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Morphological variations of *Macromitrium sulcatum* (Hook.) Brid. (Musci: Orthotrichaceae), with its four new synonyms supported by molecular data

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ABSTRACT
Macromitrium sulcatum (Hook.) Brid. is widely distributed in sub-Saharan Africa, South Asia, Indochina, Southeast Asia and Yunnan province of China. Our examination of its type and ordinary specimens showed that the species highly varied in the outline, basal cells, apical cells and upper margins of its branch leaves. On the phylogenetic tree based on *trn*L-F, *trn*G and ITS2, seventeen samples formed a strongly supported clade, which were morphologically associated with the types of *M. sulcatum* and its previous synonyms including *M. seriatum* Paris & Broth., *M. ceylanicum* Mitt., *M. belangeri* Müll. Hal. and *M. bequaertii* Thér. & Naveau, as well as those of *M. lorifolium* Paris & Broth., *M. muellerianum* Mitt., *M. pseudoramentosum* Herzog and *M. turgidum* Dixon. In this study, we compared the types and ordinary specimens of these species and found that the variations of the later four species fall within the morphological variation range of *M. sulcatum*. Therefore, we treated them as new synonyms of *M. sulcatum*.

KEY WORDS
Bryophyte,
Macromitrioideae,
morphological variations,
phylogeny.

RÉSUMÉ
Variations morphologiques de Macromitrium sulcatum *(Hook.) Brid. (Musci : Orthotrichaceae), avec quatre nouveaux synonymes étayés par des données moléculaires.*
Macromitrium sulcatum (Hook.) Brid. est largement répandu en Afrique subsaharienne, en Asie du Sud, en Indochine, en Asie du Sud-Est et dans la province du Yunnan en Chine. L'examen du spécimen type et des spécimens ordinaires a montré que l'espèce variait fortement dans le contour, les cellules basales, les cellules apicales et les marges supérieures de ses feuilles de branche. Sur l'arbre phylogénétique basé sur *trn*L-F, *trn*G et ITS2, dix-sept échantillons formaient un clade fortement soutenu, qui était morphologiquement associé aux types de *M. sulcatum* et à ses synonymes précédents, y compris *M. seriatum* Paris & Broth., *M. ceylanicum* Mitt., *M. belangeri* Müll. Hal. et *M. bequaertii* Thér. & Naveau, ainsi que ceux de *M. lorifolium* Paris & Broth., *M. muellerianum* Mitt., *M. pseudoramentosum* Herzog et *M. turgidum* Dixon. Dans cette étude, nous avons comparé les types et les spécimens ordinaires de ces espèces et nous avons trouvé que les variations des quatre dernières espèces se situent dans la gamme de variation morphologique de *M. sulcatum*. Par conséquent, nous les avons traitées comme de nouveaux synonymes de *M. sulcatum*.

MOTS CLÉS
Bryophyte,
Macromitrioideae,
variations
morphologiques,
phylogénie.

INTRODUCTION

Macromitrium Brid. (Musci: Orthotrichaceae), a pantropical genus with more than 300 species (Crosby *et al.* 1999; Allen 2002; Frey & Stech 2009; Brinda & Atwood 2024), is one of the largest moss genera in the world. Despite the large number of species in the genus, most are regional species confined to a single continent. Among the few transcontinental species of the genus is *Macromitrium sulcatum* (Hook.) Brid.

Based on the collection of Gardner from Nepal, Hooker (1820) first described *Schlotheimia sulcata* Hook. in his "*Musci Exotici* 2". In his original descriptions, Hooker briefly described the species as "Caule repente, ramis erectis brevibus, foliis lineari-lanceolatis acuminatis undulatis (siccitate crispis), seta longa, capsula ovata profunde sulcata" (stems creeping, with short erect branches, leaves linear-lanceolate, acuminate and undulate, crisped when dry, setae long, capsules ovate, deeply furrowed). Four years later Hooker & Greville (1824) transferred the species into the genus *Orthotrichum* Hedw. Finally Bridel (1826) placed the species in *Macromitrium.* Bartram (1939), Gangulee (1976), Eddy (1996), Wilbraham (2008) and Yu *et al.* (2018) described and illustrated the species in detail.

Since its inception, *M. sulcatum* has been recorded from various regions in Asia, including Borneo (Suleiman *et al.* 2006), India (Mitten 1859; Gangulee 1976), Kampuchea (Tixier 1979), Myanmar (Mitten 1856, 1883; Bartram 1943;Tixier 1973), Sri Lanka (O'Shea 2002), Thailand (Noguchi 1960; Horikawa & Ando 1964; Tixier & Smitinand 1966; Tixier 1971), The Philippines (Bartram 1939), Vietnam (Pócs 1965) and Malesia (Eddy 1996). It is also the most commonly encountered species of the genus *Macromitrium* in sub-Saharan Africa (O'Shea 2006; Wilbraham 2008, 2015) and Réunion (Ellis & Wilbraham 2008).

Macromitrium sulcatum could be identified by its robust habit, tuberculate basal cells and smooth upper cells of branch leaves and furrowed capsules with double peristome. The species has been reported as highly variable in morphology (Eddy 1996; Wilbraham 2015), particularly in branch leaves in their outline and apices, basal cells and margins near the apex (Ellis & Wilbraham 2008). Owning to the continuous variability of *M. sulcatum*, five nominal species, including *M. ceylanicum* Mitt., *M. leptocarpum* Broth., *M. neelgheriense* Müll. Hal., *M. ramentosum* Thwaites & Mitt. and *M. torulosum* Mitt., were placed under the species as variety or subspecies (Müller 1870; Fleischer 1902-1904; Tixier 1975; Yu *et al.* 2018), and twenty-three species names have been synonymized with the species (including ten invalid or illegitimate names) (Gangulee 1976; O'Shea 2006; Wilbraham 2016). However, the extent and pattern of morphological variations for *M. sulcatum* have not been visually displayed so far. With our continuing taxonomic study of the genus *Macromitrium* in the world, we have examined the types of *M. sulcatum* and its eight synonyms (*M. belangeri*, *M. bequaertii*, *M. eckendorffii*, *M. perundulatum*, *M. pseudoramentosum*, *M. ramentosum*, *M. seriatum* Paris & Brotherus and *M. trollii*), as well as numerous other type and ordinary specimens comparable to *M. sulcatum.* Therefore, we are able to reassess morphological variations of the species within the types of these synonyms. Based on our understanding of the morphological variations of *M. sulcatum*, we propose that *M. lorifolium* Paris & Broth.*, M. muellerianum* Mitt.*, M. pseudoramentosum* Herzog and *M. turgidum* Dixon are conspecific with *M. sulcatum*. The objective of the present work is to provide molecular and morphological evidence supporting the reduction of these four nominal species to synonyms with *M. sulcatum*.

MATERIAL AND METHODS

Morphological examination of specimens

Type specimens of *M. belangeri*, *M. bequaertii*, *M. ceylanicum*, *M. eckendorffii*, *M. lorifolium*, *M. muellerianum*, *M. perundulatum*, *M. pseudoramentosum*, *M. ramentosum*, *M. seriatum*, *M. sulcatum*, *M. trollii* and *M. turgidum* were requested on loan from BM, E, FH, H-BR, JE, NY, PC and S, and 33 ordinary specimens assigned with *M. sulcatum* (including its variety and subspecies, *M. sulcatum* subsp. *ramentosum* (Thwaites & Mitt.) M. Fleisch., *M. sulcatum* var. *leptocarpum* (Broth.) J.Yu, D.D.Li, Y.Li & S.L.Guo and *M. sulcatum* var. *torulosum* (Mitt.) Tixier were from BM, MO, and H-BR.

Microscopic examinations were taken with an Olympus-BX53 light microscope, while microphotographs were obtained with a DP74 camera (Olympus) mounted on the microscope. Descriptions and illustrations of upper, medial and basal leaf cells were based on leaves from the middle of the stems and branches.

Molecular protocols and phylogenetic tree construction

Forty-one samples were used for molecular analyses, representing *M. sulcatum, M. turgidum, M. lorifolium*, *M. japonicum* Dozy & Molk*, M. cavaleriei* Cardot & Thér., *M. microstomum* (Hook. & Grev.) Schwägr., *M. gymnostomum* Sull. & Lesq.*,* as well as specimens exhibiting morphological characteristics closely aligning with the type specimens of *M. muellerianum, M. pseudoramentosum* and *M. ceylanicum. Groutiella tomentosa* (Hornsch.) Wijk & Margad.*, Macrocoma tenuis* subsp. *sullivantii* (Müll. Hal.) Vitt and *Schlotheimia grevilleana* Mitt. were used as outgroups. Taxa for the analyses and their voucher specimens are listed in Appendix 1.

The nuclear ribosomal internal transcribed spacer region 5.8S-ITS2-26S (hereafter, ITS2), the tRNA (Gly) (UCC) (*trn*G), and the *trn*L-*trn*F intergenic spacer (*trn*L-F) have been widely used in phylogenetic analyses for mosses (Draper & Hedenäs 2009; Hedenäs 2012), and were therefore selected to construct a phylogenetic tree with the above taxa.

The DNA extraction method, PCR amplifications and primers for the three regions followed Li *et al.* (2018). Phylogenetic analysis of three molecular datasets were carried out using Bayesian Inferences (BI) and Maximum Likehood (ML). BI analysis followed the methods described in Li *et al.* (2018). ML analysis was performed using RAxML v.8.2.10 (Stamatakis 2014) with 1000 bootstrap replicates, employing

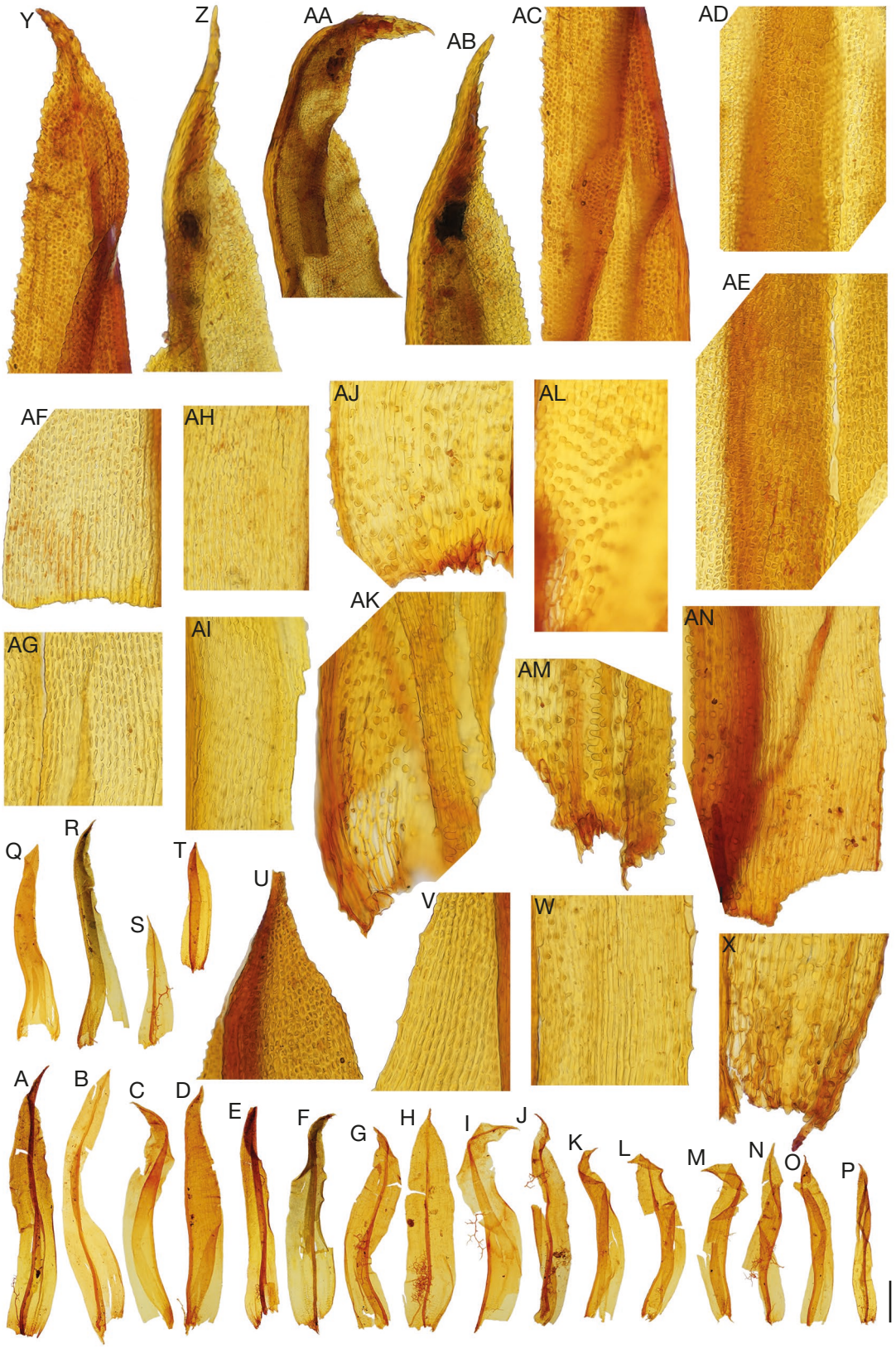

Fig. 1. — *Macromitrium sulcatum* (Hook.) Brid.: **A**-**R**, branch leaves; **S**, stem leaf; **T**, perichaetial leaf; **U**, apical cells of perichaetial lea; **V**, upper cells of perichaetial leaf; **W**, low cells of perichaetial leaf; **X**, basal cells of perichaetial leaf; **Y**-**AB**, apical cells of branch leaves; **AC**-**AE**, upper cells of branch leaves; **AF**, **AG**, medial cells of branch leaves; **AH**, **AI**, low cells of branch leaves; **AJ**-**AN**, basal cells of branch leaves (all from holotype, FH00290392). Scale bar: A-T, 500 µm; U-AN, 50 µm.

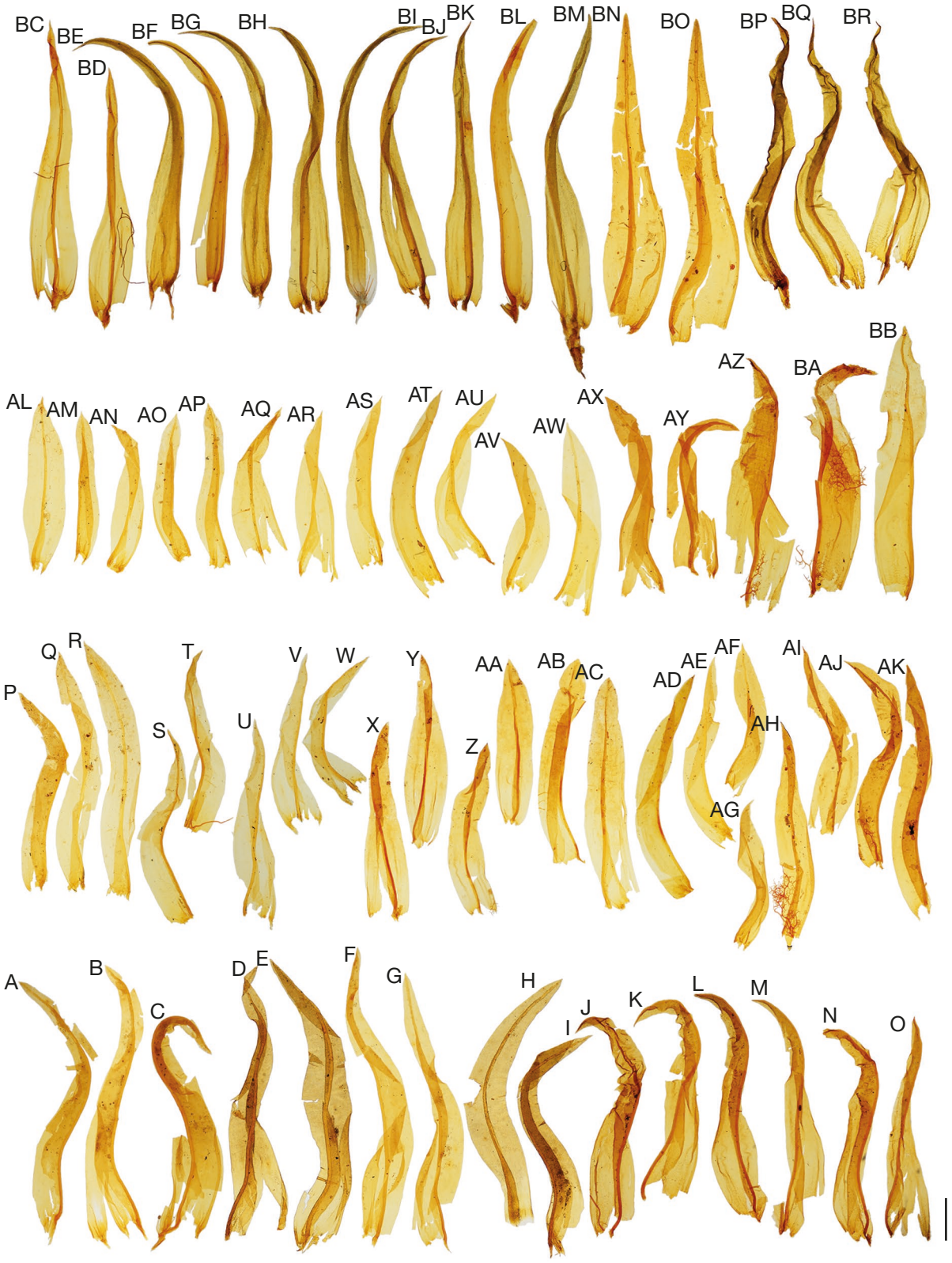

Fig. 2. — Branch leaves in the types of *Macromitrium sulcatum* (Hook.) Brid. and its synonyms: **A**-**C**, from isotype of *M. belangeri* Müll.Hal., S-B162961; **D**-**I**, from *M. belangeri*, PC0721946; **J**-**O**, from *M. nilghiriense* Müll.Hal., H-BR2630003; **P**-**U**, from holotype of *M. bequaertii* Thér. & Naveau, PC0098353; **V**, **W**, from syntype of *M. bequaertii*, JE04006256; **X**-**AD**, from holotype of *M. eckendorffii* Thér. & P.de la Varde, PC0105918; **AE**-**AK**, from isotype of *M. seriatum* Paris & Broth., PC0137555; **AL**-**AQ**, from isotype of *M. seriatum*, PC0106736; **AR**-**AW**, holotype of *M. seriatum*, PC0106738; **AX**-**BB**, isotype of *M. sulcatum*, FH00290392; **BC**-**BM**, from holotype of *M. ceylanicum* Mitt., NY00518287; **BN**, **BO**, from isotype of *M. trollii* Dixon, JE04008697; **BP**-**BR**, from holotype of *M. perundulatum* Broth., H-BR2626001. Scale bar: 500 µm.

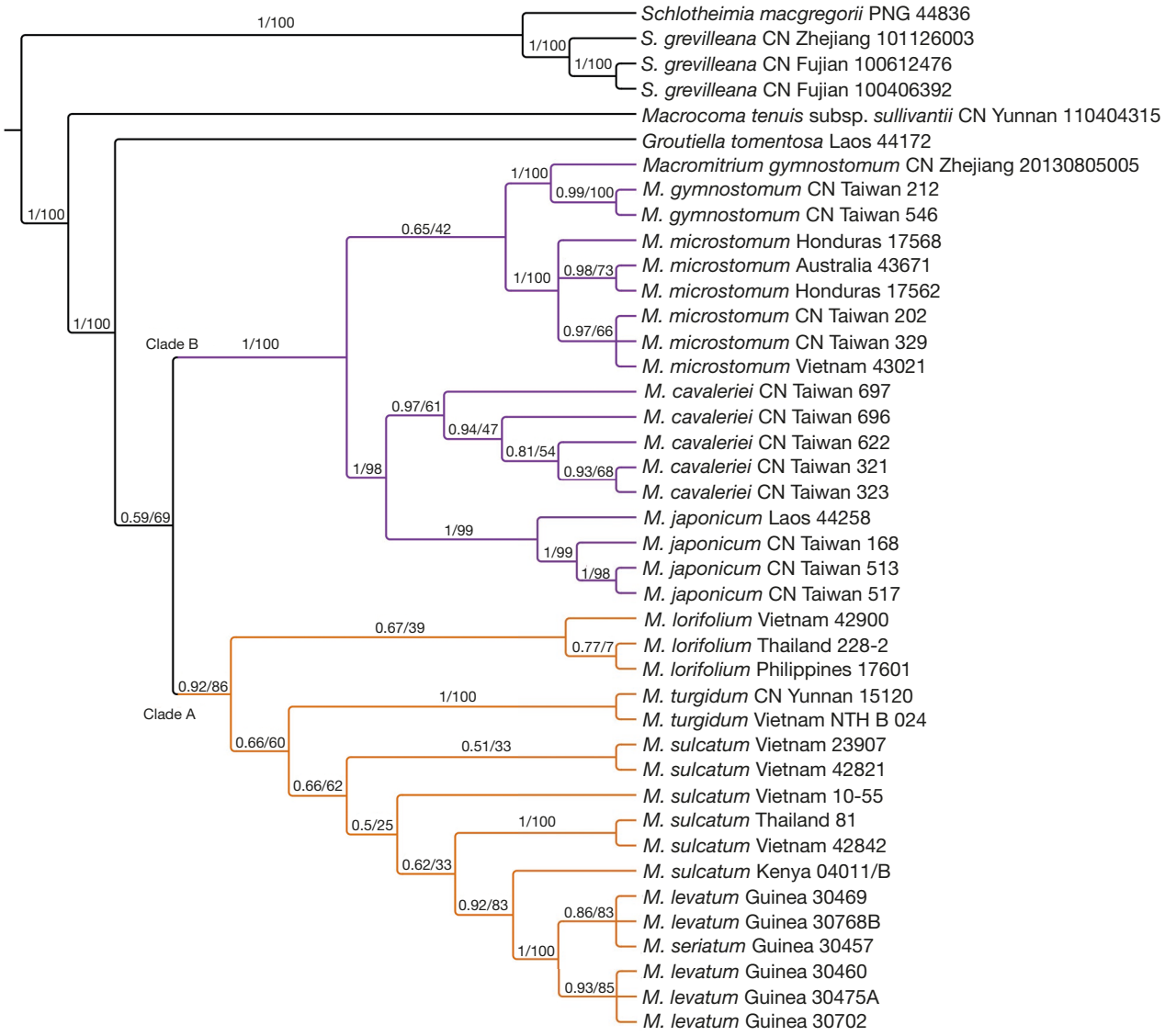

Fig. 3. — Phylogenetic tree with Bayesian posterior probabilities (PPBI) and maximum parsimony bootstrap (BSML) on the branch, inferred from the combined datasets of *trn*L-F, *trn*G and ITS2.

a GTR + G model of nucleotide substitution for each partition. Trees were visualized and annotated in TreeGraph 2.0 (Stöver & Müller 2010).

RESULTS

Morphological characteristics in the types of *M. sulcatum* and its previous synonyms

The isotype of *M. sulcatum* (FH, marked with "Nepal, *Gardner s.n.* original, type") is characterized by the following features: 1) plants medium-sized; stems long creeping, with short and erect branches; 2) branch leaves spirally, often individually contorted and twisted when dry, erect to flexuose-spreading when moist, oblong-lanceolate or ligulate-lanceolate with an acute or acuminate-acute apex, margins denticulate near the apex and entire below, slightly rugose above; costae single, ending a few cells below apex; upper cells small, subquadrate, quadrate or quadrate-rotund, smooth, sometimes incrassate, flat to slightly bulging; medial cells slightly elongate, subquadrate, short-rectangular, smooth, in longitudinal rows, gradually becoming elongate farther down; basal cells near costae rectangular to irregularly rectangular, thin-walled, smooth and pellucid, obviously larger than their ambient cells, appearing as a "cancellina region", others elongate, rectangular to sublinear, strongly thick-walled and porose, moderately tuberculate; outmost marginal cells at or near leaf insertion slightly differentiated, enlarged and hyaline, forming a more or less distinct border; 3) perichaetial leaves differentiated, shorter than branch leaves, oblong-ligulate to broadly oblong, often plicate in basal part, broadly acute at apex, with percurrent to excurrent costa; 4) setae 5.0-17 mm long, smooth, twisted to left; 5) capsule urns ovoid to ellipsoid, narrowed at mouth, strongly furrowed when dry; peristome consists of a

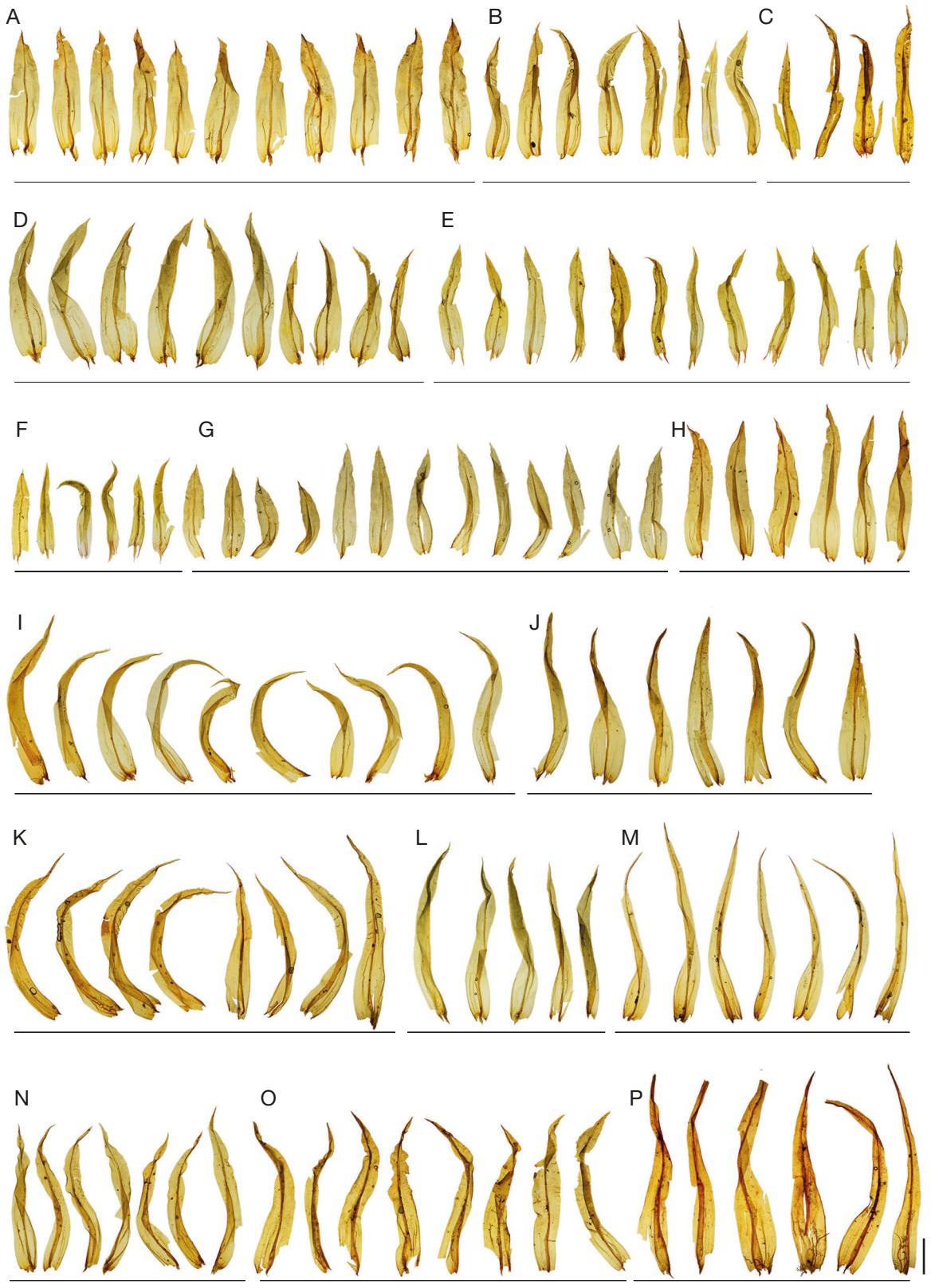

FIG. 4. — Branch leaves of *Macromitrium sulcatum* (Hook.) Brid.: **A**, *M. sulcatum* Thailand 81; **B**, *M. levatum* Mitt. Guinea 30768B; **C**, *M. levatum* Guinea 30475A; **D**, *M. levatum* Guinea 30469; **E**, *M. levatum* Guinea 30460; **F**, *M. seriatum* Paris & Broth. Guinea 30457; **G**, *M. levatum* Guinea 30702; **H**, *M. lorifolium* Paris & Broth. Philippines 17601; **I**, *M. sulcatum* Vietnam 23907; **J**, *M. sulcatum* Kenya 04011/B; **K**, *M. sulcatum* Vietnam 42842; **L**, *M. sulcatum* Vietnam 10-55; **M**, *M. lorifolium* Vietnam 42900; **N**, *M. sulcatum* Vietnam 42821; **O**, *M. turgidum* Dixon CN Yunnan 15120; **P**, *M. turgidum* Vietnam NTH B 024. Scale bar: 100 µm.

Fig. 5. — *Macromitrium lorifolium* Paris & Broth.: **A**-**J**, branch leaves; **K**, **L**, apical cells of branch leaves; **M**, upper cells of branch leaf; **N**, **O**, medial cells of branch leaves; **P**, low cells of branch leaf; **Q**, **R**, basal cells of branch leaves (all from lectotype, H-BR2630007). Scale bars: A-J, 500 µm; K-R, 50 µm.

low double membrane, exostome yellowish, densely papillose, endostome hyaline; operculum erect, conic-rostrate; spores anisosporous; and 6) calyptra mitrate, large and naked, deeply lacerate (Fig. 1).

Having examined the types of *M. sulcatum* and its partial synonyms, we found continuous variations of its branch leaves in: 1) the shape from ligulate, ligulate-lanceolate, or oblong-lanceolate, lanceolate to narrowly lanceolate (Fig. 2); 2) upper

margins from entire to serrate or denticulate; 3) basal laminal cells weakly tuberculate to strongly tuberculate; 4) upper laminal cells in radiating diagonal rows from the costa in broad ligultae to ligulate-lanceolate leavesor in longitudinal rows in narrow lanceolate leaves; and 5) the outmost marginal cells at the insertion not much different from their ambient cellsor enlarged and hyaline forming a differentiated border. Continuous variations also existed in its perichaegial leaves, from oblong-ligulate to broadly oblong (shorter than branch leaves), to oblong-lanceolate, narrowly acuminate to long acuminate or aristate (slightly longer than branch leaves).

Morphological and phylogenetic evidence for the four new synonyms of *M. sulcatum*

After deletion of incomplete regions for some samples at the beginning and ends of the alignment, the total number of aligned sites from the three genes was 1913. Among them, 580 sites were variable characters and 437 were parsimony-informative. The numbers of sites in each locus based on sequence length, parsimony variable sites, parsimony informative sites, and the optimal substitution models, which were selected for Bayesian analysis, are presented in Appendix 2. The topologies of the ML and BI trees were largely congruent. Consequently, the subsequent discussion of phylogenetic relationships is based on the BI tree, with nodes annotated by positerior probabilities (PP) from BI analysis and bootstrap values (BS) from ML analysis (Fig. 3).

In the phylogenetic tree (Fig. 3) based on the combination of ITS2, *trn*G and *trn*L-F, seventeen samples, which were morphologically associated with the types of *M. sulcatum, M. seriatum, M. lorifolium, M. turgidum, M. ceylanicum, M. mullerianum, M. pseudoramentosum, M. belangeri* and *M. bequaertii*, formed a strongly supported clade (PPBI = 0.92, BSML = 86, Clade A). Four species including *M. gymnostomum*, *M. microstomum*, *M. cavaleriei* and *M. japonicum* could be identified in the phylogeny, all with relatively high posterior probabilities and then formed a strongly supported Clade B (PPBI = 1, BSML = 100). Clade A is sister to Clade B, the former differing from the latter by their furrowed capsules with double peristomes and tuberculate basal cells of branch leaves.

Within the seventeen samples of Clade A, variations existed in outline and apices (Figs 3; 4) as well as upper margins, and laminal cells of branch leaves. The branch leaves are often oblong- to lingulate-lanceolate with acute to cuspidate-acute apices (Guinea 30702, 30457, 30460, 30469, and 30768B, Thailand 81 and Philippines 17601), but some are lanceolate to narrow lanceolate with acuminate apices (Kenya 04011/B, Vietnam NTH B 024, 23907, 10-55, 42842, 42900). The upper margins are almost entire in narrow lanceolate branch leaves to denticulate to varying degrees in broad oblong – to lingulate-lanceolate branch leaves. The upper and medium cells were often in radiating diagonal rows from the costa in broad branch leaves, but in longitudinal rows in narrow leaves. However, these variations are continuous among the specimens in Clade A, and fall within the range of *M. sulcatum* and its synonyms (Figs 1; 2). The seventeen samples of Clade A were characterized by the combination of the following features: 1) plants medium-sized to robust in dense mats; 2) branch leaves broad to narrowly lanceolate, partially ligulate– to oblong-lanceolate, upper and medial cells isodiametric, smooth, flat to slightly bulging; basal cells near costae thin-walled, smooth and pellucid, distinctly larger than their ambient cells, forming a "cancellina" region, others elongate, rectangular to sublinear, thick-walled and porose, tuberculate to various degrees; and 3) perichaetial leaves often shorter than branch leaves, oblong-ligulate to broadly oblong; 4) setae 5-18 mm long, smooth, twisted to the left; 5) capsule urns ovoid to ellipsoid, furrowed when dry; peristome consists of a low double membrane, exostome yellowish, densely papillose, endostome hyaline; and 6) calyptra mitrate large and naked, deeply lacerate. These features align with those described of *M. sulcatum* by Wilbraham (2008, 2015) and Yu *et al.* (2018), as illustrated in Figures 1 and 2. Therefore, these seventeen specimens in Clade A (Fig. 3) belong to *M. sulcatum* unquestionably.

The type specimens of *M. lorifolium* (Fig. 5) and *M. muellerianum* (Fig. 6) exhibits morphological similarities to the six specimens in Clade A (Figs 3; 4), as well as to the types of partial synonyms of *M. sulcatum*, including *M. belangeri*, *M. seriatum*, *M. perundulatum* and *M. trollii* (Fig. 2). The primary distiction is that the type specimens of *M. lorifolium* exhibit varying degrees of leaf undulation when moist. Therefore, we treated *M. lorifolium* as a synonym of *M. sulcatum*.

The types and their original descriptions of *M. pseudoramentosum* Herzog (Fig. 7) and *M. turgidum* Dixon (Fig. 8) are similar to those of *M. sulcatum* (Fig. 1) and its synomyns such as *M. belangeri*, *M. bequaertii*, *M. eckendorffii* and *M. seriatum* (Fig. 2), and also similar to some specimens in Clade A of the phylogenetic tree (such as Philippines 17601, Thailand 81, Guinea 30469, 30768B, 30457, 20460, 30457A, and 30702) (Figs 3; 4).

Considering the morphological variations of *M. sulcatum* (Fig. 1) and its synonyms (Fig. 2), and those of the seventeen specimens in Clade A of the phylogenetic tree (Figs 3; 4), we placed *M. muellerianum* Mitt., *M. lorifolium* Paris & Broth., *M. pseudoramentosum* Herzog and *M. turgidum* Dixon in synonymy with *M. sulcatum* (Hook.) Brid.

Taxonomical treatment

Family Orthotrichaceae Arn.
Gender *Macromitrium* Brid.

Macromitrium sulcatum (Hook.) Brid.

Bryologia Universa 1: 319. (Bridel 1826).

Schlotheimia sulcata Hook., *Musci Exotici* 2: 156 (Hooker 1820). Type protologue and citation: Nepal, *D. Gardner* (isotype: FH!).

Macromitrium lorifolium Paris & Broth., *Revue Bryologique* 34: 30. (Paris 1907). syn. nov. Type protologue: [Vietnam] no detail type information, but the introduction of the original paper included "Annam, Langbian, *Pinus* et *Dipterocarpus*, Par. M. le *Dr. Eberhardt*". Type citation: Annam, Langbian, *Pinus* et *Dipterocarpus*,

Fig. 6. — *Macromitrium muellerianum* Mitt.: **A**-**H**, branch leaves; **I**-**K**, apices of branch leaves; **L**-**M**, apical cells of branch leaves; **N**, upper cells of branch leaf; **O**, medial cells of branch leaf; **P**, low cells of branch leaf; **Q**-**R**, basal cells of branch leaves (all from isotype, JE04006257). Scale bar: A-H, 500 µm; I-K, 100 µm; L-Q, 50 µm; R, 20 µm.

leg. *Eberhardt, no. 433*, 1906 (with a mark: "*sp n.*!") (lectotype designated here: H-BR 2630007!; isolectotype: H-BR 263006!).

Macromitrium muellerianum Mitt., J. Proc. *Journal of the Proceedings of the Linnean Society, Botany*, Suppl. 1: 51. (Mitten 1859). syn. nov. Type protologue: no detail information about the type specimen but with information "all the specimens were collected by Missionar Bernhard Schmid from Neilgherri (Nilgiri) Mountains, India" in the introduction of the original publication. Type citation: Mont. Neelgherrenses, *Bernhard Schmidt s. n.,* as *Macromitrium uncinatum* C. Müll. (lectotype designated here: JE04006257!); Nilghiries, marked as *Macromitrium uncinatum* (isotype: E00625564!).

Macromitrium pseudoramentosum Herzog, *Hedwigia* 66: 346. (Herzog 1926). syn. nov. Type protologue: Ceylon: Auf Erde am Fuß Bäume im Urwald des Pidurutalagala, *c*. 2100 m, Nr. 147, und auf Erde am Grund der Baumstämme in einer Schlucht bei Hakgala, *c*. 1300 m, 151. Type citation: Ceylon: Auf Erde am Urwald des Pidurutalagala, *c*. 2100 m, Januar, 06, leg. *Th. Herzog Nr. 147* (lectotype designated here: JE04008742!); Auf Erde am Grund des Baumstämme in einer Schlucht bei Hakgala, *c*. 1300 m, Febuar. 06. *Th. Herzog Nr. 151.* (syntype: JE04008741!); Ceylon, Schlucht bei Hakgala, *c*. 1300 m, leg *Th. Herzog* (isosyntype: BM000982502!).

Macromitrium turgidum Dix., *Journal of the Siam Society, Natural History Supplement* 9: 22 (Dixon 1932). syn. nov. Type protologue and citation: [Thailand] *Chantaburi*. Krāt, Kao Kūap, on tree in evergreen forest, *c*. 700 m. alt., 27 Dec., 1929, Coll. *A. F. G. Kerr* (*438*), type (holotype: BM000825435!). Rāchaburī, Prachūap, Kao Lūang, on tree in open evergreen forest, 5 July, 1926, coll. *A. F. G. Kerr* (*151*) (paratype: BM000825434!).

ADDITIONAL SPECIMENS EXAMINED

Macromitrium blumei Nees ex Schwaegrichen

OTHER MATERIAL EXAMINED. — **Indonesia** • Java, Blume; Legit, misit Al. Braun ad Muellerum; Herb. Muell., comm. Schliephacke; (isotype: H-BR 2600011) • Java; *Wichma,* 2442 (H-BR 2604015). **Papua New Guinea** • Morobe; *D. H. Norris 65019* (MO4435585, H 3195800); *D.H. Norris 65393* (H 3195926); *Timo Koponen 34524* (KRAM-B-114324) • West Sepik; *A. Touw. 18543* (MO5371039). **Philippines** • Mindanao; *E. J. Reynoso, 2123b* (MO4417625). **Malaysia** • Sarawak, the Division, Gunong Mulu National park; *A. Touw 21038* (MO6362356).

Macromitrium sulcatum var. ***sulcatum*** (Hook.) Brid.

OTHER MATERIAL EXAMINED. — **China** • Xizang; *Y. G. Su 4833* (MO3676218, as *M. turgidum*); *Y. G. Su 4641* (MO3676361, as *M. turgidum*).
India • Madras; *G. Foreau s. n.* (MO2559233); *W. Griffith 153* (MO1950193) • Karnataka; *M. E. Hale 48103* (MO2569147); *50708* (MO2560513); *50540* (MO2560509) • Kerala; *M. E. Hale 47633* (MO2489245) • Tamil Nadu; *M. E. Hale 47652* (MO2489241); *M. Fleischer B 3162* (MO3080548, MO5222675, MO3080510); *B 3161* (MO3080549); *B 3160* (MO5222664); *E. Hegewald 4594* (MO5229001); *C. C. Townsend 73/569* (MO5628441); *73/572* (MO5628440) • Nilghiri; *Perrettet 16* (H-BR 2647025).
Sri Lanka • *H. Wright 3817* (H-BR 2647022); *W. Meijer 1799* (MO5361179); *W. Meijer 1936* (MO5361161) • Central Province, *Schäfer-Verwimp* & *Verwimp*, *C372* (MO5367894); *C269* (MO5367817); *Gerrit Davidse 8292* (MO2411379) • Midlands; *C. Ruinard* & *A. H. M. Jayasuriya 10/144b* (MO2859658) • Hakgala Gardens and Forest Reserve; *C. Ruinard* & *A. H. M. Jayasuriya 19/146-2* (MO2859563) • Hinidoou Kanda hills; Ceylon S.W.; *H. Wright 3817* (H-BR 2647022) • Ceylon; *Walker et Gardner no. 253* (holotype of *M. ceylanicum*, NY00518287) • Ceylon; *Dr. Thwaites.* (as *M. ramentosum*, H-BR 2630028).
Vietnam • Lam Dông; *Evrard 1383* (H 3090748); *C. M. Evrard 1383* (MO3064950); *S. He & K. Nguyen 42900* (MO6239367, as *M. lorifolium*); *Evrard 1383* (MO3064950; PC0083690, as *M. lorifolium*); *S. He & K. Nguyen 42821* (MO6239369, as *M. lorifolium*) • lac Duong District; *S. He* & *Khang Nguyen 42842* (MO6239368) • Ha Giang; *K. S. Nguyen 10-55* (6366640); *K. Nguyen 10-55*; III.2010; (MO6366640, as *M. lorifolium*); *L.V. Averyanov NT B 024* (MO5244297, as *M. turgidum*).
Thailand • Chiang Mai Province; *Schäfer-Verwimp Nr. 23767* (MO5367893); *J. F. Maxwell B-148* (MO6231592, as *M. turgidum*) • Payap; *A. Touw. 8711* (MO2163749) • Northern; *A. Schäfer-Verwimp 24021* (MO5367892) • South-eastern; Chanthaburi; *P. Sukkharak, A. Likananan & P. Kitlap 81* (MO6629346) • Udawn; *A. Touw 10544* (MO2154138); *P. Sukkharak et al. 228-2* (MO, as *M. lorifolium*) • Kao Bangto, Pang-nga, Siam; *A. F. G. Kerr 423* (BM000825436, *as M. turgidum*).
Philippines • Luzon; *M. R. Crosby 17601* (MO6162743 as *M. lorifolium*); *E. D. Merril 4936* (H-BR 2647001); *M. Ramos 5506* (H-BR 2647004); *M. L. Merritt & T. C. Zichokke 16424* (H-BR 2647007); *E. D. Merrill* (H-BR 2647036) • Prov. Benguet; *E. B. Capeland 1347* (H-BR 2467033) • Mindanao; *M. Ramon & G. Edano 37184* (H 3090746).
Guinea • *Pobéguin C.H.O., s.n.* (lectotype of *M. seriatum*, PC0137555) • Haute Téné; *Pobéguin C.H.O. s.n.* (isolectotypes of *M. seriatum*, PC0106736, PC0106737, PC0106738).
Kenya • Ostafrika, Mt. Kenia; *Troll C. 5863* (isotype of *M. trollii*, JE04008697) • Ngong Hill; *S Pócs 04011/B* (MO6095084).
Central African Republic • Bocaranga, Chute Durzoro sur la Pendé, près village Woso; *Eckendorff s.n.* (holotype of *M. eckendorffii*, PC0105918).
Congo • Kampianabulongo (Penghe - Urumu); *Bequaert s.n.* (lectotype of *M. bequaertii*, PC0098353) • Kilo-Irumu; *Pobéguin C.H.O. s.n.* (as *M. bequaertii*, PC0098352).
Rwanda • Afrique orientale, Rugege-Wald; *Mildbraed I. no. 830* (as *M. perundulatum*, H-BR 2626001).
Mauritius • *Belanger s.n.* (as *M. belangeri*, lectotype: PC0137487; isolectotype: S: B162961) • Bourbon; *L. H. Boivin s. n.* (S-B162961).

DISCUSSION

Macromitrium sulcatum is a widely distributed species in sub-Saharan Africa, South Asia, Indochina, Southeast Asia and as far north as Yunnan province of China. The species highly vary in some of its characters, particularly in the branch leaves (ligulate-, to oblong-lanceolate, broad to narrowly lanceolate) and their basal cells (tuberculate to varying degrees), upper margins near apex (denticulate to entire), apical cells (rounded to slightly elongate) (Wilbraham 2015). Wilbraham (2015) thought that it is convenient to continue with the broad species concept currently adopted for *M. sulcatum*.

The seventeen specimens in Clade A of the phylogenetic tree (Figs 3; 4) are basically divided into two groups, one with ligulate-, oblong-lanceolate to broad lanceolate leaves (Thailand 81, Guinea 30469, 30768B, 30457, 30460, Philippines 17601, 30702) and the other with lanceolate to narrowly lanceolate leaves (Vietnam 42 900, 42 842, 10-55, NTH B 024, Kenya 04011/B). It is the same case for the type specimens of *M. sulcatum* and its synonyms. Morphologically, there also exist two groups, one with ligulate-lanceolate leaves such as

FIG. 7. — *Macromitrium pseudoramentosum* Herzog: **A**-**J**, branch leaves; **K**, **L**, apices of branch leaves; **M**, **N**, basal cells of branch leaves; **O**, apical cells of branch leaf; **P**, upper cells of branch leaf; **Q**, **R**, low cells of branch leaves (all from isosyntype, BM000982502). Scale bar: A, J, 500 µm; K, L, 100 µm; M-R, 50 µm.

M. seriatum (AL-AW), *M. sulcatum* (AX-BB), *M. eckendorffii* (X-AD), *M. bequaertii* (P-U), and the other with lanceolate to narrowly lanceolate leaves such as *M. ceylanicum* (BC-BM), *M. belangeri* (A-I), *M. nilegiriense* (J-O) (Fig. 2). However, from the topological structure of the phylogenetic tree (Fig. 3), specimens with ligulate- to oblong-lanceolate leaves and those

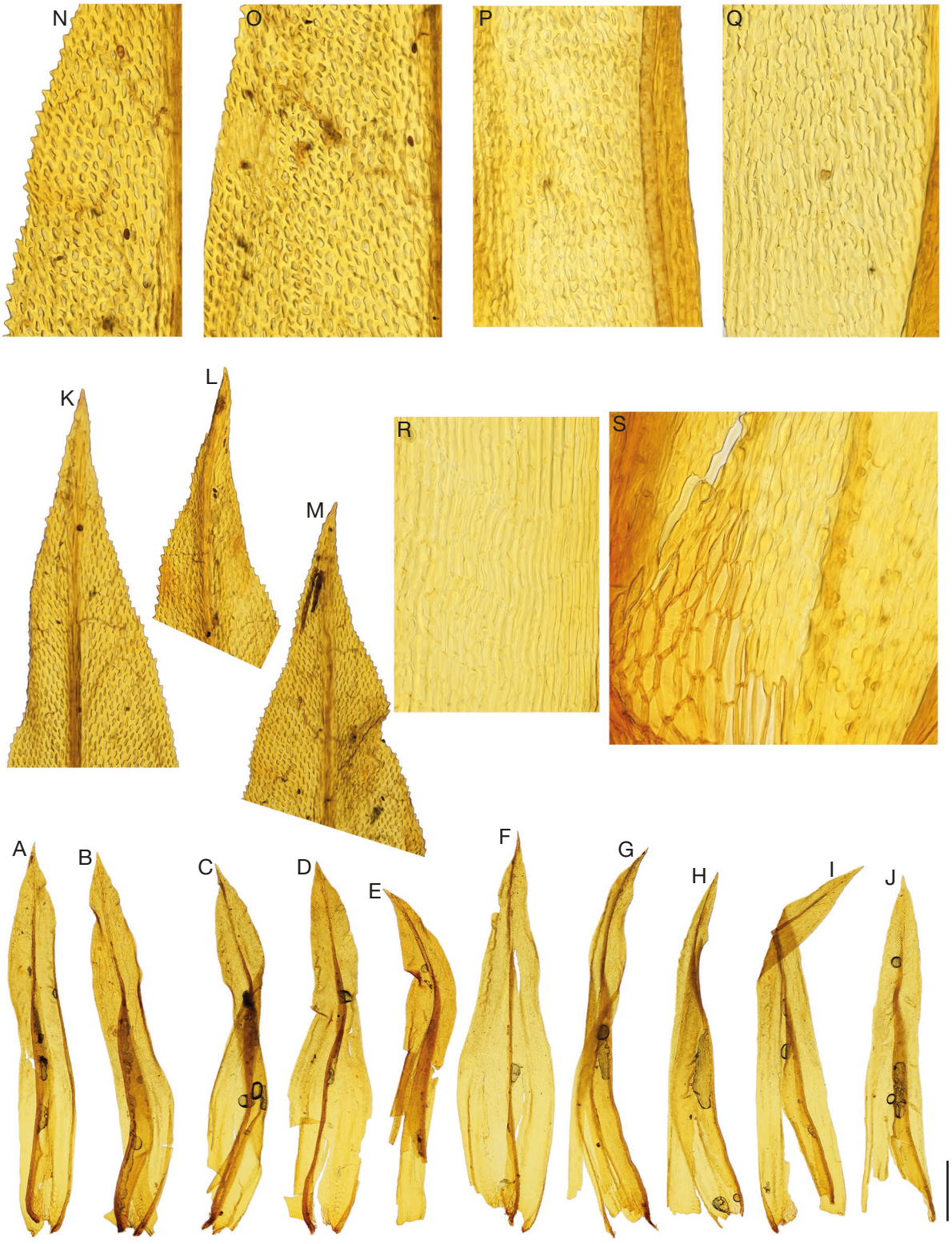

Fig. 8. — *Macromitrium turgidum* Müll. Hal.: **A**-**J**, branch leaves; **K**-**M**, apical cells of branch leaves; **N**, apical cells near margin of branch leaf; **O**, upper cells of branch leaf; **P**, medial cells of branch leaf; **Q**, **R**, low cells of branch leaves; **S**, basal cells of branch leaf (all from holotype, BM 000825435). Scale bar: A-J, 500 µm; K-M, 100 µm; N-S, 50 µm.

with lanceolate to narrowly lanceolate leaves are nested in some clades such as Thailand 81 and Vietnam 42 842, Vietnam 42 900 and Philippines 17 601, Guinea 30 702 (Fig. 4). Therefore, the intraspecific taxonomical value of the shapes of branch leaves for *M. sulcatum* is limited. In the original publications of *M. ceylanicum* (Mitten 1859), the species was

mentioned as similar to *M. sulcatum*. Fleischer (1902-1904) treated *M. ceylanicum* as a subspecies of *M. sulcatum* because the former had narrowly long lanceolate leaves. Gangulee (1976) treated *M. ceylanium* as a synonym of *M. sulcatum*, but he didn't give reasons for the taxonomic treatment of the species. According to the phylogenetic analyses with three genes and its morphological characteristics (Appendix 3), we confirmed the taxonomic treatment of the species by Gangulee.

Müller described *Macromitrium uncinatum* based on the collection by Missionar Bernhard Schmid from Neilgherri (Nilgiri) Mountains, India. In the "*Musci Indiae Orientalis, an enumeration of the mosses of the East Indies*", Mitten (1859) replaced *M. uncinatum* by *M. muellerianum* because the former is a latter homonym of *M. uncinatum* (Brid.) Brid (Bridel 1826). When Mitten substituted *M. uncinatum* Müll. Hal with *M. muellerianum*, he didn't describe the species again and only mentioned two specimens related to the species, one collected by Bernhard Schmid and the other by Gardner (no. 33). However, Müller (1853) only mentioned Bernhard Schmid as the collector of the specimens relevant to his new species in "*Musci Neilgherrenses*". There are no specimens associated with *M. uncinatum* and collected by Schmid in NY. Therefore, here we designated JE 04006257 (Mont. Neelgherrenses, *Bernh. Schmidt s.n.*, *Macromitrium uncinatum* C. Müll.) as a lectotype for *M. muellerianum*.

The types of *M. muellerianum* Mitt. is basically the same as those of *M. ceylanicum* Mitt., with narrowly lanceolate branch leaves. Though difference exists between the types of *M. muellerianum* and *M. sulcatum* in the shape of their branch leaves, such difference also exists among the 18 specimens in Clade A of the phylogenetic trees (which belong to *M. sulcatum* as analyzed above), and those of previous synonyms of *M. sulcatum*.

The types of *M. pseudoramentosum* Herzog and *M. turgidum* Dixon closely resemble those of *M. sulcatum*, only upper margin near the apex of in the former two species are almost entire while the latter slightly denticulate. Additionally, while the upper portions of branch leaves in *M. pseudoramentosum* are undulate to varying degrees, similar features have been observed in some populations of *M. sulcatum* (Wilbraham 2008). Herzog (1926) mentioned that *M. pseudoramentosum* is similar to *M. ramentosum* Thwaites & Mitt. *Macromitrium ramentosum* was placed as a subspecies of *M. sulcatum* by Fleischer (1902-1907) and Yu *et al.* (2018) confirmed *M. sulcatum* subsp. *ramentosum*. Actually, the type specimens of *M. pseudoramentosum* and *M. sulcatum* both posses naked calyptrae, distinguishing them from *M. sulcatum* subsp. *ramentosum* by the latter with hairy calyptrae.

In the original description of *M. lorifolium* by Paris (1907), there was no detailed type information, but they mentioned the collector and locality of the specimens with "Annam, Langbian, *Pinus* et *Dipterocarpus*, Par. M. le *Dr. Eberhardt*". We found two specimens H-BR 2630006 and H-BR 2630007 (Annam, Langbian, *Pinus* et *Dipterocarpus*, leg. Eberhardt, no. 433, 1906, *Macromitrium lorifolium*, *sp. n.*!), which were collected one year earlier than the publication and agree well with the original description of *M. lorifolium* by Paris (1907). Based on the status and relevance of the specimens, we designate H-BR 2630007 as the lectotype of *M. lorifolium*.

When Paris (1907) described *M. lorifolium*, they thought that the species was similar to *M. blumei* Nees ex Schwägr., *M. longicaule* Müll. Hal. and *M. longipilum* A. Braun ex Müll. Hal. However, from *M. lorifolium, M. blumei* can be distinguished by its setae papillose to varying degrees, and branch leaves with asymmetrical apices and a conspicuous apiculus or awn, *M. longicaule* can be separated by its pluripapillose upper cells of branch leaves; and *M. longipilum* can be distinguished by its strongly conic-bulging or mammillose cells and a long, smooth and flexuose hair-point. The types *M. lorifolium* have narrowly lanceolate branch leaves with undulate upper portions, which are different from those of *M. sulcatum*. The variations of the former still fall within the range of the latter according to the broad species concept for *M. sulcatum* by Wilbraham (2015) and the variations of *M. sulcatum* in Figures 1, 2 and 4.

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Author's contribution

Jun Yang and Guangyu Luo contributed equally to this article.

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APPENDICES

Appendix 1. — Names, origins and vouchers (herbarium) used for phylogenetic analyses in this study.

Taxa	Collection Locality	Coll. number	Collector	Herbarium
Schlotheimia macgregorii Broth. & Geh.	Paup New Guinea	44836	He S.	MO
Schlotheimia grevilleana Mitt.	Zhejiang, China	101126003	Guo S. L.	SHTU
Schlotheimia grevilleana	Fujian, China	100612476	Wu W.Y. & Wang Y.F.	HSNU
Schlotheimia grevilleana	Fujian, China	100406392	Wu W.Y. & Wang Y.F.	HSNU
Macrocoma tenuis subsp. *sullivantii* (Müll. Hal.) Vitt	Yunnan, China	110404315	Guo S. L.	SHTU
Groutiella tomentosa (Hornsch.) Wijk & Margad.	Laos	44172	He S.	MO
Macromitrium gymnostomum Sull. & Lesq.	Zhejiag, China	20130805005	Guo S. L.	SHTU
Macromitrium gymnostomum	Taiwan, China	212	Guo S. L. & Cao T.	SHTU
Macromitrium gymnostomum	Taiwan, China	546	Guo S. L. & Cao T.	SHTU
Macromitrium microstomum (Hook. & Grev.) Schwägr.	Taiwan, China	304	Guo S. L. & Cao T.	SHTU
Macromitrium microstomum	Honduras	17568	B. Allen	MO
Macromitrium microstomum	Australia	43671	H. Streimann	MO
Macromitrium microstomum	Honduras	17562	B. Allen	MO
Macromitrium microstomum	Taiwan, China	202	Guo S. L. & Cao T.	SHTU
Macromitrium microstomum	Taiwan, China	329	Guo S. L. & Cao T.	SHTU
Macromitrium microstomum	Vietnam	43021	He S. & N.S. Khang	MO
Macromitrium cavaleriei Cardot & Thér.	Taiwan, China	697	Guo S. L. & Cao T.	SHTU
Macromitrium cavaleriei	Taiwan, China	696	Guo S. L. & Cao T.	SHTU
Macromitrium cavaleriei	Taiwan, China	622	Guo S. L. & Cao T.	SHTU
Macromitrium cavaleriei	Taiwan, China	321	Guo S. L. & Cao T.	SHTU
Macromitrium cavaleriei	Taiwan, China	323	Guo S. L. & Cao T.	SHTU
Macromitrium japonicum Dozy & Molk.	Laos	44258	He S.	MO
Macromitrium japonicum	Taiwan, China	168	Guo S. L. & Cao T.	SHTU
Macromitrium japonicum	Taiwan, China	513	Guo S. L. & Cao T.	SHTU
Macromitrium japonicum	Taiwan, China	517	Guo S. L. & Cao T.	SHTU
Macromitrium lorifolium Paris & Broth.	Vietnam	42900	He S. & N.S. Khang	MO
Macromitrium lorifolium	Thailand	228-2	P. Sukkharak, A. Likananan & P. Kitlap	MO
Macromitrium lorifolium	Philippines	17601	Marshall R. Crosby	MO
Macromitrium turgidum Dixon	Yunnan, China	15120	Marshall R. Crosby	MO
Macromitrium turgidum	Vietnam	NTH B024	L.V. Averyanov	MO
Macromitrium sulcatum (Hook.) Brid.	Vietnam	23907	H. van der Werff, Bruce Gray, T.H. Nguyên & N.S. Khang	MO
Macromitrium sulcatum	Vietnam	42821	He S. & N.S. Khang	MO
Macromitrium sulcatum	Vietnam	10-55	N.S. Khang	MO
Macromitrium sulcatum	Thailand	81	P. Sukkharak, A. Likananan & P. Kitlap	MO
Macromitrium sulcatum	Vietnam	42842	He S. & N.S. Khang	MO
Macromitrium sulcatum	Kenya	04011/B	Sarolta Pócs & T. Pócs	MO
Macromitrium levatum Mitt.	Guinea	30469	B. Allen	MO
Macromitrium levatum	Guinea	30768B	B. Allen	MO
Macromitrium seriatum	Guinea	30457	B. Allen	MO
Macromitrium levatum	Guinea	30460	B. Allen	MO
Macromitrium levatum	Guinea	30475A	B. Allen	MO
Macromitrium levatum	Guinea	30702	B. Allen	MO
Macromitrium scleropodium Besch.	Guinea	30692	B. Allen	MO

Appendix 2. — Numbers of sites in each locus based on sequence length (**bp**), parsimony variable (**p.v.**) sites, parsimony informative (**p.i.**) sites and the models selected for Bayesian analysis.

Gene	Length (bp)	p.v. sites	p.i. sites	Model
*trn*L-F	469	101	53	HKY+G
*trn*G	577	101	89	HKY+G
its2	867	378	295	HKY+I+G
Total	1913	580	437	

Appendix 3. — *Macromitrium ceylanicum* Mitt.: **A**-**K**, branch leaves; **L**, **M**, apices of branch leaves; **N**, **O**, apical cells of branch leaves; **P**, upper cells of branch leaf; **Q**, **R**, medial cells of branch leaves; **S**, **T**, low cells of branch leaves; **U**, basal cells of branch leaf (all from holotype, NY00518287). Scale bar: A-K, 500 µm; L, M, 200 µm; N-U, 50 µm.