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THE GENUS *FABRONIA* (FABRONIACEAE, BRYOPHYTA) IN RUSSIA

РОД *FABRONIA* (FABRONIACEAE, BRYOPHYTA) В РОССИИ

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Abstract

A combined molecular-phylogenetic and morphological approach to the genus *Fabronia* resulted in recognizing of five species in the territory of Russia. *Fabronia ciliaris* is rather widespread in Russia, while *F. pusilla* and *F. rostrata* are rare. Two species are added: *F. major* is resurrected from the oblivion and *F. altaica* sp. nova is described. These species were found to be distinct from *F. ciliaris* in two studied nuclear markers of the ribosomal operon, ITS and IGS1, as well as by morphology. Detailed morphological descriptions and illustrations of all species, information on their distribution and key to identification of *Fabronia* species in Russia are given. It is shown that partial sequences of IGS1 provide a much stronger phylogenetic signal being essentially congruent with ITS.

Резюме

В результате изучения рода *Fabronia* в России с помощью молекулярно-филогенетических и морфологических методов на ее территории выявлено 5 видов. *Fabronia ciliaris* – наиболее широко распространенный вид, *F. pusilla* и *F. rostrata* – редкие. Два вида добавились к флористическому списку: *F. major,* которая ранее рассматривалась как разновидность *F. pusulla* или синоним *F. ciliaris*, восстановлена в видовом статусе; *F. altaica* sp. nova описана как новый вид. Эти два вида хорошо отличаются от *F. ciliaris* по двум ядерным маркерам рибосомного оперона, ITS и IGS1, равно как и по морфологическим признакам. Для каждого вида приводятся описание, иллюстрации и информация о распространении; дан ключ для определения видов *Fabronia* в России. Показано, что часть последовательности IGS1 имеет значительно большую вариабельность по сравнению с ITS и является перспективным маркером для решения проблем систематики на видовом уровне.

KEYWORDS: mosses, taxonomy, new species, molecular phylogenetics, ITS, IGS1

Introduction

The genus *Fabronia* Raddi has mainly a south-temperate to tropical distribution, with few species reaching north-temperate to boreal regions. In Eurasia, it has maximal diversity in China, where as much as ten species occur (Gao & Fu, 2002b). African flora includes 29 species, predominantly in its eastern regions, although many of them remain poorly known (O'Shea, 2006).

In the northern part of Holarctic, the genus *Fabronia* was usually accepted to include two widespread species: *F. ciliaris* (Brid.) Brid. and *F. pusilla* Raddi. The former one was reported from the eastern parts of both North America and Eurasia, while *F. pusilla* is primarily a western species in both continents. Some authors thought that they are not different and considered the latter merely as a subspecies of the former, *Fabronia ciliaris* subsp. *pusilla* (Raddi) Grout, or even as its synonym.

In European Russia, *F. pusilla* has been confirmed only from a single locality in Rostov Province (Ignatov & Ignatova, 2003). Most *Fabronia* collections from Asia were referred to *F. ciliaris*, although Abramova &Abramov (1968) reported *F. pusilla* from the Baikal area. *Fabronia matsumurae* Besch. was reported for the Russian Far East by Ignatov & Afonina (1992) based on unpublished record of V.Ya. Cherdantseva from Khabarovsk Territory; however, this species was excluded later (Ignatov, Afonina, Ignatova *et al.*, 2006), with the comment of Cherdantseva on the misidentification. Finally, *F. rostrata* Broth. was published by Dudov *et al.* (2015) for Amurskaya Province (Russian Far East) and Zabaikalsky Territory (Southern Siberia).

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The field work of the authors in Dagestan (East Caucasus) revealed an enormous variation in both gametophyte and sporophyte of *Fabronia* plants occurring in a small area, which forced us to explore the case more thoroughly with the DNA sequencing.

MATERIAL AND METHODS

Specimen selection

The prelinminary analysis of Caucasian specimens brought a result which lead to the expanded set. Finally, we studied DNA from 59 specimens: 49 from of *Fabronia ciliaris* s.l., nine of *F. pusilla*, and one of *F. rostrata*. Specimens were taken from MHA, MW, LE, NY and were kindly sent to us by H. Köckinger, N. Schnyder, J. Kučera, H. Hofmann and T. Kiebacher from their private collections. All collections of *Fabronia* from Russia kept in LE, MHA and MW, as well as some specimens from other regions from these Herbaria and also from H, S and NY were studied by traditional morphological methods. The images of the type collection of *F. major* from BM were kindly arranged by L. Ellis, and the type of *F. ciliaris* was studied by images of the Berlin digitized herbarium.

DNA extraction and amplification

Total genomic DNA was extracted from dry plants using the Nucleospin Plant Extraction Kit (Macherey-Nagel, Germany). Two regions of the ribosomal operon, ITS 1–5.8S–ITS2, and the first, 5'-part from 5S-side of the IGS1 were selected for this study.

For ITS region the laboratory protocol was essentially the same as in previous moss studies, described in detail by, *e.g.*, Gardiner *et al.* (2005).

The nuclear IGS1 region was amplified with primers complementary to 3' end of 26S rRNA gene - 26dR2 (forward) 5'-GAGATGAATCCTTTGCAGACG -3'and 5S rRNA gene - 5S(r)R2 (reverse) 5'-GAGTTCTGATGGGATCYGGTG -3', the latter following Wicke *et al.* (2011).

EncycloPlus PCRkit (Russia) was used for amplification. Amplification was conducted under the following conditions: 94°C – 3' (initial denaturation); 30 cycles: 94°C – 20", 62°C –20", 72°C – 40"; 72– 5' (final extension step). For some specimens, two PCR fragments of different length were obtained. Amplification products were separated on a 1% agarose gel in 1xTAE with ethidium bromide staining and purified using MinElute © Gel Extraction Kit (Qiagen, Germany). The length of IGS1 region varied from 238 to 476 bp in PCR product from different specimens. Most part of PCR product was sequenced without cloning. Heterogeneous matrixes were cloned in pTZ57R/T vector with ThermoScientificIns TAclone PCR Cloning kit (ThermoScientific). Clones were screened by length in 1,5% agarose gel; fragments of various length were sequenced. PCR products were sequenced using the ABI PRISM © BigDye™ Terminator v. 3.1 and further analyzed on an automated sequencer (Applied Biosystems) 3730 DNA Analyzer in common use facility "Genom". The specimen vauchers and GenBank accession numbers are given in Appendix 1.

Phylogenetic analyses

Sequences were aligned manually in Bioedit (Hall, 1999). ITS data of the outgroup taxa, *Catagonium nitens* (Brid.) Cardot and *Rhizofabronia perpilosa* (Broth.) Broth. were taken from the GenBank.

Bayesian Analyses (BA) were performed for both ITS and IGS1by running two parallel analyses in MrBayes 3.2.6 (Ronquist *et al*., 2012) with each run consisted of six Markov chains and 25,000,000 generations with default number of swaps chains. The sampling frequency was one tree each 5.000 generations, and the chain temperature was set at 0.02 in all analyses. Convergence of each analysis was evaluated using Tracer1.4.1 (Rambaut & Drummond, 2007) to check that all ESS values exceeded 200. Consensus trees were calculated after omitting the first 25% trees as burn-in. Analyses were performed on the Cipres Science Gateway (http://www.phylo.org/portal2) on XSEDE.

The haplotype network was built using the TCS program (Clement *et al.,* 2000) with a cut-off level of 0.95. Gaps in the datamatrix were manually coded as one mutational event regardless their length. Thus in the analysis parameter, gaps were considered as missing data.

Morphological studies

Selected specimens of *F. ciliata* s.l., including types and species included in the molecular phylogenetic analysis, were used for leaf and cell measurements with Infinity software. For each specimen, we measured for three leaves: leaf length, leaf width, and for 10 median laminal cells: cell length, cell width, with subsequent calculation cell length/width ratio and cell length/leaf length ratio.These data were analyzed in PAST (Hammer *et al*., 2001).

RESULTS

Molecular studies

For ITS, 56 out of 58 sequences were newly generated, and all 41 IGS1 sequences were newly obtained. ITS alignment included 689 positions, 51 being variable and 23 parsimony informative. Bayesian analysis of the ITS, with outgroups of *Catagonium* and *Rhizofabronia*, found *Fabronia* to be monophyletic (PP=1). *Fabronia* is represented by a terminal clade, comprising mainly a polytomy, and the basal grade, where two branches include, first, five specimens from Altai and Caucasus in polytomy (Group 2) and, second, two specimens from Texas, U.S.A., referred by morphology to *F. ciliaris* var. *wrightii* (Sull.) W.R. Buck (Fig. 1). They form a well supported clade (PP=0.99), sister to the terminal clade, which is rather poorly supported (PP=0.70). Within the terminal clade, the extensive polytomy is formed by specimens of *F. ciliaris* (most specimens), *F. rostrata* and *F. ciliaris* var. *polycarpa* (Hook.) W.R. Buck, and three clades nested within this polytomy. These three nested clades include: (1) 13 specimens from Central Europe and the Cacuasus (Group 1), and their clade has got a maximal support; (2) nine specimens of *F. pusilla* (PP=0.97); and (3) moderately supported group of four specimens of *F. ciliaris* from Dagestan (PP=0.89).

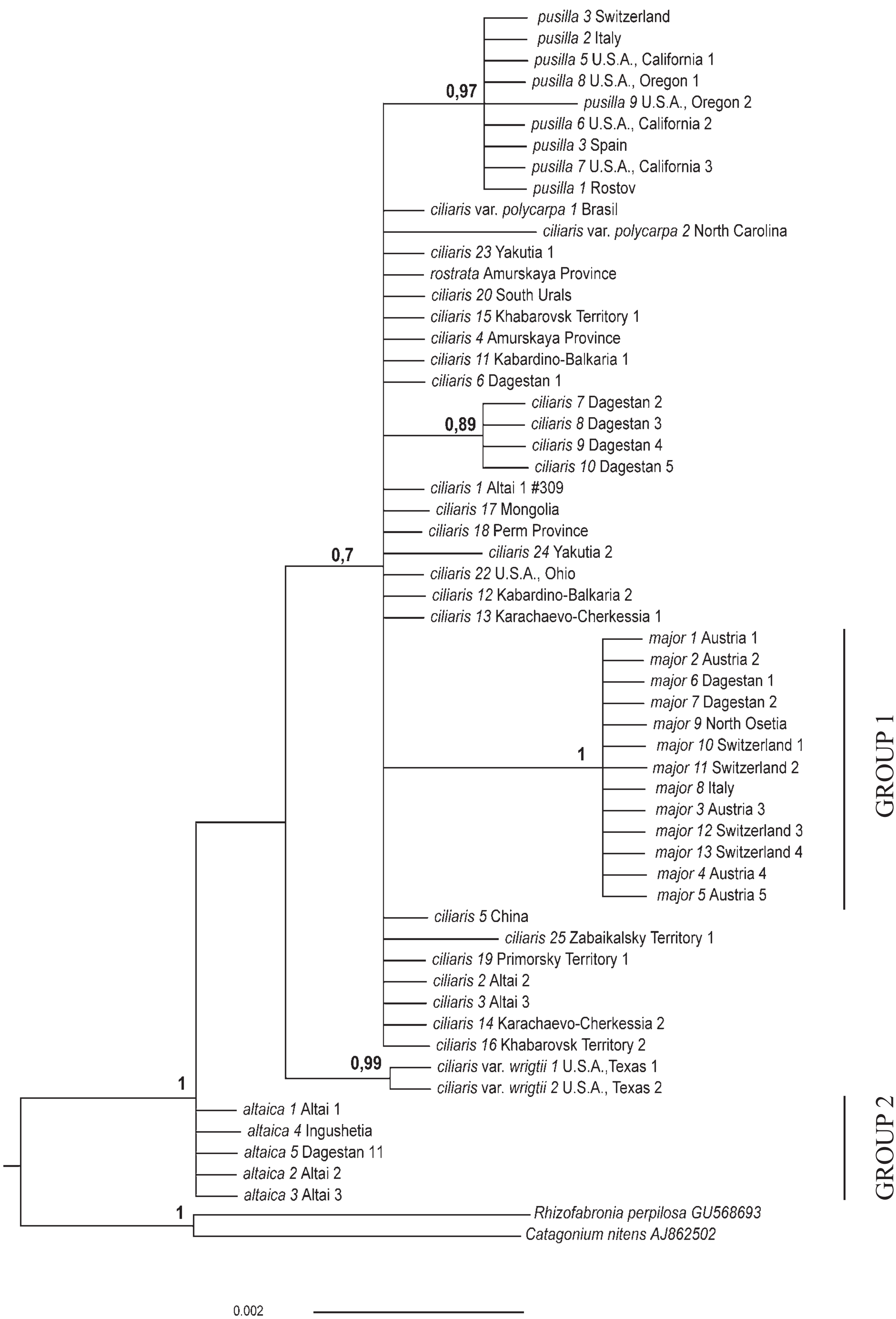

Fig. 1. Bayesian tree from dataset of nuclear ITS1-2. Posterior probabilities (>0.7) are shown above branches.

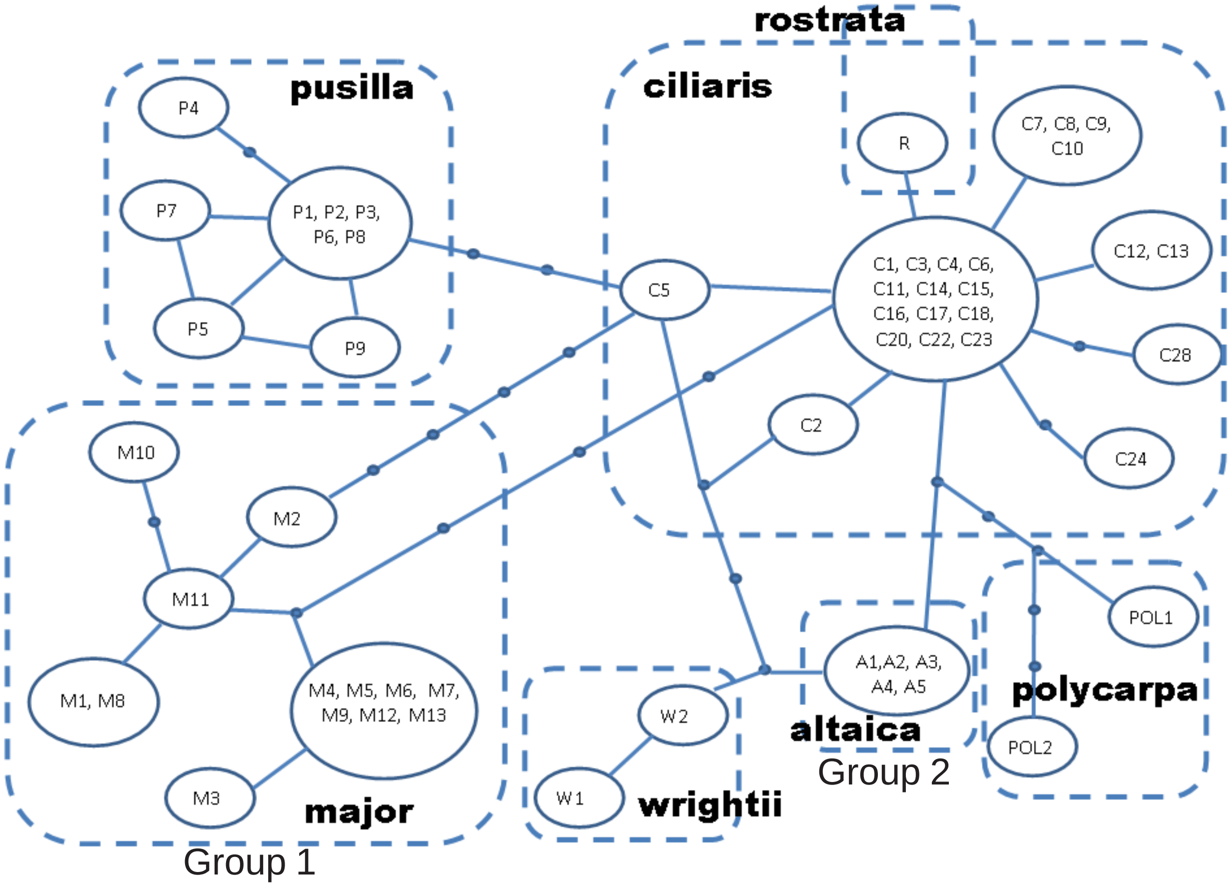

Fig. 2. Haplotype network from dataset of nuclear ITS1-2.

TCS analysis of the same set, but differing in the gap coding, demonstrated a principally similar grouping of specimens (Fig. 2). The largest number of them appeared in *F. ciliaris* cluster, where the core haplotype with 13 specimens is surrounded by 10 specimens differing in one or two mutational event. The only studied specimen of *F. rostrata* appeared to be the least differentiated genetically: it differs from the core *F. ciliaris* by only one insertion. Two substitutions differentiate all five specimens of the Group 2, which further linked with the North American *F. ciliaris* var. *wrightii* that differs by another two substitutions from the Group 2 haplotype. Another American plants, preliminary referred here to *F. ciliaris* var. *polycarpa* (from North Carolina and Brasil) appear as a branch originating from missing haplotype between core *F. ciliaris* and the Group 2. *Fabronia pusilla* is linked to *F. ciliaris* by a longer branch of three missing haplotypes and also it is linked not to core *F. ciliaris*, but to Chinese (Inner Mongolian) haplotype. The latter specimen has a very peculiar position, being immediately connected with five groups: core *F. ciliaris* (1step), *F. pusilla* (3 steps), Group 2 (4 steps), *F. ciliaris* var. *wrightii* (4 steps), and Group 1 (5 steps). Thirteen specimens of the Group 1 are only moderately compact: the most common haplotype is represented by 7 out of 13 specimens, and the distance between extremes is 5 steps (4 haplotypes, either present or missing). However, no geographical grouping is seen within specimens of the Group 1: *e.g.*, both Caucasian and Central European plants are present in haplotypes [M1,M8] and [M4...M13], as shown in Fig. 2. The group 1 has two links to *F. ciliaris*, both with 4 missing haplotypes.

IGS1 sequences were found sufficiently more variable than ITS. Their alignment includes 509 positions, where in 98 positions from the 5'-end are quite conservative: only five are variable, four being parsimony informative. Next 80 positions are somewhat more variable, but almost without indels, which appear later in the alignment (Fig 3, to the right of 177 position). One long insertion of 96 bp occurs in one specimen of *F. ciliaris*, and in the last 110 positions (400–509) there are 31variable and 20 parsimony informative. Alignment itself shows a marked differences, especially for the Group 1 (Fig. 3). Specimens of *F. pusilla* differ in fewer indels, but in a number of substitutions. *Fabronia ciliaris* is especially heterogeneous; however, specimens from the Group 2 are characterized by a stable presence of several substitutions and indels, differing them from all found haplopytes of *F. ciliaris*. *Fabronia rostrata* has no unique substitutions or indels in IGS1, being especially similar to specimens of *F. ciliaris* from a rather neighboring (within 1000 km) areas. Specimen of *F. ciliaris* var. *wrightii*

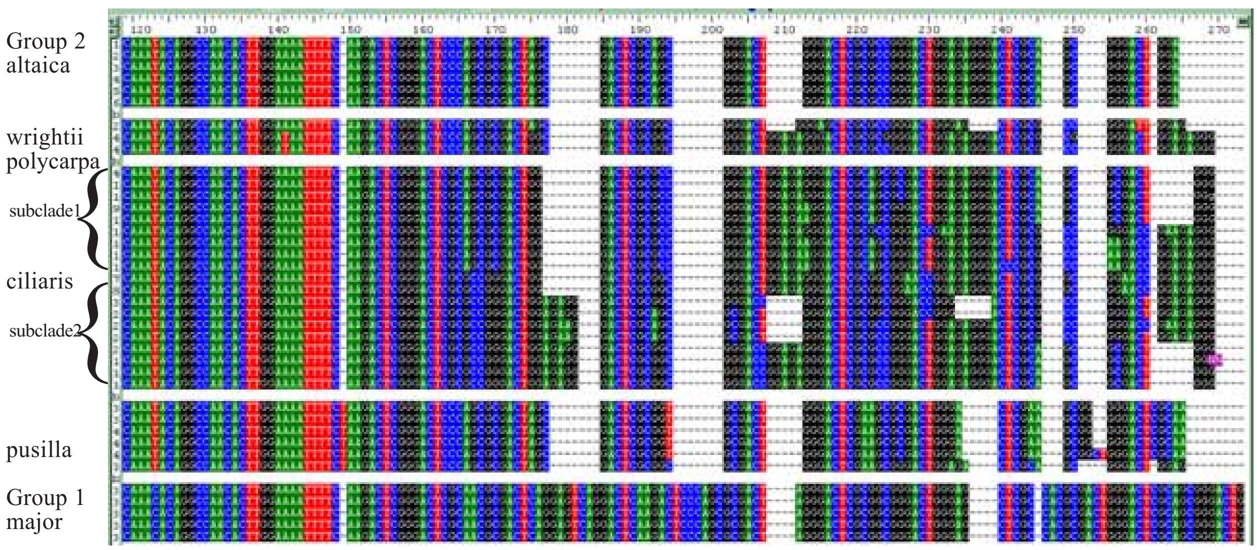

Fig. 3. Part of IGS alignment.

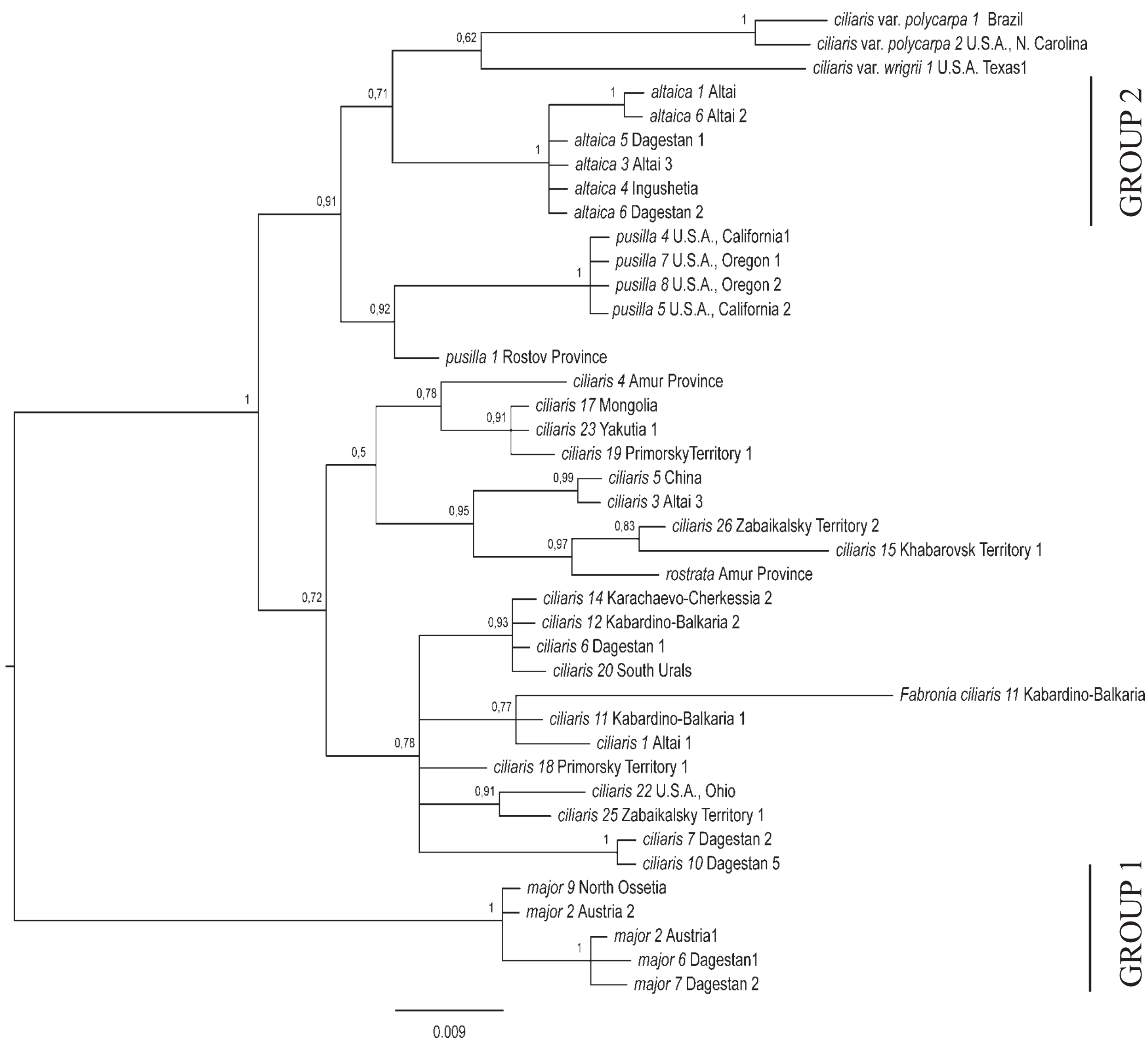

Fig. 4. Bayesian tree from dataset of nuclear IGS. Posterior probabilities (>0.7) are shown above branches.

from Texas is intermediate between specimens of the Group 2 and *F. ciliaris* s.str. + *F. ciliaris* var. *polycarpa*.

Unrooted Bayesian tree based on IGS1 sequences presents the groups well-seen from the alignment (Fig. 4). Specimens of the Group 1 form the maximally supported clade sister to all others, which appear also in the clade with the maximal support. The latter includes two clades, one of *F. ciliaris* and *F. rostrata*, and another clade, with subclades of *F. pusilla* (PP=0.92), specimens of the Group 2 (P=1), *F. ciliaris* var. *polycarpa* (PP=1) and *F. ciliaris* var. *wrightii* (one specimen). Within the better represented specimens, the following geographical delimitation is remarkable. In *Fabronia pusilla,* one specimen from the South European Russia is sister to the western North American specimens, which form a maximally supported clade. In *F. ciliaris,* there are two clades, albeit with low support. Noteworthy is that one clade comprises the mixture of North American, European and Asian (up to Pacific coast) plants, whereas the second one includes East Asian plants, with one westernmost locality in Altai Mountains.

Morphological studies

Differences between specimens of the Group 1, Group 2 and *F. ciliaris* in leaf shape, length of marginal teeth and cell areolation are shown in Figs. 5–6 (see also discussion below). Studied specimens of *F. pusilla* were rather variable in leaf shape, ranging from ovate (more common) to lanceolate (Fig. 9: 1–6); however, all of them had multicellular marginal teeth (Fig. 10: 1–5); cell length and cell length/ width ratio were also found to be variable in studied specimens (Fig. 10: 1–5), but specimens with short laminal cells, similar to *F. ciliaris*, were more numerous. Two studied specimens of *F. ciliaris* var. *wrightii* appeared to be very similar to the Group 2 in leaf shape, dentation of leaf margins, leaf length and width, cells and capsule shape (Figs. 9: 9–10, 10: 8 and 11: 19).

The results of measurements of cell length and width of seven specimens from the Group 1, five specimens from the Group 2 and seven specimens of *F. ciliaris* are shown in Fig. 7. *Fabronia ciliaris* has the shortest cells, (18–)22–39(–43) μm, cells of specimens from the Group 1 are the longest, (36–)50–70(–95) μm, while specimens of the Group 2 are intermediate between them in this parameter: (29–)35–53(–78) μm. Variability in cell length is the lowest in specimens of the Group 2 and the highest in specimens of the Group 1 (Fig. 7A). Similar trends are observed in cell length/width ratios of these specimens (Fig. 7B).

Peristomes are represented in herbaria mostly in opened capsules, they are often broken off, and their preservation is far from perfect. SEM studies in a limited material did not allow us to find any differences between *F. ciliaris* and specimens fo the Group 1, but the Group 2 is somewhat distinct from them in the following peristomial characters: (1) inner surface of exostome teeth is almost smooth at base vs. longitudinally striolate; (2) inner surface in the middle has more prominent and more densely arranged longitudinal striae vs. more distantly arranged and not that prominent ones; (3) outer surface in the middle has more prominent striae covered by regularly arranged papillae vs. striae not so prominent, papillae more variable in shape, often sitting on tooth surface, not on apparent striae.

DISCUSSION

The present results show a more complicated situation within the genus *Fabronia* than it was thought before. Separate status of *F. pusilla* is confirmed in all analyses. *Fabronia rostrata* appeared to be only slightly differentiated from *F. ciliaris* genetically, despite these species have stable morphological distinctions both in gametophyte and sporophyte structure. At the same time, specimens referred to *F. ciliaris* s.l. were resolved in a more complex topology in the molecular phylogenetic trees. The original hypothesis that '*F. ciliaris*' includes two sympatric species in the East Caucasus was over-confirmed: Dagestan plants appeared to belong to three entities instead of two: *F. ciliaris* s. str., Group 1 and Group 2.

Group 1

Fabronia ciliaris s. str. formed an unresolved polytomy with *F. rostrata* and *F. ciliaris* var. *polycarpa* in ITS-based tree, with nested clades of *F. pusilla*, *F. ciliaris* var. *wrightii* and species of Group 1 (Fig. 1). IGS1 tree found *F. ciliaris* s. str. in a poorly supported clade formed by two subclades (Fig. 4), differences between which are easy to see simply in the alignment (Fig. 3). One of these subclades includes specimens from North America, Western Europe, Caucasus and thoughout Russia up to Pacific coast, whereas another clade includes only East Asian specimens from China, Mongolia and Russia up to Altai Mountains. The latter area is known as a western limit for many eastern species (Ignatov, 1993). No morphological distinctions for specimens of these two subclades were found. All specimens of *F. ciliaris* s. str. are characterized by ovate and abruptly acuminate leaves, serrulate leaf margins with small, mainly unicellular teeth, short laminal cells and ovate capsules.

Specimens of the Group 1(13 specimens in ITS set, 5 in IGS1 set) have a restricted range from Central Europe to the Eastern Caucasus (North Ossetia and Dagestan). In both ITS and IGS1 trees, they form a maximally supported clade and are well separated in haplotype network (Figs. 1–2, 4). In the ITS tree, this clade is nested within the polytomy of *F. ciliaris*, while in IGS1 tree it is sister to the rest *Fabronia* taxa involved in the present analysis. These specimens are also well distinguished by gametophyte morphology. They have leaves different in shape from *F. ciliaris*: ovate-lanceolate or lanceolate, more or less gradually tapered and then narrowed into attenuate acumen vs. ovate, abruptly narrowed into acumen (Fig. 5: 12–15 and 1–6); leaf margins are more strongly serrate, with long unicellular teeth vs. finely serrate or serrulate, with short unicellular teeth (Fig. 6: 11–14 and 1–5); and laminal cells are longer, 50–70 μm

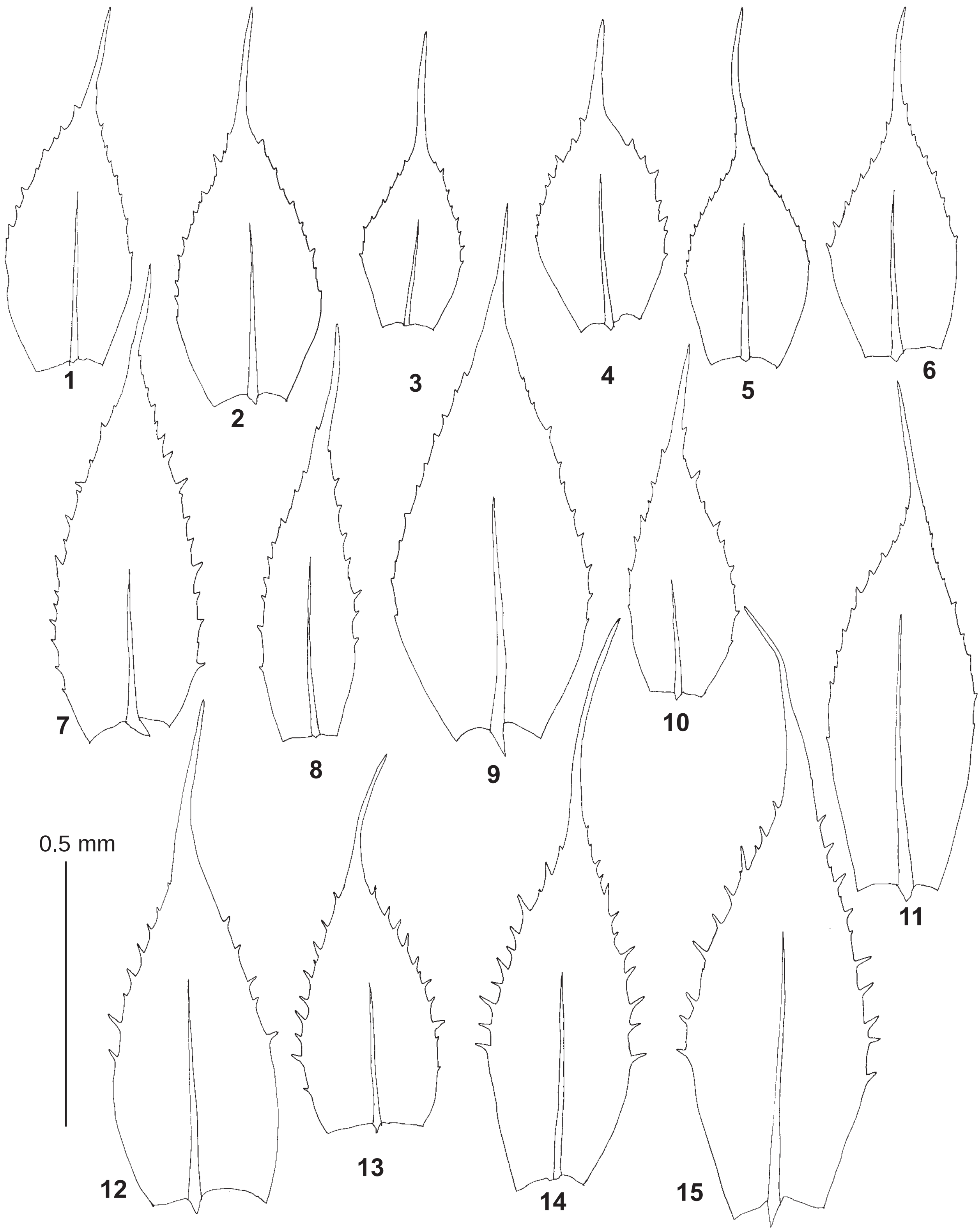

Fig. 5. 1–6 – *Fabronia ciliaris;* 7–10 – *F. altaica* (group 2); 11 – *F.* cf. *altaica*; 12–15 – *F. major* (group 1). 1 – putative isotype of *F. ciliaris*, Helvetia, LE; 2 – Russia, Dagestan, *Ignatov & Ignatova 09-766*, MHA; 3 – Russia, Altai Republic, 3.VII.1989, *Ignatov 0/43*, MHA; 4 – Russia, Khabarovsk Territory, *Ignatov & Ignatova 13-494*, MHA; 5 – Amurskaya Province, 21.VI.2011, *Bezgodov 391*, MHA; 6 – U.S.A., Ohio, *Buck 50414*, NY; 7 – Russia, Altai Republic, *Ignatov & Ignatova 12-747*, MHA; 8 – Altai, 31.VII.1991, *Ignatov & Ignatova 25/53*, MHA; 9 – Russia, Dagestan, *Ignatov & Ukrainskaya 09-480*, MHA; 10 – Russia, Dagestan, *Ukrainskaya 14098*, LE; 11 – Italy, 31.X.1898, *Artaria s.n.*, LE; 12 – Austria, 2.X.2013, *Köckinger 14991*, duplicate in MW; 13 – Austria, 18.IV.2001, *Köckinger 14992*, duplicate in MW; 14 – Russia, North Ossetia/Alania, *Ukrainskaya 15938*, LE; 15 – Russia, Dagestan, *Ignatov & Ukrainskaya 09-572*, MHA. 1–15 – leaves. Scale bar: 0.5 mm for all.

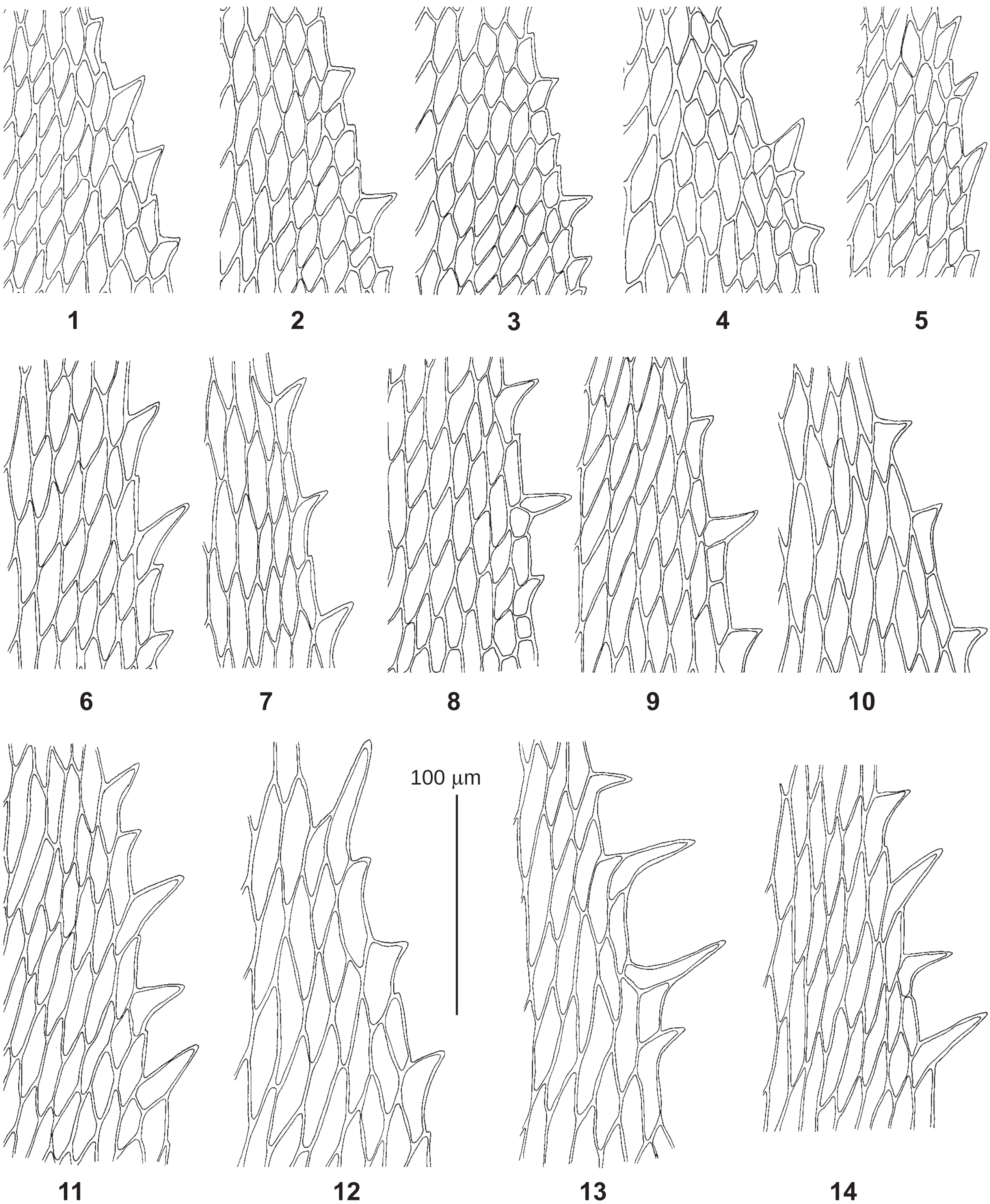

Fig. 6. 1–5 – *Fabronia ciliaris;* 6–9 – *F. altaica* (group 2)*;* 10 – *F.* cf. *altaica;* 11–14 – *F. major* (group 1). 1 – putative isotype of *F. ciliaris*, Helvetia, LE; 2 – Russia, Dagestan, *Ignatov & Ignatova 09-766*, MHA; 3 – Russia, Altai Republic, 3.VII.1989, *Ignatov 0/43*, MHA; 4 – Russia, Khabarovsk Territory, *Ignatov & Ignatova 13-494*, MHA; 5 – U.S.A., Ohio, *Buck 50414*, NY; 6 – Russia, Altai Republic, *Ignatov & Ignatova 12-747*, MHA; 7 – Altai, 31.VII.1991, *Ignatov & Ignatova 25/53*, MHA; 8 – Russia, Dagestan, *Ignatov & Ignatova 09-672*, MHA; 9 – Russia, Dagestan, *Ukrainskaya 14098*, LE; 10 – Italy, 31.X.1898, *Artaria s.n.*, LE; 11 – Austria, 18.IV.2001, *Köckinger 14992*, duplicate in MW; 12 – Russia, Dagestan, *Ignatov & Ignatova 09-254*, MHA; 13 – Russia, Dagestan, *Ignatov & Ukrainskaya 09-572*, MHA; 14 – Russia, North Ossetia/Alania, *Ukrainskaya 15938*, LE. 1–14 – median leaf cells. Scale bar: 100 µm for all.

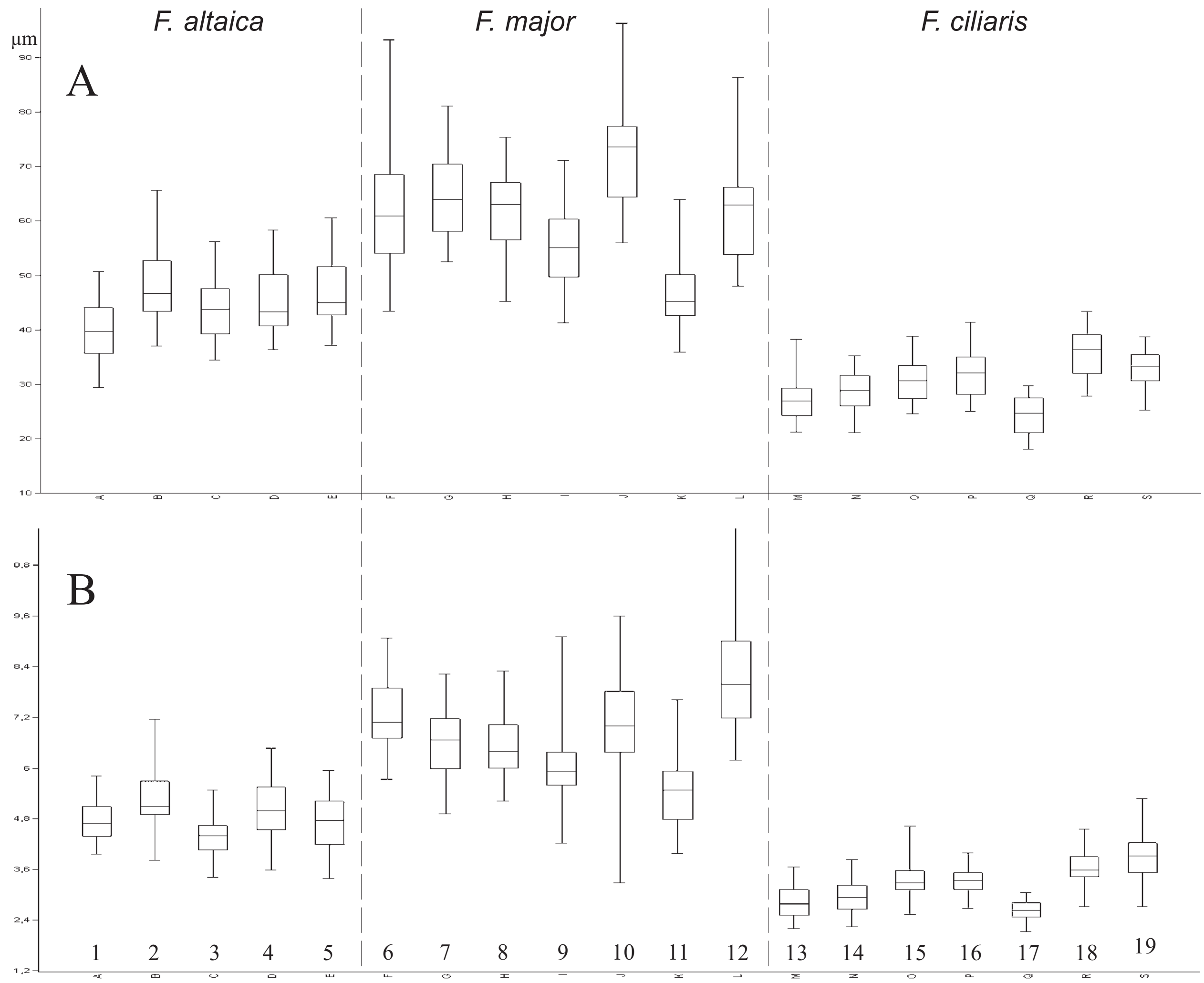

Fig. 7. Leaf cell length, µm (A) and leaf cell length/width ratios of 19 specimens of *Fabronia* (for voucher information see Appendix 1 and specimens examined sections for each species). 1–4 – *Fabronia altaica:* 1 – Altai 2; 2 – Dagestan 2; 3 – Ingushetia; 4 – Altai 1. 5 – *F.* cf. *altaica*: Italy, Como. 6–12 – *F. major:* 6 – Dagestan 1; 7 – Dagestan 2; 8 – Austria 1; 9 – North Ossetia; 10 – Switzerland 2; 11– Italy, lectotype of *F. major*; 12 – Austria 4. 13–19 – *F. ciliaris:* 13 – Amurskaya Province; 14 – Zabaikalsky Territory 1; 15 – Altai 1; 16 – Primorsky Territory, Ignatov et al. #13-1840, MHA; 17 – Yakutia 2; 18 – U.S.A., Ohio; 19 – putative isotype of *F. ciliaris*, Helvetia, LE.

vs. 20–40 µm. This combination of characters is stable and easily recognized, thus it seems that the Group 1 represents a good separate species.

The species morphology corresponds to *F. major* De Not., a species described in 1836 from northern Italy, but shortly after that referred by the authors of "Bryologia Europaea" to *F. pusilla* as a variety, var. *major* (De Not.) Schimp.[1] In this book, there are two pictures, namely Fig. 6 in the plate "*Fabronia pusilla*" and one unnumbered picture to the right of "6" that lack figure explanation. At the same time, these pictures are the only not mentioned in the text (unlike all others from this plate, accurately cited in the text of *F. pusilla*). As var. *major* is discussed in the text, we assume that these two pictures belong to this taxon. Picture 6 shows strongly serrate leaf margins, but with unicellular teeth, contarary to *F. pusilla,* where teeth are usually multicellular (illustrations of *F. pusilla* var. *pusilla* in "Bryologia Europaea" always show multicellular teeth). Also a relatively long laminal cells are specially illustrated in unnumbered figure.

The type collections of *F. major* are absent in FI, but are available in BM. Specimens that fit the protologue are kept in BM. Kind assistance of L.T. Ellis who made three photographs showing leaf shape and cell areolation of the type material of *F. major* (Fig. 14) allowed us to conclude the identity of the type of *F. major*, the drawing 6 in "Bryologia Europaea" and the plants of our Group 1.

Group 2

Specimens of the Group 2 were found in ITS tree to be sister to the rest of *Fabronia* taxa (Fig. 1), and in IGS1 tree they were resolved in a maximally supported clade sister to the clade of North American *F. ciliaris* var. *wrightii* and var. *polycarpa* (Fig. 4). Morphologically,

[1] – Authors of "Index Muscorum" referred this taxon to the synonym of *F. ciliaris* (Wijk *et al.*, 1962).

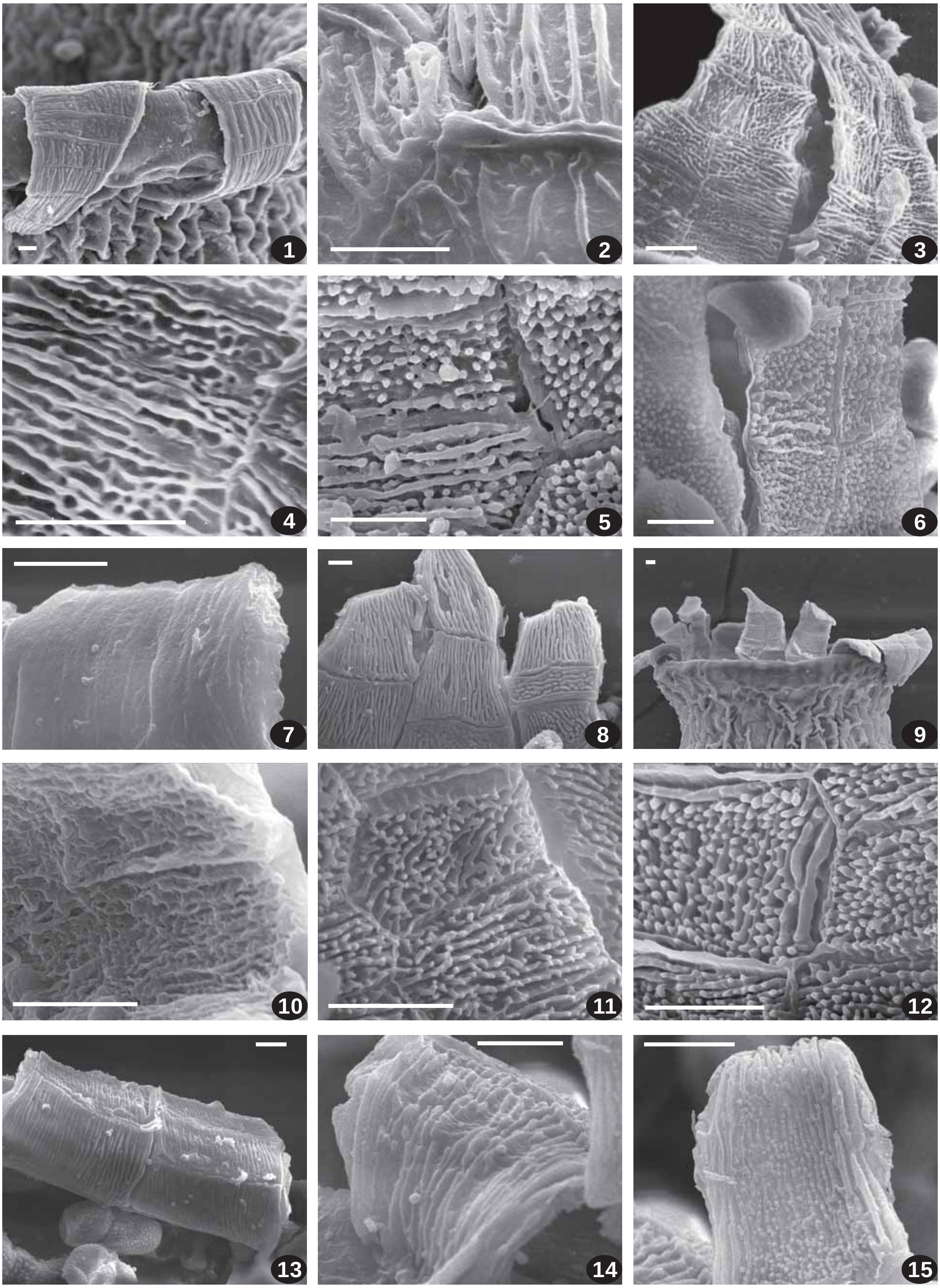

Fig. 8. Peristomes of *Fabronia:* 1–6 – *Fabronia ciliaris* (from: Russia, Altai, *Ignatov & Ignatova 12-747*, MHA); 7–12 – *F. altaica* (from: Russia, Altai, *Ignatov & Ignatova 25/151*, MHA)*;* 13–15 – *F. major* (from: Austria, *Köckinger 14992*, MHA)*.* 1–2, 7–8. 13–14 – inner surface of exostome teeth; 3–6, 10–12, 15 – outer surface of exostome teeth; 9 – whole peristome. All scale bars: 10 μm.

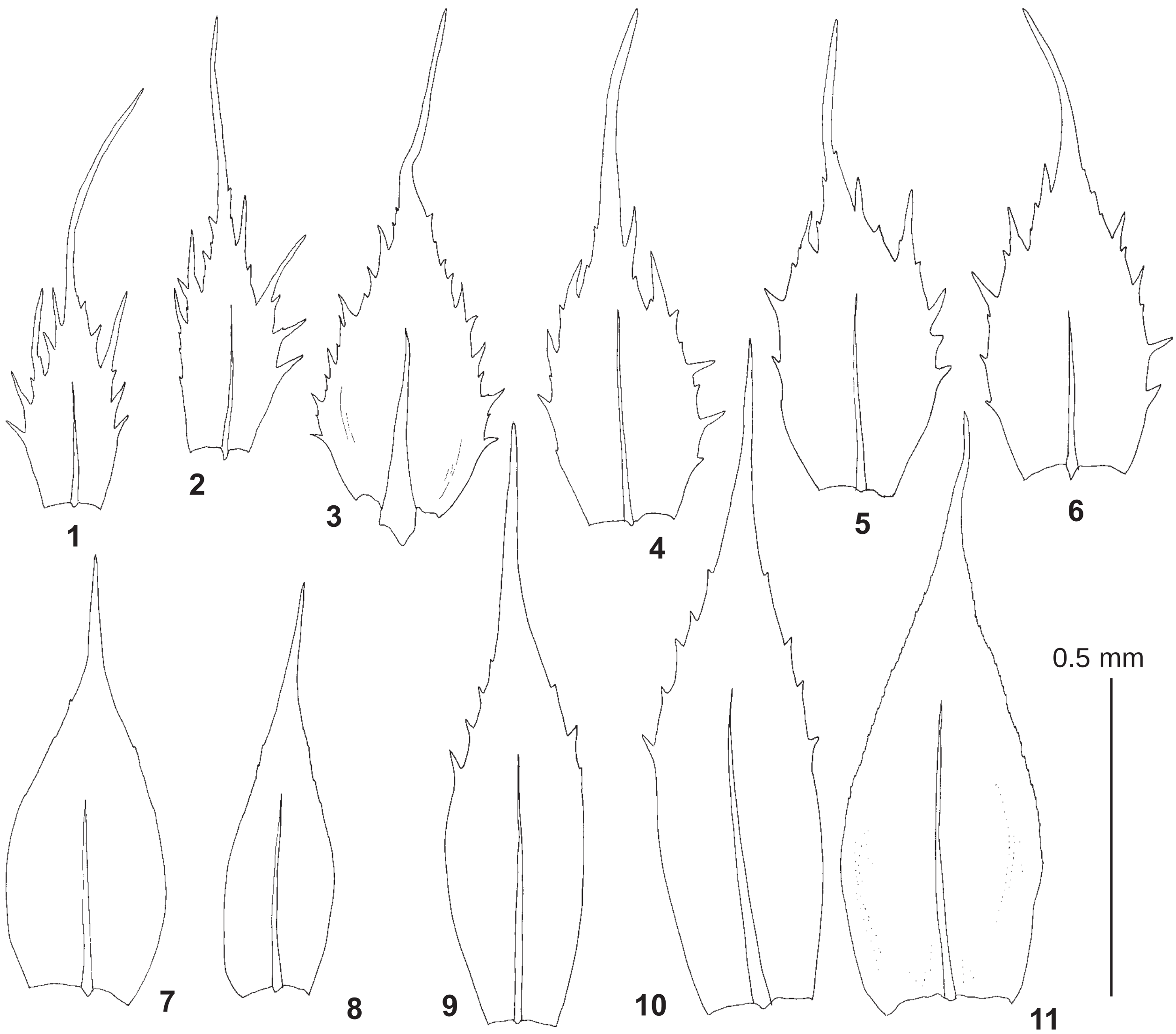

Fig. 9. 1–6 – *Fabronia pusilla;* 7–8 – *F. ciliaris* var. *polycarpa;* 9–10 – *F. ciliaris* var. *wrighti* (type); 11 – *F. rostrata.* 1–2 – Spain, 3.V.2015, *Kučera 17500*, dupl. ex herb. Jan Kučera in CBFS; 3 – Russia, Rostov Province, 16.X.2000, *Sereda s.n.*, MHA; 4 – Kyrgyzstan, 18.VI.1965, *Rakhmatulina s.n.*, LE; 5 – Russia, Buryatia, Baikal Lake, 26.VI.1956, *Bardunov s.n.*, LE; 6 – U.S.A., Oregon, *Shevock 31600*, NY; 7 – U.S.A., North Carolina, *Buck 25250*, NY; 8 – Jamaica, 15.VII.1922, *Anonymus*, LE; 9–10 – U.S.A., Texas, *Wright 251,* S #F87916; 11 – Russia, Amurskaya Province, 7.VIII.2013, *Dudov & Kotel'nikova 2013_Br_0593*, MW. 1–11 – leaves. Scale bar: 0.5 mm for all.

specimens of this group are similar to *F. major* in leaf shape: ovate-lanceolate, more or less gradually attenuate. Leaf margins are more strongly serrate in comparison to *F. ciliaris*, but marginal teeth are shorter than in *F. major*. Length of laminal cells is intermediate between *F. ciliaris* and *F. major* and ranges mainly from 30 to 50 µm (see also Fig 7). These specimens are also characterised by longer capsules compared with *F. ciliaris* and usually darker colored peristome teeth. In addition to the specimens from Dagestan, which were initially noticed as different from *F. ciliaris*, a number of collections of this taxon were found in Altai and one in Ingushetia (Eastern Cauasus).

Although some morphological characters of the plants from the Group 2 are intermediate between *F. ciliaris* s. str. and *F. major*, molecular phylogenetic data do not support such conclusion. Contrary, they point a certain affinity to southern North American and South American taxa, usually accepted at the infraspecific level of *F. ciliaris*. In the latest treatment of the genus for North America, McIntosh (2014) recognized only two species, *F. ciliaris* and *F. pusilla*. He referred to the treatment of Buck (1994) on the 'Moss Flora of Mexico' and appreciated his key to the varieties of *F. ciliaris*, but, nevertheless, considered them too variable for acceptance. These varieties include var. *ciliaris*, var. *polycarpa* and var. *wrightii* (two latter originally described as separate species). *Fabronia ciliaris* var. *polycarpa* is described by Buck as a very variable taxon, distributed in southeasten North America, Mexico (common), Jamaica and Dominican Re-

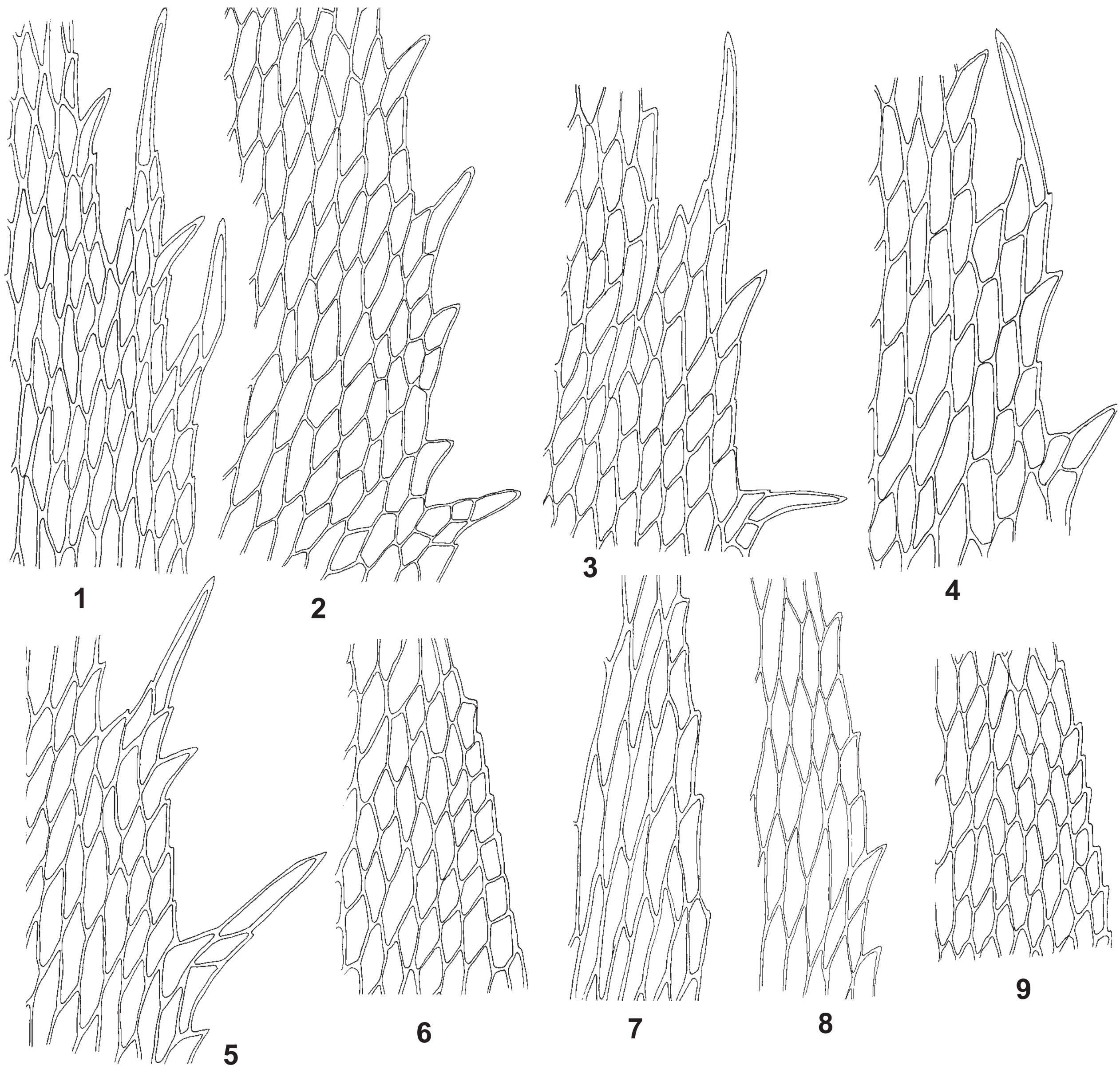

Fig.10. 1–5 – *Fabronia pusilla;* 6–7 – *F. ciliaris* var. *polycarpa;* 8 – *F. ciliaris* var. *wrightii*; 9 – *F. rostrata.* 1 – Spain, 3.V.2015, *Kučera 17500*, dupl. ex herb. Jan Kučera in CBFS; 2 – Russia, Rostov Province, 16.X.2000, *Sereda s.n.*, MHA; 3 – Kyrgyzstan, 18.VI.1965, *Rakhmatulina s.n.*, LE; 4 – Russia, Buryatia, Baikal Lake, 26.VI.1956, *Bardunov s.n.*, LE; 5 – U.S.A., Oregon, *Shevock 31600*, NY; 6 – U.S.A., North Carolina, *Buck 25250*, NY; 7 – Jamaica, 15.VII.1922, *Anonymus*, LE; 8 – U.S.A., Texas, *Wright F87916*, S; 9 – Russia, Amurskaya Province, 7.VIII.2013, *Dudov & Kotel'nikova 2013_Br_0593*, MW. 1–8 – median leaf cells. Scale bar: 100 μm for all.

public and northern South America (Buck, 1983, 1994). Likewise var. *ciliaris*, it has ovate leaves, but they are gradually short-acuminate and often have subentire margins. *Fabronia ciliaris* var. *wrightii* is also reported as common in Mexico, present in Jamaica and Dominican Republic and northern South America and also in southwestern United States. Among its diagnostic characters, Buck (1994) mentions lanceolate, long-acuminate leaves; illustration on page 864 shows weakly serrulate margins and laminal cells that are longer than in var. *ciliaris* (cf. Fig. 645 j and b). Shape of capsules is not discussed in this treatment. We have studied a syntype of *F. wrightii* in S (Texas. In agro Texano, Wright 251, B87916). This specimen is sterile; plants have lanceolate leaves, but stronger serrate margins (Fig. (9: 9–10); in these characters, as well as in cell length (Fig. 10: 8) it appeared to be similar to the plants from Group 2 (eastern Caucasus and Altai).

In our dataset, five specimens of *F. ciliaris* s.l. from America were included: two of var. *wrightii* from the U.S.A., Texas, two of var. *polycarpa* from Brasil and the U.S.A., and one of var. *ciliaris* from the U.S.A., Ohio. Such scarce sampling is insufficient for solving taxonomic problems of the genus in North America, where *Fabronia* obvious-

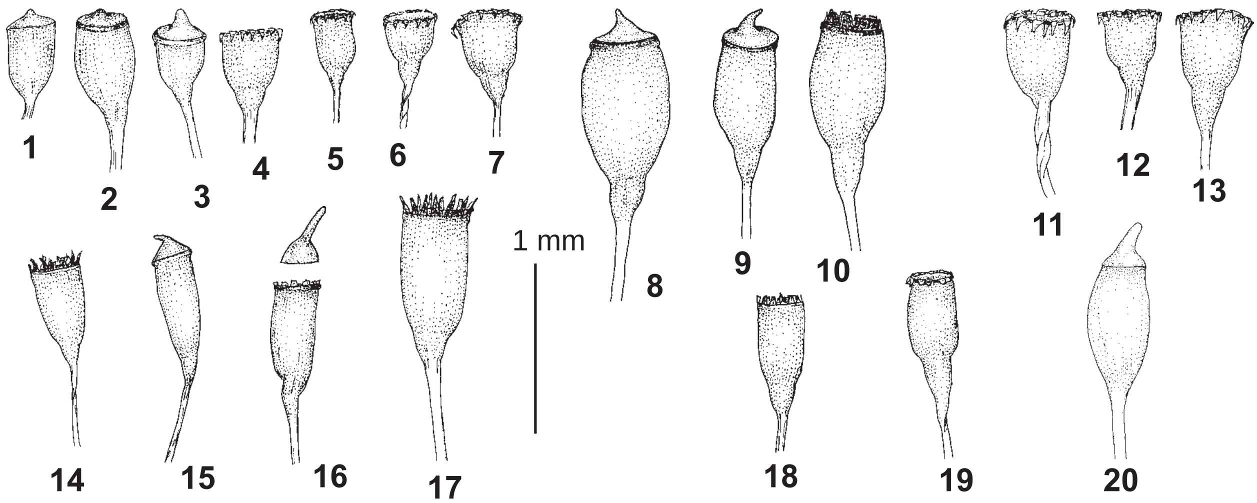

Fig. 11. 1–7 – *Fabronia ciliaris*; 8–10 – *F. major* (group 1); 11–13 – *F. pusilla*; 14–16 – *F. altaica* (group 2); 17 – 11 – *F.* cf. *altaica*; 18 – *F. ciliaris* var. *polycarpa*; 19 – *F. ciliaris* var. *wrightii*; 20 – *F. rostrata*. 1 – Russia, Bashkortostan, 2.IX.1945, *Selivanova-Gorodkova s.n.*, MHA; 2 – Russia, Altai Republic, 7.VII.1993, *Ignatov & Ignatova 34/24*, MHA; 3 – Russia, Khabarovsk Territory, *Ignatov & Ignatova 13-494*, MHA; 4 – Russia, Altai Republic, 3.VII.1989, *Ignatov 0/43*, MHA; 5 – Russia, Dagestan, *Ignatov & Ignatova 09-672*, MHA; 6 – Russia, Amurskaya Province, 21.VI.2011, *Bezgodov 391*, MHA; 7 – U.S.A., Ohio, *Buck 50414*, NY; 8–10 – Austria, 1.II.1994, *Köckinger 94-79*, duplicate in MW; 11 – Spain, 3.V.2015, Kučera 17500, dupl. ex herb. Jan Kučera in CBFS; 12 – Kyrgyzstan, 18.VI.1965, *Rakhmatulina s.n.*, LE; 13 – Russia, Irkutsk Province, Baikal Lake, 26.VI.1956, *Bardunov s.n.*, LE; 14 – Russia, Dagestan, *Ukrainskaya 14098*, LE; 13 – Russia, Altai Republic, *Ignatov & Ignatova 12-747*, MHA; 16 – Russia, Altai Republic, 31.VII.1991, *Ignatov & Ignatova 25/53*, MHA; 17 – Italy, 31.X.1898, *Artaria s.n.*, LE; 18 – Jamaica, 15.VII.1922, *Anonymus*, LE; 19 – U.S.A., Texas, 14.VIII.2005, Buck 49234 (NY); 20 – Russia, Amurskaya Province, 7.VIII.2013, *Dudov & Kotel'nikova 2013_Br_0593*, MW. 1–19 – capsules. Scale bar: 100 μm for all.

ly needs more attention. Only one specimen, from Ohio, was resolved within the group of Eurasian specimens of *F. ciliaris* s. str. by both molecular markers, which is in a full agreement with its morphology. Other four specimens appeared in different places in two obtained topologies. In ITS based tree (Fig. 1), *F. ciliaris* var. *polycarpa* was found within a grade of *F. ciliaris* s. str., while two specimens of var. *wrightii* formed a highly supported clade sister to most *Fabronia* specimens (except for the Group 2). In IGS1 tree (Fig. 4), two specimens of var. *polycarpa* formed a maximally supported clade sister to the single included specimen of *F. wightii*, and both of them were resolved in a sister relationship to the Group 2, however, with low support. TCS network (Fig. 2) illustrates a close position of the Group 2 to *F. ciliaris* var. *wrightii*, and somewhat more distant relationship to var. *polycarpa*. By morphology, these three entities are similar, so it is difficult to outline their distinctive characters, especially between the Group 2 and var. *wrightii*. There are two possible solutions: (1) to refer Eurasian specimens of the Group 2 to *F. wrightii*, resurrecting its species status, or (2) to describe specimens of the Group 2 as a separate species, awaiting a broader revision of the genus with a comprehensive representation of North American populations. We prefer the second way, considering the following: (1) a great geographical gap between the distibution of the Group 2 in central part of Eurasia and of *F. ciliaris* var. *wrightii* mostly tropical parts of America; (2) more narrow leaves in American plants, described by Buck as 0.12–0.20 mm wide (we saw occasionally 0.24 mm) versus 0.25–0.3 mm wide in specimens of the Group 2; (3) considering genetic differentiation: specimens of the Group 2 are totally invariable in ITS, while *F. ciliaris* var. *wrightii* differs in 2–3 mutational events; IGS1 sequences also almost lack variation in the Group 2 (one specimen out of five has 2 substitutions from all others), whereas *F. ciliaris* var. *wrightii* differs already in 30 substitutions. Thus plants of Group 2 are described below as a new species, *Fabronia altaica*.

Fabronia pusilla, F. rostrata, F. matsumurae

The distinction between *F. pusilla* and *F. ciliaris* is also sometimes questioned. At least some problematic specimens were mentioned by, *e.g.*, Crum & Anderson (1981). Specimens of *F. pusilla* from westernmost localities are easily recognized due to large, multicellular teeth at leaf margins. However, at the eastern edge of its distribution range, where *F. pusilla* co-occurs with *F. ciliaris*, plants with smaller marginal teeth consisting not more than three cells are often collected. Contrary to *F. major* and *F. altaica*, *F. pusilla* usually has ovate leaves abruptly narrowed into acumen, short laminal cells and short, ovate capsules, which is similar to *F. ciliaris*. In our dataset, only one specimen of *F. pusilla* in question with small marginal teeth was included (*F. pusilla 2*, Italy). It appeared in *F. pusilla*-clade in ITS-based tree (Fig. 1), belonging the the main haplotype in the haplotype network (Fig. 2). On the other hand, specimens with occasional 2–3-celled marginal teeth were observed far beyond the distributional range of *F. pusilla*, *e.g.*, in South Urals

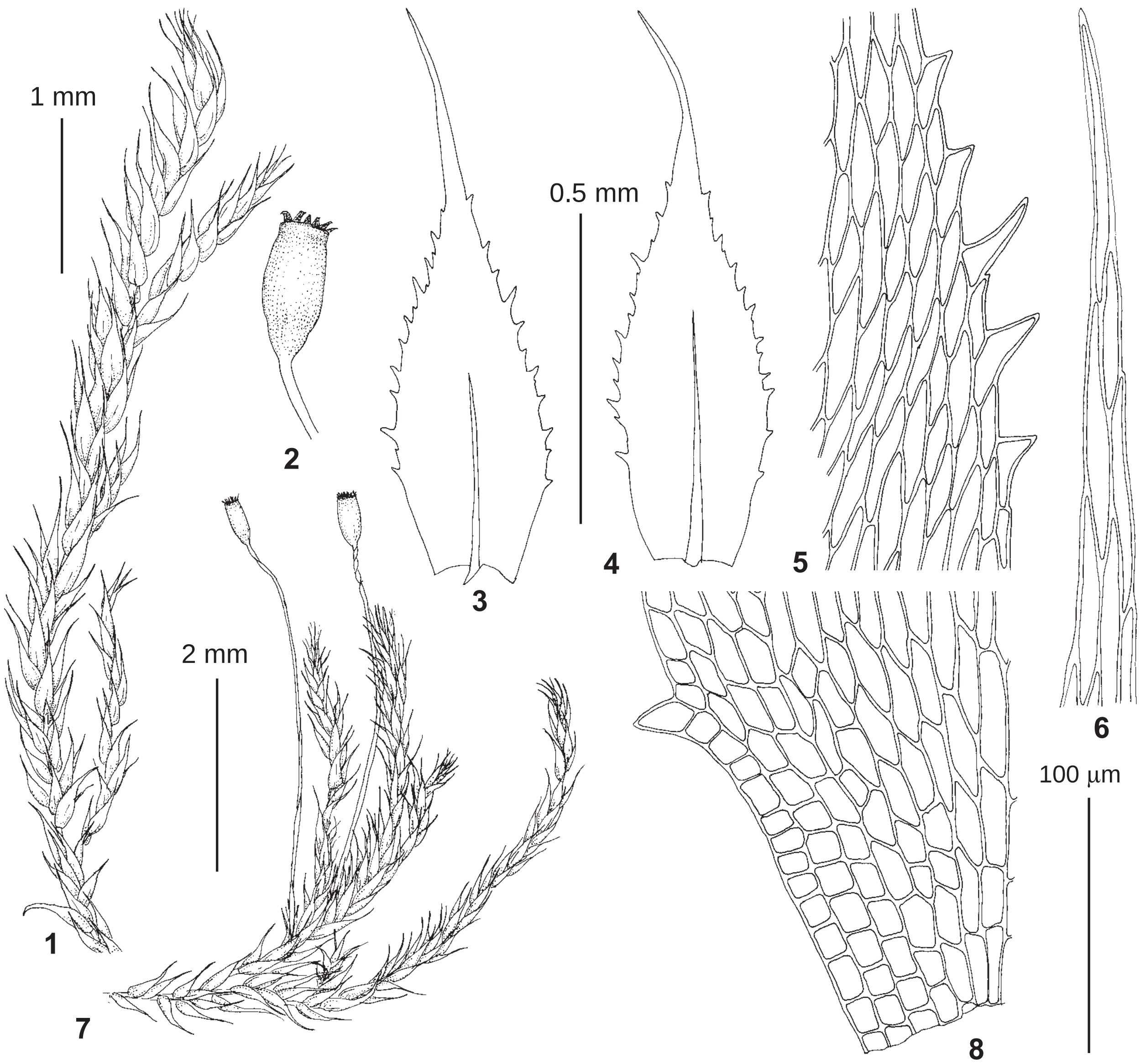

Fig. 12. *Fabronia altaica* (from holotype: Russia, Altai Republic, Chulyshman River valley, *Ignatov & Ignatova 12-747*, MHA). 1, 7 – habit, dry; 2 – capsule; 3–4 – leaves; 5 – median leaf cells; 6 – leaf apical part; 8 – basal leaf cells. Scale bars: 2 mm for 7; 1 mm for 1–2, 0.5 mm for 3–4; 100 μm for 5–6, 8.

and Khabarovsk Territory. They were resolved within *F. ciliaris* (*F. ciliaris 20* and *15* in Figs. 1–3).

We were able to confirm only one specimen of *F. pusilla* from Siberia: it is a specimen from Ol'khon Island of Baikal Lake. It is old and could not be sequenced; however, it undoubtfully belongs to this species due to leaves with very large, multicellular marginal teeth (Fig. 10: 4). Closest localities of *F. pusilla* are known in Middle Asia (Turkmenistan, Tajikistan and Kyrgyzstan); we confirm these identifications in LE. *Fabronia pusilla* was also reported from SW China, Xizang and Yunnan (Gao & Fu, 2002b); however, illustrations in Gao & Fu (2002a: page 96, Fig. 43) do not show the main character of *F. pusilla*, namely multicellular teeth at leaf margins.

Fabronia rostrata is a rare species, only recently found in Russia. The only sequenced specimen showed very subtile difference from *F. ciliaris* in ITS and none in more variable IGS1. However, a unique combination of such characters as eperistomate capsule and operculum with long, oblique beak easily separates this species from *F. ciliaris* (it is worth to note, however, that one specimen of *F. ciliaris* from the Caucasus (Kabardino-Balkaria 1) also had numerous capsules with long, oblique beak, but with perfectly developed peristome). Further studies are needed to understand such discrepancy better.

Another specimen from the Russian Far East was once identified as *F. matsumurae* due to the absence of normally developed peristome. It appeared to be identical to *F. ciliaris* in both ITS and IGS1 sequences. Some capsules in this collection have rudimentary or practically absent peristome, while in other ones pale teeth ca. 50 μm long, with papillose-striolate ornamentation were observed. This feature is unknown in *F. ciliaris*, but for *F. matsumurae* only totally eperistomate capsules were reported. In other characters, *i.e.*, leaf shape, marginal teeth, cell areolation, capsule and operculum shape and spore size these plants fit *F. ciliaris*. We consider peristomes in this collection as abnormally developed and refer this specimen to the latter species.

NrIGS1 vs. nrITS

The IGS1 is not a very widely used marker for phylogenetic studies as it is often too variable so precluding proper aligning, variable in length (Mateos & Markow, 2005), and has big reversions (Wicke *et al*., 2011).

However, in some rapidly evolving groups IGS provides a strong and clear phylogenetic signal, which is well congruent with that from ITS (Logacheva *et al*., 2011). In moss species of the genus *Schistidium,* it possessed a conservative and species-specific substitutions (Milyutina *et al*., 2015). The present study indicates a great value of IGS1 for supporting ITS-based conclusions of the species delimitation.

TAXONOMY

Fabronia Raddi, Atti Accad. Sci. Siena 9: 231–235, pl. 1. 1808.

Plants very small, soft, forming small flat mats, green or yellowish green, silky. Stems fragile, prostrate, irregularly branched, branches short, mostly densely foliate, julaceous; central strand and hyalodermis not differentiated, all cells ± thin-walled; rhizoids clastered near branch bases and developed on dorsal side of costa in lower part of leaves; paraphyllia absent; juvenile branch leaves narrow lanceolate or linear, sutuated on branch bases. Leaves loosely appressed when dry, occasionally slightly secund, spreading when moist, concave, ovate, ovate-lanceolate or lanceolate, abruptly or gradually acuminate, often piliferous; margins plane, dentate, denticulate or subentire, marginal teeth unicellular, short or long, or large, multicellular; costa slender, ending at midleaf; lamina unistratose, smooth; leaf cells rhomboidal or long-rhomboidal, with moderately thickened, non-porose walls; alar cells differentiated, quadrate and short rectangular, numerous. Autoicous. Perichaetial leaves broader than vegetative leaves. Setae erect, slender, yellowish or brownish, smooth. Capsules erect, ovoid, pyriform or cylindrical; annulus absent; exothecial cells quasrate and short rectangular, with wavy walls, stomata present, with elongate pore; peristome single, consisting of 16 exostome teeth usually fused in pairs, broadly lanceolate, blunt, light brown or dark red-brown, densely papillose-striolate on both surfaces, without trabeculae on both sides, usually reflexed when dry and appressed to the capsule wall, fragile, often broken in opened capsules. Opercula low conic or almost flat, mammillate or obliquely rostrate. Spores small, smooth or finely papillose.

Fabronia altaica Ignatova & Ignatov, sp. nova.

Type: Russia, Altai Republic, Ulagan District, left slope to Chulyshman River valley ca. 1 km downstream from Chulcha River mouth, ca. 51°05'N, 87°59'E, 550 m a.s.l., at cliff base in *Rhododendron* thickets, on rocks covered with thin layer of soil, 15.VIII.2012, coll. M. Ignatov & E. Ignatova #12-747 (Holotype MHA, isotypes MW, LE, H, S).

Illustrations: Figs. 12, 5: 7–11, 6: 6–10, 8: 7– 12; 11: 14–17.

Diagnosis: this species is close to *Fabronia ciliaris* and differs from it in lanceolate vs. ovate leaves, gradually vs. abruptly acuminate, longer leaf cells: 30–50 μm vs. 20–35 μm long, and ovate-cylindrical vs. ovate capsules.

Plants small, silky-green, glossy, in dense patches. Stems creeping, ascending at upper part, ca. 5 mm long, irregularly branching; branches 2–3 mm long, erect or arcuate, densely foliate. Stem and branch leaves similar, loosely appressed when dry, straight or ± secund, spreading when moist, ovate-lanceolate or lanceolate, gradually long acuminate, 0.65–0.90×0.25–0.30 mm; leaf margins dentate, marginal teeth unicellular, moderate in size (20–30 μm long); costa slender, smooth, ending at mid-leaf; lamina smooth, upper and median laminal cells elongate-rhomboidal, (29–)35–50(–75)×7–9 μm, with length/width ratio 4–6:1 and cell length, μm/ leaf length, mm ratio 42.7–70.9; apical leaf cell to 100 μm long; alar cells quadrate to short-rectangular, forming a weakly delimited rectangular group 3–4 cells wide and 7–11 cells along leaf margin. Autoicous, usually with sporophytes. Perigonia bud-like. Perichaetial leaves ca. 0.8 mm long and 0.4 mm wide, with oblong base and abruptly attenuate narrow acumen; costa ending in the acumen. Sporophytes single in perichaetium. Seta ca. 4 mm long, straight, flexuose when dry, yellow. Capsule ovate-cylindrical, 0.6–0.9 mm long and ca. 0.3 mm wide, slightly constricted below mouth when open, with short neck, smooth, pale brown, with dark-brown rim; annulus absent. Peristome single, consisting of 16 exostome teeth fused in pair, dark-brown, obtuse, ca. 150 μm long; outer surface densely papillose and striolate, inner surface with less prominent ornamentation, smooth in lower part of teeth and covered with low oblique ridges and occasionally with scarce papillae in distal part. Spores 13–15 μm, finely papillose. Operculum low conic, with short oblique beak.

Distribution and ecology. *Fabronia altaica* is known from Altai Republic and the Caucasus, in both regions only from the most xeric areas. In Altai, it grows on dry boulders, rock outcrops and cliffs on xeric slopes, in *Rhododendron* thickets at cliff bases and in pine forests; it was also occasionally collected on soil at cliff base. Habitats of this species in Dagestan (Eastern Caucasis) were different: it was collected several times on trunks of birch and pear trees, while in Ingushetia it grew on soil in mixed forest.

Specimens examined: RUSSIA: ASIAN RUSSIA: **Altai Republic**: Ulagan District: Chulyshman River valley 1 km downstream Chulcha River mouth, 550 m alt., 15.VIII.2012, *Ignatov & Ignatova 12-745* (MHA); Shebalino District: Katun River valley near Ust-Sema, 580 m alt., 28.VII.1991, *Ignatov & Ignatova 24/62* (MHA); Chemal District: Katun River valley

10 km upstream from Chemal, 450 m alt., 7.VII.1993, *Ignatov & Ignatova 34/24* (MHA); Edikhta Creek (Aedigan Creek tributary), 1100 m alt., 8.VII.1993, *Ignatov & Ignatova 34/111* (MHA); Ongudai District: Malyj Yaloman Settl., 900 m alt., 30.VII.1991, *Ignatov & Ignatova 25/151* (MHA); Malyj Yaloman Settl., 950 m alt., 30.VII.1991, *Ignatov & Ignatova 25/158* (MHA); Malyj Yaloman Creek 8.5 km upstream from Katun River, 1100 m alt., 31.VII.1991, *Ignatov & Ignatova 25/53* (MHA); CAUCASUS: **Dagestan Republic**: Gunib District, Gunib settlement surroundings: 1550 m alt., 22.V.2009, *Ignatov & Ignatova 09-725* (MHA, MW); 1600 m alt., 21.V.2009, *Ignatov & Ukrainskaya 09-475* (MHA); 1560 m alt., 22.V.2009, *Ignatov et al. 14095 & 14098* (LE); **Republic of Ingushetia**: Aramkhi, 1300 m alt., 12.VII.2005, *Bersanova s.n.* (MHA).

?ITALY: Como, 8.IX.1896 & 31.X.1898, *F.A. Artaria s.n.* (LE). Plants from rich collection with many duplicates (seen in LE, H and S) from the northern Italy (Lombardy) is indistingishable from *F. altaica* by morphology. However, some specimens of *F. major* from Switzerland (proved by DNA) had laminal cells also more or less similar to *F. altaica* (cf. Fig. 7). Considering this, and also the absence of any other specimens of *F. altaica* from Central Europe, admitting that this specimen may represent an ultimate modification of *F. major*. In the illustrations it is shown under the name *F.* cf. *altaica*.

Differentiation. *Fabronia altaica* is rather variable in leaf shape and size (cf. Fig. 5: 7–11); however, there is rather clear difference in shape from *F. ciliaris*: ovate-lanceolate or lanceolate vs. ovate, and more gradually narrowed to the acumen vs. abruptly acuminate. There is a statistically proved difference in cell length between these species (Fig. 7). Fertile plants of *F. altaica* are readily distinguished from *F. ciliaris* by the shape of capsules: oblong, ovate-cylindrical vs. ovate. Peristome of *F. altaica* are usually darker colored, dark-brown vs. light-brown in *F. ciliaris*, but this difference may be caused by longer remaining color of peristome in the former species, while in young, deoperculate capsules they are of the same color. Opercula were rarely seen in *F. altaica*, but it seems that they are also different, conic and with short oblique beak, while in specimens of *F. ciliaris* we observed capsules mainly with mammillate opercula (though some exceptions were also seen: at least one specimen of *F. ciliaris* from Kabardino-Balkaria has capsules with obliquely rostrate opercula). In leaf shape, *F. altaica* resembles *F. major*, and in the beginning of the present study we did not separate them from each other. However, the latter species has longer cells, (36–)50–70(–95) µm (with few exceptions: three specimens from Switzerland had shorter cells, mainly 43–50 µm) but long marginal teeth. See also above the discussion about the specimen from northern Italy which resembles *F. altaica* in cell shape but more likely represents a deviating specimens of *F. major*. Capsules were found only in few collctions of *F. major*; they resemble *F. altaica* rather than *F. ciliaris* (see Fig. 11: 8–10, 14–17 and 1–7).

Fabronia ciliaris (Brid.) Brid., Bryol. Univ. 2: 171. 1827. — *Hypnum ciliare* Brid., Muscol. Recent. Suppl. 2: 155. 1812.

Holotype. "Schleicher Botaunte *Fabronia octoblepharis*, *Fabronia ciliaris* Bryol. Univ. *Hypnum* [*sericeulum?*] Helvetia, 1807" (B 31 0677 01), http://ww2.bgbm.org/Herbarium/specimen.cfm?Barcode=B31067701 (Röpert, 2000).

Putative isotype in LE: "*Pterigynandrum obctoblepharis* Schl., am Nov. genus?, ex Helvet" [another later hardwriting at label bottom "*Fabronia*"].

Illustrations: Figs. 5: 1–6, 6: 1–5, 11: 1–7; Ignatov & Ignatova (2004): Fig 429 on page 647.

Plants small, silky-green or yellow-green, glossy, in dense patches. Stems creeping, ca. 5 mm long, irregularly branching; branches 2–3 mm long, erect, densely foliate. Stem and branch leaves similar, loosely appressed when dry, straight, often with slightly recurved apices, spreading when moist, ovate, abruptly long acuminate, 0.5–0.9×0.25–0.3 mm; leaf margins denticulate, marginal teeth unicellular, small (ca. 0.1 mm long), or, rarely, consisting of 2–3 cells; costa slender, smooth, ending at midleaf; lamina smooth, upper and median laminal cells rhomboidal, 20–35(–40)×8–11 µm, with length/width ratio 2–4:1 and cell length, µm/ leaf length, mm ratio 27.0–53.3; apical cell ca. 110 µm long; alar cells quadrate to short-rectangular, forming weakly delimited rectangular goup 3–4 cells wide and 6–9 cells along leaf margin. Autoicous, sporophytes rare. Perigonia bud-like, sometimes numerous. Perichaetial leaves 0.4–0.5 mm long and 0.3–0.4 mm wide, with oblong base and gradually attenuate narrow acumen; costa ending below apex; margins with longer, stronger recurved teeth in upper part. Sporophytes single in perichaetium. Seta 3–4 mm long, straight, flexuose when dry, yellow. Capsule ovate, with short neck, 0.35–0.45 mm long and 0.3–0.4 mm wide, often flared at mouth with age, smooth, pale brown, concolorous at rim or slightly darker; annulus absent. Peristome single, consisting of 16 exostome teeth fused in pair, light-brown or brown, obtuse, ca. 125 µm long; outer surface papillose-striolate, inner surface with less prominent ornamentation, in distal parts of teeth covered with low vertical ridges. Spores (10–)15–17 µm, papillose. Operculum low conic, mammillate or with short straight or, rarely, moderately long oblique beak.

Distribution and ecology. *Fabronia ciliaris* s. str. is considered as a widespread species throughout the world. It is known from mountain areas of Central and Southern Europe, in Asia it was reported from many provinces of China, from Korea and Japan; it is quite widespread in America, especially in the eastern part, uncommon in Mexico and central South America and becoming more frequent to the south, in mountain areas (Buck, 1983); it was also reported from Australia, New Zealand and Hawai. In Russia, *F. ciliaris* is most widespread and frequent species of the genus. It is known from Eastern and Central Caucasus, Middle and South Urals, southern Siberia and south of Russian Far East; its northernmost records were made in southern and central Yakutia and the extreme point is in Verkhoyansk District, at 67°35'N (Isakova, 2010). Most numerous collections were made in Altai Mt. and Transbaikalia. This species grows in mountain areas in a wide range of altitudes, from 150 to

1550 m a.s.l., but mainly in forest zone. It inhabits dry and moderately wet cliffs, rock outcrops and boulders, both acidic and calcareous, in open and shady places, and occasionally grows on soil in rocky places; it was also collected on tree trunks: on poplar in Khabarovk Territory, on elm in Primorsky Territory and on pear trees in Dagestan. In Yakutia, it occurs on rock outcrops on xeric and warm steppe slopes, where other southern xerophilous species where found.

Selected specimens examined: RUSSIA: CAUCASUS: **Dagestan Republic**: Gunib District: Gunib, 1550 m alt., 22.V.2009, *Ignatov & Ignatova 09-672 & 09–766* (MW); **North Ossetia/Alania**: Suargom Gorge, 800 m alt., 1.XII.2014, *Ukrainskaya 15945* (LE); **Kabardino-Balkaria**: Chereksky Disrict, Verkhnaya Balkaria Settl., 1100–1150 m alt., 28.VIII.2005, *Ignatov et al. 05-1825 & 05-1880* (MHA); Elbrussky District, Bylym, Baksan River valley, 1000 m alt., 30.VII.2004, *Ignatov et al. s.n.* (MHA); **Karachaevo-Cherkessia**: Teberda Nature Reserve, Dzhemagat Creek valley, 1550 m alt., 22.VII.1994, *Onipchenko 115/94* (MW); Aksaut Gorge, 5.VI.1989, *Ukrainskaya 14444* (LE); Daut River valley, 4.VIII.1993, *Ukrainskaya 14443* (LE). URALS: **Bashkortostan**: Bashkirsky Nature Reserve, Kaga River mouth, 2.IX.1945, *Selivanova-Gorodkova s.n.* (MHA); **Chelyabinsk Province**: Satka District, Ai River, 300 m alt., 6.VIII.2011, *Ibatullin 36* (MHA); **Perm Territory**: Kishertsky District, Kamen Vostryj, 2.VII.1999, *Bezgodov 268* (MW); ASIAN RUSSIA: **Altai Republic**: Ulagan District: Chulyshman River valley, 1950 m alt., 2.VIII.1993, Ignatov 36/95 (MHA); Chulcha River valley, 1000 m alt., 11.VII.1991, Ignatov 9/12 (MHA); northern shore of Teletzkoe Lake, Yailyu, 460 m alt., 1.VI.1989, *Ignatov 0/1054* (MHA); west of Yailyu, Izvestkovaya Mt., 650 m alt., 12.VI.1989, *Ignatov 0/669* (MHA); Artyshtu River 0.3 km of its mouth, 600 m alt., 20.IX.1989, *Zolotukhin s.n.* (MHA); Kukol stow in the valley of Karakem River, 23.VI.1989, *Ignatov 0/1055* (MHA); Sebalino District: Katun River valley near Ust-Sema, 380 m alt., 28.VII.1991, *Ignatov & Ignatova 24/163* (MHA); Chemal District: Chemal Creek 3 rm upstream mouth, 450 m alt., 12.VII.1993, *Ignatov & Ignatova 34/63* (MHA); **Irkutsk Province**, Irkutsk surroundings, 10.VII.1932, *Kostin s.n.* (LE); Baikal Lake, Maloe More, Yadyrtui Cape, 19.VII.1987, *Bardunov s.n.* (LE); **Zabaikalsky Territory**: Dul'durga District, Alkhanai National Park, Ilya River, 8.VII.2006, *Afonina 1606* (LE); Kyra District: Sokhondinsky Biosphere Reserve: Agutsa River, 1098 m alt., 18.VII.2010, *Afonina A3710* (LE); Enda River, 1320 m alt., 12.VII.2010, *Afonina A1910* (LE); Bukukun River, 1646 m alt., *Czernyadjeva 42-11* (LE); Ulota District: Ingoda River ner Leninskiy Settlement, 6.VIII.2011, *Afonina 0611* (LE); Krasnochikoisky District: Zhindokon Creek, 963 m alt., 8.VIII.2011, *Afonina 1411* (LE); Nerchinsk District: Nerchinsko-Kuenginsky Rangem Marikta River, 15.VII.2012, *Czernyadjeva 7-12* (LE); Aleksandrovsky Zavod District, Malaya Borzya River, 817 m alt., 27.VII.2012, *Afonina 4412* (LE); Tungokochin District, Ul'durga River, 618 m alt., 16.VII.2012, *Afonina 1112* (LE); Chita District, Aratsa River, 964 m alt., 13.VII.2012, *Afonina 0312* (LE); **Republic of Buryatia**: Selenga River near Novoselenginsk Settlement, 4.VII.2007, *Afonina 00707* (LE); **Amurskaya Province**: Selemdzhinsky District: Norskaya Hill, 220 m alt., 21.VI.2011, *Bezgodov 391* (MHA); Nora River, 240 m alt., 15.VII.2010, *Bezgodov 460* (MHA); **Khabarovsk Territory**: Verkhnebureinsky District: Chegdomyn, 450 m alt., *Ignatov 97-284* (MHA); Sovgavan District: Botchinsky State Reserve: Spokoiny Creek, 290 m alt., 22.VIII.2013, *Ignatov & Ignatova 13-1035* (MHA); Mulpa River, 245 m alt., 14.VIII.2013, *Ignatov & Ignatova 13-494* (MHA); **Primorsky Territory**: Partizank District: Chandolaz Mt., 250 m alt., 8.IX.2013, *Ignatov et al. 13-1840* (MHA); Shkotovo District: Ussurijsky Nature Reserve, Koryavaya Pad', Zmeinaya Mt., 331 m alt., 15.X.2008, *Ignatov 08-299* (MHA); **Republic of Sakha/Yakutia**: Khangalassky District: Lenskie Pillars National Park, Lena River downstream Labyja Creek mouth, 150 m alt., 19.VIII.2000, *Ignatov 00-164* (MHA); Verkhoyansk District, 30 rm W of Tabalakh Settl., Tuostakh Creek, 5.VIII.2009, *Isakova s.n.* (MHA).

ASIA: GEORGIA: Borzhom, pr. fl. Kura, VIII.1877, *A.H. & V.F. Brotherus s.n.* (LE); Imeretia, pr. fl. Rion, 6.VI.1877, *A.H. & V.F. Brotherus s.n.* (LE); Ossetia, Balta, ad. fl. Terek, 19.V.1881, *A.H. & V.F. Brotherus s.n.* (LE). AZERBAIJAN: Zakatalsky District, Kebeloba Settl., 14.VI.1969, *Lyubarskaya s.n.* (LE); Lenkoran, Bilyasar Mountains, 28.V.1937, *Topachevsky s.n.* (LE). MONGOLIA: **Khentii Province**, 33 km NW of Dadal, Bukukun River valley, 4.VIII.2006, *Afonina s.n.* (LE); **Bayan-Hongor Province**, Ikh-Bogd Mt., 2000 m alt., 29.VI.2001, *Ignatov 01-479* (MHA); **Omnogovi Province**, Khuren khanyn khep mountain ridge, 2000 m alt., 25.VI.2001, *Ignatov 01-456* (MHA). CHINA: **Inner Mongolia**, NE of Huhhot, Yingshan Mountains, Manhan Mt., 1650 m alt., 24.X.2008, *Ignatov 08-511* (MHA).

EUROPE: AUSTRIA: Carinthia: Drautal, Danielsberg, ca. 900 m alt., 14.VI.2003, *Köckinger 15056* (MW, ex Hb. H. Köckinger); Lavanttal, Waldensteiner Graben E of Twimberg, 700 m alt., 12.VI.2004, *Köckinger 15057* (MW, ex Hb. H. Köckinger); SWITZERLAND: Ticino, Cugnasco-Gerra, Sciarana, 350 m alt., 9.IV.2005, *Schnyder 2005070* (ex Herbarium Norbert Schnyder). HUNGARY: Ktyptogamae exsiccatae #1892, col. *Lojka* (LE). ITALY: Südtirol, Meran, no date, *Zickendrath s.n.* (LE).

NORTH AMERICA: U.S.A.: **Ohio**: Adams Co., Spring Glen National Area, 215 m alt., 22.V.2006, *Buck 50414* (NY); **Oklahoma**: Payne Co., Stillwater Creek, 22.III.1942, *Ikenberry 829* (LE); **Missouri**: Shannon Co., Jam-Up Creek, 28.XI.1961, *Redfearn 9484* (LE).

Differentiation. Distinctive characters of *F. ciliaris* include ovate, abruptly acuminate leaves, regularly denticulate margins with small marginal teeth, short laminal cells 20–45 x 18–11 µm with length/width ratio 2–4:1 and short, ovate capsules. Its difference from *F. altaica, F. major, F. pusilla* and *F. rostrata* are discussed in comments to them.

Fabronia major De Not., Mem. Reale Accad. Sci. Torino 39: 229. 1836. — *Fabronia pusilla* var. *major* (De Not.) Schimp., Bryol. Eur. 5: 71 (fasc. 44–45. Mon. 3). 1850.

Lectotype (selected here): specimen from herbarium of G. Hampe, BM 001007509 (Fig. 14).

Comments on the lectotypification: there are two specimens of *Fabronia major* in BM, which obviously belong to the same species (Fig. 14). Collection from the Hampe herbarium is preferred by the following reasons, suggested by Len Ellis: (1) it has several sporophytes (in Schimper' herbarium only one or two); (2) specimen from Hampe' herbarium is generally in a better physical condition; (3) specimen from Schimper' herbarium includes fragments of a different pleurocarp with leaves with conspicous single costa (superficially similar to *Lescurea saxi-*

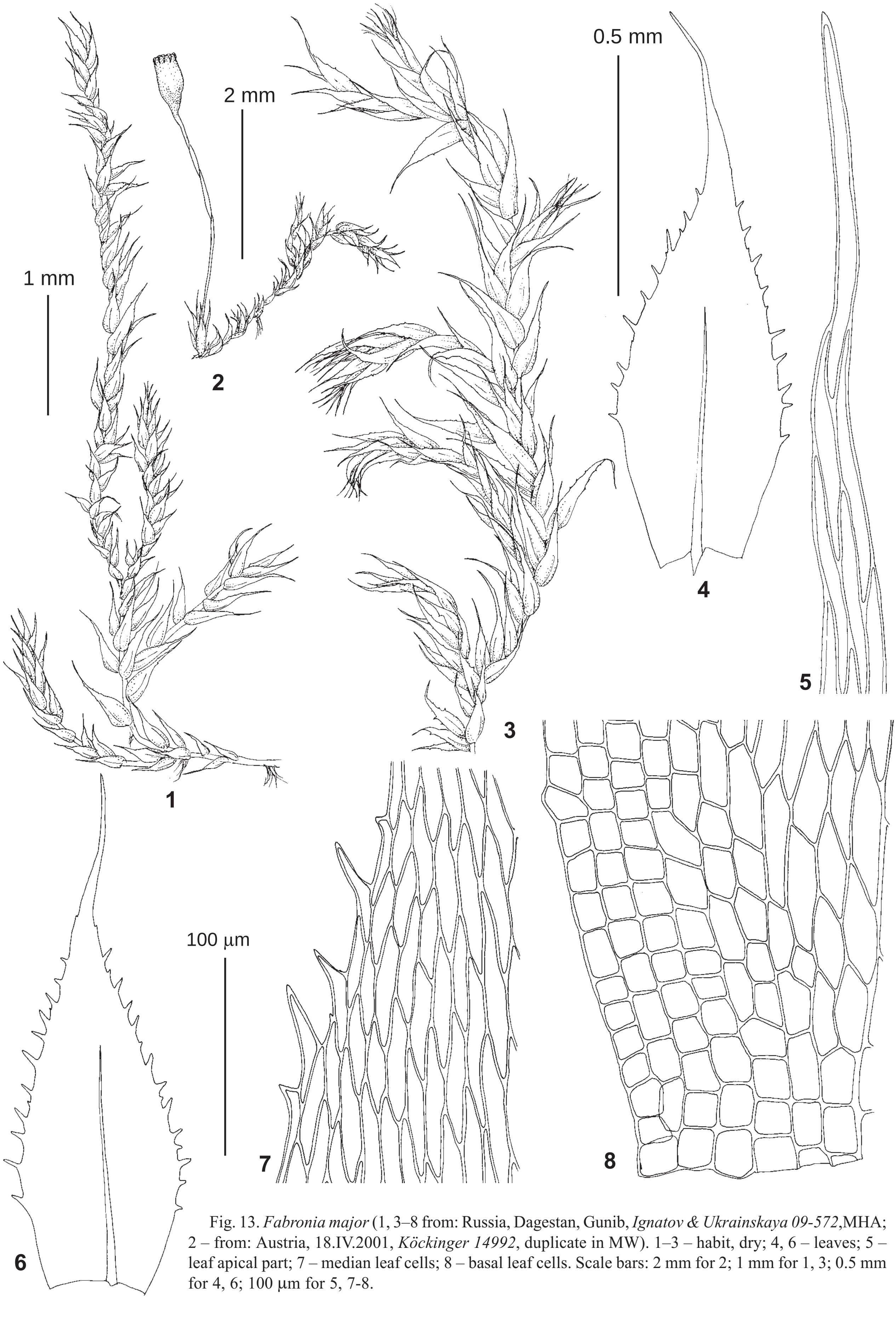

Fig. 13. *Fabronia major* (1, 3–8 from: Russia, Dagestan, Gunib, *Ignatov & Ukrainskaya 09-572*,MHA; 2 – from: Austria, 18.IV.2001, *Köckinger 14992*, duplicate in MW). 1–3 – habit, dry; 4, 6 – leaves; 5 – leaf apical part; 7 – median leaf cells; 8 – basal leaf cells. Scale bars: 2 mm for 2; 1 mm for 1, 3; 0.5 mm for 4, 6; 100 µm for 5, 7-8.

Fig. 14. *Fabronia major.* 1 – specimen from herbarium of W. Schimper, BM 001244356; 2 – specimen from herbarium of G. Hampe, BM 001007509 (lectotype of *F. major*, selected here). 3 – leaf cells from BM 001244356; 4-5 – leaf cells from BM 001007509. Scale bar: 100 μm for 3-5. Courtesy of Len Ellis.

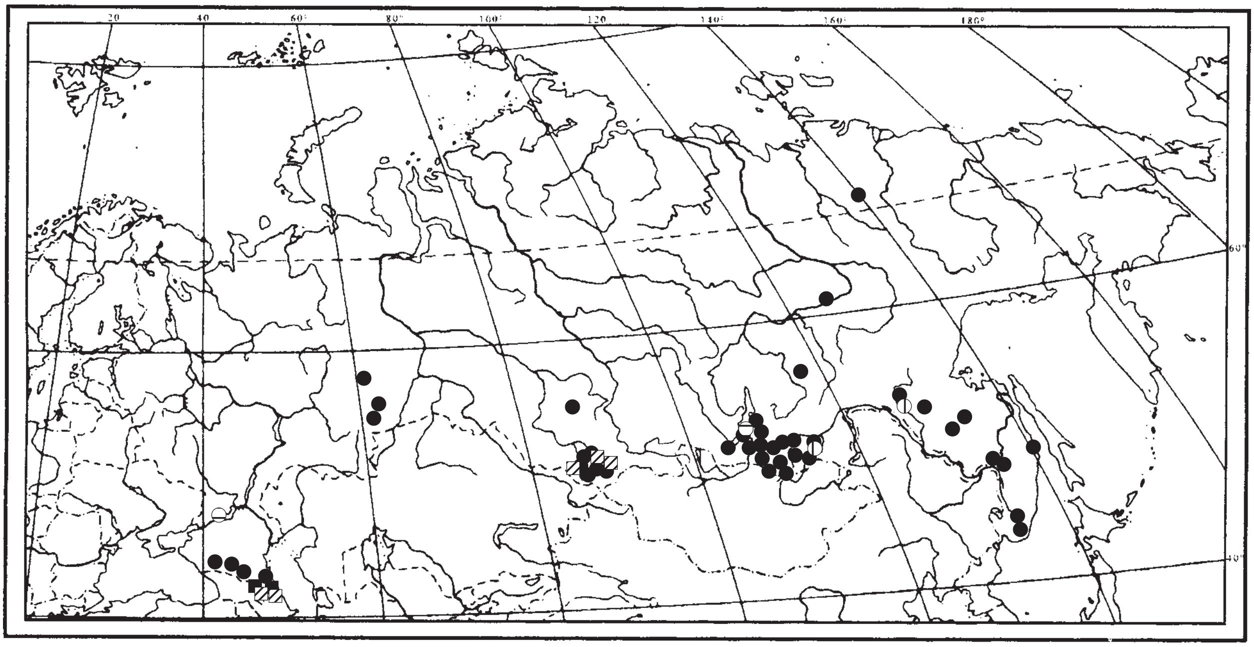

Fig. 15. Distribution of *Fabronia* species in Russia: ● – *F. ciliaris*;■ – *F. major*;▨ – *F. altaica*; ⊖ – *F. pusilla*; ⦶ – *F. rostrata*.

cola), while the specimen from Hampe herbarium has no admixtures.

Illustrations: Figs. 13–14, 5: 12–16, 6: 11–14, 8: 13–15 and 11: 8.

Plants small, yellow-green, green or grayish-green, glossy, in soft, dense patches. Stems creeping or ascending, 5–10 mm long, irregularly branching; branches 2–4 mm long, straight or arcuate, densely foliate. Stem and branch leaves similar, loosely appressed when dry, straight, occasionally secund, erect-spreading when moist, lanceolate, gradually long acuminate, 0.6–1.0(–1.3)×0.2–0.3(–0.4) mm; leaf margins dentate or ciliate, marginal teeth mainly unicellular (occasionally with additional short cell at base, long (25–35 μm, occasionally to 50 μm long); costa slender, smooth, ending at midleaf; lamina smooth, upper and median laminal cells elongate-rhomboidal, (36–)50–70(–85)×8–11 μm, with length/width ratio 4–8:1 and cell length, μm/ leaf length, mm ratio 42.8–91.2; apical leaf cell to 175 μm long; alar cells quadrate to short-rectangular, forming weakly delimited rectangular goup 3–4 cells wide and 8–13 cells along leaf margin. Autoicous, sporophytes infrequent. Perigonia bud-like. Perichaetial leaves 0.5–0.7 mm long and ca. 0.2 mm wide, with oblong base and gradually attenuate narrow acumen; costa ending above midleaf; margins with stronger dentate in upper part than stem leaves. Sporophytes single in perichaetium. Seta 3–4 mm long, straight, flexuose when dry, yellow. Capsule short cylindrical, with short neck, 0.7–0.8 mm long and 0.4–0.5 mm wide, occasionally flared at mouth with age, smooth, light brown, with dark-brown rim; annulus absent. Peristome single, consisting of 16 exostome teeth fused in pair, dark-brown, obtuse, ca. 125 μm long, with few round perforations in distal part; outer surface papillose-striolate, inner surface with less prominent ornamentation, with low vertical ridges. Spores 14–17 μm, brownish, papillose. Operculum low conic or almost flat, with very short, narrow, straight beak.

Distribution and ecology. *Fabronia major* was found in collections from the Eastern Caucasus (Dagestan and North Ossetia) and Central and Southern Europe (Austria, Switzerland and northern Italy). It grows in mountain areas at low and middle altitudes, up to 1100 m a.s.l. in the Alps and up to 1600 m in the Eastern Caucasus. In Dagestan it was collected on trunks of hornbeam and pear trees; one specimen was also gathered from the trunk of *Magnolia* and another on unknown tree in the cemetery in Switzerland. All other collections were made from siliceous cliffs and boulders, shady and open. Most Caucasian collections were sterile, while in the mountains of Central Europe sporophytes were occasionally present.

Specimens examined: RUSSIA: **Dagestan Republic**: Gunib District, Gunib Settlement surroundings: 1370 m alt., 19.V.2009, *Ignatov & Ignatova 09-254* (MHA); 1600 m alt., 21.V.2009, *Ignatov & Ukrainskaya 09-472* (MHA); **Republic of Severnaya Ossetia/Alania**: North Ossetian Nature Reserve, Tsei River valley, 25.VII.1979, *L.I. Abramova s.n.* (MW); Fiagdon Gorge, 1275 m alt., 13.VII.2015, *Ukrainskaya 16660* (LE); Nizhny Lars, 800 m alt., 1.VII.2014, *Ukrainskaya 15938* (LE).

AUSTRIA: Styria: Stadl an der Mur, 1100 m alt., 11.X.1993, *Köckinger s.n.* (MW, ex Hb. H. Köckinger); bei St. Michael, 600 m alt., 7.VII.1884, *Breidler s.n.* (LE); Upper Austria: Donautal, Schlögen, 350 m alt., 2.X.2013, *Köckinger 14991* (MW, ex Herb. H. Köckinger); Carinthia, Lavant valley, between Twimberg and Waldenstein, 650 m alt., 18.IV.2001, *Köckinger 14992* (MW, ex Hb. H. Köckinger). SWITZERLAND: Zürich, 418 m alt., 29.III.2015, *Kiebacher 781* (MW, ex Herb. T. Kiebacher); Ticino: Muralto, am Lago Maggiore, 196 m alt., 11.X.2002, *Hofmann s.n.* (MW, ex Herb. H. Hofmann); Vogomo, 510 m alt, 7.VII.2001, *Hofmann s.n.* (MW, ex Herb. H. Hofmann); Monte Carasso, Pedemonte, 395 m alt., 9.IV.2005, *Schnyder 2005052* (MW, ex Herb. Norbert Schnyder); Grisons, Bregaglia, 890 m alt., 12.X.2016, *Hofmann s.n.* (MW, ex Herb. H. Hofmann). ITALY: Piedmont, Lepontine-Verbano Alps, Cicogna, 740–750 m alt., 24.VII.2012, *Kučera 15135* (CBFS).

Differentiation. *Fabronia major* was taken for both *F. pusilla* and *F. ciliaris*, since it considered as a variety of the former and a synonym of the latter. It resembles *F. pusilla* in long marginal teeth which, however, are unicellular, like in *F. ciliaris*. At the same time, it can be readily distinguished from both these species by narrow, lanceolate vs. ovate leaves and much longer, elongate-rhomboidal laminal cells with length/width ratio 4–8:1 vs. 2–4:1. It resembles *F. altaica* in leaf and capsule shape, but that species has slightly shorter cells, 4–6:1, and shorter marginal teeth. There is some similarity in leaf shape, cell length and strong serration of leaf margins between *F. major* and South and Central American *F. macroblepharis* Schwägr., but the latter species has even longer marginal teeth which are often 2–3-celled.

Fabronia pusilla Raddi, Atti Accad. Sci. Siena 9: 231. 1808.

Type. Europe: Toscana, Raddi s.n.

Illustrations: Figs. 9: 1–6, 10: 1–5 & 11: 11–13; see also Ignatov & Ignatova (2004), Fig. 430 on page 648.

Plants very small, soft, yellowish green, glossy, in small dense tufts. Stems creeping, ascending at apex, irregularly branched; branches erect, 1–2 mm long, densely foliate. Leaves loosely appressed when dry, often with recurved piliferous acumen, occasionally slightly secund, spreading when moist, ovate, abruptly long acuminate, 0.50–0.80×0.15–0.35 mm; leaf margins coarsely dentate to ciliate, marginal teeth unequal, large 3–5-celled teeth alter with small unicellular teeth; costa slender, smooth, ending at mid-leaf; lamina smooth, upper and median laminal cells rhomboidal, 25–30(–45)×9–11 μm, with length/width ratio 3–4:1 and cell length, μm/ leaf length, mm ratio 31.8–49.6; apical leaf cell to 110 μm long; alar cells quadrate to short-rectangular, forming weakly delimited rectangular goup 3–4 cells wide and 6–11 cells along leaf margin. Autoicous, sporophytes infrequent. Perigonia bud-like. Perichaetial leaves ca. 0.5 mm long and 0.2 mm wide, with oblong base and gradually attenuate narrow acumen; costa ending at midleaf; margins moderately dentate in upper part. Sporophytes single in perichaetium. Seta 2–3 mm long, straight, yellow. Capsule ovate, with short neck, 0.4–0.6 mm long and 0.3–0.4 mm wide, smooth, light brown, concolorous at rim; annulus absent. Peristome single, consisting of 16 exostome teeth fused in pair, light brown, obtuse, ca. 75 μm long; outer surface papillose-striolate, inner surface with less prominent ornamentation, with low vertical ridges. Spores 12–14 μm, brownish, papillose. Operculum low conic, with short oblique beak or mammillate.

Distribution and ecology. Main distribution area of *Fabronia pusilla* is in the western parts of Eurasia and North America, with southernmost localities in Mexico, and in northern Africa. It was also reported from southwestern provinces of China and states of Middle Asia. In Russia it is known from two localities: in Rostov Province (south of European Russia) and in Republic of Buryatia (Asian Russia, Baikal Lake area). Both places are characterized by xeric conditions. In Rostov province *F. pusilla* was collected on dead wood in the park. In Buryatia it grew on the shore of Baikal Lake (Svyatoi Nos peninsula), in deep shady niches of dry cliffs, on eroded rock surface. In the main part of its area, *F. pusilla* grows mainly on dry rocks (volcanic, granite, limestone), but is occasionally collected from tree trunks (*e.g.*, of *Quercus pubescens*).

Specimens examined: RUSSIA: EUROPEAN RUSSIA: **Rostov Province**: Rostov-na-Donu, Kamenka Settlement, park of the health resort "Rostovsky", 16.X.2000, *Sereda s.n.* (MHA); ASIAN RUSSIA: **Republic of Buryatia**: NE shore of Baikal Lake, Svyatoi Nos peninsula, 450 m alt, 26.VI.1956, *Bardunov s.n.* (LE).

EUROPE: SPAIN: Granada, Sierra Nevada, Güejar Sierra, Vereda de la Estrella, 145 m alt., 21.V.2009, *Guerra 30176* (LE); Andalucia, Grazalema, Sierra del Endrinal, 350 m alt., 3.V.2015, *Kučera 17500* (CBFS). ITALY: South Tyrol: Etschtal, Castel Feder S of Auer, 350 m alt., 29.X.1989 *Köckinger s.n.* (MW, ex Herb H. Köckinger); prope Bozen, 260 m alt., *Sauter*, Flora Exsiccata Austro-Hungarica #717 (LE). SWITZERLAND: Ticino, Lugano, 280 m alt., 11.II.2003, *Schnyder 2003001* (MW, ex Herb. Norbert Schnyder). AUSTRIA: Styria orientalis, Hartberg, 450 m alt., X.1942, *Baumgartner*, Crypt. Exs. ed. a Museo Hist Natur. Vindobonensi #892 (LE).

ASIA: TADJIKISTAN: Darvaz Ridge, Pyandzh River basin, Egit Village, Surkh-Dara gorge, 1130 m alt., 9.VII.1964, *Mamatkulov 5218* (LE). KYRGYZSTAN: Kyrgyz Range, Dzhirly-Kaindy stow, 1900 m alt., 18.VI.1965, *Rakhmatullina s.n.* (LE).

NORTH AMERICA: U.S.A.: **Colorado**, Boulder Co., Nordseite des Boulder Canyon, 2150 m alt., 30.III.1957, *Weber*, Crypt. Exs. ed. a Museo Hist Natur. Vindobonensi #4476 (LE); **California**: Mariposa Co., Elephant Rock, ca. 975 m alt., 2.XII.2006, *Shevock 29285* (NY); San Benito Co., ca. 470 m alt., 12.II.2005, *Shevock 26293* (NY); Monterey Co., San Antonio Reservoir County Recreation Area, ca. 240 m alt., 3.I.2009, *Schevock 32581* (NY); **Oregon**: Wheeler Co., John Day River basin, 655 m alt., 23.III.2008, *Shevock 31600* (NY); Wasco Co., Colombia River Gorge National Scenic Area, 45 m alt., 27.III.2008, *Shevock 31659* (NY).

Differentiation. 'Typical' specimens of *Fabronia pusilla* are easily recognized due to large, multicellular teeth at leaf margins. However, some specimens with smaller, 2–3-celled teeth may be referred either to *F. pusilla* or *F. ciliaris* (as it is proved by DNA data) and cannot be identified with confidence. Such specimens were observed mainly in Central Europe where both species co-occur. Maybe slightly smaller spores of *F. pusilla*, 12–14 vs. 15–17 μm in *F. ciliaris*, can help in these difficult cases.

Fabronia rostrata Broth., Symb. Sin. 4: 92. 1929.

Type. China: Yunnan, Mekong, 28°11'N, Handel-Mazzetti 8018 (holotype H).

Illustrations: Figs. 9: 11; 10: 9 and 11: 20; see also Dudov *et al.*, 2015.

Plants small, in flat, loose or moderately compact mats, light green or grayish, glossy. Stems 10–15 cm, prostrate, irregularly branched, evenly foliate. Leaves appressed and imbricate when dry, erectopatent to spreading when wet, 0.6–1.0(–1.2)×0.4–0.5 mm, ovate-lanceolate, gradually narrowed into a long and narrow acumen, slightly concave; margins plane, finely serrulate; costa slender, reaching 0.4–0.6 of leaf length; laminal cells rhomboidal, thin-walled, smooth, 30–60×6–10 µm, with length/width ratio 2–4:1 and cell length, µm/ leaf length, mm ratio 19.5–33.7; apical leaf cell to 110 µm long; alar cells differentiated, quadrate, in 3–4 rows at margin. Autoicous. Seta 2–3 mm. Capsule ovoid, 0.6–0.9 mm long. Operculum almost flat, with rather long oblique beak. Peristome totally reduced. Spores 10–15 µm.

Distribution and ecology. *Fabronia rostrata* was originally collected in NW Yunnan, at 2325 m a.s.l., on granite rocks in a dry oxbow of Mekong River (Brotherus, 1929). Gao & Fu (2002) report the species from another locality in Yunnan and from Henan, describing its habitats as "rocks and tree trunks in forests". In Zabaikalsky Territory the species grew at low elevation, up to 650 m a.s.l., on rock outcrops; in Amurskaya Province it was collected at 400–650 m a.s.l., on rock in the forest and on *Tilia amurensis* trunk.

Specimens examined: RUSSIA: **Zabaikalsky Territory**, Nerchinsko-Zavodskiy District, near Nerchinsky Zavod settlement, 658 m alt., 25.VII.2012, *Afonina 3912* (LE); **Amurskaya Province**: Zeisky Disctrict, Zeya Nature Reserve, Tukhuringra range: Gilyiskiy bay of Zeya reservoir, right shore, at 0.3 km to W from cordon "Medvezhiy" 628 m alt., 2.VIII.2013, *Dudov & Kotel'nikova# 2013_Br_0021*; Izvestkoviy bay of Zeya reservoir, right shore near Izvestkoviy stream estruary 421 m alt., 4.VIII.2013. *Dudov & Kotel'nikova 2013_Br_0336* (MW).

Differentiation. In the description of this species V.F. Brotherus (1929) noted such characteristic features of the species as finely serrulate leaf margins and operculum with rather long oblique beak. These characters, as well as the absence of peristome, allow its separation from both *F. ciliata* and *F. pusilla* which possess much stronger serrate leaf margins (especially the latter species), mammillate operculum and well-developed, albeit fragile single peristome of 16 teeth, strongly reflexed in dry state and appressed to the urn of opened capsules. Even if partly brocken, teeth remains are apparent enough to indicate peristome presence in these species.

KEY TO IDENTIFICATION OF *FABRONIA* SPECIES IN RUSSIA

1. Leaves ovate, abruptly long acuminate; leaf length/ width ratio 2.4–2.8:1 2
— Leaves ovate-lanceolate or lanceolate, gradually long acuminate; leaf length/width ratio (2.4–)2.8–3.7:1 .. 4

2. Marginal teeth unequal, large 3–5-celled teeth alter with small unicellular teeth .... *F. pusilla*
— Marginal teeth equal, small, 1(–2)-celled 3

3. Peristome present .... *F. ciliaris*
— Peristome absent .... [*F. matsumurae*]

4(1) Peristome absent; operculum with a curved long beak; leaf margins finely serrulate .... *F. rostrata*
— Peristome present; operculum with a short beak or mammillate; leaf margins serrate 5

5. Upper and middle leaf cells 50–70(–85) µm long, 4–8:1; teeth at leaf margins 25–50 µm long .... *F. major*
— Upper and middle leaf cells 35–50 µm long, 4–6:1; teeth at leaf margins 20–30 µm long .... *F. altaica*

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Appendix 1. Species of *Fabronia* used in analyses, with GenBank accession numbers and voucher information for specimens

Voucher	TCS	Voucher data and extraction number	ITS	IGS
altaica Altai 1	A1	Russia, Altai Republic, Ignatov & Ignatova 12-747 (MHA), OK 939	MF417689	MF417682
altaica Altai 2	A2	Russia, Altai Republic, Ignatov & Ignatova 25/151 (MHA), OK 942	MF417692	MF417684
altaica Altai 3	A3	Russia, Altai Republic, Ignatov & Ignatova 25/53 (MHA), OK 943	MF417693	MF417685
altaica Ingushetia	A4	Russia, Ingushetia, 12.VII.2005, Bersanova s.n. (MHA), OK 1535	MF417690	MF417686
altaica Dagestan 1	A5	Russia, Dagestan, Ignatov & Ukrainskaya 09-480 (MHA)], OK 941	MF417691	MF417683
altaica Dagestan 2	A6	Russia, Dagestan, 21.V.2009, Ignatov & Ukrainskaya s.n. (LE), OK 1543		MF417687
ciliaris Altai 1	C1	Russia, Altai Republic, Ignatov 0/43 (MW), OK 309	MF417703	MF417669
ciliaris Altai 2	C2	Russia, Altai Republic, Ignatov & Ignatova 34/113 (MHA), OK 1541	MF417713	
ciliaris Altai 3	C3	Russia, Altai Republic, Ignatov & Ignatova 34/76 (MHA), OK 1540	MF417714	MF417659
ciliaris Amurskaya Province	C4	Russia, Amurskaya Province, 21.VI.2011, Bezgodov 391 (MHA), OK 937	MF417697	MF417652
ciliaris China	C5	China, Inner Mongolia, Ignatov 08-511 (MHA), OK 1534	MF417710	MF417657
ciliaris Dagestan 1	C6	Russia, Dagestan, Ignatov & Ignatova 09-672 (MHA), 0K 940	MF417699	MF417664
ciliaris Dagestan 2	C7	Russia, Dagestan, Abakarova & Ignatov 11-2013 (MHA), OK 431	MF417700	MF417650
ciliaris Dagestan 3	C8	Russia, Dagestan, Ignatov & Ignatova 09-766 (MHA), OK 299	MF417701	
ciliaris Dagestan 4	C9	Russia, Dagestan, Abakarova & Ignatov 11-2013 (MHA), OK 1007	MF417702	
ciliaris Dagestan 5	C10	Russia, Dagestan, Ignatov et al. 14098 (MHA), OK 1533	MF417709	MF417651
ciliaris Kabardino-Balkaria 1	C11	Russia, Kabardino-Balkaria, Ignatov et al. 05-1880 (MHA),	MF417698	MF417666 & MF417681
ciliaris Kabardino-Balkaria 2	C12	Russia, Kabardino-Balkaria, 30.VII.2004, Ignatov et al. s.n. (MHA), OK 1039	MF417707	MF417663
ciliaris Karachaevo-Cherkessia 1	C13	Russia, Karachaevo-Cherkessia, Onipchenko 206/96 (MW), OK 1040	MF417708	
ciliaris Karachaevo-Cherkessia 2	C14	Russia, Karachaevo-Cherkessia, Onipchenko 115/94, (MW), OK 1545	MF417715	MF417662
ciliaris Khabarovsk Territory 1	C15	Russia, Khabarovsk Territory, Ignatov & Ignatova 13-494 (MHA), OK 936	MF417696	MF417660
ciliaris Khabarovsk Territory 2	C16	Russia, Khabarovsk Territory, 12.VIII.1981, Cherdantseva s.n. (VLA), OK 1597	MF417716	
ciliaris Mongolia	C17	Mongolia, 4.VII.2006, Afonina s.n. (MW), OK 310	MF417704	MF417653
ciliaris Perm Province	C18	Russia, Perm Province, 2.VII.1999, Bezgodov 268 (MW)	AY528883	

ciliaris Primorsky Territory	C19	Russia, Primorsky Territory, Ignatov 08-299 (MHA), OK 1538	MF417712	MF417656
ciliaris South Urals	C20	Russia, Chelyabinsk Province, 6.VIII.2011, Ibatullin 36 (MHA), OK 933	MF417695	MF417665
ciliaris Switzerland	C21	Switzerland, Schnyder 2005070 (MHA, ex Herb. N. Schnyder), OK 1653	MF417717	
ciliaris U.S.A., Ohio	C22	U.S.A., Ohio, Buck 50414 (NY 00829716), OK 1016	MF417706	MF417667
ciliaris Yakutia 1	C23	Russia, Yakutia, 5.VIII.2008, Isakova s.n. (MHA), OK 932	MF417694	MF417654
ciliaris Yakutia 2	C24	Russia, Yakutia, 5.VIII.2008, Ignatov 00-164 (MHA)	MF417705	
ciliaris Zabaikalsky Territory 1	C25	Russia, Zabaikalsky Territory, 17.VI.2010, Czernyadjeva 24-10 (LE), OK 1537	MF417711	MF417668
ciliaris Zabaikalsky Territory 2	C26	Russia, Zabaikalsky Territory, 8.VII.2006, Afonina 1606 (LE), OK 1536		MF417658
major Austria 1	M1	Austria, Carinthia, 18.IV.2001, Köckinger 14992 (MW, ex Herb. H. Köckinger), OK 1037	MF417718	MF417672
major Austria 2	M2	Austria, Carinthia, 2.X.2013, Köckinger 14991 (MW, ex Herb. H. Köckinger), OK 1008	MF417719	MF417671
major Austria 3	M3	Austria, Styria, 11.X.1993, Köckinger s.n. (MHA, ex Herb. H. Köckinger), OK 1659	MF417723	
major Austria 4	M4	Austria, 1.II.1994, Köckinger 94-79 (MHA, ex Herb. H. Köckinger), OK 1657	MF417729	
major Austria 5	M5	Austria, Styria, 9.IV.1993, Köckinger s.n. 93-57 (MHA), OK 1658	MF417730	
major Dagestan 1	M6	Russia, Dagestan, Ignatov & Ignatova 09-254 (MHA), OK 1041	MF417720	MF417673
major Dagestan 2	M7	Russia, Dagestan, Ignatov & Ukrainskaya 09-572 (MHA), OK 1042	MF417721	MF417674
major Italy	M8	Italy, Piedmont, 24.VII.2012, Köckinger 15135 (MHA, ex Herb. H. Köckinger), OK 1665	MF417726	
major North Ossetia	M9	Russia, 25.VII.1979, North Ossetia, L.I. Abramova s.n. (MW), OK 1544	MF417722	MF417670
major Switzerland 1	M10	Switzerland, Grisons, 12.X.2016, Hofmann s.n. (MHA, ex Herb. H. Hofmann), OK 1663	MF417724	
major Switzerland 2	M11	Switzerland, Ticino, 11.X.2002, H. Hofmann s.n. (MHA, ex Herb. H. Hofmann), OK 1664	MF417725	
major Switzerland 3	M12	Switzerland, 9.IV.2005, Schnyder 2005052 (MHA, ex Herb. N. Schnyder), OK 1662	MF417727	
major Switzerland 4	M13	Switzerland, Zьrich, 29.III.2015, Kiebacher 781 (MHA, ex Herb. T. Kiebacher), OK 1652	MF417728	
pusilla Rostov Province	P1	Russia, Rostov Province, 16.X.2000, Sereda s.n. (MHA), OK 1038	MF417737	MF417680
pusilla Italy	P2	Italy, 29.X.1989, Köckinger s.n. (MHA, ex Herb. H. Köckinger), OK 1656	MF445046	
pusilla Spain	P3	Spain, 21.V.2009, Guerra s.n. (MHA), OK 1598	MF417735	
pusilla Switzerland	P4	Switzerland, 11.II.2003, Schnyder 2003001 (MHA, ex Herb. N. Schnyder), OK 1654	MF417738	
pusilla U.S.A., California 1	P5	U.S.A., California, Shevock 32581 (NY 01093951), OK 1009	MF417731	MF417675
pusilla U.S.A., California 2	P6	U.S.A., California, Shevock 26293 (NY 00743182), OK 1014	MF417734	MF417679
pusilla U.S.A., California 3	P7	U.S.A., California, Shevock 29285 (NY 00943898), OK 1012	MF417736	
pusilla U.S.A., Oregon 1	P8	U.S.A., Oregon, Shevock 31659 (NY 01093952), OK 1010	MF417732	MF417676 & MF417678
pusilla U.S.A., Oregon 2	P9	U.S.A., Oregon, Shevock 31600 (NY 01093775), OK 1011	MF417733	MF417677
rostrata Amurskaya Province	R	Russia, Amurskaya Province, 7.VIII.2013, Dudov & Kotelnikova #Br_0593 (MW), OK 935	MF417739	MF417661
ciliaris var. *polycarpa* Brasil	POL1	Brasil, 9.II.2006, Bordin 412 (MHA), OK 984	MF417740	MF417655
ciliaris var. *polycarpa* U.S.A., North Carolina	POL2	U.S.A., North Carolina, Buck 25250 (NY 00464920), OK 1015	MF417741	MF417688
ciliaris var. *wrigtii* U.S.A.,Texas 1	W1	U.S.A., Texas, Buck 49234 (NY 00715890), OK 1017	MF417742	MF417683
ciliaris var. *wrigtii* U.S.A., Texas 2	W2	U.S.A., Texas, Buck 49253 (NY 00729553), OK 1018	MF417743	