Finding missing diversity from synonyms of Haplopteris (Pteridaceae)

Zuo-Ying Wei¹², Zeng-Qiang Xia¹³, Xian-Chun Zhang⁴, Jian-Guo Cao², Yue-Hong Yan¹

¹ Shenzhen key laboratory for Orchid Conservation and Utilization, National Orchid Conservation center of China and the Orchid Conservation & research Center of Shenzhen, Shenzhen 518114, China ² College of Life and Environmental Sciences, Shanghai Normal University, Shanghai 201602, China ³ CAS Center for Excellence in Molecular Plant Sciences, Shanghai Institute of Plant Physiology and Ecology, Chinese Academy of Sciences, 300 Fenglin Road, Shanghai 200032, China ⁴ State Key Laboratory of Systematic and Evolutionary Botany, Institute of Botany, The Chinese Academy of Sciences, Beijing 100093, China

Corresponding author: Yue-Hong Yan (yan.yh@126.com)

Academic editor: Blanca León  |  Received 20 April 2021  |  Accepted 6 May 2021  |  Published 27 May 2021

Citation: Wei Z-Y, Xia Z-Q, Zhang X-C, Cao J-G, Yan Y-H (2021) Finding missing diversity from synonyms of Haplopteris (Pteridaceae). PhytoKeys 178: 81–94. https://doi.org/10.3897/phytokeys.178.67622

Abstract

Although taxonomists target the remote wild regions to discover new species, taxa lacking a comprehensive and modern systematic treatment may be the new hotspot for biodiversity discovery. The development of molecular systematics integrated with microscopic observation techniques has greatly improved the ability of taxonomists to identify species correctly. Vittaria centrochinensis Ching ex J.F. Cheng, regarded as a synonym of Haplopteris fudzinoi (Makino) E.H.Crane, remained hidden from the eyes of fern taxonomists for more than 20 years. Herein, we collected several population samples of V. centrochinensis by performing molecular phylogenetic analysis of five cpDNA regions (rbcL, atpA, matK, ndhF, and trnL-trnF) and through micromorphological observation of specimens which differs from H. fudzinoi by lamina width and exospores. Considering the differences in morphology, geographical range, and genetic distance between these two species, we formally recognized V. centrochinensis as an authentic species and proposed a new combination Haplopteris centrochinensis (Ching ex J.F.Cheng) Y.H.Yan, Z.Y.Wei & X.C.Zhang, comb. nov. Our findings demonstrate that several taxa in synonyms are missing, and nowadays taxonomy should also include re-evaluation of the past taxonomy.

Copyright Zuo-Ying Wei et al. This is an open access article distributed under the terms of the Creative Commons Attribution License (CC BY 4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.
Keywords
Haplopteris, molecular phylogeny, new combination, nomenclature, Pteridaceae, taxonomy

Introduction

The question “How many species are there on earth?” is one of the top 125 questions in science, and exploring it is considered equivalent to imagining the number of stars in the sky (Kennedy and Norman 2005). To understand the biodiversity of species, taxonomists should not only explore new species but also re-evaluate the published species’ names that are considered synonymous with older species’ names. According to the stasis of the web of TPL (The Plant List 2013), more than one-third of species names are unclear and approximately one-third of species names are considered synonymous. Unfortunately, once a species name is treated as a synonym, it remains in the pile of synonyms forever. With the development in molecular phylogeny research, DNA barcoding, and detailed taxonomic observations, an increasing number of species names have been re-established from the checklist of synonyms, which ranges from ferns (Shu et al. 2017; Shu et al. 2018; Wei et al. 2018; Wang et al. 2020) to spermatophyte (Luo et al. 2016; Jin et al. 2017; Wang et al. 2018). Consequently, we found that the synonym database could be a new hotspot for biodiversity discovery.

Accurate specimen identification through sequencing of the type specimens or samples from type locality is the key to solving questions regarding taxonomic synonyms. In addition, a clear understanding of the taxonomic status and barcoding database of the species suspected of being independent is required. Haplopteris C.Presl is a genus of vittarioid ferns, long treated as a synonym of Vittaria Sm. (Kramer 1990; Wu and Ching 1991; Chen et al. 2013). Recently, it has been widely adopted and followed that the Old World Vittaria species were transferred to Haplopteris (Chen et al. 2013). Because of limited morphology exhibited by members of the Haplopteris as well as convergent and parallel evolution of morphological characteristics, the circumscription of species in the genus has been ambiguous. Vittaria centrochinensis Ching ex J.F.Cheng, just one of a long sleeping suspicious species in the synonym list of Haplopteris, was initially published in “Flora of Jiangxi” (Xu 1993) as a new species and subsequently considered as a synonym of V. fudzinoi (Zhang 1999). To date, it has been regarded as a synonym of Haplopteris fudzinoi (Makino) E.H.Crane (Zhang and Gilbert 2013; Yan et al. 2016). Haplopteris fudzinoi is a species originally described in Japan, and then used to refer to a Chinese fern (Zhang 1999). During our field investigation in Wuyi Mountain (Jiangxi, China), we collected some population samples of V. centrochinensis and found some obvious differences between V. centrochinensis and H. fudzinoi.
In this study, we analyzed morphological characteristics and geographic distribution along with the molecular phylogeny to confirm the identity of *V. centrochinensis* and phylogenetic affinities of this species with *H. fudzinoi*. We hope that this study can provide a paramount example of re-evaluating of synonyms for new insights into biodiversity discovery.

**Materials and methods**

**Morphological analyses and geographical distribution**

For morphology, the *H. centrochinensis* was compared with similar species by analyzing photographs of type specimens and field photos. The features of rhizome scales were obtained using Nikon SMZ-1500 (Japan). The morphology of spores was observed with a Quanta 250 scanning electron microscope (FEI, USA), and spore size was measured using ImageJ software (Collins 2007). The descriptions of spore ornamentation abided by Wang and Dai (2010) and Ranker et al. (1993). The map of the geographical distribution of two species, namely *H. centrochinensis* and *H. fudzinoi*, was obtained through field investigation and National Specimen Information Infrastructure (NSII). The specimens of *H. centrochinensis* in this study were deposited in Shanghai Chenshan Herbarium (CSH).

**Phylogenetic analyses**

The total genomic DNA was extracted from silica-dried leaves by using a plant total genomic DNA kit (Tiangen, Beijing, China), according to the manufacturer’s instructions. The primers used for amplification and sequencing were shown in Table 1. Sequencing was performed with an ABI 3730xl DNA analyzer (Applied Biosystems, Foster City, CA, USA). The cpDNA sequences of the three samples of *H. centrochinensis* were submitted to GenBank under accession numbers: MW810047–MW810061 (Table 2). In addition, five cpDNA regions of nine species were downloaded from GenBank (Table 3). Of these, the unavailable data (Table 3) were treated as missing data when they were concatenated. The newly generated sequences were assembled and edited using SeqMan (Burland 1999). Subsequently, all sequences were aligned and manually adjusted on MEGA software (v7.0) (Kumar et al. 2016), with default alignment parameters. Alignments of five cpDNA regions were concatenated using PhyloSuite (Zhang et al. 2018). Then the matrix was used to construct phylogenetic trees with maximum likelihood (ML) and MrBayes. Maximum likelihood analysis was conducted using IQ-TREE (Nguyen et al. 2015) integrated in PhyloSuite with standard bootstrap and TVM+F+G4 model. Bayesian analysis was performed using MrBayes (v3.2.6) (Ronquist et al. 2012) with the GTR+F+G4 model. Four Markov chains were
Table 1. List of PCR amplification and sequencing primers used in the study.

| Regions | Primer name | Primer sequence (5’-3’) | Reference |
|---------|-------------|------------------------|-----------|
| rbcL    | AF          | ATGTCACCACAAACGGAGACTAAAGC | Hasebe et al. (1994) |
|         | ESRBCL1361R | TCAGGACTCCACTAATGCTTCCACG | Schuettpelz and Pryer (2007) |
| atpA    | ESATPF412F  | GCARGGGTCAAGCAAGCG       | Schuettpelz et al. (2006) |
|         | ESTRNR46F   | GTATAGGTTCRATCCTATGGAGCG | Schuettpelz et al. (2006) |
| matK    | Vt matK1610F* | GCARTCAARGTTAATRGTAA       | Chen et al. (2013) |
|         | Vt matK rRFQ | TTATACGGAATTCTGGRATCT     | Chen et al. (2013) |
| ndhF    | Vt ndhF fAYS | GCTTATCTAACHATGCCTAGYTRGGATATGG | Kuo et al. (2016) |
|         | Vt trnN 2210R | TCCTGARACGGAAAATAGCGTGTATGG | Kuo et al. (2016) |
| trnL-F  | F           | ATTTGAACCTGTCAGACAGC     | Taberlet et al. (1991) |
|         | FernL 1Ir1  | GGYATCTCGAGCCAAATC       | Li et al. (2010) |

Table 2. GenBank accession number of sequences newly generated in this study.

| Species                        | Location      | Voucher   | GenBank accession number |
|--------------------------------|---------------|-----------|--------------------------|
| Haplopteris centrochinensis    | Jiangxi, China | YYH15442-1 | M8W10047, M8W10050, M8W10053, M8W10056, M8W10059 |
| comb. nov.                     |               |           |                          |
| Haplopteris centrochinensis    | Jiangxi, China | YYH15442-2 | M8W10048, M8W10051, M8W10054, M8W10057, M8W10060 |
| comb. nov.                     |               |           |                          |
| Haplopteris centrochinensis    | Jiangxi, China | YYH15442-3 | M8W10049, M8W10052, M8W10055, M8W10058, M8W10061 |
| comb. nov.                     |               |           |                          |

run 1,000,000 generations, with the sampling frequency of 100. The standard deviation of split frequencies was set to less than 0.01 to achieve the convergence of the independent runs. A majority-rule consensus tree was constructed to estimate the posterior probabilities (PP); the first 25% of samples were discarded as the burn-in phase.

Results

Morphological comparisons and geographical distribution

The morphological and micromorphological characters of *H. centrochinensis* and *H. fudzinoi* are presented in Figure 1 and Table 4. The lamina of *H. centrochinensis* was shorter and wider than that of *H. fudzinoi* (Fig. 1A, B, F); in *H. fudzinoi* costa it was raised adaxially with two prominent long grooves beside the costa on adaxial surface (Fig. 1D). The rhizome scales were yellow-brown, margin denticulate, linear-lanceolate, and clathrate (Fig. 1E left); scale margins of *H. centrochinensis* were toothed and those of *H. fudzinoi* were subentire to minutely denticulate at lower margin and upper part, respectively. The scales length of *H. centrochinensis* were visibly longer than that of *H. fudzinoi* (Fig. 1E). Spores were monolete for both the species. Spore ornamentation observed in *H. centrochinensis* was scabrate and rugate (Fig. 1G, I), whereas it was lavegiate or inconspicuous-granulate in *H. fudzinoi* (Fig. 1H, J). Additionally, sori position was distinct between the two species; the soral line in *H. fudzinoi* was located close to the edge of lamina and immersed in groove (Fig. 1D), whereas it was immersed between the frond
costa and margin in *H. centrochinensis* (Fig. 1C). The geographical distribution for these two species was obtained on the basis of the information of the specimens. The result indicated that most distributions are shared by *H. centrochinensis* and *H. fudzinoi* (Fig. 3).

*Haplopteris centrochinensis* is an independent species according to molecular data obtained using phylogenetic analysis

The two phylogenetic analyses (BI, ML) recovered congruent topologies, with *Antrophyum parvulum* and *Antrophyum sessilifolium* as outgroups (Fig. 2). The results revealed strong support for the monophyly of *H. centrochinensis* (PP = 1.0, BS = 100) (Fig. 2), and it was strongly supported as a sister to another four species (i.e., *H. fudzinoi*, *H. doniana*, *H. taeniophylla*, and *H. linearifolia*) of *Haplopteris* (PP = 1.0, BS = 100) (Fig. 2). The genetic distance between the *H. centrochinensis* and these four *Haplopteris* species ranged from 0.073 to 0.120, and the intraspecific distances of these four species were 0 and 0.001 (Table 5).
Figure 1. Morphological observations in *H. centrochinensis* YYH15442 (A, C, F, G, I) and *H. fudzinoi* SG1654 (B, D, H, J). A habitat, C sorus position and flat lamina, F type specimen (provided by National Plant Specimen Resource Center, http://www.cvh.ac.cn); and G, I spore and ornamentation in *H. centrochinensis* YYH15442 B habitat (taken by Hong-Jin Wei) D sorus position and flat lamina (taken by Hong-Jin Wei) H, J spore and ornamentation in *H. fudzinoi* SG1654 E rhizome scale, left: *H. fudzinoi*, right: *H. centrochinensis*.
Finding missing diversity from synonyms of *Haplopteris* (Pteridaceae)

Figure 2. Majority consensus tree derived from Bayesian tree based on 5 cpDNA loci (*rbcL*, *atpA*, *matK*, *ndhF*, and *trnL-F*). Numbers above the branches are support values in the order of PP/BP/BS.

Table 5. Genetic distance between eight individuals of five *Haplopteris* species.

|   | 1    | 2    | 3    | 4    | 5    | 6    | 7    |
|---|------|------|------|------|------|------|------|
| 2 | 0.073*|      |      |      |      |      |      |
| 3 | 0.120*| 0.001|      |      |      |      |      |
| 4 | 0.120*| 0    | 0    |      |      |      |      |
| 5 | 0.120*| 0.001| 0.001| 0.001|      |      |      |
| 6 | 0.120*| 0.001| 0.001| 0.001| 0    |      |      |
| 7 | 0.120*| 0    | 0    | 0.001| 0.001| 0.001| 0    |
| 8 | 0.073*| 0    | 0    | 0.000| 0.001| 0.001| 0    |

Note: 1 = *H. centrochinensis* (YYH15442); 2 = *H. fudzinoi* (Kuo2225); 3 = *H. doniana* (Kuo 1418); 4 = *H. doniana* (Kuo1801); 5 = *H. taeniophylla* (Chen 2086); 6 = *H. taeniophylla* (Chen 1493); 7 = *H. taeniophylla* (FWL 974); 8 = *H. linearifolia* (Liu 9457); Genetic distances of *H. centrochinensis* from others species are shown with *.

Discussion

Re-evaluation of synonyms for new insights into biodiversity discovery

Synonym is the first concern in the estimation of the total number of species in one taxon, and only after its resolution can one ask the next question regarding how many additional species there are in the taxon (Joppa and Pimm 2011). Surprisingly, near-
ly two-thirds of the plant names are synonymous or recorded as unresolved in *TPL* (2013), which consists of 26,000 additional synonyms that were not listed in its earlier version (v.1.0). The increase in the number of newly discovered species has been consistent in line with the use of molecular evidence; however, information on synonyms is meager. For instance, *International Plant Names Index* (IPNI 2020) provides information on *nomen novum*, *combination nova*, and *taxa nova*, but it provides no information on new species resurrected from the established synonyms. Although many species of ferns (Liu et al. 2013; Morigengaowa et al. 2018; Shu et al. 2017; Shu et al. 2018; Sigel et al. 2014; Wang et al. 2020; Wei et al. 2018) and seed plants (Tkach et al. 2015; Hu et al. 2015) have been reinstated as independent species, this type of study has been rarely reported. The extent of biodiversity hidden in taxonomic literature is an interesting question to explore. To understand the biodiversity of our planet and for efficient conservation of valuable natural resources, the prime objective of taxonomists should be to correctly identify our planet biodiversity by using modern taxonomic facilities.

Various taxa, especially widely distributed ones, still require a comprehensive systematic treatment that also involves evaluating their nomenclature. Then, if cryptic taxa or misunderstood species have to be segregated, naming these taxa needs first to be evaluated against synonymy as potential sources of the needed name, otherwise a new name needs to be proposed. However, the number of taxonomists has significantly declined (Haas and Hauser 2005), and young taxonomists do not pay enough atten-

---

**Figure 3.** Geographic distribution of *H. centrochinensis* and *H. fudzinoi* in China. The dataset is provided by the National Specimen Information Infrastructure ([http://www.nsii.org.cn](http://www.nsii.org.cn)).
Finding missing diversity from synonyms of *Haplopteris* (Pteridaceae)

Therefore, the number of species on earth remains uncertain. Fortunately, technological advancement has considerably affected taxonomy. According to the IPNI data, two obvious turning points in taxonomy have affected the trends in new combinations and new taxa (Fig. 4), and those are related to the development of electron microscopy and molecular phylogeny in the 1970s and the 1990s, respectively (Endess et al. 2000). Although the new taxa have been displaying a steady or even a downward trend, the new combination is expected to display an upward trend in future, with the application of molecular biology in taxonomy (Fig. 4). Unsurprisingly, new combinations will continue to occur for a long time because of the abundance of listed synonyms and suspected species names, which are equivalent to the new species in the wild. Thus, synonyms and suspected species will serve as the new biological diversity hotspot for the exploration of new unknown species.

**Integrative taxonomy contributes to clarifying species delimitation**

The reason for numerous synonyms existing only in books may be the lack of sufficient morphological judgments made in the past. In the present study, the phylogeny (Fig. 2) based on the 5-locus dataset revealed strong support for the monophyly of *H. centrochinensis* (PP = 1.0, BS = 100) (Fig. 2) and strong support for *H. centrochinensis* as sister to *H. fudzinoi* (PP = 1.0, BS = 100) (Fig. 2). Although our result was different from that of a study by Zhang and Gilbert (2013) that indicated distinction between the two species, no further research was performed merely because of limited conditions at that time. Moreover, genetic distance in line with the K2P model showed an obvious hereditary difference between the *H. centrochinensis* and another three *Haplopteris* species (Table 5). For morphological comparisons, several traits were observed. Of these, the most

![Figure 4](image-url). Trends in the number of new names, new combinations, and new taxa published over 50 years (1970–2020).
unambiguous differences between the two species (*H. centrochinensis* and *H. fudzinoi*) were the wider lamina, longer rhizome scale, and shorter stipe in *H. centrochinensis*. In addition, *H. fudzinoi* costa was raised adaxially with two prominent long grooves besides the costa on adaxial surface. Furthermore, the scabrate and rugate ornamentation of spores observed in *H. centrochinensis* was found to be laevigate or inconspicuous-granulate in *H. fudzinoi*. To sum up, monophyletic clade, long genetic distance, stable morphological differentiation, and independent geographical distribution form the basis of establishing *H. centrochinensis* as a divergent species or an independent species, and therefore, it should not be considered synonymous with *H. fudzinoi*.

Here, we proposed a new combination *H. centrochinensis* (Ching ex J.F. Cheng) Y.H.Yan, Z.Y.Wei & X.C.Zhang, comb. nov. The taxonomic treatment of *H. centrochinensis* is as follows.

**Taxonomic treatment**

*Haplopteris centrochinensis* (Ching ex J.F. Cheng) Y.H.Yan, Z.Y.Wei & X.C.Zhang, comb. nov.

urn:lsid:ipni.org:names:77217251-1

*Vittaria centrochinensis* Ching ex J.F. Cheng: Fl. Jiangxi 1: 365. 1993. Basionym.

*Vittaria taeniophylla* sensu E.Zhang, non Copel.: Fl. Zhejiang 1: 111. 1993. p.p.

*Vittaria fudzinoi* sensu X.C.Zhang, non Makino: Fl. Rep. Poup. Sin. 3(2):20.1999. p.p.

*Haplopteris fudzinoi* sensu Zhang & Gilbert, non (Makino) E. H. Crane: Fl. China 2(3): 254.2013. p.p.

**Type.** China. Hubei Province, Enshi Tujia and Miao Autonomous Prefecture, Hefeng District, elev. 1200 m, October 1958, Hong-Jun Li, 8394 (holotype, PE!; isotypes, IBSC!, NAS!).

**Additional specimens examined. Guangxi Province:** Damaoshan District, 26 July 1958, Shao-Qing Chen, 15853 (IBSC); Quanzhou District, April 27, 2013, Quanzhou census team, 450324130427042LY (GXMG). **Guizhou Province:** Kaili City, census team, 3592 (CNBG); Xingren District, 9 August 1960, census team, 7872 (CNBG); Yinjiang, December 26, 1930, Y. Tsiang, 7867 (CNBG). **Hunan Province:** Shaoyang City, Dongkou District, 24 May 1983, Ze-Yong Yang, 166 (IBSC); Xinning District, September 9, 1984, Anonymous, 394 (PE). **Jiangxi Province:** Shangrao City, Yanshan District, Wuyi Mountain National Nature Reserve, 1729 m, October 7, 2019, Yue-Hong Yan, Zuo-Ying. Wei, Quan Yuan, YYH15442 (NOCC); Shangrao City, Yushan District, Sanqingshan, July 27, 1991, Sheng-Xiu Xu, 91018 (JXU); Jinggangshan City, Jinggangshan, April 13, 1983, Sheng-Xiu Xu, 83422 (JXU); Jinggangshan City, Jinggangshan, February 1982, 8210118 (JXU); Jinggangshan City, Jinggangshan, November 4, 1982, 8220349 (JXU); Jinggangshan City, Jinggangshan, July 2, 1973, Jing-Fu Cheng, 730433 (JXU); Shangrao City, Yushan District, Huayushan, July 1970, 0028466 (PEY); Pingxiang City, Luxi District, March 24, 2014, Gong-Xi, Chen and Dai-Gui Zhang, LXP-06-
Finding missing diversity from synonyms of *Haplopteris* (Pteridaceae)

1246, LXP-06-1251, LXP-06-1201 (SYS). **Zhejiang Province:** Quzhou City, Kaihua District, September 1, 2019, She-Lang Jin, Hong-Yu Wei, Jiao Zhang, JSL5850 (CSH); Longquan City, September 27, 1963, Shao-Guang Zhang, 4453 (CNBG); Linan City, May 25, 1958, Anonymous, 28714; Qingyuan District, Pei-Xi Qiu, 3935 (PE); Taishun District, July 17, 1960, Anonymous, 8576 (CNBG).

**Note.** *Vittaria centrochinensis* Ching ex J.F. Cheng was initially published in “Flora of Jiangxi” as a new species found in two distributed provinces (i.e., Jiangxi and Hubei). The type locality is situated in the Hefeng District from which a single specimen was cited. Additional specimens were cited from Jiangxi Province.

**Acknowledgments**

We thank NSII and Shanghai Chenshan Herbarium (CSH) for providing online specimen images, and Hong-Jin Wei and Yu-Feng Gu for taking photos of *H. fudzinoi*. We are grateful to Quan Yuan for helping with the field investigation. We thank Hui Shen, Rui Zhang, Dong-Mei Jin, Hui Shang, Wen Shao and Yu-Feng Gu for helping in the experiment. We appreciate the useful suggestions provided by the editor and an anonymous reviewer. We would like to thank TopEdit (www.topeditsci.com) for its linguistic assistance during the preparation of this manuscript. This project was supported by the Strategic Priority Research Program of the Chinese Academy of Sciences (project numbers XDA19050404), the Basic Project of Ministry of Science and Technology of China (project numbers 2015FY110200) and Shenzhen Key Laboratory for Orchid Conservation and Utilization.

**References**

Burland TG (1999) Dnastar’s lasergene sequence analysis software. Bioinformatics Methods and Protocols 132: 71–91. https://doi.org/10.1385/1-59259-192-2:71

Chen CW, Huang YM, Kuo LY, Chang YH, Liu YC, Chiou WL (2013) A new vittarioid fern species, *Haplopteris heterophylla* (Pteridaceae). Systematic Botany 38(4): 901–909. https://doi.org/10.1600/036364413X674805

Collins TJ (2007) ImageJ for microscopy. BioTechniques 43(1S): 25–30. https://doi.org/10.2144/000112517

Endess PK, Baas P, Gregory M (2000) Systematic plant morphology and anatomy-50 years of progress. Taxon 49(3): 401–434. https://doi.org/10.2307/1224342

Haas F, Hauser CL (2005) Taxonomists: An endangered species. Success Stories in Implementation of the Programmes of Work on Dry and Sub-Humid Lands and the Global Taxonomy Initiative, 87–79.

Hasebe M, Omori T, Nakazawa M, Sano T, Kato M, Iwatsuki K (1994) *rbcL* gene sequences provide evidence for the evolutionary lineages of leptosporangiate ferns. Proc. Proceedings
Hu H, Al-Shehbaz IA, Sun YS, Hao GQ, Liu JQ (2015) Species delimitation in *Orychophragmus* (Brassicaceae) based on chloroplast and nuclear DNA barcodes. Taxon 64(4): 714–726. https://doi.org/10.12705/644.4

IPNI (2020) International Plant Names Index. Published on the Internet http://www.ipni.org, The Royal Botanic Gardens, Kew, Harvard University Herbaria & Libraries and Australian National Botanic Gardens.

Jin WT, Schuiteman A, Chase MW, Li JW, Chung SW, Hsu TC, Jin XH (2017) Phylogenetics of subtribe Orchidinae s.l. (Orchidaceae; Orchidoideae) based on seven markers (plastid *matK, psaB, rbcL, trnL-F, trnH-psbA*, and nuclear nrits, *Xdh*): Implications for generic delimitation. BMC Plant Biology 17(1): e222. https://doi.org/10.1186/s12870-017-1160-x

Joppa LN, Pimm RSL (2011) How many species of flowering plants are there? Proceedings of the Royal Society B: Biological Sciences 278(1705): 554–559. https://doi.org/10.1098/rspb.2010.1004

Kennedy D, Norman C (2005) What Don’t We Know? Science 309(5731): 78–102. https://doi.org/10.1126/science.309.5731.78b

Kramer KU (1990) Vittariaceae. In: Kramer KU, Green PS (Eds) The Families and Genera of Vascular Plants (Vol. 1). Pteridophytes and gymnosperms. Springer-Verlag, Berlin, 272–277. https://doi.org/10.1007/978-3-662-02604-5_46

Kumar S, Stecher G, Tamura K (2016) MEGA7: Molecular evolutionary genetics analysis version 7.0 for bigger datasets. Molecular Biology and Evolution 33(7): 1870–1874. https://doi.org/10.1093/molbev/msw054

Kuo LY, Chen CW, Shinohara W, Ebihara A, Kudoh H, Sato H, Huang YM, Chiou WL (2016) Not only in the temperate zone: Independent gametophytes of two vittarioid ferns (Pteridaceae, Polypodiales) in East Asian subtropics. Journal of Plant Research 130(2): 255–262. https://doi.org/10.1007/s10265-016-0897-x

Li FW, Kuo LY, Huang YM, Chiou WL, Wang CN (2010) Tissue-direct PCR, a rapid and extraction-free method for barcoding of ferns. Molecular Ecology Resources 10(1): 92–95. https://doi.org/10.1111/j.1755-0998.2009.02745.x

Liu HM, Jiang RH, Guo J, Hovenkamp P, Perrie L, Shepherd L, Hennequin S, Schneider H (2013) Towards a phylogenetic classification of the climbing fern genus *Arthropteris*. Taxon 62(4): 688–700. https://doi.org/10.12705/624.26

Luo JP, Hong Y, Ren C, Yang QE, Yuan Q (2016) Reinstatement of the Chinese species *Cimicifuga lancifoliolata* (Ranunculaceae). Nordic Journal of Botany 000: 001–014.

Morigengawa, Luo JJ, Knapp R, Wei HJ, Liu BD, Yan YH, Shang H (2018) The identity of *Hypolepis robusta*, as a new synonym of *Hypolepis alpina* (Dennstaedtiaceae), based on morphology and DNA barcoding and the new distribution. PhytoKeys 96: 35–45. https://doi.org/10.3897/phytokeys.96.23470

Nguyen LT, Schmidt HA, von Haeseler A, Minh BQ (2015) IQ-TREE: A Fast and Effective Stochastic Algorithm for Estimating Maximum-Likelihood Phylogenies. Molecular Biology and Evolution 32(1): 268–274. https://doi.org/10.1093/molbev/msu300
Finding missing diversity from synonyms of *Haplopteris* (Pteridaceae)

Ranker TA, Tyron AF, Lugardon B (1993) Spores of the Pteridophyta: Surface, wall structure, and diversity based on electron microscope studies. Systematic Botany 18(2): 377–378. https://doi.org/10.2307/2419410

Ronquist F, Teslenko M, van der Mark P, Ayres DL, Darling A, Hohnsa S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian Phylogenetic Inference and Model Choice Across a Large Model Space. Systematic Biology 61(3): 539–542. https://doi.org/10.1093/sysbio/sys029

Schuettpelz E, Pryer KM (2007) Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. Taxon 56(4): 1037–1050. https://doi.org/10.1007/b1065903

Schuettpelz E, Korall P, Pryer KM (2006) Plastid *atpA* data provide improved support for deep relationships among ferns. Taxon 55(4): 897–906. https://doi.org/10.1007/b1065684

Shu JP, Shang H, Jin DM, Wei HJ, Zhou XL, Liu HM, Gu YF, Wang Y, Wang FG, Shen H, Zhang R, Adje B, Yan YH (2017) Re-establishment of species from synonymies based on DNA barcoding and phylogenetic analysis using *Diplopterygium simulans* (Gleicheniaceae) as an example. PLoS ONE 12(3): e0164604. https://doi.org/10.1371/journal.pone.0164604

Shu JP, Luo JJ, Wei HJ, Yan YH (2018) Clarifying the taxonomic status of *Dryopteris yepingenesis* based on materials from the type locality. Zhiwu Xuebao 53: 793–800.

Sigel EM, Windham MD, Smith AR, Dyer RJ, Pryer KM (2014) Rediscovery of *Polypodium calirhiza* (Polypodiaceae) in Mexico. Brittonia 66(3): 278–286. https://doi.org/10.1007/s12228-014-9332-6

Taberlet P, Gielly L, Pautou G, Bouvet J (1991) Universal primers for amplification of three noncoding regions of chloroplast DNA. Plant Molecular Biology 17(5): 1105–1109. https://doi.org/10.1007/BF00037152

The Plant List (2013) Version 1.1. Published on the Internet; http://www.theplantlist.org/[accessed 1st January 2021]

Tkach N, Röser M, Miehe G, Muellner-Riehl AN, Ebersbach J, Favre A, Hoffmann MH (2015) Molecular phylogenetics, morphology and a revised classification of the complex genus *Saxifraga* (saxifragaceae). Taxon 64(6): 1159–1187. https://doi.org/10.12705/646.4

Wang QX, Dai XL (2010) Spores of Polypodiales (Filicales) from China. Science Press, Beijing.

Wang L, Ren C, Yang QE (2018) Rediscovery of *Cremanthodium principis* (Asteraceae, Senecionaceae) in northwestern Yunnan, China. Phytotaxa 343(3): 277–282. https://doi.org/10.11646/phytotaxa.343.3.8

Wang T, Xiao B, Liu ED, Nguyen KS, Duan JQ, Wang KL, Yan YH, Xiang JY (2020) Rediscovery of *Angiopteris tonkinensis* (Marattiaceae) after 100 years, and its revision. PhytoKeys 161: 1–9. https://doi.org/10.3897/phytokeys.161.54912

Wei R, Ebihara A, Zhu YM, Zhao CF, Hennquin S, Zhang XC (2018) A total-evidence phylogeny of the lady fern genus *athyrium roth* (athyriaceae) with a new infrageneric classification. Molecular Phylogenetics and Evolution 119: 25–36. https://doi.org/10.1016/j.ympev.2017.10.019

Wu H, Ching RC (1991) Fern Families and Genera of China. Science Press, Beijing.

Xu SX (1993) *Vittaria* Sm. In: Editorial Committee (Eds) Flora of Jiangxi (Vol. 1 (Vittariaceae)). Jiangxi Science Technology Press Nanchang, China, 345–353.
Yan YH, Zhang XC, Zhou XL, Sun JQ (2016) Pteridaceae. Species catalogue of China. Volume 1 Plants. Pteridophytes. Science Press, Beijing, 38–60.
Zhang XC (1999) Vittariaceae. In: Chu WM (Ed.) Flora Reipublicae Popularis Sinicae 3. Science Press, Beijing, 12–31.
Zhang XC, Gilbert MG (2013) *Haplopteris* C. Presl. In: WU ZY, Raven PH, Hong DY (Eds) Flora of China (Vol. 2/3 (Pteridaceae)). Science Press, Beijing and Missouri Botanical Garden Press.
Zhang D, Gao FL, Li WX, Jakovlić I, Zou H, Zhang J, Wang GT (2018) PhyloSuite: An integrated and scalable desktop platform for streamlined molecular sequence data management and evolutionary phylogenetics studies. bioRxiv 489088. https://doi.org/10.1101/489088