BRYOPHYTES — МОХООБРАЗНЫЕ

A rare moss *Cynodontium suecicum* (Rhabdoweisiaceae, Bryophyta) on the Barents Sea coast of the Kola Peninsula: morphological and molecular study

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Abstract. Specimens of the rare species *Cynodontium suecicum* (Rhabdoweisiaceae, Bryophyta) were collected near Drozdovka Bay on the Barents Sea coast of the Kola Peninsula (Russia) in 2016. They were compared with samples of *C. suecicum* from the Teriberka area (also the coast of the Barents Sea) gathered in 1977 by R. N. Schljakov. The morphological features of both groups of samples were studied, and nucleotide sequence data for ITS1-2 nrDNA and *trn*L-F cpDNA were obtained. Molecular analysis suggested *C. suecicum* as a hybrid that inherited cytoplasmic DNA from *C. tenellum* and nuclear DNA from *Kiaeria blyttii*. Taking into account the rather clear morphological delimitation against other species, combined with the stability of genetic characters, we believe that *S. suecicum* should be retained as a species-level taxon.

Keywords: DNA, intergeneric hybridization, morphological variability, Murmansk Region, Russia.

Редкий мох *Cynodontium suecicum* (Rhabdoweisiaceae, Bryophyta) с побережья Баренцева моря Кольского полуострова: морфологические и молекулярные данные

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Резюме. В 2016 г. в районе губы Дроздовка (Баренцево море, Кольский п-ов) были собраны образцы редкого в мире мха *Cynodontium suecicum* (Rhabdoweisiaceae, Bryophyta). Проведено морфологическое и молекулярно-генетическое сравнение с образцами того же вида из района Териберки (Баренцево море), собранными в 1977 г. Р. Н. Шляковым. Приведены результаты изучения анатомо-морфологических признаков. Получены нуклеотидные последовательности ITS1-2 ядДНК и *trn*L-F хпДНК. Установлено сходство хлоропластного локуса с последовательностями *C. tenellum*, а ядерного – с последовательностями вида из другого рода, а именно *Kiaeria blyttii*. Таким образом, есть основания считать *Cynodontium suecicum*

межродовым гибридом. Учитывая довольно четкие морфологические различия в сочетании с генетическими характеристиками, мы полагаем, что *C. suecicum* является таксоном видового уровня.

Ключевые слова: ДНК, межвидовая гибридизация, морфологическая изменчивость, Мурманская область, Россия.

Originally, *Cynodontium suecicum* (Arnell et C. E. O. Jensen) I. Hagen was collected in Sweden, from surroundings of Östersund in 1870 and Hoting in 1894, and was described as a new species, *Oncophorus suecicus*, in 1895 (Arnell, Jensen, 1895). Later, Hagen transferred it to the genus *Cynodontium* (Hagen, 1899). To date, localities of this species have been recorded only within Fennoscandia (Sweden, Norway, and Finland; Hallingbäck *et al.*, 2006) including the Kola Peninsula (Murmansk Region, Russia). For a long time, the single record of *C. suecicum* on the Kola Peninsula was known from the vicinity of the Teriberka village on the Barents Sea coast (Schljakov, Konstantinova, 1982). Later, several localities were discovered in the southern and east-southern coast of the Kola Peninsula (White Sea) — near Umba town and Chavan'ga village, as well as on an island of the Porja Guba bay (Sofronova *et al.*, 2017).

In August 2016 during fieldwork on the northeastern coast of the Kola Peninsula (Barents Sea), some specimens of *C. suecicum* were gathered in the area of Drozdovka Bay (Belkina, Likhachev, 2021; Fig. 1). Due to some variability of characters in our samples, we decided to compare them with the samples collected by R. N. Schljakov in 1977 in the surroundings of the Teriberka village, 170 km northwest of Drozdovka Bay. The northern and northeastern coasts of the Kola Peninsula belong to the Kola province of the subarctic (southern) tundra subzone (Aleksandrova, 1977), but birch stands can be found along river valleys and in moist protected depressions among the tundra. Natural conditions of the region are described in more details in Belkina and Likhachev (2021).

Material and Methods

Taxon sampling. In total, 11 samples were included in this study. The list with specimen vouchers and GenBank accession numbers are shown in Table 1. Three samples of *C. suecicum* from the surroundings of Drozdovka Bay and three Schljakov's specimens of *C. suecicum* from the vicinity of the Teriberka village (doublets) were studied. Five of these samples are stored in the herbarium of the Polar-Alpine Botanical Garden and Institute (KPABG) and one — in the Komarov Botanical Institute in St. Petersburg (LE).

In sample KPABG(M) 9391 (Table 1), along with the main species (*C. suecicum*), a small turf of *C. tenellum* with sporophytes was revealed. In specimen KPABG(M) 9392, the majority of the sample consisted of *C. tenellum* plants with or without sporophytes, while in another part of the sample, we found the plants of *C. suecicum* without capsules.

The morphological features and nucleotide sequences of ITS1-2 nrDNA and *trn*L-F cpDNA were studied. For comparison, two representative samples of *C. tenel-*

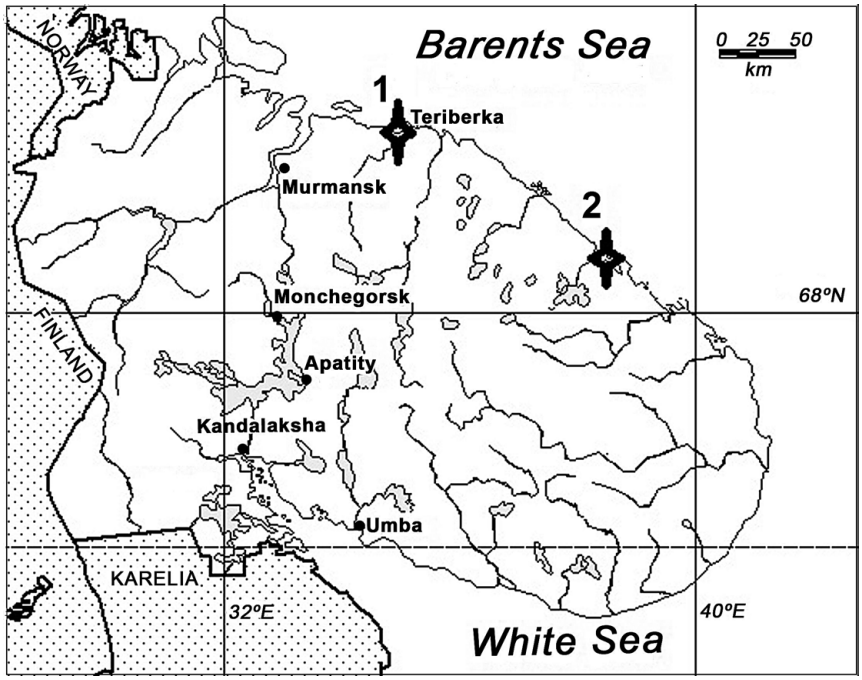

Fig. 1. The map of Murmansk Region (Russia): 1 — Teriberka village, 2 — Drozdovka Bay.

lum (Schimp.) Limpr. from Teriberka area and from Pyhälampi Lake in southeastern part of the Murmansk Region were selected. For two Schljakov's samples [KPABG(M) 9391 and KPABG(M) 9392], analyses were undertaken both for individuals of *C. suecicum* and of *C. tenellum*. In addition, one questionable sample without sporophytes and similar to *C. suecicum* was examined (Table 1, #11). It was collected near the shore of widened Ivanovka River estuary, 10–13 km east of the Drozdovka moss populations.

For morphological study, the optical microscopes Mikmed 6 and Micromed MC-5-Zoom Led were used.

Molecular analysis. DNA extraction from dried moss tissue was carried out with DNeasy Plant Mini Kit (Qiagen, Germany). Amplification and sequencing reactions were done with primers suggested by White *et al.* (1990) for ITS1-2 and Taberlet *et al.* (1991) for *trn*L-F. PCR was carried out in 20 µl volumes with the following protocol: 3 min at 94°C, 30 cycles (30 s 94°C, 40 s 56°C, 60 s 72°C), 2 min of final extension at 72°C. Amplified fragments were visualized on 1% agarose TAE gels by EthBr staining, purified using the QIAquick Gel Extraction Kit (Qiagen, Germany), and used as a template in sequencing reactions with the ABI Prism BigDye Terminator v. 3.1 Ready Reaction Kit (Applied Biosystems, USA) following the standard protocol provided for 3730 DNA Analyzer (Applied Biosystems, USA).

Obtained sequences were assembled and aligned in BioEdit 7.0.1 (Hall, 1999). BLAST search (https://blast.ncbi.nlm.nih.gov/) was implemented to determine the

Table 1

The specimen's voucher information of the studied samples of *Cynodontium suecicum*, *C. tenellum*, *Oncophorus wahlenbergii* from the Murmansk Region.

##	Herbarium number/ Field number	Taxon or inferred taxon	Description of the locality and habitat	GenBank accession numbers, ITS1-2 nrDNA / *trn*L-F cpDNA
1	KPABG(M) 9391/542	*Cynodontium suecicum*	About 69.10453°N, 35.04045°E; Teriberka River basin, left shore, to north of Dolgiy Creek, dry rock; 7 VIII 1977, *Schljakov*	No data/ No data
2		*C. tenellum*		MW996694/ MZ014505
3	KPABG(M) 9392/542a	C. *suecicum*	the same (doublet)	MW996693/ MZ014504
4		*C. tenellum*		MW996695/ MZ014506
5	LE/542	*C. suecicum*	the same (doublet)	MW996692/ MZ014503
6	KPABG(M) 121111/ Б41-4-16	*C. suecicum*	68.29776°N, 38.44112°E; shore of the Drozdovka Bay in innermost part, 4 m a. s. l., low gentle coastal rocks near littoral zone, in a crevace; 10 VII 2016, *Belkina*	MW996690/ MZ014501
7	KPABG(M) 124246/ Б48-9-16	*C. suecicum*	68.27755°N, 38.45981°E, Drozdovka Bay surroundings, 48 m a. s. l., about 0.5 km west of Drozdovjavr Lake, southeast-facing rock cliffs in birch forest, on incline wall; 11 VII 2016, *Belkina*	MW996689/ MZ014500
8	KPABG(M) 121154/ Б48-18-16	*C. suecicum*	*ibid*., in crevice in steep rock wall; 11 VII 2016, *Belkina*	MW996691/ MZ014502
9	KPABG(M) 13917/ III572-77	*C. tenellum*	About 69.15023°N, 35.10288°E; Teriberka River basin, left shore near Teriberka village, slope, turf on wet stone; 7 VIII 1977, *Schljakov*	MW996696/ MZ014507
10	KPABG(M) 13941/ III262-72	*C. tenellum*	About 66.77880°N, 29.84735°E; southwestern part of the Murmansk Region, near Pyhälampi Lake; 05 VII 1972, *Schljakov*	MW996697/ MZ014508
11	KPABG(M) 121271/ Б108-2-16	*Oncophorus wahlenbergii* Brid. (questionable sample)	68.26092°N, 38.72467°E; Ivanovskaya Bay surroundings (Barents Sea), southeastern shore of the Ivanovka River estuary, 8 m a. s. l., large rounded stones in the small stream, in cracks above the water; 20 VII 2016, *Belkina*	MW996698/ MZ014509

similarity of newly generated sequences with data from allied moss species. The molecular variability of tested samples was estimated as the value of *p*-distances for both ITS1-2 and *trn*L-F in Mega 5.1 (Tamura *et al.*, 2011) using the pairwise deletion option for counting gaps.

Results

Molecular estimation. ITS1-2 and *trn*L-F nucleotide sequences were obtained for ten samples — in total, twenty accessions were deposited into GenBank (Table 1). We were not able to obtain ITS1-2 for sample #1, despite two attempts, and it was excluded from the molecular analysis. Alignments were produced manually; all positions were taken in estimation; absent data were coded as missing. With exception of specimen #11, all studied samples possess quite similar sequences of the *trn*L-F region. BLAST search revealed their 99–100% similarity with accessions of *Cynodontium tenellum* from Sakhalin, Yamal, Taimyr (Russia), Norway, Austria, and with two samples of *C. suecicum* from the Kola Peninsula. Surprisingly, the two groups of highly distinct ITS1-2 sequences were obtained among *Cynodontium* specimens. For the first group (samples #2, 4, 9, 10), BLAST search resulted in 99% similarity to two samples of *Cynodontium asperifolium*, for the second (samples # 3, 5, 6, 7, 8) — 99–100% similarity to multiplied sampled *Kiaeria blyttii* (Bruch et Schimp.) Broth. Sample #11 is similar to *Oncophorus wahlenbergii* Brid. at 98% level for *trn*L-F and 99% for ITS1-2. The *p*-distance calculation (Table 2) revealed the presence of infraspecific variability in C. *suecicum* — 0.6% in ITS1-2 and 0.1% in *trn*L-F, whereas *C. tenellum* varied only in ITS1-2 (0.1%). The divergence between both species is absent for *trn*L-F and achieved 10.5% for ITS1-2. The specimen attended to *O. wahlenbergii* is distinct from both *Cynodontium* species at 27.5-30.3% level for ITS1-2 and at 7% for *trn*L-F.

Table 2

The value of *p*-distances for studied specimens.

	Taxon	Infraspecific *p*-distances, ITS1-2/*trn*L-F, %	*p*-distances among species, ITS1-2/*trn*L-F, %		
			1	2	3
1	*Cynodontium suecicum*	0.6/0.1			
2	*C. tenellum*	0.1/0.0	10.5/0.0		
3	*Oncophorus wahlenbergii*	n/c/n/c	30.3/15.7	27.5/15.7	

Morphological features. We compared the descriptions of the diagnostic features of *C. suecicum* in the literature sources (Arnell, Jensen, 1895; Savicz-Ljubitzkaja, Smirnova, 1970; Nyholm, 1987; Hallingbäck *et al.*, 2006). All authors indicate the following distinctive characteristics: 1) flat leaf margins throughout, 2) a more or less clearly differentiated group of cells at the angles of the leaf base, 3) a long excurrent nerve, 4) erect or almost erect, straight or hardly curved, furrowed capsule without struma, 5) an annulus composing of large cells, separating. Nyholm (1987) also poin-

ted at the width of cells in the upper part of leaf lamina — of 10–11 μm as a diagnostic feature. At the same time, some differences in the descriptions of the characters of this taxon can be found in the publications. Arnell and Jensen (1895) state that the nerve is weak, whereas Nyholm (1987) indicates a strong nerve and Hallingbäck *et al.* (2006) specifies that the nerve is widening towards the upper part of the leaf. Peristome teeth are split to 1/3 (Arnell, Jensen, 1895), to 1/2 (Savicz-Ljubitzkaja, Smirnova, 1970) or almost to the base (Nyholm, 1987; Hallingbäck *et al.*, 2006).

The morphological features of mosses in our samples from Drozdovka Bay generally correspond to those of *C. suecicum*, though with slight variations (Supplement[1]). In particular, the narrowing of the leaf into a subula can be quite sudden (sample #8), the margins of the leaf lamina in the upper part can vary from entire to crenulate-mamillose and even dentate-mamillose (the last — in specimens #7 and #8). Alar cell group can be indistinctly or clearly delimited from other cells of the lamina base and be inflated or not. A variable characteristic is the width of the cells in the upper part of the leaf, and it can differ even in the leaves of neighboring plants in the same turf. In the Barents Sea populations, these values may vary in range of 10–12 μm and up to 13.5 in sample #6. The nerve is quite strong in all populations and becomes wider by the middle of the leaf; it is always more or less long excurrent at the leaf apex. The appearance of the capsules is similar in all samples. In sample #6, some peristome teeth are divided into 3, significantly differing in size (i.e., not only split into 2 halves).

In specimens #2 and #4, individuals of *C. tenellum* have nerve ending at the leaf apex, strongly recurved leaf margins and annulus of smaller cells, but at the same time, spores are large (20–25 μm). Some features of *Cynodontium suecicum* samples from Drozdovka Bay surroundings are presented on figures 2–5.

Discussion

Recent wide-scale phylogenetic reconstruction of the family Rhabdoweisiaceae based on cpDNA and mtDNA markers (Fedosov *et al.*, 2021) elucidated great diversity within the family and revealed new and unexpected affinities among taxa traditionally associated with the same or different genera, resulting in numerous taxonomical rearrangements. The authors (l. c.) registered a high level of nucleotide markers similarity among *C. suecicum* and *C. tenellum*. Our multiplied sampling of both taxa, too, suggested an identity of *trn*L-F, but 10.5% divergence among ITS1-2 does not allow to include *C. suecicum* in synonymy with *C. tenellum*. We supposed that *C. suecicum* appears to be a hybrid between *C. tenellum* (cytoplasmic inheritance) and *Kiaeria blyttii* (nuclear inheritance) and could be treated as a species of a hybrid origin. Fedosov and coauthors deposited nucleotide sequences of ITS1-2 *Kiaeria blyttii* into GenBank, supporting this opinion (personal communication). Hybridization in mosses is possibly a frequent event that is registered among species of a single genus, among species of different genera in a single family, or even between genera from phylogenetically

[1] The Supplement is available at the end of the article page on the journal website (https://doi.org/10.31111/nsnr/2021.55.2.427).

Fig. 2. Leaves of *Cynodontium suecicum* from Drozdovka Bay surroundings.
1, 2 — from KPABG(M)#121111; 3, 4 — from KPABG(M)#124246.
Scale bar: 1 mm

remote families (cf.: Ignatov *et al*., 2019; Sawangproh, Cronberg, 2021). In our case, we discovered an example of intergeneric hybridization.

Considering the anatomical and morphological features, *C. suecicum* is a fairly well-defined species that is relatively easily identified in the presence of sporophytes. However, in the absence of mature capsules, plants can be confused with some other species. For example, on Ivanovka River shore, not far from Drozdovka Bay, we collected a specimen with sterile plants that were similar to gametophytes of the *C. suecicum* (leaves with slightly differentiated alar cells, elongate-rectangular incrassate cells in the lower part of leaf laminas, and mamillose excurrent nerves). By molecular data, it was associated with *Oncophorus wahlenbergii* (Table 1, #11). Nyholm (1987) wrote, that in habitus *Cynodontium suecicum* "may resemble *Kiaeria blyttii*" but "the latter is usually smaller and is easily recognized by its male inflorescences with several perigonial leaves". The inner perigonial leaves are wide, sheathing, suddenly narrowed to a short wide apiculus in *Cynodontium suecicum* vs. narrower, gradually tapering in *Kiaeria blyttii*.

In the Murmansk Region, *C. suecicum* is usually not very tall and is similar in height to *C. tenellum*. Sometimes it may be confused with the latter species, which can grow in adjacent or even in the same turf. In these cases, delimitation of them is difficult without preparing microscope slides. The main distinguishing features between these two species are flat leaf margins in the *C. suecicum* vs. recurved margins in the *C. tenellum*, nerve protruding from the leaf vs. apex-terminated nerve, and large cells of annulus

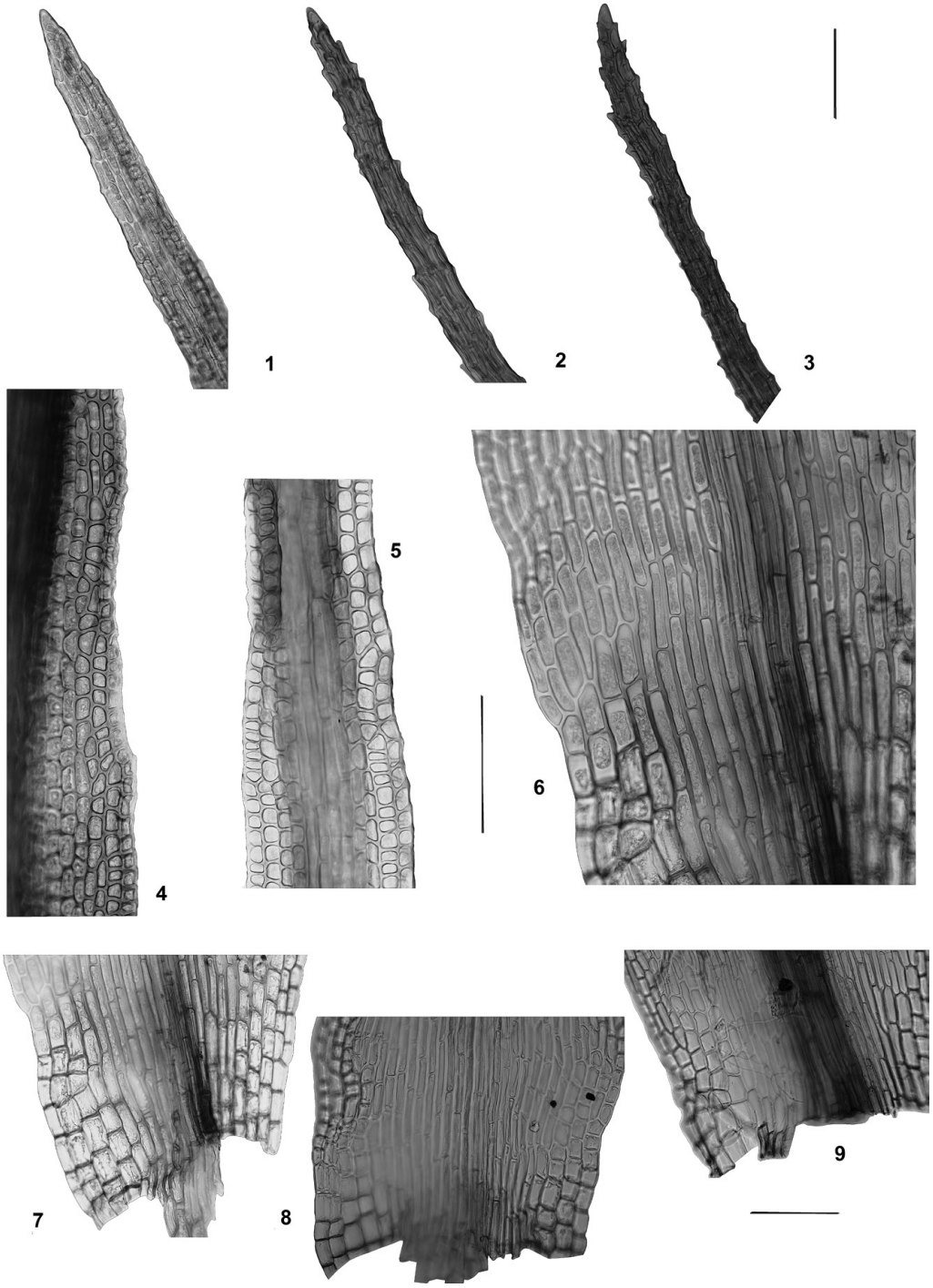

Fig. 3. Leaf lamina cells of *Cynodontium suecicum*.
1–3 — at the apex; 4, 5 — at the leaf middle, 6 — at the base; 7–9 — at the leaf angles;
1, 5–7 — from KPABG(M)#121111; 2–4, 8, 9 — from KPABG(M)#124246.
Scale bars: 100 μm.

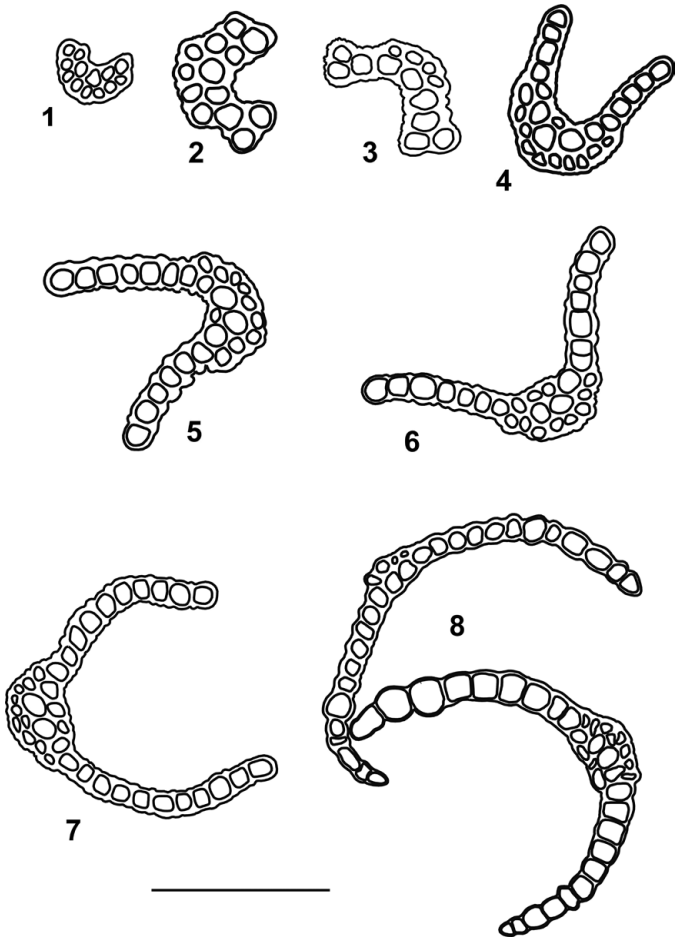

Fig. 4. Cross sections of leaves at upper (1–3), middle (4–6) and lower (7, 8) parts in *Cynodontium suecicum*.
1 — from KPABG(M)#121111; 2–8 — from KPABG(M)#124246.
Scale bar: 100 μm.

(45–55 μm) vs. smaller cells (15–20 μm). The width of the upper leaf cells is not a reliable distinguishing characteristic.

Thus, we suggest, that *C. suecicum* can be considered as a species that originated from hybridization between *C. tenellum* and *Kiaeria blyttii*, but it has clear morphological differences and sufficient genetic stability.

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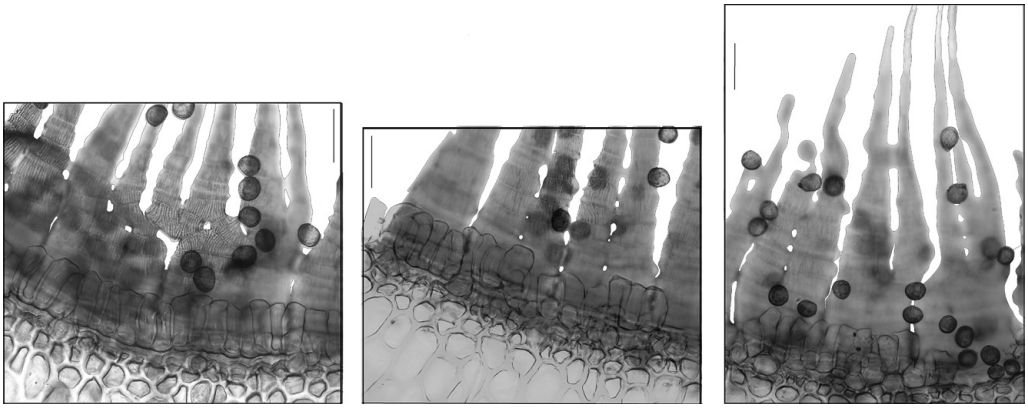

Fig. 5. Annulus at the capsules before natural opening in *Cynodontium suecicum* [KPABG(M)#124246]. Scale bars: 50 μm.

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