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Original Paper
Root anatomy of Venezuelan species of *Geonoma* (Arecaceae: Arecoideae: Geonomateae)

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Abstract

In this research we studied root anatomy of eight species and two morphotypes from the genus *Geonoma* in Venezuela, in order to explore their structural and taxonomic implications. Fresh material sampled wild population was fixed in FAA and hand-sectioned or with a rotary microtome, following standardized protocols. Histochemical tests were carried out in some components. Obtained preparations were studied under a calibrated optical microscope; some variables were quantified by means of an eyepiece micrometer. The obtained results allowed the anatomical differentiation of the studied species and the two morphotypes. Most informative diagnostic variables identified include the thickening shape of the cells in the exodermis walls (transverse section), parenchyma cells with circular contours in the cortex, length of air spaces, the differentiation of passage cells in the endodermis, shared "V" and "Y" shaped xylem arches, the shape of phloem strands and scattered metaxylem vessels in the pith. Our results are also discussed in the context of other structural studies published on roots of different members of Arecaceae.

Key words: anatomy, geonoma, roots.

Resumo

Se estudió la anatomía radical de ocho especies y dos morfotipos de Geonoma presentes en Venezuela, con el fin de explorar sus implicaciones estructurales y taxonómicas. Material fresco de poblaciones silvestres fue fijado en FAA y se seccionó a mano alzada o con un microtomo de rotación, siguiendo los protocolos estándar. Se realizaron pruebas histoquímicas en algunos componentes. Las preparaciones obtenidas se estudiaron bajo un microscopio óptico calibrado; algunas variables se cuantificaron usando un micrómetro ocular. Los resultados obtenidos permitieron la diferenciación anatómica de las especies estudiadas y de los dos morfotipos. Entre las variables diagnósticas identificadas se incluyen: la forma del engrosamiento de las paredes en las células de la exodermis (sección transversal), la presencia de células del parénquima con contornos regulares en la corteza, la longitud de los canales de aire, la diferenciación de las células de paso en la endodermis, la presencia de arcas compartidas en forma de "V" o "Y", la forma de los cordones floemáticos y la presencia de vasos de metaxilema dispersos en la médula. Nuestros resultados también se discuten en relación a otros estudios estructurales publicados sobre raíces de diferentes miembros de Arecaceae.

Palavras-chave: anatomía, geonoma, raíces.

Introduction

Among the monocotyledonous families, Arecaceae (Palmae) is a relevant taxonomic group because of its wide morphological and ecological diversity (Dransfield *et al.* 2008). Members of this family are broadly distributed all over the world, largely dominant in tropical and subtropical regions, with an over 80 millions year old fossil record (Stewart 1994; Dransfield *et al.* 2008), but molecular phylogenetic analyses suggest an earlier origin dating back to the mid cretaceous (Couvreur *et al.* 2011).

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Arecaceae is not only a diverse and ecologically important group, but also highly valued due to its many uses for human communities in a wide range of worldwide activities (Anderson & Anderson 1985). Among tropical Venezuelan ecosystems, palms stand out because of their biological growth habit, their relevance as a basic flora component and as a significant element in plant communities (Vareschi 1992). In Venezuela, the palm family is composed of 30 genera and 101 species, Arecoideae being the best represented subfamily (Stauffer 1999). Within arecoid palms the most diverse genera are *Geonoma* Willd. and *Bactris* Jacq. *ex* Scop. (Stauffer 1999). The most specialized and largest genus in tribe Geonomateae is *Geonoma*, represented by 68 species worldwide (Dransfield *et al*. 2008; Henderson 2011) and recently shown as an example of complex radiation (Loiseau *et al.* 2019). In Venezuela, there are between 19 and 20 recognized species (Stauffer 1999; Hokche *et al*. 2008), but many more may be discovered from poorly inventoried areas of the country. Currently some species are considered to be endangered due to extremely narrow distribution, overexploitation in commercially useful species and destruction of the natural ecosystems where they thrive. Venezuela's coastal mountain range is considered by Stauffer (1999) to be high in diversity and endemism for Arecaceae, with about 38 species reported for that region. This zone is severely affected by conservation threats owing to the uncontrolled increase of agricultural and urban activities that are rapidly destroying the species habitat.

In this context, it is necessary to undertake urgent conservation plans that include ecological, taxonomic and structural studies on scantly understood palm groups, especially in their natural habitats of the Andean region, coastal zone, the Venezuelan plains and Orinoco delta (Llamozas *et al*. 2003; Hokche *et al.* 2008). *Geonoma* is widely distributed in central and northwestern South America and most of the Antilles (Dransfield *et al.* 2008; Henderson 2011). In Venezuela, they grow relatively frequently in the Andes at 700–2,900 mamsl elevation in montane rainforest, in the Coastal Cordillera in Venezuela at 400–1,600 mamsl elevation in lowland to montane rainforest, in the Northwestern coastal area of Venezuela; cloud forest on summits of isolated mountains, exposed to high winds to 1,400 mamsl elevation, and to the south of the country at 100–1,200 mamsl elevation in lowland to montane rainforest (Henderson *et al.* 1995; Hoyos & Braun 2001; Dransfield *et al.* 2008; Henderson 2011). However, there is no record of the edaphoclimatic conditions of these ecosystems for analyzing the distribution of the taxa studied with the environmental conditions prevailing in each particular habitat, which would be very necessary. In this sense, Muscarella *et al.* (2019) indicated that the edaphic conditions are associated with the phylogenetic community structure of palms across western Amazonia. Specifically, *Geonoma* species showed patterns of phylogenetic clustering associated with low-fertility upland sites.

Plant anatomy can contribute to the better understanding of ecologic, taxonomic and phylogenetic relations in vascular plants, as well as highly informative concerning their physiology. Palms in particular display remarkable vegetative and reproductive anatomical variability. Studies of this variation provide useful characteristics to establish relations between different taxa and in some instances explain the evolutionary changes that have occurred (Uhl & Dransfield 1987; Tomlinson *et al.* 2011).

In recent years, studies on the vegetative organs of palms have significantly increased. However, there is still an important lack of information regarding the structure and development of vegetative organs in some critical taxa often unplaced, or not represented at all in the most recent phylogenetic analyses. This is arguably due to the great morphological variability and the difficulties hindering palm organ collection (Govaerts & Dransfield 2005; Dransfield *et al*. 2008; Tomlinson *et al*. 2011).

Tomlinson (1961) undertook pioneer efforts towards the analysis of root anatomy in a large number of palm genera, establishing general patterns for the family, whereas Seubert (1998a, b) further increased our knowledge with the study of root histology in 101 genera in the group. In this study it was highlighted the remarkable variation in the inner root structure among the different tribes. All studies carried out so far on palm root anatomy confirm that there are rather few anatomical differences among species of the same genus, most of these being rather quantitative or scarcely meaningful to propose divisions among taxonomic groups. In particular for the Geonomateae tribe (previously known as the Geonomeae), they considered that the genera therein included display homogeneous anatomical characteristics. In spite of its rich taxonomic diversity in (ca. 68 spp.) published efforts confirm that the material examined remains very scant. Thus Tomlinson (1961) only studied two species (*Geonoma vaga* Griseb., *Geonoma* sp.), and Seubert (1998a, b) included three species (*Geonoma congesta* H. Wendl. *ex* Spruce and two indeterminate species). Likewise Tomlinson *et al*. (2011), consider that a detailed investigation on the genus *Geonoma*, as the most diverse genus in the Neotropics, would be very interesting for the ecological understanding of tropical rainforest.

The taxonomy of *Geonoma* was reviewed by Henderson (2011); and supported by a recent NGS-based phylogenetic analysis of all Genomateae (Loiseau *et al*. 2019). The first study highlights the presence of very variable species, in which subspecies and morphotypes are proposed to better understand highly polymorphic characters often leading to complex taxonomic interpretations. One of the complexes pointed out by Henderson (2011) that is represented in Venezuela Palm Flora is *Geonoma undata* in which the subspecie *undata* with several morphotypes (*i.e.*, *densa*, *undata*) are included. Henderson's taxonomic proposal is in some cases challenged by the groups proposed by Loiseau *el al*. (2019), which makes clear the importance to integrate additional data to a better understanding of the complex taxonomy within Geonomateae, in particular to the species-rich genus *Geonoma*.

Based on these considerations, an anatomical study was performed on the roots of eight species of the genus *Geonoma* (Arecoideae: Geonomateae) in Venezuela, including two morphotypes of one of them. The aims of the study are: 1) to understand the taxonomical implications of the inner root structure; 2) to compare our data with similar studies carried out in the family; and 3) to relate our results with the current taxonomic and phylogenetic circumscription of *Geonoma*.

Materials and Methods

Material from eight taxa of *Geonoma* was collected from wild populations in the cloud forest of the Venezuelan Coastal Range (Tab. 1; Fig. 1). Seven of them were named using Henderson's monograph (2011) and *G. paraguanensis* which was not considered by this author but remains anintriguing, yet poorly understood palm is here kept as a valid taxonomic entity as proposed by Hokche *et al*. (2008). The studied species are listed in Table 1. Specialized bibliography of the family was reviewed and dried material was examined in the herbaria CAR, CORO, MY, and VEN, acronyms according to Thiers (continuously updated).

Roots of at least three individuals were collected for each species and samples from first order roots on adult plants were collected; these samples were 10 cm long (measured from the radical apex), and the cuts were done on the most distant portion of the latter, this was chosen because its tissues showed complete differentiation in all species, which was verified by making exploratory sections along the samples. This material was fixed in FAA (formaldehyde, glacial acetic acid and ethanol 70%) until lab processing. The samples were hand-sectioned or by means of a rotary microtome. Afterwards they were dyed with toluidine blue aqueous (1%) (O'Brien & McCully 1981) or with astra blue with safranine (Kraus & Arduin 1997). Semi-permanent slides were obtained for some of the analyses. A glycerin-water solution (1:1) was used as a mounting medium. The slides were sealed with colorless nail polish (Purvis *et al*. 1966). Samples to be sectioned with a rotary microtome were dehydrated in a graded tertiary butyl alcohol series, then infiltrated and embedded in paraplast (58 °C melting point) and cross-sectioned. Cuts were afterwards dyed with safranine-fast green, and mounted with Canada oil, creating permanent slides (Johansen 1940). Temporary slides with transverse cuts were made for histochemical tests (Johansen 1940; Kraus & Arduin 1997) in order to determine the presence of lipids with Sudan III, lignine with phloroglucinol at 1% and tannins with ferric chloride at 10%.

Preparations were studied under a Nikon calibrated optical microscope using an incorporated eyepiece micrometer, and a Leitz stereoscopic microscope. Images were captured with a digital camera coupled to this optical microscope. The description of the anatomical data obtained followed the terminology already used by Tomlinson (1961, 1990) and Tomlinson *et al*. (2011).

The following quantitative variables, registered in five visual fields per slide, were evaluated: number of layers and epidermis thickness, number of layers of exodermis, endodermis and cortex, as well as the thickness of the latter. The vascular cylinder and pith diameter, pericycle thickness, number of xylem arcs, number of metaxylem vessels, as well as the widest metaxylem vessels were also determined.

Table 1 – Information of the *Geonoma* taxa studied and vouchers deposited in MY.

Taxon	Collectors	Locality	Habitat	Altitude (mamsl)	Vouchers numbers
Geonoma deversa (Poit.) Kunth subsp. *deversa*	Briceño A, Silva K & Álvarez L	Amazonas, Venezuela, Mun. Atures, via El Muelle.	Lowland rainforest along river. Plant growing on sandy soil with dense layer of leaf litter.	100	132864
					132865
					132866
					132867
Geonoma lehmannii Dammer *ex* Burret subsp. *lehmannii*	Briceño A & Rodríguez J	Trujillo, Venezuela, Mun. Bocono National Park Guaramacal, road from Bocono to Guaramacal, SE from Bocono, via The antennas.	Montane rainforest	2450	132847
				2469	132848
					132849
				2460	132850
Geonoma orbignyana Mart. subsp. *orbignyana*	Briceño A & Rodríguez J	Trujillo, Venezuela, Mun. Bocono, Trujillo-Bocono old road.	Montane rainforest	2401	132851
				2394	132852
					132853
					132854
Geonoma paraguanensis H. Karst.	Briceño A, Castro M & Muñoz D	Falcon, Venezuela, Mun. Carirubana, Peninsula of Paraguana, summit of the hill Santa Ana.	Cloud forest on summits of isolated mountains, exposed to high winds	836	132836
					132837
					132838
					132839
					132840
					132841
	Briceño A, Castro M, Márquez L & Muñoz D			754	132859
Geonoma pinnatifrons subsp. *pinnatifrons*	Briceño A & Espinoza Y	Miranda, Venezuela, Mun. Baruta, main street "Los Guayabitos", Topotepuy Ecological Gardens, El Volcán	Montane rainforest	1461	132877
					132878
					132879
Geonoma simplicifrons Willd.	Briceño A & Rodríguez J	Aragua, Venezuela, Mun. Mario Briceño Iragorry, Rancho Grande, 100-200 m from the Paso de Portachuelo towards the Pico Periquito.	Montane rainforest	1193	132874
					132875
					132876
Geonoma spinescens H. Wendl.	Briceño A & Rodríguez J	Aragua, Venezuela, Mun. Mario Briceño Iragorry, Rancho Grande, 100-200 m from the Paso de Portachuelo towards the Pico Periquito.	Montane rainforest	1193	132869
					132871
					132873

Taxon	Collectors	Locality	Habitat	Altitude (mamsl)	Vouchers numbers
Geonoma undata Klotzsch subsp. *undata* (densa morphotype)	Briceño A, Castro M & Muñoz D	Falcon, Venezuela, Mun. Petit, Sierra of San Luis, Cumbre de Uria, Entering the road adjacent to the Guardaparques house.	Montane rainforest	1372	132842
					132843
				1390	132844
	Briceño A, Castro M & Muñoz D	Falcon, Venezuela, Mun. Petit, Sierra de San Luis, via hill Galicia, towards the antenna complex.	Montane rainforest	1486	132846
	Briceño A & Rodríguez J	Aragua, Venezuela, Mun. Mario Briceño Iragorry, Rancho Grande, 100-200 m from the Paso de Portachuelo towards the Pico Periquito	Montane rainforest	1132	132868
				1193	132870
				1198	132872
Geonoma undata Klozsch subsp. *undata* (undata morphotype)	Briceño A & Rodríguez J	Trujillo, Venezuela, Mun. Bocono, between Bocono and El Batatal	Montane rainforest	1863	132856
				1864	132857
				1861	132858

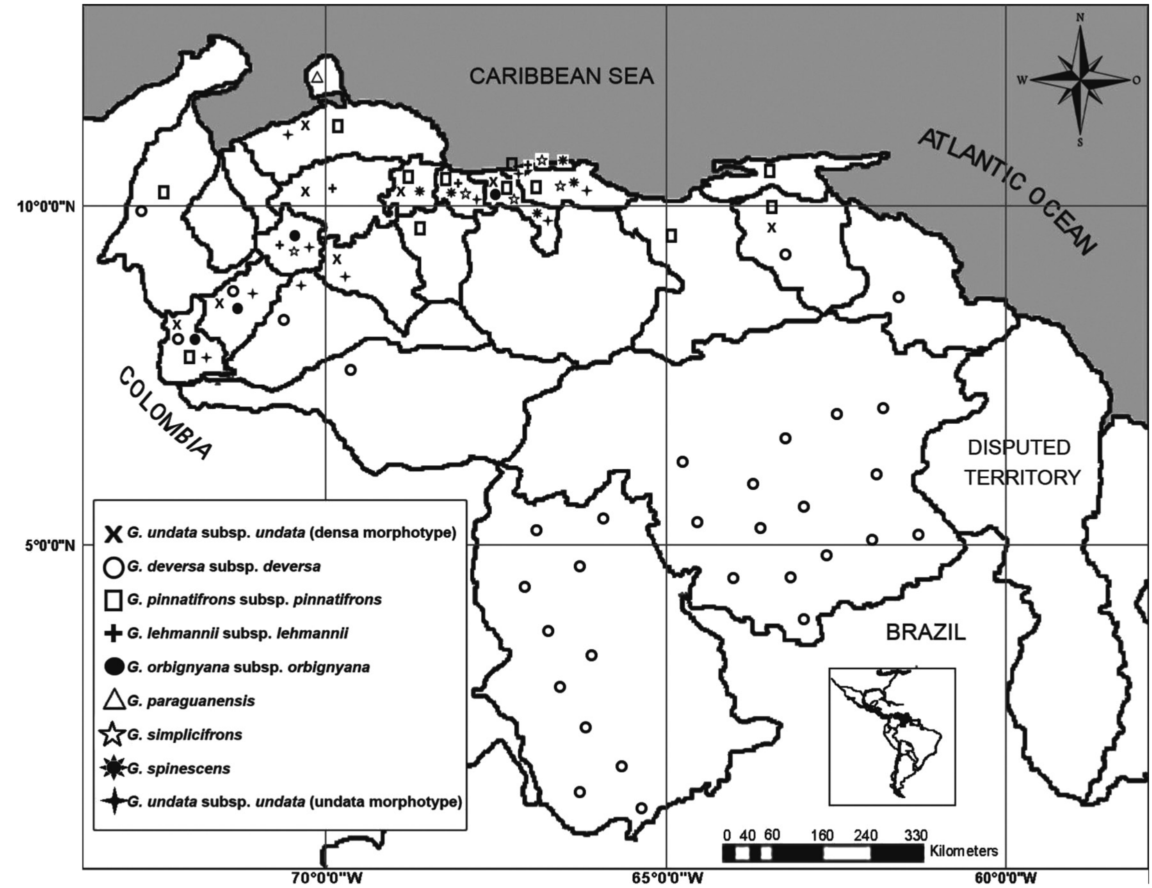

Figure 1 – Distribution map of the *Geonoma* species studied.

Results

All the studied species show in transverse section a one-layered rhizodermis, with quadrangular to rectangular cell shape, thin, pectocelullosic walls; root hairs lacking (Fig. 2a-c), the latter was verified by reviewing the exploratory sections made along the portions of sampled roots. Layer thickness varies among species, presenting the lowest values in *G. deversa*, *G. pinnatifrons* and *G. simplicifrons*; the highest value was registered in *G. paraguanensis*. In the remaining taxa it is rather uniform (Tab. 2).

The cortex is made of exodermis, heterogeneous parenchyma and endodermis. In *G. deversa*, *G. orbignyana*, *G. pinnatifrons*, *G. simplicifrons*, *G. spinescens* and *G. undata* (*densa* morphotype) (Fig. 2a), the exodermis cells are quadrangular, with thin walls in the first taxon, and thick ones for the remaining taxa. In *G. lehmannii* (Fig. 2b) rectangular cells with lignified external walls are predominant, and in *G. paraguanensis* (Fig. 2c) and *G. undata* (*undata* morphotype) this lignification occurs in both external and radial tangents forming an inverted U. On the other hand, the endodermis has strongly lignified walls in *G. deversa* (Fig. 2d), *G. pinnatifrons*, *G. paraguanensis* and the two morphotypes of *G. undata* but has thinner walls in the remaining species (*i.e.*, *G. simplicifrons*) (Fig. 2e). Likewise, there are also conspicuous passage cells in *G. spinescens* and *G. orbignyana* (Fig. 2f).

The parenchyma located between the exodermis and the endodermis shows variation in the organization and specific features of its cells (Fig. 2g). The ones located below the exodermis are relatively small cells, which increase in diameter in centripetal direction, with strongly sclerified walls in *G. deversa* (Fig. 2g), *G. lehmannii* (Fig. 2h), *G. orbignyana*, *G. pinnatifrons*, *G. spinescens* (Fig. 3a) and *G. undata* (*undata* morphotype) (Fig. 3b), and in a lower degree in *G. undata* (*densa* morphotype) (Fig. 3d), *G. paraguanensis* and *G. simplicifrons*. In this zone, in *G. undata* (*undata* morphotype) (Fig. 3b) there are parenchyma cells of variable diameter with a circular outline. Underneath this group of cells, the tissue is composed by mostly thin walled cells and between 13–23 intercellular channels of different sizes (Tab. 2), which are radially distributed and form air channels that are bordered by cells of different width (Figs. 2g, h; 3a, c; 4a-d); in species such as *G. deversa* (Fig. 4c) and *G. undata* (*densa* morphotype) the cell walls are thick and lignified. Towards the inner part of the cortex, limiting with the endodermis, the cells are oval shaped and the cell main axis parallel to the surface and radially organized in concentric layers around the vascular cylinder (Figs. 2d-h; 3c, d; 4). The number of cortex layers, as well as the thickness in this region varies among species. It is wider and with a larger number of cell layers in *G. paraguanensis* and thinner in *G. pinnatifrons*; nonetheless, the smallest number of cell layers were observed in *G. orbignyana* and *G. lehmannii* (Tab. 2). *G. paraguanensis* is the only species where fungal structures were observed invading the cells of the rhizodermis and cortical tissue.

The vascular cylinder is delimited by a pericycle layer, with rectangular or oval-shape cells, arranged with their main axis parallel to the surface. Such cells have thin pectocellulosic walls in *G. pinnatifrons*, *G. orbignyana* (Fig. 2f), *G. paraguanensis* and *G. undata* (*undata* morphotype); and rather sclerified in *G. undata* (*densa* morphotype) (Fig. 3c), *G. deversa* (Fig. 2d), *G. lehmannii*, *G. simplicifrons* and *G. spinescens* (Fig. 3d). The diameter of the vascular cylinder varies among species, the highest value was recorded for *G. deversa* and *G. undata* (*undata* morphotype), and the lowest for *G. lehmannii* (Tab. 2).

The vascular tissue consists of a variable number of xylem arches in the different species studied (Tab. 2). In most of them, the common pattern displayed was the presence of "I" shaped arches (Fig. 4c). In some cases these may share metaxylem elements showing a "V" shaped arrangement. An atypical "Y" shaped arrangement could be observed in *G. undata* (*densa* morphotype) (Fig. 4a). The number of metaxylem vessels per arch, as well as their diameter, were also different among species. The largest number of vessels per arch was registered in *G. orbignyana* and the smallest in *G. pinnatifrons*; likewise, the largest vessel diameter was observed in *G. undata* (*undata* morphotype) and the smallest was in *G. spinescens* (Tab. 2). The phloem strands are conspicuous and appear round or oval; the main axis length varies among taxa, the longest observed on *G. deversa*, *G. paraguanensis*, *G. undata* (*undata* morphotype) and *G. undata* (*densa* morphotype) (Fig. 3d) and *G. orbignyana*; and the shortest observed on *G. lehmannii* (Fig. 4b), *G. spinescens*, *G. simplicifrons* and *G. pinnatifrons* (Tab. 2).

The central region of the vascular cylinder is composed of parenchyma cells with thin walls, especially in those located towards the center, with thicker, lignified walls in the outer ones, closer to the arches. Occasionally in *G. deversa* (Fig. 4c) and

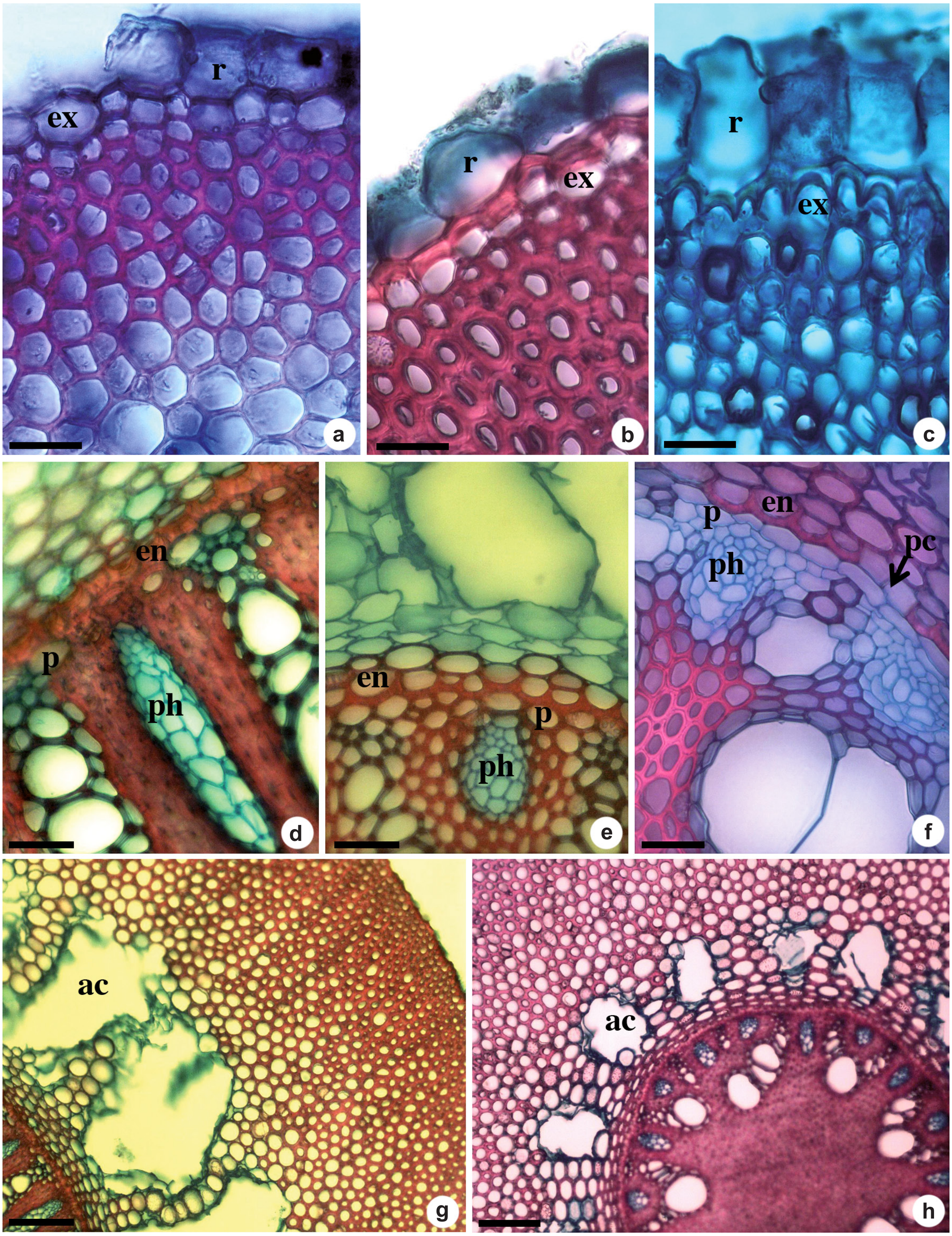

Figure 2 – a-h. Transverse sections of *Geonoma* roots – a-c. details of the rhizodermis and exodermis – a. *G. undata* (*densa* morphotype); b. *G. lehmannii*; c. *G. paraguanensis*; d-f. details of the endodermis and pericycle – d. *G. deversa*; e. *G. simplicifrons*; f. *G. orbygniana*; g. cortex in *G. deversa* (indicated with brackets), note large air channels; h. *G. lehmannii*, note small air channels. (ac = air channels; en = endodermis; ex = exodermis; pc = passage cells; ph = phloem; p = pericycle; r = rhizodermis). Bars: a-f = 30 μm; g, h = 100 μm.

Table 2 – Average values of anatomical variables in the roots of eight *Geonoma* species and two morphotypes.

Variables	***G. deversa* subsp. *deversa***	***G. lehmannii* subsp. *lehmannii***	***G. orbignyana* subsp. *orbignyana***	***G. paraguanensis***	***G. pinnatifrons* subsp. *pinnatifrons***	***G. simplicifrons***	***G. spinescens***	***G. undata* subsp. *undata* (*densa* morphotype)**	***G. undata* subsp. *undata* (*undata* morphotype)**
					Epidermis				
Thickness (µm)	19.5	35	32.5	52.5	20	19.5	32.5	30	32.5
					Fundamental System				
Number of cortex layers	44	32	32	50	33	46	43	45	47
Cortex thickness (µm)	930	560	610	1.010	520	730	610	860	840
Number air spaces	21	13	17	20	14	20	23	18	21
Maximum length air spaces	360	100	150	360	110	180	95	240	350
					Vascular Cylinder				
Cylinder vascular diameter (µm)	1,300	520	860	1,030	790	970	840	800	1,260
Number of xylem arches	29-34	19	18	23	20-26	32-40	29-32	22-25	38-41
Number of metaxylem vessels/arch	2-5	3-6	3-8	4-6	1-3	4-6	2-5	2-5	2-4
Inner diameter of wide metaxylem vessels considering the largest axe (µm)	55.5	42.5	84	72	76.5	56	39	71.5	97
Maximum length of the phloem strands (µm)	150	50	102.5	137.5	85	75	65	113	137
Pith diameter (µm)	610	270	390	480	370	650	570	480	820

G. paraguanensis (Fig. 4d) one or two metaxylem vessels distributed in the cylinder central region were evident. This area was wide in *G. undata* (*undata* morphotype) and *G. simplicifrons*, and narrow in *G. lehmannii* and *G. pinnatifrons*.

The response to the histochemical test for lignin detection of the root sections on the studied species was positive, in the exodermis, parenchyma external cortical region and even more internal portions, and in the endodermis and pericycle, when they have thick walls; in the xylem this compound was also detected.

All species showed a positive reaction for the fat test in the exodermis, in thin-walled endodermal cells or in the internal tangential wall of cells of this tissue that have U-shaped thickening and in some cells of cortical parenchyma in *G. undata* (*densa* morphotype) and in *G. orbignyana*.

Geonoma lehmmanii, *G. spinescens* y *G. undata* (morphotype *undata*) were the only species where the presence of tannins in parenchymal cortical cells near the endodermis was recorded; in the rest of the species the reaction was very scarce, located in parenchymal cells associated with xylem.

Discussion

The general anatomical features observed in roots of *Geonoma* are in congruence with those pointed out by Tomlinson (1961), Seubert (1998a) and Tomlinson *et al*. (2011). Nonetheless, our study highlights some important and non-yet reported differences at the species level.

The rhizodermis was significantly thicker in the narrow endemic *G. paraguanensis* (over 50 µm) with respect to the rest of the species, for this palm this could be interpreted as an important ecological adaptation associated with water storage, as this species grows under full sun conditions, exposed on rocky escarpments of the Santa Ana Mountain, permanently exposed to strong winds and high day-night temperature variation. According to several authors (*i.e.*, Esau 1959) one of the main characteristics of the rhizodermis is the development of root hairs; however, our study on *Geonoma* indicated that they are not present in the group. Seubert (1998a) pointed out that unlike Coryphoideae and Ceroxyloideae,

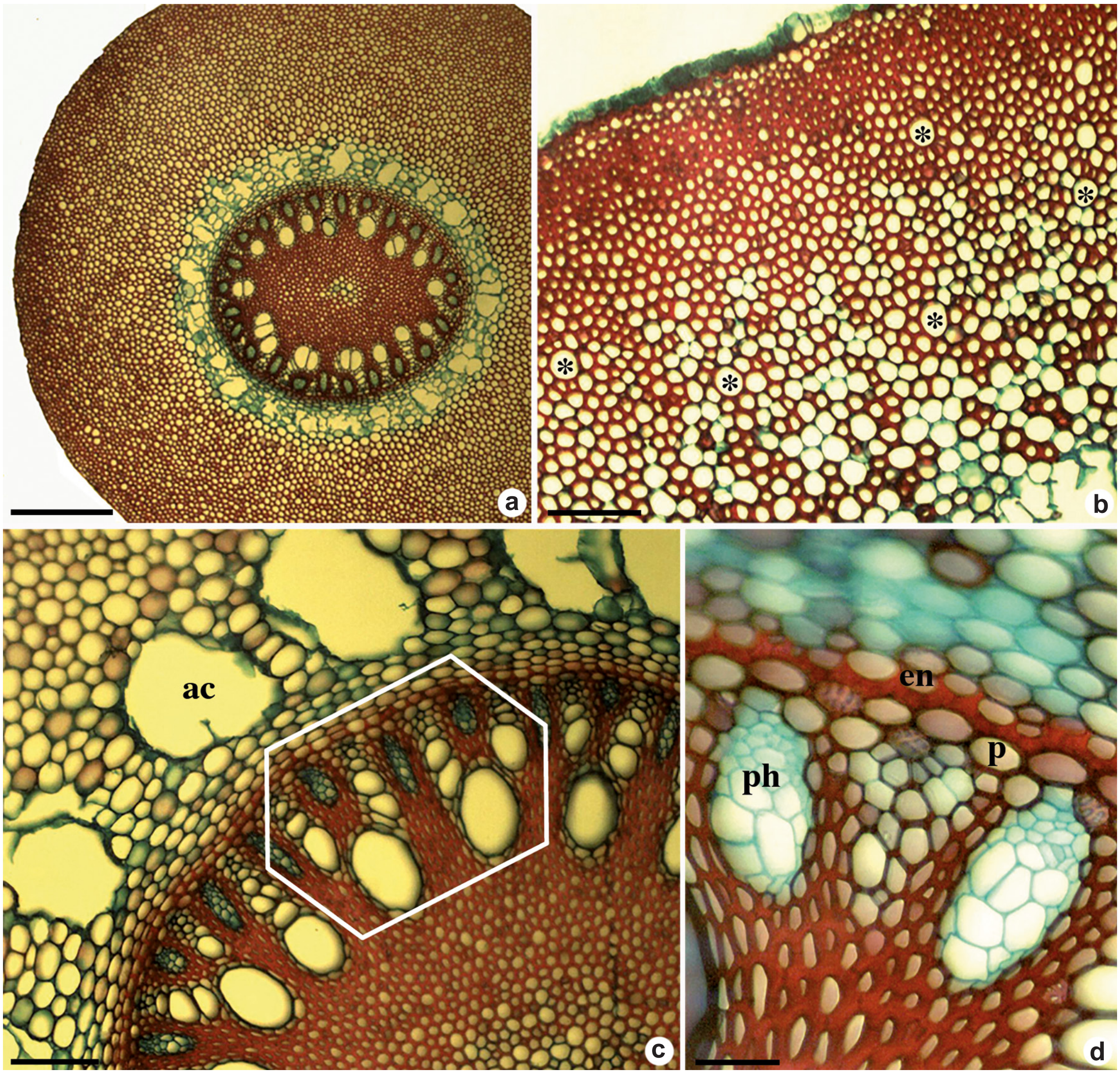

Figure 3 – a-d. Transverse sections of *Geonoma* roots – a. general view of the root of *G. spinescens*; b. *G. undata*, *undata* morphotype note rounded cells (indicated with asterisks); c. *G. simplicifrons*, note "V" shaped xylem arches (inside an hexagon); d. *G. undata* (*densa* morphotype), observe elongate phloem strands. (ac = air channel; en = endodermis; p = perycicle; ph = phloem). Bars: a = 300 µm; b,c = 100 µm; d = 30 µm.

these appendages are apparently lacking in all Arecoideae. On the other hand, Tomlinson (1961) noted for palm roots in general the development of a hairy layer is only present in very thin, high order roots.

The thin-walled exodermis observed by us in *G. undata* (*densa* morphotype), is not in congruence with previous studies (*i.e.*, Tomlinson 1961; Seubert 1998a; Tomlinson *et al*. 2011), in which thick-walled cells composing this layer were observed. Likewise, on *G. paraguanensis* and *G. undata* (*undata* morphotype) the thickness of these strata is uneven, since it is more evident on external tangential and radial walls, showing an inverted "U" shape. The thickening of the cell walls in this layer can be linked to the protection against dehydration and attack of pathogens (Enstone *et al*. 2003).

The cortex parenchyma was variable among species with respect to thickness, number of layers and degree of sclerotization, being the external cells more important regarding these features. Michael & Ehwal (2010) indicate that type of histology may reduce water loss and control the radial flow and nutrients. The presence of abundant intercellular spaces of variable size, also called air channels, is remarkable and according to Seubert (1998a) may have a lysigenous origin. Variability in the size of the air channels in a species depends on the level of intensity of the process that created them (Smirnoff & Crawford 1983). Roots of plants thriving in humid environments like the

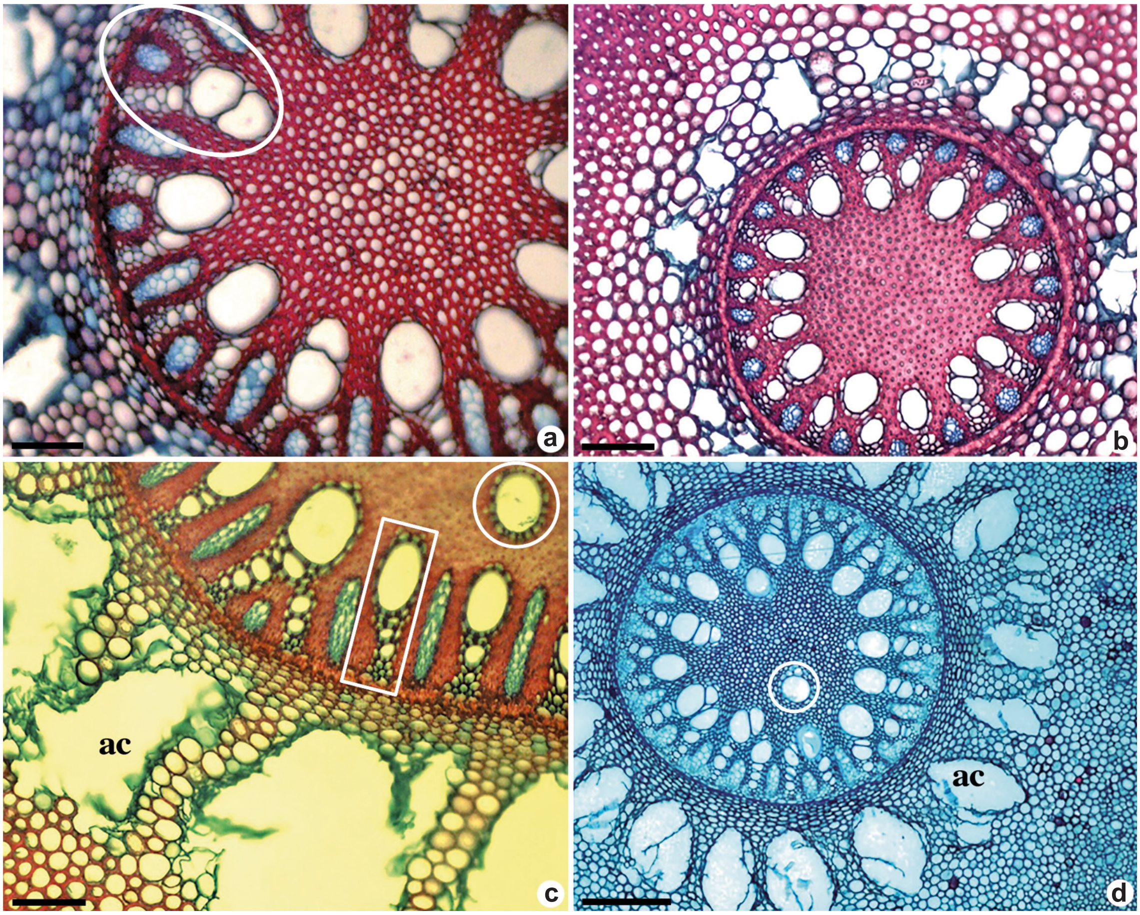

Figure 4 – a-d. Transverse sections of *Geonoma* roots – a. *G. undata* (*densa* morphotype), note "Y" shaped xylem arches (inside an oval); b. *G. lehmannii*, short phloem strands (indicated with arrowheads); c. *G. deversa*, note sclerified cells in septa (indicated with arrow), xylem arch in the shape of "I" (inside a rectangle) and metaxylem element in the pith (inside a circle); d. *G. paraguanensis* with a metaxylem element in the pith (inside a circle). ac = air channel. Bars: a-c = 100 µm; d = 300 µm.

ones observed by us in the cloud forest of the Venezuelan Coastal Range, frequently develop a spongy parenchyma, with a high number of intercellular spaces, essential for aeration (Flores-Vindas 1999). Most studied taxa grow in the understory, benefiting from almost constant environmental and soil humid conditions; the exception is the narrow endemic *G. paraguanensis* which grows in full sunny-exposed conditions. The arrangement of parenchyma cells close to the endodermis in radially organized concentric layers, which could indicate activity of a primary thickening meristem in those roots. Menezes *et al*. (2005) studied root anatomy in species from three different clades of monocotyledons, including Poales such as *Cephalostemon riedelianus* Körn (Rapateaceae), *Cyperus papyrus* L. (Cyperaceae), Alismatales, such as *Lagenocarpus rigidus* (Kunth) Nees, *L. junciformis* (Kunth) Kuntze (Cyperaceae), *Echinodorus paniculatus* Micheli (Alismataceae) and Zingiberales *Zingiber officinale* Roscoe (Zingiberaceae). These authors propose a new interpretation of the primary thickening in the group based on their observations of the presence of endodermis with meristematic activity in the roots of all these species and stated that the endodermis produces parenchyma in a centrifugal way.

The presence of a thick-walled endodermis may act as a physiological barrier restricting apoplastic diffusion of solutes from the cortex to the vascular cylinder (Flores-Vindas 1999). This feature is common in palms, but also recorded in many other monocotyledons (Tomlinson 1961). In all studied taxa, the endodermis walls were thick and "U-shaped". The thickening pattern of the secondary wall in the endodermis is one of the few informative anatomical characteristics that could by analyzed from a phylogenetic perspective (Tomlinson 1961; Seubert 1998a; Tomlinson *et al*. 2011). Two main features can be identified studying cross sections of the endodermis: 1) radial and inner tangential cell walls, unevenly thickened in -U-shape, 2) evenly thickened walls in an O-shape, the first one being regarded as synapomorphic, and the latter plesiomorphic for the family (Tomlinson *et al*. 2011). The presence of passage cells, as observed by us in *G. spinescens* and *G. orbignyana*, is an infrequent condition in palms (Tomlinson 1961). These thin-walled cells, located in front of the xylem arches, allow water and dissolved substances to pass (Roth 1976). It is important to highlight that the current investigation focused on first order roots, therefore they do not have a significant absorption function, as this is usually linked to higher order roots (Tomlinson 1961). The presence of passage cells in the roots of the above mentioned species could be considered of taxonomic value for the group, but this could be only confirmed with the inclusion of more taxa in a similar structural analysis.

The presence of fungal structures in the rhizodermis of *G. paraguanensis* was not unexpected, since mycorrhizal symbiosis has been usually reported in the palm family. In tropical forests conditions, where competition for light, nutrients and water can be high, association with arbuscular mycorrhizas may influence the capability of nutrient absorption (Zobel *et al*. 1997; Allen *et al*. 2003). The fungal structures identified in *G. paraguanensis* may be an adaptation for the harsh habitat where this species thrive: strongly subjected to strong wind, steep slopes and frequent nutrient loss could benefit the development of this type of symbiotic relationship. Palms are perennial monocots and their roots tend to form mycorrhizas (Zona 1996; Broschat & Elliott 2009). Nonetheless, there is little information about this association, probably due to the fact that palm roots have abundant lignified tissues and silica bodies, which makes the investigation difficult from a methodological perspective (Tomlinson 1990).

As previously indicated the collected roots where classified as first order roots, therefore, they can be considered as non-functional with respect to absorption. In old roots, pericycle cells can develop secondary walls (Flores-Vindas 1999) and this could partially explain the presence of a sclerified pericycle, as observed by us in *G. deversa*, *G. lehmannii*, *G. simplicifrons*, *G. spinescens* and *G. undata* (*densa* morphotype).

Considering the stele types in palm roots proposed by Cormack (1896), Drabble (1904) and Tomlinson (1961), most of the studied species can be identified as type 2, which is characterized by a cylindrical stele, with a pith surrounded by thin walls with parenchyma cells. Likewise, the stele configuration of *G. deversa* and *G. paraguanensis* corresponds to type 3, due to the presence of metaxylem vessels isolated in the pith. On the other hand, according to the simplified classification of Seubert (1998a), all species of this study would be included into vascular cylinder type 1, identified by her as the "normal" vascular cylinder.

In the same way, the presence of arches with shared metaxylem elements, "V-shaped" in most species and of "Y-shaped" restricted to *G. undata* (*densa* morphotype), matches with the observations of Cormack (1896) and Tomlinson (1961) and regarded by these authors as the most common condition in palms. However, there were also conspicuous arches where no metaxylem elements were shared (shaped as an "I"), a condition that has been previously identified in the seedling roots of *Astrocaryum* palms (Martel 2012), but otherwise reported as common elsewhere in monocotyledons (Seago & Fernando 2013). The wide phloem areas observed in *G. deversa*, *G. undata* (*undata* morphotype) and *G. paraguanensis* and the large diameter of metaxylem vessels registered on *G. undata* (*undata* morphotype), *G. orbignyana* and *G. pinnatifrons*, may be associated to a significant increase in the transportation of water, nutrients and reserve substances (Patrick & Offler 2001). Differences among these variables were used by Fatima *et al*. (2014) to separate 22 cultivars of *Phoenix dactylifera* L., but their promising use at higher taxonomic levels including species and subspecies requires further exploration in the palm family.

Two secondary metabolites, lignin and fats, were registered in all *Geonoma* roots. Lignin is the most abundant component of the wall cell, after cellulose, which appears during the formation of the secondary walls. This substance allows the strengthening and stiffness of the wall cell, giving the cell greater capacity for compressive strength (Lindorf *et al.* 2006). Fats and related substances are found in almost all living cells (Roth 1976). The presence of these substances in the exodermis, endodermis and even in the cortical parenchyma cells in *Geonoma*, represents an advantage in terms of the water economy of the group, since this hydrophobic substance confers greater resistance against apoplastic water loss (Dickinson 2000).

The accumulation of tannins in the parenchyma cells near the endodermis and pith of *G. lehmmanii* and *G. undata* (*undata* morphotype) can be associated with the synthesis of some metabolite that facilitates water retention and/or the protection of metabolic pathways, as indicated by Pyykkó (1966) and Casierra-Posada & Rodríguez (2006).

Seubert (1998b) pointed out that root anatomy allows us to clearly differentiate genera within Arecaceae; nonetheless, infra-generic differences appear to be less evident to detect. In this study, it was possible to differentiate species of *Geonoma* based on their root structure. Some of the variables that support differentiation are: thickening of exodermis walls, parenchyma cells of round shape in the cortex, passage cells in the endodermis, shared xylem arches in the shape of a "V" or a "Y", metaxylem vessels scattered in the pith, among others.

We are aware that our study remains preliminary and that supplementary anatomical features of vegetative and reproductive organs are needed to understand their evolutionary implication, relying on a stable molecular phylogenetic framework (*i.e.*, Loiseau *et al*. 2019).

Geonoma undata (*densa* morphotype) can be distinguished by the differentiation of metaxylem vessels forming a "Y", while *G. undata* (*undata* morphotype) presents parenchyma cells of circular contours. These characteristics are considered useful to distinguish morphotypes, since in the case of the first, the trait was presented in roots collected from two different states (Aragua and Falcon), which seems to indicate its stability, while the second feature was evident only in the morphotype of that species. Henderson (2011) successfully solved important systematic conflicts within *Geonoma*, in many cases supported by the investigation of Loiseau *et al.* (2019). Nonetheless, the infraspecific delimitation for categorizing correctly the so called complexes of species requires further study. *G. undata* is considered by Henderson (2011) as the second more variable specie of the group. With this study we are providing root anatomical features that allow distinguish the two of the morphotypes included in this species.

On the other hand, *G. paraguanensis*, a taxon not treated in Henderson's monography of the genus presents unique characteristics that allow its clear differentiation and may support its recognition as an isolated and well-defined taxonomic entity. These features include radical exodermis with external walls thickened in the shape of an inverted "U", and presence of isolated metaxylem vessels occupying the central region of the cylinder. This last feature was also observed in *G. deversa.*

The use of distinctive anatomical features from the root led to the delimitation of two morphotypes within the *Geonoma undata* complex, suggesting that our approach may be regarded as a promising identification tool at infraspecific taxonomic ranks in highly diverse palm genera.

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