**SYSTEMATICS AND PHYLOGENY**

**Lihengia: A new genus of Asteraceae distinct from Dubyaea**

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**Abstract** A new genus, Lihengia, is established for two species presently treated within Dubyaea, which is proved to be paraphyletic in the present study, even after exclusion of Lihengia. Dubyaea is a genus of about 15 species endemic to the Sino-Himalayan region that are treated within subtribe Crepidinae of tribe Cichorieae within Asteraceae. Stebbins suggested that Dubyaea may contain species representing direct ancestors of several widespread genera in tribe Cichorieae, thus making phylogenetic reconstruction challenging. We tested the monophyly of Dubyaea using a molecular phylogeny reconstructed from ITS and five plastid fragment sequences (petD, psbA-trnH, 5′trnL(UAA)-trnF, rpl32-trnL(UAG), trnQ(UUG)-5′rps16) and sampling comprising Dubyaea and related species within the tribe Cichorieae. We resolved Dubyaea species within at least two separate clades of tribe Cichorieae. Most species of Dubyaea occurred in subtribe Crepidinae, while Dubyaea sect. Amoena was placed in subtribe Lactucinae. Based on our findings, we erect Lihengia as a new genus to accommodate the species of D. sect. Amoena, and, consequently, we propose two new combinations. We discuss the morphological and cytological support for the new genus.

**Keywords** Asteraceae; Cichorieae; Dubyaea; Lihengia; new genus; Sino-Himalaya

**Supporting Information** may be found online in the Supporting Information section at the end of the article.

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**INTRODUCTION**

The Asteraceae is one of the largest family of flowering plants with 25,000–35,000 species (Mandel et al., 2019). Within Asteraceae, tribe Cichorieae is one of the most easily recognized and well-circumscribed tribes, having uniform characters of milky latex and homogamous capitula with ligulate flowers (Kilian & al., 2009); it includes 11 subtribes (Kilian & al., 2009). Among the sections, two are well represented in East Asia: Crepidinae and Lactucinae.

Subtribe Crepidinae includes the genus Dubyaea DC., which is composed of about 15 accepted species (Stebbins, 1940; Shih, 1993, 1995, 1997; Mamgain & Rao, 2008; Shi & Kilian, 2011), including the type D. hispida (D.Don) DC. This genus is characterized by nodding capitula, phyllaries in several series, brownish, purplish, or blackish stiff and often glandular hairs along midveins (rarely glabrous), fusiform cypselas that are weakly compressed with apices that are truncate or attenuate, and coarse and rigid pappus setae (Stebbins, 1940; Shih, 1997; Shi & Kilian, 2011). Dubyaea shows diverse morphological characteristics, such as habit caulescent or acaulescent, involucre cylindric, broadly campanulate or almost hemispheric, capitula declined, pendent or erect, florets yellow or of some shade of purple (pale, bluish, reddish, or brownish) or blue, pappus yellowish, brownish or whitish (Shi & Kilian, 2011). Dubyaea is subdivided into three sections according to Stebbins (1940), who provided a first comprehensive revision of the genus. These are D. sect. Dubyaea (“Eudubyaea”), sect. Ixeridopsis Stebbins, and sect. Amoena (Hand.-Mazz.) Stebbins. Stebbins (1940) considered Dubyaea as a relictual genus that contains direct ancestors of some or all of the extant species within larger and more widespread genera of tribe Cichorieae. Consistent with this view, representatives of all the three sections have primitive anatomical characteristics, but these differ between sections.

Among the sections of Dubyaea, the affinities of D. sect. Amoena, which contains two species, has remained the most ambiguous. Most species of Dubyaea have yellow or purple to reddish florets, whitish to yellowish pappus and distinct stems, but the two species of D. sect. Amoena, i.e., D. amoena (Hand.-Mazz.) Stebbins and D. gombalana (Hand.-Mazz.) Stebbins, have blue florets, brownish pappus and acaulescent habit (Fig. 1A,D) and are, therefore, remarkably different from other species of Dubyaea (Stebbins, 1940; Shih, 1997; Shi & Kilian, 2011). These two species were originally described as Lactuca amoena Hand-Mazz. and L. gombalana Hand.-Mazz. by Handel-Mazzetti (1924) and placed in Lactuca sect. Amoenae.
Fig. 1. Photographs of living plants of *Dubyaea amoena* and *D. gomalana*. A–C, *Dubyaea amoena* from China, Yunnan, Gongshan, 2 Aug 2018, L. Wang & M. Zhang 2057 (IBSC); D & E, *D. gomalana* from China, Yunnan, Gongshan, 31 Jul 2015, L.S. Xu & R. Ke 150145 (PE). A & D, Habit; B, Lateral view of a capitulum; C, Florets; E, Front view of a capitulum. — Photos: A–C by Long Wang; D & E by Lian-Sheng Xu.
Hand.-Mazz. Later on, Stebbins (1937) transferred these two species to *Dubyaea* because of their coarse pappus bristles, and cypselas that are fusiform and slightly beaked, more or less compressed but with five main ribs about equal in strength. Stebbins (1940) further established *D. sect. Amoenae*, and this treatment was usually accepted by later authors (Shih, 1997; Shi & Kilian, 2011). More recently, a molecular phylogenetic study using nuclear ITS and four plastid sequences (*matK, psbA-trnH, rbcL, trnL-F*) showed that *Youngia racemifera* (Hook.f.) Babcock & Stebbins is nested within *Dubyaea*, that *Dubyaea glaucescens* Stebbins belongs within the genus *Faberia* Hemsl., and that *Nabalus* is sister to *Dubyaea* (Liu & al., 2013). However, this study did not include either of the two species of *D. sect. Amoenae*.

In this study, we sought to use molecular phylogenies, and morphological and cytological evidence to further test the monophyly of *Dubyaea* and to clarify the relationships of *D. sect. Amoenae*.

## MATERIALS AND METHODS

**Plant material and sampling.** — Cypselae morphology and cypselae surface sculpturing of three species of *Dubyaea* (*D. amoena*, *D. gombalana*, *D. hispida*), one species of *Paraprenanthes* (*P. melanantha*), and one species of *Notoseris* (*N. henryi*) were observed. We also examined pollen characters of four *Dubyaea* species (*D. amoena*, *D. blinii*, *D. gombalana*, *D. hispida*). Both cypselae and pollen material were collected from plants in the wild or from herbarium specimens. Sixty-four samples were chosen for the molecular phylogenetics, and morphological and cytological characters for 20 samples representing 11 species of *Dubyaea* (*Appendix 1*). All voucher specimens were deposited in PE and IBSC. Twenty-five specimens comprising 15 taxa were sequenced for this study. The materials of molecular study were silica dried fresh leaves collected in the field.

**Observations of cypselae and pollen characters.** — The morphological diversity of fruit surface sculpturing has been previously observed using scanning electron microscopy (Barthlott, 1981, 1984; Barthlott & al., 1998). Sculpturing on fruit surfaces may not be as affected by the environmental conditions in which an individual occurs than other morphological traits (Barthlott, 1984). The abbreviations used in describing fruit epidermal morphology in the results follow Zhu & al. (2006) and Zhang & al. (2013). Descriptive terminology of pollen characters was based on Punt & al. (2007).

We mounted mature cypselae and pollen grains directly onto aluminum stubs with double-sided adhesive tape, sputter-coated with gold to a maximum thickness of 20 μm, and observed with a Hitachi S-4800 scanning electron microscope (SEM, Science Instrument Company, Beijing, China) with a voltage of 10 kV. For cypselae, microphotographs focus primarily on their centers. In addition to micrographs, we also examined mature cypselae collected from herbarium specimens using a light microscope. Samples for SEM observations are shown in Table 1.

### Cytological observation. — For cytological characteristics, we studied five individuals from one population of *Dubyaea amoena* (voucher: China, Yunnan, Gongshan County; L. Wang & M. Zhang 2057; IBSC). We obtained the individual plants from the wild and transferred them to a greenhouse. We allowed the roots of the plants to produce new growth before collecting root tips. The procedures and solution of cytological observation followed Tang & al. (2014). The root tips were pretreated with 0.1% colchicine for 2.5 h before fixing them in Carnoy’s solution (glacial acetic acid : absolute ethanol = 1 : 3). After fixation, we macerated the tips in an 1 : 1 mixture of 45% acetic acid and 1 M HCl at 37°C for 45 min, and then stained and squashed them in Carbol fuchsin.

### Sequence data. — Total genomic DNA was extracted from 20–30 mg of leaf tissue using the Universal Genomic DNA Extraction Kit Version 3.0 (TaKaRa, Dalian, China), following the manufacturer’s instructions. Using the extracted DNA, we performed PCR to amplify the nuclear ribosomal internal transcribed spacer (ITS) and five plastid DNA regions (*petD, psbA-trnH, 5′trnL/UAA*-trnF, *rpl32-trnL/UAG*, *trnE/GUG*-5′rps16) based on previously published protocols (Wang & al., 2013). Briefly, the 25 μl PCR reactions contained 20 ng of DNA template, 200 μM dNTPs, 0.25 μM of each primer, 1 U Taq polymerase, 1× Taq buffer. We performed the amplifications using TaKaRa Taq (DR001AM; Takara Biotechnology Co., Dalian, China) and a PTC-0200 DNA Engine Peltier thermal cycler (Bio-Rad, San Francisco, California, U.S.A.). We purified the PCR

### Table 1. Samples for SEM observations (specimens are kept in PE).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Collection number</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dubyaea amoena</em></td>
<td>X.L. Peng KR1602</td>
<td>China, Yunnan, Gongshan</td>
</tr>
<tr>
<td><em>Dubyaea blinii</em></td>
<td>L.S. Xu &amp; Rui Ke 160046</td>
<td>China, Yunnan, Gongshan</td>
</tr>
<tr>
<td><em>Dubuea gombalana</em></td>
<td>X.L. Peng KR1601</td>
<td>China, Yunnan, Gongshan</td>
</tr>
<tr>
<td><em>Dubuea gombalana</em></td>
<td>L.S. Xu &amp; Rui Ke 150145</td>
<td>China, Yunnan, Gongshan</td>
</tr>
<tr>
<td><em>Dubyaea hispida</em></td>
<td>Y.S. Chen &amp; al. 584</td>
<td>China, Xizang, Gyirong</td>
</tr>
<tr>
<td><em>Notoseris henryi</em></td>
<td>S.X. Zhu 168</td>
<td>China, Chongqing, Nanchuan</td>
</tr>
<tr>
<td><em>Paraprenanthes melanantha</em></td>
<td>J.H. Xiong &amp; Z.L. Zhou 92336</td>
<td>China, Chongqing, Nanchuan</td>
</tr>
</tbody>
</table>
products with Magnetic Beads DNA Gel Extraction Kit (Ensuer Biologicals, Shanghai, China), and performed sequencing on an ABI 3730XL automated DNA sequencer (Applied Biosystems, Foster City, California, U.S.A.) via Majorbio (Shanghai, China) with the same primers as used for amplification. We sequenced all regions using forward and reverse primers so that there was at least 70% overlap between reads. We assembled sequences with ContigExpress Sequencer v.4.1.4 (GeneCodes Corporation, Ann Arbor, Michigan, U.S.A.). Within this study, we generated 147 new DNA sequences, which we deposited in GenBank (accession numbers beginning with MK; Appendix 1).

**Phylogenetic analysis.** — We performed nucleotide BLAST searches against the NCBI non-redundant nucleotide database (Wheeler et al., 2007) using the web portal (https://blast.ncbi.nlm.nih.gov/Blast.cgi?PAGE_TYPE=BlastSearch) to test for contamination and to confirm the identities of the sequences. We aligned the sequences using Clustal X v.1.83 (Thompson et al., 1997) and adjusted them manually in BioEdit v.7.0.9 (Hall, 1999) (suppl. Appendices S1, S2).

We reconstructed phylogenies using the nuclear and plastid datasets separately, because previous studies of subtribe Lactu- cinae revealed several hard topological incongruences (Wang et al., 2013). Prior to performing the phylogenetic analyses, the best partitioning scheme and evolutionary models were selected using PartitionFinder2 (Lanfear et al., 2017), with rclustfer algorithm and corrected Akaike information criterion (AICc). The best models were GTR + I + Γ for ITS and GTR + Γ for each of the five plastid loci (suppl. Appendix S3). We performed Bayesian phylogenetic analyses using MrBayes v.3.1.2 (Huelsenbeck & Ronquist, 2001). Two independent analyses consisting of four Markov Chain Monte Carlo (MCMC) chains were run for 10 million generations, sampling one tree every 1000 generations. Runs were completed when the average standard deviation of split frequencies reached 0.01; the stationarity of the runs was assessed using Tracer v.1.7 (Rambaut & al., 2018). After removing the burn-in period samples (the first 25% of sampled trees), a 50% majority-rule consensus tree was constructed (suppl. Appendices S4, S5).

We performed maximum likelihood analyses using RAxML-HPC2 v.8.2.8 (Stamatakis, 2014), with 1000 bootstrap replicates under the GTRGAMMA model on the XSEDE online computing cluster accessed via the CIPRES Science Gateway (http://www.phylo.org) (suppl. Appendices S6, S7).

**RESULTS**

**Cypsela surface sculpturing and pollen characters observations.** — Surface sculpturing of the fruit was investigated focusing on the following four items proposed by Barthlott: (1) cell arrangement; (2) the shape of the epidermal cells; (3) the ornamentation of the outer cell walls; and (4) the degree of development of epicuticular wax (Table 2).

The epidermal cells of the fruits of all species examined were longitudinally elongated and had well-developed epicuticular wax. The shape of the epidermal cells could be grouped into three types: (1) oblong-shaped, end wall nearly round to slightly blunt (OBB) (*Dubyaea amoena*, Fig. 2A; *D. gombalana*, Fig. 2B); (2) unclear outline with short acute end wall (UOSA) (*Paraprenanthes melanantha*, Fig. 2D); (3) unclear outline with short blunt end wall (UOSB) (*D. hispida*, Fig. 2C; *Notoseris henryi*, Fig. 2E). Ornamentation of the outer cell wall is absent in *D. amoena* and *D. gombalana*.

The pollen grains of *Dubyaea* are 25–38 μm (*D. amoena*, 25–30 μm; *D. gombalana*, 31–38 μm; *D. hispida*, 36–38 μm; *D. blinii*, 35–36 μm) in diameter, oblate-spheroidal, elliptic in equatorial view, hexagonal with convex sides in polar view, tricolporate, and echinolophate. The paraporal lacunae are large and pentagonal. Each ectocolpus is divided into three lacunae, connected by narrow interlacunar gaps. The abporal lacunae are large, angular, and broader toward the poles. The spines are 2.4–8.7 μm long (*D. amoena*, 5.1–8.0 μm; *D. gombalana*, 6.4–8.7 μm; *D. hispida*, 2.4–4.8 μm; *D. blinii*, 4–4.8 μm) and tapered. The polar areas possess three to nine spines (Fig. 3).

**Cypsela morphological observations.** — The cypselas of *Dubyaea hispida* (Fig. 4G–I) are stick-like, weakly compressed with ca. seven ribs, apex long attenuate, without beak, and pappus yellowish white and of scabrid bristles. In contrast, the cypselas of *D. amoena* (Fig. 4A–C) and *D. gombalana* (Fig. 4D–F) are columnar, weakly compressed, with fewer inconspicuous ribs (ca. five), and pappus brown and of stout, sparsely scabrid bristles. The cypselas of *Paraprenanthes melanantha* (Fig. 4J–L) are cylindroid, weakly compressed, with ca. nine distinct ribs, apex truncate and without beak, and

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**Table 2.** Characteristics of cypsela surface sculpturing from SEM observations.  

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Cell arrangement</th>
<th>Shape of cells</th>
<th>Ornamentation</th>
<th>Epicuticular wax</th>
<th>Figure</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dubyaea amoena</em></td>
<td>PLA</td>
<td>OBB</td>
<td>SMT</td>
<td>WED</td>
<td>Fig. 2A</td>
</tr>
<tr>
<td><em>Dubuea gombalana</em></td>
<td>PLA</td>
<td>OBB</td>
<td>SMT</td>
<td>WED</td>
<td>Fig. 2B</td>
</tr>
<tr>
<td><em>Dubyaea hispida</em></td>
<td>PLA</td>
<td>UOSB</td>
<td>VEP</td>
<td>WED</td>
<td>Fig. 2C</td>
</tr>
<tr>
<td><em>Paraprenanthes melanantha</em></td>
<td>PLA</td>
<td>UOSA</td>
<td>PTR</td>
<td>WED</td>
<td>Fig. 2D</td>
</tr>
<tr>
<td><em>Notoseris henryi</em></td>
<td>PLA</td>
<td>UOSB</td>
<td>VEP</td>
<td>WED</td>
<td>Fig. 2E</td>
</tr>
</tbody>
</table>

PLA, parallel to long axis; PTR, papillae with little trichomes; OBB, oblong shaped, end wall nearly round to slightly blunt; SMT, smooth; UOSA, unclear outline with short acute end wall; UOSB, unclear outline with short blunt end wall; VEP, verrucose papillae; WED, well developed.
Fig. 2. SEM images of surface sculpturing of cypselas in Dubyaea s.l. and related genera. A, D. amoena, X.L. Peng KR1602 (PE); B, D. gombalana, X.L. Peng KR1601 (PE); C, D. hispida, Y.S. Chen & al. 584 (PE); D, Paraprenanthes melanantha, J.H. Xiong & al. 92336 (PE); E, Notoseris henryi, S.X. Zhu 168 (PE). a, Median magnification; b, High magnification.
Fig. 3. SEM images of pollen grains in Dubyaea s.l. A & B, D. amoena, X.L. Peng KR1602 (PE); C & D, D. gombalana, L.S. Xu & Rui Ke 150145 (PE); E & F, D. hispida, Y.S. Chen & al. 584 (PE); G & H, D. blinii, L.S. Xu & Rui Ke 160046 (PE). A, C, E & G, Equatorial view; B, D, F & H, Polar view. — Scale bars = 5 μm.
pappus white and of slender scabrid bristles. The cypsela of *Notoseris henryi* (Fig. 4M–O) are cylindroid to subsessile, compressed, with ca. nine distinct ribs, apex truncate and without beak, and pappus white of slender scabrid bristles.

**Cytological evidence.** — Based on the sampling of five individuals, the chromosome number of *Dubyaea amoena* is $2n = 18$ (Fig. 5) and it is reported here for the first time.

**Phylogenetic analysis.** — The aligned ITS sequences were 673 nucleotides in length and possessed 280 parsimony-informative characters. The aligned matrix for the chloroplast DNA (cpDNA) dataset was 4698 nucleotides in length (petD, 1–960 bp; psbA-trnH, 961–1572 bp; rpl32-trnL(UAG), 1573–2817 bp; trnQ(UUG)-5′rps16, 2818–4036 bp; 5′trnL(UAA)-trnF, 4037–4938 bp). It contained 555 parsimony-informative characters when the gaps were treated as missing data. We present the BI phylograms (Figs. 6, 7) with Bayesian posterior probability (PP) and ML bootstrap support (BS) values.

Analyses of the cpDNA data (Fig. 7) produced a well-supported phylogenetic tree and clearly demonstrates that *Dubyaea* is polyphyletic with *D. sect. Amoena* sister to *Notoseris* and *Paraprenanthes* (PP = 1, BS = 99). The remaining species of *Dubyaea* are paraphyletic and form a clade including *Nabalus, Syncalathium, Sinoseris* and *Soroseris* (PP = 0.99, BS = 88).

The ITS tree (Fig. 6) is relatively poorly resolved. *Dubyaea atropurpurea*, *D. sp. nov.*, *D. emeinesis*, *D. hispida*, *D. blinii*, *D. chimiliensis*, *D. jinyangensis*, *D. tsarongensis* and *D. rubra* are grouped with species of *Nabalus, Sinoseris, Soroseris, and Syncalathium* (PP = 1, BS = 92) in subtribe Crepidinae, but the relationships within this clade are not as well resolved as with cpDNA. *Dubyaea amoena* and *D. gombalana* formed a monophyletic clade (PP = 0.97, BS = 79), which is sister to *Notoseris* (PP = 1, BS = 98) in subtribe Lactucinae.

**DISCUSSION**

**Morphological evidence.** — Previous morphological studies shed light on that the species of *Dubyaea sect. Amoena* are distinct from the rest species of *Dubyaea*, such as Stebbins (1940) suggested, “*Soroseris* is most closely related to *Dubyaea*, and is most probably derived from that genus.” Morphological characters, such as involucre bracts, synflorescence, capitula, cypsela and pappus color and structure were observed carefully in this study, and the combination of these characters distinguish *D. sect. Amoena* from both *Dubyaea s.str.*, *Notoseris*, and *Paraprenanthes* clearly (Table 3).

Our results of the surface sculpturing of the fruit wall of *Paraprenanthes melanantha* (Franch.) Ze H. Wang and *Notoseris henryi* (Dunn) C. Shih of subtribe Lactucinae were consistent with previous studies of these two genera (Lu, 2013; Guan, 2014). Despite the phylogenetic position of *Dubyaea sect. Amoena* within this tribe, its two species differ markedly in their fruit surface sculpturing from *P. melanantha* and *N. henryi*, which are more similar to *D. hispida*. In particular, the outline of the epidermal cells is clear in *D. amoena* and *D. gombalana*, while those of *P. melanantha*, *N. henryi* and *D. hispida* have an obscure outline. Moreover, the epidermal cells of the cypsela of *D. amoena* and *D. gombalana* are smooth, whereas those of *P. melanantha*, *N. henryi*, and *D. hispida* have ornamentation.

Pollen characters of *Notoseris rhombiformis* C. Shih and *Paraprenanthes polypodifolia* (Franch.) C. C. Chang ex C. Shih have been studied previously, and pollen morphological data were found to provide some support for recent changes in the circumscription of genera within Crepidinae and Lactucinae (Wang et al., 2009). According to our observation of pollen in this study, palynological characters are homogeneous within *Dubyaea sect. Amoena* and other species of *Dubyaea*, and also similar to *N. rhombiformis*, but different from *P. polypodifolia*, which has a smaller polar region and less spines (4–5). Thus, the palynological characters are not useful for distinguishing *D. sect. Amoena* from *Notoseris* and *Paraprenanthes*.

**Cytological evidence.** — Previous cytological investigations have shown that *Dubyaea* has a basic chromosome number of $2n = 16$ (Stebbins, 1940). Our result shows that *D. amoena* has the same basic chromosome number as *Notoseris* and *Paraprenanthes*: $2n = 18$ (Fig. 5). This cytological evidence is consistent with the results of our phylogenetic analyses, which support the position of *D. sect. Amoena* within subtribe Lactucinae.

**Molecular phylogenetic evidence.** — *Dubyaea sect. Amoena* should be treated as an independent genus. Not only nuclear ITS demonstrates the pattern (Fig. 6), but also the chloroplast regions (Fig. 7). Our tribe-wide phylogenetic analyses indicate that *D. atropurpurea*, *D. blinii*, *D. chimiliensis*, *D. emeinesis*, *D. hispida*, *D. rubra* and *D. tsarongensis* belong within subtribe Crepidinae, while *D. amoena* and *D. gombalana* comprise a monophyletic lineage of subtribe Lactucinae. Although there are already some molecular systematics studies involving genus *Dubyaea*, none of them included the species from *D. sect. Amoena*. Based on nuclear ITS and plastid trnL-F and psbA-trnH phylogenetic trees, Zhang & al. (2011) found *D. hispida* is

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**Fig. 5.** Mitotic metaphase chromosomes of *Dubyaea amoena* (L. Wang & M. Zhang 2057 [IBSC], China, Yunnan, Gongshan), $2n = 18$. 

8 µm
Fig. 6. Phylogram of the Bayesian inference analysis of the nrITS dataset (support values: Bayesian posterior probability above and maximum likelihood bootstrap below) and distribution of chromosome number (gray bars on the right). *Dubyaea amoena* and *D. gombalana* are indicated in bold font.
Fig. 7. Phylogram of the Bayesian inference analysis of the cpDNA dataset (support values: Bayesian posterior probability above and maximum likelihood bootstrap below), distribution of chromosome number (gray bars on the right) and subtribe (black bars on the right). Dubyaea amoena and D. gombalana are indicated in bold font.
closely related to *Hololeion*, *Soroseris* and *Syncalathium*. Kilian & al. (2017) found that *Dubyaea* is closely related to *Nabalus* and *Soroseris*. With more samples of *Dubyaea* included, Liu & al. (2013) concluded *Dubyaea* is not a monophyletic group

**Lihengia: a new genus of Asteraceae.** — *Dubyaea* sect. *Amoena* currently comprises two species in the transitional zone between the eastern Himalayas and the Hengduan Mountains. The new genus *Lihengia* is proposed here based on the evidence mentioned above, to accommodate the two species formerly placed in *D*. sect. *Amoena*. *Lihengia* is distinct from *Dubyaea*, *Soroseris* and *Paraprenanthes* by its acaulescent and rosette habit, solitary and erect capitulum, columnar cypsela, cypsela ribs 3–5, pappus bristles brown, sparsely and shortly scabrid (Table 3), epidermal cells oblong, and ornamentation of the outer cell wall is absent (Table 2).

**Dubyaea s.str. is not a monophyletic group.** — Our present study shows the first comprehensive phylogenetic analysis of this lineage based on one nuclear and five plastid markers. Our present phylogenetic results support that *Dubyaea* s.str. is not a monophyletic group and that *Dubyaea-Nabalus-Soroseris-Syncalathium* is a well-supported lineage.

### TAXONOMY


Acaulescent perennials, hirsute or glabrous. Leaves all basal, rostrate, pinnatifid or entire. Scapes naked or bracteates. Involucres narrowly cylindrical-campanulate, with 10–15 florets; phyllaries imbricate, deltoid or lanceolate, glabrous or glandular-hirsute. Capitula solitary on the top of the scape; florets blue. Pappus bristles sparsely and shortly scabrid. Cypselas columnar, weakly compressed, inconspicuous ribs 3–5. Epidermal cells oblong, ornamentation of the outer cell wall is absent. Base chromosome number \( x = 9 \).

**Etymology.** — The name *Lihengia* derives from the Chinese botanist Prof. Heng Li, who has made great contributions to understanding the biodiversity of the Gaoligong Shan Mountains.

**Distribution and habitat.** — *Lihengia* includes only two rare species, restricted to a small area in northwestern Yunnan Province (Gongshan County) and southeastern Xizang (Bomi, Mêdog and Zayü Counties) of China (Fig. 8). It occurs disjunctly in only three counties. The species grow in alpine meadows, bamboo thickets, or on rocky slopes, at 3200 m to 4570 m elevation.

**Phenology.** — The two species of *Lihengia* flower from July to August.

**Conservation.** — According to the IUCN criteria (IUCN, 2012), the two species of *Lihengia* should be both considered Endangered because of their small area of occupancy.


### Table 3. Diagnostic morphological characters of *Lihengia* gen. nov., *Dubyaea* s.str., *Soroseris*, and *Paraprenanthes*.

<table>
<thead>
<tr>
<th>Characters</th>
<th>Lihengia gen. nov.</th>
<th>Dubyaea s.str.</th>
<th>Soroseris</th>
<th>Paraprenanthes</th>
</tr>
</thead>
<tbody>
<tr>
<td>Growth form</td>
<td>Acaulescent, rosette</td>
<td>Distinct stem</td>
<td>Distinct stem</td>
<td>Distinct stem</td>
</tr>
<tr>
<td>Involucre</td>
<td>Narrowly campanulate</td>
<td>Cylindric, broadly campanulate, or almost hemispheric</td>
<td>Narrowly cylindrical</td>
<td>Narrowly cylindrical</td>
</tr>
<tr>
<td>Synflorescence</td>
<td>Solitary capitulum</td>
<td>Solitary capitulum or corymbose</td>
<td>Capillaceous branches</td>
<td>Capillaceous branches</td>
</tr>
<tr>
<td>Capitula</td>
<td>Erect</td>
<td>Delineated, pendent, or erect</td>
<td>Pendent at anthesis</td>
<td>Often pendent at anthesis</td>
</tr>
<tr>
<td>Florets</td>
<td>Blue to purplish blue</td>
<td>Yellow or purple to reddish</td>
<td>Purple</td>
<td>Pale reddish to purple</td>
</tr>
<tr>
<td>Floret number</td>
<td>10–16</td>
<td>7–70</td>
<td>3–12</td>
<td>4–15</td>
</tr>
<tr>
<td>Cypselas shape</td>
<td>Cylindrical</td>
<td>Narrowly cylindrical</td>
<td>Cylindroid to subsuliform</td>
<td>Cylindroid</td>
</tr>
<tr>
<td>Cypselas ribs</td>
<td>3–5 ribs</td>
<td>5 prominent main ribs alternating with 1 to 2 more slender secondary ribs</td>
<td>5 main ribs and 2 rather similar secondary ribs in between</td>
<td>5 main ribs and 2 rather similar secondary ribs in between</td>
</tr>
<tr>
<td>Pappus color</td>
<td>Brown</td>
<td>Yellowish or whitish</td>
<td>White</td>
<td>White</td>
</tr>
<tr>
<td>Pappus bristle</td>
<td>Stout, sparsely scabrid</td>
<td>Slender, scabrid</td>
<td>Slender, densely scabrid</td>
<td>Slender, densely scabrid</td>
</tr>
</tbody>
</table>
Distribution and habitat. — Xizang (Zayü County) and Yunnan (Gongshan County) of China. Alpine meadows, bamboo thickets, or rocky slopes; 3470–4420 m.

Representative specimens examined. — CHINA. Xizang: Zayü, Tsarong [Chawalong], open alpine moorland on the Salwin-Kiuchiang divide, NW of Si-Chi-to, 4270 m, Oct 1922, G. Forrest 22936 (US); Zayü, Tsarong [Chawalong], Salween-Kiuchiang divide, 4420 m, Sep 1921, G. Forrest 20331 (US); — Yunnan: Gongshan, Mount Kenichunpo, eastern and western slopes, Salween and Irrawaddy divide, 4270 m, May–Jul 1932, J.F. Rock 21975 (US); Gongshan, Mount Kenichunpo, mountains west of Champutong, 4114 m, Oct 1932, J.F. Rock 22518 (US); Gongshan, Salween-Kiuchiang divide, Oct 1922, G. Forrest 22798 (PE); Gongshan, Bingzhongluo, about 2.8 km direct south of Gawagapu, 4270 m, 28 Aug 2006, Gaoligong Shan Biodiversity Survey 31513 (CAS, KUN, PE); Gongshan, Bingzhongluo, about 2.8 km S of Gawagapu mountain and ca. 14.7 direct km WSW of Bingzhongluo in the next basin to the E of Chukui lake, 27°59′06″N, 98°29′00″E, 4270 m, 28 Aug 2006, Gaoligong Shan Biodiversity Survey 31513 (CAS, KUN); Gongshan, Bingzhongluo, about 2.8 km direct S of Gawai-gapu mountain and ca. 14.7 direct km WSW of Bingzhongluo in the next basin to the E of Chukui lake, 27°59′06″N, 98°29′00″E, 4270 m, 28 Aug 2006, Gaoligong Shan Biodiversity Survey 31513 (CAS, KUN); Gongshan, Bingzhongluo, Gawai-gapu, 3700–4321 m, 3 Aug 2013, X.H. Jin & al. ST1876 (PE); Gongshan, Bingzhongluo, Chugancuo lake, 4000 m, 15 Oct 2016, X.L. Peng KR1602 (PE); Gongshan, Cikai, Heipu Pass along the road from Gongshan to the Dulong Jiang valley, 27°46′19″N, 98°26′47″E, 3490 m, 12 Aug 2006, Gaoligong Shan Biodiversity Survey 32051 (CAS, KUN, PE); Gongshan, Cikai, Yipsaka lake, 2.4 direct km by SE of the Heipa Pass tunnel on the new road from Gongshan to the Dulong Jiang valley, 27°45′22″N, 98°27′45″E, 3560 m, 12 Aug 2006, Gaoligong Shan Biodiversity Survey 32077 (CAS, KUN); Gongshan, Champutong, 3700–3800 m, 20 Sep 1940, K.M. Feng 7849 (KUN, PE); Gongshan, Salween-Kiuchiang divide, Lunguikala, 3500 m, 14 Sep 1938, T.T. Yu 20261 (A, KUN, PE).


Distribution and habitat. — Xizang (Bomi, Mêdog and Zayü counties) and Yunnan (Gongshan County) of China. Alpine moist meadows; 3200–4200(–4570) m.

Representative specimens examined. — CHINA. Xizang: Bomi, Gawalong pass to Mêdog, 4000 m, 19 Sep 2012, FLPH Tibet Expedition 12-1789 (PE); Mêdog, Nage, 3200 m, 31 Jul 1974, Qinghai-Xizang Expedition 74-3798 (PE); Zayü, Tsarong [Chawalong], northern slopes of Mt Kenichunpo, north of Sikitung, 4270 m, May–Jun 1932, J.F. Rock 22160 (GH, US); Zayü, Tsarong [Chawalong], Salwin-Kiuchiang divide,
28°24′N, 98°24′E, 4270–4570 m, Sep 1921, G. Forrest 20257 (US); — Yunnan: Gongshan, Bingzhongluo, Chuguanluo lake, 4000 m, 15 Oct 2016, X.L. Peng KR1601 (PE); Gongshan, Bingzhongluo, Chuguanluo lake, 3988 m, 31 Jul 2015, L.S. Xu & R. Ke 150145 (PE); Gongshan, Bingzhongluo, Chuguanluo lake, 3950 m, 18 Aug 2016, L.S. Xu & R. Ke 160092 (PE).

■ AUTHOR CONTRIBUTIONS

YSC designed the research. YSC, RK and LSX participated in the field trips. RK gathered the molecular and morphological data; LSX and RK analyzed the molecular data; HML participated in the cytological analysis. YSC and LSX prepared the manuscript. YSC, LSX and AH participated in the revision of the manuscript. — YSC, https://orcid.org/0000-0002-7729-1075; LSX, https://orcid.org/0000-0002-9874-9452; RK, https://orcid.org/0000-0001-9730-8594; AH, http://orcid.org/0000-0003-3215-1201; HML, https://orcid.org/0000-0001-6660-7620

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■ LITERATURE CITED


Appendix 1. Taxon sampling, voucher data and GenBank accession numbers.

Taxon names used in the phylogenograms are in bold italics and in alphabetical order; unique sample identifier as used in the phylograms and, in square brackets where available, the voucher specimen number and GenBank accession number (if barcode data and herbarium code) are given for all samples of newly generated sequences; GenBank accession numbers are in the following sequence: ntITS, petD, psbA-trnH, 5′trnL(UUA)-trnF, rpl32-trnL(UAG) and trnQ(UUA)-CPys16, with missing sequences indicated by a dash (−), and newly generated sequences indicated by an asterisk (*).


14 Version of Record
Appendix 1. Continued.