Partial generic revision of Barbula (Musci: Pottiaceae): Re-establishment of Hydrogonium and Streblotrichum, and the new genus Gymnobarbula

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Abstract Large genera, that were defined using a restricted suite of morphological characters, are particularly prone to be polyphyletic. We analysed a representative selection of species traditionally assigned to the genus Barbula, believed to represent the largest genus of the moss family Pottiaceae, but which recently was suggested to be polyphyletic. Special attention was paid to species traditionally assigned to Barbula sect. Hydrogonium and sect. Convolutae, in which phylogenetic relationships are likely to be incongruent with morphological traits, which could have evolved in adaptation to hydric and otherwise extreme habitats. Our phylogenetic analysis was based on nITS and chloroplast rps4 and trnM-trnV sequence data and resolved only the type of the genus, B. unguiculata, plus B. orizabensis, in subfamily Pottiioideae, while most of the species occurring in the Northern Hemisphere are part of Trichostomoideae and need to be recognized within the re-established and partly re-defined genera Hydrogonium and Streblotrichum. The phylogenetically and morphologically divergent B. bicolor needs to be removed from Streblotrichum to a newly described genus, Gymnobarbula. Numerous taxonomic changes and nomenclatural novelties, resulting from the molecular, morphological and nomenclatural studies are proposed for taxa of Hydrogonium, particularly within the H. consanguineum clade. Lectotypes are selected for Tortula angustifolia Hook. & Grev. (= Hydrogonium angustifolium) (Hook. & Grev.) Jan Kučera, comb. nov.; Tortula consanguinea Thwaites & Mitt. (= Hydrogonium consanguineum (Thwaites & Mitt.) Hilp.) and Tortula flavescens Hook. & Grev. (= Hydrogonium consanguineum (Thwaites & Mitt.) Hilp.).

Keywords Barbula; Gymnobarbula gen. nov.; Hydrogonium; ITS; nomenclature; polyphyly; Pottiaceae; rps4; Streblotrichum; taxonomy; trnM-trnV

Supplementary Material The alignment is available in the Supplementary Data section of the online version of this article (http://www.ingentaconnect.com/content/iapt/tax).

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INTRODUCTION

The genus Barbula Hedw. has been considered to represent the largest genus of the moss family Pottiaceae Schimp., with Zander (2007) estimating Barbula to contain some 200 species. The current taxonomic concept of Barbula dates back to Saito (1975), who emphasized gametophytic characters (e.g., leaf shape and anatomy and characters of axillary hairs). This allowed him to exclude the species of Didymodon Hedw. with twisted peristome teeth, and those of Bryoerythrophyllum P. Chen from the earlier concepts of Barbula, while including the species of Hydrogonium (Müll. Hal.) A. Jaeger. Saito recognized three subgenera—B. subg. Barbula with sect. Barbula and sect. Hydrogonium (Müll. Hal.) K. Saito, B. subg. Streblotrichum (P. Beauv.) K. Saito, and the newly established B. subg. Odontophyllum K. Saito. His concept was slightly extended by Zander (1993) from a global perspective. Zander classified the genus only down to section level, merging B. subg. Odontophyllum with B. sect. Convolutae (= B. subg. Streblotrichum), while retaining B. sect. Hydrogonium, and further recognizing several mostly monotypic and partly obscure sections not occurring in Japan, such as the principally Central American B. sect. Hyophila Bruch and Hyophila Brid., and envisaged the future splitting of the genus into segregate genera.

Phylogenetic inferences from rps4 data resolved Barbula as a polyphyletic entity (Werner et al., 2004). Its generitype, Barbula unguiculata Hedw., appeared in subfamily Pottiioideae (Limpr.) Broth., while the other two analyzed species, B. bolleana (Müll. Hal.) Broth. and B. indica (Hook.) Spreng., appeared in a clade in subfamily Trichostomoideae (Schimp.) Limpr. The close relationship between the latter two species was perhaps unexpected, as B. bolleana has been regarded by recent authors (Frahm et al., 1996; Zander, 2007) to be taxonomically
identical with *B. ehrenbergii* (Lorentz) M. Fleisch., the type of *B. sect. Hydrogonium*, while *B. indica* (Hook.) Spreng. represents a group of taxa which had been recognized by some pre-Saitoan authors as the genus *Semibarbularia* Herzog ex Hilp. (e.g., Hilpert, 1933; Ganglee, 1972). *Semibarbularia* has mostly been synonymized with *Barbula* in the following treatments (Saito, 1975; Li & al., 2001). Later, Cox & al. (2010) were able to confirm the isolated position of *B. agraria* Hedw., elevated to the rank of genus (*Hyophiladelphus* Müll. Hal.) by Zander (1995). The isolated position of some European members of *B. sect. Convolutae* Bruch & Schimp. could be inferred from a study by Köckinger & Kučera (2011), which essentially studied the members of tribe Pfeurowesieaeaeae (Limpr.) P.C. Chen.

It is obvious that building a robust backbone phylogeny of *Barbula* sensu Zander (1993) is a voluminous task which can be accomplished only by the combination of molecular phylogenetic analyses with the careful re-consideration of morphological and anatomical characters. The sampling for such a study will not only have to include the representatives of the genus, as understood by earlier authors, from its entire range, but also species currently assigned to the genera *Trichostomum* or *Hyphila*, which contain species morphologically similar to *Barbula*. Similarly, the relatively recently segregated genus *Pseudocrossidium* R.S. Williams should be included, because its delimitation has not been tested using molecular markers. One way of dealing with *Barbula* is the successive revision of relatively well-defined groups that will be removed from the wastebasket assemblage of the original *Barbula*, keeping in mind that the morphological delimitation must not always reflect phylogenetic relationships. Based on the molecular studies discussed above, we identified two such groups, *B. sect. Hydrogonium* and sect. *Convolutae*.

*Barbula* sect. *Hydrogonium* was first recognized as a “Gruppe”, i.e., an unranked infrageneric group, within the genus *Trichostomum* by C. Müller (Müller 1876: 297) to accommodate three similar hydrophytic taxa, *B. bolleana* and *B. ehrenbergii* (now regarded as conspecific), and *B. meidenensis* Cufod. (= *Trichostomum fontanum* Müll. Hal.), a little known Somali species that may, according to the protologue, be identical with the preceding two species. Fleischer (1904) broadened the concept of *Hydrogonium* (at subgeneric level within *Barbula*) to accommodate the hygrophilous Indo-Malayan s.l. *Barbula* species with broadly lanceolate to lingulate leaves with smooth to little papillose, relatively wide lamina cells (*B. javanica* Dozy & Molk., *B. inflexa* (Duby) Müll. Hal., *B. pseudoehrenbergii* M. Fleisch., *B. tjihodensis* M. Fleisch.). Later Hilpert (1933) included in *Hydrogonium* the less hygrophilous species with densely papillose lamina cells, such as *H. consanguineum* (Thwaites & Mitt.) Hilp., and drew attention to axillary gemmae of a type different from, e.g., *Streblotrichum*. Hilpert’s delimitation of *Hydrogonium* was accepted and applied to East Asian species by Chen (1941), who also formalized the delimitation of two groups within *Hydrogonium*, i.e., *H. sect. Hydrogonium* ["Euhydrogonium"], comprising the traditionally recognized hygrophilous taxa, and the newly distinguished *H. sect. Barbuliella* P.C. Chen comprising species with small papillose cells and sharply acute or apiculate leaves. Finally, Zander (1993) extended sect. *Hydrogonium* to include the genus *Semibarbularia*, a view that was later (Werner & al., 2004) corroborated by their molecular relationships. Zander (2007) later changed his mind and transferred the North American species of *Semibarbularia* and *H. sect. Barbuliella* to *H. sect. Convolutae*. Most of the taxa assigned historically to *Hydrogonium* have their distribution centre in the Indo-Malayan region or occur exclusively in this area.

**Barbula** sect. *Convolutae*, typified by *B. convoluta* Hedw., has been traditionally recognized to include *Barbula* s.l. species with strongly differentiated convolute perichaetial leaves, mostly yellow seta and an annulus of strongly differentiated, vesiculose cells (Limpricht, 1890; Zander, 1993). This definition agrees well only with the characters of the primarily European species *Streblotrichum convolutum*, *S. commutatum* (Jur.) Hilp., and *S. endereissii* (Garov.) Loeske, while other taxa like *S. bicolor* (Bruch & Schimp.) Loeske or *S. croceum* (Bríd.) Loeske share only some of these characters. Only a few taxa occurring exclusively outside Europe have historically been assigned to this group of mosses. Although Brotherus (1902: 410–411) listed 30 species worldwide, most of them were later transferred to other genera or synonymized.

Our aims were (1) to identify phylogenetically defined supra-specific units within the supposedly polyphyletic genus *Barbula* and to compare the phylogenetic signal from chloroplast and nrITS datasets, (2) to identify morphological and anatomical characters which match these phylogenetically defined units and permit their formal description or referral to earlier described taxa, and (3) to develop a taxonomic and nomenclatural synopsis of taxa referred to *Barbula* sect. *Convolutae* and sect. *Hydrogonium* occurring in the Northern Hemisphere, focused on the revision of specific limits within the *Barbula indica* complex where these limits are uncertain considering the contrasting treatments of Sollman (2004b), Zander (2007) and Ignatova & Ignatov (2009).

**MATERIALS AND METHODS**

**Herbarium material and sampling for the molecular analysis.** — Sampling of the material followed the main goals specified above. We sampled representative species of sect. *Convolutae* and sect. *Hydrogonium*, with a focus on exemplars from their putative centres of origin in SW Asia and the Holarctic, respectively. More detailed sampling was necessary in the *B. indica* complex. Types of the sections as well as taxa which differ in morphological characters which might prove to be taxonomically important were included in the analysis. This selection was complemented by representatives of other Pottiaceae, based on Zander (1993), Werner & al. (2004, 2005b), Cox & al. (2010) and Köckinger & Kucera (2011). The taxa sampled for this study are listed in Appendix 1.

The molecular study was complemented by the study of herbarium material and the most relevant types to ensure the correct application of names. These studies particularly concentrated on European and American collections named *Barbula*.
The remaining Barbula s.l. species appear among members of subfamily Trichostomoideae. A possible exception are listed in Appendix 1. We have also extensively utilized the study of the types obtained from BM, E and NY, and additional recent material from Southeast Asia of these taxa and of B. javanica was obtained from E. Later findings prompted us for morphological study of the types of B. subcomosa Broth. and B. majuscula Müll. Hal., which were obtained from BM. The plants studied are listed in Appendix 1. We have also extensively utilized the results of our previous morphological studies of Barbula by the first author.

Molecular protocols. — Total genomic DNA was extracted using the NaOH method (Werner et al., 2002). Three regions were selected for amplification: the chloroplast loci rps4 with the flanking rps4-trnS spacer (hereafter denoted as rps4) and trnM-trnV, and the nuclear ITS region. Chloroplast rps4 is the region best represented for Pottiaceae in GenBank, followed by nuclear ITS, which was used in the treatments of Trichostomoideae by Werner et al. (2005b) and Köckinger & Kučera (2011). The variability of trnM-trnV has been shown to be useful in the study of Werner et al. (2009). Amplification and sequencing reactions followed the protocols described in Köckinger & Kučera (2011), and primers and amplification of trnM-trnV followed Werner et al. (2009). When data obtained from the direct ITS sequencing indicated a mixed template and more than two polymorphic positions within one sequence were detected, cloning was performed following the procedure described by Košnar et al. (2012).

Sequence editing, alignment and phylogenetic analysis. — The sequences were edited in BioEdit v.7 (Hall, 1999). The partial sequences of the trnS gene were trimmed from the rps4 amplicons, as were the variable 5’ and 3’ ends of ITS amplicons which belong to the 18S and 26S rRNA genes. The sequences were aligned using the online version of MAFFT v.6 (Katoh & Toh, 2008) using the Q-INS-i strategy with 200PAM / κ = 2 scoring matrix, gap opening penalty set to 1.0, and the offset value set to 0.0. The resulting alignments were manually inspected for homology problems and edited but these interventions were limited to very obvious cases to ensure maximum reproducibility. For purposes of phylogenetic analyses, three data matrices were produced: ITS, rps4, and a concatenated matrix of rps4 and trnM-trnV. Information from indels was included in the phylogenetic analyses of the chloroplast datasets by coding them into the data matrix with SeqState v.1.4 (Müller, 2005) using the simple indel coding method (Simmons & Ochoterena, 2000).

Selection of outgroup taxa was based on earlier studies by Werner et al. (2004) and Cox et al. (2010). This selection could not be fully identical among datasets because trnM-trnV could not be amplified in Pseudephemerum and Pleuridium, and ITS sequences of Blindia, Fissidens and Scopelophila were not alignable with the rest of the dataset. Phylogenetic analyses were performed using the maximum parsimony (MP) criterion in PAUP* v.4b10 (Swofford, 2002) and Bayesian inference using MrBayes v.3.2.1 (Ronquist et al., 2012). The MP analysis was run using a heuristic search with the following settings: tree bisection-reconnection (TBR) branch swapping, random additions with 1000 replicates, hold = 1, multtrees = yes, steepest descent = yes, collapse = yes. The ‘maxtrees’ limit was not restricted in analyses of concatenated rps4+trnM-trnV data, but was set to 100,000 trees in the analysis of rps4 and to 50,000 in the analysis of ITS. A bootstrap analysis was performed with 1000 replicates using the heuristic search strategy as described, except for the following options: the ‘maxtrees’ limit was set to 10,000 and 10 replicates of random additions were used for analysis of concatenated rps4+trnM-trnV; the ‘maxtrees’ limit was set to 1000 and simple additions were used for the analysis of ITS and rps4 matrices. For Bayesian inference, we have not partitioned DNA data from the concatenated chloroplast matrix, as the phylogenetic signal from separate genes and spacers was weak (compare support for clades in the separate rps4 analysis and the analysis of the concatenated chloroplast dataset). We used a gamma model of rate variation across sites sampled across the GTR model space (iset nst = mixed rates = gamma). The analyses in MrBayes were performed using two simultaneous runs each with four separate chains, sampling one tree every 100 generations and running until the average standard deviation of split frequencies between runs dropped below 0.01. The temperature of a hot chain was set empirically to 0.05. Following the inspection of log likelihood values we found no reason to change the default setting of burn-in of the first 25% of sampled trees, and the remaining trees were used for construction of a 50% majority consensus tree. The trees were edited using TreeGraph v.2 (Stöver & Müller, 2010). Alternative topological hypotheses were evaluated using Bayesian inference. The datasets were re-analysed using the same settings as described above, except that models were constrained to monophyly/polyphyly of particular groups. The marginal model likelihoods of constrained trees were estimated using the harmonic mean of the likelihood values of the MCMC samples (Ronquist et al., 2012). Differences in log likelihoods >3 log units were considered as significant (Kass & Raftery, 1995).

RESULTS

Data matrices and phylogenetic reconstruction. — Data characteristics of the sequences are summarized in Table 1. The strict consensus trees obtained from MP had similar topologies as the 50% consensus Bayesian trees, differing only in poorly supported internal branches. Therefore, only the Bayesian trees (Figs. 1–3) are shown here with bootstrap support from the MP analyses shown where applicable. The topologies of trees inferred from each individual region as well as from the combined chloroplast data confirmed the polyphyly of Barbula sensu Zander (1993). While the type of the genus, Barbula unguiculata, plus B. orizabensis is resolved in Pottioidae, the remaining Barbula s.l. species appear among members of subfamily Trichostomoideae. A possible exception...
... only the clade comprising accessions of B. enderesii and B. convoluta was considered as Streblotrichum. While the chloroplast datasets render members of Barbula containing B. unguiculata and B. orizabensis received poor support only in the Bayesian inference of ITS data (PP = 0.94, Fig. 3). All tests using constrained trees rejected monophyly of Barbula s.str. with any other clade of other Barbula s.l. accessions (see Table 2).

While the chloroplast datasets render members of Streblotrichum (except for B. bicolor, see below) monophyletic with high support, the ITS analysis surprisingly suggests their polyphyly. While B. enderesii and one of the accessions of B. convoluta appear in a clade containing Hyophila involuta, B. bicolor and the Leptodinium + Triquetrella clade, which is largely congruent with the concatenated chloroplast dataset, the rest of accessions of B. convoluta with B. commutata appears in Pottioidae in a poorly supported clade containing Didymodon and Syntrichia.

Barbula bicolor has an uncertain position in Trichostomoidae. Chloroplast data marginally support its affinity to Hyophila involuta rather than to Streblotrichum, while ITS data failed to resolve its position with statistical support. The analysis of constrained trees strongly supported the non-monophly of Streblotrichum + B. bicolor based on the rps4 dataset and marginally did so in the analysis of the concatenated chloroplast dataset, while the ITS data marginally supported the possible monophyly of Streblotrichum + B. bicolor (Table 2). Nevertheless, the appearance of the Leptodinium + Triquetrella clade in this poorly supported clade again points to homology problems in ITS, and morphologically this grouping of taxa has no support at all.

The relationships of Hyophiladelphus could be analyzed only in the rps4 dataset, which was slightly extended compared to the last study of Cox & al. (2010). Hyophiladelphus appears closely related with Hyophila Brid., Gymnostomiella M. Fleisch., Splachnobryum Müll. Hal. and possibly Indopottia A.E.D. Daniels & al., and a close relationship with B. bicolor was rejected in the test of monophyly (Table 2).

All analyses resolved a strongly supported clade within Trichostomoidae, which contained the traditionally recognized species of sect. Hydrogonium (B. bolleana—the type of the section, B. pseudoehehrenbergii, B. javanica) together with taxa which were recognized only by some authors as members of Hydrogonium (B. amplexifolia, B. subcomosa, B. indica), and with taxa that have never been attributed to this group (B. crocea, B. convoluta var. gallinula). All the tests using constrained trees rejected monophyly of this clade with any other clade of Barbula s.l. (Table 2). The molecular analysis of samples originally identified as B. indica (incl. var. kurilensis and var.}

### Table 1. Characteristics of data matrices. Characters are listed for each of the regions in the rps4 + trnM-trnV matrix.

|          | rps4 | rps4 + trnM-trnV | ITS |
|----------|------|-----------------|-----|
| Number of sequences | 100  | 87              | 114 |
| Number of characters | 696  | 679 / 945       | 1911|
| Variable characters | 332  | 269 / 439       | 1116|
| Parsimony-informative characters | 196  | 157 / 250       | 826 |

### Table 2. Comparison of constrained trees using marginal model likelihoods.

| Group constrained to monophyly | rps4 | rps4 + trnM-trnV | ITS |
|--------------------------------|------|-----------------|-----|
| Barbula s.l.                   | –    | PPP             | PPP |
| Barbula s.str. (B. orizabensis + B. unguiculata) | –    | PP              | n.s.|
| Barbula s.str. + Gymnobarbula  | –    | PPP             | PPP |
| Barbula s.str. + Streblotrichum| –    | PPP             | PPP |
| B. orizabensis + Streblotrichum| –    | PPP             | –   |
| B. unguiculata + Streblotrichum| –    | P               | –   |
| Gymnobarbula + Hydrogonium     | –    | PP              | PP  |
| Gymnobarbula + Hydrogonium + Streblotrichum | –    | PPP             | PP  |
| Gymnobarbula + Hydrogonium     | –    | P               | M   |
| Hydrogonium + Streblotrichum   | –    | PPP             | PP  |
| Gymnobarbula + Hyophiladelphus  | PP   | –               | –   |
| Gymnobarbula + Hydrogonium + Hyophiladelphus | PPP  | –               | –   |
| Hydrogonium + Hyophiladelphus   | PPP  | –               | –   |

M, tree constrained to monophyly is significantly better, difference in marginal likelihoods >3 log units; P, tree constrained to polyphyly is significantly better, difference in marginal likelihoods >3 log units; PP, tree constrained to polyphyly is significantly better, difference in marginal likelihoods >5 log units; PPP, tree constrained to polyphyly is significantly better, difference in marginal likelihoods >30 log units; n.s., no significant difference in marginal likelihoods of constrained trees. In ITS analyses, only the clade comprising accessions of B. enderesii and B. convoluta JQ890491 was considered as Streblotrichum.
Fig. 1. Phylogenetic relationships (50% majority consensus tree) from the Bayesian inference of the rps4 dataset. Accessions of Barbula in its earlier circumscription printed in bold. Numbers above branches indicate posterior probability from the BI analysis, followed by bootstrap values of the MP analysis where applicable. Bold branches indicate clades with PP values > 0.95 and bootstrap values > 0.75, dotted lines indicate branches resolved only by the MB analysis.
Fig. 2. Phylogenetic relationships as revealed by the analysis of the concatenated rps4 and trnM-trnV datasets. For further explanation see Fig. 1.
Fig. 3. Phylogenetic relationships based on ITS. For further explanation see Fig. 1.
Barbula amplexifolia clade. — Barbula amplexifolia accessions are highly variable. Identical ITS, rps4 and trnM-trnV haplotypes were obtained only from European samples, while all Asian and North American accessions are unique. One accession (Long 18818) is so distant from other accessions that it does not appear in the B. amplexifolia clade in any of the analyses. It probably belongs to a different species, although it still matches the described morphological variability of B. amplexifolia. Barbula crocea, never before assigned to sect. Hydrogonium, appears nested within the B. amplexifolia clade in the analysis of the combined chloroplast dataset, yet its position in the ITS analysis suggests a poorly supported sister relationship to the rest of Hydrogonium excluding B. amplexifolia.

Barbula gregaria and B. cruegeri. — All inferences agree in their confirmation of no close relationship of specimens identified as B. gregaria and their putative synonyms (B. indica var. gregaria, B. cruegeri, B. horrinervis) to B. amplexifolia or B. indica s.str. Surprisingly, these inferences also resolve B. gregaria and B. cruegeri s.str. as separate entities that do not constitute a monophyletic taxon. American B. cruegeri can be morphologically defined by the characters listed below in the taxonomic synopsis, although the differentiation is not always easy. Putatively endemic North American B. convoluta var. gallinula is resolved as sister to the remaining B. gregaria accessions. It differs in two unique transitions in the coding region of rps4 and one substitution and two indels in the rps4-trnS spacer; ITS is somewhat more divergent, differing in several larger indels, but anyway B. convoluta var. gallinula forms a well-supported monophyletic group with the rest of B. gregaria except for the above-named specimen Eckel 188986.

Barbula subcomosa. — Two accessions of plants originally identified as B. consanguinea appeared in a well-supported clade separate from a clade containing other accessions of that taxon. That clade appears in a poorly supported lineage as sister to B. javanica (ITS dataset), resp. sister to a poorly supported clade of B. javanica+B. bolleana+B. cf. pseudoehrenbergii+B. indica+B. consanguinea s.l. (cp dataset). Subsequent morphological reconsideration and study of the type of B. subcomosa (see Synopsis) indicated the highly probable identity of this lineage with B. subcomosa, that has been to date regarded as synonymous with B. consanguinea.

Barbula bolleana clade. — This clade, sister to B. indica+B. consanguinea s.l., includes B. bolleana and another taxon, which consists of several accessions originally named B. consanguinea, B. javanica or B. tenuirostris, which are morphologically uniform and different from all other taxa included. This taxon may be identical to B. pseudoehrenbergii (see Taxonomic synopsis for details).

Barbula indica+B. consanguinea clade. — All Indian and the Omani sample of B. indica share identical sequences in the chloroplast regions, and the rps4 sequences are also identical with the morphologically unusual Mauritanian samples deposited in GenBank, studied earlier by Werner & al. (2003). One sample of morphologically divergent B. cf. indica from Australia (Streimann 39344) differs by three substitutions in rps4, and similarly its ITS shows multiple substitutions and indels compared to the otherwise nearly invariable B. indica. The ITS and chloroplast inferences differ mainly in the position of the Omani sample (Rothfels 2763), identified as B. indica, which in the ITS dataset is more closely related to the accessions of B. consanguinea. The possibility of a hybrid origin of Rothfels 2763 between B. indica and B. consanguinea would have some support from its intermediate morphology. The tropical accessions of B. consanguinea from SW Asia are identical in their chloroplast sequences but slightly diverge in their ITS, hence the pattern seen in the ITS tree, in which B. consanguinea sample Long 28197 clusters with North American samples of B. cancellata and European and Asian samples of B. indica var. kurilensis. The type of B. indica var. kurilensis is identical with the European plants named earlier B. indica (re-interpreted as B. consanguinea by Köckinger & al., 2012), and differs only by one substitution in the trnM-trnV spacer from North/Central American B. cancellata, and in four, respectively three substitutions in their chloroplast loci from B. consanguinea s.str. The phylogenetic signal of ITS is similar to the signal of the chloroplast regions in this clade. The three accessions of B. indica var. kurilensis are identical except for one microsatellite repetition in one of the samples. The two samples of the North American B. cancellata diverge from each other in three microsatellite motifs, and both differ from B. indica var. kurilensis in two homopolymer segments. The two B. consanguinea s.str. accessions show greater genetic divergence particularly in their ITS2 region.

### Discussion

Our results confirm that all earlier delimitations of Barbula not only do not meet the criterion of monophyly with respect to the analyzed sequence data, but show that Barbula is so clearly polyphyletic that several genera need to be re-established or newly recognized. Barbula, with more than 200 species accepted by Zander (1993, 2007) the largest genus of Pottiaceae, must be substantially restricted. In addition to monotypic Hyophiladelphus, which has already been removed from Barbula by Zander (1995), the species attributed to sections Convolutae and Hydrogonium as circumscribed by Zander (1993) must further be removed from the genus. The new delimitation of the genus Barbula within Pottioidae requires further investigation, because Barbula s.str. was not representatively sampled in this study. Especially Southern...
Hemisphere taxa seem to be of special importance for the future delimitation of *Barbula* s.str. Also the exact placement of *B. orizabensis* will be interesting, because a sister-group relationship of *B. unguiculata* and *B. orizabensis* was suggested only by the ITS data (without bootstrap support; constraining the chloroplast data to monophyly was significantly worse than the tree found). Morphology nevertheless strongly supports that the latter two taxa are congeneric as recognized by earlier authors (Thériot, 1931; Zander, 1979). Shared characters of the two species include the relatively long stems with even foliage, lowermost leaves nearly identical to the uppermost ones, leaf costa excurrent in stout muro, lingulate leaf apex, strongly recurved leaf margins, multiple simple conical papillae on lamina cells in the transition zone between the upper pluripapillose cells with c-shaped or composite papillae and smooth basal cells, dorsal superficial cells of the costa pluripapillose with simple conical and evenly distributed papillae, perichaetial leaves little differentiated, seta orange-reddish to reddish brown, long-cylindric capsule with long, sinistrorsely twisted peristome, spores to 15 μm, and axillary gemmae (sub-globose, brownish, pluricellular and spontaneously developed in *B. orizabensis*, but unicellular, and known only from cultivation in *B. unguiculata*; Zander, 1979).

*Barbula* sect. *Convolutae* needs to be recognized as a separate genus, i.e., *Streblotrichum*, although in a delimitation which partly differs from historical understanding (after *B. bicolor*, *B. crocea*, *B. hiroshii*, *B. convoluta* var. *gallinula* are removed, see Synopsis). This delimitation of *Streblotrichum* has strong support in our molecular analyses (see Results) and represents a morphologically clear-cut entity (see Synopsis) although the diversification of ITS sequences makes the genus biphyletic. The apparent non-monophyly might well reflect the problems of homology within ITS due to the low level of sequence similarity rather than really challenging the monophyly of *Streblotrichum* (similar to the case of the *Leptodontium + Triquetrella* clade, which also belongs to Pottioidae according to chloroplast data), but needs to be addressed in future studies. ITS sequences of both *Streblotrichum* clades are probably functional nrDNA molecules. Both sequence types have a conserved 5.8S gene, and no differences in free energy of RNA secondary structure nor in CG content were observed (data not shown). Nevertheless, the intrafamilial position of *Streblotrichum* could not yet be ascertained due to low support for any of the placements described above.

*Barbula bicolor* always constituted a morphologically odd element in the earlier delimitation of *Streblotrichum*, as already acknowledged by Brotherus (1902: 410), and it does not even fit the broad global description of *Barbula* s.l. by Zander (1993: 146) considering its large spores and absent peristome. As the molecular relationships based on the analysis of chloroplast regions do not support the monophyly of *Streblotrichum* s.str. + *B. bicolor*, and the results of the ITS analysis are weakly supported, the species is best accommodated in a genus of its own that is newly described below as *Gymnobarbula*.

The re-established genus *Hydrogonium* becomes one of the phylogenetically best-supported genera of Pottiaceae (Figs. 1–3). Historically, the acceptance and delimitation of *Hydrogonium* in the treatments that followed Chen (1941) varied substantially, with the majority of opinions tending towards sectional or no infrageneric rank within *Barbula*, with the notable exception of Li & al. (2001), who accepted the genus. Interestingly, they attributed *B. subcomosa* and the little known *B. dixoniana* (P.C. Chen) Redd. & B.C. Tan to *Barbula*, although they basically adopted Chen’s delimitation of *Hydrogonium*, judging from the descriptions and key characters provided. Similarly, it is not obvious why Saito (1975), along with earlier treatments, classified *B. subcomosa* within sect. *Hydrogonium* but *B. amplexifolia* (as *B. coreensis*) and *B. gregaria* (as *B. harrinervis* K. Saito) were left in sect. *Barbula*. Our molecular results are consistent with Zander’s perhaps surprising view (Zander, 1993) that the hygrophilous taxa, such as *B. bolleana*, are species with a morphology derived from xerophilous species, such as *B. indica*, and hence that their unusual morphology may reflect adaptations to a special habitat. Earlier delimitations of *Hydrogonium* always strived to look for morphological characters that were such derived adaptations, a view that was unintentionally but strongly supported by the name of the genus itself. One of the obvious differences of our treatment from Zander’s delimitation is the transfer of subg. *Odontophyllum* from the synonymy of *Streblotrichum* to the synonymy of *Hydrogonium*. The type of *Odontophyllum*, *Barbula hiroshii*, described by Saito (Saito, 1975: 499) is morphologically very similar to *B. crocea*, which was traditionally accommodated in *Streblotrichum* (Limpriht, 1890; Loecke, 1909) despite the fact that it substantially differs from other members of the genus in its perichaetial leaves (much less differentiated), colour of seta (red versus yellow in *Streblotrichum*), or anatomy of annulus (non-revoluble in *B. crocea*). These characters, which are common to *B. crocea* and *B. hiroshii*, are clearly all diagnostic characters of *Hydrogonium* and the two species are thus combined in *Streblotrichum* (Limpriht, 1890; Loecke, 1909) and will probably be refined by future revisionary studies (see below in Synopsis), the molecular relationships of *B. cruegeri*...
and *B. subcomosa* support the recognition of these taxa at the specific level. The nested position of the *B. gregaria* specimen Eckel 188986 in the nrITS dataset (within *B. cruegeri*) points towards possible hybridization or shared ancestral polymorphism of the two taxa. On the other hand, the morphological similarity of *B. convoluta* var. *gallinula* to *B. gregaria* and its sister relationship to all (cp dataset) or all but one (ITS dataset) *B. gregaria* accessions favour its recognition at the infraspecific level within *B. gregaria*, which itself is proposed to be combined under *Hydrogonium* below. Similarly, *B. indica* var. *kurilensis* and *B. cancellata*, which seem to be molecularly uniform but slightly distinct, yet closely related to the more variable *B. consanguinea* s.str., might be best recognized as infraspecific taxa of *B. consanguinea*. In all three latter cases (*B. convoluta* var. *gallinula*, *B. indica* var. *kurilensis*, *B. cancellata*), we formally propose the status of variety as most appropriate below.

The extent of polyphyly in *Barbula* sensu Zander (1993) has no known parallel in Pottiaceae and in fact has very few parallels among other bryophytes and embryophytes. Even in the largest angiosperm genera, which proved to be polyphyletic following recent molecular studies, such as *Astragalus* L. (Wojciechowski, 2005), *Euphorbia* L. (Horn & al., 2012), or *Senecio* L. (Pelser & al., 2007), and which outnumber the estimated species count in ex-*Barbula* by one order, the species removed from the core genus remained interspersed among taxa of the same tribe or subtribe. Generally speaking, polyphyly is perhaps largely confined to taxa with specialized morphology and a reduced number of easily observable characters. This may be less common in higher plants but commonly has been documented, e.g., in algae and lichens (Gaya & al., 2008; Draisma & al., 2010). In mosses polyphyly has best been documented for several lineages of pleurocarpous mosses at both generic and familial levels (Gardiner & al., 2005; Ignatov & al., 2007; Olsson & al., 2009). The situation in liverworts is generally less well known but a polyphyletic origin was demonstrated in only a few of the recently analyzed large genera, e.g., *Jungermannia* (Hentschel & al., 2007) or *Lophozia* (De Roo & al., 2007). The polyphyly in hypnalean moss lineages could be expected considering their rapid radiation concomitant with the evolution of angiosperm-dominated tropical forests in the Tertiary (Shaw & al., 2003; Pedersen & Newton, 2007). In case of the above-named liverwort genera, the broad circumscriptions were based on the lack of unequivocally differentiating morphological characters of the groups after their revision on a world-wide level (Váňa, 1973; Schuster, 2002). Pottiaceae have been monographed relatively recently and thoroughly (Zander, 1993) with great emphasis placed on the formalized cladistic phylogenetic analysis of morphological and anatomical characters. While some of the large genera seem to have withstood the test of phylogenetic relationships using DNA sequence data (*Didymodon*, Werner & al., 2005a), and most others show some level of paraphyly but do not include accessions now found in other subfamilies (*Tortula* Hedw., Werner & al., 2002; Košnar & al., 2012; *Weissia* Hedw. and *Tortella* (Lindb.) Limpr., Werner & al., 2005b), the level of polyphyly in the modern definition of *Barbula* is unique. It implies that homoplasic morphological and anatomical characters cannot be easily recognized without the help of molecular data.

**TAXONOMIC AND NOMENCLATURAL SYNOPSIS**

The synopsis applies to the taxa occurring in the Holarctic, Indomalayan, and northern part of Neotropical ecozones.

**Gymnobarbula** Jan Kučera, gen. nov. – Type: *G. bicolor*.

Closely resembling *Streblotrichum* P. Beauv. but differing in the rudimentary peristome, reddish seta, persistent annulus, large spores (> 20 μm), absence of rhizoidal gemmae, rusty brown coloured cells of the leaf base, and the little differentiated anatomy of the weak, flat leaf costa, consisting only of a row of guide cells and 1–2 rows of dorsal stereids in the lower part of leaves.

Lindberg (1863: 386) was the first who used the name *Gymnobarbula*, unfortunately without description and rank designation, i.e., having created a nomen nudum, to accommodate this morphologically odd species of *Barbula*. He noted its similarity to "*B. convolutae*, i.e., *Streblotrichum*, and particularly to *B. crocea*. The name *Gymnobarbula* also appeared in a different context as a generic nomen nudum in C. Müller’s *Genera Muscorum Frondosorum* (Müller, 1901: 456), and two specific nomina nuda, ascribed to Schimper, were listed in that genus in the same publication (*G. weddelli*, *G. subulirostris*). However, there is no other known mention of these taxa in the literature.

According to our present knowledge the genus is monotypic and its description is thus identical with the description of *Gymnobarbula bicolor* (see e.g., Bruch & Schimper, 1846: 76–77; Limpricht, 1890: 626–627).

**Gymnobarbula bicolor** (Bruch & Schimp.) Jan Kučera, comb. nov. = *Gymnostomum bicolor* Bruch & Schimp. in Bruch & al., Bryol. Europ. 1: 76, pl. 29 (fasc. 33–36. Mon. 4. pl. 1). 1846 – Type: In terra calcarea m. Radstädter Tauern Alp. Salisburgiae (Funk) et in Alpibus Julicis (Sendtner).

This is a relatively rare species, only known from the European Alps (Switzerland, Italy, Austria, Germany). The virtually absent peristome, unusually large spores, and the rusty brown cells of the leaf base are characters which are probably unknown in any other member of *Barbula* s.l., at least among the well-known taxa. In addition to the diagnostic characters of *Gymnobarbula*, *Barbula crocea* differs by the presence of axillar gemmae, much larger size, longer yellowish basal leaf cells, and hardly differentiated perichaetial leaves. The species of *Streblotrichum* differ in their yellow seta, well-developed twisted peristome, separating annulus and much smaller spores (to ca. 12 μm). In contrast to most members of tribe Hyophylleeae, to which *Gymnobarbula* might belong phylogenetically, the leaf cells of *Gymnobarbula* are not unilaterally and ventrally bulging, and are covered by dense, multiple, massive warty papillae reminding of *Anoeclatium* Schwägr. or *Molendoa* Lindb.

**Streblotrichum** P. Beauv. in Mag. Encycl. 5: 317. 1804 = *Barbula* subg. *Streblotrichum* (P. Beauv.) K. Saito in J. Hattori Bot. Lab. 39: 499. 1975 = *Barbula* sect. *Streblotrichum*
Kučera & al. • Hydrogonium, Streblotrichum, and Gymnobarbula gen. nov.

(1842) = Barbula sect. Convolutae (De Not.) Bruch & Schimp. in Bruch & al., Bryol. Europ. 2: 91 (fasc. 13–15. Mon. 29).

Barbula crocea (Mitt.) A. Jaeger, type of Barbula convoluta (Hedw.) Dick. ex With., Syst. Arr. Brit. Pl., ed. 4, 3: 799. 1801 = Tortula convoluta (Hedw.) P. Gaertn. & al., Oekon. Fl. Wetterau 3(2): 92. 1802.

= Barbula sect. Convolutae (De Not.) Bruch & Schimp. in Bruch & al., Bryol. Europ. 2: 91.

Streblotrichum (on generic, subgeneric or sectional rank) has traditionally been recognized to include Barbula s.l. species with strongly differentiated convolute perichaetal leaves, and an annulus of differentiated, vesiculose cells, which agrees well with the characters of S. convolutum, S. commutatum, S. enderesii and S. bicolor (Bruch & Schimp.) Loeske. After S. bicolor is moved to Gymnobarbula, as discussed above, the first three taxa are more or less characterized by the yellow seta, revolute annulus, and the formation of brown, spherical, rhizoidal gemmae, and these characters can be added to the revised delimitation of Streblotrichum. Barbula crocea was also traditionally assigned to Streblotrichum, but its molecular relationships, as well as the less markedly differentiated perichaetal leaves, red seta, non-revolute annulus, absence of rhizoidal gemmae and presence of axillary gemmae support its inclusion in Hydrogonium. The same applies to B. convoluta var. gallinula R.H. Zander (see below). Whether B. convoluta var. eustegia (Cardot & Thér.) R.H. Zander, which is also reported to have perichaetal leaves less markedly differentiated, is to be retained in or to be removed from Streblotrichum needs to be ascertained. Its automatic combination to Streblotrichum is to be avoided, having in mind the case of B. convoluta var. gallinula. Whether Barbula calycina (Mitt.) A. Jaeger, type of Barbula sect. Leptopogon (Mitt.) Lindb., and regarded as synonymous with Streblotrichum by Zander (1993), belongs here, also needs to be ascertained. Among the austral taxa, B. calycina Schwägr. and B. microcalycina Magill have been reported to have markedly convolute, differentiated perichaetal leaves (Magill, 1981), but other diacritical characters as identified by the analysis of the northern taxa are lacking except for the yellow seta in the latter species, and hence molecular data are necessary to resolve their affinities. As judged from illustrations, the putatively endemic Chinese Streblotrichum propaguliferum X.J. Li & M.X. Zhang seems to belong to Dichodontium Schimp., as it has no diagnostic characters of Streblotrichum. The genus Streblotrichum was synonymized with Barbula sect. Convolutae (1842) at the sectional level (Zander 1993). This is correct (Barbula sect. Streblotrichum is a later combination) except for the author citation, which should read (De Not.) Bruch & Schimp., as the basionym of the epithet is Tortula sect. Convolutae De Not. (1838), not vice versa, as stated in Index Muscorum.

Accepted species studied: Streblotrichum convolutum (Hedw.) P. Beauv., S. commutatum (Jur.) Hilp., S. enderesii (Garov.) Loeske.

Hydrogonium (Müll. Hal.) A. Jaeger in Ber. Thätigt. St. Gal. lischen Naturwiss. Ges. 1877–78: 405 (Ad. 2: 669). 1880 = Trichostomum [unranked] Hydrogonium Müll. Hal. in Linnaea 40: 297. 1876 = Barbula subg. Hydrogonium (Müll. Hal.) M. Fleisch. in Musc. Buitenzorg 1: 352. 1904 ≡ B. sect. Hydrogonium (Müll. Hal.) K. Saito in J. Hattori Bot. Lab. 39: 492. 1975 ≡ Didymodon subg. Hydrogonium (Müll. Hal.) Kindb., Eur. N. Amer. Bryin. 2: 273. 1897 – Type (designated by Saito, 1975: 492): H. ehrenbergii (Lorentz) A. Jaeger in Ber. Thätigt. St. Gallischen Naturwiss. Ges. 1877–78: 405 = Trichostomum ehrenbergii Lorentz in Abh. Königl. Akad. Wiss. Berlin 1867: 25, t. 4 f. 1–6, t. 5 f. 7–19. 1868 = Hydrogonium bolleanum (Müll. Hal.) A. Jaeger fide Frahm & al. in Trop. Bryol. 12: 123–154. 1996.

= Semibarbula Herzog ex Hilp. in Beih. Bot. Centralbl., Abt. 2, 50(2): 626. 1933 – Type: S. indica (Hook.) Herzog ex Hilp. in Beih. Bot. Centralbl., Abt. 2, 50(2): 626. 1933.

= Barbula subg. Odontophyllon K. Saito in J. Hattori Bot. Lab. 39: 499. 1975 (‘Odontophylla’), syn. nov. – Type: B. hiroshi K. Saito in J. Hattori Bot. Lab. 39: 499. 1975.

Hydrogonium is distinguished from Barbula primarily by the nearly constant presence of axillary gemmae even in natural conditions, which differ in shape from the gemmae of Barbula in being mostly markedly elongate, seriate, ellipsoid, clavate to fusiform or concinate, green, light brownish-green to red-dish brown, as opposed to spherical, unicellular to pluricellular, irregularly subsphaerical non-seriate brownish gemmae with protuberant cells of Barbula and no axillary gemmae in other segregate genera (except for the rhizoidal gemmae of Streblotrichum). The indistinct ornamentation of the cell surface together with the loose areolation of relatively large cells and the generally flaccid habit of plants holds true only for a minor part of derived Hydrogonium species, which occur in markedly wet habitats, and the non-hygrophytic species such as H. orientale may show remarkable phenotypic plasticity, acquiring the “typical” Hydrogonium characters when growing in humid places, as excellently demonstrated by Werner & al. (2003). Perichaetal leaves of Hydrogonium are slightly differentiated, mostly smaller than the vegetative leaves, and subsheathing. The peristeum is typically well-developed, composed of 32 long, sinistrorsely twisted filiform prongs, but shows a progressive reduction via shorter anastomosing teeth, as typically developed in the North American ‘Barbula cancellata’ (see below), to the short, more or less erect, fagacious teeth of H. orientale. We revised in detail the taxa related or believed to be related to Hydrogonium orientale and H. consanguineum, which form the larger part of Hydrogonium taxa. Several tropical taxa, known from the very limited number of historical observations, need to be addressed in the future, including taxa that have earlier not been assigned to Hydrogonium, such as Barbula pachyloma Broth., B. calodictyon Broth., B. sumatranana Baumg. & Dixon or B. robbinsii Bartr. However, we believe that we have addressed a significant proportion of the existing diversity of the genus.

Species addressed in this treatment, for which nomenclatural changes are proposed or taxonomic understanding was re-considered:
1. *Hydrogonium angustifolium* (Hook. & Grev.) Jan Kučera, *comb. nov.* = *Tortula angustifolia* Hook. & Grev. in Edinburgh J. Sci. 1: 298, t. 12. 1824 = *Barbula angustifolia* (Hook. & Grev.) Müll. Hal., Syn. Musc. Frond. 1: 603. 1849, non Brid. 1826 = *B. tenuirostris* Brid., Bryol. Univ. 1: 826. 1827 – **Lectotype (designated here):** Nepal, *Wallich* (E! [E00049216]).

**Typification notes.** – The herbarium material of *Tortula angustifolia* found in BM and E is extremely sparse. In BM, there are two envelopes bearing this name. One of them (BM000867496) has the seal “Herbarium Hookerianum 1867” and was annotated by Wilson (initial W) as “Tortula angustifolia Hook. [from Harvey’s own specimen], closely allied to *T. flavescens*. Nepal, Wallich”. It contains two fragments of one plant with seta but without capsule. The other type specimen at BM contains a heavy paper sheet with four miniature glued capsules. The upper two capsules (BM000867497) are annotated by Wilson in a similar manner as BM000867496 as “*Tortula angustifolia* Hook. Nepal. *Wallich* [from Harvey’s own specimen]”, and are accompanied by sketches of the plant habit, several leaves, capsule and the peristome, re-drawn after Hooker. The capsules include fragments of one plant. The lower two capsules (BM000867498) contain two and one shoot, respectively, of the type collection of *Tortula flavescens*, and both types were compared and annotated by Wilson. It appears that Wilson realized that the two types are very similar and planned to unite them under the name *Tortula crenulata* (reference to a manuscript from June 1857). His annotation under *Tortula angustifolia* reads: “differs from *T. flavescens*—see below—in the more opaque texture of leaves, which are more lax when dry; differs also in areolation, somewhat bordered with larger cells, crenate, nerve more pellucid … [illegible]”. The Greville herbarium at E contains two specimens annotated as type specimens. One (E00049216) includes a small heavy paper sheet with four glued plants (one of them with sporophyte, although deoperculated and with lost peristome) annotated as “*Tortula angustifolia* H. & Gr. Nepal. Dr. Wallich”; this seems to be a part of the original collection. The other specimen (E00049217) contains two glued tufts of *Hydrogonium javanicum* (!) but is annotated by Wilson (June 1850) as “*Tortula tenuirostris* Hook. & Grev./Greville/Tortula angustifolia Hook. & Greville”. The original Wallich collection from Nepal was obviously separated into several duplicates but the time of origin of the duplicates is unknown. Wilson’s annotations on the authenticity of the duplicates housed at BM referring to W.H. Harvey are not quite relevant with respect to the authenticity of Hooker’s material, as Harvey (b. 1811) must have acquired the material from Hooker not earlier than after 1834, when they met in Glasgow (Long, 1995). Hence, Greville’s duplicate from his own herbarium (E00049216) housed now at E is more suitable as type and is selected as lectotype here; moreover the specimen contains more material. The status of the two specimens from BM as islectotypes would be inappropriate, as they hardly originated as duplicates of the Greville specimen.

With respect to the taxonomic identity of *Hydrogonium angustifolium*, the type specimens include large-leaved plants (up to 2.8 mm long), flaccid and crisped when dry, which are superficially very similar to the types of *Tortula flavescens* Hook. & Grev. (= *Hydrogonium consanguineum*, see below). However, no gemmae were seen among the leaves and, more importantly, the cross-section of leaves shows distinctly bistratose to polystratose margins, which are nevertheless not distinct under the microscope under incident light, so that this character could easily have been overlooked. Among similar species, bi- or polystratose leaf margins have otherwise only been described for the New Guinean *Barbula pachylooma* Broth. (cf. Norris & Koponen, 1989; Eddy, 1990). The eventual identity of the two taxa needs to be studied. Anyway, the name *Hydrogonium angustifolium* (= *Barbula tenuirostris*) is thus not applicable to any taxon of the *H. orientale* complex and the synonymy proposed by Sollman (2004a, b) has to be suspended until more material can be studied, ideally using molecular tools; our attribution to *Hydrogonium* is based solely on its morphological similarity to other species of the genus from the region and may even prove erroneous in the future. *Hydrogonium angustifolium* s.str. has not been known from other than the type collections until the treatment of Sollman (2004a, 2004b), although already Chen (1941), who could not study the original material, speculated about its identity with *H. consanguineum*. Anyway, our revision of the material at E and BM has not revealed any additional specimens of *H. angustifolium*.

2. *Hydrogonium consanguineum* (Thwaites & Mitt.) Hilp. in Beih. Bot. Centralbl., Abt. 2, 50(2): 626. 1933 = *Tortula consanguinea* Thwaites & Mitt. in J. Linn. Soc., Bot. 13: 300. 1873 (prior to Oct. 9) = *Barbula consanguinea* (Thwaites & Mitt.) A. Jaeger in Ber. Thät.g. St. Gallischen Naturwiss. Ges. 1877–78: 409. 1880 – **Lectotype (designated here):** “Ins. Ceylon, ad terram, Dr. Thwaites.” (BM! [BM0001006686]).

Two varieties are recognized here:

2a. *Hydrogonium consanguineum* var. *consanguineum* = *Barbula flavicans* D.G. Long in J. Bryol. 18: 356. 1994 = *Tortula flavescens* Hook. & Grev. in Edinburgh J. Sci. 1: 297, pl. 12. 1824, non (Dicks. ex With.) P. Beauv. 1805 – **Lectotype (designated here):** “On a clayey soil. Nepal; Dr. *Wallich*” (E! [E00108463]; islectotypes: E! [E00208466, E00208467, E00246543, E00108465], BM! [BM000671526, BM000671529, BM001031296, BM000671527, BM000867498]).

**Typification notes for *Tortula consanguinea* Thwaites & Mitt. – JK was able to study the material from both NY and BM, and the additional isotype from E. The reason for all earlier confusion was the fact that the type material, consisting of many duplicates of the original collection (Thwaites 67 from Ceylon), contains a mixture of species. The two major elements of the mixture are *H. consanguineum* and *H. javanicum*, two relatively closely related and macroscopically very similar species. While the duplicates from BM contain both species either in pure tufts or mixed in quantitatively comparable proportions, the isotype at NY (NY371655) contains only *H. javanicum*
(two other packets glued on the sheet with this isotype do not have any writing on them and contain a mixture of Bryum sp. and Hydrogonium cf. pseudoehrenbergii, elements unknown from any other duplicate of Thwaites 67, and hence probably not part of the original collection), and the isotype at E contains only H. consanguineum. The sheet with the isotype of H. consanguineum from NY contains a label “Holotype of Tortula consanguinea Thw. & Mitt.≡ Hydrogonium consanguineum (Thw. & Mitt.) Hilp.”, and this confused earlier authors, particularly Sollman (2000b). This designation obviously cannot be attributed to Mitten (Hilpert’s combination dates to 1933), and must not be followed. In case of heterogeneous type material, it is important to identify which taxon was intended for the description by the author(s). The description (Mitten, 1873) unfortunately does not specifically mention the most important diacritical characters between H. consanguineum and H. javanicum as we understand them, but mentions the percurrent, dorsally scabrous costa, a condition which can rarely occur in H. javanicum (the nerve in this species mostly ends below the apex and the back of the costa is lowly papillose) but is typical for H. consanguineum, particularly under lower magnification and in optically inferior devices that scientists used at that time. It thus seems safe to typify the name H. consanguineum with the element from Thwaites’ herbarium at BM that does not belong to H. javanicum, and this is best accomplished by the homogeneous material of BM001006686. Sayre (1977) moreover identified the major part of Thwaites’ herbarium to be housed at BM. Consequently, duplicates of the original collection that contain only the admixed species H. javanicum (specimens BM000867492 and NY371655) are excluded from consideration as type material.

• Typification notes for Barbula flavicans D.G. Long.
  At least five duplicates of Wallich’s original collection of Tortula flavescens are housed at E (E00108463 containing a coloured, unsigned sketch; E00108464 annotated by Wilson in 1852; E00208466 and E00208467 [Menzies Herbarium]; and E00246543 [Arnott Herbarium]; another possible duplicate [E00108465 annotated as Tortula flavescens Nepaul—probably by Wallich himself] was bequested to E from Herb. Wight). At BM, four possible duplicates of the original Wallich collection are housed—two of them bearing the “Herbarium Hookerianum 1867” stamp and number “H.1653” (BM671526, 671529), another specimen (BM1031296) is annotated as “H.1653 dupl.”, and specimen BM671527 was labelled by “Arnott 18252, with another, differently written property designation “Hb. Benth.”—perhaps bequeathed to Bentham by Arnott. The lectotype was chosen from the Greville material at E (E00108463), which is annotated as “Nepal: Dr. Wallich to Hook.” The rest of the type material, which looks convincingly like duplicates of the original collection, is designated here as islectotypes.

Hydrogonium consanguineum was described from Sri Lanka (Ceylon) by Mitten (1873) and has been consistently in use for the taxon’s occurrences in Sri Lanka, Singapore and Java (Fleischer, 1904), Vietnam and the Philippines (Chen, 1941), and generally Malesia (Eddy, 1990), while in the Himalayas (Nepal, Bhutan) the taxon was known as Barbula flavicans, described from Nepal (Gangulee, 1972; Long, 1994). The occurrences in Japan, Taiwan and China (Chen, 1941; Saito, 1975; Li & al., 2001) have been named B. subcomosa, Hydrogonium sordidum or otherwise, although the synonymy is either dubious or wrong (see below). The above-described problems with the heterogeneous type material led to the synonymy with H. javanicum, first proposed by Saito (1975: 495–496), and followed by most later authors, including Zander (1993) and Sollman (2000b), who studied the same type material at NY. A different opinion was recently only expressed by Eddy (1990), who studied other parts of type material from BM (see above) that included H. consanguineum as understood by earlier authors, e.g., Fleischer (1904), i.e., differing from H. javanicum in the densely papillose upper lamina cells, not bulging ventrally, and strongly papillose dorsal surface of the leaf costa. The species was first described under the name Tortula flavescens in 1824, but unfortunately this name was already in use at the time of description, and even the later common usage of the replacement name Barbula fuscescens of 1849 was invalid, and hence Barbula flavicans was newly proposed for the taxon by Long (1994), who at that time did not know about the identity with H. consanguineum. According to Art. 11.4 of ICN, Tortula consanguinea Thwaites & Mitt. and combinations based on this basionym have nomenclatural priority over Barbula flavicans, first validly used in 1994. Sollman (2000b) contributed to the nomenclatural confusion, having agreed with Saito on the interpretation of the type of H. consanguineum as being identical with H. javanicum but at the same time having kept the earlier usage of H. consanguineum (spelled as Barbula consanguinea sensu Eddy). Such a treatment would have required a previous conservation of the name. The confusion has grown even bigger after Sollman (2004a) realized that ‘B. consanguinea sensu Eddy’ is taxonomically identical with Barbula flavicans but unfortunately did not realize the consequences of Art. 11.4 of ICN, and incorrectly synonymized the taxa under B. flavicans. Later he nevertheless probably realized his error, having published another (Sollman, 2004b), nearly identical article in the same volume of the journal (without any explanation of the previous nomenclatural somersaults), where the taxa, including ‘B. consanguinea sensu Eddy’ were synonymized under the valid and legitimate name B. tenuirostris, which was correct from the nomenclatural point of view but contradicts our taxonomic findings described below in the paragraph on Hydrogonium angustifolium. Among the taxa, proposed as synonyms of H. consanguineum by Sollman (2004b), no taxon except for H. angustifolium endangers its priority. However the types of Barbula gracilenta Mitt. (1859) and B. gangetica Müll. Hal. (1872), not considered by Sollman and accepted as good species by Li & al. (2001), need to be checked, although the descriptions and illustrations do not raise the suspicion of obvious identity.

2b. Hydrogonium consanguineum var. cancellatum (Müll. Hal.) Jan Kučera, comb. & stat. nov.≡ Barbula cancellata Müll. Hal. in Flora 56: 483. 1 Nov 1873 – Type: “Texas, Dallas Co., J. Boll cum Aongstroemia varia associatam legit 1870”.
North and Central American plants of *H. consanguineum* s.l. (a name never used in North America) were traditionally named *B. cruegeri*, with the type from Texas (Steere, 1938), *B. pringlei* Cardot and *B. hypselostegia* Cardot, with types from Mexico (Bartram, 1949), and *B. cancellata*, with a type from Texas (Crum & al., 1973). Zander (1979) synonymized all of these and some other types (including *B. gregaria* treated below) under *Barbula indica*, within which he later (Zander, 2007) recognized two varieties: *var. indica* with small gemmae and recurved margins, and *var. gregaria* with large gemmae and plane margins. Zander (1979) cited the observation of Crum that the taxon with small gemmae occurring predominantly in North America north of Mexico matches the type of *Barbula cancellata*. It can be inferred that this taxon has later (Zander, 2007) been identified as *B. indica var. indica*. According to the descriptions, *B. pringlei* and *B. hypselostegia* are likely identical with *B. cancellata*, although the types have not been examined by us.

Plants morphologically matching *B. cancellata* were shown above to be nested within *H. consanguineum*. In addition to the molecular differences described above, *B. cancellata* differs from *H. consanguineum* s.str. in the irregularly anastomosing rami of the peristome teeth, relatively broad, ovate-cuspidate leaves with a broadly cuspidate to lingulate leaf apex, reminding of the leaf shape of *B. gregaria*, and the dorsal superficial cells of the costa being mostly shortly rectangular to subquadrate, commonly chlorophylllose, and densely papillose with papillae not markedly associated to the cell ends. Nevertheless, the morphological differences are not always clear-cut and the molecular divergence is low, which seems to be most adequately evaluated by distingushing *B. cancellata* at the varietal level within *H. consanguineum*. The taxonomic synonymy (at the species level) of *Tortula consanguinea* with *B. cancellata* called for investigation of the dates of publication of both taxa, because both species names were published in 1873. *Barbula cancellata* was published in *Flora* (Müller, 1873), issued in clearly dated fascicles; this article was the first in No. 31 in November 1873. Dating of the description of *T. consanguinea* in Vol. 13 (1873) of the *Journal of the Linnean Society, Botany*, is more complicated, as the precise dates of publication of individual issues have not been printed. Fortunately, starting with the next volume of the journal (Vol. 14, 1875), the journal introduced the practice of printing the publication dates after completion of the volume, so that we know that No. 1 of Vol. 14 was published on 9 October 1873, which is one month earlier than the publication date for *B. cancellata*. This constitutes a good argument for considering the name *Tortula consanguinea* as having the priority over *Barbula cancellata*.

*Hydrogonium consanguineum* var. *cancellatum* is distributed mainly in the southwestern United States and the neighbouring part of Mexico (see Appendix 1 for the studied specimens), but the exact distribution needs to be elucidated as the taxon was not consistently distinguished from related taxa. According to Sollman (2000b), which escaped later attention, *B. consanguinea* occurs in Florida (Allen 7541, MO; Drouet & Nielsen s.n., L) and Hawaii (Hoe 3347, L), which may well be based on specimens of *H. consanguineum* var. *cancellatum*.

2c. *Hydrogonium consanguineum* var. *kurilense* (Ignatova & Ignatov) Jan Kučera, comb. nov. = *Barbula indica* var. *kurilensis* Ignatova & Ignatov in Arctoa 18: 138. 2010 (*2009*). – Holotype: “Russia … Kunashir Island … Ignatov no. 06–1884” (MHA; isotype MHA!).

The type of *Barbula indica* var. *kurilensis*, which has been the only specimen of the taxon known (Ignatova & Ignatov, 2009), was collected on Kunashir Island of the Kurils, today belonging to Russia. Although it was carefully compared to the type of *B. indica*, the possible identity with related Japanese taxa, particularly *B. subcomosa* in the sense of Saito (1975) was not considered, despite the geographical proximity of Japanese occurrences. Molecular affiliations clearly nest *B. indica* var. *kurilensis* within *H. consanguineum* s.str., along with the very slightly different *H. consanguineum* var. *cancellatum*. Interestingly, *B. indica* var. *kurilensis* does not seem to be morphologically differentiated from *H. consanguineum* s.str., i.e., *B. subcomosa* sensu Saito, while the differences from var. *cancellatum* can be equated to those between var. *cancellatum* and var. *consanguineum*. All European material (see Appendix 1) is morphologically identical with the Asian type, as are the DNA sequences of recent specimens, despite the considerable geographical distance that is not known to be bridged by any other occurrence in between. The ecology of the Far Eastern and European plants is also virtually identical (cf. Köckinger et al., 2012). The unknown sporophytes might differ from var. *consanguineum* in a similar way to those of var. *cancellatum*.

3. *Hydrogonium croceum* (Brid.) Jan Kučera, comb. nov. = *Tortula crocea* Brid., Muscol. Recent. Suppl. 1: 257. 1806 = *Barbula crocea* (Brid.) F. Weber & D. Mohr, Bot. Taschenbuch: 481. 1807 = *Streblotrichum croceum* (Brid.) Loeske in Hedwigia 49: 30. 1909 – Type: In monte Meissneri Cattorum [Hoher Meißen naer Kassel] Junio 1805 legi … Ex Helvetiæ etiam … = *Barbula paludosa* F. Weber & D. Mohr, Bot. Taschenbuch: 482. 1807, nom. illeg. (ICN Art. 52.2) – Type: Schleicher, Cent. 3 No. 22.

Morphological reasons for inclusion of this species in *Hydrogonium* were discussed above. The taxon is only known from Europe.

4. *Hydrogonium cruegeri* (Sond. ex Müll. Hal.) Jan Kučera, comb. nov. = *Barbula cruegeri* Sond. ex Müll. Hal., Syn. Musc. Frond. 1: 618. 1849 – Type: Insula Trinitatis Antillarum, ad La Ventille, in terra argillosa, Crieger legit Aug. 2, 1846, in muris et rupibus calcareis formam confertorem Nov. 28.

As discussed above under *H. consanguineum* var. *cancellatum*, *Barbula cruegeri* has earlier been believed to represent, together with *B. gregaria*, the taxon of the *Barbula indica* complex from Central to tropical South America with large gemmae. It can be deduced that Zander (2007) synonymized *B. cruegeri* with *B. indica* var. *gregaria*, although the synonymy has never been officially published except for the more inclusive synonymy of *B. indica* and *B. cruegeri*. Indeed, *Hydrogonium cruegeri* is morphologically very similar to *H. gregarium*, and
we realized the differences between the two only after some of the South/Central American plants were resolved in a clade separate from *H. gregarium* in the phylogenetic analysis. *Hydrogonium cruegeri* differs morphologically from *H. gregarium* in its stronger costa, which is more prominent dorsally and more highly papillose (commonly the costa remains even if the surrounding lamina erodes), by the leaf cells on both sides being ampullaceous-mammillose with extremely high papillae (this character has been observed in some specimens of *H. gregarium* as well), and by the leaf margins being mostly narrowly recurved in the proximal 1/3–2/3. The perichaetial leaves are less differentiated and not markedly sheathing basally. Although we have not yet seen the type of *B. cruegeri*, the characters listed above seem to be visible in the type material present at BM (BM000872606–7, scanned for plants.jstor.org), which is the basis of our belief in the identity of this type. We have to admit the possibility of a certain amount of gene flow between *H. cruegeri* and *H. gregarium*, as discussed above.

At present, *H. cruegeri* is believed to be a (sub)tropically distributed taxon in Central America and the northeastern part of South America (see Appendix 1), but more detailed revision work is needed to confirm this hypothesis.

### 5. Hydrogonium gregarium (Mitt.) Jan Kučera, comb. nov. ≡ Tortula gregaria Mitt. in J. Proc. Linn. Soc., Bot., Suppl. 1: 29. 1859 ≡ Barbula gregaria (Mitt.) A. Jaeger in Ber. Thätigk. St. Gallischen Naturwiss. Ges. 1871–72: 424. 1873 ≡ Barbula indica var. gregaria (Mitt.) R.H. Zander in Cryptog. Bryol. Lichénol. 2: 6. 1981 − Syntypes: In Nepaliae orient. reg. temp., J.D. Hooker (no. 166); In Tibetiae reg. temp. T. Thomson (No. 126).

Two varieties are recognized here:

#### 5a. *H. gregarium* var. *gregarium*

= *Barbula horrinervis* K. Saito in J. Hattori Bot. Lab. 39: 486. 1975 − Holotype: Japan, Nippara, *Saito 4936* (TNS).

This is a broadly distributed and in many regions probably quite common taxon from India, Nepal, Bhutan, China and Japan but extends along the Pacific coast of North America far south (see Appendix 1). Saito’s *Barbula horrinervis* (Saito, 1975) is clearly identical with *H. gregarium*, and was distinguished by overemphasizing the importance of leaf shape. Interestingly, while Zander (1979) observed the morphological transitions between *B. indica* and *B. gregaria*, Sollman (2000a) stated that “this is not correct” and that rather *B. gregaria* is “identical with, or very near *Barbula ampelophylla*”. Indeed, according to Sollman’s identification of SW Asian material of *H. gregarium* and *H. ampelophylla* at E, he did not distinguish between the two taxa, although JK could not find a single specimen that would show intermediate characters between the two species (for a more detailed discussion see Köckinger & Kučera, 2007). Li & al. (2001) also did not recognize *H. gregarium* for China, but its synonym *B. horrinervis* is listed in the synonymy of *B. indica*. In our opinion, the differentiation of *H. gregarium* from *H. ampelophylla* is quite straightforward and the problems may only emerge in the differentiation of *H. gregarium* from *H. cruegeri*, as discussed above under the latter taxon.

#### 5b. *Hydrogonium gregarium* var. *gallinulum* (R.H. Zander) Jan Kučera, comb. nov. ≡ Barbula convoluta var. *gallinula* R.H. Zander in Phytologia 44: 195, f. 15–19. 1979 − Holotype: Canada, Northwest Territories, Nahanni Natl. Park, Virginia Falls, *Scuter 22433* (NY).

Morphologically, Zander (1979) differentiates this taxon by the presence of simple papillae on the abaxial surface of the costa as opposed to the prorulae of *H. gregarium*, and by larger leaf cells (9–12 vs. 7–10 μm). The ornamentation of the costa is very variable in *H. gregarium* but we admit that the leaf cells in var. *gallinulum* are extremely large and out of the range observed in other specimens of *H. gregarium*. Moreover, the constantly obtuse leaves with a weak costa that never reaches the apex is also unusual. Hence, the taxon might at the moment most conveniently be considered a variety of *H. gregarium*, as proposed above.

### 6. Hydrogonium hiroshii (K. Saito) Jan Kučera, comb. nov. ≡ Barbula hiroshii K. Saito in J. Hattori Bot. Lab. 39: 499, f. 48: 12–22. 1975 − Holotype: Japan [Honshu], Tokyo, Okutama, Nippara, Ogawi-dani, *Saito 10379* (TNS).

The putatively endemic Japanese *Barbula hiroshii* was described by Saito (1975) as the closest relative of *H. croceum*, and a new subgenus, *Odontophyllon* (“-phyllae”), was established for it, based on the toothed leaf margin, large grape-shaped gametophytes, and differentiated hyalodermis as diacritical characters. However, toothed margins are rather typically present in many *Hydrogonium* species, though never as strongly developed. This combination is being proposed purely for morphological reasons; we have not yet studied any specimens.

### 7. Hydrogonium majusculum (Müll. Hal.) P.C. Chen in Hedwigia 80: 242, t. 46 f. 6–7. 1941 = Barbula majuscula Müll. Hal. in Nuovo Giorn. Bot. Ital., n.s., 5: 182. 1898 − Type: China interior, prov. Shan-si sept., in alveo fluminis Lao-yu-huo prope Shan-gen-ze, Martio 1897 (isotype: Giraldi s.n., BM!).

The taxon was regarded to represent a good species by Li & al. (2001), while it was synonymized with *H. consanguineum* by Sollman (2004a, b). The studied isotype of *Barbula majuscula* is indeed similar to *H. consanguineum* in its general habit and leaf and costa shape, but differs in substantially larger upper lamina cells (10–15 μm). The gametophytes were not observed in the type specimen at BM, although their presence was noted on the revision label by Sollman from 1999. Hence we regard the identity of *H. majusculum* with *H. consanguineum* unwarranted at the moment, but before additional material is studied, a final taxonomic conclusion cannot be drawn.

### 8. *Hydrogonium orientale* (F. Weber) Jan Kučera, comb. nov. ≡ Trichostomum orientale F. Weber in Arch. Syst. Naturgesch. 1(1): 129; t. 4 f. 6. 1804 = *Semibarbula orientalis* (F. Weber) Wijk & Margad. in Taxon 8: 75. 1959 − Type: Ex India orientali misit Rottleri.

= *Barbula indica* (Hook.) Spreng., Nomencl. Bot. 2: 122. 1824

≡ *Tortula indica* Hook., Musci Exot. 2: 135. 1819 ≡ *Semibarbula indica* (Hook.) Herzog ex Hilp. in Beih. Bot. 35
Centralbl., Abt. 2, 50(2): 626. 1933 – Type: In India orientali. Röttler. In murs Botanici Calcuttæ. Gul. Wallich, M.D.

This is the closest relative of *H. consanguineum*, and as discussed above, a certain amount of gene flow between the two cannot be ruled out. However, the pattern of known morphological and molecular variability still allows recognizing both taxa at species level.

9. *Hydrogonium subcomosum* (Broth.) P.C. Chen in Hedwigia 80: 236. 1941 = *Barbula subcomosa* Broth. in Hedwigia 38: 211. 1899 – Holotype: Kanagawa, *Wichura 1400* (H-BR; isotypes: BM!)

The two studied isotypes superficially match *H. consanguineum* except for being slightly more robust (plants to ca. 4 cm high, leaves to about 2.5 mm long). Importantly, no gemmae were observed in the two duplicates present at BM, despite Sollman’s (2004a) explicit reference to this character. However, his revision labels were not present in the herbarium sheet from BM. The gemmae were also not mentioned in the protologue, which is important, as we cannot automatically assume that they were neglected as was commonly the case with older authors. The reason for our belief is that the next species treated in Brotherus (1899) was the equally newly described *Hyophila propagulifera* Broth. with gemmae similar to *H. consanguineum*. Also Chen (1941) did not mention the gemmae despite his careful observation of this character. We can also confirm his observation that the leaf apex of *H. subcomosum* is gradually tapered and the costa is not excurrent, as opposed to the more abruptly narrowed, broader apex in *H. consanguineum* with a mucronate excurrent costa, although this character does not seem to be sufficiently constant in additional material studied of the two taxa. The foliage of *H. subcomosum* is less dense, exposing the stem between the leaves. An identical condition was observed in recent collections of ‘*Barbula consanguinea*’ from Bangladesh and Bhutan, which also differed in their molecular affinities as described above. Hence we refer to these plants as *H. subcomosum*. It needs to be underlined, however, that Saito’s (1975) description refers to both *H. subcomosum* and *H. consanguineum*, as the axillary gemmae were explicitly mentioned and illustrated; whether both var. *consanguineum* and var. *kuri-lense* occur in Japan and if they differ in their regional distribution, needs to be ascertained.

10. *Hydrogonium* sp. In the course of the revision of *Hydrogonium consanguineum*, we encountered plants similar in morphology to *H. consanguineum* and *H. orientale* that produced nearly identical axillary gemmae but had broader leaves with a broadly cuspidate apex, much more pellucid, less papillose and bigger cells (9–12 μm), markedly bulging on both sides in cross-section. This taxon is very closely related to *H. bolleanum* as discussed above. According to the descriptions of Fleischer (1904), Chen (1941) and Eddy (1990), the taxon might be identical with *H. pseudoehrenbergii* (M. Fleisch.) P.C. Chen but until the type has been studied, this identity is not certain.

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Appendix 1. Newly updated species with GenBank accession numbers.

Acoula trisperma (Spruce) Müll. Hal.: Austria, Seidlwinkltal, 
Barbula recurvirostrum (Hedw.) Dixon: Austria, Seidlwinkltal, 
Barbula sida (Hedw.) R.H. Zander: Czechia, Pouzdřany, 
Barbula recurvirostrum (Hedw.) Dixon: Austria, Seidlwinkltal, 
Barbula recurvirostrum (Hedw.) Dixon: Austria, Seidlwinkltal,
Appendix 1. Continued.

556, JQ890479, —, JQ890532. **Pseudocrossidium hornschuchianum** (Schultz) R.H. Zander: Austria, Plankowitzpitze, Kučera 12610, CBFS, 309, JQ890481, JQ890420, JQ890535. **Pseudocrossidium revolutionum** (Brind.) R.H. Zander: UK, Kindrogan, Kučera 1009J, CBFS, 310, JQ890482, JX679913, JQ890534(direct), JX679941(clone1), JX679942(clone2). **Scopelophila cataractae** (Mitt.) Broth.: U.S.A: Silver Hill Mine, Davidson Co., NC, B. Shaw s.n., CBFS:15042, 575, JX679983, JX679933, JX679959-JX679962 (clones 1–4). **Syntrichia ruralis** (Hedw.) F. Weber & D. Mohr: Czechia, Kojátky, Košnar 1035, CBFS, 576, —, —, JX679963–4 (clones 1–2). **Tortella fragilis** (Hook. & Wilson) Limpr.: Switzerland, Mt. Sidelhorn, Košnar 954, CBFS, 564, JX679975, JX679925, JX679951.

**Tortula muralis** Hedw.: Czechia, Studanka, Košnar 771, CBFS, T56, —, JQ890421, —. **Trichostomum crispulum** Bruch: Spain, Bullas, Ros & Werner s/n, MUB, OW1507, —, JQ890418, —. **Tuercchia nivea** (E.B. Bartram) R.H. Zander: U.S.A: Miami, Miami-Dade Co., CO 1974, BM; Etchū, Yabuda(?), Dixon(?), 19 Aug. 1915. — Bangladesh, Rangamati, Long 28158, E.

Appendix 1. Continued.

**Weissia controversa** Hedw.: Switzerland, Mt. Sidelhorn, Košnar 954, CBFS, 564, JX679975, JX679925, JX679951. **Weissia subantarctica** Hedw.: Northern Territories, Australia, 1809, E. **Weissia variabilis** (Hedw.) F. Weber & D. Mohr: Brazil, 1819, E. **Weissia simplex** (Hedw.) F. Weber & D. Mohr: Brazil, 1819, E. **Weissia falcata** (Hedw.) F. Weber & D. Mohr: Brazil, 1819, E. **Weissia fuciformis** (Hedw.) F. Weber & D. Mohr: Brazil, 1819, E.

**Additional specimens studied** (for list of Barbula ampeloxifolia specimens see Kockinger & Kučera, 2007): **Barbula arcuata** Griff.: India: Darjeeling, R.S. Chopra & Singh 39, BM. — Nepal: Mardi Kholi, Stainton & al. 7193a, BM (cf. B. gangetica Müll. Hal.). **Barbula bolleana** (Müll. Hal.) Broth.: Spain: Caravaca de la Cruz, Kučera 13685, CBFS. — Switzerland: Rämikon, E. Steiger s.n., Z. **Barbula cancellata** Müll. Hal.*: (all specimens from DUKE) U.S.A.: Alabama: Bowers 12234, 15227, Anderson 26721, 27769; Florida: Anderson 14310, 24671, Peck 8, Small 7831, Rapp 136, Purcell 300MF49, Ris & al. 6155, Schornheir 20. — Mexico, S. Luis Potosí, Frye 2143, DUKE. **Barbula consanguinea** (Thwaites & Mitt.) A. Jaeger*: India: Uttarakhund, Mussoorie, Dubhie s.n., BM; Mohan Pass, Dubhie s.n., BM; Doiwala, Brotherus s.n., E; Maharashtra, Poona [Pune], Sedgwick s.n., BM; Odisha, Jeypore, Walker 552, 564, 568, 56, 56, 56, 56, 56, Karnataka, Shiggaon, Dixon 3487, BM; Kerala, Kumily, Foreau s.n., BM; W. Bengal, Calcutta [Kolkata], Barbula amplexifolia (Mitt.) A. Jaeger*: India: Darjeeling, F. Zemp 13724, 13725, BM (cf. B. gangetica Müll. Hal.). **Barbula gregaria** 14.8.1943, BP 179185. **Barbula kurilensis** (Hedw.) F. Weber & D. Mohr: Czechia, Kojátky, Košnar 1035, CBFS, 576, —, —, CBFS, 577, JX679984, JX679934, JX679965; New Zealand, J. Beever 99-94, MUB, OW2100, —, JQ890419, —.

**Additional specimens studied** (for list of Barbula ampeloxifolia specimens see Kockinger & Kučera, 2007): **Barbula arcuata** Griff.: India: Darjeeling, R.S. Chopra & Singh 39, BM. — Nepal: Mardi Kholi, Stainton & al. 7193a, BM (cf. B. gangetica Müll. Hal.). **Barbula bolleana** (Müll. Hal.) Broth.: Spain: Caravaca de la Cruz, Kučera 13685, CBFS. — Switzerland: Rämikon, E. Steiger s.n., Z. **Barbula cancellata** Müll. Hal.*: (all specimens from DUKE) U.S.A.: Alabama: Bowers 12234, 15227, Anderson 26721, 27769; Florida: Anderson 14310, 24671, Peck 8, Small 7831, Rapp 136, Purcell 300MF49, Ris & al. 6155, Schornheir 20. — Mexico, S. Luis Potosí, Frye 2143, DUKE. **Barbula consanguinea** (Thwaites & Mitt.) A. Jaeger*: India: Uttarakhund, Mussoorie, Dubhie s.n., BM; Mohan Pass, Dubhie s.n., BM; Doiwala, Brotherus s.n., E; Maharashtra, Poona [Pune], Sedgwick s.n., BM; Odisha, Jeypore, Walker 552, 564, 568, 56, 56, 56, 56, 56, Karnataka, Shiggaon, Dixon 3487, BM; Kerala, Kumily, Foreau s.n., BM; W. Bengal, Calcutta [Kolkata], Barbula amplexifolia (Mitt.) A. Jaeger*: India: Darjeeling, F. Zemp 13724, 13725, BM (cf. B. gangetica Müll. Hal.). **Barbula gregaria** 14.8.1943, BP 179185.