SYSTEMATICS AND PHYLOGENY

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 nrITS and chloroplast *rps4* and *trnM-trnV* sequence data and resolved only the type of the genus, *B. unguiculata*, plus *B. orizabensis*, in subfamily Pottioideae, 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).

■ 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.C. 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. *Odontophyllon* 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. *Odontophyllon* 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. *Hyophiladelphus* Müll. Hal., or the Central to South African *B.* sect. *Bulbibarbula* Müll. Hal. This delimitation of *Barbula* has never been challenged in later treatments and hence it has been widely accepted, except by Li & al. (2001), who retained *Hydrogonium* distinct from *Barbula*. Even Zander (1993), however, acknowledged the difficult delimitation of *Barbula* with respect to, e.g., *Trichostomum* 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 & al., 2004). Its generitype, *Barbula unguiculata* Hedw., appeared in subfamily Pottioideae (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 & 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 *Semibarbula* Herzog ex Hilp. (e.g., Hilpert, 1933; Gangulee, 1972). *Semibarbula* has mostly been synonymized with *Barbula* sect. *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.) R.H. Zander) 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 Pleuroweisieae (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 *Hyophila*, 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. meidensis* 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. tjibodensis* 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 *Semibarbula*, 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 *Semibarbula* 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. enderesii* (Garov.) Loeske, while other taxa like *S. bicolor* (Bruch & Schimp.) Loeske or *S. croceum* (Brid.) 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 phylogenetially 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 & Kučera (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*

indica (BP, DUKE, Z, priv. herb. G. Amann) and *B. indica* var. *kurilensis* (MHA). Following the treatment of Sollman (2004b), who synonymized many taxa of the *B. indica* complex under *B. tenuirostris* Brid., the type material of *B. tenuirostris* and their taxonomically and nomenclaturally most relevant synonyms, *B. flavicans* D.G. Long and *B. consanguinea* were 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 *B. amplexifolia* and *B. gregaria* (Köckinger & Kučera, 2011), as well as unpublished morphological studies of European species of *Barbula* by the first author.

Molecular protocols. — Total genomic DNA was extracted using the NaOH method (Werner & 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 & al. (2005b) and Köckinger & Kučera (2011). The variability of *trnM-trnV* has been shown to be useful in the study of Werner & al. (2009). Amplification and sequencing reactions followed the protocols described in Köckinger & Kučera (2011), and primers and amplification of *trnM-trnV* followed Werner & 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 & 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 invariable 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 & al. (2004) and Cox & 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 & 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, multrees = yes, steepest = 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 (lset 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 & 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* are resolved in Pottioideae, the remaining *Barbula* s.l. species appear among members of subfamily Trichostomoideae. A possible exception

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

is the position of *Streblotrichum*, which is ambiguous: sister to Trichostomoideae+Pottioideae (*rps4* dataset, Fig. 1), basal within Trichostomoideae (concatenated chloroplast dataset, Fig. 2) or even polyphyletic (ITS dataset, Fig. 3), with low support for any of these placements. Monophyletic *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 *Leptodontium+Triquetrella* clade, which is largely congruent with the concatenated chloroplast dataset, the rest of accessions of *B. convoluta* with *B. commutata* appears in Pottioideae in a poorly supported clade containing *Didymodon* and *Syntrichia*.

Barbula bicolor has an uncertain position in Trichostomoideae. 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-monophyly 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 *Leptodontium+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 Trichostomoideae, which contained the traditionally recognized species of sect. *Hydrogonium* (*B. bolleana*—the type of the section, *B. pseudoehrenbergii, 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 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 + Streblotrichum	PP	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*.
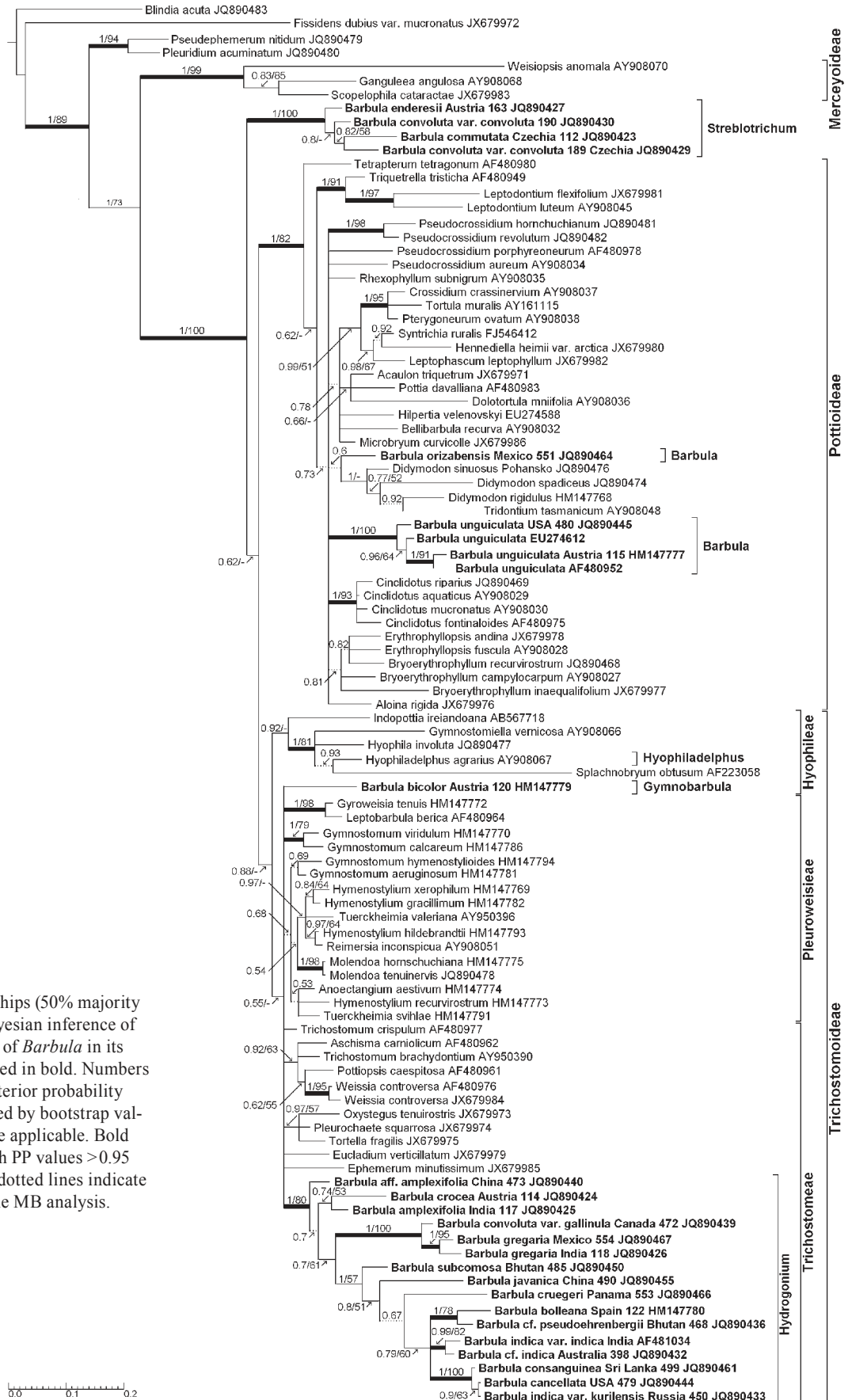
Blindia acuta JQ890483
Fissidens dubius var. mucronatus JX679972
1/94 Pseudephemerum nitidum JQ890479
Pleuridium acuminatum JQ890480
1/99
0.83/85 Weisiopsis anomala AY908070
Ganguleea angulosa AY908068
Scopelophila cataractae JX679983
1/100 Barbula enderesii Austria 163 JQ890427
Barbula convoluta var. convoluta 190 JQ890430
0.82/58 Barbula commutata Czechia 112 JQ890423
0.8/- Barbula convoluta var. convoluta 189 Czechia JQ890429
Tetrapterum tetragonum AF480980
1/91 Triquetrella tristicha AF480949
1/97 Leptodontium flexifolium JX679981
Leptodontium luteum AY908045
1/98 Pseudocrossidium hornchuchianum JQ890481
Pseudocrossidium revolutum JQ890482
Pseudocrossidium porphyreoneurum AF480978
Pseudocrossidium aureum AY908034
Rhexophyllum subnigrum AY908035
1/95 Crossidium crassinervium AY908037
Tortula muralis AY161115
Pterygoneurum ovatum AY908038
0.92 Syntrichia ruralis FJ546412
Hennediella heimii var. arctica JX679980
0.98/87 Leptophascum leptophyllum JX679982
Acaulon triquetrum JX679971
Pottia davalliana AF480983
Dolotortula mniifolia AY908036
Hilpertia velenovskyi EU274588
Bellibarbula recurva AY908032
Microbryum curvicolle JX679986
0.6 Barbula orizabensis Mexico 551 JQ890464] Barbula
Didymodon sinuosus Pohansko JQ890476
0.77/52 Didymodon spadiceus JQ890474
0.92 Didymodon rigidulus HM147768
Tridontium tasmanicum AY908048
1/100 Barbula unguiculata USA 480 JQ890445
Barbula unguiculata EU274612
0.96/64 1/91 Barbula unguiculata Austria 115 HM147777 Barbula
Barbula unguiculata AF480952
1/93 Cinclidotus riparius JQ890469
Cinclidotus aquaticus AY908029
Cinclidotus mucronatus AY908030
Cinclidotus fontinaloides AF480975
0.82 Erythrophyllopsis andina JX679978
Erythrophyllopsis fuscula AY908028
Bryoerythrophyllum recurvirostrum JQ890468
Bryoerythrophyllum campylocarpum AY908027
Bryoerythrophyllum inaequalifolium JX679977
Aloina rigida JX679976
Indopottia ireiandoana AB567718
0.92/- Gymnostomiella vernicosa AY908066
1/81 Hyophila involuta JQ890477
0.93 Hyophiladelphus agrarius AY908067] Hyophiladelphus
Splachnobryum obtusum AF223058
Barbula bicolor Austria 120 HM147779] Gymnobarbula
1/98 Gyroweisia tenuis HM147772
1/79 Leptobarbula berica AF480964
Gymnostomum viridulum HM147770
Gymnostomum calcareum HM147786
0.69 Gymnostomum hymenostylioides HM147794
Gymnostomum aeruginosum HM147781
0.84/64 Hymenostylium xerophilum HM147769
Hymenostylium gracillimum HM147782
Tuerckheimia valeriana AY950396
0.97/64 Hymenostylium hildebrandtii HM147793
Reimersia inconspicua AY908051
1/98 Molendoa hornschuchiana HM147775
Molendoa tenuinervis JQ890478
0.53 Anoectangium aestivum HM147774
Hymenostylium recurvirostrum HM147773
0.55/- Tuerckheimia svihlae HM147791
Trichostomum crispulum AF480977
0.92/63 Aschisma carniolicum AF480962
Trichostomum brachydontium AY950390
Pottiopsis caespitosa AF480961
1/95 Weissia controversa AF480976
Weissia controversa JX679984
0.97/57 Oxystegus tenuirostris JX679973
0.62/55 Pleurochaete squarrosa JX679974
Tortella fragilis JX679975
Eucladium verticillatum JX679979
Ephemerum minutissimum JX679985
Barbula aff. amplexifolia China 473 JQ890440
0.74/53 Barbula crocea Austria 114 JQ890424
1/80 Barbula amplexifolia India 117 JQ890425
1/100 Barbula convoluta var. gallinula Canada 472 JQ890439
1/95 Barbula gregaria Mexico 554 JQ890467
0.7 Barbula gregaria India 118 JQ890426
0.7/61 Barbula subcomosa Bhutan 485 JQ890450
1/57 Barbula javanica China 490 JQ890455
Barbula cruegeri Panama 553 JQ890466
1/78 Barbula bolleana Spain 122 HM147780
0.8/51 Barbula cf. pseudoehrenbergii Bhutan 468 JQ890436
0.99/82 Barbula indica var. indica India AF481034
0.67 Barbula cf. indica Australia 398 JQ890432
0.79/60 1/100 Barbula consanguinea Sri Lanka 499 JQ890461
Barbula cancellata USA 479 JQ890444
0.9/63 Barbula indica var. kurilensis Russia 450 JQ890433

1/89
1/73
1/82
1/100
0.62/-
0.99/51
0.78
0.66/-
0.73
0.62/-
0.81
0.88/-
0.97/-
0.68
0.54

Streblotrichum

Merceyoideae
Pottioideae
Hyophileae
Pleuroweisieae
Trichostomoideae
Trichostomeae
Hydrogonium

0.0　0.1　0.2

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.

Pleuridium acuminatum JQ890533
Pseudephemerum nitidum JQ890532
1/100
0.94
Barbula orizabensis Mexico 551 JQ890523
Barbula orizabensis Jamaica 552 JQ890524
1/100 **Barbula unguiculata Austria 115 HM147804**
Barbula unguiculata AY437129
0.65 **Barbula unguiculata USA 480 JQ890507**
Aloina rigida JX679952
0.89 Pseudocrossidium hornschuchianum JQ890535
0.66 0.7/100 Pseudocrossidium revolutum clone JX679941
0.74/100 Pseudocrossidium revolutum clone JX679942
Cinclidotus riparius JX679940
0.62 0.93/- Bryoerythrophyllum inaequalifolium JX679953
1 Bryoerythrophyllum ferruginascens FJ952611
0.88/52 Bryoerythrophyllum recurvirostrum JQ890527
Erythrophyllopsis andina JX679954
0.95/89 Didymodon rigidulus HM147795
0.6/- Didymodon sinuosus JQ890529
0.63 Didymodon spadiceus JQ890528
0.56 Syntrichia ruralis clones JX679963, JX679964
1/100 **Barbula commutata B112 JQ890485**
Barbula commutata B308 HM147816
1/100 **Barbula convoluta B113 HM147803**
Barbula convoluta B189 JQ890490
Barbula (Barbula group)
Streblotrichum
1/100 Acaulon triquetrum JX679947
Microbryum curvicolle JX679969
1 Leptophascum leptophyllum clone JX679958
1/80 Tortula muralis AY437132
0.69 Hennediella heimii var. arctica clone JX679956
Tortula hoppeana AY934544
1/- 0.76/- Tortula subulata AY934573
1/100 Tortula protobryoides AY934591
Hilpertia velenovskyi isolate AJ973251
1/100 Leptodontium flexifolium JX679957
0.67/- Triquetrella arapilensis AY437126
1/100 **Barbula bicolor Austria 120 HM147806**
Barbula bicolor Austria 164 JQ890489
Gymnobarbula **Hyophileae**
0.55
0.76 1/100, **Barbula enderesii Austria 525 JQ890522**
1/100 **Barbula enderesii Austria 163 JQ890488**
Barbula convoluta var. convoluta Czechia 190 JQ890491
Streblotrichum
Hyophila involuta JQ890530 **Hyophileae**
0.96/- 1/100 Gyroweisia tenuis HM147799
Leptobarbula berica AY796283
Gymnostomum viridulum HM147797
0.97 Anoectangium aestivum HM147801
1 Gymnostomum hymenostylioides HM147819
Tuerckheimia svihlae HM147817
Molendoa tenuinervis JQ890531
1/- Hymenostylium recurvirostrum HM147800
Hymenostylium gracillimum HM147809
1/98 Hymenostomum xerophilum HM147796
Tuerckheimia valeriana AY854431
1/100 Hymenostylium hildebrandtii AY796282
0.96/- Eucladium verticillatum JX679955
0.99/72 Pottiopsis caespitosa DQ988950
Chionoloma bombayense HM049777
1/99 Oxystegus recurvifolius HM049794
1/100 Oxystegus tenuirostris JX679948
0.85/- Pleurochaete squarrosa JX679950
1/52 Tortella fragilis JX679951
0.91/- Tortella humilis AY796261

Pottioideae
Pleuroweisieae

1/100
Barbula cf. amplexifolia China 473 JQ890502
Barbula amplexifolia Canada 471 JQ890500
1/100 **Barbula amplexifolia Austria 111 JQ890484**
1/60 **Barbula amplexifolia Macedonia 469 JQ890499**
Barbula amplexifolia India 117 clones JX679937, JX679938
1/- **Barbula amplexifolia India 475 JQ890504**
Barbula amplexifolia Nepal 336 JQ890492
0.93/61 **Barbula amplexifolia Russia 116 HM147805**
1/100 **Barbula crocea Austria 114 JQ890486**
0.95 **Barbula crocea Slovakia 500 JQ890521**
0.97/90 **Barbula convoluta var. gallinula Canada 472 JQ890501**
1/99 **Barbula gregaria China 474 JQ890503**
0.72 **Barbula gregaria India 118 JQ890487**
1/100 **Barbula gregaria China 476 JQ890505**
1/96 **Barbula gregaria Mexico 554 JQ890526**
1 1/- **Barbula cruegeri Mexico 483 clones JX679945, JX679946**
1/100 **Barbula cruegeri Ecuador B482 JQ890508**
Barbula cruegeri Panama B553 JQ890525
1/100 **Barbula subcomosa Bhutan 485 JQ890510**
1/100 0.65 **Barbula subcomosa Bangladesh 492 JQ890517**
1/100 **Barbula javanica India 494 JQ890519**
Barbula javanica Bhutan 493 JQ890518
0.68/- **Barbula javanica China 490 JQ890515**
0.93/100 **Barbula cf. indica Australia 398 AY796286**
0.99/73 **Barbula indica var. indica India 399 JQ890493**
1/100 **Barbula indica var. indica India 467 JQ890497**
0.98/100 **Barbula bolleana Spain 122 HM147807**
1/100 **Barbula bolleana Spain 400 JQ890494**
1/100 **Barbula cf. pseudoehrenbergii Bangladesh 487 JQ890512**
0.64 **Barbula cf. pseudoehrenbergii Nepal 489 JQ890514**
1/100 **Barbula cf. pseudoehrenbergii Bhutan 468 JQ890498**
0.91 **Barbula consanguinea Bangladesh 491 JQ890516**
1/- **Barbula consanguinea Bangladesh 488 JQ890513**
Barbula consanguinea Bangladesh 486 JQ890511
0.98/100 **Barbula indica var. indica Oman 484 JQ890509**
Barbula cancellata USA 479 JQ890506
1/- **Barbula cancellata Mexico 481 JX679943**
0.9/- **Barbula indica var. kurilensis Russia 450 JQ890495**
Barbula indica var. kurilensis Switzerland 452 JQ890496
Barbula indica var. kurilensis Austria 498 JQ890520

Hydrogonium **Trichostomeae**

Trichostomoideae

0.96

1/100 Trichostomum brachydontium AY796252
0.95/87 Trichostomum crispulum AY796249
Weissia controversa JX679965
1/100 Weissia brachycarpa AY796243
Weissia controversa AY796242
1/- Aschisma carniolicum isolate AY796270
Ephemerum minutissimum clones JX679966, JX679967, JX679968
Ephemerum sessile AY796285

0.0 0.1 0.2

gregaria), *B. tenuirostris*, *B. consanguinea* and *B. convoluta* var. *gallinula* revealed that the morphological characters used in Floras and other treatments for the differentiation of these taxa do not reflect molecular relationships. The morphological re-consideration of the samples nevertheless showed that it is possible to find characters which are in good agreement with the pattern detected by the molecular study. These characters will be described and discussed in the taxonomic synopsis and were used for the final identification of taxa. The individual clades within *Hydrogonium* will be described in more detail in the following text.

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. indicav* + *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 Pottioideae 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 mucro, 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 (subglobose, 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 Pottioideae 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 been 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) Redf. & 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. horrinervis* 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. *Odontophyllon* from the synonymy of *Streblotrichum* to the synonymy of *Hydrogonium*. The type of *Odontophyllon*, *Barbula hiroshii*, described by Saito (Saito, 1975: 499) is morphologically very similar to *B. crocea*, which was traditionally accommodated in *Streblotrichum* (Limpricht, 1890; Loeske, 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 this genus in the Synopsis below. Starting with Hilpert (1933), earlier authors correctly pointed out unclear morphological limits between *Hydrogonium* and *Hyophila*, which differ only in the absence of a peristome in members of the latter genus, while sharing leaf shape, hygric habitat, ventrally bulging leaf cells in some species and densely papillose in others of both genera, and production of axillary gemmae. Unfortunately, molecular data have been acquired only for *Hyophila involuta*, which is not even the type of the genus. *Hyophila involuta* was resolved in a group of its own within Trichostomoideae that can be identified with tribe Hyophileae, but in a delimitation that differs both from Chen's original (Chen, 1941) and Zander's later concepts (Zander, 1993).

The unexpected grouping of *Hydrogonium* taxa called for several reconsiderations at specific and infraspecific levels. The first of these is the confirmation of the status of *B. gregaria* as distinct from *B. amplexifolia* and *B. indica*, which was advocated on morphological grounds by Köckinger & Kučera (2007). Further, *B. cruegeri* and *B. subcomosa* should be distinguished from *B. gregaria* and *B. consanguinea*, respectively. Although the morphological differentiation is not always easy 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 concommitant 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 homoplastic 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. weddellii*, *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 axillary 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 Hyophileae, 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 *Anoectangium* 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*

(P. Beauv.) Limpr., Laubm. Deutschl. 1: 626. 1888 – Type (designated by Saito, 1975: 499): *S. convolutum* (Hedw.) P. Beauv., Prodr. Aethéogam.: 89. 1805 ≡ *Barbula convoluta* Hedw., Sp. Musc. Frond.: 120. 1801 ≡ *Bryum convolutum* (Hedw.) Dicks. 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 (fasc. 13–15. Mon. 29). 1842 ≡ *Tortula* sect. *Convolutae* De Not. in Mem. Reale Accad. Sci. Torino 40: 287. 1838.

Streblotrichum (on generic, subgeneric or sectional rank) has traditionally been recognized to include *Barbula* s.l. species with strongly differentiated convolute perichaetial 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 moreover characterized by the yellow seta, revoluble 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 perichaetial leaves, red seta, non-revoluble 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 perichaetial 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 calyculosa* (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 perichaetial 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. Thätigk. St. Gallischen 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., Musci 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. Thätigk. 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. hiroshii* 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 corniculate, green, light brownish-green to reddish 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). Perichaetial leaves of *Hydrogonium* are slightly differentiated, mostly smaller than the vegetative leaves, and subsheathing. The peristome 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, fugacious teeth of *H. orientale*. We revised in detail the taxa related or believed to be related to *Hydrogonium orientale* and *H. consaguineum*, 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. sumatrana* 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 cellules, 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 "*Tort. 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. & 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 isolectotypes 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 pachyloma* 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. Thätigk. St. Gallischen Naturwiss. Ges. 1877–78: 409. 1880 – **Lectotype (designated here):** "Ins. Ceylon, ad terram, Dr. Thwaites." (BM! [BM001006686]).

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. Nepaul; Dr. *Wallich*" (E! [E00108463]; isolectotypes: 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 from 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 isolectotypes.

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 Trinidad (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 chlorophyllose, 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 distinguishing *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 #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 affinities 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 & 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 Meissner Cattorum [Hoher Meißner near Kassel] Junio 1805 legi … Ex Heluetiâ 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, *Crüger* legit Aug. 2, 1846, in muris et rupibus calcareis formam confertiorem 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 amplexifolia*". Indeed, according to Sollman's identification of SW Asian material of *H. gregarium* and *H. amplexifolium* 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. amplexifolium* 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, *Scotter 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 gemmae, 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. Schen-si sept., in alveo fluminis Lao-y-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 gemmae 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 *Rottler*.
= *Barbula indica* (Hook.) Spreng., Nomencl. Bot. 2: 72. 1824 ≡ *Tortula indica* Hook., Musci Exot. 2: 135. 1819 ≡ *Semibarbula indica* (Hook.) Herzog ex Hilp. in Beih. Bot.

Centralbl., Abt. 2, 50(2): 626. 1933 – Type: In India orientali. *Röttler*. In muris Horti 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. *kurilense* 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 acquired sequences with GenBank accession numbers.

Species, country, locality, collector, collector number, herbarium code, isolate number, GenBank accession numbers in the order *rps4*, *trnM-trnV*, ITS. * denotes species for which taxonomic changes (tranfer to the genera *Streblotrichum*, *Gymnobarbula* or *Hydrogonium*) are proposed.

Acaulon triquetrum (Spruce) Müll. Hal.: Czechia, Pouzdřany, *Košnar 356*, CBFS, 558, JX679971, JX679921, JX679947. *Aloina rigida* (Hedw.) Limpr.: Czechia, Pavlov, *Košnar 954*, CBFS, 565, JX679976, JX679926, JX679952. *Anoectangium aestivum* (Hedw.) Mitt.: Austria, Heiligenblut, *Kučera 12848*, CBFS, 104, HM147774, JX679910, HM147801. *Barbula amplexifolia* (Mitt.) A. Jaeger*: Austria, Seidlwinkltal, *Kučera 12792*, CBFS, 111, JQ890422, JQ890363, JQ890484; Russia, Sakha, Selyakh, *Ignatov 00-36*, MHA, 116, HM147778, JQ890367, HM147805; India, Nainital, *Hallingbäck s.n.*, CBFS, 117, JQ890425, JQ890368, JX679937(clone2), JX679938 (clone3); Nepal, Phulchowki, *Townsend 92/89*, E, 336, JQ890431, –, JQ890492; Macedonia, Popova Šapka, *Kučera 13775*, CBFS, 469, JQ890437, JQ890378, JQ890499; Canada, NWT, Virginia Falls, *Steere 76-605*, MO, 471, JQ890438, JQ890379, JQ890500; India, Sikkim, *Long 26378*, E, 475, JQ890442, JQ890381, JQ890504; *Barbula* aff. *amplexifolia* (Mitt.) A. Jaeger*: China, Yunnan, Gang Ho Ba, *Long 18818*, E, 473, JQ890440, JQ890380, JQ890502. *Barbula bicolor* (Bruch & Schimp.) Lindb.*: Austria, Seidlwinkltal, *Košnar 1540*, CBFS, 120, HM147779, JQ890370, HM147806; Mt. Bielschitza, *Köckinger 14262*, CBFS, 164, 170, JQ890428, JQ890372, JQ890489; *Barbula bolleana* (Müll. Hal.) Broth.*: Spain, Motril, *Vadam s.n.*,CBFS, 122, HM147780, JQ890371, HM147807; Spain, Bullas, *Kučera 13670*, CBFS, 400, JX679970, JQ890374, JQ890494. *Barbula cancellata* Müll. Hal.*: U.S.A., Berkeley Co. (NC), *B.Shaw 8846*, DUKE, 479, JQ890444, JQ890383, JQ890506; Mexico, Tabasco, S. Fé, *Zamudio 1181*, DUKE, 481, JQ890446, JQ890384, JX679943. *Barbula commutata* Jur.*, Czechia, Rabí, *Kučera 12658*, CBFS, 112, JQ890423, JQ890364, JQ890485; *Barbula convoluta* Hedw. var. *convoluta*: Czechia, Hus, *Kučera 3882*, CBFS, 113, HM147776, –, HM147803; Czechia, Vilémovice, *Kučera 13021*, CBFS, 189, JQ890429, JQ890401, JQ890490; Czechia, Suchý žleb, *Kučera 13023*, 190, JQ890430, JQ890402, JQ890491; *Barbula convoluta* var. *gallinula* R.H. Zander*: Canada, NWT, Virginia Falls, *Steere 76-605*, MO, 472, JQ890439, JX679916, JQ890501. *Barbula consanguinea* (Thwaites & Mitt.) A. Jaeger*: Bangladesh, Chittagong, *Long 28072*, E, 486, JQ890451, JQ890389, JQ890511; Bangladesh, Alikadam, *Long 28197*, E, 488, JQ890453, JQ890391, JQ890513; Bangladesh, Kaptai, *Long 28117*, E, 491, JQ890456, JQ890394, JQ890516; Sri Lanka, Ella, *Townsend 73/1093*, E, 499, JQ890461, JQ890393, –. *Barbula crocea* (Brid.) F. Weber & D. Mohr*: Austria, Rotgülden, *Kučera 12556*, CBFS, 114, JQ890424, JQ890365, JQ890486; Slovakia, Motyčky, *Kučera 1087*, CBFS, 500, JQ890462, JQ890399, JQ890521; *Barbula cruegeri* Müll. Hal.*: Ecuador, Pichincha, *Arts 19/003*, DUKE, 482, JQ890447, JQ890385, JQ890508(direct read), JX679944 (clone1); Mexico, Chiapas, *Eggers & Frahm 23*, DUKE, 483, JQ890448, JQ890386, JX679945(clone2), JX679946(clone3); Panama, Cerro Jefe, *Allen 9020*, DUKE, 553, JQ890466, JQ890405, JQ890525. *Barbula enderesii* Garov.*: Austria, Pfarreben, *Köckinger 14261*, CBFS, 163, JQ890427, JX679911, JQ890488; Austria, Lechnergraben, *Köckinger 14911*, CBFS, 525, JQ890463, JQ890400, JQ890522. *Barbula gregaria* (Mitt.) A. Jaeger*: India, Nainital, *Hallingbäck s.n.*, CBFS, 118, JQ890426, JQ890369, JQ890487; China, Yunnan, Bapo, *Long 33624*, E, 474, JQ890441, JX679917, JQ890503; Yunnan, Bawan Cun, *Long 32244*, E, 476, JQ890443, JQ890382, JQ890505; Mexico, Guerrero, Puentecilla, *Eckel 188986*, DUKE, 554, JQ890467, JQ890406, JQ890526. *Barbula indica* (Hook.) Spreng. var. *indica*: Australia, Wombarella Gap, *Streimann 39344*, NY, 399, JQ890432, –, AY796286; India, Naini Tal, *Arts 08/05*, MUB, 399, AF481034, JQ890373, JQ890493; India, Lucknow, *Long 30794*, E, 467, JQ890435, JQ890377, JQ890497; Oman, Wadi Tiwi, *Rothfels 2763*, DUKE, 484, JQ890449, JQ890387, JQ890509. *Barbula indica* var. *kurilensis* Ignatova & Ignatov*: Russia, Mt Ruruy, *Ignatov 06-1884*, MHA, 450, JQ890433, JQ890375, JQ890495; Switzerland, Rottenschwil, *Hofmann 183139*, Z, 452, JQ890434, JQ890376, JQ890496; Austria, Hard, *Amann s.n.*, CBFS, 498, JQ890460, JX679919, JQ890520. *Barbula javanica* Dozy & Molk.*: China, Yunnan, Kunming, *Long 24613*, E, 490, JQ890455, JQ890393, JQ890515; Bhutan, Gaylegphug, *Long 8159*, E, 493, JQ890458, JQ890396, JQ890518; India, Sikkim, *Long 22418*, E, 494, JQ890459, JQ890397, JQ890519. *Barbula orizabensis* Müll. Hal. Mexico, Tzitzio, *Delgadillo 5010*, 551, JQ890464, JQ890403, JQ890523; Jamaica, Cedar Valley, *Crosby 3370*, DUKE, 552, JQ890465, JQ890404, JQ890524 I. *Barbula* sp., cf. *pseudoehrenbergii* M. Fleisch.*: Bhutan, Phuntsholing, *Long 10352*, E, 468, JQ890436, JX679915, JQ890498; Bangladesh, Manichari, *Long 28169*, E, 487, JQ890452, JQ890390, JQ890512; Nepal, Chitwan Lodge, *Townsend 92/318*, E, 489, JQ890454, JQ890392, JQ890514. *Barbula subcomosa* Broth.*: Bhutan, Phuentsholing, *Long 7725*, E, 485, JQ890450, JQ890388, JQ890510; Bangladesh, Teknaf, *Long 28215*, E, 492, JQ890457, JQ890395, JQ890517. *Barbula unguiculata* Hedw. Austria, Heiligenblut, *Kučera 12829*, CBFS, 115, HM147777, JQ890366, HM147804; USA, Davidson Co. (SC), *AJ Shaw 5692*, DUKE, 480, JQ890445, JX679918, JQ890507; *Blindia acuta* (Hedw.) Bruch & Schimp.: Portugal, Peneda, *Kučera 10525*, CBFS, 121, JQ890483, JQ890416, JX679939; *Bryoerythrophyllum inaequalifolium* (Taylor) R.H. Zander: Russia: Sokhondo, Agutsa River, *Czernyadyeva 36-10*, CBFS:15095, 567, JX679977, JX679927, JX679953. *Bryoerythrophyllum recurvirostrum* (Hedw.) P.C. Chen: Czechia, Šumperk, *Kučera 12925*, CBFS, 361, JQ890468, JQ890407, JQ890527. *Cinclidotus riparius* (Host ex Brid.) Arn.: Czechia, Sokolohrady, *Košnar s.n.*:CBFS, 197, JQ890469, JX679912, JX679940. *Didymodon rigidulus* Hedw.: Czechia, Hříběcí Boudy, *Kučera 12905*, CBFS, 15, HM147768, JQ890408, HM147795. *Didymodon spadiceus* (Mitt.) Limpr.: Czechia, Ostravice, *Plášek s.n.*, CBFS:12722, 78, JQ890474, JQ890409, JQ890528. *Didymodon sinuosus* (Mitt.) Delogne: Czechia, Pohansko, *Kučera 12059*, CBFS, 85, JQ890476, JQ890410, JQ890529. *Ephemerum minutissimum* Lindb.: Czechia, Velká nad Veličkou, *Košnar 692*, CBFS, 578, JX679985, JX679935, JX679966(clone1), JX679967(clone2), JX679968(clone3). *Erythrophyllopsis andina* (Sull.) R.H. Zander: Ecuador: Mt Chimborazo, *Soldán s.n.*, CBFS:7418, 568, JX679978, JX679928, JX679954. *Eucladium verticillatum* (Hedw.) Bruch & Schimp.: Czechia, Tetín, *Kučera 14692*, CBFS, 570, JX679979, JX679929, JX679955. *Fissidens dubius* var. *mucronatus* (Breidl. ex Limpr.) Kartt., Hedenäs & L. Söderstr.: Czechia, Velká nad Veličkou, *Košnar 696*, CBFS, 559, JX679972, JX679922, JX679949. *Gymnostomum hymenostylioides* (Broth. & Dixon) R.H. Zander: India, Nainital, *Long 30847*, CBFS:13299, HM147794, JQ890411, HM147819. *Gymnostomum viridulum* Brid.: Czechia, Lukov, *Hradílek s.n.*, CBFS:12914, 99, HM147770, JQ890412, HM147797. *Gyroweisia tenuis* (Schrad. ex Hedw.) Schimp.: France, Mont-Dore, *Kučera 10748*, CBFS, 102, HM147772, JX679908, HM147799. *Hennediella heimii* var. *arctica* (Lindb.) R.H. Zander: Norway, Svalbard, Petuniabukta, *Košnar 1932*, CBFS, 571, JX679980, JX679930, JX679956(clone1). *Hymenostylium xerophilum* Köckinger & Jan Kučera: Austria, Reiting, *Köckinger 05-954*, CBFS:12913, 62, HM147769, JQ890415, HM147796. *Hymenostylium gracillimum* (Nees & Hornsch.) Köckinger & Jan Kučera: Austria, Tiboldgraben, *Köckinger 14264*, CBFS:12972, 165, HM147782, JQ890413, HM147809. *Hymenostylium recurvirostrum* (Hedw.) Dixon: Austria, Seidlwinkltal, *Kučera 12780*, CBFS, 103, HM147773, JX679909, HM147800. *Hyophila involuta* (Hook.) A. Jaeger: Costa Rica, Barra Honda, *T.Hauer s.n.*, CBFS:14557, 495, JQ890477, JQ890414, JQ890530. *Leptodontium flexifolium* (Dicks.) Hampe: Russia: Duldurga, Elo-Rakhanai, *Afonina s.n.*, CBFS:14332, 572, JX679981, JX679931, JX679957. *Leptophascum leptophyllum* (Müll. Hal.) J. Guerra & Cano: Spain: Los Pulpites, *Kučera 13661*, CBFS, 573, JX679982, JX679932, JX679958(clone1). *Microbryum curvicolle* (Hedw.) R.H. Zander: Czechia, Pouzdřany, *Košnar 358*, CBFS, 579, JX679986, JX679936, JX679969. *Molendoa tenuinervis* Limpr. Mongolia, Mt. Ikh-Bogd, *Ignatov 01-789*, MHA, CBFS:12954, 134, JQ890478, JQ890417, JQ890531. *Oxystegus tenuirostris* (Hook. & Taylor) A.J.E. Sm.: Czechia, Třísov-Dívčí Kámen, *Košnar 431*, CBFS, 561, JX679973, JX679923, JX679948. *Pleuridium acuminatum* Lindb.: Czechia, Mokrsko, *Kučera 13738*, CBFS, 557, JQ890480, –, JQ890533. *Pleurochaete squarrosa* (Brid.) Lindb.: Czechia, Tmaň-Kotýz, *Košnar 1266*, CBFS, 562, JX679974, JX679924, JX679950. *Pseudephemerum nitidum* (Hedw.) Loeske: Czechia, Pořešín, *Kučera 13593*, CBFS,

556, JQ890479, –, JQ890532. ***Pseudocrossidium hornschuchianum*** (Schultz) R.H. Zander: Austria, Plankowitzspitze, *Kučera 12610*, CBFS, 309, JQ890481, JQ890420, JQ890535. ***Pseudocrossidium revolutum*** (Brid.) R.H. Zander: UK, Kindrogan, *Kučera 10091*, 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 (clones1–4). ***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, Studánka, *Košnar 771*, CBFS, T56, –, JQ890421, –. ***Trichostomum crispulum*** Bruch: Spain, Bullas, *Ros & Werner s/n*, MUB, OW1507, –, JQ890418, –. ***Tuerckheimia svihlae*** (E.B. Bartram) R.H. Zander: U.S.A: Marianna Caverns, FL, *Cash & Rapp M193*, DUKE, 312, HM147791, JX679914, HM147817. ***Weissia controversa*** Hedw.: Czechia, Hrubá Vrbka, *Košnar 1253,* CBFS, 577, JX679984, JX679934, JX679965; New Zealand, *J. Beever 99-94*, MUB, OW2100, –, JQ890419, –.

Additional specimens studied (for list of *Barbula amplexifolia* specimens see Köckinger & Kučera, 2007): ***Barbula arcuata*** Griff.*: India: Darjeeling, *R.S. Chopra & Singh 39*, BM. — Nepal: Mardi Khola, *Stainton & al. 7193a*, BM (cf. *B. gangetica* Müll. Hal.). ***Barbula bolleana*** (Müll. Hal.) Broth.*: Spain: Caravaca de la Cruz, *Kučera 13685*, CBFS. — Switzerland: Rümikon, *E. Steiger s.n.*, Z. ***Barbula cancellata*** Müll. Hal.*: (all specimens from DUKE) U.S.A.: Alabama: *Bowers 12234, 15227, Anderson 26721, 27769*; Forida: *Anderson 14310, 24671, Peck 8, Small 7831, Rapp 136, Purcell 300MF49, Ris & al. 6155, Schornherst 20*. — Mexico, S. Luis Potosí, *Frye 2143*, DUKE. ***Barbula consanguinea*** (Thwaites & Mitt.) A. Jaeger*: India: Uttarakhand, Mussoorie, *Duthie s.n.*, BM; Mohand Pass, *Duthie s.n.*, BM; Doiwala, *Brotherus s.n.*, E; Maharashtra, Poona [Pune], *Sedgwick s.n.*, BM; Odisha, Jeypore, *Walker 552, 564, 568*, BM; Karnataka, Shiggaon, *Dixon 3487*, BM; Kerala, Kumily, *Foreau s.n.*, BM; W. Bengal, Calcutta [Kolkata], *Gangulee s.n.*, BM. — Philippines: Luzon, Mt. S. Isidro, *Fénix s.n.* Nov. 1917, E. ***Barbula indica*** var. ***kurilensis*** Ignatova & Ignatov*: Switzerland: Aargau, Rottenschwil, Reuss, *H. Hofmann 170396*, *N. Müller 171213*, Bad Ragaz, Rhein, *N. Müller 171894*, Emmen, Reuss, *F. Zemp 183290*. — Hungary: Budapest, *Boros 8.1925*, BP 107073. — Croatia: Kotoriba-Alsódomború [D. Dubrava], *Boros 14.8.1943*, BP 179185. ***Barbula gregaria*** (Mitt.) A. Jaeger*: Mexico, Chiapas, *Hermann 26399*, DUKE; Puebla, Xicotepec de Juarez, *Delgadillo 1220*, L. Bhutan, Pemagatshel, *Long 8561*, E; Chendebi, *Long 8737*, E; Chapcha, *Long 8824*, E. — India, Himachalpradesh, Mount Jako, *Gollan s.n.* 26.6.1906, PC; Beas, *Lillie 1372*, L; West Bengal, Tiger Hill, *Long 22375*, E; Ghum, *Long 23036*, E; Uttaranchal, Rajpur, *Bowen s.n.*, L; Mussoorie, *Maas Geesteranus 14730-1, de Haas B6, B-34, B-44, B-54A*, L; Mallital, *Long 30799*, E; Sikkim, Bop, *Long 26378*, E; Samiti Lake, *Long 22791*, E; Bitu, *Long 26337*, E; Tista valley, *Long 26365*, E. — China, Yunnan: Stone Forest, *Touw 23504C*, L; Zhongdian, *Long 18720*, E; Gang Ho Ba, *Long 18842*, E; Lijiang, *Long 18886*, E; Qionhzu Temple, *Long 23540*, E; Bawan, *Long 32161*, E; Shabadi, *Long 32573*, E; Nankang, *Long 32652*, E; Bingzhongluo, *Long 33522*, E; Liuku, *Long 34272*, E; Qinlangdang, *Long 36260*, E; Nu Jiang, *Long & Shevock 37061*, E. Sichuan, Jinfu Shan, *Wu 21156*, MO; Taiwan: Li-shan, Nantou, *Chuang & Schofield 869A*, L. — Indonesia, Sumatra, Prapat on Toba Lake, *Staal S-4*, L; Lombok, Rinjani, *Elbert 1285F*, L; — Japan, Ōita,. Mt. Sobo, *Iwatsuki* 7 Aug. 1962, L. — Thailand, Payap, Doi Chiengdao, *Touw 9361*, L. ***Barbula javanica*** Dozy & Molk.*: China: Yunnan, Weixi, *Long 24513*, E. — India: Maharashtra, Mahabaleshwar, *Townsend 73/416, 445, 473*, E; Sikkim, Raniphul, *Long 26302*, E. — Indonesia: Java, Sindanglaya, *M. Fleischer, Musci Archipelagi Indici, Ser. III. 1900. No. 124*, E; Tjipannas, *M. Fleischer. Musci Archipelagi Indici, Ser. V. 1902. No. 214*, E. — Nepal: Godawari, *Long 17597–8*, E. — Sri Lanka: Peradeniya, *M. Fleischer, Musci Archipelagi Indici, Ser. X. 1908. No. 460*, E; Rapava, *illegible coll.* No. 2083, BM. ***Barbula subcomosa*** Broth.*: Japan: Kanagawa, *Wichura* 1400 (isotype of *Barbula subcomosa* Broth., 2 duplicates, BM); Etchū, Yabuda(?), *Dixon(?)* 19 Aug. 1915. — Bangladesh, Rangamati, *Long 28158*, E.