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Plant anatomy: history and future directions

Comparative leaf anatomy of the nothospecies ×*Butyagrus nabonnandii* (Arecaceae) with its parental species

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Abstract

Anatomical studies of the leaf blade have been used to complement the morphological data and aid circumscription and identification in Arecaceae. The hybrid palm *×Butyagrus nabonnandii* results from the natural cross between *Butia odorata* and *Syagrus romanzoffiana*. This study aimed to verify if the leaf anatomy can help identify the hybrid and differentiate it from the parental *taxa*. Samples from the middle portion of the pinnae were collected and subjected to the usual techniques for light microscopy. Three portions of the pinnae were sampled: margin, intermediate region, and midrib. The main characteristics considered were the arrangement of fibre and vascular bundles. Pinnae anatomy proved to be useful in the identification of *×B. nabonnandii*, because it showed a distinctive pattern, highlighting the importance of leaf anatomy in differentiating the hybrid from parental *taxa*. The pinnae anatomy of the hybrid was a combination of parental taxa's characters, similar to the external morphology.

Key words: *Butia*, hybrid palm, plant anatomy, *Syagrus*, taxonomy.

Resumo

Estudos anatômicos da lâmina foliar têm sido usados para complementar os dados morfológicos e ajudar na circunscrição taxonômica em Arecaceae. A palmeira híbrida *×Butyagrus nabonnandii* é o resultado de cruzamento natural entre *Butia odorata* e *Syagrus romanzoffiana*. Objetivou-se verificar se a anatomia foliar pode ajudar na identificação do híbrido, bem como diferenciá-lo dos *taxa* parentais, ajudando em possíveis dúvidas sobre a identificação taxonômica envolvendo esses três *taxa*. Amostras da porção mediana de pinas foram coletadas e sujeitas a técnicas usuais para microscopia óptica. Três regiões da pina foram amostradas: margem, região intermediária e nervura mediana. O arranjo das fibras e feixes vasculares foram os principais caracteres considerados. A anatomia da pina provou ser útil na identificação de *×B. nabonnandii*, porque mostrou um padrão distinto, demonstrando a importância da anatomia foliar na diferenciação do híbrido dos *taxa* parentais. A anatomia do híbrido revelou uma combinação de caracteres de ambos os parentais, da mesma maneira como é observado na morfologia externa.

Palavras-chave: *Butia*, palmeira híbrida, anatomia vegetal, *Syagrus*, taxonomia.

Introduction

In Brazil, there are 87 genera, 388 species and 18 natural hybrids of Arecaceae, the most of them from interspecific crosses (Lorenzi 2010; Noblick 2010a,b, 2017a; Soares *et al*. 2023). Although rare, natural hybrids from intergeneric crosses are also observed. The most common intergeneric hybrid among palms originate from *Syagrus romanzoffiana* (Cham.) Glassman and species belonging to the *Butia* genus, creating

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the nothogenus ×*Butyagrus* Vorster, with three nothospecies recorded to Brazil: ×*B. nabonnandii* (Prosch.) Vorster, ×*B. alegretensis* K. Soares, and ×*B. paranaensis* Engels, T.A. Meyer & K. Soares (Noblick 2010a; Soares *et al*. 2014a; Engels *et al*. 2021).

×*Butyagrus nabonnandii* is the result of a cross between *B. odorata* (Barb. Rodr.) Noblick and *S. romanzoffiana*, and it occur in far southern Brazil and in the southeastern region of Uruguay (Noblick 2010a, 2011; Rivas *et al*. 2017; Oliveira-Neves *et al*. 2022; Rosa *et al*. 2023). However, artificially bred specimens of this hybrid have been cultivated in Europe and in the USA since the end of the 19th century (Tournay 2009).

To date, plant morphology has been the only taxonomic tool used to identify Arecaceae hybrids in Brazil, indicated by the presence of intermediate characters of each parental species (Noblick 2012; Soares *et al*. 2014b; Soares & Assis 2015; Silveira *et al*. 2022). Regarding ×*B. nabonnandii*, the external morphology helps identify reproductive specimens, but this tool is not equally efficient for non-reproductive specimens. Furthermore, herbaria vouchers of ×*B. nabonnandii* are challenging to identify using solely morphology or based on incomplete labels. Such difficulty was also reported by Noblick (2013) for *Syagrus*, whose pressed and dried specimens appear similar but show characters in the field that are not well preserved on herbarium sheets or not recorded on the labels. However, leaf anatomy is well preserved after the pressing and drying process, even in older samples (see Fig. 3 in Firmo *et al*. 2021), allowing the differentiation of morphologically similar species not only on a herbarium sheet but also in the field.

In Arecaceae, leaf anatomical studies have helped identify several species and infer systematic relationships within the family (Silva & Potiguara 2008; Sanín & Galeano 2011; Noraini *et al*. 2012; Martins *et al*. 2015; Defaveri *et al*. 2015; Kikuchi *et al*. 2016; Pinedo *et al*. 2016; Vianna 2017; Vianna *et al*. 2017; Silva & Lemos 2020). In *Butia* and *Syagrus*, several anatomical studies became prominent along with morphological data to identify and circumscribe species within these two genera (Glassman 1970; Tomlinson *et al*. 2011; Noblick 2013, 2014, 2017b, 2018; Sant'Anna-Santos *et al*. 2015, 2018, 2023a,b,c; Sant'Anna-Santos 2021; 2023; Firmo *et al*. 2021; Noblick & Sant'Anna-Santos 2021).

For instance, the *Butia* genus was first considered a section of *Syagrus* by Glassman (1970). Later, he performed a systematic survey of the leaf anatomy in *Syagrus* (Glassman 1972), which prompted him to reinstate *Butia* as a valid genus (Glassman 1979) - based on a distinctive pinna anatomy, in which the adaxial and abaxial leaf surfaces and mesophyll are alike (Horn *et al*. 2009). Therefore, disregarding the polarity of the vascular bundles, the pinna anatomy of *Butia* is about mirror-image equivalents on cross-sections (Horn *et al*. 2009). The so-called mirrored mesophyll in the literature is rather uncommon in Arecaceae but is the most striking pinna character to identify the *Butia* genus (Tomlinson *et al*. 2011; Noblick 2014; Sant'Anna-Santos *et al*. 2015; 2018; Noblick & Sant'Anna-Santos 2021; Sant'Anna-Santos 2021, 2023). In *Syagrus*, the mirrored mesophyll has never been observed (Noblick 2013, 2017a, 2018; Firmo *et al*. 2021; Sant'Anna-Santos *et al*. 2023a,b).

Therefore, this study aimed to evaluate whether the leaf anatomy in ×*B. nabonnandii* can be a valuable tool for identifying the hybrid and differentiating it from its parental species.

Materials and Methods

Specimens of ×*B. nabonnandii*, *B. odorata* and *S. romanzoffiana* were collected in five municipalities of Rio Grande do Sul state: Venâncio Aires, Porto Alegre, Cachoeira do Sul, Manoel Viana and São Vicente do Sul (Fig. 1). Vouchers were deposited in the Bruno Edgar Irgang Herbarium (HBEI) at the Universidade Federal do Pampa (UNIPAMPA). Complete voucher information is available as supplementary material (Tab. S1, available at <https://doi.org/10.6084/m9.figshare.25475860.v1>).

Leaf samples for anatomical analysis were collected from five specimens of *B. odorata* and *S. romanzoffiana* at each municipality and a total of 17 specimens of ×*B. nabonnandii*. The leaf of palms is pseudo-compound and dissected, and in the present work, we adopted the long-established term "pinna" to refer to each unit, following the terminology adopted by Dransfield *et al*. (2008). For the anatomical data, the pinnae were sampled from the middle of the leaves and sectioned into three portions: leaf margin, midrib portion, and the intermediate region between the former and the latter (Firmo *et al*. 2021). The previously collected dried samples were subjected to a herborisation reversion process adapted from Meira & Martins (2003), then softened according to Firmo *et al*. (2021). Next, they were dehydrated and stored in

70% ethyl alcohol. After that, the samples were freehand-sectioned with a disposable razor blade following Firmo *et al*. (2021). The microscopic features were measured and examined by bright-field microscopy using an Axio Imager A2 microscope (Carl Zeiss, Germany) equipped with Axiocam MRc (Carl Zeiss, Germany) and the ZEN 2 v 4.0 software. The distribution of the three sampled *taxa* was mapped using QGIS v.3.10.13 (QGIS.org 2020), and municipalities data were taken from IBGE (2018).

The qualitative anatomical characters examined in the present study follow Glassman (1972), Noblick (2013, 2017b), and Noblick & Sant'Anna-Santos (2021). For the pinnae margin and intermediate region, the following characteristics were analysed: (1) vascular bundles with exaggerated fibrous sheath; (2) vascular bundles arrangement and location in the mesophyll; and (3) location and size of non-vascular fibre bundles (henceforth fibre bundles). For the midrib, the following characteristics were analysed: (1) shape; (2) number of collateral bundles; (3) connection to the hypodermis, (4) abaxial projection of the fibrous ring (MFR); (5) accessory bundles partially or completely surrounding the MFR; and (6) expansion tissue. The terminology adopted here for leaf anatomical descriptions follows Noblick (2013, 2017b) for the margin and Glassman (1972), Sant'Anna-Santos *et al*. (2018) and Firmo *et al*. (2021) for midrib and intermediate regions. The midrib shapes in cross-section used for *Butia* and *Syagrus* - truncate, round and triangular - were here adopted to characterise the midrib of ×*B. nabonnandii*, *B. odorata* and *S. romanzoffiana* (see Glassman 1972; Sant'Anna-Santos *et al*. 2015, 2018; Firmo *et al*. 2021; Sant'Anna-Santos 2021, 2023).

Results and Discussion

Intermediate region

Two patterns of arrangement of fibre bundles and vascular bundles were observed in ×*B. nabonnandii*. The most common is pattern 1, characterised by fibre bundles attached to the adaxial hypodermis, tertiary vascular bundles attached to both surfaces (adaxial and abaxial) and rare minute fibre bundles (Fig. 2a). The pattern 2 is characterised solely by tertiary vascular bundles attached to both surfaces (Fig. 2b), and this pattern was observed only in the population from Venâncio Aires municipality.

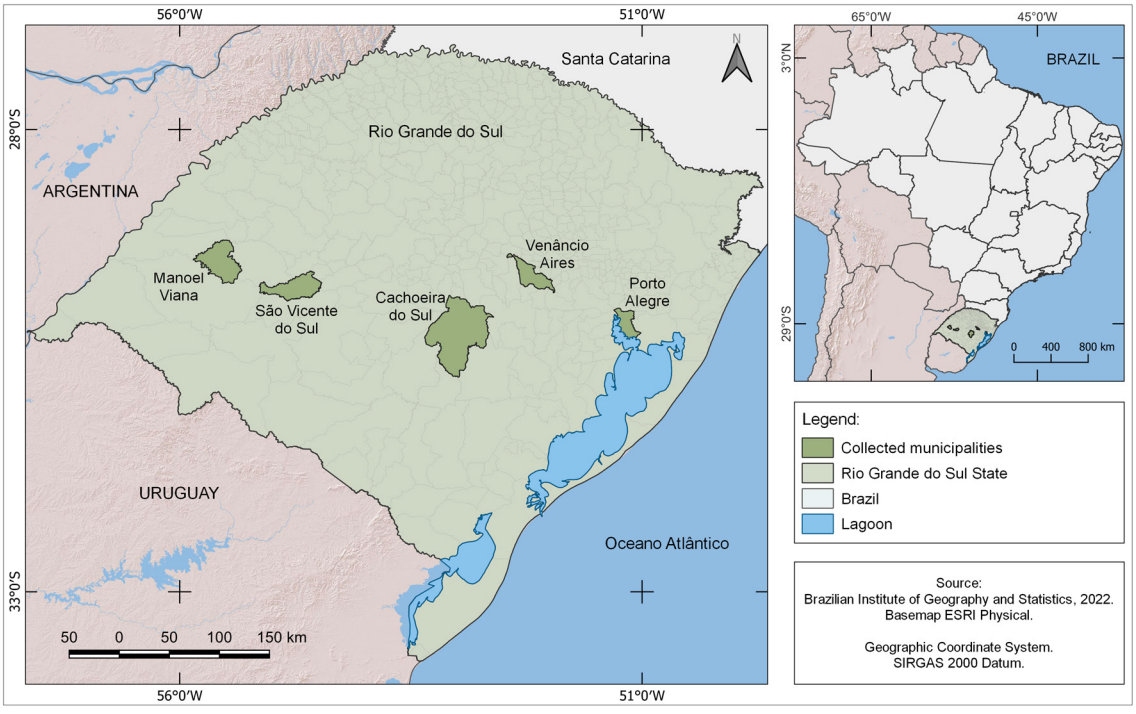

Figure 1 – Localization of the municipalities where the specimens of ×*Butyagrus nabonnandii*, *Butia odorata* and *Syagrus romanzoffiana* were collected in Rio Grande do Sul state, Brazil.

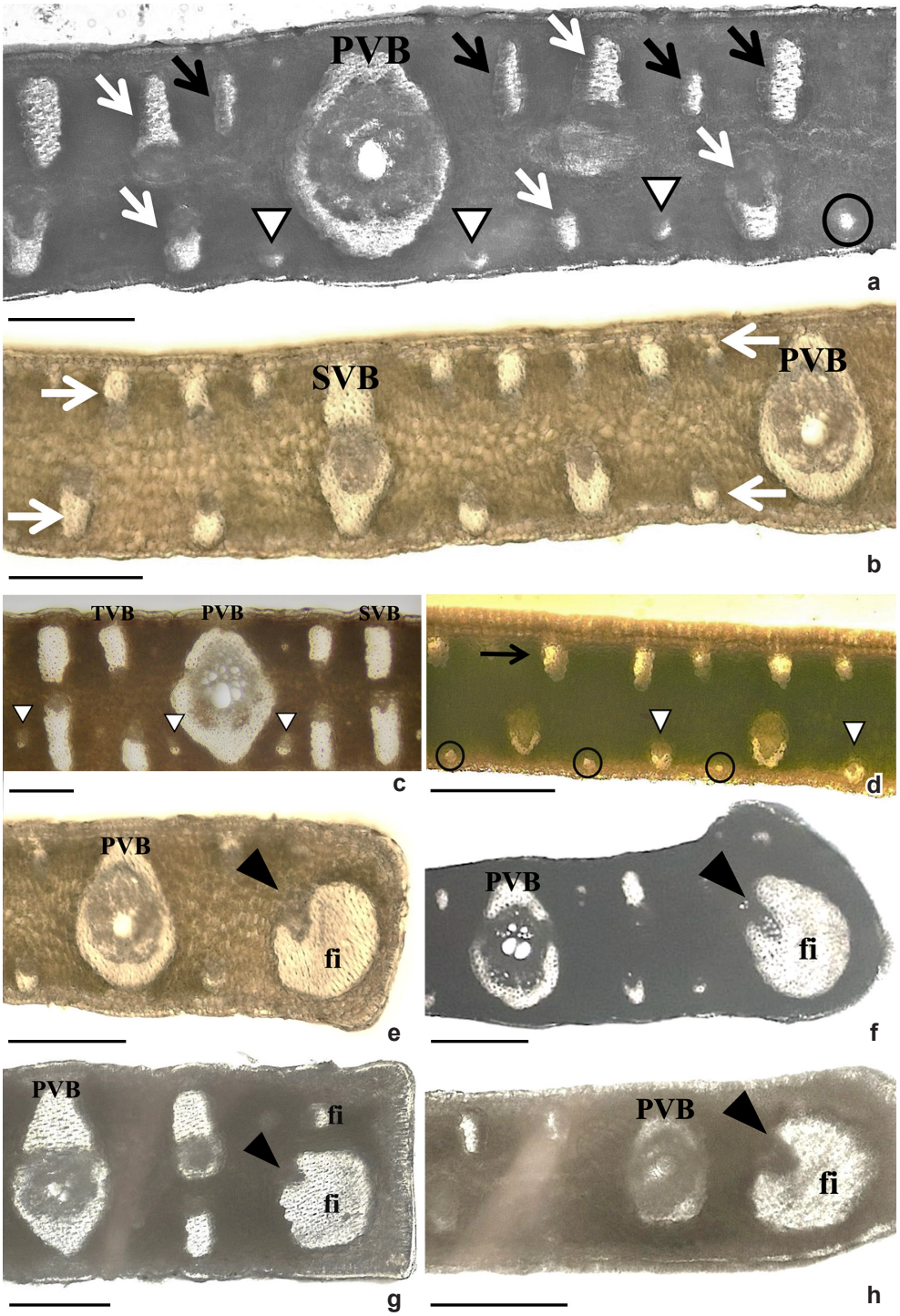

Figure 2 – a-b, e-f. Pinnae anatomy of ×*Butyagrus nabonnandii*. c, g. *Butia odorata*. d, h. *Syagrus romanzoffiana* under light microscopy (cross sections). a-d. intermediate region. e-h. margin. a-b. pattern 1 and 2 of fibre and vascular bundles arrangement, respectively. c. mirrored anatomy. d. non mirrored anatomy. e, g-h. quadrangular shape. f. deltoid shape. (white arrows = tertiary vascular bundles; black arrows = fibre bundles on the adaxial surface; white arrowheads = minute vascular bundles; black circles = fibres on the abaxial surface; black arrowheads = vascular bundle with an exaggerated fibrous sheath in the leaf margin; Fi = fibres; PVB = primary vascular bundle; SVB = secondary vascular bundle; TVB = tertiary vascular bundle). Scale bars = 200 µm.

Currently, 11 species of *Syagrus* possess different patterns in the pinnae anatomy of intermediate region (Noblick *et al*. 2014; Noblick 2017b; Sant'Anna-Santos *et al*. 2023a,b). It could indicate intra-specific variation within a single species or even a complex of several closely related unresolved species (Noblick 2017b).

The vascular arrangement in *B. odorata* is clearly mirrored because the vascular bundles on the adaxial side are more or less reflected on the abaxial side (Fig. 2c), as shown by Sant'Anna-Santos *et al*. (2015, 2018) and also observed in other *Butia* species (Noblick 2014). In specimens of *B. odorata* studied here, the abaxial surface possesses, near the primary vascular bundles, smaller tertiary vascular bundles, which are not attached to the hypodermis (Fig. 2c), corroborating previous descriptions (see Sant'Anna-Santos *et al*. 2015, 2018; Noblick & Sant'Anna-Santos 2021).

In *Syagrus*, the presence and relative abundance of fibre bundles on adaxial and abaxial surfaces were some of the criteria used by Glassman (1972) to separate groups within *Syagrus*. For example, *S. romanzoffiana* is characterised by the presence of fibre bundles attached only to the adaxial hypodermis (Glassman 1972; Noblick 2013, 2017b) (Fig. 2d). On the abaxial surface, minute fibre bundles and tertiary vascular bundles are observed in *S. romanzoffiana* (Fig. 2d) and ×*B. nabonnandii* also presented the same pattern (Fig. 2a). Other *Syagrus* species also presented the same fibre and vascular bundles arrangement on the abaxial surface (Glassman 1972; Noblick 2013, 2017b, 2018; Firmo *et al*. 2021; Sant'Anna-Santos *et al*. 2023a,b).

The fibre and vascular bundles arrangement of ×*B. nabonnandii* in the intermediate region is easily distinguishable from the parental *taxa*, considering that the two patterns presented by the hybrid are not observed in *S. romanzoffiana* and neither *B. odorata*.

Margin

In ×*B. nabonnandii*, it was observed only one tertiary vascular bundle with exaggerated fibrous sheath in the margin (Fig. 2e-f) and variation in the shape of the margin on cross-sections: quadrangular (Fig. 2e) and deltoid (Fig. 2f).

Butia odorata specimens here analysed showed a quadrangular margin with two tertiary bundles; the abaxial bundle has an exaggerated fibrous sheath compared to the adaxial bundle (Fig. 2g). These results are similar to those found by Sant'Anna-Santos *et al*. (2018) for *B. odorata* specimens collected in Tapes municipality (Rio Grande do Sul state, Brazil). Despite this congruence in *B. odorata*, the margin shape must be used cautiously since Sant'Anna-Santos *et al*. (2018) demonstrated that it is not a reliable character to distinguish some species of *Butia*.

Pinnae margin has identified *Syagrus* species effectively, showing variations in anatomical patterns of some species (Noblick 2013, 2017b; Noblick *et al*. 2014). Noblick (2013) developed an identification key based solely on anatomical characters of the pinnae margin for acaulescent *Syagrus* species because morphology alone could not identify certain species complexes. Noblick (2017b) discussed this variation in *taxa* of wide geographic distribution, such as *Syagrus glazioviana* Becc., and hypothesised that these differences could either represent intraspecific variation or mean that the species is, in fact, a complex of several closely related unresolved species. However, as shown by Sant'Anna-Santos *et al*. (2023a, b) in *Syagrus cabraliensis* (Noblick & Lorenzi) Sant'Anna-Santos and *Syagrus carvalhoi* B.F. Sant'Anna-Santos, narrow endemics could also show this variation.

In *Syagrus romanzoffiana*, for example, two margin patterns were observed by Noblick (2017b): the first in specimens collected in Brazil and the second in specimens collected in Paraguay. The *S. romanzoffiana* specimens studied here are similar to the specimens from Paraguay studied by Noblick (2017b), where the margin has a quadrangular shape and has only a single tertiary bundle with exaggerated fibrous sheath (Fig. 2h). This might be explained by the greater proximity of the collection areas of the present study to the territory of Paraguay. *Syagrus romanzoffiana* is one of the most widely distributed species in South America and is known to be polymorphic in response to differences in soil and altitude, which has been widely discussed in the literature (for a comprehensive review of this issue, see Noblick 2017a).

Midrib

In ×*B. nabonnandii*, the midrib is truncate because of the two tips that project outwards (sensu Sant'Anna-Santos *et al*. 2018), ranging from less (Fig. 3a) to more vertically elongated (Fig. 3b). The main vascular system is composed of 4 to 10 collateral bundles (Fig. 3a-b) and is surrounded by a continuous fibrous ring, projected abaxially and not connected to the abaxial hypodermis. Moreover,

accessory vascular bundles around the fibrous ring are present, surrounding it completely (Fig. 3a) or not (Fig. 3b), and at least one has an exaggerated fibrous sheath. Accessory vascular bundles are miniveins, which partially or completely surround the fibrous ring in the midrib (Noblick & Sant'Anna-Santos 2021). In addition, fibre bundles surround the fibrous ring, and they can also be present within the expansion tissue (not shown), as previously shown in *Syagrus* (see Fig. 4 in Firmo *et al*. 2021). In *Butia*, fibre bundles within the expansion tissue have not yet been observed (see Sant'Anna-Santos *et al.* 2015, 2018; Sant'Anna-Santos 2021, 2023). The expansion tissue is interrupted and is formed by three (Fig. 3a) to four (Fig. 3b) layers of expansion cells.

Butia odorata and *S. romanzoffiana* midribs present some similarities when compared to ×*B. nabonnandii*. The main similarities are observed in the midrib: the number of collateral bundles (more than three), continuous fibrous ring and an interrupted expansion tissue (Fig. 3c-d).

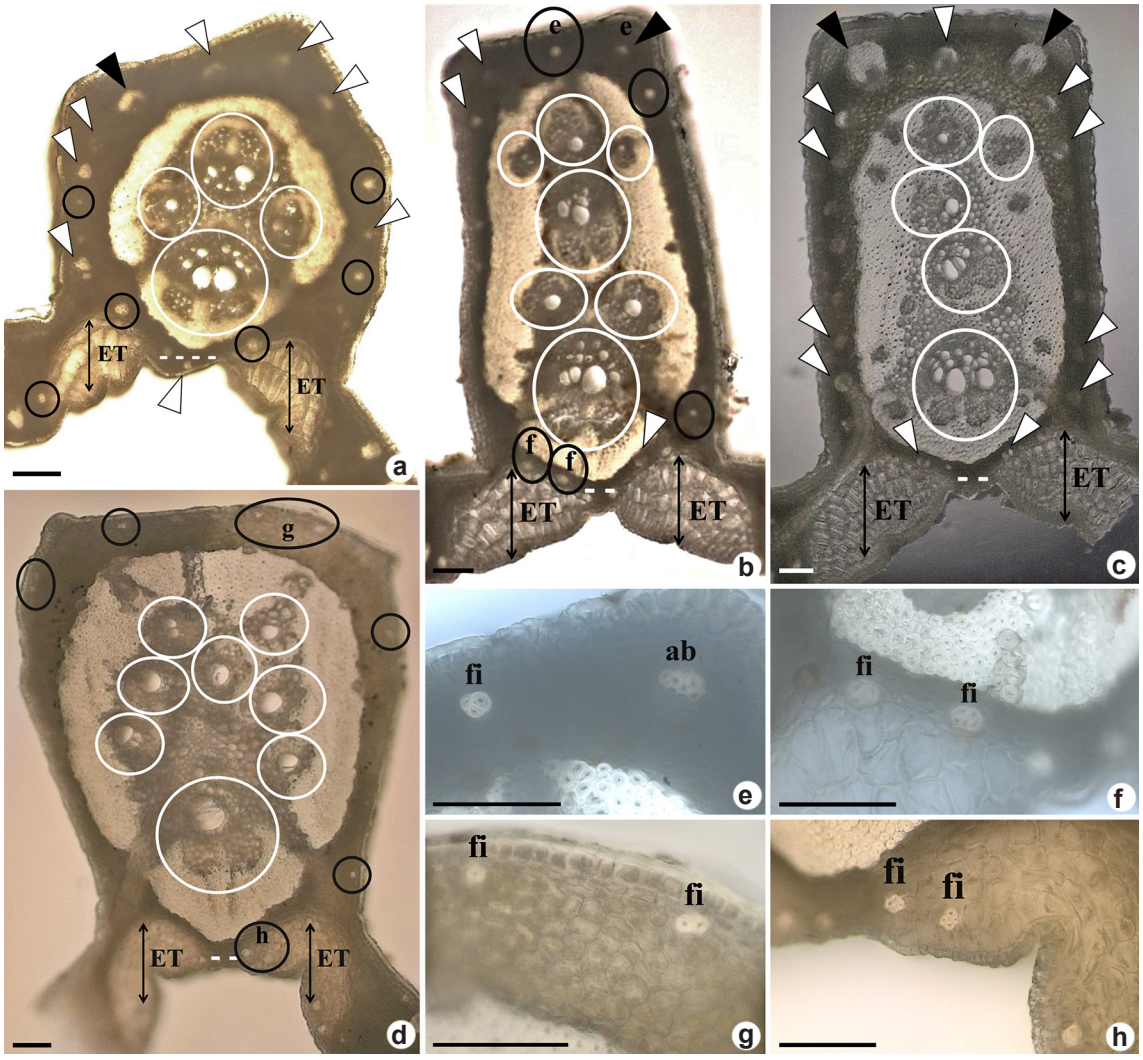

Figure 3 – a-h. Cross sections of midrib region under light microscopy a-b, e-f. ×*Butyagrus nabonnandii*. c. *Butia odorata*. d, g-h. *Syagrus romanzoffiana*. a-c. accessory bundles around the fibrous ring (white arrowheads); vascular bundles with sheath reiforcement (black arrowheads). a-b, d. nonvascular fibers around the fibrous ring and in the expansion tissue (ET) (black circles). a-d. expansion tissue interrupted (dotted white line); collateral bundles in the main vascular system (white circles). e. Detail of b: nonvascular fiber bundle (fi) and accessory bundle (ab) near the adaxial surface. f. detail of b: fibre bundles (fi) near the expansion tissue. g. detail of d: fibre bundles (fi) near the adaxial surface. h. detail of d: fibre bundles (fi) in the expansion tissue. Scale bars = 100 µm.

Several midrib characteristics have been useful for *Butia* and *Syagrus* taxonomy, such as size, shape, expansion tissue and fibrous ring characteristics, vascular bundles around the fibrous ring, and the number of vascular bundles in the main vascular system (see Glassman 1972; Sant'Anna-Santos *et al*. 2015, 2018, 2023a, b; Firmo *et al*. 2021; Noblick & Sant'Anna-Santos 2021; Sant'Anna-Santos 2021, 2023). For example, the presence of accessory bundles that completely surround the midrib fibrous ring is one of the main characters distinguishing *Butia odorata* from *Butia capitata* (Mart.) Becc. (Sant'Anna-Santos *et al.* 2015).

In *Syagrus*, *e.g.*, Firmo *et al*. (2021) suggested the existence of a new species from a very isolated mountain in Brazil, based on its geographical isolation associated with morphological and exclusive anatomical characters of the midrib (uniseriate adaxial hypodermis and a fibrous ring reaching the abaxial hypodermis). Recently, this new species was formally described as *Syagrus aristeae* B.F. Sant'Anna-Santos (Sant'Anna-Santos *et al*. 2023c).

In *B. odorata*, fibre bundles around the fibrous ring and within the expansion tissue were absent (Fig. 3c), corroborating with the previously showed by Sant'Anna-Santos *et al.* (2018). Only accessory bundles surrounding completely the fibrous ring were observed, with two of them showing sclerenchymatic sheath reinforcement in the adaxial surface (Fig. 3c). This last character is an important taxonomic character for *Butia* as shown by Sant'Anna-Santos *et al*. (2018). In general, the presence of fibre bundles in the midrib region was not observed in *Butia* (Sant'Anna-Santos *et al*. 2015, 2018; Noblick & Sant'Anna-Santos 2021), except in *B. buenopolensis* B. F. Sant'Anna-Santos (Sant'Anna-Santos 2021).

Regarding *S. romanzoffiana*, all specimens analysed here presented truncate midrib, and were observed only fibre bundles surrounding completely the fibrous ring and within the expansion tissue (Fig. 3d, 3g-h). In several species of *Syagrus*, the presence of fibre bundles in the midrib and within the expansion tissue are commonly observed (see Glassman 1972; Firmo *et al*. 2021; Sant'Anna-Santos 2023a, b, c). However, to our knowledge, this is the first report to *S. romanzoffiana* with images.

The presence of fibre and accessory vascular bundles in the midrib region of ×*B. nabonnandii* (Fig. 3e-f), characteristics observed in all specimens sampled, becomes this pinnae region more useful in identifying the hybrid, in comparison with margin and intermediate region.

The comparative description of the anatomical characters from the intermediate region, margin, and midrib of *S. romanzoffiana*, *B. odorata* and ×*B. nabonnandii* are shown in Table 1.

Table 1 – Pinnae anatomy differences among ×*Butyagrus nabonnandii*, *Butia odorata* and *Syagrus romanzoffiana*.

Characters	***×B. nabonnandii***	***B. odorata***	***S. romanzoffiana***
Intermediate region			
Tertiary vascular bundles on the adaxial surface	Present	Present	Absent
Nonvascular bundles on the adaxial surface	Absent/Present	Absent	Present
Leaf margin			
Shape	Deltoid/Quadrangular	Quadrangular	Quadrangular
Number tertiary vascular bundles	1	2	1
Midrib			
Accessory vascular bundles completely surrunding the main vascular system	Absent/Present	Present	Absent
Number of accessory bundles with exaggerated fibrous sheath	1–2	2	0
Expansion tissue (ET) estratification	3–4	4	4
Fibers in the hypodermis and ET	Absent/Present	Absent	Present

Pinnae anatomy proved useful in the identification of the hybrid ×*Butyagrus nabonnandii* and also differentiated it from both parental *taxa*. In addition to the morphological aspects, the recognition of a hybrid individual in areas where *Butia* and *Syagrus* are sympatric, and even specimens deposited in herbaria, can be done using an easy and fast method of leaf anatomy analysis. The pinnae anatomy of the hybrid revealed a combination of characters of both parental taxa, as observed in the external morphology.

Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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