Arctoa (2009) **18**: *151-162*

TWO NEW SPECIES OF JUNGERMANNIACEAE FROM ASIATIC RUSSIA
ДВА НОВЫХ ВИДА JUNGERMANNIACEAE ИЗ АЗИАТСКОЙ ЧАСТИ РОССИИ

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Abstract

Two species of Jungermanniaceae are described as new to science. *Solenostoma pseudopyriflorum* Bakalin et Vilnet is characterized by paroicous inflorescence, rigid shoots, purple colouration of a stem and leaf bases, as well as rhizogenous basal portion of the perianth. The species is most closely related to *S. pyriflorum*, but the latter has dioicous inflorescense and not so deep purple colour of a stem and basal portion of leaves. *Jungermannia konstantinovae* Bakalin et Vilnet is characterized by penta-plicate perianth, paroicous inflorescence, very oblique inserted leaves and prostrate growth form. The species is superficially most similar to *J. atrovirens*, but the latter species is dioicous and has a typical for *Jungermannia* fusiform perianth, that is gradually contracted to the mouth. *Solenostoma pyriflorum* is excluded from Russian flora, as all so-called collections belong to *S. pseudopyriflorum*. Also, *S. rishiriense* is excluded from the liverwort flora of Primorskij Territory and Sakhalin Island, as all collections from these regions were proved to be *S. pseudopyriflorum* as well. *Solenostoma pocsii* (Váňa) Bakalin *comb. nov*. is proposed

Резюме

Описаны два новых для науки вида из семейства Jungermanniaceae. *Solenostoma pseudopyriflorum* Bakalin et Vilnet характеризуется парецией, жесткими побегами, пурпурно окрашенными стеблем и основаниями листьев, а также ризоидами, образующимися в основании периантия. Вид наиболее близок к *S. pyriflorum*, который отличается двудомностью и отсутствием яркой пурпурной окраски стебля и оснований листьев. *Jungermannia konstantinovae* Bakalin et Vilnet характеризуется 5-складчатым периантием, парецией, очень косо прикрепленными листьями, стелющейся формой роста. По внешнему облику вид напоминает *J. atrovirens*, отличающийся от него двудомностью и типичным для рода веретеновидным периантием, постепенно сужающимся к устью. *Solenostoma pyriflorum* исключена из флоры России, поскольку все ее указания были основаны на образцах, относимых нами к *S. pseudopyriflorum*, а *S. rishiriense* исключена из флоры Приморского края и о-ва Сахалин, поскольку все имеющиеся указания относятся к *S. pseudopyriflorum*. Предлагается новая комбинация *Solenostoma pocsii* (Váňa) Bakalin *comb. nov*.

KEYWORDS: *Jungermannia, Solenostoma,* Hepaticae, taxonomy, *trn*L-F, Asia

Introduction

In the course of revision of liverwort flora of the Russian Far East we found specimens of *Solenostoma* and *Jungermannia* s. str., which do not fit any described species. To confirm the species status of both taxa we additionally used sequence analysis of *trnL-F* region of cpDNA.

Materials and methods

The present study is based on both traditional morphological studies as well as molecular phylogenetic analyses. At first, both species were recognized during the taxonomic revision of material from the Russian Far East. Later on, we verified our results by *trnL-F* cpDNA loci analyses.

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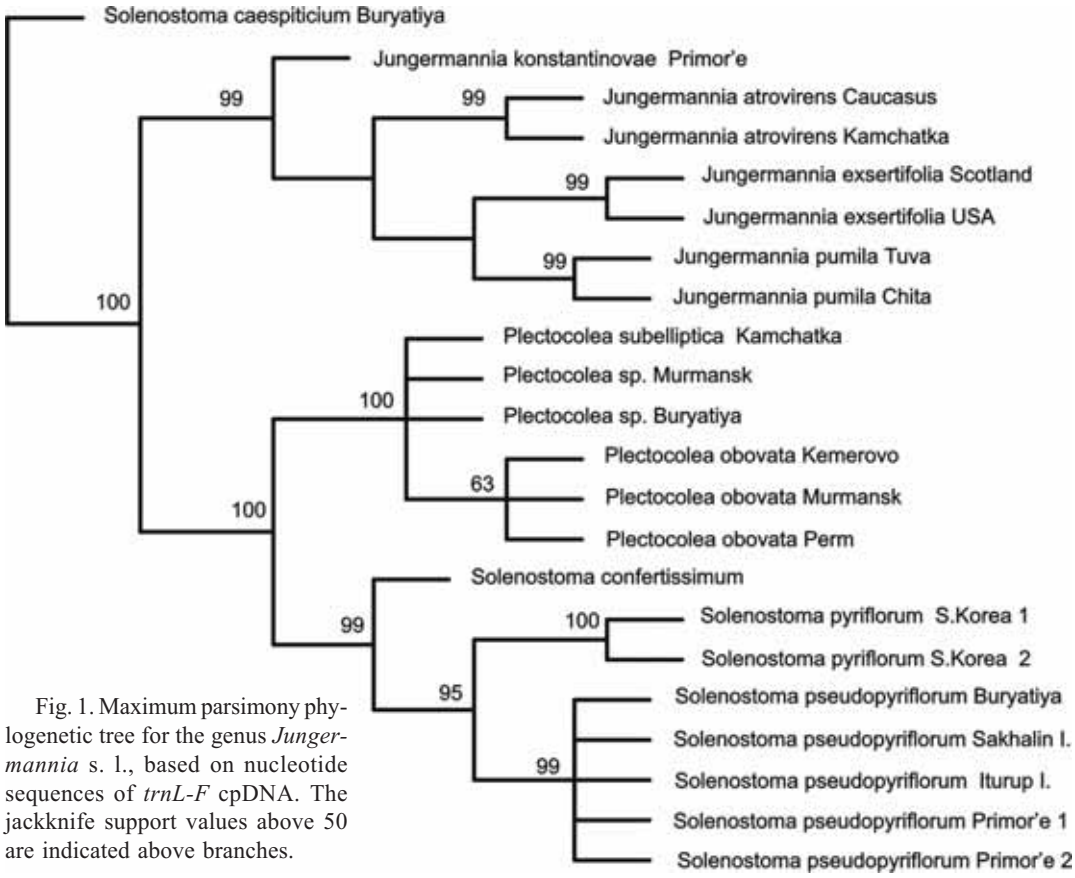

Fig. 1. Maximum parsimony phylogenetic tree for the genus *Jungermannia* s. l., based on nucleotide sequences of *trnL-F* cpDNA. The jackknife support values above 50 are indicated above branches.

For the study, we obtained sequences of *trnL-F* for five samples of *Solenostoma pseudopyriflorum* Bakalin & Vilnet (described below) from the Russian Far East and South Siberia. *Jungermannia konstantinovae* Bakalin & Vilnet (described below) is presented in analyses only by the plants from holotype. Previously studied closely related species with few additions from GenBank data were used for testing position of these putatively new species. Totally, the *trnL-F* sequences of 22 *Jungermannia* s.l. (including *Solenostoma* and *Plectocolea*) samples were analyzed. Specimen vouchers and GenBank accession numbers are given in Table 1. The protocol of DNA extraction and amplification was the same as in Vilnet et al. (2008). The sequences were aligned manually using the BioEdit program (Hall, 1999). Two analytical procedures were implemented for phylogenetic analysis: maximum parsimony method (MP) with the TNT program (Goloboff et al., 2003) and maximum likelihood (ML) method with the PHYML (Guindon & Gascuel, 2003). The parsimony analysis includes a New Technology Search with search minimal length tree by five reiterations, 2000 jackknife resamplings with deletion of 36% positions, gaps were treated as fifth nucleotide. The (GTR+Γ+I) model of nucleotide substitution and eight gamma rate categories were employed for phylogeny estimation by the ML method; support for individual nodes was assessed using a bootstrap resampling procedure with 2000 replicates.

Trees were rooted on *Solenostoma caespiticium*, a species obviously related to *Jungermannia* s.l., but in our opinion without a definite affinity to species of either *Jungermannia* s. str. or *Solenostoma*; its current placement in *Solenostoma* should be changed, but this problem is out of scope of the present paper.

RESULTS

The entire alignment of 22 sequences consists of 523 positions which were included into

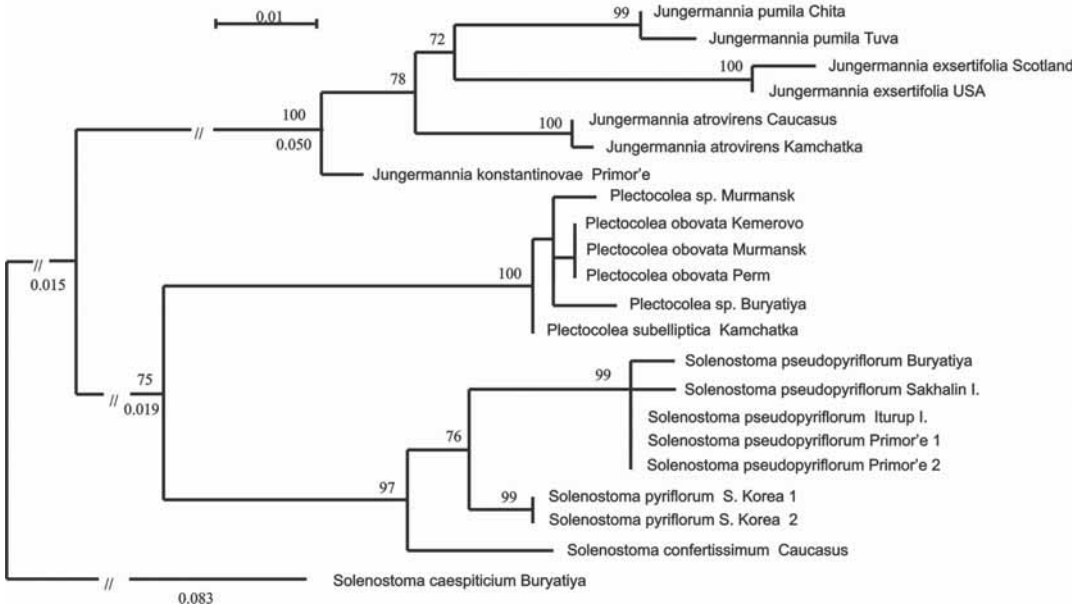

Fig. 2. Maximum likelihood phylogenetic tree for the genus *Jungermannia* s. l., based on nucleotide sequences of *trnL-F* cpDNA (loglk = -1569.046270). The bootstrap support values >50 are shown above branches and means of length for cut branches are indicated below branches.

analysis. Among them, 115 (21.0%) are variable, and 80 (15.3%) are parsimony informative.

The MP analysis with TNT yielded in three maximum parsimonious trees, L=300. The topology of its strict-consensus tree is identical with that of jackknife tree shown on Fig. 1.

The MP tree with jackknife supports is shown in Fig. 1. The ML calculation resulted in a tree with logL = -1569.046270 (Fig. 2).

Topologies of both trees are quite similar: *Jungermannia* s.str. is resolved in a clade sister to the clade with two subclades, one including species of *Plectocolea* and another one of *Solenostoma* species. Clades of all three genera have high support, in MP analysis of 99, 100 and 99 respectively, and in ML: 100, 100, and 97 (Figs. 1, 2). Within *Solenostoma* clade, *S. confertissimum* is sister to the clade formed by *S. pyriflorum* and *S. pseudopyriflorum*, each of them receiving support of 100 or 99, while the clade formed by both these species has support of 95 in MP and 76 in ML. The samples of *Jungermannia atrovirens*, *J. pumila* and *J. exsertifolia* compose its own clades within *Jungermannia* s.str. clade with support of 100 or 99. The common clade of *J. pumila* and *J. exsertifolia* is not supported in MP and in ML it obtained 72 bootstrap support. *Jungermannia atrovirens* is in sister relation to *J. pumila*+*J. exsertifolia* clade without support in MP and 78 bootstrap support in ML. The new described species *J. konstantinovae* takes a robust basal position in *Jungermannia* s.str. clade.

The length of *trn*L-F sequence of *S. pseudopyriflorum* is 475 bp, of *S. pyriflorum* 451 bp, being different in two indels (23 bp and 1 bp) in P8 stem-loop region of *trnL*-intron, seven substitutions in *trnL*-intron and three substitutions in intergenic spacer (Fig. 3). The specimen of *S. pseudopyriflorum* from Buryatiya has two substitutions in 5'-exon *trnL* and specimen from Sakhalin Island – two substitutions in *trnF* compared with other analyzed samples. The sequences of both *S. pyriflorum* samples are identical.

The length of *trn*L-F sequence of *J. konstantinovae* is 472 bp, *J. atrovirens* and *J. exsertifolia* – 471 bp, *J. pumila* – 464 bp. Two deletions (1 bp and 6 bp) in *trnL*-intron are found for *J. pumila* sequences (the sample downloaded from GenBank has two deletions by 1 bp in intergenic spacer). Both *J. atrovirens* and *J. exsertifolia* differ from *J. konstantinovae* in a single 1 bp deletion in *trnL*-intron. No specific indels and five specific substitutions in *trnL*-intron and one in

```
                  10         20         30         40         50         60         70         80         90
kon Prim.    TCGAAATCGG TAGACGCTAC GGACTTAATT TGATTGAGCC TTGGTCAAGA TATTGACTGA GTGATTGTTT CCATATTCAG GGAAATCTGG
atr Cauc.    .......... .......... .......... .C........ .C........ .......... .......... .......... ..........
atr Kamch.   .......... .......... .......... .C........ .C........ .......... .......... .......... ..........
pum Chita    .......... .......... .......... .T........ .C........ .......... .......... .......... ..........
pum Tuva     NNNNNNNNNN NNNNNNNNNN NNNNNNNNNN NNNNNNNNNN NNNN...... .......... .......... .......... ..........
exs USA      .......... .......... .......... .T........ .CA....... C......... .......... .......... ..........
exs Scot.    NNNNNN.T.. ........G. .......... .T........ .CA....... C......... .......... .......... ..........

                 100        110        120        130        140        150        160        170        180
kon Prim.    GTTGAAAGAA AAACATAGTA GGTGATCCTG AGCCAAATTT TAATTACGAA ATAGGTGCAG AGACCCAAAG GGAACTATCC AATTGAAAAA
atr Cauc.    .......... .......... .......... .......... ...G...A.. .......... .......... .......... ....._....
atr Kamch.   .......... .......... .......... .......... ...G...A.. .......... .......... .......... ....T.....
pum Chita    .......... .......... .......... .......... A..G...A.. .......... .......... .A........ ......-...
pum Tuva     .......... .......... .......... .......... A..G...A.. .......... .......... .A........ ......-...
exs USA      .......... .......... .......... .......... ...G...A.. .......... ....T.G... .A........ ......-...
exs Scot.    .......... .......... .......... .......... ...G...A.. .......... ....T.G... .A........ ......-...

                 190        200        210        220        230        240        250        260        270
kon Prim.    CTATAATATT TAGAGATAAA TATAAATAAA TTTATGTTAG ATGTGGATAA AGATAGAGTC CATTTTTTAC ATGCTATATC TAGTTAGCAA
atr Cauc.    .......... ......G... .......... .......... ..A....... .......... .......-.. .......... ..........
atr Kamch.   .......... ......G... .......... .......... ..A....... .......... .......-.. .......... ..........
pum Chita    .......... .---------- ....G..... .......... ..A....... .......... .......-.. .......... ..........
pum Tuva     .......... .---------- ....G..... ...N...... ..A....... .......... .......-.. .......... ..........
exs USA      .......... .......... ...G...... .......... ..AC...... .......... .......... G......... ..........
exs Scot.    .......... .......... ..G....... .......... ..AC...... .......... .......... G......... ..........

                 280        290        300        310        320        330        340        350        360
kon Prim.    CGATGTAAAT CATTGTAAAA AGAAAATCCG TTGGCTTTTT AGACCGTGAG GGTTCAAGTC CCTCTACCCC CATGCAAAAC TCAATCTATT
atr Cauc.    .......... .......... .......... .......... .......... .......... .......... .......... ....C....C
atr Kamch.   .......... .......... .......... .......... .......... .......... .......... .......... ....C....C
pum Chita    .......... .......... .......... .......... .......... .......... .......... .........T ..........
pum Tuva     .......... .......... .......... .......... .......... .......... .......... ...-.....T ..........
exs USA      .......... .......... .......... ......A... .......... .......... .......... .....T.... ..........
exs Scot.    .......... .......... .......... ......A... .......... .......... ..NNNNNNNN NNNNNNNNNN NNNNNNNNNN

                 370        380        390        400        410        420        430        440        450
kon Prim.    ACACCGTTGA CAAAAATTTC ATTTTTATGT TAAAATTACG CATCTAAAAT TGCCGGAATA GCTCAGTTGG CAGAGCAGAG GACTGAAAAT
atr Cauc.    .......... ..T....... .......... ...G.....A A......... .......... .......... .......... ..........
atr Kamch.   .......... ..T....... .......... ...G.....A A......... .......... .......... .......... ..........
pum Chita    .......... ..TT...... C.....G..G .......G.. .......... .......... .......... T......... ..........
pum Tuva     .......... ..TT....-. C.....G..G ......CNNN NT........ .......... ......NNNN NNNNNNNNNN NNNNNNNNNN
exs USA      .AT....... ..T....... G......... ..G....... .......... .......... .......... T......... ..........
exs Scot.    NNNNNNNNNN NNNNNNNNNN NNNNNNNNNN NNNNNNNNNN NNNNNNNNNN NNNNNNNNNN NNNNNNNNNN NNNNNNNNNN NNNNNNNNNN

                 460
kon Prim.    CCTCGTGTCA CCAGT
atr Cauc.    .......... .....
atr Kamch.   .......... ...NN
pum Chita    .......... .....
pum Tuva     NNNNNNNNNN NNNNN
exs USA      .......... .....
exs Scot.    NNNNNNNNNN NNNNN
```

Fig. 3. The alignment of *trn*L-F cpDNA for *Solenostoma pseudopyriflorum* and *S. pyriflorum* (names abbreviated, compare with Table 1.)

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                  10         20         30         40         50         60         70         80         90
pyr S. Kor. 1 TCGAAATCGG TAGACGCTAC GGACTTAATT TGATTGAGCC TTGGTCAAGA AATTGACTAA GTGACTGTTT CCAGATTCAG GGAACCCTAG
pyr S. Kor. 2 .......... .......... .......... .......... .......... .......... .......... .......... ..........
pseud Sakh.   .......... .......... .......... .......... ..T....... .......... .......... ........G. ..........
pseud Itur.   .......... .......... .......... .......... ..T....... .......... .......... ........G. ..........
pseud Prim. 1 .......... .......... .......... .......... ..T....... .......... .......... ........G. ..........
pseud Prim. 2 .......... .......... .......... .......... ..T....... .......... .......... ........G. ..........
pseud Bur.    .......T.. ........G. .......... .......... ..T....... .......... .......... ........G. ..........

                 100        110        120        130        140        150        160        170        180
pyr S. Kor. 1 GTTGAAGAAG AACATAGTAG GTAATCCTGA GCCAAATTTT GTTTACGAAA TAGGTGCAGA GACTCAAAGG GAACTATCCA GTTAAAAAAA
pyr S. Kor. 2 .......... .......... .......... .......... .......... .......... .......... .......... ..........
pseud Sakh.   ......T... ......A... .......... .......... .......... .......... .......... ........G ...GG.....
pseud Itur.   ......T... ......A... .......... .......... .......... .......... .......... ........G ...GG.....
pseud Prim. 1 ......T... ......A... .......... .......... .......... .......... .......... ........G ...GG.....
pseud Prim. 2 ......T... ......A... .......... .......... .......... .......... .......... ........G ...GG.....
pseud Bur.    ......T... ......A... .......... .......... .......... .......... .......... ........G ...GG.....

                 190        200        210        220        230        240        250        260        270
pyr S. Kor. 1 CTATATATAA TATTTAGCGA TAAA------ ---------- -------TTT ATTATTACAG ATTATATTAG ATATGGATAA AGATAGAGTC
pyr S. Kor. 2 .......... .......... ....------ ---------- ---------- .......... .......... .......... ..........
pseud Sakh.   .......... .......... ....TATAAA TAACATTATT TTAATAA... .......... .......... .......... ..........
pseud Itur.   .......... .......... ....TATAAA TAACATTATT TTAATAA... .......... .......... .......... ..........
pseud Prim. 1 .......... .......... ....TATAAA TAACATTATT TTAATAA... .......... .......... .......... ..........
pseud Prim. 2 .......... .......... ....TATAAA TAACATTATT TTAATAA... .......... .......... .......... ..........
pseud Bur.    .......... .......... ....TATAAA TAACATTATT TTAATAA... .......... .......... .......... ..........

                 280        290        300        310        320        330        340        350        360
pyr S. Kor. 1 CTTTTTTACA TGCTATATT- GGTTAGCAAC GATGCAAATC ATTGTAAAAA GAAAATCCGT TGGCTTTTTA GACCGTGAGG GTTCAAGTCC
pyr S. Kor. 2 .......... .........- .......... .......... .......... .......... .......... .......... ..........
pseud Sakh.   .......... .........C .......... .......... .......... .......... .......... .......... ..........
pseud Itur.   .......... .........C .......... .......... .......... .......... .......... .......... ..........
pseud Prim. 1 .......... .........C .......... .......... .......... .......... .......... .......... ..........
pseud Prim. 2 .......... .........C .......... .......... .......... .......... .......... .......... ..........
pseud Bur.    .......... .........C .......... .......... .......... .......... .......... .......... ..........

                 370        380        390        400        410        420        430        440        450
pyr S. Kor. 1 CTCTACCCCC ATCATAAATC AAATTTATGG GTTCAAATAA CGCATCAAAA AATTGCCGGA ATAGCTCAGT TGGTAGAGCA GAGGACTGAA
pyr S. Kor. 2 .......... .......... .......... .......... .......... .......... .......... .......... ..........
pseud Sakh.   .......... .......... .......... ........T. ..T...C... .......... .......... .......... ..........
pseud Itur.   .......... .......... .......... ........T. ..T...C... .......... .......... .......... ..........
pseud Prim. 1 .......... .......... .......... ........T. ..T...C... .......... .......... .......... ..........
pseud Prim. 2 .......... .......... .......... ........T. ..T...C... .......... .......... .......... ..........
pseud Bur.    .......... .......... .......... ........T. ..T...C... .......... .......... .......... ..........

                 460        470
pyr S. Kor. 1 AATCCTCGTG TCACCAGTTC AAATA
pyr S. Kor. 2 .......... ..... .....
pseud Sakh.   .......... ....AG.... .....
pseud Itur.   .......... ..... .....
pseud Prim. 1 .......... ..... .....
pseud Prim. 2 .......... ..... .....
pseud Bur.    .......... ..... .....
```

Fig. 4. The alignment of *trn*L-F cpDNA for *Jungermannia* spp. (names abbreviated, compare with Table 1.)

Table 1. Specimens used in molecular phylogenetic analysis and their GenBank data for *trnL-F* cpDNA. The sequences downloaded from GenBank are marked by asterisk.

Taxon	Herbarium voucher	GenBank no.
Jungermannia atrovirens Dumort.	Russia, Caucasus, Karachaevo-Cherkessia, Konstantinova, K 421-6-05 (KPABG)	GQ220763
J. atrovirens Dumort.	Russia, Kamchatka Prov., Bakalin, K-74-13a-04 (KPABG)	GQ220764
J. exsertifolia Steph.	U.S.A., Wyoming, Konstantinova, A69/5-95	AY327775*
J. exsertifolia Steph.	UK, Scotland, West Sutherland, Gleann Dubh, Long 29178	AY453774*
J. konstantinovae Bakalin et Vilnet	Russia, Primor'e, Nakhodka City area, Bakalin, P-69-16-08 (VLA)	GU220586
J. pumila With.	Russia, Tuva, Bakalin, 10.VII.1999	AY327771*
J. pumila With.	Russia, Chita Prov., Afonina, 11606 (KPABG)	GU220588
Plectocolea obovata (Nees) Mitt.	Russia, Murmansk Prov., Konstantinova, 196-6-02 (KPABG)	GQ220754
P. obovata (Nees) Mitt.	Russia, Kemerovo Prov., Konstantinova, 72-2-00 (KPABG)	GQ220753
P. obovata (Nees) Mitt.	Russia, Perm Territory, Konstantinova, K 324-1-04 (KPABG)	GQ220755
P. subelliptica (Lindb. Ex Kaal.) A. Evans	Russia, Kamchatka Prov., Bakalin, K-48-13-03 (KPABG)	GQ220752
P. sp.	Russia, Murmansk Prov., Konstantinova, 30-1-97 (KPABG)	GQ220761
P. sp.	Russia, Buryatiya, Konstantinova, 70-2-01 (KPABG)	GQ220751
Solenostoma caespiticium (Lindenb.) Steph.	Russia, Buryatiya, Konstantinova 101-1-01 (KPABG)	GU220585
S. confertissimum (Nees) Schljakov	Russia, Caucasus, Karachaevo-Cherkesia, Konstantinova K 459-8a-05 (KPABG)	GQ220758
S. pyriflorum Steph. 1	South Korea, KyongNam Prov., Chiri, Bakalin, Kor-8-5-09 (VLA)	GU220590
S. pyriflorum Steph. 2	South Korea, KyongNam Prov., Chiri, Bakalin, Kor-10-8-09 (VLA)	GU220591
S. pseudopyriflorum Bakalin et Vilnet	Russia, Sakhalin Prov., **Sakhalin** Island, Bakalin, S-25-1a-06 (VLA)	GU220592
S. pseudopyriflorum Bakalin et Vilnet	Russia, Sakhalin Prov., **Iturup** Island, Bakalin, K-12-8-07 (VLA)	GU220593
S. pseudopyriflorum Bakalin et Vilnet 1	Russia, **Primor'e**, Bakalin, P-74-79a-05 (VLA)	GU220594
S. pseudopyriflorum Bakalin et Vilnet 2	Russia, **Primor'e,** Bakalin, P-65-1-06 (VLA)	GU220595
S. pseudopyriflorum Bakalin et Vilnet	Russia, **Buryatiya**, Konstantinova, 30-2-01 (KPABG)	GQ220759

intergenic spacer differentiate *J. konstantinovae* from the other studied taxa (Fig. 4).

Discussion

Both phylogenetic trees resolved species of *Jungermannia* s. str., *Plectocolea*, and *Solenostoma* (except *Solenostoma caespiticium*) in three clades with high support. Hentschel et al. (2007) in their study among other taxa of Jungermanniinae analyzed *rbcL* sequences of two *Solenostoma* species and four of *Plectocolea* (cited as *Solenostoma*). These species composed an intermingled clade and authors suggested the inclusion of *Plectocolea* into *Solenostoma* (Hentschel et al., 2007). Our *trnL-F* analysis of two *Plectocolea* species and three *Solenostoma* species demonstrates the segregation of these taxa from each other. Thus, here we accept these two genera, *Plectocolea* and *Solenostoma*, as a separate ones.

Solenostoma pseudopyriflorum demonstrates a stable and almost invariable sequence pattern over extensive territory of about 3000 km, from Baikal to Kuril Islands. Its infraspecific variation in *trn*L-F is 0.5-0.9%, while the difference between *S. pseudopyriflorum* and *S. pyriflorum*

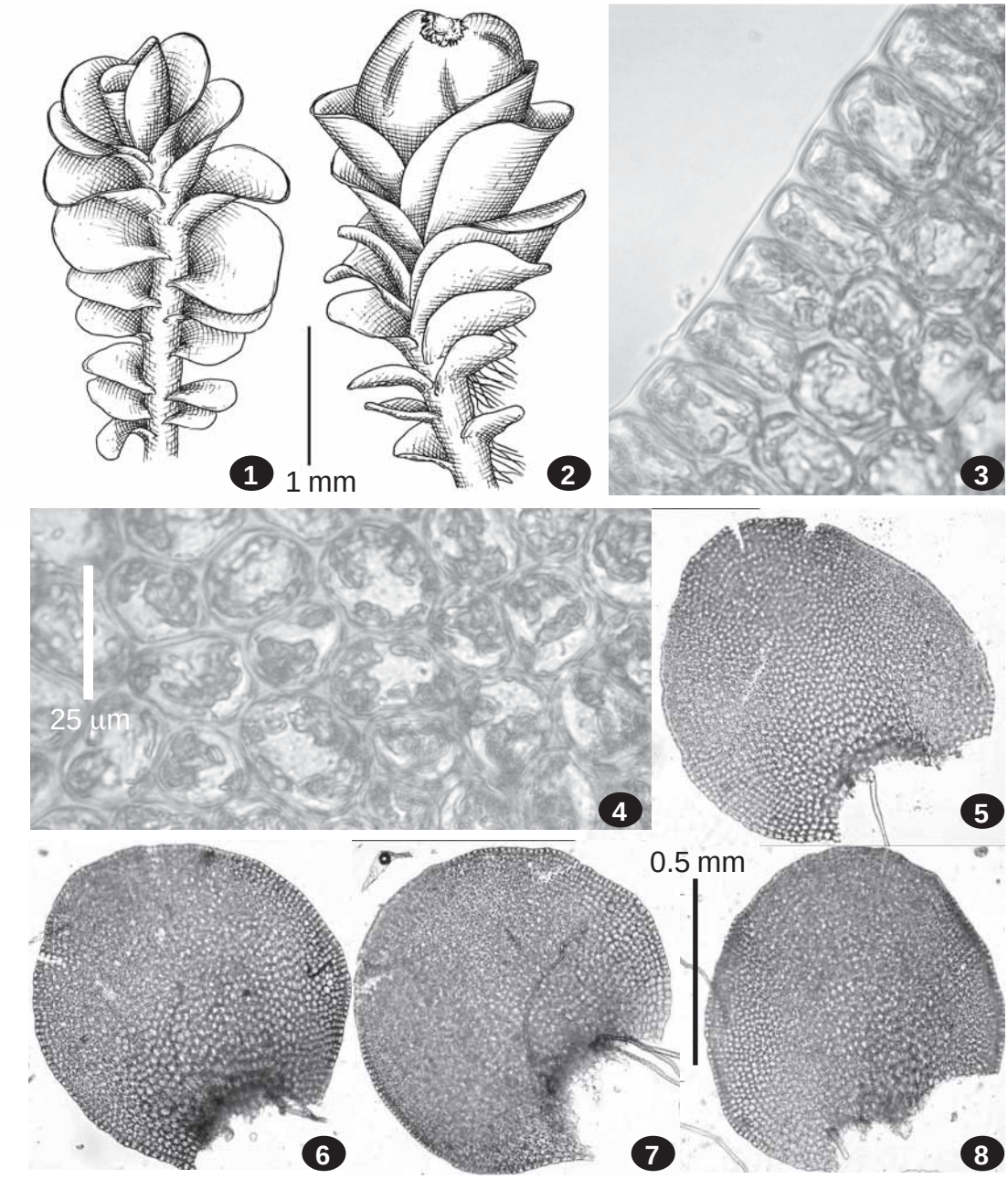

Fig. 5. *Solenostoma pseudopyriflorum* Bakalin et Vilnet. (from holotype, Bakalin K-12-8-07): 1 – sterile plant; 2 – perianthous plant; 3 – cells near leaf margin; 4 – mid-leaf cells, 5-8- leaves. Scale bars: 1 mm for 1-2; 0.5 mm for 4-8; 25 μm for 3-4.

is much greater, 7.2-7.6%, that is similar to the level of difference between species in the genus *Lophozia* s.str. (Vilnet et al., 2008). These data support the segregation of *Solenostoma pseudopyriflorum* as a separate species dictinct from *S. pyriflorum*.

Although the only one sequence of *J. konstantinovae* was studied, it differs from other analyzed *Jungermannia* species by 2.9-5.2%. The infraspecific sequence variation in this clade is 0.3% for *J. atrovirens*, 1.4% for *J. pumila* and 0.7% for *J. exsertifolia.* Thus the level of *trn*L-F

Table 2. A comparison of *Solenostoma pseudopyriflorum* Bakalin et Vilnet with related species.

Character	*S. pseudopyriflorum*	*S. pyriflorum*	*S. rishiriense*	*S. confertissimum*	*S. sphaerocarpum*
Plant color	light or yellow-green to brown	deep green to brown	pale brown to whitish green	light green to green or yellowish green	light to dirty green, with sepia tint to olive-green and brownish black
Purple pigmentation	in leaf base and sometimes in stem and perianth	sometimes near stem apex	commonly at leaf margins and perianth beak	near stem apex and especially at leaf margins and upper portion of perianth	absent
Shoot width, mm	1.0-2.5	1.0-2.0	0.5-1.0	0.5-1.0(-2.0)*	0.8-2.0
Stem width, μm	(150-)200-300(-400)	200-300	150-240	150-210	180-400
Rhizoid color	purple to purplish brownish light rose, rarely colorless (in some part of shoots);	colorless to purple	colorless to brownish and purple	colorless to brownish, rarely purplish	colorless to brownish
Rhizoids	scattered to numerous	numerous	numerous	numerous	numerous
Rhizoid position	on ventral side of stem and at perianth base	on ventral side of stem and at perianth base	on ventral side of stem	on ventral side of stem and base of sterile leaves	on ventral side of stem
Inflorescence	paroicous	dioicous	dioicous	paroicous	paroicous
Distribution in Russia	mountains of south Siberia and Far East	not present	South Kurils and Okhotsk Sea coast	widespread north of 53°N	widespread mostly north of 53°N

* – Schljakov (1980) gives the shoot width for *S. confertissima* being 1-2 mm, and it is correct for European populations, while in East Asian ones (not studied by Schljakov) we observed plants with 0.5-1.0 mm width only.

Table 3. A comparison of *Jungermannia konstantinovae* Bakalin et Vilnet with related species.

Character	*J. konstantinovae*	*J. atrovirens*	*J. pumila*	*J. polaris*
Growth type	creeping	creeping	erect to ascending	ascending to creeping
Shoot width, mm	1.0-1.2(-1.5)	0.7-1.5	0.75-1.35	0.22-0.3
Stem diameter, μm	150-180	120-300	100-280	90-150
Leaves concavity	flattened, rarely slightly concave or channeled	flattened to concave	shallowly channeled to almost flat, with semifunnelate base	concave to channeled-concave
Angle fromed by leaf with stem or branch	15-25°	45-80°	30-40°	30-60°
Leaf size (l x w), μm	300-500 x 350-600 (0.8-0.9:1)	600-750 x 600-650 (1:0.8-0.9)	570-1050 x 500-820 (1:0.8-0.9)	280-300 x 250-300 (1:0.95-1)
Midleaf cell size, μm	15-28 x 13-18	26-30 x 14-17	25-45 x 13-21	25-35 x 12-18
Inflorescence	paroicous	dioicous	paroicous	paroicous
Perianth shape	oval to rhomboidal, 5-plicate	rhomboidal	fusiform to rhomboidal	oval to obpyriform
Substrate acidity	Basic	Basic	Acidic to neutral	Acidic to neutral

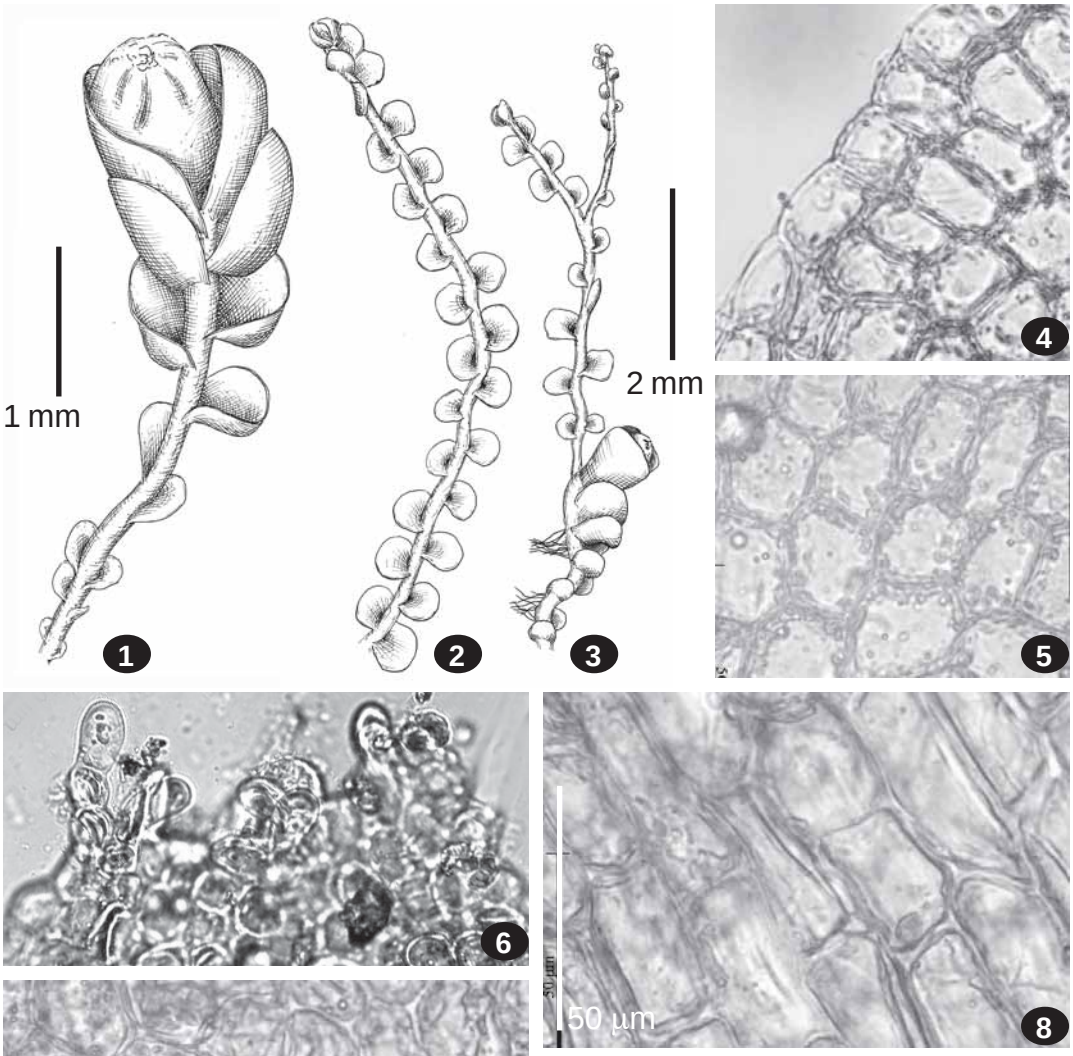

Fig. 5. *Jungermannia konstantinovae* Bakalin et Vilnet (from holotype, Bakalin P-69-16-08): 1 – perianthous plant; 2 – sterile plant; 3 – perianthous plant with ventral innovation; 4 – cells near leaf margin; 5 – mid-leaf cells; 6 – perianth mouth; 7 – cells in upper part of perianth; 8 – cells in perianth middle; 9-11 – leaves. Scale bars: 1 mm for 1; 2 mm for 2-3; 0.2 mm for 9-11; 50 μm for 4-8.

sequence divergence of *J. konstantinovae* also supports its acceptance as a distinct species.

TAXONOMIC CONCLUSIONS

Solenostoma pseudopyriflorum Bakalin et Vilnet, sp. nov. Fig. 5.

Plantae paroicae, erectes vel ascendentes, vivide virides vel brunneolae vel purpurescens. Rhizoides purpurescens, erectes vel fasciculates. Folia subtransverse inserta, convava, trigonis triangularis vel convexis. Perianthium ad orem abrupte contractum, tri- vel tetraplicatum.

Plants rigid, erect to ascending, light green to yellow-green, yellowish brown and purplish brown, characteristically with purplish to purple-red colour in leaf base and stem, and (sometimes) perianth. Shoots (3-)5-15 mm long, 1.0-1.7 mm wide in sterile plants, (1.5-)2.0-2.5 mm wide in fertile ones. Stem (0.15-)0.2-0.3(-0.4) mm wide, orbicular in cross section, branching rarely occurs, ventral or lateral, originated as innovations, but gives rise to normally developed shoots, dorsal surface cell walls slightly to moderately thickened, walls brown, brownish to purplish, with small concave trigones, (28-)60-90(-120) ×(15-)20-26(-32) μm. Rhizoids scattered to numerous, erect or decurrent down stem in indistinct fascicles, purple to purplish brown, light rose, rarely colorless (in some part of shoots). Leaves distant to subincumbent and subimbricate, erect, inserted at their middle (3/4 of insertion line length) at angle of (45-)60-85° with stem, dorsally decurrent for 1/6–1/3(–2/3) of stem width, on ventral side subtransversely inserted where insertion line arcuate, not or barely decurrent or decurrent up to 1/2 of stem width, widely ovoid to widely triangular, suborbicular and transversely oval, flattened to concave and loosely channeled, frequently with deflexed apex, rarely undulate at margin, wider than long, 0.72-1.20×0.72-1.50 mm (1:0.8-0.9(-1)), to longer than wide, 0.68-0.90×0.66-0.83 mm (0.9-1:1). Cells in midleaf thin-walled, lumen subquadrate to rounded, (17-)25-40(-45)×(14-)15-28(-32) μm, walls colourless to rose and purplish, trigones small to large in size, concave to convex, near margin (14-)17-26(-30) μm, thin-walled, trigones distinct, triangle to convex, external walls frequently thickened, cuticle smooth throughout. Paroicous. Perianth terminal, deep green to purple-green, obpyriform or widely clavate to cylindrical, emergent up to 2/3 of its length from bracts, smooth or weakly 3-4-plicate in upper part, sometimes with 1 ventral innovation (once dorsal innovation was found - VLA, K-12-8-07, Iturup Island), weakly rhizogenous in basal part (both dorsal, lateral and ventral sides), ca. 1.8-2.2×1.0 mm, perigynium indistinct or up to 1/5 of perianth length, archegonia 5-15 per perichaetium, female bracts equal in size with antheridial bracts, undulate at margin, loosely clinging perianth in lower part, bracteole absent. Androecia in (1-)2(-3) pairs of bracts below perichaetium, or separated from the latter by 1 pair of sterile leaves; antheridia 1-2 in each bract, easily disintegrate; antheridial body nearly spherical, ca. 120 μm in diameter, stalk with 2 (rarely, near stalk base with 1) cell rows, ca. 70 μm long, bracts concave, widely oval to nearly orbicular, ca. (0.75-)0.95-1.10×(1.00-)1.10-1.30 μm, loosely inflated at base and purplish in inflated area, with deflexed apex. Capsule ellipsoidal, ca. 500×300 μm, bistratose, inner cells flexuous-linear, ca. 60-80×9 μm with 6-11 annular thickenings, outer cells ca. 32×28 μm, subquadrate, with 2 nodular thickenings on each vertical wall, seta ca. 70 mm in diameter and ca. 5 mm long. Spores ca. 18 μm, finely papillose, reddish brown, elaters ca. 150-180×5-9 μm, bispiral, with elongated (up 25 μm long) gradually narrowed endings (Figs. 2, 3).

Holotypus: the Russian Far East, Kurils Islands, Iturup Island, Bogatyr' Range (44°54'57"N 147°30'20"E), 395 m alt. Stone along stream in *Sasa* thickets, leg. 8 August 2007 V.A. Bakalin (VLA, K-12-8-07, isotype in KPABG 112860)

Other specimens examined: The Russian Far East, Sakhalin Island, Nabilsky Range (50°46'04"N 143°15'18"E), 350 m alt. Cliffs near waterfall, leg. 14.VIII.2006 Ignatov (VLA, duplicate in KPABG 112849); Sakhalin Island, Belaya River near Sokol Settlement, 6 km upstream (47°15'17"N 142°48' 47"E), 68 m alt. Vertical cliffs along river bank, built with sedimentary grounds and surrounded by *Abies-Picea* forest. leg. Bakalin, S-25-1a-06 (VLA, duplicate in KPABG 112846K); Sakhalin Island, Vostochno-Sakhalinskiye Mts., nature reserve "Vaida" (49°53'16"N 143°27'06"E), 394 m alt. Limestone cliffs in deep ravine. leg. Bakalin, S-34-3-06 (VLA, duplicate in KPABG 112848); Primorskij Territory, Vladivostok City area, Bogataya Griva Range near Bogataya River (43°14'N 132°04'E), ca. 200 m alt.

Wet stone in full shade, leg. 4.VIII.1952 Woroshilov (MHA, NB: was identified as "*Jungermannia pyriflora* Steph. *ad* var. *minutissima* (Amak.) Amak. *vergens*" by J. Váňa); Primorskij Territory, South of Sikhote-Alin Range, Pidan Mt., Oyry Stream valley (43°05'05"N 132°41'40"E), 699 m alt. Wet stones in mountain lighted dark coniferous forest, leg. Bakalin, P-56-19-08 (VLA); Primorskij Territory, South of Sikhote-Alin Range, area near the top of Pidan (Livadijskaya) Mt. (43°04'15"N 132°41'37"E), 1200 m alt. Boulders along stream in *Abies-Picea-Betula* subalpine lighted forest intermingled with gravely barrens fields, leg. Bakalin, P-74-79a-05 (VLA: was identified as *S.* cf. *pyriflorum* Steph. by Bakalin); Primorskij Territory, Alekseevskij Range, Area near the top of Olkhovaya Mt. (43°20'50"N 133°39'22"E), 1500 m alt. Stones along stream in *Picea-Betula* forest with admixture of *Abies* and *Alnus* and fern-forb cover, leg. Bakalin, P-65-2a-06, P-65-22-06, P-65-37-06, P-65-1-06 (VLA, the last duplicate in KPABG-110327); Primorskij Territory, Chuguevskij District, Snezhnaya Mt. (ca. 43°43'N 134°25'E), 800 m alt. Wet cliffs near stream, leg. 1.IX.1974 Bardunov (VLA, KPABG-112871, NB: was identified as *S. minutissima* Amak. by R.N. Schljakov); Khabarovskij Territory, Solnechnyj District, Silinka River valley (50°44'25"N 136°23'28"E), 630 m alt. Wet shaded cliffs in *Picea* forest, leg. Bakalin, Kh-7-8-07 (VLA); South Siberia, Rupublic of Buryatiya, Chamar-Daban Range, Baikalsky Nature State Reserve, Pravaya Anosovka River valley (ca. 51°30'N 130°50'E). Wet cliff in dark coniferous forest, leg. 5.VIII.2001 N.A. Konstantinova (KPABG-102426); Altai Mts., Uedinennoye Lake (51°49'N 87°48'E), 880 m alt. Rock outcrops, on N-facing slope, leg. 6.VI.1989 Ignatov (MHA, duplicate in VLA, NB: identified as *J. pyriflora* Steph. by Váňa).

As it is seen from cited specimens, the species described above has a rather wide range of distribution and it is not very rare in the Russian Far East and South Siberia. One of its striking features is an easy disintegration of antheridia and only loosely or almost not inflated base of male bracts. This was probably a reason for the repeated confusions. Gambaryan (1992) recorded it as *Solenostoma rishiriense*, Váňa & Ignatov (1995) as *Jungermannia pyriflora* and Bakalin (2007, 2008a) as *Solenostoma pyriflorum* and *S. rishiriense*. Later on, the senior author observed a surprising fact that all samples identified as *S. pyriflorum* (or sometimes closely related *S. rishiriense*) from Russia have numerous and fertilized archegonia, developed perianthia and sometimes even sporangia, but at the same time, in all of those samples androecia were supposedly absent. Intense search of antheridia was undertaken and yield in discovery of them or their remains in all the listed specimens. In most cases only a very small and hardly discernible stalks of antheridia were found, while in a few cases the antheridial bodies remained on them, thus proving the paroicous sexual condition in this species.

The new species belongs to *Solenostoma* sect. *Solenostoma.* Váňa (1975) listed 35 species for this section worldwide; recent addition may increase the number up to 40 species. Only four of them are paroicous: *Solenostoma pseudopyriflorum*, *S. jenseniana* (Grolle) Bakalin (boreal to arctic Europe and subarctic Asia), *S. pocsii* (Váňa) Bakalin *comb. nov*. Basionym: *Jungermannia pocsii* Váňa, Folia Geobot. Taxonom. 10: 365. 1975. (known from Kenya, Tanzania and Natal) and *S. sphaerocarpum* (Hook.) Steph. (with arcto-boreal circumpolar distribution). In adjacent area of China, provinces of Heilongjiang and Jilin only one species of the sect. *Solenostoma* (*S. pyriflorum*) is known (Piippo, 1990). Indeed *S. pseudopyriflorum* is superficially very similar to and may be readily confused with *S. pyriflorum,* which have been made repeatedly. The confusion with smaller and pale to whitish *S. rishiriense* is less likely.

Monoicous inflorescence is rather rare in the genus, and present mainly in northern species. The formal identification using keys of Schljakov (1981) and Amakawa (1960), would lead to *S. confertissimum* (Nees) Schljakov (sect. *Desmorhiza* Amak.) and *S. sphaerocarpum* (Hook.) Steph. (sect. *Solenostoma*). The comparison of *S. pseudopyriflorum*, with them and other related and superficially similar taxa are given in Table 1.

Most of collections of *Solenostoma pseudopyriflorum* are from spruce and fir forests in mountains of asiatic Russia, south of 51°N. It occurs on wet and usually shaded rocks and cliffs. The distribution and ecology of species is rather similar to that of *Lophozia lantratoviae* Bakalin, except the latter is not yet recorded in South Kurils, and *Solenostoma pseudopyriflorum* is not known in the Caucasus. Both species belong to mountain boreo-temperate flora element.

Two last years Bakalin conducted hepatic exploration in mountainous areas of South Ko-

rea but failed to collect *Solenostoma pseudopyriflorum*, in contrast to *S. pyriflorum* that was found to be very common both in broad-leaved and coniferous mountain belts in the latter area. *Solenostoma pyriflorum* was described from Japan (Nagano Prefecture in Middle Honshu) and is currently known from Japan, South Korea (Amakawa, 1960) and China, in Xizang and Jilin (Piippo, 1990).

Based on the above data, as well as on the reidentification of *S. pyriflorum* from the Altai Mountains, we exclude *S. pyriflorum* from the hepatic flora of Russia; all studied specimens being referred to *S. pseudopyriflorum*. Also *S. rishiriense* is excluded now from the liverwort flora of Primorskij Territory and Sakhalin. However, this species occurs in Russia in the South Kuril Islands and northern coast of the Sea of Okhotsk

Selected specimens examined of *Solenostoma rishiriense*: Khabarovskij Territory, Okhotskij District, Lanzhinskiye Mts. (59°26'39"N 143°28'13"E), 212 m alt. Clayish soil in roadside, leg. 24 July 2008 Bakalin, VLA, Kh-33-3-08; Kurils Islands, Iturup Island, Belyye Skaly cliffs area (45°15'48"N 148°13'03"E), 18 m alt. Crumble slope of white pumice deposits, leg. 23 September 2005 Bakalin, VLA, K-67-7b-05; Kurils Islands, Kunashir Island, Ozernaya River mouth area (43°53'04"N 145°27'43"E), 30 m alt. Spots of bare ground in wind stressed meadow on slope to sea, leg. 6 September 2006 Bakalin, VLA, K-46-14a-06).

Jungermannia konstantinovae Bakalin et Vilnet sp. nov.

Plantae paroicae, prostrates, vivide virides vel brunneolae, calcicolae. Rhizoides decolorates, erectes vel fasciculates. Folia oblique inserta, convava, trigonis indistinctis. Perianthium ad orem abrupte contractum, pentaplicatum.

Plants deep green to brownish green. Shoots 1.0-1.2(-1.5) mm wide, 10-20 mm long, prostrate, creeping. Stem 150-180 μm wide, orbicular in cross section, branching lateral, terminal, rarely ventral, dorsal surface cells slightly thickened with indistinct trigones, 50-120×24-28 μm. Rhizoids scattered, colorless to grayish, erect, sometimes in indistinct fascicles. Leaves distant, flattened, rarely slightly concave or channeled (especially near androecia), broadly ovoid to transverse oval, rarely slightly retuse at apex, 300-500×350-600 μm (1:0.8-0.9), inserted in their middle (3/4 of insertion line length) at angle of 15-25° with axis, dorsal margin forming angle up to 45°, not decurrent, ventral margin deviating up to 80°, not or slightly decurrent, insertion line arcuate. Cells in midleaf thin-walled, with brownish walls, 15-28×13-18 μm, trigones indistinct, near margin 15-28 μm, cuticle smooth. Oil bodies 2-4(-8) per cell, nearly smooth. Paroicous. Perianths terminal, deep green, oval to rhomboidal, 5-plicate (2 lateral, 1 dorsal, 2 ventral), almost always with 1 ventral innovation, ca. 1.0×0.7 mm, unistratose to base, cells in perianth middle 24-35×20-30 μm, subisodiametric, with concave to triangle trigones, perigynium indistinct, archegonia ca. 7 per perichaetium, bracts equal in size to male bracts. Androecia in 2-3 pairs below perichaetium, bracts strongly concave to cupped 0.85×1.00-1.05 mm or smaller in lower pairs.

Holotypus: the Russian Far East, Primorskij Territory, Nakhodka City area, Sestra Mt. (42°49'40"N 132°59'40"E), 328 m alt. Wet calcareous cliffs in deep ravine, surrounded scattered oak and *Rhododendron* shrubs, leg. 17 October 2008 Bakalin (VLA, P-69-16-08, isotype in KPABG 112870).

When first observed in the field, the plant was referred to *Jungermannia atrovirens* by its habit. Subsequent study revealed unistratose perianth composed of isodiametric cells and 5-plicate in upper part, which are characteristics of *Solenostoma*, not *Jungermannia* s. str. The DNA data, discussed above, however indicate the position of the new species within the latter one. In addition, the prostrate growth (even in perianth bearing plants), very obliquely inserted leaves, deep green color of plants, rhizoids with no trace of reddish pigmentation, and calciphilous ecology indicate rather *Jungermannia* s.str. than *Solenostoma*.

Jungermannia s. str. includes ca. 10 species worldwide. Seven of them were listed in world list by Váňa (1975). It seems that *J. konstantinovae* can be confused with three species distributed in adjacent areas of Japan, Korea and China: *J. atrovirens*, *J. pumila* and *J. polaris*. Their distinction is given in Table 3.

ACKNOWLEDGEMENTS

Authors thank Mr. M.A. Bakalin for preparing of line drawings of plant habit (figs. 2, 5). This research has been supported by program for

Basic Research of Presidium RAS "Biodiversity (Gene pools and genetic diversity)" and RFBR 09-04-00281.

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