Mohamedia, a new genus of Lejeuneaceae (Marchantiophyta) from Oceania and tropical Asia

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Abstract. Lejeuneaceae is the largest family of liverworts with an estimated 1800 species in about 73 genera. The systematic position of a number of taxa in the family remains ambiguous owing to the lack of molecular data and morphological observations especially on oil bodies and ocelli in fresh samples. *Drepanolejeunea brunnea* Mizut. and *Lepidolejeunea borneensis* (Steph.) R.M.Schust. are two examples of these taxa. Here we investigate the phylogenetic relationships of these two species by using the nuclear ribosomal ITS region and two chloroplast regions (*rbc*L, *trn*L–*trn*F). The molecular data show that *Drepanolejeunea brunnea* and *Lepidolejeunea borneensis* form a well-supported clade unrelated to *Drepanolejeunea* (Spruce) Steph. and *Lepidolejeunea* R.M.Schust. On the basis of the combined molecular-phylogenetic and morphological data, a new genus in the subtribe Lepidolejeuneinae, *Mohamedia* R.L.Zhu et L.Shu, is described to accommodate *Drepanolejeunea brunnea* and *Lepidolejeunea borneensis*. *Mohamedia* is closely related to *Otolejeunea* Tixier endemic to Madagascar, but differs in the thinner stem with only 3(–4) rows of medullary cells, perianths with 4–5 crenulate to weakly dentate keels and without auricles, and lack of an unbroken row of ocelli in leaf lobes. Two new subgenera, *Mohamedia* subg. *Mohamedia* and *Mohamedia* subg. *Piippolejeunea* R.L.Zhu et L.Shu, are described and the new combinations (*Mohamedia brunnea* (Mizut.) R.L.Zhu et L.Shu and *M. borneensis* (Steph.) R.L.Zhu et L.Shu) are proposed.

Keywords. Brunei, *Drepanolejeunea, Lepidolejeunea*, ocellus, oil body, surface wax.

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Lejeuneaceae, the largest family of liverworts (Marchantiophyta), comprises an estimated 1800 species in about 73 genera (Zhu et al. 2018b). Although much progress in molecular phylogenetics has been made in recent years, the division of the diverse family into natural genera has not yet been completed (Zhu & Shu 2018). A number of taxa of the family are still poorly known owing to the lack of molecular data and detailed morphological observations especially on oil bodies and ocelli. *Drepanolejeunea brunnea* Mizut. is a rare species previously known only from the type locality in Borneo (Mizutani 1970). It was placed in *Ophthalmolejeunea* R.M.Schust. as *O. brunnea* (Mizut.) R.M.Schust. by Schuster (1992) but the latter genus (type: *O. monophthalma* R.M.Schust.) is a synonym of *Drepanolejeunea* (Spruce) Steph. (e.g., He et al. 2012; this study). *Lepidolejeunea borneensis* (Steph.) R.M.Schust., first described by Stephani (1914 as *Hygrolejeunea borneensis* Steph.), was moved to *Pycnolejeunea* (Spruce) Schiffn. as *P. borneensis* (Steph.) Mizut. (*nom. illeg*., Mizutani 1972) and *P. acutifolia* Mizut. (Mizutani 1976), but accepted in *Lepidolejeunea* R.M.Schust by Piippo (1986) in her monograph of the latter genus. It is the only autoicous species of *Lepidolejeunea* and is known from Indonesia (Borneo), Malaysia (Sarawak), Singapore and the Pacific region (Juslén et al. 2001; Piippo 1986; Pócs et al. 2011). The generic

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placement of both *Lepidolejeunea borneensis* and *Drepanolejeunea brunnea* remains in doubt owing to the lack of molecular data and morphological observations especially on oil bodies and ocelli in fresh samples. Recent molecular-phylogenetic studies on Lejeuneaceae revealed that *Lepidolejeunea* was a well-supported monophyletic group belonging in its own subtribe Lepidolejeuneinae Gradst. together with seven other genera (Schäfer-Verwimp et al. 2017; Zhu et al. 2018a,b). *Drepanolejeunea*, however, proved not fully monophyletic and a new genus, *Soella* R.L.Zhu et al. known from China and Japan, was described based on *Drepanolejeunea obtusifolia* T.Yamag. (Zhu et al. 2018b). In this work, we present a first molecular and morphological analysis of fresh samples of *Drepanolejeunea brunnea* and *Lepidolejeunea borneensis*. Our results show that *Drepanolejeunea brunnea* and *Lepidolejeunea borneensis* form a well-supported clade unrelated to *Drepanolejeunea* and *Lepidolejeunea* (**Fig. 4**). On the basis of the combined molecular-phylogenetic and morphological data we propose the new genus *Mohamedia* to accommodate these two species.

MATERIALS AND METHODS

Taxon sampling. The taxon sampling consists of 143 samples of 126 species of Lejeuneaceae, including two samples of *Drepanolejeunea brunnea*, three of *Lepidolejeunea borneensis*, and 119 further members (138 samples) of all 13 subtribes of the tribe Lejeuneeae (Zhu et al. 2018a,b) to which these two species belong. Since *Drepanolejeunea brunnea* and *Lepidolejeunea borneensis* were placed in the subtribes Drepanolejeuneinae Gradst. and Lepidolejeuneinae, respectively (Söderström et al. 2016), we made a broad and representative sampling of these two subtribes, including 33 accessions of 23 species of Lepidolejeuneinae and 26 accessions of 25 species of Drepanolejeuneinae. Several recently described genera in the tribe Lejeuneeae, such as *Cumulolejeunea* R.L.Zhu & L.Shu, *Gaolejeunea* R.L.Zhu et W.Ye, *Soella* R.L.Zhu et al., *Reinerantha* Gradst. et R.L.Zhu and *Yanoella* R.L.Zhu et al. (Gradstein et al. 2018; Ye & Zhu 2018; Zhu et al. 2018a,b; Zhu & Shu 2018) were also included in our analysis. Five species belonging to five genera in the subfamily Ptychanthoideae Mizut., including *Archilejeunea fuscescens* (Hampe ex Lehm.) Fulford, *Lopholejeunea eulopha* (Taylor) Schiffn., *Neurolejeunea breutelii* (Gottsche) A.Evans, *Ptychanthus striatus* (Lehm. et Lindenb.) Nees, and *Thysananthus spathulistipus* (Reinw. et al.) Lindenb., were selected as an outgroup. Sequences of seven species were newly generated in the present study; the remaining sequences were downloaded from GenBank. A complete list of taxa, voucher information, and GenBank numbers is shown in **Table 1** and **Supplementary Table S1.**

Morphological observation. Field images were photographed with a Sony ILCE-6000 digital camera. Micrographs were made with an Olympus BX43 microscope equipped with a DP71 digital camera. The confirmation of surface wax projections was by using washing of leaves in chloroform for three minutes prior to observation.

DNA extraction, amplification, sequencing and alignment. Total DNA was isolated from fresh or silica-dried specimens using DNeasy Plant Mini Kits (Qiagen, Hilden, Germany), following the manufacturers' instructions, with minor modifications. For a high concentration of total DNA, we chose 70 µL (micro sign + capital L) buffer AE to elute in the last step and repeat it with the eluent.

Three molecular markers were investigated, nrITS, *trn*L–F and *rbc*L as in earlier papers about Lejeuneaceae (Zhu et al. 2017; Zhu et al. 2018a,b; Zhu & Shu 2018). Sequencing was carried out bidirectionally by Jie Li Biology Inc., China (http://www.genebioseq.com). DNA sequence edition and consensus assembly were performed using PhyDE v.0.997. Sequences aligned through the MAFFT v.7 (Katoh & Standley 2013) and manually corrected with PhyDE v.0.997. For nrITS, the program Gblocks v.0.91b (Castresana 2000; Talavera & Castresana 2007) was used to delimit and remove regions of alignment uncertainty with options for a "less stringent" selection on Gblocks web server (http://molevol.cmima.csic.es/castresana/Gblocks_server.html). The final alignments are available on TreeBASE (http://purl.org/phylo/treebase/phylows/study/TB2:S23882).

Phylogenetic analyses. Phylogenetic analyses were performed using three different strategies, i.e., maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI). Dataset congruence was accessed analyzing each with the "fast" stepwise-addition parsimony bootstrapping procedure implemented in PAUP* V4.0 (Swofford

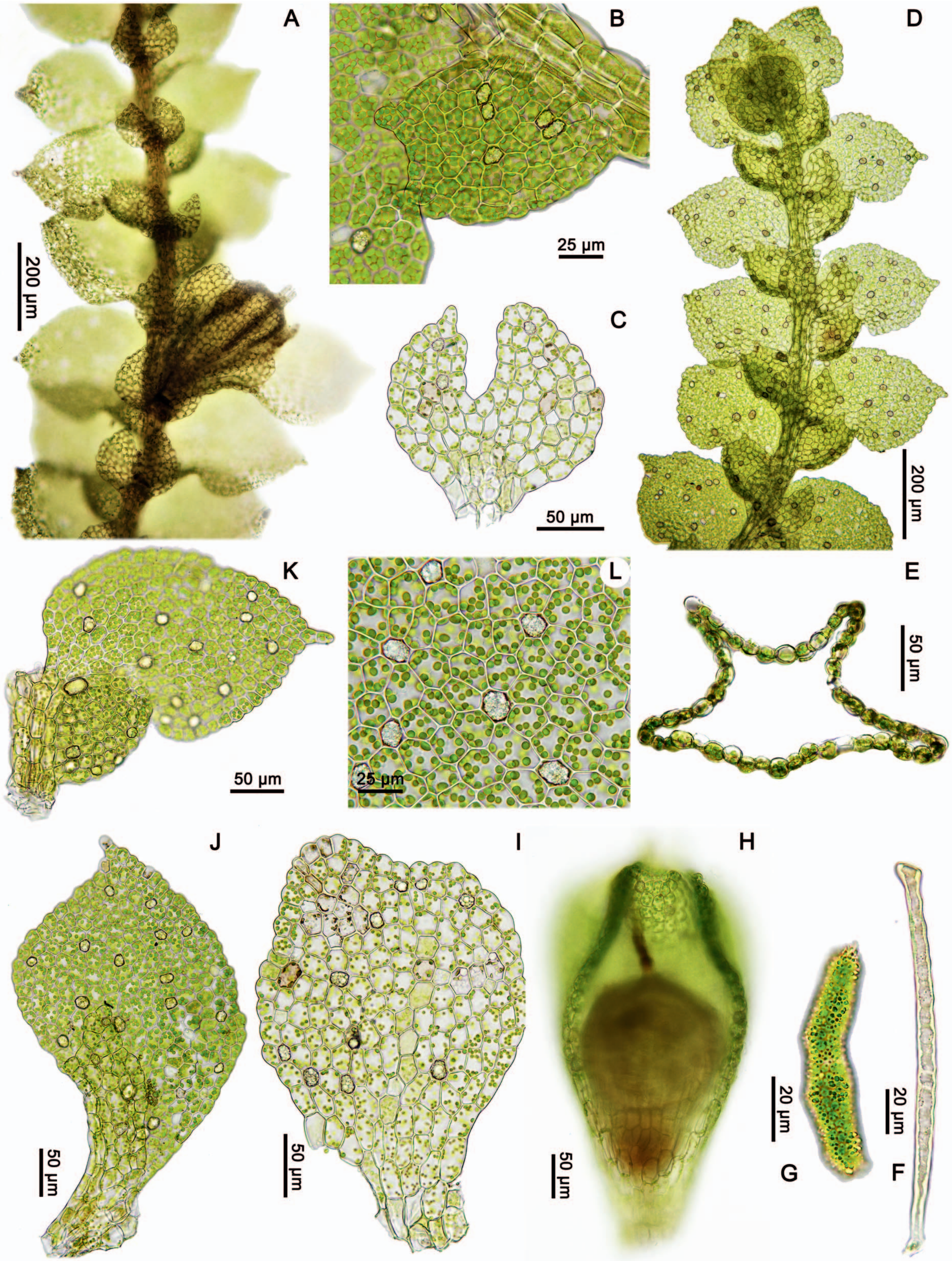

Figure 1. *Mohamedia borneensis* (Steph.) R.L.Zhu et L.Shu. **A.** Portion of shoot showing a gynoecium and pycnolejeuneoid leaf sequence, ventral view. **B.** Leaf lobule showing proximal hyaline papilla. **C.** Underleaf. **D.** Portion of shoot, ventral view. **E.** Transverse section of perianth. **F.** Elater. **G.** Spore. **H.** Perianth, ventral view. **I.** Female bracteole. **J.** Female bract, ventral view. **K.** Leaf showing the basal ocellus belonging to the basal type. **L.** Median cells of leaf lobe showing scattered ocelli. All from *B. C. Ho & Y.M. Wei 20181005-49* (HSNU).

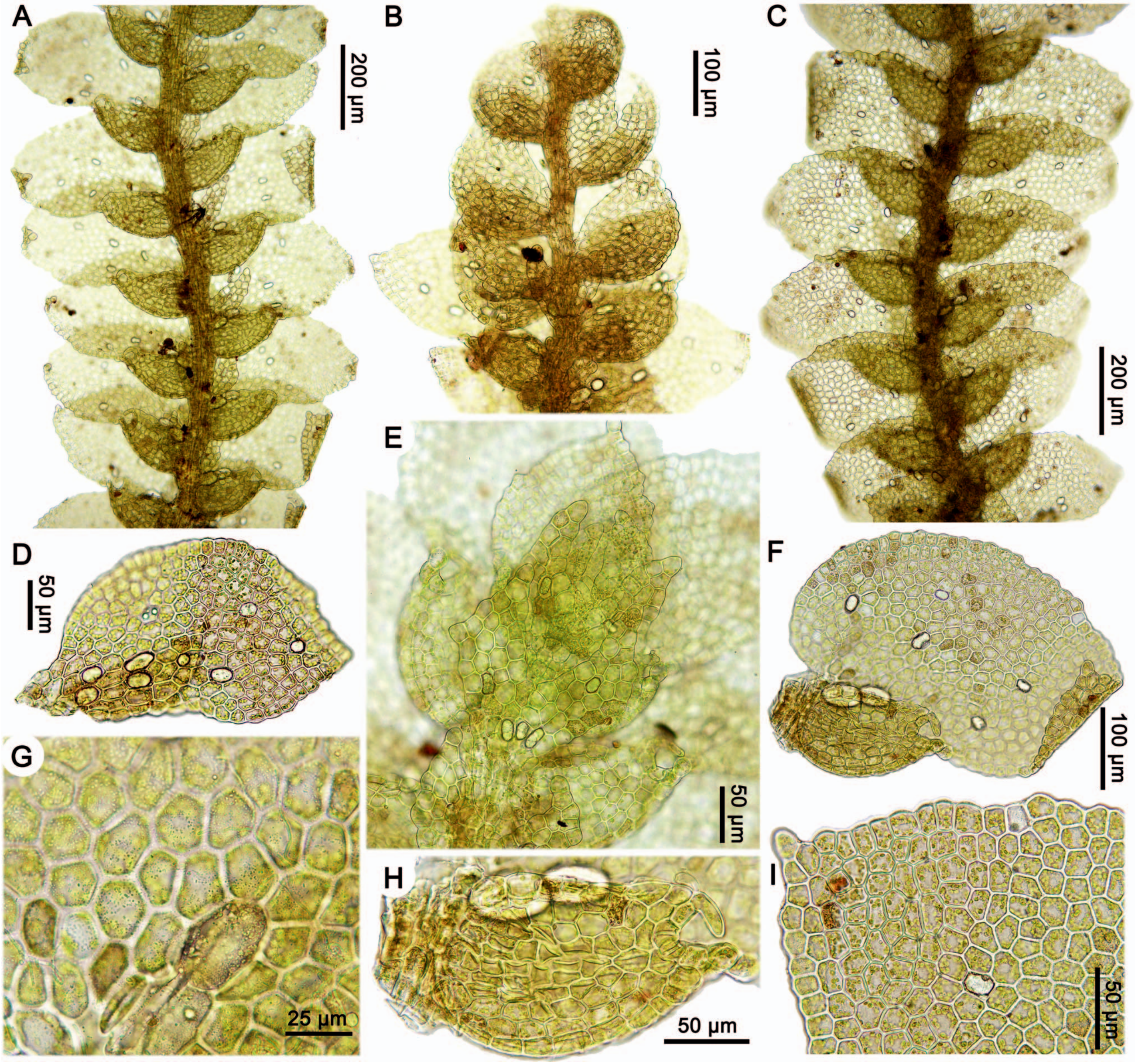

Figure 2. *Mohamedia brunnea* (Mizut.) R.L.Zhu et L.Shu. **A.** Portion of shoot, ventral view. **B.** Androecium, ventral view. **C.** Portion of shoot. **D.** Female bract. **E.** Apex of shoot showing ocellate underleaves, ventral view. **F.** Leaf, ventral view. **G.** Basal cells of leaf lobe showing surface wax projections. **H.** Leaf lobule showing hyaline papilla and free lateral margin of leaf lobule. **I.** Apex of leaf lobe. All from *R.-L. Zhu et al. 20151218-3B* (HSNU).

2003), performing 1000 non-parametric bootstrap replicates (Felsenstein 1985). Conflict between datasets was considered to exist when a significant supported clade (bootstrap support ≥70%) from one marker was contradicted by another significantly supported clade from a different marker. When no conflicts were detected, the different datasets were combined.

MP analysis was conducted with PAUP* V4.0 (Swofford 2003), performing heuristic searches with "Mul-Trees" in effect, TBR as branch-swapping algorithm, Max-Trees = 1000, and branches collapsing when maximum branch length is zero. All characters were equally weighted and coded indels were treated as binary data. Non-parametric bootstrap searches (Felsenstein 1985) were used to calculate branch supports (MP_{BS}), performing 1000 replicates with the full-heuristic option and the same parameters used in the heuristic search.

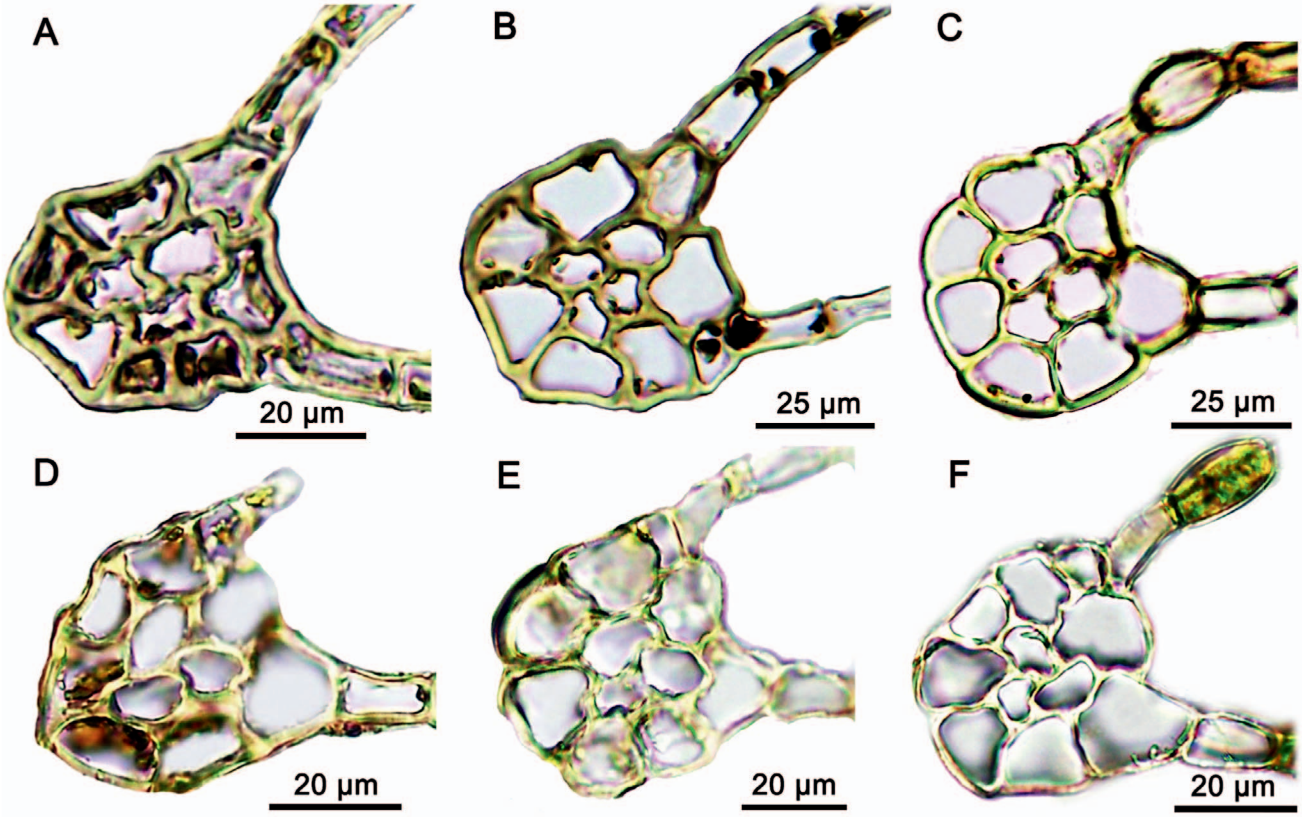

Figure 3. Transverse section of stem. **A.** *Mohamedia brunnea* (Mizut.) R.L.Zhu et L.Shu. **B–F.** *Mohamedia borneensis* (Steph.) R.L.Zhu et L.Shu. A from *R.-L. Zhu et al. 20151218-3B* (HSNU), B and D from *A. Juslén 671* (SINU), C from *R.-L. Zhu et al. 20151216-25* (HSNU), E from *S. & T. Pocs 03297/G* (EGR), and F from *B.C. Ho & Y.-M. Wei 20181005-49* (HSNU).

RAxML-HPC V.8.2.6 (Stamatakis 2014) was used to conduct maximum likelihood (ML) analyses on the combined dataset, excluding gaps. The nucleotide substitution model was set to GTR+γ. We performed 1000 ML bootstrap (BS) replicates, followed by a thorough ML search for the best tree.

In addition, the Bayesian analysis was done using Metropolis Coupled Markov Chain Monte Carlo strategy implemented in MrBayes v.3.2.6 (Huelsenbeck & Ronquist 2001; Ronquist & Huelsenbeck 2003). The different genes were partitioned as separate subsets, with topology linked across subsets, but separate model parameter values for

Table 1. Sequences newly generated in the study, including taxa, vouchers and GenBank accession numbers. "—" missing sequences.

Taxon	Voucher	*rbc*L	*trn*L–F	nrITS
Drepanolejeunea brunnea Mizut. I	Brunei, Zhu et al. 20151216-9 (HSNU)	MK313089	MK313099	MK313078
Drepanolejeunea brunnea Mizut. II	Brunei, Zhu et al. 20151218-3B (HSNU)	—	—	MK313080
Lepidolejeunea bidentula (Steph.) R.M.Schust. II	Indonesia, Zhu et al. 20170518-28 (HSNU)	MK313090	MK313101	MK313079
Lepidolejeunea borneensis (Steph.) R.M.Schust. I	Malaysia, Zhu et al. 20160916-12 (HSNU)	MK313093	MK313100	MK313088
Lepidolejeunea borneensis (Steph.) R.M.Schust. II	Brunei, Zhu et al. 20151216-25 (HSNU)	MK313091	—	MK313087
Lepidolejeunea borneensis (Steph.) R.M.Schust. III	Brunei, Zhu et al. 20151218-4 (HSNU)	MK313092	MK313102	MK313086
Lepidolejeunea novae-caledoniae (Piippo) R.L.Zhu et Frank Müll	New Caledonia, Müller NC19J (DR, HSNU)	MK313094	MK313107	MK313081
Vitalianthus aphanellus (Spruce) Bechteler et al. I	Brazil, Zhu & Shu 20171125-6B (HSNU)	MK313095	MK313103	MK313085
Vitalianthus lamyii R.L.Zhu et al.	Brunei, Zhu et al. 20151215-64A (HSNU)	MK313096	MK313105	MK313084
Vitalianthus guangxianus R.L.Zhu et al. I	China, Wei et al. 20150629-7 (HSNU)	MK313097	MK313106	MK313083
Vitalianthus guangxianus R.L.Zhu et al. II	China, Wei 20110217-24 (HSNU)	MK313098	MK313104	MK313082

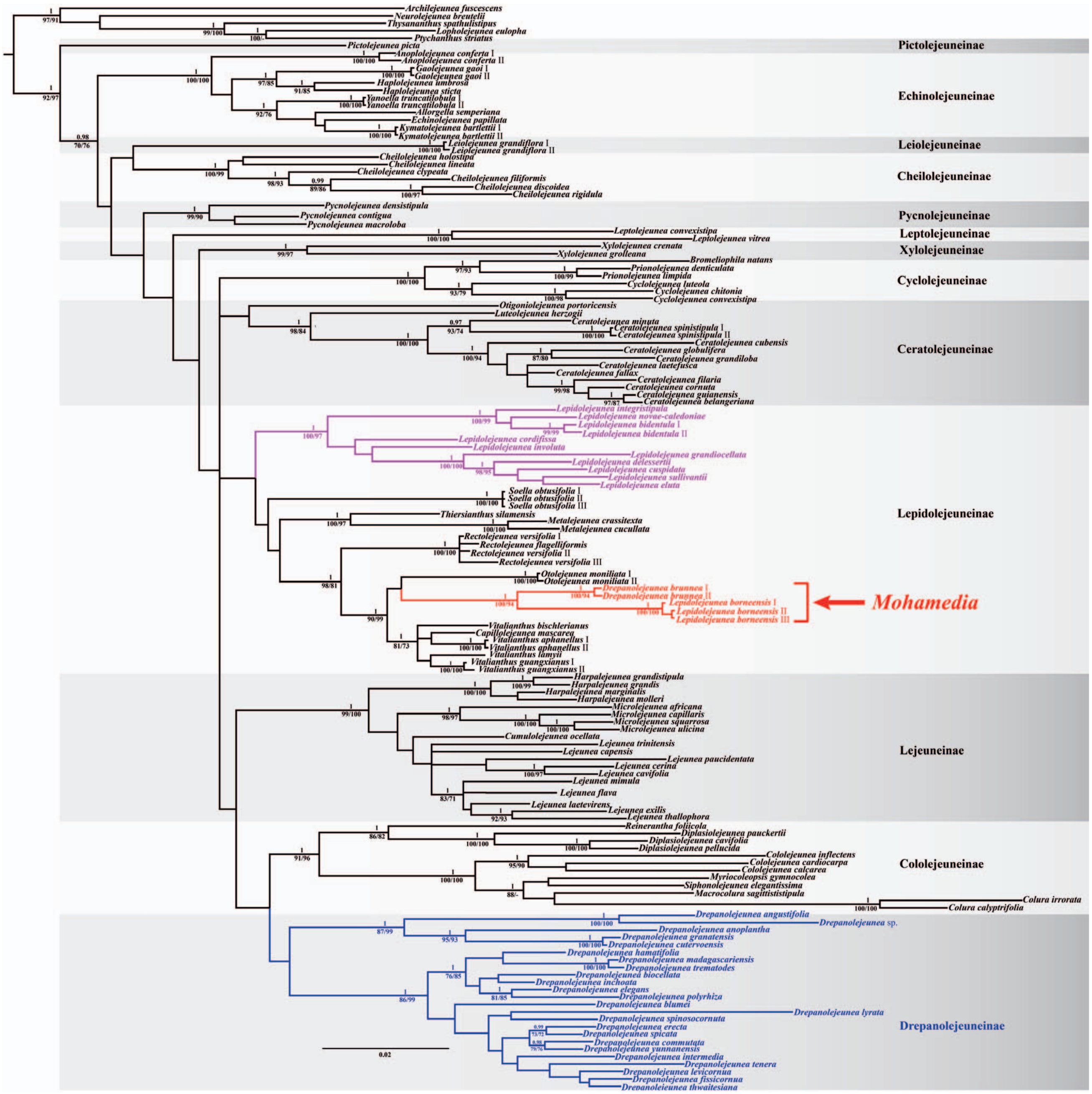

Figure 4. Phylogeny of Lejeuneaceae illustrating position of *Drepanolejeunea brunnea* Mizut. and *Lepidolejeunea borneensis* (Steph.) R.M.Schust., inferred from combined dataset (*rbc*L, *trn*L–*trn*F and nrITS) and topology displayed as majority rule consensus tree of trees recovered in stationary phase of Bayesian search with posterior probabilities (PP_{BI}) ≥ 0.98, Maximum likelihood bootstrap support (ML_{BS}) ≥ 80, and Maximum parsimony bootstrap support (MP_{BS}) ≥ 70 displayed besides the nodes with PP_{BI} on the branch and below the branch with ML_{BS} at left and MP_{BS} at right.

each. Nucleotide substitution models were selected with MrModeltest 2.3 (Nylander 2004). Several analyses were conducted with Markov chains on each of two independent runs with the following settings: 10^7 generations, it was found that the standard deviation of split frequencies was below 0.01, and the analysis was discontinued. In each analysis, by examining the decrease in the standard deviation of the split frequencies, it was found that chains had achieved stability within the first quarter of the samples; thus burn-in was set to 25000. From the 75001 trees remaining after burn-in was discarded, a 50% majority-rule consensus tree was calculated with posterior probabilities (PP) for support of the branches.

Results

A test for congruence after maximum parsimony bootstrapping revealed no significant conflicts among the different markers and the three datasets were therefore concatenated for further phylogenetic analyses. The final matrix of the combined dataset had 2140 characters (601 in nrITS, 606 in *trn*L–F, 933 in *rbc*L), 1171 of which were constant, 208 parsimony-uninformative and 761 parsimony-informative. Search for trees with MP retained 94 best trees with a length of 5193 steps. Parsimony tree scores were identical for all trees: consistency index = 0.309, retention index = 0.655, rescaled consistency index = 0.203, and homoplasy index = 0.691.

The phylogenetic reconstructions from the ML analysis yielded the best tree with an overall topology similar to that of MP trees concerning well-supported clades, with minor variations in some unsupported groups. The consensus tree of Bayesian analysis had an almost identical topology to that of ML tree (**Fig. 4**).

The results of the phylogenetic analyses were largely consistent with previous studies of the subtribes of subfamily Lejeuneoideae (Zhu et al. 2018a,b). *Drepanolejeunea brunnea* and *Lepidolejeunea borneensis* formed a highly supported clade ($MP_{BS} = 94$, $ML_{BS} = 100$, $PP_{BI} = 1$) separate from *Drepanolejeunea* and *Lepidolejeunea*. This monophyletic group was nested in a clade together with *Otolejeunea* Grolle et Tixier, *Vitalianthus* R.M.Schust. et Giancotti and *Capillolejeunea* S.W.Arnell ($MP_{BS} = 99$, $ML_{BS} = 90$, $PP_{BI} = 1$) and belonging to the subtribe Lepidolejeuneinae (**Fig. 4**).

Morphological observations on fresh samples show that *Drepanolejeunea brunnea* has several diagnostic features including 1) ocellate underleaves, 2) lack of oil bodies in non-ocellate leaf cells, and 3) verrucose leaf cell cuticle resulting from surface waxes (**Figs. 2 & 6**). These characters were previously unknown in *Drepanolejeunea*. In typical *Drepanolejeunea*, ocelli are absent in underleaves, ordinary leaf cells have granular oil bodies, and the cuticle is smooth (Schuster 1992; Zhu & So 2001). Our examination of numerous specimens of *Lepidolejeunea borneensis* revealed that the stem consists of three rows of medullary cells as is typical of *Drepanolejeunea*, *Leptolejeunea* (Spruce) Steph., *Metalejeunea* Grolle and *Microlejeunea* (Spruce) Steph. (**Fig. 3A & 3C–F**), and that the ocelli at the base of the leaf lobes are of the basal type (**Fig. 1K**) as in *Drepanolejeunea brunnea*. In typical *Lepidolejeunea*, the stem has usually more than four rows of medullary cells (four medullary rows only in *L. serrulata* (Steph.) Grolle, cf. Piippo 1986) and the ocelli at the base of the leaf lobes are of the suprabasal type. Both *D. brunnea* and *L. borneensis* share several diagnostic characters such as 1) stems with three rows of medullary cells, 2) presence of ocelli in underleaves, 3) ocelli at the base of the leaf lobes of the basal type, 4) 4–5-keeled perianths without horns, 5) bilobed underleaves with erect lobes, and 6) pycnolejeuneoid gynoecial innovations. Therefore, a new genus, *Mohamedia* R.L.Zhu et L.Shu, is formally proposed to accommodate the clade composed of these two species.

Taxonomy

Mohamedia R.L.Zhu et L.Shu, *gen. nov.*

Type species: *Mohamedia brunnea* (Mizut.) R.L.Zhu et L.Shu (≡*Drepanolejeunea brunnea* Mizut., J. Hattori Bot. Lab. 33: 231. 1970).

Mohamedia is recognized by the following set of characters: autoicous sexuality, ocellate leaf lobes and underleaves, ocelli at the base of leaf lobes belonging to the basal type, absence in the leaf lobe of an unbroken row of ocelli, lack of oil bodies in non-ocellate leaf cells, pycnolejeuneoid gynoecial innovations, and 4(–5)-keeled perianths without horns.

Etymology. The genus is named in honor of Dr. Haji Mohamed of the University of Brunei Darussalam and University of Malaya for his remarkable contributions to our knowledge of the bryophyte diversity of Brunei Darussalam and Malaysia.

Habitats and distribution. At present *Mohamedia* comprises two species in two monospecific subgenera which usually grow on tree roots, tree bases, tree trunks, and decaying logs, sometimes on living leaves dominantly in lowland rain forests in tropical Asia and Oceania (**Fig. 5**).

Mohamedia subg. Piippolejeunea R.L.Zhu et L.Shu, *subg. nov.*

Type species: *Mohamedia borneensis* (Steph.) R.L.Zhu et L.Shu.

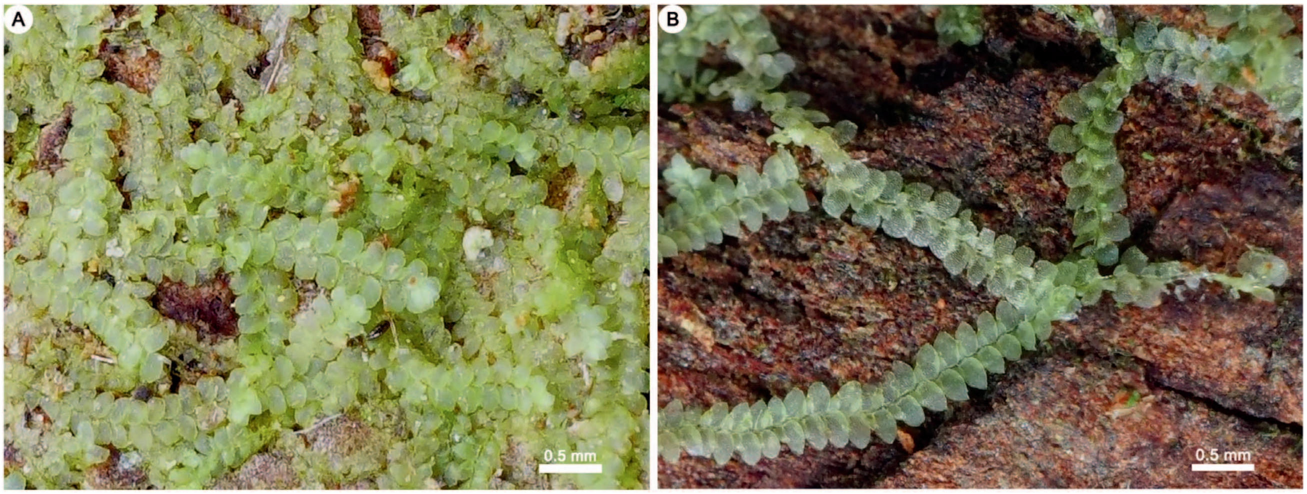

Figure 5. A. Epiphytic population of *Mohamedia brunnea* (Mizut.) R.L.Zhu et L.Shu in lowland rain forests in Brunei Darussalam. **B.** Epiphytic population of *Mohamedia borneensis* (Steph.) R.L.Zhu et L.Shu in lowland rain forests in Brunei Darussalam, mixed with *M. brunnea*. A from *R.-L. Zhu et al. 20151216-7* (HSNU), B from *R.-L. Zhu et al. 20151216-25* (HSNU).

Mohamedia subg. *Piippolejeunea is close to subg. Mohamedia, but differs in the ocellate leaf lobules, non-curved lobular tooth, and smooth cuticle of leaf cells.*

Etymology. The subgenus is named in honor of Dr. Sinikka Piippo of the University of Helsinki in recognition of her important contributions to bryology, especially her monograph of *Lepidolejeunea* (Lejeuneaceae) in 1986.

At present subg. *Piippolejeunea* is monospecific, and known from Oceania and tropical Asia. The two subgenera can be separated by the following key:

1. Ocelli in leaf lobule absent; leaf cells verrucose owing to surface wax projections; lobular tooth long and curved.. ***Mohamedia* subg. *Mohamedia***
1. Ocelli in leaf lobule present; leaf cells smooth, without surface wax projections; lobular tooth short and straight... ***Mohamedia* subg. *Piippolejeunea***

Mohamedia borneensis (Steph.) R.L.Zhu et L.Shu, *comb. nov.* **Figs. 1, 3B–F & 5B**

≡ *Hygrolejeunea borneensis* Steph., Sp. Hepat. 5: 557. 1914. ≡ *Pycnolejeunea borneensis* (Steph.) Mizut., J. Hattori Bot. Lab. 35: 404. 1972 *nom. illeg.* (*non P. borneensis* Steph., Sp. Hepat. 5: 632. 1914). ≡ *Pycnolejeunea* "*Phynolejeunea*"*acutifolia* Mizut., J. Hattori Bot. Lab. 40: 446. 1976, *nom. nov. pro.* ≡ *Lepidolejeunea borneensis* (Steph.) R.M.Schust., Phytologia 45(5): 425. 1980. Type: INDONESIA. West Borneo: Silnas Sambas, 24 July 1903, *W. Micholitz s.n.* (holotype: G 00043977!; isotype: JE!).

Description. Autoicous. Plants green to yellowish green, minute, 3 to 8 mm long. Shoots 0.50–0.80 mm wide, irregularly branched, branches *Lejeunea*-type, leaf sequence of vegetative branches lejeuneoid. Stems 30–52 μm in diameter, in transverse section with 7 cortical cells and 3(–4) medullary cells, cortical cells subquadrate to oblong, 10–20(–23) × 9–17 μm, slightly thick-walled, medullary cells ± isodiametric, 9–19 × 8–12 μm, thin-walled or slightly thick-walled; ventral merophyte 2 cells wide, ocelli absent in stem cells, rhizoids at base of underleaves, few, tufted, usually hyaline, rhizoid disc usually present, mostly horizontally oblong. Leaves contiguous to imbricate, diverging from stem at an angle of 50–75°; leaf lobes asymmetrically ovate, falcate, 0.20–0.45 mm long, 0.15–0.40 mm wide, margins crenulate, apex acute to apiculate, sometimes round to obtuse, usually incurved, ventral margin usually weakly arched, dorsal margin arched near base; leaf lobules ovoid, strongly inflated, 1/3–2/5 as long as the lobes, sometimes strongly reduced, ocelli 3–5, lateral free margin usually slightly incurved (except at apex), proximal to the notch bordered by 5–6 subquadrate to rectangular marginal cells, apex usually slightly constricted, with a unicellular, short and blunt, straight apical tooth (13–16 × 7.5–14 μm) almost parallel to stem; keel arched, almost smooth, hyaline papilla oblong,

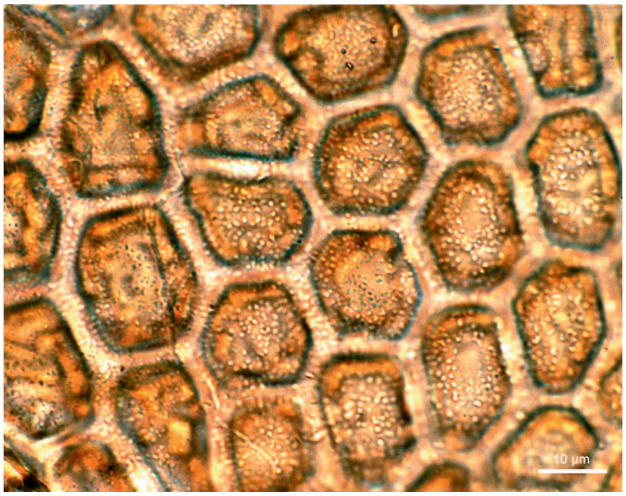

Figure 6. *Mohamedia brunnea* (Mizut.) R.L.Zhu et L.Shu. Cells of leaf lobe showing surface wax projections, from *M. Mizutani 3011* (NICH).

15–18 × 8.7–10 µm, situated at the proximal base of apical tooth. Cells of leaf lobe with thin walls and very small trigones, cuticle smooth, surface wax projections absent, intermediate thickenings absent; cells at the margin quadrate to rectangular, 13–19(–25) × 11–15(–21) µm, in the middle ± hexagonal, 17–28(–32) × 15–22(–30) µm, near base similar to median cells in shape, but slightly larger. Oil bodies absent in non-ocellate leaf cells. Ocelli 6–11(–15) per leaf lobe, 1 at base, 5–10(–14) at middle; basal ocelli slightly larger than adjacent leaf cells, oblong, 25–42 × 16–22 µm, of the basal type (adjacent to a stem cell, cf. Zhu & Shu 2001), median ocelli almost as large as non-ocellate cells, scattered, hexagonal. Underleaves remote, suborbicular, usually slightly wider than long, 3–4(–5) times as wide as stem, bilobed to 1/2 their length, sinus V-shaped, lobes mostly triangular, erect, usually obtuse at apex, 5–7 cells long, 4–7 cells wide at base, inner lateral margin nearly entire, outer lateral one more or less crenulate, insertion line slightly arched, base cuneate; ocelli in underleaves 1–5, as large as non-ocellate cells. Androecia terminal on a short or long branch, capitate, bracts in 3–5 pairs, hypostatic, strongly concave and inflated, shortly and subequally bifid, apex rounded, nearly entire; lobule slightly shorter, keels strongly arched, slightly crenulate; bracteoles 1–2, borne only at the basal portion of the androecium, similar to ordinary underleaves; antheridia 2 per bract. Gynoecia on short or long branches, always with 1(–2) pycnolejeuneoid innovations; bracts deeply and unequally bifid, the lobe obovate-oblong to oblong-ovate, 0.47–0.60 mm long, 0.25–0.4 mm wide, apex acute to acuminate, rarely to obtuse to rounded, margin almost entire to crenulate, base with 0–1 ocellus, middle with 9–17 ocelli; lobule oblong, 0.20–0.27 mm long, 0.06–0.09 mm wide, 1/2–2/3 as long as the bract lobe, apex obtuse to apiculate, keel sinuate, ca. 3/4 as long as the lobule, without wing; bracteole connate with bracts usually on both sides at base, obovate to oblong, 0.30–0.50 mm long, 0.18–0.40 mm wide at middle, margin slightly crenulate, apex emarginated or to 1/5-bilobed, sinus usually V-shaped, lobes obtuse at apex, ocelli present in female bracteole. Perianths about 1/4–1/3 exserted, obovoid, 0.40–0.50 mm long, 0.25–0.32 mm wide at middle, slightly dorsiventrally compressed, with 4–5 keels, dorsal keels usually indistinct (**Fig. 1E**), keels usually crenulate to denticulate, surface of perianth almost smooth, beak short, 1(–2) cells long, ocelli in perianth numerous. Capsules almost spherical, 160–210 µm in diameter, dehiscing from apex down into four valves when mature, valves non-recurving, 190–220 µm long, 115–130 µm wide at middle, capsule wall thick, smooth on surface, consisting of 2(–3) layers of cells, trigones and intermediate thickenings indistinct; seta articulate, 350–560 µm long, with 8–9 articulations, 12 outer cells surrounding 4 inner cells in transverse section; foot with 2–3 transversal cell rings; elaters linear, marginal elaters 22 per capsule,150–250 µm long, 9–18 µm wide, wall sinuately thickened. Spores rectangular in shape, 45–75 × 12–15 µm, minutely papillose on surface, rosettes several, but usually indistinct. Asexual reproduction not seen.

Distribution and habitat. Known from Fiji (Pócs et al 2011 as *Lepidolejeunea borneensis*), Indonesia (West Borneo) (Mizutani 1972 as *Pycnolejeunea borneensis*), Malaysia (Sarawak) (Piippo 1986 as *L. borneensis*) and Singapore (Juslén et al. 2001 as *L. borneensis*; Piippo et al. 2002 as *L. borneensis*; Zhu et al. 2018d as *L. borneensis*). New to Brunei Darussalam and Sabah. On tree roots, tree bases, tree trunks and decaying logs, and occasionally on living leaves in lowland forests.

Representative specimens examined. BRUNEI DARUSSALAM. TEMBURONG: Kuala Belalong Field Studies Centre of University Brunei Darussalam, 04°32′53.01″N, 115°09′29.98″E, 89 m, on tree trunks, 16 Dec. 2015, *R.-L. Zhu et al. 20151216-25*

(HSNU); *ibid.*, 04°32′53.89″N, 115°09′20.28″E, 140 m, epiphyllous, *R.-L. Zhu et al. 20151217-54a* (HSNU); *ibid.*, 04°32′50.71″N, 115°09′32.27″E, 150 m, on decaying logs, 18 Dec. 2015, *R.-L. Zhu et al. 20151218-4* (HSNU). FIJI. TAVEUNI ISLAND: above Korovou village, around the first Tavoro Waterfall, 16°49.564–620′S, 179°52.420–800′W, 10–100 m, on planted ornamental shrub, 8 Sept. 2003, *S. & T. Pocs 03297/G* (EGR, HSNU). MALAYSIA. SABAH: Lahad Datu, Sepagaya Forest Reserve, Mount Silam, along trail to Silam water spring, 04°58′26.91″N, 118°10′59.07″E, 332 m, on tree bases, 16 Sept. 2016, *R.-L. Zhu et al. 20160916-12* (HSNU). SINGAPORE. Bukit Timah Nature Reserve, Lasia Valley, on tree bases, 13 Nov. 1998, *A. Juslén 671* (SINU); Bukit Timah Nature Reserve, Cave Path, on tree bases, 5 Oct. 2018, *B.C. Ho & Y.-M. Wei 20181005-49* (HSNU; SING).

Mohamedia brunnea (Mizut.) R.L.Zhu et L.Shu, *comb. nov.* **Figs. 2, 3A, 5A & 6**

≡ *Drepanolejeunea brunnea* Mizut., J. Hattori Bot. Lab. 33: 231. 1970. ≡ *Ophthalmolejeunea brunnea* (Mizut.) R.M.Schust., J. Hattori Bot. Lab. 72: 323. 1992. TYPE: MALAYSIA. SABAH: in forest between Hot Spring, Poring and Royal Soc. Bungalow, E slope of Mt. Kinabalu, 600–1100 m, on tree trunk, 28 May 1963, *M. Mizutani 3011* (holotype: NICH!).

Description. Autoicous. Plants yellowish green, minute, 2 to 6 mm long. Shoots 0.35–0.80 mm wide, irregularly branched, branches *Lejeunea*-type, leaf sequence of vegetative branches lejeuneoid. Stems 35–51 μm in diameter, in transverse section with 7 cortical cells and 3 medullary cells, cortical cells subquadrate to oblong, 8.8–19 × 8.0–16 μm, thick-walled, medullary cells ± isodiametric, 10–18 × 7.4–10 μm, slightly thick-walled; ventral merophyte 2 cells wide, ocelli absent in stem cells, rhizoids at base of underleaves, few, tufted, usually hyaline, rhizoid disc not seen. Leaves imbricate, diverging from stem at an angle of 50–80°; leaf lobes asymmetrically ovate, falcate, 0.20–0.35 mm long, 0.15–0.30 mm wide, margins usually irregularly denticulate or weakly crenulate, apex acute to apiculate, usually incurved, ventral margin usually weakly arched, dorsal margin ± arched near base; leaf lobules ovoid-rectangular, strongly inflated, 2/5(–1/2) as long as the lobes, sometimes strongly reduced, ocelli absent, lateral free margin usually slightly incurved (except at apex), proximal to the notch bordered by 5–6 subquadrate to rectangular marginal cells, apex usually slightly constricted, with a unicellular, long and curved apical tooth (25–33 × 7.5–11 μm) directed towards leaf apex; keel arched, almost smooth, hyaline papilla oblong, 17–23 × 6.5–8 μm, situated at the proximal base of apical tooth. Cells of leaf lobe with slightly thick walls and very small trigones, cuticle verrucose owing to surface wax projections, intermediate thickenings absent; cells at the margin quadrate to rectangular, 10–18(–20) × 9–14 (–15) μm, in the middle ± hexagonal, 12–24(–26) × 11–18(–20) μm, near base similar to median cells in shape, but slightly larger. Oil bodies absent (occasionally with 0–5 minute oil droplets) in non-ocellate leaf cells. Ocelli 4–7(–10) per leaf lobe, 1–2 at base, 3–5(–8) at middle; basal ocelli larger than adjacent leaf cells, oblong, 35–42(–48) × 17–28 μm, of the basal type (the lowermost ocellus adjacent to stem cell, cf. Zhu & Shu 2001), two ocelli usually in a longitudinal row bordering each other, median ocelli almost as large as non-ocellate cells, scattered, hexagonal. Underleaves remote, longer than wide, 1.5–3(–4) times as wide as stem, bilobed to 2/3 their length, sinus V-shaped, lobes lanceolate to narrowly triangular, erect, acute at apex, 3–5(–6) cells long, 2–5 cells wide at base, apex ending in 1–2 uniseriate cells, inner lateral margin nearly entire, outer lateral one irregularly and remotely dentate, occasionally entire, insertion line almost straight, base cuneate, ocelli 1–5 in underleaf. Androecia terminal on short or long branch, capitate, bracts in 2–6 pairs, hypostatic, strongly concave and inflated, shortly and subequally bifid, apex rounded, nearly entire; lobule slightly shorter, keels strongly arched, slightly crenulate; bracteoles 1–2, borne only at the basal portion of the androecium, similar to ordinary underleaves; antheridia 2 per bract. Gynoecia on short or long branches, always with 1 pycnolejeuneoid innovation; bracts deeply and unequally bifid, the lobe ovate to oblong-ovate, 0.30–0.45 mm long, 0.18–0.25 mm wide, apex acute to acuminate, margin almost entire to irregularly and remotely dentate or crenulate, base with 1–2 ocelli, middle with 3–7 ocelli; lobule oblong, 0.21–0.25 mm long, 0.06–0.08 mm wide, 2/5–2/3 as long as the bract lobe, apex obtuse to apiculate, keel slightly sinuate to straight, 1/2–2/3 as long as the lobule, without wing; bracteole connate with bracts on both sides at base, oblong, 0.30–0.40 mm long, 0.15–0.18 mm wide at middle, margin slightly denticulate, apex bilobed to 1/5–1/4 its length, sinus usually V-shaped, ocelli present in female bracteole. Perianths about 1/3 exserted, obovoid, 0.39–0.50 mm long, 0.28–0.38 mm wide at middle, dorsiventrally compressed, with 4 keels (dorsal keel absent or indistinct), keels usually crenulate to denticulate, surface of perianth almost smooth, beak short, 1(–2) cells long, ocelli in perianth numerous. Capsules almost spherical, 175–230 μm in diameter, dehiscing from apex down into four valves when mature, valves non-recurving, 200–250 μm long, 115–135 μm wide at middle, capsule wall thick, smooth on surface, consisting of 2(–3) layers of cells, trigones and intermediate thickenings not distinct; seta articulate, 450–580 μm long, with 8–9 articulations, 12 outer cells surrounding 4 inner cells in transverse section; foot with 2–3 transversal cell rings; elaters linear, marginal elaters 22 per capsule,145–200 μm long, 7.5–12 μm wide, wall sinuately thickened. Spores rectangular in shape, 30–46 × 12–16 μm, minutely papillose on surface, rosettes several, but usually indistinct. Asexual reproduction not seen.

Distribution and habitat. Previously known only from Sabah, Malaysia (Mizutani 1970 as *Drepanolejeunea brunnea*); new to Brunei Darussalam. In Brunei Darussalam *Mohamedia brunnea* was found on tree bases, tree trunks and tree branches in lowland rain forests, at 50–260 m. In Sabah the species was collected on tree trunks at altitudes of 600–1100 m (Mizutani 1970). The species may be expected to be more widely distributed in lowland rain forests of tropical Asia.

Representative specimens examined. BRUNEI DARUSSALAM. Temburong: Kuala Belalong Field Studies Centre of University Brunei Darussalam, 04°32′55.82″N, 115°09′39.02′′E, 260 m, on tree trunks, 16 Dec. 2015, *R.-L. Zhu et al. 20151216-70* (hsnu); *ibid*., 04°32′49.76′′N, 115°09′31.89′′E, 153 m, on tree trunks, 18 Dec. 2015, *R.-L. Zhu et al. 20151218-3B* (hsnu); *ibid*., 04°32′54.34′′N, 115°09′21.39′′E, 141 m, on tree trunks, 17 Dec. 2015, *R.-L. Zhu et al. 20151217-65A* (hsnu); *ibid*., 04°32′52.40′′N, 115°09′27.38′′E, 61 m, on tree branches, 16 Dec. 2015, *R.-L. Zhu et al*. 20151216-7 (hsnu); *ibid*., 04°32′52.38′′N, 115°09′27.49′′E, 62 m, on tree trunk, 16 Dec. 2015, *R.-L. Zhu et al. 20151216-9* (hsnu).

Discussion

Our new phylogenetic analysis clearly shows that *Mohamedia* is nested within the lineage of the subtribe Lepidolejeuneeinae, and sister to *Otolejeunea*, a monospecific epiphyllous genus endemic to Madagascar, but with low support values ($MP_{BS} = 73$, $ML_{BS} = 71$, $PP_{BI} = 0.79$). *Otolejeunea* is morphologically well characterized by the two-keeled perianths with auricles, an unbroken vitta consisting of 3–5 moniliate ocelli in leaf lobe, a stem with over five rows of cortical cells, and the lack of scattered ocelli in leaf lobes (Tixier 1980). *Mohamedia* and *Otolejeunea* share many similarities, e.g., the autoicous condition, ocellate leaf lobes, pycnolejeuneoid gynoecial innovations, single lobular tooth, thin- to moderately thick-walled leaf cells without distinct intermediate thickenings and large trigones, remote bilobed underleaves with erect lobes, proximal hyaline papilla, and lack of vegetative reproductive organs. Although we have not checked whether oil bodies are also absent in *Otolejeunea* as in *Mohamedia, Mohamedia* clearly differs from *Otolejeunea* in its thinner stem with 3(–4) rows of medullary cells, 4–5-keeled perianths with crenulate to weakly dentate keels and without auricles, and lack of an unbroken basal vitta consisting of 3–5 ocelli in leaf lobes.

Lepidolejeunea is a pantropical genus of 17 currently accepted species (Schäfer-Verwimp et al. 2017; Shu et al. 2016; Söderström et al. 2016). It was divided into three subgenera: *Kingiolejeunea* (H.Rob.) R.M.Schust., *Lepidolejeunea*, and *Perilejeunea* (Kachroo et R.M.Schust.) R.M.Schust. mainly based on stem structure and underleaf insertion (Piippo 1986; Söderström et al. 2016). Recently, the new subgenus *Caribeolejeunea* Schäfer-Verw. et al. has been described based on a collection from Jamaica (Schäfer-Verwimp et al. 2017). In addition, recent molecular-phylogenetic studies revealed that *Lepidolejeunea* is a well-supported monophyletic genus belonging to Lepidolejeuneinae Gradst. together with seven other genera (Schäfer-Verwimp et al. 2017; Zhu et al. 2017, 2018a,b). Although the type of the genus, *L. falcata* (Herzog) R.M.Schust., a rare species from New Caledonia (Piippo 1986; Thouvenot et al. 2011), has not yet been sequenced, two new accessions of *L. bidentula* (Steph.) R.M.Schust., thought to be most similar to the type species (Piippo 1986), were included in the present analyses.

Lepidolejeunea borneensis (= *Mohamedia borneensis*) the only autoicous species assigned to *Lepidolejeunea*, was placed in *Lepidolejeunea* subg. *Kingiolejeunea* by Piippo (1986). In the recent world checklist of liverworts and hornworts (Söderström et al. 2016), however, it was treated as "*incertae sedis*". According to Piippo (1986), the stem in transverse section of *Lepidolejeunea borneensis* contains seven cortical cells and four slightly smaller medullary cells. Our examination of numerous specimens from various regions, however, reveals that the stem normally consists of only three rows of medullary cells (**Fig. 3C**–**F**), only occasionally of four rows (**Fig. 3B**). The stem is quite similar to that of *Drepanolejeunea* and *Leptolejeunea*, and very different from *Lepidolejeunea* which usually has more than four rows of medullary cells. An examination of basal ocelli in fresh samples, moreover, shows that the ocelli at the base of the leaf lobes of *Lepidolejeunea borneensis* are of the basal type. In the remaining species in *Lepidolejeunea*, however, they are of the suprabasal type (basal-most ocellus separated by one to several non-ocellate cells from the stem cells, cf. Zhu & So 2001). As observed by Piippo (1986 as *L. borneensis*), *Mohamedia borneensis* shows much variation especially in the leaf apex. In most specimens the leaf apexes are acute to apiculate (**Fig. 1**), but sometimes obtuse, occasionally rounded. The apiculate to rounded apexes sometimes occur even on the same stem in specimens from Brunei Darussalam (*R.-L. Zhu et al. 20151218-4, 20151217-69A*).

Drepanolejeunea brunnea was originally placed in *Drepanolejeunea* mainly owing to the presence of ocelli in leaf lobes, three rows of medullary cells of the stem, and pycnolejeuneoid gynoecial innovations (Mizutani 1970). But the oil bodies of leaf cells and ocelli in underleaves were not described or illustrated in the protologue (Mizutani 1970). Our examination of fresh samples reveals that this species has ocellate underleaves as in *Lepidolejeunea* and *Pictolejeunea* (**Fig. 2E**), and that oil bodies are lacking in ordinary leaf cells as in typical *Lepidolejeunea* (Piippo 1986; Schuster 1992). *Mohamedia brunnea* is quite similar to the Bornean *Vitalianthus lamyii* R.L.Zhu et al. in the minute plants, remote underleaves with two erect and narrow lobes, usually acute to apiculate and incurved leaf apex, stem consisting of only three rows of medullar cells, single lobular tooth, thin- to moderately thick-walled leaf cells without distinct intermediate thickenings, pycnolejeuneoid gynoecial innovations, and obovate perianths with crenulate to weakly dentate keels. The two species are not easy to be distinguished especially when ocelli and oil bodies are disintegrated (herbarium specimens). *Vitalianthus lamyii*, however, differs in the smooth cuticle of leaf cells, less falcate leaves, and leaf keels only weakly arched (Zhu et al. 2018d).

An unusual feature of *Mohamedia brunnea* is the occurrence of wax crystals in the cuticle. Surface waxes in leafy liverworts are still poorly known. In *Plagiochila*, wax crystals are restricted to a single clade (*Plagiochila* sect. *Fuscoluteae*) (Heinrichs & Reiner-Drehwald 2012). In Lejeuneaceae surface waxes have been reported only in three species of the genus *Lejeunea* (Heinrichs & Reiner-Drehwald 2012; Lee et al. 2014). *Mohamedia* is the second known genus with distinct surface wax projections in Lejeuneaceae. The presence of surface waxes in Lejeuneaceae may be much more widespread.

Mohamedia is well characterized by the autoicous sexuality, ocellate underleaves with two erect lobes, lack of oil bodies in non-ocellate cells, ocelli at the base of the leaf lobe of the basal type, pycnolejeuneoid gynoecial innovations, stem with usually only three rows of medullary cells, lack of cladia, proximal hyaline papilla, scattered ocelli in leaf lobes, usual presence of surface waxes on leaf cells (absent in *M. borneensis*), and the absence of an unbroken row of ocelli in the leaf lobe.

The subtribe Lepidolejeuneinae now contains nine genera (**Fig. 4**). *Mohamedia* is possibly confused with *Lepidolejeunea,* but the latter is easily distinguished by the basal ocelli belonging to the suprabasal type, dioicous condition, stem with over four rows of medullary cells. *Rectolejeunea*, a small neotropical genus with only three species (Zhu et al. 2018a; Zhu & Shu 2018), most resembles *Mohamedia* in several important characters such as ocellate leaf lobes, pycnolejeuneoid gyonecial innovations, and basal ocelli in leaf lobes belonging to the basal type. *Rectolejeunea,* however, is readily separated by the special flagelliform branches, stem with over four rows of medullary cells, and round apex of leaf lobes. *Mohamedia* is also similar to *Thiersianthus* R.L.Zhu et L.Shu, a currently described genus known only from Borneo (Zhu et al. 2017) in the lack of oil bodies, bilobed underleaves with two erect lobes, ocellate leaf lobes, reduced second tooth of the leaf lobule, and pycnolejeuneoid gyonecial innovations. *Thiersianthus* is easily recognized by the basal ocelli belonging to the suprabasl type and stem with over six rows of medullary cells. Four other small genera in the subtribe Lepidolejeuneinae: *Capillolejeunea S*.W.Arnell, *Metalejeunea* Grolle, Soella et al., and *Vitalianthus* R.M.Schust. et Giancotti, share some characters with *Mohamedia:* the single lobular tooth, thin- to moderately thick-walled leaf cells without distinct intermediate thickenings, stem consisting of only three rows of medullar cells, pycnolejeuneoid gyonecial innovations, and proximal hyaline papilla. *Capillolejeunea* and *Vitalianthus* easily differ from *Mohamedia* in having the leaves with moniliate rows of ocelli, lack of ocelli in underleaves, and granular oil bodies (He et al. 2014; Zhu et al. 2018c). The relationship between *Capillolejeunea* and *Vitalianthus* remains unresolved (**Fig. 4**). The further treatment of *Vitalianthus* will be discussed in a separate paper. *Metalejeunea* is the only genus without ocelli in the subtribe Lepidolejeuneinae. Moreover the leaves in *Metalejeunea* are remote and suberect with very large leaf lobules and granular oil bodies, which are rather different from those of *Mohamedia. Soella* is a monospecific genus known in China and Japan (Zhu et al. 2018b). It is at once distinct from *Mohamedia* in having distinct oil bodies, larger leaf cells, (2–)3–4 basal ocelli in a transverse row belonging to the suprabasal type.

Mohamedia and *Drepanolejeunea* share the ocellate leaf lobes, stem usually with only three rows of medullary cells, proximal hyaline papilla, reduced second tooth of the leaf lobule, and pycnolejeuneoid gyonecial innovations. *Drepanolejeunea*, however, differs cytologically: presence of oil bodies and lack of ocelli in underleaves. Furthermore, *Drepanolejeunea* usually has special cladia for vegetative reproduction.

Besides the presence of ocelli in leaf lobules in *Mohamedia borneensis, M. brunnea* is immediately distinguished from *M. borneensis* by the usual presence of surface wax projections, smaller leaf cells, lanceolate to narrowly triangular lobes of the underleaf, and long lobular tooth.

Ophthalmolejeunea (R.M.Schust.) R.M.Schust., a small Asian genus with only two species, was established based on *O. monophthalma* R.M.Schust. (=*Ophthalmolejeunea erecta* (Steph.) R.M. Schust.≡-*Drepanolejeunea erecta* (Steph.) Mizut.) (Grolle & Reiner-Drehwald 1999; Schuster 1980, 1992, 2001). *Ophthalmolejeunea erecta* is nested in *Drepanolejeunea* (**Fig. 4** as *Drepanolejeunea erecta*). The molecular data support the reduction of *Ophthalmolejeunea* to *Drepanolejeunea* as proposed by He et al. (2012) by morphological evidence. The other species in *Ophthalmolejeunea, O. brunnea*, is moved to *Mohamedia* (this study).

Three hundred and sixty-nine genera have been accepted in liverworts (Marchantiophyta) (Zhu et al. 2018b). With the description of *Mohamedia* and the most recent addition of *Udaria* Singh et al. (Lophocoleaceae) (Singh et al. 2018) from India, the number of liverwort genera is raised to 371, including 74 in Lejeuneaceae.

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Supplementary document online:

Supplementary Table S1. Sequences from GenBank used in this study, including taxa, locations, vouchers, and GenBank accession numbers. "—" missing data.