RESEARCH ARTICLE

Phylogenetic revision of Dennstaedtioideae (Dennstaedtiaceae: Polypodiales) with description of *Mucura*, gen. nov.

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DOI https://doi.org/10.1002/tax.12858

Abstract We undertook a molecular phylogenetic revision of hayscented ferns (Dennstaedtiaceae: Dennstaedtioideae) using four plastid markers. Our sampling represents ca. 40% of the extant diversity and includes the type species for each of the relevant segregate genera. We coded 18 discrete morphological characters which we used to find diagnosable clades. We show that *Dennstaedtia* is polyphyletic, with the majority of species forming three morphologically distinct clades, but its type (*D. flaccida*) is nested within *Microlepia*. As such, we support the conservation of *Dennstaedtia* with a new type, *D. dissecta*. Following our results, we develop a classification of four genera: *Dennstaedtia*, *Microlepia*, *Mucura* (gen. nov.) and *Sitobolium*. Beyond the inclusion of *D. flaccida*, we propose to maintain *Microlepia* with its current circumscription. Except for a single adventive species in the Neotropics, *Microlepia* is a Paleotropical genus of about 60 species diagnosed by their distinctive perispore ornamentation of rodlets, and by petioles that lack epipetiolar buds. *Mucura* is a Neotropical genus of two species that differ from all other Dennstaedtiaceae by the combination of dichotomously branching rhizomes, petioles that lack epipetiolar buds, marginal sori with both abaxial and adaxial indusia, and trilete spores with a unique perispore ornamentation. As defined here, *Dennstaedtia* is a pantropical genus of about 55 species recognized by having unbranched rhizomes, petioles bearing epipetiolar buds, and by often bearing proliferous buds upon the leaves. *Sitobolium* is a small clade of ca. five species distinguished by their relatively small leaves that have elongate catenate hairs. These hairs often bear a capitate non-glandular terminal cell. In support of our classification, we provide a key to the eleven genera of Dennstaedtiaceae, and for the four genera of Dennstaedtioideae we provide morphological and geographic synopses, a list of constituent species, and necessary new combinations.

Keywords *Dennstaedtia*; fern genera; *Microlepia*; morphology; *Patania*; perispore; *Sitobolium*

Supporting Information may be found online in the Supporting Information section at the end of the article.

■ INTRODUCTION

Dennstaedtia Bernh. was described by Bernhardi in 1801 based upon *Trichomanes flaccidum* G.Forst., a little-known species from western Pacific islands. The circumscription of *Dennstaedtia* has changed considerably over time but has generally united plants with marginal sori derived from the marginal initials during leaf development (Bower, 1928), that bear both abaxial and adaxial indusia (sometimes referred to as inner and outer, respectively), and long-creeping solenotostelic rhizomes (Holttum, 1968; Mickel, 1973). Moore (1859) was perhaps the first to establish its modern conception (Tryon & Tryon, 1980), as a genus of about 70 species with a nearly cosmopolitan distribution, defined by a terrestrial habit, pubescent rhizomes, petioles that frequently bear epipetiolar buds (branch buds), marginal sori with cup- or purse-shaped indusia, and trilete spores (Kramer, 1990; Moran, 1995; Navarrete & Øllgaard, 2000; PPG-I, 2016). However, early (Wolf & al., 1994; Wolf, 1995; Schuettpelz & Pryer, 2007) and recent phylogenetic studies (Perrie & al., 2015; Testo &

Article history: Received: 16 Mar 2022 | returned for (first) revision: 16 May 2022 | (last) revision received: 11 Oct 2022 | accepted: 20 Oct 2022 | published online: 14 Dec 2022 | **Associate Editor:** Li-Bing Chang |

Sundue, 2016; Shang & al., 2018; Schwartsburd & al., 2020; Wang & al., 2021) demonstrated that this concept is not monophyletic by the inclusion of *Microlepia* C.Presl and its small segregate genera *Leptolepia* Prantl and *Oenotrichia* Copel., genera that were differentiated from *Dennstaedtia* by having abaxial sori, with a single abaxial indusium.

Polyphyly of *Dennstaedtia* was not unexpected; some forty years after its initial publication, J. Smith (1842) placed the type, *D. flaccida*, within the recently coined *Microlepia* (Presl, 1836). Copeland (1947) came to similar conclusions based upon its echinate spore morphology, and Tryon & Tryon (1980) later did as well, using SEM images. Copeland (1958) and Holttum (1968) also questioned whether the sorus position could be relied upon to distinguish *Dennstaedtia* and *Microlepia*. They commented that differences between the genera were slight, and that some species appear intermediate between the two genera, differing only by whether the indusium is strictly marginal or slightly removed from the margin and situated upon the abaxial leaf surface. They suspected that transitions between marginal and abaxial sori probably occurred multiple times. This was recently demonstrated by phylogenetic analyses, in which Schwartsburd & al. (2020) showed the evolution from marginal to abaxial sori occurred at least five times within Dennstaedtiaceae, and by Wang & al. (2021), who found that *D. smithii* (Hook.) T.Moore, a species with marginal sori, was nested in the *Microlepia* clade that otherwise have sori positioned abaxially (i.e., indicating a reversal to marginal position).

Rather than merge *Microlepia* into *Dennstaedtia*, Tryon & Tryon (1980) attempted to retain *Dennstaedtia* by conserving a later publication of the same name based upon a type that fit their concept of the genus. They proposed to conserve *Dennstaedtia* T.Moore (1859) based upon *D. cicutaria*, against *Dennstaedtia* Bernh. This proposal also conserved *Dennstaedtia* T.Moore against several other genera, namely *Sitobolium* Desv. (based upon *D. punctilobula*), *Patania* C.Presl (based upon *D. obtusifolia*) and *Adectum* Link (based upon *Dicksonia pilosiuscula*) that were not in active use at the time. The Committee for Pteridophyta voted against their proposal, however. Holttum commented that it was premature to act without further knowledge of Asian taxa, particularly *D. flaccida*, and Pichi Sermolli concluded that *Dennstaedtia* T.Moore should be inferred to have the same type of that *Dennstaedtia* Bernh. (Pichi-Sermolli, 1982). Despite the ruling, Tryon and Tryon adopted *Dennstaedtia* T.Moore based upon *D. cicutaria* as the accepted name in their influential 1982 publication, which may have delayed the adoption of a resolution that was in accord with the *ICBN*.

Schwartsburd & al. (2020) outlined possible nomenclatural solutions to the non-monophyly of *Dennstaedtia* by either broadly defining it to include *Microlepia* or by adopting a series of more narrowly defined genera: *Coptidipteris* (based upon *D. wilfordii*), *Patania* (based upon *D. obtusifolia*) and *Sitobolium* (based upon *D. punctilobula*). Any nomenclatural solution, however, is incumbent upon the phylogenetic positions of these type species, and the circumscription of genera that taxonomists find useful. While type species for most of the relevant genera have been included in recent studies (e.g., Perrie & al., 2015; Schwartsburd & al., 2020), those of *Dennstaedtia* and *Patania* have not previously been subject to phylogenetic analysis.

These previous studies demonstrating the polyphyly of *Dennstaedtia*, and the problematic handling of the principle of priority by Tryon & Tryon (1982) led us to conduct a molecular phylogenetic analysis of the family with a robust sampling of *Dennstaedtia* representing ca. 40% of the extant diversity. We included type species for each of the relevant segregate genera including the types of *Patania* and *Dennstaedtia*. We also map morphological character states allowing us to evaluate their taxonomic value in generic circumscription and infrafamilial classification. Our results lead us to recircumscribe genera of Dennstaedtioideae, including the resurrection of *Sitobolium*, and the establishment of *Mucura* gen. nov. Finally, in an associated publication we propose to conserve *Dennstaedtia* with a new type in order to maintain nomenclatural stability (Triana-Moreno & al., 2022).

■ MATERIALS AND METHODS

Taxonomic sampling. — Our goal was to sample broadly across the Dennstaedtiaceae, and densely within the Dennstaedtioideae. In this study, our sampling of Dennstaedtiaceae included all 13 genera (sensu Shang & al., 2018; Schwartsburd & al., 2020) and 93 species. For *Dennstaedtia* sensu PPG-I (2016), 29 species were included, representing approximately 40% of the diversity in this group. We also included 26 species in 13 genera of other Polypodiales and Cyatheales as outgroups. In total, phylogenetic sampling of Dennstaedtiaceae and outgroups included 158 terminals. Of these, 25 were collected during this research in various locations in the Andes of Colombia, for the genera *Dennstaedtia* (16 samples), *Mucura* gen. nov. (1), *Blotiella* (1), *Hypolepis* (2), *Lindsaea* (1), *Paesia* (1), *Pteridium* (1) and *Saccoloma* (2). Other samples were taken from the collection of tissues preserved in silica gel in the VT herbarium, of which 28 come from the Neotropics, three from North America and 38 from the Old World. Three samples were taken from herbarium specimens (*Dennstaedtia arborescens*, *Castro 756*; *D. distenta*, *Sundue 4998*; *Mucura bipinnata* comb. nov., *Fawcett 470*). For other taxa with no available samples and for the outgroup the sequences were downloaded from GenBank (Appendix 1). We excluded sequences of Dennstaedtiaceae that were shown by Shang & al. (2018) to be problematic.

Extraction, amplification, sequencing, and alignment. — Total DNA was extracted, mainly from silica gel dehydrated laminar tissue samples, or from small fragments of herbarium specimens (ca. 1 cm^2) using a CTAB protocol (Doyle & Doyle, 1987) with the addition of polyvinylpyrrolidone (PVP) to avoid inhibition of amplification by phenolic compounds (John, 1992). We PCR-amplified four regions of the chloroplast (*rbcL* coding gene, *rpl16* intron, *rps4* coding region along with the *rps4-trnS* intergenic spacer, and the

trnL-F intergenic spacer) using previously published primers (Table 1).

For *rbcL*, denaturation was started at 94°C for 5 min, followed by 35 cycles of 94°C for 30 s, 56°C for 30 s and 72°C for 1 min; and final extension at 72°C for 10 min. For *rpl16*, denaturation at 94°C for 5 min, followed by 35 cycles of 94°C for 30 s, 50.5°C for 30 s and 72°C for 1 min; and final extension at 72°C for 10 min. And for *rps4-trnS* and *trnL-F*, denaturation at 94°C for 5 min, followed by 35 cycles of 94°C for 30 s, 50°C for 30 s and 72°C for 1 min; and final extension at 72°C for 8 min. Amplification was confirmed by 1.2% agarose gel electrophoresis at 100 V. The PCR products were purified by applying 1 µl of ExoSAP-IT (Thermo Fischer Scientific, Lithuania) and incubating at 37°C for 15 min, followed by a further 15 min at 80°C. Each region was sequenced using the "forward" and "reverse" end primers used for amplification, and internal primers were additionally used for *rbcL* (Table 1). Sequencing was carried out at The Vermont Integrative Genomics Resource DNA Facility (Burlington, Vermont, U.S.A.). Resulting sequences were examined and assembled in Geneious Prime 2019.2.1 (Kearse & al., 2012). Alignments were made using MAFFT v.7.035b (Katoh & Standley, 2013) and are publicly available at https://doi.org/10.5061/dryad.5hqbzkh99.

Phylogenetic analysis. — Sequence contigs for *rbcL*, *rpl16*, *rps4-trnS*, and *trnL-trnF* were assembled from raw reads and edited using Geneious. We aligned our resulting sequences along with those harvested from GenBank using MAFFT v.7.035b (Katoh & Standley, 2013) and then concatenated them. Best-fitting models of nucleotide substitution were determined for each partitioned marker using ModelFinder (Chernomor & al., 2016; Kalyaanamoorthy & al., 2017). We chose the edge-linked proportional substitutional model and GTR+F was inferred to be the best model for each partition. The maximum likelihood (ML) and Bayesian phylogenetic (BI) and parsimony (MP) reconstructions were implemented using the CIPRES Science Gateway (Miller & al., 2010). Our ML reconstructions were conducted using IQ-tree2 (Minh & al., 2020), and branch support was inferred from 1000 ML bootstrap (BS) replicates. Our Bayesian reconstructions were conducted using MrBayes v.3.2 (Ronquist & al., 2012). The Markov Chain Monte Carlo analysis was performed with four chains run for 6 million generations, sampling every 1000 generations. The resulting log files were inspected for convergence and adequate sampling using Tracer v.1.6 (Rambaut & al., 2018). The first 25% of trees were discarded as burn-in, and a majority-rule consensus tree was generated from the remaining trees. Branch support was inferred from posterior probabilities (PP). Our parsimony analyses were performed with PAUPRat (Sikes & Lewis, 2001), which executes Nixon's (1999) ratchet. All characters were treated as equally weighted and unordered, gaps were treated as missing data, and non-informative characters were removed for analysis. Heuristic searches were performed using the Tree Bisection Reconnection algorithm. PAUP* v.4.a169 (Swofford, 2002) was used to calculate strict consensus trees, and also to assess bootstrap branch supports with heuristic searches on 1000 pseudo-replicates.

Morphological character analysis. — We scored 18 discrete characters for ancestral state analysis of traits determined to be of value in systematic treatments for the family. These included morphological features of the sporophyte and its spores, and chromosome base numbers. Data were scored from literature (e.g., Holttum, 1968; Tryon & Tryon, 1982; Jermy & Walker, 1985; Kramer, 1990; Tryon & Lugardon, 1990; Moran, 1995; Brownsey, 1998; Navarrete & Øllgaard, 2000; Mickel & Smith, 2004; Yan & al., 2013; Yañez & al., 2014, 2016a,b; Shang & al., 2018; Schwartsburd & al., 2020) or by direct observation of specimens at COL, MO, NY, and VT. Character states were mapped onto the most likely tree resulting from our RAxML analyses using both parsimony and likelihood employing an equal rate transition model (Lewis, 2001) in MESQUITE v.3.5 (Maddison, 2008). We then visualized the distribution of these character states on the phylogeny using the "plotTree" and "add.simmap.legend" functions in the R package phytools v.0.7.70

Table 1. Primers used for amplification and sequencing.

Marker	Primer name	Primer Sequence 5′–3′	Source
rbcL	1F	ATG TCA CCA CAA ACA GAG ACT AAA GC	Hasebe & al. (1994)
	ESRBCL628F*	CCA TTY ATG CGT TGG AGA GAT CG	Schuettpelz & Pryer (2007)
	ESRBCL654R*	GAA RCG ATC TCT CCA ACG CAT	Schuettpelz & Pryer (2007)
	1351R	GCA GCA GCT AGT TCC GGG CTC CA	Hasebe & al. (1994)
rpl16	rpL16F	ATG CTT AGT GTG YGA CTC GTT	Small & al. (2005)
	rpL16R	TCC SCN ATG TTG YTT ACG AAA T	Small & al. (2005)
rps4-trnS	RPS4TRNSF	AGT TGT TAG TTG TTG AGT AT	Skog & al. (2004)
	RPS4TRNSR	TAC CGA GGG TTC GAA TC	Smith & Cranfill (2002)
trnL-F	tab-f	ATT TGA ACT GGT GAC ACG AG	Taberlet & al. (1991)
	tab-e	GGT TCA AGT CCC TCT ATC CC	Taberlet & al. (1991)

* used only for sequencing.

(Revell, 2012) and the "tiplabels" function from ape v.5.5, using the "ace" function (Paradis & al., 2004). Characters and their states are provided in Appendix 2.

Characterization of perispore morphology. — Perispore morphology was characterized by making semi-permanent light microscope (LM) slides in glycerin-jelly. These were observed without any acetolysis, since it can affect spore morphology (Erdtman, 1960). The perispore was characterized according to the predominant ornamental types and their arrangement on the surface, from the observation of 25 spores per specimen. Specimens studied are listed in Appendix 3. We followed the terminology employed by Tryon & Lugardon (1990), Lellinger (2002) and Punt & al. (2007).

Taxonomic treatment. — Specimens from the herbaria BA, COL, LP, and VT, and the virtual collections from AAU, MO and NY were studied using PteridoPortal (pteridoportal.org); type specimens were examined using virtual collections when necessary.

■ RESULTS

Characterization of the sequences. — Two hundred and tweny-four new nucleotide sequences were generated (Appendix 1). The variability of the characters in the markers varied between 42.4% (*rbcL*) and 91.5% (*trnL-trnF*), while in the concatenated matrix it was 66.4%. The percentage of parsimony informative characters varied between 33.7% (*rbcL*) and 76.7% (*trnL-F*) and was 52.8% for the concatenated matrix. These and other attributes of the markers are summarized in Table 2.

Phylogenetic analyses. — Dennstaedtiaceae was recovered as monophyletic (PP = 1, BS = 98), as were its subfamilies, the Monachosoroideae (PP = 1, BS = 100), Hypolepidoideae (PP = 1, BS = 100, MP = 94) and Dennstaedtioideae (PP = 1, BS = 100, MP = 96). The six genera of Hypolepidoideae were recovered as monophyletic (Fig. 1). In contrast, genera of the Dennstaedtioideae exhibited phylogenetic relationships in conflict with current classification. *Dennstaedtia* s.l was divided into four clades. The first split within Dennstaedtioideae separates a large clade of tropical *Dennstaedtia* along with *Oenotrichia* and *Leptolepia* from the remaining Dennstaedtioideae (PP = 1, BS = 100). This clade is also home to the type of *Patania*. Among the remaining Dennstaedtioideae, all analyses resolved a split separating a small clade of two species—*D. bipinnata* and *D. globulifera*—from the remaining taxa. Support for the sister relationship of the two species was high (PP = 1, BS = 100), and the BI support for them as sister to the remaining Dennstaedtioideae was high as well (PP = 1), but support for this clade was weak in our ML (BS = 63) and MP results (MP = 59, suppl. Fig. S1). Support for the sister relation of the two remaining clades was high in all analyses (PP = 1, BS = 100, MP = 95). The first of these included species of relatively high latitude from eastern North America and eastern Asia. It included the type species of *Coptidipteris*, and *Sitobolium* (PP = 1, BS = 100, MP = 96). The remaining clade included species of *Microlepia*, along with its type, and the type of *Dennstaedtia* (PP = 1, BS = 100, MP = 95).

Morphological character evolution. — Our reconstructions found that the presence of abaxial and adaxial indusia (Fig. 2A,B), sorus position (Fig. 3B), and rhizome indument (suppl. Fig. S2G) were useful characters at the family level; that is, they exhibited low homoplasy and were generally consistent within large clades. As for characters that help diagnose the genera that we recognized (see below), we found that the presence/absence of epipetiolar buds (Fig. 2C), the shape of the petiole base (suppl. Fig. S2C), the presence/absence of wings along the rachis-costa junction (suppl. Fig. S2D) and the perispore ornamentation (Figs. 3D, 4) were most useful. In particular, the spores of *Mucura* gen. nov. were defined by verrucae, prominent ridges and irregular reticles (Fig. 4A). The perispore of *Microlepia* was consistently defined by a three-dimensional network of rodlets (Fig. 4D). *Sitobolium* and *Patania* were variable in spore ornamentation, but morphologies were consistent within subclades, e.g., the clade corresponding to species previously recognized as *Coptidipteris*, which had tuberculate perispores (Fig. 4B).

In contrast, the presence/absence of proliferous buds upon the lamina (Fig. 2D), rhizome branching (suppl. Fig. S2F), aculeae upon axes (suppl. Fig. S2A), and lamina division (suppl. Fig. S2B), had sufficient homoplasy or missing data such that they have less diagnostic power at this rank. Chromosome base numbers corresponded closely to the genera within the Hypolepidoideae—most genera have a single number distinct from other genera, but there is no similar pattern in the Dennstaedtioideae (Fig. 3C). The clade including *Microlepia* exhibited a base number of $x = 43$ (86), while the remaining Dennstaedtioideae tended to be bimodal, either $x = 30–34$ or $x = 46–47$.

Characters found useful to differentiate the genera of the Dennstaedtioideae recognized here are summarized in Table 3, and the complete morphological data matrix is available as suppl. Table S1.

■ DISCUSSION

Systematics and morphology of Dennstaedtiaceae. — Our recovery of a monophyletic Dennstaedtiaceae along with its subfamilies, the Dennstaedtioideae, Hypolepidoideae, and Monachosoroideae, agrees with previous studies (Schuettpelz & Pryer, 2007; Testo & Sundue, 2016; Shang & al., 2018, Schwartsburd & al., 2020). Morphological characters that help diagnose the family are abundant, and include long-creeping rhizomes, rhizomes protected by an indument of trichomes, the presence of epipetiolar buds, marginal sori, and the presence of an adaxial indusium (Fig. 2B). Although not included in our analysis, family characters also include leaves provided with multicellular catenate hairs, and rhizome vasculature forming solenosteles (Becari-Viana & Schwartsburd, 2017). Some of these characters however are not necessarily synapomorphies due to losses and to the aberrant character states of

Table 2. Characterization of the alignments, and statistics for each marker and combination.

				Characters															
	ILD test (*p*-value)	Number of taxa	Number of samples	Alignment length	Constant characters	(%)	Variable characters	(%)	Non-informative variable characters under parsimony	(%)	Informative characters under parsimony	(%)	Most parsimonious trees	Tree length	Consistency index (CI)	Retention index (RI)	Rescaled consistency index (RC)	Resolved clades in the strict consensus tree	Polytomies in the strict consensus tree
rbcL	---	71	92	1393	802	57.6	591	42.4	122	8.8	469	33.7	9756	1783	0.379	0.778	0.294	66	11
rpl16	---	46	65	817	180	22.0	637	78.0	168	20.6	469	57.4	9918	1580	0.520	0.748	0.389	48	5
rps4-trnS	---	62	101	534	65	12.2	469	87.8	76	14.2	393	73.6	9974	1261	0.602	0.929	0.559	51	19
trnL-F	---	66	94	494	42	8.5	452	91.5	73	14.8	379	76.7	10001	1729	0.495	0.832	0.412	66	7
rbcL + *rpl16*	1.00	78	111	2210	982	44.4	1228	55.6	290	13.1	938	42.4	8698	3372	0.444	0.786	0.349	74	9
rbcL + *rps4-trnsS*	0.95	91	138	1917	857	44.7	1060	55.3	198	10.3	862	45.0	9555	3290	0.506	0.865	0.438	112	9
rbcL + *trnL-F*	0.97	87	127	1887	844	44.7	1043	55.3	195	10.3	848	44.9	9212	3521	0.435	0.805	0.350	92	9
rpl16 + *rps4-trnS*	0.90	72	118	1351	245	18.1	1106	81.9	244	18.1	862	63.8	9964	2852	0.554	0.882	0.489	66	18
rpl16 + *trnL-F*	0.93	75	114	1311	222	16.9	1089	83.1	241	18.4	848	64.7	9949	3314	0.506	0.818	0.414	95	6
rps4-trnS + *trnL-F*	0.26	78	125	1028	107	10.4	921	89.6	149	14.5	772	75.1	9961	3011	0.536	0.886	0.475	85	11
rbcL + *rpl16* + *rps4-trnS*	0.97	91	146	2744	1047	38.2	1697	61.8	366	13.3	1331	48.5	8743	4654	0.485	0.848	0.411	94	9
rbcL + *rpl16* + *trnL-F*	1.00	90	140	2704	1024	37.9	1680	62.1	363	13.4	1317	48.7	9168	5107	0.461	0.803	0.370	90	9
rbcL + *rps4-trnS* + *trnL-F*	0.89	93	149	2421	909	37.5	1512	62.5	271	11.2	1241	51.3	9227	4808	0.476	0.854	0.406	104	11
rpl16 + *rps4-trnS* + *trnL-F*	0.68	81	134	1845	287	15.6	1558	84.4	317	17.2	1241	67.3	9961	4622	0.527	0.863	0.455	97	12
rbcL + *rpl16* + *rps4-trnS* + *trnL-F*	0.96	93	156	3238	1089	33.6	2149	66.4	439	13.6	1710	52.8	6616	6400	0.486	0.843	0.410	115	10

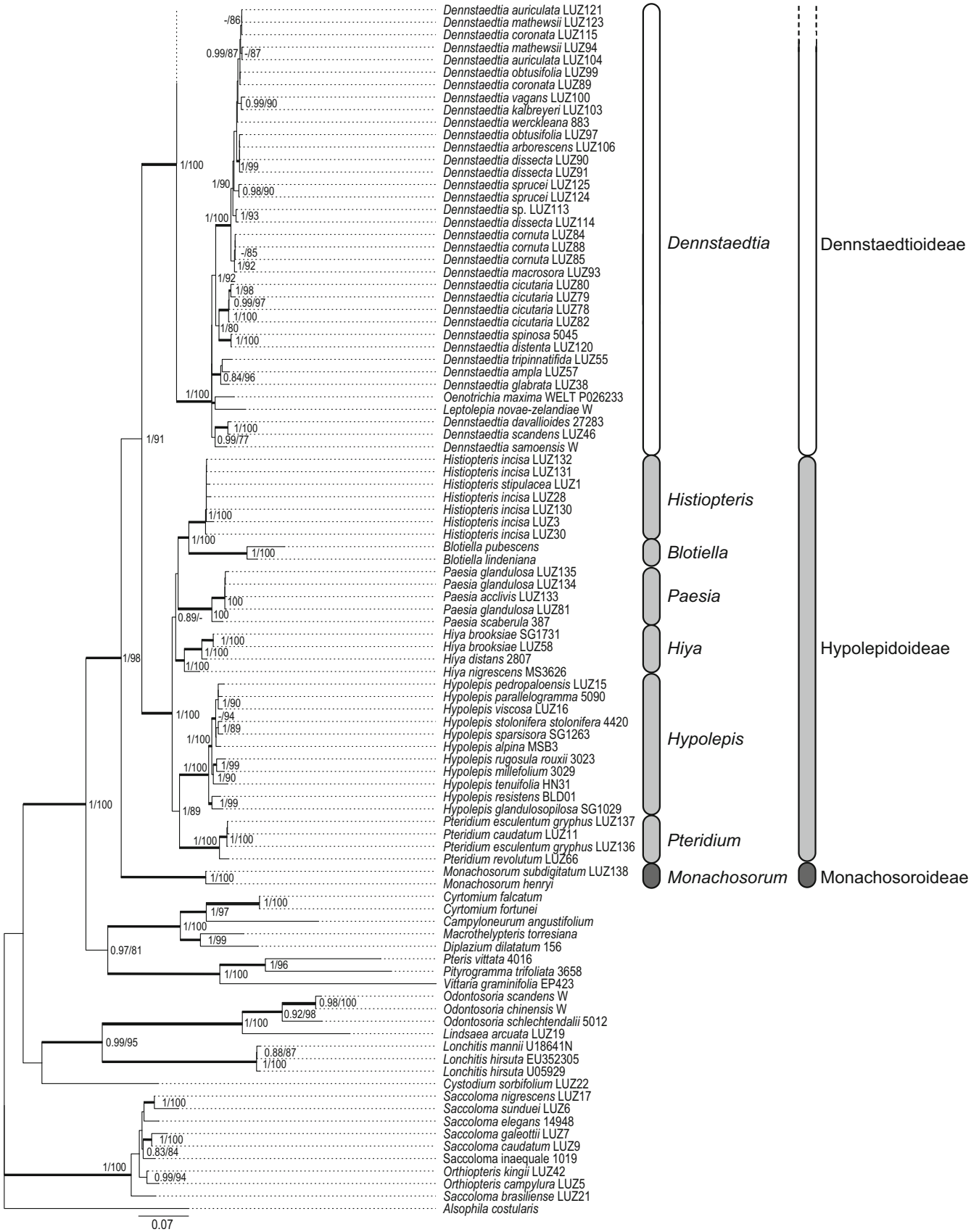

Fig. 1. Best tree resulting from the maximum likelihood phylogenetic tree search using IQ-Tree2. Bootstrap support values >80% from 1000 iterations are presented at nodes. Clades with posterior-support of 1 and ML bootstrap values >90% are indicated with a thickened bar.

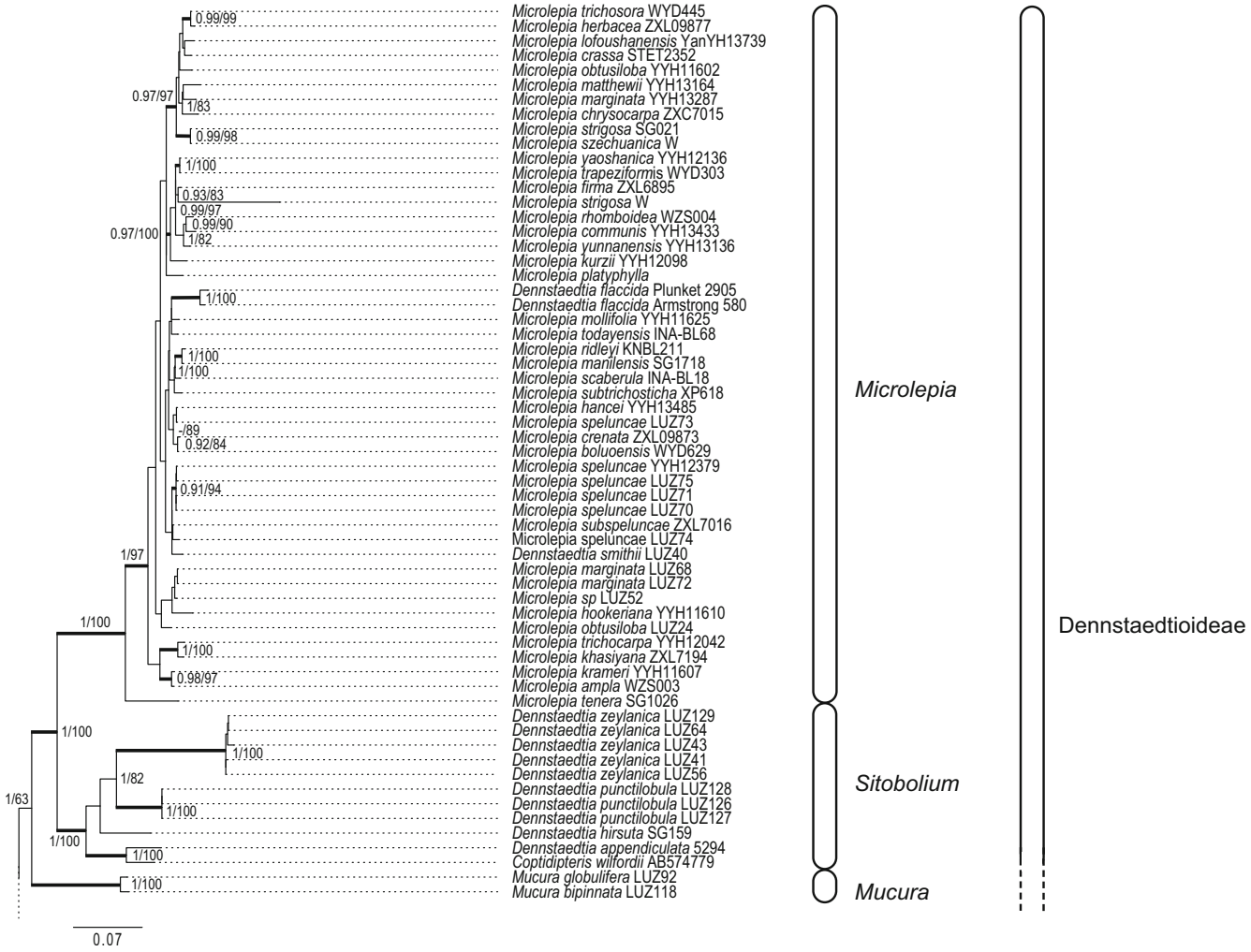

Fig. 1. Continued.

Monachosorum, which is sister to all other Dennstaedtiaceae (Ebihara & al., 2016; Shang & al., 2018; Schwartsburd & al., 2020).

Characters of the subfamilies exhibit some homoplasy but remain useful for diagnosing the clades. With a few exceptions, Dennstaedtioideae are characterized by trilete spores and round sori protected either by a single abaxial indusium or by both abaxial and adaxial indusia (Figs. 2A,B, 3A). In the latter case, these tend to form a cup-shaped indusium widely referred to as the "*Dennstaedtia* type". In contrast, Hypolepidoideae mostly have monolete spores, except for *Pteridium* (Fig. 3A). Elongate sori are only found in Hypolepidoideae, and most genera in this subfamily lack an abaxial indusium, but they are present in *Pteridium* and *Paesia* (Fig. 2A).

Within the family, we find most of the currently recognized genera are reciprocally monophyletic; results that agree with other recent amplicon phylogenetic studies (Shang & al., 2018; Schwartsburd & al., 2020; Wang & al., 2021), and a phylogenetic analysis of complete plastomes (Lu & al., 2022). These are *Blotiella*, *Histiopteris*, *Hiya*, *Hypolepis*, *Monachosorum*, *Paesia*, and *Pteridium*. Our finding that *Dennstaedtia* is polyphyletic is also in accord with previous studies (Wolf & al., 1994, Wolf, 1995; Schuettpelz & Pryer, 2007; Perrie & al., 2015; Shang & al., 2018; Schwartsburd & al., 2020; Wang & al., 2021); however, here our dense sampling of *Dennstaedtia* provides additional insight. Like previous studies, we recover a principally tropical clade including the types of *Leptolepia*, *Patania*, and *Oenotrichia*, and a clade from higher latitudes including the types of *Coptidipteris* and *Sitobolium*. Previous studies also recovered a clade of *Microlepia*, but unlike those studies, we find that the type of *Dennstaedtia* (*D. flaccida*) nests within it. Another difference from previous studies is that we recover a clade comprising the Neotropical species *D. bipinnata* and *D. globulifera*. These species had been previously discussed as morphologically aberrant compared to other Neotropical *Dennstaedtia* (Tryon, 1960; Navarrete & Øllgaard, 2000), but neither had previously been subject to phylogenetic analysis.

Despite our findings of nested and paraphyletic taxa, we find that morphological traits have low homoplasy with the main

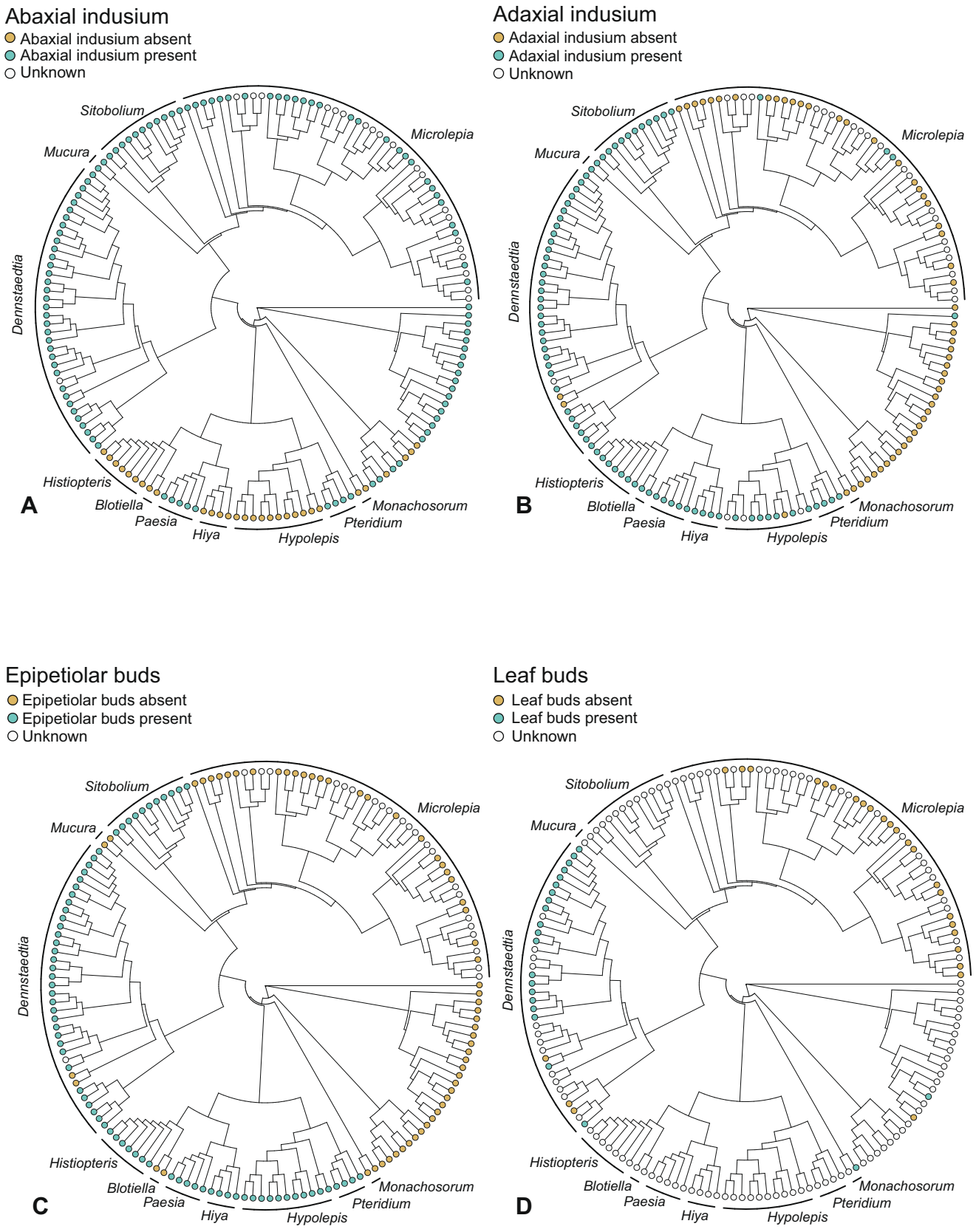

Fig. 2. Character state maps for four traits. **A**, Abaxial indusium present (blue) vs. absent (yellow); **B**, Adaxial indusium present (blue) vs. absent (yellow); **C**, Epipetiolar buds present (blue) vs. absent (yellow); **D**, Leaf buds present (blue) vs. absent (yellow). White circles indicate taxa for which character state data is missing.

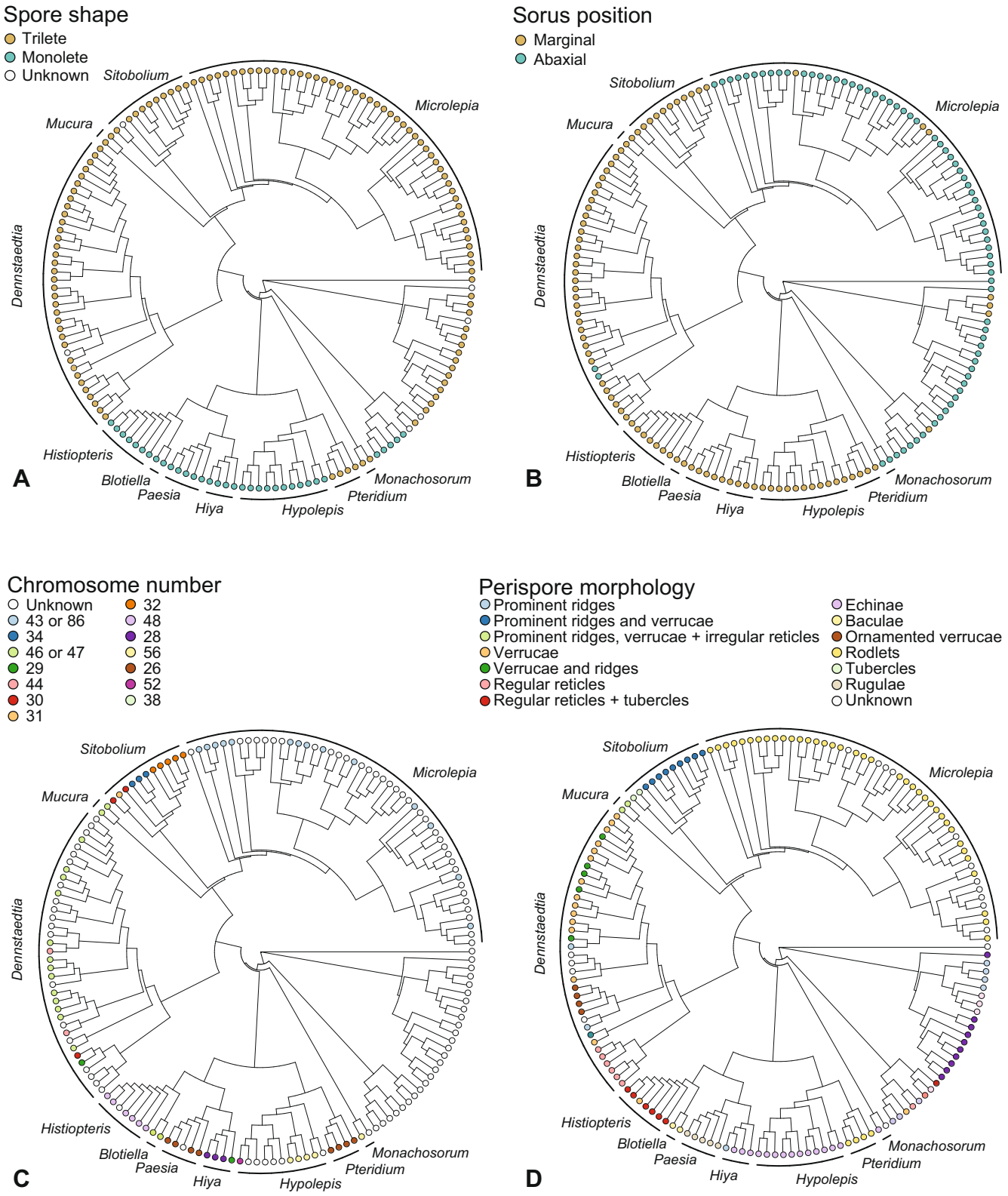

Fig. 3. Character state maps for four traits. **A**, Spore shape: monolete (blue), trilete (yellow); **B**, Sorus position: abaxial (blue), marginal (yellow). **C**, Chromosome base number: 43 or 86 (light blue), 34 (blue), 46 or 47 (light green), 29 (green), 44 (pink), 30 (red), 31 (light orange), 32 (orange), 48 (light purple), 28 (purple), 56 (yellow), 26 (brown), 52 (magenta), 38 (aquamarine); **D**, Perpispore morphology: prominent ridges (light blue), prominent ridges and verrucae (blue), prominent ridges, verrucae + irregular reticles (light green), verrucae (orange), verrucae and ridges (green), regular reticles (pink), regular reticles + tubercles (red), echinae (purple), baculae (light yellow), ornamented verrucae (brown), rodlets (yellow), tubercles (aquamarine), rugulae (light brown). White circles indicate taxa for which character state data is missing.

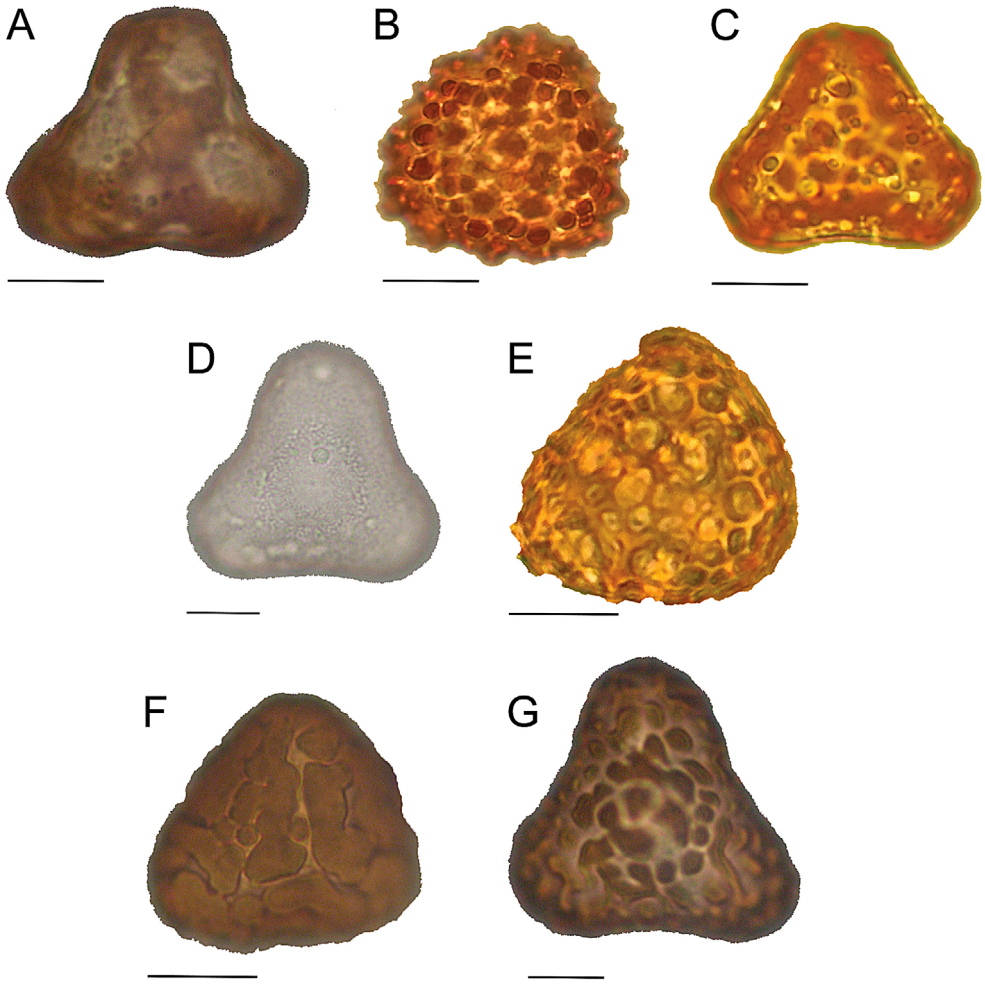

Fig. 4. Examples of perispore morphology of spores in distal view. **A**, Verrucae and irregular reticles with prominent ridges covering the corners, *Mucura globulifera* (*Yañez & Márquez 86*, LP); **B**, Tubercles, *Sitobolium wilfordii* (*Unknown coll. s.n.*, UVMVT192145, VT); **C**, Verrucae and prominent ridges to the spore sides, *Sitobolium hirsutum* (*Rothfels & al. 5282*, VT); **D**, Network of rodlets, *Microlepia speluncae* (*Rojas 4878*, MO); **E**, Regular reticle, *Dennstaedtia glabrata* (*James & Sundue 1593*, VT); **F**, Prominent ridges, *Dennstaedtia distenta* (*Mickel 4163*, LP); **G**, Verrucae and ridges, *Dennstaedtia dissecta* (*Palacios 1296*, LP). — Scale bars = 10 µm.

Table 3. Morphological characters found useful to differentiate the genera of the Dennstaedtioideae.

	Dennstaedtia	*Microlepia*	*Mucura*	*Sitobolium*
Epipetiolar buds	Present usually	Absent	Absent	Present
Petiole base shape	Sulcate	Sulcate	Subterete	Sulcate
Rachis-costa wings	Absent	Absent	Present	Absent
Leaf buds	Present or absent	Absent	Absent	Absent
Rhizome branching	Usually unbranched	Branched (or unknown)	Branched	Regularly branched
Sorus position	Marginal usually	Abaxial (rarely marginal)	Marginal	Marginal
Adaxial indusium	Present usually	Absent (rarely present)	Present	Present
Perispore ornamentation	Verrucae / Ornamented verrucae / Ridges / Prominent ridges / Regular reticles	Rodlets, evenly distributed or forming a network	Verrucae / Prominent ridges and irregular reticles	Tubercles / Verrucae and prominent ridges

clades and are therefore useful for delineating genera. Characters most useful for defining genera within Dennstaedtioideae included the presence/absence of epipetiolar buds (Fig. 2C), the presence/absence of wings along the rachis-costa junction (suppl. Fig. S2D), the shape of the petiole base (suppl. Fig. S2C), and perispore ornamentation (Fig. 3D). These results for the utility of macromorphological characters corroborate the findings of Navarrete & Øllgaard (2000), who argued that groups of Neotropical Dennstaedtioideae could be distinguished, but that most taxonomic treatments had neglected the most useful characters, those of the rhizomes and petioles. Similarly, our findings corroborate the conclusions of Tryon & Tryon (1980), Tryon & Lugardon (1990), and Yañez & al. (2016b), who found perispore morphology to be highly diagnostic.

In contrast, our results demonstrate that sorus position—the historically most heavily relied upon character in the classification of Dennstaedtioideae—is homoplastic, changing from abaxial to marginal (Fig. 3B), sometimes within traditional genera. We show that sorus position changes from marginal to abaxial in the ancestor of the *Microlepia* clade, and then back to marginal in both *D. smithii* and *D. flaccida*. This plasticity was anticipated by Bower (1928) while working on *Hypolepis*, who then concluded that sorus position should not be rigidly used when defining genera as was commonly done by 18th and 19th century botanists (Paris & Barrington, 1990). Our results corroborate that sorus position is labile within the Dennstaedtioideae and does not follow a pattern that corresponds to a useful circumscription of genera.

Taken together, our results demonstrate that clades of Dennstaedtioideae are morphologically diagnosable, particularly using rhizome, petiole, and perispore characters, and that previous classifications overemphasized sorus position, leading to polyphyletic genera.

Classification of Dennstaedtioideae. — Our finding that the type of *Dennstaedtia* (*D. flaccida*) is nested within *Microlepia* confirms taxonomic suspicions dating back over 150 years (Smith, 1842). Similar conclusions were drawn by Copeland (1947), Holttum (1968), Tryon (1960), and Tryon & Tryon (1980). This result combined with the polyphyly of *Dennstaedtia* and previous disregard for the *ICBN* rule of priority (e.g., in Tryon & Tryon, 1982) have led to an unfortunate nomenclatural situation, where the type of the largest Dennstaedtioideae genus (*Dennstaedtia*) is embedded within the second-largest genus (*Microlepia*).

One solution to this taxonomic problem would be to maintain a single globally distributed *Dennstaedtia* of ca. 130 species comprising morphologically disparate clades. The name *Dennstaedtia* would have priority. This classification would be convenient for users accustomed to that name, particularly for North American workers, and would be relatively unaffected by the loss of *Microlepia*. However, such a broadly defined *Dennstaedtia* would also be unwieldy in size and would fail to reflect the morphological disparity or evolutionary distinctions in the group. We do not think that users would find a single-genus classification more useful. Instead, we prefer smaller genera because they help emphasize evolutionary, morphological and geographic differences among lineages (Schuettpelz & al., 2018). This approach is also in line with sentiments presented by Perrie & al. (2015), Schwartsburd & al. (2020), Weakley (2020), and Wang & al. (2021) each of whom discussed a classification comprising several genera as an option in light of the polyphyly of *Dennstaedtia*.

Considering taxonomic solutions that recognize multiple genera within Dennstaedtioideae, there are several options. Our results lead us to propose a classification that recognizes four morphologically diagnosable and geographically coherent clades as genera: one that consists of the bulk of species traditionally recognized in *Dennstaedtia* (the oldest genus name available for this clade is *Patania*); one that includes *D. globulifera* and *D. bipinnata*; one that includes a set of north-temperate species including the types of *Sitobolium* and *Coptidipteris*; and one that includes the species traditionally recognized in *Microlepia*, but which also includes the type of *Dennstaedtia*. To avoid the large number of name changes that would be associated with transferring *Microlepia* species to *Dennstaedtia* and the bulk of *Dennstaedtia* to *Patania*, in parallel with this paper we have submitted a proposal to conserve *Dennstaedtia* with a new type (*D. cicutaria*; Triana-Moreno & al., 2022). Our classification thus recognizes these four clades as *Dennstaedtia*, *Microlepia*, *Mucura* (gen. nov.), and *Sitobolium*.

Previous authors have further split *Coptidipteris* from *Sitobolium*, but we do not see value in recognizing this small genus. *Coptidipteris* is based upon *Dennstaedtia wilfordii*, a species that differs from other Dennstaedtioideae by its glabrous leaves. In our results, it is sister to *D. appendiculata*, a pubescent species with a very different leaf shape. These two species share a distinctive perispore morphology of broad folds, but otherwise don't have any conspicuous shared characters we can point to. In order to maintain monophyletic genera, recognizing *Coptidipteris* would lead us to either combine *D. appendiculata* in *Coptidipteris* creating a morphologically heterogenous genus, or to recognize a yet additional genus, a monotypic *Emodiopteris* based on *D. appendiculata*. Neither of these options seem more useful than a single *Sitobolium*, which we find to be morphologically and geographically coherent.

In support of our classification, we provide morphological and geographic synopses, constituent species, and the necessary new combinations. For these, we provide basionyms and other recent combinations. For additional synonymy see Moran (1995), Mickel & Smith (2004), Navarrete & Øllgaard (2000), Yan & al. (2013), Fraser-Jenkins & al. (2017), Schwartsburd & al. (2017), Brownsey & Perrie (2018), and Hassler (2019). Species are assigned to genera either by molecular phylogenetic evidence and/or morphology. For species placed by morphology alone, we particularly emphasize rhizome morphology, epipetiolar buds, and perispore characters, which our results demonstrate are robust indicators of phylogenetic position. Species lacking sufficient evidence are listed separately and without combinations beneath the clade to which we consider them most likely to belong. Finally, we list excluded species for taxa combined under a genus to which they no longer belong.

■ TAXONOMIC TREATMENT

Key to the genera of Dennstaedtiaceae

1. Sorus supplied by a single vein, marginal or abaxial……2
1. Sorus supplied by two or more veins, marginal……8
2. Rhizome short-creeping or ascending, dictyostelic; petiole with two vascular bundles; sori exindusiate ……. ***Monachosorum***
2. Rhizome long-creeping, solenostelic; petiole with one vascular bundle; sori indusiate or exindusiate …… 3
3. Abaxial indusium absent or minute and vestigial; spores monolete…… 4
3. Abaxial indusium present; spores trilete …… 5
4. Fiddlehead of developing leaf apex protected by reduced basal pinnules; axes armed, the spines curved, apically black when mature…… ***Hiya***
4. Fiddlehead of developing leaf apex not protected by reduced basal pinnules; axes armed or not, when present, the spines straight, green to stramineous……***Hypolepis***
5. Sori abaxial, submarginal (rarely marginal); indusia usually scarious; perispore morphology comprising of rodlets that are evenly distributed or forming a network……***Microlepia***
5. Sori marginal; lower indusia similar in texture to the upper indusia; perispore morphology various, never rodlets 6
6. Epipetiolar buds absent; adaxial axes (rachis-costae) with raised wing, the wings decurrent onto the next order; petiole bases subterete, not clearly sulcate……***Mucura***
6. Epipetiolar buds usually present; adaxial axes (rachis-costae) without raised wings; petiole adaxially sulcate, the groove confluent between orders …… 7
7. Rhizome branched regularly, ca. 0.5 cm diam.; leaves less than 1 m long, lacking leaf buds; glabrous or pubescent, hairs catenate, spreading, the apex often with a capitate terminal cell; plants with a north-temperate distribution……***Sitobolium***
7. Rhizome usually unbranched, thick, ca. 0.5 to 4 cm diam.; leaves often 1–2 m long, sometimes up to ca. 12 m, often with proliferous buds, hairs various, but lacking capitate terminal cells; plants primarily tropical in distribution……***Dennstaedtia***
8. Veins anastomosing; pinnae opposite or subopposite ….9
8. Veins free; pinnae all or mostly alternate …… 10
9. Laminae glabrous or somewhat scaly, often glaucous; rhizomes scaly; unfurling leaf protected by reduced basal pinnules…… ***Histiopteris***
9. Laminae pubescent, green, not glaucous; rhizomes pubescent; unfurling leaf not protected by reduced basal pinnules…… ***Blotiella***
10. Rachises flexuous; spores monolete……***Paesia***
10. Rachises straight; spores trilete …… ***Pteridium***

I. ***Microlepia*** C.Presl, Tent. Pterid.: 124, t. 4, fig. 21–23. 1836, nom. cons. prop. – Type (designated by Smith, Hist. Fil.: 260. 1875): *Microlepia polypodioides* (Sw.) C.Presl. (≡ *Dicksonia polypodioides* Sw.) (= *Microlepia speluncae* (L.) T.Moore ≡ *Polypodium speluncae* L.).

= *Scyphofilix* Thouars, Gen. Nov. Madagasc.: 1. 1806, nom. rej. prop. – Type (designated by Farwell in Amer. Midl. Naturalist 12: 237. 1931): *Polypodium speluncae* L. (≡ *Microlepia speluncae* (L.) T.Moore).

Description. – *Plants* terrestrial or rarely rupestral; *rhizomes* short to long creeping, with trichomes or bristles, branching (or unknown); *petioles* grooved, lacking epipetiolar buds, rarely aculeate; *leaves* large, erect, decompound, usually distant, or sometimes closely spaced, lamina 1–4-pinnate with strigose, acicular hairs, axes inalate; *veins* free, with slender apices; *sori* generally abaxial and protected by an abaxial indusium, indusium half cup-shaped directed outward, or rarely sori cup-shaped, protected by adaxial and abaxial indusia, and directed downward; *spores* trilete with perispore ornamentation of rodlets. (Fig. 5)

Synopsis. – *Microlepia* is a monophyletic group of about 60 species resolved as sister to *Sitobolium*. *Microlepia* can be diagnosed by its distinctive perispore ornamentation of rodlets (Fig. 4D), and by petioles that lack epipetiolar buds (Mickel, 1973). The sori are generally abaxial and protected by an abaxial indusium, but marginal sori with both abaxial and adaxial indusia evolved at least twice as demonstrated by our results and those of Wang & al. (2021). Although nearly all Dennstaedtiaceae bear catenate hairs, those of *Microlepia* are often distinctively strigose and acicular, and never glandular. *Microlepia* is essentially an Old-World genus, distributed primarily in tropical and east Asia but extending to Africa and Madagascar, Australia, the western Pacific, and Hawaii. One species, *M. speluncae*, is widespread in the Neotropics where it appears to be adventive (Tryon & Tryon, 1982).

History of use. – *Microlepia* has been in use since it was described by Presl (1836). The largely overlooked name *Scyphofilix* Thouars was published 30 years before *Microlepia* and would have priority (Farwell, 1931), had Schwartsburd's (2017) proposal to conserve *Microlepia* against it not been approved by the General Committee. Similarly, our proposal to conserve *Dennstaedtia* with a new type aims to maintain nomenclatural stability of *Microlepia*.

Taxonomic treatments. – Wang & al. (2017) reported this as one of the most taxonomically challenging clades. Species estimates vary widely, from 33 (Moore, 2010) to 60 (PPG-I, 2016), or 100 (Yuan & al., 2012). Important regional treatments include Cambodia (Sun, 2014), China (Yan & al., 2013), India (Fraser-Jenkins & al., 2017), Japan (Nakaike, 1975), Nepal (Fraser-Jenkins & al., 2015), Taiwan (Knapp, 2011; TPG, 2019, 2021), and Thailand (Tagawa & Iwatsuki, 1979). We include 44 species and 4 named hybrids here based upon molecular phylogenetic and morphological evidence. We list an additional 25 species and 1 named hybrid that remain insufficiently known to us at this time.

Constituent species

Microlepia ×***adulterina*** W.H.Wagner in Contr. Univ. Michigan Herb. 22: 153. 1999.

Microlepia ×***austroizuensis*** N.Nakato & Seriz. in J. Jap. Bot. 56: 164. 1981.

Microlepia* ×*bipinnata (Makino) Y.Shimura in J. Phytogeogr. Taxon. 27: 41. 1979 ≡ *Microlepia marginata* var. *bipinnata* Makino in J. Jap. Bot. 3: 47. 1926.

Microlepia boluoensis Y.Yuan & L.Fu in Nordic J. Bot. 30(2): 170. 2012.

Microlepia calvescens (Wall. ex Hook.) C.Presl in Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 455. 1851 ≡ *Davallia calvescens* Wall. ex Hook., Sp. Fil. 1: 172. 1845.

Microlepia caudigera T.Moore, Index Fil.: 303. 1861.

Microlepia chrysocarpa Ching in Sinensia 1(1): 3. 1929.

Microlepia crassa Ching in Chien & Chun, Fl. Reipubl. Popularis Sin. 2: 360. 1959.

Microlepia dubia (Roxb.) C.V.Morton in Contr. U.S. Natl. Herb. 38: 342. 1974 ≡ *Polypodium dubium* Roxb. in Calcutta J. Nat. Hist. 4(16): 496. 1844.

Microlepia firma Mett. ex Kuhn in Linnaea 36: 146. 1869.

Microlepia flaccida (G.Forst) Fée, Mém. Foug. 5 (Gen. Filic.): 327. 1852 ≡ *Trichomanes flaccidum* G.Forst., Fl. Ins. Austr.: 85. 1786 ≡ *Dennstaedtia flaccida* (G.Forst.) Bernh. in J. Bot. (Schrader) 1800(2): 124, t. 1, fig. 3. 1801.

Microlepia hallbergii (J.F.R.Almeida) C.Chr., Index Filic., Suppl. Tert.: 127. 1934 ≡ *Davallia hallbergii* J.F.R.Almedia in J. Indian Bot. Soc. 5: 19, t. [unum.]. 1926.

Microlepia hookeriana (Wall. ex Hook.) C.Presl in Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 455. 1851 ≡ *Davallia hookeriana* Wall. ex Hook., Sp. Fil. 1: 172, t. 47B. 1845.

Microlepia intramarginalis (Tagawa) Seriz. in J. Jap. Bot. 47: 48. 1972 ≡ *Microlepia strigosa* var. *intramarginalis* Tagawa in Act. Phytotax. Geobot. 10(3): 202. 1941.

Microlepia izu-peninsulae Sa.Kurata in J. Geobot. 11: 4. 1962.

Microlepia* ×*kandelii Fraser-Jenk., Annot. Checkl. Ind. Pterid. 1: 175. 2016.

Microlepia kerrii S.J.Moore in Phytotaxa 324(2): 193, fig. 1. 2017.

Microlepia krameri C.M.Kuo in Taiwania 30: 59. 1985.

Microlepia kurzii (C.B.Clarke) Bedd., Handb. Ferns Brit. India: 66. 1883 ≡ *Davallia kurzii* C.B.Clarke in Trans. Linn. Soc. London, Bot. 1(7): 446. 1880.

Microlepia majuscula (E.J.Lowe) T.Moore, Index Fil.: 297. 1861 ≡ *Davallia majuscula* E.J.Lowe, Ferns 8: 93, t. 33. 1859.

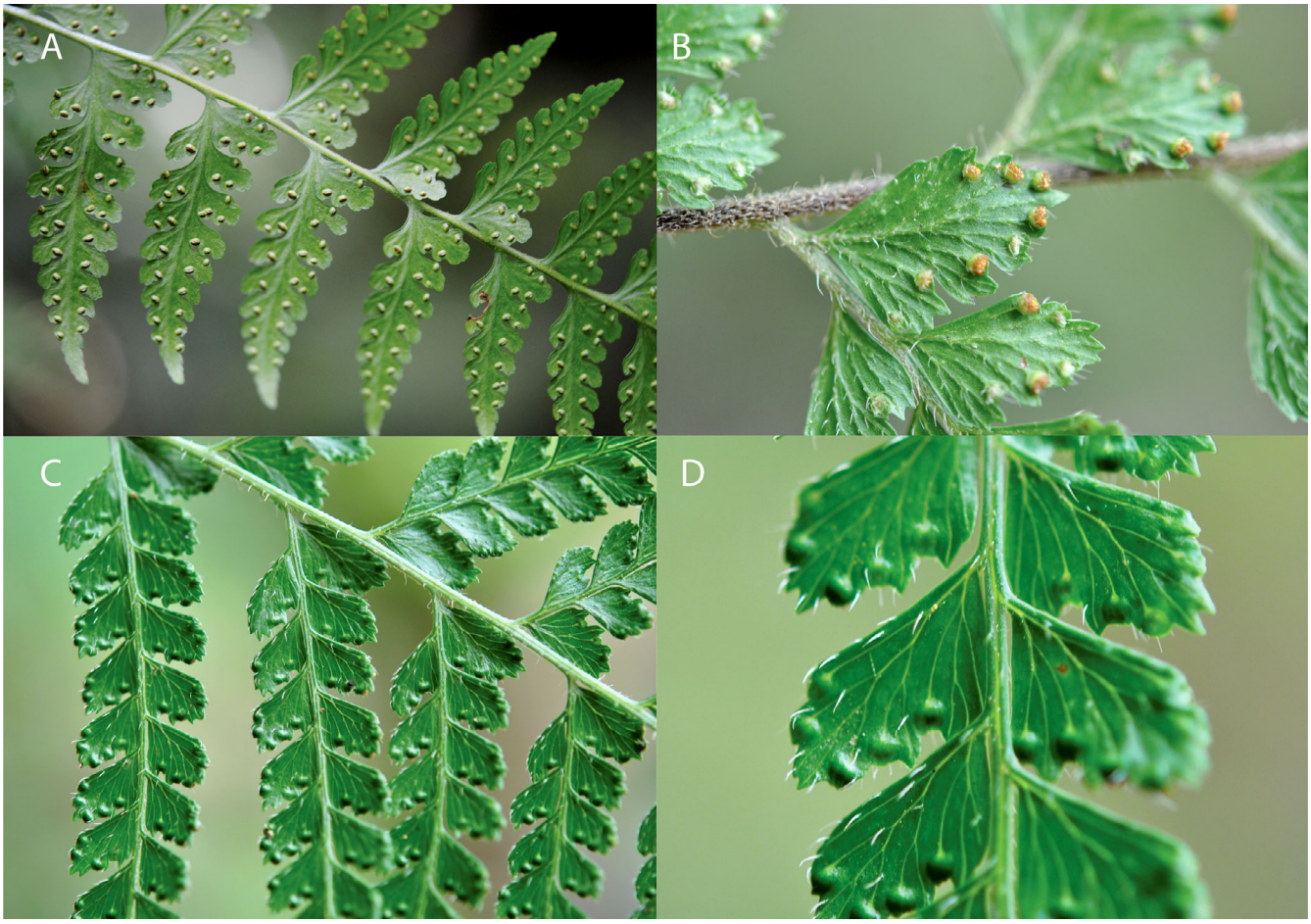

Fig. 5. Characters of *Microlepia*. **A**, Lower leaf surface; **B**, Detail of abaxial sori; **C**, Upper leaf surface; **D**, Detail of pinna costae. — All from *Microlepia strigosa*, Philippines, *Sundue 3163* (CMUH, TAIF, VT). All photos by M. Sundue.

Microlepia manilensis (Goldm.) C.Chr., Index Filic.: 427. 1906 ≡ *Davallia manilensis* C.Presl ex Goldm. in Nov. Actorum Acad. Caes. Leop.-Carol. Nat. Cur. 19(Suppl. 1): 465. 1843.

Microlepia marginata (Panz.) C.Chr., Index Filic. 4: 212. 1905 ≡ *Polypodium marginatum* Panz. in Christmann & Panzer, Vollst. Pflanzensyst. 13(1): 199. 1786.

Microlepia matthewii Christ in Notul. Syst. (Paris) 1(2): 54. 1909.

Microlepia mollifolia Tagawa in Acta Phytotax. Geobot. 5(3): 189. 1936.

Microlepia nepalensis (Spreng.) Fraser-Jenk., Kandel & Pariyar, Ferns Fern-Allies Nepal 1: 172. 2015 ≡ *Davallia nepalensis* Spreng., Syst. Veg. 4(1): 121. 1827.

Microlepia nipponica (Miq.) C.Chr., Index Filic.: 427. 1906 ≡ *Davallia nipponica* Miq. in Ann. Mus. Bot. Lugduno-Batavi 3: 180. 1867.

Microlepia obtusiloba Hayata in Bot. Mag. (Tokyo) 23: 27. 1909.

Microlepia platyphylla (D.Don) J.Sm. in London J. Bot. 1: 427. 1842 ≡ *Davallia platyphylla* D.Don, Prodr. Fl. Nepal.: 10. 1825.

Microlepia proxima (Blume) C.Presl in Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 455. 1851 ≡ *Davallia proxima* Blume, Enum. Pl. Javae 2: 238. 1828.

Microlepia pseudohirta Rosenst. in Repert. Spec. Nov. Regni Veg. 9: 425. 1911.

Microlepia pseudostrigosa Makino in Bot. Mag. (Tokyo) 28: 337. 1914.

Microlepia rhomboidea (Wall. ex Kunze) Prantl in Arbeiten Königl. Bot. Gart. Breslau 1: 31. 1892 ≡ *Davallia rhomboidea* Wall. ex Kunze in Bot. Zeitung (Berlin) 8(8): 158. 1850.

Microlepia ridleyi Copel. in Philipp. J. Sci., C, 11: 39. 1916.

Microlepia scaberula Mett. ex Kuhn in Linnaea 36(2): 148. 1869.

Microlepia setosa (Sm.) Alston in Philipp. J. Sci. 50: 177, t. 1, fig. 3. 1933 ≡ *Davallia setosa* Sm. in Rees, Cycl. 10: *Davallia* no. 18. 1808.

Microlepia shubhangiae S.Sharma & Kholia in Webbia 73(2): 192. 2018.

Microlepia smithii (Hook.) Y.H.Yan in Taxonomy 1(3): 256 ≡ *Dicksonia smithii* Hook., Sp. Fil. 1: 80, t. 28D. 1844 ≡ *Dennstaedtia smithii* (Hook.) T.Moore, Index Fil.: 308. 1861.

Microlepia speluncae (L.) T.Moore, Index Fil.: 93 1857 ≡ *Polypodium speluncae* L., Sp. Pl.: 1093. 1753.

Microlepia strigosa (Thunb.) C.Presl in Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 455. 1851 ≡ *Trichomanes strigosum* Thunb. in Murray, Syst. Veg., ed. 14: 941. 1784 ≡ *Dennstaedtia strigosa* (Thunb.) J.Sm., Hist. Fil.: 265. 1875.

Microlepia substrigosa Tagawa in Acta Phytotax. Geobot. 5(3): 189. 1936.

Microlepia subtrichosticha Ching in Chien & Chun, Fl. Reipubl. Popularis Sin. 2: 368. 1959.

Microlepia tenera Christ in Notul. Syst. (Paris) 1(2): 53. 1909.

Microlepia thailandensis S.J.Moore in Phytotaxa 324(2): 193, fig. 1. 2017.

Microlepia todayensis Christ in Philipp. J. Sci., C, 3: 272. 1908.

Microlepia trapeziformis (Roxb. ex Griff.) Kuhn in Festschr. 50 Jähr. Jub. Königstädt. Realschule Berlin: 347. 1882 ≡ *Davallia trapeziformis* Roxb. ex Griff. in Calcutta J. Nat. Hist. 4: 516. 1844.

Microlepia trichocarpa Hayata, Icon. Pl. Formos. 4: 210, fig. 142. 1914.

Microlepia trichosora Ching in Chien & Chun, Fl. Reipubl. Popularis Sin. 2: 358. 1959.

Microlepia yakusimensis Tagawa in Acta Phytotax. Geobot. 11(3): 238. 1942.

Insufficiently known taxa

Microlepia communis Ching in Chien & Chun, Fl. Reipubl. Popularis Sin. 2: 367. 1959 [recognized by Wang & al. (2021), considered syn. of *Microlepia rhomboidea* by Hassler (2019)].

Microlepia concinna R.M.Tryon & A.F.Tryon in Rhodora 83: 135. 1981 ≡ [nom. nov. for] *Dennstaedtia concinna* Rosenst. in Hedwigia 56: 349. 1915, non *D. concinna* C.Presl in Moore, Index Fil.: xcvii. 1857 [insufficiently known, possible affinity with *Dennstaedtia smithii*].

Microlepia crenata Ching in Chien & Chun, Fl. Reipubl. Popularis Sin. 2: 368. 1959 [recognized by Wang & al. (2021), considered a syn. of *Microlepia todayensis* by Hassler (2019)].

Microlepia fadenii Pic.Serm. in Webbia 27: 406. 1973 [possible syn. of *Microlepia hallbergii*].

Microlepia fujianensis Ching in Wuyi Sci. J. 1(1): 1. 1981 [doubtful, known only from the type].

Microlepia ×hirtiindusiata P.S.Wang in Wang & Wang, Pterid. Fl. Guizhou: 441. 2001 [presumed to be a sterile hybrid, more study is needed].

Microlepia hancei Prantl in Arbeiten Königl. Bot. Gart. Breslau 1: 35. 1892 [recognized by Wang & al. (2021), considered a syn. of *M. nepalensis* by Hassler (2019)].

Microlepia herbacea Ching & C.Chr. ex Tardieu & C.Chr. in Notul. Syst. (Paris) 6: 6, t. 1(1–2). 1937 [recognized by Wang & al. (2021), considered a syn. of *M. mathewii* by Hassler (2019)].

Microlepia khasiyana (Hook.) C.Presl in Abh. Königl. Böhm. Ges. Wiss., ser. 5, 6: 455. 1851 ≡ *Davallia khasiyana* Hook., Sp. Fil. 1: 173, t. 47A. 1856 [recognized by Wang & al. (2021), considered a syn. of *M. strigosa* by Fraser-Jenkins (2008)].

Microlepia lofoushanensis Ching in Chien & Chun, Fl. Reipubl. Popularis Sin. 2: 364. 1959 [recognized by Wang & al. (2021), considered a syn. of *M. rhomboidea* by Hassler (2019)].

Dennstaedtia macgregorii Copel. in Philipp. J. Sci. 81: 4, t. 2. 1952 [insufficiently known by us, Copeland (1958) suggested an affinity with *D. smithii*, here treated in *Microlepia*].

Microlepia melanorhachis Rosenst. in Repert. Spec. Nov. Regni Veg. 12: 526. 1913 [insufficiently known].
Microlepia membranacea B.S.Wang in Acta Sci. Nat. Univ. Sunyatseni 1961(2): 46. 1961 [insufficiently known].
Microlepia nudisora C.Chr. in Bull. Bernice P. Bishop Mus. 177: 34. 1943 [insufficiently known].
Microlepia pilosiuscula (Sm.) C.V.Morton in Contr. U.S. Natl. Herb. 38: 313. 1974 ≡ *Davallia pilosiuscula* Sm. in Rees, Cycl. 11: *Davallia* no. 10. 1808 [possibly an earlier name for *D. trapeziformis* (Fraser-Jenkins, 2008)].
Microlepia protracta Copel. in Philipp. J. Sci. 81: 5. 1952 [insufficiently known].
Microlepia puberula Alderw. in Bull. Jard. Bot. Buitenzorg, sér. 2, 11: 17. 1913 [possible syn. of *D. majuscula* (Fraser-Jenkins & al. (2017)].
Microlepia rheophila K.Iwats. & M.Kato in Acta Phytotax. Geobot. 31(1–3): 35. 1980 [insufficiently known].
Microlepia sinostrigosa Ching in Chien & Chun, Fl. Reipubl. Popularis Sin. 2: 360. 1959 [considered a syn. of *M. pseudostrigosa* Makino by Knapp (2011)].
Microlepia subspeluncae Ching in Chien & Chun, Fl. Reipubl. Popularis Sin. 2: 244. 1959 [recognized by Wang & al. (2021), considered a syn. of *M. speluncae* by Hassler (2019), forming a clade with *M. speluncae* in our results].
Microlepia szechuanica Ching in Chien & Chun, Fl. Reipubl. Popularis Sin. 2: 363. 1959 [recognized by Wang & al. (2021), considered a syn. of *M. strigosa* by Hassler (2019)].
Microlepia vitiensis Brownlie in Beih. Nova Hedwigia 55: 118. 1977 [insufficiently known].
Microlepia yaoshanica Ching in Bull. Fan Mem. Inst. Biol., n.s., 1: 299. 1949 [recognized by Wang & al. (2021), considered a syn. of *M. trapeziformis* by Hassler (2019), and is sister to that taxon in our phylogenetic results].
Microlepia yunnanensis Ching in Chien & Chun, Fl. Reipubl. Popularis Sin. 2: 366. 1959 [recognized by Wang & al. (2021), considered a syn. of *M. trichocarpa* by Hassler (2019)].

Excluded names

Microlepia fluminensis Fée, Crypt. Vasc. Brésil 1: 151, t. 51, fig. 1. 1869 ≡ *Dennstaedtia fluminensis* (Fée) C.Chr., Index Filic.: 217. 1905 (= *Dennstaedtia cornuta* (Kaulf.) Mett.).
Microlepia lindsayiformis Fée, Crypt. Vasc. Brésil 1: 152, t. 51, fig. 2. 1869 ('*lindsayaeformis*') ≡ *Dennstaedtia lindsayiformis* (Fée) C.Chr., Index Filic.: 217. 1905 (= *Dennstaedtia cornuta* (Kaulf.) Mett.).

II. ***Dennstaedtia*** Bernh. in J. Bot. (Schrader) 1800(2): 124. 1801, nom. cons. prop. – Type: *Dennstaeaedtia dissecta* (Sw.) T.Moore (*Dicksonia dissecta* Sw.), typ. cons. prop.
= *Patania* C.Presl, Tent. Pterid: 137, t. 5, fig. 12–14. 1836 – Type (designated by Christensen, Index Filic.: xxix. 1906): *Patania obtusifolia* (Willd.) C.Presl (≡ *Dicksonia obtusifolia* Willd.).
= *Leptolepia* Prantl in Arbeiten Königl. Bot. Gart. Breslau 1: 23. 1892 – Type (designated by Christensen, Index Filic.: xxviii. 1960): *Leptolepia novae-zelandiae* (Colenso) Mett. ex Diels. (≡ *Davallia novae-zelandiae* Colenso).
= *Costaricia* Christ in Bull. Soc. Bot. Genève, ser. 2, 1(5): 229. 1909 – Type: *Costaricia werckleana* Christ.
= *Oenotrichia* Copel. in Univ. Calif. Publ. Bot. 16: 82. 1929 – Type: *Oenotrichia maxima* (E.Fourn.) Copel. (≡ *Leucostegia maxima* E.Fourn.).
= *Paradennstaedtia* Tagawa in J. Jap. Bot. 27(6): 213. 1952 – Type: *Paradennstaedtia glabrata* (Ces.) Tagawa (≡ *Dicksonia glabrata* Ces.).

Description. – *Plants* terrestrial or rupestral (or rarely epiphytic); *rhizomes* short to long creeping, unbranched, with catenate hairs; *petioles* grooved, adaxially sulcate, usually bearing epipetiolar buds, rarely aculeate; *leaves* large, erect, decompound, 2–4-pinnate, often with proliferous buds, axes inalate; *veins* free, with enlarged or slender apices; *sori* usually marginal, usually provided with abaxial and adaxial indusia fused into purse- or cup-shaped involucre; *spores* trilete, perispore regular reticles, ridges and verrucate. (Fig. 6)

Synopsis. – As defined here, *Dennstaedtia* is generally a pantropical genus but absent from continental Africa. It includes ca. 55 species sister to all other Dennstaedtioideae. *Dennstaedtia* is recognized by having rhizomes that are usually unbranched, petioles bearing epipetiolar buds, and by often bearing proliferous buds upon the leaves. The leaves of most species are large, and some species such as *D. scandens* are indeterminate and scandent over other vegetation. The spores of Neotropical species exhibit verrucae and ridges (Fig. 4F,G), whereas regular reticles are found among Paleotropical species (Fig. 4E). Neotropical species of *Dennstaedtia* are fairly morphologically homogenous, whereas Paleotropical species exhibit more trait variation, at least in our analysis. This is particularly true of species formerly treated in the small genera *Leptolepia* (*Dennstaedtia novae-zelandiae*) and *Oenotrichia* (*Dennstaedtia maxima*) which differ by branched rhizomes, the lack of epipetiolar buds, and abaxial sori along with the constituent loss of the adaxial indusia. *Dennstaedtia maxima* further differs by rhizomes provided with scales instead of hairs and by having monolete (rarely trilete) spores. These taxa are part of an unresolved polytomy. If they prove to be sister to the remainder of *Dennstaedtia*, some users may prefer to recognize them as small genera.

The early Eocene *Dennstaedtia christophelii* Pigg & al. (2021) has been placed in this clade based upon its similarity to *D. mathewsii* (Hook.) C.Chr. and *D. producta* Mett. This age sits between two recent clade age estimates; Testo & Sundue (2016) estimated the crown group of *Dennstaedtia* to have diverged during the late Eocene, and Schwartsburd & al. (2020) estimated it to diverge during the mid-Miocene.

History of use. – This circumscription retains the familiar circumscription of *Dennstaedtia* minus the two species of *Mucura* gen. nov., the two species moved to *Microlepia*, and the temperate clade here recognized as *Sitobolium*. The oldest available name for this clade is *Patania* Presl (1836), but our

Fig. 6. Characters of *Dennstaedtia*. **A**, Upper Leaf surface with leaf buds present in pinna axils; **B**, Upper leaf surface and grooved rachis-costa axes without raised wings; **C**, Lower leaf surface and marginal sori; **D**, Creeping unbranched rhizome; **E**, Subterete petioles with prominent epipetiolar buds. — All photos by M. Sundue except E by P.H. Hovenkamp.

proposal (Triana-Moreno & al., 2022) to conserve *Dennstaedtia* with *D. dissecta* as the type would permit its continued use and avoid further name changes. The New Zealand endemic *D. novae-zelandiae* was previously recognized as the monotypic genus *Leptolepia*. *Dennstaedtia maxima*, endemic to New Caledonia, was previously recognized as *Oenotrichia*.

Taxonomic treatments. – The Neotropical species of Ecuador were revised by Navarrete & Øllgaard (2000), who pioneered the emphasis of rhizome characters. Schwartsburd & al. (2017) treated the Bolivian species, and Mexican and Mesoamerican species were treated by Mickel & Smith (2004) and Moran (1995), respectively. Brownsey & Perrie (2018) treated the species from New Zealand, and those from the Western Pacific were treated by Nakamura (2008). Copeland (1958) recognized several narrowly distributed species in his treatment of Philippine ferns that presumably belong here, but which are insufficiently known by us. We include 37 constituent species of *Dennstaedtia* based upon molecular phylogenetic and morphological evidence, and we make necessary combinations for two of them. We list an additional 15 that remain insufficiently known to us at this time.

New combinations and constituent species

Dennstaedtia ampla (Baker) Bedd. in J. Bot. 31: 227. 1893 ≡ *Dicksonia ampla* Baker in J. Linn. Soc. 22: 223. 1886.

Dennstaedtia antillensis (Jenman) C.Chr., Index Filic.: 216. 1905 ≡ *Dicksonia antillensis* Jenman in J. Bot. 24: 267. 1886.

Dennstaedtia arborescens (Willd.) E.Ekman ex Maxon in Proc. Biol. Soc. Wash. 43: 88. 1930 ≡ *Davallia arborescens* Willd., Sp. Pl. 5: 470. 1810.

Dennstaedtia arcuata Maxon in Amer. Fern J. 35(1): 22. 1945.

Dennstaedtia articulata Copel. in Leafl. Philipp. Bot. 2: 396. 1908.

Dennstaedtia auriculata Navarr. & B.Øllg. in Nordic J. Bot. 20(3): 337, fig. 5a–d. 2000.

Dennstaedtia canaliculata Alderw. in Bull. Jard. Bot. Buitenzorg, ser. 2, 16: 6. 1914.

Dennstaedtia cicutaria (Sw.) T.Moore, Index. Fil.: 97. 1857 ≡ *Dicksonia cicutaria* Sw. in J. Bot. (Schrader) 1800(2): 91. 1801.

Dennstaedtia cornuta (Kaulf.) Mett. in Ann. Sci. Nat., Bot., sér. 5, 2: 260. 1864 ≡ *Dicksonia cornuta* Kaulf., Enum. Filic.: 227. 1824.

Dennstaedtia coronata (Sodiro) C.Chr., Index Filic.: 216. 1905 ≡ *Dicksonia adiantoides* var. *coronata* Sodiro, Recens. Crypt. Vasc. Quit.: 23. 1883.

Dennstaedtia davallioides (R.Br.) T.Moore, Index Fil.: 305. 1861 ≡ *Dicksonia davallioides* R.Br., Prodr.: 158. 1810.

Dennstaedtia dissecta (Sw.) T.Moore, Index Fil.: 305. 1861 ≡ *Dicksonia dissecta* Sw. in J. Bot. (Schrader) 1800(2): 91. 1801.

Dennstaedtia distenta (Kunze) T.Moore, Index Fil.: 306. 1861 ≡ *Dicksonia distenta* Kunze, Analecta Pteridogr.: 39. 1837.

Dennstaedtia elmeri Copel., Leafl. Philipp. Bot. 1: 233. 1907.

Dennstaedtia glabrata (Ces.) C.Chr., Index Filic.: 217. 1905 ≡ *Dicksonia glabrata* Ces. in Rendiconto Accad. Sci. Fis & Mat. 16: 24, 28. 1877.

Dennstaedtia glauca (Cav.) C.Chr. ex Looser in Revista Chilena Hist. Geogr. 69: 184. 1932 ≡ *Davallia glauca* Cav., Descr. Pl.: 278. 1802.

Dennstaedtia hooveri Christ in Philipp. J. Sci., C, 2: 169. 1907.

Dennstaedtia kalbreyeri Maxon in Proc. Biol. Soc. Wash. 51: 40. 1938 ≡ *Dicksonia pubescens* Baker in J. Bot. 19: 203. 1881, nom. illeg, non Schkuhr 1809 ≡ *Dennstaedtia pubescens* C.Chr., Index Filic.: 218. 1905, nom. illeg.

Dennstaedtia macrosora Navarr. & B.Øllg. in Nordic J. Bot. 20(3): 340, fig. 6N–O. 2000.

Dennstaedtia magnifica Copel. in Univ. Calif. Publ. Bot. 18: 218. 1942.

Dennstaedtia maxima (E.Fourn.) L.A.Triana & Sundue, **comb. nov.** ≡ *Leucostegia maxima* E.Fourn. in Ann. Sci. Nat., Bot., sér. 5, 18: 334. 1873 ≡ *Oenotrichia maxima* (E.Fourn.) Copel. in Univ. Calif. Publ. Bot. 16: 82. 1929.

Dennstaedtia mathewsii (Hook.) C.Chr., Index. Filic.: 218. 1905 ≡ *Deparia mathewsii* Hook., Sp. Fil. 1: 85, t. 30B. 1844.

Dennstaedtia novae-zelandiae (Colenso) Keyserl., Polyp. Herb. Bunge.: 22. 1873 ≡ *Davallia novae-zelandiae* Colenso in Tasmanian J. Nat. Sci. 2: 182. 1842 ≡ *Microlepia novae-zelandiae* (Colenso) J.Sm., Cat. Ferns Kew: 67. 1856 ≡ *Leptolepia novae-zelandiae* (Colenso) Mett. ex Diels in Engler & Prantl, Nat. Pflanzenfam. 1: 212, fig. 11a, b. 1899.

Dennstaedtia novoguineensis (Rosenst.) Alston in J. Bot. 77: 289. 1939 ≡ *Dennstaedtia smithii* var. *novoguineensis* Rosenst. in Repert. Spec. Nov. Regni Veg. 10: 323. 1912.

Dennstaedtia obtusifolia (Willd.) T.Moore, Index Fil.: 306. 1861 ≡ *Dicksonia obtusifolia* Willd., Sp. Pl. 5(1): 483. 1810.

Dennstaedtia paucirrhiza Navarr. & B.Øllg. in Nordic J. Bot. 20(3): 333, fig. 3a–e. 2000.

Dennstaedtia producta Mett. in Ann. Sci. Nat., Bot., sér. 5, 2: 260. 1864.

Dennstaedtia resinifera (Blume) Mett. ex Kuhn in Ann. Mus. Bot. Lugduno-Batavi 4: 290. 1869 ≡ *Cheilanthes resinifera* Blume, Enum. Pl. Javae: 138. 1828.

Dennstaedtia samoensis (Brack.) T.Moore, Index Fil.: 307. 1857 ≡ *Sitolobium samoense* Brack., U.S. Expl. Exped., Filic.: 274, t. 38, fig. 1. 1854.

Dennstaedtia scandens (Blume) T.Moore, Index Fil.: 307. 1861 ≡ *Dicksonia scandens* Blume, Enum. Pl. Javae: 240. 1828.

Dennstaedtia spinosa Mickel in Amer. Fern J. 58(1): 90. 1968.

Dennstaedtia sprucei T.Moore, Index Fil.: 308. 1861.

Dennstaedtia tripinnatifida Copel. in Philipp. J. Sci. 60: 109, t. 16. 1936.

Dennstaedtia tryoniana Navarr. & B.Øllg. in Nordic J. Bot. 20(3): 334, fig. 2a–j. 2000.

Dennstaedtia vagans (Baker) Diels in Engler & Prantl, Nat. Pflanzenfam. 1(4): 218. 1899 ≡ *Dicksonia vagans* Baker in J. Bot. 162. 1871.

Dennstaedtia werckleana (Christ) Navarr. & B.Øllg. in Nordic J. Bot. 20(3): 344, fig. 8h–j. 2000 ≡ *Costaricia werckleana* Christ in Bull. Soc. Bot. Genéve 1(5): 229. 1909.

Dennstaedtia wercklei (Christ) R.M.Tryon in Contr. Gray Herb. 187: 50. 1960 ≡ *Saccoloma wercklei* Christ in Bull. Herb. Boiss., sér. 2, 4(11): 1100. 1904.

Insufficiently known species

Dennstaedtia anthriscifolia (Bory) T.Moore, Index Fil: 303. 1861 ≡ *Lonchitis anthriscifolia* Bory in Willd., Sp. Pl. 5: 461. 1810 [treated in *Dennstaedtia* by Tardieu-Blot (1958), who described the spores as minutely spiny, an uncommon character state for the clade].

Dennstaedtia dennstaedtioides (Copel.) Copel. in Philipp. J. Sci., C, 2: 126. 1907 ≡ *Microlepia dennstaedtioides* Copel. in Philipp. J. Sci. 1, Suppl. 2: 148, fig. 4. 1906 [insufficiently known].

Dennstaedtia fusca Copel. in Philipp. J. Sci. 81: 4, t. 3. 1952 [insufficiently known].

Oenotrichia macgillivrayi (E.Fourn.) Copel. in Univ. Calif. Publ. Bot. 16: 82. 1929 ≡ *Leucostegia maxima* E.Fourn. in Ann. Sci. Nat., Bot., ser. 5, 18: 344. 1873 [insufficiently known].

Dennstaedtia madagascariensis (Kunze) Tardieu in Humbert, Fl. Madag. Fam. 5(1): 11. 1958 ≡ *Dicksonia madagascariensis* Kunze, Analecta Pteridogr.: 38. 1837 [the long-creeping rhizomes appear to lack epipetiolar buds].

Dennstaedtia merrillii Copel. in Philipp. J. Sci., C, 2: 126. 1907 [insufficiently known].

Dennstaedtia parksii Copel. ex Morton in Bull. Bernice P. Bishop Mus. 220: 28, fig. 4. 1959 [insufficiently known].

Dennstaedtia penicillifera Alderw. in Bull. Jard. Bot. Buitenzorg, ser. 2, 28: 17, t. 1. 1918 [insufficiently known].

Dennstaedtia philippinensis Copel. in Leafl. Philipp. Bot. 9: 3107. 1920 [insufficiently known].

Dennstaedtia remota (Christ) Diels in Engler & Prantl, Nat. Pflanzenfam. 1(4): 218. 1899 ≡ *Dicksonia remota* Christ in Verh. Naturf. Ges. Basel 11: 423. 1896 [insufficiently known].

Dennstaedtia rufidula C.Chr. in Gard. Bull. Straits Settlem. 7: 226, t. 51. 1934 [insufficiently known].

Dennstaedtia shawii Copel. in Philipp. J. Sci. 30: 326. 1926 [insufficiently known].

Dennstaedtia sumatrana Alderw. in Bull. Dép. Agric. Indes Néerl. 18: 6. 1908 [insufficiently known].

Dennstaedtia terminalis Alderw. in Bull. Jard. Bot. Buitenzorg, ser. 2, 16: 6, t. 4. 1914 [insufficiently known, the apparently long-creeping rhizome is aberrant for this clade].

Dennstaedtia williamsii Copel. in Philipp. J. Sci. 1, Suppl. 2: 148. 1906 [insufficiently known].

Excluded names

Dennstaedtia appendiculata (Wall. ex Hook.) J.Sm., Hist. Fil.: 265. 1875 ≡ *Dicksonia appendiculatum* Wall. ex Hook., Sp. Fil. 1: 79, t. 27C. 1844 ≡ *Sitobolium appendiculatum* (Wall. ex Hook.) L.A.Triana & Sundue.

Dennstaedtia elwesii (Baker) Bedd., Handb. Ferns Brit. India: 26. 1883 ≡ *Dicksonia elwesii* Baker in Hooker & Baker, Syn. Fil., ed. 2: 54. 1874 [= *Sitobolium appendiculatum* (Wall. ex Hook.) L.A.Triana & Sundue].

Dennstaedtia scabra (Wall. ex Hook.) T.Moore, Index Fil.: 307. 1861 ≡ *Dicksonia scabra* Wall. ex Hook, Sp. Fil. 1: 80, t. 28B. 1844 [= *Sitobolium zeylanicum* (Sw.) L.A. Triana & Sundue].

III. ***Sitobolium*** Desv. in Mém. Soc. Linn. Paris 6: 262. 1827 [*Sitolobium* J.Sm. in J. Bot. (Hooker) 3: 418. 1841, orth. var., *Litolobium* Newman in Phytologist 5: 236. 1854, orth. var.] – Type: *Sitobolium punctilobulum* (Michx.) Desv. (≡ *Nephrodium punctilobulum* Michx.).

= *Adectum* Link, Fil. Spec.: 42. 1841 – Type: *Adectum pilosiusculum* (Willd.) Link (≡ *Dicksonia pilosiuscula* Willd.).

= *Coptidipteris* Nakai & Momose in Cytologia, Vol. Fuji Jub. 1: 365. 1937 [*Coptodipteris*, orth. var.] – Type: *Coptidipteris wilfordii* (T.Moore) Nakai & Momose (≡ *Microlepia wilfordii* T.Moore).

= *Fuziifilix* Nakai & Momose in Cytologia, Vol. Fuji Jub. 1: 365. 1937 – Type: *Fuziifilix pilosella* (Hook.) Nakai & Momose (≡ *Davallia pilosella* Hook.).

= *Emodiopteris* Ching & S.K.Wu in Acta Phytotax. Sin. 16(4): 21. 1978 – Type: *Emodiopteris appendiculata* (Wall. ex Hook.) Ching & S.K.Wu (≡ *Dicksonia appendiculata* Wall. ex Hook.).

Description. – *Plants* terrestrial or rupestral; *rhizomes* short to long creeping, generally branched, with catenate hairs; *petioles* grooved, adaxially sulcate, bearing epipetiolar buds, unarmed; *leaves* small to moderately sized, generally less than 1 m long, erect, decompound, 2–4-pinnate, usually with catenate hairs and sometimes glandular hairs, without proliferous leaf buds, axes inalate; *veins* free, with enlarged apices; *sori* marginal, provided with abaxial and adaxial indusia fused into a cup-shaped involucre; *spores* trilete, perispore of prominent ridges and verrucae, or tubercles. (Fig. 7)

Synopsis. – *Sitobolium* is a small clade of ca. five species sister to *Microlepia. Sitobolium* are distinguished by their relatively small leaves that have elongate catenate hairs. These hairs often bear a capitate non-glandular terminal cell. *Sitobolium punctilobulum* and *S. appendiculatum* additionally have glandular hairs. *Sitobolium wilfordii*, however, is glabrous. All *Sitobolium* have epipetiolar buds, enlarged vein endings, and marginal cup-shaped sori comprised of both abaxial and adaxial indusia. The epipetiolar buds distinguish them from their closest relatives, *Microlepia* and *Mucura*, but this character is homoplastic and widespread in the family. *Sitobolium appendiculatum* and *S. wilfordii* have

previously been treated as *Emodiopteris* and *Coptidipteris* respectively. The two are united in having tuberculate perispore morphology (Fig. 4B) (vs. the verrucate perispore, with prominent ridges seen in other *Sitobolium* species), but otherwise lack diagnostic characters to distinguish them as a distinct genus and are therefore included here. The geographical distribution of *Sitobolium* is the Northern Hemisphere; most species are East Asian—*S. punctilobulum* is the single North American species. We recovered it as a sister to the East Asian *S. zeylanica* (as *S. scabra*) as did Schwartsburd & al. (2020), who inferred an early Miocene divergence time between the two. This age estimate corresponds well with a major dispersal event from Asia to North America for many plant groups using the Bering land bridge or North Atlantic land bridges (Lee & al., 2020).

History of use. – *Sitobolium* was in use by early authors until Moore (1859) subsumed it under his concept of *Dennstaedtia* (Tryon & Tryon, 1980). The original spelling by Desvaux was altered by J. Smith to '*Sitolobium*', but there is no reason to believe that Desvaux's spelling was incorrect.

Taxonomic treatments. – The Asian species have been treated (in *Dennstaedtia*) by Knapp (2011) and Yan & al. (2013), and by Fraser-Jenkins & al. (2015, 2017), who updated some taxonomy and nomenclature. *Sitobolium punctilobulum*, the only species in the Western Hemisphere, was monographed by Conard (1908). We include five constituent species of *Sitobolium* based upon molecular phylogenetic and morphological evidence, and we make necessary combinations for four of them.

Fig. 7. Characters of *Sitobolium*. **A**, Habit; **B**, Lower leaf surface and marginal sori with cup-shaped indusia; **C**, Creeping branched rhizome and petioles with epipetiolar buds; **D**, Grooved adaxial rachis-costa axes without raised wings. — All photos by M. Sundue except B by R.C. Moran.

New combinations and constituent species

Sitobolium appendiculatum (Wall. ex Hook.) L.A.Triana & Sundue, **comb. nov.** ≡ *Dicksonia appendiculata* Wall. ex Hook., Sp. Fil. 1: 79, t. 27C. 1844 ≡ *Dennstaedtia appendiculata* (Wall. ex Hook.) J.Sm., Hist. Fil.: 265. 1875. = *Dicksonia elwesii* Baker in Hooker & Baker, Syn. Fil., ed. 2: 54. 1874 ≡ *Dennstaedtia elwesii* (Baker) Bedd., Handb. Ferns Brit. India: 26. 1883.

Sitobolium hirsutum (Sw.) L.A.Triana & Sundue, **comb. nov.** ≡ *Davallia hirsuta* Sw. in J. Bot. (Schrader) 1800(2): 87. 1801 ≡ *Dennstaedtia hirsuta* (Sw.) Mett. ex Miq. in Ann. Mus. Bot. Lugduno-Batavi 3(6): 181. 1867.

Sitobolium punctilobulum (Michx.) Desv. in Mém. Soc. Linn. Paris 6: 263. 1827 ≡ *Nephrodium punctilobulum* Michx., Fl. Bor.-Amer. 2: 268. 1803 ≡ *Dennstaedtia punctilobula* (Michx.) T.Moore, Index Fil.: 97. 1857.

Fig. 8. Characters of *Mucura*. **A**, Habit; **B**, Upper leaf surface and alate rachis-costa axes; **C**, Lower leaf surface and marginal sori with cylindrical indusia; **D**, Unbranched rhizome and petiole lacking epipetiolar buds. — All photos by M. Sundue.

Sitobolium wilfordii (T.Moore) L.A.Triana & Sundue, **comb. nov.** ≡ *Microlepia wilfordii* T.Moore, Index Fil.: 299. 1861 ≡ *Dennstaedtia wilfordii* (T.Moore) Christ, Geogr. Farne: 192, 195. 1910 ≡ *Coptidipteris wilfordii* (T.Moore) Nakai & Momose in Cytologia, Vol. Fuji Jub. 1: 365, fig. 1a, 2i, 3c, 4c, d. 1937.

Sitobolium zeylanicum (Sw.) L.A.Triana & Sundue, **comb. nov.** ≡ *Dicksonia zeylanica* Sw. in J. Bot. (Schrader) 1800(2): 91. 1801 ≡ *Dennstaedtia zeylanica* (Sw.) Zink ex Fraser-Jenk. & Kandel in Fraser-Jenkins & al., Ferns Fern-Allies Nepal 1: 161. 2015.

= *Dicksonia scabra* Wall. ex Hook., Sp. Fil. 1: 80, t. 28B. 1844 ≡ *Dennstaedtia scabra* (Wall. ex Hook.) T.Moore, Index Fil.: 307. 1861

= *Dennstaedtia melanostipes* Ching in Chien & Chun, Fl. Reipubl. Popularis Sin. 2: 357. 1959.

Excluded names

Sitobolium adiantoides J.Sm. in London J. Bot. 1: 434. 1842 [= *Dicksonia bipinnata* Cav. ≡ *Dennstaedtia bipinnata* (Cav.) Maxon in Proc. Biol. Soc. Wash. 51: 39. 1938].

Sitobolium dubium (R.Br.) Brack., U.S. Expl. Exped., Filic. 16: 273 ≡ *Davallia dubia* R.Br., Prodr.: 157. 1810 ≡ *Calochlaena dubia* (R.Br.) M.D.Turner & R.A.White in Amer. Fern J. 78: 92. 1988.

Sitobolium plumieri (Hook.) J.Sm., Ferns Brit. For., ed. 2: 319. 1877 ≡ *Dicksonia plumieri* Hook., Sp. Fil. 1: 72. 1846 [= *Davallia domingensis* Spreng., Anleit. Kenntn. Gew. 3: 149, t. 4, fig. 33. 1804 ≡ *Saccoloma domingense* (Spreng.) C.Chr., Arbeiten Königl. Bot. Gart. Breslau 1: 21. 1815.

Sitobolium rubiginosum (Kaulf.) J.Sm. in London J. Bot. 1: 434 ≡ *Dicksonia rubiginosa* Kaulf., Enum. Filic.: 226. 1824 [= *Dicksonia cicutaria* Sw. in J. Bot. (Schrader) 1800(2): 91. 1801 ≡ *Dennstaedtia cicutaria* (Sw.) T.Moore., Index Fil.: 97. 1857].

Sitobolium stramineum (Labill.) Brack., U.S. Expl. Exped., Filic.: 16. 1854 ≡ *Dicksonia straminea* Labill., Sert. Austro-Caledon.: 7. 1824 ≡ *Calochlaena straminea* (Labill.) M.D.Turner & R.A.White in Amer. Fern J. 78: 92. 1988.

IV. ***Mucura*** L.A.Triana & Sundue, **gen. nov.** – Type: *Mucura bipinnata* (Cav.) L.A.Triana & Sundue (≡ *Dicksonia bipinnata* Cav.).

Diagnosis. – Differing from all other Dennstaedtiaceae by having dichotomously branching rhizomes, petioles that lack epipetiolar buds, marginal sori with both abaxial and adaxial indusia forming a cylindrical or cup-shaped involucre, and trilete spores with a verrucate and broadly ridged perispore, and sometimes irregular reticles.

Description. – *Plants* terrestrial; *rhizomes* long creeping, dichotomously branching, pubescent; *petioles* subterete, without an adaxial sulcus, with an omega-shaped vascular bundle, lacking epipetiolar buds; *leaves* large, erect, decompound, laminar axes alate, the wings decurrent onto the next order, lacking proliferous leaf buds; *veins* free, with slender apices; *sori* marginal, provided with abaxial and adaxial indusia that together form a cylindrical cup-shaped involucre; *spores* trilete, broadly ridged and verrucate, and sometimes irregular reticles. (Fig. 8)

Distribution and habitat. – Distributed from Mexico and the West Indies to the southern cone of South America, in humid forests, from sea level to 3500 m. Largely absent from Amazonia.

Etymology. – This name is a Spanish feminine noun [mú·ku·ra] derived from the Caribbean and Chibcha linguistic families (Flórez, 1955) that refers to a fired clay pot, commonly made by indigenous people living within the geographic distribution of the genus. These clay pots are characterized by having a globose base, like the indusium of *Mucura globulifera*, and a long narrow neck, reminiscent of the cylindrical indusium of *M. bipinnata*.

Discussion. – *Mucura* comprises two Neotropical species that may be sister to the clade of *Microlepia* and *Sitobolium*. It is distributed from Mexico and the West Indies to the southern cone of South America but not distributed in Amazonia. Previously treated in *Dennstaedtia*, Navarrete & Øllgaard (2000) emphasized the morphological disparity between species treated here as *Mucura* and other Neotropical species of *Dennstaedtia*. We agree, and our ancestral character state reconstruction recovers several autapomorphic states. It has a rachis-costa architecture found in no other lineage where the axes are provided with adaxial wings that are continuous between orders (from the rachis to the pinna costae, and pinna costae to pinnule costules). *Mucura* has a unique perispore ornamentation consisting of verrucae, broad ridges, and irregular reticles on the distal face (Fig. 4A). Also unique to *Mucura* are the subterete petiole bases; as far as we have seen, all other Dennstaedtioideae have petioles that are adaxially sulcate. Notably, *Mucura* lacks epipetiolar buds which are present in nearly all other Dennstaedtiaceae. They can further be distinguished from *Dennstaedtia* by their elongate, and branched rhizomes. These distinct morphological features, along with its phylogenetic position, warrant recognition of this clade at the rank of genus.

New combinations and constituent species

Mucura bipinnata (Cav.) L.A.Triana & Sundue, **comb. nov.** ≡ *Dicksonia bipinnata* Cav., Descr. Pl.: 174. 1802 ≡ *Dennstaedtia bipinnata* (Cav.) Maxon in Proc. Biol. Soc. Wash. 51(8): 39. 1938.

Mucura globulifera (Poir.) L.A.Triana & Sundue, **comb. nov.** ≡ *Polypodium globuliferum* Poir. in Lamarck, Encycl. 5: 554. 1804 ≡ *Dicksonia globulifera* (Poir.) Kuntze, Revis. Gen. Pl. 3(3): 378. 1898 ≡ *Dennstaedtia globulifera* (Poir.) Hieron. in Bot. Jahrb. Syst. 34(4): 455. 1904.

■ AUTHOR CONTRIBUTIONS

LATM conceived of the project, and LATM and MS contributed to all aspects of the research. AY contributed to the analysis of the evolution of morphological characters in general and to the palynological analysis. CJR and LYK contributed samples. All authors contributed to writing

and revising the manuscript. — LATM, https://orcid.org/0000-0002-5344-0697; AY, https://orcid.org/0000-0002-4508-2148; LYK, https://orcid.org/0000-0002-3388-3757; CJR, https://orcid.org/0000-0002-6605-1770; NTLP, https://orcid.org/0000-0002-3145-8183; PBS, https://orcid.org/0000-0002-5305-9300; MS, https://orcid.org/0000-0003-1568-150X

■ ACKNOWLEDGMENTS

We would like to thank Robbin Moran for helpful discussion and checking specimens at MO. Susan Fawcett, David Barrington, and Weston Testo provided valuable comments on the manuscript. Alejandra Vasco, Jonathan Castro, Susana Vega, Alejandro Marín, Sarah Morris, and Verónica Bedoya assisted MS with field work. We acknowledge The New York Botanical Garden for providing leaf tissue samples. This article is part of the Ph.D. thesis of LATM, which was partially supported by a grant from Universidad Nacional de Colombia (HERMES-40890). The Bogotá Botanical Garden allowed LATM to join some field trips of their project "Conservación ex situ de los helechos de Cundinamarca". Angélica Aponte, Ayda Patiño, Miguel Triana and Amparo Moreno assisted LATM with fieldwork. José Murillo provided DNA samples, assisted LATM with some fieldwork and made useful comments and suggestions on the preliminary analyses. NTLP thanks FAPEMIG and IAPT (2020). PBS thanks CNPq (204998/2017-4).

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Appendix 1. Species names and GenBank accession numbers of DNA sequences used in this study. Names are presented using the classification presented in this paper.

List of GenBank accessions used in this study presented as follows: Taxon, unique identifier, collector and collection number for the voucher, GenBank accession number for *rbcL*, *rpl16*, *rps4-trnS*, *trnL-F*. A dash (–) indicates data that were unavailable. Sequences generated as part of this study are marked with an asterisk (*).

Alsophila costularis Baker, NC_044080, *T. Wang & al. s.n.*, NC_044080, NC_044080, NC_044080, NC_044080. ***Blotiella lindeniana*** (Hook.) R.M.Tryon, 3401, *P.B. Schwartsburd 3401*, MT409883, –, –, –. ***Blotiella lindeniana*** (Hook.) R.M.Tryon, LUZ20, *L.A. Triana 1041*, Colombia (COL), –, –, OK092426*, OK092317*. ***Blotiella pubescens*** R.M.Tryon, U05911, *D. Strasberg s.n.* (UTC, REU), U05911, –, –, –. ***Campyloneurum angustifolium*** (Sw.) Fée, MA28464, *Martínez 28464* (NY), MF317986, –, –, MF318327. ***Cyrtomium falcatum*** (L.f.) C.Presl, 2397, *X.C. Zhang 2397*, EF394238, –, –, –. ***Cyrtomium falcatum*** (L.f.) C.Presl, 26520908, *YNUH DDCF2014*, –, 26520908, –, –. ***Cyrtomium falcatum*** (L.f.) C.Presl, EF177268, *Driscoll & Barrington s.n.*, –, –, –, EF177268. ***Cyrtomium fortunei*** J.Sm., –, *S. Li & al. s.n.*, NC_037510, NC_037510, NC_037510, NC_037510. ***Cystodium sorbifolium*** (Sm.) J.Sm., LUZ22, *C.W. Chen 3196*, Solomon Islands (TAIF), –, –, –, OK092318*. ***Dennstaedtia* sp.**, LUZ113, *M. Sundue 3991*, Costa Rica (VT), –, –, OK092474*, OK092346*. ***Dennstaedtia ampla*** (Baker) Bedd., LUZ57, *Wade 4671*, Malaysia (TAIF), –, OK092384*, OK092427*, –. ***Dennstaedtia arborescens*** (Willd.) E.Ekman & Maxon, LUZ106, *J. Castro 756*, Colombia (COL), OK092514*, OK092385*, OK092428*, –. ***Dennstaedtia auriculata*** Navarr. & B.Øllg., LUZ104, *J. Murillo 4791*, Colombia (COL), –, –, OK092429*, OK092319*. ***Dennstaedtia auriculata*** Navarr. & B.Øllg, LUZ121, *C.J. Rothfels 4973*, Peru (UC), OK092515*, –, OK092430*, OK092320*. ***Dennstaedtia cicutaria*** (Sw.) T.Moore, LUZ78, *L.A. Triana 993*, Colombia (COL), OK092517*, OK092386*, OK092432*, OK092322*. ***Dennstaedtia cicutaria*** (Sw.) T.Moore, LUZ79, *L.A. Triana 1016*, Colombia (COL), OK092518*, OK092387*, OK092433*, OK092323*. ***Dennstaedtia cicutaria*** (Sw.) T.Moore, LUZ80, *L.A. Triana 1036*, Colombia (COL), OK092519*, OK092388*, OK092434*, OK092324*. ***Dennstaedtia cicutaria*** (Sw.) T.Moore, LUZ82, *L.A. Triana 1043*, Colombia (COL), OK092520*, OK092389*, OK092435*, OK092325*. ***Dennstaedtia cornuta*** (Kaulf.) Mett., LUZ84, *L.A. Triana 1017*, Colombia (COL), OK092521*, OK092390*, OK092436*, OK092326*. ***Dennstaedtia cornuta***

Appendix 1. Continued.

(Kaulf.) Mett., LUZ85, *L.A. Triana 1022*, Colombia (COL), OK092522*, OK092391*, OK092437*, OK092327*. ***Dennstaedtia cornuta*** (Kaulf.) Mett., LUZ88, *L.A. Triana 1040*, Colombia (COL), –, OK092392*, OK092438*, –. ***Dennstaedtia coronata*** (Sodiro) C.Chr., LUZ89, *L.A. Triana 1033*, Colombia (COL), –, OK092393*, OK092441*, –. ***Dennstaedtia coronata*** (Sodiro) C.Chr., LUZ115, *W.L. Testo 758*, Costa Rica (VT), –, OK092394*, OK092442*, OK092328*. ***Dennstaedtia davallioides*** (R.Br.) Moore, 27283, *L. Perrie 3585* (WELT), KT983819, MH918674, –, –. ***Dennstaedtia dissecta*** (Sw.) Moore, LUZ114, *W.L. Testo 721*, Costa Rica (VT), –, –, OK092447*, OK092330*. ***Dennstaedtia dissecta*** (Sw.) Moore, LUZ90, *L.A. Triana 1025*, Colombia (COL), OK092523*, OK092395*, OK092443*, OK092329*. ***Dennstaedtia dissecta*** (Sw.) Moore, LUZ91, *L.A. Triana 1030*, Colombia (COL), –, OK092396*, OK092444*, –. ***Dennstaedtia distenta*** (Kunze) T.Moore, LUZ120, *M. Sundue 4998*, Mexico (VT), OK092524*, OK092397*, OK092448*, OK092331*. ***Dennstaedtia glabrata*** (Ces.) C.Chr., LUZ38, *L.Y. Kuo 1926*, Philippines (TAIF), –, –, OK092451*, –. ***Dennstaedtia kalbreyeri*** Maxon, LUZ103, *J. Murillo 4790*, Colombia (COL), OK092528*, OK092400*, OK092454*, –. ***Dennstaedtia macrosora*** Navarr. & B.Øllg. LUZ93, *L.A. Triana 990*, Colombia (COL), OK092529*, –, OK092456*, OK092335*. ***Dennstaedtia mathewsii*** (Hook.) C.Chr., LUZ123, *C.J. Rothfels 5068*, Peru (UC), –, –, OK092459*, OK092336*. ***Dennstaedtia mathewsii*** (Hook.) C.Chr., LUZ94, *L.A. Triana 991*, Colombia (COL), OK092530*, –, OK092457*, –. ***Dennstaedtia maxima*** (E.Fourn.) L.A.Triana & Sundue, WELT_P026233, *WELT P026233* (WELT), KT983830, –, –, –. ***Dennstaedtia novae-zelandiae*** (Colenso) L.A.Triana & Sundue, W, *P.G. Wolf 682*, U18639, –, –, –. ***Dennstaedtia obtusifolia*** (Willd.) T.Moore, LUZ97, *L.A. Triana 1015*, Colombia (COL), OK092531*, –, OK092460*, –. ***Dennstaedtia obtusifolia*** (Willd.) T.Moore, LUZ99, *L.A. Triana 1038*, Colombia (COL), OK092532*, OK092401*, OK092461*, OK092337*. ***Dennstaedtia samoensis*** (Brack.) T.Moore, W, *P.G. Wolf 425*, U18637, –, –, –. ***Dennstaedtia scandens*** (Blume) Moore, LUZ46, *L.Y. Kuo 2806*, Taiwan (TAIF), –, –, OK092472*, –. ***Dennstaedtia spinosa*** Mickel, *M. Sundue 5045*, MT416337, MT470019, MT593216, –. ***Dennstaedtia sprucei*** T.Moore, LUZ124, *C.J. Rothfels 4974*, Peru (UC), OK092539*, OK092404*, OK092475*, OK092347*. ***Dennstaedtia sprucei*** T.Moore, LUZ125, *C.J. Rothfels 4975*, Peru (UC), OK092540*, –, OK092476*, OK092348*. ***Dennstaedtia tripinnatifida*** Copel., LUZ55, *Wade 4441*, Solomon Islands (TAIF), –, OK092405*, OK092477*, –. ***Dennstaedtia vagans*** (Baker) Diels, LUZ100, *L.A. Triana 1019*, Colombia (COL), OK092541*, –, OK092478*, –. ***Dennstaedtia werckleana*** (H.Christ) Navarrete & B.Øllg., 883, *J.H. Nitta 883* (CR, UC), MW138147, –, –, –. ***Diplazium dilatatum*** Blume, 156, *X.C. Zhang 156*, KC254418, KY427344, –, KC254497. ***Histiopteris incisa*** (Thunb.) J.Sm., LUZ130, *C.J. Rothfels 4956*, Peru (UC), OK092544*, OK092409*, OK092481*, OK092354*. ***Histiopteris incisa*** (Thunb.) J.Sm., LUZ131, *C.J. Rothfels 5051*, Peru (UC), OK092545*, OK092410*, OK092482*, OK092355*. ***Histiopteris incisa*** (Thunb.) J.Sm., LUZ132, *C.J. Rothfels 5050*, Peru (UC), OK092546*, OK092411*, OK092483*, OK092356*. ***Histiopteris incisa*** (Thunb.) J.Sm., LUZ28, *L.Y. Kuo 2685*, Philippines (TAIF), OK092543*, OK092407*, –, OK092351*. ***Histiopteris incisa*** (Thunb.) J.Sm., LUZ3, *M. Sundue 3947*, Mexico (VT), OK092542*, OK092406*, OK092479*, OK092349*. ***Histiopteris incisa*** (Thunb.) J.Sm., LUZ30, *L.Y. Kuo 3286*, China (TAIF), –, OK092408*, –, OK092352*. ***Histiopteris stipulacea*** Copel., LUZ1, *M. Sundue 3635*, Papua New Guinea (VT), –, OK092412*, OK092484*, OK092357*. ***Hiya brooksiae*** (Alderw.) H.Shang, LUZ58, *Wade 4710*, Malaysia (TAIF), –, OK092413*, OK092485*, OK092358*. ***Hiya brooksiae*** (Alderw.) H.Shang, SG1731, *SG1731*, MH289639, MH289746, MH289711, –. ***Hiya distans*** (Hook.) Brownsey & Perrie, 2807, *L. Perrie 2807*, MT416341, MT470023, –, MT593239. ***Hiya nigrescens*** (Hook.) H.Shang, MS3626, *M. Sundue 3626*, MH289641, MH289737, MH289703, MT593240. ***Hypolepis alpina*** (Blume) Hook., MSB3, *MSB3*, –, MH289729, MH289697, MT593277. ***Hypolepis glandulosopilosa*** H.G.Zhou & H.Li, SG1029, *HygSG1029*, MH289632, MH289720, MH289688, MT593258. ***Hypolepis millefolium*** Hook., 3029, *Perrie 3029* (WELT), EF469956, MH918677, –, MT593262. ***Hypolepis parallelogramma*** (Kunze) C.Presl, 5090, *Rodríguez 5090*, MT416326, MT633763, MT559743, MT593267. ***Hypolepis pedropaloensis*** Schwartsb. & J.Prado, LUZ15, *L.A. Triana*, Colombia *1011* (COL), OK092547*, –, OK092486*, OK092359*. ***Hypolepis resistens*** (Kunze) Hook., BLD01, *BLD01*, MG944782, MH289724, MH289692, MG944788. ***Hypolepis rugosula*** (Labill.) J.Sm., 3023, *Roux 3023*, MT426184, MT470050, MT593223, MT593283. ***Hypolepis sparsisora*** (Schrad.) Kuhn, SG1263, *HysSG1263*, MH289631, MH289732, MH289700, MT593286. ***Hypolepis stolonifera*** Fée var. ***stolonifera***, 4420, *P.B. Schwartsburd 4420*, MT426189, MT470062, MT563116, MT593296. ***Hypolepis tenuifolia*** (G.Forst.) Bernh., HN31, *HN31*, MG944786, MH289733, MH289701, MG944791. ***Hypolepis viscosa*** H.Karst., LUZ16, *L.A. Triana 1012*, Colombia (COL), OK092548*, OK092414*, OK092487*, OK092360*. ***Lindsaea arcuata*** Kunze, LUZ19, *L.A. Triana 1028*, Colombia (COL), OK092549*, –, –, OK092361*. ***Lonchitis hirsuta*** L., EU352305, *F. Axelrod 9601* (UTC), EU352305, –, –, –. ***Lonchitis hirsuta*** L., U05929, *F. Axelrod 4221* (UPRRP, UTC), U05929, –, –, –. ***Lonchitis mannii*** Alston, U18641N, *Wolf 339*, LMU18641, –, –, –. ***Macrothelypteris torresiana*** (Gaudich.) Ching, 33947882, *R. Wei & al. s.n.*, –, NC_035858, –, –. ***Macrothelypteris torresiana*** (Gaudich.) Ching, PE4087, *Zhang 4087* (PE), JN572346, –, –, JN572265. ***Microlepia* sp.**, LUZ52, *L.Y. Kuo 3226*, China (TAIF), –, –, OK092492*, OK092364*. ***Microlepia ampla*** Ching, *Wei Hongjin* (PE), MK051603.1, –, MK051946.1, MK052476.1. ***Microlepia boluoensis*** Y.Yuan & L.Fu, WYD629, *Yan Yuehong & al.* (PE), MK051673.1, –, MK051922.1, MK052452.1. ***Microlepia chrysocarpa*** Ching, ZXC7015, *Zhang Xianchun* (PE), MK051808.1, –, MK052061.1, MK052599.1. ***Microlepia communis*** Ching, YYH13433, *Yan Yuehong & al.* (PE), MK051638.1, –, MK051882.1, MK052412.1. ***Microlepia crassa*** Ching, STET2352, *Li Zhongyang* (PE), MK051799.1, –, MK052052.1, MK052590.1. ***Microlepia crenata*** Ching, ZXL09873, *Zhou Xile & al.* (PE), MK051701.1, –, MK051954.1, MK052484.1. ***Microlepia firma*** Mett. ex Kuhn, ZXL6895, *Zhou Xile & al.* (PE), MK051813.1, –, MK052070.1, MK052608.1. ***Microlepia flaccida*** (G.Forst) L.A.Triana & Sundue, A580, *K. Armstrong 580*, Vanuatu, OK092525*, OK092398*, OK092449*, OK092332*. ***Microlepia flaccida*** (G.Forst) L.A.Triana & Sundue, P2905, *G. Plunket 2905*, Vanuatu, OK092526*, OK092399*, OK092450*, OK092333*. ***Microlepia hancei*** Prantl, YYH13485, *Yan Yuehong & al.* (PE), MK051726.1, –, MK051978.1, MK052515.1. ***Microlepia herbacea*** Ching & C.Chr. ex Tardieu & C.Chr., ZXL09877, *Zhou Xile & al.* (CNS, PE), MK051794.1, –, MK052047.1, MK052586.1. ***Microlepia hookeriana*** (Wall. ex Hook.) C.Presl, YYH11610, *Yan Yuehong* (PE), MK051844.1, –, MK052105.1, MK052650.1. ***Microlepia khasiyana*** (Hook.) C.Presl, ZXL7194, *Zhou Xile* (PE), MK051627.1, –, MK052087.1, MK052625.1. ***Microlepia krameri*** C.M. Kuo, YYH11607, *Yan Yuehong* (PE), MK051595.1, –, MK051873.1, MK052403.1. ***Microlepia kurzii*** (C.B.Clarke) Bedd., YYH12098, *Yan Yuehong* (PE), MK051631.1, –, MK051874.1, MK052404.1. ***Microlepia lofoushanensis*** Ching, YanYH13739, *Yan Yuehong* (PE), MK051727.1, –, MK051979.1, MK052516.1. ***Microlepia manilensis*** (Goldm.) C.Chr., SG1718, *Yan Yuehong & Shang Hui* (PE), MK051865.1, –, MK052118.1, MK052670.1. ***Microlepia marginata*** (Panz.) C.Chr., LUZ68, *T.Y. Nwe 332*, Myanmar (NY), –, OK092415*, OK092489*, –. ***Microlepia marginata*** (Panz.) C.Chr., LUZ72, *T.Y. Nwe 476*, Myanmar (NY), –, –, OK092490*, OK092362*. ***Microlepia marginata*** (Panz.) C.Chr., YYH13287, *Yan Yuehong* (PE), MK051720.1, –, MK051972.1, MK052509.1. ***Microlepia matthewii*** Christ, YYH13164, *Yan Yuehong* (PE), MK051636.1, –, MK051880.1, MK052410.1. ***Microlepia mollifolia*** Tagawa, YYH11625, *Yan Yuehong* (PE), MK051709.1, –, MK051962.1, MK052494.1. ***Microlepia obtusiloba*** Hayata, LUZ24, *L.Y. Kuo 2427*, Taiwan (TAIF), –, –, OK092491*, OK092363*. ***Microlepia obtusiloba*** Hayata, YYH11602, *Yan Yuehong* (PE), MK051842.1, –, MK052103.1, MK052648.1. ***Microlepia platyphylla*** (D.Don) J.Sm., –, *P.G. Wolf 673*, U18642, –, –, –. ***Microlepia rhomboidea*** (Wall. Ex Kunze) Prantl, WZS004, *Wei Hongjin* (PE), MK051786.1, –, MK052039.1, MK052578.1. ***Microlepia ridleyi*** Copel., KNBL211, *Yan Yuehong* (PE), MK051864.1, –, MK052117.1, MK052669.1. ***Microlepia scaberula*** Mett. Ex Kuhn, INA-BL18, *Yan Yuehong* (PE), MK051645.1, –, MK051889.1, MK052419.1. ***Microlepia smithii*** (Hook.) Y.H.Yan, LUZ40, *L.Y. Kuo 2319*, Taiwan (TAIF), OK092550*, OK092416*, OK092493*, –. ***Microlepia speluncae*** (L.) T.Moore, LUZ70, *T.Y. Nwe 140*, Myanmar (NY), –, OK092417*, –, –. ***Microlepia speluncae*** (L.) T.Moore, LUZ71, *T.Y. Nwe 159*, Myanmar (NY), –, OK092418*, –, –. ***Microlepia speluncae*** (L.) T.Moore, LUZ73, *T.Y. Nwe 530*, Myanmar (NY), –, OK092419*, OK092494*, OK092365*. ***Microlepia speluncae*** (L.) T.Moore, LUZ74, *T.Y. Nwe 874*, Myanmar (NY), OK092551*, OK092420*, –, OK092366*. ***Microlepia speluncae*** (L.) T.Moore, LUZ75, *T.Y. Nwe 580*, Myanmar (NY), OK092552*, OK092421*, –, OK092367*. ***Microlepia speluncae*** (L.) T.Moore, YYH12379, *Yan Yuehong 12379* (Herbarium), MK051712.1, –, MK052078.1, MK052501.1. ***Microlepia strigosa*** (Thunb.) C.Presl, SG021, *Shang Hui* (PE), MK051656.1, –, –, MK052433.1. ***Microlepia strigosa*** (Thunb.) C.Presl, W, *P. Wolf s.n.*, U05931, –, –, –. ***Microlepia subspeluncae*** Ching, Chien & Chun, ZXL7016, *Zhou Xile & al.* (PE), MK051871.1, –, –, MK052616.1. ***Microlepia subtrichosticha*** Ching, XP618, *Yan Yuehong & al.* (PE), MK051699.1, –, MK051951.1, MK052481.1. ***Microlepia szechuanica*** Ching, Chien & Chun, W, *P. Wolf 660*, U18643, –, –, –. ***Microlepia tenera*** Christ, SG1026, *Shang Hui* (PE), MK051801.1, –, MK052054.1, MK052592.1. ***Microlepia todayensis*** Christ, INA-BL68, *Yan Yuehong* (PE), MK051735.1, –, MK051983.1, MK052524.1. ***Microlepia trapeziformis*** (Roxb. ex Griff.) Kuhn, WYD303, *Yan Yuehong & al.* (PE), MK051667.1, –, MK051916.1,

Appendix 1. Continued.

MK052446.1. ***Microlepia trichocarpa*** Hayata, YYH12042, *Yan Yuehong* (PE), MK051607.1, –, MK051964.1, MK052498.1. ***Microlepia trichosora*** Ching in Chien & Chun, WYD445, *Yan Yuehong* (PE), MK051855.1, –, MK052110.1, MK052662.1. ***Microlepia yaoshanica*** Ching, YYH12136, *Yan Yuehong* (PE), MK051834.1, –, MK052095.1, MK052640.1. ***Microlepia yunnanensis*** Ching, Chien & Chun, YYH13136, *Yan Yuehong* (PE), MK051719.1, –, MK051971.1, MK052508.1. ***Monachosorum henryi*** Christ, –, *R. Moran 5461* (HAST, MO, F), U05932, –, –, –. ***Monachosorum subdigitatum*** (Blume) Kuhn, LUZ138, *C.J. Rothfels 4744*, Peru (UC), OK092553*, OK092422*, OK092496*, –. ***Mucura bipinnata*** (Cav.) L.A.Triana & Sundue, LUZ118, *S. Fawcett 470*, Puerto Rico (VT), OK092516*, –, OK092431*, OK092321*. ***Mucura globulifera*** (Poir.) L.A.Triana & Sundue, LUZ92, *L.A. Triana 1013*, Colombia (COL), OK092527*, –, OK092453*, OK092334*. ***Odontosoria chinensis*** (L.) J.Sm., W, *T. Ranker 1231* (COLO), U05934, –, –, –. ***Odontosoria scandens*** (Desv.) C.Chr., W, *F. Axelrod 5353* (UPRRP), U05935, –, –, –. ***Odontosoria schlechtendalii*** (C.Presl) C.Chr., 5012, *M. Sundue 5012*, MT633753, –, –, –. ***Orthiopteris campylura*** (Kunze) Copel., LUZ5, *C.W. Chen 4025*, Solomon Islands (TNM), –, –, OK092497*, OK092369*. ***Orthiopteris kingii*** (Bedd.) Holttum, LUZ42, *L.Y. Kuo 2571*, Philippines (TAIF), –, –, OK092498*, –. ***Paesia acclivis*** (Kunze) Kuhn, LUZ133, *C.J. Rothfels 4920*, Peru (UC), OK092554*, OK092423*, OK092499*, OK092370*. ***Paesia glandulosa*** (Sw.) Kuhn, LUZ134, *C.J. Rothfels 5113*, Peru (UC), OK092556*, –, OK092501*, OK092372*. ***Paesia glandulosa*** (Sw.) Kuhn, LUZ135, *C.J. Rothfels 5138*, Peru (UC), OK092557*, –, OK092502*, OK092373*. ***Paesia glandulosa*** (Sw.) Kuhn, LUZ81, *L.A. Triana 1042*, Colombia (COL), OK092555*, OK092424*, OK092500*, OK092371*. ***Paesia scaberula*** (A.Rich.) Kuhn, 387, *P.G. Wolf 387* (UTC), U05937, –, –, –. ***Pityrogramma trifoliata*** (L.) R.M.Tryon, 3658, *C.J. Rothfels 3658* (DUKE), KM008145, 38745998, –, KM007920. ***Pteridium caudatum*** (L.) Maxon, LUZ11, *L.A. Triana 983*, Colombia (COL), –, –, OK092503*, OK092374*. ***Pteridium esculentum*** (G.Forst.) Cockayne, LUZ136, *C.J. Rothfels 5031*, Peru (UC), OK092558*, –, OK092504*, OK092375*. ***Pteridium esculentum*** (G.Forst.) Cockayne, LUZ137, *C.J. Rothfels 4896*, Peru (UC), OK092559*, –, OK092505*, OK092376*. ***Pteridium revolutum*** (Blume) Nakai, LUZ66, *T.Y. Nwe 807*, Myanmar (NY), OK092560*, OK092425*, OK092506*, OK092377*. ***Pteris vittata*** L., 4016, *C.J. Rothfels 4016* (DUKE), KM008232, –, –, KM008008. ***Saccoloma brasiliense*** Mett., LUZ21, *C. Mynssen 1091*, Brasil (TUR), –, –, OK092507*, OK092378*. ***Saccoloma caudatum*** Copel., LUZ9, *M. Sundue 3101*, Mexico (VT), –, –, OK092508*, OK092379*. ***Saccoloma elegans*** Kaulf., 14948, *Tuomisto 14948* (TUR), HQ157302, –, –, GU478728. ***Saccoloma galeottii*** (Fée) A.Rojas, LUZ7, *M. Sundue 3507*, Mexico (VT), –, –, OK092509*, OK092380*. ***Saccoloma inaequale*** (Kunze) Mett., 1019, *M.M. Jones 1019* (TUR), KJ628823, –, MG561410, MG561418. ***Saccoloma nigrescens*** (Mett.) A.Rojas, LUZ17, *L.A. Triana 1020*, Colombia (COL), –, –, OK092512*, OK092382*. ***Saccoloma sunduei*** A.Rojas, LUZ6, *M. Sundue 3186*, Colombia (VT), –, –, OK092513*, OK092383*. ***Sitobolium appendiculatum*** (Wall. ex Hook.) L.A.Triana & Sundue, 5294, *X.C. Zhang 5294*, MK051807, –, –, –. ***Sitobolium hirsutum*** (Sw.) L.A.Triana & Sundue, SG159, *SG159*, –, –, –, MK052591. ***Sitobolium punctilobulum*** (Michx.) Desv., LUZ126, *C.J. Rothfels 3812*, United States (DUKE), OK092533*, –, OK092462*, OK092338*. ***Sitobolium punctilobulum*** (Michx.) Desv., LUZ127, *C.J. Rothfels 4568*, Canada (DUKE), OK092534*, –, OK092463*, OK092339*. ***Sitobolium punctilobulum*** (Michx.) Desv., LUZ128, *C.J. Rothfels 4581*, Canada (DUKE), OK092535*, OK092402*, OK092464*, OK092340*. ***Sitobolium wilfordii*** (T.Moore) L.A.Triana & Sundue, AB574779, *TNS-763999* (TNS), AB574779, –, –, –. ***Sitobolium zeylanicum*** (Sw.) L.A.Triana & Sundue, LUZ129, *C.J. Rothfels 4747*, Malaysia (UC), OK092538*, –, OK092471*, OK092344*. ***Sitobolium zeylanicum*** (Sw.) L.A.Triana & Sundue, LUZ41, *L.Y. Kuo 2352*, Taiwan (TAIF), OK092536*, –, OK092467*, –. ***Sitobolium zeylanicum*** (Sw.) L.A.Triana & Sundue, LUZ43, *L.Y. Kuo 2722*, Philippines (TAIF), OK092537*, OK092403*, OK092468*, OK092341*. ***Sitobolium zeylanicum*** (Sw.) L.A.Triana & Sundue, LUZ56, *Wade 4659*, Malaysia (TAIF), –, –, OK092469*, OK092342*. ***Sitobolium zeylanicum*** (Sw.) L.A.Triana & Sundue, LUZ64, *T.Y. Nwe 365*, Myanmar (NY), –, –, OK092470*, OK092343*. ***Vittaria graminifolia*** Kaulf., EP423, *E. Schuettpelz 1772* (US), 38747268, 38747299, –, –.

Appendix 2. Characters and their states.

Character number. **Character name.** (State number) State name.

1. **Rhizome branching.** (0) Unbranched; (1) branched.
2. **Rhizome indument.** (0) Trichomes; (1) scales; (2) glabrous.
3. **Petiole base shape.** (0) Subterete; (1) grooved.
4. **Rachis-costae grooves.** (0) Decurrent; (1) not decurrent.
5. **Sorus position.** (0) Marginal; (1) abaxial.
6. **Sorus vasculature.** (0) Single vein; (1) several veins.
7. **Spore shape.** (0) Trilete; (1) monolete.
8. **Perispore morphology.** (0) Rodlets; (1) prominent ridges and verrucae; (2) tubercles; (3) prominent ridges, verrucae and irregular reticles; (4) verrucae; (5) verrucae and ridges; (6) prominent ridges; (7) ornamented verrucae; (8) irregular reticles; (9) regular reticles; (10) irregular reticles and tubercles; (11) baculae; (12) rugulae; (13) echinae; (14) folds; (15) ridges and tubercles; (16) grains; (17) plain; (18) striate; (19) rodlets and grains.
9. **Venation.** (0) Free; (1) anastomosing.
10. **Vein tips.** (0) Slender; (1) enlarged.
11. **Chromosome number.** (0) 43 or 86; (1) 34; (2) 46 or 47; (3) 29; (4) 44; (5) 30; (6) 31; (7) 32; (8) 33; (9) 48; (10) 28; (11) 56; (12) 49; (13) 26; (14) 38; (15) 52.
12. **Aculeae.** (0) Unarmed; (1) armed.
13. **Lamina division.** (0) Simple; (1) up to 1-pinnate; (2) up to 2-pinnate; (3) up to 3-pinnate; (4) up to 4-pinnate; (5) up to 5-pinnate.
14. **Leaf buds.** (0) Absent; (1) present.
15. **Epipetiolar buds.** (0) Absent; (1) present.
16. **Abaxial indusium.** (0) Absent; (1) present.
17. **Adaxial indusium.** (0) Absent; (1) present.
18. **Rachis-costa wing.** (0) Absent; (1) present.

Appendix 3. Voucher information for specimens used in palynological analysis.

Species, country, *collector and collection number* (herbarium).

Dennstaedtia arborescens, Costa Rica, *Mickel 2045* (LP), *2589* (LP), *3111* (LP); *Testo 1841* (FLA). ***Dennstaedtia auriculata***, Colombia, *Grubb P-87* (COL); Costa Rica, *Mickel 2535* (LP); Panama, *M.A. Cornman 860* (VT). ***Dennstaedtia coronata***, Colombia, *Triana-Moreno 1033* (COL). ***Dennstaedtia dissecta***, Argentina, *Palacios 1296* (LP). ***Dennstaedtia distenta***, Mexico, *Mickel 4163* (LP); *Rzedowski 21106* (LP). ***Dennstaedtia glabrata***, Papua New Guinea, *James & Sundue 1593* (VT); *Sundue & al. 3776* (VT). ***Dennstaedtia kalbreyeri***, Colombia, *Croat 51798* (COL). ***Dennstaedtia macrosora***, Colombia, *Rodríguez 3567* (COL); *Triana-Moreno 990* (COL). ***Dennstaedtia mathewsii***, Colombia, *Jaramillo 3557* (COL); *Triana-Moreno 991* (COL), *1031* (COL). ***Dennstaedtia samoensis***, Solomon Islands; *Cheng-Wei Chen & al. SITW07662* (VT). ***Dennstaedtia scandens***, Papua New Guinea, *James & Sundue 1690* (VT); Philippines, *Elmer 11516* (VT). ***Dennstaedtia sprucei***, Colombia, *Acosta-Arteaga 1042* (COL). ***Dennstaedtia vagans***, Colombia, *Franco 4790* (COL); *Triana-Moreno 1019*

Appendix 3. Continued.

(COL). ***Microlepia speluncae***, Paraguay, *Rojas 4878* (MO). ***Mucura bipinnata***, Bolivia, *Krukoff 10331* (LP); Colombia, *Echeverry 149A* (COL); Costa Rica, *Mickel 2697* (LP), *3505* (LP); *De la Sota 5226* (LP). ***Mucura globulifera***, Argentina, *Yañez & Marquez 86* (LP). ***Patania werckleana***, Costa Rica, *Testo & al. 1237* (VT). ***Sitobolium hirsutum***, China, *Rothfels & al. 5282* (VT); Japan, *Togasi 1637* (VT). ***Sitobolium punctilobulum***, United States, *Cook 352* (VT); *McQueen 1570* (VT); *Seymour 27739* (VT). ***Sitobolium wilfordii***, Japan, *Unknown, s.n.* (VT-192144); *Science College, Imperial University s.n.* (VT-192145). ***Sitobolium zeylanicum***, China, *Rothfels 5308* (VT); Japan, *Boufford 20014* (VT); Nepal, *Cronin F1052* (VT).