Phytotaxa 167 (3): 223–234
www.mapress.com/phytotaxa/

Article

ISSN 1179-3155 (print edition)
PHYTOTAXA
ISSN 1179-3163 (online edition)

http://dx.doi.org/10.11646/phytotaxa.167.3.1

Molecular phylogeny of *Faberia* (Asteraceae: Cichorieae) based on nuclear and chloroplast sequences

GUANG-YAN WANG[1,2,4], YING MENG[1,2,3], TAO DENG[1] & YONG-PING YANG[1,2,3,5]

[1]*Key Laboratory of Biodiversity and Biogeography, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China.*
[2]*Plant Germplasm and Genomics Center, the Germplasm Bank of Wild Species, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming 650201, China.*
[3]*Institute of Tibetan Plateau Research at Kunming, Chinese Academy of Sciences, Kunming 650201, China.*
[4]*University of the Chinese Academy of Sciences, Beijing 100049, China.*
[5]*Author for correspondence. E-mail: yangyp@mail.kib.ac.cn.*

Abstract

Faberia is a perennial herbaceous member of Asteraceae that is mainly distributed in central and southwestern China. Nuclear (ITS) and plastid (*psbA–trnH*, *rbcL*, *matK*, and *trnL–F*) sequences representing five *Faberia* species were analyzed with maximum parsimony, maximum likelihood, and Bayesian inference, all of which strongly supported the monophyly of *Faberia*. *Faberia nanchuanensis*, *F. cavaleriei*, and *F. faberi* from central China form a well-supported clade. Additionally, *F. sinensis* and *F. thibetica* from southwestern China also form a well-supported clade. Incongruence between nuclear and plastid fragments was interpreted as hybridization or limited character evolution in the plastid DNA. *Faberia* may have descended from hybridization between Lactucinae and Crepidinae. Besides phylogenetic results, *Faberia nanchuanensis* is recorded for the first time from Hunan Province, and *F. sinensis* from the Tibet Autonomous Region.

Key words: China, Compositae, *Faberia*, hybridization, phylogeny

Introduction

Faberia Hemsl. is a perennial herbaceous genus of Cichorieae in Asteraceae. Ling & Shih (1997) recognized four species in the genus and listed another three as potential but imperfectly known members because of a lack of available material. Shih & Kilian (2011) included in the genus seven species that were distributed in central and southwestern China. *Faberia* is characterized by a campanulate or cuneiform involucre, a slender style with papillae or setae, and a brown or pale yellow to white pappus of equal bristles. All species of *Faberia* occur in moist places in woods, or in rocky, grassy places along streams or under waterfalls.

The genus *Faberia* was established based on *F. sinensis* Hemsl., a species endemic to southwestern China (Forbes & Hemsley 1888). Taxonomists held different opinions on the delimitation of this genus. Some botanists considered *Faberia* a separate genus (Hoffmann 1890–1894, Beauverd 1910, Léveillé 1914, Anthony 1934, Shih 1995, Shih & Chen 1996, Ling & Shih 1997, Kilian *et al*. 2009), while others reduced *Faberia* into *Lactuca* L. (Franchet 1895) or into *Prenanthes* L. (Babcock 1947, Lauener 1976, Sennikov & Illarionova 2001, Lack 2007). Sennikov & Illarionova (2008) transferred *Youngia racemifera* (Hook. f.) Babc. et Stebbins, *Y. silhetensis* (DC.) Babc. & Stebbins, and *Y. silhetensis* subsp. *bhutanica* Grierson & Spring. into *Faberia*. Shih & Kilian (2011) associated *Prenanthes glandulosa* Dunn with *Faberia*. Moreover, Kilian *et al*. (2009) and Shih & Kilian (2011) merged *Faberiopsis* Shih & Y. L. Chen with *Faberia*. Liu *et al*. (2012) strongly supported *Faberia* as a separate genus and merged *Faberiopsis* with *Faberia* based on karyological analyses.

Previous studies were restricted to morphological and chromosomal characters; no molecular approach have been undertaken for *Faberia*. DNA data, particularly DNA sequences, greatly contributed to understanding of the phylogeny, evolution, and taxonomy of Asteraceae (Jansen & Kim 1996). In this study, we used nuclear DNA (nrDNA; the internal transcribed spacer of ribosomal DNA; ITS) and plastid DNA (cpDNA; *psbA–trnH*, *rbcL*,

Accepted by Alexander Sennikov: 21 Jan. 2014; published: 14 May 2014

matK, and *trnL–F*) sequences to (1) test the monophyly of *Faberia* and (2) reconstruct its phylogeny and systematic position.

Materials and methods

Taxon sampling

We sampled five species of *Faberia* for this molecular study (Table 1). We were not able to obtain any material for *F. ceterach* Beauverd and *F. lancifolia* J. Anthony. *Warionia saharae* Benth. et Coss. was chosen as an outgroup in line with Kilian *et al*. (2009). To evaluate the monophyly, phylogeny, and systematic position of *Faberia*, sequences of its close relatives in Cichorieae (representing Crepidinae, Hypochaeridinae, Hyoseridinae, Lactucinae, Microseridinae, Cichoriinae, Hieraciinae, Scolyminae, and Scorzonerinae) were obtained from GenBank (Table 1). Living plants were cultivated in a greenhouse at the Kunming Institution of Botany. Voucher specimens were deposited in KUN.

DNA extraction and sequencing

Total DNA was extracted from about 15 mg of silica-gel dried leaf material using the CTAB method of Doyle & Doyle (1987) and the Plant Genomic DNA Extraction (Bioteke, Beijing, China) following the manufacturer's instructions. Polymerase chain reaction (PCR) amplifications were performed using 10 ng of genomic DNA, 4 pmol of each primer (see below), 0.5 U Taq polymerase (Promega, Fitchburg, WI, USA), and 2.5 mM $MgCl_2$ in a volume of 20 μL under the following conditions: 3 min at 94°C; followed by 30 cycles of 30 s at 94°C, 30 s at 50°C, and 1 min at 72°C, and then a final 10 min extension at 72°C.

Primers used in the amplification and sequencing were as follows. For the nuclear ITS region: primers ITS1 and ITS4 (White *et al*. 1990). The plastid *psbA–trnH*: primers *psbA-F* and *trnH-R* (Sang *et al*. 1997, Hamilton *et al*. 1999); *rbcL*: primers Z1 and 1024R (Zurawski *et al*. 1981, Olmstead *et al*. 1993); *matK*: primers 3F and 1R (Sang *et al*. 1997); *trnL–F*: primers Tab-c and Tab-f (Taberlet *et al*. 1991).

The PCR products were purified using the polyethylene glycol (PEG) precipitation procedure following the manufacturer's protocols. Cycle sequencing was carried out using the following profile: 35 cycles of 97°C for 15 s, 50°C for 5 s, and 60°C for 4 min. Dideoxy cycle sequencing was performed using the chain-termination method and the ABI PRISM BigDye v.3.1 reaction kit (Applied Biosystems, Foster City, CA, USA) following the manufacturer's protocols. Products were run on an ABI 3100 genetic analyzer (Applied Biosystems) using the manufacturer's protocols. The sequence fragments from forward and reverse primers were assembled using Sequencer v.4.1.4 (GeneCodes Corporation, Ann Arbor, MI, USA). The sequences were aligned with ClustalX v.1.83 (Thompson *et al*. 1997). Manual adjustments were made using Bioedit v.7.0.5 (Hall 1999).

Phylogenetic analyses

Phylogenetic trees were reconstructed using maximum parsimony (MP), maximum likelihood (ML), and Bayesian inference (BI). Parsimony analyses were performed with heuristic searches of 1,000 replicates with random stepwise addition using tree bisection–reconnection (TBR) branch swapping, MulTrees, and the Collapse option selected in PAUP* v.4.0b10 (Swofford 2003). Gaps were treated either as missing data or as new characters. All characters and character state transformations were weighted equally. The bootstrap percentages (BP) were calculated from 1,000 replicates using a heuristic search with simple addition with the TBR and MULPARS options implemented (Felsenstein 1985).

Before the model-based analytical approaches, the model of DNA evolution that best fit the sequence data was explored. A hierarchical likelihood ratio test as implemented in the software MrModeltest (Nylander 2004) suggested the generalized time reversible model (GTR + I + G) fit the data best. In the following ML and BI analyses the substitution models and parameters were adjusted according to the estimates of MrModeltest. Maximum likelihood analyses were performed in Garli v.0.96 beta (Zwickl 2006) and BI in MrBayes v. 3.1.2 (Huelsenbeck & Ronquist 2001). The Bayesian Markov chain Monte Carlo (MCMC) algorithm was run for 2,000,000 generations with four incrementally heated chains, starting from random trees and sampling every 100 generations. The first 2000–5000 trees were discarded as burn-in, depending on when chains appeared to have become stationary. The remaining trees were assumed to represent the posterior probability (PP) distribution and used to calculate a majority rule consensus tree with PP values on the nodes in PAUP*.

TABLE 1. Voucher information and GenBank accession numbers for *Faberia* and related taxa in this study.

Taxa	Voucher	Collector	Locality	ITS	*psbA–trnH*	*rbcL*	*matK*	*trnL–F*
Outgroup								
Warionia saharae Benth. & Coss.	---		---	L35876	---	EU385027	EU385407	AY702089S2
Andryala								
A. integrifolia L.	---	---	---	AY879153	JX501942	HM849774	HM850614	AY879119
Catananche								
C. caerulea Georgi	---	---	---	AJ633467	EU531696	---	EU531675	AF118912
Chaetoseris								
C. cyanea (D. Don) C. Shih	slNie1094 (KUN)	Ze-Long Nie, Ying Meng, Tao Deng	China: Sichuan, Yanyuan	KF739608	GU109329	---	---	GU109298
Cicerbita								
C. alpina (L.) Wallr.	---		---	AJ633340	---	---	---	---
Cichorium								
C. intybus L.	---	---	---	AJ746410	GU818354	---	GU817441	GU817987
Crepis								
C. capillaris (L.) Waller	---		---	HQ161936	FJ395464	HM849923	FJ395373	---
Faberia								
F. cavaleriei Levl.	dt090715001 (KUN)	Tao Deng	China: Guizhou, Suiyang	KF739618	---	KF739633	---	---
F. faberi (Hemsley) N. Kilian	zz09074 (KUN)	Jian-Jun Zhou	China: Chongqing, Jinfoshan	KF739619	---	KF739634	---	---
F. sinensis Hemsl.	nie2062 (KUN)	Ze-Long Nie, Ying Meng, Tao Deng	China: Yunnan	KF739621	---	---	KF739652	---
	nie3157 (KUN)	Ze-Long Nie, Ying Meng, Tao Deng	China: Xizang, Gongbujiangda	KF739622	---	---	KF739651	---
F. thibetica (Franch.)	A4721 (KUN)	Tao Deng	China: Sichuan, Kangding	KF739620	KF739626	---	KF739653	KF739642
Faberiopsis								
F. nanchuanensis (C. Shih) C. Shih & Y. L. Chen	WGY010 (KUN)	Guang-Yan Wang, Liang Xu, Jian-Jun Zhou	China: Hunan, Yongshun	KF739612	KF739623	KF739630	KF739647	KF739638
	WGY021 (KUN)	Guang-Yan Wang, Liang	China: Hunan,	KF739613	KF739624	KF739631	KF739648	KF739639

..... *continued on the next page*

TABLE 1 (continued)

		Xu, Jian-Jun Zhou	Baojing					
	WGY007 (KUN)	Guang-Yan Wang, Liang Xu, Jian-Jun Zhou	China: Hunan, Yongshun	KF739614	KF739625	KF739632	KF739649	KF739640
	ZZ090 (KUN)	Jian-Jun Zhou	China: Chongqing, Nanchuan	KF739615	---	---	---	---
	ZZ09037 (KUN)	Jian-Jun Zhou	China: Chongqing, Sanhui	KF739616	---	---	---	---
	dt090622001 (KUN)	Tao Deng	China: Chongqing, Jinfoshan	KF739617	---	---	KF739650	KF739641
Ixeris								
I. stolonifera A. Gray	---		---	AJ633284	KF739629	---	AJ633156	---
Lactuca								
L. indica L.	---		---	AY862579	GU109320	---	EU749319	GU109288
Lapsana								
L. communis Linn.	---		---	HQ161939	FJ395498	---	FJ395399	---
Melanoseris								
M. leptantha (C. Shih) N. Kilian	nie1159 (KUN)	Ze-Long Nie, Ying Meng, Tao Deng	China: Sichuan, Muli	KF739607	---	---	---	---
Notoseris								
N. psilolepis C. Shih	nie2280 (KUN)	Ze-Long Nie, Ying Meng, Tao Deng	China: Guangxi, Nandan	KF739609	---	KF739637	KF739657	KF739646
Paraprenanthes								
P. diversifolia (Vaniot) N. Kilian	---		---	KF739610	---	---	---	---
P. yunnanensis (Franch.) C. Shih	---		---	---	GU109330	---	---	GU109299
Podospermum								
P. jacquinianum C. A. Mey.	---	---	---	---	EF374295	---	---	EF374378
P. meyeri K. Koch	---	---	---	AY508196	---	---	---	---
Prenanthes								
P. purpurea L.	---		---	AJ633342	AF208383	---	DQ840440	HQ324003
Pterocypsela								
P. elata Maxim.	ZDG339 (KUN)	Dai-Gui Zhang	China: Hunan, Sangzhi	KF739606	---	KF739636	KF739656	KF739645

..... *continued on the next page*

TABLE 1 (continued)

Rhagadiolus								
R. edulis DC.	---	---	---	---	---	---	AF542066	AF528402
Sonchus								
S. oleraceus (L.) L.	ZDG094 (KUN)	Dai-Gui Zhang	China: Hunan, Qianzhou	KF739611	HQ596853	HM850373	HQ593454	---
Soroseris								
S. glomerata (Decne.) Stebbins	---		---	HQ436216	HQ436184	JF944489	JF956528	HQ436151
Taraxacum								
T. coreanum F. H. Wigg.	nie1414 (KUN)	Ze-Long Nie	China: Sichuan, Daocheng	KF739605	---	KF739635	KF739654	KF739643
Tragopogon								
T. dubius Scop.	---	---	---	HQ161962	HQ596868	HQ590305	HQ593471	---
Uropappus								
U. lindleyi (DC.) Nutt.	---	---	---	AF473652	---	---	AJ633242	AF061948
Youngia								
Y. japonica (L.) DC.	---		---	HQ161935	KF739627	EU385029	EU385409	EU385123
Y. erythrocarpa (Vant.) Babcock & Stebbins	ZDG632 (KUN)	Dai-Gui Zhang	China: Hunan, Yongshun	KF739604	KF739628	---	KF739655	KF739644

Notes: --- indicates unpublished sequence.

To evaluate the congruence of the nuclear and plastid datasets, we first employed the incongruence length difference (ILD) test (Farris *et al*. 1994). The ILD test was conducted with 1000 replicates of heuristic search using TBR branch swapping with 10 random sequence additions in PAUP* v.4.0b10 (Swofford 2003).

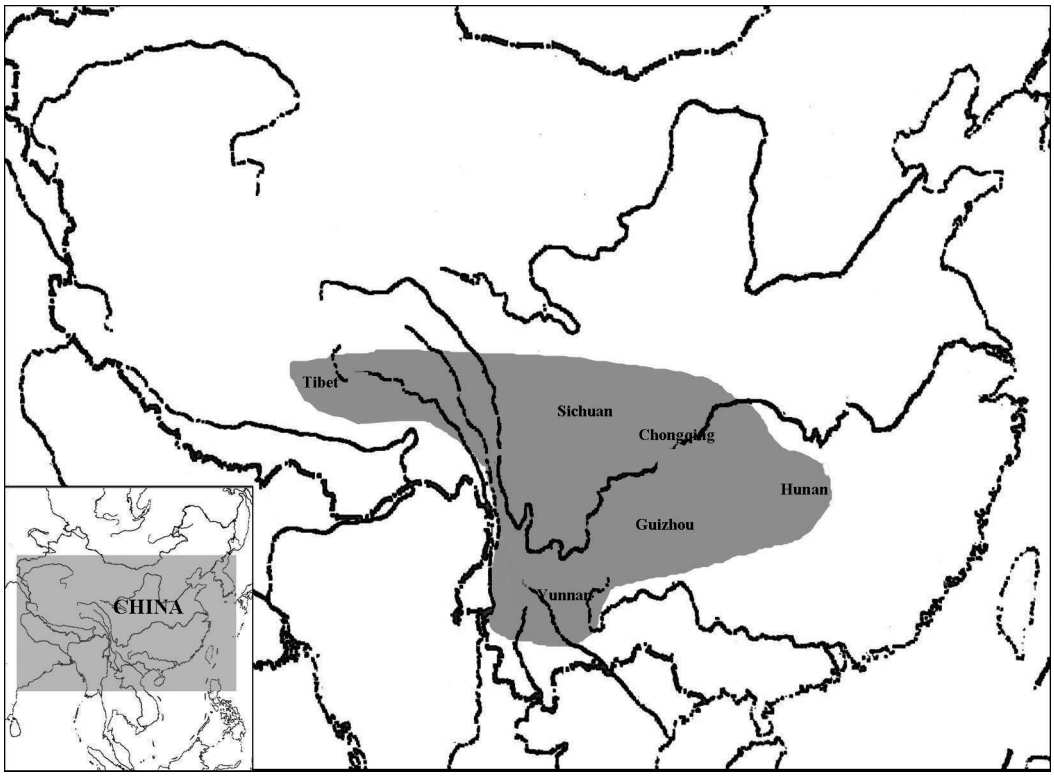

FIGURE 1. Distribution of *Faberia* in central and southwestern China based on field observations and herbarium collections.

Results

The aligned sequences of the ITS region generated a data matrix of 678 base pairs (bp) with 261 parsimony-informative sites (261/678 = 38.50%), while the *psbA–trnH* data set had 515 aligned bp, 54 of which were parsimony-informative (54/515 = 10.49%). The aligned *rbcL* data set was 1,358 bp in length, with 24 parsimony-informative sites (24/1358 = 1.78%). The *matK* data set had 879 aligned bp, 48 of which were parsimony-informative sites (48/879 = 5.46%). The *trnL–F* data set had 888 aligned bp, 43 of which were parsimony-informative site (43/888 = 4.84%). We combined all the plastid data in our analyses. The combined cpDNA matrix data had 3,804 characters including 248 parsimony informative sites (248/3804 = 6.52%). The ILD test indicated that chloroplast sequences (*psbA–trnH*, *rbcL*, *matK* and *trnL–F*) and nuclear ITS data sets were incongruent (P = 0.01). The strict consensus tree of the nuclear ITS sequences is shown in Fig. 2, while that of the chloroplast sequences (*psbA–trnH*, *rbcL*, *matK* and *trnL–F*) is shown in Fig. 3.

The monophyly of *Faberia* was well supported, with BP = 100 and PP = 1.00 (Figs. 2 and 3). Two clades corresponding to their distributions were supported within *Faberia* (Fig. 3): *F. nanchuanensis*, *F. cavaleriei* H. Léveillé and *F. faberi* (Hemsl.) N. Kilian from central China formed a strongly supported clade (PP = 0.99), while *F. sinensis* and *F. thibetica* (Franch.) Beauverd from southwestern China formed another robust clade (PP = 0.99). The clades recovered with cpDNA data were inconsistent with the nrDNA tree (Fig. 2). *Faberia* was located at basal-most position of Lactucinae in the nrDNA tree, but was derived within Crepidinae in the cpDNA tree. Fig. 4 represents a phylogram of *Faberia* and its relatives based on ITS data. *Faberia* species formed a closely knit clade with very little sequence divergence.

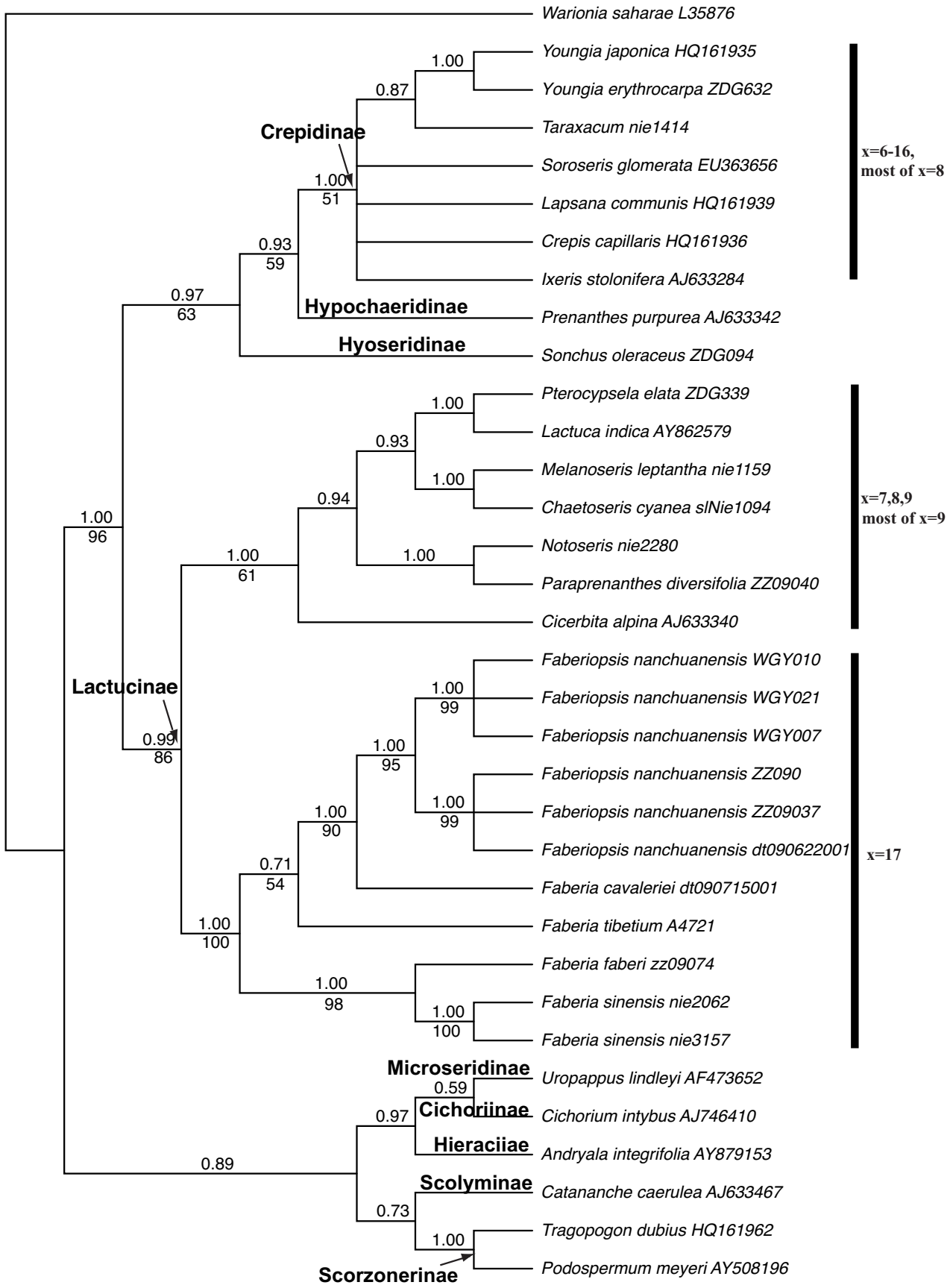

FIGURE 2. Strict consensus tree of *Faberia* and relatives based ITS sequences. Tree length = 1227 steps, CI = 0.50, RI = 0.55, and RC = 0.28. Bootstrap values greater than 50% are above the lines and Bayesian posterior probabilities are below the lines.

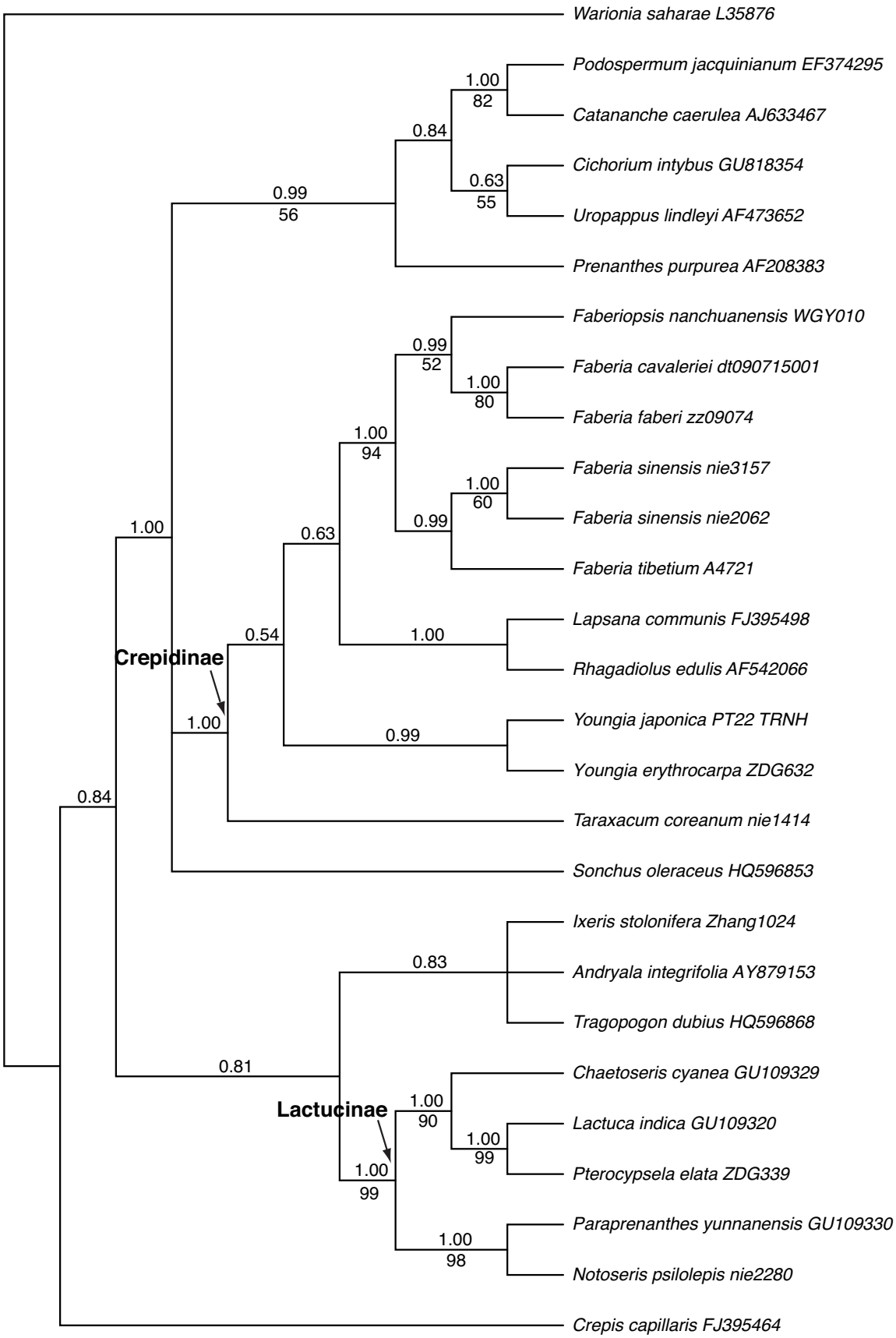

FIGURE 3. Strict consensus tree of *Faberia* and relatives based on the combined chloroplast sequences. Tree length = 624, CI = 0.83, RI = 0.67, and RC = 0.56. Bootstrap values greater than 50% are above the lines and Bayesian posterior probabilities are below the lines.

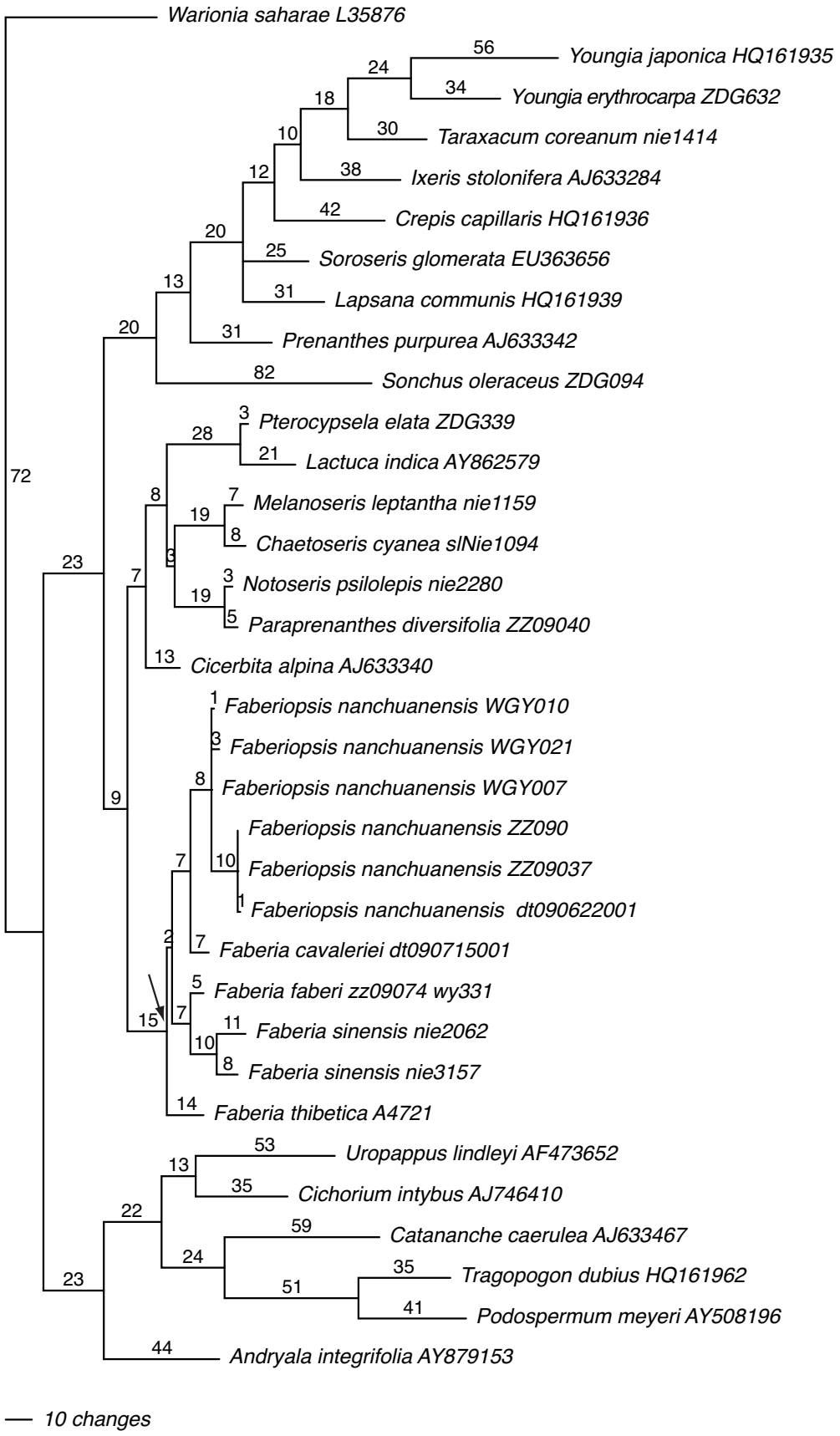

FIGURE 4. Phylogram of *Faberia* and relatives derived from internal transcribed spacer (ITS) nrDNA data. Values above each branch are branch length.

Discussion

Monophyly of Faberia

Both nrDNA and cpDNA (Figs. 2 and 3) data indicated that all sampled species of *Faberia* formed a well-supported monophyletic group. Morphological evidence for monophyly included campanulate or cuneiform involucres, slender styles with papillae or sweeping hairs, and a brown or pale yellow to white pappus of equal bristles. A chromosome comparison also supported the monophyly of the genus. All species have $2n = 34$ with the karyotype of Stebbins's 2B type (Liu *et al*. 2012).

Another argument supporting the monophyly of *Faberia* is that the species formed a closely knit clade with very little internal sequence divergence (Fig. 4). The pattern suggests a rapidly speciating group that diverged into new habitats throughout a recent radiation (Chen *et al*. 2005), which offered new opportunities for colonization, establishment, and morphological modification. Based on the *Flora Reipublicae Popularis Sinicae* and *Flora of China*, *Faberiopsis nanchuanensis* is endemic to Jinfoshan, Chongqing; and *Faberia sinensis* is restricted to Yunnan and Sichuan provinces. In our study, *F. nanchuanensis* is recorded for the first time also from Hunan Province (WGY007, WGY010, WGY021), and *F. sinensis* from the Tibet Autonomous Region (nie3157). We inferred that this may be related to fragmented areas which were formerly wider. Our results, based on extensive sampling from within its distribution areas, suggested that *Faberiopsis* was nested within *Faberia* (Figs. 2 and 3).

Phylogeny and systematic position of Faberia

Seven species of *Faberia* have been reported to be restricted to central and southwestern China (Shih & Kilian 2011; Fig. 1). In our analyses, five species from these two regions formed a robustly supported clade (PP = 1.00, BP = 100, Fig. 2; PP = 1.00, MB = 94, Fig. 3). Two clades within *Faberia* corresponded to their distributions in central and southwestern China (Fig. 3). *Faberiopsis nanchuanensis*, *Faberia cavaleriei*, and *F. faberi* from central China formed a robust clade (PP = 0.99, Fig. 3) of morphologically diverse species. Their stem leaves varied from ovate to elliptic to lanceolate and the ligules from five-toothed to trisect including a series of intermediate forms. *Faberia sinensis* and *F. thibetica* from southwestern China formed another strongly supported clade (PP = 0.99, Fig. 3) that was characterized by rosette leaves. However, the cpDNA tree was inconsistent with the nrDNA tree (Fig. 2). We inferred that *Faberia* appers to be severely differentiated.

The phylogenetic position and limits of *Faberia* are not well resolved. *Faberia* was synonymized with *Lactuca* (Franchet 1895) or *Prenanthes* (Babcock 1947, Lauener 1976, Sennikov & Illarionova 2001, Lack 2007) in the subtribe Lactucinae. Sennikov & Illarionova (2008) placed *Youngia racemifera*, *Y. silhetensis*, and *Y. silhetensis* subsp. *bhutanica* into *Faberia*. Shih & Kilian (2011) associated *Prenanthes glandulosa* with *Faberia*. In the present study, the nrDNA and cpDNA trees were incongruent, with *Faberia* being basal-most within Lactucinae in the nrDNA tree, and nested within Crepidinae in the cpDNA tree. One possible interpretation of this incongruence could be hybridization in the nrDNA region or limited character evolution in plastid DNA (İkinci 2011), which is supported by morphological and cytological evidence. Based on petal color, most species of Lactucinae have yellow, purple red, or blue flowers, while those of Crepidinae are yellow. *Faberia* flowers are reddish to bluish-purple. We inferred that petal color in Lactucinae and Crepidinae may be a fundamental character. The basic chromosome number of *Faberia* is $x = 17$ (Liu *et al*. 2012), which is a very rare number in Cichorieae. The chromosome numbers of 61 genera in Cichorieae range from $x = 3$ to $x = 11$. Notably, $x = 17$ was also present in *Warionia* Benth. et Coss. (Katinas *et al*. 2008) and the American species of *Lactuca canadensis* L. and *L. graminifolia* Michx. (Babcock *et al*. 1937; Tomb *et al*. 1978, Doležalová *et al*. 2002) was also found. Nevertheless, Katinas *et al*. (2008) indicated that *Warionia* was so unique that it belonged to a new subtribe, Warioniinae. In addition, they inferred that this genus was distantly related to *Faberia*. The karyotypes of the American *Lactuca* species with $x = 17$ were found rather asymmetric, consisting of predominantly subterminal centromeric (st) chromosomes (Babcock *et al*. 1937, Doležalová *et al*. 2002), thus having been also remarkably different from *Faberia*. Babcock *et al*. (1937) argued that the American *Lactuca* species with $x = 17$ had probably descended through hybridization between the diploid $x = 8$ and $x = 9$ species, followed by polyploidization. It is of great importance to distinguish the origin of the species with basic chromosome number $x = 17$ from the closest relative of *Faberia*. Moreover, the most common basic number in Lactucinae and Crepidinae are $x = 9$ and $x = 8$, respectively. In conclusion, our results suggest that the origin of $x = 17$ in *Faberia* was similar to that in *Lactuca*; *Faberia* may have descended through hybridization between Lactucinae and Crepidinae.

Acknowledgements

We are grateful to Wen-Cai Wang and Yun-Ting Lei for their valuable assistance in revising this manuscript, and to Ze-Long Nie, Dai-Gui Zhang, Liang Xu and Jian-Jun Zhou for providing the materials. The study was supported by grants from the National Natural Science Foundation of China (NSFC 40930209 to H. Sun) and the Ministry of Science and Technology of China, Major State Basic Research Development Program (2010CB951704).

References

Anthony, J. (1934) Diagnoses specierum novarum in herbario Horti Regii Botanici Edingburgensis cognitarum. *Notes from the Royal Botanic Garden*, *Edinburgh* 18: 189–217.

Babcock, E.B. (1947) The genus *Crepis* 2. *University of California Publications in Botany* 22: 199–1030.

Babcock, E.B., Stebbins, G.L. & Jenkins, J.A. (1937) Chromosomes and phylogeny in some genera of the Crepidinae. *Cytologia* 1: 188–210.
http://dx.doi.org/10.1508/cytologia.fujiijubilaei.188

Beauverd, G. (1910) Contributions à l'étude des Composées Asiatiques. *Bulletin de la Société Botanique de Genève* 2: 36–51.

Chen, S.T., Guan, K.Y., Zhou, Z.K., Olmstead, R. & Cronk, Q. (2005) Molecular Phylogeny of *Incarvillea* (Bignoniaceae) based on ITS and trnL-F sequences. *American Journal of Botany* 94(4): 625–633.
http://dx.doi.org/10.3732/ajb.92.4.625

Doležalová, I., Lebeda, A., Janeček, J., Číhalíková, J., Křístková, E. & Vránová, O. (2002) Variation in chromosome numbers and nuclear DNA contents in genetic resources of *Lactuca* L. species (Asteraceae). *Genetic Resources and Crop Evolution* 49: 383–395.
http://dx.doi.org/10.1023/a:1020610129424

Doyle, J.J. & Doyle, J.L. (1987) A rapid DNA isolation procedure for small quantities of fresh leaf tissue. *Phytochemical Bulletin* 19: 11–15.

Farris, J.S., Källersjö, M., Kluge, A.G. & Bult, C. (1994) Testing significance of incongruence. *Cladistics* 10: 315–319.
http://dx.doi.org/10.1111/j.1096-0031.1994.tb00181.x

Felsenstein, J. (1985) Confidence limits on phylogenies: An approach using the bootstrap. *Evolution* 39: 783–791.
http://dx.doi.org/10.2307/2408678

Forbes, F.B. & Hemsley, W.B. (1888) An enumeration of all the plants known from China proper, Formosa, Hainan, Corea, the Luchu Archipelago, and the Island of Hongkong, together with their distribution and synonymy. *Botanical Journal of the Linnean Society* 23: 1–489.
http://dx.doi.org/10.1111/j.1095-8339.1888.tb00535.x

Franchet, M.A. (1895) Plants nouvelles de la Chine occidentale. *Journal de Botanique* (Morot) 9: 258–265.

Hall, T.A. (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95–98.

Hamilton, M.B. (1999) Four primer pairs for the amplification of chloroplast intergenic regions with intraspecific variation. *Molecular Ecology* 8: 521–523.

Hoffmann, O. (1890–1894) Compositae. *In*: Engler, A. & Prantl, K. (eds.) *Die natürlichen Pflanzenfamilien* 4(5). Engelmann, Leipzig, pp. 87–391.

Huelsenbeck, J.P. & Ronquist, R. (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17: 754–755.
http://dx.doi.org/10.1093/bioinformatics/17.8.754

İkinci, N. (2011) Molecular phylogeny and divergence times estimates of *Lilium* section *Liriotypus* (Liliaceae) based on plastid and nuclear ribosomal ITS DNA sequence data. *Turkish Journal of Botany* 35: 319–330.

Jansen, R.K. & Kim, K.J. (1996) Implications of chloroplast DNA data for the classification and phylogeny of the Asteraceae. *In*: Hind, D.J.N. & Beentje, H.J. (eds.) *Compositae: Systematics. Proceedings of the International Compositae Conference, Kew, 1994*, vol. 1. Royal Botanic Gardens, Kew, pp. 317–339.

Katinas, L., Tellería, M.C., Susanna, A. & Ortiz, S. (2008) *Warionia* (Asteraceae): a relict genus of Cichorieae? *Anales del Jardin Botanico de Madrid* 65: 367–381.
http://dx.doi.org/10.3989/ajbm.2008.v65.i2.299

Kilian, N., Gemeinholzer, B. & Lack, H.W. (2009) Tribe Cichorieae. *In*: Funk, V.A., Susanna, A., Stuessy, T.E. & Bayer, R.J. (eds.) *Systematics, evolution and biogeography of Compositae*. IAPT, Vienna, pp. 343–383.

Lack, H.W. (2007) Tribe Cichorieae. *In*: Kadereit, J.W. & Jeffrey, C. (eds.) K. Kubitzki's *The families and genera of vascular plants* 8. Springer-Verlag, Berlin & Heidelberg, pp. 180–199.

Lauener, L.A. (1976) Catalogue of the names published by Hector Léveillé: IX [Compositae]. *Notes from the Royal Botanic Garden*, *Edinburgh* 34: 327–402.

Léveillé, H. (1914) Decades plantarum novarum. LIX–LXX. *Repertorium specierum novarum regni vegetabilis* 13: 337–345.
http://dx.doi.org/10.1002/fedr.4870092706

Ling, Y. & Shih, C. (1997) Compositae-Lactuceae. *In*: Ling, Y. & Shih, C. (eds.) *Flora Reipublicae Popularis Sinicae* 80.

Science Press, Beijing, pp. 1–302.
Liu, Y., Deng, T. & Yang, Q.E. (2012) Karyology of the genus *Faberia* (Cichorieae-Asteraceae) and its systematic implications. *Nordic Journal of Botany* 30(3): 365–371. http://dx.doi.org/10.1111/j.1756-1051.2011.01305.x
Nylander, J.A.A. (2004) *MrModeltest*, version 2 [computer program]. Evolutionary Biology Centre, Uppsala University, Uppsala, Sweden.
Olmstead, R.G., Bremer, B., Scott, K. & Palmer, J.D. (1993) A parsimony analysis of the Asteridae *sensu lato* based on *rbcL* sequence. *Annals of the Missouri Botanical Garden* 80: 700–722. http://dx.doi.org/10.2307/2399855
Sang, T., Crawford, D.J. & Stuessy, T.F. (1997) Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). *American Journal of Botany* 75: 408–430. http://dx.doi.org/10.2307/2446155
Sennikov, A.N. & Illarionova, I.D. (2001) Morphological and anatomical structure of achenes in the genus *Prenanthes* s.l. (Asteraceae). *Botanicheskii Zhurnal* 86: 56–66.
Sennikov, A.N. & Illarionova, I.D. (2008) Generic delimitation of the subtribe Ixeridinae newly segregated from Crepidinae (Asteraceae-Lactuceae). *Komarovia* 5: 57–117.
Shih, C. (1995) New Species of the Chinese Compositae. *Acta Phytotaxonomica Sinica* 33: 181–197.
Shih, C. & Chen, Y.L. (1996) *Faberiopsis* C. Shih et Y.L. Chen, Genus Novum Familiae Compositarum Sinensium. *Acta Phytotaxonomica Sinica* 34: 438–439.
Shih, C. & Kilian, N. (2011) *Faberia* Hemsley. *In*: Wu, Z.Y., Raven, P.H. & Hong, D.Y. (eds.) *Flora of China* 20. Science Press, Beijing & Missouri Botanical Garden, St Louis, pp. 357–361.
Swofford, D.L. (2003) *PAUP*: Phylogenetic analysis using parsimony (*and other methods)*, version 4.0b10. Sinauer, Sunderland, Massachusetts, USA.
Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. (1991) Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Molecular Biology* 17: 1105–1109. http://dx.doi.org/10.1007/bf00037152
Thomson, J.D., Gibson, T.J., Plewniak, F., Jeanmougin, F. & Higgins, D.G. (1997) The ClustalX windows interface: flexible strategies for multiple sequence alignment aided by quality analysis tools. *Nucleic Acids Research* 24: 4876–4882. http://dx.doi.org/10.1093/nar/25.24.4876
Tomb, A.S., Chambers, K.L., Kyhos, D.W., Powell, A.M. & Raven, P.H. (1978) Chromosome numbers in the Compositae. XIV. Lactuceae. *American Journal of Botany* 65: 717–721. http://dx.doi.org/10.2307/2442146
White, T.J., Bruns, T.D. & Lee, S. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *In*: Innis, M.A., Gelfand, D.H., Sninsky, J.J. & White, T.J. (eds.) *PCR protocols, a guide to methods and applications*. Academic Press, San Diego, pp. 315–322.
Zurawski, G., Perrot, B., Bottomley, W. & Whitfeld, P.R. (1981) The structure of the gene for the large subunit of ribulose 1, 5-bisphosphate carboxylase from spinach chloroplast DNA. *Molecular Ecology* 9: 3251–3270. http://dx.doi.org/10.1093/nar/9.14.3251
Zwickl, D.J. (2006) *Genetic algorithm approaches for the phylogenetic analysis of large biological sequence data sets under the maximum likelihood criterion*. Ph.D. dissertation, The University of Texas at Austin, Austin, Texas, USA.