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ORIGINAL ARTICLE

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*, Dennstaedtioideae, leptosporangiate ferns, Neotropics

Cuidado com meus espinhos: uma nova samambaia espinhosa (*Dennstaedtia*, Dennstaedtiaceae) da Amazônia central e ocidental

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*, Dennstaedtioideae, samambaias leptosporangiadas, região neotropical

INTRODUCTION

Dennstaedtia Bernh. belongs to the family Dennstaedtiaceae, a Cretaceous lineage that diverged early among the leptosporangiate ferns (Schwartsburd *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; Schwartsburd *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* Schwartsburd *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 cup-shaped, cilindrical, or an hemi-globose structure (Tryon and Tryon 1982; Mickel and Smith 2004; Schwartsburd 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

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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; Schwartsburd *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 hebarium 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 Dennstaedtioideae 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.

MATERIAL AND METHODS

This study is part of an ongoing comprehensive review of the genus *Dennstaedtia* from Brazil and neighboring countries. For this purpose, specimens from the following herbaria have been examined: CEPEC, CESJ, COR, BHCB, FUEL, FURB, HAS, HUCS, HUEFS, HRCB, IAN, ICN, INPA, MBML, MCN, MG, OUPR, SAMES, SJRP, UEC, UFP, UFRGS, UPCB, VIES and VIC (Brazil); SGO (Chile); UPRRP (Puerto Rico); NY and VT (U.S.A) (Thiers 2022). In addition, we examined unidentified specimens from TUR (University of Turku, Finland) and AAR (Aarhus University, Denmark) and *Dennstaedtia* specimens from the online repositories SpeciesLink (CRIA 2022), Reflora (http://reflora.jbrj.gov.br/reflora/herbarioVirtual/), and Pteridophyte Collections Consortium (https://www.pteridoportal.org/portal/index.php).

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).

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 acampamento do PPBio, aproximadamente 1:30 horas de barco, em beira do igarapé), 1º47'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 adaxilly 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, formed by the fusion of the inner and the outer indusia. Spores tetrahedral-globose, trilete, verrucate with partly fused verrucae.

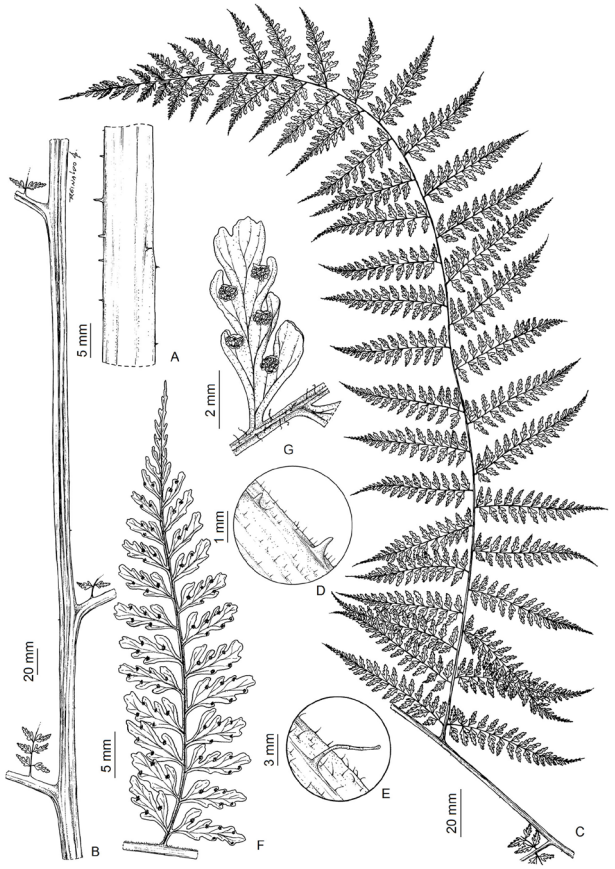

Figure 1. *Dennstaedtia aculeata*. **A** – Section of the petiole, showing spinescence; **B** – Rachis showing alternate pinnae; **C** – Pinna; **D** – Detail of rachis showing spines and acicular hairs; **E** – Detail of rachis showing acicular and catenate hairs with prominent base; **F** – Pinnule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

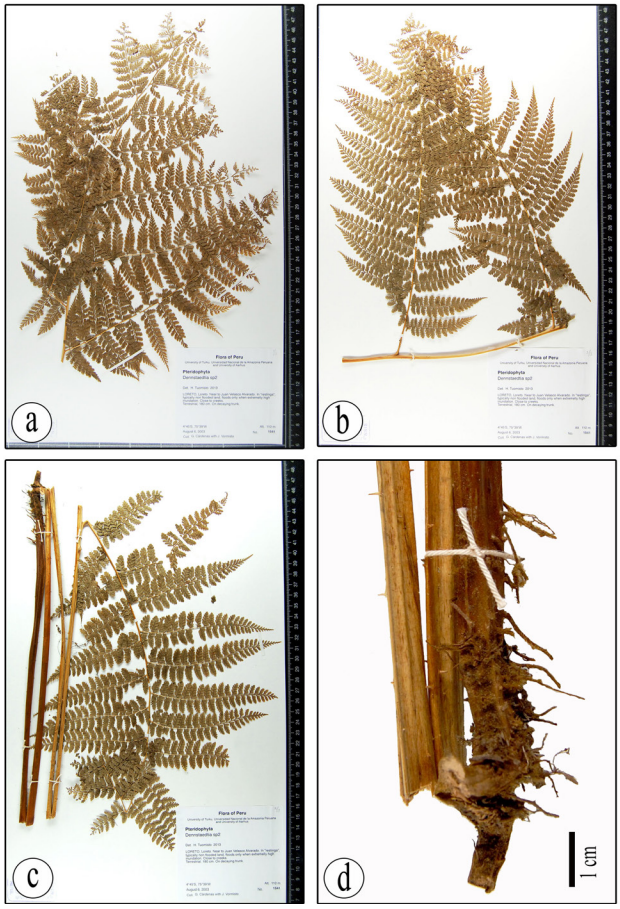

Figure 2. *Dennstaedtia aculeata* (sp. nov.) (*G. Cárdenas & J. Vormisto 1541*, TUR-599750, TUR-599751, TUR-599752). **A** – Laminar apex; **B** – Medial pinnae; **C** – Basal pinna and petiole; **D** – Petiole and part of the rhizome in detail. Credits: G. Zuquim; edited by N.T.L. Pena. This figure is in color in the electronic version.

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

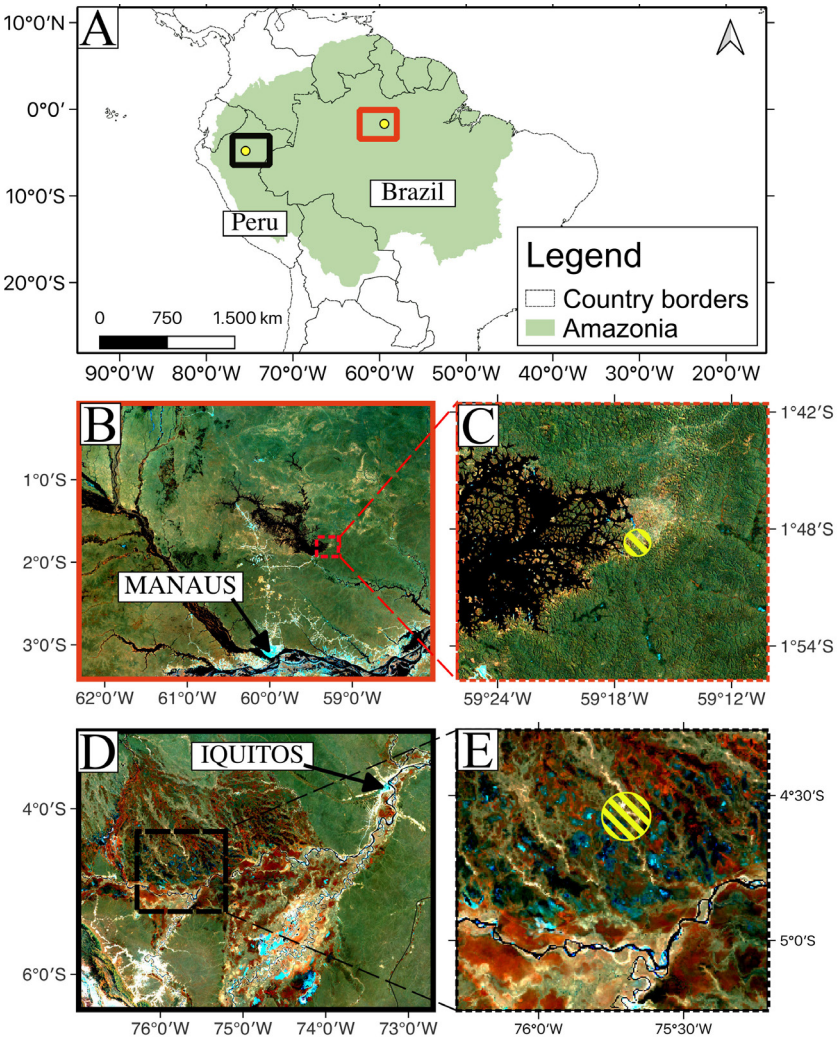

Figure 3. Distribution map of *Dennstaedtia aculeta* (sp. nov.). **A** – Known location records of *Dennstaedtia aculeata* in the Amazon region; **B-C** – Collection site of the type specimen near the artificial lake of the Balbina hydroeletric dam in Amazonas, Brazil; **D-E** – Collection site of the 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.

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).

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 (Schwartsburd and Prado 2015), thus being superficially similar to *D. aculeata.* However, unlike *D. aculeata*, *Hypolepis* has only outer indusium and monolete spores (Schwartsburd 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.) (Schwartsburd *et al.* 2020). Secondly, their base chromosome numbers are very different, with *Dennstaedtia* (group *Patania*) having 46 and 47, and *Hypolepis* 52 (Schwartsburd *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; Schwartsburd *et al.* 2020), especially in subfamily Hypolepidoideae. According to Shang *et al.* (2018) and Schwartsburd *et al.* (2020), they appeared in the ancestors of the genus *Hiya* H. Shang and in the Neotropical clade of *Hypolepis* (see also Schwartsburd 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 unnarmed species, such as *Hiya distans* (Hook.) Brownsey & Perrie, and some Neotropical *Hypolepis* (Shang *et al.* 2018; Schwartsburd *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; Schwartsburd *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).

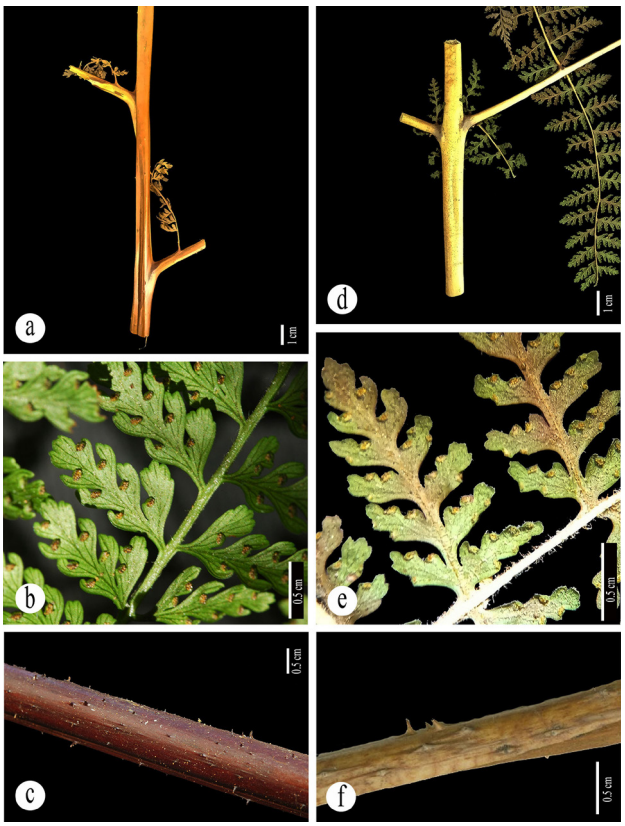

Figure 4. *Dennstaedtia aculeata* (sp. nov.) (*G. Zuquim & R. Braga-Neto 172*, INPA-219630). **A** – Rachis with alternating pinnae; **B** – Pinules and ultimate segments, abaxially; **C** – Petiole dark brown to vinaceus and densely spiny. *Dennstaedtia spinosa* (*M. Sundue et al. 5045*, VT-290463; *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.

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.* cilindrical). 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).

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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