



A new species, *Bryobrothera tambuyukonensis* (Daltoniaceae, Bryopsida), from Sabah, Borneo Island

HIROYUKI AKIYAMA¹ & MONICA SULEIMAN²

¹Museum of Nature and Human Activities & Phylogenetic Division/ Institute of Natural and Environmental Science, Hyogo Prefectural University, Yayoigaoka-6, Sanda, Hyogo 669-1546, Japan

²Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Jalan UMS, 88400 Kota Kinabalu, Sabah, Malaysia.

Abstract

We report a new species *Bryobrothera tambuyukonensis*, based on the specimens collected in Sabah, Borneo Island. Phylogenetic analyses with plastid (*rps4* and *trnL-F*) and mitochondrial (*nad5*) genes along with a number of morphological features (for example, undulate lamina, oblong-lanceolate leaves with a single strong costa reddish brown in color, and thick-walled and porose laminal cells) confirmed its distinctiveness from *B. crenulata* and also close relationship to the elimbata group comprised of *Adelothecium bogotense* and *Benitotania elimbata*.

Key words: mosses, *nad5*, phylogeny, *rps4*, *trnL-F*

Introduction

Mount Tambuyukon (2570 m) in Kinabalu Park (Sabah, Malaysia) is the largest ultramafic mountain on Borneo Island and quite rich in plant species (Van der Ent *et al.*, 2014). During a field survey carried out on this mountain in August 2008, the junior author collected a curious moss in a mossy forest looking quite similar to *Benitotania elimbata* H.Akiyama *et al.* (2003: 456), formerly reported from Kinabalu Park (Akiyama *et al.* 2003). The plants were collected again during a scientific expedition to Sungai Imbak Forest Reserve (Sabah, Malaysia) in April 2014. The second locality is also an ultramafic outcrop. The highest point of this outcrop is only 1460 m, but due to compression effect of forest zones on a small mountain (Richard 1996, Van der Ent *et al.* 2014), a mossy forest developed at a lower elevation even as low as 1100 m (Suleiman *et al.* 2011) and the plants were found in this kind of forest.

External morphology of the plants showed several different features from those expressed in plants of *Benitotania* Akiyama *et al.* (2003: 454), *Bryobrothera* Thériot (1921: 26), and *Adelothecium* Mitten (1869: 391), all of which have been suggested to form a well-supported monophyletic clade by phylogenetic analyses using molecular markers (Pokorny *et al.* 2012). Denticulate upper leaf margins and a strongly undulate upper leaf lamina are the most distinctive characteristics and are quite different from the three genera in these features. Therefore, we examined its identity using molecular markers as well as detailed morphological comparisons described below.

Material and Methods

Taxon sampling

In order to settle the systematic position of the present moss, we carried out phylogenetic analyses using *rps4* and *trnL-F* sequences from chloroplast DNA and *nad5* from mitochondrial DNA. We included in our analyses other members of the Hookeriales, especially other members of the family Daltoniaceae on the basis of previous phylogenetic analyses (Ho *et al.* 2012, Pokorny *et al.* 2012). Three taxa of the Hypopterygiaceae, i.e., *Cyathophorum bulbosum* (Hedwig 1801: 43) Müller (1850: 14), *Hypopterygium tamarisci* (Hedwig 1801: 212) Müller (1850: 8), and *Lopidium plumarium* (Mitten 1869: 329) Hampe (1879: 162) were used as outgroup terminals. The specimens used in the analysis and their accession numbers are listed in Appendix 1. As for the target taxon, we tried to extract DNA from those collected at different localities, but were able to obtain DNA only from a single sample.

DNA extraction, amplification, and sequencing

Nucleotide sequences were obtained from three regions, including nine newly generated nucleotide sequences for this study (Appendix 1). Sequenced regions are: (1) the plastid *trnS-rps4* region [i.e., *rps4* plus the *trnS-rps4* intergenic spacer (IGS), hereafter *rps4*], (2) the plastid *trnL-F* region, including the *trnL*_{UAA} group I intron and the *trnL-F* IGS (hereafter *trnL-F*), and (3) the mitochondrial *nad5* group I intron (hereafter *nad5*). We did not use plastid *rbcL* because of the deficiency of data in GenBank for the Daltoniaceae and related genera for this locus.

The procedures in the present analysis are mostly similar to those detailed in Chang *et al.* (2006) and Akiyama *et al.* (2010). We extracted total genomic DNA from herbarium material, using the usual CTAB method (Doyle & Doyle 1987) with 2% CTAB used for fresh materials within one month of their collection in the field. The PCR profile had an initial denaturing at 94°C for 3 min, followed by 35 cycles of 94°C for 30 sec, 56°C for 40 sec, 72°C for 1 min, with a final extension at 72°C for 5 min for *rps4*; an initial denaturing at 94°C for 3 min, followed by 30 cycles of 94°C for 30 sec, 58°C for 40 sec, 72°C for 1 min, with a final extension at 72°C for 5 min for *trnL-F*; an initial denaturing at 94°C for 1 min, followed by 30 cycles of 97°C for 1 min, 52°C for 1 min, 72°C for 3 min, with a final extension at 72°C for 7 min for *nad5*.

Primers both for PCR and sequencing are *rps5* and *trnas* for *rps4* (Cox *et al.* 2000), *trnC* and *trnF* for *trnL-F* (Taberlet *et al.* 1991), and *nad5-4F* and *nad5-3R* for *nad5* (Cox *et al.* 2004). Cleaning of the PCR products and sequencing were performed by MacroGen Inc., Japan (www.macrogen-japan.co.jp). Nucleotide sequence data reported are available in the DDBJ/EMBL/GenBank databases under the accession numbers listed in Appendix 1. We used MUSCLE (Edgar 2004) to manually align the final consensus sequences, together with previously published sequences from GenBank.

Phylogenetic analyses

Preliminary analyses using *rps4*, *trnL-F*, and *nad5* datasets separately suggest almost similar topologies, and thus combined data sets of all three sequences were used for further analyses. We performed Maximum Likelihood (ML) and Maximum Parsimony (MP) analyses using MEGA5.2.2. (Tamura *et al.* 2011). For MP analyses, we used default settings with TBR branch-swapping with 1000 random addition replicates. We used T92+G+I model in the ML analysis with all the terminals and T92+G model for smaller analysis described below with selected terminals as they were determined as the optimal models according to the Akaike's Information Criterion (AIC: Akaike 1973) as implemented in MEGA5.2.2. We did non-parametric bootstrapping analyses for ML and MP analyses. This was performed with 1000 pseudo-replicates with simple taxon addition in both ML and MP analyses.

To better understand the relationships of *Benitotania elimbata*, *Adelothecium bogotense* (Hampe 1866: 303) Mitten (1869: 391), *Bryobrothera crenulata* (Brotherus & Paris 1908: 19) Thériot (1921: 26), and the Sabah plant, additional analyses were performed with a small dataset containing *Ephemeropsis tjibodensis* Goebel (1892: 116) and *E. trentepohlioides* (Renner 1934: 88) Sainsbury (1951: 2) as outgroup terminals following the results obtained by Pokorny *et al.* (2012) and Ho *et al.* (2012).

Results

We got five most parsimonious trees for MP analysis with 1076 steps in tree length (CI= 0.61710, RI= 0.614593). Regarding the phylogenetic relationships, ML (Fig. 1) and MP (Fig. 2) results are largely congruent and there are no conflicts for the relationship between *Bryobrothera* and related three genera. Therefore, the following discussion is based on the results of the ML analysis.

Our present datasets of *rps4*, *trnL-F*, and *nad5* do not contain enough information to elucidate the relationships the terminals recognized as members of the Daltoniaceae sensu Pokorny *et al.* (2012). Except for some terminal pairs of genera, only two clades can be distinguished as monophyletic with high support values. One of these is the clade including the elimbate species of Daltoniaceae, that is *Benitotania*, *Adelothecium*, and *Bryobrothera* as well as the Sabah plant (indicated as *Bryobrothera tambuyukonensis* in Figs. 1–3), and the other clade including some other members of the family.

In the first clade, three specimens of *Benitotania elimbata*, and two of *Bryobrothera crenulata* form a monophyletic clade with high support values [bootstrap values (bv) =100 at both clades]. The Sabah plant forms a monophyletic clade with high support value with two specimens of *B. crenulata* (1–2; bv = 92). Subsequently, this clade become monophyletic with the addition of its sister group, including three specimens of *B. elimbata* (1–3) and *Adelothecium bogotense*, with moderate support values (bv = 88).

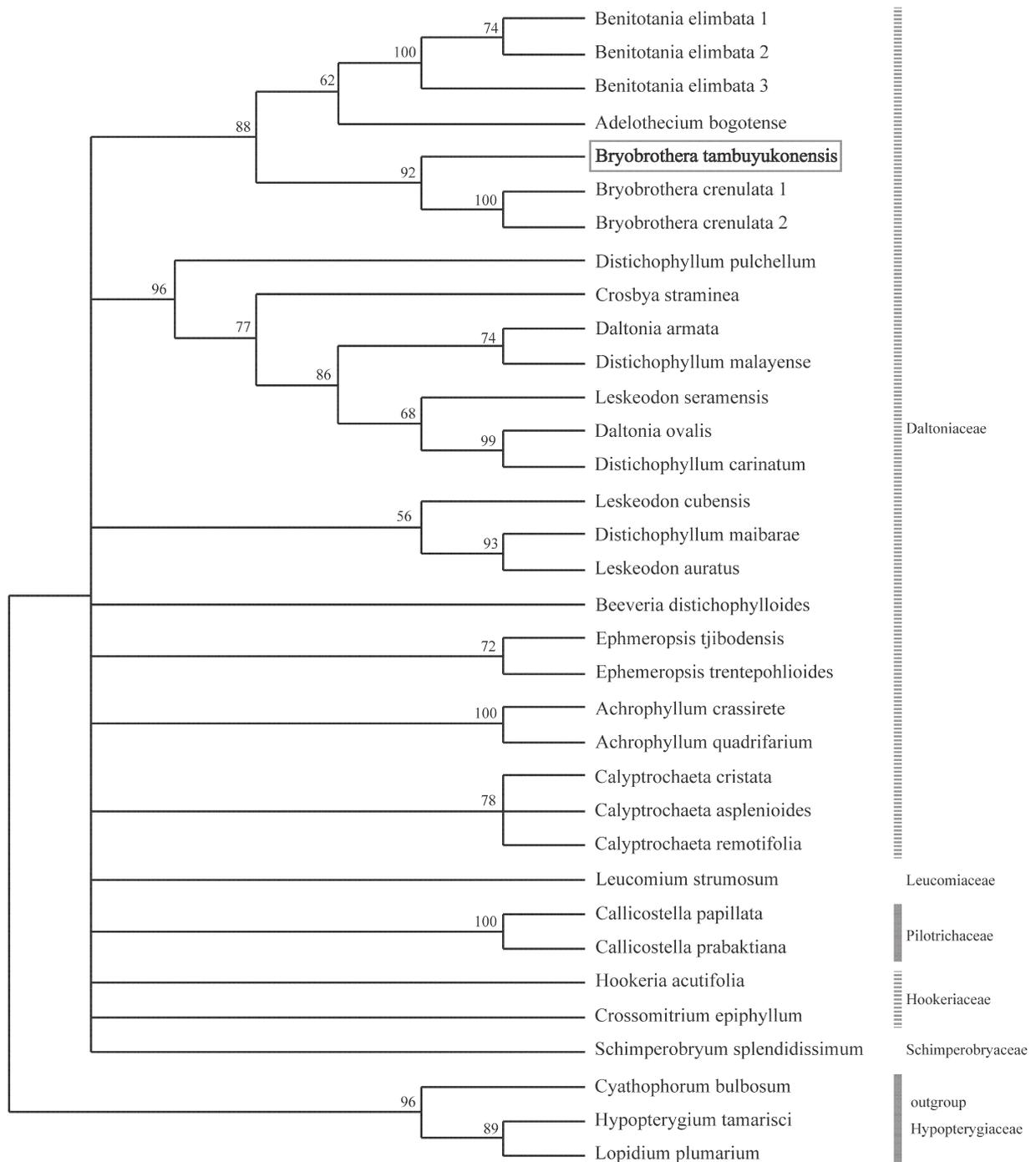


FIGURE 1. Maximum likelihood tree based on data set of *rps4*, *trnL-F*, and *nad5* sequences. Figures by the nodes are reliabilities estimated by bootstrap methods (1000 duplicates). The present new species *Bryobrothera tambuyukonensis* forms a monophyletic group with *Adelothecium*, *Benitotania*, and *Bryobrothera*.

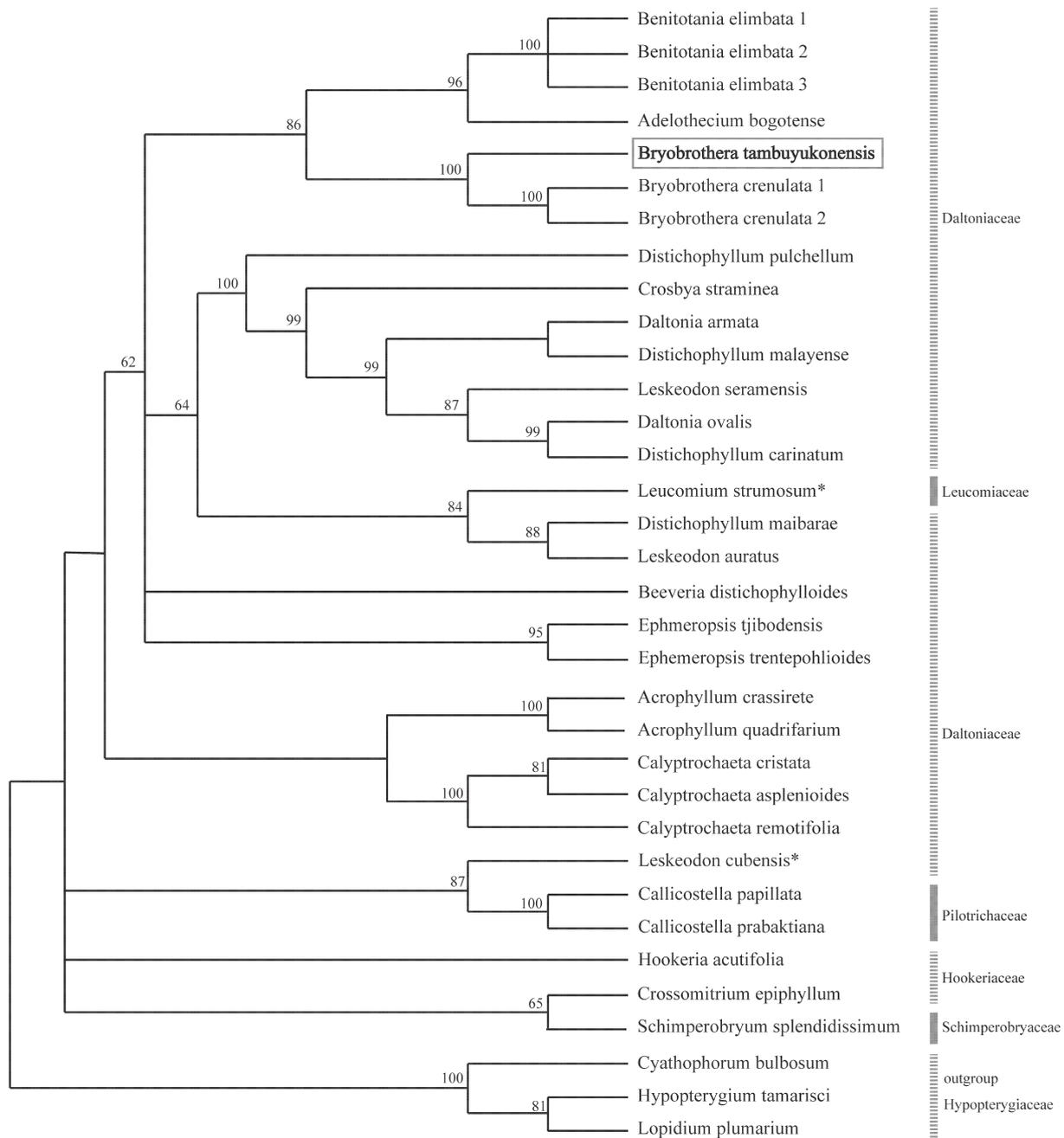


FIGURE 2. Strict consensus tree of Maximum parsimony based on data set of *rps4*, *trnL-F*, and *nad5* sequences. Figures by the nodes are reliabilities estimated by bootstrap methods (1000 duplicates). *Leucomium strumosum* and *Leskeodon cubensis* (with asterisks) changes their places in the tree comparing to that obtained from Maximum likelihood method.

Figure 3 shows the results of an analysis using a small dataset of *rps4*, *trnL-F*, and *nad5* and only including specimens of the four genera as well as two species of *Ephemeropsis* Goebel (1892: 98) as outgroup terminals. The Sabah plants form a monophyletic clade with high support value ($bv = 100$) with two specimens of *Bryobrothera crenulata*, and this is a sister to the clade including *Adelotheceium bogotense* and three specimens of *Benitotania elimbata*. Each of these four genera, however, is separated from the others by distinctive genetic distances.

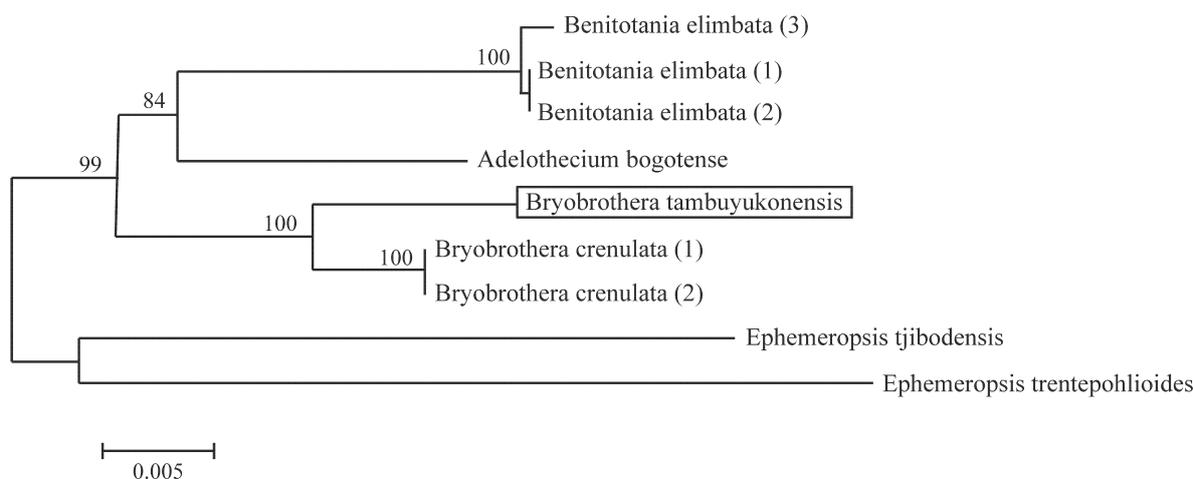


FIGURE 3. ML tree indicating phylogenetic interrelationships among the four species of the genera *Adelotheceium*, *Benitotania*, and *Bryobrothera* inferred from the small data set of *rps4*, *trnL-F*, and *nad5* sequences. Two *Ephemeroopsis* species are attributed as outgroup terminals of these three genera on the basis of results presented by Ho *et al.* (2012) and Pokorny *et al.* (2012). Scale bar indicates base substitution.

Discussion

Present molecular analyses suggest that the Sabah plant shows mostly close affinity to *Bryobrothera crenulata*. They share morphological and ecological features, such as (1) a single, subpercurrent, often reddish costae, (2) porose and thick-walled laminal cells, and (3) epiphytic habitat often found on tree trunks. However, *B. crenulata* differs from the Sabah plant in (1) much smaller plant size (stems 1.0–2.1 mm long), (2) presence of gemmae on rhizoids, (3) broadly elliptical to obovate to spatulate-obovate leaves with shorter length (0.6–1.2 mm long), (4) totally plane lamina, (5) round-hexagonal upper laminal cells, and (6) thin-walled alar cells arranged in a single row (Norris & Robinson 1979, Streimann 1999).

The Sabah plant and *Bryobrothera crenulata* then form a monophyletic clade with *Benitotania elimbata* and *Adelotheceium bogotense*. Pokorny *et al.* (2012) already showed the monophyly of these elimbate Daltoniaceae genera on the basis of five gene molecular analyses. As for morphology and habitat preference, the Sabah plants and the two genera share the following features; (1) growing on trunks and branches of small trees in mossy montane forests, (2) more or less flat foliation in aerial shoots, (3) leaves with distinctly narrowed bases, (4) narrow but clearly differentiated alar regions with quadrate, pitted cells, (5) fusiform and distinctly porose lower laminal cells, (6) quadrate to short-rectangular, thick-walled upper laminal cells, and (7) single, thick costa reaching more than 4/5 of leaf length.

The Sabah plant also looks similar to *Benitotania elimbata* in appearance in the field and leaf shape. It is also notable that the *B. elimbata* and the Sabah plants are known only from Sabah (northern part of the Borneo Island) and no sporophytes or asexual reproductive organs are known for these two species. *Benitotania elimbata*, however, differs from the Sabah plant in a number of morphological features, such as (1) shorter leaves (ca. 2.0 mm long), (2) totally plane lamina, (3) short rectangular to hexagonal upper and median laminal cells, (4) slight mamillation on laminal cells, (5) slender costa not reaching near leaf apices, and (6) short 3–4 cells axillary hairs (Akiyama *et al.* 2003). While, *Adelotheceium bogotense* differs from the Sabah plant in the features, such as (1) presence of microphyllous and gemmiferous tips of secondary stems bearing clusters of minute gemmae, (2) broadly ovate to obovate, rounded or rounded-obovate leaves, (3) totally plane lamina, and (4) nearly isodiametric upper lamina cells (Ochyra *et al.* 1992, Whittemore & Allen 1989).

Judging from the morphology and phylogeny analyses, we propose a new species under the genus *Bryobrothera* to accommodate the Sabah plants as described below.

Taxonomy

Bryobrothera tambuyukonensis H.Akiyama & Suleiman, *sp. nov.* (Figs. 4–23)

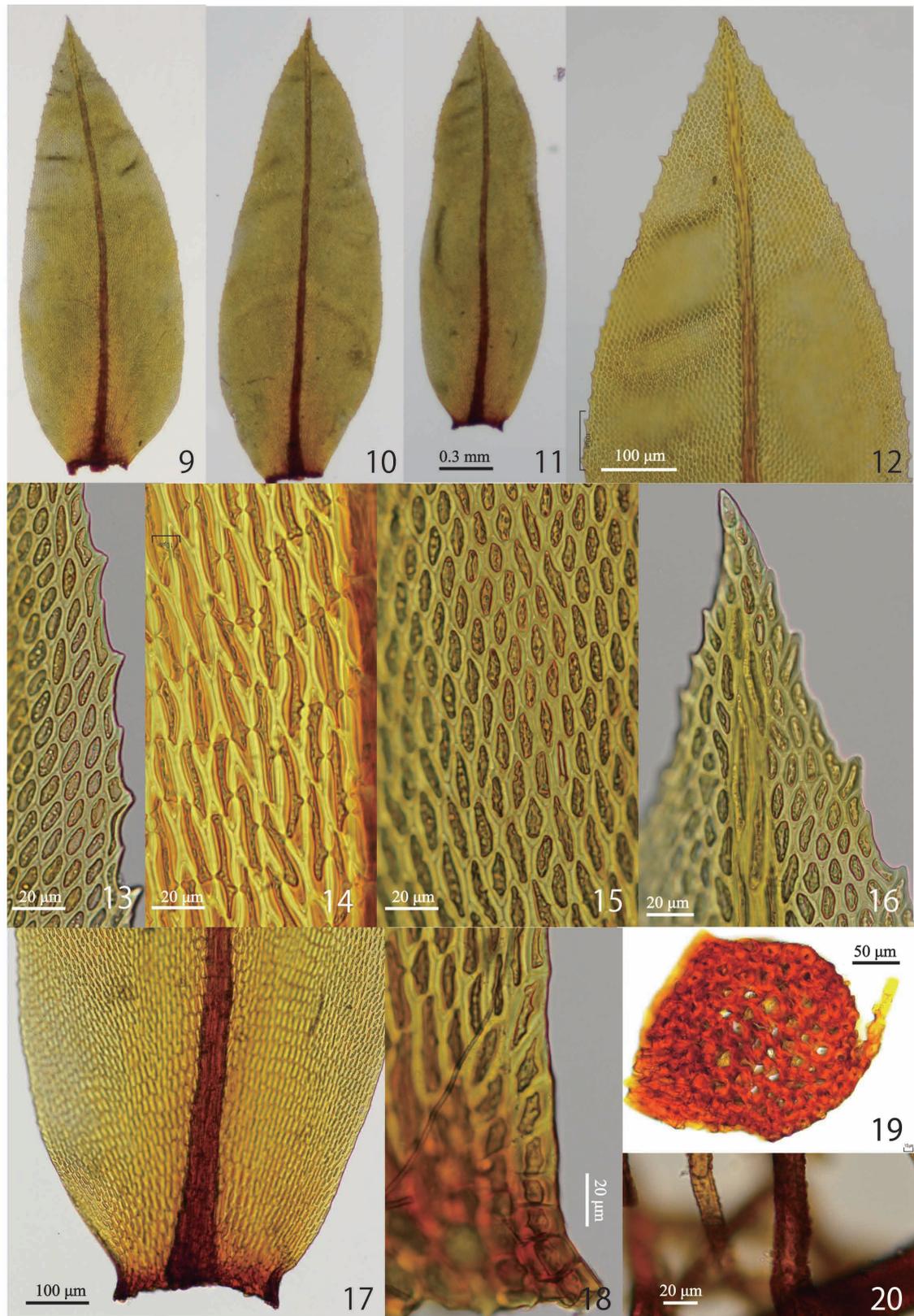
Type:—MALAYSIA. Sabah: Tongod District, Sg. Imbak Forest Reserve, Block IID, ridge zone, 05°04'35.2" N, 117°11'7.2" E, 1300 m asl., 2 April 2014, *M. Suleiman 5871* (holotype BORH; isotypes BM, HYO, L, MO, NY, SAN).

Plants light green or yellowish brown except for shoot tips, and quickly turning to brownish yellow in herbarium specimens. **Primary stems** short, tightly attached to substrata, bearing a number of aerial secondary stems. **Secondary stems** densely tufted, 3–7 cm long, scarcely branching, ± complanate-foliate, blackish brown, opaque, thick-walled except for pale green younger portions at tips, ca. 0.2–0.3 mm in diameter, round in transverse section, without central strand; stem leaves arranged in 10 rows and ± complanate-foliate; leaves of upper portion often caducous and the stems becoming naked, with lower portions of stems covered with old leaves, often decayed to only costae. **Pseudoparaphyllia** linear-lanceolate. **Axillary hairs** (Fig. 21) transparent, 3–6 cells long including a slightly differentiated single basal cell. **Rhizoids** mainly emerging from lower part of secondary stems, not restricted to around buds, reaching 7 mm long, sparsely branched, with intricately pinnately branched side branches; cells of main and side branches densely and minutely papillose. **Asexual reproductive organs** not found, but easily detached leaves may serve as vegetative propagules.



FIGURES 4–8. Plants of *Bryobrothera tambuyukonensis*.

4, 6–8: *M. Suleiman 5871* (Sg. Imbak; holotype). 5: *M. Suleiman 3698* (Tambuyukon).



FIGURES 9–20. *Bryobrothera tambuyukonensis*.

9–11: Stem leaves. 12: Upper half of a leaf; note the denticulate margins. 13: Midleaf marginal cells. 14: Midleaf juxtacostal cells. 15: Median laminal cells. 16: Leaf apex. 17: Leaf base. 18: Alar region with quadrate cells. 19: Transverse section of an aerial stem. 20: Rhizoids. (All from the holotype.)

Stem leaves oblong-lanceolate, distinctly narrowed at base, $2.2\text{--}3.2 \times 0.6\text{--}0.9$ mm, conspicuously undulate in upper portions of lamina when both dry and wet (Figs. 4–7); margins plane, denticulate except for basal portion;

marginal 1–2 cells slightly differentiated, longer than inner ones; costa single, reddish brown in color, subpercurrent, ending 2–3 cells below the leaf apex, protruding only on dorsal side, only with dorsal stereids. **Laminal cells** pale green at first, but soon turning deep reddish brown or brownish yellow by conspicuous deposition inside; juxtacostal cells much longer than median and marginal cells; upper laminal cells round to shortly elliptic, $7\text{--}15 \times 5\text{--}8 \mu\text{m}$, evenly thick-walled, smooth; median laminal cells elliptic to fusiform, sinuate, \pm porose, $12\text{--}30 \times 5\text{--}8 \mu\text{m}$, evenly thick-walled, smooth, becoming shorter and smaller toward the margin; lower laminal cells elongate, distinctly porose, $20\text{--}40 \times 5\text{--}8 \mu\text{m}$, evenly thick-walled, smooth; alar region differentiated with a few short-rectangular to quadrate cells, pale green at first, turning deeply reddish brown.

Dioicous? Male plants and antheridia not found. **Perichaetia** lateral on secondary stems. **Prefertilization perichaetial leaves** (Figs. 22–23) much smaller than stem leaves, linear-lanceolate, narrowed at base, 0.8 mm (innermost one)–1.3 mm (outermost one) long, with single costa; margins plane, serrate except for the basal portion; laminal cells smooth, similar to those of ordinary stem leaves in shape but with narrower and longer cells at margin; alar cells differentiated. **Archegonia** ca. 10 per perichaetium, without paraphyses. **Sporophytes** unknown.

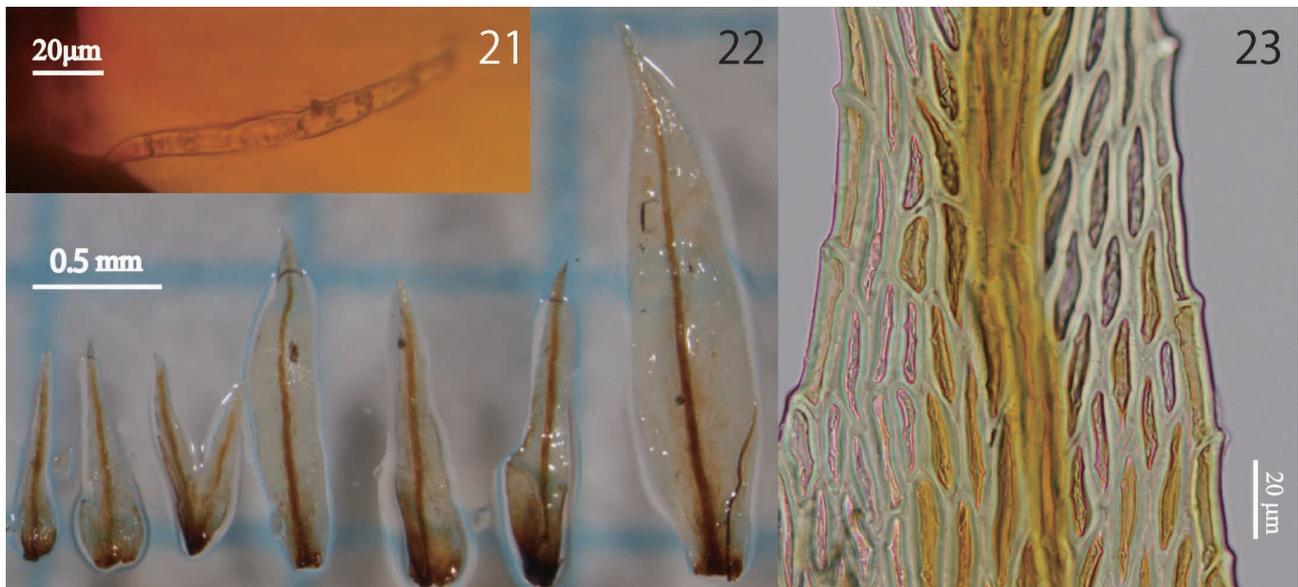
Other specimens examined: MALAYSIA. Sabah: Ranau District, Kinabalu Park, Mount Tambuyukon, Musang Camp (Km10) to the summit, $6^{\circ}11'56.5''\text{--}6^{\circ}12'42.7''\text{N}$, $116^{\circ}39'41.4''\text{--}116^{\circ}40'53.1''\text{E}$, 1450–1670 m asl., 14 August 2008, *M. Suleiman & D.P. Masundang* 3640 & 3690 (both BORH, KLU), 3687, 3690 & 3700 (all BORH, HIRO, KLU), 3702 (BORH, HYO, KLU, SNP), 3704 (BORH, HYO, KLU, NY, SNP): Tongod District, Sg. Imbak Forest Reserve, Block IID, ridge zone, $5^{\circ}04'56.0''\text{--}5^{\circ}04'35.2''\text{N}$, $117^{\circ}09'16.3''\text{--}117^{\circ}11'7.4''\text{E}$, 900–1300 m asl., 2 April 2014, *M. Suleiman* 5807 (BORH), 5820 & 5824 (both BORH, SAN).

Habitat: Forming compact and dense tufts on trunks and branches of small trees and shrubs in mossy forests.

Distinguishing features: (1) epiphytic habit, (2) complanate foliation, (3) distinctly undulate upper lamina, (4) evenly thick-walled, porose, and smooth laminal cells, and (5) denticulate upper leaf margins.

Note 1: The rhizoid branching pattern of *Bryobrothera tambuyukonensis* resembles that reported in the genus *Adelothecium bogotense* (Whittemore and Allen 1989), that is, with intricately pinnately branched side branches. They are, however, not restricted around branch primordia as in the case of *A. bogotense*.

Note 2: Axillary hairs of *B. tambuyukonensis* are almost similar in size and the number of cells to those of *B. crenulata* and *Benitotania elimbata*. While they are shorter than those of *Adelothecium bogotense* [10 or more cells according to Norris & Robinson (1979) and illustrated by Buck (1998: p. 18)] and have a single basal cell, which is absent in axillary hairs of *A. bogotense*.



FIGURES 21–23. *Bryobrothera tambuyukonensis*. 21: Axillary hair. 22: Perichaetial leaves. 23: Margin of inner perichaetial leaf. (All from the holotype.)

Note 3: According to our field observation, this species, although much larger and often brownish in color, has a habit similar to that of *Benitotania elimbata*. These two species grow in the same locality, as seen in Sungai Imbak Forest Reserve. It prefers small tree trunks in steep upper montane forests with high humidity, at elevations of 900–1700 m. A large population of this species was observed by a mountain stream in Sungai Imbak Forest Reserve.

Interestingly, this species was not found at the Silau-Silau Trail in the vicinity of the Headquarter office of Kinabalu Park or at the summit zone of Mount Alab where *B. elimbata* thrives. Neither of these sites is ultramafic.

Keys to *Bryobrothera tambuyukonensis* and related species

1. Inner cortical cells of stems large and thin-walled and outer ones small and thick-walled. Gemmae on reduced axillary branches. Axillary hairs 5–10-celled, with a hardly differentiated basal cell (rarely with single, slightly pigmented basal cell). Central and South America, and Africa (Tanzania and Madagascar) *Adelothecium bogotense*
- Cortical cells of stems small and thick-walled throughout. Gemmae on reduced axillary branches absent (except for rhizoidiform ones reported from *Bryobrothera*). Axillary hairs less than 6-celled, with 1–2 ± pigmented basal cells2.
2. Leaves broadly elliptical to obovate or spatulate-obovate, 0.3–0.6 mm long. Rhizoidiform gemmae in leaf axils. Pseudoparaphyllia filamentous, 3-celled. Philippines, Indonesia (Seram), Australia, Solomon Island, New Caledonia, Fiji.....
.....*Bryobrothera crenulata*
- Leaves narrowly ovate to lanceolate, usually more than 2 mm long. Gemmae absent. Pseudoparaphyllia linear-lanceolate. Only known from North Borneo3.
3. Leaf apex acute, not mucronate. Lamina distinctly undulate in dry and wet conditions. Laminal cells smooth. Leaf margin denticulate above.....
.....*Bryobrothera tambuyukonensis*
- Leaf apex obtuse, mucronate. Lamina plane, never undulate. Laminal cells minutely verrucose. Leaf margin almost entire.....
.....*Benitotania elimbata*

Acknowledgements

We would like to thank Sabah Parks for research permission at Mount Tambuyukon and Sabah Forestry Department for the invitation to participate in the Heart of Borneo (HoB) scientific expedition to Sungai Imbak Forest Reserve. We also thank to Dr. A. Takano (Museum of Nature and Human Activities, Hyogo) for kind help in molecular analyses in a laboratory, Dr. W. R. Buck (New York Botanical Garden) for linguistic corrections of the text. This study was financially supported by JSPS KAKENHI no. 24570108 to HA and no. 24255007 to Dr. M. Kanzaki (Kyoto University) and Nagao Natural Environment Foundation (NEF) of Japan to MS.

References

- Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. *In*: Petrov, B.N., and Caski, F. (Eds.) *Proceedings of the 2nd International Symposium on Information Theory*. Akadimiai Kiado, Budapest, pp. 267–281.
- Akiyama, H., Tsubota, H., Yamaguchi, T. & Suleiman, M. (2003) The new genus *Benitotania* (Daltoniaceae, Bryopsida) from Mt. Kinabalu. *Bryologist* 106: 454–459.
<http://dx.doi.org/10.1639/13>
- Akiyama, H., Chiang, Y. & Tan, B.C. (2010) *Clastobryopsis imbricata* (Pylaisiadelphaceae) *sp. nov.* from Doi Inthanon, northern Thailand. *Bryologist* 123: 752–759.
<http://dx.doi.org/10.1639/0007-2745-113.4.752>
- Brotherus, V.F. & Paris, J.É.G.N. (1908–1909) Contribution à la flore bryologique de la Nouvelle Calédonie II. *Oefversigt af Förhandlingar, Finska Vetenskaps-Societeten* 51A(17): 1–31.
- Buck, W.R. (1998) Pleurocarpous mosses of the West Indies. *Memoirs of The New York Botanical Garden* 82: 1–400.
- Chang, Y., Khiong, C.-W., Graham, S.W. & Tan, B.C. (2006) Molecular evidence for the systematic positions of two enigmatic mosses: *Pterogonidium pulchellum* (Sematophyllaceae, Musci) and *Piloecium pseudorufescens* (Myuriaceae, Musci). *Canadian Journal of Botany* 84: 501–507.
<http://dx.doi.org/10.1139/b06-002>
- Cox, C.J., Goffinet, B., Newton, A.E., Shaw, A.J. & Hedderson, A.J. (2000) Phylogenetic relationships among the diplolepidous-alternate

- mosses (Bryidae) inferred from nuclear and chloroplast DNA sequences. *Bryologist* 103: 224–240.
[http://dx.doi.org/10.1639/0007-2745\(2000\)103\[0224:pratda\]2.0.co;2](http://dx.doi.org/10.1639/0007-2745(2000)103[0224:pratda]2.0.co;2)
- Cox, C.J., Goffinet, B., Shaw, A.J. & Boles, B. (2004) Phylogenetic relationships among the mosses based on heterogeneous Bayesian analysis of multiple genes from multiple genomic compartments. *Systematic Botany* 29: 234–250.
<http://dx.doi.org/10.1600/036364404774195458>
- Doyle, J.J. & Doyle, L.L. (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11–15.
- Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32: 1792–1797.
<http://dx.doi.org/10.1093/nar/gkh340>
- Goebel, K. von (1892) Archegoniatenstudien. *Flora* 76: 92–116 + 2 plates.
- Hampe, E. (1866) Prodromus Flore Novo-Granatensis. [sér. 5] *Annales des Sciences Naturelles, Botanique* 5: 301–342.
- Hampe, E. (1879) Enumeratio muscorum hactenus in provinciis Brasiliensibus Rio de Janeiro et São Paulo detectorum. *Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn* 1879: 73–164.
<http://dx.doi.org/10.5962/bhl.title.4410>
- Hedwig, J. (1801). *Species Muscorum Frondosorum: Descriptae et tabulis*. Sumpta J.A. Barthii, Leipzig, vi+352 pp.
<http://dx.doi.org/10.5962/bhl.title.26>
- Ho, B.-C., Pokorny, L., Tan, B.C., Frahm, J.-P., Shaw, A.J. & Quandt, D. (2012) Molecular evolution and diversification of the moss family Daltoniaceae (Hookeriales, Bryophyta) with emphasis on the unraveling of the phylogeny of *Distichophyllum* and its allies. *Botanical Journal of the Linnean Society* 170: 157–175.
<http://dx.doi.org/10.1111/j.1095-8339.2012.01279.x>
- Mitten, W. (1869) Musci Austro-Americani. *Journal of the Linnean Society, Botany* 12: 1–659.
- Müller, C. (1849–1851) *Synopsis Muscorum Frondosorum omnium hucusque Cognitorum* 2. Alb. Foerstner, Berlin.
<http://dx.doi.org/10.5962/bhl.title.31>
- Norris, D.H. & Robinson, H. (1979) The systematic position of *Bryobrothera crenulata*. *Bryologist* 82: 305–309.
<http://dx.doi.org/10.2307/3242094>
- Ochyra, R., Bednarek-Ochyra, H., Pócs, T. & Crosby, M.R. (1992) The moss *Adelothecium bogotense* in Continental Africa, with a review of its world range. *Bryologist* 95: 287–295.
<http://dx.doi.org/10.2307/3243487>
- Pokorny, L., Ho, B.-C., Frahm, J.-P., Quandt, D. & Shaw, A.J. (2012) Phylogenetic analyses of morphological evolution in the gametophyte and sporophyte generations of the moss order Hookeriales (Bryopsida). *Molecular Phylogenetics and Evolution* 63: 351–364.
<http://dx.doi.org/10.1016/j.ympev.2012.01.005>
- Renner, O. (1934) Javanische Kleinigkeiten. Über Ephemeroopsis, Archephemeroopsis n. g., Leptocolea, Cuscuta, Casuarina, Ficus. *Annales du Jardin Botanique de Buitenzorg* 44: 65–100
- Richard, P.W. (1996) *The tropical rain forest*. 2nd ed. Cambridge University Press, Cambridge, 600 pp.
- Sainsbury, G.O.K. (1951) The taxonomy of moss *Archephemeroopsis trentepohlioides* Renn. *Transactions and Proceedings of the Royal Society of New Zealand* 79: 203–205.
- Streimann, H. (1999) Taxonomic studies on Australian Hookeriaceae (Musci) 2. The genera *Distichophyllum* and *Bryobrothera*. *Journal of the Hattori Botanical Laboratory* 86: 89–119.
- Suleiman, M., Chua, M.S. & Awang-Kanak, F. (2011) Mosses from the southern part of Imbak Canyon Conservation area. In: Latiff, A. & Sinun, W. (Eds.) *Imbak canyon Conservation Area, Sabah - Geology, Biodiversity and Socio-economic Environment*, Akademi Sains Malaysia & Yayasan Sabah, Kota Kinabalu, pp. 269–281.
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular Evolutionary Genetics Analysis using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. *Molecular Biology and Evolution* 28: 2731–2739.
<http://dx.doi.org/10.1093/molbev/msr121>
- Thériot, I. (1921) Considérations sur la flore bryologique de la Nouvelle-Calédonie et diagnoses d'espèces nouvelles. *Revue Bryologique et Lichénologique* 48: 22–28, 54–59.
- Van der Ent, A. (2014) *The ultramafic flora of Sabah: An introduction to the plant diversity on ultramafic soils*. Natural History Publications (Borneo), Kota Kinabalu, 251 pp.
- Whittemore, A. & Allen, B. (1989) The systematic position of *Adelothecium* Mitt. and the familial classification of the Hookeriales (Musci). *Bryologist* 92: 261–272.
<http://dx.doi.org/10.2307/3243392>

Appendix 1. The specimens and their accession numbers (in order of *rps4*, *trnL-F*, and *nad5*) and voucher information used in the present analyses. New accessions are indicated with an asterisk (*) before species names and with voucher information.

Achrophyllum crassirete (Matter) Matteri, HQ443812, HQ443849, HQ443781 (*J.-P. Frahm 21-10*, BONN). *A. quadrifarum* (Sm.) Vitt & Crosby, AY449660, HQ443850, AY452316 (*W. Frey & T. Pfeiffer 98-T2*, CHR and *H. Streimann 51258*, NY). *Adelothecium bogotense* (Hampe) Mitt., AY306856, AY306690, AY452318 (*Vital & W. R. Buck 19649*, NY). *Beeveria distichophylloides* (Broth. & Dixon) Fife, AY306867, AY306701, AY452320 (*A. Fife 11150*, NY). *Benitotania elimbata* H. Akiyama, T. Yamag. & Suleiman (1), AY449661, AY449669, AY452321 (*Akiyama & Suleiman 2002*, NY). **B. elimbata* (2), AB971207, AB971210, AB971213 (Malaysia, Sabah, Gunong Alab, *H. Akiyama 23554*, HYO). **B. elimbata* (3), AB971208, AB971211, AB971214 (Malaysia, Sabah, Sungai Imbak, *M. Suleiman 5823*, HYO). *Bryobrothera crenulata* (Broth. & Paris) Thér. (1), AY306869, AY306703, AY452325 (*H. Streimann 57716*, NY). *B. crenulata* (2), HQ443814, HQ443852, HQ443783 (*H. Streimann & T. Pócs 64341*, S). **B. tambuyukonensis*, AB971209, AB971212, AB971215 (Malaysia, Sabah, Sungai Imbak, *Suleiman 5871*, HYO, isotype). *Callicostella papillata* (Mont.) Mitt., HQ443816, HQ443854, HQ443784 (*B.C. Ho 07-003*, SING). *C. prabaktiana* (Müll.Hal.) Bosch & Sande Lac., HQ443817, HQ443855, HQ443785 (*B.C. Ho 07-008*, SING). *Calyptrochaeta asplenioides* (Brid.) Crosby, HQ613603, HQ398739, HQ613542 (*Arts RSA27/11*, EGR). *C. remotifolia* (Müll.Hal.) Z.Iwats., B.C.Tan & A.Touw, HQ443820, HQ443857, HQ443788 (*Linis s.n.*, 28 VI 2007, SING). *C. cristata* (Hedw.) Desv., HQ443819, HQ443856, HQ443787 (*J.-P. Frahm 1-11*, BONN). *Crosbya straminea* (Mitt. ex Beckett) Vitt, AY306887, AY306721, AY908490 (*A. Fife 10379*, NY). *Crossomitrium epiphyllum* (Mitt.) Müll.Hal., AY306885, AY306719, AY452337 (*W. R. Buck 33259*, NY). *Cyathophorum bulbosum* (Hedw.) Müll.Hal., AY306889, AY306723, AY452339 (*H. Streimann 55638*, NY). *Daltonia armata* E.B.Bartram, HQ443826, HQ443863, HQ443793 (*B.C. Ho 08-007*, SING). *D. marginata* Griff., HQ443829, GQ906139, HQ443796 (*W. R. Buck 39344*, NY). *Distichophyllum carinatum* Dixon & W.E.Nicholson, HQ613618, HQ613682, HQ613555 (*D.G. Long 24419*, E). *D. maibarae* Besch., HQ613637, HQ613700, HQ613567 (*M. Mizutani 14977*, S). *D. malayense* Damanhuri & Mohamed, HQ613638, HQ613701, HQ613568 (*M. Suleiman 1608*, BORH). *D. pulchellum* (Hampe) Mitt., HQ613649, HQ613712, HQ613577 (*H. Streimann 63444*, S). *Ephemeropsis tjibodensis* K.I.Goebel, HQ443840, HQ443873, HQ443806 (*Bisang & L. Hedenäs s.n. 'B57686'*, S). *E. trentepohlioides* (Renner) Sainsbury, AY306906, AY306740, AY90849 (*Macmillan 95/94*, NY). *Hookeria acutifolia* Hook. & Grev., HQ443843, HQ443875, HQ443807 (*B.C. Ho 07-004*, SING). *Hypopterygium tamarisci* (Hedw.) Müll.Hal., EF647964, EF657194, EF667887 (*Holst 4910*, NY). *Leskeodon seramensis* H.Akiyama, HQ613671, HQ613734, HQ613596 (*T. & S. Pócs 03279/DB*, EGR). *L. auratus* (Müll. Hal.) Broth., HQ613669, HQ613732, HQ613594 (*B. Allen 15351*, NY). *L. cubensis* (Mitt.) Thér., HQ443845, HQ443879, HQ443808 (*Djan-Chékar 94-340*, NY). *Leucomium strumosum* (Hornsch.) Mitt., AY306943, AY306777, AY908488 (*Holz FG 00-268*, NY). *Lopidium concinnum* (Hook.) Wilson, AY306947, AY306781, AY452375 (*Vital & W. R. Buck 20001*, NY). *Schimperobryum splendidissimum* (Mont.) Margad., AY306988, AY306822, AY452385 (*Holz & Franzaring Ch 00-156*, NY).