

Phylogenetic Relationships and Morphological Evolution in a Major Clade of Leafy Liverworts (Phylum Marchantiophyta, Order Jungermanniales): Suborder Jungermanniineae

Blanka Shaw,^{1,8} Barbara Crandall-Stotler,² Jiří Váňa,³ Raymond E. Stotler,^{2†} Matt von Konrat,⁴ John J. Engel,⁴ E. Christine Davis,⁵ David G. Long,⁶ Pavel Sova,⁷ and A. Jonathan Shaw¹

¹Department of Biology, Duke University, Durham, North Carolina 27708, U. S. A.

²Department of Plant Biology, Southern Illinois University, Carbondale, Illinois 62901-6509 U. S. A.

³Department of Botany, Charles University, Benátská 2, CZ-12801 Praha 2, Czech Republic.

⁴Department of Botany, The Field Museum, 1400 South Lake Shore Drive, Chicago, Illinois 60605–2496, U. S. A.

⁵Department of Biology, University of Florida, 614 Carr Hall, Gainesville Florida 32611, U. S. A.

⁶Royal Botanic Garden, Edinburgh EH3 5LR, Scotland.

⁷University of South Bohemia, Faculty of Science, Branisovska 31, 370 05 Ceske Budejovice, Czech Republic.

[†]Ray Stotler died in December, 2013, before this paper was accepted for publication; he played a major role in the research, including preparation of this manuscript.

⁸Author for correspondence (blanka@duke.edu)

Communicating Editor: Thomas L. P. Couvreur

Abstract—The suborder Jungermanniineae of the Jungermanniales is a major lineage of leafy liverworts, recognized in recent classifications to include 15 families. Gametophytes within the suborder are morphologically diverse, but commonly anisophyllous to distichous, usually with succubous, rarely transverse or incubuous, leaf insertions. Sporophytes are frequently, but not universally, enclosed by stem-derived perigynia or coelocauls, often accompanied by perianth reduction or loss and some level of geocauly or marsupial development. We herein provide the first comprehensive molecular phylogeny of this geographically widespread suborder, using sequences generated from one nuclear (*rpb2*), two mitochondrial (*nad1* and *rps3*), and seven plastid (*atpB*, *psbA*, *psbT-H*, *rbcL*, *rps4*, *trnG* and *trnL*) loci, sampled from 279 accessions representing 163 species in 57 genera. Ancestral states were reconstructed for 14 morphological characters generally considered taxonomically diagnostic for families in the suborder. Our phylogenetic analyses support the return of *Leiomylia* (= *Mylia anomala*) to the Myliaceae, removal of Myliaceae from the Jungermanniineae, and validation of the monogeneric suborder **Myliineae** subord. nov. to house it. Eighteen families are recognized within the Jungermanniineae, nine of which are monogeneric; namely, Endogemmataceae, Harpanthaceae, Gyrothyraeaceae, Arnelliaceae, Saccogynaceae, Geocalyceae, Jackiellaceae, **Notoscyphaceae** stat. nov., and Trichotemnomataceae. The generic compositions of other families are modified as follows: *Saccogynidium* is transferred from Geocalyceae to a newly named subfamily of Acrobolbaceae, **Acrobolbaceae subf. Saccogynidioidae**, and one other subfamily of the Acrobolbaceae is validated, **Acrobolbaceae subf. Austrolophozioideae**; *Hygrobiella* is included in Antheliaceae (previously in Cephaloziaceae or its own family); Jungermanniineae is broadened to include Mesoptychiaceae and Delavayellaceae; *Cryptocoleopsis* and *Nardia* are transferred from Solenostomataceae to Gymnomitriaceae; *Gottschelia*, *Herzogobryum*, and *Nothogymnomitrium* are excluded from the Jungermanniineae; Solenostomataceae is recognized to include *Solenostoma*, *Arctoscyphus*, *Cryptocolea*, and *Diplocolea*. Additional nomenclatural changes include recognizing *Horikawaella* as a synonym of *Solenostoma* and *Apomarsupella* as a synonym of *Gymnomitrium*, establishing two new subgenera of *Solenostoma*, ***Solenostoma* subg. Metasolenostoma** and ***Solenostoma* subg. Eucalyx**, and transferring *Jungermannia conchata* to *Cephalozia*. Morphological character state reconstructions identify dioecious inflorescences, gametangia on leading stems, flagelliform or stoloniferous branches absent, dorsal leaf insertions not overlapping the stem midline, large underleaves, and lack of gemmae as ancestral within the Jungermanniineae. All morphological characters appear to be moderately to highly homoplasious within the suborder.

Keywords—Chloroplast sequence data, Jungermanniaceae, liverwort phylogeny, mitochondrial sequence data, morphological character evolution, nuclear sequence data

Fossil records suggest that the early Paleozoic era, some 500–350 mya, marked the beginnings of land plant diversification, with the ancestors of several major clades established by the Devonian epoch (Kenrick and Crane 1997). Megafossils that are morphologically similar to extant simple thalloid liverworts are known from this epoch, including *Riccardiothallus* Guo et al., *Pallaviciniites* R. M. Schust., and *Metzgeriothallus* Hernick et al., and there is evidence that liverworts may be the earliest-diverging clade among the bryophyte lineages (Qiu 2008; but see also Finet et al. 2010; Wodniok et al. 2011; Cox et al. 2014). Over the last ten years, molecular phylogenetic analyses have resolved the deep clades of liverworts (Davis 2004; He-Nygrén et al. 2004; Forrest et al. 2006), and made progress in resolving relationships among major lineages of the largest clade, the leafy liverworts, i.e. subclass Jungermanniidae Engl. Fine-scale relationships within many speciose lineages, however, are still poorly understood. The suborder Jungermanniineae R.M. Schust. ex Stotler & Crand.-Stotl., as circumscribed by Crandall-Stotler et al. (2009), comprise one such group.

Concepts of the suborder have changed dramatically since its validation by Crandall-Stotler and Stotler (2000), primarily as a consequence of molecular phylogenetic studies (Forrest et al. 2006; He-Nygrén et al. 2006; Heinrichs et al. 2007; Vilnet et al. 2010). When first proposed by Schuster in 1953, the suborder encompassed all families of what is currently recognized as the Jungermanniales, but by 2000 several additional suborders had been established, and the Jungermanniineae were limited to a very broadly defined Jungermanniaceae, a monotypic Mesoptychiaceae, the Gymnomitriaceae, and the Scapaniaceae (Crandall-Stotler and Stotler 2000). The most recently published classification of liverworts by Crandall-Stotler et al. (2009), which incorporated phylogenetic inferences from Davis (2004), He-Nygrén (2007), He-Nygrén et al. (2004, 2006), Schill et al. (2004), Yatsentyuk et al. (2004), Heinrichs et al. (2005, 2007), Forrest et al. (2006), Hentschel et al. (2006, 2007), de Roo et al. (2007), Vilnet et al. (2007), and Feldberg et al. (2009), recognized 15 families in the Jungermanniineae. Our study is designed to assess the relationships among genera

and families included in this circumscription of the suborder. We also address species relationships within one clade (Solenostomataceae) by sampling multiple accessions, when available, of the included species.

Within the suborder Jungermanniineae, circumscriptions of the Jungermanniaceae and the genus *Jungermannia* L. have been diverse. In early morphology-based classifications (e.g. Schuster 1970; Váňa 1973), the family was broadly circumscribed to include *Jungermannia*, *Nardia* Gray, *Notoscyphus* Mitt., *Cryptocolea* R.M. Schust., *Cryptocoleopsis* Amak., *Diplocolea* Amak., *Scaphophyllum* Inoue, *Horikawaella* Hatt. & Amak., and *Hattoria* R.M. Schust. in the subfamily Jungermannioideae and numerous other genera classified in eight additional subfamilies (Crandall-Stotler and Stotler 2000). *Jungermannia* was circumscribed to include four subgenera, namely *J.* subg. *Jungermannia*, *J.* subg. *Liochlaena* (Nees) S. Arnell, *J.* subg. *Solenostoma* (Mitt.) Amak., and *J.* subg. *Plectocolea* (Mitt.) Amak. As a consequence of their molecular analysis, Hentschel et al. (2007) proposed to split this broadly interpreted genus into three genera corresponding to the subgenera, *Jungermannia*, *Liochlaena* Nees, and *Solenostoma* Mitt. (incl. *Plectocolea* (Mitt.) Mitt.). This system, including the broad concept of *Solenostoma*, has been accepted by most recent authors (e.g. Crandall-Stotler et al. 2009; Feldberg et al. 2009; Váňa and Long 2009; Váňa et al. 2010a) although some (e.g. Vilnet et al. 2011; Bakalin and Vilnet 2012) continue to recognize *Solenostoma* and *Plectocolea* as distinct genera. Hentschel et al. (2007) proposed that Jungermanniaceae should include only *Jungermannia*, *Delavayella* Steph., *Eremonotus* Lindb. & Kaal., *Leicolea* (Müll. Frib.) H. Buch, and *Liochlaena*, but they did not suggest a family placement for the remaining genera usually classified in the subfamily Jungermannioideae. Crandall-Stotler et al. (2008) recognized three families for the jungermannioid complex, placing *Delavayella* in Delavayellaceae, *Leicolea* and *Liochlaena* in Mesoptychiaceae, and the residue of the Jungermannioideae in the Jungermanniaceae, excluding other subfamilies from the family. In 2009, these families were redefined, the Mesoptychiaceae was combined with the Jungermanniaceae, and the Solenostomataceae was erected (Crandall-Stotler et al. 2009). There is, however, still ambiguity as to the relationships of these taxa. Addressing the phylogenetic affinities of taxa previously considered subgenera of *Jungermannia*, namely, *Liochlaena*, *Solenostoma*, and *Plectocolea* (Amakawa 1959, 1960; Váňa 1973) and related genera of the Jungermanniaceae and Solenostomataceae is, therefore, an additional focus of our study.

Within the Jungermanniineae, leaves are usually succubous, rarely transverse or incubous, in arrangement; sporophytes are often, but not always, protected by stem perigynia or coelocauls; perianths are frequently reduced or lacking; and marsupia may be present or absent (Crandall-Stotler et al. 2009). In addition, the suborder is heterogeneous with regards to leaf form, underleaf presence or absence, branching types and patterns, and form and position of reproductive structures, all characters considered of taxonomic importance in the delimitation of genera and families (He-Nygrén 2007). It has been suggested that the presence of perigynia is a synapomorphy for the suborder (He-Nygrén 2007), but patterns of evolutionary change in the key taxonomic characters of the suborder have never been reconstructed. Our evaluation of relationships within

the suborder includes analyses of morphological trait evolution in the context of phylogenetic relationships inferred from molecular data.

The present phylogenetic analysis is based on nucleotide sequence variation from 10 genomic regions representing all three genomes, mitochondrial, plastid, and nuclear, and includes 279 accessions representing 57 genera. The specific goals of this work were to (1) resolve relationships among species, genera, and families within the Jungermanniineae, (2) reconstruct ancestral states for selected morphological characters, and (3) propose a revised classification for the Jungermanniineae based on results from our analyses. Our general goals for the morphological reconstructions were to infer ancestral states for the Jungermanniineae as a whole and to assess, qualitatively, the degree to which morphological characters commonly used to delineate genera and families in this group are or are not homoplasious.

MATERIALS AND METHODS

Taxon Sampling—Our total data set includes 163 species representing 57 of the 63 genera classified in 15 families of the Jungermanniineae (Crandall-Stotler et al. 2009). In the absence of unambiguous information about circumscription of the Jungermanniaceae, our sampling includes multiple species within those genera included in the family, taxa that have been classified in proximity to the Jungermanniaceae, and selected more distant taxa to resolve polarity within a phylogenetically circumscribed in-group. Voucher information and GenBank accession numbers are provided in Appendix 1.

Genomic Sampling—Sequences were generated for one nuclear, two mitochondrial, and seven plastid loci (Table 1). RNA polymerase II (*rpb2*) represented the nuclear genome, and the mitochondrial genome was represented by intron sequences in the NADH protein-coding subunit 1 (*nad1*) and ribosomal small subunit protein 3 (*rps3*). From the plastid genome we sequenced CF1 ATPase beta-subunit gene (*atpB*), photosystem II (PSII) reaction center protein D1 (*psbA*), photosystem II reaction center protein T (*psbT-H*), ribulose-bisphosphate carboxylase gene (*rbcL*), ribosomal small protein 4 (*rps4*), tRNA(Gly) (UCC) (*trnG*), and the *trnL* (UAA) 59 exon *trnF* (GAA) region (*trnL*).

Extractions, amplifications, and sequencing followed methods and used primers described by Shaw et al. (2003) except for *atpB* and *rpb2*. Primer sequences for all the loci used in this study were provided in Cooper et al. (2011).

Phylogenetic Analyses—Sequences were initially aligned using MUSCLE (vers. 3.7; Edgar 2004) with default options and then adjusted manually with PhyDE® 0.995 (Müller et al. 2007). Regions of ambiguous alignment were identified and excluded from further analysis. Optimal substitution models were selected to maximize the Akaike information criterion (AIC) statistic for each locus using the software MrModeltest (vers. 2.3; Nylander 2004) in conjunction with PAUP* (vers. 4.0b10; Swofford 1998). Incongruence among loci (defined as conflicting clades supported by > 70 bootstrap (BS) support) were identified using the TCT (Tree Congruence Tester) program available at <http://www.biology.duke.edu/bryology/cymon.html#software>. No significant conflicts were detected so no taxa were removed from the concatenated data set.

Two data sets were analyzed. One included all 279 accessions and the other was pruned to include just one accession per 169 species. For the larger unpruned data set, maximum likelihood (ML) trees were constructed for a series of concatenated data sets to test the effects of missing data on topology and clade support. Analyses were run with only those accessions represented by eight or more loci, six or more, five or more, and with all accessions including those represented by only one locus. We found no topological differences among the restricted data sets. Results described below are based on all accessions, even those represented in the combined data set by only one of the 10 loci. Single locus bootstrap trees are available upon request. Trees from concatenated data sets with taxa having minimum numbers of successfully sequenced loci (as described above) are not presented, but are available upon request. Reconstructions were obtained using GARLI, version 1.0 (Zwickl 2006) not specifying nor fixing model parameters. These analyses were run on the Cipres portal (<http://www.phylo.org/portal2/>, Miller et al. 2010). Clade support was estimated

TABLE 1. Genomic regions sequenced for phylogenetic analyses of the Jungermanniineae (shown in Figs. 1, 2, and Fig. S1). *atpB*, *psbA*, *psbT*, *rbcL*, *rps4*, *trnG*, and *trnL* are from the plastid genome, *nad1* and *rps3* are from the mitochondrial genome, and *rpb2* is from the nuclear genome. N tree S1 = sample size in the analysis shown in Fig. S1; N Fig. 1 = sample size in the analysis shown in Fig. 1. PS = potentially informative

Marker	Genome	N tree S1	% Missing data (Fig. S1)	N tree Fig. 1	% Missing data (Fig. 1)	Aligned length	Analyzed length	Autapomorphic sites	Invariant sites	PS sites	% PS sites	Model
<i>atpB</i>	cp	70	75%	67	60%	1,181	997	595	68	334	34%	GTR+I+G
<i>psbA</i>	cp	225	19%	154	9%	1,473	1,206	769	101	336	28%	GTR+I+GHKY+I+G
<i>psbT</i>	cp	184	34%	131	22%	589	443	199	46	198	45%	GTR+I+G
<i>rbcL</i>	cp	137	51%	106	37%	1,551	1,346	797	74	475	35%	GTR+I+G
<i>rps4</i>	cp	204	27%	148	12%	751	583	200	58	325	56%	GTR+I+G
<i>trnG</i>	cp	160	43%	113	33%	1,013	656	123	67	466	71%	GTR+I+G
<i>trnL</i>	cp	229	18%	136	20%	913	518	214	50	254	49%	GTR+I+G
<i>nad1</i>	mt	202	28%	140	17%	990	844	590	79	175	21%	GTR+I+G
<i>rps3</i>	mt	167	40%	125	26%	1,186	1,104	690	146	268	24%	GTR+I+G
<i>rpb2</i>	nc	98	65%	66	61%	765	695	434	21	240	35%	GTR+I+G
combined	10 loci	279	40%	169	30%	10,412	8,391	4,611	710	3,071	37%	GTR+I+G

using GARLI, with 300 bootstrap replicates. The best substitution model for every gene in the unpruned data set was found to be GTR+I+ Γ so the concatenated data were analyzed using that single model.

Additional phylogenetic analyses were conducted on a pruned data set containing one accession per species (supplementary Table S1). The reconstruction from this more restricted data set is provided as Fig. 1, but the more taxon-inclusive reconstruction (all samples) is provided as supplementary Fig. S1. The ML reconstruction based on all samples (including multiple accessions per species) for the Solenostomataceae s. s. is presented as Fig. 2, since that family is also a focus of the study. Relationships among the 169 accessions (one per species; Fig. 1) were reconstructed under ML using the search methods described above. In addition to the ML analyses, Bayesian analyses were conducted on the pruned data set using MrBayes v3.1.2. We ran heterogeneous Bayesian analysis with site-specific (variable) rates for each partition with the following settings: unlink ratio=(all) revmat=(all); statefreq=(all) shape=(all) pinvar=(all); lset applyto=(all) ngammacat=4; prset ratepr=variable. Based on results from MrModeltest, all partitions for this data set, pruned to include one accession per species, were run with the GTR+I+G substitution model with the exception of *psbA*, for which the HKY+I+G model was optimal among those tested. The Bayesian search was run as follows: mcmc ngen=60000000; samplefreq=5000; printfreq=10000; nchains=4; nruns=2 temp=0.05. Tracer v1.5 (Rambaut and Drummond 2007) was used to evaluate the burn-in and to examine log likelihoods, ensuring that the runs were in the stationary phase and that adequate effective sample sizes (ESS) were attained. Construction of the consensus tree and estimation of clade posterior probabilities were based on the trees sampled after the chains converged. Consensus topologies and support values from the different methodological approaches were compiled and drawn using TreeGraph 2.0.42–187 beta (<http://treegraph.bioinfweb.info/>) and Figtree v.1.3.1. (<http://tree.bio.ed.ac.uk/software/figtree/>). The datasets used for phylogenetic analyses were deposited in TreeBASE (<http://purl.org/phylo/treebase/phyloids/study/TB2:S16128>).

Morphological Character State Reconstruction—Fourteen morphological characters were scored for all species included in the molecular analyses. Eight of the characters were binary and the other six were multistate. All scoring was based on personal study of the vouchers and knowledge of the taxa, supplemented with published descriptions; none were taken solely from literature sources. Ancestral state reconstructions were accomplished using the data set pruned to include one sample per species (Table S1). The characters and their states are listed in Table 2; character state scores for each species are listed in supplementary Table S2.

Character state reconstructions were performed with Mesquite vers. 2.75 (Maddison and Maddison 2011). Traits were mapped onto the maximum likelihood tree derived from Garli analyses of the pruned data set (Fig. 1). Reconstructions were performed using the mk1 model. Ancestral states at the base of the Jungermanniineae clade were inferred for those characters where the state was not “ambiguous” in the Mesquite analyses. Levels of homoplasy for each character were evaluated qualitatively by examination of character state reconstructions mapped onto the ML tree.

RESULTS

Molecular Variation—Sequence characteristics and amounts of missing data for the 10 loci included in phylogenetic analyses

are provided in Table 1. Among the plastid loci, *trnG* was most variable (in terms of potentially synapomorphic substitutions) and *psbA* was least variable. The two mitochondrial loci (*nad1*, *rps3*) were relatively nonvariable (21% and 24% synapomorphic sites, respectively). The nuclear locus, *rpb2*, was the least variable of the non-organellar loci (Table 1). The unpruned data set (279 taxa; Fig. S1) contained 39% missing data; the pruned data set (169 taxa; Fig. 1) contained 30% missing data. Specifically, 18 accessions were represented by data from all of the ten genomic regions sequenced, 36 for nine, 40 for eight, 41 for seven, 41 for six, 27 for five, 22 for four, 17 for three, eight for two, and 29 for only one.

Phylogenetic Relationships: Jungermanniineae—ML bootstrap values and Bayesian posterior probabilities were moderate to high for many of the important nodes that define major clades (Figs. 1, 2). The phylogeny was rooted with *Schistochila laminigera* Hook. f. & Taylor (suborder Perssoniellineae) as the outgroup (Fig. 1). For purposes of describing the reconstruction shown in Fig. 1, clades are labeled with family names. Some of the families, as defined in the figure, have modified circumscriptions relative to current classifications (e.g. Crandall-Stotler et al. 2009). The labels are included to facilitate the description of our results, while modifications of family circumscriptions are highlighted in the Discussion section below.

The Myliaceae, represented by *Mylia taylorii* (Hook.) Gray and *Leiomylia anomala* (Hook.) J.J. Engel & Braggins in our data set, has sometimes been included in the Jungermanniineae, but is resolved as sister to all other ingroup taxa in the current analyses. Although some taxa in the next two clades (moving up the tree in Fig. 1) have similarly been associated with the Jungermanniineae, these clades are best considered representative of suborders Lophocoleineae and Cephaloziineae, respectively (Fig. 1). Accessions resolved in the Lophocoleineae include representatives of the Lepidoziaceae, Pseudolepidoziaceae, Plagiochilaceae, and Lophocoleaceae, including the genus *Bragginsella* R. M. Schust., whose relationships have been controversial but which is supported with 100% BS as being nested within Lophocoleaceae. *Nothogymnomitrium* R. M. Schust. and *Herzogobryum* Grolle, both formerly classified in the Gymnomitriaceae of the Jungermanniineae, are likewise nested among representatives of the Cephaloziineae. The Jungermanniineae (from the Acrobolbaceae upward in Fig. 1) is strongly supported (BS = 100%) as monophyletic.

Within the Jungermanniineae, species of the genera *Lethocolea* Mitt. nom. cons., *Saccogynidium* Grolle, *Goebelobryum* Grolle,

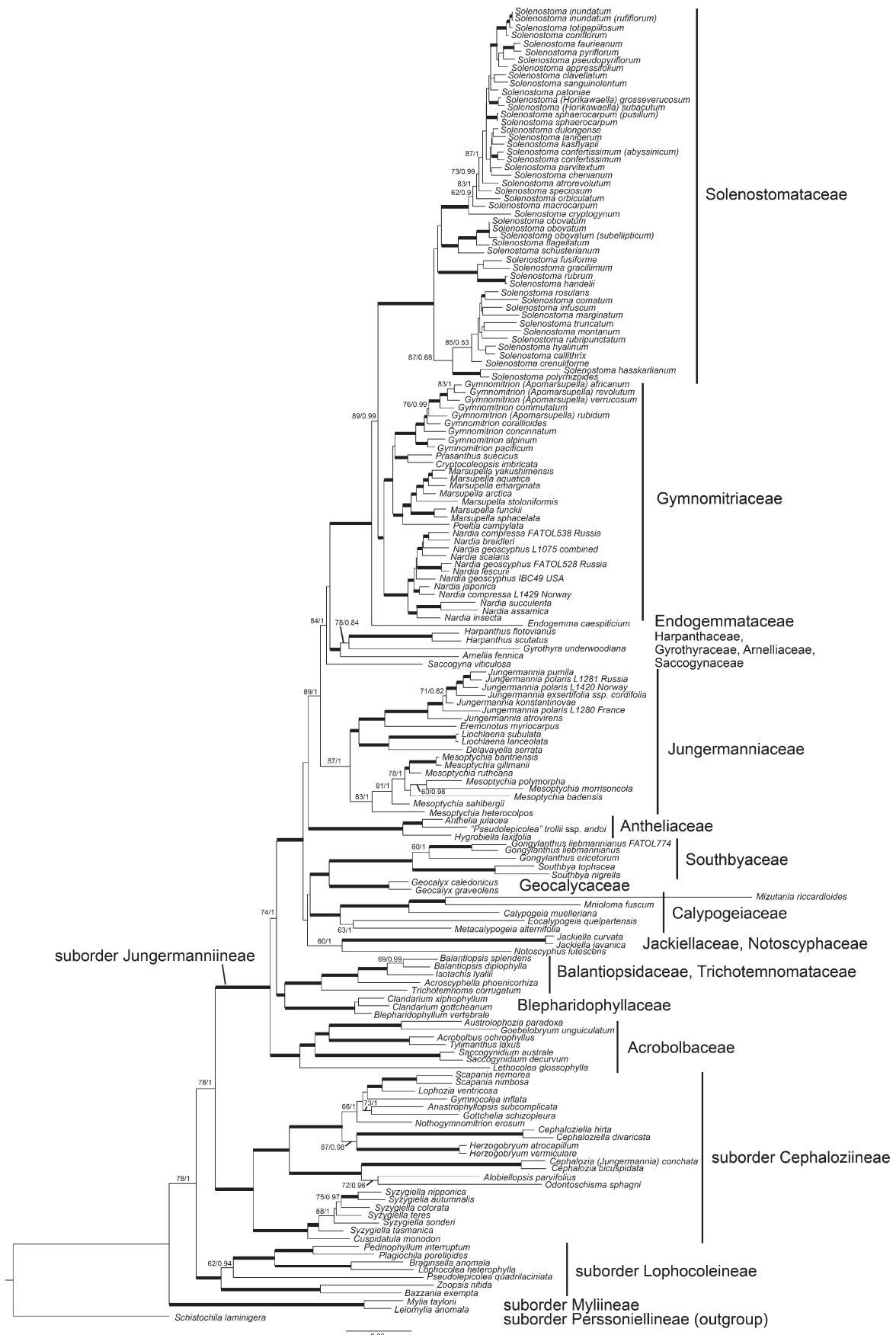


FIG. 1. Maximum likelihood phylogenetic reconstruction of the Jungermanniaceae (and outgroups) using GARLI (see Materials and Methods for analytical details). Multiple accessions per species were pruned from the data set; see Fig. S1 for an ML reconstruction based on the unpruned data set. Values above branches are ML bootstrap percentages / Bayesian PP. Thickened branches indicate ML bootstrap < 90% and Bayesian PP = 1.0.

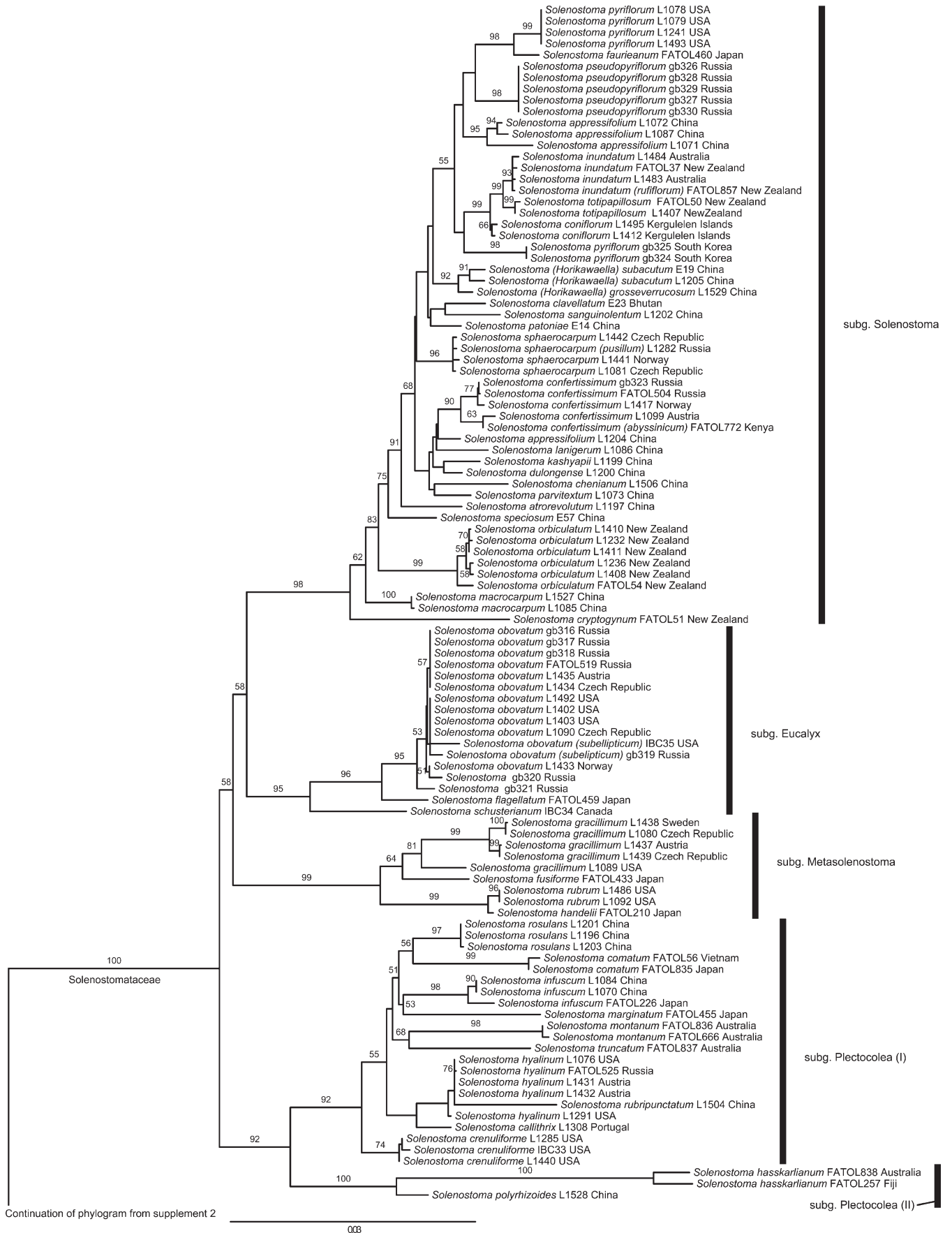


FIG. 2. Maximum likelihood phylogenetic reconstruction of the Solenostomataceae using GARLI (see Materials and Methods for analytical details). Multiple samples per species included where available. Based on the same data set as in Fig. S1. Values above branches are ML bootstrap percentages.

TABLE 2. Morphological characters and states scored for all species included in the phylogenetic analyses.

1. Underleaves: 0 = conspicuous; 1 = reduced to a few cells or papillae; 2 = absent
2. Interlocking merophytes: 0 = absent; 1 = present
3. Leaf form: 0 = undivided or emarginate; 1 = distinctly lobed
4. Frullania-type branching: 0 = absent; 1 = present
5. Flagelliform or stoloniferous branches: 0 = absent; 1 = present
6. Gemmae: 0 = absent; 1 = exogenous, angulate; 2 = exogenous, spherical to ovoid elliptical; 3 = endogenous
7. Sexual condition: 0 = dioecious; 1 = monoecious
8. Position of androecia: 0 = on leading axes; 1 = on short specialized branches
9. Position of gynoecia: 0 = on leading axes; 1 = on short specialized branches
10. Stem perigynium: 0 = absent or very low, < 0.2 length of the perianth; 1 = > 0.3 < 1.0 length of the perianth; 2 = ≥ the length of the perianth
11. Perianth: 0 = present, well developed; 1 = absent or very reduced
12. Calyptra type: 0 = with little or no shoot involvement; 1 = at least upper third of venter origin (shoot calyptra); 2 = little or no venter tissue present (coelocaula)
13. Geocauly: 0 = absent; 1 = moderate (Nardia or Harpanthus type); 2 = extensive (elongate marsupium)
14. Capsule shape: 0 = spheroidal, length = width; 1 = ovoid or short elliptical, < 2x as long as wide; 2 = long elliptical or cylindrical, > 2x as long as wide

Austrolophozia R. M. Schust., *Acrobolbus* Nees, and *Tylimanthus* Mitt. form a well-supported clade (Acrobolbaceae) that is resolved as sister to the rest of the Jungermanniineae (PP = 1.0). A small, strongly supported clade containing *Blepharidophyllum* Ångstr., *Clandarium* (Grolle) R. M. Schust., *Trichotemnoma* R. M. Schust., *Acroscyphella* N. Kitag. & Grolle, *Isotachis* Mitt., and *Balantiopsis* Mitt. (Blepharidophyllaceae, Trichotemnaceae, Balantiopsaceae) is then sister to the remaining taxa. *Notoscyphus*, *Jackiella* Schiffn., *Metacalyptogea* (S. Hatt.) Inoue, *Eocalypogea* (R.M. Schust.) R. M. Schust., *Mizutania* Furuki & Z. Iwats., *Mnioloma* Herzog, *Calypogea* Raddi, *Geocalyx* Nees, *Southbya* Spruce, and *Gongylanthus* Nees form a clade resolved in the ML reconstruction that is in turn sister to all remaining taxa in the study, but without support. However, within that clade, the Calypogeiaceae, Geocalyceae, and Southbyaceae are each strongly supported as monophyletic (Fig. 1).

The ML tree shows a clade (Antheliaceae, including Hygrobiellaceae), supported by 100% BS, that includes *Hygrobiella* Spruce, *Pseudolepicolea trollii* Grolle & Ando, and *Anthelia* (Dumort.) Dumort. The sister group relationship of this clade to the remaining taxa of Jungermanniineae is, however, without BS support. The Jungermanniaceae, including *Jungermannia* s. s. (with *J. atrovirens* Dumort., the type of *Jungermannia*), *Eremonotus*, *Liochlaena*, and *Delavayella*, and the Mesoptychiaceae (including *Mesoptychia* (Lindb.) A. Evans and formerly recognized genera *Hattoriella* (Inoue) Inoue and *Leiocolea* form sister clades, and this more inclusive, fairly well supported clade that includes both families is resolved sister to the rest of the Jungermanniineae (i.e. above it in Fig. 1), albeit with poor support.

Monophyly of the remaining terminal clade, while resolved in the ML tree, is not supported by the bootstrap. *Saccogyna viticulosa* (L.) Dumort. is resolved as an early diverging lineage within that group. A well-supported clade with *Arnellia fennica* (Gottsche & Rabenh.) Lindb., two species of *Harpanthus* Nees, and *Gyrothyra underwoodiana* M. Howe, is sister to the remaining taxa (Endogemmataceae, Gymnomitriaceae,

Solenostomataceae). Within the latter group, *Endogemma caespitium* (Lindenb.) Konstant., Vilnet & A. V. Troitsky is sister (with strong support; 89% ML bootstrap, 0.99 Bayesian PP) to the Gymnomitriaceae plus Solenostomataceae. The six accessions of *E. caespitium* from Eurasia and North America are on an exceptionally long stem branch (and distinguished as the Endogemmataceae), but are little differentiated from one another (Fig. S1).

The Gymnomitriaceae contain nine species of *Nardia* and although several of the species represented by multiple accessions are non-monophyletic (Fig. S1), the genus is very strongly supported. Seven species of *Marsupella* Dumort. form a monophyletic group sister to *Poeltia campylata* Grolle within the Gymnomitriaceae (Fig. 1). *Prasanthus suecicus* Lindb. is sister to *Cryptocoleopsis imbricata* Amakawa with strong support. The Gymnomitriaceae also encompass nine species of *Gymnomitrium* Corda, including four species often classified as *Apomarsupella* R. M. Schust. that are nested within the *Gymnomitrium* clade (shown in Fig. 1).

Species Relationships Within the Solenostomaceae—The Solenostomataceae form a monophyletic group supported by 100% BS and 1.00 PP. Our sampling of this clade includes approximately 51 species of *Solenostoma* (of an estimated 140 species recognized worldwide), and although the species fall into multiple subclades that are each well-supported, relationships among those subclades are in some cases ambiguous (Fig. 2). We herein (below) describe one new subgenus (*Metasolenostoma*) and elevate *Eucalyx* from sectional to subgeneric rank within *Solenostoma* to formalize two of these monophyletic groups. These two groups each contain accessions representing *Solenostoma* species from the Northern Hemisphere, including North America, Europe, and Asia. Multiple accessions of *S. obovatum* (Nees) C. Massal. (subg. *Eucalyx*) from North America and Europe are very similar at the nucleotide sequence level. A third clade (with 92% BS support) consisting of 12 *Solenostoma* species is here assigned to the subgenus *Plectocolea*. Seven of the species in this clade are from Asia and three are from Australia, with *S. crenuliforme* (Aust.) Steph., *S. callithrix* (Lindenb. et Gottsche) Steph. and *S. hyalinum* (Lyell) Mitt. from North America and Europe nested within the group. A collection referred to *S. rubripunctatum* (S. Hatt.) R. M. Schust., from China, is nested within *S. hyalinum*, on a long branch, without support. The relationship between these two taxa warrants further study.

Subgenera *Plectocolea* (92% BS), *Metasolenostoma* (99% BS), and *Eucalyx* (BS=95%) form a paraphyletic grade basal to subgenus *Solenostoma* (98% BS). The subgenus *Solenostoma* includes Asian accessions from Bhutan, China, Japan, and South Korea plus accessions from New Zealand and the Kerguelen Islands, as well as *S. pyriferum* Steph. from North America (resolved with 100% support as sister to *S. fairieanum* (Beauvd.) R. M. Schust. from Japan), *S. pseudopyriferum* Bakalin & Vilnet from Asiatic Russia, *S. sphaerocarpum* (Hook.) Steph. from Europe, *S. confertissimum* (Nees) Schljakov, also from Europe, and *S. abyssinicum* (Nees) Steph. (reduced to *S. confertissimum* in this study) from Africa. Species formerly segregated as the genus *Horikawaella*, namely, *H. grosse-verrucosa* (Amakawa & S. Hatt. and *H. subacuta* (Herzog) S. Hatt. & Amakawa, from China, are nested within *Solenostoma* subg. *Solenostoma*. Some species are clearly non-monophyletic; e.g. American accessions attributed to *S. pyriferum* appear to be only

distantly related to Korean accessions, and one accession of *S. appressifolium* (Mitt.) Vána & D. G. Long from China is not resolved with the other three, also from China.

Morphological Character Reconstructions—Ancestral states for morphological characters are summarized in supplementary Fig. S2. Although character states for some traits are ambiguous, it appears likely that the ancestor of Jungermanniineae had dioecious inflorescences, gametangia on leading stems, flagelliform or stoloniferous branches absent, dorsal leaf insertions not overlapping the stem midline, large underleaves, and no gemmae.

The ancestral sexual condition in the Jungermanniineae was unambiguously dioecious, but monoecy appears to have evolved at least 16 times (Fig. S2). Gemmae evolved multiple times in distantly related families of the Jungermanniineae. Underleaves were gained multiple times in the Jungermanniineae and appear to be present in the ancestor of *Mesoptychia*, *Delavayella*, *Liochlaena*, *Eremonotus*, and *Jungermannia* within the Jungermanniaceae (Fig. 1, Fig. S2). Underleaves were also present in the common ancestor of the Southbyaceae (Fig. 1, Fig. S2) but absent in the common ancestor of the Gymnomitriaceae+Solenostomataceae clade. Underleaves were subsequently regained in the common ancestor of *Nardia* species. There appear to have been at least 4–5 additional losses of underleaves in the Jungermanniineae (Table S2 and Fig. S2). We cannot accurately count the numbers of gains and losses for all characters because our sampling was not exhaustive at the species level and some additional character state transitions occurred within families. A qualitative assessment of additional transitions can be gained from studying Fig. S2.

All morphological traits are characterized by extensive homoplasy, including parallel losses and gains. Reversals also appear to have occurred repeatedly. This is true of both gametophytic and sporophytic characters; capsule shape has clearly transitioned between ovoid and spheroidal in multiple lineages. Early-diverging lineages within the Jungermanniineae repeatedly evolved more narrowly elongate to cylindrical capsules but this capsule shape seems not to have re-evolved in more derived lineages, which are characterized by shorter and broader capsules (Fig. S2). Gynoecea and androecea were borne on the leading axes of ancestral Jungermanniineae, but shifts to short lateral branches occurred multiple times; in some lineages this shift in the position of female and male reproductive structures occurred together, but shifts in gynoecea or androecea, but not both, occurred in a few lineages. Flagelliform or stoloniferous branches evolved multiple times, but do not currently characterize large clades but rather one or a few species scattered across the phylogeny. One of the least homoplasious characters pertains to the dorsal leaf insertion overlapping (or not) the stem midline, but even that character shows some homoplasy.

DISCUSSION

New Phylogenetic and Taxonomic Inferences—Early molecular phylogenetic analyses addressed primarily the backbone relationships among classes, orders and suborders of liverworts (e.g. Davis 2004; Forrest and Crandall-Stotler 2004, 2005; Heinrichs et al. 2005; He-Nygrén et al. 2006; Forrest et al. 2006). These and subsequent family level studies, such as those of de Roo et al. (2007), He-Nygrén

(2007), Hentschel et al. (2006, 2007), Wilson et al. (2007) and Vilnet et al. (2007) resulted in numerous new insights, most of which were incorporated in the most recent comprehensive classification of liverworts by Crandall-Stotler et al. (2009). Our results extend previous inferences and provide support for additional realignments of several taxa of the Jungermanniineae.

The Myliaceae are excluded from the Jungermanniineae and recognized to comprise the new suborder Myliineae subord. nov. Although the suborder was proposed by Engel and Braggins (2005), and referred to by He-Nygrén (2007), it has never been validly published. Although Engel and Braggins (2005) indicated in the abstract that *Trabacellula* Fulford should also be included in the suborder based on similar cell wall architecture, in the taxonomic section of their manuscript, that genus is retained in the Cephaloziaceae subfam. *Trabacelluloideae* (Fulford) R. M. Schust. Cell wall architecture aside, *Trabacellula* is morphologically congruent with the Cephaloziaceae, where it has traditionally been placed. Because *Trabacellula* was not included in our molecular sampling, we cannot assess whether transfer out of the Cephaloziaceae is justified and therefore we retain it in that family.

Within the Myliaceae, the taxonomic status of *Leiomylia* J. J. Engel & Braggins, erected to include only *Mylia anomala* (Hook.) Gray, is equivocal. Our results mirror those of de Roo et al. (2007) in resolving *L. anomala* and *M. taylorii* as sister taxa in a strongly supported clade. These results indicate a much closer relationship between *L. anomala* and *M. taylorii* than that proposed by Engel and Braggins (2005), who placed them in separate suborders, and clearly support the return of *Leiomylia* to the Myliaceae. What cannot be determined with certainty is whether *Leiomylia* should be reduced to *Mylia*, as proposed by de Roo et al. (2007). There is disagreement among us as to whether *Leiomylia* should be recognized, but our molecular results do not support any particular taxonomic conclusion regarding the two genera. For now, the best decision seems to be to recognize *Leiomylia*, pending more expansive population-level studies of the Myliaceae and more exhaustive studies of the chemical and cellular features of the cell wall grids.

Monophyly of the Myliineae is strongly supported in our analyses, but its phylogenetic position is ambiguous. It is resolved as sister to the large Lophocoleineae/Cephaloziineae/Jungermanniineae clade but with poor support (Fig. 1), a position also resolved in the parsimony analysis of He-Nygrén (2007). But in other analyses, e.g. those of de Roo et al. (2007), Heinrichs et al. (2007), Hentschel et al. (2007) and the maximum likelihood analysis of He-Nygrén (2007), it was resolved as the earliest diverging lineage of the Jungermanniineae. Considering the unique blend of morphological characters displayed by the group, in combination with our molecular data, recognition of a separate suborder seems justified.

Circumscription of the Acrobolbaceae is broadened to include *Saccogynidium*, a genus formerly aligned with the Geocalycaceae (Grolle 1960; Crandall-Stotler et al. 2009), with which it shares many morphological features, and a new subfamily, Acrobolbaceae subf. *Saccogynidioideae* subf. nov., is established for it. Schuster (2001) recognized three subfamilies in the Acrobolbaceae, namely, subf. *Acrobolboideae* R. M. Schust. nom. inval. (without diagnosis) comprising *Acrobolbus*, *Marsupidium* Mitt., and *Tylimanthus*,

a monogeneric subf. Austrolophozioideae R. M. Schust. nom. inval. (without diagnosis), and subf. Lethocoleoideae, as established and delimited by Grolle (1972) to include *Lethocolea* and *Goebelobryum*. Although all taxa in the Acrobolbaceae form well-developed marsupia, in the latter subfamily the marsupia are hollow and derived from a stem perigynium; i.e. *Calypogeia* type, while in the other two subfamilies, they are solid and derived from a coelocaul; i.e. *Tylimanthus* type. In our study, *Goebelobryum*, which has a *Calypogeia* type marsupium and *Austrolophozia*, with a *Tylimanthus* type marsupium, are resolved as sister taxa in a strongly supported lineage; therefore, *Goebelobryum* is transferred to the subfamily Austrolophozioideae. Despite these significant differences in marsupial development, the taxa share the following suite of characters: leaves spinose-dentate to lobulate, often with reddish to brown pigments, cell walls smooth, oil bodies large and few in number, rhizoids in dense mats that often form decurrent bundles on the ventral surface of the stem, branches only of the lateral *Plagiochila* type, and male bracts little modified from the leaves (Schuster 2001; Engel and Glenny 2012). *Saccogynidium* is resolved as a separate lineage within the family (Fig. 1) and is also morphologically distinct in having large, bilobed underleaves and gametangia always borne on very short, determinant ventral branches. Although *Marsupidium* sometimes produces androecia and occasionally gynoecia on short to long ventral branches, the androecium-bearing branches can continue growth after gametangial maturation (Engel and Grolle 1971; Engel and Glenny 2008), in contrast to the very specialized reduced sexual branches of *Saccogynidium*. In *Saccogynidium* marsupia are of the *Calypogeia* type, developmentally most like those of *Goebelobryum*, and its capsule wall is multistratose, a character shared with all other taxa in the Acrobolbaceae. In addition to naming a new subfamily for *Saccogynidium*, we also provide a diagnosis (below) to validate subfamily Austrolophozioideae; A. subfam. Acrobolboideae has recently been validated by Briscoe et al. (2015).

No changes are proposed to the circumscriptions of Blepharidophyllaceae, Trichotemnomataceae, Balantiopsidaceae, Jackiellaceae and Gyrothyraeaceae in Crandall-Stotler et al. (2009), and the Calypogeiaceae is the modified only by the inclusion of *Mizutania*, as already proposed by Masuzaki et al. (2010). Our molecular data show that *Blepharidophyllum* and *Clandarium* are closely related, and Grolle (1965) suggested that they be classified in a single genus. Since *B. densifolium* (Hook.) Ångstr. ex C. Massal., the type of *Blepharidophyllum*, was not included in our study, we maintain them here as separate genera pending future studies. The Trichotemnomataceae is strongly supported as sister to the Balantiopsidaceae, as also shown by He-Nygrén (2007). In agreement with the analysis of Hendry et al. (2007), *Jackiella* is resolved as a monophyletic lineage of the Jungermanniiineae, but with ambiguity as to its precise relationships (Fig. 1). A weakly supported sister relationship to *Notoscyphus* is suggested, and there are shared morphological characters that support at least a distant relationship between these taxa; e.g. unlobed leaves, restriction of branching to the ventral *Bazzania* type, leaf cells with large trigones and 1–3 large, granular oil bodies, a seta comprised of eight rows of large epidermal cells and a core of much smaller inner cells, and elongate capsules with 2-stratose walls. On the other hand, substantial mor-

phological and molecular differences between them justify their placement in separate families, accommodated by the elevation of Jungermanniiaceae subfam. Notoscyphoideae (Schuster 1970, 2002) to the monogeneric Notoscyphaceae.

Geocalycaceae, in the sense of Crandall-Stotler et al. (2009), is polyphyletic and is consequently now recognized to include only the genus *Geocalyx*. Additional monogeneric families are established for *Notoscyphus*, *Saccogyna*, and *Harpanthus* (see taxonomic section below) and *Saccogynidium* is transferred to the Acrobolbaceae as already discussed. The characters that have suggested a relationship among these genera; i.e. the restriction of gametangia to abbreviated ventral branches, *Calypogeia* type marsupia and bifid underleaves, have evolved multiple times in the Jungermanniiineae and are not indicative of a family level relationship, as previously assumed.

Hygrobliella and *Anthelia* are included in a single family, as previously postulated by Müller (1948, 1954), who placed them in the Hygrobliellaceae. Much later, Konstantinova and Vilnet (2009: 65) proposed to establish Hygrobliellaceae as a new family, but this publication of the name was not valid since the proper basionym was not cited; however, the name was validly published by Konstantinova et al. (2014). Based on the principle of priority, nonetheless, the family name that must be applied to this lineage is Antheliaceae, validly published by Schuster (1963). In more recent treatments, *Hygrobliella* has been classified in the Cephaloziaceae based on Schuster's (1973) transfer of the genus to that family (e.g. Paton 1999; Damsholt 2002; Crandall-Stotler et al. 2009). Schuster (1979), in contrast to earlier workers, considered *Anthelia* to be a "highly isolated taxon" unrelated to *Hygrobliella* and proposed its placement in a monogeneric suborder Antheliineae, which was subsequently recognized and validly published by Crandall-Stotler and Stotler (2000). In 2006 He-Nygrén et al. showed that *Anthelia* belongs in the Jungermanniiineae, a concept accepted by Crandall-Stotler et al. (2009), while Vilnet et al. (2012) resolved *Hygrobliella* as an outlier of the Cephaloziineae. Ours is the first study to include both genera, and resolve their close relationship.

The strongly supported resolution of *Pseudolepicolea trollii* ssp. *andoi* (R. M. Schust.) S. Hatt. & Mizut. within the Antheliaceae lineage is puzzling, considering its very different morphology from its sister taxon, *Anthelia*. These results also render the genus *Pseudolepicolea* Fulford & J. Taylor, as circumscribed by Hässel de Menéndez and Solari (1975), Grolle (1983) and Crandall-Stotler et al. (2009), polyphyletic, with the generitype, *P. quadrilaciniata* (Sull.) Fulford & J. Taylor, resolved in the Lophocoleineae. We have verified that the voucher specimen for the *P. trollii* ssp. *andoi* sequences is correctly identified. Female plants with young sporophytes found in the collection have perianths that are elongate, 6-keeled, and deeply 12-lobed at the mouth, with the lobes long, acuminate. Sporophytes are enclosed in a well-developed shoot calyptra and penetrate the stem to the level of the bracts; the capsule is shortly ellipsoidal, with a 2-layered wall, and the seta averages six cells in diameter, with 18–22 rows of epidermal cells that are slightly larger than the internal cells. These features are held in common with *P. fryei* (Perss.) Grolle & Ando, a species recognized by Schuster (1960) as the type of the genus *Lophochaete* R. M. Schust., and differ from the true calyptra and multistratose capsule

wall of *P. quadrilaciniata* (Schuster 1966; Hässel de Menéndez and Solari 1975). It is tempting to conclude from our analysis that *Lophochaete* should be recognized as a genus, but we have no molecular data on *P. fryei* or other species of *Pseudolepicolea*. In addition, there seems to be little morphological connection between *P. trollii* ssp. *andoi* and the other genera of the Antheliaceae. Consequently, we are reserving judgment on the disposition of this taxon, pending additional sampling within the Pseudolepicoleaceae.

Jungermanniaceae is broadened to include five genera, namely *Jungermannia*, *Eremonotus*, *Liochlaena*, *Delavayella*, and *Mesoptychia*, including all species of the former *Leiocolea* and *Hattoriella* (Váňa et al. 2012b). As in earlier analyses by de Roo et al. (2007), Hentschel et al. (2007) and Vilnet et al. (2010, 2011), three lineages are resolved within the Jungermanniaceae clade, each of which has been previously recognized as a family; i.e. Jungermanniaceae, Delavayellaceae, and Mesoptychiaceae (e.g. He-Nygrén et al. 2006). Our analyses suggest that these lineages are closely related and we therefore agree with Hentschel et al. (2007) and define the Jungermanniaceae to include all three. Morphological characters that also support recognition of a single family include the following: branching only from lateral merophytes, gynoecia and androecia only on leading stems, long emergent perianths that are contracted at the mouth, bistratose capsule walls, and in all taxa except *M. sahlbergii* (Lindb. & Arnell) A. Evans, calyptral development with little or no shoot involvement, no perigynial development, and no geocauly.

The Arnelliaceae are resolved as polyphyletic, with *Arnellia* sister to a *Gyrothyra*/*Harpanthus* clade and the *Southbya*/*Gongylanthus* lineage sister to the Geocalycaee. These results support the transfer of *Southbya* and *Gongylanthus* to the recently named Southbyaceae as discussed by Váňa et al. (2012a), and the circumscription of Arnelliaceae as a monogeneric family. A close phylogenetic relationship among *Arnellia*, *Gyrothyra*, and *Harpanthus* lineages is moderately supported, but substantial levels of molecular and morphological divergence among them lead us to recognize three separate families, as labeled in Fig. 1. The transfer of *Stephaniella* and *Stephaniellidium* Winkler ex Grolle to Arnelliaceae by Crandall-Stotler et al. (2009) was based on the nested position of *Stephaniella* between *Southbya* and *Gongylanthus* in de Roo et al. (2007). Personal study of the voucher specimen for the *Stephaniella* sequence confirmed, however, that it had been misidentified, and was actually *Gongylanthus liebmannianus* (Lindenb. et Gottsche) Steph. (labeled FATOL774 in Table S1 and Fig. 1). In the absence of molecular data, the phylogenetic affinities of *Stephaniella* and *Stephaniellidium* remain equivocal, but there is no evidence to support their placement in either the Arnelliaceae or Southbyaceae. Morphologically they have more characters in common with the Gymnomitriaceae, in which they were placed by Schuster (1984), than in other families represented in our dataset. In 2002 Schuster elevated his subfamily Stephanielloideae of the Gymnomitriaceae to family status, still noting, however, a close relationship to that family.

The Gymnomitriaceae is modified to include *Nardia* and *Cryptocoleopsis*, previously classified in the Solenostomataceae (Crandall-Stotler et al. 2009), and to exclude *Herzogobryum* and *Nothogymnomitrium*. In our study, the 19 accessions of *Nardia* form a lineage that is sister to a group that includes five genera: *Poeltia*, *Marsupella*, *Cryptocoleopsis*, *Prasanthus*,

and *Gymnomitrium*, a topology also resolved in Vilnet et al. (2010, 2011). The fairly small molecular distance between the two lineages and several shared morphological features (e.g. the development of stem perigynia, reduction in size of perianths, occurrence of two or three large, granular oil bodies per cell, and isodiametric outer capsule wall cells with nodular thickenings on all walls) support our transfer of *Nardia* to the Gymnomitriaceae. The major morphological divergences between the two lineages are the evolution of underleaves in *Nardia* and dorsally overlapping leaf insertions (i.e. dorsally interlocking merophytes) in the “*Poeltia* to *Gymnomitrium* clade,” but both of these traits are homoplasious (see supplementary Fig. S2). Although nine species of *Nardia* were included in our sampling, interspecific relationships within the genus are unclear, due in part to the non-monophyly of multiple accessions of *N. geoscyphus* (De Not.) Lindb. and *N. compressa* (Hook.) Gray. *Nardia succulenta* (Rich. ex Lehm. & Lindenb.) Spreng. and *N. assamica* (Mitt.) Amakawa, which were recognized as related taxa by Váňa (1976) and Engel (1988), are strongly supported as sister taxa. However, *N. insecta* Lindb., a species that is morphologically unlike them and quite like *N. geoscyphus* and *N. lescurii* (Austin) Underw. (Schuster 1969; Váňa 1976) is sister to them, forming a clade that is sister to the rest of the genus. Although our sampling within *Nardia* is more extensive than any previously published treatment, expanded population level studies are needed to resolve species level relationships and evolutionary groups within the genus.

Since its erection by Amakawa (1959), *Cryptocoleopsis* has been aligned with taxa of the Jungermanniaceae, although some resemblance to *Prasanthus* was noted by Amakawa (1959). Inoue (1983) reduced *Gymnomitrium integerrimum* N. Kitag., named by Kitagawa (1959), to synonymy under *Cryptocoleopsis imbricata*, with an indication that the taxon should remain in Jungermanniaceae. It is noteworthy that *Cryptocoleopsis* is not only resolved within the Gymnomitriaceae, but sister to *Prasanthus*, which it resembles in lacking a perianth and in expressing moderate geocauly.

Also within the Gymnomitriaceae, *Poeltia*, considered a subgenus of *Marsupella* by Schuster (1996, 2002), is resolved as sister to the *Marsupella* clade, and is herein recognized as a monotypic genus. Although *Poeltia* is related to *Marsupella*, it is unique in the family in having strongly patent, squarrose leaves and gynoecia borne on short, endogenous branches (Grolle 1966). *Apomarsupella* is nested within *Gymnomitrium* and is reduced to it. This reduction is morphologically supported by the absence of perianth and perigynial development in *Apomarsupella*, as is also diagnostic of *Gymnomitrium* (Schuster 1996; Vilnet et al. 2010). The inclusion of *Herzogobryum* in the Gymnomitriaceae has been equivocal since *H. teres* (Carrington & Pearson) Grolle was resolved in the Cephaloziineae (Clade B) by Davis (2004) and Forrest et al. (2006). Although this species has recently been transferred to *Syzygiella* (Váňa et al. 2013) because of its morphological similarities to that genus, the phylogenetic affinities of the generitype have not previously been tested. In our study *Herzogobryum vermiculare* (Schiffn.) Grolle (= *H. cucullatum* (Herzog) Grolle, the type of *Herzogobryum*) and *H. atrocipillum* (Hook. f. & Taylor) Grolle were resolved in the Cephaloziineae, near the Cephaloziellaceae, and the genus is, therefore, removed from Gymnomitriaceae; *H. teres* is nested in *Syzygiella*, confirming its transfer to that genus. The monospecific genus

Nothogymnomitrium was also resolved in the Cephaloziineae, in the vicinity of the Anastrophyllaceae and Cephaloziellaceae, supporting its removal from the Gymnomitriaceae as well. Whether *Acrolophozia* R. M. Schust., *Aponardia* (R. M. Schust.) Váňa, *Nanomarsupella* R. M. Schust. ex A. Hagborg, L. Söderstr. & von Konrat and *Paramomitrium* R. M. Schust. should remain in the family remains to be tested. Schuster (2002) and Engel and Glenny (2008) placed *Paramomitrium* in the Jungermanniaceae near *Eremonotus*, but it is still recognized in Gymnomitriaceae by Váňa et al. (2010b).

Solenostomataceae was erected by Crandall-Stotler et al. (2009) to accommodate *Solenostoma* and the presumably related *Arctoscyphus*, *Bragginsella*, *Cryptocolea*, *Cryptocoleopsis*, *Cryptostipula*, *Diplocolea*, *Horikawaella*, *Nardia*, and *Scaphophyllum*. Because the family included *Nardia*, the type of the earlier named Mesophyllaceae Heeg (= the superfluous Aliculariaceae Warnst., published 11 yr later), Solenostomataceae was incorrect at the time of its naming. With the transfer of *Nardia* to the Gymnomitriaceae, however, it becomes a correct family name, the type of which is *Solenostoma*. Our results support the placement of *S. caespiticium* (Lindenb.) Steph. in the monotypic Endogemmataceae by Vilnet et al. (2011), the transfer of *Gottschelia patoniae* Grolle, D. B. Schill & D. G. Long and *Scaphophyllum speciosum* (Horik.) Inoue to *Solenostoma* by Feldberg et al. (2009), and the removal of the genus *Gottschelia*, based on *G. schizopleura* (Spruce) Grolle, from the Jungermanniineae to the Cephaloziineae. In our analyses, both species of *Horikawaella* are nested in *Solenostoma* subg. *Solenostoma*, supporting the synonymy of that genus under *Solenostoma*. *Cryptocoleopsis* is transferred to Gymnomitriaceae (as already discussed), *Bragginsella* has been placed in Lophocoleaceae (Glenny and Malcolm 2005; Söderström et al. 2013) and *Cryptostipula* has been synonymized with *Hepatostolonophora* J. J. Engel & R. M. Schust. in Lophocoleaceae (Engel 2011). The phylogenetic affinities of *Arctoscyphus*, *Cryptocolea* and *Diplocolea* remain to be tested.

Our analyses resolved four major clades within a broadly defined, strongly supported *Solenostoma* (Solenostomataceae) clade (Fig. 2). Subgeneric status is proposed for each of these lineages as indicated in Fig. 2, namely, *S.* subg. *Solenostoma*, *S.* subg. *Eucalyx*, *S.* subg. *Metasolenostoma*, and *S.* subg. *Plectocolea*. Relationships among these subgenera are not unambiguously resolved, and there are clear morphological overlaps among them, especially as regards perigynial and perianth characters. Taxa in *S.* subg. *Eucalyx* and *S.* subg. *Plectocolea* have plectocoleoid perianths that are fusiform, comprised of elongate cells, and contracted but not beaked at the mouth. Of species sampled, all resolved in *S.* subg. *Eucalyx* have well-developed perigynia that are 1–2 times the length of the perianths, which are barely emergent from the bracts, whereas all resolved in *S.* subg. *Plectocolea* have perigynia that are shorter than the perianths, which generally extend well beyond the bracts. Whether species that were not included in our sampling will also sort into these two subgenera based on this difference in perigynial development remains to be tested. Solenostomatoid perianths that are pyriform, comprised of isodiametric cells in the upper and middle part, and contracted into a distinct beak at the mouth, and low to scarcely developed perigynia are characteristic of both *S.* subg. *Solenostoma* and *S.* subg. *Metastolenostoma*. All species resolved in *S.* subg. *Metastolenostoma* have leaves

that are bordered by a row of larger cells, whereas those resolved in *S.* subg. *Solenostoma* do not express this character, but whether this character is constantly diagnostic is equivocal since not all species with solenostomatoid perianths and bordered leaves have been tested. No other morphological characters, including those used by Amakawa (1960, 1966); e.g. plant size, growth form, or rhizoid distribution, separate infrageneric groups, nor do our results support the sectional classifications proposed by Amakawa (1960, 1966). In this regard, note that *S. hasskarlianum* and *S. rosulans*, the only species of *S.* subg. *Plectocolea* sect. *Plectocolea* included in our dataset are resolved in separate clades of *S.* subg. *Plectocolea*, the former in *S.* subg. *Plectocolea* II and the latter in *S.* subg. *Plectocolea* I (Fig. 2). Since our current dataset does not include *S. radiculosum* Mitt., the type of *S.* subg. *Plectocolea*, we prefer to recognize both of these clades in *S.* subg. *Plectocolea*. Although Bakalin and Vilnet (2012) recover clades that are comparable to our four subgeneric lineages, their analysis differs in several regards, the most significant of which is the resolution of *S. hyalinum* sister to the *Solenostoma* clade. In all of our analyses, accessions of *S. hyalinum*, including one from Russia, form a clade that is nested in *S.* subg. *Plectocolea*, with which it shares perianth and perigynial characters. Since there is little support for the clade designated by Bakalin and Vilnet (2012) as *Solenostoma*, but strong support for the clade that includes both the *Solenostoma* and *Plectocolea* lineages, it seems more reasonable to recognize *Plectocolea* as one of four subgenera of *Solenostoma*, as we propose, than to modify its circumscription as a genus (Bakalin and Vilnet 2012).

In addition to the transfer of *Horikawaella subacuta* and *H. grosse-verrucosa* to *S.* subg. *Solenostoma*, our analyses suggest that *S. abyssinicum* is nested within *S. confertissimum*, and *S. subellipticum* (Lindb. ex Heeg) R. M. Schust. is nested within *S. obovatum*. We propose (below) that the two nested taxa be synonymized with their respective inclusive species. Schuster (1988) postulated that *Jungermannia subellipticum* (Lindb. ex Heeg) Levier was likely an ecological variant of *J. obovata* Nees, and Damsholt (2002) reduced it to infrageneric status as *J. obovata* subsp. *minor* (Carrington) Damsh. (Basionym: *Nardia obovata* Lindb. var. *minor* Carrington. Brit. Hep.: 33. 1876). Since *S. subellipticum* is nested within *S. obovatum* and not recovered as a monophyletic group (see also Bakalin and Vilnet 2012), this subspecies is not recognized. Váňa (1974a) noted that *S. abyssinicum* is morphologically very similar to *S. confertissimum* and likely should be reduced to it, as supported by its nested position in that clade.

That *Solenostoma rufiflorum* (Colenso) J. J. Engel is not resolved as distinct from *S. inundatum* (Hook. f. & Taylor) Mitt. ex Steph. supports the reduction of this species to *S. inundatum* by Váňa (1975) based on morphology alone. Our evidence does not refute this reduction. At the same time, the two samples identified as *S. totipapillosum* (E. A. Hodgs.) R. M. Schust. are resolved as sister to the *S. inundatum*/*S. rufiflorum* clade. Although these results indicate that *S. inundatum* and *S. totipapillosum* are closely related, they do not necessarily contradict the species-level recognition of *S. totipapillosum*. Cell walls are always coarsely papillose in *S. totipapillosum*, a relatively small plant, as compared to usually smooth to finely striolate,

or with delicate, low papillae, in *S. inundatum*, which is typically larger (Schuster 2002; Engel and Glenny 2008). However, the two taxa are quite similar in other aspects of their morphology, including leaf shape and stance, perianth/perigynial structure, subglobose capsule shape and color, capsule wall anatomy and spore wall architecture. Resolution of their taxonomic status requires additional sampling of both populations and genomic regions. Likewise, determining the significance of the apparent polyphyly of *S. pyriflorum* and *S. appressifolium* requires expanded population level studies within *Solenostoma*.

Solenostoma pusillum (C. E. O. Jensen) Steph. and *S. sphaerocarpum* are not resolved as distinct with our data. According to Schuster (1969), Váňa (1974b) and Damsholt (2002), there are only minor morphological differences between these species, the most notable being the frequent presence of small-leaved shoots, reddish brown pigmentation and a tendency for leaves to be reniform in the former, as compared to an absence of these features in the latter. However, these differences are not consistently expressed, making separation of the two taxa also questionable on morphological grounds. Based on their similar morphologies and our molecular evidence, we propose the reduction of *S. pusillum* to *S. sphaerocarpum*.

Morphological Evolution—Despite ambiguities for some characters at the base of the Jungermanniineae tree, we were able to reconstruct ancestral conditions for a number of characters. Molecular analyses have repeatedly shown that traditional hypotheses of morphological evolution in hepatics (e.g. Evans 1939; Schuster 1966) are incongruent with phylogenetic relationships that have been resolved across the phylum (Davis 2004; He-Nygrén et al. 2004, 2006; Heinrichs et al. 2005; Forrest et al. 2006). Maximum parsimony reconstructions of morphological character state evolution have further verified that many characters once considered taxonomically diagnostic are homoplasious (Crandall-Stotler et al. 2005; Yu et al. 2013), therein challenging the utility of morphological data in liverwort systematics. Our results support that view; we were not able to identify a single one of the 14 characters we scored as having evolved without homoplasy. It is impossible to count the precise number of state transitions for any character without exhaustive sampling at the species level, but even with our incomplete sampling we demonstrated that most character states evolved 4–10 times across the Jungermanniineae tree as we reconstructed it.

We did not quantify correlations among state transitions in this study, but examination of our reconstructions indicates largely independent patterns of homoplasy across characters. The correlation between the position of gynoecia and androecia is not surprising, and possibly adaptive. When gametangia are produced on short branches, they are ventrally exposed, being overlaid by the stem and/or leaves of the parent plant, while those on leading stems are dorsally exposed. Having archegonia and antheridia in the same plane would presumably enhance fertilization. Future work on morphological evolution in this group should also include assessments of habitat shifts in order to assess possible adaptive processes underlying trait homoplasy. Transitions from dioecy to monoecy might involve polyploidization, but too few data are available at present to test that hypothesis.

TAXONOMIC TREATMENT

New Taxa—We here name and describe a new suborder, two new subfamilies, a new family, and two new subgenera.

Myliiineae J. J. Engel & Braggins ex Crand.-Stotl., Váňa, Stotler & J. J. Engel, subord. nov. —TYPE: *Mylia* Gray, Nat. Arr. Brit. Pl. I: 693. 1821.

Plants sparsely branched, with branches of the *Frullania*-type; leaves succubous, undivided, orbicular to oblong-ovate, usually with cell wall grids and perforations, margins entire; underleaves lanceolate to subulate, entire, smaller than the leaves; gynoecia and androecia on leading axes; antheridial stalks uniseriate; sporophytes enclosed by a shoot calyptra and perianth; perianths laterally compressed above, with the mouth broad, bilabiate; capsules ovoid, with the wall 3- to 5-stratose; gemmae 1- or 2-celled, on leaf tips.

This suborder includes only the Myliaceae Schljakov, which was formerly included in the Jungermanniineae (Crandall-Stotler et al. 2009). Engel and Braggins (2005) suggested that this suborder should be erected, but did not validly publish it. They proposed the suborder to include *Mylia* and *Trabacellula* Fulford, having segregated *Mylia anomala* (Hook.) Gray to the monotypic genus *Leiomylia* J. J. Engel & Braggins, which they retained in the Jungermanniaceae Rchb. of the suborder Jungermanniineae R. M. Schust. ex Stotler & Crand.-Stotl. As discussed previously, we retain *Trabacellula* in the Cephaloziaceae Mig. (suborder Cephaloziineae Schljakov), and return *Leiomylia* to the Myliaceae, suborder Myliiineae. Even though our circumscriptions of the Myliiineae differ, we ascribe the name to Engel and Braggins (2005).

Acrobolbaceae E. A. Hodgs. subfam. **Saccogynidioideae** Crand.-Stotl., Váňa & Stotler, subfam. nov. —TYPE: *Saccogynidium* Grolle, J. Hattori Bot. Lab. 23: 43. 1960 [1961].

Plants green to brown, irregularly branched, with all branches of the *Bazzania*-type; leaves succubous, unlobed, with the apices rounded or emarginate; leaf cells papillose, with the oil bodies small, finely granulate, ellipsoidal to fusiform, eight to 20 per cell; underleaves large, deeply bilobed, with margins entire; androecia on very short catkin-like ventral branches; gynoecia also on very short ventral branches; perianths lacking; marsupia hollow, of the *Calypogeia*-type; capsule ellipsoidal, beaked, with the wall 4- to 6-layered; asexual reproductive structures lacking.

Saccogynidium, the only genus recognized in this subfamily, was previously classified in the Geocalycaceae H. Klinggr. (Crandall-Stotler et al. 2009). Its transfer to the Acrobolbaceae is supported not only by our analysis, but also by its possession of a thick multistratose capsule wall that is structurally different from the bistratose wall characteristic of Geocalycaceae, and by its highly papillose leaf cell walls. The subfamily differs from other subfamilies of Acrobolbaceae by the presence of large, bilobed underleaves and androecia and gynoecia borne on very short ventral branches.

Acrobolbaceae E. A. Hodgs. subfam. **Austrolophozioideae** R. M. Schust. ex Crand.-Stotl., Váňa & Stotler, subfam. nov. —TYPE: *Austrolophozia* R. M. Schust., J. Hattori Bot. Lab. 26: 282. 1963.

Plants with branches only of the lateral *Plagiochila* type; leaves succubous, spinose-dentate to lobulate, often with reddish to brown pigments, with the cell walls smooth; oil bodies large and few in number; rhizoids in dense mats that often form decurrent bundles on the ventral surface of the stem; androecia on leading stems, with male bracts little modified from the leaves; gynoecia terminal on leading stems; perianths vestigial or lacking; marsupium of either the solid *Tylimanthus*-type (*Austrolophozia*) or hollow *Calypogeia*-type (*Goebelobryum*); capsule ellipsoidal, not beaked, with the wall 4- or 5-layered; gemmae, if present, 2-celled from reduced leaves.

This subfamily includes *Austrolophozia* R. M. Schust. and *Goebelobryum* Grolle. Although Schuster (1980: 543; 2001: 107) included "subf. *Austrolophozioideae* Schust." in treatments of the Acrobolbaceae, he failed to provide a Latin description or diagnosis for the subfamily, rendering it invalid (ICN Art. 39.1). We here validate this name with an English description (ICN Art. 39.2), and circumscribe it to include *Austrolophozia* and *Goebelobryum*.

Notoscyphaceae Crand.-Stotl., Váňa & Stotler, fam. et stat. nov. —TYPE: *Notoscyphus* Mitt. in B. C. Seemann, Fl. Vitiensis: 407. 1873. [The date of this publication is often cited as 1871 and on p. 405 of our copy is printed "published June 1, 1871," but Grolle (1983) pointed out that it was not actually issued until Feb 1873.]

This monogeneric family is here validated by the diagnosis of Jungermanniaceae Rchb. subfamily Notoscyphoideae R. M. Schust., Trans. Brit. Bryol. Soc. 6: 94–95. 1970. Note that in accordance with Article 49.2 (McNeill et al. 2012) parenthetical authors are not cited for suprageneric names, even if validly published by reference.

Schuster (2002: 447) remarked that following intensive restudy of *Notoscyphus*, he thought it ought to be placed in its own family although he did not do so. He stated that the affinities of the genus were probably with *Geocalyx* Nees and that it should go into the Geocalycaceae or else be a family adjoining the Geocalycaceae. Our molecular data support his view that it should be placed in its own family, but do not support a close relationship with *Geocalyx*.

Solenostoma Mitt. subg. *Metasolenostoma* Váňa, Crand.-Stotl. & Stotler, subg. nov. —TYPE: *Solenostoma gracillimum* (Sm.) R. M. Schust., Hepat. Anthocerotae N. Amer. 2: 972. 1969. Basionym: *Jungermannia gracillima* Sm. in Sowerby, Engl. Bot. 32. pl. 2238. 1811.

Plants with leaves bordered by one row of larger cells (only in well-developed plants in *S. gracillimum* and *S. fusiforme* (Steph.) R. M. Schust.); perianth of the *Solenostoma*-type, pyriform, suddenly contracted to a beaked mouth and made up of isodiametric (not elongated) cells; perigynium scarcely developed or less than 0.2 times the length of the perianth.

Previous classifications of *Solenostoma* Mitt. often recognized two subgenera, *S. subg. Solenostoma* and *S. subg. Plectocolea* Mitt. (Schuster 2002, Hentschel et al. 2007), based primarily on the form of the perianth cells and absence or presence of a well-developed perigynium. However, in our analyses four well-supported, monophyletic lineages are resolved within *Solenostoma*, with *S. subg. Solenostoma* and *S. subg. Plectocolea*, as previously circumscribed, paraphyletic. In addition to recognizing

these subgenera, two new subgenera are established to accommodate these lineages. Of the species treated by us, *Solenostoma* subg. *Metasolenostoma* includes *S. gracillimum*, *S. fusiforme* (Steph.), *S. rubrum* (Gottsche ex Underw.) R. M. Schust., and *S. handelii* (Schiffn.) Müll. Frib., species previously classified in *S. subgenus Solenostoma*.

Solenostoma Mitt. subg. *Eucalyx* (Lindb.) Váňa, Crand.-Stotl. & Stotler, stat. et comb. nov.; Basionym: *Nardia* sect. *Eucalyx* Lindb., Not. Sällsk. Fauna Fl. Fennica Förh. 13: 369. 1874. ≡ *Nardia* subg. *Eucalyx* (Lindb.) Lindb., Musci Scand.: 8. 1879. —TYPE: *Solenostoma obovatum* (Nees) C. Massal., Epat. Erb. Critt. Ital.: 17 [=Accad. Sci. Med. Nat. Ferrara 1903: 199]. 1903. Basionym: *Jungermannia obovata* Nees, Naturgesch. Eur. Leberm. 1: 279, 332. 1833.

Plants often with reddish-purple pigmentation on stems and leaf bases; stoloniferous, flagelliform branches common, of the *Plagiochila*-type; rhizoids purple; perianth of the *Plectocolea*-type, 4- to 6- plicate, with the cells elongated and the mouth lobulate, scarcely emergent from the bracts; perigynium terete, bearing the bracts on its surface, exceeding the perianth in length.

The name *Eucalyx* was first proposed as a subgenus of *Nardia* Gray nom. cons. by Lindberg (Bot. Not. 1872: 167. 1872) but was not validly published because it was not described. In 1874 it was described as *Nardia* sect. *Eucalyx* Lindb. in the publication "Manipulus Muscorum Secundus" (Lindberg 1874), which validated the name. The Lindberg use of this epithet as a subgenus of *Nardia* (stat. nov.) is therefore valid in any of the Lindberg publications after that date, the first of which is *Nardia* A. *Eucalyx* (Lindb.) Lindb., Musci Scand.: 8. (8 Nov.- 30 Dec. 1879) according to Isoviiita (1980: 72). Of the species resolved in the *S. subg. Eucalyx* clade, namely, *S. obovatum*, *S. flagellatum* (Hatt.) Váňa & Long, and *S. schusterianum* (J. D. Godfrey & G. Godfrey) Váňa, Hentschel & Heinrichs, only *S. obovata* (≡ *Jungermannia obovata* Nees ≡ *Nardia obovata* (Nees) Lindb.) was included in Lindberg's original treatment (1872) and in the validly published section (1874); we, therefore, designate this as the type of the subgenus. Other species placed by Lindberg in subgenus *Eucalyx* have been resolved in *S. subg. Plectocolea*. Although both *S. subg. Eucalyx* and *S. subg. Plectocolea* have perigynia and *Plectocolea*-type perianths, only those species resolved in the *S. subg. Eucalyx* lineage have frequent flagelliform branches and very long perigynia, with scarcely emergent perianths.

New Combinations—Six new combinations at the species level are provided based on results of this study.

Grolle and Váňa (1992) named *Jungermannia conchata* Grolle & Váňa based on a collection of small, entire-leaved plants from 4100 m elevation in Nepal. At the time of the naming, neither males nor sporophytes were known. In our analyses this taxon is resolved in *Cephalozia*, as also supported by new findings of male plants (Váňa, unpubl. data).

Cephalozia conchata (Grolle & Váňa) Váňa, comb. nov.; Basionym: *Jungermannia conchata* Grolle & Váňa, Fragm. Flor. Geobot. 37: 3. 1992.

The genus *Apomarsupella* R.M. Schust. was established by Schuster in 1996 to include four taxa that resemble *Marsupella* in vegetative characters, but *Gymnomitrium* in

gynoecial characters, namely, *A. revoluta* (Nees) R.M. Schust. (the generitype), with two subspecies, *A. africana* (Steph. ex Bonner) R.M. Schust., and *A. rubida* (Mitt.) R.M. Schust. In 1999, Váňa transferred two additional species from *Marsupella*, *A. crystallocaulon* (Grolle) Váňa and *A. verrucosa* (Nichols.) Váňa. Since all species of *Apomarsupella*, including the generitype, are nested in *Gymnomitrium*, we place *Apomarsupella* in synonymy of *Gymnomitrium* (see below), necessitating the following new combinations:

Gymnomitrium crystallocaulon (Grolle) Váňa, Crand.-Stotl. & Stotler, comb. nov.; Basionym: *Marsupella crystallocaulon* Grolle, Khumbu Himal: 281. 1966.

Gymnomitrium revolutum (Nees) H. Philib. subsp. *novoguineanensis* (R. M. Schust.) Váňa, Crand.-Stotl. & Stotler, comb. nov.; Basionym: *Apomarsupella revoluta* (Nees) R. M. Schust. subsp. *novoguineanensis* R. M. Schust., J. Hattori Bot. Lab. 80: 90. 1996.

Gymnomitrium rubidum (Mitt.) Váňa, Crand.-Stotl. & Stotler, comb. nov.; Basionym: *Jungermannia rubida* Mitt., J. Proc. Linn. Soc., Bot. 5: 90. 1860.

Both of the named species of *Horikawaella* S. Hatt. & Amakawa are nested with strong support within *Solenostoma* subg. *Solenostoma*. Placement of the two genera in synonymy (see below) is supported, not only by our analysis, but also by their similar morphologies, with acute, rather than rounded, leaf apices, being the major distinguishing character of the *Horikawaella* species, which are herein transferred to *Solenostoma*.

Solenostoma subacutum (Herzog) Váňa, Crand.-Stotl. & Stotler, comb. nov.; Basionym: *Anastrophyllum subacutum* Herzog, Ann. Bryol. 12: 75. 1939.

Solenostoma grosse-verrucosum (Amakawa & S. Hatt.) Váňa, Crand.-Stotl. & Stotler, comb. nov.; Basionym: *Horikawaella grosse-verrucosa* Amakawa & S. Hatt. in Hara, Bull. Univ. Mus. Univ. Tokyo 8 [Fl. East Himalaya, third Rep.]: 216. 1975.

New Synonyms—The following new synonyms are provided based on this study:

Delavayellaceae R. M. Schust., Bryologist 64: 202. 1961, syn. nov. = JUNGERMANNIACEAE Rchb., Bot. Damen: 256. 1828.

Hygrobicellaceae Konstant. & Vilnet, Phytotaxa 167(2): 217. 2014 (Arctoa 18: 65. 2009[2010], nom. inval.), syn. nov. = ANTHELIACEAE R. M. Schust., J. Hattori Bot. Lab. 26: 236. 1963.

Apomarsupella R. M. Schust., J. Hattori Bot. Lab. 80: 79. 1996, syn. nov. = GYMNOMITRIUM Corda in Opiz, Naturalientausch 12: 651. 1829.

Horikawaella S. Hatt. & Amakawa, Misc. Bryol. Licheol. 5: 164. 1971, syn. nov. = SOLENOSTOMA Mitt., J. Proc. Linn. Soc., Bot. 8: 51. 1865.

Solenostoma abyssinicum (Nees) Steph., Bull. Herb. Boissier, sér. 2, 1(5): 491 [=Sp. Hepat. 2: 53]. 1901. Basionym: *Jungermannia abyssinica* Nees in Gottsche, Lindenberg & Nees, Syn. Hepat.: 93. 1844, syn. nov. = SOLENOSTOMA CONFERTISSIMUM (Nees) Schljakov, Pečen. Mhi Severa SSSR 4: 51. 1981. Basionym: *Jungermannia confertissima* Nees, Naturgesch. Eur. Leberm. 1: 277, 291. 1833.

Solenostoma pusillum (C. E. O. Jensen) Steph., Sp. Hepat. 6: 83, 1917. Basionym: *Aplozia pusilla* C. E. O. Jensen, Rev. Bryol. 39: 92, 1912, syn. nov. = SOLENOSTOMA SPHAEROCARPUM (Hook.) Steph., Bull. Herb. Boissier, sér. 2, 1(5): 499 [Sp. Hepat. 2: 61], 1901. Basionym: *Jungermannia sphaerocarpa* Hook., Brit. Jungerm. Table 74, 1815.

Solenostoma subellipticum (Lindb. ex Heeg) R. M. Schust., Hepat. Anthocerotae N. Amer. 2: 1021. 1969. Basionym: *Nardia subelliptica* Lindb. ex Heeg, Verh. K. K. Zool.-Bot. Ges. Wien 43: 69. 1893, syn. nov. = SOLENOSTOMA OBOVATUM (Nees) C. Massal., Epat. Erb. Critt. Ital.: 17. [= Accad. Sci. Med. Ferrara 1903: 199.] 1903. Basionym: *Jungermannia obovata* Nees, Naturgesch. Eur. Leberm. 1: 332. 1833. This agrees with the concept of Damsholt (2002: 230) who reduced *J. subelliptica* to *J. obovata* subsp. *minor* Carrington.

New Circumscriptions—New circumscriptions for seven families are required based on results of this study.

The following three families were all validly published but were incorrect when named because they included the type genus of an earlier published family name. However, by exclusion of that genus from each of these families, they become the correct family name with new circumscriptions. In accordance with Article 49.2 (McNeill et al. 2012), parenthetical authors are not cited for suprageneric names. HARPANTHACEAE Arnell in Holmberg, Skand. Fl. 2(a): 147. 1928. Type: *Harpanthus* Nees, Naturg. Eur. Leberm. 2: 351. 1836. We here recognize this family as monogeneric. When published, this family name was incorrect because it included *Geocalyx*, the type genus of the older Geocalycaceae. With the removal here of *Geocalyx* from Harpanthaceae and its retention in the Geocalycaceae, this family becomes correct under Article 52.3 (McNeill et al. 2012; ex. 18). SACCOGYNACEAE Heeg, Verh. Zool.-Bot. Ges. Wien 41: 571. 1891. Type: *Saccogyna* Dumort., Comment. Bot.: 113. 1822. We here recognize this family as being monogeneric. When published, this family name was incorrect because it included *Geocalyx*, the type genus of the older Geocalycaceae. As with the Harpanthaceae, the removal here of *Geocalyx* from Saccogynaceae and its retention in the Geocalycaceae, makes this family name correct under Article 52.3 (McNeill et al. 2012; ex. 18). SOLENOSTOMATACEAE Stotler & Crand.-Stotl., Edinburgh J. Bot. 66: 190. 2009. Type: *Solenostoma* Mitt., J. Proc. Linn. Soc., Bot. 8: 51. 1865. The genera that now remain in Solenostomataceae are *Solenostoma* Mitt. [including *Plectocolea* (Mitt.) Mitt.], *Arctoscyphus* Hässel, *Cryptocolea* R. M. Schust., and *Diplocolea* Amak. When published, this family name was incorrect because it included *Nardia*, which is the type genus of the earlier Mesophyllaceae Heeg (*Mesophylla* ≡ *Nardia*). With transfer of *Nardia* to the older Gymnomitriaceae, this family becomes correct under Article 52.3 (McNeill et al. 2012; ex. 18). In addition to the removal of *Nardia* here, the following genera formerly placed here are transferred or reduced as follows: *Bragginsella* R. M. Schust. transferred to Lophocoleaceae (Söderström et al. 2013); *Cryptocoleopsis* Amak. transferred to Gymnomitriaceae (done here); *Cryptostipula* R. M. Schust. reduced to *Hepatostolonophora* J. J. Engel & R. M. Schust. (Lophocoleaceae) (Engel 2011: 402); *Horikawaella* S. Hatt. & Amakawa reduced to *Solenostoma* Mitt. (done here), and *Scaphophyllum* Inoue reduced to *Solenostoma* Mitt. (Feldberg et al. 2009).

Circumscriptions of the following four families have also been modified by having genera added or genera transferred to other families without nomenclatural consequences: ANTHELIACEAE, ARNELLIACEAE, GYMNOMITRIACEAE and JUNGERMANNIACEAE. Full details of these changes and their justifications are provided in the Discussion section.

ACKNOWLEDGMENTS. This research was supported by a multi-institutional, collaborative grant from the Assembling the Tree of Life program at NSF. The following NSF grants supported this work: EF-0531730-002 (to AJS) EF-0531680 (to MvK and JJE), EF-0531750 (to BC-S & RES). Numerous collectors supplied collections for the phylogenetic analyses and all such collaborators are gratefully acknowledged. This work would be impossible without assistance from many talented collectors. We thank Sandra Boles, Lisa Karst, Nicolas Devos, and Laura Briscoe for technical assistance.

LITERATURE CITED

- Amakawa, T. 1959. Family Jungermanniaceae of Japan. I. *The Journal of the Hattori Botanical Laboratory* 21: 248–291.
- Amakawa, T. 1960. Family Jungermanniaceae of Japan. II. *The Journal of the Hattori Botanical Laboratory* 22: 1–90.
- Amakawa, T. 1966. New or little known Asiatic species of the family Jungermanniaceae. II. *The Journal of the Hattori Botanical Laboratory* 29: 253–266.
- Bakalin, V. A. and A. A. Vilnet. 2012. New combinations and new species of *Solenostoma* and *Plectocolea* (Solenostomataceae) from the Russian Far East. *The Bryologist* 115: 566–584.
- Briscoe, L., J. J. Engel, L. Söderström, A. Hagborg, and M. von Konrat. 2015. Notes on Early Land Plants Today. Nomenclatural notes on Acrobolbaceae. *Phytotaxa* (in press).
- Cooper, E. D., A. J. Shaw, B. Shaw, M. J. Henwood, M. M. Heslewood, and E. A. Brown. 2011. A multi-locus molecular phylogeny of the Lepidoziaceae: laying the foundations for a stable classification. *Molecular Phylogenetics and Evolution* 59: 489–509.
- Cox, C. J., B. Li, P. G. Foster, T. M. Embley, and P. Cíván. 2014. Conflicting phylogenies for early land plants are caused by composition biases among synonymous substitutions. *Systematic Biology* 63: 272–279.
- Crandall-Stotler, B. and R. E. Stotler. 2000. Morphology and classification of the Marchantiophyta. Pp. 21–70 in *Bryophyte Biology*, eds. Shaw A. J. and B. Goffinet. Cambridge: Cambridge University Press.
- Crandall-Stotler, B. J., L. L. Forrest, and R. E. Stotler. 2005. Evolutionary trends in the simple thalloid liverworts (Marchantiophyta, Jungermanniopsida subclass Metzgeriidae). *Taxon* 54: 299–316.
- Crandall-Stotler, B. J., R. E. Stotler, and D. G. Long. 2008. Morphology and classification of the Marchantiophyta. Pp. 1–54 in *Bryophyte Biology* 2nd ed., eds. Goffinet B. and A. J. Shaw. Cambridge: Cambridge University Press.
- Crandall-Stotler, B. J., R. E. Stotler, and D. G. Long. 2009. Phylogeny and classification of the Marchantiophyta. *Edinburgh Journal of Botany* 66: 155–198.
- Damsholt, K. 2002. *Illustrated Flora of Nordic Liverworts and Hornworts*. Lund: Kleinstaub.
- Davis, E. C. 2004. A molecular phylogeny of leafy liverworts (Jungermanniidae: Marchantiophyta). Pp. 61–86 in *Molecular systematics of bryophytes: progress, problems & perspectives* eds. Goffinet B., V. C. Hollowell, and R. E. Magill. Monographs in Systematic Botany from the Missouri Botanical Garden. Vol. 98. St. Louis: Missouri Botanical Garden.
- de Roo, R. T., T. A. Hedderson, and L. Söderström. 2007. Molecular insights into the phylogeny of the leafy liverwort family Lophoziaaceae Cavers. *Taxon* 56: 301–314.
- Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.
- Engel, J. J. 1988. The taxonomic position of *Apotomanthus* (Hepaticae). *Beihfte zur Nova Hedwigia* 90: 203–221.
- Engel, J. J. 2011. Studies of New Zealand Hepaticae. 56–68. A miscellanea of new taxa and combinations. *Nova Hedwigia* 93: 401–410.
- Engel, J. J. and J. E. Braggins. 2005. Are *Mylia* and *Trabacellula* (Hepaticae) related? Unsuspected links revealed by cell wall morphology, with the transfer of *Mylia anomala* to a new genus (*Leiomylia* J. J. Engel & Braggins) of Jungermanniaceae. *Taxon* 54: 665–680.
- Engel, J. J. and D. Glenny. 2008. A flora of the liverworts and hornworts of New Zealand, Vol. 1. *Monographs in Systematic Botany from the Missouri Botanical Garden* 110: 1–897.
- Engel, J. J. and D. Glenny. 2012. Austral Hepaticae 48. *Goebelobryum* Grolle (Acrobolbaceae). *Nova Hedwigia* 95: 319–336.
- Engel, J. J. and R. Grolle. 1971. *Marsupidium* in South America. *The Journal of the Hattori Botanical Laboratory* 34: 437–444.
- Evans, A. W. 1939. The classification of the Hepaticae. *Botanical Review* 5: 49–96.
- Feldberg, K., J. Hentschel, A. Bombosch, D. G. Long, J. Váňa, and J. Heinrichs. 2009. Transfer of *Gottschelia grollei*, *G. patoniae* and *Scaphophyllum speciosum* to *Solenostoma* based on chloroplast DNA *rbcL* sequences. *Plant Systematics and Evolution* 280: 243–250.
- Finet, C., R. E. Timme, C. F. Delwiche, and F. Marlétaz. 2010. Multi-gene phylogeny of the green lineage reveals the origin and diversification of land plants. *Current Biology* 20: 2217–2222.
- Forrest, L. L. and B. J. Crandall-Stotler. 2004. A phylogeny of the simple thalloid liverworts (Jungermanniopsida, Metzgeriidae) as inferred from five chloroplast genes. Pp. 119–140 in *Molecular systematics of bryophytes: progress, problems & perspectives* eds. B. Goffinet, V. C. Hollowell, and R. E. Magill. Monographs in Systematic Botany from the Missouri Botanical Garden. Vol. 98. St. Louis: Missouri Botanical Garden.
- Forrest, L. L. and B. J. Crandall-Stotler. 2005. Progress towards a robust phylogeny for the liverworts, with particular focus on the simple thalloids. *The Journal of the Hattori Botanical Laboratory* 97: 127–159.
- Forrest, L. L., E. C. Davis, D. G. Long, B. J. Crandall-Stotler, A. Clark, and M. L. Hollingsworth. 2006. Unraveling the evolutionary history of the liverworts (Marchantiophyta): multiple taxa, genomes and analyses. *The Bryologist* 109: 303–334.
- Glenny, D. and B. Malcolm. 2005. *Key to the Australasian genera of liverworts and hornworts. ABRs identification series. ABRs/CBIT*, Canberra.
- Grolle, R. 1960. Über *Saccogyna* Dum. und *Saccogynidium*, eine neue Lebermoosgattung. *The Journal of the Hattori Botanical Laboratory* 23: 41–67.
- Grolle, R. 1965. Die Lebermoosgattungen *Blepharidophyllum* Ångstr. und *Krunodiplophyllum* nov. gen. (Scapaniaceae). *The Journal of the Hattori Botanical Laboratory* 28: 55–74.
- Grolle, R. 1966. Die Lebermoose Nepals. *Ergebnisse Forschung-Unternehmen Nepal-Himalaya* 1: 262–298.
- Grolle, R. 1972. Die Namen der Familien und Unterfamilien der Lebermoose (Hepaticopsida). *Journal of Bryology* 7: 201–236.
- Grolle, R. 1983. Nomina generica Hepaticarum; references, types and synonymies. *Annales Botanici Fennici* 121: 1–62.
- Grolle, R. and J. Váňa. 1992. Eine neue *Jungermannia* (Hepaticae, Jungermanniaceae) aus Nepal. *Fragmenta Floristica Geobotanica* 37: 3–6.
- Hässel de Menéndez, G. G. and S. S. Solari. 1975 [1976]. Bryophyta Hepaticopsida: Calobryales, Jungermanniales, Vetaformaceae, Balantiopsaceae. Pp. 1–181 in *Flora Criptogámica de Tierra del Fuego. Guarrera, S.A.*, vol. 15, no. 1, eds. I. Gamundi de Amos and D. Rabinovich de Halperin. Buenos Aires: Fundación para la Educación, la Ciencia y la Cultura.
- Heinrichs, J., G. R. Gradstein, R. Wilson, and H. Schneider. 2005. Towards a natural classification of liverworts (Marchantiophyta) based on the chloroplast gene *rbcL*. *Cryptogamie Bryologie* 26: 131–150.
- Heinrichs, J., J. Hentschel, R. Wilson, K. Feldberg, and H. Schneider. 2007. Evolution of leafy liverworts (Jungermanniidae, Marchantiophyta): Estimating divergence times from chloroplast DNA sequences using penalized likelihood with integrated fossil evidence. *Taxon* 56: 31–44.
- Hendry, T. A., B. Wang, Y. Yang, E. C. Davis, J. E. Braggins, R. M. Schuster, and Y.-L. Qiu. 2007. Evaluating phylogenetic positions of four liverworts from New Zealand, *Neogrollea notabilis*, *Jackiella curvata*, *Goebelobryum unguiculatum*, and *Herzogianthus vaginatus*, using three chloroplast genes. *The Bryologist* 110: 738–751.
- Hentschel, J., J. A. Paton, H. Schneider, and J. Heinrichs. 2007. Acceptance of *Lioclaena* Nees and *Solenostoma* Mitt., the systematic position of *Eremonotus* Pearson and notes on *Jungermannia* L. s.l. (Jungermanniidae) based on chloroplast DNA sequence data. *Plant Systematics and Evolution* 268: 147–157.
- Hentschel, J., R. Wilson, M. Burghardt, H. J. Zündorf, H. Schneider, and J. Heinrichs. 2006. Reinstatement of Lophocoleaceae (Jungermanniopsida) based on chloroplast gene *rbcL* data: Exploring the importance of female involucre for the systematics of Jungermanniales. *Plant Systematics and Evolution* 258: 211–226.

- He-Nygrén, X. 2007. Multi-gene phylogeny supports single origin of jungermannioid perigynium. *Annales Botanici Fennici* 44: 450–462.
- He-Nygrén, X., I. Ahonen, A. Juslén, D. Glenny, and S. Piippo. 2004. Phylogeny of liverworts—beyond a leaf and a thallus. Pp. 87–118 in *Molecular systematics of bryophytes: progress, problems & perspectives* eds. B. Goffinet, V. C. Hollowell, and R. E. Magill. Monographs in Systematic Botany from the Missouri Botanical Garden. Vol. 98. St. Louis: Missouri Botanical Garden.
- He-Nygrén, X., A. Juslén, I. Ahonen, D. Glenny, and S. Piippo. 2006. Illuminating the evolutionary history of liverworts (Marchantiophyta) — towards a natural classification. *Cladistics* 22: 1–31.
- Inoue, H. 1983. Taxonomic miscellany on hepatics (2). *Journal of Japanese Botany* 58: 65–70.
- Isoviita, P. 1980. S. O. Lindberg's bryological reports in Finnish newspapers. Critically annotated facsimile collection. *Pam. Bot. Mus. Univ. Helsinki* 8: 1–88.
- Kenrick, P. and P. R. Crane. 1997. *The Origin and Early Diversification of Land Plants: A Cladistic Study*. Washington, DC: Smithsonian Institution Press.
- Kitagawa, N. 1959. New or interesting species of *Gymnomitrium* (Hepaticae) in Japan. *Acta Phytotaxonomica et Geobotanica* 18: 33–38.
- Konstantinova, N. A. and A. A. Vilnet. 2009. [2010]. New taxa and new combinations in Jungermanniales (Hepaticae). *Arctoa* 18: 65–67.
- Konstantinova, N. A., A. A. Vilnet, L. Söderström, A. Hagborg, and M. von Konrat. 2014. Notes on early land plants today: 53. Hygrobiellaceae (Marchantiophyta) validated. *Phytotaxa* 167: 217.
- Lindberg, S. O. 1874. Manipulus muscorum secundum. *Notiser ur Sällskapet pro Fauna et Flora Fennica Förhandlingar* 13: 351–418.
- Maddison, W. P. and D. R. Maddison. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75 <http://mesquiteproject.org>.
- Masuzaki, H., M. Shimamura, T. Furuki, H. Tsubota, T. Yamaguchi, H. Mohamed Abdul Majid, and H. Deguchi. 2010. Systematic position of the enigmatic liverwort *Mizutania* (Mizutaniaceae Marchantiophyta) inferred from molecular phylogenetic analyses. *Taxon* 59: 448–458.
- McNeill, J., F. R. Barrie, W. R. Buck, V. Demoulin, W. Greuter, D. L. Hawksworth, P. S. Herendeen, S. Knapp, K. Marhold, J. Prado, W. F. Prud'homme van Reine, G. F. Smith, J. H. Wiersema, and N. J. Turland (eds.). 2012. *International Code of Nomenclature for Algae, Fungi and Plants (Melbourne Code)*. Adopted by the Eighteenth International Botanical Congress Melbourne, Australia, July 2011. Ruggell, Liechtenstein: Gantner Verlag. [Regnum Vegetabile 154].
- Miller, M. A., W. Pfeiffer, and T. Schwartz. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. Pp. 1–8 in *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 Nov. 2010, New Orleans, LA.
- Müller, K. 1948. Der systematische Wert von Sporophytenmerkmalen bei den beblätterten Lebermoosen. *Svensk Botanisk Tidskrift Utgåvan af Svenska Botaniska Foreningen* 42: 1–16.
- Müller, K. 1954. *Die Lebermoose Europas* (Dr. L. Rabenhorst's *Kryptogamen-Flora von Deutschland*, 3 aufl.) 6 Band, 4 Lieferung. Leipzig: Akademische Verlagsgesellschaft.
- Müller, K., D. Quandt, J. Müller, and C. Neinhuis. 2007. PhyDe: phylogenetic data editor. Version 0.997. Available at: <<http://www.phyde.de>>.
- Nylander, J. A. A. 2004. *MrModeltest v. 2*. Program distributed by the author. Evolutionary Biology Centre, Uppsala University.
- Paton, J. A. 1999. *The Liverwort Flora of the British Isles*. Martins UK: Harley Books.
- Qiu, Y.-L. 2008. Phylogeny and evolution of charophytic algae and land plants. *Journal of Systematics and Evolution* 46: 287–306.
- Rambaut, A. and A. J. Drummond. 2007. Tracer v1.4. Available from <<http://beast.bio.ed.ac.uk/Tracer>>.
- Schill, D. B., D. G. Long, M. Moeller, and J. Squirrell. 2004. Phylogenetic relationships between Lophoziaaceae and Scapaniaceae based on chloroplast sequences. Pp. 141–149 in *Molecular systematics of bryophytes: progress, problems & perspectives* eds. B. Goffinet, V. C. Hollowell, and R. E. Magill. Monographs in Systematic Botany from the Missouri Botanical Garden. Vol. 98. St. Louis: Missouri Botanical Garden.
- Schuster, R. M. 1960. [1961]. Notes on nearctic Hepaticae. XIX. The relationships of *Blepharostoma*, *Temnoma* and *Lepicolea*, with descriptions of *Lophochaete* and *Chandonanthus* subg. *Tetralophozia*, subg. n. *The Journal of the Hattori Botanical Laboratory* 23: 192–210.
- Schuster, R. M. 1963. Studies on antipodal Hepaticae. I. Annotated key to the genera of antipodal Hepaticae with special reference to New Zealand and Tasmania. *The Journal of the Hattori Botanical Laboratory* 26: 185–309.
- Schuster, R. M. 1966. A memoir on the family Belpharostomataceae, I. *Candollea* 21: 59–136.
- Schuster, R. M. 1969. *The Hepaticae and Anthocerotae of North America*, Vol. II. Columbia University Press, New York.
- Schuster, R. M. 1970. Studies on Hepaticae XVIII. The family Jungermanniaceae, s. lat.: A reclassification. *Transactions of the British Bryological Society* 6: 86–107.
- Schuster, R. M. 1973. [1972]. Phylogenetic and taxonomic studies on Jungermanniidae. *The Journal of the Hattori Botanical Laboratory* 36: 321–405.
- Schuster, R. M. 1979 [1980]. The phylogeny of the Hepaticae. Pp. 41–82 in *Bryophyte Systematics* eds. G. C. S. Clarke and J. G. Duckett J.G. London: Academic Press.
- Schuster, R. M. 1980. *The Hepaticae and Anthocerotae of North America, East of the Hundredth Meridian*. Vol. IV. Columbia University Press, New York.
- Schuster, R. M. 1984. *New Manual of Bryology*, Vol. 2. Nichinan, Japan: Hattori Botanical Laboratory.
- Schuster, R. M. 1988. The Hepaticae of South Greenland. *Beihfte zur Nova Hedwigia* 92: 1–255.
- Schuster, R. M. 1996. Studies on antipodal Hepaticae. XII. Gymnomitriaceae. *The Journal of the Hattori Botanical Laboratory* 80: 1–147.
- Schuster, R. M. 2001. Revisionary studies on Austral Acrobolbaceae, I. *The Journal of the Hattori Botanical Laboratory* 90: 97–166.
- Schuster, R. M. 2002. Austral Hepaticae, Part II. *Beihfte zur Nova Hedwigia* 119: 1–606.
- Shaw, A. J., C. J. Cox, and S. B. Boles. 2003. Polarity of peatmoss evolution: who says mosses have no roots? *American Journal of Botany* 90: 1777–1787.
- Söderström, L., B. Crandall-Stotler, R. E. Stotler, J. Váña, A. Hagborg, and M. von Konrat. 2013. Notes on Early Land Plants Today. 36. Generic treatment of Lophocoleaceae (Marchantiophyta). *Phytotaxa* 97: 36–43.
- Swofford, D. L. 1998. PAUP*: Phylogenetic Analysis Using Parsimony (and Other Methods) Sunderland: Sinauer Associates.
- Váña, J. 1973. Studien über die Jungermannioideae (Hepaticae). 1. Allgemeine Charakteristik. *Folia Geobotanica et Phytotaxonomica* 8: 181–201.
- Váña, J. 1974a. Studien über die Jungermannioideae (Hepaticae). 5. *Jungermannia* subg. *Plectocolea* und subg. *Solenostoma*: Afrikanische Arten. *Folia Geobotanica et Phytotaxonomica* 9: 277–312.
- Váña, J. 1974b. Studien über die Jungermannioideae (Hepaticae). 5. *Jungermannia* subg. *Plectocolea* und subg. *Solenostoma*: Europäische und nordamerikanische. *Folia Geobotanica et Phytotaxonomica* 9: 369–423.
- Váña, J. 1975. Studien über die Jungermannioideae (Hepaticae). 8. *Jungermannia* subg. *Plectocolea* und subg. *Solenostoma* In Australien, Neuseeland und Ozeanien. *Folia Geobotanica et Phytotaxonomica* 10: 277–323.
- Váña, J. 1976. Studien über die Jungermannioideae (Hepaticae). 10. *Nardia*. *Folia Geobotanica et Phytotaxonomica* 11: 367–425.
- Váña, J., R. Grolle, and D. Long. 2012a. Taxonomic realignments and new records of *Gongylanthus* and *Southbya* (Marchantiophyta: Southbyaceae) from the Sino-Himalayan region. *Nova Hedwigia* 95: 183–196.
- Váña, J., J. Hentschel, and J. Heinrichs. 2010a. New combinations in Jungermanniales: transfer of 32 taxa to *Solenostoma* Mitt. *Cryptogamie Bryologie* 31: 135–139.
- Váña, J. and D. Long. 2009. Jungermanniaceae of the Sino-Himalayan region. *Nova Hedwigia* 89: 485–517.
- Váña, J., L. Söderström, A. Hagborg, and M. von Konrat. 2012b. Early land plants today. 8. New combinations and some lectotypifications in *Mesoptychia*. *Phytotaxa* 65: 52–56.
- Váña, J., L. Söderström, A. Hagborg, and M. von Konrat. 2013. Notes on early land plants today. 17. Transfers of some taxa in Adelantheaceae (Marchantiophyta). *Phytotaxa* 76: 35–36.
- Váña, J., L. Söderström, A. Hagborg, M. von Konrat, and J. J. Engel. 2010b. Early land plants today: taxonomy, systematics and nomenclature of Gymnomitriaceae. *Phytotaxa* 11: 1–80.
- Vilnet, A. A., N. A. Konstantinova, and A. V. Troitsky. 2010. Molecular insight on phylogeny and systematics of the Lophoziaaceae, Scapaniaceae, Gymnomitriaceae and Jungermanniaceae. *Arctoa* 19: 31–50.
- Vilnet, A. A., N. A. Konstantinova, and A. V. Troitsky. 2011. Taxonomical rearrangements of Solenostomataceae (Marchantiophyta) with

description of new family Endogemmataceae based on trnL-F DNA analysis. *Folia Cryptogamica Estonica* 48: 125–133.

Vilnet, A. A., N. A. Konstantinova, and A. V. Troitsky. 2012. Molecular phylogeny and systematics of the suborder Cephalozieae with special attention to the family Cephalozieaceae s. l. (Jungermanniales, Marchantiophyta). *Arctoa* 21: 113–132.

Vilnet, A. A., I. A. Milyutina, N. A. Konstantinova, M. S. Ignatov, and A. V. Troitsky. 2007. Phylogeny of the genus *Lophozia* (Dumort.) Dumort. s. s. inferred from nuclear and chloroplast sequences ITS1–2 and TRNL-F. *Russian Journal of Genetics* 43: 1306–1313.

Wilson, R., S. R. Gradstein, H. Schneider, and J. Heinrichs. 2007. Unraveling the phylogeny of Lejeuneaceae (Jungermanniopsida): evidence for four main lineages. *Molecular Phylogenetics and Evolution* 45: 270–282.

Wodniok, S., H. Brinkmann, G. Glöckner, A. J. Heide, H. Philippe, M. Melkonian, and B. Becker. 2011. Origin of land plants: do conjugating green algae hold the key? *BMC Evolutionary Biology* 11: 104.

Yatsentyuk, S. P., N. A. Konstantinova, M. S. Ignatov, J. Hyvönen, and A. V. Troitsky. 2004. On phylogeny of Lophozieae and related families (Hepaticae, Jungermanniales) based on TrnL-TrnF intron-spacer sequences of chloroplast DNA. Pp. 151–167 in *Molecular systematics of bryophytes: progress, problems & perspectives* eds. B. Goffinet, V. C. Hollowell, and R. E. Magill. Monographs in Systematic Botany from the Missouri Botanical Garden. Vol. 98. St. Louis: Missouri Botanical Garden.

Yu, Y., T. Pócs, A. Schäfer-Verwimp, J. Heinrichs, R.-L. Zhu, and H. Schneider. 2013. Evidence for rampant homoplasy in the phylogeny of the epiphyllous liverwort genus *Cololejeunea* (Lejeuneaceae). *Systematic Botany* 38: 553–563.

Zwickl, D. J. 2006. Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. Ph.D. dissertation. Austin: University of Texas.

APPENDIX 1. List of sampled taxa by family, voucher information, and GenBank Accession numbers (*atpB*, *psbA*, *psbT*, *rbcL*, *rps4*, *trnG*, *trnL*, *nad1*, *rps3*, *rpb2*, respectively).—: missing data. Voucher numbers beginning with “gb” designate sequences downloaded from GenBank.

Acrobolbaceae: *Acrobolbus ochrophyllus*: FATOL118, Chile, J.J. Engel 26633 (F), KF852005, KF851834, KJ451735, KF852285, KF851387, KJ802044, KJ802071, KF852430, KF851532,—; *Austrolophozia paradoxa*: FATOL785, New Zealand, J.J. Engel & M. von Konrat 28538 (F), KF852035, KF851889,—, KF851427,—, KF852475, KF851567,—; *Goebelobryum unguiculatum*: L1274, New Zealand: North Island, Y. Qiu, M.A.M. Renner & R.M. Schuster NZ-03054 (AK), KF852077, JF513406,—, JF513466, JF513487,—, JF513386, KF851638,—; *Lethocolea glossophylla*: IBC41, Ecuador, E.C. Davis 259 (DUKE), KF852059, AY607963, KF852195, DQ439692, AY608084, KJ802051, KJ802080, KF852498, KF851602, KJ802025; *Saccogymidium australe*: FATOL135, New Zealand, J.J. Engel, M. von Konrat & J.E. Braggins 24166 (F)—, KF942473, KF943272,—, KF943404, KF942832, KF942960,—, KF942712,—; *S. decurvum*: L1368, Australia: Tasmania, B. Shaw 6410 (DUKE), KF852088,—, KF852368, KF852389, KF851479,—, KF852555, KF851652,—; *Tylimanthus laxus*: IBC44, Costa Rica, G. Dauphin 2920 (NY)—, KF852499, KF851603, KJ802035. **Adelanthaceae:** *Cuspidatula monodon*: L1210, New Zealand, J.J. Engel & M. von Konrat 28380 (F)—, KF851922,—, KF852364, KF851455,—, KJ802087, KF852523, KF851626,—; *Syzygiella autumnalis*: L1300, USA: Vermont, B. Shaw 6969 (DUKE), KF852084, KF851944, KF852226, KF852382, KF851473, KJ802054, KJ802092, KF852544, KF851646, KJ802034; *S. colorata*: L1371, Australia: Tasmania, B. Shaw 6533 (DUKE), KF942447, KF942564, KF943333, KF943589, KF943481, KF942888, KF943049, KF943205, KF942766, KF942671; *S. nipponica*: E22, Nepal, D.G. Long 30702 (E)—, KF942461, KF943261,—, KF943397, KF942822, KF942950, KF943116,—, KF942631; *S. sonderi*: FATOL108, Gough Island, N.J.M. Gremmen 2000-0374 (F)—, KF942472, KF943270,—, KF943402, KF942831,—, KF943124, KF942710,—; *S. tasmanica*: FATOL02, New Zealand: South Auckland Province, J.J. Engel, M. von Konrat, & J.E. Braggins 23900 (F)—, KF942471, KF943269,—, KF943548,—, KF942713,—; *S. teres*: FATOL39, New Zealand, J.J. Engel, M. von Konrat & J.E. Braggins 24539 (F), KF852010, KF851847, KF852129, KF852296, KF851398,—, KF852444,—; L1225, New Zealand, J.J. Engel & M. von Konrat s.n. (F)—, KF942549,—, KF943582, KF943469,—, KF943035, KF943191, KF942753, KF942665. **Anastrophyllaceae:** *Anastrophyllopsis subcomplicata*: FATOL483, Australia, D. A. Meagher & N. Klazenga 07-142 (F), KF942423, KF942484, KF943280, KF943550, KF943414, KF942838, KF942968,

KF943135, KF942720,—; *Gottschelia schizopleura*: L1206, Malaysia: Pahang, D.G. Long 36922 (E)—, KF851920,—, KF852362, KF851453,—, KJ802085, KF852521, KF851624, KJ802021; *Gymnocolea inflata*: FATOL535, Svalbard, N.A. Konstantinova & A.N. Savchenko K118-1-04 (F), KF852019, KF851861, KF852141, KF852306, KF851412, KJ802048, KJ802076, KF852452, KF851553, KJ802022. **Antheliaceae:** “*Pseudolepicolea*” *trollii* subsp. *andoi*: E53, China: Yunnan, D.G. Long 33719 (E)—, KF943263, KF943547, KF943399,—, KF943117, KF942703,—; *Anthelia julacea*: E67, UK: Scotland, D.G. Long 31292 (E)—, KF851830, KF852121, KF852280, KF851384, KJ802043, KJ802070,—, KF852428, KF851527, KJ802014; L1404, USA: Alaska, B. Shaw F952/5 (DUKE)—, KF942570, KF943340, KF943594, KF943488, KF942894, KF943055, KF943212, KF942772, KF942677; *Hygrobliella laxifolia*: FATOL512, Russia, N.A. Konstantinova 31-2-03 (F)—, KF942489, KF943285,—, KF943420,—, KF942683, Russia, V. A. Bakalin s.n. (F)—, KF852154, KF852320, KF851422,—, KF852462, KF851560,—. **Arnelliaceae:** *Arnellia fennica*: L1498, Finland, B. Shaw 1250 (DUKE), KF852098, KF851969, KF852251, KF852402, KF851493, KJ802096,—, KF802058,—. **Balantiopsidaceae:** *Acroscephella phoenicorhiza*: FATOL865, New Zealand, J.E. Braggins & M.A.M. Renner 4174 (F), KF852039, KF851900, KF852165, KF852339,—, KF852339,—; *Balantiopsis diplophylla*: IBC7, Australia, H. Streimann 59554 (NY)—, KF852201, KF852348,—, KF851610,—; *B. splendens*: FATOL783, Chile, J.J. Engel 25363 (F)—, KF851887,—, KF852330,—, KF852330,—; *Isotachis lyallii*: IBC30, New Zealand, J.J. Engel 21825 (F), AY607905, AY607952, AY608010, KF852343, AY608073, AY608178, AY608130, KF852497, KF851600,—. **Blepharidophyllaceae:** *Blepharidophyllum vertebrale*: L1209, New Zealand, J.J. Engel & M. von Konrat s.n. (F), KF852073, KF851921, KF852217, KF852363, KF851454,—, KJ802086, KF852522, KF851625,—; *Clandarium gottscheanum*: FATOL777, Chile, J.J. Engel 26229 (F), KF852032, KF851885,—, KF852329, KF851425,—, KF852472, KF851564,—; *C. xiphophyllum*: L1373, Australia: Tasmania, B. Shaw 6433 (DUKE), KF942448,—, KF943334, KF943590, KF943482,—, KF943206, KF942767,—. **Calypogeaceae:** *Eocalypogeia quelpartensis*: gb242, Japan, T. Furuki 20233 (HIRO)—, AB476566, AB476605,—, KF942466, KF943266,—, KF942826, KF942955, KF943121, KF942707, KF942633; IBC11, USA, E.C. Davis 130 (DUKE), JF315941, AY6079311, JF316196, JF316291, AY6080521, AY608169, AY608121, AY607870, AY608169, KJ802016; *Metacalypogeia alternifolia*: E30, Bhutan, D.G. Long 28712 (E)—, JF513396, JF513412, JF513455, JF513474, KJ802040, KJ802068, KF852423, KF851522,—; *Mizotania riccardioides*: L1510, Malaysia: Pahang, D.G. Long, D.S. Rycroft & B. O’Shea 36926 (E)—, KF851971, KF852254,—, KF852568, KF851664,—; *Mnioloma fuscum*: L1516, Fiji, J.E. Braggins et al. 16. IV. 2008 (NSW)—, KF852256, KF852404, KF851498,—, KJ802100, KF852569, KF851665, KJ802029. **Cephalozieaceae:** *Alobiellopsis parvifolius*: L1532, Japan: Honshu, B. Shaw 8240 (DUKE), KF852105, KF851979, KF852262, KF852411, KF851505, KJ802064, KJ802104, KF852576, KF851672,—; *Cephalozia (Jungermannia) conchata*: L1198, China: Yunnan, D.G. Long 34888 (E)—, KF942541, KF943323, KF943576, KF943462, KF942883, KF943028, KF943183, KF942748,—; L1526, China: Yunnan, D. G. Long & J. Shevock 37157 (DUKE)—, KF942623, KF943389,—, KF942942, KF943107,—, KF942814,—; *Cephalozia bicuspidata*: FATOL587, Russia, N.A. Konstantinova s.n. (F)—, KF942504, KF8543295, KF943563, KF943435, KF942855, KF942986, KF943151,—, L1240, Ireland, R.E. Stotler & B.J. Crandall-Stotler s.n. (ABSH)—, JF513405, KF852220, JF513465, JF513486,—, KJ802090, JF513385, KF851633,—; *Odontoschisma sphagnum*: L1494, Canada: Newfoundland, B. Shaw 6684 (DUKE)—, KF942613, KF943377,—, KF943531, KF942930, KF943097,—, KF943377,—. **Cephalozieaceae:** *Cephalozia divaricata*: L1426, Czech Republic, P. Sova s.n. (DUKE), KF852095, KF851965, KF852248, KF852399, KF851489, KJ802056, KJ802094, KF852565, KF851660, KJ802017; *C. hirta*: IBC14, Australia, H. Streimann 59793 (NY), KF942433,—, JF513433,—, KF942864, KJ802079,—, KF942739, KF942650; *Herzogobryum atrocipillum*: L1497, Marion Island, R. Ochrya 1402/01 (DUKE)—, KF943380,—, KF943534, KF942933,—, KF942933,—; *H. vermiculare*: L1351, Iles Kerguelen, R. Ochrya 1011/06 (DUKE)—, KF942562, KF943332, KF943587, KF943479, KF942886, KF943047,—, KF942764, KF942669; *Nothogymnomitrium erosum*: FATOL177, New Zealand, J.J. Engel, M. von Konrat & J.E. Braggins 24569 (F)—, KF942474,—, KF943548, KF943395,—, KF942713,—; gb046, Australia, H. Streimann 53475 (JE)—, GQ900110,—, GQ900318,—, GQ900216,—, L1235, New Zealand, J.J. Engel & M. von Konrat s.n. (F)—, KF851928,—, KF852369, KF851461,—, KJ802089, KF852528, KF851632,—. **Endogemmataceae:** *Endogemma caespiticium*: FATOL505, Russia, N.A. Konstantinova 213-02 (F)—, KF942486,—, KF943417,—, KF942970,—, KF942970,—; gb322, Russia: Buryatiya, N.A. Konstantinova 101-1-01 (KPABG)—, GU220585,—, L1413, USA: Alaska,

- L1076, USA: North Carolina, B. Shaw Fza553 (DUKE),—, KF942521, KF943313,—, KF943450,—, KF943168,—, L1291, USA: Oregon, B. Shaw 6259b (DUKE), KF942446,—, KF942560, KF943330, KF943586, KF943477, KF942884, KF943045, KF943202, KF942763,—, L1431, Austria, P. Sova s.n. (DUKE),—, KF942593, KF943358, KF943609, KF943511, KF942914, KF943077, KF943235, KF942789,—, L1432, Austria, P. Sova s.n. (DUKE),—, KF942594, KF943359, KF943610, KF943512, KF942915, KF943078, KF943236, KF942790,—, S. infusum: FATOL226, Japan, H. Deguchi s.n. (221) (F),—, KF942476,—, KF943406,—, KF942962, KF943127,—, L1070, China: Jilin, B. Shaw 5448 (DUKE),—, KF942516,—, KF942870, KF943008,—, L1084, China: Jilin, B. Shaw 5424 (DUKE), KF942439, KF942529,—, KF943453,—, KF943018, KF943174,—, S. inundatum: FATOL37, New Zealand, J.J. Engel & M. von Konrat 23589 (F),—, KF942478, KF943274,—, KF943408,—, KF943130,—, L1483, Australia: Tasmania, B. Shaw 6391 (DUKE),—, KF942606, KF943371, KF943619, KF943524, KF942926, KF943090, KF943247, KF942799,—, L1484, Australia: Tasmania, B. Shaw 6395 (DUKE),—, KF942607, KF943372, KF943620, KF943525,—, KF943091, KF943248, KF942800,—, S. inundatum (rufiflorum): FATOL857, New Zealand, D. Glenny 9944 (F),—, KF942514, KF943302, KF943569, KF943445, KF942861, KF942996, KF943160,—, S. kashyapii: L1199, China: Yunnan, D.G. Long 34448 (E),—, KF942542,—, KF943577, KF943463,—, KF943029, KF943184,—, KF942662; S. lanigerum: L1086, China: Yunnan, B. Shaw 5604 (DUKE), KF942440, KF942531,—, KF943454, KF942880, KF943020, KF943176,—, S. macrocarpum: L1085, China: Yunnan, B. Shaw 5573 (DUKE),—, KF942530, KF943317,—, KF942879, KF943019, KF943175,—, L1527, China: Yunnan, D.G. Long 35702 (DUKE), KF942455, KF942624, KF943390,—, KF943542, KF942943, KF943108, KF943256, KF942815,—, S. marginatum: FATOL455, Japan, T. Yamaguchi 29073 (F), KF942422, KF942480, KF943276,—, KF943410, KF942834, KF942964, KF943132, KF942717,—, S. montanum: FATOL666, Australia, T. Pócs & H. Streimann s.n. (F),—, KF942505, KF943296, KF943564, KF943436,—, KF942987, KF943152,—, FATOL836, Australia, T. Pócs & H. Streimann 99105/F (F),—, KF942509, KF943299,—, KF943441, KF942858, KF942992, KF943158,—, S. obovatum: FATOL519, Russia, N.A. Konstantinova & A.N. Savchenko K382-3e-04 (F),—, KF942491,—, KF943552, KF943422, KF942843, KF942974, KF943139, KF942722,—, gb316, Russia: Murmansk, N.A. Konstantinova 196-6-02 (KPABG),—, GQ220754,—, gb317, Russia: Kemerovo, N.A. Konstantinova 72-2-00 (KPABG),—, GQ220753,—, gb318, Russia: Perm, N.A. Konstantinova K 324-1-04 (KPABG),—, GQ220755,—, L1090, Czech Republic, B. Shaw 1777 (DUKE),—, KF942533,—, L1402, USA: Alaska, B. Shaw F960/6 (DUKE),—, KF942568, KF943338,—, KF943486, KF942892, KF943053, KF943210, KF942770, KF942675; L1403, USA: Alaska, B. Shaw F961/14 (DUKE),—, KF942569, KF943339, KF943593, KF943487, KF942893, KF943054, KF943211, KF942771, KF942676; L1433, Norway, P. Sova s.n. (DUKE),—, KF942595, KF943360, KF943611, KF943513, KF942916, KF943079, KF943237, KF942791, KF942693; L1434, Czech Republic, P. Sova s.n. (DUKE),—, KF942596, KF943361, KF943612, KF943514, KF942917, KF943080, KF943238, KF942792, KF942694; L1435, Austria, P. Sova s.n. (DUKE),—, KF942597, KF943362, KF943613, KF943515, KF942918, KF943081, KF943239, KF942793, KF942695; L1492, USA: Alaska, B. Shaw 7755 (DUKE),—, KF942611, KF943375,—, KF943529, KF942928, KF943095,—, KF942804,—, S. obovatum (subellipticum): gb319, Russia: Kamchatka, V.A. Bakalin K-48-13-03 (KPABG),—, GQ220752,—, IBC35, USA, W.B. Schofield 111132 (DUKE),—, KF943005,—, S. orbiculatum: FATOL54, New Zealand: Westland Province, J. J. Engel, M. von Konrat & J.E. Braggins 24788 (F),—, KF942496,—, KF943427, KF942848, KF942979, KF943144, KF942728,—, L1232, New Zealand, J.J. Engel & M. von Konrat 28158 (F),—, KF942550,—, KF943583,—, KF943036, KF943192, KF942754,—, L1236, New Zealand, J.J. Engel & M. von Konrat 28166 (F),—, KF942552,—, KF943585,—, KF943037, KF943194, KF942756,—, L1408, New Zealand, M. Renner 4137 (DUKE),—, KF942574, KF943343, KF943597, KF943492, KF942898, KF943059, KF943216, KF942775, KF942679; L1410, New Zealand, M. Renner s.n. (DUKE),—, KF942575, KF943344, KF943598, KF943493, KF942899, KF943060, KF943217, KF942776, KF942680; L1411, New Zealand, M. Renner s.n. (DUKE),—, KF942576, KF943345, KF943599, KF943494, KF942900, KF943061, KF943218, KF942777, KF942681; S. parvitextum: L1073, China: Yunnan, B. Shaw 5775 (DUKE), KF942436, KF942519, KF943311, KF943571, KF943448, KF942873, KF943011, KF943166,—, S. patoniae: E14, China: Yunnan, D.G. Long 34743 (E),—, KF942459, KF943260,—, KF942820, KF942947, KF943114,—, S. polyrhizoides: L1528, China: Yunnan, D.G. Long 36119 (DUKE),—, KF942625, KF943391,—, KF943543, KF942944, KF943109,—, KF942816,—, S. pseudopyriflorum: gb326, Russia: Sakhalin, V.A. Bakalin S-25-1a-06 (VLA),—, GU220592,—, gb327, Russia: Sakhalin, V.A. Bakalin K-12-8-07 (VLA),—, GU220593,—, gb328, Russia: Primor'e, V.A. Bakalin P-74-79a-05 (VLA),—, GU220594,—, gb329, Russia: Primor'e, V.A. Bakalin P-65-1-06 (VLA),—, GU220595,—, gb330, Russia: Buryatiya, N.A. Konstantinova 30-2-01 (KPABG),—, GQ220759,—, S. pyriflorum: gb324, South Korea: KyongNam, V.A. Bakalin Kor-8-5-09 (VLA),—, GU220590,—, gb325, South Korea: KyongNam, V.A. Bakalin Kor-10-8-09 (VLA),—, GU220591,—, L1078, USA: North Carolina, B. Shaw 12988 (DUKE),—, KF942523,—, KF943014, KF943169,—, L1079, USA: North Carolina, B. Shaw pSchF (DUKE),—, KF942524,—, KF943170,—, L1241, USA: North Carolina, B. Shaw D-4A (DUKE),—, KF942553,—, KF943471,—, KF943038, KF943195, KF942757,—, L1493, USA: North Carolina, B. Shaw SchF 2007 (DUKE),—, KF942612, KF943376,—, KF943530, KF942929, KF943096,—, KF942805,—, S. rosulans: L1196, China: Yunnan, D.G. Long 36185 (E),—, KF942539,—, KF943574, KF943460,—, KF943026, KF943181, KF942746,—, L1201, China: Yunnan, D.G. Long 36011 (E),—, KF942544,—, KF943578, KF943465,—, KF943030, KF943186, KF942750,—, L1203, China: Yunnan, D.G. Long 33911 (E),—, KF942546,—, KF943579, KF943466,—, KF943032, KF943188, KF942751,—, S. rubripunctatum: L1504, China, D.G. Long 32517 (DUKE),—, KF942808,—, S. rubrum: L1092, USA: Oregon, B. Shaw F595 (DUKE),—, KF942534, KF943319,—, KF943456, KF942881, KF943022, KF943177,—, KF942657; L1486, USA: Alaska, B. Shaw 7845 (DUKE),—, KF942608, KF943373,—, KF943526,—, KF943092, KF942801,—, S. sanguinolentum: L1202, China: Yunnan, D.G. Long 35755 (E),—, KF942545,—, KF943031, KF943187,—, S. schusterianum: IBC34, Canada, E.C. Davis 431 (DUKE),—, KF943394,—, KF943004,—, S. sp.: gb320, Russia: Murmansk, N.A. Konstantinova 30-1-97 (KPABG),—, GQ220761,—, gb321, Russia: Buryatiya, N.A. Konstantinova 70-2-01 (KPABG),—, GQ220751,—, S. speciosum: E57, China: Yunnan, D.G. Long 33745 (E),—, JF513397, JF513413, JF513456,—, KF942825, KF942953, JF513346, KF942706,—, S. sphaerocarpum: L1081, Czech Republic, B. Shaw 3503 (DUKE),—, KF942526, KF943315,—, KF942877, KF943016, KF943172,—, L1441, Norway, P. Sova s.n. (DUKE),—, KF942602, KF943367, KF943618, KF943520, KF942923, KF943086, KF943244, KF942798,—, L1442, Czech Republic, P. Sova s.n. (DUKE), KF852096, KF851966, KF852249, KF852400, KF851490, KJ802057, KJ802095, KF852566, KF851661,—, S. sphaerocarpum (pusillum): L1282, Russia: Murmanskaya Oblast, J. Kučera 11462 (CBFS),—, KF942556, KF943326,—, KF943041, KF943198, KF942759,—, S. totipapillosum: FATOL50, New Zealand, J.J. Engel, M. von Konrat & J.E. Braggins 24933 (F),—, KF943281, KF943551, KF943415,—, L1407, New Zealand, M. Renner 4201 ? 4021 (DUKE),—, KF942573, KF943342, KF943596, KF943491, KF942897, KF943058, KF943215, KF942774,—, S. truncatum: FATOL837, Australia, T. Pócs & H. Streimann 9969/J (F),—, KF942510, KF943300,—, KF943442, KF942859, KF942993, KF943159,—, **Southbyaceae:** *Gongylanthus ericetorum*: L1139, Sicily, B. Buryová 593 (DUKE),—, KF943321,—, KF943458,—, KF943179, KF942744,—, *Gongylanthus liebmannianus*: FATOL774, Venezuela: Merida, L. Söderström, P. Manyanga & R. de Roo 2004/030b (F), KF852031, KF851883,—, KF852471, KF851563,—, L1479, Colombia, J.C. Benavides s.n. (SIU),—, KF851967,—, KF851491,—, *Southbya nigrella*: L1140, Italy, B. Buryová 621 (DUKE),—, KF851914, KF852211, KF852355, KF851446,—, KJ802083, KF852514, KF851618, KJ802020; *Southbya tophacea*: E60, Italy, D.G. Long 35466 (E),—, KF942465, KF943265,—, KF942954, KF943120,—, KF942632. **Trichotemnomataceae:** *Trichotemnomma corrugatum*: L1279, New Zealand: South Island, Y. Qiu & J.E. Braggins NZ-03123 (AK),—, KF851940,—, KF852379, KF851469,—, KF852540, KF851642,—.