

Thiersianthus (Marchantiophyta: Lejeuneaceae), a new genus from lowland rainforests in Borneo

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ABSTRACT. The tropical lowland rainforest is a paradise for Lejeuneaceae. Borneo is located in the heart of the biodiversity hotspots of Philippines, Sundaland and Wallacea. During an expedition to explore liverwort diversity of Sabah, Borneo we found an undescribed ocellate taxon in the lowland ultramafic rainforests. Our phylogenetic analyses based on the nuclear ribosomal ITS region and two chloroplast regions (*rbcl*, *trnL-trnF*) suggest that this unknown species belongs to the subtribe Lepidolejeuneinae of Lejeuneaceae. On the basis of the combined molecular phylogenetic and morphological data, here we propose a new genus, *Thiersianthus*, to accommodate this new species. *Capillolejeunea* known only from the East African Islands and *Kymatolejeunea* endemic to New Zealand were included in molecular analysis for the first time.

KEYWORDS. Hepaticae, liverwort, Malaysia, Mt. Silam, new species, Sabah.



Lejeuneaceae is the largest family of liverworts with 1873 species in 70 genera (Zhu & Shu 2017). Lejeuneaceae has been subdivided into two subfamilies, Ptychanthoideae and Lejeuneoideae. The latter subfamily was further classified into three tribes, Brachiolejeuneae, Symbiezidiaceae and Lejeuneae (Gradstein 2013; Söderström et al. 2016). Lejeuneae is the largest tribe and was recently subdivided into 13 subtribes: Ceratolejeuneinae Gradst., Cheilolejeuneinae Gradst., Cololejeuneinae Gradst., Cyclolejeuneinae Gradst., Drepanolejeuneinae Gradst., Echinolejeuneinae Gradst., Leiolejeuneinae Schäf.-Verw. et Heinrichs, Lejeuneinae Gradst., Lepidolejeuneinae Gradst., Leptolejeuneinae Heinrichs et Schäf.-Verw., Pictolejeuneinae Bechteler et al., Pycnolejeuneinae Heinrichs et Schäf.-Verw., and Xylolejeuneinae Heinrichs et Schäf.-Verw. (Bechteler et al. 2016a; Gradstein 2013). Recent molecular phylogenetic studies of Lejeuneaceae have led to a considerable reduction of genera, e.g., *Myriocolea*

Spruce = *Colura* (Dumort.) Dumort. (Heinrichs et al. 2012a), *Oryzolejeunea* (R.M.Schust.) R.M.Schust. and *Sphaerolejeunea* Herzog = *Lejeunea* Lib. (Heinrichs et al. 2012b; Ye et al. 2013), *Trocholejeunea* Schiffn. = *Acrolejeunea* (Spruce) Schiffn. (Wang et al. 2014), *Chondriolejeunea* (Benedix) Kis et Pócs = *Cololejeunea* (Spruce) Steph. (Yu et al. 2013), *Aureolejeunea* R.M.Schust., *Cyrtolejeunea* A.Evans, *Cystolejeunea* A.Evans, *Leucolejeunea* A.Evans and *Omphalanthus* Lindenb. et Nees = *Cheilolejeunea* (Spruce) Steph. (Ye et al. 2015; Ye & Zhu 2010), *Mastigolejeunea* (Spruce) Steph. = *Thysananthus* Lindenb. (Sukkharak & Gradstein 2017), *Physantholejeunea* R.M.Schust. = *Otigoniolejeunea* (Spruce) Schiffn. (Czumay et al. 2013; Wei et al. 2014). At the same time several small genera, such as *Allorgella* Tixier (Bechteler et al. 2016b), *Capillolejeunea* S.W.Arnell (He et al. 2014), *Otigoniolejeunea* (Wei et al. 2014) and *Dibrachiella* (Spruce) X.Q.Shi et al. (Shi et al. 2015), have been reinstated or erected. In the framework of the generic revision of Lejeuneaceae, we found an ocellate taxon from Malaysian Borneo not assignable to any known genera of the

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DOI: 10.1639/0007-2745-120.4.xxx

Table 1. New sequences used in this study, including taxa, locations, vouchers and GenBank accession numbers.

Taxon	Voucher	<i>rbcL</i>	<i>trnL-F</i>	nrITS
<i>Capillolejeunea mascarena</i> S.W.Arnell	Reunion Island, Pócs 08058/F (HSNU)	MG459427	MG459428	MG459426
<i>Kymatolejeunea bartlettii</i> Grolle I	New Zealand, Glenny 10793 (CHR)	MG365630	MG365632	MG365631
<i>Kymatolejeunea bartlettii</i> Grolle II	New Zealand, Glenny 11768 (CHR)	MG365633	MG365635	MG365634
<i>Thiersianthus silamensis</i> R.L.Zhu et L.Shu	Malaysia, Zhu et al. 20160916-23A (HSNU)	MG365636	MG365637	MG365638

family. Based on the morphological and molecular study of this material, we propose a new genus, *Thiersianthus* known only from Sabah state, Malaysia.

MATERIALS AND METHODS

Taxon sampling, morphological observation, DNA extraction and sequencing. Over 200 specimens of the subtribe *Lepidolejeuneinae* Gradst. containing *Capillolejeunea*, *Lepidolejeunea* R.M.Schust., *Metalejeunea* Grolle, *Otolejeunea* Grolle et Tixier, *Rectolejeunea* A.Evans, and *Vitalianthus* R.M.Schust. et Giancotti (Bechteler et al. 2016a; He et al. 2014) were examined. All morphological and anatomical characters were based on an examination using an Olympus BX43 microscope equipped with a DP71 digital camera. The field pictures were photographed with a digital camera (Sony ILCE-6000). Line drawings were made with the aid of a Nikon drawing tube.

For our study we included 100 species in 34 genera from the tribe *Lejeuneae* Dumort. Phylogenetic analyses indicated that the unknown taxon is nested within the subtribe *Lepidolejeuneinae* of subfamily *Lejeuneoideae*, and we accordingly included 19 accessions representing all known genera of *Lepidolejeuneinae*. This sampling represents both morphological and geographic variation in the subtribe. The sequences of the genera *Capillolejeunea* and *Kymatolejeunea* Grolle were newly generated in the present study together with the sequences of the unknown taxon, and the remaining sequences were downloaded from Genbank. Outgroups consisted of 13 species from subfamily *Ptychanthoideae*. The complete list with sample names, voucher information and GenBank accession numbers is presented in **Table 1** and **Supplementary Table S1**.

Total DNA were extracted from dried herbarium specimens or fresh samples using DNeasy Plant Mini Kits (Qiagen, Hilden, Germany) after grind pre-treatment in a multi-sample tissue lyser (Jinxin technology, China). Sequence data from three

molecular markers (*rbcL*, *trnL-trnF* and nrITS) were used in this study as in previous publications (Gradstein et al. 2006; Hartmann et al. 2006; Taberlet et al. 1991). Bidirectional sequencing was generated by Jie Li Biology Inc., China (<http://www.genebioseq.com>).

Phylogenetic analyses. Initial sequences were produced using PhyDE v.0.997 (<http://www.phyde.de/>) and then manually edited after aligned in MAFFIT version 7 (Katoh & Standley 2013). The maximum parsimony method was used to check the incongruent nodes between the individual makers. No evident incongruent nodes were found and subsequently three data sets were combined to conduct phylogeny analyses. Maximum parsimony (MP) analyses were run using PAUP* V4.0 (Swofford 2002). Branch swapping was performed using TBR and 500 random sequence addition replicates, and the strict consensus of most parsimonious tree was computed. Automorphic and constant characters were excluded prior to the analysis. Clade support was accessed by conducting 10000 bootstrap replicates with ten random taxon additions and heuristic search options. Maximum Likelihood (ML) analyses were performed with the program RAXML-Blackbox (Stamatakis, 2014) through the Cipres Science Gateway services (Miller et al. 2010). The GTRGAMMA model of evolution was independently specified for each partition. Nodal support was estimated using 500 bootstrap replicates through the “rapid bootstrapping” option of RAXML. Bayesian inference (BI) analyses were conducted with MrBayes 3.2.6 (Fredrik et al. 2012) through the Cipres Science Gateway service (Miller et al. 2010). The models of evolution selected by MrModeltest 2.3 (Nylander 2004) were set for each independent partition. Default priors of model parameters were also defined for each partition. Two parallel MCMC runs of 50000000 generations were conducted, each run containing three heated chains and one cold chain. The default value of temperature coefficient was used for all analyses. Trees and estimated

parameter values were sampled every 1000 generations, thus obtaining a total of 50000 samples from which the first 12500 were discarded as burn-in. A 50% majority-rule consensus tree, with each branch lengths and posterior probabilities of clades was generated to summarize the results of the post burn-in posterior distribution of trees.

RESULTS

Phylogenetic analyses using MP, ML and BI show highly congruent topologies that differed in the degree of resolution for some clades and do not produce well-supported incongruent clades among them. Of 2233 base pairs analysed, 1154 are constant and 226 variable characters are parsimony-uninformative while 853 are unparsimony-uninformative. The MP analyses result in 12 equally parsimonious trees with a length of 1856 steps, a consistency index of 0.300 and a retention index of 0.608. A BI topology tree with bootstrap values is shown in **Fig. 1**. Our results agree with the previous molecular study on the classification of *Lejeuneae* (Bechteler et al. 2016a; Heinrichs et al. 2014a,b; Schäfer-Verwimp et al. 2014; Ye et al. 2015). The topology shows that the unknown taxon is nested within the lineage of *Lepidolejeuneinae*, but not a member of *Lepidolejeunea* and appears to be a sister of *Metalejeunea* with strong support (MP=100, ML=100, PP=1.00). All the representative species from *Lepidolejeuneinae* form a well-supported monophyletic clade (MP=80, ML=81, PP=1.00), which is split into three subclades. One subclade is composed of *Lepidolejeunea*, sister with the other two subclades containing *Capillolejeunea*, *Metalejeunea*, *Otolejeunea*, *Rectolejeunea*, *Vitalianthus* and the unknown taxon. *Capillolejeunea*, a small genus with two species, is distributed only in the East African Islands (He et al. 2014). The type species of this genus, *C. mascarena* S.W.Arnell, is nested within the subtribe *Echinolejeuneinae*, and sister to *Vitalianthus*, a small genus known only from Brazil and China (Bechteler et al. 2016; He et al. 2012) (**Fig. 1**). *Kymatolejeunea*, a monospecific genus endemic to New Zealand (Grolle 1984; Schuster 2001), is nested within the subtribe *Echinolejeuneinae* as proposed by Grolle (1984), Schuster (2001) and Gradstein (2013) based on morphological evidence (**Fig. 1**).

Morphological observations are illustrated in **Figs. 2–3** and treated in detail in the following sections.

TAXONOMIC TREATMENT

Thiersianthus silamensis R.L.Zhu & L.Shu, *gen. et sp. nov.* **Fig. 2A–F & Fig. 3**

Plants autoicous. Shoots irregularly pinnately branched, branches Lejeunea-type. Stems in transverse section with seven cortical cells and 6–8 medullary cells, ventral merophyte two cells wide. Leaves imbricate. Leaf lobes asymmetrically ovate, margins entire, apex obtusely rounded to rounded, cells thin-walled, trigones small, intermediate thickenings absent, ocelli numerous, scattered in leaf lobe, median ocelli larger than surrounding cells, suprabasal ocelli 1–4, very large (ca. 2–5 times as large as surrounding cells), usually isodiametric, oil bodies absent in non-ocellate cells (replaced by minute oil droplets), cuticle smooth. Leaf lobules ovoid to rectangular, sometimes strongly reduced, apex with a unicellular tooth, hyaline papilla at proximal base of tooth. Underleaves small, bilobed, outer lateral margin entire or with a small tooth. Gynoeceia with one pycnolejeuneoid innovation, female bract lobes entire, bracteole shortly bilobed. Perianths emergent, ocelli numerous, keels five, smooth. Androeceia terminal on short branches, bracteoles present only at base. Vegetative reproductive organs absent.

TYPE: MALAYSIA. SABAH: Lahad Datu, Sepagaya Forest Reserve, Mount Silam, along trail to Silam water spring, 04°58'28.50"N, 118°10'52.62"E, 303 m, on tree roots, 16 Sept. 2016, *Rui-Liang Zhu, Lei Shu & Xiang-Bo Yin* 20160916-23A (holotype: HSNU!; isotypes: BORH!, SAN!, SNP!).

Description. Autoicous. Plants green to yellowish green, minute, delicate, 3–7 mm long. Shoots (0.50–) 0.55–0.75 (–0.85) mm wide, irregularly pinnately branched, branches *Lejeunea*-type, leaf sequence of vegetative branches lejeuneoid. Stems 49–70 µm in diam., in transverse section with seven cortical cells surrounding 6–8 medullary cells, cortical cells subquadrate to oblong, 10–21 × 9–14 µm, larger than medullary cells, medullary ones ± isodiametric, 7–11 × 6–10 µm; ventral merophyte two cells wide. Rhizoids at base of underleaves, rhizoid disc absent. Leaves imbricate, flattened, shallowly inserted to stem, diverging from stem at an angle of 50–90°. Leaf lobes asymmetrically ovate, falcate, 0.30–0.45 mm long, 0.25–0.40 mm wide, margins entire, apex rounded to obtusely rounded,

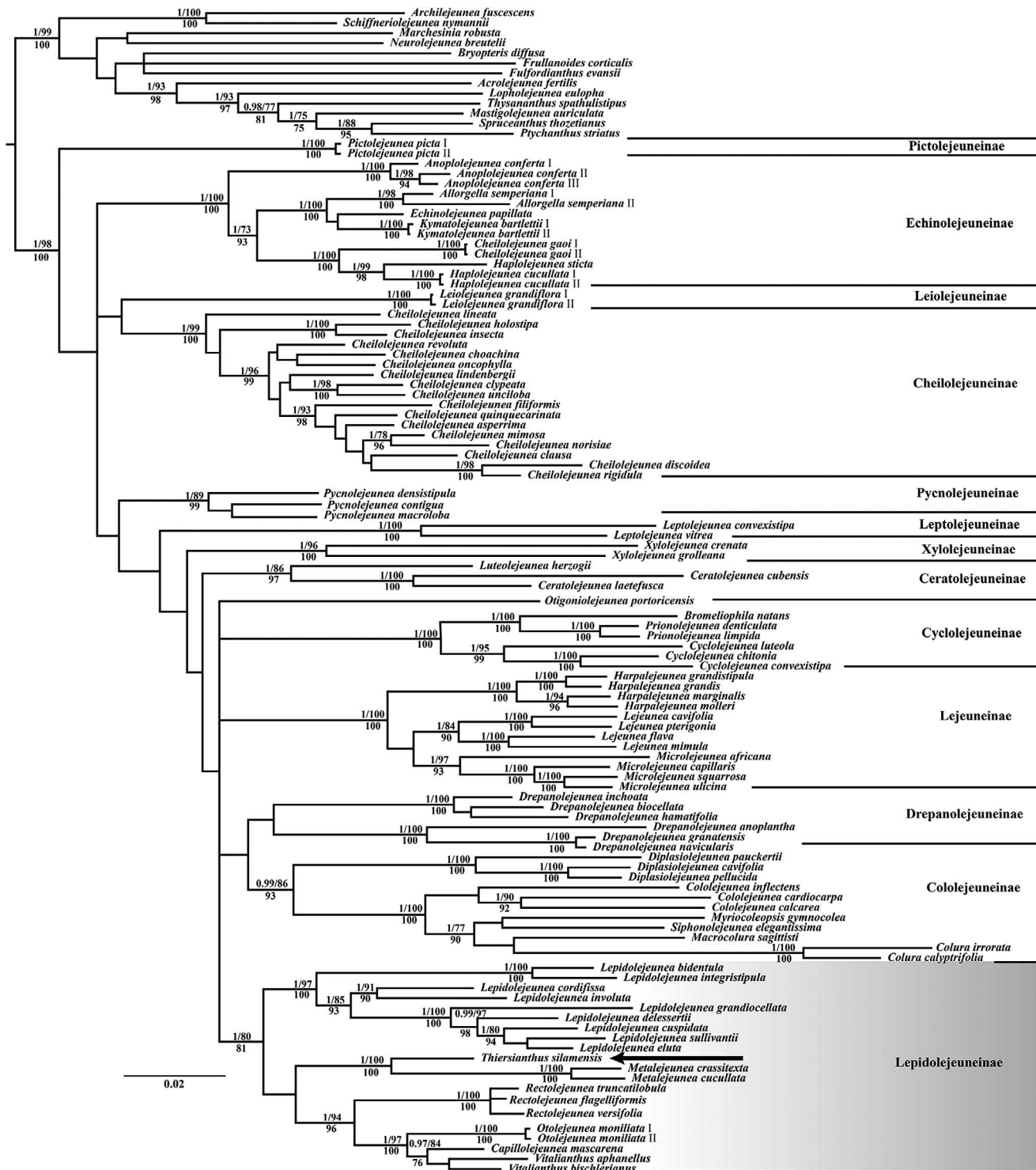


Figure 1. Bayesian majority consensus tree calculated from the results of Bayesian analysis of the combined dataset. Bayesian posterior probabilities and MP bootstrap percentage values are indicated above the branches, while the ML bootstrap percentage values are presented under the branches.

ventral margin usually strongly sinuated, dorsal margin strongly arched. Leaf lobules ovate, strongly inflated, 1/5–1/4 as long as the lobes (sometime strongly reduced), lateral free margin arched, usually

slightly incurved (except for apex), bordered by 5–7 usually rectangular marginal cells, apex usually constricted, with a unicellular, usually subquadrate, not curved apical tooth, usually directed towards

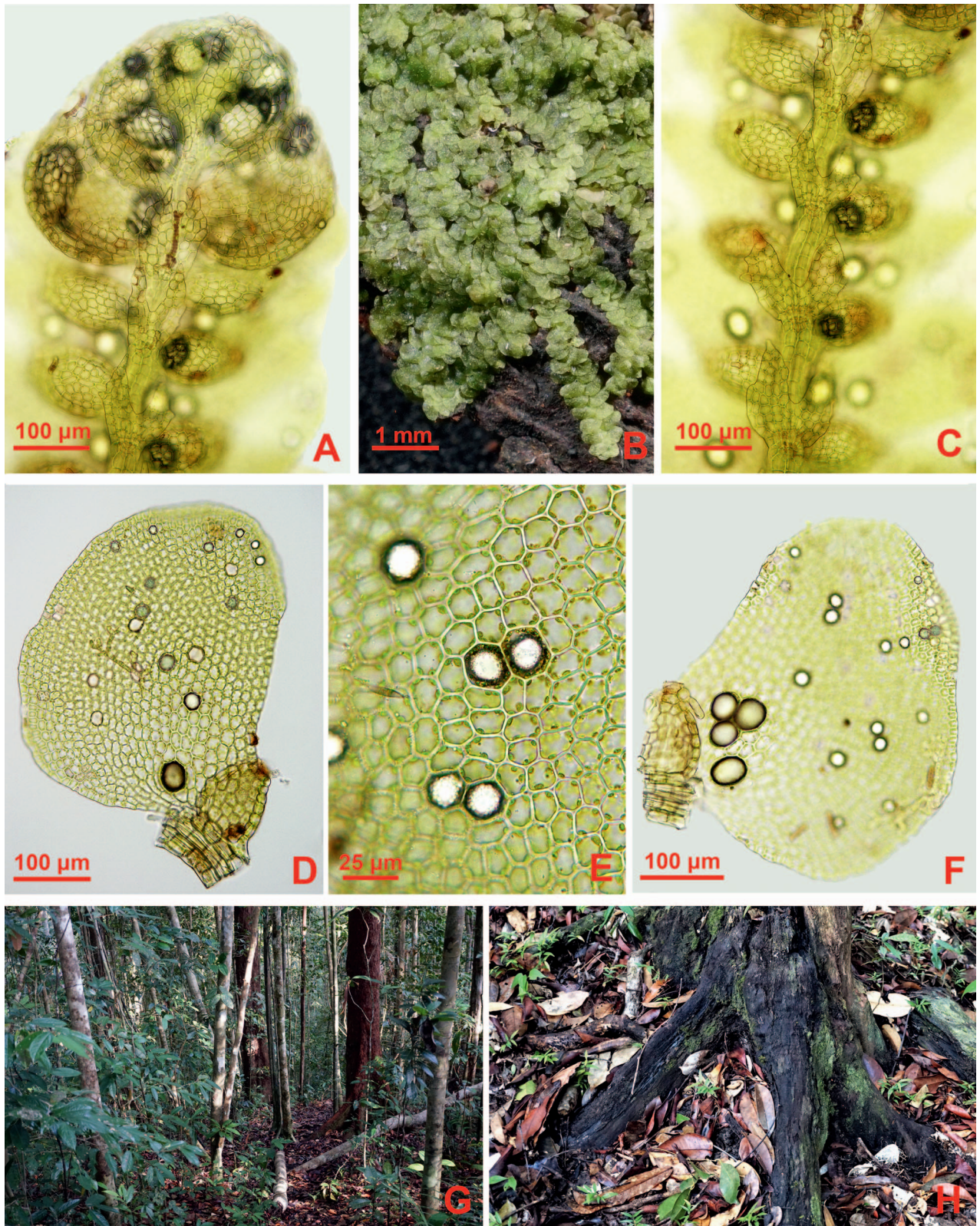


Figure 2. *Thiersianthus silamensis*. A. Androecium, ventral view. B. Plants creeping on tree roots. C. Portion of shoot showing underleaves and lack of ocelli in underleaves. D. Leaf and portion of stem, showing a single basal ocellus and scattered ocelli, dorsal view. E. Median cells of leaf lobe, showing ocelli. F. Leaf and portion of stem, showing four basal ocelli and scattered ocelli, ventral view. G. Type locality. H. Habitat, showing tree roots with *Thiersianthus silamensis*. A–F from Zhu et al. 20160916-23A (holotype).

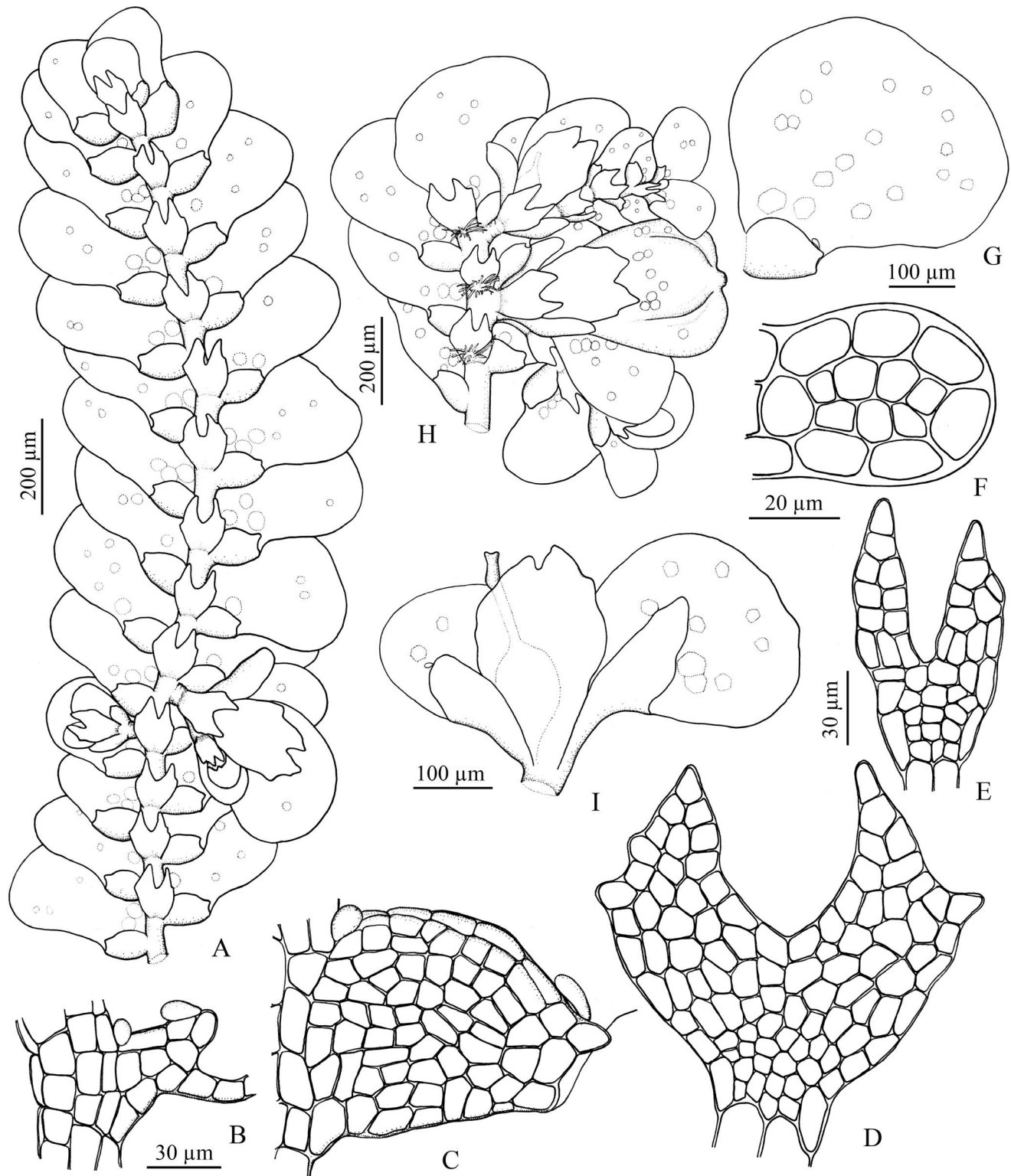


Figure 3. *Thiersianthus silamensis*. A. Plant with a gynoecium, ventral view. B. Reduced leaf lobule with a hyaline papilla and a stylus. C. Well-developed leaf lobule, ventral view. D, E. Underleaves. F. Transverse section of stem. G. Leaf, ventral view. H. Portion of shoots with a perianth. I. Gynoecium, ventral view. All drawn from Zhu et al. 20160916-23A (holotype).

shoot apex, keel arched, smooth, hyaline papilla oblong, $20\text{--}30 \times 8\text{--}14 \mu\text{m}$, situated at the proximal base of apical tooth. Stylus unicellular, oblong, $12\text{--}20 \times 7.5\text{--}11 \mu\text{m}$. Cells of leaf lobe with thin walls and very small trigones, without intermediate thickenings, at margin quadrate to rectangular, $11\text{--}25 \times 10\text{--}14 \mu\text{m}$, in the middle \pm hexagonal, $15\text{--}25 \times 12\text{--}18 \mu\text{m}$, near base similar to median ones in shape, slightly larger than median cells. Oil bodies absent in non-ocellate cells (replaced by minute “oil droplets”), oil bodies in ocelli 1 per cell, large, finely granular. Scattered ocelli present in leaf lobes, female bract lobes and perianths, usually isodiametric, $17\text{--}25 \times 15\text{--}25 \mu\text{m}$, usually larger than non-ocellate leaf cells, basal ocelli 1–4 per leaf lobe, very large, almost isodiametric, $(30\text{--})37\text{--}50 \times (25\text{--}) 36\text{--}50 \mu\text{m}$, ca. 2–5 times as large as surrounding non-ocellate cells, the lowermost ocellus separated by one to several non-ocellate leaf cells from stem cells (of the suprabasal type, cf. Zhu & So 2001). Underleaves remote, longer than wide, 1.5(–2) times as wide as stem, bilobed to ca. 1/2 their length, sinus V-shaped, lobes narrowly triangular, erect, acute at apex, 5–7 cells long, 3–5 cells wide at base, inner lateral margin nearly entire, outer lateral one usually with a unicellular tooth, insertion line almost straight to subtransverse, base cuneate (never cordate). Androecia frequent, intercalary, usually on long lateral branches or on main shoots, bracts in 2–4 pairs, hypostatic, strongly concave and inflated, shortly and subequally bifid, lobes 0.15–0.21 mm long, 0.12–0.17 mm wide, apex rounded, nearly entire, lobule slightly shorter, keels strongly arched, almost entire, antheridia two per bract, subspherical, ca. 76 μm in diameter, bracteoles 1–2, borne only at the basal portion of androecium, similar to ordinary underleaves. Gynoecia usually on short or long branches, with one pycnolejeuneoid innovation; bracts obovate, 0.28–0.42 mm long, 0.16–0.27 mm wide, deeply and unequally bifid, the lobe broadly obovate, apex rounded, margin entire, with 5–12 ocelli as in leaf lobe, lobule oblong or lingulate, ca. 2/3 as long as the bract lobe, ca. 0.2 mm long, 0.08 mm wide, margin entire, apex obtuse, keel sinuate to almost straight, 1/2–2/3 as long as the lobule; bracteole connate with bracts on both sides at base, oblong, 0.22–0.30 mm long, 0.15–0.16 mm wide at middle, margin nearly entire, apex bilobed to 1/7–1/4 its length, sinus V-shaped, lobes triangular. Perianths rare, about 1/3 exerted, obovoid, 0.40–0.48 mm long, 0.30–0.35 mm wide at middle,

inflated, with five entire keels, antical keel a little lower than the others and sometimes indistinct, surface of perianth smooth, beak short, 1–2 cells long, ocelli in perianth several to numerous, scattered. Sporophyte not seen. Asexual reproductive organs absent.

Etymology. *Thiersianthus* is named after Barbara Thiers of the New York Botanical Garden in honor of her outstanding contributions to bryology and plant taxonomy. The specific epithet refers to the locality where the new species was found.

Habitats and distribution. On tree roots and decaying logs in lowland ultramafic rainforests at an altitude of ca. 300 m, usually associated with *Cololejeunea dilatata* (Steph.) Mizut., *Lopholejeunea javanica* (Nees) Schiffn. and *Lejeunea cocoes* Mitt.; known only from Mount Silam, Sepagaya Forest Reserve, Lahad Datu, Sabah, Malaysian Borneo.

Additional specimens examined. MALAYSIA. SABAH: Lahad Datu, Sepagaya Forest Reserve, Mount Silam, along trail to Silam water spring, $04^{\circ}58'30.45''\text{N}$, $118^{\circ}10'52.22''\text{E}$, 291 m, on decaying logs, 16 Sept. 2016, *Rui-Liang Zhu, Lei Shu & Xiang-Bo Yin 20160916-30B* (HSNU).

DISCUSSION

Our molecular analysis based on a representative sampling of Lejeuneae shows that this new genus is a member of the subtribe Lepidolejeuneinae and amazingly sister to *Metalejeunea* Grolle, a pantropical non-ocellate genus with only three species (Pócs et al. 2011; Zhu & Grolle 2002; Zhu & So 2001) (Fig. 1). *Thiersianthus* and *Metalejeunea* share several characters including the minute size of plants, small and thin-walled leaf cells without intermediate thickenings, pycnolejeuneoid gynoecial innovation, small, distant and bilobed underleaves, smooth keels of perianths, single non-curved lobular tooth, proximal hyaline papilla, and lack of vegetative reproductive organs. *Metalejeunea*, however, is immediately distinguished from *Thiersianthus* by 1) rigid plants, 2) lack of ocelli in leaf lobes, 3) zig-zag stem with only 3 rows of medullary cells, and 4) presence of segmented oil bodies in all leaf cells. The last three characters are often served as most useful characters in recent generic delimitations of Lejeuneaceae (Czumay et al. 2013; Dong et al. 2013; Gradstein 2013; Gradstein et al. 2003; He et al. 2014; Wei & Zhu 2013; Zhu & So 2001). *Metalejeunea* is the unique genus lacking ocelli in the subtribe

Lepidolejeuneinae. As concluded in Dong et al. (2013), the lack of ocelli in this genus may be explained by the loss of this character during the evolution of Lejeuneaceae.

Thiersianthus is well characterized and readily recognized by the lack of distinct oil bodies in non-ocellate leaf cells, very large, usually isodiametric basal ocelli in leaf lobes, lack of ocelli in underleaves, transverse section of stem with over 5 rows of medullary cells, and small, remote and bifid underleaves whose lobes are narrow and usually with 0–1 tooth at the lateral margin (Figs. 2–3).

Lepidolejeunea is a medium-sized pantropical genus of 17 currently accepted species (Schäfer-Verwimp et al. 2017; Shu et al. 2016; Söderström et al. 2016). *Thiersianthus* and *Lepidolejeunea* share extreme similarities in the soft-textured plants, presence of scattered ocelli in leaf lobes, proximal hyaline papilla, pycnolejeuneoid gynoecial innovation, thin-walled leaf cells without intermediate thickenings, lack of distinct oil bodies in non-ocellate leaf cells, presence of ocelli in perianths, and similar stem structure. These morphological similarities may be due to rampant homoplasy for adaptation to similar environmental conditions in tropical rainforests owing to the high degree of morphological homoplasy within Lejeuneaceae (Gradstein et al. 2003; Wilson et al. 2007; Yu et al. 2013). *Thiersianthus* is separated from *Lepidolejeunea* by the lack of ocelli in both underleaves and leaf lobules, basal ocelli always larger than non-ocellate cells in leaf lobes, and non-crenulate margin of leaf lobes. The presence of ocelli in underleaves is one of the striking characters of *Lepidolejeunea* (Piippo 1986). *Rectolejeunea queenslandica* (B.M.Thiers) Xiao L.He, a rare species endemic to Queensland, Australia (He 1997; Thiers 1987 as *Lepidolejeunea queenslandica* B.M.Thiers) also resembles *Thiersianthus* in the small and distant underleaves, presence of scattered ocelli in leaf lobes, proximal hyaline papilla, thin-walled leaf cells without intermediate thickenings, lack of distinct oil bodies in non-ocellate leaf cells, presence of ocelli in perianths, larger basal ocelli of leaf lobes, and pycnolejeuneoid gynoecial innovation. The presence of scattered ocelli in underleaves in *Rectolejeunea queenslandica* (Thiers 1987 as *Lepidolejeunea queenslandica*), however, can immediately distinguish it from *Thiersianthus*. Owing to the lack of molecular data, the phylogenetic position of *Rectolejeunea queenslandica*, however, remain ambiguous. An intensive study on

the genus *Rectolejeunea* will be addressed in a separate study (Zhu & Shu, in preparation).

With the addition of *Thiersianthus*, the subtribe Lepidolejeuneinae now contains seven genera (*Capillolejeunea*, *Lepidolejeunea*, *Metalejeunea*, *Otolejeunea*, *Rectolejeunea*, *Thiersianthus*, and *Vitalianthus*) (Fig. 1). This subtribe is characterized by the green to yellowish green plants, single lobular tooth, proximal hyaline papilla, pycnolejeuneoid gynoecial innovations, thin-walled leaf cells without distinct intermediate thickenings, and usual presence of ocelli in leaf lobes (except for *Metalejeunea*). The seven genera in this subtribe can be keyed out in the following key.

KEY TO GENERA IN THE SUBTRIBE LEPIDOLEJEUNEINAE

1. Ocelli absent in leaf lobes; transverse section of stem with 3 rows of medullary cells; stem zig-zag *Metalejeunea*
1. Ocelli present in leaf lobes; transverse section of stem usually with over four rows of medullary cells; stem not zig-zag 2
2. Unbroken basal vitta of 3–5 ocelli present in leaf lobes 3
2. Unbroken basal vitta of 3–5 ocelli absent in leaf lobes 5
3. Transverse section of stem with over 5–9 rows of medullary cells; perianths with two auriculate keels *Otolejeunea*
3. Transverse section of stem with three rows of medullary cells; perianths with 4–5 keels 4
4. Leaves falcate; leaf apex usually with 2–5 ciliate teeth; leaf cells large, usually with distinct trigones; distributed in East African Islands *Capillolejeunea*
4. Leaves non-falcate; leaf margin entire; leaf cells small, without distinct trigones; distributed in Asia and Neotropics *Vitalianthus*
5. Ocelli present in underleaves *Lepidolejeunea*
5. Ocelli absent in underleaves (except for *Rectolejeunea*, cf. Reiner-Drehwald & Grolle 2012) 6
6. Lobular tooth usually long and sharp; flagelliform branches usually present *Rectolejeunea*
6. Lobular tooth short and blunt; flagelliform branches absent *Thiersianthus*

The tropical lowland forest is a paradise for Lejeuneaceae with up to 70% of liverwort species belonging to Lejeuneaceae (Gradstein 2006; Zartman 2003). Borneo is located in the heart of the biodiversity hotspots of Philippines, Sundaland and Wallacea (Myers et al. 2000). More detailed investigations of bryophytes in pristine lowland forests in this island may lead to find more interesting taxa, especially of Lejeuneaceae (Zhu et al. 2017).

ACKNOWLEDGMENTS

The authors would like to thank Sabah Biodiversity Centre for the research permit, Datuk Sam Mannan (Chief Conservator of Forests) for the access permission, Lee Ying Fah (Deputy Chief Conservator of Forests: Research & Development), Jurimin Ebin (District Forest

Officer of Lahad Datu), and the curator of Sandakan Herbarium and staff for their kind support during the field trip. Special thanks are due to S. R. Gradstein (PC), T. Pócs and A. Gyarmati (EGR) for sending samples of Lejeuneaceae for our study, the curators and staff of CANB, CHR, EGR, G, GOET, HSNU, JE, NICH and NY for making specimens available for study through loans or visits, the herbarium CHR for allowing DNA analysis of the material, Xiang-Bo Yin (HSNU) for field assistance, and C. Promma, You-Liang Xiang and Xia-Fang Cheng (HSNU) for the preparation of partial plates. This research was supported by the National Natural Science Foundation of China (nos. 31370238 and 31570206).

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manuscript received October 12, 2017; accepted November 2, 2017.

Supplementary documents online:

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