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ON THE LEAF FRAGILITY IN *DICRANUM* (DICRANACEAE, BRYOPHYTA)

О ЛОМКОСТИ ЛИСТЬЕВ ВИДОВ DICRANUM (DICARANACEAE, BRYOPHYTA)

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Abstract

A study of relationship of leaf tip fragility to the leaf cell net is performed for for four species, *Dicranum fragilifolium, D. hakkodense, D. tauricum,* and *D. viride*. Differences in the leaf fragility is correlated with species ecology, and the higher fragiality at sectorial borders is discussed.

Резюме

Проведено исследование связи ломкости верхушек листьев у четырех видов: *Dicranum fragilifolium, D. hakkodense, D. tauricum,* и *D. viride*. Различия в ломкости связываются с экологией вида. Повышенная ломкость обнаруживается на границах клеточных секторов, образующих лист.

KEYWORDS: *Dicranum*, morphology, vegetative reproduction, cell net structure

INTRODUCTION

The fragile leaf tips provide a rather common way of vegetative reproduction in mosses. It is known in genera of a number of families: Pottiaceae (*Didymodon, Tortella*, etc.), Calymperaceae (*Calymperes*), Polytrichaceae (*Polytrichastrum*), and Dicranaceae (*Dicranum*). In *Dicranum* fragile leaves occasionally occur in widespread Arctic species, e.g., in *D. elongatum* Schleich. ex Schwägr. and *D. spadiceum* Zett., but invariably fragile leaves are characteristic of a group of species close to *D. viride* (Sull. & Lesq.) Lindb. Within the latter species, the Asiatic population has been recently resurrected as a separate species, *D. hakkodense* Cardot, which was for a long time treated as a variety of *D. viride* (Takaki, 1964) or just as its synonym (Iwatsuki, 2004). Recent molecular data indicate a distinct status of *D. hakkodense*, in addition to numerous morphological differences (Ignatova & Fedosov, 2008).

Originally the idea of the study was to compare the pattern of fragility in these two species, but later two other species, *D. fragilifolium* Lindb. and *D. tauricum* Sapjegin were added to this study.

MATERIAL AND METHODS

Material: Specimens from herbarium collections were taken. One specimen of each species was taken for measurements of 50-60% of apices, while 2-4 other specimens from the neighboring areas were used to check if the fragility pattern is the same. As most of specimens of the same species gave the same results, all apices of one species are analysed as a one massive of data.

Plants were somewhat pressed, so many leaves got broken. Broken apices found in the envelope bottoms were used as well. Separated in this way upper parts of leaves were placed in water slides, photographed under light microscope and measured in the ScopePhoto Program (http://www.scopetek.com). Only fragments with the leaf apex were taken into account, i.e. fragments broken on both ends were not included in count. Data were analyzed in Mathcad (Makarov, 2008) and PAST (Hammer et al., 2008).

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Table 1. Length of leaf apices of four species of *Dicranum*, presenting n – number of measurements; M – mathematical expectation; σ – dispersion; P – relative error; SKEW – skewness; KUR –kurtosis.

	n	M, μm	σ, μm	P, %	SKEW	KUR
D. fragilifolium	1222	1128 ±19	663 ±13	1,68 ±0,04	1,13 ±0,07	1,1 ±0,1
D. hakkodense	1146	1720 ±29	980 ±20	1,68 ±0,05	0,89 ±0,07	0,2 ±0,1
D. tauricum	1137	1044 ±19	625 ±14	1,85 ±0,05	1,40 ±0,07	2,0 ±0,1
D. viride	1190	1135 ±16	544 ±11	1,53 ±0,04	1,02 ±0,07	0,8 ±0,1

The distribution of lengths of leaf apices for smoothened by Gaussian function (cf. Schmidt, 1984), where y= coefficient.

$$F(x) = \sum_{n=1}^{n_{MAX}} \left[\frac{1}{y \cdot \sqrt{2\pi}} \cdot e^{\frac{-(x-t_n)}{2 \cdot y^2}} \right] \qquad (1)$$

RESULTS

The main parameters of the leaf apical fragments are given in Table 1 and their distribution is shown in Fig. 1.

The distribution of leaf apices length (Fig. 1) is similar to log-normal (this will be discussed in more details below), but with a rather regular alternation of peaks and hollows in the interval 1-2 mm from leaf apex. Therefore, the distribution has been tested for the sinusoidal one.

In order to do this test, the overall distribution was at first tested for a better approximation. Three distributions were considered, log-normal (2), Rayleigh (3) and Gamma (4), where θ, ω, ε – coefficients, μ – mean of log-normal distribution, Γ – gamma function. The log-normal distribution showed the lowest value of chi-squared test (Table 2), thus indicating a better approximation.

$$F_L(x) = \frac{-\left(\frac{\ln(x) - \mu}{\omega}\right)^2 \Big/ 2}{x \cdot \omega \cdot \sqrt{2\pi}} \qquad (2)$$

$$F_R(x) = \frac{x}{\varepsilon^2} \cdot e^{-\frac{x^2}{2 \cdot \varepsilon^2}} \qquad (3)$$

$$F_G(x) = x^{k-1} \cdot \frac{e^{-\frac{x}{\theta}}}{\Gamma(k) \cdot \theta^k} \qquad (4)$$

Table 2. Pearson's chi-squared test (χ^2) of approximation of distribution of length of broken apices by Rayleigh. Gamma and log-normal distributions (χ^2, p=0.99, =3141; k = 2959).

	Rayleigh	Gamma	log-normal
D. fragilifolium	734	80	57
D. hakkodense	681	97	34
D. tauricum	4892	93	87
D. viride	232	125	103

Thus the log-normal distribution was subtracted from the distribution of lengths of leaf apices (Fig. 1). This was done by subtracting the log-normal function value from the corresponding values at each integral micron, thus for 4000 values:

$D(x) = F(x) - F_L(x)$, $x \in (0, 400)$.

The resulting graphs are shown in Fig. 2. Their approximation with sinusoidal distribution was tested by correlation analysis in PAST, by comparison of data for each micron (Table 3). Parameters of sinusoid (period and from zero along *x*) were identified visually for each species.

As it is shown in Table 3, the sinusoidal distribution has got a high support.

In order to find a correspondence between the sinusoid parameter and leaf structure, on the one hand, and, first of all, areolation pattern, additional measurements were carried out, targeting at the lengths of leaf sectors.

The sectorial leaf structure in mosses has been alredy described by Lorenz (1864), Müller (1898) and subsequently discussed by Frey (1971), Donskov (2008), etc. A moss leaf is built by descendants of rather few cells that are cut off from the leaf apical cell and then undergo divisions forming square or rectangular sectors with the sides of 2, 4, 8, 16, etc., cells long. Along the margin these sectors and their subsectors are well seen by exceptionally large teeth (cf. Fig.

Table 3. Correlation between the distribution of leaf length apices and sinusoidal function: m = b – 2 – degrees of freedom, where b – number of values with the interval of 1 μm (roughly at the distance between 1 and 2 mm from the apex) ; Cor – correlation; Cor_{st} = critical value for p=0.999; UnCor - probablility of the anti-correlation.

	Cor	Cor_{st}	UnCor	m
D. fragilifolium	0,538	0,146	<0,0001	828
D. hakkodense	0,634	0,146	<0,0001	1168
D. tauricum	0,428	0,146	<0,0001	840
D. viride	0,295	0,146	<0,0001	967

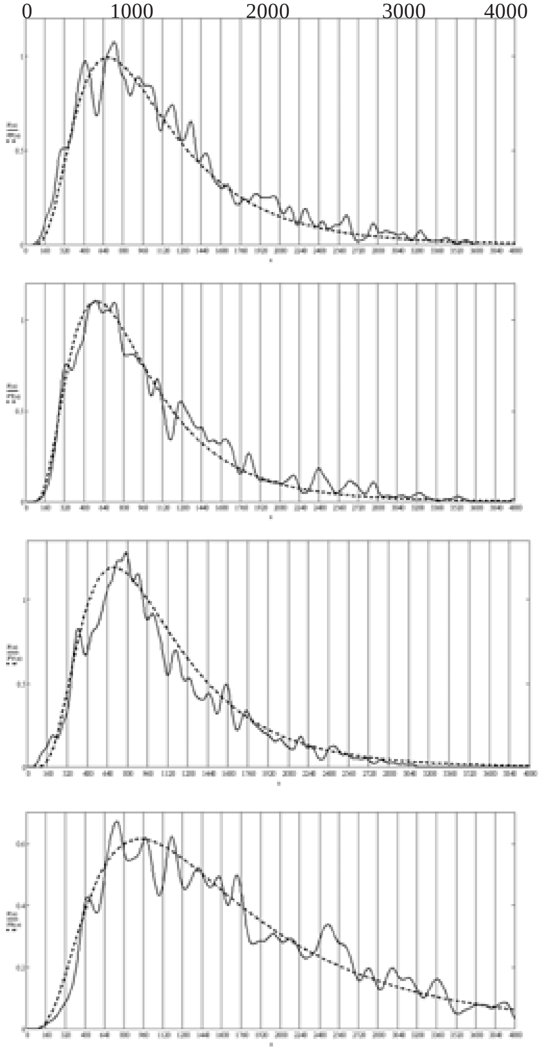


Fig.1. Distribution diagrams of broken off leaf apices lengths of *Dicranum fragilifolium* (1), *D. tauricum* (2), *D. viride* (3), and *D. hakkodense* (4). Log-normal approximation is given as dash-line. X – length of apices in μm, Y – number of fragments smoothened by Gaussian function, (1) in page 100.

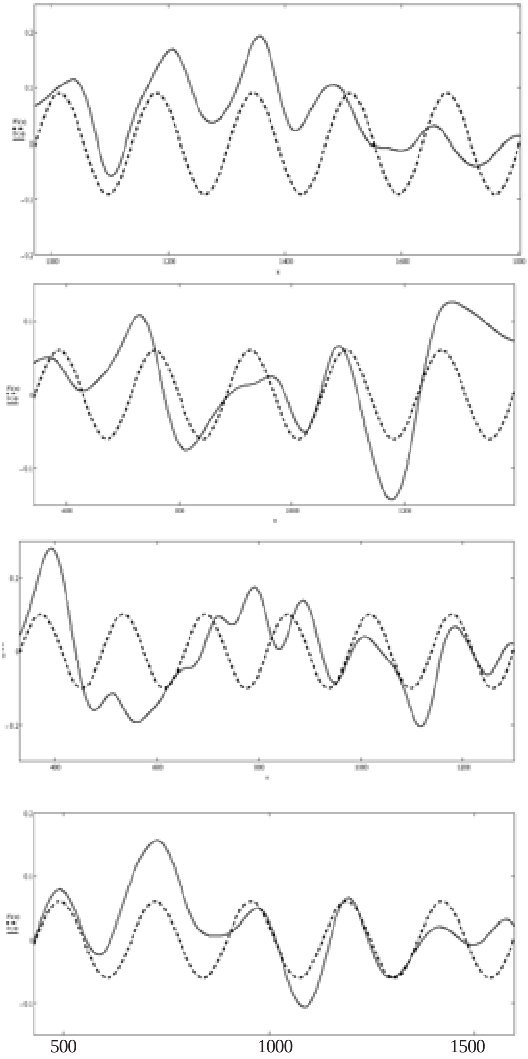


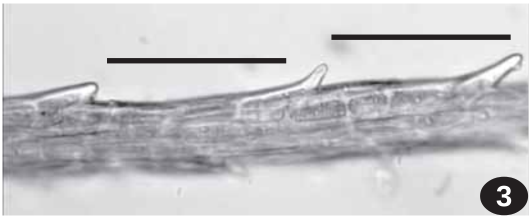
Fig.2. Distribution of length of apices of four species of *Dicranum*, after subtract of log-normal distribution: *D. fragilifolium* (1), *D. tauricum* (2), *D. viride* (3), and *D. hakkodense* (4). Approximating sinusoid distribution is given as dash-line:

	interval, μm	period, μm
D. fragilifolium	972–1803	165
D. tauricum	537–1376	166
D. viride	332–1300	161
D. hakkodense	428–1597	237

3,4, 9, etc.). This was especially easy to see in *D. tauricum* and *D. hakkodense*, the species with a serrate margin.

The sector structure in a mature leaf is not always easy to recognize. However, the marginal teeth often indicate the sectorial borders, being especially large at distances of 4, 8, or 16 cells. It is usually impossible to find out the difference between sectorial, half-subsectorial (as well as quarter-sectorial, etc) borders, but more or less clear borders are generally well seen and so measurements from border to next border are apparent, and in most cases well marked by marginal serration.

The illustrations of measurements in *D. tauricum* and *D. hakkodense* are shown in Figs. 3-30 and data on them are given in Table 4.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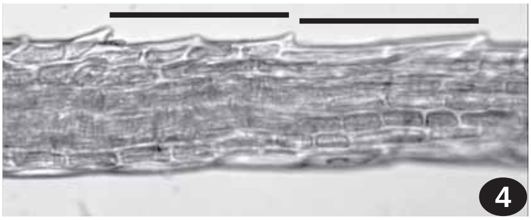
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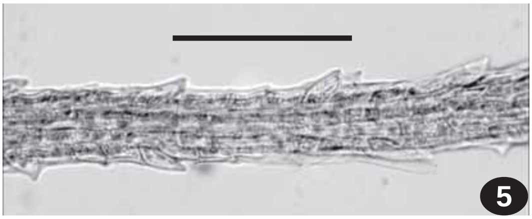
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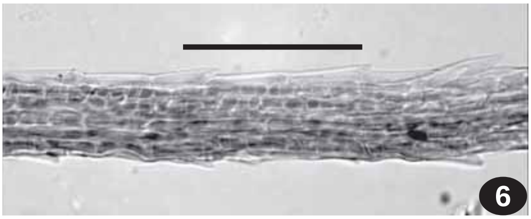
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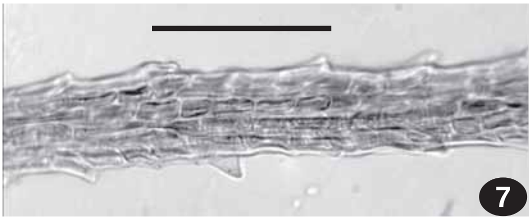
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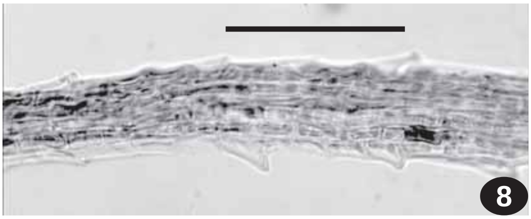
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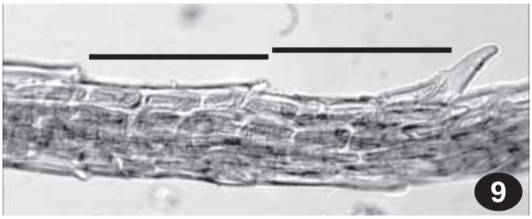
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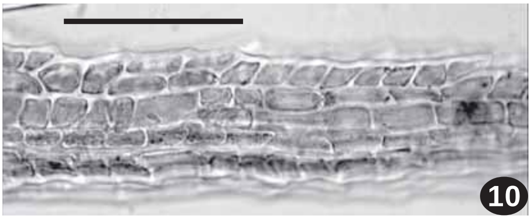
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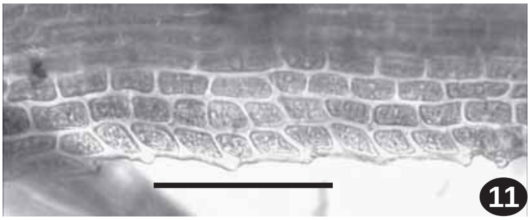
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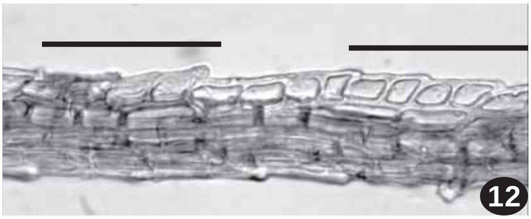
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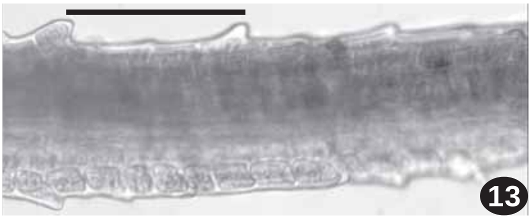
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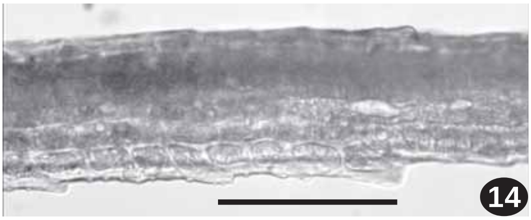
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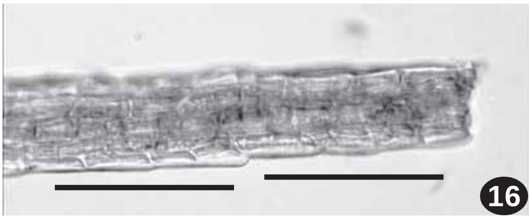
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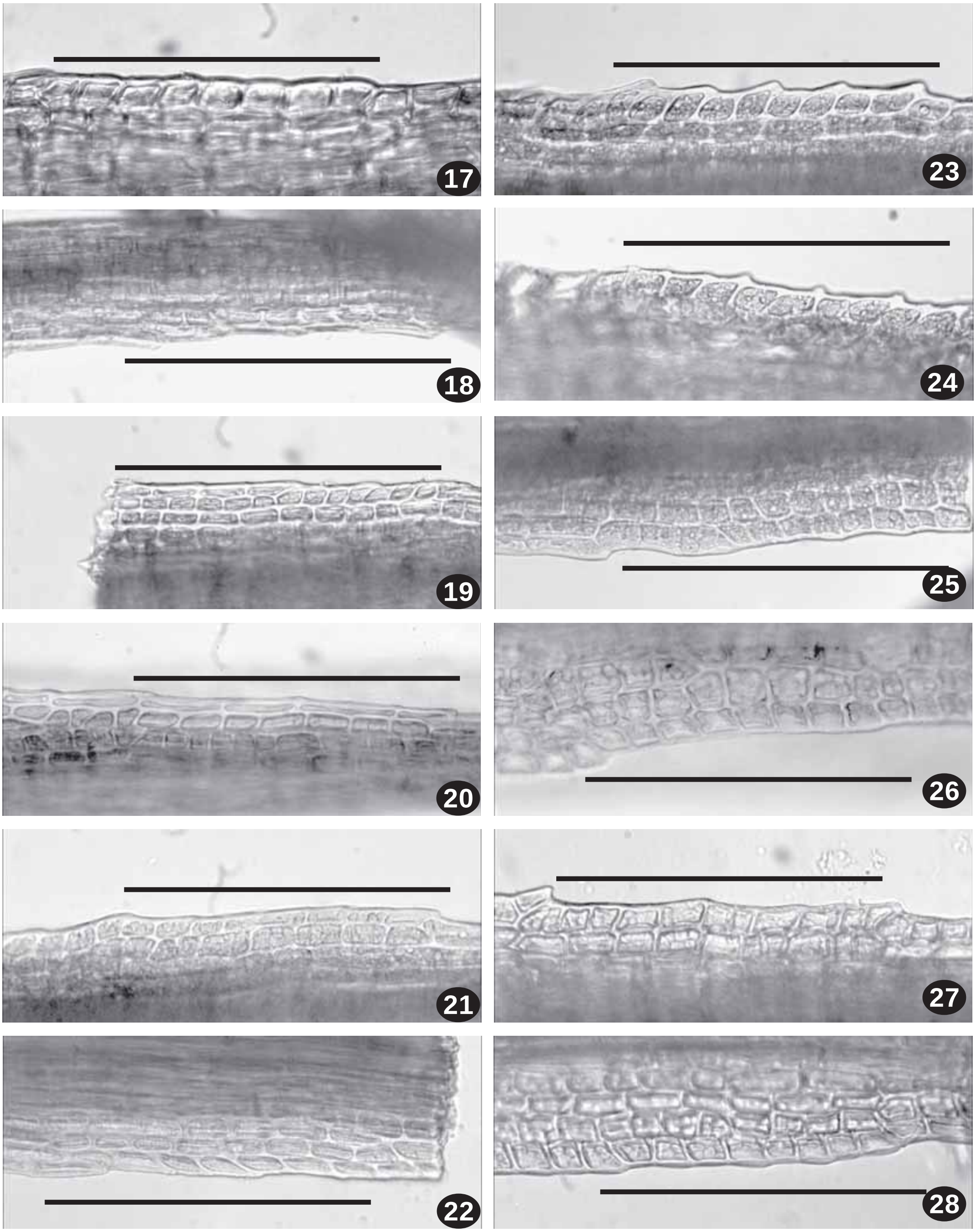
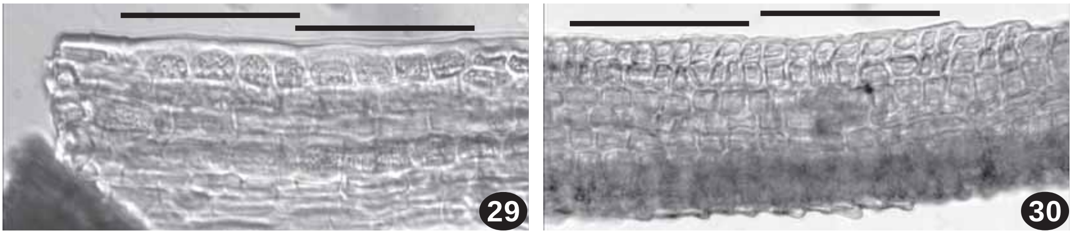


Figs. 17-28. Broken leaf apices of *Dicranum hakkodense* (17-22) and *D. tauricum* (23-28), showing part at about 1 mm from the leaf apex. Compare scale bar of 160 μm. with the leaf sectorial subdivison as it is seen from areolation pattern: groups of 4 and 8 cells more or less delimited from neigboring cells.

Figs. 3-16 (opposite page). Broken leaf apices of *Dicranum hakkodense* (3-9) and *D. tauricum* (10-16), showing upper part (part ca. 0.5 mm at about 1 mm from the leaf apex). Compare scale bar of 80 μm. with the leaf sectorial subdivison as it is seen from areolation pattern.



Figs. 29-30. Leaf apices of *Dicranum fragilifolium* (29) and *D. viride* (30). Scale bar 80 µm. Note blocks of 4 and 8 cells.

Two other species, *D. viride* and *D. fragilifolium,* were not possible to involve in this analysis, because the marginal serration in *D. viride* is weak (Fig. 30), with only solitary teeth, while in the studied specimens of *D. fragilifolium* the leaf margin was totally entire (Fig. 29). Although in some places segments borders were clear, in the majority of places those bounds were highly controversial for the analysis.

Discussion

The correspondence between fragility and segment structure of leaf. – The sinusoidal distribution is apparent at a certain distance from the apex in graphs showing lengths of broken apices. Especially interesting in this fact is that the period of sinusoid is about the same as the length of leaf sectors that include cells descendant from one cell.

Visual observation on the places of breakage shows that in most, although far from all, cases the cells above it are forming tetrads, thus indicating that the borders of leaf sectors have a somewhat higher probability of leaf breakage.

This, however, usually cannot be traced in the uppermost leaf where division at the latest stage of development appears to be less regular. On the contrary, at the distance between 1 and 2 mm from the leaf apex the leaf breakage is fairly regular (Fig. 2, Table 3), and cells commonly form apparent blocks of 4 or 8 cells (Figs. 17-28, Table 4), which have length ca. 80 µm.

This value seems to correspond to the synusoid period of ca. 160 µm and 240 µm in *D. hakkodense*, i.e. 2×80 or 3×80 µm. This can be considered as an indirect evidence of leaf breakage along the leaf sectorial borders, although additional observations would be needed to prove this.

Dicranum hakkodense vs. other species. – Fig. 1 shows that *D. hakkodense* differs from three other species with fragile leaves. Its broken-off apices are on average longer and are more variable than in other species. Also they have lower skewness, which means that the distribution is less asymmetric, and a lower kurtosis value, which indicates that the peak is less compact (Table 1).

Dicranum fragilifolium and *D. tauricum* form an opposite group: their leaf apices are shorter and more homogeneous in size; *D. viride* is closer to these two species, although has different values, being somewhat intermediate between extremes.

The specific position of *D. hakkodense* can probably be explained by the cell net pattern: in the upper leaf *D. hakkodense* has strongly oblique teeth, so the cell walls between the outer cells and a next upper cell makes their appears to be longer and therefore stronger (Figs. 3,5,9, etc.). It looks at places (Figs. 4, 6, 20) even as a kind of border.

In other species marginal teeth are either not expressed, or are not strong enough and directed at a very broad angle (60-80°) to leaf length.

Fragility and species ecology. – The discussed patterns indicate that *D. hakkodense* has a

Table 4. The distance between teeth in two species of *Dicranum*, where n_{MAX} – number of measurements; M – mean of distribution; σ – dispersion; P – relative error.

	n_{MAX}	M, µm	σ, µm	P_t, %
D. hakkodense	103	79 ± 1	11,7 ± 0,8	1,5 ± 0,1
D. tauricum	117	77 ± 1	13,5 ± 0,8	1,6 ± 0,1

somewhat less fragility compared with other species of the group, and probably did not evolve so deeply in this direction. This fact has an interesting parallel in species ecology. *Dicranum fragilifolium* and *D. tauricum* grow usually on decaying wood, on stumps, fallen logs, and the former also at trunk bases; *Dicranum viride* (population from European Russia, maybe not identical with the American and Central European ones) is a plant of hardwood trunks, growing usually quite high above ground, although preferring somewhat inclined trunks, thick branches (where it is likely abundant in some crown parts, as evident from occasional fall of plants by birds), *D. hakkodense* is common on trunks of coniferous trees, and also not rare on rocks. This overview shows that the two former species occur in habitats that require frequent change of place, as their substrates exist for a shorter time tham those for *D. viride* and *D. hakkodense*. The latter species is able to inhabit long-term existing substrates and therefore is not so much dependant on frequent dissemination, thus its "perfect" fragility may not be so much pressed by natural selection.

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Appendix 1. Specimens used for the study, all from Russia, kept in MHA.

Dicranum fragilifolium

Arkhangelsk Province, 10.VIII.1988 Ignatov
Arkhangelsk Province, 30.VII.1988 Ignatov
Arkhangelsk Province, 2.VIII.1988 Ignatov

Dicranum hakkodense

Khabarovsk Territory, Ignatov #97-959
Primorsky Territory, Ignatov #07-233
Kuril Islands, Ignatov #06-1171
Kuril Islands, Ignatov #06-1411
Primorsky Territory, Ignatov, Ignatova & Cherdantseva #06-2624

Dicranum tauricum

Karachaevo-Cherkessiya, Ignatov & Ignatova #05-3342
Karachaevo-Cherkessiya, 9.VIII.1986 Ignatova
Karachaevo-Cherkessiya, 16.VIII.1986 Ignatova
Adygeya Republic, 20.VIII.1999 Ignatov
Karachaevo-Cherkessiya, Ignatov & Ignatova #05-3025

Dicranum viride

Tatarstan, 18.VIII.2003 Ignatov & Ignatova,
Bashkortostan, Ignatova #05-1
Moscow Province, 24.VII.1986, Ignatov
Moscow Province, 29.VI.1988, Ignatov
Perm Province. 4.V.2004, Bezgodov #94