

NELSON TÚLIO LAGE PENA

**REVISÃO TAXONÔMICA E FILOGENIA DE *DENNSTAEDTIA S.L.*
(DENNSTAEDTIACEAE) PARA AMERICA DO SUL**

Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

Orientador: Pedro Bond Schwartzburd

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Tese apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Doctor Scientiae*.

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*"The answer, my friend, is blowin' in the wind, the answer
is blowin' in the wind".*

(Bob Dylan)

RESUMO

PENA, Nelson Túlio Lage, D.Sc., Universidade Federal de Viçosa, julho de 2022. **Revisão taxonômica e filogenia de *Dennstaedtia* (grupo *Patania*) para a América do Sul.** Orientador: Pedro Bond Schwartzburd.

No presente trabalho, 13 espécies de *Dennstaedtia*, seis de *Mucura* e duas de *Microlepia* são reconhecidas para a América do Sul, totalizando um total de 20 espécies revisadas na tese. Destas, três táxons são propostos como novos para a ciência, e cinco novas combinações foram realizadas, principalmente relacionadas aos complexos de espécies *Dennstaedtia dissecta/D. cornuta* e *Mucura bipinnata/M. globulifera*. Foram propostas três novas espécies, a saber: *Dennstaedtia aculetata* sp. nov., *D. andina* sp. nov. e *Mucura alata* sp. nov. Cinco combinações novas também são propostas, a saber: *Dennstaedtia concinna* comb. nov., *D. fluminensis* comb. nov., *Mucura baccifera* comb. nov., *M. tamandarei* comb. nov. e *M. tenera* comb. nov. Os estudos moleculares apresentam uma nova proposta filogenética para a família Dennstaedtiaceae, com foco nas espécies brasileiras da subfamília Dennstaedtioideae. Os marcadores utilizados foram *rbcL*, *trnL-trnF* e *rps4-trnS*. As reconstruções filogenéticas se basearam em análises de Máxima Verossimilhança e Bayesiana. A topologia resgatou as subfamílias Dennstaedtioideae, Hypolepidoideae e Monachosoroideae como monofiléticas, apresentando elevado valor de bootstrap para os clados em nível de gênero. Os complexos de espécies, principalmente envolvendo espécies brasileiras, foram melhor compreendidos e resolvidos taxonomicamente. As espécies resgatadas da sinonímia, *Dennstaedtia concinna*, *D. fluminensis*, *Mucura tamandarei* e *M. tenera*, foram sustentadas como espécies válidas no estudo filogenético aqui apresentado.

Palavras-chave: Neotropical. Polypodiales. Samambaias.

ABSTRACT

PENA, Nelson Túlio Lage, D.Sc., Universidade Federal de Viçosa, July 2022. **Taxonomic review and phylogeny of *Dennstaedtia* (*Patania* group) for South America.** Adviser: Pedro Bond Schwartsburd.

In the present work, 13 species of *Dennstaedtia*, six of *Mucura* and two of *Microlepia* are recognized for South America, totaling 20 species reviewed in the thesis. Of these, three taxa are proposed as new to science, and five new combinations were performed, mainly related to the complexes of *Dennstaedtia dissecta*/*D. cornuta* and *Mucura bipinnata*/*M. globulifera* species. Three new species were proposed, namely *Dennstaedtia aculetata* sp. nov., *D. andina* sp. nov. and *Mucura alata* sp. nov. Five new combinations are also proposed, namely: *Dennstaedtia concinna* comb. nov., *D. fluminensis* comb. nov., *Mucura baccifera* comb. nov., *M. tamandarei* comb. nov. and *M. tenera* comb. nov. Molecular studies present a new phylogenetic proposal for the family Dennstaedtiaceae, focusing on the Brazilian species of the subfamily Dennstaedtioideae. The markers used were *rbcL*, *trnL-trnF* and *rps4-trnS*. The phylogenetic reconstructions were based on Maximum Likelihood and Bayesian analyses. The topology rescued the subfamilies Dennstaedtioideae, Hypolepidoideae and Monachosoroideae as monophyletic, presenting a high bootstrap value for the clades at the genus level. Species complexes, mainly involving Brazilian species, were better understood and resolved taxonomically. The species rescued from synonymy, *Dennstaedtia concinna*, *D. fluminensis*, *Mucura tamandarei* and *M. tenera*, were sustained as valid species in the phylogenetic study presented here.

Keywords: Neotropical. Polypodiales. Ferns.

SUMÁRIO

1. INTRODUÇÃO GERAL.....	12
Figura 1. Proposta filogenética apresentada por Triana-Moreno <i>et al.</i> (<i>in prep.</i>) .	13
Artigos científicos.....	17
Trabalhos técnicos e workshop	18
Capítulos de livro	19
REFERÊNCIAS BIBLIOGRÁFICAS	20
Capítulo I: Taxonomic revision of South American <i>Microlepia</i> and <i>Mucura</i> (Dennstaedtiaceae), including new species, new circumscriptions, and nomenclatural clarifications.....	23
ABSTRACT	24
1. INTRODUCTION	25
2. MATERIAL AND METHODS	26
3. RESULTS AND DISCUSSION	27
TAXONOMIC TREATMENT.....	28
<i>Microlepia speluncae</i>	29
<i>Microlepia strigosa</i>	32
<i>Mucura alata</i>	33
<i>Mucura globulifera</i>	35
<i>Mucura tamandarei</i>	38
<i>Mucura tenera</i>	39
4. EXCLUDED SPECIES FROM THE STUDY AREA	46
<i>Mucura baccifera</i>	46
5. EXCLUDED NAMES.....	49
<i>Mucura bipinnata</i>	49
6. DOUBTFUL NAMES.....	49
<i>Dicksonia punctulata</i>	49
7. ACKNOWLEDGEMENTS	50
8. LITERATURE CITED.....	50
Figure 1. <i>Microlepia speluncae</i>	53
Figure 2. <i>Mucura alata</i> ; <i>Mucura baccifera</i>	54
Figure 3. <i>Mucura globulifera</i> ; <i>Mucura tamandarei</i> ; <i>Mucura tenera</i>	55
Map 1. Distribution of <i>Microlepia speluncae</i>	56
Map 2. Distribution of <i>Mucura alata</i>	57
Map 3. Distribution of <i>Mucura globulifera</i>	58

Map 4. Distribution of <i>Mucura tamandarei</i>	59
Map 5. Distribution of <i>Mucura tenera</i>	60
Capítulo II. Beware my spines: a new spiny fern (<i>Dennstaedtia</i> , Dennstaedtiaceae) from central and western Amazonia	62
ABSTRACT	62
RESUMO	62
1. INTRODUCTION	63
2. MATERIAL AND DISCUSSION	64
3. RESULTS	64
<i>Dennstaedtia aculeata</i>	64
4. DISCUSSION	67
5. CONCLUSIONS	68
6. ACKNOWLEDGMENTS	69
7. REFERENCES	69
Figure 1. Illustration of <i>Dennstaedtia aculeata</i>	72
Figure 2. Photo board of <i>Dennstaedtia aculeata</i>	73
Figure 3. Distribution map of <i>Dennstaedtia aculeata</i>	74
Figure 4. <i>Dennstaedtia aculeata</i> ; <i>D. spinosa</i>	75
Capítulo III. Taxonomic revision of <i>Dennstaedtia</i> s. str. (Dennstaedtiaceae) for South America, except the for the northern Andes	77
ABSTRACT	78
1. INTRODUCTION	79
2. MATERIAL AND METHODS	79
3. RESULTS AND DISCUSSION	80
TAXONOMIC TREATMENT	81
<i>Dennstaedtia aculeata</i>	82
<i>Dennstaedtia andina</i>	83
<i>Dennstaedtia arcuata</i>	84
<i>Dennstaedtia auriculata</i>	85
<i>Dennstaedtia cicutaria</i>	86
<i>Dennstaedtia concinna</i>	92
<i>Dennstaedtia cornuta</i>	93
<i>Dennstaedtia coronata</i>	108
<i>Dennstaedtia fluminensis</i>	109
<i>Dennstaedtia glauca</i>	112
<i>Dennstaedtia mathewsii</i>	113

<i>Dennstaedtia obtusifolia</i>	115
<i>Dennstaedtia sprucei</i>	118
4. EXCLUDED NAMES AND SPECIES FROM THE AREA	119
5. DOUBTFUL NAMES.....	119
6. ACKNOWLEDGEMENTS	120
7. LITERATURE CITED.....	120
Figure 1. A-D. <i>Dennstaedtia aculeata</i> ; <i>D. arcuata</i> ; <i>D. auriculata</i> ; <i>D. cicutaria</i>	123
Figure 2. <i>Dennstaedtia concinna</i> ; <i>D. cornuta</i> ; <i>D. coronata</i>	124
Figure 3. <i>Dennstaedtia fluminensis</i> ; <i>D. glauca</i> ; <i>D. mathewsii</i>	125
Figure 4. A-D. <i>Dennstaedtia obtusifolia</i> ; <i>D. sprucei</i> ; <i>D. andina</i>	126
Map 1. Geographic distribution of <i>Dennstaedtia aculeata</i> ; <i>D. arcuate</i> ; <i>D. auriculata</i>	127
Map 2. Geographic distribution of <i>Dennstaedtia cicutaria</i> ; <i>D. concinna</i>	128
Map 3. Geographic distribution of <i>Dennstaedtia cornuta</i>	129
Map 4. Geographic distribution of <i>Dennstaedtia coronata</i> ; <i>D. fluminensis</i> ; <i>D. glauca</i>	130
Map 5. Geographic distribution of <i>Dennstaedtia mathewsii</i> ; <i>D. obtusifolia</i>	131
Map 6. Geographic distribution of <i>Dennstaedtia andina</i> ; <i>D. sprucei</i>	132
Capítulo VI. A filogenia molecular como ferramenta taxonômica para a resolução de complexos de espécies	134
RESUMO	135
ABSTRACT	135
1. INTRODUÇÃO.....	136
2. MATERIAL E MÉTODOS	138
3. RESULTADOS	140
4. DISCUSSÃO.....	140
5. AGRADECIMENTOS.....	144
6. REFERÊNCIAS	144
Fig.1. Hipótese filogenética para Dennstaedtiaceae baseada em análise de máxima verossimilhança. Os números são valores de bootstrap.	147
Fig.2. Hipótese filogenética para Dennstaedtiaceae de Triana-Moreno <i>et al.</i> (<i>in press</i>).....	148
Figure 3. Topologia com foco nos gêneros <i>Dennstaedtia</i> e <i>Mucura</i> . Os números são valores de bootstrap. As setas em vermelho representam os nomes resgatados da sinonímia.	149
Apêndice 1.	150
Capítulo V. Fern flora of Viçosa: Dennstaedtiaceae, Lindsaeaceae, and Saccolomataceae.....	154

ABSTRACT	155
RESUMO	156
1. INTRODUCTION	157
2. MATERIAL AND METHODS	158
3. RESULTS AND DISCUSSION	158
<i>Dennstaedtia cicutaria</i>	160
<i>Pteridium esculentum</i> subsp. <i>arachnoideum</i>	161
<i>Lindsaea lancea</i> var. <i>lancea</i>	163
<i>Lindsaea quadrangularis</i> subsp. <i>quadrangularis</i>	164
<i>Lindsaea stricta</i> var. <i>stricta</i>	164
<i>Saccoloma elegans</i>	165
4. ACKNOWLEDGEMENTS	166
5. LITERATURE CITED.....	166
Figure 1. <i>Dennstaedtia cicutaria</i> ; <i>Pteridium esculentum</i> subsp. <i>arachnoideum</i> ..	171
Figure 2. <i>Lindsaea lancea</i> var. <i>lancea</i> ; <i>L. quadrangularis</i> subsp. <i>quadrangularis</i>	172
Figure 3. <i>Lindsaea stricta</i> var. <i>stricta</i> ; <i>Saccoloma elegans</i>	173

1. INTRODUÇÃO GERAL

Dennstaedtiaceae Lotsy é uma família de samambaia pertencente ao clado Polypodiales e a subclasse Polypodiidae, que compreende ao grupo de samambaias mais biodiverso chamadas lepto-esporangiadas (PPG I 2016). Dennstaedtiaceae possui ca. 270 espécies com distribuição mundial e hábito de colonização relacionadas as bordas dos fragmentos florestais, característica peculiar entre as samambaias (Schwartzburd *et al.* 2020). Ainda, a família Dennstaedtiaceae é constituída por três subfamílias que são denominadas: Monachosoroideae, Dennstaedtioidae e Hypolepidoideae (Triana-Moreno *et al. in pres.*).

Morfologicamente, a família Dennstaedtiaceae pode ser reconhecida por apresentar as seguintes características: rizoma curto a longo rastejante; glabros ou com tricomas catenados. As folhas possuem ca. de 4 m de comprimento; lâminas 1-pinado à 4-pinado-pinatifido; nervuras livres; indumento catenado, mais raramente acicular ou ausentes. Soros marginais ou próximos a margem, discretos, formado apenas por indúcio abaxial, pseudo-indúcio, ou pela fusão pela fusão do indúcio abaxial a porção da lâmina adaxial, originando indúcio com morfologia cupuliforme, de bolsa, cilíndrico ou jara (Smith *et al.* 2006; Triana-Moreno *et al. in pres.*).

Em relação as subfamílias, Monachosoroideae é monogenérica, representada pelo gênero monofilético *Monachosorum* Kunze. Hypolepidoideae é atualmente representada por seis gêneros que nos estudos filogenéticos mais recentes, se apresentam em dois clados: 1. Clado formado pelos gêneros *Hiya* H.Sanhg, *Paesia* A.St-Hil., *Histiopteris* (J.Agardh) J.Sm. e *Blotiella* R.M.Tryon; 2. Clado formado pelos gêneros *Pteridium* Gled. ex Scop., *Hypolepis* Bernh. (Schwartzburd *et al.* 2020; Triana-Moreno *et al. in prep.*).

A subfamília Dennstaedtioidae, até então, sempre foi reafirmada como uma subfamília contendo gêneros não monofiléticos, especialmente por demonstrar *Dennstaedtia* Bernh. *s.l.* como polifilético (*e.g.* Perrie *et al.*, 2015; Schwartzburd *et al.*, 2020). No entanto, os estudos realizados por Triana-Moreno *et al. (in prep.)*, sugerem novas classificações genéricas, de modo a deixá-los natural. Desta forma, Triana-Moreno *et al. (in prep.)*, segregou o gênero *Dennstaedtia s.l.* em três gêneros distintos, à saber: *Dennstaedtia s.str.*, *Mucura* Triana & Sundue e *Sitobolium* Desv.

Assim, a subfamília Dennstaedtioideae passou a ser composta por quatro gêneros naturais: *Dennstaedtia* s.str., *Mucura*, *Sitobolium* e *Microlepia* C.Presl (Figura 1).



Figura 1. Proposta filogenética apresentada por Triana-Moreno et al. (in prep.).

Durante os estudos filogenéticos de Triana-Moreno *et al.* (*in prep.*), a espécie tipo do gênero *Dennstaedtia*, *D. flaccida* (Forst.) Bernh. (sob o basônimo: *Trichomanes flaccidum* G.Forst.), uma espécie pouco conhecida da Indonésia e ilhas do Pacífico ocidental e que foi descrita por Bernhardt em 1801, agrupou ao clado das espécies do gênero *Microlepia*. Uma vez que o gênero *Dennstaedtia* tem prioridade por ter sido descrito primeiro que *Microlepia*, descrita em 1836, para solucionar o problema apresentado, poderia apenas sinonimizar *Microlepia* em *Dennstaedtia*. Por sua vez, o gênero até então considerado *Dennstaedtia* seria transferido para *Patania*, de modo que Tryon (1960) sinonimizou o gênero *Patania*, sob o basônimo *Patania obtusifolia* (Willd.) C.Presl em *Dennstaedtia*. No entanto, esta solução também exigirá que o ca. 60 espécies de *Microlepia* sejam combinadas em *Dennstaedtia*, e a circunscrição de *Dennstaedtia* alterada significativamente, para um conceito mais amplo e desconhecido, e que a maioria de *Dennstaedtia*, como atualmente reconhecida, seja transferida para a desconhecida *Patania*, causando assim enorme instabilidade nomenclatural. Por este motivo, Triana-Moreno *et al.* (2022), propuseram a conservação dos nomes *Microlepia* e *Dennstaedtia*, com a escolha de *D. dissecta* (Sw.) T. Moore (= *Dicksonia dissecta* Sw.) como novo Tipo para *Dennstaedtia*.

O gênero *Dennstaedtia* s.l. teve seus primeiros estudos de revisão iniciados por Tryon (1960 – ver também Tryon e Tryon, 1982), que teve as Américas como foco de seu estudo, onde apenas 11 espécies foram consideradas válidas. Após os trabalhos de Tryon, floras regionais apresentaram gradualmente novidades taxonômicas em relação ao gênero *Dennstaedtia* s.l., como: Flora da Mesoamérica (Moran, 1995; Rojas-Alvarado e Villalobos-Brenes, 2018), Flora do Equador (Navarrete e Øllgaard, 2000), Flora do México (Mickel e Smith, 2004) e Flora da Argentina (Yañez *et al.*, 2014). Para o Brasil, menciona-se a Flora Ilustrada Catarinense – “Pteridáceas” (Sehnem, 1972), Flora de Minas Gerais (Assis e Salino, 2011), Flora do Espírito Santo (Schwartzburd, 2017).

Nos últimos anos, a família Dennstaedtiaceae foi alvo de diversos estudos filogenéticos com a finalidade de estabelecer relações evolutivas entre os gêneros, aos quais, revelam o gênero *Dennstaedtia* como polifilético (Perrie *et al.* 2015; Schneider *et al.* 2016; Shang *et al.* 2018; Schwartzburd *et al.* 2020). Os autores mencionados anteriormente apontam para dois principais clados envolvendo as espécies de *Dennstaedtia* s.l.: clado I - representado pelas espécies do hemisfério

sul, ao qual espécies já foram chamadas de *Patania* C.Presl (baseado em *D. obtusifolia*), e que formam clado irmão aos gêneros *Leptolepia* Prantl e *Oenotrichia* Copel.; clado II - representado pelas espécies do hemisfério norte e que formam clado irmão ao gênero *Microlepia* C.Presl. Contudo, os estudos realizados por Triana-Moreno *et al.* (*in prep.*), sugerem novas classificações genéricas, tornando a circunscrição deles mais natural, onde *Dennstaedtia s.l.* foi então segregado em três gêneros distintos: *Dennstaedtia s.str.* (equivalente a “*Dennstaedtia* grupo *Patania*”), *Mucura* Triana & Sundue e *Sitobolium* Desv. Desta forma, a atual filogenia posiciona *Sitobolium* como grupo irmão de *Microlepia*, que por sua vez indica *Sitobolium* + *Microlepia* como irmãos de gênero *Mucura*, que por fim estabelece [*Sitobolium* + *Microlepia*] + *Mucura*] como gêneros-irmãos de *Dennstaedtia s.str.* (Triana-Moreno *et al.*, *in prep.*). As linhagens de Dennstaedtioideae ainda compreendem os gêneros *Leptolepia* Prantl e *Oenotrichia* Copel., os quais estão posicionados dentro do clado de *Dennstaedtia s.str.*, e por este motivo estão sendo propostos como sinônimos do gênero por Triana-Moreno *et al.* (*in prep.*).

Para além das problemáticas cladística acitadas acima, as espécies circunscritas em *Dennstaedtia s.l.*, necessitavam de estudos taxonômicos mais atualizados para uma melhor delimitação de suas espécies, uma vez que a depender do autor, as monografias apresentam uma grande divergência em relação a real diversidade taxonômica, onde pode ser considerada ca. 15 a 25 espécies válidas (Tryon 1960, Tryon & Tryon 1982, Navarrete & Øllgaard 2000, Rojas-Alvarado & Villalobos-Brenes 2018). Certamente, um dos principais motivos para a não exatidão taxonômica são os complexos específicos que geram erros nas identificações. Na América do Sul, há pelo menos dois principais complexos que necessitavam de revisão: 1. o complexo *Dennstaedtia dissecta/D. cornuta* e nomes relacionados; e 2. o complexo, *Dennstaedtia bipinnata/D. globulifera* e nomes relacionados, que após a criação do novo gênero *Mucura*, passaram a se chamar complexo *Mucura bipinnata/M. globulifera*.

De modo a solucionar as problemáticas apresentadas, a tese teve sete objetivos:

1. Realizar revisão taxonômica das espécies de *Dennstaedtia*, *Microlepia* e *Mucura* para América do Sul.
2. Atualizar as áreas de distribuição dos táxons de Dennstaedtioide ocorrentes na América do Sul, não poderia ser um objetivo?

3. Resolver problemas nomenclaturais relativos à nomenclatura das espécies de Dennstaedtioidae.
4. Propor chaves de classificação para o reconhecimento das espécies de Dennstedtioidae encontradas na área de estudo.
5. Produzir descrições morfológicas a fim de auxiliar no reconhecimento das espécies estudadas na área de estudo.
6. Utilizar ferramentas moleculares para auxiliar nas decisões taxonômicas, tendo como base uma filogenia preliminar, pois a mesma será acrescida de sequência que serão disponibilizadas após a publicação do trabalho de Triana-Moreno *et al.* (*in prep.*).
7. Realizar o tratamento taxonômico das famílias Dennstaedtiaceae, Lindsaeaceae e Saccolomataceae, a fim de contribuir com o projeto "Samambaias e Licófitas da região de Viçosa, Minas Gerais".

A tese conta com 13 espécies de *Dennstaedtia s.str.*, seis de *Mucura* e 1 de *Microlepia* que são reconhecidas para a América do Sul, totalizando um total de 20 espécies revisadas. Destas, três táxons são propostos como novos para a ciência (*Dennstaedtia aculetata*, *sp. nov.*, *D. andina*, *sp. nov.* e *Mucura alata*, *sp. nov.*), e cinco novas combinações foram realizadas, principalmente relacionadas aos complexos de espécies *Dennstaedtia dissecta*/*D. cornuta* (*Dennstaedtia concinna*, *comb. nov.*, *D. fluminensis*, *comb. nov.*) e *Mucura bipinnata*/*M. globulifera* (*Mucura baccifera*, *comb. nov.*, *M. tamandarei*, *comb. nov.*, *M. tenera*, *comb. nov.*). Os estudos moleculares resgataram as subfamílias Dennstaedtioidae, Hypolepidoideae e Monachosoroideae como monofiléticas, apresentando elevado valor de bootstrap para os clados em nível de gênero. Os complexos de espécies, principalmente envolvendo espécies brasileiras, foram melhor compreendidos e resolvidos taxonomicamente. As espécies resgatadas da sinonímia, *Dennstaedtia concinna*, *D. fluminensis*, *Mucura tamandarei* e *M. tenera*, foram sustentadas como espécies válidas no estudo filogenético aqui apresentado.

Portanto, a tese encontra-se dividida em cinco capítulos principais, onde cada um deles segue as normas da revista a que foi ou será submetido.

Capítulo I. Pena, N.T.L. & P. B. Schwartzburd. Taxonomic revision of South American *Microlepia* and *Mucura* (Dennstaedtiaceae), including new species, new circumscriptions, and nomenclatural clarifications. – a ser submetido ao

periódico *American Fern Journal*. Este capítulo trata principalmente das espécies dos gêneros *Microlepia* e *Mucura* da América do Sul.

Capítulo II. Pena, N.T.L.; Zuquim, G. & Schwartzburd, P.B. (2022). Beware my spines: a new spiny fern (*Dennstaedtia*, Dennstaedtiaceae) from central and western Amazonia. *ACTA Amazonica*, 52: 142–148. O presente capítulo descreve uma nova espécie de samambaia espinhosa para o gênero *Dennstaedtia* com ocorrência para a Amazônia brasileira e peruana.

Capítulo III. Pena, N.T.L. & P. B. Schwartzburd. Taxonomic revision of *Dennstaedtia* s. str. (Dennstaedtiaceae) for South America, except the for the northern Andes. – a ser submetido ao periódico *American Fern Journal*. Este capítulo trata das espécies do gênero *Dennstaedtia* da América do Sul, com exceção dos Andes do norte.

Capítulo IV. Pena, N.T.L. & P. B. Schwartzburd. Estudos filogenéticos em Dennstaedtiaceae, como foco nas espécies brasileiras da subfamília Dennstaedtioideae. – periódico a ser definido. Este capítulo abordou o uso de ferramentas moleculares para auxiliar nas decisões taxonômicas, principalmente das espécies brasileiras, pertencentes a família Dennstaedtiaceae.

Capítulo V. Pena, N.T.L. & P. B. Schwartzburd. Fern flora of Viçosa, Minas Gerais, Brazil: Dennstaedtiaceae, Lindsaeaceae, and Saccolomataceae. – aceito para publicação na *Hoehnea*. O presente capítulo faz parte de um projeto em andamento sobre samambaias e licófitas da região de Viçosa, Minas Gerais, Brasil, onde foi realizado o tratamento taxonômico das famílias Dennstaedtiaceae, Lindsaeaceae e Saccolomataceae.

Durante o desenvolvimento da Tese, além dos trabalhos específicos com os gêneros *Dennstaedtia*, *Microlepia* e *Mucura*, houve outras produções científicas com foco nas Pteridófitas:

Artigos científicos:

- a. Triana-Moreno, L.A.; Schwartzburd, 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>

- b. Schwartzburd, P.B. & Pena, N.T.L. (2022). Flora of Espírito Santo: Saccolomataceae. *Rodriguesia*, 73: 1–7. <https://doi.org/10.1590/2175-7860202273021>
- c. Alves-Araújo, A.; & al. Pena, N.T.L.; & al. (2022). Floristic survey of vascular plants of a poorly known area in the Brazilian Atlantic Forest (Flona do Rio Preto, Espírito Santo). *Biodiversity Data Journal*, 10: 1–21. doi: 10.3897/BDJ.10.e75910
- d. Pena, N.T.L. & Schwartzburd, P.B. (2021). *Pleopeltis guttisquamata* (Polypodiaceae): a new epiphytic fern from the inselbergs of Espírito Santo, Brazil. *Brittonia*, 73: 152–159. DOI 10.1007/s12228-020-09656-8
- e. BGF - The Brazil Flora Group; Pena, N.T.L. 2021. Brazilian Flora 2020: Leveraging the power of a collaborative scientific network. *TAXON*, 71: 1–21. Disponível em: <https://doi.org/10.1002/tax.12640>
- f. Pena, N.T.L. & Miranda, C.V. (2020). Ferns and lycophytes from a forest associated with quartzite fragments in southern Espírito Santo state, Brazil. *Heringeriana*, 14: 33–48. <https://doi.org/10.17648/heringeriana.v14i1.917912>
- g. Schwartzburd, P.B.; Oliveira, A.G.S. & Pena, N.T.L. (2020). (004-005) Proposals to include the term -type-species- in the Code. *TAXON*, 69: 624–624. <https://doi.org/10.1002/tax.12246>
- h. Triana-Moreno, L.A., Yañez, A., Kuo, L-Y., Rothfels, C.J., Pena, N.T.L., Schwartzburd, P.B. & Sundue, M. (*in prep.*). Phylogenetic revision of Dennstaedtioidae (Dennstaedtiaceae: Polypodiales) with description of *Mucura*, gen. nov. Obs.: manuscrito submetido e em processo de revisão na *TAXON*.

Trabalhos técnicos e workshop:

- a. Avaliador *on line* das espécies de Anemiaceae e Pteridaceae para o Projeto Revisão da Lista das Espécies Ameaçadas do Espírito Santo. Disponível no livro: Fraga *et al.* (orgs.) (2019). Fauna e flora ameaçadas de extinção no estado do Espírito Santo. ISBN 978-65-81414-01-6.
- b. Avaliador no workshop "Revisão da Lista das Espécies Ameaçadas de Extinção do Espírito Santo", realizado no período de 28 de abril a 01 de maio de 2019, na Universidade Vila Velha, Vila Velha-ES. Na categoria de Avaliador do grupo "Samambaias e Licófitas". Disponível no livro: Fraga *et al.* (orgs.) (2019). Fauna

e flora ameaçadas de extinção no estado do Espírito Santo. ISBN 978-65-81414-01-6.

- c. Monografias das famílias Culcitaceae, Lindsaeaceae e Salviniaceae e para os gêneros Doryopteris e Lytoneuron, no projeto Flora do Brasil 2020. Disponível em:

<http://floradobrasil.jbrj.gov.br/reflora/listaBrasil/ConsultaPublicaUC/ResultadoDaConsultaNovaConsulta.do#CondicaoTaxonCP>

Capítulos de livro:

- a. BFG - The Brazil Flora Group; Pena, N.T.L. (2021). Coleção Flora do Brasil 2020. 0. ed. Rio de Janeiro: Jardim Botânico do Rio de Janeiro, v. 1. 36p.
- b. BFG - The Brazil Flora Group; Pena, N.T.L. (2021). Flora do Brasil 2020. 1. ed. Rio de Janeiro: Jardim Botânico do Rio de Janeiro, v. 1. 28p.
- c. Sylvestre, L.S.; Schwartsburd, P.B.; Prado, J.; Salino, A.; Hirai, R.Y.; Matos, F.B.; Gonzatti, F.; Weigand, A.; Mynssen, C.M.; Pena, N.T.L.; Contaifer, L. & Caitano, H. A. (2019). Samambaias e Licófitas ameaçadas de extinção no estado do Espírito Santo. *In*: Claudio Nicoletti de Fraga; Mileide de Holanda Formigoni; Flávia Guimarães Chaves. (Org.). Fauna e flora ameaçadas de extinção no estado do Espírito Santo. 1ed.Santa Teresa: Instituto Nacional da Mata Atlântica, 1: 124–135.
- d. Fraga, C.N.; Peixoto, A.L.; & al.; Pena, N.T.L.; & al. (2019). Lista da fauna e flora ameaçadas de extinção no estado do Espírito Santo. *In*: Claudio Nicoletti de Fraga; Mileide de Holanda Formigoni; Flávia Guimarães Chaves. (Org.). Fauna e flora ameaçadas de extinção no estado do Espírito Santo. 1ed.Santa Teresa: Instituto Nacional da Mata Atlântica, 1: 342–419.

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Capítulo I. Pena, N.T.L. & P. B. Schwartzburd. Taxonomic revision of South American *Microlepia* and *Mucura* (Dennstaedtiaceae), including new species, new circumscriptions, and nomenclatural clarifications. – a ser submetido ao periódico American Fern Journal.

Capítulo I: Taxonomic revision of South American Microlepia and Mucura (Dennstaedtiaceae), including new species, new circumscriptions, and nomenclatural clarifications

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ABSTRACT

We present the taxonomic revision of the South American species of *Microlepia* and *Mucura*, a genus recently segregated from *Dennstaedtia* s.l. Here, seven species are recognized: *Micr. speluncae*, *Micr. strigosa*, *Muc. alata*, sp. nov., *Muc. baccifera*, comb.nov., *Muc. globulifera*, *Muc. tamandarei*, comb. nov., and *Muc. tenera*, comb. nov. In *Mucura*, a new species is proposed and three names presenting new combination are rescued from synonymy and have their circumscriptions and geographical distributions updated. We also suggest new circumscriptions for the two species previously accepted in the genus: *Muc. baccifera* (not occurring in South America) and *Muc. globulifera*. *Mucura baccifera* is a substitute name for the Mesomaerican/Antillean plants traditionally named as *Muc. bipinnata* (= *Dennstaedtia bipinnata*), whose type represents *D. dissecta*, in fact.. *Mucura globulifera* is widespread in the Neotropics; *Muc. baccifera* occurs in northern and western South America; *Muc. tamandarei* is endemic to Brazil and Paraguay; and *Muc. tenera* occurs in southern and eastern South America. *Microlepia speluncae* is an invasive species that has spread in some places within the Neotropics, not forming a cohesive geographical distribution. We present key to species, comprehensive descriptions, illustrations, type information, examined specimens, maps of distribution, and comments for all taxa, including nomenclatural clarifications.

KEYWORD.—Amazon, Andes, Atlantic Forest, Dennstaedtioid ferns, Pteridophyta

1. INTRODUCTION

The family Dennstaedtiaceae Lotsy is monophyletic and presents 11 genera and ca. 265 species in the latest classifications (Shang *et al.*, 2018; Schwartsburd *et al.*, 2020; Triana-Moreno *et al.*, 2022a). In the last decade, Dennstaedtiaceae has been the subject of several phylogenetic studies which indicated the paraphyly (or polyphyly) of some genera, which were later re-circumscribed in order to reach a monophyletic classification within the family; also, a few genera were described as new (*e.g.* Perrie *et al.*, 2015; Shang *et al.*, 2018; Schwartsburd *et al.*, 2020; Wang *et al.*, 2021; Triana-Moreno *et al.*, 2022a, 2022b).

Until 2016, ten genera of Dennstaedtiaceae have been recognized, namely: *Blotiella* R.M.Tryon; *Dennstaedtia* Bernh.; *Histiopteris* (J.Agardh) J.Sm.; *Hypolepis* Bernh.; *Leptolepia* Mett. ex Prantl; *Microlepia* C.Presl; *Monachosorum* Kunze; *Oenotrichia* Copel.; *Paesia* A.St.-Hil., and *Pteridium* Gled. ex Scop. (PPG I, 2016). However, the latest phylogenetic studies revealed two more genera for the family, *Mucura* L.A. Triana & Sundue and *Hiya* H. Shang, the rescue of *Sitobolium* Desv., and the synonymization of *Leptolepia* and *Oenotrichia* (Shang *et al.*, 2018; Triana-Moreno *et al.*, 2022a). Genus *Mucura* refers to the former group of species of *Dennstaedtia s.l.* with adaxial wings continuous from pinna-rachises onto costae, as well as continuous from costae onto costules. *Hiya*, on the other hand, was segregated from *Hypolepis s.l.* by its segregated position in the phylogeny, as well as the presence of recurved black-tipped prickles, truly scandent leaves with indeterminate rhythmic growth, stipule-like pinnules, and rachis-costa architecture where the adaxial grooves of the axes are confluent between orders (Shang *et al.*, 2018).

Dennstaedtia s.l. had its first revisionary studies initiated by Tryon (1960 – see also Tryon and Tryon, 1982), which had the Americas as a focus of his study, from where he considered only 11 valid species. After Tryon's work, regional works have gradually presented taxonomic novelties, such as: Flora of Mesoamerica (Moran, 1995; Rojas-Alvarado and Villalobos-Brenes, 2018), Flora of Ecuador (Navarrete and Øllgaard, 2000), Flora of México (Mickel and Smith, 2004), and Flora of Argentina (Yañez *et al.*, 2014). For Brazil, mention is made to Flora Ilustrada Catarinense – “Pteridáceas” (Sehnem, 1972), Flora of Minas Gerais (Assis and Salino, 2011), Flora

of Espírito Santo (Schwartzburd, 2017), and Flora do Brasil 2020 (Schwartzburd and Pena, in <<https://floradobrasil.jbrj.gov.br/FB90915>>). With the current circumscription of Dennstaedtiodeae presented by Triana-Moreno *et al.* (2022a), it is estimated that the genus *Dennstaedtia s. str.* has ca. 55 species with Pantropical distribution.

The genus *Mucura*, until the present moment, had only two species ascribed to it: *M. bipinnata* (Cav.) Maxon and *M. globulifera* (Poir.) Hieron., both with Neotropical distribution (Tryon, 1960; Triana-Moreno *et al.*, 2022a). Finally, *Microlepia* has ca. 60 species with Tropical and Subtropical distribution, being essentially an Old-World genus, which is distributed mainly in Tropical and eastern Asia and extends into Africa and Madagascar, Australia, New Zealand, the western Pacific islands, and Hawaii (*e.g.* Tryon and Tryon, 1982; Yuehong *et al.*, 2013; Triana-Moreno *et al.*, 2022a). In the Neotropics, the only known species of the genus is *Micr. speluncae* (L.) T.Moore, which has sub-cosmopolitan distribution. *Microlepia speluncae* occurs in many places within the Neotropics, but without presenting a cohesive and continuous range. This uncommon distribution, allied to the spreadness of the species worldwide, has led some authors to consider it an invasive species in the Neotropics, as well as in many other parts of the World (Tryon and Tryon, 1982; Kramer and Cremers, 1990; Mickel and Smith, 2004; Yuehong *et al.*, 2013). Another species, *Micr. jamaicensis* Fée, has once been considered an endemic species from Jamaica, but it has lately been synonymized under *Micr. speluncae* (Tryon and Tryon, 1982; Proctor, 1985).

Here, we present the taxonomic revision of *Microlepia* and *Mucura* from South America (Figures 1-3, Maps 1-5), of which seven species are recognized: *Micr. speluncae*, *Micr. strigose*, *Muc. alata*, *sp. nov.*, *Muc. adiantoides*, *comb. nov.*, *Muc. globulifera*, *Muc. tamandarei*, *comb. nov.*, and *Muc. tenera*, *comb. nov.* The three names presenting new combination into *Mucura* are rescued from synonymy and have their circumscriptions and geographical distribution updated. We also suggest new circumscriptions for the two species previously accepted in the genus: *Muc. baccifera* (previously treated as *Muc. bipinnata* or *Dennstaedtia bipinnata*, and not occurring in South America) and *Muc. globulifera*.

2. MATERIAL AND METHODS

The studies were carried out between the years 2018 to 2022, in which Neotropical specimens of Dennstaedtiodeae from were analyzed. Unfortunately, we were not able to examine a comprehensive number of specimens from Venezuela, Colombia, and Ecuador, as well as from Central and North Americas. Therefore, our revision was concentrated on South America, except for northern Andes. During this period, collection expeditions were carried out in Brazilian territory. Specimens from the following herbaria were examined: BHCB, CEPEC, CESJ, COR, FURB, HAS, HUCCS, HUEFES, HRCB, IAN, ICN, INPA, MA, MBML, MG, OUPR, PACA, SAMES, SJRP, SP, SPF RB, UEC, UFP, UPCB, VIC, VIES (Brazil); SGO (Chile); UPRRP (Puerto Rico); NY, UC and VT (USA) (Thiers, continuous update). We also examined specimens online, through the websites of SpecieLink (<http://www.splink.org.br/>), Reflora – Flora do Brasil 2020 (<http://reflora.jbrj.gov.br/reflora/herbarioVirtual/>), GBIF (<https://www.gbif.org/>) and Pteridophyte Collections Consortium (<https://pteridoportal.org/>), including types.

Fieldwork occurred place in the states of Bahia, Espírito Santo, Minas Gerais and Rio de Janeiro. The collections were carried out according to the usual herborization techniques proposed by Windisch (1992). The collected specimens were deposited in the herbarium VIC, and their duplicates to be sent mainly to NY, RB, and SP (Thiers, continuous update). Descriptions of general morphological characters follow Lellinger (2002) and the names and authors of the species were confirmed through IPNI (<http://www.ipni.org>) and in original publication. Maps were prepared in QGIS v. 3.22 (https://qgis.org/pt_BR/site/index.html).

3. RESULTS AND DISCUSSION

Key to *Dennstaedtia**, *Microlepia* and *Mucura* from South America

1. Sori submarginal, protected only by the lower indusia 2
 - Sori marginal, protected by the lower indusia fused to the upper indusia 3
2. Fronds > 1 m long; petioles light to dark brown; the abaxial surfaces of the costae and veins with light brown catenate hairs *Microlepia speluncae*
 - Fronds < 1 m long; petioles yellow-brown to red-brown; costae and veins bear abundant, colorless or pale brown, multicellular, non-glandular hairs *Microlepia strigosa*

3. Adaxial axes (rachises-costae) not winged *Dennstaedtia s. str.* (not in this work*)
 Adaxial axes (rachises-costae) winged 4
4. Sori and indusia cylindrical 5
 Sori rounded, indusia spherical to hemi-spherical 6
5. Laminae 4-pinnate to 4-pinnate-pinnatifid; costae, veins and laminar tissue between the veins abaxially glabrous; ultimate pinnules lanceate; sori ≤ 0.6 mm *Mucura alata*
 Laminae 3-pinnate-pinnatifid to 4-pinnate; costae, veins and laminar tissue between the veins abaxially with catenate hairs; ultimate pinnules ovate to oblong; sori ≥ 0.8 mm *Mucura baccifera* (not in Soth America)
6. Segments falcate, inequilateral, overlapping the pinnules above *Mucura tamandarei*
 Segments oblong, equilateral, not overlapping the pinnules above 7
7. Costules, veins, and laminar tissue between the veins adaxially with catenate hairs; sori ≥ 1.2 mm *Mucura globulifera*
 Costules, veins, and laminar tissue between the veins adaxially glabrous; sori ≤ 1 mm *Mucura tenera*

TAXONOMIC TREATMENT

Microlepia C.Presl, Tent. Pteridogr. 124, pl. 4, figs. 21–23. 1836. LECTOTYPE (designated by Smith 1875): *Microlepia polypodioides* (Sw.) C.Presl. (*Dicksonia polypodioides* Sw.) [= *Microlepia speluncae* (L.) T.Moore].

Scyphofilix Thouars, Gen. Nov. Madagac. 1. 1806, *nom. rej.* LECTOTYPE (designated by Farwell 1931): *Scyphofilix speluncae* (L.) Farwell (*Polypodium speluncae* L.; *Microlepia speluncae* (L.) T.Moore).

Plants terrestrial or rarely rupestral; rhizomes short to long creeping, with trichomes or bristles, branching ; petioles grooved, lacking epipetiolar buds, rarely aculeate; leaves large, erect, decompose, usually distant, or sometimes closely spaced, lamina 1–4-pinnate with strigose, acicular hairs, axes inalate; veins free, with slender apices; sori generally submarginal and protected by a lower indusium, the indusium half cup-shaped directed outward, or rarely the sori marginal, protected by

lower and upper indusia fused into a cup-shaped structure, and directed downwards; spores trilete with perispore ornamentation of rodlets.

Microlepia speluncae (L.) T.Moore, Ind. Filic. 93. 1857. *Polypodium speluncae* L., Sp. Pl. 2: 1093. 1753. *Aspidium speluncae* (L.) Willd., Sp. Pl., Ed. 4, 5(1–2): 269. 1810. *Davallia speluncae* (L.) Baker, Syn. Filic. 100. 1867. *Scyphofilix speluncae* (L.) Farw., Amer. Midl. Naturalist 12: 263. 1931. LectoTYPE (designated here): Ceylon, s.d., Hermann s.n. (BM-000621939, image!; isolectotype: BM-000621951, image!). (Fig. 1, map. 1).

For heterotypic synonymy see Sledge (1956), Proctor (1985), and Yuehong et al. (2013).

Plants terrestrial or rupestral. Rhizomes creeping, 0.5–1 cm diam, densely covered with orange-yellow, catenate hairs. Fronds determinate, 1–3 m long; petioles light to dark brown, 0.35–1 m × 0.5–1 cm, inermous, with small aerophores, densely covered with catenate hairs; laminae 3–4-pinnate, herbaceous, 1–2 m long, with alternate pinnae; rachises light to dark brown, adaxially sulcate, abaxially and adaxially with catenate hairs, with small aerophores; basal pinnae alternate, equilateral, lanceate, obtuse at the base, acute at the apex, (13–)23–50 cm × (4–)7–20 cm; costae abaxially and adaxially with densely light brown, catenate hairs, small aerephores, lacking adaxial wings; ultimate segments lanceate to ovate, 1–2 × 0.5–1 cm, inequilateral, with the first acroscopical segment reduced, proximally obtuse and sessile, distally round and crenate, shallow sinus not forming segments; costules and veins abaxially and adaxially with light brown catenate hairs, laminar tissue between the veins abaxially and adaxially with catenate and acicular hairs; lamina margins glabrous, entire and crenate to undulate at apex. Sori abaxial, 0.5–0.8 × 0.5–0.1 mm; indusia half cup-shaped directed downwards, with catenate hairs.

DISTRIBUTION.—Widespread in the Old World; probably introduced in the Netropics, where it is found on the Greater Antilles (except Puerto Rico) Trinidad (Proctor 1985), Ecuador (Tryon & Stolze, 1989), and Brazil, Bolivia, French Guiana, and Paraguay.

SPECIMENS EXAMINED.—FRENCH GUIANA. Cayenne: in sylvis montosis circa Cayenne Maouri, May 1837, *F. M. R. Leprieur 37* (US); in paludibus prope Cagnac, 1836, *F.M.R. Leprieur s.n.* (L-3568136).

BRAZIL.—Pará: Belém, bosque Rodrigues Alves, quadrante III, canteiro 104, 10 Feb 2004, *S.M. Rosário 45* (MG). Rio de Janeiro: Cachoeira de Macacu, estrada para a direita, 22°27'50.4"S, 42°45'21.6"W, 50 m, 18 Nov 2017, *P.B. Schwartsburd & M.P. Schwartsburd 4417* (VIC); Cachoeira de Macacu, Estrada Funchau para Mineradora de Água, 22°30'13"S, 42°46'35"W, 35 m, *P.B. Schwartsburd & M.P. Schwartsburd 4417* (VIC); Cachoeira de Macacu, Fazenda Vital Brazil, 22°33'S, 42°55'W, 100–200 m, 03 Jul 2014, *P.B. Schwartsburd et al. 3290* (VIC); Cachoeira de Macacu, Fazenda Vital Brazil, 22°33'S, 42°55'W, 100–200 m, 03 Jul 2014, *P.B. Schwartsburd et al. 3310* (VIC); Cachoeira de Macacu, Fazenda Vital Brazil, 22°33'S, 42°55'W, 100–200 m, 03 Jul 2014, *P.B. Schwartsburd et al. 3311* (VIC); Cachoeira de Macacu, Fazenda Vital Brazil, 22°33'S, 42°55'W, 100–200 m, 03 Jul 2014, *P.B. Schwartsburd et al. 3314* (VIC); Cachoeira de Macacu, Fazenda Vital Brazil, 22°33'S, 42°55'W, 100–200 m, 03 Jul 2014, *P.B. Schwartsburd et al. 3315* (VIC); Cachoeira de Macacu, street between Funchal and Guapiaçu, near Regua, 22°28'14"S, 42°45'21"W, 31 m, 18 Oct 2009, *K. Baber & J. Wesenberg KB273* (RB); Rio de Janeiro: Cachoeira de Macacu, street between Funchal and Guapiaçu, near Regua, 22°28'11"S, 42°45'36"W, 56 m, 08 Nov 2009, *K. Baber & J. Wesenberg KB340* (RB); Rio de Janeiro: Cachoeira de Macacu, street between Funchal and Guapiaçu, near Regua, 22°28'16"S, 42°45'42"W, 29 m, 16 Nov 2009, *K. Baber & J. Wesenberg KB404* (RB); Engenheiro Paulo de Frontin, Morro Azul, IZMA, trilha da Fazenda Santa Margarita, 29 Sep 2002, *E.F. Laranjeira et al. 5* (RB); Guapimirim, Estação Ecológica Estadual do Paraíso, trilha para Mariquitas, partindo do rio Paraíso, próximo a represa, Área FP08, 22°26'00"S, 42°50'00"W / 22°32'00"S, 42°56'00"W, 20 m, Nov 1991, *L. Sylvestre et al. 630* (RB); Guapimirim, Estação Ecológica Estadual do Paraíso, rio Paraíso, margem esquerda na direção da subida da trilha Estação Ecológica Estadual do Paraíso, 01 Dec 2008, *C.E.S. Jascone 1161* (RB); Guapimirim, Parque Nacional da Serra dos Órgãos, trilha das ruínas, 22°29'38.2"S, 43°00'04.9W, 390 m, 15 Apr 2011, *J.A. Lombardi et al. 8416* (RB); Guapimirim, Estação Ecológica Estadual de Paraíso, Centro de Primatologia do RJ, 22°26'00"S, 42°50'00"W / 22°32'00"S, 42°56'00"W, 250 m, 07 Nov 1984, *G. Martinelli & G. Bromley 10249* (RB); Magé, 3 km ESE Santo Aleixo, 22°35'S, 43°02'W, 50 m, 26 Oct 1980, *R. Guedes & L. Pereira-Gonzaga s.n.* (RB–224699). Nova Iguaçu, Reserva Biológica de Tinguá, ao longo da Estrada Real, 200–500 m, 26 Jan 2021, *P.B. Schwartusburd & N.T.L. Pena 4775* (VIC); Nova Iguaçu, Reserva Biológica de Tinguá, estrada para a

represa do Macuco, 200 m, 27 Jan 2021, *P.B. Schwartzburd & N.T.L. Pena 4805* (VIC); Nova Iguaçu, Reserva Biológica de Tinguá, núcleo Boa Esperança, caminho para estação Colomy, 100–300 m, 28 Jan 2021, *N.T.L. Pena & P.B. Schwartzburd 1034* (VIC); Nova Iguaçu, Reserva Biológica de Tinguá, trilha entre a Represa do Macuco e as piscinas e cachoeiras turísticas, 150–200 m, 27 Jan 2021, *P.B. Schwartzburd & N.T.L. Pena 4810* (VIC); Nova Iguaçu, Reserva Biológica de Tinguá, represa da Serra Velha, 300 m, 27 Jan 2021, *P.B. Schwartzburd & N.T.L. Pena 4814* (VIC); Petrópolis, Serra da Estrela, 22 Apr 1937, *J.G. Kuhlmann & A. Brade 15741* (RB); Rio de Janeiro, 22 Apr 1937, *J.G. Kuhlmann & A.C. Brade 15741* (VIC; RB); Rio de Janeiro, cultivado no Jardim Botânico, Obs.: Exemplar colhido por A. Ducke no Pará em 1932, 1935, *A.C. Brade 1933* (RB); Rio de Janeiro, Jardim Botânico do Rio de Janeiro, Arboreto, Canteiro 20H, 21 Jul 2003, *F.R. Simões et al. 59* (RB); Rio de Janeiro, Jardim Botânico do Rio de Janeiro, canteiro 26D, 09 Oct 2003, *F.R. Simões 97* (RB); Rio de Janeiro, Jardim Botânico do Rio de Janeiro, trilha pelo orquidário, 07 Jan 1994, *C.M. Mynssen 81* (RB); Rio de Janeiro, 17 Mar 1994, *C.M. Mynssen 84* (RB); Rio de Janeiro, Jardim Botânico do Rio de Janeiro, canteiro 2D, 03 Feb 1999, *C.G. Pinto 24* (RB); Rio de Janeiro, Parque Lage, 29 Sep 1994, *L. Kishida 3* (SJRP). Rio Grande do Sul: Tenete Portela, P.F.E. do Turvo, 20 Nov 1982, *R.M. Bueno 3946* (ICN). São Paulo: Teodora Sampáio, Parque Estadual Morro do Diabo, trilha Lago Verde, 22°32', 52°11', 300 m, 30 Jan 1995, *M.R. Pietrobon-Silva 1680* (SJRP).

BOLIVIA.—La Paz: Franz Tamayo, Parque Nacional Madidi, sector Sumpulo, pasando el río Mojos, entre Mojos y Pata., -14.581 -68.7760834, 976 m, 26 Sep 2009, *D. Alanes 115* (UC); Iturrealde, San Buena Ventura, -14.47, -67.58, 427 m, 13 Nov 1901, *R.S. Williams 1260* (US).

PARAGUAY.—Alto Parana: 1909, *K. Fiebrig 5779* (US); Sapucay: Paraguaria Centralis, 1913, *E. Hassler s.n.* (L-3568079).

Microlepia speluncae can be recognized by the 3 to 4-pinnate laminae, which are 1 to 2 m long. In the laminar tissue and veins, on both surfaces, there are catenate hairs, and in the laminar tissue between the veins there are also both catenate and acicular hairs. The sori is abaxial with only the lower indusia, which are half cup-shaped directed downwards, therefore differing from *Dennstaedtia* and *Mucura*, whose species present marginal sori, provided with lower and upper indusia. *Microlepia speluncae* differs from *M. strigosa* by fronds greater than 1 m wide (less

than 1 m wide); petioles light to dark brown (vs. yellow-brown to red-brown), and the abaxial surfaces of the costae and veins with light brown catenate hairs (vs. costae and veins bear abundant, colorless or pale brown, multicellular, non-glandular hairs).

Microlepia strigosa (Thunb.) C.Presl, Epimel. Bot. 95 (1851). *Trichomanes strigosum* Thunb. in Murray, Syst. Veg., ed. 14 (J. A. Murray) 941 (1784).

Plants terrestrial. Rhizomes long-creeping. Fronds determinate, 0.30–0.95 m long; Petioles yellow-brown to red-brown, 3.5–5 cm × 0.5–1 cm, inermous, with small aerophores; laminae 2–3-pinnate-pinnatifid, herbaceous, 0.4–0.6 m long, with alternate pinnae; basal pinnae alternate, equilateral, lanceate, obtuse at the base, acute at the apex, 7–20 cm × 3–10 cm; rachises, costae, costules and veins abaxially glabrous, and rachises, costae, costules and veins adaxially bear abundant, colourless or pale brown, multicellular, non-glandular hairs; lamina margins glabrous, entire and crenate to undulate at apex. Sori are submarginal, and the indusia are half-cup-shaped, attached on three sides, bearing hairs at the base and on the abaxial surface.

DISTRIBUTION.—For South America it is known only on Ilha de Páscoa in Chile. However, occurs naturally in India, Sri Lanka, China, south-east Asia, New Caledonia, Vanuatu, Fiji and Hawaii (Lüer 1984).

SPECIMENS EXAMINED.—CHILE. Ilha de Páscoa: Crater of Rano Kao, 23 Jan 1917, *C.J.F. Skottsberg* 125 (BISH); Shady slope near floor of crater of Rano Kao, 15 Jan 1935, *J.P. Chapin* 1005 (BISH); Tongariki, 15m, 19 Jan 1935, *J.P. Chapin* 1050 (BISH).

See comment in *Microlepia speluncaea*.

Mucura L.A. Triana & Sundue, Taxon 00: 00. 2022. TYPE: *Mucura globulifera* (Poir.) L.A.Triana & Sundue (*Polypodium globuliferum* Poir.; *Dennstaedtia globulifera* (Poir.) Hieron.).

Plants terrestrial or rarely epipetric; rhizomes long creeping, dichotomously branching, pubescent; petioles subterete, without an adaxial sulcus, with an omega-shaped vascular bundle, lacking epipetiolar buds; leaves large, erect, decompose, laminar axes alate, the wings decurrent onto the next order, lacking proliferous leaf buds; veins free, with slender apices; sori marginal, provided with lower and upper

indusia that together form a cylindrical, cup-shaped involucre; spores trilete, broadly ridged and verrucate, and sometimes with irregular reticles.

Mucura alata N.T.L. Pena & Schwartsb. ***sp. nov.*** TYPE: PERU. Dep. Loreto: above Pongo de Manseriche, mouth of Rio Santiago, in dense forest, 200 m, 19 Nov 1931, Y. Mexia 6127 (holotype: UC-509312, image!; isotypes: F-C0646142F, image!; MO-2056826, n.v.; NY-4008376, image!; US-1615549, image!; US-1615550, image!). (Fig. 2. A-E, Map. 2).

Dicksonia apiifolia var. *dissecta* Desv., Mém. Soc. Linn. Paris 6(2): 318 (1827).
Lectotype (designated here): PERU. *Pöppig s.n.* (LE-00007996, image!).

Plants terrestrial. Rhizomes creeping, sometimes dichotomously branched, 0.7–1.5 cm diameter, densely with ferruginous catenate hairs. Fronds determinate, 1–2 m long; petioles dark brown with densely catenate hairs at base, light brown and sparsely catenate hairs to glabrous towards the apex, 0.5–1 m × 0.5–1 cm, inermous, small aerophores; laminae 4-pinnate to 4-pinnate-pinnatifid, glossy, herbaceous, 0.50–1 m long, with alternate pinnae; rachis light brown to dark brown, adaxially sulcate, abaxially and adaxially sparsely with catenate hairs to glabrescent, more densely at base of axis, small aerophores, adaxially wings continuous pinna-rachises onto costae; basal pinnae alternate, lanceate, 30–60 × 10–20 cm, inequilateral, first pinnule reduced basioscopically, obtuse base, acute to acuminate apex; costae abaxially and adaxially with rarely light catenate hairs to glabrous, catenate hair is more dense from the base of the axis two to three times that of the costae, small aerophore, straight adaxially wings continuous costae onto costules; ultimate segments alternate, lanceate, 1–3 × 0.5–1.5 cm, inequilateral, with the first acroscopical segment reduced, proximally obtuse and pedicellate, distally round and dentate, deep sinus forming segments; costules and veins abaxially and adaxially glabrous, adaxially straight wings continuous pinna-rachises onto costae; laminar tissue between the veins abaxially and adaxially glabrous; laminar margins glabrous, base entire and dentate at apex; sori round 0.4–0.6 × 0.4–0.6 mm; indusia cylindrical, glabrous.

ETYMOLOGY.—The specific epithet “*alata*” is a reference to the wing present straight adaxially wings continuous pinna-rachises onto costae and costae onto costules.

DISTRIBUTION.—Venezuela, Colombia, Ecuador, Peru, Bolivia, and Brazil, in the sub-Adean/ Amazon forested regions; from 200 to 500 m.

SPECIMENS EXAMINED.—VENEZUELA. Carabobo: Puerto Cabello, San Esteban, 1893, *A. Mocquerys s.n.* (US-1431037). Zulia: Faldas inferiores, selva macrotérmica, a lo largo de la Quebrada Perayra, afluente del Río Tukuku (tocucu), Suroeste de la Mission de Los Angeles de Tukuku (tocucu), al Suroeste de Machiques, 450-475 m, 29 Aug 1967, *J.A. Steyermark s.n.* (F-99836).

COLOMBIA.—Magdalena: Santa Marta (Dist. Esp.), 26 Jan 1898, *H.H. Smith 2431* (TEX); 1898, *H.H. Smith 2431* [Magdalena: Santa Marta (Dist. Esp.), 26 Jan 1898, *H.H. Smith 2431*] (F).

ECUADOR.—Manabí: Wet forest, just inland from La Tuna, on coast, 30 Jun 1942, *O.L. Haught 3368* (US); Napo: Tena, Jatun Sacha Biological Station. 8 km east of Misahualli, 1°04'S, 77°36'W, 400 m, 9–19 Dec 1990, *A. Fay 2789* (UC).

PERU.—Loreto: Above Pongo de Manseriche, mouth of Rio Santiago, -4.466667°, -77.616667°, 200 m, 19 Nov 1931, *Y. Mexia 6127* (UC); 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, 12° 49' S, 69° 17' W, 260 m, 19 Nov 1931, *P.J. Barbour 5331* (F).

BRAZIL.—Rio de Janeiro: Mangaratiba, Reserva Rio das Pedras (Particular), trilha da Lagoa Seca, 16 May 1998, *C.M. Myssen 191* (RB; VIC); Rondônia: Colorado do Oeste, Linha 5, norte, 14 Apr 1992, *P.J. Pivetta 1527* (SJRP).

BOLIVIA.—Cochabamba: Ayopaya, Cruzando el rio Ipiri, subiendo a la cima de la serrania de Mosetenez, ladera superior, -16.05 -66.683333, 1112m, 21 Sep 2004, *H. Huaylla 1337* (UC); La Paz: Sud Yungas, 1 Jul 1939, *B.A. Krukoff 10331* (F).

The specimens of *Mucura alata* were traditionally classified as *Dennstaedtia bipinnata*. However, the name *Dennstaedtia bipinnata* has nomenclatural issues (see the comments of *Mucura baccifera*, below). In addition, we here recognize *Dennstaedtia bipinnata* sensu Tryon (1960; and Amparo-Triana 2022a) as two distinct taxa: *Mucura alata* occurring in South America and *Mucura baccifera* occurring in North America, Central America, and the Antilles.

Mucura alata differs from *M. baccifera* by deeply indented pinnules lanceate and more indented with deeper segments (vs. pinnules ovate to oblong and less indented with shallow segments); apex of pinnules with deep and wide tooth (vs. apex of pinnae with shallow and thin tooth); pinnules commonly glabrous, sometimes

with rare catenate trichomes (vs. frequent catenate trichomes); straight adaxially wings (vs. gently curved adaxially wings) measuring sori 0.4–0.6 × 0.4–0.6 mm (vs. 0.8–1 × 0.8–1 mm).

Mucura adiantoides has a homogeneous geographic distribution, occurring in the low lands of sub-Andean and Amazonian vegetation. Strangely, there is one collection from the state of Rio de Janeiro, southeastern Brazil, making an odd disjunctive distribution. This material (*Mynssen 191*) completely agrees with the morphology of the specimens from northern/western South America, and was previously identified as *Dennstaedtia bipinnata* by Mynssen & Windisch (2004) and Schwartsburd (2020). That sole collection from Rio de Janeiro is from an international resort (Rio das Pedras), which makes us wonder it is an alien species in Rio de Janeiro.

Mucura globulifera (Poir.) L.A.Triana & Sundue, Taxon in prep. 2022. Polypodium globuliferum Poir., Lam. & al., Encycl. 5: 554. 1804. *Dicksonia globulifera* (Poir.) O.Kuntze, Rev. Gen. Pl. 3(2): 378. 1898. *Dennstaedtia globulifera* (Poir.) Hieron., Engl. Jahrb. 114: 455. 1904. *Dicksonia altissima* (Poir.) Sm., Rees Encycl. 11. 1808, nom. nov.. HOLOTYPE: Plumier, Traité Foug. Amér., Pl. 30!, 1705. (Fig. 3. A-E, map. 3).

Dennstaedtia bradeorum Rosenst., Repert. Spec. Nov. Regni Veg. 22: 3. 1925. LECTOTYPE (designated by Tryon 1960): Costa Rica, A.C. Brade 634 (S–S-R-1444, image!); isolectotypes: GH-00020956, n.v., UC-405622, image!, NY-00149035, image!

Dicksonia exaltata Kunze, Bot. Zeitung (Berlin) 8: 59. 1850, nom. sup. *Dennstaedtia exaltata* Hieron., Bot. Jahrb. Syst. 34(4): 454. 1904. HOLOTYPE: Plumier, Traité Foug. Amér., Pl. 30!, 1705.

Dennstaedtia gracilis A.Rojas & Tejero, Revista Biol. Trop. 50(3-4): 1008, figs. 1–3. 2002. Type: MEXICO. Hidalgo: Mpio. de Molango, Km 118 de la Carretera Federal 105, entre Zacualtipan y Molango, A. Rojas and J.D. Tejero-Díaz 5376 (MEXU-01348008, image!; isotypes: MEXU-00359514, image!; MEXU-00359523, n.v., NY-01043117, image!, UAMIZ-0056107, image!, UAMIZ-0056108, image!, US-01105778, image!).

Dicksonia lagerheimii Sodiro, Crypt. Vasc. Quit. 50. 1893. *Dennstaedtia lagerheimii* (Sodiro) C.Chr., Index Filic. 217. 1905. LECTOTYPE (designated here): ECUADOR. Cresce en los bosques del Volcán “el Corazón”, 2000–2800m, May 1873, A.L. Sodiro s.n. (NY-00149030, image!; isolectotypes: P-00633289, image!, S-S-R-1482, image!, US-00066390, frag., image!).

Plants terrestrial. Rhizomes creeping, dichotomously branched, 1–2 cm diam, densely covered with orange-yellow (amber) to ferruginous, catenate hairs. Fronds determinate, 1–4 m long.; petioles light to dark brown, 1–1.20 m × 0.5–1 cm, inermous, with small aerophores, densely covered with catenate hairs at the base, glabrescent above; laminae 3-pinnate-pinnatifid, 1–3 m long (estimated), with alternate pinnae; rachises light to dark brown, adaxially sulcate, abaxially and adaxially with catenate hairs, more densely at the base of axes, with small aerophores, adaxially curved wings continuous pinna-rachises onto costae; basal pinnae alternate, lanceolate to ovate, 30–65 cm × 20–35 cm, equilateral, proximally obtuse to truncate, distally acute; costae abaxially densely light brown catenate hairs, adaxially sparsely light brown catenate hairs, catenate hair more densely at base of axis, small aerephore, curverd adaxially wings continuous costae onto costules; ultimate segments oblong to ovate, 1.5–2.5 × 0.8–1.5 cm, with the first acroscopical segment reduced, proximally obtuse and sessile, distally crenate to dentate, shallow sinus forming not segmentes; costules and veins abaxially densely light brown catenate hairs, adaxially sparsely light brown catenate hairs; laminar tissue between the veins abaxially densely catenate hairs, adaxially sparsely catenate hairs; lamina margins glabrous, entire and crenate to dentate at apex. Sori rounded, 1.2–1.5 × 1.2–1.5 mm; indusia spherical with catenate hairs.

DISTRIBUTION.—Antilles, Central America, Venezuela, Colombia, Ecuador, Peru, and Bolivia; from 1000 to 3000 m.

SPECIMENS EXAMINED.—VENEZUELA. Distrito Federal, Wooded valley, Los Venados, south side of Pico Avila, just north of Caracas, 1300–1500m, 12 Sep 1961, *R.M. Tryon & A.F. Tryon 5723* (US). Trujillo: Boconó, Parque Nacional Guaramacal, sector quebrada Honda-Pele Ojo, El Santuario, 1950-2100 m, Jan 2001, *B. Stergios & R. Caracas 18956* (URRP-42554, US).

COLOMBIA.—Santa Marta, United States of Colombia., 11.227559 -74.19111; 1898, *H.H. Smith 1118* (UC); Santander, Eastern Cordillera. Vicinity of Charta, 2000–2600 m, 1 Feb 1927, *E.P. Killip & A.C. Smith 19111* (US).

ECUADOR.—Chimborazo, Cañon of the río Chanchan, about 5 km. north of Huigra, 1524–1981 m, 19 Sep 1945, *W.H. Camp E-3462* (US); Napo, Quijos, Streamside and roadside banks between Baeza and Quijos, -0.45138, -77.93472, 1920 m, 02 Agu 1992, *A. Fay 3808* (UC).

PERU.—Cusco: La Convención, Dist. Huayopata, Huyro, Calquiña, -12.980833, -72.058611, 1750m, 27 Jun 2003, *E. Bonino 740* (UC); Cusco, La Convención, Dist. Santa Ana, Tunquimayo, -13.05, -72.93, 2800m, 12 Jun 2003, *E. Suclli Montañés 947* (NY); Junín: Pichis Trail, Yapas, 1350–1600m, 28 Jun 1929, *E. P. Killip 25473* (F).

BOLIVIA.—Tarija: Arce, 29.2 km S of Emborozú-Sidras road on road to Bermejo, (12.7 km S of Naranjo Agrio), -22.36666, -64.48333, 600 m, 21 Apr 1983, *J.C. Solomon 9990* (UC).

Additional Specimens Examined. DOMINICAN REPUBLIC. Prov. Azua: Civ. Santo Domingo, San José de Ocoa, Bejucal, in a cañada, 1300 m, 04 Mar 1929, *E.L. Ekman 11778* (NY-1903177); Cordillera Central, el Poblado rural de Pocilga, aprox. 1.5 km norte de Sabana de San Juan, 18°39'N, 70°44'O, 4000–4400 ft. [1200–1350 m], 27 Jul 1982, *T. Zanoni & J. Pimentel s.n.* (NY-1903168); Prov. La Estrelleta: Sierra de Neiba, 31-34 km by road NNW of La Descubierta, 11-14 km N of Angel Felix, Elevation 1850-1900 m, 21 Feb 1983, *J.T. Mickel 8751* (NY); Sierra de Neiba, along the Carratera International near the crest of the range. Along the Haitian border, vic. line between provinces of San Rafael and Independencia, 1700-2000 m, 7 Aug 1967, *G.J. Gastony et al. 590* (NY); Prov. La Pedernales: Sierra Bahoruco, Los Arroyos, 18.2590°N, 71.7395°W, 1700 m, 8 Dec 2018, *P.B. Schwartsburd et al. 4536* (VIC; VT); Prov. La Pedernales: Sierra Bahoruco, en la caleta internacional subindo hacia Los Arroyos, 18.25°N, 71.74°W, 8 Dec 2018, *P.B. Schwartsburd et al. 4535* (VIC; VT); Prov. La Pedernales: Sierra Bahoruco, Sector Las Abejas, 18.05°, 71.29°W, 7 Dec 2018, *P.B. Schwartsburd et al. 4519* (VIC; VT).

PUERTO RICO.—Florida: Bo. Florida Adentro, trail N up limestone hill, 0.5 km along dirt road E of old quarry at Rt 140, km 50.75, 150-250 m, 11 Jun 1992, *F. Axelrod et al. 4653* (UFRRP); Juana Diaz: Bo. Collores dirt road from end of Rt 512 (c. 3 km N of jct Rt 517), Wet mountain forest, 600-750 m, 4 Oct 1992, *F. Axelrod and I. Sastre 5262* (UPRRP).

Mucura globulifera differs from *M. tenera* by costules and veins adaxially with catenate hairs (vs. costules and veins adaxially glabrous), laminar tissue between the

veins abaxially densely catenate hairs, adaxially sparsely catenate hairs (vs. laminar tissue between the veins abaxially sparsely catenate hairs, adaxially glabrous), curved adaxially wings (vs. strongly curved adaxially wings); sori 1.2 to 1.5 mm (vs. sori 0.5 to 1 mm). *Mucura globulifera* are generally larger and more robust plants than *M. tenera*.

Mucura tamandarei (Rosenst.) N.T.L.Pena & Schwartsb. **comb. nov. pro** *Dennstaedtia tamandarei* Rosenst., *Hedwigia* 56: 359. 1915. LECTOTYPE (designated here): BRAZIL. São Paulo: Hector Legrú, Jan 1913, F. Tamadaré and A.C. Brade 5421 (NY-00815783, image!; isolectotypes: S-1447, image!; UC-442210, image!). (Fig. 3. F-J., map. 4).

Plants terrestrial. Rhizomes creeping, dichotomously branched, 0.5–1 cm diam, densely covered with bright orange-yellow (light brown) catenate hairs. Fronds determinate, 1–3 m long (estimated); petioles light to dark brown, sometimes with dark brown stains at the base, 0.5–1 m (estimated) × 0.3–0.8 cm, inermous, with small aerophores, densely covered with catenate hairs at the base, glabrescent above; laminae 3-pinnate-pinnatifid, herbaceous, 1–2 m long (estimated), with alternate pinnae; rachises light to dark brown sometimes with dark brown stains, adaxially sulcate, abaxially and adaxially with catenate hairs, more densely at the base of axes, with small aerophores, curved adaxially wings continuous pinna-rachises onto costae; ultimate segments falcate, 1–2 × 0.5–1 cm, with the first acroscopical segment reduced, sometimes overlapping the above pinnules, proximally oblong and sessile, distally falcate and dentate apex, shallow sinus forming segmentes; costules and veins abaxially with light brown catenate hairs, adaxially glabrous; laminar tissue between the veins abaxially with catenate hairs, adaxially glabrous; lamina margins glabrous, entire and dentate at apex. Sori rounded, 0.8–1.5 × 0.8–1.5 mm; indusia spherical with catenate hairs.

DISTRIBUTION.—Occurrence recorded for Bolivia, Brazil and Paraguay, occurring in the Brazilian states of Rio Grande do Sul, Santa Catarina, Paraná, São Paulo, Minas Gerais, and Mato Grosso do Sul.

SPECIMENS EXAMINED.—BOLIVIA. La Paz: Bautista Saavedra, 10 km de Camata hacia Apolo, -15.21666 -68.68333, 1300m, 25 Jun 1997, *M. Kessler 10336* (UC).

BRAZIL.—Mato Grosso do Sul: Corumbá. Morro Urucum, Córrego Banda Alta, 9°11'15.148"S, 57°34'53.081"W, 15 Jun 2001, *no col. 155* (UPCB-66497); Corumbá, Morro Santa Cruz, Córrego Bandalta, 14 mar 2001, *E.L.M. Assis 94* (BHCB, COR, RB). Minas Gerais: Ouro Preto, 1968, *L. Rennó s.n.* (BHCB-741); Ouro Preto, 1937, *J. Badini 131* (BHCB); Hervario [Herbário] "Jose Badini", 1936, *J. Badini 199* (RB); locality unknown, *Anonymous s.n., ex Herb. Damasio* (RB-36241). Paraná: Foz do Iguaçu, Parque Nacional do Iguaçu, estrada para o Poço Preto, 25°37'30"S, 54°25'30"W, 180 m, 2 Oct 2006, *P.H. Labiak et al. 3756* (UPCB). Rio Grande do Sul: Rio Grande, Estrada para o Cassino, 32°06'04"S, 52°10'09"W, 5 m, 25 May 2014, *F. Gonzatti 1246* (CESJ, UCS); Tenente Portela, P.F. Turvo, 09 jan 1982, *R. Bueno 3955* (ICN); Santa Catarina: Dr. Pedrinho, Véu da Noiva, 26,65347°S, 49,52498°W, 620 m, 28 mar 2008, *P.B. Schwartsburd et al. 1597* (UPCB); São Paulo: Analandia, Serra do Cruzeiro, 22°08'S, 47°40'W, 24–26 Oct 1986, *A. Salino 49 [49a]* (BHCB, UEC); Hector Legu-rib. dos Patos, jan 1993, *T.T. Toledo Jr. 377* (RB); Ypiranga, 1876, *H. Luederwaldt s.n.* (NY); State unknown: *C.F. von Martius s.n.* (RB-505417). PARAGUAY.—Asuncion, Trinidad, Ytororó - Ypaná. Monte sombrio húmedo, 31 Jan 1918, *C. Rojas 2714* (US).

Mucura tamandarei differs from *M. tenera* by the opposite to subopposite basal pinnae (vs. alternate), the costae abaxially with long, light brown, catenate hairs (vs. with short, light brown, catenate hairs), the falcate, inequilateral segments, which overlap the pinnules above (vs. oblong, equilateral segments, not overlapping the pinnules above) and curved adaxially wings (vs. strongly curved adaxially wings).

Mucura tenera (C.Presl) N.T.L.Pena & Schwartsb., **comb. nov. pro** *Dicksonia tenera* C.Presl, *Delic. Prag.* 188. 1822. *Dennstaedtia tenera* (C.Presl) Mett., *Ann. Sci. Nat., Bot., sér. 5, 2:* 261. 1864. *Dennstaedtia cicutaria* var. *tenera* (C.Presl) Fée, *Mém. Foug., 11. Hist. Foug. Antil.* 94. 1866. LECTOTYPE (designated here): BRAZIL. [Rio de Janeiro], in montosis ad Tijura [Tijuca] prope Rio de Janeiro, s.d., J.B.E. Pohl s.n. (PRC-455346, image!; probable isoelectotype: BR0000006870546, image! [as "Serra de Tingua, Pohl 4536"]). (Fig. 3. K-N., map. 5).

Plants terrestrial. Rhizomes creeping, dichotomously branched, 0.5–1 cm diam, densely covered with orange-yellow (amber) to ferruginous, catenate hairs. Fronds determinate, 1–3 m long; petioles dark brown at the base, light to dark brown

above, 0.5–1 m × (0.3–) 0.5–1 cm, inermous, with small aerophores, densely covered with catenate hairs at the base, glabrescent above; laminae 3-pinnate-pinnatifid, 1–2 m long, herbaceous, with alternate pinnae; rachises light to dark brown, adaxially sulcate, abaxially and adaxially with catenate hairs, more densely at the base of axes, with small aerophores, adaxially wings continuous pinna-rachises onto costae; basal pinnae alternate, lanceolate, 30–53 cm × 12–28 cm, truncate at the base, acute at the apex, equilateral; costae abaxially with light brown catenate hairs, adaxially glabrescent, catenate hair more densely at base of axis, small aerephore, strongly curved adaxially wings continuous costae onto costules; ultimate segments oblong to ovate, 1–2 × 0.5–1 cm, proximally obtuse and sessile, distally round and crenate, shallow sinus not forming segmentes, strongly curved adaxially wings continuous costae onto costules; costules and veins abaxially moderately light brown catenate hairs, adaxially glabrous; laminar tissue between the veins abaxially sparsely catenate hairs, adaxially glabrous; lamina margins glabrous, entire and crenate at apex. Sori rounded, 0.5–1 × 0.5–1 mm; indusia hemi-spherical to tubular with catenate hairs.

DISTRIBUTION.—Southern and eastern South America, mainly in the Atlantic Forest, in Argentina, Brazil Paraguay, and Uruguay; from sea level to 2000 m.

SPECIMENS EXAMINED.—BRAZIL. Bahia: Itanhém, Estrada de Itanhém a Batinga, 17°8'17"S, 40°25'34"W, 29 Dec 2004, *A.M. Amorim et al. 4654* (CEPEC); Jussari, R.P.P.N. Serra do Teimoso, 15°09'15.8"S, 39°31'24.2"W, 260–400 m, 02 Nov 2002, *A Salino & J.G. Jardim 8189* (BHCB). Ceará: Baturité, Sítio São João, 14 Dec 1939, *J. Eugenio 43* (RB); Maranguape, Serra de Maranguape, Morro (Serra) da Pedra Rajada, 3°54'05"S, 38°43'12"W, 750 m, 8 Apr 2011, *P.B. Schwartsburd 2463* (VIC); Maranguape, Serra de Maranguape, trilha para Pedra Rajada, 3°50'S, 38°43'W, 650 m, 18 Feb 1998, *M. Almeida-Neto 371* (SJRP). Espírito Santo: Cariacica, Reserva Biológica Duas Bocas, Represa Velha, 20°15'31"S, 40°29'51"W, 170 m, 11 Jun 2010, *A. Salino et al. 14864* (BHCB); Castelo, Parque Estadual Mata das Flores, 20°36'49"S, 41°10'05"W, 120 m, 24 Jun 2008, *A. Salino et al. 13486* (BHCB); Castelo, Parque Estadual Mata das Flores, 20°36'41"S, 41°10'11"W, 120 m, 27 Jun 2008, *A. Salino et al. 13669* (BHCB); Castelo, Parque Estadual Mata das Flores, 20°35'S, 41°10'W, 400 m, 28 Feb 2016, *P.B. Schwartsburd et al. 3715* (VIC, VIES, VT); Castelo, Parque Estadual Mata das Flores, 20°35'S, 41°10'W, 400 m, 28 Feb 2016, *P.B. Schwartsburd et al. 3702* (VIC); Pancas, Lajinha, Sítio Floresta,

19°9'16.7"S, 40°47'15.5"W, 150 m, 26 Aug 2009, *A. Salino 14451* (BHCB). Mato Grosso do Sul: Corumbá, Morro Santa Cruz, nascente do córrego Bandalta, 15 Sep 2001, *E.L.M. Assis 286* (BHCB). Minas Gerais: Apr 1842, *A.M. Claussen 1242* (RB); Araponga, Parque Estadual Serra do Brigadeiro, Pico do Boné, 20°40'30"S, 42°26'50"W, 1500 m, 23 Feb 2014, *P.B. Schwartsburd et al. 3069* (VIC); Araponga, Parque Estadual Serra do Brigadeiro, Pedra do Pato, 20°39'34.6"S, 41°00'39.9", 1228 m, 11 Dec 2018, *N.T.L. Pena et al. 762* (VIC); Arcos, Fazenda Faroeste, Margem esquerda do Rio São Miguel, 20°15'54"S, 45°40'13"W, 700-800 m, 25 May 2003, *P.H.A. Melo & F.A. Carvalho 690* (BHCB); Arcos, Fazenda Faroeste, próximo a margem direita ao Rio São Miguel, 20°16'08.8"S, 45°39'38.3"W, 650-700 m, 11 Apr 2004, *A. Salino et al. 9569* (BHCB); Arcos, Fazenda Faroeste, ao lado da Calciolândia, 20°16'14"S, 45°39'34"W, 650-700 m, 15 Jul 2007, *A. Salino et al. 13107* (BHCB); Bandeira, área a ca. 14 km da sede da Bandeira, na divisa com a Bahia, 15°49'30.2"S, 40°31'15.8"W, 500–550 m, 06 Oct 2003, *A. Salino et al. 9123* (BHCB); Brazópolis, divisa com o estado de São Paulo, próximo a Paiol Grande, 22°39'01"S, 45°39'56"W, 1265 m, 30 Oct 2008, *T.E. Almeida et al. 1568* (BHCB); Brazópolis, divisa com o estado de São Paulo, próximo a Paiol Grande, 22°39'01"S, 45°39'56"W, 1265 m, 30 Oct 2008, *T.E. Almeida et al. 1574* (BHCB); Camanducaia, Mata do Chico Rei, 1405 m, 07 Feb 2002, *L.C.N. Melo 202* (BHCB); Carangola, 1907, *A.T. Baeta-Neves s.n.* (OUPR-10638); Caratinga, Estação Biológica de Caratinga, Trilha da Gameleira, 12 Dec 1995, *A. Salino et al. 2388* (BHCB); Caratinga, Estação Biológica de Caratinga, Trilha da Gameleira, 25 Mar 2000, *A. Salino et al. 5146* (BHCB); Coronel Pacheco, Fazenda da Argentina, 450 m, 29 May 1944, *E. P. Heringer 1269* (RB); Delfim Moreira, Estrada que leva da Barreira até o Distrito de São Francisco e Campos do Jordão, 22°34'43"S, 45°15'52"W, 1775 m, 01 Nov 2008, *T.E. Almeida et al. 1629* (BHCB); Delfim Moreira, Fazenda do Onça, trilha do Pico do Carrasco, 22°37'02"S, 45°20'W, 2005 m, 17 Mar 2011, *A.L. Gasper et al. 2678* (BHCB); Gonçalves, fragmento de floresta da Pousada Lua de Pedra, 22°41'6.9"S, 45°55'21.2"W, 1650 m, 20 Jul 2007, *A. Salino et al. 12825* (BHCB); Itabirito, Serra da Moeda, 20°19'26.03"S, 43°55'55.59"W, 1157 m, 09 Sep 2006, *G. Heringer 107* (BHCB); Januária, Vale do rio Peruaçu, 15°07'23"S, 44°14'37"W, 20 Jul 1997, *A. Salino 3251* (BHCB); Lima Duarte, Nascente do Pirapitinga, 11 Oct 1989, *L. Krieger & M. Brugger 24242* (BHCB; CESJ); Marliéria, Parque Estadual do Rio Doce, trilha Vinhático, 29 Mar 1996, *A. Salino 2666* (BHCB); Marliéria, Parque Estadual do

Rio Doce, trilha Vinhático, 13 Sep 1997, *A. Salino & L.C.N. Melo 3418* (BHCB); Marliéria, Parque Estadual do Rio Doce, trilha Vinhático, 02 Mar 1999, *A. Salino 4463* (BHCB); Nova Lima, Estação Ecológica Catarina, 20°04'09.8"S, 44°00'07.0"W, 08 Sep 2001, *L.C.R.S. Teixeira et al. 41* (BHCB); Ouro Preto, 1935, *J. Bradini 131* (BHCB; RB); Ouro Preto, Parque Estadual do Itacolomi, Fazenda do Manso, 1328 m, 29 Oct 2003, *L.B. Rolim & L. Silva 76* (BHCB; OUPR); Ouro Preto, Parque Estadual do Itacolomi, Fazenda do Manso, 1328 m, 29 Dec 2003, *L.B. Rolim & L. Silva 76* (BHCB; OUPR-17.165); Paraisópolis, Parque Ecológico do Brejo Grande, 22°34'74"S, 45°48'52"W, 1265 m, 31 Oct 2008, *T.E. Almeida et al. 1607* (BHCB); Santa Maria do Salto, Distrito de Talismã, Fazenda Duas Barras, 16°24'16.5"S, 40°03'27.4"W, 750-850 m, 09 Oct 2003, *A. Salino 9179* (BHCB). Paraná. Araucária, REPAR Petrobrás, 13 Feb 2001, *R. Kersten & S.M. Silva 565* (UPCB); Apucarana, Pirajó, Jun 1951, *G. Tessmann s.n.* (RB- 76834); Campina Grande do Sul, Parque Estadual Pico Paraná, Morro Camapuã, 25°15'S, 48°52'W, 950-1150 m, 20 Dec 2008, *J.B.S. Pereira & F. Marinero 412* (VIC, UPCB); Cândói, 18 Jun 2004, *P.B. Schwartsburd et al. s.n.* (UPCB-54419); Cerro Azul, Rio Ponta Grossa, 16 Jul 1992, *G. Hatschbach and O.S. Ribas 59449* (HUCS); Francisco Beltrão, Parque Municipal Irmão Sirilo, 25 Oct 2006, *P.B. Schwartsburd et al. 1115* (UPCB); Fênix, Parque Estadual Vila Rica do Espírito Santo, 23°54'54"S, 51°57'13"W, 350 m, 09 Nov 2004, *P.H. Labiak et al. 3450* (UPCB); Foz do Iguaçu, Parque Nacional do Iguaçu, Rodovia Cataratas, 25°37'33"S, 54°28'26"W, 193 m, 12 Sep 2010, *R.S. Viveiros & A.G. Pastro 153* (BHCB); Foz do Iguaçu, Parque Nacional do Iguaçu, trilha Poço Preto, 25°36'15"S, 54°24'06"W, 196 m, 19 Sep 2010, *R.S. Viveiros & A.G. Pastro 163* (BHCB); Foz do Iguaçu, Parque Nacional do Iguaçu, trilha Poço Preto, 31 Apr 2013, *M. Lautert & A. Salino 254* (BHCB); Foz do Iguaçu, Margem do Rio São João Paraná, 25 May 1949, *A.P. Duarte 1884* (RB); Iretama, Rio Muquião, 24°24'26"S, 52°02'33"W, 14 Nov 2013, *E.D. Lozano & E.L. Siqueira 1832* (RB); Londrina, Parque Estadual Mata dos Godoy, 15 Dec 1992, *A. Salino et al. 1598* (UEC); Ortigueira, 02 Dec 2011, *C. Michelin 1170* (UPCB); Palotina, Linha São Vicente, 03 Dec 1992, *P.J. Pivetta & M.R. Silva 1551* (SJRJ); Rio Branco do Sul, Represa da Votoran, 04 Jul 2004, *A. Dunaiski Jr. and W. do Amaral 2621* (UPCB); Santa Maria do Oeste, Rio Feio, 25 Aug 2001, *G. Hatschbach 72281* (RB); São João do Triunfo, Fazendo Experimental da UFPR, 23 Jan 2005, *P.B. Schwartsburd et al. 642* (UPCB); Tibagi, Parque Estadual do Guartelá, 870 m, 18 May 2011, *C. Michelin et al. 1106* (UPCB);

Três Barras do Paraná, Fazenda Guarani, 22 Feb 1993, *M.C.M. Marques s.n.* (BHCB-31508; UPCB-20822); Telemaco Borba, Parque Ecológico da Klabin, Trilha Ecológica, 29 Jun 2004, *C.R. Sakagami and K. Sakagami 112* (UPCB); idem, 19 Jan 2005, *C.R. Sakagami and N.K. Sakagami 257* (UPCB). Pernambuco. Jaqueira, Usina Colônia, RPPN Feri Caneca, Mata do Córrego do Guariba, 8°43'S, 35°50'20"W, 650 m, 17 Mar 2011, *P.B. Schwartzburd & S. Dejavu 2338* (VIC); Jaqueira, Mata da Serra do Quengo, 08°42'37"S, 35°50'01"W, 600-700 m, 25 Mar 2003, *R.A.G. Gueiros 47* (UFP!). Rio de Janeiro. Guapimirim. Estação Ecológica do Paraíso, 22°28'58"S, 42°55'3"W, 175 m, 24 Sep 2010, *K. Baber 555* (RB); Itatiaia, Parque Nacional do Itatiaia, cerca de 800 m antes do hotel Ipê, 10 Feb 2020, *N.T.L. Pena and P.B. Schwartzburd 906* (VIC); idem, *N.T.L. Pena and P.B. Schwartzburd 904* (VIC); idem, *N.T.L. Pena P.B. Schwartzburd 903* (VIC); Itatiaia, Parque Nacional do Itatiaia, trilha do Hotel Simon para o Três Picos, 29 Sep 2005, *L. Sylvestre 1840* (RB); Mangaratiba, Reserva Rio das Pedras, trilha do Corisco, 06 Jan 2000, *C.M. Mynssen 303* (RB); Mendes, Fazenda São José das Paineiras, 03 Dec 1993, *C.M. Mynssen 72* (RB); Nova Iguaçu, Estrado do Ouro/ estado dos escravos, 22°53'66"S, 43°40'76"W, 200-500 m, 25 Jan 2021, *N.T.L. Pena & P.B. Schwartzburd 996* (VIC); Nova Iguaçu, Estrado do Ouro/ estado dos escravos, 22°53'66"S, 43°40'76"W, 200-500 m, 26 Jan 2021, *N.T.L. Pena & P.B. Schwartzburd 1010* (VIC); Nova Iguaçu, Estrado do Ouro/ estado dos escravos, 22°53'66"S, 43°40'76"W, 200-500 m, *N.T.L. Pena & P.B. Schwartzburd 1020* (VIC); Nova Iguaçu, Estrado do Ouro/ estado dos escravos, 22°53'66"S, 43°40'76"W, 200-500 m, 27 Jan 2021, *N.T.L. Pena & P.B. Schwartzburd 1031* (VIC); Nova Iguaçu, Núcleo Boa Esperança, Colomy, 22°53'66"S, 43°40'76"W, 100-300 m, 28 Jan 2021, *N.T.L. Pena & P.B. Schwartzburd 1043* (VIC); Nova Iguaçu, Núcleo Boa Esperança, Colomy, 22°53'66"S, 43°40'76"W, 100-300 m, 28 Jan 2021, *N.T.L. Pena & P.B. Schwartzburd 1043* (VIC); Pão de Açúcar, 02 Aug 1936, *A.C. Brade 15339* (RB); Rio das Ostras (IBAMA), antiga estrada do Cardoso, Reserva Biológica União, 23 Aug 2000, *J.M.A. Braga 6178* (RB); Tijuca, Parque Nacional da Tijuca, Mata do Pai Ricardo, 300–500 m, 10 Jun 1976, *J.P.P. Carauta 2070* (RB); Idem, trilha dos estudantes, primeiro trecho, 22°57'36"S, 43°16'34"W, 337 m, 31 Jul 2018, *M. Bicalho et al. 65* (RB). Rio Grande do Sul. Barracão, Parque do Espigão Alto, 11 Jun 1988, *C. Mondin 391* (HAS); Caxias do Sul, Vila Olivia, 07 Jan 2000, 780 m, *A. Kegler 520* (UCS); Caraá, Fraga, APA Municipal de Caraá, 20 May 2009, *R.M. Senna et al. 1366* (HAS); Caxias do

Sul, Estrada Santa Lúcia do Piaí, 12 Jul 1988, *C. Mondin 430* (HAS); Caxias do Sul, Vila Oliva, 780 m, 17 Jan 2003, *A. Kegler 1526* (HUCS); Derrubadas, Parque Estadual do Turvo, 440 m, 17 Jul 2004, *C.D. Inácio 28* (ICN); Erechim, Parque Longines Malinowski, 25 Feb 1994, *A. Butzke et al. s.n.* (HUCS-10969); Esmeralda, 29 Set 1982, *R. Bueno 3958* (ICN); Esmeralda, E.E. Aracuri, 31 Jul 1982, *R. Bueno 3952* (ICN); Farroupilha, Salto Ventoso, 16 Nov 1998, *C. Glufke s.n.* (HAS-40599); Garibaldi, São José de Costa Real, estrada para São Pantaleão, 29°13'19"S, 51°37'57"W, 29 Sep 2019, *F. Gonzatti 5135* (VIC; UCS); Gramado, Vila Olivia, 29 Nov 1993, *R.M. Bueno s.n.* (ICN-155003; ICN-193926; VIC-54739; VIC-54733); Gramado, Vila Olivia, 29 Nov 1993, *R. Bueno s.n.* (ICN-155003); Jaguarí, 31 May 1991, *R. Bueno 4127* (ICN); Itaara, RPPN Fundação Motã, 29°00'00"S, 53°44'17"W, 340 m, 10 Set 2016, *F. Gonzatti and M.D. Ferrarese 2725* (HUCS; UFP); Jaguarí, Morro da Gruta, 31 May 1991, *R. Bueno 4130* (ICN; VIC); Monte Belo do Sul, Linha 80 da Leopoldina, 28 Agu 2011, *F. Gonzatti 127* (HUCS); Morro Reuter, São José do Herval, 736 m, 24 Apr 2002, *C.R. Lehn 300* (HASU, HUCS); Não-Me-Toque, zona rural, ca. De % Km do centro, 28°28'00"S, 52°45'00"W, 12 Oct 2009, *P.G. Windisch 10524* (ICN; VIC); Santa Cruz do Sul, 03 Nov 1903, *C. Jürgens and A. Stier 29a* (HUCS); Santa Cruz do Sul, 08 Feb 1903, *C. Jürgens and A. Stier 28* (HUCS); Santa Maria, Reserva Biológica Corsan, 20 Sep 1991, *R.M. Bueno s.n.* (ICN-155027; ICN-155028; VIC-54732; VIC-54734); Santa Maria, mata marginal do rio Ibicuí-Mirim, área de brragem Saturnino de Brito, 06 Jul 1982, *O. Bueno 3528* (HAS); Santa Maria, Silveira Martins, 28 Mar 2008, *P.B. Schwartsburd 1500* (UPCB; VIC); São Francisco de Paula, *P.G. Windisch 10801* (ICN); São Francisco de Paula, 19 Apr 1982, *R. Bueno s.n.* (ICN-155018); São Francisco de Paula, Linha Juá, 29°08'05"S, 50°48'10"W, 828 m, *F. Gonzatti 2331* (VIC; UCS); São Vendelino, Estrada de acesso ao Morro Canastra, 29°24'S, 51°15'W, 600 m, 01 May 2001, *F.P.F. Athayde & P.G. Windisch 937* (HASU, SJRP); Silveira Martins, Rota Gastronômica, chácara do Mezzomo, 28 Mar 2008, *P.B. Schwartsburd 1500* (SMDB; VIC); Selbach, entroncamento de Colorada em direção a Selbach, 28°37'S, 52°57'W, 13 Oct 2009, *P.G. Windisch 10587* (ICN); Sinimbu, Acima da Serra, entre Sinibu e Pinhal de Santo Antônio, 25 Jan 2009, *P.B. Shwartsburd et al. 1910* (VIC); Idem, Santa Cruz, 5 Jan 1942, *P.R. Reitz 103* (RB); Tapera, 1 km do entroncamento de Espumoso, 28°38'S, 52°51', 13 Oct 2009, *P.G. Windisch 10596* (ICN); Tenente Portela, P.F. Turvo, 15 Jan 1982, *R.M. Bueno 3954* (ICN; VIC); Tenente Portela, P.F. Turvo, 07 Jul 1982,

R.M. Bueno 3956 (ICN; VIC); Tenente Portela, P.F. Turvo, 26 Oct 1982, *R.M. Bueno 3957* (ICN); Tenente Portela, P.F. Turvo, 09 Jan 1982, *R.M. Bueno s.n.* (ICN-155022); Tenente Portela, P.F. Turvo, 07 Jul 1982, *R. Bueno 3956* (ICN); Tenente Portela, Parque Estadual Florestal do Turvo, na estrada para Porto Garcia, 09 Nov 1983, *J. Mattos et al. 25298* (HAS; VIC); Tenente Portela, Parque Estadual Florestal do Turvo, na estrada para Porto Garcia, 23 Dec 1987, *N. Bassan & J. Meyer s.n.* (HAS-55952; VIC-54730); Terra de Areia, Morro Azul, 29°16'58"S, 49°56'59"W, 487 m, 13 Oct 2013, *M.H. M.H. Nervo and F.S.C. Velho 1338* (ICN). Santa Catarina. Anita Garibaldi, Cachoeira Primeira, 27°43'24"S, 51°12'45"W, 866 m, 13 Dec 2008, *A. Stival-Santos & S. Silveira 70 29* (FURB); Araranguá, Turvo, ao lado do caminho na mata virgem, 11 Nov 1943, *R. Reitz C 196* (RB); Blumenau, RPPN Bougerkopf, trilha da cachoeira, 27°00'22"S, 49°04'21"W, 302, 06 Feb 2013, *L.A. Funez 1711* (FURB); Jaraguá do Sul, Campo Alegre, 26°21'S, 49°8'W, 140 m, 10 Feb 2008, *M.J.M. Christenhusz et al. 4745* (UPCB); Nova Teutônia, 20 Dec 1944, *F. Plaumann 539* (RB); Piratuba, Linha Navegantes, 06 Jun 2000, *A.D. Nilson s.n.* (HAS-40601); Praia Grande, P.N. Aparados da Serra, 5 Agu 2009, *P.B. Schwartsburd et al. 2254* (VIC); Quilombo Manoel Mayer, Propriedade Onorino Cesco, 26°45'16"S, 52°45'09", 422 m, 14 Mar 2018, *F. Gonzatti and O. Cesco 4264* (HUCS); Riozinho, Bom Retiro, 1.000 m, 24 Dec 1948, *Reitz 2791* (RB); Tunápolis, Canaleta, 26°57'17.00"S, 53°35'43.00"O, 590 m, 02 Mar 2009, *M. Verdi et al. 1647* (BHCB); Xavantina, Linha Rondon, 27°00'00"S, 52°22'48.00"W, 649 m, 25 Mar 2009, *S. Dreveck & F.E. Carneiro 757* (BHCB). São Paulo. Cedral, Fazenda Dallas, 20°54'S, 49°16'W, 09-06 Nov 1999, *R. Bousi & T. Vasconcelos s.n.* (SJRP-21280); Cedral, sítio ca. 5 km de Cedral, barranco afluente do rio São Domingo, 23°53'S, 49°22'W, 23 Jul 1995, *A.P.N. Soares 20* (SJRP-15553); Iporanga/ Apiai, Parque Estadual Turístico do Alto Ribeira (PETAR), Núcleo Santana, 24°32'22"S, 48°41'36"W, *F.F.F. Mazzeiro & A. Soller 660* (UPCB); São Paulo, Ypiranga, *H. Luederwaldt s.n.* (VIC-54602); Mirassol, Grota de Mirassol, 06 Dec 1987, *A. Salino 224* (BHCB); Mirasol, Grota de Mirasol, 23 Nov 1994, *F.R. Torres* (SJRP); Mogi das Cruzes, Serra do Itapeti, 700 m, 22 Oct 2005, *V.A.O. Dittrich et al. 1378* (BHCB); São José do Barreiro, Parque Nacional da Serra da Bocaina, 1000 m, 05 Jan 2008, *P.H. Labiak et al. 4267* (UPCB); Vinhedo, Fazenda Rio da Prata, 23°02'S, 46°58'W, 590 m, 28 Jul 1993, *C.E. Rodrigues Jr. & M.R. da Silva 518* (SJRP); Ypiranga, *H. Luederwaldt s.n.* (SFP-; VIC-54.602).

PARAGUAY.—Alto Paraná, Estancia, Rio Bonito: Forest II, around Rio Bonito on eastern side of property, 25°37'55"S, 54°48'17"W, 240 m, 27 Nov 1995, *E.M. Zardini & L. Guerrero 43780* (RB); Canindeyú, 17 Dec 1982, *A. Schinini 23161* (F); Departamento de Guaira, região da Cascata se Syî, 23-24 May 1989, *P.G. Windisch 5484* (SJRP); Itapua, El Tirol, 19.5 km. by road +/- Encarnacion., 14 Oct 1981, *M. Foster 81-21* (UC).

URUGUAY.— Tacuarembó, Gruta de los Cuervos, 18 Jan 1944, *D. Legrand 3313* (US); Tacuarembó, Gruta de los Cuervos, 11 Jan 1965, *D. Puerto 3940* (US).

ARGENTINA.—Córdoba: Rio Cuarto, 26°37'51"S, 54°6'12"O, Bobbosque Terrestrial, 10 Oct 2011, *M. Arana & A. Oggero s.n.* (VIC-41909); Misiones: Concepcion, 14 Feb 1947, *H. Huidobro 5435* (RB); Jujuy, Cainguás, Salto Encantador, prox arroyo Tabay, 06 Aug 1950, *E. Schwindt 4718* (RB); San Javier, 14 Feb 1947, *R. Huidobro 5435* (RB); San Pedro, Parque Providencial Esmeralda, 15 Mar 2011, *A. Yañez and C. Macluf 91* (VIC, LP); San Pedro, Parque Provincial Cruce Caballero, 26°33'S, 54°03'W, 600 m, 17 Dec 2006, *R. Kersten 1117* (UPCB); San Pedro. Puerto Piraý, 06 Jul 1948, *G.J. Schwarz 6817* (RB); Tucuman: Famailla, Caspinchango, 20 Sep 1949, *B. Sas 118* (RB); Rio Chico, entre col. 17 y Arroyo Aradito, 28 Mar 1942, *T. Meyer 4378* (RB).

For difereentiation with other species, see the comments of *Mucura globulifera* and *M. tamandarei*.

4. EXCLUDED SPECIES FROM THE STUDY AREA

Mucura baccifera (Poir.) N.T.L.Pena & Schwartsb. **comb. nov. pro** Polypodium bacciferum Poir. *Encycl. [J. Lamarck & al.] 5: 554. 1804. Dicksonia globuligera* Desv. *Mém. Soc. Linn. Paris 6: 317. 1827, nom. nov. LECTOTYPE* (designated here): Plumier, *Traité Foug. Amér., Pl. 31!, 1705. (Fig. 2. F-J).*

Dicksonia adiantoides Humb. & Bonpl. ex Willd. *Sp. Pl. 5: 488. 1810., nom. sup. Dennstaedtia adiantoides* (Humb. & Bonpl. ex Willd.) T.Moore, *Ind. Fil. xcvi. 1857. Syntypes: Venezuela, Caripe, Humboldt & Bonpland s.n. (B-W-20165-020, image!); Puerto Rico, Ventenat s.n. (MA-213495, image!); Puerto Rico, Ventenat s.n. (B-W-20165-010, image!, US-00745250, frag., image!).*

Plants terrestrial. Rhizomes long creeping, sometimes dichotomously branched, 0.5–0.1 cm diameter, densely with light brown to ferruginous catenate hairs. Fronds determinate, ca. 1–3 m long; petioles light brown to dark brown, at base dark brown, 0.60–1.5 m × 0.5–1 cm, with densely ferruginous catenate hairs, above with sparsely ferruginous catenate hairs to glabrescent, inermous, small aerophores; laminae 3-pinnate-pinnatifid to 4-pinnate, glossy, herbaceous, 0.50–2 m long, with alternate pinnae; rachises light brown to dark brown, adaxially sulcate, abaxially and adaxially sparsely with catenate hairs to glabrescent, more densely at base of axis, small aerophores; basal-pinnae alternate, equilateral, lanceate, proximally obtuse, distally acute to cuneate, 25–60 × 14–27 cm; costae abaxially moderate with ferruginous catenate hairs, adaxially glabrous with gently curved wings continuous along the costae and at the costules, catenate hair is more dense from the base of the axis are similar to the costae, small aerephore, gently curved adaxially wings continuous costae onto costules; ultimate pinnules alternate, ovate to oblong, 1–3 × 0.5–1.5 cm, inequilateral, with the first acrosopical segment reduced, proximally ovate to oblong and sessile, distally round and dentate apex, deep sinus forming segments; costules and veins abaxially moderate with light brown to ferruginous catenate hairs, adaxially glabrous; laminar tissue between the veins abaxially moderate with light brown to ferruginous catenate hairs, adaxially glabrous; laminar margins glabrous, base entire and dentate at apex; sori cylindrical 0.8–1 × 0.8–1 mm ; indusia cylindrical, glabrous, abaxially rarely with sparsely catenate hairs.

DISTRIBUTION.—Antilles and Central America.

SPECIMENS EXAMINED.—HONDURAS. Atlántida: Miramar-San Isidro, Zona de Amortiguamiento, 10 Km SO de Tela, 350 m, 20 Nov 1989, *R. Cruz 393* (TEFH). El Paríso: Rio arriba, 8 km de la ciudad, 820 m, 10 Jan 1982, *A. Jorge & N. Escobar 238* (TEFH). Francisco Morazán: Reserva Biológica Montaña de Misoco, 100 Km al Noroeste de Tegucigalpa, Sendero Los Olingos, Comunidad de Monte Galan, Municipio de Guaimaca, 1729 msnm, UTM 0520691 y 1617044, 11 Oct 2012, *R. Hernández & R. Moreno 1092* (TEFH). Olancho: Montana Piedra Blanca al E de Catacamas, 1000 m, 17 Nov 1988, *M.A. Palacios* (TEFH); Represa de Santa Maria del Real, 15 Km, NO, de Catacamas, 1000 m, 30 Apr 1988, *C. Nelson & R. Andino 10148* (TEFH).

MEXICO.—Veracruz: San Andrés Tuxtla, Ejido Bairro Lerdo, faldas del Volcán San Martín Tuxtla, 18°34N, 95°10W, 1000 m, 11 Aug 2005, *T. Krömer & A. Acebey 2473*

(XAL); San Andrés Tuxtla, SE slopes of Volcán San Martín Tuxtla, 12 Km, N of San Andrés Tuxtla, 18°33'N, 95°12'W, 1100 m, 1 Jul 1982, *G. Diggs et al. 2701* (XAL); Tepetzintla, La Pagua a 25 km al NE de Tepetzintla em la falda de la sierra de otontepec, 700 m, 29 Aug 1981, *G. Castillo O. & A. Benavides M. 2336* (XAL).

PANAMA.—Province of Chiriqui: Burica Peninsula, 8 mi West of Puerto Armuelles, 200 m, 2 Mar 1973, *R.L. Liesner 351* (TEFH).

PUERTO RICO.—Adjuntas: Along PR Rt. 518 at Logo de Garzas, growing in wooded slopes along by stream, 18.15405°N, 66.74039°W, 545 m, 17 May 2011, *R. James-Hickey et al. #11-45 s.n.* (UPRRP-50904; MU); Bosque Estadual de Monte Guilarte, intersection of hwy 131 and hwy 518, 18.14317N, 66.76839W, 1100 m, 11 Jan 2016, *S. Fawcett & A.A. Reznicek 470* (UPRRP). Arecino: Río Arriba, Río Abajo Forest Reserve, at sinkhole Midway along pilot road for proposed Rt 10, 225 m, 19 Aug 1994, *A. Axelrod 8260* (UPRRP). Cayey: In sylvia ad Planaje, 25 Sep 1885, *P. Sintenis 2391* (UPRRP-51739). Ciales: Los Tres Picachos, up E slopes along jeep road (from Rt 149 near jct Rt 157) through old coffee plantation, 700–800 m, 12 Jul 1992, *F. Axelrod & B. Axelrod 4831* (UPRRP). Jayuya: Las Tres Palmas, trail off Rt 533, Km 5.4, and then up slope, 700–850 m, 10 Mar 1991, *F. Axelrod & J. Wells 2181* (UPRRP). Maricao: Bo. Maricao Afuera, along Maricao River, upstream from the Fish Hatchery, 18°10'11"N, 66°59'10"W, 460–580 m, 11 Jan 1996, *P. Acevedo-Rdgz et al. s.n. [7748]* (UPRRP-32065). Olimpia: Bo. Olimpia: Finca Olimpia, Headwaters of Río de la Ciénaga, 18°08.37'N, 66°42.57'W, 720 m, 24 Sep 2005, *J.D. Ackerman 3952* (UPRRP). Peñuelas: Bo. Rucio, ridge just S of Cerro Garrote, Wet mountain forest, 18°07.56'N, 66°42.02'W, 975 m, 27 Feb 2011, *F. Axelrod & Y. García 14700* (UPRRP); Prov. Pedernales, Parque Nacional Sierra de Bahoruco, Sector Las Abejas, 18.05°N, 71.29°W, 07 Dec 2018, *P.B. Schwartsburd et al. 4525* (VIC; VT). San Lorenzo: Bo. Jagual, Summit area of Cerro Gregorio, 18°08.96N, 65°00.66'W, 625–640 m, *F. Axelrod & R. Thomas 11860* (UPRRP). Serro Bauruco: Prov. Barahona, Polo, Loma La Jó, Bosque Nublado, al topo de la Loma, próximo a las antenas, 6 Dec 2018, *P.B. Schwartsburd et al. 4514* (VIC; VT); Serro Bauruco: Prov. Barahona, Polo, Loma La Jó, Bosque Nublado, al topo de la Loma, próximo a las antenas, 6 Dec 2018, *P.B. Schwartsburd et al. 4515* (VIC; VT). Vicinity of Utuado: Roadside bank, 07 Mar 1915, *E.G. Britton 5214* (NY). Utuado: Bo. Caonillas Arriba, Cerro Morales, NW slope, along trail to summit, second-growth mountain forest with relict forest, 750 m, 21 Feb 1993, *F. Axelrod et al. 5788* (UPRRP). Yauco: Bo. Río

Prieto, Monte Membrillo, along trail on N slope above jeep road from Hacienda Assunción, 850-950 m, -3 Apr 1994, F. Axelrod & A. Axelrod 7652 (UPRRP).

The specimens of *Mucura baccifera* were traditionally named as *Dennstaedtia bipinnata* (Sw.) T.Moore by many authors, such as (= *Mucura bipinnata*) by Tryon (1960), Navarrete and Øllgaard (2000), Mickel and Smith (2004), and Triana-Moreno *et al.* (2022a). These authors also regarded a Neotropical distribution for this species. Here, we consider the South American specimens as distinct from those of Central America and Antilles – for differentiation, see the comments of *Mucura alata*. Furthermore, the lectotype of *Dennstaedtia bipinnata* at the MA herbarium does not have adaxial wings, and, in fact, represents a specimen of *Dennstaedtia dissecta* (see excluded names, below). The previous “isotypes” at herbaria B and US correspond to the traditional concept of “*Dennstaedtia bipinnata*” (i.e., they have adaxial wings), but, since they are taxonomically distinct from the lectotype at MA, they can no longer be considered isolectotypes.

The name *Dennstaedtia adiantoides* has also been applied to this taxon, but *D. adiantoides* is a superfluous name, as in Willdenow (1809) original description, he included *D. bipinnata* in the synonymy, hence its type (MA-213495) – see also Maxon (1938) and Mickel and Smith (2004). Thus, the oldest valid name for the present taxon is *Polypodium bacciferum*, here combined in *Mucura*. For differentiation with other species, see the comments of *Mucura alata*.

5. EXCLUDED NAMES

Mucura bipinnata (Cav.) L.A.Triana & Sundue, Taxon *in prep.* 2022. *Dicksonia bipinnata* Cav., Descr. Pl. 174. 1802. *Dennstaedtia bipinnata* (Cav.) Maxon, Proc. Biol. Soc. Wash. 51: 39. 1938. Lectotype (designated by Tryon 1960): Puerto Rico, *Ventenat s.n.* (MA-213495, image!) = ***Dennstaedtia dissecta*** (Sw.) T. Moore – see the comments of *Mucura baccifera* above.

6. DOUBTFUL NAMES

Dicksonia punctulata Poir., Lam. Encycl. Suppl. 2: 475. 1811. Holotype: *Hb. Desfontines* (P? – not found). We have not found the type of this name.

7. ACKNOWLEDGEMENTS

Pena thanks Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) for the PhD scholarship, the International Association for Plant Taxonomy (IAPT) for the "Grant 2020", and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES-PROAP) for the graduate grant; we also thank the students, Curators, and staff at Herbarium VIC, the Curators and staff of the herbaria which sent loans or were visited (see material and methods), and Joelcio Freitas and Reinaldo Pinto for the illustrations.

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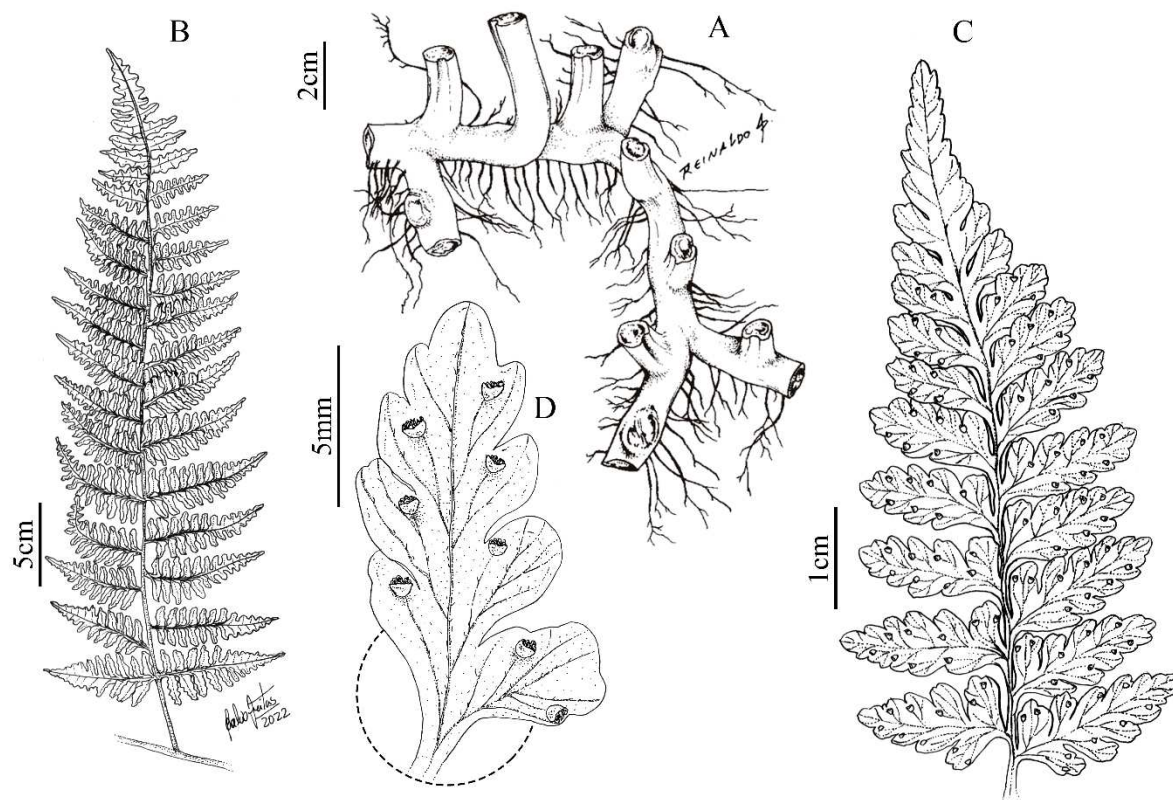


Figure 1. A-D. *Microlepidia speluncae*. A. rhizomes; B. basal pinnae; C. pinnule, abaxially; D. ultimate segments with indusia half cup-shaped directed downwards.

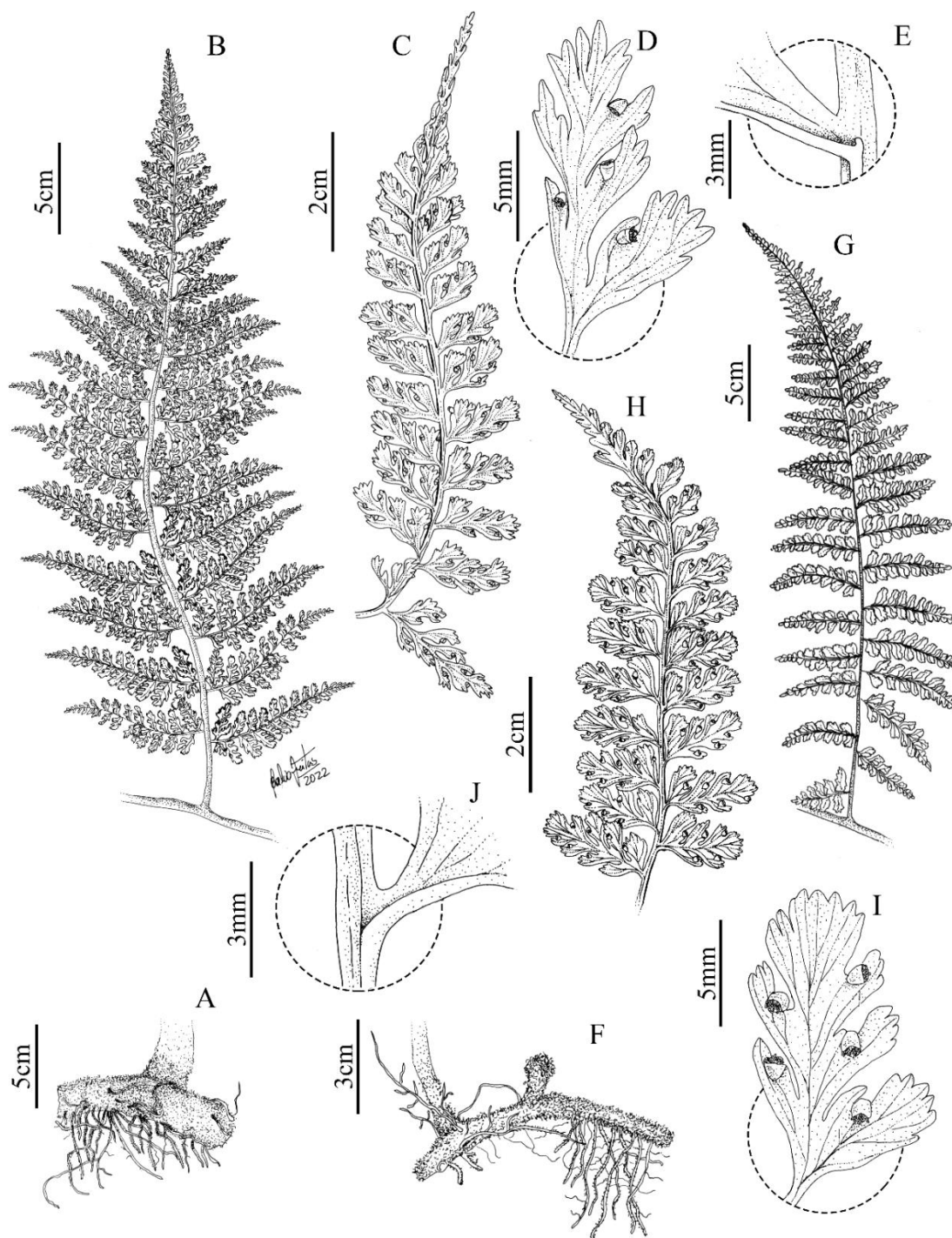


Figure 2. A-E. *Mucura alata*. A. rhizomes; B. basal pinnae; C. pinnule, abaxially; D. ultimate segments with apex of pinnules with deep and wide tooth, and indusia cylindrical; E. segment, adaxially, showing straight wings. F-J. *Mucura baccifera*. F. rhizomes; G. basal pinnae; H. pinnule, abaxially; I. ultimate segments with apex of pinnae with shallow and thin tooth, and indusia cylindrical; J. segment, adaxially, showing curved wings.

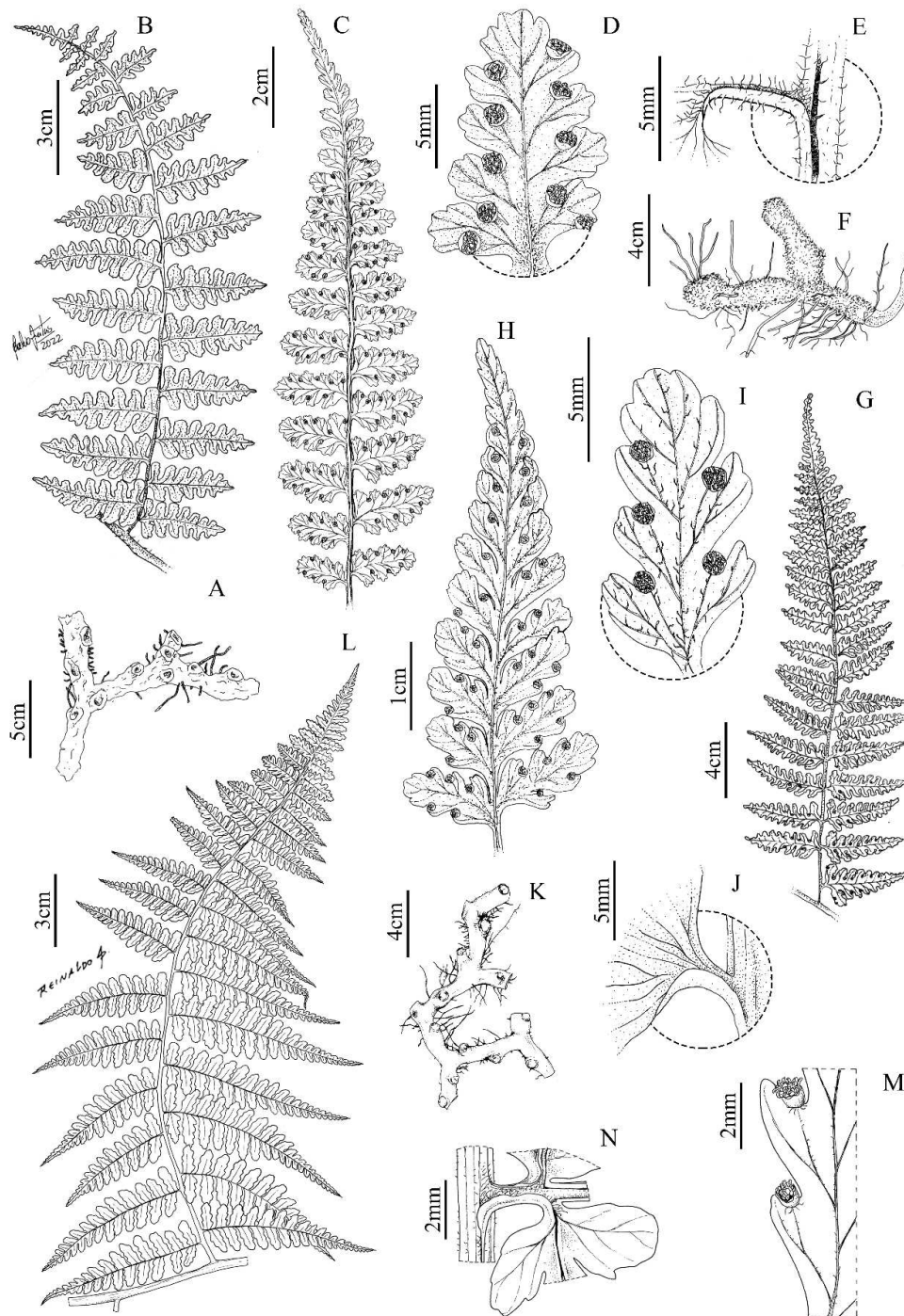
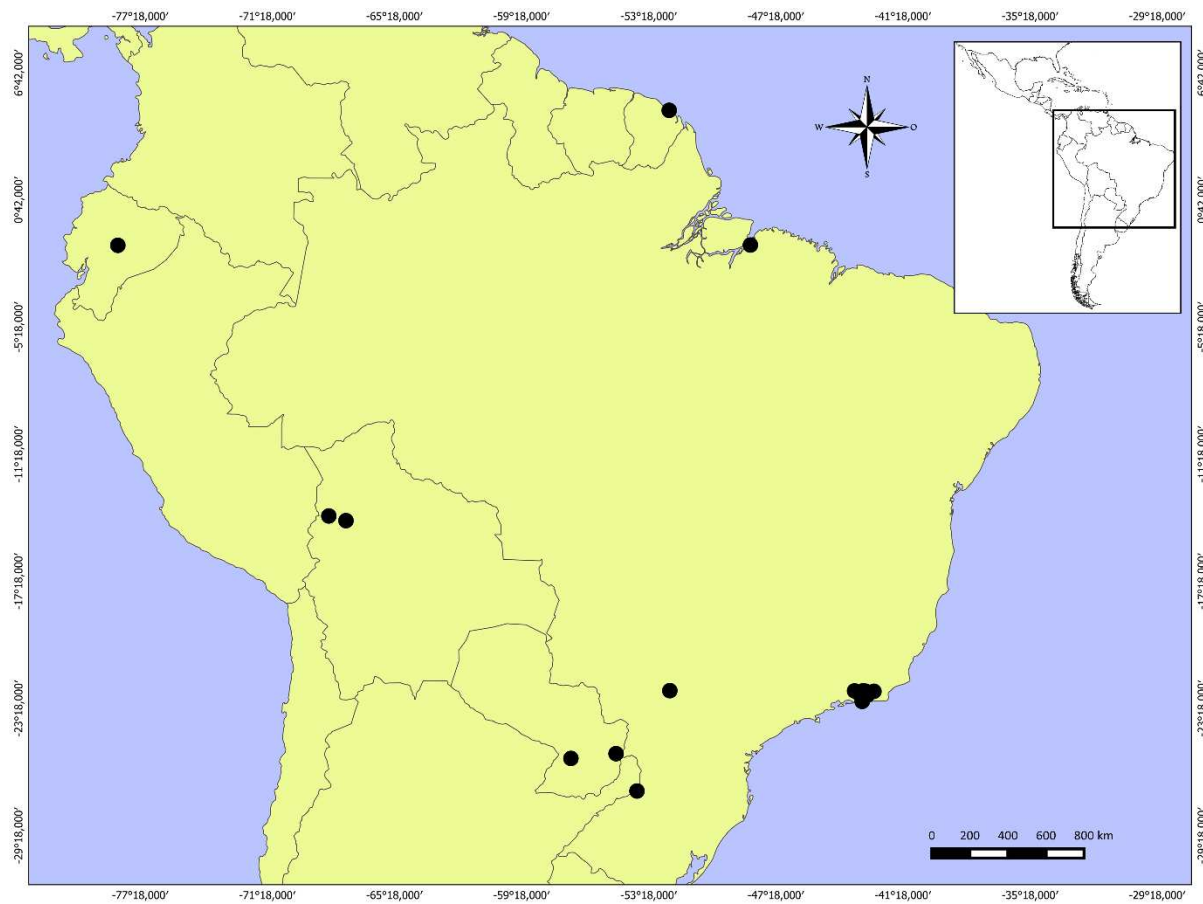
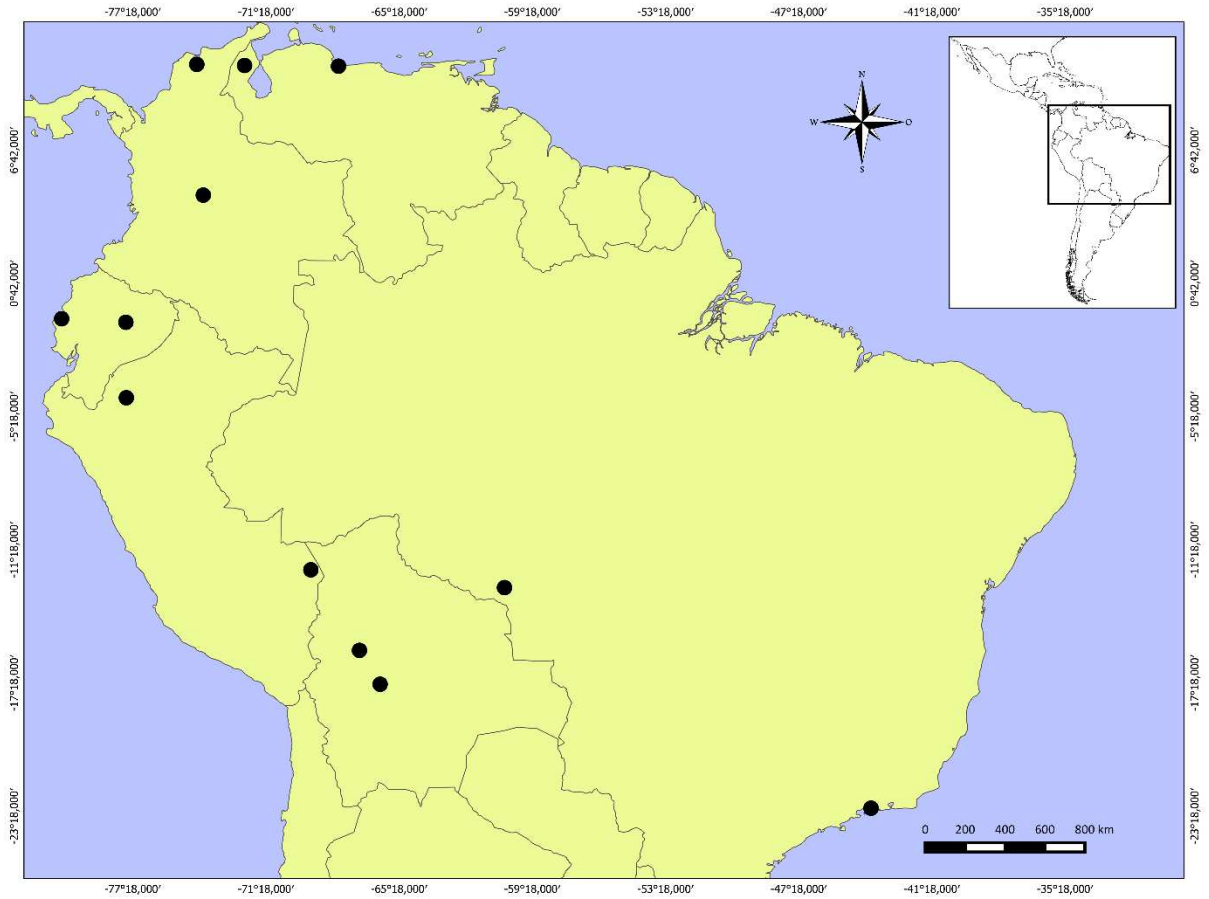


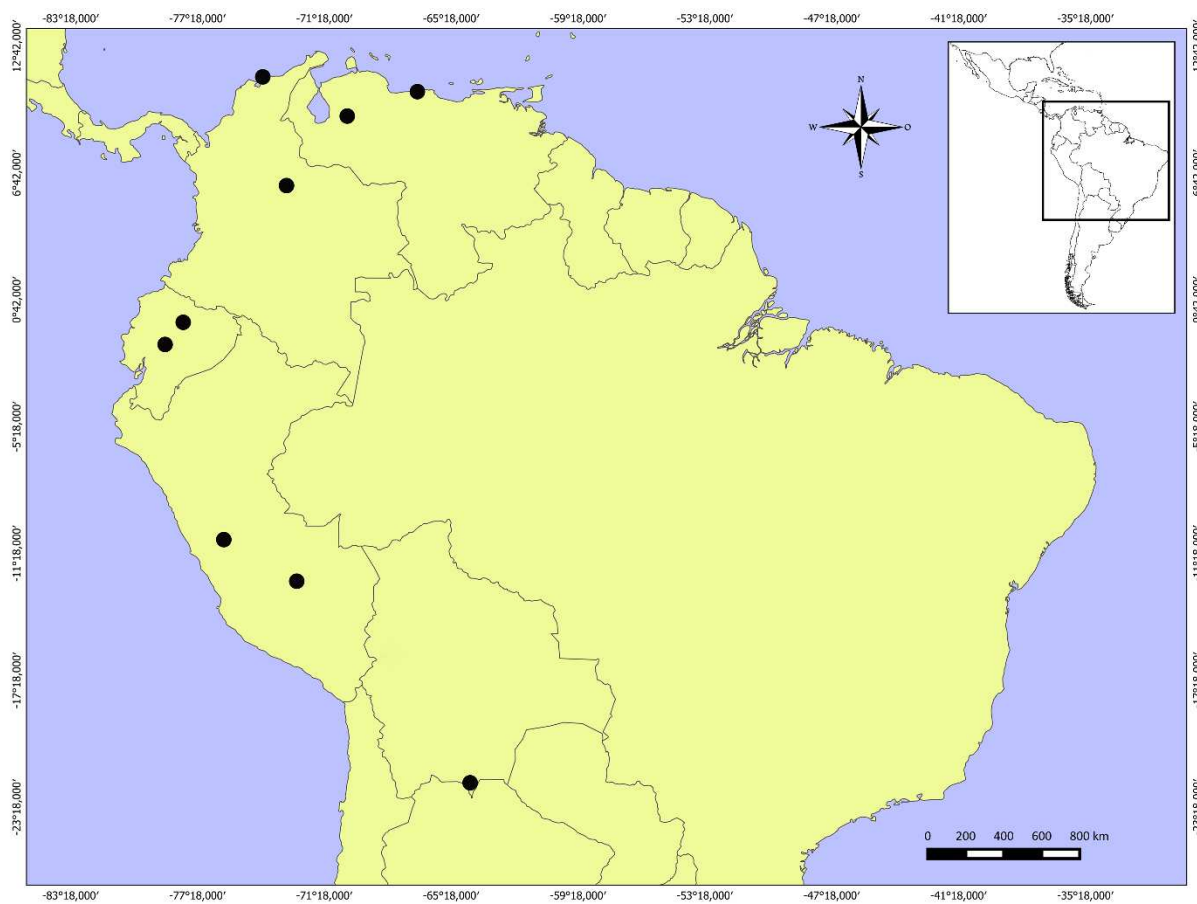
Figure 3. A-E. *Mucura globulifera*. A. rhizomes, dichotomously branched; B. basal pinnae; C. pinnule, abaxially; D. ultimate segments with indusia spherical; E. segment, adaxially, showing curved wing. F-J. *Mucura tamandarei*. F. rhizomes, dichotomously branched. G. basal pinnae; H. pinnule, abaxially; I. ultimate segments with indusia spherical. J. segment, adaxially, showing curved wing. K-N. *Mucura tenera*. K. rhizomes, dichotomously branched; L. basal pinnae; M. ultimate segments with indusia hemi-spherical to tubular; N. segment, adaxially, showing strongly curved wing.



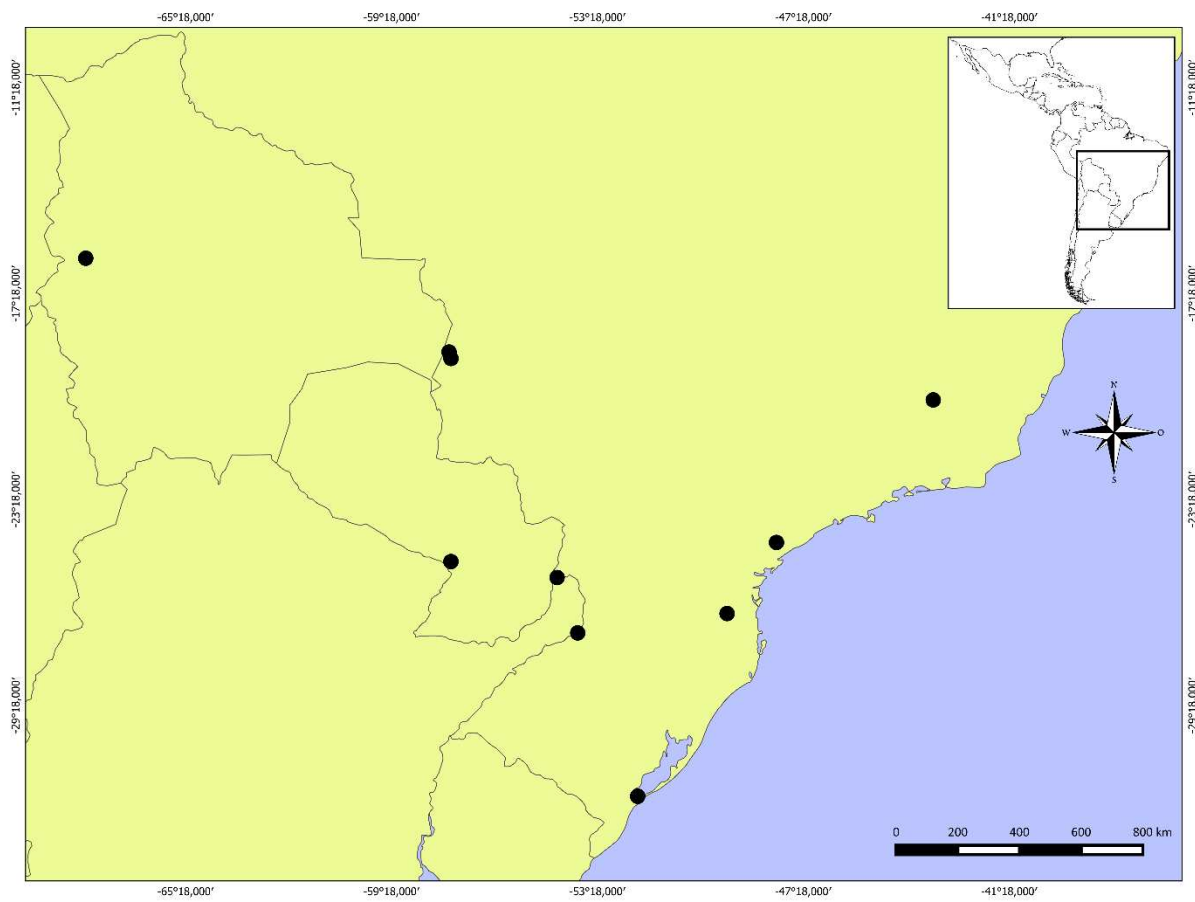
Map 1. Distribution of *Microlepia speluncae*.



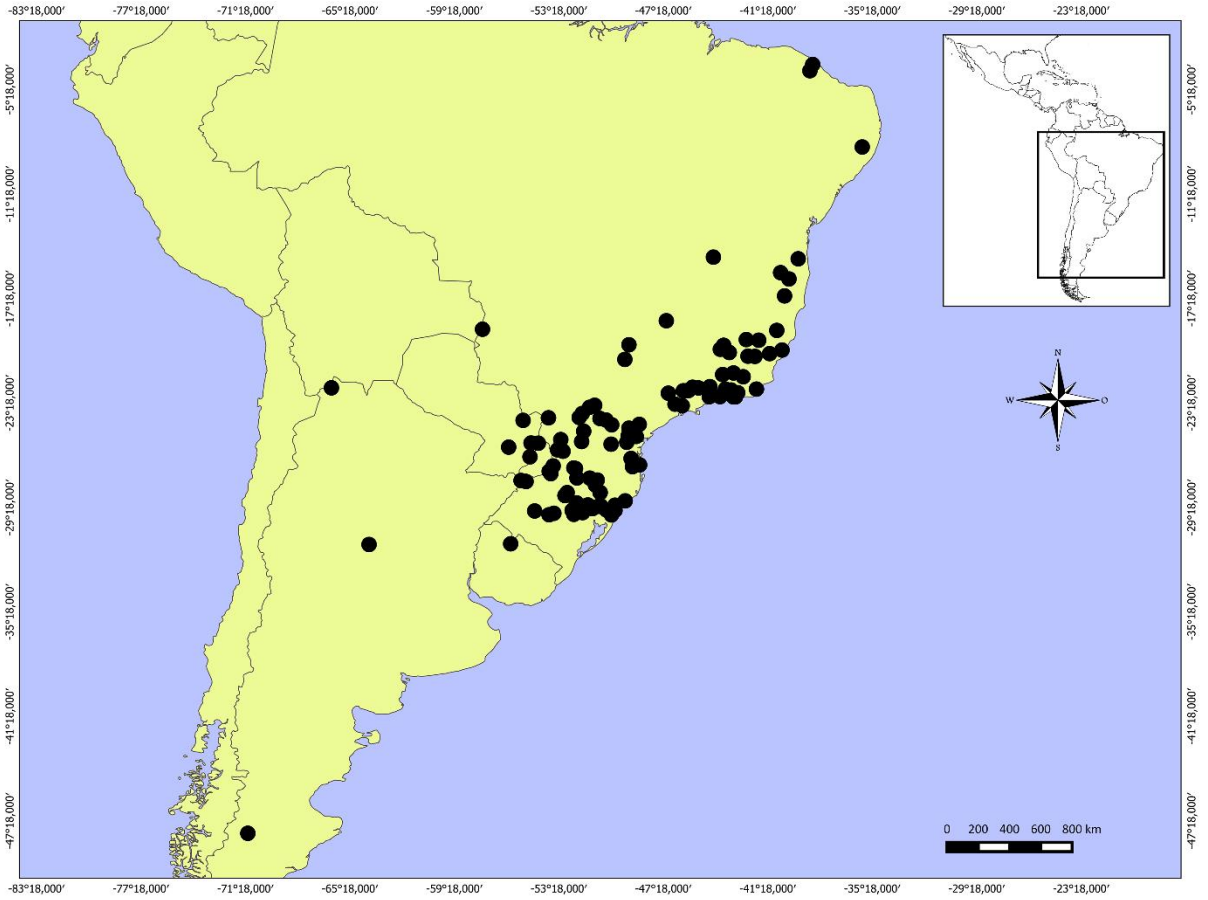
Map 2. Distribution of *Mucura alata*.



Map 3. Distribution of *Mucura globulifera*.



Map 4. Distribution of *Mucura tamandarei*.



Map 5. Distribution of *Mucura tenera*.

Capítulo II. Pena, N.T.L.; Zuquim, G. & Schwartzburd, P.B. (2022). Beware my spines: a new spiny fern (*Dennstaedtia*, Dennstaedtiaceae) from central and western Amazonia. Publicado na ACTA Amazonica, 52: 142–148. Doi: <https://doi.org/10.1590/1809-4392202103661>

Capítulo II. Beware my spines: a new spiny fern (*Dennstaedtia*, *Dennstaedtiaceae*) from central and western Amazonia

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ABSTRACT

A new spiny fern belonging to the genus *Dennstaedtia* is described from Brazilian and Peruvian Amazonia. *Dennstaedtia aculeata* (sp. nov.) is the third spiny species known for the genus, and the first in South America. It is compared with another Neotropical spiny *Dennstaedtia*, *D. spinosa*. We also present images, illustrations and a distribution map of the specimens, and discuss the habitat preference of the species towards nutrient-richer soils and spinescence in the family.

KEYWORDS: *Dennstaedtia aculeata*, *Dennstaedtia spinosa*, Dennstaedtiaceae, leptosporangiate ferns, Neotropics

RESUMO

Uma nova espécie de samambaia espinhosa do gênero *Dennstaedtia* é descrita para a Amazônia brasileira e peruana. *Dennstaedtia aculeata* (sp. nov.) é a terceira espécie espinhosa conhecida para o gênero e a primeira na América do Sul. A comparamos com outra *Dennstaedtia* espinhosa da região neotropical, *D. spinosa*. Também apresentamos imagens, ilustrações e um mapa de distribuição dos espécimes, e discutimos a preferência da espécie por habitats de solos ricos ou relativamente ricos em nutrientes e a espinescência na família.

PALAVRAS-CHAVE: *Dennstaedtia aculeata*, *Dennstaedtia spinosa*, Dennstaedtiaceae, samambaias leptosporangiadas, região neotropical

1. INTRODUCTION

Dennstaedtia Bernh. belongs to the family Dennstaedtiaceae, a Cretaceous lineage that diverged early among the leptosporangiate ferns (Schwartzburd *et al.* 2020). The genus has pantropical distribution and comprises about 70 species (PPG I 2016), but it has been recovered as polyphyletic by recent molecular phylogenetic studies (Perrie *et al.* 2015; Shang *et al.* 2018; Schwartzburd *et al.* 2020). Due to the absence of DNA sequences of the type of the genus (*D. flaccida* (J.R. Forst.) Bernh.), Neotropical species are still classified into *Dennstaedtia* s.l., but into the informal group of “*Patania*” (sensu Schwartzburd *et al.* 2020).

As currently circumscribed, *Dennstaedtia* is defined by creeping rhizomes, which are glabrous or with catenate hairs; by the large fronds to 4 m long, with 1–5-pinnate laminae; and by the marginal, discrete sori, that are borne at the tip of single veins, and which are protected by the fusion of the inner and outer indusia, becoming a purse-shaped, a cupshaped, cylindrical, or an hemi-globose structure (Tryon and Tryon 1982; Mickel and Smith 2004; Schwartzburd 2020).

For the Americas, Tryon (1960) (see also Tryon and Tryon 1982), made the first major contribution to *Dennstaedtia* studies, in which nine species were recognized. From the 2000s onwards, taxonomic novelties were reported including the description of seven new species to science and some species brought back from synonymy (e.g., Navarrete and Øllgaard 2000; Rojas-Alvarado and Villalobos-Brenes 2018). In addition, new occurrence records were reported in Mesoamerica and South America (Yañez *et al.* 2014; Rojas-Alvarado and Villalobos-Brenes 2018).

Currently, 15 species of *Dennstaedtia* are recognized for the Amazon region (Tryon and Stolze 1989; Cremers and Kramer 1991; Smith and Kramer 1995; Navarrete and Øllgaard 2000; Murillo-Pullido *et al.* 2008; Zuquim *et al.* 2009; Prado *et al.* 2017; Schwartzburd *et al.* 2017). Of these, the 15 species are known to occur in western Amazonia (Tryon and Stolze 1989; Navarrete and Øllgaard 2000; Prado *et al.* 2017) and three of them have known occurrence for the Guiana Shield (Smith and Kramer 1995).

During a review of *Dennstaedtia* specimens in the herbarium of Instituto Nacional de Pesquisas da Amazônia - INPA (Manaus, Brazil), we found a spiny specimen collected 15 years ago in central Amazonia which had been reported as *Dennstaedtia* sp. (Zuquim *et al.* 2009). Spines are fairly common in

Dennstaedtiaceae, but only in the subfamily Hypolepidoideae. Within Dennstaedioideae and *Dennstaedtia* s.l., spines have been previously reported only in the paleotropical *D. scandens* (Blume) T. Moore and in *D. spinosa* Mickel from Mexico and Honduras (Moran 1995; Mickel and Smith 2004; Yan *et al.* 2013; Reyes-Chávez *et al.* 2021), but never in South America. We later identified further spiny *Dennstaedtia* material among unidentified specimens collected in the Peruvian Amazon and deposited in the herbarium of the University of Turku (Finland). Our work brings as a novelty the description of a new spiny species for Amazonia, the only one known to occur in central Amazonia, the first spiny *Dennstaedtia* from South American species, and the third spiny species in the genus, increasing to 16 the total number of *Dennstaedtia* species known to Amazonia. We also present illustrations and diagnostic images comparing the new species with *D. spinosa*, and a distribution map of the known occurrence records.

2. MATERIAL AND DISCUSSION

Descriptions of general morphological characters follow Lellinger (2002), Mickel and Smith (2004), and Schwartsburd (2020). The conservation status of the species was evaluated according to the IUCN Red List categories and criteria (IUCN 2012; IUCN Standards and Petitions Committee 2019). Extent of occurrence (EOO) was estimated using the GeoCat geospatial conservation assessment tool (Bachman *et al.* 2011) for extinction risk assessment. Due to the small number of observed records, it was not possible to calculate the Area of Occupancy (AOO). Maps were prepared in QGIS v. 3.22 (https://qgis.org/pt_BR/site/index.html).

3. RESULTS

Dennstaedtia aculeata N.T.L. Pena, Zuquim & Schwartsb., ***sp. nov.*** Type: Brazil, Amazonas, Presidente Figueiredo, old-growth terra-firme forest on the edge of the lake of the Balbina Hydroelectric Power Plant, docking port of the future PPBio camp, approximately 1:30 hours by boat, on the margin of a small stream. (Terra firme na beira do lago da Usina Hidrelétrica de Balbina, porto de atracagem do futuro campamento do PPBio, aproximadamente 1:30 horas de barco, em beira do igarapé), 1°47'S, 59°17'W, 06 August 2006, G. Zuquim & R. Braga-Neto 172 (holotype: INPA-219630!; isotype: EAFM-3627!). (Figures 1, 2, 3, 4a–c).

Diagnosis: *Dennstaedtia aculeata* is characterized by the presence of spines, as well as acicular and catenate hairs on the petioles and rachises. (Figure 1).

Plants terrestrial. Rhizomes long creeping with catenate hairs, and roots with setose hairs. Fronds determinate, to ca. 2 m long; petioles vinaceous, 0.5–1 m × 0.8–1 cm, spiny, the spines reddish brown, 0.5–3 mm long, with small aerophores, glabrescent, moderately covered by acicular and catenate hairs in the adaxial sulcus, proximally with roots; laminae 4-pinnate to 4-pinnate-pinnatifid, ca. 1 m long, with alternate pinnae; rachises dark brown, spiny, with small aerophores, adaxially sulcate, densely covered by light brown catenate hairs, abaxially covered by light brown, acicular hairs and sparsely covered by catenate hairs with prominent base; basal pinnae alternate, equilateral, 60 × 40 cm, lanceate, proximally obtuse, distally acute to cuneate; costae abaxially with acicular and catenate hairs, adaxially with catenate hairs, with small aerophores, lacking adaxial wings; ultimate segments oblong, proximally sessile, distally round and dentate, 1–1.5 × 0.5–0.7 cm, with deep sinuses forming segments; costules and veins abaxially and adaxially with acicular and catenate hairs; laminar tissue between the veins abaxially with acicular and catenate hairs, adaxially glabrous; lamina margins glabrous, entire and dentate at the segment apices. Sori rounded, 0.5–0.8 × 0.5–0.8 mm; indusia purse-shaped, glabrous, formed by the fusion of the inner and the outer indusia. Spores tetrahedralglobose, trilete, verrucate with partly fused verrucae.

Paratype: Peru, Loreto, near Juan Velascos Alvarado, in “restinga”, typically non flooded land, floods only when extremely high inundation, close to creeks, 4°45’S, 75°39’W, 110 m, 6 Aug 2003, G. Cárdenas & J. Vormisto 1541 (on three sheets: TUR-599750, TUR-599751, TUR-599752)

Distribution: *Dennstaedtia aculeata* is known from central Brazilian Amazonia, Amazonas state, Brazil, and from northeastern Peruvian Amazonia, Loreto, Peru (Figure 2). The type specimen from Brazil was collected near the bank of a small creek (locally known as igarapé) in the Uatumã Biological Reserve (REBio Uatumã). In Peru, *D. aculeata* was collected almost 2000 km away from the type, in the Pastaza region (Figure 3). The species potentially occurs in other areas between the two known locality records and further into eastern Brazilian Amazonia, as well as in areas with similar conditions in western Amazonian countries such as Colombia and Ecuador.

Habitat: The type specimen was collected in a terra-firme forest in REBio Uatumã, near the artificial lake of the Balbina hydroelectric dam. The climate in the region is humid and without a dry season (no months with less than 50 mm of rainfall; Sombroek 2001). The region is located on the contact between two geological formations: the Paleozoic sandstone of the Trombetas Formation, in which overlaying soils tend to be poor in nutrients, and the Precambrian igneous rocks of the Iricoumé Formation, which is part of the Guiana Shield, with mosaic soils of varying fertility (Irion 1978; Sombroek 2000). The fern was growing on the margin of a small stream near *Saccoloma inaequale* (Kunze) Mett., *Pteris tripartita* Sw., and *Didymochlaena truncatula* (Sw.) J.Sm., which typically occur on relatively nutrient-rich soils (Zuquim *et al.* 2014). Interpretation of reflectance data of Landsat images (Van doninck and Tuomisto 2018; Tuomisto *et al.* 2019) and soil samples taken near the location of the type specimen (Figueiredo *et al.* 2014) and the paratype (Normand *et al.* 2006) suggest that the species might be an intermediate to nutrient-rich soil specialist. The paratype occurred in a patch of soil of volcanic origin along the Urituyaco River (Normand *et al.* 2006), in the geological area of the Pastaza Fan. The Pastaza Fan is a vast Holocene volcanoclastic alluvial fan draining from the Cotopaxi volcano (Räsänen *et al.* 1990). Intermingled with the nutrient-rich soils, which mainly occur along river valleys, the Pastaza region comprises a mosaic of different edaphic characteristics and vegetation types, with poor-soil swamps and slightly elevated areas which are dominated by the palm *Mauritia flexuosa* L.f. (locally known as aguajales in Peru or buritizais in Brazil).

Etymology: The specific epithet “*aculeata*” is a reference to the spines present on the petioles and rachises of the plant, which are uncommon in the genus. Conservation status: According to the IUCN Red List criteria, *Dennstaedtia aculeata* should be considered as Data Deficient (DD), as there is not enough information to make a direct or indirect assessment of its risk of extinction based on the distribution and/or population status of the new species. As *Dennstaedtia aculeata* is known only from isolated individuals in its type and paratype localities, there is no solid information about its current status or potential threats. For example, it was not possible to calculate the Extent of Occurrence (EOO) with only two known occurrence records. The DD category indicates that more information is needed about the geographic distribution and biology of *D. aculeata*, and that further

research is needed to determine the appropriate threat classification (IUCN 2012; IUCN Standards and Petitions Committee 2019).

4. DISCUSSION

We placed *Dennstaedtia aculeata* in Polypodiales, due to its stalked sporangia with vertical, interrupted annuli. We placed it in Dennstaedtiaceae and *Dennstaedtia* due to the long creeping rhizomes with catenate hairs, long and highly dissected fronds (to 4-pinnate-pinnatifid), free veins, discrete, marginal sori protected by purse-shaped indusia (formed by the fusion of inner and outer indusia), and tetrahedral-globose, trilete spores (Tryon 1960; Navarrete and Øllgaard 2000).

Hypolepis Bernh. is a genus in Dennstaedtiaceae with many species having spines, as well as discrete, marginal sori (Schwartzburd and Prado 2015), thus being superficially similar to *D. aculeata*. However, unlike *D. aculeata*, *Hypolepis* has only outer indusium and monolete spores (Schwartzburd and Prado 2015). We discarded the possibility of *D. aculeata* being an intergeneric hybrid between *Dennstaedtia* and *Hypolepis* for several reasons. First, the lineages of these two genera are very distantly related, having diverged in the Cretaceous (ca. 80 m.y.a.) (Schwartzburd *et al.* 2020). Secondly, their base chromosome numbers are very different, with *Dennstaedtia* (group *Patania*) having 46 and 47, and *Hypolepis* 52 (Schwartzburd *et al.* 2020). Finally, the sporangia and spores of *D. aculeata* are perfectly well-developed, with similar morphology to those of *D. cicutaria* (Yañez *et al.* 2016).

Spines (or aculei, prickles, thorns, depending on each author's interpretation) are common epidermal structures found in the Dennstaedtiaceae (Shang *et al.* 2018; Schwartzburd *et al.* 2020), especially in subfamily Hypolepidoideae. According to Shang *et al.* (2018) and Schwartzburd *et al.* (2020), they appeared in the ancestors of the genus *Hiya* H.Shang and in the Neotropical clade of *Hypolepis* (see also Schwartzburd and Prado 2015), sometimes contributing to the so-called "scandent syndrome" (when the spines aid the individual plant to grow supported by other elements of the vegetation). Within these two different clades, there were also secondary reversals, giving origin to unarmed species, such as *Hiya distans* (Hook.) Brownsey & Perrie, and some Neotropical *Hypolepis* (Shang *et al.* 2018; Schwartzburd *et al.* 2020).

In subfamily Dennstaedtioideae, spines are extremely rare. Out of the approximately 130 species in the subfamily, spines were previously reported only for

one Paleotropical species (*Dennstaedtia scandens*), and for one Neotropical species from Mexico and Honduras (*D. spinosa*) (e.g., Mickel and Smith 2004; Schwartzburd *et al.* 2020). Therefore, *D. aculeata* is the third known spiny species in the subfamily. Morphologically, the spines of *D. scandens* are different from those of *D. spinosa* and *D. aculeata*: they are stout and curved, whereas in the other two species they are conical and straight. Unfortunately, we were not able to extract DNA from *D. aculeata* to check if it is a sister taxon to *D. spinosa*, and thus their spines had the same origin.

Dennstaedtia aculeata differs from *D. spinosa* by the alternate pinnae (vs. opposite), the vinaceous and densely spiny petioles (vs. light brown and sparsely spiny), the dark brown rachises (vs. stramineous), by the costae, veins and laminar tissue between the veins with acicular and catenate hairs (vs. with only catenate hairs), and by the glabrous indusia (vs. hairy) (Figure 4). Another morphologically close species to *D. aculeata* is *D. cicutaria*, due to the similar indument on the rachises, costae and veins (copiously furnished by acicular and catenate hairs) (Tryon 1960). However, *D. cicutaria* has absolutely no spines, and *D. aculeata* presents rachises abaxially sparsely covered by catenate hairs, with prominent base (vs. densely covered by catenate hairs, with homogeneous base).

We also compared *D. aculeata* with *D. bipinnata* (Cav.) Maxon, which was the only *Dennstaedtia* species previously known from Brazilian Amazonia (Prado *et al.* 2017). *Dennstaedtia aculeata* can be easily distinguished from *D. bipinnata* by the presence of spines on petioles and rachises (vs. no spines), by the lack of wings adaxially continuous from pinna-rachises onto costae (vs. presence of wings adaxially continuous), and indusia purse-shaped (vs. cylindrical). The description of this new species advances our knowledge of the taxonomy and systematics of Neotropical ferns in the botanically undersampled and understudied Amazon region (Nelson *et al.* 1990; Hopkins 2007; Schulman *et al.* 2007).

5. CONCLUSIONS

We describe a new fern species, *Dennstaedtia aculeata* (Dennstaedtiaceae), from Brazilian and Peruvian Amazonia. This species is unique among South American *Dennstaedtia* for having spines on petioles, and rachises and was immediately recognized as a new species. Furthermore, the species presents two types of hairs (catenate and acicular), which can be observed in the rachises and

laminae. This is the 16th species of *Dennstaedtia* described for Amazonia, the first to be recorded in central Amazonia.

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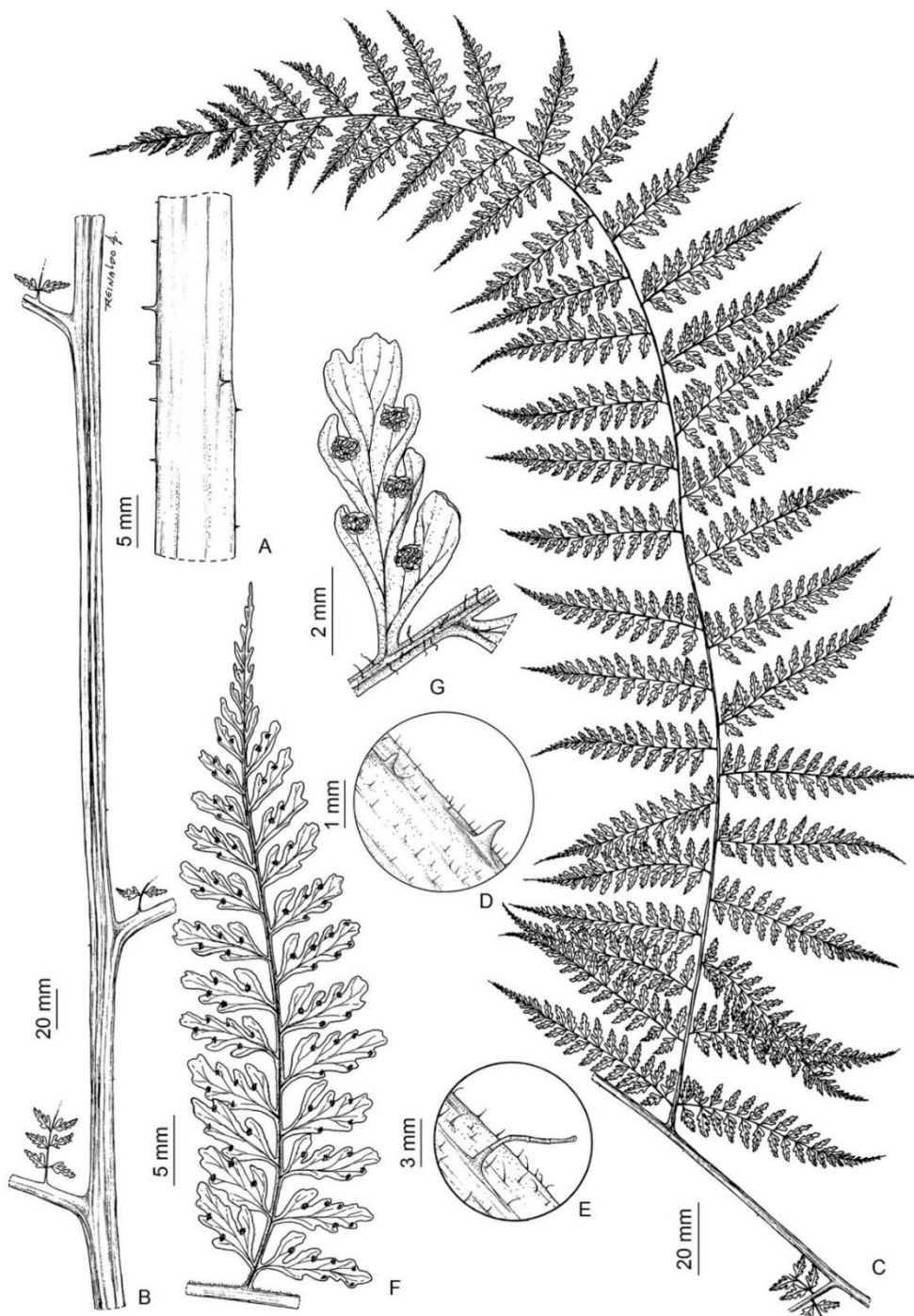


Figure 1. *Dennstaedtia aculeata*. A – Section of the petiole, showing spinescence; B – Rachis showing alternate pinnae; C – Pinna; D – Detail of rachis showing spines and acicular hairs; E – Detail of rachis showing acicular and catenate hairs with prominent base; F – Pinnule abaxially; G – Ultimate segment, abaxially, showing sori. Credits: Reinaldo Pinto.

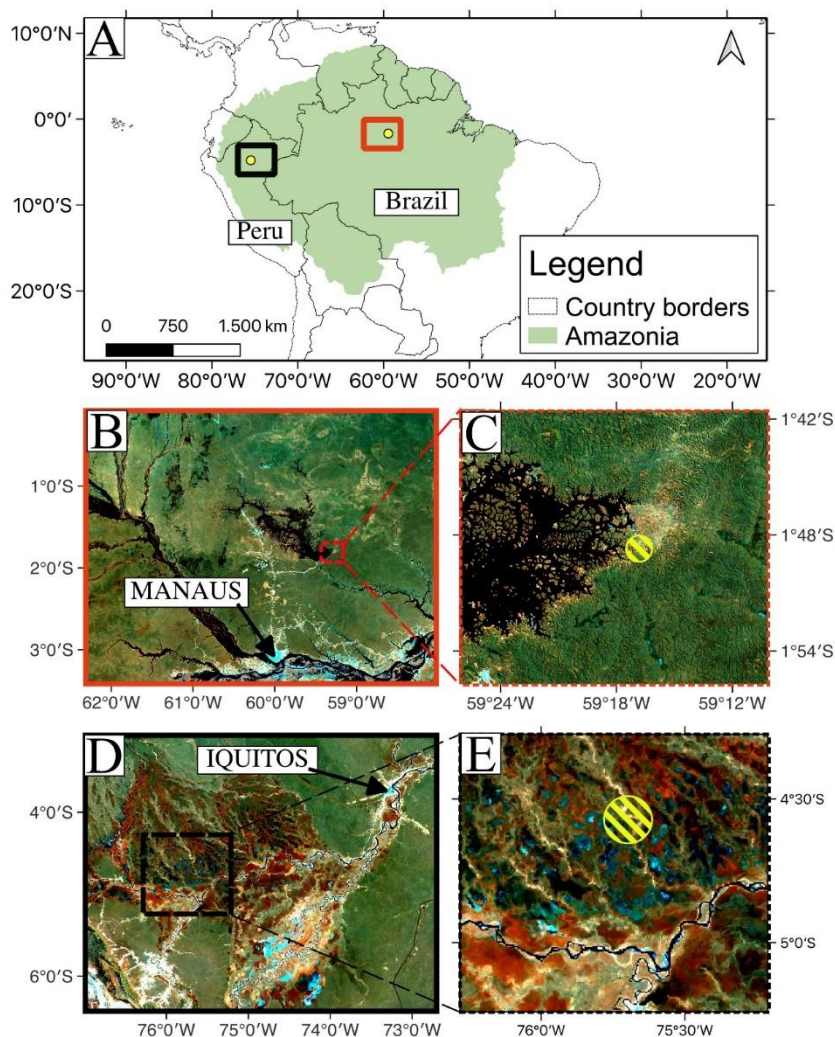


Figure 3. Distribution map of *Dennstaedtia aculeata* (*sp. nov.*). A – Known location records of *Dennstaedtia aculeata* in the Amazon region; B-C – Collection site of the type specimen near the artificial lake of the Balbina hydroelectric dam in Amazonas, Brazil; D-E – Collection site of the paratype in the Pastaza fan, near Iquitos, Peru. Background image is the median reflectances of Landsat scenes imagery (Van doninck and Tuomisto 2018) coarsened to 450 m resolution. Red, green and blue channels have been assigned, respectively, to bands 4, 5 and 7. Reflectance ranges for each band were 2700–3500, 1100–1600 and 430–670, respectively. Amazonian limits according to Eva and Huber 2005. This figure is in color in the electronic version.

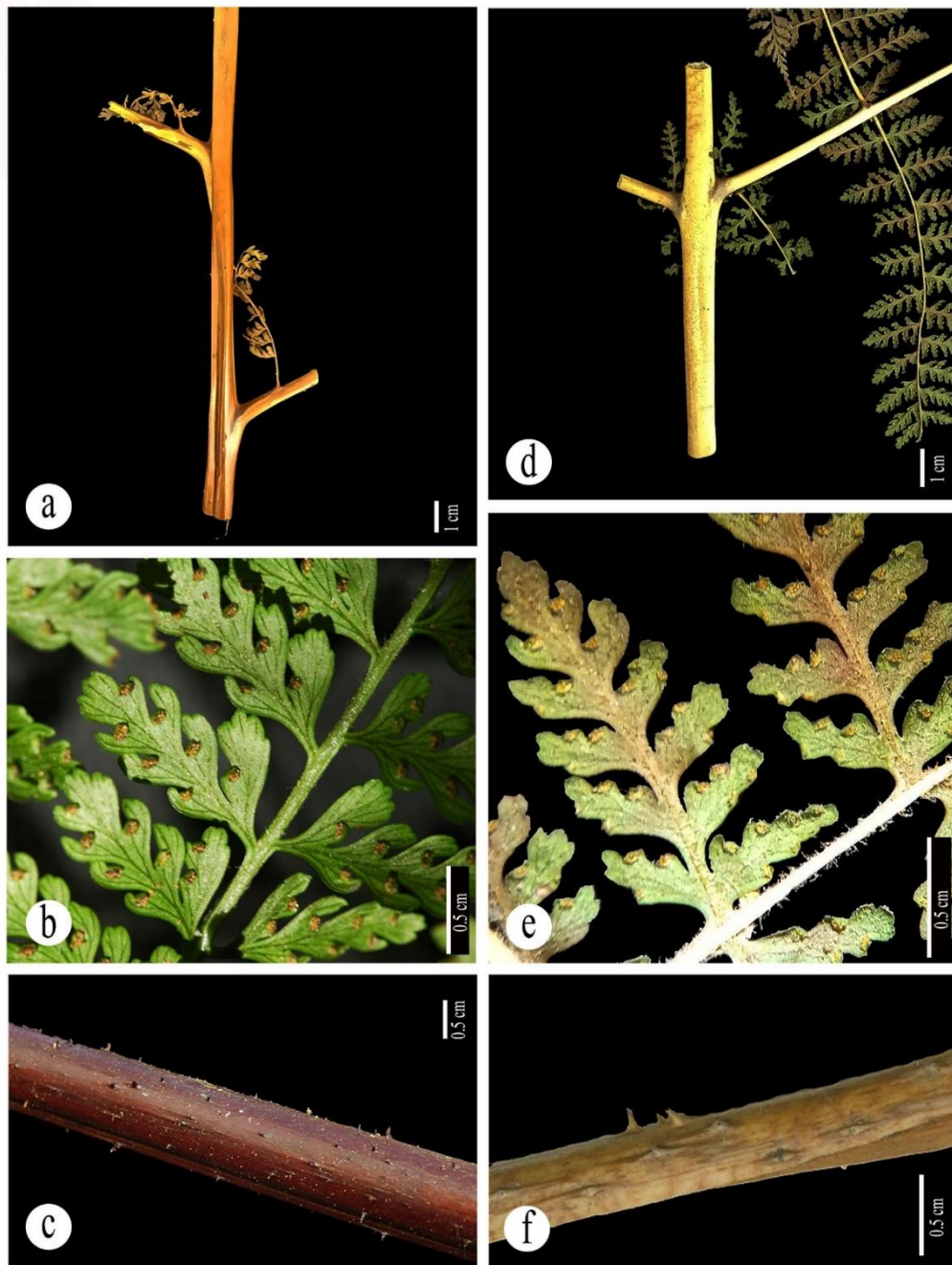


Figure 4. *Dennstaedtia aculeata* (*sp. nov.*) (G. Zuquim & R. Braga-Neto 172, INPA-219630). A – Rachis with alternating pinnae; B – Pinules and ultimate segments, abaxially; C – Petiole dark brown to vinaceous and densely spiny. *Dennstaedtia spinosa* (M. Sundue et al. 5045, VT-290463; J.T. Mickel 2730, NY-149042). D – Rachis with opposite pinnae; E – Pinules and ultimate segments, abaxially; F – Petiole light brown and sparsely spiny. Credits: N.T.L. Pena (A, D, E); G. Zuquim (B, C); NYBG virtual herbarium (F). This figure is in color in the electronic version.

Capítulo III. Pena, N.T.L. & P. B. Schwartzburd. Taxonomic revision of *Dennstaedtia* s. str. (Dennstaedtiaceae) for South America, except the for the northern Andes. – a ser submetido ao periódico *American Fern Journal*.

Capítulo III. Taxonomic revision of *Dennstaedtia* s. str. (Dennstaedtiaceae) for South America, except the for the northern Andes

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ABSTRACT

We present the taxonomic revision of *Dennstaedtia s. str.* for South America, except for the northern Andes. *Dennstaedtia s. str.* excludes the Tropical species with adaxial connecting wings (now ascribed to *Mucura*) and the Temperate species of *Sitobolium*. Here, 13 species are recognized: *D. aculeta*, *D. andina*, *sp. nov.*, *D. arcuata*, *D. auriculata*, *D. cicutaria*, *D. concinna*, *comb. nov.*, *D. cornuta*, *D. coronata*, *D. fluminensis*, *comb. nov.*, *D. glauca*, *D. mathewsii*, *D. obtusifolia*, and *D. sprucei*. A new species is proposed and two names are rescued from synonymy, for which we present new combinations and updated circumscriptions and geographical distribution. Among these new circumscriptions, *D. concinna* had been lately treated as a synonym of *D. mathewsii*, which has a distribution to the Amazon and Andean-Amazon; *D. fluminensis* was rescued from the synonymy of *D. cornuta*, and is endemic to Brazil; and *D. adina* is proposed here as a new endemic species from Peru, morphologically related to *D. arborescens* and *D. auriculata*. We present key to species, comprehensive descriptions, illustrations, type information, examined specimens, maps of distribution, and comments for all taxa.

KEYWORD.—Amazon, central Andes, Atlantic Forest, Dennstaedtioid ferns, Pteridophyta

1. INTRODUCTION

Dennstaedtia Bernh. is a genus that has about 55 species with a Pantropical distribution, and belongs to the family Dennstaedtiaceae (PPG I 2016; Tryon 1960; Tryon and Tryon 1982; Moran 1995; Rojas-Alvarado and Villalobos-Brenes 2018; Navarrete and Øllgaard 2000; Mickel and Smith 2004; Yañez et al. 2014; Schwartzburd & Pena 2022; Triana-Moreno et al. 2022a). With the new circumscription of Dennstaedtioideae proposed by Triana-Moreno et al. (2022a), the species of *Dennstaedtia s.l.* having adaxial connecting wings, forms a distinct clade to which they were circumscribed as a new genus *Mucura* L.A. Triana & Sundue. The species of *Mucura* from South America are treated in Pena & Schwartzburd (in prep. – Chapter 2).

During the phylogenetic studies carried out by Triana-Moreno et al. (2022a), it was noted that the type species of *Dennstaedtia s.l.* (*Dennstaedtia flaccida* (Forst.) Bernh.), was grouped within the clade of *Microlepia* C.Presl. As *Dennstaedtia* and *Microlepia* are widely used for names with a significant number of species, Triana-Moreno et al. (2022b), made a conservation proposal (including altering the type) of *Dennstaedtia*, in order to maintain its taxonomic stability, as well as and *Microlepia*.

Here, we present the taxonomic revision of *Dennstaedtia* from *s. str.* for South America, except for the northern Andes (Figures 1-4, Maps 1-6). Here, 13 species are recognized: *Dennstaedtia aculeta*, *D. andina*, *sp. nov.*, *D. arcuata*, *D. auriculata*, *D. cicutaria*, *D. concinna*, *comb. nov.*, *D. cornuta*, *D. coronata*, *D. fluminensis*, *comb. nov.*, *D. glauca*, *D. matheuwsii*, *D. obtusifolia* and *D. sprucei*. The two names presenting new combination into *Dennstaedtia* are rescued from synonymy and have their circumscriptions and geographical distribution updated, namely: *D. concinna* with distribution to the Amazon and Andean-Amazon, and the Brazilian endemic *D. fluminensis*.

2. MATERIAL AND METHODS

The studies were carried out between the years 2018 to 2022, in which Neotropical specimens of Dennstaedtioideae from were analyzed. Unfortunately, we were not able to examine a comprehensive number of specimens from Venezuela, Colombia, and Ecuador, as well as from Central and North Americas. Therefore, our revision was concentrated on South America, except for northern Andes. During this period,

collection expeditions were carried out in Brazilian territory. Specimens from the following herbaria were examined: BHCB, CEPEC, CESJ, COR, FURB, HAS, HUCCS, HUEFES, HRCB, IAN, ICN, INPA, MA, MBML, MG, OUPR, PACA, SAMES, SJRP, SP, SPF RB, UEC, UFP, UPCB, VIC, VIES (Brazil); SGO (Chile); UPRRP (Puerto Rico); NY, UC and VT (USA) (Thiers, continuous update). We also examined specimens online, through the websites of SpecieLink (<http://www.splink.org.br/>), Re flora – Flora do Brasil 2020 (<http://reflora.ibri.gov.br/reflora/herbarioVirtual/>), GBIF (<https://www.gbif.org/>) and Pteridophyte Collections Consortium (<https://pteridoportal.org/>), including types.

Fieldwork occurred place in the states of Bahia, Espírito Santo, Minas Gerais and Rio de Janeiro. The collections were carried out according to the usual herborization techniques proposed by Windisch (1992). The collected specimens were deposited in the herbarium VIC, and their duplicates to be sent mainly to NY, RB, and SP (Thiers, continuous update). Descriptions of general morphological characters follow Lellinger (2002) and the names and authors of the species were confirmed through IPNI (<http://www.ipni.org>) and in original publication. Maps were prepared in QGIS v. 3.22 (https://qgis.org/pt_BR/site/index.html).

3. RESULTS AND DISCUSSION

KEY TO *DENNSTAEDTIA* FROM SOUTH AMERICA, EXCEPT FOR THE NORTHERN ANDES

1. Laminae 1-pinnate *D. arcuata*
 Laminae 1-pinnate-pinnatifid or more dissected 2
2. Petioles and rachises spiny *D. aculeata*
 Petioles and rachises inermous 3
3. Petioles, rachises, and laminae with catenate and acicular hairs *D. cicutaria*
 Petioles, rachises, and laminae with only catenate hairs 4
4. Laminae 1-pinnate-pinnatifid to 2-pinnate-pinnatifid 5
 Laminae 3- pinnate to 4-pinnate-pinnatifid 9
5. Laminar margins densely covered by catenate hairs *D. sprucei*
 Laminar margins glabrous 6
6. Sori arranged continuously along the margin of the pinnae *D. coronata*
 Sori not arranged continuously along the margin of the pinnae 7
7. Sori the basiscopically and acroscopically, never in pinnae apices *D. obtusifolia*
 Sori in the pinnae apices 8

8. Sori round, willing mainly at the apex of the ultimate segments, oriented in the plane of the lamina and projected out of the blade, induzia hemi-spherical *D. concinna*
 Sori hemi-spherical, oriented in angle 90° of the laminae; induzia purse-shaped *D. andina*
9. Indusia bivalvate *D. fluminensis*
 Indusia cup-shaped or purse-shaped 10
10. Sori projected outside the pinna *D. mathewsii*
 Sori not immersed on the pinna 11
11. Sori in shallow sinus formed by auricle-shaped segment *D. auriculata*
 Sori in deep sinus, not forming auricle-shaped segment 12
12. Laminae 4-pinnate to 4-pinnate-pinnatifid *D. glauca*
 Laminae 3-pinnate to 3-pinnate-pinnatifid *D. cornuta*

TAXONOMIC TREATMENT

Dennstaedtia Bernh. in J. Bot. (Schrader) 1800(2): 124. Oct–Dec 1801. TYPE CONS.:

Dennstaedtia dissecta (Sw.) T. Moore (*Dicksonia dissecta* Sw.).

Patania C. Presl, Tent. Pterid. 137. 1836. *Dicksonia* subgen. *Patania* (C.Presl) Hook.

TYPE: LECTOYPE (designated by Christensen): Index Filic. XXIX. H. Hagerup, Copenhagen. 1906. *Patania obtusifolia* (Willd.) C. Presl [= *Dicksonia obtusifolia* Willd.].

Leptolepia Prantl, Arbeiten Königl. Bot. Gart. Breslau 23. 1892. LECTOTYPE (designated by Christensen): Index Filic. xxviii. H. Hagerup, Copenhagen. 1960.

Leptolepia novae-zelandiae (Colenso) Mett. ex Diels. [= *Davallia novae-zelandiae*].

Oenotrichia Copel., Univ. Calif. Publ. Bot. 16: 82 (1929). TYPE: *Oenotrichia maxima* (E. Fourn.) Copel. [= *Leucostegia maxima* E.Fourn.].

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, 2-4 pinnate, sometimes with proliferous buds on rachises, the axes without adaxial connecting wings; veins free, with enlarged or slender apices; sori marginal, provided with abaxial and adaxial indusia fused into purse- or cup-shaped involucre; spores trilete, the perispore with regular reticles, ridges and verrucate.

Dennstaedtia aculeata N.T.L. Pena, Zuquim & Schwartzb. *Acta Amazonica* 52(2): 142–148. 2022. TYPE: BRAZIL. Amazonas: Presidente Figueiredo, Terra firme na beira do lago da Usina Hidrelétrica de Balbina, porto de atracagem do futuro acampamento do PPBio, aproximadamente 1:30 horas de barco, em beira do igarapé, 1°47'S, 59°17'W, 06 Aug 2006, G. Zuquim & R. Braga-Neto 172 (holotype: INPA-219630!; isotype: EAFM-3627!). (Fig. 1, A-D; Map. 1)

Plants terrestrial. Rhizomes long creeping with catenate hairs, and roots with setose hairs. Fronds determinate, to ca. 2 m long; petioles burgundy, 0.5–1 m × 0.8–1 cm, spiny, the spines reddish brown, 0.5–3 mm long, with small aerophores, glabrescent, moderately covered by acicular and catenate hairs in the adaxial sulcus, proximally with roots; laminae 4-pinnate to 4-pinnate-pinnatifid, ca. 1 m long, with alternate pinnae; rachises dark brown, spiny, with small aerophores, adaxially sulcate, densely covered by light brown catenate hairs, abaxially covered by light brown, acicular hairs and sparsely covered by catenate hairs with prominent base; basal pinnae alternate, equilateral, 60 × 40 cm, lanceate, proximally obtuse, distally acute to cuneate; costae abaxially with acicular and catenate hairs, adaxially with catenate hairs, with small aerophores; ultimate segments oblong, inequilateral, with the first acroscopical segment reduced, proximally sessile, distally round and dentate, 1–1.5 × 0.5–0.7 cm, with deep sinuses forming segments; costules and veins abaxially and adaxially with acicular and catenate hairs; laminar tissue between the veins abaxially with acicular and catenate hairs, adaxially glabrous; lamina margins glabrous, entire and dentate at the segment apexes. Sori rounded, 0.5–0.8 × 0.5–0.8 mm; indusia purse-shaped, glabrous.

DISTRIBUTION.—*Dennstaedtia aculeata* is known from central Brazilian Amazonia, Amazonas state, Brazil, and from northeastern Peruvian Amazonia, Loreto, Peru. Region of the nutrient-rich soils in Amazonian forests.

SPECIMENS EXAMINED.—PERU. Loreto, near Juan Velascos Alvarado, in “restinga”, typically non flooded land, floods only when extremely high inundation, close to creeks, 4°45'S, 75°39'W, 110 m, 6 Aug 2003, G. Cárdenas & J. Vormisto 1541 (on three sheets: TUR-599750, TUR-599751!, TUR-599752!).

SPECIMENS EXAMINED.—BRAZIL. Amazonas: Presidente Figueiredo, Terra firme na beira do lago da Usina Hidrelétrica de Balbina, porto de atracagem do futuro acampamento do PPBio, aproximadamente 1:30 horas de barco, em beira do

igarapé), 1°47'S, 59°17'W, 06 Aug 2006, G. Zuquim & R. Braga-Neto 172 (holotype: INPA-219630!; isotype: EAFM-3627!).

Dennstaedtia aculeata is the only species in South America to present spines on the petiole and rachis. *Dennstaedtia aculeata* differs from *D. spinosa* (a spiny species endemic to Mexico and Honduras) by the alternate pinnae (*vs.* opposite), the burgundy and densely spiny petioles (*vs.* light brown petioles that are sparsely spiny), the dark brown rachises (*vs.* stramineous), the costae, veins and laminar tissue between the veins with acicular and catenate hairs (*vs.* with only catenate hairs), and by the glabrous indusia (*vs.* hairy).

Dennstaedtia andina N.T.L. Pena & Schwartsb. ***sp. nov.*** TYPE: PERU. Oxapampa: La Suiza, along the short trail to a cave, or by the cave itself., -10.65440N, -75.45111E, 2180 m, 19 May 2016, C.J. Rothfels 4973A, 4973B, 4973C (UC!). (Fig. 4, I-N; Map 6)

Plants terrestrial. Rhizomes ascending, 1.5–2 cm diam, verrucose and glabrous. Fronds determinate, 2–3 m long; petioles dark to light brown, with root projections, 0.8–1 m × 0.5–1.8 cm, inermous, small aerophores, densely catenate hairs; laminae 2-pinnate-pinnatifid, 1–2 m long, with alternate pinnae; rachises light brown, adaxially sulcate, abaxially and adaxially with catenate hairs, more densely at base of axis, sometimes buds in axes, small aerophores; basal pinnae alternate, lanceolate, 40–60 × 10–20 cm, equilateral, proximally obtuse, distally acute; costae abaxially and adaxially with catenate hairs, adaxially sulcate, small aerephore; ultimate pinnae lanceate, 5–10 × 1–2.5 cm, proximally sessile, distally acuminate to caudate, crenate, with shallow sinus forming round-shaped to acute-shaped segment; costules and veins abaxially with sparsely catenate hairs, adaxilly glabrescent; laminar tissue between the veins abaxially sparsely catenate hairs, adaxilly glabrous; lamina margins glabrous, entire and crenate at apex segments. Sori hemi-spherical, 0.8–1.2 × 0.4–0.7 mm; indusia purse-shaped, glabrous.

ETYMOLOGY.— The specific epithet “*andina*” is a reference to its known occurrence for the Andes region of Peru.

DISTRIBUTION.—Known only from the type locality, in La Suiza, Oxapampa, Peru.

Dennstaedtia andina is recognized by the 2-pinnate-pinnatifid laminae with buds in the axes, and the lanceate ultimate pinnae, which are proximally sessile and distally acuminate to caudate, with shallow sinuses forming round-shaped to

acute-shaped segments. *Dennstaedtia andina* differ of *D. auriculata* by the 2-pinnate-pinnatifid laminae (vs. 3-pinnate-pinnatifid), the presence of proliferous buds in the axes (vs. buds absent), the laminar tissue between the veins abaxially with sparse catenate hairs, adaxilly glabrous (vs. abaxially with dense catenate hairs, adaxilly with sparse catenate hairs), and laminar tissue between the veins abaxially sparsely catenate hairs, adaxilly glabrous (vs. abaxially densely catenate hairs, adaxilly sparsely catenate hairs). *Dennstaedtia andina* also differs from *D. arborescens* by ultimate pinnae with segments acute (vs. segments rounded), sori in shallow sinus (vs. sori in margin devoid of sinus), occurrence for South America (vs. Antilles). *Dennstaedtia andina* also differs from *D. coronata* by ultimate segments sessile (vs. pedicelated), costules and veins abaxially with sparsely catenate hairs, adaxilly glabrescent (abaxially densely catenate hairs, adaxilly glabrous), sori distant from each other, not continuous along the entire edge of the blade (vs. sori close to each other, continuous along the edge of the blade).

Dennstaedtia arcuata Maxon, Amer. Fern J. 35(1): 22. 1945. TYPE. COLOMBIA. Valle del Cauca: La cumbre, Cordillera Occidental, 1800–2100 m, 14 May 1922, E.P. Killip 5565 (holotype: US-on two sheets [US-00066382, image!, US-00066383, image!]; isotypes: GH-00022319, image!; NY-00149034, image!). (Fig. 1, E-H; Map 1)

Plants terrestrial. Rhizomes creeping (no see). Fronds determinate, 1–2 m long; petioles light to dark brown, with root projections at the base, 0.30–0.70 m × 0.4–0.8 cm, inermous, small aerophores, densely catenate hairs, without buds at base; laminae 1-pinnate, 0.70–1 m long, with alternate pinnae; rachises dark brown, adaxially sulcate, abaxially densely catenate hairs; adaxially sparsely, more densely at base of axis, with buds in axes, small aerophores; basal pinnae alternate, lanceolate to falcate, 14–22 × 3–4 cm, equilateral, proximally obtuse, distally cuneate to acuminate; costae abaxially densely catenate hairs, adaxially glabrescent and sulcate, small aerephore; ultimate segments lanceolate to falcate, 12–15 × 2–3 cm, proximally pedicellate and obtuse, distally cuneate to acuminate, crenate, without sinus; veins abaxially sparsely catenate hairs, adaxilly glabrous; laminar tissue between the veins abaxially sparsely catenate hairs, adaxilly glabrous; lamina margins glabrous, entire and crenate at apex segments. Sori hemi-spherical, next to

each other, sometimes seeming continuous, 1–1.7 × 0.5–0.7 mm; indusia purse-shaped, glabrous, sometimes catenate hairs at the base.

DISTRIBUTION.—Antilles, Costa Rica, northern Andes, and Peru; ca. 1700 m in the studied area (1300–2100 elsewhere).

SPECIMENS EXAMINED.—PERU. Province Bagua: 12 km E of La Peca (by trail), 1700 m, 29 Jun 1978, *P. Barbour 2572* (UC).

ADDITIONAL SPECIMENS EXAMINED.—COSTA RICA. Near the juncture of the Provinces of Alajuela: Guanacaste and Puntarenas, high ridge north of the television relay tower above Monteverde and bordering the Monteverde Cloud Forest Nature Reserve, 10°19'N, 83°48'W, 1750–1800 m, 27 Feb 1977, *Wm. Burger et al. s.n.* (NY-04008269).

ECUADOR.—Prov. Pastaza: Hacienda San Antonio del Barón von Humboldt, 2 km ao NE de Mera, 1°27'S, 78°06'E, 1300 m, 19 Feb 1985, *M. Baker 27* (NY).

Dennstaedtia arcuata can be recognized as the only species with 1-pinnate laminae with alternate pinnae, that are lanceolate to falcate, and equilateral, proximally obtuse, distally cuneate to acuminate, and bearing in margin hemispherical sori, that sometimes seems continuous to each other.

Dennstaedtia auriculata Navarrete & B.Øllg., *Nordic J. Bot.* 20(3): 337, fig. 5A–D. 2000. TYPE. ECUADOR. Prov. Pichincha: Km 21 de la carretera Quito-Sto. Domingo, 2200 m, H. Navarrete 449 (holotype: QCA, image!; isotypes: AAU, image!, QCNE, image!). (Fig. 1, I–K; Map 1)

Dennstaedtia obtusifolia var. *protrusa* Christ in Pittier, *Prim. Fl. Costaric.* 3: 38. 1901.—Lectotype (designated here): Costa Rica: Forêts de Copey, Mar 1898, *A. Tonduz 11785* (P-00633296, image!; isolectotypes: GH-00020961, image!; US-00066392, image!).

Plants terrestrial. Rhizomes ascending to decumbent, 1–2 cm diam, verrucose and glabrous. Fronds determinate, 2–4 m long; petioles dark brown, without root projections, 1–2 m × 0.7–1 cm, inermous, small aerophores, with catenate hairs to glabrescent; laminae 3-pinnate-pinnatifid, 1–2 m long, with alternate pinnae; rachises light to dark brown, adaxially sulcate, abaxially and adaxially with densely catenate hairs to glabrescent, more densely at base of axis, without buds in axes, small aerophores; basal pinnae alternate, lanceolate to lanceate, 30–40 × 20–25 cm, equilateral, proximally obtuse, distally acute; costae abaxially and adaxially with

densely catenate hairs, adaxially sulcate, small aerephore; ultimate segments lanceate to falcate, 2–3 × 0.8–1.5 cm, proximally sessile, distally acute to round, crenate, with shallow sinus forming auricle-shaped segment; costules and veins abaxially densely catenate hairs, adaxially sparsely catenate hairs; laminar tissue between the veins abaxially densely catenate hairs, adaxially sparsely catenate hairs; lamina margins glabrous, entire and crenate at apex segments. Sori hemi-spherical, 0.8–1.5 × 0.5–1 mm; indusia purse-shaped, glabrous.

DISTRIBUTION.—Antilles, Guatemala and Costa Rica (Navarrete & Ollgaard 2000), Colombia, Venezuela, Ecuador, Peru, and Bolivia; 1800–3350 m.

SPECIMENS EXAMINED.—PERU. Ancash: Huari, Huacachi, Estación near Muña, 1829 m, 20 May 1923, *J. F. Macbride 4176* (F). Cusco: 18 Feb 1990, *B. León 2224* (F). Departamento Cuzco: Provincia Convencion; Localidad exacta Amaibamba, 1700 m, 23 Nov 1950, *C. Vargas 9805* (UC).

BOLIVIA.—Dep. Cochabamba: Prov. José Carrasco Torrico, 113 km antigua carretera Cochabamba-Villa Tunari, 17°07'S, 65°38'W, 2900 m, 03 Jul 1996, *M. Kessler et al. 6918* (UC). La Paz: Nor Yungas, 5 km de Chuspipata hacia Coroico, -16.38333 -67.8, 2700 m, 19 Sep 1997, *M. Kessler 12089* (UC).

ADDITIONAL SPECIMENS EXAMINED.—ECUADOR. Secus fl. Pilaton: Aug 1905, *A.L. Sodiro s.n.* (NY-04008344).

See comment of *Dennstaedtia andina*, for differentiation with this species.

Dennstaedtia cicutaria (Sw.) T.Moore, Index Fil. (T.Moore) 2: xcvi. 1857. *Dicksonia cicutaria* Sw., J. Bot. (Schrader) 1800(2): 91. 1802. LECTOTYPE (designated by Tryon 1960: 30): JAMAICA. [1784–1786], O.P. Swartz s.n. (S-R-1478, image!; isoelectotypes: LD-1765556, image!, S-06-1554, image!, S-06-1555, image!, US-00066384, image!). (Fig. 1, L-N; Map 2)

Dicksonia rubiginosa Kaulf., Enum. Filic. 226. 1824. *Dennstaedtia rubiginosa* (Kaulf.) T.Moore, Index Fil. (T.Moore) 2: xcvi. 1857. LECTOTYPE (designated here): BRAZIL. Rio de Janeiro: *K.H. Mertens s.n.* (E-00417515, image!; isoelectotype: LE00008017).

Dicksonia umbrosa Liebm., Mexic. Bregn. 262. 1849. TYPE (designated by Mickel & Smith 2004): MEXICO. Veracruz: Inter Colipa et Misantla, *F.M. Liebmann 2663* [*Pl. Mex. 2663, Fl. Mex. 804*] (C-n.v.; isoelectotypes: NY-00149033-frag., image!, US-00066399, image!).

Dicksonia decomposita Christ, Bull. Soc. Roy. Bot. Belgique 35(1): 180. 1896.
Dennstaedtia decomposita (Christ) Christ, Bull. Herb. Boissier, sér. 2, 5: 732.
 1905. LECTOTYPE (designated by Mickel & Smith 2004): Costa Rica, 1 Mar 1894,
A. Tonduz & H. Pittier 8644 (P-00743725, image!; isolectotypes: BR-
 0000006870355, image!; BR-0000006870386, image!; NY-00149026, image!;
 US-00066386, image!).

Plants terrestrial. Rhizomes long creeping, 0.5–1.8 cm diam, densely with light brown catenate hairs. Fronds determinate, 1–4 m long; petioles dark brown to vinaceous at the base, with root projections, 0.5–2 m × 0.8–1.5 cm, inermous, small aerophores, densely covered acicular and catenate hairs at the base, glabrescent above; laminae 3-pinnate-pinnatifid to 4-pinnate, 1–2 m long, with alternate pinnae; rachises light to dark brown, adaxially sulcate, abaxially light brown to ferruginous acicular and catenate hairs, adaxially densely with light brown to ferruginous catenate hairs, structure dark at base of axis, small aerophores; basal pinnae alternate, equilateral, 45–75 × 23–40 cm, lanceolate, proximally truncate, distally acute; costae abaxially densely with light brown to ferruginous acicular and catenate hairs, adaxially sulcate, densely light brown to ferruginous catenate hair, small aerephore, lacking adaxial wings; ultimate segments oblong, 0.6–1 × 0.3–0.5 cm, proximally sessile, distally round and dentate, with deep sinus forming segment; costules and veins abaxially and adaxilly with light brown to ferruginous acicular and catenate hairs; laminar tissue between the veins abaxially and adaxilly with light brown to ferruginous acicular and catenate hairs; lamina margins glabrous, entire and dentate at apex segments. Sori rounded, 0.5–1 × 0.5–1 mm; indusia purse-shaped, commonly with acicular hairs.

DISTRIBUTION.—Central Mexico to Panama, the Greater Antilles, and South America (in Peru, Bolivia, Brazil and Argentina; possibly also in Paraguay and Uruguay, but not recorded so far); from sea level to 1200 m in the studied area.

SPECIMENS EXAMINED.—PERU. Depto. Loreto: above Pongo de Manseriche, mouth of Rio Santiago, edge of opening in border forest, 200 m, 20 Nov 1931, *Y. Mexia 6128* (UC); Distr. Palcazu: El Paujil, lowland rain forest, 10°20'12"S, 75°15'39"W, 700–800 m, 13 May 2005, *H. van der Werff et al.* (UC).

BOLIVIA.—Beni: Ballivian Provincia, Río Colorado, Collegio Tecnico Agropecuario de Río Colorado, 15°00'S, 67°10'W, 235 m, 22 Jun 1989, *A & L. Fay 2088* (UC). La

Paz: Caranavi, serrania Bella Vista, 36 km de Caranavi hacia Sapecho, 22 Aug 1997, *M. Kessler 11263* (UC).

BRAZIL.—Alagoas: Ibateguara, Engenho Coimbra, Grotta do Varição, 35°51'55,9S, 09°00'12,4"S, 380-400 m, 19 Dec 2000, *M.R. Pietrobon & A.C.P. Santiago 4697* (UFP); Ibateguara, usina Serra Grande, Engenho Coimbra, Grotta do Taquarí/ Porcos, 09°00'19"S, 35°51'50,8"W, 390-415 m, 10 Feb 2001, *M.R. Pietrobon & A.C.P. Santiago 4906* (CEPEC; MG; UFP); Ibateguara, usina Serra Grande, Engenho Coimbra, Grotta do Quirino, 08°59'58,3"S, 35°52'14,7"W, 390-415 m, 11 Feb 2001, *M.R. Pietrobon & A.C.P. Santiago 4964* (CEPEC/CEPLAC; MG; UFP). Bahia: Camacan, Fazenda Serra Bonita, Reserva Serra Bonita, 15°23'30"S, 39°33'55"W, 835 m, 28 Jul 2008, *F.B. Matos et al. 1529* (RB; UPCB); Ilhéus, 5 Dec 1968, *J. Almeida & T.S. Santos 278* (CEPEC/CEPLAC; RB; SJRP); Ilhéus, Distrito Rio do Braço, Fazenda Estrela da Manhã, 14°40'56"S, 39°36'09"W, 80 m, 09 Dec 2014, *J.F. Souza et al. 258* (BHCB); Ipiaú, Mirabela Mineração, 14°10'50"S, 39°41'33"W, 13 Nov 2007, *D.T. Souza 341* (BHCB). Ceará: Maranguape, Serra de Maranguape, Trilha para Pedra Rajada, 03°50'S, 38°43'W, 650 m, 18 Feb 1998, *M. Almeida-Neto 374* (SJPR). Espírito Santo: Castelo, Parque Estadual do Forno Grande, 20°31'08"S, 41°05'11"W, 1200 m, 25 Jun 2008, *A. Salino et al. 13601* (BHCB); Itaguaçu, Santa Maria, Alto Limoeiro, 23 May 1946, *A.C. Brade 18371* (RB). Goiás: Corumbataí, Serra do Padre, 700 m, *C.E. Rodrigues Jr. & M.R. da Silva 536* (SJRP). Minas Gerais: Araponga, Parque Estadual da Serra do Brigadeiro, Trilha da Pedra do Pato, 1100–1200 m, 4 May 2017, *P.B. Schwartsburd et al. 4097* (VIC); Cascata, 01 Sep 1935, *A.P. Duarte 3077* (RB); Juiz de Fora, Mata do Krambeck, Sítio Malícia, 05 Apr 2008, *F.S. Souza et al. 387* (BHCB; CESJ); Nova Lima, RPPN Mata do Jambreiro, 19°58'15.9"S, 43°53'15.7"W, 23 Mar 2004, *J.B. Figueiredo et al. 369* (BHCB); Patos de Minas, Cascata, 01 Sep 1935, *A.P. Duarte 3077* (BHCB); Sabará, R.P.P.N. Cuiabá, base da Serra da Piedade, 19°51'08.7"S, 43°44'38.1"W, 770 m, 18 Jul 2006, *T.E. Almeida & D.T. Souza 237* (BHCB); São Roque de Minas, Parque Nacional da Serra da Canastra, Casca Danta, 20°18'20"S, 40°31'12.8"W, 14 Jul 1997, *A. Salino 3196* (BHCB); Vale Verde, Parque Nacional do Caparaó, 20 Nov 2008, *A. Salino s.n.* (BHCB-123099); Viçosa, Escola Superior de Agricultura e Veterinária, Horticultural Hill, 670 m, 7 Jul 1930, *Y. Mexia 4846* (F, IAN, MO-*n.v.*, U, UC, US); Viçosa, Escola Superior de Agricultura e Veterinária, base of Horticultural Hill, 668 m, 17 Jul 1930, *Y. Mexia 4866* (IAN, F, U, UC, US, VIC, WTU); Viçosa,

Escola Superior de Agricultura e Veterinária, Jan 1934, *J.G. Kuhlmann s.n.* (VIC-1309). Paraná: Antonina, Reserva Natural Rio Cachoeira (SPVS), estrada Sede-Gervásio, 25°15'S, 48°41'W, 30 m, 30 Apr 2005, *F.B. Matos & M.O. Silva 538* (UPCB); Antonina, Reserva Natural Rio Cachoeira (SPVS), trilha do Zé Carlos, 25°18'S, 48°41'W, 30 m, 30 Apr 2006, *F.B. Matos & G. Weiss 1132* (UPCB); Guaratuba, 16 Jul 1971, *L.C.Krieger 11153* (RB); Guaraqueçaba, Morro do Quitumbê ou do Costão, 25°17'S, 48°20'W, 16 Apr 1995, *S.F. Athayde et al. 295* (UPCB); Guaraqueçaba, Reserva Natural Salto Morato, Área de Projeto Sucessão, 21 Dec 1999, *A.L.S. Gatti & G. Gatti 323* (UPCB); Guaratuba, 16 Dec 1972, *P.L.H. Krieger 11153* (UPCB). Rio de Janeiro: sem data (coleção Fée), *Glaziou 385* (RB); sem data (coleção Fée), *Glaziou 2381* (RB); Nova Friburgo, Macaé de Cima, 22°22'36"S, 42°28'58"W, 1200 m, 13 Dec 2019, *F. Gonzatti et al. 5473* (HUCS); Rio de Janeiro, estrada Dona Castorina, Vista Chinesa, *A.C. Brade 16113* (RB). Rio Grande do Sul: Barracão, caminho para Malhadinho, 15 Feb 2000, *T. Strchl 3020* (HAS; VIC); Barracão, linha Tope, 13 Jul 2000, *J. Spanholi s.n.* (HAS-37258; VIC); Itati, Arroio do Pinto, 28 Mar 2017, *R.M. Senna 1643* (HAS); Osório, Maquiné, Estação Experimental Fitotécnica, 2 Dec 1986, *J. Mattos & N. Silveira 30319* (HAS); Paratí, Parque Nacional da Serra da Bocaina, Serra do Mar, trilha para o pico do Cruzeiro, 23°18'14.4"S, 44°47'16.3"W, 400 m, 07 Aug 2001, *A. Salino et al. 7344* (BHCB); São Francisco de Paula, Serra do Umbu, 29°30'19"S, 50°19'27"W, 09 Jul 2016, *F. Gonzatti 2540a* (HUCS); Tenente Portela, P. F. Turvo, 13 Jan 1982, *R. Bueno 3947* (ICN; VIC). Santa Catarina: Araranguá, Luiz Alves, 10 Jan 1941, *P.C. Reitz 685* (RB); Blumenau, Morro do Cachorro, 26°46'36"S, 49°02'16"W, 150-759 m, 15 May 2017, *L.A. Funez 6349* (FURB); Itapoá, na saída da cidade em direção à Garuva ou BR 101, 100-200 m, 11 Jan 2020, *P.B. Schwartsburd et al. 4619* (VIC); Itajaí, Escalvado, 20 m, 12 Apr 1946, *R. Reitz 1595* (RB); Itajaí, Luiz Alves, 1941, *P.C. Reitz 676* (RB); Quilombo, cataratas do Salto Saudades, 26°40'39"S, 52°36'29"W, 435 m, 23 Dec 2021, *F. Gonzatti 6236* (HUCS); Timbé do Sul, Ecótono entre matas Nubulares, Floresta c/ Araucária e Floresta Atlântica, Serra da Rocinha, 300 m, 6 Feb 2009, *P.B. Schwartsburd & A. C. Corazzini 1988* (VIC); Witmarsum, Krauer Central, Florística IFFSC 686, 26°54'37"S, 49°46'14"W, 439 m, 13 Apr 2010, *A. Korte & A. Kniess 2705* (FURB). São Paulo: Analandia, Serra do Cruzeiro, 22°08'S, 47°40'W, 24-26 Oct 1986, *A. Salino 49a* (SJPR); Analandia, Serra do Cruzeiro, 22°08'S, 47°40'W, 750 m, 1 Apr 1988, *A. Salino 438* (SJRP); Alto da Serra,

Jun 1912, *H. Luederwaldt s.n.* (SPF; VIC-54.600); Ariranha, Faz. [Fazenda] Figueira, 03 Nov 1994, *L. Bizari et al. 1a* (SJRP); Barra do Turvo, Cachoeira Vêu da Noiva, 8 km do município de Barra do Turvo, , borda imediata do Parque Estadual do Jacupiranga, núcleo Cerdo, 24°43'12"S, 48°27'04"W, 700 m, *A. Salino et al. 10306* (BHCB); Bananal, Estação Ecológica de Bananal, 22°47'32.2"S, 44°21'32.6"W, 1200 m, 11 Sep 2001, *A. Salini et al. 7521* (BHCB); Brotas, Cachoeira Caçoroba, 22°17'S, 48°06'W, 22 May 1993, *C.E. Rodrigues Jr. & M.R. Silva 470* (SJRP); Brotas, Faz. [Fazenda] Santa Maria, Cachoeira Santo Cristo, 22°17'S, 48°47'W, 700 m, 22-23 May 1993, *R.M.C. Andrade & M.R. Silva 165* (SJRP); Sete Barras, fazenda Intervalles, 21 Jul 1994, *A. Salino 2061* (BHCB); Iporanga/ Apiaí, Parque Estadual Turístico do Alto Ribeira (PETAR), Núcleo Santana, 21°Sep 2011, *F.F.F. Mazziere & A. Soller 598* (UPCB); Iporanga/ Apiaí, Parque Estadual Turístico do Alto Ribeira (PETAR), Núcleo Cabloco, 24°32'22"S, 48°41'36"W, 29 May 2012, *F.F.F. Mazziere et al. 1042* (UPCB); Iporanga/ Apiaí, Parque Estadual Turístico do Alto Ribeira (PETAR), Núcleo Cabloco, 24°32'22"S, 48°41'36"W, 29 May 2012, *F.F.F. Mazziere et al. 1047* (UPCB); Juquiá, Reserva Votorantim, Complexo Juquiá, trilha da casa de Pedra, 24°09'55"S, 47°33'36"W, 39 m, 28 Mar 2013, *A. Salino et al. 15629* (BHCB); Juquiá, Reserva Votorantim, Complexo Juquiá, trilha de Chaminé, UHE Alecrim, 20°06'08"S, 47°30'18"W, 193 m, 01 Apr 2013, *T.E. Almeida et al. 3253* (SPF); Mendonça, Fazenda Santa Maria, 21°12'S, 49°35'W, 21 Dec 1996, *M.R. Pirotbom-Silva 3873* (SJRP); Mirassol, Grotta de Mirassol, 06 Dec 1987, *A. Salino* (UEC); Ribeirão Grande, Parque Estadual Intervalles, trilha Caçadinha, 24°16'39"S, 48°25'09"W, 780 m, 15 Apr 2003, *A. Salino et al. 8433* (BHCB); São Bento do Sapucaí, estrada para a Pedra do Baú, floresta de araucária, 28 Dec 2016, *P.B. Schwartsburd et al. 3866* (VIC); Serra da Cantareira, Ex. Herb. Damasio, Jun 1913, *F.T. Toledo s.n.* (RB-36242); São Luiz do Paraitinga, Parque Estadual da Serra do Mar, núcleo Santa Virgínia, trilha Pirapitinga, 23°20'29"S, 45°08'48"W, 900-950 m, 04 Mar 2001, *A. Salino et al. 6087* (BHCB); São Paulo, Parque Estadual da Serra do Mar, núcleo Cunha, 18 Dec 1996, *A. Salino 2954* (BHCB); Ubatuba, Parque Estadual da Serra do Mar, Núcleo Picinguaba, Sertão do Puruba, 23°20'24.0"S, 44°58'40.6"W, 40 m, 05 Aug 2001, *A. Salino et al. 7244* (BHCB). **State unknown:** locality unknown, s.d., *C.F. von Martius s.n., ex Herb. Fée* (RB-30646); locality unknown, s.d., *A.M. Claussen 118, ex Herb. Fée* (RB).

ARGENTINA.—Argentina, Jujuy, Depto. Ledesma, camino a la toma del Rio Zora. 15 km before the intake, 15 Dec 1986, *F. Zuloaga 2877* (UC); Misiones, San Pedro, Parque Provincial Esmeralda, Alrededores del la Estacion Biologica, 16 Feb 2017, *G. Marquez 364* (NY); Misiones, Parque Provincial Moconá, 22 Feb 2017, *G. Marquez 471* (NY).

ADDITIONAL SPECIMENS EXAMINED.—EQUADOR. Pichincha: San Jose de Toachi 100 kms W, of Quito, 03 Apr 1951, *P.R. Bell 201* (RB); Cacaoal, 06 May 1951, *P.R. Bell 922* (RB).

HONDURAS.—Quebrada Montañuelas, entre La Misión y Montañuelas, Departamento Comayaga, 31 Mar 1963, *A.R. Molina s.n.* (RB-168402).

JAMAICA.—Hanover Parish: Buddy Hill, 2 mi SE of Cash Hill at ca. 180 m on limestone substrate, 18°22'16N, 78°05'47"W, 23 Jul 1997, *R. O'Reilly & A. Siaca s.n.* (UPRRP-20554); Hollymount: 19-20 Sep 1906, *L. M. Underwood 3469* (NY); Near Cedarhurst: 16 Feb 1903, *L. M. Underwood 1551* (NY); Near Troy "Cock-Pit Country": 07-11 May 1903, *L. M. Underwood 2900* (NY); St. Catherine Parish, Holymount on Mount Diablo, 09 Jul 1963, *M.R. Crosby 615* (RB).

MEXICO.—Coleção Fée, *Galeotti 6292* (RB); Huatusco, Coleção Fée, Agu 1854, *W. Schaffner 257* (RB); Huatusco, *W. Schaffner 258* (RB).

PANAMÁ.—Along Quebrada Bonita, 13 Km NE of Buena Vista. 3 Km NW of Salamanca, 28 Oct 1973, *M. Nee 7646* (RB); Upstream From Puerto Pilon-Portobelo road. 6 km S of Portobelo. Province of Colon. Disturbed tropical wet forest on slope on N side of Rio Guanache, 0,5 - 1,0 Km, 25 Sep 1973, *M. Nee 7118* (RB).

PERU.—Distrito Churubamba; hacienda Mercedes, Cotirarda, damp ravine, 21 Sep 1936, *Y. Mexia 8218* (RB).

PUERTO RICO.—Bo. Limaní, Sector Guayo, 18°09.55'N, 66°49.08'W, 925-975 m, 18 Feb 2007, *F. Axelrod & J. Turnquist 13776* (UPRRP); Peñuelas, Bo. Rucio, trail to Cerrote de Peñuelas, Wet moutain forest, 955 m, 18°07.22'N, 66°42.06'W, 3 Mar 2011, *F. Axelrod et al. 14711* (UPRRP).

Dennstaedtia cicutaria can be recognized by presenting catenate and acicular hairs on the petioles, rachis and laminae. *Dennstaedtia cicutaria* by pinnae alternate (vs. opposite), pinnae pedicellate (vs. sessile) and axes brownish (vs. stramineous). *Dennstaedtia cicutaria* also differs from *D. glauca* by costules and veins abaxially and adaxilly with acicular and catenate hairs (vs. abaxially only catenate hairs and adaxially glabrous); laminar tissue between the veins abaxially and adaxilly acicular

and catenate hairs (vs. abaxially only catenate hairs, adaxially glabrous), indusia with acicular hairs (vs. glabrous).

Dennstaedtia concinna (C.Presl) T.Moore, Index Fil. (T.Moore) 2: xcvi. 1857. *Patania concinna* C.Presl, Tent. Pterid. 138. 1836. nom. nov. *Davallia concinna* C.Presl, Reliq. Haenk. 1: 66. 1825, nom. illeg. [non Schrader 1818]. *Dicksonia concinna* (C.Presl) Hook., Sp. Fil. [W.J. Hooker] 1: 74. 1844. LECTOTYPE (designated here): PERU. T.P.X. Haenke s.n. (PRC-450738!; isolectotypes: PR-on two sheets (23918a!, and 23918b!). (Fig. 2, A-C; Map 2)

Plants terrestrial. Rhizomes creeping, 0.6–1 cm diam, densely covered with “rough structure” and golden to light brown catenate hairs. Fronds determinate, 0.85–2 m long; petioles dark brown at the base, light to dark brown above, 0.35–0.60 m × 0.5–1 cm, inermous, with small aerophores, buds at the base, “rough structure” and catenate hairs to glabrescent at the base, glabrescent above; laminae 2-pinnate-pinnatifid, 0.70–1.20 m long, proximally opposite pinnae, distally alternate pinnae; rachises light to dark brown, adaxially sulcate, abaxially and adaxially with catenate hairs to glabrescent, adaxially more densely at the base of axes, with small aerophores; basal pinnae opposite to sub-opposite, equilateral, 28–50 cm × 10–26 cm, lanceolate, acute and strongly reduced at the base, acute at the apex; costae abaxially densely light brown catenate hairs, adaxially sparsely light brown catenate hairs to glabrescent, adaxially catenate hair more densely at base of axis, small aerophore; lacking adaxial wings; ultimate segments round, proximally sessile, distally crenate to dentate, 0.8–1.2 × 0.5–1 cm, shallow sinus not forming segments; costules and veins abaxially with light brown catenate hairs, adaxially light brown catenate hairs sparsely to glabrous; laminar tissue between the veins abaxially with catenate hairs, adaxially glabrous; lamina margins glabrous, entire and crenate to dentate at apex. Sori round, willing mainly at the apex of the ultimate segments, oriented in the plane of the lamina, sometimes in sinus, 0.5–0.8 × 0.5–0.8 mm; indusia hemi-spherical, glabrous. Espores trilete.

DISTRIBUTION.—*Dennstaedtia concinna* occurs in the Amazon region of Venezuela, Brazil, and Bolivia.

SPECIMENS EXAMINED.—BRAZIL. Amazonas: São Gabriel da Cachoeira, Serra do Curicuriari, 20 Oct 1978, *M. Madson et al* PFE556 (BHCB; INPA). Mato Grosso do Sul: Corumbá, Morro Urucum, Córrego Banda Alta, 19°11'15.148"S,

57°34'53.081"W, 07 Jun 2001, *E.L.M. Assis 217a* (UPCB; RB); idem, Morro Santa Cruz, Córrego Bandalta, 06 Jul 2001, *E.L.M. Assis 217b* (BHCB, COR). Rondônia: Colorado do Oeste. Linha 4, sul, 28 May 1991, *P.J. Pivetta 1487* (SJRP); idem, Sítio Angical, Linha Nova 1 Km 3, rumo Escondido, propriedade Sr. João Oliveira Corte, 17 Jan 2007, *S.Z. Neiva 348* (HBRA, image!); idem. Sítio Paraiso, Linha 01, rumo Colorado Km 18, propriedade Sr. Wladir Luiz Breitenbach, 17 Feb 2007, *S.Z. Neiva 535* (HBRA, image!).

BOLIVIA.—Beni: Ballivian Province, 25 km from Yucumo on Yucumo-Quiquibey road, in the Pilón Lajas, 15°17'S, 67°04'W, 950 m, 18 Jul 1990, *A. Fay & L. Fay 2756* (US, image!); Depto. Cochabamba: Prov. Ayopaya, 50 m del sub campamento, quebrada con agua permanente, ladera superior de la serrania de Mosetenes, 16°2'S, 66°39'W, 24 Sep 2004, 1118 m, *H. Huaylla 1411* (UC); Depto. Cochabamba, Prov. Chapare, cavernas del Repechón, PN Carrasco, 17°02'S, 65°26'W, 550 m, 8 Sep 1996, *M. Kessler et al. 8328* (UC); Prov. Carrasco, Parque Nacional Carrasco, al S al S del campamento Petrolero Ichoa, 17°38'S, 64°24'W, 767 m, 23 Sep 1997, *A. Acebey 767* (UC); Prov. Carrasco, 149 km antigua carretera Cochabamba-Villa Tunari, 17°07'S, 65°34'W, 1000 m, 31 Agu 1996, *M. Kessler et al. 7994* (UC); Prov. Chapare, Parque Ecoturítico Machia, 1 km la E de Villa Tunari, 16°58'S, 65°24'W, 300 m, 16 Sep 1996, *M. Kessler et al. 8513* (UC).

ADDITIONAL SPECIMENS EXAMINED.—VENEZUELA. Dpto. Atures: Amazonas, E slope of unnamed peak, 8 km NW of settlement of Yutaje, 4 km W of Río Coro-Coro, W of Serranía de Yutaje, 05°41'N, 66°10'W, 1500–1760 m, *R. Liesner & B. Holst 21607A* (UC).

Dennstaedtia concinna differs *Dennstaedtia mathewsii* by the costae adaxially with sparse catenate hairs to glabrescent (vs. adaxially with dense catenate hairs), the ultimate segments rounded with deeper sinus, sometimes with the sori within the sinuses (vs. oblong without deep sinuses; sori always projected out of the blade), the sori round, oriented in the plane of the lamina, and the indusia hemi-spherical, (vs. sori hemi-spherical, oriented in the plane of the lamina, along margins, indusia copulifome).

Dennstaedtia cornuta (Kaulf.) Mett., Ann. Sci. Nat. V, 2: 260. 1864. *Dicksonia cornuta* Kaulf., Enum. Fil. 227. 1824. LECTOTYPE (or NEOTYPE?, designated here): BRAZIL. [Minas Gerais]: Brasilia meridionalis, prope Santo Antônio [Santo Antônio

do Itambé], s.d. [1818-1820], F. Sellow B705 C 90 (B-200045184, image!; isolectotypes: B-200045182, image!, B-200045183, image!, B-200045185, image!). (Fig. 2, D-G; Map 3)

Dennstaedtia lindsayiformis (Fée) C. Chr. Ind. Fil. 217. 1905. *Microlepia lindsayiformis* Fée, Crypt. Vasc. Brésil 1: 152, t. 51, fig. 2. 1869.—Lectotype (designated here): BRAZIL, Rio de Janeiro, 28 Apr 1868, *Glaziou 2379* (P-00633278, image!; isolectotype: P-00633279, image!).

Plants terrestrial ou rupestral. Rhizomes long creeping, unbranched, rugged, 0.5–3 cm diam, with villous-catenate hairs to glabrous, roots with villous-catenate hairs. Fronds determinate, 1–3.5 m long; petioles dark brown, rarely light brown, frequently with petiolar bud basally, 0.5–1.5 m × 0.5–2 cm, inermous, small aerophores, abaxially and adaxially densely covered catenate hairs to glabrescent, roots coming out from the base; laminae 3-pinnate to 3-pinnate-pinnatifid, (0.5) 1–2 m long, with proximally opposite to sub-opposite pinnae, distally alternate pinnae; rachises light or dark brown, inermous, abaxially densely light or dark brown catenate hairs, adaxially sulcate, sparsely light or dark brown catenate hairs, more densely at base of axis, sometimes buds in axes, small aerophores; basal pinnae opposite to sub-opposite, inequilateral, lanceolate, with the first acroscopical pinnule reduced, obtuse base, acute apex, (5) 20–70 × (5) 10–25 cm; costae abaxially densely with light or dark brown catenate hairs, adaxially sulcate, moderate to sparsely light or dark brown catenate hair, more densely at base of axis, small aerephore, lacking adaxially wings; ultimate segments equilateral, ovate to oblong, sessile base, round to acute and entire to crenate apex, 1–2 × 0.5–1 cm, shallow sinus not forming segment; costules and veins abaxially densely with light or dark brown catenate hairs, adaxially sparsely light or dark brown catenate hairs to glabrescent; laminar tissue between the veins abaxially and adaxially with sparsely dark brown catenate with dark brown catenate to glabrous; lamina margins glabrous, entire and crenate apex. Sori rounded, 0.7–1.8 × 0.7–1.8 mm; indusia purse-shape, glabrous. Espores trilete.

DISTRIBUTION.—*Dennstaedtia cornuta* has confirmed Occurrence for Argentina, Brazil and northern South America.; altitudinal variation between 200 to 4.000 m.

SPECIMENS EXAMINED.—PERU. Distrito de Oxapampa: Parque Nacional Yanachaga-Chemillen, San Alberto sector, Cordillera de Yanachaga, 10.53964N, 75.36669, 2306

m, 25 May 2016, *C.J. Rothfels et al. 5087* (UC). Dist. Santa Ana: Poromate, boque primario, 12°56'S, 72°47'W, 2302 m, 17 Jun 2003, *G. Calatayud et al. 1495* (UC)

BOLIVIA.—Depto. Lá Paz, Prov. Caranavi, serrania Bella Vista, 38 km de Caranavi hacia Sapecho, 15°40'S, 67°29'W, 1500 m, 25 Aug 1997, *M. Kessler et al. 11406* (UC). Cochabamba, Carrasco, 116 km antigua carretera a Cochabamba-Villa Tunari, -17.1333333, -65.6333333, 2400 m, 06 Jul 1996, *M. Kessler 7034* (UC).

BRAZIL.—Alagoas: Ibataguara, Usina Serra Grande, Engenho Coimbra, Mata do Paraíba, 14 Oct 2003, *M.R. Pietrobon et al. 5611* (CESJ; UFP). Bahia: Arataca, Serra da Lontra, 15°12'10"S, 39°24'29"W, 600 m, 12 Feb 2005, *F.B. Matos et al. 405* (CEPEC; UPCB); Boa Nova, Recanto dos Pássaros, 14°24'24.78S, 40°07'14.34"W, 785-1030 m, 03 Apr 2015, *V.A.O. Dittrich & A.M. Souza 2091* (BHCB; CESJ); Boa Nova, Recanto dos Pássaros, 14°24'24.78S, 40°07'14.34"W, 785-1030 m, 03 Apr 2015, *V.A.O. Dittrich & A.M. Souza 2092* (BHCB; CESJ); Camacã, fazenda Serra Bonita, 15°23'30"S, 39°33'55"W, 835 m, 03 Feb 2005, *F.B. Matos et al. 295* (CEPEC; UPCB); Camacã, RPPN Serra Bonita, 15°23'30"S, 39°33'55"W, 835 m, 03 Mar 2006, *F.B. Matos 1063* (UPCB); Santa Terezinha, Serra da Jiboia, subida da serra pelo Monte Cruzeiro (GAMBA – REFLORESTAR), 12°52'15"S, 39°28'47"W, 435 m, 03 Mar 2001, *F.R. Nonato et al. 804* (HUEFS). Espírito Santo: Cariacica, Alegre, Mata de altitude, 20.2642°S, 40.4197°W, 24 Jun 1988, *O.J. Pereira et al. 1558* (VIC; VIES); Cariacica, Alegre, Reserva Biológica Duas Bocas, trilha do Pau Oco, 20°17'29"S, 40°31'10"W, 600 m, 15 Feb 2008, *P.H. Labiak et al. 4618* (CEPEC; MBML; UPCB; RB); Cariacica, Reserva Biológica de Duas Bocas, 20°15'31"S, 40°29'51"W, 170 m, 11 Jun 2010, *A. Salino et al. 14850* (BHCB); Cariacica, Reserva Biológica de Duas Bocas, 20°15'05"S, 40°29'60"W, 236 m, 13 Jun 2010, *A. Salino et al. 14945* (BHCB); Castelo, 20°30'39"S, 41°04'53"W, 1105 m, 26 Jun 2008, *A. Salino et al. 13570* (BHCB); Castelo, Parque Estadual do Forno Grande, 20°52'00.8"S, 41°08'79.6W, 29 Sep 2015, *N.T.L. Pena et al. 790* (VIC); Castelo, Parque Estadual do Forno Grande, 20°52'00.8"S, 41°08'79.6W, 29 Sep 2015, *N.T.L. Pena et al. 791* (VIC); Castelo, Parque Estadual do Forno Grande, 20°30'39"S, 41°04'53"W, 1105 m, 25 Jun 2008, *A. Salino et al. 13570* (BHCB); Castelo, Parque Estadual do Forno Grande, caminho para o Forninho, 20°31'18"S, 41°05'57"W, 1700 m, *A. Salino 13738* (BHCB); Castelo, Parque Estadual do Forno Grande, trilha para a Goela da Onça, 20°30'58"S, 41°06'41"W, 1500 m, 19 Jul 2008, *P.H. Labiak et al. 4846* (CEPEC; MBML; RB; UPCB); Divino de São Lourenço, Parque Nacional do Caparaó,

rio do Veado, Pedra Escorada, 20°33'07"S, 41°45'44"W, 1190 m, 10 Feb 2011, *F.S. Souza et al. 1486* (BHCB); Ibitirama, Parque Nacional do Caparaó, base de Santa Marta, 20°29'45.5"S, 41°43'55.8"W, 960 m, 11 Sep 2008, *A. Salino 13792* (BHCB); Rio Novo do Sul, comunidade Couro dos Monos, Sítio Recanto do Aconchego, 20°50'18"S, 40°53'37"W, 100 m, 14 Nov 2015, *I.O. Moura et al. 59* (BHCB); Santa Teresa, Estação Biológica de Santa Lucia, 24 Feb 1996, *A. Salino 2589* (BHCB); Santa Teresa, Estação Biológica de Santa Lucia, Museu de Biologia Melo Leitão, próximo ao rio Timbuí, 19°53'48"S, 40°36'11"W, 600 m, 11 Jul 2007, *P.H. Labiak et al. 4010* (UPCB); Santa Teresa, Nova Lombardia, Reserva Biológica Augusto Ruschi, trilha da Cachoeira, 19°55'14"S, 40°33'37"W, 750-850 m, 02 Dec 2008, *A. Salino et al. 14012* (BHCB); Santa Teresa, Nova Lombardia, Reserva Biológica Augusto Ruschi, trilha da Preguiça, 19°54'58"S, 40°32'31"W, 830-900 m, 03 Dec 2008, *A. Salino et al. 14012* (BHCB); Santa Teresa, Nova Lombardia, Reserva Biológica Augusto Ruschi, córrego próximo ao marco 112, 03 Oct 2002, *R.R. Vervloet et al. 1132* (MBML); Santa Teresa, Nova Lombardia, Reserva Biológica Augusto Ruschi, 24 Sep 2019, *N.T.L. Pena et al. 861* (VIC); Santa Teresa, Nova Lombardia, Reserva Biológica Augusto Ruschi, 24 Sep 2019, *N.T.L. Pena et al. 862* (VIC); Santa Teresa, Nova Lombardia, Reserva Biológica Augusto Ruschi, 24 Sep 2019, *N.T.L. Pena et al. 864* (VIC); Santa Teresa, Nova Lombardia, Reserva Biológica Augusto Ruschi, 24 Sep 2019, *N.T.L. Pena et al. 864* (VIC); Sooretama, Reserva Biológica de Sooretama, região da lagoa do Macuco, 19°02'21"S, 39°56'40"W, 15 m, 15 May 2008, *A. Salino et al. 13400* (BHCB). Minas Gerais: Aiuruoca, Vale do Matutu, R.P.P.N. do Matutu, cachoeira do Fundo, 22°10'92"S, 44°65'28"W, 12 Oct 2004, *A. Salino et al. 9816* (BHCB); Alto Caparaó, Parque Nacional do Caparaó, Vale Verde, 20°25'08.7"S, 41°50'33.0"W, 1200-1390 m, *A. Salino et al. 11352* (BHCB); Antônio Carlos, 31 Jan 1980, *F. Salimena 22* (UEC); Antônio Carlos, Agu 1980, *L. Krieger s.n.* (BHCB-4307; CESJ-2713); Antônio Carlos, 31 Jan 1980, *L. Krieger s.n.* (BHCB-4340); Araponga, Parque Estadual da Serra do Brigadeiro, 1400 m, 10 Aug 1999, *A. Salino 4891* (BHCB); Araponga, Parque Estadual da Serra do Brigadeiro, trilha para o Pico do Boné, 26 May 2000, *A. Salino 5481* (BHCB); Araponga, P.E. Serra do Brigadeiro, Estrada principal do Parque, 20°43'08" S, 42°28'57" W, 1300 m, 29 Apr 2013, *P.B. Schwartsburd & S. Ferreira da Silva 2764* (VIC); Araponga, Cachoeira do Remanso, propriedade particular do Sr. Dico, 20°65'65.9"S, 42°45'40.7"W, 05 Oct 2020, *N.T.L. Pena & G.V. Pena 981* (VIC);

Araponga, Parque Estadual da Serra do Brigadeiro, Pico do Boné, 20°40'30"S, 42°26'50"W, 1500 m, 23 Feb 2014, *P.B. Schwartzburd et al. 3070* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, Pico do Boné, 20°40'37"S, 42°26'57"W, 1500 m, 23 Feb 2014, *P.B. Schwartzburd et al. 3109* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, Pico do Boné, 20°40'37"S, 42°26'57"W, 1500 m, 23 Feb 2014, *P.B. Schwartzburd et al. 3110* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, Pico do Boné, 20°40'37"S, 42°26'57"W, 1500 m, 23 Feb 2014, *P.B. Schwartzburd et al. 3113* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, Pedra do Pato, 1400 m, 22 Feb 2014, *P.B. Schwartzburd et al. 3009* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, Pedra do Pato, 1200-1400 m, 04 May 2017, *P.B. Schwartzburd et al. 4135* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, Trilha dos Muriquis, 1300–1400 m, 5 May 2017, *P.B. Schwartzburd et al. 4156* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, Pedra do Pato, 20°39'34.6"S, 41°00'38.9"W, 1450 m, 11 Dec 2018, *N.T.L. Pena et al. 758* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, portaria de Arapongas, 20°42'51"S, 42°29'15"W, 1400 m, 13 Mar 2014, *P.B. Schwartzburd & J.B.S. Pereira 3144* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, trilha do Carvão, 20°42'68.4"S, 40°27'12.0"W, 1158 m, 12 Dec 2018, *N.T.L. Pena et al. 769* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, trilha do Carvão, 20°42'68.4"S, 40°27'12.0"W, 1158 m, 12 Dec 2018, *N.T.L. Pena et al. 771* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, trilha do Carvão, 20°42'68.4"S, 40°27'12.0"W, 1158 m, 12 Dec 2018, *N.T.L. Pena et al. 772* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, trilha do Carvão, 20°42'68.4"S, 40°27'12.0"W, 1232 m, 12 Dec 2018, *N.T.L. Pena et al. 773* (VIC); Araponga, Parque Estadual da Serra do Brigadeiro, trilha dos Muriquis, 1300-1400 m, 05 May 2017, *P.B. Schwartzburd et al. 4156* (VIC); Bandeira, mata do Boi Rajado, a ca. 14 km da sede Bandeira, divisa com a Bahia, 15°47'55.7"S, 40°31'35.2"W, 620-800 m, 05 Oct 2003, *A. Salino et al. 9058* (BHCB); Camanducaia, 28 Feb 2000, *R.B. Torres et al. 1108* (BHCB); Camanducaia, mata ciliar do Canela, família Barbosa, 06 Feb 2002, *L.C.N. Melo 183* (BHCB); Camanducaia, mata da nascente do Rio Camanducaia, 22°42'50"S, 45°56'12"W, 1700-1900 m, 20 Jun 2000, *A. Salino 5612* (BHCB); Caparaó, 1100 m, 29 Sep 1977, *P.L. Krieger 15082* (BHCB; CESJ); Caparaó, Parque Nacional Serra do Caparaó, 20°29'44"S, 41°49'12"W, 1500 m, 12 Mar 2014, *P.B. Schwartzburd & J.B.S. Pereira 3140* (VIC); Caparaó, Parque Nacional Serra do Caparaó, 20°29'44"S, 41°49'12"W,

1500 m, 12 Mar 2014, *P.B. Schwartzburd & J.B.S. Pereira 3141* (VIC); Caparaó, Parque Nacional Serra do Caparaó, 20°29'44"S, 41°49'12"W, 1500 m, 12 Mar 2014, *P.B. Schwartzburd & J.B.S. Pereira 3141* (VIC); Carangola, Serra do Brigadeiro, Fazenda Neblina, 1300 m, 28 May 1989, *A. Salino 801* (UEC); Catas Altas, RPPN Serra do Caraça, mata do engenho, 20°07'S, 43°27'W, 20 Nov 2004, *N.F.O. Mota et al. 78* (BHCB); Catas Altas, R.P.P.N. Santuário do Caraça, mata do engenho, 25 Aug 2008, 20,05003S, 4351639W, 847 m, *R.S. Viveiros et al. 4* (BHCB); Delfim Moreira, fazenda Boa Esperança, trilha do Marlon, 22°34'32"S, 45°19'20"W, 1313 m, *T.E. Almeida et al. 2868* (BHCB); Descoberto, Reserva Biológica da Represa do Grama, 10 Nov 2001, *J.O. Augustin et al. s.n.* (RB-377413); Descoberto, Reserva Biológica da Represa do Grama, 15 Jun 2005, *C.M. Mynssen et al. 733* (RB); Espera Feliz, Parque Nacional do Caparaó, caminho para Macieira, 20°29'35"S, 41°49'18"W, 1602 m, 04 Mar 2010, *D.R.M. Neves et al. 765* (BHCB); Itabirito, 20°24'33"S, 43°54'64"W, 28 Jan 2015, *V.T. Giorni s.n.* (BHCB-181881); Itamonte, Parque Nacional do Itatiaia, grotta úmida, 22°20'16.9"S, 44°44'66"W, 1850-2000 m, 12 Jul 2007, *A. Salino et al. 12472* (BHCB); Itamonte, Parque Nacional do Itatiaia, estrada para abrigo Rebouças, 22°22'6.3"S, 44°44'51.9"W, 1900 m, 10 Jul 2007, *A. Salino et al. 12424* (BHCB); Itamonte, Parque Nacional do Itatiaia, estrada principal para a sede do Itatiaia, km 8, 2060 m, 15 Feb 2020, *N.T.L. Pena & P.B. Schwartzburd 972* (VIC); Jequeri-Canaã, área da Usina de Cachoeira Grande, 18 Sep 1997, *A. Salino 3494* (BHCB); Nova Lima, RPPN Capitão do Mato, 19°58'41.9"S, 43°53'10.6"W, 17 Sep 2003, *J.B. Figueiredo et al. 58* (BHCB); Nova Lima, RPPN Capitão do Mato, 20°08'00.8"S, 43°53'10.6"W, 19 Sep 2003, *J.B. Figueiredo et al. 108* (BHCB); Nova Lima, RPPN Tumbá, 26 Sep 2003, *J.B. Figueiredo et al. 160* (BHCB); Olaria, São Francisco do Prata, Serra das Flores, 1500 m, 06 Sep 1079, *Bacharelados 16558* (BHCB); Ouro Preto, 1902, *C.A.W. Schwacke s.n.* (BHCB-1402); Ouro Preto, 1934, *J. Badini s.n.* (OUPR-10554); Ouro Preto, Água Limpa, 1906, *J. Badini s.n.* (OUPR-10555); Ouro Preto, Áreas Ferreas, 1936, *J. Badini s.n.* (OUPR-10556); Ouro Preto, Serra de Ouro Preto, 1950, *J. Badini s.n.* (OUPR-10553); Palmyra, Mata da Represa, 30 Sep 1937, *A.C. Brade 15904* (RB); Sabará, R.P.P.N. Cuiabá, base da Serra Piedade, 19°51'08.7S, 43°43'45.7"W, 776 m, 18 Aug 2006, *T.E. Almeida & D.T. Souza 385* (BHCB); Santa Maria do Salto, Distrito de Talismã, fazenda Duas Barras, 16°24'16.5"S, 40°03'27.4"W, 750-800 m, 09 Oct 2003, *A. Salino et al. 9173* (BHCB); Sapucaí-Mirim, Bairro Juncal, Sítio Queda d'água, 22°43'50.3"S, 45°54'33.9"W, 1535

m, *L.C.N. Melo et al. 112* (BHCB); Sapucaí-Mirim, Propriedade do Sr. Germano, 22°44'31.7"S, 45°57'42.4"W, 1430 m, 19 Jul 2007, 22°44'31.7"S, 45°57'42.4"W, 1430 m, *A. Salino et al. 12820* (BHCB); Simonésia, RPPN Mato do Sossego, 20°03'S, 42°02'W, 1000 m, 19 Sep 2014, *P.B. Schwartsburd 3355* (VIC); Simonésia, RPPN Mato do Sossego, 20°03'S, 42°02'W, 1000 m, 19 Sep 2014, *P.B. Schwartsburd 3356* (VIC); Simonésia, RPPN Mato do Sossego, 20°03'S, 42°02'W, 1000 m, 19 Sep 2014, *P.B. Schwartsburd 3357* (VIC); Serra do Frazão, 1936, *J. Badini 319* (RB); Sete Barras, Fazenda Intervalas, base de Saibadelas, trilha do Quilombo, 21 Jul 1994, *A. Salino 2018* (BHCB); Turmalina, Estação Ecológica de Acauã, 17°10'58.2"S, 42°45'58.2"W, 775 m, 03 Jul 2006, *A. Salino et al. 11251* (BHCB); Vale Verde, Parque Nacional da Serra do Caparaó, 1100 m, 29 Sep 1977, *L. Krieger et al. s.n.* (VIC-5806). Paraná. *Capanema s.n.* (RB-6841); Antonina, Reserva Natural do Rio Cachoeira, 25°19'30"S, 48°46'30"W, 200 m, 1 Sep 2006, *M.G. Gomes et al. 13* (RB; UPCB); Antonina, Reserva Natural do Rio Cachoeira, 25°19'30"S, 48°46'30"W, 100 m, 1 Sep 2006, *M.G. Gomes et al. 33* (UPCB); Antonina, Reserva Natural do Rio Cachoeira, 25°19'30"S, 48°46'30"W, 100 m, 1 Sep 2006, *M.G. Gomes et al. 37* (UPCB); Antonina, Reserva Natural do Rio Cachoeira (SPVS), trilha do Corvo, 25°18'S, 48°41'W, 60 m, 06 Oct 2005, *F.B. Matos & P.B. Schwartsburd 829* (UPCB); Antonina, Reserva Natural do Rio Cachoeira (SPVS), trilha do Gervásio, 25°15'S, 48°41'W, 50 m, 21 Dec 2004, *F.B. Matos & P.H. Labiak 140* (UPCB); Antonina, Reserva Natural do Rio Cachoeira (SPVS), trilha do Meio, 25°18'S, 48°41'W, 200 m, 28 May 2006, *F.B. Matos & M.C. Gomes 1128* (UPCB); Antonina, Reserva Natural do Rio Cachoeira (SPVS), trilha do Zé Carlos, 25°18'S, 48°41'W, 30 m, 30 Apr 2006, *F.B. Matos & G. Weiss 1128* (UPCB); Antonina, Reserva Natural do Rio Cachoeira – SPVS, 200 m, 25 Jun 2007, *P.H. Labiak & F.B. Matos 3956* (UPCB); Camabeí, Rio Jotuva, 24°56'38.34"S, 49°58'34.34"W, 934 m, 18 Mar 2013, *B.K. Canestraro et al. 598* (UPCB); Campina Grande do Sul, Parque Estadual Pico do Paraná, Morro Camapuã, 25°15'S, 48°50'W, 950-1150 m, 20 Dec 2008, *J.B.L. Pereira & F. Marinero 410* (UPCB); Campina Grande do Sul, Parque Estadual Pico do Paraná, Morro Camapuã, 25°15'S, 48°50'W, 950-1150 m, 20 Dec 2008, *J.B.L. Pereira & F. Marinero 411* (UPCB); Campina Grande do Sul, Parque Estadual Pico do Paraná, Morro Camapuã, 25°15'S, 48°50'W, 1250–1350 m, 09 Apr 2009, *J.B.S. Pereira & R. Falleiros 472* (UPCB); Campo do Tenente, Serrinha, próximo ao Rio Cascavel, 26 Jul 1992, *J. Cislinski & M.L. Nowadzki 184* (UPCB); Céu Azul, Parque Nacional do

Iguaçu, trilha atrás do Louro Pardo, acesso pela trilha da Interpretação, Ambiental, 1 Nov 2010, *R.S. Viveiros & A.G. Pastro 189* (BHCB); Curitiba, Bairro Abranches, jardim residencial, 07 Agu 2011, *B.K. Canestraro & I.F. Canestraro 179* (RB), Curitiba, Bom Retiro, Estribo, 04 Jan 1951, *G. Tessmann* (RB); Curitiba, Parque Municipal Barigui, 15 Mar 1996, *C. Kozera & V.A. de O. Dittrich 87* (UPCB); Curitiba, Estrada Garuva, 770 m, Jan 2014, *P.B. Schwartsburd 2903* (VIC); Curitiba, próximo ao Parque Municipal Tingüi, 23 Dec 2020, *P.B. Schwartsburd & R. Santana 4763* (VIC); Curitiba, próximo ao Parque Municipal Tingüi, 23 Dec 2020, *P.B. Schwartsburd & R. Santana 4764* (VIC); Curitiba, Parque Municipal Tingüi, 900 m, 10 Jul 2007, *P.B. Schwartsburd & A.C. Hatschbach 1355* (UPCB); Curitiba, Parque Municipal Tingüi, 900 m, 14 Apr 2007, *P.B. Schwartsburd & J.B.S. Pereira 1321* (UPCB); Curitiba, Parque Municipal Tingüi e arredores, 950 m, 12 Nov 2007, *P.B. Schwartsburd & H.T. Bettega 1381* (UPCB); Curitiba, Reserva Mata Viva, Centro Politécnico da UFPR, setor de Ciências Biológicas, -254463.00000S, -492338.000W, 930 m, 06 Agu 2016, *P.H. Labiak 6275* (UPCB); Esmeralda, E.E. Aracuri, 11 Dec 1982, *R.M. Bueno 3950* (ICN; VIC); Dois Vizinhos, Campus da UTFPR, 25°41'32.1"S, 53°05'35.2"W, 513 m, 09 Nov 2007, *E.L. Siqueira et al. 22* (HUFES); Foz do Iguaçu, Parque Nacional do Iguaçu, floresta ciliar do rio São João, 25°37'21"S, 54°28'20"W, 182 m, 12 Sep 2010, *R.S. Viveiros & A.G. Pastro 148* (BHCB); Guaratuba, Serra da Prata, 25°36'S, 48°43'W, 400 m, 19 Feb 2004, *P.H. Labiak 3157* (UPCB); Gramado, 29 Nov 1993, *R.M. Bueno s.n.* (ICN-155001; VIC); Palotina, Parque Estadual de São Camilo, 16 Dec 2010, *C. Kozera & A. Ribeiro 3761* (CESJ); Paranaguá, Marumbi S. do Mar, Estr. Ferro Curitiba, 25 Jan 1951, *G. Tessmann s.n.* (RB); Paranaguá, Colônia Pereira, 06 Feb 2002, *O.S. Ribas & J.M. Silva 4302* (RB); Piraquara, Mananciais da Serra, 1000 m, 24 Jan 2004, *M. Agustini 30* (UPCB); Piraquara, Parque Estadual Pico do Marumbi, Morro do Canal, 930 m, 12 Aug 2009, *C. Michelin 489* (UPCB); Ponta Grossa, 26 Dec 1985, *L. Krieger s.n.* (CESJ-21021A); Ponta Grossa, Furnas Gêmeas, *P.B. Schwartsburd & R. Moro 895* (UPCB); Ponta Grossa, Parque Estadual de Vila Velha, capão da Fortaleza, 06 Mar 2005, *P.B. Schwartsburd et al. 671* (UPCB); Morretes, Estrada Porto de Cima, Engenheiro Lange, margem esquerda do rio Nhundiaquara, 25°24'35"S, 48°53'45"W, 78 m, 09 Dec 2004, *P.H. Labiak et al. 3458* (UPCB); Morretes, Parque Estadual Pico do Marumbi, 17 Apr 1999, *C. Kozera & O.P. Kozera 1032* (UPCB); Morretes, Parque Estadual Pico do Marumbi, 600 m, 20 Apr 2004, *P.H. Labiak & M.B. paciência 3284*

(UPCB); Morretes, Parque Estadual Pico do Marumbi, 1000 m, 15 Oct 2004, *P.H. Labiak 3422* (UPCB); Morretes, Parque Estadual Pico do Marumbi, 18 May 1999, *C. Kozera & M. Borgo 1087* (UEC); Morretes, Parque Estadual Pico do Marumbi, vertente oriental da Serra do Mar, 650 m, 22 Oct 1998, *V.A. de O. Dittrich 521* (ICN); Morretes, Parque Estadual Pico do Marumbi, 650 m, 22 Jan 1999, *V.A. de O. Dittrich 521 563* (BHCB); Morretes, Parque Estadual do Pau Oco, sentido Paranaguá-Curitiba), 25°34'48"S, 48°55'10"W, 790 m, 28 Jun 2019, *F.B. Matos et al. 2704* (UPCB; VIC); Morretes, Serra da Graciosa, caminho dos Jesuitas, 1000 m, 20 Oct 2003, *P. Labiak & R. Goldenberg 3010* (UPCB); Morretes, Serra da Graciosa, 25°19'56"S, 48°53'54"W, 800 m, 30 Jun 2005, *P.H. Labiak 3537* (UPCB); Morretes, Serra da Graciosa, projeto atitudinal GR-800, 25°19'65"S, 48°53'54"W, 800 m, 30 Jun 2005, *P.H. Labiak & M.L.B. Paciencia 3543* (UPCB); Morretes, Serra da Graciosa, projeto atitudinal GR-800, 25°19'65"S, 48°53'54"W, 600 m, 30 Jun 2005, *P.H. Labiak & M.L.B. Paciencia 3561* (UPCB); Morretes, Serra da Graciosa, projeto atitudinal GR-800, 25°19'65"S, 48°53'54"W, 200 m, 08 Sep 2005, *P.H. Labiak & M.L.B. Paciencia 3580* (UPCB); Piraquara, road to mananciais da Serra, ca. 25 km from Curitiba, 25°31'S, 49°4'W, 950 m, 14 Feb 2008, *J.M. Maarten et al. 4758* (UPCB); São Jerônimo da Serra, Fazenda Nho Ó, 27 Nov 1970, *G. Hatschbach & O. Guimarães 24331* (SJR; UPCB); São João, Parque Nacional do Iguasú, 12 May 1949, *A. Pereira 1704* (RB); São João do Triunfo, Fazenda Experimental da UFPR, 25 Jan 2005, *P.B. Schwartzburd 655* (UPCB); Serra do Mar, Est. Eng^o Lange a Prainhas, 300-373 m, 13 Feb 1951, *G. Tessmann s.n.* (RB-74802); Tibagi, Parque Estadual do Quartelá, 31 Dec 2010, *C. Michelin 1032* (UPCB); Tijucas do Sul, estrada de Garuva para São José dos Pinhais, antes da saída para Tijucas do Sul, 24 Mar 2011, *P. Fiaschi et al. 3594* (SPF); Três Barras do Paraná, Fazenda do Giacometi-Marodin, 26 Mar 1993, *A. Salino s.n.* (BHCB-30176; UPCB-3405); Tunas do Paraná, Parque Estadual de Campinhos, 02 Jun 2011, *C. Michelin et al. 1116* (UPCB). Pernambuco: Jaqueira, Usina Colônia, Mata Córrego da Guariba, 08°43'0.2"S, 35°50'20.2"W, 652 m, 19 Oct 2001, *M.S. Lopes & M.R.S. Pietrobon 438* (HUEFS; RB); Rio de Janeiro: Angra dos Reis, Jussaral, 29 Jun 1935, *A.C. Brade s.n.* (RB-512747); Cachoeiras de Macacu, Boa Vista, Santa Fé, 22°27'S, 42°37'W, 4 Jul 2014, *P.B. Schwartzburd et al. 3320* (VIC); Cachoeiras de Macacu, Boa Vista, Santa Fé, 22°27'S, 42°37'W, 4 Jul 2014, *P.B. Schwartzburd et al. 3323* (VIC); Cachoeiras de Macacu, Boa Vista, Santa Fé, 22°27'S, 42°37'W, 04 Jul 2014, *P.B.*

Schwartsburd et al. 3324 (VIC); Cachoeiras de Macacu, Boa Vista, Santa Fé, 22°27'S, 42°37'W, 4 Jul 2014, *P.B. Schwartsburd et al. 3325* (VIC); Cachoeiras de Macacu, Boa Vista, Santa Fé, 22°27'S, 42°37'W, 4 Jul 2014, *P.B. Schwartsburd et al. 3326* (VIC); Cachoeiras de Macacu, Boa Vista, Santa Fé, 22°27'S, 42°37'W, 4 Jul 2014, *P.B. Schwartsburd et al. 3327* (VIC); Itatiaia, Lote 70, 12 Feb 1943, *E. Pereira 358* (RB); Itatiaia, Lote 88, 10 Feb 1942, *A.C. Brade 17176* (RB); Itatiaia, Lote 88, *P. Campos-Porto 2609* (RB); Itatiaia, Km 10, Mar 1937, *A.C. Brade 15511* (RB); Itatiaia, Monte Serrat, Jan 1938, *A.C. Brade 16044* (RB); Itatiaia, Parque Nacional de Itatiaia, Lote 88, 21 Jun 1932, *C. Porto s.n.* (VIC-3345); Itatiaia, Itatiaia Parque Nacional de Itatiaia, Maromba, 1200 m, 21 Mar 1942, *W.D. de Barros 704* (RB); Itatiaia, Parque Nacional do Itatiaia, estrada para o planalto, estrada para o planalto Km 3, 1750 m, 19 Agu 2005, *J.P.S. Condack 423* (RB); Itatiaia, Parque Nacional do Itatiaia, estrada para o planalto, 1700 m, 18 Jul 2009, *P.B. Schwartsburd et al. 2198* (VIC); Itatiaia, Parque Nacional do Itatiaia, trilha Raul Braga, Rebouças/ Sede, 22°15'19"S, 44°38'7"W, 1600 m, 25 Nov 2009, *E.R. Damasceno et al. 385* (RB); Itatiaia, Parque Nacional do Itatiaia, Trilha do lote 21, próximo ao rio, 22°27'23"S, 44°36'45"W, 800 m, 30 May 2009, *E.R. Damasceno & T.V. Costa 275* (RB); Itatiaia, Parque Nacional do Itatiaia, complexo Maromba, trilha para Cachoeira Itaporani, 22°25'34"S, 44°37'20"W, *C. Mynssen et al. 1512* (RB); Itatiaia, Parque Nacional do Itatiaia, cerca de 800 m do hotel Ipê, 10 Feb 2020, *N.T.L. Pena & P.B. Schwartsburd 902* (VIC); Itatiaia, Parque Nacional do Itatiaia, cerca de 800 m do hotel Ipê, 10 Feb 2020, *N.T.L. Pena & P.B. Schwartsburd 905* (VIC); Itatiaia, Parque Nacional do Itatiaia, trilha para os Três Picos, 22°25'49"S, 44°36'02"W, 1220 m, 10 Jan 2008, *P.H. Labiak et al. 4417* (UPCB); Itatiaia, Parque Nacional do Itatiaia, travessia Ruy Braga, partindo da cachoeira do Maromba em direção ao Rebouças, 1160 m, 11 Feb 2020, *N.T.L. Pena & P.B. Schwartsburd 908* (VIC); Itatiaia, Parque Nacional do Itatiaia, travessia Ruy Braga, partindo da cachoeira do Maromba em direção ao Rebouças, 1160 m, 11 Feb 2020, *N.T.L. Pena & P.B. Schwartsburd 909* (VIC); Itatiaia, Parque Nacional do Itatiaia, travessia Ruy Braga, partindo da cachoeira do Maromba em direção ao Rebouças, 1160 m, 11 Feb 2020, *N.T.L. Pena & P.B. Schwartsburd 910* (VIC); Itatiaia, Parque Nacional do Itatiaia, tavesia Ruy Braga, partindo da cachoeira do Maromba em direção ao Rebouças, 1160 m, 11 Feb 2020, *N.T.L. Pena & P.B. Schwartsburd 913* (VIC); Itatiaia, Parque Nacional do Itatiaia, trilha dos Três Picos, 1100-1300 m, 12 Feb 2020, *N.T.L. Pena & P.B. Schwartsburd 920* (VIC); Itatiaia,

Parque Nacional do Itatiaia, trilha dos Três Picos, 1100-1300 m, 12 Feb 2020, *N.T.L. Pena & P.B. Schwartzburd 926* (VIC); Itatiaia, Parque Nacional do Itatiaia, trilha dos Três Picos, 1100-1300 m, 12 Feb 2020, *N.T.L. Pena & P.B. Schwartzburd 927* (VIC); Itatiaia, Pico da Nova, 21 Mar 1942, *A.C. Brade 17238* (RB); Nova Friburgo, Macaé de Cima, sítio Sophronitis, trilha para a nascente do rio Flores, 28 Oct 1990, *L. Sylvestre et al. 371* (RB); Nova Iguaçu, Rebio do Tinguá, estrada do Ouro, estrada dos Escravos, 800 m, 26 Jan 2021, *N.T.L. Pena & P.B. Schwartzburd 1017* (VIC); Nova Iguaçu, Rebio do Tinguá, estrada do Ouro, estrada dos Escravos, 800 m, 26 Jan 2021, *N.T.L. Pena & P.B. Schwartzburd 1018* (VIC); Nova Iguaçu, Rebio do Tinguá, estrada do Ouro, estrada dos Escravos, 800 m, 26 Jan 2021, *N.T.L. Pena & P.B. Schwartzburd 1019* (VIC); Mangaratiba, Reserva Biológica de Rio das Pedras, trilha para a cachoeira, 420 m, 20 Jan 2000, *M. Guerra-Santos et al. 1387* (RB); Mangaratiba, Reserva Biológica de Rio das Pedras, trilha para a cachoeira, trilha da Lagoa Seca, 400-450 m, 12 Jul 1997, *J.M.A. Braga 4204* (RB); Miguel Pereira, Reserva Biológica do Tinguá, trilha para o rancho dos Bobos, Riacho Nova Estrela, 22°34'15"S, 43°28'8"W, 800 m, 14 Dec 2001, *L. Sylvestre et al. 1587* (RB); Miguel Pereira, Reserva Biológica do Tinguá, Orbel 2, trilha com acesso pelo Km 31, margem do rio São Pedro, lado esquerdo do rio, 22°32'39"S, 43°26'1"W, 789 m, 11 Jul 2007, *L. Sylvestre et al. 2069* (RB); Parati, Parque Nacional da Serra da Bocaina, 23°11'22"S, 44°50'15"W, 1200 m, 07 Jan 2008, *P.H. Labiak et al. 4368* (UPCB); Santa Maria Madalena, Murituca, 1000 m, 02 Mar 1939, *S. Lima 13156* (RB); Serra do Couto, Coleção Fée, *s.d.*, *Glaziou 3172* (RB); Serra do Itatiaia, Cachoeira Taguaril, 900 m, *A.C. Brade 10055* (IAN); Teresópolis, Parque Nacional da Serra dos Órgãos, 22°26'56"S, 42°59'06"W, 1500 m, 13 Jan 2008, *P.H. Labiak et al. 4480* (UPCB); Teresópolis, Parque Nacional da Serra dos Órgãos, 22°26'56"S, 42°59'06"W, 1900 m, 13 Jan 2008, *P.H. Labiak et al. 4489* (UPCB); Teresópolis, Parque Nacional da Serra dos Órgãos, trilha da Pedra do Sino, em direção ao abrigo 04, 22°16'09"S, 43°00'28"W, 1448 m, 26 Oct 2012, *D.O. Dinato et al. 79* (UPCB); Teresópolis, Parque Nacional da Serra dos Órgãos, Trilha da Pedra do Sino, 222716, 43912W, 1000 m, *R.A. Engelmann et al. RE0919* (RB); Teresópolis, Serra dos Órgãos, Pedra do Frade, 19 Jul 1940, *A.C. Brade 16426* (RB); Teresópolis, Parque Nacional da Serra dos Órgãos, Trilha para a Pedra do Sino, 13 Nov 2017, *P.B. Schwartzburd 4374* (VIC). Rio Grande do Sul: Barracão, Parque Estadual Espigão Alto, *N. Silveira 5273* (HAS); Monte Belo do Sul, Linha 80 da Leopoldina,

415 m, 28 Agu 2011, *F. Gonzatti 128* (UCS; RB); Cambará do Sul, Itaimbezinho, 11 May 1990, *R.M. Senna s.n.* (ICN-155002); Cambará do Sul, Parque Aparados da Serra, 29°10'32"S, 50°05'56"W, 964 m, *M.H. Nervo 1337* (ICN); Caraá, Fraga, APA Municipal de Caraá, 30 Nov 2006, *R.M. Senna 1253* (HAS); Carambá, Parque Aparados da Serra, 29°09'44"S, 50°06'02"W, 961 m, 13 Mar 2013, *M.H. Nervo & C.R. Buzato 1339* (ICN); Caxias do Sul, Jardim Botânico de Caxias do Sul, 29°08'16"S, 51°09'14"W, 818 m, 26 Mar 2021, *F. Gonzatti 5858* (HUCS); Caxias do Sul, Vila Oliva, 780 m, 29 Dec 1999, *A. Kegler 497* (UCS); Caxias do Sul, Vila Oliva, estrada para Gramado, 29°14'11"S, 50°53'50"W, 701 m, 24 Apr 2016, *F. Gonzatti 2414* (HUCS); Caxias do Sul, Vila Oliva, estrada para Gramado, 29°14'11"S, 50°53'50"W, 701 m, 24 Apr 2016, *F. Gonzatti 2420* (HUCS); Esmeralda, E.E. Aracuri, 11 Dec 1982, *R. Bueno 3950* (ICN); Encruzilhada do Sul, 30°33'47.20"S, 52°33'23.50W, *F.D. Silva 14* (ICN); Gramado, 29 Nov 1993, *R. Bueno s.n.* (ICN-155001); Itati, Reserva Biológica da Mata Paludosa, 29°30'46"S, 50°09'10"W, 33 m, 11 Feb 2016, *F. Gonzatti 2390* (UCS); Maquiné, Reserva Biológica da Serra Geral, Vale do Encantado até Sangão do Paraguai, 04 Nov 2003, *C. Bencke 527* (HAS; VIC); Maquiné, Reserva Biológica da Serra Geral, Vale do Encantado, 23 Nov 2004, *R.M. Senna 540* (HAS); Monte Belo do Sul, Linha 80 da Leopoldina, 29°10.33'97.4"S, W51°37.30'73"W, 800 m, 01 May 2011, *F. Gonzatti 88* (CESJ; MBML; UCS); Montenegro, Linha Julio Castilhos, 400 m, 27 May 1947, *A. Sehnem s.n.* (HUCS-5135); Montenegro, Linha Pinhal, 01 Oct 1953, 500 m, *A. Sehnem s.n.* (HUCS-5145); Nova Petrópolis, nos arredores da cidade, 26 Mar 1959, *J. Mattos s.n.* (HAS-54604; HAS-54929); São Francisco de Paula, Josafá, arredores da Estação Ecológica Estadual Aratinga, 25 Apr 2005, *R.M. Senna 895* (HAS); São Francisco de Paula, 08 Jan 1948, *A. Mattos s.n.* (RB-64784); São Francisco de Paula, Linha Juá, 29°08'05"S, 50°48'10"W, 828 m, 02 Feb 2016, *F. Gonzatti 2329* (HUCS); São Francisco de Paula, Tainhas, Serra do Pinto, 975 m, 10 Jun 2002, *C.R. Lehn et al. 358* (HASU); São Francisco de Paula, Estação Biológica Aratinga, 10 Dec 2004, *R.M. Senna 680* (HAS); São Leopoldo, Morro das Pedras, 100 m, 15 Jul 1942, *A. Sehnem s.n.* (HUCS-5138); Santa Cruz do Sul, 1900-1905, *C. Jüergens & A. Stier 85* (UCS); Tenente Portela, P.F. Turvo, Jul 1982, *R. Bueno 3948* (ICN; VIC); Tenente Portela, P.F. Turvo, 20 Jul 1982, *R. Bueno 3949* (ICN); Torres, Parque Estadual de Itapeva, 21 Feb 2005, *R.M. Senna 738* (HAS); Venâncio Aires, 20 May 1983, *R. Bueno 3951* (ICN). Santa Catarina. Angelina, Rio Fortuna, 27°27'02,00"S,

49°03'00,00 O, 841 m, 08 Apr 2010, *A. Stival-Santos et al. 2465* (FURB); Araranguá, Perboa Sombrio, 04 Apr 1944, *P.R.Raulino Reitz C476* (RB); Araranguá, Serra da Rocinha, ao lado da estrada, 700 m, 20 Jan 1944, *R. Reitz C407* (RB); Blumenau, 26°54'11.39"S, 49°07'08.59"O, 135 m, 05 May 2010, *T.A. Beckhauser 201* (BHCB); Blumenau, Parque Nacional da serra do Itajaí, 28 Oct 2007, *A.L. Gasper 846* (UPCB); Blumenau, Parque São Francisco, 17 Apr 1998, *H. Rosane s.n.* (FURB); Blumenau, trilha da Chuva, PNSI, 27°03'32.00"S, 49°05'11.00"W, 290 m, 21 Nov 2013, *L.A. Funez et al. 1622* (FURB); Itajaí, Luiz Alves, 1941, *P.R. Reitz C678* (RB); José Boiteux, 26°59'53"S, 49°35'22"W, 22 Feb 2018, *A. Kassner-Filho et al. 2179* (FURB); Blumenau, trilha da Chuva, PNSI, 27°03'32.00"S, 49°05'11.00"W, 290 m, *L.A. Funez et al. 1521* (FURB); Joinville, Serra Dona Francisca, 26°11'33.04"S, 49°02'52.04"W, 576 m, 10 Dec 2009, *T.J. Cadorin et al. 905* (BHCB); Luiz Alves, Braço Francês, 26°46'12,00"S, 48°58'26,00"O, 220m, *A.L. Gasper 2278* (CESJ; FURB); Orlenas, Chapadão, 28°10'41.40"S, 49°23'23.70"W, 500 m, 2013, *R. Santos-Junior s.n.* (ICN-179153); Piratuba, lote 70–71, 05 May 2000, *L. Kem s.n.* (ICN-120891); Piratuba, lote 70–71, 05 May 2000, *L.S. Kern s.n.* (HAS-37712); Rio Tavares, Ilha de Santa Catarina, 06 Jun 1948, *P.J.A. Rohr S.J. 1063* (RB); Santa Rosa de Lima, trilha Santa Barbara, caminho para o campo dos Padres, 27°58'08"S, 49°18'50"W, 1484 m, 06 Jan 2021, *F. Gonzatti 5737* (HUCS); São Bento do Sul, Bairro Progresso, Parque Florestal do SAMAE, 26°14'00"S, 49°21'36"W, 830 m, 08 Feb 2016, *P. Schwirkowski 1575* (FURB); Sertão da Lagoa, 06 oct 1946, *P.J.A. Rohr 393* (RB); Timbé do Sul, serra da Rocinha, 06 Feb 2009, 1050 m, *P.B. Schwartsburd & A.C. Corazzini 1989* (VIC); Timbé do Sul, serra da Rocinha, serra da Rocinha, 600 m, 3 Agu 2009, *P.B. Schwartsburd et al. 2233* (VIC); Timbé do Sul, subida da Serra da Rocinha, mata em frente à casa do DER-SC, 04 Nov 1991, *R. Bueno s.n.* (ICN-155004; ICN-155013; ICN-155014); Três Barras, Floresta Nacional IBAMA, 16 Sep 2003, *M.P. Runert s.n.* (UPCB-66704); São Bento do Sul, Rio Natal, linha férrea, após CEPA Rugendas, 26°19'29"S, 49°18'48"W, 600 m, 16 Jan 2016, *P. Schwirkowski 1465* (FURB); Sertão da Lagoa, Ilha de Santa Catarina, 06 Oct 1946, *P.J.A. Rohr 393* (RB); Vitor Meireles, Jacú-Paca, 24 Jun 2010, *A. Korte & A. Kniess 3449* (FURB). São Paulo: Alto da Serra, Parque Cajurú, Jun 1912, *H. Luederwaldt s.n.* (SPF-; VIC-54.601). Bananal, Estação Biológica do Bananal, nas trilhas da Estação e da Pedra Vermelha, 22°49'10"S, 44°21'58"W, 1130-1350 m, 08 Mar 2001, *A. Salino et al. 6269* (BHCB); Bananal, Estação Biológica do Bananal, nas trilhas da

Estação e da Pedra Vermelha e Córrego do Barbosa, 22°47'32.2"S, 44°21'32.6"W, 1200-1450 m, 11 Sep 2001, *A. Salino et al. 7472* (BHCB); Campos do Jordão, Parque Estadual de Campos do Jordão, trilha do rio Sapucaí, 1550 m, 07 Jun 1992, *A. Salino 1390* (BHCB; UEC); Caraguatatuba, Parque Estadual da Serra do Mar, 23°41'32"S, 45°37'06"W, 600 m, 18 Apr 2000, *A. Salino et al. 5272* (BHCB); Cruzeiro, estrada para o Pico dos Marins, ca. 2 km antes de chegar ao acampamento base, 22°30'51"S, 45°09'10"W, 1500 m, 10 Dec 2019, *F. Gonzatti 5334* (HUCS); Cubatão, Rodovia SP 150, Anchieta, Serra do Mar, 23°53'S, 46°26'W, 11 May 1995, *M.R. Pietrobom-Silva 1766* (SJR); Cunha, Parque Estadual da Serra do Mar, 19 Jul 1996, *A. Salino 3005* (BHCB); Cunha, rodovia Cunha-Parati, estrada para pedra da Marcela, 17 Dec 1996, *A. Salino 2936* (BHCB); Eldorado, Parque Estadual do Jacupiranga, trilha do Evaristo, 24°38'05"S; 48°24'28"W, 01 Apr 2005, *A. Salino 10340* (BHCB); Iguape, Serrinhas, 14 Jan 1924, *A.C. Brade s.n.* (RB-30640); Iporanga/Apiáí, Parque Estadual Turístico do Alto Ribeira (PETAR), 24°32'22"S, 48°41'36"W, 01 Dec 2011, *F.F.F. Mazziero & A. Soller. 816* (UPCB); Iporanga/Apiáí, Parque Estadual Turístico do Alto Ribeira (PETAR), 24°32'22"S, 48°41'36"W, 07 Jul 2012, *F.F.F. Mazziero et al. 990* (UPCB); Iporanga/Apiáí, Parque Estadual Turístico do Alto Ribeira (PETAR), 24°32'22"S, 48°41'36"W, 07 Jul 2012, *F.F.F. Mazziero & A. Albiero Jr. 1100* (UPCB); Iporanga, Parque Estadual Intervalas, trilha do Cipó em direção à gruta do Cipó, 24°16'09"S, 48°24'56"W, 820 m, *A. Salino et al. 8640* (BHCB; CESJ); Itirapina, Serra de Itaqueri, às margens do rio Cachoeira, 800 m, 09 Sep 1991, *A. Salino 1055* (BHCB); Miracatu, Reserva Votorantim, complexo Juquiá, trilha entre caixa d'água e vila de moradores UHE Barra, 24°01'15"S, 47°18'56"W, 503 m, 26 Mar 2013, *A. Salino et al. 15608* (BHCB); Miracatu, Reserva Votorantim, complexo Juquiá, trilha da Casa de Pedra, 24°10'05"S, 47°33'08"W, 95 m, 28 Mar 2013, *A. Salino et al. 15636* (BHCB); São José do Barreiro, Parque Nacional da Serra da Bocaina, estrada após o rio que cruza a estrada principal 22°45'7"S, 45°37'00"W, 1446 m, 04 Oct 2011, *C.M. Mynssen et al. 1262* (RB); São Lourenço da Serra, Reserva Particular do Patrimônio Natural Paiol Maria, entrono e limites bordeados a cerca acessada pela trilha das Águas, 08 Dec 2010, *J.A. Lombardi et al. 7964* (BHCB); São Lourenço da Serra, Reserva Particular do Patrimônio Natural Paiol Maria, trilhas das águas, 26 Apr 2011, *J.A. Lombardi et al. 8522* (BHCB); São Luiz do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, trilha Pirapitinga, 23°20'29"S, 45°08'48"W, 900-

950 m, 04 Mar 2001, *A. Salino 6107* (BHCB); São Luiz do Paraitinga, Parque Estadual da Serra do Mar, Núcleo Santa Virgínia, base de Vargem Grande, trilha para Cachoeira da Boneca, Ribeirão Grande, 23°25'57.2"S, 45°12'35.6"W, 800 m, 10 Aug 2001, *A. Salino 7457* (BHCB); São Sebastião, Ilha de São Sebastião, Litoral Norte do Estado, 26 Jul 1972, *B. Siegel 36* (SJRJ); Serra da Cantareira, Jun 1913, *Tamandaré 846* (RB); Serra do Itatins, Mar 1924, *A.C. Brade s.n.* (RB); Ubatuba, Parque Estadual da Serra do Mar, Poruba, 11 Sep 1993, *A. Salino 1878* (BHCB); Ubatuba, Parque Estadual da Serra do Mar, Núcleo Picinguaba, Sertão do Puruba, 23°20'24.0"S, 44°58'40.6"W, 40 m, 05 Agu 2001, *A. Salino et al. 7252* (BHCB).

ARGENTINA.—Misiones: Departamento de San Pedro, Parque Provincial Cruce Caballero, 14 Mar 2011, *G.J. Yañez & G.J. Marquez 103* (VIC); Departamento de San Pedro, Parque Provincial Cruce Caballero, 14 Mar 2011, *G.J. Yañez & G.J. Marquez 104* (VIC); Departamento de San Pedro, Parque Provincial La Araucaria, 26°37'51"S, 54°06'12"W, 10 Oct 2011, *M. Arana & A. Oggero s.n.* (VIC-41908).

Dennstaedtia cornuta differs from *D. obtusifolia* by laminae 3-pinnate to 3-pinnate-pinnatifid (v.s 1-pinnate-pinnatifid to 2-pinnate-pinnatifid), sori in sinus not projecting outward on the margin and indusia purse-shape (vs. sori in sinus or pinnules projecting outward on the margin, indusia hemi-espherical to tubular).

Dennstaedtia cornuta differs from *D. dissecta* by segments with shallower sinuses and crenate margins (vs. deeper or more dissected sinus and dentate margins), indusia purse-shaped (vs. cylindrical), distribution of South America (vs. Antilles).

Dennstaedtia cornuta differs from *D. fluminensis* by rhizomes creeping (vs. erect to ascending), segments with shallower sinuses (vs. deeper sinus or more dissected), indusia purse-shaped (vs. bivalve), distribution of South America (vs. endemic of Brazil).

Dennstaedtia cornuta is a species that tends to be larger in northern South America and smaller in southern South America. The size of the pinnae and rhizomes are variable and may be related to the environmental conditions in which they are found, causing a phenotypic variation. However, it is not possible to evidence morphological characteristics that support a possible separation of the morpho-species.

Dennstaedtia cornuta is a species of fern that belongs to the Dennstaedtiaceae Lotsy (1909: 655). *Dennstaedtia cornuta* was first cited by Kaulfuss (1824), material referring to Brazil and sent to Sprengel, but collected by naturalists

Sello Friedrich (in Brazil, Sellow). In describing it, Kaulfuss (1824) called the species of *Dicksonia cornuta* Kaulf. (1824: 227), being years later combined by Mettenius (1864) for the genera *Dennstaedtia* Bernh. (1800 [1801]: 124), where the species was renamed for *D. cornuta*.

Sellow Friedrich was a German naturalist, who invited Georg Heinrich von Langsdorff, was part of a scientific expedition in Brazil (Marchiori *et al.* 2016). During his expedition in Brazil, Sellow Friedrich sent the materials he collected to the Museum in Berlin, therefore, the botanical samples it collected were sent to herbarium B (Botanischer Garten und Botanisches Museum Berlin-Dahlem), who was bombed in World War II and lost about 10,000 important samples (Smithsonian Libraries <www.si.edu>). Due to this historical event, which led to the loss of *Dennstaedtia cornuta* Typo, the geographical distribution of the species has always been considered uncertain and controversial, but there was suspicion about its endemism in the Brazilian Atlantic Rainforest (Schwartzburd 2017).

However, Rego *et al.* (2013) traced the approximate routes Friedrich Sellow made in Brazil between 1818-1820, and among the routes is the municipality of Santo Antônio do Itambé, belonging to the state of Minas Gerais, Brazil. Garbino & Nogueira (2017) also presents cities traveled by Friedrich Sellow between 1814-1831, corroborating with the traveled route and collection record in the region near Serra do Cipó, Minas Gerais, about 150 km from Santo Antônio de Itambé. This information is very interesting since when analyzing the data brought on the label of the herbarium exsiccata B (Berlin), added to the morphological characteristics that indicate to be *Dennstaedtia cornuta*, it reads: “Brasilia meridionalis, prope Santo Antônio”. At the time, the term “Brasilia meridionalis” indicated what is now known as southeastern Brazil. In addition, according to the history of the localities visited by Friedrich Sellow (Rego *et al.* 2013; Garbino & Nogueira 2017), Santo Antônio do Itambé is the only municipality that fits the description indicated from the label of the exsiccata as “prope Santo Antônio”. On the label is the information from “Sellow legit.”, corroborating the legitimacy of the material found in herbarium B.

Through historical information, a script of field expeditions and the morphology of the present specimen (exsiccates) found in herbarium B, we present here a lectotyping (or neotype?) for *D. cornuta*.

Dennstaedtia coronata (Sodirol) C.Chr., Index Filic. 216. 1905. *Dicksonia*

adiantoides var. *coronata* Sodiro, Recens. Crypt. Vasc. Quit. 23. 1883. *Dicksonia coronata* (Sodiro) Sodiro, Crypt. Vasc. Quit. 48 (1893). LECTOTYPE (designated here): ECUADOR. Corazón, Jul 1873, P.L. Sodiro s.n. (K-000640361, image!). (Fig. 2, H-J; Map 4)

Plants terrestrial. Rhizomes ascending, 1–2 cm diam. Fronds determinate, 2–3 m long; petioles light to drack brown, without root projections, 0.7–1 m × 0.8–2 cm, inermous, small aerophores, with catenate hairs; laminae 2-pinnate-pinnatifid, 1–2 m long, with alternate pinnae; rachises light to dark brown, adaxially sulcate, abaxially and adaxially with catenate hairs, more densely at base of axis, without buds in axes, small aerophores; basal pinnae opposite to subopposite, lanceolate 35–40 × 15–25 cm, equilateral, proximally obtuse, distally acute; costae abaxially and adaxially with catenate hairs, adaxially sulcate, small aerephore; ultimate segments lanceate, 5–7 × 1–2 cm, proximally sessile, distally cuneate to caudate crenate, with shallow sinus forming round-shaped segment; costules and veins abaxially densely catenate hairs, adaxilly glabrous; laminar tissue between the veins abaxially moderately catenate hairs, adaxilly glabrous; lamina margins glabrous, entire and crenate at apex segments. Sori hemi-spherical, close to each other, 0.8–1.5 × 0.5–1 mm; induzia purse-shaped, sometimes catenate hairs at the base. Spores trilete.

DISTRIBUTION.—*Dennstaedtia coronata* has a distribution to the north of South America and the Antilles.

SPECIMENS EXAMINED.—PERU: Depto. San Martin, Prov. Huallaga, abajo de la Morada, cerca ao río Guabayacu, 6°57'LS, 77°32'LO, 1900-2000 m, 10 Aug 1997, V. Quipuscoa S. & J. Bardales 962 (UC).

We choose as lectotype the material at K (K-000640361), since is the one we observed and fits the protologue better. The materials at S (S-R-1479, image!) and US (US-00066385, image!) correspond to another species, *D. obtusifolia*, therefore we do not consider them as isolectotypes. Unfortunately, we were not able to observe the materials at Q, and QCA.

For diferentiation with *Denntaedtia andina*, see its comments.

Dennstaedtia fluminensis (Fée) C.Ch., Index Filic. 217. 1905. *Microlepia fluminensis* Fée, Crypt. Vasc. Bresil 1: 151, t. 51, fig. 1. 1869. LECTOTYPE (designated here): BRAZIL [Rio de Janeiro], Alto Macahé [Macaé], 20 May 1868, A. Glaziou A. 2378 (P-00633275, image!; isolectotypes: P-00633276, image!; P-

00633277, image!). (Fig. 3, A-D; Map 4)

Plants terrestrial or lithophytic. Rhizomes erect to ascending, viscid, with supports roots, (0.3) 0.5–1.5 cm diam, sparsely catenate hairs to glabrescent. Fronds determinate, (0.30) 0.60–1.5 m long; petioles dark brown, viscid, 0.30–0.56 m × (0.1) 0.3–1 cm, inermous, small aerophores, abaxially and adaxially densely covered catenate hairs; laminae 3-pinnate to 4-pinnate, (0.15) 0.60–1 m long, proximally opposite to sub-opposite pinnae, distally alternate pinnae; rachises dark brown, inermous, viscid, abaxially densely dark brown catenate hairs, adaxially sulcate, sparsely dark brown catenate hairs, more densely at base of axis, small aerophores; basal pinnae opposite to sub-opposite, equilateral, lanceolate, with inequilateral, first pinnule reduced acroscopically, obtuse base, acute apex, 15–60 × 5–20 cm; costae abaxially densely with dark brown catenate hairs, adaxially sulcate, sparsely dark brown catenate hair, small aerephore, lacking adaxially wings; ultimate segments inequilateral, ovate to oblong, sessile base, round and crenate to dentate apex, (.08) 1–1.5 × (0.3) 0.5–0.8 cm, shallow sinus not forming segment; costules and veins abaxially with densely dark brown catenate, adaxially with sparsely dark brown catenate to glabrous; laminar tissue between the veins abaxially and adaxially with sparsely dark brown catenate with dark brown catenate to glabrous; lamina margins glabrous, entire and crenate to dentate apex. Sori rounded, 0.1–1.5 × 0.5–1 mm; induzia obovate-spheroid, bivalvate with catenate hairs to glabrous.

DISTRIBUTION.—Endemic to Brazil, in the states of Bahia, Espírito Santo, Minas Gerais, Rio de Janeiro, São Paulo, and Santa Catarina; 350–1600 m.

SPECIMENS EXAMINED.—BRAZIL. Bahia: Camacan, Fazenda Serra Bonita, Reserva Serra Bonita, trilha da Baneba, 15°23'30"S, 39°33'55"W, 850 m, 31 Jul 2008, F.B. Matos & R.R. Santos 1563 (UPCB). Espírito Santo: Santa Maria de Jetibá, Rio Nove, Sítio L. Kollmann, 19°58'52"S, 40°38'58"W, 04 Nov 2016, *L. Kollmann 13209* (MBML); Santa Maria de Jetibá, Rio Nove, terreno de L. Kollmann, 730 m, 28 Dec 2007, *L. Kollmann 10271* (MBML). Minas Gerais: Caparaó, Parque Nacional do Caparaó, 18 Jun 1988, *L. Krieger FPNC 673* (CESJ); Lambari, Parque Estadual de Nova Baden, trilha das Sete Quedas, 900-1000 m, 06 Mar 2017, *P.B. Schwartzburd et al. 3883* (VIC); Lambari, Parque Estadual de Nova Baden, entre a 7ª queda e o topo do morro, fora da trilha, 1000-1265 m, 09 Mar 2017, *P.B. Schwartzburd & M.L. Paulo 4038* (VIC); Lambari, Parque Estadual de Nova Baden, entre a 7ª queda e o topo do morro, fora da trilha, 1000-1265 m, 09 Mar 2017, *P.B. Schwartzburd & M.L.*

Paulo 4056 (VIC); Lima Duarte, Serra Negra, RPPN Serra Negra, Cachoeira da Borboleta Azul, 25 Oct 2008, *J.H.C. Ribeiro et al. 34* (BHCB; CESJ); Olaria, 21°56'48"S, 43°53'45"W, 1050 m, 27 Aug 2017, *V.A.O. Dittrich & B.P.S. Pereira 2204* (BHCB; CESJ); Rio Acima, Rio do Peixe, bacia do córrego Fazenda Velha, 20°9'23"S, 43°49'37"W, 825-1050 m, 30 Jun 2010, *S.G. Resende et al. 4267* (BHCB); Rio Preto, Serra Negra, Serra do Funil, 19 Apr 2006, *F.S. Souza et al. 205* (BHCB); Santa Maria do Salto, Distrito de Talismã, fazenda Duas Barras, próximo a divisa com o estado da Bahia, 16°24'16.5"S, 40°03'27.4"W, 750-850 m, 10 Oct 2003, *A. Salino et al. 9261* (BHCB; CESJ); Simonésia, Mata do Sossego, Trilha das Hortências e Trilha 2, 20°04'11"S, 42°04'37"W, 1298 m, 12 Jun 2012, *J. F. Souza & A. Salino 112* (BHCB); Simonésia, RPPN Mata do Sossego, em áreas de vales e interflúvios, 20°03'55.3"S, 42°04'25.9W, 1150-1600 m, 21 May 2006, *A. Salino et al. 11181* (BHCB; CESJ); Simonésia, RPPN Mata do Sossego, 20°4'9"S, 42°4'48"W, 1347 m, 20 Mar 2009, *A. Salino et al. 14232* (BHCB); Simonésia, RPPN Mata do Sossego, 20°4'9"S, 42°4'48"W, 1347 m, *A. Salino et al. 14237* (BHCB); Simonésia, RPPN Mata do Sossego, em áreas de vales e interflúvios, 20°03'55.3"S, 42°04'25.9W, 1150-1600 m, 21 May 2006, *A. Salino et al. 11110* (BHCB; CESJ); Simonésia, trilha das hortências e trilha 2, 20°04'11"S, 42°04'37"W, 1298 m, 12 Jun 2012, *J.F. Souza & A. Salino 112* (BHCB). Rio de Janeiro: Teresópolis, RJ 81, Km 84, 22°23"S, 42°55"W, 800 m, 28 Mar 1997, *M. Almeida-Neto 122* (HUEFS; SJRP). Santa Catarina: Indaial, Warnow Alto, 27°00'00.00"S, 49°13'51.00"W, 357 m, 14 May 2010, *A. Korte & A. Kniess 3260* (FURB). São Paulo: São Luiz do Paraitinga, Parque Estadual da Serra do Mar, núcleo Santa Virgínia, base de Itamambuca, 231931.4S, 45°04'47.7"W, 920 m, 23 Jun 2004, *A. Salino et al. 9605* (BHCB); Ubatuba, Estrada para Taubaté, no início da Serra, área do Parque Estadual da Serra do Mar, Poruba, 11 Sep 1993, *A. Salino 1878* (BHCB); Ubatuba, Estrada para Taubaté, no início da Serra, área do Parque Estadual da Serra do Mar, 23°27'40"S, 45°02'11"W, 03 Feb 1996, *A. Salino 2508* (BHCB). [Procedência: Indeterminado, s/coletor, (RB-215803)].

For differentiation, see the comments of *Dennstaedtia cornuta*.

Dennstaedtia glauca C.Chr. ex Looser, Revista Chilena Hist. Geogr. 69: 184. 1932.

Davallia glauca Cav., Descr. Pl. (Cavanilles) 278. 1802. LECTOTYPE (designated by Tryon 1960): CHILE. Cordillera del Planchón: L. Neé s.n. (MA-475616, image!; isolectotype: BM-000937680, image!). (Fig. 3, E-H; Map 4)

Dennstaedtia lambertieana (J.Rémy) Hieron., Bot. Jahrb. Syst. 34(4): 455 (1904).

Dicksonia lambertieana J.Rémy in Gay, Fl. Chil. [Gay] 6: 523. 1853. Lectotype (designated by Tryon 1960, first step, and here, second step): Chile, Santiago, *Philippi s.n.* (P-01359170, image!; isolectotype: P-01359171, image!).

Plants terrestrial. Rhizomes creeping, 0.3–0.6 cm diam, densely covered with light brown catenate hairs. Fronds determinate, 0.30–2 m long; petioles dark brown to reddish at the base, light to dark brown above, 4–30 cm × 0.2–0.6 cm, inermous, with small aerophores, moderately covered with catenate hairs at the base, glabrescent above; laminae 4-pinnate to 4-pinnate-pinnatifid, 0.20–1 m long, with alternate pinnae; rachises light to dark brown, sometimes dark brown, adaxially sulcate with catenate hairs, abaxially glabrescent, more densely at the base of axes, with small aerophores; basal pinnae opposite and alternate, equilateral, lanceolate, obtuse at the base, acute at the apex, 10–30 cm × 5–12 cm; costae abaxially with light brown catenate hairs, adaxially sparsely light brown catenate hairs to glabrescent, catenate hair more densely at base of axis, small aerophore; lacking adaxially wings; ultimate segment equilateral, oblong, at the bases basiscopically sessile, round and dentate apex, 5–7 × 1.5–2 mm, sinus forming segments; costules and veins abaxially with light brown catenate hairs, adaxially glabrous; laminar tissue between the veins abaxially with catenate hairs, adaxially glabrous; lamina margins glabrous, entire and dentate at apex. Sori hemi-espherical, 0.5–1 × 0.3–0.5 mm; indusia purse-shaped, glabrous.

DISTRIBUTION.—Southern Andes forests, in Argentina, Chile, Bolivia, and Peru; with altitudinal distribution of 700 to 3600 m.

SPECIMENS EXAMINED.—PERU. Dept. Cuzco: Prov. Cuzco, San Jerónimo, Dec 1941, *C. Vargas 2320* (UC); Depto. Cuzco. Prov. Paucartambo, 1500 m, 03 Feb 1975, *T. Plowman & E. Wade Davis 4915* (F); Reg. Quebrada de Guispi. canchi, hacienda Chiraura, 3250m, 30 Jul 1929, *F. L. Herrera 3250* (US).

BOLIVIA.—Cochabamba: Carrasco, c. 0.5 km from Monte Puncu along road to Sehuencas, 3000 m, 31 Jan 2001, *J.R.I. Wood & D.J. Goyder 17058* (UC); Depto. La

Paz: Prov. Bautista Saavedra, 3600 m, 14 Jan 1980, *T. Feuerer 7865* (F); Valle de Cochabamba, Pairumani, 06 Nov 1967, *Bro. Adolfo M. 100* (US).

ARGENTINA.—Catamarca: Ambato El Potrero, 1300m, 08 May 1910, *ex herb. L. Castillon s.n.* (US-2786298). Tucumán: Jujuy, Capital El Mollar, Dep. Cafi, 24 Nov 1927, *Schreiter 5783* (RB). Tafi: Cumbre de Riaco [interpreted], 2200m, 27 Feb 1925, *S. Venturi 6891* (US, image!); entre la Cienaga J. Au fama, 2800m, 6 Feb 1933, *A.E. Burkart 5152* (US, image!). Tucumán. Dept: Trancas, Pie de la Cuesta Grande [interpreted], 2300m, 21 Apr 1926, *S. Venturi 4204* (US, F).

CHILE.—Prov. Aconcagua (Ligua): Quebrada Las Pataguas, 160 m, Jul 1968, *J. Escudero s.n.* (CONC-97590). Prov. Santiago: Dpto. Santiago, Cerro Abanico El Mirador, 1600 m, 33°28'S, 70°27'W, 26 Mar 1961, *F. Schlegel 3760* (CONC). Prov. Valparaiso: Cerro Campana, 600 m, Feb 1958, *P. Valenzuela s.n.* (CONC-97588). Región del Lib. B. O'Higgins: Hacienda Las Nieves, nascentes Río Claro, sobre Campamento Arboleda, 1885 m, 6173769-UTMN, 358944-UTME, 28 Dec 2005, *L. Faúndes & B. Larraín s.n.* (CONC-180752). VII Region: Prov. Linares, A lo largo del río Achibueno, desde junta estero Las Animas a junta estero Riecillo, 36°05'S, 71°10'W, 9 Mar 1999, *E. Ruiz & P. López 1175* (CONC); Prov. Linares, Reserva Nacional Bellotos del Melado, quebrada húmeda, 1350 m, 35°51'S, 71°05'W, 4 Jan 2000, *A. Humaña et al. 20006* (CONC); Prov. Linares, Reserva Nacional Bellotos del Melado, quebrada Hornillos, bosque de Pumo, Litre, Quillay, 970 m, 35°51'S, 71°06'W, 19 Jul 1999, *M.K. Arroyo et al. 994936* (CONC); Prov. Linares, Rio Ancoa (Hornillos), 35°51'S, 71°08'W, 950 m, 18 May 1989, *J. S. Martin 2300* (CONC); Prov. Talca, Central Los Cipresses, a orillas del río, 35°47'S, 70°48'W, 900 m, 13 Apr 2000, *V. Finot & P. López 2140* (CONC); Prov. Talca, Los Bellotos del Melado, rivera del río el comienzo de la cuesta hasta las afureas de la Reserva Nacional, 35°50'S, 71°06'W, 700-800 m, 1 Mar 2005, *M. Mihoc 64* (CONC).

See species comments on *Dennstaedtia cicutaria*.

Dennstaedtia mathewsii (Hook.) C. Chr., Index Filic. 218. 1905. *Deparia mathewsii* Hook., Sp. Fil. [W. J. Hooker] 1: 85, t. 30B. 1844. TYPE: PERU. Mathews 1782 (holotype: K-000640357, image!; isotypes: US00589426, image!; US00066391). (Fig. 3. I-L, Map 5)

Plants terrestrial or rupestral. Rhizomes creeping, 1–1.5 cm diam, verrucose and glabrous, with petiolar buds. Fronds determinate, 1.5–4 m long; petioles dark

brown, with root projections, 1–2 m × 0.5–1 cm, inermous, small aerophores, verrucose and glabrescent; laminae 2-3-pinnate, 2–3 m long, with alternate; rachises light to dark brown, adaxially sulcate, abaxially and adaxially densely catenate hairs, more densely at base of axis, without buds in axes and in sulcou, small aerophores; basal pinnae alternate, lanceolate, 40–80 × 20–40 cm, equilateral, proximally obtuse, distally acute to acuminate; costae abaxially and adaxially densely catenate hairs, adaxially sulcate, small aerephore; ultimate segments oblong, 1.5–2 × 0.5–1 cm, proximally sessile, distally rounded, crenate, with sori projected out of the liminae, without shallow sinus forming round-shaped segment; costules and veins abaxially and adaxially sparsely catenate hairs; laminar tissue between the veins abaxially sparsely catenate hairs, adaxially glabrous; lamina margins glabrous, entire and crenate at apex segments, with sori projected out of the liminae. Sori spherical to hemi-spherical along margins, projected out of the pinna, 0.8–1 × 0.8–1 mm; indusia cup-shape, glabrous.

DISTRIBUTION.—Northern South America.

SPECIMENS EXAMINED.—PERU. Cajamarca: San Ignacio, Huarango, El Progreso, Bosque secundario, 5°19'15"S, 78°40'0"W, 1300-1450 m, 17 Sep 1999, *J. Campos et al.* 6276 (UC); La Coipa, Localidad Vista Florida (Camino a la Laguna) Bosque primario, 5°26'10"S, 78°56'00"W, 1900-2000 m, 20 Jun 1997, *J. Campos & Z. García* 4048 (UC). Pasco: Oxapampa, Catarata de Rio Tigre, 10.68173N, 75.36328E, 1777m, 24 May 2016, *C.J. Rothfels et al.* 5068 (UC); Oxapampa, Parque Nacional Yanachanga, El Huampa1, primary montane forest, 10°11'S, 75°34'W, 1 Jul 2003, *H. van der Werff* 17908 (UC).

BOLIVIA.—Depeto. Beni, Prov. Gral. Bolivián, 12 km por el camino maderero, al SW del km 12 Yucumo – Rurrenabaque, 15°04'S, 67°07'W, 450 m, 16 Jul 1997, *M. Kessler et al.* 10839 (UC).

See species comments on *Dennstaedtia concinna*.

Dennstaedtia obtusifolia (Willd.) T.Moore, Index Fil. 306. 1861. *Dicksonia obtusifolia* Willd., Sp. Pl., ed. 4 [Willdenow] 5: 483. 1810. *Patania obtusifolia* (Willd.) C.Presl, Tent. Pterid. 138 (1836). LECTOTYPE (designated here): VENEZUELA. Caracas: F. Bredemeyer s.n. (B-W-20163-010, image!). (Fig. 4, A-D; Map 5)

Dennstaedtia pubescens C.Chr., Index Filic. 218. 1905. *Dicksonia pubescens* Baker, J. Bot. 19: 203 (1881). LECTOTYPE (designated here): COLOMBIA. Peñitas: 6500 m, *W.G. Kalbreyer 1859* (K-000640360, image!; isolectotypes: K-000640359, image!; GH-00135518, image!; US-00066394, image!).

Dennstaedtia deparioides (Rosenst.) Rosenst., Hedwigia 46: 71. 1906. *Dicksonia cicutaria* var. *deparioides* Rosenst. Hedwigia 43: 214. 1904. LECTOTYPE (designated by Tryon 1960): BRAZIL. São Paulo, Toledo, im Sumpf, 800 m, 10 July 1903, *A. Ulbricht 73* (S-R-1446, image!).

Plants terrestrial. Rhizomes creeping, light brown catenate hairs, (0.5–)1–2.5 cm diameter. Fronds determinate, (0.73–)1–3 m long; petioles sometimes with projections of the roots at the base, light to dark brown, (0.22–)0.50–1 m × (0.3–)0.5–1 cm, inermous, with small aerophores, light to dark brown catenate hairs, sometimes glabrescent above; laminae 1-pinnate-pinnatifid to 2-pinnate-pinnatifid, 1–2 m long, with alternate to sub opposite pinnae; rachises light to dark brown, adaxially sulcate, abaxially and adaxially with catenate hairs, more densely at the base of axes, sometimes buds in axes, with small aerophores; basal pinnae opposite to sub-opposite, equilateral, lanceate to lanceolate, truncate to obtuse at the base, cuneate to acuminate at the apex, (9–)25–52 cm × (2.5–)10–20 cm; costae abaxially with light to dark brown catenate hairs, adaxially glabrescent, sometimes catenate hair more densely at base of axis, small aerephore; lacking adaxially wings; ultimate pinnules equilateral, lanceate to ovate, at the bases basiscopically obtuse and sessile, cuneate to acuminate and crenate apex, 1.5–12 × 1–2.5 cm, shallows sinus not forming segments; costules and veins abaxially moderately light to dark brown catenate hairs, adaxially sparsely light to dark brown catenate hairs; laminar tissue between the veins abaxially with catenate hairs, adaxially glabrous; lamina margins glabrous, entire. Sori rounded to tubular, at the apex of ultimate pinnules projecting outward on the margin, 0.5–1 × 0.5–1 mm; indusia hemi-espherical to tubular, glabrous.

DISTRIBUTION.—For the regions presented in the work, *Dennstaedtia obtusifolia* occurs in Peru and Brazil. However, its distribution is recognized for Colombia and Venezuela; altitudinal distribution from 200 to 1000 m.

SPECIMENS EXAMINED.—PERU. Pasco: OXAPAMPA, along road Chatarra-Cacazu, forest on steep, rocky slopes, 10°32'S, 75°04'W, 890 m, 10 Jul 2003, *H. van der Werff et al. 18235* (UC). San Martín: Provincia Huallaga, Distrito Saposoa, entre San José y Leía Chica, margen izquierda del río Huambo, 1000 m, 10 Sep 2001, *V. Quipuscoa et al. 2673* (US).

BRAZIL.—Mato Grosso do Sul: Rio Verde de Mato Grosso, Serra Pimenteira, Cachoeira do Cervo, 18°55'S, 54°53'W, 400 m, 22 feb 1994, *C.E. Rodrigues, Jr. & M.R. da Silva 725* (SJRPI). Minas Gerais: Belo Vale, 20°26'37"S, 43°56'10"W, 1300 m, 23 oct 2001, A. Salino & A. Carvalho 7652 (BHCB); Caldas, Distrito Pocinhos do Rio Verde, 21°56'S, 46°23'W, 1150-1200 m, 16 Jun 1995, *M.R. Pietrobon-Silva 1933* (SJRPI); Caldas, Distrito Pocinhos do Rio Verde, Propriedade do Fernando, subindo para Pedra Branca, 21°58'56.8"S, 46°22'52.2"W, 1300 m, 23 Jun 2021, *N.T.L. Pena et al.1074* (VIC); Caldas, Distrito Pocinhos do Rio Verde, Propriedade do Fernando, subindo para Pedra Branca, 21°58'56.8"S, 46°22'52.2"W, 1300 m, 23 Jun 2021, *N.T.L. Pena et al.1075* (VIC); Caldas, Distrito Pocinhos do Rio Verde, Propriedade do Fernando, subindo para Pedra Branca, 21°58'56.8"S, 46°22'52.2"W, 1300 m, 23 Jun 2021, *N.T.L. Pena et al.1076* (VIC); Caldas, Distrito Pocinhos do Rio Verde, Propriedade do Fernando, subindo para Pedra Branca, 21°58'56.8"S, 46°22'52.2"W, 1300 m, 23 Jun 2021, *N.T.L. Pena et al.1077* (VIC); Caldas, Distrito Pocinhos do Rio Verde, Propriedade do Fernando, subindo para Pedra Branca, 21°58'56.8"S, 46°22'52.2"W, 1300 m, 23 Jun 2021, *N.T.L. Pena et al.1078* (VIC); Caldas, Distrito Pocinhos do Rio Verde, Estrada para Pedra Branca, 21°57'09.95"S, 46°23'04.8W, 1000 m, 24 Jun 2021, *N.T.L. Pena et al. 1080* (VIC); Caldas, Distrito Pocinhos do Rio Verde, Estrada para Pedra Branca, 21°57'09.95"S, 46°23'04.8W, 1000 m, 24 Jun 2021, *N.T.L. Pena et al. 1081* (VIC); Caldas, Distrito Pocinhos do Rio Verde, Estrada para Pedra Branca, 21°57'09.95"S, 46°23'04.8W, 1000 m, 24 Jun 2021, *N.T.L. Pena et al. 1082* (VIC); Caldas, Distrito Pocinhos do Rio Verde, Estrada para Pedra Branca, 21°57'09.95"S, 46°23'04.8W, 1000 m, 24 Jun 2021, *N.T.L. Pena et al. 1083* (VIC); Caldas, Distrito Pocinhos do Rio Verde, Estrada para Pedra Branca, 21°57'09.95"S, 46°23'04.8W, 1000 m, 24 Jun 2021, *N.T.L. Pena et al. 1084* (VIC); Caldas, zona de amortecimento da Rebio Pedra Branca, 21°56'39"S,

46°23'7"W, 1330 m, 15 Oct 2013, *E.A. Williams et al. 137* (RB); Caldas, zona de amortecimento da Rebio Pedra Branca, 21°57'8"S, 46°23'6"W, 1358 m, 23 Oct 2013, *E.A. Williams et al. 162* (RB); Caldas, zona de amortecimento da Rebio Pedra Branca, 21°56'39"S, 46°23'7"W, 1330 m, 03 Feb 2014, *E.A. Williams et al. 312* (RB); Caldas, zona de amortecimento da Rebio Pedra Branca, 21°22'55"S, 46°56'53"W, 1337 m, 16 Jul 2015, *E.A. Williams & E.J. Godoy 526* (RB); Caratinga, Estação Biológica de Caratinga, Jaó, 24 Mar 2000, *A. Salino et al. 5120* (BHCB); Conceição do Mato Dentro, no entrono do Parque Municipal Ribeirão do Campo, 19°03'13.8"S, 43°37'04.1"W, 1200 m, 8 Agu 2003, *A. Salino & R.C. Mota 8882* (BHCB); Descoberto, Reserva do Grama, 15 Jun 2005, *C.M. Mynssen et al. 732* (RB); Descoberto, Reserva Biológica da Represa do Grama, "epífita" na mata, próximo a curso d'água, 10 Nov 2001, *J.O. Augustin et al. s.n.* (CESJ-53.078); Itabirito, Área da Serra da Moeda, 20°19'9.9"S, 43°56'17"W, 1450 m, 14 Jun 2021, *A. Salino et al. 7091* (BHCB); Itabirito, Serra da Moeda, 20°19'26.03"S, 43°55'55.59"W, 1157 m, 9 Sep 2006, *G. Heringer 110* (BHCB); Juiz de Fora, Mata do Krambeck, 25 Mar 2008, *I. Almeida et al. 28* (BHCB; CESJ); Juiz de Fora, Reserva Biológica Municipal do Poço d'Anta, 21°45'40"S, 43°19'11"W, 760 m, 30 Sep 2017, *R.C.J. Garcia 128* (CESJ); Marliéria, Parque Estadual do Rio Doce, as margens do Córrego Pardo, 25 Mar 2002, *A. Salino 7971* (BHCB); Nova Lima, Mata da Mutuca, Córrego da Mutuca, 03 Sep 2001, *F.A. Carvalho et al. 09* (BHCB); Nova Lima, RPPN Capitão do Mato, 20°08'00.8"S, 43°53'10.6"W, *J.B. Figueiredo et al. 108* (BHCB); Nova Lima, RPPN Tumbá, 26 Sep 2003, *J.B. Figueiredo & N.F.O. Mota 160* (BHCB); Novo Cruzeiro, Fazenda Araras, 17°36'47.6"S, 41°57'49.3"W, 754 m, 10 Feb 2004, *J.R. Stehmann et al. 3598* (BHCB); Ouro Preto, Estação Ecológica do Tripuí, 1200 m, 19 Oct 2002, *A. Salino 8093* (BHCB); Passa Quatro, 03 May 1948, *S. Araújo 18955* (BHCB; RB); Poté, Fazenda Nossa Senhora de Fátima, 17°44'35"S, 41°13'56"W, 370-523 m, 20 Aug 2004, *J.A. Lombardi et al. 6070* (BHCB); Sabará, RPPN Cuiaba, base da Serra da Piedade, 19°51'08.7"S, 43°43'45.7"W, 776 m, 18 Jul 2006, *T.E. Almeida & D.T. Souza 235* (BHCB; RB). Paraná: Telêmaco Borba, Fazenda Monte Alegre, à beira do ribeirão Varanal, 24°20'13.4"S, 50°35'23.1"W, 31 Oct 2006, *T.I.N. de Azevedo & S.I. de Azevedo 49* (FUEL). Rio Grande do Sul: Dom Pedro de Alcântara, 29°19'49.35"S, 49°50'08.91"W, 9 m, 13 Jan 2014, *F. Gonzatti 1005* (HAS; UCS). São Paulo: Analândia, Serra do Cruzeiro, 800 m, 28 Nov 1987, *A. Salino 203* (BHCB); Águas da Prata, 21°56'S, 46°48'W, 850 m, 17 Jun 1995, *M.R. Pietrobon-Silva 1989*

(MBM; SJRP); Brotas, mata ciliar do Viveiro Municipal, 470 m, 21 Sep 1991, A. Salino 1103 (BHCB); Campinas, Barão Geraldo, Reserva Florestal Santa Genebra, 13 Feb 1992, A. Salino 1276 (BHCB, UEC); São Carlos, Rodovia Viscinal de acesso ao Broa, ca. 13 km de São Carlos, 26 Sep 1997, M.R. Pietrobon-Silva 4174 (SJRP); Teodoro Sampaio, região do Pontal do Paranapanema, Parque Estadual do Morro do Diabo, ca. 30 km da sede pela trilha córrego 7 de setembro ou rio da onça ou Angelin, 22°32'S, 52°11'W, 250-350, 16 Jan 1995, M.R. Pietrobon-Silva 1566 (SJRP); Teodoro Sampaio, região do Pontal do Paranapanema, Parque Estadual do Morro do Diabo, ca. 30 km da sede pela trilha córrego 7 de setembro ou rio da onça ou Angelin, 22°32'S, 52°11'W, 250-350 m, 19 Sep 1996, M.R. Pietrobon-Silva 3469 (SJRP); Zacarias, no date, C. Siqueira s.n. (SJRP-29391).

See species comments on *Dennstaedtia cornuta*.

Dennstaedtia sprucei T.Moore, Index Fil. (T.Moore) 308. 1861. *Dicksonia sprucei* (T. Moore) Baker, J. Bot. 15: 162. 1877. LECTOTYPE (designated here): ECUADOR, In Andibus Ecuadorensibus [Andes of Ecuador], 1857–1859, R. Spruce 5350 (BM-000937677, image!; isolectotypes: B-200119871, image!; BM-000777052, image!; COL-000006215, frag., image!; GH-00020963, image!; K-000640350, image!; K000640351, image!; LE-00008205, image!; NY-00149043, image!; NY00328996, image!; P-00633300, image!; P-00633301, image!; P00633302, image!; US-00066398, frag., image!). (Fig. 4, E-H; Map. 6)

Plants terrestrial. Rhizomes creeping, 0.5–1 cm diam, verrucose and glabrous. Fronds determinate, 2–4 m long; petioles dark brown, without root projections, 0.50–1 m × 0.4–1 cm, inermous, small aerophores, with densely catenate hairs; laminae 2-pinnate to 2-pinnate-pinnatifid, 2–3 m long, with opposite to sub opposite pinnae; rachises dark brown, adaxially sulcate, abaxially and adaxially densely catenate hairs, more densely at base of axis, without buds in axes, small aerophores; basal pinnae opposite, lanceolate, 30–40 × 10–15 cm, equilateral, proximally obtuse, distally acute; costae abaxially densely catenate hairs, adaxially glabrescent and sulcate, small aereophore; ultimate segments lanceate to falcate, 2–5 × 0.8–1.5 cm, proximally sessile, distally acute, crenate, with shallow sinus forming round-shaped segment; costules and veins abaxially densely catenate hairs, adaxilly sparsely catenate hairs; laminar tissue between the veins abaxially densely catenate hairs, adaxilly sparsely catenate hairs; lamina margins densely catenate hairs, entire and

crenate at apex segments. Sori hemi-spherical, 1.2–2.5 × 1–1.5 mm; indusia purse-shaped, with catenate hairs.

DISTRIBUTION.—Northern South America.

SPECIMENS EXAMINED.—PERU. Distrito de Oxapampa: La Suiza, along the short trail to a cave, or by the cave itself. -10.65440N, -75.45111E, 2180 m, 19 May 2016, C.J. Rothfels 4975 (UC); Pasco, along old road Oxapampa-Villa Rica, 10°38'S, 75°22'W, 2000 m, 25 Jun 2003, *H. van der Werff et al.* 17764 (UC). Prov. San Martín: Montane forest on sandstone (1) or limestone (2), 05°41'S, 77°48'W, 1950 m, 4 Mar 2001, *H. van der Werff et al.* 16715 (UC).

BOLIVIA.—Depto. Cochabamba, Prov. José Carrasco Torrico, 117 km antigua Carretera Cochabamba-Villa Tunari, 17°08'S, 65°39'W, 2350 m, 07 Jun 1996, M. Kessler 7071 (UC).

ADDITIONAL SPECIMENS EXAMINED.—ECUADOR.—Pichincha: Old road Quito-Sto. Domingo, forest remnants along road, 2900 m, *H. van der Werff & W. Palacios* 10590 (NY).

Dennstaedtia sprucei differs from *D. auriculata* by rhizomes creeping (vs. ascending to decumbent), laminae 2-pinnate to 2-pinnate-pinnatifid (vs. 3-pinnate-pinnatifid), alternate pinnae (vs. opposite to sub-opposite pinnae), laminar margins with catenate hairs (vs. glabrous), indusia with catenate hairs (vs. glabrous). *Dennstaedtia sprucei* differs from *D. arborescens* by laminar margins with catenate hairs (vs. glabrous), without buds in axes rachises-laminae (vs. buds in axes rachises-laminae), indusia densely catenate hairs (vs. glabrescent).

4. EXCLUDED NAMES AND SPECIES FROM THE AREA

Dennstaedtia bipinnata = *Dennstaedtia dissecta* – see Chapter 1.

Dennstaedtia dissecta (Sw.) T.Moore, Index Fil. (T.Moore) 305. 1861. – not occurring in the area.

5. DOUBTFUL NAMES

Dennstaedtia divaricata C.Chr., Index Filic. 217 (1905). *Dicksonia divaricata* Sodiro, Anales Univ. Centr. Ecuador 7: 104 (1893). Holotype.—ECUADOR. Bosques Occidentales del Volcán Pululahua, Sodiro s.n. (Q? – not found; AAU? – not found). We have not found the type of this name.

Dennstaedtia grossa Christ, Bull. Herb. Boissier ser. 2, 6: 192 (1906). Lectotype: Costa Rica, Navarro, Wercklé 9 (P? – not found). We have not found the type of this name.

Dennstaedtia ordinata (Kaulf.) T. Moore, Ind. Fil. 306. 1861. *Dicksonia ordinata* Kaulf. Enum. Fil. 226. 1824. Holotype: Porto Rico, *Ventenat*. We have not found the type of this name.

Dicksonia punctulata Poir., Lam. Encycl. Suppl. 2: 475. 1811. Holotype: *Hb. Desfontines* (P? – not found). We have not found the type of this name.

6. ACKNOWLEDGEMENTS

Pena thanks Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) for the PhD scholarship, the International Association for Plant Taxonomy (IAPT) for the "Grant 2020", and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES-PROAP) for the graduate grant; we also thank the students, Curators, and staff at Herbarium VIC, the Curators and staff of the herbaria which sent loans or were visited (see material and methods), and Joelcio Freitas and Reinaldo Pinto for the illustrations.

7. LITERATURE CITED

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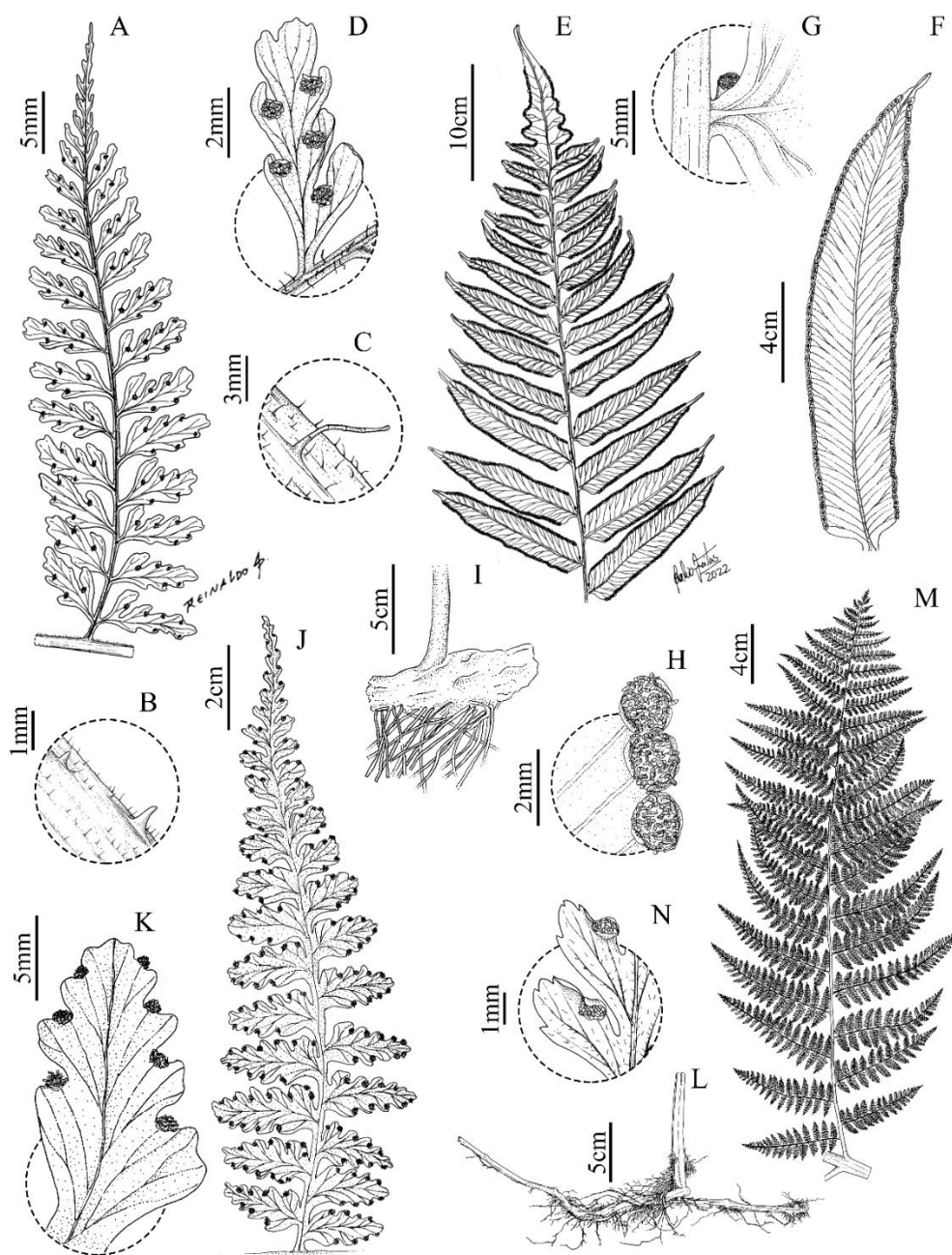


Figure 1. A-D. *Dennstaedtia aculeata*. A. pinnule, abaxially; B. detail of rachis showing spines; C. detail of rachis showing acicular and catenate hairs; D. ultimate segment, abaxially, showing sori and indusia. E-H. *Dennstaedtia arcuata*. E. lamina, abaxially; F. pinnule, abaxially; G. buds in axes; H. segment, abaxially, showing sori and indusia. I-K. *Dennstaedtia auriculata*. I. rhizome; J. pinnule, abaxially; K. ultimate segment, abaxially, showing sori and indusia. L-N. *Dennstaedtia cicutaria*. L. Rhizome; M. pinnule, abaxially; N. ultimate segment, abaxially, showing sori and indusia.

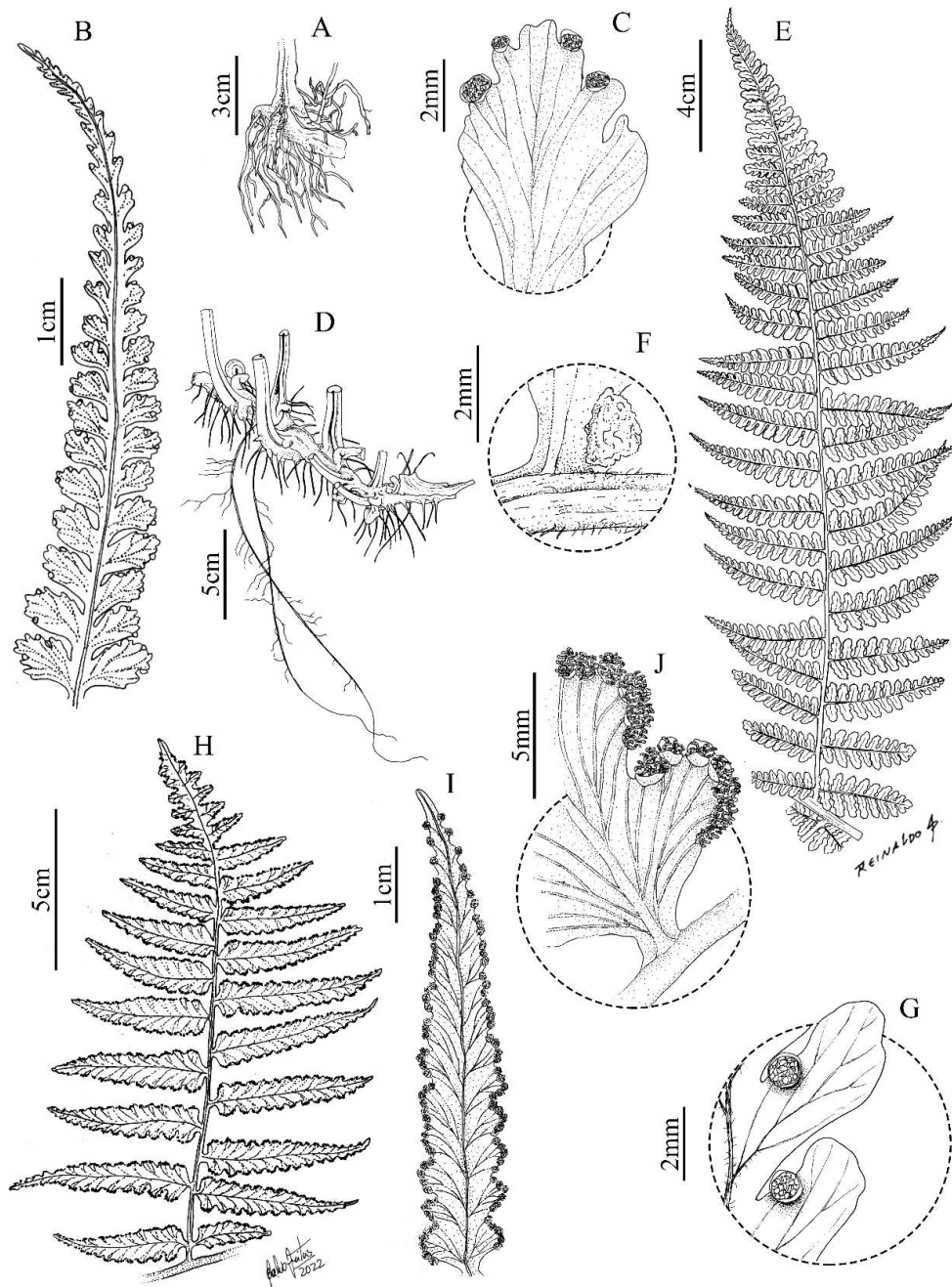


Figure 2. A-C. *Dennstaedtia concinna*. A. rhizome; B. pinnule, abaxially; C. ultimate segment, abaxially, showing sori and indusia. D-G. *Dennstaedtia cornuta*. D. rhizome; E. basal pinnae; F. buds in axes; G. segment, abaxially, showing sori and indusia. H-J. *Dennstaedtia coronata*. H. basal pinnae; I. pinnule, abaxially; J. segment, abaxially, showing sori and indusia.

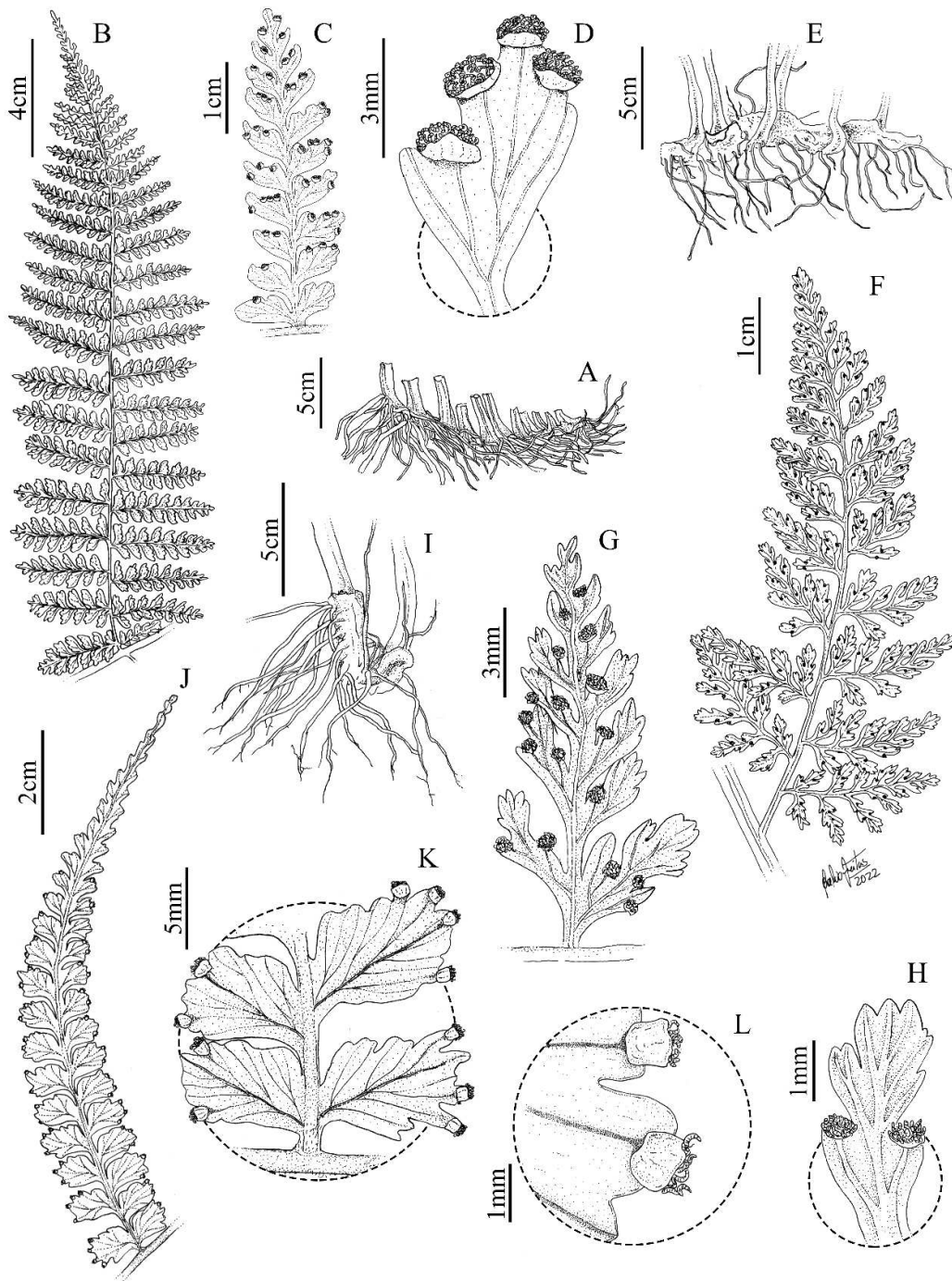


Figure 3. A-D. *Dennstaedtia fluminensis*. A. rhizome; B. pinna, abaxially; C. pinnule, abaxially; D. ultimate segment, abaxially, showing sori and indusia. E-H. *Dennstaedtia glauca*. E. rhizome; F. pinna, abaxially; G. pinnule, abaxially; H. ultimate segment, abaxially, showing sori and indusia. I-L. *Dennstaedtia mathewsii*. I. rhizome; J. pinna, abaxially; K. pinnule, abaxially; L. ultimate segment, abaxially, showing sori and indusia.

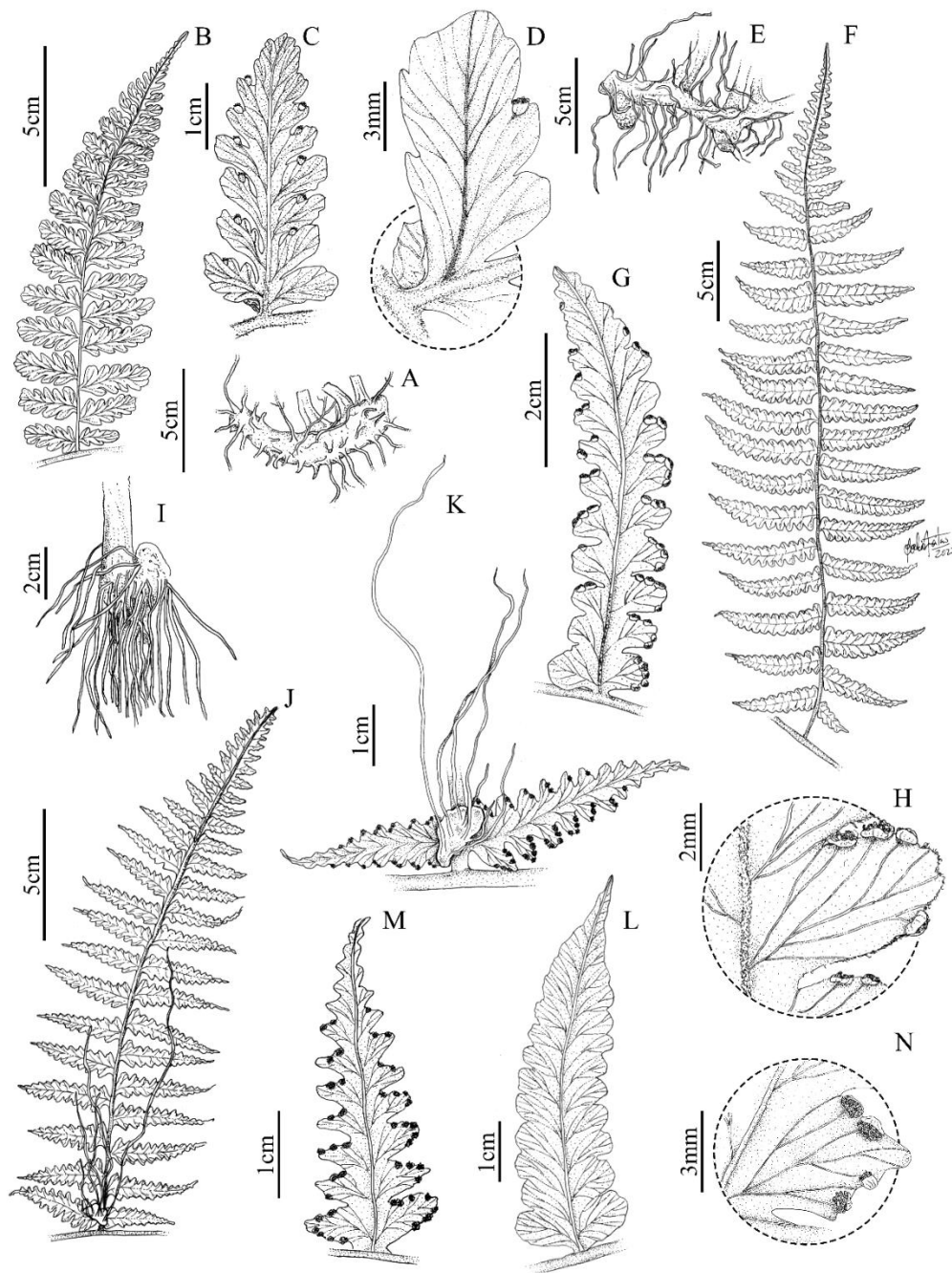
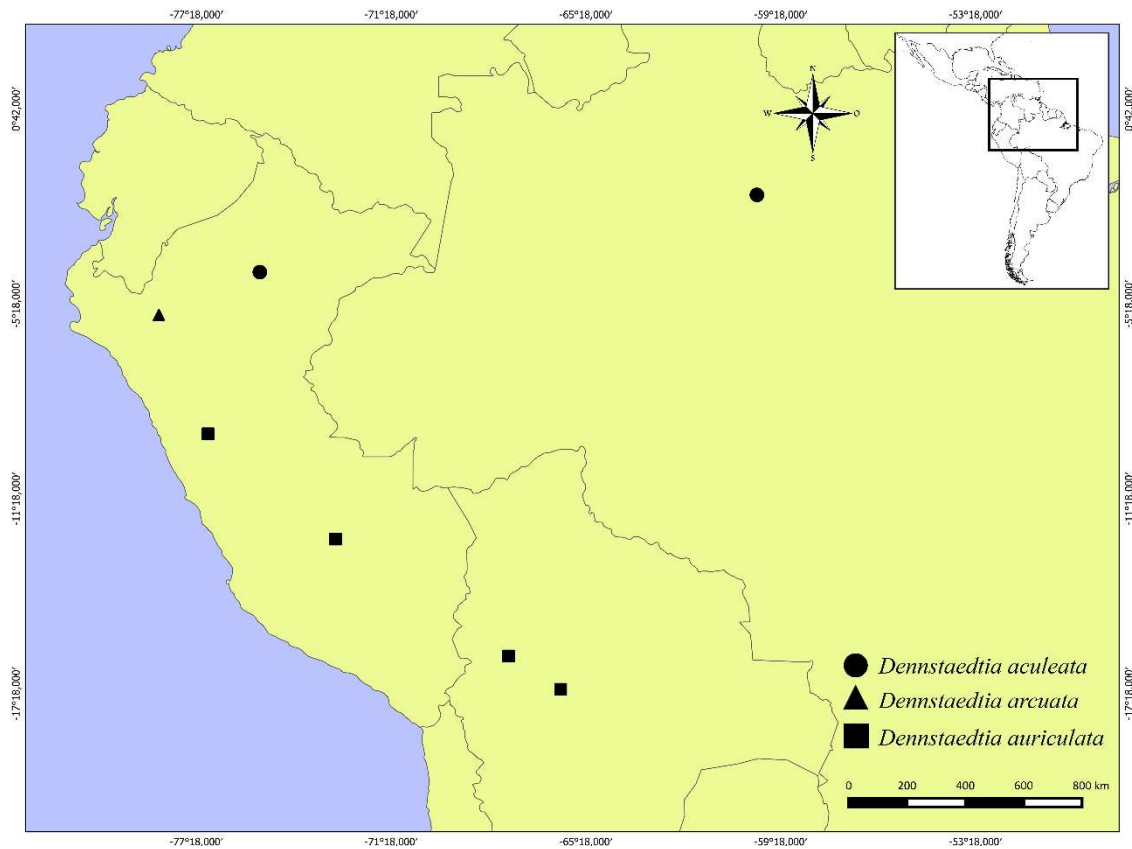
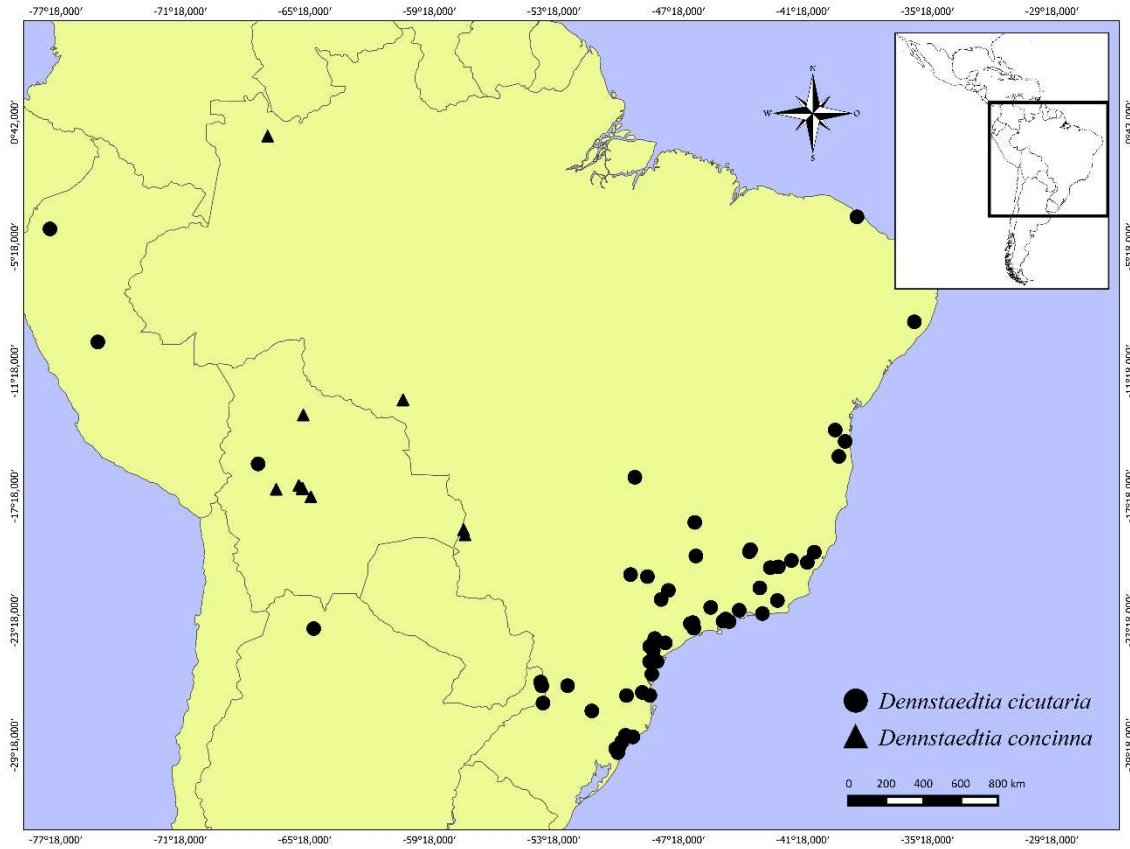


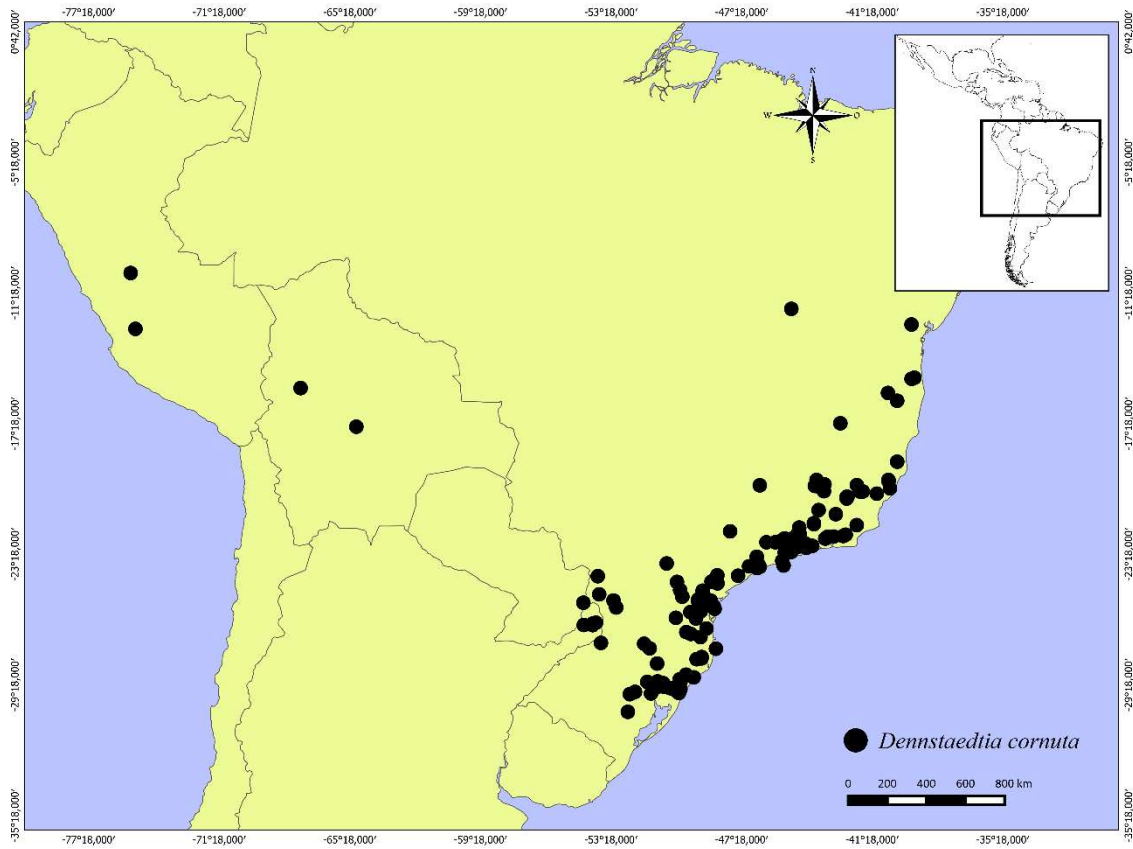
Figure 4. A-D. *Dennstaedtia obtusifolia*. A. rhizome; B. pinna, abaxially; C. pinnule, abaxially; D. ultimate segment, abaxially, showing sori, indusia, and buds in axes. E-H. *Dennstaedtia sprucei*. E. rhizome; F. pinna, abaxially; G. pinnule, abaxially; H. ultimate segment, abaxially, showing sori, indusia, and hairs in margin. I-N. *Dennstaedtia andina*. I. rhizome; J. pinna, abaxially; K. detail of buds in axes; L. ultimate segment at the apex, abaxially; M. ultimate segment at the base, abaxially; N. segment, abaxially, showing sori and indusia.



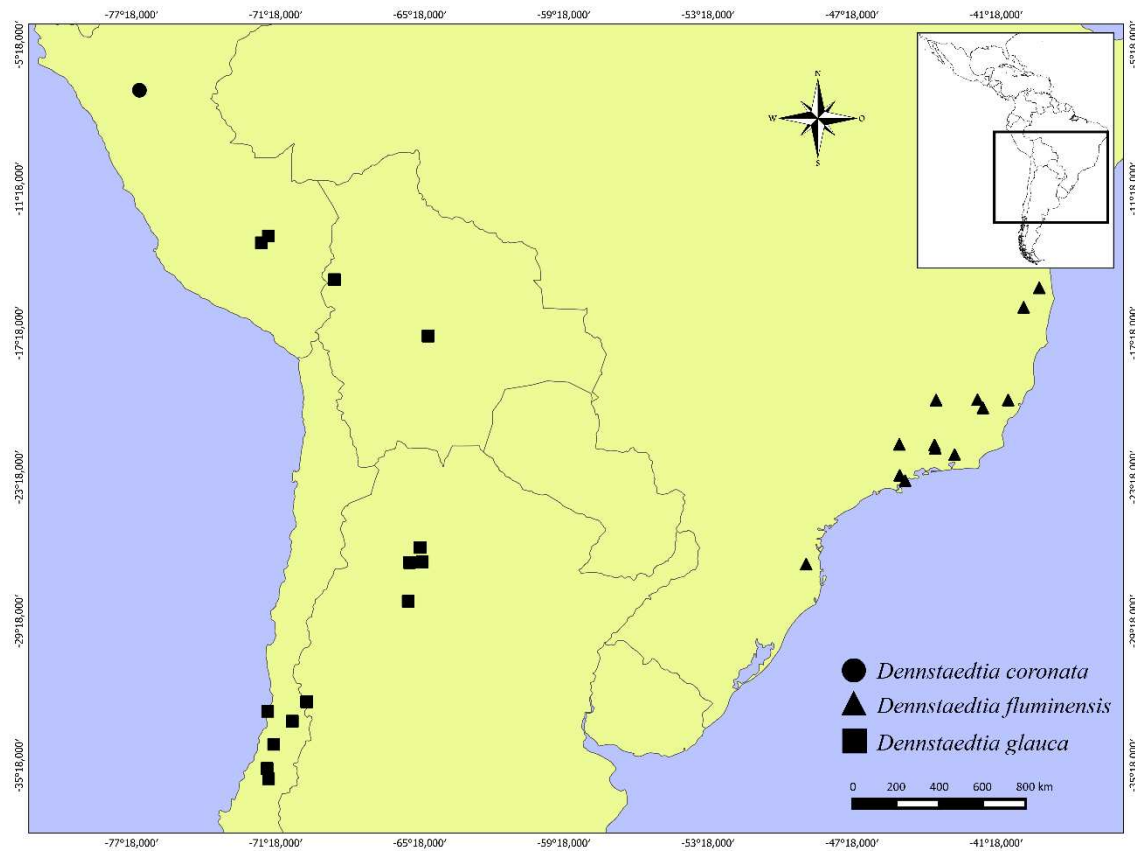
Map 1. Geographic distribution of *Dennstaedtia aculeata* (circle); *D. arcuata* (triangle); *D. auriculata* (square).



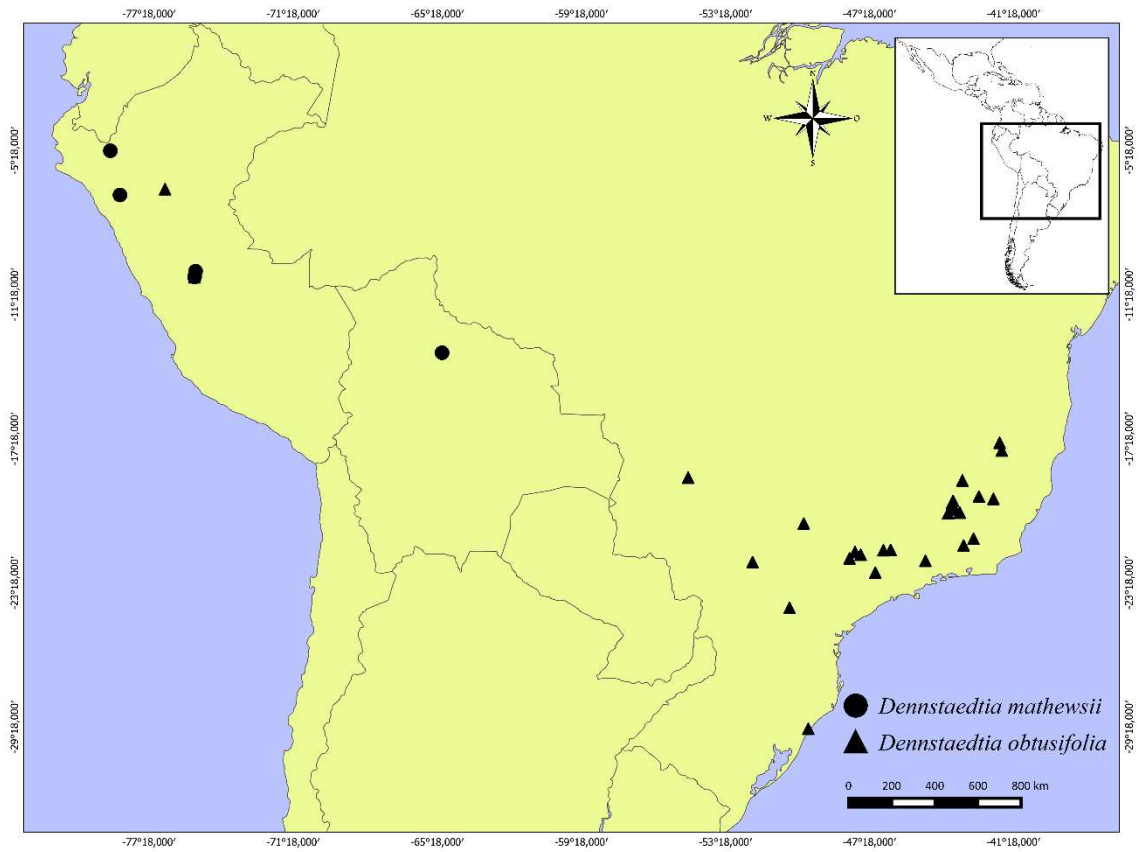
Map 2. Geographic distribution of *Dennstaedtia cicutaria* (circle); *D. concinna* (triangle).



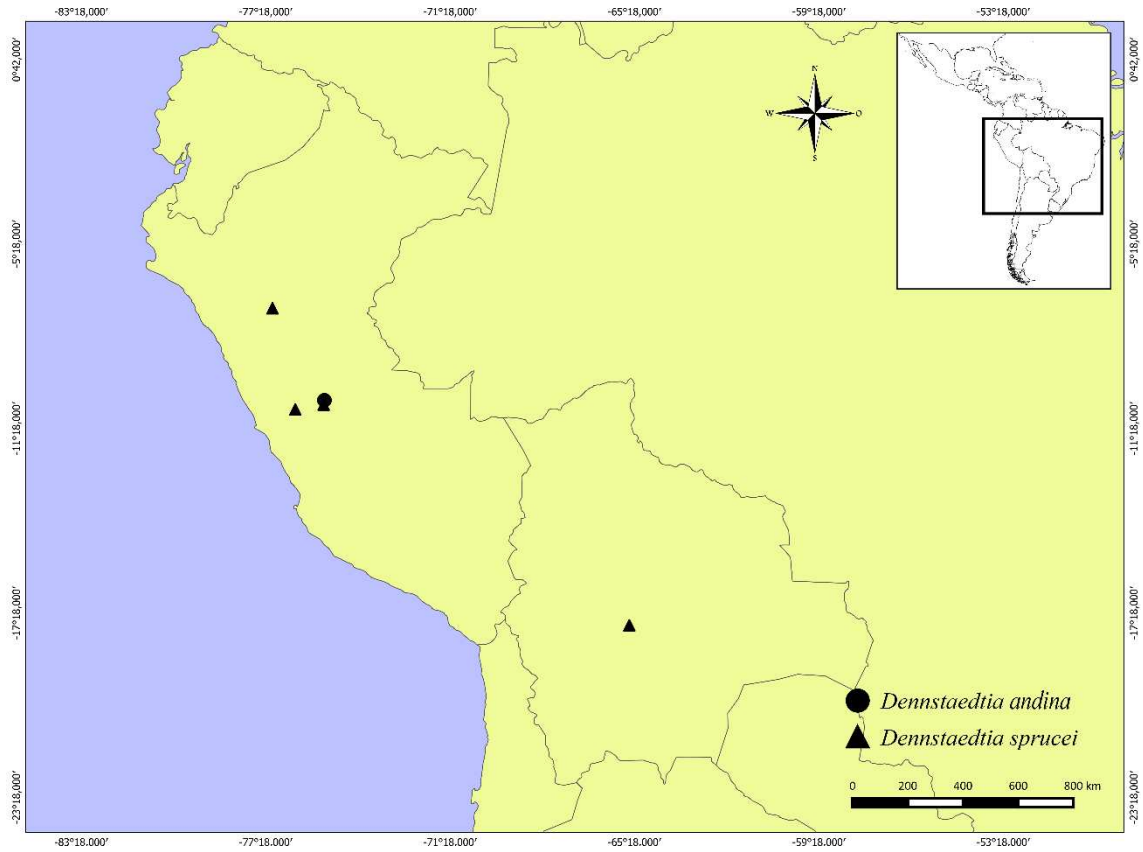
Map 3. Geographic distribution of *Dennstaedtia cornuta* (circle).



Map 4. Geographic distribution of *Dennstaedtia coronata* (circle); *D. fluminensis* (triangle); *D. glauca* (square).



Map 5. Geographic distribution of *Dennstaedtia mathewsii* (circle); *D. obtusifolia* (triangle).



Map 6. Geographic distribution of *Dennstaedtia andina* (circle); *D. sprucei* (triangle).

Capítulo IV. Pena, N.T.L. A filogenia molecular como ferramenta taxonômica para a resolução de complexos de espécies.

Capítulo VI. A filogenia molecular como ferramenta taxonômica para a resolução de complexos de espécies

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RESUMO

O presente estudo apresenta análise de filogenia molecular como ferramenta taxonômica para a resolução de complexos de espécies para a família Dennstaedtiaceae, com foco nas espécies brasileiras da subfamília Dennstaedtioideae. Para a resolução topológica, foram extraídas amostras de DNA de materiais frescos armazenados em sílica gel e de espécimes herborizados. Os marcadores utilizados foram *rbcL*, *trnL-trnF* e *rps4-trnS*. As reconstruções filogenéticas se basearam em análises de Máxima Verossimilhança e Bayesiana. A topologia resgatou as subfamílias Dennstaedtioideae, Hypolepidoideae e Monachosoroideae como monofiléticas, apresentando elevado valor de bootstrap para os clados em nível de gênero. Os complexos de espécies, principalmente envolvendo espécies brasileiras, foram melhor compreendidos e resolvidos taxonomicamente. As espécies resgatadas da sinonímia, *Dennstaedtia concinna*, *D. fluminensis*, *Mucura tamandarei* e *M. tenera*, foram sustentadas como espécies válidas no estudo filogenético aqui apresentado.

Palavras-chave: complexo de espécies, *Dennstaedtia dissecta*, *Dennstaedtia cornuta*, evolução, *Mucura*

ABSTRACT

The present study presents molecular phylogeny analysis as a taxonomic tool for the resolution of species complexes for the family Dennstaedtiaceae, focusing on the Brazilian species of the subfamily Dennstaedtioideae. For the topological resolution, DNA samples were extracted from fresh materials deposited in silica gel and herborized specimens. The markers used were *rbcL*, *trnL-trnF*, and *rps4-trnS*. The phylogenetic reconstructions were based on Maximum Likelihood. The topology showed the subfamilies Dennstaedtioideae, Hypolepidoideae, and Monachosoroideae as monophyletic, presenting a high bootstrap value for the clades at the genus level. The complexes of species, especially those involving Brazilian species, are now better understood and taxonomically resolved. Some species rescued from synonymy, *Dennstaedtia concinna*, *D. fluminensis*, *Mucura tamandarei*, and *M. tenera*, are supported as valid species in our phylogenetic study.

Key-words: *Dennstaedtia dissecta*, *Dennstaedtia cornuta*, evolution, *Mucura*, species-complexes

1. INTRODUÇÃO

Nos últimos dez anos, importantes contribuições de cunho filogenético voltaram-se aos estudos da família Dennstaedtiaceae, que confirmaram o monofiletismo da família (e.g. Perrie *et al.*, 2015; Schneider *et al.*, 2016; Shang *et al.*, 2018; Schwartsburd *et al.*, 2020; Wang *et al.*, 2021; Triana-Moreno *et al.*, *in press*). Estes estudos também apontaram para três grandes clados dentro da família, que foram reconhecidos oficialmente como três subfamílias por Schwartsburd *et al.* (2020). A relação entre as três subfamílias variaram um pouco entre os trabalhos filogenéticos, com alguns apontando a relação [Dennstaedtioideae [Monachosoroideae + Hypolepidoideae]] (Schneider *et al.* 2016), e outros a relação [Monachosoroideae [Dennstaedtioideae + Hypolepidoideae]] (Perrie *et al.*, 2015; Shang *et al.*, 2018; Schwartsburd *et al.*, 2020; Triana-Moreno *et al.*, *in press*). Esta última se apresenta como hipótese mais aceita, uma vez que ele foi gerado pelos trabalhos que incluíram amostragens mais representativas da família, apesar de terem valores de bootstrap não muito robustos, para estas relações.

A sub-família Monachosoroideae é monogenérica, representada pelo gênero *Monachosorum* Kunze. Hypolepidoideae é representada atualmente por seis gêneros, porém foram apresentadas duas topologias levemente distintas. As primeiras topologias apresentaram um clado formado apenas por *Pteridium* Gled. ex Scop., comportando-se como clado-irmão das demais Hypolepidoideae (Perrie *et al.*, 2015; Schneider *et al.* 2016; Shang *et al.*, 2018). Nos estudos filogenéticos mais recentes, contendo maior número de espécies, há a formação de dois clados principais: 1. clado formado pelos gêneros *Hiya* H.Shang, *Paesia* A.St.-Hil., *Histiopteris* (J.Agardh) J.Sm. e *Blotiella* R.M.Tryon; 2. clado formado por *Pteridium* e *Hypolepis* Bernh. (Schwartsburd *et al.*, 2020; Triana-Moreno *et al.*, *in press*). Apesar destas duas topologias levemente diferentes, a monofilia dos seis gêneros foi evidenciada em todos estes trabalhos, inclusive com a descrição do gênero *Hiya*.

Dennstaedtioideae, por outro lado, foi comumente demonstrada como uma subfamília contendo gêneros não monofiléticos, que necessitariam de rearranjos sistemáticos futuros. Perrie *et al.* (2015), Schneider *et al.* (2016) e Schwartsburd *et al.* (2020) demonstraram que *Dennstaedtia* Bernh., como tradicionalmente circunscrita, era polifilética. Nestas fileogenias, gêneros com poucas espécies, como *Leptolepia* Prantl e *Oenotrychia* Copel. apareciam dentro do clado das *Dennstaedtia* tropicais, enquanto que as *Dennstaedtia* norte-temperadas apareciam

como grupo-irmão de *Microlepia* C.Presl. Schneider *et al.* (2016) e Schwartsburd *et al.* (2020) chegaram a apontar resoluções monofiléticas, inclusive nomeado informalmente alguns grupos de *Dennstaedtia* s.l., como grupo “*Patania*” e grupo “*Sitobolium*”, porém, sem sequenciar o tipo de *Dennstaedtia*, era virtualmente impossível sair do campo da especulação.

Então, Triana-Moreno *et al.* (*in press*) se propuseram a fazer um estudo mais amplo de Dennstaedtioideae, incluindo o tipo de *Dennstaedtia*. Neste trabalho, ficou evidenciado que *Dennstaedtia* s.l. deveria ser dividida em três gêneros, para se atingir uma classificação mais natural, monofilética. Surpreendentemente, estes autores chegaram à conclusão de que o tipo de *Dennstaedtia* (*D. flaccida*) aparecia dentro de *Microlepia*, o que iria gerar uma enorme mudança nomenclatural: as espécies de *Microlepia* passariam a ser chamadas de *Dennstaedtia*; a maioria das espécies tradicionalmente classificadas em *Dennstaedtia* passariam a ser chamadas de *Patania*. Para evitar tamanhas mudanças, Triana-Moreno *et al.* (2022) propuseram, então, uma conservação de nome de *Dennstaedtia*, com um tipo conservado – alterando o tipo do gênero para *D. dissecta* (Sw.) T.Moore.

A nova classificação da subfamília proposta por Triana-Moreno *et al.* (*in press*), apresenta quatro gêneros: *Dennstaedtia* s. str. (mantendo basicamente a maioria das *Dennstaedtia* tradicionais, tropicais), *Microlepia*, o novo gênero *Mucura* Triana & Sundue (contendo duas espécies neotropicals), e *Sitobolium* Desv. (contendo as antigas *Dennstaedtia* norte-temperadas). *Leptolepia* e *Oenotrychia* foram sinonimizadas sob *Dennstaedtia* s. str.

Apesar do trabalho de Triana-Moreno *et al.* (*in press*) ser o mais completo até o momento e resolver taxonomicamente as circunscrições genéricas, ele praticamente não utilizou espécimes brasileiros e não se ateu às problemáticas taxonômicas a nível específico, dentro dos complexos de espécies. O presente autor e seu orientador participaram ativamente do trabalho de Triana-Moreno *et al.* (*in press*), porém apenas na parte taxonômica, morfológica e nomenclatural. As sequências produzidas por Triana-Moreno *et al.* (*in press*) ainda não estão disponíveis no GenBank e tampouco foram disponibilizadas para o presente autor. Aqui foram produzidas novas sequências de espécimens fundamentais para a resolução de problemas taxonômicos dentro de complexos de espécies, porém, infelizmente não foi possível acrescentá-las à filogenia principal de Triana-Moreno *et al.* (*in press*).

Obeve-se a chance de re-identificar alguns espécimens sequenciados por Triana-Moreno *et al.* (*in press*), o que trouxe ainda mais luz à identificação precisa e resolução de complexos de espécies. Portanto, o objetivo deste capítulo, foi utilizar ferramentas filogenéticas para sustentar (ou rejeitar) as decisões taxonômicas baseadas em morfologia, utilizando as duas respostas para uma melhor decisão taxonômica nos complexos.

2. MATERIAL E MÉTODOS

Amostragem taxonômica

Foi selecionado como grupo externo o gênero *Odontosoria* (C.Presl.) Fée, pertencente à família Lindsaeaceae e ao clado Lindsaeineae, grupo irmão de Saccolomatineae que foi o primeiro grupo a divergir dentro da ordem Polypodiales (PPG – The Pteridophyte Phylogeny Group 2016). A sequência do gênero foi extraída por meio do banco de dados disponível no GenBank. As amostragens de Monachosoroideae, Hypolepidoideae e Dennstaedtdioideae foram de cinco, 31 e 61 táxons, respectivamente.

Trabalho de campo

Os estudos foram realizados entre os anos de 2018 a 2022, nos quais foram analisadas as espécies dos gêneros *Dennstaedtia*, *Microlepia* e *Mucura*. Nesse período, foram realizadas expedições a campo em território brasileiro (nos estados da BA, ES, MG, RJ) para coleta de material em sílica gel. Plantas *in situ* da República Dominicana e Estados Unidos da América também tiveram amostras coletadas em sílica gel, durante o trabalho de campo de Pedro B. Schwartzburd. Durante os estudos da presente tese, foram extraídos DNA de 262 espécimes. Informações taxonômicas e quais herbários foram consultadas podem ser acessados nos capítulos 2 e 4.

Trabalho de herbário

Com o intuito de comparar as topologias filogenéticas apresentadas por Triana-Moreno *et al.* (*in press*) e as que obtivemos como resultados de nossas análises, os espécimes utilizados na filogenia de Triana-Moreno *et al.* (*in press*), foram reidentificados. O herbário UC da Califórnia, U.S.A, nos concedeu empréstimo dos espécimes utilizados na filogenia de Triana-Moreno *et al.* (*in press*). Ainda, foi

verificado imagens de espécimes disponibilizadas nos herbários virtuais. O processo de avaliação das identificações dos espécimes utilizados na filogenia de Triana-Moreno *et al.* (*in press*), foi super importante para o entendimento de relações mais específicas dos gêneros, uma vez que a existência dos complexos geram demasiada confusão nas identificações dos espécimes indexados nos herbários.

Extração de DNA, amplificação, sequenciamento e análises filogenéticas

O DNA genômico foi extraído usando o protocolo CTAB adaptado de Doyle e Doyle (1990), de tecidos foliares coletados em campo, secos com sílica gel ou de espécimes de herbário quando não havia material fresco disponível. Os três marcadores de DNA de cloroplastos que sequenciamos (*rbcL*, *trnL-trnF* e *rps4-trnS*) foram amplificados por PCR em 23 μ L de reações usando 1 μ L de DNA genômico, 12 μ L Cellco taq DNA polimerase Mix, 8 μ L de água deionizada e 1 μ L de cada primer a 10 μ mol/L.

Para o *rps4-trnS* e o *trnL-trnF*, foi utilizado um programa de PCR começando com uma etapa inicial de desnaturação de 5 min a 94°C; seguido por 35 ciclos de 30 segundos a 94°C, 30 segundos a 55°C, 1 minuto a 72°C; e um período de extensão final de 8 min a 72°C. Já para *rbcL*, o programa de PCR começou com uma etapa inicial de desnaturação de 3 min a 94°C; seguido por 30 ciclos de 30 segundos a 94°C, 30 segundos a 50°C, 1 minuto a 72°C; e um período de extensão final de 10 min a 72°C. Todos os produtos de PCR foram sequenciados por ACTGene Análises Moleculares, Alvorada, Rio Grande do Sul, Brasil. As sequências foram editadas visualmente e montadas usando o programa Geneious version 2022.1.1 (Biomatters Ltd., San Francisco, Califórnia, EUA).

Além das sequências recém-geradas, sequências disponíveis no GenBank, correspondentes aos três marcadores *rbcL*, *trnL-trnF* e *rps4-trnS* foram baixadas (Apêndice 1). Evitamos combinar sequências de diferentes espécimes da mesma espécie. Sempre que isso era feito, nos certificamos de que fossem filogeneticamente congruentes. Na filogenia principal, de um conjunto de dados de 97 espécimes, combinamos apenas as sequências de *Monachosorum henryi* Christ.

Para as análises de Máxima Verossimilhança, os padrões GTRCAT e GTRGAMMA foram utilizados, mas não apresentaram diferenças significativas. As análises de Máxima Verossimilhança foram realizadas usando o CIPRES Science Gateway, Universidade da Califórnia, San Diego, Califórnia, EUA. As análises de Bayesiana foi realizada no MrBayes (versão MrBayes 3.2.7a x86-64), com 1 milhão

de gerações. Na análise Bayesiana, o burnin foi de 25 % para o modelo GTR + I + G, obtido pelo MrModeltest (versão MrModeltest 2.4_64 bit). As topologias geradas pelas análises de Máxima Verossimilhança e Bayesiana, foram similares.

3. RESULTADOS

Para a presente análise foi gerada uma árvore de Máxima Verossimilhança e Bayesiana representando as relações filogenéticas de Dennstaedtiaceae, com um total de 106 espécimes e 97 espécies (Fig. 1). Do total de 262 espécimes que tiveram o DNA extraído, apenas 10 espécimes tiveram sucesso. A relação filogenética de Dennstaedtiaceae foi mantida como monofilética, assim como suas subfamílias, Monachosoroideae (Boot Strap = 100%), Hypolepidoideae (BS = 87%) e Dennstaedtioideae (BS = 100%). Os quatro gêneros de Dennstaedtioideae e os seis gêneros de Hypolepidoideae foram recuperados como monofiléticos. Todos os clados a nível genérico apresentam elevado valor de suporte, onde para a subfamília Dennstaedtioideae os valores foram: *Dennstaedtia s. str.* (BS = 100%), *Mucura* (BS = 100%), *Microlepia* (BS = 100%), *Sitobolium* (BS = 100%); já para a subfamília Hypolepidoideae, os valores encontrados foram: *Hiya* (BS = 88%), *Histiopteris* (BS = 100%), *Blotiela* (BS = 100%), *Paesia* (BS = 100%), *Hypolepis* (BS = 100%) e *Pteridium* (BS = 100%). A subfamília Monachosoroideae é monogenérica, representada pelo gênero *Monachosorum*, e se manteve como monofilética.

4. DISCUSSÃO

A presente topologia filogenética que recupera Dennstaedtiaceae como monofilética, junto com suas subfamílias, Dennstaedtioideae, Hypolepidoideae e Monachosoroideae (Fig. 1), concorda com estudos filogenéticos anteriormente realizados (Schuettpelz & Pryer, 2007; Testo & Sundue, 2016; Shang *et al.*, 2018, Schwartzburd *et al.*, 2020) e principalmente a os estudos filogenéticos que está sendo realizado por Triana-Moreno *et al.* (*in press*) (Fig. 2). A subfamília Dennstaedtioideae, que é foco do presente estudo, é grupo irmão do clado da subfamília Hypolepidoideae (Fig. 1). Dennstaedtioideae é caracterizada por esporos triletes e soros redondos protegidos por um único indúcio abaxial ou por ambos indúsios (abaxial e adaxial) que forma um indúcio em forma de taça, ao passo que em Hypolepidoideae os esporos são em sua maioria monoletes (exceção em *Pteridium* que é trilete), os soros podem ser alongados ou não e o indúcio abaxial é

ausente na maioria dos gêneros, porém presentes em *Pteridium* e *Paesia* (Schwartzburd *et al.*, 2020; Triana-Moreno *et al.* (*in press*)).

Os trabalhos filogenéticos anteriores realizados (e.g. Wolf *et al.*, 1994; Wolf, 1995; Schuettpelz & Pryer, 2007; Perrie *et al.*, 2015; Shang *et al.*, 2019; Schwartzburd *et al.*, 2020; Wang *et al.*, 2021, Triana-Moreno *et al.* (*in press*)) indicam *Dennstaedtia s.l.* como grupo polifilético, contudo Triana-Moreno *et al.* (*in press*) tornou *Dennstaedtia s.l.* em grupos naturais com a criação do gênero *Mucura* e o resgate do gênero *Sitobolium*. Em nosso estudo, a topologia apresentada está de acordo com os cladogramas de *Dennstaedtia*, *Mucura*, *Sitobolium* e *Microlepia* sustentados no estudo de Triana-Moreno *et al.* (*in press*) (Fig. 2). As novas combinações de *Leptolepia novae-zelandiae* (Colenso) Mett. ex Diels. para *Dennstaedtia novae-zelandiae* (Colenso) L.A. Triana & Sundue e *Oenotrichia maxima* (E. Fourn.) Copel. para *Dennstaedtia maxima* (E. Fourn.) L.A. Triana & Sundue, realizada por Triana-Moreno *et al.* (*in press*), são corroboradas em nosso estudo filogenético.

Os gêneros *Dennstaedtia* e *Mucura* sempre foram marcados por complexos específicos em relação aos estudos morfológicos (e.g. Tryon, 1960; Sehnem, 1972; Tryon & Tryon, 1982; Moran, 1995; Rojas-Alvarado & Villalobos-Brenes, 2018; Navarrete & Øllgaard, 2000; Mickel & Smith, 2004; Assis & Salino, 2011; Yañes *et al.*, 2014; Schwartzburd, 2017), e na América do Sul, há pelo menos um complexo para cada gênero que são: 1. complexo *Dennstaedtia* – *D. cornuta*/*D. dissecta*/*D. obtusifolia* e nomes relacionados; 2. complexo *Mucura* – *M. bipinnata*/*M. globulifera* e nomes relacionados (e.g. Tryon, 1960; Sehnem, 1972; Tryon & Tryon, 1982; Moran, 1995; Rojas-Alvarado & Villalobos-Brenes, 2018; Navarrete & Øllgaard, 2000; Assis & Salino, 2011; Yañes *et al.*, 2014; Schwartzburd, 2017).

Em relação ao complexo *Dennstaedtia cornuta*/*D. dissecta*/*D. obtusifolia* e nomes relacionados, Tryon (1960), havia considerado as espécies *Dennstaedtia dissecta* e *D. obtusifolia*, deixando *D. cornuta* como sinônimo de *D. dissecta*. Trabalhos subsequentes como Navarrete & Øllgaard (2000), Assis & Salino (2011) e Schwartzburd (2017), passaram a considerar a espécie *D. cornuta*. O nosso estudo filogenético corroborou a hipótese de que realmente *D. dissecta* e *D. cornuta* são táxons distintos (Fig. 3). Os dois espécimes de *Dennstaedtia cornuta* formaram um clado exclusivo que é irmão de *D. arborescens*, ao passo que *Dennstaedtia dissecta* posiciona-se como irmão do clado de *D. cicutaria*, ao qual parecem ter divergido antes do clado de [*D. fluminensis* + [*D. cornuta* + *D. arborescens*]]. Além da distância

filogenética, morfológicamente a distinção entre *Dennstaedtia dissecta* e *D. cornuta* está principalmente relacionada ao último segmento, onde em *D. cornuta* os segmentos possuem enseios rasos e margens crenadas (vs. enseios profundos ou mais dissecados e margens dentadas), indúcio em forma de bolsa “*purse-shaped*” (vs. cilíndrico) e distribuição para América do Sul (vs. Antilhas) (ver Capítulo 3).

Ainda em relação ao complexo *Dennstaedtia dissecta/D. cornuta*, nossos estudos morfológicos (ver Cap. 4) e filogenéticos sustentaram a retirada de *D. fluminensis* da sinonímia de *D. cornuta*. Na filogenia, *D. fluminensis* se posicionou como grupo irmão dos clados formados das espécies de *D. auriculata* + *D. cornuta* (Fig. 2). Morfológicamente *D. cornuta* difere de *D. fluminensis* devido ao rizoma rastejante (vs. ereto a ascendente), pelos segmentos com enseios rasos (vs. enseios profundos ou mais dissecados), indúcio em forma de “bolsa” *purse-shaped* (vs. bivalve), distribuição da América do Sul (vs. endêmica do Brasil) (Ver Cap. 3).

Dennstaedtia concinna, espécie também resgatada de sua sinonímia (ver Cap. 2), foi considerada por Tryon (1960) como sinônimo de *D. arborescens*, e por Navarrete & Øllgaard (2000) como sinônimo de *D. obtusifolia*. Em nossa filogenia, *Dennstaedtia concinna* se posicionou como irmão do clado do [novo mundo + velho mundo], longe das demais espécies Neotropicais, onde *D. arborescens* se posiciona (Fig. 5). A posição de *D. concinna* apresentada em nossa topologia, posicionando-se na árvore após *D. scandens*, sustenta que *D. concinna* realmente trata-se de um táxon distinto de *D. arborescens*. Apesar de *D. concinna* ter sido considerada espécie sinônimo de *D. arborescens* e *D. obtusifolia*, sua morfologia é mais próxima de *D. mathewsii*. Contudo, *Dennstaedtia concinna* difere de *D. mathewsii* pelas costas adaxialmente com pêlos catenados esparsos a glabrescentes (vs. adaxialmente com pêlos catenados densos), os segmentos finais arredondados com seios mais profundos, às vezes com os soros dentro dos seios (vs. oblongos sem seios profundos; soros sempre projetados para fora da lâmina), os soros redondos, orientados no plano da lâmina, e a indúcio hemisférico, (vs. soros hemisféricos, orientados no plano da lâmina, ao longo das margens, indúcio copuliforme (ver Cap. 3).

As espécies do gênero *Dennstaedtia s. str.* são reconhecidas por apresentar rizomas curto a longo reptante e não ramificado. Pecíolos com brotos epipeciolares e raramente aculeados. As folhas são 2–4-pinadas e as vezes apresentam gemas nas raques. Os soros são marginais proveniente da junção de um indúcio abaxial e

adaxial, dando origem a um indúcio em formato de bolsa ou copo (*purse-* ou *cup-shaped*). Os esporos são trilete e o perísforo com retículos regulares, sulcos e verrucados (ver Cap. 3).

Em relação ao complexo *Mucura bipinnata*/*M. globulifera*, até o presente estudo apenas duas espécies eram reconhecidas *M. bipinnata*/*M. globulifera* (e.g. Tryon, 1960; Sehnem, 1972; Tryon & Tryon, 1982; Moran, 1995; Rojas-Alvarado & Villalobos-Brenes, 2018; Navarrete & Øllgaard, 2000; Assis & Salino, 2011; Yañes *et al.*, 2014; Schwartsburd, 2017). No entanto, com base em nossas contribuições morfológicas (ver Cap. 2), duas espécies foram resgatadas da sua sinonímia de *Mucura globulifera*, que são: *M. tamandarei* e *M. tenera*. Em nossa análise filogenética *Mucura tamandarei* e *M. tenera* formam um clado irmão ao clado [*M. globulifera* + *M. baccifera*] (Fig. 6). O fato de *M. tamandarei* e *M. tenera* se posicionarem no clado do gênero *Mucura*, corrobora para a sustentação do gênero proposto por Triana-Moreno *et al.* (*in press*). Em nossas análises filogenéticas é possível perceber que o clado compartilhado pelas espécies *Mucura tamandarei* e *M. tenera*, não ficou totalmente bem resolvido. Talvez a inclusão mais de mais marcadores ou de mais amostras possa apresentar uma melhor resolução.

Os espécimes de *Mucura baccifera* foram tradicionalmente denominados como *Dennstaedtia bipinnata* (Sw.) T.Moore por vários autores, como (= *Mucura bipinnata*) por Tryon (1960), Navarrete e Øllgaard (2000), Mickel e Smith (2004), e Triana-Moreno *et al.* (*in press*). Os autores citados também consideraram uma distribuição Neotropical para esta espécie. Em nossos estudos, consideramos os espécimes sul-americanos distintos dos da América Central e das Antilhas, uma vez que *Mucura alata* (espécimes Sul-Americanas) difere de *M. baccifera* (espécimes da América Central e Antilhas) pelas pínulas lanceadas profundamente recortadas e mais recortadas com segmentos mais profundos (*vs.* pínulas ovais a oblongas e menos recortadas com segmentos rasos); ápice das pínulas com dente profundo e largo (*vs.* ápice das pinas com dente raso e fino); pínulas comumente glabras, às vezes com tricomas catenados raros (*vs.* tricomas catenados freqüentes); asas adaxialmente retas (*vs.* asas adaxialmente curvadas suavemente) medindo soros 0,4–0,6 × 0,4–0,6 mm (*vs.* 0,8–1 × 0,8–1 mm). Para ver as resoluções nomenclaturais, ver capítulo 2.

As espécies do gênero *Mucura* são reconhecidas por apresentarem rizomas ramificados dicotomicamente, com feixe vascular em forma de ômega, folhas

decompostas com eixos laminares alados que decorrem para a ordem seguinte, soros marginais, providos de indúcio inferior e superior que juntas formam um invólucro cilíndrico em forma de taça; esporos triletes, amplamente estriados e verrucados, e às vezes com retículos irregulares.

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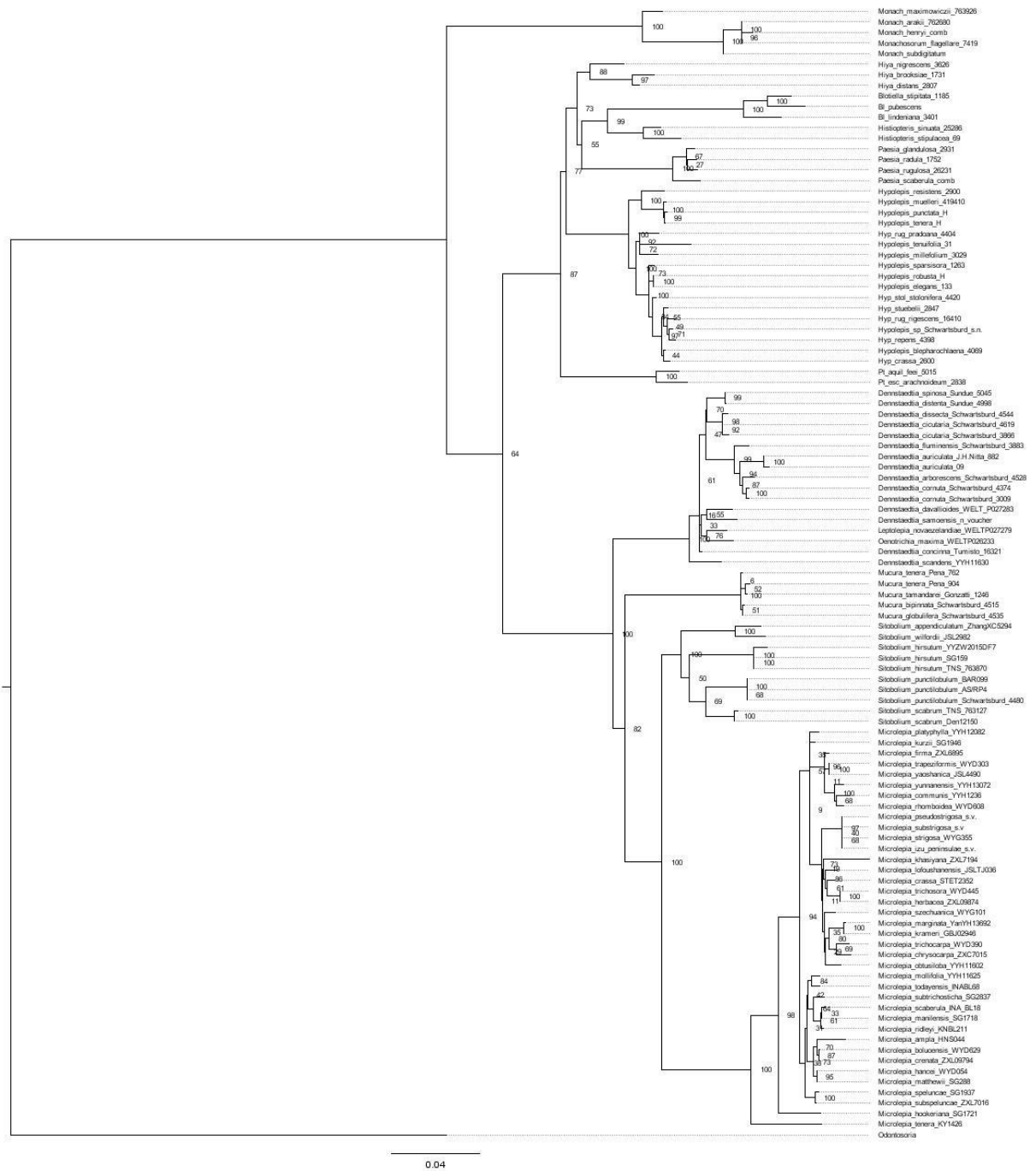


Fig.1. Hipótese filogenética para Dennstaedtiaceae baseada em análise de máxima verossimilhança. Os números são valores de bootstrap.

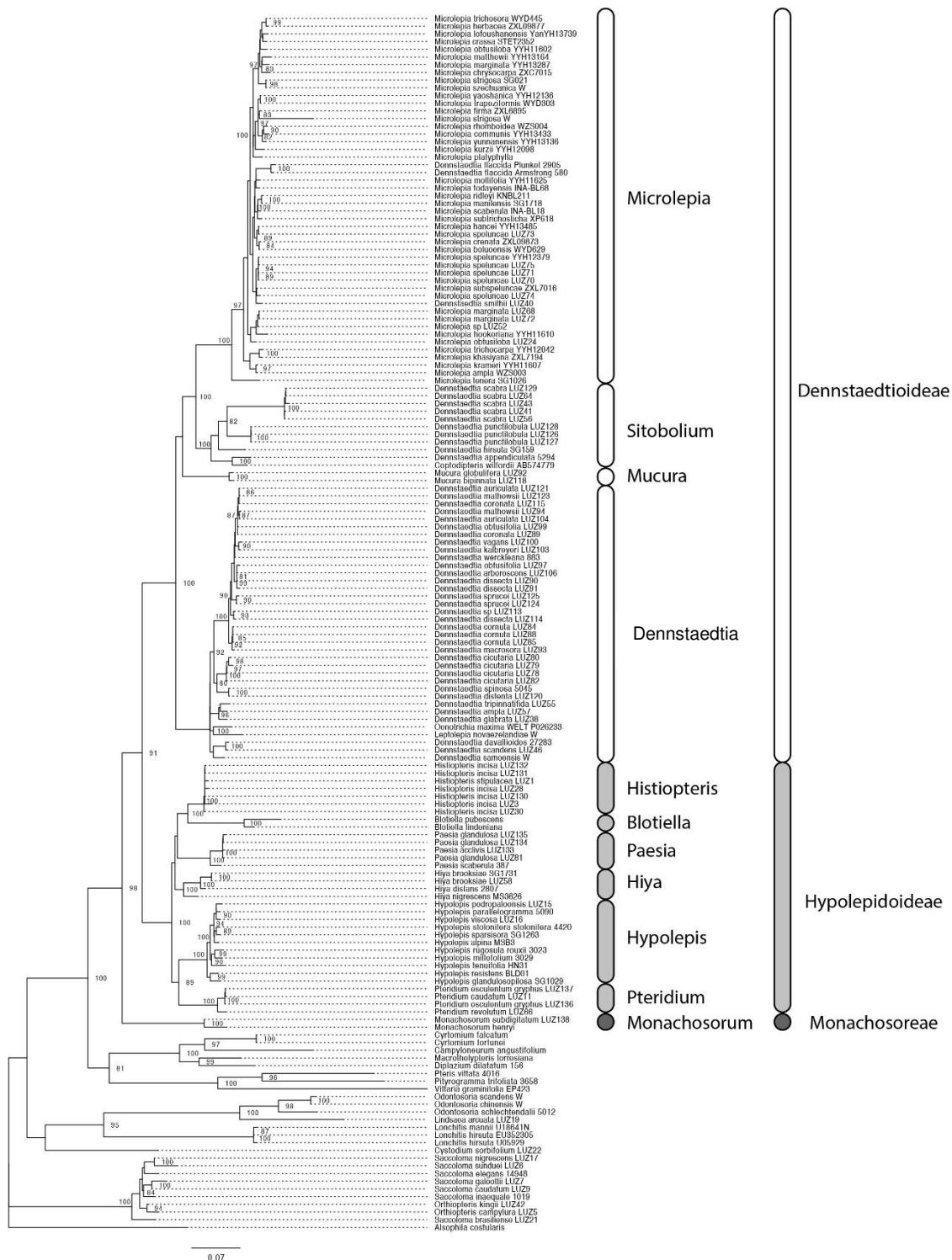


Fig.2. Hipótese filogenética para Dennstaedtiaceae de Triana-Moreno *et al.* (in press).

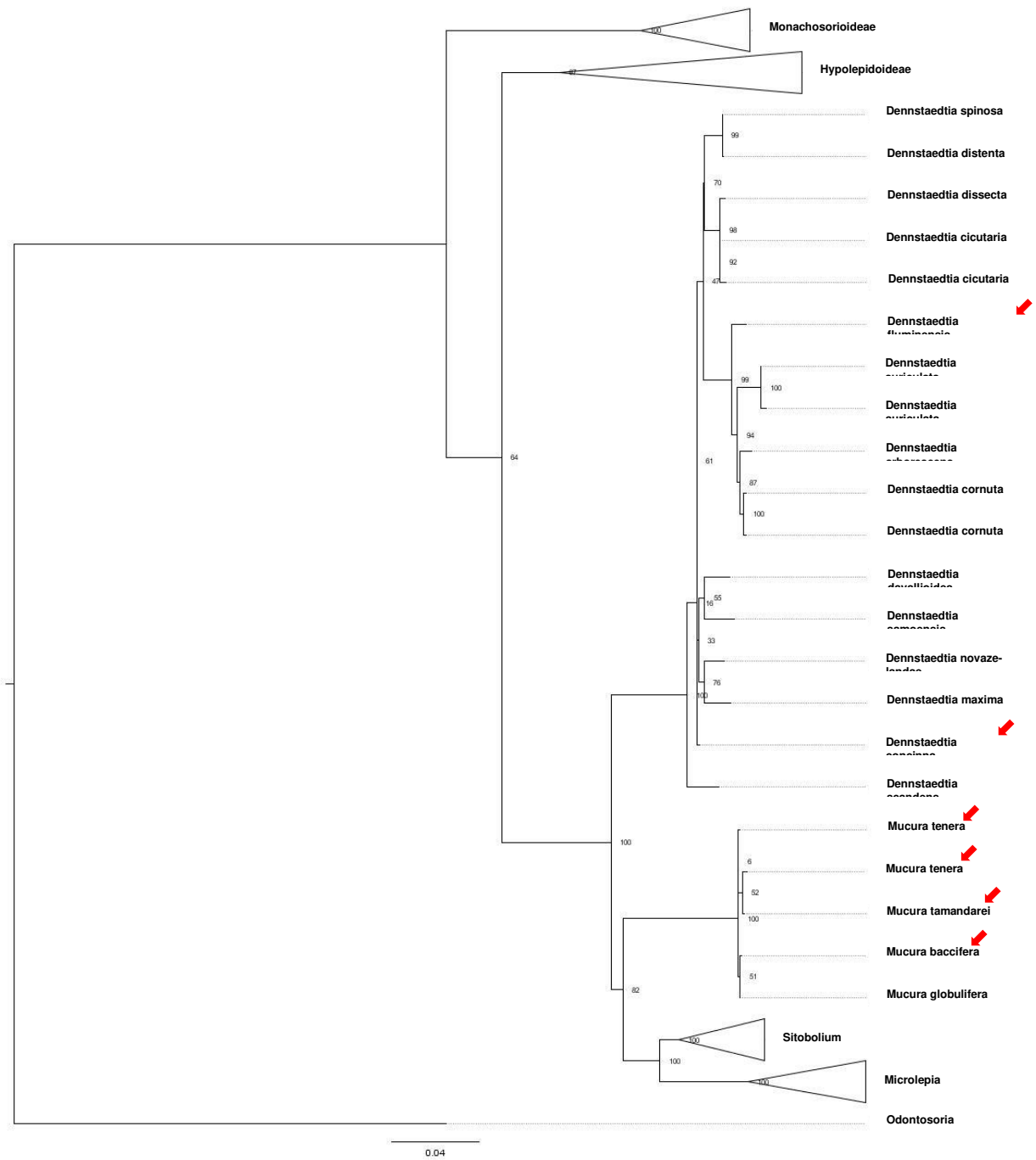


Figure 3. Topologia com foco nos gêneros *Dennstaedtia* e *Mucura*. Os números são valores de bootstrap. As setas em vermelho representam os nomes resgatados da sinonímia.

Apêndice 1. Táxons, informações de vouchers (quando disponíveis) e números de acesso GenBank de *rbcL*, *trnL-trnF* e *rps4-trnS*, O hífen (–) significa “não disponível”; asterisco (*) significa “em processo de submissão ao GenBank”.

Blotiella lindeniana (Hook.) R.M.Tryon, *Schwartsburd 3401*, MT470015, MT593230, –. *Blotiella pubescens* (Kaulf.) R.M.Tryon, –, BPUU05911, –, –. *Blotiella stipitata* (Alston) Faden in Agnew, *SG1185*, MG944780, MG944795, MH289683. *Dennstaedtia appendiculata* (Wall.) J.Sm. [=*Sitobolium appendiculatum*], *ZhangXC5294*, MK051807, MK052598, MK052060. *Dennstaedtia arborescens* Ekman ex Maxon, *Schwartsburd 4528*, TP13*, TP13*, –. *Dennstaedtia auriculata* Navarrete & B.Øllg., *Schuettpelz 9*, EF463166, –, –; *J.H. Nitta 882*, MW138148, –, –. *Dennstaedtia bipinnata* (Cav.) Maxon [=*Mucura baccifera*], *Schwartsburd 4515*, TP03*, TP03*, –. *Dennstaedtia cicutaria* (Sw.) T.Moore, *Schwartsburd 3866*, MT593213, –, –. *Dennstaedtia cornuta* (Kaulf.) Mett., *Schwartsburd 3009*, MT593214, –, –; *Schwartsburd 4374*, MT470018, –, MT559747. *Dennstaedtia davallioides* (R.Br.) T.Moore, *WELT P027283*, MH918674, –, –. *Dennstaedtia dissecta* (Sw.) T.Moore, *Schwartsburd 4544*, PV132*, PV132*, –. *Dennstaedtia distenta* (Kunze) T.Moore, *Sundue 4998*, –, –, MT559732. *Dennstaedtia fluminensis* C.Chr., *Schwartsburd 3883*, MT416334, –, MT593215. *Dennstaedtia globulifera* Hieron. [=*Mucura globulifera*], *Schwartsburd 4535*, PV12*, PV12*, –. *Dennstaedtia hirsuta* Mett. [=*Sitobolium hirsutum*], *SG159*, MK051800, MK052053, MK052591. *Dennstaedtia punctilobula* (Michx.) T.Moore [=*Sitobolium punctilobulum*], *Schwartsburd 4480*, MT416336, –, –; *AS/RP4*, KJ663802, –, –. *Dennstaedtia samoensis* (Brack.) T.Moore, –, DSU18637, –, –. *Dennstaedtia scabra* (Wall.) T.Moore [=*Sitobolium scabrum*], *Den12150*, MH289649, –, –; *TNS:763127*, –, –. *Dennstaedtia tamandarei* Rosenst. [=*Mucura tamandarei*], *F. Gonzatti 1246*, TP40*, –, TP40*. *Dennstaedtia tenera* (Pr.) Mett. [=*Mucura tenera*], *N.T.L. Pena 762*, TP06*, TP06*, –.; *N.T.L. Pena 904*, TP79*, TP79*, –. *Dennstaedtia wilfordii* (T.Moore) Christ [=*Sitobolium wilfordii*], *JSL2982*, MK051796, MK052049, MK052588. *Histiopteris sinuata* J.Sm., *WELT P025286*, KT983823, –, –. *Histiopteris stipulacea* (Hook.) Copel., *HisC069*, MH289645, MT593235 –. *Hiya brooksiae* (Alderw.) H.Shang, *SG1731*, MH289639, MT593237, MH289711. *Hiya distans* (Hook.) Brownsey & Perrie, *Perrie 2807*, MT416341,

MT593239, –. *Hiya nigrescens* (Hook.) H.Shang, MS3626, MH289641, MT593240, MH289703. *Hypolepis crassa* Maxon, *Sundue 2600*, MT426169, MT593252, MT559738. *Hypolepis repens* (L.) C.Presl, *Schwartsburd 4398*, –, MT593271, MT563103. *Hypolepis rugosula* subsp. *pradoana* Schwartsb., *Schwartsburd 4404*, MT426183, MT593281, MT563109. *Hypolepis rigescens* var. *rigescens*, *Wood 16410*, MT426180, MT593276, MT563105. *Hypolepis stolonifera* var. *stolonifera*, *Schwartsburd 4420*, MT426189, MT593296, MT563116. *Hypolepis stuebelii* Hieron., *Smith 2847*, –, MT593297, MT593228. *Hypolepis blepharochlaena* Mickel & Beitel, MS4069, MH289740. *Hypolepis elegans* Carruth., *Perrie 133*, MT426171, MT593254, –. *Hypolepis millefolium* Hook., *WELT P20798*, EF469956, MT593262, –. *Hypolepis muelleri* Wakef., *WELT 419410*, MT426179, MT593266, –. *Hypolepis punctata* Mett. ex Kuhn, *FLX6*, MG944784, MG944790, –. *Hypolepis resistens* Hook., *SG2900*, MG944785, MG944800, MH289694. *Hypolepis sparsisora* (Schrad.) Kuhn, *HysSG1263*, MH289631, MT593286, MH289700. *Hypolepis tenera* Ching in Chien & Chun, *HyyZGD17*, MH289633, MT593298, –. *Hypolepis tenuifolia* (Forst.) Bernh., *HN31*, MG944786, MG944791, MH289701. *Leptolepia novae-zelandiae* (Colenso) Mett. ex Diels [= *Dennstaedtia novae-zelandiae*], *WELT P027279*, KT983829, –, –. *Microlepia ampla* Ching in Chien & Chun, *HNS044*, MK051598, MK051897, MK052427. *Microlepia boluoensis* Y.Yuan & L.Fu, *WYD629*, MK051673, MK052452, –. *Microlepia chrysoarpa* Ching, *ZXC7015*, MK052599, MK052061, –. *Microlepia communis* Ching in Chien & Chun, *YYH1236*, MK051835, MK052641, MK052096. *Microlepia crassa* Ching in Chien & Chun, *STET2352*, MK051799, MK052590, MK052052. *Microlepia crenata* Ching in Chien & Chun, *ZXL09794*, MK052583, MK052044, –. *Microlepia firma* Mett.; Kuhn, *ZXL6895*, MK051813, MK052608, MK052070. *Microlepia hancei* Prantl, *WYD054*, –, MK052661, –. *Microlepia herbacea* Ching & C.Chr. ex Tardieu & C.Chr., *ZXL09874*, MK051853, MK052660, –. *Microlepia hookeriana* (Wall.) C.Presl, *SG1721*, MK051866, MK052671, –. *Microlepia izu-peninsulae* Sa.Kurata, *TNS:766448*, AB574783, –, –. *Microlepia khasiyana* C.Presl, *ZXL7194*, MK051627, MK052625, MK052087. *Microlepia krameri* C.M.Kuo, *GBJ02946*, MK051839, MK052645, MK052100. *Microlepia kurzii* (C.B.Clarke) Bedd., *SG1946*, MK051868, MK052673, –. *Microlepia lofoushanensis* Ching in Chien & Chun, *JSL-TJ036*, MK051827, –, –. *Microlepia manilensis* C.Presl, *SG1718*, MK051865, MK052670, MK052118. *Microlepia marginata* (Panz.) C.Chr.,

YanYH13692, MK052632, –, –. *Microlepia obtusiloba* Hayata, YYH11602, –, MK052648, –. *Microlepia pseudostrigosa* Makino, TNS:766447, AB574786, –, –. *Microlepia rhomboidea* C.Presl, WYD608, MK051830, MK052636, –. *Microlepia ridleyi* Copel., KNBL211, MK051864, MK052669, MK052117. *Microlepia scaberula* Mett.; Kuhn, INA-BL18, MK051645, MK052419, MK051889. *Microlepia spelunca* (L.) T.Moore, SG1937, MK051867, MK052672, MK052119. *Microlepia strigosa* (Thunb.) C.Presl, WYG355, MK051861, MK052666, –. *Microlepia subspelunca* Ching in Chien & Chun, ZXL7016, MK051871, MK052078, MK052616. *Microlepia substrigosa* Tagawa, TNS:763302, AB574785, –, –. *Microlepia tenera* Christ, KY1426, MK051802, –, MK052055. *Microlepia todayensis* Christ, INA-BL68, MK051735, MK052524, MK051983. *Microlepia trapeziformis* (Roxb.) Kuhn, WYD303, MK051667, MK052446, MK051916. *Microlepia trichocarpa* Hayata, WYD390, –, MK052550, –. *Microlepia trichosora* Ching in Chien & Chun, WYD445, MK051855, MK052662, MK052110. *Microlepia yaoshanica* Ching, JSL4490, MK051862, MK052667, MK052115. *Microlepia yunnanensis* Ching in Chien & Chun, YYH13072, MK051850, MK052657, –. *Monachosorum arakii* Tagawa, TNS:762680, –. *Monachosorum maximowiczii* Hayata, TNS:763926, AB574792, –, –. *Monachosorum flagellare* Hayata, ZXL7419, –, –, MH289702. *Odontosoria* (C.Presl) Fée, –, PV62*, PV62*, –. *Oenotrichia maxima* (Fourn.) Copel. [=Dennstaedtia maxima], WELT P026233, KT983830, –, –. *Paesia rugulosa* Diels, WELT P026231, KT983831, –, –. *Paesia scaberula* (A.Rich.) Kuhn, WELT P027282, KT983832, –, –. *Pteridium aquilinum* (L.) Kuhn, –, PV64*, PV64*, PV64*. *Pteridium aquilinum* f. *arachnoidea* Hieron., –, PV64*, PV64*, PV64*.

Capítulo V. Pena, N.T.L. & P. B. Schwartzburd. Fern flora of Viçosa, Minas Gerais, Brazil: Dennstaedtiaceae, Lindsaeaceae, and Saccolomataceae. – submetido e aceito para publicação na *Hoehnea*.

Capítulo V. Fern flora of Viçosa: Dennstaedtiaceae, Lindsaeaceae, and Saccolomataceae

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ABSTRACT

(Fern flora of Viçosa, Minas Gerais, Brazil: Dennstaedtiaceae, Lindsaeaceae, and Saccolomataceae). As part of an ongoing project treating the ferns and lycophytes from the region of Viçosa, Minas Gerais, Brazil, we here present the taxonomic treatment of the early divergent lineages of the leptoesporangiate ferns: the families Dennstaedtiaceae, Lindsaeaceae, and Saccolomataceae. We have been sampling the remnant forest patches since 2012; we also fully reviewed the collection of herbarium VIC, and other online collections: F, IAN, NY, PH, RB, U, UC, UPCB, US, and WTU. In the region of Viçosa, six taxa belonging to those families occur: *Dennstaedtia cicutaria* and *Pteridium esculentum* subsp. *arachnoideum* (Dennstaedtiaceae); *Lindsaea lancea* var. *lancea*, *L. quadrangularis* subsp. *quadrangularis*, and *L. stricta* var. *stricta* (Lindsaeaceae); and *Saccoloma elegans* (Saccolomataceae). Among these taxa, only *L. quadrangularis* subsp. *quadrangularis* and *S. elegans* are endemic to the Brazilian Atlantic Rainforest; the remaining are widespread in the Neotropics. We present keys, descriptions, illustrations, examined specimens, and comments.

Keywords: Brazilian Atlantic Rainforest, Polypodiales, pteridophytes, southeast Brazil, taxonomy

RESUMO

(Flora de samambaias de Viçosa, Minas Gerais, Brasil: Dennstaedtiaceae, Lindsaeaceae, and Saccolomataceae). Como parte de um projeto em andamento sobre samambaias e licófitas da região de Viçosa, Minas Gerais, Brasil, o tratamento taxonômico das primeiras linhagens divergentes de samambaias leptosporangiadas: as famílias Dennstaedtiaceae, Lindsaeaceae e Saccolomataceae são apresentadas. Expedições de campo são realizadas desde 2012 em remanescentes florestais da região. Também foi realizada uma revisão completa da coleção do herbário VIC, cuja data de início é 1930, bem como de outras coleções online de herbários: F, IAN, NY, PH, RB, U, UC, UPCB, US, and WTU. Na região de Viçosa, existem seis táxons pertencentes a essas famílias: *Dennstaedtia cicutaria* e *Pteridium esculentum* subsp. *arachnoidum* (Dennstaedtiaceae); *Lindsaea lancea* var. *lancea*, *L. quadrangularis* subsp. *quadrangularis* e *L. stricta* var. *stricta* (Lindsaeaceae); e *Saccoloma elegans* (Saccolomataceae). Dentre esses táxons, apenas *L. quadrangularis* subsp. *quadrangularis* e *S. elegans* são endêmicos da Mata Atlântica brasileira; as demais estão amplamente distribuídas na região Neotropical. São apresentadas chaves, descrições, ilustrações, materiais examinados e comentários.

Palavras-chave: Mata Atlântica Brasileira, Polypodiales, pteridófitas, sudeste do Brasil, taxonomia.

1. INTRODUCTION

At the end of the era in which the plant Classification Systems were mostly based on morphological data, Dennstaedtiaceae was considered a big family, comprehending three subfamilies (or tribes) and about 17 genera (Tryon & Tryon 1982, Kramer 1990). With the advent of molecular data, those subfamilies were raised to family-level, some families were created, and now the early-diverging leptoesporangiate ferns are represented by Cystodiaceae (one genus), Dennstaedtiaceae with a stricter circumscription (11–12 genera), Lindsaeaceae (seven genera), Lonchitidaceae (one genus), Saccolomataceae (one or two genera), as well as the great Pteridaceae (+50 genera) (Smith *et al.* 2006, PPG I 2016, Shang *et al.* 2018, Schwartsburd *et al.* 2020).

Brazil is represented by Dennstaedtiaceae with eight genera and 26 species, Lindsaeaceae with one genus and 34 spp., Lonchitidaceae with one genus and one sp., and Saccolomataceae with one genus and nine spp., leaving Pteridaceae apart (which is subject to another paper) (Kramer 1957, Pena *et al.* 2020, Schwartsburd 2020, Schwartsburd & Pena 2020). In general, these plants present characters considered plesiomorphic that are typical of the early-diversing lineages of Polypodiales, such as solesnotelic rhizomes clothed with hairs or primitive scales, large, highly dissected leaves, the sori that are truly marginal and protected by inner and outer indusia, and trilete spores (Tryon & Tryon 1982, Kramer 1990, PPG I 2016, Schwartsburd *et al.* 2020).

Pteridium is spread all across the globe (except for Antarctic) and may be the one most important to mankind by if directly affects the local human populations: it behaves as a pioneer weed invading croplands; it spreads its underground rhizomes making it hard to be removed; it intoxicates the cattle and horses; and it also intoxicates humans, when ingested – some studies also pointed out the transmittion of its toxins (the psilatoquinis) via cow milk (e.g., Tryon 1941, Evans 1976, Page 1976, Marrs *et al.* 2000, Martini-Santos *et al.* 2010, Oliveira *et al.* 2018, Schwartsburd *et al.* 2018).

In the state of Minas Gerais, Dennstaedtiaceae is represented by 14 species, Lindsaeaceae by 11, and Saccolomataceae by three (Pena *et al.* 2020 Schwartsburd 2020, Schwartsburd & Pena 2020, Schwartsburd 2022). Here, we present the taxonomic treatment of these families for the region of Viçosa, Minas Gerais, Brazil, as part of the ongoing project on the Fern Flora of this region with fascicles in

preparation and others already published: Miranda & Schwartzburd (2016 – Salviniaceae), Rabelo & Schwartzburd (2016 – Schizaeales), and Gonçalves da Silva & Schwartzburd (2017 – Polypodiaceae).

2. MATERIAL AND METHODS

In the region of Viçosa, Minas Gerais, Brazil, the remaining forest patches are classified as Semi-Deciduous Seasonal Forest (IBGE 2012). The local elevation ranges from 600 to 900 m a.s.l. (personal observations), and the annual temperatures range from 5° to 30°C (INMET <<http://www.inmet.gov.br>>).

We have been sampling the remnant forest patches since 2012. Specimens were collected and dried according to usual methods for fern collections (Windisch 1992) and then incorporated in herbarium VIC (acronyms following Thiers, continuously updated), with duplicates to be sent to other herbaria. We also fully reviewed the collection of herbarium VIC and collections of other herbaria online: F, IAN, NY, PH, RB, U, UC, UPCB, US, and WTU. Although the classification system adopted for the previous fascicles was based on an adaptation of Kenrick & Crane (1997) and Smith *et al.* (2006), we here adopt the system of PPG I (2016). Morphological terms are according to Lellinger (2002).

3. RESULTS AND DISCUSSION

Dennstaedtiaceae, Lindsaeaceae, and Saccolomataceae, presented a total of four genera and six species occurring in the region of Viçosa. Four of those species have also infra-specific classifications, which were adopted here. The six taxa are: *Dennstaedtia cucutaria* (Sw.) T. Moore, and *Pteridium esculentum* subsp. *arachnoideum* (Kaulf.) Thomson (Dennstaedtiaceae); *Lindsaea lancea* (L.) Bedd. var. *lancea*, *L. quadrangularis* Raddi subsp. *quadrangularis*, and *L. stricta* (Sw.) Dryand. var. *stricta* (Lindsaeaceae); and *Saccoloma elegans* Kaulf. Among them, only *L. quadrangularis* subsp. *quadrangularis* and *S. elegans* are endemic to the Brazilian Atlantic Rainforest; the remaining taxa are widespread in the Neotropics. Differently from the other studied families: Salviniaceae (Miranda & Schwartzburd 2016); Anemiaceae (Rabelo & Schwartzburd 2016); Polypodiaceae (Gonçalves da Silva & Schwartzburd 2017), we have not recollected half of the taxa involved in this paper, which were collected on the 1930s and never again. Probably, they went locally

extinct due to forest fragmentation and disturbance. We have not recollected *D. cicutaria*, *L. lancea* var. *lancea*, nor *L. quadrangularis* subsp. *quadrangularis*.

Key to taxa of Dennstaedtiaceae, Lindsaeaceae, and Saccolomataceae from the region of Viçosa:

1. Sori born at the tip of single veins 2
2. Laminae 1-pinnate; sori along the laminar margins, parallel to each other *Saccoloma elegans* (Saccolomataceae)
2. Laminae 3-pinnate-pinnatifid to 4-pinnate; sori born on sinuses of the segments *Dennstaedtia cicutaria* (Dennstaedtiaceae)
1. Sori born at the tip of multiple veins (on a commissural vein) 3
3. Rhizomes with hairs; laminae 3–4-pinnate-pinnatifid *Pteridium esculentum* subsp. *arachnoideum* (Dennstaedtiaceae)
3. Rhizomes with scales; laminae 1–2-pinnate (or rarely 3-pinnate) (Lindsaeaceae) 4
4. Stipes abaxially terete, adaxially flattened *Lindsaea stricta* var. *stricta*
4. Stipes quadrangular in cross section 5
5. Stipes and rachises reddish-brown; sori interrupted *Lindsaea quadrangularis* subsp. *quadrangularis*
5. Stipes proximally dark brown, stramineous above; rachises stramineous; sori not interrupted *Lindsaea lancea* var. *lancea*

Dennstaedtiaceae

Rhizomes generally long-creeping, solenostelic or rarely dyctiostelic or polycyclic, bearing hairs or rarely with primitive scales. Leaves monomorphic; stipes often with epipetiolar buds, usually with a omega-shaped vascular strand; laminae 2–5-pinnate, rarely less dissected; veins free or rarely anastomosing and then without included veinlets; indument formed by hairs or glandular hairs, or absent. Sori marginal or submarginal, linear or discrete, introrse or extrorse, protected by outer and/or inner indusia or rarely not protected; spores tetrahedral and trilete, or reniform and monolete (Smit et al. 2006).

The family is cosmopolitan, composed of eleven genera and ca. 270 species (PPG I 2016; Shang *et al.* 2018; Schwartsburd *et al.* 2020). The clade containing

Dennstaedtia, *Leptolepia*, *Microlepia*, and *Oenotrichia* still needs recircumscriptio, due to a polyphyletic *Dennstaedtia* (Schwartzburd *et al.* 2020).

***Dennstaedtia* Bernh.**

Rhizomes short to long-creeping, glabrous or with catenate hairs. Leaves large, to 4 m long; laminae 2–4-pinnate; veins free; indument formed by catenate hairs, acicular hairs, or absent; sori marginal, discrete, at the tip of single veins; inner and outer indusia fused into purse- or cup-shaped or hemi-globose indusia (Smit *et al.* 2006).

About 70 species, but polyphyletic in current circumscription (Schwartzburd *et al.* 2020). In Brazil, six species (Schwartzburd & Pena 2020), but there are probably about eight to ten species (*pers. obs.*).

***Dennstaedtia cicutaria* (Sw.) T. Moore**, *Ind. Filic.* [T. Moore] 2: xcvi. 1857.

Dicksonia cicutaria Sw., *J. Bot.* (Schrad.) 1800(2): 91. 1801.

Figure 1a-c

Plants terrestrial. Rhizomes long-creeping, with brownish catenate hairs. Leaves 1–3.5 m long; stipes 0.5–2.5 m long, proximally brown, lighter brown above, with acicular hairs or glabrescent; laminae 0.5–2 m long, proximally 3-pinnate-pinnatifid to 4-pinnate; rachises light brown, pilose, with brownish catenate hairs, without proliferous buds; basal pinnae 25–100 cm × 12–35 cm, subequilateral; pinnules sessile, lanceolate to oblong, margins dentate; costae abaxially and adaxially pilose, with light brown to reddish catenate hairs; costules abaxially and adaxially pilose, with light brown to reddish catenate hairs; veins free, abaxially and adaxially hirsute, with erect, light brown to reddish acicular hairs; laminar tissue between the veins abaxially and adaxially with catenate and acicular hairs; sori oblong or rounded, born at the tip of single veins, in sinuses of segments; indusia purse-shaped, commonly with acicular and catenate hairs.

Geographical distribution: Neotropical.

Specimens examined: BRAZIL. MINAS GERAIS: Viçosa, Agricultural College land, Horticultural Hill, 670 m, 7 Jul 1930, *Y. Mexia 4846* (F, MO-*n.v.*, U, UC, US); Viçosa, Escola Superior de Agricultura e Veterinária, base of Horticultural Hill, 668 m, 17-VII-1930, *Y. Mexia 4866* (IAN, F, U, UC, US, VIC, WTU); Viçosa, Escola Superior de Agricultura e Veterinária, Jan 1934, *J.G. Kuhlmann s.n.* (VIC-1309).

Dennstaedtia cicutaria is recognized by veins and laminar tissue between the veins densely with catenate and acicular hairs, indusia purse-shaped with acicular and catenate hairs.

Pteridium Gled. ex Scop., *nom. cons.*

Rhizomes long-creeping, with setose hairs. Leaves large, to 4.5 m long; laminae 3–5-pinnate; veins free; indument formed by catenate hairs, acicular hairs, arachnoid hairs, and/or minute gnarled hairs; sori marginal, linear, continuous along the laminar margins, born on comissural veins; inner indusia vestigial; outer indusia linear (Smit et al. 2006).

Two species and two species with hybrid origin are currently recognized (Thomson 2012, Zhou *et al.* 2014, Schwartsburd *et al.* 2018, 2020). In addition, a total of ca. 20 morpho-taxa are also recognized as infra-specific entities, such as subspecies, varieties, forms, or combinations of more than one rank (e.g., Tryon 1941, Page 1976, Thomson 2012, Schwartsburd *et al.* 2018). In Brazil, the following taxa are currently recognized: *Pteridium caudatum* (L.) Maxon, *P. esculentum* subsp. *arachnoideum* (Kaulf.) Thomson, *P. esculentum* subsp. *campestre* (Schrad.) Schwartsb. & J. Prado, *P. esculentum* subsp. *gryphus* Schwartsb., *P. esculentum* var. *harpianum* Schwartsb. & A. Yanez, and *P. esculentum* var. *paedomorphicum* Schwartsb. & J. Prado (Schwartsburd 2020). The most common taxon in southeastern Brazil is *P. esculentum* subsp. *arachnoideum*, which invades crops and is toxic for cattle, horses, and human ingestion (Schwartsburd *et al.* 2018).

Pteridium esculentum subsp. ***arachnoideum*** (Kaulf.) Thomson, *Telopea* 14: 45. 2012.

Figure 1d-g

Plants terrestrial, ticket-forming. Rhizomes long-creeping, with ciliform hairs. Leaves 1.5–4.5m long; stipes 0.75–2.5 m long, proximally dark brown, stramineous above, glabrous; laminae 0.75–2.5m m long, proximally 3–4-pinnate-pinnatifid; rachises stramineous, glabrous; basal pinnae 60–100 × 25–70cm, equilateral; pinnae and pinnules distally with free lobes between the segments; compound distal segments inequilateral, irregularly dissected, caudate at apex; simple distal segments linear, up to 3(–4) cm long; costae abaxially with reddish catenate hairs, adaxially glabrous; costules abaxially with reddish catenate hairs, adaxially glabrous;

veins abaxially lanose, with lax, arachnoid hairs, adaxially glabrous; laminar tissue between the veins abaxially and adaxially glabrous; sori marginal, linear, along segment margins, born at the tip of multiple veins; inner indusia vestigial; outer indusia linear.

Geographical distribution: Neotropical.

Specimens examined: BRAZIL. MINAS GERAIS: Entre Viçosa e Visconde do Rio Branco, 11-V-2013, *P.B. Schwartsburd et al. 2837* (VIC); Entre Viçosa e Visconde do Rio Branco, 11-V-2013, *P.B. Schwartsburd et al. 2838* (VIC). Viçosa, State Agricultural School, 24-II-1957, *H.S. Irwin 2721* (F, TEX-*n.v.*, UC, US, VIC); Viçosa, Escola Superior de Agricultura e Veterinária, 1943, *P. Alvin s.n.* (VIC-3537); Viçosa, Universidade Federal de Viçosa, Fazendinha, 11-IX-1977, *Rosane & Rosângela s.n.* (VIC-7962); Viçosa, Universidade Federal de Viçosa, Fazendinha, 11-IX-1977, *Rosane & Rosângela s.n.* (VIC-7963); Viçosa, Universidade Federal de Viçosa, Fazendinha, 11-IX-1977, *Rosane & Rosângela s.n.* (VIC-7964); Viçosa, Universidade Federal de Viçosa, Fazendinha, 11-IX-1977, *Rosane & Rosângela s.n.* (VIC-7965); Universidade Federal de Viçosa, Mata do Paraíso, Trilha dos Alpes, 9-II-2017, *P.B. Schwartsburd et al. 3877* (VIC); Universidade Federal de Viçosa, Mata do Paraíso, Trilha dos Alpes, 9-II-2017, *P.B. Schwartsburd et al. 3879* (VIC); Viçosa, Universidade Federal de Viçosa, Mata da Biologia, 27-III-2019, *N.T.L. Pena et al. 783* (VIC); Viçosa, Universidade Federal de Viçosa, Mata da Biologia, 27-III-2019, *N.T.L. Pena et al. 784* (VIC).

Pteridium esculentum subsp. *arachnoideum* is recognized by the pinnae and pinnules distally with free lobes between the segments, veins abaxially with arachnoid hairs, and glabrous laminar tissue between the veins. The outer indusia is always present, even in sterile leaves.

Lindsaeaceae

Rhizomes short to long-creeping, protostelic with internal phloem, or rarely solenostelic, bearing basally attached, nonclathrate scales or hairs. Leaves monomorphic; laminae simple to 3-pinnate or rarely more dissected; veins usually free, occasionally anastomosing and then without included veinlets; indument generally absent or formed by 2-celled glandular hairs. Sori marginal or submarginal, extrorse, elongate to linear, protected by outer (not modified) and inner (modified)

indusia; spores tetrahedral and trilete, or rarely bilateral and monolete (Smit et al. 2006).

Lindsaea Dryand. ex Sm.

Rhizomes short-creeping, with primitive scales. Leaves small to medium-sized, ca. 20 cm to 1 m long; laminae simple to 3-pinnate; indument absent or formed by 2-celled glandular hairs; veins generally free; sori marginal or submarginal, elongate, born on commissural veins; inner indusia modified, elongate; outer indusia not modified (Smit et al. 2006).

About 180 species, with 34 occurring in Brazil (Kramer 1957, PPG I 2016, Pena *et al.* 2020).

Lindsaea lancea (L.) Bedd. var. ***lancea***, Suppl. Ferns S. Ind. 6.: 292. 1876. *Adiantum lancea* L., Sp. Pl. ed. 2. 2: 1557. 1763.

Figure 2a-d

Plants terrestrial. Rhizomes short-creeping, with dark brown, lanceolate scales. Leaves 30–50 cm long; stipes 15–25 cm long, dark brown proximally, stramineous above, quadrangular, proximally with dark brown, acuminate scales and sparse 2-celled glandular hairs; laminae 15–25 cm long, 2-pinnate; rachises not winged, stramineous, with sparse 2-celled glandular hairs; basal pinnae 10–15cm × 2.5–3.5cm equilateral; pinnules petiolulate, dimidiate, 1.5–2 cm long; costae abaxially and adaxially with sparse 2-celled glandular hairs or glabrescent; veins abaxially and adaxially glabrous; laminar tissue between the veins abaxially and adaxially glabrous; sori continuous, born at the tip of multiple veins; inner indusia membranaceous to papyraceous, the margins entire, wavy, glabrous.

Geographical distribution: Neotropical.

Specimens examined: BRAZIL. MINAS GERAIS: Viçosa, 1930, Y. Mexia 4639-a (GH-n.v., UC, US, VIC).

All *Lindsaea* spp. from Viçosa are similar in having 2-pinnate laminae and dimidiate pinnules. *Lindsaea lancea* var. *lancea* differs from the other two by having continuous sori; *L. quadrangularis* subsp. *quadrangularis* differs from the other two by having reddish-brown, winged rachises; and *L. stricta* var. *stricta* differs from the other two by having petioles that are terete abaxially. In addition, pinnule lengths are different between the three taxa: 1.5–2 cm in *L. lancea* var. *lancea*, 1.2–1.5 cm in *L. quadrangularis* subsp. *quadrangularis*, and to 1 cm in *L. stricta* var. *stricta*.

Lindsaea quadrangularis Raddi subsp. ***quadrangularis***, Opusc. Sci. 3: 294. 1825.

Figure 2e-h

Plants terrestrial. Rhizomes short-creeping, with light brown, lanceolate scales. Leaves 40–75 cm long; stipes 25–40 cm long, entirely reddish-brown, quadrangular, proximally with light brown, acuminate scales and sparse 2-celled glandular hairs; laminae 20–40 cm long, 2-pinnate; rachises winged, reddish-brown, with sparse 2-celled glandular hairs; basal pinnae 10–18 × 2–3 cm; pinnules short-petiolulate, dimidiate, 1.2–1.5 cm long; costae abaxially and adaxially with sparse 2-celled glandular hairs; veins abaxially and adaxially glabrous; laminar tissue between the veins abaxially with sparse 2-celled glandular hairs, adaxially glabrous; sori interrupted, born at the tip of multiple veins; indusia membranaceous, the margin dentate, glabrous.

Geographical distribution: endemic to the Brazilian Atlantic Forest.

Specimens examined: BRAZIL. MINAS GERAIS: Viçosa, Agricultural College lands, Hillside of Cha-Cha Valley, 1-III-1930, *Y. Mexia 4410-a* (UC, US-*n.v.*); Viçosa, 1935, *J.G. Kuhlmann s.n.* (VIC-1894).

Lindsaea stricta (Sw.) Dryand. var. ***stricta***, Trans. Linn. Soc. London 3: 42. 1797. *Adiantum strictum* Sw., Prodr. [O. P. Swartz] 135. 1788.

Figure 3a-d

Plants terrestrial. Rhizomes short-creeping, with dark brown, lanceolate scales. Leaves 35–80 cm long; stipes 15–50 cm long, dark brown proximally, stramineous above, abaxially terete, adaxially flattened, proximally with dark brown, acuminate scales; laminae 20–35 cm long, 2-pinnate or rarely 1- or 3-pinnate; rachises not winged, stramineous, with sparse 2-celled glandular hairs or glabrescent; basal pinnae 12–25 cm × 1–2 cm; pinnules short-petiolate, dimidiate or flabellate, to 1 cm long; costae abaxially and adaxially with sparse 2-celled glandular hairs or glabrescent; veins abaxially and adaxially with sparse 2-celled glandular hairs or glabrous; laminar tissue between the veins abaxially and adaxially with sparse 2-celled glandular hairs or glabrous; sori interrupted, born at the tip of multiple veins; inner indusia membranaceous, the margins dentate, glabrous.

Geographical distribution: Neotropical.

Specimens examined: BRAZIL. MINAS GERAIS: Viçosa, road to Cajurí, Moro Grande, 750 m, 7-I-1931, *Y. Mexia 5486* (B-*n.v.*, BM-*n.v.*, C-*n.v.*, F, G-*n.v.*, GH-*n.v.*, K-*n.v.*, MO-*n.v.*, NY-*n.v.*, PH-*n.v.*, S-*n.v.*, TEX-*n.v.*, U-*n.v.*, UC, US, VIC); Viçosa, Silvestre, 10-IV-1999, *M.G. Bovini 1624* (VIC); Viçosa, Universidade Federal de Viçosa, Mata da Silvicultura, em direção ao Cristo, 740 m, 20°46'S, 42°52'W, 31-X-2014, *P.B. Schwartzburd et al. 3421* (VIC); Viçosa, Universidade Federal de Viçosa, Mata da Silvicultura, em direção ao Cristo, 740 m, 20°46'S, 42°52'W, 31-X-2014, *P.B. Schwartzburd et al. 3423* (VIC); Universidade Federal de Viçosa, Mata do Paraíso, Trilha dos Alpes, 9-II-2017, *P.B. Schwartzburd et al. 3881* (VIC); Viçosa, Universidade Federal de Viçosa, Recanto das Cigarras, 8-VII-2019, *N.T.L. Pena et al. 1049* (VIC).

Saccolomataceae

Rhizomes erect or rarely short-creeping, sometimes forming small trunks, dictyostelic, bearing peltate scales. Leaves monomorphic; stipes with an omega-shaped vascular strand; laminae 1–4-pinnate; veins free; indument formed by caduceus scales or rarely by scattered catenate hairs. Sori marginal or submarginal, discrete, extrorse, protected by outer (not modified) and inner (modified) indusia; spores tetrahedral-globose and trilete (Smit et al. 2006).

One pantropical genus with about 24 species (Rojas-Alvarado 2010, Luong *et al.* 2015, Schwartzburd 2020, Schwartzburd 2022). The adoption of genus *Orthiopteris* for the Paleotropical species is phylogenetically justified, but lacks morphological support; thus, regarding only *Saccoloma* in Saccolomataceae is more convenient (Schwartzburd 2022). In Brazil, nine species are currently recognized (Schwartzburd 2022).

***Saccoloma* Kaulf.**

***Saccoloma elegans* Kaulf.**, Berlin. Jahrb. Pharm. Verbundenen Wiss. 21: 51. 1820.

Figure 1e-l

Plants terrestrial. Rhizomes erect to decumbent, stout to trunk-like, glabrescent; leaves 1.2–2.2 m long; petioles proximally burgundy, stramineous above, 40–80 cm long, proximally wrinkled to minutely spiny; petiolar scales peltate, blackish, with or without lighter, dentate margins; laminae 1-pinnate 80–140 cm long; rachises stramineous, glabrous; basal pinnae 15–25 × 2.5–3.5 cm; costae abaxially and

adaxially glabrous; veins commonly 1-furcate, rarely simple or 2 or 3-furcate (at the base of pinnae), abaxially and adaxially glabrous; sori marginal, discrete, born at the tip of single veins, placed side by side; outer indusia not modified; inner indusia hemi-umbonate, commonly forming wings connecting adjacent sori.

Geographical distribution: Endemic to the Brazilian Atlantic Forest, from Pernambuco to Santa Catarina.

Specimens examined: BRAZIL. MINAS GERAIS: Estrada São Miguel–Viçosa [Road to São Miguel], 25-IV-1930, *Y. Mexia* 4639 (F, IAN, MO-*n.v.*, NY, PH, VIC, UC, US); Viçosa, Escola Superior de Agricultura e Veterinária, s.d., *Y. Mexia* 4964 (MO-*n.v.*, NY, US, VIC); Viçosa, woods on slope, 710 m, 6-X-1930, *Y. Mexia* 5385-*a* (UC-2 sheets); Viçosa–Coimbra, km 120, Sítio Bom Sucesso, 13-IX-2002, *G.E. Valente & M.L. Batista* 1071 (VIC); Viçosa, Mata do Seu Nico, 20°47'S, 42°51'W, 800 m, 6-XI-2012, *P.B. Schwartsburd & E. Guatimosin* 2618 (NY, RB, UPCB, VIC).

Saccoloma elegans is recognized by the 1-pinnate laminae and the discrete sori placed side by side and opening extrorsely.

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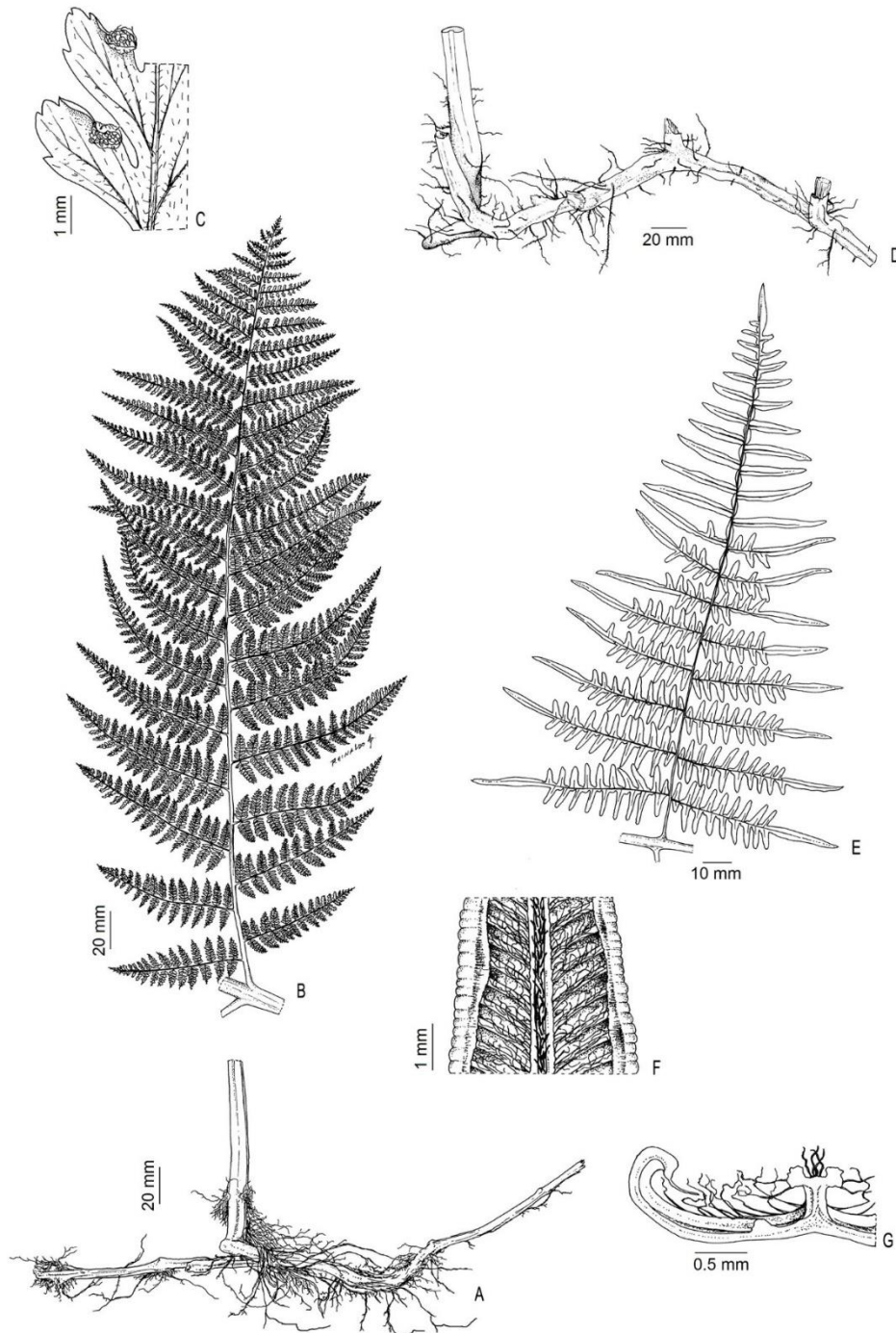


Figure 1. a–c. *Dennstaedtia cicutaria*. a. rhizome. b. basal pinna. c. segments, abaxially, showing indument and sori. d–g. *Pteridium esculentum* subsp. *arachnoideum*. d. rhizome. e. pinnule. f. segment, abaxially, showing indument and sori. g. segment in cross section, showing indument and outer indusium (abaxial surface up).

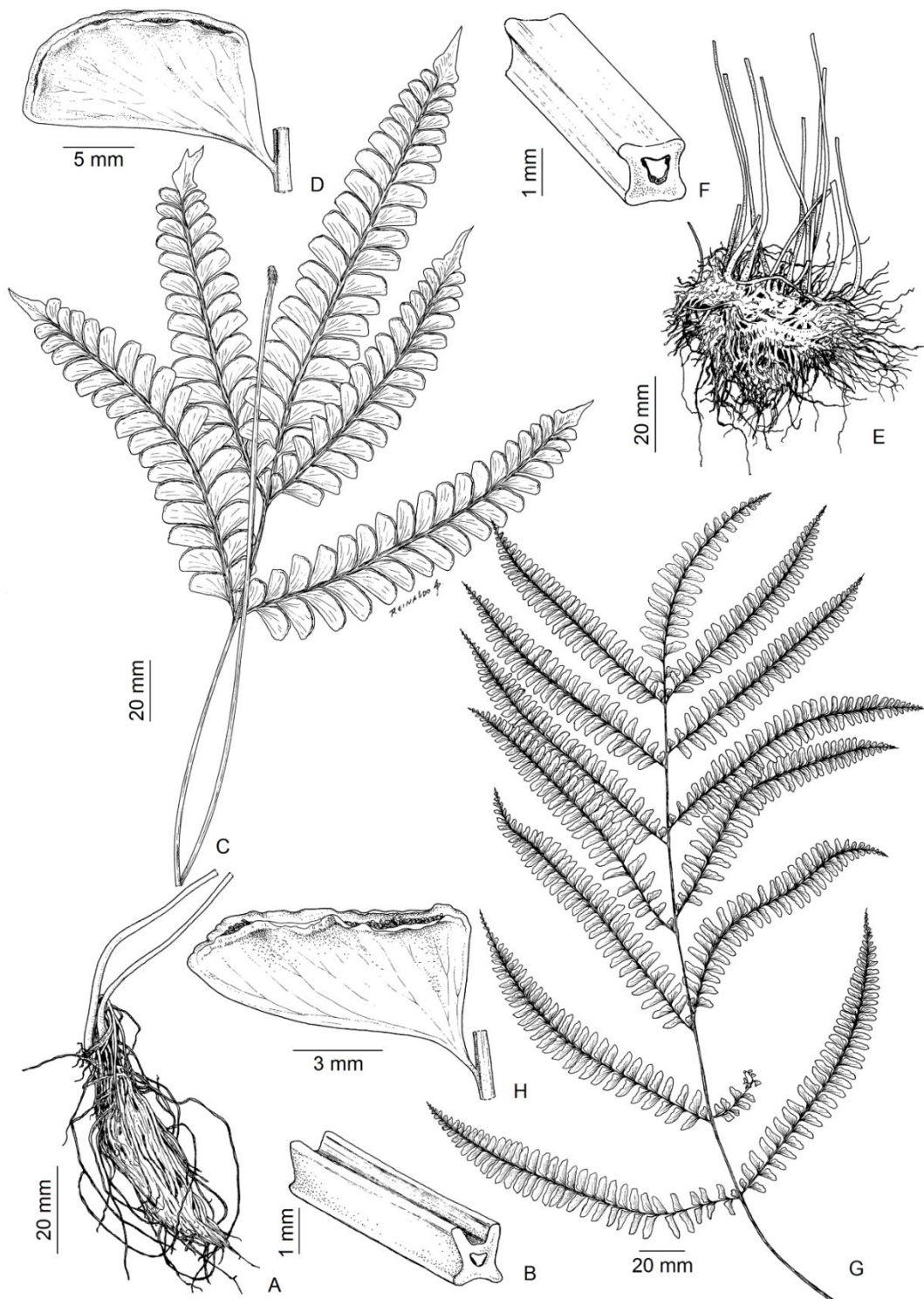


Figure 2. a–d. *Lindsaea lancea* var. *lancea*. a. rhizome. b. petiole, in cross section. c. leaf. d. pinnule, abaxially, showing sorus. e–h. *Lindsaea quadrangularis* subsp. *quadrangularis*. e. rhizome. f. petiole, in cross section. g. leaf. h. pinnule, abaxially, showing sorus.

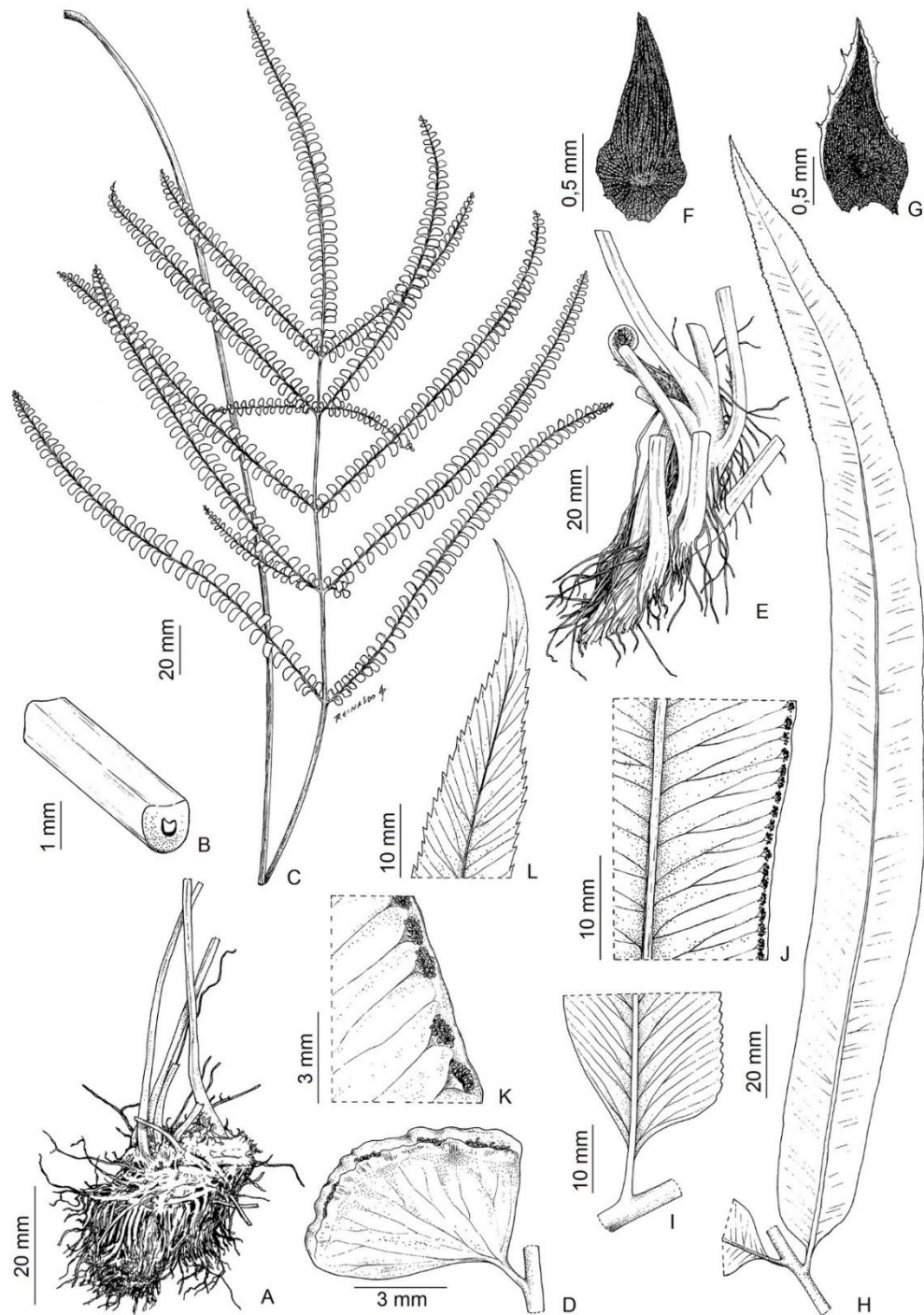


Figure 3. a–d. *Lindsaea stricta* var. *stricta*. a. rhizome. b. petiole, in cross section. c. leaf. d. pinnule, abaxially, showing sorus. e–l. *Saccoloma elegans*. e. rhizome. f. and g. petiolar scales. h. medium pinna. i. base of pinna. j. pinna, abaxially, showing venation pattern. k. pinna, abaxially, showing sori. l. apex of pinna.