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Hacia la resolución filogenética de los helechos Dennstaedtioides

Contribución de las especies neotropicales del género *Dennstaedtia* (Dennstaedtiaceae)

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Resumen

Hacia la resolución filogenética de los helechos Dennstaedtioides: Contribución de las especies neotropicales del género *Dennstaedtia* (Dennstaedtiaceae)

Se presenta una revisión filogenética molecular de la subfamilia Dennstaedtioideae (Dennstaedtiaceae) en la cual se analizaron cuatro marcadores del cloroplasto para aproximadamente el 40% de las especies de la subfamilia. Adicionalmente, se codificaron 18 caracteres morfológicos que se emplearon para encontrar clados diagnosticables morfológicamente. Se encontró que *Dennstaedtia s.l.* es polifilético y su tipo está anidado dentro de *Microlepia*. Los géneros *Leptolepia* y *Oenotrichia* fueron transferidos a *Dennstaedtia*, y *Coptidipteris* fue transferido a *Sitobolium*. Otras especies tradicionalmente reconocidas en *Dennstaedtia* fueron transferidas a *Sitobolium*, *Mucura* (gen. nov.), y dos especies a *Microlepia*, entre éstas *D. flaccida*, el tipo de *Dennstaedtia s.l.* Este resultado motivó la presentación de una propuesta ante el comité de nomenclatura del Código Internacional de Nomenclatura para algas, hongos y plantas para conservar *Dennstaedtia* con un nuevo tipo. *Microlepia* es un género con alrededor de 60 especies distribuidas en el viejo mundo, con excepción de una especie en el Neotrópico; se reconoce por su distintiva ornamentación de perisporio con bastones, y por sus pecíolos que carecen de yemas epipeciolares. *Dennstaedtia* es un género pantropical con aproximadamente 55 especies

reconocidas por tener rizomas no ramificados, pecíolos con yemas epipeciolares y, a menudo, por tener yemas prolíficas sobre las hojas. *Sitobolium* es un pequeño clado de aproximadamente cinco especies que se distinguen por sus hojas relativamente pequeñas provistas de pelos catenados alargados. Estos pelos suelen tener una célula terminal capitada no glandular. Se presenta el género nuevo *Mucura*, con dos especies de distribución neotropical que se diferencian de todas las demás Dennstaedtiaceae por tener rizomas ramificados dicotómicamente, pecíolos que carecen de yemas epipeciolares, soros marginales con indusio tanto abaxial como adaxial, y esporas triletes con una ornamentación única del perisporio. Para complementar esta clasificación, se presenta una sinopsis morfológica y geográfica, una lista de las especies constituyentes y las nuevas combinaciones necesarias. Se proporciona una clave para los once géneros de Dennstaedtiaceae, y se presenta una revisión taxonómica para el nuevo género *Mucura*.

Palabras clave: *Dennstaedtia*; filogenia; *Microlepia*; morfología; *Mucura*, *Patania*; perispora; nomenclatura; *Sitobolium*; taxonomía.

Abstract

Towards the phylogenetic resolution of the Dennstaedtioid ferns: contribution of the neotropical species of the genus *Dennstaedtia* (Dennstaedtiaceae)

A molecular phylogenetic review of the subfamily Dennstaedtioideae (Dennstaedtiaceae) is presented, in which four chloroplast markers were analyzed for approximately 40% of the species of the subfamily. Additionally, 18 morphological characters were coded and used to find morphologically diagnosable clades. *Dennstaedtia s.l.* was found to be polyphyletic and its type is nested within *Microlepia*. The genera *Leptolepia* and *Oenotrichia* were transferred to *Dennstaedtia*, and *Coptidipteris* was transferred to *Sitobolium*. Other species traditionally recognized in *Dennstaedtia* were transferred to *Sitobolium*, *Mucura* (gen. nov.), and two species to *Microlepia*, including *D. flaccida*, the type of *Dennstaedtia s.l.* This result motivated the application of a proposal to the nomenclature committee of the International Code of Nomenclature for Algae, Fungi and Plants to conserve *Dennstaedtia* with a new type. *Microlepia* is a genus with about 60 species distributed in the old world, with the exception of one species in the Neotropics; it is recognized by its distinctive perispore ornamentation with rodlets, and by its petioles that lack epipetiolar buds. *Dennstaedtia* is a pantropical genus with approximately 55 species recognized as having unbranched rhizomes, petioles with epipetiolar buds, and often having prolific buds on the leaves. *Sitobolium* is a

small clade of about five species distinguished by their relatively small leaves bearing elongated catenate hairs. These hairs usually have a non-glandular capitate terminal cell. The new genus *Mucura* is presented, with two species of neotropical distribution that differ from all other Dennstaedtiaceae by having dichotomously branched rhizomes, petioles lacking epipetiolar buds, marginal sori with both abaxial and adaxial indusium, and trilete spores with unique ornamentation. of the perisporium. To complement this classification, a morphological and geographical synopsis is presented, as well as a list of the constituent species and the necessary new combinations. A key to the eleven genera of the Dennstaedtiaceae is provided, and a taxonomic revision for the new genus *Mucura* is presented.

Key words: *Dennstaedtia*; *Microlepia*; morphology; *Mucura*; nomenclature; *Patania*; perispore; phylogeny; *Sitobolium*; taxonomy.

Introducción

Los sistemas de clasificación propuestos recientemente para los helechos se han sustentado en las relaciones filogenéticas inferidas a partir de datos moleculares (Smith & al. 2006, Christenhusz & Chase 2014, PPG I 2016). Sin embargo, para algunos grupos han sido escasos los estudios filogenéticos, el muestreo taxonómico y las fuentes de evidencia, lo cual se refleja en relaciones contradictorias y, por ende, en clasificaciones discordantes para estos grupos (PPG I 2016). Tal es el caso de la familia Dennstaedtiaceae, cuyas relaciones con Pteridaceae y 'Eupolypods' no fueron resueltas en la clasificación de Smith & al. (2006). Desde entonces, se han realizado análisis basados en diferentes fuentes de evidencia, en los que se han obtenido relaciones filogenéticas resueltas pero incongruentes entre sí, pues a partir de genes del cloroplasto se ha inferido que el clado hermano de Dennstaedtiaceae es ''Eupolypods'+Pteridaceae' (Wolf 1995, Perrie & al. 2015, Testo & Sundue 2016), mientras que los marcadores nucleares restringen el grupo hermano de la familia al clado 'Eupolypods' (Rothfels & al. 2015, PPG I 2016) (Figura 1).

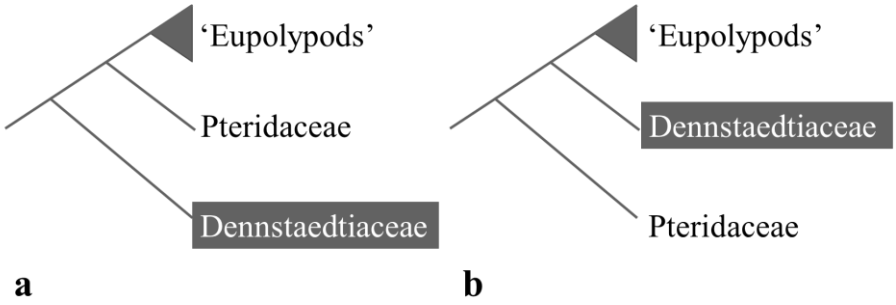

Figura 1. Hipótesis filogenéticas alternativas entre las familias Dennstaedtiaceae y Pteridaceae, y el clado 'Eupolypods', inferidas a partir de **(a)** marcadores del cloroplasto (Schuettpelz & Pryer 2007, Christenhusz & Chase 2014, Testo & Sundue 2016) y **(b)** marcadores nucleares (Rothfels & al. 2015, PPG I 2016).

Dentro de la familia también se han recuperado relaciones incongruentes. Para Dennstaedtiaceae se reconocen las subfamilias Dennstaedtioideae (D), Hypolepidoideae (H) y Monachosoroideae (M), pero las relaciones filogenéticas entre éstas también continúan inciertas, aunque la topología (M+(H+D)) recibe mayor soporte con respecto a la alternativa (D+(H+M)) (Schwartsburd & al. 2020).

En lo referente al género *Dennstaedtia* Bernh. ha sido escaso el muestreo taxonómico y geográfico en los estudios filogenéticos, pues para este género pantropical se han empleado, como máximo, diez de las aproximadamente 70 especies que lo componen (Moran 1995), y sólo cuatro de las 23 especies neotropicales (Schwartsburd & al. 2020). En dichos estudios, la fuente de evidencia filogenética que predomina son genes del cloroplasto (Wolf 1995, Perrie & al. 2015, Testo & Sundue 2016, Schwartsburd & al. 2020) y en menor medida marcadores nucleares (Rothfels & al. 2015). La evolución de caracteres morfológicos sólo ha sido explorada a la luz de los resultados de la filogenia molecular por Schwartsburd & al. (2020).

Los caracteres morfo-anatómicos diagnósticos del género *Dennstaedtia* son los rizomas reptantes, pilosos o glabrescentes; las frondas grandes (>1 m largo), 1-4 pinnadas (Figura 2a), con venas libres; los pecíolos acanalados por la cara adaxial, con un haz vascular que presenta forma de "Ω" invertida en sección transversal (Figura 2b); los soros marginales en el ápice de las venas; los indusios dobles compuestos por una porción marginal de la lámina foliar, y otra originada en la epidermis abaxial, que pueden configurar un indusio bivalvado (Figura 2c, 2d) (Moran 1995, Navarrete & Øllgaard 2000). Aunque este conjunto de caracteres permite reconocer claramente las especies de *Dennstaedtia*, Perrie & al. (2015) detectaron que algunas veces es difícil diferenciarlas morfológicamente de especies de *Microlepia* (Dennstaedtiaceae), género de distribución predominantemente asiática.

Otros estudios para el género en el Neotrópico han examinado la morfología y desarrollo del gametofito (Martínez & al. 2014) y la micromorfología de las esporas (Yáñez & al. 2016). En el primer estudio se encontró que *Dennstaedtia globulifera* presenta gametofitos cordiformes unisexuales, y en el segundo estudio se reconoció que las esporas de las cinco especies trabajadas son triletes y que entre ellas pueden ocurrir tres tipos de ornamentación: verrugosa, verrugoso-rugosa y reticulada.

Comúnmente los especímenes de herbario de *Dennstaedtia* corresponden a muestras insuficientemente recolectadas, lo cual ha dificultado su estudio taxonómico (Rojas-Alvarado & Tejero-Díez 2002). Esta limitación ha impedido que se aborde su estudio filogenético a partir de la morfología. Aún durante el auge de la sistemática molecular, estos helechos han recibido poca atención, y sus relaciones filogenéticas todavía son inciertas. Por tal razón, esta investigación pretende contribuir a la resolución de las relaciones filogenéticas

de los helechos Dennstaedtioides por medio de la incorporación de evidencia morfológica y molecular, obtenida principalmente de las especies neotropicales de *Dennstaedtia*, uno de los géneros más diversos de la familia en esta región del mundo.

Figura 2. Algunos caracteres distintivos del género *Dennstaedtia*. **A.** *D. cornuta*, fronda >1 m de longitud; nótese la lámina varias veces pinnada. **B.** *D. cicutaria*, sección transversal del pecíolo que muestra el haz vascular (lado adaxial abajo) **C.** *D. coronata*, soros marginales, bivalvados en el ápice de venas libres. **D.** *D. cornuta*, soros marginales, nótense las porciones adaxial (estrella) y abaxial (flecha) del indusio bivalvado (Fotos: L.A Triana, 2018).

Marco conceptual

Este proyecto se enmarca en los postulados de la sistemática filogenética (Hennig 1968), escuela que busca reconstruir las relaciones entre los organismos biológicos sobre la base de la ancestralidad en común, inferida a través de caracteres derivados y compartidos (sinapomorfías) entre las especies. Uno de los principios fundamentales de la sistemática filogenética es que estos patrones filogenéticos reflejen el orden jerárquico de la naturaleza. Dicho orden jerárquico se representa gráficamente con cladogramas o hipótesis de parentesco entre taxones.

En la construcción de estos patrones entra en juego el concepto de homología, tanto su interpretación previa al análisis cladístico (homología primaria), como su inferencia *a posteriori* resultante del o los árboles filogenéticos (homología secundaria). En el caso de las secuencias de ADN la homología primaria se establece por medio de un procedimiento operacional llamado alineamiento, mediante el cual se optimiza la similitud entre las secuencias (Patterson 1988).

A partir de esta información será posible ejecutar análisis filogenéticos que permitan elegir las hipótesis con un mayor grado de consistencia y soporte con respecto a los datos, mediante la implementación del principio de parsimonia, el cual busca minimizar el número de explicaciones *ad-hoc* para los resultados. En otras palabras, se prefieren los cladogramas que muestran mayor congruencia entre los caracteres que sustenten los clados (agrupaciones) recuperados (Page & Holmes 1998).

Desde la perspectiva cladística se reconoce que la base para proponer clasificaciones biológicas es la inferencia filogenética, disciplina basada en la detección de caracteres homólogos y en el reconocimiento de grupos monofiléticos, lo cual incrementa el rigor metodológico suficiente para sustentar con la mayor cantidad de evidencia las hipótesis filogenéticas y extenderlas a las clasificaciones biológicas propuestas (de Luna 1995).

Dentro los métodos de inferencia filogenética basados en caracteres se encuentran la parsimonia, la máxima verosimilitud y la inferencia bayesiana, los dos últimos preferidos para los análisis de datos moleculares, los cuales pueden ser analizados a través de aproximaciones probabilísticas calculadas a través de modelos explícitos de evolución molecular (Abascal & al. 2014).

Antecedentes

La familia Dennstaedtiaceae pertenece al suborden Dennstaedtiinae (PPG I 2016) del orden Polypodiales (Smith & al. 2006). Se estima que su diversificación inició durante el Triásico, hace 235 Ma, en condiciones más cálidas y secas que las actuales (Testo & Sundue 2016). Según los estudios de Schuettpelz & Pryer (2007), Christenhusz & Chase (2014) y Testo & Sundue (2016), basados en marcadores del cloroplasto, esta familia es el grupo hermano del clado (Pteridaceae + ‘Eupolypods’), que incluye 21 familias más (Figura 1a). Sin embargo, Rothfels & al. (2013, 2015) tuvieron en cuenta que el genoma nuclear ofrece un mayor poder de resolución filogenética a niveles taxonómicos poco profundos, debido a su alta tasa de evolución, por lo cual exploraron las relaciones filogenéticas de los helechos a partir de 25 genes nucleares de copia única; para el grupo de interés en esta investigación Rothfels & al.

(2015) obtuvieron la relación filogenética (Pteridaceae + (Dennstaedtiaceae + 'Eupolypods')), aunque sólo dos especies de la familia Dennstaedtiaceae fueron incluidas en el análisis. Esta última relación fue implementada en la clasificación propuesta por PPG I (2016) (Figura 1b).

Las relaciones evolutivas dentro de los 'Polypodiales no-Eupolypods' han sido poco estudiadas. Mickel (1973) realizó una primera exploración y analizó la variabilidad morfológica de los soros y las esporas, los patrones de ramificación del rizoma, la anatomía del pecíolo, el tipo de indumento, los patrones estomáticos y el desarrollo de la hoja. Dado que dicho estudio no se enmarcó en los postulados de la cladística, sino en los de la escuela evolutiva, sus conclusiones no se dan en términos de la inferencia de grupos monofiléticos y sus relaciones filogenéticas, sino en términos de relaciones ancestro-descendiente entre los taxones estudiados, por lo cual, con respecto a *Dennstaedtia*, Mickel (1973) concluyó que el género es la base a partir de la cual divergen tres líneas filéticas de la familia.

Wolf (1995) realizó un análisis filogenético de la familia Dennstaedtiaceae, empleando caracteres moleculares. En lo concerniente a *Dennstaedtia*, el análisis sólo incluyó tres especies, una sudamericana, una norteamericana y una asiática, y el género resulta parafilético con respecto a los géneros paleotropicales *Leptolepia* y *Microlepia*. Los tres géneros conformaron un grupo monofilético, en el cual se configuraron dos subclados, uno de ellos integrado por *Microlepia* y la especie norteamericana (*D. punctilobula*), y el otro subclado con *Leptolepia* y las dos especies restantes (*D. samoensis* y *D. auriculata*). Schuettpelz & Pryer (2007), en un análisis filogenético molecular que incluyó 400 especies

de helechos leptosporangiados, corroboraron los hallazgos de Wolf (1995) al obtener en un clado conformado por los mismos tres géneros.

Más recientemente, Perrie & al. (2015) realizaron un estudio filogenético con secuencias de marcadores cloroplásticos, orientado a explorar las relaciones filogenéticas del género australiano *Oenotrichia* (Dennstaedtiaceae). Dicho análisis incluyó siete especies de *Dennstaedtia*, dos de ellas ampliamente distribuidas en el Paleotrópico y en el Nuevo Mundo, una en Norteamérica y las restantes en Asia y Oceanía. Schwartsburd & al. (2020) emplearon el mismo tipo de marcadores, incrementaron en tres el número de especies neotropicales de *Dennstaedtia* con respecto a estudios previos, y obtuvieron resultados congruentes con éstos. Los dos estudios refutaron la monofilia de *Dennstaedtia*, pues sus especies resultan disgregadas en dos grupos dentro de un gran clado que contiene a otros cuatro géneros paleotropicales, *Coptidipteris*, *Leptolepia*, *Microlepia* y *Oenotrichia*. Este gran clado corresponde al grupo actualmente reconocido como la subfamilia Dennstaedtioideae (Figura 3). Ninguno de los dos grupos de *Dennstaedtia* resultó restringido geográficamente, ya que ambos incluyen tanto especies presentes en el Nuevo Mundo como especies paleotropicales. A la luz de estos hallazgos se establece la necesidad de redefinir la clasificación de la familia, y ampliar el muestreo con un mayor número de especies.

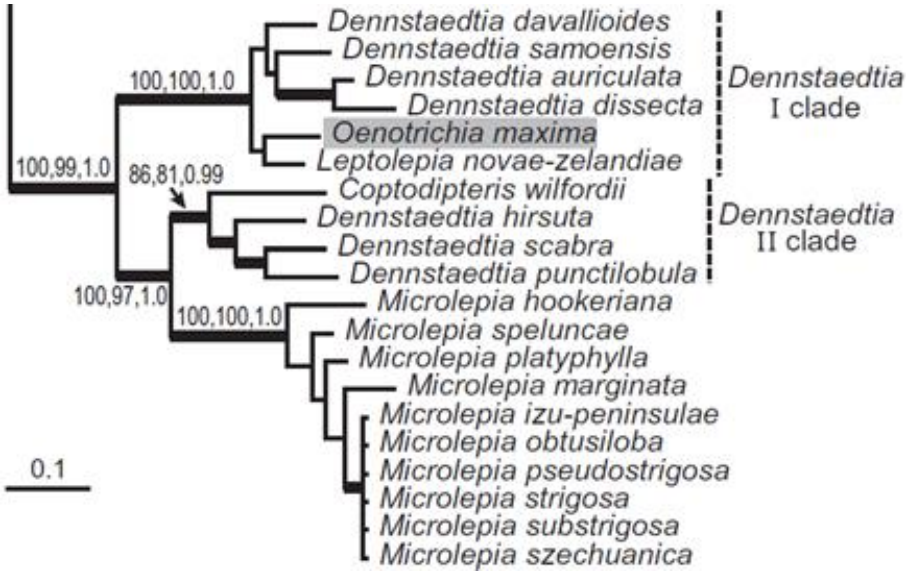

Figura 3. Porción del árbol filogenético de Perrie & al. (2015) que ilustra la condición polifilética de *Dennstaedtia*. *D. auriculata* y *D. dissecta* están presentes en el Neotrópico. *D. punctilobula* se encuentra en Norteamérica, y las especies restantes se distribuyen en Asia, Australia e islas del Pacífico.

A pesar de la escasa representatividad de *Dennstaedtia* en los análisis más recientes, la similitud entre los resultados de estos estudios constituye una evidencia recurrente que refuta la monofilia del género. La corroboración de este resultado implicaría una reorganización de por lo menos cinco géneros de la familia. Adicionalmente, el escaso muestreo impide proponer una reconstrucción más detallada de las relaciones filogenéticas dentro del género *Dennstaedtia* y los géneros afines. Con el desarrollo de esta investigación se contribuye considerablemente a la resolución de estas incógnitas.

Planteamiento del problema

Los estudios filogenéticos existentes que involucran a *Dennstaedtia* están orientados a reconstruir la filogenia a nivel de géneros o familias del orden Polypodiales (Smith & al. 2006, Schuettpelz & Pryer 2007, Christenhusz & Chase 2014, Rothfels & al. 2015,

Schwartsburd & al. 2020), o a explorar las relaciones filogenéticas de otros géneros de la familia Dennstaedtiaceae (Perrie & al. 2015). No obstante, *Dennstaedtia* permanece poco representado en dichos análisis, a pesar de que la monofilia del género y las relaciones filogenéticas de sus especies no se han evaluado en detalle.

Los estudios antes mencionados tienen en común que el muestreo taxonómico del género es limitado, pues el que presenta mayor número de especies sólo cuenta con diez. Además, estos estudios se han basado solamente en datos de secuencias de nucleótidos (Wolf 1995, Smith & al. 2006, Schuettpelz & Pryer 2007, Christenhusz & Chase 2014, Perrie & al. 2015, Rothfels & al. 2015, Schwartsburd & al. 2020), por lo cual la informatividad filogenética de los caracteres morfológicos aún continúa inexplorada.

En general, es poco el conocimiento que se tiene sobre la evolución de los caracteres morfológicos dentro de Dennstaedtiaceae. El único estudio de las relaciones intragenéricas que ha tomado en consideración los caracteres morfológicos es el de Mickel (1973). A su vez, Navarrete & Øllgaard (2000) analizaron algunos caracteres morfológicos poco convencionales como herramienta para el reconocimiento taxonómico de las especies, entre ellas la morfología del rizoma y del pecíolo y el desarrollo de yemas en el pecíolo y la lámina. No obstante, los estudios filogenéticos existentes no consideran estos caracteres como elementos de análisis y discusión. Estos caracteres deben ser examinados en detalle, a fin de evaluar su informatividad filogenética, y la congruencia con los caracteres moleculares empleados en los análisis moleculares recientes de *Dennsteadtia* y géneros afines, en cuyas relaciones podrían revelarse novedades. Por lo tanto, el desarrollo de esta investigación tendrá un efecto tanto en el conocimiento de *Dennstaedtia*, como en el de los géneros afines

que conforman la subfamilia Dennstaedtioideae propuesta por Becari-Viana & Schwartsburd (2017) (Figura 3).

Justificación

Un análisis filogenético combinado (morfológico y molecular) de miembros de la subfamilia Dennstaedtioideae, incrementando el muestreo taxonómico de *Dennstaedtia*, permitirá (1) evaluar la congruencia de estos dos tipos de caracteres; (2) incrementar de manera significativa el muestreo con el fin de explorar de manera más rigurosa las relaciones filogenéticas; (3) los resultados obtenidos permitirán verificar o refutar la monofilia del género y generar una revisión de la clasificación genérica de las Dennstaedtiaceae; (4) los taxones muestreados y la información obtenida ampliarán la representatividad de especies del Nuevo Mundo, con la cual será posible proyectar estudios posteriores que analicen el grupo en todo su rango de distribución, o incorporar fuentes adicionales de evidencia.

La inclusión de especies neotropicales en el presente proyecto de investigación es fundamental, ya que cerca de un tercio de las especies de *Dennstaedtia*, y seis de los 10 géneros de la familia se encuentran en el trópico del Nuevo Mundo, por lo cual se examinará de forma significativa la variabilidad morfológica para un mejor entendimiento de la diversificación de la familia. Adicionalmente, la riqueza del género en Colombia (18 especies) permitirá incrementar las colecciones del material requerido para los estudios morfológicos y moleculares.

Preguntas de investigación

Esta investigación dará respuesta a los siguientes interrogantes:

1. ¿Cómo se configuran las relaciones filogenéticas de la subfamilia Dennstaedtioideae al enriquecer el muestreo taxonómico con especies neotropicales de *Dennstaedtia*?
2. ¿Qué relaciones filogenéticas se reconstruyen entre las especies estudiadas de *Dennstaedtia*?
3. ¿Cómo han evolucionado los caracteres morfológicos que sustentan las relaciones interespecíficas del género *Dennstaedtia* y las relaciones genéricas de la subfamilia Dennstaedtioideae?

Hipótesis

Teniendo en cuenta la escasa representatividad de los helechos Dennsteadtioides en los análisis filogenéticos existentes, el uso exclusivo de caracteres moleculares en estos estudios, y los resultados obtenidos en ellos, se propone abordar esta investigación orientada por el siguiente supuesto:

> El análisis filogenético de los helechos de la subfamilia Dennstaedtioideae, enriquecido con la inclusión de las especies neotropicales de *Dennstaedtia*, y con la integración de caracteres morfológicos que brindarán soporte adicional a los moleculares, proporcionará evidencia para lograr una aproximación a las relaciones filogenéticas de la familia Dennstaedtiaceae, para someter a prueba la monofilia de

Dennstaedtia, para precisar la posición filogenética de las especies neotropicales estudiadas, y para redefinir la clasificación genérica de la familia.

Objetivos

General

- Proponer una hipótesis filogenética para *Dennstaedtia* (Dennstaedtiaceae) y para la subfamilia Dennstaedtioideae a partir del estudio de especies neotropicales del género.

Específicos

1. Esclarecer las relaciones filogenéticas de las especies neotropicales de *Dennstaedtia* dentro de la subfamilia Dennstaedtioideae mediante los análisis filogenéticos de caracteres morfológicos y moleculares.
2. Evaluar la informatividad filogenética de los caracteres moleculares y morfológicos obtenidos a partir de un muestreo representativo de las especies neotropicales de Dennstaedtiaceae.
3. Analizar la evolución de los caracteres morfológicos tradicionalmente propuestos como diagnósticos del género *Dennstaedtia* y de sus especies.
4. Proponer una clasificación intrafamiliar basada en la filogenia obtenida.

Literatura citada

Abascal, F., Irisarri, I., Zardoy, R. 2014. Filogenia y evolución molecular. pp. 57-85. En: Á. Sebastián, A. Pascual-García (Eds.). 2014. Bioinformática con Ñ. Arquitectura viva. Madrid. 558 pp.

Becari-Viana, I., Schwartsburd, P. B. 2017. Morpho-anatomical studies and evolutionary interpretations of the rhizomes of extant Dennstaedtiaceae. American Fern Journal 107: 105-123.

Christenhusz, M.J.M., Chase, M.W. 2014. Trends and concepts in fern classification. Annals of Botany 113: 571-594.

De Luna, E. 1995. Bases filosóficas de los análisis cladísticos para la investigación taxonómica. Acta Botánica Mexicana 33: 63-79.

Hennig, W. 1968. Elementos de una sistemática filogenética. Eudeba. Buenos Aires.

Martínez, O.G., Chambi, C.J., Avilés, Z. 2014. Gametophytic phase of two Neotropical ferns, *Dennstaedtia globulifera* (Poir.) Hieron and *Hypolepis poeppigii* Mett. ex Maxon (Dennstaedtiaceae). Plant Systematics and Evolution 300: 909-915.

Mickel, J.T. 1973. The classification and phylogenetic position of the Dennstaedtiaceae, pp. 135-144. En: Jermy, A.C., Crabbe, J.A., Thomas, B.A. (eds.) The phylogeny and classification of the ferns. Academic Press. Londres.

Moran, R.C. 1995. *Dennstaedtia*. pp. 150-163. En R.C. Moran., Riba, R. (eds.). Flora Mesoamericana. Volumen 1. Psilotaceae a Salviniaceae. Universidad Nacional Autónoma de México. México D.F.

Navarrete, H., Øllgaard, B. 2000. The fern genus *Dennstaedtia* (Dennstaedtiaceae) in Ecuador, new characters, new species and new combinations. Nordic Journal of Botany 20: 311-346.

Page, R.D.M., Holmes, E.C. 1998. Molecular evolution. A Phylogenetic Approach. Blackwell Science. Oxford.

Patterson, C. 1988. Homology in classical and molecular biology. Molecular Biology and Evolution 5: 603-625.

Perrie, L.R., Shepherd, L.D., Brownsey, P.J. 2015. An expanded phylogeny of the Dennstaedtiaceae ferns: *Oenotrichia* falls within a non-monophyletic *Dennstaedtia*, and *Saccoloma* is polyphyletic. Australian Systematic Botany 28: 256-264.

PPG I. 2016. A community-derived classification for extant lycophytes and ferns. Journal of Systematics and Evolution 56: 563-603.

Rojas-Alvarado, A.F., Tejero-Díez, D. 2002. Una nueva especie de *Dennstaedtia* (Filicales: Dennstaedtiaceae) para México. Revista de Biología Tropical 50: 1007-1012.

Rothfels, C.J., Larsson, A., Li, F.W., Sigel, E.M., Huiet, L., Burge, D.O., Ruhsam, M., Graham, S.W., Stevenson, D.W., Wong, G.K.S., Korall, P., Pryer, K.M. 2013. Transcriptome-Mining for Single-Copy Nuclear Markers in Ferns. PLoS ONE 8(10): e76957.

Rothfels, C.J., Li, F.W., Sigel, E.M., Huiet, L., Larsson, A., Burge, D.O., Ruhsam, M., Deyholos, M., Soltis, D.E., Stewart, C.N., Shaw, S.W., Pokorny, L., Chen, T., dePamphilis, C., DeGironimo, L., Chen, L., Wei, X., Sun, X., Korall, P., Stevenson, D.W., Graham, S.W., Wong, G.K.S., Pryer, K.M. 2015. The evolutionary history of ferns inferred from 25 low-copy nuclear genes. American Journal of Botany 102: 1-19.

Schuettpelz, E., Pryer, K.M. 2007. Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. Taxon 56: 1037-1050.

Schwartsburd, P.B., Perrie, L.R., Brownsey, P., Shepherd, L.D., Shang, H., Barrington, D.S., Sundue, M.A. 2020. New insights into the evolution of the fern family Dennstaedtiaceae from an expanded molecular phylogeny and morphological analysis. Molecular Phylogenetics and Evolution 150: 106881. https://doi.org/10.1016/j.ympev.2020.106881.

Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., Wolf, P.G. 2006. A classification for extant ferns. Taxon 55: 705-731.

Testo, W., Sundue, M. 2016. A 4000-species dataset provides new insight into the evolution of ferns. Molecular Phylogenetics and Evolution 105: 200-211.

Wolf, P.G. 1995. Phylogenetic analysis of *rbcL* and nuclear ribosomal RNA gene sequences in Dennstaedtiaceae. American Fern Journal 85: 306-327.

Yáñez A., Márquez, G.J., Morbelli, M.A. 2016. Spore morphology and ultrastructure of Dennstaedtiaceae from Paranaense Phytogeographic Province I.: Genus *Dennstaedtia*. Review of Palaeobotany and Palynology 224: 181-194.

Chapter 1. Phylogenetic relationships of Dennstaedtioideae (Dennstaedtiaceae: Polypodiales) with description of *Mucura*, gen. nov.

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Abstract

We undertook a molecular 32 phylogenetic revision of hayscented ferns (Dennstaedtioideae: Dennstaedtiaceae) 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 20 discrete morphological characters which we use to find diagnosable clades. We show that the *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 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*

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, 1974). 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 & 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, *Dennstaedtia 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 *Dennstaedtia 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 nomenclature committee for the International Code of Botanical Nomenclature (ICBN) 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. (Voss, 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 ICBN rule 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 relevant segregate genera including the type 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 et 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), 93 species and 2 subspecific taxa. For *Dennstaedtia* sensu PPGI (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 samples. Of these, 25 were collected during this research in various locations in the Andes of Colombia, for the genera *Dennstaedtia* (16 samples), *Mucura* (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 (Thiers, 2022), 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, 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 et al. (2020) 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 *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 sec, 56°C for 30 sec 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 sec, 50.5°C for 30 sec 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 sec, 50°C for 30 sec 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, VT, USA).

Resulting sequences were examined and assembled in Geneious Prime 2019.2.1 (Kearse & al., 2012). Alignments were made using MAFFT v7.035b (Katoh & Standley, 2013).

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 v7.035b (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. Both maximum likelihood

(ML) and Bayesian phylogenetic 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 (BI) reconstructions were conducted using MrBayes v.3.2 (Ronquist et 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).

Morphological Character Analysis. — We scored 20 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; Wan, 2013; Yañez & al., 2014, 2016a, 2016b; 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 (Maddison, 2008) 212 . 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 version 0.7.70 (Revell, 2012) and the “tiplabels” function from ape, 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 the herbaria AAU, MO and NY were studied using PteridoPortal (pteridoportal.org); type specimens were examined using virtual collections when necessary.

Results

Characterization of the sequences. — Three-hundred and two new sequences were generated: 64 from *rbcL*, 58 from *rpl16*, 103 from *rps4-trnS*, and 77 from *trnL-trnF* (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 58.2% 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 = 99), as were its subfamilies, the Monachosoroideae (PP=1, BS = 100), Hypolepidoideae (PP=1, BS = 100) and Dennstaedtioideae (PP=1, BS = 100). 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 that 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 in our ML results support for this clade was weak (BS = 65). Support for the sister relation of the two remaining clades was high in all analyses (PP=1, BS = 100). 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). The remaining clade included species of *Microlepia*, along with its type, and the type of *Dennstaedtia* (BS = 100).

Morphological character evolution. — Our reconstructions found that the presence of abaxial and adaxial indusia (Fig. 2A–B), sorus position (Fig. 3D), and rhizome indument 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, the presence/absence of wings along the rachis-costa junction and the perispore ornamentation (Figs. 3B, 4 A–G) were most useful. In particular, the spores of *Mucura* 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 (SI), aculeae upon axes (SI), and lamina division (SI), 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 included in the Supplementary Information.

Discussion

Systematics and morphology of Dennstaedtiaceae. — Our recovery of a monophyletic *Dennstaedtiaceae* along with its subfamilies, the Dennstaedtioideae, Hypolepidoideae, and Monachosorioideae, agree 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 *Monachosorum* which is sister to all other *Dennstaedtiaceae* (Ebihara et 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., 2019; Schwartsburd & al., 2020; Wang & al., 2021), and a forth-coming phylogenetic analysis of complete plastomes (Lu et al, in press). 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., 2019; 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 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 (SI), the shape of the petiole base (SI), and perispore ornamentation (Fig. 3B). 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. 2D), 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, would 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 et al., 2022). Our classification thus recognizes these four clades as *Dennstaedtia, Mucura* (gen. nov.), *Sitobolium*, and *Microlepia*.

Previous authors have further split *Coptidipteris* from *Sitobolium*, but we do not see value in recognizing this small genus. *Coptidipteris* is based upon *D. 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 do have any conspicuous share characters we can point to. In order to maintain monophyletic genera, recognizing *Coptidipteris* would lead us to either combine *D. appendicualta* 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.Short-creeping or ascending, dictyostelic rhizome; two vascular bundles in the petiole; sori exindusiate ..... *Monachosorum*

    2. Long-creeping, solenostelic rhizome; one vascular bundle in the petiole; sori indusiate or exindusiate.

        3. Abaxial indusium absent or minute and vestigial; spores monolete.

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*

3. Abaxial indusium present; spores trilete.

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. Epipetiolar buds usually present; adaxial axes (rachis-costae) without raised wings; petiole adaxially sulcate, the groove confluent between orders.

7. Rhizome branched regularly, *ca*. 0.5 cm diam.; leaves less than 1 m long, lacking leaf buds; glabrous or pubescent, the 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*

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*

1. Sorus supplied by two or more veins, marginal.

8. Veins anastomosing; pinnae opposite or subopposite

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*

8. Veins free; pinnae all or mostly alternate

10. Rachises flexuous; spores monolete ..... *Paesia*

10. Rachises straight; spores trilete ..... *Pteridium*

I. *Microlepia* C. Presl, Tentamen Pteridographiae 124–125, pl. 4, f. 21–23. 1836, **nom. cons. prop.** Lectotype designated by J. Smith, Hist. Filicum 260. 1875: *Microlepia polypodioides* (Sw.) C. Presl. — *Dicksonia polypodioides* Swartz) [=*Microlepia speluncae* (L.) T. Moore – *Polypodium speluncae* L.)]. **Fig. 5**

Scyphofilix Thouars, Gen. Nov. Madagac. 1. 1806. Lectotype designated by Farwell, O. A. 1931, **nom. rej. prop.** Fern notes. II. Ferns in the herbarium of Parke Davis & Co., Amer. Midl. Naturalist 12: 237: *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.

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, *Microlepia 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 (2017) not conserved *Microlepia* against it. Similarly, our proposal to conserve *Dennstaedtia* with a new type maintains 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 & al., 2014), China (Yan & al., 2013), India (Fraser-Jenkins & al., 2017), Japan (Nakaike, 1975), Nepal (Fraser-Jenkins & al., 2009), Taiwan (Knapp, 2011; TPG, 2019, 2021), and Thailand (Tagawa & Iwatsuki, 1979). We include 44 species and four named hybrids here based upon molecular phylogenetic and morphological evidence. We list an additional 25 species and one named hybrid that remain insufficiently known to us at this time.

Constituent species

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

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

Microlepia* × *bipinnata (Makino) Y.Shimura, J. Phytogeogr. Taxon. 27: 41. 1979.

Microlepia boluoensis Y.Yuan & L.Fu, Nordic J. Bot. 30: 170. 2012.

Microlepia calvescens (Wall. ex Hook.) C.Presl, Epimel. Bot. 95. 1851.− *Davallia calvescens* Wallich ex Hook., Sp. Fil. 1: 172. 1845.

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

Microlepia chrysocarpa Ching, Sinensia 1: 3. 1929.

Microlepia crassa Ching. Fl. Reipubl. Pop. Sin.2: 360. 1959.

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

Microlepia firma Mett. ex Kuhn, Linn. 36: 146. 1869.

Microlepia flaccida (G.Forst) Fée, Mem. Foug., 5. Gen. Filic. 327. 1852. − *Dennstaedtia flaccida* (G.Forst.) Bernh., Schrad., J. Bot. 1800: 124, t. 1, f. 3. 1801. — *Trichomanes flaccidum* G.Forst., Prod. 85. 1786.

Microlepia hallbergii (J.F.R.Almeida) C.Chr., Index Filic., Suppl. Tert. 127. 1934. − *Davallia hallbergii* J.F.R.Almedia, J. Indian Bot Soc 5: 19 et t. 1926. —

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

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

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

Microlepia* × *kandelii Fraser-Jenk., Annot. Checkl. Ind. Pterid. 175–176.

Microlepia kerrii S.J.Moore, Phytotaxa 324: 193–195, f. 1. 2017.

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

Microlepia kurzii (C.B.Clarke) Bedd., Handb. 66. 1883. − *Davallia kurzii* C.B. Clarke, Transactions of the Linnean Society of London, 2nd series: Botany 1: 446. 1880.

Microlepia majuscula (E.J.Lowe) T.Moore, Index Fil. 297. 1861.

Microlepia manilensis (Goldm.) C.Chr., Index Filic. 427. 1906.

Microlepia marginata (Panz.) C.Chr., Index Fil. 4: 212. 1905. − *Polypodium marginatum* Panz., Vollst. Pflanzensyst.13(1): 199. 1786. —

Microlepia matthewii Christ, Notul. Syst. (Paris) 1: 54

Microlepia mollifolia Tagawa, Acta Phytotax. Geobot. 5: 189. 1936.

Microlepia nepalensis (Spreng.) Fraser-Jenk., Kandel & Pariyar, Ferns Fern-Allies Nepal 1: 172. 2015. − *Davallia nepalensis* Spreng., Systema Vegetabilium, editio decima sexta 4(1): 121. 1827.

Microlepia nipponica (Miq.) C.Chr., Ind Fil. 427. 1906. − *Davallia nipponica* Miq., Ann. Lugd.-Bat. 3: 180. 1867. —

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

Microlepia platyphylla (D.Don) J.Sm., London Journal of Botany 1: 427. 1842. − *Davallia platyphylla* D. Don, Prodromus Florae Nepalensis 10. 1825. —

Microlepia proxima (Blume) C.Presl, Epimel. Bot. 95. 1851. − *Davallia proxima* Blume, Epim. bot. 238. 1828. —

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

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

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

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

Microlepia scaberula Mett. ex Kuhn, Linnaea 36: 148. 1869.

Microlepia setosa (Sm.) Alston, Philipp. J. Sci. 50: 177, t.1, f.3. 1933.

Microlepia shubhangiae S.Sharma & Kholia, Webbia 73: 192. 2018.

Microlepia smithii (Hook.) Y.H. Yan, Wang, T. & al., 2021. Taxonomy 1: 256−265. − *Dennstaedtia smithii* (Hook.) T.Moore, Ind. 308. 1861. — *Dicksonia smithii* Hook., Sp. 1: 80, t. 28D. 1844.

Microlepia speluncae (L.) T.Moore, Index Fil. (T.Moore) 93 (1857). — *Polypodium speluncae* L., Species Plantarum 2: 1093–1094. 1753.

Microlepia strigosa (Thunb.) C.Presl, Abhandlungen der Königlichen Böhmischen Gesellschaft der Wissenschaften, ser. 5 6: 455. 1851. − *Dennstaedtia strigosa*

(Thunb.) J. Sm., Hist. Fil. 265. 1875. — *Trichomanes strigosum* Thunb., Systema Vegetabilium. Editio decima quarta 941. 1784.

Microlepia substrigosa Tagawa, Acta Phytotaxonomica et Geobotanica 5: 189–190. 1936.

Microlepia subtrichosticha Ching, Flora Reipublicae Popularis Sinicae 2: 368. 1959.

Microlepia tenera Christ, Notulae Systematicae. Herbier du Museum de Paris 1: 53–54. 1909.

Microlepia thailandensis S.J.Moore, Phytotaxa 324: 193–195, f. 1. 2017.

Microlepia todayensis Christ, The Philippine Journal of Science. Section C, Botany 3: 272. 1908.

Microlepia trapeziformis (Roxb. ex Griff.) Kuhn; Chaetopt. [Festschr. 50jähr. Jubiläum Königst. Realschule zu Berlin] 347. 1882.

Microlepia trichocarpa Hayata, Icones plantarum formosanarum nec non et contributiones ad floram formosanam. 4: 210–211, f. 142. 1914.

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

Microlepia yakusimensis Tagawa, Acta Phytotax. Geobot. 11: 238. 1942.

Insufficiently known taxa

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

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

Microlepia crenata [recognized by Wang & al., (2021), considered a **syn. of** *Microlepia todayensis* by Hassler & Schmitt (2021)].

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

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

Microlepia* × *hirtiindusiata P.S.Wang, Pterid. Fl. Guizhou 441 (-442) 2001 [presumed to be a sterile hybrid, more study is needed].

Microlepia hancei Prantl, Arb. bot. Gart. Breslau 1: 35. 1892. [recognized by Wang & al., 2021, consdidered to be a **syn. of** *M. nepalensis* by Hassler & Schmitt (2021)].

Microlepia herbacea Ching & C.Chr. ex Tardieu & C.Chr., Notul. Syst. (Paris) 6: 6, t. 1(1−2) (1937). [recognized by Wang & al., 2021, consdidered to be a **syn. of** *M. mathewii* by Hassler & Schmitt (2021)].

Microlepia khasiyana (Hook.) C.Presl, Abh. Königl. Böhm. Ges. Wiss. 5(6) (Epim. Bot.): 95 (1851) [recognized by Wang & al. (2021), considered **syn. of** *M. strigosa* by Fraser-Jenkins (2008)].

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

Dennstaedtia macgregori Copel., Phil. J. Sci. 81: 4, t. 2. 1952. [Insufficiently known by us, Copeland (1958) suggested an affinity with *D. smithii*].

Microlepia melanorhachis Rosenst., Repert. Spec. Nov. Regni Veg. 12: 526. 1913. [insufficiently known].

Microlepia membranacea B.S.Wang, Acta Sci. Nat. Univ. Sunyatsenia 1961: 46. 1961. [insufficiently known].

Microlepia nudisora C.Chr., Bull. Bernice P. Bishop Mus. 177: 34 1943. [insufficiently known].

Davallia pilosiuscula Sm., Rees, Cycl. 11. no. 10 (1808). — *Microlepia pilosiuscula* (Sm.) C.V.Morton, Contr. U.S. Natl. Herb. 38: 313. 1974. [possibly an earlier name for *D. trapeziformis* (Fraser-Jenkins, 2008).]

Microlepia protracta Copel., Philipp. J. Sci. 81: 5. 1952. [insufficiently known].

Microlepia puberula Alderw., Bull. Jard. Bot. Buitenzorg Ser. 2, XI: 17. 1913. [possible syn. of *D. majuscula* (Fraser-Jenkins & al., (2017)].

Microlepia rheophila K.Iwats. & M.Kato, Acta Phytotax. Geobot. 31(1−3): 35. 1980. [insufficiently known].

Microlepia sinostrigosa Ching [considered a syn. of *M. pseudostrigosa* Makino by Knapp (2011)].

Microlepia subspeluncae Ching, Chien & Chun, Fl. Reipubl. Pop. Sin. 2: 244. 1959. [recognized by Wang & al. (2021), considered **syn. of** *M. speluncae* by Hassler & Schmitt (2021), forming a clade with *M. speluncae* in our results].

Microlepia szechuanica Ching, Chien & Chun, Fl. Reipubl. Pop. Sin. 2: 363 1959. [recognized by Wang & al. (2021), considered **syn. of** *M. strigosa* by Hassler & Schmitt (2021)].

Microlepia trapeziformis (Roxhburgh) Kuhn [considered a syn. of *D. pilosiuscula* (Sm.) L.A. Triana & Sundue by Maxon (1974)]

Microlepia vitiensis Brownlie, Beih. Nova Hedwigia 55: 118. 1977. [insufficiently known].

Microlepia yaoshanica Ching, Bull. Fan Mem. Inst. Biol. Bot. 2, 1: 299 (1949) [recognized by Wang & al. (2021), considered a **syn. of** *M. trapeziformis* by Hassler & Schmitt (2021), and sister to that taxon in our phylogenetic results].

Microlepia yunnanensis Ching, Chien & Chun, Fl. Reipubl. Pop. Sin. 2: 366 (1959) [recognized by Wang & al. (2021), considered a **syn. of** *M. trichocarpa* by Hassler & Schmitt (2021)].

Excluded names

Microlepia fluminensis Fée, Crypt. Vasc. Bresil 1: 151, t.51, f.1 (1869). *Dennstaedtia fluminensis* C.Chr., Index Filic. 217 (1905). [= *Patania cornuta* (Kaulf.) L.A. Triana & Sundue].

Microlepia lindsayiformis Fée, Crypt. Vasc. Bresil 1: 152, t.51, f.2 (1869) (as "*lindsayaeformis*"). *Dennstaedtia lindsayiformis* (Fée) C.Chr., Index Filic. 217 (1905). [= *Patania cornuta* (Kaulf.) L.A. Triana & Sundue].

II. *Dennstaedtia* Bernh. in J. Bot. (Schrader) 1800(2): 124. Oct–Dec 1801, nom. cons. prop. Type: *D. dissecta* (Sw.) T. Moore (*Dicksonia dissecta* Sw.), typ. cons. prop. **Fig. 6**

Patania C. Presl, Tentamen Pteridographiae 137–138, pl. 5, f. 12–14. 1836. Lectoype designated by Christensen (Index Filic. XXIX. H. Hagerup, Copenhagen. 1906): *Patania obtusifolia* (Willd.) C. Presl [≡*Dicksonia obtusifolia* Willd.].

Leptolepia Prantl, Arbeiten aus dem Königl. Botanischen Garten zu Breslau 1: 23. 1892. Lectotype designated by Christensen (Index Filic. xxviii. H. Hagerup, Copenhagen. 1960): *Leptolepia novae-zelandiae* (Colenso) Mett. ex Diels. [≡ *Davallia novae-zelandiae*]

Costaricia Christ, Bull. Soc. Bot. Genève ser. 2, 1: 229. 1909. Type: *Costaricia werckleana Christ, Bull. Soc. bot. Genéve 1: 229 1909.*

Oenotrichia Copel., University of California Publications in Botany 16: 82. 1929. Type: *Oenotrichia maxima* (E. Fourn.) Copel. [≡*Leucostegia maxima* E. Fourn.]

Paradennstaedtia Tagawa, J. Jap. Bot. 27: 213. 1952. Type: *Paradennstaedtia glabrata* (Ces.) Tagawa, J. Jap. Bot. 27: 213 (1952). [≡*Dicksonia glabrata* Ces.]

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

Synopsis. — As defined here, *Dennstaedtia* is a pantropical genus of *ca.* 55 species sister to all other Dennstaedtioideae. *Dennstaedtia* is recognized by having unbranched rhizomes, 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. 4, f, g), whereas regular reticles are found among paleotropical

species (Fig. 4, e). 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-zealandiae*) 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. *Patania 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 to this clade based upon its similarity to *Dennstaedtia mathewsii* (Hook.) L.A. Triana & Sundue and *D. producta* (Mett.) L.A. Triana & Sundue. 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*, 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 proposal (Triana-Moreno et al., 2022) to conserve *Dennstaedtia* with *D. dissecta* as the type permits its continued use and avoids further name changes. The New Zealand endemic *Dennstaedtia 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 at the time of writing. We include 37 constituent species of *Patania* based upon molecular phylogenetic and morphological evidence, and we make necessary combinations for 36 of them. We list an additional fifteen that remain insufficiently known to us at this time.

New combinations and constituent species

Dennstaedtia ampla (Baker) Bedd., J. Bot. 227. 1893. — *Dicksonia ampla* Baker, J. Linn. Soc. 22: 223. 1886.

Dennstaedtia antillensis (Jenman) C.Chr., Ind. 216. 1905.— *Dicksonia antillensis* Jenman, J. Bot. 267. 1886.

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

Dennstaedtia arcuata Maxon, Amer. Fern J. 36: 22. 1945.

Dennstaedtia articulata Copel., Leafl. Phil. Bot. 2: 396. 1908.

Dennstaedtia auriculata Navarr. & B.Øllg., Nordic J. Bot. 20: 337. 2000.

Dennstaedtia canaliculata Alderw., Bull. Jard. Bot. Buitenz. II, 16: 6. 1914.

Dennstaedtia cicutaria (Sw.) T.Moore, Ind. Fil. 97. 1857. — *Dicksonia cicutaria* Sw., Schrad., J. Bot. 1800: 91. 1801.

Dennstaedtia cornuta (Kaulf.) Mett., Ann. sc. nat. V, 2: 260. 1864.— *Dicksonia cornuta* Kaulf., Enum. Fil. 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; Parker´s Cat. 1858.— *Dicksonia davallioides* R.Br., Prodr. Fl. Nov. Holl. 158. 1810.

Dennstaedtia dissecta (Sw.) T.Moore, Ind. 305. 1861. — *Dicksonia dissecta* Sw., Schrad., J. Bot. 1800: 91. 1801.

Dennstaedtia distenta (Kunze) T.Moore, Ind. Fil. 306. 1861. — *Dicksonia distenta* Kunze, Analecta Pteridogr. 39. 1837.

Dennstaedtia elmeri Copel., Elmer, Leafl. Phil. Bot. 1: 233. 1907.

Dennstaedtia glabrata (Ces.) C.Chr.; Ind. 217. 1905.— *Dicksonia glabrata* Ces., Rend. Ac. Napoli 16: 24, 28. 1877.

Dennstaedtia glauca (Cav.) C.Chr. ex Looser, Revista Hist. Géogr. Chile 69: 184. 1932.— *Davallia glauca* Cav., Descr. Pl. 278. 1802.

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

Dennstaedtia kalbreyeri Maxon, Proc. Biol. Soc. Washington 51: 40. 1938., nom. nov. for *Dicksonia pubescens* Baker, J. Bot. 19: 203. 1881, not Schkuhr 1809. — *Dennstaedtia pubescens* (Baker) C. Chr., Index Fil. 218. 1905.

Dennstaedtia macrosora Navarr. & B.Øllg., Nordic J. Bot. 20: 340. 2000.

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

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

Dennstaedtia mathewsii (Hook.) C.Chr., Ind. 218. 1905.— *Deparia mathewsii* Hook., Sp. 1: 85, t. 30B. 1844.

Dennstaedtia novae-zelandiae (Colenso) L.A. Triana & Sundue, **comb. nov. —** *Davallia novae-zelandiae* Colenso, Tasmanian J. Nat. Sci. 2: 182. 1845. — *Leptolepia novae-zelandiae* (Colenso) Mett. ex Diels in Engler & Prantl, Nat. Pflanzenfam. 1, 52 212, f. 11a, b. 1899.

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

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

Dennstaedtia paucirrhiza Navarr. & B.Øllg., Nordic J. Bot. 20: 333. 2000.

Dennstaedtia producta Mett., Ann. sc. nat. V, 2: 260. 1864.

Dennstaedtia resinifera (Blume) Mett. ex Kuhn, Ann. Mus. Bot. Lugd. -Bat. 4: 290. 1869.— *Cheilanthes resinifera* Blume, Enum. Fil. 138. 1828.

Dennstaedtia samoensis (Brack.) T.Moore, Ind. Fil. 307. 1857. **—** *Sitolobium samoense* Brack., U. S. Expl. Exp. 16: 274, t. 38, f. 1. 1854.

Dennstaedtia scandens (Blume) T.Moore, Parker´s Cat. 1858. — *Dicksonia scandens* Blume, Enum. Pl. Javae 240. 1828.

Dennstaedtia spinosa Mickel, Amer. Fern J. 58: 90. 1968.

Dennstaedtia sprucei T.Moore, Ind. 308. 1861. — *Dicksonia sprucei* (T.Moore) Baker, J. Bot. 162. 1877.

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

Dennstaedtia tryoniana Navarr. & B.Øllg., Nordic J. Bot. 20: 334. 2000.

Dennstaedtia vagans (Baker) Diels, Nat. Pfl. 1: 218. 1899. — *Dicksonia vagans* Baker, J. Bot. 162. 1871.

Dennstaedtia werckleana (Christ) Navarr. & B.Øllg., Nordic J. Bot. 20: 344. 2000. — *Costaricia werckleana* Christ, Bull. Soc. bot. Genéve 1: 229. 1909.

Dennstaedtia wercklei (Christ) R.M.Tryon, Contr. Gray Herb. 187: 50. 1960. — *Saccoloma wercklei* Christ, Bull. Herb. Boiss. II, 4: 1100. 1904. —

Insufficiently known species

Dennstaedtia anthriscifolia (Bory) T.Moore, Ind. 303. 1861. — *Lonchitis anthriscifolia* Bory, Willd., Sp. 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., Philipp. J. Sci., Bot.2: 126. 1907. — *Microlepia dennstaedtioides* Copel., Phil. J. Sci. 1, Suppl. II: 148, f. 4. 1906. [insufficiently known].

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

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

Dennstaedtia madagascariensis (Kunze) Tardieu, Humbert, Fl. Madag. Fam. 5, 1: 11. 1958. [the long-creeping rhizomes appear to lack epipetiolar buds].

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

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

Dennstaedtia penicillifera Alderw., Bull. Jard. Bot. Buitenz. II, 28: 17, t. 1. 1918. [insufficiently known].

Dennstaedtia philippinensis Copel., Elmer, Leafl. Phil. Bot. 9: 3107. 1920. [insufficiently known].

Dennstaedtia remota (Christ) Diels, Nat. Pfl. 1: 218. 1899. — *Dicksonia remota* Christ, Verh. Naturf. Ges. Basel 11: 423. 1896. [insufficiently known].

Dennstaedtia rufidula C.Chr., Gard. Bull. Str. Settl. 7: 226, t. 51. 1934. [insufficiently known].

Dennstaedtia shawii Copel., Phil. J. Sci. 30: 326. 1926. [insufficiently known].

Dennstaedtia sumatrana Alderw., Bull. Dépt. agric. Ind. néerl. 18: 6. 1908. [insufficiently known].

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

Dennstaedtia williamsii Copel., Phil. J. Sci. 1, Suppl. II: 148. 1906. [insufficiently known].

Excluded names

Dennstaedtia appendiculata (Wall. ex Hook.) J. Sm., Hist. Fil. 265. 1875 [= *Sitobolium appendiculatum* (Wall ex Hook.) L.A. Triana & Sundue].

Dennstaedtia elwesii (Baker) Bedd., Handb. Ferns Brit. India, Suppl. 2, t. 347. 1876 [≡ *Sitobolium elwesii* (Baker) L.A. Triana & Sundue].

Dennstaedtia scabra (Wall. ex Hook.) T.Moore, Ind. Fil. 307. 1861. [≡ *Sitobolium zeylanicum* (Sw.) L.A. Triana & Sundue].

III. *Sitobolium* Desv., Mém. Soc. Linn. Paris 6: 262. 1827. *Sitolobium* J. Sm., J. Bot. (Hooker) 3: 418 (1841). [orth. variant]. *Litolobium* Newman, Phytologist 5: 236. 1854. [orth. variant]. Type: *Sitobolium punctilobulum* (Michx.) Desv. [= *Nephrodium punctilobulum* Michx.] **Fig. 7**

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

Coptidipteris Nakai & Momose, Cytologia (Fujii Jub. Vol.) 1: 365. 1937. *Coptodipteris* [orth. variant]. Type: *Coptidipteris wilfordii* (T. Moore) Nakai & Momose [= *Microlepia wilfordii* T. Moore]

Emodiopteris Ching & S.K. Wu, Acta Phytotax. Sin. 16: 21. 1978. Type: *Emodiopteris appendiculata* (Wall. ex Hook.) Ching & S.K. Wu [=*Dicksonia appendiculata* Wall. ex Hook.]

Fuziifilix Nakai & Momose, Cytologia (Fujii Jub. Vol.) 1: 365. 1937. Type: *Fuziifilix pilosella* (Hook.) Nakai & Momose [=*Davallia pilosella* 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, 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.

Synopsis. — *Sitobolium* is a small clade of *ca.* five species sister to *Microlepia*. *Sitobolium* are distinguished by their relatively small leaves that are provided with elongate catenate hairs. These hairs often bear a capitate non-glandular terminal cell. *Sitobolium punctilobulum* and *S. appendiculatum* are additionally provided with 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 *Coptidipteris* (based upon *Microlepia wilfordii*). The two are united in having tuberculate perispore morphology (Fig. 4, b) (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 distinctly northern. Most species are East Asian, *Sitobolium punctilobulum* is the single North American species. We recovered it as a sister to the East Asian *S. scabra* as did Schwartsburd & al. (2020) who calculated an early Miocene divergence time between the two. This age estimate corresponds well with 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 by Knapp (2011) and Wan (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.

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. 27 C. 1844. — *Dennstaedtia appendiculata* (Wall. ex Hook.) J.Sm., Hist. Fil. 265. 1875.

Dennstaedtia elwesii (Baker) Bedd., Handb. Ferns Brit. India, Suppl., t. 347. 1876.

Sitobolium hirsutum (Sw.) L.A. Triana & Sundue, **comb. nov. —** *Davallia hirsuta* Sw., Schrad., J. Bot. 1800: 87. 1801. — *Dennstaedtia hirsuta* (Sw.) Mett. ex Miq., Ann. Mus. Bot. Lugd. -Bat. 3: 181. 1867.

Sitobolium punctilobulum (Michx.) Desv., Mem. Soc. Linn. Paris 6, 2: 263. 1827. — *Nephrodium punctilobulum* Michx., Fl. bor. Amer. 2: 268. 1803. — *Dennstaedtia punctilobula* (Michx.) T.Moore, Ind. Fil. 97. 1857.

Sitobolium wilfordii (T.Moore) L.A. Triana & Sundue, **comb. nov. —** *Microlepia wilfordii* T.Moore, Ind. 299. 1861. — *Dennstaedtia wilfordii* (T.Moore) Christ, Geogr. d. Farne 192, 195. 1910. — *Coptidipteris wilfordii* (T.Moore) Nakai & Momose, Cytologia, Fujii Jub. Vol. 365, f. 1(a), 2(i) e 3(c) g 4(c−d). 1937.

Sitobolium zeylanicum (Sw.) L.A. Triana & Sundue, **comb. nov. —** *Dicksonia zeylanica* Sw., Schrad., J. Bot. 1800: 91. 1801. — *Dennstaedtia zeylanica* (Sw.) Zink ex Fraser-Jenk. & Kandel; Ferns and Fern-allies of Nepal 1: 161. 2015.

Dennstaedtia scabra (Wall. ex Hook.) T.Moore, Ind. Fil. 307. 1961.

Dennstaedtia melanostipes Ching, Chien & Chun, Fl. Reipubl. Pop. Sin. 2: 357 1959.

Excluded species

Sitobolium adiantoides J. Sm. [=*Dicksonia bipinnata* Cav.]

Sitobolium dubium (R. Br.) Brack [=*Calochlaena dubia* (R. Br.) M.D. Turner & R.A. White]

Sitobolium plumieri (Hook.) J. Sm. [=*Saccoloma domingense* (Spreng.) C. Chr.]

Sitobolium rubiginosum (Kaulf.) J. Sm. [=*Patania cicutaria* (Sw.) L.A. Triana & Sundue]

Sitobolium stramineum (Labill.) Brack. [=*Culcita straminea* (Labill.) Maxon]

IV. *Mucura* L.A. Triana & Sundue, **gen. nov. —** Type: *Mucura bipinnata* (Cav.) L.A. Triana & Sundue (=*Dicksonia bipinnata* Cav.). Fig. 8

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.

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 · ɾa] derived from the Caribbean and Chibcha linguistic families (Flórez, 1955), which 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 *M. globulifera*, and a long narrow neck, reminiscent of the cylindrical indusium of *M. bipinnata*.

Discussion. — *Mucura* comprises two neotropical species that are 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. Navarrete & Øllgaard (2000) emphasized the morphological disparity between its species and other neotropical species (here treated as *Patania*). 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. 4, a). 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 *Dennstaedtia*ceae. They can further be distinguished from *Patania* by their narrow, 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, Proc. Biol. Soc. Wash. 51: 39. 1938.

Mucura globulifera (Poir.) L.A. Triana & Sundue, **comb. nov. —** *Polypodium globuliferum* Poir., Lam. & al., Encycl. 5: 554. 1804. — *Dennstaedtia globulifera* (Poir.) Hieron., Engl. Jahrb. 114: 455. 1904.

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Literature Cited

Becari-Viana, I. & Schwartsburd, P.B. 2017. Morpho-anatomical studies and evolutionary interpretations of the rhizomes of extant Dennstaedtiaceae. *Amer. Fern J.* 107: 105−123. https://doi.org/10.1640/0002-8444-107.3.105

Beddome, R.H. 1876. *Supplement to The Ferns of Southern India and British India: Containing a Revised List of All the Ferms of India, Ceylon, Birmah, and the Malay Peninsula and 45 Plates of Hitherto Unfigured Species*. Madras: Gantz Brothers.

Bower, F.O. 1928. The Ferns (Filicales) treated comparatively with a view to their natural classification. Vol. 3: the leptosporangiate ferns. Cambridge: Cambridge University Press.

Brownsey, P.J. 1998. Dennstaedtiaceae. Pp. 214–228 in: Orchard, A.E., & McCarthy, P.M. (eds.), *Flora of Australia*, vol. 48. Melbourne: ABRS/CSIRO.

Brownsey, P.J. & Perrie, L.R. 2018: Dennstaedtiaceae. Pp. 1−53 in: Breitwieser, I. & Wilton, A.D. (eds.), *Flora of New Zealand - Ferns and Lycophytes*. Fascicle 19. Lincoln: Manaaki Whenua Press.

Chernomor, O., von Haeseler, A. & Minh, B.Q. 2016. Terrace aware data structure for phylogenomic inference from supermatrices. *Syst. Biol*. 65: 997–1008. https://doi.org/10.1093/sysbio/syw037

Conard, H.S. 1908. *The structure and life-history of the hay-scented fern* (No. 7). Washington: Carnegie Institution of Washington.

Copeland, E.B. 1947. Genera Filicum-the genera of ferns. *Genera Filicum-the genera of ferns.* Waltham, Mass.: Chronica Botanica Co.

Copeland, E.B. 1958. *Fern flora of the Philippines.* Manila: Bureau of Printing.

Doyle, J.J. & Doyle, J.L., 1987. *A rapid DNA isolation procedure for small quantities of fresh leaf tissue*.Phytochemical Bulletin 19: 11–15

Ebihara, A., Nakato, N., Amoroso, V.B., Hidayat, A. and Kuo, L.Y., 2016. *Monachosorum arakii* Tagawa (Dennstaedtiaceae) is a relict "international" hybrid: a reassessment of the *Monachosorum* species. Systematic Botany 4: 586–595.

Farwell, O.A. 1931. Fern notes II. Ferns in the herbarium of Parke, Davis & Co. *Amer. Midl. Naturalist* 12: 233−311.

Erdtman, G. 1960. The acetolysis method. A revised description. *Svensk Bot. Tidskr.* 54: 561−564.

Flórez, L. 1955. Algunas voces indígenas en el español de Colombia. *Revista Colombiana de Antropología* 4: 286−310.

Fraser-Jenkins, C.R., Kandel, D.R. & Pariyar, S. 2015. Ferns and fern-allies of Nepal. *Indian Fern J.* 342.

Fraser-Jenkins, C.R., Gandhi, K.N., Kholia, B.S. & Benniamin, A. 2017. *An annotated checklist of Indian Pteridophytes*. Part 1. Dehra Dun: Bishen Singh Mahendra Pal Singh.

Hasebe M, Omori, T., Nakazawa, M., Sano, T., Kato, M., & Iwatsuki, K. 1994. *rbcL* gene sequences provide evidence for the evolutionary lineages of leptosporangiate ferns. *Proc. Natl. Acad. Sci. U.S.A.* 91: 5730−5734. https://doi.org/10.1073/pnas.91.12.5730

Hassler, M. & Schmitt, B., 2021. World Ferns. Synonymic checklist and distribution of ferns and lycophytes of the world.

Holttum, R.E. 1968. *Flora of Malaya*. Singapore: Government Printing Office.

Jermy, A.C. & Walker, T.G. 1985. *Cytotaxonomic studies of the ferns of Trinidad*. London: British Museum (Natural History).

Jermy, A.C., Crabbe, J.A. & Thomas, B.A. (eds.). 1973. *Phylogeny and classification of the ferns.* London: Academic Press.

John, M.E. 1992. An efficient method for isolation of RNA and DNA from plants containing polyphenolics. *Nucl. Acids Res.* 20: 2381. https://doi.org/10.1093/nar/20.9.2381

Kalyaanamoorthy, S., Minh, B.Q., Wong, T.K., Von Haeseler, A. & Jermiin, L.S. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. *Nat. methods* 14: 587−589. https://doi.org/10.1038/nmeth.4285

Katoh, K., & Standley, D.M. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molec. Biol. Evol.* 30: 772−780. https://doi.org/10.1093/molbev/mst010

Kearse, M., Moir, R., Wilson, A., Stones-Havas, S., Cheung, M., Sturrock, S., Buxton, S., Cooper, A., Markowitz, S., Duran, C., Thierer, T., Ashton, B., Meintjes, P. & Drummond, A. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Knapp, R., 2011. *Ferns and Fern Allies of Taiwan (英文版)*. Taipei: KBCC Press and Yuan−Liou Publishing.

Kramer, K.U. 1990. Dennstaedtiaceae. Pp. 81−94 in: Kramer, K.U., Green, P.S., & Kubitzki, K. (eds.), *The families and genera of vascular plants. V. 1: Pteridophytes and gymnosperms*. Berlin, Heidelberg: Springer.

Lee, G.E., Condamine, F.L., Bechteler, J., Pérez-Escobar, O.A., Scheben, A., Schäfer-Verwimp, A., Pocs, T. & Heinrichs, J. 2020. An ancient tropical origin, dispersals via land bridges and Miocene diversification explain the subcosmopolitan disjunctions of the liverwort genus *Lejeunea*. *Sci. Rep.* 10: 1−13. https://doi.org/10.1038/s41598-020-71039-1

Lellinger, D.B. 2002. A modern multilingual glossary for taxonomic pteridology. *Pteridologia* 3: 1–263.

Lewis, P.O. 2001. A likelihood approach to estimating phylogeny from discrete morphological character data. *Syst. Biol.* 50: 913−925. https://doi.org/10.1080/106351501753462876

Maddison, W.P. 2008. Mesquite: a modular system for evolutionary analysis. *Evolution*, *62*: 1103–1118.

Mickel, J.T. 1973. The Classification and Phylogenetic Position of the Dennstaedtiaceae. Pp. 135−144 in: Jermy, A.C., Crabbe, J.A. & Thomas, B.A. (eds.), *Phylogeny and classification of the ferns.* London: Academic Press.

Mickel, J.T. & Smith, A.R. 2004. *The Pteridophytes of Mexico*. New York: New York Botanical Garden Press.

Minh, B.Q., Schmidt, H.A., Chernomor, O., Schrempf, D., Woodhams, M.D., Von Haeseler, A. & Lanfear, R. 2020. IQ-TREE 2: new models and efficient methods for phylogenetic inference in the genomic era. *Molec. Biol. Evol.* 37: 1530−1534. https://doi.org/10.1093/molbev/msaa015

Miller, M.A., Pfeiffer, W. & Schwartz, T. 2010. Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *Gateway Computing Environments Workshop (GCE)* 2010: 1−8. https://doi.org/10.1109/GCE.2010.5676129.

Moore, S.J. 2010. Monographic study on the fern genus *Microlepia* (Dennstaedtiaceae). Ph. D. thesis of Department of Life Science, National Taiwan Normal University, Taipei, Taiwan.

Moore, T. 1859. *Index filicum: a synopsis, with characters, of the genera, and an enumeration of the species of ferns, with synonyms, references.* (Vol. 1). London: William Pamplin.

Moran, R.C. 1995. *Dennstaedtia*. Pp. 150−163 in: Moran, R.C. & Riba, R. (eds.). *Flora Mesoamericana. Vol. 1. Psilotaceae a Salviniaceae*. México D.F.: Universidad Nacional Autónoma de México.

Nakaike, T. 1975. *Enumeratio Pteridophytarum Japoniucm, Filicales*. Tokyo: University of Tokyo Press.

Nakamura, M. (ed.). 2008. Illustrated Flora of Ferns and Fern Allies of South Pacific Islands. National Museum of Nature and Science, Series No. 8. Tokyo: Tokai University Press.

Nakato, N. and Ebihara, A., 2011. Chromosome number of *Microlepia hookeriana* (Dennstaedtiaceae) and chromosome number evolution in the genus *Microlepia*. *Bull Natl Mus Nat Sci Ser B, 37*: 75−78.

Navarrete, H. & Øllgaard, B. 2000. The fern genus *Dennstaedtia* (Dennstaedtiaceae) in Ecuador, new characters, new species and a new combination. *Nordic J. Bot.* 20: 319−346. https://doi.org/10.1111/j.1756-1051.2000.tb00747.x

Paris, C.A. & Barrington, D.S. 1990. William Jackson Hooker and the generic classification of ferns. *Ann. Missouri Bot. Gard.* 77: 228−238. https://doi.org/10.2307/2399536

Paradis, E., Claude, J. & Strimmer, K. 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20: 289−290. https://doi.org/10.1093/bioinformatics/btg412

Perrie, L.R., Shepherd, L.D. & Brownsey, P.J. 2015. An expanded phylogeny of the Dennstaedtiaceae ferns: *Oenotrichia* falls within a non-monophyletic *Dennstaedtia*, and *Saccoloma* is polyphyletic. *Austral. Syst. Bot.* 28: 256−264. https://doi.org/10.1071/SB15035

Pigg, K.B., DeVore, M.L., Greenwood, D.R., Sundue, M., Schwartsburd, P. & Basinger, J.F. 2021. Fossil Dennstaedtiaceae and Hymenophyllaceae from the Early Eocene of the Pacific Northwest. *Int. J. Pl. Sci.* 182: 793−807. https://doi.org/10.1086/715633

PPG-I. 2016. A community-derived classification for extant lycophytes and ferns. *J. Syst. Evol.* 54: 563−603. https://doi.org/10.1111/jse.12229

Presl, K.B. 1836. *Tentamen Pteridographiae seu genera Filicacearum*. Prague: Typis Filiorum Theophili Haase.

Punt, W., Hoen, P.P., Blackmore, S. & Le Thomas, A. 2007. Glossary of pollen and spore terminology. *Rev. Palaeobot. Palynol.* 143: 1–81. https://doi.org/10.1016/j.revpalbo.2006.06.008

Revell, L.J. 2012. phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol Evol.* 3: 217−223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Ronquist, F., Teslenko, M., van der Mark, P., Ayres, D.L., Darling, A., Höhna, S., Larget, B., Liu, L., Suchard, M.A. & Huelsenbeck, J.P. 2012. MRBAYES 3.2: Efficient Bayesian phylogenetic inference and model selection across a large model space. *Syst. Biol.* 61: 539−542. https://doi.org/10.1093/sysbio/sys029

Shang, H., Sundue, M., Wei, R., Wei, X.P., Luo, J.J., Liu, L., Schwartsburd, P.B., Yan, Y.H. & Zhang, X.C. 2018. Hiya: a new genus segregated from *Hypolepis* in the fern family Dennstaedtiaceae, based on phylogenetic evidence and character evolution. *Molec. Phylogen. Evol.* 127: 449−458. https://doi.org/10.1016/j.ympev.2018.04.038

Schuettpelz, E., & Pryer, K.M. 2007. Fern phylogeny inferred from 400 leptosporangiate species and three plastid genes. *Taxon* 56: 1037−1050. https://doi.org/10.2307/25065903

Schuettpelz, E., Rouhan, G., Pryer, K.M., Rothfels, C.J., Prado, J., Sundue, M., Windham, M.D., Moran, R.C. & Smith, A.R. 2018. Are there too many fern genera? *Taxon* 67: 473−480. https://doi.org/10.12705/673.1

Schwartsburd, P.B. 2017. (2508) Proposal to conserve the name *Microlepia* against *Scyphofilix* (Dennstaedtiaceae). *Taxon* 66: 516−516. https://doi.org/10.12705/662.20

Schwartsburd, P.B., Navarrete, H., Smith, A.R. & Kessler, M. 2017. Prodromus of a fern flora for Bolivia. XXVI. Dennstaedtiaceae. *Phytotaxa* 332: 251−268. https://doi.org/10.11646/phytotaxa.332.3.2

Schwartsburd, P.B., Perrie, L.R., Brownsey, P., Shepherd, L.D., Shang, H., Barrington, D.S. & Sundue, M. 2020. New insights into the evolution of the fern family

Dennstaedtiaceae from an expanded molecular phylogeny and morphological analysis. *Molec. Phylogen. Evol.* 150: 106881. https://doi.org/10.1016/j.ympev.2020.106881

Skog, J.E., Mickel, J.T., Moran, R.C., Volovsek, M. & Zimmer, E.A. 2004. Molecular studies of representative species in the fern genus *Elaphoglossum* (Dryopteridaceae) based on cpDNA sequences *rbcL*, *trnL-F*, and *rps4-trnS*. *Int. J. Pl. Sci.* 165: 1063–1075. https://doi.org/10.1086/423877

Small, R.L., Lickey, E.B., Shaw, J. & Hauk, W.D. 2005. Amplification of noncoding chloroplast DNA for phylogenetic studies in lycophytes and monilophytes with a comparative example of relative phylogenetic utility from Ophioglossaceae. *Molec. Phylogen. Evol.* 36: 509−522. https://doi.org/10.1016/j.ympev.2005.04.018

Smith, A.R. & Cranfill, R.B. 2002. Intrafamilial relationships of the thelypteroid ferns. *Amer. Fern J.* 92: 131−149. https://doi.org/10.1640/0002-8444(2002)092[0131:IROTTF]2.0.CO;2

Smith, J. 1842. An arrangement and definition of the genera of ferns, with observations on the affinities of each genus. *London J. Bot.* 1: 659–668.

Stamatakis, A. 2014. RAxML Version 8: A tool for Phylogenetic Analysis and Post-Analysis of Large Phylogenies. *Bioinformatics* 30: 1312−1313. https://doi.org/10.1093/bioinformatics/btu033

Suissa, J.S., Sundue, M. & Testo, W.L. 2021. Mountains, climate and niche heterogeneity explain global patterns of fern diversity. *J. Biogeogr.* 48: 1296−1308. https://doi.org/10.1111/jbi.14076

Sullivan, J. & Joyce, J. 2005. Model Selection in Phylogenetics. *Annu. Rev. Ecol. Evol.* 36: 445−466. https://doi.org/10.1146/annurev.ecolsys.36.102003.152633.

Sun, B.Y. 2014. *Biodiversity of Cambodia: Lycophytes and ferns*. Incheon: National Institute of Biological Resources.

Taberlet, P., Gielly, L., Pautou, G. & Bouvet, J. 1991. Universal primers for amplification of three non-coding regions of chloroplast DNA. *Plant Mol. Biol.* 17: 1105–1109. https://doi.org/10.1007/BF00037152

Tagawa, M. & Iwatsuki, K. 1979. Pteridophytes. Pp. 1−128 in: Smitinand, T. & Larsen, K. (eds.), *Flora of Thailand, vol. 3, part 1*. Bangkok: Royal Forest Department.

Tardieu-Blot, M. 1958. — Polypodiaceae *s.l.* Pp. 1−391 in: Humbert, H. (ed.), *Flore de Madagascar et des Comores, famille 5*. Paris: Firmin-Didot.

Testo, W. & Sundue, M. 2016. A 4000-species dataset provides new insight into the evolution of ferns. *Molec. Phylogen. Evol.* 105: 200−211. https://doi.org/10.1016/j.ympev.2016.09.003

Thiers, B. 2022**.** Index Herbariorum: A global directory of public herbaria and associated staff. New York: The New York Botanical Garden. http://sweetgum.nybg.org/science/ih/.

TPG 2019. Updating Taiwanese pteridophyte checklist: a new phylogenetic classification. *Taiwania* 64: 367–395. https://doi.org/10.6165/tai.2019.64.367

TPG 2021. Taiwan Pteridophyte Checklist v2021.2. https://groups.google.com/forum/#!forum/taiwan-pteridophyte-group [accessed 02.07.2021]

Triana- Moreno, L.A., Schwartsburd, P.B., Yañez, A., Pena, N.T.L., Kuo, L.Y., Rothfels, C. & Sundue, M. 2022. (2892) Proposal to conserve the name *Dennstaedtia* (Dennstaedtiaceae) with a conserved type. *Taxon 71*: 688–690. https://doi.org/10.1002/tax.12756

Tryon, R.M. 1960. A review of the genus *Dennstaedtia* in America. *Contr. Gray Herb.* 187: 23−52. https://www.jstor.org/stable/41764824

Tryon, A.F. & Lugardon, B. 1990. *Spores of the Pteridophyta: surface, wall structure, and diversity based on electron microscope studies*. New York: Springer.

Tryon, R.M. & Tryon, A.F. 1980. Proposal to conserve the name *Dennstaedtia* T. Moore (1859) (Pteridophyta) against *Dennstaedtia* Bernh. (1801), *Sitobolium* Desv. (1827), *Patania* Presl (1836), and *Adectum* Link (1841). *Taxon* 29: 512−513.

Tryon, R.M. & Tryon, A.F. 1981. Taxonomic and nomenclatural notes on ferns. *Rhodora* 83: 133−137. https://www.jstor.org/stable/23314057

Tryon, R.M. & Tryon, A.F. 1982. *Ferns and allied plants: with special reference to tropical America*. New York: Springer.

Voss, E.G. 1982. Nomenclature Committee Reports. *Taxon* 31: 310−318. https://doi.org/10.2307/1219998.

Wan, J.K. 2013. Dennstaedtiaceae. Pp: 147−168 in: Wu, C.-Y., Raven, P.H. & Hong, D.-Y. (eds.), *Flora of China, vol. 2–3, Lycopodiaceae through Polypodiaceae*. Beijing: Science Press. St. Louis: Missouri Botanical Garden Press.

Wang, J.C., Chang, Y., Chiou, W.L. & Liu, H. 2017. Two new species of *Microlepia* (Dennstaedtiaceae, Polypodiopsida) from Thailand. *Phytotaxa* 324: 193−197. https://doi.org/10.11646/phytotaxa.324.2.8

Wang, T., Liu, L., Luo, J.J., Gu, Y.F., Chen, S.S., Liu, B., Shang, H. & Yan, Y.H. 2021. Finding Hidden Outliers to Promote the Consistency of Key Morphological Traits and Phylogeny in Dennstaedtiaceae. *Taxonomy* 1: 256−265. https://doi.org/10.3390/taxonomy1030019

Weakley, A.S. 2020. *Flora of the southeastern United States*. Chapel Hill: University of North Carolina Herbarium, North Carolina Botanical Garden.

Wolf, P.G., Soltis, P.S. & Soltis, D.E. 1994. Phylogenetic relationships of dennstaedtioid ferns: evidence from rbcL sequences. *Molec. Phylogen. Evol.* 3: 383−392. https://doi.org/10.1006/mpev.1994.1044

Wolf, P.G. 1995. Phylogenetic analyses of rbcL and nuclear ribosomal RNA gene sequences in Dennstaedtiaceae. *Amer. Fern J.* 85: 306−327. https://doi.org/10.2307/1547812

Yan, Y.H., Qi, X.P., Liao, W.B., Xing, F.W., Ding, M.Y., Wang, F.G., Zhang, X., Wu, Z., Serizawa, S., Prado, J., Funston, A., Gilbert, M., & Nooteboom, H.P. 2013. Dennstaedtiaceae. *Flora of China* 2−3: 147−168.

Yañez, A., Arana, M.D., Marquez, G.J. & Oggero, A.J. 2014. The genus *Dennstaedtia* Bernh. (Dennstaedtiaceae) in Argentina. *Phytotaxa* 174: 69−81. https://doi.org/10.11646/phytotaxa.174.2.1

Yañez A., Márquez, G.J., & Morbelli, M.A. 2016a. Spore morphology and ultrastructure of Dennstaedtiaceae from Paranaense Phytogeographic Province I.: Genus *Dennstaedtia*. *Rev. Palaeobot. Palynol.* 224: 181−194. https://doi.org/10.1016/j.revpalbo.2015.06.012

Yañez A., Márquez, G.J., & Morbelli, M.A. 2016b. Palynological analysis of Dennstaedtiaceae taxa from the Paranaense Phytogeographic Province that produce Trilete spores II: *Microlepia speluncae* and *Pteridium arachnoideum*. *Anais Acad. Brasil. Ci.* 88: 877−890. https://doi.org/10.1590/0001-3765201620150230

Yuan, Y., Fu, L. & Ma, C.Y. 2012. *Microlepia boluoensis* sp. nov. (Dennsteadtiaceae) from Guangdong, China. *Nordic J. Bot.* 30: 168−173. https://doi.org/10.1111/j.1756-1051.2011.01318.x

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 in particular. CJR and LYK contributed samples. All authors contributed to writing and revising the manuscript.

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Tables

Table 1. Primers used for amplification and sequencing. Those marked with an asterisk (*) were used only for 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)

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

				Characters														
	ILD test (*p-value*)	Number of taxa	Number of terminals	Alignment length	Constant characters	(%)	Variable characters	(%)	Non-informative variable characters	(%)	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

Table 3. Characters found useful to differentiate the genera of the Dennstaedtioideae.

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

Figures

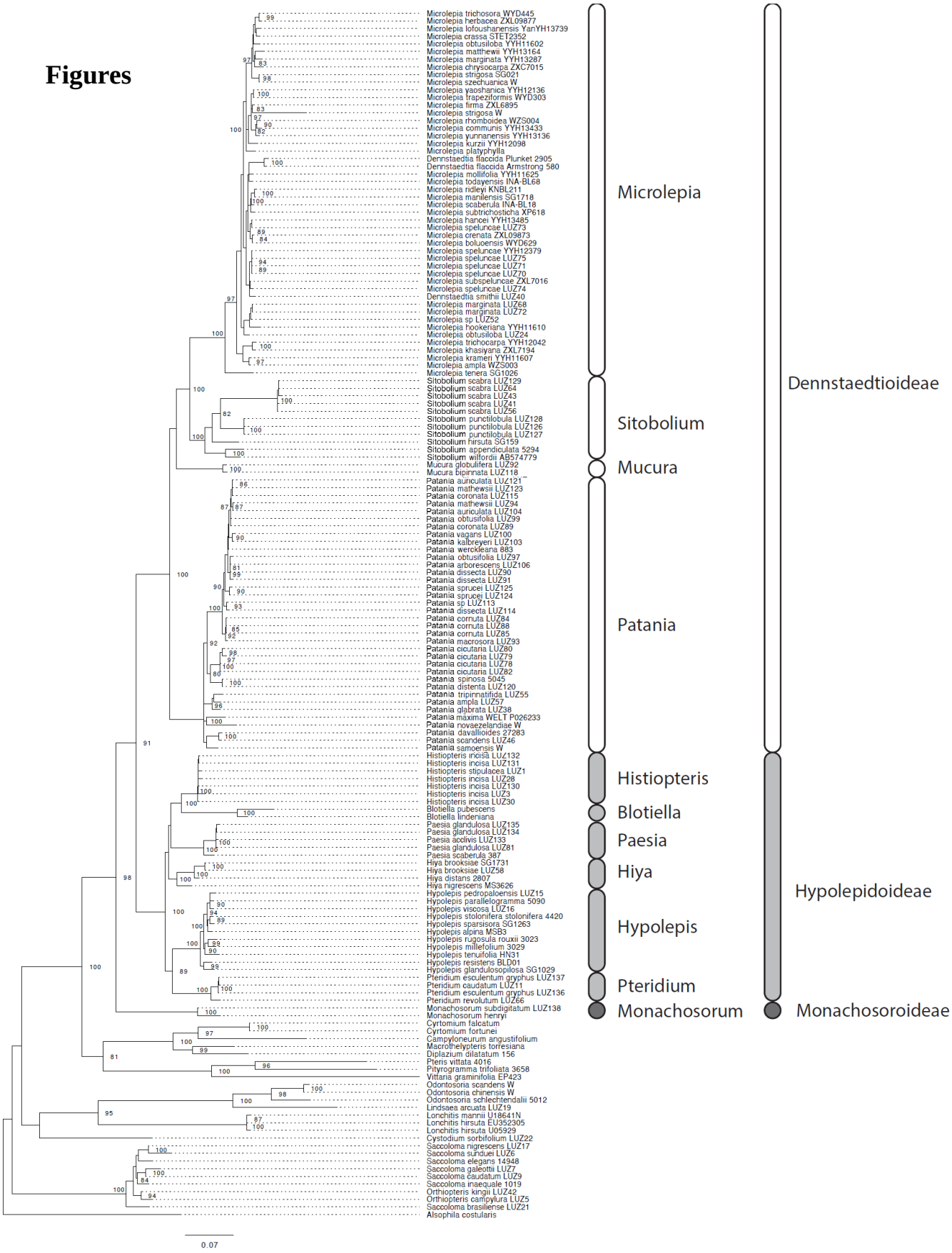

Figure 1. Best tree resulting from the maximum likelihood phylogenetic tree search using IQ-Tree2 Bootstrap support values >80% from 1,000 iterations are presented at nodes.

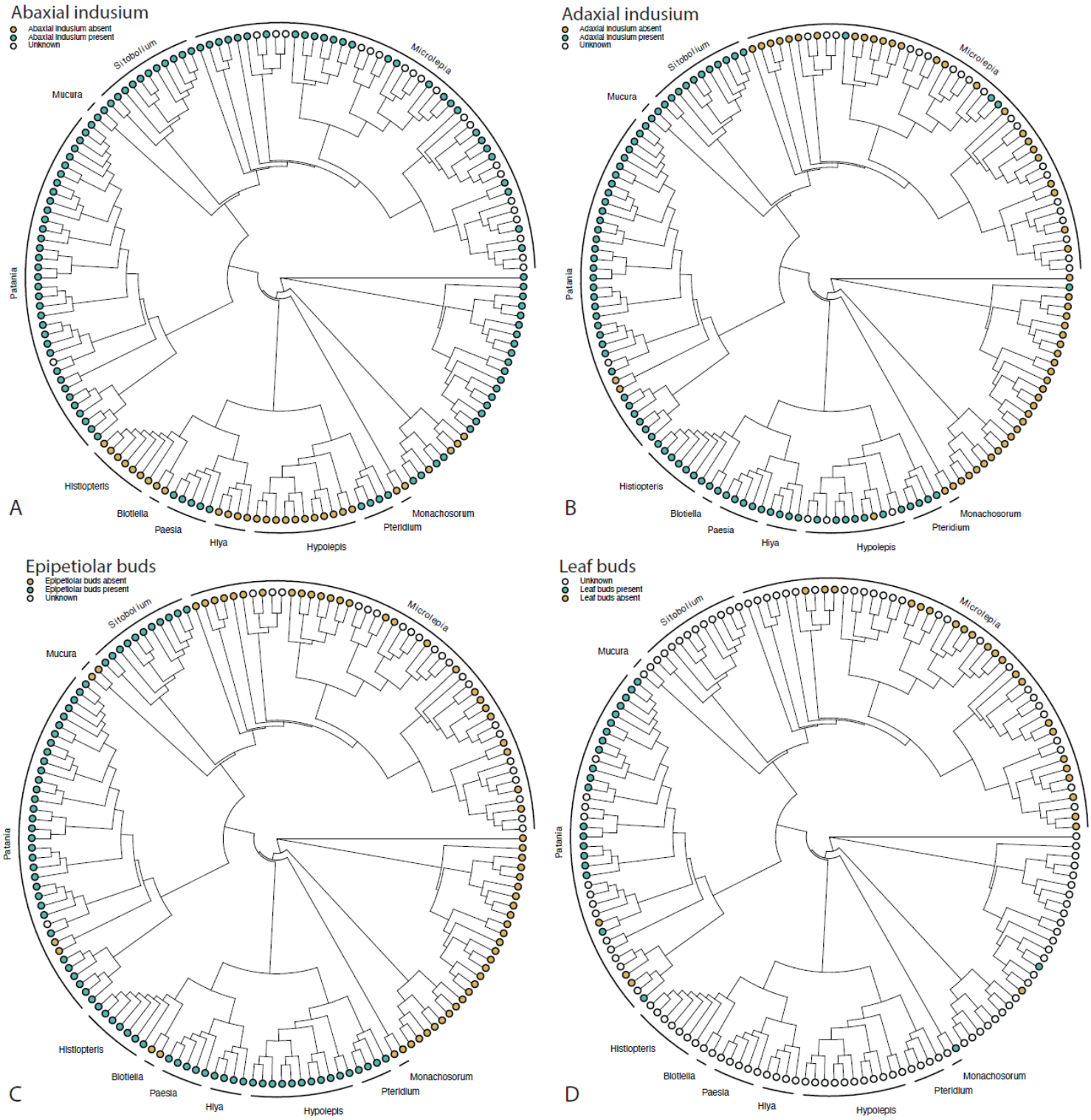

Figure 2. Character state maps for four traits. **A**. Abaxial indusium present vs. absent. **B**. Adaxial indusium present vs. absent. **C**. Epipetiolar buds present vs. absent. **D**. Leaf buds present vs. absent.

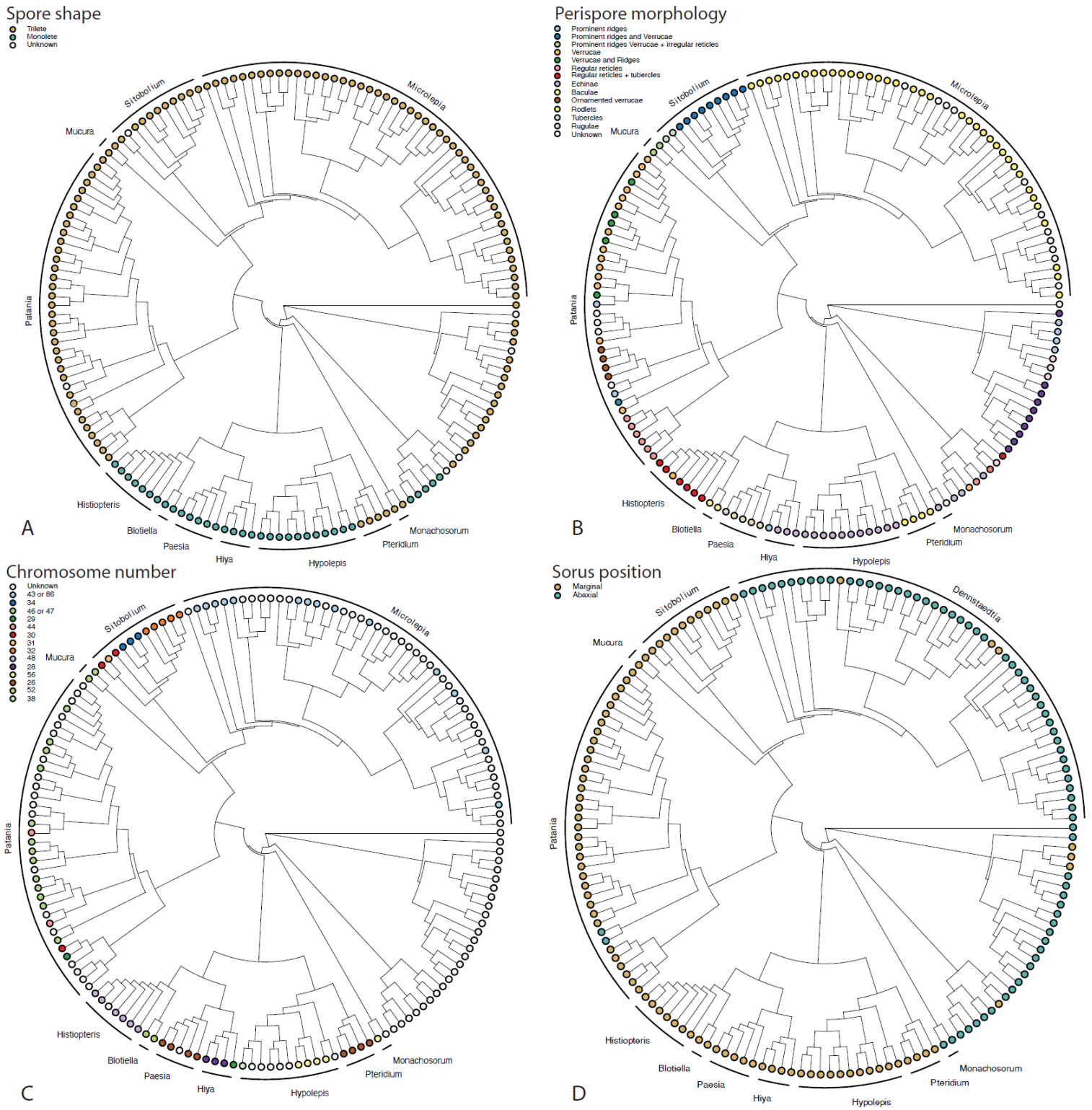

Figure 3. Character state maps for four traits. **A**. Spore shape: monolete (blue), trilete (yellow). **B**. Perpispore morphology: prominent ridges (light blue), prominent ridges and verrucae (blue), prominent ridges, verrucae + irregular reticles (light green), verrucae (orange), verrucae and ridges (green), regular reticles (pink), regular reticles + tubercles (red), echinae (purple), baculae (light yellow), ornamented verrucae (brown), rodlets (yellow), tubercles (aquamarine), rugulae (light brown). **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**. Sorus position: abaxial (blue), marginal (yellow). White circles indicate taxa for which character state data is missing.

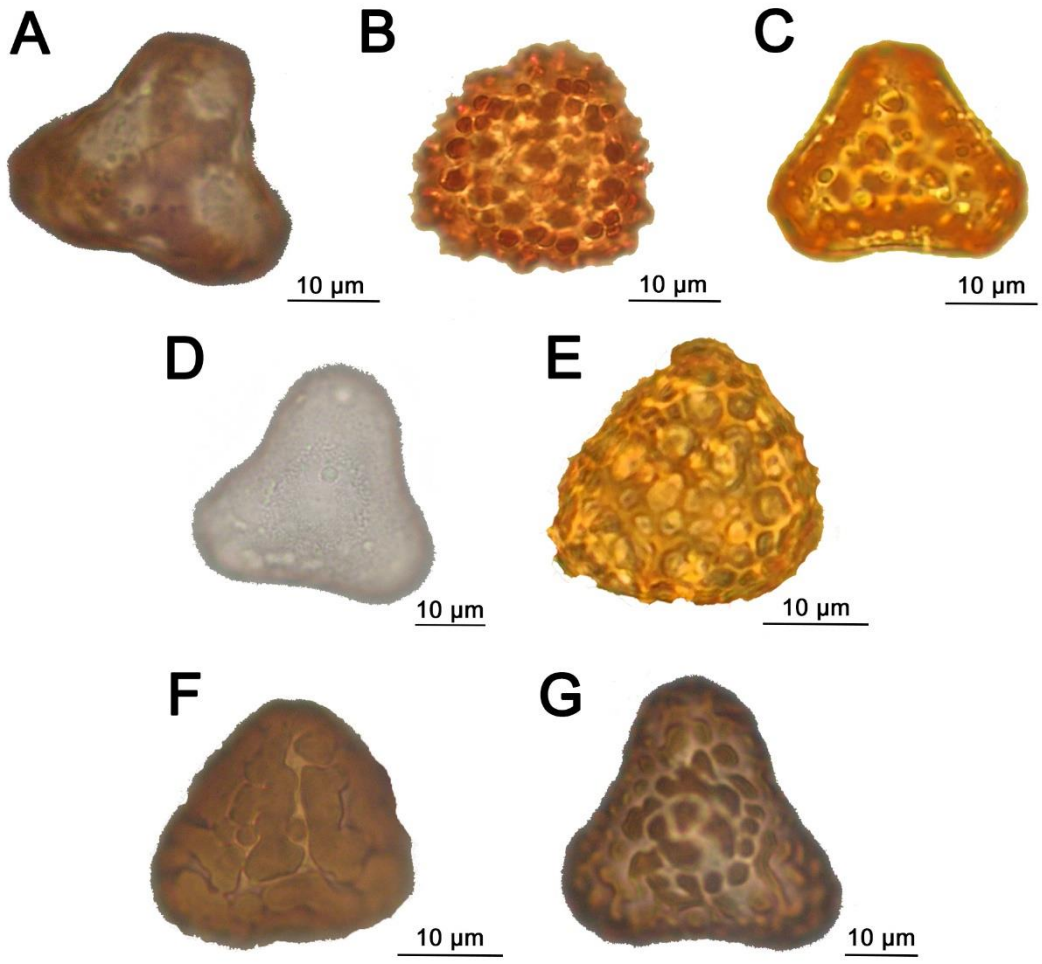

Figure 4. Examples of perispore morphology of spores in distal view. **A**. Verrucae and irregular reticles with prominent ridges covering the corners, *Mucura globulifera* (*Yañez & Márquez 86*, LP). **B**. Tubercles, *Sitobolium wilfordii* (*Unknown s.n.*, UVMVT192145). **C**. Verrucae and prominent 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).

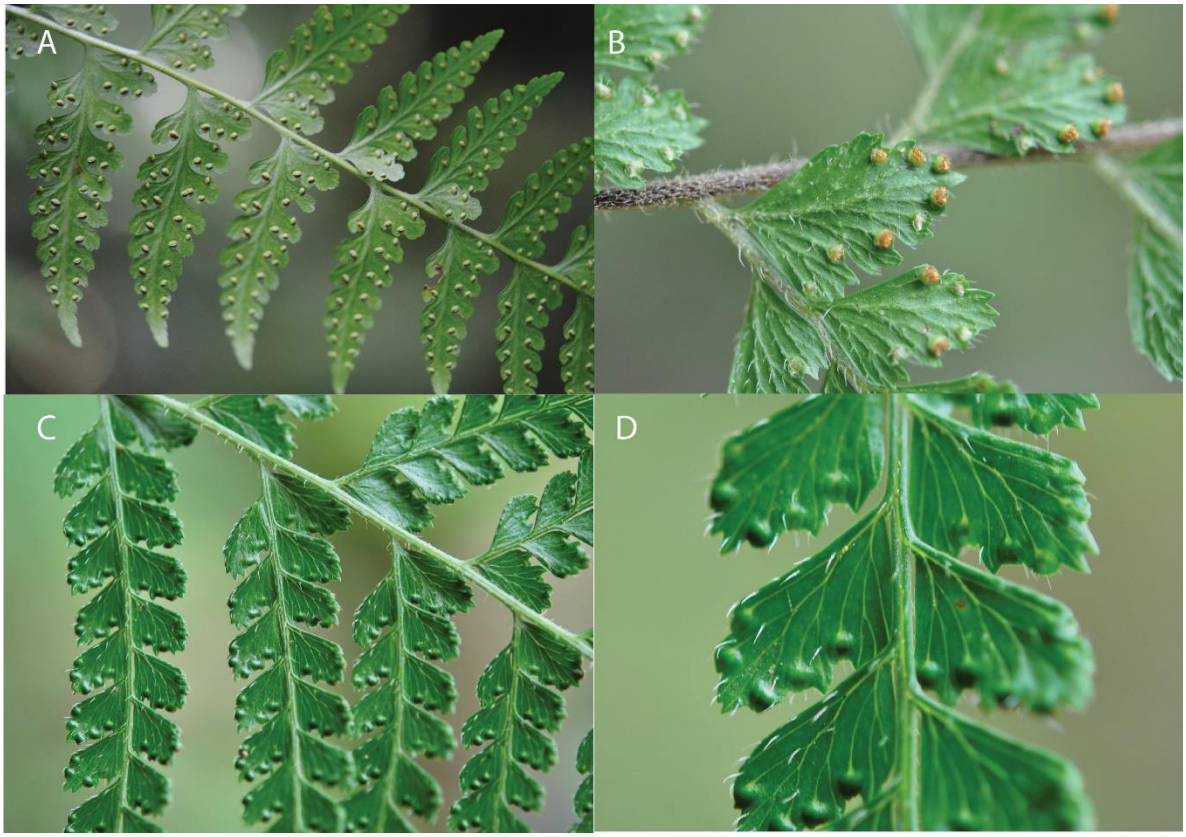

Figure 5. Characters of *Microlepia*. **A**. Lower leaf surface. **B**. Detail of abaxial sori. **C**. Upper leaf surface. **D**. Detail of pinna costae. All from *Microlepia strigosa*, Philippines, *Sundue 3163* (CMUH, TAIF, VT).

Figure 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.

Figure 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.

Figure 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.

Appendix 1. Species names and GenBank accession numbers of DNA sequences used in this study.

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* (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, *Dirscoll & 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* (TAIF), —, —, —, *OK092318. ***Dennstaedtia*** *sp.*, LUZ113, *M. Sundue 3991* (VT), —, —, *OK092474, *OK092346. ***Dennstaedtia ampla*** (Baker) L.A. Triana & Sundue, LUZ57, *Wade 4671* (TAIF), —, *OK092384, *OK092427, —. ***Dennstaedtia arborescens*** (Willd.) L.A. Triana & Sundue, LUZ106, *J. Castro 756* (COL), *OK092514, *OK092385,

*OK092428, —. ***Dennstaedtia auriculata*** (Navarr. & B.Øllg.) L.A. Triana & Sundue, LUZ104, *J. Murillo 4791* (COL), —, —, *OK092429, *OK092319. ***Dennstaedtia auriculata*** (Navarr. & B.Øllg.) L.A. Triana & Sundue, LUZ121, *C.J. Rothfels 4973* (UC), *OK092515, —, *OK092430, *OK092320. ***Dennstaedtia cicutaria*** (Sw.) L.A. Triana & Sundue, LUZ78, *L.A. Triana 993* (COL), *OK092517, *OK092386, *OK092432, *OK092322. ***Dennstaedtia cicutaria*** (Sw.) L.A. Triana & Sundue, LUZ79, *L.A. Triana 1016* (COL), *OK092518, *OK092387, *OK092433, *OK092323. ***Dennstaedtia cicutaria*** (Sw.) L.A. Triana & Sundue, LUZ80, *L.A. Triana 1036* (COL), *OK092519, *OK092388, *OK092434, *OK092324. ***Dennstaedtia cicutaria*** (Sw.) L.A. Triana & Sundue, LUZ82, *L.A. Triana 1043* (COL), *OK092520, *OK092389, *OK092435, *OK092325. ***Dennstaedtia cornuta*** (Kaulf.) L.A. Triana & Sundue, LUZ84, *L.A. Triana 1017* (COL), *OK092521, *OK092390, *OK092436, *OK092326. ***Dennstaedtia cornuta*** (Kaulf.) L.A. Triana & Sundue, LUZ85, *L.A. Triana 1022* (COL), *OK092522, *OK092391, *OK092437, *OK092327. ***Dennstaedtia cornuta*** (Kaulf.) L.A. Triana & Sundue, LUZ88, *L.A. Triana 1040* (COL), —, *OK092392, *OK092438, —. ***Dennstaedtia coronata*** (Sodiro) L.A. Triana & Sundue, LUZ89, *L.A. Triana 1033* (COL), —, *OK092393, *OK092441, —. ***Dennstaedtia coronata*** (Sodiro) L.A. Triana & Sundue, LUZ115, *W.L. Testo 758* (VT), —, *OK092394, *OK092442, *OK092328. ***Dennstaedtia davallioides*** (R.Br.) L.A. Triana & Sundue, 27283, *L. Perrie 3585* (WELT), KT983819, MH918674, —, —. ***Dennstaedtia dissecta*** (Sw.) L.A. Triana & Sundue, LUZ114, *W.L. Testo 721* (VT), —, —, *OK092447, *OK092330. ***Dennstaedtia dissecta*** (Sw.) L.A. Triana & Sundue, LUZ90, *L.A. Triana 1025* (COL), *OK092523, *OK092395, *OK092443, *OK092329. ***Dennstaedtia dissecta*** (Sw.) L.A. Triana & Sundue, LUZ91, *L.A. Triana 1030* (COL), —, *OK092396, *OK092444, —. ***Dennstaedtia distenta*** (Kunze) L.A. Triana & Sundue, LUZ120, *M. Sundue 4998* (VT),

*OK092524, *OK092397, *OK092448, *OK092331. ***Dennstaedtia glabrata*** (Ces.) L.A. Triana & Sundue, LUZ38, *L.Y. Kuo 1926* (TAIF), —, —, *OK092451, —. ***Dennstaedtia kalbreyeri*** (Maxon) L.A. Triana & Sundue, LUZ103, *J. Murillo 4790* (COL), *OK092528, *OK092400, *OK092454, —. ***Dennstaedtia macrosora*** (Navarr. & B.Øllg.) L.A. Triana & Sundue, LUZ93, *L.A. Triana 990* (COL), *OK092529, —, *OK092456, *OK092335. ***Dennstaedtia mathewsii*** (Hook.) L.A. Triana & Sundue, LUZ123, *C.J. Rothfels 5068* (UC), —, —, *OK092459, *OK092336. ***Dennstaedtia mathewsii*** (Hook.) L.A. Triana & Sundue, LUZ94, *L.A. Triana 991* (COL), *OK092530, —, *OK092457, —. ***Dennstaedtia maxima*** (E. Fourn.) L.A. Triana & Sundue, WELT_P026233, *WELT P026233* (WELT), KT983830, —, —, —. ***Dennstaedtia novae-zealandiae*** (Colenso) L.A. Triana & Sundue, W, *P.G. Wolf 682*, U18639, —, —, —. ***Dennstaedtia obtusifolia*** (Willd.) C.Presl, LUZ97, *L.A. Triana 1015* (COL), *OK092531, —, *OK092460, —. ***Dennstaedtia obtusifolia*** (Willd.) C.Presl, LUZ99, *L.A. Triana 1038* (COL), *OK092532, *OK092401, *OK092461, *OK092337. ***Dennstaedtia samoensis*** (Brack.) L.A. Triana & Sundue, W, *P.G. Wolf 425*, U18637, —, —, —. ***Dennstaedtia scandens*** (Blume) L.A. Triana & Sundue, LUZ46, *L.Y. Kuo 2806* (TAIF), —, —, *OK092472, —. ***Dennstaedtia spinosa*** (Mickel) L.A. Triana & Sundue, 5045, *M. Sundue 5045*, MT416337, MT470019, MT593216, —. ***Dennstaedtia sprucei*** (T.Moore) L.A. Triana & Sundue, LUZ124, *C.J. Rothfels 4974* (UC), *OK092539, *OK092404, *OK092475, *OK092347. ***Dennstaedtia sprucei*** (T.Moore) L.A. Triana & Sundue, LUZ125, *C.J. Rothfels 4975* (UC), *OK092540, —, *OK092476, *OK092348. ***Dennstaedtia tripinnatifida*** (Copel.) L.A. Triana & Sundue, LUZ55, *Wade 4441* (TAIF), —, *OK092405, *OK092477, —. ***Dennstaedtia vagans*** (Baker) L.A. Triana & Sundue, LUZ100, *L.A. Triana 1019* (COL), *OK092541, —, *OK092478, —. ***Dennstaedtia werckleana*** (Christ) L.A. Triana & Sundue, 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* (UC), *OK092544, *OK092409, *OK092481, *OK092354. ***Histiopteris incisa*** (Thunb.) J. Sm., LUZ131, *C.J. Rothfels 5051* (UC), *OK092545, *OK092410, *OK092482, *OK092355. ***Histiopteris incisa*** (Thunb.) J. Sm., LUZ132, *C.J. Rothfels 5050* (UC), *OK092546, *OK092411, *OK092483, *OK092356. ***Histiopteris incisa*** (Thunb.) J. Sm., LUZ28, *L.Y. Kuo 2685* (TAIF), *OK092543, *OK092407, —, *OK092351. ***Histiopteris incisa*** (Thunb.) J. Sm., LUZ3, *M. Sundue 3947* (VT), *OK092542, *OK092406, *OK092479, *OK092349. ***Histiopteris incisa*** (Thunb.) J. Sm., LUZ30, *L.Y. Kuo 3286* (TAIF), —, *OK092408, —, *OK092352. ***Histiopteris stipulacea*** Copel., LUZ1, *M. Sundue 3635* (VT), —, *OK092412, *OK092484, *OK092357. ***Hiya brooksiae*** (Alderw.) H. Shang, LUZ58, *Wade 4710* (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 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* (COL), *OK092548, *OK092414, *OK092487, *OK092360. ***Lindsaea arcuata*** Kunze, LUZ19, *L.A. Triana 1028* (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* (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*, *OK092525, *OK092398, *OK092449, *OK092332. ***Microlepia flaccida*** (G.Forst) L.A. Triana & Sundue, P2905, *G. Plunket 2905*, *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* (NY), —, *OK092415, *OK092489, —. ***Microlepia marginata*** (Panz.) C.Chr., LUZ72, *T.Y. Nwe 476* (NY), —, —, *OK092490, *OK092362. ***Microlepia marginata*** (Panz.) C.Chr., YYH13287, *Yan Yuehong* (PE), MK051720.1, —, MK051972.1, MK052509.1. ***Microlepia mathewii*** 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* (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* (TAIF), *OK092550, *OK092416, *OK092493, —. ***Microlepia speluncae*** (L.) T.Moore, LUZ70, *T.Y. Nwe 140* (NY), —, *OK092417, —, —. ***Microlepia speluncae*** (L.) T.Moore, LUZ71, *T.Y. Nwe 159* (NY), —, *OK092418, —, —. ***Microlepia speluncae*** (L.) T.Moore, LUZ73, *T.Y. Nwe 530* (NY), —, *OK092419, *OK092494, *OK092365. ***Microlepia speluncae*** (L.) T.Moore, LUZ74, *T.Y. Nwe 874* (NY), *OK092551, *OK092420, —, *OK092366. ***Microlepia speluncae*** (L.) T.Moore, LUZ75, *T.Y. Nwe 580* (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, 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* (UC), *OK092553, *OK092422, *OK092496, —. ***Mucura bipinnata*** (Cav.) L.A. Triana & Sundue, LUZ118, *S. Fawcett 470* (VT), *OK092516, —, *OK092431, *OK092321. ***Mucura globulifera*** (Poir.) L.A. Triana & Sundue, LUZ92, *L.A. Triana 1013* (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* (TNM), —, —, *OK092497, *OK092369. ***Orthiopteris kingii*** (Bedd.) Holttum, LUZ42, *L.Y. Kuo 2571* (TAIF), —, —, *OK092498, —. ***Paesia acclivis*** (Kunze) Kuhn, LUZ133, *C.J. Rothfels 4920* (UC), *OK092554, *OK092423, *OK092499, *OK092370. ***Paesia glandulosa*** (Sw.) Kuhn, LUZ134, *C.J. Rothfels 5113* (UC), *OK092556, —, *OK092501, *OK092372. ***Paesia glandulosa*** (Sw.) Kuhn, LUZ135, *C.J. Rothfels 5138* (UC), *OK092557, —, *OK092502, *OK092373. ***Paesia glandulosa*** (Sw.) Kuhn, LUZ81, *L.A. Triana 1042* (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* (COL), —, —, *OK092503, *OK092374. ***Pteridium esculentum*** (G. Forst.) Cockayne, LUZ136, *C.J. Rothfels 5031* (UC), *OK092558, —, *OK092504, *OK092375. ***Pteridium esculentum*** (G. Forst.) Cockayne, LUZ137, *C.J. Rothfels 4896* (UC), *OK092559, —, *OK092505, *OK092376. ***Pteridium revolutum*** (Blume) Nakai, LUZ66, *T.Y. Nwe 807* (NY), *OK092560, *OK092425, *OK092506, *OK092377. ***Pteris vittata*** L., 4016, *C.J.*

Rothfels 4016 (DUKE), KM008232, —, —, KM008008. ***Saccoloma brasiliense*** Mett., LUZ21, *C. Mynssen 1091* (TUR), —, —, *OK092507, *OK092378. ***Saccoloma caudatum*** Copel., LUZ9, *M. Sundue 3101* (VT), —, —, *OK092508, *OK092379. ***Saccoloma elegans*** Kaulf., 14948, *Tuomisto 14948* (TUR), HQ157302, —, —, GU478728. ***Saccoloma galeottii*** (Fée) A. Rojas, LUZ7, *M. Sundue 3507* (VT), —, —, *OK092509, *OK092380. ***Saccoloma inaequale*** (Kunze) Mett., 1019, *M.M. Jones 1019* (TUR), NC_044686, —, NC_044686, NC_044686. ***Saccoloma nigrescens*** (Mett.) A. Rojas, LUZ17, *L.A. Triana 1020* (COL), —, —, *OK092512, *OK092382. ***Saccoloma sunduei*** A. Rojas, LUZ6, *M. Sundue 3186* (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* (DUKE), *OK092533, —, *OK092462, *OK092338. ***Sitobolium punctilobulum*** (Michx.) Desv., LUZ127, *C.J. Rothfels 4568* (DUKE), *OK092534, —, *OK092463, *OK092339. ***Sitobolium punctilobulum*** (Michx.) Desv., LUZ128, *C.J. Rothfels 4581* (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* (UC), *OK092538, —, *OK092471, *OK092344. ***Sitobolium zeylanicum*** (Sw.) L.A. Triana & Sundue, LUZ41, *L.Y. Kuo 2352* (TAIF), *OK092536, —, *OK092467, —. ***Sitobolium zeylanicum*** (Sw.) L.A. Triana & Sundue, LUZ43, *L.Y. Kuo 2722* (TAIF), *OK092537, *OK092403, *OK092468, *OK092341. ***Sitobolium zeylanicum*** (Sw.) L.A. Triana & Sundue, LUZ56, *Wade 4659* (TAIF), —, —, *OK092469, *OK092342. ***Sitobolium zeylanicum*** (Sw.) L.A. Triana & Sundue, LUZ64, *T.Y. Nwe 365* (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.

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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; (16) 38.

12. **Aculeae.** (0) Absent; (1) present.

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. **Lamina 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.

MATRIX

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Alsophila_costularis_NC_044080          -1101-0-00?1300100
Blotiella_lindeniana_LUZ20              001001-51-E0200010
Blotiella_pubescens_U05911              001001-51-E0200010
Campyloneurum_angustifolium_MA28464     011010111-?0100000
Coptidipteris_wilfordii_2982            101100-A0060201110
Cyrtomium_falcatum_2397                 011110171-?0100100
Cyrtomium_fortunei                      011110171-?0100100
Cystodium_sorbifolium_LUZ22             001010-400?0200110
Dennstaedtia_ampla_LUZ57                0010000200?0301110
Dennstaedtia_appendiculata_5294         -211000A0150301110
Dennstaedtia_arborescens_LUZ106         0010000101?0201110
Dennstaedtia_auriculata_LUZ104          0010000101?0311110
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Dennstaedtia_macrosora_LUZ93            0010000101?0211110
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Dennstaedtia_mathewsii_LUZ123          0010000101?0211110
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Dennstaedtia_obtusifolia_LUZ99         0010000(1 8)0120211110
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Hypolepis_resistens_BLD01              -010001300B04010?0
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Lindsaea_arcuata_LUZ19                 -11011-(9 B)00?0200100
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Microlepia_rhomboidea_WZS004            ?0??1009??????????
Microlepia_ridleyi_KNBL211              ?0??100??????????
Microlepia_scaberula_INA                ?0??100??????????
Microlepia_speluncae_LUZ70              -01010090000400100
Microlepia_speluncae_LUZ71              -01010090000400100
Microlepia_speluncae_LUZ73              -01010090000400100
Microlepia_speluncae_LUZ74              -01010090000400100
Microlepia_speluncae_LUZ75              -01010090000400100
Microlepia_speluncae_YYH12379           ?0??10090000400100
Microlepia_sp_LUZ52                     -010100?00?0400100
Microlepia_strigosa_LUZ34               -01010090000200100
Microlepia_strigosa_W                   -01010090000200100
Microlepia_subspeluncae_ZXL7016         ?0??100?00???00100
Microlepia_subtrichosticha_XP618        ?0??100?00???00100
Microlepia_szechuanica_W                -010100900???00100
Microlepia_tenera_SG1026                ?0??100900???00100
Microlepia_todayensis_INA               1010100900?1300100
Microlepia_trapeziformis_WYD303         ?0??100?00???00100
Microlepia_trichocarpa_YYH12042         ?010100900?0300100
```

Microlepia_trichosora_WYD445	1010100?00???00100
Microlepia_yaoshanica_YYH12136	?0??100900???00100
Microlepia_yunnanensis_YYH13136	?0??100?00???00100
Monachosorum_henryi	0010100?00?0310000
Monachosorum_subdigitatum_LUZ138	0010100300B0410000
Mucura_bipinnata_LUZ118	1001000(0 1 E)0020400111
Mucura_globulifera_LUZ92	1001000(0 1 E)0020300111
Odontosoria_chinensis_W	-111100B00?0400100
Odontosoria_scandens_W	-111100B00?0100100
Odontosoria_schlechtendalii_5012	-111100B00?0500100
Oenotrichia_maxima_WELT_P026233	111-101E00?0300100
Orthiopteris_campylura_LUZ5	0111100400?0300100
Orthiopteris_kingii_LUZ42	0111100400?0300100
Paesia_acclivis_LUZ133	-011011C00?0201110
Paesia_glandulosa_LUZ134	-011011C00D0401110
Paesia_glandulosa_LUZ135	-011011C00D0401110
Paesia_glandulosa_LUZ81	-011011C00D0401110
Paesia_scaberula_387	1011011C00D0401110
Pityrogramma_trifoliata_3658	01101-0B00?0100000
Pteridium_caudatum_LUZ11	1010010900D0401110
Pteridium_esculentum_gryphus_LUZ136	1010010900D0401110
Pteridium_esculentum_gryphus_LUZ137	1010010900D0401110
Pteridium_revolutum_LUZ66	1010010900D0301110
Pteris_vittata_4016	011001-(8 A)00?0200000
Saccoloma_brasiliense_LUZ21	0111100400?0300100
Saccoloma_caudatum_LUZ9	0111100400????0100
Saccoloma_elegans_14948	0111100400?0100100
Saccoloma_galeottii_LUZ7	0111100400?0200100
Saccoloma_inaequale_1019	0111100400?0400100
Saccoloma_nigrescens_LUZ17	0111100400?0300100
Saccoloma_sunduei_LUZ6	0111100400?0310100
Sitobolium_punctilobula_LUZ126	1010000(0 1)0110401110
Sitobolium _punctilobula_LUZ127	1010000(0 1)0110401110
Sitobolium _punctilobula_LUZ128	1010000(0 1)0110401110
Vittaria_graminifolia_EP423	011011-D00?0100000

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* (COL). ***Dennstaedtia werckleana***, Costa Rica, *Testo & al. 1237* (VT). ***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). ***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).

Chapter 2. (2892) Proposal to conserve the name *Dennstaedtia* (Dennstaedtiaceae) with a conserved type

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(0000) ***Dennstaedtia*** Bernh., Schrad., J. Bot. 1800(2): 124. Oct-Dec 1801, nom. cons. prop.

Typus: *D. dissecta* (Sw.) T. Moore. (*Dicksonia dissecta* Sw.) typ. cons. prop.

Dennstaedtia Bernh. and *Microlepia* C.Presl are two sub-cosmopolitan genera belonging to the bracken fern family, Dennstaedtiaceae. They are the second and third richest genera in the family, with respective estimates of 70 and 60 species (Yan & al. in Wu & al., Fl. China 2–3: 147–168. 2013; PPG I, in J. Syst. Evol. 54: 563–603. 2016). The circumscription of these genera has remained stable since the half of the 19th century (Moore, Ind. Filic. xcvii. 1859; Christensen, Filicinae, in Verdoorn, Manual of Pteridology: 522-550. 1938; Holttum, Biol. Rev. 24: 267–269. 1949; Copeland, Genera Filicum, 1947; Alston, Taxon: 5: 23–25.1956; Nayar in Taxon 19: 229–236. 1970; Tryon & Tryon, Ferns Allied Pl. 1982; Kramer, Dennstaedtiaceae, in Kramer & al., Fam. Gen. Vasc. Pl.: 81-94, 1990), and they have been largely accounted for in floras worldwide (Mickel & Smith, Pterid. Mexico, 2004; Roux, in Strelitzia 23: 111–112. 2009; Yan & al. *l.c.*, Schwartsburd in Forzza & al., Cat. Pl. Fungi Bras. 1: 530. 2010; Murillo-P. & al., *Dennstaedtia*, in Bernal & al., Cat. Pl. Liq. Colombia: 469–470, 2016; Cámara-Leret & al. in Nature 584: 579–583, suppl. 1 .2020.). They are morphologically close, and their delimitation and differentiation have traditionally relied on the sorus shape and position: *Dennstaedtia* has marginal sori protected by the inner and outer indusia fused into a specialized purse- or cup-shaped structure; whereas *Microlepia* has abaxial sori protected only by the modified inner indusium (Tryon & Tryon *l.c.* 1982; Kramer *l.c.*).

When Tryon & Tryon (in Taxon 29: 512–513. 1980) added spore morphology to differentiate these two genera, they realized that the type of *Dennstaedtia* (*D. flaccida*) had

delicately tuberculate spores, similar to *Microlepia* spp., whereas the remaining *Dennstaedtia* had verrucate-tuberculate, reticulate, or ridged spores. Tryon & Tryon (*l.c.* 1980) further proposed the spore ornamentation to be taxonomically more reliable than sorus shape and position, and they predicted a huge nomenclatural change among these two genera, with: (1) the synonymization of *Microlepia* under *Dennstaedtia;* (2) all *Microlepia* species combined into *Dennstaedtia;* and (3) most *Dennstaedtia* species combined into *Sitobolium* Desv., except for *D. flaccida*. Tryon & Tryon (*l.c.* 1980) estimated about 90 new combinations – at that time, the estimates of *Dennstaedtia* and *Microlepia* were about 45 species, each. In order to maintain nomenclatural stability, Tryon & Tryon (*l.c.* 1980) presented an unusual conservation proposal, in which they tried to alter the type of *Dennstaedtia,* its original place of publication, and its authorship: from *Dennstaedtia* Bernh. (in Schrader *l.c.*; type: *D. flaccida*), to *Dennstaedtia* T. Moore (*l.c.*; type: *D. cicutaria* (Sw.) T.Moore). Since, in their view, the "modern" circumscription of *Dennstaedtia* was initiated by Moore (*l.c.*). In accepting this proposal, both *Dennstaedtia* and *Microlepia* would retain their circumscriptions in use (*i.e,* from the 1850s to 1980s) and 90 name changes would be avoided.

Tryon & Tryon's (*l.c.* 1980) proposal was rejected by the Nomenclatural Committee for Pteridophyta (Voss, in Taxon 31: 314–315. 1982): Holttum argued their prediction was taxonomically premature, and Pichi-Sermolli argued Moore (*l.c.*) never intended to describe a new genus *Dennstaedtia* – he was adopting Bernhardi's genus and expanding upon it. Even with the rejection of the Committee, Tryon & Tryon (*l.c.* 1982), in their comprehensive monograph of Neotropical pteridophytes, pursued this idea, and cited *Dennstaedtia* as authored by Moore and with *D. cicutaria* as type.

With the advent of molecular phylogenetics, Perrie & al. (in Austral. Syst. Bot. 28: 256−264. 2015), Schneider & al. (in Perspect. Pl. Ecol. Evol. Syst. 18:70–78. 2016), Shang & al. (in Molec. Phylogen. Evol. 127: 449−458. 2018), Schwartsburd & al. (in Mol. Phylogen. Evol.: 106881. 2020), and Wang & al. (in Taxonomy 1: 256–265. 2021) demonstrated the paraphyly (or polyphyly) of *Dennstaedtia*, with *Microlepia* and small segregates (*Leptolepia* Prantl, *Oenotrichia* Copel.) nested within. These papers also proposed that sorus position in Dennstaedtiaceae is a homoplastic character, evolving from marginal to abaxial (sub-marginal for the authors) at least five times in the family, and reversing again to marginal at least two times (Schwartsburd & al., *l.c.:* Fig. 5, c; Wang & al. *l.c.*).

Some taxonomic solutions have been suggested (e.g., Schneider & al. *l.c.*, Schwartsburd & al. *l.c.*), but these precluded the addition of *D. flaccida* which has only recently been placed into a phylogenetic analysis (Triana-Moreno & al *in prep.* – the same authors of this proposal, submitted to *Taxon*). We now confirm the placement by Tryon & Tryon (*l.c.* 1980) that *D. flaccida*, the type of *Dennstaedtia*, is nested within *Microlepia* spp. (37 species in our sampling, but probably representing *ca*. 60 spp.). Three other clades are formed: one with five north-temperate species currently classified in *Dennstaedtia* (with alternative names in *Sitobolium* and *Coptidipteris* Nakai & Momose); another clade with only two Neotropical species, currently classified in *Dennstaedtia* (with no genus name available in synonymy); and another, a more distant clade, representing the main core of "*Dennstaedtia*", with 26 pantropical species in our sampling (but probably representing *ca*. 50–60 spp.), currently classified in *Dennstaedtia* (and *Leptolepia* and *Oenotrichia*, with one species each), with alternative names in *Patania*.

In order to reach a natural, monophyletic classification, nomenclatural changes will be necessary. One solution is to merge these four clades into *Dennstaedtia s.l.*, synonymizing

all those generic names, including *Microlepia*. In doing so, the *ca*. 60 species of *Microlepia* will need to be combined into *Dennstaedtia,* and the circumscription of *Dennstaedtia* will be expanded to comprise a large and morphologically diverse clade.

A second solution is to merge the three first mentioned clades in *Dennstaedtia s. medio* and classify the other one as *Patania* (which has been the main core of *Dennstaedtia sensu* 1850s until 2020s). This solution will also require that the *ca*. 60 species of *Microlepia* be combined into *Dennstaedtia,* and the circumscription of *Dennstaedtia* altered significantly, to a broader and unfamiliar concept. The north-temperate clade and those two Neotropical species would remain in *Dennstaedtia.* There seems to be little value in this solution; concepts are changed but the resulting genera are not necessarily more useful.

The third solution is to consider each of the four clades as four distinct genera. This solution is the best in our judgment, since the resulting genera are morphologically distinct and geographically coherent (Triana-Moreno, *l.c.*). In doing so, following priority of names and type placement in the phylogeny, *Dennstaedtia* as we know it would drastically change its circumscription, keeping the type and those *ca*. 60 species of *Microlepia; ca*. 5–10 north-temperate species will become (or return to) *Sitobolium*; a new genus will be described to accommodate two Neotropical species; and the *ca*. 50–60 pantropical species of *"Dennstaedtia"* will become (or return to) *Patania.* "*Microlepia*" and *"Dennstaedtia*" in the traditional sense (1850s to 2020s) will drastically change their circumscription, and at least 100 combinations are needed. Therefore, in order to reduce the number of new combinations associated with this option, we propose the conservation of *Dennstaedtia* with *D. dissecta* (Sw.) T. Moore (Index Fil.: 305. 1861) (≡ *Discksonia dissecta* Sw. in J. Bot (Schrader) 1800(2): 91. 1801) – a core member of the clade as currently cincunscribed – as conserved type. In doing so, the circumscription of both *Dennstaedtia* and *Microlepia* will be largely

maintained (the latter altered by the inclusion *D. flaccida* and *D. smithii* (Hook.) T. Moore): the other 70 species of *Dennstaedtia* and the 60 species of *Microlepia* will retain their name.

As a complementary information to support this proposal, we should mention that *Microlepia* is already in the process of becoming a conserved name. Schwartsburd (in Taxon 66: 216. 2017) uncovered that *Scyphofilix* Thouars (Gen. Nov. Madagasc.: 1. 1806), has priority proposed the conservation of *Microlepia* against *Scyphofilix* in order to prevent 60 name changes. This conservation was approved by the Nomenclature Committee for Vascular Plants (Applequist, in Taxon 68: 850. 2019). Thus, retention of *Microlepia* (1836) against the much older name *Scyphofilix* (1806) is already authorized (Art, 14, 15 of the *ICN*; Turland & al., Regnum Veg. 159. 2018).

In summary, acceptance of this modern equivalent of Tryon & Tryon's (l.c. 1980) unsuccessful conservation proposal, will ensure continued application of *Dennstaedtia* and *Microlepia* to the vast majority of species traditionaly assigned to these genera.

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Capítulo 3. Revisión taxonómica del género *Mucura* (Dennstaedtiaceae)

Resumen

Se presenta un tratamiento taxonómico para el género neotropical *Mucura* (Dennstaedtiaceae) basado en la revisión de especímenes de herbario y colecciones virtuales. El género está compuesto por dos especies distribuidas ampliamente en el Neotrópico. Este estudio provee herramientas para la identificación taxonómica, tales como una clave para los géneros de la familia y una clave para las especies del género. Adicionalmente, se presentan descripciones del género y de las especies, e información sobre su distribución geográfica y altitudinal en toda su área de distribución.

Palabras clave. Dennstaedtioideae, Helechos, Neotrópico, Pteridophyta.

Abstract

A taxonomic treatment for the neotropical genus *Mucura* (Dennstaedtiaceae) based on the review of herbarium specimens and virtual collections is presented. The genus comprises two species widely distributed in the Neotropics. This study provides tools for taxonomic

identification, such as a key to the genera of the family and a key to the species of the genus. Additionally, descriptions of the genus and species are presented, as well as information on their geographical and altitudinal distribution throughout their range.

Key words. Dennstaedtioideae, Ferns, Neotropics, Pteridophyte.

Mucura L.A. Triana & Sundue es un género de helechos perteneciente a la subfamilia Dennstaedtioideae de la familia Dennstaedtiaceae (Triana-Moreno & al., *en imprenta*). El gènero está constituido por dos especies, *M. globulifera* (Poir.) L.A. Triana & Sundue y *M. bipinnata* (Cav.) L.A. Triana & Sundue, de amplia distribución geogràfica en el Neotrópico. Son plantas terrestres con frondas 3-4-pinnado-pinnatífidas. Se reconocen fácilmente de otros helechos con hábito y fronda semejante porque sus pecíolos carecen de yemas, los canales adaxiales de los ejes de la lámina son decurrentes sobre el eje de siguiente orden, y están bordeados por un ala herbácea. El aspecto de sus soros también es muy característico, pues son marginales y presentan un involucro globoso o cilíndrico formado por la fusión de los indusios adaxial y abaxial. Sus esporas también presentan una morfología distintiva, pues son triletes, verrugadas, con crestas anchas y retículos irregulares en la cara distal.

Las especies de *Mucura* se encontraban circunscritas en *Dennstaedtia* Lotsy. género del que se conocen varios tratamientos taxonómicos en el Neotrópico, incluídos los de las especies presentes en Perú (Tryon & Stolze 1989), Mesoamérica (Moran 1995), Venezuela (Smith & Kramer 1995), Ecuador (Navarrete & Øllgaard 2000), México (Rojas & Tejero-Díez 2002, Mickel & Smith 2004), Brasil (Assis & Salino 2011) y Argentina (Yáñez & al. 2014). En Colombia se registran las dos especies (Rodríguez-Rey & al. 2006).

Los caracteres diagnósticos de *Mucura* han sido reconocidos consistentemente a partir de los estudios morfológicos realizados a sus especies mientras se encontraban circunscritas en *Dennstaedtia*. Navarrete & Øllgaard (2000) clasificaron las especies ecuatorianas de *Dennstaedtia* en cinco grupos, uno de ellos conformado por las dos especies hoy pertenecientes a *Mucura*. El grupo fue definido por caracteres no compartidos con otras especies de *Dennstaedtia*, como los rizomas ramificados y la ausencia de yemas peciolares, y otros caracteres no exclusivos, como la continuidad de los canales adaxiales del raquis (*vs*. discontinuos en otras especies), las raíces fibrosas (*vs*. gruesas, o delgadas y rígidas), y el ápice de las venas no engrosado (*vs*. ápice claviforme). Estos caracteres fueron incluidos en un análisis filogenético basado en datos morfológicos que fue el primero en inferir la monofilia de las especies de *Dennstaedtia* que fueron transferidas posteriormente a *Mucura* (Triana-Moreno 2018. Véase también el estudio filogenético en esta tesis).

Mucura globulifera fue objeto de un estudio palinológico minucioso en el que Yáñez & al. (2016a) describieron los caracteres micromorfológicos y ultraestructurales específicos de sus esporas, y concluyeron que éstos tienen valor sistemático y son una fuente de información útil para la identificación taxonómica. Con la incorporación de *M. bipinnata* en el análisis de la evolución de los caracteres micromorfológicos del perisporio, Triana-Moreno & al. (*en imprenta*) corroboraron que la ornamentación de las esporas de *Mucura* es constante dentro del género y única dentro de la familia.

En un análisis filogenético basado en caracteres moleculares del cloroplasto, que incorporó especies de todos los géneros de la familia, pero que estuvo particularmente enfocado en las especies neotropicales de *Dennstaedtia*, se recuperó de manera consistente la monofilia de

Mucura como género hermano del clado conformado por los géneros *Sitobolium* y *Microlepia*. Este sustento filogenético fundamentó la propuesta de *Mucura* como novedad taxonómica (Triana-Moreno & al., *en imprenta*).

Materiales y métodos

El sistema de clasificación de referencia para este tratamiento es PPG-I (2016), complementado con la clasificación intrafamiliar propuesta por Becari-Viana & Schwartsburd (2017). Se estudiaron directamente los especímenes de los herbarios BA, COL y VT, y las colecciones virtuales de los herbarios AAU, MO y NY (acrónimos de herbarios según Thiers 2022); los ejemplares tipo fueron examinados en las colecciones virtuales donde están disponibles.

Se elaboró una clave taxonómica para la familia Dennstaedtiaceae y otra para las especies de *Mucura*. Las descripciones emplean los términos técnicos propuestos por Lellinger (2002). La descripción de cada especie está acompañada por una lámina que detalla los caracteres morfológicos del esporofito, y la micromorfología de las esporas fotografiadas al Microscopio Electrónico de Barrido (MEB). Las esporas se trataron con carbonato de sodio al 3% caliente, se lavaron, se deshidrataron, se suspendieron en etanol al 96% y se transfirieron a placas de acetato (Morbelli 1980). Después del secado, se recubrieron con oro. Las observaciones fueron realizadas con un microscopio electrónico Jeol JSM-6360LV del servicio de microscopía de la Facultad de Ciencias Naturales y Museo de La Plata (Argentina).

Aunque en el tratamiento taxonómico sólo se cita un espécimen de referencia para cada país, tanto los mapas como las distribuciones geográficas y altitudinales que se describen en el texto están basados en la georreferencia de los especímenes presentados en el Anexo 1, que incluye todos los ejemplares examinados directamente y los vistos en los herbarios virtuales antes mencionados.

Tratamiento taxonómico

Para identificar los géneros de la familia Dennstaedtiaceae se presenta la siguiente clave dicotómica elaborada a partir de observaciones propias o datos disponibles en la literatura (Kremp & Kawasaki 1972, Tryon & Tryon 1982, Tryon & Lugardon 1991, Moran 1995, Navarrete, H., Øllgaard 2000, Becari-Viana & Schwartsburd 2017, Perrie & al. 2015, Yáñez & al. 2016a, 2016b, Brownsey & Perrie 2018, Triana-Moreno & al. *en imprenta*).

Clave para los géneros de la familia Dennstaedtiaceae

1. Suministro vascular del soro por una sola vena 2

1. Suministro vascular del soro por dos o más venas 8

2. Rizoma cortamente reptante, dictiostélico; pecíolo con dos haces vasculares; soros sin indusio ..... *Monachosorum*

2. Rizoma largamente reptante, solenostélico; pecíolo con un haz vasculares; soros con o sin indusio 3

3. Indusio abaxial presente, fusionado basalmente a la lámina, o fusionado al indusio adaxial formando un involucro bivalvado, globoso o cilíndrico 4

3. Indusio abaxial ausente, el adaxial formado por la margen revoluta de la lámina, escuamiforme 7

4. Base del pecíolo subterete, sin yemas epipeciolares. Indusios cilíndricos o globosos ..... ***Mucura***

4. Base del pecíolo acanalado por el lado adaxial, yemas epipeciolares presentes o ausentes. Indusios bivalvados o escuamiformes 5

5. Soros marginales con indusio bivalvado 6

5. Soros submarginales con indusio escuamiforme fusionado basalmente a la lámina ..... ***Microlepia***

6. Yemas epipeciolares presentes ..... ***Dennstaedtia***

6. Yemas epipeciolares ausentes ..... ***Sitobolium***

7. Aguijones de los ejes de la lámina, cuando presentes, verdes o estramíneos; cayados no protegidos por pínnulas basales reducidas ..... ***Hypolepis***

7. Aguijones de los ejes de la lámina negros, al menos apicalmente; cayados protegidos por pínnulas basales reducidas ..... ***Hiya***

8. Venas anastomosadas; pinnas opuestas o subopuestas 7

8. Venas libres; pinnas generalmente alternas 10

9. Láminas glabras o algo escamosas, generalmente glaucas; rizomas escamosos; cayados protegidos por pínnulas basales reducidas ..... ***Histiopteris***

9. Lámina pubescente, verde, no glauca; rizomas pubescentes; cayados no protegidos por pínnulas basales reducidas ..... ***Blotiella***

10. Raquis flexuosos; esporas monoletes ..... ***Paesia***

10. Raquis rectos; esporas triletes ..... ***Pteridium***

Mucura L.A. Triana & Sundue, Taxon *en imprenta*.

TIPO: *Mucura bipinnata* (Cav.) L.A. Triana & Sundue. (≡*Dicksonia bipinnata* Cav.)

Descripción. RIZOMA ramificado dicotómicamente, densamente pubescente con pelos castaño-dorados. PECÍOLO subterete en la base, inserto subdorsalmente en el rizoma, sin raíces ni yemas peciolares; cubierto con pelos similares a los del rizoma, al menos en la base; acanalado adaxialmente. LÁMINA deltada a ovado lanceolada, 3-4-pinnado-pinnatifida, con canales continuos entre ejes de diferentes órdenes. PINNAS deltado-lanceoladas; PÍNNULAS con margen dentada; ejes de los penúltimos segmentos con alas herbáceas perpendiculares que bordean los canales de los ejes decurrentes sobre el eje de siguiente orden; venas estériles con el ápice tan ancho como la vena. SOROS naciendo en los senos; indusio cilíndrico o globoso. ESPORAS triletes, verrugosas y crestadas.

Distribución. Desde el sur de Estados Unidos hasta Uruguay y el norte de Argentina. 0-3500 m.

Etimología. Este nombre es un sustantivo femenino en español [mú·ku·ɾa] derivado de las familias lingüísticas caribe y chibcha (Flórez 1955), que hace referencia a un cántaro de arcilla cocida, propia de los pueblos aborígenes en el área de distribución del género. Se caracteriza por tener una base globosa, como el indusio de *M. globulifera*, y un cuello estrecho y largo, que recuerda al indusio cilíndrico de *M. bipinnata* (Triana-Moreno & al. *en imprenta*).

Clave para las especies de *Mucura*

1. Lámina lustrosa en ambas caras; segmentos basales de tercer orden alternos, el proximal acroscópico más largo que el basiscópico; ápices de los últimos segmentos en su mayoría agudos y profundamente dentados; canales adaxiales de los ejes de la lámina glabrescentes o con pelos como los de la lámina. Soros cilíndricos ..... ***M. bipinnata***

1. Lámina opaca en ambas caras; segmentos basales de tercer orden subopuestos, aproximadamente igual de largos entre sí; ápices de los últimos segmentos en su mayoría con dientes obtusos y poco profundos; canales adaxiales de los ejes de la lámina pubescentes con pelos adpresos diferentes a los de la lámina. Soros globosos ..... ***M. globulifera***

Mucura bipinnata (Cav.) L.A. Triana & Sundue, Taxon *en imprenta*. Figs. 4, 5.

≡ *Dicksonia bipinnata* Cav., Descr. Pl. 174. 1802. *Dennstaedtia bipinnata* (Cav.) Maxon, Proc. Biol. Soc. Washington 51(8): 39. 1938. TIPO: ¿Puerto Rico? *Ventenat s.n*. (Holotipo: MA!; Isotipos: B-W-20165 (foto, GH; fragm., US)).

Descripción. RIZOMA largamente rastrero, 0.5-1 cm de ancho, con entrenudos de 5-9 cm de largo, cubierto con pelos catenados de 0.5-3 mm de largo; con raíces laterales. FRONDA 2-3×1-1.6 m. PECIOLO 0.8-1.5 cm de ancho, proximalmente pubescente, distalmente glabrescente; ligeramente lustroso, castaño oscuro, tornándose estramíneo en la región distal. LÁMINA deltada a ovado lanceolada, 3-4-pinnado-pinnatífida, tan larga como el pecíolo, arqueada, anádroma, glabrescente, lustrosa por ambos lados. PINNAS alternas, deltado-lanceoladas, las basales hasta 80×25 cm, largamente pediculadas, el pedículo 2-5 cm. PÍNNULAS fuertemente dentadas, segmentos basales de tercer orden alternos, el proximal acroscópico más largo que el basiscópico; últimos segmentos agudos; canales adaxiales de

los ejes glabrescentes o con pelos septados, castaño claro; costas y cóstulas pelosas abaxialmente, los tricomas generalmente más densos cerca de las uniones. SOROS 0.6 a 0.8 mm de diámetro, indusio cilíndrico, glabro.

Especímenes de referencia. Estados Unidos: Florida, Seminole Co, Stand covering about 1/2 acre in Black Hammock near Oviedo, 29 may 1983, *Popenoe, J. 2312* (NY). **México:** Veracruz, Zontecomatlán, Along Huayacocotla-Zontecomatlán road 1 km. NE of San Antonio Ixtatetla, 1300 m, 20°42'N, 98°22'W, 27 abr 1983, *Nee, M.H. 26801* (NY). **Guatemala:** Sololá, Santiago Atitlán, 1600 m, 14°36'N, 91°15'W, 01 sep 1999, *Morales Can, J. 454* (MO). **Belice:** Cayo, 740 m, 16°32'N, 89°05'W, 08 mar 2000, *Monro, A.K. 3197* (BM, BRH, MEXU, MO, PMA). **Honduras:** El Paraíso, El Paraíso, Mata de Plátano. 5 km E de El Paraíso, 600 m, 13°54'N, 86°33'W, 10 ene 1982, *Soto, J.V. 136* (MO). **El Salvador:** 13°42'N, 89°00'W, *Standley, P.C. 19760* (GH). **Nicaragua:** Matagalpa, 1400 - 1500 m, 12°59'N, 85°52'W, 1-31 oct 1975, *Gómez P, L.D. 6311* (CR). **Costa Rica:** Guanacaste, Rincón de la Vieja National Park slopes of Volcán Santa Maria, 700-900 m, 10°46'N, 85°18'W, 26 ene 1986, *Smith, A.R. 1969* (NY). **Panamá:** Chiriquí, Burica Península. Rabo de Puerco 8 km west of Puerto Armuelles, 50 - 150 m, 08°16'N, 82°54'W, 18 feb 1973, *Croat, T.B. 21976* (MO). **Cuba:** 600-660 m, 20°09'N, 75°30'W, 6-10 feb 1911, *Shafer, J.A. 8499* (MO). **Jamaica:** Saint Ann, Fern Gully St. Ann, 200-300 m, 18°22'42"N, 77°05'38"W, 23 jul 1926, *Maxon, W.R. 10385* (NY). **Haiti:** L'Artibonite, Vicinity of Kalacroix Section Dessalines. Departement de l'Artibonite, 700 m, 11 dic 1925, *Leonard, E.C. 7919* (NY). **República Dominicana:** La Vega, 1100 - 1200 m, 19°03'N, 70°51'W, 13 jul 1967, *Gastony, G.J. 144* (MO). **Puerto Rico:** Arecibo, Río Arriba, Río Abajo Forest Reserve at sinkhole midway along pilot road for proposed Rt 10, 225-225 m, 18°20'51"N, 66°40'59"W, 19 ago

1994, *Axelrod, F.S. 8260* (NY). **Guadalupe:** Rivière Noire (au dessus de Saut de Constantin), 280-700 m, 16°01'56.6"N, 61°40'59.3"W, 1894, *Duss, A. 4181* (NY). **Colombia:** Meta, PNN Tinigua, 1200 m, 2°40'N, 74°10'W, 26 nov 1990, *Churchill, S.P. 16893* (COL, MO, NY). **Venezuela:** Yaracuy, Bolívar, Caserío de Quebrada Seca, 133 m, 10° 33' 0"S, 68° 51' 56"W, 02 jul 1953, *Aristeguieta & Pannier 1822* (COL). **Trinidad & Tobago:** Trinidad. Mount Tucuche trail from base to the peak, 152-936 m, 10°44'47.8"N, 61°24'16.6"W, 12 jul 1984, *Mickel, J.T. 9567* (NY). **Ecuador:** Morona-Santiago, Mutinza, foothills of Cord. Cutucú just E of village, 660-800 m, 02°11'S, 077°44'W, 19 nov 1995, *Øllgaard, B. 1520* (AAU). **Perú:** Madre de Dios, Tambopata, ca. 30 air km or 70-80 river km SSW Puerto Maldonado at effluence Rio La Torre (Rio D'Orbigny)/ Rio Tambopata (SE bank) Tambopata Nature Reserve, 260 m, 12°49'12"S, 69°16'48"W, 19 may 1980, *Barbour, P.J. 5345* (NY). **Brasil:** Acre, Manoel Urbano, Rio Chandless (tributary of Rio Purus) left bank Colocaçao Iracema, 9°21'36"S, 69°56'15"W, 18 mar 2002, *Daly, D.C. 11418* (NY). **Bolivia:** Santa Cruz, Florida, 4 km (by air) NE of Bermejo in or near bottom of valley of "Refugio Los Volcánes", 1120 m, 18°06'S, 63°36'W, 28 jul 2003, *Sundue, M.A. 751* (NY).

Distribución. Desde el sur de Estados Unidos, Mesoamérica e islas del Caribe hasta el sur de Brasil. 0-3500 m.

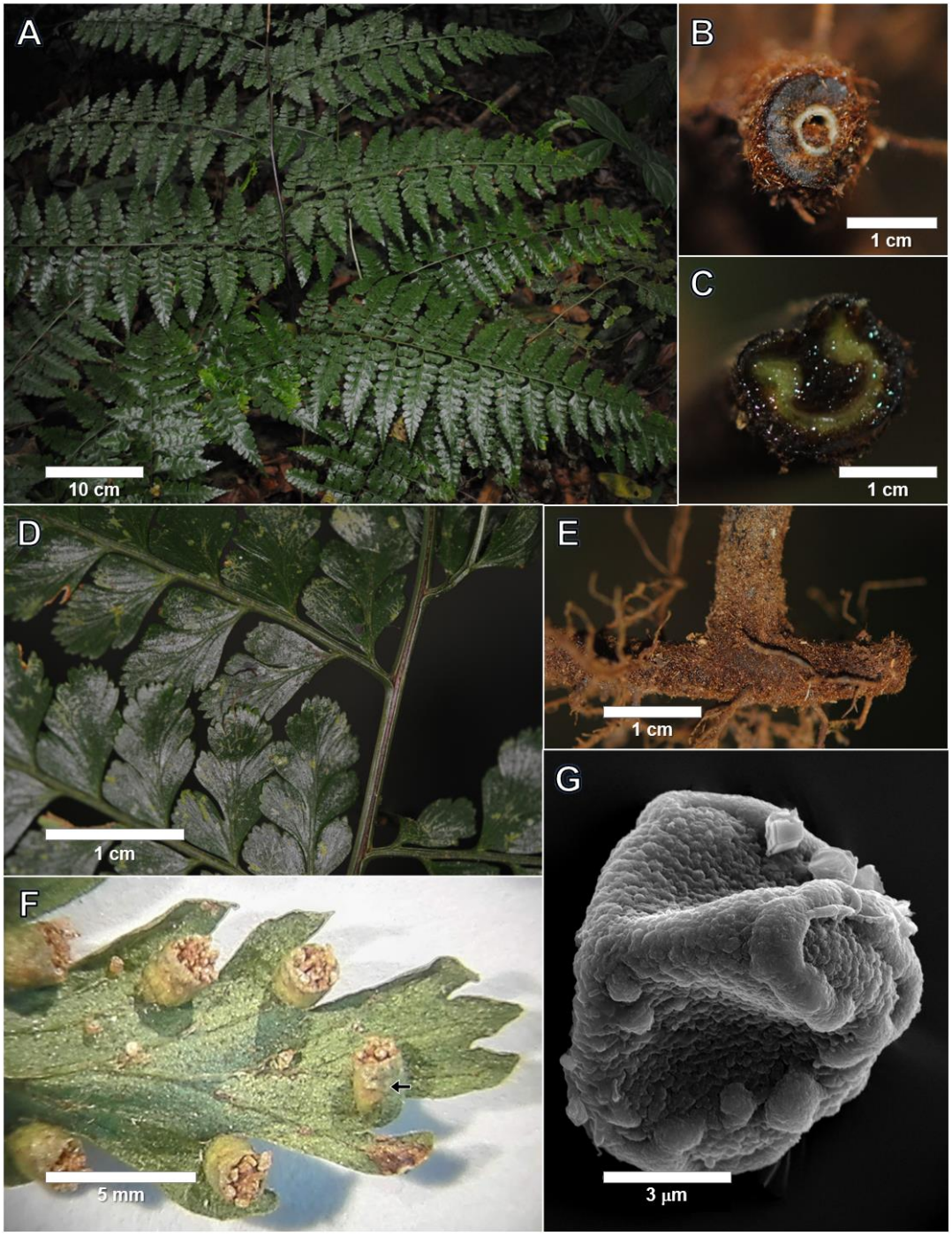

Figura 4. *Mucura bipinnata*. **A.** Vista general de una fronda, superficie adaxial. **B.** Corte transversal del rizoma cubierto con pelos. **C.** Corte transversal del pecíolo con haz vascular en forma de Ω invertida. **D.** Detalle de la lámina lustrosa con los segmentos basales de tercer orden alternos. **E.** Ausencia de yemas epipeciolares. **F.** Soros marginales con indusio cilíndrico (flecha). **G.** Vista ecuatorial de una espora trilete; nótese la ornamentación verrugosa con retículos que forman crestas engrosadas. (**A-E.** *Testo 743* (CR, VT) en http://www.fernsoftheworld.com/2015/04/17/dennstaedtia-bipinnata/. **F.** *Fawcett 470* (VT). **G.** *Krukoff 10331* (LP).

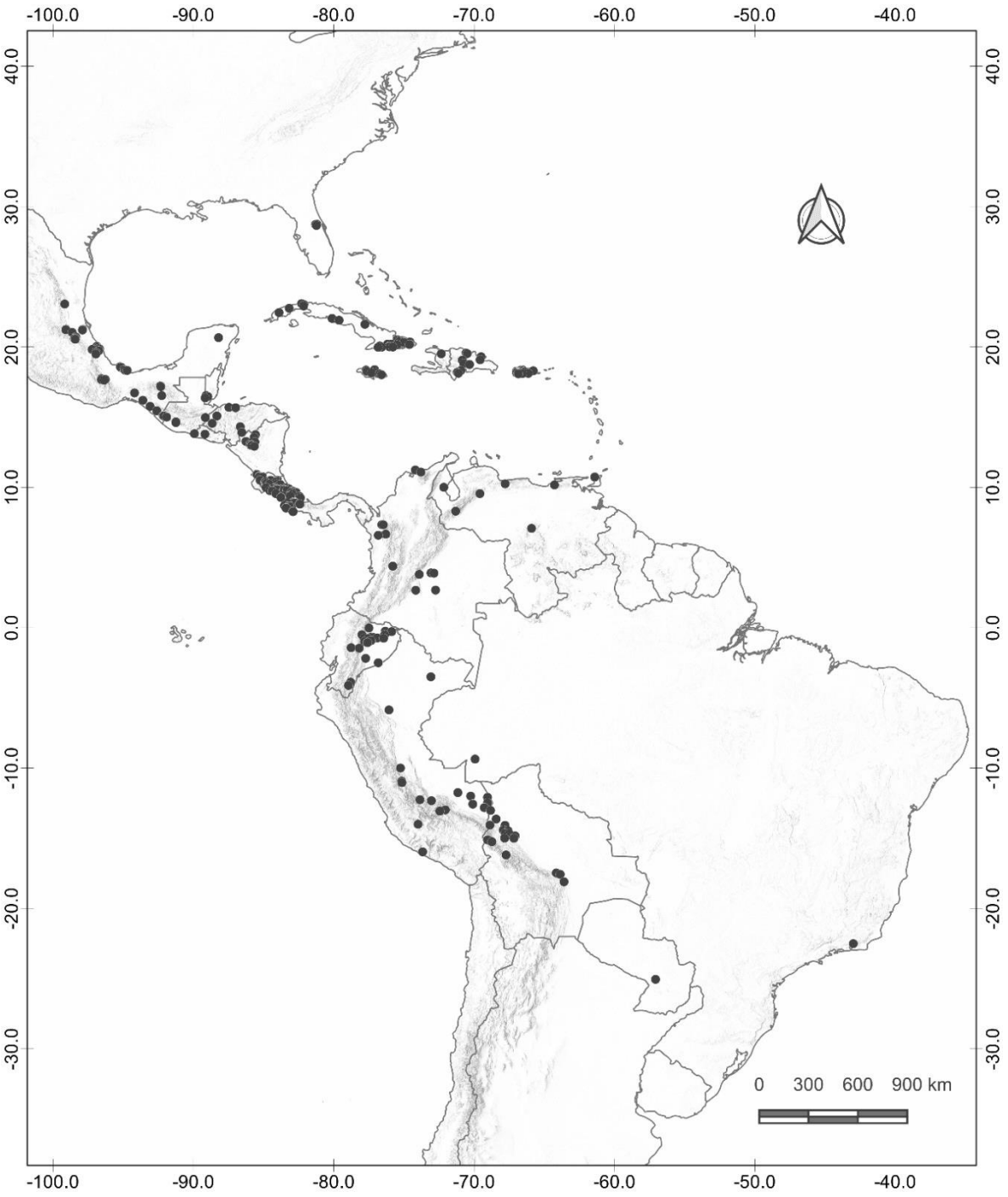

Figura 5. Distribución geográfica de *Mucura bipinnata*.

Mucura globulifera (Poir.) L.A. Triana & Sundue, Taxon *en imprenta*. Figs. 6, 7.

≡ *Polypodium globuliferum* Poir. Encyclopédie Méthodique, Botanique 5: 554. 1804. *Dicksonia globulifera* (Poir.) Kuntze, Revis. Gen. Pl. 3(3): 378. 1898. *Dennstaedtia globulifera* (Poir.) Hieron., Botanische Jahrbücher für Systematik 34: 455. 1904. TIPO: Hispaniola (Holotipo: *Plumier* Tract. Fil. Amer.: 24, tab. 30. 1705).

= *Dicksonia tenera* C. Presl, Delic. Prag. 1: 189. 1822. *Dennstaedtia tenera* (C. Presl) Mett., Ann. Sci. Nat., Bot., sér. 5, 2: 261. 1864. TIPO. Brasil, *J.B.E. Pohl 4536* (lectotipo, BR 0000006870546!, designado por Yáñez & Arana en Flora Argentina 2: 18. 2016).

= *Dicksonia lagerheimii* Sodiro, Anales Univ. Centr. Ecuador 7: 106. 1892. *Dennstaedtia lagerheimii* (Sodiro) C. Chr., Index Filic. 217. 1905. TIPO. Ecuador. Pichincha, crece en los bosques del volcán «el Corazón», entre 2000-2800 m, Dic 1893, *L. Sodiro s.n.* (NY 149030!, P 00633289, S-R-1482, US 00066390).

= *Dennstaedtia tenera* (C. Presl) Mett. var. *dentata* Hieron., Bot. Jahrb. Syst. 22(3): 362. 1897. TIPO. Argentina. «Tucumán: in feuchten schattigen Schluchten bei Siambon in der Sierra von Tucuman» 27 Ene 1874, *P.G. Lorentz & G. Hieronymus s.n. 794* (lectotipo, CORD 00056011, designado por Yáñez & Arana en Flora Argentina 2: 18. 2016; isolectotipo, CORD 00056012).

= *Dennstaedtia tamandarei* Rosenst., Hedwigia 56: 359. 1915. TIPO. Brasil. São Paulo. Hector Legrú, in silvis umbrosis, Ene 1913, Firmiano Tamandaré, *A.C. Brade 5421* (holotipo, S-R-1447; isotipo, UC 442210).

= *Dennstaedtia bradeorum* Rosenst., Repert. Spec. Nov. Regni Veg. 22(606-608): 3. 1925. TIPO. Costa Rica. Candelaria, 1600 m, 3 Nov 1910, *A. Brade & C. Brade 634* (GH 00020956, NY 00149035!, S-R-1444, UC 405622, US).

= *Dennstaedtia gracilis* A. Rojas & Tejero, Revista Biol. Trop. 50(3-4): 1008. 2003. TIPO. México. Hidalgo. Municipio de Molango, km 118 de la Carretera Federal 105, entre

Zacualtipán y Molango, 20º28’21"N, 98º40’32"W, 1400 m, 15 Mayo 2000, *A. Rojas & D. Tejero-Díez 5376* (holotipo, MEXU 00359514; isotipos, CR, F, NY 01043117!, UAMIZ 0056107, UAMIZ 0056108, UC, US 01105778).

Descripción. RIZOMAS subterráneos o reptantes, 30-50 cm de largo, 0.8-3 cm de ancho, entrenudos 1-4 cm de largo, las ramificaciones frecuentemente algo desiguales en longitud; cubiertos con pelos pluricelulares de hasta 15 mm de largo, ondulados; raíces ventrales. PECÍOLOS erectos o ascendentes; hasta 2.5 cm de ancho en la base; pubescentes con pelos similares a los del rizoma; canal adaxial poco profundo, densamente pubescente con pelos adpresos, pluricelulares, agudos, castaño oscuro, hasta 3 mm de largo. LÁMINA ascendente o escandente, ovado lanceolada, opaca en ambos lados, más corta que el peciolo, 3-pinnado-pinnatifida, menos disectadas en frondas jóvenes, con canales continuos entre ejes de diferentes órdenes; raquis pubescente. PINNAS subdeltoide-lanceoladas, algo traslapadas, pínulas basales opuestas, no o ligeramente reducidas, ocasionalmente decurrentes sobre el raquis; PÍNNULAS subdeltoide-lanceoladas, últimos segmentos glabros, ápices de los últimos segmentos en su mayoría con dientes obtusos y poco profundos; segmentos basales de tercer orden subopuestos, aproximadamente igual de largos entre sí; canales adaxiales de los ejes de la lámina pubescentes con pelos adpresos diferentes a los de la lámina; venas hundidas axialmente, prominentes abaxialmente, pubescentes con pelos catenados. SOROS hasta 2 mm; indusio globoso, esparcidamente pubescente o glabrescente.

Especímenes de referencia. Estados Unidos: Texas, Val Verde Co., Fern Cave on Martin J. Rose Jr. Ranch 18 miles north of Comstock, 29°56'44.5"N, 101°10'22.8"W, 1 oct 1962, *Correll, D.S. 26140* (NY). **México:** Chiapas, Motozintla, 1900 m, 15°19'N, 092°16'W, 17

nov 1971, *Breedlove, D.E. 22653* (MO). **Guatemala:** Amatitlán, Palin, 1085 m, 14°24'N, 090°41'W, feb 1892, *Smith, J.D. 2709* (NY). **Honduras:** Francisco Morazán, Distrito Central, 1900-2000 m, 14°12'N, 087°05'W, 22 mar 1951, *Morton, C.V. 7291* (MO). **Nicaragua:** Managua, 800 m, 12°01'N, 086°17'W, 06 ene 1941, *Grant, V.E. 982* (US). **Costa Rica:** High ridge north of the television relay tower above Monteverde and bordering the Monteverde Cloud Forest Nature Reserve. Near the juncture of the Provinces of Alajuela Guanacaste and Puntarenas, 1750-1800 m, 10°19'12"N, 83°48'00"W, 27 feb 1977, *Burger, W.C. 10813* (NY). **Panamá:** Panama Canal Zone. Around Los Siguas Camp southern slope of Cerro de la Horqueta Chiriquí, 1000-1300 m, 2 mar 1911, *Maxon, W.R. 4969* (NY). **Cuba:** Loma del Gato and vicinity. Cobre range of Sierra Maestra, 1000-1100 m, 11 jul 1921, *Fr. León, 10177* (NY). **Jamaica:** Portland, Hardwar Gap Hollywell Recreational Park ravine E of Hollywell near parking and toad down to waterfall, 1200 m, 18°04'48"N, 76°43'12"W, 13 ene 2004, *Christenhusz, M.J.M. 3025* (NY). **Haití:** Massif de La Selle: Dept. Sud'Est: 8 Km. "Norte" de Seguin en la carretera a Furcy y Petionville: "Cajacqué" (Casa Jacque en Español), 1900 m, 18°19'48"N, 72°16'12"W, 21 nov 1982, *Zanoni, T.A. 24545* (NY). **República Dominicana:** La Vega, Prope Constanza, 1190-1190 m, 18°54'46.1"N, 70°44'19.7"W, jun 1910, *von Türckheim, H. 3075* (NY). **Puerto Rico:** Utuado, Cerro Roncador, 800-900 m, 18°13'58.8"N, 66°45'35.3"W, 25 ago 1981, *Liogier, A.H. 32210* (NY). **Colombia:** Boyacá, Santa María, Vereda Caño Negro, camino a Copa Blanca, 1600-1720 m, 4°50'50.6"N, 73°17'52.3"W, 06 nov 2003, *Murillo, J. 3494* (COL). **Venezuela:** Miranda, Parque Nacional El Ávila. Cordillera de la Costa: Silla de Caracas: vertiente sur: entre No Te Apures (pica puesto de guardaparques Sabas Nieves hacia la Silla) y la cueva de los palmeros, 1500-1800 m, 10°31'30"N, 66°51'00"W, abr 2001, *Meier, W. 8182* (NY). **Guyana:** Upper Takutu-Upper Essequibo, Acarai Mts Tinarnau Creek at NW'ern base of Tinarnau Peak, 500 m, 1°16'12"N,

58°36'00"W, 5 mar 1994, *Henkel, T.W. 4969* (NY). **Ecuador:** Napo, Oyacachi, sector Río Chalpi, ca. 15 km al E del pueblo. Bosque maduro, 2500 m, 0°15'S, 77°58'W, 25 may 1996, *Navarrete, H. 1679* (AAU). **Perú:** Junín, Chanchamayo, Chilpez ca. 26km S of San Ramón, 1720-1850 m, 10°16'12"S, 75°22'12"W, 19 oct 1982, *Smith, D.N. 2638* (NY). **Brasil:** Minas Gerais, Araponga, Parque Estadual da Serra do Brigadeiro nas proximidades da Sede, 1400-1400 m, 20°40'00.8"S, 42°31'14.2"W, 10 jul 1999, *Salino, A. 4891* (NY). **Bolivia:** Tarija, Aniceto Arce, Municipio Padcaya. Reserva Nacional de Flora y Fauna Tariquía. Saliendo de Cambarí hacia el quebrada Cangrejo, 1060 m, 22°09'08.6"S, 64°24'10.8"W, 16 ene 2005, *Huaylla Limachi, H. 1659* (NY). **Paraguay:** Paraguarí, Macizo Acahay. in forest on eastern peak, 500 m, 25°54'S, 57°09'W, 5 sep 1988, *Zardini, E.M. 7007* (NY). **Argentina:** Misiones, San Pedro, Parque Provincial Esmeralda, 485 m, 26°53'47.8"S, 53°52'50.2"W, dic 2010, *Yañez, A. 71* (NY). **Uruguay:** Rivera, 01 nov 1996, *Bonifacino, J. M. s.n.* (SI).

Distribución. Desde el sur de Estados Unidos, Mesoamérica e islas del Caribe hasta Uruguay y el norte de Argentina. 140-3300 m.

Figura 6. *Mucura globulifera*. **A.** Vista general. **B.** Ausencia de yemas epipeciolares. **C.** Lámina opaca con los segmentos basales de tercer orden subopuestos. Ejes acanalados adaxialmente, canales decurrentes bordeados por un ala herbácea. **D.** Soros marginales con indusio globoso. **E.** Vista distal de una espora trilete. Ornamentación verrugoso-reticulada formando crestas engrosadas. Fuentes: **A.** *Velazco* en https://www.flickr.com/photos/aztekium/2925345636/. **B.** *Hatschbach 59449* (ASU). **C.** Yáñez & al. (2014). **D.** *Velazco* en https://www.flickr.com/photos/aztekium/2924495197/. **E.** *Gómez-Noguez 237* en http://www.fernsoftheworld.com/2015/03/24/dennstaedtia-globulifera/.

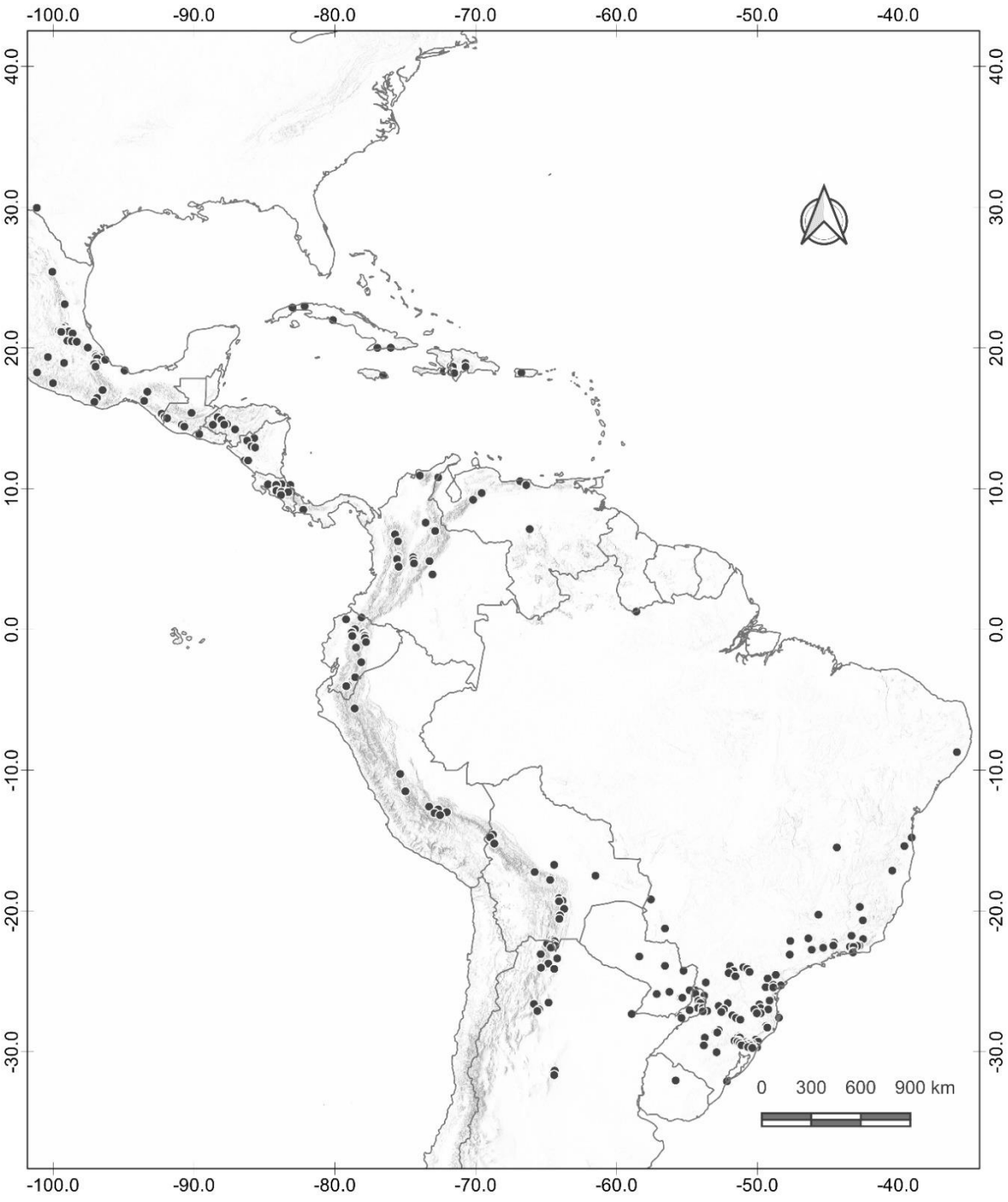

Figura 7. Distribución geográfica de *Mucura globulifera*.

Agradecimientos

Este estudio recibió apoyo económico de la Universidad Nacional de Colombia por medio del proyecto HERMES-40890. Agustina Yáñez contribuyó al estudio de las esporas de *M. bipinnata*. Michael Sundue aportó valiosos comentarios al tratamiento taxonómico. Susana Velásquez-Franco elaboró los mapas. Los herbarios BA, COL y VT permitieron el estudio presencial de sus especímenes.

Literatura citada

Assis, F., Salino, A. 2011. Dennstaedtiaceae (Polypodiopsida) no estado de Minas Gerais, Brasil. Rodriguésia 62: 11-33.

Becari-Viana, I., & Schwartsburd, P. B. 2017. Morpho-anatomical studies and evolutionary interpretations of the rhizomes of extant Dennstaedtiaceae. American Fern Journal, 107(3), 105-123.

Brownsey, P.J., Perrie, L.R. 2018. Dennstaedtiaceae. En: Breitwieser, I., Wilton, A.D. (Eds.) Flora of New Zealand - Ferns and Lycophytes 19. Manaaki Whenua Press, Lincoln. http://dx.doi.org/10.7931/B11G9K

Flórez, L. 1955. Algunas voces indígenas en el español de Colombia. Revista Colombiana de Antropología 4: 286-310.

Kremp, G.O.W., Kawasaki, T. 1972. The spores of the pteridophytes. Hirokawa publishing company. Tokyo.

Lellinger, D.B. 2002. A modern multilingual glossary for taxonomic pteridology. Pteridologia 3: 1-263.

Mickel, J.T., Smith, A.R. 2004. The pteridophytes of Mexico. Memoirs of the New York Botanical Garden 88: 1-1055.

Moran, R.C. 1995. *Dennstaedtia*. pp. 150-163. En R.C. Moran., Riba, R. (eds.). Flora Mesoamericana. Volumen 1. Psilotaceae a Salviniaceae. Universidad Nacional Autónoma de México. México D.F.

Morbelli, M.A. 1980. Morfología de las esporas de las Pteridophyta presentes en la Región Fuego-Patagónica. República Argentina. Opera Lilloana 28: 1-138.

Navarrete, H., Øllgaard, B. 2000. The fern genus *Dennstaedtia* (Dennstaedtiaceae) in Ecuador, new characters, new species and new combinations. Nordic Journal of Botany 20: 311-346.

Perrie, L.R., Shepherd, L.D., Brownsey, P.J. 2015. An expanded phylogeny of the Dennstaedtiaceae ferns: *Oenotrichia* falls within a non-monophyletic *Dennstaedtia*, and *Saccoloma* is polyphyletic. Australian Systematic Botany 28: 256-264.

PPG I. 2016. A community-derived classification for extant lycophytes and ferns. Journal of Systematics and Evolution 56: 563-603. DOI: 10.1111/jse.12229.

Rodríguez-Rey, G., Chica-Balaguera, N., Murillo A., J. 2006. Revisión del género *Dennstaedtia* (Dennstaedtiaceae) en Colombia. p. 629. En: Mejía P., M, & al. (Eds.) Libro de Resúmenes IX Congreso Latinoamericano de Botánica. Jardín Botánico Nacional Dr. Rafael Ma. Moscoso. Santo Domingo.

Rojas-Alvarado, A.F., Tejero-Díez, D. 2002. Una nueva especie de *Dennstaedtia* (Filicales: Dennstaedtiaceae) para México. Revista de Biología Tropical 50: 1007-1012.

Smith, A.R., Kramer, K.U. 1995. Dennstaedtiaceae. Pp. 46-71. En: Steyermark, J.A., Berry, P.E., Holst, B.K. (Eds.) Flora of the venezuelan Guayana, vol. 2. Timber press. Portland.

Thiers, B. 2022 (en actualización permanente). Index Herbariorum. The New York Botanical Garden. Nueva York. Disponible en: http://sweetgum.nybg.org/science/ih/.

Triana-Moreno, L.A. 2018. Relaciones filogenéticas de las especies neotropicales de *Dennstaedtia* (Dennstaedtiaceae) inferidas a partir de caracteres morfológicos. p. 28. En: Alzate G., F. & al. (Eds.). Memorias Segundo Simposio Colombiano en Sistemática de Plantas. Instituto de Biología, Universidad de Antioquia. Medellín.

Tryon, A.F., Lugardon, B. 1991. Spores of the Pteridophyta: surface, wall structure, and diversity based on electron microscope studies. Springer. Nueva York.

Tryon, R.M., Stolze, R.G. 1989. Pteridophyta of Peru II, 13. Pteridaceae - 15. Dennstaedtiaceae. Fieldiana Botany New Series 22: 1-128.

Tryon, R.M., Tryon, A.F. 1982. Ferns and allied plants: with special reference to tropical America. Springer. Nueva York.

Yáñez, A., Arana, M.D., Márquez, G.J., Oggero, A.J. 2014. The genus *Dennstaedtia* Bernh. (Dennstaedtiaceae) in Argentina. Phytotaxa 174: 69−81.

Yáñez A., Márquez, G.J., Morbelli, M.A. 2016a. Spore morphology and ultrastructure of Dennstaedtiaceae from Paranaense Phytogeographic Province I.: Genus *Dennstaedtia*. Review of Palaeobotany and Palynology 224: 181-194.

Yáñez A., Márquez, G.J., Morbelli, M.A. 2016b. Palynological analysis of Dennstaedtiaceae taxa from the Paranaense Phytogeographic Province that produce Trilete spores II: *Microlepia speluncae* and *Pteridium arachnoideum.* Anais da Academia Brasileira de Ciências 88: 877-890. DOI: http://dx.doi.org/10.1590/0001-3765201620150230.

Anexo 1

La lista de especímenes presenta los nombres de los colectores, los números de colección y la especie referenciada con el número entre paréntesis: (1) *Mucura bipinnata*, (2) *Mucura globulifera*.

Abbott, W.L. 1592 (1), **Alston, A.H.G.** 7829 (1), 7892 (1), **Anderson, L.C.** 5376 (2), **Ankersen, H.** 81 (2), **Annies, J.** 247 (2), **Araujo, A.** 1082 (1), **Arbeláez, A.L.** 264 (1), 361 (1), **Aristeguieta & Pannier** 1822 (1), **Axelrod, F.S.** 8260 (1), 4831 (1), **Azofeifa, A.** 464 (1), **Badini** 3082 (2), **Baker, M.A.** 6084 (1), **Barbosa, C.E.** 280 (1), **Barbour, P.J.** 5331 (1), 5345 (1), 5349 (1), **Barker, E.E.** 47 (1), **Barkley, F.A.** 18C734 (1), **Basualdo, I.** 1993 (2), 2031 (2), **Belgrano, M.J.** 608 (2), 731 (2), **Bello C., E.** 4457 (2), **Bockus S.M. & J.S. Hall** 7895 (2), **Bonino, E.** 758 (1), 740 (2), **Bourgeau, E.** 2342 (2), 2362 (2), **Boza E., T.E.** 2350 (1), 2716 (2), **Brade, A.C.** 7728 (2), **Brandbyge, J.S.** 33332 (1), **Breedlove, D.E.** 21616 (2), 22653 (2), 22777 (2), 23292 (1), 24809 (2), 25757 (2), 31351 (2), 32360 (1), 34441 (1), 34620 (1), **Bridarolli, A.J.** 810 (2), **Britton, E.G.** 446 (1), 747bis (1), 5214 (1), **Britton, N.L.** 5250 (1), 2096 (1), 6189 (1), **Bro. Clement,** 619 (1), **Bro. Hioram,** 256 (2), **Broadway, W.E.** 6020 (1), **Brown, A.** 1343 (2), **Buchtien, O.** 313 (1), **Bunting, G.S.** 12079 (2), **Burger, W.C.** 10813 (2), **Cammack, J.** 2 (1), **Camp, W.H.** E-3462 (2), **Cárdenas, M.** 1854 (1), **Chávez A., R.** 3424 (2), **Christenhusz, M.J.M.** 3025 (2), 3264 (2), 4745 (2), **Churchill, S.P.** 16893 (1), **Clark, O.M.** 7375 (2), **Clausen, P.** 2109 (2), **Correll, D.S.** 26140 (2), **Croat, T.B.** 12122 (1), 16429 (1), 21976 (1), 25228 (1), 26758A (1), 27022 (1), 35072 (1), 78547 (1), **Daly, D.C.** 11418 (1), **Davidse, G.** 36883 (1), 19197 (1), **de la Quintana, D.**