



Discovery and genomic analysis of two newly recorded *Hydrobryum* in China (Podostemaceae), revealing underestimated biodiversity and phylogenetic insights

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ABSTRACT: During a botanical survey conducted from 2022 to 2023 in Fujian, China, initial identification through morphoanatomical studies and molecular phylogenetic analyses using the *matK* gene confirmed the presence of two species from the genus *Hydrobryum*: *H. floribundum* and *H. koribanum*. These findings represent new species records for China and established *Hydrobryum* as a newly recorded genus in Fujian. Previously known as endemic and rare in Japan, the discovery of these species in Fujian expands their geographical range and suggests a greater ecological adaptability than previously understood. Further analysis of their chloroplast genomes helped illuminate adaptive genetic variations that may contribute to the ecological success of these species in diverse environments.

KEY WORDS: Chloroplast genome, *Hydrobryum*, newly recorded species, phylogeny, taxonomy.

INTRODUCTION

Podostemaceae, an aquatic angiosperm family commonly known as river-weeds, is notable for its unique ecological and morphological adaptations to turbulent aquatic environments, such as waterfalls and rapids, which are predominantly found in tropical and subtropical regions (Philbrick and Alejandro, 1995; Cook and Rutishauser, 2007; Kato, 2016). These plants have evolved specialized features, including tenacious roots that adhere to submerged rock surfaces and a growth pattern transitioning from vertical to horizontal, enabling them to withstand seasonal water level changes and persist even during drought periods (Koi and Kato, 2012; Xue *et al.*, 2020). Consequently, Podostemaceae are valued as a model system for studying evolutionary and morphological dynamics in aquatic plants, attracting significant interest from evolutionary biologists (Koi and Kato, 2007; Rutishauser, 2016; Bedoya *et al.*, 2019; Katayama *et al.*, 2019; 2022; Koi and Kato, 2020; Xue *et al.*, 2020; Kato *et al.*, 2022; Chen *et al.*, 2022; Zhang *et al.*, 2022, 2024).

Phylogenetically, Podostemaceae belongs to Malpighiales, specifically the clusioid clade, and is closely related to Hypericaceae (Jin *et al.*, 2020a). Podostemaceae comprises over 340 species distributed across 60 genera, with a wide geographical distribution: approximately 155 species in the Americas, 90 in Africa and Madagascar, and around 100 in Asia and Australia (Katayama *et al.*, 2022; Kato *et al.*, 2022). Based on extensive *matK* data, Podostemaceae is classified into three subfamilies: Podostemoideae, Weddellinoideae,

and Tristichoideae, with Podostemoideae being the most diverse and globally distributed (Costa *et al.*, 2011; Koi and Kato, 2012; APG IV, 2016).

Hydrobryum, an Asian-endemic genus and the most taxonomically diverse within the subfamily Podostemoideae (Koi and Kato, 2019), is characterized by its crustose and foliose roots that spread over rock surfaces, short leafy shoots, and distinctive flattened, ribbed capsules (Cusset, 1992; Suzuki *et al.*, 2002; Kita and Kato, 2004; Cook and Rutishauser, 2007). Embryologically, *Hydrobryum* species exhibit a hypocotyl and two cotyledons, lacking a primary shoot and root during the embryo-seedling stage but developing adventitious and exogenous roots (Suzuki *et al.*, 2002; Koi *et al.*, 2012; Koi and Kato, 2020). With 33 recognized species, *Hydrobryum* has a broad geographical distribution across numerous Asian countries, including Assam, Bangladesh, China, East Himalaya, Japan, Laos, Myanmar, Nepal, Thailand and Vietnam (Grierson and Long, 1987; Hara *et al.*, 1982; Kato, 2008; Kato, 2011; Koi and Kato, 2012; Kress *et al.*, 2003; Mao *et al.*, 2016; Newman *et al.*, 2007; Pasha *et al.*, 2013; Wu and Raven, 2003). Thailand and Laos are particularly notable for hosting the highest species diversity within this genus, each with 16 known species (Werukamkul *et al.*, 2016, 2018; Koi and Kato, 2019). In China, historical records provide detailed documentation of two species: *H. griffithii* and *H. japonicum* (Tao, 1983; Kato and Kita, 2003).

In 2022–2023, during extensive fieldwork in Fujian province, China, we unexpectedly collected two additional specimens of *Hydrobryum*. Through morphological studies and phylogenetic analyses utilizing the *matK* gene, we

**Table 1.** Species accession of phylogenetic tree based on the *matK* sequences.

Species	Accession	Species	Accession	Species	Accession
<i>Cladopus austrosumiensis</i>	AB048371.1	<i>Hy. griffithii</i>	AB048373.1	<i>Hy. subcylindricoides</i>	LC384155.1
<i>Cl. fallax</i>	AB537378.1	<i>Hy. hapteron</i>	LC384149.1	<i>Hy. subcylindricum</i>	AB537405.1
<i>Cl. fukienensis</i>	LC144912.1	<i>Hy. japonicum</i>	AB537396.1	<i>Hy. taeniatum</i>	LC422807.1
<i>Cl. japonicus</i>	AB038189.1	<i>Hy. kaengsophense</i>	AB104565.1	<i>Hy. takakioides</i>	AB610241.1
<i>Cl. javanicus</i>	AB066175.1	<i>Hy. khaoyaiense</i>	LC151343.1	<i>Hy. varium</i>	AB610252.1
<i>Cl. nymanii</i>	AB104577.1	<i>Hy. koribanum</i>	AB048374.1	<i>Hy. verrucosum</i>	LC422816.1
<i>Cl. pierrei</i>	AB610228.1	<i>Hy. koribanum</i>	PP882865	<i>Hy. vientianense</i>	AB610250.1
<i>Cl. queenslandicus</i>	AB300702.1	<i>Hy. loeicum</i>	LC151346.1	<i>Hydrodiscus koyamae</i> 1	AB537382.1
<i>Cl. taiensis</i>	AB698212.1	<i>Hy. micrantherum</i>	AB104576.1	<i>Hyd. koyamae</i> 2	AB537381.1
<i>Ctenobryum mangkonense</i> 1	LC375211.1	<i>Hy. nakaiense</i>	LC384152.1	<i>Paracladopus chiangmaiensis</i> 1	AB537420.1
<i>Ct. mangkonense</i> 2	LC375212.1	<i>Hy. phetchabunense</i>	LC151352.1	<i>Pa. chiangmaiensis</i> 2	AB698348.1
<i>Hanseniella heterophylla</i> 1	AB104562.1	<i>Hy. phurueanum</i>	AB610251.1	<i>Podostemum distichum</i>	AB698349.1
<i>Ha. heterophylla</i> 2	LC151325.1	<i>Hy. puncticulatum</i>	AB104572.1	<i>Po. saldanhanum</i> 1	AB698354.1
<i>Hydrobryum bifoliatum</i>	AB104564.1	<i>Hy. ramosum</i>	LC422797.1	<i>Po. saldanhanum</i> 2	AB698355.1
<i>Hy. clandestinum</i>	LC384148.1	<i>Hy. somranii</i>	AB537402.1	<i>Thawatchaia laotica</i>	LC151396.1
<i>Hy. floribundum</i>	AB104571.1	<i>Hy. stellatum</i>	LC422798.1	<i>T. trilobata</i>	AB610476.1
<i>Hy. floribundum</i>	PP882864				

Notes: *Hydrobryum floribundum* (PP882864) and *H. koribanum* (PP882865) obtained from current study.

confirmed the discovery of two newly recorded species: *H. floribundum* and *H. koribanum*. This study aims to comprehensively describe these new records and provide phylogenetic insights that enhance the understanding of *Hydrobryum* within Podostemaceae.

MATERIALS AND METHODS

Material

Plant samples of *Hydrobryum floribundum* were collected from Jiuxi river, Xianyou County, Fujian province. *H. koribanum* was collected from Tingjiang river, Changting County, Fujian province. The voucher specimens (*Hydrobryum floribundum*: specimen No. FNU0041423, catalogue No. CBH04687; *Hydrobryum koribanum*: specimen No. FNU0041440, catalogue No. CBH04696) were deposited in the Herbarium of College of Life Sciences, Fujian Normal University (FNU).

Total DNA extract, genome assembly and annotation

In this study, total DNA was extracted from the fresh leaves of *Hydrobryum floribundum* and *H. koribanum* collected from Xianyou and Changting Counties, respectively, using the DNeasy Plant Mini Kit (Qiagen, Valencia, CA, USA). The DNA quantification, qualification and library preparation were performed by Berry Genomics Co. Ltd. (Beijing, China). The specific steps are as follows: The quality of isolated genomic DNA was through a combination of two methods: (1) DNA degradation and contamination were monitored on 1% agarose gels; (2) DNA concentration was measured using the Qubit® DNA Assay Kit in Qubit® 2.0 Fluorometer (Life Technologies, CA, USA). Library preparation was performed using the VAHTS® Universal Plus DNA Library Prep Kit for Illumina V2 (ND627-C1-

P1 (24 times /kit)). Genomic DNA samples were taken and enzymatically fragmented to a size of 350 bp. Subsequently, the DNA fragments were end polished, A-tailed, and ligated with the full-length adapter for Illumina sequencing. Finally, the libraries were analyzed for size distribution using agarose gels and were quantified by real-time PCR. Genome skimming was performed using next-generation sequencing technologies on the Illumina Novaseq 6000 platform (150 bp paired-end reads) by Berry Genomics Co. Ltd. (Beijing, China). To control library insert size, a dual-round magnetic based selection process was employed after Adapter Ligation when input DNA was ≥ 100 ng, utilizing 53 μ l magnetic beads in the first round and 12 μ l magnetic beads in the second to achieve a 400 bp insert size. Both species yielded 10 GB of data. The paired-end reads were filtered and assembled into the complete plastome using GetOrganelle v1.7.5, following the parameters described in Jin *et al.* (2020b). Specifically, the K-mer was set to '21, 45, 65, 85, 105' and the word size was set to 0.6. Following previous studies, our workflow includes five key steps as well: 1. Mapping reads to seed and assembling seed-mapped reads for parameter estimation; 2. Recruiting more target-associated reads through extending iterations; 3. Conducting de novo assembly; 4. Roughly filtering for target-like contigs; 5. Identifying target contigs and exporting all configurations (Langmead and Salzberg, 2012; Bankevich *et al.*, 2012; Camacho *et al.*, 2009; Jin *et al.*, 2020b). The final assembly graphs were visualized using Bandage (Wick *et al.*, 2015) to assess completeness. Gene annotation was performed using CPGAVAS2 (Shi *et al.*, 2019) and PGA (Qu *et al.*, 2019). Protein coding sequence annotations were confirmed using BLASTx. tRNAs were checked using tRNAscan-SE v2.0.3. Final chloroplast genome

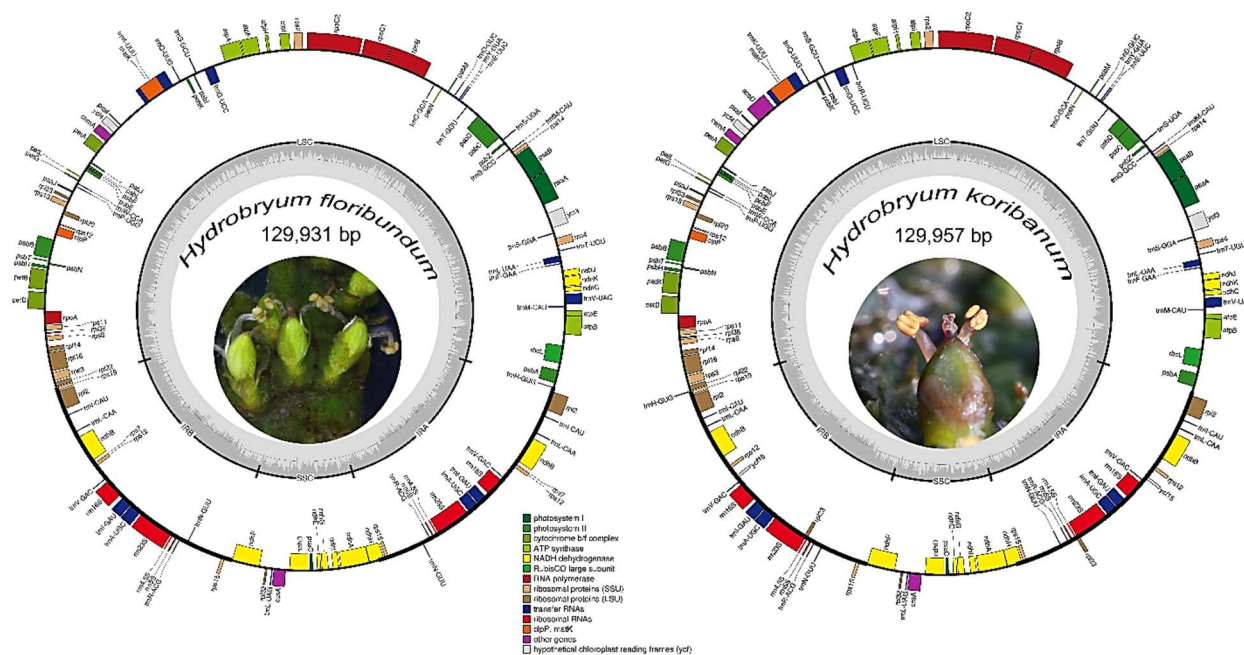


Fig. 1. Gene maps of *Hydrobryum floribundum* and *H. koribanum* complete chloroplast genomes. Genes inside the circle are transcribed clockwise, genes outside the circle counter clockwise.

maps were created using OGDRAW v1.3.1 (Greiner *et al.*, 2019). The *matK* gene was extracted from the chloroplast genome using Geneious prime v 2024.0.5.

Phylogenetic analyses

To confirm our identification results based on morphological characters, and to reveal the phylogenetic relationship of two newly recorded species within *Hydrobryum* and other closely related genera of the *Hydrobryum* subclade, we downloaded the *matK* sequences from Genbank and subsequently constructed a phylogenetic tree, which contains 49 species from 8 genera of Podostemaceae (Table 1). Among them, three species of *Podostemum* were used as outgroups.

To align the *matK* sequences for the phylogenetic analysis, we employed MAFFT v7.310 (Katoh and Standley, 2013) with default settings. For the phylogenetic analyses, different model - testing procedures were employed in IQ - TREE v1.6.8 and MrBayes v3.2.6. In IQ - TREE, ModelFinder evaluated 286 DNA models (sample size: 1831). Using the Bayesian Information Criterion (BIC), the optimal model was TVM+F+R3 (BIC = 16872.870) (Kalyanamoorthy *et al.*, 2017), which was selected by ModelFinder. Maximum likelihood phylogenies were inferred using IQ-TREE v1.6.8 (Nguyen *et al.*, 2015) under the model automatically selected by IQ-TREE ('Auto' option in IQ-TREE) for 2000 ultrafast (Minh *et al.*, 2013) bootstraps. In MrBayes v3.2.6 (Ronquist *et al.*, 2012), ModelFinder tested up to 24 DNA models (same sample size). Based on BIC, the best - fit model was GTR+F+G4 (BIC =

16911.739) (Kalyanamoorthy *et al.*, 2017). Bayesian Inference phylogenies were inferred with this model in two parallel runs of 2,000,000 generations, discarding the initial 25% of data as burn - in. Phylograms were visualized in ChiPlot v2.6.1 (Xie *et al.*, 2023).

RESULTS

The complete chloroplast genomes

Podostemaceae is notable for possessing one of the smallest chloroplast genomes within the Malpighiales order, with typical sizes around 130 kb (Bedoya *et al.*, 2019; Jin *et al.*, 2020a). In this study, we reported the complete chloroplast genomes of *Hydrobryum floribundum* and *H. koribanum*. The chloroplast genome of *H. floribundum* is 129,931 bp long and has a GC content of 35 % (Fig. 1). It exhibits the typical quadripartite structure found in chloroplast genomes, consisting of a pair of IR regions (20,329 bp), separated by an SSC region (11,761 bp) and an LSC region (77,512 bp). The genome encodes a total of 106 genes, including 73 protein-coding genes, 29 transfer RNA (tRNA), and 4 ribosomal RNA (rRNA) genes. Among these, 10 protein-coding genes and 6 tRNA genes contain introns (Table 2). Eight genes were identified as absent, including *rpl23*, *trnR-UCU*, *trnT-CGU*, *infA*, *ycf15*, and *rps16*, as well as the uncommon losses of *ycf1* and *ycf2*. Furthermore, an inversion of ~ 50 kb is observed in the LSC region, spanning from *rbcL* to *trnK-UUU*. The annotated chloroplast genome has been deposited in GeneBank, under accession number PP882864.

**Table 2.** Gene contents of the chloroplast genomes of *Hydrobryum floribundum* and *H. koribanum*.

Category, Group of Genes	<i>Hydrobryum floribundum</i>	<i>Hydrobryum koribanum</i>
Photosynthesis:		
Subunits of photosystem I	<i>psaA, psaB, psaC, psal, psaj</i>	<i>psaA, psaB, psaC, psal, psaj</i>
Subunits of photosystem II	<i>psbA, psbB, psbC, psbD, psbE, psbF, psbH, psbl, psbJ, psbK, psbL, psbM, psbN, psbT, psbZ</i>	<i>psbA, psbB, psbC, psbD, psbE, psbF, psbH, psbl, psbJ, psbK, psbL, psbM, psbN, psbT, psbZ</i>
Subunits of NADH dehydrogenase	<i>ndhA*, ndhB*(2), ndhC, ndhD, ndhE, ndhF, ndhG, ndhH, ndhI, ndhJ, ndhK</i>	<i>ndhA*, ndhB*(2), ndhC, ndhD, ndhE, ndhF, ndhG, ndhH, ndhI, ndhJ, ndhK</i>
Subunits of cytochrome b/f complex	<i>petA, petB*, petD*, petG, petL, petN</i>	<i>petA, petB*, petD*, petG, petL, petN</i>
Subunits of ATP synthase	<i>atpA, atpB, atpE, atpF*, atpH, atpI</i>	<i>atpA, atpB, atpE, atpF*, atpH, atpI</i>
Large subunit of rubisco	<i>rbcL</i>	<i>rbcL</i>
Self-replication:		
Proteins of large ribosomal subunit	<i>rpl14, rpl16*, rpl2*(2), rpl20, rpl22, rpl32, rpl33, rpl36</i>	<i>rpl14, rpl16*, rpl2*(2), rpl20, rpl22, rpl23(2), rpl32, rpl33, rpl36</i>
Proteins of small ribosomal subunit	<i>rps11, rps12*(2), rps14, rps15(2), rps18, rps19, rps2, rps3, rps4, rps7(2), rps8</i>	<i>rps11, rps12*(2), rps14, rps15(2), rps18, rps19, rps2, rps3, rps4, rps8</i>
Subunits of RNA polymerase	<i>rpoA, rpoB, rpoC1, rpoC2</i>	<i>rpoA, rpoB, rpoC1*, rpoC2</i>
Ribosomal RNAs	<i>rrn16S(2), rrn23S(2), rrn4.5S(2), rrn5S(2)</i>	<i>rrn16S(2), rrn23S(2), rrn4.5S(2), rrn5S(2)</i>
Transfer RNAs	<i>trnA-UGC*(2), trnC-GCA, trnD-GUC, trnE-UUC, trnF-GAA, trnG-GCC, trnG-UCC*, trnH-GUG, trnI-CAU(2), trnI-GAU*(2), trnK-UUU*, trnL-CAA(2), trnL-UAA*, trnL-UAG, trnM-CAU, trnN-GUU(2), trnP-UGG, trnQ-UUG, trnR-ACG(2), trnS-GCU, trnS-GGA, trnS-UGA, trnT-GGU, trnT-UGU, trnV-GAC(2), trnV-UAC*, trnW-CCA, trnY-GUA, trnM-CAU</i>	<i>trnA-UGC*(2), trnC-GCA, trnD-GUC, trnE-UUC, trnF-GAA, trnG-GCC, trnG-UCC*, trnH-UUC, trnI-CAU(2), trnI-GAU*(2), trnK-UUU* GUG, trnL-CAU(2), trnL-GAU*(2), trnK-UUU* trnL-CAA(2), trnL-UAA*, trnL-UAG, trnM-CAU, trnN-GUU(2), trnP-UGG, trnQ-UUG, CAU, trnR-ACG(2), trnR-UCU, trnS-GCU, trnS-GGA, trnS-UGA, trnT-UGU, trnT-GGU, trnT-UGU, trnV-GAC(2), trnV-UAC*, trnW-CCA, trnY-GUA, trnM-CAU</i>
Other genes:		
Maturase	<i>matK</i>	<i>matK</i>
Protease	<i>clpP</i>	<i>clpP</i>
Envelope membrane protein	<i>cemA</i>	<i>cemA</i>
Acetyl-CoA carboxylase	<i>accD</i>	<i>accD*</i>
c-type cytochrome synthesis gene	<i>ccsA</i>	<i>ccsA</i>
Genes of unknown function:		
Conserved hypothetical chloroplast ORF	<i>ycf3*, ycf4</i>	<i>ycf15(2), ycf3*, ycf4</i>

Notes: Gene*: Gene with one intron; Gene**: Gene with two introns; Gene (2): Number of copies of multi-copy genes.

Similarly, the chloroplast genome of *H. koribanum* measures 129,957 bp and has a GC content of 35.16% (Fig. 1). It also exhibits the quadripartite structure, with IR regions totaling 20,143 bp, an SSC region of 11,901 bp, and an LSC region of 77,770 bp. The genome encodes 109 genes, consisting of 75 protein-coding genes, 30 transfer RNA (tRNA), and 4 ribosomal RNA (rRNA) genes (Table 2). Among these, 11 protein-coding genes and 6 tRNA genes contain introns. A total of six genes were lost, including *trnT-CGU*, *infA*, *rps7*, *rps16*, *ycf1*, and *ycf2*. An inversion of ~ 50 kb is also present in the LSC region, spanning from *rbcL* to *trnK-UUU*. The annotated chloroplast genome has been deposited in GeneBank under accession number PP882865.

The phylogenetic analysis

The Phylogenetic analysis was constructed using the *matK* sequences (Fig. 2), which were extracted from the complete chloroplast genomes of *Hydrobryum floribundum* and *H. koribanum*, both 1,530 bp in length. The resultant phylogenetic tree exhibited a clustering pattern among samples from Fujian Province, China, and

Japan, with strong statistical support (Bootstrap probabilities /Bayesian posterior probabilities (BP/PP) = 100/1.00), which consistent with the results obtained through morphological identification. Notably, there were discrepancies in the phylogenetic relationships among *Thawatchia*, *Hydrobryum*, and *Hanseiella* when the trees constructed using different methodologies were compared. In the Maximum Likelihood (ML) phylogenetic tree, *Thawatchia* demonstrated a closer affinity to *Hydrobryum* (BP = 52) (Fig. 2A). Conversely, in the Bayesian phylogenetic tree, *Thawatchia* exhibited a closer relationship with *Hanseiella*, forming a sister group (PP = 0.44) (Fig. 2B). It is noteworthy that the phylogenetic analysis based on *matK* sequences provided only limited support for certain branches within the *Hydrobryum* clade. In particular, the clade comprising *H. loicum*, *H. phetchabunense*, and *H. vientianense* exhibited weak support (PP = 0.38) when grouped with the clade containing *H. japonicum*, *H. floribundum*, and *H. koribanum* (Fig. 2B). This observation suggests that the resolving power of *matK* sequences varies among species within the genus.

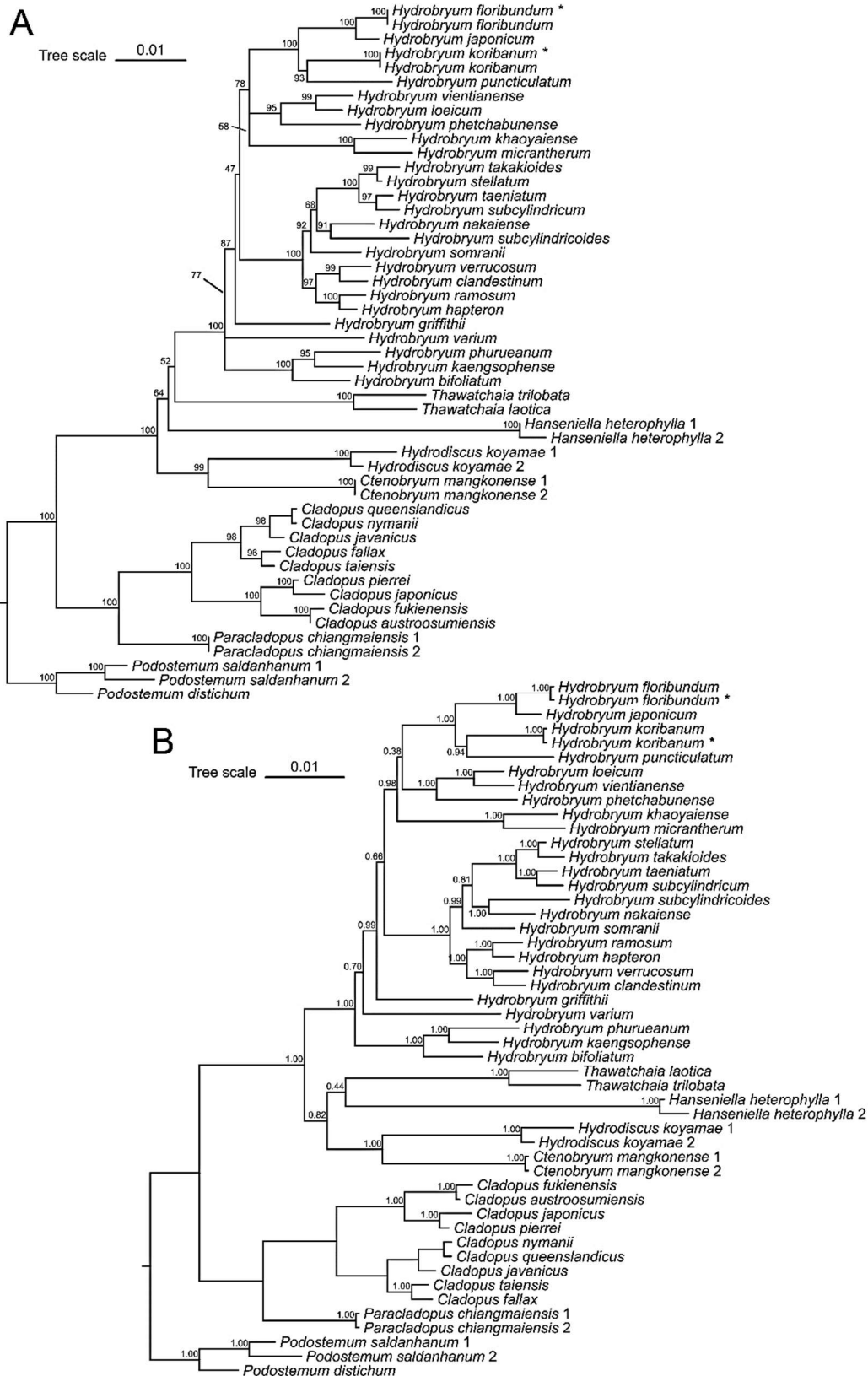


Fig. 2. The phylogram of **Podostemaceae** based on the *matK* sequences, **A.** The maximum likelihood (ML) phylogram, Numbers above the branches indicate bootstrap probabilities (BP). **B.** The Bayesian phylogram, Numbers above the branches indicate posterior probabilities (PP). *Hydrobryum floribundum** and *H. koribanum** are newly recorded species from China.



TAXONOMIC TREATMENT

Key to the species of *Hydrobryum* in China

1. Bracts 6; Ovules 52–54 per capsule 1. *H. griffithii*
– Bracts 2–4; Ovules 24–40 per capsule 2
2. Capsule ribs 11–13; leaves 8–10 per tuft 2. *H. japonicum*
– Capsule ribs ≤ 10 ; leaves ≤ 7 per tuft 3
3. Root 0.4–0.8 mm thick; Ovules 32–36 per capsule; leaves 2–5 per tuft 3. *H. koribanum*
– Root 0.2–0.3 mm thick; Ovules 26–30 per capsule; leaves 4–7 per tuft 4. *H. floribundum*

Hydrobryum floribundum Koidz, J. Jap. Bot. 6: 1 (1929)

Fig. 3

Examined specimens: CHINA. Fujian province, Xianyou County, Jiuxi river, elevation 400 m, 25°32' N, 118°37' E. 9 Dec. 2023, *Bing-Hua Chen* No. FNU0041423, catalogue No. CBH04687

Perennial aquatic herb; root thalloid, resembles lichen, adhere to the surface of underwater rocks, 0.22–0.25 mm thick, during the vegetative stage (Fig. 3A). Leaves linear, fascicled, 4–7 per tuft, 5.39–6.08 mm long (Fig. 3B–C). Flowers hermaphroditic, solitary, scattered on dorsal surface of root; spathe, ellipsoid, fascicled, 2.18–2.38 mm long, 1.21–1.32 mm wide, rupturing irregularly near the apex (Fig. 3D–E). Tepals 2, linear, almost equalling ovary; stamens 2, Y-shaped, 2.15–2.41 mm long; anthers 2, ovoid, yellow (Fig. 3F–G). Ovary single, ellipsoid, bright green, two-chambered, 2.05–2.44 mm long, 0.96–1.04 mm wide; stigmas 2, short, thickly subulate (Fig. 3F). Capsules ellipsoid, oblate, dark reddish brown, 2.12–2.59 mm long, 1.02–1.15 mm wide, slender longitudinal ribs on the surface, ribs 10, capsule sperm 0.84–0.95 mm long (Fig. 3H). Placenta, oval; seeds long oval, 26–30 per capsule, attached to entire placenta (Fig. 3I–J).

Phenology: Florescence occurs from November to December, with the fruiting season from December to January.

Distribution and habitat: Japan (Kagoshima Pref., southern Kyushu); new record for China (Guangxi province; Fujian province, Xianyou County, Jiuxi river). Originally described from Japan (Kyushu) and considered endemic.

Etymology: It is recommended to name it in Chinese: “Duō Huā Shuǐ Shí Yī” (多花水石衣), according to specific epithet “*floribundum*” meaning multi-flowered.

Hydrobryum koribanum Imamura ex Nakay. & Minamitani, J. Jap. Bot. 74: 314 (1999)

Fig. 4

Examined specimens: CHINA. Fujian province, Changting County, Tingjiang river, elevation 370 m, 25°55' N, 116°29' E. 21 Jan. 2024, *Bing-Hua Chen* No. FNU0041440, catalogue No. CBH04696

Perennial aquatic herb; lives in turbulent rivers, adhering to submerged rock surface in open and sunny habitat (Fig. 4A). Root thalloid, resembles lichen, 0.35–0.78 mm thick, during the vegetative stage (Fig. 4B–C).

Leaves linear, fascicled, 2–5 per tuft, 2.87–4.34 mm long (Fig. 4B–D). Flowers hermaphroditic, solitary, scattered on dorsal surface of root; spathe, ellipsoid, flattened, 1.55–1.65 mm long, 1.12–1.30 mm wide (Fig. 4E–F). Stamens 2, 2.93–3.01 mm long; anther 2, ovoid, yellow; tepals 2, linear, almost equalling ovary (Fig. 4G–I). Ovary single, ellipsoid, bright green, two-chambered, 1.91–2.38 mm long, 1.09–1.50 mm wide; stigmas 2, short, V-shaped (Fig. 4J). Capsules ellipsoid, dark reddish brown, 2.10–2.38 mm long, 1.13–1.33 mm wide, slender longitudinal ribs on the surface, ribs 8, capsule sperm 0.92–1.16 mm long (Fig. 4K). Placenta oval; seeds long oval, 32–36 per capsule, attached to entire placenta (Fig. 4L–N).

Phenology: Florescence October to November, fruiting season November to January.

Distribution and habitat: Japan (Yakushima Island, southern Kyushu); new record for China (Fujian province, Changting County, Tingjiang river). Originally described from Japan (Kyushu) and considered endemic.

Etymology: It is recommended to name it in Chinese: “Gōng Qí Shuǐ Shí Yī” (宫崎水石衣), which was firstly discovered in Japan Kyushu Miyazaki-ken (Nakayama and Minamitani, 1999).

DISCUSSION

This study substantially revises the known distribution of *Hydrobryum floribundum* and *H. koribanum*, species previously believed to be endemic to Japan, with *H. floribundum* first discovered in 1928 in the Maegawa River, Shibushi, Kagoshima Prefecture, Kyushu (Koidzumi, 1929), and *H. koribanum* discovered by S. Imamura in the Iwase River, Nishimorokata, Miyazaki Prefecture, Kyushu, and described in detail by Nakayama and Minamitani in 1999 (Nakayama and Minamitani, 1999). Their endemism and scarcity in Japan were confirmed in 2008 (Kato, 2008). However, between 2022 and 2023, we found abundant wild populations of both species in Fujian Province, China. While the chloroplast genome of *H. floribundum* has been reported (Li *et al.*, 2024), detailed morphological and geographic distribution analyses were lacking. Our findings suggest a continuous distribution of both species across East Asia, with mainland China possessing richer resources. Notably, *H. floribundum* exhibits a broader distribution, indicating a primary concentration in China.

Climate has emerged as a pivotal factor in determining the distribution of *Hydrobryum* species. Both *H. floribundum* and *H. koribanum* thrive in regions characterized by a subtropical monsoon climate, as observed in Fujian, China, and along the Iwase River in Japan. This preference for monsoon climates is consistent with observations made by Kato *et al.* (2022), who noted a similar habitat selection among other Podostemaceae species. The presence of related species such as *H. japonicum* and *H. griffithii* in comparable climatic zones

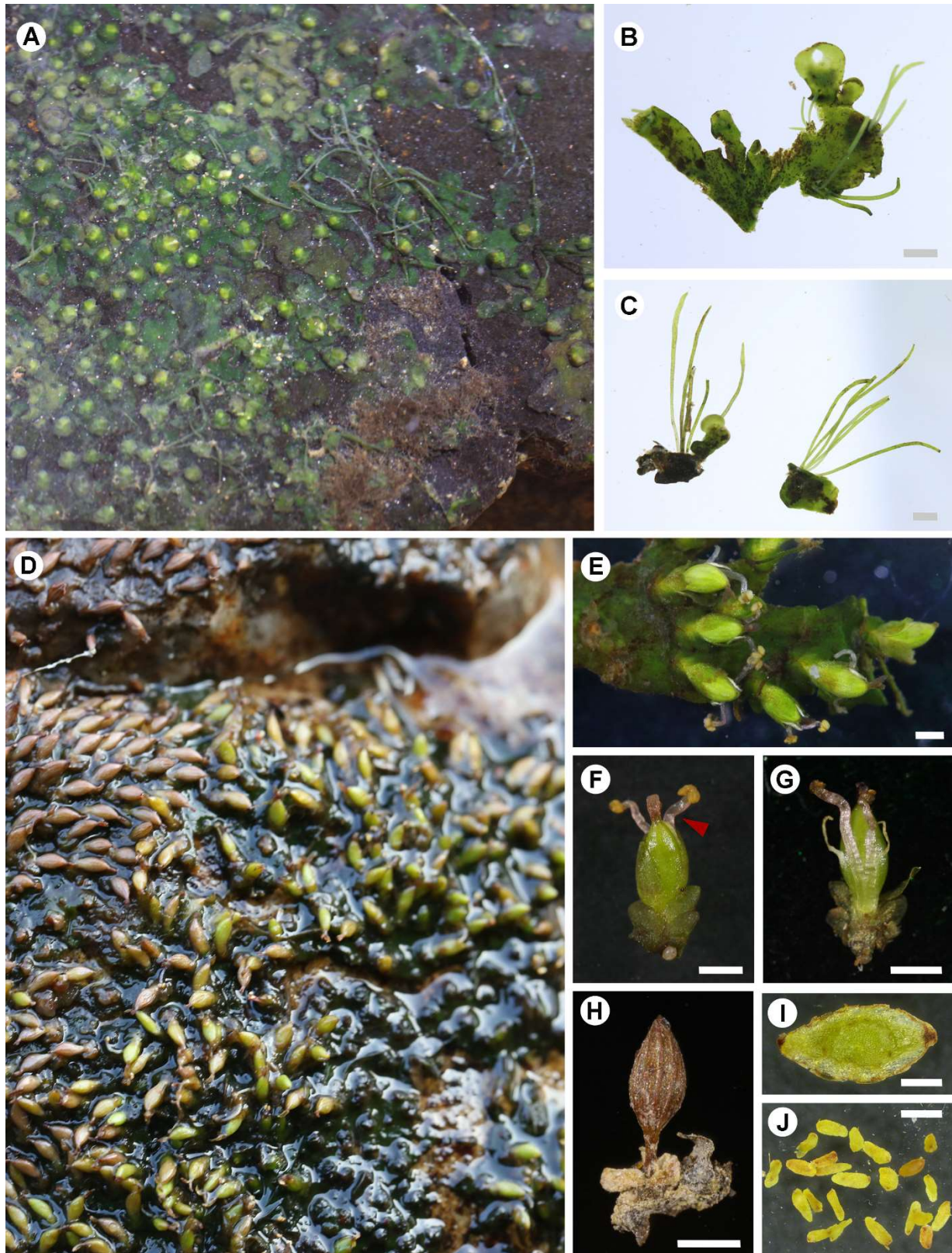


Fig. 3. *Hydrobryum floribundum*. **A.** Habitat, showing leaves, buds and flaky root; **B.** Flaky root with trophophyll; **C.** Trophophyll, a cluster including 5–6 leaves. Scale bars: B–C= 1 mm. **D.** Flowering and fruiting period, showing flowers, unripe fruits and flaky root; **E.** Fully blooming flowers; **F.** Frontal view of a flower, two stamens as shown by the arrow; **G.** A flower (spatella removed), showing two stamens and two filaments; **H.** Ripe fruits; **I.** Oval placenta; **J.** Seeds. Scale bars: E–G=1 mm; H–I=200 μ m.

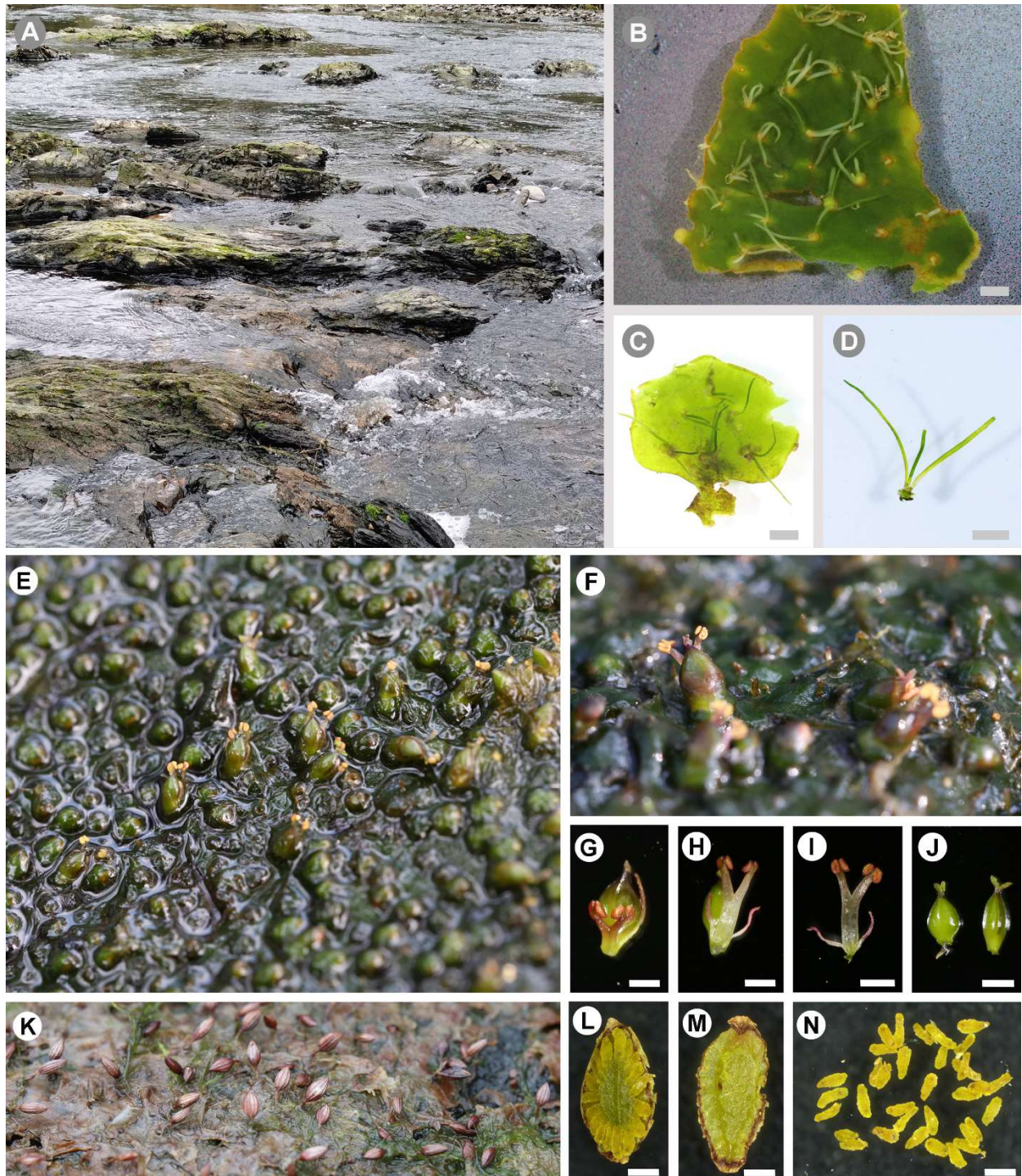


Fig. 4. *Hydrobryum koribanum*. **A.** Habitat; **B–C.** Flaky root with trophophyll; **D.** A tuft of trophophyll, including 3 leaves. Scale bars: B–D=1 mm. **E.** Flowering and fruiting period, showing flowers, unripe fruits and flaky root; **F.** Fully blooming flowers; **G–H.** The internal structure of the flower (spathella removed), showing two stamens and two filaments; **I.** Stamens and filaments (ovary removed); **J.** Two oval ovaries; **K.** Ripe fruits; **L.** Oval placenta with seeds; **M.** Oval placenta (seeds removed); **N.** Seeds. Scale bars: G–J=1 mm; L–N=150 μ m.

further corroborates this pattern. Nonetheless, to fully understand the intricacies of this relationship, further studies incorporating long-term climate data, detailed plant physiological research, and genetic analyses are essential.

The abundant resources of *Hydrobryum* in neighboring Thailand and Laos, which each host 16 species as documented by Koi and Kato (2012, 2015, 2019) and Werukamkul *et al.* (2016, 2018), suggest a



promising potential for similar biodiversity in the tropical and subtropical regions of southern China. The continuous distribution and climatic adaptability of these species underscore the likelihood of undiscovered *Hydrobryum* resources within China. This inference is supported by recent genomic advancements and discoveries in China, such as the decoding of the complete genome of *Cladopus chinensis* (Xue *et al.*, 2020), and the identification of new species and records like *Polypleurum chinense* (Chen *et al.*, 2022), *Paracladopus chiangmaiensis* (Wu *et al.*, 2022), and *Terniopsis yongtaiensis* (Zhang *et al.*, 2022). These findings indicate that the diversity of Podostemaceae in China has been significantly underestimated. Continued in-depth investigations are essential to reveal the full extent of Podostemaceae distribution and to validate the potential richness of this genus in China.

The analysis of the chloroplast genomes of *H. floribundum* and *H. koribanum* has provided important insights into the genomic evolution within Podostemaceae. Both species exhibit the loss of the *rps16* gene, a trait commonly observed in most Malpighiales, which underscores a conserved evolutionary pattern (Bedoya *et al.*, 2019). Notably, *H. floribundum* also exhibits the loss of the *ycf15* gene, found in the IR region of the chloroplast genome. Since its initial identification in the chloroplast genome of *Nicotiana* (Shinozaki *et al.*, 1986), the functionality of the *ycf15* gene has been questioned, with many studies suggesting it may be a pseudogene or that its evolutionary loss in many angiosperms affects its protein-coding capability (Chumley *et al.*, 2006; Shi *et al.*, 2013; Steane, 2005). The specific absence of *ycf15* in *H. floribundum* points to potential adaptive variations, highlighting the need for further studies to explore its functional implications and adaptive significance. Additionally, the relocation of the *rps15* gene from the SSC to the IR region aligns with similar genomic rearrangements observed in other Podostemaceae, except for *Tristicha trifaria*, where it is located at the SSC/IRA boundary (Bedoya *et al.*, 2019; Jin *et al.*, 2020a; Chen *et al.*, 2022; Zhang *et al.*, 2022). Moreover, the uncommon loss of *ycf1* and *ycf2*, along with the major inversion between *rbcL* and *trnK-UUU*, are consistent features within Podostemaceae (Bedoya *et al.*, 2019; Wu *et al.*, 2022). These genomic rearrangements likely represent synapomorphies that distinguish Podostemaceae from other Malpighiales (Bedoya *et al.*, 2019) and may reflect adaptive responses to environmental pressures or historical biogeographical events. Further comparative genomic studies across more species within Podostemaceae could clarify the evolutionary importance of these genomic features and their role in the family's diversification.

The phylogenetic analysis of the *Hydrobryum* subclade reveals a complex evolutionary history with unresolved relationships among its members (Koi and

Kato, 2012; Werukamkul *et al.*, 2018; Wu *et al.*, 2022). This subclade is divided into two primary clades: one comprising *Hydrobryum*, *Hanseniella*, and *Thawatchaia*, and the other formed by *Ctenobryum* and *Hydrodiscus*, suggests an intricate pattern of divergence and convergence influenced by both genetic and environmental factors. Previous studies have indicated weak statistical support (BS_{ML}=47) for the subclade formed by *Hanseniella* and *Thawatchaia* (Koi and Kato, 2012, 2020; Wu *et al.*, 2022). Conversely, our phylogenetic reconstruction shows low bootstrap support (BP=52) for a closer relationship between *Thawatchaia* and *Hydrobryum* in the maximum likelihood phylogram of Podostemaceae (Fig. 2A). Morphological similarities between *Thawatchaia* and *Hydrobryum*, including the structure of flowering shoots (appressed or oblique or only flowers erect) and bracts (in two ranks, uniform, simple or trilobed) (Kato and Koi, 2009), further complicate the phylogenetic scenario. These similarities suggest potential instances of convergent evolution or the retention of ancestral traits. Limited molecular data, especially for *Thawatchaia*, *Hanseniella*, *Ctenobryum*, and *Hydrodiscus*, contributes to these uncertainties. Thus, extensive field investigation and comprehensive data collection in China are crucial to resolve these phylogenetic relationships and deepen our understanding of the evolutionary history of *Hydrobryum* subclade.

To effectively conserve the biodiversity of this genus, maintaining the integrity of its natural habitats is paramount. Specific actions proposed include prohibiting the construction of reservoirs within the habitats, banning modifications to river channels and the extraction of stream stones, and enforcing stringent controls on wastewater discharges in the surrounding areas. Furthermore, considering these two species are not currently included in the "Updated List of National Key Protected Wild Plants (Decree No. 15)," it is essential to advocate for their addition in the next update of the list. These measures are critical for the preservation of the unique ecosystems these riverine species inhabit.

CONCLUSION

This study contributes to the understanding of the *Hydrobryum* genus in China by documenting two species, *Hydrobryum floribundum* and *H. koribanum*, that were not previously recorded in the country. This discovery increases the known number of *Hydrobryum* species within Chinese flora from two to four. For the first time, the complete chloroplast genome of *H. koribanum* was analyzed, providing valuable genetic information. The presence of these species in China extends the known distribution of *Hydrobryum* beyond Japan, highlighting the underestimated biodiversity of this genus in the region. Genomic analyses identified common gene losses, such as *rps16* in both species, and specific losses of *ycf15* in *H.*



floribundum, suggesting the presence of adaptive genetic variations that may contribute to the ecological success of these species. Phylogenetic analysis using *matK* sequences has confirmed the taxonomic identification of these newly recorded species and has illuminated the relationships within the *Hydrobryum* subclade, although some phylogenetic links remain unresolved. In conclusion, this research significantly expands our knowledge of *Hydrobryum* diversity and the evolutionary dynamics of *Hydrobryum* in China, emphasizing the importance of genomic investigations and continued field explorations to uncover the hidden richness of this understudied region.

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