

Transfer of *Gottschelia grollei*, *G. patoniae* and *Scaphophyllum speciosum* to *Solenostoma* based on chloroplast DNA *rbcL* sequences

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Abstract Maximum parsimony and Bayesian analyses of a chloroplast DNA *rbcL* dataset indicate a position of *Gottschelia schizopleura* in Scapaniaceae (Jungermanniales suborder Cephaloziineae). *Gottschelia grollei*, *G. patoniae* and *Scaphophyllum speciosum* are nested in *Solenostoma* (Solenostomataceae, Jungermanniales suborder Jungermanniidae) and are transferred to this genus. Accessions of *G. schizopleura* from Africa and Asia are separated by long branches.

Keywords Cryptic speciation · *Gottschelia* · Jungermanniales · Molecular phylogeny · *Scaphophyllum* · *Solenostoma* · *rbcL*

Introduction

Molecular phylogenetic studies have substantiated the position of liverworts (Marchantiophyta) as the earliest diverging extant main lineage of land plants (Qiu et al.

2006) and provided numerous new insights into their classification (Crandall-Stotler et al. 2009). The leafy liverworts represent a derived lineage that basically splits into two main clades assigned to as Jungermanniales and Porellales (Heinrichs et al. 2005, 2007; He-Nygrén et al. 2006). Molecular data allowed for a subdivision of Jungermanniales into four suborders (He-Nygrén et al. 2006) and pointed at numerous incongruences of morphology-based classification schemes and topologies derived from DNA sequence evidence (Heinrichs et al. 2004; Hentschel et al. 2006, 2007a; De Roo et al. 2007; Hendry et al. 2007; Vilnet et al. 2008). Schill et al. (2004) demonstrated that the family Lophoziaceae is nested in Scapaniaceae. Heinrichs et al. (2005) formalized the synonymy of Lophoziaceae and Scapaniaceae and showed that Lophoziaceae subfam. Jamesonielloideae (Inoue 1966) forms a separate lineage. Subsequently, this subfamily was included in Adelanthaceae (Heinrichs et al. 2007) or treated as a family of its own (He-Nygrén et al. 2006).

In the framework of a study on the molecular phylogeny of Adelanthaceae s. l. (Feldberg et al., unpublished), we produced chloroplast DNA *rbcL* sequences of several genera that earlier were assigned to Lophoziaceae subfam. Jamesonielloideae or related clades (Horikawa 1934; Schuster 2002; Long and Váňa 2007). Here we present our results with regard to the genera *Gottschelia* Grolle and *Scaphophyllum* Inoue. *Gottschelia* was set up to include two species with a jungermannialean habit that have exceedingly elongated, cylindrical perianths with the female bracts not accompanied by a bracteole, and slenderly ellipsoidal to cylindrical capsules with linear valves, and angular-stellate gemmae (Grolle 1968; Schuster 2002). Grolle et al. (2003) and Long and Váňa (2007) added two further species that have broadly ellipsoid to ellipsoid-cylindric perianths and do not produce gemmae. *Scaphophyllum* includes a

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single species with canoe-shaped, strongly concave leaves (Schuster 1998).

Materials and methods

DNA extraction, PCR amplification and sequencing

DNA extraction, PCR amplification and sequencing were carried out as described in Hentschel et al. (2006). If no product was detected, a second (nested) PCR was performed using the forward primer *rbcL*-210-F and the reverse primer *rbcL*-1200-R (Gradstein et al. 2006).

Taxon sampling and phylogenetic analyses

Nineteen new sequences of the genera *Adelanthus* Mitt., *Gottschelia*, *Scaphophyllum*, *Syzygiella* Spruce and *Wettsteinia* Schiffn. were generated. The new *rbcL* sequences were compared with GenBank sequences using the BLASTN program (Altschul et al. 1990) and incorporated into a large alignment of *rbcL* sequences of various taxa of Jungermanniopsida. The BLAST searches and preliminary maximum parsimony (MP) analyses of the Jungermanniopsida dataset (results not shown) indicated an affiliation of the new sequences to either Jungermanniales suborder Cephaloziineae or Jungermanniineae sensu He-Nygrén et al. (2006). Further sequences of representatives of these suborders were sampled based on the results of Hentschel et al. (2007a). Representatives of Jungermanniales suborder Lophocoleineae [*Bazzania* Gray, *Chiloscyphus* Corda, *Mastigophora* Nees, *Plagiochila* (Dumort.) Dumort., He-Nygrén et al. 2006] were chosen as outgroups.

The sequences (Table 1) were manually aligned in BioEdit version 5.09 (Hall 1999) resulting in a dataset including 1,053 homologous sites. Missing parts of sequences were coded as “N” (A, C, G or T). Phylogenetic trees were inferred using maximum parsimony as implemented in PAUP* version 4.0b10 (Swofford 2000). MP analyses were performed with the following options implemented: heuristic search mode with 1,000 random-addition sequence replicates, tree bisection-reconnection branch swapping (TBR), MULTrees option on, and collapse zero-length branches off. All characters were treated as equally weighted and unordered. Bootstrap support (BS) values were estimated by calculating 1,000 bootstrap replicates (Felsenstein 1985), each with 10 random-addition-sequence replicates, TBR branch swapping, and MULTrees on. Rearrangements were limited to 10 million per replicate. Bootstrap percentage values above 70 were regarded as good support (Hillis and Bull 1993). Bayesian inference of phylogeny was conducted using a general time reversible model (GTR) as implemented in MrBayes version

3.1.2 (Huelsenbeck and Ronquist 2001). A Bayesian search was carried out using four simultaneous Markov chains, 5 million generations and sampling every 100th generation. The software tool Tracer version 1.3 (Rambaut and Drummond 2003) was used to examine the parameters and determine the number of trees needed to reach stationarity (burn-in). Bayesian posterior probability (BPP) confidence values were generated from trees found after this initial burn-in period. Bayesian clade credibility values were regarded as significant when exceeding $BPP \geq 0.95$ (Larget and Simon 1999).

Results

Three hundred and eight of the 1,053 aligned characters were parsimony informative, 90 autapomorphic and 655 constant. The strict consensus of 432 maximally parsimonious trees (length 1,659 steps, consistency index excluding uninformative characters 0, 29) is depicted in Fig. 1. Bayesian searches sampled 45,001 trees (mean $\ln = -9.465955$). The Bayesian topology (Fig. 2) is largely congruent with the MP topology. The ingroup is divided into Cephaloziineae (BS 76, BPP 1.00) and Jungermanniineae (BS 52, BPP 1.00). Seven accessions of the generitype *Gottschelia schizopleura* (Spruce) Grolle form a monophyletic lineage (BS 100, BPP 1.00) that is placed sister to *Chaetophyllopsis whiteleggei* (Carrington and Pearson) R. M. Schust. (BS 96, BPP 1.00). Asian and African accessions of *G. schizopleura* are separated by a deep split (Fig. 2). The *G. schizopleura*/*Chaetophyllopsis* clade is placed sister to a clade with representatives of Scapaniaceae (Cephaloziineae) (BS 98, BPP 1.00). Two accessions of *Gottschelia patoniae* Grolle, Schill and D. G. Long and three accessions of *Scaphophyllum speciosum* (Horik.) Inoue form monophyletic lineages within the *Solenostoma* Mitt. clade (Jungermanniineae) (BS 77, BPP 1.00). An accession (type material) of *Gottschelia grollei* D. G. Long and Váña is placed sister to *Solenostoma sphaerocarpum* (Hook.) Steph.

Based on the molecular topologies, we propose a transfer of *G. grollei*, *G. patoniae*, and *S. speciosum* to *Solenostoma*:

Solenostoma grollei (D. G. Long and Váña) K. Feldberg, J. Hentschel, A. Bombosch, D. G. Long, Váña and J. Heinrichs, comb. nov. Bas.: *Gottschelia grollei* D. G. Long and Váña, J. Bryol. 29: 167. 2007.

Solenostoma patoniae (Grolle, Schill and D. G. Long) K. Feldberg, J. Hentschel, A. Bombosch, D. G. Long, Váña and J. Heinrichs, comb. nov. Bas.: *Gottschelia patoniae* Grolle, Schill and D. G. Long, J. Bryol. 25: 3. 2003.

Solenostoma speciosum (Horik.) J. Hentschel, K. Feldberg, A. Bombosch, D. G. Long, Váña and J. Heinrichs,

Table 1 Taxa used in the present study, including information about the origin of the studied material, voucher information and the herbaria where the vouchers are deposited, as well as GenBank accession numbers

Taxon	Origin	Voucher	Accession number
<i>Adelanthus decipiens</i> (Hook.) Mitt.	St. Helena	Wigginton 05/613 (GOET)	FJ984934
<i>Adelanthus lindenbergianus</i> (Lehm.) Mitt.	Argentina	Long 31828 (GOET)	FJ984933
<i>Anthelia julacea</i> (L.) Dumort.	Nepal	Long 31292 (H)	DQ026581
<i>Balantiopsis diplophylla</i> (Hook.f. and Taylor) Mitt.	New Zealand	Engel 20853 (GOET)	DQ312476
<i>Barbilophozia barbata</i> (Schreb.) Loeske	Bulgaria	Hentschel Bryo 0753 (GOET)	DQ312477
<i>Bazzania tricrenata</i> (L.) Gray	Austria	Heinrichs 4388 (GOET)	AY699990
<i>Calypogeia cordifolia</i> Steph.	Japan	Ohnishi 5523 (HIRO)	EF503673
<i>Calypogeia muelleriana</i> (Schiffn.) Müll.Frib.	Germany	Hentschel Bryo 01340 (GOET)	AM392302
<i>Cephalozia bicuspidata</i> (L.) Dumort.	Germany	Hentschel Bryo 0362 (GOET)	AM392307
<i>Cephaloziella divaricata</i> (Sm.) Schiffn.	Germany	Hentschel Bryo 01159 (GOET)	DQ312481
<i>Chaetophyllopsis whiteleggei</i> (Carrington and Pearson) Hamlin	Australia	Curnow 4804 (H)	AY462292
<i>Chiloscyphus polyanthos</i> (L.) Corda	Finland	He-Nygrén and Piippo 1469 (H)	AY149851
<i>Cylindrocolea recurvifolia</i> (Steph.) Inoue	Japan	Deguchi 36641 (HIRO)	AM392306
<i>Diplophyllum albicans</i> (L.) Dumort.	Germany	Hentschel Bryo 0240 (GOET)	AM392309
<i>Geocalyx graveolens</i> (Schrad.) Nees	Germany	Meinunger s. n. (JE)	DQ312490
<i>Gongylanthus ericetorum</i> (Raddi) Nees	Greece	Düll 63. (35.) (GOET)	AM392303
<i>Gottschelia schizopleura</i> (Spruce) Grolle (1)	Réunion	Schäfer-Verwimp et al. 19823 (GOET)	FJ984938 ^a
<i>Gottschelia schizopleura</i> (2)	Réunion	Gradstein 12032 (GOET)	FJ984939 ^a
<i>Gottschelia schizopleura</i> (3)	Madagascar	Ah-Peng R96 (GOET)	FJ984940 ^a
<i>Gottschelia schizopleura</i> (4)	Indonesia	Gradstein 12065 (GOET)	FJ984941 ^a
<i>Gottschelia schizopleura</i> (5)	Indonesia	Gradstein 12064 (GOET)	FJ984942 ^a
<i>Gottschelia schizopleura</i> (6)	Sri Lanka	Schäfer-Verwimp et al. 5488/II (GOET)	FJ984943 ^a
<i>Gottschelia schizopleura</i> (7)	Malaysia	Schäfer-Verwimp et al. 18695 (GOET)	FJ984944 ^a
<i>Gyrothyra underwoodiana</i> M.Howe	Canada	Hong 98-558 (MO-5241752)	DQ026584
<i>Harpanthus flotovianus</i> (Nees) Nees	Austria	Heinrichs et al. 4390 (GOET)	DQ312492
<i>Isotachis lyallii</i> Mitt.	New Zealand	Engel 21825 (F)	AY608032
<i>Jackiella curvata</i> Allison and E.A. Hodgs.	New Zealand	Qiu et al. NZ-03064 (AK)	DQ787461
<i>Jamesoniella autumnalis</i> (DC.) Steph.	China	Koponen et al. 55912 (H)	AY462303
<i>Jamesoniella rubricaulis</i> (Nees) Grolle	Ecuador	Sauer MS-E 251 (GOET)	GQ120508
<i>Jamesoniella undata</i> (Mont.) Steph.	Bolivia	Churchill et al. 22807 (GOET)	AM392305
<i>Jungermannia atrovirens</i> Dumort.	Germany	Hentschel Bryo 01784 (GOET)	EF503675
<i>Jungermannia pumila</i> Whit.	Russia	Bakalin P-72-2-05 (GOET)	EF503677
<i>Leiocolea collaris</i> (Nees) Jörg.	Slovakia	Hentschel Bryo 0864 (GOET)	DQ312501
<i>Liochlaena lanceolata</i> Nees	USA	Stotler and Crandall-Stotler 107 (ABSH)	AY507409
<i>Liochlaena subulata</i> (A.Evans) Schljakov	Japan	Inoue BSE 859 (GOET)	EF503678
<i>Marsupella emarginata</i> (Ehrh.) Dumort.	Germany	Hentschel Bryo 01638 (GOET)	DQ312505
<i>Mastigophora dicladus</i> (F.Weber) Nees	Indonesia	Schäfer-Verwimp and Verwimp 24898 (GOET)	EF503679
<i>Nardia compressa</i> (Hook.) Gray	Belgium	Heinrichs et al. 3806 (GOET)	DQ312507
<i>Nardia geoscyphus</i> (De Not.) Lindb.	Germany	Hentschel Bryo 01874 (GOET)	EF503680
<i>Nardia scalaris</i> Gray	Germany	Hentschel and Wilson Bryo 01618 (GOET)	DQ312508
<i>Nardia succulenta</i> (Lehm. and Lindenb.) Spruce	Bolivia	Churchill et al. 22796 (GOET)	EF503681
<i>Neesioscyphus argillaceus</i> (Nees) Grolle	Brazil	Schäfer-Verwimp and Verwimp 11107 (GOET)	DQ312509
<i>Notoscyphus lutescens</i> (Lehm. and Lindenb.) Mitt.	Vietnam	Pócs et al. 98101/D (GOET)	EF503682
<i>Nowellia curvifolia</i> (Dicks.) Mitt.	Mexico	Burghardt 4493 (GOET)	DQ312510
<i>Pedinophyllum truncatum</i> Inoue	China	Koponen 46768	AY149855
<i>Plagiochila porelloides</i> (Nees) Lindenb.	Germany	Heinrichs and Groth 4340 (GOET)	AY699998
<i>Saccogyna viticulosa</i> (L.) Dumort.	Tenerife	Gradstein 9977 (GOET)	DQ312514

Table 1 continued

Taxon	Origin	Voucher	Accession number
<i>Scapania aspera</i> M. Bernet and Bernet	Bulgaria	Hentschel Bryo 0762 (GOET)	AM392310
<i>Sphenobolus minutus</i> (Schreb.) Berggr.	Spitsbergen	Hentschel Bryo 0421 (GOET)	DQ312475
<i>Solenostoma callithrix</i> (Lindenb. and Gottsche) Steph.	Mexico	Burghardt 45 09 (GOET)	DQ312497
<i>Solenostoma crenulatum</i> Mitt.	Belgium	Heinrichs et al. JH 3822 (GOET)	EF503684
<i>Solenostoma grollei</i> (D.G. Long and Váňa) K. Feldberg et al.	China	Long 35715 (GOET)	FJ984948 ^a
<i>Solenostoma hyalinum</i> (Lydell) Mitt.	?	Qiu 01041 (MICH)	DQ645970
<i>Solenostoma infusum</i> (Mitt.) J. Hentschel	Japan	Deguchi s. n. (GOET)	DQ312498
<i>Solenostoma obovatum</i> (Nees) C. Massal.	Austria	Heinrichs et al. 4391 (GOET)	DQ312499
<i>Solenostoma patoniae</i> (Grolle et al.) K. Feldberg et al.(1)	China	Long 34886 (GOET)	FJ984946 ^a
<i>Solenostoma patoniae</i> (2)	China	Long 37161 (GOET)	FJ984947 ^a
<i>Solenostoma speciosum</i> subsp. <i>villosum</i> (R.M. Schust.) J. Hentschel et al. (1)	China	Long 34713 (GOET)	FJ984949 ^a
<i>Solenostoma speciosum</i> subsp. <i>villosum</i> (2)	Bhutan	Miehe 00-444-08-A (GOET)	FJ984950 ^a
<i>Solenostoma speciosum</i> subsp. <i>villosum</i> (3)	Bhutan	Miehe 00-444-08-B (GOET)	FJ984951 ^a
<i>Solenostoma sphaerocarpum</i> (Hook.) Steph.	Germany	Hentschel and Wilson Bryo 01594 (GOET)	EF503686
<i>Syzygiella concreta</i> (Gottsche) Spruce	Bolivia	Churchill 22744 (GOET)	AM392304
<i>Syzygiella liberata</i> Inoue	Bolivia	Churchill 22577 (GOET)	FJ984936 ^a
<i>Syzygiella ovalifolia</i> Inoue	Sulawesi	Gradstein 11025c (GOET)	FJ984937 ^a
<i>Tylimanthus saccatus</i> (Hook.) Mitt.		Qiu 02044; W. Frey and T. Pfeiffer 98-Mo 41 A (BSB)	DQ645975
<i>Tylimanthus laxus</i> (Lindenb.) Steph.	Ecuador	Gradstein and Mandl 10147 (GOET)	DQ312515
<i>Wettsteinia inversa</i> (Sande Lac.) Mitt.	Sulawesi	Gradstein 11014 (GOET)	FJ984935 ^a

Herbarium acronyms follow Holmgren et al. (1990)

^a Accession numbers of newly generated sequences

comb. nov. Bas.: *Anastrophyllum speciosum* Horik., J. Sci. Hiroshima Univ., Ser. B, Div. 2, Bot. 2: 147. 1934.

Solenostoma speciosum subsp. *villosum* (R. M. Schust.) J. Hentschel, K. Feldberg, A. Bombosch, D. G. Long, Váňa and J. Heinrichs, comb. nov. Bas.: *Scaphophyllum speciosum* subsp. *villosum* R. M. Schust., Bryologist 101: 434. 1998.

Discussion

The recent progress in liverwort phylogeny is reflected in the new liverwort classification of Crandall-Stotler et al. (2009). However, several genera have not yet been sequenced or been tested for their monophyly. Therefore we anticipate that modifications of the current classification will prove to be necessary to arrive at a natural subdivision.

Several recent molecular phylogenetic studies demonstrated that genus concepts need to be modified both in Scapaniaceae (De Roo et al. 2007; Vilnet et al. 2008) and Adelanthaceae s. l. (De Roo et al. 2007; He-Nygrén et al. 2006). Recent molecular work also demonstrated the

need for modified family concepts in Jungermanniineae (Hentschel et al. 2007a). The present study adds to growing evidence that many current genus concepts do not reflect ancestral relationships within these clades. Accessions of three species currently assigned to *Gottschelia* (Long and Váňa 2007) are placed in two different suborders of Jungermanniales, Cephaloziineae (*G. schizopleura*) and Jungermanniineae (*G. grollei*, *G. patoniae*). The generitype *G. schizopleura* is resolved in Scapaniaceae (including Lophoziaceae, Heinrichs et al. 2005) as suggested by earlier authors (Grolle et al. 2003; Long and Váňa 2007). This position is supported by the stellate gemmae, and the long-cylindrical, slender perianth with a plicate, crenulate-dentate mouth (Grolle 1968). *G. grollei* and *G. patoniae* lack gemmae and are provided with broadly ellipsoid to ellipsoid-cylindric perianths (Long and Váňa 2007). These characters link the two species with *Solenostoma*. The concave, unlobed leaves with rough cuticle are also known from some representatives of *Solenostoma* (Váňa 1973, 1974). Based on the outcome of the molecular phylogenetic analyses and the morphological similarities, we transfer *G. grollei* and *G. patoniae* to *Solenostoma*. Attempts to

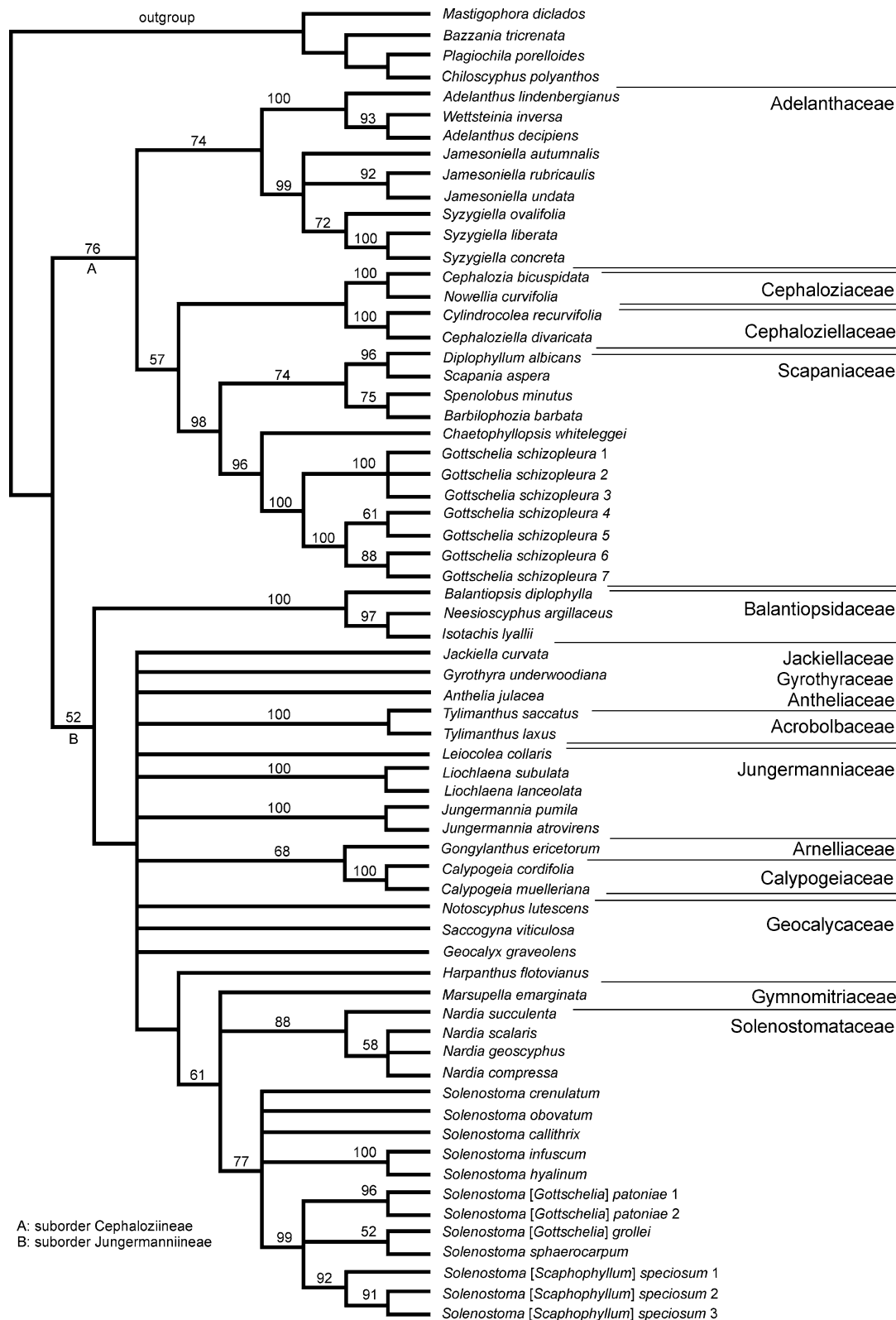


Fig. 1 Strict consensus of the 432 most parsimonious trees recovered during 1,000 random-taxon-addition heuristic searches of the *rbcL* data set. Bootstrap support is indicated at branches. The family

classification is based on Heinrichs et al. (2007, Adelanthaceae), Hentschel et al. (2007a, Jungermanniaceae) and Crandall-Stotler et al. (2009)

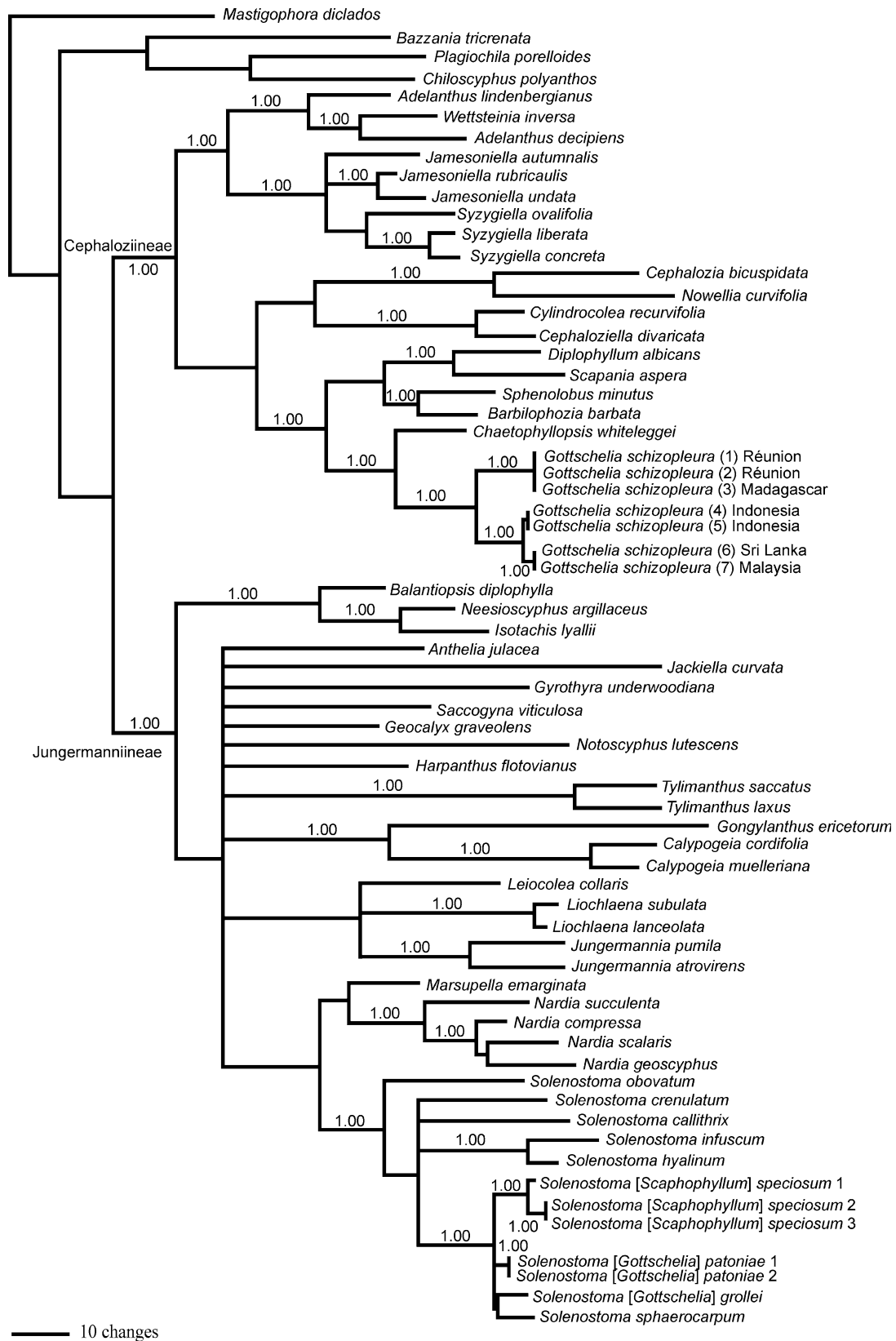


Fig. 2 Majority-rule consensus tree of trees recovered in stationary phase of Bayesian search. Bayesian posterior probabilities (≥ 0.95) are indicated at branches

sequence the fourth *Gottschelia* species, *G. maxima* (Steph.) Grolle (Long and Váňa 2007), remained unsuccessful. This species [epitype, designated by Grolle et al. (2003: 6), JE!] closely resembles *G. schizopleura* but differs in the crenulate-dentate leaf margins. Judging from morphology, it can remain in *Gottschelia*.

The monospecific genus *Scaphophyllum* (Schuster 1998) differs from *Gottschelia* and *Solenostoma* by canoe-shaped, strongly concave leaves, and a loosely to densely ciliate stem surface. Based on these differences, Schuster (1998, 2002) placed *Scaphophyllum* in its own subfamily, Scaphophylloideae. However, already Váňa (1973) pointed at striking similarities of *Scaphophyllum* and several species of *Jungermannia* L. s. l. that are now placed in *Solenostoma*. The present study supports Váňa's (1973) view: *Scaphophyllum* is nested in a robust subclade of *Solenostoma*. Based on the molecular topologies (Figs. 1, 2) and the morphological similarities of *Scaphophyllum* and *Solenostoma*, we transfer *Scaphophyllum* to the latter genus.

The African and Asian accessions of *G. schizopleura* are separated by long branches (Fig. 2), indicating a considerable period of isolation of the respective populations. Genetic variation within morphologically circumscribed liverwort species seems to be a common phenomenon and has been observed for several clades, e.g., *Bryopteris* (Nees) Lindb. (Hartmann et al. 2006), *Frullania* Raddi (Hentschel et al. 2009), *Herbertus* Gray (Feldberg et al. 2007), *Porella* L. (Hentschel et al. 2007b) and *Ptychanthus* Nees (Ahonen et al. 2005). In many cases, the phylogenetic structure follows a geographical pattern and could be indicative of cryptic speciation (Heinrichs et al. 2009). The Madagascan and Réunion accessions of *G. schizopleura* are more robust than the accessions from Indonesia, Malaysia and Sri Lanka. A detailed morphological investigation could possibly reveal morphological characters that would allow for a separation of the main clades of *G. schizopleura*. The type of *G. schizopleura* originates from Madagascar (Spruce 1885). Grolle (1968, 1971) lowered several (Austral-)asian taxa to synonyms of *G. schizopleura*. If two species are actually at hand, the basionym *Jungermannia colorata* δ *microphylla* Nees should be picked up to name the Asian populations.

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