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Taxonomic Novelties in *Solenostoma* – *Plectocolea* Complex (Solenostomataceae, Hepaticae) in East Asia

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ABSTRACT

The involving of poorly known taxa from East Asia into integrative analysis allows clarifying the taxonomic structure of *Plectocolea* – *Solenostoma* complex. Due to data in hand this complex includes four distinct genera. The genus *Metasolenostoma* Bakalin et Vilnet is described. *Jungermannia* sect. *Protosolenostoma* is elevated to generic rank – *Protosolenostoma* (Amak.) Bakalin et Vilnet. The species rank for *Plectocolea shinii*, *Solenostoma minutissimum* and *S. rishiriense* is confirmed. *Plectocolea ariadne* fits well in *Plectocolea*, but not in *Solenostoma*. The name *Solenostoma major* is showed to be incorrectly used before and the new name *S. sunii* Bakalin et Vilnet is proposed for the taxon. The new species *Metasolenostoma orientale* Bakalin et Vilnet and *Plectocolea higuchii* Bakalin et Vilnet are described. The paper provides morphological descriptions as well as figures based on studied material for newly described or re-evaluated taxa. Some evolutionary pathways within *Plectocolea* – *Solenostoma* complex are discussed: 1) perigynium reduction and specification of perianth, 2) further development of perigynium conjugate with perianth reduction, 3) specialization of 'oil cells' in the leaf lamina and 4) the growth form evolution.

Keywords

Solenostomataceae, *Plectocolea*, *Solenostoma*, *Metasolenostoma*, *Protosolenostoma*, integrative taxonomy, *trnL-F*, *trnG-intron*

РЕЗЮМЕ

Бакалин В.А., Вильнет А.А., Фуруки Т., Катагири Т. Таксономические изменения в комплексе *Plectocolea* – *Solenostoma* (Solenostomataceae, Hepaticae) в Восточной Азии

Вовлечение малоизученных восточноазиатских представителей в интегративное исследование прояснило структуру комплекса *Plectocolea* – *Solenostoma*. Установлено, что этот комплекс включает 4 рода, один из которых (*Metasolenostoma* Bakalin et Vilnet) описан впервые, а другой впервые рассматривается как самостоятельный род – *Protosolenostoma* (Amak.) Bakalin et Vilnet (= *Jungermannia* sect. *Protosolenostoma*). Подтвержден видовой статус *Plectocolea shinii*, *Solenostoma minutissimum* и *S. rishiriense*. *Plectocolea ariadne* должна рассматриваться как представитель рода *Plectocolea*, а не *Solenostoma*. Показано некорректное использование названия *Solenostoma major*, которое заменено на *S. sunii* Bakalin et Vilnet. Описаны новые виды: *Metasolenostoma orientale* Bakalin et Vilnet и *Plectocolea higuchii* Bakalin et Vilnet. Приводятся морфологические описания и иллюстрации впервые описанных видов и таксонов, статус которых пересмотрен. На основе интегративного анализа сделаны наблюдения о следующих путях эволюции в комплексе *Plectocolea* – *Solenostoma*: 1) редукция перегиния и увеличение периантия, 2) увеличение перегиния и уменьшение периантия, 3) специализация 'масляных клеток' в листе, 4) развитие форм роста.

Ключевые слова

Solenostomataceae, *Plectocolea*, *Solenostoma*, *Metasolenostoma*, *Protosolenostoma*, интегративная таксономия, *trnL-F*, *trnG-intron*

In the course of exploration of *Solenostoma* – *Plectocolea* complex we revealed some new for science taxa or re-evaluated epithets regarded before as synonyms (Bakalin & Vilnet 2012, Bakalin 2013). Recently we had an opportunity to involve new material into the analysis to make further clarification in this complex, one of the most difficult taxonomic entities in temperate East Asia, that resulted in some nomenclatural changes as well as the creation of two new genera. The main goals of the present study are to describe

these novelties and to reveal evolutionary pathways in this complex.

MATERIALS AND METHODS

Taxon sampling

To continue our study of East Asian Solenostomataceae we sequenced *trnL-F* and *trnG-intron* cpDNA from 24 specimens morphologically assigned to 11 species of the genus

Plectocolea, four species of the genus *Solenostoma*, one sample tentatively assigned to *Solenostoma* and ambiguously identified specimen of *Jungermannia pumila*. With exception of several specimens from Russia, South Korea, Japan, Cambodia and U.S.A. other studied samples were gathered by first author during the field trip in China and Japan in 2013–2014. Newly generated nucleotide sequences were analyzed with previously published data for 86 specimens. Species of the genus *Marsupella* were chosen as an outgroup (Bakalin & Vilnet 2012). The samples studied here are listed in Table 1 with GenBank accession numbers and voucher details.

DNA isolation, amplification and sequencing

DNA was extracted using the NucleoSpin Plant Kit (Macherey-Nagel, Germany) from dried liverwort shoots that were isolated from herbarium samples. The amplification and sequencing were performed using the primers suggested by Taberlet et al. (1991) for *trnL-F* and Shaw et al. (2005) for *trnG-intron*.

PCR was carried out in 20 µl volumes according to the following procedure: 3 min at 94°C, 30 cycles of 30 s at 94°C, 40 s at 56°C for *trnL-F* or 64°C for *trnG-intron*, and 60 s at 72°C, followed by 2 min of extension time at 72°C. Amplified fragments were visualized on 1 % agarose TAE gels by EthBr staining, purified using GFXTM PCR DNA and Gel Band Purification Kit (Amersham Biosciences, U.S.A.), and then used as a template in sequencing reactions with the ABI Prism BigDye Terminator Cycle Sequencing Ready Reaction Kit (Applied Biosystems, U.S.A.) following the standard protocol provided for the 3100 Avant Genetic Analyzer (Applied Biosystems, U.S.A.).

Phylogenetic analyses

Nucleotide data of *trnL-F* and *trnG-intron* of each sequenced specimen were combined and included in produced earlier alignment for 86 specimens from genera *Solenostoma* and *Plectocolea* (Bakalin & Vilnet 2012) using BioEdit v. 7.0.1 (Hall 1999); all positions of the alignment were included in the phylogenetic analysis. The infrageneric and infraspecific variability of each DNA locus was evaluated as the value of the *p*-distances between samples and species of each genera, as calculated in Mega 5.1 (Tamura et al. 2011) using the pairwise deletion option for counting gaps.

The combined alignment of *trnL-F+trnG-intron* was analyzed using three analytical procedures: the maximum parsimony method (MP) using the TNT program (Goloboff et al. 2003), the maximum likelihood method (ML) using PhyML (Guindon & Gascuel 2003) and the Bayesian method (BA) using the MrBayes v. 3.2.1 (Ronquist et al. 2012).

The MP analysis involved a New Technology Search with a search for the minimum-length tree by five 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 program ModelGenerator (Keane et al. 2004) determined that the GTR+I+G model was the best-fit evolutionary model of nucleotide substitutions for the produced alignment. In ML analysis the GTR+I+G model 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 $\rho_{100} = 0.993238$ realized in RAxML v. 7.2.6 (Stamatakis 2006).

In the Bayesian analysis each partition of combined alignment (*trnL-F*, *trnG-intron*) 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 3000000, and trees were saved once every 100th generation. The software tool Tracer (Rambaut & Drummond 2007) reveals effective sample size (ESS) is 747.6505 and auto-correlation time (ACT) is 3611.3263 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.

RESULTS

Phylogeny

Sequences of *trnL-F* were obtained for 24 specimens, *trnG-intron* – 21 specimens. Combined alignment for 111 (including outgroup) specimens consists of 1295 positions, among them 543 belong to *trnL-F*, 752 to *trnG-intron*. The number of constant positions are 791 (61.08 %) in *trnL-F+trnG-intron*, 344 (63.35 %) in *trnL-F*, 447 (59.44 %) in *trnG-intron*. The number of variable positions are 460 (35.52 %) in *trnL-F+trnG-intron*, 180 (33.15 %) in *trnL-F*, 280 (37.23 %) in *trnG-intron*. The number of parsimoniously informative positions are 339 (26.18 %) in *trnL-F+trnG-intron*, 137 (25.23 %) in *trnL-F*, 202 (26.86 %) in *trnG-intron*.

The MP analysis yielded 6 equally parsimonious trees with a length of 1845 steps, with CI=0.553879 and 0.898330 calculated in Mega 5.1. The ML calculation resulted in a single tree, the arithmetic means of Log likelihood was -7680.29713. Arithmetic means of Log likelihoods in the BA analysis in both runs sampled were -7951.62 and -7954.85.

The enlarged dataset analyzed in this study leads to changes in tree topologies compared with those in Bakalin & Vilnet (2012). There are four main clades with partially weak supported relation (Fig. 1) opposite to two clades – *Plectocolea*- and *Solenostoma*-clades – obtained earlier (Bakalin & Vilnet 2012: Figs 1, 2). Moreover, some internal nodes within clades were not obtained sufficient supports in all analyses that unresolved relation between complexes of taxa. The representatives of the genus *Solenostoma* dispersed in three supported clades. The first diverged clade consists of two specimens of *Solenostoma koreanum* (= *S. fusiforme*) from

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

Provisional identification based on morphological data	Taxon	Specimen voucher (Herbarium)	GenBank accession numbers	
			<i>trnL-F</i>	<i>trnG-intron</i>
<i>Plectocolea ariadnae</i>	<i>Plectocolea ariadnae</i> (Tayl.) Mitt.	Cambodia: Pursat Prov., S.-S. Choi, C8348c (JNU, VBGI, KPABG)	KM102705	no data
<i>P. comata</i>	<i>P. comata</i> S. Hatt.	Japan: Miyazaki Pref., V. Bakalin, M. Matsumoto, J-2-12-14 (VBGI, KPABG)	KM102706	KM102685
<i>P. erecta</i>	<i>P. erecta</i> Amakawa	South Korea, S.-S. Choi, Exs. 22 (VBGI, KPABG)	KM102707	no data
<i>P. erecta</i>	<i>P. erecta</i> Amakawa	Japan: Kyushu Isl. Fukuoka Pref., V. Bakalin, J-7-32-14 (VBGI, KPABG)	KM102708	KM102686
<i>Solenostoma</i> sp.	<i>P. higuchii</i> Bakalin et Vilnet	China: Yunnan Prov., M. Higuchi, 48795 (VBGI, KPABG)	KM102709	KM102687
<i>P. infusca</i>	<i>P. infusca</i> Mitt.	Japan: Kyushu Isl. Fukuoka Pref., V. Bakalin, J-7-50-14 (VBGI, KPABG)	KM102710	KM102688
<i>P. horikovana</i>	<i>P. kurilensis</i> (Bakalin) Bakalin & Vilnet	Japan: Miyazaki Pref., V. Bakalin, M. Matsumoto, J-2-26-11 (VBGI, KPABG) 1	KM102711	KM102689
<i>P. horikovana</i>	<i>P. kurilensis</i> (Bakalin) Bakalin & Vilnet	Japan: Kyushu Isl. Fukuoka Pref., V. Bakalin, J-4-67-14 (VBGI, KPABG)	KM102712	KM102690
<i>P. infusca</i>	<i>P. kurilensis</i> (Bakalin) Bakalin & Vilnet	Japan: Miyazaki Pref., V. Bakalin, M. Matsumoto, J-2-33-14 (VBGI, KPABG) 2	KM102713	KM102691
<i>P. radiculosa</i>	<i>P. radiculosa</i> (Mitt.) Mitt.	Japan: Miyazaki Pref., M. Matsumoto, 2841 (VBGI, KPABG)	KM102714	KM102692
<i>P. shinii</i>	<i>P. shinii</i> (Amakawa) Bakalin	Japan: Kagoshima Pref., T. Katagiri, 3889 (VBGI, KPABG)	KM102715	KM102693
<i>P. tetragona</i>	<i>P. tetragona</i> (Lindenb.) Meijer	Japan: Miyazaki Pref., V. Bakalin, J-1-8-14 (VBGI, KPABG)	KM102716	KM102694
<i>P. truncata</i>	<i>P. truncata</i> (Nees) Bakalin	Japan: Miyazaki Pref., V. Bakalin, M. Matsumoto, J-2-2-14 (VBGI, KPABG) 1	KM102717	KM102695
<i>P. truncata</i>	<i>P. truncata</i> (Nees) Bakalin	Japan: Miyazaki Pref., V. Bakalin, J-1-24-14 (VBGI, KPABG) 2	KM102718	KM102696
<i>P. unispiris</i>	<i>P. unispiris</i> Amakawa	Japan: Miyazaki Pref., V. Bakalin, M. Matsumoto, J-2-5-14 (VBGI, KPABG)	KM102719	KM102697
<i>P. unispiris</i>	<i>P. unispiris</i> Amakawa	Japan: Kyushu Isl. Fukuoka Pref., V. Bakalin, J-4-72-14 (VBGI, KPABG)	KM102720	KM102698
<i>Solenostoma koreanum</i>	<i>Protosolenostoma fusiforme</i> (Steph.) Vilnet et Bakalin	South Korea: Jeju-do Prov., S.-S. Choi, 111411 (1) (JNU, VBGI, KPABG) 1	KM102721	no data
<i>S. koreanum</i>	<i>Protosolenostoma fusiforme</i> (Steph.) Vilnet et Bakalin	South Korea: Jeju-do Prov., S.-S. Choi, 111411 (2) (JNU, VBGI, KPABG) 2	KM102722	KM102699
<i>Jungermannia pumila</i>	<i>Solenostoma confertissimum</i> (Nees) Schljakov	Russia: Altay 18/101 (MHA)	KM102723	KM102700
<i>S. macrocarpum</i>	<i>S. macrocarpum</i> (Stephani) Váňa & D.G. Long	China: Guizhou Prov., V. Bakalin, China-55-54-13 (VBGI, KPABG) 1	KM102724	KM102701
<i>S. macrocarpum</i>	<i>S. macrocarpum</i> (Stephani) Váňa & D.G. Long	China: Guizhou Prov., V. Bakalin, China-56-75-13 (VBGI, KPABG) 2	KM102725	KM102702
<i>S. minutissimum</i>	<i>S. minutissimum</i> (Amakawa) Bakalin. Vilnet et Furuki	Japan: Kyushu Isl. Fukuoka Pref., V. Bakalin, J-6-32-14 (VBGI, KPABG)	KM102726	KM102703
<i>S. fusiforme</i>	<i>Metasolenostoma</i> cf. <i>orientale</i> Bakalin et Vilnet	USA: California, J.C. Brinda, 2836 (MO, VBGI, KPABG)	KP113541	KP113540
<i>P. rubripunctata</i> cf.	<i>M. rubripunctatum</i> (S. Hatt.) Vilnet et Bakalin	Japan: Kyushu Isl. Fukuoka Pref., V. Bakalin, J-7-25-14 (VBGI, KPABG)	KM102727	KM102704

South Korea, gathered in *locus classicus*. Unexpected molecular divergence together with morphological uniqueness allows us to elevate section *Protosolenostoma* with this species to generic rank (see below). The second diverged clade was presented by *S. ochotensis*, *S. gracillima*, *S. fusiforme* (as treated in Bakalin & Vilnet 2012) and specimens identified as *P. rubripunctata* (Japan) (BS=94 % in MP, BS=100 % in ML, PP=1.00 in BA) from main *Solenostoma*-clade. Relation of this clade to *Plectocolea* and *Solenostoma* was supported by BS=77 % in MP and PP=1.00 in BA compared with supports of its previous affinity to *Solenostoma*-clade BS=59 % in MP, BS=71 % in ML, PP=0.69 in BA in Bakalin & Vilnet (2012: Figs. 1, 2). Based on the complex of mole-

cular and morphological data we suppose to include this group of species into a new genus – *Metasolenostoma* gen. nov. Specimens indicated in Bakalin & Vilnet (2012) as *S. fusiforme* from Russian Far East are phylogenetically distinct from *S. koreanum* l.c. (= *S. fusiforme*) and treated here as a new species – *Metasolenostoma orientale* sp. nov. the newly sequenced specimen identified as *S. fusiforme* from U.S.A. is placed in sister relation to *Metasolenostoma orientale*-clade. The third clade of *Solenostoma* species (BS=51 % in ML, PP=0.91 in BA) with generic type *S. sphaerocarpum* is in agreement with *Solenostoma*-clade in our previous study with the exclusion of species assigned here to *Metasolenostoma* (BS=60 % in MP, BS=79 % in ML, PP=0.99 in BA in Bakalin & Vilnet

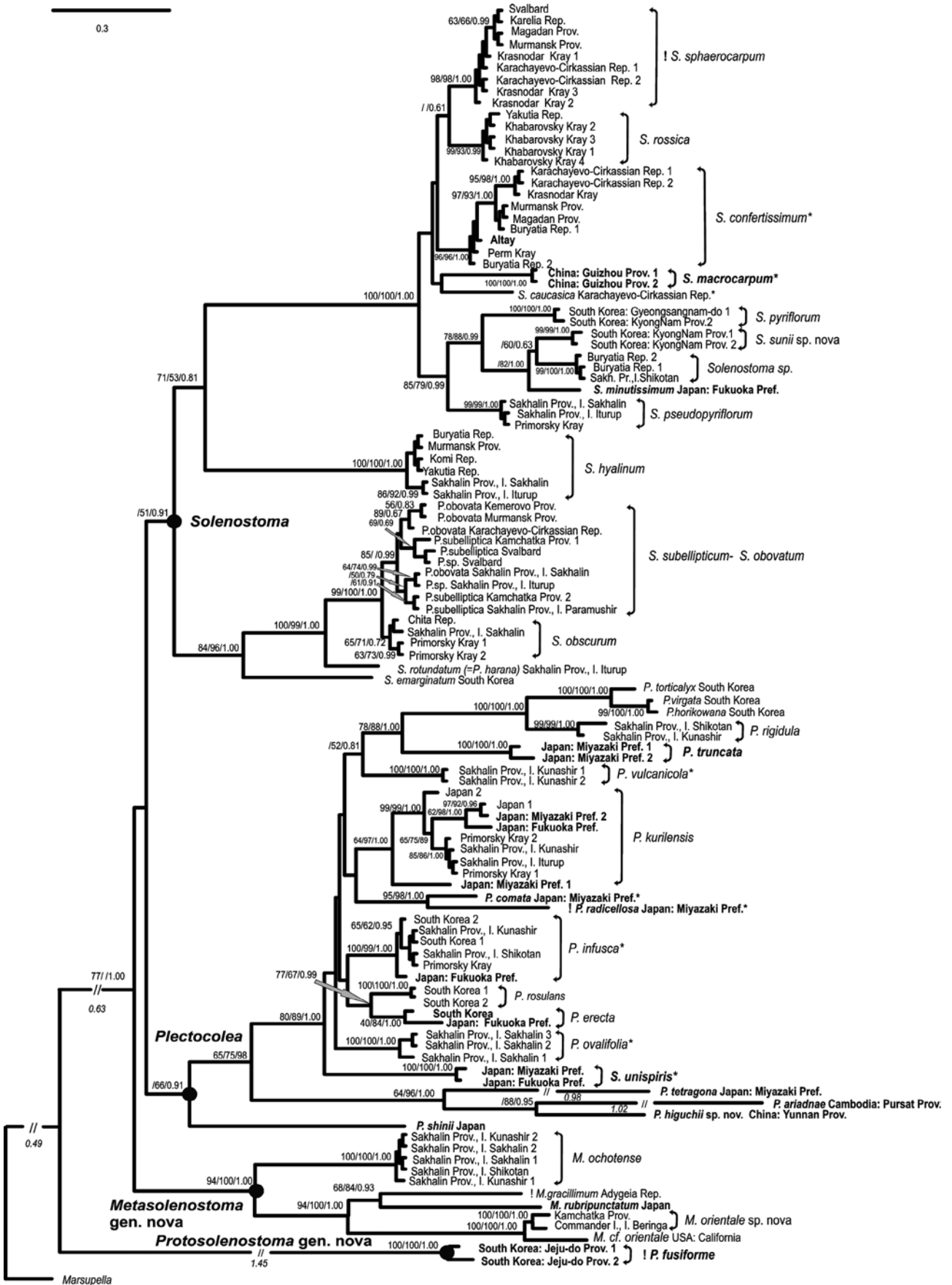


Figure 1 Phylogenetic tree for the *Solenostoma* – *Plectocolea* taxa based on the combined *trnL*-F+*trnG*-intron nucleotide sequence data using a Bayesian approach. The bootstrap support greater than 50 % calculated using maximum parsimony, maximum likelihood methods and Bayesian posterior probabilities greater than 0.50 are indicated after the slashes. The value of length for cut branches is pointed under phyla. Taxa with incongruent positions achieved in all phylogenetic calculations are marked by asterisks. The generitype species for each genus is marked by “!”. Specimens sequenced for this study are in bold. All taxa names are given in treatment provided in this study

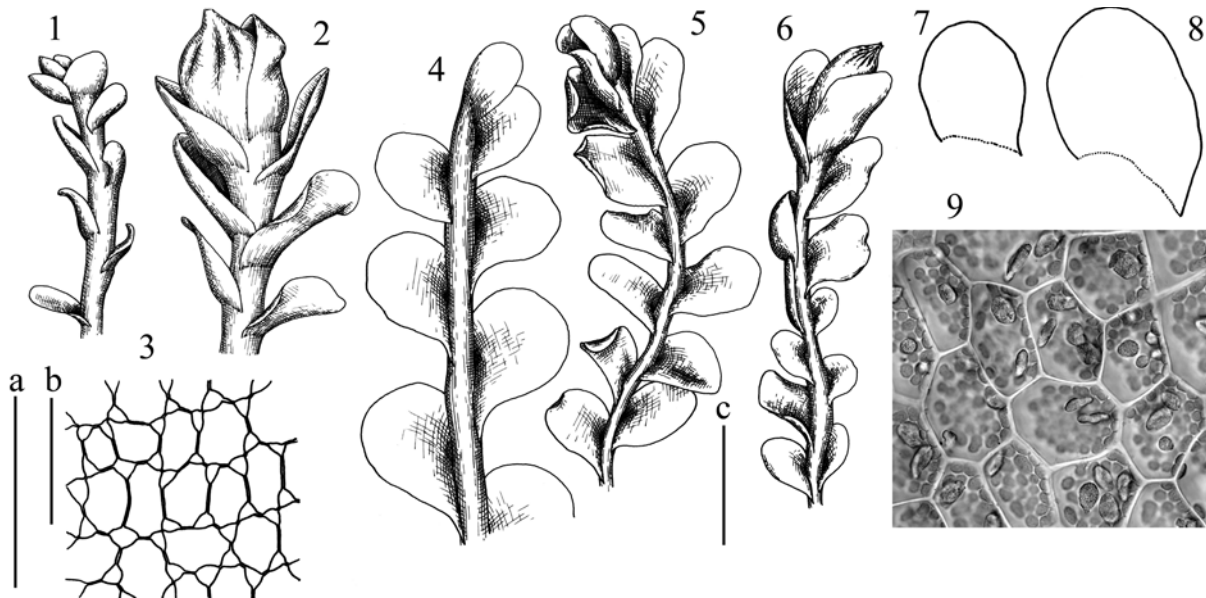


Figure 2 *Solenostoma rishiriense* Amak. (1–3): 1 – sterile plant, 2 – perianthous plant, 3 – midleaf cells. *Plectocolea shinii* (Amakawa) Bakalin: (4–8): 4, 5 – sterile plants, 6 – perianthous plant, 7, 8 – leaves, 9 – oil-bodies in the midleaf. Scales a – 500 μ m, for 1, 2; b – 50 μ m, for 3; a – 1 mm, for 4–8; c – 50 μ m, for 9. 1–3 – from NICH-53527 (holotype of *Solenostoma rishiriense*), 4, 9 – from Katagiri 3398 (HIRO), 5–8 – from NICH-104560 (holotype of *Jungermannia shinii*)

2012: Figs. 1, 2). We insist on the treatment of the species robustly nested in this clade – *P. hyalina*, *P. subelliptica*, *P. obovata*, *P. obscura*, *P. emarginata*, *P. barana* – as the members of the genus *Solenostoma* and pointed on Fig. 1 corresponding nomenclatural combinations. The newly sequenced specimen of *Solenostoma macrocarpum* from China is of an ambiguous relation, whereas the specimen of *S. minutissimum* from Japan was found to have a sister affinity (BS=82 % in ML, PP=1.00 in BA) to clade composed by the specimens of *S. sunii* sp. nov. and *Solenostoma* sp. (BS=60 % in ML, PP=0.63 in BA). Erroneously identified specimen of *Jungermannia pumila* from Russia (Altay) fits well in clade of *S. confertissimum*.

The type species of genus *Plectocolea* – *P. radiculosa* from Japan was firstly sequenced and found to be related to *P. comata* from Japan (BS=95 % in MP, BS=98% in ML, PP=1.00) in clade of *Plectocolea*-species, and this supported the treatment of the genus provided earlier in Bakalin & Vilnet (2012). The phylogenetic relations of taxa within *Plectocolea*-clade are also weakly supported. Additionally to *P. vulcanicola* from previous study, the affinity of *P. infusca*, *P. ovalifolia* and newly sequenced *P. unispiris* from Japan was not clarified here. On the contrary, *P. rosulans* having uncertain relationships compose a clade with two South Korean specimens of *P. erecta* (BS=77 % in MP, BS=67 % in ML, PP=0.99 in BA). Two Japanese specimens of *P. truncata* are in sister relation to clade of *P. rigidula*, *P. horikowana*, *P. virgata* and *P. torticalyx* (BS=78 % in MP, BS=88 % in ML, PP=1.00 in BA). After molecular investigation of two Japanese specimens morphologically assigned to *P. infusca* only one of them was attend to this species, whereas the other one was found in *P. kurilensis*-clade – taxon with high level of morphological and molecular variability (Table 3). Two Japanese specimens named *P. horikowana* on the molecular data are diverged from each other but also found within *P. kurilensis*-clade. The long branches in the base of *Plectocolea*-clade

belong to sister related *P. ariadne* from Cambodia, *P. tetragona* and *Solenostoma* sp. (*trnL*-F sequenced) specimens from Japan (BS=64 % in MP, BS=96 % in ML, PP=1.00 in BA), as well as to *P. shinii* from Japan (BS=66 % in ML, PP=0.91 in BA). After morphological reinvestigation specimen of *Solenostoma* sp. was assigned to a new species – *Plectocolea higuchii* sp. nov.

The value of *p*-distances for *trnL*-F and *trnG*-intron counted for species of genera *Solenostoma*, *Plectocolea* and *Metasolenostoma* in current treatment are shown in Tables 2–4 and partially discussed in species delimitation in taxonomical part. The most variable species according to the value of infraspecific *p*-distances counted separately for *trnL*-F and *trnG*-intron is *Plectocolea kurilensis*. The reason for high level of *p*-distances in *trnL*-F of *Metasolenostoma orientale* is incomplete sequence data for AY327777. The species delimitation is robustly supported by the value of *p*-distances with the exception of slightly genetically different species pairs discussed in Bakalin & Vilnet (2012) – *S. rossica* / *S. sphaerocarpum*, *P. subelliptica* / *P. obovata* / *P. obscura*, *P. horikowana* / *P. virgata* / *P. torticalyx*. Below we provide the morphological discussion of newly recognized or re-evaluated taxa.

Morphology and taxonomy

1. *Plectocolea shinii* (Amakawa) Bakalin, Polish Bot. Journ., 58(1): 132, 2013 (= *Jungermannia shinii* Amakawa, J. Hattori Bot. Lab. 33: 156, 1970. Type: JAPAN, Kagoshima Pref., Amami Islands, Okinoerabu Isl., 200 m alt., wet clay in limestone cave, leg. Shin T. 27.VII.1966 (NICH 104560))

The name (as *Jungermannia shinii*) was established by Amakawa (1970) based on material from Amami Islands (Japan). Amakawa (l. c.) recognized it as characterized by (l. c.: 158): “(1) the small, flaccid, light yellow-orange plant. (2) ligulate-ovate leaves, (3) thin-walled leaf cells without trigones and with nearly smooth of faintly verrucose cu-

ticle, (4) light brown rhizoids scattered on the stem, and (5) the shortly exerted, ovate perianth with a wide mouth". This species was recognized for a short time until it was considered as the synonym of *P. truncata* by Váňa & Inoue (1983) without giving detailed reasons (only the indication that the "taxon" is "extremely variable", l.c.: 134 was provided). Bakalin (2013) regarded that solution to be premature, but Bakalin's point of view was refused by Váňa et al. (2013) who suggested (again without explanations) that *P. shinii* as well as other related taxa are better to keep in the collective group *P. truncata*. In the course of the current research we were able to collect the fresh material from the *locus classicus* of the species and involve it in the DNA analysis that obviously confirmed that morphological differences noted by Amakawa (1970) support the recognition *P. shinii* at the species level. The value of *p*-distances between *P. shinii* and *P. truncata* achieved 8.4 % in *trnL*-F and 3.9 % in *trnG*-intron. We also found this species in a lot of additional localities and studied oil-bodies from the fresh material in the *locus classicus*. Since data on morphology and distribution were strongly improved, below we provide the description of the taxon based on available materials, as well as illustrations and specimens examined of the species.

Plants prostrate, soft, lax, pallid, pale brownish to yellowish brownish, semi-pellucid, 0.6–1.5 mm wide and 8–15 mm long, forming loose mats. Stem 100–150 µm in diameter, sparsely laterally branched (no subfloral innovations), brownish. Rhizoids rather numerous, colorless to brownish and grayish, obliquely spreading and united into unclear fascicles, or decurrent down the stem, but not forming distinct fascicle. Leaves subhorizontally inserted and subhorizontally oriented, only near perianth leaves inserted obliquely; distant to contiguous, obliquely ovate, 450–800 × 400–800 µm. Midleaf cells very thin-walled, subsodiametric to shortly oblong, 25–37 × 20–32 µm, trigones wanting to very small, concave, cuticle slightly striolate; cells along leaf margin 17–25 µm, very thin-walled, trigones very small, concave, cuticle striolate to nearly smooth. Dioicous. Perianth ca. 1000 × 600 µm, conical, pluriplicate, gradually narrowed to not beaked mouth, composed by elongate cells, exerted for 1/2 of its length; perigynium 1/5 of perianth length of lower; bracts transversely elliptic, larger than leaves, sheathing perianth in lower half and loosely obliquely spreading above. (Fig. 2).

Specimens examined: JAPAN, Kagoshima Pref., Amami Islands, Okinoerabu Isl., Syoryu limestone cave, 100 m alt., on moist limestone (paratype of *Jungermannia shinii*), leg. Takaki and Katsurayama 31.III.1967 (HIRO, s.n.), Shorhyu-do limestone cave, south opening (27°21'36.6"N 128°32'55.7"E), 150 m alt., on moist clay by stream, leg. Katagiri T., 3889 23.II.2014 (HIRO, duplicate in VBG and KPABG); MALAYSIA, Borneo Sabah, Mt. Gunung Emas Highland, 1600 m alt., on soil in evergreen forest, leg. Furuki T., 18931 14.XII.2003 (CBM 29596); THAILAND, Kanchanaburi Sai Yok Noi, Surisawat District, 150 m alt., limestone hill, on soil, leg. Kitagawa N., 24758 06.XI.1979 (KYO, s.n.), Nakhon Sawan (16°45'N 99°00'E), 800 m alt., steep loamy bank at roadside, leg. Touw A., 8259 20.XI.1965 (KYO, s.n.), Langsang National Park (16°50'N 99°05'E), 340 m alt., evergreen forest on limestone, along stream; on wet rocks, leg. Touw A. 8057 18.XI.1965 (KYO, s.n.), 8071 (KYO, s.n.).

Plectrocolea shinii may be separated from other morphologically similar species using the key published by Amakawa

(1970). It seems to be most similar to *P. granulata*, but differs from the latter in vestigial trigones, colorless, although rather common rhizoids and smooth or nearly so cuticle. This species also has unique ecological requirements occurring in limestone only (or nearly so), whereas the most other species of *Plectrocolea* (with the exception of such species as *P. vul canicola* that occurs on travertines) strongly avoid rocks with basic reaction.

The species has basal position within *Plectrocolea*-clade and probably it is one of the most primitive members of the genus due to the complex of features: poorly developed perigynium, unstable perianth shape and light-colored rhizoids. It is characterized by rather disjunctive distribution, although this thesis need to be verified since few data on the distribution of this taxon are available. Japanese Amami Islands, from where this species was described, are probably the northernmost locality of the species whose vast area is lying within South-East Asia.

2. *Plectrocolea ariadne* (Tayl.) Mitt. Trans. Linn. Soc. London, ser. 2, 3:198, 1891 (= *Jungermannia ariadne* Tayl. in Lehm. Pugillus, 8: 9, 1844)

This taxon was regarded by Amakawa (1968) and Váňa (1975) as the member of subgen. *Solenostoma* (and this point of view was accepted in many subsequent publications) due to barely developed perigynium. However, Mitten (1891) has showed this taxon to belong to the genus *Plectrocolea* and that was followed by Meijer (1959) who also revealed the similarity of oil bodies characteristic to other *Plectrocolea* with 'oil cells', i.e. *P. hasskarliana* and *P. tetragona*. In the practice, especially in sterile conditions, the delimitation of *P. hasskarliana* and *P. ariadne* presents considerable difficulty. The minor differences in leaf cell size and coloration are not constant. Even when perianthous material is available, the identification sometimes is very formal and reduced to measurements of relative perigynium length that is very variable. Thus *P. hasskarliana* and *P. ariadne* may be conspecific or may be very closely related. On the other hand *P. ariadne* and *P. tetragona* are highly divergent species, the value of *p*-distances for them is till 10.6 % in *trnL*-F and 9.6 % in *trnG*-intron. Thus, conducted DNA analysis evidently confirmed *P. ariadne* as a member of *Plectrocolea* in the narrow sense, but not of *Solenostoma*.

3. *Plectrocolea radiculosa* (Mitt.) Mitt. Trans. Linn. Soc. London, ser. 2, 3: 176, 1891. (= *Jungermannia radiculosa* (Mitt.) Steph., Sp. Hepat., 2: 75, 1901)

The previous publication (Bakalin & Vilnet 2012) showed at the tree of *Solenostoma* – *Plectrocolea* complex the presence of well defined clades; those were named as *Solenostoma* and *Plectrocolea*-clades. Whereas the name *Solenostoma* does not cause any doubts since the type species of this 'group' was sequenced for many times, the usage of '*Plectrocolea*' was somewhat doubtful, because the type species was not studied genetically before. Last spring, due to courtesy of Ms. Matsumoto (NICH) we were able to obtain fresh material of *Plectrocolea radiculosa* from Miyazaki Prefecture in Japan. That material was included in the present analysis and invariably showed the equivalence of *Plectrocolea* sensu Mitten (1891) and the clade tentatively named as *Plectrocolea*-clade in our

previous study (Bakalin & Vilnet, 2012). *P. radiculosa* was found to be related to *P. comata*, and that is not surprising if the character of rhizoids origin (mostly near ventral leaf base in *P. comata* and entirely so in *P. radiculosa*) will be taken into account. The main differences between two species are their growth form (with erect form of *P. radiculosa* seems to be more advanced), genetically they differ by 1.9 % in *trnL-F* and by 3.3 % in *trnG*-intron.

Table 2. The value of intraspecific and infrageneric *p*-distances for species: attended to the genus *Solenostoma*, n/c – non calculated due to presence of nucleotide data for single specimen only

Species	Intraspecific <i>p</i> -distances, <i>trnL-F</i> / <i>trnG</i> -intron, %	Infrageneric <i>p</i> -distances, <i>trnL-F</i> / <i>trnG</i> -intron, %														
		<i>sphaeroc.</i>	<i>rossica</i>	<i>confjert.</i>	<i>pyriflorum</i>	<i>sumii</i>	indet.	<i>pseudopyriflorum</i>	<i>minut.</i>	<i>caucasic.</i>	<i>maurac.</i>	<i>hyalina</i>	<i>subell/obov.</i>	<i>obscura</i>	<i>rotund.</i>	<i>emarg.</i>
<i>S. sphaerocarponum</i>	0.1/0															
<i>S. rossica</i>	0.08/0	0.8/1.0														
<i>S. onjerissimum</i>	0.3/0.2	1.7/1.1	2.3/0.5													
<i>S. pyriflorum</i>	0.2/0	1.7/2.9	2/2.7	2.5/2.5												
<i>S. sumii</i>	0.2/0	2.7/2.6	2.9/2.5	3.7/2.3	2.2/1.6											
<i>Solenostoma</i> indet.	0/0	3.1/2.4	3.4/2.2	4.4/2.0	3.4/2.0	1.6/0.9										
<i>S. pseudopyriflorum</i>	0/0	2/1.7	2.1/1.5	3.1/1.4	2.3/2.4	2.8/2.2	2.3/1.9									
<i>S. minutissimum</i>	n/c	3.1/2.9	3.9/2.9	4.5/2.7	3.1/2.2	1.1/1.7	1.7/1.4	2.8/2.5								
<i>S. caucasicum</i>	0/0	1.6/1.4	2.2/1.6	2.4/1.3	2.6/2.7	3.5/2.6	3.8/2.6	2.8/2.0	3.3/3.0							
<i>S. macrocarpum</i>	0/0	2.1/2.2	2.4/1.7	2.8/1.9	3.2/3.9	4.1/3.8	4.1/3.5	3.3/2.4	4.0/4.0	2.1/2.5						
<i>S. lyallianum</i>	0.3/0	5/7.6	5.1/7.4	6.1/6.9	6.1/8.8	6.5/8.1	6.4/8.0	5.1/8.3	7.6/8.5	5.5/7.7	6.3/9.0					
<i>S. subellipticum/obovatum</i>	0.5/0.2	5.8/6.5	5.8/6.4	6.4/6.1	6.2/7.3	6.1/6.9	7.2/7.1	6.7/7.2	7.4/7.9	6.4/6.4	6.8/8.1	6.7/6.2				
<i>S. obscurum</i>	0.2/0	5.9/6.2	5.9/6.1	6.5/5.8	6.3/7.0	6.2/6.6	7.4/6.8	6.7/6.9	7.6/7.6	6.7/6.1	7.7/7.8	6.6/6.0	0.9/0.3			
<i>S. rotundatum</i>	n/c	6.1/6.3	6.1/6.3	6.8/6.0	6.3/7.1	6.6/6.9	6.5/7.1	5.6/7.0	6.7/7.6	7.1/6.3	7.2/7.8	6.3/6.3	2.2/2.0	2/1.7		
<i>S. emarginatum</i>	n/c	5.6/6.7	5.8/6.4	6.1/5.9	6.4/7.4	6.7/7.0	7.7/7.3	6.2/7.1	8/8.2	6.6/6.4	7.7/7.4	6.6/6.2	4.4/3.6	4.2/3.3	4.1/3.9	

Table 3. The value of intraspecific and infrageneric *p*-distances for species: attended to the genus *Plectocolea*, n/c – non calculated due to presence of nucleotide data for single specimen only

Species	Intraspecific <i>p</i> -distances, <i>trnL-F</i> / <i>trnG</i> -intron, %	Infrageneric <i>p</i> -distances, <i>trnL-F</i> / <i>trnG</i> -intron, %																		
		<i>vulcan.</i>	<i>ovul.</i>	<i>kauri.</i>	<i>influsca</i>	<i>comata</i>	<i>radical.</i>	<i>tortic.</i>	<i>bor/nir</i>	<i>rigid.</i>	<i>trun.</i>	<i>rosul.</i>	<i>unisp.</i>	<i>erecta</i>	<i>shimii</i>	<i>tetragona</i>	<i>ariadnae</i>	<i>bignubii</i>		
<i>P. vulcanicola</i>	0/0																			
<i>P. ovalifolia</i>	0.3/0.2	2.1/2.8																		
<i>P. kauriensis</i>	1/0.7	2.8/2.6	2.6/3.0																	
<i>P. influsca</i>	0.1/0.1	2.5/2.2	1.8/2.3	2.4/2.2																
<i>P. comata</i>	n/c	3.6/2.6	3.2/3.0	3.3/3.3	2.6/2.6															
<i>P. radiculosa</i>	n/c	4.4/4.3	4/5.1	3.9/5.1	3.2/4.4	1.9/3.3														
<i>P. torticalyx</i>	n/c	4.1/5.3	4.5/5.7	4.6/5.8	3.9/5.5	5.7/6.6	6.4/7.6													
<i>P. horicomana/virgata</i>	0.2/0	4.3/5.9	4.5/6.0	4.9/6.0	4.2/5.4	6/7.2	6.8/8.2	0.7/1.1												
<i>P. rigidula</i>	0.4/0.4	4.5/4.3	4.6/4.7	4.8/4.2	4.2/3.9	5.9/5.6	6.8/7.2	1.9/3.1	2.2/3.0											
<i>P. truncata</i>	0.5/0.3	4.1/3.2	4.8/3.5	5.2/3.5	4.2/2.8	5.6/3.6	6.3/5.4	6.2/4.9	6.5/5.4	6.5/3.9										
<i>P. rosulans</i>	0/0	2.5/1.9	1.9/2.2	2.7/2.4	1.9/1.5	3.2/2.8	3.8/4.4	3.9/4.7	4.2/5.3	4.6/4.1	5.2/2.7									
<i>P. unispinis</i>	0.2/0	5.1/2.8	4.6/2.8	4.8/2.6	4.3/2.2	4.3/3.2	5.7/4.9	7.6/5.8	7.7/6.1	7.8/4.5	6.6/3.0	4.9/2.3								
<i>P. erecta</i>	0.6/n/c	2.2/2.7	1.6/2.9	2.3/3.0	1.9/2.2	3.2/3.4	3.7/5.2	4.1/5.3	4.6/6.0	4.6/4.8	4.4/3.5	1.5/1.3	4.5/2.4							
<i>P. shimii</i>	n/c	7.1/3.4	7.1/4.2	7.9/4.0	7/3.5	7.6/4.9	8.6/6.3	9.1/5.7	9.1/6.0	9.5/5.9	8.4/3.9	6.5/3.2	8.1/4.3	6.9/4.0						
<i>P. tetragona</i>	n/c	6.8/11.7	6.7/11.7	7.5/12	6.3/11.9	6.4/11.8	8.1/13.2	8.2/12.4	8.2/12.6	8.3/13.3	9.4/12.0	6.1/11.3	7.9/11.9	6.7/11.6	8.1/10.1					
<i>P. ariadnae</i>	n/c	10.9/8.3	11.2/8.4	11.4/8	10.9/8.2	9.8/8	12/9.3	11.2/11.0	11.9/11	12/10.6	10.8/9.1	11.3/8.1	10.9/8.0	11.1/8.6	12.9/7.1	10.6/9.6				
<i>P. bignubii</i>	n/c	6.1/n/c	6.3/n/c	6.6/n/c	6.5/n/c	7.2/n/c	8.6/n/c	8/n/c	8/n/c	8.3/n/c	8.4/n/c	6.3/n/c	8.1/n/c	6.4/n/c	6.2/n/c	8.8/n/c				

Table 4. The value of infraspecific and infrageneric *p*-distances for species. attended to the genus *Metasolenostoma*. n/c – non calculated due to presence of nucleotide data for single specimen only

Species	Intraspecific <i>p</i> -distances. <i>trnL-F/trnG-intron</i> . %	Infrageneric <i>p</i> -distances. <i>trnL-F/trnG-intron</i> . %				
		<i>ochotensis</i>	<i>gracillima</i>	<i>rubripun.</i>	<i>orientale</i>	cf. <i>orientale</i>
<i>M. ochotense</i>	0.1/0					
<i>M. gracillimum</i>	n/c	3/6.2				
<i>M. rubripunctatum</i>	n/c	4.8/6.2	3.4/4.9			
<i>M. orientale</i>	1.0/0	5.4/6.3	3.6/5.6	5.3/5.1		
<i>M. cf. orientale</i>	n/c	6.0/6.9	4.8/6.1	6.4/5.8	2.5/1.3	

4. *Plectocolea higuchii* Bakalin et Vilnet *sp. nov.*

Plants pallid, semi-pellucid, erect in loose patches, soft, whitish to pale greenish, with markedly violet tinged of evidently colored shoot apices (especially obvious near leaf margins), 2.5–3.5 mm wide and 20–40 mm long. Stem whitish, 425–525 µm in diameter, rarely laterally intercalary branched (branches produces by weakly developed shoots only). Rhizoids rather numerous, obliquely spreading or decurrent down the stem, but not forming distinct fascicle, originated from leaf lamina and ventral side of stem (mostly originated from stem near ventral leaf base), colorless to grayish. Leaves subtransversely to slightly obliquely inserted, dorsally for 1/2–4/3 of stem width decurrent, ventrally arcuately to transversely inserted, up 1/2 of stem width decurrent, contiguous to subimbricate, rather distant, concave-canaliculate to concave, erect to obliquely spreading, undulate to slightly crispate at margin, transversely elliptic, commonly with cordate base, rarely retuse, truncate to emarginate at apex, 1125–1875 × 1875–2750 µm. Cells in the midleaf subisodiametric to oblong, 37.5–80.0 × 32.5–55.0 µm, thin-walled, trigones small, concave, cuticle distinctly papillose; cells along margin 25.0–37.5 µm, thin to slightly thick-walled, with loosely to evidently thickened external wall, trigones small to moderate in size, concave, cuticle loosely papillose. [other unknown] (Fig. 3).

Holotypus: CHINA. Yunnan Prov. Dali State, South of Caojian (25,40956N 99,20695E), wet cliffs at roadside, 1800 m alt. leg. M. Higuchi, 48795 17 Sept. 2008 (TNS 209341, isotypes in VBG and KPABG).

In the course of study of the material from Yunnan, collected by Dr. M. Higuchi, we were able to find one peculiar specimen that, due to morphology and DNA evidences, should be regarded as the new taxon of the species rank. At the first look, the plants of this species are strongly similar to *Metasolenostoma orientale* due to erect growth form, pellucid and soft plants with evident violet tint. Later, in microscope studies, it was found that rhizoids are produced by leaf lamina, and this does not allow to apply the name *M. orientale*. Due to DNA analysis, the species obviously belongs to *Plectocolea*-clade and relates to *Plectocolea ariadne* and *P. hasskarliana* (from which it differs in the absence of red to purple pigmentation and the presence of violet color, a few rhizoids originated from leaf lamina, versus very dense and common laminar rhizoids in the both later species) and *Plectocolea tetragona* (differs in colorless not fasciculate rhizoids, versus deep purple and united in clear fascicle that decurrent down the stem rhizoids). The values of *p*-distances to the closest relative species (with *P. ariadne* – 8.8 % in

trnL-F, with *P. tetragona* – 6.2 % in *trnL-F*) suggest *Plectocolea higuchii* as a robust species.

Unfortunately this species was collected only once in sterile condition, thus no features of perianth and androecia are available for study, as well as oil-bodies structure was not studied. Only little is known about ecological preferences of this new species. Most probably it grows in open places at temperate broadleaved forest belt in south-east China.

5. *Metasolenostoma* Bakalin et Vilnet *gen. nov.*

Description. Plants delicate, pellucid, mostly flaccid, soft. Epidermal stem cells elongate (2–5 times longer than wide). Rhizoids colorless or only slightly colored. Leaves very obliquely inserted. Leaf cells with small to wanting trigones, along margin mostly larger than in the midleaf and commonly with thickened cell walls.

Type species: *Metasolenostoma gracillimum* (Sm.) Vilnet et Bakalin *comb. nov.*

Basionym: *Jungermannia gracillima* Sm. English Botany 32: 2238. 1811. (= *Solenostoma gracillimum* (Sm.) R.M. Schust. Hepat. Anthocerotae N. Amer. 2: 972. 1969.

Other taxa:

Metasolenostoma gracillimum f. *crenulatum* (J.E. Smith) Vilnet et Bakalin *comb. nov.* Basionym: *Jungermannia crenulata* J.E. Smith in Sowerby, Eng. Bot., pl. 1463, 1805

Metasolenostoma orientale Bakalin et Vilnet *sp. nov.* (see below)

Metasolenostoma rubripunctatum (S. Hatt.) Vilnet et Bakalin *comb. nov.* Basionym: *Plectocolea rubripunctata* S. Hatt. J. Hattori Bot. Lab. 3: 41. f. 36. 1948[1950].

Metasolenostoma ochotense Vilnet et Bakalin *comb. nov.* Basionym: *Solenostoma ochotensis* Bakalin and Vilnet The Bryologist 115(4): 575, 2012.

The involving of additional material into reconstruction of phylogenetic relationships within *Solenostoma* – *Plectocolea* group revealed the separation of clade previously placed as a poorly supported subclade in *Solenostoma*-clade (Bakalin & Vilnet 2012, Figs 1, 2) including at least four species ‘*S. ochotensis*’, ‘*S. orientale*’, ‘*S. gracillimum*’ and ‘*P. rubripunctata*’. The species of this group (was also discussed before on the example of ‘*S. ochotensis*’, cf. Bakalin and Vilnet 2012) are characterized by the presence of low perigynium, prostrate growth form, colorless or nearly so rhizoids, larger cells along leaf margin and pellucid to pale colored plants. The only one exception is ‘*S. orientale*’ that is characterized by erect growth form and is one of the most advanced variants of the group. This clade appears to be a transitional one between ‘true’ *Solenostoma* and *Plectocolea* and currently we regard it as distinct genus of the *Solenostoma* – *Plectocolea* complex.

6. *Metasolenostoma rubripunctatum* (S. Hatt.) Vilnet et Bakalin

This is one of a few species of old ‘*Jungermannia* s.l.’ bearing gemmae. One of them (*Liochlaena lanceolata* Nees) was transferred to another family – Delavayellaceae R.M. Schust. and another (*Endogemma caespiticia* (Lindenb.) Konstant., Vil-

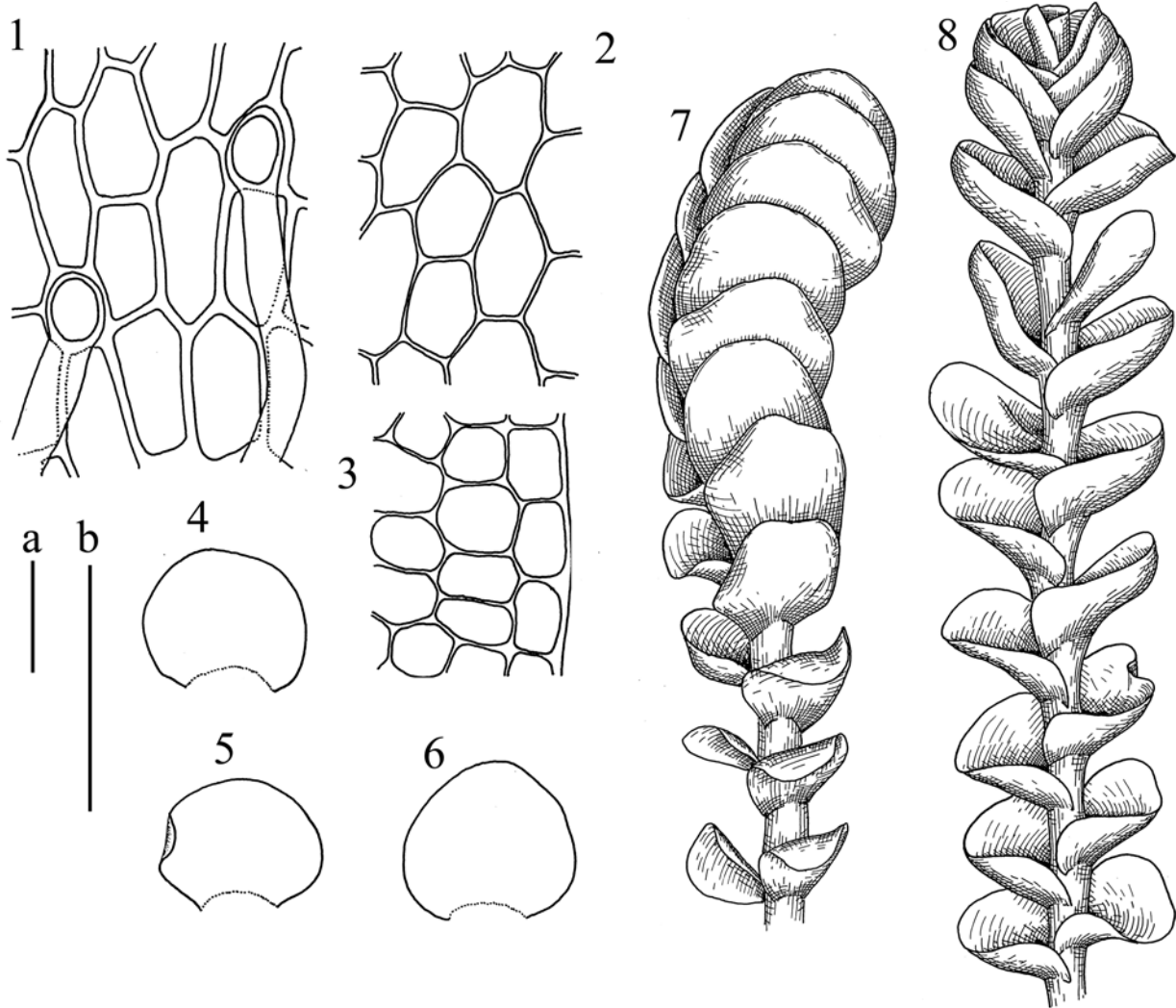


Figure 3 *Plectocolea biguchii* Bakalin et Vilnet. 1 – rhizogenous cells in leaf lamina in lower half of the leaf, 2 – midleaf cells, 3 – cells along leaf margin, 4–6 – leaves, 5, 6 – plant habit. Scales: a – 100 μ m, for 1–3, b – 3 mm, for 4–6. All from TNS-209341

net and A.V. Troitsky) – to specially described monotypic genus and corresponding monotypic family (Endogemmataceae Konstant., Vilnet et A.V. Troitsky). Thus the rather principal question existed, whether representatives of *Solenostoma* – *Plectocolea* complex are able to produce gemmae. Due to available data this is the first attempt to sequence this gemmae-bearing taxon. As far as we found this species is related to *Metasolenostoma gracillimum*, which is not surprising. Aside of gemmae production both taxa are very similar in morphology (and *M. rubripunctata* was also many times misidentified by F. Stephani as *M. gracillimum*). Both taxa are similar in prostrate growth form, swollen and larger cells along leaf margin, poorly developed leaf cells trigones and short perigynium. Rather more difficult to find robust differentiations, that are unstable aside distribution (East Asian versus amphi-Atlantic), ability to develop the gemmae and only slightly larger cells along leaf margin (versus noticeable larger in most common phases of *M. gracillimum*). Nevertheless, the value of *p*-distances between *M. rubripunctata* and *M. gracillimum* are 3.4 % in *trnL*-F and 4.9 % in *trnG*-intron that characterized these taxa as ‘good’ species.

Specimens examined: CHINA, Fujiang Prov., Nanjing Co., subtropical rainforest reservation, on soil in subtropical rain forest,

leg. Chang K.C., 542 (IFP 00024592), Guizhou Prov., Kaijiang Co., Xiang Zhi Stream (26°46'59.5"N 106°54'44.5"E), 1200 m alt., broadleaved (mostly evergreen) forest on steep slope to valley of stream, moist clay on slope, in part shade, leg. Bakalin V.A., 19.XI.2013. China-51-52-13 (VBGI), Hunan Prov., Dayong Co., Zhangjiajie, on soil, 580 m alt., leg. Li D.K., 17955 (IFP 00024593), Yanling Co. (26°30'N 114°04'E), 1100 m alt., on sand in evergreen broadleaved forest, leg. Koponen T. et al., 57094 13.X.1998 (F, C0076960F), Yunnan Prov., Bijiang Co., Mt. Gaoligongshan, leg. Zang M., 5502 (IFP 00000427), Tengchong Co., Heshun, near Dalongtan, on soil, leg. Li X.J., 292 (IFP 00024589); INDIA Darjeeling, 2000 m alt., leg. Saxena B.N. X.1979 (NICH 378927), JAPAN, Hokkaido Pref., Rebun Island, Momiowa, leg. Fukuhara M., 182.07.VIII.1954 (NICH 75653), Chiba Pref., Choushi-shi, Saruta Shrine, 30 m alt., on soil in forest, leg. Furuki T., 9403 29.IX.1990 (CBM 13593), Aichi Pref., route from Gyojagoe to Yuya, 400 m alt., leg. Deguchi H., 4129 27.X.1969 (KYO, s.n.), Awa Pref., Nanishi-gun, Yakiyamadera Mt. (paratype of *Plectocolea rubripunctata*), leg. Iba T., 14 10.III.1944 (NICH 12339), Fukuoka Pref., Tagamagun, Soeda-machi, Hiko-san Mt., along upper course of Shioi River (33°28'20"N 130°54'07"E), 770–900 m alt., broadleaved (evergreen and deciduous)-coniferous (*Cryptomeria-Chamaecyparis*) mixed forest along stream, wet cliff on slope, in partial shade, leg. Bakalin V.A., J-7-25-14 17.III.2014 (VBGI), J-7-36-14 (VBGI), Miyazaki Pref., Minaminaka-gun, Kitago, in terra nuda (paratype of *P. rubripunctata*), leg. Hattori S., 9873 02.XII.1948 (NICH 12349), Kochi Pref., Tosa (was identified as *Nardia crenulata* by F. Stephani), leg. Makino T., XI.1895 (SAP, s.n.), Kyoto Pref., Kamo, Kizu-cho, on exposed surface of cuts, leg. Deguchi H., 2204 24 01 69 (KYO, s.n.), route from Ide-cho to Emon shrine, 200 m alt., leg.

Deguchi H., 4195 09.IX.1969 (KYO, s.n.), Mie Pref., Gochi, 50 m alt., on cliffs (Hepaticae Japonicae Exsiccatae ser. 16 (1969) n. 778 *Jungermannia rubripunctata*), leg. Yamada K. 04.I.1969 (SAP, s.n.), Miyazaki Pref., Nakago, 300 m alt., ad tophum explanata, mesophila (Hepaticae Japonicae Exsiccatae ser. 2 (1947) n. 60 *Plectocolea rubripunctata* spec. nov., 'materia originalis'), leg. Hattori S. X.1946 (SAP, s.n.), Nakago 300 m alt., ad tophum explanata, mesophila (isoparatype of *Plectocolea rubripunctata*, published in Hepaticae Japonicae ser. 2., 1947, N 60), leg. Hattori S. X.1946 (NICH, 41667), Nagasaki Pref., Taradake Mt., 250 m alt., on bank, leg. Amakawa T., 2268/2221 24.III.1957 (HIRO, s.n.), Oita Pref., Bungonakamura - Handa Plateau, on bank, leg. Amakawa T., 1822/2222 13.III.56 (HIRO, s.n.), Kagoshima Pref., Kimotuki-gun, Tashimura, between Tashiro and Uchimonaki, bank (holotype of *Plectocolea rubripunctata*), leg. Hattori S., 1337 01.IV.1939 (NICH 11965); NEPAL, East Nepal, 1650 m alt., on soil, leg. Higuchi M., 18366 05.XI.1988 (HIRO, s.n.).

7. *Metasolenostoma orientale* Bakalin et Vilnet sp. nov.

Description. Plants ascending to erect, in loose patches 1.0–2.8 mm wide, up 15–40 mm in length, pale green to whitish, sometimes with brownish tint become brownish to black and violet in leaf margin, especially near apex and perianth. Stem 170–300 µm in diameter, orbicular in cross section, rarer elliptic 315–420 × 280–390 µm, branching ventral, rarely occur, dorsal surface cells thin-walled to slightly thick-walled, trigones indistinct or small concave, 78–200 × 17–42 µm. Rhizoids isolated to dense or virtually absent, erect to obliquely spreading, separated or united into indistinct fascicles, rarely forming mat under ventral side of stem, colorless to brownish. Leaves distant to contiguous and subimbricate, on big shoots with undulate leaf margin, rarely retuse in apex, commonly with blackish to brownish border on leaf margin, inserted at angle of (10)40–70(80)° with axis, dorsally decurrent for 1/3–3/3 of stem width, on ventral side insertion line arcuate to straight, transverse, not or barely decurrent, (615)1000–1750 × (665)1200–2135 µm ((0.7–0.9) 1–1.3:1), widely obliquely elliptic-triangular to orbicular and widely ovoid, at the base sheathing the stem, loosely canalicate to concave or flattened above, obliquely spreading laterally. Cells in the midleaf thin, rarely slightly thickened, mostly oblong to hexagonal, 30–75 × 25–54 µm, with small concave trigones, along margin 28–52 µm, mostly with thickened and colored external wall, cuticle papillose to smooth in lower half of leaf and smooth above, rarely finely striolate throughout. Dioicous. Perianth colorless to blackish commonly becoming brownish, black and violet in the keels, terminal, rhomboidal, 4–5-keeled with distinct 2 lateral and 1 dorsal keels and smoothed or indistinct 2 ventral keels, ca. 2200 × 1100 µm; perigynium virtually absent; female bracts the same size with sterile leaves, bracteole absent. Androecia intercalary, in 5–8 pairs, with 2(–3) antheridia per bract, stalk biseriate; bracts similar to sterile leaves, but inflated near the base. Sporophyte unknown (Fig. 4).

Holotypus: RUSSIA, Kamchatka Peninsula, Central Kamchatka (55°45'N 157°53'E), 900 m alt., wet travertine cone, leg. Bakalin V.A., K-88-13-01 29.VIII.2001 (KPABG 103946, duplicate in VBG1)

Other specimens examined (paratypes): CANADA, British Columbia, Queen Charlotte Islands, Craham I., leg. Schofield W.B., 19.V.1961 (ny00099055); JAPAN, Akita Pref., Kurikoma Mt., leg. Saito K. 15.VIII.1965 (NICH 78293), Hokkaido Pref., Hidaka Mt., valley of small river with cliffy shores in orohemiboral (*Abies-Picea-Cercidiphyllum-Acer-Ulmus-Alnus*) woodland, leg. Koponen T.,

14307 28.VII.1970 (NICH 116770), Akita Pref., Kurikoma Mt., leg. Saito K. 15.VIII.1965 (NICH 78293), Kyoto Pref., Otodaninotaki, 400 m alt., moist rocks, leg. Kodama T., 39491 22.IX.1969 (NICH 104338); RUSSIA, Kurils Islands, Kunashir Island (44°00'20"N 145°46'23"E), 100 m alt., hollows in thermal mire, leg. Bakalin V.A., K-52-18-06 10.IX.2006 (VBG1), (44°29'20"N 146°06'16"E), 50 m alt., hot (40°C) strata of travertine, leg. Bakalin V.A., K-41-4-06 30.VIII.2006 (VBG1), (43°51'52"N 145°30'10"E), 150 m alt., along hot thermal spring, leg. Bakalin V.A., K-45-10-06 04.IX.2006 (VBG1), (43°53'04"N 145°27'43"E), 30 m alt., cliffs near waterfall, leg. Bakalin V.A., K-46-19a-06 06.IX.2006 (VBG1), Iturup Island (45°02'21"N 147°59'00"E), 301 m alt., stream with traces of sulphur, leg. Bakalin V.A., K-54-1-05 15.IX.2005 (VBG1), (45°06'13"N 147°59'16"E), 416 m alt., along sulphur stream, leg. Bakalin V.A., K-53-2-05 15.IX.2005 (VBG1); U.S.A., California, Plumas Co., leg. Brinda J.C., 2836 26.III.2011 (MO, duplicates in VBG1 and KPABG), Colorado, Mineral Co., leg. Cooper D.J. 09.VIII.1999 (NY00580773), Oregon, Douglas Co., leg. Wagner D.H. 03.IV.1977 (NY00244529), Lincoln Co., on rock at back end of beach where it meets the bluff, wet seepy area, leg. Halse R.R. 22.VI.2000 (NY00693682), Washington, Rainier Co., leg. Jilett J.G. VII.1919 (NY 00243847), Baker Mt. (47°35'N 122°17'W), 1400 m alt., path in the forest, leg. Konstantinova N.A., A79/8-95 13.IX.1995 (KPABG, duplicate in VBG1).

When starting the special research of hepatic flora in the Russian Far East, Bakalin (2010, etc.) referred all *Solenostoma*-like plants growing in volcanically modified habitats (travertine cones, thermal springs, etc.) and characterized by the presence of leaf rim of slightly swollen cells, to widely distributed in eastern Asia *S. fusiforme* or to misinterpreted in that time *S. koreanum*. It was also discussed and illustrated for North America (Bakalin 2012) under the name of *Solenostoma fusiforme*. However, after study of type specimens in G, Bakalin found the specimens of *Solenostoma fusiforme* and *S. koreanum* are to be identical, and that confirms synonymization of these names by Inoue (1975) and Vána (1975). Nevertheless *S. fusiforme* is different from the specimens named as '*S. fusiforme*' from the Russian Far East. Due to this evidence we included the material of 'true' *S. fusiforme* from South Korea to this study and did not register their relation with previously tested specimens of *S. fusiforme* from the Russian Far East (Bakalin & Vilnet 2012). According to tree topologies we regard the first species to belong in a new separate genus – *Protosolenostoma* gen. nov. (see below) whereas another one is considered to be a new species – *Metasolenostoma orientale*.

The new species is characterized by: 1) pellucid soft texture, 2) elongated stem epidermal cells, 3) sheathing leaves, commonly overlapping lower half of the next situated leaf, 3) wanting or nearly so trigones in the leaf cells, 4) slightly enlarged leaf cells along leaf margin (sometimes with unclearly thickened walls). Due to very special habit of this species there are only a few taxa it may be easily mistaken for. It probably may be confused with *Plectocolea vulcanicola*, especially lax forms in sterile conditions, when two taxa are sometimes impossible to separate. It should be mentioned that phylogenetic affinity of *P. vulcanicola* in *Plectocolea*-clade still is not resolved. The perianthous plants strictly differ in the presence/absence of perigynium. In sterile conditions two species may be separated due to sheathing leaves of *Metasolenostoma orientale*, those commonly overlap the half of the next situated leaf versus obliquely spreading leaves in *Plectocolea vulcanicola*. The species has some similarities with *Protosolenostoma fusiforme*, from which it differs in: 1) common presence of blackish to black pigmentation

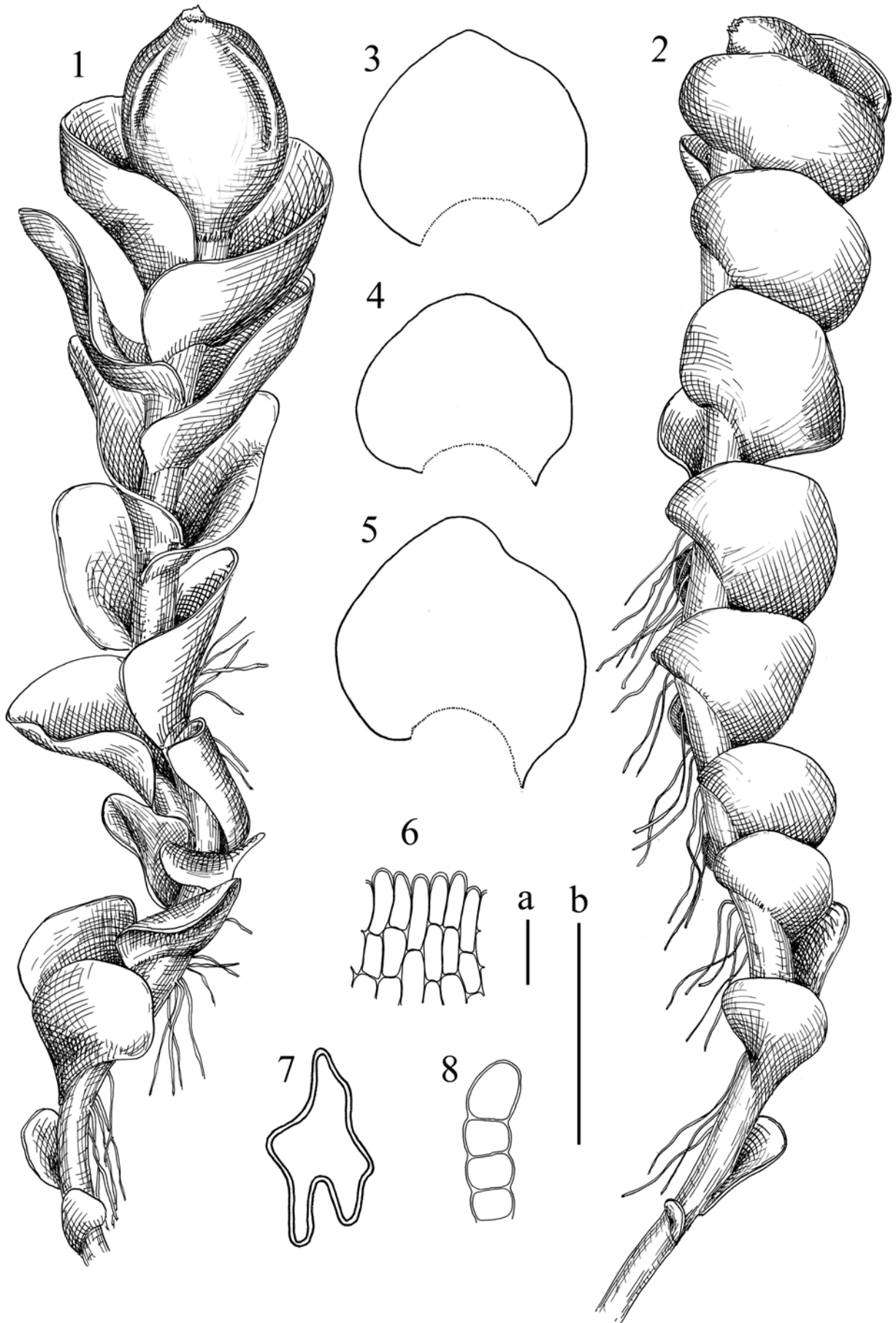


Figure 4 *Metasolenostoma orientale* Bakalin et Vilnet. 1 – perianthous plant, 2 – sterile plant, lateral view, 3–5 – leaves, 6 – perianth mouth, 7 – perianth cross section in its middle part, 8 – leaf cross section near leaf margin. Scales: a – 50 μ m, for 6, 8; b – 2 mm, for 1–5, 7. All from K-88-13-01 (VBGI)

with violet tint in shoot apices, 2) ascending to erect growth form versus prostrate to ascending (evident in perianthous plants only) in *P. fusiforme*, 3) although general shoot widths measurements are largely overlapping, *M. orientale* looks larger, because leaves commonly sheathing the stem, while in *P. fusiforme* they are subhorizontally oriented and laterally spreading, this corresponds to 4) strong difference in leaves size that mostly fits $1000\text{--}1750 \times 1200\text{--}2135 \mu\text{m}$, when in *P. fusiforme* they are mostly $550\text{--}725 \times 575\text{--}875 \mu\text{m}$, and 5) *P. fusiforme* has evidently developed perigynium, that reach 1/4 of perianth length, versus virtually absent perigynium in *M. orientale*.

Distribution. Azonal nearly Amphi-Pacific. Within the latter area the taxon is very common in volcanically modified habitats along North Pacific part of 'Pacific Ring of Fire'. Within the Russian Far East, it is locally abundant in Eastern Kamchatka and South Kurils (surprisingly absent in North Kurils). Southward it was recorded in some localities in Japan (Hokkaido, Akita, and southernmost in Kyoto Prefectures). In North America, the distribution is confined to its western half and seems to bear relict character. The species occurs in some isolated localities in Aleutians (Vána 1975), Washington, Oregon and, surprisingly, Colorado in the U.S.A., and in British Columbia in Canada. At least half of the localities are in the areas of extinct volcanism. In comparison with *Protosolenostoma fusiforme*, *Metasolenostoma orientale* seems to have much northern distribution and is going to New World via Aleutians, versus distribution confined to temperate to subtropical Japan and southern tip of Korean Peninsula.

Ecology. Nearly neutrophilic to acid tolerate hygrophyte. The preferable habitats of the species in the Russian Far East are wet travertine cones, where water is enriched not only by sulphur, but also compound of arsenic and a lot of rare earth elements, e.g. uranium (Dulchenko, pers. comm.). Other habitats are thermal pools and streams (acidic to neutral reaction), where the species survives in the diapason of pH varying from 1.8 to 6.8 (Bakalin et al. 2011). The habitats of *M. orientale* do not freeze in winter due to the abovementioned specificity. The species is growing from Subarctic zone in Kamchatka (starting from mountain tundra belt, at the elevation over than 1300 m alt.) to broadleaved deciduous forests in South Kurils, but only along these peculiar and certainly azonal habitats.

The specimen provisionally identified as *Solenostoma fusiforme* from U.S.A. (Brinda, 2836, MO) molecularly is closely related to *Metasolenostoma orientale*-clade, although quite different from both specimens from the Russian Far East. The values of *p*-distance count 2.5 % in *trnL-F* and 1.3 %, in *trnG*-intron that higher than level of infraspecific variability but significantly lower than level of infrageneric variability in related taxa (Table 4). Both Russian specimens of *M. orientale* revealed variation only in *trnL-F* (*p*-distances – 1 %). The current process of speciation is traced only in DNA level, whereas morphological differentiation of geographically remote populations is still absent. It is possible to elevate two subspecies within *M. orientale*, but due to restricted data we prefer to treat Californian specimen as *M. cf. orientale*.

8. ***Protosolenostoma* (Amak.) Bakalin et Vilnet stat. nov.** (Basionym: *Jungermannia* sect. *Protosolenostoma* Amak. Journ. Hattori Bot. Lab. 22: 55. 1960)

Type species: *Solenostoma koreanum* Steph. Sp. Hepat. 6: 81. 1917., = ***Protosolenostoma fusiforme*** (Steph.) Vilnet et Bakalin **comb. nov.** Basionym: *Nardia fusiformis* Steph. Bull. Herb. Boissier 5: 99. 1897.

Amakawa (1960) described *Jungermannia* sect. *Protosolenostoma* to place '*Jungermannia koreana*' and '*J. fusiformis*'. This section was regarded as the 'transition' to '*Jungermannia* subgen. *Luridae*' and '*J.* subgen. *Plectocolea*' from *J.* subgen. *Solenostoma* due to often weakly rostellate fusiform 3(4)-plicate perianth. Later Vána (1975) and Inoue (1975) suggested the identity of *Solenostoma koreanum* and *Jungermannia fusiforme*, with the latter as priority name. Thus the section became monotypic. Morphologically *Protosolenostoma fusiforme* is characterized (in comparison with the majority of other species of *Solenostoma-Plectocolea* complex) by lax and soft texture, almost constant presence of low perigynium (with the exception of some submerged or nearly so phases), and mostly fusiform to 3-plicate perianth that commonly is not evidently rostellate. This species is similar to *Metasolenostoma ochotense*, from which it may be differentiated by very small to wanting trigones, and evident rim along leaf margin (sometimes with strongly thick-walled and swollen cells) and distant and subhorizontally inserted leaves, versus small and concave, but distinct trigones, 4–5-plicate perianth, weakly developed or absent rim with thin-walled cells and subtransversely to obliquely inserted leaves in *M. ochotense*. Despite the aforementioned features two species may be hardly different in untypical phases, although their genetic distance is rather high. Below we provide the list of examined specimens of *Protosolenostoma fusiforme*.

Specimens examined: JAPAN, Akita Pref., Ogachi District, leg. Yoshioka K and K. Saito 15.VIII.1965 (HIRO s.n.), Yuri-gun, 520 m alt., on submerged humus in stream, leg. Higuchi M. 21532 25.X.1992 (INS 100838), Aomori Pref., Sukayu, Arakawa, Aomori-city, Hakkoda-san, 1000 m alt., leg. Kitagawa N., 3992 05.IX.1959 (KYO, s.n.), 4110 06.IX.1959 (KYO s.n.), (holotype of *Solenostoma aomorense* Steph.) leg. Faurie U., 1260 (G00112198), (isotype of *Solenostoma aomorense* Steph.), leg. Faurie U., 1259 XI.1902 (KYO, s.n.), Hakkoda, eaux chaude de Shikaya, thermal, leg. Faurie U., 12791 07.VII.1894 (KYO, s.n.), Fukuoka Pref., Kambukusan, Hiko Mt., 600 m alt., on wet rock, leg. Amakawa T. 2719/2422 11.VIII.1958 (HIRO, s.n.), Seburiyama Mt., 700 m alt., on wet rock, leg. Kuwahara Y., 1760 04.I.1953 (NICH 51888), Gifu Pref. Anzudani, 150 m alt., on wet rocks, leg. Mizutani M., 14962 26.X.1991 (F, C0029082F), Gunma Pref., Oshimizu, Oze, 1300 m alt., on soil, leg. Sakuma E., 2331 18.VIII.1964 (HIRO, s.n.), Tanigawa Mt., 900 m alt., deciduous broadleaved forest, leg. Inoue H., 6032 28.VII.1956 (INS 200776), 700 m alt., leg. Inoue H., 6007 VII.1956 (NICH 62262), Hokkaido Pref., Daisetsu Mt., 1900 m alt., wet soil in old crater (holotype of *Jungermannia kuwaharae*), leg. Kuwahara Y., 10.VII.1956 (NICH 73007), (isotype of *J. kuwaharae*) (NICH 176526), Rebun Island, Kafukai, 30 m alt., roadside, Hasegawa J., leg. 7970 27.VIII.1984 (KYO, s.n.), Otaru (isotype of *Nardia fusiformis*) Faurie U., 88 28.XII.1885 (KYO, s.n.), (holotype of *Nardia fusiformis*), leg. Faurie U., 88 28.XII.1885 (G00112194), *Noboribetsu, thermalis*, leg. Faurie U., 9965, 9966 1893 (KYO, s.n.), Kagoshima Pref., Yakushima Isl.: between Kosugidani and Hananoego, submerged (holotype of *Plectocolea yakushimensis*), leg. Hattori S., 7467 26.IX.1940 (NICH 11585), 1000 m alt., leg. Inoue H., 24807 27.X.1979 (INS 55489), Miyano-ura, 600 m alt., on moist rocks (Hepaticae Japonicae Exsiccatae, ser. 22 (1982), 1075), leg. Kodama T. 28.XII.1974 (F, C0029084F), 1000 m alt., moist bank along trail (Bryophyta Selecta Exsiccata, n. 511, as *J. fusiformis*), leg. Inoue H. 27.X.1979 (F, C0029085F), Motcho-

mudake Mt., 300 m alt., along rivulet in open place, leg. Tagawa M and Kitagawa N., 949 26.XII.1959 (KYO, s.n.), 700 m alt., in spongy tufts on wet granite (Hepaticae Japonicae Exsiccatae ser. 4 (1951) n. 187 *Plectocolea yakushimensis* 'e loco originali'), leg. Mayebar K. VII.1951 (SAP, s.n.), between Kosugidani and Hananoego (paratype of *Plectocolea yakushimensis*), leg. Hattori S., 7537 26.IX.40 (NICH 11590), Kigen-sugi, along road (30°17'57"N 130°33'28"E), 1225 m alt., on wet gravels of granite on cutting face of road, leg. Furuki T. 23530 05.III.2014 (CBM, 37260), Kyoto Pref., Oohara, 300 m alt., wet cliffs, leg. Nakajima T., 1211 03.V.1953 (NICH 61716), Koshihata-Gonokuchi, Kameoka, 250 m alt., leg. Kodama T., 39696/2417 16.XII.1969 (HIRO, s.n.), Mie Pref., from Shin Ousugibashi to Chaya, Ousugi-mura, 400 m alt., on wet rock, leg. Yamada K., 7590 04.V.66 (NICH 198487), 500, on soil, leg. Yamada K., 21216 11.X.2003 (NICH 243417), Nagano Pref., Togakushi Mt., 1800 m alt., on rock, leg. Sakuma E., 5568/2413 10.X.1965 (HIRO, s.n.), Niigata Pref., Seki warm spring, Myoko Mt., 850 m alt., on soil leg. Sakuma E. 5187/2416, 19.IX.1965 (HIRO, s.n.), Kuroiwa, Kakisaki-machi, 200 m alt., on soil, leg. Sakuma E., 14295/2410 13.X.1968 (HIRO, s.n.), Oita Pref., Sobo Mt., Kobaru-Kunumi Pass, Inochinomizu, 1300 m alt., on wet rock, leg. Amakawa T., 5262/2412 22.VII.1965 (HIRO, s.n.), Shiga Pref., Ohkawara-rindo, Tsuchiyama-cho, leg. Kodama T., 34091 25.VII.1967 (KYO, s.n.), Hira Mt., 960 m alt., granite ledge, leg. Kodama T., 22965 24.XI.1963 (KYO, s.n.), Yamagata Pref., Momizi-kyo, 300 m alt., on moist rock, leg. Sato Y., 27.V.1973 (INS 27719); SOUTH KOREA, Quelpart (Jeju Island) (holotype of *Solenostoma koreanum* Steph.), leg. Faurie U., 236 1906 (G16635/00112199), Jeju-do, Halla Mt., (33°21'49"N 126°26'55"E), 992 m alt., shaded wet soil in broadleaved forest, leg. Choi S.S., 8035, 26.VIII.2010 (JNU, duplicate in VBG), Bolla Orum (33°21'20"N 126°28'35"E), 1230 m alt., leg. Choi S.S., 111424, 111411 (*locus classicus* of *Solenostoma koreanum* Steph.) 01.XI.2011 (JNU, duplicate in VBG).

9. The note on *Solenostoma major* (S. Hatt.) Bakalin et Vilnet

This taxon was elevated to the species level based on our study of South Korean material (Bakalin & Vilnet 2012) that was regarded as identical with Japanese '*Jungermannia pyriformis* var. *major*' based on the treatment by Amakawa (1960). However, in the course of later researches we found the material used by Amakawa to be heterogeneous. Firstly it includes the type specimen of '*J. monticola* var. *major*' and secondly the material from other herbaria and is probably identical with *Solenostoma hikoense* Amak. (its type specimen was not found in NICH, TNS, KYO and HIRO). On the one hand, the type material contains lax plants with colorless rhizoids and may be treated as a variety of *Solenostoma pyriformis*. On the other hand, other specimens named by Amakawa as '*Jungermannia pyriformis* var. *major*' are morphologically identical with the specimens from South Korea which served as the basis for our concept of *S. major* (flattened undulate leaves, purple rhizoids, etc.). Thus the name for the taxon evaluated by Bakalin and Vilnet should be changed and the new formal description should be proposed. Since we studied genetically only South Korean material (Japanese is very old for that purpose) we prefer to designate as holotype the specimen from Korean Peninsula. This formally new taxon was discussed in details before (Bakalin & Vilnet 2012).

Solenostoma sunii* Bakalin et Vilnet *sp. nov.* (= ?*Solenostoma hikoense* Amak. in Amak. et Osada, Enumer. Pl. Mt. Hikosan, 2. Bryophyta, 4, 1957, nom. nud.; *Solenostoma major* (S. Hatt.) Bakalin et Vilnet, auct. non *Jungermannia monticola* S. Hatt. f. *major* S. Hatt. J. Hattori Bot. Lab. 3: 8, 1950)

Description**. The species is superficially similar to *Solenostoma pyriformis* Steph., but characterized by deep purple

colored rhizoids, wide, flattened, undulate and distant leaves and the tendency to occupy very wet habitats (banks of streams, where it is sometimes growing submerged).

Holotypus: REP. OF KOREA, KyongNam Province, Chiri Mt. (35°19'46"N 127°44'07"E), 1800 m alt., wet and shady crevices in cliffs, leg. Bakalin V.A., Kor-10-27-09 14.VI.2009 (VBGI, isotype in KPABG).

Other specimens examined (paratypes): JAPAN, Oita Pref., Sobo Mt., Tenguiwa, 1500 m alt., on rocks, leg. Amakawa T., 5277/2176 24.VII.1966 (HIRO, s.n.), Fukuoka Pref., Hiko Mt., 800 m alt., on wet rock, leg. Amakawa T., 2152 31.VII.1961 (HIRO, s.n.), Tochigi Pref., Kuzuu, 600 m alt., on wet rocks along trail, leg. Inoue H. 24.IX.1989 (TNS, s.n.); SOUTH KOREA, KyongNam Province, Chiri Mt. (35°19'46"N 127°44'07"E), 1800 m alt., wet and shady crevices in cliffs, leg. Bakalin V.A., Kor-10-28-09 14.VI.2009 (VBGI), (35°21'10"N 127°34'13"E), 981 m alt., wet cliffs along stream, leg. Bakalin V.A., Kor-18-21-09 20.VI.2009 (VBGI), (35°19'46"N 127°44'97"E), 1447 m alt., wet cliffs along stream, leg. Bakalin V.A., Kor-7-7-09 14.VI.2009 (VBGI), Jeju-do, Halla Mt. (33°21'49"N 126°26'55"E), 992 m alt., on shaded wet soil in broadleaved forest, leg. Choi S.S., 8041, 26.VIII.2010 (JNU, duplicate in VBG).

*This species is named in honor of famous South Korean pteridologist, Prof. B.Y. Sun (JNU), who involved Bakalin into study of Korean liverworts and supported the travels around Korean Peninsula when the presented species was collected.

**The species was described in detail, discussed and illustrated before (Bakalin & Vilnet 2012) under the name of *Solenostoma major*.

10. ***Solenostoma minutissimum*** (Amak.) Bakalin. Vilnet et Furuki *comb. nov.* Basionym *Jungermannia pyriformis* var. *minutissima* Amak. Journ. Hattori Bot. Lab. 22: 61, 1961 (= *Solenostoma minutissimum* Amak. in Amak. et Osada, Enumer. Pl. Mt. Hikosan, 2. Bryophytes, 4, 1959, nom. nud.)

Just within one year after this species was revealed (Amakawa 1959 b) the author (Amakawa 1960) has changed its position and treated the taxon as a variety within *Solenostoma pyriformis*. On obtained tree topologies, the specimens of *Solenostoma minutissimum* and *Solenostoma pyriformis* are located in separated phyla. The values of *p*-distances between these taxa are till 3.1 % in *trnL*-F and 2.2 % in *trnG*-intron that are a little bit higher than between other related species pairs from the same clade (Table 2). Thus, the treatment of *S. minutissimum* as a distinct species is more natural. Morphologically this taxon is more similar to *Solenostoma* sect. *Nematocaulon* Amakawa (distant leaves, plants becoming much wider to the perianth, cf. Amakawa 1966), but not to *S. pyriformis* complex and should be treated as separate species. Below we provide the morphological description based both on type specimen and other available material, as well as illustrations and list of specimens examined.

Plants prostrate to ascending (female branches), yellowish brownish to brownish, forming loose to dense mats, 0.4–0.9 mm wide and 3–5 mm long. Stem 50–80 µm in diameter, not branched, even as subfloral innovations, brownish. Rhizoids colorless to deep purple (color varies on the same shoot, becoming purple where stem incurved and/or touch substratum), not numerous, erect spreading, separated or united into unclear fascicles. Leaves distant to contiguous, obliquely inserted, not or shortly decurrent in

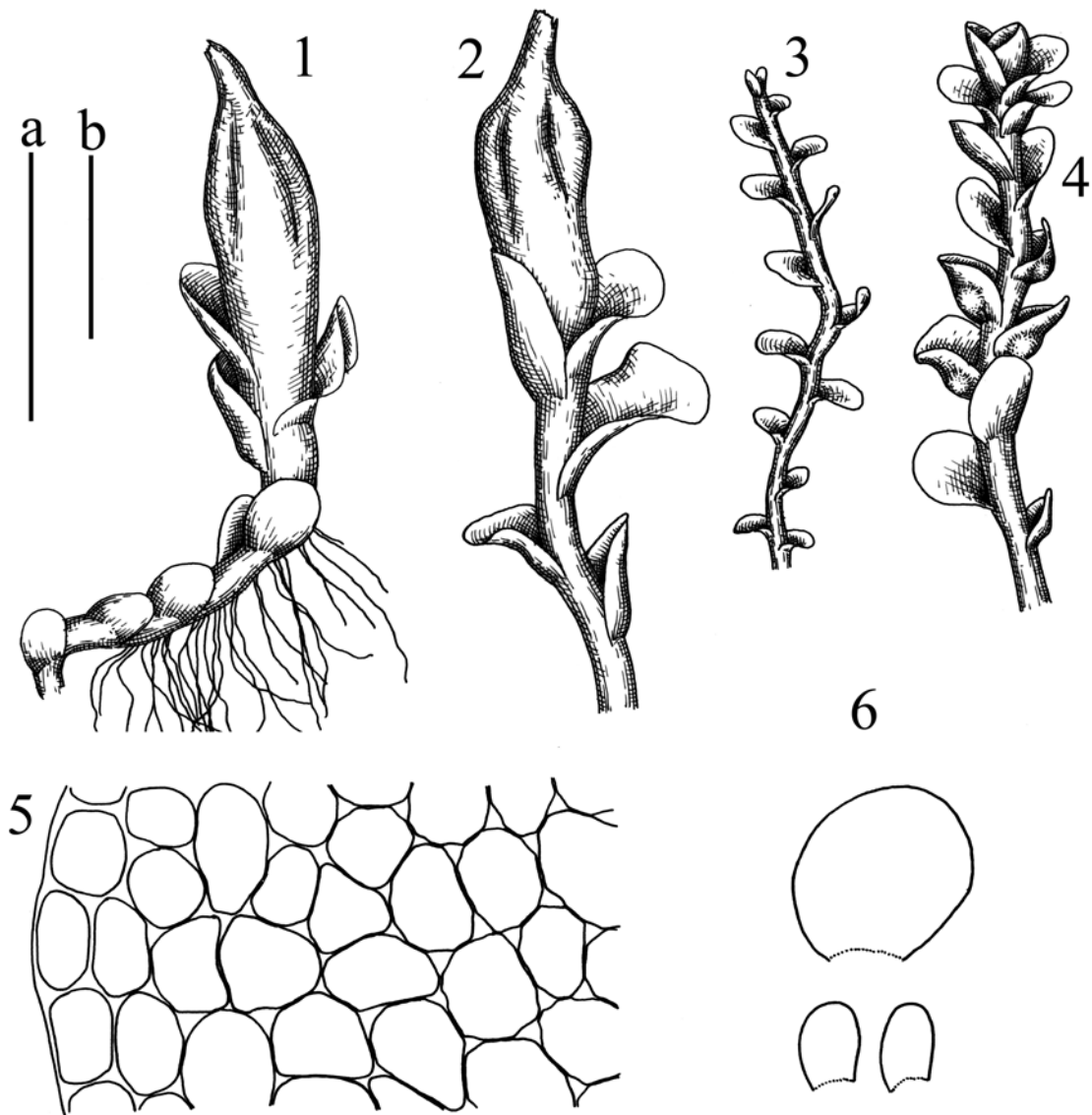


Figure 5 *Solenostoma minutissimum* (Amak.) Bakalin et Vilnet. 1, 2 – perianthous plants, 3 – sterile plant, 4 – male plant, 5 – cells from leaf margin to the middle, 6 – leaves. Scales: a – 1 mm, for 1–4, b – 50 μ m, for 5, 6. All from NICH-73012 (holotype of *Solenostoma minutissimum*)

the both sides, concave-canaliculate to nearly flattened, or sometimes sheathing the stem in lower 1/3 of the length and deflexed above, obliquely oriented, 250–500 \times 150–360 μ m (near base and in depauperate branches smaller), ovate to obliquely ovate. Midleaf cells 22–32 \times 20–27 μ m, thin-walled, trigones moderate in size to small, triangle to concave, cuticle smooth; cells along margin 15–20 μ m, thin-walled, with moderate in size to large, sometimes loosely confluent (and then wall unequally thickened) in tangential wall, external wall thickened, cuticle smooth. Dioicous. Androecia intercalary, with 3–4 pair of bracts, bracts cupped, with deflexed margin. Perianth without subfloral innovations, nearly fusiform to clavate, 700–1000 \times 250–300 μ m, 3-plicate in upper half, mostly gradually narrowed to beaked or rather conical abruptly ended mouth, composed by subsodiametric cells, bistratose in lower 1/3, exerted for 3/4 or for almost whole extent; perigynium wanting or shorter than 1/5 of perianth length; female bracts sheathing perianth to obliquely spreading (Fig. 5).

The distribution of species is poorly understood, we have revealed it from South-East China (Yunnan), Indian

Mardas State and several localities in Japan as well as in isolate local in Jeju-do in South Korea. It is possible to expect much wider occurrence of this species in Chinese Himalaya, as well as in adjacent territories.

Specimens examined: CHINA, Yunnan Prov., Ailaoshan Mts., 2100–2400 m alt., on soil of rock crevice in forest, leg. Furuki T., 17719 07.X.2002 (CBM 26671); INDIA, Madras State, Madura District, Palni Hills, Kodaikanal and surroundings, 1660 m alt., on the ground, leg. Foreau S.J. 09.IX.1932 (HIRO s.n., ex NICH 364555); JAPAN, Chiba Pref., Awa-gun, Kiosumi-ji, 200 m alt., on soil in valley, leg. Furuki T., 16556 12.I.2001 (CBM 25356), Fukuoka Pref., Gozen Mt., 1050 m alt., on rock (holotype of *Solenostoma minutissimum*), leg. Kuwahara Y., 4335 28.XII.1955 (NICH 73012), Homan Mt., 750 m alt., on moist rock, leg. Kuwahara Y., 3379/2150 18.I.1953 (HIRO, s.n.), Kagoshima Pref. Kirishima Mt. on rock, leg. Hattori S. 08.IV.1941 (NICH 8985), Amami-oshima Isl., Sumiyou River, 200 m alt., on soil along road, leg. Furuki T. 11893b 04.II.1995 (CBM 21438), Fukuoka Pref., Tagama-gun, Soeda-machi, Hiko-san Mt., Takasumi Shrine area, (33°28'49"N 130°56'04"E), 800–1100 m alt., broadleaved (evergreen and deciduous)-coniferous (*Cryptomeria-Chamaecyparis*) mixed forest on N-facing slope, cliff in partial shade, in mesic conditions, leg. Bakalin V.A. J-6-32-14 16.III.2014 (VBGI), Kyoto Pref. Shugakuin, Hiei-zan, lower elevation, leg. Kitagawa N., 2227 18.III.1959 (KYO, s.n.), Mie Pref. Akamekyo, Nabari, on rock, leg. Magofuku T. 126/2163 07.VII.1903 (HIRO, s.n.), along Minami-dani near

Yanoko-toge, 600 m alt., leg. Kitagawa N. 7370 19.III.1963 (KYO, s.n.), Nara Pref. Hegri-mura, Narukawa, 350 m alt., on soil, leg. Kodama T., 7527/2161 10.X.1954 (HIRO, s.n.); SOUTH KOREA, Jeju-do, Seogwipo-si (33°18'39"N 126°33'11"E), 541 m alt., leg. Choi S.S., 111307 28.X.2011 (JNU, duplicate in VBGJ).

11. Note on *Solenostoma risbiriense* Amak. Journ. Jap. Bot. 31: 48, 1956

Váňa (1975) synonymized *Solenostoma risbiriense* with *Jungermannia pyriflora* var. *minutissima* (as in l.c.) and founded this decision based on observation that (l.c.: 212): “*Solenostoma risbiriense* Amak. seems to be only a habitat modification of the present variety”. Contrary to him we regard this taxon as independent species not closely related to *Solenostoma minutissimum*. *S. risbiriense* differs from *S. minutissimum* in smaller size of shoots that not or only slightly dilated to the perianth, absence of red to purple pigmentation, spherical perianth that only shortly exerted from the bracts and also in geographic distribution. When *S. minutissimum* has large (although probably disjunctive) area in eastern Asia, spreading to Chinese Yunnan and Indian Himalaya, *S. risbiriense* has distribution restricted to alpine zone of mountains in Hokkaido, although with southernmost isolated record in alpine zone of Hiuchigatake Mt. in Fukushima Pref. Below we provide the description based on type material as well as other available specimens.

Plants prostrate to ascending, brownish to yellowish brown and blackish brown, 0.3–0.6 mm wide and 3–5 mm long, incrustated by soil particles. Stem 60–150 µm in diameter, sparsely laterally branched, brownish to brown. Rhizoids sparse, colorless to grayish and brownish, separated and erect spreading. Leaves distant to contiguous (in perianthous shoots mostly), obliquely spreading, concave-canaliculate to concave, subtransversely inserted, up 1/2 of stem width decurrent in the both sides, 330–750 × 280–830 µm, ovate to obovate and nearly rounded (bigger ones). Mid-leaf cells subisodiametric to shortly oblong, 16–25 × 12–18 µm, thin-walled, walls brownish, trigones moderate in size, triangle to slightly concave or convex, cuticle smooth; cells along leaf margin 10–17 µm, thin-walled, with rather small, concave trigones, cuticle smooth. Dioicous? Perianth exerted for 2/5–1/2 of its length or hidden within bracts, nearly spherical, ca. 600 × 550 µm, loosely 3-plicate in upper part, loosely beaked, mouth crenulate, composed by oblong, clavate cells with thickened walls, seems unistratose to base, composed by nearly isodiametric cells, 13–20 µm in diameter, thin-walled, with moderate in size, triangle to slightly concave or convex trigones; perigynium virtually absent; bracts sheathing the perianth or obliquely spreading in upper 1/3 (Fig. 2).

Specimens examined: JAPAN, Fukushima Pref., Hiuchigatake Mt., 2200 m alt., leg. Yuzawa, 1563/2647 10.VIII.1966 (HIRO, s.n.), Hokkaido Pref., Rishiri Isl., near summit 1600–1719 m alt., on andesite rocks in exposed condition (holotype of *Solenostoma risbiriense*), leg. Shimizu D., 22.VII.1954 (NICH 53527), Hidaka, Poroshiri Mt., 1600–1700 m alt., *Pinus pumila* and alpine meadow, on soil, leg. Iwatsuki Z., 390 25.VII.71 (NICH 120780).

CONCLUSIONS

The complex *Solenostoma* – *Plectocolea* shows the great genetic and morphological diversity and includes four distinct genera: *Plectocolea*, *Solenostoma*, *Metasolenostoma* and *Protosole-*

nostoma. The integrative approach to the evaluation of taxonomic value of morphological features have showed robust importance of such features as growth form, coloration (including ability to produce peculiar pigmentation), distance between leaves, general increasing of shoot width to the top, as well as ecological preferences. The species rank of such taxa as *Plectocolea shinii* and *Solenostoma minutissimum* was robustly supported in the course of the present study.

The phylogenetic tree presented herein is the largest of constructed until today for *Solenostoma* – *Plectocolea* complex and some evolutionary trends in *Solenostoma* – *Plectocolea* complex are possible to reveal. Before only a few such observations were published. Müller (1956) regarded perianth reduction line as one of evolutionary trends within *Jungermannia* s.l., this well corresponds to Amakawa's (1959) statement on *Plectocolea radiculosa* (characterized by low perigynium) as one of the most primitive within *Plectocolea* (*Jungermannia* subgen. *Plectocolea* in l.c.).

The present research showed basal groups formed by species with slightly (but evidently) developed perigynium (*Protosolenostoma*, *Metasolenostoma*) and unspecified unistratose perianth. Further evolution within *Solenostoma* and *Plectocolea* (in this respect) showed two opposite ways: 1) perigynium reduction and specification of perianth, with final variant in absence of perigynium and specified (rostellate) bi-polystratose perianth, 2) further development of perigynium conjugate with perianth reduction, with the final variant with two (rarely three) pairs of female bracts on the perigynium and short conical perianth hidden within bracts. Noticeable these two ways were realized in the both large genera. Following way 1 the most advanced *Solenostoma* are *Solenostoma sphaerocarpum*, *S. marcescens* (Mitt.) Bakalin, etc., and the most advanced in *Plectocolea* are *P. radiculosa*, etc. Following to the way 2 the most advanced species in *Solenostoma* are *S. subellipticum* (Lindb. ex Heeg) R.M. Schust. and *S. obscurum* (A. Evans) R.M. Schust., when in *Plectocolea* this should be ‘*Virgata*-group’.

The third way, realized within *Plectocolea* only, is the specialization of oil cells in the leaf lamina (correlate with perigynium reduction) in the complex *Plectocolea ariadne* – *P. basskarliana*–*P. tetragona*.

The fourth way might be the growth form evolution. When basal *Protosolenostoma* characterized by only prostrate growth form, within *Metasolenostoma* one species (*M. orientale*) showed advance in erect growth form that also corresponds to loss of perigynium, although the bulk of other taxa characterized by prostrate growth form. In more advanced *Solenostoma* and *Plectocolea* erect growth form prevails over prostrate growth form. Noticeable erect growth form commonly correlate with other tentatively advanced features: rostellate perianth (e.g. *Solenostoma pyriflorum*, *S. marcescens* and related taxa), presence of “oil cells” in leaf lamina (e.g. *P. radiculosa*, etc.), lack of perigynium or, contrary, its large development (e.g. *P. unispiris* and related taxa). The latter may be regarded as the evidence of correlate feature evolution.

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