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Homaliodendron maolanense sp. nov. (Neckeraceae, Bryophyta), a new species from China based on molecular and morphological data

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ABSTRACT
The new species *Homaliodendron maolanense* sp. nov. is described and illustrated based on its morphological and molecular evidence. The new species can be distinguished from all congeners by the combination of the following features: 1) plants strongly flattened and frondose; 2) secondary stems with bi- to tripinnate branches and a few foliose pseudoparaphyllia; 3) stem leaves rather asymmetric, strongly falcate, ovate-spathulate, widest at the middle, strongly tapered to base, with a truncate or apiculate apex, as well as double and distinct costae; 4) margins of stem leaves irregularly biserrate with 6-12 sharp teeth, the terminal tooth curved, larger than the others, multicellular, coarse and blunt, entire below; and 5) cells of stem leaves strongly incrassate and smooth, strongly porose at low and basal portions. A key and digital image are presented to separate *H. maolanense* sp. nov. from other nine Chinese species.

KEY WORDS
Moss,
Neckeraceae,
Homaliodendron,
molecular phylogeny,
new species.

RÉSUMÉ

Homaliodendron maolanense *sp. nov. (Neckeraceae, Bryophyta), une nouvelle espèce originaire de Chine basée sur des données moléculaires et morphologiques.*

La nouvelle espèce *Homaliodendron maolanense* sp. nov. est décrite et illustrée sur la base de ses caractéristiques morphologiques et moléculaires. La nouvelle espèce se distingue de toutes les espèces apparentées par la combinaison des caractéristiques suivantes : 1) plantes fortement aplaties et frondées ; 2) tiges secondaires avec des branches bi- à tripennées et quelques pseudoparaphyllia foliacées ; 3) feuilles caulinaires plutôt asymétriques, fortement falciformes, ovales-spatulées, plus larges au milieu, fortement effilées à la base, avec un apex tronqué ou apiculé, ainsi que des côtes doubles et distinctes ; 4) les bords des feuilles caulinaires sont irrégulièrement biserrés avec 6 à 12 dents acérées, la dent terminale étant courbée, plus grande que les autres, multicellulaire, grossière et émoussée, entière en dessous ; 5) et les cellules des feuilles caulinaires sont fortement épaissies et lisses, fortement poreuses dans les parties basses et basales. Une clé et une image numérique sont présentées pour distinguer *H. maolanense* sp. nov. des neuf autres espèces chinoises.

MOTS CLÉS
Mousse,
Neckeraceae,
Homaliodendron,
phylogénie moléculaire,
espèce nouvelle.

INTRODUCTION

Homaliodendron Fleisch. *sensu stricto* is predomainantly reported from tropical and subtropical regions (Wijk *et al.* 1964; Crosby *et al.* 1999). Approximately twelve species of the genus are currently recognized worldwide (Fleischer 1906; Iwatsuki & Noguchi 1973; Gangulee 1976; Scott & Stone 1976; Miller *et al.*1978; Iwatsuki & Tan 1979; Florschütz-de Ward & Florschütz 1979; Kis 1985; Enroth 1989; Noguchi & Iwatsuki 1989; Allen 2010; Forzza 2025; Olsson *et al.* 2010; Enroth & Koponen 2017). Among them, nine species have been recorded in China (Ninh 1984; Redfearn *et al.* 1996; Su 1988; Pei *et al.* 2011; Wu 2011; Jia & He 2013; Enroth & Koponen 2017).

Species in the genus *Homaliodendron* are characterized by their pleurocarpous growth habit, flattened or slightly complanate branching, and ovate to lanceolate leaves. The leaf margins are often serrate or biserrate, and the upper laminal cells tend to be elongate or linear, which distinguishes them from closely related genus *Homalia* Brid. Additionally, almost members of this genus exhibit strongly flattened and frondose plants with wide-spreading complanate leaves, which is a key diagnostic feature for genus-level identification.

To accurately identify whether a moss specimen belongs to *Homaliodendron*, careful examination of the leaf arrangement, costal structure, and leaf margin dentation is required. The presence of a distinctly single costa, biserrate leaf margins with multicellular teeth, and falcate or curved leaves are key features distinguishing *Homaliodendron* from similar genera.

During a field excursion in Guizhou province, China, we collected a moss with a *Homaliodendron*-like habit growing on stones. Morphologically, it is characterized by its strongly falcate branch and stem leaves with distinctly double costae. The leaf upper margins and apex are biserrate, coarse and blunt multicellular teeth, which further supports its placement in *Homaliodendron*. To confirm its genus identity, we constructed a phylogenetic tree including the newly collected moss and six other *Homaliodendron* species, with *Neckera pennata* Hedw. as an outgroup. The resulting phylogenetic tree clearly supports the placement of the moss within the genus *Homaliodendron*. According to its morphological features and the position on the phylogenetic tree, we confirmed that the moss clearly represented a hitherto undescribed species.

MATERIAL AND METHODS

Examination of specimens

Specimen examinations and measurements were conducted using an Olympus-BX53 light microscope, while microphotographs were obtained with a DP74 camera mounted on this microscope. For detailed analysis, leaves located at the middle of stems and branches were selected. Observations and illustrations focused on the upper, medial, and basal leaf cells. Leaf width measurements were taken at the widest part.

Molecular protocols

A total of 27 samples were selected for molecular analyses, representing six other species of *Homaliodendron* including *H. flabellatum* (Sm.) M.Fleisch., *H. ligulifolium* (Mitt.) M.Fleisch., *H. montagneanum* (Müll. Hal.) M.Fleisch., *H. papillosum* Broth., *H. pulchrum* L.Y.Pei & Y.Jia, *H. scalpellifolium* (Mitt.) M.Fleisch. These samples were collected from various regions across China, encompassing diverse ecological and geographical regions. Additionally, two species of *Circulifolium* S.Olsson, Enroth & D.Quandt were included in the analysis. *Neckera pennata* Hedw. was used as an outgroup. Taxa for the analyses and their voucher specimens are listed in Table 1.

The nuclear ribosomal internal transcribed spacer region 5.8S-ITS2-26S (hereafter, ITS2), the tRNA (Gly) (UCC) (*trn*G), and the *trn*L-*trn*F intergenic spacer (*trn*L-F) have been widely used in phylogenetic analyses for mosses (Draper & Hedenäs 2009; Hedenäs 2012). These three markers were used to construct a phylogenetic tree with the above taxa. The DNA extraction method, PCR amplifications and primers for the three regions followed Li *et al.* (2018).

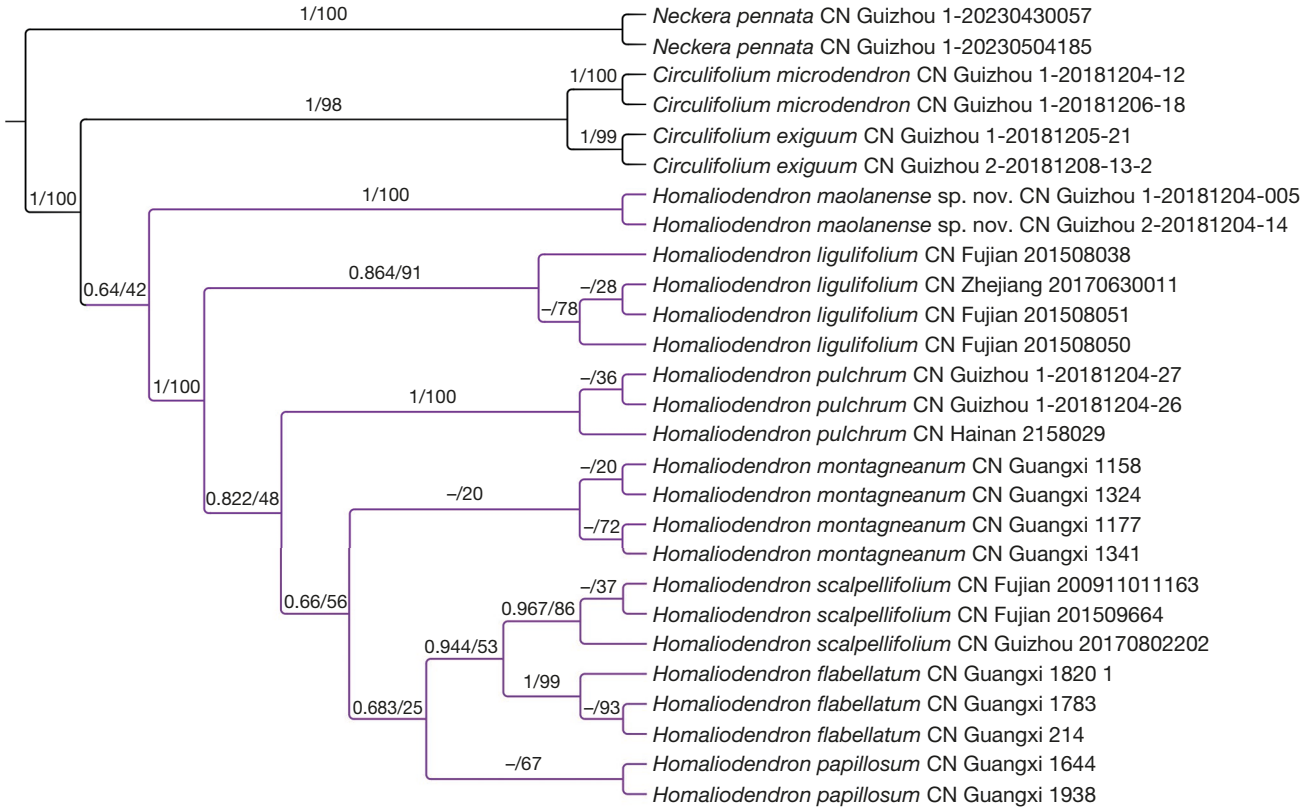

Fig. 1. — Phylogenetic tree with Bayesian posterior probabilities (PPBI) and maximum parsimony bootstrap support (BSML) on the branch, inferred from the combined datasets of *trn*L-F, *trn*G and ITS2. In **violet**, the clade of genus *Homaliodendron* Fleisch.

Phylogenetic tree construction

All sequences were manually aligned using PhyDE 0.9971 (Müller *et al.* 2010). After deletion of incomplete regions for some samples at the beginning and ends of the alignment, the total number of aligned sites from the three genes was 1701. Among them, 756 sites were variable characters and 268 were parsimony-informative. The numbers of sites in each locus based on sequence length, parsimony variable sites, parsimony informative sites, and the optimal substitution models, which were selected for Bayesian analysis, are presented in Table 2.

Phylogenetic analysis of three molecular datasets were carried out using Bayesian Inferences (BI) and Maximum Likehood (ML). The best-fitting nucleotide substitution models for each gene region were determined using MrModeltest v. 2.4 (Nylander 2004) in conjunction with PAUP 4.0b10 (Swofford 2003), employing the Akaike Information Criterion (AIC). Bayesian phylogenetic tree was constructed using a Markov Chain Monte Carlo (MCMC) approach implemented in MrBayes v3.2.7 (Ronquist *et al.* 2012).

Four independent MCMC runs, each with four chains, were performed for 1 000 000 generations, with trees sampled every 1 000 generations. Posterior probabilities were calculated after discarding the first 25% of trees as burn-in (Huelsenbeck & Ronquist 2001). Maximum Likelihood analysis was performed using RAxML v.8.2.10 (Stamatakis 2014) with 1 000 bootstrap replicates, employing a GTR + G model of nucleotide substitution for each partition. Phylogenetic trees were visualized and annotated using TreeGraph 2.0 (Stöver & Müller 2010).

RESULTS

The phylogenetic analysis incorporating the *trn*L-F, *trn*G, and ITS2 regions consistently identified all ten Neckeraceae Schimp. species, with high posterior probabilities (PP) and robust bootstrap support (BS) (Fig. 1).

Notably, two samples collected from Maolan National Natural Reserve in Guizhou Province formed a single clade ($PP_{BI} = 1$; $BS_{ML} = 100$), sister to a major clade consisting of *H. flabellatum, H. ligulifolium*, *H. montagneanum*, *H. papillosum*, *H. pulchrum* and *H. scalpellifolium* ($PP_{BI} = 1$; $BS_{ML} = 100$). The phylogenetic analyses show that the above two samples belong to the genus *Homaliodendron*, and should be placed in *Homaliodendron sensu stricto* because of their multicellular teeth at the leaf apex and foliose pseudoparaphyllia.

The two samples of *Homaliodendron* from Maolan are morphologically different from the other congeners by their branch and stem leaves, which are strongly falcate with widest part at the middle, and have irregularly biserrate margins with

TABLE 1. — Names, origins and vouchers (herbarium) used for phylogenetic analyses in this study as well as GenBank accession numbers.

Taxa	Collection locality	Coll. number	Collector	Herbarium	GenBank Accession		
					*trn*L-F	*trn*G	nrITS2
Circulifolium exiguum (Bosch & Sande Lac.) S. Olsson, Enroth & D. Quandt	Guizhou, China	1-20181205-21	Guo S. L., Li D.D. & Zhang Y. C.	SHTU	PV600085	PV600058	PV603899
C. exiguum	Guizhou, China	2-20181208-13-2	Guo S. L., Li D.D. & Zhang Y. C.	SHTU	PV600086	PV600059	PV603900
C. microdendron (Mont.) S. Olsson, Enroth & D. Quandt	Guizhou, China	1-20181204-12	Guo S. L., Li D.D. & Zhang Y. C.	SHTU	PV600087	PV600060	PV603901
C. microdendron	Guizhou, China	1-20181206-18	Guo S. L., Li D.D. & Zhang Y. C.	SHTU	PV600088	PV600061	PV603902
Homaliodendron flabellatum (Sm.) M.Fleisch.	Guangxi, China	1783	Wang Y. F. & Zuo Q.	HSNU	PV600089	PV600062	PV603903
H. flabellatum	Guangxi, China	1820-1	Wang Y. F. & Zuo Q.	HSNU	PV600090	PV600063	PV603904
H. flabellatum	Guangxi, China	214	Wang Y. F. & Zuo Q.	HSNU	PV600091	PV600064	PV603905
Homaliodendron ligulifolium (Mitt.) M.Fleisch.	Zhejiang, China	20170630011	Guo S. L.	SHTU	PV600092	PV600065	PV603906
H. ligulifolium	Fujian, China	201508038	Wang Y. F., Wei Q. Q. & Zhang B. Y.	HSNU	PV600093	PV600066	PV603907
H. ligulifolium	Fujian, China	201508050	Wang Y. F., Wei Q. Q. & Zhang B. Y.	HSNU	PV600094	PV600067	PV603908
H. ligulifolium	Fujian, China	201508051	Wang Y. F., Wei Q. Q. & Zhang B. Y.	HSNU	PV600095	PV600068	PV603909
Homaliodendron maolanense sp. nov.	Guizhou, China	1-20181204-005	Yang J. *et al.*	SHTU	PV600096	PV600069	PV603910
H. maolanense sp. nov.	Guizhou, China	2-20181204-14	Yang J. *et al.*	SHTU	PV600097	PV600070	PV603911
Homaliodendron montagneanum (Müll. Hal.) M. Fleisch.	Guangxi, China	1158	Wang Y. F. & Zuo Q.	HSNU	PV600098	PV600071	PV603912
H. montagneanum	Guangxi, China	1177	Wang Y. F. & Zuo Q.	HSNU	PV600099	PV600072	PV603913
H. montagneanum	Guangxi, China	1324	Wang Y. F. & Zuo Q.	HSNU	PV600100	PV600073	PV603914
H. montagneanum	Guangxi, China	1341	Wang Y. F. & Zuo Q.	HSNU	PV600101	PV600074	PV603915
Homaliodendron papillosum Broth.	Guangxi, China	1644	Wang Y. F. & Zuo Q.	HSNU	PV600102	PV600075	PV603916
H. papillosum	Guangxi, China	1938	Wang Y. F. & Zuo Q.	HSNU	PV600103	PV600076	PV603917
Homaliodendron pulchrum L.Y. Pei & Y. Jia	Guizhou, China	1-20181204-27	Guo S. L., Li, D.D. & Zhang Y. C.	SHTU	PV600104	PV600077	PV603918
H. pulchrum	Guizhou, China	1-20181204-26	Guo S. L., Li, D.D. & Zhang Y. C.	SHTU	PV600105	PV600078	PV603919
H. pulchrum	Hainan, China	2158029	Wang Q. H. & Yu N. N.	PE	PV600106	PV600079	PV603920
Homaliodendron scalpellifolium (Mitt.) M.Fleisch.	Guizhou, China	20170802202	Guo S. L., Li, D.D. & Zhang Y. C.	SHTU	PV600107	PV600080	PV603921
H. scalpellifolium	Fujian, China	200911011163	Wang Y. F., Wei Q. Q. & Zhang B. Y.	HSNU	PV600108	PV600081	PV603922
H. scalpellifolium	Fujian, China	201509664	Wang Y. F., Wu W. Y. & Liu Q.	HSNU	PV600109	PV600082	PV603923
Neckera pennata Hedwig.	Guizhou, China	1-20230430057	Guo S. L., Yu J. & Huang R. L.	SHTU	PV600083	PV600056	PV603897
N. pennata	Guizhou, China	1-20230504185	Guo S. L., Yu J. & Huang R. L.	SHTU	PV600084	PV600057	PV603898

6-12 sharp teeth, and a large, curved, multicellular, coarse and blunt terminal tooth. Based on the results of the morphological comparisons and molecular phylogenetic analyses, we thought that these two specimens represented a hitherto undescribed species. Here we named the species as *Homaliodendron maolanense* J.Yang, F.M.Lei, R.L.Huang, Y.C.Zhang, L.He, S.L.Guo, J.Yu & D.D.Li, sp. nov., indicating its type locality in Maolan, Libo County, Guizhou Province, China.

TAXONOMIC TREATMENT

Family NECKERACEAE Schimp.
Genus *Homaliodendron* Fleisch.

Homaliodendron maolanense J.Yang, F.M.Lei, R.L.Huang, Y.C.Zhang, L.He, S.L.Guo, J.Yu & D.D.Li, sp. nov. (Fig. 2)

KEY TO *HOMALIODENDRON* SPECIES IN CHINA

1. Capsules immersed ..... *H. neckeroides* Broth.
— Capsules exserted 2

2. Stipe leaf apices rounded-obtuse ..... *H. montagneanum* (Müll. Hal.) M.Fleisch.
— Stipe leaf apices acute or narrowly obtuse 3

3. Upper cells of stem leaves long rhomboid 4
— Upper cells of stem leaves rounded, quadrate to hexagonal 5

4. Branch leaves nearly similar in width throughout, acute or narrowly obtuse at the apex ..... *H. ligulifolium* (Mitt.) M.Fleisch.
— Branch leaves usually wider at the base, acute at the apex ..... *H. scalpellifolium* (Mitt.) M.Fleisch.

5. Branch leaf cells more or less distinctly mammillose ..... *H. papillosum* Broth.
— Branch leaf cells smooth 6

6. Costae single, strong or slender 7
— Costae absent or short and double 9

7. Branch leaves with the same width from base to upper, costae slender 8
— Branch leaves with the base broader than the apex, costa strong ..... *H. crassinervium* Thér.

8. Stipe leaves appressed, seta 2.5-4 mm ..... *H. flabellatum* (Sm.) M.Fleisch.
— Stipe leaves spreading, seta longer than 1.5 cm ..... *H. fruticosum* (Mitt.) S.Olsson, Enroth & D.Quandt

9. Branch leaf margins irregularly dentate at the apex, and costae double, short, sometimes indistinct or absent ..... *H. pulchrum* L.Y.Pei & Y.Jia
— Branch leaf margins strongly, irregularly biserrate teeth at the apex and costae distinctly double ..... *H. maolanense* J.Yang, F.M.Lei, R.L.Huang, Y.C.Zhang, L.He, J.Yu & D.D.Li, sp. nov.

TYPE MATERIAL. — **China** • Guizhou Province, Libo County, Maolan National Natural Reserve, Forest of Stone Scenic Spot; on rocks; 874 m alt.; 25°17'31.41"N, 107°56'16.75"E; 04.XII.2018; *leg.* J. Yang *et al.* 1-20181204-005 (holotype: SHTU!; isotype: KUN!).

ETYMOLOGY. — The specific epithet indicates the type locality: Maolan, Libo County, Guizhou Province, China.

HABITAT. — Growing on rocks under broadleaved forest, along roads.

DIAGNOSIS. — Similar to *Homaliodendron pulchrum*, but differing in having strongly falcate, asymmetrial leaves widest in midleaf, apices with irregularly biserrate teeth, and costae distinctly double.

DESCRIPTION

Plants medium to large-sized, to 10 cm long, strongly flattened, frondose, mostly with glossy, green or yellowish green, becoming tawny with age. Primary stems prostrate, with few reddish rhizoids, secondary stems erect, bipinnately or tripinnately branched, with few foliose pseudoparaphyllia. Central strand absent, outer cortex of 6-8 layers of thick-walled collenchymatous cells, inner cortex of thin-walled parenchymatous cells. Stipe leaves oblong-spathulate to obovate, obtuse at apices, 2.9-3.3 mm long, decurrent; costae double, short, distinct. Stem leaves, 2.3-3.3 mm, horizontally spreading, very asymmetric, strongly falcate, ovate-spathulate, with widest part at the middle, 0.85-1.45 mm wide, strongly tapered to base, 0.35-0.55 mm at base; apex truncate or apiculate, irregularly biserrate with 6-12 sharp teeth, the terminal tooth curved, larger than the others, 0.2-0.28 mm long, multicellular, coarse and blunt, entire below; often inflexed on one side at base; costae double, disitinct; cells strongly incrassate, smooth, round to longly rhomboidal, 4-8 × 10-18 µm at tip and margin, gradually longer below, 5-10 × 16-38 µm in mid-leaf, 5-9 × 35-95 µm at base near costa, basal leaf cells distinctly porose, at margin becoming smaller, shortly rhomboid to irregular rectangular. Branch leaves similar to stem leaves in shape, but smaller in size, 2.0-2.5 mm long, strongly falcated, costae double, dentate at the apex, with widest part at the middle, 0.75-0.90 mm wide, 0.32-0.34 mm at base; cells similar to those of stem leaves but smaller. Sporophytes not seen.

DISCUSSION

Fleischer (1905-1906) established the genus *Homaliodendron*, dividing it into two sections: *Homaliodendron* and *Circulifolia* Fleisch. Species in section *Circulifolia* differ from these in section *Homaliodendron* by having smaller, complanate leaves, minute, crenulate leaf apices and filiform pseudoparaphyllia (Ninh 1984; Buck 1998). Olsson *et al.* (2010) elevated *Circulifolia* to the generic level, naming it *Circulifolium* S.Olsson, Enroth & D.Quandt.

In our phylogenetic analyses, *Circulifolium exiguum* and *C. microdendron* are confirmed as a distinct genus, differing from *Homaliodendron stricto sensu* by their strongly complanate leaves with minute, crenulate leaf dentation and filiform pseudoparaphyllia, consistent with the findings on the phylogenetic

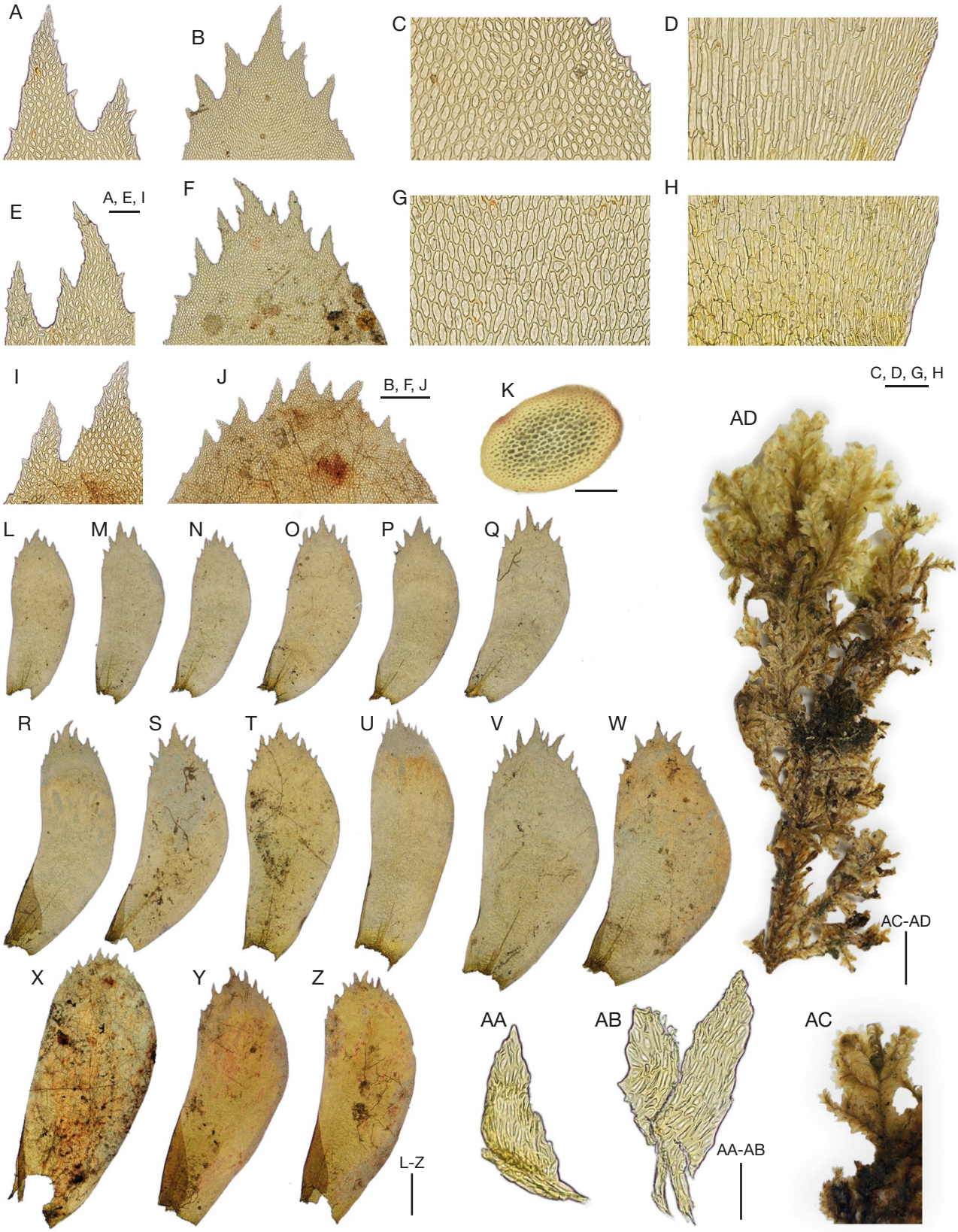

FIG. 2. — *Homaliodendron maolanense* sp. nov.: **A**, **B**, apical cells of branch leaves; **C**, upper cells of branch leaf; **D**, basal cells of branch leaf; **E**, **F**, apical cells of stem leaves; **G**, upper cells of stem leaf; **H**, basal cells of stem leaf; **I**, **J**, apical cells of stipe leaves; **K**, cross-section of stem; **L**-**Q**, branch leaves; **R**-**W**, stem leaves; **X**-**Z**, stipe leaves; **AA**, **AB**, pseudoparaphyllia; **AC**, plant when wet; **AD**, plant when dry (all from SHTU 2-20181204-14). Scale bars: A, C-E, G-I, AA, AB, 50 µm; B, F, J, 200 µm; K, 100 µm; L-Z, 500 µm; AC, AD, 500 mm.

TABLE 2. — Numbers of sites in each locus based on sequence length (**bp**), parsimony variable (**p.v.**) sites, parsimony informative (**p.i.**) sites, and the models selected for Bayesian analysis.

Gene	Length (bp)	p.v. sites	p.i. sites	Model
*trn*L-F	497	137	34	HKY+I
*trn*G	632	345	148	GTR+G
its2	572	274	86	GTR+G
Total	1701	756	268	—

relationships within the *Pinnatella* clade of the Neckeraceae (Olsson *et al.* 2010). Additionally, the newly identified species *H. maolanense* sp. nov., along with six other species of *Homaliodendron stricto sensu*, form a well-supported monophyletic clade.

In the study of Indochinese *Homaliodendron*, Ninh (1984) highlighted that the shape and arrangement of stem leaves and branch leaves were the most important characteristics for species identification. In the clade of seven *Homaliodendron* species on the phylogenetic tree, *H. ligulifolium* can be easily distinguished from other species by their lingulate, oblong-lingulate or broadly lingulate stem leaves.

Homaliodendron pulchrum, first described by Pei *et al.* (2011), is characterized by its oblong-spathulate to ovate leaves with indistinct or short double costae. Our phylogenetic analysis places three specimens of *H. pulchrum*, collected from Guizhou and Hainan Provinces, within a distinct clade. This clade is sister to *H. montagneanum*, *H. scalpellifolium*, *H. flabellatum* and *H. papillosum*. These findings reinforce the recognition of *H. pulchrum* as a unique species within the genus *Homaliodendron*.

Among the other four species on the phylogenetic tree, *H. montagneanum* was also distinct and mostly easily identified by its broadly triangular to lanceolate stem leaves, and acute or narrowly obtuse stipe leaf apices. Leaf characters such as the margin, cell structure and costa are also valuable for distinguishing *Homaliodendron* species (Ninh 1984; Olsson et al. 2010). *Homaliodendron papillosum* is unique within the genus for its medial cells of branch leaves and stem leaves more or less distinctly mammillose, a feature that clearly differentiates it from other species(Wu 2011; Enroth & Koponen 2017).

Homaliodendron maolanense sp. nov. and *H. pulchrum* exhibit morphological similarities, notably in their leaf apices, which are characterized by multicellular dentate structures, as well as in their thick-walled laminal cells and distinctly porose basal laminal cells. However, the leaves of *H. maolanense* sp. nov. are strongly falcate with widest part at the middle, distinctly asymmetric, strongly and irregularly biserrate teeth at the apex and costae distinctly double, while the leaves of *H. pulchrum* are oblong-spatulate to obovate, slightly asymmetric, irregularly dentate at the apex, and costae double, short, sometimes indistinct or absent (Pei et al. 2011).

The new species, *Homaliodendron maolanense* sp. nov., could be identified by the combination of the following features: 1) primary stems prostrate secondary stems erect, bi- or tri-pinnately branched, with few foliose pseudoparaphyllia; 2) branch and stem leaves strongly falcate with widest part at the middle; 3) costae double, short, distinct; 4) the teeth of upper margins and apex of leaves multicellular, biserrate, coarse and blunt; and 5) basal leaf cells distinctly porose.

Our results indicate that the new species, *H. maolanense* sp. nov., belongs to *Homaliodendron stricto sensu*. This placement is supported by both molecular data and morphylogical characteristics: notably presence of multicellular teeth at the leaf apex and foliose pseudoparaphyllia. So far, a total of ten species of *Homaliodendron* have been reported from China. The following key facilitates the identification of *H. maolanense* sp. nov. among the nine other Chinese species in the genus.

Acknowledgements

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