

REVISION OF PHYLOGENETIC RELATIONSHIPS OF *DIDYMODON* SECT. *RUFIDULI*
(POTTIACEAE, MUSCI)

ПЕРЕСМОТР ФИЛОГЕНЕТИЧЕСКОГО ПОЛОЖЕНИЯ *DIDYMODON* SECT. *RUFIDULI*
(ПОТТИАСЕАЕ, МУСЦИ)

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Abstract

Molecular phylogenetic analysis of the *Didymodon* species, which were assigned to Sect. *Rufiduli* (P.C. Chen) R.H. Zander by different authors showed that most of these species constitute a monophyletic lineage which largely fits the original concept of Chen. *Didymodon asperifolius*, *D. sinuosus*, and surprisingly also *D. revolutus* need to be included in the section, while *D. anserinocapitatus* is more closely related to *D. cordatus* of the sect. *Didymodon*. The genus *Fuscobryum* R.H. Zander (sect. *Rufiduli* in the sense of Zander) represents a well-supported lineage within sect. *Didymodon*, and is therefore combined as a subsection thereof, after *D. norrisii* is removed to sect. *Vineales*. *Didymodon gaochienii* and *D. asperifolius* have been found polyphyletic in present morphological circumscriptions and hybridization between *D. hedysarifformis* and the Russian lineage of *D. gaochienii* s.l. has been suggested by incongruence between nuclear and chloroplast data. Revision of types revealed that *D. murrayae* seems to be identical with the type of *D. gaochienii* and at the same time, current understanding of these taxa differs from what is represented by their types, which will probably necessitate description of new taxa following a dedicated study. Additions to known distribution of *Didymodon hedysarifformis*, *D. johansenii*, *D. murrayae*, *D. rivicola* and *D. zanderi* are listed.

Резюме

Согласно данным молекулярно-филогенетического анализа виды, относимые разными авторами к секции *Rufiduli* (P.C. Chen) R.H. Zander, образуют монофилетическую группу, соответствующую изначальной концепции секции, предложенной Ченом. *Didymodon asperifolius*, *D. sinuosus*, а также, неожиданно, и *D. revolutus* должны быть включены в эту секцию, в то время как *D. anserinocapitatus* оказался близок к *D. cordatus* из секции *Didymodon*. Род *Fuscobryum* R.H. Zander (Sect. *Rufiduli* в смысле Зандера) представляет собой хорошо поддержанную группу в секции *Didymodon* и рассматривается в ранге подсекции, при этом *D. norrisii* должен быть перемещен в секцию *Vineales*. Показана полифилетичность *Didymodon gaochienii* и *D. asperifolius* в их известных морфологических границах, а также выявлен факт гибридизации между *D. hedysarifformis* и представленной в России линией *D. gaochienii* s.l. на основании несоответствия данных ядерной и хлоропластной ДНК. Тип *D. murrayae* оказался идентичен типу *D. gaochienii*, так что виды в их современном понимании, по-видимому, должны быть описаны. Перечислены данные, уточняющие распространение *Didymodon hedysarifformis*, *D. johansenii*, *D. murrayae*, *D. rivicola* и *D. zanderi*.

KEYWORDS: *Didymodon* section *Rufiduli*, Pottiaceae, molecular phylogeny, ITS, *rps4*, *trnM-trnV*

INTRODUCTION

Phylogenetic affinities among species of the large genus *Didymodon* based on molecular data have to date been published only in the paper of Werner *et al.* (2005), who studied the relationships among 29 taxa, and tested the monophyly of the genus in the sense of Zander (1993), based on the nuclear ITS sequence data. The authors confirmed the monophyly of *Didymodon* as understood by Zander (l.c.) and clearly refuted the earlier suggested transfer of *D. sinuosus* to *Oxystegus*. Also, they questioned the need for separating the genera *Geheebia* and

Trichostomopsis. Infrageneric affinities were much less clearly obvious, confirming the monophyly of the only section, *Asteriscium*, and even this was not possible before *D. bistratosus*, a species morphologically close to *D. vinealis*, and *D. paramicola*, earlier segregated into a monotypic genus (*Kingiobryum*) of the family Dicranaceae, was understood as a member of the section. Chloroplast data have been published only for a subset of the taxa employed in the Werner *et al.*'s study. The most comprehensive picture of chloroplast phylogeny to date can be drawn from the paper by Jiménez *et al.* (2012), who

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described a new South American genus, *Andina*, which combined several species earlier recognized within both *Pseudocrossidium* and *Didymodon*. Having analyzed a concatenated matrix of chloroplast *trnL-F* and *trnG* regions, they were able to confirm the monophyly of sections *Fallaces* (with the inclusion of *D. luridus*, as suggested by Werner *et al.*, 2005) and of the sect. *Vineales*, with *D. bistratosus* in the sister position to the clade containing both of these sections, and *Andina* + *Gertrudiella* sister to *Didymodon* as a whole.

The results of above named studies need to be supplemented by information from additional species, other geographic regions and multiple genomic compartments before they can be generally accepted. Unfortunately, the selection of taxa for the study of Werner *et al.* (2005), which was intended just as a preliminary investigation into the phylogenetic relationships, included only taxa occurring in Europe and North America and was based on a single hypervariable nuclear marker. Similarly, only European taxa of sections *Fallaces* and *Vineales* and the North American *D. norrisii* were included in the study of Jiménez *et al.* (2012), which might compromise the obtained results. Again, the marker selection included only two regions from one genomic compartment. Zander (2013) published another, rather revolutionary classification scheme of *Didymodon*, based on the re-interpretation of Werner *et al.* (2005), which resulted in splitting the genus into six genera – *Didymodon*, *Trichostomopsis* (re-established), *Geheebia* (amended to include the earlier concept of sect. *Fallaces*), *Vinealobryum* (= sect. *Vineales*), *Fuscobryum*, established for taxa putatively related to *D. nigrescens* (*D. perobtusus*, *D. subandreaeoides*, *D. norrisii*), and monotypic *Exobryum* with *D. asperifolius*.

One of the species groups in *Didymodon* that has not yet been representatively covered by the above named molecular phylogenetic treatments was the group of taxa with fragile leaf tips, which seems to be particularly well represented in the Central Asian and South Siberian mountains and was taxonomically treated using conventional methods by Otnyukova (2002). Besides the relatively well-known species, *D. johansenii*, she accepted two species previously described from China, *D. anserinocapitatus* and *D. gaochienii* (synonymized later by Sollman (2006) with *D. fragilicuspis*), and described two new species, *D. hedysarififormis* from Tuva and *D. murrayae* from Altai, the two neighbouring regions of southernmost part of Siberia, situated along the Mongolian border. Later, another species was described from southern Siberia (Aga-Buryatia of Transbaikalia), *Didymodon zanderi* Afonina & Ignatova (Afonina & Ignatova, 2007), putatively related to *D. hedysarififormis*. Phylogenetic affinities of all these species have never been thoroughly discussed, nor studied using molecular approaches. *D. johansenii* and *D. anserinocapitatus* have been considered the only members of section *Didymodon* besides the

generitype, *D. rigidulus* by Zander (2013), who merged *D. acutus*, *D. icmadophilus* and *D. validus* into the infraspecific variability of *D. rigidulus*. *Didymodon murrayae* was placed in the section *Vineales* in the same treatment based on swapping that species with *D. sinuosus*, the name under which *D. murrayae* was earlier reported from North America. The phylogenetic position of *D. sinuosus* is nevertheless not clearly established. Although most authors acknowledge morphological and anatomical similarities between that species and the typical representatives of the section *Vineales* (reddish colour, red KOH reaction of lamina walls, absent ventral stereids of the costa), there are also characters not seen among members of *Vineales*, such as the fragile lamina or denticulation of upper leaf margins. Phylogenetic affinities based on nrITS data (Werner *et al.*, 2005) neither support the close relationship of *D. sinuosus* with the section *Vineales*.

Alternative placement of *D. sinuosus*, *D. murrayae* and potentially the other taxa with fragile leaf apices could be within the section *Rufiduli*. That section was originally described within *Barbula* to account for three Chinese species with mammillose cells and costa ending below apex – *B. rufidula* (= *D. rufidulus*), *B. rivicola* (= *D. rivicola*) and *B. subrivicola* (synonymized later by Saito, 1975 with *Didymodon nigrescens*). The section was largely neglected by recent authors until Zander (1999) revived it for placing the newly described *D. norrisii*, along with the morphologically similar *D. nigrescens*, *D. perobtusus* and *D. subandreaeoides*. He underlined the characters of bulging lamina cells, papillose crenulate upper leaf margins and dark red – blackish color, red in KOH, whereas Chen (1941) stressed the costa ending well below apex, bulging lamina cells and the leaves twisted in dry state. *Didymodon nigrescens* and *D. perobtusus* were placed by Chen in subsect. *Rigidulae* (roughly equivalent to usual current delimitation of sect. *Didymodon*). However, bulging leaf cells occur also in species that were never compared to species of sect. *Rufiduli* in the sense of either author, such as *D. occidentalis* of the sect. *Vineales* or the South American taxa *Didymodon fuscus* or *D. santessonii*, which are also similar to members of the latter section and were tentatively compared to *D. vinealis* by Jiménez & Cano (2006).

MATERIAL AND METHODS

The sampling included the selection of above named species with fragile leaf apices in multiple accessions covering as much as possible of the distribution area, species of sect. *Rufiduli* in the sense of both Chen (1941) and Zander (1999), as well as several accessions of *D. sinuosus*, *D. asperifolius*, and *D. fuscus*. These were complemented by the representatives of other groups of *Didymodon*, as well as the selection of most probable outgroups, based on the studies of Werner *et al.* (2004), Kučera *et al.* (2013) and unpublished results of our team. Table 1 lists the accessions used in this study. We employed one nuclear (ITS) and two chloroplast markers (*rps4*, *trnM-trnV*), which were successful-

ly used in our previous phylogenetic studies in Pottiaceae (Köckinger & Kučera 2011; Kučera *et al.* 2013) and enabled the re-use of earlier results and easier interpretation of new data. Authors of names in the whole text follow the TROPICOS database (www.tropicos.org).

Molecular protocols

Total genomic DNA was extracted using the NaOH method (Werner *et al.*, 2002). The target regions (ITS, *rps4*, *trnM-trnV*) were amplified from diluted crude extracts, and the purified DNA sequenced as specified in our earlier studies (*e.g.*, Köckinger & Kučera, 2011).

Sequence editing, alignment, and phylogenetic analysis

Obtained raw sequences were edited (trimming of primer complements, 18S and 26S rRNA in ITS amplicons, interpretation of ambiguities where possible) in BioEdit v.7.1.7 (Hall, 1999) and Geneious v. 7 (Biomatters Ltd, available from <http://www.geneious.com/>). Three datasets were built, ITS, chloroplast concatenation (*rps4* + *trnM-trnV*), and ITS + cp concatenation for accessions which were successfully amplified for all regions. The sequences in the above described datasets were aligned using the online interface of MAFFT v7.213 (Kato & Standley, 2013), employing the Q-INS-i strategy with 20 PAM/ê = 2 scoring matrix, gap opening penalty set to 1.0, and offset value set to 0.0 for ITS sequences (including the ITS part of the concatenated dataset before concatenation) and E-INS-i strategy with the same settings for chloroplast sequences. The resulting alignments were manually inspected for homology problems and manually edited, but these interventions were limited to minimum cases to ensure maximum reproducibility. Indels were scored for chloroplast partitions with SeqState v.1.4 (Müller, 2005) using the simple indel coding method (Simmons & Ochoterena, 2000). Phylogenetic analyses were performed using the Bayesian inference (BI), maximum likelihood (ML), and maximum parsimony (MP) criteria on partitioned datasets with partitions assigned to individual DNA regions (ML, BI), and binary indel data. MrBayes v. 3.2.2 (Ronquist *et al.*, 2012) was used for BI, with the gamma model of rate variation across sites sampled across the GTR model space (nst = mixed, rates = gamma) with unlinked parameters for the respective partitions and performed two simultaneous runs with temp set to 0.05 and otherwise default settings for 1 million generations. The convergence between runs in all cases dropped below 0.01. Twenty-five percent of the sampled trees were discarded as burn-in and the rest were used for construction of the majority consensus tree. ML analysis was executed in RaxML using the raxmlGUI interface v 1.3 (Silvestro & Michalak, 2012) using the GTR model of nucleotide substitution with the Γ model of rate heterogeneity. Bootstrap support for the lineages was calculated using the ‘thorough bootstrap’ option with 500 replicates. MP analysis, with gaps scored as missing data, was executed in TNT ver. 1.1 (Goloboff *et al.*, 2008). Trees were sought using a heuristic search starting by 1000 random addition sequences followed by

TBR and keeping 99 trees in each replication. Strict consensus tree was constructed from the most parsimonious trees found and bootstrap support plotted for resolved lineages using 1000 replicates.

RESULTS

Molecular affinities

The chloroplast (cp), ITS, and ITS+cp alignments comprised 1382, 1466, and 2838 nucleotide sites, respectively, with additional 41 characters from the indel scoring of the chloroplast partitions in the latter two datasets. Topology of trees agrees among methods of phylogenetic inference, although with different levels of support, essentially similar for BI and ML, and lower from MP for some of the branches. Hence we present only the topology with branch lengths from the BI and add the support indication from other methods on the respective trees (Figs. 1-3).

The inference from analysed chloroplast regions (Fig. 1) and the ITS (Fig. 2) agrees in most aspects. Most of the species with caducous leaf apices except *D. anserinocapitatus* group into a well-supported clade, which also includes *D. rivicola* and *D. asperifolius*, essentially in agreement with the original delimitation of sect. *Rufiduli* by Chen (1941). Chloroplast data support the inclusion of *D. sinuosus* and *D. revolutus* in the sister position to the rest of the clade, while the ITS data separate these two taxa into a poorly supported position sister to the rest of analysed *Didymodon* taxa. All accessions of *D. anserinocapitatus* are nested within other representatives of sect. *Didymodon*, in a sister position to *D. cordatus*, which itself is closely related to *D. validus* (data not shown but compare also Werner *et al.*, 2005). Members of *Fuscobryum* (sect. *Rufiduli* sensu Zander, 1999) except *D. norrisii* form a well-supported clade within the sect. *Didymodon*, and *D. norrisii* appears to be nested within sect. *Vineales*. South Hemisphere taxa with bulging cells, represented by *D. fuscus* and *D. xanthocarpus*, form a moderately supported clade in a sister position to the clade formed by sect. *Asteriscium* and sect. *Didymodon* in the analysis of chloroplast data but one of the *D. fuscus* s.l. accessions appears unsupported sister to sect. *Rufiduli* in the ITS tree (ML analysis nevertheless supports a clade containing this accession in a sister position to *D. fuscus* s.str. + *D. xanthocarpus*). Conflict between chloroplast and ITS data is also seen in the positions of *D. rigidulus*, *D. acutus* and *D. icmadophilus* but the chloroplast information is poorly supported. The concatenation of all regions (Fig. 3) supports the chloroplast-based phylogeny with respect to the position of *D. sinuosus* and *D. revolutus*, as well as retaining *D. fuscus* s.l. and *D. anserinocapitatus* accessions in monophyletic lineages but in case of *D. rigidulus*, *D. acutus* and *D. icmadophilus* the signal from ITS data is stronger.

The species-level view surprisingly shows many of the analysed taxa of sect. *Rufiduli* non-monophyletic. *D. hedysarififormis* is monophyletic only after about half of

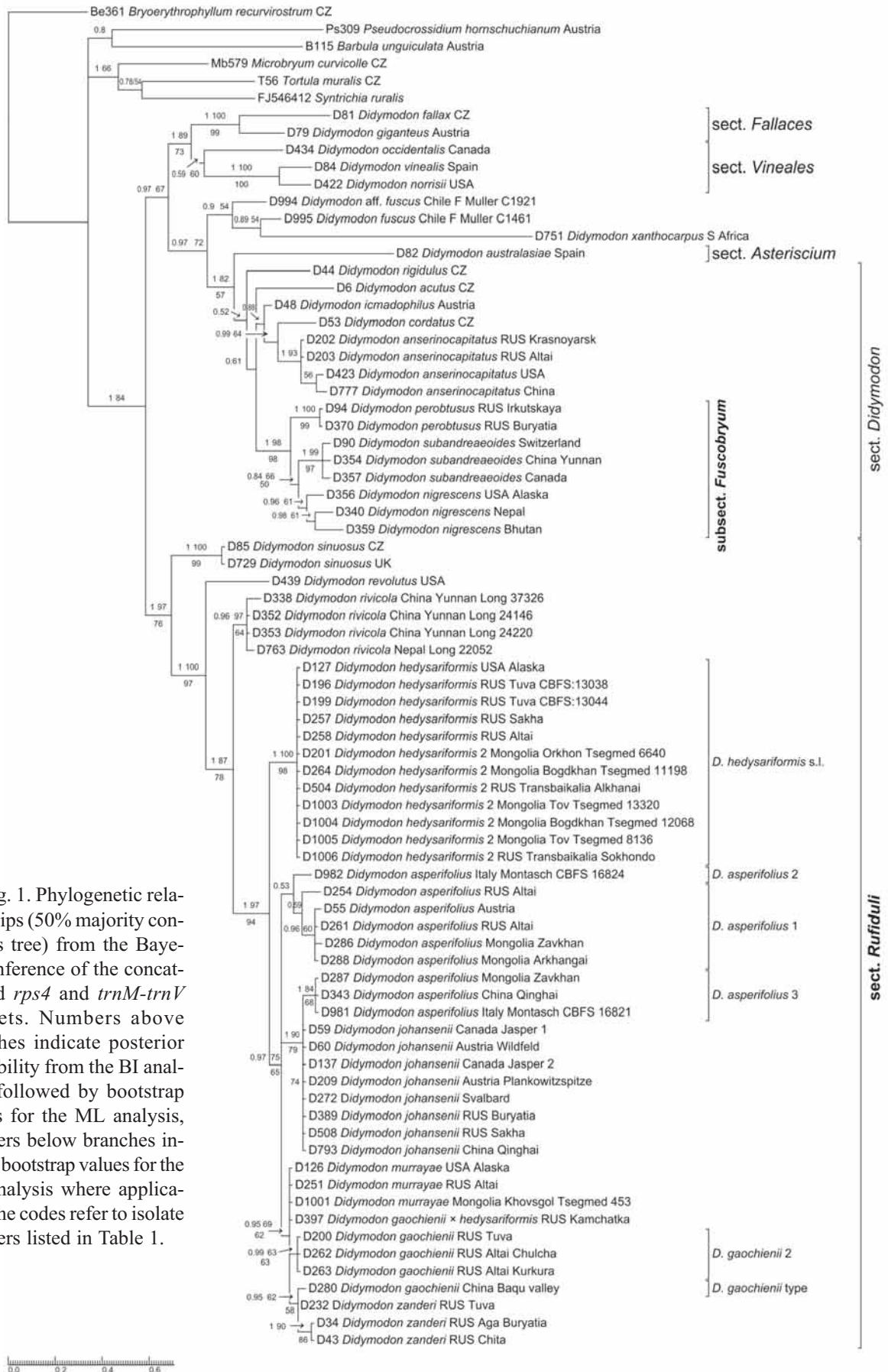


Fig. 1. Phylogenetic relationships (50% majority consensus tree) from the Bayesian inference of the concatenated *rps4* and *trnM-trnV* datasets. Numbers above branches indicate posterior probability from the BI analysis, followed by bootstrap values for the ML analysis, numbers below branches indicate bootstrap values for the MP analysis where applicable. The codes refer to isolate numbers listed in Table 1.

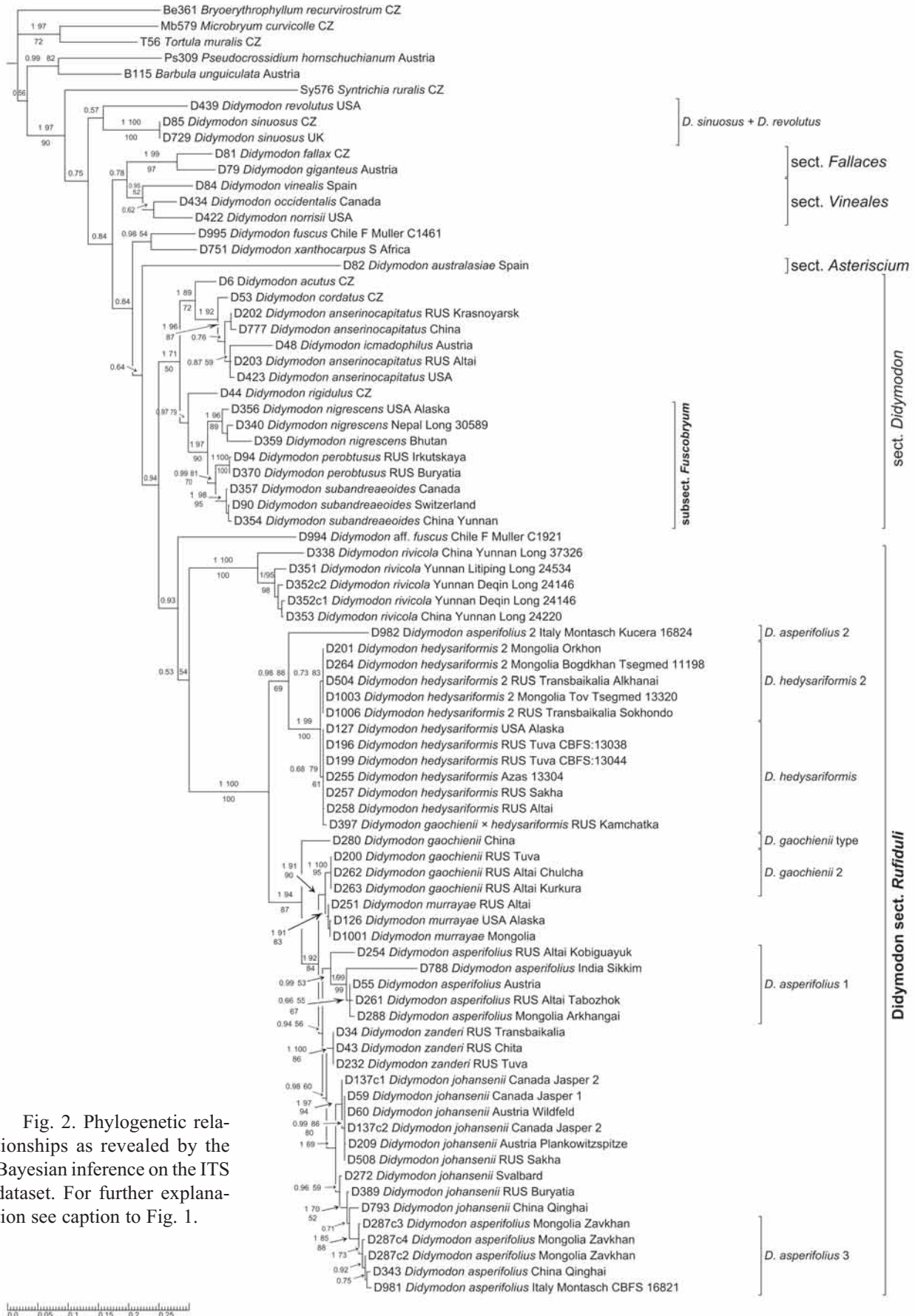


Fig. 2. Phylogenetic relationships as revealed by the Bayesian inference on the ITS dataset. For further explanation see caption to Fig. 1.

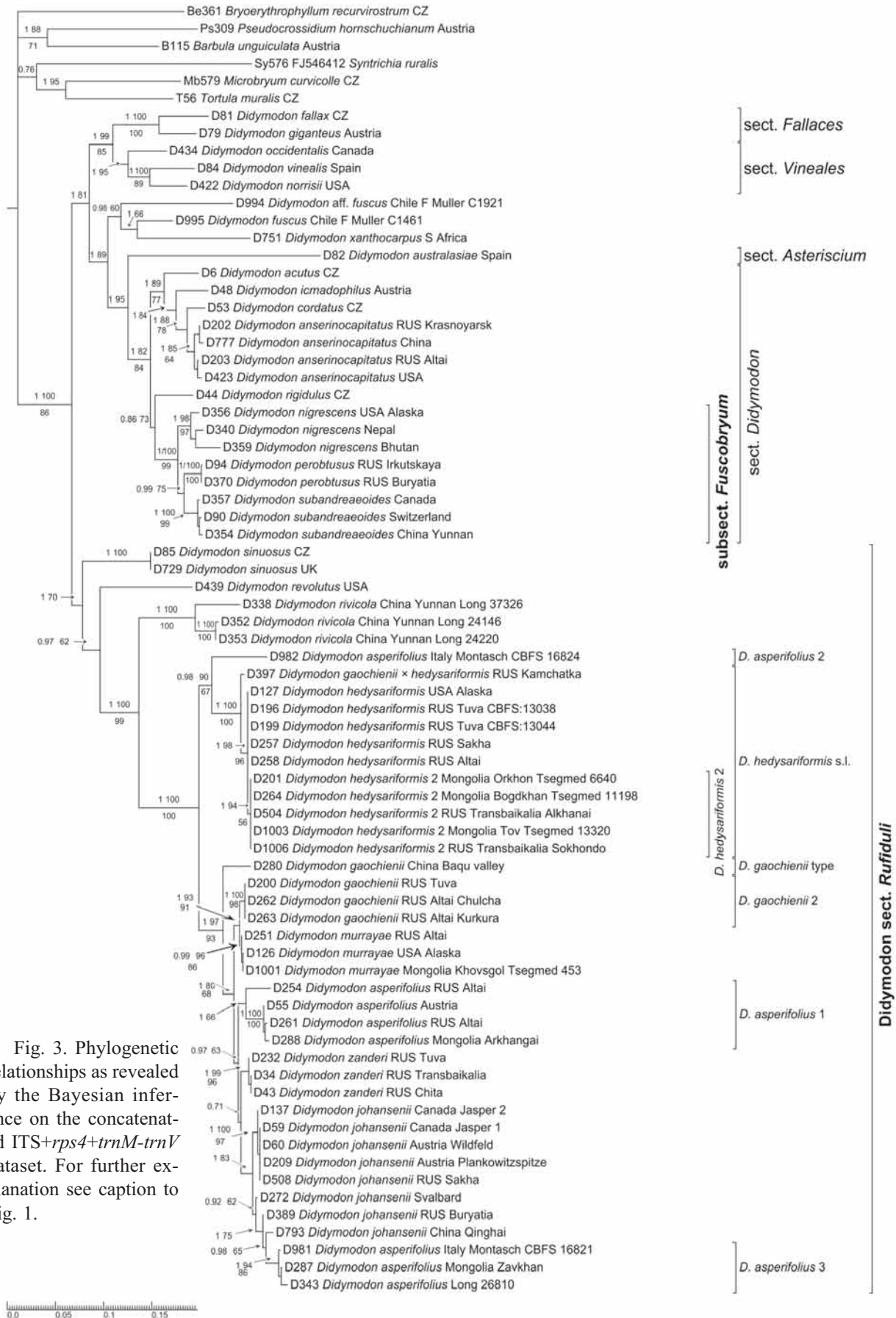


Fig. 3. Phylogenetic relationships as revealed by the Bayesian inference on the concatenated ITS+*rps4*+*trnM*-*trnV* dataset. For further explanation see caption to Fig. 1.

the analysed accessions with the morphology of *D. gaochienii* sensu Otnyukova (2002) is recognized as '*D. hedysarifformis*-2', a taxon with the chloroplast sequence identical to *D. hedysarifformis* and ITS sequence differing in one constant ITS1 substitution and two 2-bp deletions from the rest of otherwise rather variable *D. hedysarifformis* accessions. Neither the rest of analysed accessions, morphologically corresponding to *Didymodon gaochienii*, is monophyletic. The isotype specimen has a completely unique sequence, different in one *rps4* site and two *trnM-trnV* sites from the Russian accessions of that taxon and being only distantly related to the rest of the section members in its ITS sequence. Interestingly, its chloroplast sequence is identical to *D. murrayae* except for one unique substitution which has not been observed in any other of the analysed accessions. The ITS sequence with many deletions and scarcely alignable regions in ITS1 might however have likely resulted as partial artefact during the cloning procedure. In one of the samples from Kamchatka (isolate 397), the chloroplast sequence is identical to *D. murrayae* (different in only one base of the *trnM-trnV* region from Russian *D. gaochienii*) but the ITS sequence corresponds to *D. hedysarifformis*, suggesting the possible hybridization between the two taxa. *Didymodon johanssenii* is monophyletic only based on chloroplast data (with their sequences completely uniform), otherwise it necessitates the inclusion of '*D. asperifolius*-3' into one of its ITS clades. *Didymodon asperifolius* in its current morphological understanding is deeply polyphyletic, with individual accessions belonging to at least three lineages, named here provisionally *D. asperifolius* 1–3.

South American taxa with bulging lamina cells, which share the general habit and costa anatomy with typical representatives of sect. *Vineales*, do not seem to be related with this lineage. Rather, they might represent a basal lineage within *Didymodon* together with the South African *D. xanthocarpus*, sister to both sections *Asteriscium* and *Didymodon*. However, this hypothesis needs to be tested with a better representation of South Hemisphere taxa.

Morphological considerations

There is a reasonable level of match between the partly surprising molecular affinities and morphological characters if some of the existing sectional and species-level concepts are reconsidered. The addition of *D. zanderi*, *D. hedysarifformis*, *D. gaochienii*, *D. murrayae*, *D. johanssenii*, and *D. sinuosus* into the Chen's concept of sect. *Rufiduli* necessitates no significant morphological amendments except for accounting for the variability in costa excurrency, which is percurrent to excurrent in some of these taxa. On the other hand, in addition to the rufous colour and bilaterally bulging to mammillose lamina cells, all these taxa share characters that have not been mentioned by Chen, such as the fragile and disintegrating lamina in the upper part of the leaf and disintegrating and caducous tip of the costa in taxa with its excurrent part. Also, in contrast to other representatives of

Didymodon, the members of sect. *Rufiduli* in the amended sense share a disproportionately narrow costa with reduced anatomical differentiation. This character is useful e.g. in the differentiation of *D. anserinocapitatus* (sect. *Didymodon*) from the superficially similar *D. johanssenii*, in addition to the colour differences. Both *D. anserinocapitatus* and *D. johanssenii* were recognized as species closely related to *D. rigidulus*, and hence considered to represent two of few taxa recognized within the sect. *Didymodon* by Zander (2013). While *D. anserinocapitatus* indeed belongs within sect. *Didymodon*, as evidenced by the well-differentiated costa anatomy and absence of rufous colour of plants, *D. johanssenii* only shares the obviously convergent character of swollen breaking excurrent parts of costa (Figs. 32–33), but otherwise matches well the delimitation of sect. *Rufiduli*, with rufous colour of plants, reduced costa anatomy and bulging lamina cells. The addition of *D. asperifolius* in sect. *Rufiduli* might look more surprising, as even Chen (1941) recognized this taxon within the sect. *Fallaces* (named there incorrectly *Barbula* subsect. *Reflexae* Mönk.), followed by most other authors (Zander, 1993; Jiménez *et al.*, 2005 but not Saito, 1975), until Zander (2013) established a genus of its own, *Exobryum*, to account for the unusual combination of morphological characters found in this species. However, *D. asperifolius* shares the rufous colour and proportionally weak costa with reduced anatomy, as well as the sometimes fragile upper leaf lamina and sometimes bulging leaf cells with the other members of the section, hence only the robust habit, patent to squarrose leaves in wet state, porose basal cells, and mostly absent central strand of the stem are the alien characters of the species, shared with some species of sect. *Fallaces*. Much more problematic is the inclusion of *Didymodon revolutus*. This seems to be an extremely specialized species of the genus with characters hardly attributable to any of the generally recognized sections, such as the broadly obtuse leaves with revolute margins up to the apex and costa ending below apex, with bifurcations (spurs) in its terminal part. The unusual combination of characters led Cardot (1909) to the establishment of a new monotypic genus, *Husnotiella* at the time of the description and since then, its affinities have never been thoroughly discussed, neither by Williams (1913), who synonymized *Husnotiella* with *Didymodon*, nor by Zander (2013), who combined the species into *Trichostomopsis* (= *Didymodon* sect. *Asteriscium*). Although *D. revolutus* shares the somewhat reduced costa anatomy with other members of sect. *Rufiduli* as recognized here, it is also strikingly different in the absence of rufous colour, non-fragile leaf lamina and hardly bulging lamina cells except for the ventral epidermal cells of the costa. Hence, its inclusion in sect. *Rufiduli* is only tentative at the moment and should be tested more thoroughly in the future, although one should bear in mind that analogical surprising affinities of highly specialized taxa are not so exceptional (compare, e.g., the affinity of *Hydrogrim-*

mia mollis with members of *Grimmia* subgenus *Orthogrimmia*; Streiff 2006; Hernández-Maqueda *et al.*, 2008, or the affinity of *Ephemerum* with *Pottiaceae* trib. *Trichostomeae*; Werner *et al.*, 2004; Cox *et al.*, 2010; Goffinet *et al.*, 2011; Kučera *et al.*, 2013).

One of the serious potential flaws of this study is the absence of *Didymodon rufidulus* in our molecular analysis and the lectotypification of the sect. *Rufiduli* with this species at the same time. Chen (1941) has not typified his newly established *Barbula* sect. *Rufidulae* and after *B. subrivicola* has been synonymized with *Didymodon nigrescens*, the choice of the lectotype is only possible with either *D. rufidulus* or *D. rivicola*. The latter species would unequivocally match the original description of the section, has been analysed molecularly and clearly belongs to the lineage recognized here as sect. *Rufiduli*, but the name and the first position in Chen's listing the species favours *D. rufidulus* as the first choice candidate for the lectotypification. The first author was able to study the isotype of *D. rufidulus* from herbarium JE and the isotype of *Didymodon handelii* from E, synonymized with *D. rufidulus* by Chen (1941). Although the isotype of *D. rufidulus* only includes one stem fragment of the plant, it matches well the Chen's illustration and the original description and in fact resembles the recently described *D. zanderi* in both shape of narrowly lanceolate leaves with costa ending below apex and occasionally fragile upper part of the lamina, and bilaterally bulging leaf cells (hardly papillose in the type of *D. rufidulus* but slightly papillose in the type of *D. handelii*). The short straight peristome teeth are also very similar in both taxa, which together provide strong arguments for inclusion of *D. rufidulus* into the lineage of molecularly barcoded taxa containing *D. rivicola*. The type of *D. handelii* looks similar to the type of *D. rufidulus* but it is smaller in stature, its leaves are more similar in shape to *D. fallax* and the upper cells are not conspicuously bulging, hence the identity with *D. rufidulus* is in our opinion not certain.

Molecular data have shown that the morphological characteristics related to the shape of the segments of the fragile costa or upper lamina, which were used to the delimitation of *D. hedyariformis* from *D. gaochienii* (Otnyukova, 1998, 2002) are not in agreement with the molecular data, and probably are to be considered homoplastic. Unfortunately it is not possible to solve this discrepancy between morphological and molecular data by the synonymization of the two taxa, as the *D. hedyariformis* clade, which includes the Mongolian *D. gaochienii*-like accessions appears sister to all other taxa of the sect. *Rufiduli*, including the morphologically very different *D. zanderi*, *D. johansenii* and *D. asperifolius*, and the synonymization all these taxa would bring little sense to the practical taxonomy of the group. It is also not quite impossible that the deep polyphyly of the three lineages within *D. gaochienii*, seen in the three studied gene regions from two genomic compartments arises from

the conflict between gene trees and species trees due to the deep coalescence / incomplete lineage sorting and might not reflect the situation of the whole genome. It is interesting to mention that similar deep polyphyly was seen in the analysed accessions of *Streblotrichum convolutum* in the study by Kučera *et al.* (2013). Another important fact was found following the detailed comparison of types of *D. gaochienii* and *D. murrayae*. The characteristically toothed acute apex of *D. murrayae* was found on plants of the studied isotype of *D. gaochienii* (Fig. 8), which, together with the above mentioned molecular data constitutes a solid argument for synonymization of the two taxa, although the molecular affinities should be studied on more accessions from the Tibetan area to account for uncertainties which result from the incompletely preserved DNA in the type of *D. gaochienii*. Anyway, the highly probable identity of the two types necessitates the formal description of *D. gaochienii sensu Otnyukova* (2002), here named *D. gaochienii 2*, which nevertheless should not be accomplished prior to the examination of the type of *D. fragilicuspis*, regarded identical to *D. gaochienii* by Sollman (2006).

The polyphyly of *D. asperifolius* in present circumscription is only superficially similar to the situation of *D. gaochienii*. Upon the morphological examination of the specimens, assigned to the three revealed lineages within the contemporary concept of the species, we were able to find differences, which might later prove sufficient for the description of new taxa corresponding to the molecularly barcoded lineages. These characters include the presence of stem central strand, character of papillosity of lamina cells, the stature of the plants and subtle differences in the leaf shape. It may be noted that Jiménez *et al.* (2005), in agreement with Saito (1975) have not observed the central strand in the stem of studied specimens, while the other authors did (Zander, 1979; Kučera, 2000). Nevertheless, given the large collection numbers of *D. asperifolius* worldwide and the existence of several older types that have been put into synonymy with *D. asperifolius*, we prefer to perform a more thorough revision before attempting at describing new taxa within the complex.

Molecular support for Zander's delimitation of the genus *Fuscobryum* (recognized as a subsection of *Didymodon* sect. *Didymodon* here, see below) only requires the removal of *Didymodon norrisii*, which seems to be closely related to *D. vinealis*, in agreement with earlier results of Jiménez *et al.* (2012), based on different chloroplast genes. Moreover, as already pointed out by Zander (1999), *D. norrisii* differs from the members of sect. *Rufiduli* in the stout costa and pluripapillose lamina cells, both characteristic of sect. *Vineales*. The differences of subsect. *Fuscobryum* from sect. *Rufiduli* include deep brown to blackish, rather than rusty brownish colour and non-fragile lamina. An interesting autapomorphy of the section might include the flattened, spirally twisted seta,

as seen in *D. nigrescens*, the type species of the subsection; in other species of that group the sporophyte is unfortunately not known.

TAXONOMIC SYNOPSIS OF THE TAXA

In the following synopsis, we list the taxa accepted and excluded from *Didymodon* sect. *Rufiduli*. We refer to existing sources for synonymy, descriptions and distribution data and only list additional information if applicable.

***Didymodon* Sect. *Rufiduli* ‘*Rufidulus*’ (P.C. Chen) R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 162. 1993. Lectotype: *Didymodon rufidulus* (Müll. Hal.) Broth., **here designated**.**

Barbula Sect. *Rufidulae* ‘*Rufidula*’ P.C. Chen, Hedwigia 80: 210. 1941.

Exobryum R.H. Zander, Framew. Post-Phylogenet. Syst. p. 96. 2013. (14 Sep 2013), **syn. nov.** Type: *Exobryum asperifolium* (Mitt.) R.H. Zander (= *Didymodon asperifolius* (Mitt.) H.A. Crum, Steere & L.E. Anderson).

Husnotiella Cardot, Rev. Bryol. 36: 71, **syn. nov.** Type: *Husnotiella revoluta* Cardot (= *Didymodon revolutus* (Cardot) R.S. Williams).

Characteristics of the section include rusty red coloration, dark green in less exposed parts of plants, tendency towards development of fragile upper part of leaf lamina and/or excurrent part of costa, serving for vegetative propagation, bilaterally bulging lamina cells with often only single papillae, and relatively weak costa with few guide cells in one row and ventral stereids absent. Sporophyte production is rare; the peristome (when known) is reduced, of short, straight, irregularly divided filiform teeth.

ACCEPTED SPECIES

Didymodon asperifolius (Mitt.) H.A. Crum, Steere & L.E. Anderson, Bryologist 67: 163. 1964.

Barbula asperifolia Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 34. 1859, basionym.

Exobryum asperifolium (Mitt.) R.H. Zander, Framew. Post-Phylogenet. Syst. p. 96. 2013. (14 Sep 2013); *Didymodon rufus* var. *gorodkovii* Abramova & I.I. Abramov, *Didymodon gorodkovii* (Abramova & I.I. Abramov) Schljakov, *Didymodon asperifolius* var. *gorodkovii* (Abramova & I.I. Abramov) Afonina, Problemy Briologii v SSSR p. 13. 1989.

For additional synonymy, see Jiménez *et al.* (2005).

Description and distribution summarized in Jiménez *et al.* (2005).

It is probable that at least one new taxon will be described from within the current circumscription of the species. Nevertheless, the type, according to existing descriptions, seems to agree with representatives of the first lineage (*asperifolius* 1) and these at least overwhelmingly show the typical characters reported for the species, such as the large stature, completely absent stem central strand and papillose upper lamina cells.

Didymodon gaochienii B.C. Tan & Y. Jia, J. Hattori Bot. Lab. 82: 309. f. 12–19. 1997. Figs. 4–8, 17–22(–26)

(?= *Didymodon fragilicuspis* Broth., Ann. Bryol. 1: 31. 1928)

(?= *Didymodon murrayae* Otnyukova, Arctoa 11: 345. f. 6. 2002)

The description and illustration of Tan & Jia (1997) and Otnyukova (2002) do not fully correspond to our examination. Morphologically, the type of *D. gaochienii* (Figs. 4–8) matches the type of *D. murrayae* (Figs. 9–13), whereas the other examined plants of these species show subtle morphological differences, as well as molecular differences, which are nevertheless much smaller than the position in phylogenetic trees suggests. Broader sampling, particularly in the Chinese part of the distribution area, is necessary to resolve the question. Moreover, *D. gaochienii* sensu Otnyukova (2002), which probably should be described as a taxon of its own, falls within two molecularly defined lineages and we have not found characters which would allow assigning the specimens to them. Whether deep coalescence / incomplete lineage sorting is responsible for the polyphyletic nature of ‘*D. gaochienii*’ lineages, or indeed more species should be recognized with morphological characteristics that we were not able to elaborate, needs to be addressed in future studies. Moreover, hybridization probably occurs between *D. gaochienii* 2 (*D. gaochienii* sensu Otnyukova) and *D. hedysarifformis*. Adding to the complexity of problems, Sollman (2006) synonymized *D. gaochienii* with the older *D. fragilicuspis* Broth., described from Kashmir (Brotherus, 1928), which would also mean a significant range extension for the species (known distribution until that study included the eastern part of Tibetan plateau, Southern Siberia and Mongolia but see below). Unfortunately, we were not able to check the type material (the loan request to herbarium H was not answered) and Sollman provides no details on the Brotherus’s type (“The type collections of *D. f.* and *D. g.* were carefully compared and were found to match well”). In conclusion, the application of the name *Didymodon gaochienii* (or *D. fragilicuspis*) remains problematic and cannot be matched to molecularly resolved lineages at present. The only guaranteed specimen, which can be unequivocally assigned to *D. gaochienii* s. str. is the type specimen, and very probably, the type of *D. murrayae* from Russia, Altai belongs here as well.

Didymodon hedysarifformis Otnyukova, Arctoa 7: 207. f. 1–36. 1998. Figs. 29–31

[+14–16 for *D. hedysarimosmis* 2]

For description and illustration, see Otnyukova (1998, 2002). Reported characters only apply to the lineage described here as *hedysarifformis* 1, which has been using molecular data confirmed to occur in Russian Altai, Tyva (Otnyukova, 2002), Yakutia (Ivanova *et al.*, 2005), Kamchatka (Czernyadjeva, 2012), and North American Alaska (which is a new record for America). The occurrence in Mongolia, reported by Tsegmed (2001), is nevertheless probable.

Other records: Afonina (2007): Transbaikal Territory; Bezgodov *et al.* (2013): Amurskaya Province.

New record: U.S.A., Alaska: Talkeetna Quad. Denali State Park, Lower Troublesome Creek state recreation site, George Parks Hwy, 62°37'N, 150°14'W, on bark of roadside mature *Populus balsamifera*, 7.7.1991 A.R. Perry 7670 (NMW).

Didymodon johansenii (R.S. Williams) H.A. Crum, *Canad. Field-Naturalist* 83: 157. 1969. Figs. 32-34

Barbula johansenii R.S. Williams, *Rep. Canad. Arctic Exped. 1913-1918*, 4(E): 4. f. 1-12. 1921.

For description and illustration, see Otnyukova (2002).

Previous records: Otnyukova (2002): Chukotka, Altai, Khakassia; Ivanova *et al.* (2005): Yakutia; Fedosov *et al.* (2011): Taimyr; Bardunov (2000) and Fedosov (2008): Irkutsk Province; Afonina (2009): Buryatia; Jiménez (2006): Tajikistan; Redfearn *et al.* (1996): China (Qinghai); Sollman (2008, 2010): Bhutan, Pakistan; Zander (2007): NW North America.

Didymodon murrayae Otnyukova, *Arctoa* 11: 345. f. 6. 2002. Figs. 9-13, 27-28

For description and illustration, see Otnyukova (2002). Toothed apex of excurrent part of the costa in juvenile leaves has been found to be the best diagnostic character of *D. murrayae*. As mentioned above, the type seems to be identical with the type of *D. gaochienii*. The differences in the invariable sequences of Siberian *D. murrayae* and the type of *D. gaochienii* might well be found to be not important but should their differentiation be confirmed, *D. murrayae* would stay a species of its own, pending the amendment of morphological characteristics with respect to *D. gaochienii*.

Previous records: Asia: Altai (Russia, Altai Rep.), North America: Alaska, British Columbia (Zander 2007).

New country record: Mongolia: Khövsgöl Province (Aimag), Renchinlkhümbe Sum, Mt Khar-Murugu-Uul, stony fields, on rocks, 21.6.2006 Ts. Tsegmed 453 (CBFS).

Didymodon revolutus (Cardot) R.S. Williams, *Bryologist* 16: 25. 1913.

Basionym: *Husnotiella revoluta* Cardot, *Rev. Bryol.* 36: 71. 1909.

Trichostomopsis revoluta (Cardot) R.H. Zander, *Framew. Post-Phylogenet. Syst.* p. 93. 2013. (14 Sep 2013).

For additional synonymy, description and illustration see Allen (2002), Jiménez *et al.* (2005), or Zander (2007). The reasons for transferring the species to *Trichostomopsis* have not been specified by Zander (2013) but Allen (2002) lists similarities between *D. australasiae* and *D. revolutus*, which include the bulging ventral epidermal cells of the costa and the slightly developed stem hyalodermis. On the other hand, thickened non-hyaline basal leaf cells and costa guide cells in one row in *D. revolutus* contradict the affinity with *Didymodon* sect. *Asteriscium* on morphological reasons.

Didymodon rivicola (Broth.) R.H. Zander, *Ann. Bot. Fenn.* 20: 222. 1983. Figs. 40, 49-50

Barbula rivicola Broth., *Symb. Sin.* 4: 41. 1929.

For description and illustration see Chen (1941) or Li *et al.* (2001). The species is quite similar to *D. zanderi*, from which it differs in broader leaves and shorter apices, and more pronouncedly mammillose bulging lamina cells. The leaves show also less pronounced tendency for disintegration of the upper lamina.

The species was believed to be endemic to China, where it is quite broadly distributed with the centre of distribution in Yunnan (Li *et al.*, 2001). Miede (1991) however also published a record from Central Nepal. Below, we list new regional occurrences for India (Jammu and Kashmir, Uttarakhand) and Nepal.

INDIA: Jammu and Kashmir: Gangabal, W end of the larger lake, ca. 3640 m, damp rock crevice in a rock bluff descending almost to the water, 12.8.1989 C.C. Townsend 89/469 (E); Uttarakhand, Garhwal Himal: between Dhanolti and Mussoorie, 30°26'N, 78°13'E, on half-shaded rock in a cultured land 2360 m, M. Lüth 6686 (herb. Lüth, dupl. CBFS).

NEPAL: Rasuwa distr., N bank of Langthang Khola between Lama Hotel and Ghora Tabela, 28°10'N, 85°27'E, 2610 m, on boulder, 24.4.1992, Long 22052 (E).

Didymodon rufidulus (Müll. Hal.) Broth., *Nat. Pflanzenfam.* I(3): 405. 1902. Figs. 38, 42-44, 47

Basionym: *Barbula rufidula* Müll. Hal., *Nuovo Giorn. Bot. Ital.*, n.s. 3: 102. 1896.

?= *Didymodon handelii* Broth.

According to Chen (1941), followed by other authors, additional synonyms include *Trichostomum sulphuripes* Müll. Hal. and *T. nodiflorum* Müll. Hal. (not seen).

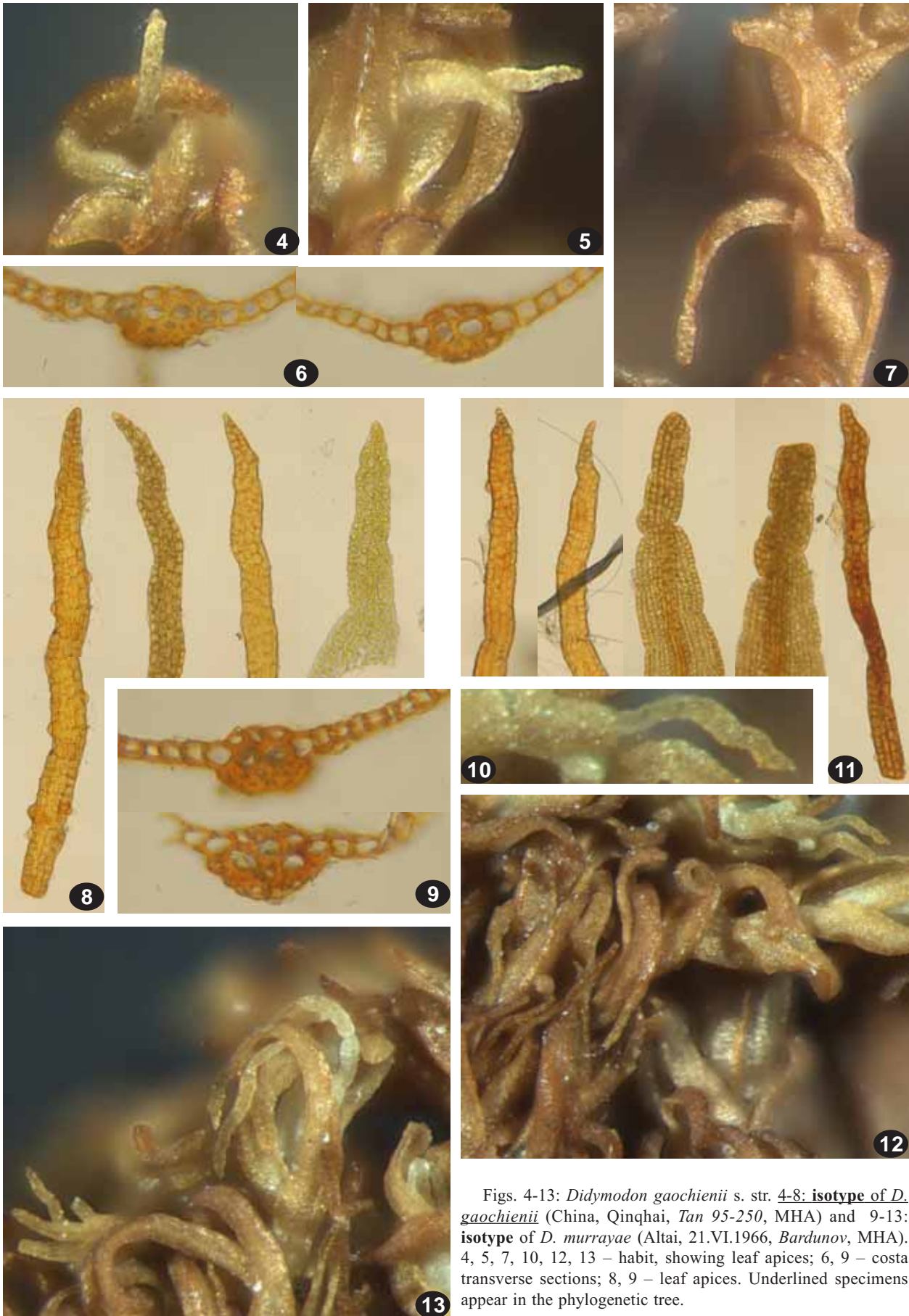
For description and illustration see Chen (1941) or Li *et al.* (2001). It seems that the taxon has not been generally well understood. For instance, none of the (anyway few) specimens housed in herbarium E with generally large collections of Sino-Himalayan bryophytes matches the type, except perhaps the isotype of *Didymodon handelii*. The other specimens belonged either to *D. icmadophilus* or to *D. asperifolius* s.l. The species seems to be morphologically transitional between *D. zanderi* and *D. rivicola*, as illustrated in Figs. 38-50.

Didymodon sinuosus (Mitt.) Delogne, *Bull. Soc. Roy. Bot. Belgique* 12: 423. 1873.

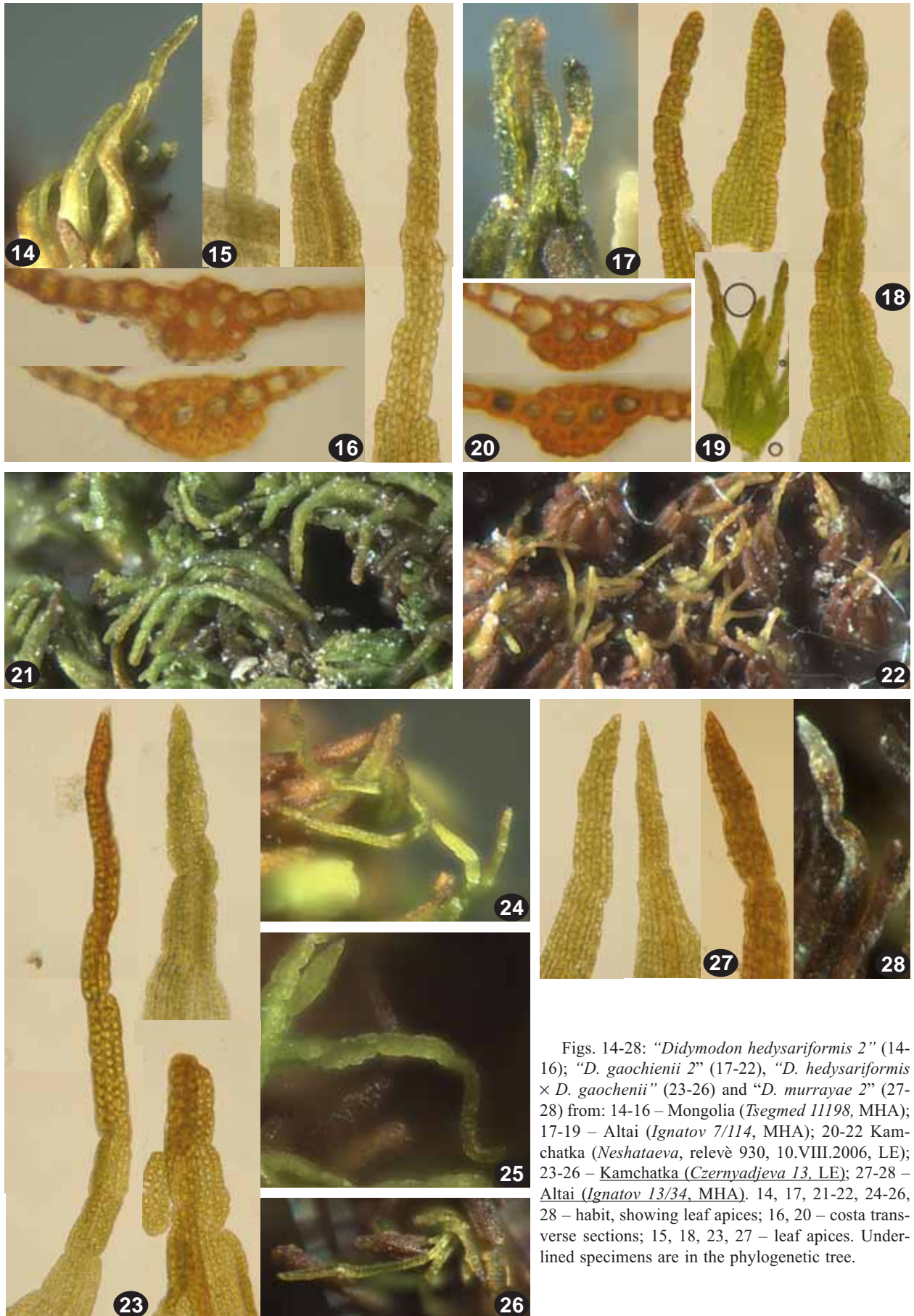
Basionym: *Tortula sinuosa* Mitt., *J. Bot.* 5: 327. 1867.

For additional synonymy, description and illustration see Jiménez (2006).

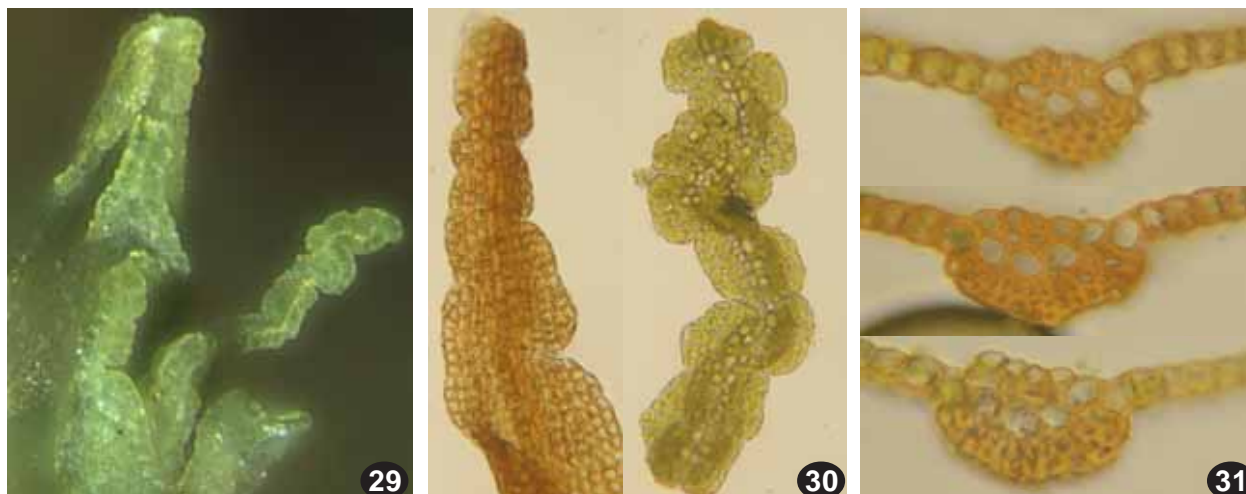
The species matches well the morphology of sect. *Rufiduli* except for the relatively stout costa with commonly present two rows of guide cells, typical of species of sect. *Vineales* and denticulate leaf apices and costa in younger leaves, which are unique for this species (the character of denticulation is different in *D. erosodenticulatus*). Jiménez (2006) also reports the occurrence of multicellular gemmae developed on the upper ventral part of the costa seen in a sample from Azerbaijan, but this character has never been observed in any other specimen.



Figs. 4-13: *Didymodon gaochienii* s. str. 4-8: **isotype** of *D. gaochienii* (China, Qinqhai, *Tan 95-250*, MHA) and 9-13: **isotype** of *D. murrayae* (Altai, 21.VI.1966, *Bardunov*, MHA). 4, 5, 7, 10, 12, 13 – habit, showing leaf apices; 6, 9 – costa transverse sections; 8, 9 – leaf apices. Underlined specimens appear in the phylogenetic tree.



Figs. 14-28: "*Didymodon hedysarifformis* 2" (14-16); "*D. gaochienii* 2" (17-22), "*D. hedysarifformis* × *D. gaochienii*" (23-26) and "*D. murrayae* 2" (27-28) from: 14-16 – Mongolia (*Tsegmed 11198*, MHA); 17-19 – Altai (*Ignatov 7/114*, MHA); 20-22 Kamchatka (*Neshataeva*, relevè 930, 10.VIII.2006, LE); 23-26 – Kamchatka (*Czernyadjeva 13*, LE); 27-28 – Altai (*Ignatov 13/34*, MHA). 14, 17, 21-22, 24-26, 28 – habit, showing leaf apices; 16, 20 – costa transverse sections; 15, 18, 23, 27 – leaf apices. Underlined specimens are in the phylogenetic tree.



Figs. 29-31: *Didymodon hedysarifformis* from isotype: Tuva (13.VII.1996, *Otnyukova*, MHA), 29 – habit, showing leaf apices; 30 – leaf apices; 31 – costa transverse sections. Underlined specimen is in phylogenetic tree.

Previous records: Europe, Middle East, Caucasus. In Russia was reported from Gelendzhik, Caucasus (Abramova & Abramov, 1962). Some additional collections were made along Black Sea coast, from Sochi area (Ignatov & Ignatova, 1.VIII.2002, MHA) to Utrish (e.g. Ignatov & Ignatova #05-178, MHA).

Didymodon zanderi Afonina & Ignatova, *Arctoa* 16: 135. f. 1–3. 2007. Figs. 39, 45-46, 48

For description and illustration, see Afonina & Ignatova (2007). Relationship to *D. hedysarifformis* has already been suggested by the authors of the description

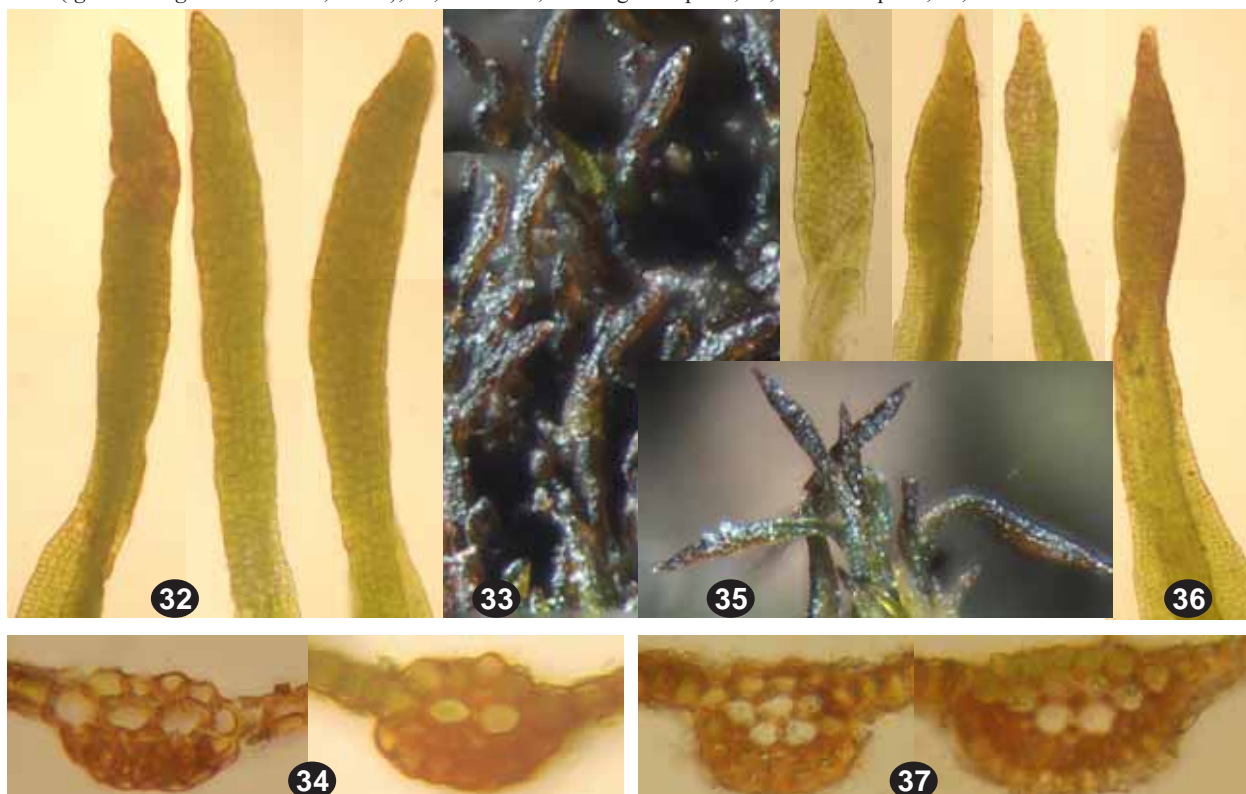
and in fact, this species is morphologically closest to *D. rufidulus*, as argued above.

In addition to distribution in original description (Transbaikalia, Buryatia, Yakutia, Taimyr, Altai, Kamchatka, Primorsky Territory), the species was found in Khabarovsk Territory (Ignatova *et al.*, 2013), Mongolia (Tsegmed, 2010) and Inner Mongolia Province of China (Bai *et al.*, 2008).

Didymodon* sect. *Didymodon* subsect. *Fuscobryum (R.H. Zander) J. Kučera, *comb. nova*

Basionym: *Fuscobryum* R.H. Zander, *Framev. Post-Phylogenet. Syst.* p. 98. 2013. (14 Sep 2013).

Figs. 32-37: *Didymodon johansenii* (32-34) and *D. anserinocapitatus* (35-37). 32-34 – Yakutia (*Ignatov* 11-4049, MHA), 35-37 – Altai (*Ignatov & Ignatova* 12-346, MHA); 33, 35 – habit, showing leaf apices; 32, 36 – leaf apices; 34, 37 – costa transverse sections.





Figs. 38-50. *Didymodon rufidulus*, **isotype**, JE (38, 42-44, 47); *D. zanderi*, **holotype**, Transbaikalia, *Afonina* 3406, MHA (41) and *Afonina* 3405, CBFS (39, 45-46, 48); *D. rivicola*, China, Long 24146, E (40, 49-50). 38-

40 – costa transverse sections; 44, 46, 50 – leaves; 41, 47-49 – habit, showing leaf apices; 42, 44, 45 – leaf apices. Underlined specimens are in phylogenetic trees.



Type: *Didymodon nigrescens* (Mitt.) K. Saito, J. Hattori Bot. Lab. 39: 510. 1975.

Characteristics of the subsection include dark brown to blackish coloration, upper part of leaf lamina not fragile, costa hardly excurrent, and vegetative propagation occasional by means of axillary gemmae. Lamina cells bilaterally bulging or not, commonly conspicuously thick-walled, with multiple/branched papillae. Costa in well-developed plants with a single row of guide cells and a weak band of ventral and a larger group of dorsal stereids. Sporophyte production known only in *D. nigrescens*; the seta is flattened and twisted dextrorsely.

ACCEPTED SPECIES

Didymodon nigrescens (Mitt.) K. Saito, J. Hattori Bot. Lab. 39: 510. 1975. *Barbula nigrescens* Mitt., J. Proc. Linn. Soc., Bot., Suppl. 1: 36. 1859.

Fuscobryum nigrescens (Mitt.) R.H. Zander, Framew. Post-Phylogenet. Syst. p. 99. 2013. (14 Sep 2013).

For description and illustration see Chen (1941), Allen (2002), Li *et al.* (2001) and Zander (2007).

Didymodon subandreaeoides (Kindb.) R.H. Zander

Fuscobryum subandreaeoides (Kindb.) R.H. Zander, Framew. Post-Phylogenet. Syst. p. 99. 2013. (14 Sep 2013).

For additional synonymy, description and illustration see Kučera & Köckinger (2000) and Jiménez (2006).

Didymodon perobtusum Broth., Rev. Bryol., n.s., 2: 1. 1928.

Barbula perobtusum (Broth.) P.C. Chen, Hedwigia 80: 194. 28 f. 1–5. 1941.

Fuscobryum perobtusum (Broth.) R.H. Zander, Framew. Post-Phylogenet. Syst. p. 99. 2013. (14 Sep 2013).

For description and illustration see Chen (1941) or Zander (2007).

SPECIES EXCLUDED FROM SECTIONS *RUFIDULI* AND *DIDYMODON* SUBSECT. *FUSCOBRYUM*

Didymodon anserinocapitatus (X.J. Li) R.H. Zander, Bull. Buffalo Soc. Nat. Sci. 32: 162. 1993 (*Barbula anserinocapitata* X.J. Li, Acta Bot. Yunnan. 3: 103. f. 2: 1–9. 1981.) Figs. 35–37

For description and illustration see Otnyukova (2002) or Jiménez (2006). The species has convergent shape of swollen excurrent part of the costa (Figs. 35–36) serving vegetative propagation to *D. johansenii* (Figs. 32–33) but in fact is closely related to *D. cordatus* / *validus* / *tectorum* group of taxa, which belong to *Didymodon* Hedw. sect. *Didymodon* subsect. *Didymodon*. Morphological evidence for the relationship with the above named taxa includes the relatively strong costa with several layers of dorsal stereids, two rows of guide cells at least sometimes seen in all of the above named taxa and green to dark green colour of plants without reddish tones. In contrast to species of sect. *Vineales* which can have convergently identical anatomy of the costa, the red KOH reaction of cell walls and multiple branched papillae are not present.

Didymodon norrisii R.H. Zander, Bryologist 102: 112. f. 1–11. 1999. (*Fuscobryum norrisii* (R.H. Zander) R.H. Zander, Framew. Post-Phylogenet. Syst. p. 99. 2013. (14 Sep 2013).

For description and illustration see Zander (1999). This species shares the general look with *D. nigrescens*, owing to the typically dark brown colour and quite similar leaf shape. However, the anatomy of the costa is typical for other species of *Didymodon* sect. *Vineales* with two rows of guide cells and absent ventral stereids. The papillosity is less developed than in most species of the section but similar to, e.g., *D. brachyphyllus*, and still more developed than in *D. nicholsonii*. Bulging lamina cells approach those of *D. occidentalis* R.H. Zander, another rather similar species of sect. *Vineales*.

KEY TO THE TREATED TAXA

(*DIDYMODON* SECT. *RUFIDULI*, SUBSECT. *FUSCOBRYUM*, *D. ANSERINOCAPITATUS* AND *D. NORRISII*)

1. Plants green, with imbricate, not contorted, ovate-lanceolate rounded leaves, margin revolute up to the apex *D. revolutus*
— Plants rufous to dark brown or blackish at least in exposed parts, margin recurved not up to the apex 2
2. Leaves mostly ovate to broadly ovate-lanceolate with ± rounded apex 3
— Leaves mostly longer, from the ovate or oblong base long-lanceolate; if ovate, apex hardly rounded 4
3. Vegetative propagation by regularly formed deciduous flagelliform innovations with reduced, cochleariform leaves, axillary gemmae absent
..... *D. subandreaeoides*
— Occasional vegetative propagation by means of mostly unicellular axillary gemmae, flagelliform innovations with reduced leaves absent *D. perobtusum*
4. Specialized vegetative propagation by means of swollen excurrent parts of costa 5
— Specialized vegetative propagation by means of irregularly disintegrating upper lamina or disintegrating apices formed mostly by costa, but the costa not swollen 6
5. Plants green to dark green, costa strong, with two layers of guide cells and well developed dorsal stereids in multiple rows, upper lamina cells around 8 µm *D. anserinocapitatus*
— Plants typically rufous, costa weak, with a single layer of guide cells and weak dorsal stereid band, upper lamina cells mostly over 10 µm *D. johansenii*
6. At least young leaf apices with mostly regularly toothed margins *D. sinuosus*
— Leaf apices with margins entire or with few irregular teeth in the apical caducous part of the leaf ... 7
7. Leaves mostly patent to squarrose when wet, from ovate base gradually tapering to apex; plants typically robust, with long and porose basal cells and stem central strand absent *D. asperifolius* s.l.

- Leaves spreading, never squarrose when wet, from oblong-ovate base more abruptly narrowed to long-lanceolate apical part; basal cells never porose and at least weak stem central strand always present. 8
- 8. Leaf apices acute, gradually tapering, only occasionally fragile and disintegrating into variously large lamina parts, not containing the costa 9
- Leaf apices narrow and nearly lingulate, conspicuously fragile and mostly broken, disintegrating into segments containing costa and adjacent parts of lamina 13
- 9. Plants dark chestnut brown to blackish 10
- Plants dark green or rufous 11
- 10. Leaf cells typically with extremely thickened cell walls, costa weak, hardly ventrally prominent, with a single layer of guide cells, leaf apex not cucullate *D. nigrescens*
- Leaf cells with moderately thickened cell walls, costa stout, ventrally prominent, with two layers of guide cells and ventral stereids absent, leaf apex cucullate *D. norrisii*
- 11. Leaves broadly lanceolate or ovate-lanceolate, gradually tapering to acute apex *D. rivicola*
- Leaves lanceolate with long apex; if broadly lanceolate, than apiculate or blunt 12
- 12. Plants mostly dark green, leaf apex narrowly acuminate to apiculate, somewhat cucullate, in cross-section hollow, leaf cells bulging and papillose *D. zanderi*
- Plants mostly rufous, leaf apex gradually acuminate, not cucullate, keeled, leaf cells bulging, hardly papillose *D. rufidulus*
- 13. Terminal part of the caducous leaf tip acute, slightly irregularly toothed, solid for (15–)20–30 cells, which falls off as one fragment, composed mostly of the excurrent costa; below near transition to lamina notched and separates into fragments of usually 4–8(–12) cells long 14
- Terminal part of the caducous leaf tip blunt, composed of the costa lined with narrow lamina border, not toothed, notched and easily broken into fragments 4–8(–12) cells long 15
- 14. Terminal part of the caducous leaf tip composed of thin-walled cells, some of them conspicuously bulging *D. gaochienii* s.str.
- Terminal part of the caducous leaf tip composed of moderately thick-walled cells, without bulging cells *D. murrayae* 2
- 15. Leaf apex formed by irregularly notched fragments in a flexuose line, leaf cells around 8 µm *D. hedysarifformis* s.str.
- Leaf apex formed by relatively regularly notched fragments in a ± straight line, leaf cells mostly 10–14 µm *D. gaochienii* 2 incl. the *D. hedysarifformis*-2 lineage

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Table 1. Label data and accession numbers of studied specimens. New accessions are boldfaced.

Species	Isolate	Provenance	Collector_No	Herbarium	ITS	rps4	trnM-trnV
<i>Barbula unguiculata</i>	B115	Austria, Carinthia, Heiligenblut	Kučera 12829	CBFS	HM147804	HM147777	JQ890366
<i>Bryoerythrophyllum recurvirostrum</i>	Be361	Czech Republic, Sumperek, Mestske skaly	Kučera 12925	CBFS	JQ890527	JQ890468	JQ890407
<i>Didymodon acutus</i>	D6	Czech Republic, Breclav, Sedlec	Kučera 12684	CBFS	KP307477	KP307551	KP307667
<i>D. anserinocapitatus</i>	D202	Russia, Krasnoyarsk	Otnyukova	CBFS:13039	KP307480	KP307545	KP307640
<i>D. anserinocapitatus</i>	D203	Russia, Altai Republic, Malyi Yaloman	Ignatov & Ignatova				
			25/155	CBFS:13045	KP307485	KP307558	KP307664
<i>D. anserinocapitatus</i>	D423	U.S.A., Colorado, Vrain Canyon	Weber & Wittmann				
			B-114031	DUKE	KP307497	KP307544	KP307636
<i>D. anserinocapitatus</i>	D777	China, Yunnan, Diqing, Deqin	Long 23918	E	KP307466	KP307582	KP307616
<i>D. asperifolius</i>	D55	Austria, Carinthia, Mt Gr. Hafner	Kučera 12575	CBFS	KP307455	JQ890472	KP307600
<i>D. asperifolius</i>	D254	Russia, Altai Republic, Kobiguayuk Cr	Ignatov 0/113	CBFS:13302	KP307494	KP307597	KP307665
<i>D. asperifolius</i>	D261	Russia, Altai Republic, Mt Tabozhok	Ignatov 31/281	CBFS:13303	KP307492	KP307596	KP307659
<i>D. asperifolius</i>	D286	Mongolia, Zavkhan, Tsagaan Gol	F-Muller	DR:039336	–	KP307595	KP307605
<i>D. asperifolius</i>	D288	Mongolia, Arkhangai, Ogtojin Am	F-Muller	DR:039402	KP307502	KP307553	KP307631
<i>D. asperifolius</i>	D788	India, Sikkim, Goichang	Long 26560	E	KP307489	–	–
<i>D. asperifolius 2</i>	D982	Italy, Friuli, Mt Montasch	Kučera 16824	CBFS	KP307457	KP307588	KP307608
<i>D. asperifolius 3</i>	D287	Mongolia, Zavkhan, Tsagaan Gol	F-Muller	DR:039368			
				clone 2:	KP307516		
				clone 3:	KP307522		
				clone 4:	KP307499	KP307587	KP307622
<i>D. asperifolius 3</i>	D343	China, Qinghai, Huashixia	Long 26810	E	KP307514	KP307540	KP307660
<i>D. asperifolius 3</i>	D981	Italy, Friuli, Mt Montasch	Kučera 16821	CBFS	KP307510	KP307590	KP307637
<i>D. australasiae</i>	D82	Spain, Granada, Trevelez	Kučera 5425	CBFS	KP307472	KP307571	KP307651
<i>D. cordatus</i>	D53	Czech Republic, Breclav, Dolni Vestonice	Kučera 12702	CBFS	KP307460	KP307564	KP307668
<i>D. fallax</i>	D81	Czech Republic, Breclav, Klentnice	Kučera 2023	CBFS	KP307504	KP307552	KP307663
<i>D. aff. fuscus</i>	D994	Chile, Reg. XI, Puyuhapi	F-Muller C1921	CBFS:16866	KP307476	KP307546	KP307615
<i>D. fuscus</i>	D995	Chile, Reg. VII, Altos de Lircay	F-Muller C1461	CBFS:16865	KP307467	KP307537	KP307601
<i>D. gaochienii</i>	D280	China, Qinghai, Baqu valley	Tan 95-250	MHA (isotype)	KP307474	KP307538	KP307658
<i>D. gaochienii 2</i>	D200	Russia, Tuva, Lake Kadysh	Otnyukova	CBFS:13040	KP307461	KP307591	KP307641
<i>D. gaochienii 2</i>	D262	Russia, Altai Republic, Chulcha River	Ignatov 9/42	CBFS:13318	KP307488	KP307532	KP307649
<i>D. gaochienii 2</i>	D263	Russia, Altai Republic, Kurkura Range	Ignatov 8/329	CBFS:13319	KP307482	KP307592	KP307623
<i>D. gaochienii 3</i>	D397	Russia, Kamchatka, Pravyi Kikhchik	Chernyadyeva 13	CBFS:13724	KP307506	KP307541	KP307620
<i>D. giganteus</i>	D79	Austria, Salzburg, Mt Waldhorn	Kučera 12897	CBFS	KP307468	KP307548	KP307669
<i>D. hedysariformis</i>	D127	U.S.A., Alaska, Denali	Perry 7670	CBFS:12916	KP307525	KP307569	KP307629
<i>D. hedysariformis</i>	D196	Russia, Tuva, Toora-Khem River	Otnyukova	CBFS:13038	KP307465	KP307555	KP307618
<i>D. hedysariformis</i>	D199	Russia, Tuva, Toora-Khem	Otnyukova	CBFS:13044	KP307464	KP307557	KP307628
<i>D. hedysariformis</i>	D255	Russia, Tuva, Azas River	Otnyukova	CBFS:13304	KP307462	–	–
<i>D. hedysariformis</i>	D257	Russia, Sakha, Ezhantsy	Ignatov 00-67	CBFS:13305	KP307478	KP307550	KP307624
<i>D. hedysariformis</i>	D258	Russia, Altai Republic, Ust-Sema	Ignatov 24/53	CBFS:13306	KP307486	KP307574	KP307632
<i>D. hedysariformis 2</i>	D201	Mongolia, Orkhon River basin	Tsegmed 6640	CBFS:13041	KP307518	KP307556	KP307655
<i>D. hedysariformis 2</i>	D264	Mongolia, Ulan Bator, Bogdkhan Uul	Tsegmed 11198	CBFS:13317	KP307529	KP307581	KP307635
<i>D. hedysariformis 2</i>	D504	Russia, Transbaikalia, Alkhanai	Afonina 07507	CBFS:14104	KP307495	KP307580	KP307666
<i>D. hedysariformis 2</i>	D1003	Mongolia, Tov, Khustain Ridge	Tsegmed 13320	CBFS:14930	KP307528	KP307572	KP307612
<i>D. hedysariformis 2</i>	D1004	Mongolia, Ulan Bator, Bogdkhan Uul	Tsegmed 12068	CBFS:14941	–	KP307578	KP307610
<i>D. hedysariformis 2</i>	D1005	Mongolia, Tov, Hentei Ridge	Tsegmed 8136	CBFS:14942	–	KP307560	KP307634
<i>D. hedysariformis 2</i>	D1006	Russia, Transbaikalia, Sokhondo, Enda	Czemjadjeva 47-11	CBFS:15096	KP307458	KP307561	KP307633
<i>D. icmadophilus</i>	D7/D48	Austria, Styria, Mt Hochwildstelle	Kučera 12490	CBFS	KP307475	KP307598	KP307604
<i>D. johansenii</i>	D59	Canada, Alberta, Jasper, Devona cabin	Cleavitt	CBFS:4472	KP307470	KP307542	KP307662
<i>D. johansenii</i>	D60	Austria, Styria, Mt Wildfeld	Kučera 7204	CBFS	KP307517	KP307593	KP307602
<i>D. johansenii</i>	D137	Canada, Alberta, Jasper, Snake Indian River	N. Cleavitt	CBFS:4473			
				clone 1:	KP307487		
				clone 2:	KP307493	KP307583	KP307603

<i>D. johansenii</i>	D209	Austria, Salzburg, Mt Plankowitzspitze	Köckinger 97-631	CBFS:13254	KP307471	KP307577	KP307614
<i>D. johansenii</i>	D272	Norway, Svalbard, Petuniabukta	Kosnar	CBFS:13322	KP307526	KP307579	KP307653
<i>D. johansenii</i>	D389	Russia, Buryatia, Sorok River	Afonina 02408	CBFS:13718	KP307456	KP307573	KP307626
<i>D. johansenii</i>	D508	Russia Sakha, Suntar Khayata ridge	Ivanova & Krivoshapkin	CBFS:14105	KP307481	KP307530	KP307645
<i>D. johansenii</i>	D793	China, Qinghai, Jungun Naichong	Long 26962	E	KP307515	KP307594	KP307657
<i>D. murrayae</i>	D126	U.S.A., Alaska, Liberty Falls	Perry 7912	CBFS:12917	KP307503	KP307563	KP307650
<i>D. murrayae</i>	D251	Russia, Altai Republic, Kayru Creek	Ignatov	CBFS:13300	KP307513	KP307576	KP307613
<i>D. murrayae</i>	D1001	Mongolia, Khovsgol, Khar-Murugu-Uul	Tsegmed 453	CBFS:14920	KP307521	KP307567	KP307639
<i>D. nigrescens</i>	D340	Nepal, Langtang valley	Long 30589	E	KP307498	KP307543	KP307611
<i>D. nigrescens</i>	D356	U.S.A., Alaska, Izembek NWR	Schofield 109554	NY	KP307512	KP307554	KP307656
<i>D. nigrescens</i>	D359	Bhutan, Bumthang Road	Andreas	NY	KP307505	KP307562	KP307648
<i>D. norrisii</i>	D422	U.S.A., California, Upper Chico Canyon	Shevock 27907	DUKE	KP307509	KP307585	KP307617
<i>D. occidentalis</i>	D434	Canada, British Columbia, Botaniae Mt	McIntosh 7521	DUKE	KP307524	KP307533	KP307599
<i>D. perobtusius</i>	D94	Russia, Irkutskaya, Lake Baykal	Pujmanova	CBFS:12920	KP307523	KP307539	KP307609
<i>D. perobtusius</i>	D370	Russia, Buryatia, River Sorok	Afonina 02408	CBFS:13691	KP307490	KP307549	KP307654
<i>D. revolutus</i>	D420/439	U.S.A., Oklahoma, Hinton	Merrill 13249	DUKE	KP307501	JQ890471	KP307646
<i>D. rigidulus</i>	D44	Czech Republic, C. Budejovice	Kučera 1815	CBFS	KP307473	KP307589	KP307647
<i>D. rivicola</i>	D338	China, Yunnan, Gaoligong Shan	Long & Shevock 37326	E	KP307491	KP307566	KP307607
<i>D. rivicola</i>	D351	China, Yunnan, Diqing, Litiping Plateau	Long 24534	E	KP307507	–	–
<i>D. rivicola</i>	D352	China, Yunnan, Diqing, Deqin	Long 24146	E	clone 1: KP307479		
					clone 2: KP307520	KP307565	KP307661
<i>D. rivicola</i>	D353	China, Yunnan, Diqing, Benzilan	Long 24220	E	KP307500	KP307575	KP307652
<i>D. rivicola</i>	D763	Nepal, Langtang Khola	Long 22052	E	–	KP307568	KP307619
<i>D. sinuosus</i>	D85	Czech Republic, Breclav, Pohansko	Kucera 12059	CBFS	JQ890529	JQ890476	JQ890410
<i>D. sinuosus</i>	D729	United Kingdom, Scotland, Allt Mor	Hodgetts 8230	CBFS:16366	KP307508	KP307536	KP307627
<i>D. subandreaeoides</i>	D90	Switzerland, Schwyz, Mt Rigi	Kučera 7389	CBFS	KP307483	KP307570	KP307630
<i>D. subandreaeoides</i>	D354	China, Yunnan, Wo Tu Di	Long 19030	E	KP307519	KP307547	KP307642
<i>D. subandreaeoides</i>	D357	Canada, NWT, Virginia Falls	Steere 76-603	NY	KP307484	KP307531	KP307644
<i>D. vinealis</i>	D84	Spain, Malaga, Ronda Mts	Kučera 5567	CBFS	KP307469	JQ890475	KP307606
<i>D. xanthocarpus</i>	D751	South Africa, Cape, Mt Synott	Magill & Schelpe 4030	E	KP307459	KP307534	KP307638
<i>D. zanderi</i>	D34	Russia, Transbaikalia, Alkhanay, Ubzholgos	Afonina 3405	CBFS:12909	KP307527	KP307535	KP307621
<i>D. zanderi</i>	D43	Russia, Chita, Kyra	Afonina 11706	CBFS:12907	KP307463	KP307559	KP307643
<i>D. zanderi</i>	D232	Russia, Tuva, Lake Kadysh	Otnyukova	CBFS:13273	KP307496	KP307586	KP307625
<i>Microbryum curvicolle</i>	Mb579	Czech Republic, Breclav, Pouzdrany	Kosnar 358	CBFS:15119	JX679969	JX679986	JX679936
<i>Syntrichia ruralis</i>		Canada, Alberta, Bow River		UC/JEPS	–	FJ546412	FJ546412
<i>Syntrichia ruralis</i>	Sy576	Czech Republic, Vyskov, Kojatky	Kosnar 1035	CBFS:15126	clone 1	–	–
<i>Tortula muralis</i>	T56	Czech Republic, Tachov, Studanka	Kosnar 771	CBFS	JN544795	JN581679	JQ890421