

SYSTEMATICS AND PHYLOGENY

Toward a new circumscription of the twinsorus-fern genus *Diplazium* (Athuriaceae): A molecular phylogeny with morphological implications and infrageneric taxonomy

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Abstract *Diplazium* and allied segregates (*Allantodia*, *Callipteris*, *Monomelangium*) represent highly diverse genera belonging to the lady-fern family Athuriaceae. Because of the morphological diversity and lack of molecular phylogenetic analyses of this group of ferns, generic circumscription and infrageneric relationships within it are poorly understood. In the present study, the phylogenetic relationships of these genera were investigated using a comprehensive taxonomic sampling including 89 species representing all formerly accepted segregates. For each species, we sampled over 6000 DNA nucleotides of up to seven plastid genomic regions: *atpA*, *atpB*, *matK*, *rbcL*, *rps4*, *rps4-trnS* IGS, and *trnL* intron plus *trnL-trnF* IGS. Phylogenetic analyses including maximum parsimony, maximum likelihood and Bayesian methods congruently resolved *Allantodia*, *Callipteris* and *Monomelangium* nested within *Diplazium*; therefore a large genus concept of *Diplazium* is accepted to keep this group of ferns monophyletic and to avoid paraphyletic or polyphyletic taxa. Four well-supported clades and eight robust subclades were found in the phylogenetic topology. Reconstruction of the evolutionary pattern of morphological characters, such as dissections of leaves, petiole/rachis scales, and shapes of sori, recovered some character combinations of systematic value for infrageneric classification. In light of morphological characters and our molecular phylogeny, a re-defined *Diplazium* and an infrageneric classification are proposed.

Keywords *Allantodia*; *Callipteris*; *Diplazium*; molecular phylogeny; *Monomelangium*; morphological character evolution; subgeneric classification

Supplementary Material The alignment file is available in the Supplementary Data section of the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

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■ INTRODUCTION

The twinsorus-fern genus *Diplazium* Sw. is the most species-rich lineage of the lady-fern family Athuriaceae (Christenhusz & al., 2011). There are about 350 to 400 species placed either in a single broadly defined genus *Diplazium* (Christensen, 1906; Kato, 1977) or in two to seven segregate genera (e.g., Tryon & Tryon, 1982; Kramer & Kato, 1990; Wu & Ching, 1991; Z.-R. Wang, 1997; Chu & He, 1999; Pacheco & Moran, 1999; M.-L. Wang & al., 2004). This group of ferns has a pantropical distribution with species diversity mainly harbored in Malesia (ca. 70%) and the Neotropics (ca. 25%; Tryon & Tryon, 1982; Pacheco & Moran, 1999; Mickel & Smith, 2004), and less than 5% in the Afromadagascan region (Roux, 2009) and Australia (Jones, 1998) (Fig. 1A–G). Most species are distributed in tropical and subtropical climates, but few species have been found in cold-temperate to even arctic regions in Eurasia (Tryon & Tryon, 1982; Wu & Ching, 1991; Chu & He, 1999). Plants are mainly terrestrial,

growing in humid lowland to high mountain forests and occasionally on limestone rocks.

Generic delimitation of *Diplazium* has been a subject of strong controversy among pteridologists (Ching, 1964, 1978; Kato, 1977; Mickel, 1979; Tryon & Tryon, 1982; Lellinger, 1985; Kramer & Kato, 1990; Chu & He, 1999; Pacheco & Moran, 1999). *Diplazium* has been widely accepted as a natural group due to shared characters such as base chromosome number ($x = 41$) and the linear single or double sori (called diplazioid sori; Swartz, 1801; Christensen, 1906; Kato, 1977; Kramer & Kato, 1990; but see Copeland, 1947; Holttum, 1954), whilst several allied genera, such as *Allantodia* R. Br. (Brown, 1810: 149), *Callipteris* Bory (Bory, 1804), *Diplaziosis* C. Chr. (Christensen, 1906), *Monomelangium* Hayata (Hayata, 1928), and *Rhachidosorus* Ching (Ching, 1964), have been disputed (Christensen, 1906; Ching, 1964; Kato, 1977; Pichi-Sermolli, 1977; Pacheco & Moran, 1999). Ching (1964) separated *Allantodia* from *Diplazium* mainly based on characters such as the non-imparipinnate fronds and continuous

grooves from rachis to costa. Chu & He (1999) revised the subgeneric classification of *Allantodia* with three sections and ten series. More recently, Pacheco & Moran (1999) resurrected *Callipteris* in their revision of the Neotropical species, and found diagnostic characters such as anastomosing veins and petiole/rachis scales with bifid-toothed margins. However, they hesitated to extend their revision to a global scale because of the lack of taxonomic studies of Old World representatives, especially of the exclusively Paleotropical type of the genus, *Diplazium* (*Callipteris*) *proliferum* (Lam.) Thouars. Plants of the monotypic *Monomelangium* show a unique combination of morphological characters including *Asplenium*-like linear sori, multicellular hairs on both petiole and rachis, and spores with a unique ornamentation described as trichomanoid or hairlike (Ching, 1964; Q.-X. Wang & al., 1997). However, several authors interpreted these unique features as part of the variation of a broadly defined *Diplazium* (Kato, 1973; 1977; Tryon & Lugardon, 1991). This interpretation appeared to be consistent with the result of a molecular systematic study (Sano & al., 2000a), but the evidence provided in that study was considered ambiguous due to the lack of bootstrap values above 50% at several critical nodes. A later phylogenetic study (M.-L. Wang & al., 2003) suggested that *Allantodia*, *Callipteris* and *Monomelangium* were nested within *Diplazium*. Up to the present, studies of the lady ferns confirmed that *Diplaziopsis* and *Rhachidosorus* were well resolved as distinct lineages in eupolypods II (Sano & al., 2000a; Wei & al., 2010; Christenhusz & al., 2011; Kuo & al., 2011; Rothfels & al., 2012a, b; also see Li & al., 2011), which refuted previous suggestions about the close relationship between them (Kato, 1977; Kramer & Kato, 1990; M.-L. Wang & al., 2003, 2004). However, exact relationships among the remaining genera (including *Allantodia*, *Callipteris*, *Diplazium* and *Monomelangium*) stayed unclear.

The uncertainty about generic classification without doubt was caused by different interpretations of the observed morphological diversity. Some characters considered to be informative to discriminate genera may not be informative. It has been argued for other groups of ferns that frequent homoplasy and the usage of plesiomorphic character states resulted in instable generic classifications (Hovenkamp, 1996; Schneider & al., 2009). For example, *Allantodia* was distinguished from *Diplazium* by the pinnatifid leaf apex contrasting with undivided apical pinnae (Ching, 1964; Chu & He, 1999). However, this character is rather unstable, and several species of *Diplazium* from East and Southeast Asia (*Diplazium pinfaense* Ching or *D. lobatum* (Tagawa) Tagawa) also have pinnatifid leaf apices (Kato, 1977; Tryon & Tryon,

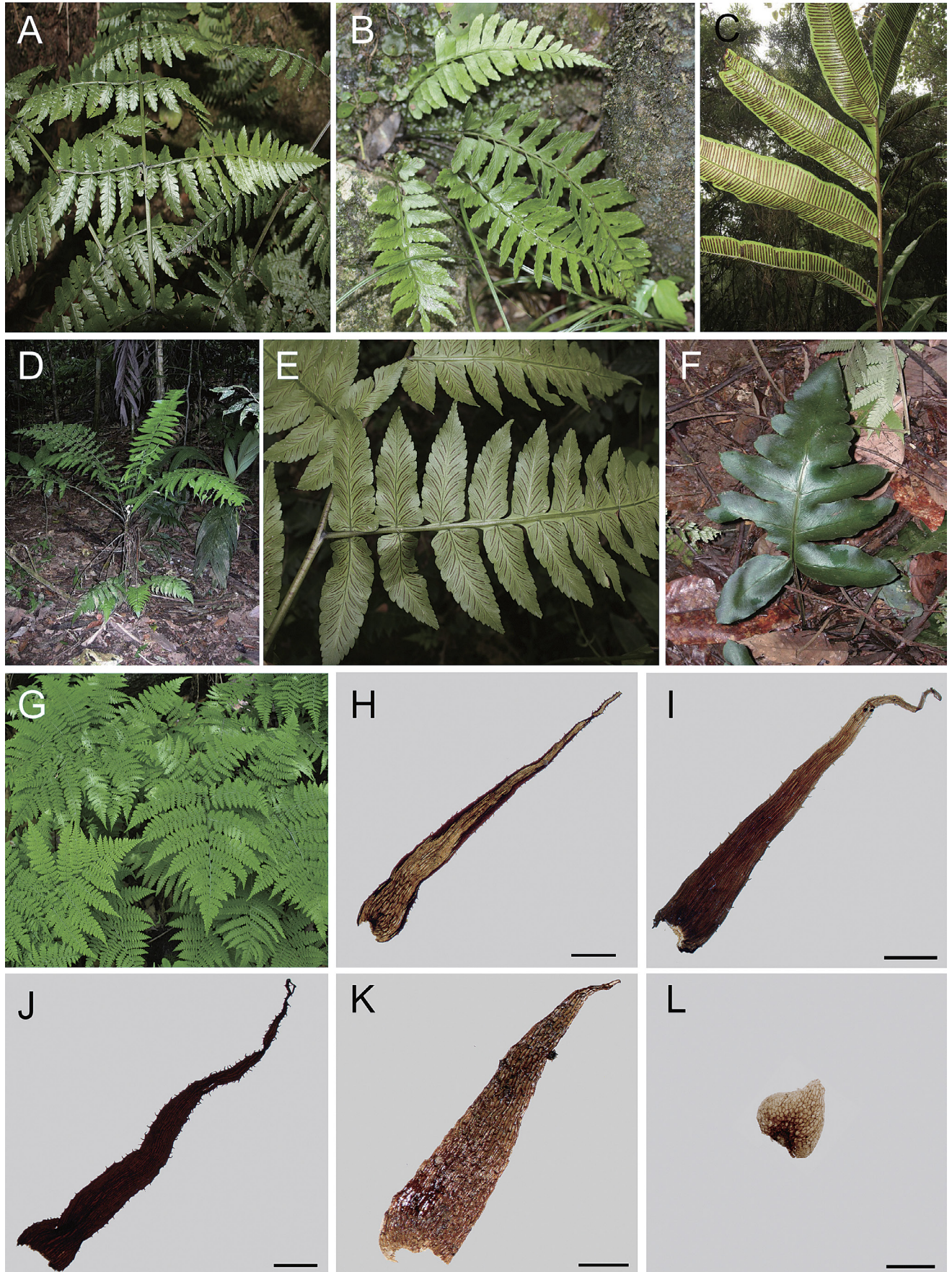
1982). In contrast to leaf morphology, scales on rhizomes and petioles were often ignored in the taxonomy of Athyriaceae. However, scales were considered to be one of the two key characters defining *Callipteris* (Pacheco & Moran, 1999). Unlike other members of Athyriaceae, rhizome/petiole scales of *Diplazium* present a notable disparity in shape, marginal structure and color. The shape of scales varies from lanceolate (Fig. 1H–K) to ovate (Fig. 1L), while the color of scales was found to be either concolorous (Fig. 1I–L) or bicolorous (Fig. 1H), i.e., bicolorous scales with two thickened marginal strands. The margins of scales also vary in the presence or absence of marginal teeth as well as the micromorphology of these teeth, e.g., bifid teeth. High rates of morphological divergence are a challenge to morphology-based classification because some of this variation originated by parallel evolution whereas other characters are apomorphic (Hovenkamp, 1996; Schneider & al., 2009). The problem was, however, to identify the apomorphic characters.

As a result, previous studies of *Diplazium* were inadequate not only due to poor analyses of morphological characters with systematic value, but also due to scant species sampling. For example, only seven out of 350 species were sequenced respectively in Sano & al. (2000a) and M.-L. Wang & al. (2003), and ten taxa were sampled in Schuettpelz & Pryer (2007). Therefore, a DNA sequence based phylogenetic study was designed to uncover the relationships between *Diplazium* and putative segregates such as *Allantodia*, *Callipteris*, and *Monomelangium*. To address arguments about generic delimitation, the evolution of taxonomically important morphological characters was reconstructed using the obtained phylogenetic framework. Besides erecting a natural circumscription of *Diplazium*, we also addressed questions concerning the infrageneric classification of the redefined genus.

■ MATERIALS AND METHODS

Taxon sampling and molecular data. — Ninety ingroup taxa representing eighty-nine species were sampled including representatives of the four genera (*Allantodia*, *Callipteris*, *Diplazium*, *Monomelangium*) accepted by some authors (Ching, 1964, 1978; Kato, 1977; Z.-R. Wang, 1997; Chu & He, 1999; M.-L. Wang & al., 2004). The sample included the type, i.e., *Callipteris prolifera* (Lam.) Bory (= *Diplazium proliferum* (Lam.) Thouars), *Diplazium plantaginifolium* (L.) Urb. (neotype designated by Proctor, 1985), and *Monomelangium hancockii* (Maxim.) Hayata (synonym of *Monomelangium pullingeri* (Baker) Tagawa, *Diplazium pullingeri* (Baker) J. Sm.).

Fig. 1. Diversity in leaf shape and scale morphology in *Diplazium*. Information in brackets are photographers or vouchers. **A**, *Diplazium bellum* [R. Wei]; **B**, *D. heterocarpum* [X.-C. Zhang]; **C**, *D. lechleri* [R.C. Moran]; **D**, *D. striatum* (syn.: *D. striatastrum*) [R.C. Moran]; **E**, *D. simile* [Z.-Y. Li]; **F**, *D. pinnatifidum* [R.C. Moran]; **G**, *D. sibiricum* var. *sibiricum* [R. Wei]; **H**, bicolorous and toothed scale of *D. dilatatum* [China: Yunnan, Z.-R. Wang 567 (PE)]; **I**, concolorous brown and toothed scale of *D. squamigerum* [China: Henan, D0479 (PE)]; **J**, concolorous black and toothed scale of *D. crassiusculum* [China: Zhejiang, C.-F. Zhang 9156 (PE)]; **K**, concolorous brown and entire scale of *D. wichurae* var. *wichurae* [China: Anhui, 5310 (PE)]; **L**, concolorous and entire scale of *D. muricatum* [China: Yunnan, 11552-2 (PE)]. — Scale bars = 1 mm.



Since Brown (1810) did not designate the type for *Allantodia*, we here accept that the type was designated by Ching (1964) as *Allantodia australis* R. Br. (= *Diplazium australe* (R. Br.) N.A. Wakef.). Moreover, our sampling covered all parts of the distribution range of the four genera including the Paleotropics and Neotropics. Of the Neotropical species, we sampled representatives of all morphological groups recognized by Tryon & Tryon (1982) and also took into consideration most recent treatments (Stolze, 1981; Proctor, 1985; Tryon & Stolze, 1991; Stolze & al. 1994; Pacheco & Moran, 1999; Mickel & Smith, 2004). With *Diplazium (Callipteris) proliferum*, we included the most critical of the Afromadagascan *Diplazium* species because it is the type of the segregate *Callipteris* (Pacheco & Moran, 1999). The majority of Afromadagascan species appear to resemble Asian species of *Diplazium* or also occur in Asia. Also, the Afromadagascar region harbors only 17 species in total (Roux, 2009). The sample also comprised eight species from the remaining four genera of Athyriaceae: *Anisocampium* C. Presl, *Athyrium* Roth, *Cornopteris* Nakai, and *Deparia* Hook. & Grev. (Sano & al., 2000a, b; M.-L. Wang & al., 2003, 2004; Y.-C. Liu & al., 2011). They were treated as part of the ingroup. As for outgroup taxa, we included representatives from eupolypods II known to be closely related to Athyriaceae: Aspleniaceae were represented by *Asplenium* L. and *Hymenasplenium* Hayata, Blechnaceae by *Blechnum* L. and *Woodwardia* Sm., Cystopteridaceae by *Cystopteris* Bernh. and *Gymnocarpium* Newman, Diplaziopsidaceae by *Diplaziopsis*, Onocleaceae by three species of *Onoclea* L. as defined in Christenhusz & al. (2011) and including *Matteuccia* Tod. and *Pentarhizidium* Hayata, Thelypteridaceae by *Thelypteris* Schmidel, and Woodsiaceae by *Woodsia* R. Br. The most recent studies of the phylogeny of eupolypods II (Schuettpehlz & Pryer, 2007; Kuo & al., 2011; Lehtonen, 2011; Rothfels & al., 2012b) were taken into consideration when selecting our outgroup taxa.

DNA sequence data were sampled for up to seven plastid DNA markers including five coding regions, *atpA*, *atpB*, *matK*, *rbcL*, *rps4*, and two non-coding regions *rps4-trnS* intergenic spacer (IGS) and *trnL* intron plus *trnL-trnF* IGS. For simplification, the *rps4* gene together with *rps4-trnS* IGS will be called *rps4-trnS* and the *trnL* intron plus *trnL-trnF* IGS will be called *trnL-F* throughout this paper. Besides the newly generated 466 sequences, 108 DNA sequences were downloaded from GenBank at the National Centre for Biotechnology Information (<http://www.ncbi.nlm.nih.gov>). All newly generated sequences were deposited at GenBank (Appendix 1).

DNA isolation, amplification and sequencing. — Total genomic DNA was extracted from silica gel-dried leaves (Chase & Hills, 1991) or fresh tissue using the Plant Genomic DNA Kit (Tiagen Biotech, Beijing, China) following the manufacturer's instructions, or using the modified cetyltrimethyl-ammonium-bromide (CTAB) procedure (Doyle & Doyle, 1987). All seven plastid DNA regions were amplified separately with standard polymerase chain reaction (PCR). The *atpA* and *atpB* regions were amplified following the primers (Table 1) and procedure reported in Schuettpehlz & al. (2006) and Schuettpehlz & Pryer (2007). The *rbcL* region was amplified using primers 1F and 1351R, following the PCR protocol outlined in Hasebe & al. (1994). The *matK* region was amplified using primers and PCR protocols introduced by the CBoL Plant Barcoding Working Group (http://www.barcodinglife.org/index.php/Public_Primer_PrimerSearch). The *rps4-trnS* region was amplified following Nadot & al. (1995) and Smith & Cranfill (2002). The *trnL-F* region was amplified using the primers and PCR protocol described in M.-L. Wang & al. (2003). Successful DNA amplification was verified by running aliquots of the PCR product on a 1% agarose gel in TAE buffer. All PCR products were purified using PEG8000 or TIANgel Midi Purification Kit (Tiagen Biotech) following the manufacturer's protocol, and were then directly

Table 1. List of primers used for DNA amplification and sequencing.

DNA region	Primer name	Sequence (5'–3')	Source
<i>atpA</i>	ESATPF412F	GARCARGTTCGACAGCAAGT	Schuettpehlz & al., 2006
	ESTRNR46F	GTATAGGTTTCRARTCCTATTGGACG	Schuettpehlz & al., 2006
<i>atpB</i>	ESATPB172F	AATGTACTTGTGAAGTWCAACAAT	Schuettpehlz & Pryer, 2007
	ESATPE45R	ATTCCAAACWATTTCGATTWGGAG	Schuettpehlz & Pryer, 2007
<i>matK</i>	PolypodF1	ATTTYTGARGAYAGAYTDCC	CBoL Plant Barcoding Working Group
	PolypodR1	CGTRGTATATATCTCRATYTACGC	CBoL Plant Barcoding Working Group
<i>rbcL</i>	1F	ATGTCACCACAAACAGAGACTAAAGC	Hasebe & al., 1994
	1351R	GCAGCAGCTAGTTCGGGCTCCA	Hasebe & al., 1994
	<i>rbcLsF</i>	ATCCAGCCATTCATGCGT	This study
<i>rps4-trnS</i>	F	ATGTCCTGTTATCGAGGACCT	Nadot & al., 1995
	R	TACCGAGGGTTCGAATC	Smith & Cranfill, 2002
<i>trnL-F</i>	c	CGGAATTGGTAGACGCTACG	M.-L. Wang & al., 2003
	f	ATTGAACTGGTGACACGAG	M.-L. Wang & al., 2003

sequenced using BigDye chemistry with an ABI 3730XL genetic analyzer (Applied Biosystems, Foster City, California, U.S.A.). A newly designed internal primer *rbcLsF* was added to the sequencing reaction of the *rbcL* region, but otherwise the same primer sets were employed for DNA amplification and sequencing. Sequence data were edited and assembled in the ContigExpress program of the Vector NTI Suite v.6.0 (Informax, North Bethesda, Maryland, U.S.A.). Newly obtained combined with downloaded sequences were assembled in single-region datasets that were aligned using CLUSTAL X v.1.83 (Thompson & al., 1997) followed by manual adjustment in BioEdit v.7.1.11 (Hall, 1999) and Mesquite v.2.7.5 (Maddison & Maddison, 2011). An ambiguously aligned string of polyA-bases was visually detected in the *rps4-trnS* region and excluded from all phylogenetic analyses. No further ambiguously aligned regions and inversions were detected in the visual inspection of the alignments. Compatibility of the chloroplast regions was explored by visual comparison of the bootstrap consensus trees obtained from independent maximum parsimony analyses (see below for the procedure) of each region. Bootstrap values of similar nodes less than 75% were not considered as incongruent among DNA markers (Mason-Gamer & Kellogg, 1996). In the absence of evidence for conflicting nodes, all data were assembled in a single combined dataset.

Phylogenetic analyses. — Maximum parsimony (MP), maximum likelihood (ML) and Bayesian inference (BI) phylogenetic reconstructions were performed for each region separately and a combined DNA dataset including all regions. MP analyses were carried out using PAUP* v.4.0b10 (Swofford, 2002). All characters were weighted equally and gaps were treated as missing data. The most parsimonious trees were obtained with heuristic searches of 1000 replicates with random stepwise sequence addition (RAS), tree bisection-reconnection (TBR) branch swapping, and 10 trees from each random sequence addition were saved. MP bootstrap values (BS_{MP}) were calculated with 1000 replicates with simple sequence addition, TBR branch swapping, and 10 trees saved per replicate.

For the ML analysis, two partitions were recognized within the combined dataset representing coding and non-coding regions. We employed jModelTest v.0.11 (Posada, 2008) that uses PhyML for ML tree-searches (Guindon & Gascuel, 2003) to determine the appropriate DNA substitution model, rate of invariable sites, and gamma rate heterogeneity according to the Akaike information criterion (AIC; Akaike, 1974). ML trees were generated by performing a rapid bootstrap analysis on the RAxML web-server (Stamatakis & al., 2008) with the selected GTR+I+ Γ model for both partitions. All parameter values for tree search were calculated using our selected settings. After the rapid bootstrap search step, ML bootstrap values (BS_{ML}) of each node were checked in FigTree v.1.4 (Rambaut, 2012).

The BI analysis was performed in MrBayes v.3.2.1 (Huelsenbeck & Ronquist, 2001; Ronquist & al., 2012) based on the best model (GTR+I+ Γ) for both partitions suggested by the Bayesian information criterion (BIC; Schwarz, 1978) implemented in jModelTest. Four chains were run, each for

1,000,000 generations, and were sampled every 1000 generations, with a random starting tree. The convergence of runs and estimation of burn-in were checked using Tracer v.1.5 (Rambaut & Drummond, 2009). Bayesian Posterior Probabilities (PP_{BI}) were calculated for the majority consensus tree of all sampled trees after discarding trees sampled within the burn-in phase in MrBayes v.3.2.1.

Chromosome counts. — A single specimen of *Diplazium* (*Allantodia*) *bellum* (C.B. Clarke) Bir (Appendix 1) was examined cytologically. Observations of somatic chromosomes followed the protocols given in R.-X. Wang & Lu (2008). Juvenile pinnae were pretreated with a 1 : 1 solution of 0.002 M 8-hydroxyquinoline and 0.2% colchicine for 4 h at about 20°C. After fixation in 45% acetic acid at 4°C for 20 min, the pinnae were hydrolyzed in 60°C 1 M HCl for 20 s. The tissues were stained with a solution of 10% carbol-fuchsin for 5 min and directly squashed after rinsed with distilled water.

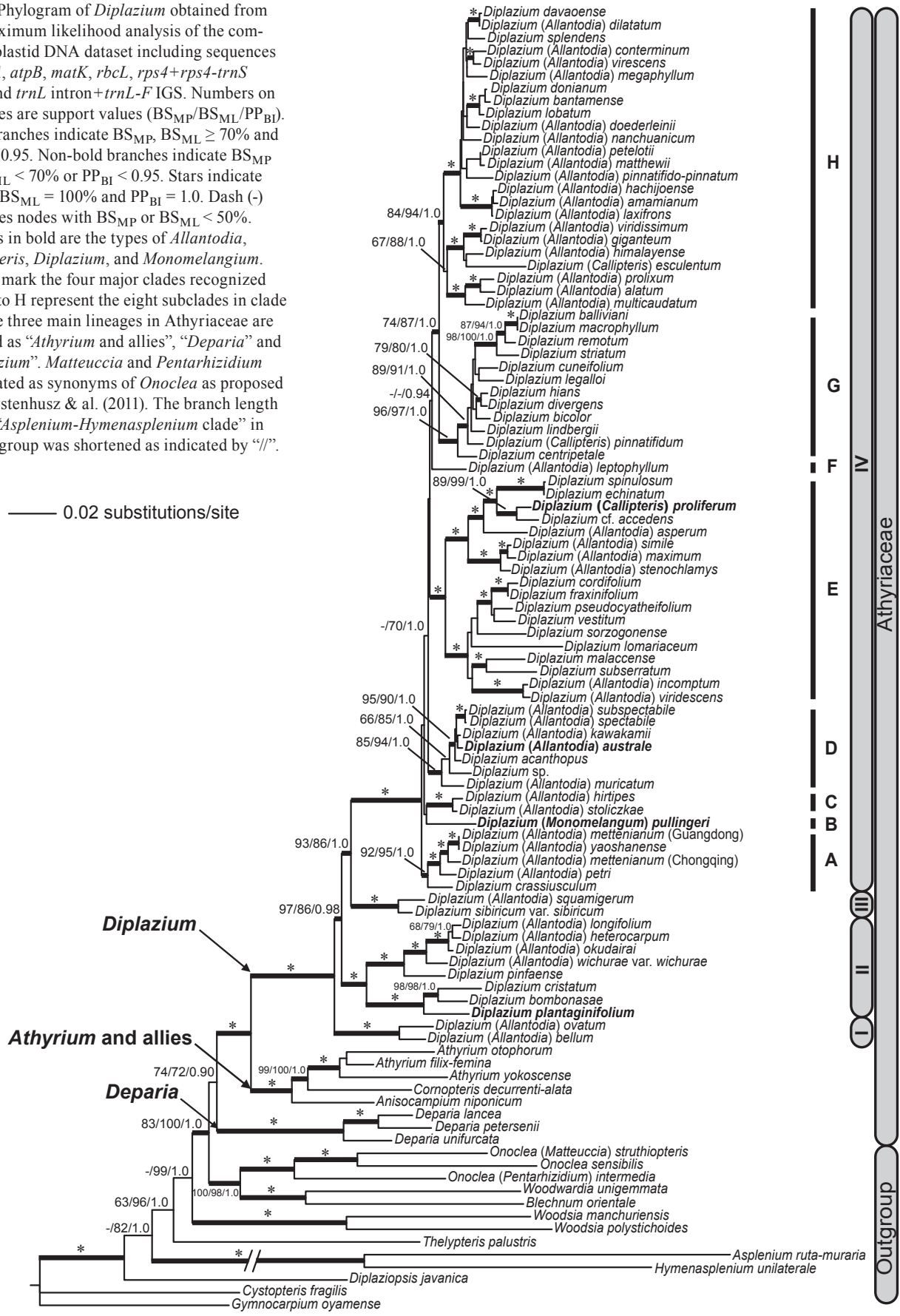
Morphological character evolution. — The data employed for the reconstruction of the evolution of morphological characters were obtained from publications (Ching, 1964; Kato, 1977; Tryon & Tryon, 1982; Chu & He, 1999; Pacheco & Moran, 1999) and our own observations of morphological character variation using herbarium specimens held at PE or NY. In addition, we considered observations made during fieldwork. All characters were scored as discrete binary or multistate characters (Appendix 2). Among these characters, particular care was given to the observation of color and margin of scales from the basal part of the petiole. Characters were selected because they were either considered to be diagnostic in previous taxonomic treatments or were considered as putative apomorphic character states for the recovered clades.

The evolution of morphological characters was reconstructed with likelihood and parsimony methods implemented in Mesquite v.2.7.5 (Maddison & Maddison, 2011). All characters were treated as unordered and equally weighted. Missing data were coded as unknown. To reconstruct character evolution, a maximum likelihood approach using Markov k-state 1 parameter model (Mk1; Lewis, 2001) was used. To account for phylogenetic uncertainty, the “Trace-characters-over-trees” command was used to calculate ancestral states at each node including probabilities in the context of likelihood

Table 2. Descriptive statistics of analyzed plastid DNA sequence data matrices.

DNA region	Aligned length	Excluded sites	Constant characters (%)	Parsimony-informative characters (%)
<i>atpA</i>	1747	0	1126 (64.5)	448 (25.6)
<i>atpB</i>	1218	0	857 (70.4)	251 (20.6)
<i>matK</i>	811	0	256 (31.6)	416 (51.3)
<i>rbcL</i>	1206	0	842 (69.8)	260 (21.6)
<i>rps4-trnS</i>	968	16	396 (40.9)	419 (43.3)
<i>trnL-F</i>	1016	0	384 (37.8)	430 (42.3)
Combined	6966	16	3859 (55.4)	2224 (31.9)

Fig. 2. Phylogram of *Diplazium* obtained from the maximum likelihood analysis of the combined plastid DNA dataset including sequences of *atpA*, *atpB*, *matK*, *rbcL*, *rps4+rps4-trnS* IGS, and *trnL* intron+*trnL-F* IGS. Numbers on branches are support values (BS_{MP}/BS_{ML}/PP_{BI}). Bold branches indicate BS_{MP}, BS_{ML} ≥ 70% and PP_{BI} ≥ 0.95. Non-bold branches indicate BS_{MP} or BS_{ML} < 70% or PP_{BI} < 0.95. Stars indicate BS_{MP}, BS_{ML} = 100% and PP_{BI} = 1.0. Dash (-) indicates nodes with BS_{MP} or BS_{ML} < 50%. Species in bold are the types of *Allantodia*, *Callipteris*, *Diplazium*, and *Monomelangium*. I to IV mark the four major clades recognized and A to H represent the eight subclades in clade IV. The three main lineages in Athyriaceae are marked as “*Athyrium* and allies”, “*Deparia*” and “*Diplazium*”. *Matteuccia* and *Pentarhizidium* are treated as synonyms of *Onoclea* as proposed in Christenhusz & al. (2011). The branch length of the “*Asplenium-Hymenasplenium* clade” in the outgroup was shortened as indicated by “//”.



reconstructions. To carry out these analyses, characters were plotted onto 900 trees that were sampled in the Bayesian analyses of the combined dataset using MrBayes v.3.2.1 with the settings: 1,000,000 generations with a sample frequency of one sample every 1000 generations, and a burn-in phase discarding the first 101 sampled trees. The results were finally summarized as percentage of changes of character states on a given branch among all 900 trees utilizing the option of “Average-frequencies-across-trees”.

■ RESULTS

The combined data matrix included up to 6966 nucleotides for each of the 101 taxa (Table 2). The three phylogenetic analyses (MP, ML, BI) unraveled congruent topologies. As for the MP analyses, the combined dataset resulted in 100 most parsimonious trees with a length of 9210 steps based on a dataset with 3859 constant characters, 2224 parsimony-informative characters, consistency index (CI) = 0.44, retention index (RI) = 0.67, and rescaled consistency index (RC) = 0.29. The optimal ML phylogram had an $-\ln L = 57102.9361$ (Fig. 2).

Diplazium together with *Allantodia*, *Callipteris* and *Monomelangium* was recovered to be monophyletic ($BS_{MP} = 100$; $BS_{ML} = 100$; $PP_{BI} = 1.00$), while the last three putative segregates were all found to be nested within *Diplazium* (Fig. 2). *Allantodia* and *Callipteris* were also polyphyletic. In total, four well-supported main clades (Fig. 2, I–IV) and eight robust subclades (Fig. 2, A–H) were resolved in our phylogenetic topology.

Main clade I was composed of two East Asian species, *Diplazium (Allantodia) bellum* and *D. (Allantodia) ovatum*

(W.M. Chu) R. Wei & X.C. Zhang ($BS_{MP} = 100$; $BS_{ML} = 100$; $PP_{BI} = 1.00$). This clade was resolved as the putative sister to the remaining clades ($BS_{MP} = 97$; $BS_{ML} = 86$; $PP_{BI} = 0.98$). Main clade II ($BS_{MP} = 100$; $BS_{ML} = 100$; $PP_{BI} = 1.00$) consisted of two subclades with high bootstrap and posterior probability values. One of these two lineages included exclusively Neotropical species (*Diplazium plantaginifolium*, *D. cristatum* (Desr.) Alston, *D. bombonasae* Rosenst., Fig. 2). Sister to the Neotropical subclade, the other subclade of main clade II comprised Asian species that were treated as belonging to either *Diplazium* or *Allantodia*. Main clade III ($BS_{MP} = 100$; $BS_{ML} = 100$; $PP_{BI} = 1.00$) comprised species mainly distributed in Laurasian temperate climate zones such as *Diplazium (Allantodia) squamigerum* (Mett.) Christ and *D. sibiricum* var. *sibiricum* (Turcz. ex Kunze) Sa. Kurata. Main clade IV ($BS_{MP} = 100$; $BS_{ML} = 100$; $PP_{BI} = 1.00$) included eight well-supported subclades that arise from a poorly resolved backbone phylogeny. Within this main clade, Neotropical species were restricted to subclade G ($BS_{MP} = 96$; $BS_{ML} = 97$; $PP_{BI} = 1.0$) while Paleotropical species composed the remaining subclades. Clade IV, the most species-rich clade, included the majority of species classified as *Allantodia*, and also the proposed segregates *Callipteris* and *Monomelangium*. *Callipteris* was found to be polyphyletic with species located in subclades E, G, and H. The sister relationships of *Monomelangium* was not robustly supported ($BS_{MP} < 50\%$, $BS_{ML} < 50\%$ and $PP_{BI} < 0.95$).

The somatic chromosome number of *Diplazium bellum* was $2n = 82$ (Fig. 3); thus, the specimens we examined was a diploid based on $x = 41$.

■ DISCUSSION

Monophyly of *Diplazium* with *Allantodia*, *Callipteris* and *Monomelangium*. — The present study provides a comprehensive analysis of the phylogeny of *Diplazium* based on a moderately dense taxon sampling by including ca. 25% of the species diversity and covering the whole geographic range and morphological diversity. Our results recovered *Diplazium* together with *Allantodia*, *Callipteris* and *Monomelangium* as a monophyletic group ($BS_{MP} = 100$, $BS_{ML} = 100$, $PP_{BI} = 1.00$), which is supported by morphological evidence such as the uninterrupted grooves of rachis and costae, diplazioid sori (the linear sori singular or paired back-to-back along the same vein with the end never J- or U-shaped crossing the vein), and the same base chromosome number ($x = 41$) (Bir, 1962; Ching, 1964; Kato, 1977; Tryon & Tryon, 1982; Kramer & Kato, 1990). Thus this lineage is easily recognized as a natural group (Kato, 1977; Tryon & Tryon, 1982; Z.-R. Wang, 1997; M.-L. Wang & al., 2004; Rothfels & al., 2012a). However, a few species previously assumed to be related to the group were not supported as close relatives in recent studies, and *Diplaziopsis-Homalosorus* (Wei & al., 2010; Christenhusz & al., 2011; Li & al., 2011) and *Rhachidosorus* (Christenhusz & al., 2011; Li & al., 2011) were excluded from Athyriaceae, and *Triblemma* transferred to *Deparia* (Sano & al., 2000b).

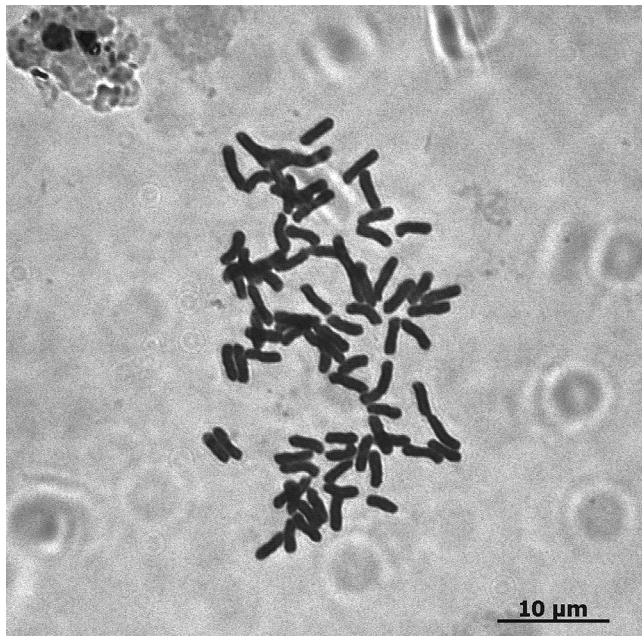


Fig. 3. Somatic metaphase chromosomes of *Diplazium bellum* ($2n = 82$). Scale bar = 10 μ m.

Generic circumscription of *Diplazium*. — Although *Diplazium* s.str. was widely accepted as the core genus of *Diplazium* s.l. (Kato, 1977; Mickel, 1979; Lellinger, 1985; Kramer & Kato, 1990), several segregates such as *Allantodia*, *Callipteris*, and *Monomelangium* were also recognized (Ching, 1964, 1978; Chu & He, 1999; Pacheco & Moran, 1999). In contrast to the monophyly of *Diplazium* s.l., the putative segregates, *Allantodia*, *Callipteris* and *Monomelangium*, were all found to be nested in *Diplazium* s.str. rendering it paraphyletic. This result is consistent with previous studies based on molecular evidence (Sano & al., 2000a; M.-L. Wang & al., 2003; Schuettpelz & Pryer, 2007; Lehtonen, 2011), although the conclusions of these studies were limited by their insufficient taxon sampling.

Given the considerably dense sampling that included many taxonomically important species, we are now in a position to re-evaluate arguments about the generic delimitation of *Diplazium*. As discussed above, our results are consistent with the concept of a broadly defined *Diplazium* s.l., and no support for the monophyly of *Allantodia* and *Callipteris* was recovered. Moreover, there were no morphological characters that could be used as diagnostic indicators allowing unequivocal assignment of species to these segregates. According to Chu & He (1999), the occurrence of flattened sori characterizes *Diplazium*, whilst tumid sori are restricted to *Allantodia*. However, our study did not provide evidence to verify this argument because the differences in sorus structure appeared to be continuous and not discrete as assumed by Chu & He (1999).

The alternative to recognizing *Diplazium* s.l., recognition of the four clades recovered, would require the introduction of two new genera and a large number of new combinations. Thus, this alternative creates taxonomic instability that should be avoided. Considering the apparent morphological and phylogenetic consistency of these four clades, we recognize them as infrageneric groups. Some potential morphological characters for distinguishing these four groups were explored. Similar cases have recently been documented when re-circumscribing large genera of ferns with high diversity including *Asplenium* (Schneider & al., 2004a), *Dryopteris* Adans. (H.-M. Liu & al., 2007; Zhang & al., 2012) and *Pteris* L. (Schuettpelz & al., 2007). Furthermore, our study of *Diplazium* may also provide insights for studies addressing the generic classification of the other two main clades of Athyriaceae, as all show similar ambiguity in the number of recognized genera. In the *Deparia* lineage, most authors tend to recognize a single genus despite considerable diversity in critical characters such as sorus morphology (Kato, 1984; Sano & al., 2000a, b). Their approach in delimiting *Deparia* is similar to our preference of a broadly defined *Diplazium*. In contrast, the most recent studies of the *Athyrium* lineage revealed arguments to recognize three genera, i.e., *Anisocampium*, *Athyrium*, and *Cornopteris* (Y.-C. Liu & al., 2011).

Phylogenetic relationships among clades within *Diplazium*. — Our study unraveled four well-supported main clades and eight robust subclades within *Diplazium* (Fig. 2).

Main clade I included two species mainly occurring in southwest China extending to Myanmar, Bhutan and India.

These two species share characters such as more or less opposite pinnae of the lower order and a single ovate-shaped sorus crossing over one vein. The sister relationship of this clade to the remaining clades appears to be supported by this sorus character which resembles the arrangement of sori found in most non-diplazioid lineages (e.g., *Deparia* and *Cornopteris*) in Athyriaceae. Although some authors regarded this clade as member of *Athyrium* (Ching, 1934), its morphological characters diverge strongly from *Athyrium* (Chu & He, 1999) with a non-inflated basal part of the petioles and a base chromosome number of $x = 41$ (Fig. 3) versus $x = 40$ in *Athyrium*. In contrast, species of this clade show consistency with *Diplazium* concerning leaf shape (Chu & He, 1999), grooves on petiole/rachis (Kato, 1977), spore morphology (Chang & al., 2001) and base chromosome number.

Species of clade II fell into two lineages representing Old World and New World elements, respectively. Auricular pinnae (Fig. 1B) are typically present in most members of this clade excluding the type of *Diplazium* (*D. plantaginifolium*) and one species of *Diplazium* occurring in east China and Japan (*D. pinfaense*). Species of this clade are further characterized by entire lanceolate scales and linear sori. In previous taxonomic studies, the placement of some species belonging to this clade is highly variable (Kurata, 1963; Smith, 1976; Tryon & Tryon, 1982; Chu & He, 1999). Tryon & Tryon (1982) suggested a group comprising the Neotropical elements of this clade but they excluded the type species as a “highly distinctive species of uncertain affinity” based only on its simple lanceolate lamina. However, the evolution of simple leaves is complex within *Diplazium* (Fig. 2), and some Asian and Neotropical lineages also comprise species with simple fronds closely related to species with a complex dissection of leaves (e.g., *D. subserratum* (Blume) T. Moore to *D. malaccense* C. Presl and *D. pinnatifidum* Kunze to *D. lindbergii* (Mett.) Christ) (Fig. 2). Thus, this character cannot be regarded as decisive for classification. Leaf dissection was also found to be misleading in the generic classification of other groups of derived ferns such as Aspleniaceae (Schneider & al., 2004) and Polypodiaceae (Ranker & al., 2004; Schneider & al., 2004; Kreier & al., 2008; Otto & al., 2009). In contrast, several morphological characters observed in the Old World species appeared to be putatively apomorphic states restricted to clade II or its subclades, such as biserrate pinnae (Chu & He, 1999) and a U-shaped groove without flat base on petioles and rachis (Kato, 1977). This suggests that more detailed taxonomic studies involving not only the Old World species but also their New World relatives (such as *D. lonchophyllum* Kunze, *D. subsilvaticum* Christ and *D. unilobum* Hieron.) are required to evaluate the consistency of these morphological characters in this clade.

The distribution of the two species of clade III ranges from temperate to boreal regions in Eurasia. Both species are deciduous as an adaptation to withstand water stress during winter periods. Kato (1977) assumed a close relationship of the species belonging to this clade and species like *Diplazium dilatatum* Blume belonging to clade IV because they share some morphological similarities, i.e., the U-shaped groove with a flat base

and non-clathrate scales. However, the results of our phylogenetic analysis revealed these similarities either as homoplastic or plesiomorphic (Fig. 2). Considering their deciduous habit and concolorous toothed scales, ovate pinnule, and variable petiolar anatomy (Ogata, 1933, 1935; Bir, 1962), we propose to treat species of this clade as a distinct subgenus in *Diplazium* (see Taxonomic treatment below).

Clade IV harbors a more diversity in morphology and distribution than any of the other clades. This clade likely contains more than 70% of the species diversity of *Diplazium*. Species in this clade were found to be separated into eight robustly supported subclades (Fig. 2, A–H). However, phylogenetic relationships among these subclades are unresolved given the weak support of the branches leading to them. Clade IV also displays a pattern of short branches connecting deeper nodes and long branches leading to tip nodes. This pattern may indicate the occurrence of an initial rapid radiation in the early history of the clade. Evidence for ancient rapid radiations has been reported for many lineages of land plants and is considered to reflect geological events and/or climatic fluctuations in the last 60 million years (e.g., Whitfield & Lockhart, 2007; Jian & al., 2008; Fiz-Palacios & al., 2011). Such rapid radiation may underlie the poor resolution of phylogenetic relationships among subclades. However, the recovered topology of clade IV exhibits some biogeographic patterns. For instance, all members belonging to subclade E are found in Southeast Asia and adjoining regions including southern China extending to various Pacific islands such as Taiwan, Fiji and Polynesia, and some species like *Diplazium proliferum* even reside in the Afromadagascan region. Subclade G was found to be restricted to the Neotropical region while its putative sister clade, subclade H, showed an Asian occurrence.

Although we are making major strides in understanding phylogenetic relationships of this widely distributed group of ferns, future studies are needed to improve species sampling in various areas including Afromadagascar, the Neotropics, and Malesia. However, our sample included representatives of all groups that were suggested to reflect the morphological divergence of *Diplazium* in the New World (Tryon & Tryon, 1982). Our sample, therefore, likely reflects the species and morphological diversity of *Diplazium* in the Neotropics better than that of the Asian tropics/subtropics. For example, *D. centripetale* (Baker) Maxon, *D. lindbergii* and *D. pinnatifidum* occurring in the Neotropics were included. This sample represents about 10% of species recognized in recent floristic treatments (Stolze, 1981; Proctor, 1985; Tryon & Stolze, 1991; Stolze & al., 1994; Mickel & Smith, 2004) which is a much higher percentage than our sample of tropical Asian taxa of which we cover only 8.7%. In conclusion, an increased sampling is unlikely to alter the main phylogenetic topology and may be only of interest to studies that aim to test hypotheses concerning local diversity or aim to reconstruct the colonization of the Neotropics in greater detail. In this context, we should also point out that the other genera of Athyriaceae are either restricted to the Old World or, as in *Athyrium*, contain only a few derived species in the New World (Tryon & Tryon, 1982; Kramer & Kato, 1990; Mickel & Smith, 2004).

Morphological character evolution. — Two previously studied characters (dissection of leaves and shape of sori) were used in the reconstruction of the evolution of morphological characters because they are widely utilized as diagnostic characters for infrageneric and specific taxonomy of *Diplazium* (Holttum, 1954; Ching, 1964; Kato, 1977; Chu & He, 1999). In addition, two other characters (margin and color of scales) assumed to have diagnostic potential were also taken into consideration. All four morphological characters contain some phylogenetic information (Figs. 4–5).

Flattened sori is the most common state in most clades (Fig. 4A), and this state is inferred as plesiomorphic for *Diplazium*, while species with tumid sori are restricted to three non-closely related lineages, i.e., main clade I, and subclades D and H in main clade IV. This result suggests a parallel origin of this character in four lineages. Interestingly, no convincing evidence for a reversal from tumid to flattened sori was found.

The evolution of leaf dissection was recovered as highly complex, that is, most nodes were reconstructed with mixed ancestral states (Fig. 4B). The majority of species studied have bi- to tripinnate leaves but only a few clades show this character consistently with the exception of the main clade I. In contrast, imparipinnate leaves is the second-most frequent state and appears to dominate main clade II and several subclades of main clade IV. Simple leaves evolved independently four times. Various authors considered the evolution of simple leaves the result of heterochronic mutations (e.g., Imaichi & Kato, 1992; Masuyama, 1996; Christenhusz & el., 2008; Pryer & Hearn, 2009) that result in the conservation of juvenile characters in adult individuals (paedomorphism). The main argument to support this hypothesis is based on the observation that many ferns with complex leaves have leaves with simple blades in their early development. For example, young plants of *Diplazium cordifolium* Blume have simple leaves, whereas older plants may form both simple and imparipinnate leaves (Holttum, 1954). Several species (such as *D. lomariaceum* (Christ) M.G. Price, *D. subserratum*, *D. pinnatifidum* and *D. plantaginifolium*) retain simple or lobed leaves as adults (Holttum, 1954; Tryon & Tryon, 1982). Thus, in our analyses leaf dissection of these species has been coded as simple and that of *D. cordifolium* as imparipinnate. Under the assumption that simple leaves originated from compound leaves, our analyses revealed the bi- to tripinnate leaf as the most probable plesiomorphic leaf shape of *Diplazium* (likelihood = 56%), but the alternative states with probabilities of 11% for simple leaf and 33% for imparipinnate leaf need to be considered.

Our likelihood analysis confirmed concolorous scales to be the most probable ancestral state (99.9%; Fig. 11–L) in *Diplazium* (Fig. 5A), and the reconstruction of scale margin features indicated entire scales with a probability of 76% for the most common ancestor of *Diplazium* (Fig. 5B). The occurrence of bicolorous scales is restricted to main clade IV, but evolved several times independently in this clade according to our results. Toothed scales either originated in the common ancestor of main clades III and IV (likelihood probability of 50%) or evolved independently at least twice. In clade IV, scales

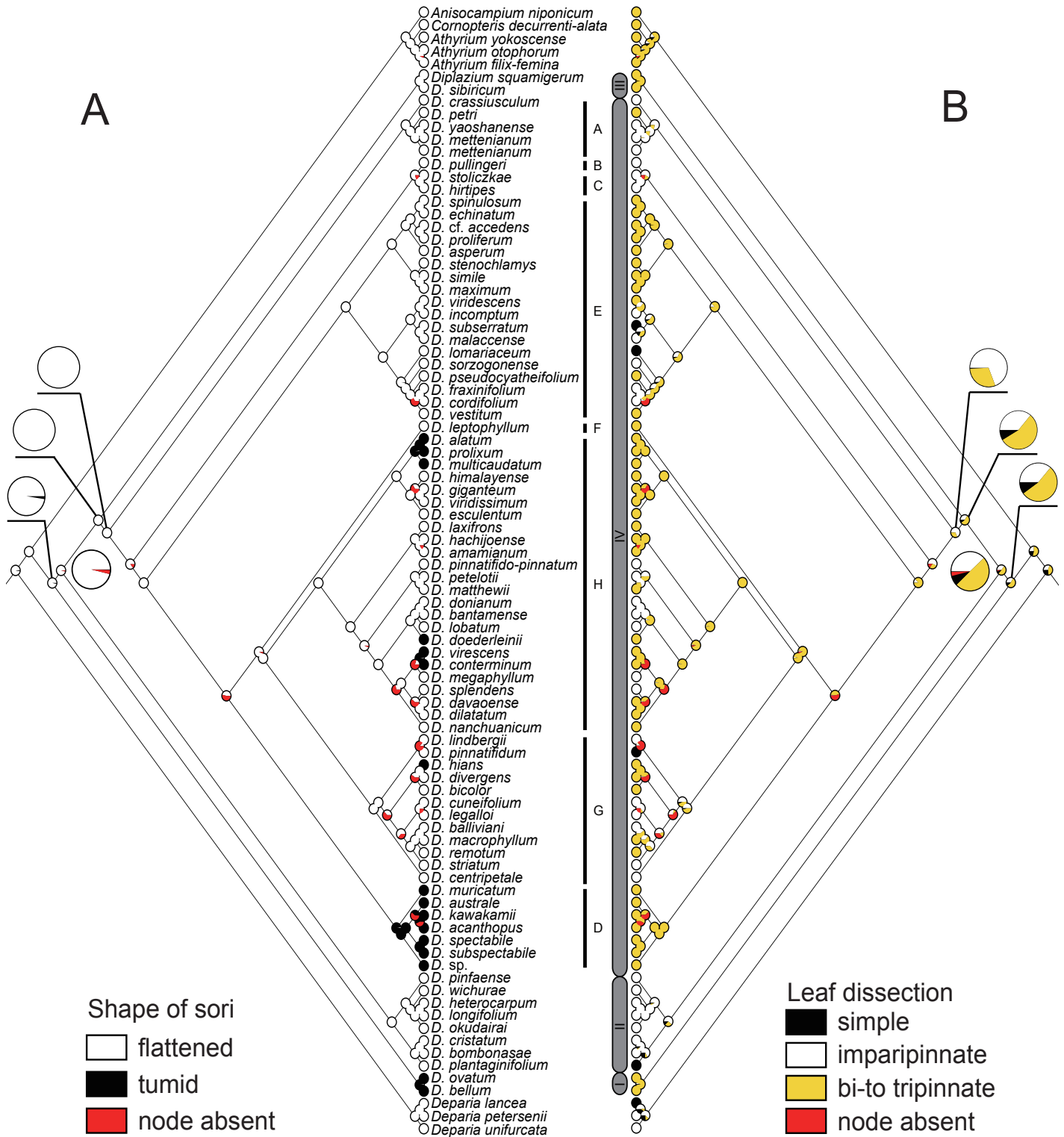


Fig. 4. Evolution of previously widely used morphological characters reconstructed with maximum likelihood over 900 trees obtained in the plateau phase of the Bayesian inference analysis of the combined plastid DNA dataset. The phylogeny was reduced to members of Athyriaceae. Pie charts show the percentage of node absence in the input 900 trees and the average likelihood received by each state across all input trees possessing that node. **A**, shape of sori: flattened or tumid; **B**, dissection of leaves: simple, imparipinnate, bi- to tripinnate. — Letters A to H mark subclades as in Fig. 2 and the text. The four enlarged pie charts show the reconstructed character states of the putative ancestors of the four main clades (see Fig. 2).

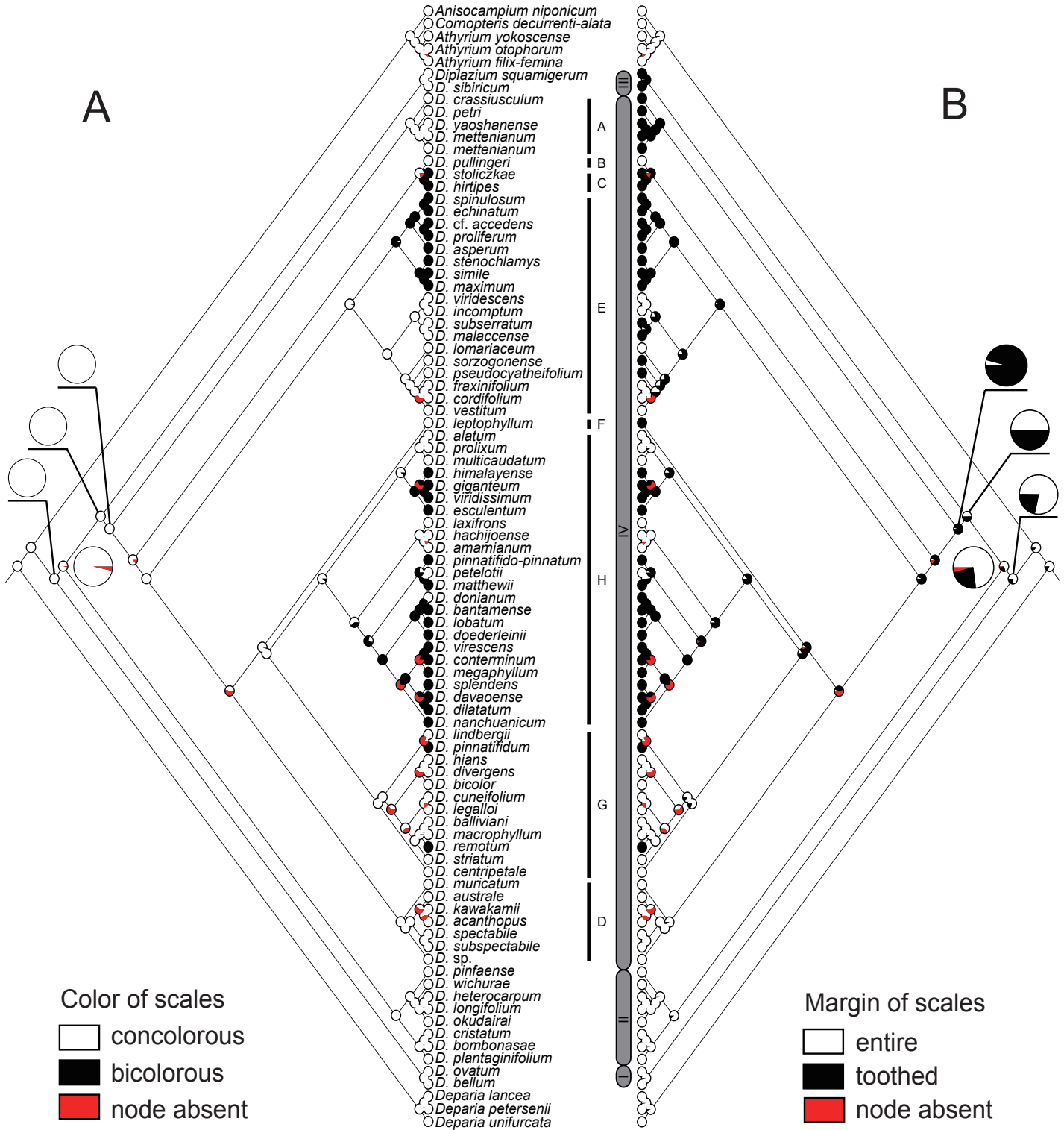


Fig. 5. Evolution of petiole/rachis scale characters reconstructed with maximum likelihood over 900 trees obtained in the plateau phase of the Bayesian inference analysis of the combined plastid DNA dataset. The phylogeny was reduced to members of Athyriaceae. Pie charts show the percentage of node absence in the input 900 trees and the average likelihood received by each state across all input trees possessing that node. **A**, color scales: concolorous or bicolorous; **B**, scale margin: entire or toothed. — Letters A to H mark subclades as in Fig. 2 and the text. The four enlarged pie charts show the reconstructed character states of the putative ancestors of the four main clades (see Fig. 2).

with toothed margins are probably ancestral (96%) and were repeatedly lost more than seven times. However, a reversal to scales with toothed margins may have happened twice in subclade G according to our results. The reconstruction of the evolution of this character has to be considered as ambiguous given the limited number of species incorporated and the lack of robustness of the backbone of clade IV.

Our results recovered a high level of homoplasy in some key morphological characters which may make the relationships among clades or subclades more ambiguous. However, the combined morphological characters can potentially distinguish clades/subclades by avoiding the homoplasy of single characters. As an example, clades I and III have a similar pattern of leaf dissection, but they are distinct in scales and sori.

■ TAXONOMIC TREATMENT

Subgeneric classification. — Several studies have addressed the taxonomy of *Diplazium* in the past fifty years, some providing an infrageneric classification of *Diplazium* (Ching, 1964; Kato, 1977; Tryon & Tryon, 1982; Chu & He, 1999). These studies recognized the importance of parallel evolution of many morphological characters that resulted in conflicting concepts of the classification of these ferns (Bory, 1804; Brown, 1810; Christensen, 1906; Hayata, 1928; Copeland, 1947; Holttum, 1954; Ching, 1964; Kato, 1977; Kramer & Kato, 1990; Chu & He, 1999; Pacheco & Moran, 1999). Our molecular phylogenetic study provides the basic framework for an improved classification and a better understanding of character evolution and species diversification. As discussed, here we propose to treat this group of ferns as a single genus. To manage the morphological diversity of this broadly defined genus, we introduce an infrageneric classification that considers the DNA sequence-based phylogeny, morphological variation and geographic distribution.

Diplazium Sw. in J. Bot. (Schrader) 1800: 4, 61. 1801 [“1800”]

– Type: *D. plantaginifolium* (L.) Urb., Symb. Antill. 4: 31. 1903 ≡ *Asplenium plantaginifolium* L., Syst. Nat., ed. 10, 2: 1323. 1759 (neotype, designated by Proctor, Ferns Jamaica: 392. 1985).

= *Allantodia* R. Br., Prodr.: 149. 1810 – Type: *A. australis* R. Br., Prodr.: 149. 1810 (lectotype designated by Ching in Acta Phytotax. Sin. 9: 44. 1964).

= *Callipteris* Bory, Voy. Îles Afrique 1: 282. 1804, non *Callipteris* Brongn. 1849 – Type: *C. prolifera* (Lam.) Bory, Voy. Îles Afrique 1: 283. 1804 ≡ *Asplenium proliferum* Lam., Encycl. 2: 307. 1786.

= *Monomelanium* Hayata in Bot. Mag. (Tokyo) 42: 343. 1928 – Type: *M. pullingeri* (Baker) Tagawa in J. Jap. Bot. 12: 539. 1936 ≡ *Asplenium pullingeri* Baker in Gard. Chron., n.s., 4: 484. 1875 (= *M. hancockii* (Maxim.) Hayata in Bot. Mag. (Tokyo) 42: 343. 1928).

Plants medium-sized to large; terrestrial and occasionally lithophytic. Rhizomes long creeping to short erect, bearing scales. Rhizome scales ovate to lanceolate; concolorous (i.e.,

no incrassate strands on both margins of scales) or bicolorous (i.e., two incrassate strands on both margins of scales); margins entire to toothed, teeth often bifid. Petioles glabrous to hairy, or scaly to echinate; scales identical with those of rhizomes. Fronds ovate-triangular to triangular; simple to tripinnate, apical pinnae usually pinnatifid or similar to lateral pinnae. Rachis and costae glabrous to hairy, or scaly to muricate, sulcate adaxially, lacking a free central ridge; rachis grooves continuous to costae or not, sometimes U-shaped without flat base or U-shaped with flat base; veins free or sometimes anastomosing. Sori ovate to elongate, flattened to tumid, single or paired back-to-back along the same vein, never hooked crossing over the vein at one end; indusia splitting from one side or sometimes dorsally split when sori tumid.

Key to the subgenera of *Diplazium*

1. Laminae symmetric, pinnae and pinnules more or less opposite and orthogonal; sori ovate, single, crossing over one vein, rarely paired back-to-back along the same vein subg. *Pseudallantodia*
1. Laminae asymmetric, pinnae and pinnules usually alternate and oblique; sori flattened and elongate, sometimes tumid, always paired back-to-back along the same vein 2
2. Laminae simple to bipinnate; pinnae (pinnules) usually prominently auriculate on the acroscopic side at the base; margins of pinnae (pinnules) usually biserrate; scales concolorous with entire margins; petioles and rachis glabrous; rachis groove U-shaped without flat base subg. *Diplazium*
2. Laminae bi- to tripinnate, rarely simple or imparipinnate; pinnae (pinnules) usually without prominent auricle on the acroscopic base; margins of pinnae (pinnules) usually entire or serrate; scales concolorous or bicolorous, margins usually toothed or sometimes entire; petioles and rachis scaly to muricate, or sometimes hairy; rachis groove U-shaped with a flat base 3
3. Plants deciduous; laminae and pinnae ovate; lobes usually obtuse; scales lanceolate, concolorous with toothed margins; mainly distributed in temperate region subg. *Sibirica*
3. Plants evergreen; laminae and pinnae triangular or lanceolate; lobes usually lanceolate; scales usually lanceolate or sometimes ovate, usually bicolorous, sometimes concolorous, margins toothed or entire; mainly distributed in subtropics to tropics subg. *Callipteris*

Diplazium subg. *Diplazium* ≡ *Asplenium* subg. *Diplazium* (Sw.) C.B. Clarke in Trans. Linn. Soc. London, Bot. 1(8): 495. 1880 – Type: *D. plantaginifolium* (L.) Urb., Symb. Antill. 4: 31. 1903 ≡ *Asplenium plantaginifolium* L., Syst. Nat., ed. 10, 2: 1323. 1759 (neotype designated by Proctor in Ferns Jamaica: 1985: 392).

Plants evergreen, medium-sized. Rhizomes long-creeping to short erect. Scales concolorous with entire margins. Laminae simple to bipinnate, if imparipinnate or bipinnate, laminae usually asymmetric; pinnae and pinnules alternate and usually

auriculate, margins biserrate. Petioles and rachises glabrous; grooves U-shaped. Veins free with one forked end in every serrature. Sori linear and elongate, usually paired back-to-back along the same vein.

Diplazium subg. *Pseudallantodia* (C.B. Clarke) R. Wei & X.C. Zhang, **comb. nov.** \equiv *Asplenium* subg. *Pseudallantodia* C.B. Clarke in Trans. Linn. Soc. London, Bot. 1: 495. 1880 – Type: *D. bellum* (C.B. Clarke) Bir in Res. Bull. Panjab Univ. Sci. 15: 148. 1964 \equiv *Asplenium bellum* C.B. Clarke in Trans. Linn. Soc. London, Bot. 1: 496. 1880 \equiv *Allantodia bella* (C.B. Clarke) Ching in Acta Phytotax. Sin. 9: 48. 1964 (lectotype designated by Fraser-Jenkins in Taxon. Revis. Ind. Subcont. Pterid.: 269. 2008).

Plants evergreen, medium-sized to large. Rhizomes recumbent to short erect. Scales concolorous with entire margins. Laminae usually bipinnate, symmetric; pinnae and pinnules orthogonal, more or less opposite. Petioles and rachises usually glabrous; grooves U-shaped with a flat base. Veins free with two-forked end in one serrature. Sori ovate, singular crossing over one vein and rarely paired back-to-back along the same vein.

Diplazium subg. *Sibirica* R. Wei & X.C. Zhang, **subg. nov.** – Type: *D. sibiricum* (Turcz. ex Kunze) Sa. Kurata in Namageta & Kurata, Enum. Jap. Pterid.: 292, 340. 1961 \equiv *Asplenium sibiricum* Turcz. ex Kunze, Analecta Pteridogr.: 25, t. 15. 1837.

Plants deciduous, medium-sized; mainly distributed in temperate regions. Rhizomes long-creeping to recumbent. Scales concolorous with toothed margins. Laminae bipinnate, asymmetric; pinnae and pinnules oblique and alternate; lobes usually obtuse, margins crenate. Petioles and rachises scaly or slightly hairy; grooves U-shaped with a flat base. Veins free with forked end. Sori oblong to elongate, usually paired back-to-back along the same acroscopic vein at the base of pinnae or pinnules.

Diplazium subg. *Callipteris* (Bory) R. Wei & X.C. Zhang, **comb. & stat. nov.** \equiv *Callipteris* Bory, Voy. Îles Afrique 1: 282. 1804 non *Callipteris* Brongn. 1849 – Type: *D. proliferum* (Lam.) Thouars, Esquisse Fl. Tristan d'Acugna: 35. 1808 \equiv *Asplenium proliferum* Lam., Encycl. 2: 307. 1786 \equiv *Callipteris prolifera* (Lam.) Bory, Voy. Îles Afrique 1: 283. 1804.

Plants evergreen, medium-sized to large; mainly distributed in subtropics to tropics. Rhizomes usually short erect or sometimes long-creeping to recumbent. Scales bicolorous, sometimes concolorous, lanceolate or sometimes ovate; margins toothed, sometimes entire. Laminae simple to tripinnate, asymmetric; pinnae and pinnules triangular to lanceolate, margins usually serrate. Petioles and rachises scaly or muricate, sometimes hairy; grooves U-shaped with a flat base. Veins free or sometimes anastomosing. Sori linear or sometimes tumid, usually paired back-to-back along the same acroscopic vein at the base of pinnae or pinnules.

New combinations. — Four new combinations in *Diplazium* are necessary based on our analysis:

Diplazium multicaudatum (Wall. ex C.B. Clarke) R. Wei & X.C. Zhang, **comb. nov.** \equiv *Asplenium multicaudatum* Wall. ex C.B. Clarke in Trans. Linn. Soc. London, Bot. 1: 502. 1880 – **Lectotype (designated here):** Napalia [NEPAL]: 1821, *N. Wallich 229* (Z no. Z-000002055 photo!; isolectotype: US no. 00065565 photo!)

Diplazium nanchuanicum (W.M. Chu) R. Wei & X.C. Zhang, **comb. nov.** \equiv *Allantodia nanchuanica* W.M. Chu in Acta Phytotax. Sin. 21: 219. 1983 – Holotype: CHINA. Chongqing: Jinfo Mountain, Sanhui, Honghegou, by stream side, on the margin of mixed forest, in limestone gorge, alt. 750 m, 28 Sep 1977, *W.-M. Chu & Z.-Y. Liu 7617* (PYU).

Diplazium ovatum (W.M. Chu) R. Wei & X.C. Zhang, **comb. nov.** \equiv *Allantodia ovata* W.M. Chu in Bull. Bot. Res., Harbin 4: 12–13. 1984 – Holotype: CHINA. Chongqing: Jinfo Mountain, Daheba, alt. 900 m, 19 Mar 1983, *Z.-Y. Liu 3865* (PE!).

Diplazium subspectabile (Ching & W.M. Chu) R. Wei & X.C. Zhang, **comb. nov.** \equiv *Allantodia subspectabilis* Ching & W.M. Chu in Fl. Xizang. 1: 148–150. 1983 – Holotype: CHINA. Xizang: Zayu, alt. 2000 m, 16 Jul 1973, *C.-W. Chang 748* (PE!).

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Appendix 1. Species names and GenBank accession numbers of DNA sequences used in this study. Voucher information is given for accessions for which DNA sequences were newly obtained, using the following order: taxon, locality (including province or provenance of cultivated information, when known), collector and number and (herbarium) for voucher specimen, GenBank accession number of *atpA*; *atpB*; *matK*; *rbcL*; *rps4-trnS*; *trnL-F*. A dash (–) indicates missing data; an asterisk (*) indicates newly generated sequences.

INGROUP TAXA: *Anisocampium niponicum* (Mett.) Y.C. Liu, W.L. Chiou & M. Kato, JF832097; JF832155; JF832257; JF832057; JN168077; AF515256. *Athyrium filix-femina* (L.) Roth, JF832096; JF832154; JF303941; JF832056; AF425152; EU329076. *Athyrium otophorum* (Miq.) Koidz., JF832098; EF463563; JF832258; EF463305; JN168076; AF515236. *Athyrium yokoscense* (Franch. & Sav.) Christ, EF463905; EF463564; –; EU329055; JN168078; EU329098. *Cornopteris decurrenti-alata* (Hook.) Nakai, JF832104; JF832159; JF832263; JF832061; –; EU329106. *Deparia lancea* (Thunb.) Fraser-Jenk., JF832109; EF463567; JF303940; EF463306; AF425153; AF515238; *Deparia petersenii* (Kunze) M. Kato, JF832110; JF832161; JN673852; JF832065; JN168086; JN673894. *Deparia unifurcata* (Baker) M. Kato, JF832111; EF463569; JF832271; EF463307; JN168087; AF515235. *Diplazium acanthopus* C. Chr., Indonesia: Sulawesi, *M. Kessler Cicuzza806* (Z), KC254238*; KC254158*; KC254391*; KC254546*; KC254466*. *Diplazium* cf. *accedens* Blume, U.S.A.: cultivated in Missouri Botanical Garden, *G. Yatskievych MBG2001-1125* (MO), KC254229*; KC254308*; KC254150*; KC254383*; KC254537*; KC254457*. *Diplazium alatum* (Christ) R. Wei & X.C. Zhang, China: Yunnan, *R. Wei WR0259* (PE), KC254250*; KC254329*; KC254171*; KC254402*; KC254558*; KC254480*. *Diplazium amamianum* Tagawa, China: Taiwan, *X.-P. Qi XP333* (TAI), KC254258*; KC254337*; KC254179*; KC254410*; KC254566*; KC254488*. *Diplazium asperum* Blume, China: Hainan, *X.C. Zhang 545* (PE), KC254224*; KC254303*; KC254145*; KC254379*; KC254531*; KC254451*. *Diplazium australe* (R. Br.) N.A. Wakef., New Zealand: cultivated, *B.S. Parriss Bar01* (PE), KC254239*; KC254318*; KC254159*; KC254392*; KC254547*; KC254467*. *Diplazium balliviani* Rosenst., Bolivia, *P. Weigelt PW09232* (UC), –; –; KC254169*; –; KC254556*; KC254478*. *Diplazium bantamense* Blume, Indonesia: Sulawesi, *M. Kessler Cicuzza455* (Z), KC254271*; –; KC254192*; KC254422*; KC254579*; KC254502*. *Diplazium bellum* (C.B. Clarke) Bir, China: Yunnan, *R. Wei WR0206* (PE), KC254200*; KC254279*; KC254121*; KC254356*; KC254507*; KC254428*. *Diplazium bicolor* Stolze, Bolivia, *M. Kessler MK13009* (Z), KC254243*; KC254322*; KC254163*; KC254396*; KC254549*; KC254471*. *Diplazium bombonense* Rosenst., JF832115; EF463570; EF463308; JF832273; –; –. *Diplazium centripetale* (Baker) Maxon, EF463912; EF463571; EF463309; –; –. *Diplazium conterminum* Christ, China: Chongqing, *R. Wei WR0056* (PE), KC254344*; KC254186*; KC254416*; KC254573*; KC254495*. *Diplazium cordifolium* Blume, Philippines, *M. Kessler Karger1516* (Z), KC254220*; KC254299*; KC254141*; –; KC254527*; KC254448*. *Diplazium crassiusculum* Ching, China: Jiangxi, *R. Wei JGS066* (PE), KC254214*; KC254293*; KC254135*; KC254370*; KC254521*; KC254442*. *Diplazium cristatum* (Desr.) Alston, Bolivia, *P. Weigelt PW90474* (UC), KC254206*; KC254285*; KC254127*; KC254362*; KC254515*; KC254434*. *Diplazium cuneifolium* Rosenst., Bolivia, *P. Weigelt PW090230* (UC), KC254248*; KC254326*; KC254168*; –; KC254554*; KC254476*. *Diplazium davaoense* Copel., Philippines, *M. Kessler Karger816* (Z), KC254268*; KC254347*; KC254189*; KC254419*; KC254576*; KC254498*. *Diplazium dilatatum* Blume, China: Guangxi, *X.-C. Zhang 156* (PE), KC254267*; KC254346*; KC254188*; KC254418*; KC254575*; KC254497*. *Diplazium divergens* Rosenst., Bolivia, *M. Kessler MK13068* (UC), KC254244*; KC254323*; KC254164*; KC254397*; KC254550*; KC254472*. *Diplazium doederleinii* (Luerss.) Makino, China: Guangdong, *R. Wei & al. WXP24* (PE), KC254260*; KC254339*; KC254181*; KC254412*; KC254568*; KC254490*. *Diplazium donianum* (Mett.) Tardieu, China: Hainan, *X.-C. Zhang 5562* (PE), KC254272*; KC254349*; KC254193*; KC254423*; KC254580*; KC254502*. *Diplazium echinatum* C. Chr., Fiji, *L.R. Perrie FJ11-99* (WELT), KC254226*; KC254305*; KC254147*; KC254381*; KC254533*; KC254453*. *Diplazium exculentum* (Retz.) Sw., China: Yunnan, *X.-C. Zhang 2983* (PE), KC254254*; KC254333*; KC254175*; KC254406*; KC254562*; KC254484*. *Diplazium fraxinifolium* C. Presl, Philippines, *M. Kessler Karger631* (Z), –; –; –; KC254536*; KC254456*. *Diplazium giganteum* (Baker) Ching, China: Sichuan, *C.-H. Li LCH012* (PE), KC254252*; KC254331*; KC254173*; KC254404*; KC254560*; KC254482*. *Diplazium hachijoense* Nakai, China: Chongqing, *R. Wei WR0057* (PE), KC254256*; KC254335*; KC254177*; KC254408*; KC254564*; KC254486*. *Diplazium heterocarpum* Ching, China: Hunan, *X.-C. Zhang 6176* (PE), KC254203*; KC254282*; KC254124*; KC254359*; KC254510*; KC254431*. *Diplazium hians* Kunze ex Klotzsch, Bolivia, *I. Jienez LJ1329* (UC), KC254245*; KC254324*; KC254165*; KC254398*; KC254551*; KC254473*. *Diplazium himalayense* (Ching) Panigrahi, China: Yunnan, *R. Wei WR0222* (PE), KC254255*; KC254334*; KC254176*; KC254407*; KC254563*; KC254485*. *Diplazium hirtipes* Christ, China: Yunnan, *X.-C. Zhang 4454* (PE), KC254211*; KC254290*; KC254132*; KC254367*; KC254518*; KC254439*. *Diplazium incomptum* Tagawa, China: Taiwan, *L.-Y. Kuo Kuo2500* (TAI), KC254218*; KC254297*; KC254139*; KC254374*; KC254525*; KC254446*. *Diplazium kawakamii* Hayata, China: Yunnan, *R. Wei WXP172* (PE), KC254236*; KC254315*; KC254157*; KC254390*; KC254544*; KC254464*. *Diplazium laxifrons* Rosenst., China: Yunnan, *X.-C. Zhang 6359* (PE), KC254257*; KC254336*; KC254178*; KC254409*; KC254565*; KC254487*. *Diplazium legalloii* Proctor, EF463916; EF463575; EF463313; –; –. *Diplazium leptophyllum* Baker ex Christ, China: Yunnan, *R. Wei WR0246* (PE), KC254240*; KC254319*; KC254160*; KC254393*; –; KC254468*. *Diplazium lindbergii* (Mett.) Christ, Bolivia, *M. Kessler MK12992* (Z), KC254246*; –; KC254166*; KC254399*; KC254552*; KC254474*. *Diplazium lobatum* (Tagawa) Tagawa, China: Yunnan, *R. Wei WR0258* (PE), KC254270*; –; KC254191*; KC254421*; KC254578*; KC254500*. *Diplazium lomariaceum* (Christ) M.G. Price, Philippines, *M. Kessler Karger1582* (Z), KC254221*; KC254300*; KC254142*; KC254376*; KC254528*; KC254449*. *Diplazium longifolium* T. Moore, China: Yunnan, *X.-C. Zhang 6301* (PE), KC254204*; KC254283*; KC254125*; KC254360*; KC254511*; KC254432*. *Diplazium macrophyllum* Desv., Bolivia, *P. Weigelt PW090229* (UC), KC254247*; KC254325*; KC254167*; KC254400*; KC254553*; KC254475*. *Diplazium malaccense* C. Presl, Indonesia: Sulawesi, *M. Kessler Cicuzza168* (Z), KC254228*; KC254307*; KC254149*; –; KC254535*; KC254455*. *Diplazium matthewii* (Copel.) C. Chr., China: Guangxi, *X.-C. Zhang 101* (PE), KC254263*; KC254342*; KC254184*; KC254415*; KC254571*; KC254493*. *Diplazium maximum* (D. Don) C. Chr., China: Jiangxi, *R. Wei JGS068* (PE), KC254231*; KC254310*; KC254152*; KC254385*; KC254539*; KC254459*. *Diplazium megaphyllum* (Baker) Christ, location unknown, *H.-M. Liu LHM101* (PE), KC254264*; KC254343*; KC254185*; –; KC254572*; KC254494*. *Diplazium mettenianum* (Miq.) C. Chr., China Chongqing, *R. Wei WR0070* (PE), KC254212*; KC254291*; KC254133*; KC254368*; KC254519*; KC254440*. *Diplazium mettenianum* (Miq.) C. Chr., China: Guangdong, *R. Wei WR0194* (PE), KC254216*; KC254295*; KC254137*; KC254372*; KC254523*; KC254444*. *Diplazium multicaudatum* (Wall. ex C.B. Clarke) R. Wei & X.C. Zhang, China: Yunnan, *R. Wei WR0227* (PE), KC254251*; KC254330*; KC254172*; KC254403*; KC254559*; KC254481*. *Diplazium muricatum* (Mett.) Alderw., China: Yunnan, *R. Wei WR0197* (PE), KC254235*; KC254314*; KC254156*; KC254389*; KC254543*; KC254463*. *Diplazium nanchuanicum* (W.M. Chu) R. Wei & X.C. Zhang, China: Chongqing, *J.-Q. Sun S034* (PE), KC254259*; KC254338*; KC254180*; KC254411*; KC254567*; KC254489*. *Diplazium okudairai* Makino, China: Chongqing, *R. Wei WR0153* (PE), KC254201*; KC254280*; KC254122*; KC254357*; KC254508*; KC254429*. *Diplazium ovatum* (W.M. Chu) R. Wei & X.C. Zhang, China: Chongqing, *R. Wei WR0098* (PE), KC254199*; KC254278*; KC254120*; KC254355*; KC254506*; KC254427*. *Diplazium petelotii* Tardieu, China: Yunnan, *R. Wei WR292* (PE), KC254262*; KC254341*; KC254183*; KC254414*; KC254570*; KC254492*. *Diplazium petri* Tardieu, China: Guangxi, *R.-H. Jiang JRH1407* (PE), KC254213*; KC254292*; KC254134*; KC254369*; KC254520*; KC254441*. *Diplazium pinfaense* Ching, China: Sichuan, *C.-H. Li LCH007* (PE), KC254202*; KC254281*; KC254123*; KC254358*; KC254509*; KC254430*. *Diplazium pinnatifido-pinnatum* (Hook.) T. Moore, China: Yunnan, *R. Wei WR269* (PE), KC254261*; KC254340*; KC254182*; KC254413*; KC254569*; KC254491*. *Diplazium pinnatifidum* Kunze, Bolivia, *M. Kessler MK12988* (Z), KC254241*; KC254320*; KC254161*; KC254394*; –; KC254469*. *Diplazium plantaginifolium* (L.) Urb., U.S.A.: cultivated in the Missouri Botanical Garden, *R.C. Moran 339* (MO), KC254205*; KC254284*; KC254126*; KC254361*; KC254514*; KC254433*. *Diplazium proliferum* (Lam.) Thouars,

Appendix 1. Continued.

JF304008; EF463577; JF303939; EF463315; –; –. *Diplazium prolixum* Rosenst., China: Chongqing, *R. Wei WR0099* (PE), KC254249*; KC254328*; KC254170*; KC254401*; KC254557*; KC254479*. *Diplazium pseudocyathifolium* Rosenst., Philippines, *M. Kessler Karger1584* (Z), KC254222*; KC254301*; KC254143*; KC254377*; KC254529*; KC254450*. *Diplazium pullingeri* (Baker) J. Sm., China: Guangxi, *X.-C. Zhang 2826* (PE), KC254209*; KC254288*; KC254130*; KC254365*; KC254516*; KC254437*. *Diplazium remotum* Fée, Bolivia, *I. Jienez JI1566* (UC), –; –; KC254327*; –; –; KC254555*; KC254477*. *Diplazium sibiricum* (Turcz. ex Kunze) Kurata, China: Beijing, *R. Wei WR0176* (PE), KC254208*; KC254287*; KC254129*; KC254364*; KC254513*; KC254436*. *Diplazium simile* (W.M. Chu) R. Wei & X.C. Zhang, China: Yunnan, *R. Wei WR0243* (PE), KC254230*; KC254309*; KC254151*; KC254384*; KC254538*; KC254458*. *Diplazium sorogonense* C. Presl, Indonesia: Sulawesi, *M. Kessler Cicuzza990* (Z), KC254223*; KC254302*; KC254144*; KC254378*; KC254530*; –. *Diplazium sp.*, Philippines, *M. Kessler Karger785* (Z), KC254237*; KC254316*; –; –; KC254545*; KC254465*. *Diplazium spectabile* (Wall. ex Mett.) Ching, China: Xizang, *Z.-Y. Li 2737* (PE), KC254234*; KC254313*; KC254155*; KC254388*; KC254542*; KC254462*. *Diplazium spinulosum* Blume, Indonesia: Sulawesi, *M. Kessler 940* (Z), KC254225*; KC254304*; KC254146*; KC254380*; KC254532*; KC254452*. *Diplazium splendens* Ching, China: Yunnan, *R. Wei WR0288* (PE), KC254269*; KC254348*; KC254190*; KC254420*; KC254577*; KC254499*. *Diplazium squamigerum* (Mett.) Christ, China: Chongqing, *R. Wei WR0115* (PE), KC254207*; KC254286*; KC254128*; KC254363*; KC254512*; KC254435*. *Diplazium stenochlamys* C. Chr., China: Yunnan, *R. Wei WR0304* (PE), KC254232*; KC254311*; KC254153*; KC254386*; KC254540*; KC254460*. *Diplazium stoliczkae* Bedd., China: Yunnan, *X.-C. Zhang 6340* (PE), KC254210*; KC254289*; KC254131*; KC254366*; KC254517*; KC254438*. *Diplazium striatum* (L.) C. Presl, Bolivia, *M. Kessler MK13350* (Z), KC254242*; KC254321*; KC254162*; KC254395*; KC254548*; KC254470*. *Diplazium subserratum* (Blume) T. Moore, Philippines, *L.-Y. Kuo Chiou15146* (TAI), KC254219*; KC254298*; KC254140*; KC254375*; KC254526*; KC254447*. *Diplazium subspectabile* (Ching & W.M. Chu) R. Wei & X.C. Zhang, China: Xizang, *Z.-Y. Li 1209* (PE), KC254233*; KC254312*; KC254154*; KC254387*; KC254541*; KC254461*. *Diplazium vestitum* C. Presl, Indonesia: Sulawesi, *M. Kessler Cicuzza972* (Z), KC254227*; KC254306*; KC254148*; KC254382*; KC254534*; KC254454*. *Diplazium virescens* Kunze, China: Guangxi, *R.-H. Jiang JRH082* (PE), KC254266*; KC254345*; KC254187*; KC254417*; KC254574*; KC254496*. *Diplazium viridescens* Ching, China: Hainan, *R.-H. Jiang JRH096* (PE), KC254217*; KC254296*; KC254138*; KC254373*; KC254524*; KC254445*. *Diplazium viridissimum* Christ, China: Sichuan, *C.-H. Li LCH006* (PE), KC254253*; KC254332*; KC254174*; KC254405*; KC254561*; KC254483*. *Diplazium wichurae* var. *wichurae* (Mett.) Diels, JF832117; EF463579; JF832275; AB042743; –; AF515245. *Diplazium yaoshanense* (Wu ex Wu, Wong & Pong) Tardieu, China: Guangdong, *R. Wei WR0193* (PE), KC254215*; KC254294*; KC254136*; KC254371*; KC254522*; KC254443*. **OUTGROUP TAXA:** *Asplenium ruta-muraria* L., EF463608; EF463344; JF832253; AF525273; AY549763; HQ676517. *Blechnum orientale* L., China: Guangdong, cultivated in Shenzhen Fairy Lake Botanical Garden, *X.-C. Zhang 2565* (PE), KC254194*; KC254273*; KC254115*; KC254350*; KC254504*; KC254424*. *Cystopteris fragilis* (L.) Bernh., JF832108; JF832160; JF832062; AF425148; HQ676522. *Diplaziopsis javanica* (Blume) C. Chr., China: Hainan, *S.Y. Dong 426* (PE), JF832114; JF832163; JF303928; HQ380212; HQ380219; KC254503*. *Gymnocarpium oyamense* Ching, JF832121; JF832166; JF832278; JF832069; AF425149; AF515248. *Hymenasplenium unilaterale* (Lam.) Hayata, JF832127; EF452020; EF452020; EF452140; AY459170; AF525232. *Matteuccia struthiopteris* (L.) Tod., voucher information unknown, KC254197*; KC254276*; KC254118*; KC254353*; –; KC254425*. *Onoclea sensibilis* L., U.S.A.: Virginia, *X.-C. Zhang 3791* (PE), KC254196*; KC254275*; KC254117*; KC254352*; –; –. *Pentari-hizidium intermedium* Hayata, China: Hubei, *X.-C. Zhang 3394* (PE), KC254198*; KC254277*; KC254119*; KC254354*; KC254505*; KC254426*. *Thelypteris palustris* Schott, JF832146; JF832182; JF832292; JF832085; AF425189; HQ676538. *Woodsia manchuriensis* (Hook.) Ching, JF832138; JF832179; JF832284; HQ380214; HQ380221; –. *Woodsia polystichoides* D.C. Eaton, JF832150; JF832186; JF303930; JF832089; HQ380220; –. *Woodwardia unigemmata* (Makino) Nakai, China: Chongqing, *X.-C. Zhang 2717* (PE), KC254195*; KC254274*; KC254116*; KC254350*; –; –.

Appendix 2. Data matrix for four morphological characters: (1) margin features of rhizome/petiole scales: 0 = entire; 1 = toothed; (2) color of rhizome/petiole scales: 0 = concolorous; 1 = bicolorous; (3) shape of sori: 0 = flattened; 1 = tumid; (4) dissection of leaf: 0 = imparipinnate, 1 = bi- to tripinnate; 2 = simple.

Anisocarpium niponicum, 0; 0; 0; 1. *Athyrium filix-femina*, 0; 0; 0; 1. *Athyrium otophorum*, 0; 0; 0; 1. *Athyrium yokoscense*, 0; 0; 0; 1. *Cornopteris decurrenti-alata*, 0; 0; 0; 1. *Deparia lancea*, 0; 0; 0; 2. *Deparia petersenii*, 0; 0; 0; 0. *Deparia unifurcata*, 0; 0; 0; 0. *Diplazium ovatum*, 0; 0; 0; 1. *Diplazium bellum*, 0; 0; 1; 1. *Diplazium okudairai*, 0; 0; 0; 0. *Diplazium wichurae* var. *wichurae*, 0; 0; 0; 0. *Diplazium pinfaense*, 0; 0; 0; 0. *Diplazium heterocarpum*, 0; 0; 0; 0. *Diplazium longifolium*, 0; 0; 0; 0. *Diplazium bombonense*, 0; 0; 0; 0. *Diplazium plantaginifolium*, 0; 0; 0; 2. *Diplazium cristatum*, 0; 0; 0; 0. *Diplazium squamigerum*, 1; 0; 0; 1. *Diplazium sibiricum* var. *sibiricum*, 1; 0; 0; 1. *Diplazium pullingeri*, 0; 0; 0; 0. *Diplazium stoliczkae*, 1; 1; 0; 0. *Diplazium hirtipes*, 1; 1; 0; 0. *Diplazium mettenianum* (Chongqing), 1; 0; 0; 0. *Diplazium petri*, 1; 0; 0; 0. *Diplazium crassiusculum*, 1; 0; 0; 0. *Diplazium yaoshanense*, 1; 0; 0; 0. *Diplazium mettenianum* (Guangdong), 1; 0; 0; 0. *Diplazium viridescens*, 0; 0; 0; 1. *Diplazium incomptum*, 0; 0; 0; 0. *Diplazium cordifolium*, 0; 0; 0; 1. *Diplazium lomariaceum*, 0; 0; 0; 2. *Diplazium pseudocyathifolium*, 1; 0; 0; 1. *Diplazium sorogonense*, 1; 0; 0; 0. *Diplazium asperum*, 1; 1; 0; 1. *Diplazium spinulosum*, 1; 1; 0; 1. *Diplazium echinatum*, 1; 1; 0; 1. *Diplazium vestitum*, 0; 0; 0; 1. *Diplazium malaccense*, 1; 0; 0; 0. *Diplazium fraxinifolium*, 0; 0; 0; 0. *Diplazium acedens*, 1; 1; 0; 1. *Diplazium proliferum*, 1; 1; 0; 1. *Diplazium simile*, 1; 1; 0; 1. *Diplazium maximum*, 1; 1; 0; 1. *Diplazium stenochlamys*, 1; 1; 0; 1. *Diplazium subspectabile*, 0; 0; 1; 1. *Diplazium spectabile*, 0; 0; 1; 1. *Diplazium muricatum*, 0; 0; 1; 1. *Diplazium kawakamii*, 0; 0; 1; 1. *Diplazium sp.*, 0; 0; 1; 1. *Diplazium acanthopus*, 0; 0; 1; 1. *Diplazium australe*, 0; 0; 1; 1. *Diplazium leptophyllum*, 1; 0; 0; 1. *Diplazium pinnatifidum*, 1; 1; 0; 2. *Diplazium striatum*, 0; 0; 0; 0. *Diplazium bicolor*, 0; 0; 0; 1. *Diplazium divergens*, 0; 0; 1; 1. *Diplazium hians*, 0; 0; 1; 1. *Diplazium lindbergii*, 0; 0; 0; 0. *Diplazium macrophyllum*, 0; 0; 0; 1. *Diplazium centripetale*, 0; 0; 0; 0. *Diplazium legalloii*, 0; 0; 0; 0. *Diplazium cuneifolium*, 0; 0; 0; 0. *Diplazium remotum*, 1; 1; 0; 1. *Diplazium balliviani*, 0; 0; 0; 0. *Diplazium prolixum*, 0; 0; 1; 1. *Diplazium alatum*, 0; 0; 1; 1. *Diplazium multicaudatum*, 0; 0; 1; 1. *Diplazium giganteum*, 1; 1; 0; 1. *Diplazium viridissimum*, 1; 1; 0; 1. *Diplazium esculentum*, 1; 1; 0; 1. *Diplazium himalayense*, 1; 1; 0; 1. *Diplazium hachijoense*, 0; 0; 0; 1. *Diplazium laxifrons*, 0; 0; 0; 1. *Diplazium amamanum*, 0; 0; 0; 1. *Diplazium nanchuanicum*, 1; 1; 0; 1. *Diplazium doederleinii*, 1; 1; 1; 1. *Diplazium pinnatifido-pinnatum*, 1; 1; 0; 0. *Diplazium petelotii*, 0; 0; 0; 0. *Diplazium matthewii*, 1; 1; 0; 1. *Diplazium megaphyllum*, 1; 1; 0; 0. *Diplazium conterminum*, 1; 1; 1; 1. *Diplazium virescens*, 1; 1; 1; 1. *Diplazium dilatatum*, 1; 1; 0; 1. *Diplazium davaoense*, 1; 1; 0; 1. *Diplazium splendens*, 1; 1; 0; 0. *Diplazium lobatum*, 1; 1; 0; 0. *Diplazium bantamense*, 1; 1; 0; 0. *Diplazium donianum*, 1; 0; 0; 0.