

DIDYMODON GAOCHIENII (POTTIACEAE, BRYOPHYTA) IN RUSSIA

DIDYMODON GAOCHIENII (POTTIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

Didymodon gaochienii, a species described from Qinghai Province of China, is found in Yakutia (NE Asian Russia). This species was recently placed into synonymy of *D. fragilicuspis*, but the new molecular phylogenetic data challenge this decision. The new Yakutian specimen is almost identical with the type of *D. gaochienii* in nrITS1-2 sequence, and they differ contrastingly from all other sequences obtained from plants of *Didymodon* with fragile leaf tips. Taking into account the great distance, ca. 5100 km, between Qinghai and Yakutian localities, and the identity of Yakutian and Chinese specimens both in sequences and morphology, we suggest a reconsideration of species delimitation in this group.

Резюме

Didymodon gaochienii, описанный из провинции Цинхай в Китае, найден в Якутии (на северо-востоке азиатской части России). Этот вид был недавно помещен в синонимы *D. fragilicuspis*, однако новые молекулярно-филогенетические данные оспаривают это решение. Образцы из Якутии полностью согласуются с типовым образцом *D. gaochienii* по ядерному маркеру ITS1-2, и они контрастно отличаются от других видов *Didymodon* с ломкими верхушками листьев. Принимая во внимание значительное расстояние, около 5100 км, между цинхайской и якутской популяциями и их идентичность по морфологии и по изученным последовательностям ядерной ДНК, мы считаем необходимым пересмотр границ между видами в этой группе.

KEYWORDS: mosses, molecular marker, nrITS1-2, species delimitation

INTRODUCTION

The genus *Didymodon* Hedw. s.l. is one of the most speciose and therefore difficult for identification in the family Pottiaceae. Its recently published phylogenetic analysis by Jiménez *et al.* (2022) suggests splitting *Didymodon* into eight morphologically homogeneous genera. However, the species level taxonomy, especially in Northern and Central Asia, still remains insufficiently understood, judging from numerous publications with the descriptions of new species from this region (Feng *et al.*, 2022a, b, c; Jiménez *et al.*, 2023; Wu *et al.*, 2023).

One of the difficult complexes in *Didymodon* is the group of species with fragile leaf tips. These plants occur mainly in Siberia and are poorly represented in Europe, thus they appeared in the focus of special studies only recently. In the last treatment of the genus *Didymodon* in Russia, still within the genus *Barbula* that time, Savicz-Lyubitskaya and Smirnova (1970) accepted only one species, *D. johansenii* (R.S. Williams) H.A. Crum, excepting fragile-leaved forms of species of *Didymodon icmadophilus*–*D. rigidulus* affinites.

Otnyukova & Zander (1998) and Otnyukova (1998, 2002) added to the Russian moss flora several more species of *Didymodon* with fragile leaf tips, including previously described from China *D. anserinocapitatus* (X.J. Li) R.H. Zander and *D. gaochienii* B.C. Tan & Y. Jia (Tan & Jia, 1997), and two new species, *D. hedysarifomis* Otnyukova from Tyva and *D. murrayae* Otnyukova from Altai. Shortly after that, Afonina & Ignatova (2007) described *Didymodon zanderi* Afonina & Ignatova from the Trans-Baikal Territory, which also belongs to this group, regardless the non-fragile leaves.

Kučera & Ignatov (2015) revised this group with the combined morphological and molecular approach, finding it to be rather diverse, with some species having fragile leaf tips, while some having totally non-fragile leaves, e.g. *D. asperifolius* (Mitt.) H.A. Crum, Steere & L.E. Anderson. Altogether nine species were accepted in the *Didymodon* sect. *Rifiduli* (P.C. Chen) R.H. Zander by these authors, leaving, however, three other lineages of this group under informal names, denoted by species name + number.

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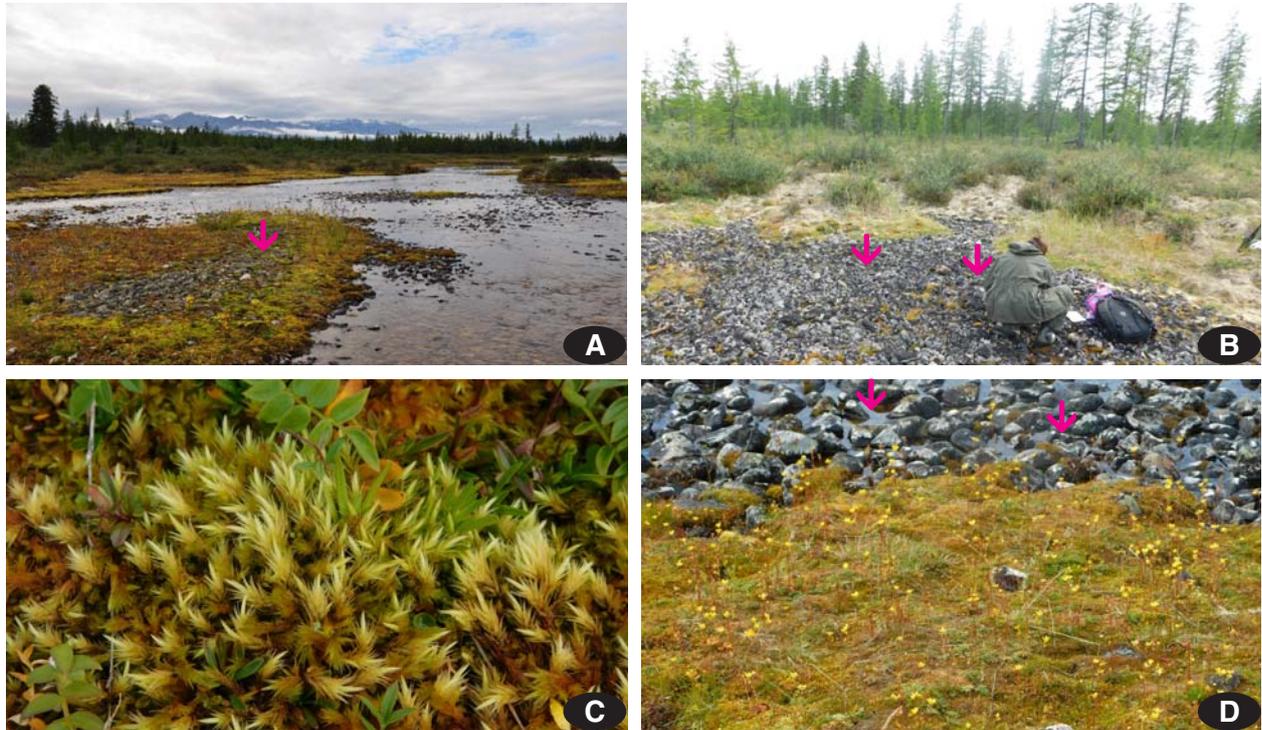


Fig. 1. The unnamed creek in the foothills of Chersky Range (A) on the left bank of Tirekhtyakh River ca. 10 km from Sasyr Settlement, where *Didymodon gaochienii* has been collected (arrows) on rocky bank (cf. 'B'); in this place, *Aulacomnium acuminatum* ('C') and *Saxifraga hirculus* ('D') are also abundant.

Other authors considered the differences in structure of leaf apices insufficient for separating distinct taxa. Sollman (2006) put *D. gaochienii* into the synonymy of *D. fragilicuspis* Broth., and this decision was followed by Zander (2019) and Jiménez *et al.* (2022). The two latter publications also added *D. murayae* to the synonymy of *D. fragilicuspis*.

It is worthy noting that *Didymodon* species with caducous leaf tips are rare mosses, known from quite a few specimens. One our recent collection from Yakutia apparently provides an evidence for challenging the current approach to the species delimitation in this group.

MATERIAL AND METHODS

Yakutian population

The collection of *D. gaochienii*, which initiated the present study, has been done in Eastern Yakutia, the area known as the coldest among lowland regions of the Northern Hemisphere, reaching -55 – -60°C in winter, and experiencing snowfalls in mid-summer, with snow cover lasting for several days. The collecting locality is between Kolyma and Indigirka Rivers of the Arctic Ocean Basin, slightly to the south from the Arctic Circle ($65^{\circ}10'\text{N}$).

The vegetation in the area is comprised mostly of *Larix* stands, while in valleys of rivers and creeks an extensive semi-permanent ice-fields are often present, surrounded by treeless vegetation. Despite of permafrost several hundred meters deep below the ground surface, some springs in the foothills of the Chersky Mountain

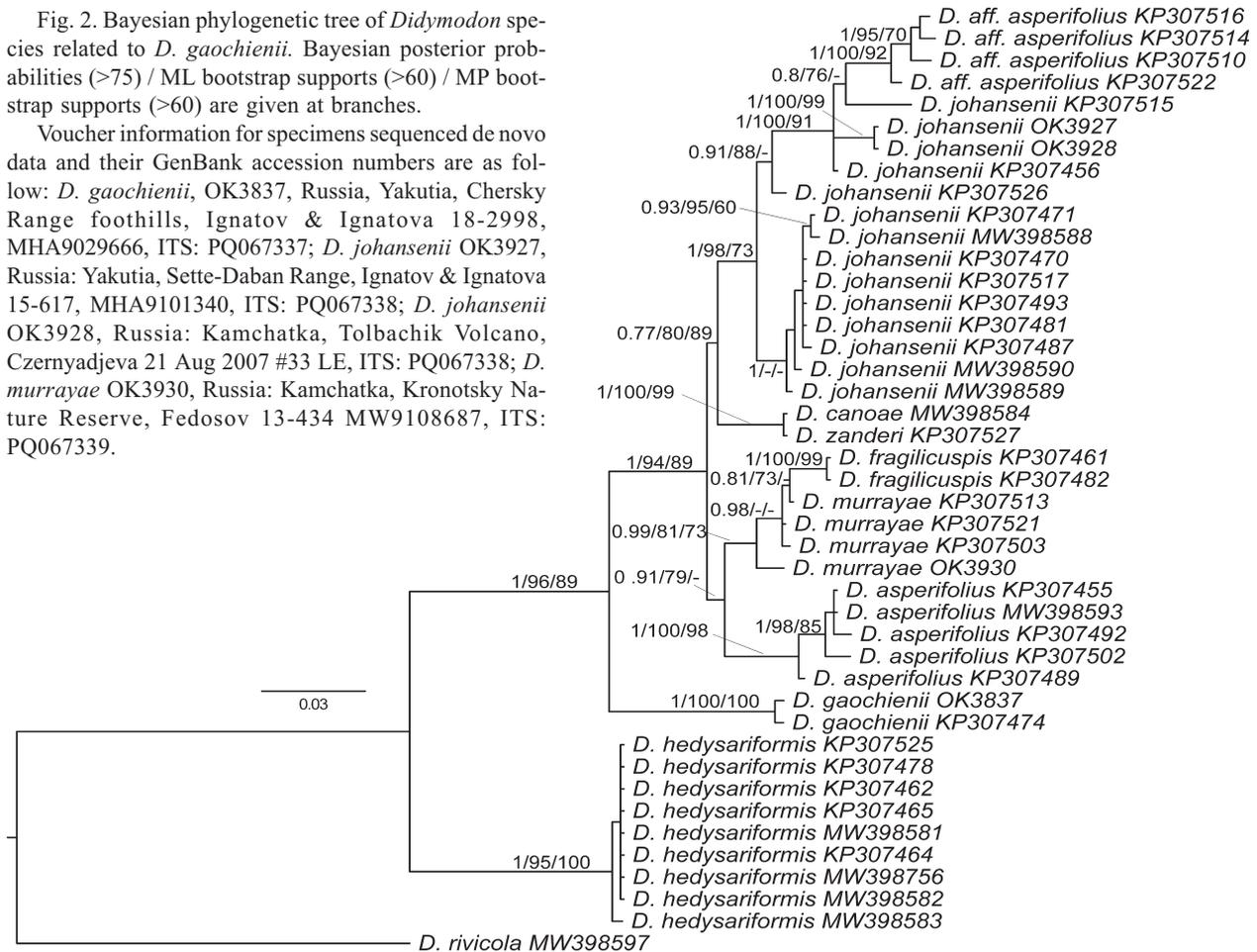
Range are getting frozen only in October. One of such spring areas has been explored by us in 2018 (Fig. 1). An extensive flow of shallow water is surrounded by *Betula nana* L. s.l. shrubs with scattered *Larix cajanderi* Mayr trees. *Sphagnum fuscum* (Schimp.) H. Klinggr. forms hummocks, and especially common mosses here are *Tomentypnum nitens* (Hedw.) Loeske and *Aulacomnium acuminatum* (Lindb. & Arnell) Kindb. *Saxifraga hirculus* L. gives yellow aspect to the bank vegetation of this rivulet. This *Saxifraga* species is severely vulnerable in most parts of European Russia, where rich fen vegetation is rapidly declining. *Saxifraga hirculus* is still locally not rare in Yakutia, but its abundance in the area shown in Fig. 1 was outstanding. Large gravel pieces along this brook were covered by *Didymodon* with caducous leaves, different from any species of the genus we've ever seen.

Sampling

The sampling included GenBank accessions most similar to the sequence obtained from the Yakutian plant. These were species of *Didymodon* with caducous leaf tips grouped together in the phylogenetic trees in previous analyses by Kučera & Ignatov (2015) and Jiménez *et al.* (2022), including *Didymodon hedysarififormis*, *D. gaochienii*, *D. zanderi*, *D. canoae* C. Feng, J. Kou & L. Feng, *D. asperifolius*, *D. murrayae*, and *D. fragilicuspis*. Specimen data are provided by Kučera & Ignatov (2015) in Table 1. Specimen data for Yakutian sample and few collections sequenced de novo are included in the legend to Fig. 2.

Fig. 2. Bayesian phylogenetic tree of *Didymodon* species related to *D. gaochienii*. Bayesian posterior probabilities (>75) / ML bootstrap supports (>60) / MP bootstrap supports (>60) are given at branches.

Voucher information for specimens sequenced de novo data and their GenBank accession numbers are as follow: *D. gaochienii*, OK3837, Russia, Yakutia, Chersky Range foothills, Ignatov & Ignatova 18-2998, MHA9029666, ITS: PQ067337; *D. johansenii* OK3927, Russia: Yakutia, Sette-Daban Range, Ignatov & Ignatova 15-617, MHA9101340, ITS: PQ067338; *D. johansenii* OK3928, Russia: Kamchatka, Tolbachik Volcano, Czernyadjeva 21 Aug 2007 #33 LE, ITS: PQ067338; *D. murrayae* OK3930, Russia: Kamchatka, Kronotsky Nature Reserve, Fedosov 13-434 MW9108687, ITS: PQ067339.



DNA extraction, amplification, and sequencing

DNA extraction was done with the Qiagene Extractor. Primers L and B were used for amplification of ITS (White, 1990). The sequencing protocols were essentially the same as in our previous studies (Gardiner *et al.*, 2005).

Molecular phylogenetic analysis

Sequences were aligned using MAFFT v7.213 (Kato & Standley, 2013), using E-INS-i strategy. No indel coding was made.

Bayesian analysis was performed in MrBayes 3.2.6 (Ronquist *et al.*, 2012), with four parallel runs each consisting of six Markov chains, with 20 000 000 generations, chain temperature 0.02, GTR model, reaching ESS>200, with GTR+G+I model for spacers and HKY+I for coding region.

Maximum likelihood analysis was done at W-IQ-TREE server (Trifinopoulos *et al.*, 2016), 1000 replications and otherwise default parameter, 1000 replications. Substitution models were selected by the server as follow: ITS1: TNe+G4; 5.8S RNA gene K2P; ITS2: K2P+G4.

Maximum parsimony analyses were performed in Nona (Goloboff, 1994) in the Winclada shell (Nixon, 1999), with bootstrap calculations for 1000 replications

(using the following parameters: N search reps 100, starting trees per rep 100, max trees 100, ‘do max’).

The tree was rooted on *D. rivicola* (Broth.) R.H. Zander, the species sister to the clade of the above mentioned species in the analyses of both Kučera & Ignatov (2015) and Jiménez *et al.* (2019). Other related species were not included due to difficulties in ITS aligning, and even *D. rivicola* was already quite different from the rest of analyzed species.

RESULTS

The phylogenetic tree (Fig. 2) found *D. hedysariformis* clade (PP=1, ML BS=100, MP BS=100) sister to the clade of all other studied species (PP=1, ML BS=96, MP BS=89). The latter has two subclades, one of *D. gaochienii* type and Yakitian specimen in question (PP=1, ML BS=100, MP BS=100) and another one (PP=1, ML BS=94, MP BS=89) of 31 remaining specimens. The latter is subdivided further into the low supported clade (PP=0.91, ML BS=79) that includes subclades of *D. asperifolius* (PP=1, ML BS=98, MP BS=85) and of *D. murrayae*+*D. fragillicuspis* [following for the latter the species naming used by Jiménez *et al.* (2019)]. *Didymodon fragillicuspis* clade (PP=1, ML BS=100, MP BS=99) was found nested in the mutual clade with *D. murrayae* (PP=0.99, ML BS=81, MP BS=73).

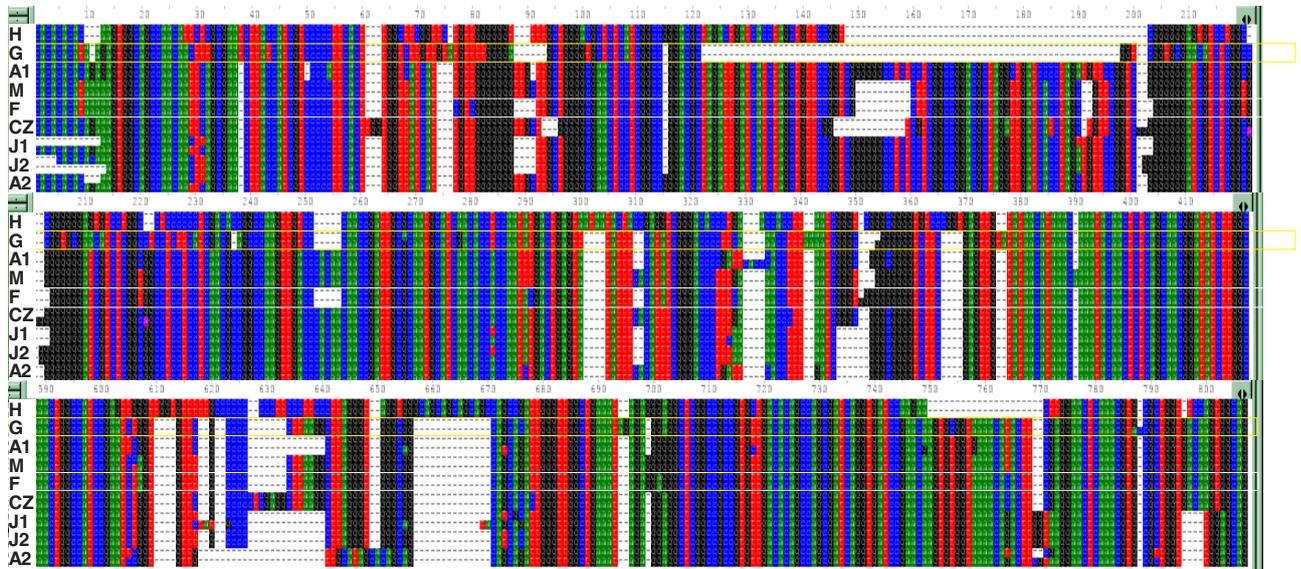


Fig. 3. Alignment of *Didymodon* species related to *D. gaochienii*: two upper parts are ITS1, the lower part is ITS2 (5.8S gene and low variable 3' end of ITS are not included). Two samples of each species are represented according to the order of phylogenetic tree in Fig. 2. Very variable *D. asperifolius* and *D. johansenii* are given by two pairs each, representing contrastingly different groups of haplotypes, while *D. canoae* and *D. zanderi* are given in one pair, because only one complete ITS sequence is available for each of them, and also they form a highly supported clade and have very similar ITS sequences.

Abbreviations are as follow: H: *D. hedysariformis*, G: *D. gaochienii*, A1: *D. asperifolius*, M: *D. murrayae*, F: *D. fragilicuspis*, CZ: *D. canoae* & *D. zanderi*, J1 and J2: *D. johansenii*, A2: *D. aff. asperifolius*. Sequences of *D. gaochienii* are in yellow frame, and of *D. fragilicuspis* in white frame.

The clade sister to *D. asperifolius*+(*D. murrayae*+*D. fragilicuspis*) clade was found poorly supported, but it included two nearly maximally supported clades, one of two specimens: one of *D. zanderi* and another of *D. canoae* (PP=1, ML BS=100, MP BS=99), and another (PP=1, ML BS=98, MP BS=73) of numerous specimens of *D. johansenii* and plants with non-fragile leaves reported by Kučera & Ignatov (2015) as *D. aff. asperifolius*.

In addition to the phylogenetic tree, we provide parts of ITS1 and ITS2 alignments to illustrate the level of variations among species in this group (Fig. 3).

Morphological distinctions of specimens are given in Discussion section. Illustrations show the 'Yakutian *D. gaochienii*' by photo (Fig. 4) and line drawings (Fig. 6), type of *D. gaochienii* (Fig. 5), plants referred by Kučera & Ignatov to *D. gaochienii* 2 by photo (Fig. 7) and line drawings (Fig. 8), and then some other species of this group by photo (Figs. 9–10).

DISCUSSION

Kučera & Ignatov (2015) provided an expanded discussion of species delimitation in *Didymodon* sect. *Rufiduli* based of variation in plastid and nuclear sequences. Among others, they mentioned that the type of *D. gaochienii* is only distantly similar to the rest members of the section in its ITS sequence. Such numerous deletions and scarcely alignable regions in ITS1 could raise the suspect that they might be merely an artifact during the cloning procedure. Kučera & Ignatov (2015) also admitted that so different ITS probably resulted from incompletely preserved DNA in the type of *D. gaochienii*.

The present discovery of the second population of *D. gaochienii* with subidentical ITS sequence requires a reconsideration of the unusual ITS sequence of the Quinhai specimen. Considering a huge distance between two populations—over 5100 km estimated by Google map service—and also their high similarity in morphology, only a little doubt remains that they represent a good, rare species.

This discovery poses a problem of the distinction of this species from similar taxa, as well as nomenclatural issue. On the one side, Sollman (2006) put *D. gaochienii* into the synonymy of *D. fragilicuspis*, a species described from Kashmir. On the other side, Zander (2019) selected the lectotype of *D. fragilicuspis* and stated that "the type conformed with key, discussion and illustrations of '*D. gaochienii*' given by Otnyukova (2002)". The illustrations of Siberian '*D. gaochienii*' sensu Otnyukova (2002) are based on a collection referred by Kučera & Ignatov (2015) to '*D. gaochienii* 2' (one of two sequenced specimens). '*D. gaochienii* 2' is shown in the present phylogenetic tree under the name *D. fragilicuspis* (so to be consistent with names used by Jiménez *et al.*, 2022), and it seems evident that plants with the names *D. gaochienii* and *D. fragilicuspis* in the tree in Fig. 2 and also in Fig. 3 are unlikely conspecific. Illustrations of *D. gaochienii* (Figs. 4–6) and of *D. fragilicuspis*, as the application of this name explained above (Figs. 7–8) may additionally support their distinctness.

We did not study the type of *D. fragilicuspis* personally; however, we assume that until the sequence data for

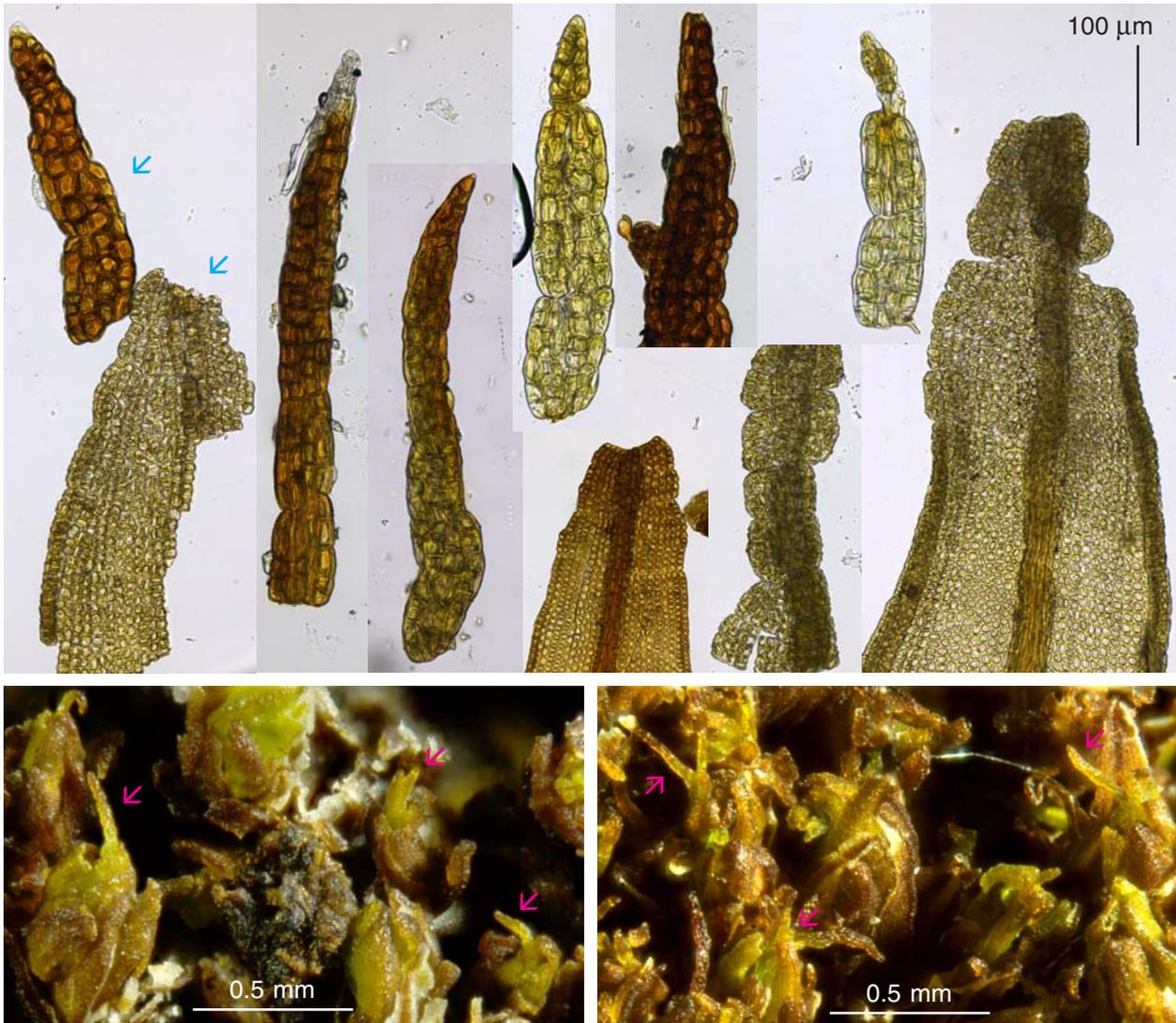


Fig. 4. Yakutian specimen of *Didymodon gaochienii* (MHA9029666), showing variation in fragile leaf tips (above, one scale for all pictures) and habit (below). Rare occurrence of fragile elements on plants is arrowed.

Didymodon with caducous leaf tips from Kashmir will be available, the stable nomenclatural solution can not be achieved. Therefore, to minimize inconsistencies, we call *D. gaochienii* sensu Otnyukova (2002) = *D. gaochienii* 2 sensu Kučera & Ignatov (2015) as *D. fragilicuspis*.

***Distinctions of D. gaochienii* s. str. and *D. fragilicuspis*.**

It is difficult to describe the difference between these two species in a key to identification, as they concern more the style of variation rather than some definite characters.

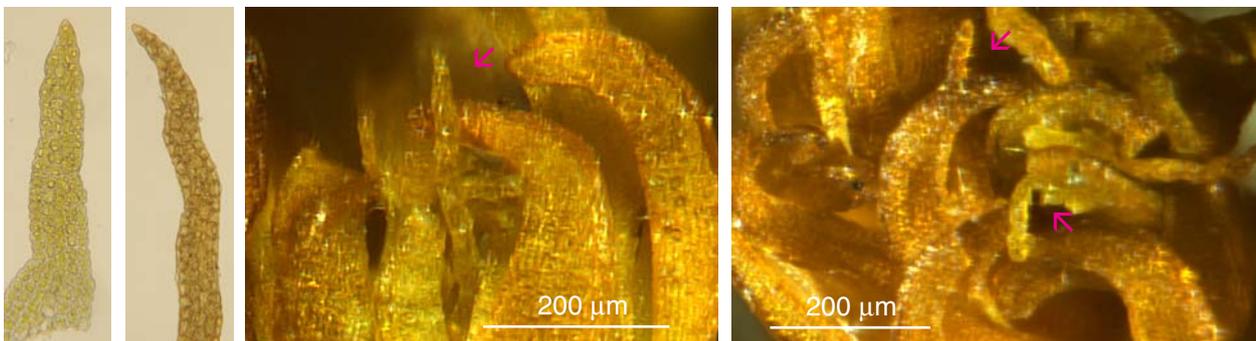


Fig. 5. *Didymodon gaochienii* (Qunghai, Tan 95-250, MHA9066369), showing fragile leaf apices (left) and habit, fragile leaf tips arrowed.

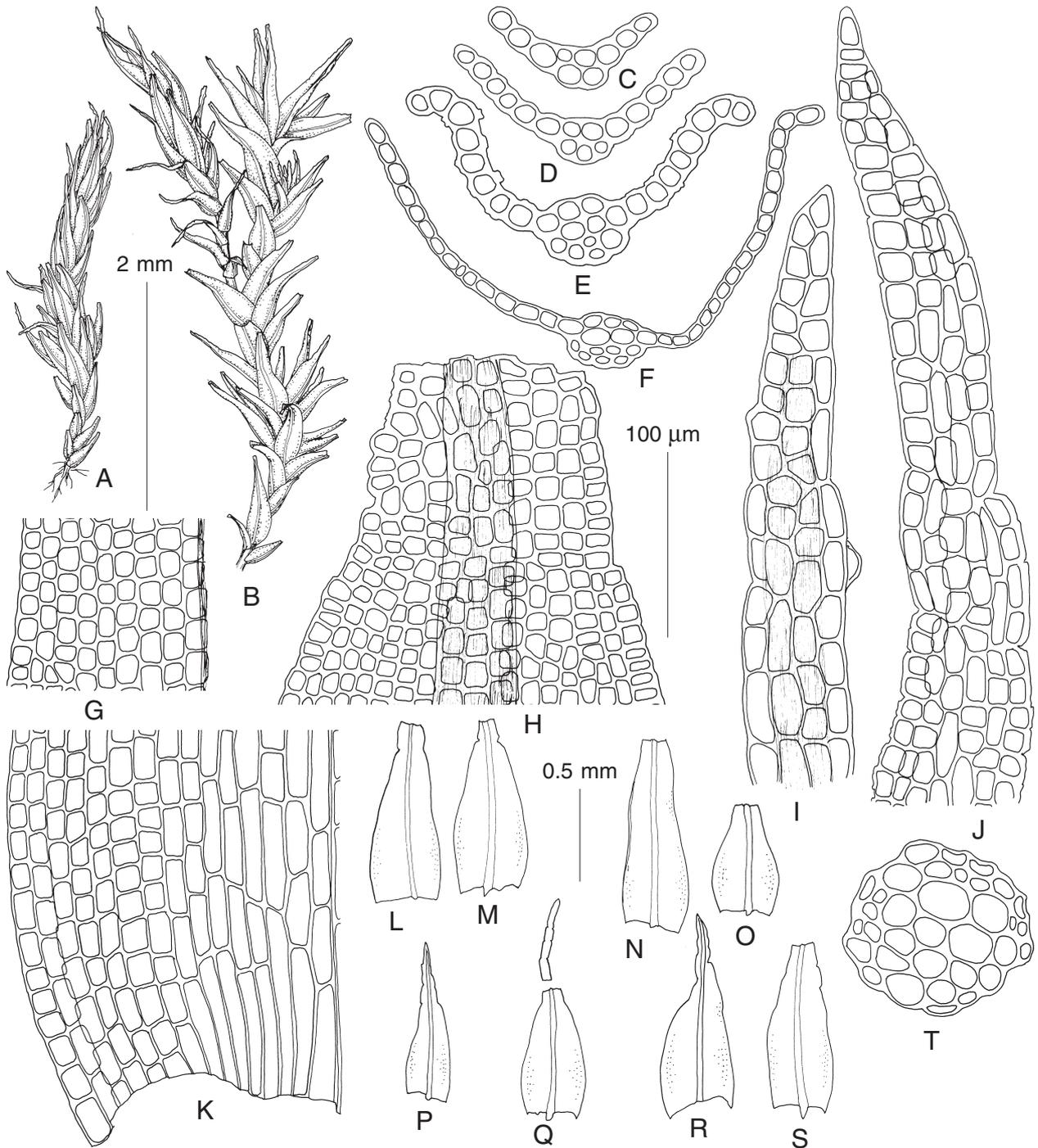


Fig. 6. *Didymodon gaochienii* (from Russia, Yakutia, Momsy Distr., Ignatov & Ignatova 18-2998, MHA9029666). A: habit, dry; B: habit, wet; C-F: leaf transverse sections; G: mid-leaf cells; H: cells in the upper part of broken leaf; I-J: caducous leaf tips; K: basal leaf cells; L-S: leaves; T: stem transverse section. Scale bars: 2 mm for A-B; 0.5 mm for L-S; 100 µm for C-J, K, T.

The first what is apparent is a different degree of leaf fragility between these species. In tufts of *D. gaochienii*, most leaf tips are usually fallen off due to their outstanding fragility, so only few intact leaf tips are usually observed (pink arrows in Figs. 4 and 5). In contrast, tufts of *D. fragilicuspis* or at least some of their parts look like a brush of spiculose leaf tips with constrictions, still remaining attached or being ready to fall off (Fig. 6 A-B). The mentioned difference probably depends of the leaf

shape and mode of its tapering to fragile part. In *D. gaochienii*, leaves are narrowed more or less abruptly from ovate or ovate-lanceolate basal part, having scalloped margins at the joint with the distal linear part, similar to those in *D. hedysarifformis*. In *D. fragilicuspis*, leaves taper to the linear part much more gradually, and their fragile portions appear to be sufficiently longer than in *D. gaochienii*. In *D. gaochienii*, caducous leaf tips are composed of fewer segments, which are uneven in shape,

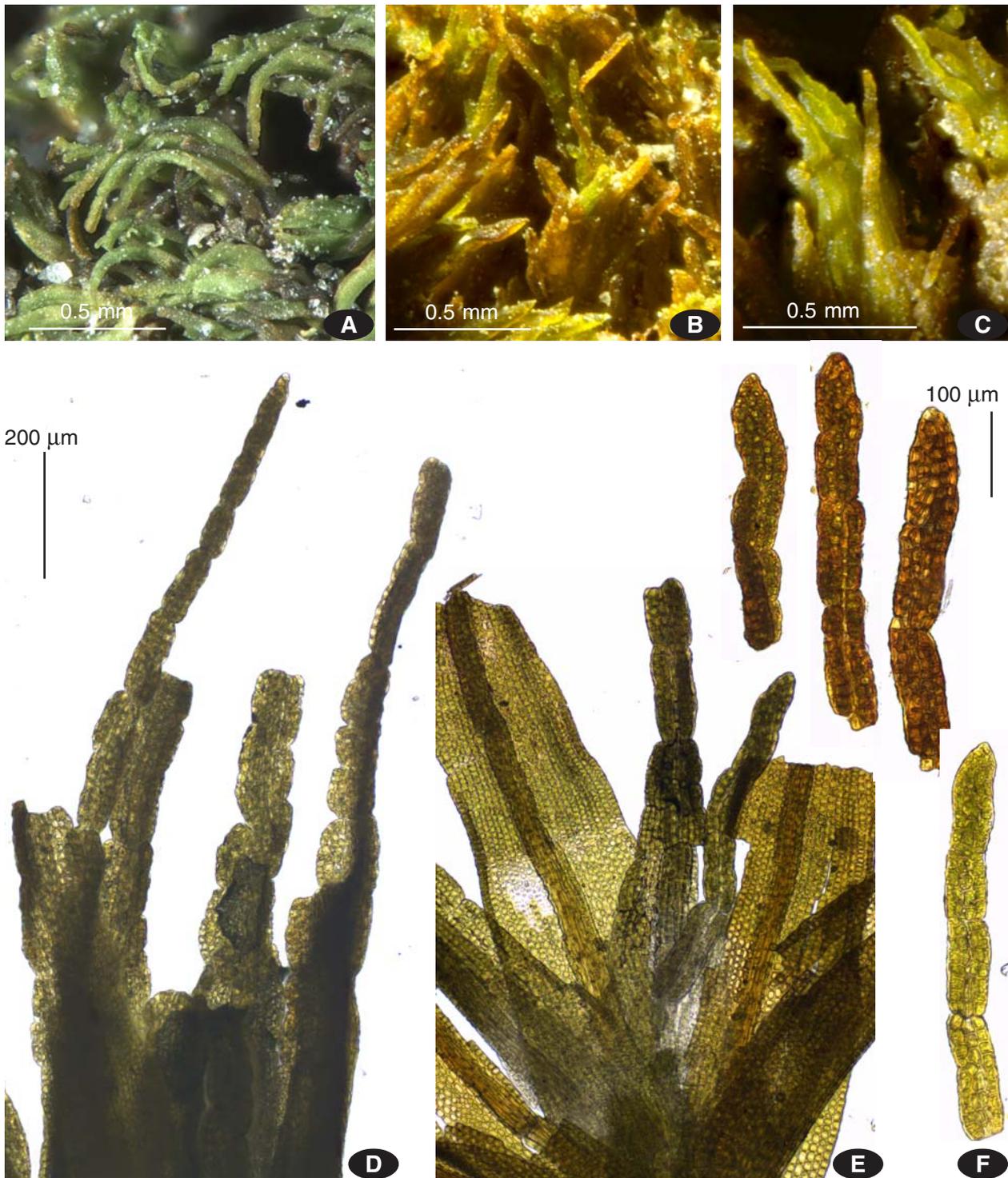


Fig. 7. *Didymodon fragilicuspis* A: from Kamchatka (Neshataeva 3-2-00, LE); B, C, E, F: from Altai Republic (Ignatov 8/239, MHA); D: from Trans-Baikal Territory (Urbanavichus 23_7_2000_LE). A–C: habit, showing copiose occurrence of fragile leaf tips. D–E: upper part of stem, showing remaining parts of leaves; F: leaf apices fallen off. Scale bars: 200 μm for D–E, 100 μm for F (fallen off apices).

whereas in *D. fragilicuspis*, leaf tips consist of more numerous, regular, barrel-like segments (Fig. 7 F), similar to fragile leaf tips of *Tortella alpicola* Dix. Also, in *D. gaochienii*, cells at the transitional zone from base to fragile leaf portion are often much smaller than cells in

the uppermost, caducous leaf portion. Fig. 4 shows the contrasting difference in cell size in different leaf fragments from the same plant, found in a slide (blue arrows). At first sight it would be difficult to believe that such two pieces are taken from the same plant, or sus-

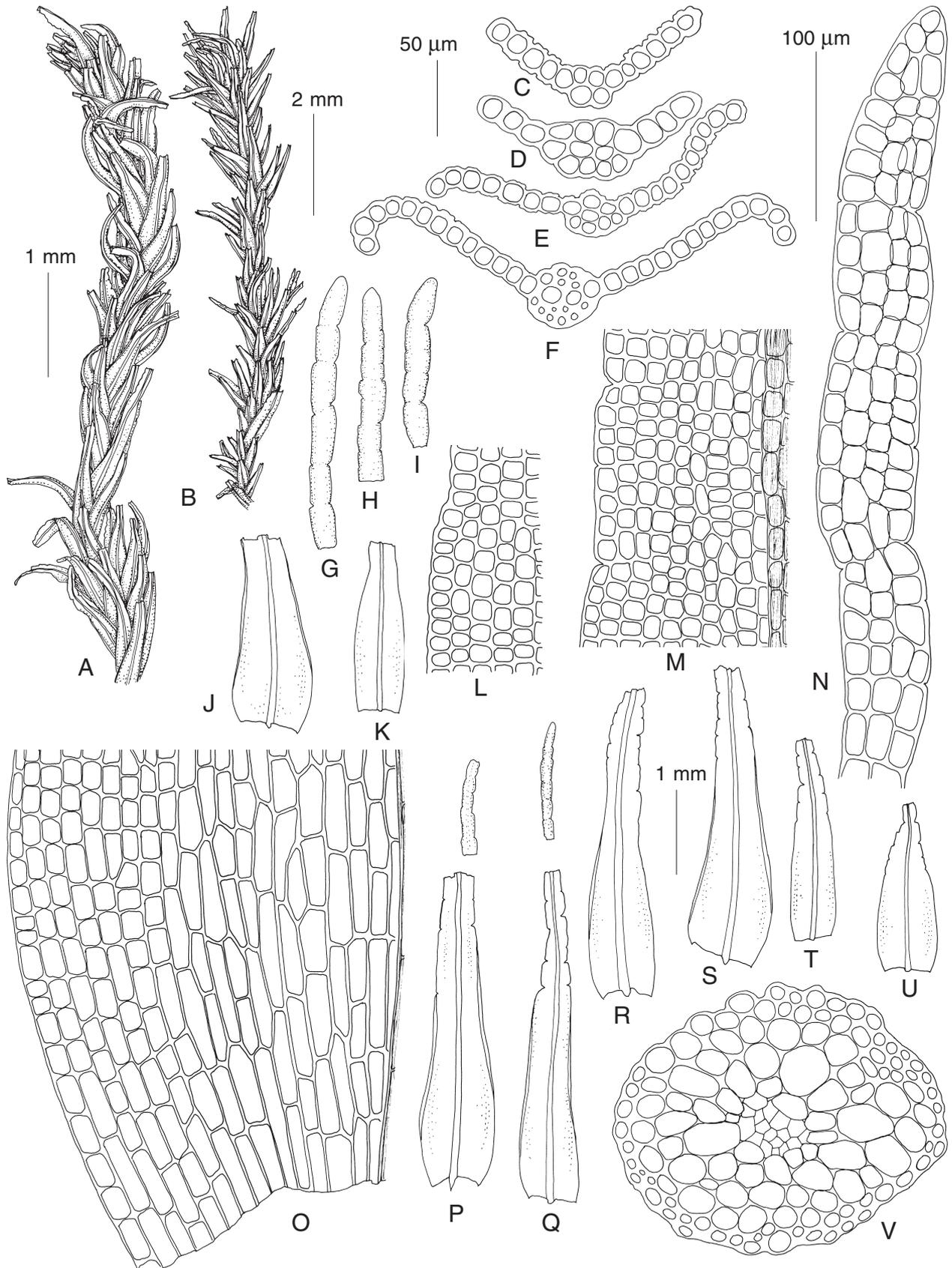


Fig. 8. *Didymodon fragilicuspis* (from Russia, Buryatia, Tunka Distr., Mondy Settl. outskirts, Pisarenko op23160, MHA). A: habit, dry; B: habit, wet; C–F: leaf transverse sections; G–I: caducous leaf tips; J–K, P–U: leaves; L–M: mid-leaf cells; N: upper leaf cells; O: basal leaf cells; V: stem transverse section. Scale bars: 2 mm for B; 1 mm for A; 0.5 mm for G–K, P–U; 100 μm for L–O; 50 μm for C–F, V.



Fig. 9. *Didymodon hedysarififormis* (Altai, locality of specimen MW9035929): habitat, photo in nature and under microscope.

pect that the photos were made under different magnification. In *D. fragilicuspis*, nothing like this was observed.

The distinctions of other *Didymodon* species with caducous leaves from *D. fragilicuspis* and *D. gaochienii* were discussed and illustrated by Kučera & Ignatov (2015). Thus, they are shown here only briefly.

Didymodon hedysarififormis (Fig. 9) forms an extensive, moderately dense to rather lax tufts. Upper parts of its leaves are usually already fallen off, and it is very difficult to find them. The common habit of plants, as they are represented in herbarium specimens, is shown in Fig. 9 (right): leaves are exceedingly contorted and broken, unless the plant is collected at a very early stage of development, with great care, and delivered to herbarium in a special box, without pressing from above, as usually happens if a gathered tuft is put in the envelope, which then is put in a bag with other collections. *Didymodon hedysarififormis* grows on rocks and frequently on tree trunks, usually in flood plains (Fig. 9, left). Sporophytes in this species are more frequent than in any other species of *Didymodon* sect. *Rufiduli*.

Didymodon johansenii (Fig. 10, right) differs from other species with caducous leaf tips in having dark green to rufulous-blackish color. Its attenuate leaf tips are

formed by excurrent costa; they are swollen and only moderately fragile. Plants are saxicolous or growing on lithosoil on rock outcrops or in rocky tundra vegetation.

Didymodon johansenii possesses a considerable internal differentiation, which is apparent from the present molecular phylogenetic tree (Fig. 2) and from the parts of alignment (Fig. 3). It is a rare species, and its additional collections may help to discover its still neglected morphological heterogeneity.

Didymodon murrayae remains the most controversial taxon in the group. Kučera & Ignatov (2015) found that the type of this species might be conspecific with the type of *D. gaochienii* (Fig. 5), because of their identical plastid sequences. However, by ITS sequences (Fig. 2) and morphology (Fig. 10A), *D. murrayae* has only moderate similarity with *D. gaochienii*, being more difficult to separate from *D. fragilicuspis*. Since the latter is nested in the clade of *D. murrayae* in the ITS tree (Fig. 2), the hybrid origin of *D. murrayae* from *D. gaochienii* and *D. fragilicuspis* is very likely. For identification purposes, the straight, divided into numerous barrel-like segments apical parts of *D. fragilicuspis* are essential distinction from *D. murrayae*, which has leaves with slightly geniculate apical parts, splitting to fewer fragments.

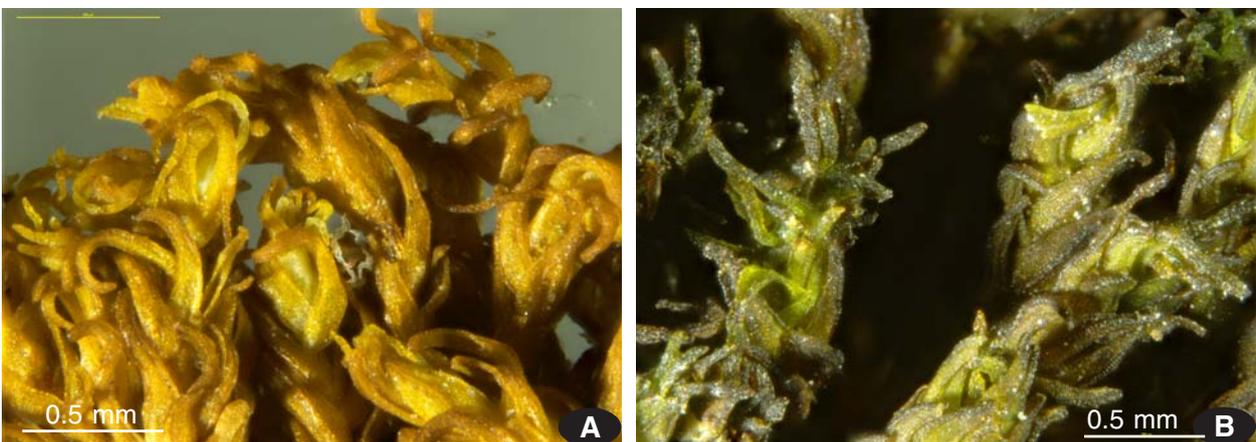


Fig. 10. Habits of A: *Didymodon murrayae* (Altai, isotype, Bardunov 21.VI.1966, MHA) and *D. johansenii* (Buryatia, Afonina 02408, LE).

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