Arctoa (2015) **24**: *294-313*
doi: 10.15298/arctoa.24.26

REVISION OF THE RUSSIAN MARCHANTIALES. II. A REVIEW OF THE GENUS *ASTERELLA* P. BEAUV. (AYTONIACEAE, HEPATICAE)

РЕВИЗИЯ ПОРЯДКА MARCHANTIALES В РОССИИ. II. ОБЗОР РОДА *ASTERELLA* P. BEAUV. (AYTONIACEAE, HEPATICAE)

EUGENY A. BOROVICHEV[1,2], VADIM A. BAKALIN[3,4] & ANNA A. VILNET[2]

ЕВГЕНИЙ А. БОРОВИЧЕВ[1,2], ВАДИМ А. БАКАЛИН[3,4], АННА А. ВИЛЬНЕТ[2]

Abstract

The genus *Asterella* P. Beauv. includes four species in Russia: *A. leptophylla* and *A. cruciata* are restricted to the southern flank of the Russian Far East and two others, *A. saccata* and *A. lindenbergiana* occur mostly in the subartcic zone of Asia and the northern part of European Russia. *Asterella cruciata* is recorded for the first time in Russia. The study of the ribosomal LSU (or 26S) gene and *trn*L-F cpDNA intron confirmed the placement of *Asterella gracilis* in the genus *Mannia* and revealed the close relationship of *A. leptophylla* and *A. cruciata,* and the rather unrelated position of *A. saccata* and *A. lindenbergiana*. The phylogenetic tree includes robustly supported terminal clades, however with only weak support for deeper nodes. In general, *Asterella* species and *M. gracilis* from Russia show low levels of infraspecific variation. An identification key and species descriptions based on Russian specimens are provided, along with details of specimens examined, ecology and diagnostic characters of species.

Резюме

Род *Asterella* P. Beauv. представлен в России четырьмя видами: *A. leptophylla* и *A. cruciata* ограничены в распространении югом российского Дальнего Востока, а два других вида, *A. saccata* и *A. lindenbergiana,* распространены преимущественно в субарктической Азии и северной части европейской России. *Asterella cruciata* впервые выявлена в России. Анализ нуклеотидных последовательностей части гена LSU (или 26S) ядДНК и *trn*L-F хпДНК подтверждает положение *Asterella gracilis* в роде *Mannia* и показывает, что *A. leptophylla* и *A. cruciata* являются филогенетически близкими видами. Однако, последние виды четко отличаются морфологически. Все четыре известные в России вида *Asterella* и *M. gracillis* характеризуются низким уровнем внутривидовой вариабельности по изученным последовательностям ДНК, образцы видов формируют надежно поддержанные клады, что однозначно подтверждает видовой статус этих таксонов. В то же время, полученная филогения рода *Asterella* характеризуется низкими поддержками внутренних узлов на построенных филогенетических деревьях. Приводятся ключ для определения российских видов, список изученных образцов, а также морфологические описания с указанием особенностей изученных видов и предпочитаемых ими местообитаний, составленные по российскому материалу.

KEYWORDS: *Asterella*, Aytoniaceae, Russia, liverworts, phytogeography, taxonomy, Hepaticae, LSU, 26S, *trn*L-F

INTRODUCTION

Asterella is one of the largest genera of the order Marchantiales, including 45-50 species worldwide with 15 taxa occurring in Eurasia (Long, 2006). The checklist of Russian liverworts (Konstantinova, Bakalin *et al*., 2009) reported four *Asterella* species: *A. gracilis* (F. Weber) Underw., *A. leptophylla* (Mont) Grolle, *A. lindenbergiana* (Corda ex Nees) Arnell and *A. saccata* (Wahlenb.) A. Evans. However, since then, *Asterella gracilis* was transferred to *Mannia* (Schill *et al*., 2010), basing on two estimations of molecular phylogeny of the family Aytoniaceae based on *mat*K and *trn*L-intron cpD-

1 – Institute of Industrial Ecology Problems of the North of the Kola Science Center of RAS, Apatity, Murmansk Province, 184209, Russia – Россия, 184209, г. Апатиты, Мурманская область, Институт проблем промышленной экологии Севера Кольского научного центра РАН; e-mail: borovichyok@mail.ru
2 – Polar-Alpine Botanical Garden-Institute of the Kola Science Center of RAS, Kirovsk, Murmansk Province, 184256, Russia – Россия, 184256, г. Кировск, Мурманская область, Полярно-альпийский ботанический сад-институт им. Н.А. Аврорина Кольского НЦ РАН; e-mail: anya_v@list.ru
3 – Botanical Garden-Institute FEB RAS, Makovskogo Street, 142, Vladivostok, 690024, Russia – Ботанический сад-институт ДВО РАН, ул. Маковского, 142, Владивосток, 690024
4 – Institute of Biology and Soil Science FEB RAS, Stoletiya Vladivostoka Avenue, 159, Vladivostok, 690022, Russia, Биолого-почвенный институт ДВО РАН, пр. Столетия Владивостока, 159, Владивосток, 690022; e-mail: v_bak@list.ru

NA (Long *et al*., 2000) and LSU (or 26S) gene and *trn*L-F cpDNA (Schill *et al*., 2010). In another DNA barcoding study including a single sample of *Asterella gracilis,* this was also found among *Mannia* species by the test of *rbc*L cpDNA (Hollingsworth *et al*., 2009). However, this taxonomic transfer is quite incongruent with morphological evidences. The traditional differentiating feature between *Asterella* and *Mannia* is presence of an individual preudoperianth around each sporophyte in *Asterella* (Müller, 1954; Schljakov, 1982; Schuster, 1992; etc.). A pseudoperianth is found in *A. gracilis*, but not in any other *Mannia* species. In this case, the results of molecular study demonstrate the problem of morphological delimitation of the two genera. Some differences between *Mannia gracilis* (*Asterella gracilis*) and other *Asterella* were found in spore morphology (Long, 2006). In the present study, we treat *A. gracilis* as a member of the genus *Mannia*, but include it in discussion on morphology and key, so it will not be overlooked during specimen identification.

In the course of recent studies on the liverwort flora of Russia we examined (both morphologically and genetically) material of *Asterella* from Russia available to us, clarifying the distribution of previously recorded taxa. The main goal of the present study is to revise this genus in Russia utilizing an integrative taxonomic approach, and to provide keys, morphological descriptions and illustrations of species based on collections from Russia.

Material and methods

Taxon samping

The morphological study was based on ca. 70 specimens of *Asterella* from Russia kept in KPABG, VBGI, LE, MHA, TUR, KW and IRK.

For molecular studies, nucleotide sequences were newly obtained for 37 specimens of the family Aytoniaceae, 33 of them were gathered mostly in geographically remote regions of Russia and four from neighboring countries: Norway, Ukraine, Japan and China (Table 1). The genus *Asterella* was represented by 8 specimens referred by morphology to the 4 species known in Russian liverwort flora. Additionally, 20 specimens from 6 taxa of the genus *Mannia*, 6 specimens from 2 species of *Plagiochasma* and 3 specimens of *Reboulia hemisphaerica* were tested.

For phylogenetic testing the partial nuclear ribosomal LSU gene (ca. 1100 bp fragment from the 5'-end of the gene) and *trn*L-F cpDNA were selected due to suitable taxa sampling in Long *et al*. (2000) and Schill *et al*. (2010). The part of *rbc*L gene cpDNA suggested by Hollingsworth *et al*. (2009) is almost twice as short as the part of the nuclear ribosomal LSU gene in Schill *et al*. (2010), but the number of variable and parsimony informative positions in this *rbc*L region is significantly lower than in part of LSU gene (in two and 1.5 times, consequently). All analyzed specimens are listed in Table 1, including data on morphological identification, GenBank accession numbers and voucher details. The newly generated data were combined with 78 GenBank accessions (LSU and *trn*L-F) belonging to 39 specimens of 24 marchantioid liverworts taxa from Schill *et al*. (2010: Appendix 1) and 18 GenBank accessions (*trn*L-intron) of 16 *Asterella* species from Long *et al*. (2000). Following these studies, *Targionia hypophylla* L. was used as an outgroup taxon for the phylogenetic analyses.

DNA isolation, PCR amplification and DNA sequencing

DNA was extracted from dried liverwort tissue using the NucleoSpin Plant Kit (Macherey-Nagel, Germany). The amplification and sequencing were performed using primers suggested by Taberlet *et al*. (1991) and Shaw (2000) for the *trn*L-F and LSU, respectively.

PCRs were carried out in 20 µl volumes according to the following procedure: 3 min at 94°C, 30 cycles (30 s 94 °C, 40 s 56 °C for *trn*L-F or 50°C for LSU, 60 s 72 °C) and 2 min of extension time at 72 °C. Amplified fragments were visualized on 1 % agarose TAE gels by EtBr staining, purified using the GFX PCR DNA and Gel Band Purification Kit (Amersham Biosciences, USA), and then used as a template for sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, USA) following the standard protocol provided for 3100 Avant Genetic Analyzer (Applied Biosystems, USA).

Phylogenetic analysis

Two datasets, LSU and *trn*L-F, were automatically aligned using BioEdit 7.0.1 (Hall, 1999) with ClustalW option and then manually corrected. The strict-consensus trees of non-parametric bootstrap analyses revealed a lack of incongruence between both datasets and subsequently they were combined.

The combined LSU+*trn*L-F dataset for 76 specimens (with exclusion of specimens with *trn*L-intron data only) was analyzed by the maximum parsimony method (MP) with the TNT program (Goloboff *et al*., 2003). This analysis involved a New Technology Search with a search for the minimum-length tree by one reiteration and 1000 bootstrap resamplings; the default settings were used for other parameters; indels were taken into account by a modified complex coding algorithm in SeqState (Müller, 2005). The Bayesian method (BA) with MrBayes v. 3.2.1 (Ronquist *et al*., 2012) and the maximum likelihood method (ML) with PhyML 3.0 (Guindon *et al*., 2010) were implemented for full dataset with 94 specimens, absent data were treated as missing.

The program ModelGenerator (Keane *et al*., 2004) determined the GTR+I+G model as the best-fit evolutionary model of nucleotide substitutions for LSU+*trn*L-F dataset. This model of nucleotide substitutions was used and the rate heterogeneity among sites was modeled using a gamma distribution with four rate categories. Bootstrap support (BS) for individual nodes was assessed using a resampling procedure with 500 replicates. According to stopping frequency criterion (FC) for bootstrapping procedure (Pattengale *et al*., 2010) for our dataset even 200 replicates are enough for reaching BS convergence with Pearson average c100=0.992940 realized in RAxML v7.2.6 (Stamatakis, 2006).

For the Bayesian analysis each of the partitions of the combined alignment (LSU and *trn*L-F) was separately assigned the GTR+I+G model, and gamma distributions were approximated using four categories. Two independent runs of the Metropolis-coupled MCMC were used to sample parameter values in proportion to their posterior probability. Each run included three heated chains and one unheated chain, and the two starting trees were chosen randomly. The number of generations was 3 million, and trees were saved every 100th generation. Average standard deviation of split frequencies between two runs was 0.005226. The software tool Tracer (Rambaut, Drummond, 2007) reveals effective sample size (ESS) is 1832,5766 and auto-correlation time (ACT) is 2946,6817 for our data. The 3000 trees as determined by Tracer were discarded in each run, and 54000 trees from both runs were sampled after burning. Bayesian posterior probabilities were calculated as branch support values from trees sampled after burn-in.

The infrageneric and infraspecific variability of each DNA locus (LSU, *trn*L-F, *trn*L–intron) for all included in the full dataset *Asterella* species was estimated as the value of the *p*–distances between specimens and species, as calculated in Mega 5.1 (Tamura *et al*., 2011) using the pairwise deletion option for counting gaps.

Results

In total, 22 sequences of partial LSU gene and 36 sequences of *trn*L-F for 37 Aytoniaceae specimens were obtained and combined in a newly produced alignment with accessions from Schill *et al*. (2010) and Long *et al*. (2000). The combined alignment for 94 specimens of marchantioid liverworts consists of 1958 character sites; among them 1185 sites belong to LSU, 773 sites to the *trn*L-F region. The number of constant positions in the LSU region and *trn*L-F region are 930 (78.48 %) and 415 (53.69 %), variable positions are 221 (18.64 %) and 284 (36.74 %), parsimony informative positions 150 (12.66 %) and 207 (26.78 %). Totally, in combined alignment there are 1345 (68.69 %) constant positions, 505 (25.79 %) are variable and 357 (18.23 %) are parsimony informative positions. Thus, the variability of *trn*L-F region almost in two times higher than variability of partial LSU gene, evidently, this cpDNA locus is more suitable for phylogenetic reconstruction.

The MP analysis yielded two equally parsimonious trees with a length of 2465 steps, with CI = 0.615019 and RI = 0.832159 calculated in Mega 5.1. The ML calculation resulted in a single tree, the arithmetic means of Log likelihood was -9294.95184. Arithmetic means of Log likelihoods in the BA analysis for both runs sampled were -9208.32 and -9208.82 respectively.

The trees topologies achieved by three methods are highly congruent. The MP tree for 76 specimens with indication of bootstrap support values (BS) is shown in Fig. 1, the ML tree for 94 specimens with indication of BS and posterior probabilities (PP) calculated in BA analysis – in Fig. 2.

The constructed topologies are quite similar to the trees published in Schill *et al*. (2010). The phylogenetic affinity among *Asterella* species resembles those obtained by Long *et al*. (2000). The robustly supported subclades with multiplied sampled five species of the genus *Mannia* and *Asterella gracilis* compose a terminal clade on obtained trees (BS=93% in ML, PP=1.00 in BA) (Fig. 1. 2). Seven Russian accessions of *A. gracilis* comprise a subclade with three previously analyzed specimens from Europe (BS=99% in ML, PP=1.00 in BA) in relation to *Mannia triandra* and *M. pilosa* (BS=93% in MP, BS=97% in ML, PP=1.00 in BA) that supports its treatment as *Mannia gracilis* as concluded by Schill *et al*. (2010). Based on DNA analysis the morphological identification of four *Mannia* specimens was corrected: *Mannia androgyna* (instead erroneously *M. fragrans*) was suggested for Russian Far East, two specimens were referred to *M. triandra*, specimens of erroneously determined *Mannia androgyna* from the Republic of Adygeia was found in a subclade along with Austrian samples of *M. californica* that as suggested in Schill *et al*. (2010) could be an evidence of cryptic speciation in this taxon.

Asterella californica and *A. grollei* compose their own separated phyla with support on phylogenetic trees partly resembling results of Schill *et al*. (2010) and Long *et al*. (2000). Other *Asterella* species were placed in an unsupported clade with genera *Plagiochasma* and *Reboulia* in MP tree (Fig. 1) or dispersed among two clades on ML/BA trees (Fig. 2): *A. lindenbergiana*+*A.saccata*+8 species of *Asterella* represented by single specimen (PP=0.77 in BA) and *A. leptophylla*+*A. cruciata*+*A. khasyana*+*A. africana*+*A. tenella*+*A. wallichiana* (PP=1.00 in BA). Thus, our estimation demonstrate polyphyly of the genus *Asterella* as previously achieved also by Schill *et al*. (2010) and Long *et al*. (2000).

Four species of *Asterella* from the Russian flora were found in one clade in the MP tree (Fig. 1) or as a result of ML/BA analyses of extended taxa sampling *A. lindenbergiana* and *A. saccata* were placed in a distinct clade from *A. leptophylla* and *A. cruciata* (Fig. 2). All studied specimens of *A. lindenbergiana* from Russia compose one subclade and possess a common nucleotide sequence of *trn*L–intron with Norwegian specimen (BS=100% in MP, BS=96% in ML, PP=1.00 in BA). A Russian specimen of *A. saccata* is similar to those from Switzerland (BS=100% in MP, BS=100% in ML, PP=1.00 in BA). The specimens of *A. leptophylla* from Primorsky Territory of Russia and from Japan compose a clade with moderate support (BS=65% in ML, PP=0.89 in BA). The clade that shows a sister position of *A. cruciata* to *A.*

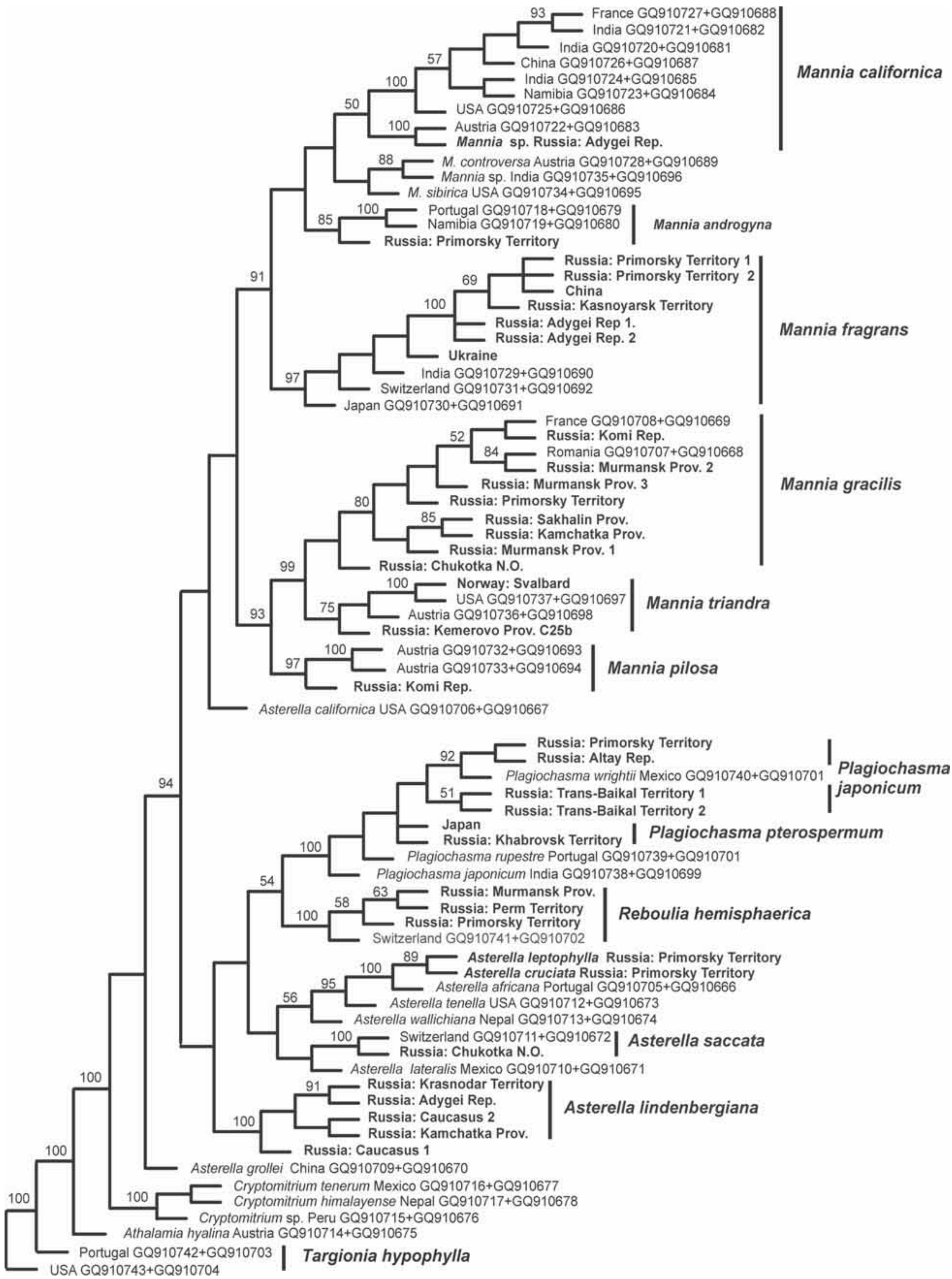

Fig 1. Phylogram obtained in a maximum parsimony calculation for the family Aytoniaceae and related taxa based on combined nucleotide sequences dataset of LSU nrDNA and *trn*L-F cpDNA (76 specimens). Bootstrap support values more than 50% are indicated. Samples sequenced for this study are in bold, for specimens from Schill *et al*. (2010) the GenBank accessions numbers are provided (LSU+*trn*L-F).

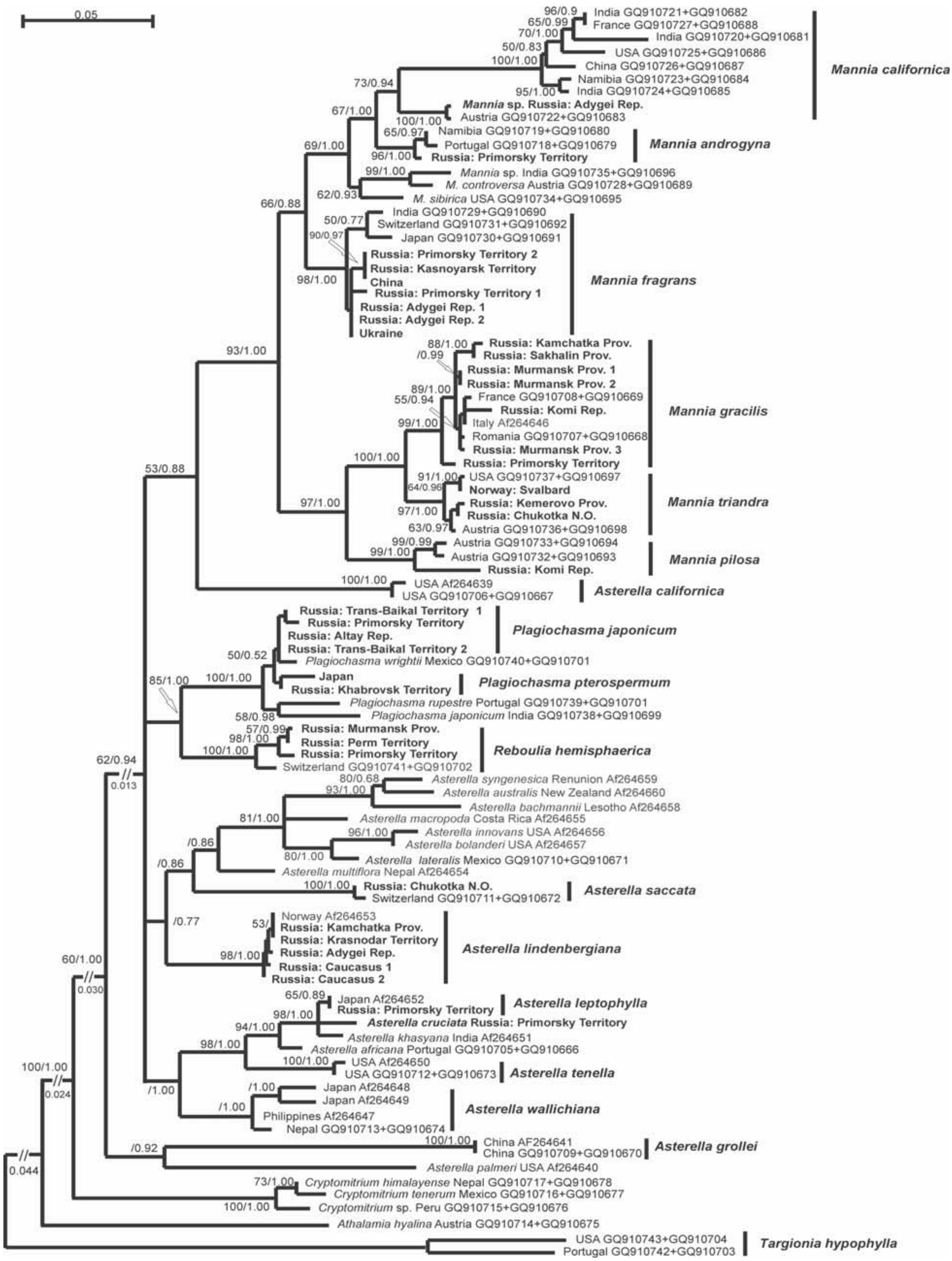

Fig 2. Phylogram obtained in a maximum likelihood calculation for the family Aytoniaceae and related taxa based on combined nucleotide sequences dataset of LSU nrDNA and *trn*L-F cpDNA (94 specimens). Bootstrap support values of maximum likelihood analysis and Bayesian posterior probabilities more than 50% (0.50) are indicated. The values of length for cut branches are shown. Samples sequenced for this study are in bold, for specimens from Schill *et al*. (2010) and Long *et al*. (2000) the GenBank accessions numbers are provided (LSU+*trn*L-F or *trn*L-intron, consequently).

Table 1. The list of taxa, specimens vouchers and GenBank accession numbers for sequenced in this study specimens.

Taxon	Voucher specimen	GenBank accession numbers	
		*trn*L-F	LSU (26S)
Asterella cruciata	Russia: Primorsky Territory, Bardunov, s.n., 9.IX.1978 (VBGI, KPABG)	KR024222	KR024186
A. leptophylla	Russia: Primorsky Territory, Bakalin, P-40-24-12 (VBGI, KPABG)	KR024221	KR024185
A. lindenbergiana	Russia: Adygei Rep., Konstantinova, K409-3-12 (KPABG)	KR024219	KR024183
A. lindenbergiana	Russia: Kamchatka Prov., Karagynsky Isl., Bakalin, K-18-20-05 (VBGI, KPABG)	KR024215	—
A. lindenbergiana	Russia: Krasnodar Territory, Konstantinova, K437-1-07 (KPABG)	KR024218	KR024182
A. lindenbergiana	Russia: Caucasus, **1**, Konstantinova, K409-3-12 (KPABG)	KR024217	KR024181
A. lindenbergiana	Russia: Caucasus, **2**, N. Konstantinova, K427-12 (KPABG)	KR024216	KR024180
A. saccata	Russia: Chukotka N.O., Afonina, s.n., 14.VIII.1979 (LE, KPABG)	KR024220	KR024184
Mannia androgyna	Russia: Primorsky Territory, Gambaryan, 16.VII.1997 (VBGI, KPABG)	KR024188	—
M. fragrans	China: Great Khingan Range, Bakalin, China-33-3-10 (KPABG)	KR024191	—
M. fragrans	Russia: Adygei Rep., **1**, Konstantinova & Savchenko, K104-4-09 (KPABG)	KR024194	KR024168
M. fragrans	Russia: Adygei Rep., **2**, Konstantinova & Savchenko, K168-2-09 (KPABG)	KR024193	KR024167
M. fragrans	Russia: Krasnoyarsk Territory, Stolby NSR, Vasil'ev, s.n., 3.VIII.1985 (KPABG)	KR024192	KR024166
M. fragrans	Russia: Primorsky Territory, **1**, Bakalin, P-1-5-11 (VBGI, KPABG)	KR024189	—
M. fragrans	Russia: Primorsky Territory, **2**, Kozhevnikov, s.n., 13.IX.2000 (VBGI, KPABG)	KR024190	—
M. fragrans	Ukraine, Zerov, s.n., 10.VI.1953 (KW, KPABG)	—	KR024169
M. gracilis	Russia: Kamchatka Prov., Bakalin, K-62-2-03 (KPABG)	KR024202	—
M. gracilis	Russia: Komi Rep., Dulin, MVD-1113 (KPABG)	KR024198	KR024172
M. gracilis	Russia: Murmansk Prov., **1**, Borovichev, B23-1-06 (KPABG)	KR024199	—
M. gracilis	Russia: Murmansk Prov., **2**, Borovichev, BE17-1-06 (KPABG)	KR024200	KR024173
M. gracilis	Russia: Murmansk Prov., **3**, Borovichev, P-305-6-13 (KPABG)	KR024203	KR024174
M. gracilis	Russia: Primorsky Territory, Bakalin, P-84-1-07 (VBGI, KPABG)	KR024204	—
M. gracilis	Russia: Sakhalin Prov., Sakhalin Isl., Bakalin, S-60-17-09 (VBGI, KPABG)	KR024201	—
M. pilosa	Russia: Komi Rep., Dulin, s.n., 21.VI.2007 (KPABG)	KR024205	KR024175
M. sp.	Russia: Adygei Rep., Konstantinova, K105-2-09 (KPABG)	KR024187	KR024165
M triandra	Norway: Svalbard, Borovichev, BE171-5-09 (KPABG)	KR024195	KR024170
M. triandra	Russia: Chukotka N.O., Vangelya Isl., Polozova, s.n., 1.IX.1985 (LE, KPABG)	KR024196	—
M. triandra	Russia: Kemerovo Prov., Konstantinova, 82-1-00 (KPABG)	KR024197	KR024171
Plagiochasma japonicum	Russia: Altay Rep., Zolotuchin, s.n., 23.V.1982 (KPABG, MHA)	KR024206	—
P. japonicum	Russia: Primorsky Territory, Gambaryan, 148d (VBGI, KPABG)	KR024209	—
P. japonicum	Russia: Trans-Baikal Territory, **1**, Mamontov, YuSM-265-3-9 (KPABG)	KR024208	KR024177
P. japonicum	Russia: Trans-Baikal Territory, **2**, Mamontov, YuSM-278-2-1 (KPABG)	KR024207	KR024176
P. pterospermum	Japan, Yamaguchi, Bryophytes of Asia #147 (KPABG)	KR024210	—
P. pterospermum	Russia: Khabarovsk Territory, Bakalin, Kh-72-22-09 (VBGI, KPABG)	KR024211	—
Reboulia hemisphaerica	Russia: Perm Territory, Konstantinova, K391-4-04 (KPABG)	KR024213	KR024179
R. hemisphaerica	Russia: Primorsky Territory, Gambaryan, s.n., 4.VIII.1995 (VBGI, KPABG)	KR024214	—
R. hemisphaerica	Russia: Murmansk Prov., Borovichev, BE13-6-07 (KPABG)	KR024212	KR024178

leptophylla is supported in the MP tree (Fig. 1, BS=89%), while in the ML/BA analysis these species appears in a polytomy with other species (Fig. 2).

The *p*–distances in the genus *Asterella* indicate robust species differentiation by *trn*L-F and *trn*L–intron sequences whereas variation of LSU is quite low to distinguished closely related species (Table 2). *Asterella lindenbergiana* and *A. saccata* reveal the low level of infracpecific variation among the studied loci (*trn*L–intron/*trn*L-F/LSU: 0/0.1/0.1 and 0/0/0.3 consequently) whereas *M. gracilis* appears to be a more variable species even within Europe (*trn*L–intron/*trn*L-F/LSU: 1.1/0.7/0.3) and could be a candidate taxon for cryptic species estimation. The differences in *trn*L–intron sequences between two specimens of *A. leptophylla* are absent, but their differentiation from *A. cruciata* partially exceeds the level of infraspecific variation found in a sufficiently sampled species (*trn*L–intron/*trn*L-F/LSU: 1.6/1.3/0.4). Similar level of infrageneric *p*–distances was obtained for related species *A. africana* and *A. khasyana.* It should be mentioned that two specimens from China of *A. leptophylla* and *A. cruciata* are also only slightly differentiated from *rbc*L cpDNA (Hollingsworth *et al*., 2009). However morphologically *A. cruciata* and *A. leptophylla* are well differentiated.

The implemented study does not resolve the deep nodes in *Asterella* phylogeny, but supported terminal clades appeared to be useful for practical taxonomy. The results confirmed the position of *Asterella gracilis* in *Mannia*, the close relationship of *A. leptophylla* and the newly reported for Russian flora *A. cruciata.* The single specimen of *Asterella saccata* from Russia was found in a clade with a specimen of this species from Switzerland, being clearly separated from other *Asterella* species and supporting the presence of *Asterella saccata* in Russia. *Asterella lindbergiana* and *M. gracilis* reveal a low level of infraspecific

Table 2. The values of *p*-distances within species (INT, shaded) and between species (INF) of *Astereалla* (calculated with data on LSU and *trn*L-F by Schill et al. (2010) and *trn*L-intron by Long et al. (2000). Three values are given for three loci as follow: *trn*L-intron/*trn*L-F/LSU. Dashes mark non calculated values due to single specimen only.

	INT	INF																			
Taxon		*gracilis*	*lindenb.*	*austr.*	*syng.*	*bachm.*	*lateralis*	*bolan.*	*innov.*	*macr.*	*palmeri*	*californ.*	*saccata*	*afric.*	*mult.*	*leptoph.*	*cruciata*	*khas.*	*tenella*	*wallichiana*	*grollei*
gracilis	1.1/0.7/0.3																				
lindenbergiana	0/0.1/0.1	6.7/6.9/2.8																			
australis	-/-/-	8.3/-/-	4.7/-/-																		
syngenesica	-/-/-	7.6/-/-	3.7/-/-	1.8/-/-																	
bachmannii	-/-/-	7.5/-/-	4.4/-/-	3.1/-/-	2.9/-/-																
lateralis	-/-/-	7.1/7.7/3.3	3.8/4.1/2.0	3.8/-/-	2.8/-/-	4.1/-/-															
bolanderi	-/-/-	7.2/-/-	4.1/-/-	4.9/-/-	3.9/-/-	5.1/-/-	1.9/-/-														
innovans	-/-/-	8.1/-/-	4.7/-/-	5.1/-/-	4.6/-/-	5.9/-/-	2.5/-/-	0.5/-/-													
macropoda	-/-/-	7.3/-/-	3.5/-/-	3.7/-/-	3.8/-/-	4.5/-/-	2.9/-/-	2.9/-/-	3.0/-/-												
palmeri	-/-/-	9.0/-/-	8.7/-/-	8.7/-/-	8.0/-/-	9.0/-/-	8.8/-/-	9.3/-/-	9.9/-/-	9.6/-/-											
californica	0.2/-/-	5.9/6.4/3.7	5.5/4.4/3.0	7.2/-/-	6.5/-/-	6.7/-/-	6.3/6.0/3.5	6.2/-/-	7.0/-/-	6.5/-/-	6.6/-/-										
saccata	0/0/0.3	8.8/8.6/2.8	6.8/5.6/2.1	8.3/-/-	8.2/-/-	8.3/-/-	6.8/6.5/1.6	6.8/-/-	7.6/-/-	7.1/-/-	9.5/-/-	7.2/6.2/2.9									
africana	-/-/-	6.6/8.1/4.1	4.3/4.0/2.5	7.4/-/-	6.5/-/-	6.6/-/-	5.4/6.1/2.4	5.7/-/-	6.4/-/-	5.7/-/-	8.4/-/-	5.5/5.3/4.3	6.0/6.0/2.6								
multiflora	-/-/-	7.7/-/-	3.9/-/-	5.0/-/-	4.8/-/-	5.8/-/-	3.8/-/-	4.0/-/-	4.7/-/-	3.8/-/-	9.5/-/-	6.1/-/-	5.2/-/-	4.9/-/-							
leptophylla	0/-/-	6.6/8.1/4.0	4.3/4.2/2.6	7.4/-/-	7.0/-/-	6.6/-/-	5.4/6.0/2.5	5.7/-/-	6.4/-/-	5.7/-/-	9.2/-/-	5.2/5.3/4.0	6.2/6.3/2.3	1.9/1.9/0.6	4.9/-/-						
cruciata	-/-/-	6.8/8.4/3.9	5.8/5.5/2.5	8.9/-/-	8.5/-/-	8.1/-/-	6.9/7.2/2.6	7.1/-/-	7.9/-/-	7.1/-/-	10.3/-/-	6.2/6.1/4.3	7.7/7.5/2.6	3.0/2.9/0.6	6.4/-/-	1.6/1.3/0.4					
khasyana	-/-/-	6.6/-/-	4.9/-/-	8.0/-/-	7.6/-/-	7.2/-/-	6.0/-/-	6.2/-/-	7.0/-/-	6.2/-/-	9.8-/-	5.8/-/-	6.8/-/-	2.1/-/-	5.5/-/-	0.8/-/-	1.9/-/-				
tenella	0.3/-/-	9.1/9.2/3.9	6.7/5.1/2.7	9.0/-/-	8.6/-/-	8.7/-/-	7.2/7.0/2.5	8.0/-/-	8.7/-/-	8.0/-/-	11.6/-/-	8.2/6.5/4.5	8.8/7.7/2.4	4.4/3.5/0.8	7.0/-/-	4.4/4.2/1.0	5.6/5.3/1.1	5.0/-/-			
wallichiana	1.2/-/-	6.8/6.9/3.6	4.5/4.3/2.2	7.7/-/-	6.9/-/-	7.5/-/-	6.2/5.8/2.0	6.4/-/-	7.0/-/-	6.4/-/-	9.3/-/-	6.3/5.3/4.0	6.8/6.5/2.4	4.1/4.3/1.8	5.5/-/-	4.7/4.8/1.8	6.2/6.1/2.2	5.1/-/-	6.8/5.7/1.5		
grollei	0/-/-	9.9/12.4/3.9	8.3/9.1/3.9	10.0/-/-	9.6/-/-	10.3/-/-	9.3/10.4/3.3	9.5/-/-	10.0/-/-	9.5/-/-	7.0/-/-	7.7/9.1/3.8	9.5/10.0/3.1	8.1/9.5/3.6	9.1/-/-	8.6/10.4/3.3	10.0/11.5/3.6	9.2/-/-	11.1/11.3/3.0	7.6/10.0/4.0	

sequence variation in studied DNA loci, thus confirming barcoding ability of the latter.

TAXONOMIC TREATMENT

Asterella P. Beauv. in Cuvier (ed.), Dict. Sci. Nat. 3: 257. 1805. – *Fimbraria* Nees, Horae Phys. Berol.: 44. 1820.

Type: *Asterella tenella* (L.) P. Beauv. in Cuvier (ed.), Dist. Sci. Nat. ed. 1, 3: 257. 1805. – *Marchantia tenella* L., Sp. Pl., ed. 1, 2:1137. 1753.

Thalli medium-sized to relatively large; prostrate; forming more or less pure patches or mats; without or with smell of rotten fish; regularly dichotomously branched, sometimes with stipitate-based ventral innovations; **segments** linear to oblong or obcordate; **upper surface** almost flat or with air chambers slightly convex; **color of upper surface** pale green to green, sometimes with reddish tint; not rarely in older parts becoming reddish- to brownish; **thallus margins** undulate to crispate; reddish to purplish, thin, slightly to strongly enrolled in dry condition. **Dorsal epidermis** delicate to firm, mostly colorless, with **cells** thin-walled, with small to distinct trigones; **pores** simple, not stellate, one per air chamber, slightly to moderately elevated above epidermis, surrounded by 2–3(–4) concentric rings of 6–8 cells in each; **oil-cells** usually scattered. **Aerenchyma** well-developed, loose, occupying ca. 1/4 to 1/2 of the thallus height in the middle and all of height in the wings, with **oil-cells** scattered; **air chambers** isodiametric in cross section to slightly transversely elliptic, 1–3(–4)-layered in the middle, and 1(–2)-layered in the wings, with or without free secondary filaments. **Ventral tissue** parenchymatous, consisting of cells with slightly thickened walls, with **oil-cells** scattered. **Oil-bodies** lacking or present in both aerenchyma and ventral tissue, one per specialized oil cell, filling cell lumen. **Midrib** weakly to strongly prominent beneath. **Rhizoids** smooth and pegged, hyaline, covering ventral surface of midrib of thallus. **Ventral scales** in two rows on midrib, covered by dense rhizoids; small to large, colorless to dark red or purplish. **Gemmae** lacking. **Sexual condition** monoicous. **Antheridia** arising dorsally on leading thallus shortly behind the female receptacle or forming dorsal compact cushions on small heart-shaped ventral branches. **Gynoecia** terminal**,** arising in apical notch of leading thallus; **stalk of receptacle** delicate to rigid; erect; pale green to purplish or dark brown, with single rhizoidal furrow. **Archegonial scales** numerous at apex and forming conspicuous reddish cluster or absent, almost linear and with ring of reddish linear scales around stalk base or absent. **Carpocephalum** green to reddish-tinged, conical, conical-hemispheric to flattened and disk-like or umbrella-shaped; **disc** convex, divided into 2–6 lobes, with each involucre often expanded, narrow to broad, containing and partly sheathing a single pseudoperianth and sporogonium; free margin entire or bilobed; **pseudoperianth** colorless to pinkish; lobes hyaline, brownish or pinkish, delicate; exerted from involucre, 5–16 in number, lanceolate. **Capsule** globose, purplish to black, outer wall-cells thin, lacking thickenings. **Spores** yellow, yellowish red, carrot-red to dark purple; alveolate. **Elaters** 1–2-spiral.

The genus is subdivided into five subgenera (Grolle, 1976, 1983; Long, 2001, 2005); three of them (*Asterella*, *Saccatae* (Grolle) D.G. Long, and *Phragmoblepharis* Grolle) are known in Russia. The main features for infrageneric classification include characters of the pseudoperianths and carpocephalum as well as spore morphology (Long, 2005). One of the valuable features for identification of Russian members of the genus is the sex distribution types which are sometimes different from those recognized in leafy liverworts. Below we provide the sex distribution types recognized in Aytoniaceae, following Long (2006) with our modifications:

paroicous – the type, as in leafy liverworts, characterized by position of male organs behind the female ones on the same thallus. Antheridia situated dorsally on leading thallus behind female receptacle;

terminal autoicous – antheridia borne on main branches of the thallus (the same with bearing female receptacles);

female-ventral autoicous – female gametangia borne on ventral, often reduced branches, male ones – on the main branches;

male-ventral autoicous – antheridia borne on ventral, often reduced branches, female ones on the main branches;

dioicous – male and female branches are born on separate thalli;

pseudodioicous – any case of the monoicous inflorescence which appears to be dioicous due to early-decaying thallus bases that give the appearance of dioicy.

KEYS TO THE SPECIES OF *ASTERELLA* AND RELATED SPECIES RECORDED IN RUSSIA

Key to species in Russia for specimens in fertile conditions and ripe spores

1. Sexual condition female-ventral autoicous; thalli thin and semi-translucent .... *Asterella leptophylla*
— Sexual condition predominantly paroicous; thalli more or less firm 2
2. Female receptacle hemispherical; spores proximally alete; distally irregularly and incompletely areolate .... *Mannia gracilis*
— Female receptacle conical, conical-hemispheric or disk-shaped; spores proximally trilete; distally with regular complete areolae 3
3. Plants in fresh condition with strong smell of rotten fish; appendages of ventral scales not forming a cluster at apex;, thalli with not or only slightly enrolled margins in dry condition 4
— Plants have not smell of rotten fish in fresh condition; ventral scales with conspicuously projecting appendages that form noticeable cluster at the apex; margins of thallus strongly inrolled when dry .... *Asterella saccata*
4. Thalli relatively large, 8–26 mm long and 4–8 mm wide; upper surface of thallus commonly with strong reddish to brownish secondary pigmentation; ventral scales rounded triangular to ovate with 1–2 appendages; stalk of female receptacle 10–15 mm long and longer; spores dark purple, (76–)80–90 µm in diameter, distal face with many small alveoli .... *Asterella lindenbergiana*
— Thalli smaller, 8–15 mm long and 2–5 mm wide; upper surface of thallus mostly pale green to green, rarely with reddish tint; ventral scales triangular to lanceolate with single appendage per ventral scale; stalk of female receptacle 2–6 mm length; spores yellowish-red to carrot red, (55–)60–70 µm in diameter; distal face with not many larger alveoli .... *Asterella cruciata*

Key to species in Russia for sterile specimens (not applicable for some deviant modifications)

1. Thalli mostly thin and delicate; specimens from South of the Russian Far East only 2
— Thalli mostly thick and leathery; predominantly arctomontane sub- to circumpolar 3
2. Plants in fresh condition with strong smell of rotten fish; lacking xeromorphic branches and tubers .... *Asterella cruciata*
— Plants have not smell[1] of rotten fish in fresh condition; thalli segments have both hygroshoots and vegetative xeroshoots or tubers ... *Asterella leptophylla*
3. Appendages of scales not forming a cluster at apex; thalli with not or only slightly enrolled margins in dry condition 4
— Ventral scales with conspicuously projecting appendages that form noticeable cluster at the apex; margins of thallus strongly enrolled when dry .... *Asterella saccata*
4. Plants in fresh condition with strong smell of rotten fish; thalli relatively large, 8–26 mm long and 4–8 mm wide; ventral scales rounded triangular to ovate with 1–2 appendages .... *Asterella lindenbergiana*
— Plants have not smell of rotten fish in fresh condition; thalli smaller, 6–15 mm long and 1.5–3 mm wide; ventral scales semicircular with single elongated appendage .... *Mannia gracilis*

Asterella subgenus **Phragmoblepharis** Grolle, Feddes Repert. 87: 246. 1976.

Thalli thick, relatively large; aromatic or non aromatic; regularly dichotomously branched, sometimes with stipitate-based ventral innovations. **Aerenchyma** well-

[1] – According to personal correspondence of David Long, in Indian region this species does smell of rotten fish, which however never observed in Russian plants

developed; **air chambers** isodiametric in cross section to slightly transversely elliptic, (1–)2–3(–4)-layered in the middle; without free secondary filaments. **Ventral scale appendages** 1–2 per scale; lanceolate to oblong-lanceolate; hyaline or reddish; not- to weakly constricted **at base**. **Sexual condition** paroicous. **Carpocephalum** conical, deeply 2–4-lobed, **involucres margin** free, deeply sinuate-lobed; **pseudoperianth** pinkish, tubular, fringed at apex into 12–16 equal reddish-brown lanceolate segments, connate at apex. **Spores** dark purple; outer face with many small alveoli. **Elaters** 1–2-spiral; purplish to red-violet.

Type: *Asterella elegans* (Spreng.) Trevis. Reale Ist. Lombardo Sci., Rendiconti 7: 785. 1874.

Asterella lindenbergiana (Corda ex Nees) Arnell, Lebermosstud. Nordl. Norwegen: 2. Jönköping. 1892. – *Fimbraria lindenbergiana* Corda ex Nees, Naturg. Europ. Leberm. 4: 266, 283. 1838. – *Fimbraria lindenbergiana* Corda ex Nees var. ß angustior Nees, Naturg. Europ. Leberm. 4: 283. 1838 – *Fimbraria major* Hampe in Nees, Naturg. Europ. Leberm. 4: 283. 1838. – *Marchantia alpina* Schleich., Cat. Pl. Helv., ed. 3, 36. 1815. – *Fimbraria bonjeanii* De Not., Mem. Reale Accad. Sci. Torino, ser. 2, 1: 335. 1839. – *Asterella bonjeanii* (De Not.) Trevis., Rendiconti Reale Ist. Lombardo Sci. 7: 785. 1874. – *Hypenantron bonjeanii* (De Not.) Trevis., Mem. Reale Ist. Lombardo Sci., 4: 397. 1877. (Fig. 3).

Illustrations: Frye & Clark, 1937 (p. 80); Müller, 1954 (p. 359, fig. 70); Schljakov, 1982 (p. 94, fig. 34 (3 a-â); Damsholt, 2002 (p. 725, pl. 273); Long, 2006 (p. 92, fig. 22; p. 128, fig. 32b). **Maps:** Söderström, 1995 (p. 9, map 22); Damsholt, 2002 (p. 727, fig. 290); Long, 2006 (p. 195, fig. 45).

Description (Fig. 3): **Thalli** thick, relatively large, 8–26 mm long, 4–8 mm wide (wider in the area of bifurcation), prostrate, forming more or less pure patches or mats, not xeromorphic habit, with smell of rotten fish both in fresh condition and in the course of short-time boiling of herbarium specimens, regularly dichotomously branched, sometimes with stipitate-based ventral innovations; **segments** oblong to lingulate-obcordate; leathery; **apex** strongly notched; **upper surface** not reticulate, almost flat or with air chambers slightly convex; **color of upper surface** pale-green to green, sometimes with reddish tinged, in older parts becoming reddish to brownish; **thallus margins** undulate to crispate; reddish to purplish; thin, often only slightly enrolled in dry condition. **Dorsal epidermis** delicate to firm, mostly colorless; **cells** (25–)30–35(–40)×(20–)25–30 µm; thin, without trigones; **oil-cells** scattered in epidermis; **cuticule** smooth; **pores** simple, slightly to moderately elevated above epidermis, (15–)20–30 µm in diameter, surrounded by 2–3(–4) concentric rings of 6–8 cells in each, cell walls thin or slightly thickened. **Aerenchyma** well-developed, loose, occupying ca. 1/4 to 1/3 of the thallus height in the middle and all of height in the wings; **air chambers** isodiametric in cross section to slightly transversely elliptic, (1–)2–3(–4)-layered in the middle, and 1(–2)-layered in the wings; without free secondary filaments. **Ventral tissue** parenchymatous, consisting of cells with slightly thickened walls, occupying ca. 2/3–3/4 the thallus thickness in the middle and almost absent beneath the wing. **Oil-bodies** lacking or present in both aerenchyma and ventral tissue. **Midrib** prominent; in cross-section ± triangular, suddenly disappear toward thin thallus wings, distinctly and narrowly keeled; thallus over midrib 900–1100(–1320) µm thick in cross-section. **Rhizoids** smooth and pegged, hyaline, covering ventral surface of midrib of thallus. **Ventral scales** reddish to purple; on both sides of the midrib, slightly overlapping; rounded triangular to ovate; **body** (1050–)1200–1800 µm long and (800–)900–1000 µm wide; **body cells** 60–110(–130) µm long and 20–25 µm wide in the middle, with numerous scattered oil-cells, 23–30 µm in diameter; marginal slime papillae numerous; **appendages** 1–2 per scale, lanceolate to oblong-lanceolate; hyaline or reddish; **appendage size** (200–)250–500 µm long and (50–)80–100 µm wide, with a few marginal slime-papillae near base; **appendage base** not- to weakly constricted. **Sexual condition** paroicous. **Antheridia** arising dorsally on leading thallus shortly behind the female receptacle, forming elliptical to circular disc; **ostioles** conical, in clusters or loosely dispersed, conspicuous, without scales. **Gynoecia** arising in apical notch of leading thallus; **stalk of receptacle** robust, purplish to dark brown, smooth, 10–15 mm long, with single very deep rhizoidal furrow. **Archegonial scales** at apex numerous, forming conspicuous reddish cluster, almost linear and forming ring of reddish linear scales around stalk base. **Carpocephalum** conical, reddish green, 3–5 mm in diameter; **disc** convex, deeply 2–4-lobed, each involucre with a single sporophyte; **lobes** inclined at angle of 30° to stalk; **involucres margin** free, deeply sinuate-lobed, rounded; **pseudoperianth** pinkish, tubular, fringed at apex into 12–16 equal reddish-brown lanceolate segments, connate at apex. Capsule globose, purplish, wall-cells thin, lacking thickenings. **Spores** dark purple, (76–)80–90 µm in diameter, outer face with many small alveoli, winged, wing margin undulate, inner face incompletely sculptured, with an indistinct trilete scar. **Elaters** 1–2-spiral, purplish to red-violet; 100–150 µm long, 12–16 µm wide.

Differentiation. When sterile the species may be readily confused with *Reboulia hemisphaerica* due to similar size, coloration of dorsal surface as well as general habit. *A. lindenbergiana* differs from *Reboulia* in: 1. having smell of rotten fish versus no rotten fish smell; 2. pores surrounded by 2–3 concentric rings of thin-walled cells versus pores usually surrounded by 4–6 cell rings with thickened walls in *Reboulia*; 3. distinctly and narrowly keeled midrib versus unkeeled thallus of *Reboulia*; 4. reddish ventral scales with 1–2 lanceolate to ob-

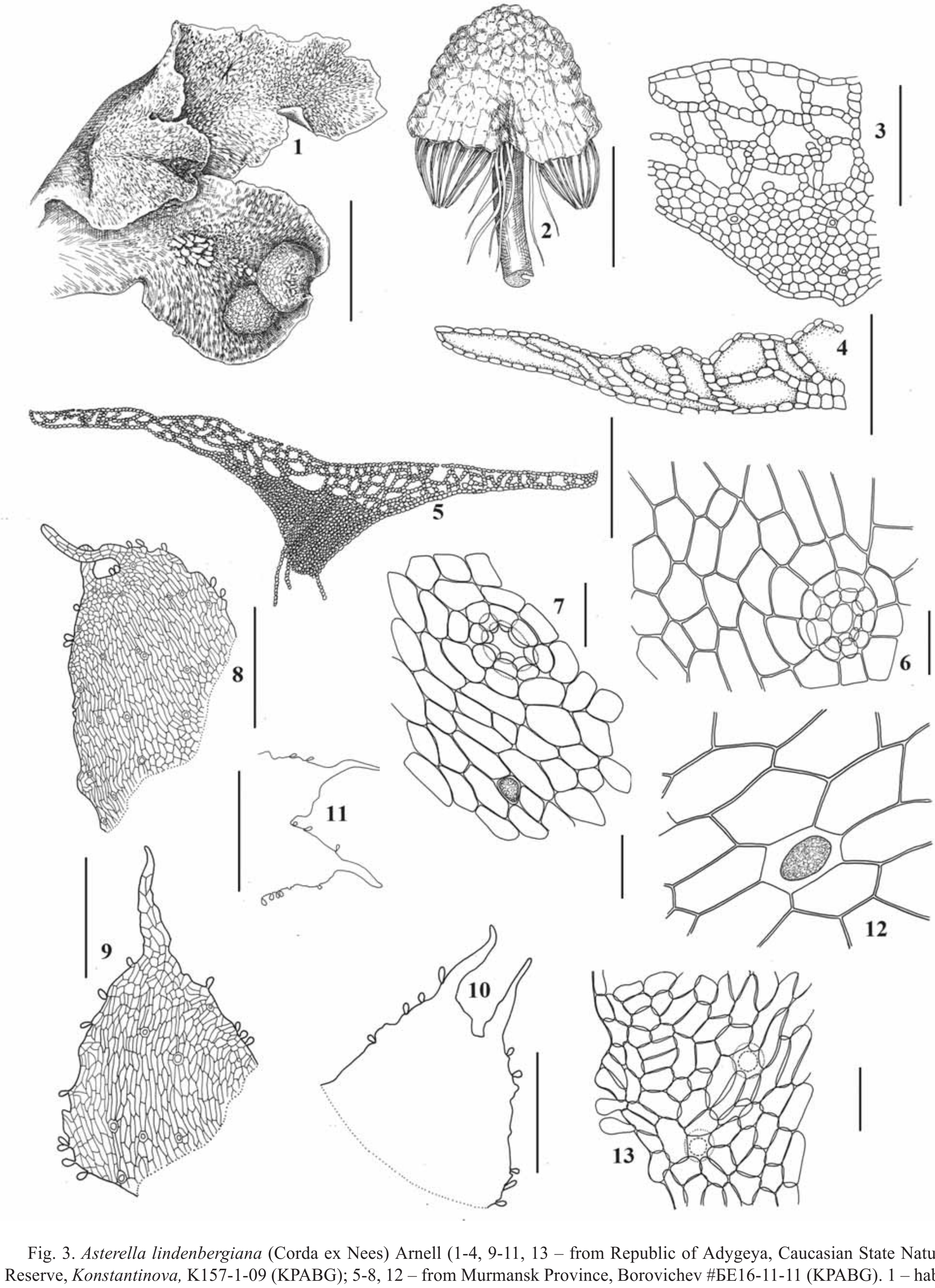

Fig. 3. *Asterella lindenbergiana* (Corda ex Nees) Arnell (1-4, 9-11, 13 – from Republic of Adygeya, Caucasian State Nature Reserve, *Konstantinova,* K157-1-09 (KPABG); 5-8, 12 – from Murmansk Province, Borovichev #БЕ16-11-11 (KPABG). 1 – habit of plant, dorsal view; 2 – carpocephalum of female receptacle; 3 – median part of thallus transverse section; 4 – basal part of thallus transverse section; 5 – thallus transverse section; 6-7 – air-pores from dorsal epidermis of thallus; 8-11 – ventral scales with appendages; 12 – part of thallus dorsal epidermis with oil-body; 13 – basal part of ventral scale. Scale bars: 5 mm for 1; 3 mm for 2; 1 mm for 5, 11; 750 µm for 8-10; 500 µm for 3; 300 µm for 4; 60 µm for 13; 30 µm for 6-7, 12.

long-lanceolate appendage versus purplish ventral scales with 2–3 narrowly linear to filiform appendages. In the field *Asterella lindenbergiana* may be mistaken with *Preissia quadrata.* The main differences are the following: 1. *A. lindenbergiana* has smell of rotten fish, whereas *P. quadrata* has not smell; 2. simple pores versus barrel-shaped in *P. quadrata*; 3. ventral scales with 1–2 appendages versus ventral scales in *P. quadrata* with single lanceolate appendage; 4. compact male disk versus male receptacle stalked in *P. quadrata*; 5. female receptacle stalk with one rhizoidal stalk versus stalk with two rhizoidal furrows *Preissia*.

Distribution. *Asterella lindenbergiana* is montane subcircumpolar liverwort. The area of the species covers alpine belt in large mountainous systems both North America (Evans, 1920, 1923; Frey & Clark, 1937) and Europe: Italy, France, Austria, Switzerland, Germany, Poland, Romania, Slovakia, Slovenia, Sweden, Norway (Long, 2006); Spain (Allorge, 1956), Finland (Koponen *et al*., 1977) and Ukraine (Borovichev & Nyporko, 2014). In Russia, *A. lindenbergiana* is known from Caucasus: Republic of Adygeya (Konstantinova & al., 2009), North-West part of Russia: Murmansk Province (Borovichev, 2011), East Siberia: Republic of Yakutiya (Andrejeva, 2009) and Far East: Chukotka Autonomous District (Konstantinova & Vilnet, 2014), Magadan and Amur Provinces (Borovichev & Bakalin, 2013, Kamchatka Territory (present study).

Ecology. Calciphilous mesophyte, growing in the base of cliffs covered with humus or mineral soils; on wet shady soil in deep canyons; along streams on slopes consisting of lime or other *Ca*-rich subsrtrata. The species often forms more or less pure mats, or growing as admixture to other hepatics, most commonly with *Blepharostoma trichophyllum* (L.) Dumort*., Pressia quadrata* (Scop.) Nees*, Leiocolea gillmanii* (Aust.) Evans*, Mannia fragrans* (Balb.) Frye et L.Clark and *Tritomaria quinquedentata* (Huds.) H. Buch. The species shows only weak connection to the vegetation in the surroundings of the mineral substrata where it is growing and found both in tundra, crooked forests and dark coniferous forest biomes, rarely descending to broadleaved-coniferous forests (Caucasus, Western Europe). According to published data (Mårtensson, 1955; Damsholt, 2002; Long, 2006) *Asterella lindenbergiana* is a typically alpine species in Europe and occurs in humus-filled crevices and in small caves on limestone, *etc*., and in calcareous snow-bed habitats in the alpine belt of mountains. In the upper parts of the subalpine belt species occurs mainly in caves under boulders or over-hanging rocks and at the foot of calcareous cliffs.

Specimens examined. **RUSSIA: Murmansk Province**, Lovozero District, Voron'i Tundry Mts., VII.2011, Borovichev #БЕ16-11-11; 16-14-11; 16-18-11 (KPABG; VBGI); **Republic of Adygeya,** Caucasian State Nature Reserve, Lagonaki Plateau, Psenodah Lake valley, 18.X.2012, Konstantinova K408-12 (KPABG); ibidem, 18.X.2012, Konstantinova K409-3-12 (KPABG); ibidem, 18.X.2012, Konstantinova K410-1b-12 (KPABG); ibidem, piedmont of Psheho-Su Mt., 18.X.2012, Konstantinova K415-7-12 (KPABG); Malaya Laba River Basin, Snegovalka Ridge, cirque of Armovka Mountain, 25.IX.2009, Konstantinova K157-1-09 (KPABG); ibidem, 24.IX.2009, Konstantinova K146-1-09 (KPABG); Kurdgips River valley, slope of the Abadzesh Murzikau Ridge, 12.X.2007, Konstantinova K437-1-07 (KPABG); **Republic of Yakutiya**, Verchoyansk Region, 30.VIII.1935, Yarovoj (LE, det. K. Ladyzhenskaya, tested by E. Andrejeva & R. Grolle); **Kamchatka Territory**, west part of the Bering Sea, Karaginskij Island, North-West macroslope of Vysokaya Mt., 1.VIII.2005, Bakalin K18-19-05, K18-20-05 (VBGI, as *Reboulia hemisphaerica* (L.) Raddi); **Magadan Province,** Magadan City Vicinity, Gertnera Bay, 16.VII.2010, Bakalin #Mag22-20-10 (VBGI); **Amur Province**, Zeya District, 18.VIII.1908, Prochorov & Kuzeneva #59 (VBGI; KPABG); **FINLAND:** Enontekio, Kilpisjarvi, Saanajarvi, 27.V.1968, Laine 1844 (TUR); ibidem, 11.VII.2008 Syrjanen (TUR); ibidem, 7.VII.2009, Syrjanen (TUR); **SWITZERLAND**, Kanton Bern, VIII.1906, Culmann (TUR, KPABG, V. Schiffner's Hepaticae europaeae exsiccatae #1200 as *Fimbraria lindenbergiana* var. *angustior*); Austia, Salzburg, 30.IX.1905, Baumgartner (TUR, KPABG, V. Schiffner's Hepaticae europaeae exsiccatae #1199 as *Fimbraria lindenbergiana*); Tirol, 8.VIII.1903, Schiffner & Handel-Mazzetti (TUR, KPABG, V. Schiffner's Hepaticae europaeae exsiccatae #1198 as *Fimbraria lindenbergiana*); Slovakia, Hohe Tatra, 7.X.1907, Raciborski (TUR, KPABG, V. Schiffner's Hepaticae europaeae exsiccatae #1197 as *Fimbraria lindenbergiana*).

Asterella subgenus **Asterella**

Thalli thin and very delicate; aromatic or non aromatic; vegetative branches terminal and ventral. **Aerenchyma** well-developed; **air chambers** isodiametric to elongated, without free secondary filaments, 1–2(–3)-layered both in the middle and the wings. **Ventral scale appendages** single, oblong to ovate, with a few marginal slime-papillae; **appendage apex** short acute to obtuse, constricted or not at base, margins entire. **Sexual condition** paroicous or ventral-male autoicous. **Antheridia** forming in dorsal, compact disc (cushions), situated on leading thallus behind the female receptacle or situated on small heart-shaped ventral branches. **Carpocephalum** flattened to disk-like or umbrella-shaped, involucre with free margin entire or cleft; **pseudoperianth** colourless to hyaline or rose, with undivided base bless than half total length or undivided basal cape. **Spores** yellow to carrot-red-yellow, regularly areolate on distal surface.

Type: *Asterella tenella* (L.) P. Beauv.

Asterella cruciata (Steph.) Horik., Hikobia 1: 79. 1951. – *Fimbraria cruciata* Steph., Sp. Hep. 6: 12. 1917. – *Asterella odora* S. Hatt., Bot. Mag. (Tokyo) 58: 44. 1944. – *Asterella chichibuensis* Shimizu & S. Hatt., J. Hattori Bot. Lab. 8: 46. 1952. – *Asterella mitsuminensis* Shimizu & S. Hatt., J. Hattori Bot. Lab. 8: 48. 1952. (Fig. 4).

Illustrations: Shimizu & Hattori, 1952 (p. 46, fig. 1, as *A. chichibuensis*; p. 51, fig. 3, as *A. mitsuminensis*); Inoue, 1976 (pl. 169, as *A. odora*); Iwatsuki, 2001 (pl. 186); Long, 2006 (p. 87, fig. 17; p. 127, fig. 31f). **Map:** Long, 2006 (p. 167, fig. 40).

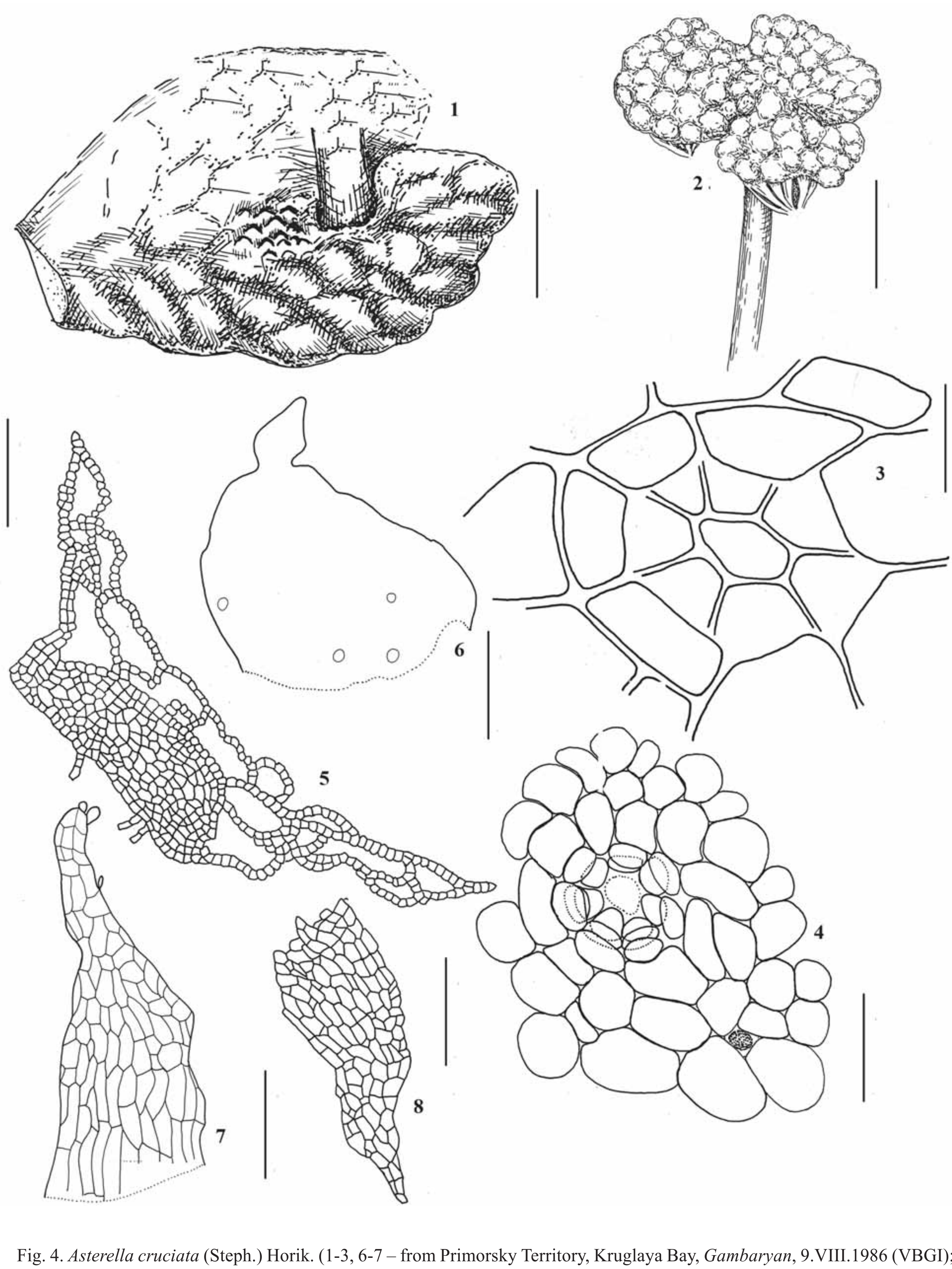

Fig. 4. *Asterella cruciata* (Steph.) Horik. (1-3, 6-7 – from Primorsky Territory, Kruglaya Bay, *Gambaryan*, 9.VIII.1986 (VBGI); 4-5, 8 – rom Primorsky Territory, Kedrovaya Pad‘ State Reserve, *Bardunov*, 9.IX.1978 (VBGI). 1 – habit of plant, dorsal view; 2 – carpocephalum of female receptacle; 3-4 – air-pores from dorsal epidermis of thallus; 5 – thallus transverse section; 6-8 – ventral scales with appendage. Scale bars: 1 mm for 1-2; 400 µm for 5, 7-8; 300 µm for 6; 60 µm for 4; 50 µm for 3.

Description: **Thalli** thin and very delicate, small, 8–15 mm long, 2–5 mm wide, forming more or less pure small patches; dichotomously branched, frequently with ventral innovations with stipitate base; **segments** oblong, cordate to obcordate, broadest towards apex; **apex** notched; **upper surface** not reticulate, almost flat; **color of upper surface** pale-green to green, sometimes with reddish tinged; **thallus margins** rather delicate, undulate; greenish to slightly pinkish, xeromorphic branches and tubers lacking. **Dorsal epidermis** delicate, lustrous, mostly colorless to rose tinged; **cells** (15–)18–30(–32) ×(20–)25–35(–45) μm, with thin or slightly thickened walls and small trigones; **oil-cells** scattered in epidermis with single oil-body; **pores** simple, not elevated to slightly elevated above epidermis, (15–)18–25 μm in diameter, surrounded by 2(–3) concentric rings of 6–8 cells in each, cell walls thin. **Aerenchyma** well-developed, occupying ca. 1/2 of the thallus height in the middle and all height in the wings; **air chambers** isodiametric to elongated, without free secondary free filaments, 1–2(–3)-layered both in the middle and the wings. **Ventral tissue** parenchymatous, consisting of thin-walled cells, occupying ca. 1/4–1/3 the thallus thickness in the middle and absent beneath the wing. **Midrib** ±relatively well-defined, thallus over midrib 300–550 μm thick in cross-section. **Rhizoids** smooth and pegged, hyaline, covering ventral surface of midrib of thallus. **Ventral scales** reddish, scattered thought ventral surface rarely slightly overlapping, triangular to lanceolate, sometimes with a few slime-papillae on outer margin; **body size** (500–)600–900 μm long and (300–)500–600 μm wide; **body cells size** 30–60(–85) μm long and 23–40 μm wide, with numerous scattered oil-cells, 25–30 μm in diameter; **appendage** by one per ventral scale, oblong to ovate, hyaline or reddish; **appendage size** (120–)150–500 μm long and (80–)100–150 μm wide, with a few marginal slime-papillae and rarely oil-cells; **appendage apex** short acute to obtuse; **appendage base** weakly constricted. **Sexual condition** paroicous. **Antheridia** forming dorsal compact disc (cushions), situated on leading thallus behind the female receptacle; **disc** elliptical to circular; **ostioles** conical, without scales. **Gynoecia** arising in apical notch of leading thallus; **stalk of receptacle** greenish to purplish, smooth, short 3–5(–8) mm long, with single rhizoidal furrow. **Archegonial scales** at apex numerous, lanceolate to almost linear, hyaline to purplish, with 1–2 slime papillae and a few scattered scales along stalk. **Carpocephalum** flattened, green, **disc** flat to convex or slightly verrucose, deeply irregularly 3–5-lobed, each involucre with a single sporophyte; **involucres** margin undivided; **pseudoperianth** colorless, with undivided base less than half total length, lobes 9–15 in number, lanceolate, free at maturity, not deciduous. **Spores** yellow-reddish to orange, globose; (55–)60–70 μm in diameter, distal face with not many, large and highly ornamented dentate alveolae, trilete. **Elaters** 2-spiral, 170–220 μm long, 7–10 μm wide.

Ecology. Neutrophilic mesophyte, occurring on fine soil along water courses (streams, small rivers) or in cliff crevices filled with fine ground, always occupying partly to fully shaded areas. The species occurs in temperate broadleaved deciduous to evergreen subtropical forest zones.

Distribution. *Asterella cruciata* is temperate-subtropical East Asian species known from limited numbers of locations in Japan (Honshu), China (Sichuan, Yunnan) and Korea (Long, 2006). We suggest the distribution of the species is poorly understood and it should be much more common in eastern China than is it suggested. In the course of recent studies we have revealed it in southern flank of the Russian Far East and Guizhou Province of China.

Differentiation and variation. *Asterella cruciata* may be readily mistaken for *A. leptophylla*. The main differentiation features from latter are in: 1. lacking xeromorphic branches versus both hygroshoots and vegetative xeroshoots often present; 2. paroicous inflorescence versus lateral-autoicous inflorescence; 3. very short stalk of female receptacle (ca. 2–6 mm long) versus longer (6–15 mm long); 4. deeply-lobed carpocephala versus shortly lobed ones, and 5. spores with highly ornamented dentate reticulations versus larger spores with almost smooth reticulations.

The specimens from Russia fall within the variability of the species as it was described by Long (2006), with the exception: 1. smaller dorsal epidermal cells size (15–)18–30(–32)×(20–)25–35(–45) μm; 2. longer stalk of female receptacle, 3–5(–8) mm, whereas it was described by Shimizu and Hattori (1952) and Long (2006) for *Asterella cruciata* as: 1. epidermal cells size are 35–62×15–37 μm and 2. female receptacle stalk very short, 0.8–3 (–6.8) mm.

Specimens examined (newly reported areas marked by asterisk). ***RUSSIA: Primorsky Territory,** Khasan District, Kedrovaya Pad' State Reserve, ~43°21'N – 131°38'E, rocks, on gravel 9.IX.1978, Bardunov (VBGI, as *A. leptophylla*); 2 km from Nerpa Bay, Kruglaya Bay, ~42°52'N 131°25'E, foot of coastal cliffs, on humus covering stones in cliff crevices, with *A. leptophylla*, 9.VIII.1986, Gambaryan (VBGI as *A. leptophylla*); Ol'ginsky District, 2 km from Margaritovka Settlement, valley of the right tributary of river Margaritovka, 43°48'38"N – 134°33'41" E, on humic soil, 24.VII.1980, Gambaryan (VBGI, as *A. leptophylla*); southern spoors of Krestovaya Mt. in Ol'ga Bay, in 4 km along road to Lazo Settlement from Ol'ga Settlement, 43°44'38"N 135°12'24.3"E, 25 m alt., rocky outcrops surrounded by *Quercus* forest, fine-grained soil in crevice of cliffs partly shaded by *Quercus* and *Lespedeza,* 22.IX.2007. Bakalin P84-11-07 (VBGI, KPABG); **SOUTH KOREA**: Deokgyu-san, Chonlabukdo, Musu, Deokgyu National Park, southern part of Park Sasgak, 30.VI.2008, Bakalin Kor16-3-08 (VBGI); **CHINA**: *Guizhou Province, Kaijang County, Nanjiang Gorge, 26°56'52.5"N 106°58'51.7"E, 900 m alt., broadleaved (mostly evergreen) forest on steep slope and within valley of stream, moist clay on steep slope, 20.XI.2013, Bakalin China-53-21-13, China-53-24-13 (VBGI, KPABG).

Asterella leptophylla (Mont.) Grolle, Feddes Repert. 87: 246. 1976. – *Fimbraria leptophylla* Mont., Ann. Sci. Nat., Bot., sér. 2 18: 19. 1842. – *Fimbraria reticulata* Kashyap, J. Bombay Nat. Hist. Soc. 25: 279. 1917. – *Asterella reticulata* (Kashyap) Pandé, K.P. Srivast. & Sultan Khan, J. Hattori Bot. Lab. 11: 9. 1954, ex Kachroo, Hattori Bot. Lab. 19: 4. 1958, *nom. illeg.* non *A. reticulata* A. Evans – *Asterella kashyapii* Maheshw., Taxon 18: 599. 1969. – *Fimbraria yoshinagana* Horik., Sci. Rep. Tôhoku Imp. Univ., Ser. 4, Biol. 4: 395. 1929. – *Asterella yoshinagana* (Horik.) Horik., Hikobia 1: 79. 1951. – *Asterella pusilla* Shimizu & S. Hatt., J. Hattori Bot. Lab. 8: 50. 1952. – *Asterella sanoana* Shimizu & S. Hatt., J. Hattori Bot. Lab. 9: 25. 1953. – *Asterella umbelliformis* Shimizu & S. Hatt., J. Hattori Bot. Lab. 9: 25. 1953. (Fig. 5).

Illustrations: Shimizu & Hattori, 1952 (p. 52, fig. 4, as *A. pusilla*); Shimizu & Hattori, 1953 (p. 26, fig. 5 as *A sanoana*; p. 28, fig. 6 as *A. umbelliformis*; p. 30, fig. 7 as *A sanoana*); Long, 2006 (p. 89, fig. 19; p. 127, fig. 31g). **Map:** Long, 2006 (p. 181, fig. 42).

Description. **Thalli** thin and delicate, small, 5–10(–12) mm long, 3–5 mm wide, forming more or less pure small patches, dichotomously branched, frequently with ventral innovations with stipitate base; **segments dimorphic**: **hygroshoots** cordate to obcordate, rarely oblong, tapering to stipitate base, broadest towards apex; **apex** deeply notched; **upper surface** not reticulate, flat; **color of upper surface** pale-green to green, sometimes with reddish tint; **thallus margins** rather delicate, undulate, frequently violet or purplish and **vegetative xeromorphic shoots** as short tuber-like at apex and stipitate-based ventral branches or short tuber-like thickened terminal part of **hygromorphic shoots** forming in dry conditions above main thallus, broadly spatulate or subovate; **apex** entire, dense covered by ventral scales appendages; **color of upper surface** pale-green to green, often with reddish tint; **thallus margins** purple, rather delicate, undulate. **Dorsal epidermis** delicate, lustrose, mostly colorless to rose tinged; **cells** almost isodiametric, (20–)25–35(–40)×(1–20–30(–35) µm, with thin or slightly thickened walls and visible triangle trigones,; **oil-cells** scattered in epidermis; **cuticule** smooth; **pores** simple, not to slightly elevated above epidermis, one per air-chambers, 15–25 µm in diameter, surrounded by 2–3 concentric rings of 6–8 cells in each, cell walls thin. **Aerenchyma in hygromorphic shoots** well-developed, occupying 1/2–2/3 of the thallus height in the middle and all of height in the wings; **air chambers** isodiametric, without free secondary filaments, 1–2(–3)-layered in the middle and elongated and 1-layered in the wings: **aerenchyma in xeromorphic shoots** compact, occupying 1/2–2/3 of the thallus height in the middle; **air chambers** 2–3-layered in the middle. **Ventral tissue in hygromorphorphic shoots** parenchymatous, consisting of thin-walled cells, occupying ca. 1/3–1/2 the thallus thickness in the middle and absent beneath the wing. **Midrib in hygromorphic shoots** relatively well defined, thallus over midrib 400–600 µm thick in cross-section; gradually tapering laterally into wings; **midrib in xeromorphic shoots** wide, thick, fleshy; thallus over midrib 300–450 µm thick in cross section. **Rhizoids** smooth and pegged, hyaline, covering ventral surface of midrib of thallus. **Ventral scales** in several irregular longitudinal rows, not overlapping, purple or reddish to rose, triangular to more or less lunate; **body size** 500–800(–900) µm long and 650–925 µm wide; **body cells size** 45–65(–72) µm long and 15–30 µm wide, with numerous scattered oil-cells, 25–30 µm in diameter; **appendage** one per ventral scale, oblong to lanceolate, hyaline or reddish; **appendage size** (300–)350–450 µm long and (100–)150–200 µm wide, without oil-cells; **appendage apex** obtuse to shortly acuminate; **appendage margin** crenate to denticulate. **Sexual condition** ventral-male autoicous. **Antheridia** forming in dorsal, compact cushions, situated on small heart-shaped ventral branches with smaller than vegetative and female branches; **disc** elliptical to circular, surrounded by a few reddish linear scales; **ostioles** conspicuously conical. **Gynoecia** arising from apex notch of leading thallus; **stalk of receptacle** delicate, pale purple and hyaline, smooth, 10–15 mm long, with single rhizoidal furrow. **Archegonial scales** at apex numerous and forming ring, with a few scales towards base, when mature almost naked except apical part; lanceolate to almost linear, hyaline to pinkish, apex with a single slime papilla, with margin entire, except for occasional slime-papillae, lacking oil-cells. **Carpocephalum** disk-like or umbrella-shaped, green to grayish-green frequently with reddish tint; **disc** flat to convex, with 4–5 lobes (very rarely 6–7-lobed), unequal in size; more or less rectangular, moderately deep, each involucre with a single sporophyte; **involucres margin** entire; **pseudoperianth** colorless to hyaline or slightly rose, undivided at basal part, 9–12-lobed, lobes lanceolate, mostly free at maturity towards the base. **Spores** yellow; 55–85 µm in diameter, distal face with not many, large, with almost smooth ornamented alveolae, trilete, distal surface areolated. **Elaters** 2-spiral, 220–250 µm long, 10–12 µm wide, yellowish.

Ecology. Neutrophilic to acid tolerant meso-xerophyte, one of the most common representatives of Marchantiales in southern flank of the Russian Far East. It occupies dry to mesic fine soils filled cliff crevices near (although aside of direct impact of running water) or far of watercourses, sometimes growing in manmade habitats in road rock cuts. The species prefers open to semi-shaded habitats in broadleaved deciduous forests (in the Russian Far East) to evergreen forests in subtropical and temperate belts southward.

Distribution. *Asterella leptophylla* is temperate-subtropical Asian species covering Paleo-Tethyan area in Pakistan, India, Nepal, Bhutan and widely spreading to oceanic East Asia and South-East Asia as to Indonesia, Philippines, China, Korea, Japan (Long, 2006), with

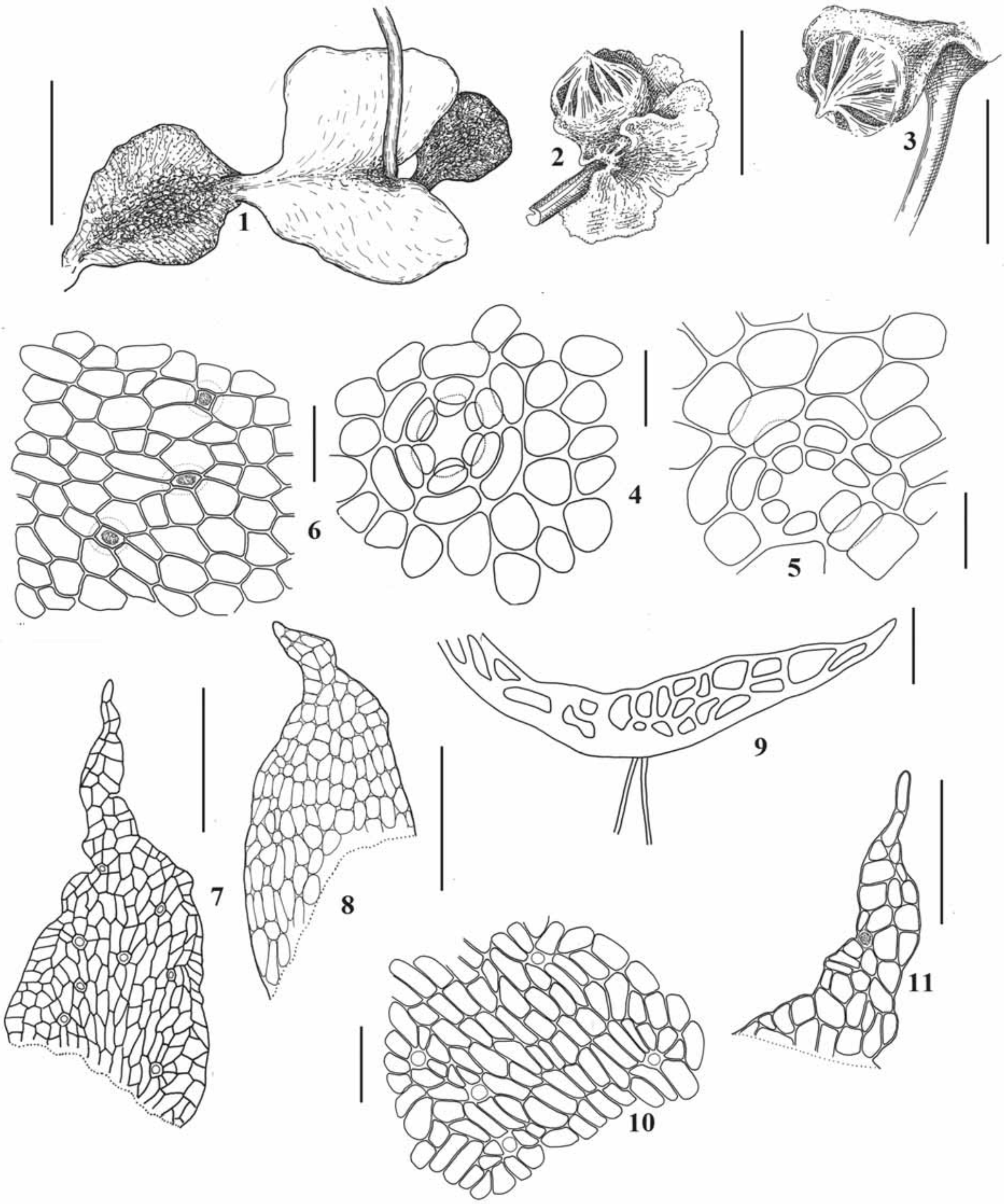

Fig. 5. *Asterella leptophylla* (Mont) Grolle (1, 4-5 – from Primorsky Territory, Schkotovsky District, Smol'nyj Klyuch Stream valley, *Bakalin* P40-24-12 (VBGI); 2-3, 6-7 – ibidem, P40-21-12 (VBGI); 8-11 – from Primorsky Territory, Lazo State Reserve, *Bardunov,* 23.IX.1974, (KPABG #116201). 1 – habit of plant, dorsal view; 2-3 – carpocephalum of female receptacle; 4-5 – airpore from dorsal epidermis of thallus; 6 – part of thallus dorsal epidermis with oil-bodies; 7-8 – ventral scales with appendages; 9 – thallus transverse section; 10 – median part of ventral scale; 11 – appendage of ventral scale. Scale bars: 3 mm for 1; 2 mm for 2-3; 400 µm for 9; 300 µm for 7-8; 150 µm for 11; 80 µm for 6; 60 µm for 10; 40 µm for 4-5.

the northernmost localities in the Russian Far East. *Asterella leptophylla* was included to the Red Data Book of Russia as rare species (Bakalin, 2008), being known in that time from limited number of localities in Primorsky Territory (many of which were re-identified for *A. cruciata*, see above). Nowadays many additional localities of this species were revealed and we suggest this species cannot be regarded as a rarity in the Ruissian flora, although it is limited in distribution by the southern flank of the Russian Far East (doubtless reflecting southern relation of Russian liverwort flora) that should be explained by climatic and phytogeographic reasons.

Specimens examined. **RUSSIA: Primorsky Territory,** Khasan District, Kedrovaya Pad‘ State Reserve, 9.IX.1953, Voroschilov (MHA, det. R. Grolle); ibidem, 9.IX.1978, Bardunov (VBGI); ibidem, 10.IX.1978, Bardunov (VBGI, KPABG #104746); ibidem, 13.X.1974, Bardunov (VBGI); ibidem, 16.X.1974, Bardunov (VBGI, IRK, KPABG #116199); ibidem, 18.VIII.1977, Gambaryan (VBGI, det. R. Grolle); ibidem, 19.VIII.1982, Gambaryan (VBGI, det. R. Grolle); ibidem, Kedrovka River, 8.IX.2002, Potemkin & Kotkova #2163 (LE); Gamov‘s Peninsula, Vityaz‘ Bay, 13.X.1978, Bardunov (VBGI, det. R. Grolle); Kravtsovka Village, Kravtsoka‘s waterfalls area, 20.IX.2010, Bakalin #P46-4-10 (VBGI); Vladivostok City, 31.VIII.1962, Bardunov (VBGI, det. R. Grolle); Botanical Garden-Institute, in 1 km from road Vladivostok-Khabarovsk, 18.X.2003 Bakalin (KPABG #105670); Partizansk District, Lozovyj Settlement, 13.IX.1974, Bardunov (VBGI); ibidem, 13.IX.1974, Bardunov & Cherdantzeva (VBGI, IRK, KPABG #104747); Schkotovsky District, Livadijsky Range, Litovka (Falaza) Mt., Smol‘nyj Klyuch Stream valley, 18.IX.2012, Bakalin P40-20-12, 40-21-12, 40-24-12 (VBGI); ibidem, 20.IX.2012 Bakalin P43-21-12 (VBGI); Lazo District, Alekseevsky Range, area near the top of Olkhovaya Mt., 4.X.2006, Bakalin P66-12-06 (VBGI); ibidem, Elomovsky stream, area near Benevskiye waterfalls6.X.2006, Bakalin #P68-32a-06 (VBGI, as *Reboulia hemisphaerica*); Przhevalskogo Range, 6.IX.2010, Mamontov Prim-104 (KPABG); Ol‘ginsky District, Moryak-Rybolov, 11.IX.1977 Bardunov (KPABG #104744, VBGI, det. R. Grolle); ibidem, Lazo State Reserve, middle course of Perekatnaya River, , 23.IX.1974, Bardunov (VBGI, IRK, KPABG #116201); ibidem, south-eastern spoor of Snezhnaya Mt. in the head of Ostantsovyj Stream, 18.IX.2007, Bakalin P-77-14-07 (VBGI; Hepaticae Rossicae Exsiccatae, VII, #153). **REPUBLIC OF KOREA: Kyong-Nam Province**, Chiri Mts. National Park, lower course of Jungsan-ri Steram, 13.VI.2009, Bakalin Kor-3-1-09, Kor-3-2-09 (VBGI).

Asterella subgen. **Saccatae** (Grolle) D.G. Long, J. Bryol. 22: 113. 2000.

Thalli thick, leathery, of strongly xeromorphous habit; not aromatic, regularly dichotomously branched, sometimes with ventral innovations at apex. Aerenchyma well-developed, compact; air chambers narrow, 1(–2)-layered in the middle, but narrowly elongated towards margins and 1-layered in the wings; with a few free filamentous. Ventral scales with 1–2 hyaline appendages per scale; lanceolate to oblong-lanceolate, entire or dentate. Sexual condition paroicous, rarely terminal-autoicous. Androecia forming low elliptical to elongated median group or rarely as 1–2 ostiole. Carpocephalum conical-hemispheric, shortly-lobed, involucre margins free, with broad bluntly V-shaped median incisure, margin weakly sinuate. Spores yellow-brownish color, on distal surface with weak primary wavy minutely reticulate lamellae.

Type: *Asterella saccata* (Wahlenb.) A. Evans

Asterella saccata (Wahlenb.) A. Evans, Contr. U.S. Natl. Herb. 20: 276. 1920. – *Marchantia saccata* Wahlenb., Ges. Naturf. Freunde Berlin Mag. Neuesten Entdeck. Gesammten Naturk. 5: 296. 1811. – *Fimbraria saccata* (Wahlenb.) Nees, Horae Phys. Berol. 45. 1820. – *Hypenantron saccatum* (Wahlenb.) Trevis, Memor. del‘ Inst. Lombardo Sci e Let. 4: 440. 1887. – *Marchantia fragrans* Schleich., [Pl. Crypt. Exsic. Hedvet. 3: 64. 1805, *nom. nudum*] ex DC in Lam. & DC, Fl. Fr. 4:423. 1805. *hom. illeg*. non Balb. 1804. – *Hypenantron ciliatum* Corda, Naturalientausch [12] (Beitr. Naturg. [1]): 648. 1829. – *Marchantia umbonata* Wallr., Linnaea 14: 686. 1841[1840]. – *Fimbraria umbonata* (Wallr.) Wallr., [Linnaea 14: 686. 1841, *nom. nudum*] ex Nees in Gottcsche, Lindenberg & Nees, Syn. Hepat. 559. 1846. – *Hypenantron umbonatum* (Wallr.) Trevis., Memor. Inst. Lomb. Sci. Let. 4: 440. 1887. – *Fimbraria fragrans* Nees, Horae Phys. Berol. 45. 1820. *p.p.* – *Hypenantron fragrans* Trevis., Herb. Crypt. Trevis. 32, 1853. – *Asterella fragrans* Trevis., Rend. ist. Lomb. 7:785. 1874. (Fig. 6).

Illustrations: Frye & Clark, 1937 (p. 77); Müller, 1954 (p. 355, fig. 68, as *Fimbraria saccata*); Schljakov, 1982 (p. 94, fig. 34 (1 a-â); p. 95, fig. 35 (1 a-â); Schuster, 1992 (p. 258, fig. 957; p. 262, fig. 958 (1-10); Long, 2006 (p. 92, fig. 11); Damsholt, 2013 (p.559, fig. 185). **Map:** Long, 2006 (p. 134, fig. 33).

Description (Fig. 6): **Thalli** thick, leathery, medium-sized, 5–10 mm long, 1–4 mm wide (near apex up to 5–6 mm wide), forming more or less pure patches, strongly xeromorphous habit, non aromatic, regularly dichotomously branched, sometimes with ventral innovations at apex; **segments** oblong to lingulate-obcordate; **apex** strongly notched, with conspicuous whitish ventral scale appendages forming white beard-like cluster; **upper surface** not reticulate, concave, rarely almost flat; **color of upper surface** green to grayish-green and ochre-yellow in older parts; **thallus margins** undulate, reddish to dark-purplish or whitish, strongly erect and/or inrolled in dry condition. **Dorsal epidermis** delicate, mostly colorless; **cells** 20–30×10–16 µm; **cell walls** thin to slightly thickened, with small concave trigones; **oil-cells** scattered in epidermis; **cuticle** smooth; **pores** simple, moderately elevated above epidermis, (10–)15–25 µm in diameter, surrounded by 2(–3) concentric rings of 6–7 cells in each, cell walls thin. **Aerenchyma** well-developed, compact, subdivided, occupying ca. 1/4 to 1/2 of the thallus height in the middle and all of height in the wings; **air chambers** narrow, 1(–2)-layered in the middle, but narrowly elongated towards margins and 1-layered in the wings, with a few free filaments. **Ventral tissue** parenchymatous, consisting of thin-walled cells, occupying ca. 1/2–3/4 the thallus thickness in the middle and almost absent beneath the wing; with scattered oil-cells both in aerenchyma and ventral tissue; **oil-cells** yellow-purple, globose, (15–)17–30 µm in diameter, rarely elliptical, 30–35×30–32 µm. **Midrib** prominent, broadly rounded or bluntly keeled, gradually narrowed to thinner wings, thick, thallus over midrib 600–950 µm thick in cross-section. **Rhizoids** smooth and pegged, hyaline or rose to brownish, covering ventral surface of midrib of thallus. **Ventral scales** dark red to purplish; they are attached to

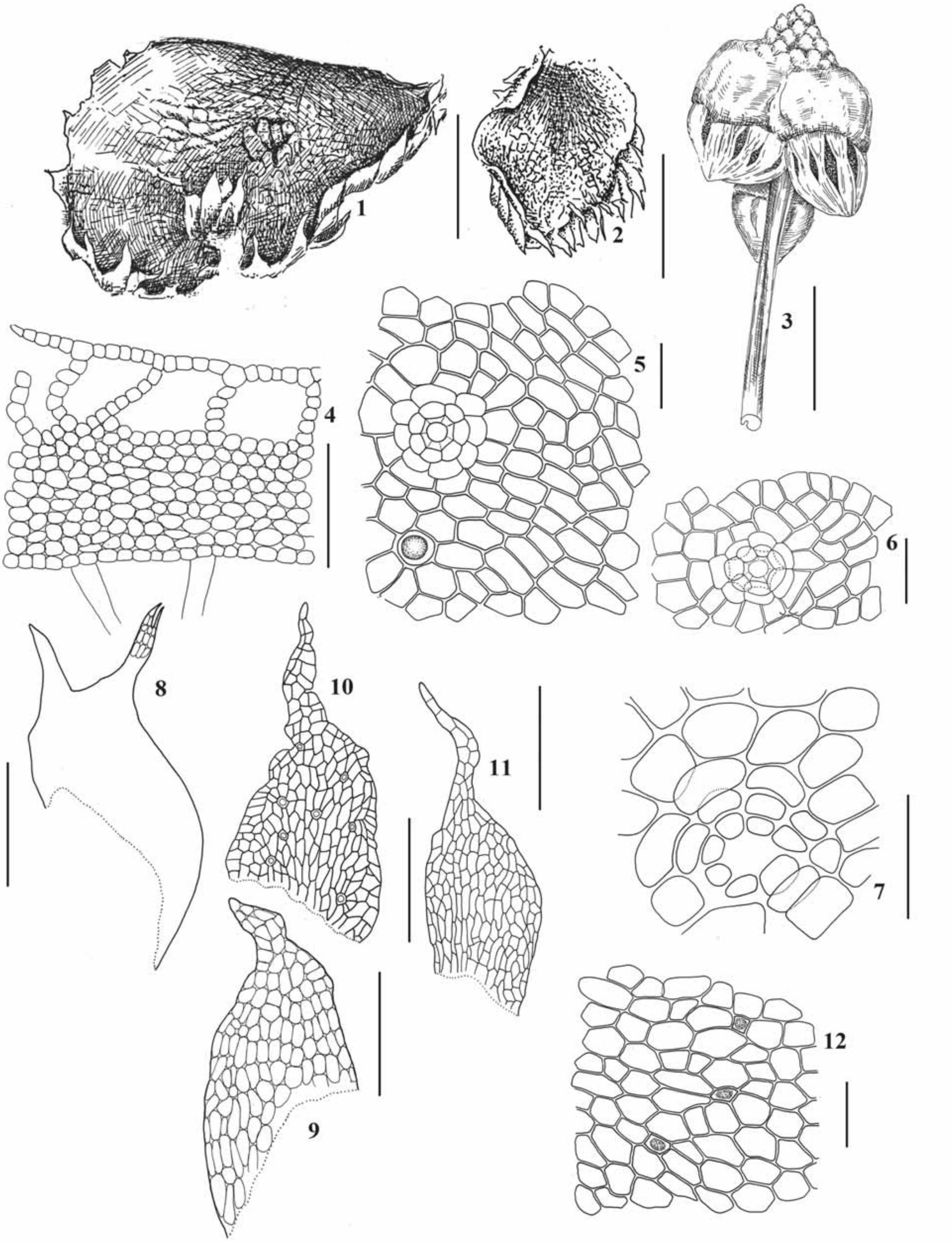

Fig. 6. *Asterella saccata* (Wahlenb.) A. Evans (All from Altay Republic, Altay State Nature Reserve, *Zolotukhin, Tyaplyakova*, 27.IV.1978 (MHA). 1-2 – habit of plant, dorsal view; 3 – carpocephalum of female receptacle; 4 – median part of thallus transverse section; 5-7 – air-pore from dorsal epidermis of thallus; 8-11 – ventral scales with appendages; 12 – median part of ventral scale with oil-bodies. Scale bars: 2 mm for 1-3; 600 µm for 8-11; 500 µm for 4; 50 µm for 5-7, 12.

the middle of the lower side of the thallus, so clearly expressed strip midline between the bases of the scales along the thallus is free from ventral scales; rounded triangular to obliquely semilunate; **body** 1100–1800 µm long and 500–750 µm wide, marginal slime papillae numerous; **body cells** 50–80(–100) µm long and 20–30 µm wide, with numerous scattered pale oil-cells; **oil cells** 22–30 µm in diameter; **appendage** 1–2 per scale, lanceolate to oblong-lanceolate, hyaline; **appendage** 500–900 µm long and 200–300 µm wide, quickly tapering above broad base; slime- papillae absent. **Sexual condition** paroicous, rarely terminal-autoicous. **Antheridia** arising dorsally on leading thallus shortly behind the female receptacle or rarely on separate terminal branch; forming low elliptical to elongated median group, rarely as 1–2 ostiole; **ostioles** conical, greenish to purplish, without scales. **Gynoecia** arising in apical notch of leading thallus; **stalk of receptacle** yellowish to rarely robust, smooth, 5–15 mm long, with single rhizoidal furrow. **Archegonial scales** at base numerous, forming conspicuous dense cushion of hyaline scales and a few at apex, almost linear to filiform, margin entire. **Carpocephalum** conical-hemispheric, green to yellowish-green; **disc** convex, shortly 2-4-lobed, each with a single sporophyte, lobes almost vertical or up to 20° to stalk; **involucres margin** free, with broad bluntly V-shaped median incisures, margin weakly sinuate; **pseudoperianth** white, compressed laterally when young and with strongly connate apical part of lobes when mature, with free margins recurved when dry. **Spores** yellow-brown, globose, (85–)90–105 µm in diameter, on distal surface with weak primary wavy lamellae with minute reticulations. **Elaters** 2-spiral, yellowish, 170–210 µm long, 15–18 µm wide.

Differentiation. When lacking female receptacle the species is most likely to be mistaken with *Mannia fragrans* because of similarity of general habit in dry condition: whitish brush of scales at apex of female branches and usually blackish and enrolled (when dry) thallus. *A. saccata* differs from *Mannia fragrans* in: 1. not fragrant thalli in fresh conditions versus commonly aromatic (cedar-oil smell) in *M. fragrans*; 2. thin to slightly thickened cell walls of dorsal epidermis, with small trigones versus thickened cell walls and large to bulging trigones in *M. fragrans;* 3. margin of ventral scales without slime-papillae versus margin of ventral scales with a few marginal slime-papillae in *M. fragrans*; 4. ventral scales are situated at some distance from the middle of thallus lower side in such a way that there is clearly expressed strip on both sides of middle ridge of thallus free from ventral scales versus ventral scales on either side of the midrib, strongly overlapping in *M. fragrans*.

Sometimes*, Asterella saccata* may be misidentified as *A. lindenbergiana*. However, *A. saccata* differs from latter in: 1. lacking rotten fish smell versus obvious smell of rotten fish in fresh condition in *A. lindenbergiana*; 2. smaller thallus of 1–4 mm wide only, versus 4–8 mm wide in *A. lindenbergiana*; 3. presence of apical cluster conspicuously projecting appendages of ventral scales versus appendages of scale not forming a white cluster at apex; 4. margins of thallus strongly incurved when dry versus often only slightly enrolled margins of thallus in dry condition.

Ecology. Calciphilous xerophyte, growing in open to full sun places in S- to SW-faced cliff crevices filled with fine soil; mostly in alpine belt or tundra zone. The species often forms more or less pure mats often with an admixture of other hepatics, or, sometimes, hidden between mosses.

Distribution. *Asterella saccata* is arctomontane subcircumpolar species whose area covers subalpine to alpine belts in large mountainous systems in Eurasia and North America (Schuster, 1992; Long, 2006; Damsholt, 2013). Recent revision by Long (2006) confirmed the species in Eurasia for Austria, Switzerland, Czech Republic, Slovakia, Italy, Makedonia, Hungary, Germany), eastward to Russia and China (Xinjing). Older records (not all of the specimens on which these records were based were checked by Long, l.c., thus we cannot eliminate them) includes Spain, France, Romania, Poland (Söderström *et al*., 2002) and Greece (Bory, 1832). The species also occurs in North America, where known from Yukon, British Columbia (Canada) and Alaska, Idaho, Montana, Washington, Oregon, Wyoming, New Mexico (U.S.A.), Mexico (Schuster, 1992) and Greenland (Schuster & Damsholt 1974; Damsholt, 2013). The species was also provisionally reported by Zerov (1964) for Ukraine, but still time the occurrence in the country was not confirmed. *Asterella saccata* was known in the Russia from European part: Perm‘ Province (Lindberg & Arnell, 1889; Long, 2006), Siberia: Krasnoyarsk Territory (Lindberg & Arnell, 1889; Konstantinova & Vasiljev, 1994; Long, 2006), Altay Republic (Váňa & Ignatov, 1995), Republic of Yakutiya (Sofronova, 2005), Chukotka Autonomous District (Afonina & Duda, 1993; Afonina, 2000), Kamchatka Territory (Wahlenberg, 1811; Bakalin, 2009), Amur Province (Lindberg & Arnell, 1889; Long, 2006; Andrejeva, 2009). According to personal communication of Dr. E.V. Sofronova the record of *Asterella saccata* for Resource Reserve «Orulgan Sis» (North-Eastern Yakutia) (Sofronova & Sofronov, 2012) should be referred to *A. lindenbergiana*.

In the course of the present research we were able to identify this species for Altay Republic, Krasnoyarsk Territory and Chukotka Autonomous District. It is noteworthy that this species was described from Avacha Bay in the Kamchatka Peninsula based on collections by H. Tilesius (Wahlenberg, 1811), however numerous attempts to collect it in *locus classicus* by Bakalin have failed. On the contrary, Bakalin found as more or less frequent in that area *Mannia gracilis.* This was described four years later as *Marchantia gracilis* (Weber, 1815) and might be easily mistaken with *Asterella saccata*. We could not study the type of *A. saccata* and Long (2006) did not cite the type specimen too (probably it was lost), since it is rather puzzling question whether the widely accepted understanding of *Asterella saccata* in modern literature is really congruent with the original treatment of *Marchantia saccata* by Wahlenberg.

***Specimens examined*. RUSSIA: Altay Republic**, Altay State Nature Reserve, Chulyshman Stream, 27.IV.1978, Zolotukhin, Tyaplyakova (MHA, KPABG, VBGI); **Krasnoyarsk Territory,** Krasnoyarsk City vicinity, Vereschagin, det. 17.VI.1936 Zerov (KW, KPABG); **Chukotka Autonomous District**, Pekul'ney Range, middle part of the Yuzhnij Pekul'nejveem River, 14.VIII.1979, Afonina (LE; KPABG); Anadyr River Basin, Enmyvaam River, 4.VII.1982, Afonina (LE; KPABG).

ACKNOWLEDGEMENTS

We are greatly indebted to the curators of LE (Dr. A. Potemkin), MHA (Dr. M. Ignatov), IRK (Dr. S. Kazanovskij), TUR (Dr. S. Huhtinen) and KW (Dr. V. Virchenko) for specimens loan. Authors are sincerely grateful to Dr. D. Long (E) for confirmation of the identification of *Asterella cruciata* as well as for comments and English improvement. We thank Dr. M. Ignatov as well as Dr. Yu. Mamontov for helpful criticism and suggestions. The figures were kindly prepared by Mr. M. Bakalin, to whom authors are sincerely grateful. The work was partially supported by the Russian Foundation of Basic Researches (grants no. 13-04-00775, 15-04-03479, 15-34-20101) and President's Program for support of PhD researches (МК-2926.2015.4).

LITERATURE CITED

[AFONINA, O.M.] АФОНИНА О.М. 2000. Мохообразные. – [Bryophytes] *В кн: Флора и фауна заповедников. Вып. 88. Мохообразные и лишайники заповедника "Остров Врангеля" (ред. Корнеева Т.М.)* [*In: Korneeva, T.M. (ed.) Flora i fauna zapovednikov. 88. Mokhoobraznye i lishajniki zapovednika "Ostrov Vrangelya"*] *M., Гриф и К°* [*Moscow, Grif & Co*]*: 6–46.*

[AFONINA, O.M. & J. DUDA] АФОНИНА О.М., Й. ДУДА. 1993. Печеночные мхи Чукотки. – [Liverworts of Chukotka] *Ботанический журнал* [*Botanicheskij Zhurnal*] **78**(3): *77–93.*

ALLORGE, V. 1956. Sur quelques Muscinees du Pic de Midi-de-Bigorre (Pyrénées Centrales). – *Revue Bryologique et Lichénologique* **25**: *304–307.*

ANDREJEVA, E.N. 2009. New rare liverwort records from Russian Federation Regions. – *Arctoa* **18**: *281–286.*

[BAKALIN, V.A.] БАКАЛИН В.А. 2008. *Asterella leptophylla* (Mont.) Grolle. – *В кн.: Красная книга Российской Федерации (растения и грибы) (ред. Л.В. Бардунов, В.С. Новиков)*[*In: Bardunov, L.V. & V.S. Novikov (eds.) Red-list of Russian Federation (plants and fungi)*] *Москва* [*Moscow*]: *638–639.*

[BAKALIN, V.A.] БАКАЛИН В.А. 2009. Флора и фитогеография печеночников Камчатки и прилегающих островов. – [Flora and phytogeography of liverworts of Kamchatka and adjacent islands] *M., КМК* [*Moscow, KMK Scientific Press*], *250 pp.*

BOROVICHEV, E.A. 2011. New liverwort records from Murmansk Province. 3. – *Arctoa* **20**: *247.*

BOROVICHEV, E.A. & V.A. BAKALIN. 2013. New national and regional bryophyte records. *Asterella lindenbergiana* (Corda ex Nees) Lindb. ex Arnell (Southern Far East, Russia). – *Journal of Bryology* **35**(3): *228.*

[BOROVICHEV, E.A. & S.A. NYPORKO] БОРОВИЧЕВ Е.А., С.А. НЫПОРКО. 2014. Три таксона из семейства Aytoniaceae (Marchantiophyta) новые для флоры печеночников Украины. – [Three new for the Ukrainian liverwort flora taxa of the family Aytoniaceae (Marchantiophyta)] *Украинский ботанический журнал* [*Ukrainian Botanical Journal*] **71**(1): *66–70.*

BORY DE SAINT-VINCENT, J.B.G.M. 1832. Hepaticae. – *In.: Expedition scientifique de Moree, Section des Sciences Physiques (3)2 Botanique*: *296–300.*

DAMSHOLT, K. 2002. Illustrated flora of Nordic liverworts and hornworts. – *Nordic Bryological Society, Lund*, *840 pp.*

DAMSHOLT, K. 2013. The liverworts of Greenland. – *Nordic Bryological Society, Lund*, *626 pp.*

EVANS, A.W. 1920. The North American species of *Asterella*. – *Contributions from the United States National Herbarium* **20**: *247–312.*

EVANS, A.W. 1923. Family 5. Rebouliaceae. – *In: North American Flora. New-York: New York Botanical Garden*. **14**(1): *39–56.*

FRYE, T. C. & L. CLARK. 1937. Hepaticae of North America. Part I. – *University of Washington Publications in Biology* **6**: *1–162.*

GOLOBOFF, P., FARRIS, S. & K. NIXON. 2003. T.N.T.: Tree analysis using New Technology. Program and documentation. – *Available from the authors, and at www.zmuc.dk/public/phylogeny.*

GROLLE, R. 1976. Verzeichnis der Lebermoose Europas und benachbarter Gebiete. – *Feddes Repertorium* **87**: *171–279.*

GROLLE, R. 1983. Nomina generica Hepaticarum; references, types & synonyms. – *Acta Botanica Fennica* **121**: *1–62.*

GUINDON, S., DUFAYARD, J.F., LEFORT, V., ANISIMOVA, M., HORDIJK, W., & O. GASCUEL. 2010. New Algorithms and Methods to Estimate Maximum-Likelihood Phylogenies: Assessing the Performance of PhyML 3.0. – *Systematic Biology* **59**: *307–321.*

HALL, T.A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. – *Nucleic Acids Symposium Series* **41**: *95–98.*

HOLLINGSWORTH, M.L., A. CLARK, L.L. FORREST, J. RICHARDSON, R.T. PENNINGTON, D. G. LONG, R. COWAN, M. CHASE, M. GAUDEUL & P.M. HOLLINGSWORTH. 2009. Selecting barcoding loci for plants: Evaluation of seven candidate loci with species level sampling in three divergent plant groups. – *Molecular Ecology Resources* **9**: *439–457.*

INOUE, H. 1976. Illustrations of Japanese Hepaticae. – *Tsukiji Shokan, Tokio* **2**: *1–193.*

IWATSUKI, Z. (ed.). 2001. Mosses and Liverworts of Japan. – *Heibonsha, Tokyo: 355 pp.* (in Japanese).

KEANE, T.M., NAUGHTON, T.J. & J.O. McINERNEY. 2004. Model-Generator: amino acid and nucleotide substitution model selection. – *http://bioinf.may.ie/software/modelgenerator.*

KONSTANTINOVA, N.A. & V.A. BAKALIN, E.N. ANDREJEVA, A.G. BEZGODOV, E.A. BOROVICHEV, M.V. DULIN, YU.S. MAMONTOV. 2009. Check-list of liverworts (Marchantiophyta) of Russia. – *Arctoa* **18**: *1–63.*

KONSTANTINOVA, N.A., T. AKATOVA & A.N. SAVCHENKO. 2009. Hepatics of Caucasian State Nature Reserve (North-west Caucasus, Russia). – *Arctoa* **18**: *121–134.*

KONSTANTINOVA, N.A. & A.N. VASILJEV. 1994. On the hepatic flora of Sayan Mountains (South Siberia). – *Arctoa* **3**: *123–132.*

KONSTANTINOVA, N.A. & A.A. VILNET. 2014. New liverwort records from Chukotka Autonomous District. 1. – *In: Sofronova E.V. (ed.) New bryophyte records. 3, Arctoa* **23**: *234–235.*

KOPONEN, T., P. ISOVIITA & T. LAMMES. 1977. The bryophytes of Finland: an annotated checklist. – *Flora Fennica* **6**: *1–77.*

LINDBERG, S.O. & H.W. ARNELL. 1889. Musci Asiae Borealis. – *Kongliga Svenska Vetenskaps Academiens Handlinga* **23**(10): *163 pp.*

LONG, D.G. 2001. Studies on the genus *Asterella* (Aytoniaceae). V. Miscellaneous notes on Asiatic Asterella. – *Lindbergia* **26**: *43–45.*

LONG, D.G. 2005. Studies on the genus Asterella (Aytoniaceae). VI. infrageneric classification in Asterella. – *Journal of the Hattori Botanical Laboratory* **97**: *249–261.*

LONG, D.G. 2006. Revision of the genus *Asterella* P. Beauv. in Eurasia. – *Bryophytorum Bibliotheca* **63**: *1–299*.

LONG, D.G., M. MOELLER & J. PRESTON. 2000. Phylogenetic relationships of *Asterella* (Aytoniaceae, Marchantiopsida) inferred from chloroplast DNA sequences. – *Bryologist* **103**: *625–644*.

MÅRTENSSON, O. 1955. Bryophytes of the Torneträsk Area, Northern Swedish Lappland. I. Hepaticae. – *Almqvist & Wiksells boktryckeri AB, Stockholm*, *107 pp.*

MÜLLER, K. 1954. Die Lebermoose Europas. – *In: Rabenhorst's Kryptogamenflora von Deutschland, Österreich und der Schweiz. 3. Auflage* **6**(1): *1–756*.

MÜLLER, K. 2005. SeqState. Primer design and sequence statistic for phylogenetic DNA datasets. – *Advances and Applications in Bioinformatics and Chemistry* **4**: *65–69*.

PATTENGALE, N.D., M. ALIPOUR, O.R.P. BININDA-EMONDS, B.M.E. MORET & A. STAMATAKIS. 2010. How many bootstrap replicates are necessary? – *Journal of Computational Biology* **17**: *337–354*.

RAMBAUT, A. & A.J. DRUMMOND. 2007. Tracer v1.4. – *http://beast.bio.ed.ac.uk/Tracer.*

RONQUIST, F., M. TESLENKO, P. VAN DER MARK, D.L. AYRES, A. DARLING, S. HÖHNA, B. LARGET, L. LIU, M.A. SUCHARD & J.P. HÜLSENBECK. 2012. MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. – *Systematic Biology* **61**: *539–542*.

SCHILL, D.B., D.G. LONG & L.L. FORREST. 2010. A molecular phylogenetic study of *Mannia* (Marchantiophyta, Aytoniaceae) using chloroplast and nuclear markers. – *Bryologist* **113**(1): *164–179*.

[SCHLJAKOV, R.N.] ШЛЯКОВ Р.Н. 1982. Печеночные мхи Севера СССР. – [The Hepatics of the North of the USSR] *Л., Наука* [*Leningrad, Nauka*] **5**: *1–196*.

SCHUSTER, R.M. 1992. The Hepaticae and Anthocerotae of North America east of the hundredth meridian. Vol. 6. – *Chicago, 937 pp.*

SCHUSTER, R.M. & K. DAMSHOLT. 1974. The Hepaticae of West Greenland from ca. 66° N to 72° N. – *Meddelelser om Grønland* **199**(1): *5–373*.

SHAW, A.J. 2000. Phylogeny of the Sphagnopsida based on chloroplast and nuclear DNA sequences. – *Bryologist* **103**: *277–306*.

SHIMIZU, D. & S. HATTORI. 1952. Studies on the Japanese species of *Asterella* (1). – *Journal of the Hattori Botanical Laboratory* **8**: *46–54*.

SHIMIZU, D. & S. HATTORI. 1953. Studies on the Japanese species of *Asterella* (2). – *Journal of the Hattori Botanical Laboratory* **9**: *25–31*.

SÖDERSTRÖM L. 1995. Preliminary distribution maps of bryophytes in Norden. – *In: Hepaticae and Anthocerotae. Trondheim, 51 pp.*

SÖDERSTRÖM, L., E. URMI & J. VÁŇA. 2002. Distribution of Hepaticae and Anthocerotae in Europe and Macaronesia. – *Lindbergia,* **27**: *3–47.*

[SOFRONOVA, E.V.] СОФРОНОВА Е.В. 2005. Печеночные мхи. – [Liverworts] *В кн: Разнообразие растительного мира Якутии (ред. Данилова Н.С.)* [*In: Danolova, N.S. (ed.) Raznoobrazie rastitelnogo mira Yakutii*] *Новосибирск, СО РАН* [*Novosibirsk, Sib. Div. of Russ. Acad. Sci.*]: *92–104*.

[SOFRONOVA, E.V. & R.R. SOFRONOV] СОФРОНОВА Е.В., Р.Р. СОФРОНОВ. 2012. Печеночники ресурсного резервата «Орулган-Сис» (хребет Орулган, Ссеверо-восточная Якутия). – [The liverworts of the Orulgan Resource Reserve (Orulgan Ridge, North-Eastern Yakutia)] *Ботанический журнал* [*Botanicheskij Zhurnal*] **97**(4): *487–496*.

STAMATAKIS, A. 2006. RAxML-VI-HPC: Maximum Likelihood-based Phylogenetic Analyses with Thousands of Taxa and Mixed Models. – *Bioinformatics* **22**: *2688-2690*.

TABERLET, P., L. GIELLY, G. PAUTOU & J. BOUVET. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. – *Plant Molecular Biology* **17**: *1105–1109*.

TAMURA, K., D. PETERSON, N. PETERSON, G. STECHER, M. NEI & S. KUMAR. 2011. MEGA 5: Molecular Evolutionary Genetics Analysis Using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Method. – *Molecular Biology and Evolution* **28**: *2731–2739*.

VÁŇA, J. & M.S. IGNATOV. 1995. Bryophytes of Altai Mountains. Preliminary list of Altaian hepatics. – *Arctoa* **5**: *1–14*.

WAHLENBERG, G. 1811. Kamtschadalische Laub- und Lebermoose, gesammelt auf der russischen Entreckungstreise von dem Herrn Hofrath Tilesius. – *Magazin für die neuesten Endeckungen in der gesammten Naturkunde* **5**: *289–297*.

WEBER, F. 1815. Historiae Muscorum Hepaticorum Prodromus. – *Kiliae: 1–204*.

[ZEROV, D.K.] ЗЕРОВ Д.К. 1964. Флора печіночних і сфгнових мохів України. – [The flora of hepatics and peat-mosses of Ukraine]. *Київ* [*Kiev*]: *356 pp.*