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Research paper

Phylogeny, character evolution, and classification of Selaginellaceae (lycophytes)

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ABSTRACT

Selaginella is the largest and most taxonomically complex genus in lycophytes. The fact that over 750 species are currently treated in a single genus makes Selaginellales/Selaginellaceae unique in pteridophytes. Here we assembled a dataset of six existing and newly sampled plastid and nuclear loci with a total of 684 accessions (74% increase of the earlier largest sampling) representing *ca.* 300 species to infer a new phylogeny. The evolution of 10 morphological characters is studied in the new phylogenetic context. Our major results include: (1) the nuclear and plastid phylogenies are congruent with each other and combined analysis well resolved and strongly supported the relationships of all but two major clades; (2) the *Sinensis* group is resolved as sister to *S.* subg. *Pulviniella* with strong support in two of the three analyses; (3) most morphological characters are highly homoplasious but some characters alone or combinations of characters well define the major clades in the family; and (4) an infrafamilial classification of Selaginellaceae is proposed and the currently defined *Selaginella s.l.* is split into seven subfamilies (corresponding to the current six subgenera + the *Sinensis* group) and 19 genera (the major diagnosable clades) with nine new species-poor genera. We support the conservation of *Selaginella* with a new type, *S. flabellata*, to minimize nomenclatural instability. We provide a key to subfamilies and genera, images illustrating their morphology, their morphological and geographical synopses, a list of constituent species, and necessary new combinations. This new classification will hopefully facilitate communication, promote further studies, and help conservation.

1. Introduction

Selaginella (Selaginellaceae) is the largest genus in lycophytes and known for its special phylogenetic position in vascular plants, its heterospores, its resurrection ability, and its pharmacological value (Banks et al., 2009). *Selaginella* is among the earliest diverging lineages of vascular plants and diverged from its closest living relative about 383 million years ago (Ma) in the Devonian Period (Klaus et al., 2017).

Following PPG I (2016), *Selaginella* alone constitutes the family Selaginellaceae and the order Selaginellales. However, it is unique for an order/family in pteridophytes with 700 or more species (Jermy, 1990; Tryon and Lugardon, 1991; Zhou and Zhang, 2015) to contain only one genus, considering the most recent classifications of pteridophytes, for example, *ca.* 380 species in 17 genera in Lycopodiales (Chen et al., 2022; Zhang and Zhou, 2022), the sister order of Selaginellales + Isoëtales, *ca.* 265 species in 25 genera in Blechnaceae (PPG I, 2016; de Gasper et al., 2016; González et al., 2020), *ca.* 1200 species in 37 genera in Thelypteridaceae (Fawcett and Smith, 2021), and *ca.* 900 species in 42 genera in Polypodiaceae subfam. Grammitidoideae (Yang et al., 2023; Zhou et al., 2023).

In fact, morphological heterogeneity within the broadly defined *Selaginella* or Selaginellaceae has been observed for a long time and a number of studies to recognize several genera in Selaginellaceae have been published. Splitting *Selaginella* into several genera dates back to Palisot de Beauvois (1803) when he described and recognized *Didiclis* P. Beauv., *Diplostachyum* P. Beauv., *Gymnogynum* P. Beauv., and *Stachygynandrum* P. Beauv. ex Mirb (1802) in the same

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work, two years before *Selaginella* was described (Palisot de Beauvois, 1804). Kuntze (1891) transferred a number of species of *Selaginella* to *Lycopodioides* but he actually did not split the genus into two, because he recognized *Lycopodioides* only. Börner (1912) separated *Heterophyllium* Hieron. ex Börner from *Selaginella* based on *Selaginella helvetica*, although this generic name is a later homonym of *Heterophyllium* (Schimp.) Müll. Hal. ex Kindb. (1894) and a nomenclatural synonym of *Diplostachyum*. Rothmaler (1944) recognized three genera in Selaginellaceae: *Didiclis* with a single macrosporangium at the base of strobili surrounded by sterile sporophylls, *Lycopodioides* with multiple macrosporangia at the base of strobili without any sporophylls, and *Selaginella* with uniform and spirally arranged leaves. Kung (1988) divided *Selaginella s.l.* into *Lycopodioides* and *Selaginella s.s.* and restricted the latter to *Selaginella selaginoides* and its allies that have no rhizophores and have loosely spirally arranged sterile leaves and cylindric strobili (*S.* subg. *Selaginella* sensu Zhou and Zhang, 2015). *Selaginella* sensu Kung (1988) has the same circumscription as Rothmaler's (1944). Satou (1997) and Tzvelev (2004) adopted Rothmaler's (1944) and Kung's (1988) classifications. Soják (1993) accepted *Selaginella* sensu Rothmaler (1944) and Kung (1988) and split *Lycopodioides* sensu Kung (1988) into the narrowly defined *Lycopodioides* and *Bryodesma* Soják; the latter was based on *Selaginella rupestris* (L.) Spring and included those species with spirally arranged sterile leaves and decussate sporophylls. Most recently, Weakley (2012) has recognized three genera in the family, *Bryodesma*, *Lycopodioides*, and *Selaginella s.s.*, for the Flora of the Southern and Mid-Atlantic States. Weakley (2022) and Weakley and Southeastern Flora Team (2022) included one more genus in the family, *Gymnogynum*, in the Flora of the Southeastern United States.

One of the major reasons that the broadly defined *Selaginella* was often adopted (e.g., Jermy, 1990; Valdespino, 1993; Zhang et al., 2013; PPG I, 2016) is that the current type of the genus, *S. selaginoides* (L.) P. Beauv. ex Schrank & Mart., is a member of a two-species subunit with no rhizophores at all, dramatically different from all other species in the genus. Recognizing multiple genera would result in name changes of all but the two species without rhizophores, although the name *Selaginella* may be proposed for conservation with a conserved type (Turland et al., 2018).

The second major reason that the broadly defined *Selaginella* was often adopted is that the phylogenetic relationships within the genus had been largely unclear in spite of earlier phylogenetic studies (Korall et al., 1999; Korall and Kenrick, 2002, 2004; Arrigo et al., 2013) and the morphological homoplasy had not been adequately assessed in an appropriate phylogenetic context. These have been improved greatly in the past few years. Weststrand and Korall (2016a) and Zhou et al. (2016; available online in 2015) published large-scale phylogenies based on plastid and nuclear markers. Based on plastid *rbcL* and nuclear ITS data of 394 accessions representing *ca*. 200 species (*ca*. 25% of the extant diversity of the genus) of *Selaginella*, Zhou et al. (2016) identified six deep-level clades and 20 major clades with strong resolution of the relationships among most of these clades. Zhou and Zhang (2015) thus recognized these six deep-level clades as six subgenera of *Selaginella* (*S.* subg. *Selaginella*, *S.* subg. *Boreoselaginella* Warb., *S.* subg. *Pulviniella* Li Bing Zhang & X.M. Zhou, "*S.* subg. *Ericetorum* Jermy" (= *S.* subg. *Gymnogynum* (P. Beauv.) Weststrand & Korall), *S.* subg. *Heterostachys* Baker, and *S.* subg. *Stachygynandrum* (P. Beauv. ex Mirb.) Baker) and three of subgenera (*S.* subg. *Ericetorum*, *S.* subg. *Heterostachys*, and *S.* subg. *Stachygynandrum*) were further classified into six, five, and seven sections, respectively. However, some relationships, e.g., those of the *Selaginella sanguinolenta* clade, were not strongly supported in Zhou et al. (2016) and the enigmatic *Sinensis* group, which had caused poor phylogenetic resolution in the previous study (Korall and Kenrick, 2002), was not sampled in their study. Based on plastid *rbcL* and nuclear *pgiC* and *SQD1* data of 340 accessions representing 223 species of *Selaginella* including 10 species of the *Sinensis* group, Weststrand and Korall (2016a) resolved the *Sinensis* group as sister to those taxa (*S.* subg. *Pulviniella*, *S.* subg. *Ericetorum*, *S.* subg. *Heterostachys*, and *S.* subg. *Stachygynandrum* sensu Zhou and Zhang (2015)) with rhizophores clearly originated on the ventral side of the stem with moderate support (PP = 0.97) in Bayesian inference (BI). The relationships of five out of the seven major clades identified by Weststrand and Korall (2016a) were not resolved. Depending on different DNA markers, the relationships of *S.* subg. *Boreoselaginella* [including *Selaginella nummularifolia* Ching, *Selaginella rossii* (Baker) Warb., *S. sanguinolenta* (L.) Spring, etc.)] were resolved differently (Weststrand and Korall, 2016a; Zhou et al., 2016). Based on plastid gnomes of 26 species of *Selaginella*, Zhang et al. (2019) resolved *S.* subg. *Boreoselaginella* as sister to the superclade with ventral rhizophores with strong support, same as the position β found by Weststrand and Korall (2016a). Zhang et al. (2020, 2022) then speculated that high GC content, extensive RNA editing sites, and elevated substitution rate of plastid genomes maybe strongly shook the stability of phylogenetic topology of *Selaginella*. A recent phylogenomic analysis based on 59 plastomes failed to well resolve the phylogenetic relationships in *Selaginella* with confidence, highlighting the difficulty in resolving the phylogeny and evolution of this particularly important land plant lineage (Zhou et al., 2022).

Morphologically, state of rhizophores, arrangement of vegetative leaves and sporophylls, and spore morphology are traditionally used for the classification of *Selaginella* (e.g., Jermy, 1986; Zhou and Zhang, 2015; Weststrand and Korall, 2016b). However, because of the homoplastic nature of some morphological characteristics, some taxa are very difficult to define and identify clearly (Zhou et al., 2015; Weststrand and Korall, 2016b). For example, rosette-forming habit is present in three subgenera: *S.* subg. *Stachygynandrum* [e.g., *Selaginella pallescens* (C. Presl) Spring), *S.* subg. *Gymnogynum* [e.g., *Selaginella lepidophylla* (Hook. & Grev.) Spring, *Selaginella novoleonensis* Hieron.), and *S.* subg. *Pulviniella* [e.g., *Selaginella pulvinata* (Hook. & Grev.) Maxim., *S. tamrscina* (P. Beauv.) Spring), and dimorphic sporophylls appear in *S.* subg. *Stachygynandrum* [e.g., *Selaginella flagellata* Spring, *Selaginella moritziana* Spring, *Selaginella radiata* Baker, *Selaginella simplex* Baker] and *S.* subg. *Heterostachys* [e.g., *Selaginella leptophylla* Baker, *Selaginella nipponica* Franch. & Sav., *Selaginella repanda* (Desv. ex Poir.) Spring]. Similarly, some morphological character states, e.g., rhizophores borne on dorsal sides of the stem, reticulate surfaces of megaspores, stele with more than two vascular bundles, and diverse sporangial arrangement on the strobili, are also present in more than one section and/or subgenus.

Selaginella is heterosporous. A number of studies on the morphology of megaspores and microspores (especially megaspores) of *Selaginella* have been published (e.g., Zhou et al., 2015; Valdespino et al., 2015; Valdespino et al. (2018a); Valdespino et al. (2018b); Valdespino, 2015, 2017a, 2020; Bauer et al., 2016; Wang et al., 2018). These studies showed that *Selaginella* holds extremely high diversity in spore morphology. Spore data have provided very important and useful taxonomic information which has been incorporated in the recent classifications of the genus (Zhou and Zhang, 2015; Weststrand and Korall, 2016a, 2016b). In addition to spore ornamentation, the size of both megaspores and microspores also shows great variation in *Selaginella*. Megaspore sizes range from 150 to 1500 μm and microspore sizes from 15 to 50 μm (Mickel and Hellwig, 1969; Zhou et al., 2015; Bauer et al., 2016). Taxonomically, species of *S.* subg. *Gymnogynum* often have larger (500−1000 μm) megaspores, whereas those of *S.* subg. *Heterostachys* and *S.* subg. *Pulviniella* usually have smaller (200−400 μm) megaspores.

Plastome studies (Tsuji et al., 2007; Smith, 2009; Wicke et al., 2011; Jansen and Ruhlman 2012; Ruhlman and Jansen 2018; Mower et al., 2019; Xu et al., 2018; Zhang et al., 2019a, Zhang et al., 2019b; Kang et al., 2020; Xiang et al., 2022; Zhou et al., 2022) showed that plastomes of Selaginellaceae and their infrafamilial lineages known so far have a number of unique and diverse features: (a) plastomes of most plant lineages are highly conserved with quadripartite structure composed by a large single copy (LSC), a small single copy (SSC), and two inverted repeats (IRa and IRb), whereas plastomes of Selaginellaceae exhibit DR structure (also can be R, DR, IR, or DR-IR coexisting types) with small to medium repeats existed in SC, and plastome conformations ranged from one to 24 (Zhou et al., 2022); (b) plastome sizes in most land plants are 120–160 kb but those in Selaginellaceae are 78–190 kb; (c) a plastome in other vascular plants usually contains approximately 120–130 genes but those of Selaginellaceae contain 36–128 gene; (d) *accD/cemA/infA/psaM/rpl20/rpl21/rpl32/rpl33/rps12/rps15/rps16/ycf66/ycf94* and most of the rRNA, tRNA, and introns are generally lost or pseudogenetized in Selaginellaceae; (e) GC content in land plant plastomes ranges from 34% to 40%, but plastomes of Selaginellaceae often are extremely GC-rich (>50%); and (f) overall distinctions of plastomes among subgenera even among sections in *Selaginella* are much greater than those among orders/families/subfamilies/genera in other vascular plants.

In this study our goals included: (1) better resolving the relationships within *Selaginella* with expanded taxon sampling by including the elusive *Sinensis* group and with expanded character sampling by including two highly conserved nrDNA markers, 18S and 26S, to be sampled for the first time for *Selaginella*; (2) for the first time evaluating the evolution of gross morphology and micromorphology of megaspores and microspores and identifying morphological synapomorphies of various clades in the context of the new phylogeny; and (3) proposing a infrafamilial classification of Selaginellaceae based on new molecular and morphological results.

2. Materials and methods

2.1. Taxon sampling

Silica gel-dried materials and herbarium samples either were collected in the fields or herbaria (CDBI, KUN, MO, and PYU). Taxon sampling for this study consisted of 686 accessions representing *ca*. 300 species in *Selaginella* including all subgenera/sections recognized by Zhou and Zhang (2015) and Weststrand and Korall (2016b). For morphological analysis, 291 accessions to represent *ca*. 275 species of *Selaginella* were included.

2.2. DNA extraction, amplification and sequencing

Total genomic DNA was extracted from silica-dried material or sometimes from herbarium specimens using a TIANGEN plant genomic DNA extraction kit (TIANGEN Biotech., Beijing, China) following the manufacturers' protocols. In total six genes, one plastid marker (*rbcL*), two single-copy nuclear genes (*pgiC* and *SQD1*), and three nuclear rDNA markers (18S, 5.8S, and 26S), were used in the phylogenetic study. The primer sequences and PCR conditions are listed in Table S1. PCR products were purified and sequenced by TSINGKE Biological Technology (Chengdu, China). Sequencher 4.14 (Gene Codes Corp., Ann Arbor, MI, USA) was used to assemble and edit contiguous sequences.

2.3. Sequence alignment and phylogenetic analysis

Sequences for each marker were initially aligned with MAFFT v.7 (Katoh and Standley, 2013) and manually adjusted in BioEdit (Hall, 1999). The ambiguously aligned areas were deleted. jModeltest 2.1.7 (Darriba et al., 2012) was used to select the best-fitting likelihood model for Bayesian analyses. The Akaike information criterion (Akaike, 1974) was used to select among models instead of the hierarchical likelihood ratio test, following Pol (2004) and Posada and Buckley (2004). The best-fitting models and parameter values are provided in Table 2. The alignment has been deposited in FigShare with study number #22730093.

Equally weighted maximum parsimony (MP) jackknife (JK) analyses (Farris et al., 1996) for each locus and the combined sequence data were conducted using PAUP* v.4.0b10 (Swofford, 2002), with insertions and deletions coded as missing data, the removal probability set to approximately 37%, and "jac" resampling emulated analyses. One thousand replicates were performed with 10 TBR searches per replicate and a maximum of 100 trees held per TBR search.

For the concatenated analysis of all nucleotide characters, maximum likelihood (ML; Felsenstein, 1973) tree searches and ML bootstrapping (BS) were conducted using the web server RAxML-HPC2 on TG v.7.2.8 on CIPRES web server (Miller et al., 2010), with 1000 rapid bootstrap analyses and -m GTRCAT as the default model followed by a search for the best-scoring tree in a single run (Stamatakis et al., 2008).

Bayesian inference (BI) was conducted using MrBayes 3.2.7 (Ronquist and Huelsenbeck, 2003) on CIPRES (Miller et al., 2010), transition/transversion rate ratio set as a free parameter, and GTR + I+Γ model (lset nst = 6 rates = invgamma) for all partitions, all model parameters were unlinked across four partitions (unlink statefreq = [all], revmat = [all], shape = [all], pinvar = [all]), and all partitions were allowed to have different rates (prset applyto = [all] ratepr = variable). Two independent runs, each with four chains (one cold, three heated), were conducted, each beginning with a random tree and sampling one tree every 1000 generations of 10,000,000 generations. Convergence among generations and stationarity were assessed using Tracer v.1.4 (Rambaut and Drummond, 2007) and the first 25% of the trees was discarded as burn-in to ensure that stationarity in log-likelihood had been reached. The remaining trees were used to calculate a 50% majority-rule consensus topology and posterior probabilities (PP).

2.4. Morphological studies

Morphological data (habit, sterile leaves, states of rhizophores, strobilus morphology, sporophylls, etc.) were obtained from field observations, herbarium investigations (specimens at CDBI, MO, NY, PYU, SING, and UC), and literature studies. Megaspores and microspores for some representative species were observed and studied using scanning electron microscope (SEM) (QUANTA 200 Scanning Electron Microscope, FEI Co., USA) at Yunnan University, Kunming, China.

Table 1
Data matrices and tree statistics for each of the dataset. PI chars. include the outgroups.

Region	# Accessions	# Characters	# PI chars. (%)
rbcL	665	1323	715 (54.0%)
18S	187	1637	392 (23.9%)
26S	144	909	222 (24.4%)
5.8S	284	166	63 (38.0%)
pgiC	128	480	293 (61.0%)
SQD1	143	543	338 (62.2%)
18S + 26S + ITS + *pgiC* + *SQD1*	292	3735	1308 (35.0%)
18S + 26S + ITS + *pgiC* + *SQD1*+*rbcL*	665	5058	2023 (40.0%)

Table 2
Best-ftting models and parameter values for separate (*rbcL*, 18S, 26S, 5.8S, *pgiC*, and *SQD1*), simultaneous nuclear, and simultaneous nuclear + plastid datasets and in this study. “G” = gamma distribution shape parameter (Yang, 1994). “GTR” = general-time-reversible model (Tavaré, 1986). “I” = proportion of invariable sites. “pInv” = proportion of invariable sites. “Simultaneous-1” = 18S + 26S + 5.8S + *pgiC* + *SQD1*. “Simultaneous-2” = 18S + 26S + 5.8S + *pgiC* + *SQD1*+*rbc*L.

Region	Model (AIC)	Base frequencies				Substitution model (rate matrix)							
		A	C	G	T	A–C	A–G	A–T	C–G	C–T	G–T	pInv	G
rbcL	GTR + I + G	0.2857	0.2433	0.2255	0.2455	0.4631	3.9209	0.2720	0.5053	2.4318	1.0000	0.3140	1.0406
18S	GTR + I + G4	0.2781	0.2738	0.2168	0.2313	0.6532	6.6774	1.4011	0.3697	2.5304	1.0000	0.6271	0.5937
26S	GTR + I + G	0.2181	0.3153	0.2171	0.2496	0.8700	9.0898	1.9289	0.3311	3.0681	1.0000	0.5842	0.7472
5.8S	TIM2ef + I + G4	0.2500	0.2500	0.2500	0.2500	1.8204	4.9269	1.8204	1.0000	11.7664	1.0000	0.3311	0.5161
pgiC	TVM + I + G4	0.2169	0.2487	0.2353	0.2990	1.5604	8.0577	1.8589	1.6658	8.0577	1.0000	0.4050	1.2491
SQD1	TIM3+I + G	0.2077	0.2875	0.3089	0.1959	1.3327	3.7081	1.0000	1.3327	5.8799	1.0000	0.4093	1.0064
Simultaneous-1	GTR + F + I + G4	0.2410	0.2790	0.2310	0.2480	0.9487	5.8027	1.1042	0.8629	4.0430	1.0000	0.5810	0.6100
Simultaneous-2	GTR + I + G4	0.2488	0.2598	0.2411	0.2503	0.7940	5.0369	0.7221	0.7775	3.7732	1.0000	0.4813	0.6299

2.5. Character evolution analysis

Based on previous morphological works and our studies of the morphology of *Selaginella* species worldwide, 10 morphological characters were analyzed: presence of rhizophores (absent, present), positions of rhizophores (dorsal side of stems and/or branches, ventral side of stems or/and branches, uncertain), dimorphism of overall sterile leaves (dimorphic, monomorphic), dimorphism of sterile leaves at the base of main stems (dimorphic, monomorphic), arrangement of sterile leaves [(spiral, four rows, decussate (at least on stem)], number of megasporophylls on strobili (only one to few at base, several on dorsal or/and ventral side), dimorphism of sporophylls on strobili (dimorphic, monomorphic), resupination of strobili with dimorphic sporophylls (resupinate, non-resupinate, N/A), surfaces of megaspores (reticulate, non-reticulate), reticulate megaspores [the *Bryodesma* type (with prominent and dense muri: Fig. 5Q), the *Gymnogynum* type (with often high and strong or wing-like muri and slightly regular meshes: Fig. 5N–Q), the *Stachygynandrum* type (with more or less open and irregular meshes: Fig. 10H, K–N), the *Tetragonostachyae* type-1 (with very fine muri and open meshes: Fig. 9M and N), and the *Tetragonostachyae* type-2 (with fine muri formed by verrucate ornamentation: Fig. 9L), N/A]. Similar to megaspores, microspores of *Selaginella* also showed high variation (e.g., Valdespino et al., 2015; Zhou et al., 2015; Wang et al., 2018), but microspore data were often unavailable and thus were not included in our analysis. Mesquite v.2.75 (Maddison and Maddison, 2011) was used to optimize morphological features on the most likely ML tree. The ancestral states were estimated based on parsimony criterion. For most species with multiple samples, only one or two samples of each species were selected on the tree for analysis.

3. Results

3.1. Molecular phylogeny

A total of 1551 sequences including 665 sequences of *rbcL*, 128 of *pgiC*, 143 of *SQD1*, 187 of 18S, 284 of 5.8S, and 144 of 26S were used in the study, of which 420 (*ca*. 30% of total sequences) sequences were newly sequenced for this study. An additional 1131 sequences were downloaded from GenBank. Voucher information and GenBank accession numbers for all sequences are listed in Table S1. Characteristics of alignments are summarized in Table 1. The tree topologies using maximum likelihood, Bayesian inference, and maximum parsimony analyses were generally concordant when using the concatenated dataset.

A comparison of the trees resulting from MPJK analyses of the plastid marker, individual nuclear markers, combined nuclear markers, and combined plastid and nuclear dataset did not identify any well-supported conflicts in MP analyses (MPJK >70%; Mason-Gamer and Kellogg, 1996; Zhang and Simmons, 2006). The ML tree based on the plastid marker is shown in Fig. S1, that based on the combined nuclear markers is in Fig. S2, that based on combine plastid and nuclear markers is in Fig. S3, and the simplified Fig. S3 is in Fig. 1. The results described below were based on combined plastid and nuclear markers.

The monophyly of *Selaginella* was strongly supported (MLBS: 100%; MPJK: 100; BIPP: 1.00). Within *Selaginella*, seven deep-level clades corresponding to *S.* subg. *Selaginella*, *S.* subg. *Boreoselaginella, S.* subg. *Gymnogynum* (“*S.* subg. *Ericetorum*” sensu Zhou and Zhang, 2015), *S.* subg. *Pulviniella*, *S.* subg. *Heterostachys*, *S.* subg. *Stachygynandrum* sensu Zhou and Zhang (2015), and the *Sinensis* group were strongly supported (MLBS: 100%; MPJK ≥99; BIPP: 1.00).

Selaginella subg. *Selaginella*, *S.* subg. *Boreoselaginella*, and *S.* subg. *Gymnogynum* were resolved as the first, second, and third diverging lineages, respectively, all with strong ML and BI support. *Selaginella* subg. *Pulviniella* was resolved as sister to the *Sinensis* group with strong ML and BI support. They together were sister to *S.* subg. *Heterostachys* + *S.* subg. *Stachygynandrum*. The MPJK values were generally low for the inter-subgeneric relationships. Within the *Sinensis* group, three deep geographically differentiated clades were identified: one with Asian and northern African species, one with *Selaginella australiensis*, and one with species from Indian Ocean islands. Within *S.* subg. *Gymnogynum*, six major clades corresponding six sections sensu Zhou and Zhang (2015) were strongly supported as monophyletic: sect. *Megalosporarum* was strongly supported as sister to *S.* sect. *Myosurus*, and *S.* sect. *Lepidophyllae* was strongly supported as sister to *S.* sect. *Homoeophyllae*, but other inter-sectional relationships were not strongly supported. Within *S.* subg. *Heterostachys*, five sections defined by Zhou and Zhang (2015) were all strongly supported as monophyletic (MLBS ≥99%; MPJK ≥88; BIPP: 0.98) and their relationships were well resolved and strongly supported (MLBS ≥95%; MPJK ≥80; BIPP: 1.00), but same as those in Zhou et al. (2016). Within *S.* subg. *Stachygynandrum*, *S.* sect. *Ascendentes* was resolved as sister to the rest, followed by *S.* sect. *Circinatae* and *S.* sect. *Plagiophyllae* which formed a clade sister to the remaining four sections sensu Zhou and Zhang (2015).

3.2. Morphological evolution

Ten common morphological characters and their states are shown in Fig. 2A–J. It took one step for the parsimony reconstruction of rhizophores (Fig. 2A); three steps for that of positions of rhizophores (Fig. 2B), four steps for that of dimorphism of overall sterile leaves (Fig. 2C); 20 steps for that of dimorphism of sterile leaves at the base of main stems (Fig. 2D); three steps for that of arrangement of sterile leaves (Fig. 2E); four steps for that of number of megasporophylls on strobili (Fig. 2F); 15 steps for that of dimorphism of sporophylls on strobili (Fig. 2G); 15 steps for that of

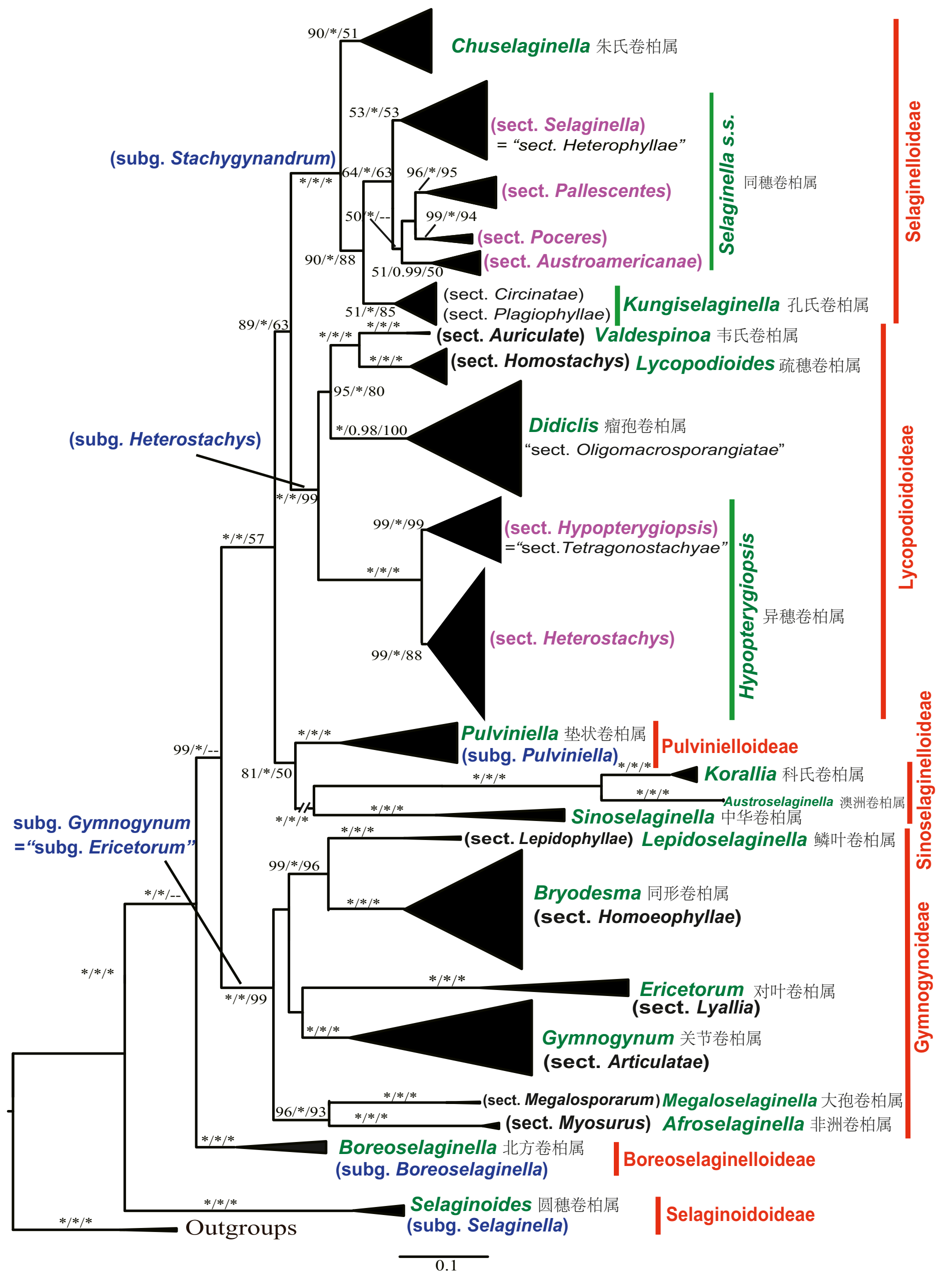

Fig. 1. Simplified maximum likelihood phylogeny of Selaginellaceae based on plastid *rbcL* and nuclear ITS sequences. The sizes of black triangles are in proportion to the sample sizes of individual clades. Support values (maximum likelihood bootstrap support, maximum parsimony jackknife support, and posterior probability) are shown along the branches. "*" indicates a 100% support value. Red and green names indicate the 7 subfamilies and 19 genera, respectively, recognized in the current classification. Blue and black Latin names indicate the subgenera and sections recognized by Zhou and Zhang (2015). Black Chinese names indicate Chinese vernacular names of the genera. Purple names indicate the 8 sections recognized by Zhou and Zhang (2015) and this study at the same rank.

resupination of strobili with dimorphic sporophylls (Fig. 2H); seven steps for that of surfaces of megaspores (Fig. 2I); and eight steps for that of reticulate megaspores (Fig. 2J).

4. Discussion

4.1. Major new findings in the phylogeny

With the largest phylogeny so far in terms of the number of species sampled, our study made a number of new findings in comparison with earlier such works (Weststrand and Korall, 2016a; Zhou et al., 2016). These new findings might provide foundation for future studies of interspecific relationships and discoveries of hidden diversity. Below we focus on and update the major relationships in the genus. In order to compare our current results with previous ones, we use subgeneric and sectional names in the Zhou and Zhang (2015) classification except the *Sinensis* group, which was not treated in our earlier classification, and *S.* subg. *Ericetorum* which is changed to *S.* subg. *Gymnogynum* here (Weststrand and Korall, 2016a).

Overall, the major new findings include: (1) The *Sinensis* group is resolved as sister to *S.* subg. *Pulviniella* with strong support in two of the three analyses; (2) *S.* sect. *Circinatae* and *S.* sect. *Plagiophyllae* formed a clade with strong support in two of the three analyses; (3) *S.* sect. *Megalosporarum* and *S.* sect. *Myosurus* are resolved as sister to each other; (4) *S.* sect. *Ascendentes* is resolved as sister to the rest

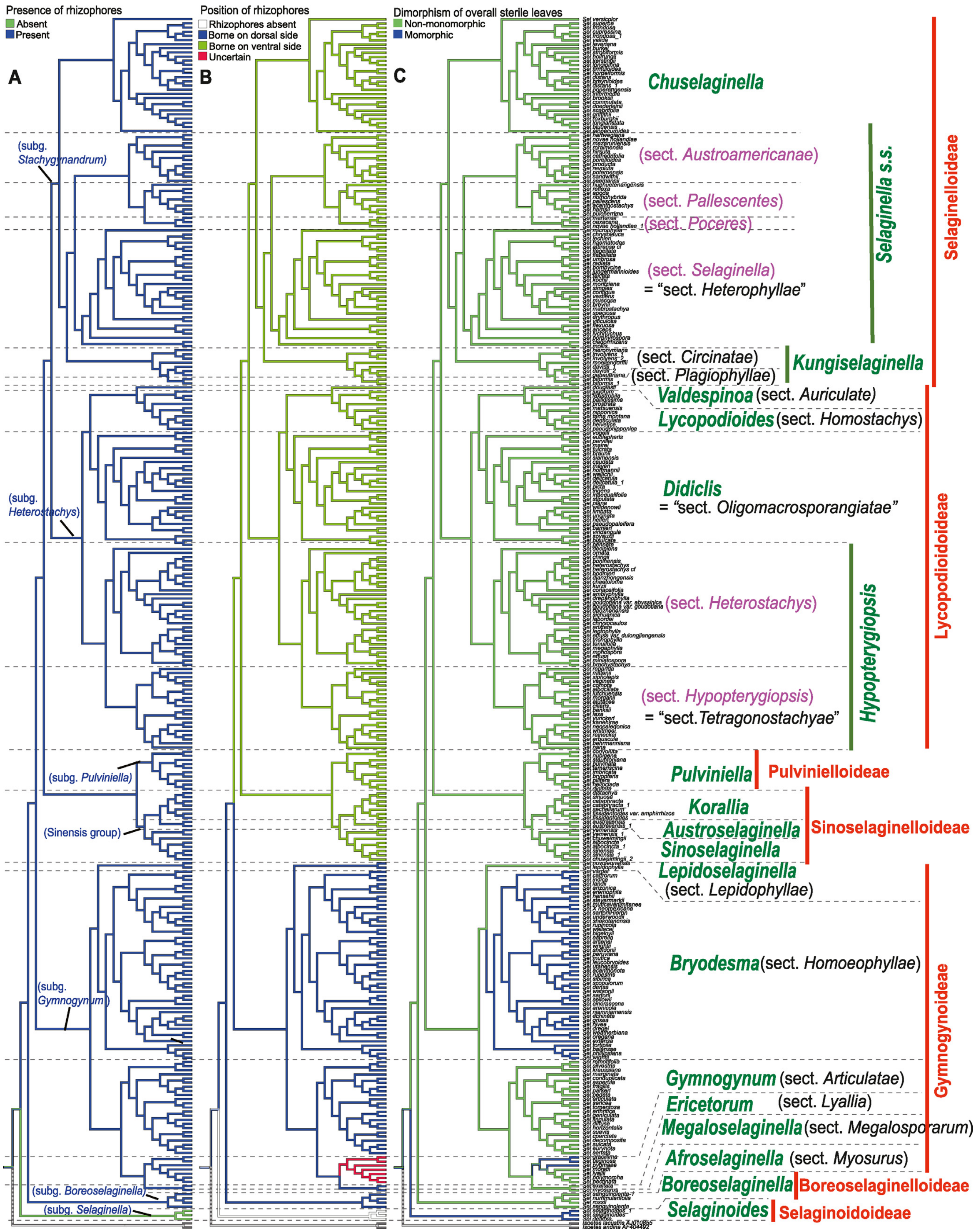

Fig. 2. Morphological characters of Selaginellaceae optimized onto the maximum likelihood tree. **A.** Presence of rhizophores; **B.** Position of rhizophores; **C.** Dimorphism of overall sterile leaves. **D.** Dimorphism of sterile leaves at the base of main stems

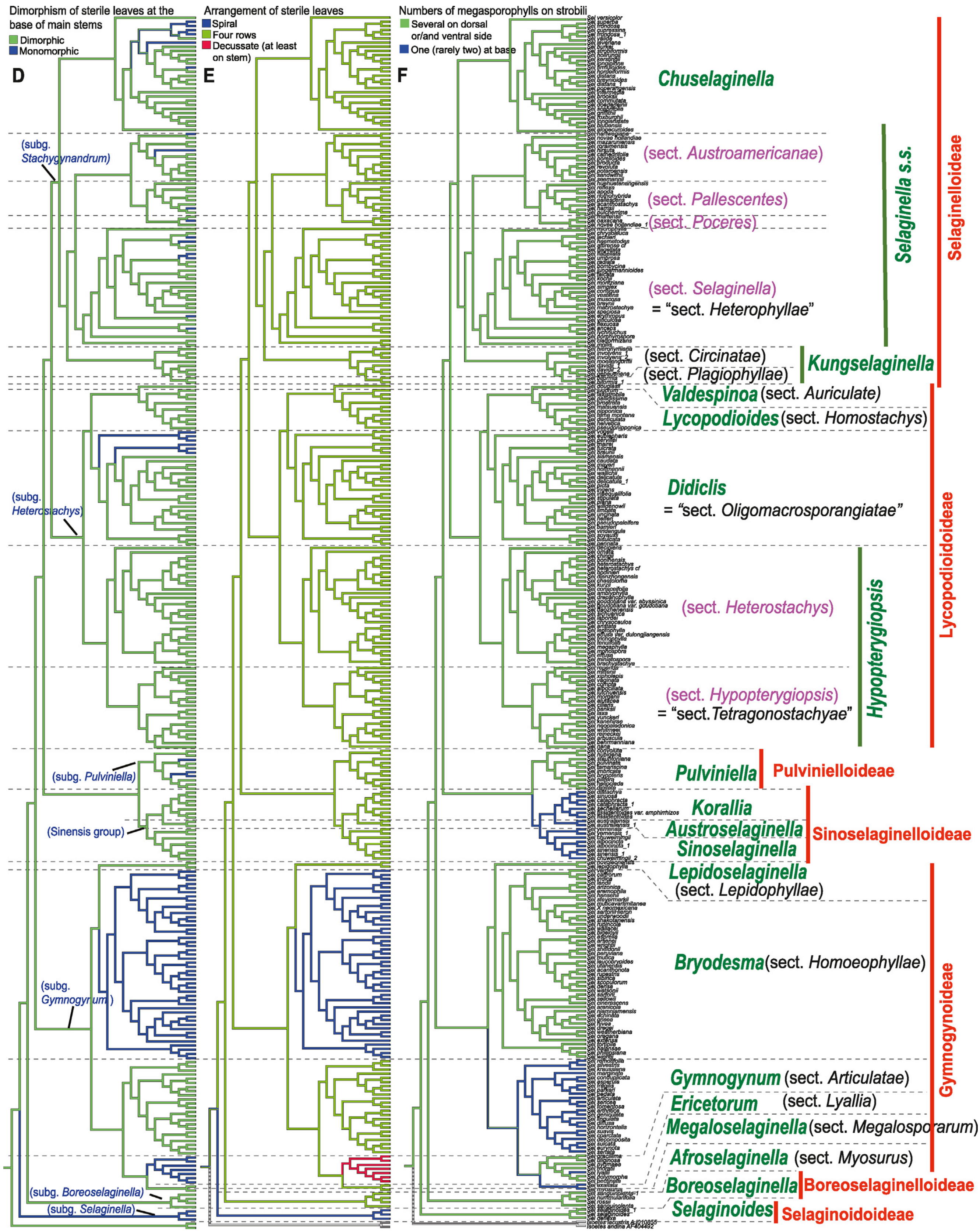

Fig. 2. (*continued*).

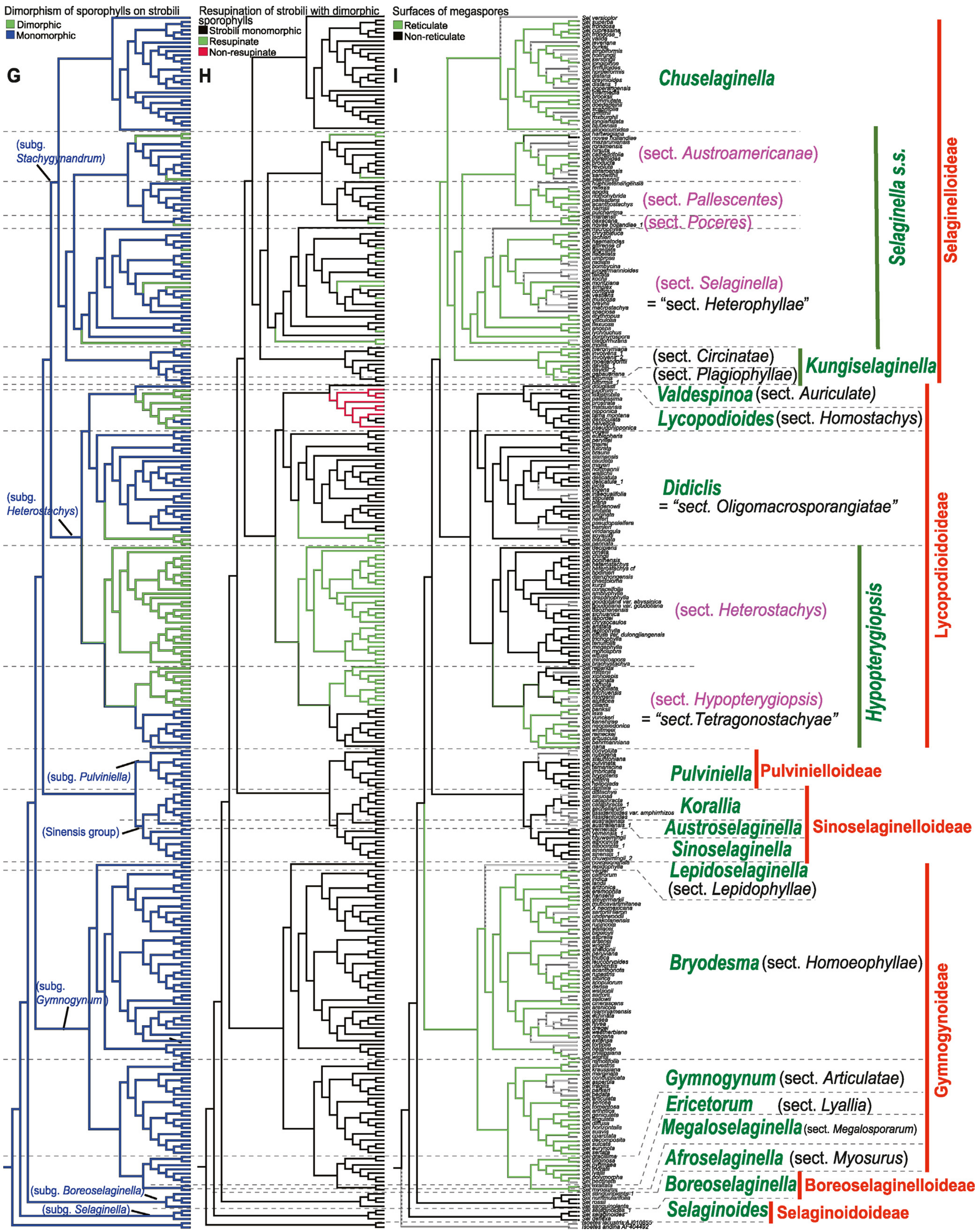

Fig. 2. (*continued*).

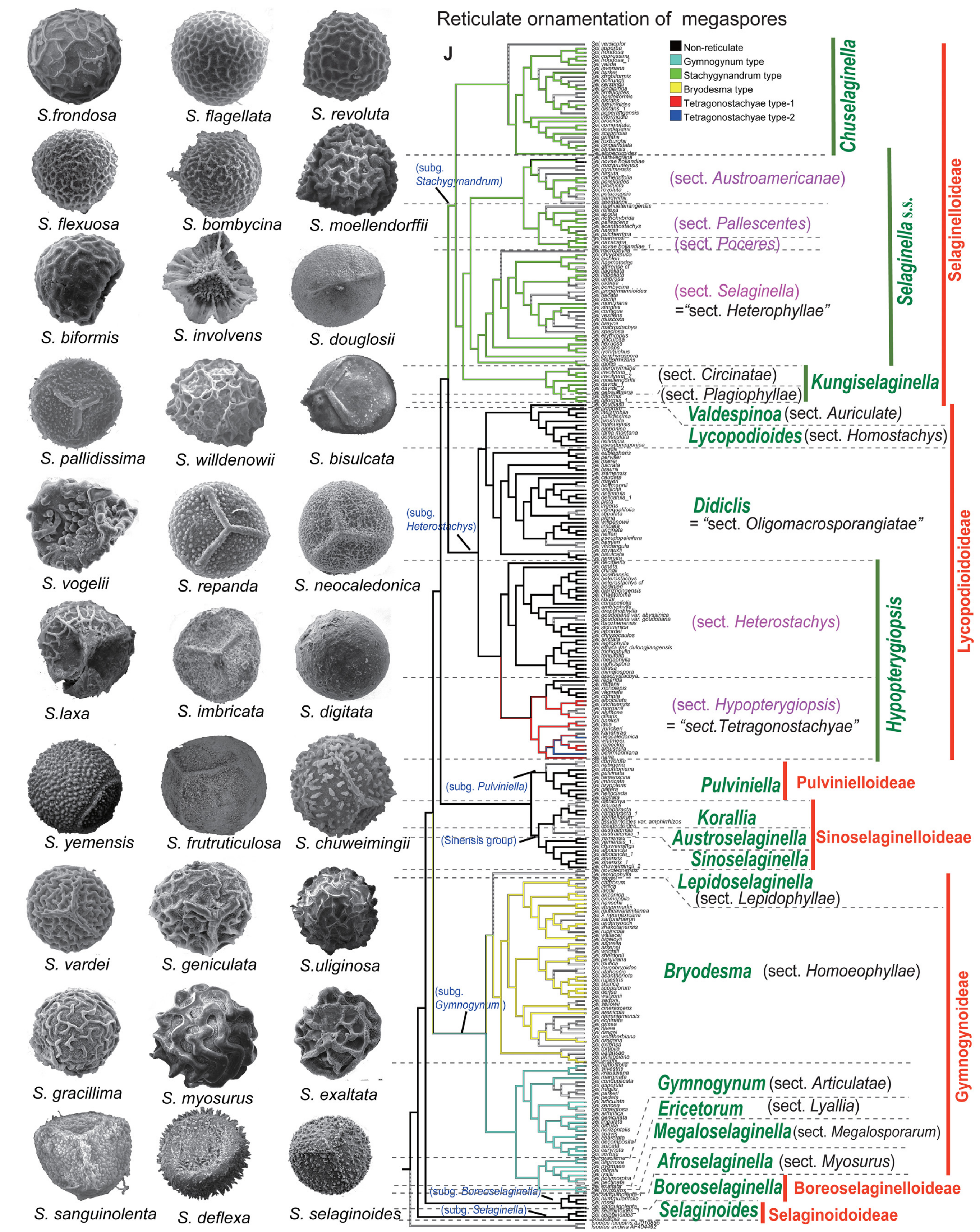

Fig. 2. (*continued*).

of *S.* subg. *Stachygynandrum* with strong support; and (5) *S.* sect. *Ascendentes* is found to contain African species. We will discuss them in detail below.

4.2. Deep relationships in Selaginella

4.2.1. Selaginella subg. Selaginella (Fig. 3)

Selaginella subg. *Selaginella* is the first diverging lineage in *Selaginella*. It contains only two species, *S. selaginoides* (L.) P. Beauv. ex Schrank & Mart. and *Selaginoides deflexa* Brack. Its relationships have been quite consistent (Korall et al., 1999; Korall and Kenrick, 2002, 2004; Arrigo et al., 2013; Weststrand and Korall, 2016a; Zhou et al., 2016). This clade is well characterized by spiral and monomorphic sporophylls and absence of rhizophores (Fig. 2A, C, E and 3).

4.2.2. Selaginella subg. Boreoselaginella (Fig. 4)

It corresponds to the *Sanguinolenta* group (Weststrand and Korall, 2016a). The resolutions of *Selaginella* subg. *Boreoselaginella* have been controversial. Depending on datasets and analysis methods, there have been three resolutions: (1) sister to the remaining taxa with rhizophores [e.g., BI based on *rbcL*, *SQD1*, or *rbcL* + *SQD1*: Weststrand and Korall (2016a); BI and ML based on *rbcL* + ITS: Zhou et al. (2016)]; (2) sister to a clade containing *S.* subg. *Pulviniella* + *S.* subg. *Heterostachys* + *S.* subg. *Stachygynandrum* sensu Zhou and Zhang (2016) based on *pgiC* data (Weststrand and Korall, 2016a) and based on plastome data (Zhou et al., 2022); and (3) sister to the ventral-rhizophore clade with strong support based on plastid gnomes of 26 species of *Selaginella* but only a few species of *Selaginella* were sampled and did not include the *Sinensis* group (Zhang et al., 2020).

Morphologically, *Selaginella* subg. *Boreoselaginella* has large number of inexplicable features in *Selaginella*, e.g., nearly monomorphic sterile leaves, rhizophores borne on dorsal side of stems and branches, xerophytic habit, monomorphic sporophylls, larger megaspores, and rugate surface of microspore. It is similar to *S.* sect. *Articulatae*, *S.* sect. *Megalosporarum*, and *S.* sect. *Myosurus* in having large spore size, dimorphic sterile leaves, and rhizophores borne on dorsal side of stems and branches. It is similar to *S.* sect. *Homoeophyllae* in having xerophytic habit, rhizophores borne on dorsal side, and rugate surface of microspores (Fig. 4L–N). Some species (*S. sanguinolenta* and *S. nummularifolia*) with nearly monomorphic sterile leaves are similar to *S.* sect. *Lepidophyllae*. However, this subgenus also has some characters (e.g., strobili with more than one megasporophylls, sterile leaves dimorphic and in four rows) similar to *S.* subg. *Heterostachys* and *S.* subg. *Stachygynandrum* sensu Zhou and Zhang (2015). In particular, except rhizophores borne on dorsal side and strobili with more than one megasporophyll, this subgenus is strongly similar to some species (e.g., *S. albocinata*) of the *Sinensis* group in Asia in having xerophytic habit and monomorphic sporophylls, and they usually share same distribution area in Asia.

In our current study *Selaginella* subg. *Boreoselaginella* is well supported as the second diverging lineage in our ML and BIanalyses (second resolution above), although the support value is <50% in our MP analysis (Fig. 1). Being the second diverging lineage has so far most frequently supported.

4.2.3. Selaginella subg. Gymnogynum (Fig. 5)

We used *Selaginella* subg. *Ericetorum* in our earlier papers (Zhou and Zhang, 2015; Zhou et al., 2016) which turned out to be a synonym of *S.* subg. *Gymnogynum* (Weststrand and Korall, 2016a). This subgenus is strongly supported as the third diverging lineage in our current study, consistent with our earlier results (Zhou et al., 2016). It shares a synapomorphy of rhizophores borne on dorsal side of stems; this character state is undetermined in some species in *S.* sect. *Lyallia*, one of the six sections in the subgenus (Zhou and Zhang, 2015). Reticulate megaspore surfaces are a synapomorphy of this subgenus (see below). Within this subgenus, six well-supported clades/sections, *S.* sect. *Lyallia*, *S.* sect. *Megalosporarum*, S. sect. *Myosurus*, S. sect. *Articulatae*, S. sect. *Homoeophyllae*, and *S.* sect. *Lepidophyllae* are well identified. *Selaginella* sect. *Homoeophyllae* and *S.* sect. *Lepidophyllae* are strongly supported as sister to each other (Weststrand and Korall, 2016a; Zhou et al., 2016; our Fig. 1 and S3). *Selaginella* sect. *Megalosporarum* and *S.* sect. *Myosurus* are resolved as sister to each other, which was not found in our earlier study (Zhou et al., 2016), but consistent with the results of Weststrand and Korall (2016a). Other internal relationships of this subgenus are poorly resolved as previous studies (Weststrand and Korall, 2016a; Zhou et al., 2016) and more studies are needed.

Selaginella subg. *Exaltatae* sensu Weststrand and Korall (2016b) includes our *S.* sect. *Megalosporarum* and *S.* sect. *Myosurus* (Zhou and Zhang, 2015). These two sections, not recognized by Weststrand and Korall (2016b), have different geographical distributions (the former in America and the latter in Africa) and specialized gross morphology and microspores (Fig. 5). *Selaginella* sect. *Megalosporarum* has microspores with rod-like ornamentation on surfaces, but *S.* sect. *Myosurus* has microspores with equatorial ring and verrucous ornamentation on surfaces (Fig. 5S vs. 5T). In addition, the divergence between them has been dated as *ca.* 200 million years ago (Klaus et al., 2017).

4.2.4. The Sinensis group (Fig. 6)

Weststrand and Korall (2016a) resolved the *Sinensis* group as sister to the rest of their *Selaginella* subg. *Stachygynandrum* (= *Selaginella* subg. *Pulviniella* + *S.* subg. *Heterostachys* + *S.* subg. *Stachygynandrum* sensu Zhou and Zhang (2015)). In our current study, the *Sinensis* group is for the first time resolved as sister to *S.* subg. *Pulviniella* with relatively strong support in ML and BIanalyses, although only 50% support value in MP analysis (Fig. 1 and S3). The monophyly of the *Sinensis* group is strongly supported. Morphologically, the *Sinensis* group can be easily distinguished from other taxa in *Selaginella* in having rhizophores borne on the ventral side of stems, only one (to a few) megasporophyll at the base of strobili, large megaspores (usually >600 μm in diam.) (Fig. 2B, F and 6). Within the *Sinensis* group, three well-supported subclades (the *Selaginella sinensis* subclade, the *S. australiensis* subclade, and the *Selaginella fissidentoides* subclade) are identified, consistent with results by Weststrand and Korall (2016a). These subclades can be easily distinguished from one another by gross morphology, microspores, megaspores, and geographical distributions (see below). Although strobili with only one megasporophyll (megasporangium) at the base are also present in *S.* subg. *Gymnogynum*, the latter has rhizophores borne on dorsal side of stems, reticulate ornamentation on megaspore surfaces, and often spiny ornamentation on microspore surfaces (Fig. 5).

Recent plastome study has shown that 48 species of *Selaginella* sampled had high GC content (>50%) but all three species in the *Sinensis* group had ~ 30% GC content in plastomes, similar to most vascular plants; the *Sinensis* group has the smallest plastomes in land plants except some parasitic plants, and their plastomes do not contain any tRNAs (Zhou et al., 2022).

4.2.5. Selaginella subg. Pulviniella (Fig. 7)

Selaginella subg. *Pulviniella* was resolved as sister to *S.* subg. *Heterostachys* + *S.* subg. *Stachygynandrum* sensu Zhou and Zhang (2015) with moderate support in our earlier study (Zhou et al., 2016) but the *Sinensis* group was not sampled. Weststrand and Korall (2016a) sampled the *Sinensis* group but only BIanalysis was presented. Our current study resolved *S.* subg. *Pulviniella* as sister to the *Sinensis* group with relatively strong support in ML and BI analyses, although only 50% support value in MP analysis (Fig. 1 and S3). This resolution has not been found before. Morphologically and ecologically, this subgenus comprises species mostly with rosette-forming habit and extremely drought habitat. This subgenus and the *Sinensis* group share drought habitat, but morphological synapomorphies to support their sister relationship are unclear.

4.2.6. *Selaginella subg. Heterostachys (Figs. 8 and 9)*

Consistent with our previous results (Zhou et al., 2016), our current study resolved *Selaginella* subg. *Heterostachys* as sister to *S.* subg. *Stachygynandrum* with strong support and identified five strongly supported clades within the subgenus corresponding to the five sections proposed by Zhou and Zhang (2015): *S.* sect. *Auriculate*, *S.* sect. *Homostachys*, *S.* sect. *Heterostachys*, *Didiclis* ("*S.* sect. *Oligomacrosporangiatae*"), and *S.* sect. *Tetragonostachyae*. Although Weststrand and Korall (2016a, b) did not recognize this subgenus and our sections, their results were consistent with ours with five sections sensu Zhou and Zhang (2015) strongly supported. This subgenus, strongly supported as monophyletic (Weststrand and Korall, 2016a; Zhou et al., 2016; our Fig. 1 and S3) and characterized by non-reticulate megaspores (Fig. 2I), mainly comprises species with dimorphic sporophylls of strobili in Asia and those species with verrucate ornamentation on their microspore surfaces but this reversed to finely reticulate ornamentation (*Tetragonostachyae* type-1 and type-2) in some pacific island species of *S.* sect. *Tetragonostachyae* (Fig. 2I and J).

4.2.7. *Selaginella subg. Stachygynandrum (Fig. 10)*

This subgenus is also always strongly supported as monophyletic (Korall and Weststrand, 2016a; Zhou et al., 2016; our Fig. 1 and S3). Reticulate megaspore surfaces are a synapomorphy of *S.* subg. *Stachygynandrum* (see below). In our earlier study, we recognized seven sections/clades in this subgenus: *S.* sect. *Ascendentes*, *S.* sect. *Austroamericanae*, *S.* sect. *Circinatae*, *S.* sect. *Heterophyllae*, *S.* sect. *Pallescentes*, *S.* sect. *Plagiophyllae*, and *S.* sect. *Poceres* (Zhou and Zhang, 2015) and resolved two paraphyletic clades, *S.* sect. *Circinatae* and *S.* sect. *Plagiophyllae*, as the first diverging lineages with weak support (Zhou et al., 2016). In our current study, these two clades formed a clade strongly supported as monophyletic in two of the three analyses and as the second diverging lineage in the subgenus with strong support. *Selaginella* sect. *Ascendentes* is resolved as sister to the rest of the subgenus. These results are consistent with those in Korall and Weststrand (2016a). *Selaginella* sect. *Ascendentes* was only known to be distributed in Asia and Pacific islands (Zhou et al., 2016), but now an African species (*Selaginella versicolor*) is also resolved in this clade (Korall and Weststrand, 2016a; our Fig. 1 and S3). Korall and Weststrand (2016b) recognized this subgenus with a very broad circumscription of 600+ species including three of our subgenera: *S.* subg. *Heterostachys*, *S.* subg. *Pulviniella*, and *S.* subg. *Stachygynandrum*, plus the *Sinensis* group. They recognized none of our sections in this subgenus either, although five out of our seven sections were strongly supported and the remaining two formed a strongly supported monophyletic clade in their study (our Table 3).

4.3. *Morphological evolution in Selaginella*

4.3.1. *Character 1—Presence of rhizophores (Fig. 2A)*

Two species of *Selaginella*, *S. selaginoides* and *S. deflexa*, have no rhizophores (Fig. 3C), and all other species have. These two species are the only member of *S.* subg. *Selaginella* (Zhou and Zhang, 2015). The ancestral state of rhizophores in *Selaginella* is ambiguous because the character state in *Isoëtes* is unknown or not applicable. Absence of rhizophores can be a synapomorphy or a symplesiomorphy of *S.* subg. *Selaginella*. Presence of rhizophores can also be a synapomorphy or a symplesiomorphy of the rest of *Selaginella* excluding *S.* subg. *Selaginella* (Fig. 2A).

4.3.2. *Character 2—Position of rhizophores (Fig. 2B)*

The rhizophores in *Selaginella* can be borne on dorsal or ventral side of stems or/and branches. The rhizophores borne on dorsal side are the ancestral state of rhizophores in *Selaginella* (Fig. 2B). The rhizophores of *S.* sect. *Lyallia* are strictly restricted to the base of erect stems and the dorsal/ventral position of rhizophores is unknown (Fig. 5C). The ventrally borne rhizophores evolved once in *Selaginella* and are a synapomorphy of *S.* subg. *Pulviniella* + *S.* subg. *Heterostachys* (Fig. 8D, G) + *S.* subg. *Stachygynandrum* + the *Sinensis* group (Fig. 6B).

4.3.3. *Character 3—Dimorphism of overall sterile leaves (Fig. 2C)*

The sterile leaves of *Selaginella* can be monomorphic or dimorphic. Although only about 8% of the species have monomorphic sterile leaves in *Selaginella*, monomorphic sterile leaves have been frequently used to identify and define some taxa, e.g., *S.* subg. *Selaginella* (Fig. 3A–D), *S.* sect. *Homoeophyllae* Spring sensu Zhou and Zhang (2015) (Fig. 5A, H), and *S.* subg. *Ericetorum* sensu Jermy (1986) (Fig. 5C, K). Our morphological analysis suggests that the ancestral state of sterile leaves in *Selaginella* is ambiguous. The widespread dimorphic sterile leaves evolved only once from monomorphic state in *Selaginella*. Dimorphic sterile leaves evolved to monomorphic leaves once independently each in *S.* sect. *Homoeophyllae* and *S.* sect. *Lyallia*.

4.3.4. *Character 4— Dimorphism of sterile leaves at the base of main stems (Fig. 2D)*

Except all species of *Selaginella* subg. *Selaginella* and *S.* sect. *Homoeophyllae*, and some of *S.* sect. *Lyallia* with monomorphic sterile leaves throughout plants in Character 3, those species with erect stems and dimorphic sterile leaves on branches can have monomorphic sterile leaves at the base of the main stem. Most species have dimorphic sterile leaves at the base of the main stem (Figs. 3–10) in *Selaginella* and this dimorphism is a morphological synapomorphy or ancestral state of *Selaginella* excluding *S.* subg. *Selaginella*. Monomorphic sterile leaves at the base of the main stem have evolved at least 18 times from dimorphic sterile leaves independently in the genus. Monomorphic sterile leaves at the base of the main stem (Fig. 5C) appear to be a synapomorphy of *S.* sect. *Lyallia* and it is reversed to dimorphic sterile leaves on lower parts of main stem independently.

4.3.5. *Character 5—Arrangement of sterile leaves (Fig. 2E)*

Arrangement of sterile leaves in *Selaginella* can be spiral (Fig. 3A, B, D, F and 5A, H), in four rows (Fig. 4A–H, 5B, D, E, I, 6A–H, 7A–D, 8A–L and 10A–C, F), or decussate (at least on stem; Fig. 5C, K). The ancestral state of arrangement of sterile leaves in *Selaginella* is ambiguous and can be either spiral or in four rows. Sterile leaves in four rows can be a synapomorphy or a symplesiomorphy of *Selaginella* excluding *S.* subg. *Selaginella*. Sterile leaves in four rows evolved to spiral sterile leaves once in *S.* sect. *Homoeophyllae.* Decussate sterile leaves evolved from those in four rows and are a synapomorphy of *S.* sect. *Lyallia*. Decussate sterile leaves on branches are restricted to *S.* sect. *Lyallia*, while some other species with decussate sterile leaves on main stems have sterile leaves in four rows on branches. We hypothesize that decussate sterile leaves in *S.* sect. *Lyallia* are homologous, but more developmental and anatomical studies are necessary.

4.3.6. Character 6—Number of megasporophylls on strobili (Fig. 2F)

Number of megasporophylls on strobili can be only one (to a few) at base of strobili (Fig. 5G and 6D–F) or more than two on dorsal side or/and ventral side of strobili (Fig. 3G, 4E–G, 5G, L, 7D, 9A–J and 10D–F). Having several megasporophylls on strobili is a synapomorphy of *Selaginella s.l.* Only one (to a few) megasporophyll on strobili is a morphological synapomorphy of the *Sinensis* group. The ancestral state of the clade containing S. sect. *Articulatae* + *S.* sect. *Megalosporarum* + S. sect. *Myosurus* + *S.* sect. *Lyallia* is ambiguous.

4.3.7. Character 7— Dimorphism of sporophylls on strobili (Fig. 2G)

Sporophylls on strobili in *Selaginella* can be dimorphic (Fig. 8B, D, 9A–D, F, G, I, and 10D, E) or monomorphic (Fig. 3A, B, D, E, G, 4E–G, 5G, H, J, L, 6D, F, 7D, 9E, H, J and 10F). Traditionally, based on the dimorphic sporophylls in *Selaginella*, *S.* subg. *Heterostachys* sensu Jermy (1986) was widely accepted. However, phylogenetic analyses showed that these species with dimorphic sporophylls in *Selaginella* are polyphyletic (Weststrand and Korall, 2016a; Zhou et al., 2016; our Fig. 1 and S1–S3). Our morphological analysis suggests that monomorphic sporophylls on strobili are the ancestral state of *Selaginella*. Dimorphic sporophylls do not appear in other subgenera or the *Sinensis* group but only evolved in the two latest-diverging subgenera, *S.* subg. *Heterostachys* and *S.* subg. *Stachygynandrum*. Dimorphic sporophylls evolved at least 14 times in these two subgenera, but are dominant in *S.* subg. *Heterostachys*. The ancestral state of dimorphism of sporophylls on strobili in *S.* subg. *Heterostachys* is ambiguous.

4.3.8. Character 8—Resupination of strobili with dimorphic sporophylls (Fig. 2H)

Based on the relative position between dimorphic sporophylls and sterile leaves, strobili with dimorphic sporophylls (those taxa with dimorphic sporophylls in character 7) in *Selaginella* can be resupinate (Fig. 8B, D, 9A–D, I and 10D, E) or non-resupinate (Fig. 9F and G). Non-resupinate strobili evolved from monomorphic sporophylls and is a synapomorphy of *S.* sect. *Homostachys*. *Selaginella* sect. *Auriculate*, the sister of *S.* sect. *Homostachys*, has monomorphic sporophylls. Resupinate strobili evolved once or twice in *S.* subg. *Heterostachys* depending on the ancestral state and evolved at least 10 times in *S.* subg. *Stachygynandrum*. The ancestral state of resupination of strobili in *S.* subg. *Heterostachys* is ambiguous.

4.3.9. Character 9—Surfaces of megaspores (Fig. 2I)

Based on the main elements of ornamentation, surfaces of megaspores in *Selaginella* can be reticulate (Fig. 5N–R and 9L–N) or non-reticulate (Fig. 3H, L, 4J–K, 6I–L, 7E–H, 9K, S–V, X). Our morphological analysis suggests that non-reticulate surfaces are the ancestral state of megaspores in *Selaginella*. Reticulate megaspores in the genus are not homologous but could have evolved only three times in *Selaginella* independently. Reticulate surfaces of megaspores are unambiguously a synapomorphy of *S.* subg. *Stachygynandrum* and a synapomorphy of *S.* subg. *Gymnogynum* as well. The ancestral state of *S.* sect. *Tetragonostachyae* of *S.* subg. *Heterostachys* is ambiguous. Reticulate megaspores reversed to non-reticulate megaspores once in *S.* subg. *Stachygynandrum* and at least once in *S.* sect. *Tetragonostachyae*. Reticulate megaspores in *S.* sect. *Tetragonostachyae* can be a symplesiomorphy. Based on the morphology and size of muri, five types of reticulate ornamentation can be identified (see below).

4.3.10. Character 10—Reticulate megaspores (Fig. 2J)

Based on the density, size, and shape of muri of reticulate ornamentation, reticulate megaspores can be divided into the *Gymnogynum* type (with often high and strong or wing-like muri and slightly regular meshes: Fig. 5N–P, R), the *Bryodesma* type (with prominent and dense muri: Fig. 5Q), the *Stachygynandrum* type (with more or less open and irregular meshes: Fig. 10H, K–N), the *Tetragonostachyae* type-1 (with fine muri and open meshes: Fig. 9M–N), and the *Tetragonostachyae* type-2 (with fine muri formed by connected verrucate ornamentation, Fig. 9L). The *Stachygynandrum* type of megaspores is a synapomorphy of *S.* subg. *Stachygynandrum*. The *Gymnogynum* type of megaspores is shared by *S.* subg. *Gymnogynum* excluding *S.* sect. *Homoeophyllae*, which supports a close relationship, not resolved by our molecular data, among *S.* sect. *Articulatae*, *S.* sect. *Lyallia*, *S.* sect. *Megalosporarum*, and *S.* sect. *Myosurus*. The *Bryodesma* type of megaspores is a synapomorphy of *S.* sect. *Homoeophyllae* (*Bryodesma*). The *Tetragonostachyae* type-1 and -2 of megaspores characterize *S.* sect. *Tetragonostachyae* but the ancestral state of the section is ambiguous.

4.4. Splitting Selaginella into seven subfamilies and 19 genera

With our new molecular and morphological results and results from previous studies (Zhou and Zhang, 2015; Weststrand and Korall, 2016a, 2016b; Zhou et al., 2016), it appears that the major monophyletic clades in the currently defined *Selaginella s.l.* or Selaginellaceae can be morphologically defined by some characters alone or combinations of characters. We propose to recognize these major clades as genera. The question is how many genera should be recognized. Jermy (1986) recognized four subgenera, Zhou and Zhang (2015) accepted six subgenera excluding the *Sinensis* group and three subgenera were further classified into six, five, and seven sections, respectively, and Weststrand and Korall (2016b) recognized seven subgenera with 600+ species in one subgenus and excluding the *Sanguinolenta* group. The major differences between the two recent classifications by Zhou and Zhang (2015) and by Weststrand and Korall (2016b) lie mainly in how to treat *S.* subg. *Stachygynandrum*. Weststrand and Korall (2016b) combined *S.* subg. *Stachygynandrum* sensu Zhou and Zhang (2015), *S.* subg. *Heterostachys* sensu Zhou and Zhang (2015), *S.* subg. *Pulviniella*, and the *Sinensis* group based on their largely unresolved relationships. We prefer to divide their *S.* subg. *Stachygynandrum* further for two reasons: (a) their *S.* subg. *Stachygynandrum* contains 600+ species with heterogeneous morphologies and distributions and is not informative; and (b) the relationships within it are now well resolved and strongly supported (at least in the nuclear phylogeny) in our current study (Fig. 1 and S3).

Here we propose to recognize our six earlier subgenera and the *Sinensis* group as seven subfamilies and the 19 major clades in our phylogenies as 19 genera in Selaginellaceae (list of subfamilies and genera below) for the following reasons:

(1) Although recognizing 19 genera for 700–800 species in Selaginellaceae/Selaginellales may be viewed as dramatic deviation from the current single-genus classification, there is a history of dividing Selaginellaceae into more than one genus (Palisot de Beauvois, 1803, 1804; Kuntze, 1891; Börner, 1912; Rothmaler, 1944; Sakurai, 1943; Kung, 1988; Soják, 1993; Satou, 1997; Tzvelev, 2004; Weakley, 2012, 2022; Weakley and Southeastern Flora Team, 2022). Schuettpelz et al. (2018) argued that there are too few fern genera. Our current classification is also in agreement with recent classifications of pteridophytes, e.g., 25 genera for *ca.* 265 species in Blechnaceae (PPG I, 2016; de Gasper et al., 2016; González et al., 2020), 17 genera for *ca.* 380 species in Lycopodiales (Øllgaard, 2012; PPG I, 2016; Chen et al., 2022; Zhang and Zhou, 2022), 37 genera for *ca.* 1200 species in Thelypteridaceae (Fawcett et al., 2021; Fawcett and Smith, 2021), and

42 genera for *ca.* 900 species in Polypodiaceae subfam. Grammitidoideae (Yang et al., 2023; Zhou et al., 2023). Many of these recent generic segregates are not necessarily clearer phylogenetically or morphologically than the genera of Selaginellaceae we recognize here.

(2) The relationships in Selaginellaceae, especially those within *Selaginella* subg. *Stachygynandrum* sensu Weststrand and Korall (2016b), which were not well resolved in Weststrand and Korall (2016a), have been well resolved (Zhou et al., 2016), even with the *Sinensis* group sampled (Fig. 1 and S3). The genus-level units are well-supported phylogenetically, such that the circumscription of the genera won't need to change in the near future as more phylogenetic information becomes available.

(3) These 19 genera are all deeply diverged lineages in Selaginellaceae and mostly among the oldest lineages in vascular plants. Molecular dating by Klaus et al. (2017) estimated the 15 out of the 19 genera to have diverged from their sisters (stem ages) about 120–373 million years ago and the remaining four about 75–80 million years ago. The stem ages of the 15 genera are older than any polypod families and genera and the 19 genera we recognize here are older than those of most genera of pteridophytes as estimated by Schuettpelz and Pryer (2009) and Du et al. (2021). Notably, all 42 grammitid fern genera recognized in recent studies diverged from their sisters in the past 30 million years (Sundue et al., 2014; Yang et al., 2023; Zhou et al., 2023). Lu et al. (2020), Zhang et al. (2020), and Zhang and Zhang (2022) used relatively old ages as an argument for generic recognition in Woodsiaceae, Lepisoreae (Polypodiaceae), and Ophioglossaceae, respectively.

(4) Most of the 19 genera and seven subfamilies are morphologically definable, although combinations of morphological characters are sometimes needed (Zhou and Zhang, 2015; Weststrand and Korall, 2016a, b; Zhou et al., 2016, Figs. 2–10; Tables 4 and 5). In fact, as shown below, five out of the seven subfamilies (except Lycopodioidoideae and Selaginelloideae) and 16 out of the 19 genera (except *Didiclis, Hypopterygiopsis, Selaginella s.s.*) can be distinguished from one another using macromorphological features only. Spore features and distribution information are useful in distinguishing Lycopodioidoideae from Selaginelloideae, and are critical in distinguishing *Didiclis* from *Hypopterygiopsis* and in distinguishing *Selaginella s.s.* from *Chuselaginella* and *Kungiselaginella.*

(5) Most of the 19 genera are geographically coherent: *Afroselaginella* is endemic to Africa; *Austroselaginella* is endemic to Australia; *Boreoselaginella*, *Chuselaginella,* and *Kungiselaginella* occurs in the Old World; *Bryodesma* occurs in Africa, East Asia, and North America; *Didiclis* occurs in Africa, Asia, and Australasia; *Ericetorum* occurs in Africa and Australia; *Gymnogynum* occurs in North to South Americas, and rarely in Asia and Africa; *Hypopterygiopsis* occurs in Asia and Pacific islands and a few in Africa and Madagascar; *Korallia* is endemic to Madagascar and adjacent islands; *Lepidoselaginella* is endemic to North America; *Lycopodioides* occurs in Eurasia; *Megaloselaginella* is endemic to Central to South America; *Pulviniella* occurs in Africa and Asia and rarely in Americas; *Selaginella s.s.* is nearly endmics to Americas except one or a few species in Africa; *Selaginoides* is endemic to the boreal area and Hawaii; *Sinoselaginella* occurs in China extending to the Arabic area and eastern Africa (Ethiopia, Kenya, Somalia); and *Valdespinoa* is endemic to North America.

(6) This 19-genus classification is largely in line with our earlier classification (Zhou and Zhang, 2015), albeit the taxa have different ranks (Fig. 1). We recognized six subgenera and three of them were further divided into five, six, and seven sections, respectively (Zhou and Zhang, 2015). Fifteen out of our 21 subgenera/sections are recognized as genera here, whereas our *S.* sect. *Heterostachys* and *S.* sect. *Tetragonostachyae* are combined to form *Hypopterygiopsis*, and *S.* subg. *Stachygynandrum* sensu Zhou and Zhang (2015) collectively forms Selaginelloideae. The major difference is that the *Sinensis* group was not treated by Zhou and Zhang (2015) and is divided into three genera here. This 19-genus classification is in fact not contradictory with the one proposed by Weststrand and Korall (2016b) in which seven subgenera were recognized. Five of their subgenera, *S.* subg. *Ericetorum*, *S.* subg. *Gymnogynum*, *S.* subg. *Lepidophyllae*, *S.* subg. *Rupestrae*, *S.* subg. *Selaginella*, are circumscribed exactly the same as the corresponding five of our 19 genera. Their *S.* subg. *Exaltatae* is divided into our *Afroselaginella* and *Megaloselaginella.* Their unplaced *Sanguinolenta* group is our *Boreoselaginella.* The biggest difference is that we recognize 11 genera in their *S.* subg. *Stachygynandrum*, which formed an unresolved polytomy in their phylogeny (Weststrand and Korall, 2016a), but is well resolved in our current study, especially in the nuclear phylogeny (Fig. 1 and S1–S3).

(7) Although segregating these 19 clades will cause disruption of a number of species names, in parallel with this paper we have published a proposal to conserve *Selaginella* with a new type (*S. flabellata* (L.) Spring) in the most species-rich major clade in *Stachygynandrum* (Wan et al., 2023), which will largely reduce nomenclatural instability. In fact, most American species belong to the newly defined *Selaginella s.s.* The current type of *Selaginella*, *S. selaginoides*, is resolved in the *Selaginoides* clade which contains only two species. There is already a generic name available, *Selaginoides*, for this clade. In addition to the names *Selaginella* and *Selaginoides*, five generic names, *Bryodesma*, *Didiclis*, *Gymnogynum*, *Hypopterygiopsis*, and *Lycopodioides*, are available and a number of species have already been transferred to these genera (Kuntze, 1891; Sakurai, 1943; Rothmaler, 1944; Kung, 1988; Soják, 1992; Satou, 1997; Tzvelev, 2004; Weakley, 2022). Three generic names, *Boreoselaginella, Ericetorum*, and *Pulviniella*, are raised from existing subgeneric names (Warburg, 1900; Jermy, 1986; Zhou and Zhang, 2015; Weststrand and Korall, 2016b). Therefore, only nine new generic names are needed and they mostly contain only one to a few species and will not cause mass disruption of names: *Afroselaginella* for *S.* sect. *Myosurus* with about four species, *Austroselaginella* for *S. australiensis* and additional three species, *Chuselaginella* for *S.* sect. *Ascendentes* with *ca.* 70 speices, *Kungiselaginella* for *S.* sect. *Circinatae* and *S.* sect. *Plagiophyllae* with *ca.* two dozen species, *Lepidoselaginella* for *S.* sect. *Lepidophyllae* with about three species, *Megaloselaginella* for *S.* sect. *Megalosporarum* with about two species, *Korallia* for *S.* sect. *Fissidentoides* with about 15 species, and *Sinoselaginella* for portion of the *Sinensis* group with five species, and *Valdespinoa* for *S.* sect. *Auriculate* with about one species.

(8) Subdividing *Selaginella s.l.* into homogeneous and manageable genera is good for the purposes of analysis, communication, and conservation. It will be easier for botanists to undertake monographic work, for example, on the subunits, and to identify and communicate meaningful phylogenetic/evolutionary changes. Treating *Selaginella* as a single genus devalues it as a triage level for judging biodiversity value and ignores the ancient diversity of its deeply diverged clades. It has been argued that there are too few genera in

pteridophytes, which does not foster more precise and efficient communication, promote additional research, or facilitate herbarium curation (Schuettpelz et al., 2018).

In a very parallel case, *Thelypteris* Schmidel was reduced to a tiny (2 species) genus, with all other species being placed in "new" genera (Fawcett et al., 2021; Fawcett and Smith, 2021). The same could be done in *Selaginella*, but we prefer to conserve *Selaginella* with a new type to maximally stabilize the names (Wan et al., 2023). *Thelypteris* had been to a much greater degree already treated and split into many genera, whereas, despite some movement over the centuries towards splitting *Selaginella*, much less had been done and segregates had been much less discussed, used, combinations made, in *Selaginella* until the modern era of gene sequencing and phylogenetic trees.

Treating these 19 genera at the rank of subgenus or section within *Selaginella* is an alternative (Jermy, 1986, 1990; Zhou and Zhang, 2015; Weststrand and Korall, 2016b), but those ranks are almost always ignored except by professional plant systematists, and there is nothing like the name of a species (incorporating the genus) to emphasize less relationship (different genus names) or more relationship (same genus name; A. Weakley, pers. comm.).

It will be more inconvenient for today's botanists to adopt a dramatically different classification than to use the existing one with all 750+ species together in one genus, but in the long run the next-generation botanists will find it informative to distinguish the deeply diverged clades at the generic rank because of their molecular, morphological, and geographical distinctiveness. Treating all 750+ species in a single genus is comparable to lumping all then 33 genera of Polypodiaceae subfam. Grammitidodeae into *Grammitis* Sw. or lumping all 24 genera of cheilanthoid ferns into *Hemionitis* L. (Pteridaceae) as done by Christenhusz et al. (2018).

5. Taxonomic treatment

Our current phylogeny based on the largest taxon and character (nuclear and plastid) sampling corroborated earlier findings (Weststrand and Korall, 2016a; Zhou et al., 2016) that *Selaginella* is well resolved into a number of major clades. Our morphological analysis of 10 important characters showed that the major phylogenetic clades can be defined morphologically (Weststrand and Korall, 2016a; our Fig. 2). Our earlier classification (Zhou and Zhang, 2015) recognized six subgenera and three of them further into five, six, and seven sections, respectivel, excluding the *Sinensis* group. Our new results confirm the monophyly of all but two sections (the relationships between *S.* sect. *Circinatae* and *S.* sect. *Plagiophyllae* are not well resolved but they together are monophyletic). Considering all evidence available, earlier classifications of *Selaginella* (Palisot de Beauvois, 1803; Kuntze, 1891; Walton and Alston, 1938; Sakurai, 1943; Rothmaler, 1944; Jermy, 1986, 1990; Kung, 1988; Soják, 1992; Satou, 1997; Tzvelev, 2004; Weakley, 2012, 2020; Zhou and Zhang, 2015; Weststrand and Korall, 2016b), and recent trend of pteridophyte classifications, we here propose to split the currently defined *Selaginella s.l.* into seven subfamilies corresponding our earlier six subgenera (Zhou and Zhang, 2015) and the *Sinensis* group, four of which are monogeneric and three of which are further divided into 3, 4, and 6 genera, respectively. The 7 subfamilies and 19 genera include: Boreoselaginelloideae (*Boreoselaginella*), Gymnogynoideae (*Afroselaginella*, *Bryodesma*, *Ericetorum*, *Gymnogynum*, *Lepidoselaginella*, *Megaloselaginella*), Lycopodioidoideae (*Didiclis*, *Hypopterygiopsis*, *Lycopodioides*, *Valdespinoa*), Pulvinielloideae (*Pulviniella*), Selaginelloideae (*Chuselaginella, Kungiselaginella, Selaginoides s.s.*), Selaginoidoideae (*Selaginoides*), and Sinoselaginelloideae (*Austroselaginella*, *Korallia*, *Sinoselaginella*). A comparison of our current and earlier classifications is listed in Table 3 and Fig. 1 and S1−S3.

We provide a key to subfamilies and genera below. For each subfamily and genus, we provide morphological, phylogenetic, and geographical synopses, constituent species, and the necessary new combinations. For these, we provide basionyms and other recent combinations. For additional synonymy see Tryon (1955), Kung (1988), Soják (1993), Valdespino (1993), Jermy and Holmes (1998), Mickel and Smith (2004), Chu (2006), Roux (2009), Zhang et al. (2013), Fraser-Jenkins et al. (2015, 2017), Valdespino and Zimmer (2016), and Hassler (2022). We list all species of each genus currently known to us. Species lacking sufficient evidence are listed at the end of "Taxonomic treatment" without combinations pending further studies. We provide Chinese vernacular names for all subfamilies, genera, and sections in the family and for all species occurring in China.

Key to subfamilies and genera of Selaginellaceae

1. Rhizophore absent; sterile leaves loosely spirally arranged; strobili cylindric (circumboreal areas and Hawaii; 2n = 18) [subfam. I. **Selaginoidoideae** 圆穗卷柏亚科] ***Selaginoides*** 圆穗卷柏属
1. Rhizophore present; sterile leaves densely and spirally, in four rows, or decussately arranged; strobili tetragonal or dorsiventrally complanate (2n = 16−60) 2
2. Rhizophores borne on dorsal side of stems and/or branches; if rhizophores strictly restricted to the base of stem, sterile leaves at least decussately arranged on stem or throughout plants 3
2. Rhizophores borne on ventral side of stems and/or branches; if rhizophores strictly restricted to the base of stem, sterile leaves on stem never decussately arranged 9
3. Plants xerophytic, non-rosette-forming, creeping; sterile leaves in 4 rows, strobili with many megasporangia on dorsal and/or ventral side; megaspore surfaces densely contiguous-tuberculate, non-reticulate...... [subfam. II. **Boreoselaginelloideae** 北方卷柏亚科] ***Boreoselaginella*** 北方卷柏属
3. Plants non-xerophytic (if xerophytic, plants rosette-forming or with spirally monomorphic leaves on sterile stem and branch), erect, suberect, ascending, scandent, or creeping (if creeping, plants with monomorphic leaves throughout the plant or strobili with only one megasporangium at base); megaspore surfaces reticulate (the *Gymnogynum* type and the *Bryodesma* type) [subfam. III. **Gymnogynoideae** 关节卷柏亚科] 4
4. Sterile leaves strictly monomorphic throughout the plant or at least on stem 5
4. Sterile leaves dimorphic or slightly monomorphic throughout the plant 6
5. Sterile leaves monomorphic and spirally arranged throughout the plant ...... ***Bryodesma*** 同形卷柏属
5. Sterile leaves monomorphic and decussately arranged throughout the plant or at least at the base of stems ***Ericetorum ......*** 对叶卷柏属
6. Plants rosette-forming ***Lepidoselaginella ......*** 鳞叶卷柏属
6. Plants non-rosette-forming 7
7. Stems inarticulate; microspores with an equatorial flange and surfaces verrucate ...... ***Afroselaginella*** 非洲卷柏属
7. Stems often articulate; microspores without an equatorial flange and surfaces echinate or pillared 8
8. Plants extremely large (up to 1 m tall); stem's vascular system actino-plectostele; megaspores *ca.* 1.5 mm; microspore surfaces pillared ...... ***Megaloselaginella*** 大孢卷柏属
8. Plants normally shorter than 80 cm; stem's vascular system haplostele, actinostele, or plectostele; megaspores smaller

Table 3
A comparison of this classification to two recent classifications [Zhou and Zhang's (2015) and Weststrand and Korall's (2016b)] and Weststrand and Korall's (2016a) phylogeny.

This classification	Zhou and Zhang (2015)	Weststrand and Korall (2016b)	Weststrand and Korall (2016a)
subfam. I. **Selaginoidoideae [*Selaginoides*]**	**subg. *Selaginella***	**subg. *Selaginella***	***Selaginella* clade (pp = 1.00)**
subfam. II. **Boreoselaginelloideae** [***Boreoselaginella***]	subg. Boreoselaginella	**in subg. *Stachygynandrum***	the sanguinolenta group clade (pp = 1.00)
subfam. III. **Gymnogynoideae**	**subg. *Ericetorum***	**subg. *Rupestrae* +*Gymnogynum*/ +*Exaltatae* +*Lepidophyllae* +*Ericetorum***	***S. rupestrae* +*Lepidophyllae*+*Gymnogynum* +*exaltatae*+*Ericetorum* clade (pp = 1.00)**
Afroselaginella	sect. *Myosurus*	in subg. *Exaltatae*	the *S. congoensis* to *S. Myosurus* E clade (pp = 1.00)
Bryodesma	sect. *Homoeophyllae*	subg. *Rupestrae*	*S. rupestrae* clade (pp = 1.00)
Ericetorum	sect. *Lyallia*	subg. *Ericetorum*	*S. ericetorum* clade (pp = 1.00)
Gymnogynum	sect. *Articulatae*	subg. *Gymnogynum*	*S. Gymnogynum* clade (pp = 1.00)
Lepidoselaginella	sect. *Lepidophyllae*	subg. *Lepidophyllae*	*S. Lepidophyllae* clade (pp = 1.00)
Megaloselaginella	sect. *Megalosporarum*	subg. *Exaltatae*	the *S. exaltata* A-B clade (pp = 1.00)
subfam. V. **Pulviniellоideae [*Pulviniella*]**	**subg. *Pulviniella***	**in subg. *Stachygynandrum***	**the *S. nubigena* to *S. digitata* A-C clade (pp = 1.00)**
subfamily IV. **Sinoselaginelloideae**	**Unsampled**	**in subg. *Stachygynandrum***	**the *S. yemensis* A to *S. schellarum* clade (pp = 1.00)**
Austroselaginella	Unsampled	in subg. *Stachygynandrum*	the *S. australiensis* A-B clade (pp = 1.00)
Korallia	Unsampled	in subg. *Stachygynandrum*	the *S. distachya* to *S. sechellarum* clade (pp = 1.00)
Sinoselaginella	Unsampled	in subg. *Stachygynandrum*	the *S. yemensis* A to *S. sinensis* clade (pp = 1.00)
subfam. VI. **Lycopodioidoideae**	**subg. *Heterostachys***	**in subg. *Stachygynandrum***	**the *S. douglasii* A to *S. arbuscula* clade (pp = 1.00)**
Didiclis	sect. Oligomacrosporangiatae	in subg. *Stachygynandrum*	the *S. siamensis* to *S. mayeri* B clade (pp = 1.00)
Hypopterygiopsis	sect. *Heterostachys* + Sect. *Tetragonostachyae*	in subg. *Stachygynandrum*	the *S. monospora* A to *S. arbuscula* clade (pp = 1.00)
sect. *Heterostachys*	sect. *Heterostachys*	in subg. *Stachygynandrum*	the *S. monospora* A to *S. labordei* E clade (pp = 1.00)
sect. *Hypopterygiopsis*	Sect. *Tetragonostachyae*	in subg. *Stachygynandrum*	the *S. repanda* to *S. arbuscula* clade (pp = 1.00)
Lycopodioides	sect. *Homostachys*	in subg. *Stachygynandrum*	the *S. tama–montana* to *S. helavetica* B clade (pp = 1.00)
Valdespinoa	sect. *Auriculate*	in subg. *Stachygynandrum*	the *S. douglasii* clade (pp = 1.00)
subfamily VII. **Selaginelloideae**	**subg. *Stachygynandrum***	**in subg. *Stachygynandrum***	**the clade *S. versicolor* A-C to *S. contigua* clade (pp = 1.00)**
Chuselaginella	sect. *Ascendentes*	in subg. *Stachygynandrum*	the *S. versicolor* A-C to *S. roxburghii* C clade (pp = 1.00)
Kungiselaginella	sect. *Circinatae* + sect. *Plagiophyllae*	in subg. *Stachygynandrum*	the *S. moellendorffii* A-B to *S. biformis* B clade (pp = 1.00)
***Selaginella* s.s.**	subg. *Stachygynandrum*	in subg. *Stachygynandrum*	the *S. versicolor* A-C to *S. contigua* clade (pp = 1.00)
sect. *Austroamericanae*	sect. *Austroamericanae*	in subg. *Stachygynandrum*	the *S. hirsuta* to *S. revoluta* C clade (pp = 0.99)
sect. *Pallescentes*	sect. *Pallescentes*	in subg. *Stachygynandrum*	the *S. huehuetenangensis* A-B to *S. pulcherrima* clade (pp = 1.00)
sect. *Poceres*	sect. *Poceres*	in subg. *Stachygynandrum*	the *S. novae-hollandiae* B to *S. oaxacana* B clade (pp = 1.00)
sect. *Selaginella*	sect. *Heterophyllae*	in subg. *Stachygynandrum*	the *S. cladorrhizans* to *S. contigua* clade (pp = 0.99)

than 1 mm; microspore surfaces often echinate ...... ***Gymnogynum*** 关节卷柏属

9. Plants xerophytic; often forming rosettes, rarely stems erect, rhizophores strictly restricted to the base of stem and stems tufted and curling inward when dry; megaspore surfaces coarse without clear ornamentation; microspores spherical, surface scabrate or verrucate ...... [subfam. V. **Pulvinielloideae**垫状卷柏亚科] ***Pulviniella***垫状卷柏属
9. Plants growing in wet habitats or rarely slightly xerophytic; stems erect, suberect, ascending, creeping, or scandent, rarely rosette-forming but megaspore surfaces reticulate, and microspores often hemispherical 10
10. Sporophylls monomorphic [if sporophylls dimorphic, then megaspore surfaces typical reticulate ornamentation (all these species with dimorphic sporophylls in America)]; megaspore surfaces reticulate (the *Stachygynandrum* type); microspore surfaces often verrucate to baculate on distal surfaces 16
10. Sporophylls dimorphic [if sporophylls monomorphic, megaspore surfaces verrucate, low-rugate, tuberculate, finely reticulate (or fenestrate)]; microspore surfaces verrucate, blunt spiny, lamellate, cristate, plain but with globules or spherules, or rarely baculate on distal surfaces (Old World, only *Didiclis hoffmannii* in the New World] ...... [subfam. VI. **Lycopodioidoideae** 异穗卷柏亚科] 11
11. Sporophylls dimorphic, non-resupinate or resupinate (or sporophylls monomorphic but strobili strongly loose and not distinct from sterile parts) 12
11. Sporophylls monomorphic, and strobili distinct from sterile parts 14
12. Strobili non-resupinate (sporophylls dimorphic) or rarely slightly lax (monomorphic); sporophylls loosely arranged ...... ***Lycopodioides*** 疏穗卷柏属
12. Strobili resupinate (sporophylls dimorphic); sporophylls densely arranged 13
13. Dorsal leaves obovate ...... ***Didiclis*** (the *D. bisulcata* group) 瘤孢卷柏属
13. Dorsal leaves non-obovate, often ovate ...... ***Hypopterygiopsis*** 异穗卷柏属
14. Plants small, *ca.* 10 cm, strictly creeping forming loose mats ...... ***Valdespinoa*** 韦氏卷柏属
14. Plants medium-to large-sized, more than 20 cm, erect, scandent, rarely creeping, not forming loose mats 15
15. Megaspore surfaces tuberculate and usually interconnected to form reticula-like structure; microspore surfaces blunt spiny, laminate, or cristate ...... ***Didiclis*** 瘤孢卷柏属
15. Megaspore surfaces finely reticulate (*Tetragonostachyae* type-1 and -2); microspore surfaces low-verrucate or smooth with irregular spherules ...... ***Hypopterygiopsis*** 异穗卷柏属
16. Strobili with several megasporophylls (sporangia) on the ventral and/or dorsal side; megaspores smaller than 400 μm, surfaces non-reticulate ...... [subfamily VII. **Selaginelloideae** 同穗卷柏亚科] 17
16. Strobili with only one (to a few) megasporophyll (sporangium) at the base; megaspores larger than 500 μm, surfaces

Table 4
Comparison of gross morphology of 7 subfamilies and 19 genera in Selaginellaceae recognized in the current classification.

Subfamilies/Genera	Growth forms	Rhizophores borne on stem/branch	Strobili	Dimorphism of sporophylls	Arrangement of sporophylls	Dimorphism of sterile leaves	Arrangement of sterile eaves	Numbers of megasporophylls on strobili
Subfamily I Selaginoidoideae [*Selaginoides*]	Erect	Absent	Cylindrical	Monomorphic	Spiral	Monomorphic	Spiral	Several on dorsal or/ and ventral sides
Subfamily II Boreoselaginelloideae [*Boreoselaginella*]	Creeping	Dorsal	Tetragonal	Monomorphic	Four rows	Dimorphic to nearly monomorphic	Four rows	Several on dorsal or/ and ventral sides
Subfamily III Gymnogynoideae	Creeping, ascending, erect, rosette-forming	Dorsal or restricted to base of stem	Tetragonal	Monomorphic	Four rows	Monomorphic to dimorphic	Four rows	Several on dorsal or/ and ventral sides; or only one (to a few) at base
Gymnogynum	Creeping, ascending, and erect	Dorsal	Tetragonal	Monomorphic	Four rows	Dimorphic	Four rows	Only one (to a few) at base
Bryodesma	Creeping	Dorsal	Tetragonal	Monomorphic	Four rows	Monomorphic	Spiral	Several on dorsal or/ and ventral sides
Lepidoselaginella	Rosette-forming	Dorsal	Tetragonal	Monomorphic	Four rows	Dimorphic	Four rows	Several on dorsal or/ and ventral sides
Ericetorum	Erect	Restricted to base of stem	Tetragonal	Monomorphic	Four rows	Monomorphic (rarely dimorphic on branches)	Decussate (some four rows on branches)	Several on dorsal or/ and ventral sides; or only one (to a few) at base
Megaloselaginella	Erect	Dorsal	Tetragonal	Monomorphic	Four rows	Dimorphic	Four rows	Only one (to a few) at base
Afroselaginella	Creeping	Dorsal	Tetragonal	Monomorphic	Four rows	Dimorphic	Four rows	Only one (to a few) at base
Subfamily IV Sinoselaginelloideae	Creeping, ascending	Ventral	Tetragonal	Monomorphic	Four rows	Dimorphic	Four rows	Only one (to a few) at base
Austroselaginella	Creeping	Ventral	Tetragonal	Monomorphic	Four rows	Dimorphic	Four rows	Only one (to a few) at base
Korallia	Creeping, ascending	Ventral	Tetragonal	Monomorphic	Four rows	Dimorphic	Four rows	Only one (to a few) at base
Sinoselaginella	Creeping	Ventral	Tetragonal	Monomorphic	Four rows	Dimorphic	Four rows	Only one (to a few) at base
Subfamily V Pulviniellоideae [*Pulviniella*]	Rosette-forming or Erect	Ventral	Tetragonal	Monomorphic	Four rows	Dimorphic (rarely monomorphic on stems)	Four rows	Several on dorsal or/ and ventral sides
Subfamily VI Lycopodioidoideae	Ascending, creeping, erect, prostrate, scandent	Ventral	Complanate to Tetragonal	Dimorphic to slightly dimorphic (resupinate) or monomorphic	Four rows	Dimorphic	Four rows	Several on dorsal or/ and ventral sides
Valdespinoa	Prostrate	Ventral	Tetragonal	Monomorphic	Four rows	Dimorphic	Four rows	Several on dorsal or/ and ventral sides
Hypopterygiopsis	Creeping, ascending, erect, or prostrate	Ventral	Complanate to Tetragonal	Dimorphic to slightly dimorphic (resupinate) or monomorphic	Four rows	Dimorphic	Four rows	Several on dorsal or/ and ventral sides
Lycopodioides	Creeping, or prostrate	Ventral	Complanate but lax	Dimorphic (non-resupinate), rarely monomorphic)	Four rows	Dimorphic	Four rows	Several on dorsal or/ and ventral sides
Didiclis	Ascending, creeping, erect, or scandent	Ventral, rarely restricted to base of stem	Tetragonal (only complanate in the Bisulcata group)	Monomorphic [only dimorphic (resupinate) in the *Bisulcata* group]	Four rows	Dimorphic (rarely monomorphic on stem)	Four rows	Several on dorsal or/ and ventral sides
Subfamily VII Selaginelloideae	Erect, ascending, or creeping (rarely rosette-forming)	Ventral, or restricted to base of stem	Tetragonal, rarely complanate	Monomorphic [rarely dimorphic (resupinate) in America]	Four rows	Dimorphic (or monomorphic on stem)	Four rows	Several on dorsal or/ and ventral sides

Chuselaginella	Mainly ascending, some erect	Ventral, rarely restricted to base of stem	Tetragonal	Monomorphic	Four rows	Dimorphic (or monomorphic on stem)	Four rows	Several on dorsal or/ and ventral sides
Kungiselaginella	Mainly erect, few creeping	Restricted to base of stem, few ventral	Tetragonal	Monomorphic	Four rows	Dimorphic (or monomorphic on stem)	Four rows	Several on dorsal or/ and ventral sides
Selaginella s.s.	Erect, ascending, or creeping (rarely rosette-forming)	Ventral or restricted to base of stem	Tetragonal, rarely complanate	Monomorphic or few dimorphic (resupinate)	Four rows	Dimorphic (or monomorphic on stem)	Four rows	Several on dorsal or/ and ventral sides

Table 5
Comparison of spore (megaspore and microspore) morphology, distribution, and constituent species of 7 subfamilies and 19 genera in the current classification of Selaginellaceae.

Subfamilies/Genera	Megaspores	Microspores	Distribution	Constituent species
Subfamily I Selaginoidoideae [*Selaginoides*]	Baculate to verrucate	Spiny	Circumboreal areas and Hawaii	2 species (*Selaginoides deflexa*; *S. selaginoides*)
Subfamily II Boreoselaginelloideae [*Boreoselaginella*]	With densely contiguous tubercles and verrucae	Rugulate, tuberculate, or verrucate	Eastern to western Asia, and extending to Russia.	6 species (*B. aitchisonii, B. borealis, B. jacquemontii, B. nummularifolia, B. rossii, B. sanguinolenta*)
Subfamily III Gymnogynoideae	*Gymnogynum* type or *Bryodesma* type	Rugulate, spiny, or verrucate	Worldwide	All species with dorsal rhizophores excluding *Boreoselaginella*; all species with sterile leaves decussately arranged on the stem
Afroselaginella	*Gymnogynum* type	With an equatorial flange	Southern Africa	Except *S. kraussiana*, all African species with rhizophores born on dorsal side of stems and branches (*Afroselaginella chevalieri, A. congoensis, A. myosurus, A. volubilis*)
Bryodesma	*Bryodesma* type	Rugulate and verrucate	Americas, Africa and Asia	All species with dorsal rhizophores + spirally arranged monomorphic sterile leaves
Ericetorum	*Gymnogynum* type	Rugulate or verrucate	Australasia and Afro-Malagasy	All species with rhizophores restricted to the base of stems and sterile leaves decussately arranged on stem
Gymnogynum	*Gymnogynum* type	Spiny	Americas (a few in Africa and Asia)	All species in Americas with dorsal rhizophores + only one (to a few) megasporophyll at the base of strobili + African *Gymnogynum kraussianum* and Asian *G. remotifolium*
Lepidoselaginella	*Gymnogynum* type	Several curved ridges	Mexico and USA	3 rosette-forming species (*L. lepidophylla, L. novoleonensis, L. ribae*).
Megaloselaginella	*Gymnogynum* type	Columned	Central and South Americas	2 species *(Megaloselaginella exaltata, M. gigantea)* with extremely large plants

(*continued on next page*)

Table 5 (*continued*)

Subfamilies/Genera	Megaspores	Microspores	Distribution	Constituent species
Subfamily IV Sinoselaginelloideae	Verrucate, tuberculate, lamellate	Rugulate, tuberculate, verrucate	Old World	Only one (to a few) megasporophyll at the base + rhizophores borne on ventral side of stems or branches
Austroselaginella	Verrucate, tuberculate	Coarse	Queensland in Australia	All species in Queensland of Australia with strobili with only one (to a few) megasporophyll at the base + rhizophores borne on ventral side of stems or branches
Korallia	Verrucate, tuberculate	Verrucate	Madagascar and adjacent Indian Ocean islands	All species in Madagascar and adjacent Indian Ocean islands with strobili with one (to a few) megasporophyll at the base + rhizophores borne on ventral side of stems or branches
Sinoselaginella	Verrucate, tuberculate	Rugulate, tuberculate, verrucate	China to the Arabic area and eastern Africa	All species in China (extending to the Arabic area and eastern Africa) with strobili with only one (to a few) megasporophyll at the base + rhizophores borne on ventral side of stems or branches
Subfamily V Pulvinielloideae [*Pulviniella*]	Coarse or small verrucate or granular	Rugulate, verrucate, coarse	Africa, Asia, and North and Central Americas	All rosette-forming species except *Lepidoselaginella* and two species of *Selaginella* (*S. pallescens* and *S. nothohybrida*); some species with extremely xerophytic habit and erect plants (e.g., *Pulviniella helioclada, P. stauntoniana*)
Subfamily VI Lycopodioidoideae	Tuberculate to verrucate	Tuberculate, verrucate or granular (rarely baculate)	Old World (a few in Americas)	All Old-World species with resupinate strobili and dimorphic to slightly dimorphic sporophylls; all species in the Old World with strictly monomorphic sporophylls + sterile leaves in four rows + non-reticulate megaspore surfaces; two American species: *Didiclis hoffmannii* and *Valdespinoa douglasii*
Didiclis	Tuberculate to verrucate, often interconnected; or smooth	Verrucate, blunt-spiny, cristate, and lamellate	Asia and Africa (a few in Americas)	All Old-World species with strictly monomorphic sporophylls + sterile leaves four rows + non-reticulate megaspore surfaces; species with dimorphic sporophylls in the *Bisulcata* group: *Didiclis bisulcata, D. obovata, D. opaca, D. pennata,* and *D. soyauxii;* and American *D. hoffmannii*)
Hypopterygiopsis	Verrucate, tuberculate, *Tetragonostachyae* type-1 or -2	Granular, verrucate, smooth	Asia, Africa, and south Pacific islands	All species with resupinate strobili + dimorphic or slightly dimorphic sporophylls in the Old World except the *Bisulcata* group of *Didiclis* (*D. bisulcata, D. obovata, D. opaca, D. pennata,* and *D. soyauxii*) in South and Southeast Asia
Lycopodioides	Tuberculate and/or vermiculate or ridged	Verrucate	Europe to South and East Asia (only 1 sp. in Java, Indonesia)	All species with non-resupinate strobili + dimorphic sporophylls (but including *Lycopodioides denticulata* and *L. helvetica*)
Valdespinoa	Granular to verrucate	Surfaces smooth but fossulate	USA	Only *Valdespinoa douglasii*
Subfamily VII Selaginelloideae	*Stachygynandrum* type; rarely verrucate	Baculate, blunte spiny, some tubercare, verrucate, papillate, or coarse etc.	Asia, Americas, Pacific islands, a few in Africa	All species with rhizophores born on ventral side of stems and branches or restricted at the base of stem + many megasporophylls born on dorsal or ventral side of strobili + no rosette-forming habit (except *S. pallescens, S. nothohybrida*) + often reticulate megaspore surfaces + often baculate microspores surfaces
Chuselaginella	*Stachygynandrum* type	Baculate	Asia, Pacific islands, and a few in Africa	All Asian species with a zonal on the proxiaml surface of megaspores + microspores with baculate ornamentation, and African *Chuselaginella versicolor*, etc.
Kungiselaginella	*Stachygynandrum* type	Blunte spiny	Asia	All Asian species without a zonal on the proxiaml surface of megaspores + microspores with blunte or tubercate ornamentation
Selaginella s.s.	*Stachygynandrum* type or few tubercate on surfaces	Baculate, blunte spiny, verrucate, papillate, or coarse etc.	Americas and one (or a few) in Africa	All species with rhizophores born on ventral side of stems and branches or restricted at the base of stem + many megasporophylls born on dorsal or ventral side of strobili + no rosette-forming habit (except *S. pallescens, S. nothohybrida*), and the African *S. cathedrifolia*.

reticulate ...... [subfamily IV. **Sinoselaginelloideae** 中华卷柏亚科] 19

17. Microspore surfaces coarse, baculate, blunt spiny, papillate, or verrucate, rarely ridged (Americas, except *S. cathedrifolia* in Africa) ...... ***Selaginella s.s.*** 同穗卷柏属
17. Microspore surfaces often baculate or with blunt spines (Old World) 18
18. Plants often ascending to suberect, a few strictly erect; sides of veins of ventral leaves with two light-colored bands; megaspores without a zonal structure on proximal surface; microspore surfaces blunt spiny (Asia) ...... ***Kungiselaginella*** 孔氏卷柏属
18. Plants often strictly erect, a few creeping; sides of veins of ventral leaves without light-colored bands; megaspores with a zonal structure on proximal surface; microspore surfaces baculate with extending tips (Asia, Pacific islands to Africa) ...... ***Chuselaginella*** 朱氏卷柏属
19. Plants xerophytic; microspore surfaces prominently tuberculate (East and South Asia extending to Arabic area and northern Africa) ...... ***Sinoselaginella*** 中华卷柏属
19. Plants non-xerophytic; microspore surfaces verrucate or coarse (Australia, Madagascar and adjacent islands) 20
20. Ventral leaves usually auriculate at basiscopic and acroscopic bases; microspores with three holes on proximal surfaces (Madagascar and adjacent islands) ...... ***Korallia*** 科氏卷柏属
20. Ventral leaves non-auriculate at base; microspore surfaces without holes on proximal surfaces (Australia) ...... ***Austroselaginella*** 澳洲卷柏属

Subfamily I. **Selaginoidoideae** Li Bing Zhang & X.M. Zhou, subfam. nov. 圆穗卷柏亚科(新拟) – type: *Selaginoides* Ség

Plants erect, with no rhizophores; sterile leaves monomorphic and spirally arranged; sporophylls monomorphic; megaspore

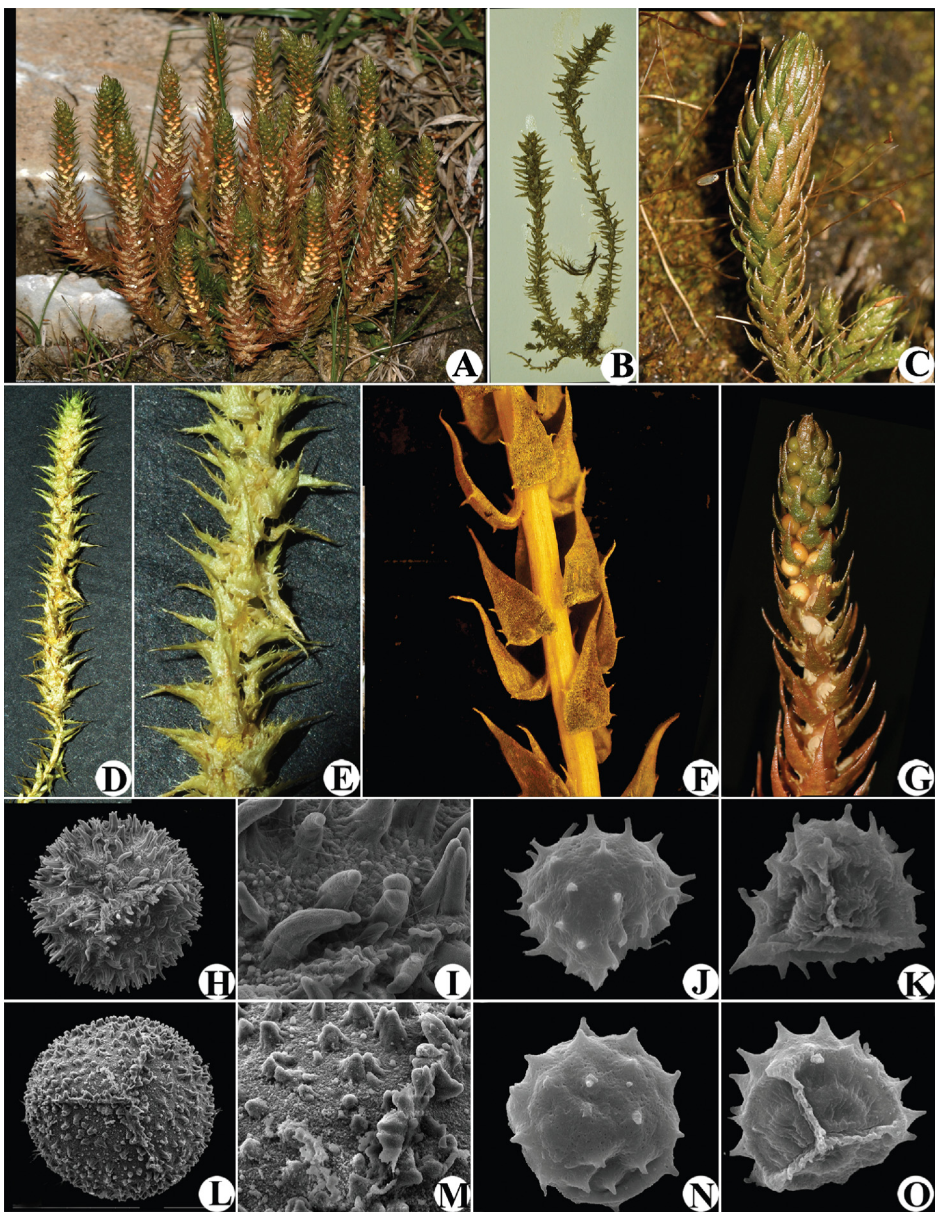

Fig. 3. Morphology of subfamily Selaginoidoideae 圆穗卷柏亚科 (*Selaginella* subg. *Selaginella*; Zhou and Zhang, 2015). **A–C, G and L–O. *Selaginoides spinosa*** (B. Habit; C. Showing plant without rhizophore; G. Showing densely and spirally arranged sporophylls. L and M. Spiny or verrucate ornamentation on megaspore surface. N and O. Spiny ornamentation on microspore surface (N. Distal surface in tetrad and O. Proximal surface). **D, E, F, and H–K. *S. deflexa*** (A. Habit; D and E. Densely and spirally arranged sporophylls; F. Spirally arranged sterile leaves on stem; H and I. Spiny ornamentation on megaspore surface; J and K. Spiny ornamentation on microspore (J. proximal surface and K. distal surface).

surfaces blunt echinate to tuberculate; microspore surfaces with echinate (Fig. 3); 2n = 18 (Takamiya, 1993).

This subfamily corresponds to *Selaginella* subg. *Selaginella* sensu Zhou and Zhang (2015) and Weststrand and Korall (2016b).

It contains one genus: *Selaginoides*, occurring in circumboreal areas and Hawaii.

Selaginoides Ség., Pl. Veron. 3: 51. 1754. 圆穗卷柏属(新拟) ≡ *Mirmau* Adans., Fam. Pl. (Adanson) 2: 491. (1763) ≡ *Polycocca* Hill, Gener. Nat. Hist., ed. 2, 2(Hist. Pl.): 116 (1773) – Type: *Lycopodium selaginoides* L. ≡ *Selaginella selaginoides* (L.). P. Beauv. ex Schrank & Mart., Hort. Reg. Monac. 3 (1829) = *Selaginoides spinulosa* (A. Braun ex Döll) Li Bing Zhang & X.M. Zhou ≡*Selaginella spinulosa* A. Braun ex Döll, Rhein. Fl.: 38 (1843) ≡ *Lycopodina spinulosa* (A. Braun ex Döll) Bubani, Fl. Pyren. 4: 445 (1901) = *Selaginella* subg. *Homoeophyllum* Hieron. & Sadeb., Engler & Prantl, Nat. Pflanzenfam. l(4): 669. 1902 – Type: *Selaginella selaginoides* (L.) P. Beauv. ex Mart. & Schrank.

Selaginoides is resurrected here. *Selaginella* has been proposed to be conserved with a conserved type, *Selaginella flabellata* (L.) Spring (Wan et al., 2023; also see below). *Selaginella spinosa* P. Beauv. (Prodr. Aethéogam.: 112. 1805) is an illegitimate name – the epithet '*selaginoides*' (from *L. selaginoides* L., Sp. Pl.: 1101. 1753) was available for use by Palisot de Beauvois in *Selaginella*. The epithet '*selaginoides*' from *L. selaginoides* would create a tautonym in *Selaginoides* (Art. 23.4 of the ICN). The earliest available epithet in *Selaginoides* is '*spinulosa*'.

Selaginoides is the earliest diverging lineage in Selaginellaceae (Korall et al., 1999; Korall and Kenrick, 2004; Zhou et al., 2016, 2022; Weststrand and Korall, 2016a).

Morphologically, this genus differs from the rest of species in the family in having no rhizophores and monomorphic and spirally arranged leaves (Fig. 2A, E).

The genus contains two species: *Selaginella spinulosa* (circumboreal area) and *S. deflexa* (Hawaii) (Fig. 3).

Members:

Selaginoides deflexa (Brack.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella deflexa* Brack., U.S. Expl. Exped., Filic. 16: 332, no. 3, t.45, f.3 (1854) ≡ *Lycopodioides deflexa* (Brack.) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Selaginoides spinulosa (A. Braun ex Döll) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella spinulosa* A. Braun ex Döll, Rhein. Fl.: 38 (1843) ≡ *L. spinulosa* (A. Braun ex Döll) Bubani, Fl. Pyren. 4: 445 (1901).

Subfamily II. **Boreoselaginelloideae** Li Bing Zhang & X.M. Zhou, ***subfam. nov.*** 北方卷柏亚科(新拟) – type: *Boreoselaginella* (Warb.) Li Bing Zhang & X.M. Zhou

Plants xerophytic, creeping (Fig. 4A–C); sterile leaves in four rows, nearly monomorphic (Fig. 4D) or dimorphic (Fig. 4H), axillary leaves present; rhizophores borne on dorsal side of stem (Fig. 4D); sporophylls monomorphic; megaspore surfaces with dense contiguous tubercles; microspore surfaces rugate to verrucate; 2n = 30 (Takamiya, 1993).

This subfamily corresponds to *Selaginella* subg. *Boreoselaginella* sensu Zhou and Zhang (2015). It is likely the second earlier diverging lineage in the family (Zhou et al., 2016; our Fig. 1, S3).

Plastome conformation of Boreoselaginelloideae known so far (Zhou et al., 2022) was DR structure with only one conformation. In addition, these genes (*psaM*/*rpl20*/*rpl21*/*rpl33*) tend to be lost or pseudogenized, but are preserved in other taxa of Selaginellaceae. Furthermore, genes (*psaM*/*trnI-CAU*/*trnP-GGG*/*trnS-GCU*/*trnS-UGA*) only existed in Boreoselaginelloideae. Except *ndhE*, all *ndh* genes were lost or pseudogenized in Boreoselaginelloideae (Zhang et al., 2022; Zhou et al., 2022).

It contains one genus: *Boreoselaginella*, occurring from eastern to western Asia, and extending to Russia.

Boreoselaginella (Warb.) Li Bing Zhang & X.M. Zhou, *stat. nov.* 北方卷柏属(新拟) –Basionym: *Selaginella* subg. *Boreoselaginella* Warb., Monsunia 1: 100. 1900 – Lectotype (designated by Zhou and Zhang, 2015: 1129): *Boreoselaginella borealis* (Kaulf.) Li Bing Zhang & X.M. Zhou ≡ *Selaginella* borealis (Kaulf.) Spring (= *Selaginella sanguinolenta* (L.) Spring).

Boreoselaginella has rhizophores borne on the dorsal side of the stem, monomorphic and spirally arranged sterile leaves throughout, and non-reticulate megaspores. This combination of the morphology is unique in the family.

It contains about six species distributed from eastern to western Asia and extending to Russia.

Members:

Boreoselaginella aitchisonii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella aitchisonii* Hieron., Engl. & Prantl, Nat. Pfl. 1 (4) 674 (1902) ≡ *Lycopodioides aitchisonii* (Hieron.) Tzvelev, Novosti Sist. Vyssh. Rast. 36: 25 (2004) ≡ *Selaginella sanguinolenta f. aitchisonii* (Hieron.) Alston, Proc. Nat. Inst. Sci. India 11: 215 (1945).

Boreoselaginella borealis (Kaulf.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium boreale* Kaulf., Enum. Fil. 17–18 (1842) ≡ *Selaginella borealis* (Kaulf.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10 (1): 141, no. 40 (1843) ≡ *Lycopodioides borealis* (Kaulf.) Kuntze, Rev. Gen. Pl. 1: 826 (1891). 北方卷柏(新拟)

Boreoselaginella jacquemontii (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella jacquemontii* Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 226, no. 104 (1843).

Boreoselaginella nummularifolia (Ching) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella nummularifolia* Ching, Fl. Xizangica 1: 21 (1983). 钱叶北方卷柏(新拟)

Boreoselaginella rossii (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella mongholica* var. *rossii* Baker, J. Bot. 21: 45 (1883) ≡ *Selaginella rossii* (Baker) Warb., Monsunia 1: 101 (1900) ≡ *Lycopodioides rossii* (Baker) Tzvelev, Novosti Sist. Vyssh. Rast. 36: 25 (2004). 鹿角北方卷柏(新拟)

Boreoselaginella sanguinolenta (L.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium sanguinolentum* L., Sp. Pl. 2: 1100 (1753) ≡ *Stachygynandrum sanguinolentum* (L.) P. Beauv., Prodr. aethéogam. 114 (1805) ≡ *Selaginella sanguinolenta* (L.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 135, no. 2 (1843) ≡ *Lycopodioides sanguinolenta* (L.) Kuntze, Rev. Gen. Pl. 1: 827 (1891). 红枝北方卷柏(新拟)

Subfamily III. **Gymnogynoideae** Li Bing Zhang & X.M. Zhou, ***subfam. nov.*** 关节卷柏亚科 (新拟) – Type: *Gymnogynum* P. Beauv

Plants erect, ascending, or creeping, rarely scandent or rosette-forming (Fig. 5A–E), with rhizophores borne on dorsal side of stems and/or branches (Fig. 5F, H–L); a few species with rhizophores strictly restricted to the base of stem (Fig. 5C); sterile leaves monomorphic and decussately arranged at least in lower portion of plants (*Ericetorum*) (Fig. 5C, K); sporophylls monomorphic, with only one megasporophyll at the base of strobili (Fig. 5J); reticulate megaspore surfaces with wing-like and highly convoluted laesurae forming a complex mass close to the pole (*Ericetorum*) (Fig. 5P); megaspore surfaces reticulate (mainly *Gymnogynum* type with high or wing-like muri and often closed meshes) (Fig. 5N–R); microspore surfaces verrucate to rugate or echinate (Fig. 5S–W; Zhou et al., 2015); 2n = 18, 20 (Jermy et al., 1967; Takamiya, 1993; Marcon, 2003).

The plastome conformations of Gymnogynoideae known so far (Zhou et al., 2022) have all four types of structures (IR, DR, IR-DR coexisting, and NR). In addition, genes *ndh* and *matK* tend to

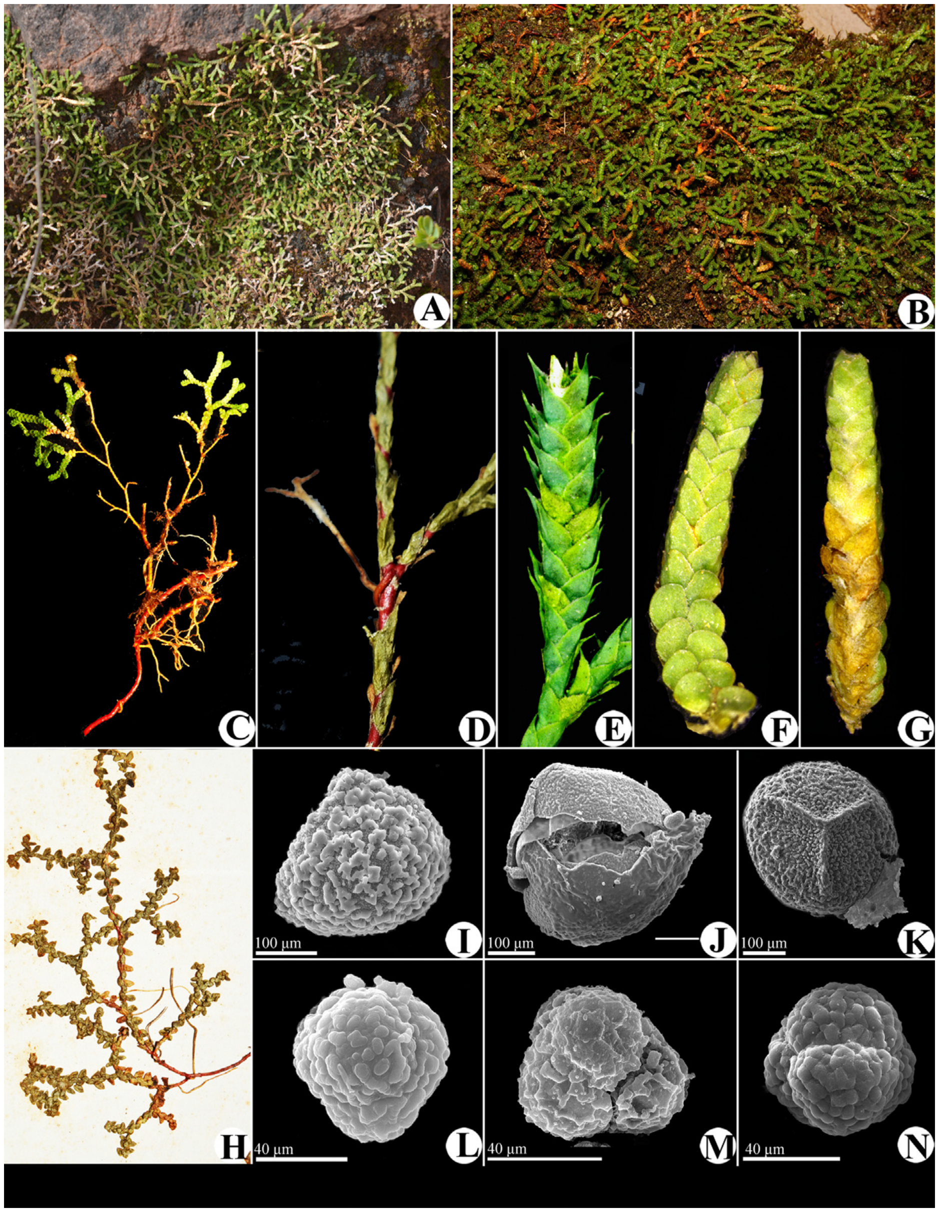

Fig. 4. Morphology of subfamily Boreoselaginelloideae 北方卷柏亚科 (*Selaginella* subg. *Boreoselaginella*; Zhou and Zhang, 2015). **A, D, E, I and L. *Boreoselaginella sanguinolenta*** (A. Habit; D. Rhizophore bore on dorsal side of stem; E. Strobilus tetragonal and sporophylls monomorphic; I. Megaspore; L. Microspore). **B, C, F, G, J and M. *B. nammularifolia*** (B. Habit; C. Plant; F and G. Strobilus (F. Dorsal side and G. Ventral side); J. Megaspore; M. Microspore). **H, K and N. *B. rossii*** (H. Plant; K. Megaspore; N. Microspore).

lose or pseudogenize except in *Gymnogynum*. The *rpl14* (except pseudogenetization in *Lepidoselaginella*) and *ycf3* intron2 (except preserved in *Megaloselaginella*) have been lost in all genera.

This subfamily corresponds to "*Selaginella* subg. *Ericetorum*" (= *S.* subg. *Gymnogynum*) sensu Zhou and Zhang (2015). Weststrand and Korall (2016b) recognized five subgenera in this clade.

It contains six genera, *Afroselaginella*, *Bryodesma*, *Ericetorum*, *Gymnogynum*, *Lepidoselaginella*, and *Megaloselaginella*, occurring in Africa, Australasia, the Caribbeans, and Americas.

Afroselaginella Li Bing Zhang & X.M. Zhou, *gen. nov.* 非洲卷柏属(新拟) – Type: *Afroselaginella myosurus* (Sw.) Li Bing Zhang & X.M. Zhou [*Lycopodium Myosurus* Sw.; *Selaginella myosurus* (Sw.) Alston].

= *Selaginella* sect. *Myosurus* Li Bing Zhang & X.M. Zhou, Taxon 64 (6): 1133 (2015) – Type: *Selaginella Myosurus* (Sw.) Alston.

Etymology: "*Afro-*" derived from *Africa*, referring to the African distribution of the genus.

Plants creeping, stems inarticulate, with a single large megasporangium per strobilus, reticulate megaspores with extremely wide and high muri (Fig. 5N), microspores with an equatorial ring (Fig. 5S).

Afroselaginella has the smallest plastome size (*ca.* 100 kb) in Gymnogynoideae known so far (Zhou et al., 2022). Plastome structure of *Afroselaginella* has only SC region (single copy region) but lacking repeat region and has one ribosomal operon (Zhou et al., 2022).

Afroselaginella circumscribed here corresponds to *Selaginella* sect. *Myosurus* sensu Zhou and Zhang (2015) and part of *S.* subg. *Exaltatae* sensu Weststrand and Korall (2016b).

It contains about five species in Africa.

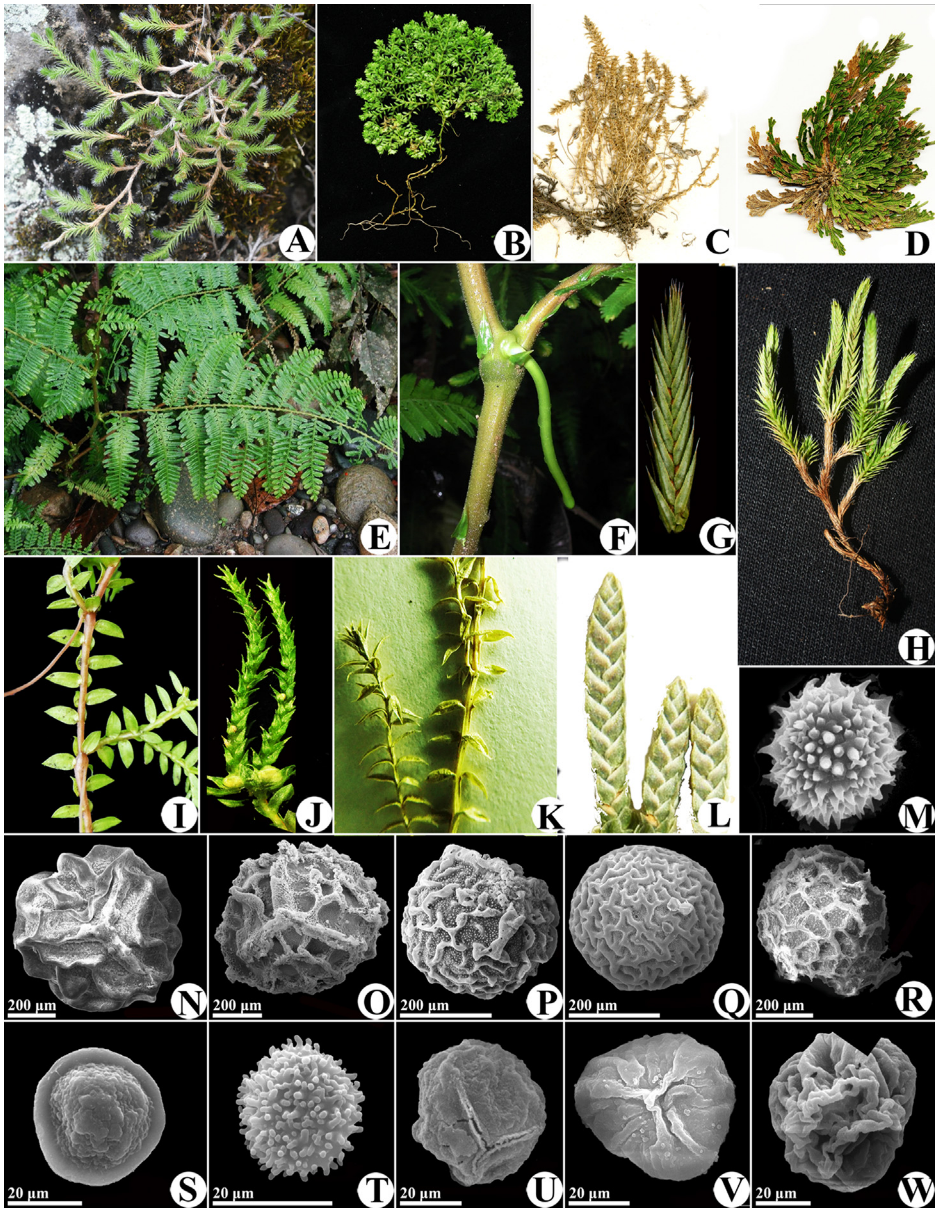

Fig. 5. Morphology of subfamily Gymnogynoideae 关节卷柏亚科 (*Selaginella* subg. *Gymnogynum* " = subg. *Ericetorum*"; Zhou and Zhang, 2015). **A, G, H, Q and V. *Bryodesma vardei*** (A. Habit; G. Strobilus tetragonal and sporophylls monomorphic; H. Plant; Q. Megaspore; V. Microspore). **B & J. *Gymnogynum kraussianum*** (B, Plant; J. Strobili with only one megasporophyll at base). **C, P and U. *Ericetorum gracillimum*** (C. Plants; P. Megaspore; U. Microspore). **D, L and W. *Lepidoselaginella lepidophylla*** (D. Rosset plants; L. Strobili tetragonal and sporophylls monomorphic; W. Microspore). **E, F, O and T. *Megaloselaginella exaltata*** (E. Plant; F. Rhizophore bore on dorsal side of stem and stem swollen on branch; O. Megaspore; T. Microspore). **I. *Gymnogynum remotifolium*** (I. Rhizophore bear on dorsal side of stem and stem swollen on branch). **K. *Ericetorum lyallii*** (K, Deccuately arranged leaves on stem). **M and R. *Gymnogynum marginatum*** (M. microspore; R. Megaspore). **N and S. *Afroselaginella myosurus*** (N, Megaspore; S. Microspore).

Members:

Afroselaginella chevalieri (Hieron. ex Bonap.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella chevalieri* Hieron. ex Bonap., Notes pterid. 1: 124 (1915).

Afroselaginella congoensis (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella congoensis* Alston, Mém. Inst. Fr. Afr. Noire 50: 30, t. 6, f. 1–8 (1957).

Afroselaginella grallipes (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella grallipes* Alston, Mem. Soc. Linn. Normandie Bot. 1(3): 80 (1938).

Afroselaginella myosurus (Sw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium myosurus* Sw., Schrad., J. Bot. (1800) (2): 118 (1801) ≡ *Selaginella myosurus* (Sw.) Alston, J. Bot. 70: 64, no. 6 (1932). J. Bot. 70: 64, no. 6 (1932).

Afroselaginella volubilis (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella volubilis* Alston, Bol. Soc. Broter. Ser. 2, 30: 25 (1956).

Bryodesma Soják, Preslia 64(2): 154 (1993) 同形卷柏属(新拟) – Type: *Bryodesma rupestre* (L.) Soják, Preslia 64(2): 155 (1993) ≡ *Lycopodium rupestre* L., Sp. Pl. 2: 1101 (1753) ≡ *Selaginella rupestris* (L.) Spring, Flora 21(1): 182. 1838.

Selaginella sect. *Homoeophyllae* Spring in Martius, Fl. Bras. 1(2): 118 (1840) ≡ *Selaginella* sect. *Homotropae* A. Broun, App. Ind. Sem. Hort. Berol. 11. ([1857] 1858) – Type: *Selaginella rupestris* (L.) Spring.

Selaginella subg. *Tetragonostachys* Jermy, Fern Gaz. 13: 118. 1986, non Hook. & Grev. in Bot. Misc. 2: 382 (1831) – Type: *Selaginella rupestris* (L.) Spring.

Bryodesma corresponds to *Selaginella* sect. *Homoeophyllae* sensu Zhou and Zhang (2015) and to *S.* subg. *Rupestrae* sensu Weststrand and Korall (2016b), and approximates "*S.* subg. *Tetragonostachys*" sensu Jermy (1986). It also approximates *S.* sect. *Tetragonostachys* sensu Tryon (1955) who recognized four series (*S.* ser. *Arenicolae* Tryon, *S.* ser. *Sartorii* Tryon, *S.* ser. *Rupestres* Tryon, and *S.* ser. *Eremophilae* Tryon) based on the habit and leaf morphology. The relationships of the four series in our phylogeny are unresolved (Fig. S3). Two plastid genomes of species from this section [*Selaginella vardei* H. Lév. and *S. indica* (Milde) R.M. Tryon] were studied and extremely rare short dispersed repeats have been found (Zhang et al., 2019).

Morphologically, *Bryodesma* can be easily distinguished in having xerophytic habit (Fig. 5A), rhizophores borne on dorsal side of the stem (Fig. 5H), sterile leaves spirally arranged throughout (Fig. 5A–H), and axillary leaves absent (Fig. 5H). The proximal surfaces of microspores always present rough and irregularly rugate ornamentation (Fig. 5V), which is also found in these xerophytic species of *S.* subg. *Boreoselaginella* (Zhou et al., 2015).

Plastome structures of nearly all species in *Bryodesma* known so far (Zhou et al., 2022) are DR (direct repeats) structure and without small or medium repeats existed in SC (single-copy region).

Bryodesma contains about 60 species, about 40 species in Americas (nearly all in North America), about 12 species in Africa and Madagascar and adjacent islands, and about five species in Asia (Tryon and Lugardon, 1991; Valdespino, 1993a; Roux, 2009; Weakley, 2012; 2020; Arrigo et al., 2013; Fraser-Jenkins et al., 2015, 2017; Zhou and Zhang, 2015; Weststrand and Korall, 2016b; Hassler, 2022). *Bryodesma corallinum* (Riddell) Weakley has recently been transferred to the genus (Weakley, 2022).

Members:

Bryodesma acanthonota (Underw.) Skoda, Preslia 68(4): 343 (1997). Basionym: *Selaginella acanthonota* Underw., Torreya 2: 172 (1902).

Bryodesma aethiopicum (Bizzarri) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella caffrorum* var. *aethiopica* Bizzarri, Webbia 29: 556 (1975).

Bryodesma arenaria (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella arenaria* Baker, J. Bot. 21: 82, no. 23 (1883).

Bryodesma arenicola (Underw.) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella arenicola* Underw., Bull. Torrey Bot. Club 25: 541 (1898).

Bryodesma arizonicum (Maxon) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella arizonica* Maxon, Smithsonian Misc. Collect. 72: 5–6 (1920).

Bryodesma arsenei (Weath.) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella arsenei* Weath., J. Arnold Arbor. 25: 417, t. 2, f. 8 (1944).

Bryodesma asprellum (Maxon) Soják; Preslia 64(2): 154 (1992 publ. 1993) Basionym: *Selaginella asprella* Maxon, Smithsonian Misc. Collect. 72: 6 (1920).

Bryodesma balansae (A. Braun) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella balansae* (A. Braun) Hieron., Hedwigia 39: 318 (1900).

Bryodesma bigelovii (Underw.) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella bigelovii* Underw., Bull. Torrey Bot. Club 25: 130, no. 6 (1898).

Bryodesma caffrorum (Milde) Soják; Preslia 64(2): 15,4 (1992 publ. 1993). Basionym: *Selaginella caffrorum* (Milde) Hieron., Hedwigia 39: 313 (1900).

Bryodesma basipilosum (Valdespino) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella basipilosa* Valdespino, Brittonia 44(3): 314(1992 publ. 1993).

Bryodesma carinatum (R.M. Tryon) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella carinata* R.M. Tryon, Ann. Mo. Bot. Gard. 42: 50, f. 25–26, map 31 (1955).

Bryodesma carnerosanum (T. Reeves) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella carnerosana* T. Reeves, Brittonia 32(3): 365 (1980).

Bryodesma cinerascens (A.A. Eaton) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella cinerascens* A.A. Eaton; Fern Bull. 7: 33 (1899).

Bryodesma corallina (Riddell) Weakley; J. Bot. Res. Inst. Texas 16(2): 405 (2022). Basionym: *Lycopodium corallinum* Riddell; New Orleans Med. Surg. J. 9: 617 (1853).

Bryodesma densum (Rydb.) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella densa* Rydb.; Mem. New York Bot. Gard. 1: 7 (1900).

Bryodesma dregei (C. Presl) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Lycopodium dregei* C. Presl; Abh. Königl. Böhm. Ges. Wiss., Math.-Naturw. Cl. V, 3 (1845), reimpr. in Bot. Bemerk. (C. Presl) 153 (1846).

Bryodesma echinatum (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella echinata* Baker, J. Linn. Soc. Bot. 22: 536 (1887).

Bryodesma emodi (Fraser-Jenk.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella emodi* Fraser-Jenk., in Fraser–Jenkins, Kandel & Pariyar, Ferns Fern-Allies Nepal 1: 67–68. 2015. 印度同形卷柏(新拟)

Bryodesma eremophilum (Maxon) Soják; Preslia 64(2): 154 (1992 publ. 1993). *Selaginella eremophila* Maxon; Smithsonian Misc. Collect. 72(5): 3, t. 2 (1920).

Bryodesma extensum (Underw.) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella extensa* Underw.; Bull. Torrey Bot. Club 25: 131 (1898).

Bryodesma griseum (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella grisea* Alston, J. Bot. 77: 222 (1939).

Bryodesma hansenii (Hieron.) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella hansenii* Hieron., Hedwigia 39: 301 (1900).

Bryodesma landii (Greenm. & N. Pfeiff.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella landii* Greenm. & N. Pfeiff., Ann. Mo. Bot. Gard. 5: 205 (1918).

Bryodesma macratherum (Weath.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella macrathera* Weath., J. Arnold Arbor. 24: 326 (1943).

Bryodesma niveum (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella nivea* Alston, Dansk Bot. Ark. 7: 194, t. 78(1–4) (1932), nom. nud., et Cat. Pl. Madagasc., Pterid. 71 (1932).

Bryodesma humbertii (Stefanov. & Rakotondr.) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella nivea* subsp. *Humbertii* Stefanov. & Rakotondr., Novon 6(2): 207 (1996).

Bryodesma leucobryoides (Maxon) Skoda; Preslia 68(4): 343 (1997). Basionym: *Selaginella leucobryoides* Maxon, Smithsonian Misc. Collect. 72(5): 8, t. 5 (1920).

Bryodesma limitaneum (Weath.) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella mutica* var. *Limitanea* Weath., J. Arnold Arbor. 25: 414 (1944) ≡ *Bryodesma muticum* var. *Limitaneum* (Weath.) Skoda, Preslia 68(4): 343 (1997).

Bryodesma muticum (D.C. Eaton ex Underw.) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella mutica* D.C. Eaton ex Underw., Bull. Torrey Bot. Club 25: 128 (1898)

Bryodesma × ***neomexicanum*** (Maxon) Skoda; Preslia 68(4): 343 (1997). Basionym: *Selaginella* ×*neomexicana* Maxon, Smithsonian Misc. Collect. 72: 2 (1920).

Bryodesma njamnjamense (Hieron.) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella njamnjamensis* Hieron., Hedwigia 39: 312 (1900).

Bryodesma oreganum (D.C. Eaton) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella oregana* D.C. Eaton; Wats., Bot. California 2: 350 (1880).

Bryodesma parishii (Underw.) Soják; Preslia 64(2): 154 (1992 publ. 1993). Basionym: *Selaginella parishii* Underw., Bull. Torrey Bot. Club 33: 202 (1906).

Bryodesma peruvianum (Milde) Soják; Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella peruviana* (Milde) Hieron., Hedwigia 39: 307 (1900).

Bryodesma phillipsianum **(**Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella wightii* var. *phillipsiana* Hieron., Hedwigia 39: 320 (1900) ≡ *Selaginella phillipsiana* (Hieron.) Alston, J. Bot. 77: 222 (1939).

Bryodesma proximum (R.M. Tryon) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella proxima* R.M. Tryon, Ann. Mo. Bot. Gard. 42: 56, f. 33–35, map 37 (1955).

Bryodesma rupestre (L.) Soják; Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella rupestris* (L.) Spring; Flora 21: 149 and 182, no. 12 (1838).

Bryodesma rupincola (Underw.) Soják; Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella rupincola* Underw.; Bull. Torrey Bot. Club 25: 129 (1898).

Bryodesma sartorii (Hieron.) Soják, Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella sartorii* Hieron.; Hedwigia 39: 304 (1900).

Bryodesma scopulorum (Maxon) Skoda & Holub, Preslia 68(4): 343 (1997). Basionym: *Selaginella scopulorum* Maxon; Am. Fern J. 11: 36 (1921).

Bryodesma sellowii (Hieron.) Soják, Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella sellowii* Hieron., Hedwigia 39: 306 (1900).

Bryodesma shabaense (Bizzarri) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella shabaensis* Bizzarri, Webbia 36(1): 204 (1982).

Bryodesma shakotanense (Franch. ex Takeda) Soják, Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella shakotanensis* (Franch. ex Takeda) Miyabe & Kudô; Fl. Hokkaido 63 (1930). 北海道同形卷柏(新拟)

Bryodesma sibiricum (Milde) Soják, Preslia 64(2): 155 (1992 publ. 1993). *Selaginella sibirica* (Milde) Hieron.; Hedwigia 39: 290, no. 1 (1900). 西伯利亚同形卷柏(新拟)

Bryodesma standleyi (Maxon) Skoda; Preslia 68(4): 343 (1997). Basionym: *Selaginella standleyi* Maxon; Smithsonian Misc. Collect. 72(5): 9 (1920).

Bryodesma steyermarkii (Alston) Soják, Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella steyermarkii* Alston, Ann. Mag. Nat. Hist. XII, 7: 638, t. XII.9, f. a–c. Aug (1954).

Bryodesma tortipilum (A. Braun) Soják, Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella tortipila* A. Braun, Ann. Sci. Nat., Bot., sér. V, 3: 271 (1865).

Bryodesma underwoodii (Hieron.) Soják, Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella underwoodii* Hieron. in Engl. & Prantl, Nat. Pflanzenfam. 1: 714 (1901).

Bryodesma utahense (Flowers) Skoda & Holub, Preslia 68(4): 343 (1997). Basionym: *Selaginella utahensis* Flowers, Am. Fern J. 39: 83 (1949).

Bryodesma vardei (H. Lév.) Soják, Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella vardei* H. Lév., Cat. Pl. Yun-Nan 172, f. 41 (1915)-17. 细瘦同形卷柏(新拟)

Bryodesma viridissimum (Weath.) Soják, Preslia 64(2): 155 (1992 publ. 1993). *Selaginella viridissima* Weath., J. Arnold Arbor. 24: 326 (1943).

Bryodesma wallacei (Hieron.) Soják, Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella wallacei* Hieron., Hedwigia 39: 297 (1900).

Bryodesma watsonii (Underw.) Soják; Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella watsonii* Underw., Bull. Torrey Bot. Club 25: 127 (1898).

Bryodesma weatherbianum (R.M. Tryon) Soják, Preslia 64(2): 155 (1992 publ. 1993). Basionym: *Selaginella weatherbiana* R.M. Tryon, Am. Fern J. 40: 69 (1950).

Bryodesma wightii (Hieron.) Soják, Preslia 64(2): 155 (1992). Basionym: *Selaginella wightii* Hieron., Hedwigia 39: 319 (1900).

Bryodesma wrightii (Hieron.) Soják; Preslia 64(2): 155 (1992). Basionym: *Selaginella wrightii* Hieron, Hedwigia 39: 298–299 (1900).

Ericetorum (Jermy) Li Bing Zhang & X.M. Zhou, stat. nov. 对叶卷柏属(新拟) – Basionym: *Selaginella* subg. *Ericetorum* Jermy, Fern Gaz. 13(2): 117. 1986 – Type: *Ericetorum uliginosa* (Labill.) Li Bing Zhang & X.M. Zhou (≡ *Selaginella uliginosa* (Labill.) Spring).

Didiclis sect. *Lyallia* Rothm., Feddes Repert. Spec. Nov. Regni Veg. 54: 70 (1944) ≡ *Selaginella* sect. *Lyallia* (Rothm.) Li Bing Zhang & X.M. Zhou, Taxon 64(6): 1133 (2015) – Type: *Selaginella lyallii* (Hook. & Grev.) Spring.

=*Selaginella* (unranked) *Tetrastichae* A. Braun, App. Ind. Sem. Hort. Berol. 11. [1857] 1858 – Lectotype (designated by Zhou and Zhang 2015: 1133): *Selaginella uliginosa* (Labill.) Spring.

=*Selaginella* subser. *Pleiostelicae* Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanzenf. I.(4): 707. 1902, non Hieronymus and Sadebeck, 1901 (1902: 700, 710) – Lectotype (designated by Zhou and Zhang 2015: 1133): *Selaginella lyallii* (Hook. & Grev.) Spring.

Ericetorum circumscribed here corresponds to *Selaginella* sect. *Lyallia* (Rothm.) Li Bing Zhang & X.M. Zhou (2015) and to *S.* subg. *Ericetorum* sensu Weststrand and Korall (2016b). Its geographical distribution and constituent species are same as those reported in previous studies (Zhou and Zhang, 2015; Weststrand and Korall, 2016b).

Morphologically, *Ericetorum* can be easily identified in having erect plant, solenostelic rhizome (Weststrand and Korall, 2016a), rhizophores strictly restricted to the base of stem (Fig. 5C), sterile leaves monomorphic and decussately arranged (or at least on stem) (Fig. 5K; Stefanović et al., 1997; Schulz et al., 2013). Megaspore surfaces are reticulate and have convoluted laesurae forming a complex mass close to the pole on proximal surfaces (Fig. 5P; Stefanović et al., 1997; Schulz et al., 2013). Microspore surfaces are gemmate, foveolate, verrucate to rugate ornamentation or scabrate often covered with microstructure being spines or gemmae (Fig. 5U; Stefanović et al., 1997; Schulz et al., 2013).

The plastome of *Ericetorum* known so far (Zhou et al., 2022) has DR structure, the lowest GC content (*ca.* 50%), and the smallest LSC (*ca.* 45 kb) in Gymnogynoideae.

Eight species are currently known in this genus containing four Australasian and four Afro-Malagasy species (Stefanović et al., 1997; Roux, 2009; Schulz et al., 2013).

Members:

Ericetorum aboriginale (C. Schulz & Homberg) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella aboriginalis* C. Schulz & Homberg, Syst. Bot. 38(1): 11 (2013).

Ericetorum gracillimum (Kunze) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium gracillimum* Kunze, Lehm., Pl. Preiss. 2: 109 (1846–47) ≡ *Lycopodioides gracillima* (Kunze) Kuntze, Rev. Gen. Pl. 1: 825 (1891) ≡ *Selaginella gracillima* (Kunze) Spring ex Salomon; Nomencl. 353 (1883).

Ericetorum lyallii (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium lyallii* Hook. & Grev., Enum. Fil. J. Bot. (Hook.) Kew Misc. 2: 387, no. 120 (1831) ≡ *Selaginella laevigata* var. *Lyallii* (Hook. & Grev.) Baker, J. Bot. 23: 116 (1885) ≡ *S. lyallii* (Hook. & Grev.) Spring; Bull. Acad. Roy. Soc. Bruxelles 10: 146, no. 84 (1843).

Ericetorum moratii (W. Hagemann & Rauh) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella moratii* W. Hagemann & Rauh; Pl. Syst. Evol. 176(3–4): 205 (1991).

Ericetorum pygmaeum (Kaulf.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium pygmaeum* Kaulf., Enum. Fil. 9 (1824) ≡ *Lycopodium pumilum* var. *pygmaeum* (Kaulf.) Schltdl., Adumbr. Fl. Aethiop. 6 (1825) ≡ *Lycopodioides pygmaeum* (Kaulf.) Kuntze, Rev. Gen. Pl. 1: 825 (1891) ≡ *Selaginella pygmaea* (Kaulf.) Alston; J. Bot. (London) 69: 257 (1931).

Ericetorum pectinatum (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella pectinata* Spring, Bull. Acad. Roy. Sci. Bruxelles 10(1): 146. 1843, nom. nov. for *Lycopodium pectinatum* Willd., Sp. Pl., ed. 4. 5(1):44. 1810, nom. illeg., non Lamarck (1792: 651). – *Selaginella polymorpha* Badre', Fl. Madagasc. fam. 14:25. 1997, a nom. nov. but superfl. for *L. pectinatum* Willd. – Lectotype (designated by Smith et al., 2016): "America meridionale?" [protologue], "Habitat in Madagascar" [specimens], B–W 19400-02 0.

Ericetorum royenii (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella royenii* Alston; Nova Guinea ser. 2, 7: 2 (1956).

Ericetorum uliginosum (Labill.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium uliginosum* Labill., Nov. Holl. pl. spec. 2: 154, t. 251, f. 1 (1806) ≡ *Lycopodioides uliginosa* (Labill.) Kuntze, Rev. Gen. Pl. 1: 827 (1891) ≡ *L. uliginosum* Labill., Nov. Holl. pl. spec. 2: 154, t. 251, f. 1 (1806) ≡ *Selaginella uliginosa* (Labill.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 136 (1843).

Gymnogynum P. Beauv., Mag. Encycl. 9(5): 480 (1804) 关节卷柏属(新拟) ≡ *Lycopodium* subg. *Gymnogynum* (P. Beauv.) Rchb., Consp. Regn. Veg.: 78 (1828) ≡ *Didiclis* sect. *Gymnogynum* (P. Beauv.) Rothm., Feddes Repert. Spec. Nov. Regni Veg. 54: 70 (1944) – Type: *Gymnogynum* domingense P. Beauv., Mag. Encycl. 9(5): 480 (1804) [= *Selaginella* plumosa (L.) C. Presl ≡ *Lycopodium plumosum* L.].

= *Selaginella* sect. *Articulatae* (Spring) Li Bing Zhang & X.M. Zhou, Taxon 64(6): 1132 (2015) ≡ *Selaginella* (unranked) *Articulatae* Spring in Mém. Acad. Sci. Belg. 24: 53 (1850) ≡ *S.* ser. *Articulatae* (Spring) Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanzenf. l(4): 707 (1902) ≡ *Didiclis* sect. *Articulatae* (Spring) Rothm. in Feddes Repert. Spec. Nov. Regni Veg. 54: 71. (1944) – Lectotype (designated by Rothmaler, 1944: 71): *Didiclis sulcata* (Desv. ex Poir.) Rothm. (= *Selaginella sulcata* (Desv. ex Poir.) Spring ex Mart.).

= *Selaginella* (unranked) *Ascendentes* A. Braun in App. Ind. Sem. Hort. Berol. 11 ([1857] 1858) non A. Braun (1858: 11) – Lectotype (designated by Zhou and Zhang, 2015: 1132): *Selaginella galeottii* Spring (= *Selaginella stellata* Spring).

= *Selaginella* (unranked) *Repentes* A. Braun in App. Ind. Sem. Hort. Berol. 12. [1857] 1858, non A. Braun (1858: 11) – Lectotype (designated by Zhou and Zhang 2015: 1132): *Selaginella hortensis* Mett. (= *Selaginella kraussiana* (G. Kunze) A. Braun).

Selaginella (unranked) *Caulescentes* A. Braun in App. Ind. Sem. Hort. Berol. 12 ([1857] 1858), non A. Braun (1858: 11) – Type: *Selaginella asperula* Spring.

Selaginella subser. *Pleiostelicae* Hieron. & Sadeb. in Engler. & Prantl, Nat. Pflanzenf. l(4): 710 (1902) non Hieronymus and Sadebeck, 1901 (1902: 700, 707) – Type: *Selaginella kraussiana* (G. Kunze) A. Braun.

= *Selaginella* subser. *Monostelicae* Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanzenf. l(4): 708 (1902) non Hieronymus and Sadebeck, 1901 (1902: 673, 704) – Type: *Selaginella remotifolia* Spring.

Gymnogynum corresponds to *Selaginella* sect. *Articulatae* sensu Zhou and Zhang (2015) and to *S.* subg. *Gymnogynum* sensu Weststrand and Korall (2016b). *Gymnogynum* is always well supported as monophyletic in morphology (Mickel et al., 2004) and phylogeny (Weststrand and Korall, 2016a; Zhou et al., 2016; our Fig. 1 and S1–S3).

Morphologically, *Gymnogynum* has articulation (presenting swellings or nodules: Fig. 5I) on stems and branches (Lopes et al., 2020), strobilus with only one large megasporophyll at the base (Fig. 5J), rhizophores borne on dorsal side of stem or/and branch (Fig. 5B, F–I), megaspores large and with reticulate ornamentation on surfaces (Korall and Taylor, 2006; Zhou et al., 2015, Fig. 5R), and microspore surfaces usually spiny or echinate (Fig. 5M; Zhou et al., 2015; Valdespino and Lòpez, 2020).

The *ndh* gene of plastomes in *Gymnogynum* is preserved (Zhou et al., 2022).

This genus contains about 50 species mainly in North to South Americas and a few in Africa and Asia. *Gymnogynum kraussianum* is native to Africa and has been cultivated throughout the world and has been recently transferred to *Gymnogynum* by Weakley as *G. kraussianum* (Kunze) Weakley (2022).

Members:

Gymnogynum atirrensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella atirrensis* Hieron., Nat. Pflanzenfam. 1(4): 711 (1901).

Gymnogynum anaclastum (Alston ex Crabbe & Jermy) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella anaclasta* Alston ex Crabbe & Jermy, Am. Fern J. 63(3): 135 (1973).

Gymnogynum angustifolium (A. Braun) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella sericea* var. *angustifolia* A. Braun; Ann. Sci. Nat., Bot., sér. V, 3: 299 (1865).

Gymnogynum arthriticum (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella arthritica* Alston, Arch. Bot. (Forli) 11: 43 (1935).

Gymnogynum articulatum **(**Kunze) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium articulatum* Kunze, Linn. 9: 10 (1834 publ. 1835) ≡ *Selaginella articulata* (Kunze) Spring, Flora 21: 182 (1838) ≡ *Lycopodioides articulata* (Kunze) Kuntze, Rev. Gen. Pl. 1: 825 (1891).

Gymnogynum asperulum (Mart. ex Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: ≡ *Lycopodium asperulum* C.Mart. ex Spring in Mart. Fl. Bras. 1(2): 127, no. 15 (1840) ≡ *Lycopodioides asperula* (Mart. ex Spring) Kuntze, Rev. Gen. Pl. 1: 825 (1891) ≡ *Selaginella asperula* Mart. ex Spring, Mart., Fl. Bras. 1(2): 127 (1840).

Gymnogynum asplundii (Alston ex Crabbe & Jermy) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella asplundii* Alston ex Crabbe & Jermy, Fern Gaz. 11(4): 257 (1976).

Gymnogynum buchtienii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella buchtienii* Hieron., Med. Rijks Herb. Leiden, no. 27: 2 (1915).

Gymnogynum caluffii (Shelton) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella caluffii* Shelton, Willdenowia 33(1): 159 (2003).

Gymnogynum coarctatum (Mart. ex Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella coarctata* Mart. ex Spring, Mart., Fl. Bras. 1(2): 126, no. 14 (1840) ≡ *Lycopodioides coarctata* (Mart. ex Spring) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Gymnogynum conduplicatum (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella conduplicata* Spring, Mart., Fl. Bras. 1(2): 129 (1840) ≡ *Selaginella geniculata* subsp. *conduplicata* (Spring) Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 712 (1901 publ. 1902) ≡ *Selaginella geniculata* var. *conduplicata* (Spring) A. Braun, Ann. sc. nat. V, 3: 303 (1865).

Gymnogynum decompositum (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella decomposita* Spring, Mart., Fl. Bras. 1(2): 123, no. 10 (1840).

Gymnogynum diffusum **(**C. Presl) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium diffusum* C. Presl, Rel. Haenk. 1(1): 78 (1825) (nom. illeg., non R. Br. (1810)) ≡ *Selaginella diffusa* (C. Presl) Spring, Bull. Acad. Roy. Soc. Bruxelles 10 (1): 143 (1843).

Gymnogynum eurynotum (A. Braun) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella eurynota* A. Braun, Ann. sc. nat. V, 3: 293 (1865) ≡ *Lycopodioides eurynota* (A. Braun) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Gymnogynum expansum (Sodiro) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella expansa* Sodiro, Rec. Cr. vasc. quit. 95, no. 12 (1883) ≡ *Lycopodioides expansa* (Sodiro) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Gymnogynum flabellum (Desv.) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella flabellum* (Desv.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 234, no. 157 (1843).

Gymnogynum fragile (A. Braun) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella fragilis* A. Braun, Ann. sc. nat. V, 5, 3: 305 (1865).

Gymnogynum filicaule (Sodiro) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella filicaulis* Sodiro, Rec. Cr. vasc. quit. 600 (1893), et Anal. Univ. Centr. Ecuador 12: 413 (1895).

Gymnogynum fuertesii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella fuertesii* Hieron., Urban, Symb. Ant. 7: 164 (1912).

Gymnogynum geniculatum (C. Presl) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium geniculatum* C. Presl, Rel. Haenk. 1(1): 80 (1825) ≡ *Selaginella geniculata* (C. Presl) Spring, Bull. Acad. Roy. Soc. Bruxelles 10(1): 230 (1843) ≡ *Lycopodioides geniculata* (C. Presl) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Gymnogynum germinans (Valdespino & C. López) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella germinans* Valdespino & C. López, Botany Letters 165(3–4): 488 (2018).

Gymnogynum horizontale (C. Presl) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium horizontale* C. Presl, Rel. Haenk. 1(1): 78 (1825) ≡ *Selaginella horizontalis* (C. Presl) Spring; Bull. Acad. Roy. Soc. Bruxelles 10(1): 226 (1843).

Gymnogynum humboldtianum (A. Braun) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella humboldtiana* A. Braun; Ann. Sci. Nat., Bot., sér. V, 5, 3: 293 (1865).

Gymnogynum ivanii (Shelton & Caluff) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella ivanii* Shelton & Caluff, Willdenowia 33(1): 162 (2003).

Gymnogynum kraussianum (Kunze) Weakley; J. Bot. Res. Inst. Texas 16(2): 405 (2022). Basionym: *Lycopodium kraussianum* Kunze; Linnaea 18: 114 (1844). 小翠云 (栽培)

Gymnogynum kunzeanum (A. Braun) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella kunzeana* A. Braun, Ann. sc. nat. V, 3: 296–297, no. 35 (1865) ≡ *Lycopodioides kunzeana* (A. Braun) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Gymnogynum lingulatum (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella lingulata* Spring, Mém. Acad. Roy. Sci. Belg. 24: 224 (1849) ≡ *Lycopodioides lingulata* (Spring) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Gymnogynum marginatum (Humb. & Bonpl. ex Willd.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium marginatum* Humb. & Bonpl. ex Willd., Sp. Pl. 5: 41, no. 58 (1810) ≡ *Selaginella marginata* (Humb. & Bonpl. ex Willd.) Spring, Flora 21: 194 (1838) ≡ *Lycopodioides marginata* (Kunth) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Gymnogynum microtus (A. Braun) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella microtus* A. Braun, Ann. sc. nat. V, 3: 293, no. 32 (1865).

Gymnogynum moranianum (Valdespino & C. López) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella moraniana* Valdespino & C. López, Brittonia 72(1): 24 (2019).

Gymnogynum parkeri (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium parkeri* Hook. & Grev., Enum. Fil. J. Bot. (Hook.) Kew Misc. 2: 388, no. 123 (1831) ≡ *Selaginella parkeri* (Hook. & Grev.) Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 146 (1843) ≡ *Lycopodioides parkeri* (Hook. & Grev.) Kuntze, Rev. Gen. Pl. 2: 827 (1891).

Gymnogynum parviarticulatum (W.R. Buck) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella parviarticulata* W.R. Buck, Brittonia 38(1): 45 (1986).

Gymnogynum pedatum (Klotzsch) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella pedata* Klotzsch, Linn. 17: 521 (1844).

Gymnogynum plumosum (L.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *L. plumosum* L., Sp. Pl. 2: 1100 (1753) ≡ *Stachygynandrum plumosum* (L.) P. Beauv., Fl. D'Oware, 1: 10 (1805) ≡ *Lycopodioides plumosa* (L.) Kuntze, Rev. Gen. Pl. 1: 825 & 827 (1891) ≡ *Selaginella plumosa* (L.) C. Presl, Abh. (K.) Böhm. Ges. Wiss., Math.-Naturw. Cl. V, 3: 583 (1845).

Gymnogynum poeppigianum (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium poeppigianum* Hook. & Grev., Enum. Filic. J. Bot. (Hook.) Kew Misc. 2: 392–393, no. 143 (1831). ≡ *Selaginella poeppigiana* (Spring) Spring, Flora 21: 185 (1838). ≡ *Lycopodioides poeppigiana* (Spring.) Kuntze, Revis. Gen. Pl. 2: 827 (1891).

Gymnogynum remotifolium (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella remotifolia* Spring, Miq. Pl. Jungh. 3: 276, no. 5 (1854) ≡ *Lycopodioides remotifolia* (Spring) H.S. Kung, Fl. Sichuan. 6: 65–67, t. 19, 10–15 (1988). 疏叶关节卷柏 (新拟)

Gymnogynum schizobasis (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella schizobasis* Baker, J. Bot. 21: 333, no. 86 (1883) ≡ *Lycopodioides schizobasis* (Baker) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Gymnogynum sericeum (A. Braun) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella sericea* A. Braun, Ann. sc. nat. V, 3: 298–299, no. 37 (1865) ≡ *Lycopodioides sericea* (A. Braun) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Gymnogynum sertatum (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella sertata* Spring, Mém. Acad. Roy. Sci. Belg. 24: 104 (1849) ≡ *Lycopodioides sertata* (Spring) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Gymnogynum silvestre (Aspl.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella silvestris* Aspl., Ark. för Bot. 20A(7): 30, f. 3–5 (1926).

Gymnogynum stellatum (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella stellata* Spring, Flora 21: 188 (1838) ≡ *Selaginella parkeri* var. *stellata* (Spring) Baker, J. Bot. 23: 120 (1885) ≡ *Selaginella stolonifera* var. *stellata* Spring, Flora 21: 194 (1838).

Gymnogynum suave (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella sulcata* ssp. *suavis* Spring, Flora 21: 185 (1838) ≡ *Selaginella suavis* (Spring) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 229 (1843) ≡ *Lycopodioides suavis* (Spring) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Gymnogynum sulcatum (Desv. ex Poir.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium sulcatum* Desv. ex Poir., Lam., Encycl. suppl. 3: 549, no. 74. (1813 publ. 1814) ≡ *Selaginella sulcata* (Desv. ex Poir.) Spring ex Mart., Flora 20 (2): 126 (1837) ≡ *D. sulcata* (Desv.) Rothm., Fedde, Repert. Spec. Nov. 54: 71 (1944) ≡ *Lycopodioides sulcata* (Desv.) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Gymnogynum tardum (Mickel & Beitel) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella tarda* Mickel & Beitel, Mem. New York Bot. Gard. 46: 353, f. 128H–N (1988).

Gymnogynum tenuissimum (Fée) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella tenuissima* Fée, Cr. vasc. Br. 2: 98, no. 6/2, t. 108 (1873) ≡ *Lycopodioides tenuissima* (Fée) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Gymnogynum tomentosum (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella tomentosa* Spring, Mém. Acad. Roy. Sci. Belg. 24: 231 (1849) ≡ *Selaginella geniculata* var. *tomentosa* (Spring) Baker, J. Bot. 23: 121 (1885).

Gymnogynum trisulcatum (Aspl.) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella trisulcata* Aspl., Ark. för Bot. 20A(7): 34, f. 6 (1926).

Gymnogynum versatile (A.R.Sm.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella versatilis* A.R.Sm., Ann. Mo. Bot. Gard. 77(2): 270 (1990).

Lepidoselaginella Li Bing Zhang & X.M. Zhou, gen. nov. 鳞叶卷柏属(新拟) – Type: *Lepidoselaginella lepidophylla* (Hook. & Grev.) Li Bing Zhang & X.M. Zhou ≡ *Lycopodium lepidophyllum* Hook. & Grev., Icon. Filic. 2(9): 162 (1830) ≡ *Selaginella lepidophylla* (Hook. & Grev.) Spring, Fl. Bras. (Martius) 1(2): 126 (1840).

= *Selaginella* sect. *Lepidophyllae* Li Bing Zhang & X.M. Zhou, Taxon 64(6): 1133 (2015) – Type: *Selaginella lepidophylla* (Hook. & Grev.) Spring.

Etymology: "*Lepido-*" derived from *lepidophylla*, referring to the scales-looking leaves of the type species.

Lepidoselaginella corresponds to *Selaginella* sect. *Lepidophyllae* sensu Zhou and Zhang (2015) and *S.* subg. *Lepidophyllae* sensu Weststrand and Korall (2016b). It is strongly supported as sister to *Bryodesma* (Weststrand and Korall, 2016a; Zhou et al., 2016; our Fig. 1 and S1–S3).

Morphologically, *Lepidoselaginella* has rosette habit (Fig. 5D) and rhizophores borne on dorsal side of the stem. Although some taxa in other genera (e.g., *S. pallescens*, *Selaginella nothohybrida*, and most members of *Pulviniella*) also have rosette habit, they have rhizophores borne on ventral side of the stem. *Lepidoselaginella* has megaspores with ridges on the distal surface (Korall and Tryon, 2006) and microspores with striped ornamentation which are different from rest of species in the family (Fig. 5W).

The plastome of *Lepidoselaginella* has IR structure (Zhou et al., 2022).

Lepidoselaginella contains about three species occurring in Mexico and USA (Mickel and Smith, 2004; Weststrand and Korall, 2016a; Zhou et al., 2016).

Members:

Lepidoselaginella lepidophylla (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *L. lepidophyllum* Hook. & Grev., Icon. Fil. 2(9): 162 (1830), et Enum. Fil. J. Bot. (Hook.) Kew Misc. 3: 106 (1833) ≡ *Selaginella lepidophylla* (Hook. & Grev.) Spring, Mart., Fl. Bras. 1(2): 126 (1840) ≡ *Lycopodioides lepidophylla* (Hook.) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Lepidoselaginella novoleonensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella novoleonensis* Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 676, no. 56. (1901 publ. 1902).

Lepidoselaginella ribae (Valdespino) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella ribae* Valdespino, Mem. New York Bot. Gard. 88 (Pterid. Mexico): 591–592 (2004).

Megaloselaginella Li Bing Zhang & X.M. Zhou, *gen. nov.* 大孢卷柏属(新拟) – Type: *Megaloselaginella exaltata* (Kunze) Li Bing Zhang & X.M. Zhou (≡ *Lycopodium exaltatum* Kunze ≡ *Selaginella exaltata* (Kunze) Spring).

= *Selaginella* sect. *Megalosporarum* Li Bing Zhang & X.M. Zhou, Taxon 64(6): 1133 (2015).

Etymology: "*Megalo-*" derived from *Megalosporarum*, referring to the extremely large megaspores (*ca.* 1.5 mm).

Megaloselaginella corresponds to *Selaginella* sect. *Megalosporarum* sensu Zhou and Zhang (2015) and part of *S.* subg. *Exaltatae* sensu Weststrand and Korall (2016b).

Megaloselaginella is very similar to *Gymnogynum* in having rhizophores borne on dorsal side of the stem and only one megasporophyll at the base of strobili (Fig. 5F). However, *Megaloselaginella* has large erect plants (up to 1 m) (Fig. 5E), several steles in a special actino-plectoste (a sort of three-lobed plectostele) (Lopes et al., 2020), largest megaspores in the family (*ca.* 1.5 mm; Mickel and Hellwig, 1969, Fig. 5O), and pillared to baculate ornamentation on microspore surfaces (Fig. 5T).

The plastome of *Megaloselaginella* known so far (Zhou et al., 2022) has DR-IR coexisting structure and the intron2 of *ycf*3 (Zhou et al., 2022).

This genus contains about two species in Central and South Americas (Steyermark et al., 1986; Zhou et al., 2016; Hassler, 2022).

Members:

Megaloselaginella exaltata (Kunze) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *L. exaltatum* Kunze, Linn. 9: 8 (1834 [1835]) ≡ *Selaginella exaltata* (Kunze) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 234 (1843) ≡ *Lycopodioides exaltata* (Kunze) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Megaloselaginella gigantea (Steyerm. & A.R. Sm.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella gigantea* Steyerm. & A.R.Sm., Ann. Mo. Bot. Gard. 73(1): 209 (1986).

Subfamily IV. **Sinoselaginelloideae** Li Bing Zhang & X.M. Zhou, ***subfam. nov.*** 中华卷柏亚科 (新拟) – type: *Sinoselaginella* Li Bing Zhang & X.M. Zhou

Plants erect, ascending, or creeping (Fig. 6A, G), with ventral rhizophores (Fig. 6B); sterile leaves dimorphic (Fig. 6A–C, E, G, H); sporophylls monomorphic (Fig. 6D, F); strobili with only one (to a few) megasporophyll at the base (Quanansah, 1988; Zhao et al., 2001); megaspore surfaces verrucate, prominent elements composed by long curved baculate (Fig. 6P) or rope microstructure (Zhou et al., 2015); microspore surfaces rugate (Fig. 6M–O), coarse (Fig. 6Q–T), sometimes with holes on proximal surfaces (Fig. 6Q–S).

The plastomes of Sinoselaginelloideae known so far (Zhou et al., 2022) have the smallest size (78–90 kb) in Selaginellaceae and the plastome structure is more like "network" rather than looping. Except *rrn16* and *rrn23*, most of the plastid tRNA and rRNA genes are lost in Sinoselaginelloideae. Sinoselaginelloideae have the least protein-coding genes in Selaginellaceae (*ca.* 27) (Zhou et al., 2022).

Some species of this subfamily like most of land plant lineages have a low GC content (*ca.* 30%).

This subfamily corresponds to the *Sinensis* group sensu Korall and Kenrick (2004) and Weststrand and Korall (2016a).

It contains three genera: *Austroselaginella*, *Korallia*, and *Sinoselaginella*, occurring in Africa, Asia, Australia, and Indian Ocean islands.

Austroselaginella Li Bing Zhang & X.M. Zhou, gen. nov. 澳洲卷柏属(新拟) – Type: *Austroselaginella australiensis* (Baker) Li Bing Zhang & X.M. Zhou (≡ *Selaginella australiensis* Baker, J. Bot. 21: 144, no. 55 (1883)).

Austroselaginella has creeping plants, monomorphic strobili, and only one (to a few) megasporophyll at the base of strobili (Fig. 6F). *A. australiensis* is very similar to *G. remotifolium* and *G. kraussianum*, but the former has the rhizophores borne on ventral side and non-articulate stems. *Austroselaginella* is also similar to some species with creeping plants in *Korallia*, but the former has the base of ventral leaves not auriculate (Fig. 5E vs. 5H) and microspores without holes on proximal surfaces (Fig. 5T vs. 5Q–S). *Austroselaginella* has very large megaspores (600–750 μm in diam.). Although Korall and Taylor (2006) reported that the megaspore surfaces of *A. australiensis* were strongly reticulate, their recent study (Weststrand and Korall, 2016) clarified that the "reticulate surfaces of megaspores" was probably based on a misidentified specimen. Jermy and Holmes (1998) reported that the megaspore surfaces of *A. australiensis* are faintly reticulate. We did not examine the megaspores of *A. australiensis* but its microspore surfaces are somewhat smooth (Fig. 6T).

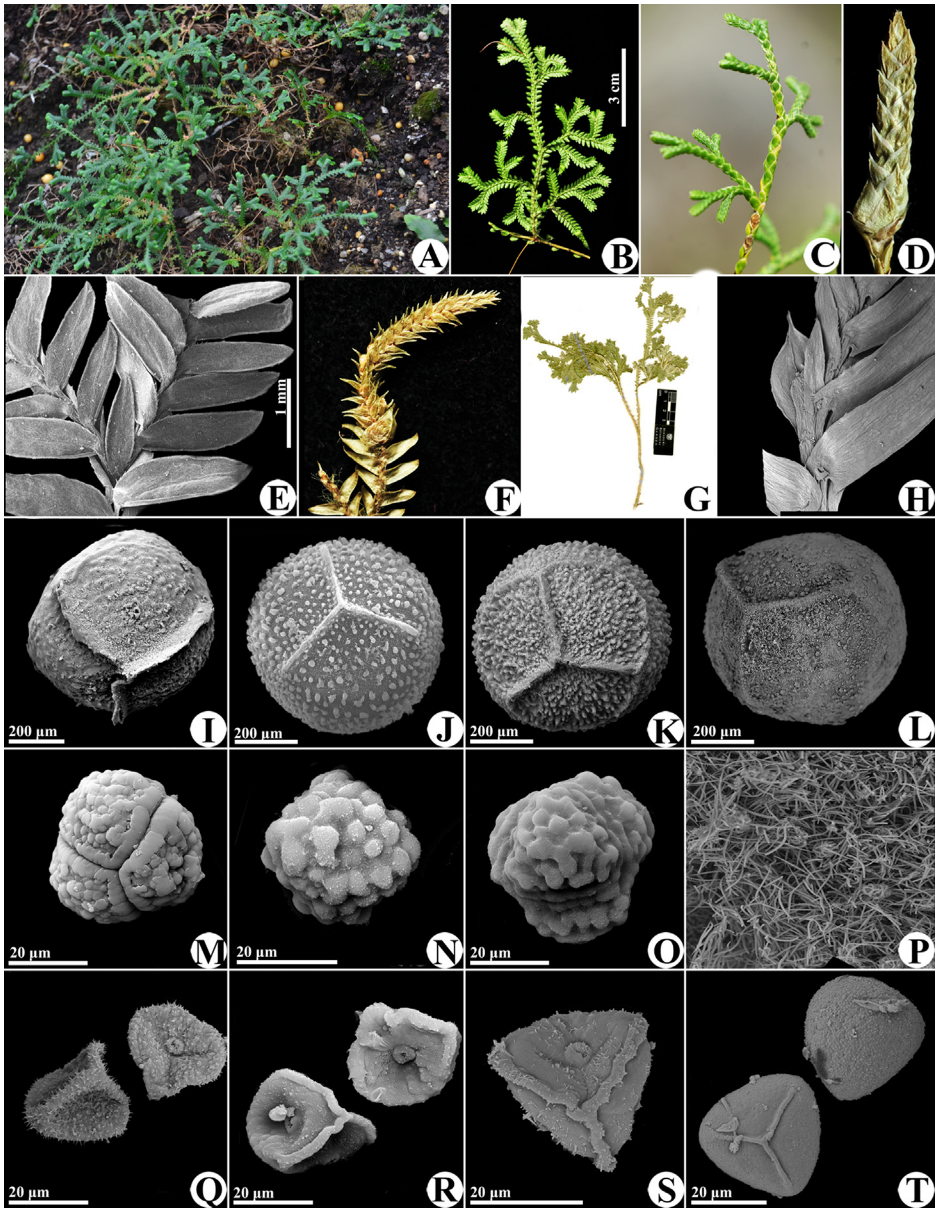

Fig. 6. Morphology of subfamily Sinoselaginelloideae 中华卷柏亚科 (the *Sinensis* group; Weststrand and Korall, 2016b). **A, B, I, and M. *Sinoselaginella sinensis*** (A. Habit; B. Showing part of plant with ventral rhizophore bore on ventral side and strobilus with only one megasporophyll on base; I. Megaspore; M, Microspore). **C, D, J, and N. *S. albocincta*** (C. Part of plant; D. Strobilus with only one megasporophyll at base; J. Megaspore; N. Microspore). **E, F and T. *Austroselaginella australiensis*** (E. Ventral side of part of plant; F. Strobilus with only one megasporophyll (megasporangium) at base; T. Microspore). **K and O. *Sinoselaginella yemensis*** (K. Megaspore; O. Microspore). **L, P and S. *Korallia cataphracta*** (L and P. Megaspore; S. Microspore).

It contains about four species distributed in rain-forested regions of north-eastern Queensland in Australia (Jermy and Holmes, 1998).

Members:

Austroselaginella andrewsii (Jermy & J.S. Holmes) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella andrewsii* Jermy & J.S. Holmes, Fl. Australia 48: 705 (1998).

Austroselaginella australiensis (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella australiensis* Baker, J. Bot. 21: 144, no. 55 (1883) ≡ *Lycopodioides australiensis* (Baker) Kuntze, Rev. Gen. Pl. 1: 825 (1891).

Austroselaginella brisbanensis (F.M. Bailey) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella brisbanensis* F.M. Bailey, Queensl. Fl. Suppl. 62 (1886) ≡ *Lycopodioides brisbanensis* (F.M. Bailey) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Austroselaginella leptostachya (F.M. Bailey) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella leptostachya* F.M. Bailey, Proc. Roy. Soc. Queensl. 1: 13 (1884) ≡ *Selaginella australiensis* var. *Leptostachya* (F.M. Bailey) Domin, Bibl. Bot. 85: 237 (1913).

Korallia Li Bing Zhang & X.M. Zhou, *gen. nov.* 科氏卷柏属(新拟) — Type: *Korallia fissidentoides* (Hook. & Grev.) Li Bing Zhang & X.M. Zhou (≡ *Lycopodium fissidentoides* Hook. & Grev., Enum. Fil. Hook. Bot., Misc. 2: 305, no. 151 (1831)).

= *Selaginella* sect. *Oligomacrosporangiatae* Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanzenf. l(4): 704 (1902) ≡ *Didiclis* subg. *Oligomacrosporangiatae* (Hieron. & Sadeb.) Rothm. in Feddes Repert. Spec. Nov. Regni Veg. 54: 70 (1944)

["*Oligomacrosporangiata*"] – Lectotype (designated by Rothmaler, 1944: 70): *Selaginella fissidentoides* (Hook. & Grev.) Spring.

= *Selaginella* subser. *Monostelicae* Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanzenf. I(4): 704 (1902) non Hieronymus and Sadebeck, 1901 (1902: 673, 708) – Lectotype (designated by Zhou and Zhang, 2015: 1135): *Selaginella fissidentoides* (Hook. & Grev.) Spring.

Etymology:— From *korall*-, in honor of Prof. Petra Korall of Uppsala University, Sweden, for her contributions to the study of ferns in general and that of *Selaginella* in particular (e.g., Korall et al., 1999; Korall and Kenrick, 2002, 2004; Weststrand and Korall, 2016a, b).

In our earlier classification (Zhou and Zhang, 2015), we thought *Selaginella fissidentoides* should be resolved in *Didiclis* and misapplied *S.* sect. *Oligomacrosporangiatae* to *Didiclis*. *Korallia* is a member of the *Sinensis* group and sister to *Austroselaginella* (Weststrand and Korall, 2016; our Figs. S1–S3).

Species of *Korallia* have erect, creeping or ascending plants and often a biauriculate base of ventral leaves (Fig. 6H). The megaspore surfaces are often covered with dense and thin thorns (Fig. 6P). Microspores have a special hole on each proximal district of the proximal surfaces (Fig. 6Q–S)—such structure was never found or reported in other genera in the family.

The master plastome of *Korallia* known so far (Zhou et al., 2022) can mediate 12 isomers through repeats in SC. Almost all genes do not have copies (except *rrn16/23* and *ndhE*) and the GC content is larger than 50% in *Korallia*. *Korallia* is the only genus with two copies of *ndhE* in Selaginellaceae.

Korallia contains about 15 species distributed in Madagascar and adjacent Indian Ocean islands (e.g., Mauritius, Mayotte, Reunion, and Seychelles; Badré, 2008).

Members:

Korallia amphirrhizos (A. Braun ex Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella amphirrhizos* A. Braun ex Hieron., Nat. Pfl. 1(4): 705 (1902) ≡ *S. fissidentoides* var. *amphirrhizos* (A. Braun ex Hieron.) Stefanov. & Rakotondr., Novon 6(2): 208 (1996).

Korallia balfourii (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella balfourii* Baker, Fl. Maurit. 522, no. 2 (1877) ≡ *Lycopodioides balfourii* (Baker) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Korallia cataphracta (Willd.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium cataphractum* Willd., Sp. Pl. 5: 43, no. 62 (1810) ≡ *Selaginella cataphracta* (Willd.) Spring, Flora 21: 209 (1839).

Korallia concinna (Sw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium concinnum* Sw., Syn. Fil. 182, 408, no. 52 (1806) ≡ *Selaginella concinna* (Sw.) Spring, Flora 21: 188, no. 15 (1838).

Korallia distachya (Cordem.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella distachya* Cordem., Bull. Soc. Sc. Arts La Réunion,104 (1890–91).

Korallia fissidentoides (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *L. fissidentoides* Hook. & Grev., Enum. Fil. Hook. Bot., Misc. 2: 305, no. 151 (1831) ≡ *Selaginella fissidentoides* (Hook. & Grev.) Spring, Bull. Acad. Roy. Soc. Bruxelles 8(12): 142 (1841) ≡ *Didiclis fissidentoides* (Hook. & Grev.) Rothm., Fedde, Repert. Spec. Nov. 54: 70 (1944) ≡ *Lycopodioides fissidentoides* (Hook. & Grev.) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Korallia fruticulosa (Bory ex Willd.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium fruticulosum* Bory ex Willd., Sp. Pl. 5: 41, no. 59 (1810) ≡ *Selaginella fruticulosa* (Bory) Spring, Flora 21: 202 (1838).

Korallia obtusa (P. Beauv.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium obtusum* (P. Beauv.) Desv. ex Poir., Lam., Encycl. suppl. 3: 548. (1813 publ. 1814) ≡ *Selaginella obtusa* (P. Beauv.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 228 (1843) ≡ *Lycopodioides obtusa* (P. Beauv.) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Korallia rodriguesiana (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella rodriguesiana* Baker, Fl. Maurit. 523, no. 4 (1877) ≡ *Lycopodioides rodriguesiana* (Baker) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Korallia sechellara (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella sechellarum* Baker, Fl. Maurit. 523, no. 523 (1877) ≡ *Lycopodioides sechellarum* (Baker) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Korallia serrulata (Desv.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium serrulatum* Desv. ex Poir., Lam., Encycl. suppl. 3: 550, no. 78. (1813 publ. 1814) ≡ *Selaginella serrulata* (Desv.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 228, no. 113 (1843).

Korallia sinuosa (Desv.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium sinuosum* Desv. ex Poir., Lam., Encycl. suppl. 3: 558. (1813 publ. 1814) ≡ *Selaginella sinuosa* (Desv.) Alston, J. Bot. 72: 230 (1934).

Korallia sparsifolia (Desv.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium sparsifolium* Desv. ex Poir., Lam., Encycl. suppl. 3: 553, no. 95. (1813 publ. 1814) ≡ *Selaginella sparsifolia* (Desv.) Badré, Fl. Mascar. Ptérid. 1: 45 (2008).

Korallia tereticaulis (Desv.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium tereticaulon* Desv. ex Poir., Lam., Encycl. suppl. 3: 551, no. 85. (1813 publ. 1814) ≡ *Selaginella tereticaulis* (Desv.) Spring, Flora 21: 210 (1838).

Korallia viridula (Bory) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium viridulum* Bory ex Willd., Sp. Pl. 5: 37, no. 50 (1810) ≡ *Selaginella viridula* (Bory) Spring, Flora 21: 190 (1838).

Sinoselaginella Li Bing Zhang & X.M. Zhou, *gen. nov.* 中华卷柏属(新拟) – Type: *S. sinensis* (Desv.) Li Bing Zhang & X.M. Zhou [≡ *Lycopodium sinense* Desv., Mém. Soc. Linn. Paris 6: 189 (1827) ≡ *Selaginella sinensis* (Desv.) Spring, Bull. Acad. Roy. Sci. Bruxelles 10(1): 137 (1843)].

Etymology:— "*Sino*-" derived from *sinensis*, referring to the Chinese distribution of the type species.

Sinoselaginella is part of the *Sinensis* group. It is sister to *Austroselaginella* + *Korallia*. Morphologically, *Sinoselaginella* is xerophytic and has creeping stems (Fig. 6A), rhizophores borne on ventral side in axils of branches (Fig. 6B), intervals throughout the main stem (Fig. 6A and B), only one megasporophyll on the ventral side of the base of strobili (Fig. 6F), large and usually verrucate and tuberculate ornamentation on megaspore surfaces and this prominent elements comprised by ropes (Fig. 6I–K; Zhou et al., 2015), and microspore surfaces with prominent verrucae, and/or somewhat ridges (Fig. 6M–N). Species of *Sinoselaginella* are very similar to some species of *Boreoselaginella*, especially *Sinoselaginella albocincta* and *B. sanguinolenta*, two species with extremely similar appearance (Kung, 1981) and overlapping distribution (Zhang et al., 2013), but *B. sanguinolenta* has strobili with several megasporophylls rather than one (Fig. 4E–G) and rhizophores borne on the dorsal side of stems (Fig. 4D).

Nearly all species in *Sinoselaginella* known so far (Zhou et al., 2022) have protein-coding genes with two or three copies. GC content of the plastome is *ca.* 30% in *Sinoselaginella* which is different from other taxa in Selaginellaceae (Zhou et al., 2022).

Sinoselaginella contains about five species (*Sinoselaginella adunca, S. albocincta*, *Sinoselaginella chuweimingii*, *S. sinensis*, and *Sinoselaginella yemensis*) distributed in China extending to the Arabic area and eastern Africa (Somalia, Ethiopia, Kenya) (Zhang et al., 2013; Fraser-Jenkins et al., 2015, 2017; Zhou et al., 2015).

Members:

Sinoselaginella adunca (A. Braun ex Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella adunca* A. Braun ex Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 674 (1901 publ. 1902).

Sinoselaginella albocincta (Ching ex H.S. Kung) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella albocincta* Ching ex H.S. Kung, Acta Bot. Yunnan. 3(2): 251–252, f. 1: 9–14 (1981) ≡ *Selaginella adunca* ssp. *albocincta* (Ching) Fraser-Jenk., Indian Fern J. 25(1–2): 8 (2008 publ. 2009) ≡ *Lycopodioides albocincta* (Ching ex H.S. Kung) H.S. Kung, Fl. Sichuan. 6: 61 (1988). 白边中华卷柏(新拟)

Sinoselaginella chuweimingii (X.M. Zhou, Z.R. He, Liang Zhang & Li Bing Zhang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella chuweimingii* X.M. Zhou, Z.R. He, Liang Zhang & Li Bing Zhang, Phytotaxa 231(3): 284 (2015). 维明中华卷柏(新拟)

Sinoselaginella sinensis (Desv.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *L. sinense* Desv., Mém. Soc. Linn. Paris 6: 189 (1827) ≡ *Selaginella sinensis* (Desv.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 137, no. 19 (1843) ≡ *Lycopodioides sinensis* (Desv.) Satou, Hikobia 12(3): 269 (1997). 中华卷柏(新拟)

Sinoselaginella yemensis (Sw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium yemense* Sw., Syn. Fil. 182, 407, no. 49, t. 4, f. 4 (1806) ≡ *Selaginella yemensis* (Sw.) Spring ex Decne., Arch. Mus. Paris 2: 191 (1941–42) ≡ *Lycopodioides yemensis* (Sw.) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Subfamily V. **Pulvinielloideae** Li Bing Zhang & X.M. Zhou, ***subfam. nov.*** 垫状卷柏亚科(新拟) – type: *Pulviniella* (Li Bing Zhang & X.M. Zhou) Li Bing Zhang & X.M. Zhou

Plants often rosette-forming (Fig. 7A and B), or erect and tufted when dry (Fig. 7C), with ventral rhizophores; sterile leaves dimorphic, four rows (Fig. 7A); sporophylls monomorphic (Fig. 7D); megaspores surface coarse, usually without obvious ornamentation (Fig. 7E–H); microspores globose, surfaces coarse or non-prominent verruca and granule (Fig. 7I–L); 2n = 20.

The plastome of Pulvinielloideae known so far (Zhou et al., 2022) has DR structure and only one conformation. Genes *rpl*16 tend to pseudogenize, and *trnC*-GCA and *rps18* are lost in

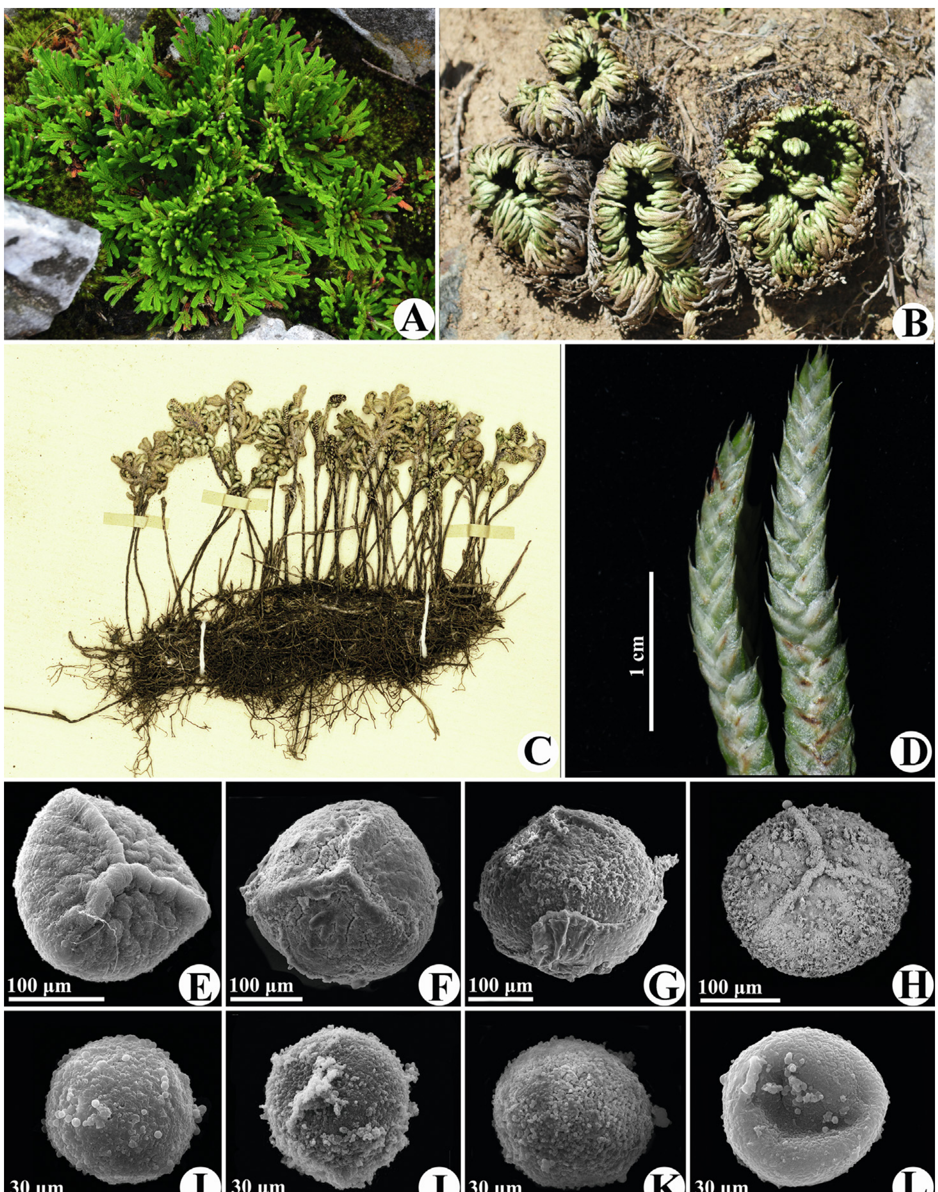

Fig. 7. Morphology of subfamily Pulvinielloideae 垫状卷柏亚科 (*Selaginella* subg. *Pulviniella*; Zhou and Zhang, 2015). **A, B, D, E, and I. *Pulviniella pulvinata*** (A and B. Habit; D. Strobili tetragonal and sporophylls monomorphic; E. Megaspore; I. Microspore). **C, F, and J. *P. digitata*** (C. Plants; F. Megaspore; J. Microspore)**. G and K. *P. imbricata*** (G. Megaspore; K. Microspore). **H and L. *P. stauntoniana*** (H. Megaspore; L. Microspore).

Pulvinielloideae. All *ndh* genes are lost or pseudogenized in Pulvinielloideae.

This subfamily corresponds to *Selaginella* subg. *Pulviniella* sensu Zhou and Zhang (2015).

It contains one genus, *Pulviniella*, occurring in Africa, Asia, and North and Central Americas.

Pulviniella (Li Bing Zhang & X.M. Zhou) Li Bing Zhang & X.M. Zhou, **stat. nov.** 垫状卷柏属 (新拟) – Basionym: *Selaginella* subg. *Pulviniella* Li Bing Zhang & X.M. Zhou, Taxon 64 (6): 1133 (2015) – Type: *Pulviniella pulvinata* (Hook. & Grev.) Li Bing Zhang & X.M. Zhou ≡ *S. pulvinata* (Hook. & Grev.) Maxim.

Pulviniella corresponds to *Selaginella* subg. *Pulviniella* Li Bing Zhang & X.M. Zhou and our data resolved it as sister to the *Sinensis* group (Fig. 1 and S3). However, Weststrand and Korall's (2016a) study found it to be sister to a clade including *S.* subg. *Heterostachys* sensu Zhou and Zhang (2015) and *S.* subg. *Stachygynandrum* sensu Zhou and Zhang (2015).

Most species of *Pulviniella* have rosette habit. The rosette habit evolved at least three times in Selaginellaceae: once in *Pulviniella* (e.g., *S. pulvinata*), once in *Lepidoselaginella* (e.g., *L. lepidophylla* and *L. novoleonensis*), and once in *Selaginella s.s.* (e.g., the *S. pallescens* + *S. nothohybrida* clade), respectively. However, except those in *Pulviniella,* all species with rosette habit in Selaginellaceae have reticulate ornamentation. 2n = 20 or 24 (Jermy et al., 1967; Takamiya,1993; Marcon et al., 2005).

Pulviniella and some species of *Sinoselaginella* often overlap in distribution and share xerophyte habit in China. For example, the *S. chuweimingii-P. pulvinata* pair and the *S. sinensis-P. tamariscana* pair, respectively, usually co-occur in a same habitat in China (Chu et al., 2006; Zhang et al., 2013; our field observations), but they are not sister to each other, which is consistent with morphology.

Pulviniella contains *ca.* 15 species occurring through Africa, Asia, and North & Central Americas (Zhang et al., 2013; Fraser-Jenkins et al., 2015, 2017; Zhou et al., 2015; Yang et al., 2022).

Members:

Pulviniella algida (Jie Yang bis & X.C. Zhang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella algida* Jie Yang bis & X.C. Zhang, Taxon 72: 14–15 (2023). 高寒垫状卷柏(新拟)

Pulviniella bryopteris (L.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium bryopteris* L., Sp. Pl. 2: 1103 (1753) ≡ *Selaginella bryopteris* (L.) Baker, J. Bot. 22: 376 (1884) ≡ *Lycopodioides bryopteris* (L.) Kuntze, Rev. Gen. Pl. 1: 825 (1891) ≡ *Stachygynandrum bryopteris* P. Beauv., Prodr. aethéogam. 109 (1805).

Pulviniella convoluta (Arn.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium convolutum* Arn., Mem. Wern. Nat. Hist. Soc. 5: 199 (1824) ≡ *Lycopodioides convoluta* (Arn.) Kuntze, Rev. Gen. Pl. 1: 826 (1891) ≡ *Selaginella convoluta* (Arn.) Spring, Mart., Fl. Bras. 1 (2): 131 (1840).

Pulviniella digitata (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella digitata* Spring, Mém. Acad. Roy. Sci. Belg. 24: 75 (1850) ≡ *Lycopodioides digitata* (Spring) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Pulviniella graniticola (Jie Yang bis & X.C. Zhang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella graniticola* Jie Yang bis & X.C. Zhang, Taxon 72: 15. 2023. 花岗岩垫状卷柏(新拟)

Pulviniella gypsophila (A.R.Sm. & T. Reeves) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella gypsophila* A.R.Sm. & T. Reeves, Sida 10(3): 211 (1984).

Pulviniella helioclada (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella helicoclada* Alston, Dansk Bot. Ark. 7: 195, t. 78(10–12) (1932), nom. nud., et ex C. Chr., Perrier Cat. 71 (1932).

Pulviniella imbricata (Forssk.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium imbricatum* Forssk., Fl. Aegypt.-Arab. 125: 1 (1775) ≡ *Selaginella imbricata* (Forssk.) Spring ex Decne., Arch. Mus. Hist. Nat. 2: 193, t. 7 (1841) ≡ *Lycopodioides imbricata* (Forssk.) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Pulviniella iridescens (X.C. Zhang & Y.R. Wang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella iridescens* X.C. Zhang & Y.R. Wang, Taxonomy 1: 305. (2021). 彩虹垫状卷柏(新拟)

Pulviniella nubigena (J.P. Roux) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella nubigena* J.P. Roux, Bothalia 38(2): 154 (2008).

Pulviniella orientali-chinensis (Ching & C.F. Zhang ex Hao Wei Wang & W.B. Liao) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella orientali-chinensis* Ching & C.F. Zhang ex Hao Wei Wang & W.B. Liao, Acta Sci. Nat. Univ. Sunyatsenia 61(2): 305 (2022). 华东垫状卷柏(新拟)

Pulvinae pilifera (A. Braun) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella pilifera* A. Braun, Sitz. Ges. Naturf. Freunde, Jan. 1857 ex Index 1866, p. 2 ≡ *Lycopodioides pilifera* (A. Braun) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Pulviniella pseudotamariscina (X.C. Zhang & C.W. Chen) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella pseudotamariscina* X.C. Zhang & C.W. Chen, Guihaia: 42 (10): 1635 (2022).

Pulviniella pulvinata (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium pulvinatum* Hook. & Grev., J. Bot. (Hook.) Kew Misc. 2: 381 (1831) ≡ *Selaginella pulvinata* (Hook. & Grev.) Maxim., Mém. Ac. Imp. Sci. St. Pétersb. 9: 335 (1859) ≡ *Lycopodioides pulvinata* (Hook. & Grev.) H.S. Kung, Fl. Sichuan. 6: 64, t. 18, 1–3 (1988) ≡ *Selaginella tamariscina* var. *pulvinata* (Hook. & Grev.) Alston, Bull. Fan Mem. Inst. Biol. Bot. 5: 271 (1934). 垫状卷柏(新拟)

Pulviniella qinbashanica (Jie Yang bis & X.C. Zhang) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. ≡ *Selaginella pulvinata* subsp. *qinbashanica* Jie Yang bis & X.C. Zhang, Taxon 72: 16–17 (2023). 秦巴垫状卷柏(新拟)

Pulviniella stauntoniana (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella stauntoniana* Spring, Mém. Acad. Roy. Sci. Belg. 24: 71 (1850) ≡ *Lycopodioides stauntoniana* (Spring) Kuntze, Rev. Gen. Pl. 1: 827 (1891). 旱生垫状卷柏(新拟)

Pulviniella tamariscina (P. Beauv.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Stachygynandrum tamariscinum* P. Beauv., Mag. Encycl. 9(5): 483 (1804), also Prodr. aethéogam. 106 (1805) ≡ *Lycopodium tamariscinum* (P. Beauv.) Desv. ex Poir., Lam., Encycl. suppl. 3: 540. (1813 publ. 1814) ≡ *Selaginella tamariscina* (P. Beauv.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 136, no. 9 (1843) ≡ *Lycopodioides tamariscina* (P. Beauv.) H.S. Kung, Fl. Sichuan. 6: 62–64, t. 18, 4–6 (1988). 卷柏.

Subfamily VI. **Lycopodioidoideae** Li Bing Zhang & X.M. Zhou, ***subfam. nov.*** 异穗卷柏亚科(新拟) – type: *Lycopodioides* Kuntze

Plants creeping (Fig. 8B, D–H, K), prostrate, ascending (Fig. 8E), scandent (Fig. 8L) or erect (Fig. 8A, I, J), with ventral rhizophores(Fig. 8D, G); sterile leaves dimorphic (Fig. 8), four rows; sporophylls monomorphic (Fig. 9E, H, J) or dimorphic [non-resupinate (Fig. 9F and G) or resupinate (Fig. 9B–D, I)]; megaspore surfaces often verrucate to tuberculate, few reticulate, smooth (Fig. 9K–N, S–V); microspore surfaces can be cristate, verrucate, granulate, laminate, blunt spiny, baculate, or smooth, depending on different genera (Fig. 9O–R, W, Y, Z); 2n = 16, 18, 20, 32 (Jermy, 1967; Loyal and Kumar, 1984; Takamiya, 1993; Mukhopadhyay and Goswami, 1996; Marcon et al., 2005).

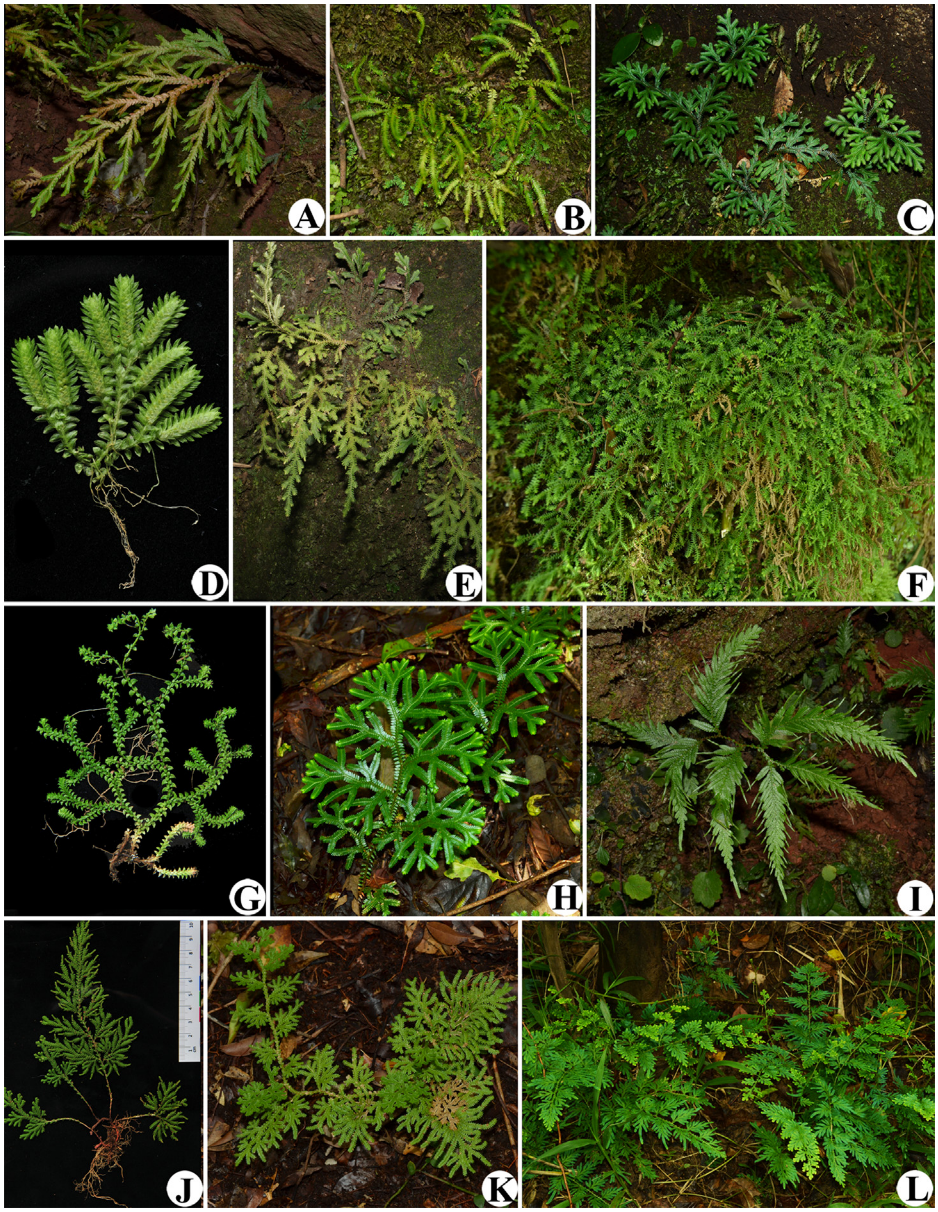

Fig. 8. Growth forms of subfamily Lycopodioidoideae 异穗卷柏亚科 (*Selaginella* subg. *Heterostachys*; Zhou and Zhang, 2015). **A.** ***Hypopterygiopsis bodinieri***; **B.** ***H. heterostachys***; **C.** ***H. monospora***; **D.** ***H. ciliaris***; **E.** ***H. repanda***; **F.** ***H. vaginata***; **G.** ***Lycopodioides nipponica***; **H.** ***Didiclis bisulcata***; **I.** ***D. delicatula***; **J.** ***D. mairei***; **K.** ***D. siamensis***; **L.** ***D. willdenowii***.

This subfamily corresponds to *Selaginella* subg. *Heterostachys* sensu Zhou and Zhang (2015).

Lycopodioidoideae comprise those species with dimorphic or slightly dimorphic and resupinate sporophylls (*Hypopterygiopsis*), dimorphic and non-resupinate sporophylls (most species of *Lycopodioides*), or monomorphic sporophylls (*Valdespinoa* and nearly all species of *Didiclis*).

Traditionally, *Selaginella* subg. *Heterostachys* only contains those species with dimorphic and resupinate sporophylls in *Selaginella* (e.g., Baker, 1883, 1887; Warburg, 1900; Walton and Alston,1938; Jermy, 1986, 1990) before our classification (Zhou and Zhang, 2015). However, morphological analysis shows that species with dimorphic sporophylls are not monophyletic (Zhou et al., 2016) and dimorphic sporophylls have evolved at least 13 times in the family (Fig. 2G).

Based on our study on the phylogeny, gross morphology, spore morphology, and geographic distribution, all species with dimorphic sporophylls and resupinate strobili in the Old World (Asia, Pacific islands, Africa, and Madagascar) should belong to Lycopodioidoideae. However, based on the morphology of megaspores andmicrospores and molecular data, those species with dimorphic sporophylls and resupinate strobili in the New World (mainly in South and Central Americas) are members of Selaginelloideae (see below). The dimorphic sporophylls and resupinate strobili evolved many times independently in Lycopodioidoideae and Selaginelloideae (Fig. 2G and H).

Lycopodioidoideae known so far (Zhou et al., 2022) have the most complicated and diverse plastome structures in Selaginellaceae. Two genera (*Lycopodioides* and *Valdespinoa*) have three ribosomal operon copies and the largest plastome size in Selaginellaceae. All of known plastome structures of Lycopodioidoideae are DR-IR coexisting structure (Zhou et al., 2022).

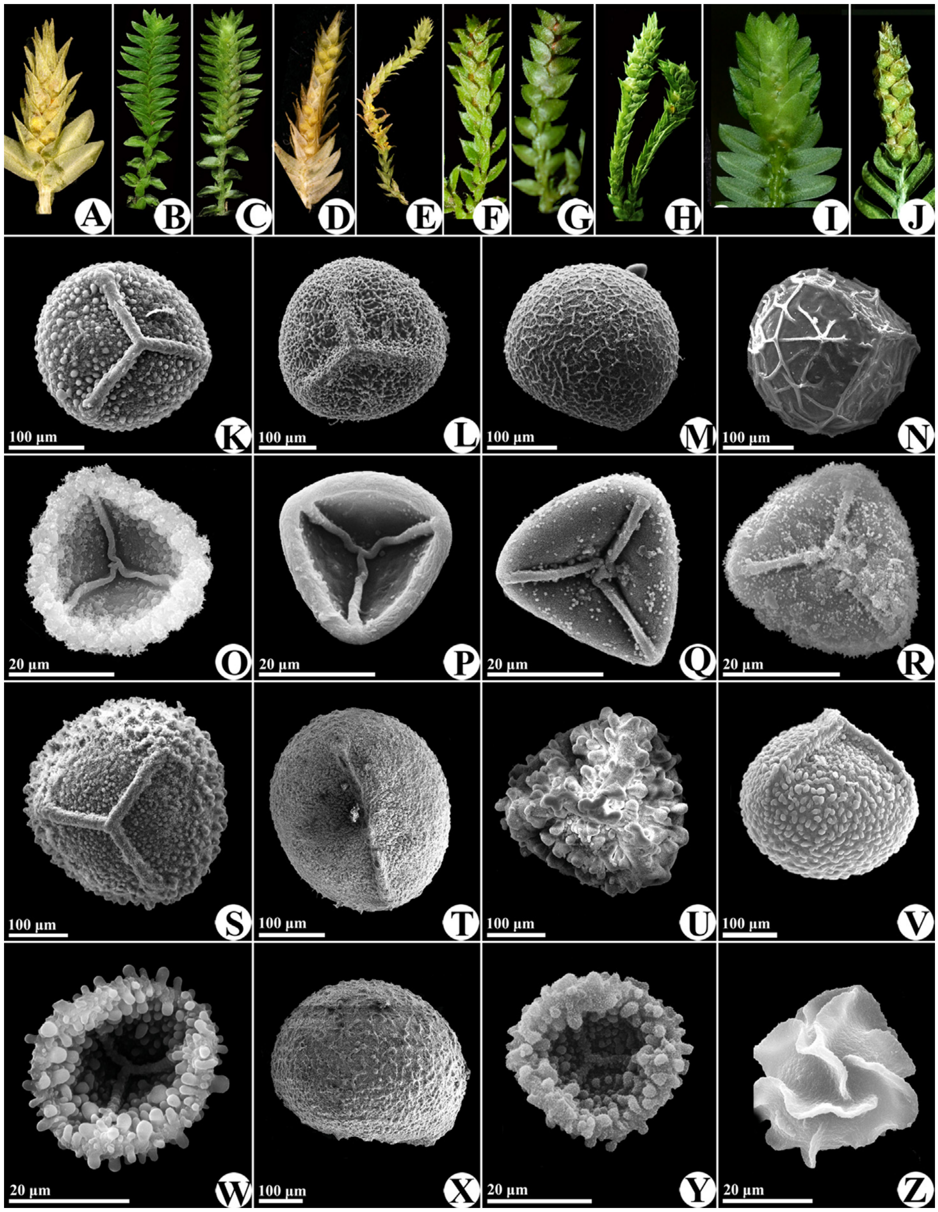

Fig. 9. Morphology of subfamily Lycopodioidoideae 异穗卷柏亚科 (*Selaginella* subg. *Heterostachys*; Zhou and Zhang, 2015). **A. *Hypopterygiopsis monospora*** (A. Strobilus), **B and C. *H. ciliaris*** (B. Dorsal side of strobilus; C. Ventral side of strobilus), **D, K and O. *H. repanda*** (D. Strobilus; K. Megaspore; O. Microspore); **E. *Lycopodioides helvetica*** (E, strobilus); **F and G. *L. nipponica*** (F, Dorsal side of strobilus; G, Ventral side of strobilus); **H, T and X. *Valdespinoa douglosii*** (H. Strobilus; T. Proximal surface of megaspore; X. Distal surface of megaspore), **I. *Didiclis bisulcata*** (I. Strobilus); **J. *D. braunii***; **L and P. *H. neocaledonica*** (L. Megaspore; P. Microspore); **M and Q. *H. arbuscula*** (M. Megaspore; O. microspore); **N and R. *H. ciliaris*** (N. megaspore; R. microspore); **S and W. *H. effusa*** (S. Megaspore; W. Microspore); **U and Y. *Didiclis vogelii*** (U. Megaspore; Y. Microspore)**; V and Z. *D. siamensis*** (V. Megaspore; Z. Microspore).

Lycopodioidoideae contain four genera, *Didiclis*, *Hypopterygiopsis*, *Lycopodioides*, and *Valdespinoa*, occurring in the Old World and New World.

Didiclis P. Beauv. ex Mirb., Hist. Nat. Vég. 3: 477, 4: 314 (1802) 瘤孢卷柏属(新拟) – Type: *Didiclis ornithopodioides* (L.) P. Beauv. ex J. St.-Hil (*Selaginella ornithopodioides* (L.). Spring, Flora 21(14): 216 (1838)).

= *Lycopodium* (unranked) *Platystachya* Hook. & Grev. in Bot. Misc. 2: 380 (1831) ≡ *Selaginella* (unranked) *Platystachyae* (Hook. & Grev.) Spring in Mém. Acad. Sci. Belg. 24: 53 (1850) – Lectotype (designated by Zhou and Zhang, 2015: 1134): *Selaginella chrysocaulos* (Grev. & Hook.) Spring.

= *Selaginella* ser. *Brachystachyae* Warb. in Monsunia 1: 110 (1900) – Type: *Selaginella brachystachya* (Hook. & Grev.) Spring.

= *Lycopodium* (unranked) *Planifolia* Hook. & Grev., Bot. Misc. 2: 382 (1831) ≡ *Selaginella* (unranked) *Planifoliae* (Hook. & Grev.) Spring in Martius, Fl. Bras. 1(2): 118. (1840) – Lectotype (designated by Zhou and Zhang, 2015: 1135): *Lycopodium tetragonostachyum* Wall. ex Grev. & Hook.

= *Selaginella* (unranked) *Pronae* A. Braun, App. Ind. Sem. Hort. Berol. 12 ([1857] 1858) – Lectotype (designated by Zhou and Zhang, 2015: 1135): *Selaginella ciliaris* Spring.

= *Selaginella* ser. *Proniflorae* Warb., Monsunia 1: 108 (1900) – Type: *Selaginella proniflora* (L.) Baker.

Didiclis corresponds to "*Selaginella* sect. *Oligomacrosporangiatae*" sensu Zhou and Zhang (2015). The type of *Selaginella* sect. *Oligomacrosporangiatae*, *S. fissidentoides*, turned out to be a member of the *Sinensis* group (now *Korallia*) shown by Weststrand and Korall (2016a). The type shares one megasporangium only at the base of strobili with the *Sinensis* group (Quansah, 1988; Stefanović et al., 1997; also see above).

Although species of *Didiclis* show high diversity of gross morphology, they share tuberculate or verrucate megaspores and blunt-spiny to lamellate or cristate microspores (Zhou et al., 2015; Wang et al., 2018).

Comparing with other subfamilies and genera, *Didiclis* known so far has the most diverse master conformations ranging from 2 to 10 in their plastomes (Zhou et al., 2022).

Didiclis contains *ca.* 80 species from Asia and some species from Africa (e.g., *Didiclis pervillei*) and one species from America (*D. hoffmannii*) in the subfamily (Fig. S3).

Based on the morphology and phylogeny, *Didiclis* can be divided into six well identifiable groups (the *Braunii* group, the *Bisulcata* group, the *Delicatula* group, the *Pervillei* group, the *Siamensis* group, and the *Willedenowii* group) corresponding to six subclades in the phylogeny.

(1) The *Braunii* group: This group is characterized by xerophytic and erect plants with monomorphic sterile leaves on stem, broadly ovate sporophylls, and sterile leaves usually involute when dry. Based on our field observations and specimen examination, this group contains about five species (*Didiclis braunii*, *D. fulcrata*, *D. mairei*, *D. ostenfieldii*, and *D. pubescens*) in South and Southeast Asia.
(2) The *Delicatula* group: This group is similar to the *Willedenowii* group in having nearly entire leaves (except *D. hoffmannii* from America), erect and suberect plants, but has blunt-spiny ornamentation on microspores. This group contains more than seven species (*Didiclis caudata*, *D. delicatula*, *D. picta*, *D. plana*, *D. mayeri*, *D. stipulata*, and *D. wallichii*).
(3) The *Bisulcata* group: This group is characterized by resupinate and extremely complanate strobili with dimorphic sporophylls, obovate dorsal leaves, and nearly smooth surfaces on megaspores. Dimorphic sporophylls and resupinate strobili evolved independently or reversed in this group. This group contains about five species (*Didiclis bisulcata*, *D. obovata, D. opaca*, *D. pennata*, and *D. soyauxii*) in South and Southeast Asia.
(4) The *Pervillei* group: This group is very similar to the *Braunii* group in having xerophytic habit, erect and pubescent plants, and involute leaves when dry, but species of this group have verrucate ornamentation in microspores and are only distributed in Madagascar and South Africa. This group contains about three species (*Didiclis eublepharis*, *D. pervillei*, and *D. vogelii*).
(5) The *Siamensis* group: This group has long-creeping, ascending or scandent plants. It is similar to some species in the *Willedenowii* group, but has leaf margins ciliolate (*vs.* entire in the *Willedenowii* group), only one vascular bundle (vs. usually 3 vascular bundles in the *Willedenowii* group), and slightly xerophytic habit. This group contains only one species, *Didiclis siamensis*, in Southeast Asia.
(6) The *Willedenowii* group: This group is easily distinguished in having a large plant size (up to 1 m), scandent habit, entire leaves, and lamellate to cristate ornamentation on microspores. This group contains *ca.* 60 species, the most of species in *Didiclis* (e.g., *D. bamleri*, *D. helferi*, *D. limbata*, *D. pseudopaleifera*, *D. uncinata*, *D. viridangula*, *D. willdenowii*, etc.) (Chen et al., 2017; Zhang et al., 2013).

These groups might deserve some taxonomical rank, but more samples need to be included and detailed morphological studies are necessary.

Members:

Didiclis axillifolia (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella axillifolia* Alderw., Bull. Jard. Bot. Buitenz. II, 11: 37 (1913).

Didiclis bamleri (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella bamleri* Hieron., Engl. Bot. Jahrb. 56: 239, no. 51 (1920).

Didiclis bisulcata (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella bisulcata* Spring, Mém. Acad. Roy. Sci. Belg. 24: 259 (1850) ≡ *Lycopodioides bisulcata* (Spring) Kuntze, Rev. Gen. Pl. 1: 826 (1891). 双沟瘤孢卷柏(新拟)

Didiclis braunii (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella braunii* Baker, Gard. Chr. (1867): 783, 1120, no. 24 ≡ *Lycopodioides braunii* (Baker) Kuntze, Rev. Gen. Pl. 1: 826 (1891). 布朗瘤孢卷柏(新拟)

Didiclis buergersiana (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella buergersiana* Hieron., Engl. Bot. Jahrb. 56: 231, no. 30 (1920).

Didiclis canaliculata **(**L.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Stachygynandrum canaliculatum* (L.) P. Beauv., Prodr. aethéogam. 110 (1805) ≡ *Selaginella canaliculata* (L.) Spring, Flora 21: 201, no. 21 (1838) ≡ *Lycopodioides canaliculata* (L.) Kuntze, Rev. Gen. Pl. 1: 824 (1891).

Didiclis caudata (Desv.S) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium caudatum* Desv., Lam., Encycl. suppl. 3: 558 (1813 publ. 1814) ≡ *Selaginella caudata* (Desv.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 144 (1843) ≡ *Selaginella canaliculata* var. *caudata* (Desv.) Warb., Monsunia 1: 107, 122 (1900).

Didiclis commersonii (Spring) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella caudata* var. *commersonii* Spring; Mém. Acad. Roy. Sci. Belgique 24 [Monogr. Lyc. 2]: 140 (1849).

Didiclis conferta (T. Moore) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella conferta* T. Moore, Proc. Roy. Hort. Soc. 1: 133 (1861) ≡ *Lycopodioides conferta* (T. Moore) Kuntze, Rev. Gen. Pl. 1: 826 (1891)

Didiclis decurrens (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella decurrens* Hieron., Engl. & Prantl, Nat. Pfl. 1(4): 703, no. 7 (1901 publ. 1902).

Didiclis delicatula **(**Desv. ex Poir.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium delicatulum* Desv. ex Poir., Lam., Encycl. suppl. 3: 554, no. 99. (1813 publ. 1814) ≡ *Selaginella delicatula* (Desv. ex Poir.) Alston, J. Bot. 70(838): 282 (1932) ≡ *Lycopodioides delicatula* (Desv. ex Poir.) H.S. Kung, Fl. Sichuan. 6: 67–68, t. 20, 1–6 (1988). 薄叶瘤孢卷柏(新拟)

Didiclis dixitii (Madhus. & S. Nampy) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella dixitii* Madhus. & S. Nampy, Nordic J. Bot. 14(5): 527 (1994).

Didiclis dolichoclada (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella dolichoclada* Alston, J. Bot. 70: 64, no. 5 (1932).

Didiclis engleri (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella engleri* Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 704, no. 374. (1901 publ. 1902).

Didiclis eublepharis (A. Braun ex Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella eublepharis* A. Braun ex Hieron., Nat. Pfl. 1 (4): 677 (1902).

Didiclis finium (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella finium* Alderw., Bull. Jard. Bot. Buitenz. II, 16: 52 (1914).

Didiclis fulcrata **(**Buch.-Ham. ex D. Don) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium fulcratum* Buch.-Ham. ex

D. Don, Prodr. Fl. Nepal. 17 (1825) ≡ *Selaginella fulcrata* (Buch.-Ham. ex D. Don) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 231 (1843) ≡ *Lycopodioides fulcrata* (Buch.-Ham. ex D. Don) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Didiclis fulvicaulis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella fulvicaulis* Hieron., Hedwigia 50: 29, no. 21 (1910).

Didiclis furcillifolia (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella furcillifolia* Hieron., Hedwigia 50: 31, no. 22 (1910).

Didiclis gastrophylla (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella gastrophylla* Warb., Monsunia 1: 107, 121, no. 103, t. 4, f. D (1900).

Didiclis gaudichaudiana (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella gaudichaudiana* Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 145, no. 72 (1843).

Didiclis gracilis (T. Moore) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella gracilis* T. Moore, Gard. Chr. 25, 1: 752, 2: 407 (1886).

Didiclis hainanensis (X.C. Zhang & Noot.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella hainanensis* X.C. Zhang & Noot., Bot. J. Linn. Soc. 148(3): 323 (2005). 海南瘤孢卷柏(新拟)

Didiclis helferi (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella helferi* Warb., Monsunia 1: 107, 121, no. 106 (1900). 攀缘瘤孢卷柏(新拟)

Didiclis hewittii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella hewittii* Hieron., Hedwigia 51: 262, no. 12 (1911 publ. 1912).

Didiclis hindsii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella hindsii* Hieron., Engl. Bot. Jahrb. 50: 2, 43, no. 18 (1913).

Didiclis hochreutineri (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella hochreutineri* Hieron., Ann. Jard. Cons. Bot. Genève 15–16: 228–230 (1912).

Didiclis hoffmannii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella hoffmannii* Hieron., Hedwigia 41: 184 (1902).

Didiclis inaequalifolia (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium inequalifolium* Hook. & Grev., J. Bot. (Hook.) Kew Misc. 2. 391 (1831) ≡ *Selaginella inaequalifolia* (Hook. & Grev.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 145 (1843) ≡ *Lycopodioides inaequalifolia* (Hook. & Grev.) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Didiclis ingens (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella ingens* Alston, J. Bot. 72: 229 (1934).

Didiclis kittyae (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella kittyae* Alderw., Bull. Jard. Bot. Buitenz. II, 7: 35 (1912).

Didiclis lacerata (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella lacerata* Warb., Monsunia 1: 106, 120, no. 97 (1900).

Didiclis latupana (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella latupana* Alderw., Bull. Jard. Bot. Buitenz. II, 16: 54 (1914).

Didiclis limbata (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella limbata* Alston, J. Bot. 70(831): 62 (1932). 具边瘤孢卷柏(新拟)

Didiclis lobbii (Veitch ex A. Braun) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella lobbii* Veitch ex A. Braun, Ind. Sem. Hort. Berol., 20 (1858) ≡ *Lycopodioides lobbii* (Veitch ex A. Braun) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Didiclis mairei (H. Lév.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella mairei* H. Lév., Sert. Yunnan. 299 (1916). 狭叶瘤孢卷柏(新拟)

Didiclis maxima (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella maxima* Alderw., Bull. Jard. Bot. Buitenz. II, 16: 53 (1914).

Didiclis mayeri (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella mayeri* Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 700, no. 343. (1901 publ. 1902).

Didiclis megalura (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella megalura* Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 702, no. 358 (1901 publ. 1902).

Didiclis megastachya (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella megastachya* Baker, J. Bot. 23: 20, no. 202 (1885) ≡ *Lycopodioides megastachya* (Baker) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Didiclis obovata (S.Y. Dong) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella obovata* S.Y. Dong, Syst. Bot. 47(1): 88 (2022). 倒卵叶瘤孢卷柏(新拟)

Didiclis opaca (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella opaca* Warb., Monsunia 1: 108, 122, no. 112 (1900).

Didiclis ornithopodioides (L.) Spring Basionym: *Lycopodium ornithopodioides* L., Sp. Pl. 2: 1105, no. 23 (1753) ≡ *Selaginella ornithopodioides* (L.) Spring, Flora 21: 216, no. 25 (1838) ≡ *Lycopodioides ornithopodioides* (L.) Kuntze, Rev. Gen. Pl. 1: 824 & 827 (1891) ≡ *Stachygynandrum ornithopodioides* (L.) P. Beauv., Prodr. aethéogam. 110 (1805).

Didiclis ostenfeldii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella ostenfeldii* Hieron., Bull. Herb. Boiss. II, 5: 721, no. 98 (1905).

Didiclis padangensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella padangensis* Hieron., Hedwigia 50: 34, no. 23 (1910).

Didiclis pennata (D. Don) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium pennatum* D. Don, Prodr. Fl. Nepal. 18 (1825) ≡ *Selaginella pennata* (D. Don) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 232 (1843) ≡ *Lycopodioides pennata* (D. Don) Kuntze, Rev. Gen. Pl. 2: 827 (1891). 拟双沟瘤孢卷柏(新拟)

Didiclis permutata (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella permutata* Hieron., Hedwigia 50: 24, no. 19 (1910).

Didiclis pervillei (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella pervillei* Spring, Mém. Acad. Roy. Sci. Belg. 24: 169 (1850) ≡ *Lycopodioides pervillei* (Spring) Kuntze, Rev. Gen. Pl. 1: 825 (1891).

Didiclis picta (Griff.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium pictum* Griff. ex Baker, J. Bot. 23: 19 (1885) ≡ *Selaginella picta* (Griff.) A. Braun ex Baker, J. Bot. 23(265): 19 (1885) ≡ *Lycopodioides picta* (Griff.) Kuntze, Rev. Gen. Pl. 1: 827 (1891). 黑顶瘤孢卷柏(新拟)

Didiclis plana (Desv. ex Poir.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium planum* Desv. ex Poir., Lam., Encycl. suppl. 3: 554, no. 98. (1813 publ. 1814) ≡ *Selaginella plana* (Desv. ex Poir.) Hieron., Nat. Pfl. 1(4): 703 (1901).

Didiclis polystachya (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella wallichii* var. *polystachya* Warb., Monsunia 1: 106 (1900) ≡ *Selaginella polystachya* (Warb.) Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 702, no. 362. (1901 publ. 1902).

Didiclis praetermissa (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella praetermissa* Alston, J. Bot. 70: 65 (1932).

Didiclis pseudopaleifera (Hand.-Mazz.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella pseudopaleifera* Hand.-Mazz., Sitzungsber. Akad. Wiss. Wien, 61: 82 (1924). 耳叶瘤孢卷柏(新拟)

Didiclis pubescens (Wall. ex Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium pubescens* Wall., Num. List no. 123 (1829), nomen, ex Hook. & Grev., Enum. Fil. J. Bot. (Hook.)

Kew Misc. 1: 383, no. 103 (1831) ≡ *Selaginella pubescens* (Wall. ex Hook. & Grev.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 225 (1843). 二歧瘤孢卷柏(新拟)

Didiclis rechingeri (Hieron. ex Rech.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella rechingeri* Hieron. ex Rech., Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 89: 486 (1914).

Didiclis retroflexa (v.A.v.R.) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella axillifolia* var. *retroflexa* v.A.v.R., Bull. Jard. Bot. Buit. II, 11: 38. (1913).

Didiclis schlechteri (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella schlechteri* Hieron., Bot. Jahrb. Syst. 50: 2, 41, no. 17 (1913).

Didiclis semicordata (Wall. ex Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium semicordatum* Wall., (Cat. n. 126-3, 11 & 13 (1829), nom. nud.) ex Hook. & Grev., J. Bot. (Hook.) Kew Misc. 2: 396 (1831) ≡ *Lycopodioides semicordata* (Wall. ex Hook. & Grev.) Kuntze, Rev. Gen. Pl. 1: 827 (1891) ≡ *Selaginella semicordata* (Wall. ex Hook. & Grev.) Spring, Mart., Fl. Bras. 1 (2): 122 (1840).

Didiclis siamensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella siamensis* Hieron., Bot. Tidsskr. 24: 113 (1901). 泰国瘤孢卷柏(新拟)

Didiclis soyauxii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella soyauxii* Hieron., Engl. & Prantl, Nat. Pfl. 1(4): 697, no. 305. (1901 publ. 1902).

Didiclis stipulata (Blume) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium stipulatum* Blume, Enum. Pl. Jav. 2: 268, no. 18 (1830) ≡ *Selaginella stipulata* (Blume) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 145, no. 70 (1843).

Didiclis subbiflora (Hieron ex Brause) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. ≡ *Selaginella gracilis* var. *subbiflora* Hieron ex Brause, Engl. Bot. Jahrb. 56: 238, no. 47. (1920).

Didiclis trichoclada (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella trichoclada* Alston, J. Bot. 70: 63, no. 3 (1932). 毛枝瘤孢卷柏(新拟)

Didiclis tylophora (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella tylophora* Alderw., Bull. Jard. Bot. Buitenz. II, 16: 50 (1914).

Didiclis uncinata (Desv. ex Poir.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium uncinatum* Desv. ex Poir., Lam., Encycl. Suppl. 3: 558 (1814) ≡ *Lycopodioides uncinata* (Desv.) Kuntze, Rev. Gen. Pl. 1: 825 (1891) ≡ *Selaginella uncinata* (Desv. ex Poir.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 141 (1843). 翠云草.

Didiclis usterii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella usterii* Hieron., ex Usteri, Beitr. Phil. Veg., 135 (1905), et Leafl. Phil. Bot. 6: 2055 (1913).

Didiclis velutina (Ces.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella velutina* Ces., Rec. Ac. Sci. Nap. 16: 28, 31 (1877).

Didiclis victoriae (J.W. Moore) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella victoriae* J.W. Moore, Cat. n. 143: 8, t. 6 (1878) ≡ *Lycopodioides victoriae* (J.W. Moore) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Didiclis viridangula (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella viridangula* Spring, v. Heurck, Pl. Nov., 29 (1870) ≡ *Lycopodioides viridangula* (Spring) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Didiclis vogelii (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella vogelii* Spring, Monogr. Lyc. 2: 170, no. 111 (1850).

Didiclis wallichii (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium wallichii* Hook. & Grev., Enum. Fil. J. Bot. (Hook.) Kew Misc. 2: 384, no. 106 (1831) ≡ *Selaginella wallichii* (Hook. & Grev.) Spring, Mart., Fl. Bras. 1 (2): 124 (1840). 瓦氏瘤孢卷柏(新拟)

Didiclis willdenowii (Desv.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium willdenovii* Desv. ex Poir., Lam., Encycl. suppl. 3: 540, 552, no. 87. (1813 publ. 1814) ≡ *Selaginella willdenowii* (Desv.) Baker, Gard. Chr. 783, 950 (1867) ≡ *Lycopodioides willdenowii* (Desv.) Kuntze, Rev. Gen. Pl. 1: 827 (1891). 藤瘤孢卷柏(新拟)

Hypopterygiopsis Sakurai, Bot. Mag. (Tokyo) 57: 255 (1943) 异穗卷柏属(新拟) – Type: *Hypopterygiopsis reptans* Sakurai, Bot. Mag. (Tokyo) 57: 255 (1943) (≡ *Selaginella sakuraii* H.A. Mill.).

= *Selaginella* ser. *Suberosae* Warb. in Monsunia 1: 110 (1900) – Type: *Selaginella suberosa* Spring.

= *Selaginella* (unranked) *Erectae* A. Braun in App. Ind. Sem. Hort. Berol. 11 ([1857] 1858) – Type: *Selaginella inaequalifolia* Spring.

= *Selaginella* (unranked) *Scandentes* A. Braun in App. Ind. Sem. Hort. Berol. 11 ([1857] 1858) ≡ *Selaginella* ser. *Scandentes* (A. Braun) Baker in J. Bot. Lond. 21: 4 (1883) – Lectotype (designated here): *Selaginella laevigata* Spring (= *S. willdenowii* (Desv. ex Poir.) Baker).

= *Selaginella* ser. *Sarmentosae* Baker in J. Bot. Lond. 21: 4 (1883) – Lectotype (designated by Zhou and Zhang, 2015: 1135): *Selaginella inaequalifolia* Spring.

= *Selaginella* subser. *Pleurophyllae* Warb. in Monsunia 1: 106 (1900) – Lectotype (designated by Zhou and Zhang, 2015: 1135): *Selaginella willdenowii* (Desv. ex Poir.) Baker.

= *Selaginella* ser. *Bisulcatae* Warb. in Monsunia 1: 108 (1900) – Type: *Selaginella bisulcata* Spring.

= *Selaginella* ser. *Pleiostelicae* Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanzenf. I(4): 700. (1902) ≡ *Lycopodioides* sect. *Pleiostelica* (Hieron. & Sadeb.) Rothm. in Feddes Repert. Spec. Nov. Regni Veg. 54: 69 (1944), "*Pleiostele*" – Lectotype (designated by Rothmaler, 1944: 69): *Selaginella uncinata* (Desv. ex Poir.) Spring.

The type of *Hypopterygiopsis* was described as a "moss" species (Sakurai, 1943) but it turned out to be a Selaginellaceae (Miller, 1967). Our examination of the type confirmed this. The type is not sampled in our molecular work and is assigned here based on the morphology.

This genus contains about 170 species in Africa and Asia. Based on the synapomorphy of strobili with dimorphic sporophylls, we combined *Selaginella* sect. *Heterostachys* and *S.* sect. *Tetragonostachyae* sensu Zhou and Zhang (2015) to form *Hypopterygiopsis* here. Within *Hypopterygiopsis*, we recognize two sections.

Hypopterygiopsis sect. ***Hypopterygiopsis*** 藓状异穗卷柏组(新拟)

= *Selaginella* (unranked) *Tetragonostachyae* (Hook. & Grev.) Spring in Mém. Acad. Sci. Belg. 24: 53 (1850). Basionym: *Lycopodium* (unranked) *Tetragonostachya* Hook. & Grev. in Bot. Misc. 2: 382 (1831) ≡ *S.* sect. *Tetragonostachyae* (Hook. & Grev.) Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanzenf. 1(4): 669 (1902) ≡ *S.* sect. *Tetragonostachyae* (Hook. & Grev.) Rothm. in Feddes Repert. Spec. Nov. Regni Veg. 54: 68 (1944), "*Tetragonostachya*" ≡ *Lycopodioides* subg. *Tetragonostachya* (Hook. & Grev.) Tzvel. in Novosti Sist. Vyssh. Rast. 36: 25 (2004) – Type: *L. tetragonostachyum* Wall. ex Grev. & Hook. [≡ *Hypopterygiopsis tetragonostachya* (Wall. ex Grev. & Hook.) Li Bing Zhang and X.M. Zhou].

This section corresponds to *Selaginella* sect. *Tetragonostachyae* sensu Zhou and Zhang (2015).

Based on the evolution of strobilus morphology, monomorphic sporophylls are reversed in this section. Although some species from Pacific islands have monomorphic to submonomorphic sporophylls, they have same megaspores as those species with dimorphic sporophylls in Asia. Species of this section have megaspore surfaces reticulate (*Tetragonostachyae* type-1 and type-2 with very fine muri and open meshes: Fig. 9L–N) and usually microspore surfaces smooth (Fig. 9P and Q), verrucate (Fig. 9O, R) or baculate (*S. ciliaris*; Zhou et al., 2015).

This section contains two well-supported clades in our phylogenetic analysis. One clade contains species with monomorphic sporophylls (e.g., *Hypopterygiopsis arbuscula*, *Hypopterygiopsis kanehirae, Hypopterygiopsis whitmeei*) mainly from Pacific islands (Kato, 2008; Chen et al., 2017), and the other contains species with strongly (*Hypopterygiopsis ciliaris* and *Hypopterygiopsis xipholepis*) or slightly dimorphic (*Hypopterygiopsis repanda* and *Selaginella vaginata*) sporophylls mainly in Asia and some in Africa and Madagascar (Figs. S1–S3) (Quansah and Thomas, 1985; Stefanović, 1997; Zhang et al., 2013).

Hypopterygiopsis sect. ***Heterostachys*** (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. 异穗卷柏组(新拟) – Basionym: *Selaginella* subg. *Heterostachys* Baker in J. Bot. Lond. 21: 3 (1883) ≡ *Selaginella* sect. *Heterostachys* (Baker) Li Bing Zhang & X.M. Zhou, Taxon 64(6): 1134 (2015) – Lectotype (designated by Jermy, 1986: 118): *Hypopterygiopsis heterostachys* (Baker) Li Bing Zhang & X.M. Zhou (≡ *H. heterostachys* (Baker) Li Bing Zhang & X.M. Zhou).

This section corresponds to *Selaginella* sect. *Heterostachys* sensu Zhou and Zhang (2015). This section contains the most species with resupinate strobili and dimorphic sporophylls from Asia and Africa (Quansah and Thomas, 1985; Stefanović, 1997; Zhang et al., 2013).

Morphologically, *Selaginella* sect. *Heterostachys* has often creeping (Fig. 8B and C), sometimes ascending or erect plants (Fig. 8A); resupinate strobili and dimorphic sporophylls (Fig. 9A); megaspore surfaces papillate, tuberculate, and verrucate (Fig. 9S, U; Zhou et al., 2015), sometimes elements connected (9U); and microspore surfaces often verrucate, gemmulate, and spherulate (Fig. 9W–Y), rarely few tuberculate and rugate (Zhou et al., 2015).

Although dimorphic sporophylls and resupinate strobili also exist in *Hypopterygiopsis* sect. *Hypopterygiopsis* and some America species of *Selaginella s.s.* (see below), these species of the latter usually have megaspores with reticulate ornamentation (Figs. 9 and 10; Korall and Taylor 2006; Bauer et al., 2016; Valdespino (2017c)).

Members of the genus:

Hypopterygiopsis abyssinica (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella abyssinica* Spring, Monogr. Lyc. 2: 99, no. 44 (1850) ≡ *Selaginella goudotiana* var. *abyssinica* (Spring) Bizzarri, Webbia 29: 585 (1975) ≡ *Lycopodioides abyssinica* (Spring) Kuntze, Rev. Gen. Pl. 1: 825 (1891).

Hypopterygiopsis albociliata (P.S. Wang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella albociliata* P.S. Wang, J. Arnold Arbor. 71(2): 269 (1990). 白毛异穗卷柏(新拟)

Hypopterygiopsis alutacea (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella alutacea* Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 233, no. 154 (1843) ≡ *Lycopodioides alutacea* (Spring) Kuntze, Rev. Gen. Pl. 1: 825 (1891).

Hypopterygiopsis amblyphylla (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella amblyphylla* Alston, Bull. Fan Mem. Inst. Biol. Bot.5(6): 287–288 (1934). 钝叶异穗卷柏(新拟)

Hypopterygiopsis angustifolia (Hieron. ex Jeanpert) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella usta* var. *angustifolia* Hieron. ex Jeanpert, Bull. Mus. Paris 17: 579 (nomen) (1911).

Hypopterygiopsis antimonanensis (B.C. Tan & Jermy) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella antimonanensis* B.C. Tan & Jermy, Fern Gaz. 12(3): 170 (1981).

Hypopterygiopsis apoensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella apoensis* Hieron., Elmer, Leafl. Phil. Bot., 6: 2023, no. 18 (1913).

Hypopterygiopsis arbuscula (Kaulf.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium arbusculum* Kaulf., Enum. Fil. 19 (1824) ≡ *Selaginella arbuscula* (Kaulf.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 227 (1843) ≡ *Lycopodioides arbuscula* (Kaulf.) Kuntze, Rev. Gen. Pl. 1: 825 (1891).

Hypopterygiopsis arbusculoides (J.W. Moore) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella arbusculoides* J.W. Moore, Bull. Bernice P. Bishop Mus. 102: 15 (1933).

Hypopterygiopsis aristata (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella aristata* Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 232, no. 152 (1843) ≡ *Selaginella circinalis* var. *aristata* C. Presl, Bot. Bem. 153 (1845).

Hypopterygiopsis atimonanensis (B.C. Tan & Jenny) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella atimonanensis* B.C. Tan & Jenny, Fern Gaz. 12(3): 170 (1981).

Hypopterygiopsis auquieri (Bizzarri) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella auquieri* Bizzarri, Bull. Jard. Bot. Belg. 51(1–2): 220 (1981).

Hypopterygiopsis austro-orientalis (H.J. Wei & X.M. Zhou) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella austro-orientalis* H.J. Wei & X.M. Zhou; Phytotaxa 579(2): 91 (2023). 东南异穗卷柏(新拟)

Hypopterygiopsis bankii (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella banksii* Alston; Bull. Bernice P. Bishop Mus. 93: 15, 83 (1932).

Hypopterygiopsis beccariana (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella beccariana* Baker, J. Bot. 23: 154, no. 254 (1885) ≡ *Lycopodioides beccariana* (Baker) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Hypopterygiopsis behrmanniana (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella behrmanniana* Hieron., Engl. Bot. Jahrb. 56: 233 (1920).

Hypopterygiopsis bemarahensis (Stefanović & Rakotondr.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella bemarahensis* Stefanović & Rakotondr., Novon 6(2): 203 (1996).

Hypopterygiopsis blepharophylla (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella blepharophylla* Alston, Mém. Inst. Fr. Afr. Noire 50: 40, t. 6, ff. 9–15 (1957).

Hypopterygiopsis bodinieri (Hieron. ex Christ) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella bodinieri* Hieron. ex Christ, Bull. Ac. Géogr. Bot. Mans 11: 273, no. 109 (1902), nomen, et Hedwigia 43: 6, no. 25 (1904). 大叶异穗卷柏(新拟)

Hypopterygiopsis boninensis (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella boninensis* Baker, J. Bot. 23 (270): 178 (1885) ≡ *Lycopodioides boninensis* (Baker) Kuntze, Rev. Gen. Pl. 1: 826 (1891). 小笠原异穗卷柏(新拟)

Hypopterygiopsis brachystachya (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium brachystachyum* Hook. & Grev., J. Bot. (Hook.) Kew Misc. 3:107 (1833) ≡ *Selaginella brachystachya* (Hook. & Grev.) Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 232 (1843) ≡ *Lycopodioides brachystachya* (Hook. & Grev.) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Hypopterygiopsis buchholzii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella buchholzii* Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 696, no. 272 (1901 publ. 1902).

Hypopterygiopsis burbidgei (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella burbidgei* Baker, J. Bot. 23: 154, no. 253 (1885).

Hypopterygiopsis busuensis (Alderw.) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella darmandvillei* var. *busuensis*Alderw.; Bull. Jard. Bot. Buitenzorg, sér. 2, 16. 50 (1914).

Hypopterygiopsis calcicola (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella calcicola* Hieron., Hedwigia 51: 258, no. 9 ((1911) 1912).

Hypopterygiopsis calostachya (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium calostachyum* Hook. & Grev., Enum. Fil. J. Bot. (Hook.) Kew Misc. 3: 108 (1833) ≡ *Selaginella calostachya* (Hook. & Grev.) Alston, J. Bot. 70: 65, no. 8 (1932).

Hypopterygiopsis cataractarum (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella cataractarum* Alston, Proc. Nat. Inst. Sci. India 11: 228 (1945).

Hypopterygiopsis chaetoloma (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella chaetoloma* Alston, J. Bot. 70: 67, no. 12 (1932). 毛边异穗卷柏(新拟)

Hypopterygiopsis chaii (Jermy) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella chaii* Jermy, Kew Bull. 41(3): 551 (1986).

Hypopterygiopsis chingii (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella chingii* Alston, Jour. Bot. 70: 66, no. 10 (1932). 秦氏异穗卷柏(新拟)

Hypopterygiopsis chrysocaulos (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium chrysocaulon* Hook. & Grev., Enum. Fil. J. Bot. (Hook.) Kew Misc. 2: 401, no. 182 (1831) ≡ *Selaginella chrysocaulos* (Hook. & Grev.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 232 (1843) ≡ *Lycopodioides chrysocaulos* (Hook. & Grev.) H.S. Kung, Fl. Sichuan. 6: 78 (1988). 块茎异穗卷柏(新拟)

Hypopterygiopsis chrysorrhizos (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella chrysorrhizos* Spring, Mém. Acad. Roy. Sci. Belg. 24 (2): 251 (1850) ≡ *Lycopodioides chrysorhiza* (Spring) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Hypopterygiopsis ciliaris (Retz.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium ciliare* Retz., Obs. Bot. 5: (1789) ≡ *Selaginella ciliaris* (Retz.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 231 (1843) ≡ *Lycopodioides ciliaris* (Retz.) Kuntze, Rev. Gen. Pl. 1: 826 (1891). 睫毛异穗卷柏(新拟)

Hypopterygiopsis ciliata (Alston) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella selangorensis* var. *ciliata* Alston, Gard. Bull. Straits Settlem. 8: 44 (1934).

Hypopterygiopsis cochleata (Hook. & Grev.) Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium cochleatum* Hook. & Grev., Enum. Fil. J. Bot. (Hook.) Kew Misc. 2: 395, no. 153 (1831) ≡ *Lycopodioides cochleata* (Hook. & Grev.) Kuntze, Rev. Gen. Pl. 1: 826 (1891) ≡ *Selaginella cochleata* (Hook. & Grev.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 143, no. 55 (1843).

Hypopterygiopsis compta (Hand.-Mazz.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella compta* Hand.-Mazz., Symb. Sin. 6: 9, pl. 2. (1929). 缘毛异穗卷柏(新拟)

Hypopterygiopsis coonooriana (R.D. Dixit) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella coonooriana* R.D. Dixit, Bull. Bot. Surv. India 25(1–4): 223 (1983 publ. 1985).

Hypopterygiopsis coriaceifolia (X.M. Zhou, N.T. Lu & Li Bing Zhang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella coriaceifolia* X.M. Zhou, N.T. Lu & Li Bing Zhang, Phytotaxa 453(2): 125 (2020).

Hypopterygiopsis crassipes (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella crassipes* Spring, Monogr. Lyc. 2: 243, no. 181 (1850) ≡ *Lycopodioides crassipes* (Spring) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Hypopterygiopsis curtisii (Ridl.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella curtisii* Ridl., J. Roy. As. Soc., Str. Br., No. 80: 148, no. 2 (1919).

Hypopterygiopsis daozhenensis (Li Bing Zhang, Q.W. Sun & Jun H. Zhao) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella daozhenensis* Li Bing Zhang, Q.W. Sun & Jun H. Zhao, Phytotaxa 207(2): 187 (2015). 道真异穗卷柏(新拟)

Hypopterygiopsis darmandvillei (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella darmandvillei* Alderw., Bull. Jard. Bot. Buitenz. II, 1: 23–24 (1911).

Hypopterygiopsis decipiens (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella decipiens* Warb., Monsunia 1: 127 (1900).

Hypopterygiopsis densiciliata (X.M. Zhou, Liang Zhang & Bo Xu) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella densiciliata* X.M. Zhou, Liang Zhang & Bo Xu, PhytoKeys 227: 135–149 (2023). 密毛异穗卷柏(新拟)

Hypopterygiopsis devolii (H.M. Chang, P.F. Lu & W.L. Chiou) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella devolii* H.M. Chang, P.F. Lu & W.L. Chiou, Blumea 56(1): 21 (2011). 棣氏异穗卷柏(新拟)

Hypopterygiopsis dianzhongensis (X.C. Zhang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella dianzhongensis* X.C. Zhang, PhytoKeys 118: 77 (2019). 滇中异穗卷柏(新拟)

Hypopterygiopsis drepanophylla (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella drepanophylla* Alston, J. Bot. 70(831): 66–67 (1932). 镰叶异穗卷柏(新拟)

Hypopterygiopsis dulongjiangensis (W.M. Chu) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella effusa* var. *Dulongjiangensis* W.M. Chu, Fl. Yunnan. 20: 718 (2006). 独龙江异穗卷柏(新拟)

Hypopterygiopsis effusa (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella effusa* Alston, J. Bot. 70: 65, no. 9 (1932). 疏松异穗卷柏(新拟)

Hypopterygiopsis elegantissima (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella elegantissima* Warb., Monsunia 1: 111, no. 175 (1900).

Hypopterygiopsis eschscholzii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella eschscholzii* Hieron., Elmer, Leafl. Phil. Bot. 6: 2041, no. 26 (1913).

Hypopterygiopsis exasperata (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella exasperata* Warb., Monsunia 1: 109, 126, no. 139 (1900).

Hypopterygiopsis firmula (A. Braun ex Kuhn) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella firmula* A. Braun ex Kuhn; Verh. K. K. Zool.-Bot. Ges. Wien 19: 585, no. 132 (1869).

Hypopterygiopsis goudotiana (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella goudotiana* Spring, Bull. Acad. Roy. Soc. Bruxelles 8 (12): 140 (1841) ≡ *Lycopodioides goudotiana* (Spring) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Hypopterygiopsis heterostachys (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella heterostachys* Baker, J. Bot. 23: 177, no. 264 (1885) ≡ *Lycopodioides heterostachya* (Baker) Kuntze, Rev. Gen. Pl. 1: 826 (1891). 异穗卷柏.

Hypopterygiopsis hildebrandtii (A. Braun ex Kuhn) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella hildebrandtii* A. Braun ex Kuhn, v. Decken, Reis. III, 3, Bot.: 71, no. 88 (1879).

Hypopterygiopsis hollrungii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella hollrungii* Hieron. Engl. Bot. Jahrb. 50: 35, no. 14 (1913).

Hypopterygiopsis intertexta (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella intertexta* Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 233, no. 156 (1843).

Hypopterygiopsis jainii (R.D. Dixit) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella jainii* R.D. Dixit, Bull. Bot. Surv. India 25: 225, f. 2 A–H (1985).

Hypopterygiopsis kaernbachii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella kaernbachii* Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 700, no. 335 (1901 publ. 1902).

Hypopterygiopsis kalbreyeri (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella kalbreyeri* Baker, J. Bot. 22: 276, no. 157 (1884).

Hypopterygiopsis kanehirae (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella kanehirae* Alston, J. Bot. 72: 227 (1934).

Hypopterygiopsis keralensis (R.D. Dixit) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella keralensis* R.D. Dixit, Bull. Bot. Surv. India 27 (1–4): 123–124. 1987 ("1986").

Hypopterygiopsis ketra-ayam (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella ketra-ayam* Alderw., Bull. Jard. Bot. Buitenz. II, 1: 24–25 (1911).

Hypopterygiopsis kivuensis (Bizzarri) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella kivuensis* Bizzarri, Bull. Jard. Bot. Belg. 53(1–2): 174 (1983).

Hypopterygiopsis kouytcheensis (H. Lév.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella kouytcheensis* H. Lév., Fedde, Repert. 9 (222–226): 451 (1911). 贵州异穗卷柏(新拟)

Hypopterygiopsis kurzii (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella kurzii* Baker, J. Bot. 23: 249, no. 283 (1885) ≡ *Lycopodioides kurzii* (Baker) Kuntze, Rev. Gen. Pl. 1: 826 (1891). 缅甸异穗卷柏(新拟)

Hypopterygiopsis labordei (Hieron. ex Christ) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella labordei* Hieron. ex Christ, Bull. Ac. Inst. Géogr. Bot. III, 11: 272, no. 168 (1902) ≡ *Lycopodioides labordei* (Hieron. ex Christ) H.S. Kung, Fl. Sichuan. 6: 77–78 (1988). 细叶异穗卷柏(新拟)

Hypopterygiopsis lanceolata (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella lanceolata* Warb., Monsunia 1: 108, 123, no. 117 (1900).

Hypopterygiopsis lauterbachii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella lauterbachii* Hieron., Bot. Jahrb. Syst. 50: 31, no. 12 (1913).

Hypopterygiopsis laxa (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella laxa* Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 233, no. 153 (1843) ≡ *Lycopodioides laxa* (Spring) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Hypopterygiopsis leoneensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella leoneensis* Hieron., Engl. & Prantl, Nat. Pfl. 1(4): 697(1901 publ. 1902).

Hypopterygiopsis leptophylla (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella leptophylla* Baker, J. Bot. 23 (269): 157 (1885) ≡ *Lycopodioides leptophylla* (Baker) Kuntze, Rev. Gen. Pl. 1: 826 (1891). 膜叶异穗卷柏(新拟)

Hypopterygiopsis lewalleana (Bizzarri) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella lewalleana* Bizzarri, Bull. Jard. Bot. Belg. 51(1–2): 222 (1981).

Hypopterygiopsis lindhardtii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella lindhardtii* Hieron., Bull. Herb. Boiss. II, 5: 723, no. 99 (1905).

Hypopterygiopsis llanosii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella llanosii* Hieron., Elmer, Leafl. Phil. Bot. 6: 2039, no. (1913).

Hypopterygiopsis longiciliata (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella longiciliata* Hieron., Engl., Bot. Jahrb. 50: 2, 33, no. 13 (1913).

Hypopterygiopsis loriai (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella loriai* Hieron., Engl. Bot. Jahrb. 50: 2, 27, no. 10 (1913).

Hypopterygiopsis lutchuensis (Koidz.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella lutchuensis* Koidz., Pl. Nov. Amamio-Oshimensis, Ins. Adjasc., 4 (1928), et Acta Phytotax. Geobot. 1: 165 (1932). 琉球异穗卷柏(新拟)

Hypopterygiopsis macroblepharis (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella macroblepharis* Warb., Monsunia 1: 108, 124, no. 126, t. 3C (1900).

Hypopterygiopsis mannii (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella mannii* Baker, J. Bot. 23: 180, no. 277 (1885) ≡ *Lycopodioides mannii* (Baker) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Hypopterygiopsis marinii (Stefanović & Rakotondr.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella marinii* Stefanović & Rakotondr., Novon 6(2): 205 (1996).

Hypopterygiopsis megaphylla (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella megaphylla* Baker, J. Bot. 23: 180 (1885) ≡ *Lycopodioides megaphylla* (Baker) Kuntze, Rev. Gen. Pl. 1: 826 (1891). 宽叶异穗卷柏(新拟)

Hypopterygiopsis menziesii (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium menziesii* Hook. & Grev., Enum. Fil. 1: 2, no. 131 (1831) ≡ *Selaginella menziesii* (Hook. & Grev.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 227, no. 109 (1843) ≡ *Lycopodioides menziesii* (Hook. & Grev.) Kuntze, Rev. Gen. Pl. 1: 826 (1891) ≡ *Selaginella arbuscula* var. *menziesii* (Hook. & Grev.) Skottsb., Medd. Göteborgs Bot. Trädgard, 15: 145 (1944).

Hypopterygiopsis miniatospora (Dalzell) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium miniatosporum* Dalzell, J. Bot. (Hook.) 4: 114 (1852) ≡ *Selaginella miniatospora* (Dalzell) Baker, J. Bot. 23: 249 (1885) ≡ *Lycopodioides miniatospora* (Dalzell) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Hypopterygiopsis minutifolia (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella minutifolia* Spring, Monogr. Lyc. 2: 239, no. 176 (1850) ≡ *Lycopodioides minutifolia* (Spring) Kuntze, Rev. Gen. Pl. 1: 826 (1891). 小叶异穗卷柏(新拟)

Hypopterygiopsis mittenii (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella mittenii* Baker, J. Bot. (London) 21: 18 (1883).

Hypopterygiopsis molleri (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella molleri* Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 697, no. 292. (1901 publ. 1902).

Hypopterygiopsis molliceps (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella molliceps* Spring, Mém. Acad. Roy. Sci. Belg. 24: 257 (1850) ≡ *Lycopodioides molliceps* (Spring) Kuntze, Rev. Gen. Pl. 1: 826 (1891).

Hypopterygiopsis monodii (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella monodii* Alston, Bull. Inst. Franc. Afr. Noire, A, 21: 440 (1959).

Hypopterygiopsis monospora (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium monosporum* (Spring) Hook., Bot. Misc. 9: 362 (1857) ≡ *Selaginella monospora* Spring, Mém. Acad. Roy. Sci. Belg. 24: 135 (1850) ≡ *Selaginella plumosa* var. *monospora* (Spring) Baker, J. Bot. 21: 145 (1883). 单子异穗卷柏(新拟)

Hypopterygiopsis morganii (Zeiller) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella morganii* Zeiller, Bull. Soc. Bot. France 32: 78 (1985).

Hypopterygiopsis myosuroides (Kaulf.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium myosuroides* Kaulf., Enum. Fil. 19 (1824) ≡ *Selaginella myosuroides* (Kaulf.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 232, no. 150 (1843) ≡ *Lycopodioides myosuroides* (Kaulf.) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis nairii (R.D. Dixit) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella nairii* R.D. Dixit, Bull. Bot. Surv. India 26: 106 (1985).

Hypopterygiopsis namdaphaensis (Sarn. Singh & Panigrahi) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella namdaphaensis* Sarn. Singh & Panigrahi, Ferns & Fern-Allies of Arunachal Pradesh 1: 64. (2005).

Hypopterygiopsis nana (Desv.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium nanum* Desv. ex Poir., Lam., Encycl. suppl. 3: 554, no. 96. (1813 publ. 1814) ≡ *Selaginella nana* (Desv.) Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 232, no. 151 (1843) ≡ *Lycopodioides nana* (Spring) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis nayarii (R.D. Dixit) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella nayarii* R.D. Dixit, Bull. Bot. Surv. India 27(1–4): 123 (1987).

Hypopterygiopsis neocaledonica (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella neocaledonica* Baker, J. Bot. 22: 245, no. 143 (1884) ≡*Lycopodioides neocaledonica* (Baker) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis nummularia (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella nummularia* Warb., Monsunia 1: 108, 123, no. 121 (1900).

Hypopterygiopsis ornata **(**Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium ornatum* Hook. & Grev., Enum. Fil. J. Bot. (Hook.) Kew Misc. 3: 108 (1883) ≡ *Selaginella ornata* (Hook. & Grev.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 232 (1843) ≡ *Selaginella brachystachya* var. *ornata* (Hook. & Grev.) Baker, J. Bot. 23: 180 (1885). 微齿异穗卷柏(新拟)

Hypopterygiopsis panchghaniana (R.D. Dixit) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella panchghaniana* R.D. Dixit, Bull. Bot. Surv. India 25: 226 (1985).

Hypopterygiopsis panigrahii (R.D. Dixit) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella panigrahii* R.D. Dixit, Bull. Bot. Surv. India 25: 226, f. 4. A—H (1985).

Hypopterygiopsis parachrysocaulos (M.H. Zhang & X.C. Zhang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella parachrysocaulos* M.H. Zhang & X.C. Zhang, Taxon 71(6): 1167 (2022). 拟块茎异穗卷柏(新拟)

Hypopterygiopsis perpusilla (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella perpusilla* Baker, J. Bot. 23: 292 (1885) ≡ *Lycopodioides perpusilla* (Baker) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis phanotricha (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella phanotricha* Baker, J. Bot. 23: 156, no. 261 (1885) ≡ *Lycopodioides phanotricha* (Baker) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis philippina (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella philippina* Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 140 (1843) ≡ *Lycopodioides philippina* (Spring) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis pricei (B.C. Tan & Jermy) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella pricei* B.C. Tan & Jermy, Fern Gaz. 12(3): 170 (1981).

Hypopterygiopsis proniflora **(**Lam.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium proniflorum* Lam., Encycl. 3: 652, no. 25. (1789 publ. 1791) ≡ *Selaginella proniflora* (Lam.) Baker, J. Bot. 22: 156 (1885) ≡ *Stachygynandrum proniflorum* (Lam.) P. Beauv., Prodr. aethéogam. 110 (1805) ≡ *Lycopodioides proniflora* (Lam.) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis protensa (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella protensa* Alston, Mém. Inst. Fr. Afr. Noire 50: 41 (1957).

Hypopterygiopsis qingchengshanensis (Li Bing Zhang & X.M. Zhou) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella qingchengshanensis* Li Bing Zhang & X.M. Zhou, Phytotaxa 522(4): 286 (2021). 青城山异穗卷柏(新拟)

Hypopterygiopsis radicata **(**Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium radicatum* Hook. & Grev., Enum. Fil. J. Bot. (Hook.) Kew Misc. 2: 397, no. 160 (1831) ≡ *Selaginella radicata* (Hook. & Grev.) Spring, Mém. Acad. Roy. Sci. Belg. 24 (2) 114 (1850) ≡ *S. plumosa* var. *radicata* (Hook. & Grev.) Warb., Monsunia 1: 102 (1900).

Hypopterygiopsis raiateensis (J.W. Moore) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella raiateensis* J.W. Moore, Bull. Bernice P. Bishop Mus. 102: 15 (1933).

Hypopterygiopsis rajasthanensis (Gena, Bhardwaja & A.K. Yadav) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella rajasthanensis* Gena, Bhardwaja & A.K. Yadav, Am. Fern J. 69: 119 (1979).

Hypopterygiopsis rasoloheryi (Rakotondr.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella rasoloheryi* Rakotondr., Candollea 71(1): 144 (2016).

Hypopterygiopsis reineckei (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella reineckei* Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 678, no. 83. (1901 publ. 1902).

Hypopterygiopsis repanda **(**Desv. & Poir.) Spring Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium repandum* Desv. ex Poir., Lam., Encycl. suppl. 3: 558. (1813 publ. 1814) ≡ *Selaginella repanda* (Desv. & Poir.) Spring, Gaudich., Voy. Bonite Bot. 1: 329 (1846). 高雄异穗卷柏(新拟)

Hypopterygiopsis reptans Sakurai, Bot. Mag. (Tokyo) 57: 255 (1943) ≡ *Selaginella sakuraii* H. Miller, Taxon 16: 70 (1967).

Hypopterygiopsis reticulata **(**Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium reticulatum* Hook. & Grev., J. Bot. (Hook.) Kew Misc. 2: 402 (1831) ≡ *Selaginella reticulata* (Hook. & Grev.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 233 (1843).

Hypopterygiopsis robinsonii (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella robinsonii* Alderw., Phil. J. Sci. Bot., 11C: 118 (1916).

Hypopterygiopsis roesickeana (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella roesickeana* Hieron., Engl. Bot. Jahrb. 56: 235, no. 36 (1920).

Hypopterygiopsis sambiranensis (Stefanov. & Rakotondr.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella sambiranensis* Stefanov. & Rakotondr., Adansonia ser. 3, 3: 19(1): 166, f. 1—2 (1997).

Hypopterygiopsis scabrida (Ridl.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella scabrida* Ridl., J. Roy. As. Soc., Str. Br., No. 80: 159, no. 32 (1919) ≡ *Selaginella alutacea* var. *scabrida* (Ridl.) Alston, Gard. Bull. Str. Settl. 8: 56 (1934).

Hypopterygiopsis schefferi (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella schefferi* Hieron., Engl. Bot. Jahrb. 50: 2, 24, no. 8 (1913).

Hypopterygiopsis selangorensis (Bedd. ex Ridl.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella selangorensis* Bedd. ex Ridl., J. As. Soc., Str. Br., No. 80: 148, no. 3 (1919).

Hypopterygiopsis sespillifolia (Brownlie) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella sespillifolia* Brownlie, Fl. Nouv.-Caléd. 3: 32 (1969).

Hypopterygiopsis setchellii (O.C. Schmidt) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella setchellii* O.C. Schmidt, Fedde, Repert, 20: 158 (1924).

Hypopterygiopsis sichuanica (H.S. Kung) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella sichuanica* H.S. Kung, Acta Bot. Yunnan. 3(2): 252 (1981). 四川异穗卷柏(新拟)

Hypopterygiopsis singalanensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella singalanensis* Hieron., Hedwigia 50: 18, no. 12 (1910).

Hypopterygiopsis societatis (J.W. Moore) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella societatis* J.W. Moore; Bull. Bernice P. Bishop Mus. 102: 13 (1923).

Hypopterygiopsis spinulosovena (G.Q. Gou & P.S. Wang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella spinulosovena* G.Q. Gou & P.S. Wang, Acta Bot. Yunnan. 27(2): 145—146 (2005). 刺脉异穗卷柏(新拟)

Hypopterygiopsis squarrosa (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella squarrosa* Baker, J. Bot. 23: 180, no. 276 (1885).

Hypopterygiopsis stolleana (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella stolleana* Hieron., Engl. Bot. Jahrb. 56: 236, no. 37 (1920).

Hypopterygiopsis strigosa (Bedd.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella strigosa* Bedd., Kew Bull. (1911), 192, no. 600 (1911).

Hypopterygiopsis subcordata (A. Braun ex Kuhn) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella subcordata* A. Braun ex Kuhn; Fil. Afr. 193 (1868) ≡ *Lycopodioides subcordata* (A. Braun) Kuntze, Rev. Gen. Pl. 1: 827 (1891) ≡ *Stachygynandrum subcordatum* (A. Braun) Carruth., Cat. Afr. Pl. coll. by Dr. F. Welwitsch in 1853–1861, 2(2): 262 (1901).

Hypopterygiopsis subeffusa (Shalimov et X.C. Zhang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella subeffusa* Shalimov & X.C. Zhang, Turczaninowia 25(3): 58 (2022). 近疏松异穗卷柏(新拟)

Hypopterygiopsis subdiaphana (Wall. ex Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium subdiaphanum* Wall., (Cat. n. 136 (1829), nom. nud.) ex Hook. & Grev., Enum. Fil. J. Bot. (Hook.) Kew Misc. 2: 401, no. 183 (1831) ≡ *Selaginella subdiaphana* (Wall. ex Hook. & Grev.) Spring, Bull. Acad. Roy. Sci. Bruxelles 10: 232 (1843) ≡ *Lycopodioides subdiaphana* (Wall. ex Hook. & Grev.) Kuntze, Rev. Gen. Pl. 1: 825 (1891). 近透明异穗卷柏(新拟)

Hypopterygiopsis subisophylla (Jermy) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella subisophylla* Jermy, Brit. Fern Gaz. 10: 30, f. 1–9 (1968).

Hypopterygiopsis subchaetoloma (X.M. Zhou, Li Bing Zhang & Z.R. He) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella subchaetoloma* X.M. Zhou, Li Bing Zhang & Z.R. He, *Phytotaxa* 603(3): 225 (2023). 近毛边异穗卷柏(新拟)

Hypopterygiopsis submonospora (Shalimov & X.C. Zhang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella submonospora* Shalimov & X.C. Zhang, Turczaninowia 25(1): 154 (2022). 拟单子异穗卷柏(新拟)

Hypopterygiopsis subspinulosa (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella subspinulosa* Spring, Miq. Pl. Jungh. 3: 277, no. 10 (1854).

Hypopterygiopsis subvaginata (X.C. Zhang & Shalimov) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella subvaginata* X.C. Zhang & Shalimov, J. Sp. Res. 9(3): 222 (2020). 拟鞘舌异穗卷柏(新拟)

Hypopterygiopsis tectissima (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella tectissima* Baker, Jour. Bot. 22: 89, no. 119 (1884).

Hypopterygiopsis temehaniensis (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella temehaniensis* J.W. Moore; Bull. Bernice P. Bishop Mus. 102: 13 (1933).

Hypopterygiopsis tenera (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium tenerum* Hook. & Grev., J. Bot. (Hook.) Kew Misc. 2: 400 (1831) ≡ *Selaginella tenera* (Hook. & Grev.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 232 (1843) ≡ *Lycopodioides tenera* (Hook. & Grev.) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis tenerrima (A. Braun ex Kuhn) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella tenerrima* A. Braun ex Kuhn, Fil. Afr. 193 (1868) ≡ *Lycopodioides tenerrima* (A. Braun) Kuntze, Rev. Gen. Pl. 1: 827 (1891) ≡ *Stachygynandrum tenerrimum* (A. Braun) Carruth., Cat. Afr. Pl. coll. by Dr. F. Welwitsch in 1853–1861, 2(2): 262 (1901).

Hypopterygiopsis tenuifolia (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella tenuifolia* Spring, Mém. Acad. Roy. Sci. Belg. 24(2): 253 (1850) ≡ *Lycopodioides tenuifolia* (Spring) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis thomensis (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella thomensis* Alston, Exell, Cat. Vasc. Pl. S. Tomé, 97, f. 3 (1944).

Hypopterygiopsis trichophylla (K.H. Shing) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella trichophylla* K.H. Shing, Vasc. Pl. Hengduan Mount. 1: 11 (1993), without Latin descr. et Acta Phytotax. Sin. 31(6): 569 (1993) ≡ *Selaginella monospora* ssp. *trichophylla* (K.H. Shing) X.C. Zhang, Fl. Reipubl. Popularis Sin. 6(3): 189 (2004). 毛叶异穗卷柏(新拟)

Hypopterygiopsis unilateralis (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella unilateralis* Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 232, no. 140 (1843) ≡ *Lycopodioides unilateralis* (Spring) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis usta (Vieill. ex Baker) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella usta* Vieill. ex Baker, Jour. Bot. 23: 23, no. 212. 1885.

Hypopterygiopsis vanderystii (Bizzarri) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella vanderystii* Bizzarri, Bull. Jard. Bot. Belg. 53(1–2): 171 (1983).

Hypopterygiopsis vaginata (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella vaginata* Spring, Mém. Acad. Roy. Sci. Belg. 24: 87 (1850) ≡ *Lycopodioides vaginata* (Spring) Kuntze, Rev. Gen. Pl. 1: 827 (1891). 鞘舌卷柏(新拟)

Hypopterygiopsis vieillardii (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella vieillardii* Warb., Monsunia 1: 125, no. 138 (1900).

Hypopterygiopsis wangpeishanii (Li Bing Zhang, H. He & Q.W. Sun) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella wangpeishanii* Li Bing Zhang, H. He & Q.W. Sun, Phytotaxa 164(3): 195 (2014). 培善异穗卷柏(新拟)

Hypopterygiopsis wattii (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella wattii* Baker, Handb. Fern-Allies 109 (1887) ≡ *Lycopodioides wattii* (Baker) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis weinlandii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. ≡ *Selaginella weinlandii* Hieron., Engl. Bot. Jahrb. 50: 21, 29, no. 11 (1913).

Hypopterygiopsis whitmeei (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella whitmeei* Baker, J. Bot. 23: 24, no. 215 (1885) ≡ *Lycopodioides whitmeei* (Baker) Kuntze, Rev. Gen. Pl. 1: 827 (1891).

Hypopterygiopsis wuyishanensis (K.W. Xu, X.M. Zhou & Y.F. Duan) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella wuyishanensis* K.W. Xu, X.M. Zhou & Y.F. Duan, PhytoKeys 202: 111 (2022). 武夷山异穗卷柏(新拟)

Hypopterygiopsis xichouensis (W.M. Chu) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella xichouensis* W.M. Chu, Fl. Yunnan. 20: 720 (2006). 西畴异穗卷柏(新拟)

Hypopterygiopsis xipholepis (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella xipholepis* Baker, J. Bot. 23: 155, no. 258 (1885) ≡ *Lycopodioides xipholepis* (Baker) Kuntze, Rev. Gen. Pl. 1: 827 (1891). 剑叶异穗卷柏(新拟)

Hypopterygiopsis xishuiensis (G.Q. Gou & P.S. Wang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella xishuiensis* G.Q. Gou & P.S. Wang, Acta Phytotax. Sin. 43(1): 71 (2005). 习水异穗卷柏(新拟)

Hypopterygiopsis yunckeri (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella yunckeri* Alston, Bull. Bernice P. Bishop Mus. 220: 44 (1959).

Hypopterygiopsis zechii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella zechii* Hieron., Engl. & Prantl, Nat. Pfl. 1(4): 697, no. 298 (1901 publ. 1902).

Hypopterygiopsis zhangii (S.Y. Dong) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella zhangii* S.Y. Dong, Syst. Bot. 47(1): 91 (2022). 宪春异穗卷柏(新拟)

Hypopterygiopsis zollingeriana (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella zollingeriana* Spring, Miq., Pl. Jungh. 3: 278, no. 11 (1854).

Lycopodioides Boehm., Def. Gen. Pl. (ed. 3). 485. 1760. 疏穗卷柏属(新拟) – isonym: *Lycopodioides* Kuntze, Revis. Gen. Pl. 2: 824

(1891) ≡ *Trispermium* Hill, Gener. Nat. Hist., ed. 2, 2(Hist. Pl.): 112 (1773) – Type: *Lycopodium denticulatum* L., Sp. Pl. 2: 1106 (1753) ≡ *Selaginella denticulata* (L.) Spring, Flora 21(10): 149 (1838) ≡ *Lycopodioides denticulata* (L.) Kuntze, Revis. Gen. Pl. 1–2: 824 (1891).

= *Diplostachyum* P. Beauv., Mag. Encycl. 5: 481. (1804) ('*Diplostachium*'). *Lycopodioides* sect. *Diplostachyum* (P. Beauv.) Rothm. *Lycopodium* sect. *Diplostachyum* (P. Beauv.) Rchb. ≡ *Selaginella* sect. Diplostachyum (P. Beauv.) T. Moore ≡ *Heterophyllium* Hieron. ex Börner. Lectotype (designated by Pfeiffer, Nom. 1: 1100. 1874): *Lycopodium helveticum* L., Sp. Pl. 2: 1104 (1753) ≡ *Bernhardia helvetica* (L.) Gray, Nat. Arr. Brit. Pl. 2: 23 (1821) ≡ *Selaginella helvetica* (L.) Spring, Flora 21(1): 149 (1838) ≡ *Lycopodioides* helvetica (L.) Kuntze, Revis. Gen. Pl. 2: 826 (1891) ≡ *Heterophyllium helveticum* (L.) Börner, Fl. Deut. Volk 285 (1912).

Lycopodioides is the most frequently recognized genus in addition to *Selaginella* in the family, but our circumscription is different from those in earlier literature and corresponds to *Selaginella* sect. *Homostachys* sensu Zhou and Zhang (2015). The latter has been recognized in earlier classifications of *Selaginella* (e.g., Walton and Alston, 1938; Warburg, 1900). Walton and Alston (1938) included *Selaginella rothertii*, a species from high mountain in Java (Alston, 1935) as a member of *S.* subg. *Homostachys. S. rothertii* might be the southernmost species in subg. *Homostachys*, whereas the remaining species are distributed from East Asia to Europe (Zhang et al., 2021). Warburg (1900) recognized *S.* subg. *Homostachys*, but included *S. ciliaris* and *Selaginella pallidissima* in it. Although *S. ciliaris* has creeping plant, similar to those species in subg. *Homostachys*, this species has dimorphic but resupinate strobili and reticulate megaspore and is a member of *Hypopterygiopsis* sect. *Hypopterygiopsis*.

This genus is characterized by creeping stems (Fig. 8G), dimorphic sporophylls (Fig. 8F and G) (except for *S. denticulata* Spring and *S. helvetica* (L.) Spring with nearly monomorphic but loose sporophylls (Fig. 9E)), loose and non-resupinate (with the smaller ones in the same plane as the median leaves and the larger ones in the same plane as the ventral leaves) strobili (Fig. 8F and G). Species in *Lycopodioides* usually grow in wet habitat. Although megaspore surfaces with papillate, tuberculate, and verrucate ornamentation are similar to those of *Hypopterygiopsis* sect. *Hypopterygiopsis*, but the laesurae of megaspores in *Lycopodioides* are usually disconnected at the pole (Zhou et al., 2015; Zhou and Zhang, 2015). 2n = 18 (Reese,1951; Jermy et al., 1967; Loyal et al., 1984; Takamiya, 1993).

Lycopodioides known so far (Zhou et al., 2022) has large plastome size (*ca.* 187 kb) with the most genes (128) in Selaginellaceae. *Lycopodioides* has three ribosomal operon copies, and its master conformation of plastomes can mediate eight isomers (Zhou et al., 2022).

This genus contains *ca.* 12 species mainly occurring in Asia and Europe (Zhang et al., 2021).

Members:

Lycopodioides denticulata (L.) Kuntze in Revis. Gen. Pl. 2: 824. 1891. Basionym: *L. denticulatum* L., Sp. Pl. 2: 1106 (1753).

Lycopodioides helvetica (L.) Kuntze, Revis. Gen. Pl. 2: 826. 1891. Basionym: *L. helveticum* L., Sp. Pl. 2: 1104–1105 (1753). 小疏穗卷柏(新拟)

Lycopodioides jiulongensis H.S. Kung, Li Bing Zhang & X.S. Guo in Acta Bot. Yunnan. 17(4): 420, Fig. 1(1–5) (1995). 九龙疏穗卷柏(新拟)

Lycopodioides laxistrobila (K.H. Shing) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella laxistrobila* K.H. Shing, Acta Phytotax. Sin. 31(6): 569 (1993). 疏穗卷柏(新拟)

Lycopodioides longistrobilina (P.S. Wang, X.Y. Wang & Li Bing Zhang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella longistrobilina* P.S. Wang, X.Y. Wang & Li Bing Zhang, Novon 22: 260. 2012. 长穗疏穗卷柏(新拟)

Lycopodioides nipponica (Franch. & Sav.) Kuntze, Revis. Gen. Pl. 2: 827. 1891 ('nipponicum'). Basionym: *Selaginella nipponica* Franch. & Sav., Enum. Pl. Jap. 2(2): 199, 615 (1879). 伏地疏穗卷柏(新拟)

Lycopodioides pallidissima (Spring) Kuntze; Revis. Gen. Pl. 2: 827 (1891). *Selaginella pallidissima* Spring in Bull. Acad. Roy. Sci. Bruxelles 10: 231 (1843). 平疏穗卷柏(新拟)

Lycopodioides prostrata H.S. Kung, Fl. Sichuan. 6: 76 (1988). 地疏穗卷柏(新拟)

Lycopodioides pseudonipponica (Tagawa) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella pseudonipponica* Tagawa, Acta Phytotax. Geobot. 25: 177 (1973) ≡ *Selaginella helvetica* subsp. *pseudonipponica* (Tagawa) H.M. Chang, W.L. Chiou & J.C. Wang, Fl. Taiwan, Selaginellaceae 38 (2012). 拟伏地疏穗卷柏(新拟)

Lycopodioides rothertii (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella rothertii* Alderw., Bull. Jard. Bot. Buitenz. II, 7: 30 (1912).

Lycopodioides shensiensis (Christ) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella shensiensis* Christ; Nuov. Giorn. Bot. Ital. n. s. 4: 102 (1897). 陕西疏穗卷柏(新拟)

Lycopodioides tama–montana (Seriz.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella tama–montana* Seriz., J. Jpn. Bot. 53(8): 242 (1978). 高山疏穗卷柏(新拟)

Valdespinoa Li Bing Zhang & X.M. Zhou, gen. nov. 韦氏卷柏属(新拟) – Type: *Valdespinoa douglasii* (Hook. & Grev.) Li Bing Zhang & X.M. Zhou (≡ *Selaginella douglasii* (Hook. & Grev.) Spring).

Etymology: In honor of Prof. Iván A. Valdespino currently based at PMA for his contributions to the study of *Selaginella* (e.g., Valdespino, 1993a, 2015, 2016; Valdespino (2017b); 2018; 2020; Valdespino et al., 2015).

Valdespinoa corresponds to *Selaginella* sect. *Auriculate* sensu Zhou and Zhang (2015).

Valdespinoa is sister to *Lycopodioides* with strong support. However, *Valdespinoa* has monomorphic sporophylls and is only distributed in America. We recognize the monospecific *Valdespinoa* containing *V. douglasii* only. Hieronymous and Sadebeck (1902) recognized the *Douglasii* group which contains *S. accharata*, *S. delicatissma*, *S. douglasii*, and *Selaginella reflexa*. Phylogenetic analyses showed that *S. reflexa* is member of our *Selaginella* s.s (Weststrand and Korall, 2016a; Zhou et al., 2016). Based on the morphology, *S. delicatissma* (including *S. accharata*) might be members of *Valdespinoa*, but more studies are necessary.

Valdespinoa has the largest plastome size (>187 kb) known in Selaginellaceae. Its plastome has three ribosomal operon copies and its master conformation can mediate 24 isomers (Zhou et al., 2022).

Valdespinoa currently contains *Selaginella douglasii* in USA only (Valdespino, 1993a).

Member:

Valdespinoa douglasii (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium douglasii* Hook. & Grev. Bot. Misc. 2: 396 (1831) ≡ *Selaginella douglasii* (Hook. & Grev.) Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 138 (1843).

Subfamily VII. **Selaginelloideae** Li Bing Zhang & X.M. Zhou, ***subfam. nov.*** 同穗卷柏亚科(新拟) – type: *Selaginella* P. Beauv

Plants erect, suberect, ascending, or creeping, rarely rosette-forming, with ventral rhizophores borne on ventral side of stems and/or branches; sterile leaves dimorphic, decussate; sporophylls monomorphic or dimorphic (resupinate); megaspore surfaces reticulate (*Stachygynandrum* type with low and open muri; Fig. 2Z), rarely verrucate; microspore surfaces often baculate, sometimes verrucate to blunt echinate; 2n = 18, 20, 22, 36, 36–40, or 50–60

(Jermy et al., 1967; Love and Love, 1976; Takamiya, 1993; Marcon et al., 2005).

This subfamily corresponds to *Selaginella* subg. *Stachygynandrum* sensu Zhou and Zhang (2015).

Morphologically, Selaginelloideae are characterized by creeping, ascending or erect (never scandent) plants (Fig. 10A–F and 11A–D), monomorphic sporophylls (Fig. 10G and H and 11B, E, F) (but including all these species with dimorphic or subdimorphic sporophylls in new world) (Fig. 11G and H). Megaspores usually have more or less a slightly developed zona at the end of laesurae (Fig. 10K–N) or obviously equatorial flange (e.g., *S. involvens*: Fig. 11I) and surfaces with reticulate ornamentation usually with often open mesh (Fig. 10I, K–N and 11J, M–P). Microspore surfaces are usually baculate (Fig. 10J, O–R), blunt spiny (Fig. 10 Q–R), papilary (K–L), or verrucate (Fig. 10S and T) (Valdespino, 1993, 2015, 2016, 2017, 2018; 2020; Valdespino et al., 2015; Zhou et al., 2015).

Following our current classification, nearly all New World species with ventral rhizophores, except *D. hoffmannii*, *Pulviniella*, and *V. douglasii*, should be members of this subfamily. Selaginelloideae are mainly pantropical distribution, some species can extend to subtropical and temperate Asia and Americas (Valdespino, 1993a; Zhang et al., 2013).

In our previous analysis (Zhou et al., 2015, 2016) and classification (Zhou and Zhang, 2015), megaspore data have been well explored and used and their taxonomic significance was intensively discussed (Korall and Taylor, 2006; Zhou and Zhang, 2015; Zhou et al., 2015, 2016; Weststrand and Korall, 2016a). In contrast, the microspore morphology of Selaginelloideae was rarely observed and reported except that of the Old World (especially Asian) species

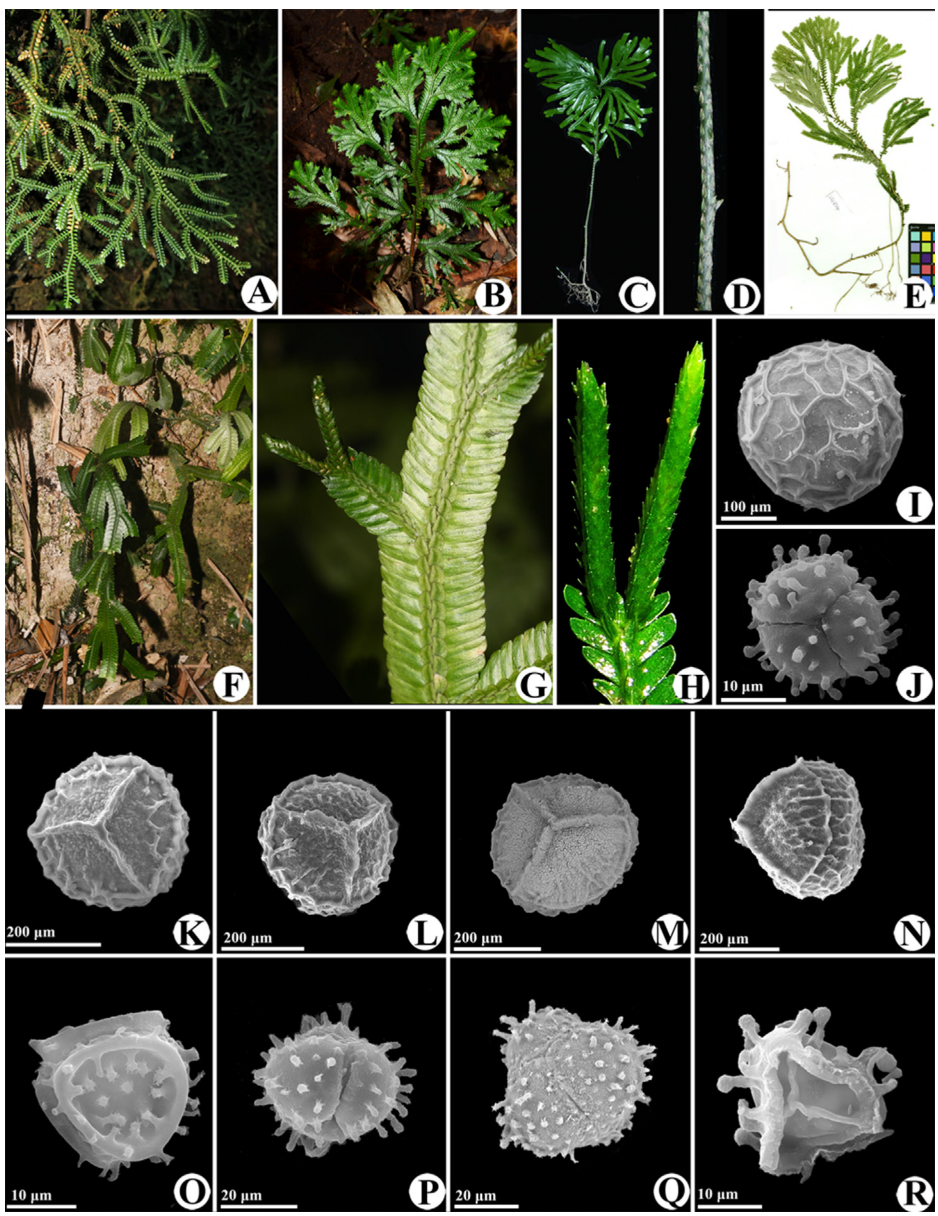

Fig. 10. Morphology of *Chuselaginella* 朱氏卷柏属in subfamily Selaginelloideae (*Selaginella* subg. *Stachygynandrum*; Zhou and Zhang, 2015). **A, K, and O. *Chuselaginella petelotii*** (A. Habit; K. Megaspore; O. Microspore); **B, H, M, and Q. *C. doederleinii*** (B. Habit; H. Strobili; M. Megaspore; Q. Microspore); **C, D, I, and J. *C. frondosa*** (C. Habit; D. Sterile leaves on stem; I. Megaspore; J. Microspore); **E. *C. intermedia*** (Habit); **F, G, L, and P. *C. rolandi-principis*** (F. Habit; G. Sterile leaves and strobili; L. Megaspore; P. Microspore); **N and R, *C. trachophylla*** (N. Megaspore; R. Microspore).

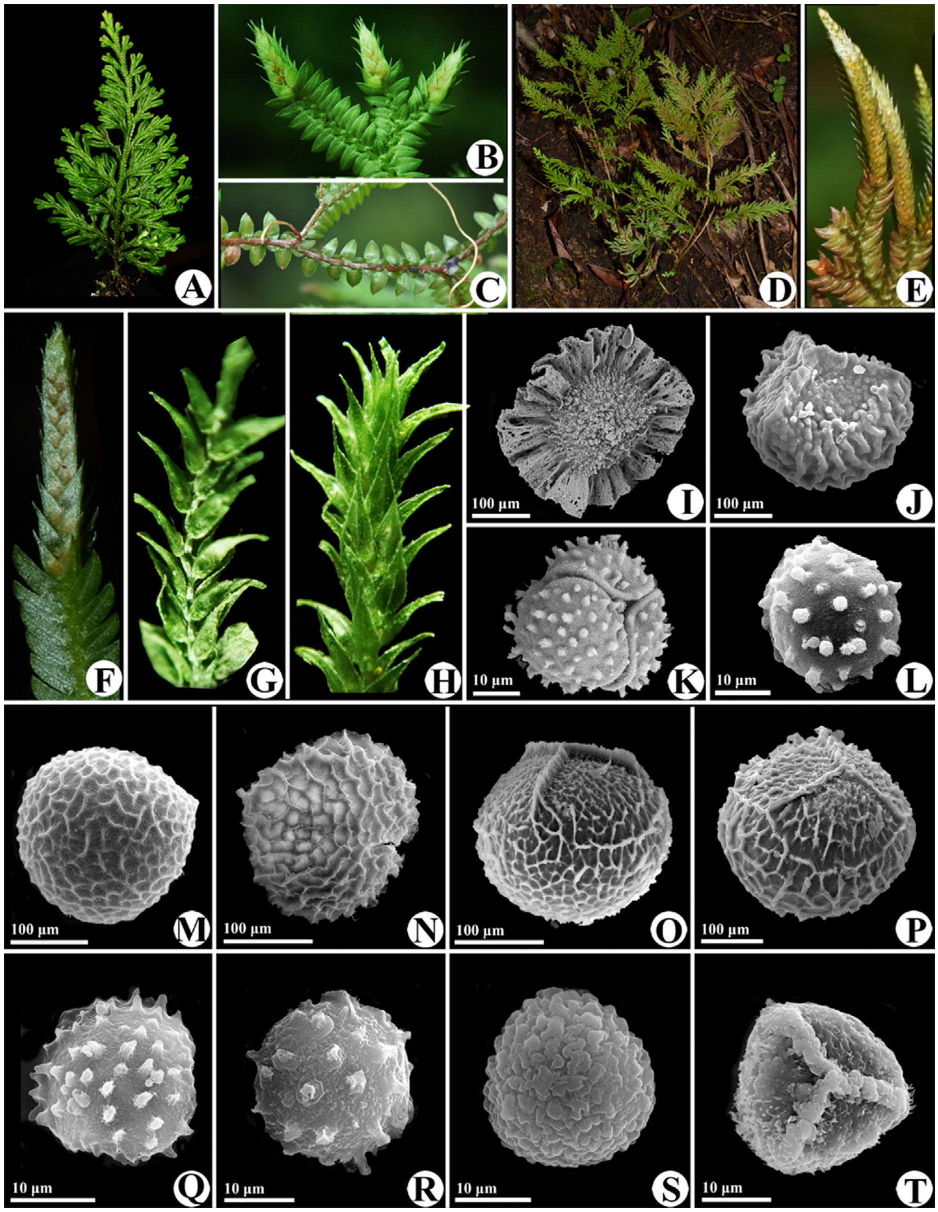

Fig. 11. Morphology of *Kungiselaginella* 孔氏卷柏属 and *Selaginella* s.s. 同穗卷柏属 in subfamily Selaginelloideae (*Selaginella* subg. *Stachygynandrum*; Zhou and Zhang, 2015). **A, F, I and K. *Kungiselaginella involvens*** (A. Habit; F. Strobilus; I. Megaspore; K. Microspore); **B and C. *K. davidii*** (B. Strobili; C. Habit); **D, E, J, L. *K. moellendorffii*** (D. Habit; E. Strobilus; J. Megaspore; L. Microspore); **G, H, M and Q. *Selaginella flagellata*** (G. Dorsal side of strobilus; H. Ventral side of strobilus; M. Megaspore; Q. Microspore); **N & R. *S. porphyrospora*** (N. Megaspore; R. Microspore); **O and S. *S. pallescens*** (O. Megaspore; S. Microspore); **P & T. *S. apoda*** (P. Megaspore; T. Microspore).

(e.g., Zhou et al., 2015). In recent years, as a large number of new species from the New World have been described and microspore data have been provided by Valdespino and co-authors (e.g., Valdespino, 2015, 2016; 2017; 2018; 2020; Valdespino et al., 2015), we now know that New-World sections have more diverse of microspore surfaces than those of the Old-World species (Zhou et al., 2015; unpublished data).

Jermy (1986) defined *Selaginella* subg. *Stachygynandrum* as containing only those species with monomorphic sporophylls, but phylogenetic analyses showed that some species with dimorphic strobili in the New World are also mixed with species with monomorphic sporophylls in the tree and the dimorphism of sporophylls have evolved 10 times (Zhou et al., 2016; Weststrand and Korall, 2006a; our Fig. 2G). Based on previous studies and our observations, species with dimorphic sporophylls from the New World also have same reticulate ornamentation as those species with monomorphic sporophylls in *S.* subg. *Stachygynandrum* sensu Jermy (1986) [e.g., *Selaginella hyalogramma* Valdespino (Valdespino et al., 2017); *Selaginella mucronata* (Valdespino et al., 2015); *Selaginella pellucidopunctata* Valdespino (Valdespino et al., 2015); and our observations for *S. flagellata* and *S. simplex*]. These are entirely different from species with dimorphic sporophylls in *Lycopodioides* and *Didiclis* which do not occur in the New World except *D. hoffmannii.* The dimorphism of sporophylls in those species from the Old World and that in those from the New World independently evolved (Fig. 2G). Evidence so far showed that the New-World species with dimorphic sporophylls are typically reticulate on megaspores and baculate on microspores. It is clear that reticulate megaspores and baculate or verrucate microspores are diagnosing features of Selaginelloideae newly defined here.

In addition, tuberculate or verrucate microspores were also observed in some New-World species in the subfamily [(e.g., *Selaginella pubimarginata* Valdespino (2020); *Selaginella brigitteana* Valdespino (Valdespino, 2019); *Selaginella neospringiana* Valdespino (2015c); *Selaginella mucugensis* Valdespino; *Selaginella saltuicola* Valdespino; *Selaginella sematophylla* Valdespino (Valdespino et al., 2015)]. Also, some morphological characters, e.g., dimorphic or monomorphic sporophylls, reticulate or non-reticulate megaspores, baculate or non-baculate microspores, etc., reversed and/or independently evolved many times in the New-World Selaginelloideae (Fig. 2J).

The plastomes of Selaginelloideae known so far (Zhou et al., 2022) are extremely conserved and have the same gene order. Species of Selaginelloideae have no more than two pairs of small repeats in SC and their plastomes have up to five conformations. Those of *Selaginella moellendorffii* and its close relatives have IR and a pair of repeats existed in SC with four conformations, whereas those of the remaining species in the subfamily have DR or DR-IR coexisting.

This subfamily contains about 330 species in three genera, *Chuselaginella, Kungiselaginella,* and *Selaginella* s.s., the former two occurring in the Old World only, and the latter in Americas only except one (a few) species in Africa. *Chuselaginella* and *Kungiselaginella* are morphologically distinguishable from each other (see below and our key) and have slightly different distributions: Asia to Pacific islands and Africa for *Chuselaginella*, and Asia for *Kungiselaginella*. *Kungiselaginella moellendorffii* (= *S. moellendorffii*) in America is introduced from the Old World. *Selaginella s.s.* is morphologically nearly indistinguishable from the other two. Alternatively, these three genera could be combined into a broadly defined *Selaginella*, but we prefer to separate them because of their molecular divergence (especially in nuclear phylogeny; Fig. S2), geographical coherence, and more manageable size.

Chuselaginella Li Bing Zhang & X.M. Zhou, gen. nov. 朱氏卷柏属(新拟) – Type: *Chuselaginella alopecuroides* (Baker) Li Bing Zhang & X.M. Zhou (= *Selaginella alopecuroides* Baker, J. Bot. British & Foreign 19: 368, no. 83. (1881)).

≡ *Selaginella* sect. *Ascendentes* (Baker) Li Bing Zhang & X.M. Zhou, Taxon 64(6): 1136. 2015 ≡ *S.* ser. *Ascendentes* Baker, J. Bot. Lond. 21: 3 (1883) – Lectotype (designated by Zhou and Zhang, 2015: 1136): *S. alopecuroides* Baker.

≡ *S.* ser. *Radicantes* Warb., Monsunia 1: 102 (1900) – Lectotype (designated by Zhou and Zhang, 2015: 1136): *S. alopecuroides* Baker.

Etymology:—From *Chu*-, in honor of Prof. Wei-Ming Chu of Yunnan University (herbarium PYU), China, for his contributions to the study of ferns in general and those of *Selaginella* of Yunnan in particular (Chu et al., 2006).

Chuselaginella corresponds to *Selaginella* sect. *Ascendentes* sensu Zhou and Zhang (2015). This genus is supported as monophyletic in all of our analyses (Fig. 1 and S1–S3). Species of this genus have plants ofter ascending (a few strictly erect), microspores always baculate with expanded tips and megaspores with reticulum and a unique zonal structure at the ends of laesurae (Fig. 10K–N) (e.g., Liu et al., 1989 for *Selaginella doederleinii* Hieron.; Liu et al., 2001 for *Selaginella frondosa* Warb.; Zhao et al., 2006b for *Selaginella commutata* Alderw.; Zhou et al., 2015, for *S. trichophylla* K.H. Shing and *Selaginella scabrifolia* Ching & Chu H. Wang; and Korall and Taylor, 2006 for additional species).

Chuselaginella contains more than 70 species from Africa, Asia, Australia, and South Pacific islands.

Members:

Chuselaginella aenea (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella aenea* Warb., Monsunia 1: 104, 115, no. 58 (1900).

Chuselaginella agusanensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella agusanensis* Hieron., Leafl. Philipp. Bot. 6: 1998.

Chuselaginella alligans (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella alligans* Hieron., Elmer, Leafl. Phil. Bot. 6: 1998, 2012, no. 15 (1913).

Chuselaginella alopecuroides (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella alopecuroides* Baker, J. Bot. 19: 368, no. 83 (1881).

Chuselaginella auriculata (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella auriculata* Spring, Bull. Acad. Roy. Soc. Bruxelles 10: 142, no. 147 (1843).

Chuselaginella bluuensis (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella bluuensis* Alderw., Bull. Jard. Bot. Buitenz. II, 11: 29 (1913).

Chuselaginella borneensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella frondosa* var. *borneensis* Hieron., Bot. Jahrb. Syst. 44: 511 (1910).

Chuselaginella brachyblepharis (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella brachyblepharis* Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 11: 24 (1913)

Chuselaginella brevipes (A. Braun) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella brevipes* A. Braun, App. Ind. Sem. Hort. Berol. 1 (1867)

Chuselaginella breynioides (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella breynioides* Baker, J. Bot. 23: 45, no. 222 (1885).

Chuselaginella brooksii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella brooksii* Hieron., Hedwigia 51: 252, no. 6 ((1911) 1912).

Chuselaginella burkei (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella burkei* Hieron., Engl. Bot. Jahrb. 50: 2, 16, no. 5 (1913).

Chuselaginella carnea (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella carnea* Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 24: 7 (1917).

Chuselaginella cesatii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella cesatii* Hieron., Hedwigia 50: 6, no. 5 (1910).

Chuselaginella ciliata (Alderw.) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella frondosa* var. *ciliata* Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 16: 48 (1914).

Chuselaginella commutata (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella commutata* Alderw., Bull. Jard. Bot. Buitenz. II, 28: 46 (1918). 长芒朱氏卷柏(新拟)

Chuselaginella copelandii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella copelandii* Hieron. Repert. Spec. Nov. Regni Veg. 10: 106 (1911).

Chuselaginella cumingiana (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella cumingiana* Spring Bull. Acad. Roy. Soc. Bruxelles 10: 146, no. 81 (1843).

Chuselaginella cuprea (Ridl.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella cuprea* Ridl.; J. Straits Branch Roy. Asiat. Soc. 80: 152, no. 14 (1919)

Chuselaginella cupressina (Willd.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium cupressinum* Willd., Sp. Pl. 5: 43 (1810).

Chuselaginella dielsii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella dielsii* Hieron.; Hedwigia 51: 254, no. 7 (1911 publ. 1912).

Chuselaginella distans (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella distans* Warb., Monsunia 1: 106, 120, no. 86 (1900).

Chuselaginella doederleinii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella doederleinii* Hieron., Hedwigia 43(1): 41–42 (1904). 深绿朱氏卷柏(新拟)

Chuselaginella dolichocentrus (K.M. Wong) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella intermedia* var. *Dolichocentrus* K.M. Wong, Gard. Bull. Singapore 35(2): 125 (1982 publ. 1983)

Chuselaginella elmeri (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella elmeri* Hieron., Repert. Spec. Nov. Regni Veg. 10: 46, no. 5 (1911).

Chuselaginella fenixii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella fenixii* Hieron. Repert. Spec. Nov. Regni Veg. 10: 98, no. 10 (1911).

Chuselaginella frondosa (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella frondosa* Warb. Monsunia 1: 105, 117, no. 75 (1900). 繁叶朱氏卷柏(新拟)

Chuselaginella grabowskyi (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella grabowskyi* Warb., Monsunia 1: 107, 122, no. 109a (1900).

Chuselaginella grandis (T. Moore) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella grandis* T. Moore, Gard. Chron. 18(2): 40, t. 8 (1882).

Chuselaginella griffithii (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella griffithii* Spring Bull. Acad. Roy. Soc. Bruxelles 10: 145, no. 80 (1843).

Chuselaginella guihaia (X.C. Zhang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella guihaia* X.C. Zhang PhytoKeys 80: 44 (2017). 桂海朱氏卷柏(新拟)

Chuselaginella hordeiformis (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella hordeiformis* Baker J. Bot. 23: 47, no. 229 (1885).

Chuselaginella hosei (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella hosei* Hieron.; Hedwigia 51: 243, no. 3. (1911 publ. 1912).

Chuselaginella intermedia (Blume) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium intermedium* Blume, Enum. Pl. Javae 2: 269, no. 20 (1830). ≡ *Selaginella intermedia* (Blume) Spring Bull. Acad. Roy. Soc. Bruxelles 10: 144 (1843).

Chuselaginella jagorii (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella jagorii* Warb. Monsunia 1: 104, 116, no. 68 (1900).

Chuselaginella kerstingii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella kerstingii* Hieron. Engl. Bot. Jahrb. 50: 2, 21, no. 7 (1913).

Chuselaginella kusaiensis (Hosok.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella kusaiensis* Hosok. Trans. Nat. Hist. Soc. Formosa 25 (147): 440 (1935).

Chuselaginella latifrons (Warb. non Hort. ex Williams) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella latifrons* Warb. non Hort. ex Williams Monsunia 1: 106, 120, no. 89 (1900).

Chuselaginella lebongtandaiana (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella lebongtandaiana* Alderw. Bull. Jard. Bot. Buitenz. II, 23: 23 (1916).

Chuselaginella leveriana (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella leveriana* Alston J. Bot. 77: 225 (1939).

Chuselaginella longiaristata (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella longiaristata* Hieron. Hedwigia 50: 16, no. 11 (1910).

Chuselaginella longipinna (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella longipinna* Warb. Monsunia 1: 105, 119 (1900).

Chuselaginella longirostris (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella longirostris* Alderw. Bull. Jard. Bot. Buitenz. II, 11: 25 (1913).

Chuselaginella lonko-batu (Hieron. & Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella lonko-batu* Hieron. & Alderw. Bull. Jard. Bot. Buitenz. II, 16: 42 (1914).

Chuselaginella louisiadensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella burkei* var. *Louisiadensis* Hieron., Bot. Jahrb. Syst. 50: 2, 18 (1913).

Chuselaginella luzonensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella luzonensis* Hieron. Engl. & Prantl, Nat. Pfl. 1(4): 681, no. 113. (1901 publ. 1902).

Chuselaginella magnifica (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella magnifica* Warb. Monsunia 1: 103, 114, no. 45, t. 3A (1900).

Chuselaginella melanesica (Kuhn) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella melanesica* Kuhn, Forschungsr. Gazelle 4, Bot: 17 (1889).

Chuselaginella moszkowskii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella moszkowskii* Hieron. Bot. Jahrb. Syst. 50: 2, 14, no. 4 (1913).

Chuselaginella opaca (Seriz.) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella doederleinii* var. *opaca* Seriz., J. Phytogeogr. Taxon. 30(1): 44 (1982).

Chuselaginella parvifolia (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella parvifolia* Alderw.; Bull. Jard. Bot. Buitenzorg, sér. 2, 11: 30 (1913).

Chuselaginella paxii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella paxii* Hieron.; Bot. Jahrb. Syst. 44: 512 (1910).

Chuselaginella pentagona (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella pentagona* Spring Mém. Acad. Roy. Sci. Belg. 24(2): 150 (1850).

Chuselaginella petelotii (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella petelotii* Alston H. Lecomte, Fl. Indo-Chine 7: 562, t. 66, f. 1–5 (1951).

Chuselaginella poperangensis (Hieron. ex Rech.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella poperangensis* Hieron. ex Rech. Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 89: 483, t.7, f.13C (1914).

Chuselaginella posewitzii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella posewitzii* Hieron. Hedwigia 51: 241, no. 1. (1911 publ. 1912).

Chuselaginella procera (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella procera* Alston J. Bot. 72: 227 (1934).

Chuselaginella puberulipes (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella puberulipes* Alderw., Nova Guinea, Rés. d. Expéd. á Nouv. Guin. 14 (Bot.): 66 (1924).

Chuselaginella quadrivenulosa (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella quadrivenulosa* Alderw. Nova Guinea, Rés. d. Expéd. á Nouv. Guin. 14 (Bot.): 65 (1924).

Chuselaginella ramosii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella ramosii* Hieron. Repert. Spec. Nov. Regni Veg. 10: 52, no. 8 (1911).

Chuselaginella rivalis (Ridl.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella rivalis* Ridl. Bull. Misc. Inform. Kew 1924: 266 (1924).

Chuselaginella rolandi-principis (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: Selaginella rolandi-principis Alston J. Bot. 72: 228–229 (1934). 海南朱氏卷柏(新拟)

Chuselaginella roxburghii ((Hook. & Grev.) Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella roxburghii* (Hook. & Grev.) Spring Bull. Acad. Roy. Soc. Bruxelles 10: 228, no. 115 (1843).

Chuselaginella rugulosa (Ces.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella rugulosa* Ces. Felci Borneo, Atti della R. Acad. Sc. 7 (8): 35 (1876).

Chuselaginella sambasensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella sambasensis* Hieron. Hedwigia 50: 9, no. 7 (1910).

Chuselaginella sarawakensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella sarawakensis* Hieron. Hedwigia 50: 13, no. 10 (1910).

Chuselaginella scabrifolia (Ching & Chu H. Wang) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella scabrifolia* Ching & Chu H. Wang Acta Phytotax. Sin. 8(2): 157 (1959). 糙叶朱氏卷柏(新拟)

Chuselaginella schatteburgiana (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella schatteburgiana* Hieron. Engl. Bot. Jahrb. 56: 229, no. 29 (1920).

Chuselaginella sepikensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella sepikensis* Hieron. Bot. Jahrb. Syst. 56: 243, no. 58 (1920).

Chuselaginella spanielema (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella spanielema* Alston, J. Bot. 72: 229 (1934) (spanioclema, sphalm.)

Chuselaginella strigosa (Ridl.) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella trichobasis* var. *strigosa* Ridl., J. Straits Branch Roy. Asiat. Soc. 80: 153 (1919). ≡ *Selaginella roxburghii* var. *strigosa* (Ridl.) K.M. Wong, Gard. Bull. Singapore 35(2): corrigendum slip [131 (1982 publ. 1983).

Chuselaginella subalpina (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella subalpina* Alderw. Bull. Jard. Bot. Buitenz. II, 20: 26 (1915).

Chuselaginella subcalcarata (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella subcalcarata* Alderw. Bull. Jard. Bot. Buitenz. II, 16: 49 (1914).

Chuselaginella subpedalis (Alderw.) Li Bing Zhang & X.M. Zhou, comb. & stat. nov. Basionym: *Selaginella paxii* var. *subpedalis* Alderw., Bull. Jard. Bot. Buitenzorg, sér. 2, 11: 30 (1913).

Chuselaginella subserpentina (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella subserpentina* Alderw. Bull. Jard. Bot. Buitenz. II, 1: 17 (1911).

Chuselaginella suffruticosa (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella suffruticosa* Alderw.; Bull. Jard. Bot. Buitenzorg, sér. 2, 1: 22 (1911).

Chuselaginella superba (Alston) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella superba* Alston, J. Bot. 70. 70: 63–64, no. 4, t. 600, f. A–F (1932). 粗茎朱氏卷柏(新拟)

Chuselaginella thurnwaldiana (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella thurnwaldiana* Hieron. Engl. Bot. Jahrb. 56: 227, no. 28 (1920).

Chuselaginella trachyphylla (A. Braun) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella trachyphylla* A. Braun Sitz. Ges. Naturf. Freunde Berl. Berl. 8 (1863). 粗叶朱氏卷柏(新拟)

Chuselaginella versicolor (Spring) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella versicolor* Spring Bull. Acad. Roy. Soc. Bruxelles 10: 143, no. 57 (1843).

Chuselaginella vestita (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella vestita* Alderw. Bull. Jard. Bot. Buitenz. II, 28: 54 (1918).

Chuselaginella vonroemeri (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella vonroemeri* Alderw. Bull. Jard. Bot. Buitenz. II, 24: 7 (1917).

Chuselaginella wariensis (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella wariensis* Hieron. Engl. Bot. Jahrb. 50: 2, 19, no. 6 (1913).

Chuselaginella zahnii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella zahnii* Hieron. Engl. Bot. Jahrb. 50: 2, 37, no. 15 (1913).

Kungiselaginella Li Bing Zhang & X.M. Zhou, gen. nov. 孔氏卷柏属(新拟) – Type: *Kungiselaginella involvens* (Sw.) Li Bing Zhang & X.M. Zhou (= *Lycopodium involvens* Sw., Syn. Fil. 182, no. 50 (1806)).

≡ *Selaginella* sect. *Circinatae* (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, Taxon 64(6): 1136. 2015 ≡ *Lycopodium* (unranked) *Circinatae* Hook. & Grev., Bot. Misc. 2: 380. 1831 ["*Circinata*"] ≡ *S.* (unranked) *Circinatae* (Hook. & Grev.) Spring in Mart., Fl. Bras. 1(2): 118 (1840) – Lectotype (designated by Zhou and Zhang, 2015: 1136): *S. involvens* (Sw.) Spring.

≡ *S.* (unranked) *Caulescentes* A. Braun, App. Ind. Sem. Hort. Berol. 11. [1857] 1858 ≡ *S.* ser. *Caulescentes* (A. Braun) Baker, J. Bot. Lond. 21: 3 (1883) – Type: *S. caulescens* Spring [= *S. involvens* (Sw.) Spring].

≡ *S.* (unranked) *Rosulatae* A. Braun, App. Ind. Sem. Hort. Berol. 11 ([1857] 1858), nom. illeg. ≡ *S.* ser. *Rosulatae* (A. Braun) Baker, J. Bot. Lond. 2: 21: 3 (1883) ≡ *Lycopodioides* sect. *Rosulatae* (A. Braun) Tzvel., Novosti Sist. Vyssh. Rast. 36: 25 (2004) – Type: *S. involvens* (Sw.) Spring.

= *S.* sect. *Plagiophyllae* (Warb.) Li Bing Zhang & X.M. Zhou, Taxon 64(6): 1137 (2015) ≡ *S.* subser. *Plagiophyllae* Warb., Monsunia 1: 103 (1900) – Lectotype (designated by Zhou and Zhang, 2015: 1137): *Selaginella biformis* A. Braun ex Kuhn.

Etymology:—From *Kung*-, in honor of the late Prof. Hsian-Shiu Kung of Chengdu Institute of Biology, Chinese Academy of Sciences (herbarium CDBI), for his contributions to the study of ferns in general and those of Sichuan in particular (e.g., Kung, 1988). He was one of the early authors who recognized more than one genus in Selaginellaceae.

This genus circumscribed here corresponds to *Selaginella* sect. *Circinatae* and *S.* sect. *Plagiophyllae* sensu Zhou and Zhang (2015) combined. The genus is strongly supported as monophyletic in two of the three analyses based on concatenated data and strongly supported in nuclear tree (Fig. 1 and S2).

Plants of *Kungiselaginella* are strictly erect (a few creeping). Ventral leaves of members of this genus usually have two light-colored bands on the sides of veins (Chu, 2006). Their microspores are either slightly baculate (e.g., *Kungiselaginalla davidii* (Franch.) Li Bing Zhang & X.M. Zhou, and *K. moellendorffii* (Hieron.) Li Bing Zhang & X.M. Zhou) or tuberculate to blunt-spiny (e.g., *K. involvens*) (Zhou et al., 2015). Two forms of habit and usually sterile microspores are present in *S. biformis* (Zhou et al., 2015).

This genus contains more than two dozen species in Asia.

Members:

Kungiselaginella argentea (Wall. ex Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium argenteum* Wall. ex Hook. & Grev., Bot. Misc. 2: 384 (1831).

Kungiselaginella biformis (A. Braun ex Kuhn) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella biformis* A. Braun ex Kuhn Fil. Afr. 189 (1868), nomen, ex Baker, J. Bot. 21: 145 (1883). 二形孔氏卷柏(新拟)

Kungiselaginella davidii (Franch.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella davidii* Franch., Pl. David. 1: 344 (1884). 蔓生孔氏卷柏(新拟)

Kungiselaginella hellwigii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella hellwigii* Hieron., Bot. Jahrb. Syst. 50: 2, 12, no. 3 (1913).

Kungiselaginella hieronymiana (Alderw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella hieronymiana* Alderw. Bull. Jard. Bot. Buitenz. II, 7: 31 (1912).

Kungiselaginella involvens (Sw.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *L. involvens* Sw., Syn. Fil. 182, no. 50 (1806). 兖州孔氏卷柏(新拟)

Kungiselaginella moellendorffii (Hieron.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella moellendorffii* Hieron. in Engl. & Prantl, Nat. Pfl. 1(4): 680, no. 102 (1901 publ. 1902). 江南孔氏卷柏(新拟)

Kungiselaginella muelleri (Baker) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella muelleri* Baker, J. Bot. 23: 122, no. 123 (1885).

Kungiselaginella pallida (Hook. & Grev.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Lycopodium pallidum* Hook. & Grev.; Enum. Filic. J. Bot. (Hook.) Kew Misc. 2: 389, no. 130 (1831) (non Beyr.) 灰白孔氏卷柏(新拟)

Kungiselaginella peltata (C. Presl) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella peltata* C. Presl Abh. Königl. Böhm. Ges. Wiss., ser. 5.

Kungiselaginella polyura (Warb.) Li Bing Zhang & X.M. Zhou, comb. nov. Basionym: *Selaginella polyura* Warb., Monsunia 1: 104, 116, no. 64, t. VI, f. A. (1900).

Selaginella P. Beauv., Mag. Encycl. 9(5): 478 (1804), nom. cons. 同穗卷柏属(新拟) – Type: *S. flabellata* (L.) Spring. conserved type. prop (Wan et al., 2023).

= *Selago* P. Browne, Civ. Nat. Hist. Jamaica 82. 1756 – Lectotype (designated by Pichi Sermolli, Webbia 26: 158 (1971)): *Lycopodium serpens* Desv. ex Poir. non L. (1753).

≡ *Stachygynandrum* P. Beauv. ex Mirb. in Lamarck & Mirbel, Hist. Nat. Vég. 3: 477 (1803) ≡ *Selaginella* subg. *Stachygynandrum* (P. Beauv. ex Mirb.) Baker, J. Bot. Lond. 21: 3. 1883 ≡ *Lycopodium* subg. *Stachygynandrum* (P. Beauv. ex Mirb.) Spreng., Anleit., ed. 2, 2(1): 109 (1817) ≡ *L.* (unranked) *Stachygynandrum* (P. Beauv. ex Mirb.) Hook. & Grev., Bot. Misc. 2: 380 (1831) ≡ *L.* (unranked) *Stachygynandrum* (P. Beauv. ex Mirb.) Kunze, Linnaea 9: 8. 1834, "*Stachygynandra*" ≡ *Didiclis* subg. *Stachygynandrum* (P. Beauv. ex Mirb.) Rothm., Feddes Repert. Spec. Nov. Regni Veg. 54: 70 (1944) – Lectotype (designated by Pichi Sermolli, Webbia 26: 164 (1971)): *Selaginella flabellata* (L.) Spring.

≡ *Selaginella* subg. *Heterophyllum* Hieron. & Sadeb. in Engler & Prantl, Nat. Pflanzenf. I(4): 673 (1902) – Lectotype (designated by Zhou and Zhang, 2015: 1136): *Selaginella flabellata* (L.) Spring.

Selaginella s.s. in this study corresponds to *S.* subg. *Stachygynandrum* Zhou and Zhang (2015) excluding *S.* sect. *Ascendentes*, *S.* sect. *Circinatae*, and *S.* sect. *Plagiophyllae*. The monophyly of the genus is strongly supported with nuclear data but its relationships are unresolved with plastid data. The combined dataset supported its monophyly strongly in BI analysis but weakly in ML and MP analyses.

Species of *Selaginella s.s.* have erect, suberect, creeping, asscending (a few rosette-forming) plants. Megaspore surfaces are often reticulate (Fig. 11J, M–P). Microspore surfaces are baculate, blunt spiny, verrucate, papillate, coarse, or ridge (Fig. 11Q–T).

The newly defined genus *Selaginella s.s.* contains about 230 species nearly endemic to Americas except one (to a few) species in Africa. Within *Selaginella s.s.*, four sections, *S.* sect. *Austroamericanae*, *S.* sect. *Heterophyllae*, *S.* sect. *Poceres*, and *S.* sect. *Selaginella* (= *S.* sect. *Pallescentes sensu* Zhou and Zhang (2015)), can be recognized.

Section 1. ***Selaginella*** sect. ***Selaginella*** 同穗卷柏组(新拟)

= *Selaginella* sect. *Heterophyllae* Spring in Mart., Fl. Bras. 1(2): 118 (1840) – Lectotype (designated by Zhou and Zhang, 2015: 1137): *Selaginella flexuosa* Spring.

= *S.* (unranked) *Enodes* Spring in Mart., Fl. Bras. 1(2): 118 (1840) – Lectotype (designated by Zhou and Zhang, 2015: 1136): *S. flexuosa* Spring.

= *S.* (unranked) *Continuae* Spring, Mém. Acad. Sci. Belg. 24: 53 (1850) ≡ *S.* ser. *Continuae* (Spring) Hieron. & Sadeb. in Engl. & Prantl, Nat. Pflanzenf. I(4): 704 (1902) – Lectotype (designated by Zhou and Zhang, 2015: 1137): *Selaginella microphylla* (Kunth) Spring.

= *S.* (unranked) *Pusillae* Spring, Mém. Acad. Sci. Belg. 24: 53 (1850) – Lectotype (designated by Zhou and Zhang, 2015: 1137): *S. microphylla* (Kunth) Spring.

= *S.* (unranked) *Ascendentes* A. Braun, App. Ind. Sem. Hort. Berol. 11 ([1857] 1858) – Lectotype (designated by Zhou and Zhang, 2015: 1137): *S. flexuosa* Spring.

= *S.* (unranked) *Persistentes* A. Braun, App. Ind. Sem. Hort. Berol. 11 ([1857] 1858) – Lectotype (designated by Zhou and Zhang, 2015: 1137): *S. flexuosa* Spring.

= *S.* sect. *Dichotropae* A. Braun, App. Ind. Sem. Hort. Berol., 11. ([1857] 1858). nom. illeg. – Lectotype (designated by Zhou and Zhang, 2015: 1137): *S. flexuosa* Spring.

= *S.* (unranked) *Resupinatae* A. Braun, App. Ind. Sem. Hort. Berol. 12. ([1857] 1858) – Lectotype (designated by Zhou and Zhang, 2015: 1137): *Selaginella stenophylla* A. Braun.

= *S.* ser. *Decumbentes* Baker, J. Bot. Lond. 21: 3 (1883) – Lectotype (designated by Zhou and Zhang, 2015: 1137): *S. microphylla* (Kunth) Spring.

= *S.* sect. *Pleiomacrosporangiatae* Hieron. & Sadeb. in Engl. & Prantl, Nat. Pflanzenf. I(4): 673. (1902) – Lectotype (designated by Zhou and Zhang, 2015: 1137): *S. flexuosa* Spring.

= *S.* ser. *Monostelicae* Hieron. & Sadeb. in Engl. & Prantl, Nat. Pflanzenf. I(4): 673 (1902) – Lectotype (designated by Zhou and Zhang, 2015: 1137): *S. flexuosa* Spring.

≡ *S.* sect. *Stachygynandrum* (P. Beauv. ex Mirb.) T. Moore, Ind. Fil. Cxxviii (1857) ≡ *Lycopodioides* sect. *Stachygynandrum* (P. Beauv. ex Mirb.) Tzvel., Novosti Sist. Vyssh. Rast. 36: 25 (2004) – Type: *S. flabellata* (L.) Spring.

Because the genus has been proposed to be conserved with a conserved type, *Selaginella flabellata* (Wan et al., 2023), our *S.* sect. *Heterophyllae* sensu Zhou and Zhang (2015) now becomes a synonym of the autonym.

This section is weakly supported as monophyletic in two but strongly in one of our three analyses based on the concatenated data (Fig. 1) and is composed of New-World (South & Central Americas) species only. They are suberect, rarely creeping or erect (if plants erect, main stems with monomorphic leaves), and have dimorphic leaves and various chromosome numbers: 2n = 18 (*S. simplex* Baker) (Graustein, 1930; Marcon et al., 2005), 2n = 20 [*Selaginella erythropus* Spring and *S. flabellata* (L.) Spring] (Jermy et al., 1967).

Section 2. ***Selaginella*** sect. ***Austroamericanae*** Li Bing Zhang & X.M. Zhou, Taxon 64(6): 1136 (2015) 南美同穗卷柏组(新拟) – type: *S. hartwegiana* Spring

= *S.* (unranked) *Redivivae* A. Braun, App. Ind. Sem. Hort. Berol. 11 ([1857] 1858) – Lectotype (designated by Zhou and Zhang, 2015: 1136): *S. ciliata* (Willd.) A. Braun [= *Selaginella novae-hollandiae* (Sw.) Spring].

The monophyly of this section is weakly supported (Fig. 1). Species of this section have stem nearly erect, different from those species with dimorphic sporophylls from America that often have creeping stems. They have dimorphic sterile leaves on stem, different from those species with erect stem and monomorphic sporophylls species from America that have monomorphic sterile leaves on stem (Valdespino, 1993b). Moreover, at least *Selaginella hartwegiana* tend to have monomorphic leaves below first branch of the stems.

About 13 species of this section are sampled in our phylogenetic analysis (Fig. S3). This section mainly occurs in North to South America and a few possibly occur in Africa (currently only *Selaginella cathedrifolia* known).

Section 3. ***Selaginella***. sect. ***Pallescentes*** Li Bing Zhang & X.M. Zhou 白变同穗卷柏组(新拟), Taxon 64(6): 1137 (2015) – type: *S. pallescens* (C. Presl) Spring

Members of this section have monomorphic sporophylls [*Selaginella apoda* (L.) C. Morren has slightly dimorphic sporophylls, but generally its sporophylls are considered to be monomorphic; Valdespino, 1993a], but variable numbers of chromosomes, e.g., *S. apoda*: 2n = 18; *S. pallescens* (C. Presl) Spring: 2n = 20, 22; *Selaginella pulcherrima* Liebm.: 2n = 20 (Tschermak-Woes and Doležal-Janish, 1959; Jermy et al., 1967).

About eight species of this section were sampled in our phylogenetic analysis (Fig. S3). However, it is necessary that more morphological and molecular studies are needed to confirm which species in Americas should be placed in this section.

Section 4. ***Selaginella*** sect. ***Proceres*** (Spring) Li Bing Zhang & X.M. Zhou, Taxon 64(6): 1137 (2015) 高贵同穗卷柏组(新拟) ≡ *S.* (unranked) *Proceres* Spring, Mém. Acad. Sci. Belg. 24: 53 (1850) – Lectotype (designated by Zhou and Zhang, 2015: 1137): *S. oaxacana* Spring

This section is strongly supported as monophyletic and resolved as sister to *Selaginella* sect. *pallescentes* (Fig. 1). Species of this section have monomorphic sporophylls and reticulate megaspore surfaces (*Selaginella martensii* Spring: Giorgi et al., 1997; Korall and Taylor, 2006; *Selaginella oaxacana* Spring: Hellwig, 1969]. Only three species were included in our phylogenetic analysis (Fig. S3). More studies are needed.

Members of the genus

Selaginella acanthostachys Baker, J. Bot. 21: 99, no. 40 (1883).

Selaginella achotalensis Shelton & Caluff, Willdenowia 33(1): 163 (2003).

Selaginella aculeatifolia Valdespino, Nordic J. Bot. 34(3): 372 (2016).

Selaginella acutifolia (Stolze) Valdespino, Mem. New York Bot. Gard. 88 (Pterid. Mexico): 558 (2004).

Selaginella agioneuma Valdespino & C. López, PeerJ 6(e4708): 4 (2018).

Selaginella alampeta M. Kessler & A.R.Sm., Edinburgh J. Bot. 63(1): 86 (2006).

Selaginella albolineata A.R.Sm., Ann. Mo. Bot. Gard. 77: 262, f. 7A–E (1990).

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Declaration of competing interest

The authors declare no conflict of interest.

Author contributions

Conceptualization: LBZ; Investigation: XMZ; Writing, Reviewing, and Editing: LBZ and XMZ; Visualization: XMZ and LBZ; Supervision: LBZ.

Conflicts of Interest

We declare no conflicts of interest.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.pld.2023.07.003.

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