1. Introduction

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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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Abstract

A single small population of chasmophytic plants is described as Mojjiangia 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 hybrid-ogenous 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 Mojjiangia, caused by chloroplast capture as a result of hybridisation and introgression with Faberia.

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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 documented in the field during 2017 and 2018 as well as on the herbarium collection made on these occasions. For morphological
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 newly generated nrITS and plastid DNA sequences with specimen data of samples used.

Table 1

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

2.5. 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 1 (glacial acetic acid–absolute ethanol = 1:3), then stained and squashed in carbol fuchsin.

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-Dubynowski-Nabalus clade, the Central to E Asia centred Ixeris-Taraxacum clade, the chiefly Irano-Turanian Heteracia-Garthadiolus clade and the Central Asian monogenic 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 ateleichoric 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 E. cavalieri 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. 4f and 5e–f), coarse brownish pappus bristles (Figs. 4j and 5g), moderately many-flowered capitula (Fig. 4a–c), a small (7 mm long) involucr of 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
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.
population are also present in Sonchella, in many species of Crepis, 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, Sorosseris 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

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.
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 nrtS 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).

*Descrip*tion* gen*ero-specifica*/*generic-specific description (Shen*zhen* code art. 38.5; Tur*l*and et al., 2018): Perennial rossett*e herb to c. 50 cm high, with spar*sely branched woody caudex and usu*ally few to several, often densely spaced leaf rosettes; rossette 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 × 1–3.5 cm, acipically 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 purpurish 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 axis. 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 synflorescentiform, of up to 90 capitula; peduncles mostly 0.5–1 cm long, somewhat brown-woolly. Capitula with 18–26 florets. involucre narrowly cylindric to narrowly campanulate, c. 7 mm long, clearly differentiated into outer and inner series of phyllaries; outer phyllaries mostly 9–12, imbricate, triangular to linear-lanceolate, acute, the outermost 1–1.5 × 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 echinopholate, trilicate, 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 subfusciform 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 μm (Fig. 5F); main ribs 5, very prominent, each ± 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.
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 *Moijiangia* population. Its location near the foot of a cliff face of the summit area could, however, be extremely

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**Fig. 5.** *Moijiangia oreophila* Ze H. Wang, N. Kilian et H. Peng – A–C: pollen. (A) polar view; (B) equatorial view; (C) paraporal 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).
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., 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 Boulford, *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 triradiate 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 Mojiang 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 Mojiang population may have been the maternal Crepidinae ancestor of *Faberia*. This hypothesis is the more
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 *Soroseris-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 Cripedinae, it is assumed that the $x = 8$ genome comes from the maternal Cripedinae 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.

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