Soella (Marchantiophyta: Lejeuneaceae), a new genus from China and Japan

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Abstract. Lejeuneaceae is the largest family of liverworts with over 1800 species distributed mostly in moist tropical and subtropical regions. *Drepanolejeunea* (Spruce) Steph. is the fourth largest genus of this family with over 120 species currently listed in the updated checklist of liverworts and hornworts, however no phylogenetic studies of this genus based on an extensive taxon sampling have been done. Here we for the first time elucidate phylogenetic relationships of *Drepanolejeunea* by using the nuclear ribosomal ITS region and two chloroplast regions (*rbc*L, *trn*L–*trn*F). Our molecular phylogenetic results reveal that *Drepanolejeunea* as currently circumscribed is not monophyletic. On the basis of the combined molecular phylogenetic and morphological data, a new genus in the subtribe Lepidolejeuneinae, *Soella,* is proposed to include the remarkable and rare species, *Drepanolejeunea obtusifolia* T.Yamag. previously known from Japan. *Drepanolejeunea* subg. *Acantholejeunea* R.M.Schust. (≡ *Acantholejeunea* (R.M.Schust.) R.M.Schust.), one of five subgenera currently accepted in *Drepanolejeunea*, is suggested to be synonymous with *Ceratolejeunea* (Spruce) J.B.Jack et Steph. *Soella obtusifolia* (T.Yamag.) R.L.Zhu et al. *comb. nov*. and *Ceratolejeunea spinistipula* (Herzog) R.L.Zhu et al. *comb. nov*. are proposed. *Drepanolejeunea tenera* K.I.Goebel is new to the liverwort flora of China. With the description of *Soella*, the liverworts (Marchantiophyta) so far contain 369 genera, including 73 genera belonging to Lejeuneaceae.

Keywords. *Acantholejeunea, Ceratolejeunea*, liverwort, new combination, new synonym, ocellus.

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Lejeuneaceae is the largest family of liverworts with over 1800 species in 70 genera (Zhu et al. 2017b). Most recent molecular phylogenetic studies of this family have led to the recognition of over a half-dozen new genera, e.g., *Cumulolejeunea* R.L.Zhu et L.Shu (Zhu & Shu 2018), *Dibrachiella* (Spruce) X.Q.Shi et al. (Shi et al. 2015), *Gaolejeunea* R.L.Zhu et W.Ye (Ye & Zhu 2018), *Gradsteinianthus* R.L.Zhu et Jian Wang bis (Wang et al. 2016), *Reinerantha* Gradst. et R.L.Zhu (Gradstein et al. 2018), *Thiersianthus* R.L.Zhu et L.Shu (Zhu et al. 2017b), and *Yanoella* R.L.Zhu et al. (Zhu et al. 2018). *Drepanolejeunea* (Spruce) Steph. with 126 species (including doubtful species) (Söderström et al. 2016; Zhu et al. 2017a) is the fourth largest genus of Lejeuneaceae, following *Cololejeunea* (Spruce) Steph., *Lejeunea* Lib., and *Cheilolejeunea* (Spruce) Steph.) (He et al. 2012b; Zhu et al. 2017a). Around 6–11 species of *Drepanolejeunea* (all belonging to subg. *Drepanolejeunea*) have been included in a molecular dataset of Lejeuneaceae, and nested in a separate subtribe Drepanolejeuneinae Gradst. (e.g., Heinrichs et al. 2014; Zhu et al. 2017b). On the basis of limited

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DOI: 10.1639/0007-2745-121.3.324

0007-2745/18/$1.75/0

sampling, He et al. (2012a) hypothesized that *Drepanolejeunea* is not monophyletic, and that *Drepanolejeunea obtusifolia* T.Yamag. may represent a new genus. In the recent classification of Lejeuneaceae in the world checklist of liverworts and hornworts (Söderström et al. 2016), *Drepanolejeunea* was placed in its own subtribe Drepanolejeuneinae containing three genera (*Capillolejeunea* S.W.Arnell, *Drepanolejeunea*, and *Vitalianthus* R.M.Schust. et Giancotti). The most recent molecular-phylogenetic studies, however, reveal that *Capillolejeunea* and *Vitalianthus* accurately belong in the subtribe Lepidolejeuneinae (Zhu et al. 2017b).

In the present study, we included 116 species, representing 38 genera in all known 13 subtribes of tribe Lejeuneeae in Lejeuneaceae, and for the first time addressed phylogenetic relationships of *Drepanolejeunea* by using the sequences of nuclear ribosomal ITS region and two chloroplast regions (*rbc*L, *trn*L–*trn*F) of 26 *Drepanolejeunea* species in all five currently accepted subgenera. As a result of our investigation, *Drepanolejeunea* as currently conceived (Söderström et al. 2016) is polyphyletic, as already anticipated by He et al. (2012a). Here we propose a new genus *Soella* to accommodate *Drepanolejeunea obtusifolia* T.Yamag., a rare species previously known only from Japan (Iwatsuki et al. 2008). *Drepanolejeunea* subg. *Acantholejeunea* R.M.Schust. (≡ *Acantholejeunea* (R.M.Schust.) R.M.Schust.) is reduced to a new synonym of *Ceratolejeunea* (Spruce) J.B.Jack et Steph. and its type species, *Drepanolejeunea spinistipula* Herzog, is transferred to *Ceratolejeunea*.

Materials and Methods

Taxon sampling. In the present study 121 species of Lejeuneaceae, representing 43 genera (38 genera in all known 13 subtribes of tribe Lejeuneeae in subfamily Lejeuneoideae) were included. Owing to the lack of samples for DNA extraction, the following five extremely rare small genera in Lejeuneoideae: *Aphanotropis* Herzog (Herzog 1952), *Calatholejeunea* K.I.Goebel (Mizutani 1984), *Dactylophorella* R.M.Schust. (Schuster 1980), *Hattoriolejeunea* Mizut. (Mizutani 1987) and *Schusterolejeunea* Grolle (Grolle 1980), could not be included in our analysis. The five genera mentioned above are morphologically very distinctive from *Drepanolejeunea* especially in the non-ocellate leaves. Five species in five genera belonging to the subfamily Ptychanthoideae of Lejeuneaceae were selected as out groups. A total of 26 species representing all five subgenera currently accepted in *Drepanolejeunea* were analysed to assess their phylogenetic placement, including 12 species in subg. *Drepanolejeunea*, one in subg. *Acantholejeunea* R.M.Schust., four in subg. *Kolpolejeunea* Grolle, three in subg. *Pristolejeunea* Grolle, and four in subg. *Rhaphidolejeunea* (Herzog) Grolle et R.L.Zhu. Except for subg. *Rhaphidolejeunea*, all type species of the remaining four subgenera were included in the present analysis. Although the Asian *Drepanolejeunea cyclops* (Sande Lac.) Grolle et R.L.Zhu, the type species of subg. *Rhaphidolejeunea*, was not included, we first included four other species of this subgenus in the present analysis: the Neotropical *Drepanolejeunea polyrhiza* (Nees) Grolle et R.L.Zhu, and the Asian *Drepanolejeunea commutata* Grolle et R.L.Zhu, *Drepanolejeunea spicata* (Steph.) Grolle et R.L.Zhu and *Drepanolejeunea yunnanensis* (P.C.Chen) Grolle et R.L.Zhu. *Drepanolejeunea cyclops* is morphologically similar to and easily confused with *D. spicata* (Steph.) Grolle et R.L.Zhu and *D. yunnanensis* (Grolle & Zhu 2000). Our sampling represented both morphological and geographic variations in *Drepanolejeunea*. The sequences of 20 *Drepanolejeunea* species were newly generated in the present study, and the remaining sequences were downloaded from GenBank (**Supplementary Table S1**). A total of 29 accessions of *Drepanolejeunea* were included in the final analyses. The taxa, voucher information and GenBank accession numbers are presented in **Table 1** and **Supplementary Table S1**.

Morphological observation. Field images were photographed with a digital camera (Canon G11) in Shiwandashan Natural Forest Park, Guangxi, China. Micrographs were made with a Zeiss Imager A1 microscope equipped with a Spot Flex digital camera or using an Olympus BX43 microscope equipped with a DP71 digital camera. The terminology used for the descriptions in this paper mainly follows Gradstein et al. (2001) and Zhu & So (2001). Habitat data were gathered based on the study of collections of herbarium specimens and published literature.

DNA extraction and sequencing. Total genomic DNA was isolated from silica-dried samples of shoots using the DNeasy Plant Mini Kits (Qiagen, Hilden, Germany). As in the previous analyses (Gradstein et al. 2018; Heinrichs et al. 2014; Schäfer-Verwimp et al. 2017; Zhu et al. 2017b,

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 angustifolia (Mitt.) Grolle	China, Zhu & Wei 20110418-65A (HSNU)	MH680754	MH680797	MH680792
Drepanolejeunea blumei Steph.	Thailand, Inuthai 967 (HSNU)	MH680772	MH680799	MH680774
Drepanolejeunea commutata Grolle et R.L.Zhu	China, Promma 20170406-7 (HSNU)	MH680758	MH680807	MH680783
Drepanolejeunea elegans Herzog	Thailand, Promma et al. 1177 (HSNU)	MH680763	MH680805	MH680775
Drepanolejeunea erecta (Steph.) Mizut.	Vietnam, Zhu et al. 20131026-36 (HSNU)	MH680765	MH680817	MH680780
Drepanolejeunea fissicornua Steph.	Malaysia, Zhu et al. 20160922-531 (HSNU)	—	MH680800	MH680776
Drepanolejeunea intermedia Zwickel	Indonesia, Zhu et al. 20170524-78j (HSNU)	MH680773	MH680803	MH680795
Drepanolejeunea levicornua Steph.	China, Zhu et al. 20050902-92 (HSNU)	MH680752	MH680802	MH680777
Drepanolejeunea lyrata Grolle	Indonesia, Zhu et al. 20170522-74A (HSNU)	MH680762	MH680811	MH680794
Drepanolejeunea madagascariensis (Steph.) Grolle	Madagascar, Pócs 9889/BD (HSNU)	MH680756	MH680808	MH680784
Drepanolejeunea obtusifolia T.Yamag. I	China, Zhu et al. 20140414-16 (HSNU)	MH680768	MH680812	MH680788
Drepanolejeunea obtusifolia T.Yamag. II	China, Zhu et al. 20140417-38 (HSNU)	MH680769	MH680813	MH680789
Drepanolejeunea obtusifolia T.Yamag. III	China, Wei 20100211-66A (HSNU)	MH680767	MH680814	MH680787
Drepanolejeunea polyrhiza (Nees) Grolle et R.L.Zhu	Brazil, Zhu & Shu 20171128-11 (HSNU)	MH680766	MH680810	MH680796
Drepanolejeunea sp.	China, Zhu & Wei 20110419-5 (HSNU)	MH680755	MH680798	MH680793
Drepanolejeunea spicata (Steph.) Grolle et R.L.Zhu	China, Yu & Peng 20100714-47A (HSNU)	MH680764	MH680819	MH680781
Drepanolejeunea spinistipula Herzog I	Brunei, Zhu et al. 20151216-10B (HSNU)	MH680770	MH680815	MH680790
Drepanolejeunea spinistipula Herzog II	Brunei, Zhu et al. 20151217-27 (HSNU)	MH680771	MH680816	MH680791
Drepanolejeunea spinosocornuta Steph.	Indonesia, Zhu et al. 20170524-92 (HSNU)	MH680760	MH680801	MH680779
Drepanolejeunea tenera K.I.Goebel	China, Wang & Peng 20110513-15A (HSNU)	MH680753	MH680804	MH680786
Drepanolejeunea thwaitesiana (Mitt.) Steph.	China, Zhu et al. 20150810-48 (HSNU)	MH680761	MH680818	MH680778
Drepanolejeunea trematodes (Nees) Bischl.	Madagascar, Pócs 9889/BE (HSNU)	MH680757	MH680809	MH680785
Drepanolejeunea yunnanensis (P.C.Chen) Grolle et R.L.Zhu	China, Lu et al. 20170927-102 (HSNU)	MH680759	MH680806	MH680782

2018; Zhu & Shu 2018), a nuclear ribosomal ITS region and two chloroplast regions (*rbc*L, t*rn*L–*trn*F) were chosen to reconstruct the phylogeny of Lejeuneaceae. Three short PCR fragments including nrITS, *rbc*L, *trn*L–F were amplified as in previous publications (Zhu et al. 2017b). PCR products were purified and sequenced bidirectionally by Jie Li Biology Inc., China (http://www.genebioseq.com).

Phylogenetic analyses. Sequences were automatically aligned with MAFFIT version 7 (Katoh & Standley 2013). The automatically aligned data matrix was subsequently fine-tuned by hand in PhyDE v.0.9971 (http://www.phyde.de/index.html).

We performed maximum parsimony (MP), Bayesian posterior probability, and maximum likelihood (ML) analyses of the regions individually and in combination.

The ITS, *trn*L–*trn*F, and *rbc*L were assessed for congruence, to determine whether the sequences could be appropriately concatenated, using maximum parsimony (MP) as implemented in PAUP* version 4.0b10 (Swofford 2002). We carried out heuristic searches with TBR branch swapping and 1000 replicates of random stepwise additions, saving 10 trees per replicate. All characters were unordered and had equal weight. We measured support for reconstructed clades using 1000 bootstrap (BP) replicates, with the starting tree generated by sample addition and tree bisection-reconnection branch swapping. The three gene trees differed in their topology, but many clades were resolved in all trees and showed no incongruence. Accordingly, the concatenated dataset was used for further analyses.

A Bayesian analysis was performed using Markov chain Monte Carlo (MCMC) sampling in MrBayes 3.2.6 (Ronquist & Huelsenbeck 2003). The data were portioned into three regions, with srartfrq, revmat, shape and pinvar parameters all unlinked between the partitions. Following the recommendation of MrModeltest 2.3 (Nylander 2004), the most complex model, GTR+G+I, was implemented for each partition. Several analyses were conducted with Markov chains on each of two independent runs with the following settings: 10^7 generations, with trees sampled every 100th generation. After 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 the burn-in was discarded, a 50% majority-rule consensus tree was calculated with posterior probabilities (PP) for support for the branches.

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

Results

The combined dataset comprised 2232 investigated molecular characters, of which 830 were parsimony informative, 227 variable but parsimony uninformative, and 1175 constant. The MP analysis resulted in 64 equally parsimonious trees with a length of 6009 steps, a consistency index 0.30 and a retention index of 0.63.

All three analysis methods (BI, ML, MP) gave a largely congruent result; the topology of BI 50% majority-rule consensus tree of the concatenated dataset is given in **Fig. 1** with the support values of MP and ML on the branches. The MP, ML, and Bayesian analyses of the concatenated dataset recovered *Drepanolejeunea* as polyphyletic, with *D. spinistipula* completely nested within *Ceratolejeunea* (BS_{MP}=100, BS_{ML}=97, PP_{BI}=1.00), and *D. obtusifolia* nested in subtribe Lepidolejeuneinae (BS_{MP}=70, BS_{ML}=87, PP_{BI}=1.00). The monophyly of the rest of the accessions of *Drepanolejeunea* were well supported with the MP and ML analyses (BS_{MP}=82, BS_{ML}=84), but the Bayesian analysis was recovered with a poor value (PP_{BI}=0.84). The clade of *Ceratolejeunea* was divided into two subclades, one of which composed of *Drepanolejeunea spinistipula* and *C. minuta* (BS_{MP}=71, BS_{ML}=84, PP_{BI}=0.7). Although *Drepanolejeunea obtusifolia* was recovered as a member of Lepidolejeuneinae, the relationship between *D. obtusifolia* and other genera of Lepidolejeuneinae was unresolved.

Our examination of fresh samples from China reveals that (2–)3–4(–6) enlarged basal ocelli are arranged in an unbroken transverse row in leaf lobes (**Fig. 2B, F, H–J**). Such a distribution pattern of ocelli does not occur in typical *Drepanolejeunea*. The vegetative reproduction of this species is by the ribbon-like regenerants at leaf margins which are also absent in the typical *Drepanolejeunea*. In addition, oil bodies in leaves are granular, but usually shining and almost homogeneous in *D. obtusifolia* (**Fig. 2D–F**). Our molecular analyses also indicate a highly isolated position of *Drepanolejeunea obtusifolia* (**Fig. 1**). On the basis of the combined molecular phylogenetic and morphological data, *Drepanolejeunea obtusifolia* obviously merits recognition as a new genus in subtribe Lepidolejeuneinae.

Morphological observations in the field showed that *Drepanolejeunea spinistipula* has the glossy pale brown green color of plants, transverse section of stem with 12–18 medullary cells, presence of scattered ocelli in leaf lobes, and horn-like projections of the perianth as in typical *Ceratolejeunea* (**Figs. 4–5**). In typical *Drepanolejeunea*, plants are never pale brown green. In addition, the stem in *Drepanolejeunea* is slender with only three rows of medullary cells. Both morphological and molecular evidence support the position of *Drepanolejeunea spinistipula* in *Ceratolejeunea*.

Discussion

Drepanolejeunea is a diverse pantropical genus (He et al. 2012b). Currently this genus is divided into five subgenera: *Acantholejeunea*, *Drepanolejeunea*, *Kolpolejeunea*, *Pristolejeunea*, and *Rhaphidolejeunea* (Söderström et al. 2016). *Acantholejeunea* was first segregated as a subgenus of *Drepanolejeunea* based on *D. spinistipula* by Schuster (1963) who later raised it to generic rank (Schuster 1968). *Acantholejeunea* is a controversial genus. Schuster (1992), Pócs et al. (1995) and Schuster (2001) recognized it as a separate genus which might have some connections with the Neotropical *Cyclolejeunea*. Gradstein (2013), however, considered it as a subgenus of *Drepanolejeunea* following Schuster (1963). At present two species are placed in subg. *Acantholejeunea*: *D. dentistipula* Steph. and *D. spinistipula* Herzog (Söderström et al. 2016). Our examination of fresh samples revealed that the type species, *D. spinistipula*, has the glossy pale brown green color of plants and a stem with over 4 rows of medullary cells as in typical *Ceratolejeunea*. On the contrary, in typical *Drepanolejeunea* the stem has only three rows of medullary cells as in *Leptolejeunea* (Spruce) Steph., *Microlejeunea* (Spruce) Steph., *Metalejeunea* Grolle, etc. (Gradstein et al. 2001; Shu et al. 2016; Zhu & So 2001). Our molecular analyses also showed that *D. spinistipula* is nested

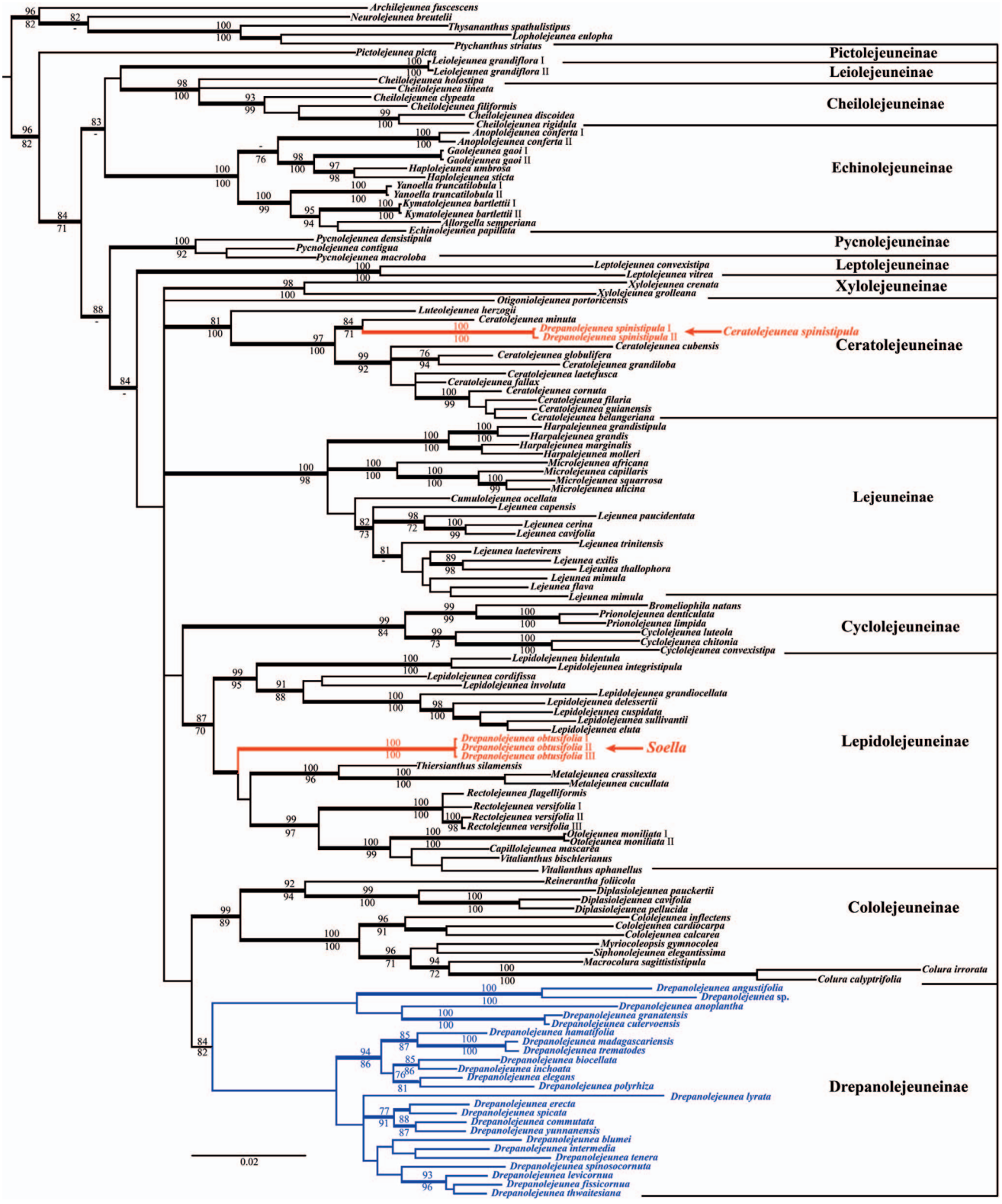

Figure 1. Phylogeny of Lejeuneaceae illustrating position of *Drepanolejeunea obtusifolia* and *Drepanolejeunea spinistipula*, inferred from combined dataset (*rbc*L, *trn*L–*trn*F and nrITS) and topology displayed as majority rule consensus tree of trees recovered in stationary phase of Bayesian search with branches thickened when $PP_{BI} \geq 0.95$. $BS_{ML} \geq 80$, $BS_{MP} \geq 70$ are displayed besides the nodes with the former above the branch and the later below the branch.

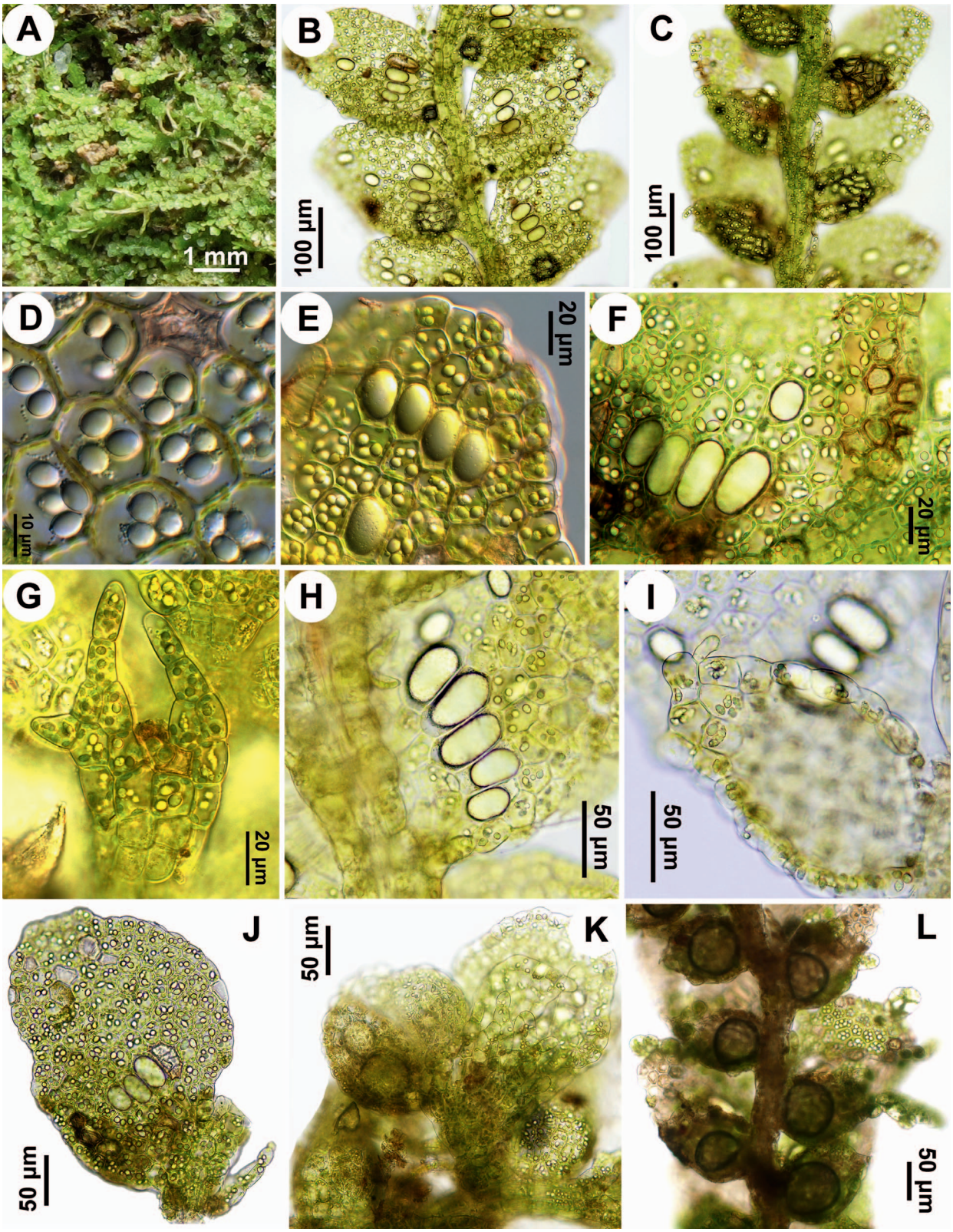

Figure 2. *Soella obtusifolia*. **A.** Close-up of *S. obtusifolia* on tree base. **B.** Portion of shoot. **C.** Portion of shoot, ventral view. **D.** Oil bodies of median cells of leaf lobe. **E.** Leaf apex showing five ocelli. **F.** Leaf base showing four basal ocelli in a transverse row. **G.** Underleaf. **H.** Leaf base showing six basal ocelli in a transverse row. **I.** Leaf lobule showing hyaline papilla and free lateral margin of leaf lobule. **J.** Leaf. **K.** Androecium and a young gynoecium, ventral view. **L.** Ribbon-like marginal regenerants. A, D, E and G from *R.-L. Zhu et al. 20141129-37* (HSNU), H–L from *R.-L. Zhu et al. 20141129-53B* (HSNU), the others from *Y.-M. Wei et al. 20140417-18* (HSNU).

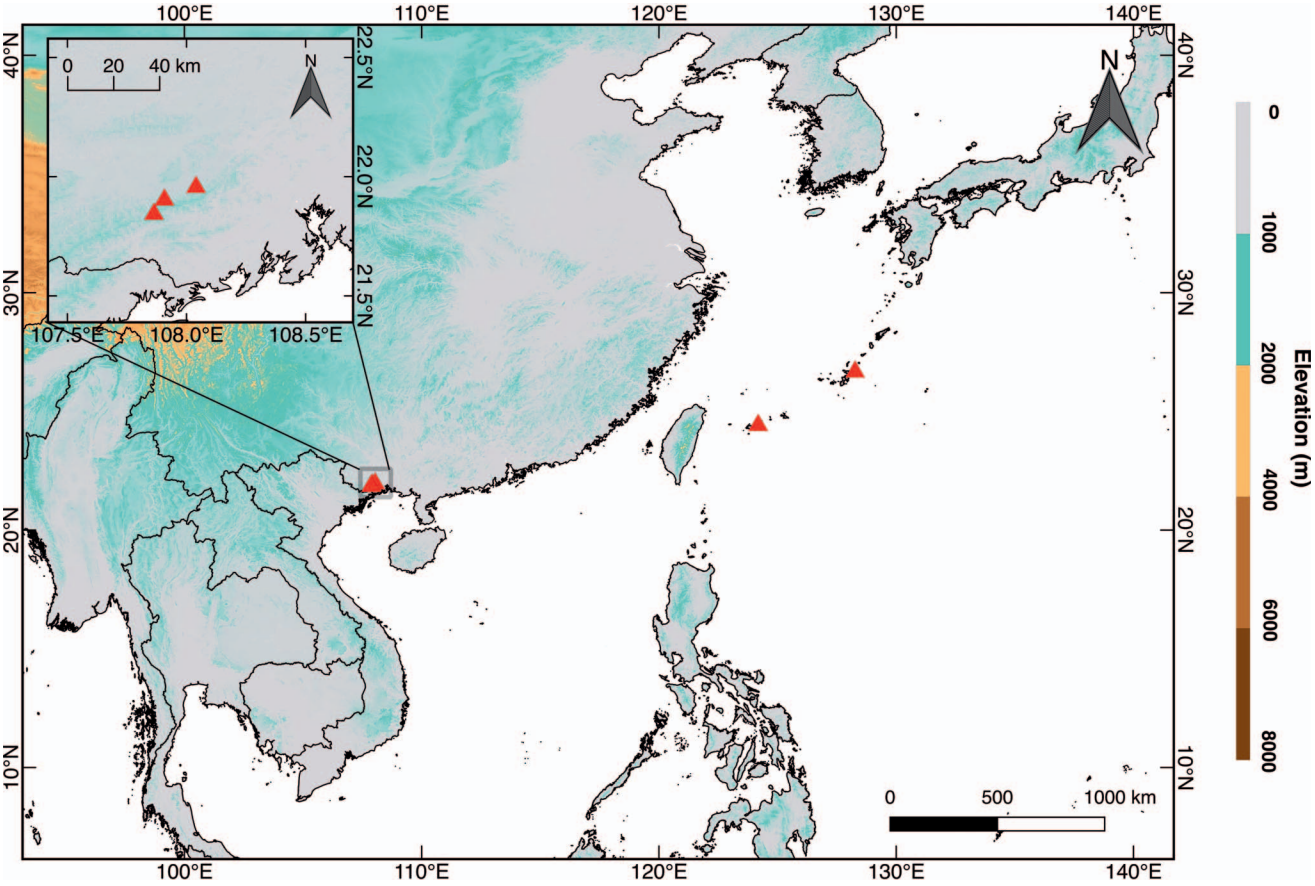

Figure 3. Known distribution of *Soella obtusifolia* (triangles).

within *Ceratolejeunea*, and sister to *Ceratolejeunea minuta* G.Dauphin. Therefore, *Acantholejeunea* is proposed to be synonymous with *Ceratolejeunea*. *Ceratolejeunea spinistipula* is readily distinguished from the other *Ceratolejeunea* species by the basal ocelli almost as large as non-ocellate basal cells (**Fig. 4B**). The second species in *Acantholejeunea*, *A. dentistipula*, is a very rare species known only from the type specimen collected from the Philippines (Tan & Engel 1986). Our examination of type specimens reveal that *A. dentistipula* has typical characters of *Drepanolejeunea* such as only three rows of medullary cells in transverse section of stem, obovate perianths with five horizontally keels usually winged, and presence of cladia for vegetative reproduction. *Acantholejeunea dentistipula* thus has to be placed in *Drepanolejeunea* as suggested by Stephani (1913). *Drepanolejeunea dentistipula* is easily recognized by the enlarged ocelli in leaf lobes, erect, spinose to dentate lobes of underleaves, and usual absence of gynoecial innovations (**Fig. 6**). *Drepanolejeunea dentistipula* is quite like the tropical Asian *D. tricornua* Herzog in the scattered ocelli in leaf lobes, enlarged ocelli in leaf lobes, and shape of leaf and leaf lobule, but the latter species can be immediately separated by the horizontally spreading underleaf lobes, very frequent gynoecial innovations, and long wings of perianths.

Drepanolejeunea obtusifolia T.Yamag. was originally described based on a single specimen collected from Ishigaki Island, Ryukyu, Japan (Yamaguchi 1984). The plant has many interesting characters, including thin-walled large cells, usually almost homogeneous oil bodies, and shining ocelli much larger than non-ocellate cells as in *Leptolejeunea*, three rows of medullary cells of the stem as in *Drepanolejeunea* and *Vitalianthus* R.M.Schust. et Giancotti, basal ocelli usually arranged in a transverse line as in *Yanoella*, pycnolejeuneoid gynoecial innovations as in *Thiersianthus*, and presence of ribbon-like marginal regenerants as in *Pictolejeunea* Grolle. Our new phylogenetic analysis clearly shows that *Drepanolejeunea obtusifolia* is nested within the lineage of the subtribe Lepidolejeuneinae, and sister

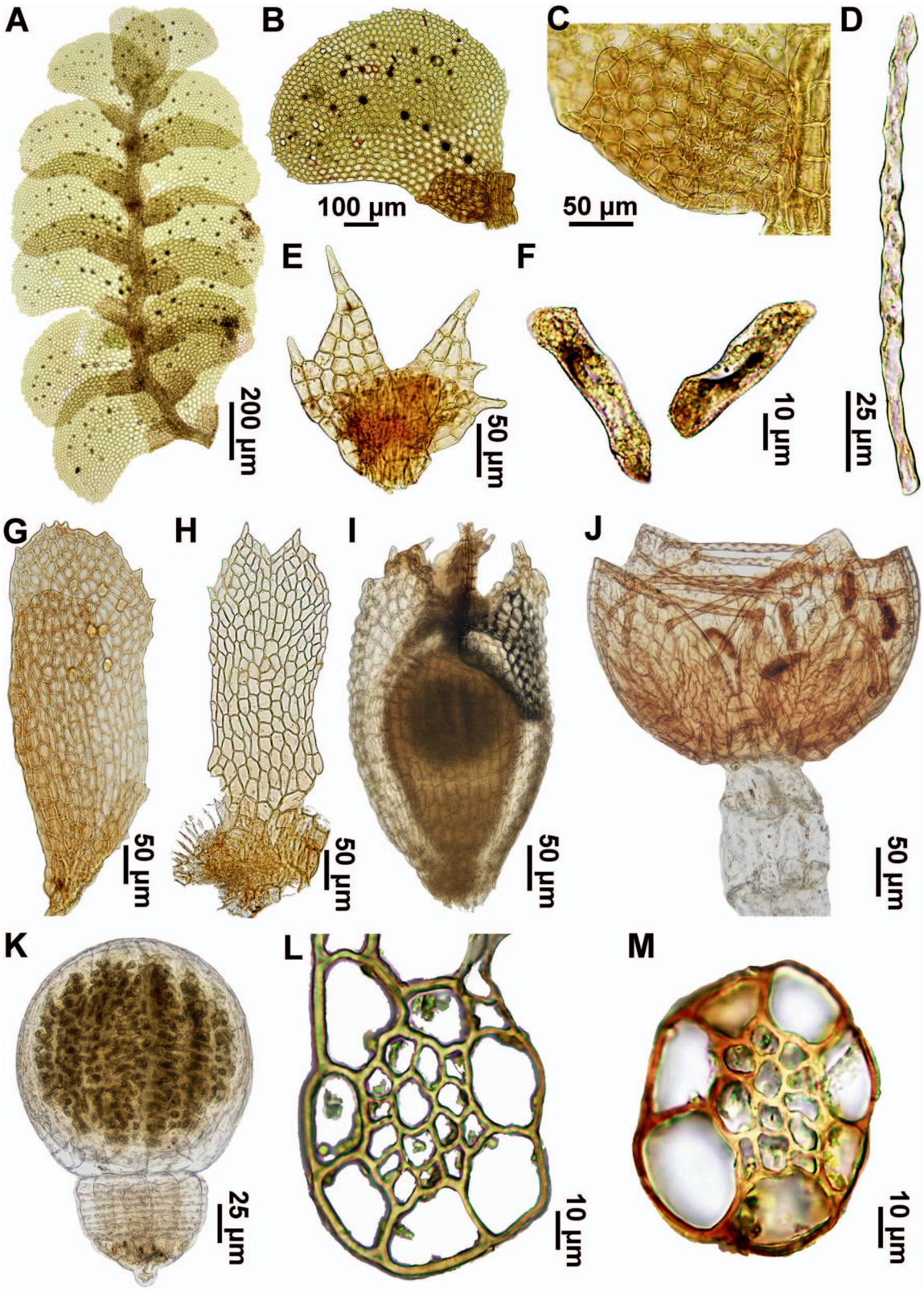

Figure 4. *Ceratolejeunea spinistipula*. **A.** Portion of shoot, ventral view. **B.** Leaf, ventral view. **C.** Leaf lobule. **D.** Elater. E. Underleaf. **F.** Spores. **G.** Female bract, ventral view. **H.** Female bracteole. **I.** Perianth, ventral view. **J.** Capsule after dehiscence. **K.** Sporophyte before elongation of seta. **L, M.** Transverse section of stem. A–C, E and L from *R.-L. Zhu et al. 20151215-13A* (HSNU), D and F–K from *R.-L. Zhu et al. 20151217-28A*, M from *R.-L. Zhu et al. 20160915-79B* (HSNU).

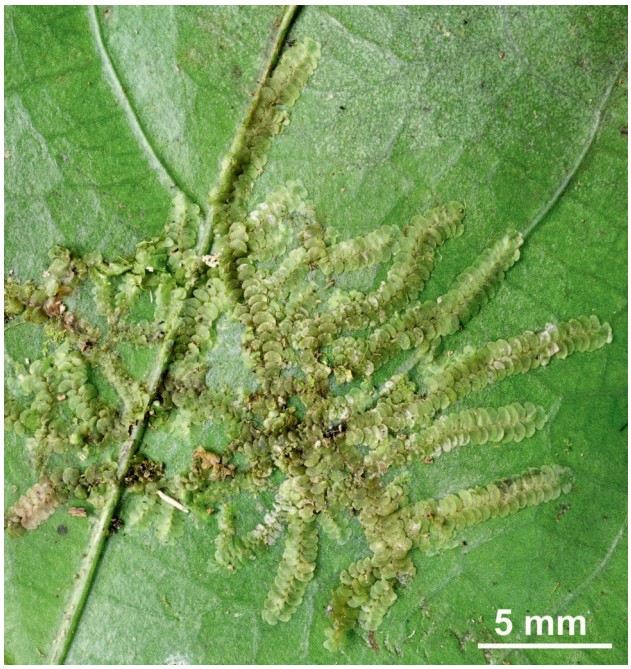

Figure 5. Close-up of *Ceratolejeunea spinistipula* on living leaves. From *R.-L. Zhu et al. 20151215-13A* (HSNU).

to the other members of subtribe Lepidolejeuneinae (**Fig. 1**). *Drepanolejeunea obtusifolia* shares with Lepidolejeuneinae several characters: 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*). *Drepanolejeunea obtusifolia*, however, is readily separated morphologically from the known genera of Lepidolejeuneinae by (2–)3–4(–6) enlarged basal ocelli arranged in an unbroken transverse row in leaf lobes (**Fig. 2**). Therefore, distinct morphological data and isolated phylogenetic position of *D. obtusifolia* within subtribe Lepidolejeuneinae clearly indicate that *D. obtusifolia* does not fit in any of the known genera of Lepidolejeuneinae. *Drepanolejeunea obtusifolia* merits recognition as a new genus, proposed in this paper as *Soella*. *Thiersianthus*, a monospecific genus known only from lowland forests of Sabah, Malaysia (Zhu et al. 2017b), is most similar to *Soella* in having scattered median ocelli in leaf lobes, enlarged basal ocelli, and pycnolejeuneoid gynoecial innovations. The former, however, is distinctive in the lack of distinct oil bodies in non-ocellate leaf cells, transverse section of stem with over five rows of medullary cells, lack of ribbon-like marginal regenerants for vegetative reproduction, and frequent gynoecial innovations. *Soella* may be confused with *Leptolejeunea* owing to the similarity in minute plants, shining scattered ocelli larger than non-ocellate cells, and usually almost homogeneous oil bodies, but *Leptolejeunea* differs in the underleaf disc composed of numerous small cells surrounded by six large marginal cells, frequent intermediate thickenings of leaf cells, presence of cladia for asexual reproduction, and absence of gynoecial innovations.

Drepanolejeunea tenera K.I.Goebel was previously known from Australia, Fiji, Indonesia, Malaysia, New Caledonia, Papua New Guinea, Thailand and Vietnam (Goebel 1928; Miller et al. 1983; Pócs & Podani 2015; Shu et al. 2017; Streimann 1991; Thouvenot et al. 2011). It is newly reported for China (voucher specimen: China, Yunnan, Mengla Co., 21°37′646″ N, 101°35′293″ E, 730 m, epiphyllous, 13 May 2011, *Wang & Peng 20110513-15A* (HSNU)).

Three hundred and sixty-three genera of liverworts have been accepted in the recent checklist of liverworts (Söderström et al. 2016), including 70 genera (excluding *Taxilejeunea* (Spruce) Steph., a synonym of *Lejeunea*) in Lejeuneaceae. With the addition of *Soella,* liverworts (Marchantiophyta) now contain 369 genera. Lejeuneaceae is thus far represented by 73 genera accounting for 20% of total liverwort genera. Additional new genera in the extremely diverse family are still expected to be described when molecular phylogenetic studies based on a more extensive taxon sampling are carried out.

Taxonomy

Soella R.L.Zhu, L.Shu, Qiong He & Y.M.Wei, *gen. nov*.

Type species: *Soella obtusifolia* (T.Yamag.) R.L.Zhu, L.Shu, Qiong He & Y.M.Wei (≡*Drepanolejeunea obtusifolia* T.Yamag., J. Jap. Bot. 59(11): 332. 1984).

Plants autoicous, epiphytic, yellowish green. Shoots scarcely and irregularly branched, branches Lejeunea-type. Stems in transverse section with 7 cortical cells and 3 smaller medullary cells, ventral merophyte 2 cells wide. Leaves usually imbricate, obliquely spreading. Leaf lobes asymmetrically ovate to triangular-ovate, ± falcate, margins entire, sometimes irregularly and remotely crenulate, apex obtuse to rounded, cells thin-walled,

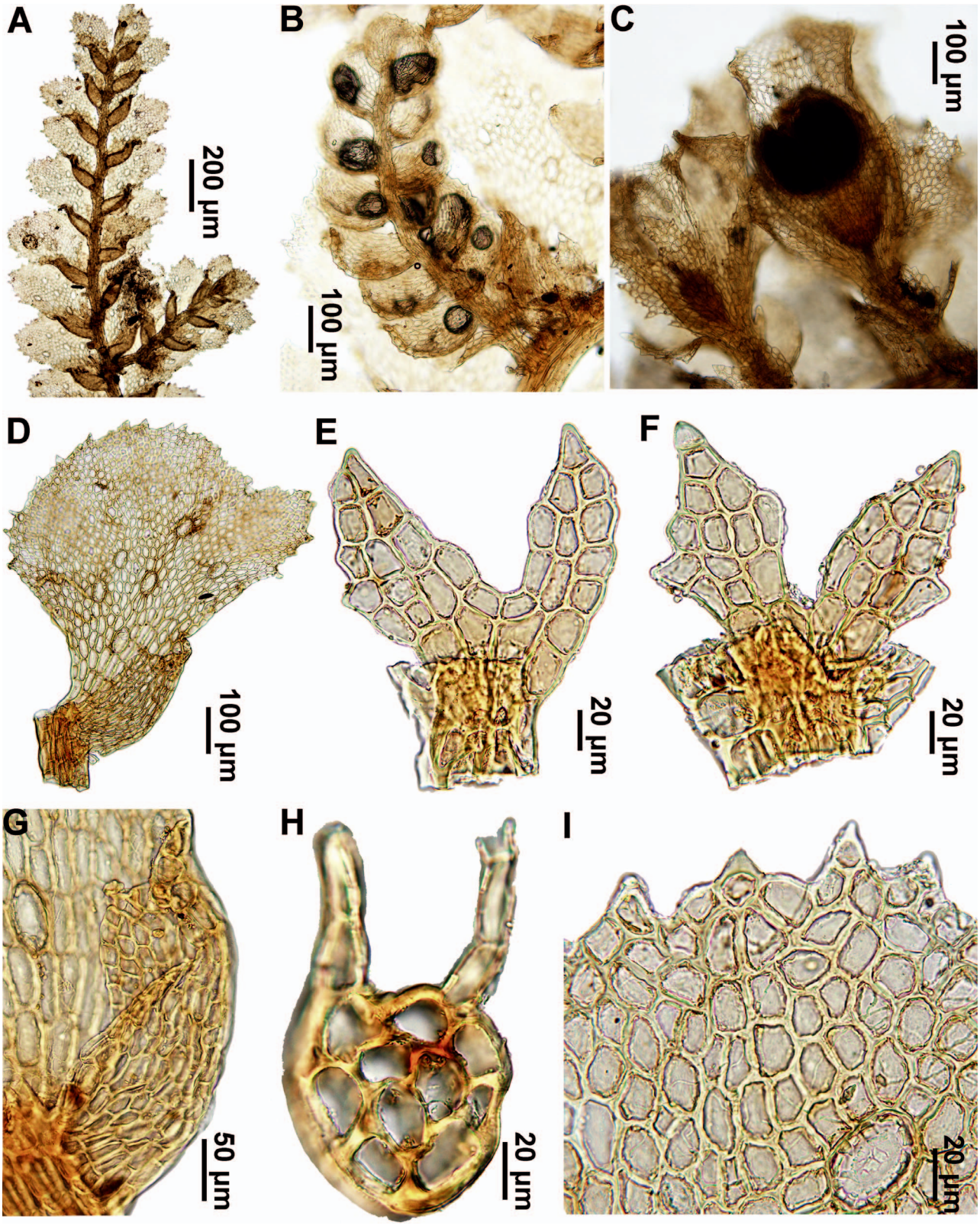

Figure 6. *Drepanolejeunea dentistipula*. **A.** Portion of shoot, ventral view. **B.** Androecium, ventral view. **C.** Gynoecia, ventral view. **D.** Leaf, ventral view. **E, F.** Underleaves. **G.** Leaf lobule. **H.** Transverse section of stem. **I.** Leaf apex. All from *C. B. Robinson s.n.* (FH).

trigones very small, intermediate thickenings absent, laminar ocelli 3–6 (–21), scattered in leaf lobe, basal ocelli usually (2–)3–4(–6) in a transverse row, much bigger than non-ocellate cells. Oil bodies granular, but usually almost homogeneous, (2–)3–5(–7) per median cell. Leaf lobules ovoid-rectangular to subquadrate, apex with a unicellular, slightly curved tooth, hyaline papilla proximal. Underleaf 1 per pair of leaves, bilobed to 1/2–2/3 their length, sinus U-shaped, rhizoid disc and ocelli absent. Androecia terminal, usually on a female subfloral innovation, with bracteoles present only at base. Gynoecia on short or long branches, occasionally with 1 pycnolejeuneoid innovation, female bract lobe almost entire, female bracteole bilobed to 2/5–1/2 its length. Perianth emergent, 5-keeled, keels almost entire to weakly denticulate due to projecting cells. Capsules almost spherical, elaters linear, spores irregularly rectangular, minutely papillose on surface, rosettes indistinct. Vegetative reproduction by means of ribbon-like marginal regenerants.

Etymology. Named after May Ling So of the Hong Kong Baptist University in recognition of her important contributions to bryology.

Soella obtusifolia (T.Yamag.) R.L.Zhu, L.Shu, Qiong He & Y.M.Wei, *comb. nov.* **Figs. 2–3**
≡ *Drepanolejeunea obtusifolia* T.Yamag., J. Jap. Bot. 59(11): 332. 1984. Type: JAPAN. Okinawa: Yaeyama Isls., Ishigaki Island, Mt. Omoto, 24°25′N, 124°11′E, 470 m, on tree trunk in evergreen forest, 11 July 1982, *T. Yamaguchi ty-2666* (holotype: HIRO (n.v.); isotype: NICH!).

Description. Autoicous. Plants yellowish green, minute, 2 to 5 mm long. Shoots 0.32–0.60 mm wide, scarcely and irregularly branched, branches *Lejeunea*-type, leaf sequence of vegetative branches lejeuneoid. Stems 45–55 μm in diameter, in transverse section with 7 cortical cells and 3 medullary cells, cortical cells subquadrate to oblong, 13–20 × 12–17 μm, slightly thick-walled, medullary cells ± isodiametric, 8–12 × 6–10 μm, slightly thick-walled; ventral merophyte 2 cells wide, rhizoids at base of underleaves, few, tufted, usually hyaline, rhizoid disc and ocelli absent. Leaves imbricate, diverging from stem at an angle of 50–85°; leaf lobes asymmetrically ovate to triangular-ovate, ± falcate, 0.18–0.32 mm long, 0.15–0.22 mm wide, margins entire to irregularly and remotely crenulate, apex obtuse to rounded, plane, ventral margin straight or weakly sinuate, dorsal margin ± arched near base; leaf lobules ovoid-rectangular to subquadrate, strongly inflated, 2/5–1/2 as long as the lobes, sometimes strongly reduced, 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, somewhat curved apical tooth directed towards leaf apex; keel arched, almost smooth, hyaline papilla oblong, 6–8 × 10–13 μm, situated at the proximal base of apical tooth. Cells of leaf lobe with thin walls and very small trigones, without intermediate thickenings, at margin quadrate to rectangular, 12–22 × 9–17 μm, in the middle ± hexagonal, 16–28 × 14–23 μm, near base similar to median cells in shape, but slightly larger. Oil bodies (2–)3–5(–7) per median cell of leaf lobe, granular, granules less than 0.7 μm in diameter, weakly knobbly on surface, but usually almost homogenous, ovoid or oblong, greyish, 4.0–6.9 × 3.7–6.0 μm. Ocelli 3–6 (–21) per leaf lobe, 1–5 (–18) at middle, 1–5 at base, median ocelli oblong, 21–29 × 15–21 μm, scattered, occasionally 2–4 in a transverse unbroken row, basal ocelli usually (2–)3–4(–6) in a transverse unbroken row, oblong, much larger than median ones, 43–55 × 20–30 μm, the lowermost ocellus always separated by one or two basal ordinary leaf cell from the stem cell (the suprabasal type, cf. Zhu & So, 2001). Underleaves remote, longer than wide, 1.0–1.5 times as wide as stem, bilobed to 1/2–2/3 their length, sinus U-shaped, lobes narrowly triangular, erect, acute at apex, 3–5 cells long, (1–)2–3(–4) cells wide at base, inner lateral margin nearly entire, outer lateral one entire or with a small tooth, insertion line almost straight, base cuneate (never cordate). Androecia terminal, capitate, usually on a female subfloral innovation, bracts in 1–3 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. Gynoecia on short or long branches, occasionally with 1 pycnolejeuneoid innovation; bracts obovate to spathulate, 0.24–0.34 mm long, 0.14–0.18 mm wide, deeply and unequally bifid, the lobe spathulate, apex rounded, margin entire, base with (0–)1–4 ocelli, middle with 0–11 ocelli; lobule oblong, 0.17–0.24

mm long, 0.04–0.08 mm wide, 1/2–4/5 as long as the bract lobe, apex obtuse, keel slightly sinuate to straight, 1/3–3/4 as long as the lobule; bracteole connate with bracts on both sides at base, oblong, 0.18–0.25 mm long, 0.12–0.19 mm wide at middle, margin entire, apex bilobed to ca. 2/5 its length, sinus usually U-shaped. Perianths about 1/3 exserted, obovoid, 0.25–0.40 mm long, 0.22–0.30 mm wide at middle, inflated, with 5 keels (2 lateral, 2 ventral, 1 dorsal), dorsal keel almost entire, a little lower than the others, ventral and lateral keels usually crenulate to denticulate owing to projecting cells, surface of perianth almost smooth, beak short, 1(–2) cells long, ocelli in perianth not seen. Calyptra one cell thick, apex usually with an obsolete archegonium. Sporophytes slightly longer than perianths, capsules almost spherical, 160–200 μm in diameter, dehiscing from apex down into four valves when mature, valves non-recurving, 193–212 μm long, 112–125 μm wide at middle, capsule wall smooth on surface, consisting of 2 layers of cells, trigones and intermediate thickenings not distinct; seta articulate, 295–330 μm long, with 7–8 articulations, 12 outer cells surrounding 4 inner cells in transverse section; foot with 2–3 transversal cell rings; elaters linear, 110–142 μm long, 7–8 μm wide, wall sinuately thickened, tip attached to valve, truncate, free base dilated. Spores irregularly rectangular in shape, 21–50 × 12–19 μm, minutely papillose on surface, rosettes indistinct. Asexual reproduction by means of ribbon-like marginal regenerants.

Habitats and distribution. *Soella obtusifolia* was found on tree bases and tree trunks in lowland evergreen forests at altitudes of 110–610 m. It was previously known only from Ishigaki Island (Yamaguchi 1984 as *Drepanolejeunea obtusifolia*) and Okinawa Island, Japan (Furuki & Fujita 2006 as *D. obtusifolia*) as one of endangered bryophytes in Japan (Iwatsuki et al. 2008). *Soella obtusifolia* is new to China and restricted to Shangsi Co. (three small localities: Pinglongshan, Shiwandashan National Forest Park, and Huangpaushan) belonging to the border areas of China and Vietnam (**Fig. 3** in the magnified area). This species, however, was not found in the Vietnamese part of the border areas of China and Vietnam (Shu et al. 2017). The total distribution of this genus is shown in **Fig. 3**. Its occurrence in Taiwan and Hainan may be expected after intensive and thorough surveys.

Representative specimens examined. CHINA. Guangxi: Shangsi Co., Shiwandashan National Nature Reserve, Shiwandashan National Forest Park, 21°54.163′N, 109°54.444′E, on tree base, 280 m, 29 Nov. 2014, *R.-L. Zhu et al. 20141129-37* (HSNU); *ibid.*, Shiwandashan National Forest Park, Shiziguanhai, 21°53.066′N, 107°54′865″E, 530 m, on tree base, 29 Nov. 2014, *R.-L. Zhu et al. 20141129-53B* (HSNU); *ibid.*, Shiwandashan National Forest Park, 21°53′52.32″N, 107°54′14.61″E, 360 m, on tree base, 17 April 2014, *Y.-M. Wei et al. 20140417-18* (HSNU); *ibid.*, Shiwandashan National Forest Park, 21°53′25.34″N, 107°54′14.19″E, 375 m, on tree trunk, 17 April 2014, *Y.-M. Wei et al. 20140417-38* (HSNU); *ibid.,* Shiwandashan National Forest Park, 21°53.720′N, 107°54.365′E, 349 m, on tree base, 10 Feb. 2010, *Y.-M. Wei et al. 20100210-66A* (HSNU); Shiwandashan National Nature Reserve, Pinglongshan, 21°50′35.50″N, 107°51′49.78″E, 451 m, on tree base, 29 June 2015, *Y.-M. Wei et al. 20150629-24* (HSNU); Shangsi Co., Huangpaushan, 21°57′21.69″N, 108°02′24.27″E, 281 m, on tree trunk, 14 April 2014, *R.-L. Zhu et al. 20140414-16* (HSNU). JAPAN, Okinawa: Okinawa Island, Kunigami-son, near Kaisui-Yosui Power Station, 26°40′N, 128°16′E, 110 m, along steam through evergreen forest at gully, on trunk of tree, 24 Dec. 2002, *T. Furuki 18197* (HSNU ex CBM-BB 25896).

With the addition of *Soella*, the subtribe Lepidolejeuneinae contains eight genera that can be separated in the following key (modified from Zhu et al. 2017b).

Key to genera in the subtribe Lepidolejeuneinae

1. Ocelli absent in leaf lobes; stem zig-zag ..... ***Metalejeunea***
1. Ocelli present in leaf lobes; 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. Transverse section of stem with three rows of medullary cells; oil bodies present in non-ocellate cells of leaf lobe ..... ***Soella***
5. Transverse section of stem with over four rows of medullary cells; oil bodies absent in non-ocellate cells of leaf lobe (replaced by minute oil droplets) 6

6. Basal ocelli in leaf lobe the basal type; flagelliform branches usually present ..... ***Rectolejeunea***
6. Basal ocelli in leaf lobe the suprabasal type; flagelliform branches absent 7
7. Ocelli present in underleaves; basal ocelli in leaf lobes almost as large as or slightly larger than non-ocellate cells .... ***Lepidolejeunea***
7. Ocelli absent in underleaves; basal ocelli in leaf lobes always much larger than non-ocellate cells..... ***Thiersianthus***

Ceratolejeunea (Spruce) J.B.Jack et Steph., Hedwigia 31: 16. 1892.

≡ *Lejeunea* subg. *Ceratolejeunea* Spruce, Trans. & Proc. Bot. Soc. Edinburgh 15: 198. 1884, '*Cerato-Lejeunea*'. Lectotype species (designated by Grolle 1983): *Ceratolejeunea cubensis* (Mont.) Schiffn. (≡*Lejeunea cubensis* Mont.).

= *Drepanolejeunea* subg. *Acantholejeunea* R.M.Schust., Beih. Nova Hedwigia 9: 115. 1963. Type species: *Drepanolejeunea spinistipula* Herzog, Svensk Bot. Tidskr. 42(3): 238. 1948. *Syn. nov*.

= *Acantholejeunea* (R.M.Schust.) R.M.Schust., J. Elisha Mitch. Ser. Soc. 83: 210. 1968 [1967]. Type species: *Acantholejeunea spinistipula* (Herzog) R.M.Schust. *Syn. nov*.

Ceratolejeunea spinistipula (Herzog) R.L.Zhu, L.Shu, Qiong He & Y.M.Wei, *comb. nov*. **Figs. 4–5**

≡ *Drepanolejeunea spinistipula* Herzog, Svensk Bot. Tasks. 42 (3): 238. 1948. ≡ *Acantholejeunea spinistipula* (Herzog) R.M.Schust., J. Elisha Mitch. Ser. Soc. 83: 210. 1968 "1967". Type: INDONESIA. Borneo: Amai Ambit, *H. B. G. Hallier 3290a* (Herb. Hort. Bot. Bog. no. 105) (lectotype designated here: JE!).

Description. Autoicous. Plants glossy greenish-brown, 10–22 mm long. Shoots 1.4–1.9 mm wide, scarcely and irregularly branched, branches *Lejeunea*-type, leaf sequence of vegetative branches lejeuneoid. Stems 60–80 μm in diameter, in transverse section with 7 cortical cells and 12–18 medullary cells, cortical cells subquadrate to oblong, 17–32 × 11–22 μm, slightly thick-walled, medullary cells ± isodiametric, 8–13 × 5–10 μm, slightly thick-walled; ventral merophyte 2 cells wide. Rhizoids at base of underleaves, few, tufted, usually hyaline, rhizoid disc absent. Leaves imbricate, diverging from stem at an angle of 60–90°; leaf lobes obliquely ovate, usually falcate, 0.60–0.90 mm long, 0.40–0.60 mm wide, margins dentate, apex rounded, plane, ventral margin straight or weakly sinuate, dorsal margin arched; leaf lobules ovoid-rectangular to subquadrate,, slightly inflated, (1/8–)1/4–1/3 as long as the lobes, sometimes strongly reduced, lateral free margin slightly incurved (except at apex), proximal to the notch bordered by 6–7 subquadrate to rectangular marginal cells, apex usually slightly constricted, with a unicellular apical tooth directed towards stem; keel slightly arched, almost smooth, hyaline papilla oblong, 18–23 × 9–12 μm, situated at the proximal base of apical tooth. Cells of leaf lobe with thin walls and very small trigones, without intermediate thickenings, at margin quadrate to rectangular, 10–14 × 7–13 μm, in the middle ± hexagonal, 17–25 × 16–25 μm, near base similar to median cells in shape, but slightly larger. Oil bodies unknown. Ocelli 9–21 per leaf lobe, subquadrate, almost as large as non-ocellate cells, 22–33 × 20–30 μm, scattered, the lowermost ocellus separated by three basal ordinary leaf cell from the stem cell (the suprabasal type, cf. Zhu & So, 2001). Underleaves remote, longer than wide, ca. 1.5 times as wide as stem, bilobed to 2/3–3/4 of their length, sinus V-shaped, lobes narrowly triangular, erect, acute at apex, 4–7 cells long, 4–6 cells wide at base, inner lateral margin nearly entire, outer lateral one entire or with 1–2 small teeth, insertion line almost straight, base cuneate (never cordate). Androecia terminal, capitate, usually on short lateral branches; 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. Gynoecia on short or long branches, with 1 pycnolejeuneoid innovation; bract lobe narrowly oblong, ca. 0.45 mm long, 0.18 mm wide, apex rounded, margin slightly dentate, ocelli as in leaf lobe, bract lobule narrowly oblong, ca. 0.36 mm long, 0.11 mm wide, 4/5 as long as the bract lobe, apex ± obtuse, keel slightly sinuate to straight, ca. 7/8 as long as the lobule; bracteole connate with bracts on both sides at base, narrowly oblong, ca. 0.4 mm long, 0.14 mm wide at middle, margin entire or weakly dentate, apex bilobed to ca. 1/8 of its length, sinus usually V-shaped. Perianths slightly exserted, obovoid, ca. 0.40 mm long, 0.26 mm wide at middle, inflated, with 3 horns, horns smooth to weakly dentate, surface of perianth almost smooth, beak 2–3 cells long, ocelli in perianth not seen. Calyptra one cell thick. Sporophytes slightly longer than perianths, capsules almost spherical, 150–170 μm in diameter,

dehiscing from apex down into four valves when mature, valves non-recurving, 165–185 μm long, 105–120 μm wide at middle, capsule wall smooth on surface, consisting of 2 layers of cells, trigones and intermediate thickenings not distinct; seta articulate, with 7–8 articulations, 12 outer cells surrounding 4 inner cells in transverse section; foot with 2–3 transversal cell rings; elaters linear, 110–145 μm long, 6–8 μm wide, wall sinuately thickened, tip attached to valve, truncate, free base dilated. Spores irregularly rectangular in shape, 35–59 × 8.5–15 μm, minutely papillose on surface, rosettes indistinct. Asexual reproduction unknown.

Distribution and habitat. Known from Indonesia (Amai Ambit), Malaysia (Johore, Sarawak), and Papua New Guinea (Pócs et al. 1995). New to Brunei. Epiphyllous usually in lowland forests in Brunei, Indonesia and Malaysia. In Papua New Guinea, *Ceratolejeunea spinistipula* was found in montane rainforests at an altitude of 1250–1300 m (Pócs et al. 1995).

Representative specimens examined. BRUNEI. TEMBURONG: Kuala Belalong Field Studies Centre of University Brunei Darussalam, 04°32′49.57″N, 115°09′23.64″E, 105 m, epiphyllous, *R.-L. Zhu et al. 20151217-27* (HSNU); *ibid.*, 04°32′52.01″N, 115°09′27.67″E, 60 m, epiphyllous, *R.-L. Zhu et al. 20151216-10B* (HSNU); *ibid.*, 04°32′49.65″N, 115°09′25.41″E, epiphyllous, 15 Dec. 2015, *R.-L. Zhu et al. 20151215-15A* (HSNU); *ibid.*, 04°32′51.89″N, 115°09′27.40″E, 75 m, epiphyllous, 16 Dec. 2016, *R.-L. Zhu et al. 20151216-13A* (HSNU). MALAYSIA, SABAH: Lahad Datu, Sepagaya Forest Reserve, Mount Silam, along Kalung-Kalungan trail, 04°57′57.33″N, 118°10′22.62″E, 727 m, epiphyllous, *R.-L. Zhu et al. 20160915-79B* (HSNU).

Drepanolejeunea dentistipula Steph., Sp. Hepat. 5: 343. 1913. **Fig. 6**

≡ *Acantholejeunea dentistipula* (Steph.) R.M.Schust., J. Elisha Mitchell Sci. Soc. 83: 210. 1968[1967]. TYPE: THE PHILIPPINES. "Luzon, Province Tayabas, Infanta, Mount Binuang", Aug. 1909, *C. B. Robinson s.n.* (Bureau of Science No. 9583) (holotype: G00060868!; isotype: FH!).

Description. Dioicous (?). Plants pale brown in herbaria, 10 to 20 mm long. Shoots 1.1–1.4 mm wide, densely and irregularly branched, branches *Lejeunea*-type, leaf sequence of vegetative branches lejeuneoid. Stems 80–100 μm in diameter, in transverse section with 7 cortical cells and 3 medullary cells, cortical cells subquadrate to oblong, 14–26 × 12–17 μm, thick-walled, medullary cells ± isodiametric, 11–22 × 10–17 μm, slightly thick-walled; ventral merophyte 2 cells wide, rhizoids at base of underleaves, few, tufted, usually hyaline, rhizoid disc and ocelli absent. Leaves imbricate, diverging from stem at an angle of 45–70°; leaf lobes obliquely ovate, ± falcate, 0.45–0.70 mm long, 0.30–0.48 mm wide, margins dentate, apex obtuse to rounded, plane, ventral margin straight or weakly arched, dorsal margin arched; leaf lobules rectangular, slightly inflated, 1/3–2/5 as long as the lobes, lateral free margin usually slightly incurved (except at apex), proximal to the notch bordered by 6–8 subquadrate to rectangular marginal cells, apex usually slightly constricted, with a unicellular, rectangular apical tooth directed towards stem; keel slightly arched, almost smooth, hyaline papilla oblong, ca. 11 × 8 μm, situated at the proximal base of apical tooth. Cells of leaf lobe with thick walls and small trigones, intermediate thickenings usually frequent, at margin quadrate to rectangular, 7–18 × 5–13 μm, in the middle ± hexagonal, 15–25 × 7.5–16 μm, near base similar to median cells in shape, but slightly larger. Oil bodies unknown. Ocelli 5–11 per leaf lobe, median ocelli 2–10, oblong, much bigger than non-ocellate cells, 38–50 × 30–40 μm, scattered, basal ocelli 1, much larger than median ones, 55–65 × 27–37 μm, the lowermost ocellus always separated by three basal ordinary leaf cells from the stem cell (the suprabasal type, cf. Zhu & So 2001). Underleaves remote, longer than wide, 1.5–2.0 times as wide as stem, bilobed to 2/3 of their length, sinus V-shaped, lobes narrowly triangular, erect to oblique, acute at apex, 4–5 cells long, 2–4 cells wide at base, inner lateral margin nearly entire, outer lateral one entire or with a small tooth, insertion line almost straight, base cuneate (never cordate). Androecia terminal, capitate, 0.5–1.4 mm long, 0.2–0.28 mm wide, usually on short lateral branches; bracts in 4–25 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. Gynoecia on short or long branches, innovation usually absent, very occasionally with 1 pycnolejeuneoid innovation; bracts ovate to oblong, ca. 0.4 mm long, 0.3 mm wide, apex acute to obtuse, lobule oblong, 3/

4–4/5 as long as the bract lobe, margin dentate; bracteole connate with bracts on both sides at base, oblong, 0.30–0.39 mm long, 0.16–0.25 mm wide at middle, margin dentate, apex bilobed to ca. 1/3 of its length, sinus usually V-shaped. Perianths about 1/3 exserted, obovoid, 0.50–0.60 mm long, 0.45–0.50 mm wide at middle, inflated, with 5 wings, wings triangular, apex usually dentate, perianth surface almost smooth, beak short, 1(–2) cells long. Sporophytes not seen. Asexual reproduction by means of cladia.

Habitats and distribution. Known only from the type specimen collected by C. B. Robinson in 1909 in Mount Binuang, Tayabas, the Philippines where it is epiphyllous.

Acknowledgments

We are grateful to the curators and staff of ALCB, CANB, CHR, CBM, EGR, FH, G, GOET, HSNU, JE, NICH and NY for making specimens available for study through loans or visits, to T. Pócs, T. Furuki, S. Chantanaorrapint and J. Inutha for providing important samples for our study, to P. A. Riupassa, H. Mohamed, A. Mustapeng, M. Suleiman, T. V. Do, T. N. Lu, C. Zartman and A. Sierra for sincere assistance in field collections, to the Guangxi Shiwandashan National Nature Reserve for the research permit and kind help during the field trips, and to T. Yamaguchi for sharing his collection experience of *Drepanolejeunea obtusifolia* in Japan. This research was supported by the Special Program for the National Basic Work of the Ministry of Science and Technology, China (no. 2012FY110600), the National Natural Science Foundation of China (nos. 31370238, 30825004 and 31570206), and the Program of Shanghai Subject Chief Scientist (no. 08XD14016).

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manuscript received June 23, 2018; accepted August 12, 2018.

Supplementary document online:

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