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.

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).
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 Geonomatinae 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 m above sea level in montane rainforest, in the Coastal Cordillera in Venezuela at 400–1,600 m above sea level 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 m above sea level, and to the south of the country at 100–1,200 m above sea level 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 Geonomatinae tribe (previously known as the Geonomiae), 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 et 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. paraguianensis which was not considered by this author but remains an intriguing, 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 Guaracacal, road from Bocono to Guaracacal, SE from Bocono, via The antennas. | Montane rainforest | 2450             | 132847           |
|                                            |                                      |                                               |               |                  | 132848           |
|                                            |                                      |                                               |               |                  | 132849           |
|                                            |                                      |                                               |               |                  | 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           |
|                                            |                                      |                                               |               |                  | 132855           |
|                                            |                                      |                                               |               |                  | 132856           |
|                                            |                                      |                                               |               |                  |                  |
| *Geonoma paraguanensis* H. Karst.          | Briceño A, Castro M & Muñoz D         | Falcon, Venezuela, Mun. Carirubana, Peninsula of Paraguan, summit of the hill Santa Ana. | Cloud forest on summits of isolated mountains, exposed to high winds | 836              | 132836           |
|                                            |                                      |                                               |               |                  | 132837           |
|                                            |                                      |                                               |               |                  | 132838           |
|                                            |                                      |                                               |               |                  | 132839           |
|                                            |                                      |                                               |               |                  | 132840           |
|                                            |                                      |                                               |               |                  | 132841           |
|                                            |                                      |                                               |               |                  |                  |
| *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  | 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           |
| (densa morphotype)                     |                             |                                                                          |                      | 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 Irarrory, Rancho Grande, 100-200 m from the Paso de Portachuelo towards the Pico Periquito | Montane rainforest  | 1132             | 132868           |
| Geonoma undata Klotzsch subsp. undata  | Briceño A & Rodríguez J     | Trujillo, Venezuela, Mun. Bocono, between Bocono and El Batatal          | Montane rainforest  | 1863             | 132856           |
| (undata morphotype)                    |                             |                                                                          |                      | 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, pectocellulosic 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. paraguauensis.

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. paraguauensis (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. paraguauensis 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. paraguauensis 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. paraguauensis and thinner in G. pinnatifrons; nonetheless, the smallest number of cell layers were observed in G. orbignyana and G. lehmannii (Tab. 2). G. paraguauensis 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. paraguauensis 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. paraguauensis, 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                                      | Epidermis | Fundamental System | Vascular Cylinder |
|------------------------------------------------|-----------|--------------------|-------------------|
| Thickness (µm)                                 | 19.5      | 35                 | 32.5              |
| Number of cortex layers                        | 44        | 32                 | 32                |
| Cortex thickness (µm)                          | 930       | 560                | 610               |
| Number air spaces                              | 21        | 13                 | 17                |
| Maximum length air spaces                      | 360       | 100                | 150               |
| Cylinder vascular diameter (µm)                | 1,300     | 520                | 860               |
| Number of xylem arches                         | 29-34     | 19                 | 18                |
| Number of metaxylem vessels/arch               | 2-5       | 3-6                | 3-8               |
| Inner diameter of wide metaxylem vessels       | 55.5      | 42.5               | 84                |
| Maximum length of the phloem strands (µm)     | 150       | 50                 | 102.5             |
| Pith diameter (µm)                             | 610       | 270                | 390               |

*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.

*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*.

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 lehmannii*, *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 = perycycle; 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

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**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 be 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 symbioses 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. deerassa*, *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. deerassa* 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*
Briceño A, Jáuregui D & Stauffer F, may be associated to a significant undata, represents an advantage in (2014) to separate 22 cultivars of undata and morphotype), matches with the observations, a taxon densa morphotype) can be and the large diameter of metaxylem vessels registered on 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 Pyykkö (1966) and Casiera-Posada & Rodriguez (2006).

Seubert (1998b) pointed out that root anatomy allows us to clearly differentiate genera within Arecales; 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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