.7(–0.8) cm long. Leaves curved to flexuose, usually spirally twisted around the stem when dry, (1–)1.2–1.8 × 0.3–0.45 mm, ovate-lanceolate to lanceolate, acute; margins entire or minutely crenulate, often gently sinuose distally, recurved in the lower half, bistratose distally or nearly throughout; costa excurrent as short yellow or brownish mucro; lamina unistratose, median laminal cells (8–)9–12(–16) × 10–13 μm; basal cells rectangular, 15–30 × 12–13 μm, often with incrassate transverse walls. Inner perichaetial leaves 1.8–2.2 mm, often reaching capsule base, broadly acute and then abruptly contracted to an apiculus or short acumens of 0.05–0.15 times the leaf length. Setae ca 2 mm. Capsules ovoid, 0.8–1.0 × 0.5–0.7 mm, light, smooth; exothecial cells elongate, moderately thick-walled, rather irregularly arranged. Operculum conical-rostrate; peristome teeth weakly to distinctly paired, 200–250 μm long, with one or two columns of PLL cells. Spores (45–)50–60 μm. Calyptra ca 1.5 mm.

Differentiation and variation. Glyphomitrium humillimum differs from other members of the genus in the combination of small size, relatively broad leaves that are often curved when dry (resembling Anoectangium Schwägr.), excurrent costa, unistratose leaf lamina (except along the margins), and inner perichaetial leaves broadly acute and contracted to an apiculus or a short narrow acumen.

Distribution. Glyphomitrium humillimum is an East Asian species that occurs in Japan, the Korean Peninsula, China, and the Russian Far East. However, the Russian distribution of this species has been treated too broadly: as became evident during the course of this study, most collections of Glyphomitrium from Russia belong to either G. crispifolium or G. ambiguum (see below), whereas G. humillimum occurs in Russia in Amur Province (a single collection from Zeya State Reserve), the Primorsky Territory (two collections), and Shikotan Island. One collection from the Zabaikalsky Territory is poorly preserved, so its identification is uncertain.

Ecology. This species inhabits tree trunks and outcrops, generally preferring more xeric habitats than those of Glyphomitrium crispifolium. Russian specimens, which form a separate clade within G. humillimum s.l., were collected mostly from rock, whereas almost all the Japanese collections were from trees. The collection from Shikotan Island was on the trunk of a Juniperus sargentii (A.Henry) Takeda ex Nakai and was made above the treeline. Most specimens are from lower elevations, although in the Zabaikalsky Territory G. humillimum was collected at 1062 m.

Specimens examined. RUSSIA. Zabaikalsky Territory: Borzya Distr., Daurski Reserve, 16 July 2010, E.S. Prelovskaya s.n. (MW, dupla ex LE).

Amur Province: Zeysky Reserve, Tukuringra Mt Range, right side of the Gilyui River valley, below the mouth of the Stepanak River, 27 August 2016, S.V. Dudov (MW9079203).

Primorsky Territory: Ussuriysky State Reserve, Zmeinaya Mt, Ignatov 08-276 (MW9040205, MHA9120760); ibid., Ignatov 06-2327 (MHA9120764); vicinity of Vladivostok City, Vityaz Bay, 15 October 1978, Bardunov s.n. (MW9111821).

Sakhalinskaya Province: Shikotan Island, vicinity of Notoro Mt, 13 August 2021, Fedosov & Shkurko s.n. (MW 9116135).

JAPAN. Honshu: Kyoto, 50 m alt., Nakajima #35311 (MHA dupla ex NIC); Gunma-ken, Katashina-mura, Mt
Glyphomitrium ambiguum Fedosov, Ignatova & Ignatov, sp. nov.

(Figures 8, 9, 10)

Type. Primorsky Territory, Terneysky District, Sikhote-Alin’sky State Reserve, Yasnoe field station, 45°13’N, 136°30’E, 175 m alt., polydominant mixed forest in valley, 2 October 2019, M.A. Kolesnikova 19-171 (holotype: MHA).

Etymology. The species name originates from the rather poor morphological differentiation from the widely distributed and not clearly morphologically circumscribed Glyphomitrium humillimum.
**Diagnosis.** Leaves flexuose to contorted, lamina unistratose except for the bistratose distal margins, costa excurrent, cells rather large, \((8–)9–12(–16) \times 10–12 \mu m\); inner perichaetial leaves reaching the capsule base, broadly narrowed above and then abruptly contracted to short narrow acumen, spores multicellular, 50–70 \(\mu m\).

**Description.** Plants small to medium-sized, green to brownish green, in loose tufts. Stems 0.5–1 cm long, erect or ascending, not or weakly branched, brown-tomentose at base. Leaves flexuose to contorted, usually spirally twisted when dry, erect-spreading when moist, \((1.2–)1.8–2.4(–2.5) \times 0.35–0.6 \text{ mm}\), lanceolate to narrowly lanceolate, keeled distally, acute;
margins entire or distally weakly sinuose, minutely crenulate, recurved in the lower half, bistratose distally; costa strong, shortly excurrent as green to brownish mucro or rarely percurrent, with dorsal and occasionally also ventral stereid bands, 3 or 4 guide cells, ventral and dorsal epidermis present; lamina unistratose; median laminal cells quadrate, rounded-quadrate or rarely transverse short rectangular, (8–)9–12(–16) × 10–12 μm, moderately thick-walled, smooth or indistinctly bulging; basal cells rectangular, 25–65 × 5–12 μm, often with incrassate transverse walls. Autoicous, perigonia in leaf axils well below perichaetia. Inner perichaetial leaves 2.4–4.0 mm long, reaching the capsule base and partly covering it, broadly narrowed.
above and then abruptly contracted to narrow acumen of 0.10–0.20 times the leaf length; costae slender, single, subpercurrent to excurrent. Setae 2.0–2.8 mm long, yellow. Capsules erect, symmetrical, ovoid to short cylindrical, 1–1.2 × 0.7 mm, pale, smooth, narrowly red-rimmed; exothecial cells elongate, thick-walled, irregularly arranged, near the mouth thick-walled subquadrate or oblate in a few rows; annulus not differentiated. Operculum conical-rostrate. Peristome deeply inserted, teeth indistinctly to distinctly paired, reflexed and appressed to the outer capsule wall when dry, 200–250 μm long, narrowly triangular, entire, strongly trabeculate from the outside, smooth and glossy from the inside, orange to brownish, composed of one or two rows of PPL cells. Spores multicellular, 50–65(–70) μm, densely papillose, green to brownish. Calyptra ca 1.5 mm.

**Differentiation.** *Glyphomitrium ambiguum* differs:

- from *G. humillimum* in having larger plants and leaves, and with inner perichaetial leaves contracted to longer acumens;
- from *G. crispifolium* in the unistratose leaf lamina, and with broader leaves with excurrent costae;
- from *G. formosanum* in the contorted vs crisped leaves, and the excurrent costae;
- from *G. warburgii*, as it was originally described by Brotherus (1899), in having smaller plants, 0.5–1 cm vs 1.5 cm high, shorter setae 2–2.5 mm vs 4 mm, and leaf cells and peristome smooth vs papillose;
- from *G. acumatum* in larger spores 50–65(–70) μm vs 38–46(–65) μm, and smaller plants, 0.5–1 cm vs 1.5 cm; and
- from *G. calycinum*, as it was described by Mitten (1859), in not having densely branched plants nor broad and short peristome teeth.

**Distribution.** *Glyphomitrium ambiguum* occurs in the southern part of the Khabarovsk Territory, in the Primorsky Territory, and on Kunashir Island. According to the distribution model presented here, it may also occur in Korea and Northeast China. In Russia, this species is generally associated with a rather warm and dry climate, being typically confined to East Asian broadleaved forests.

**Ecology.** This species inhabits tree trunks at lower elevations. Its altitudinal distribution differs from that
of *Glyphomitrium crispi folium*, which is more common in hemiboreal and boreal forest belts at higher elevations and generally has a more northern distribution in more humid climates.

**Other specimens examined.** RUSSIA. **Khabarovsk Territory:** Bol’shekheltsyrsy State Reserve, 15 August 1981, *Cherdantseva* s.n. (MW9075463, MW9110195, dupla ex VGBI); ibid., 9 August 1983, *Cherdantseva* s.n. (MW9075425, dupla ex VGBI).

**Primorsky Territory:** Olga Distr., *Ignatov* 07-337 (MHA9120761); Sikhote-Alin’sky Reserve, 16 October 1978, I.A. *Flyagina* s.n. (MW9110194 dupla ex VGBI); Chuguevsky Distr., Verkhne-Ussuriysky Scientific Station of Far Eastern branch of Russian Academy of Sciences, 1976, *Timofeeva* s.n. (MW9110193 dupla ex VGBI); Vladivostok City, Lynchikhe Creek basin, *Ignatov* 06-2042 (MHA9120767); Terney Distr., Isakov Creek, *Ignatov*, *Ignatova* & *Malashkina* 13-1707; Lozovsky Distr., 18 September 1974, *Bardunov, Cherdantseva & Olinovich* (MW9110196 dupla ex VGBI); Vicinity of Vladivostok City, Okeansky Ridge, *Ignatov* 06-3501 (MHA9120758).

**Sakhalinskaya Province:** Kunashir Island, vicinity of Yuzho-Kurilsk, *Ignatov* 06-3003 (MHA9120754); ibid., vicinity of Tet’yakovo settl., T.I. *Koroteeva* 15-10/5-4 (MHA9101386); ibid., T.I. *Koroteeva* 15-10/8-3 (MHA9101403, + *G. crispi folium*).

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**Supplemental material**

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### Table A1. Specimens used for molecular phylogenetic analysis and their GenBank accession numbers.

| Species | Isolate | Country | Specimen voucher | ITS | trnS-trnF |
|---------|---------|---------|------------------|-----|-----------|
| *Cnestrum alpestre* (Wahlenb.) Nyholm | RF9 | Russia | — | MN092459, | — |
| *Cnestrum schistii* (F.Weber & D.Mohr) J.Hagen | RF11 | Russia | — | MN092464, | — |
| *Glyphomitrium ambiguum* Fedosov, sp. nov. | GF9 | Russia | Kolesnikova 19-171 (MHA) | MZ647678 | MZ664398 |
| *Glyphomitrium ambiguum* | GF14 | Russia | MHA9120754 | MZ647679 | MZ664399 |
| *Glyphomitrium ambiguum* | GF15 | Russia | MHA9120764 | MZ647680 | MZ664400 |
| *Glyphomitrium crispifolium* Nog. | GF16 | Russia | Kolesnikova 19-85 (MHA) | MZ647681 | MZ664401 |
| *Glyphomitrium crispifolium* | GF10 | Russia | Fedosov s.n. 14.IX.2014 (MW) | MZ647682 | MZ664402 |
| *Glyphomitrium crispifolium* | OK076 | Russia | Ignatov & Ignatova 13-1589 (MHA) | MZ647683 | MZ664403 |
| *Glyphomitrium crispifolium* | OK077 | Russia | Ignatov & Ignatova 13-1945 (MHA) | MZ647684 | MZ664404 |
| *Glyphomitrium crispifolium* | OK705 | Russia | Ignatov & Ignatova 13-1213 (MHA) | MZ647685 | MZ664405 |
| *Glyphomitrium crispifolium* | GF4 | Russia | — | MF353235 | MN092500, |
| *Glyphomitrium crispifolium* | GF5 | Russia | — | MF353236 | MN092501, |
| *Glyphomitrium crispifolium* | GF6 | Russia | — | MF353237 | MN092502, |
| *Glyphomitrium daviesii* (Dicks.) Brid. | RF78 | Norway | — | MN718554, | — |
| *Glyphomitrium humillimum* (Mitt.) Cardot | GF13 | Russia | Ignatov 08-276 (MHA) | MZ647675 | MZ664394 |
| *Glyphomitrium humillimum* | GF12 | Russia | MW9079203 | MZ647676 | MZ664395 |
| *Glyphomitrium humillimum* | GF1 | Japan | Yamaguchi s.n., 9 May 2014 (HIRO, MW) | — | MZ6464396 |
| *Glyphomitrium humillimum* | GF2 | Japan | Sakamoto s.n., 10 September 2013 (HIRO, MW) | MZ647677 | MZ664397 |
| *Oncophorus virens* (Hedw.) Brid. | RF110 | Russia | MW9050594 | OL435101 | MN092556, |
| *Oreas martiana* (Hopp & Hornsch.) Brid. | RF5 | Russia | — | MN092429 | MN092431 |
| *Pseudoblindia falcata* (Hedw.) Fedosov, M.Stech & Ignatov | 250 | Russia | — | MN092516, | — |
| *Rhabdoweisia fugax* (Hedw.) Bruch & Schimp. | RF2 | Russia | — | MN092568, | — |
| *Rhabdoweisia crispata* (Dicks.) Lindb. | RF4 | Russia | — | MN092566, | — |
| *Symblepharis elongata* (I.Hagen) Fedosov, M.Stech & Ignatov | RF24 | Russia | — | MN092551, | — |
| *Symblepharis vaginata* (Hook. ex Harv.) Wijk & Margad. | RF127 | Russia | O.M. Afonina 2-10 (LE) | OL435100 | MN092570, |

*aAccessions generated for the present study are in bold. For newly studied specimens, voucher information is provided.*