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Scapania paraphyllia, a new synonym of *Scapania koponenii* (Marchantiophyta, Scapaniaceae) with special reference to paraphyllia, pseudoparaphyllia, and paraphyses

Wei-Ping Zhang¹, Lei Shu¹, Rui-Liang Zhu^{1,2}

¹School of Life Sciences, East China Normal University, Shanghai, China, ²Tiantong National Station of Forest Ecosystem, Shanghai Key Lab for Urban Ecological Processes and Eco-Restoration, East China Normal University, Shanghai, China

Scapania paraphyllia T.Cao, C.Gao, J.Sun & B.R.Zuo and *S. koponenii* Potemkin are both endemic to China. They share considerable morphological similarities except that the former species has pseudoparaphyllia. In order to elucidate the taxonomic status of the two species, we investigated morphological characters possessed by their type specimens and additional collections, and reconstructed a species phylogeny for *S. koponenii*, *S. paraphyllia*, and closely related species. The phylogenetic trees were constructed using maximum parsimony, maximum likelihood and Bayesian inference analyses based on the nuclear marker nrITS and the plastid markers *trnL-F* region and *atpB-rbcL* spacer. Both morphological and molecular evidence contradicted the hypothesis that *S. paraphyllia* and *S. koponenii* are separate species. The pseudoparaphyllia reported for *S. paraphyllia* are confirmed as paraphyses. The paraphyllia, paraphyses, and pseudoparaphyllia in *Scapania* are discussed.

Keywords: China, Hepaticae, Liverwort, Molecular phylogeny, Taxonomy

Introduction

Scapania (Dumort.) Dumort., with 100 currently accepted species (Söderström *et al.*, 2016), is the largest genus in its own family Scapaniaceae, most species of which occur in northern temperate regions. The genus is well characterised and easily recognised by the (1) lack of underleaves, (2) prominently lateral-intercalary branching, (3) leaves complicate-bilobed, with ventral leaf lobes (also called leaf lobules) often rotund to ovate or even lingulate and larger than dorsal leaf lobes (also called leaf lobes), (4) presence of a usually winged keel, (5) leaf-margins usually denticulate, occasionally entire, (6) cuticles smooth to coarsely verruculose or obviously verrucose, and (7) dorso-ventrally compressed perianths, usually with truncate and entire mouths. *Scapania* was extensively studied using both morphological (Müller, 1905; Amakawa & Hattori, 1953, 1954, 1955; Amakawa, 1964; Schuster, 1974; Potemkin, 1998, 1999a, 1999b, 2002) and molecular

data to resolve species delimitations and supraspecific classifications (Vilnet *et al.*, 2010; Heinrichs *et al.*, 2012).

So far, about 50 *Scapania* species have been recognised in China (Cao & Sun, 2008; Jia & He, 2013). Among them, *Scapania paraphyllia* T.Cao, C.Gao, J.Sun & B.R.Zuo is a species endemic to China, and known only from the two type specimens found in Zhejiang province (Zuo *et al.*, 2007; Jia & He, 2013). This species is characterised by the keel being about 1/4–1/3 the length of the leaf lobule, cuticle of leaves verrucose with large papillae, and shoots with pseudoparaphyllia in the leaf axils or on stems (Zuo *et al.*, 2007). During recent studies of *Scapania* in China, we observed that *S. paraphyllia* shared numerous common characters with *S. koponenii* Potemkin, another endemic species of China, previously known from south-eastern China (Potemkin, 2000). It seemed that the presence of ‘pseudoparaphyllia’ was the only character differing between these two species.

This study aimed to test the circumscription of *S. paraphyllia* and *S. koponenii* by conducting phylogenetic analyses based on 38 samples including

Correspondence to: Rui-Liang Zhu, Department of Biology, School of Life Sciences, East China Normal University, 3663 Zhong Shan North Road, Shanghai 200062, China. Email: rlzhu@bio.ecnu.edu.cn

S. paraphyllia and *S. koponenii* from their type localities and neighbouring provinces of China using nuclear and plastid DNA regions (nrITS, *trnL-F* region, and *atpB-rbcL* spacer). In conclusion, we propose a new synonym in accordance with the evidence from the morphological characters and molecular topologies.

Materials and Methods

Taxon sampling

To assess the phylogenetic relationship between *S. paraphyllia* and *S. koponenii*, we used a dataset consisting of 38 samples from 15 species in eight sections belonging to subg. *Scapania*. Among them, the sequences of 11 samples were newly obtained and those of the remaining 27 samples were downloaded from GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>). According to the phylogenies generated by Heinrichs *et al.* (2012) and Vána *et al.* (2012), *S. aequiloba* (Schwagr.) Dumort. and *S. curta* (Mart.) Dumort., representing the sections *Aequilobae* and *Curtae*, respectively, were chosen as the outgroup in this study. Voucher specimens for the 11 new samples were carefully examined by light microscopy (Olympus BX 43). Voucher information and GenBank accession numbers for all sequences used in the current study are listed in Appendix 1.

DNA extraction, PCR amplification, and sequencing

Tissue from the distal parts of gametophyte shoots was isolated from herbarium specimens collected within the last three years. Total genomic DNA was extracted with Qiagen DNeasy Plant® Mini Kit. Primers for PCR were those described in previous studies: *trnL-F* region from Taberlet *et al.* (1991), *atpB-rbcL* spacer from Feldberg *et al.* (2010), and nrITS region from Groth *et al.* (2003). PCR amplification was carried out as follows. For *trnL-F* and *atpB-rbcL*, an initial denaturation at 94°C for 4 min was followed by 33 cycles of 1 min denaturation at 94°C, 1 min annealing at 51°C (*trnL-F*) or 50°C (*atpB-rbcL*), and 1 min elongation at 72°C, then a final elongation step of 10 min at 72°C. For nrITS, an initial denaturation step at 94°C for 4 min was followed by 33 cycles of 1 min denaturation at 94°C, 1 min annealing at 51°C and 1.5 min elongation at 72°C, then a final 10 min elongation at 72°C. The PCR products were first tested by electrophoresis in an agarose gel to confirm successful amplification. The successful amplifications were sent to Shanghai Majorbio Bio-Pharm Technology Co. Ltd., China (<http://www.majorbio.com.cn>) for bidirectional sequencing with the same primers as used in PCR.

Phylogenetic analysis

In the phylogeny analyses, 108 sequences were included in the final dataset, of which 32 sequences were newly generated, whilst 76 were obtained from Genbank. All sequences were assembled and manually aligned in PhyDE@0.9971 (Müller *et al.*, 2005). Ambiguous positions in the dataset were excluded from subsequent phylogenetic analyses; the gaps and missing nucleotides were scored as missing data. Maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI) phylogenetic methods were employed to infer phylogenies.

Maximum parsimony analyses were conducted in PAUP 4.0b10 (Swofford, 2003). Command files based on the parsimony ratchet (Nixon, 1999) were generated by the programme PRAP2 (Müller, 2007). All characters were equally weighted and treated as unordered and heuristic searches were performed for 10,000 replicates with tree bisection and reconnection (TBR) branch swapping. The three single locus datasets were first subjected to separate MP analyses to examine for possible incongruence. The 70% bootstrap criterion was used to identify incongruent signals (Mason-Gamer & Kellogg, 1996) by visual comparisons of the tree topologies and support values. No evidence of incongruence was shown and thus the three datasets were combined for subsequent phylogenetic analyses. Maximum likelihood analyses were conducted using RAxML8.2 (Stamatakis, 2014). A rapid bootstrap analysis was run using the GTRGAMMAI substitution model with 1000 replicates. Partitioned BI analyses were performed in MrBayes v.3.0 (Huelsenbeck & Ronquist, 2001). The optimal nucleotide substitution models for each region: HKY + G (*trnL-F*), GTR + I (*atpB-rbcL*), and GTR + I + G (nrITS) were calculated using MrModeltest v.2.3 (Nylander, 2004) as implemented in PAUP* v.4.0b10 and based on the Akaike Information Criterion (AIC). The data were analysed using Markov Chain Monte Carlo (MCMC), performing four parallel analyses with four chains each run for 2 million generations, and sampling trees every 1000 generations. The first 10% of the sampled trees were discarded as burn-in determined by Tracer v1.5 (Rambaut & Drummond, 2009). From the remaining tree set, a single majority-rule consensus tree with the posterior probabilities (PP) was generated. Trees were depicted in TreeGraph v.2 (Stöver & Müller, 2010).

Results

The combined alignment consists of 1698 characters of 38 samples, including 377 in the locus *trnL-F*, 595 in *atpB-rbcL* and 726 in nrITS. Of the total characters, 1375 were constant, 228 were parsimony informative, 95 were variable but parsimony uninformative. The

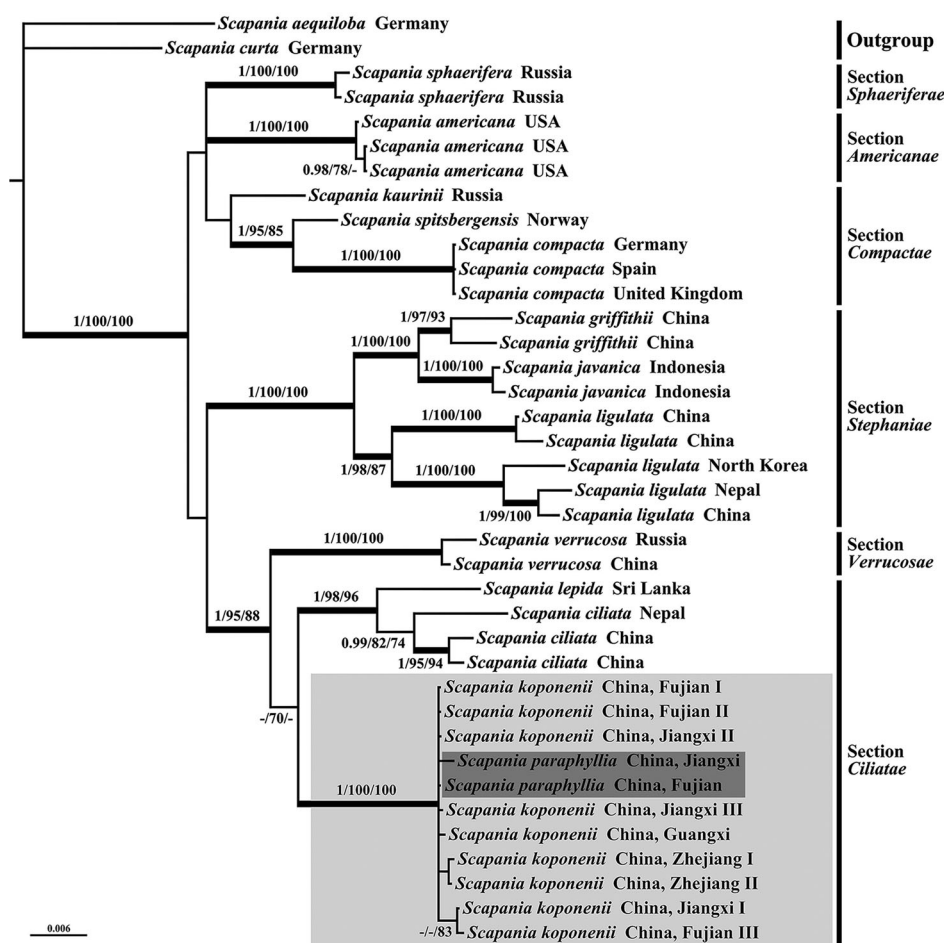


Figure 1 Majority-rule consensus tree based on Bayesian analyses of the combined dataset of *trnL-F*, *atpB-rbcL*, and *nrITS*. Bayesian posterior probability values (PP) followed by bootstrap percentage values from maximum likelihood (MLBS) and maximum parsimony (MPBS) are indicated at branches (from left to right: PP/MLBS/MPBS). Branches in bold are highly supported by all analytical methods (PP \geq 0.99; MLBS \geq 95; MPBS \geq 85). Support values of PP $<$ 0.95, MLBS $<$ 70, and MPBS $<$ 70 are not shown or indicated by a dash (-).

MP analyses generated four maximally parsimonious trees by a length of 525 steps, with a consistency index (CI) of 0.749 and a retention index (RI) of 0.884. BI and ML analyses resulted in topologies congruent with the topology from MP analyses. Thus the consensus tree from the Bayesian inference analyses is presented in Figure 1, with posterior probabilities (PP \geq 0.95) indicated on the branches as well as bootstrap support values (BS \geq 70) obtained from the likelihood and parsimony analyses separately.

In the phylogenetic topology (Figure 1), the ingroup contained 13 species. Nine species with multiple accessions were resolved in monophyletic lineages (PP = 1; MLBS \geq 97; MPBS \geq 87), while only *S. ciliata* Sande Lac. was moderately supported in both the ML and MP analyses (MLBS = 82; MPBS = 74). The 13 species represent six sections of the Heinrichs *et al.* (2012) phylogeny of *Scapania* (Figure 1). In sect. *Ciliatae*, nine samples of *S. koponenii* with two samples of *S. paraphyllia* were grouped together to form a clearly

monophyletic clade with strong support (PP = 1; MLBS = 100; MPBS = 100).

Discussion

Scapania paraphyllia was described based on two herbarium specimens (*Z.L. Liu 554*, holotype; *Z.L. Liu 553*, paratype) originally determined as *S. stephanii* Müll.Frib. from Zhejiang province (Zuo *et al.*, 2007). Our examination reveals that both holotype and paratype contain both male and female plants, and that the so-called ‘pseudoparaphyllia’ in *S. paraphyllia* are actually in male bract-axils or occasionally on stems just out of the bract-base of androecia (Figure 2D, N). The paraphyses in *S. paraphyllia* seem to have been misidentified as ‘pseudoparaphyllia’ because pseudoparaphyllia are restricted to the areas of the stem around branch primordia, and not associated with antheridia and archegonia (Magill, 1990).

Scapania koponenii was originally described by Potemkin (2000) based on samples from five provinces of China, including Fujian, Guangdong, Hunan,

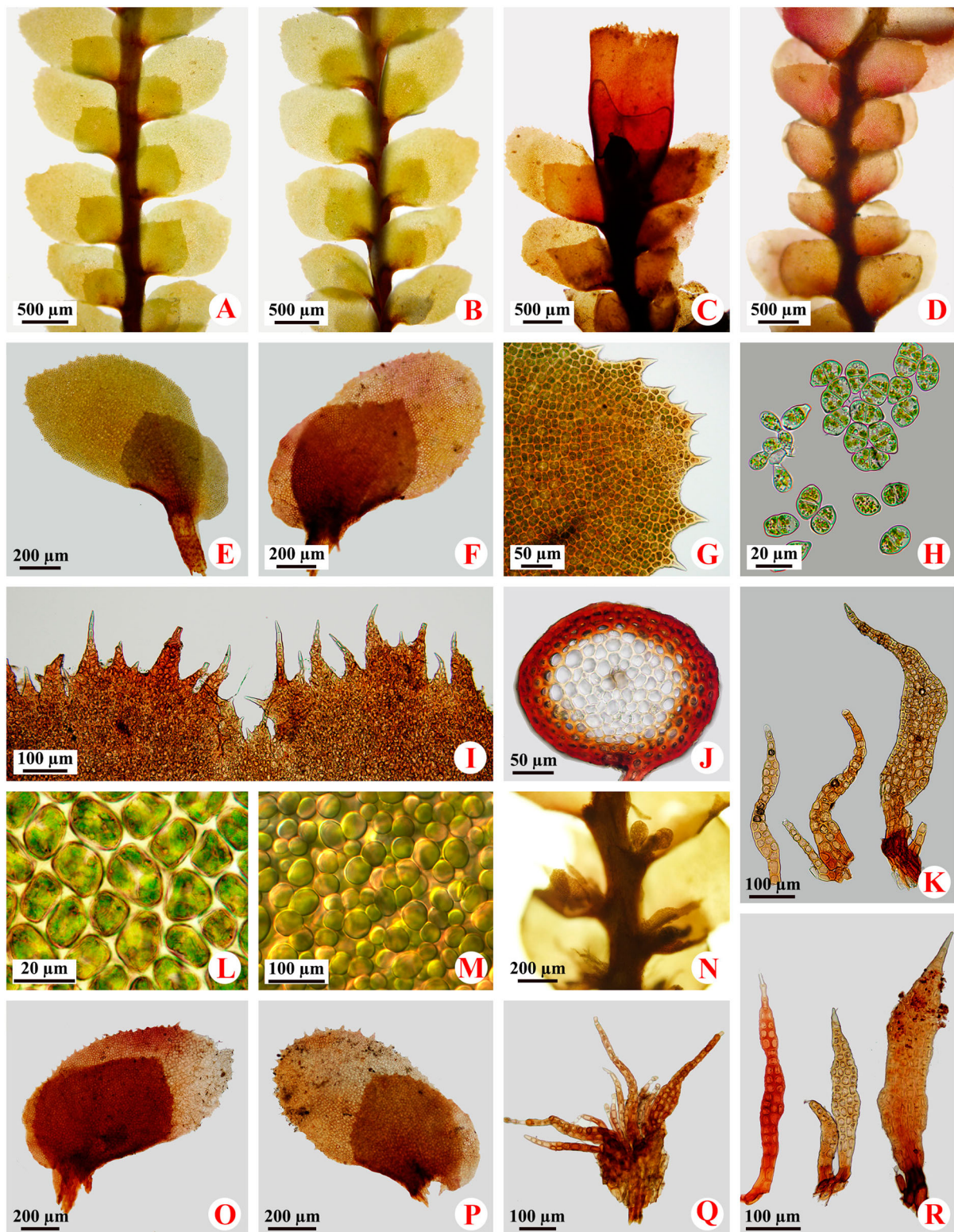


Figure 2 *Scapania koponenii* Potemkin. (A) Portion of shoot, ventral view. (B) Portion of shoot, dorsal view. (C) Portion of shoot with perianth, ventral view. (D) Portion of shoot with androecia, ventral view. (E) Leaf. (F, O, P) Male bracts. (G) Apical portion of leaf lobule. (H) Gemmae. (I) Sector of perianth mouth. (J) Cross section of stem. (K, Q, R) Paraphyses. (L) Median cells of leaf lobule. (M) Papillae of leaf lobule. (N) Portion of male plant, showing antheridia and paraphyses in male bracts. A–J, L–N, and Q from Zhang et al. 20150830-178A (HSNU), K and O from Li 95233 (paratype of *S. koponenii*, HSNU), P and R from Liu 554 (holotype of *S. paraphyllia*, HSNU).

Jiangxi, and Zhejiang. It has thus far only been found in China, but does not seem rare. It is widely distributed in Fujian, Guangdong, Guangxi, Guizhou, Hunan, Jiangxi, and Zhejiang (Zhu et al., 2006; Cao

& Sun, 2008); it mainly grows on wet cliffs, wet rocks or rocks with a thin layer of soil, usually in clumps in moist habitats at altitudes of 400–1800 m. This species is well characterised and easily recognised

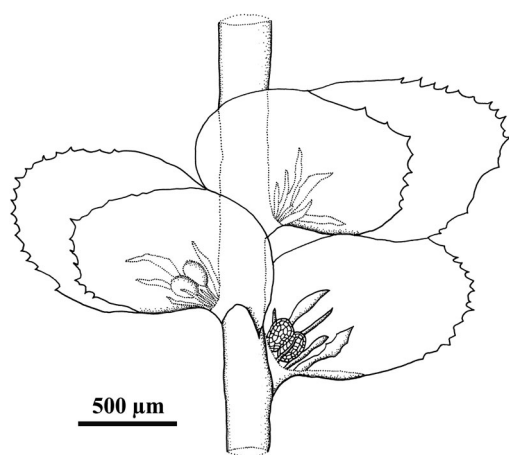


Figure 3 *Scapania koponenii* Potemkin. Portion of male plant, showing antheridia associated with paraphyses. Drawn from Zhang et al. 20150830-178A (HSNU).

by the small plants (mostly 1–2 cm long) (Figure 2A, B), the leaf lobe about 1/3–1/2 the size of leaf lobule, the keel about 1/4–2/5 the length of the leaf lobule (Figure 2E), the irregular marginal toothed leaf and perianth mouth (Figure 2C, G, and I), and the cuticle densely to coarsely papillose (Figure 2M). In addition, the androecia of this species are short with subequally bilobed male bracts in 2–3 pairs with a longer keel (Potemkin, 2000) (Figure 2D, F, and O). Male plants of numerous specimens contain numerous paraphyses which are the same as those in the type specimens of *S. paraphyllia* (Figure 2D, K, N, Q, and R; Figure 3). Morphological observations on *S. koponenii* and *S. paraphyllia* reveal that the two taxa have no significant differences as suggested by our molecular analyses. *Scapania paraphyllia* is thus proposed as a new synonym of *S. koponenii*.

In bryophytes paraphyses are hyaline or yellowish, usually uniseriate, hairs often associated with antheridia and archegonia (Magill, 1990; Merced-Alejandro & Sastre-De Jesús, 2009). Back in 1905, paraphyses were reported in *Scapania americana* Mull.Frib., *S. aspera* M.Bernet & Bernet, *S. compacta* (Roth) Dumort., *S. ligulata* subsp. *stephanii* (Mull.Frib.) Potemkin, Piippo & T.J.Kop., *S. irrigua* (Nees) Nees, *S. kaurinii* Ryan., *S. secunda* Steph., *S. umbrosa* (Schrad.) Dumort., and *S. undulata* (L.) Dumort. (Müller, 1905). Schuster (1974) and Amakawa (1964, 1967, 1968) also described paraphyses in further species, e.g., *S. brevicaulis* Taylor, *S. curta*, *S. hyperborea* Jørg., *S. komagadakensis* Amakawa, *S. nemorea* (L.) Grolle (as *S. nemorosa* (L.) Dumort.), *S. nipponica* (Amakawa & S.Hatt.) Amakawa, *S. obcordata* (Berggr.) S.W.Arnell., *S. okamurana* Steph. ex Amakawa & S.Hatt. (= *S. parvitexta* Steph.). Recently Potemkin (2000, 2001) also reported

the occurrence of paraphyses in *S. davidii* Potemkin, *S. koponenii* Potemkin and *S. sinikkae* Potemkin. The paraphyses reported in all species mentioned above are associated with antheridia, except for *S. davidii* whose paraphyses also occur in female bracts (Majumdar et al., 2016). Paraphyses are variable in size and shape in *Scapania*. They are usually linear, lanceolate, subulate, lamellate, and foliaceous and their margins are entire, or densely ciliate to dentate (Schuster, 1974; Majumdar et al., 2016). In *Scapania koponenii*, the paraphyses are yellowish to reddish-brown, linear to lanceolate, 21–128 × 188–562 μm, entire or occasionally with teeth at the margin (Figure 2K, N, Q, R; Figure 3). Although reduced paraphyses were treated as advanced morphological characters in *Scapania* (Potemkin, 2002), the taxonomic value of paraphyses still needs to wait for further studies.

The word pseudoparaphyllium was first used by Warnstorff (1904–1906) who defined it as a foliose structure around the branch primordia in *Rhynchostegium confertum* (Dicks.) Schimp. (a moss). The term, however, was later confused (Ireland, 1971; Schofield & Hebant, 1984), and it was difficult to separate from the term paraphyllium. Ignatov & Hedenäs (2007) explored the homologies of pseudoparaphyllia in pleurocarpous mosses and suggested that the term pseudoparaphyllium be used for any structures developed near or at the base of branch primordia. In *Scapania* pseudoparaphyllia have been reported in only two species, *S. macroparaphyllia* T.Cao C.Gao & J.Sun (Cao et al., 2004) and *S. paraphyllia* (Zuo et al., 2007). In the latter the pseudoparaphyllia proved to be mis-interpreted paraphyses. Owing to the limited samples available in the present study it remains unknown whether the same mis-understanding has occurred in *S. macroparaphyllia*.

Paraphyllia are tiny filaments, scales, or leaf-like structures scattered on the stems of some leafy liverworts and pleurocarpous mosses (Malcolm & Malcolm, 2006). Although paraphyllia are not frequent in liverworts, they have been reported and used as one of the key characters in the taxonomy of *Plagiochila* (Dumort.) Dumort. (Grolle & So, 1999; So, 2001). In *Scapania*, paraphyllia have been known in only a few species, e.g., *S. bolanderi* Austin, *S. maxima* Horik., *S. ornithopodioides* (With.) Waddell, and *S. robusta* Horik. (= *S. subnimbosa* Steph.) (Amakawa & Hattori, 1953; Inoue, 1972), but seem to have been confused with paraphyses because the male bracts are usually extremely similar to vegetative leaves and they are very difficult to recognise, especially when the antheridia shrivel in herbarium specimens. The terms paraphyllia and pseudoparaphyllia have also been used

interchangeably in earlier reports (e.g. Cao et al., 2004; Cao & Sun, 2008). It is still necessary to investigate the occurrence of the true paraphyllia, and evaluate their taxonomic value in *Scapania*.

Scapania koponenii may be confused with the European *S. aspera*. The former, however, differs mainly in its smaller size (1.2–2 mm wide and 5–20 mm long), smaller leaf cells (median 13–16 × 16–20 μm), dense ± hemispherical papillae, and the more elongated, ± spinose terminal tooth cells in the leaf margins (Potemkin, 2000; Borovichev et al., 2016). The molecular phylogenetic study also reveals the two species belong to different main clades of *Scapania* (Heinrichs et al., 2012). In China, *S. koponenii* is most similar to *S. ciliata*, but in the latter the plants are 2–4 cm long, with marginal teeth of the leaf often unicellular, rather strongly elongated and notably spinose, dense, and hyaline, leaf lobes usually 1/2 the leaf lobule in size, and perianth mouth with cilia 1–4 cells long.

Taxonomic treatment

Scapania koponenii Potemkin, Ann. Bot. Fenn. 37 (1): 41. 2000. (Figures 2–3)

Type: China, Hunan Prov.: Yizhang Co., Mt. Mangshan, Guizhizhai, core area of the forest reserve. Primeval subtropical (warm temperate) *Cyclobalanopsis* Oerst., *Lithocarpus* Blume, *Pinus kwangtungensis* Chun & Tsiang, *Rhododendron* L, *Schisma* Dumort. forest on slope, 24°57'N, 112°55'E, 1160 m, on cliff on open moist slope, 2 Oct. 1997, T. Koponen, S. Huttunen & P.-C. Rao 50767a (holotype: H; isotypes: LE and herb. Forest Botanical Garden, Changsha).

= *Scapania paraphyllia* T.Cao, C.Gao, J.Sun & B.R.Zuo, Acta Phytotax. Sin. 45 (3): 311. 2007. *syn. nov.* **Type:** China, Zhejiang Prov.: Suichang Co., Mt. Jiulong, 1360 m, on rock, 23 Apr. 1981, Z. L. Liu 554 (holotype: HSNU!).

Representative specimens examined: China: Fujian, Wuyishan Co., Wuyishan National Nature Reserve, 27°44'59.57"N, 117°40'46.10"E, 695 m, on rock with a thin layer of soil, 31 Aug. 2015, Zhang et al. 20150831-101 (HSNU), *ibid.*, 27°44'59.96"N, 117°40'46.37"E, 695 m, on rock with a thin layer of soil, 31 Aug. 2015, Zhang et al. 20150831-107 (HSNU), *ibid.*, 27°43'58.85"N, 117°38'44.19"E, 1061 m, on rock with a thin layer of soil, 30 Aug. 2015, Zhang et al. 20150830-145 (HSNU), *ibid.*, 27°43'58.96"N, 117°39'22.83"E, 937 m, on rock, 30 Aug. 2015, Zhang et al. 20150830-178, 20150830-178A (HSNU); Guangdong, Ruyuan Co., Babaoshan Nature Reserve, 800–900 m, on rock, 2 Nov. 1995, Li et al. 95233 (paratype of *S. koponenii*: HSNU!, SYS!); Guangxi, Xingan Co., Longtangjiang, 25°48'43.61"N, 110°25'48.55"E, 446 m, 10 Jul. 2015,

Wei et al. 20150710-3 (HSNU); Guizhou, Leishan Co., Leigongshan National Nature Reserve, 26°22.163'N, 108°08.994'E, 964 m, on rock, 26 Aug. 2010, Zhu et al. 20100826-92B (HSNU); Jiangxi, Jinggangshan Co., Jinggangshan National Nature Reserve, on rock with a thin layer of soil, 15 Oct. 2014, Wang 20141015-13 (HSNU), Zixi Co., Matoushan National Nature Reserve, 27°47'58.63"N, 117°12'07.93"E, 438 m, on wet cliff, 27 Jul. 2015, Zhang 20150727-52 (HSNU), Yanshan Co., Wuyishan National Nature Reserve, 27°50'17.39"N, 117°44'32.82"E, 1532 m, on wet cliff, 3 Aug. 2015, Zhang 20150803-137 (HSNU), *ibid.*, 27°50'26.46"N, 117°43'55.69"E, 905 m, on rock with a thin layer of soil, 4 Aug. 2015, Zhang 20150804-76 (HSNU); Zhejiang, Longquan City, Fengyangshan National Nature Reserve, 27°54.444'N, 119°10.452'E, 1293 m, on rock, 19 Apr. 2011, Zhu & Wei 20110419-12 (HSNU), Suichang Co., Mt. Jiulong, on rock, 1360 m, 23 Apr. 1981, Z. L. Liu 553 (paratype of *Scapania paraphyllia*: HSNU!). Taishun Co., Wuyanling National Nature Reserve, on wet rock, 28 Jul. 2001, Cao 010281 (SHTU).

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Taxonomic Additions and Changes: *Scapania koponenii* Potemkin (*S. paraphyllia* T.Cao, C.Gao, J.Sun & B.R.Zuo *syn. nov.*).

References

- Amakawa, T. 1964. A short revision of Himalayan *Scapania* (Hepaticae). *Journal of the Hattori Botanical Laboratory*, 27: 1–19.
- Amakawa, T. 1967. *Scapania* sect. *Gracilidae* of the areas around the north Pacific Ocean. *Journal of the Hattori Botanical Laboratory*, 30: 315–27.
- Amakawa, T. 1968. New or critical species of the genus *Scapania* of Japan I. *Journal of the Hattori Botanical Laboratory*, 31: 94–100.
- Amakawa, T. & Hattori, S. 1953. A revision of the Japanese species of Scapaniaceae (I). *Journal of the Hattori Botanical Laboratory*, 9: 45–62.
- Amakawa, T. & Hattori, S. 1954. A revision of the Japanese species of Scapaniaceae (II). *Journal of the Hattori Botanical Laboratory*, 12: 91–112.
- Amakawa, T. & Hattori, S. 1955. A revision of the Japanese species of Scapaniaceae (III). *Journal of the Hattori Botanical Laboratory*, 14: 71–90.

- Borovichev, E., Fedosov, V. & Vilnet, A. 2016. An unexpected record of the European liverwort *Scapania aspera* (Scapaniaceae, Marchantiophyta) in East Siberia. *Cryptogamie, Bryologie*, 37: 445–54.
- Cao, T. & Sun, J. 2008. Scapaniaceae. In: C. Gao & Y.-H. Wu, eds. *Flora bryophytorum Sinicorum, volume 10*. Beijing: Science Press, pp. 82–141. In Chinese.
- Cao, T., Gao, C., Sun, J., Yu, J., Song, G.-Y. & Zuo, B.-R. 2004. *Scapania macroparaphyllia*, a new species of *Scapania* (Scapaniaceae) from Xizang, China. *Acta Phytotaxonomica Sinica*, 42(2): 180–2. In Chinese.
- Feldberg, K., Váňa, J., Long, D.G., Shaw, A.J., Hentschel, J. & Heinrichs, J. 2010. A phylogeny of Adelanthaceae (Jungermanniales, Marchantiophyta) based on nuclear and chloroplast DNA markers, with comments on classification, cryptic speciation and biogeography. *Molecular Phylogenetics and Evolution*, 55(1): 293–304.
- Grolle, R. & So, M.L. 1999. On the *Plagiochila* species of sect. *Zonatae* with paraphyllia or mammillose stems (Hepaticae). *Systematic Botany*, 24(3): 297–310.
- Groth, H., Lindner, M., Wilson, R., Hartmann, F.A., Schumler, M., Gradstein, S.R. & Heinrichs, J. 2003. Biogeography of *Plagiochila*: natural species groups span several floral kingdoms. *Journal of Biogeography*, 30(7): 965–78.
- Heinrichs, J., Bombosch, A., Feldberg, K., Kreier, H.-P., Hentschel, J., Eckstein, J., Long, D., Zhu, R.-L., Schäfer-Verwimp, A., Schmidt, A.R., Shaw, B., Shaw, A.J. & Váňa, J. 2012. A phylogeny of the Northern temperate leafy liverwort genus *Scapania* (Scapaniaceae, Jungermanniales). *Molecular Phylogenetics and Evolution*, 62(3): 973–85.
- Huelsenbeck, J.P. & Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics*, 17(8): 754–5.
- Ignatov, M.S. & Hedenäs, L. 2007. Homologies of stem structures in pleurocarpous mosses, especially of pseudoparaphyllia and similar structures. In: A. Newton & R.S. Tangney, eds. *Pleurocarpous mosses systematics and evolution*. Systematics Association Special Volume 71. New York: CRC Press, pp. 269–86.
- Inoue, H. 1972. Studies on Formosan Hepaticae I. Introduction and Scapaniaceae. *Journal of Japanese Botany*, 20: 311–27.
- Ireland, R.R. 1971. Moss pseudoparaphyllia. *Bryologist*, 74: 312–30.
- Jia, Y. & He, S. 2013. *Species catalogue of China 1 (Plants): [i-vii]*. Beijing: Science Press. In Chinese.
- Magill, R.E. 1990. *Glossarium Polyglottum Bryologiae: a multilingual glossary for bryology*. Saint Louis: Missouri Botanical Garden.
- Majumdar, S., Singh, D.K., Potemkin, A.D. & Singh, D. 2016. Female plants and range extensions in *Scapania davidii* Potemkin (Scapaniaceae, Marchantiophyta). *Journal of Bryology*, 38(2): 103–9.
- Malcolm, B. & Malcolm, N. 2006. *Mosses and other bryophytes, an illustrated glossary*, edn. 2. Nelson, New Zealand: Micro-Optics Press.
- Mason-Gamer, R.J. & Kellogg, E.A. 1996. Testing for phylogenetic conflict among molecular data sets in the tribe Triticeae (Gramineae). *Systematic Biology*, 45(4): 524–45.
- Merced-Alejandro, A. & Jesús, S.D. 2009. A developmental sequence for paraphyses in *Neckeropsis* (Neckeraceae). *Bryologist*, 112(2): 342–53.
- Müller, K. 1905. Monographie der Lebermoosgattung *Scapania* Dum. *Nova Acta Academiae Caesareae Leopoldino-Carolinae Germanicae Naturae Curiosorum*, 83: 1–312.
- Müller, K. 2007. PRAP2: Parsimony and likelihood ratchet analyses with PAUP, v.0.9 [accessed 31 December 2010]. Available at: <http://systevol.nees.uni-bonn.de/software/PRAP2>
- Müller, K., Quandt, D., Müller, J. & Neinhuis, C. 2005. *PhyDE: Phylogenetic Data Editor*, ver. 0.9971, computer program [accessed 23 November 2010]. Available at: <http://www.phyde.de>
- Nixon, K.C. 1999. The Parsimony Ratchet, a new method for rapid parsimony analysis. *Cladistics*, 15(4): 407–14.
- Nylander, J.A.A. 2004. MrModeltest v.2. Computer program. Uppsala: Evolutionary Biology Centre, Uppsala University [accessed 2 November 2010]. Available at: <http://www.abc.se/~nylander/>
- Potemkin, A.D. 1998. On the origin, evolution and classification of the genus *Scapania* (Dum.) Dum. (Scapaniaceae, Hepaticae). *Journal of the Hattori Botanical Laboratory*, 85: 33–61.
- Potemkin, A.D. 1999a. An analysis of the practical taxonomy of some critical northern species of *Scapania* (Scapaniaceae, Hepaticae). *Bryologist*, 102(1): 32–8.
- Potemkin, A.D. 1999b. On the evolution and classification of *Scapania* (Hepaticae) — subgenus *Plicatilyx*. *Annales Botanici Fennici*, 36(2): 127–36.
- Potemkin, A.D. 2000. Bryophyte flora of Hunan Province, China. 2. *Scapania koponenii* sp. nova (Scapaniaceae, Hepaticae). *Annales Botanici Fennici*, 37(1): 41–4.
- Potemkin, A.D. 2001. Three new species of *Scapania* (Hepaticae) from India and China. *Annales Botanici Fennici*, 38(1): 83–9.
- Potemkin, A.D. 2002. Phylogenetic system and classification of the family Scapaniaceae Mig. *emend.* Potemkin (Hepaticae). *Annales Botanici Fennici*, 39(4): 309–34.
- Rambaut, A. & Drummond, A.J. 2009. Tracer v1.5 (online). <http://beast.bio.ed.ac.uk/Tracer>
- Schofield, W.B. & Hebert, C. 1984. The morphology and anatomy of the moss gametophyte. In: R.M. Schuster, ed. *New manual of bryology, vol. 2*. Nichinan: The Hattori Botanical Laboratory, pp. 627–57.
- Schuster, R.M. 1974. *The Hepaticae and Anthocerotae of North America. III*. New York: Columbia University Press, pp. 171–617.
- So, M.L. 2001. *Plagiochila* (Hepaticae, Plagiochilaceae) in China. *Systematic Botany Monographs*, 60: 1–214.
- Söderström, L., Hagborg, A., von Konrat, M., Bartholomew-Began, S., Bell, D., Briscoe, L., Brown, E., Cargill, D.C., Cooper, E.D., Costa, D.P., Crandall-Stotler, B.J., Dauphin, G., Engel, J.J., Feldberg, K., Glenny, D., Gradstein, S.R., He, X., Ilkui-Borges, A.L., Heinrichs, J., Hentschel, J., Katagiri, T., Konstantinova, N.A., Larrain, J., Long, D.G., Nebel, M., Pócs, T., Puche, F., Reiner-Drehwald, E., Renner, M.A.M., Sass-Gyarmati, A., Schäfer-Verwimp, A., Segarra Moragues, J.G., Stotler, R.E., Sukkharak, P., Thiers, B.M., Uribe, J., Váňa, J., Villareal, J.C., Wigginton, M., Zhang, L. & Zhu, R.-L. 2016. World checklist of hornworts and liverworts. *PhytoKeys*, 59(1): 1–828.
- Stamatakis, A. 2014. RAxML Version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics*, 30(9): 1312–3.
- Stöver, B.C. & Müller, K.F. 2010. TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinformatics*, 11: 7.
- Swofford, D.L. 2003. *PAUP*: Phylogenetic analysis using parsimony (*and other methods), version 4.0b10*. Sunderland: Sinauer Associates.
- Taberlet, P., Gielly, L., Patou, G. & Bouvet, J. 1991. Universal primers for amplification of three noncoding regions of chloroplast DNA. *Plant Molecular Biology*, 17(5): 1105–9.
- Váňa, J., Hentschel, J., Müller, J. & Heinrichs, J. 2012. Taxonomic novelties in *Scapania*. *PhytoKeys*, 10: 13–7.
- Vilnet, A.A., Konstantinova, N.A. & Troitsky, A.V. 2010. Molecular insight on phylogeny and systematics of Lophoziaaceae, Scapaniaceae, Gymnomitriaceae and Jungermanniaceae. *Arctoa*, 19(1): 31–50.
- Warnstorf, C. 1904–1906. *Kryptogamenflora der Mark Brandenburg und angrenzender Gebiete. Laubmoose*, Zweiter Band. Leipzig: Verlag von Gebrüder Borntraeger.
- Zhu, R.-L., Wang, D., Xu, L., Shi, R.-P., Wang, J. & Zheng, M. 2006. Antibacterial activity in extracts of some bryophytes from China and Mongolia. *Journal of the Hattori Botanical Laboratory*, 100: 603–15.
- Zuo, B.-R., Cao, T., Gao, C. & Sun, J. 2007. *Scapania paraphyllia* T. Cao, C. Gao, J. Sun & B.R. Zuo, a new species of Hepaticae (Scapaniaceae) from Zhejiang, China. *Acta Phytotaxonomica Sinica*, 45(3): 311–4.

Appendix 1

Voucher information and GenBank accession numbers for the taxa used for this study. Sequences newly generated are in bold. A long dash indicates missing sequences.

Taxon	Locality and voucher	GenBank accession number		
		nrITS	trnL-F	atpB-rbcL
<i>Scapania aequiloba</i> (Schwagr.) Dumort.	Germany, Thuringia, Grosburschla, <i>Marstaller 2-7-2001</i> (JE)	JN631360	JN631498	JN631629
<i>Scapania curta</i> (Mart.) Dumort.	Germany, Saxony-Anhalt, Breitenbach, <i>Hentschel Bryo 3174</i> (GOET)	JN631404	JN631542	JN631671
<i>Scapania americana</i> Mull.Frib.	U.S.A., Oregon, Douglas Co., <i>Shevock 26373</i> (GOET)	JN631367	JN631505	JN631636
<i>Scapania americana</i>	U.S.A., California, San Mateo Co., <i>Shevock 27851</i> (GOET)	JN631365	JN631503	JN631634
<i>Scapania americana</i>	U.S.A., California, San Mateo Co., <i>Shevock 27855</i> (GOET)	JN631366	JN631504	JN631635
<i>Scapania ciliata</i> Sande Lac.	Nepal, Kangchenjunga, Sikdim — Chauki, <i>Long 17560</i> (JE)	JN631393	JN631530	JN631661
<i>Scapania ciliata</i>	China, Guizhou, Yuao, <i>Peng 20100518-13</i> (HSNU)	JN631391	JN631528	JN631659
<i>Scapania ciliata</i>	China, Guangxi, Laibin, <i>Ye & Wei 20090719-10</i> (HSNU)	JN631390	JN631527	JN631658
<i>Scapania compacta</i> (Roth) Dumort.	Germany, Saxony Anhalt, Treseburg-Thale, <i>Eckstein 1409</i> (GOET)	JN631398	JN631534	JN631663
<i>Scapania compacta</i>	Spain, La Palma, Cubo de Galga, <i>Huneck JE-H3294</i> (JE)	JN631399	JN631537	JN631666
<i>Scapania compacta</i>	United Kingdom, Argyll, Glencoe, <i>Long & Murray 11492</i> (JE)	JN631400	JN631538	JN631667
<i>Scapania griffithii</i> Schiffn.	China, Fujian, Dehua Co., <i>Zhu et al. 20100403-21</i> (HSNU)	JN631419	JN631557	JN631684
<i>Scapania griffithii</i>	China, Fujian, Dehua Co., <i>Zhu et al. 20100403-25</i> (HSNU)	JN631420	JN631558	JN631685
<i>Scapania javanica</i> Gottsche	Indonesia, Central Sulawesi, Mt. Rorekatimbu, <i>Gradstein 12046</i> (GOET)	JN631435	JN631571	JN631697
<i>Scapania javanica</i>	Indonesia, Sumatra, Berastagi, <i>Schafer-Verwimp & Verwimp 24861</i> (GOET)	JN631436	JN631572	JN631698
<i>Scapania kaurinii</i> Ryan	Russia, Chita Prov., <i>Bakalin 11-1-00</i> (KPABG)	EU791759	EU791650	—
<i>Scapania koponenii</i> Potemkin	China, Zhejiang, Suichang Co., <i>Zhu et al. 20090630-22</i> (HSNU)	JN631438	JN631574	JN631700
<i>Scapania koponenii</i>	China, Zhejiang, Suichang Co., <i>Zhu et al. 20090630-48</i> (HSNU)	JN631437	JN631573	JN631699
<i>Scapania koponenii</i>	China, Fujian I, Wuyishan Co., <i>Zhang et al. 20150830-178A</i> (HSNU)	KY311839	KY311849	KY311860
<i>Scapania koponenii</i>	China, Fujian II, Wuyishan Co., <i>Zhang et al. 20150830-145</i> (HSNU)	KY311840	KY311850	KY311861
<i>Scapania koponenii</i>	China, Fujian III, Wuyishan Co., <i>Zhang et al. 20150831-107</i> (HSNU)	KY311841	KY311851	KY311862
<i>Scapania koponenii</i>	China, Jiangxi I, Yanshan Co., <i>Zhang 20150804-76</i> (HSNU)	KY311842	KY311852	KY311863
<i>Scapania koponenii</i>	China, Jiangxi II, Jinggangshan Co., <i>Wang 20141015-13</i> (HSNU)	KY311843	KY311853	KY311864
<i>Scapania koponenii</i>	China, Jiangxi III, Zixi Co., <i>Zhang 20150727-52</i> (HSNU)	KY311844	KY311854	KY311865
<i>Scapania koponenii</i>	China, Guangxi, Xingan Co., <i>Wei et al. 20150710-3</i> (HSNU)	—	KY311855	KY311866
<i>Scapania lepida</i> Mitt.	Sri Lanka, Central Prov., Nuwara Eliya, <i>Eggers SL 5,01</i> (JE)	JN631439	JN631575	—
<i>Scapania ligulata</i> Steph.	North Korea, Kumgangsán, Manmulsang, <i>Huneck KDVR 88-36</i> (JE)	JN631443	JN631579	JN631704
<i>Scapania ligulata</i>	Nepal, Kangchenjunga, Nesum-Buje Daurali, <i>Long 17499</i> (JE)	JN631442	JN631578	JN631703
<i>Scapania ligulata</i>	China, Guangxi, Maozhou, <i>Wei 20090705124</i> (HSNU)	JN631440	JN631576	JN631701
<i>Scapania ligulata</i>	China, Fujian, Dehua Co., <i>Zhu et al. 20100406-1B</i> (HSNU)	JN631441	JN631577	JN631702
<i>Scapania ligulata</i>	China, Jiangxi, Yanshan Co., <i>Zhang 20150803-120A</i> (HSNU)	KY311845	KY311856	KY311867
<i>Scapania paraphyllia</i> T.Cao, C.Gao, J.Sun & B.R.Zuo	China, Jiangxi, Yanshan Co., <i>Zhang 20150803-137</i> (HSNU)	KY311846	KY311857	KY311868
<i>Scapania paraphyllia</i>	China, Fujian, Wuyishan Co., <i>Zhang et al. 20150830-178</i> (HSNU)	KY311847	KY311858	KY311869
<i>Scapania sphaerifera</i> H.Buch & Tuom.	Russia, Siberia, Buryatiya Rep., <i>Konstantinova 92-2-01</i> (KPABG)	EU791765	EU791656	—
<i>Scapania sphaerifera</i>	Russia, Siberia, Buryatiya Rep., <i>Konstantinova, Hep. Ross. Exs. 20</i> (JE)	JN631471	JN631605	JN631730
<i>Scapania spitsbergensis</i> (Lindb.) Mull.Frib.	Norway, Spitsbergen, <i>Konstantinova 90-2-06</i> (KPABG)	EU791761	EU791752	—
<i>Scapania verrucosa</i> Heeg	Russia, Caucasus, Karachayev-Cherkessian Rep., <i>Konstantinova 609/6-05</i> (KPABG)	EU791763	EU791654	—
<i>Scapania verrucosa</i>	China, Xizang, Linzhi Pre., <i>Wang et al. 20140826-21</i> (HSNU)	KY311848	KY311859	KY311870