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Original Article

Ontogenetic Characterization of the Mangaba Pericarp (*Hancornia speciosa* Gomes) (Apocynaceae)

William Cezar Trindade do Patrocinio[1,*], Lucas Nicioli Bandeira[2], Letícia de Almeida Gonçalves[2], Dalva Graciano-Ribeiro[2], Lucimeire Pilon[3], Eli Regina Barboza de Souza[4], Flávio Alves da Silva[4]

[1] Universidade Federal de Goiás, Escola de Agronomia, Goiânia, GO, Brazil
[2] Universidade Federal de Goiás, Instituto de Ciências Biológicas, Goiânia, GO, Brazil
[3] Empresa Brasileira de Pesquisa Agropecuária, Embrapa Hortaliças, Brasília, DF, Brazil
[4] Universidade Federal de Goiás, Escola de Agronomia, Goiânia, GO, Brazil
*Corresponding Author: william.cezar17@hotmail.com

ABSTRACT

The anatomical characterization of mangaba fruit at different developmental stages remains largely unexplored. This study aims to describe the anatomical features of the mangaba pericarp across distinct phenological stages. Conventional anatomical techniques were employed for fruit characterization, along with histochemical assays. Throughout all developmental stages, the exocarp remains uniseriate and bears stomata and papillae; however, only the cuticle undergoes substantial changes, being thin during the early stages and becoming thicker as development progresses. As ripening progresses, the cuticle becomes thicker. The mesocarp is divided into three regions: outer, middle, and inner. In the outer region, the parenchyma cells elongate in the periclinal direction and display a denser organization. Idioblasts containing phenolic compounds are more abundant at the onset of fruit development but decrease as the fruit matures. Articulated and anastomosed laticifers occur throughout the middle mesocarp, along with concentric and collateral vascular bundles, whose vessel elements exhibit a helical pattern. In the endocarp, elongated trichomes develop as the fruit ripens. The pericarp analysis enabled the description of key structures associated with the survival and perpetuation of the species. Moreover, it provides valuable insights for postharvest studies of the fruit.

Keywords: anatomy, Apocynaceae, Cerrado, Goiás, native fruit

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Introduction

Apocynaceae comprises approximately 366 genera and 5,100 species distributed worldwide (Christenhusz & Byng, 2016), including trees, shrubs, and herbs with potential medicinal uses (Islam & Lucky, 2019). The mangabeira (*Hancornia speciosa* Gomes) is a fruit-bearing tree species that occurs in several regions of Brazil. The known varieties include *Hancornia speciosa* var. *speciosa*, *H. speciosa* var. *cuyabensis*, *H. speciosa* var. *gardneri*, *H. speciosa* var. *pubescens*, *H. speciosa* var. *maximilliani*, and *H. speciosa* var. *lundii* (Monachino, 1945; Collevatti *et al.*, 2018).

According to the national production scenario, Brazil produced 2,560 tons of mangaba in 2023, with the states of Paraíba and Sergipe as the leading producers, yielding 955 tons and 350 tons, respectively. In the same year, the state of Goiás ranked tenth in fruit production, with a total of two tons (IBGE, 2023).

In addition to fresh consumption, the fruits are also used in various processed forms, such as ice creams, jellies, preserves, and candied sweets (Vieira *et al.*, 2017). Mangaba is a multifunctional food with high antioxidant activity and is rich in bioactive compounds, including carotenoids, vitamin C, and vitamin E (Cardoso *et al.*, 2014).

In *H. speciosa*, the ovary is superior, bicarpellate, and syncarpous, differing from the predominantly apocarpous pattern observed in most Apocynaceae species (Simões & Kinoshita, 2002). The fruits, botanically classified as bacoid (Barroso *et al.*, 1999), exhibit variation in shape and color, depending on the variety of the species, as well as within the same plant (Ganga *et al.*, 2010).

Understanding the organs and reproductive structures of plants is essential for comprehending the life cycle of species, serving as a key element in biodiversity studies as well as in the analysis of taxonomic and phylogenetic relationships among genera and species (Giacomin *et al.*, 2022). The anatomical characterization of fruits contributes significantly to understanding the evolutionary processes related to their development and is highly relevant to research in ecology, biology, and genetic conservation (Thadeo *et al.*, 2015). This knowledge is also fundamental to elucidating seed dispersal mechanisms, thereby supporting biodiversity conservation (Fagundes & Mariath, 2010). Furthermore, the anatomical composition of fruits directly influences their quality and shelf life (Li *et al.*, 2013).

Information on the fruit development of *H. speciosa* remains limited. Existing studies include investigations of leaf anatomy (Campos *et al.*, 2021), anatomical comparisons among fruit varieties (Abdalla *et al.*, 2021), and anatomical analyses of roots under aluminum stress (Rodrigues *et al.*, 2017; Silva *et al.*, 2020). Therefore, the anatomical description of the pericarp throughout fruit development is needed.

In the study conducted by Abdalla *et al.* (2021), the pericarp of four mangaba varieties (*H. speciosa* var. *pubescens*, *H. speciosa* var. *gardneri*, *H. speciosa* var. *speciosa* e *H. speciosa* var. *cuyabensis*) was characterized (including the exocarp, mesocarp, and endocarp). However, that study examined fruits only at the mature-green stage. It is necessary, therefore, to understand how the pericarp develops throughout fruit growth, as it undergoes structural modifications during ontogeny. A study by Aguiar *et al.* (2009) on *Prestonia riedelii* (Müll.Arg.) Markgr. reported cuticle thickening, reduced trichome abundance in the epidermis, increased pecto-cellulosic wall development in the mesocarp, complete differentiation of fibers and phloem, and more distinguishable laticifer canals as fruit ontogeny progresses.

Therefore, the objective of this study was to anatomically characterize the pericarp of *H. speciosa* var. *gardneri* occurring in the Brazilian Cerrado throughout its development until full maturity.

Materials and Methods

Mangaba fruits (*H. speciosa* var. *gardneri*) were collected from the native plant collection of the Federal University of Goiás, in Goiânia, GO (16°35'38" S, 49°17'23" W). According to the Köppen–Geiger climate classification, the climate is classified as Aw (hot and semi-humid, with a dry season from May to September) (Silva *et al.*, 2017). The soil is classified as a Latossolo Vermelho distrófico with a medium texture (Embrapa, 2013). The air temperature and relative humidity (RH) on the day of fruit collection were 27 °C and 63%, respectively.

Fruits of *H. speciosa* var. *gardneri* were collected at different sizes corresponding to five phenological stages. The stages were determined based on fruit size, considering the length and diameter of 20 fruits randomly collected from four distinct populations (Fig. 1).

For each phenological stage, four fruits were collected from four *H. speciosa* individuals. Each fruit was considered one replicate, totaling four replicates. After collection, the fruits were taken to the Plant Anatomy Laboratory at the Institute of Biological Sciences, UFG, for anatomical and histochemical analyses.

Samples were taken from the middle region of fruits at stages S2, S3, S4, and S5. Given their reduced size, samples from stage S1 were considered as whole fruits. The material was fixed in FAA 50 (formaldehyde, propionic acid, 50% ethanol) at a 1:1:18 (v/v) ratio for 24 hours and then stored in 70% ethyl alcohol (Johansen, 1940).

The material was embedded in paraffin, then transverse and longitudinal sections were obtained using a rotary microtome (RM2245, Leica, Germany) at a thickness of 17 µm. After deparaffinization, the sections were stained with 0.5% Astra blue and 1% safranin, each for 15 minutes, to differentiate between non-lignified primary walls and lignified secondary walls, respectively. Permanent slides were mounted using vitral varnish (Paiva *et al.*, 2006).

Figure 1. Phenological stages of *Hancornia speciosa* Gomes var. *gardneri*. S1: stage 1 (8–11 mm in length and diameter); S2: stage 2 (12–17 mm in length and diameter); S3: stage 3 (24–29 mm in length and diameter); S4: stage 4 (30–38 mm in length and diameter); S5: stage 5 (45–52 mm in length and diameter).

Histochemical tests to identify phenolic compounds were performed using 10% ferric chloride (Johansen, 1940). For this procedure, freehand transverse sections were obtained from fresh mangaba fruits.

Stomatal visualization was carried out through paradermal sections of the fruit epidermis using a steel blade. The samples were then cleared in a 1% sodium hypochlorite solution for five minutes and subsequently stained with toluidine blue (Abbade *et al.*, 2009). Photomicrographs were obtained using an optical microscope (BX53F2, Olympus, Japan).

Results

Exocarp

The exocarp of mangaba is uniseriate, with cells elongated primarily in the anticlinal direction (Fig. 2A-D). At the beginning of development, stage S1, the cells exhibit a more prominent nucleus and a visually denser cytoplasm, resulting in a slightly more intense staining (Fig. 2A). From stage S2 onward, the cells display a papillose appearance (Fig. 2B–C). Stomata undergo differentiation at stage S1 (Fig. 2D) and are fully developed by stage S5 (Fig. 2E).

In the early developmental stages (S1 and S2), the exocarp cells are covered by a thin cuticle. However, as growth progresses from stage S3 onward, the cuticle becomes thicker (Fig. 2F). At fruit maturity, the cuticle shows a pronounced thickening, which is clearly evident at stage S5 (Fig. 2F).

Mesocarp

Based on fruit development, the mesocarp of mangaba can be divided into three regions, outer, middle, and inner, across all phenological stages (Fig. 3A).

Outer Region

In stages S1 and S2, the outer mesocarp is composed of up to eight layers of isodiametric parenchyma cells (Fig. 3B), with inconspicuous intercellular spaces. As the fruit develops, the parenchyma cells elongate in the periclinal direction (Fig. 3C), resulting in five densely arranged layers, similar to those observed in stages S3, S4, and S5. In the outer mesocarp, idioblasts containing phenolic compounds are abundant; in stages S1 and S2, they occur closer to the epidermis (Fig. 3D), reaching up to eight layers.

Middle Region

In the middle mesocarp, the parenchyma cells are visibly larger at all phenological stages (Fig. 3A). However, idioblasts containing phenolic compounds were observed only during the early stages (S1 and S2) (Fig. 3D). In stages S3, S4, and S5, these idioblasts were not detected in the parenchyma (Fig. 3E).

The laticifers are of the articulated and anastomosing type (Fig. 4A) and are distributed throughout the middle region of the mesocarp (Fig. 4B). However, from stage S3 onward, the laticifers appear to be less abundant.

The vascular bundles are of the concentric and collateral types (Fig. 4C), and the predominant vessel elements exhibit a helical pattern across all five phenological stages (Fig. 4D).

Inner Region

In the inner region of the fruits, idioblasts containing phenolic compounds can also be identified in stages S1 and S2 (Fig. 5A), but they are not observed in later stages. From stage S2 onward, laticifers appear to be less abundant. Furthermore, the cells of the outermost layers of this region are lignified at the S4 stage (Fig. 5B).

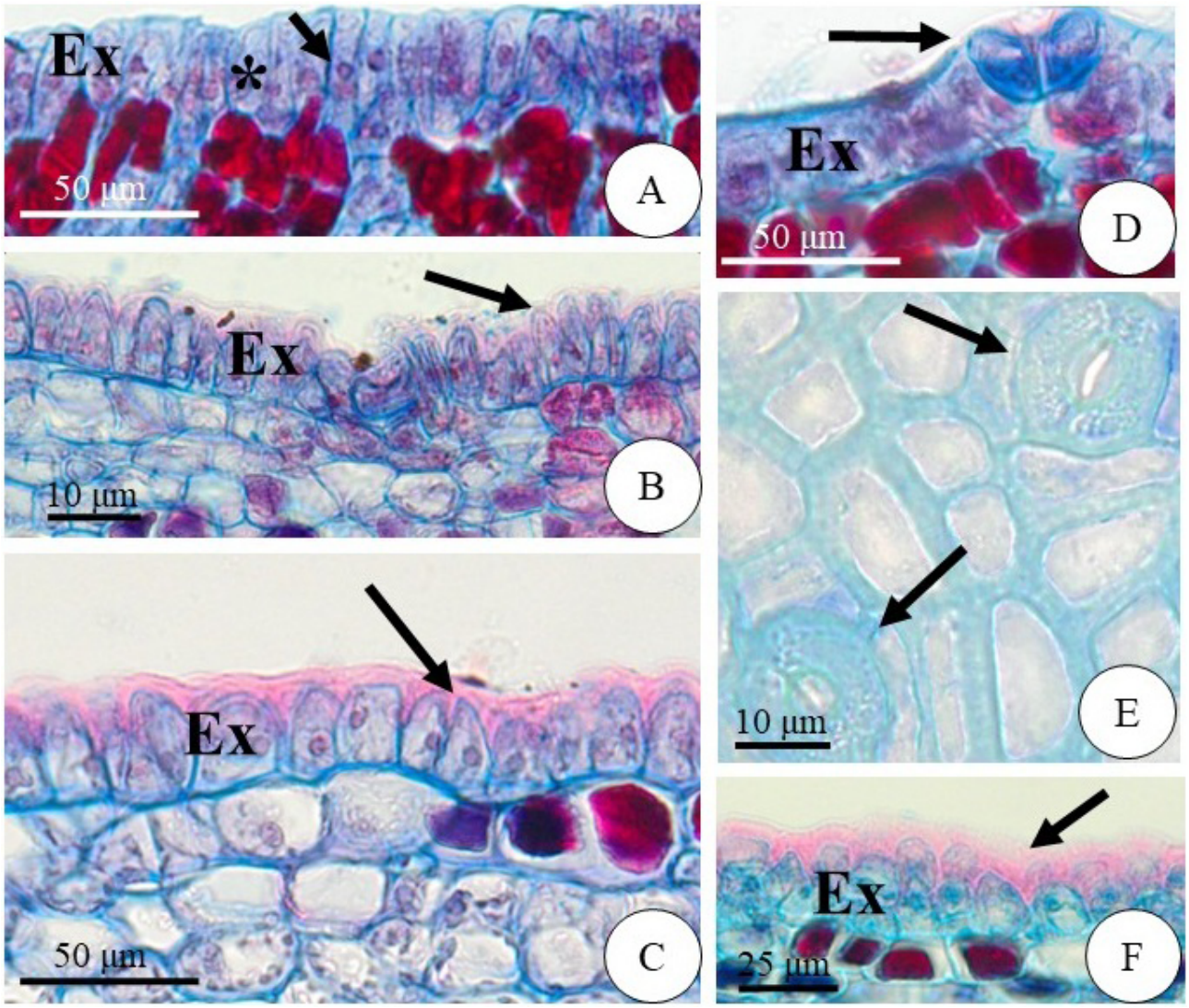

Figure 2. Photomicrographs of transverse (A–B), longitudinal (C, D–F), and paradermal (E) sections of mangaba fruit at various developmental stages. A) Stage S1: exocarp composed of anticlinally elongated cells (*) with a prominent nucleus (arrow). B) Stage S2 and C) Stage S5: exocarp cells exhibiting a papillose appearance (arrow). D) Stomata in development at stage S1 (arrow). E) Fully developed stomata at stage S5 (arrow). F) Thick cuticle at stage S5 (arrow). Ex = exocarp.

Endocarp

The endocarp, the innermost layer of the pericarp, is uniseriate, as observed in stage S2 (Fig. 5C), and remains attached to the seed coat, which bears elongated trichomes (Fig. 5B). These trichomes fit into indentations of the endocarp, which become more developed as the fruit grows, as observed at stage S2 (Fig. 5B).

Discussion

The uniseriate exocarp observed in mangaba fruits has also been reported in other Apocynaceae species (El-Fiki *et al.*, 2019; Pirolla-Souza *et al.*, 2019; Abdalla *et al.*, 2021), suggesting that this may be a common characteristic of the family. In *Prestonia riedelii* (Apocynaceae), the exocarp is uniseriate with a thin cuticle during the early developmental stages, becoming progressively thicker as the fruit matures (Aguiar *et al.*, 2009). Species that naturally occur in dry environments tend to develop thick cuticles (Riederer & Müller, 2006; Domínguez *et al.*, 2011), as observed in mangaba (Fig. 2F).

One of the main functions of the cuticle is to reduce excessive water loss (Muller & Riederer, 2005). In mangaba, cuticle thickening plays a crucial role, particularly because mature fruits have a high water content and an uniseriate exocarp that can promote dehydration. Thus, the thick cuticle contributes to maintaining fruit quality (Abdalla *et al.*, 2021).

From stage S2 onward, the cells of the exocarp become papillose, a feature not previously reported in studies of

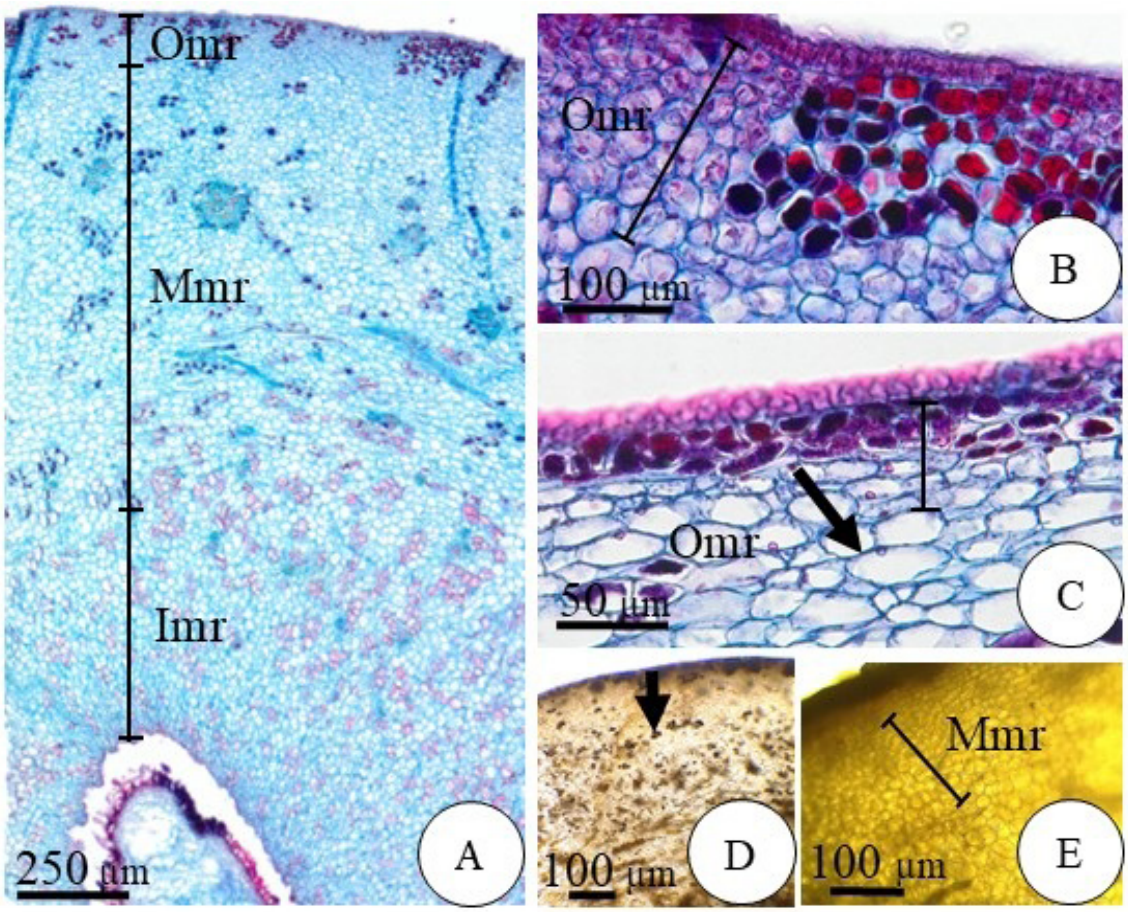

Figure 3. Photomicrographs of transverse sections of mangaba fruit at various developmental stages, highlighting the mesocarp. A) Stage S1: mesocarp regions outer, middle, and inner. B) Stage S2: isodiametric parenchyma cells. C) Stage S5: parenchyma cells elongated in the periclinal direction (arrow). D) Stage S1: parenchyma with idioblasts containing phenolic compounds (arrow). E) Stage S5: parenchyma. Omr = outer mesocarp region; Mmr = middle mesocarp region; Imr = inner mesocarp region.

mangaba fruit. Papillae are epidermal cells with an outer, projected periclinal wall (Mantovani *et al.*, 1995) and play a crucial role in reducing excessive transpiration (Toderich *et al.*, 2010; Ribeiro *et al.*, 2012). Additionally, they serve as a crucial physical barrier against the penetration of pathogenic fungi (Sherwood & Vance, 1976).

The growth of mangaba fruits was characterized by an increase in the size of the mesocarp parenchyma cells, a pattern particularly evident between S3 and S5 phenological stages. This increase in volume may be attributed to cell division, cell expansion, or a combination of both processes (Pabón-Mora & Litt, 2011), with cell expansion being directly related to the accumulation of fleshy tissue (Houel *et al.*, 2010; Zhang *et al.*, 2020). In fleshy bacoid-type fruits (Barroso *et al.*, 1999), such as the mangaba, expansion occurs predominantly in the mesocarp, while the exocarp and endocarp remain thin until maturity (Cerri & Reale, 2020; Judkevich *et al.*, 2022). This type of fruit has seeds surrounded by attractive pulp and is directly associated with attracting frugivorous animals (Ridley, 1930), which facilitates its dispersal and the establishment of the species in new environments.

In the early developmental stage, mangaba fruits contain numerous idioblasts with phenolic compounds located in the outer region of the mesocarp. The higher concentration of phenolics during the initial phase of fruit development may be associated with protection against ultraviolet radiation (Inostroza-Blancheteau *et al.*, 2014) and herbivore attack (Singh *et al.*, 2021), serving as a chemical defense strategy (Rodrigues *et al.*, 2017; Jańczak-Pieniążek *et al.*, 2023), as well as protection against high temperatures (Rivero *et al.*, 2001).

The amount of phenolic compounds decreases as the fruit ripens, a pattern also observed in fruits of *Butia capitata* (Ventura *et al.*, 2022), *Rubus ulmifolius* (Castro *et al.*, 2023), *Malus domestica* (Wojdylo & Oszmianski, 2020), and *H. speciosa* (Freitas, 2013; Morgado *et al.*, 2020). During ripening, the substrates produced are directed primarily toward fruit growth rather than the biosynthesis of phenolic compounds (Seraglio *et al.*, 2018; Pereira *et al.*, 2021).

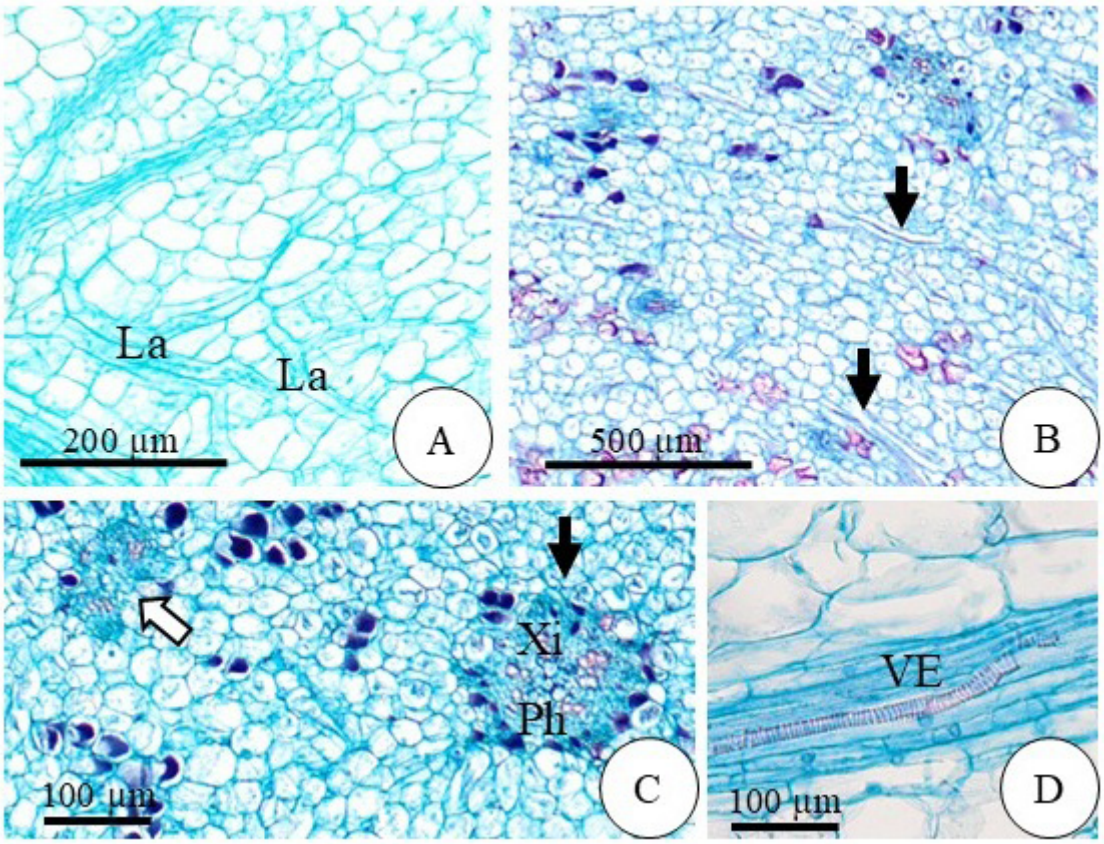

Figure 4. Photomicrographs of transverse (C) and longitudinal (A, B–D) sections of mangaba fruit at various developmental stages, highlighting the middle mesocarp. A) Stage S2: laticifers. B) Stage S1: arrowhead indicating laticifers distributed throughout the region. C) Stage S1: vascular bundles of the concentric type (arrow with black fill) and collateral type (arrow with white fill). D) Stage S5: vessel elements exhibiting a helical pattern. La = laticifers. Xi = xylem. Ph = phloem. VE = vessel elements.

Moreover, as maturation progresses, the concentration of these compounds tends to decrease, resulting in fruits that become less astringent (Freitas, 2013).

The phenolic compounds present in idioblasts are associated with plant defense (Ribeiro *et al.*, 2021). In *H. speciosa*, the accumulation of these compounds may be related to detoxification strategies against aluminum toxicity in the soil, also functioning as antioxidants under stress conditions (Tolrá *et al.*, 2009; Rodrigues *et al.*, 2017; Coimbra *et al.*, 2023). Considering that Cerrado soils are naturally acidic and rich in aluminum (Ratke *et al.*, 2021), the presence of phenolic compounds becomes essential for the adaptation and survival of mangabeira in this environment.

The presence of laticifer canals is a common feature among species of the Apocynaceae family (Gonçalves *et al.*, 2018; Campos *et al.*, 2021). The latex produced by these structures plays important defensive roles in plants, acting against herbivores and phytopathogens, while also helping to reduce water loss and contributing to wound healing (Tan *et al.*, 2017; Ramos *et al.*, 2019).

In the analyzed fruits of *H. speciosa*, the laticifers were characterized as articulated and anastomosed. In shoot apices of the same species, Souza *et al.* (2021) describe laticifers with ramifications originating from anastomoses, which corroborates the results obtained in this study. On the other hand, Abdalla *et al.* (2021), when analyzing exclusively mature fruits of *H. speciosa* var. *pubescens*, described laticifers as non-articulated and branched. This divergence may indicate structural differences between the studied materials, but it may also be related to different criteria of morphoanatomical interpretation and the stage of development considered. In this sense, the importance of ontogenetic studies that evaluate the formation of laticifers in many varieties of the species is reinforced.

The presence of trichomes on the seed coat was also reported by Abdalla *et al.* (2021) in all *H. speciosa* varieties analyzed. These structures play an important role in anchoring the seed to the soil, promoting hydration, and regulating internal temperature (Mamut *et al.*, 2014). Mangaba seeds are recalcitrant, naturally exhibiting high moisture content, and maintaining this moisture is essential for ensuring their viability (Nunes *et al.*, 2022). In this context, the increase in trichomes from stage S3 onward contributes significantly to retaining internal moisture.

The vascular system of mangaba fruits is composed of concentric and collateral bundles, which is consistent with

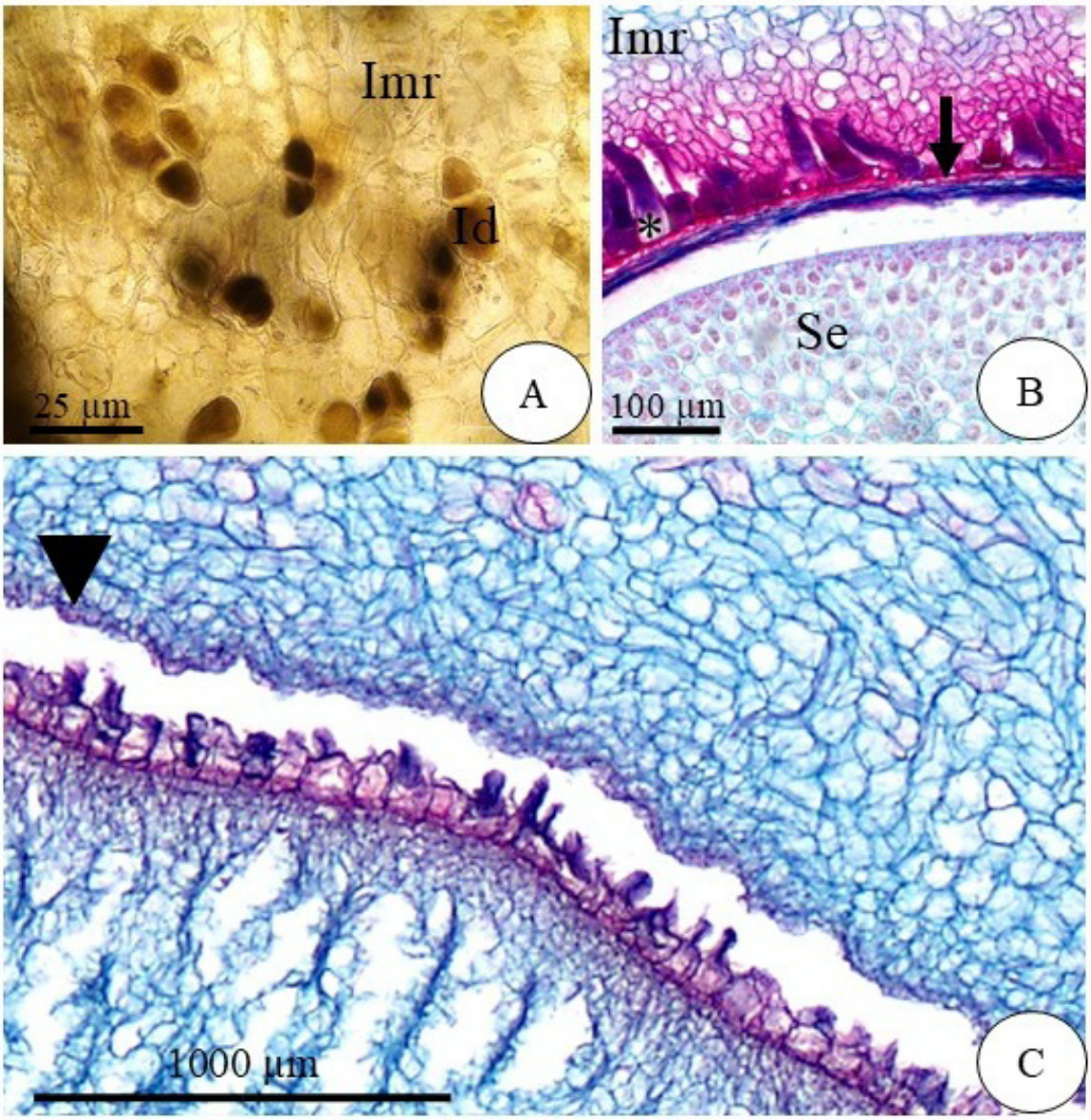

Figure 5. Photomicrographs of transverse (A) and longitudinal (B) sections of mangaba fruit at various developmental stages, highlighting the inner mesocarp and the endocarp. A) Stage S1: idioblasts containing phenolic compounds. B) Stage S4: seed coat (arrow) and trichomes (*). C) Stage S2: uniseriate endocarp (arrowhead); Imr = inner mesocarp region. Id = idioblasts. Se = seed.

other Apocynaceae species that exhibit concentric bundles (Esemann-Quadros *et al.*, 2008; Shewale *et al.*, 2022) and collateral bundles (Aguiar *et al.*, 2009; Neto *et al.*, 2020). This study represents the first characterization of vessel elements in *H. speciosa*, providing meaningful anatomical evidence that may support future taxonomic refinements within the species.

During mangaba fruit development, an increase in cuticle thickness, the presence of a papillose epidermis, and a reduction in the number of laticifers were observed. These anatomical changes are directly related to the final quality of the fruit. Additionally, the presence of phenolic compounds, which tend to decrease throughout ontogeny, also plays a significant role in this process. The laticifer canals present in the pericarp are of the articulated and anastomosing type, with a significant reduction beginning at stage S3.

The endocarp remains attached to the seed coat, which bears trichomes, a consistent feature across all developmental stages and essential for the species' perpetuation.

The vascular bundles identified are of the concentric and collateral types, with a predominance of helical vessel elements present at all phenological stages. This study represents the first characterization of vessel elements in *H. speciosa* Gomes.

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Authors' Contributions

[William Patrocinio] Conceptualization, Visualization, Investigation, Methodology, Writing – original draft. [Lucas Bandeira] Visualization, Investigation, Methodology, Writing – original draft. [Letícia Gonçalves] Conceptualization, Investigation, Methodology, Writing – review & editing. [Dalva Graciano-Ribeiro] Conceptualization, Investigation, Methodology, Writing – review & editing. [Lucimeire Pilon] Writing – review & editing. [Eli Regina Souza] Conceptualization, Writing – review & editing. [Flávio Silva] Conceptualization, Writing – review & editing.

Conflicts of Interest

The authors declare that there are no conflicts of interest related to the publication of this manuscript.

Data Availability

All data supporting the findings of this study are included in the article.

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