



OPEN ACCESS

EDITED BY
Saraj Bahadur,
Hainan University, China

REVIEWED BY
Hanwen Xiao,
Nanjing Forestry University, China
Liang Jin,
Zhejiang Academy of Agricultural
Sciences, China
Senthilkumar Umapathy,
Madras Christian College, India

*CORRESPONDENCE
Wen-Zhuan Huang
✉ wzhmoss@163.com
Yu-Huan Wu
✉ yuhuanwu@hznu.edu.cn

RECEIVED 30 March 2026
REVISED 18 May 2026
ACCEPTED 20 May 2026
PUBLISHED 09 June 2026

CITATION

Huang W-Z, Liu Y-S, Ma X-Y, Wang Q-H,
Ma W-Z, Zhu R-L, Zheng T-X and
Wu Y-H (2026) New moss taxa from
Eastern Himalaya: Plastid genomics
supports the establishment of
Scabridentaceae fam. nov. and the
description of *Scabridens gaochienii*
sp. nov. (Hypnales, Bryophyta).
Front. Plant Sci. 17:1842480.
doi: 10.3389/fpls.2026.1842480

COPYRIGHT

© 2026 Huang, Liu, Ma, Wang, Ma, Zhu,
Zheng and Wu. This is an open-access
article distributed under the terms of the
[Creative Commons Attribution License](#)
(CC BY). The use, distribution or
reproduction in other forums is
permitted, provided the original
author(s) and the copyright owner(s) are
credited and that the original publication
in this journal is cited, in accordance
with accepted academic practice. No
use, distribution or reproduction is
permitted which does not comply with
these terms.

New moss taxa from Eastern Himalaya: Plastid genomics supports the establishment of Scabridentaceae fam. nov. and the description of *Scabridens gaochienii* sp. nov. (Hypnales, Bryophyta)

Wen-Zhuan Huang^{1,2,3*}, Yu-Si Liu^{2,3}, Xin-Yin Ma^{2,3},
Qing-Hua Wang⁴, Wen-Zhang Ma⁵, Rui-Liang Zhu⁶,
Tian-Xiong Zheng⁷ and Yu-Huan Wu^{2,3*}

¹College of Life Sciences, South China Agricultural University, Guangzhou, China, ²College of Life and Environmental Sciences, Hangzhou Normal University, Hangzhou, China, ³Zhejiang Provincial Key Laboratory of Wetland Intelligent Monitoring and Ecological Restoration, Hangzhou Normal University, Hangzhou, China, ⁴State Key Laboratory of Plant Diversity and Specialty Crops, Institute of Botany, Chinese Academy of Sciences, Beijing, China, ⁵Herbarium, Key Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan, China, ⁶Bryology Laboratory, Department of Biology, School of Life Sciences, East China Normal University, Shanghai, China, ⁷Hattori Botanical Laboratory, Nichinan, Japan

The Himalayas represent a globally significant biodiversity hotspot, yet bryophyte diversity remains insufficiently explored, especially in some inaccessible areas. During recent field surveys in Motuo County, Xizang, China, we collected an unusual moss species resembling *Scabridens* E.B.Bartram but differing in gametophyte morphology, most notably by a short double costa. To clarify its taxonomic position, we assembled and annotated 20 complete chloroplast genomes from Cryphaeaceae, Leucodontaceae, and Pterobryaceae, and analyzed these alongside 29 additional Hypnales accessions. Comparative plastome analyses revealed conserved structures across these lineages, with minor variations in genome size, GC content, and IR boundary regions. Phylogenomic analyses revealed the unknown taxon as sister to *S. sinensis* E.B.Bartram with strong support. Morphologically, it differs from *S. sinensis* by a short double costa, leaf margins revolute from the base to near the apex, and longer setae. Both morphological and molecular evidence support the recognition of this unknown taxon as a new species, which we described here as *S. gaochienii* W.Z.Huang & Y.Huan Wu. Furthermore, although *Scabridens* is sister to Cryphaeaceae in plastid phylogenies, its pronounced morphological distinctiveness supports the recognition of a new family, Scabridentaceae W.Z.Huang & Y.Huan Wu, to accommodate the genus. Our results highlight the power of plastid phylogenomics in resolving complex relationships in Hypnales and underscore the eastern Himalayas as a priority region for bryophyte diversity exploration.

KEYWORDS

China, chloroplast genome, mosses, new family, new species

1 Introduction

The Himalayas are recognized as one of the world's major biodiversity hotspots (Mittermeier et al., 2004; Orme et al., 2005) and rank among the most bryophyte-rich regions globally (Groombridge, 1992). Characterized by lush vegetation, this region serves as a repository for numerous globally significant plant species (Kandel et al., 2019), and has long been known as the “world's biological gene bank” (Zhu et al., 2023). Motuo County, located in the eastern Himalayas, encompasses an exceptional elevation gradient of 7,000 m, ranging from tropical rainforests to a permanent glacier, and supports highly heterogeneous habitats with abundant light, heat, and water resources. This county was the last area to be connected to the outside by highway, with the road completed in 2013. Due to its difficult access, biodiversity surveys have been limited, and many areas remain poorly explored. In recent years, several new taxa have been described from this region based on recent collections, such as *Vaccinium motuoense* Y.H.Tong & Y.J.Guo (Tong et al., 2021), *Ficus motuoensis* Zhen Zhang & Hong Qing Li (Zhang et al., 2022), *Stellaria motuoensis* Meng Li & Y.F.Song (Li et al., 2022), *Kuhlhasseltia motuoensis* X.H.Jin & C.Ye (Ye et al., 2023), *Uncifera motuoensis* M.Z.Huang, Xue D.Chen & M.K.Li (Huang et al., 2024), etc. However, few of these discoveries pertain to bryophytes, with the exception of *Dicranum motuoense* W.Z.Huang, Tubanova & Y.Huan Wu (Huang et al., 2025), *Pseudotrachypus motuoensis* Y.X.Tian, Q.Zuo & Li Zhang (Tian et al., 2025), and *Ptychanthus striatus* var. *motuoensis* Jian Wang bis, Gradst. & R.L.Zhu (Dai et al., 2021). Obviously, the bryophyte diversity of Motuo County remains substantially underestimated.

Leucodontaceae is a family of mosses primarily distributed in the temperate zones, often growing on tree trunks and branches (Zhang, 2011a). Currently, this family comprises five genera worldwide (Brinda and Atwood, 2026): three monotypic genera (*Dozya* Sande Lac., *Eoleucodon* H.A.Mill. & H.Whittier, and *Scabridens* E.B.Bartram); *Pterogoniadelphus* M.Fleisch. with two species; and *Leucodon* Schwägr. with 33 species. *Scabridens* is a genus endemic to China, consisting solely of one rare species, *S. sinensis* E.B.Bartram (Bartram, 1935), found in the southwestern region (Zhang, 2011a; Jia and He, 2013). Morphologically, the genus is characterized by erect and simple stems, a single long costa, papillose peristome teeth, smooth capsules, serrate upper leaf margins, and an autoicous sexual condition (Bartram, 1935; Frey and Stech, 2009). Notably, this sexual condition is unusual in Leucodontaceae, where all other taxa are dioicous. Recent plastome-based phylogenetic analyses have shown that *Scabridens* and *Leucodon* Schwägr. do not form a monophyletic group; instead, *Scabridens* is revealed as sister to Cryphaeaceae (Li et al., 2024). However, as the study did not discuss this topological relationship or propose corresponding taxonomic treatments, the systematic placement of *Scabridens* remains unresolved and requires further reassessment.

During our fieldwork in Motuo County, Xizang, China (Huang et al., 2025; Tian et al., 2025), we collected an unusual moss with gametophytic features reminiscent of *Leucodon*, including clearly differentiated alar cells and a short double costa (Frey and Stech, 2009; Zhang, 2011a). However, its sporophytic features are markedly

different, such as a reduced endostome, papillose exostome teeth, and an autoicous sexual condition, which are more consistent with *Scabridens* (Bartram, 1935; Frey and Stech, 2009; Zhang, 2011a). Nevertheless, this unknown taxon can be distinguished from known *Scabridens* species by a unique combination of traits, notably a short double costa and leaf margins strongly revolute from the base to near the apex. These unique morphological characters prompted further integrative investigation.

The reconstruction of a reliable and unequivocal phylogeny of bryophytes is essential for elucidating the mechanisms underlying plant terrestrialization (Bechteler et al., 2023; Shen et al., 2024; Xu et al., 2026). However, phylogenetic reconstructions based on limited DNA loci are inadequate to resolve the relationships within Hypnales (Cox et al., 2010; Li et al., 2024). Compared with short DNA markers, complete chloroplast genomes provide substantially more phylogenetically informative characters and greater structural stability, and have emerged as powerful tools for resolving bryophyte evolution relationships (Yu et al., 2019; Xiang et al., 2022; Li et al., 2024; Xu et al., 2026). In this study, we conduct a plastid phylogenomic investigation of Hypnales, with a particular focus on the Cryphaeaceae, Leucodontaceae, and Pterobryaceae clades, by integrating newly sequenced and publicly available plastome data across 18 families. Specifically, we aim to: (1) generate and annotate complete plastomes for 20 newly sampled accessions within the focal clades; (2) characterize plastome evolution in these clades through comparative analyses of genome structure and sequence variation; (3) test the taxonomic status of the Motuo taxon, and evaluate whether it represents a new species using combined morphological and phylogenetic evidence; and (4) reassess higher-level relationships and family delimitation surrounding *Scabridens*, and provide formal taxonomic revisions where warranted.

2 Material and methods

2.1 Taxon sampling and sequencing

A total of 20 specimens were newly collected and sequenced for this study, including eight from Cryphaeaceae, five from Leucodontaceae, two from Pterobryaceae, four representing *Scabridens*, and one unidentified lineage from the Himalayas (Table 1). All specimens were identified by Wen-Zhuan Huang. Voucher specimens are deposited in the Herbarium of Hangzhou Normal University (HTC), the Herbarium of East China Normal University (HSNU), and the Herbarium, Institute of Botany, CAS (PE). To broaden the phylogenetic context, 29 additional Hypnales accessions were included, and three Orthotrichaceae accessions were selected as outgroups.

Prior to DNA extraction, visible contaminants (e.g., algae, fungi, and soil debris) were removed from all samples. Total genomic DNA was extracted using a modified CTAB protocol (Huang et al., 2019). PCR-free libraries with an insert size of 800 bp were constructed using the Illumina TruSeqTM DNA PCR-free library preparation kit (Illumina, CA, USA), and sequenced on the Illumina NovaSeq 6000 platform (Novogene, Beijing, China) to

TABLE 1 Taxa, DNA code, voucher, herbarium acronyms, localities, and GenBank accession numbers of species newly sequenced in this study.

No.	Species	DNA Code	Vouchers (herbarium code)	Locality	GenBank
1.	<i>Cyrtodontopsis leveillei</i>	HTC478	W.-Z. Ma 13-5136 (KUN)	China: Yunnan	PZ196757
2.	<i>Dozya japonica</i>	HTC422	T. Yamaguchi 42638 (HIRO)	Japan: Kyushu	PZ196758
3.	<i>Leucodon exaltatus</i>	HTC421	W.-Z. Huang 20250928-15 (HTC)	China: Xizang.	PZ196759
4.	<i>Leucodon sciurioides</i>	HTC305	M. Sulayman 281783 (XJU)	China: Xinjiang	PZ196760
5.	<i>Leucodon secundus</i> var. <i>strictus</i>	HTC318	W.-Z. Huang 20250830-29 (HTC)	China: Qinghai	PZ196761
6.	<i>Leucodon secundus</i> var. <i>strictus</i>	HTC393	W.-Z. Huang 20250929-110 (HTC)	China: Xizang	PZ196762
7.	<i>Pilotrichopsis dentata</i>	HTC151	W.-Z. Huang et al., 20250322-18 (HTC)	China: Zhejiang	PZ196763
8.	<i>Pterobryopsis acuminata</i>	HTC419	W.-Z. Huang 20250929-115 (HTC)	China: Xizang	PZ196764
9.	<i>Scabridens sinensis</i>	HTC166	W.-Z. Ma 20-10936 (KUN)	China: Xizang	PZ196765
10.	<i>Scabridens sinensis</i>	HTC167	W.-Z. Ma 19-10918 (KUN)	China: Xizang	PZ196766
11.	<i>Scabridens sinensis</i>	C89	L. Lian 206 (PE)	China: Sichuan	PZ196767
12.	<i>Scabridens sinensis</i>	HTC168	W.-Z. Ma 15253 (KUN)	China: Sichuan	PZ196768
13.	<i>Scabridens gaochienii</i>	HTC083	W.-Z. Huang & F.-Y. Zhang 20241012-71 (HTC)	China: Xizang	PZ196769
14.	<i>Schoenobryum concavifolium</i>	H53	W.-Z. Huang & S.-H. Lu 20210908-26 (HSNU)	China: Yunnan	PZ196770
15.	<i>Schoenobryum concavifolium</i>	HTC488	W.-Z. Ma 12588 (KUN)	China: Yunnan	PZ196771
16.	<i>Schoenobryum concavifolium</i>	HTC489	J.R. Shevock 54140 (KUN)	China: Yunnan	PZ196772
17.	<i>Schoenobryum concavifolium</i>	W16	Q.-H. Wang 2002 (PE)	China: Yunnan	PZ196773
18.	<i>Sphaerotheciella sphaerocarpa</i>	C88	M.-Z. Wang 202104-0792 (PE)	China: Sichuan	PZ196774
19.	<i>Sphaerotheciella sinensis</i>	H50	W.-Z. Huang et al., 20210529-19 (HSNU)	China: Yunnan	PZ196775
20.	<i>Sphaerotheciella sinensis</i>	H51	W.-Z. Huang et al., 20210529-15 (HSNU)	China: Yunnan	PZ196776

generate paired-end 150 bp reads, About 5 Gb of raw sequences were accumulated. All newly assembled plastomes were deposited in GenBank (Table 1).

2.2 Plastome assembly and annotation

Raw reads were quality-filtered by removing low-quality bases (Phred score < 30). High-quality reads were assembled using GetOrganelle v.1.7.5 (Jin et al., 2020). Initial plastome annotation was performed with CPGAVAS2 (Shi et al., 2019) and manually refined in Geneious Prime 2022 (www.geneious.com), using *Calyptothecium philippinense* Broth. (GenBank accession number: OL415138) as the reference. Genome visualization was conducted using CPGView (Liu et al., 2023).

2.3 Comparative analyses of plastomes

To assess structural conservation and potential rearrangements, plastomes were compared using mVISTA under the LAGAN model (Frazer et al., 2004). Expansion and contraction patterns at inverted repeat (IR) boundaries were further examined, and junction shifts among the LSC/IR/SSC regions were visualized using IRScope (https://irscope.shinyapps.io/IRplus/).

2.4 Phylogenetic analyses

82 protein-coding genes were aligned individually using MAFFT v.7.505 (Katoh and Standley, 2013) with the “-auto” strategy. Ambiguously aligned regions were removed manually,

and the processed alignments were concatenated for downstream analyses. Phylogenetic inference was conducted using both maximum likelihood (ML) and Bayesian inference (BI). For ML analysis, IQ-TREE v2.0.6 was used (Minh et al., 2020) with the GTR+F+I+R4 substitution model, selected under the Bayesian Information Criterion (BIC) in Modeltest v.3.7 (Chernomor et al., 2016; Kalyaanamoorthy et al., 2017). Node support was evaluated with 1,000 bootstrap replicates (ML-BS). For BI analysis, MrBayes v.3.2.6 (Ronquist et al., 2012) was run under the GTR+I+G model selected by PartitionFinder2 based on the Akaike Information Criterion (AIC) (Lanfear et al., 2017). The Markov chain Monte Carlo (MCMC) algorithm was run for 5,000,000 generations, with two parallel runs and default settings, a random starting tree and tree sampling every 1000 generations. The posterior distribution of trees was summarized by a > 50% majority-rule consensus tree after discarding the first 25% of samples as burn-in. Convergence was assessed by examining likelihood plots in Tracer v.1.7 (Rambaut et al., 2018).

3 Result

3.1 Characteristics of plastomes

All plastomes from Cryphaeaceae, Leucodontaceae, and Pterobryaceae exhibited the typical quadripartite structure of land plant chloroplast genomes, consisting of a large single-copy (LSC) region, a small single-copy (SSC) region, and two inverted repeats

(IRs) (Figure 1A). Total plastome size varied only slightly, ranging from 124,390 to 127,332 bp. The LSC region ranged from 86,527 to 87,405 bp, the SSC region from 18,389 to 18,706 bp, and each IR from 18,742 to 21,884 bp (Figure 1B; Supplementary Table 1). In particular, plastomes of *Leucodon* were consistently larger (127,297 bp–127,332 bp) than those of the remaining genera (123,390 bp to 125,117 bp) (Figure 1B; Supplementary Table 1). Overall GC content was highly conserved across taxa (28.2% to 28.7%) (Figure 1B; Supplementary Table 1). As expected, GC content was lower in LSC (25.3%–25.8%) and SSC (24.8%–25.4%) regions than in the IR regions (42.6%–44.9%). Notably, IR GC content was lower in *Leucodon* (42.6%–42.8%) than in other genera (44.2% to 44.9%) (Figure 1B; Supplementary Table 1).

All sampled plastomes contained 127 genes, including 82 protein-coding genes (CDS), 37 transfer RNA (tRNA) genes and 8 ribosomal (rRNA) genes (Figure 1A; Supplementary Table 2). Eighteen genes contained introns. Among them, *rps12*, *clpP* and *ycf3* each contained two introns, whereas *atpF*, *ndhA*, *ndhB*, *petB*, *petD*, *rpoC1*, *rpl2*, *rpl16*, *trnA-UGC*, *trnG-UCC*, *trnI-GAU*, *trnK-UUU*, *trnL-UAA*, *trnV-UAC*, and *ycf66* each contained a single intron (Supplementary Table 2).

3.2 Comparative analysis of plastomes

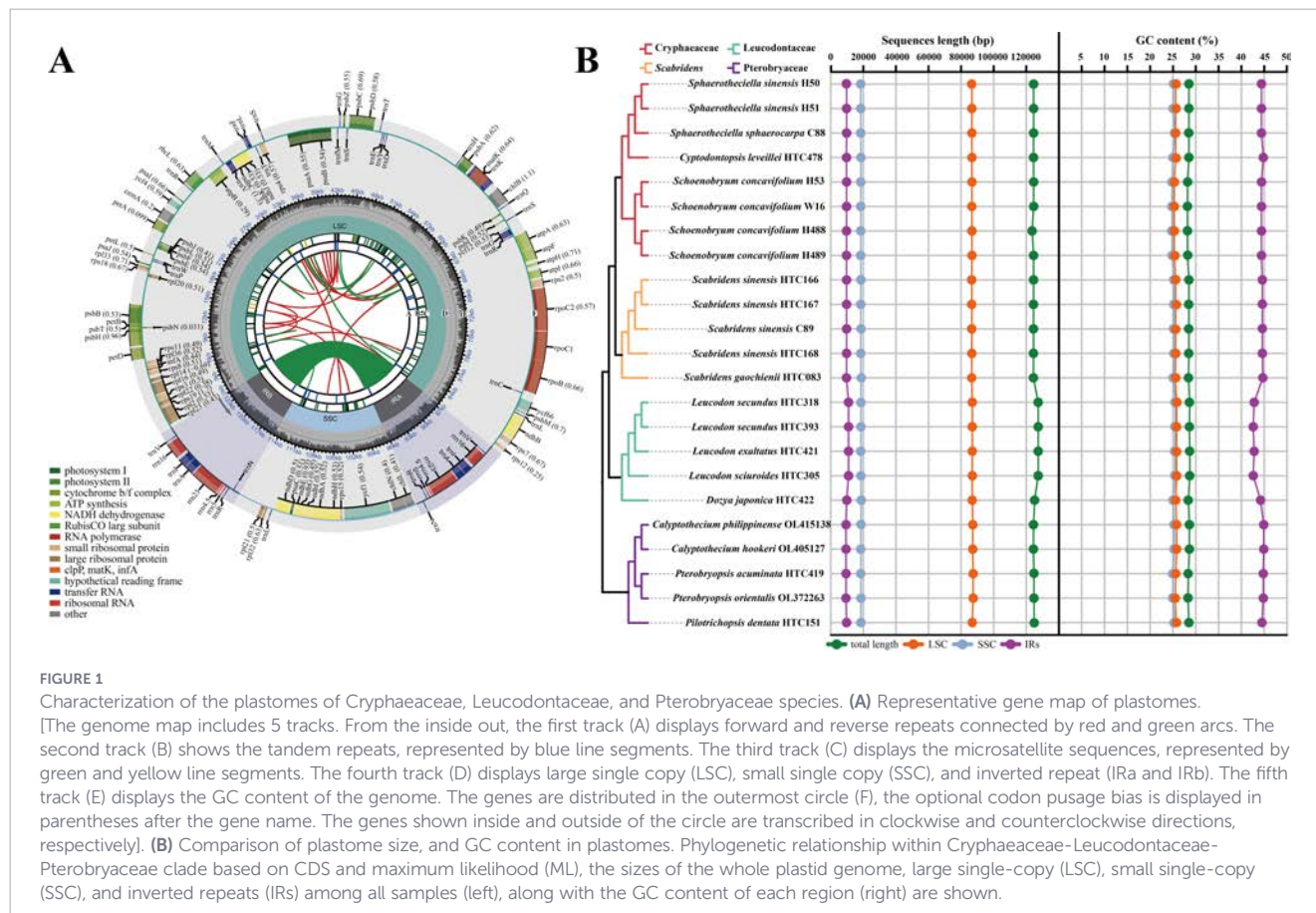
Comparative analysis of IR boundaries revealed generally conserved plastome structure across the Cryphaeaceae, Leucodontaceae, and Pterobryaceae clades, with no significant expansion or contraction

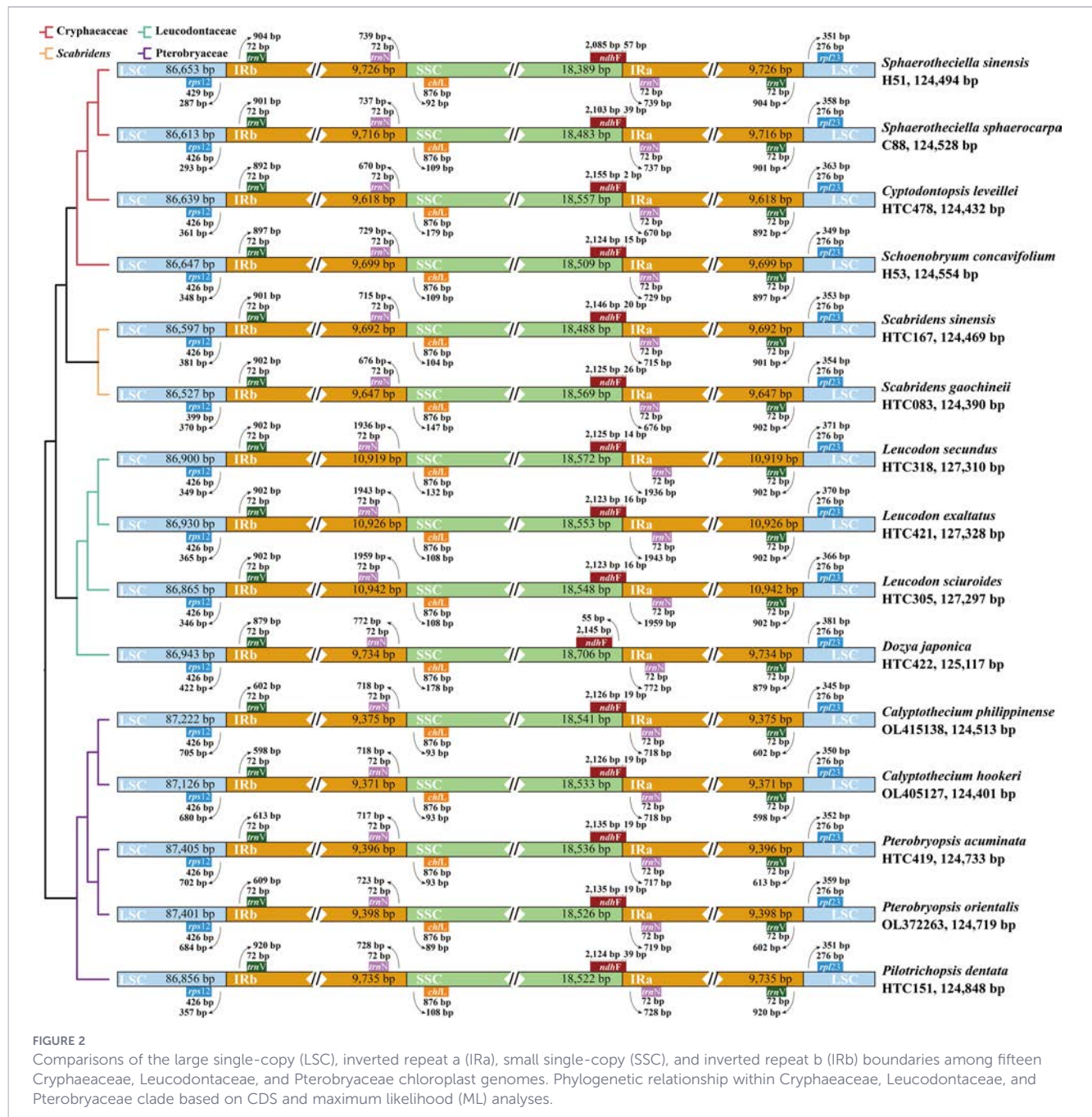
events (Figure 2). The *ndhF* gene spanned the SSC/IRa boundary in all taxa except *Dozya japonica*, with 2,085–2,155 bp located in the SSC and 2–57 bp in the IRa region (Figure 2). A lineage-specific shift was detected for *trnN* at SSC/IR junctions in *Leucodon*, where the distance to the boundary was 1,936–1,959 bp, compared with 670–772 bp in the other genera (Figure 2).

Whole plastome comparisons showed high collinearity among the 15 representative genomes, with highly conserved gene content and order and no evidence of inversions or translocations (Figures 3, 4). Sequence divergence was concentrated mainly in non-coding regions (intergenic spacers and introns), and was greater in LSC and SSC regions than in IR regions (Figure 3). Relatively variable regions included *rpl12*, *psbJ*~*petA*, *ycf4*~*psbA*, *rbcL*~*atpB*, *trnM*-CAU~*trnC*-UAC, *trnS*~*psbA*, *psaB*~*rps14*, *psbD*~*trnT*-GGU, *trnD*-GUC~*ycf2*, *matK*~*chlB*, *psbK*~*psbI*, *atpF*~*atpH*, *rpoC1*, *rpoB*~*ycf66*, *ycf66*, *trnL*-CAA~*ndhB*, *ndhA*, and *rpl21*~*ndhF* (Figure 3).

3.3 Phylogenetic analyses

The concatenated dataset of 82 protein-coding genes comprised 71,517 aligned nucleotide positions, including 53,570 constant sites, 6,616 singleton sites, and 11,331 parsimony-informative sites. Maximum-likelihood (ML) and Bayesian inference (BI) analyses generated almost congruent topologies with strong support at most nodes (Figure 5). The ML tree, annotated with bootstrap values (BS_{ML}) and Bayesian posterior probabilities (PP_{BI}), is shown in Figure 5.

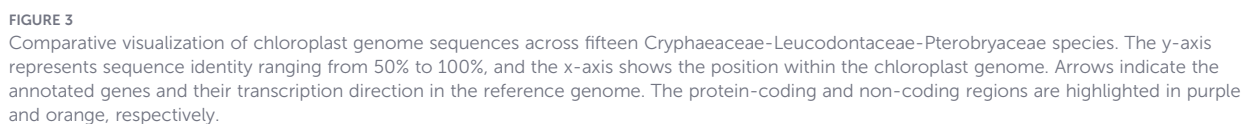




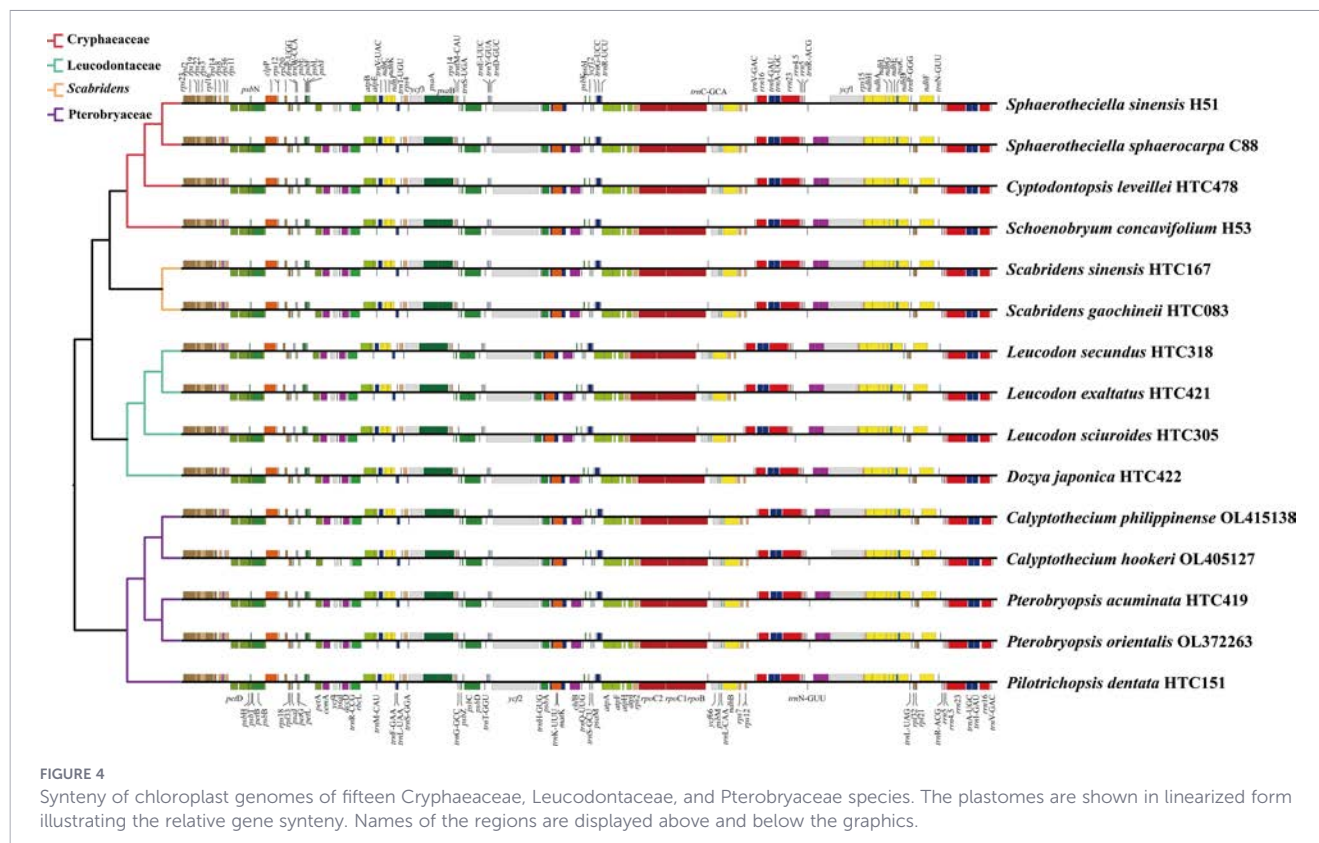
In the phylogenetic trees (Figure 5), all sampled Hypnales formed a maximally supported clade ($PP_{BI}=1$, $BS_{ML}=100\%$). Within Hypnales, Cryphaeaceae, Leucodontaceae, Scabridens, and Pterobryaceae together formed a strongly supported lineage ($PP_{BI}=1$, $BS_{ML}=100\%$). The unknown taxon from Motuo County, China, was sister to the four *S. sinensis* accessions ($PP_{BI}=1$, $BS_{ML}=100\%$). Importantly, *Scabridens* was sister to Cryphaeaceae ($PP_{BI}=1$, $BS_{ML}=100\%$) rather than to Leucodontaceae. In addition, *Dozya japonica* was sister to the *Leucodon* clade ($PP_{BI}=1$, $BS_{ML}=100\%$), and *Pilotrichopsis dentata* (Mitt.) Besch. was nested within Pterobryaceae ($PP_{BI}=1$, $BS_{ML}=91\%$).

4 Discussions

Our phylogenetic analyses strongly support that the unknown species from Motuo county is closely related to *Scabridens* (Figure 5), and morphological evidence further indicates that this species represents a distinct taxon. Compared with *S. sinensis*, this unknown taxon shows a short and often inconspicuous double costa (Figures 6B, 7B), (vs. a single costa reaching the upper-middle leaf region; Supplementary Figure 1B; Bartram, 1935; Zhang, 2011a, b; Zhang and He, 2011), leaf margins revolute from the base to near the apex (Figures 6B, K, 7B) (vs. revolute mainly in the



Noguchi, 1989; Zhang, 2011a, b; Reese and Zander, 2014), and exerted capsules (Figures 6A, 7A, 8C, D; Noguchi, 1989; Frey and Stech, 2009; Zhang, 2011a, b; Reese and Zander, 2014). However, the Motuo plants differ from *Leucodon* by having a short double costa (Figures 6B, 7B), which is typically absent in *Leucodon* (Frey and Stech, 2009; Reese and Zander, 2014), an autoicous sexual condition (vs. Dioicous; Noguchi, 1989; Frey and Stech, 2009; Zhang, 2011a, b; Reese and Zander, 2014), and alar cells restricted to the basal portion (vs. alar cells extend along both sides, forming a large region; Zhang, 2011a, b; Reese and Zander, 2014).



Notably, retention of the species from Motuo County within *Scabridens* is strongly supported. First, this species matches the core diagnostic framework of *Scabridens* in overall plant architecture and reproductive morphology, including erect and simple stems, serrate upper leaf margins, and an autoicous sexual condition (Bartram, 1935; Frey and Stech, 2009). Second, molecular evidence corroborates this placement, with the Motuo lineage forming a maximally supported sister relationship to *S. sinensis*. Though this Motuo species exhibits obviously different by short double costa compared to single long costa in *S. sinensis* (Bartram, 1935; Frey and Stech, 2009; Zhang, 2011a, b), variation in costa expression is not uncommon in bryophyte genera, and transitions among single, double-short, or even reduced costae have been documented in multiple lineages (e.g., *Forsstroemia* Lindb., Frey and Stech, 2009; *Campylium* (Sull.) Spruce, Kučera and Hedenäs, 2020; *Tetradontium* Schwägr., Ignatov and Ignatova, 2017; Lüth, 2019; and *Braunfelsia* Paris, Eddy, 1988). Therefore, recognizing the Motuo taxon within *Scabridens* is both morphologically coherent and phylogenetically robust. Together, these stable character combinations support recognition of this Motuo taxon as a species new to science, here described as *Scabridens gaochienii* W.Z.Huang & Y.Huan Wu.

The familial placement of *Scabridens* remains a central systematic issue. When this genus was first described, Bartram (1935) noted in the discussion that “the genus may not be far out of place in Leucodontaceae near *Dozya*”, because both species possess a single costa and an undifferentiated inner peristome (Noguchi, 1989; Zhang, 2011a, b). However, M. Thériot holds an opposing view, arguing that this genus may not belong to Leucodontaceae or Pterobryaceae (Bartram, 1935). Notably, a recent study by Li et al.

(2024) revealed that *Scabridens sinensis* does not form a clade with *Leucodon*, but rather constitutes a sister group to species of Cryphaeaceae. Regrettably, they did not propose any formal taxonomic decisions and merely marked this species under Cryphaeaceae in their appendix phylogeny tree (Li et al., 2024). Similarly, our phylogenetic results also show that *Scabridens* and Cryphaeaceae form a sister group (Figure 5). Whether *Scabridens* should be classified within Cryphaeaceae?

According to the morphological definition of Cryphaeaceae in the protologue (Schimper, 1856) and various monograph (e.g., Noguchi, 1989; Frey and Stech, 2009; Zhang, 2011a; Reese and Zander, 2014), this family was characterized by: (1) Costa single, percurrent to excurrent; (2) seta very short, capsule typically immersed; (3) lamina cells short, smooth or prorate; and (4) perichaetial leaves often with long-aristate. On the contrary, *Scabridens* exhibits (1) a short double costa or a single costa (Figure 6B, 7B; Supplementary Figure 1B; Bartram, 1935; Frey and Stech, 2009; Zhang, 2011a, b), (2) long setae with exserted capsules (Figures 8C, D, 6A, 7A; Supplementary Figure 1A; Bartram, 1935; Frey and Stech, 2009; Zhang, 2011a, b), (3) rhomboid to elongate laminal cells (Figures 6L, M, 7I; Supplementary Figures 1G, K, L, M; Bartram, 1935; Zhang, 2011a, b), and mucronate perichaetial leaves (Figures 6H, 7F; Supplementary Figure 1H). These significant morphological differences (Table 2) do not support the placement of *Scabridens* within Cryphaeaceae, unless we expand the definition of Cryphaeaceae. However, extending Cryphaeaceae to encompass these differences would substantially blur family-level morphological boundaries among Cryphaeaceae, Leucodontaceae, and Pterobryaceae, and would create additional taxonomic problems (Frey and Stech, 2009).

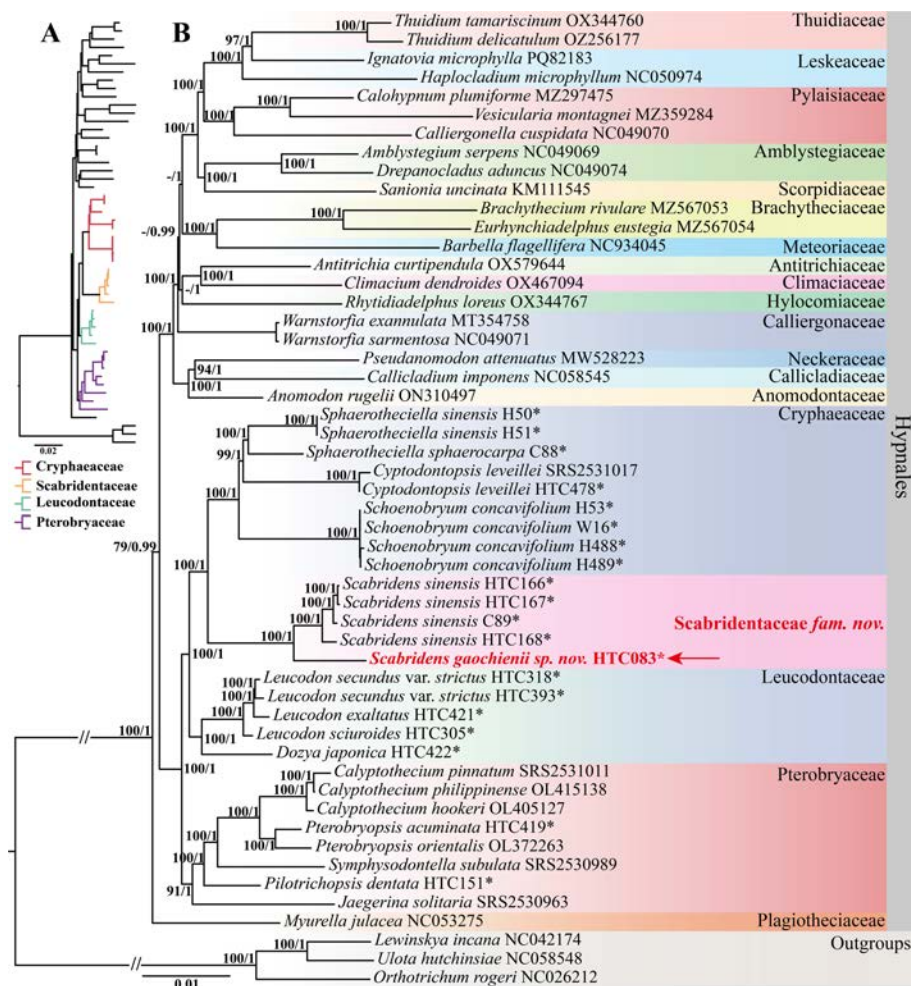


FIGURE 5

Phylogenetic tree of Hypnales inferred from concatenated 82 nucleotide sequences (analyzed using maximum likelihood (ML) (B) and Bayesian inference (BI) (A)). The phylogenetic positions of different families are highlighted in different colors. Numbers at nodes indicate ML bootstrap values (BS; before the slash) and Bayesian posterior probabilities (PP; after the slash). Dash (–) indicates nodes with ML<75 or PP<0.95. “*” means newly sequenced accessions in this study. “//” means that the branch length shown in the representative picture is only half the actual length.

Therefore, we propose to elevate *Scabridens* to family rank as Scabridentaceae W.Z.Huang & Y.Huan Wu.

Additionally, our results also support a formal transfer of *Pilotrichopsis* Besch. to Pterobryaceae. Although *Pilotrichopsis* has traditionally been placed in Cryphaeaceae (e.g., Brothier, 1905; Buck, 1998; Buck et al., 2000; Frey and Stech, 2009; Jia and He, 2025; Sugimura and Uzawa, 2025), molecular studies have repeatedly shown that *Pilotrichopsis dentata* is nested within Pterobryaceae (Cox et al., 2010; Li et al., 2024), a pattern corroborated here (Figure 5). Over recent decades, molecular phylogenetics has substantially reshaped the traditional classification of bryophytes (Bechteler et al., 2023; Li et al., 2024; Xu et al., 2026), given that monophyly is a primary criterion for modern family delimitation, retaining *Pilotrichopsis* in Cryphaeaceae is no longer tenable. We therefore adopt the taxonomic transfer of *Pilotrichopsis* to Pterobryaceae.

5 Taxonomy

Scabridentaceae W.Z.Huang & Y.Huan Wu, fam. nov.

Diagnosis:—Plants medium-sized, erect or sparingly branched. Stem cross-section without a central strand. Leaves densely clustered, slightly concave, not plicate, broadly ovate at the base and gradually narrowed to an attenuate apex. Margins revolute from the base to near the apex or only in the lower half, serrate in the upper portion, crenulate or nearly smooth in the middle and lower portion. Costa single, reach the middle-upper part of the leaf, or double and short. Laminal cells rhomboid to elongate, alar cells well differentiated, quadrate to short rectangular. Sexual condition autoicous. Perichaetial leaves are smaller than stem leaves, ecostate. Setae long, capsules exserted. Stomata superficial at urn base. Peristome teeth 16, endostome reduced, papillose throughout.

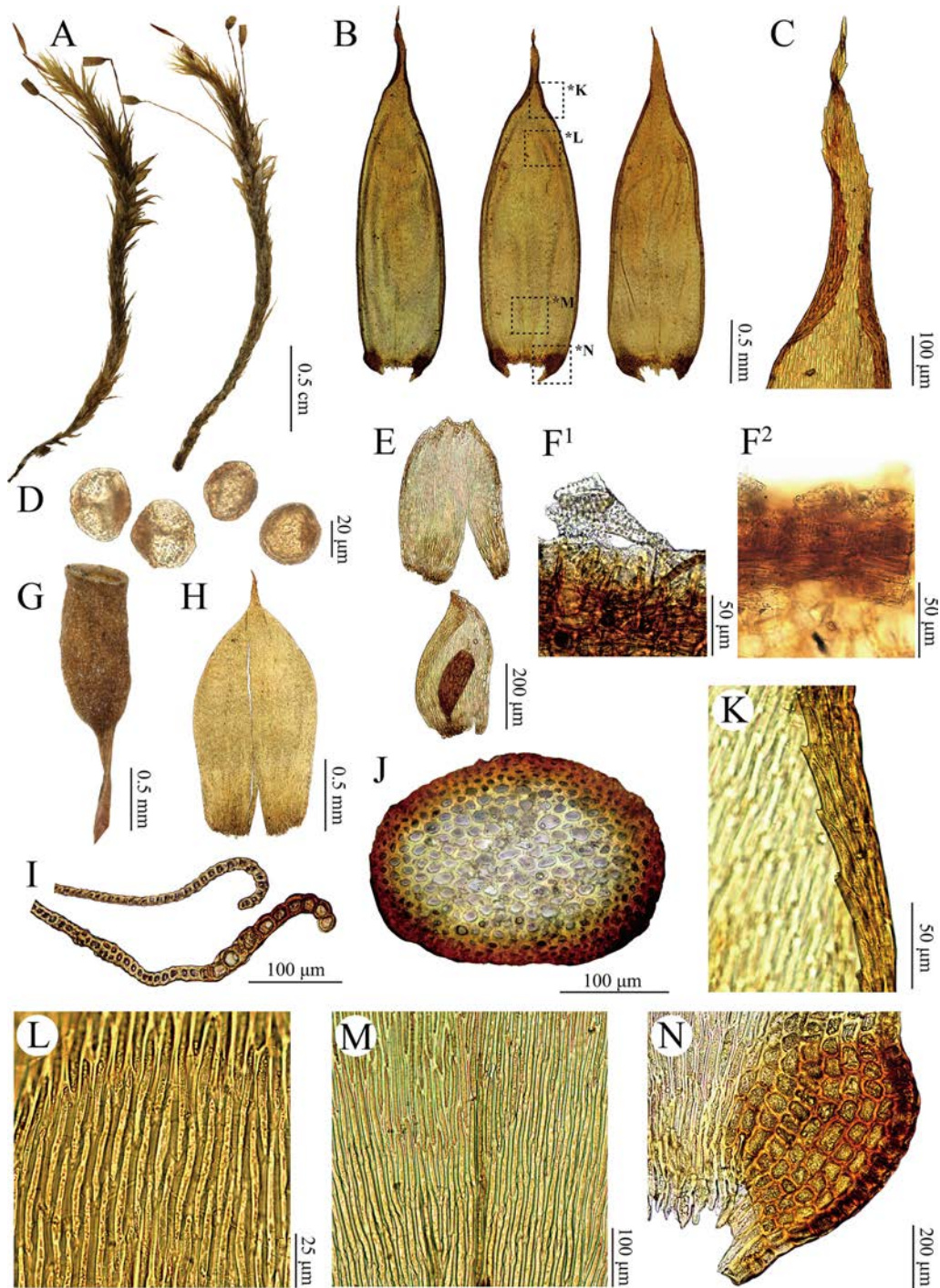


FIGURE 6

Scabridens gaochienii W.Z.Huang & Y.Huan Wu. (A) Plants; (B) Leaves; (C) Apex; (D) Spores; (E) Perigonial bracts; (F¹) Teeth (dorsal view); (F²) Teeth, ventral view, show fragile and with only a residual basal portion; (G) Capsule; (H) Perichaetial leaf; (I) Transverse section of leaves, upper one show section in middle leaf marginal portion, and lower one show section in alar portion; (J) Transverse section of stem; (K) Upper marginal cells of leaf; (L) Upper laminal cells of leaf; (M) Basal laminal cells of leaf; (N) Alar cells. All from holotype specimen. Photographed by Xin-Yin Ma (A–C, E–N) and Yu-Si Liu (D).

Type Genus:—*Scabridens* E.B.Bartram, Ann. Bryol. 8: 16. 1935.

Included species: *Scabridens sinensis* E.B.Bartram, and *S. gaochienii* W.Z.Huang & Y.Huan Wu.

Emended diagnosis: Consistent with the diagnosis of Scabridentaceae.

Type species: *Scabridens sinensis* E.B.Bartram, Ann. Bryol. 8: 16. 1935.

Type: China. Kweichow (Guizhou) Province, Nin Tao Shan, on bark, alt. 2000 m., 2 October 1931, S. Y. Cheo 825a (holotype: FH [00220367], n. v.; isotypes: FH [00220368], n.v.; NY [00845582], n. v.; PC [101249], n. v.).

Illustrations and descriptions: Bartram (1935): 16–17, Figure 10), Chen (1978): 35–37, Figure 214), Zhang (2005): 86, Figure 33), Zhang

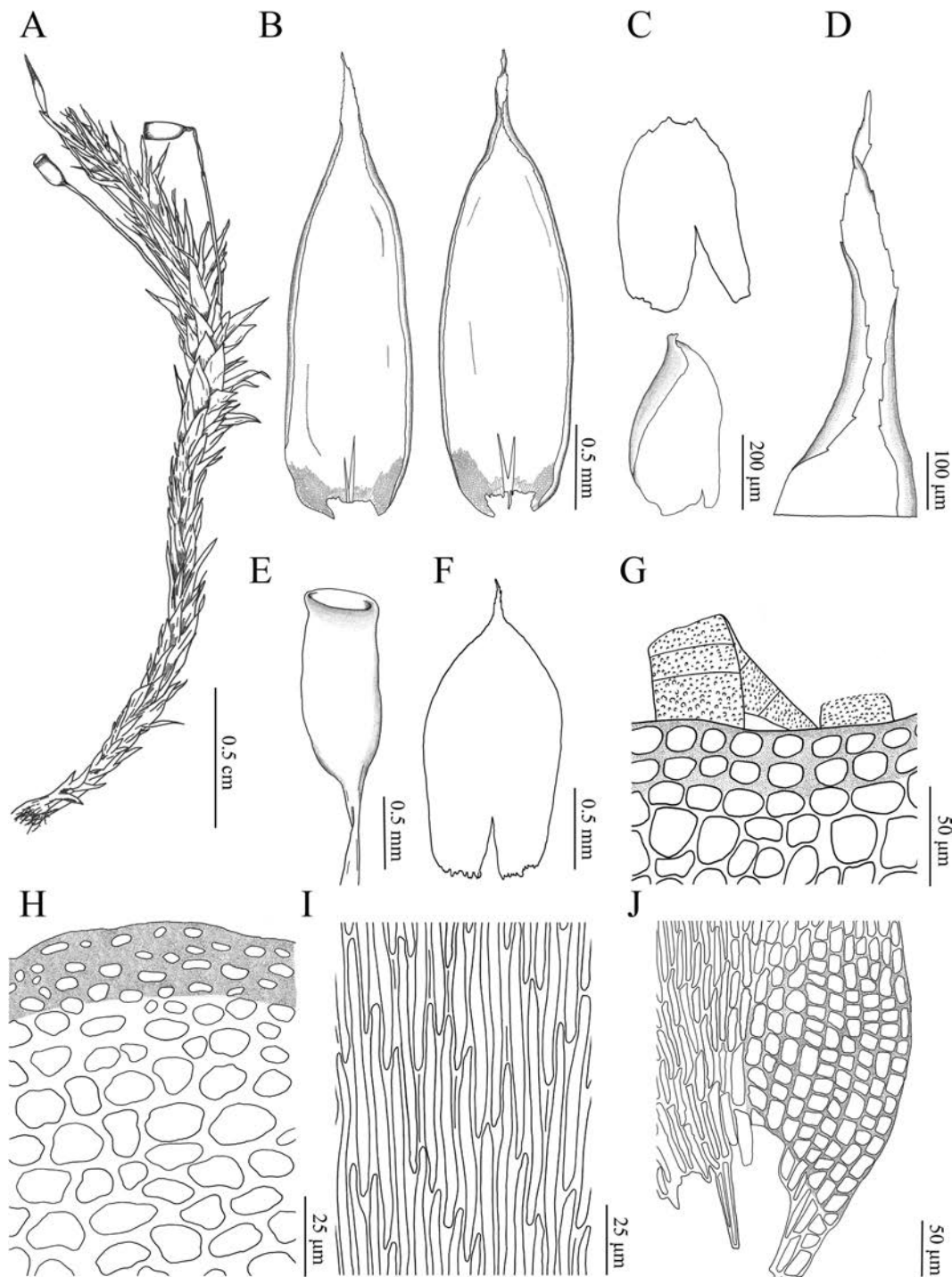


FIGURE 7

Scabridens gaochienii W.Z.Huang & Y.Huan Wu. (A) Plants; (B) Leaves; (C) Perigonal bracts; (D) Apex; (E) Capsule; (F) Perichaetial leaf; (G) Teeth; (H) Transverse section of stem; (I) Upper marginal cells of leaf; (J) Alar cells. All from holotype specimen. Drawn by Xin-Yin Ma.

(2011a: 189–190, Figure 81), Zhang and He (2011): 180–181, Figure 323), Zhang (2011b: 347–348, Figure 193), Zhang et al. (2016): 273–274, Figure 34–37), and Supplementary Figure 1.

Scabridens gaochienii W.Z.Huang & Y.Huan Wu, sp. nov. (Figures 6–8).

Chinese name: 高氏疣齿藓 [Gāo Shì Yóu Chǐ Xiǎn].

Diagnosis: Similar to *Scabridens sinensis*, but can be distinguished by the short double costa, revolute margins from the base to near the apex, longer seta (0.55–0.70 cm), and shorter peristome teeth (150–170 μ m), usually fragile and with only a residual basal portion on oral.



Type: China. Xizang Autonomous Region, Linzhi City, Motuo County, Yarlung Zangbu Grand Canyon National Nature Reserve, from Pai Town to Beibeng Village, along Paimo Road, Xiaoyandong, 29°24'56.52" N, 95°4'7.88" E, 2691 m a.l.t., on tree trunk, 12 Oct. 2024, W.-Z. Huang & F.-Y. Zhang 20241012-71 (holotype: HTC!; isotype: HSNU!).

Description: Plants in loose tufts, yellowish green in upper part and dark brown below. Stems erect, 2.3–3.5 cm high, simple or sparingly branched, with brownish to dark rhizoids at base. Cross-section of stem

rounded to oval, epidermis with 2–4(–5) layers of smaller, brownish, thick-walled cells, and 9–11 rows of larger lumen, thick-walled inner cortical cells, central strand absent. Leaves densely clustered, slightly concave, without plicate, appressed or erecto-patent when dry, erect spreading when moist, broadly ovate at base and gradually narrowed into an attenuate apex, broadest slightly above the middle, apex usually twisted, 2.7–3.3 × 0.65–0.8 cm. Margins revolute from the base to near the apex, serrate in the upper portion, crenulate or nearly smooth in the middle and lower portion. Costa slender, double, short, usually not

TABLE 2 Difference among Cryphaeaceae, Leucodontaceae, and Scabridentaceae.

Family	Cryphaeaceae	Leucodontaceae	Scabridentaceae
Plants	Medium-sized, stems erect to pendulous, often sparsely, regularly or irregularly pinnately branched	Medium-sized to large, stems simple or sparsely branched to fecondose	Medium-sized, stems erect or sparingly branched
Central strand	Absent	Weak or absent	Absent
Leaf	Ovate to narrowly lanceolate	Broadly ovate to lanceolate	Broadly ovate at base and gradually narrowed to an attenuate apex
Sexual condition	Autoicous, rarely dioicous	Dioicous	Autoicous
Costa	Single, percurrent to excurrent.	Single, reach the middle-upper part of the leaf, or absent	Single, reach the middle-upper part of the leaf, or short double
Laminal cells	Short, smooth or prorate	Oval to elongate, smooth to rarely prorate	Rhomboid to elongate, smooth
Alar cells	Differentiated, homochromatic	Differentiated, homochromatic	Differentiated, reddish brown to brownish black
Perichaetial leaf	With long-aristate	With mucronate apex.	With mucronate apex.
Setae	Very short, capsule immersed	Rather short to elongate, capsule usually exerted	Elongate, capsules exerted
Teeth	Exostome teeth papillose, endostome ± reduced, rarely absent	Exostome teeth papillose; endostome usually rudimentary	Peristome teeth papillose, endostome reduced

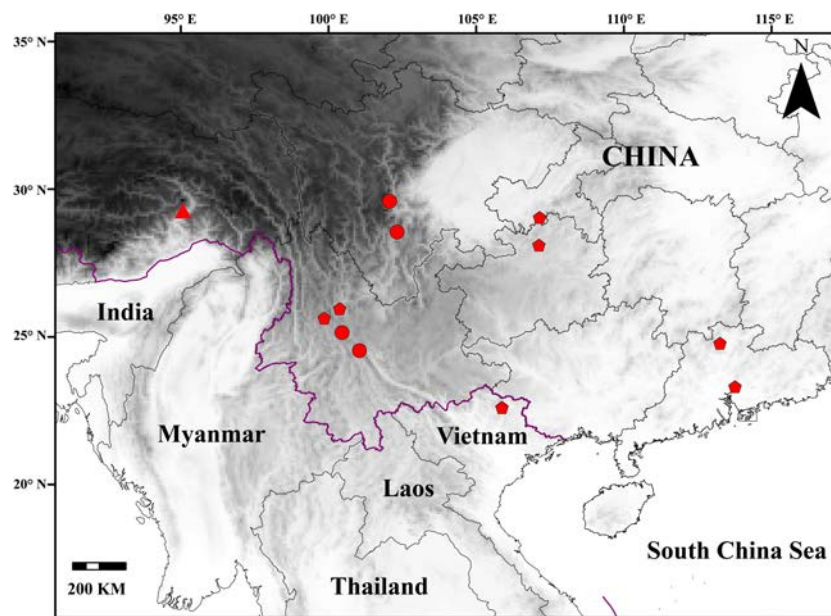


FIGURE 9

Distribution of *Scabridens gaochienii* and *S. sinensis*. Red triangles: *S. gaochienii* collection sites; red pentagons: *S. sinensis* historical records; red circles: *S. sinensis* newly discovered sites in this study.

obvious. Upper and middle laminal cells rhomboid or linear, $55\text{--}73 \times 3.5\text{--}5.5 \mu\text{m}$; basal laminal cells linear, $70\text{--}95 \times 8\text{--}12 \mu\text{m}$; alar cells well differentiated, reddish brown to dark brown, quadrate or short rectangular, $33\text{--}65 \times 25\text{--}42 \mu\text{m}$, unistratose. Sexual condition autoicous. Androecium small, axillary, perigonal bract concave, tongue-shaped or broadly ovate and short acuminate, costa absent, ca. 0.5 mm long, 0.3 mm wide. Perichaetial leaves are smaller than stem leaves, ovate-lanceolate, broadest at the middle, serrate near apex, mucronate, without a costa. Setae yellowish-brown, smooth, 0.55–0.70 cm long, helically coiled near capsules. Capsules yellowish-brown, oblong-cylindric, $1.2\text{--}1.4 \times 0.55\text{--}0.68 \text{ mm}$; exothecial cells irregular hexagonal, thick-walled; stomata superficial, only present at the urn base. Annulus not seen. Peristome teeth 16, exostome lanceolate, 150–170 μm in length, pellucid, papillose, usually fragile and with only a residual basal portion on oral, endostome undeveloped. Spores 28–40 μm in diameter, papillose under the light microscope.

Etymology. The species epithet is to honor an early Chinese bryologist, Qian Gao, in appreciation for his important contributions to our knowledge of the Chinese bryoflora.

Distribution and habitat. *Scabridens gaochienii* is currently known only from the Yarlung Zangbu Grand Canyon National Nature Reserve in Motuo County, Linzhi City, Xizang Autonomous Region, China (Figure 9). The species grows on the tree trunk in an alpine coniferous forest at an elevation of 2,691 meters. The forest mainly comprises *Abies delavayi* var. *motuoensis* W.C.Cheng & L.K.Fu, *Ilex fragilis* Hook. f., *Tsuga dumosa* (D.Don) Eichler, *Sorbus thibetica* (Card.) Hand.-Mazz., etc (Figures 8A, B). In our collected, *S. gaochienii* is found only in association with *Symblepharis vaginata* (Hook. ex Harv.) Wijk & Margad.

6 Key to the species of *Scabridens*

1. Costa single, reach middle-upper part of leaf; margins revolute from base to middle; seta short, 0.2–0.3 cm; peristome teeth ca. 250 μm , complete...*Scabridens sinensis*.

1. Costa short, double; margins revolute from base to near apex; seta 0.55–0.70 cm; peristome teeth 150–170 μm , usually fragile, incomplete...*Scabridens gaochienii*.

Data availability statement

The data presented in the study are deposited in the NCBI (<https://www.ncbi.nlm.nih.gov/>) repository. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

Author contributions

W-ZH: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. Y-SL: Software, Visualization, Writing – review & editing. X-YM: Software, Visualization, Writing – review & editing. Q-HW: Data curation, Investigation, Visualization, Writing – review & editing. W-ZM:

Investigation, Visualization, Writing – review & editing. R-LZ: Investigation, Methodology, Visualization, Writing – review & editing. T-XZ: Visualization, Writing – review & editing. Y-HW: Conceptualization, Funding acquisition, Project administration, Visualization, Writing – review & editing.

Funding

The author(s) declared that financial support was received for this work and/or its publication. This research was funded by National Natural Science Foundation of China, grant numbers 32270215 and 32500183, and the Postdoctoral Research Start-up Fund of Hangzhou Normal University (4105C5022521509).

Acknowledgments

We are grateful to the curators and staff of KUN, PE, HIRO, NICH, and HSNU for making specimens available for study through loans.

Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

References

- Bartram, E. B. (1935). Additions to the moss flora of China. *Ann. Bryol.* 8, 6–21. doi: 10.5962/p.315978
- Bechteler, J., Peñaloza-Bojacá, G., Bell, D., Burleigh, J. G., McDaniel, S. F., Davis, E. C., et al. (2023). Comprehensive phylogenomic time tree of bryophytes reveals deep relationships and uncovers gene incongruences in the last 500 million years of diversification. *Am. J. Bot.* 110, e16249. doi: 10.1002/ajb2.16249
- Brinda, J. C., and Atwood, J. J. (2026). The bryophyte nomenclator. Available online at: <https://www.bryonames.org/> (Accessed May 25, 2026).
- Brotherus, V. F. (1905). “Cryphaeaceae, Leucodontaceae,” in *Die natürlichen pflanzenfamilien. I, abt. III halfte II*. Eds. A. Engler and K. Prantl (W. Englemann, Leipzig), 736–762.
- Buck, W. R. (1998). Pleurocarpous mosses of the West Indies. *Mem. New York Bot. Gard.* 82, 1–400. doi: 10.2307/3244482
- Buck, W. R., Goffinet, B., and Shaw, J. (2000). Testing morphological concepts of orders of pleurocarpous mosses (Bryophyta) using phylogenetic reconstructions based on trnL-trnF and rps4 sequences. *Mol. Phylogenet. Evol.* 16, 180–198. doi: 10.1006/mpev.2000.0796
- Chen, P. J. (1978). *Genera Muscorum Sinicorum (Paes Secunda)* (Beijing: Science Press).
- Chernomor, O., von Haeseler, A., and Minh, B. Q. (2016). Terrace aware data structure for phylogenomic inference from supermatrices. *Syst. Biol.* 65, 997–1008. doi: 10.1093/sysbio/syw037
- Cox, C. J., Goffinet, B., Wickett, N. J., Boles, S. B., and Shaw, A. J. (2010). Moss diversity: A molecular phylogenetic analysis of genera. *Phytotaxa* 9, 175–195. doi: 10.11646/phytotaxa.9.1.10
- Dai, Z., Xing, S. C., Gradstein, S. R., Chen, X., Zhu, R. L., and Wang, J. (2021). New species or infraspecific variation? A case study of *Ptychanthus striatus* var. *motuoensis* var. nov. (Marchantiophyta: Lejeuneaceae) from Xizang, China. *Bryologist* 124, 475–483. doi: 10.1639/0007-2745-124.4.475
- Eddy, A. (1988). *A handbook of malesian mosses. Volume 1. Sphagnales to dicranales* (London: British Museum (Natural History)).
- Frazer, K. A., Pachter, L., Poliakov, A., Rubin, E. M., and Dubchak, I. (2004). VISTA: computational tools for comparative genomics. *Nucleic Acids Res.* 32, 273–279. doi: 10.1093/nar/gkh458
- Frey, W., and Stech, M. (2009). “Marchantiophyta, bryophyta, anthocerotophyta,” in *Syllabus of Plant Families - A. Engler's Syllabus der Pflanzenfamilien Part 3: Bryophytes and seedless Vascular Plants*. Ed. W. Frey (Gebrüder Borntraeger, Stuttgart), 9–263.
- Groombridge, B. (1992). *Global biodiversity: status of the Earth's living resources* (New York: Chapman and Hall).
- Huang, M. Z., Chen, X. D., Li, M. K., Zhu, R. J., Zhao, G. F., Yang, H. B., et al. (2024). *Uncifera motuoensis* (Orchidaceae), a new species from Xizang, China. *Taiwania* 69, 20–23. doi: 10.6165/tai.2024.69.20
- Huang, W. Z., Ma, W. Z., Schneider, H., Yu, Y., and Wu, Y. H. (2019). Mitochondrial genome from *Andreaea wangiana* reveals structural conservatism and a trend of size reduction in mosses. *Bryologist* 122, 597–606. doi: 10.1639/0007-2745-122.4.597
- Huang, W. Z., Ma, X. Y., Tubanova, D. Y., Dugarova, O. D., Zhang, F. Y., Hu, J., et al. (2025). *Dicranum motuoense* (Bryophyta): a new taxon from China, with special references to its complete organelle genomes. *Plants* 14, 650. doi: 10.3390/plants14050650
- Ignatov, M. S., and Ignatova, E. A. (2017). “Tetraphidopsida,” in *Moss flora of Russia. Volume 2: oedipodiales – grimmiales*. Ed. M. S. Ignatov (KMK Scientific Press Ltd, Moscow), 115–123.
- Jia, Y., and He, S. (2013). *Species catalogue of China. Volume 1: plants. Bryophytes* (Beijing: Science Press).
- Jia, Y., and He, S. (2025). *A catalogue of Asian mosses* (Beijing: Science Press).
- Jin, J. J., Yu, W. B., Yang, J. B., Song, Y., de Pamphilis, C. W., Yi, T. S., et al. (2020). GetOrganelle: A fast and versatile toolkit for accurate de novo assembly of organelle genomes. *Genome Biol.* 21, 241. doi: 10.1186/s13059-020-02154-5

Generative AI statement

The author(s) declared that generative AI was not used in the creation of this manuscript.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2026.1842480/full#supplementary-material>.

- Kalyaanamoorthy, S., Minh, B. Q., Wong, T. K. F., von Haeseler, A., and Jermin, L. (2017). ModelFinder: Fast model selection for accurate phylogenetic estimates. *Nat. Meth.* 14, 587–589. doi: 10.1038/nmeth.4285
- Kandel, P., Chettri, N., Chaudhary, R. P., Badola, H. K., Gaira, K. S., Wangchuk, S., et al. (2019). Plant diversity of the kangchenjunga landscape, eastern Himalayas. *Plant Divers.* 41, 153–165. doi: 10.1016/j.pld.2019.04.001
- Katoh, K., and Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: Improvements in performance and usability. *Mol. Biol. Evol.* 30, 772–780. doi: 10.1093/molbev/mst010
- Kučera, J., and Hedenäs, L. (2020). Revisiting the genus campyliadelphus (Amblystegiaceae, bryophyta). *Nova Hedwigia* 150, 165–178. doi: 10.1127/nova_hedwigia/2020/0601
- Lanfear, R., Frandsen, P. B., Wright, A. M., Senfeld, T., and Calcott, B. (2017). PartitionFinder 2: New methods for selecting partitioned models of evolution for molecular and morphological phylogenetic analyses. *Mol. Biol. Evol.* 34, 772–773. doi: 10.1093/molbev/msw260
- Li, M., Tian, C. F., Song, Y. F., Ju, W. B., Pathak, M. L., and Xu, B. (2022). *Stellaria motuoensis* (Caryophyllaceae), a new species from Xizang, China. *Nord. J. Bot.* 2022, e03683. doi: 10.1111/njb.03683
- Li, Y. F., Luo, L., Liu, Y., He, Q., Yu, N. N., Gaowa, N. R., et al. (2024). The Bryophyte Phylogeny Group: A revised familial classification system based on plastid phylogenomic data. *J. Syst. Evol.* 62, 577–588. doi: 10.1111/jse.13028
- Liu, S. Y., Ni, Y., Li, J. L., Zhang, X. Y., Yang, H. Y., Chen, H. M., et al. (2023). CPGView: A package for visualizing detailed chloroplast genome structures. *Mol. Ecol. Resour.* 23, 694–704. doi: 10.1111/1755-0998.13732
- Lüth, M. (2019). *Mosses of Europe—a photographic flora. Vol. 1* (Freiburg: Michael Lüth).
- Minh, B. Q., Schmidt, H. A., Chernomor, O., Schrempf, D., Woodhams, M. D., von Haeseler, A., et al. (2020). IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. *Mol. Biol. Evol.* 37, 1530–1534. doi: 10.1093/molbev/msaa015
- Mittermeier, R. A., Gil, P. R., Hoffmann, M., Pilgrim, J., Brooks, T., Mittermeier, C. G., et al. (2004). *Hotspots revisited: Earth's biologically richest and most endangered terrestrial ecoregions* (Mexico: Conservation International).
- Noguchi, A. (1989). *Illustrated moss flora of Japan. Part 3* (NiChinan-Shi: Hattori Botanical Laboratory).
- Orme, C. D. L., Davies, R. G., Burgess, M., Eigenbrod, F., Pickup, N., Olson, V. A., et al. (2005). Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436, 1016–1019. doi: 10.1038/nature03850
- Rambaut, A., Drummond, A. J., Xie, D., Baele, G., and Suchard, M. A. (2018). Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Syst. Biol.* 67, 901–904. doi: 10.1093/sysbio/syy032
- Reese, W. D., and Zander, R. H. (2014). “Cryphaeaceae schimper,” in *Flora of North America. North of Mexico. Volume 28. Bryophyta, part 2*. Ed. F. of N. A. Committee (Oxford University Press, Oxford), 584–589.
- Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D. L., Darling, A., Höhna, S., et al. (2012). MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Syst. Biol.* 61, 539–542. doi: 10.1093/sysbio/sys029
- Schimper, W. P. (1856). *Corollarium bryologiae europaeae* (Stuttgart: E. Schweizerbart).
- Shen, C., Li, H., Shu, L., Huang, W. Z., and Zhu, R. L. (2024). Ancient large-scale gene duplications and diversification in bryophytes illuminate the plant terrestrialization. *New Phytol.* 245, 2292–2308. doi: 10.1111/nph.20221
- Shi, L. C., Chen, H. M., Jiang, M., Wang, L. Q., Wu, X., Huang, L. F., et al. (2019). CPGAVAS2, an integrated plastome sequence annotator and analyzer. *Nucleic Acids Res.* 47, W65–W73. doi: 10.1093/nar/gkz345
- Sugimura, K., and Uzawa, M. (2025). Distribution and habitat of an endangered *Pilotrichopsis dentata* (Mitt.) Besch. rediscovered in Ibaraki Prefecture after 90 years. *Bull. Ibaraki Nat. Mus.* 28, 1–11.
- Tian, Y.-X., Zuo, Q., Huang, W.-Z., Ren, Z.-J., and Zhang, L. (2025). *Pseudotrachypus motuoensis* (Metoriaceae, Bryophyta), a new species from Xizang (Tibet), China. *Bryologist* 128, 37–42. doi: 10.1639/0007-2745-128.1.037
- Tong, Y. H., Zhao, W. L., Wang, B. M., Liu, E. D., Cai, J., and Guo, Y. J. (2021). *Vaccinium motuoense* (Ericaceae), a new species from Xizang, China. *PhytoKeys* 181, 105–111. doi: 10.3897/phytokeys.181.69352
- Xiang, Y. L., Jin, X. J., Shen, C., Cheng, X. F., Shu, L., and Zhu, R. L. (2022). New insights into the phylogeny of the complex thalloid liverworts (Marchantiopsida) based on chloroplast genomes. *Cladistics* 38, 649–662. doi: 10.1111/cla.12520
- Xu, H., Shen, C., Huang, W.-Z., Cargill, D. C., Villarreal, A. J. C., Chantanaorapint, S., et al. (2026). Evolution and classification of hornworts: new insights from the first plastome-based phylogeny. *New Phytol.* 249, 1491–1508. doi: 10.1111/nph.20345
- Ye, C., Li, J., Tian, H., Lin, D., and Jin, X. (2023). *Kuhlthasseltia motuoensis* (Orchidaceae, Orchidoideae, Cranichideae), a new species from Xizang, China. *Phytotaxa* 626, 141–144. doi: 10.11646/phytotaxa.626.2.7
- Yu, Y., Yang, J. B., Ma, W. Z., Pressel, S., Liu, H. M., Wu, Y. H., et al. (2019). Chloroplast phylogenomics of liverworts: a reappraisal of the backbone phylogeny of liverworts with emphasis on Ptilidiales. *Cladistics* 36, 184–193. doi: 10.1111/cla.12398
- Zhang, B. Y., Shu, L., Zhao, C. X., Wei, Y. M., Wang, J., Do, T. V., et al. (2016). New moss records for Vietnam. *Cryptogamie Bryolo.* 37, 259–281. doi: 10.7872/cryb/v37.iss3.2016.259
- Zhang, M. X. (2005). “Leucodontaceae,” in *Flora yunnanica, tomus 19 (Bryophyta: musci)* (Science Press, Beijing), 78–86.
- Zhang, M. X. (2011a). “Leucodontaceae,” in *Flora bryophytorum sinicorum. Volum. 5. Isobryales*. Eds. P. C. Wu and Y. Jia (Science Press, Beijing), 153–191.
- Zhang, M. X. (2011b). “Leucodontaceae,” in *Bryophyte flora of Guangdong*. Eds. D. L. Wu and L. Zhang (Guangdong Science and Technology Press, Guangdong), 346–349.
- Zhang, M. X., and He, S. (2011). “Leucodontaceae,” in *Moss flora of China, english version, volume 5. Erpodiaceae–climaciaceae*. Eds. P. C. Wu, M. R. Crosby and S. He (Science Press and St. Louis: Missouri Botanical Garden Press, Beijing), 153–181.
- Zhang, Z., Zhang, M., Zhang, J., Zhang, D., and Li, H. (2022). *Ficus motuoensis* (Moraceae), a new species from southwest China. *Phytokeys* 206, 119–127. doi: 10.3897/phytokeys.206.89580
- Zhu, A. H., Song, Z. K., Wang, J. F., Guan, H. W., and Ma, H. X. (2023). Multi-locus phylogeny and morphology reveal two new species of Hypoxylon (Hypoxylaceae, Xylariales) from Motuo, China. *Microorganisms* 12, 72. doi: 10.3390/microorganisms12010072