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Research paper

A revision of *Dryopteris* sect. *Diclisodon* (Dryopteridaceae) based on morphological and molecular evidence with description of a new species

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ABSTRACT

Dryopteris sect. *Diclisodon* is a small section of ferns with about 12 species mainly distributed in East Asia. Here, we carried out morphological and phylogenetic analyses of this section. A new species from southwest China, *D. gaoligongensis*, is described and illustrated. *Dryopteris gaoligongensis* resembles *D. indonesiana* and *D. sparsa*, but differs by having a creeping rhizome and large 4-pinnate fronds. We also show that *D. glabrior* Ching & Z.Y. Liu is a distinct species; however, because it is a later homonym of *D. glabrior* Copel., it should be renamed *D. renchangiana*. We conclude that a species previously known as *D. nitidula,* also an illegitimate homonym, should be recognized with a new name, *D. sinonepalensis*. We resolve the phylogenetic position of *D. yoroii* as sister to other sampled species of *D.* sect. *Diclisodon*. Our phylogenetic analyses confirm the distinctiveness of *D. gaoligongensis*, *D. renchangiana*, and *D. sinonepalensis*. A key to species of *D.* sect. *Diclisodon* in China is provided.

1. Introduction

Comprising approximately 400 species, *Dryopteris* Adanson (1763) (Dryopteridaceae) is one of the largest fern genera (PPG, 2016). *Dryopteris* consists of terrestrial plants distributed worldwide that usually grow in forests, and occasionally in rocky areas of temperate mountain regions, with the highest species diversity occurring in East Asia, especially in the Himalaya and the Hengduan Mountains Area (Fraser-Jenkins, 1986; Wu and Lu, 2000; Wu et al., 2013; Sessa et al., 2015). Currently *Dryopteris* is divided into four subgenera with about 24 sections (Zhang, 2012; Zhang et al., 2012; Zhang and Zhang, 2012; Wu et al., 2013; Kuo et al., 2016).

Although *Dryopteris* sect. *Nephrocystis* H. Itô was widely accepted by Asian pteridologists (Itô, 1935; Fraser-Jenkins, 1986; Wu and Lu, 2000; Wu et al., 2013), it is actually a later synonym of *D.* sect. *Diclisodon* (T. Moore) C. Chr (Christensen, 1905; Widén et al., 2001). The type of *D.* sect. *Diclisodon*, *Diclisodon deparioides* T. Moore (= *Dryopteris deparioides* (T. Moore) Kuntze) belongs to *D.* sect. *Nephrocystis*, although the morphology of *D. deparioides* is special and does not represent the 'typical' morphological characteristics of this section. *Dryopteris* sect. *Diclisodon* is characterized by typical asymmetrical bases of pinnales, basiscopic pinnule of basal pair of pinnae elongated as pinnatifid, and brown, lanceolate to ovate scales, and is distributed in East Asia and South Asia, and extends to the Pacific Islands. Mainly based on different morphological characters, *D.* sect. *Diclisodon* was placed in *D.* subg. *Eudryopteris* C. Chr (Itô, 1935), *D.* subg. *Nephrocystis* (H. Itô) Fras.-Jenk (Fraser-Jenkins, 1986; Widén et al., 2001), or *D.* subg. *Dryopteris* (Wu and Lu, 2000). A previous molecular phylogeny indicated that most members of this section should be placed in *D.* subg. *Dryopteris* (Zhang et al., 2012). Fraser-Jenkins (1986) included 14 species in *D.* sect. *Nephrocystis*. Darnaedi et al. (1989a) described three new species related to the widespread *D. sparsa* (D. Don) Kuntze, and recognized two other synonyms of Fraser-Jenkins (1986) as distinct species in this section. Wu et al. (2013) recorded ten species in this section in *Flora of China* after removing several members of *D.* sect. *Acrorumohra* (H. Itô) Li Bing Zhang & H.

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He (He et al., 2013) based on molecular phylogenetic study (Zhang et al., 2012). A central piece of the taxonomic problem in *D.* sect. *Diclisodon* is the relationships among the *D. sparsa* complex, which has about ten names (Fraser-Jenkins, 1986, 1989; Darnaedi et al., 1989a; Fraser-Jenkins et al., 2018). This may be related to their complicated polyploidy ($2n = 82$, $2n = 123$, $2n = 164$, apomictic 'n' = 82, and apomictic 'n' = 123) (Gibby, 1985; Darnaedi and Iwatsuki, 1987; Imaichi et al., 1987; Darnaedi et al., 1989b; Weng, 1989; Tindale and Roy, 2002; Fraser-Jenkins, 2008; Hori et al., 2021). During our recent fieldwork, we collected many samples of *D.* sect. *Diclisodon* in China, which enabled us to address some significant taxonomic issues of this section.

2. Material and methods

2.1. Morphological study

We checked 332 specimens of *Dryopteris* sect. *Diclisodon* deposited in the herbaria of BM, HNNU, IBSC, K, KUN, P, PE, PYU, TI, and TNS, particularly digitalized type specimens at BM, K, P, TI, and TNS. Sixteen related species were chosen from morphological comparisons and previous studies (Fraser-Jenkins, 1986; Darnaedi et al., 1989a; Zhang et al., 2012; Wu et al., 2013) (Table 1). Eleven morphological features of these species were extracted from specimens and species descriptions of previous studies, and particular attentions were paid to the diagnostic morphological characters adopted in *Flora of China* (Wu et al., 2013).

2.2. Molecular phylogeny

2.2.1. Taxon sampling, DNA extraction, sequencing, and plastome assembly

Leaf material was collected from living plants in the field or from herbarium specimens. Total DNA of 12 samples (Table S1) was extracted from 15 mg of silica-gel-dried leaf material using a modified 4 × CTAB DNA extraction method (Doyle and Doyle, 1987). For plastid DNA, library preparation and Illumina sequencing were conducted at the Germplasm Bank of Wild Species, Kunming Institute of Botany (CAS), and BGI Genomics Co., Ltd (Shenzhen, China), respectively. More than 2 Gb of clean data of 150 bp pair-end reads were generated for each sample. Read data were *de-novo* assembled using GetOrganelle v.1.7.0 (Jin et al., 2020). Connection and annotation were subsequently conducted using Bandage 0.8.1 (Wick et al., 2015) and Geneious 9.1.4 (Kearse et al., 2012) based on the previously published plastome of *Dryopteris filix-mas* (L.) Schott (LT618774). For the low-copy nuclear gene *AK1*, primer design and reaction procedures followed Hori et al. (2021). The voucher information and GenBank accession numbers of complete plastomes, plastid regions, and the nuclear gene *AK1* used in this study are provided in Tables S1–S3, respectively.

2.2.2. Data matrices and phylogenetic analyses

We acquired 93 sequences of nine chloroplast regions (*atpB*, *psbA-trnH*, *rbcL*, *rbcL-accD*, *rps4-trnS*, *trnG-trnR*, *trnL*, *trnL-F*, and *trnP-petG*) from 32 samples, and ten additional plastomes from GenBank. We extracted nine chloroplast regions from 22 plastomes and constructed a combined plastid matrix of 54 samples. Fourteen *AK1* sequences from nine samples were newly obtained in this study and 18 sequences were acquired from GenBank. The plastid and nuclear matrices were aligned using MAFFT v.7.017 (Katoh et al., 2002) and were subsequently corrected in Geneious 9.1.4 (Kearse et al., 2012).

Maximum Likelihood (ML) and Bayesian Inference (BI) analyses were performed to infer the phylogenetic relationships within *Dryopteris* sect. *Diclisodon* based on the combined plastid regions and nuclear *AK1* gene, respectively. ML analyses were conducted using RAxML 8.2.10 (Stamatakis, 2014). A thorough tree search for the best ML tree was performed, and bootstrap analyses were performed with 1000 replications; bipartition information from the bootstrap trees was drawn on the best ML tree. BI analyses were conducted with MrBayes 3.2.6 (Ronquist et al., 2012), using ten million generations with one tree sampled every 1000 generations; four runs with four chains were performed in parallel. The first 25% of trees were discarded as burn-in. The Markov chain Monte Carlo (MCMC) output was examined to check for convergence and to ensure that all the effective sample size (ESS) values were above 200.

3. Results and discussion

3.1. Morphology

The diagnostic morphological characters of *Dryopteris* sect. *Diclisodon* are mainly related to leaves, e.g., lamina dissection and colors of the upper part of the stipe and rachis. Nevertheless, the creeping rhizome, irregularly lacerated indusia, and marginal sori are also important in distinguishing different species (Table 1).

The new species, *Dryopteris gaoligongensis* Z.Y. Zuo, Jin Mei Lu & D.Z. Li, resembles the Southeast Asian *D. indonesiana* Darnaedi, M. Kato & K. Iwats (Darnaedi et al., 1989a), but it can be easily distinguished from the latter and other known related species by its creeping rhizome (Figs. 1D and 2B; Table 1) and having large 4-pinnate fronds long than 1 m (Fig. 1A). The creeping rhizome was previously only known in *D. maximowiczii* (Baker) Kuntze in *D.* sect. *Diclisodon*. Actually, it can be found in *D. gaoligongensis* and the newly recognized *D. renchangiana* Z.Y. Zuo & D.Z. Li (Fig. 3C; Table 1). Compared with *D. gaoligongensis*, the pinnae of *D. renchangiana* are usually sessile or subsessile, and the laminae are bipinnate to tripinnatifid at the basal pinnae (Fig. 3A; Table 1). The other species, *D. sinonepalensis* Z.Y. Zuo & Fraser-Jenkins, is similar to *D. yoroii* Seriz., but can be easily distinguished from it morphologically. *Dryopteris yoroii* has monomorphic fronds, distinct pinnae stalks, and usually triangular-ovate pinnule of the upper pinnae (Fig. 4A–D), whereas *D. sinonepalensis* usually has slightly dimorphic fronds, very short pinnae stalks, and lanceolate pinnule of upper pinnae (Fig. 4F–I). In addition, the scales of the two species are different. The stipe base of *D. yoroii* is densely clothed with bicolorous (brown with pale edges) spreading scales (Fig. 4C and E), whereas that of *D. sinonepalensis* is sparsely clothed with concolorous (pale brown) adpressed scales (Fig. 4H and G).

3.2. Phylogenetic relationships

The concatenated matrix of nine plastid regions was 8466 bp in length, with 1692 variable sites and 1093 parsimony informative sites. The phylogenetic analyses based on the concatenated plastid matrix resolved the relationships among clades and subclades in *Dryopteris* sect. *Diclisodon* with strong support values (Fig. 5). There was no substantial conflict between the topologies that resulted from BI and ML analyses. *Dryopteris polita* Rosenst. is not

Table 1
Comparisons of eleven morphological characters in *Dryopteris* sect. *Diclisodon*.

Taxon	Characters										
	Rhizome	Frond dimorphism	Color of upper part of stipe and rachis	Basal pinnae of well-developed fronds	Lamina dissection of well-developed fronds except for the basal pinnae	Length of pinnae stalks	Pinnule shape of upper pinnae	Pinnule apices	Appendage on rachis and pinna rachis	Indusia	Sori location
D. angustipalea Darnaedi, M. Kato & K. Iwats.	Erect to ascendent	Monomorphic	Stramineous	Tripinnate	Tripinnate	Longer than 10 mm, with distinct stalks	Lanceolate	Obtuse	Glabrous	Entire	Medial
D. cacaina	Erect	Monomorphic	Castaneous to purplish brown	Tripinnate	Bipinnate	Longer than 10 mm, with distinct stalks	Triangular-ovate	Obtuse	Glands	Entire	Close to costule
D. deparioides	Erect	Monomorphic	Stramineous	Tripinnate	Bipinnate	Less than 5 mm, sessile or subsessile	Lanceolate	Acuminate	Glabrous	Entire	Marginal
D. gaoligongensis	**Creeping**	**Monomorphic**	**Stramineous to castaneous**	**4-pinnate**	**Tripinnate**	**Longer than 10 mm, with distinct stalks**	**Triangular-ovate**	**Acuminate**	**Hairy**	**Entire**	**Close to costule**
D. indonesiana	Erect	Monomorphic	Stramineous	4-pinnate	Tripinnate	Longer than 10 mm, with distinct stalks	Lanceolate	Acuminate	Glabrous	Entire	Close to costule
D. maximowiczii	Creeping	Monomorphic	Stramineous	4-pinnate	Tripinnate	Longer than 10 mm, with distinct stalks	Triangular-ovate	Obtuse	Scales	Entire	Submarginal
D. melanocarpa	Erect	Monomorphic	Stramineous	Tripinnate	Tripinnate	Longer than 10 mm, with distinct stalks	Triangular-ovate	Obtuse	Glands	Entire	Submarginal
D. platypus (Kunze) Kuntze	Erect	Slightly dimorphic	Castaneous to purplish brown	Tripinnate	Bipinnate	Less than 5 mm, sessile or subsessile	Lanceolate	Obtuse	Glands	Entire	Close to costule or medial
D. polita	Erect	Monomorphic	Stramineous	Bipinnatifid to tripinnate	Bipinnate	Longer than 10 mm, with distinct stalks	Triangular-ovate to Lanceolate	Acuminate to obtuse	Glabrous	Exindusiate	Medial to submarginal
D. renchangiana	**Creeping**	**Monomorphic**	**Castaneous to purplish brown**	**Bipinnate to tripinnatifid**	**Bipinnate**	**Less than 5 mm, sessile or subsessile**	**Lanceolate**	**Obtuse to Acuminate**	**Glands**	**Entire**	**Medial**
D. sabaei (Franch. & Sav.) C. Chr.	Erect	Monomorphic	Stramineous	Tripinnate	Bipinnate	Longer than 10 mm, with distinct stalks	Lanceolate	Acuminate	Scales	Entire	Medial
D. sinonepalensis	**Erect**	**Monomorphic**	**Stramineous**	**Tripinnate**	**Tripinnate**	**Less than 5 mm, sessile or subsessile**	**Lanceolate**	**Obtuse to Acuminate**	**Glabrous**	**Entire**	**Close to costule**
D. sparsa TYPE [a]	?	Monomorphic	Stramineous	Tripinnate	Tripinnate	Longer than 10 mm, with distinct stalks	Lanceolate	Acuminate	Glabrous	Entire	Close to costule
D. sparsa [b]	Erect to ascendent	Monomorphic, sometimes slightly dimorphic	Stramineous to castaneous	Bipinnatifid to tripinnate	Bipinnate to tripinnate	Longer than 10 mm, with distinct stalks	Lanceolate to ovate	Obtuse, acuminate or truncate	Glabrous or with glands	Entire	Medial
D. sparsa var. *ryukyuensis*	Erect	Monomorphic	Stramineous	Tripinnate	Bipinnate	Longer than 10 mm, with distinct stalks	Lanceolate	Obtuse	Glands	Entire	Medial
D. sparsa subsp. *rectipinnula* Fraser-Jenk. [c]	Erect	Monomorphic	Stramineous	Tripinnate	Tripinnate	Longer than 10 mm, with distinct stalks	Lanceolate	Obtuse	Glabrous	Entire	Medial
D. subexaltata [d]	Erect	Monomorphic	Stramineous	Bipinnatifid to bippinnate	Bipinnate	Less than 5 mm, sessile or subsessile	Ovate	Truncate	Glabrous	Irregularly lacerate	Medial
D. yakusilvicola	Erect	Monomorphic	Stramineous	Tripinnate	Tripinnate	Longer than 10 mm, with distinct stalks	Lanceolate	Acuminate	Glands	Entire	Medial
D. yoroii	Erect	Monomorphic	Purplish brown	Tripinnate	Bipinnate to tripinnate	Longer than 10 mm, with distinct stalks	Triangular-ovate	Obtuse to Acuminate	Glands or scales	Entire	Medial

A new species *Dryopteris gaoligongensis* and two newly recognized species with new names, *Dryopteris renchangiana* and *D. sinonepalensis* are showed in Bold.
[a] Information was extracted from the holotype (from Nepal, BM001066027).
[b] Information was extracted from *Flora Reipublicae Popularis Sinicae* (Wu and Lu, 2000), *Flora of China* (Wu et al., 2013), Ebihara (2017), and most specimens from China and Japan.
[c] Three names were submerged in this species: *Dryopteris sinosparsa* Ching & Shing, *D. viridescens* (Baker) Kuntze (Fraser-Jenkins, 1986) and *D. rheophila* Mitsuta ex Darnaedi, M. Kato & K. Iwats. (Fraser-Jenkins et al., 2018).
[d] Including samples identified as *Dryopteris hayatae* Tagawa.

Fig. 1. *Dryopteris gaoligongensis* Z.Y. Zuo, Jin Mei Lu & D.Z. Li. A. Habitat and well-developed fronds. B. 4-pinnate lower pinnae. C. The bipinnate-pinnatifid fronds in a young plant. D. Rhizome. E. Sori on ultimate pinnules. F. Scales.

nested in *D.* sect. *Diclisodon*, which is congruent with previous studies (Sessa et al., 2012; Zhang et al., 2012). *Dryopteris* sect. *Diclisodon*, which excludes *D. polita* and *Acrorumohra* group, is strongly supported as a monophyletic group and sister to the Pallidae clade in the plastid phylogeny. *Dryopteris* sect. *Diclisodon* is divided into three clades. The Yoroii clade, consisting of only one species *D. yoroii*, is the sister group to other sampled species of *D.* sect. *Diclisodon*. *Dryopteris yoroii* is only found in alpine habitat above the tree line (alt. 2900–3500 m) of the Himalaya to the Hengduan Mountains, and Taiwan Island, and three samples are included in the present study (Fig. 5). The Sabaei clade consists of three species distributed in Japan and the Korean Peninsula, i.e., *D. maximowiczii*, *D. sabaei* (Franch. & Sav.) C. Chr, and *D. yakusilvicola* Sa. Kurata (Fig. 5), of which *D. yakusilvicola* has been previously reported as a hybrid species (Darnaedi et al., 1990; Ebihara, 2017; Hori et al., 2021). The Sparsa clade is composed of two subclades (hereafter referred to as Subclade A and Subclade B). Subclade A consists of *D. gaoligongensis*, *D. deparioides*, and three samples of *D. sparsa* from the Himalaya, the Hengduan Mountains, and their adjacent areas (Fig. 5); *D. gaoligongensis* is sister to all other members of this subclade. Subclade B consists of *D. cacaina* Tagawa, *D. melanocarpa* Hayata, *D. renchangiana*, *D. sinonepalensis*, *D. subexaltata* (Christ) C. Chr., and several samples of *D. sparsa* (including *D. sparsa* var. *ryukyuensis* Seriz.). Within subclade B, *D. cacaina* and *D. sinonepalensis* together are sister to other species.

The *AK1* matrix was 631 bp in length, with 131 variable sites and 90 parsimony informative sites. The relationships among different clades and subclades have not been well resolved in the *AK1* phylogeny, although most terminal nodes are strongly supported (Fig. 6). Three haplotypes in *D. renchangiana*, two haplotypes in *D. gaoligongensis* and *D. yoroii*, and only one haplotype in *D. sinonepalensis* were detected. The results show that *D. yoroii* is sister to other species of *D.* sect. *Diclisodon* and *D. gaoligongensis* is sister to the Nepalese *D. sparsa* (*Liou804*).

Previous studies showed that *Dryopteris sparsa* was a polymorphic species complex (Imaichi et al., 1987; Darnaedi et al., 1989a) or possibly a polyphyletic group (Liou, 2010). A recent study also showed that many hybridization events occurred in *D. sparsa* and related species in Japan (Hori et al., 2021). The samples of previous studies were mainly collected from the Sino-Japanese region (Liou, 2010; Hori et al., 2021). Our study confirmed that *D. sparsa* from the Himalaya to the Hengduan Mountains, and their adjacent areas, is not monophyletic. All *D. sparsa* samples can be divided into at least six groups (Sparsa groups A–F in Fig. 5). The *AK1* phylogeny also implies that these

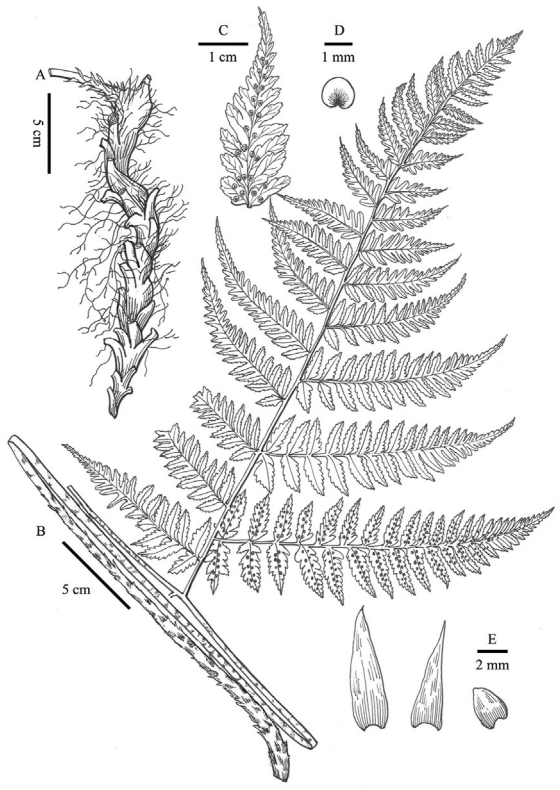

Fig. 2. Illustration of *Dryopteris gaoligongensis* Z.Y. Zuo, Jin Mei Lu & D.Z. Li. A. Rhizome. B. Stipe and basal pinna. C. Sori on ultimate pinnules. D. Indusia. E. Scales (Drawn by Ling Wang, based on the holotype (*Z.Y. Zuo1610*)).

groups are probably different taxa (Sparsa groups A, D, E & F in Fig. 6). It seems that the speciation of the *D. sparsa* complex is complicated, given the diversity of ploidy levels of this complex. Further studies are needed to elucidate the relationships among the *D. sparsa* complex with potentially cryptic species.

4. Taxonomic treatment

4.1. Dryopteris gaoligongensis Z.Y. Zuo, Jin Mei Lu & D.Z. Li, sp. nov. (Figs. 1 and 2). 高黎贡山鳞毛蕨 【*gāo lí gòng shān lín máo jué*】

Diagnosis: *Dryopteris gaoligongensis* is different from other species in *D.* sect. *Diclisodon* by being a large plant with a creeping rhizome. It is similar to some species of *D.* sect. *Marginatae* (e.g., *D. subimpressa* Loyal.) in leaf shape. However, it can be identified as a member of *D.* sect. *Diclisodon* by typical asymmetrical bases of pinnales, basiscopic pinnule of basal pair of pinnae elongated as pinnatifid.

Type: CHINA. **Yunnan**: Baoshan, 25°17′N, 98°46′E, alt. 2338 m, 20 April 2019, *Z.Y. Zuo 1610* (Holotype, KUN, in 3 cross-referenced sheets.)

Plants 50–120 cm tall. Rhizome stout, creeping, up to 20 cm long and 3 cm in diameter, densely clothed with brown, ovate-lanceolate, entire scales. Fronds approximate, stipe shorter than lamina, ca. 30–50 cm, brown at base, with spreading ovate-lanceolate, entire, brown scales, glabrous upward. Rachis and costae sparsely bearing fibrillose scales. Lamina broadly deltate-lanceolate to ovate-lanceolate, ca. 40–60 × 30–50 cm, tripinnate to 4-pinnate, base not narrowed, apex acuminate. Pinnae 15–30 pairs, opposite, oblique, stalked up to 5 cm. Pinnae lanceolate, basal pinnae largest, deltate-lanceolate, up to 30 × 15 cm on each side, apex caudate-acuminate. Pinnules 20–30 pairs, opposite at base and alternate upward, lanceolate, base broadly cuneate, usually asymmetrical, apex long acuminate. Basiscopic pinnule at base of basal pinnae longer than acroscopic ones, ca. 5 × 2 cm, base widest, 2-pinnate. Segments oblong, apices obtuse and spinulose, margin shallowly lobed to several serrate. Lamina papery, glossy, veins pinnate, forked, distinct on both surfaces. Sori close to costa on pinnules, with wide sterile belt on both sides of costa distal to sori; indusia orbicular-reniform, entire.

Distribution and habitat: Presently, only known from southern part of the Gaoligong Mountains. Forest, on the ground.

Etymology: The specific epithet "*gaoligongensis*" refers to its type locality, the Gaoligong Mountains, on the border of Yunnan of China and Myanmar.

Additional specimens examined (Paratypes):

CHINA. **Yunnan**: Baoshan, 25°17′N, 98°46′E, alt. 2317°m, 17 October 2019, *DLJ2019398* (KUN); Tengchong, 25°18′N, 98°46′E, alt. 2367 m, 18 April 2019, *Z.Y. Zuo 1539* (KUN).

4.2. Dryopteris renchangiana Z.Y. Zuo & D.Z. Li, nom. nov. (Fig. 3). 仁昌鳞毛蕨【*rén chāng lín máo jué*】

Dryopteris glabrior Ching & Z.Y. Liu in Bull. Bot. Res., Harbin 4(4): 11 (1984), *nom. illeg.* **Type**: CHINA. **Chongqing**: Jinfoshan, 21 July 1983, *Z.Y. Liu 4231* (Holotype PE01863796; Isotype IMC0007913). Non *Dryopteris glabrior* Copel. in Philipp. J. Sci. C, 5(4): 283 (1910). **Type**: Borneo. August 1908, *Brooks C.J. s.n.* (Holotype P00630771).

Distribution and habitat: It is currently known in Chongqing (Nanchuan) and Sichuan (Xuyong), China. Montane forest, on wet cliffs or the mouths of caves by streams, at 500–1500 m.

Etymology: We name *Dryopteris renchangiana* in honor of late Prof. Ren-Chang Ching (1898–1986), for his great contributions to the study of ferns. He proposed the classification system of the families and genera of the Chinese Pteridophytes, and made a revision of the Chinese and Sikkim-Himalayan *Dryopteris*.

Additional specimens examined:

CHINA. **Chongqing**: Nanchuan, *Z.Y. Liu 840758* (IMC), *Z.Y. Zuo 3496* (KUN).

Sichuan: Xuyong, *Z.Y. Zuo 3498 & 3510* (KUN).

Notes: Copeland (1910) published *Dryopteris glabrior*, but it was transferred to *Hypodematium glabrius* (Copel.) Holttum (Hassler, 2018). Ching and Liu (1984) published *D. glabrior* Ching & Z.Y. Liu based on a different specimen collected in Chongqing, which was treated as an unresolved species in *Flora of China* (Wu et al., 2013). The name *D. glabrior* Ching & Z.Y. Liu is a later homonym and is illegitimate according to Art. 53 of the Shenzhen Code (Turland et al., 2018). We collected the specimens of "*D. glabrior* Ching & Z.Y. Liu" from its type locality (Chongqing, China) and found one more population of the same species in Sichuan, China. Morphological and molecular phylogenetic studies suggest that "*D. glabrior* Ching & Z.Y. Liu" is a distinct species, and a new name is needed.

4.3. Dryopteris sinonepalensis Z.Y. Zuo & Fraser-Jenkins, nom. nov. 中尼鳞毛蕨 【*zhōng ní lín máo jué*】

Aspidium nitidulum Wallich in Num. List: no. 392 (1828), *nom. nud.*;

Fig. 3. *Dryopteris renchangiana* Z.Y. Zuo & D.Z. Li. A. Habitat and well-developed fronds. B. Sori on ultimate pinnules. C. Rhizome.

Aspidium nitidulum Wallich ex Kuhn in Linnaea 36: 117 (1869), *nom. illeg.*; Non *A. nitidulum* (C.Presl) Kunze ex Mett. in Pheg. u. Asp. 105, n.249c (1858), Basionym: *Nephrodium nitidulum* C.Presl in Epimel. Bot. 46 (1851). Type: PHILIPPINES. 1849. *Hugh Cuming, s.n.* (Type BM001045024 & PRC450276);

Lastrea sparsa var. *nitidula* Beddome in Suppl. ferns S. Ind, 17, pl. 374 (1876);

Nephrodium sparsum var. *nitidulum* (Beddome) C.B. Clarke in Trans. Linn. Soc. Lond. II (Bot.) 1: 524 (1880);

Dryopteris sparsa subsp. *nitidula* (Beddome) C. Chr. in Index flic, 293 (1905);

Dryopteris sparsa var. *nitidula* (Beddome) Ching in Bull. Fan Mem. Inst. Biol (Bot.) 8: 472 (1938);

Dryopteris nitidula (Wall. ex Kuhn) Mitsuta et S.K. Wu in Vasc. Pl. Hengduan Mount. 1: 131 (1993), *nom. illeg.* Non *Dryopteris nitidula* (C.Presl) Kuntze in Revis. Gen. Pl. 2: 813 (1891) (Basionym: *N. nitidulum* C.Presl).

Type: NEPAL. **Nagarjum**, 1821, *Wallich 392* (Lectotype K001109948) (selected by Fraser-Jenkins, 1989).

Distribution and habitat: Montane forest, on the ground at alt. 2000–3000 m in the Himalaya and the Hengduan Mountains.

Notes: Two specimens collected from Tibet (Xizang) and Yunnan were initially identified as *Dryopteris yoroii*. However, the characteristics of these two samples were obviously different from those of the holotype of *D. yoroii* and other specimens from the type locality (Taiwan). After checking and comparing more specimens and records (including the lectotype of *D. sparsa* subsp. *nitidula* and the holotype of *D. yoroii*), we concluded that the two specimens are not truly *D. yoroii*. *Dryopteris nitidula* (Wall. ex Kuhn) Mitsuta et S.K. Wu is a later homonym of *D. nitidula* (C.Presl) Kuntze and is therefore illegitimate. In this case, a new name, *D. sinonepalensis* is proposed here as the lectotype of the substituted name was collected from Nepal, but widely distributed in Southwest China. The scale color is one of key characters to distinguish *D. sinonepalensis* and *D. yoroii*. However, the scales easily fall off and are rarely present on specimens, and we are usually unable to find complete scales on specimens, leading to confusion and misidentification of many specimens of *D. sinonepalensis* and *D. yoroii*. The descriptions of *D. yoroii* in *Flora Reipublicae Popularis Sinicae* (Wu and Lu, 2000) and *Flora of China* (Wu et al., 2013) may be partly based on specimens of *D. sinonepalensis* as they mentioned the fronds are usually dimorphic. The cytotype of one sample (*Z.R. Wang & Z.X. Zhang C188*) of *D. sinonepalensis* was reported as sexual diploid (Wang and Zhang, 1981).

Additional specimens examined:

CHINA. **Chongqing**: Youyang, *Z.Y. Liu 6720, 6976 & 6978* (IMC). **Sichuan**: Chongzhou, *W.B. Ju & D.K. Chen AZH00521* (CDBI). Meishan, *Z.R. Wang* et al. *519* (PE), *Z.R. Wang & Z.X. Zhang C188* (PE),

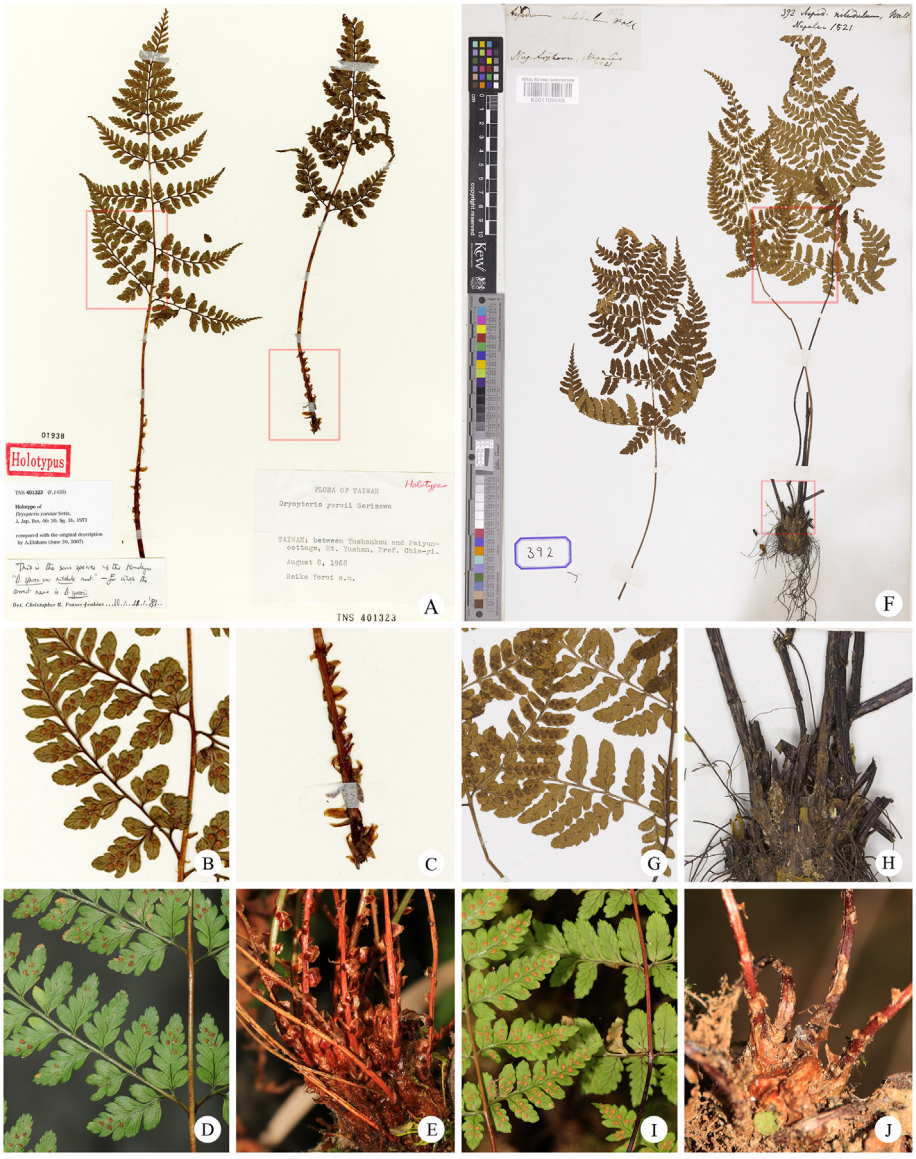

Fig. 4. Comparison of *Dryopteris yoroii* (Holotype: A, B & C; *Z.Y. Zuo, 1857*: D & E) and *D. sinonepalensis* (Lectotype: F, G & H; *Z.Y. Zuo 1331*: I & J). A & F. Overview. B, D, G & I. Sori on ultimate pinnules. C, E, H & J. Scales on stipe base.

K.J. Guan et al. *2695* (PE); Hanyuan, *X.X. Kong 3928 & 4081* (PE). Shimian, *L.B. Zhang 523* (CDBI). **Tibet (Xizang)**: Mêdog, *S.Y. Dong & Z.Y. Zuo DZ5281* (IBSC, KUN). **Yunnan**: Daguan, *W.M. Chu 5255* (PE, PYU); Lijiang, *W.M. Chu 23,153* (HGAS, PYU), *K.M. Feng 2630 & 9499* (PE), *Z.Y. Zuo 3330* (KUN); Mengzi, *W. Hancock 20* (PE); Yangbi, *Jinshajiang Team 4298* (PE, PYU), *Z.Y. Zuo 1331* (KUN); Yingjiang, *Z.Y. Zuo 1289* (KUN).

Nepal, **Makawanpu**r: Daman, *Fraser-Jenkins* 29,111 (FN 5086) (BM).

4.4. Dryopteris yoroii Serizawa, J. Jap. Bot. 46: 20. 1971. 栗柄鳞毛蕨 【*lì bǐng lín máo jué*】

Type: CHINA. **Taiwan**: between Yushankou and Paiyun cottage, Mt Yushan, 8 August 1968, *Reiko Yoroi s.n.* (Holotype TNS401323).

Distribution and habitat: Montane forest, growing on wet cliffs or on the ground above the tree line (2900–3500 m) of the Himalaya to the Hengduan Mountains, and Taiwan Island.

Notes: The distribution of *Dryopteris yoroii* has the highest altitude of all species in *D.* sect. *Diclisodon*. The sample of *D. yoroii* from Yunnan (*S.K. Wu* et al. *64*) was reported as an apomictic diploid (Xiang et al., 2006).

Additional specimens examined:

CHINA. **Sichuan**: Hanyuan, *X.X. Kong 3965* (PE); Meishan, *Z.Y. Zuo 3397* (KUN). **Taiwan**: Hualien, *C.M. Kuo 428* (TAI); Nantou, *W.T. Liou 552* (TNU). Tibet (Xizang): Mêdog, *Z.Y. Zuo 2519 & 2566* (KUN); **Yunnan**: Gongshan, *DLJ2019040* (KUN), *DLJ-ET 2240* (PE), *S.K. Wu* et al. *64* (KUN), *Z.Y. Zuo 1857* (KUN).

INDIA. **Sikkim**: Yakla, *C.B.Clarke 9876* (BM).

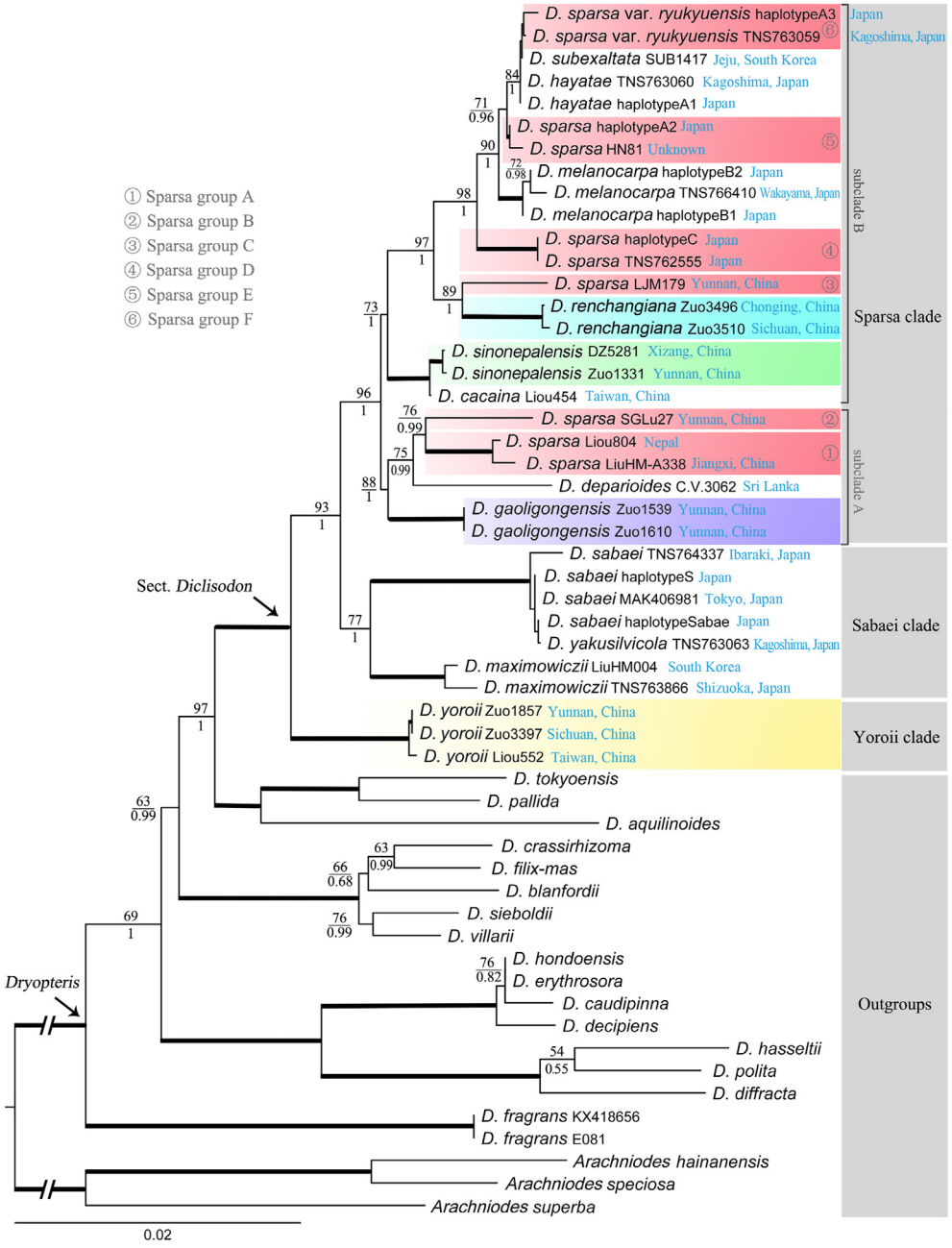

Fig. 5. ML phylogeny of *Dryopteris* sect. *Diclisodon* based on nine plastid regions. ML bootstrap support (MLBS) values and the posterior probabilities of Bayesian inference (BIPP) are indicated near nodes, with MLBS over the branches and BIPP under the branches. The thickened branch indicates 100% MLBS and 1.00 PP.

Key to species of *Dryopteris* sect. *Diclisodon* in China

1a Pinnae caudate-acuminate; indusia irregularly lacerate. ***D. subexaltata***
1b Pinnae acuminate; indusia entire.
2a Rhizome creeping.
3a Basal pinnae bipinnate to tripinnatifid. ***D. renchangiana***
3b Basal pinnae tripinnate to 4-pinnate. ***D. gaoligongensis***
2b Rhizome erect to ascendent.
4a Stipe scales bicolorous: brown with pale edge. ***D. yoroii***
4b Stipe scales concolorous: pale brown or brown.
5a Stipe and rachis brown to castaneous.
6a Fronds slightly dimorphic, pinnae with short stalks. ***D. sinonepalensis***
6b Fronds monomorphic, pinnae with distinct stalks. ***D. cacaina***
5b Stipe mostly stramineous, at least in middle to upper part, only brown in lower part.
7a Basal pinnae bipinnatifid to bipinnate. ***D. sparsa***
7b Basal pinnae bipinnate to tripinnatifid. ***D. melanocarpa***

Dryopteris polita was included in *D.* sect. *Nephrocystis* in *Flora of China* (Wu et al., 2013). A recent molecular phylogenetic study

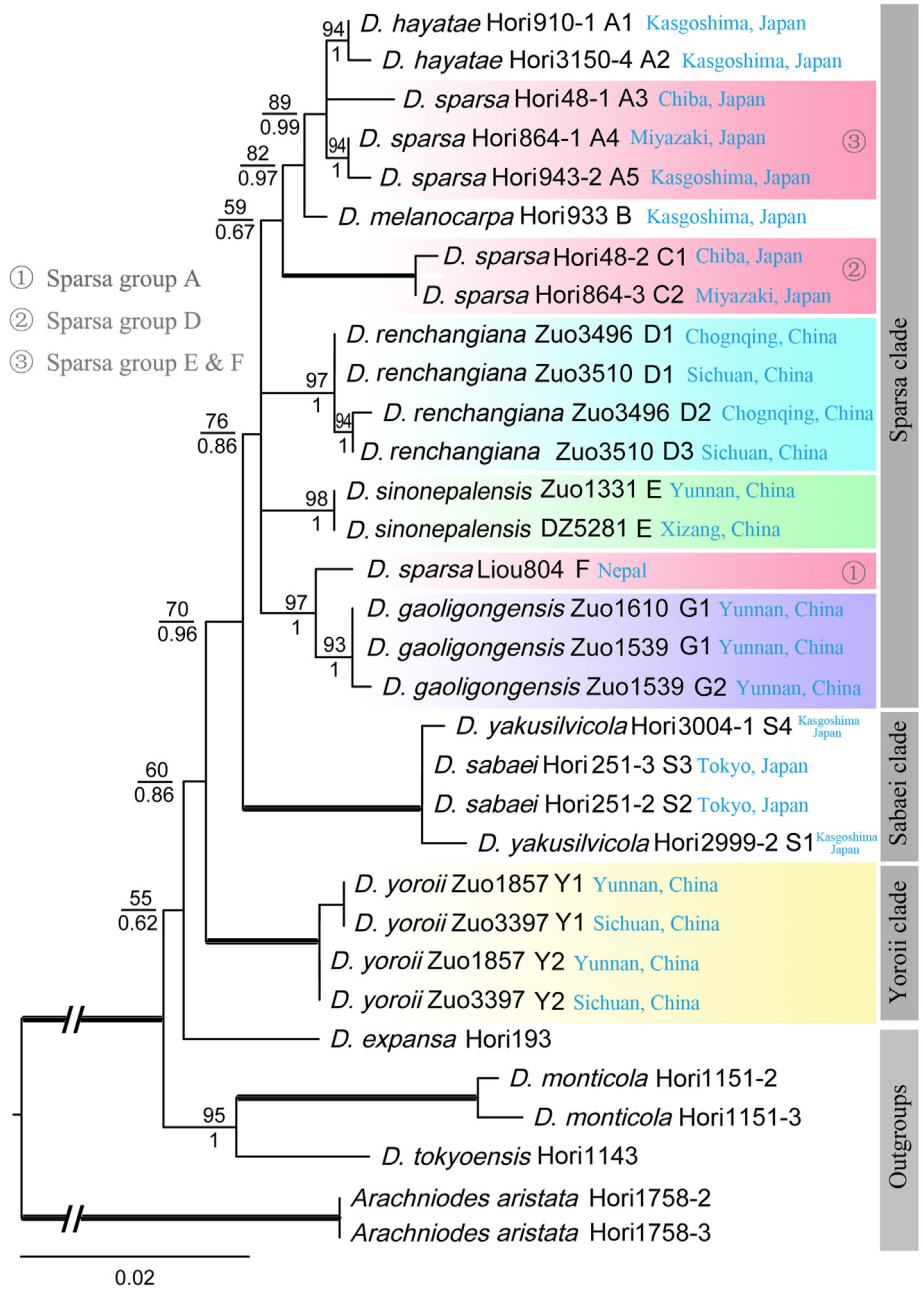

Fig. 6. ML phylogeny of *Dryopteris* sect. *Diclisodon* based on nuclear gene *AK1*. ML bootstrap support (MLBS) values and the posterior probabilities of Bayesian inference (BIPP) are indicated near nodes, with MLBS over the branches and BIPP under the branches. The thickened branch indicates 100% MLBS and 1.00 PP.

(Zhang et al., 2012) and our phylogeny suggest that it should be excluded from *D.* sect. *Diclisodon*.

5. Conclusion

In this study, we proposed three nomenclatural novelties in *Dryopteris* sect. *Diclisodon*: a new species, *D. gaoligongensis*; and two newly recognized species with new names, *D. renchangiana* and *D. sinonepalensis*. Our findings lead us to recommend that rhizome morphology be taken into account and more carefully recorded in future specimen collection of *Dryopteris*. We reconstructed the first phylogeny of *D.* sect. *Diclisodon* using combined sequence data of plastid regions and the nuclear *AK1* gene. Our phylogeny implies that *D. sparsa* is a complex group that contains many genotypes. Future research on *D.* sect. *Diclisodon* should take an integrative approach that includes both morphological observation and molecular phylogeny based on a greater number of species, especially those from the *D. sparsa* complex.

Author contributions

ZYZ and DZL designed research. ZYZ, TZ, and YX collected the materials. ZYZ, and DXY analyzed data. ZYZ, JML, DZL, as well as TZ, DXY wrote the paper.

Declaration of competing interest

The authors declare no competing interests.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2021.09.005.

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