Early leaf development in Euterpe oleracea Mart. (Arecaceae, Arecoideae): Leaflets, pinnae or segments? 1

Authors: Pinedo, André Silva, and Gomes, Sueli Maria

Source: The Journal of the Torrey Botanical Society, 149(3) : 219-229

Published By: Torrey Botanical Society

URL: https://doi.org/10.3159/TORREY-D-21-00040.1

Journal of the Torrey Botanical Society 149(3): 219–229, 2022.

Early leaf development in *Euterpe oleracea* Mart. (Arecaceae, Arecoideae): Leaflets, pinnae or segments?[1]

André Silva Pinedo[2] and Sueli Maria Gomes
Postgraduate Program in Botany, Department of Botany, University of Brasilia, P.O. Box 04.457, Asa Norte, Brasília, Distrito Federal, 70919-970, Brazil

Abstract. *Euterpe oleracea* presents long leaves with divisions in the blade frequently referred to as leaflets or pinnae, as if they were compound. The purpose of this article is to present the first leaf ontogeny study for this species. Buds of dissected *E. oleracea* were classified according to their size and morphology and examined under scanning electron and light microscopy. The youngest leaf primordia are conical. The first foldings in the leaf blade appear in primordia *ca*. 0.8 mm in length and already have procambium. When young leaves reach 1.5 mm long, these plications separate from one another. Segments change their orientation throughout leaf development. Leaf blade in *E. oleracea* is initially entire (nonplicate), becoming plicate at a later stage, and plications separate from each other as a final step. This developmental process has some similarities with what is observed in other palm species. According to early stages of the leaf ontogeny, these plants have simple pinnatisect and not compound pinnate leaves. The use of terminology such as "leaflets" or "pinnae" is incongruent with simple leaves, and we recommend that adult leaf blade subdivisions of Arecaceae should be called "leaf segments" instead. This work contributed to the understanding of histological changes during palm leaf development, being a contemporary report on both histological and micromorphological study on palm leaf ontogeny.

Key words: apical meristem, compound leaves, ontogeny, plications, simple leaves

The tribe Euterpeae (Arecoideae) is monophyletic (Pichardo-Marcano *et al*. 2019), comprising five genera that occur primarily at low altitudes in humid rain forests in Central and South America, including the Caribbean (Dransfield *et al*. 2008). *Euterpe* Mart. encompasses seven species and is easily differentiated from other palms in this tribe by its pendulous leaf segments (Henderson and Galeano 1996, Henderson 1999).

Euterpe oleracea Mart. inhabits lowland and flooded forest habitats in the Amazon region, occurring from Ecuador to the Guyanas (Smith 2014). Different from *E. precatoria* Mart. and *E. edulis* Mart., *E. oleracea* is sympodial, making extraction of palm hearts possible without killing the individual (Smith 2014). Moreover, the fruits of this species, popularly known as *açaí* in Brazil, have high energetic and nutritional content (Ribeiro *et al*. 2012) and are one of the Amazonian products that stand out in the international market (Smith 2014).

Leaves are organs formed on the shoot apical meristem by the action of hormones, such as auxin and cytokinin (Shani *et al*. 2010). An interesting question is how development differs between compound and simple leaves. Some recent works were carried out approaching these two leaf types (Efroni *et al*. 2010; Conklin *et al*. 2019), but their main focus is on the genes that determine leaf complexity, and we still lack studies about the meristematic differentiation that occur during leaf ontogenesis. It is important to understand the process of cell proliferation activity during leaf morphogenesis, as this mechanism may be responsible for controlling leaf complexity (Kang and Sinha 2010). A typical palm leaf primordium emerges in the shoot apical meristem with a hood-shaped apex in its earliest stages, when the stem-encircling leaf base is formed, distinguishing the primordium regionally into a distal hooded blade and a proximal tubular base (Kaplan *et al*. 1982a).

Concerning the ontogeny of *Euterpe* species, researchers have focused on seeds (Panza *et al*. 2004; Neto *et al*. 2010) and fruits (Ribeiro *et al*. 2012). Studies of *Euterpe* leaves focus on its ecology (Gatti *et al*. 2011), leaf epidermis in seedlings (Ceolin *et al*. 2007), or the developmental process that affects its populations (Carvalho *et al*. 1999; Portela and Santos 2011). Barabé *et al*. (2010) analyzed the shoot apical meristem of *E.*

---

[1] We acknowledge Capes for the doctoral grant for the first author and the Microscopy and Microanalyses Laboratory of Universidade de Brasília for support in preparing the scanning electron microscopic images.

[2] Author for correspondence: adpinedo20@gmail.com.

doi: 10.3159/TORREY-D-21-00040.1

Received for publication November 28, 2021, and in revised form April 2, 2022; first published May 18, 2022.

oleracea only in the first developmental stage, when plications are still not present, as the work aimed to understand the phyllotaxis. Thus, there is no research about the micromorphological and anatomical changes that occur along the process of leaf development in this species.

This research aimed to investigate *E. oleracea* leaf micromorphology and anatomy at distinct stages of development, focusing on the meristematic activity during ontogeny. Moreover, we aim to question some terminology frequently employed for palm leaves since incongruences were detected.

Materials and Methods. Material Preparation. Seedlings of *E. oleracea* at about 100–150 cm in height (Fig. 1A) were purchased from nurseries. The vouchers *Pinedo 35*, *46*, *47*, *48*, *49*, and *50* were stored at the University of Brasilia Herbarium (Thiers 2021) under register numbers 217308, 217309, 217310, 217311, 217312, and 217313, respectively. Shoot apices dissection was made carefully with the naked eye. The axillary buds were delicately removed from the main axis and dissected separately under a stereomicroscope. The developmental stages were isolated in distilled water based on their size and morphology.

A total of 60 dissected buds 0.2–200 mm in length were employed in this work. Stages ranging in size from 0.2 to 50 mm were examined under scanning electron microscopy, according to the protocol presented by Kuo (2007). Light microscopy was performed with stages between 2 and 200 mm, according to the methodology employed by Kraus and Arduin (1997), with adaptations tested by Paiva *et al.* (2006).

Scanning Electron Microscopic Analyses: Samples were fixed in Karnovsky solution at 4 °C for at least 1 hr (Kuo 2007), and then sodium phosphate buffer 0.1 M (pH 6.8) ratio 1:1 (v:v) was added. The material stayed for 24–72 hr in this solution (Kuo 2007) and was washed three times in the same buffer solution. Leaf primordia were postfixed in 2% osmium tetroxide for 2 hr and washed three more times in phosphate buffer. Samples were dehydrated in an ethanol series (10, 20, 30, 40, 50, 60, 70, 80, 90, and 100%) for at least 20 min in each solution, twice in each concentration higher than 60%. The primordia were dried in the critical point using liquid CO_2 (Kuo 2007) and assembled on copper stubs using black double-sided tape. The metallization was performed with 8 nm of gold. Images were taken in the scanning electron microscope at the Microscopy and Microanalysis Laboratory of the Universidade de Brasilia, Brazil.

Histological Analyses: Samples were fixed at room temperature (*ca.* 24 °C) in FAA50 (Johansen 1940) for at least 12 hr. The primordia were dehydrated in an ethanol gradient (50, 60, 70, 80, 90, and 100%). The larger structures were soaked longer in each concentration up to 4 hr. Thereafter, samples passed through a series of ethanol butyl acetate solutions (25, 50, 75, and 100%) for at least 1 hr in each concentration.

The specimens were infiltrated with melted paraffin 3:1 butyl acetate and were maintained overnight at 60 °C for 24 hr. The samples were replaced in pure paraffin, and paraffin blocks were mounted, positioning the primordia in such a way that plications appeared in the sections, with the aid of a stereomicroscope.

Serial sections were obtained on a rotary microtome according to the size of the sample: 2.0–3.0 mm, 10-μm thickness; more than 3.0 mm, 15-μm thickness. Longitudinal sections were made with buds of 2.0–20 mm and cross sections in a 2-mm primordium.

The sections were stained with safranin and alcian blue, according to Kraus and Arduin (1997). Colorless vitral varnish sealed up the slides with coverslips (Paiva *et al.* 2006). Observations were made, and images were captured with the program LAS ES on an Olympus photomicroscope associated to the computer.

Results. A fully developed leaf of an *E. oleracea* seedling (Fig. 1B) contains about 8–14 vegetative units. During its development, all these segments are vertically oriented and remain closely appressed to the midrib (Fig. 1C). A leaf cross section at this stage reveals the segments well fitted in a pattern, with all main vascular bundles aligned in the middle of the structure, making a distinct separation between leaf sides (Fig. 1D).

Concerning leaf ontogenesis, the *E. oleracea* leaf primordium is initiated as a horn near the dome of the shoot apical meristem. The group of meristematic cells of this horn is the first visible step in the leaf ontogenesis (Fig. 2B). A tubular base of the horn develops and embraces the shoot apical meristem (Fig. 2A), forming the young leaf sheath. The leaf blade has no plications, and the apex of the leaf primordium is promeristematic (Fig. 2B, D, E).

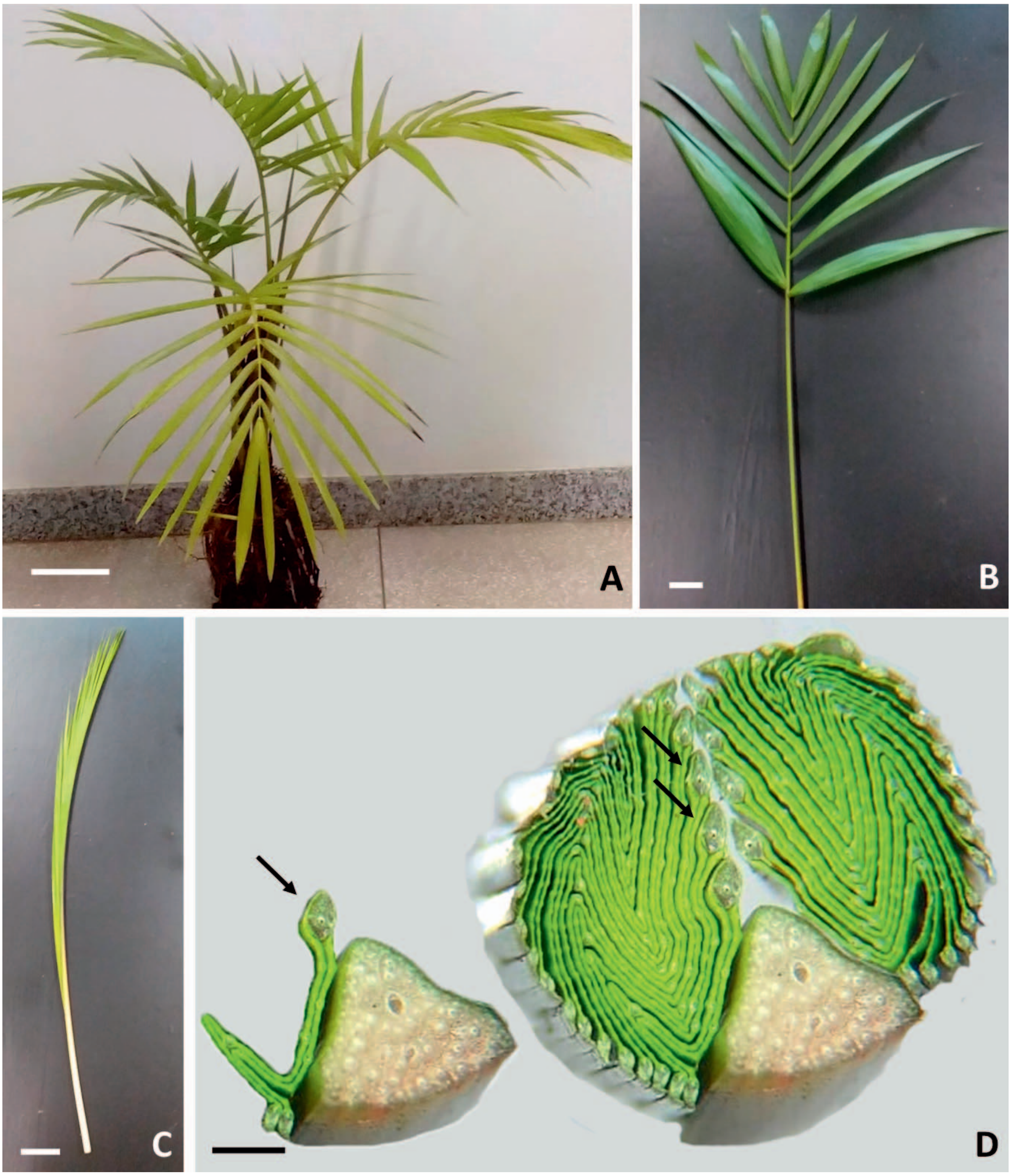

FIG. 1. *Euterpe oleracea* Mart. segments organization along development. (A) Plant seedling. (B) Completely developed leaf. (C) Leaf expanding. (D) A single segment (left) and the organization of the whole group of segments (right) around the midrib (hand-made cross section). Arrows: vascular bundles. Scale bars: A: 10 cm; B–C: 5 cm; D: 1 mm.

A larger number of cells is soon added by anticlinal and periclinal divisions, and the horn grows, being more evident when buds are more than 200 μm in length (Fig. 2D). The leaf blade primordium maintains its characteristic conical shape at the distal region, and a longitudinal plication develops from apex to base of this apical horn (Fig. 2C, E, arrow). This longitudinal region will originate the leaf midvein, and both sides will form the blade wings.

The first lateral plications normally emerge when the bud is about 700 μm in length. These plications initially resemble a series of very slight mounds or undulations on each wing of the

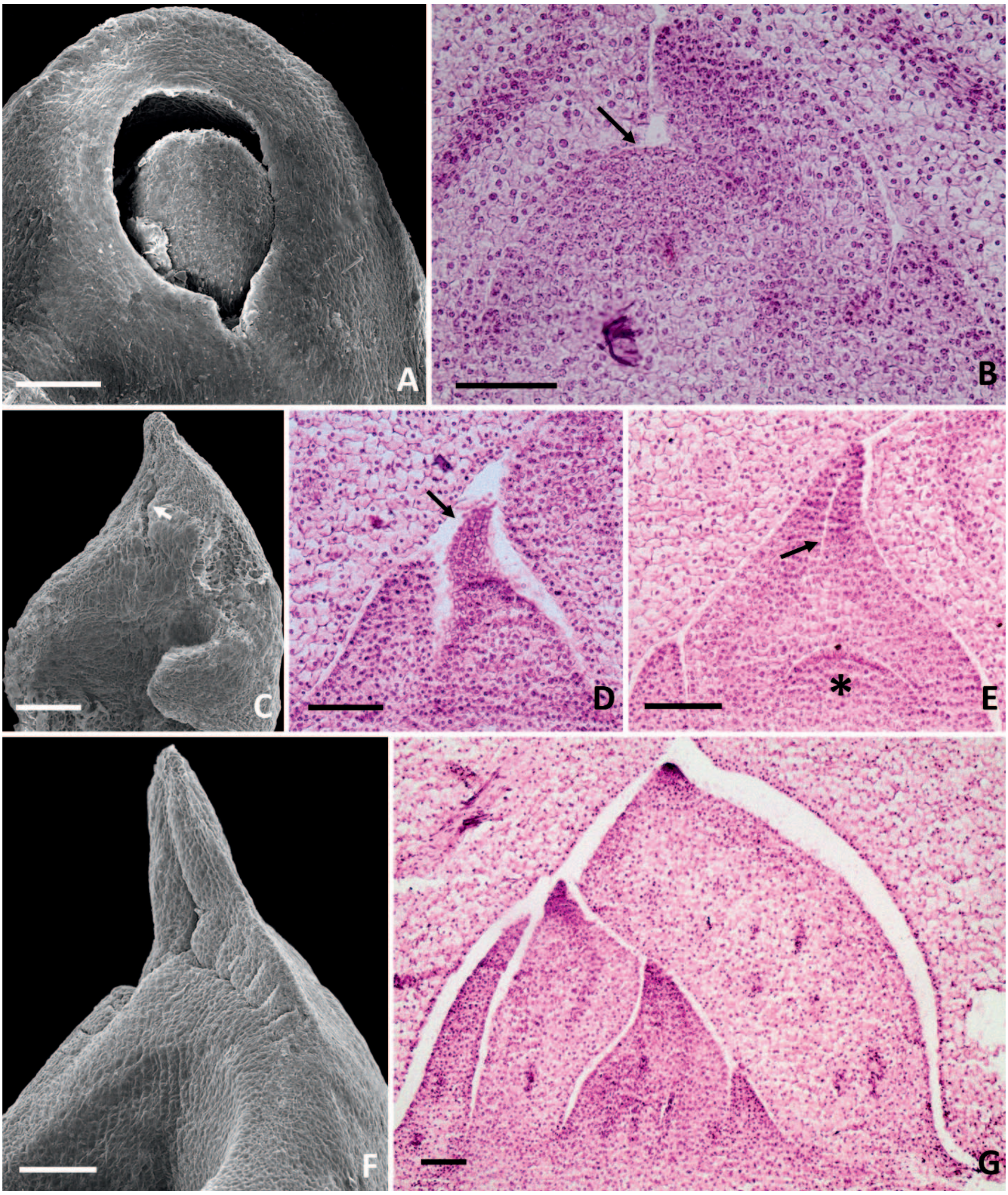

FIG. 2. Leaf ontogenesis of *Euterpe oleracea* Mart. I: primordia 0.2–1.0 mm long. (A) Shoot apical meristem with first leaf primordium emerging. (B) Group of meristematic cells (arrow) embedded in a leaf sheath. (C) Leaf primordium with apical horn, with longitudinal plication (arrow). (D) Both sides of a primordium with an apical horn (arrow). (E) Apical furrow (arrow) delimitating the sides of the leaf primordium, which surrounds the shoot apical meristem (asterisk). (F) Leaf segments in vertical orientation. (G) Smaller stages of development inside later stages. A, C, F: scanning electron microscopic; B, D, E, G: light microscopy. Scale bars: A–G: 100 μm.

primordium and first appear and are more developed on the adaxial side (Fig. 2F). Anatomically, it is clearly seen that younger stages of development grow inside the older ones (Fig. 2G), and the shoot apical meristem is always embedded in the youngest leaf primordium (Fig. 2E).

There are about six to eight plications in a 1-mm-long primordium (Fig. 3A). The developmen-

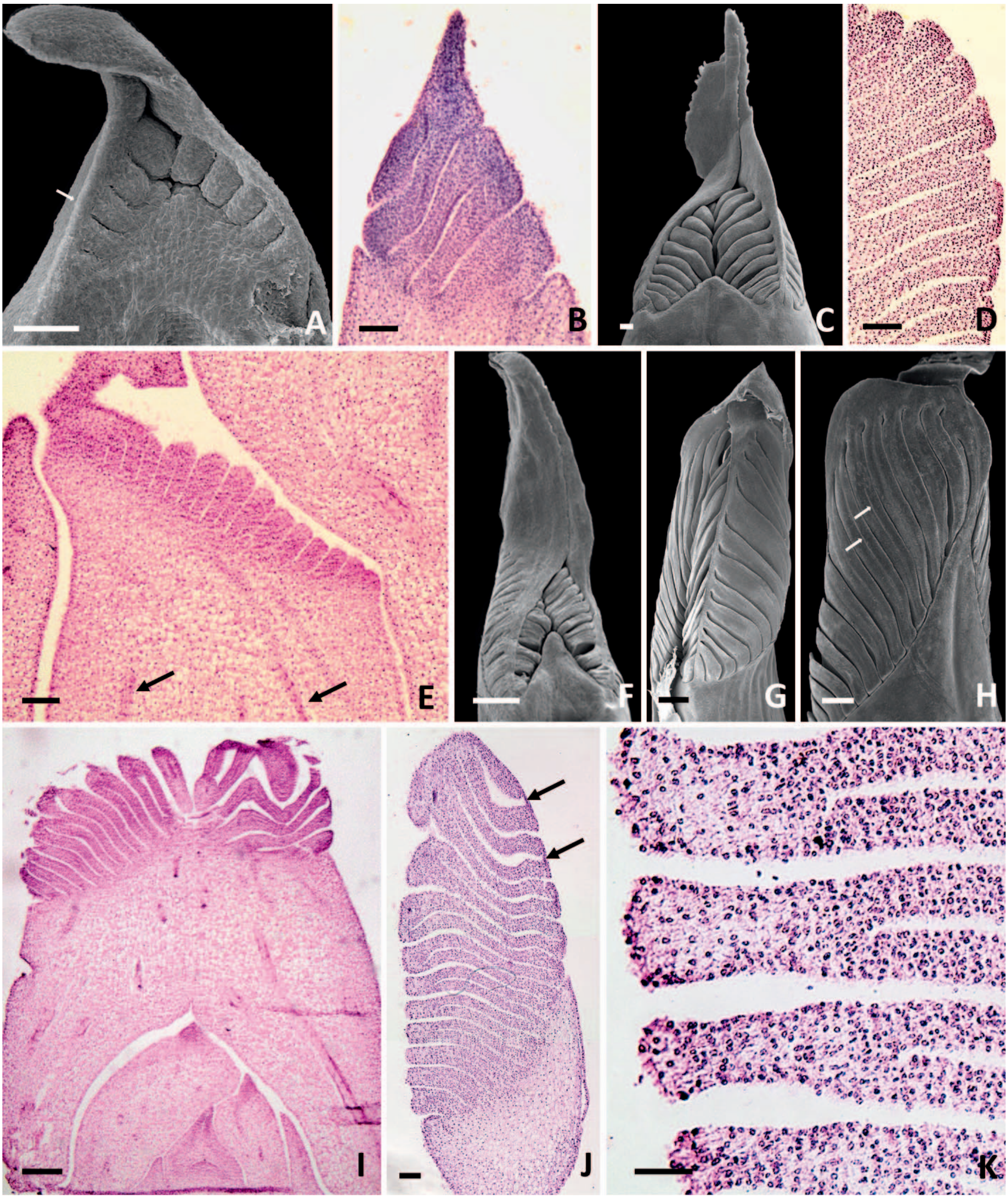

FIG. 3. Leaf ontogenesis of *Euterpe oleracea* Mart. II: primordia 1.0–5.0 mm long. (A) Horizontal plications and nonplicated marginal strip (arrow). (B) Plicated pattern in the blade. (C, D) Plications enlarge and become more distant apart. (E) Plications in a vertical orientation in primordium with procambial strands (arrows). (F, G) Apical horn present (F) and missing (G). (H) Projection at the middle of plications (arrows), indicating future ripping zone. (I, J) Vertical and horizontal segments in the same leaf. (K) Procambial strands in ridges of plications. A, C, F–H: scanning electron microscopic; B, D, E, I–K: light microscopy. Scale bars: A–E, J: 100 μm; F–H: 500 μm; I: 200 μm; K: 50 μm.

tal size distinction among young leaf wings, more evident in previous stages (Fig. 2C–E), becomes inconspicuous, while the longitudinal plication that delimits the sides deepens and becomes more evident. A smooth (nonplicate) margin strip, which divides abaxial- from adaxial-side plications (Fig. 3A), grows less and becomes narrower than the rest of the blade (compare Fig. 3A with Fig. 3F) and forms the ramenta in the adult leaf. Anatomically, the plicate pattern along the blade is in an advanced stage, with deep furrows and ridges (Fig. 3B).

In a later stage, plications have already grown to 100 μm in width and are spaced farther apart (Fig. 3C), contrasting with their closely appressed organization during the initial stages (Fig. 2F, 3A). However, as development advances, plications seem to be again more closely appressed (Fig. 3F, G). The apical horn elongates more, and plications on both adaxial and abaxial sides are completely formed at this stage (Fig. 3C). The midvein region elongates, while the plications change from a horizontal (Fig. 3C) to a vertical position (Fig. 3G). The difference in size of the two sides virtually does not exist at this stage. Anatomically, procambial strands are evident along the leaf blade (Fig. 3D), and they also start to form in each plication.

As leaf primordia approach 4 mm in length, plications are more vertically oriented (Fig. 3E–G). The apical horn has less growth and maintains a reduced size in comparison with the rest of the leaf blade (Fig. 3F, G). From this point on, the young leaf is almost entirely constituted by the plicate zone of the blade on both sides of the conical midvein (Fig. 3F–H).

The anatomical sections allow us to observe again that many younger primordia are embedded inside older ones (Fig. 3I). In some samples, the most basal segments are oriented horizontally, and the most apical ones are oriented vertically (Fig. 3I). Moreover, in Fig. 3I, it can be observed that most basal plications separate from one another at first, while the ones situated at the apex of the primordia are connected between them for a longer period. Procambial strands are observed on the ridges of the developed plications (Fig. 3J), being distinguished by the long and narrow cells.

CROSS SECTIONS: An external young leaf (Fig. 4A–E) embraces two leaf primordia (Fig. 4J) and the shoot apical meristem (Fig. 4J, K). The external young leaf has two wings of the blade united by a reduced midvein at the apex (Fig. 4A–C), while the midvein is well developed below (Fig. 4D, E), followed by the petiole with two series of vascular regions (Fig. 4F–H) and the sheath with only one vascular series (Fig. 4I–K).

The two leaf wings are different in size because of an asymmetrical development (Fig. 4A–D), being one wing twice larger than the other at the leaf apex (Fig. 4A, 40 μm below the tip). In a lower level, the bigger wing presents three well-developed plications, and the smaller one has none (Fig. 4B; 170 μm below the tip). Below, there are four plications with different sizes *versus* two smaller plications with similar sizes (Fig. 4C, 300 μm below the apex).

The midvein region is much more developed at the leaf base (Fig. 4D, E) than at the apex (Fig. 4A–C). The connection of the innermost plication to the midvein at the leaf apex is shown in Fig. 4A–C. Below, the connection of other plications to the midvein is presented (Fig. 4D, 440 μm below the apex) up to the union of the most external plications to the midvein, just at the base of the leaf lamina (Fig. 4E, 580 μm below the apex).

The petiole region has an adaxial depression distally and embraces the next primordium (Fig. 4F, star, 690 μm below the apex). This depression is deeper in the middle of the petiole (Fig. 4G, 820 μm, and Fig. 4H, 940 μm, below the apex), and the sulcate petiole accommodates the youngest leaf primordia (Fig. 4G, H). Beneath, the petiole margins are very narrow (Fig. 3I, 1,070 μm below the apex), transitioning to the sheath region (Fig. 4J, 1,220 μm, Fig. 4K, 1,440 μm, and Fig. 4L, 1,570 μm, below the apex).

Analyzing the vascularization from the base to the distal region, procambial strands form a circle in the leaf sheath (Fig. 4J, K), two levels of a semicircle in the petiole (Fig. 4G–I), and a scattered pattern in the midvein (Fig. 4D, E). In the leaf margin, there is a vascular bundle from the leaf base to its apex (Fig. 4A–E), and it is more developed than those of the adaxial plications. The vascularization is poorly differentiated in the abaxial plications, which have fewer cell layers than the adaxial ones.

The two youngest primordia embraced by the external young leaf also exhibit one side larger than the other (Fig. 4F–I).

Discussion. Here we report for the first time the leaf development process in *E. oleracea*. Previous studies on leaf ontogenesis in palm species with pinnate leaves (Table 1) give support to our understanding of the events observed here.

More than two decades separate the most recent studies on leaf ontogeny (Nowak *et al*. 2007, 2008) from previous contributions (Table 1). The present work comprises a contemporary and detailed report of a palm leaf ontogenesis and

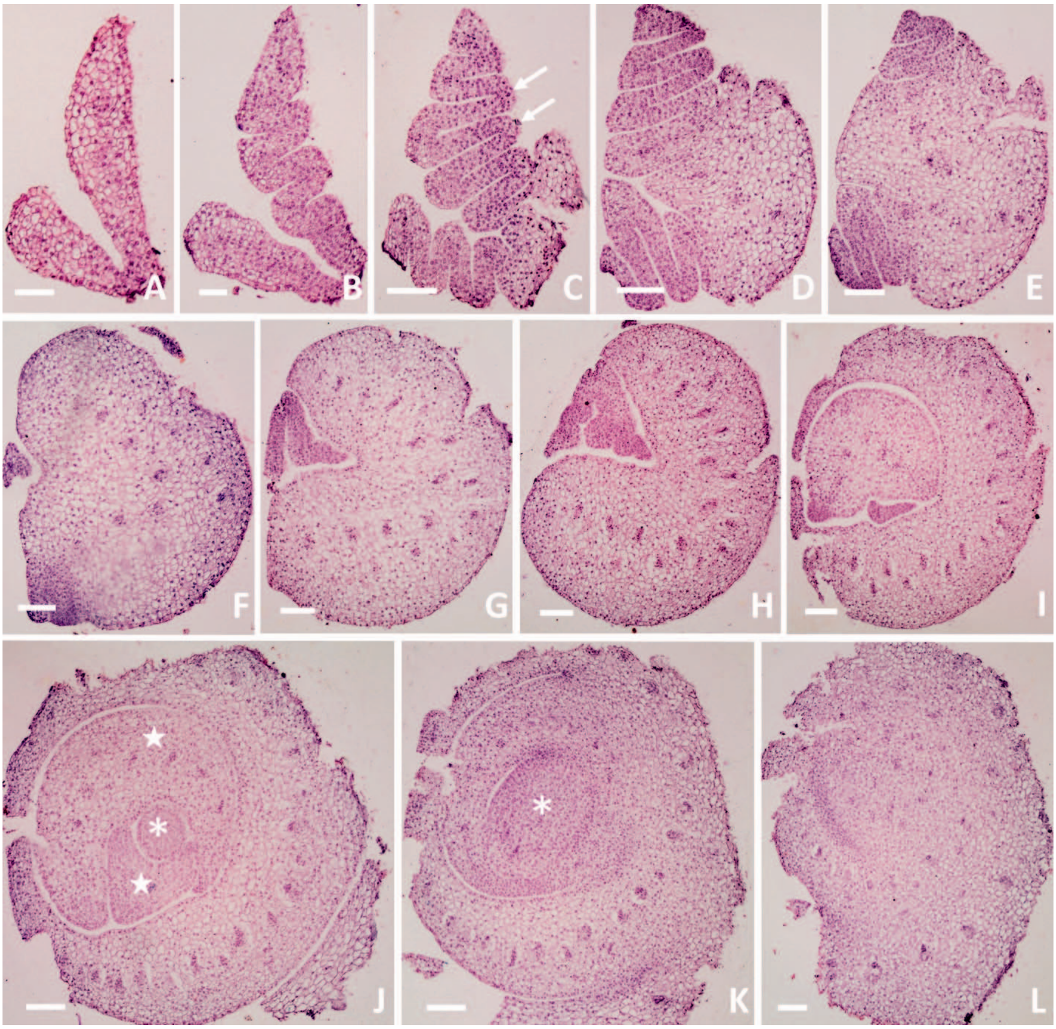

FIG. 4. Leaf ontogenesis of *Euterpe oleracea* Mart. III: primordium 2.0 mm long. Cross sections were performed at the following levels below apical tip: (A) 40 µm, (B) 170 µm, (C) 300 µm, (D) 440 µm, (E) 580 µm, (F) 690 µm, (G) 820 µm, (H) 940 µm, (I) 1,070 µm, (J) 1,220 µm, (K) 1,440 µm, and (L) 1,570 µm. Arrows: plications; stars: leaf primordia; asterisk: shoot apical meristem. Scale bars: A, B: 50 µm; C–L: 100 µm.

combines both micromorphological and histological illustration of the events.

Palms have complete amplexicaule leaves, and the origin of the distal lamina and tubular sheath is well documented (Eichler 1861; Arber 1918; Kaplan 1973). The leaf primordium emerges in the shoot apical meristem with a hood-shaped apex in their earliest stages, when the stem-encircling leaf base is formed, distinguishing the primordium regionally into a distal hooded lamina and a proximal tubular base (Kaplan *et al*. 1982a; Fig. 2A, B, F).

The bud is organized with several stages of development within a larger structure. An asymmetry was observed between both sides of the primordium mainly in the first stages of the palm leaf ontogeny, being called "cathodic" and "anodic" sides by some authors (Kaplan *et al*. 1982a; Nowak *et al*. 2007). This asymmetry is also well documented in the present work (Fig. 3C). According to Kaplan *et al*. (1982a), since the smallest side of the leaf is located within the leaf base of an older stage, it is subjected to compression, and it is reasonable to consider that

Table 1. Studies that approach the ontogeny of pinnate palm leaves. AR: Arecoideae; CO: Coryphoideae.

Species	Subfamily, tribe	References
Chamaedorea elegans Mart.	AR, Chamaedoreeae	Nowak *et al.* (2007)
Chamaedorea seifrizii Burret	AR, Chamaedoreeae	Kaplan *et al.* (1982a) Nowak *et al.* (2008)
Chrysalidocarpus lutescens H.Wendl. (now *Dypsis lutescens* (H.Wendl.) Beentje & J.Dransf.)	AR, Areceae	Kaplan *et al.* (1982b) Dengler *et al.* (1982)
Cocos nucifera L.	AR, Cocoseae	Venkatanarayana (1957)
Elaeis guineensis Jacq.	AR, Cocoseae	Yampolsky (1922)
Jubaeopsis caffra Becc.	AR, Cocoseae	Robertson (1983)
Phoenix dactylifera L.	CO, Phoeniceae	Naumann (1887) Deinega (1898)
Phoenix reclinata Jacq.	CO, Phoeniceae	Goebel (1884)
Phoenix sylvestris (L.) Roxb.	CO, Phoeniceae	Periasamy (1962) Padmanabhan (1967)
Roystonea O.F. Cook	AR, Roystoneeae	Eames (1953)

many processes that occur during leaf development may be due to a reduced space and mechanical constraints.

In the earliest stages of development, all cells present about the same size, but cells of the apical meristem of the leaf primordium are the smallest of all and are present in greater number than the others situated in different regions (Fig. 2B, D). According to Periasamy (1965), primordia first grow by perpetuative growth (growth due to an increase in the number of cells of nearly the same volume), but a differentiative growth (growth due to an increase in the volume of units of constant number) takes place in their regions that will not form plications. These processes seem to be occurring in the early stages of *E. oleracea* leaf development (Fig. 2D, E).

The differences between the two leaf sides could result in asymmetrical leaves. This asymmetry is observable mainly in the first stages of leaf development in *Chamaedorea* Willd. and *Dypsis* Noronha *ex*. Mart. (Kaplan *et al*. 1982a, 1982b). However, such asymmetry is not so evident when we analyze cross sections of *Syagrus inajai* (Spruce) Becc. embryos (Genovese-Marcomini *et al*. 2014). In our observations, cross sections through the primordia also revealed a clear asymmetry between the sides of the young leaf of *E. oleracea* (Fig. 4).

The presence of procambium on a still non-plicated primordium was observed in the classical works of Kaplan *et al*. (1982a, 1982b) and Dengler *et al*. (1982). Indeed, these authors state that there is a correlation among procambium emergence and plication formation since high cell proliferation within the original procambial strand causes provascular tissue to increase in coordination with the uprise of the adaxial ridge. A later vascular differentiation is present in *E. oleracea* since procambium appears in the primordium from about 2 mm, when virtually all plications are already developed, a result that matches with the palm genera *Cocos* L., *Borassus* L., *Caryota* L., and *Phoenix* L. by Periasamy (1966).

According to Nowak *et al*. (2008), segments in *Chamaedorea* are initially disposed in a vertical orientation, then they become oriented horizontally and assume again a vertical disposition in later stages of development, as we observed for *E. oleracea* in the present study (Fig. 3A, C, G). This change in plication orientation seems to be related to the amount of space available for the primordium, but it may also have a genetic influence. It was curious to observe some segments oriented horizontally and others vertically on the same primordium (Fig. 3I), indicating that leaf primordium sides do not change their orientation simultaneously, presenting a delay among them. The ecological meaning of this intriguing pattern can be the topic of further research concerning palm leaves.

The lines observed along the segments of primordia about 4 mm long (Fig. 3F, G) represent the first step of the stage of individual segments separating. This process is not exactly an abscission; it is rather an abscission-like mechanism since abscission requires that a given plant part become detached (Nowak *et al*. 2007). In palms with reduplicate leaves, such as *Elaeis oleifera* (Kunth) Cortés and *Cocos nucifera* L., a zone of schizogeny develops between major vascular bundles and involves epidermal and ground tissues only (Gunawardena and Dengler 2006), and this statement also seems to be true for *E. oleracea* (Fig. 3G, arrows).

The mechanism of leaf folding is not exclusive to palms. Other groups of monocots, such as Cyclanthaceae, also present plicated leaves in their ontogenetic process (Wilder 1976; Rudall 1990). However, despite their resemblance, Cyclanthaceae leaves evolved independently from Arecaceae leaves since there are significant differences among them, such as initiation site, presence of sheath and petiole morphology, number of costae, and direction of newly formed plications (Wilder 1976). Since Arecaceae and Cyclanthaceae are not closely related phylogenetically, this feature seems to have evolved independently in the two groups.

A Review on Some Leaf Terminologies. The very tip of primordia, which is formed in the initial stage of plant leaf development (Melo-de-Pinna and Cruz 2020), forms two longitudinal projections. Plications arise only below these projections, in the region that will become the adult leaf lamina, so leaves in palms are simple and dissected and not compound, just as pointed by De Candolle (1827), possibly the first to make the observation that palms have simple leaves.

In this sense, it is necessary to review the terminology to describe palm leaves in respect to their segmentation. For instance, Dransfield *et al.* (2008) consider “segments” the palm leaf units in palmatisect leaves and “pinnae” or “leaflets” in the pinnatisect ones. Nevertheless, since palm leaves are simple, the terms employed for pinnate leaves are questionable once they apply only for plants with compound leaves.

In some studies, the individual subunit of a mature palm leaf is sometimes referred to as “pinna” (*e.g.*, Defaveri *et al.* 2015; Simozrag *et al.* 2016; Salem and Ali 2020) or “leaflet” (*e.g.*, Kaplan *et al.* 1982a; Nowak *et al.* 2009; Noblick 2013; Vianna *et al.* 2017), while some works even employ both terms apparently as synonyms (Dransfield 1986; Kaplan 2001; Horn *et al.* 2009). Although Glassman (1972) uses only the term “pinna” in his classical work, his successor Noblick (2017) is one of the few researchers who adopts both terminologies, with the term “leaflet” most frequently employed throughout his article. Nevertheless, since both terms are used for eudicot compound leaves (Harris and Harris 1994; Vidal and Vidal 2000), we consider they are inadequate to be employed for the subunits of the palm leaves.

According to Bell and Bryan (2008), leaflets of pinnate-leaved plants develop from an isolated patch of marginal meristem, and hence each unit will be organized in a similar manner to a whole simple leaf. The authors also state that each leaflet has at its base a small petiole, named petiolule. This is clearly not the case for palms with simple pinnatisect leaves.

On the other hand, for palms with palmate leaves, the terminology “segment” is commonly used by Dransfield *et al.* (2008) to designate the blade subunits. “Segment” is employed in plant sciences with a much wider meaning to refer to the sections or divisions of a plant organ (Harris and Harris 1994). Thus, we propose that the term “segment” be used to name all units of palm leaves regardless of being pinnatisect or palmatisect. In a previous work, we already used the terminology “segment” instead of “pinna” and “leaflet” precisely thinking about the consistency of this hypothesis (Pinedo *et al.* 2016).

The term “rachis” is also inadequate since it is employed to designate the midvein of compound leaves (Font Quer 1953). We propose to renounce the term “rachis” and standardize the terminology “midrib” for palm leaves, as is seen for the simple leaves of other plants. This can also be applied to other plants with simple sectioned leaves, such as Cyclanthaceae.

Conclusion. The monitoring of the distinct stages of development of *E. oleracea* revealed many similarities with previous works for pinnate palms, highlighting that the ontogeny of palm leaves tends to follow a general pattern, with some few peculiarities for each species. The review of terminologies proposed in the present study, despite being used for a long time by researchers, allows an appropriate description of the palm leaves. Moreover, *E. oleracea* ontogeny in later stages of development is still unknown, and the process of segment separation needs to be analyzed.

Literature Cited

Arber, A. 1918. The phyllode theory of the monocotyledonous leaf, with special reference to anatomical evidence. Annals of Botany 32: 465–501.

Barabé, D., L. Bourque, X. Yin, and C. Lacroix. 2010. Phyllotaxis of the palm *Euterpe oleracea* Mart. at the level of the shoot apical meristem. Botany 88: 528–536.

Bell, A. D. and A. Bryan. 2008. Plant Form: An Illustrated Guide to Flowering Plant Morphology. Timber Press, Portland, OR. 342 pp.

Carvalho, R. M., F. R. Martins, and F. A. Santos. 1999. Leaf ecology of pre-reproductive ontogenetic stages of the palm tree *Euterpe edulis* Mart. (Arecaceae). Annals of Botany 83: 225–233.

Ceolin, G. B., A. Rücker, and J. G. Kray. 2007. Análise epidérmica foliar na diferenciação de plântulas de *Geonoma schottiana* e *Euterpe edulis* (Arecaceae). Revista Brasileira de Biociências 5: 18–20.

Conklin, P. A., J. Strable, S. Li, and M. J. Scanlon. 2019. On the mechanisms of development in monocot and eudicot leaves. New Phytologist 221: 706–724.

De Candolle, A. P. 1827. Organographie végétale ou description raisonnée des organes des plantes: Pour servir de suite et de développement à la Théorie élémentaire de la botanique et d'introduction à la Physiologie végétale et à la Description des familles, Vol. 1. Germer Baillère, Libraire-Éditeur, Paris, France. 558 pp.

Defaveri, A. C. A., C. F. Barros, R. C. O. Arruda, N. K. Simas, and A. Sato. 2015. *Allagoptera arenaria* (Arecaceae): Leaf anatomy of a palm from the Brazilian shore. Brittonia 67: 336–349.

Deinega, V. 1898. Beiträge zur Kenntnis der Entwickelungsgeschichte des Blattes und der Anlage der Gefassbündel. Flora (Jena, 1818–1965) 85: 439–498.

Dengler, N. G., R. E. Dengler, and D. R. Kaplan. 1982. The mechanism of plication inception in palm leaves: Histogenetic observations on the pinnate leaf of *Chrysalidocarpus lutescens*. Canadian Journal of Botany 60: 2976–2998.

Dransfield, J. 1986. A guide to collecting palms. Annals of the Missouri Botanical Garden 73: 166–176.

Dransfield, J., N. W. Uhl, C. B. Asmussen, W. J. Baker, M. M. Harley, and C. E. Lewis. 2008. Genera Palmarum: The Evolution and Classification of Palms. Board of Trustees of Royal Botanic Gardens, London, UK. 732 pp.

Eames, A. J. 1953. Neglected morphology of the palm leaf. Phytomorphology 3: 172–189.

Efroni, I., Y. Eshed, and E. Lifschitz. 2010. Morphogenesis of simple and compound leaves: A critical review. The Plant Cell 22: 1019–1032.

Eichler, A. W. 1861. Zur Entwicklungsgeschichte des Blattes mit besonderer Berucksichtigung der Nebenblatt-Bildungen: Mit 2. Tafeln, Marburg, Germany. 60 pp.

Font Quer, P. 1953. Diccionario de botánica. Labor, Barcelona, Spain. 1280 pp.

Gatti, M. G., P. I. Campanello, and G. Goldstein. 2011. Growth and leaf production in the tropical palm *Euterpe edulis*: Light conditions versus developmental constraints. Flora-Morphology, Distribution, Functional Ecology of Plants 206: 742–748.

Genovese-Marcomini, P. R., M. S. Mendonça, and S. M. Carmello-Guerreiro. 2014. Embryonic development of *Syagrus inajai* (Spruce) Becc. (Arecaceae, Arecoideae), an Amazonian palm. Australian Journal of Botany 61: 611–621.

Glassman, S. 1972. Systematic studies in the leaf anatomy of palm genus *Syagrus*. American Journal of Botany 59: 775–788.

Goebel, K. 1884. Vergleichende Entwickelungsgeschichte der Pflanzenorgane. Schenk's Handbuch der Botanik, Vol. 3. Verlag von Eduard Trewendt, Breslau, Germany. 432 pp.

Gunawardena, A. H. and N. G. Dengler. 2006. Alternative modes of leaf dissection in monocotyledons. Botanical Journal of the Linnean Society 150: 25–44.

Harris, J. G. and M. W. Harris. 1994. Plant Identification Terminology: An Illustrated Glossary. Spring Lake Publishing, Genola, UT. 216 pp.

Henderson, A. J. 1999. A phylogenetic analysis of the Euterpeinae (Palmae; Arecoideae; Areceae) based on morphology and anatomy. Brittonia 51: 106–113.

Henderson, A. J. and G. Galeano. 1996. *Euterpe*, *Prestoea*, and *Neonicholsonia* (Palmae). Flora Neotropica 72: 1–89.

Horn, J. W., J. B. Fisher, P. B. Tomlinson, C. E. Lewis, and K. Laubengayer. 2009. Evolution of lamina anatomy in the palm family (Arecaceae). American Journal of Botany 96: 1462–1486.

Johansen, D. A. 1940. Plant Microtechnique. McGraw-Hill, London, UK, 530 pp.

Kang, J. and N. R. Sinha. 2010. Leaflet initiation is temporally and spatially separated in simple and complex tomato (*Solanum lycopersicum*) leaf mutants: A developmental analysis. Botany 88: 710–724.

Kaplan, D. R. 1973. Monocotyledons—Their evolution and comparative biology. 7. Problem of leaf morphology and evolution in monocotyledons. Quarterly Review of Biology 48: 437–457.

Kaplan, D. R. 2001. Fundamental concepts of leaf morphology and morphogenesis: A contribution to the interpretation of molecular genetic mutants. International Journal of Plant Sciences 162: 465–474.

Kaplan, D. R., N. G. Dengler, and R. E. Dengler. 1982a. The mechanism of plication inception in palm leaves: Problem and developmental morphology. Canadian Journal of Botany 60: 2939–2975.

Kaplan, D. R., N. G. Dengler, and R. E. Dengler. 1982b. The mechanism of plication inception in palm leaves: Histogenetic observations on the palmate leaf of *Rhapis excelsa*. Canadian Journal of Botany 60: 2999–3016.

Kraus, J. E. and M. Arduin. 1997. Manual básico de métodos em morfologia vegetal. Ed. Universidade Federal Rural do Rio de Janeiro, Rio de Janeiro, Brazil.

Kuo, J. 2007. Electron Microscopy: Methods and Protocols, Vol. 369. Humana Press. Totowa, NJ. 817 pp.

Melo-de-Pinna, G. F. A. and R. Cruz. 2020. Leaf development in vascular plants, pp. 83–105. *In* Demarco, D., org. Plant Ontogeny: Studies, Analyses and Evolutionary Implications. Nova Science Publishers, New York, NY.

Naumann, A. 1887. Beiträge zur Entwickelungsgeschichte der Palmenblätter. Flora 70: 193–257.

Neto, M. A. M., A. D. S. Lobato, J. D. Alves, P. F. P. Goulart, and H. D. Laughinghouse IV. 2010. Seed and seedling anatomy in *Euterpe oleracea* Mart. during the germination process. Journal of Food, Agriculture and Environment 8: 1147–1152.

Noblick, L. R. 2013. Leaflet anatomy verifies relationships within *Syagrus* (Arecaceae) and aids in identification. PhytoKeys 26:75–99.

NOBLICK, L. R. 2017. A revision of the genus *Syagrus* (Arecaceae). Phytotaxa 294: 1–262.

NOWAK, J., N. G. DENGLER, AND U. POSLUSZNY. 2007. The role of abscission during leaflet separation in *Chamaedorea elegans* (Arecaceae). International Journal of Plant Sciences 168: 533–545.

NOWAK, J., N. G. DENGLER, AND U. POSLUSZNY. 2008. Abscission-like leaflet separation in *Chamaedorea seifrizii* (Arecaceae). International Journal of Plant Sciences 169: 723–734.

NOWAK, J., A. NOWAK, AND U. POSLUSZNY. 2009. Developmental comparison of leaf shape variation in three *Chamaedorea* species. Botany 87: 210–221.

PADMANABHAN, D. 1967. Some aspects of histogenesis in the leaf of *Phoenix sylvestris* L. Proceedings of the Indian Academy of Science – Section B 65: 221–229.

PAIVA, J. G. A. D., S. M. FANK-DE-CARVALHO, M. P. MAGALHÃES, AND D. GRACIANO-RIBEIRO. 2006. Verniz vitral incolor 500®: Uma alternativa de meio de montagem economicamente viável. Acta Botanica Brasilica 20: 257–264.

PANZA, V., V. LAINEZ, AND S. MALDONADO. 2004. Seed structure and histochemistry in the palm *Euterpe edulis*. Botanical Journal of the Linnean Society 145: 445–453.

PERIASAMY, K. 1962. Morphological and ontogenetic studies in palms. I. Development of the plicate condition in the palm-leaf. Phytomorphology 12: 54–64.

PERIASAMY, K. 1965. Morphological and ontogenetic studies in Palms. II. Growth pattern of the leaves of *Cocos nucifera* and *Borassus flabellifer* after the initiation of plications. Australian Journal of Botany 13: 225–234.

PERIASAMY, K. 1966. Morphological and ontogenetic studies in Palms. IV. Ontogeny of the vascular pattern in four genera. Australian Journal of Botany 14: 277–291.

PICHARDO-MARCANO, F. J., M. E. NIETO-BLÁZQUEZ, A. N. MACDONALD, G. GALEANO, AND J. RONCAL. 2019. Phylogeny, historical biogeography and diversification rates in an economically important group of Neotropical palms: Tribe Euterpeae. Molecular Phylogenetics and Evolution 133: 67–81.

PINEDO, A. S., R. C. MARTINS, R. C. OLIVEIRA, AND S. M. GOMES. 2016. Leaf anatomy in *Allagoptera* (Arecaceae). Botanical Journal of the Linnean Society 182: 361–375.

PORTELA, R. D. C. Q. AND F. A. M. D. SANTOS. 2011. Ontogenetic stages characterization for three palm species: A proposal of standardization for population dynamics studies. Brazilian Journal of Botany 34: 523–535.

RIBEIRO, G., J. PESSOA, AND M. ARDUIN. 2012. Anatomia e ontogenia dos frutos do açaizeiro: aspectos estruturais e microquímicos, pp. 63–80. *In* Pessoa, J. D. C. and G. H. A. Teixeira, eds. Tecnologias para inovação nas cadeias *Euterpe*. Embrapa, Brasilia, Brazil.

ROBERTSON, B. L. 1983. Leaf development in *Jubaeopsis caffra* (Becc.). Annals of Botany 51: 555–557.

RUDALL, P. 1990. Comparative leaf morphogenesis in Iridaceae. Botanische Jahrbücher für Systematik 112: 241–260.

SALEM, E. H. AND H. A. ALI. 2020. Effect of slow-release fertilizers on growth and fruiting of Khalas date palm. SVU-International Journal of Agricultural Sciences 2: 30–44.

SHANI, E., H. BEN-GERA, S. SHLEIZER-BURKO, Y. BURKO, D. WEISS, AND N. ORI. 2010. Cytokinin regulates compound leaf development in tomato. The Plant Cell 22: 3206–3217.

SIMOZRAG, A., A. CHALA, A. DJEROUNI, AND M. E. BENTCHIKOU. 2016. Phenotypic diversity of date palm cultivars (*Phoenix dactylifera* L.) from Algeria. Gayana Botanica 73: 42–53.

SMITH, N. 2014. Palms and People in the Amazon. Springer, Heidelberg, Germany. 513 pp.

THIERS, B. 2021. Continuously updated. Index Herbariorum: A Global Directory of Public Herbaria and Associated Staff. New York Botanical Garden's Virtual Herbarium, New York, NY. http: //sweetgum.nybg.org/ih. Retrieved August 9, 2021.

VENKATANARAYANA, G. 1957. On certain aspects of the development of the leaf of *Cocos nucifera* L. Phytomorphology 7: 297–305.

VIANNA, S. A., S. M. CARMELO-GUERREIRO, L. R. NOBLICK, AND C. A. COLOMBO. 2017. Leaf anatomy of *Acrocomia* (Arecaceae): An additional contribution to the taxonomic resolution of a genus with great economic potential. Plant Systematics and Evolution 303: 233–248.

VIDAL, W. N. AND M. R. R. VIDAL. 2000. Botânica: Organografia. Editora UFV, Viçosa, Brazil. 113 pp.

WILDER, G. J. 1976. Structure and development of leaves in *Carludovica palmata* (Cyclanthaceae) with reference to other Cyclanthaceae and Palmae. American Journal of Botany 63: 1237–1256.

YAMPOLSKY, C. 1922. A contribution to the study of the oil palm *Elaeis guineensis* Jacq. Bulletin du Jardin Botanique de Buitenzorg 5: 107–174.