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Angiopteris involuta (Marattiaceae), a new endangered fern species from southern Yunnan, China, based on morphology and molecular evidence

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Abstract

A new fern species, *Angiopteris involuta* L.J. Jiang & Z.R. He, is described from southern Yunnan, China. This taxon exhibits intermediate morphology between *Angiopteris s.s.* and *Archangiopteris*, characterized by its ascending rhizome, once pinnate to bipinnate, involute fertile pinnules, and long-linear, medial sori. Molecular phylogenetic analysis based on plastome data indicates that *A. involuta* is closely related to species of *Archangiopteris s.s. (A. bipinnata, A. chingii, A. latipinna,* and *A. nodosipetiolata)*, but distinct from other intermediate species belonging to *Angiopteris s.s.* (*A. itoi*, *A. sparsisora*, and *A. sugongii*). The species is assessed as Critically Endangered (CR) under IUCN criteria due to habitat loss and its extremely limited distribution.

Key words: Marattiaceae, eusporangiate, plastome, phylogeny, morphology

Introduction

The genus *Angiopteris* Hoffmann (1796: 29) *s.s.* was established based on *Angiopteris evecta* (G. Forster 1786: 81) Hoffmann (1796: 29). The segregate genus *Archangiopteris* Christ & Giesenhagen (1899: 72) was originally described based on the specimens collected in Mengzi, Yunnan, namely *Archangiopteris henryi* Christ & Giesenhagen (1899: 78), which is now recognized as *Angiopteris latipinna* (Ching 1958b: t.207) Z.R. He, W.M. Chu & Christenh (2013: 85). *Archangiopteris* can be distinguished from *Angiopteris* by its once-pinnate fronds, elongate linear sori positioned medially on the veins (far from the pinnule margins), numerous sporangia, and the absence of false veins (Christ & Giesenhagen 1899). Additional diagnostic features included long rhizome with dorsiventral orientation, branched paraphyses, and spores with dense spinose ornamentation (Ching 1958a, Chang 1973). However, the discovery of morphologically intermediate species, such as *A. itoi* (W.C. Shieh 1970: 205) J.M. Camus (1989: 35) and *A. sparsisora* Ching (1982: 347), has gradually blurred the taxonomic boundaries between these two genera (Ching & Wang 1982, Wu 2002, Hsieh *et al.* 2008). Camus (1989) subsequently advocated a broadly generic circumscription of *Angiopteris*. Due to the non-monophyletic of *Angiopteris s.s.,* molecular phylogenetic evidence supported merging *Angiopteris s.s.*, *Archangiopteris*, *Clementea* Cavanilles (1802: 553), *Macroglossum* Copeland (1909: 342), *Protangiopteris* Hayata (1928: 305, 346), *Protomarattia* Hayata (1919: 88), and *Psilodochea* C. Presl (1845: 28) into a monophyletic group (Li & Lu 2006, Mudock 2008a, b, He 2009). A broadly defined *Angiopteris s.l.* concept is now widely accepted (He & Christenhusz 2013, PPG I 2016, Wang *et al.* 2021, 2024, Zhao *et al.* 2023), comprising the

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ancient lineages of approximately 60 species (Tropicos, www.tropicos.org), primarily distributed across tropical to subtropical Asia and the Pacific Islands (Chu & He 2006, He & Christenhusz 2013).

Intermediate species between *Angiopteris s.s.* and *Archangiopteris* typically exhibit fertile fronds with laminae that are both once pinnate and bipinnate. Six such species have been reported: *Angiopteris caudatiformis* Hieronymus (1919: 278), *A. annamensis* C. Christensen & Tardieu (1935: 11), *A. bipinnata* (Ching 1958b: t.203) Camus (1989: 35), *A. itoi*, *A. sparsisora*, and *A. sugongii* Gui L. Zhang, J.Y. Xiang & Ting Wang tris (2021: 276). Among these, two species (*A. annamensis* and *A. caudatiformis*) have short linear sori positioned close to the pinnule margins, while the other four species (*A. itoi*, *A. bipinnata*, *A. sparsisora*, and *A. sugongii*) bear elongate linear sori positioned in the middle of the leaf vein, far from the pinnule margins. The newly described taxon here represents another intermediate taxon, belonging to the latter group but is morphologically distinct from these four species. Based on detailed morphological and molecular evidence, we confirm that these materials represent an undescribed species, here named *Angiopteris involuta* L.J. Jiang & Z.R. He.

Materials and methods

Sampling and morphological analysis—The new species (three individuals, collection No. 0591) was originally collected by Mr. Guo-Da Tao in 2008 from Jiangcheng County, Yunnan Province, China, and subsequently maintained in the greenhouse of Xishuangbanna Tropical Botanical Garden (XTBG), Chinese Academy of Sciences. Morphological observations were conducted continuously from 2022 to 2025. In 2024, the exact collection locality and habitat characteristics were confirmed through consultation with Mr. Guo-Da Tao. Field investigations were carried out by the authors in June 2024 and May 2025, during which the species was found to occur in remnant secondary forest fragments bordering rubber plantations, with only five surviving wild adult individuals detected.

Both cultivated and wild individuals were examined. Four consecutive years of comparative observation confirmed the stability of key morphological characteristics. Voucher specimens are deposited in the Herbarium of Yunnan University (PYU) and XTBG Herbarium (HITBC). Gross morphology was examined and photographed using SMZ1270 stereo microscope (Nikon, Japan). Spore materials were attached to Carbon Adhesive Tape under anatomical lens, then samples were coated with gold using the BAL-TEC SCD 005 Cool Sputter Coater (BAL-TEC AG., Liechtenstein) and visualized via QUANTA 200 Scanning Electron Microscope (FEI Co., USA) at 25 kV at Yunnan University, Kunming, China.

Taxonomic sampling, DNA extraction, and sequencing—To explore the phylogenetic relationships, the new species and its putative closely related taxa were included in the phylogenetic analysis (Table 1). In total, seven new plastomes of *Angiopteris s.l.* were newly sequenced in this study (Table 1). Total genomic DNA was extracted from silica-dried leaf material using the TIANGEN plant genomic DNA extraction kit (TIANGEN Biotech., Beijing, China) following the manufacturers' protocols. All samples were sequenced at Biomaker Technology Co., Ltd. (Beijing, China) for Illumina sequencing, in which the libraries were prepared using the NEB Next® UltraTM DNA Library Prep Kit for Illumina (New England Biolabs, USA) following the manufacturer's protocol. Paired-end reads of 2 × 150 bp were then generated on an Illumina NovaSeq 6000 instrument (2G raw data for each sample). To ensure meaningful downstream analysis, Fastp v0.23.1 (Chen *et al.*, 2018) was used to perform basic statistics on the quality of the raw reads.

Plastome assembly and annotation—The organelle reads of plastomes were identified and assembled referring to the previous published plastomes (*Angiopteris angustifolia* C. Presl (1845: 21) GenBank ID: NC026300). Then plastomes were assembled using GetOrganelle v1.7.1 (Jin *et al.* 2020). The organelle-only assembly graph was imported into Bandage v0.8.1(Wick *et al.* 2015) to visualize and learn the plastome structure. Based on each output of FASTA files representing one type of genome structure, we chose the master conformation which tried to be consistent with the published data in GenBank. In order to detect and annotate all genes, assembled complete plastomes were initially annotated using PGA (Qu *et al.* 2019). All tRNAs were confirmed using tRNAscan-SE v2.0.7 (Chan & Lowe 2019). For further validation of annotation, the positions of starts, stops, and introns of the annotated sequences were manually adjusted in Geneious Prime 2019.2.1. Circular genome maps were drawn with OrganellarGenomeDRAW v1.3.1 (Greiner *et al.* 2019)

Phylogenetic analyses—Two concatenated matrices were generated: (1) complete plastomes, and (2) 86 protein-coding gene sequences. Matrices of the complete plastomes and protein-coding sequences for each gene were aligned in Geneious Prime 2019.2.1 with the plugins MAFFT v7.450 (Katoh & Standley 2013) using "E-INS-i" strategy.

Poorly-aligned regions were removed using Gblocks v0.91b (Talavera *et al.* 2007). Concatenated analysis of all nucleotide characters of all accessions were carried out in PhyloSuite v1.2.3 (Zhang *et al.* 2020). ModelFinder tool was used to infer the appropriate nucleotide substitution model based on the corrected Akaike Information Criterion (AICc). Maximum likelihood (ML) bootstrapping was conducted with 5,000 rapid bootstrap (BS) analyses in IQ-tree v2.1.3 (Nguyen *et al.* 2015) followed by a search for the best-scoring tree in a single run. Bayesian inference (BI) was conducted for the combined dataset using MrBayes v3.2.2 (Ronquist *et al.* 2012) with two runs of four Markov Chain Monte Carlo (MCMC) chains, each beginning with a random tree and sampling one tree every 1,000 generations of 2,000,000 generations. The standard deviation of splits frequencies below 0.001, and the MCMC output was examined to check for convergence and to ensure that all of the effective sample size (ESS) values were >200. Maximum Likelihood bootstrap support values (ML-BS) and Bayesian Inference posterior probability (BI-PP) were generated and visualized in Figtree v1.4.3 (Rambaut 2017).

Flow cytometry—To determine ploidy levels, flow cytometry was used to measure the genome size for the same samples used for sequencing. Fresh leaves (0.5 g) from each sample were collected and frozen at − 80 °C. In flow cytometry assays, the amount of stained nuclear DNA is measured by its fluorescence and correlated to an internal standard of which the DNA amount is known. Experiments were carried out by the Molecular Biology Experiment Center (Germplasm Bank of Wild Species in Southwest China) using the leaves of *Zea mays* Linnaeus (1753: 971) (2C = 2.96 pg) as the internal standard. The genome size of each sample was analyzed with a BD FACSCalibur flow cytometer.

TABLE 1. Overview of the plastomes used in this study.

Species	Voucher	Location	GenBank ID	Reference
Angiopteris angustifolia C. Presl	Unknown	Unknown	NC026300	Zhu *et al.* 2016
Angiopteris bipinnata (Ching) J.M. Camus	JLJ-09-0646 (HITBC)	Yunnan, China	PX138845	this study
Angiopteris caudatiformis Hieron.	JLJ-09-0207 (HITBC)	Yunnan, China	PX138846	this study
Angiopteris chingii J.M. Camus	JLJ-09-2022 (HITBC)	Yunnan, China	PX138847	this study
Angiopteris chingii J.M. Camus -1	YYH16228-1	Yunnan, China	PP056126	Wang *et al.* 2024
Angiopteris chingii J.M. Camus -2	YYH22077	Yunnan, China	PP056122	Wang *et al.* 2024
Angiopteris fokiensis Hieron.	Unknown	China	NC068854	Qin, unpublished
Angiopteris involuta L.J. Jiang & Z.R. He	JLJ-09-1591 (PYU)	Yunnan, China	PX138848	this study
Angiopteris itoi (W.C. Shieh) J.M. Camus	Pan2024-a (PYU)	Taiwan, China	PX138849	this study
Angiopteris itoi (W.C. Shieh) J.M. Camus -1	Pan2024-b (PYU)	Taiwan, China	PX138850	this study
Angiopteris latipinna (Ching) Z.R. He, W.M. Chu & Christenh.	YYH16502	Yunnan, China	PP056125	Wang *et al.* 2024
Angiopteris nodosipetiolata Ting Wang tris, H.F. Chen & Y.H. Yan	GLQ-1 (SWFU)	Yunnan, China	PP056124	Wang *et al.* 2024
Angiopteris nodosipetiolata Ting Wang tris, H.F. Chen & Y.H. Yan -1	GLQ-2 (CSH)	Yunnan, China	PP056123	Wang *et al.* 2024
Angiopteris sparsisora Ching	JLJ-09-0864 (HITBC)	Yunnan, China	PX138851	this study
Angiopteris yunnanensis Hieron.	Liu-CP05 (HITBC)	Yunnan (Cult.), China	NC052844	Jiang *et al.* 2019

Results

The assembled the chloroplast genomes were composed of a single circular double-stranded DNA molecule based on the generated genome skimming data, and the complete plastome of the new species displayed the typical quadripartite structure, consisting of a pair of inverted repeats (IRA and IRB), separated by the large single copy region (LSC) and small single copy region (SSC) (Figure 1). The overall GC content of plastome was 35.40 %, and the length in the LSC, SSC, and IR regions were 89,742 bp, 20,564 bp, and 21,424 bp, respectively (Figure 1). The plastomes encoded an identical set of 138 genes, including 89 protein-coding genes, 41 tRNA genes and eight rRNA genes (Figure 1). The 5-end exon of the *rps*12 gene was in the LSC region, and the intron and 3-end exon of the gene were situated in the IR region (Figure 1).

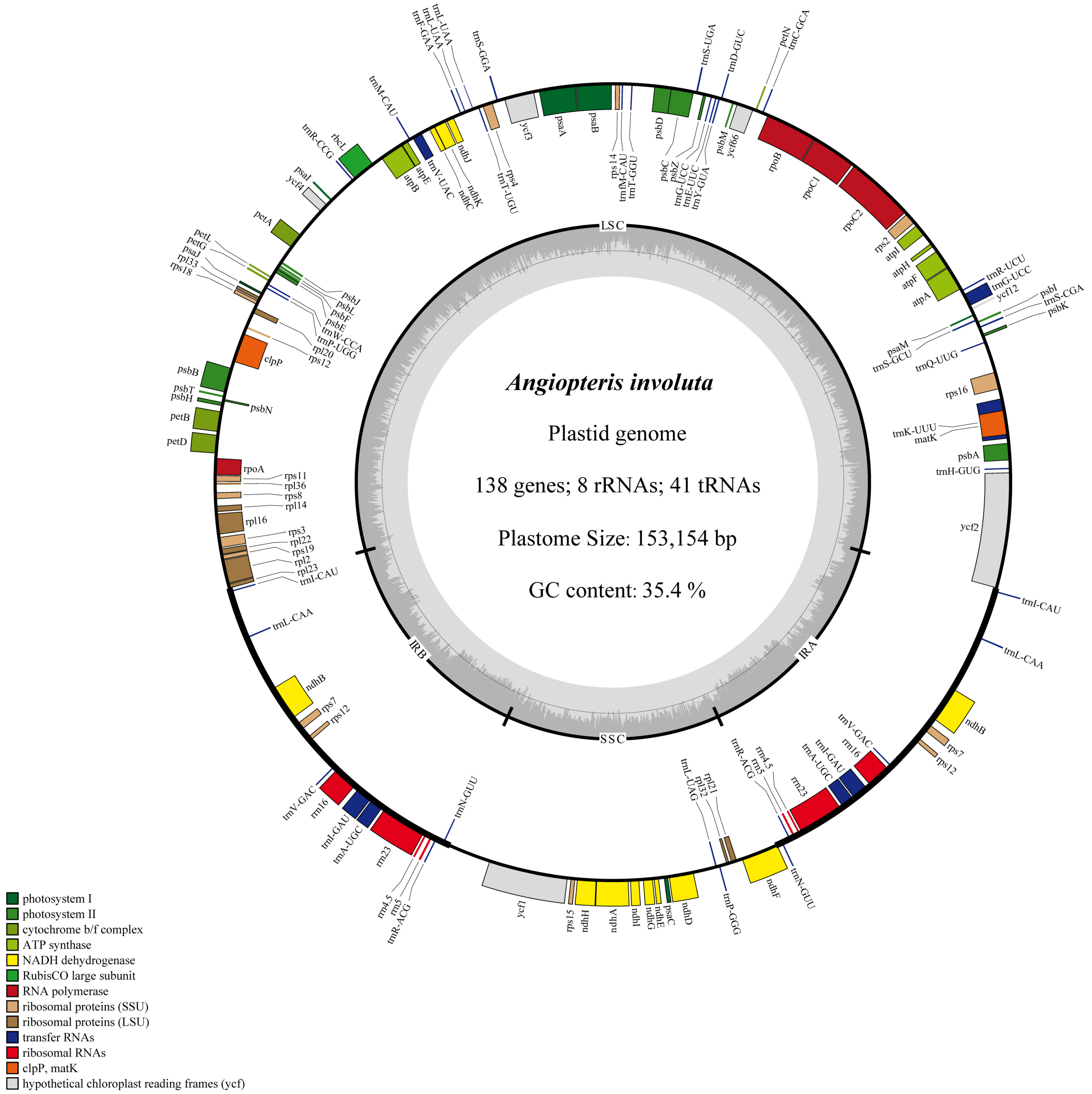

FIGURE 1. Gene map of the chloroplast genome of the *Angiopteris involuta*. Genes transcribed clockwise are depicted on the side of the circle, and gene transcribed counter clockwise on the outside. GC content is shown on the inner circle in dark gray bars. Functional group of each gene is represented in different colors.

The concatenated datasets were 156,397 bp and 82,923 bp in length, respectively (Table 2). The TIM+F+I model was employed as the best substitution model for ML analyses based on both different datasets (Table 2). The best model of evolution selected for BI analyses was GTR+F+I for both datasets (Table 2). The ML and BI phylogenetic analyses based on different datasets revealed generally congruent topologies (Figure 2). *Angiopteris involuta* was resolved as sister to *A. chingii* J.M. Camus (1989: 35) with full support (ML-BS = 100, BI-PP = 1.00; Figure 2). The results obtained from flow cytometry revealed that *Angiopteris s.l.* contains only two cytotypes (Table 3). The genome size of *A. itoi* was 7.00 Gb, approximately 1.5 times larger than other species (Table 3), indicating it is a triploid. All remaining species of *Angiopteris s.l.* were recognized as diploids, with genome sizes ranging from 4.13 Gb to 5.13 Gb (Table 3).

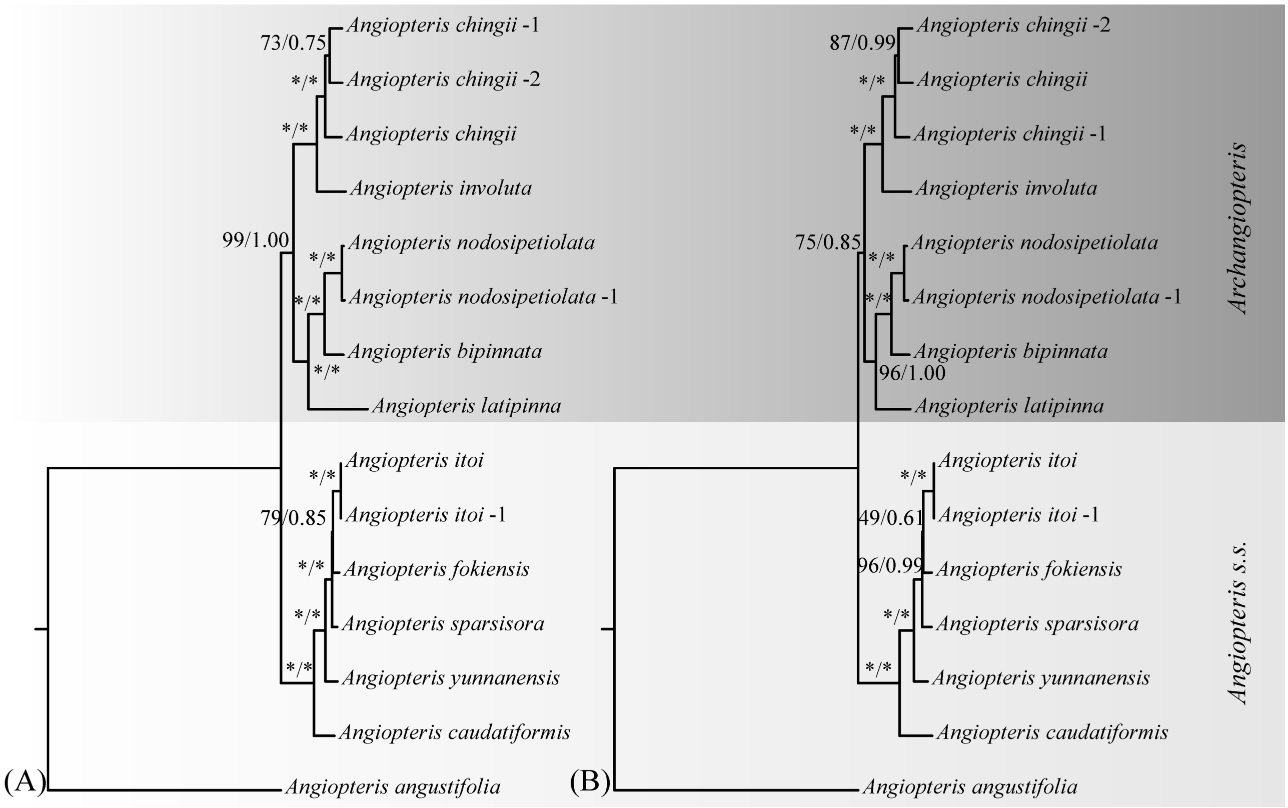

FIGURE 2. Maximum likelihood and Bayesian inference tree of *Angiopteris involuta* and its putative closely related taxa based on different datasets.—A. The complete plastome dataset.—B. The 86 protein-coding genes dataset. Maximum likelihood bootstrap support (ML-BS) and Bayesian inference posterior probability (BI-PP) are given above the branches. Values of 100 or 1.00 are indicated by asterisk.

TABLE 2. Best-fitting models and characteristics in different datasets in this study.

Datasets	Plastome	86 protein-coding genes
Number of informative sites	349	140
Number of invariable sites	151,102	82,278
Sequence length (bp)	156,397	82,923
Pairwise identity	98.80%	99.80%
Identical sites	95.90%	99.20%
Average GC content	35.50%	35.00%
Maximum likelihood model	TIM+F+I	TIM+F+I
Bayesian inference model	GTR+F+I	GTR+F+I

TABLE 3. Results of flow cytometry.

Species	Internal standard	Internal reference fluorescence intensity	Fluorescence intensity of the sample to be tested	Ratio	Genome (Gb)
Angiopteris sparsisora	*Zea mays* L.	388	815	2.10	4.83
Angiopteris bipinnata	*Zea mays* L.	383	711	1.86	4.27
Angiopteris itoi	*Zea mays* L.	398	1,212	3.05	7.00
Angiopteris itoi -1	*Zea mays* L.	398	1,212	3.05	7.00
Angiopteris chingii	*Zea mays* L.	401	720	1.80	4.13
Angiopteris involuta	*Zea mays* L.	534	1,153	2.16	4.97
Angiopteris caudatiformis	*Zea mays* L.	396	883	2.23	5.13

Discussion

Historically, *Archangiopteris* was recognized as a genus distinct from *Angiopteris* based on morphological criteria (Hayata 1919, Ching 1958a, Chang 1973, He 2009). However, the discovery of several taxa exhibiting markedly intermediate morphological traits, including *Angiopteris itoi*, *A. sparsisora*, and *A. sugongii*, has obscured the taxonomic boundaries between these two genera (Ching & Wang 1982, Wu 2002, Hsieh *et al.* 2008, Wang *et al.* 2021). Molecular phylogenetic analyses using plastid markers (e.g., Li & Lu 2006, Murdock 2008a) have demonstrated that *Archangiopteris* is nested within *Angiopteris* and forms a coherent clade. Subsequent studies further revealed that the intermediate taxa (*A. itoi*, *A. sparsisora*, and *A. sugongii*) cluster with Angiopteris species, while *A. tonkinensis* (Hayata 1919: 88) J.M. Camus (1989: 34), which exhibits characteristic features of *Archangiopteris*, is also nested within *Angiopteris* (Wang *et al.* 2024). These phylogenetic relationships underscore the evolutionary complexity within the group and support the taxonomic consolidation of *Angiopteris* and *Archangiopteris* into a single monophyletic genus.

Notably, the distinctly intermediate morphology of *Angiopteris involuta* provides novel insights. Morphologically, this species resembles *A. itoi*, *A. sparsisora*, and *A. sugongii* (Table 4). However, molecular phylogenetic analyses place *A. involuta* not with these species but rather with taxa originally assigned to *Archangiopteris* (Figure 2), thereby complicating the evolutionary narrative of *Angiopteris*. The prevailing hypothesis attributes these intermediate morphologies to hybrid origins, specifically resulting from hybridization events between plants exhibiting distinct *Angiopteris* and *Archangiopteris* characteristics. For example, *A. sparsisora* was initially described as a "putative bigeneric hybrid" (Ching & Wang 1982). Additional hybridization hypotheses within *Angiopteris* have been proposed based on morphological and biogeographical data. *A. wangii* Ching (1959: 338), for instance, has been suggested as a potential hybrid between *A. hokouensis* Ching (1959: 339) and *A. yunnanensis* Hieronymus (1919: 277) (He 2009), while *A. sugongii* is considered likely to represent a natural hybrid between former *Angiopteris* and *Archangiopteris* lineages (Wang *et al.* 2021). More detailed investigations have provided empirical support for these hybridization scenarios; for example, the triploid *A. itoi* from Taiwan Province has been identified as a hybrid between diploid and tetraploid progenitors, *A. evecta* and *A. somae* (Hayata 1915: 256) Makino & Nemoto (1925: 1563) (Hayata 1915, Makino & Nemoto 1925, Hsieh *et al.* 2008). Morphologically, *A. involuta* may likewise represent a hybrid between *Angiopteris* and *Archangiopteris*, although definitive conclusions regarding its origin require further comprehensive study.

Taxonomy

Angiopteris involuta L.J. Jiang & Z.R. He, ***sp. nov.*** **(**Figure 3)

Type:—Qushui Town, Jiangcheng Hani and Yi Autonomous County, Yunnan Province, China, tropical seasonal rainforest along stream, alt. 324 m, 10 May 2024, *L.J. Jiang240510* (Holotype: PYU *JLJ-09-1591*!; Isotype: HITBC*0133890*!).

Diagnosis:—Differs from related species by the combination of characters: mature individuals generally less than 120 cm tall (vs. up to 150 cm in *Angiopteris itoi* and *A. sugongii*); rhizome ascending (vs. erect in *A. itoi*); petioles minutely tuberculate (vs. smooth in congeners); fertile pinnules involute (boat-shaped with upturned margins, exposing partial sori abaxially; vs. flat in others); sori long linear, of intermediate length (2–8 mm; vs. 2–4 mm in *A. sparsisora* and *A. caudatiformis*; 10–20 mm in *A. bipinnata* and *A. itoi*); and leaf margins finely serrate (vs. coarsely dentate in *A. bipinnata*). The morphological comparison between *A. involuta* and the other three most similar species is provided in Table 4.

Description:—Plants terrestrial, 60–120cm tall. **Rhizome** stout, ascending. **Fronds** clustered, once pinnate or bipinnate. **Stipes** 45–60 cm × 5–8 mm, terete, sparsely tuberculate, densely covered with brown filamentous hairs when young (caducous), Sparsely covered with black, narrowly lanceolate scales (ca. 0.5–1.2 × 0.1 cm), as the leaves age, the color of the Stipe scales gradually changes from black to brown. **Lamina** to 120 cm, 1–2-pinnate; rachis wingless. **Pinnae** 5–6 pairs, narrowly lanceolate, 16–22 × 18–23 cm; bipinnate subtriangular, 45–55 × 18–23 cm, with 4–8 pairs of oblong pinnules 5–14 × 1.5–3 cm (apical ones slightly larger), base broadly cuneate, asymmetrical, with 2–4 mm petiolules, margins serrate; **Veins** sparse, simple or forked, false veins absent; texture herbaceous, adaxially green, abaxially pale green when dry. Fertile pinnules with margins strongly revolute toward adaxial surface (boat-shaped), partially exposing abaxial sori. **Sori** long linear, 2–8 mm, of 7–30 sporangial pairs, 2–3 mm from margin; paraphyses inconspicuous. **Spores** brown, trilete; exospores with densely tuberculate-spinose ornamentation. The spore mature from May to June.

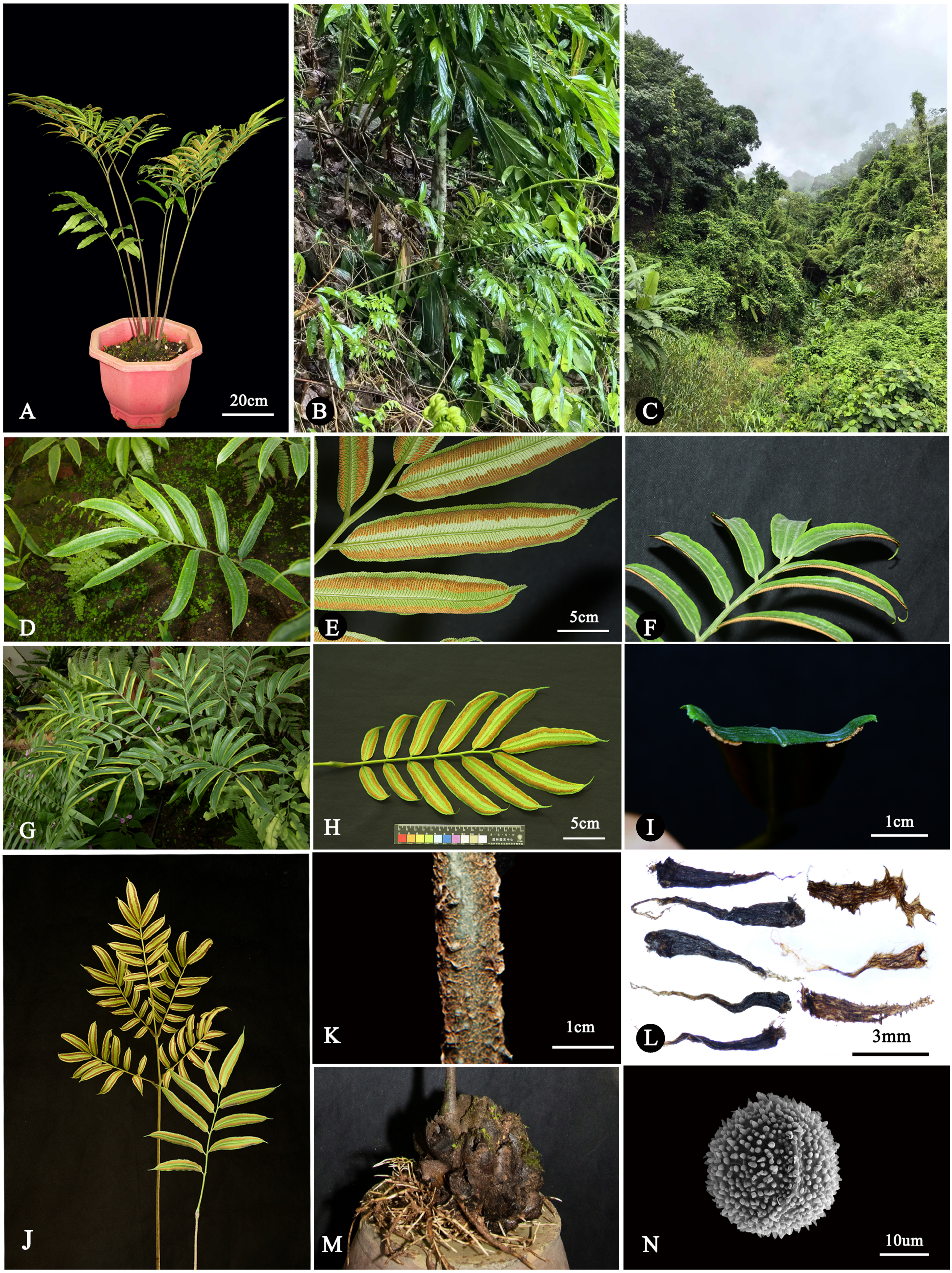

FIGURE 3. *Angiopteris involuta* L.J. Jiang & Z.R. He.—A. Cultivated plant.—B. Wild individual.—C. Habitat.—D & E. Once pinnate fertile frond.—J. Once pinnate and bipinnate fertile frond.—G & H. Bipinnate fertile frond.—F & I. Involute mature pinnules.—K. Stipe sparsely tuberculate.—L. Petiole scales, initially black with relatively neat edges (left), gradually turn dark brown over time, with the bristle-like or fringed edges and the long-pointed hairs on the scales being worn away (right).—M. Ascending rhizome.—N. Exospores with densely tuberculate-spinose ornamentation.

Additional specimens examined (paratypes):—Qushui Town, Jiangcheng Hani and Yi Autonomous County Yunnan, CHINA, tropical seasonal rainforest along stream, alt. 350 m, 26 May 2025, *L.J. Jiang250526* (PYU!).

Etymology:—The epithet *involuta* refers to its involute fertile pinnules. The Chinese name is suggested as '卷叶观音座莲 (juan ye guan yin zuo lian)'.

Distribution and habitat:—Endemic to southern Yunnan (Jiangcheng County) and grows in tropical seasonal rainforest understory along streams (270–350 m).

Conservation status:—Critically Endangered (CR B2ab (iii)). Only five wilds adult individuals and four ex situ specimens (XTBG nursery) are known. The type locality has been converted to rubber plantations, highlighting the urgent need for further field surveys in adjacent areas to assess potential remaining populations.

Notes: Molecular data place *Angiopteris involuta* in a clade with the species of *Archangiopteris* (*A. bipinnata*, *A. chingii*, *A. latipinna*, and *A. nodosipetiolata* Ting Wang tris, H.F. Chen & Y.H. Yan (2024: 181)), while *A. itoi*, *A. sparsisora*, and *A. sugongii* form a separate lineage (Wang *et al.* 2024) (Figure 2).

Keys to the species with fertile fronds with both once pinnate and bipinnate laminae of *Angiopteris* in China and surrounding regions:

1. Sori short-linear, usually less than 5 mm long, marginal 2
- Sori long-linear, usually more than 5 mm long, medial 4
2. Rhizome ascending; sori ca. 3–4 mm long, positioned 3–4 mm from the pinna margin .... *A. sparsisora*
- Rhizome erect; sori ca. 1 mm long, positioned 0.5–1 mm from the pinna margin 3
3. Stipe smooth; pinnules lanceolate .... *A. caudatiformis*
- Stipe with transversely raised stripes; pinnules oblanceolate, apex abruptly acute with a short caudate tip .... *amamensis*
4. Rhizome erect (Taiwan) .... *A. itoi*
- Rhizome ascending (Yunnan) 5
5. Plants small, mature fronds usually < 1 m; veins sparse, 5–6 per cm; leaf margins coarsely serrate,sori ca. 4 mm from margin .... *A. bipinnata*
- Plants large, mature fronds > 1 m; veins dense, 8–10 per cm; leaf margins undulate or minutely serrate, sori ca. 1–2 mm from margin 6
6. Stipes smooth, petiole scales reddish brown; fertile pinnules flat; exospores with spiculose ornamentation .... *A. sugongii*
- Stipes sparsely tuberculate, petiole scales black or dark brown; fertile pinnules with revolute margins (boat-shaped); exospores with densely tuberculate-spinose ornamentation .... *A. involuta*

TABLE 4. Morphological comparison of *Angiopteris involuta*, *A. itoi*, *A. bipinnata*, *A. sparsisora*, and *A. sugongii.*

Characters	***Angiopteris involuta***	***A. bipinnata***	***A. itoi***	***A. sparsisora***	***A. sugongii***
Frond	60–120 cm	50–80 cm	150 cm	100–120 cm	70–160 cm
Stipe	35–70 cm, sparsely tuberculate	60–70 cm, smooth	100–120 cm, smooth	35–70 cm, smooth	50–120 cm, smooth
Rhizome	ascending	ascending	erect	long-creeping	ascending
Laminae	pinnae 5–7 pairs, 5–14 × 1.5–3 cm, bases cuneate, margin serrate to crenulate, fertile pinnules with revolute margins (boat-shaped)	pinnae 10–12 pairs, 12–17 × 2–2.8 cm, bases cuneate, margin subentire, undulate, fertile pinnules flat	pinnae 7–8 pairs, 26–34 × 3–5 cm, bases cuneate, margin undulate, fertile pinnules flat	pinnae 7–15 pairs, 7–16 × 1.5–2.5 cm, bases cuneate, margin serrate to crenulate	pinnae 5–12 pairs, 25–35 × 3–5.5 cm, bases cuneate, fertile coarsely dentate, fertile pinnules flat
False veins	absent (or obscure)	absent	present	absent (or obscure)	absent (or obscure)
Sori	ca. 1–2 mm from margin, ca. 0.2–0.8 cm, with 14–60 sporangia	medial, ca. 4 mm from margin, 1–2 cm, with 20–40 sporangia	medial, 1–1.2 cm, with 40–90 sporangia	2–3 mm from margin, 2–4 mm, with 5–16 sporangia	ca. 1–2 mm from margin, ca. 0.2–1.2 cm, with 20–80 sporangia
Exospores	tuberculate-spinose	forked	verrucose	verrucose	spiculose
Distribution	Jiangcheng, Yunnan, China	Malipo, Yunnan, China	Lianhuachi, Taiwan, China	Xichou, Yunnan, China	Hekou, Yunnan, China
Reference	this study	He & Christenhusz 2013	Shieh 1970, Hsieh 2008	Ching & Wang 1982	Wang *et al.* 2021

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