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A taxonomic study of the *Didymodon rigidulus* group (Bryopsida, Pottiaceae) in Europe

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Summary of the doctoral dissertation thesis

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Introduction and Aims of the Thesis

The aim of the PhD thesis was the taxonomic treatment of the *Didymodon rigidulus* group of the moss genus *Didymodon*, which is regarded to be taxonomically one of the most complicated genera in the world's largest moss family Pottiaceae. The reasons of this fact are (1) a high number of the genus' representatives (only in Europe the number of species ranges between 20 and 35 depending on the species delimitation), (2) a considerable similarity among species due to the limited number of taxonomically usable characters and the enormous variability of these characters along the ecological and geographical gradients and (3) the large volume of material requisite to the sound critical evaluation of the existing characters.

From the three European taxonomically critical groups in genus *Didymodon*, namely the *Didymodon fallax*, *D. vinealis* and *D. rigidulus* groups, the last was chosen for the intensive taxonomic study. It was delimited in the sense of Zander (1993) as consisting of the taxa *Didymodon rigidulus* Hedw., its subspecies *andreaeoides* (Limpr.) Wijk & Margad. and varieties *validus* (Limpr.) Düll, *gracilis* (Hook. & Grev.) R. H. Zander, *icmadophilus* (Müll. Hal.) R. H. Zander and *glaucus* (Ryan) Wijk & Margad. The study included following areas:

- excerption of the literature
- study of the herbarium material, selection and recording of some quantitative and qualitative characters in a representative part of the specimens
- field study of the taxa in order to obtain the empirical knowledge of the studied taxa's ecology
- statistical evaluation of the obtained data, consisting of the descriptive statistics and the multivariate data analysis
- study of data obtained by the analysis of isozymes
- study of nomenclature, proposals for the typification of the taxa not typified yet

The result of this complex taxonomic study should be the attempt at the possibly objective and balanced classification of the *Didymodon rigidulus* group, resulting in the possible extent from the objective and reproducible course of the work.

Material and Methods

Nine taxa were described originally in the species rank in the *Didymodon rigidulus* group and these were selected for the intensive taxonomic treatment. They included *Didymodon rigidulus* Hedw., *D. validus* Limpr., Grimmia *andreaeoides* Limpr., *D. mamillosus* (Crundw.) M. O. Hill, *D. acutus* (Brid.) K. Saito, *D. icmadophilus* (Müll. Hal.) K. Saito, *Barbula abbreviatifolia* H. Müll., *D. glaucus* Ryan and *D. verbanus* (W. E. Nicholson and Dixon) Loeske.

As the author's collections were not sufficient for the study of the variability, a larger amount of the material loans was done. The loans came from most of the larger European herbaria – B, BG, BM, BP, BRNM, BRNU, E, ERE, FI, G, GJO, GZU, LAU, LE, M, MSTR, O, PC, PR, PRC, RO, S, TRH, W, WBM, Z, ZT and the private herbarium of H. Köckinger (Graz, Austria). In total, more than 2 400 herbarium specimens of the nine taxa were studied and annotated.

The taxa were studied from three points of view. First of them was the "classical" taxonomic study of the herbarium specimens. The data of the specimens were recorded in a tally containing the columns for the label details, habitus and growth form of the plants, colour, branching, length and anatomy of the stem, axillary hairs, leaves (shape, dimensions (see below), width and anatomy of the costa, leaf margin anatomy and recurvature), shape, size and ornamentation of the upper and basal cells, presence, shape and size of the axillary gemmae, gametangia, calyptra, seta (length, colour, twist), capsule (shape, size, colour, stomata, annulus, exothecium, operculum), peristome (teeth number, ornamentation, height, twist, basal membrane) and spores (size and ornamentation). All taxa were continuously studied in the field in order to find out their ecological demands, as the label details on ecology were mostly very sparse. Although all treated taxa were seen in nature by the author, some of them (namely *Didymodon verbanus*, *D. glaucus*, *D. validus*) only in a very limited number of cases, so that the given data on ecology definitely are not fully exhaustive.

The second part of the study was the compilation of the statistically evaluable data for the purposes of the exact description of the taxa's variability in the quantitative characters.

221 specimens were evaluated statistically, about 30 from each taxon. Three plants out of each specimen (representing here a population) and three leaves out of each plant were measured. Seven, in some cases eight leaf dimensions were recorded:

- leaf length (abbreviated LL in the following text and graphs)
- maximum leaf width (MW)

- basal leaf width (BW)
- distance from the leaf base to the point of the maximum leaf width (LB-MW)
- upper leaf recurvature end (distance to the lamina end, LaL-RECup)
- lower leaf recurvature end (distance to the lamina end, LaL-RECIo, recorded only in *Didymodon rigidulus* s. str. and *Grimmia andreaeoides*)
- costa excurrency (CoE)
- costa width at the leaf base (CoW)

Seven index numbers were calculated out of these dimensions:

- relative leaf length (LL/MW)
- relative base width (BW/MW)
- relative distance of the maximum leaf width from the base (LB-MW/LL)
- end of the leaf recurvature end related to the lamina length (REC[up]/LaL)
- beginning of the leaf recurvature end related to the lamina length (RECIo/LaL)
- relative excurrency of the costa (CoE/LL)
- relative costa width at the leaf base (CoW/BW)

Further, six upper and six basal cells were measured on one leaf out of each plant for one to six dimensions:

- upper cell width (UpCW, measured only in *Didymodon rigidulus*, *D. mamillosus* and *G. andreaeoides*)
- upper cell lumen width (UpCLW)
- basal cell width (BaCW, measured only in *Didymodon rigidulus*, *D. mamillosus* and *G. andreaeoides*)
- basal cell lumen width (BaCLW, not measured in *Didymodon glaucus* and *D. verbanus*)
- basal cell height (BaCH, measured only in *Didymodon rigidulus*, *D. mamillosus* and *G. andreaeoides*)
- basal cell lumen height (BaCLH, not measured in *Didymodon glaucus* and *D. verbanus*)

Eight index numbers were calculated out of these dimensions (where available):

- upper cell wall width (UpCWW, i. e. UpCW–UpCLW)
- relative width of the upper cell wall (UpCWW/UpCW)
- horizontal basal cell wall width (BaCWWh, i. e. BaCW–BaCLW)
- relative width of the horizontal basal cell wall (BaCWWh/BaCW)

- vertical basal cell wall width (BaCWWv, i. e. BaCH–BaCLH)
- relative width of the vertical basal cell wall (BaCWWv/BaCH)
- relative length of the basal cells (BaCH/BaCW)
- relative length of the basal cell lumens (BaCLH/BaCLW)

The different number of measured cell dimensions in various taxa is due to the fact that the taxa were measured successively and some dimensions were added during this process. Also, the differences in the cell and cell lumen dimensions could be measured with the adequate accuracy first after the image analysis was enabled on the digital camera OLYMPUS DP-10, which was available to me only shortly before all the data were already gained.

The classical descriptive statistics includes the tables with average values, standard deviation, minimum, maximum, median, first and third quartile. For the taxonomically important characters, histograms and percentile graphs are presented.

The multivariate data analysis methods included principal component analysis (PCA) and discriminant analysis. The aim of the PCA was to visualize the relations, similarities and dissimilarities among the populations that were epitomized by the log-transformed specimen averages of all measured characters. This method is free of the subjective intent of classification, and can help to visualize the relations in the multidimensional space. Nevertheless the first two axes of the ordination space that were drawn usually responded for only about 60 % of the variability in the data file.

The discriminant analysis was made in order to choose the best discriminating characters between the classified objects and the statistical tests of significance of those characters. Both multivariate analyses were carried out mainly with the CANOCO 4.0 package (ter Braak & Šmilauer 1998).

The third part of the study was the attempt at obtaining the molecular data, which could help test the taxonomic hypotheses, resulting from the previous study. The isozyme analysis was chosen for this goal. The living material of *Didymodon rigidulus*, *Grimmia andreaeoides*, *D. acutus*, *D. icmadophilus* and *D. glaucus* was available for isozyme studies, which were carried out at the Botanical Institute of the Czech Academy of Sciences in Průhonice near Prague. The laboratory methods of extracting and visualizing the isozymes followed to a great extent the ones described in Akiyama 1994, Boisselier-Dubayle & Bischler 1994 or Shaw & Rooks 1994, the stained isozymes included AAT, ADH, EST, GDH, GPI, IDH, LAP, 6PGDH, PGM, NADH-DH and SHDH. Also, the pattern of SOD was well visible at gels stained by the tetrazolium salts. In total, 69 specimens were extracted for the isozymes.

As there was no previous isozyme study in this genus, some technical problems were encountered during the staining process. It has not been succeeded in staining the systems PGM and LAP, and in the systems of ADH, IDH, 6PGDH, NADH-DH and SHDH the staining was incomplete. The other great problem was that all living specimens were sterile which caused that the formal genetic analysis of the progeny or the hybridization attempts could not be done. This disabled the interpretation of the zymograms in genetic terms.

Results and Discussion

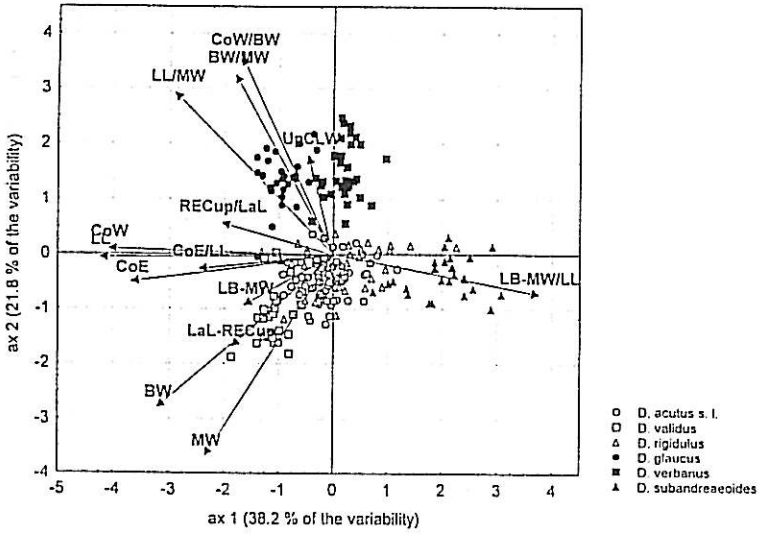
1. Didymodon glaucus

In contrast with the taxonomic views of Zander (1993) and some others, all results of my study imply that this taxon is sufficiently distinct from *Didymodon rigidulus* to deserve the specific status. The main reasons come from the analysis of the qualitative characters. The following table compares the qualitative characters of the two taxa.

Character	*Didymodon glaucus*	*Didymodon rigidulus*
ventral stereids of the costa	absent	present
guide cells of the costa	in 2 or more rows	in 1 row
dorsal superficial cells of the costa	elongate	isodiametrical
axillary gemmae	on long axillary or subterranean rhizoids, sphaerical, usually 25 – 35 µm in diam., with non-protuberant cells	on short axillary rhizoids, usually irregularly ellipsoid, usually 38 – 48 µm, with protuberant cells
basal leaf cells	hyaline, often inflated, thin-walled, sharply differentiated against the upper lamina cells	often coloured, thick-walled, slightly differentiated against the upper lamina cells

The quantitative characters of *D. glaucus* are also quite distinctive, as can be seen in the following graph from the PCA.

Graph 1: Principal component analysis of all measured objects



The main discriminating characters against *Didymodon rigidulus* are the relative leaf length (higher in more than 90 % of all leaves in *D. glaucus*) and the relative base width (higher in more than 75 % of all leaves in *D. glaucus*)

The isozyme analysis revealed the species-specific patterns in SOD and GDH, however the single analyzed colony of *Didymodon glaucus* does very probably not respond to the species' isozyme diversity in these systems. The genetically fixed differences can be seen also from the existence of mixed stands of both species.

Didymodon glaucus is a rare species endemic to Europe. All studied specimens (about 100) come from only 27 localities scattered through the whole continent and the species was found only 7 times in the last 20 years and its localities have often been destroyed in the past. It is therefore a highly threatened taxon important from the world's perspective.

2. Didymodon verbanus

This has been a nearly forgotten taxon which at best is named in the flora lists and taxonomic treatments (Corley & al. 1981, Zander 1993) as the synonym of *Didymodon glaucus*.

The differences from *Didymodon rigidulus* are indeed nearly the same as the differences between. *D. rigidulus* and *D. glaucus* with the exception of the quantitative character of relative leaf length, which falls here within the value range of *D. rigidulus*. These similarities together with the narrow distribution area which includes with a few exceptions only the canton Ticino of the southern Switzerland and the nearby area of Italy (insubric element) lead even the authors of the taxon's description to the consideration of their synonymy. However, the two taxa are not identical in their characters, neither quantitative, as can be seen from the Graph 1, nor qualitative – these include mainly the exclusively male gametangia (the gametangia in *D. glaucus* are only female), often little papillose or smooth upper lamina cells, the usual absence of gemmae and a somewhat different ecology (*D. glaucus* is a sciophilous taxon of limestone rock overhangs while *D. verbanus* is a heliophilous taxon found mostly in wet niches on mortar of the old stone walls).

There is nothing known about the genetics of *D. verbanus*, mixed stands exist with *D. rigidulus* but not with *D. glaucus* as the two taxa seem to exclude one another in their distribution.

The possible explanation of the differences between *D. glaucus* and *D. verbanus* by the existence of a single taxon with its male and female populations geographically separated was rejected as little probable. Such a case is not known among mosses, as far as I'm aware. The

male and female plants of the dioicous mosses always grow more or less intimately close. Purely male populations are known only among dioicous mosses where only the male plants were dispersed over a long distance (the case of *Telaranea murphyae* in England). The more probable explanations are thus (1) the long-distance dispersal of an unknown dioicous taxon that naturalized in the insubric area or (2) the change of sex in some population of *D. glaucus* that spread vegetatively in this area.

Didymodon verbanus is now regarded to be also a threatened taxon despite the fact that there is quite a lot of material from the insubric area in the European herbaria. The habitat of this taxon has been massively destroyed in the past 50 years with the restoration of the old stone walls.

3. Grimmia andreaeoides

The taxon has not been much known in Europe and is recently mostly regarded to be a subspecies (e. g. Zander 1993) or synonym (e. g. Corley & al. 1981) of *D. rigidulus*. However, the qualitative, and to a lesser extent the quantitative characters of this taxon were found sufficiently distinctive to merit the specific status. The differences in qualitative characters are summarized in the following table.

Character	*Grimmia andreaeoides*	*Didymodon rigidulus*
axillary gemmae	absent	present
flagelliform deciduous innovations	present	absent
leaves	dimorphic: the basal flagellum leaves are nearly orbicular, cochleariform and with the completely smooth cells. Upper flagellum and stem leaves are ovate or ovate-lanceolate, only slightly concave and their upper cells are papillose	monomorphic: if innovations are present, they are not deciduous and their leaves are not substantially different in shape from the stem leaves
central strand of the stem	absent or extremely reduced	present
stem hyalodermis	regularly present	usually absent
stem cortex cells	thick walled, walls brown-pigmented	± thin walled, walls hyaline
life form	compact tufts	variously compact turfs
colour	ferrugineous	usually dull green

The taxon is well characterized also by its quantitative characters, mainly the relative width of the basal cell width and the costa width despite some overlap with the values of *D. rigidulus* (see Graph 1).

The isozyme analyses revealed distinct species-specific patterns in the systems of SOD and GDH, mixed stands with *D. rigidulus*, which also witness of the genetically fixed differences are common in the Alps.

Although the taxon is quite poorly documented in European herbaria, especially the recent records from the Eastern Alps by H. Köckinger (Austria) prove that it is no rarity in convenient habitats, which are sunny exposed rocks (which may not be snow-covered for a longer period) of basic contents (but not pure dolomite or limestone with exception of the limestone with some contents of silicate).

During the taxonomic study, the conspecifity of the European Grimmia *andreaeoides* Limpr. and the North American *Didymodon subandreaeoides* (Kindb.) R. H. Zander was found and both taxa were synonymized with the latter name after the study of the type specimens. The known distribution of the species is thus disjunct holarctic, including north-western part of North America, Beringian part of Russian Siberia and the European Alps and Carpathians. One doubtful specimen studied comes from British Wales (Snowdon area), other two specimens which could eventually belong to another undescribed species were annotated from the Eastern Alps.

4. Didymodon rigidulus

It was confirmed that this species is extremely variable in all quantitative and many qualitative characters, however the two main qualitative differences against the other studied taxa of the group, namely the bistratose margins in the upper part of the leaves and the presence of ellipsoid axillary gemmae on short modified rhizoids in the leaf axils does not seem to be easily modified by the environment and it can be used in an absolute majority of cases for the reliable identification.

Some specimens from the arid areas of south-eastern Spain and from the Canary Islands are however too different in their qualitative (often unistratose margins, smaller axillary gemmae with non-protuberant cells) and quantitative (substantially smaller, nearly ovate leaves) characters from the typical form of *D. rigidulus* from the other areas of Europe and other parts of North Hemisphere to be regarded unequivocally conspecific. Differentiation of such plants towards *Didymodon cordatus*, especially its modification(?) called *Didymodon austriacus* is very puzzling. Also, very similar plants described as *Didymodon reedii* H. Rob., *Didymodon tectorum* (Müll. Hal.) K. Saito and *Didymodon brachyphyllus*

(Sull.) R. H. Zander are known from other parts of Holarktis and the whole range of these taxa has to be studied in future.

The species is variable enzymatically but it does not seem to coincide with the morphological variability.

5. Didymodon mamillosus

This taxon described rather recently from the Scottish Highlands (Crundwell 1976) was characterized against the most similar *D. rigidulus* by (1) the leaves and stems much smaller, (2) leaves when dry much straighter and more appressed towards the stem, (3) different leaf shape, (4) leaves less regularly recurved and (5) upper cells mamillose.

I could study the isotype specimen (E), one specimen collected in Prague, which was determined as *D. mamillosus* by the author of the description and about 20 specimens from the Eastern Alps, which could be identified as *D. mamillosus* on behalf of the above stated characters.

There was found no reason to discriminate between *D. rigidulus* and *D. mamillosus*, as both taxa are connected by innumerable transitive forms. The type specimen is indeed an extremely stunted form but about 10 % of measured leaves of *D. rigidulus* (with non-mamillose cells) have the same length. The more appressed leaves of the type specimen than the usual state in *D. rigidulus* is caused by the smaller size in combination with the smaller relative size, which is normal in stunted specimens of *D. rigidulus*. The different shape of the leaves of the type of *Didymodon mamillosus* can probably best be interpreted as the smaller ratio of leaf length to maximum width. Based on my measurements, almost 25 % of leaves in *D. rigidulus* have the same or smaller ratio. Less regularly recurved leaves in the type specimen were not observed during my study. The mamillose cells are no rarity in *D. rigidulus* and the mamillosity is not correlated with the leaf length, leaf shape or any other character.

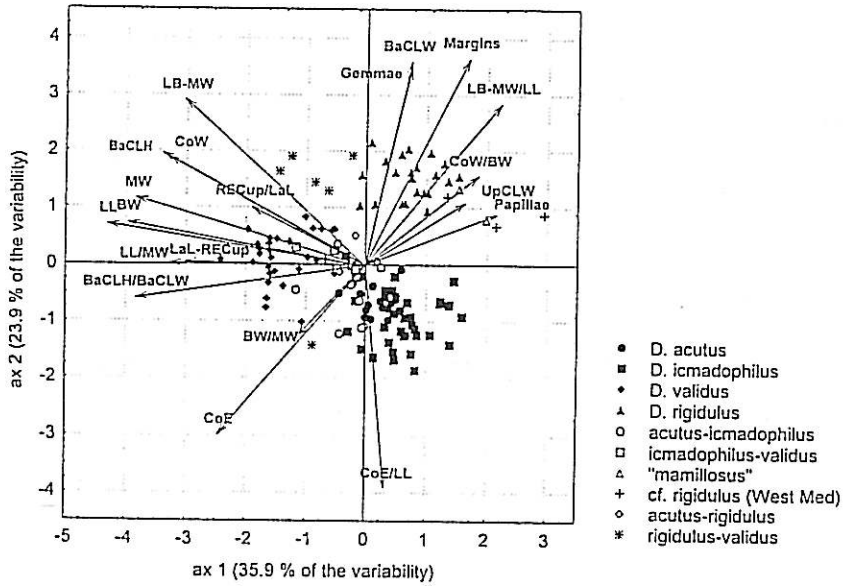
The isozyme analysis of the type specimen could of course not be executed, the analyses of the mamillose *D. rigidulus* specimens from the Alps together with the non-mamillose specimens did not reveal any coincidence.

6. Didymodon validus

The taxon was found to be probably the most complicated case in the taxonomy of *Didymodon rigidulus* group. None of the existing taxonomic opinions on *D. validus* (i. e. (1) the specific status, (2) infraspecific taxon or form of *D. rigidulus*, (3) infraspecific taxon or form of *D. acutus*) can be excluded with certainty after this study.

The position of the objects, which can be classified as *D. validus*, in the ordination space with other objects of *D. rigidulus* s. l. (*D. rigidulus*, *D. acutus*, *D. icmadophilus*, depicting also the objects which could not be classified unequivocally) is shown on the Graph 2 from PCA.

Graph 2: Principal component analysis of the objects belonging to *Didymodon rigidulus* s. l.



From this graph we can see that *Didymodon validus* represents a rather well-defined group within *D. rigidulus* s. l., based on the measured characters, with some transitions to both *D. rigidulus* s. str. and *D. acutus* s. l. (including *D. icmadophilus*). The transitions to *D. acutus* s. l. are somewhat more frequently documented.

I however does not accept the slightly more frequent transitions to *D. acutus* in quantitative characters as the evidence of the closer relationship to this taxon. The close relationship to *D. rigidulus* can be seen from some of the shared qualitative characters like the occasional presence of axillary gemmae of the same type as *D. rigidulus* or the thickness of stereid bands, which both are regarded to be taxonomically important characters in the *Didymodon rigidulus* group. On the other hand, the unistratose margins characteristic of *D. validus* can be, albeit rarely, modified in *D. rigidulus* under the special environmental conditions (especially shade). As the other evidence of the closer relationship of *D. validus* to *D. rigidulus* than to *D. acutus* can be given that in the centre of distribution of *D. validus*, transitional types to *D. rigidulus* are rather frequently documented (distinguishable virtually only

on behalf of the unistratose margins), whereas the plants transitive to *D. acutus* are not documented. On the other hand, I could name as *D. validus* only two specimens from Scandinavia without greater hesitation, while the forms transitive to *D. acutus* s. l. were much more frequent.

The isozyme data are not yet available but I could observe the evident mixed stands of *D. validus* and *D. rigidulus* in East Tyrol, Austria. Mixed stands with *D. acutus* s. l. were documented in three herbarium specimens.

The taxon is very rare (three recent localities) and its centre of distribution lies in the south-eastern Alps and their southern foothills (South Tyrol of today's Italy, Slovenia). Few other localities are known throughout Europe and from Central Asia, the biological identity of e. g. the Scandinavian and Central Asian populations on one hand and the south-alpine populations on the other hand is yet uncertain.

7. Didymodon acutus

Basically, I found no substantial difficulties in distinguishing European samples of *D. acutus* and *D. rigidulus* in the absolute majority of cases (only 5 out of ca. 1100 specimens could be interpreted as transitional between the two taxa). The major distinguishing characters can be summarized in the following table:

Character	*Didymodon acutus*	*Didymodon rigidulus*
Margins in the upper part of leaf	unistratose	bistratose
axillary gemmae	absent	present
costal stereids	ventrally in 1 – 3 rows, dorsally in 2 – 4 rows	ventrally extremely reduced, dorsally in 1 row
upper leaf cells	smooth, rarely slightly papillose	usually mamillose and papillose
capsule shape	long cylindrical	ovate

The quantitative characters are hardly distinguishing, with the exception of the costa excurrency, which however has only statistical validity and cannot be used in single cases.

The question of the possible occurrence of axillary gemmae, given in the literature, could not be answered with the absolute certainty. Five studied specimens had the combination of unistratose margins, non-mamillose leaf cells and presence of axillary gemmae. In one of the specimens this was however a case of an evident mixed stand, with a typical *D. acutus* and the controversial plants, which had more twisted leaves and broader costa than the typical *D. acutus* from the same specimen, both indicating the probable identity with *D. rigidulus*. Therefore it is advocated that the problematic gemmiferous specimens of *D. acutus* can better be viewed as the modifications of *D. rigidulus*.

Mixed stands of *D. acutus* and *D. rigidulus* have been observed quite often, implying that the genetically fixed differences exist. The isozyme analyses could not however detect any species-specific patterns in none of the system working in other taxa.

The species is not very rare in Europe, its distribution pattern may nevertheless be somewhat different and more restricted compared to the one given in literature. The distribution centre of *D. acutus* does not probably lie in the Mediterranean area, since the absolute majority of revised specimens belonged to other two similar taxa – *Didymodon fallax* and *D. vinealis*. This corresponds also to my modest experience with the Mediterranean when both latter taxa were everywhere very common but true *D. acutus* was rather rare. The majority of correctly identified specimens in European herbaria was gathered in the Pannonic lowland, e. g. the area of Hungary, part of southern Slovakia, south-eastern Czechia (Moravia) and part of Austria. The borders of the taxon's area of distribution is hard to delimit, as it creates numerous transitional forms to *D. icmadophilus* (above ca. 1000 – 1500 m in the Alps and essentially everywhere in the British Isles, Scandinavia and Caucasus) or other small taxa of the *D. rigidulus* group in Asia and America. It seems to be probable that *D. acutus* s. str. does not extend the European subcontinent with the exception of the Mediterranean area of North Africa and Middle East.

8. Didymodon icmadophilus

The differentiation between *D. icmadophilus* and *D. rigidulus* is essentially the same as between *D. acutus* and *D. rigidulus*. It is thereby easier that the axillary gemmae in *D. icmadophilus* have never been reported, and also, the isozyme analyses, especially in the system of SOD show taxon-specific patterns against *D. rigidulus*, despite quite a large variability of this system in both taxa.

Much more complicated is nevertheless the distinction between *D. acutus* and *D. icmadophilus*. The differences between the taxa given in literature include (1) the costa more excurrent in *D. icmadophilus*, (2) ± quadrate cell lumens in *D. icmadophilus* versus ± rounded lumens in *D. acutus*, (3) longer capsule with longer and more twisted peristome in *D. icmadophilus* as well as (4) the annulus cells inflated and separating in *D. icmadophilus* versus the cells not inflated and not separating in *D. acutus*. *D. icmadophilus* is reported as a montane to alpine taxon of rather wet sites, *D. acutus* as a lowland taxon of sunny dry sites.

The costa excurrency in both taxa was found to be correlated with the environmental conditions, especially the moisture rather than with other factors. *D. icmadophilus* is however far from being hydrophilous or only hydrophilous species. It can tolerate relatively dry sites in the subalpine and alpine belt and specimens from such sites have their costas little excurrent. The shape of cell lumens varies in both taxa, however it has probably some rationale. The sporophyte in both taxa is very rare, especially in *D. icmadophilus*, where it was found only in plants from the type locality in the Alps and about 5 sites of middle Norway. The sporophyte characters can thus only hardly be profoundly evaluated considering the enormous variability in the sporophyte characters in other members of the genus and the whole family. The differences on annulus could be confirmed on all studied specimens. Probably the best gametophytic character was found to be the papillosity of the upper leaf cells, which best correlates with the sporophyte characters and the probable and logical distribution pattern. Neither this character can nevertheless be used in all cases.

The species-specific isozyme patterns against *D. acutus* in the SOD system must be taken with caution due to the probably underestimated variability, mixed stands of both taxa have not been observed.

The distribution of the taxon cannot therefore be given with certainty, the obvious centres are however the Alps, Scandinavian and Scottish mountains. Unlike *D. acutus*, the taxon can be confirmed to North America (although I have not seen fertile plants).

9. Barbula abbreviatifolia

The description of this taxon was based on the quantitative differences towards *Didymodon acutus* and *D. icmadophilus* (Müller 1866), namely its shorter leaves (0.57 – 0.70 mm) and smaller ratio of length to maximum width (1.62 – 2.23). No recent publication, as far as I'm aware, gives this taxon the specific status, it is usually considered the variety, subspecies or synonym of either *D. acutus* or *D. icmadophilus*.

No gap in values of the absolute or relative leaf length was found on basis of my measurements of both taxa, and no other reason was found for distinguishing any short-leaved taxon in *Didymodon acutus* s. l.

The type specimen is sterile but its upper leaf cells with ± quadrate lumens and numerous papillae, as well as the locality (about 1500 – 1600 m in the Central Alps) correspond with *D. icmadophilus*.

Conclusions

From the nine intensively studied taxa in *Didymodon rigidulus* group, three were found to be better excluded from the close relationship with *Didymodon rigidulus*. They are *Didymodon glaucus*, *D. verbanus* and *Grimmia andreaeoides*, found to be conspecific with the North American *Didymodon subandreaeoides*.

Both *Didymodon glaucus* and *Didymodon subandreaeoides* merit specific status, their differences from *D. rigidulus* were well illustrated by a number of qualitative and quantitative characters, including the species-specific patterns in some isozyme systems.

Didymodon verbanus is definitely specifically distinct from *D. rigidulus* in a similar manner as *D. glaucus*, not fully explained is its relation to *D. glaucus*. Although both taxa are distinct in some qualitative and quantitative characters to a great extent, so that they could be regarded at least geographically segregated subspecies of one taxon, the innocence of the biological matter of the observed differences compels to distinguish *D. verbanus* as a species, until new facts emerge.

The other studied taxa are definitely closely related. *Didymodon validus* is seen as the most closely related taxon, based on the shared qualitative characters (occasional presence of axillary gemmae and the same anatomy of the leaf costa) and some transitions towards *D. rigidulus* in the centre of its distribution.

Didymodon acutus is regarded to be specifically distinct from *D. rigidulus*, though related. Its distribution is suspected not to extend substantially the European subcontinent, and the difficulties in distinguishing this taxon from *D. rigidulus* in America seem to be caused by the occurrence of other minor taxa of the *D. rigidulus* group, similar but not identical with *D. acutus*.

Didymodon icmadophilus is also regarded to be specifically distinct from *D. rigidulus*, the differences are in addition to the existence of mixed stands confirmed by the species-specific patterns in the isozymes of SOD system. The numerous transitions towards *D. acutus* in the gametophytic characters could not be sufficiently explained, and the taxon is, at the present state of knowledge, best considered to be a variety of *D. acutus*. *Barbula abbreviatifolia* is shown to be a synonym of *D. icmadophilus*.

Didymodon mamillosus was found to fall within the variability of *Didymodon rigidulus* in all of its characters. On the other hand, the existence of another taxon, extremely closely related to *D. rigidulus*, was outlined to be possible in the western Mediterranean area but the variability of this taxon there has to be studied with respect to other Holarctic taxa close to *D. cordatus* and *D. rigidulus*.

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