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New taxonomic treatments in the *Pteris fauriei* group (Pteridaceae)

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Abstract

The dividing lines between species in the *Pteris fauriei* group (Pteridaceae) are questionable and the systematic positions of some species in this group remain unclear. To help comprehensively understand the phylogenetic relationships and resolve the taxonomic problems in this group a phylogenetic tree was reconstructed based on five chloroplast DNA regions (*atpA*, *matK*, *rbcl*, *rps4-trnS* & *trnL-trnF*) from 22 *Pteris* taxa. Additionally, their spore morphology and type materials were studied. Based on the molecular and morphology evidence, we made treatments as follow: *P. oshimensis* Hieron. var. *paraemeiensis* Ching ex Ching et S.H. Wu was raised as a species from a variety of *P. oshimensis* Hieron; *P. fauriei* Hieron. var. *chinensis* Ching et S.H. Wu was treated as a synonym of *P. austrotaiwanensis* Y.S. Chao, rather than a synonym of *P. latipinna* Y.S. Chao & W.L. Chiou; and *P. omeiensis* Ching was restored to species status from a synonym of *P. oshimensis* Hieron.

Key words: *Pteris paraemeiensis*, *P. omeiensis*, taxonomic treatment, morphology character, phylogeny

Introduction

Pteris L. (Pteridaceae) is a large genus with relatively high species diversity, including about 200–250 species, distributed in tropical, subtropical and temperate regions on all continents except Antarctica (Tryon & Tryon, 1982; Tryon *et al.*, 1990). The *Pteris* species are adapted to various habitats and can vary in morphology considerably (Zhang *et al.*, 2013). For instance, *Pteris* includes a wide range of frond dissection, and their venation can be anastomosing or free. Frequent hybridization (Walker, 1954, 1958), apogamy (Walker, 1958; Chao *et al.*, 2012a; Jaruwattanaphan *et al.*, 2013; Picard *et al.*, 2021) and polyploidy (Walker, 1956, 1962; Kuriachan & Ninan, 1976; Wang, 1989; Chao *et al.*, 2012b) have contributed to the various morphological traits and the high species diversity of *Pteris*.

Due to the high morphological similarity and complex genetic relationships, the infrageneric relationships of *Pteris* are complicated. The infrageneric division of *Pteris* was originally made by Presl (1836) and Christensen (1906) and was based on venation patterns. Shieh (1966) proposed a new infrageneric classification based mainly on patterns of leaf architecture, which was supported by Zhu *et al.* (2006), Song *et al.* (2010) and Yang (2011). Recent molecular phylogenetic studies have since determined the genetic relationships among *Pteris* (Chao *et al.*, 2012a;

Jaruwattanaphan *et al.*, 2013; Schneider *et al.*, 2013; Zhang & Zhang, 2018). Based on these phylogenies *Pteris* has now been classified into three subgenera, which include 16 major clades (Zhang & Zhang, 2018).

In the latest global phylogeny of *Pteris*, Section *Campteria* is the largest section and contains about 60 species, distributed widely in subtropical and tropical regions (Zhang & Zhang, 2018). The morphological characters of the section strongly support its monophyly: lamina 2-pinnatifid to 2-pinnate, pinnae regularly pectinate, basal pairs of pinnae often with 1–3 pinnules, and veins free (except *P. biaurita* L. (1753: 1076)). However, the molecular variation detected among species in the section was very low and thus the genetic relationships within this section were poorly resolved (Zhang & Zhang, 2018). The *P. fauriei* group is in this section, with bipinnatisect laminae and entire pinnules. Except *P. fauriei*, the other taxa in the group have a narrow distribution, mainly distributed in China and Japan.

The morphological delimitation within this group is unclear. Some species are distinguished from *P. fauriei* Hieron. (1914: 345) by several subtle characteristics, such as the size of pinnae, the distance between segments and the length of sori (Ching & Wu, 1983; Chao *et al.*, 2021). Wang *et al.* (2016) concluded that there are five taxa from mainland China in the *P. fauriei* group, which could be divided into four groups based on their spore ornamentation, and pointed out that *P. fauriei* and *P. fauriei* Hieron. var. *chinensis* Ching et S.H. Wu (1983: 10) shared similar spore morphology and were difficult to distinguish. Wang *et al.* (2019) used three chloroplast marker, *atpB*, *matK* and *trnL-F* to reconstruct a phylogeny of the *P. fauriei* group in mainland China, which showed that *P. majestica* Ching (1983: 12) was phylogenetically well-separated from other species and was probably of hybrid origin, and *P. fauriei* and *P. fauriei* var. *chinensis* were in the same clade, suggesting a close relationship. Based on phylogenies of two chloroplast genes, *rbcL* and *matK*, Chao *et al.* (2017) named a new *Pteris* species, *P. latipinna* Y.S. Chao & W.L. Chiou (2017: 100), which was previously identified as *P. fauriei*, but could be morphologically distinguished by its wide lateral pinnae, large terminal pinnae, and triangular basal segments of the lateral pinnae. *Pteris fauriei* var. *chinensis* was later treated as a synonym of *P. latipinna* (Chao *et al.* 2021), because the type materials of the former species was considered identical to the latter one. Chao *et al.* (2021) also published two new species in the *P. fauriei* group, *P. austrotaiwanensis* Y.S. Chao (2021: 313) and *P. pseudowulaiensis* Y.S. Chao (2021: 314), mainly based on subtle morphological differences and the phylogeny constructed with two chloroplast genes, *rbcL* and *matK*. Chao *et al.* (2022) later revealed a complicated reticulate evolution of the *P. fauriei* group via chloroplast and nuclear DNA markers. Seven parental taxa and 58 hybrids were found. It was also found that apogamy is dominant in this group and the ploidy levels are diploid and triploid (Table 1). Chao *et al.* (2022) proposed that frequent hybridizations within this group lead to novel genetic combinations, niche differentiation and apogamy, and contribute to the significant genetic diversity and the similar but varied morphology in this group. There were 18 taxa selected in this group in the studies of Chao *et al.* (2021, 2022), mainly from Taiwan Island and Japan.

TABLE 1. Ploidy levels and reproductive modes in the *Pteris fauriei* group.

Taxon	Sex 2X	Apo 2X	Apo 3X	Apo	Reference
<i>P. arisanensis</i>		√	√		Chao <i>et al.</i> , 2022
<i>P. austrotaiwanensis</i>		√			Chao <i>et al.</i> , 2022
<i>P. boninensis</i>	√				Chao <i>et al.</i> , 2022
<i>P. fauriei</i>		√	√		Chao <i>et al.</i> , 2022
<i>P. kawabatae</i>		√	√		Chao <i>et al.</i> , 2022
<i>P. kiuschiuensis</i>		√	√		Chao <i>et al.</i> , 2022
<i>P. latipinna</i>		√			Chao <i>et al.</i> , 2022
<i>P. laurisilvicola</i>			√		Chao <i>et al.</i> , 2022
<i>P. minor</i>	√				Chao <i>et al.</i> , 2022
<i>P. natiensis</i>		√	√		Chao <i>et al.</i> , 2022
<i>P. oshimensis</i>	√				Chao <i>et al.</i> , 2022
<i>P. paraemeiensis</i>				√	Chao <i>et al.</i> , 2022
<i>P. pseudowulaiensis</i>		√			Chao <i>et al.</i> , 2022
<i>P. satsumana</i>		√			Chao <i>et al.</i> , 2022
<i>P. setuloso-costulata</i>			√		Chao <i>et al.</i> , 2022
<i>P. wulaiensis</i>		√			Chao <i>et al.</i> , 2022
<i>P. angustipinnula</i>				√	this study
<i>P. fauriei</i> var. <i>chinensis</i>				√	this study
<i>P. omeiensis</i>				√	this study

Due to the above studies, the current research focusing on the *P. fauriei* group has obvious regional limitations, mainly on the species from mainland China or from Taiwan Island and Japan. Therefore, the taxonomic issues in *P. fauriei* group require a more comprehensive study. The objectives of this study were: (i) to review the phylogenetic relationships among all the species within the *P. fauriei* group; (ii) to better resolve the taxonomic treatments of some newly named species.

Materials and methods

DNA sequencing and phylogenetic study

Based on the results of Chao *et al.* (2021, 2022) and Zhang & Zhang (2018), thirty-seven samples representing 21 taxa in the *P. fauriei* group, including one sample of outgroup *P. puberula* Ching (1941: 52) were selected for phylogenetic study (Table 2). Twelve *Pteris* samples were collected from the field by us and five chloroplast DNA (cpDNA) regions (*atpA*, *matK*, *rbcL*, *rps4-trnS* & *trnL-trnF*) were obtained using the primers and protocol in Zhang *et al.* (2015). The cpDNA sequences of other *Pteris* samples were downloaded from GenBank mentioned in previous studies (Chao *et al.*, 2014; Zhang *et al.*, 2015; Chao *et al.*, 2017; Zhang & Zhang 2018, Chao *et al.*, 2021). DNA sequences were aligned with BioEdit v7.2.5 and manually edited. The combined cpDNA data set was applied to construct phylogenetic trees using maximum likelihood (ML), maximum parsimony (MP) and Bayesian methods. For ML analysis, the default “GTRCAT” model was used and 1,000 bootstrap replicates were conducted in RAxML software (Stamatakis, 2014). For MP analysis, 1,000 tree-bisection-reconnection (TBR) searches were used for equally weighted maximum-parsimony analyses conducted for each locus in PAUP* v4.0. One thousand replicates were performed with 10 TBR searches per replicate and a maximum of 100 trees held per TBR search (Zhang & Zhang, 2018). For Bayesian analysis, a phylogenetic tree was constructed using MrBayes v3.1.2 with the best-fit model (TVM+I+G) selected by AIC in jModelTest 2.1.10 (Darriba *et al.*, 2012). Four chains were run for 1,000,000 generations, with sampling every 1,000 generation. It was confirmed that the runs had converged by verifying that the standard deviation of the split frequencies was below 0.01. The majority-rule consensus tree was finally constructed with the first 25% of samples discarded as burn-in.

TABLE 2. Taxa, locations and GenBank accession numbers of *Pteris* used for phylogenetic analysis in this study.

Taxon	Location	Voucher	Reference	GenBank accession no.				
				<i>atpA</i>	<i>matK</i>	<i>rbcL</i>	<i>rps4-trnS</i>	<i>trnL-trnF</i>
<i>P. arisanensis</i>	Taiwan	Y.S. Chao 2135 (TAIF)	Chao <i>et al.</i> , 2021	/	MZ340403	MZ291651	/	/
<i>P. angustipinnula</i>	Ceheng, Guizhou, China	J.M. Wang 20150511003 (IBSC)	this study	OQ868407	OQ868424	OQ868441	OQ868458	OQ868475
<i>P. angustipinnula</i>	Maolan, Guizhou, China	J.M. Wang 20150514008 (IBSC)	this study	OQ868408	/	OQ868442	OQ868459	OQ868476
<i>P. austrotaiwanensis</i>	Taiwan	Y.S. Chao 3255 (TAIF)	Chao <i>et al.</i> , 2021	/	MZ340419	MZ291667	/	/
<i>P. boninensis</i>	Japan	Y.S. Chao 1941 (TAIF)	Chao <i>et al.</i> , 2014	/	KF289613	KF289743	/	/
<i>P. fauriei</i>	Taiwan	Y.S. Chao 2082 (TAIF)	Chao <i>et al.</i> , 2021	/	MZ340402	MZ291650	/	/
<i>P. fauriei</i>	Maolan, Guizhou, China	J.M. Wang 20150514013 (IBSC)	this study	OQ868410	OQ868426	OQ868444	OQ868461	OQ868478
<i>P. fauriei</i>	Chongyi, Jiangxi, China	D.M. Yang 201912 (IBSC)	this study	OQ868411	OQ868427	OQ868445	OQ868462	OQ868479
<i>P. fauriei</i>	Wuzhishan, Hainan, China	L. Zhang 1308 (CDBI)	Zhang & Zhang, 2018	MF972643	MF972748	MF972810	MF972830	MF972851
<i>P. fauriei</i> var. <i>chinensis</i>	Longzhou, Guangxi, China	J.M. Wang 20150129 (IBSC)	Guo <i>et al.</i> , 2022 (<i>rbcL</i> , <i>atpA</i> , <i>trnL-trnF</i> , <i>rps4-trnS</i>); this study (<i>matK</i>)	OM397912	OQ868440	OM397922	OM397942	OM397932
<i>P. fauriei</i> var. <i>chinensis</i>	Longzhou, Guangxi, China	J.M. Wang 20150129-3 (IBSC)	this study	OQ868412	OQ868428	OQ868446	OQ868463	OQ868480

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TABLE 2 (Continued)

Taxon	Location	Voucher	Reference	GenBank accession no.				
				<i>atpA</i>	<i>matK</i>	<i>rbcL</i>	<i>rps4-trnS</i>	<i>trnL-trnF</i>
<i>P. kawabatae</i>	Taiwan	Y.S. Chao 1637 (TAIF)	Chao <i>et al.</i> , 2014	/	KF289525	KF289655	/	/
<i>P. kiuschiuensis</i>	Kaihua, Zhejiang, China	D.M. Yang 201972 (IBSC)	this study	OQ868413	OQ868429	OQ868447	OQ868464	OQ868481
<i>P. latipinna</i>	Taiwan	Y.S. Chao 2092 (TAIF)	Chao <i>et al.</i> , 2017	/	MF416326	MF416320	/	/
<i>P. latipinna</i>	Taiwan	P.F. Lu 24585 (TAIF)	Chao <i>et al.</i> , 2017	/	MF416323	MF416317	/	/
<i>P. latipinna</i>	Taiwan	P.F. Lu 25108A (TAIF)	Chao <i>et al.</i> , 2017	/	MF416324	MF416318	/	/
<i>P. laurisolivicola</i>	Japan	Y.S. Chao 1848 (TAIF)	Chao <i>et al.</i> , 2014	/	KF289608	KF289738	/	/
<i>P. laurisolivicola</i>	Japan	Y.S. Chao 2555 (TAIF)	Chao <i>et al.</i> , 2021	/	MZ340411	MZ291659	/	/
<i>P. majestica</i>	Emeishan, Sichuan, China	L. Zhang 1381 (CDBI)	Zhang & Zhang, 2018	MF972645	MF972768	MF972817	MF972836	MF972857
<i>P. minor</i>	Nanji Island, Zhejiang, China	L. Chen 20220815-2 (IBSC)	this study	OQ868415	/	OQ868449	OQ868466	OQ868483
<i>P. minor</i>	Taiwan	Y.S. Chao 2078 (TAIF)	Chao <i>et al.</i> , 2017	/	MF416327	MF416321	/	/
<i>P. natiensis</i>	Japan	Y.S. Chao 1842 (TAIF)	Chao <i>et al.</i> , 2021	/	MZ340396	MZ291644	/	/
<i>P. natiensis</i>	Japan	Y.S. Chao 1906 (TAIF)	Chao <i>et al.</i> , 2014	/	KF289612	KF289742	/	/
<i>P. omeiensis</i>	Weng'an, Guizhou, China	J.M. Wang 20150516001 (IBSC)	this study	OQ868416	OQ868431	OQ868450	OQ868467	OQ868484
<i>P. omeiensis</i>	Weng'an, Guizhou, China	J.M. Wang 20150516009 (IBSC)	this study	OQ868417	OQ868432	OQ868451	OQ868468	OQ868485
<i>P. oshimensis</i>	Japan	Y.S. Chao 1881 (TAIF)	Chao <i>et al.</i> , 2014	/	KF289611	KF289741	/	/
<i>P. oshimensis</i> var. <i>paraemeiensis</i>	Ceheng, Guizhou, China	J.M. Wang 20150506002 (IBSC)	this study	OQ868418	OQ868433	OQ868452	OQ868469	OQ868486
<i>P. oshimensis</i> var. <i>paraemeiensis</i>	Ceheng, Guizhou, China	J.M. Wang 20150506008-1 (IBSC)	this study	OQ868419	OQ868434	OQ868453	OQ868470	OQ868487
<i>P. oshimensis</i> var. <i>paraemeiensis</i>	China	J.B. Zhang sn. 20100430109 (TAIF)	Chao <i>et al.</i> , 2021	/	MZ340415	MZ291663	/	/
<i>P. pseudowulaiensis</i>	Taiwan	T.C. Hsu 8437 (TAIF)	Chao <i>et al.</i> , 2021	/	MZ340422	MZ291670	/	/
<i>P. pseudowulaiensis</i>	Libo, Guizhou, China	J.M. Wang 20150517011 (IBSC)	this study	OQ868422	OQ868437	OQ868456	OQ868473	OQ868490
<i>P. puberula</i>	Gongshan, Yunnan, China	X.H. Jin 11305 (CDBI)	Zhang <i>et al.</i> , 2015 (<i>rbcL</i> , <i>atpA</i> , <i>trnL-trnF</i> , <i>rps4-trnS</i>); Zhang & Zhang, 2018 (<i>matK</i>)	KM007648	MF972782	KM008214	KM007879	KM008102 & KM007990
<i>P. satsumana</i>	Japan	Y.S. Chao 1925 (TAIF)	Chao <i>et al.</i> , 2021	/	MZ340397	MZ291645	/	/
<i>P. setulosus-costulata</i>	Sichuan, China	L. Zhang 1379 (CDBI)	Zhang <i>et al.</i> , 2015 (<i>rbcL</i> , <i>atpA</i> , <i>trnL-trnF</i> , <i>rps4-trnS</i>); Zhang & Zhang, 2018 (<i>matK</i>)	KM007652	MF972787	KM008218	KM007883	KM008106 & KM007994
<i>P. spinescens</i>	India	C.R. Fraser-Jenkins FN113 (TAIF)	Chao <i>et al.</i> , 2014	/	KF289565	KF289695	/	/
<i>P. wulaiensis</i>	Taiwan	Y.S. Chao 1743 (TAIF)	Chao <i>et al.</i> , 2014	/	KF289548	KF289678	/	/
<i>P. wulaiensis</i>	Taiwan	P.F. Lu 26667-1 (TAIF)	Chao <i>et al.</i> , 2017	/	MF537504	MF537503	/	/

Bold GenBank accession numbers are new sequences generated for this study. Backslash (/) indicates missing data.

SEM observation

Mature spores from eight *Pteris* species were mounted on double-sided tape on stubs directly after being collected. The spores were sputter-coated with gold-palladium and then observed and measured using a S-3000N Scanning Electron Microscope (HITACHI, Japan). Spore numbers of five sporangia were counted. Twenty spores per species were measured. The spore morphological data of the other three *Pteris* species was cited from Yang (2011). In total there are 11 *Pteris* species for spore morphological analysis (Table 3). Due to the limited specimens with spores, only one individual was examined, and some of them were not from the same population that DNA sequences have been obtained from. Terms for describing the decorations of spores follow Wang & Yu (2003). According to Yang (2011), lophate decoration, ornate-lophate decoration, distal ridges, proximal ridges and laesural ridges were regarded as the ridge-like decorations. The sexual *Pteris* plants produce 64 spores per sporangium and apogamous plants produce 32 or fewer spores per sporangium (Chao *et al.* 2022), which was used to infer the reproductive mode of each sample in this study.

Results

Molecular phylogenetic analysis

The entire combined data matrix was 6449 bp. The score of final ML optimization likelihood was -10922.971937. The number of parsimony-informative characters was 58. Average standard deviation of split frequencies was 0.004628. The accession numbers of the DNA sequences were listed in Table 2.

The main taxa of the *P. fauriei* group were divided into four subgroups with acceptable support values (Fig. 1), such as MLBS > 70%, MPJK > 88%, or BIPP = 1. *Pteris arisanensis* Tagawa (1936: 102) and *P. spinescens* C. Presl (1825: 56) are successive sisters to them. Genetic differentiation of the taxa in the *P. fauriei* group was small, but the delimitation of the subgroups was clear according to the integrated results of morphological and molecular evidence. *Pteris fauriei* was nested in three of the five subgroups.

Subgroup I included five species, such as *Pteris boninensis* H. Ohba (1971: 89), *P. fauriei*, *P. minor*, *P. laurisilvicola* Sa. Kurata (1967: 85), and *P. oshimensis*. In addition, they shared identical cpDNA characters, except *P. boninensis* and *P. minor* (Sample L. Chen 20220815-2).

Subgroup II included only two taxa, *P. fauriei* and *P. kawabatae* Sa. Kurata (1969: 59). The support values of this subgroup were the highest (ML BS=92, MP JK=88, PP=1).

Subgroup III included four taxa, *P. satsumana* Sa. Kurata (1968: 66), *P. majestica*, *P. setuloso-costulata* Hayata (1914: 241–242) and *P. oshimensis* var. *paraemeiensis*. All of them formed a polytomy.

Subgroup IV was the largest within the *P. fauriei* group, with 11 species. *Pteris fauriei* var. *chinensis* and *P. austrotaiwanensis* formed a clade and were separated from the other species within this subgroup, so did *P. kiuschiuensis* Hieron. (1914: 341) and *P. omeiensis*. *Pteris wulaiensis* C.M. Kuo (1989: 143–145), *P. pseudowulaiensis*, *P. angustipinnula* Ching et S.H. Wu (1983: 11) and *P. fauriei* was also nested in a clade, but the support values within the clade were low.

Morphological analysis

Each spore observed had an equatorial flange. Most were hemispherical in equatorial view and triangular in polar view. Nine *Pteris* species had spores with the ridge-like ornamentation on the distal face, and three of them had a distal ridge each (Table 3). The length of equatorial axis of spores ranged from 35 µm to 50 µm (Table 3), indicating different genome sizes in the *P. fauriei* group. The presence and the pattern of the ridge-like decorations, and the spore size were the valuable features to delimit *Pteris* species (Fig. 2). For example, a combination of the distal ridge, the small size of spores and the spore number made *P. minor* (Hieron.) Y.S. Chao (2021: 314) unique among the *P. fauriei* group; *P. fauriei* var. *chinensis* had large spores with ornate-lophate decoration, which was different from *P. fauriei*. However, some taxa were hard to distinguish based on spore morphology alone. For instance, the spores of *P. omeiensis* Ching (1949: 312), *P. oshimensis* Hieron. var. *paraemeiensis* Ching ex Ching et S.H. Wu (1983: 10) and *P. oshimensis* Hieron. (1914: 367) all had the ridge-like decorations. It was also difficult to recognize the spores of *P. pseudowulaiensis* from those of *P. fauriei*, though the former are larger.

TABLE 3. Comparison of spore morphology in the *Pteris fauriei* group.

Taxon character	<i>P. angustipinnula</i>	<i>P. fauriei</i>	<i>P. fauriei</i> var. <i>chinensis</i>	<i>P. kiuschiuensis</i>	<i>P. minor</i>	<i>P. omeiensis</i>	<i>P. oshimensis</i>	<i>P. paraemeiensis</i>	<i>P. pseudowuliensis</i>	<i>P. sentoso-costulata</i>	<i>P. majestica</i>
Shape in equatorial view. Hemispherical: 0; Subhemispherical: 1; Other: 2.	0	0	1	0, 2	0	0	0, 2	0	0	0	0, 2
Shape in polar view. Triangular: 0; Other: 1.	0	0	0	0, 1	0	0	0	0	0	0, 1	0
Decoration on distal face. With a distal ridge: 0; Ornate-lophate or lophate: 1; Verrucately rugulate: 2; Other: 3.	1, 2, 3	2, 3	1, 2	1, 2, 3	0, 1, 2	1, 2, 3	0, 2, 3	1, 2, 3	2, 3	1, 3	0, 1, 2, 3
Decoration on proximal face. With a proximal ridge: 0; With a laesural ridge: 1; Lophate: 2; Verrucately rugulate: 3; Other: 4.	3, 4	3, 4	3, 4	1, 3, 4	1, 3, 4	3, 4	3, 4	3, 4	3, 4	1, 4	0, 2, 4
Length of equatorial axis (µm). 35–40: 0; 40–45: 1; 45–50: 2.	1	1	2	2	0	2	2	1	2	1	2
Length of polar axis (µm). 24–30: 0; 30–35: 1; 35–40: 2.	0	0	0	/	0	/	1	1	0	1	2
Equatorial flange. With equatorial flange: 0; Without equatorial flange: 1.	0	0	0	0	0	0	0	0	0	0	0
Spore number. 32 spores per sporangium: 0; 64 spores per sporangium: 1.	0	0	0	0	1	0	0	0	0	0	0
Voucher specimen	J.M. Wang 20150511003 (IBSC), Guizhou, China	D.M. Yang 201912 (IBSC), Jiangxi, China	J.M. Wang 20150129-3 (IBSC), Guangxi, China	D.M. Yang 201972 (IBSC), Zhejiang, China	L. Chen 20220815-2 (IBSC), Zhejiang, China	J.M. Wang 20150516001 (IBSC), Guizhou, China	C.H. Li 09013 (IBSC), Sichuan, China	J.M. Wang 20150506008-1 (IBSC), Guizhou, China	J.M. Wang 20150517011 (IBSC), Guizhou, China	W.M. Zhu & Z.Z. Jin 9265 (PYU), Yunnan, China	S.E. Liu 22592 (IBSC), Yunnan, China
Reference	this study	this study	this study	this study	this study	this study	Yang, 2011	this study	this study	Yang, 2011	Yang, 2011

Backslash (/) indicates the length of polar axis is unavailable.

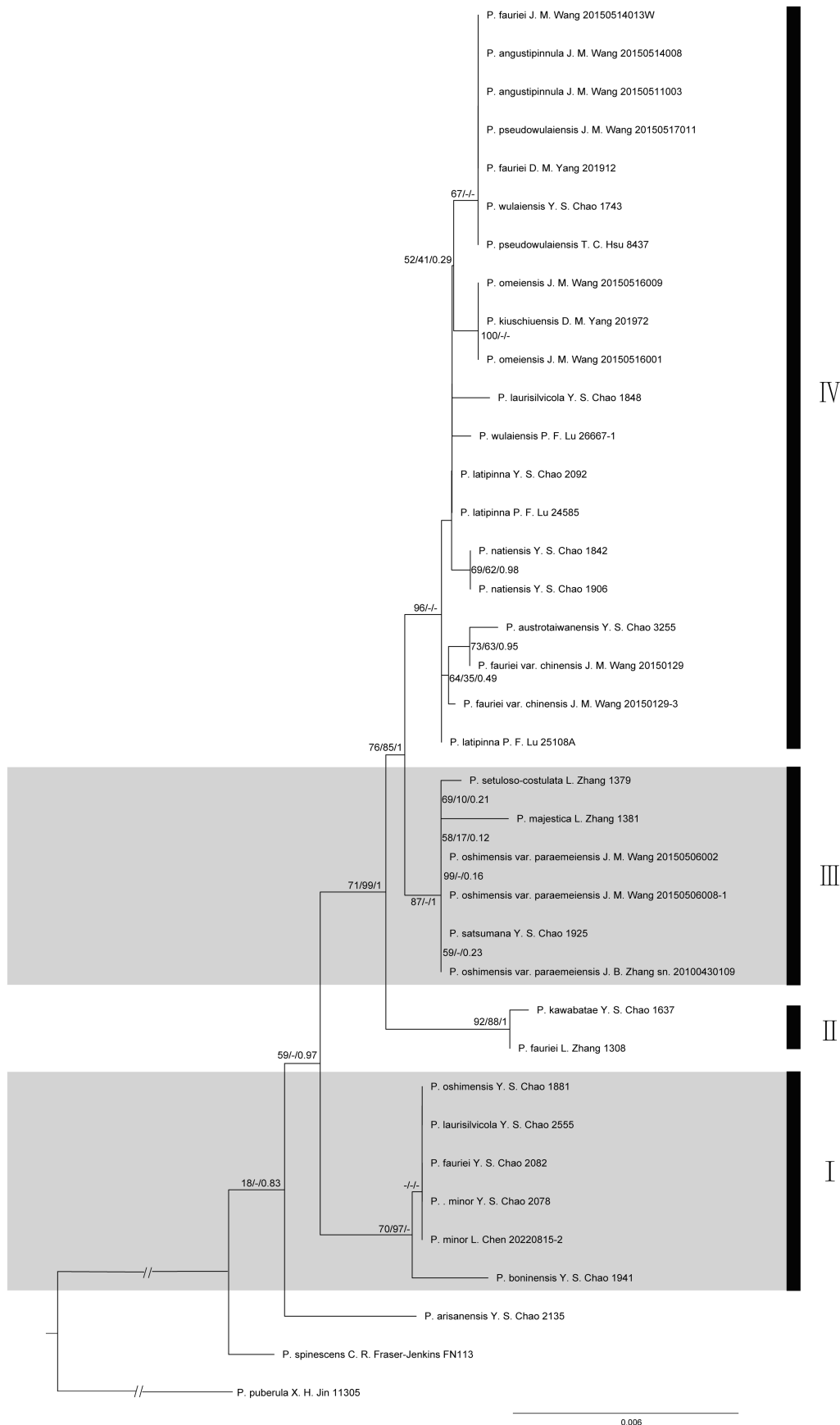


FIGURE 1. Maximum likelihood phylogeny of the *Pteris fauriei* group based on five cpDNA regions (*atpA*, *matK*, *rbcL*, *rps4-trnS* & *trnL-trnF*). The main taxa of the *P. fauriei* group are divided into four subgroups (I, II, III, IV), with *P. arisanensis* and *P. spinescens* as successive sisters. Support values (maximum likelihood bootstrap support, maximum parsimony jackknife support and Bayesian inference posterior probability) are shown along the branches. Dash (-) indicates nodes with MLBS < 10%, MPJK < 10%, or BIPP < 0.1.

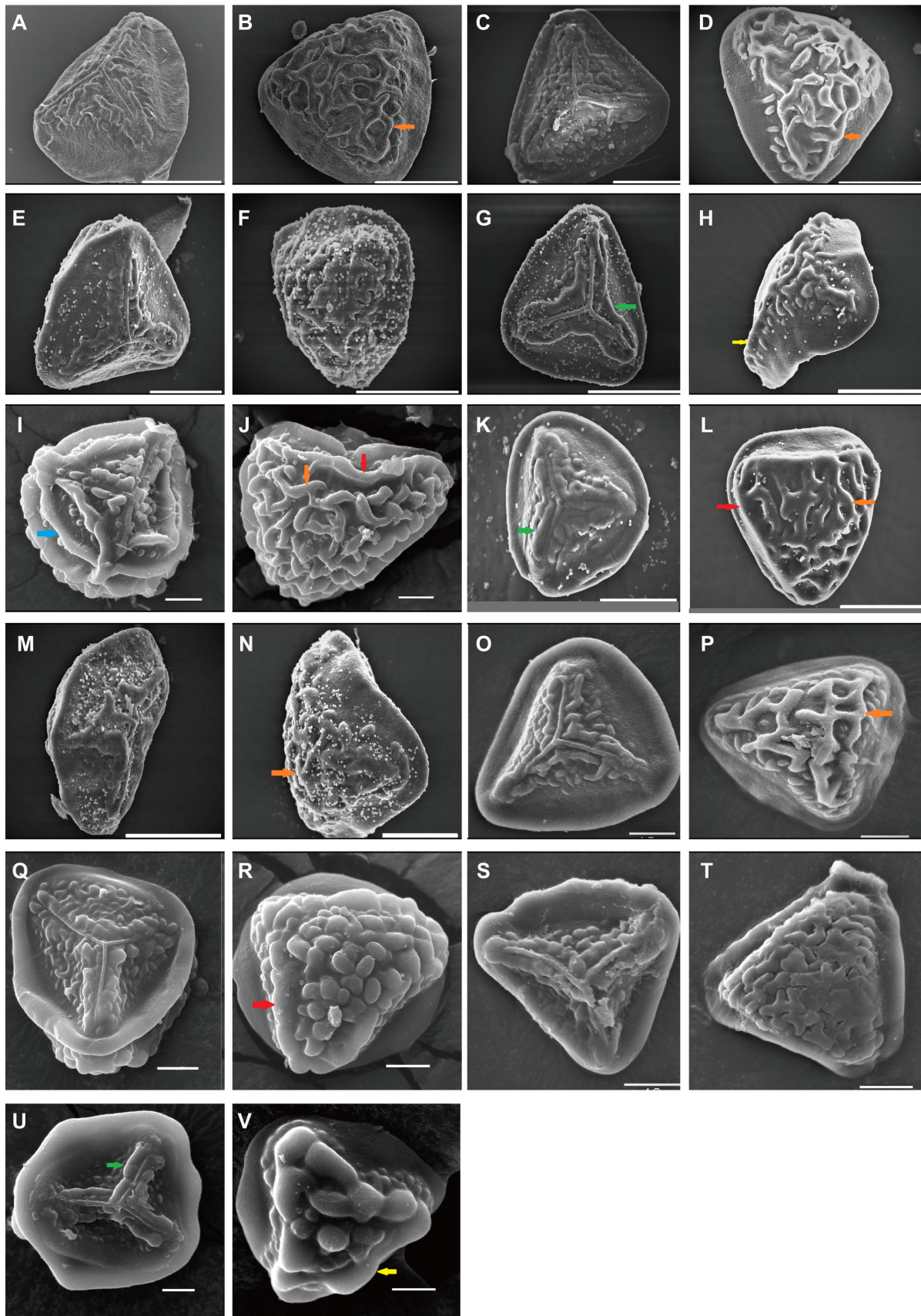


FIGURE 2. Spores of the *Pteris fauriei* group. A–B. *P. angustipinnula*. C–D. *P. fauriei* var. *chinensis*. E–F. *P. fauriei*. G–H. *P. kiuschiuensis*. I–J. *P. majestica*. K–L. *P. minor*. M–N. *P. omeiensis*. O–P. *P. paraemeiensis*. Q–R. *P. oshimensis*. S–T. *P. pseudowulaiensis*. U–V. *P. setuloso-costulata*. I–J, Q–R, U–V cited from Yang (2011). Red arrow: a distal ridge; Orange arrow: ornate-lophate decoration; Yellow arrow: lophate decoration; Blue arrow: a proximal ridge; Green arrow: a laesural ridge. A, C, E, G, I, K, M, O, Q, S, U are proximal faces; others are distal faces. A–E, K–L, N. Scale bar = 20 μm ; F–G, H, M. Scale bar = 30 μm ; I–J, O–V. Scale bar = 10 μm .

Discussion

Phylogenetic position of three taxa

Pteris oshimensis var. *paraemeiensis* was designated as a variety of *P. oshimensis* because it resembled *P. oshimensis*, but with longer lateral pinnae (14–25 cm) and longer tips (4–9 cm) (Ching & Wu, 1983). However, based on the plastid phylogenetic tree in our study, *P. oshimensis* var. *paraemeiensis* is distinct from *P. oshimensis*, and instead clustered with *P. setuloso-costulata*, *P. majestica*, and *P. satsumana*. Furthermore, we checked the type materials of these taxa except *P. satsumana*, and found that *P. oshimensis* var. *paraemeiensis* resembled *P. setuloso-costulata* rather than *P. oshimensis*. *Pteris oshimensis* var. *paraemeiensis* has more and longer lateral pinnae, and its laminae are papery, while *P. oshimensis* has sparse, short and tender pinnae (Fig. 3). In conclusion, although *P. oshimensis* var. *paraemeiensis* and *P. oshimensis* had similar spore decorations, they had different laminae and a distant phylogenetic relationship. Chao *et al.* (2022) also realized the differences, and suggested that var. *paraemeiensis* could be treated as a proper species. Therefore, we raise the status of *P. oshimensis* var. *paraemeiensis* from a variety to a distinct species.



FIGURE 3. Types of seven taxa in the *Pteris fauriei* group. **A.** *P. austrotaiwanensis* (holotype: Y.S. Chao 3255, TAIF!). **B.** Illustration of *P. latipinna* based on holotype (Y.S. Chao 2092, TAIF!). **C–D.** *P. setuloso-costulata* (iso-syntype: B. Hayata & S. Sasaki s.n., TAIF!). **E–F.** *P. fauriei* var. *chinensis* (holotype: C. Wang 31659, IBSC!; Isotype: PE!). **G–H.** *P. paraemeiensis* (holotype: W.P. Fang 3270, PE!). **I–K.** *P. omeiensis* (lectotype: C.S. Chang 755, PE!; syntype: T.C. Lee 3209, PE!). **L.** *P. oshimensis* (isotype: U. Faurie 4613, KYO!).

Pteris fauriei var. *chinensis* was published as a variety of *P. fauriei* due to its broader lateral pinnae (16–22 × 4–6 cm) and wider segments of pinnae (20–35 × 6–8 mm). *Pteris fauriei* var. *chinensis* was later treated as a synonym of *P. latipinna* without molecular evidence, but based on their type materials, which were considered to be identical (Chao *et al.*, 2021). Chao *et al.* (2017) emphasized that widely ovate sterile lamina (the ratio of length to width approximately 5:4) was the critical diagnostic character of *P. latipinna*. Simultaneously, *P. austrotaiwanensis* was found to be distinct from *P. latipinna* based on the molecular data from two cpDNA regions (Chao *et al.*, 2021) and nrDNA sequences (Chao *et al.* 2022), and thus was designated as a species, despite its similarity to *P. latipinna* in morphology and habitat. From the study of Chao *et al.* (2017, 2021), we can see that it is difficult to delimit *P. fauriei* var. *chinensis*, *P. latipinna* and *P. austrotaiwanensis* by morphology. However, according to our molecular data, *P. fauriei* var. *chinensis* was separated from *P. fauriei* and *P. latipinna* but positioned in the same clade with the newly published species *P. austrotaiwanensis* (Fig. 1). Besides, the type specimens of *P. fauriei* var. *chinensis* and *P. austrotaiwanensis* are identical in morphology (Fig. 3). Moreover, *P. fauriei* var. *chinensis* was different from *P. fauriei* in spore morphology (Table 3). The spores of the former one had ornate-lophate decoration rather than the latter one. Therefore, we conclude that it is not reasonable to treat *P. fauriei* var. *chinensis* as a synonym of *P. latipinna* and treat *P. fauriei* var. *chinensis* as a synonym of *P. austrotaiwanensis*, due to the rule that a previously published “intraspecific taxon” do not have priority over a subsequently published “species”, according to the International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code) Chapter II Section 3 Art. 11. 2 (Turland *et al.* 2018).

Pteris omeiensis was treated as a synonym of *P. oshimensis* by Wu (1990), mainly due to its oblique spreading, lanceolate lateral pinnae. However, comparing the type specimens of these two species, we found that they were significantly different (Fig. 3). *Pteris omeiensis* has stout stipes, more and longer pinnae and chartaceous laminae, while *P. oshimensis* looks short and tender, with sparser and shorter pinnae and herbaceous laminae. *Pteris omeiensis* can be also easily distinguished from *P. oshimensis* by the absence of a distal ridge despite the similar spore decorations on proximal face (Table 3, Fig. 2). Their distant genetic relationship also supports the recognition of *P. omeiensis* at species rank (Fig. 1). Thus, we confirm it is an independent species and restore its species status.

Genetic admixture between *P. fauriei* and other taxa in the *P. fauriei* group

Pteris minor, *P. latipinna*, and *P. oshimensis* are parental species of several hybrid species, such as *P. fauriei*, *P. kiuschiensis*, *P. laurisilvicola*, and *P. natiensis* Tagawa (1938: 109) (Chao *et al.*, 2022). *Pteris fauriei* is one of the most complicated taxa in the *P. fauriei* group. For instance, *P. fauriei* derives from *P. minor* and *P. latipinna* (Chao *et al.*, 2022). Additionally, five individuals named *P. cf. fauriei* derive from *P. wulaiensis* and *P. latipinna* or from *P. oshimensis* and *P. latipinna* (Chao *et al.*, 2022). In our study, *P. fauriei* falls into two separate clades with *P. minor* (clade I) and *P. wulaiensis* (clade IV), respectively. It may be that the *P. fauriei* individuals in clade IV represent another undescribed species. Due to the hybrid origins, the morphological characters to delimit the taxa in the *P. fauriei* group are subtle and unstable, lying mainly in the color of stipes, the angle of pinnae and the distance between segments. Chao *et al.* (2022) concluded that hybridization is the main reason why the genetic relationships within this group were not well resolved, leading to difficult taxonomic issues.

Taxonomic treatments

Pteris paraemeiensis (Ching et S.H. Wu) D.M. Yang, *stat. nov.*

Pteris oshimensis Hieron. var. *paraemeiensis* Ching ex Ching et S.H. Wu in Acta Bot. Austro Sin. 1: 10. 1983. Type:—CHINA. Sichuan: Mt. Omei, *W.P. Fang 3270* (holotype PE!).

Description:—Plants 50–90 cm tall. Rhizome erect, with linear-lanceolate brown scales. Fronds clustered; stipe 30–60 cm long, basally reddish brown, sparsely scaly, upper part and rachis and costae pale green or light brown; lamina 2 (or 3)-pinnatifid, oblong, 30–60 × 20–35 cm; lateral pinnae 4–11 pairs, 14–25 × 1.8–3 cm, 3–4.5 cm apart, alternate or opposite, ascending-oblique, sessile, lanceolate, apex long-caudate, 4–9 cm long, base cuneate, lowest pair of pinnae often with 1–2 basiscopic short pinnules, terminal pinna same as lateral pinnae, with stalk ca. 1 cm long, pectinately pinnatifid nearly down to costa; segments in 24–32 pairs, falcate, sometimes oblong, 5–8 × 10–15 mm, entire; costae glabrous, abaxially grooved, with needlelike flat spines along costules; veins free, 2-forked at base; lamina pale green and papery when dried. Sori linear; spore number 32; spore size 43.9 × 32.8 μm.

Distribution and conservation status:—In forests, alt. 500–1000 m. It is found in Southwest China, Guangxi, Hunan and Jiangxi. Due to its broad distribution and its occurrence in reserves we suggest that it should be classified as “Least Concern”, according to the IUCN Red List criteria (IUCN 2012).

Etymology:—When naming *P. oshimensis* var. *paraemeiensis*, Ching and Wu gave it the Chinese name “尾头凤尾蕨”, because of its tail-like tips of pinnae. Here we kept “*paraemeiensis*” for its Latin name and “尾头” for its Chinese name, to commemorate the contributions of Ching and Wu to the taxonomy of Pteridaceae.

Common name (assigned here):—Wei Tou Feng Wei Jue (尾头凤尾蕨; Chinese name)

Specimens examined:—CHINA. Guangxi: *Huanan Expedition Group 1986* (IBSC). Hunan: *S.L. Jin & J.B. Zhang JSL-WLSQ 819* (CSH), *K.G. Li, D.G. Zhang et al. TY20141225_1062* (JIU), *L. Xie 080713XL01* (JIU). Jiangxi: *D.G. Zhang & G.X. Chen LXP-06-2410* (JIU). Sichuan: *X.C. Zhang et al. 0453* (PE), *X.L. Zhou & J.B. Zhang ZXL05675* (CSH), *W.P. Fang 17405, 17956 & 17899* (IBSC), *T.H. Tu 5152* (IBSC). Chongqi: *Z.Y. Liu 4810, 9372, 10259* (IMC), *Fengdu Expedition Group 500230-001-0891-01* (IMC). Yunnan: *Z.Y. Liu 2022944* (IMC). Guizhou: *J.M. Wang 20150506002, 20150506008-1, 20150508001* (IBSC).

Taxonomic notes:—The papery laminae and lamina shape of *P. paraemeiensis* are similar to *P. setuloso-costulata*. However, it differs in having pale green costa, fewer pinnules on the basisopic side (1–2) and it occurs at lower altitudes (500–1000 m), compared to the light brown costa, 2–4 basisopic pinnules and higher altitude occurrence (1000–2500 m) of *P. setuloso-costulata* (Fig. 3). It differs from *P. oshimensis* by papery laminae, longer lateral pinnae (14–25 cm), and longer tips of pinnae (4–9 cm) (Fig. 3).

Chao *et al.* (2021) pointed out that *P. oshimensis* was rare in China and some plants identified with this name could be *P. pseudowulaiensis* or *P. paraemeiensis*. Furthermore, Fraser-Jenkins (2008) treated *P. setuloso-costulata* as a synonym of *P. spinescens*. However, the molecular evidence in our study did not support his treatment, because they were positioned in two distant clades. Actually, *P. setuloso-costulata* had a close genetic relationship with *P. paraemeiensis* rather than *P. spinescens* in our study.

Pteris austrotaiwanensis Y.S. Chao in *Taiwania* 66(3): 313, f. 1A–C. 2021. Type:—CHINA. Taiwan: Kaohsiung, Mt. Meilun, *Y.S. Chao 3255* (holotype TAIF!, isotype TAIF!)

Pteris fauriei Hieron. var. *chinensis* Ching et S.H. Wu in *Acta Bot. Austro Sin.* 1: 10. 1983. Type:—CHINA. Guangdong: Qujiang, *C. Wang 31659* (holotype IBSC!, isotype PE!)

Description:—Rhizomes short-creeping, densely covered with linear-lanceolate black-brown scales. Fronds clustered, 50–80 cm long, nearly monomorphic; stipes 20–40 cm long, stramineous or abaxially red, sparsely scaly at base; laminae green to dark green, herbaceous, ovate, 15–44 cm long, 15–30 cm wide, bipinnatisect; lateral pinnae lanceolate, 3–6 pairs, 16–22 × 1.8–6 cm, opposite, sessile, with one pair of basisopic pinnules, apex caudate, 2–3 cm long; segments falcate, 20–35 × 3–8 mm, apex acute or obtuse, margins entire; veins forked, free. Sori linear; spore number 32, spore size 48.9 × 26.8 μm.

Distribution:—In dense forests, below 1000 m, South China, Guizhou and Taiwan.

Specimens examined:—CHINA. Guangdong: *C. Wang 40734* (PE), *Y.H. Yan, S.L. Jin, Y. Wang & X.F. Zhu WYD198* (CSH). Guangxi: *R.H. Jiang, J.C. Yang & S.S. Mo 11493* (IBK), *L.Y. Yu, B.Y. Huang, D.X. Nong et al. 451422121209016LY* (GXM), *J.M. Wang 20150129, 20150129-3* (IBSC). Hainan: *W.T. Tsang 616* (PE), *S.Y. Dong 499* (PE). Guizhou: *H.J. Wei, J.B. Zhang & Y. Wang WYG047* (CSH).

Taxonomic notes:—*Pteris austrotaiwanensis* is different from *P. fauriei* by broader lateral pinnae (up to 6 cm wide) and wider segments of pinnae (up to 8 mm wide). Its herbaceous laminae, ovate lamina shape, broad lateral pinnae, and wide segments are similar to *P. latipinna*, but the laminae of *P. austrotaiwanensis* are green to dark green, while those of *P. latipinna* are light green.

According to the study of Chao *et al.* (2022), the very similar *P. austrotaiwanensis* and *P. latipinna* have different chloroplast and nuclear DNA haplotypes but share similar habitat preferences and the same ploidy level. Therefore, their similarity in morphology is probably caused by adaption to this specific habitat.

Pteris omeiensis Ching in *Bull. Fan. Mem. Inst. Biol.* new ser. 1: 312. 1949. Type:—CHINA. Szechuan: Mt. Omei, *C.S. Chang 755* (lectotype PE!), *T.C. Lee 3209* (syntype PE!), *Nos. 17899, 17956, 18018 ex Dept. Biol. Nat. Szechuan University* (paratype SZ!)

Description:—Plants 50–80 cm tall. Rhizome short, thick, erect, sparsely scaly but apex with dense, linear-lanceolate brown scales. Fronds clustered; stipe hard, stout, 50–60 cm long, basally reddish brown, sparsely scaly, upper part and rachis and costae pale green; lamina 2(or 3)-pinnatipartite, narrowly oblong, 30–35 × 10–20 cm; lateral pinnae 8–12 pairs, 12–16 × 1.5–1.7 cm, 3–4 cm apart, ascending-oblique, sessile, narrow lanceolate, apex long-caudate, base cuneate, lowest pair of pinnae 7 cm apart from the next pinnae, often with 1–2 basispic short pinnules, terminal pinna same as lateral pinnae, with stalk ca. 1 cm long, pectinately pinnatifid nearly down to costa; segments in 30–35 pairs, falcate, alternate or opposite, 10 × 3.5 mm, entire; costae glabrous, abaxially grooved, with stout spines along costules; veins free, 2-forked at base; lamina pale green when dried, chartaceous. Sori linear; spore number 32; spore size 46 µm.

Distribution and conservation status:—At the edge of woods, at 500–1200 m. It is only found in Sichuan and Guizhou, Southwest China. Due to its limited distribution, we suggest it should be classified as “Near Threatened”, according to the IUCN Red List criteria (IUCN, 2012).

Common name (assigned here):—E Mei Feng Wei Jue (峨眉凤尾蕨; Chinese name)

Specimens examined:—CHINA. Guizhou: *Unknown collector 1835* (PE), *J.M. Wang 20150516001, 20150516009* (IBSC).

Taxonomic notes:—*Pteris omeiensis* is distinct from *P. kiuschiuensis* by ascending and narrow lanceolate lateral pinnae. It also differs from *P. oshimensis* by stout stipes, more and longer pinnae and chartaceous laminae, while *P. oshimensis* is short and tender with herbaceous laminae, and sparser and shorter pinnae (Fig. 3).

Despite the difference in plant morphology, *P. omeiensis* is sister to *P. kiuschiuensis* in the cpDNA phylogenetic tree, and they are similar in spore morphology, indicating a close genetic relationship.

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