

Research paper

Mojiangia oreophila (Crepidinae, Cichorieae, Asteraceae), a new species and genus from Mojiang County, SW Yunnan, China, and putative successor of the maternal *Faberia* ancestor

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ARTICLE INFO

Article history:

Received 9 September 2020

Received in revised form

15 June 2021

Accepted 22 June 2021

Available online 29 June 2021

Keywords:

Asteraceae

Crepidinae

Phylogeny

Taxonomy

Reticulate evolution

Cytonuclear discordance

ABSTRACT

A single small population of chasmophytic plants is described as *Mojiangia oreophila*, a monotypic genus in the subtribe Crepidinae, characterised by a unique combination of morphological features, in particular densely long-papillose homomorphic achenes with five main ribs each accompanied by two secondary ribs, coarse brownish pappus bristles, moderately many-flowered capitula, a small involucre with numerous outer phyllaries, perennial rosette herb growth and brown-woolly caudex and leaf axils. Molecular phylogenetic analysis detected that in the nrITS phylogeny *M. oreophila* forms a clade of its own in the Crepidinae; in the plastid DNA phylogeny it is nested in the clade formed by the hybridogenous genus *Faberia*, the maternal ancestor of which comes from the Crepidinae and the paternal ancestor from the Lactucinae, where *Faberia* is placed in nrITS phylogenies. *M. oreophila* shares several morphological features with *Faberia* and also shares the expected chromosome number of $2n = 16$ with its hitherto unknown maternal ancestor. *M. oreophila* may therefore be a successor of the maternal ancestor of *Faberia*. Alternatively, cytonuclear discordance is to be assumed in *Mojiangia*, caused by chloroplast capture as a result of hybridisation and introgression with *Faberia*.

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1. Introduction

During the course of field work in 2017, we discovered a single population of yellow-flowered chasmophytic Asteraceae plants of the tribe Cichorieae in the mountains of the Mojiang Hani Autonomous County in SW Yunnan (Fig. 1). No other populations of these plants have yet been identified. Our attempt to identify the plants as a known species of the tribe in China failed; moreover, it became evident that the combination of morphological features of these plants does not match any of the known genera of the tribe.

Morphological analysis indicated that the newly discovered plants had an affinity to plants in the subtribe Crepidinae. This is the largest subtribe in the Cichorieae, with 21 genera and >360 species (the *Taraxacum* microspecies not counted), and it is distributed across most of the northern hemisphere with a centre of diversity in E Asia (Kilian et al., 2009a; 2009b). Our knowledge of the Crepidinae has increased considerably during the last decade and an up-to-date classification with the relevant references is provided by Kilian et al. (2009b). However, given the paucity of diagnostic morphological features and frequent homoplasies in the tribe Cichorieae (Kilian

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Peer review under responsibility of Editorial Office of Plant Diversity.

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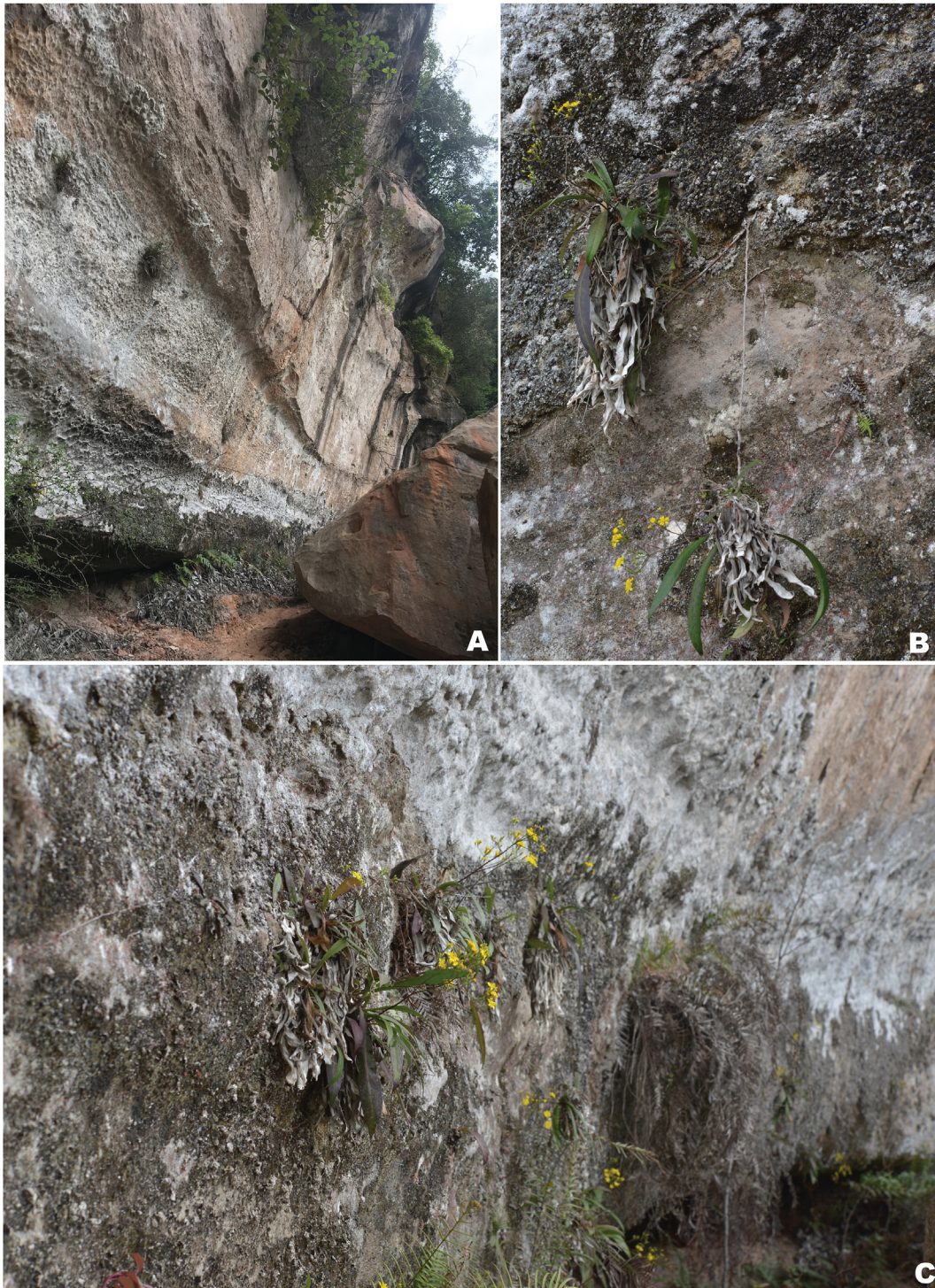


Fig. 1. *Mojiangia oreophila* Ze H. Wang, N. Kilian et H. Peng – (A) the cliff; (B) secondary trailing roots; (C) plants growing in the rock face. Photographs from type population by Zhi-jian Yin in April, 2018.

et al., 2009a), no reliable systematic placement of the Mojiang population appeared possible based on morphology alone.

Consequently, the aims of our study were to infer the systematic position of the Mojiang population from molecular phylogenetic and cytological analyses, to characterize it by morphological comparison with the closer allies and to draw the necessary taxonomic conclusions.

2. Material and methods

2.1. Plant material

The study was based on live plants observed and photo-documented in the field during 2017 and 2018 as well as on the herbarium collection made on these occasions. For morphological

comparison we consulted specimens in the herbaria of Berlin (B), Kunming (KUN) and Beijing (PE).

2.2. Morphological studies

For scanning electron microscopic (SEM) study, achenes and pollen were mounted on SEM stubs with double-sided sticky tape, coated with 20 nm Pt–Pd using a Cressington 108 Auto sputter-coater and examined using a ZEISS SIGMA 300.

2.3. Karyological study

Root-tips were obtained by germinating achenes (collected from the type population by *Zhi-jian Yin s.n.* on 23 Jun 2020) on wet filter paper in Petri dishes at approximately 20–27 °C. For chromosome counting, root-tips were pre-treated with 0.1% colchicine for at least 2.5 h, fixed in Carnoy I (glacial acetic acid–absolute ethanol = 1:3), then stained and squashed in carbol fuchsin.

2.4. Sampling, DNA extraction, amplification, sequencing and phylogenetic analysis

Molecular phylogenetic analyses were carried out using four individuals of the possible new species from its only known population. DNA was extracted, and the nuclear ribosomal internal transcribed spacer (nrITS) region and three plastid DNA markers (*trnL-F*, *psbA-trnH*, *matK*) were amplified and sequenced as described by Wang et al. (2020). Sequences were aligned into somewhat extended versions of the Crepidinae backbone matrices for nrITS and plastid DNA used by Wang et al. (2020) and the same indel coding and partitioning was applied. The GenBank accession numbers of the newly generated sequences are given in Table 1; those of the published sequences included in the matrices follow the taxon name in the phylogenetic trees (Figs. 2 and 3). Phylogenetic relationships were inferred with maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) on the high-performance computing system of the Freie Universität Berlin (Bennett et al., 2020), using the same software as described by Wang et al. (2020): PRAP v.2.0 (Müller, 2004) and PAUP v.4.0b10 (Swofford, 2003) for MP, ModelTest-NG (Darrriba et al., 2019) and RAxML-NG 0.9.0 (Kozlov et al., 2019) for ML, and MrBayes (Ronquist et al., 2012) for BI, SeqState (Müller, 2005) for indel coding, and TreeGraph v.2 (Stöver and Müller, 2010) for displaying the trees with statistical node support, and also applying the same parameters.

3. Results

3.1. Molecular phylogenetics

The nrITS sequences of three individuals investigated deviate only in one case (sample *Mojiangia* 1), which is the result of a few low-quality stretches of that single sequence and not of actual genetic differences. The aligned nrITS region had a length of 695 characters; together with the coded indels the matrix included a total of 807

characters, of which 378 were parsimony-informative. The MP analysis resulted in 827 most parsimonious trees ($L = 1946$, $CI = 0.433$, $RI = 0.697$, $RC = 0.301$, $HI = 0.567$), largely congruent in topology with the trees of the BI and ML analyses. Fig. 2 shows the BI majority consensus phylogram with the BI posterior probabilities (PP) and ML bootstrap (BS) support values (bootstrapping converged after 700 replicates with a cut-off set to 3%) below the branches and the MP jackknife (JK) support values above the branches.

The plastid DNA sequences of three individuals investigated were identical (i.e., only one accession number in Table 1). The aligned concatenated plastid DNA markers had a length of 2302 characters; together with the coded indels the matrix included a total of 2395 characters, of which 272 were parsimony-informative. The MP analysis resulted in 56 most parsimonious trees ($L = 759$, $CI = 0.775$, $RI = 0.793$, $RC = 0.615$, $HI = 0.225$), largely congruent in topology with the trees of the BI and ML analyses. Fig. 3 shows the BI majority consensus phylogram with the BI posterior probabilities (PP) and ML bootstrap (BS) support values (bootstrapping converged after 1300 replicates with a cut-off set to 3%) below the branches and the MP jackknife (JK) support values above the branches.

The Mojiang population is resolved in the nrITS phylogeny (Fig. 2) as member of a polytomy in the Crepidinae, which otherwise includes the large E Asian–North American *Soroseris-Dubyaea-Nabalus* clade, the Central to E Asia centred *Ixeris-Taraxacum* clade, the chiefly Irano–Turkic *Heteracia-Garhadiolus* clade and the Central Asian monogeneric *Acanthocephalus* clade. The genera of the last two clades are small or monospecific and show derived features, such as annuality, pronounced heterocarpy mostly combined with atelechoric adaptations and, as far as is known, a low basic chromosome number of $x = 3$ to 5 (Kilian et al., 2009b+); *Acanthocephalus benthamianus* Regel has recently also been reported for China (Ya et al., 2018).

In the plastid DNA phylogeny (Fig. 3), of which all deeper nodes lack statistical support, the Mojiang population is nested in the well-supported *Faberia* clade, which solely includes the Chinese endemic genus *Faberia*, and is resolved as sister to *F. cavaleriei* H. Lév., but this latter relationship is not supported statistically.

3.2. Morphological comparison

The combination of morphological features present in the Mojiang population (Table 2) — in particular densely long-papillose homomorphic achenes with 5 main ribs each accompanied by 2 secondary ribs (Figs. 4I and 5E–F), coarse brownish pappus bristles (Figs. 4J and 5G), moderately many-flowered capitula (Fig. 4A+C), a small (7 mm long) involucre with numerous (9–12) outer phyllaries 1/3 to 1/2 as long as the inner ones (Fig. 4D), and the perennial rosette herb growth (Figs. 1 and 4A) — is unique in the subtribe Crepidinae. Achenes with 15 ribs, of which 5 are stronger, is the state considered plesiomorphic for the tribe Cichorieae, and in the Crepidinae it is much less frequent than a reduction or an increase in the number of secondary ribs often combined with an equaling in the shape of main and secondary ribs (Stebbins, 1940; Kilian et al., 2009a). Achenes with a ribbing pattern like the Mojiang

Table 1
GenBank accession numbers of newly generated nrITS and plastid DNA sequences with specimen data of samples used.

Marker	Taxon name	Specimen	Locality	GenBank acc. no.
ITS	<i>Mojiangia oreophila</i>	Yin Zhi-Jian & Zhao Ming-Xu YZJ 0515 (KUN)	China, Yunnan Province, Puer Municipality, Mojiang County, Xinfu Town	<i>Mojiangia</i> 1: MW790611 <i>Mojiangia</i> 2&4: MW790612
<i>trnL-F</i>				MW984537
<i>psbA-trnH</i>				MW984539
<i>matK</i>				MW984538

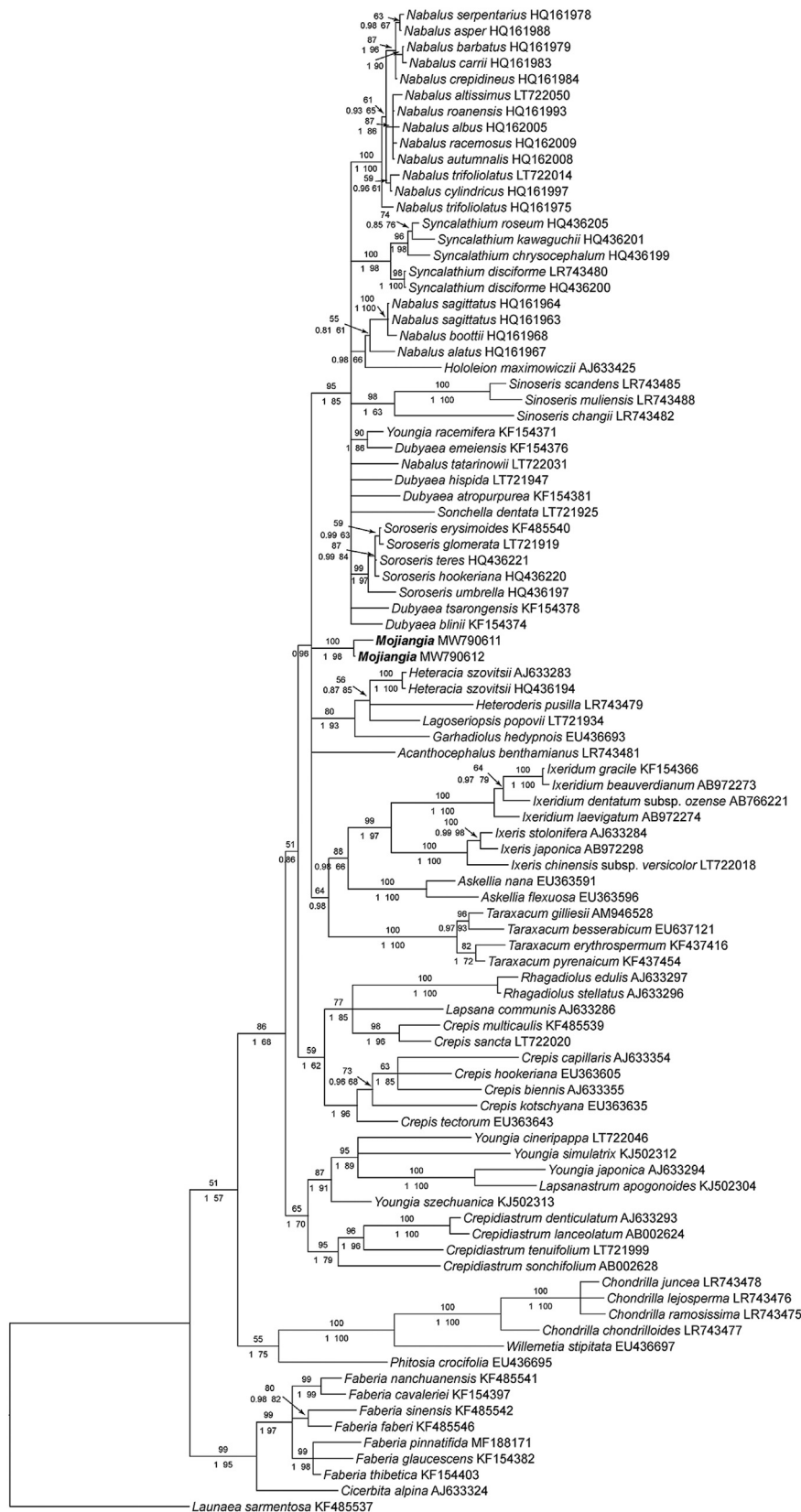


Fig. 2. Majority consensus phylogram of the Crepidinae from Bayesian analysis (support values: first line: maximum parsimony jackknife, second line: Bayesian posterior probability/maximum likelihood bootstrap) based on the nrITS region.

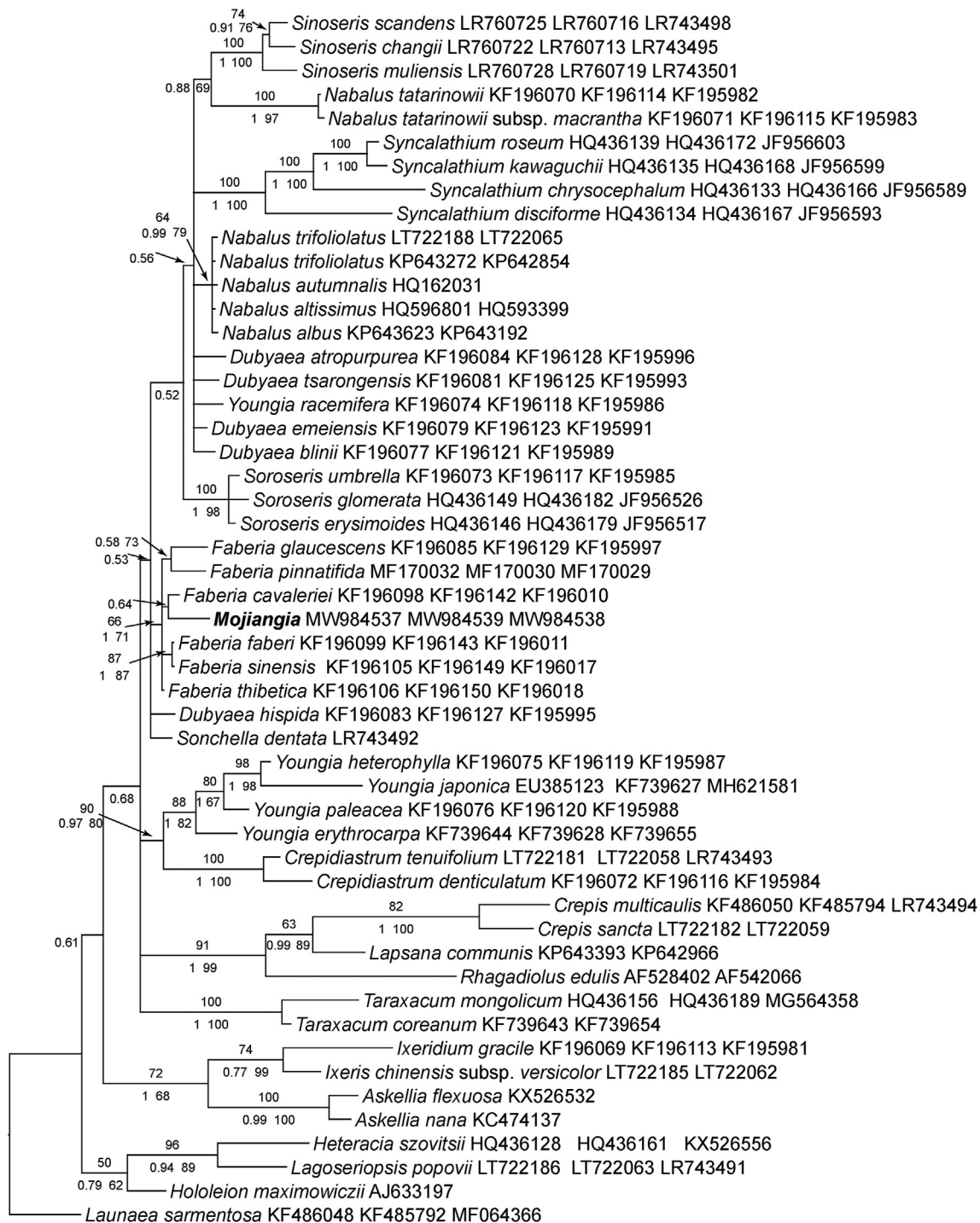


Fig. 3. Majority consensus phylogram of the Crepidinae from Bayesian analysis (support values: first line: maximum parsimony jackknife, second line: Bayesian posterior probability/maximum likelihood bootstrap) based on plastid DNA *trnL-F*, *psbA-trnH*, *matK* sequences.

population are also present in *Sonchella*, in many species of *Crepidiastrum*, *Dubyaea* and *Youngia*; achenes with only 10 ribs, by fusion of the adjacent secondary ribs, are a synapomorphy of the *Askellia-Ixeris-Ixeridium* clade, and progressive reduction towards 10 ribs is also found in the *Youngia-Crepidiastrum* clade; achenes with no secondary ribs are found in *Syncalathium*. Increases in the number of secondary ribs are present in *Crepis*, *Nabalus*, *Sinoseris*, *Soroseris* and *Taraxacum*. Densely long-papillose achenes are particularly rare in the Crepidinae; coarse pappus bristles are rather common only in

the *Dubyaea-Nabalus-Soroseris-Syncalathium* clade and rarely in *Crepis*, but are then usually white; numerous and sizable outer phyllaries are present in some genera but in others their number and size are conspicuously small. *Faberia*, in the clade in which the Mojiang population is nested in the plastid DNA phylogeny, also has numerous and sizable outer phyllaries (in single species), coarse and brownish pappus bristles, but never long-papillose achenes and always cyanic instead of yellow flowers. The pollen, which is of the most widespread *Cichorium* type (Blackmore, 1986), is tricolpate in

Table 2
 Diagnostically relevant morphological features of the Mojiang population and their presence in other Crepidinae genera and *Faberia*.

Features of Mojiang population	Presence in Crepidinae	Presence in <i>Faberia</i>
Perennial rosette herb	In all genera except <i>Acanthocephalus</i> , <i>Garhadiolus</i> , <i>Heteracia</i> , <i>Heteroderis</i> and <i>Lagoseriopsis</i>	+
Leaf axiles brown-woolly	Rare, e.g. in <i>Nabulus</i>	+
Synflorescence corymbiform with up to 90 capitula	In many genera	Corymbiform synflorescences only sparsely branched
Capitula with 18–26 flowers	In many genera	+
Involucre small (7 mm long)	In many genera	Involucre \geq 10 mm
Involucre differentiated into inner and outer phyllary series	In all genera except <i>Syncalathium</i> (there uniseriate)	+
Outer phyllaries 9–12, up to 1/3 to 1/2 as long as inner	Numerous outer phyllaries rather rare, chiefly in <i>Crepis</i> , <i>Dubyaea</i> , <i>Holeleion</i> , <i>Nabulus</i> s.l., <i>Taraxacum</i>	+
Inner phyllaries 11–13	More than 8 only in <i>Crepis</i> , <i>Dubyaea</i> , <i>Holeleion</i> , <i>Nabulus</i> s.l., <i>Soroseris</i>	+
Corolla yellow	In all genera	Always cyanic
Achenes with 15 ribs (5 main ribs and each with 2 secondary ribs)	In a minority of genera, e.g. <i>Crepidiastrum</i> , <i>Dubyaea</i> , <i>Sonchella</i> and <i>Youngia</i>	+
Achene surface densely long-papillose	Only in <i>Heteroderis</i> , <i>Lagoseriopsis</i> and apically in <i>Sinoseris</i>	Always glabrous
Pappus bristles coarse, pale brown	Frequently coarse in the <i>Dubyaea-Nabulus-Soroseris-Syncalathium</i> clade and p.p. in <i>Crepis</i> , but at the same time brownish only in <i>Dubyaea</i> and <i>Holeleion</i>	+
Pollen of the <i>Cichorium</i> type, tricolpate	In all genera	+, but always tetracolpate
Polar area of pollen small with 1–3 isolated central echinae	In several genera such as <i>Crepidiastrum</i> , <i>Crepis</i> , <i>Holeleion</i> , <i>Youngia</i>	+ p.p.

the Mojiang population (Fig. 5A–C), but always tetracolpate in *Faberia* (Liu et al., 2013, Liu et al., 2018).

3.3. Chromosome counts

Root tip mitoses revealed a chromosome complement of $2n = 16$ (Fig. 6), of which one pair has satellite chromosomes.

4. Taxonomic treatment

Both the molecular phylogenetic and morphological findings support the Mojiang population to represent a lineage of its own that is consistently resolved as a member of the Crepidinae in both the plastid and nrITS trees. Classification of the plants as a new monotypic genus thus appears appropriate.

Mojiangia oreophila Ze H. Wang, N. Kilian et H. Peng, **gen. et sp. nov.**

Holotype: China, Yunnan Province, Puer Municipality, Mojiang County, Xinfu Town, 23°39'22.64"N, 101°15'3.38"E, 1400 m, in soil

on cliffs or rocks, 4 Apr 2017, Yin Zhi-jian et Zhao Ming-Xu YZJ 0515 (KUN, see Fig. 7; isotypes: B, PE).

Further material: Type population, 7 August 2019, Zhi-jian Yin s.n. (KUN, achenes only); type population 23 Jun 2020, Zhi-jian Yin s.n. (KUN, achenes only).

Descriptio generico-specifica/generic-specific description (Shenzhen code art. 38.5; Turland et al., 2018): Perennial rosette herb to c. 50 cm high, with sparsely branched woody caudex and usually few to several, often densely spaced leaf rosettes; rosette shoots with the marcescent remains of older leaves below the actual leaf rosette, and further below covered with the scars of former leaf bases and brown-woolly indumentum (Fig. 4G); with taproot usually rooted in rock face crevices or holes, funiform secondary roots sometimes trailing clung to the rock surface (Fig. 1B). Rosette leaves narrowly elliptic to narrowly spatulate, 6–30 \times 1–3.5 cm, apically acute to acuminate, basally attenuate, margin (almost) entire to, mostly shallowly, sinuate-dentate, sometimes revolute, lamina papery to thickly papery on drying, fresh to dark green and sometimes purplish with age on upper face, paler green on lower face, glabrous on upper face and sparsely hairy on lower face especially along the midrib, brown-woolly in leaf axils. Flowering stems usually one per leaf rosette, erect, sparsely to richly branched from base or more frequently in distal half or third, leafless except for linear-lanceolate bracts subtending the branches, purplish and with brownish indumentum more densely in the axils; remnants of withered flowering stems from previous years frequently present in a leaf rosette. Synflorescence of a flowering stem corymbiform, of up to 90 capitula; peduncles mostly 0.5–1 cm long, somewhat brown-woolly. Capitula with 18–26 florets. Involucre narrowly cylindrical to narrowly campanulate, c. 7 mm long, clearly differentiated into outer and inner series of phyllaries; outer phyllaries mostly 9–12, \pm imbricate, triangular to linear-lanceolate, acute, the outermost 1–1.5 \times 0.6–0.8 mm, the longest of the outer phyllaries 1/3–1/2 as long as the inner ones; inner phyllaries 11–13, linear-lanceolate and similar in length, green and with narrow scarious margin, towards apex sparsely brown-woolly on outer face. Receptacle epaleate and glabrous. Florets with bright yellow corolla, tube 2.1–2.3 mm long, ligule broadly elliptical to obovate, 6.4–6.7 mm long and up to c. 2 mm wide; anther tube yellow, fertile part 2.6–2.8 mm long, apical appendages rounded, c. 0.3 mm long, basal appendages c. 0.5 mm long; pollen echinolophate, tricolpate, of the *Cichorium* type (sensu Blackmore 1986) with moderately extensive polar areas with only one or a few spines in addition to those bordering the adjacent lacuna, and with moderately narrow interlacunar gaps (Fig. 5A–C); style and style arms yellow. Achenes 2.7–3 mm long, columnar to subfusiform with largest diameter in lower third and stronger attenuate toward the truncate apex than towards the somewhat oblique base, brown, densely covered with antrorse, subulate, laterally flattened papillae to c. 60 μ m (Fig. 5F); main ribs 5, very prominent, each \pm differentiated, except for the very basal portion, into triplets with a secondary rib on either side. Pappus c. 3.5 mm long, persistent, pale brownish, with one series of rather coarse bristles similar in length and diameter, at base of c. 12–16 (or more?) rows of cells in cross section.

4.1. Habitat and ecology

The species occurs in secondary sub-humid evergreen broad-leaved forest at an elevation of about 1400 m near the summit of a mountain. It grows in vertical sandstone cliffs, rooting in crevices, holes, niches or steps of the rock face (Fig. 1). If holes or crevices are not deep enough, secondary roots are clung to the rock surface and trailing. Flowering March to May, fruiting May to August.

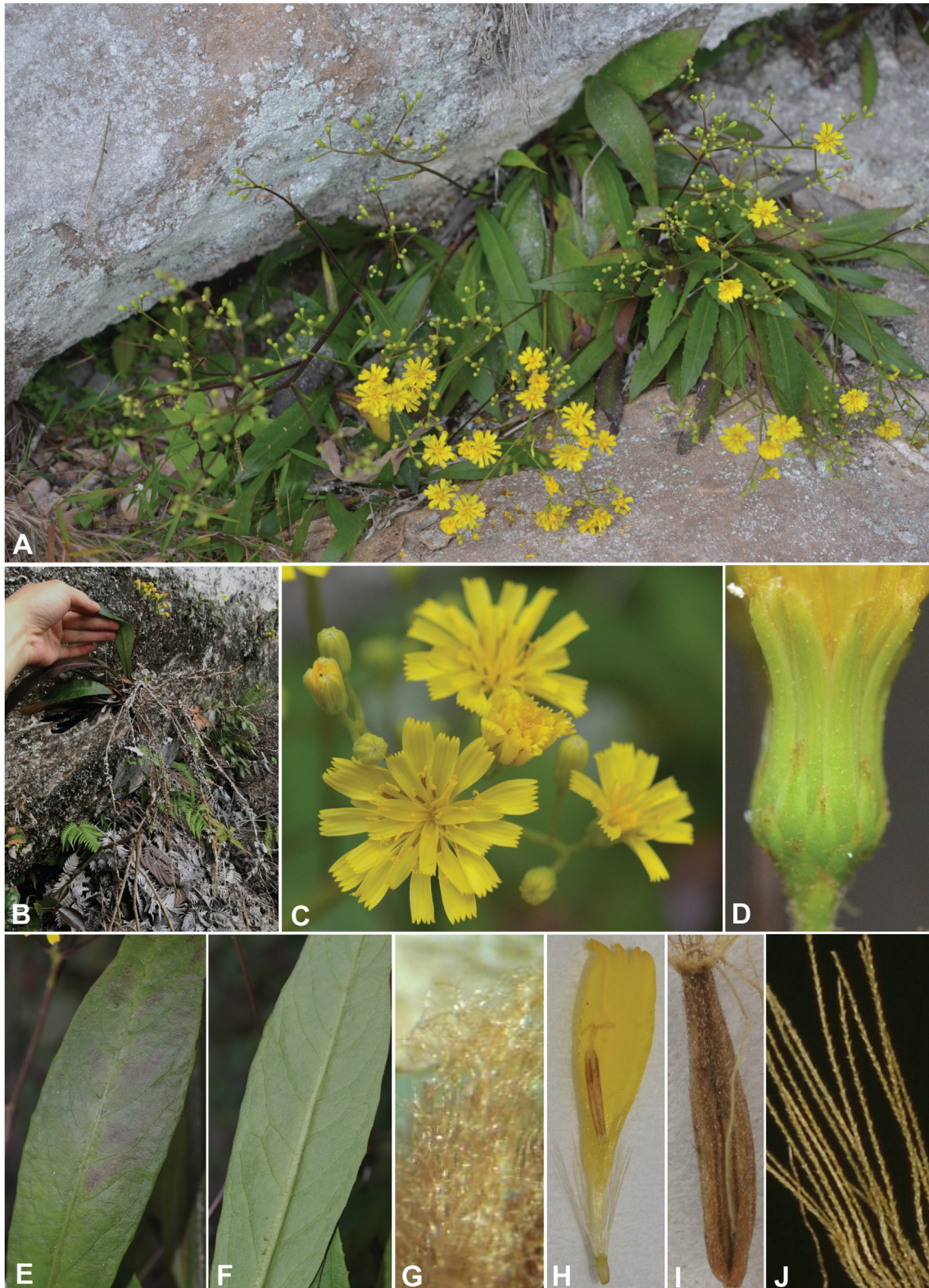


Fig. 4. *Mojiangia oreophila* Ze H. Wang, N. Kilian et H. Peng – (A) plants *in situ*; (B) roots; (C) capitulum; (D) involucre; (E) upper face of leaves; (F) lower face of leaves; (G) brown-woolly indumentum of stem base; (H) floret; (I) achene; (J) bristles of pappus. All photographs from type population by Zhi-jian Yin in April, 2018, except I and J from the same population by Ming-xu Zhao in July, 2018.

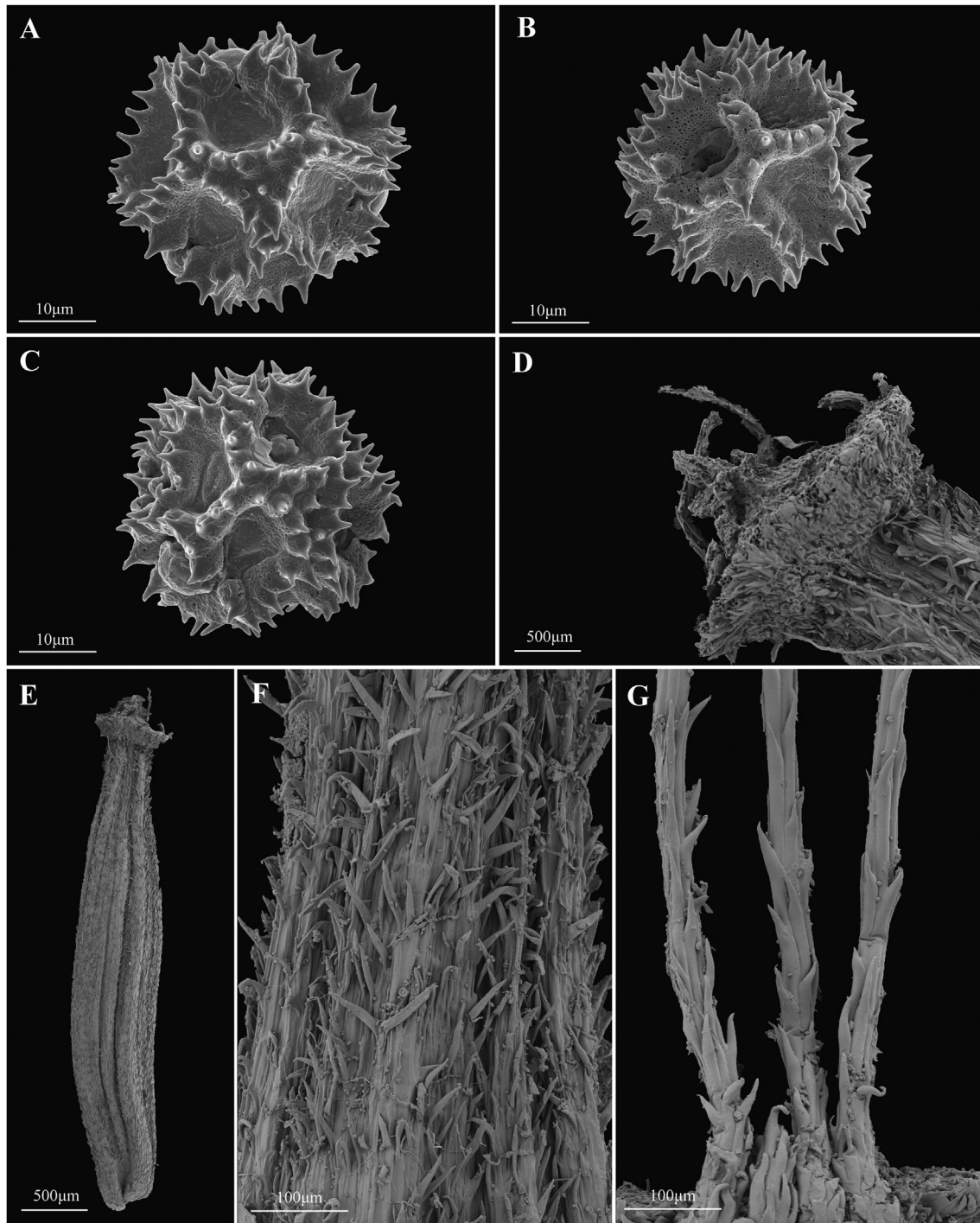


Fig. 5. *Mojiangia oreophila* Ze H. Wang, N. Kilian et H. Peng – A–C: pollen. (A) polar view; (B) equatorial view; (C) parapolar view. D–G: achene. (D) pappus disk; (E) the overall view of achene; (F) apex of corpus; (G) bristles of pappus. Pollen photographs from material of type collection; achene photographs from achenes collected on 7 August, 2019 from the type population (Zhi-jian Yin s.n., KUN).

4.2. Distribution

Only known from the type population near Xinfu in the Mojiang County, SW Yunnan, China.

4.3. Threat status

The only known population of *M. oreophila* consists of about 60 individuals in a tiny area of 300–400 m². The very small extent of

occurrence and low individual number of the species suggests it is very threatened. If further field work in the area does not detect other populations, the species must be considered as Endangered (EN) because the estimated number of individuals is lower than 250 (IUCN Standards and Petitions Subcommittee, 2019). The habitat and its environment are part of the Mojiang National Forest Park, Yunnan, which was established in 2017 and thus guarantees some protection to the *Mojiangia* population. Its location near the foot of a cliff face of the summit area could, however, be extremely

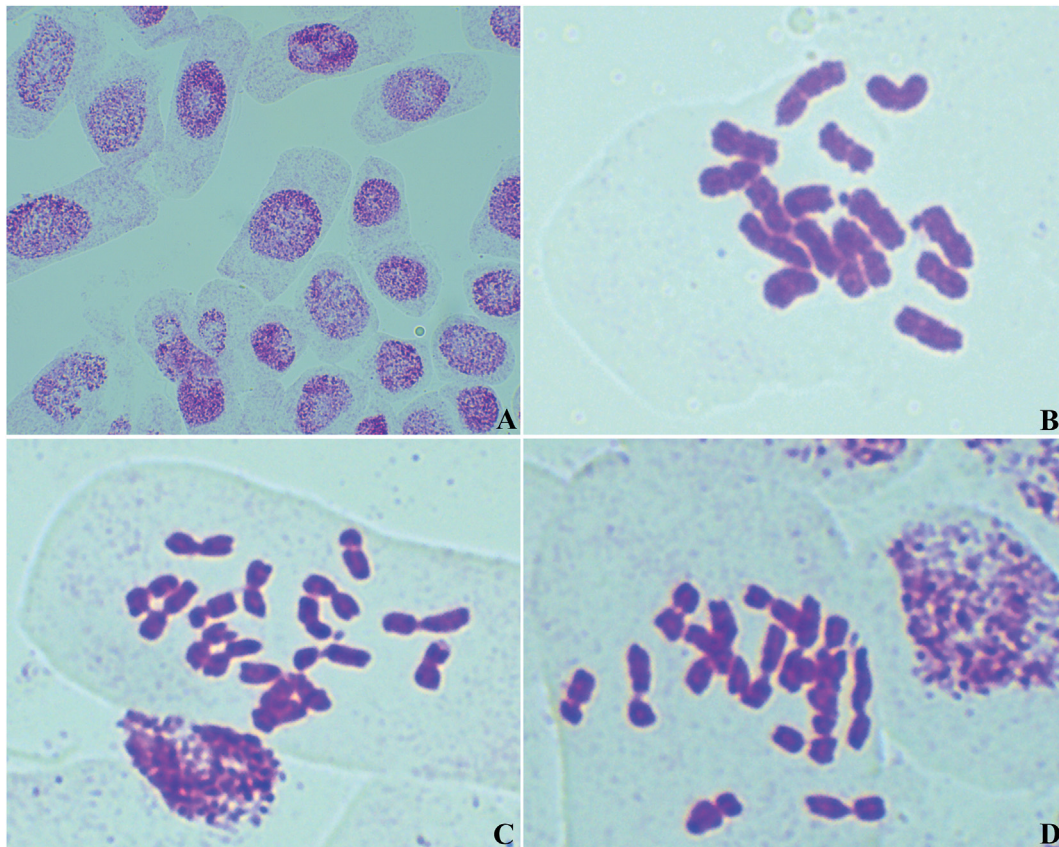


Fig. 6. *Mojiangia oreophila* Ze H. Wang, N. Kilian et H. Peng – (A) interphase nucleus; B–D: metaphase plates of root tip mitoses showing $2n = 16$. (B) mitotic metaphase of sample 1; (C) one mitotic metaphase cell of sample 2; (D) another mitotic metaphase cell of sample 2. Preparations from germinating achene samples of the type population.

threatened if this summit cliff face should be used to establish a scenic spot for park visitors.

5. Discussion

Morphological comparison shows that all diagnostically relevant features of *Mojiangia* are present in other genera of the subtribe Crepidinae, at least in some portion of their species, and – as in a good number of other genera – only their combination in *Mojiangia* is unique in the subtribe. This applies also to the pollen features. The *Cichorium* pollen type present in *Mojiangia* is the most common in the entire tribe Cichorieae (Blackmore, 1986) and its subtypes occur scattered across several subtribes with no correlation to their systematics (Blackmore, 1984; Blackmore and Persson, 1996; Wang et al., 2009). The *Mojiangia* pollen is of the subtype with a small polar area and only 1–4 isolated central echinae, the occurrence of which is also inconsistent with generic boundaries, e.g., in the cases of *Youngia* and *Sinoseris*, where the subtype with an extended polar area is also present (Peng et al., 2013; Wang et al., 2020).

In contrast, *Mojiangia* shares the majority of its diagnostically relevant features with *Faberia*, a genus of nine species placed in the subtribe Lactucinae (Wang et al., 2013; Kilian et al., 2017, 2009b+). This even holds true for the pollen, because apart from it being tetracolpate instead of tricolpate, a portion of its species (*Faberia pinnatifida* Ying Liu, Yousheng Chen et Boufford, *F. nanchuanensis* C. Shih, *F. sinensis* Hemsl.; Liu et al., 2018) have a similarly small polar area as *Mojiangia*, whereas the others have a moderately larger one. *Faberia* has been shown to be of intersubtribal hybrid origin, with the maternal ancestor of the Crepidinae and the parental ancestor of the Lactucinae (Liu et al., 2013, Liu et al., 2018; Wang et al., 2013,

Wang et al., 2014; Kilian et al., 2017). In the context of *Faberia*, where reticulate evolution was accompanied by genome duplication, leading to a basic number of $2n = 34$, it is notable that tetracolpate pollen is considered a deviation from the usually tricolpate pollen correlated with polyploidy (Woodhouse, 1935).

Such morphological resemblance agrees well with the remarkable finding that *Mojiangia* is nested in the plastid DNA tree in the *Faberia* clade, although resolved in the nrITS phylogeny in a clade of its own. This finding may have either of the following causes: chloroplast capture (Tsitrone et al., 2003; Lee-Yaw et al., 2018) from a *Faberia* species, or maternal ancestry of the intersubtribal hybridogenous *Faberia*. In the first case, hybridisation and introgression may have occurred between ancestors of the *Mojiangia* population and a *Faberia* species, in the course of which the chloroplasts of the invading *Faberia* ancestor were captured by the *Mojiangia* ancestor and after some time had replaced the resident *Mojiangia* ancestor chloroplast. Chloroplast capture is known from many plant taxa (Tsitrone et al., 2003) and may be a frequent cause of cytonuclear discordance; thus, the different phylogenetic patterns between nuclear and organellar genomes (Lee-Yaw et al., 2018). The strong genetic similarity of the plastid markers of *Mojiangia* and a single *Faberia* species (*F. cavaleriei*) makes alternative explanations, such as convergent evolution or incomplete lineage sorting, highly unlikely.

Only one other cause provides a plausible alternative explanation. Given that *Faberia* has evolved by reticulate evolution involving a paternal Lactucinae and a maternal Crepidinae ancestor (compare Liu et al., 2013; Wang et al., 2013; Kilian et al., 2017), the ancestor of the *Mojiangia* population may have been the maternal Crepidinae ancestor of *Faberia*. This hypothesis is the more



Fig. 7. *Mojiangia oreophila* Ze H. Wang, N. Kilian et H. Peng – holotype at KUN.

parsimonious one, because it assumes only one case of cytonuclear discordance, namely in *Faberia*, as a result of its known ancient hybridisation, whereas none in *Mojiangia*, because it contributed the plastid genome as hitherto unknown maternal ancestor of

Faberia. The chromosome number $2n = 16$, thus a basic number of $x = 8$, of *Mojiangia* agrees with this explanation. The basic number of $x = 8$ is common in the large *Sorosseris-Dubyaea-Nabalus* clade and several other genera, and is the highest in the Crepidinae, in

which other progressive reductions down to $x = 3$ have occurred. All *Faberia* species have a basic chromosome number of $x = 17$ as the result of hybrid formation of an $x = 9$ and $x = 8$ genome, and because the basic number of $x = 9$ is unknown in the Crepidinae, it is assumed that the $x = 8$ genome comes from the maternal Crepidinae ancestor (Liu et al., 2012, 2013; Liu and Ren, 2014; Liu and Yang, 2014).

Author contributions

Y.Z.J. and M.X.Z. discovered the wild population, collected the specimens and have taken the photos of it. Ze-Huan Wang prepared the DNA samples and performed the sequencing. Y.L. counted the chromosomes. N.K., Z.H.W. and H.P. elaborated the taxonomy. N.K. performed the molecular phylogenetic analyses and wrote the manuscript in discussion with and with substantial contributions from Z.H.W. All authors read and commented on the manuscript.

Declaration of competing interest

This article does not involve conflicts of interest.

Acknowledgements

The authors are grateful to the staff of KUN and the Institute of Cultivation and Processing of Chinese Medicinal Materials for research facilities. The use of high-performance computing resources at the Scientific Computing Service of the Freie Universität Berlin is also gratefully acknowledged. This study was supported by the National Natural Science Foundation of China (grant no. 31500168) and specific funds for the Fourth National Survey on Chinese Materia Medica Resources (GZY-KJS-2018-004). Finally, we would like to thank the Editors and two anonymous reviewers for their valuable comments on earlier versions of this paper.

References

Bennett, L., Melchers, B., Proppe, B., 2020. Curta: a General-Purpose High-Performance Computer at ZEDAT. Freie Universität Berlin, Refubium, Dokumente FU. <https://doi.org/10.17169/refubium-26754>. Available from: (Accessed 15 March 2021).

Blackmore, S., 1984. The Northwest European pollen flora 32. *Compositae – Lactuceae*. Rev. Paleobot. Palyno. 42, 45–85.

Blackmore, S., 1986. The identification and taxonomic significance of lophate pollen in the Compositae. Can. J. Bot. 64, 3101–3112.

Blackmore, S., Persson, V., 1996. Palynology and systematics of the Crepidinae (Compositae: Lactuceae). In: Hind, D.J.N., Beenthe, H.J. (Eds.), Proceedings of the International Compositae Conference, Kew, 1994, vol. 1. Compositae: Systematics. Royal Botanic Gardens, Kew, pp. 111–122.

Darriba, D., Posada, D., Kozlov, A.M., et al., 2019. ModelTest-NG: a new and scalable tool for the selection of DNA and protein evolutionary models. Mol. Biol. Evol. 37, 291–294.

IUCN Standards and Petitions Subcommittee, 2019. Guidelines for using the IUCN red list categories and criteria. Version 13. Available from: <http://www.iucnredlist.org/documents/RedListGuidelines.pdf>. (Accessed 30 May 2020).

Kilian, N., Gemeinholzer, B., Lack, H.W., 2009a. Tribe Cichorieae. In: Funk, V.A., Susanna, A., Stuessy, T.F., Bayer, R.J. (Eds.), Systematics, Evolution, and Biogeography of the Compositae. IAPT, Vienna, pp. 343–383.

Kilian, N., Hand, R., von Raab-Straube, E., (general ed.), 2009b+. Cichorieae systematics portal. Available from: <http://cichorieae.e-taxonomy.net/portal/>. (Accessed 30 May 2020).

Kilian, N., Sennikov, A., Wang, Z.H., et al., 2017. Sub-Paratethyan origin and Middle to Late Miocene principal diversification of the *Lactucinae* (Cichorieae, Compositae) inferred from molecular phylogenetics, divergence-dating and biogeographic analysis. Taxon 66, 675–703.

Kozlov, A.M., Darriba, D., Flouri, T., et al., 2019. RAXML-NG: a fast, scalable and user-friendly tool for maximum likelihood phylogenetic inference. Bioinformatics 35, 4453–4455.

Lee-Yaw, J.A., Grassa, C.J., Joly, S., et al., 2018. An evaluation of alternative explanations for widespread cytonuclear discordance in annual sunflowers (*Helianthus*). New Phytol. <https://doi.org/10.1111/nph.15386>.

Liu, Y., Chen, Y.S., Boufford, D.E., 2018. *Faberia pinnatifida* (Asteraceae; Cichorieae), a new species from Sichuan, China. Syst. Bot. 43, 316–324.

Liu, Y., Chen, Y.S., Yang, Q.E., 2013. Generic status, circumscription, and allopolyploid origin of *Faberia* (Asteraceae: Cichorieae) as revealed by ITS and chloroplast DNA sequence data. Taxon 62, 1235–1247.

Liu, Y., Ren, C., 2014. Cytotaxonomy of *Prenanthes faberi* (Compositae – Cichorieae). Nord. J. Bot., Le 32, 115–118.

Liu, Y., Deng, T., Yang, Q.E., 2012. Karyology of the genus *Faberia* (Cichorieae – Asteraceae) and its systematic implications. Nord. J. Bot. 30, 365–371.

Liu, Y., Yang, Q.E., 2014. Cytotaxonomy of *Dubyaea glaucescens* (Compositae – Cichorieae). Nord. J. Bot. 32, 871–874.

Müller, K., 2004. PRAP — computation of Bremer support for large data sets. Mol. Phylogenet. Evol. 31, 780–782.

Müller, K., 2005. SeqState: primer design and sequence statistics for phylogenetic DNA datasets. Appl. Bioinf. 4, 65–69.

Peng, Y.L., Gao, X.F., Peng, L., 2013. Pollen morphology of *Youngia* and six related genera (Asteraceae: Cichorieae) and its systematic significance. Phytotaxa 139, 39–62.

Ronquist, F., Teslenko, M., Van der Mark, P., et al., 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. Syst. Biol. 61, 539–542.

Stebbins, G.L., 1940. Studies in Cichorieae: *Dubyaea* and *Sorosseris*. Endemics of the Sino-Himalayan region. Mem. Torrey Bot. Club 19, 1–76.

Stöver, B.C., Müller, K., 2010. TreeGraph 2: combining and visualizing evidence from different phylogenetic analyses. BMC Bioinf. 11, 7.

Swofford, D.L., 2003. PAUP*: Phylogenetic Analysis Using Parsimony (*and Other Methods), Version 4.0b 10. Sinauer Associates Inc. Publishers, Sunderland.

Tsitroni, A., Kirkpatrick, M., Levin, D.A., 2003. A model for chloroplast capture. Evolution 57, 1776–1782.

Turland, N.J., Wiersema, J.H., Barrie, F.R., et al., 2018. International code of nomenclature for algae, fungi and plants (Shenzhen code) adopted by the Nineteenth International Botanical congress Shenzhen, China, July 2017. Regnum Veg. 159.

Wang, Z.H., Peng, H., Kilian, N., 2013. Molecular phylogeny of the *Lactuca* alliance (Cichorieae subtribe Lactucinae, Asteraceae) with focus on their Chinese centre of diversity detects potential events of reticulation and chloroplast capture. PloS One 8, e82692.

Wang, H., Wortley, A.H., Blackmore, S., 2009. Pollen morphology of Crepidinae and Lactucinae (Asteraceae: Cichorieae) and its systematic significance. Grana 48, 160–178.

Wang, Z.H., Kilian, N., Chen, Y.P., et al., 2020. *Sinoseris* (Crepidinae, Cichorieae, Asteraceae), a new genus of three species endemic to China, one of them new to science. Willdenowia 50, 91–110.

Wang, G.Y., Meng, Y., Deng, T., et al., 2014. Molecular phylogeny of *Faberia* (Asteraceae: Cichorieae) based on nuclear and chloroplast sequences. Phytotaxa 167, 223–234.

Woodhouse, R.P., 1935. Pollen Grains, Their Structure, Identification and Significance in Science and Medicine. McGraw-Hill, New York.

Ya, J.D., Cai, J., Zhang, Q.R., 2018. Two genera and five species newly recorded in China. Turk. J. Bot. 42, 239–245.