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Taxonomical rearrangements of Solenostomataceae (Marchantiophyta) with description of a new family Endogemmataceae based on *trn*L-F cpDNA analysis

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Abstract: The results of *trn*L-F cpDNA analysis of the suborder Jungermanniineae allow to re-evaluate relations and taxonomy of the morphologically distinctive species *Solenostoma caespiticium.* A new monotypic family Endogemmataceae is described. The new combination *Endogemma caespiticia* is made. Provisionally, the genus *Nardia* is placed in Gymnomitriaceae.

Kokkuvõte: Solenostomataceae (Marchantiophyta) taksonoomilised ümberkorraldused ja uue sugukonna Endogemmataceae kirjeldus *trn*L-F cpDNA analüüsi alusel

Alamseltsi Jungermanniineae *trn*L-F cpDNA põhine analüüs võimaldas ümber hinnata morfoloogiliselt eristunud liigi *Solenostoma caespiticium* asendi taksonoomilises süsteemis. Antakse uue monotüüpse sugukonna Endogemmataceae kirjeldus ja esitatakse uus taksonoomiline kombinatsioon *Endogemma caespiticia*. Perekond *Nardia* paigutatakse sugukonda Gymnomitriaceae.

INTRODUCTION

As shown by molecular studies during the latest decade (Davis, 2004; Yatsentyuk et al., 2004; Heinrichs et al., 2005; Forrest et al., 2006; He-Nygrén et al., 2006; De Roo et al., 2007; Vilnet et al., 2009) Jungermanniaceae sensu Schuster (1984) is polyphyletic (the collective family) and its taxa are now classified in two suborders: Jungermanniineae R. M. Schust. ex Stotler & Crand.-Stotl. and Cephaloziineae Schljakov (Crandall-Stotler et al., 2009). Taxa that used to belong to the family Jungermanniaceae are now allocated to 6 families: Scapaniaceae Mig., Jungermanniaceae Rchb. s. str., Solenostomataceae Stotler & Crand.-Stotl., Delavayellaceae R. M. Schust., Myliaceae Schljakov and Anastrophyllaceae L. Söderstr., De Roo & Hedd. (Crandall-Stotler et al., 2009; Söderström et al., 2010). The broad genus concept of *Jungermannia* L. (*Solenostoma* Mitt.) (Schuster, 1969; Váňa, 1973) is not supported by molecular phylogenetic studies. Particularly, species classified in the genus *Jungermannia* (*Solenostoma*) during the second half of the 20th century are now treated in different genera and even families. For instance, *Liochlaena* Nees is referred to Delavayellaceae, *Solenostoma* Mitt. emend. Zerov and *Plectocolea* (Mitt.) Mitt. to Solenostomataceae, and *Jungermannia* L. emend. Schljakov to Jungermanniaceae (Crandall-Stotler et al., 2009).

The new family Solenostomataceae includes nine genera (Crandall-Stotler et al., 2009; Feldberg et al., 2009), majority of them are monotypic, recently described and poorly studied. The largest genus of the family is *Solenostoma* Mitt. (including *Plectocolea* (Mitt.) Mitt. and *Scaphophyllum* Inoue) that comprises more than 150 species. As stressed by Schuster (2002) “the taxonomy of the genus remains in an unsatisfactory state”. This genus will most likely suffer the same fate as other large genera like *Lophozia* (Dumort.) Dumort. s. l. (Yatsentyuk et al., 2004; De Roo et al., 2007; Vilnet et al., 2008; Vilnet et al., 2009) and be split into several small genera after thorough molecular study. By now molecular data were published only for a few *Solenostoma* s.l. species (Hentschel et al., 2007; Feldberg et al., 2009) and we are only at the beginning of the creation of a real phylogenetic concept of this group. In a study of Jungermanniaceae Bakalin and Vilnet (2009) found that *trn*L-F sequences of *S. caespiticium* differ from both *Jungermannia* s. str. and *Solenostoma* s. str. and stated that “its current placement in *Solenostoma* should be changed”. So far

S. caespiticium has only once been included in one molecular phylogenetic study (De Roo et al., 2007), but the placement of this species in the resulting tree was dubious due to insufficient taxon sampling of *Jungermannia* s. l.

The genus *Nardia* Gray (traditionally treated in Jungermanniaceae) was resolved as a sister of the *Solenostoma* or Gymnomitriaceae+*Solenostoma* clade based on *rbc*L cpDNA data (Hentschel et al., 2007). Crandall-Stotler et al. (2009) placed *Nardia* in Solenostomataceae. In *rbc*L data analysis Feldberg et al. (2009) found *Nardia* in a weakly supported clade with *Marsupella emarginata.* Based on combined analysis of nuclear and chloroplast DNA loci we have showed that the family Solenostomataceae is paraphyletic and the placement of *Nardia* in the family Gymnomitriaceae is supported by 0.99 Bayesian posterior probability (Vilnet et al., 2010).

In this paper we provide descriptions of new taxa in the suborder Jungermanniineae taking molecular and morphological features into account.

MATERIALS AND METHODS

Taxa

The *trn*L-F cpDNA sequences of 50 taxa (60 samples) of liverworts from suborder Jungermanniineae were analysed. *Gymnomitrion alpinum, Marsupella sphacelata, Plectocolea obovata, Solenostoma caespiticium, S. pseudopyriflorum* and *S. pyriflorum* were represented by several specimens collected mainly in geographically diverse regions. *Trichotemnoma corrugatum* from the monotypic family Trichotemnomataceae R. M. Schust. was chosen as outgroup according with result of Forrest et al. (2006), He-Nygren et al. (2004, 2006) and our preliminarily analysis. The sequences for fifteen samples were obtained in this study, sequence data from our previous studies were used for 36 accessions (Yatsentyuk et al., 2004; Bakalin & Vilnet, 2009; Vilnet et al., 2010), and sequences for nine species were downloaded from GenBank. All studied samples are listed, including GenBank accession numbers and voucher details (Table 1).

DNA isolation, amplification and sequencing

DNA was extracted from dried liverwort tissues using the NucleoSpin Plant Kit (Macherey-Nagel, Germany). The *trn*L-F region of the chloroplast genome, including the part of the 5'-terminal exon, intron, the 3'-terminal exon of the *trn*L gene, the *trn*L-F intergenic spacer and part of the *trn*F gene, was amplified and sequenced using primers suggested by Taberlet et al. (1991).

PCR were carried out in 20 µl volumes according to the following procedure: 3 min at 94°C, 30 cycles (30s 94°C, 40s 58°C, 60s 72°C) and 2 min of final extension time at 72°C. Amplified fragments were visualized on 1% agarose TAE gels by EthBr staining, purified using the GFX^{TM} 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, USA) following the standard protocol provided for 3100 Avant Genetic Analyzer (Applied Biosystems, USA).

Phylogenetic analyses

The *trn*L-F sequences were aligned using T-Coffee (Notredame et al., 2000) and manually corrected in BioEdit (Hall, 1999). All positions of alignment were included in the phylogenetic analysis.

Two analytical procedures were used for the analysis: the maximum parsimony method (MP) with the TNT program (Goloboff et al., 2003) and the Bayesian method with the MrBayes v 3.1.2. (Ronquist & Huelsenbeck, 2003). The parsimony analysis with TNT involved a New Technology Search with search minimal length tree by one iteration and 1000 bootstrap resamplings, the default settings were used for other parameters. Gaps were treated as missing data.

For the Bayesian (BA) analysis initially a best-fit evolutionary model of nucleotide substitutions – HKY – was determined using the ModelGenerator software (Keane et al., 2004). The sequence alignment was divided into five partitions: *trn*F, *trn*L 5'-terminal exon, *trn*L 3'-terminal exon, *trn*L intron and *trn*L-F intergenic spacer. Each of these partitions was separately assigned the HKY model, 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, and two starting trees were chosen randomly. The number of generations was 5 000

Table 1. The list of taxa, specimens vouchers and GenBank accession numbers. Sequences with accession numbers beginning with JF were produced in this study.

Taxon	Specimen voucher	GenBank accession number
Acrobolbus ciliatus (Mitt.) Schiffn.	Nepal, Long 30514	DQ026613
Anthelia julacea (L.) Dumort.	Nepal, Long 31292	DQ026616
Balantiopsis cancellata (Nees) Steph.	Chili, Hyvonen 5946	AY463545
Calypogeia azurea Stotler & Crotz	Russia, Caucasus, Konstantinova N., K413-3-05 (KPABG)	JF421610
C. fissa (L.) Raddi	Russia, Caucasus, Konstantinova N., K514-05 (KPABG)	JF421609
Delavayella serrata Steph.	Nepal, Long 30388	DQ026618
Eremonotus myriocarpus (Carrington) Pearson	Russia, Caucasus, Konstantinova N., K446-6-05 KPABG)	EU791716
Gymnomitrion alpinum (Gottsche ex Husn.) Schiffn. 1	Russia, Kamchatka Prov., Bakalin V., K51-7-03 (KPABG)	JF421596
G. alpinum (Gottsche ex Husn.) Schiffn. 2	Russia, Sakhalin Prov., Bakalin V., 58-30-05 (KPABG)	EU791706
G. brevissimum (Schleich. ex Dumort.) Warnst.	Russia, Murmansk Prov., Konstantinova N., G 8171 (KPABG)	EU791711
G. concinnatum (Lightf.) Corda	Russia, Caucasus, Konstantinova N., K493-05 (KPABG)	EU791709
G. corallioides Nees	Svalbard: Spitsbergen, Konstantinova N., 155-04 (KPABG)	EU791705
G. pacificum Grolle	Russia, Kamchatka Prov., Bakalin V., K-26-4-02-VB (KPABG)	EU791713
Isotachis humectata (Hook. f. & Taylor) Steph.	Chili, Hyvonen 5180	AY463562
Jungermannia atrovirens Dumort.	Russia, Caucasus, Konstantinova N., K421-6-05 (KPABG)	GQ220763
J. exsertifolia Steph.	USA, Wyoming, Konstantinova N., A69/5-95 (KPABG)	AY327775
J. konstantinovae Bakalin & Vilnet	Russia, Primorsky Kray, Bakalin V., P-69-16-08 (KPABG)	GU220586
Jungermannia sp.	Russia, Caucasus, Konstantinova N., K429/1-07 (KPABG)	JF421608
Leiocolea badensis (Gottsche) Jörg.	Russia, Komi Rep., Dulin M., G101313 (KPABG)	EU791717
Liochlaena lanceolata Nees	Russia, Murmansk Prov., Konstantinova N., 206-2-02 (KPABG)	EU791719
Marsupella aquatica (Lindenb.) Schiffn.	Russia, Murmansk Prov., Konstantinova N., 152/5-87 (KPABG)	AF519201
M. arctica (Berggr.) Bryhn & Kaal.	Svalbard: Spitsbergen, Konstantinova N., 128-04 (KPABG)	EU791695
M. boeckii (Austin) Kaal.	Russia, Murmansk Prov., Konstantinova N., 367-2-00 (KPABG)	EU791696
M. disticha Steph.	Japan, Deguchi & Yamaguchi, Bryophytes of Asia 170 (2000)	EU791703
M. emarginata (Ehrh.) Dumort.	Russia, Murmansk Prov., Konstantinova N., 354-4-00 (KPABG)	EU791693
M. funckii (F. Weber & D. Mohr) Dumort.	Russia, Caucasus, Konstantinova N., K 516-1-05 (KPABG)	EU791700
M. sphacelata (Giesecke ex Lindenb.) Dumort. 1	Russia, Murmansk Prov., Konstantinova N., 25-1-03 (KPABG)	JF421598
M. sphacelata (Giesecke ex Lindenb.) Dumort. 2	Russia, Kemerovo Prov., Konstantinova N., 65/1-00 (KPABG)	AF519200
M. sprucei (Limpr.) Bernet	Russia, Kemerovo Prov., Konstantinova N., 54-1-00 (KPABG)	HQ833031
Marsupidium latifolium R.M. Schust.	Costa Rica, Dauphin 2920 (NY)	AY608134
Mesoptychia sahlbergii (Lindb.) A. Evans	Russia, Chukotka A.O., Afonina O., 10.08.1979 (KPABG)	AF519189
Metacalypogeia cordifolia (Steph.) Inoue	Russia, Primorsky Kray, Bakalin V., P-66-18a-06 (KPABG)	JF421597
Nardia assamica (Mitt.) Amakawa	Russia, Kamchatka Prov., Bakalin V., K54-1a-05 (KPABG)	EU791715
N. compressa (Hook.) Gray	Canada, British Columbia, Konstantinova N., A97/1-95 (KPABG)	AF519188
N. insecta Lindb.	Belgium, Konstantinova N., 102077 (KPABG)	EU791714
Neesioscyphus bicuspidatus (Steph.) Grolle	Costa Rica, Dauphin 2042	DQ354977
Plectocolea hyalina (Lyell) Mitt.	Russia, Buryatiya Rep., Konstantinova N., K106/2-02 (KPABG)	JF421599
P. infusca Mitt.	Russia, Primorsky Kray, Bakalin V., P-76-38-05 (KPABG)	JF421600
P. obovata (Nees) Lindb. 1	Russia, Murmansk Prov., Konstantinova N., 196-6-02 (KPABG)	GQ220754
P. obovata (Nees) Lindb. 2	Russia, Kemerovo Prov., Konstantinova N., 72-2-00 (KPABG)	GQ220753
P. obovata (Nees) Lindb. 3	Russia, Perm Kray, Konstantinova N., K324-1-04 (KPABG)	GQ220755

Table 1 (continued)

Taxon	Specimen voucher	GenBank accession number
P. obovata (Nees) Lindb. 4	Russia, Buryatiya Rep., Konstantinova N., 70-2-01 (KPABG)	GQ220751
P. obovata (Nees) Lindb. 5	Russia, Murmansk Prov., Konstantinova N., 30-1-97 (KPABG)	GQ220761
P. rigidula S. Hatt.	Russia, Kamchatka Prov., Bakalin V., K-49-11-07 (KPABG)	JF421601
P. rosulans (Steph.) S. Hatt.	South Korea, KyongNam Prov., Bakalin V., Kor-15-8-09 (KPABG)	JF421602
P. rupicola (Amakawa) Bakalin	Russia, Primorsky Kray, Bakalin V., P-72-17-05 (KPABG)	JF421603
P. subelliptica (Lindb. ex Kaal.) A. Evans	Russia, Kamchatka Prov., Bakalin V., K-48-13-03 (KPABG)	GQ220752
P. vulcanicola Schiffn.	Russia, Kamchatka Prov., Bakalin V., K-45-7-06 (KPABG)	JF421604
Solenostoma caespiticium (Lindenb.) Steph. 1/ *Endogemma caespiticia* (Lindenb.) Konstant., Vilnet & A.V. Troitsky 1	Russia, Buryatiya Rep., Konstantinova N., 101-1-01 (KPABG)	GU220585
S. caespiticium (Lindenb.) Steph. 2/ *Endogemma caespiticia* (Lindenb.) Konstant., Vilnet & A.V. Troitsky 2	Russia, Murmansk Prov., Konstantinova N., 2/3-02 (KPABG)	JF421605
S. confertissimum (Nees) Schljakov	Russia, Caucasus, Konstantinova N., K459-8a-05 (KPABG)	GQ220758
S. gracillimum (Sm.) R.M. Schust.	Russia, Caucasus, Konstantinova N., K412-07 (KPABG)	JF421606
S. pseudopyriflorum Bakalin & Vilnet 1	Russia, Buryatiya Rep., Konstantinova N., 30-2-01 (KPABG)	GQ220759
S. pseudopyriflorum Bakalin & Vilnet 2	Russia, Primorsky Kray, Bakalin V., P-74-79a-05 (KPABG)	GU220594
S. pseudopyriflorum Bakalin & Vilnet 3	Russia, Primorsky Kray, Bakalin V., P-65-1-06 (KPABG)	GU220595
S. pyriflorum Steph. 1	South Korea, KyongNam Prov., Bakalin V., Kor-10-8-09 (KPABG)	GU220591
S. pyriflorum Steph. 2	South Korea, KyongNam Prov., Bakalin V., Kor-8-5-09 (KPABG)	GU220590
S. sphaerocarpum (Hook.) Steph.	Russia, Caucasus, Konstantinova N., K340/3a-08 (KPABG)	JF421607
Trichotemnoma corrugatum (Steph.) R.M. Schust.	New Zealand, Glenny 8426	AY463591
Tylimanthus abbreviatus (Taylor) Hässel & Solari	Australia, Scott s.n. B. Bryo 236011	DQ533930

000, and trees were saved once every 10 generations. The first 100 000 trees were discarded in each run, and 146 984 trees from both runs were sampled after burning. Bayesian posterior probabilities were calculated as branch support values.

RESULTS

The *trn*L-F alignment consists of 623 sites, the 314 (50.40%) positions are constant, 283 (45.43%) variable and 216 (34.67%) are parsimonically informative.

The MP analysis with TNT yielded 25 equally parsimonious trees at different runs with a length of 874 steps. The tree resulting after 1000 bootstrap resamplings is shown with indicated bootstrap support values (BS) (Fig. 1).

In the BA analysis, trees were sampled after reaching stationarity; the average standard deviation of split frequencies between two runs was 0.006343. Arithmetic means of Log likelihoods for runs sampled were -5059.82 and -5060.57. 95% and 99% credible sets contain 110 904 and 138 984 trees, respectively. The BA tree with means of posterior probabilities (PP) is presented (Fig. 2).

The topologies of MP and BA trees are in good agreement. The discrepancies are caused by some unresolved groupings in the MP tree and by low support for some clades in the MP tree, which are however highly supported in BA tree. Species with different positions in the MP and BA trees are marked by asterisks (Figs. 1, 2).

The clades of families Balantiopsidaceae, Acrobolbaceae and Antheliaceae are subsequently divergent in lower part of trees. The next clade is formed by the genera *Calypogeia* and *Metacalypogeia* (PP = 0.95) from Calypogeiaceae. The families Jungermanniaceae and Delavayellaceae lie in one clade in the BA tree (PP = 1.00) but form an unresolved grade in the MP tree (BS = 56). Specimens of *Solenostoma caespiticium* form a separate clade that is a sister of the Solenostomataceae and Gymnomitriaceae clades (PP = 0.96). The intermingled clade of *Solenostoma* and *Plectocolea* is supported by BS = 72 and PP = 1.00. *Marsupella* and *Gymnomitrion* are located

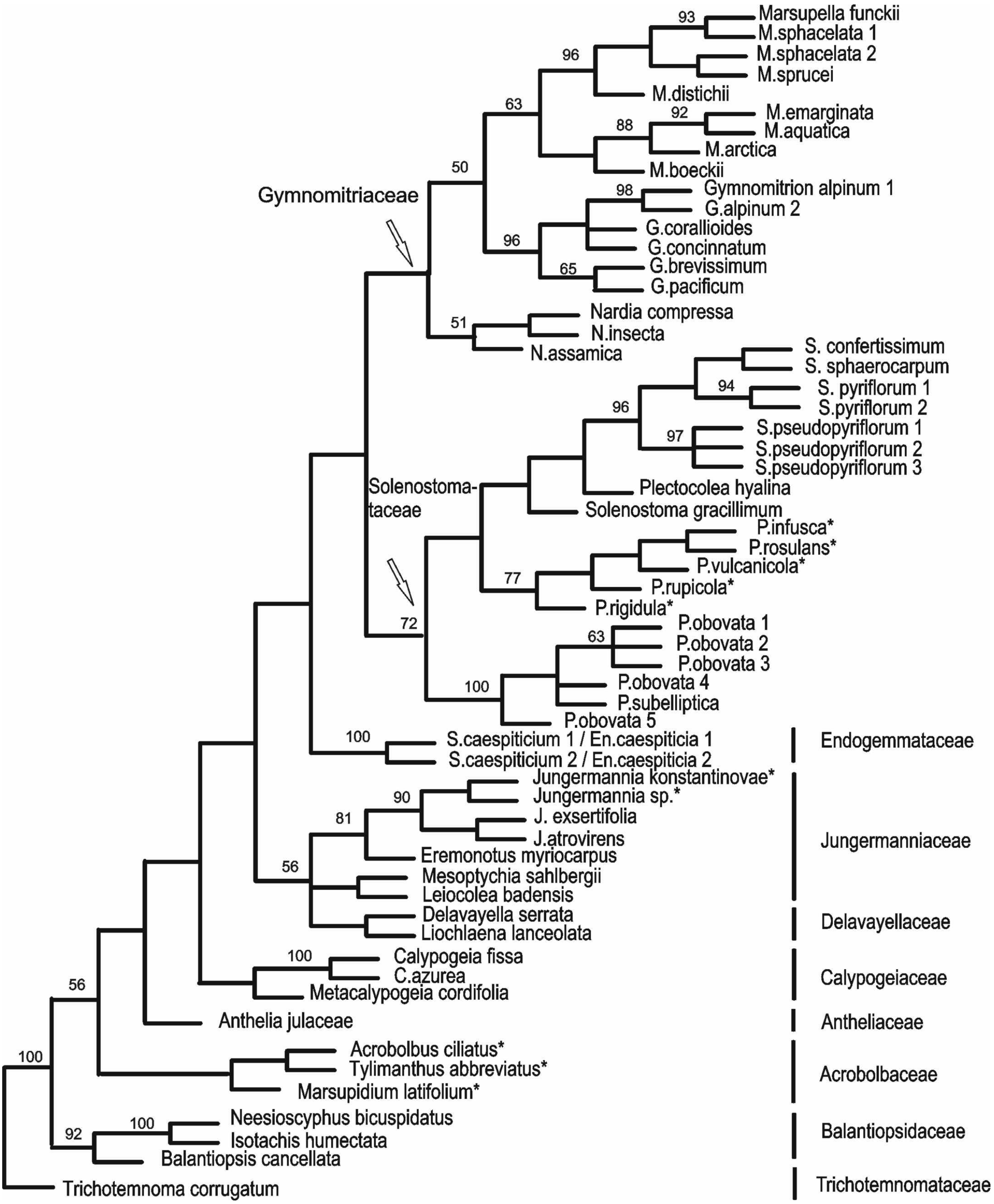

Fig. 1. Maximum parsimony phylogenetic tree for Jungermanniineae based on nucleotide sequences of *trn*L-F cpDNA. Bootstrap support values more than 50% are indicated. Taxa with flickering positions are marked by asterisks.

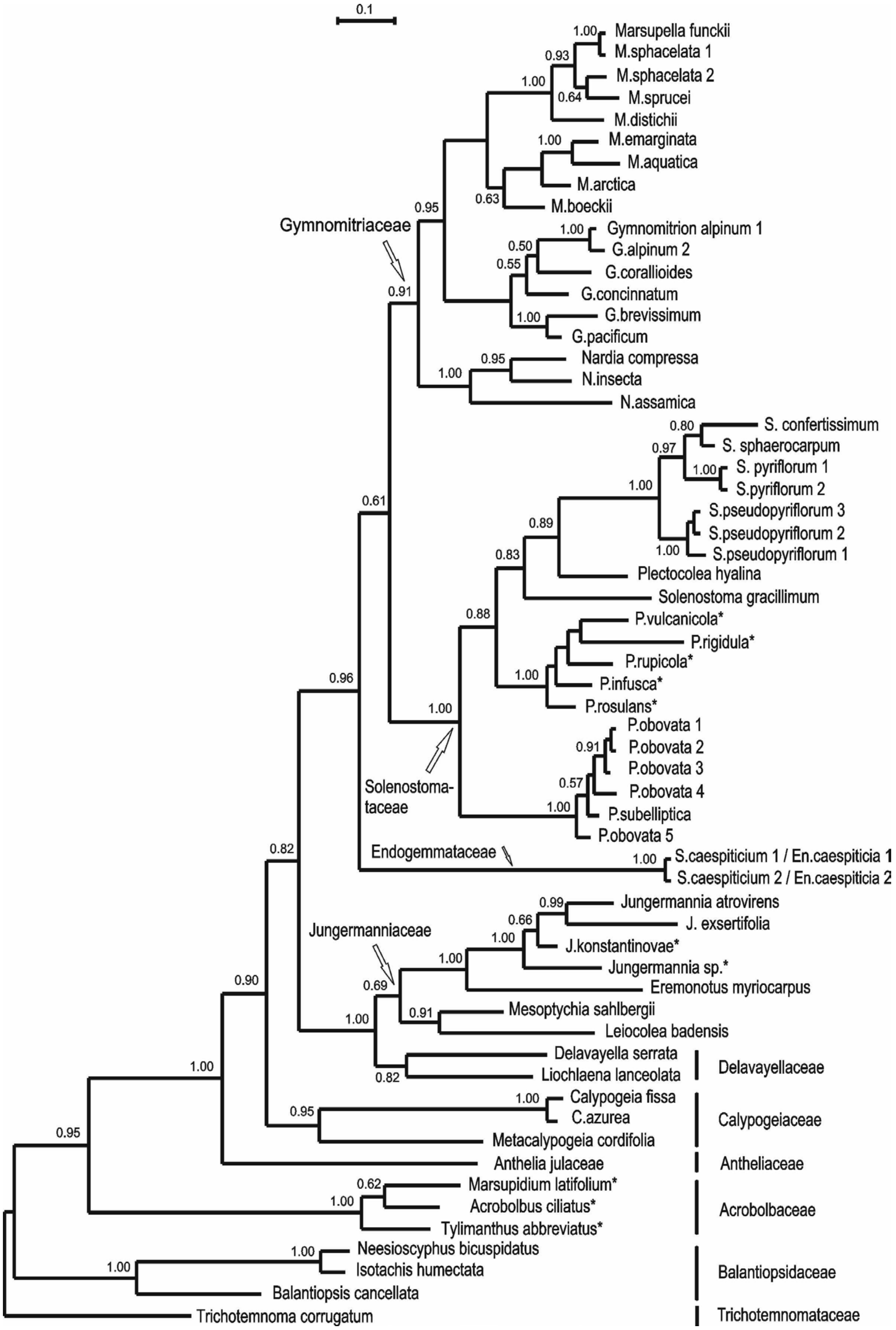

Fig. 2. Phylogenetic tree for Jungermanniineae based on nucleotide sequences of *trn*L-F cpDNA by the Bayesian approach. Bayesian posterior probabilities more than 0.50 are indicated. Taxa with flickering positions are marked by asterisks.

in a clade with BS = 50 and PP = 0.95. The genus *Nardia* is a sister of the Gymnomitriaceae clade (PP = 0.91).

DISCUSSION

The taxonomic concept of the recently described family Solenostomataceae suggested in Crandall-Stotler et al. (2009) was not supported by the results obtained here. This family is clearly polyphyletic due to the placement of *Nardia* and *Solenostoma caespiticium* in separate clades.

In both calculated trees the genus *Nardia* was found in close affinity to the family Gymnomitriaceae with high support only in the BA tree (PP = 0.91). The relation of *Nardia* to Gymnomitriaceae was earlier more strongly supported based on ITS1-2 nrDNA and *trn*L-F cpDNA on a larger taxon sampling of the order Jungermanniales (BS = 67, PP = 0.99 in Vilnet et al., 2010). The genus *Nardia* contains about 20 species, but "both perimeters of *Nardia* and the number of species to be assigned to it remain uncertain" (Schuster, 2002). In current state the genus includes morphologically heterogeneous groups of species. We studied only three species that according to Schuster (2002) belong to three different subgenera of *Nardia*: the type species *N. compressa* (subgenus *Nardia*), *N. insecta* (subgen. *Geoscypharia* Trevis.) and *N. assamica* (subgen. *Apotomanthus* Spruce). The genus is characterized in general by a combination of derived (reduced perianth and constantly well developed perigynia) and primitive (broad ventral merophytes with usually well developed underleaves etc.) features. Most *Nardia* species share the following characteristics with Gymnomitriaceae: stem-derived perigynia, reduction of perianth in the majority of accepted species, any capacity for asexual reproduction, tendency of development of 3- or even 4-spiral elaters and number and shape of oil-bodies that are usually 1 or 2–3, rarely more per cell. One striking feature that separates most *Nardia* species from both Gymnomitriaceae and Solenostomataceae is the broad ventral merophytes bearing underleaves. *Nardia* also differs from Gymnomitriaceae by the shape of the capsules (mostly ovoid-globose vs. spherical in Gymnomitriaceae). Some morphological trends could be outlined both in Gymnomitriaceae and *Nardia*: the stem anatomy (from not or slightly differentiated cortical cells to well expressed cortical layers), from clearly bilobed to shallowly bilobed or entire leaves, etc. Future careful studies of a larger set of *Nardia* spp. may possibly allow this genus to be placed in a separate family, but the molecular data available now suggest that it is more natural to assign the studied species of the genus *Nardia* to the family Gymnomitriaceae than to Solenostomataceae.

Samples of *Solenostoma caespiticium* are far apart from other *Solenostoma* species on both trees (Figs. 1, 2) and found in a clade that is a sister of the Gymnomitriaceae and Solenostomataceae clades with high support on the BA tree (PP = 0.96). The two specimens of *Solenostoma caespiticium* included in the tree reconstructions gathered in regions far from each other in Russia (Murmansk Province and Republic of Buryatiya) have identical nucleotide sequences. There are two deletions of eight and 24 nucleotides in the P8 stem-loop and insertions of 12 nucleotides in the P6 stem-loop regions of the *trn*L-intron of *Solenostoma caespiticium* which separates this taxon from the genera *Solenostoma* and *Plectocolea.*

Morphologically *Solenostoma caespiticium* is a quite distinctive species. The combination of features characteristic of both *Jungermannia* and *Solenostoma* is remarkable for this taxon. It shares the beaked mouth of the perianth with *Solenostoma* and the absence of perigynium and shoot calyptra with *Jungermannia* s. str. It differs from other Solenostomataceae and Jungermanniaceae species in the presence of endogenous gemmae that are totally lacking in these families and the characteristic very large single oil-body that is known among allied taxa only in *S. tetragonum* (Lindenb.) R. M. Schust. It is the only species among Jungermanniineae with endogenously originated gemmae. It seems that this fact was underestimated in previous classifications of hepatics. As was stressed by Schuster (1969) the absence of gemmae is one of the marked generic characters of *Solenostoma* s. l. But two species of the genus (as treated by most authors from Mitten to Schuster) have gemmae: *Solenostoma rubripunctatum* (S. Hatt.) R. M. Schust. (*Jungermannia* (*Plectocolea*) *rubripunctata* (S. Hatt.) Amak.) and *S. caespiticium.* Of them *Solenostoma rubripunctatum* have exogenous purple, one-celled rotundate gemmae restricted to tips of erect shoots or margins of reduced leaves near tip (Amakawa, 1960). Endogenous gemmae of *S. caespiticium* are quite different both in origin and shape and colour from those of *S. rubripunctatum*. Earlier Vilnet et al. (2008) showed both shape and colour of gemmae are important features reflecting some phylogenetic trends in Hepatics. So the placement in *Solenostoma* of the two species mentioned above seems unnatural. As far as we know there are no molecular studies of *S. rubripunctatum* up to date, so its affinities remain unclear. For *Solenostoma caespiticium* we suggest the new family Endogemmataceae, a monotypic family including one monotypic genus.

Endogemmataceae Konstant., Vilnet & A.V. Troitsky, *fam. nov.*

Plantae habitu Solenostomati similes sed gemmis endogenis (omnino nullis in Solenostomataceis), *corporis oleosis propriis magnis singulatim per cellulam, cellulis permagnis leptodermaticis et trn*L-F *sequentiis remotis recedit.*

Type: ***Endogemma*** **Konstant., Vilnet & A.V. Troitsky, *gen. nov.***
Plantae habitu Solenostomati similes sed gemmis endogenis (omnino nullis in Solenostomataceis), *corporis oleosis propriis magnis singulatim per cellulam, cellulis permagnis leptodermaticis et trn*L-F *sequentiis remotis recedit.*

Type: *Endogemma caespiticia* (Lindenb.) Konstant., Vilnet & A.V. Troitsky comb. nov.

Basionym: *Jungermannia caespiticia* Lindenb., Nova Acta Acad. Caes. Leop.- Carol. Nat. Cur. Suppl. 14:67, pl. I, figs. 1–8, 1829.

Type: Germany, Hamburg, Bergedorf, 1825 leg. Lindenberg, W (Lindenb. Hep. No 1930), c spor. et gem. (lectotype), 1826, leg. Lindenberg, W (Lindenb. Hep. No 1929), 1827, leg. Lindenberg, W (Lindenb. Hep. No 1926), (syntype).

Syn.: *Solenostoma caespiticium* (Lindenb.) Steph. Spec. Hep., 2:57. Geneva. 1901.

Leaves obliquely inserted, unlobed, rotundate, cells very large, pellucid, leptodermous, trigones absent, a single oil body per cell, very large, almost smooth. Gemmae endogenously formed, one-celled, roundish quadrate with a single glistening oil-body. Dioicous, perianth ”free”, without trace of perigynium or shoot calyptra 0.5–0.65 emergent, 4–5-plicate in at least the distal part with a small tubular beak.

The species is infrequent in Europe and very rare in North America (Schuster, 1969). It has recently been recorded in many regions of Russia including Siberia and the Far East (Konstantinova & Bakalin, 2009). Its distribution can be characterized as boreomontane circumpolar.

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