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Three new synonyms of *Macromitrium japonicum*
Dozy & Molk. (Bryophyta, Orthotrichaceae)
based on morphological and molecular evidence

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Three new synonyms of *Macromitrium japonicum* Dozy & Molk. (Bryophyta, Orthotrichaceae) based on morphological and molecular evidence

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ABSTRACT

Macromitrium japonicum Dozy & Molk. is an epiphytic moss mainly recorded from East Asia. To clarify its morphological variations and their potential genetic basis, we morphologically compared fourteen samples assigned to *M. japonicum*, and constructed a phylogenetic tree including these samples based on *trnL-F*, *trnG* and ITS2. On the phylogenetic tree, these fourteen samples formed a single clade, being characterized by the typical features of *M. japonicum*. Comparing the types of *M. japonicum* var. *makinoi* (Broth.) Nog., *M. dickasonii* Bartr. and *M. polygonostomum* Dixon & P. de la Varde with these samples, and the types of *M. japonicum* and its former synonyms including *Dasymitrium incurvum* Lind. and *M. bathyodontum* Cardot, we found that the variations of the former three species fall within the morphological variation range of the above fourteen samples and the types of *M. japonicum*, *D. incurvum* and *M. bathyodontum*. Therefore, we treated *M. japonicum* var. *makinoi*, *M. dickasonii* and *M. polygonostomum* as three new synonyms of *M. japonicum*. *Macromitrium giraldii* Müll.Hal. is excluded from the synonyms of *M. japonicum* and likely an acceptable species name. Additionally, *M. japonicum* is newly recorded for Myanmar.

KEY WORDS

Myanmar,
morphological variation,
phylogeny,
new synonyms,
new record.

RÉSUMÉ

Trois nouveaux synonymes de *Macromitrium japonicum* Dozy & Molk. (Bryophyta, Orthotrichaceae) sur la base de preuves morphologiques et moléculaires.

Macromitrium japonicum Dozy & Molk. est une mousse épiphyte principalement observée en Asie de l'Est. Afin de clarifier ses variations morphologiques et leur base génétique potentielle, nous avons comparé morphologiquement quatorze échantillons attribués à *M. japonicum*, et construit un arbre phylogénétique incluant ces échantillons sur la base *trnL-F*, *trnG* et ITS2. Sur l'arbre phylogénétique, ces quatorze échantillons formaient un seul clade, caractérisé par les particularités typiques de *M. japonicum*. En comparant les types de *M. japonicum* var. *makinoi* (Broth.) Nog., *M. dickasonii* Bartr. et *M. polygonostomum* Dixon & P. de la Varde avec ces échantillons, et les types de *M. japonicum* et ses anciens synonymes dont *Dasymitrium incurvum* Lind. et *M. bathyodontum* Cardot, nous avons trouvé que les variations des trois premières espèces se situent dans la gamme de variation morphologique des quatorze échantillons ci-dessus et des types de *M. japonicum*, *D. incurvum* et *M. bathyodontum*. Par conséquent, nous avons traité *M. japonicum* var. *makinoi*, *M. dickasonii* et *M. polygonostomum* comme trois nouveaux synonymes de *M. japonicum*. *Macromitrium giraldii* Müll. Hal. est exclu des synonymes de *M. japonicum* et constitue probablement un nom d'espèce acceptable. En outre, *M. japonicum* est nouvellement signalé pour le Myanmar.

MOTS CLÉS

Myanmar, variation morphologique, phylogénie, synonymes nouveaux, signalement nouveau.

INTRODUCTION

Macromitrium japonicum Dozy & Molk., an epiphytic moss of the family Orthotrichaceae (Musci), was first described by Dozy and Molkenboer in 1844 based on material from Japan. The species was once placed in *Dasymitrium* Lindb. by Lindberg (in Paris 1904-1906), but later *Dasymitrium* was synonymized with *Macromitrium* Brid. (Crosby & Magill 1981). Since its inception, *M. japonicum* has been recorded from some other Asian countries including China (Guo *et al.* 2007; Yu *et al.* 2013), India (Li *et al.* 2020), Japan (Noguchi 1967, 1989), Laos (Guo Shuiliang pers comm. 2013), Thailand (Tixier 1971; Tan & Iwatsuki 1993), Sri Lanka (O'Shea 2002), Korea (Noguchi 1989) and Vietnam (Bescherelle 1887; Ninh 1980; Tan & Iwatsuki 1993).

In the original publication of *M. japonicum*, Dozy and Molkenboer described the species as 'stem creeping, thread-like, densely branched; the branches very short, erect and simple; the leaves densely overlapping, folded at the tip, spatulate-ligulate, keeled, very intact, costae strong, ending below the apex, twisted when dry; capsule erect, ovoid-ellipsoid, opercula convex-conical, subulate-rostrate; calyptra hairy, lobed at base' (Dozy & Molkenboer 1844). According to the above description by Dozy and Molkenboer, and the lectotype designed by Noguchi, the observation of Noguchi (1967, 1989), as well as our examination of numerous specimens assigned to this species, *M. japonicum* could be distinguished from other members of the genus by a combination of the following morphological characters: 1) plants small to medium-sized in dense mats; branches short and erect, simple or with branchlets, densely leaved; 2) stem leaves recurved, from a triangular-ovate base gradually tapering to an oblong-lanceolate apex; 3) branch leaves strongly crisped and contorted when dry, spreading but often still adaxially deflexed at apex when moist, hyaline at leaf base, ligulate or sub-linear, with subacute or obtuse apices, strongly keeled; median and upper lamina cells obscure to varying degrees,

quadrate to hexagonal, thin-walled, with 3-5 small papillae; basal cells hyaline, rectangular, with slightly thickened walls, smooth; 4) vaginulae hairy, with many smooth hairs; inner perichaetial leaves ovate-lanceolate or ovate-oblong, acuminate; setae smooth; 5) capsules ovoid, ovoid-ellipsoid to subglobose, with single peristome; and 6) calyptrae campanulate but deeply cleft along on ridge as a cucullate appearance, somewhat lobed at base, with numerous, long, yellowish hairs (Figs 2-6).

Based on the collection of Mr. F. G. Dickason from Myanmar (Burma), Bartram (1943) described *M. dickasonii* E.B. Bartram. In the original publication of the species, Bartram considered *M. dickasonii* similar to *M. falcatum* Müll. Hal. reported from the Philippines, the former only different from the latter by its elongated basal cells, longer setae and longer capsules. However, *M. dickasonii* distinctly differs from *M. falcatum* by its branch leaves with smooth lower and basal laminal cells. According to the types and Bartram's description of the species, *M. dickasonii* is rather similar to *M. japonicum*, but the former has longer setae.

Dixon & Potier de la Varde (1927) described *M. polygonostomum* Dixon & P. de la Varde based on the collections of G. Foreau from Sirumalai in Tamil Nadu, India. The isosytype of the species, and the original description of the species by Dixon & Potier de la Varde (1927) agree well with those of *M. japonicum*.

Brotherus (1899) described *Dasymitrium makinoi* Broth. based on Makino's collection from Shikoku, Setton, Japan and thought that the species was similar to *M. japonicum* (as *Dasymitrium japonicum* (Dozy & Molk.) Lindb.), and different from the latter only by its short setae and small capsules. Later Paris (1900) transferred *D. makinoi* into *Macromitrium*, and Noguchi (1967) synonymized the species with *M. japonicum*. While in his *Illustrated Moss Flora of Japan* (Part 3), Noguchi (1989) treated *D. makinoi* as a variety, *M. japonicum* var. *makinoi* (Broth.) Nog. He thought that the variety differs from *M. japonicum* var. *japonicum* by its rounded-obtuse apices, shorter setae, as well as the ovoid to

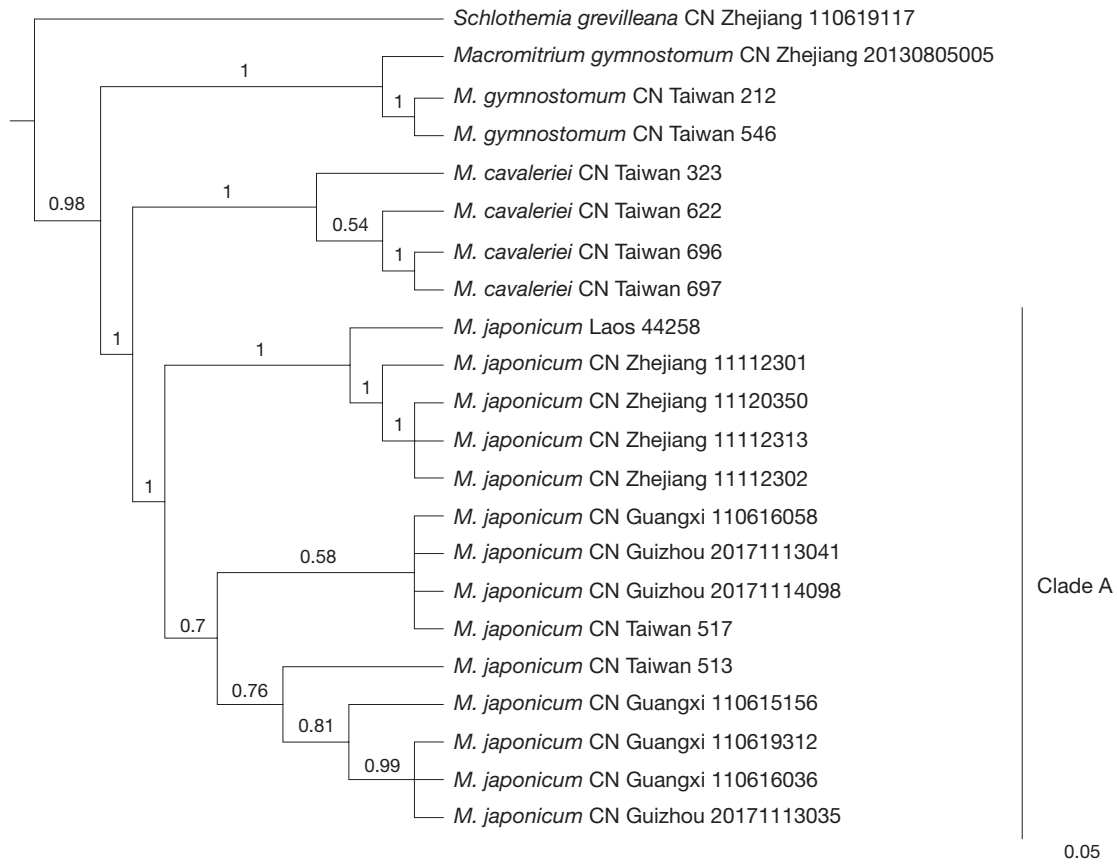


FIG. 1. — Bayesian majority consensus tree calculated from the results of Bayesian analysis of the combined datasets of *trnL-F*, *trnG* and ITS2. The Bayesian posterior probabilities are labelled above the branches.

subglobose capsules of the variety. However, the apices, seta length, and capsule shape were highly various among populations of *M. japonicum* (Noguchi 1967).

After our comparison of the types of *M. japonicum* var. *makinoi*, *M. dickasonii* and *M. polygonostomum* with that of *M. japonicum*, we speculated that the former three species names are likely synonyms of *M. japonicum*. The objective of this paper is to provide morphological and molecular evidence to confirm our opinion.

MATERIAL AND METHODS

EXAMINATION OF SPECIMENS

During the course of our global taxonomic revision of *Macromitrium*, about 96 specimens attributed to *M. japonicum*, *M. japonicum* var. *makinoi*, *M. dickasonii* and *M. polygonostomum* were examined, including types of these species names. The specimens included in this study were from FH, H (BR), L, MO, US, as well as numerous specimens collected from China by the authors (deposited at SHTU).

Microscopic examinations and measurements were taken with an Olympus-BX53 light microscope, while microphotographs were obtained with a DP74 camera 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

Twenty-two samples were used for molecular analyses, including three samples for *M. gymnostomum* Sull. & Lesq., four for *M. cavaleriei* Cardot & Thér., one for *Schlotheimia grevilleana* Mitt. as an outgroup, and fourteen samples assigned to *M. japonicum*. These fourteen samples were collected from Laos and Zhejiang, Guizhou, Guangxi, Taiwan Provinces of China (Fig. 2). Taxa for this study and voucher specimen numbers are listed in Appendix 1.

Molecular markers include one nuclear and two plastid markers: the nuclear ribosomal internal transcribed spacer region ITS1-5.8S-ITS2 (hereafter, ITS2), the tRNA (Gly) (UCC) (*trnG*), and the *trnL-trnF* intergenic spacer (*trnL-F*). These three regions have been widely used in phylogenetic analyses for *Macromitrium* (Li *et al.* 2018; Zhang *et al.* 2019; Draper *et al.* 2021) and other taxa of pleurocarpous mosses (Draper & Hedenäs 2009; Hedenäs 2012).

DNA extraction method, PCR amplifications and primers for three regions followed Zhang *et al.* (2019). Bayesian inferences (BI) was used to construct a phylogenetic tree of these twenty-two samples, which was described in Zhang *et al.* (2019). The tree was visualized and annotated in TreeGraph 2.0 (Stöver & Müller 2010).

RESULTS

After deletion of regions incomplete for some specimens at the beginnings and ends of the alignment, the total number of aligned sites from the three genes was 1756. Among them, 546 sites were variable characters and 273 were parsimony-informative. The number of sites in each locus based on sequence length, parsimony variable sites, parsimony informative sites, and the optimal substitution models selected for Bayesian analysis are given in Appendix 2.

Three species of *Macromitrium* could be identified in the Bayesian consensus tree (Fig. 1) based on the combination of ITS2, *trnG* and *trnL-F*, all with high posterior probabilities. Fourteen samples morphologically associated with *M. japonicum*, *M. dickasonii*, *M. polygonostomum*, and *M. japonicum* var. *makinoi* formed a strongly supported clade (clade A), which was a sister group to *M. cavaleriei* in the phylogenetic tree (Fig. 1). Clade A and *M. cavaleriei* belong to section *Leiostoma* Mitt., forming a sister group to *M. gymnostomum* (belonging to section *Goniostoma* Mitt.).

Within the fourteen samples of clade A, variations existed in leaf apices (from broadly acuminate, acute, obtuse to obtuse-rounded, from not, slightly to strongly adaxially enrolled when moist), leaf shapes (spathulate-ligulate, ligulate to ligulate-lanceolate) (Fig. 2), setae lengths (2-8 mm), capsule size, as well as papillosity of median and upper laminal cells (from slightly papillose to rather obscure, distinctly pluripapillose).

The type of *M. japonicum* var. *makinoi* differed from that of var. *japonicum* by its rounded-obtuse leaf apices, short setae (*c.* 2 mm long), ovoid to subglobose capsules, while the leaf apices in the type of var. *japonicum* obtuse-acute to obtuse, setae 3-4 mm long, capsules ovoid to ovoid-oblong. The type of *M. dickasonii* is basically similar to that of *M. japonicum*, only the former has slightly long setae, and unevenly spreading branch leaves with subacute apices when moist. While the type specimens of *M. polygonostomum* morphologically agree well with that of *M. japonicum*. The variations in the types of *M. japonicum*, *M. dickasonii*, *M. polygonostomum* and *M. japonicum* var. *makinoi* mainly involve branch leaf shape, laminal cell papillosity of the branch leaves, seta length and capsule size, but these variations overlap (Figs 3-6), and fall within the morphological variation range of the fourteen samples in clade A and Figure 2. Therefore, we treated *M. dickasonii*, *M. polygonostomum* and *M. japonicum* var. *makinoi* as three new synonyms of *M. japonicum*.

Family ORTHOTRICHACEAE Arn.
Genus *Macromitrium* Brid.

Macromitrium japonicum Dozy & Molk.
(Figs 3-6)

Annales des Sciences naturelles, Botanique, série 3, 2 (5): 16 (Dozy & Molkenboer 1844). — Type protologue: Japonia without exact locality and collector. — Type citation: Japan, Siebold (L910, 138-1128), lectotype!, designed by Noguchi (1967).

Macromitrium japonicum var. *makinoi* (Broth.) Nog., *Illustrated Moss Flora of Japan* 3: 606 (Noguchi 1989), **syn. nov.** — *Dasymitrium makinoi* Broth., *Hedwigia* 38: 215 (Brotherus 1899). — Type protologue: [Japan] Shikoku: Setton, ad corticem arboris (Makino). — Type citation: Japonia, Setton, leg. T. Makino, 1889 (holotype, H-BR2572002!).

Macromitrium dickasonii Bartr., *Farlowia* 1: 178 (Bartram 1943), **syn. nov.** — Type protologue: Mogok, Apr. 1934, no. 102. — Type citation: [Myanmar] Mogok, Apr. 1934, *F. G. Dickason* 102 (holotype, FH00213603!).

Macromitrium polygonostomum Dixon & P. de la Varde, *Archives de Botanique, Bulletin mensuel* 1 (8-9): 181 (Dixon & P. de la Varde 1927), **syn. nov.** — Type protologue: Hab.: Sirumalai, 4000 ft. alt., avril 1924, sterile (no 439), *ibid.*, crête rocailleuse surplombant sentier d'Emmakalapuram, mars 1927 (NOB 844A, 844B et 845). — Type citation: India, Sirumalai, mars 1927, leg. G. Foreau 844B (isotypes, US00070273!, H-BR2572016!; syntypes, PC, not seen).

DISTRIBUTION. — China (Guo *et al.* 2007; Yu *et al.* 2013), India (Li *et al.* 2020), Japan (Noguchi 1967, 1989), Laos (Guo pers. comm. 2013), Myanmar, Thailand (Tixier 1971; Tan & Iwatsuki 1993), Sri Lanka (O'Shea 2002), Korea (Noguchi 1989) and Vietnam.

HABITAT. — On trunk of broad-leaf trees, occasionally on rocks; at 10-2000 m alt.

DISCUSSION

Macromitrium japonicum is widespread in East Asia. The species often varies in shape, the apex and papillosity of median and upper laminal cells of its branch leaves (Noguchi 1967; Guo *et al.* 2007). The branch leaves are often spathulate-ligulate to ligulate, but sometimes ligulate-lanceolate; leaf apices range from broadly acuminate, acute, obtuse to broadly rounded, not or slightly to distinctly adaxially bend down when moist (Fig. 2). The median and upper laminal cells can be slightly papillose to rather obscure and distinctly pluripapillose (Guo *et al.* 2007). Considering the morphological variations of the species, Noguchi (1967) treated *Dasymitrium incurvum* Lindb., *D. makinoi* Broth., *M. bathyodontum* Cardot and *M. insularum* Sull. & Lesq. as synonyms of *M. japonicum*.

Fourteen samples of *M. japonicum* were collected from Laos and China (Guangxi, Guizhou, Taiwan, and Zhejiang). Their places in the phylogenetic tree indicate that genetic differentiation exist among some geographical populations.

Macromitrium japonicum has been reported from Laos, Thailand, Vietnam of Indochina. The present synonymization extends the distribution of the species to Myanmar.

Based on the collection of P. J. Giraldi from Tui-Kio-San, Schen-si (Shaanxi), China, Müller (1896) described *Macromitrium giralddii*. Cardot (1905) placed *M. giralddii* in synonymy with *M. incurvum* (Lindb.) Mitt. based on type material sent to him by Émile Levier. This synonymy was adopted by Brotherus (1925), and then subsequently was followed by Wijk *et al.* (1964). *Macromitrium incurvum* was later treated as a synonym of *M. japonicum* Dozy & Molk. by Noguchi (1967). After checking the types of *M. giralddii*, *M. japonicum* and *M. incurvum*, we confirmed that *M. incurvum* was conspecific with *M. japonicum*. However, *M. giralddii* was



FIG. 2. — *Macromitrium japonicum* Dozy & Molk. (all specimens deposited in SHTU).

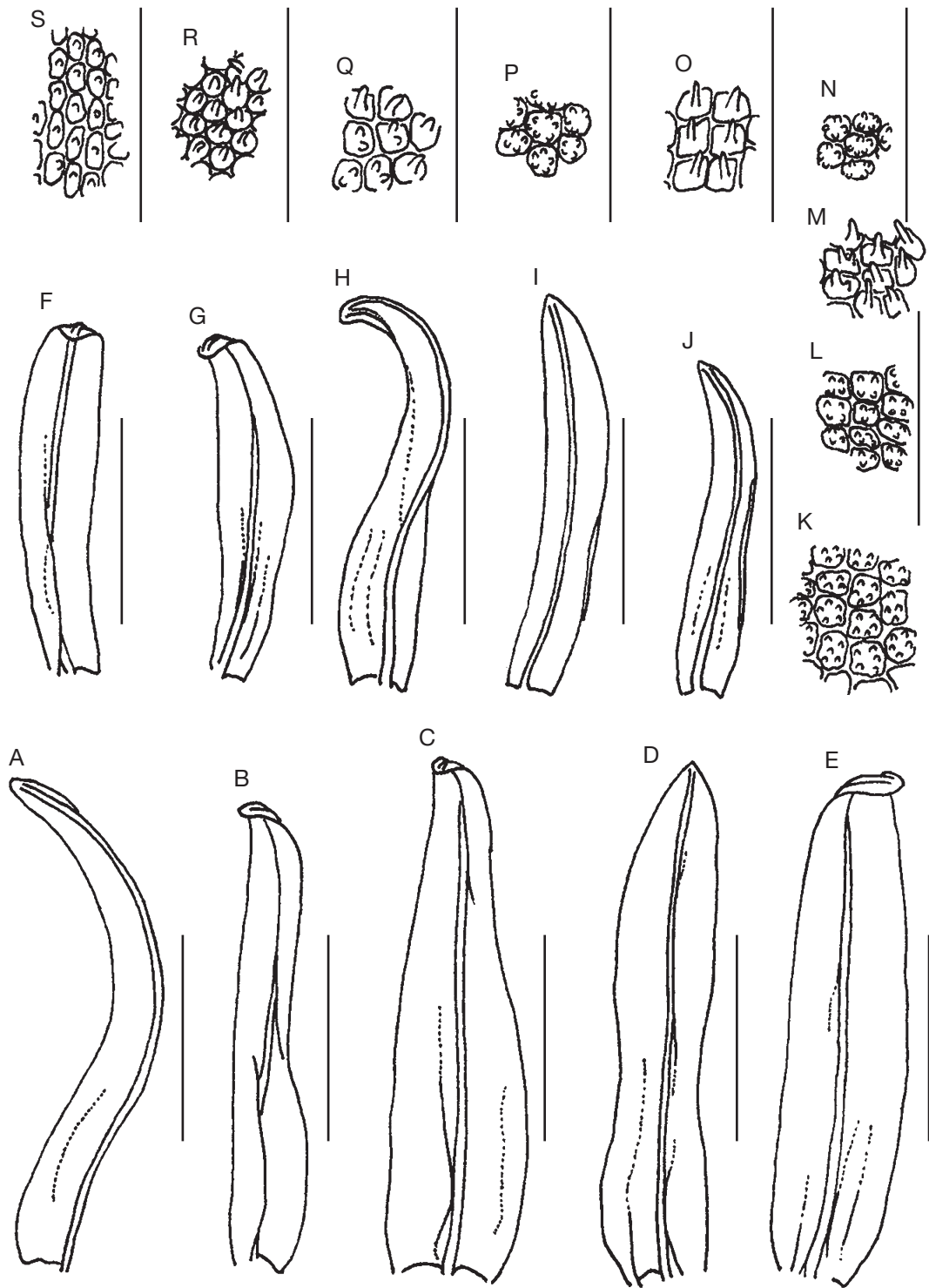


FIG. 3. — *Macromitrium japonicum* Dozy & Molk.: **A–J**, branch leaves; **K, L, Q, S**, upper cells of branch leaves; **M–P, R**, medial cells of branch leaves. **A, K**, from syntype of *M. bathyodontum* Cardot; **B, R**, from *Noguchi 45186*; **C, S**, from *Noguchi 5436*; **D, Q**, from *Noguchi 22538*; **E, P**, from *Noguchi 49319*; **F, G, L, M**, from lectotype of *M. japonicum*; **H–J, N, O**, from lectotype of *M. insularum* Sull. & Lesq. Figure modified from Noguchi 1989. Scale bars: **A–J**, 0.5 mm; **K–S**, 50 μ m.

obviously different from *M. japonicum* by having narrowly lanceolate, lanceolate to oblong-lanceolate branch leaves with acuminate apices, and unipapillose low and basal cells. Therefore, *M. giraldii* was excluded from synonyms of *M. japonicum*. In fact, *M. giraldii* is likely conspecific with

M. cavaleriei. Additionally, *M. giraldii* var. *acrophyloides* Müll.Hal., was placed in synonymy with *M. cavaleriei* (Lou *et al.* 2014). In view of nomenclature, *M. giraldii* Müll. Hal. is likely an acceptable species name. We will study and give more detailed morphological and molecular evidence

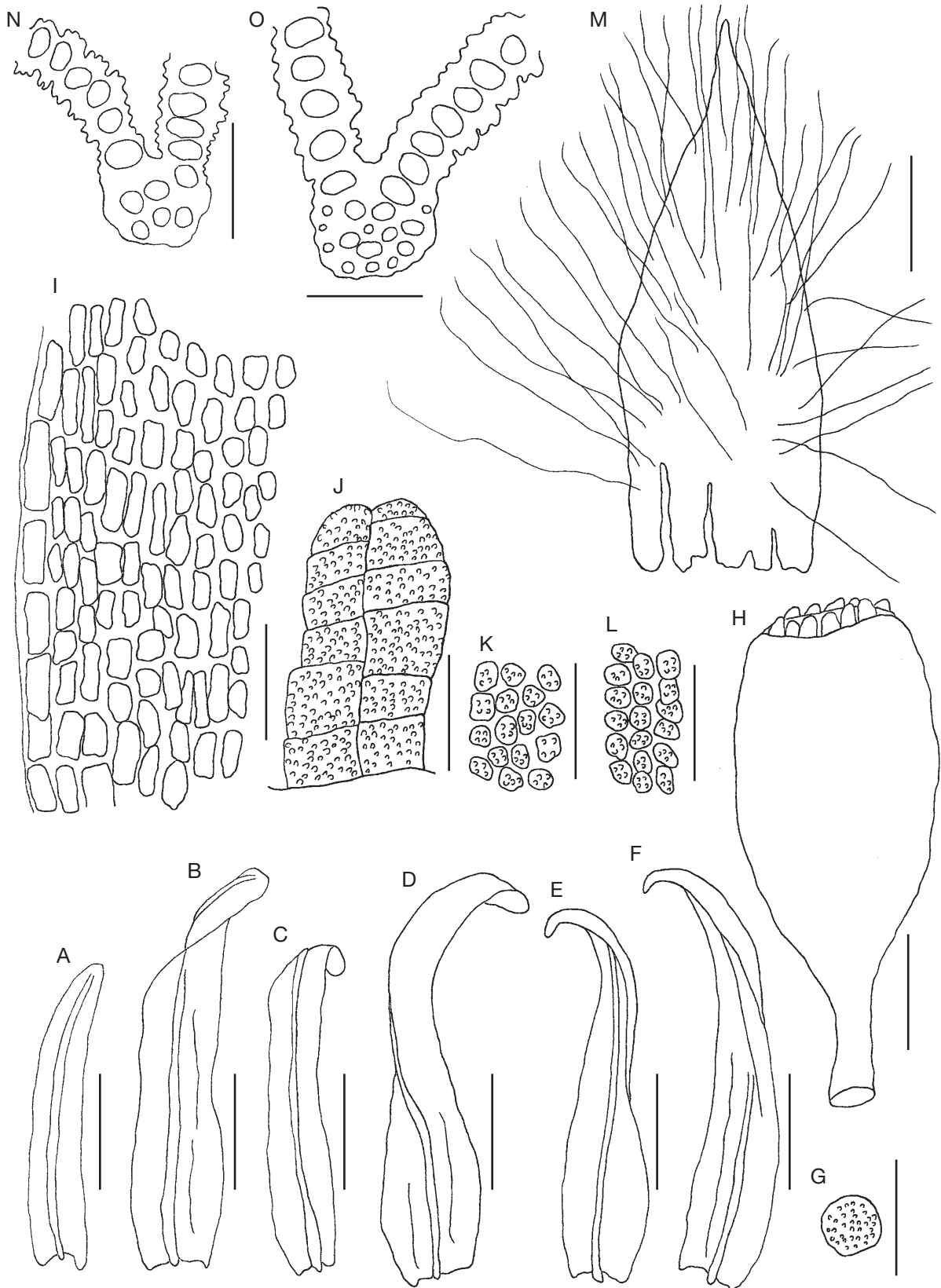


FIG. 4. — *Macromitrium japonicum* Dozy & Molk.: **A-F**, branch leaves; **G**, spore; **H**, capsule; **I**, basal leaf cells; **J**, exostome; **K**, upper cells of branch leaf; **L**, medial cells of branch leaf; **M**, calyptra; **N**, upper transverse section of branch leaf; **O**, medial transverse section of branch leaf. All from holotype of *M. japonicum* var. *makinoi* (Broth.) Nog. (H-BR2572002). Scale bars: **A-F**, **H**, **M**, 0.44 mm; **G**, **I-L**, **N**, **O**, 44 μ m.

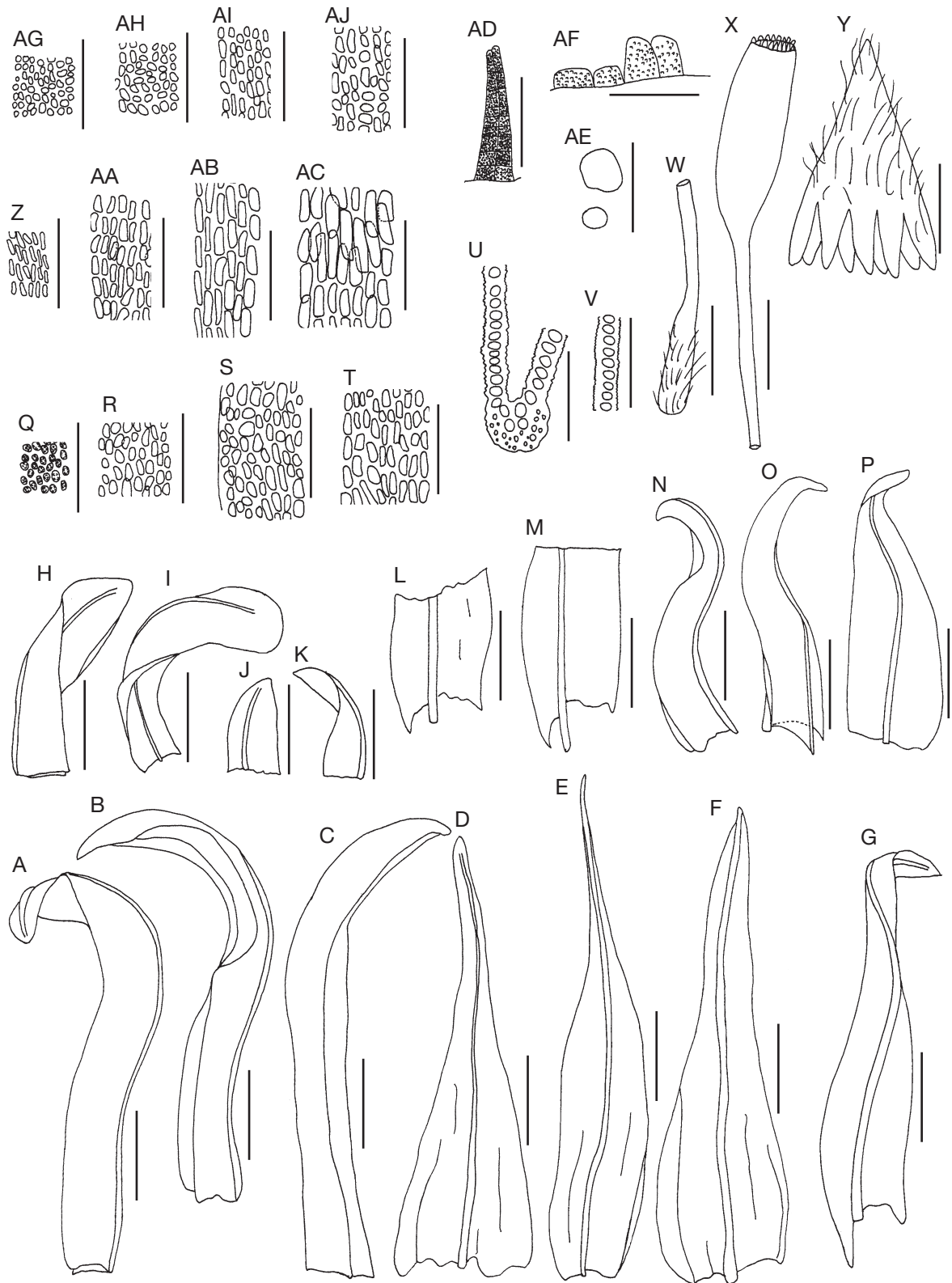


FIG. 5. — *Macromitrium japonicum* Dozy & Molk.: **A-C**, branch leaves; **D-F**, perichaetial leaves; **G**, stem leaf; **H-K**, apices of branch leaf; **L, M**, base of branch leaf; **N-P**, secondary stem leaves; **Q**, medial cells of branch leaf; **R**, lower cells of branch leaf; **S**, basal cells near margin of branch leaf; **T**, basal cells of branch leaf; **U, V**, upper transverse sections of branch leaves; **W**, vaginula; **X**, capsules; **Y**, calyptra; **Z**, upper cells of perichaetial leaf; **AA**, medial cells of perichaetial leaf; **AB**, lower cells of perichaetial leaf; **AC**, basal cells of perichaetial leaf; **AD, AF**, peristome; **AE**, spore; **AG**, upper cells of stem leaf; **AH**, medial cells of stem leaf; **AI**, lower cells of stem leaf; **AJ**, basal cells of stem leaf. All from holotype of *M. dickasonii* E.B.Bartram (FH00213603). Scale bars: A-P, W-Y, 1 mm; AF, 200 μ m; AD, 100 μ m; Q-V, Z-AC, AE, AG-AJ, 67 μ m.

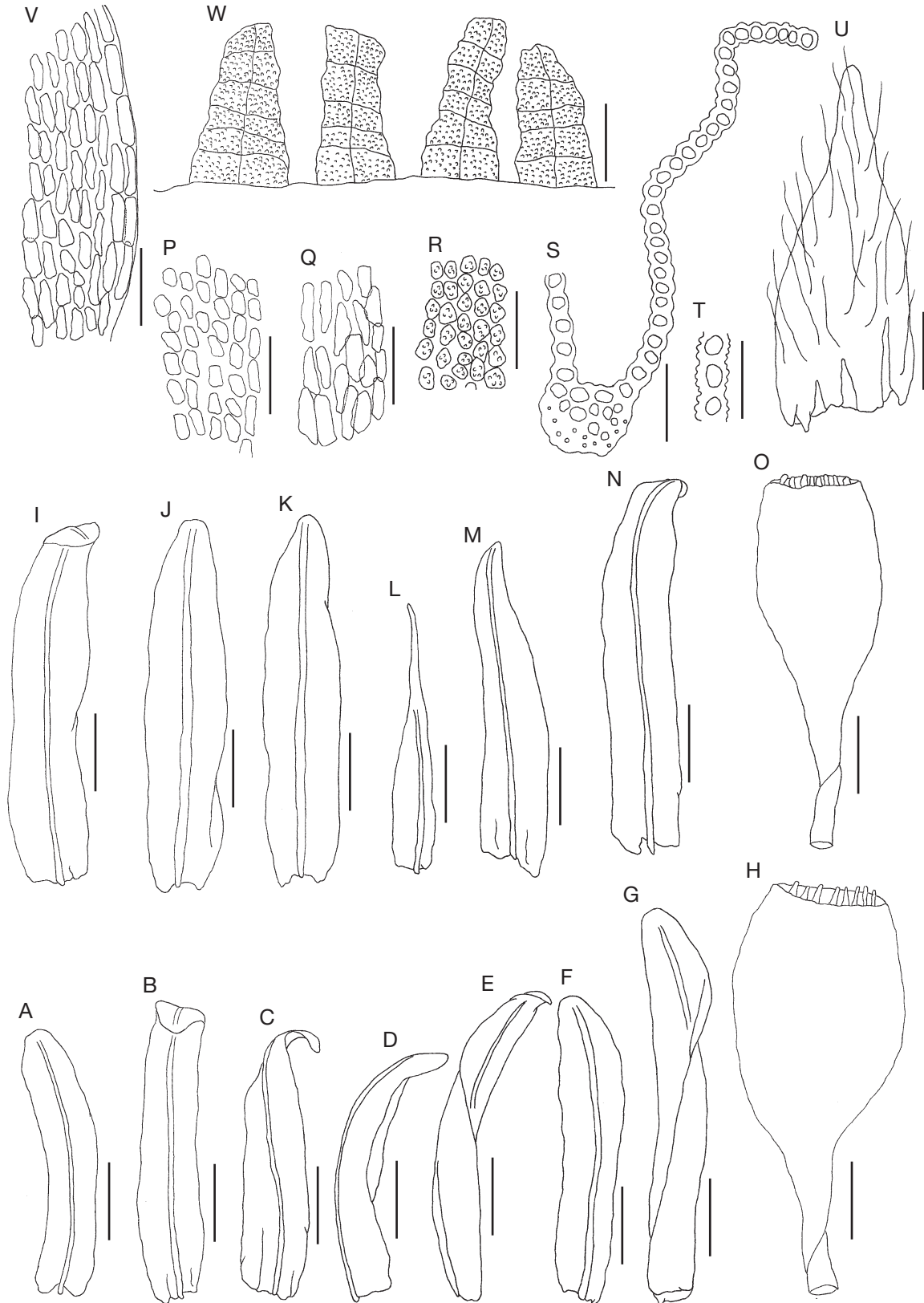


FIG. 6. — *Macromitrium japonicum* Dozy & Molk.: **A-G, I-K, M, N**, branch leaves; **L**, perichaetial leaves; **H, O**, capsules; **P, Q**, basal cells of branch leaves; **R**, medial cells of branch leaf; **S**, basal transverse section of branch leaf; **T**, upper transverse section of branch leaf; **U**, calyptra; **V**, basal cells near margin of branch leaf; **W**, peristome. All from syntype of *M. polygonostomum* Dixon & P. de la Varde (H-BR2572016). Scale bars: A-O, U, 0.44 mm; P-T, V, W, 44 μ m.

for the recognition of *M. giraldii* as an acceptable species in our subsequent study.

Macromitrium japonicum has been reported mainly from China and Japan. The other species of the genus in these two countries could be separated from *M. japonicum* as in the presented key.

Macromitrium blumei var. *zollingeri*
(Mitt. ex Bosch & Sande Lac.)
S.L.Guo, B.C.Tan & Virtanen

MATERIAL EXAMINED. — **Indonesia** • Java; *E. Nyman* 165; H-BR260006 • *C. Lauterbach* 452; H-BR2601007 • Sumatra; A. Ernst; H-BR2600017 • *Zollinger* 3716; isotype: H-BR2601008! **Malaysia** • Borneo; *J. Clemens* 3557; H-BR3090124.

Macromitrium cavaleriei Cardot & Thér.

MATERIAL EXAMINED. — **China** • Guizhou; *R. J. Cavalerie* 833; lectotype: PC0083631!; isolectotypes: PC0083629!, BM000919466! • Anhui; *Z. L. Wan & J. X. Luo* 9026, 9125, 9349, 9361; MO, PE • Fujian; *H. H. Chung* B351; PC0083733.

Macromitrium comatum Mitt.

MATERIAL EXAMINED. — **China** • Fujian; *H. H. Chung* m4; NY • Hubei; *Sino-American Expedition* 822; MO2844283. **Japan** • Honshu, Hiroshima; H. Ando; H3090196, H3090197 • Umagayeshi to Chiusenji; IX. 1886; W. Bisset; holotype: NY00518290!; isotype: NY00518291!

Macromitrium cuspidatum Hampe

MATERIAL EXAMINED. — **China** • Hainan; *P. L. Jr. Redfearn* 36210; MO3974405. **Indonesia** • Java, Salak; *S. Kurz* 845; H-BR2620014. **Malaysia** • Pahang; *A. Schäfer-Verwimp* 18535; MO5367862.

Macromitrium ferriei Cardot & Thér.

MATERIAL EXAMINED. — **China** • Shandong; Schwabe-Beha; JE • Sichuan, *B. Allen* 7249; MO • *B. Allen* 6722; MO • *P. L. Jr. Redfearn* 34843; MO • Xizang; *Y. G. Su* 2337; MO • Zhejiang; *P. C. Wu* 198; MO. **Japan** • Kyushu; *Z. Iwatsuki* 1628; MO • Kinki; *T. Nakajima* 1080; MO • Oshima; J. B. Ferrie; lectotype: PC0083650!; isolectotypes: PC0083651!, PC0083649!

Macromitrium formosae Cardot

MATERIAL EXAMINED. — **China** • Taiwan; *Faurie* 181; isotype: H3090260!

Macromitrium fortunatii Cardot & Thér.

MATERIAL EXAMINED. — **China** • Guizhou; *Fortunat* 1749; lectotype: PC0083654!; isolectotypes: PC0083657!, PC0719719!

Macromitrium gymnostomum Sull. & Lesq.

MATERIAL EXAMINED. — **China** • Zhejiang, Tianmu Mountain; *W. R. Buck* no. 23916; H • Fujian, Mt. Wuyi; *Guo* S. L. 030001-030008; SHTU.

Japan • Shizuoka Pref., Simoda; Wright; isolectotype: NY00512839! • Ousima, one of the northern Loo Choo Islands; syntype: NY00512840!

Macromitrium hainanense S.L.Guo & S.He

MATERIAL EXAMINED. — **China** • Hainan; *W. D. Reese* 17956; holotype: MO!

Macromitrium holomitrioides Nog.

MATERIAL EXAMINED. — **China** • Taiwan; *A. Noguchi* 9574; holotype: NICH!; isotype: HIRO! • Hainan; *P. C. Chen et al.* 789b; H • P. C. Wu; *W1185016*; H • *Paul L. Redfearn Jr.* 35766; MO3974398.

Macromitrium japonicum Dozy & Molck.

MATERIAL EXAMINED. — **China** • Anhui; *Z. L. Wan & J. X. Luo* 9327 • Fujian; *H. H. Chung* B4; MO • *H. H. Chung* B3; PC0083682, H3090393, NY, FH, MO • *H. H. Chung* B36/ad, B31; FH • Hance; *HB s.n.*; NY, as *M. spathylare* • *H. H. Chung* B36; S[B115577] • Zhejiang; *S. L. Guo* N 13-1; SHTU • Guangdong; *Wu Han* B 95; MO • *P. L. Jr. Redfearn* 34384; MO • *R. E. Magill, P. L. Jr. Redfearn & M. R. Crosby* 8127; MO • Hainan; *Lau & Tsang* 18295; FH • *W. D. Reese* 17498; MO • Hebei; *Q. W. Wang* 976, 864; MO • Helongjian; *Manchuria I. Kozlov* 7; H3090539 • Henan; *J. X. Luo* 128; MO • *D. E. Boufford et al.* 26349-B; FH • *J. X. Luo* 176, 196; NY, MO • *J. X. Luo* 321, 330a, 330, 352; MO • *Z. Z. He* 82; MO • Hongkong; *Herklots GAC* 363; BM • *W. T. Tsang* 29731; FH • Hubei; *Sino-American Expedition* 822b; NY • Hunan; *Handel-Mazzetti* 11064; H-BR • *Enroth* 63564, 64691, 64712, 70982, *Virtanen* 61646, 61647, 61659, 61931; H • Jiangxi; *W. B. Patterson s.n.*; FH, as *M. incurvum* • *H. H. Chung* 4045; FH • Sichuan; *P. C. Chen* 5869, *P. L. Jr. Redfearn* 35575, 34817, *A. Bruce* 6688, 7219, 7373; MO • *T. Koponen* 45900, 45958, 43425; H • Shaanxi; *J. Giraldis s.n.*; S[B88595] • *J. Giraldis* 2131; H-BR2576004, PC0083662, JE • *J. Giraldis* 1496; PC0083661 • *J. Giraldis* 1564; H-BR2576007 • *J. Giraldis* 2133; H-BR2576007 • *J. Giraldis* 1496b; NY • *J. Giraldis* 1496d; H-BR2576002 • *J. Giraldis* 2132; H-BR2576005 • *J. Giraldis* 1565; H-BR2576008 • Taiwan, Fomosa; *Schwabe-Beha*. 9, 10, 52, 56; JE • *Sasarka* 2490; H-BR2578031 • *Sasaoka* 2525; H-BR2578032 • *Suzwk* 2823; H-BR2578037 • *Suzwk* 2828; H-BR2578038 • *Suzwk* 2850; H-BR2578050 • *Wichua* 1648; H-BR2579013 • *Faurie* 95; H-BR2579014 • Yunnan; *P. C. Wu* 22152; MO • *R. E. Magill, P. L. Jr. Redfearn & M. R. Crosby* 7987; MO • *P. L. Jr. Redfearn et al.* 1730, 1844; MO • Zhejiang; *P. C. Wu* 1231, 1258, 24910, *R. L. Hu* 92; MO.

Japan • Kiushiu; *S. Hattori* 20; MO • Honshiu; *K. Sakurai* 141 • *Jhsiba* 8278; MO • Honshiu; *K. Sakurai* 16707, *M. Higuchi* 12147; MO • Yakushima; *Iwatsuki & Sharp* 1029; MO • Yoshio; *K. Mayebana* 431; MO • Kozushima; *T. Nakamura* 690; MO, JE • Kanagawa; *P. L. Jr. Redfearn* 757.

Korea • Tongduch'on-Shi; *J. R. Shevock* 16286; MO.

KEY OF *MACROMITRIUM* BRID. IN CHINA AND JAPAN

1. Peristome absent
..... *M. formosae* Cardot, *M. gymnostomum* Sull. & Lesq., *M. holomitrioides* Nog., *M. ousiense* Broth. & Paris,
M. taiheizanense Nog., *M. tuberculatum* Dixon
— Peristome present 2
2. Laminae of branch leaves irregular 1-3-stratose proliferation with pluripapillose cells
..... *M. nepalense* (Hook. & Grev.) Schwägr.
— Laminae of branch leaves unistratose or partially bistratose in median and upper portions 3
3. Laminae of branch leaves partially bistratose in median and upper portions
..... *M. maolanense* Ze Y. Zhang, D.D.Li, J.Yu & S.L.Guo
— Laminae of branch leaves unistratose 4
4. All cells of branch leaves clear and smooth
..... *M. microstomum* (Hook. & Grev.) Schwägr., *M. cuspidatum* Hampe
— Cells of branch leaves papillose (mammillose or conic-bulging) to varying degrees 5
5. Seta rather short, often 0.3-0.7 mm *M. hainanense* S.L.Guo & S.He
— Seta relatively longer, often longer than 2.0 mm 6
6. Upper cells of branch leaves with a single large linear central papilla up to 14-18 µm high
..... *M. longipapillosum* D.D.Li, J.Yu, T.Cao & S.L.Guo, *M. taiwanense* Nog.
— Upper cells of branch leaves often pluri-papillose to varying degrees or conic bulging and mammillose ... 7
7. Calyptrae smooth and naked
..... *M. blumei* var. *zollingeri* (Mitt. ex Bosch & Sande Lac.) S.L.Guo, B.C.Tan & Virtanen, *M. macrosporum* Broth.
— Calyptrae hairy 8
8. Median and upper laminal cells mammilate (conic-bulging with a blunt central projection)
..... *M. uraiense* Nog., *M. fortunatii* Cardot & Thér.
— Median and upper laminal cells pluripapillose to varying degrees 9
9. Setae shorter than 2.0 mm, branch leaves with linear and smooth basal cells, sporophytes slightly exerted the perichaetial leaves
..... *M. prolognatum* Mitt.
— Setae often longer than 3.0 mm, branch leaves with papillose cells to varying degrees, sporophytes obviously exerted the perichaetial leaves 10
10. Basal cells of branch leaves often papillose to varying degrees *M. cavaleriei* Cardot & Thér.,
M. ferriei Cardot & Thér., *M. quercicola* Brotherus, *M. tosaе* Besch., *M. turgidium* Dixon
— Basal cells of branch leaves smooth, without papillae 11
11. Apices of branch leaves spreading when moist, calyptrae with long and brown-yellowish hairs
..... *M. comatum* Mitt.
— Apices of branch leaves often adaxially incurved and inrolled when moist, calyptrae with yellowish hairs
..... *M. japonicum* Dozy & Molk.

Macromitrium longipapillosum
D.D.Li, J.Yu, T.Cao & S.L.Guo

Macromitrium maolanense
Ze Y. Zhang, D.D.Li, J.Yu & S.L.Guo

MATERIAL EXAMINED. — **Japan** • Tochigi; *J. Bisset 10*; holotype: H-BR2575009! • Honshu; *Osada T. & Suzuki N. 1530*; KRAM-B036764.

MATERIAL EXAMINED. — **China** • Guizhou; *S. L. Guo & D. D. Li 171114076*; holotype: SHTU!

Macromitrium macrosporum Broth.

MATERIAL EXAMINED. — **Papua New Guinea** • Morobe; *D.H. Norris 63347*; KRAM-B-114327 • *T. Koponen 31877*; H3195989 • *T. Koponen 31918*; H3195982 • *T. Koponen 32046*; H3195983.

Macromitrium microstomum
(Hook. & Grev.) Schwägr.

MATERIAL EXAMINED. — **China** • Yunan; *T. Cao & G. Y. Song 060194*; SHTU.

Australia • New South Wales; *W. W. Watts 1048*; H-BR2521010 • Queensland; *Stone 19542*; MEL2245721 • *Stone 2050*; MEL2249823 • Van Dieman's Land; Spence & Neill.; lectotype: E-Grev E00011665!

Macromitrium nepalense
(Hook. & Grev.) Schwägr.

MATERIAL EXAMINED. — China • Yunnan; *Crosby* 14832, 15013, 15029; MO.

India • Assam, Garo Hills; *Markb* 5873; H-BR.

Laos • *Si He* 43782; MO.

Nepal • *Wallich s.n.*; BM000982523.

Macromitrium oussiense Broth. & Paris

MATERIAL EXAMINED. — China • Anhui; *Z. L. Wan & J. X. Luo* 9290; MO5276976 • *Z. L. Wan & J. X. Luo* 9265; MO5276974 • Fujian; *H. H. Chung B* 205; FH • *H. H. Chung B* 286; PC0083705 • Jiangsu, Ou Si; 16.II.1909; leg. R. P. Courtois; isotype: PC0083704!

Macromitrium prolognatum Mitt.

MATERIAL EXAMINED. — Japan • Kyoto; *M. Tagawa* 2241; H3090655 • Yamanashi; *R. Watanabe* 827; H3090652 • Kagoshima; *Z. Iwatsuki*, A. J. Sharp & Evelyn Sharp; H3090653 • Im Shikoku; *Faurie* 1024, 1900; isotype: H-BR2573002!

Macromitrium taiheizanense Nog.

MATERIAL EXAMINED. — China • Taiwan; *A. Noguchi* 6548; isotype: NICH365243! • Guizhou; *M. R. Crosby* 15933; MO6166109 • Sichuan; *P. L. Jr. Redfearn et al.* 34709; MO3965519.

Macromitrium taiwanense Nog.

MATERIAL EXAMINED. — China • Taiwan; *A. Noguchi* 6621; holotype: HIRO; isotype: NICH365244! • Zhejiang; *P. C. Wu* 305; PE, MO5922256.

Macromitrium tuberculatum Dixon

MATERIAL EXAMINED. — China • Anhui; *K. J. Guan* 11; MO5276970 • Guangdong; *W. T. Tsang* 25592; FH • *Y. W. Taam* 402; NY, MO5130513 • Hong Kong, Tai Mo Shan, New Territories; 4.I.1931; coll. Youngsaye; *Herklots* 297 O; holotype: BM000576127! • *Herklots* 297 B; paratype: BM000576128! • White Cloud Mountains; 800 ft. alt.; Canton; 26.XII.1930; coll. Youngsaye; *Herklots* 302D; paratype: BM000576129!

Macromitrium turgidum Dixon

MATERIAL EXAMINED. — Thailand • Chantaburi; *A. F. G. Kerr* 438; holotype: BM000825435!
China • Xizang; *Y. G. Su* 4833; MO3676218 • *Y. G. Su* 4641; MO3675104.

Macromitrium uraiense Nog.

MATERIAL EXAMINED. — China • Taiwan; *A. Noguchi* 573; holotype: HIRO; isotype: NICH365246!

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APPENDICES

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

Taxa	Collection locality	Collection number	Collector	Herbarium
<i>Macromitrium gymnostomum</i> Sull. & Lesq.	Zhejiang, China	20130805005	Guo S. L.	SHTU
<i>Macromitrium gymnostomum</i>	Taiwan, China	212	Guo S. L. & Cao T.	SHTU
<i>Macromitrium gymnostomum</i>	Taiwan, China	546	Guo S. L. & Cao T.	SHTU
<i>Macromitrium cavaleriei</i> Cardot & Thér.	Taiwan, China	323	Guo S. L. & Cao T.	SHTU
<i>Macromitrium cavaleriei</i>	Taiwan, China	622	Guo S. L. & Cao T.	SHTU
<i>Macromitrium cavaleriei</i>	Taiwan, China	696	Guo S. L. & Cao T.	SHTU
<i>Macromitrium cavaleriei</i>	Taiwan, China	697	Guo S. L. & Cao T.	SHTU
<i>Macromitrium japonicum</i> Dozy & Molk.	Laos	44258	He S.	MO
<i>Macromitrium japonicum</i>	Zhejiang, China	11112301	Guo S. L.	SHTU
<i>Macromitrium japonicum</i>	Zhejiang, China	11120350	Guo S. L.	SHTU
<i>Macromitrium japonicum</i>	Zhejiang, China	11112313	Guo S. L.	SHTU
<i>Macromitrium japonicum</i>	Zhejiang, China	11112302	Guo S. L.	SHTU
<i>Macromitrium japonicum</i>	Guangxi, China	110616058	Guo S. L. & Yu J.	SHTU
<i>Macromitrium japonicum</i>	Guizhou, China	20171113041	Guo S. L. & Li D. D.	SHTU
<i>Macromitrium japonicum</i>	Guizhou, China	20171114098	Guo S. L. & Li D. D.	SHTU
<i>Macromitrium japonicum</i>	Taiwan, China	517	Guo S. L. & Cao T.	SHTU
<i>Macromitrium japonicum</i>	Taiwan, China	513	Guo S. L. & Cao T.	SHTU
<i>Macromitrium japonicum</i>	Guangxi, China	110615156	Guo S. L. & Yu J.	SHTU
<i>Macromitrium japonicum</i>	Guangxi, China	110619312	Guo S. L. & Yu J.	SHTU
<i>Macromitrium japonicum</i>	Guangxi, China	110616036	Guo S. L. & Yu J.	SHTU
<i>Macromitrium japonicum</i>	Guizhou, China	20171113035	Guo S. L. & Li D. D.	SHTU
<i>Schlotheimia grevilleana</i> Mitt.	Zhejiang, China	110619117	Guo S. L.	SHTU

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
<i>trnL-F</i>	430	30	20	HKY+G
<i>trnG</i>	639	260	130	GTR+G
ITS2	687	256	123	HKY+G
Total	1756	546	273	—