

Floral Structure in the Neotropical Tribes Leopoldinieae and Manicarieae (Arecaceae: Arecoideae)

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Floral structure is studied in detail for the first time in the monogeneric neotropical tribes Leopoldinieae and Manicarieae (Arecaceae). In order to infer taxonomic relationships of these groups, morphological and anatomical data in members of the two tribes are compared with available studies in other tribes of the basal clades of the core arecoids, as defined by recent molecular phylogenies. Our results suggest an isolated position for *Manicaria* and highlight unexpected affinities between the tribe Leopoldinieae and representatives of the western Pacific Ocean tribe Pelagodoxeae.

The genus *Leopoldinia*, dedicated to the archduchess of Austria, Josefa Carolina Leopoldina, was described in 1824 by the celebrated palm botanist Carl F. P. von Martius (1794–1868) (Figs. 1–6). It represents the single representative of the neotropical tribe Leopoldinieae (Martius 1824). The genus *Manicaria* was described in 1791 by the German botanist Joseph Gaertner (1732–1791) and corresponds with the single representative

of the tribe Manicarieae, as defined by Dransfield et al. (2008) (Figs. 7–12). These two remarkable monogeneric tribes belong to the large subfamily Arecoideae, known to be the largest and most diverse subfamily within palms (Dransfield et al. 2008). The tribes Manicarieae and Leopoldinieae represent two basal lineages of the core arecoid clade as defined by Baker and Couvreur (2012), here called “basal core arecoids,” including also

tribes Pelagodoxeae, Euterpeae and Geonomateae.

The number of species within *Leopoldinia* and *Manicaria* remains a subject of taxonomic debate. In the case of *Leopoldinia*, different numbers of species have been proposed since the description of the genus. Hence, Martius (1824) recognized two species, whereas Wallace (1853) increased the number to three, a taxonomic point of view that was supported by Henderson (1995). Bernal and Galeano (2010) recognized only two species and more recently, Henderson (2011) proposed that all species published so far for the genus (*L. piassaba* Wallace, *L. major* Wallace and *L. pulchra* Mart.) should be recognized as valid. A similar situation can be traced in *Manicaria*, a genus described by Gaertner (1791) based on only one species (*Manicaria saccifera* Gaertn.). Different taxonomic and floristic treatments on the genus have recognized three species (i.e. Wessels Boer 1988) or only one (i.e. Henderson 1995). More recently, Bernal and Galeano (2010) have recognized *M. martiana* Burret and *M. saccifera* Gaertn. as the only two accepted species for the genus.

Both genera are distributed in the neotropical region. *Manicaria* has a wide distribution, ranging from Central America, across Trinidad, the Orinoco Delta and the Guianas to the lower Amazon River (Dransfield et al. 2008). In contrast, *Leopoldinia* is an endemic palm genus of the Amazon basin, restricted to the Rio Negro and upper Orinoco region of Venezuela, Colombia and Brazil (Dransfield et al. 2008, Henderson 1995, Stauffer 2000). Representatives of both genera have been reported to be economically important for indigenous groups of the Amazon and Orinoco basins. At least two species of *Leopoldinia* (*L. piassaba*, *L. pulchra*) have been reported as economically important for their stems (Fig. 6), fibers, leaves and fruits (Putz 1979), whereas the leaves of *Manicaria* are used primarily for thatching (Dransfield et al. 2008) by ethnic groups such as the Warao Indians from the Orinoco delta region (Fig. 12).

The molecular phylogenetic relationships of Leopoldinieae and Manicarieae with the remaining tribes of Arecoideae are not yet completely understood. Both tribes are included in the "core" arecoid clade, but their precise position remains unclear (Dransfield et al. 2008). The Manicarieae was found to be sister to the Geonomateae in the RFLP tree of Uhl et al. (1995); this relationship was

suggested also by Asmussen et al. (2006) in the Plastid DNA tree and supported by the supertree of Baker et al. (2009). However, the *prk*-based phylogeny of Lewis and Doyle (2002) and the combined *prk* & *rpb2* tree of Baker et al. (2011) placed the Manicarieae as sister to a clade composed of the tribes Euterpeae, Leopoldinieae, Pelagodoxeae, Geonomateae and included the tribe Leopoldinieae in their plastid DNA tree for the first time in a molecular phylogeny of the palm family. In this analysis the tribe was resolved as sister to the Manicarieae. Later, the Leopoldinieae was resolved as sister to Euterpeae (Lewis & Doyle 2002, Loo et al. 2006) and as sister to the Areceae/Euterpeae, Geonomateae and Manicarieae clades in the plastid DNA tree of Hahn (2002). A sister relationship of Leopoldinieae with the Manicarieae/Geonomateae clade was indicated by Asmussen et al. (2006) and recovered by the study of Baker et al. (2009). In all these phylogenies the relationships of the tribe Leopoldinieae with other arecoid groups was always resolved with low bootstrap support. Norup et al. (2006) proposed a sister relationship, although with moderate bootstrap support, between Leopoldinieae and Pelagodoxeae, the latter endemic to the Marquesas Islands and the western half of the mainland New Guinea. The same relationship was recovered by Baker et al. (2011), with strong bootstrap support. This relationship is surprising because both tribes, Leopoldinieae and Pelagodoxeae, display highly disjunct and geographically isolated distribution patterns (Dransfield et al. 2008). The most recent molecular phylogenetic analysis of the palm family confirms previous studies in which Leopoldinieae is resolved as sister to a clade composed of the tribes Geonomateae and Manicarieae (Baker & Couvreur 2012). The Old World tribe Pelagodoxeae, composed of the genera *Pelagodoxa* and *Sommieria*, remains relatively close in the topology presented.

Morphology and anatomy of palm reproductive structures have been studied in detail in only 4% of the almost 2500 palm species (Stauffer et al. 2002). Floral structure, especially anatomy has never been studied in detail in *Leopoldinia* and *Manicaria*. Information on gross morphological characters has been provided for members in all tribes of the basal core arecoids (Dransfield et al. 2008), but the floral structure has been studied in detail in only three of them: Pelagodoxeae (Stauffer et al. 2004), Geonomateae (Stauffer & Endress

2003, Stauffer et al. 2003), and Euterpeae (Kuchmeister et al. 1997). As a contribution to the understanding of the reproductive structures in arecoid palms and in order to explore relationships of the two enigmatic monogeneric tribes Leopoldinieae and Manicarieae within the core arecoid clade, a thorough study of the floral structures of *Leopoldinia piassaba*, *Leopoldinia pulchra* and *Manicaria saccifera* has been conducted. The specific aims of the present study are (1) to contribute to a better understanding of the floral structure of the neotropical tribes Leopoldinieae and Manicarieae and (2) to explore the systematic relationships of Leopoldinieae and Manicarieae with other groups of the basal clade of the core arecoids using floral structural characters.

Materials and Methods

The morphological and anatomical study was based on flowers collected from wild populations and fixed in alcohol (Table 1). Inflorescences at several stages of development and young infructescences of *L. piassaba* and *L. pulchra* were collected by Dr. Lorena Guevara (Venezuelan Central University) and also obtained from the spirit collection of the L. H. Bailey Hortorium (Cornell University, Ithaca, USA). In both cases the material was originally

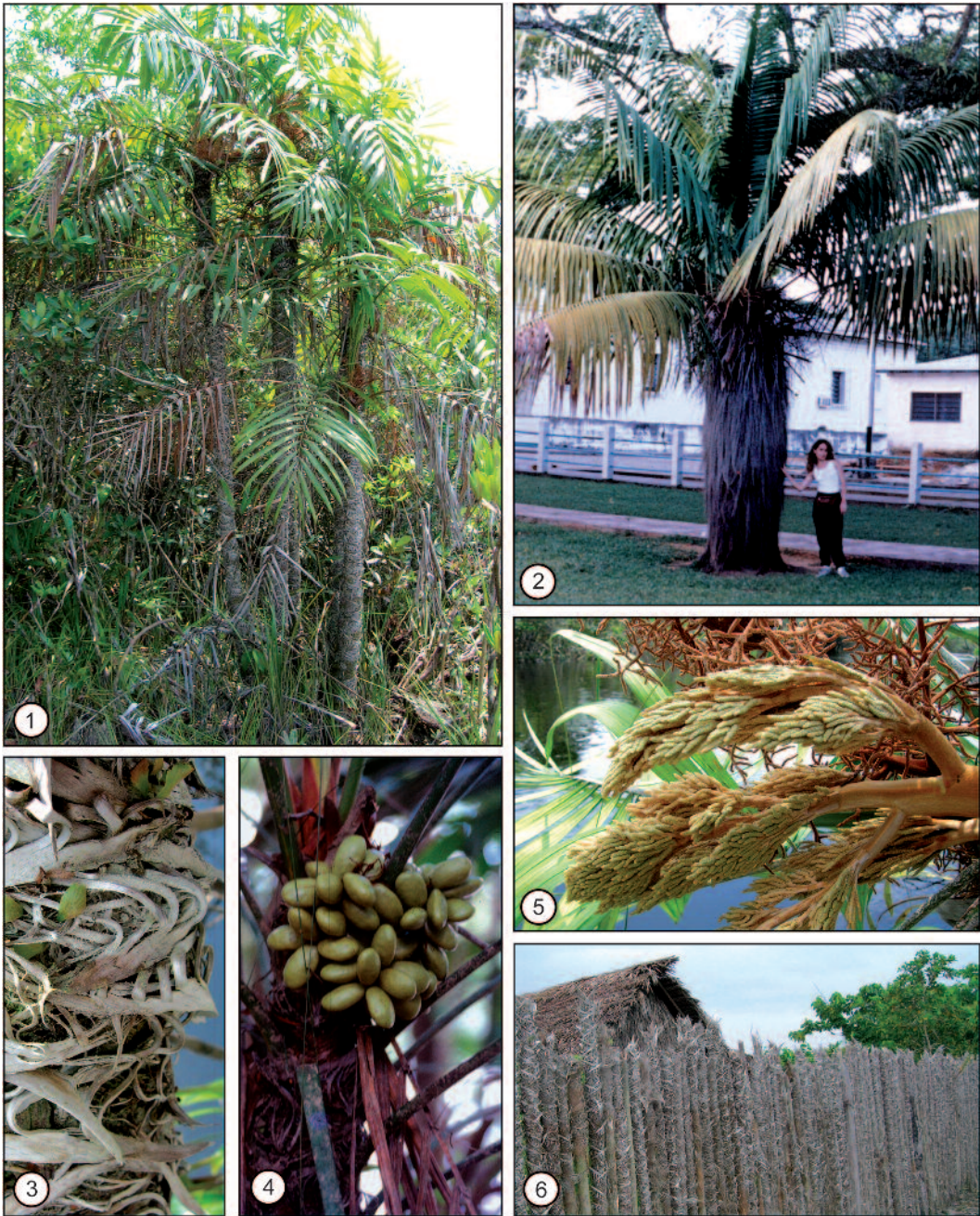
collected in the Venezuelan Amazon. Male and female flowers at bud stage of *M. saccifera* were collected by FWS in the Orinoco Delta (Venezuela).

For the anatomical investigations, small fragments of rachillae or individual flowers were evacuated, dehydrated and embedded in the resin Kulzer's Technovit 7100 (2-hydroxyethyl methacrylate [HEMA]). Further details of this techniques are given in Igersheim and Cichocki (1996). The material was serially cross sectioned and longitudinally sectioned at 7–10 µm using a rotary microtome (Leitz 1512), stained with ruthenium red and toluidine blue and mounted in Assistant-Histokitt mounting medium. Observations and photographs were made with a digital light microscope (NIKON Eclipse 80i) at the Laboratory of Cytology and Vegetal Histology (University of Geneva); the permanent slides were deposited at the Laboratory of Micro-Morphology of the Conservatory and Botanical Garden of Geneva.

For scanning electron microscopy (SEM), fragments of inflorescences, individual flowers and individual floral organs were dehydrated, critical-point dried and sputter-coated with gold. Micrographs were obtained using a Zeiss DSM 940A SEM (Orion 6.60 Imaging System)

Table 1. Plant material studied

Species	Collection	Reproductive status	Repository
<i>Leopoldinia piassaba</i>	Guanchez s.n. (19 Oct. 1990)	Fruits	L.H. Bailey
Wallace	Guanchez s.n. (22 Oct. 1990)	Fruits	Hortorium
	Guanchez s.n.	Pre-anthetic ♀ buds	
	Guanchez 5080	Late ♀ buds	
	Guanchez 5081	♀ buds	
<i>Leopoldinia pulchra</i>	Guanchez 4912	Early fruits	L.H. Bailey
Mart.	Guanchez 4911	Early fruits	Hortorium
	Guanchez s.n. (06 Oct. 1990)	♂ buds	
	Guanchez s.n.	Early ♂ and ♀ buds	
	Guevara 79a	♂ buds	Venezuelan
	Guevara 79b	Early ♂ and ♀ buds	Central Univ.
	Guevara 78	Early ♂ buds	
<i>Manicaria saccifera</i>	Stauffer (Feb. 2012)	Late ♀ and ♂ buds	Conservatory
Gaertn.			and Botanical Garden of Geneva



1. Habit of *Leopoldinia pulchra*. 2. Habit of *L. piassaba*. 3. Stem surface with leaf sheaths of *L. pulchra*. 4. Inflorescence of *L. pulchra*. 5. Inflorescence of *L. pulchra*. 6. Fences constructed with stems of *L. pulchra* by indigenous tribes of the Orinoco region. (photos: L. Guevara and F. Stauffer)

at the Natural History Museum of Geneva, Switzerland.

Results

Flower morphology and anatomy of *Leopoldinia*

The inflorescence is interfoliar and bears unisexual flowers sunken in shallow pits. The

female flowers are solitary or arranged in triads with two male flowers (Fig. 14) flanking one central female flower. Solitary female flowers are usually more robust than the ones borne in combination with male flowers. When not in floral triads, male flowers are either solitary or inserted in dyads; they are surrounded by a brown, dense tomentum (Fig. 13).

The male flowers are sessile, oblong, ovoid, 1 mm long or even smaller in diameter, in all cases smaller than the pistillate flowers. The calyx reaches one-third of the flower length and is composed of three distinct, imbricate, keeled and striate sepals, with toothed margins. The corolla is composed of three distinct, valvate, triangular-ovate petals, with entire margins. The petals are on the inner side marked by the impression of the anthers. The androecium is composed of six, latrorse, dorsifixed stamens (Figs. 15 & 16). Three stamens are antepetalous and three antesepalous. The ones in the antesepalous position are attached at a slightly lower level than the antepetalous. The filaments are short, broad and connate only at the very base; they have inflexed tips. The anthers are short and ovate in a cross-section (Fig. 17). The pistillode has a three-lobed barrel shape.

The female flowers are sessile, globose, 2.5–3 mm long and 2.5–3 mm in diameter at late bud stage. The calyx is composed of three distinct, imbricate, rounded and membranous sepals, with slightly toothed margins. The corolla is composed of three distinct, valvate, rounded petals, with entire margins. The sterile androecium is represented by six reduced staminodes, which are short, flat and truncate. The gynoecium is synascidiate, composed of three postgenitally united carpels, which at mid-height of the ovary become separated. No epithelium that could be associated with a septal nectary was identified in the carpel flanks. The gynoecium is trilocular and triovulate; however, only one ovule fully develops towards anthesis. The stage of development of the ovule characterizes the shape of the gynoecium, ranging from slightly pyramidal to rounded (Figs. 18, 19). The ovule is campylotropous, bitegmic, crassinucellate and hanging; it is laterally attached to the ventral side of the locule and fills the entire cavity (Fig. 20). Towards the micropyle the outer and inner integuments are 8 and 4 cell layers thick, respectively; the micropyle is straight and slightly expanded due to the large obturator. The three stigmatic branches are lined with unicellular papillae. The pollen tube transmitting tract (PTTT) separates downwards in three branches, corresponding to the three locules. It reaches the ovule by surrounding the funiculus.

The base of the female flower is characterized by a six cell layers thick transition zone of square or rhomboid cells that may be interpreted as an abscission zone. Tanniferous

idioblasts were observed in the mesophyll of the gynoecium, especially from the base up to the mid-height of the ovary. Tanniferous idioblasts were also observed in the pistillode of the male flowers. Raphide idioblasts were not seen in the tissues studied.

Flower morphology and anatomy of *Manicaria*

The inflorescence is interfoliar and bears unisexual flowers sunken in pits. The staminate flowers are solitary and spirally arranged on the entire rachillae, whereas only few pistillate flowers concentrate at the base of the rachilla.

The male flowers are oblong, asymmetrical, 5 mm long and 4 mm wide. The calyx is composed of three slightly imbricate, distinct sepals, which are membranous, irregular in size and shape, slightly keeled, with fibrous variously notched margins. The corolla is composed of three, very thick valvate petals (Fig. 25), one remarkably smaller than the others. The petals are distinct and adnate to the base of the filaments of the peripheral stamens. The androecium is polyandrous (Figs. 21, 22, 24), with ca. 20–25 introrsely dehiscent, dorsifixed stamens; the length of the filaments and the anthers, including the shape of the latter, vary according to the position of the stamen in the androecium. Two filaments connate up to the level of the anthers were observed in some flowers; pistillode lacking.

The pistillate flowers are oblong, ovoid, 9 mm long and 6 mm in diameter, slightly compressed and asymmetrical. The calyx is composed of three imbricate sepals, which are distinct, membranous and irregular in size and shape, with fibrous margins. The corolla is composed of three very thick petals, two notably larger than the remaining one. The petals are valvate with an obtuse apex and congenitally fused up to 4–5 mm, with entire margins. Staminodes 9, small, thin, basally adnate to the ovary, upwards free; each staminode is served by one central vascular bundle; six staminodes are antepetalous and oblong in cross-section, whereas three are antesepalous and triangular in cross-section (Fig. 28). The gynoecium is obovoid, composed of three congenitally united carpels; all of them are equally developed at late bud stage, giving to the gynoecium a triangular shape in cross-section (Fig. 29). The ovary region is ovoid, topped with a pyramidal stigma with three clearly differentiated branches; the style is short. The PTTT is common at the stigmatic-



7. Habit of *Manicaria saccifera*. 8. Leaves; 9. Inflorescence. 10. Detail of a cross-sectioned fruit. 11. Portion of inflorescence with male flowers at late bud. 12. Thatching constructed by the Warao Indians in the Orinoco Delta. (photos: L. Guevara and F. Stauffer)

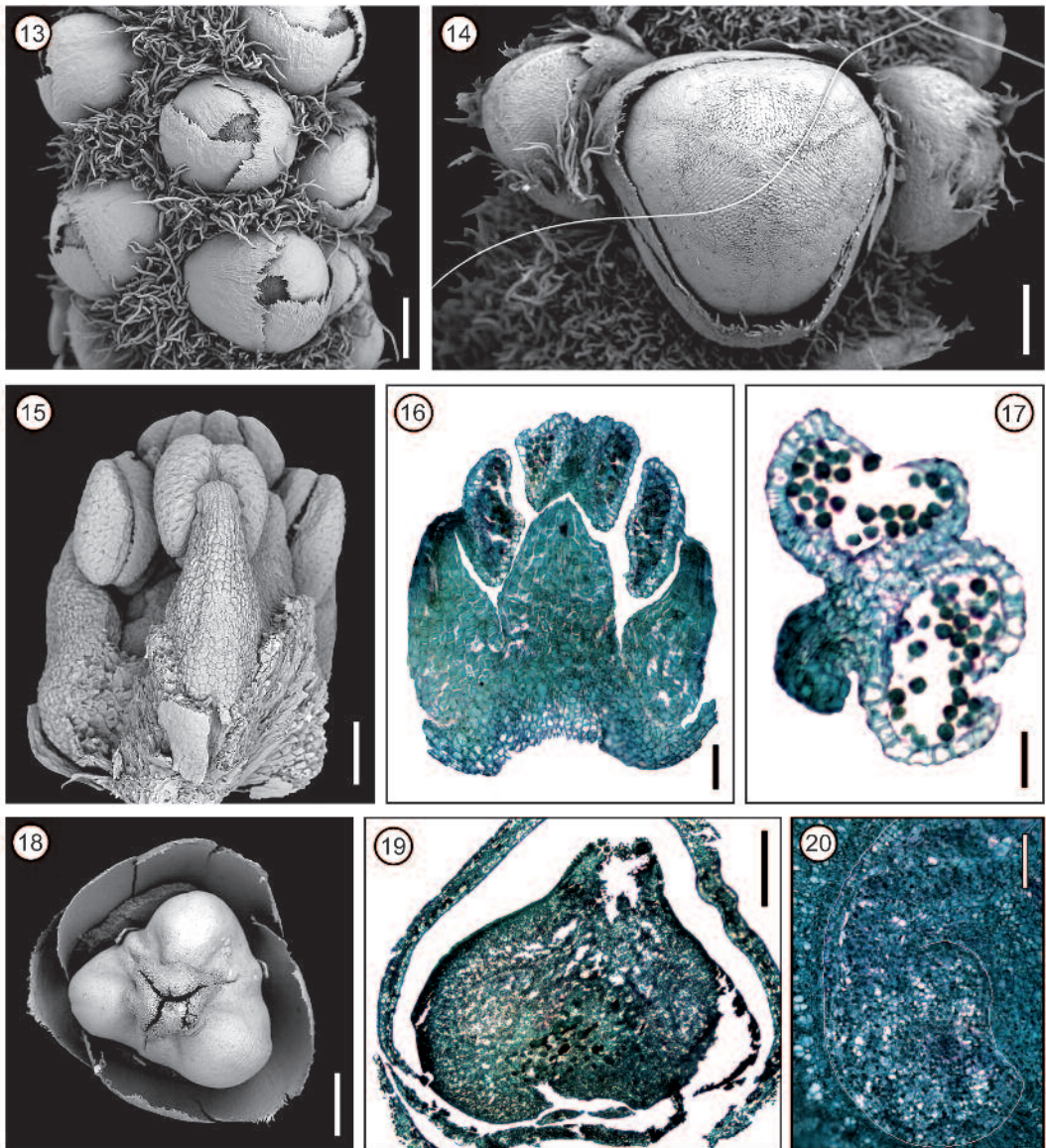
style region and separates downwards in three branches, one directing each locule. It reaches the ovule by surrounding the funiculus. The gynoecium is trilobulate and triovulate. The ovule is anatropous, bitegmic and crassinucellate (Fig. 23). It is attached to the ventral side and in the upper half of the locule and fills the entire cavity.

The whole gynoecium is highly vascularized, especially in the peripheral zones corresponding with the thick ovary walls (Fig. 27). Each carpel is served by one dorsal vascular bundle, 10–12 lateral procambial strands and four ventral vascular bundles. Vascular bundles were also clearly observed in

the region of the chalaza (Fig. 26). Tannins idioblasts concentrate at the base of the gynoecium but were also observed throughout the gynoecium, around the three ovules. These tanniferous idioblasts were not observed in the ovary walls. The lack of tannins in the ovary walls enables to distinguish two types of mesophylls in the cross-section of the gynoecium (Fig. 27). Raphide idioblasts were not seen in the tissues studied.

Discussion

This paper represents a contribution to the knowledge of the floral structure in the tribes Manicarieae and Leopoldinieae. The floral structure of *Leopoldinia* and *Manicaria* had

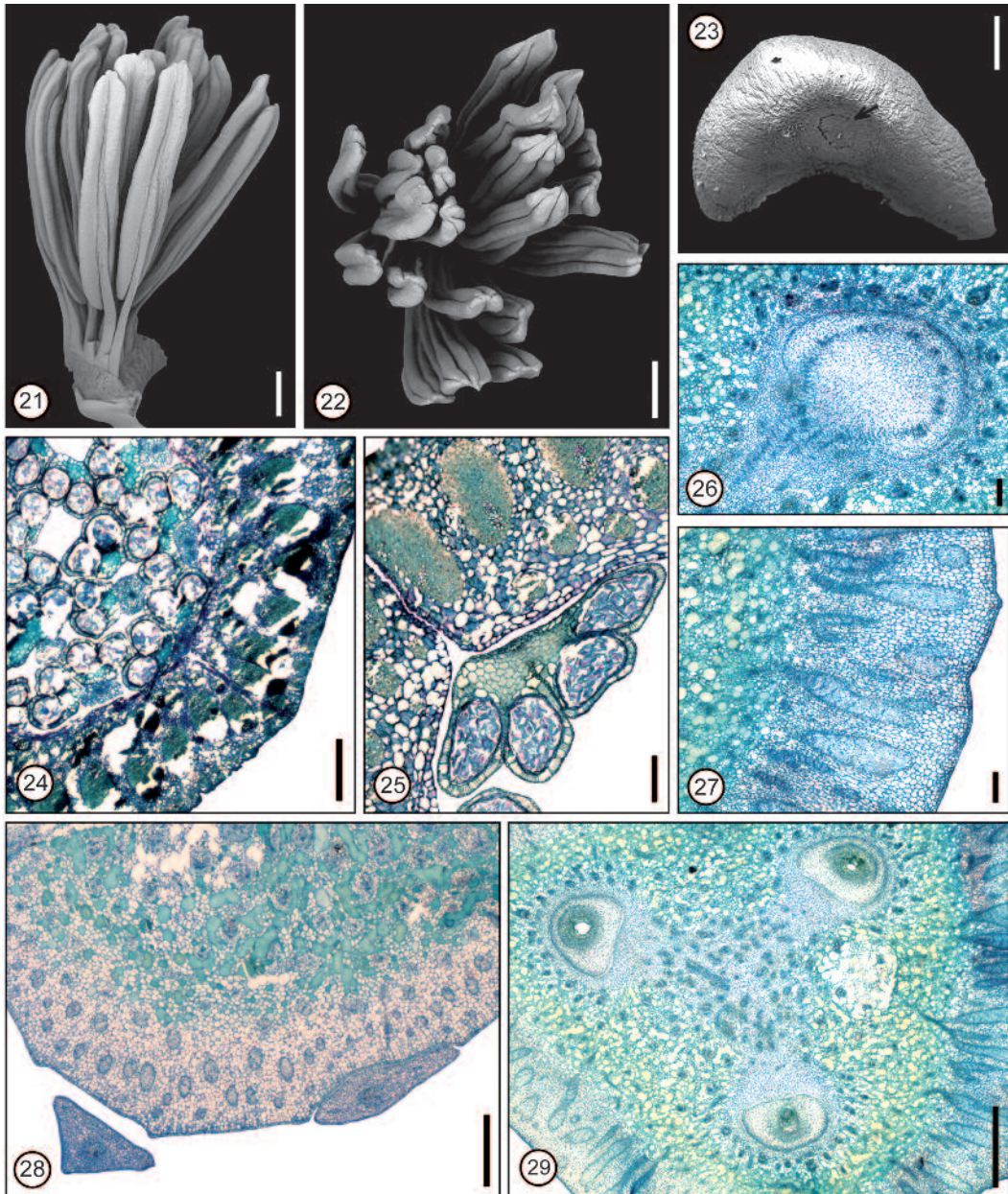


13–20. Morphology and anatomy of the flowers in *Leopoldinia*. 13. Portion of rachilla showing developing male floral buds, note dense hairs covering the rachilla, scale bar = 250 μm ; 14. Portion of rachilla showing a triad composed of one central female flower and two male flowers at bud stage, scale bar = 250 μm ; 15. Side view of a male flower at late bud stage, perianth removed, scale bar = 125 μm ; 16. Longitudinal section of a male flower at late bud stage, perianth removed, scale bar = 100 μm ; 17. Cross-section of an anther, note the well differentiated endothecium, scale bar = 50 μm ; 18. Upper view of female flower at late bud stage, petals removed, scale bar = 500 μm ; 19. Longitudinal section of a female flower at early bud stage, scale bar = 500 μm ; 20. Longitudinal section of an ovule, note micropylar region facing the ventral side of the locule, scale bar = 100 μm .

never previously been studied in detail, in spite of the large economic importance of these palms for indigenous populations in the neotropics and the fact that both taxa display unclear phylogenetic relationships among the taxa of the core arecoid clade.

Leopoldinia and *Manicaria* are characterized by floral triads, at least at the base of the rachillae,

composed of one central female flower and two lateral male flowers sunken in pits. This type of floral arrangement unequivocally supports the inclusion of these two tribes within the subfamily Arecoideae. The two genera display an important number of shared floral characters, namely oblong staminate flowers, with three distinct and imbricate



21–29. Morphology and anatomy of the flowers in *Manicaria*. 21. Side view of a polyandrous male flower, perianth removed, scale bar = 500 μm ; 22. Upper view of a polyandrous male flower, perianth removed, scale bar = 500 μm ; 23. Detail of an ovule, arrow pointing to the micropyle region, scale bar = 100 μm ; 24. Cross-section of a male flower showing anthers, scale bar = 250 μm ; 25. Cross-section of an anther with a detail on the mesophyll of the petal, scale bar = 100 μm ; 26. Cross-section of an ovule showing vascular bundles emerging from the funiculus, scale bar = 100 μm ; 27. Cross-section of the ovary, at the left side mesophyll with tanniferous cells, at the right side thick ovary wall with large vascular bundles, scale bar = 100 μm ; 28. Cross-section of the basal part of the ovary showing two staminodes with different shapes, triangular in antesepalous position and oblong in antepetalous position, scale bar = 250 μm ; 29. Cross-section of the ovary showing three equally developed ovules, scale bar = 500 μm .

sepals with variously notched or toothed margins and three valvate petals. The pistillate flowers are characterized by three distinct and imbricate sepals and three valvate petals; the

gynoecium presents distinct staminodes and a syncarpous, trilobulate, triovulate ovary topped by three stigmatic branches. Contrary to what has been observed in other arecoid groups

(Rudall et al. 2003, Stauffer et al. 2003, Stauffer et al. 2004) septal nectaries were not detected in either of the two genera, suggesting that other possible types of reward attract potential pollinators (e.g. pollen). On the other hand, raphide-containing idioblasts, suggested to be a reward for bee-pollinators (D'Arcy et al. 1996) or as defense devices (Sakai et al. 1972), were not evident in any organs of the flowers. The presence of tanniferous idioblasts throughout the gynoecium in both genera suggests that these inclusions may be regarded as a defense mechanism against herbivores. Interestingly, the absence of the septal nectaries and raphide-containing idioblasts in *Leopoldinia* and *Manicaria* appears to be unique, compared with representatives of other basal core arecoids (Table 2).

In spite of several shared characters, the flowers of *Leopoldinia* differ from *Manicaria* in several important aspects concerning the floral structure. Male flowers of *Leopoldinia* are characterized by the typical monocotyledon trimery, represented by six latrorse, basally connate stamens with broad filaments, and a three-lobed syncarpous pistillode. In the case of *Manicaria*, the male flowers have 20–25 thin, elongated and introrse stamens, and the pistillode is completely lacking. The stamen filaments are rarely connate up to the anthers and the filaments of the peripheral stamens are basally connate to the petals. The female flowers of the two genera differ mostly in the shapes of the gynoecium and perianth parts. *Leopoldinia* is characterized by a pyramidal to rounded gynoecium, rounded petals and sepals. *Manicaria* has on the contrary an obovoid gynoecium with oblong or irregular and asymmetrical sepals and petals.

Although both genera have syncarpous, trilocular and triovulate gynoecia, the gynoecium of *Manicaria* presents three equally developed ovaries at late bud stage, whereas the gynoecium of *Leopoldinia* shows what may be described as late pseudomonometry, in which the fertile ovary and the two sterile ovaries are almost equal in size and shape (Stauffer & Endress 2003). The ovules are campylotropous and hanging in *Leopoldinia*, whereas they are anatropous and laterally attached in *Manicaria*. In the case of *Leopoldinia*, the globose gynoecium is topped by three free stigmatic branches with unicellular papillae, whereas in *Manicaria*, the obovoid gynoecium is topped by a rather smooth pyramidal stigmatic region with connate stigmatic branches. Numerous

stamens in *Manicaria* is characteristic of the male flowers, and female flowers display an increased number of staminodes. *Leopoldinia* has consistently six stamens in the male flowers and six staminodes in the female flowers.

Our study explored the possible taxonomic relationships among representatives of the five tribes of the basal core arecoids, based on comparison with data presented in similar studies of floral structure (Table 2). Indeed, representatives of all five tribes share only a few common characters, namely distinct imbricate sepals, valvate petals, inflexed stamens at bud stage in the male flowers and imbricate sepals and three differentiated stigmatic branches in the female flowers. Morphological and anatomical characters associated with the floral structure of *Leopoldinia* show surprising affinities with flowers of the palm genus *Pelagodoxa* (Table 2), endemic to the Marquesas Islands, and supports the relationships proposed by the molecular studies of Norup et al. (2006) and Baker et al. (2011). *Leopoldinia* and *Pelagodoxa* present oblong male flowers, distinct and imbricate sepals, triangular-ovate valvate petals, six dorsifixed stamens and a syncarpous pistillode. Female flowers of these two genera have distinct and imbricate sepals, distinct petals and more or less rounded, pseudomonomerous, trilobulate, triovulate gynoecia, topped by three stigmas covered with unicellular papillae.

Leopoldinia resembles *Euterpe* only with respect to perianth characters. These two genera have similar distinct, rounded, variously tattered or notched, imbricate sepals, distinct, valvate petals, six wide stamens inflexed at bud stage and three-lobed pistillode in male flowers. Female flowers of *Leopoldinia* and *Euterpe* have similar, distinct, imbricate sepals and distinct petals. Flowers of *Leopoldinia* share with *Geonoma* the presence of distinct and imbricate sepals, valvate petals and three-lobed pistillode in male flowers and imbricate sepals, valvate petals, pseudomonomerous trilobulate gynoecium with papillate stigmatic branches and six staminodes in the female flowers.

Manicarieae does not show evident affinities with any other representative of the basal core arecoids. The surprisingly isolated position of this palm, already suggested by the molecular study of Baker et al. (2011), may be supported by the male flower with many stamens but lacking a pistillode and a clearly trimerous

Table 2. Main floral characters in representatives of the basal core arecoids.

(1) Stauffer et al. 2004; (2) Stauffer et al. 2002, Stauffer & Endress 2003, Dransfield et al. 2008, Wessels Boer 1968; (3) Kuchmeister et al. 1997, Dransfield et al. 2008.

Character	<i>Leopoldinia</i>	<i>Manicaria</i>	<i>Pelagodoxa</i> ¹	<i>Geonoma</i> ²	<i>Euterpe</i> ³
<i>Staminate flower</i>					
<i>Sepals - connation</i>	distinct	distinct	distinct	distinct	distinct
- <i>shape</i>	rounded	irregular	ovate	deltoid-elongate	rounded
- <i>margins</i>	toothed	notched	entire	entire	tattered
- <i>aestivation</i>	imbricate	imbricate	imbricate	imbricate	imbricate
<i>Petals - connation</i>	distinct	distinct	basal	fused up to 2/3 of length	distinct
- <i>shape</i>	triangular-ovate	irregular, triangular-ovate	triangular-ovate	ovate	asymmetrical
- <i>aestivation</i>	valvate	valvate	valvate	valvate	valvate
<i>Stamens - number</i>	6	20–25	6	(3–) 6	6
<i>Filaments - adnation</i>	free	basally with petals	with pistillode	with inner side of petals	free
- <i>connation</i>	at the very base	rarely connate	free	free	free - <i>shape</i>
triangular	thin, elongate	triangular	narrow, flat	basally wider	broad,
<i>Anthers - shape</i>	dorsifixed, oval	dorsifixed, elongate	dorsifixed, oval	divaricate	medifixed, elongate
- <i>position at bud stage</i>	inflexed	straight to inflexed	inflexed	inflexed	inflexed
- <i>dehiscence</i>	latrorse	introrse	introrse	introrse	latrorse
<i>Pistillode - presence</i>	present	absent	present	present	present
- <i>shape</i>	barrel shaped, 3-lobed	(-)	barrel shaped, 3-lobed	round, 3-lobed	columnar, 3-lobed

Table 2. Main floral characters in representatives of the basal core arecoid. (Continued)

Character	<i>Leopoldinia</i>	<i>Manicaria</i>	<i>Pelagodoxa</i> ¹	<i>Geonoma</i> ²	<i>Euterpe</i> ³
<i>Pistillate flower</i>					
<i>Sepals - connation</i>	distinct	distinct	distinct	basally connate	distinct
- shape	rounded	asymmetrical	ovate	deltoid-elongate	rounded, pointed
- margins	slightly toothed	fibrous	entire	entire	lacerate
- aestivation	imbricate	imbricate	imbricate	imbricate	imbricate
<i>Petals - connation</i>	distinct	fused up to mid-height	distinct	basally connate	distinct
- shape	rounded	irregular, triangular-ovate	triangular	ovate	ovoid
- aestivation	valvate	valvate	imbricate	valvate	imbricate
<i>Gynoeceum - type</i>	pseudomonomerous	trimerous	pseudomonomerous	pseudomonomerous	pseudomonomerous
- shape	merous		merous		
- fusion of carpels	pyramidal-rounded	obovoid	rounded	elongated	ovoid
- fusion of carpels	syncarpous	syncarpous	syncarpous	syncarpous	syncarpous
<i>Number of locules/ovules</i>	3/3	3/3	3/3	normally 1/1	1/1
<i>Number of stigmas</i>	3	3	3	3	3
<i>Stigmatic surface</i>	papillate	smooth	papillate	papillate	papillate
<i>Ovule - insertion</i>	hanging	lateral	basal	mid-height	lateral
- type	campylotropous	anatropous	anatropous	anatropous	hemianatropous
<i>Staminodes - number/connation</i>	6/distinct	9/basally fused	6/basally fused	6/united into a tube	absent
		with ovary	with ovary		
<i>Septal nectaries</i>	absent	absent	present	present	present
<i>PTTT</i>	differentiated	differentiated	differentiated	differentiated	unknown
<i>Raphide idioblasts</i>	absent	absent	present	present	present
<i>Tanniferous idioblasts</i>	present	present	present	present	unknown

gynoecium in the female flower. The presence of a completely enveloping prophyll and peduncular bract (even at fruiting stage) may be added as a unique character for *Manicaria* among the basal core arecoid tribes. Male flowers of *Manicaria* and *Pelagodoxa* have an oblong shape, distinct and imbricate sepals, distinct petals and dorsifixed introrse stamens. The female flowers of these two taxa share distinct, imbricate sepals, a trilobulate, triovulate gynoecium with anatropous ovules. *Manicaria* shares with *Euterpe* the same group of characters that is shared with *Leopoldinia*, namely distinct, imbricate sepals with variously notched margins, distinct, valvate and asymmetrical petals in male flowers, and distinct, imbricate sepals and an ovoid gynoecium in the female flowers. The male flowers of *Manicaria* and *Geonoma* share distinct sepals, valvate petals and introrse stamens, whereas the female flowers of both genera have imbricate sepals, valvate, basally united petals and trilobulate gynoecium with an anatropous ovule. Finally, flowers in representatives of Geonomateae and Euterpeae show some affinities with Manicarieae and Leopoldinieae, but further studies may be necessary to infer more defined relationships between these groups.

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Literature Cited

- ASMUSSEN, C.B. AND M.W. CHASE. 2001. Coding and noncoding plastid DNA in palm systematics. *American journal of botany* 88: 1103–1117.
- ASMUSSEN, C.B., J. DRANSFIELD, V. DEICKMANN, A.S. BARFOD, J.-C. PINTAUD AND W.J. BAKER. 2006. A new subfamily classification of the palm family (Arecaceae): evidence from plastid DNA phylogeny. *Botanical Journal of the Linnean Society* 151: 15–38.
- BAKER, W.J. AND T.L.P. COUVREUR. 2012. Global biogeography and diversification of palms sheds light on the evolution of tropical lineages. I. Historical biogeography. *Journal of Biogeography* 40: 274–285.
- BAKER, W.J., M.V. NORUP, J.J. CLARKSON, T.L.P. COUVREUR, J.L. DOWE, C.E. LEWIS, J.-C. PINTAUD, V. SAVOLAINEN, T. WILMOT AND M.W. CHASE. 2011. Phylogenetic relationships among arecoid palms (Arecaceae: Arecoidae). *Annals of Botany* 108: 1417–1432.
- BAKER, W.J., V. SAVOLAINEN, C.B. ASMUSSEN-LANGE, M.W. CHASE, J. DRANSFIELD, F. FOREST, M.M. HARLEY, N.W. UHL AND M. WILKINSON. 2009. Complete generic-level phylogenetic analyses of palms (Arecaceae) with comparisons of supertree and supermatrix approaches. *Systematic Biology* 58: 240–56.
- BERNAL, R. AND G. GALEANO. 2010. Notes on *Mauritiella*, *Manicaria* and *Leopoldinia*. *Palms* 54: 119–132.
- 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*. Kew Publishing, London.
- D'ARCY, W.G., R.C. KEATING AND L.S. BUCHMANN. 1996. The calcium oxalate package or so-called resorption tissue in some angiosperm anthers. Pp 159–191 in D'ARCY, W.G. AND R.C. KEATING (eds.) *The Anthers: Form, Function and Phylogeny*. Cambridge University Press, New York.
- GAERTNER, J. 1791. *De Fructibus et Seminibus Plantarum*. Stuttgart.
- HAHN, W.J. 2002. A phylogenetic analysis of the Arecoid Line of palms based on plastid DNA sequence data. *Molecular Phylogenetics and Evolution* 23: 189–204.
- HENDERSON, A. 1995. *The Palms of The Amazon*. Oxford University Press, Inc.
- HENDERSON, A. 2011. A revision of *Leopoldinia* (Arecaceae). *Phytotaxa* 32: 1–17.
- IGERSHEIM, A. AND O. CICHOCKI. 1996. A simple method for microtome sectioning of prehistoric charcoal specimens, embedded in 2-hydroxyethyl methacrylate (HEMA). *Review of Palaeobotany and Palynology* 92: 389–393.
- KUCHMEISTER, H., I. SILBERBAUER-GOTTSBERGER AND G. GOTTSBERGER. 1997. Flowering, pollination, nectar standing crop, and nectaries of *Euterpe precatoria* (Arecaceae), an Amazonian rain forest palm. *Plant Systematics and Evolution* 206: 71–97.

- LEWIS, C.E. AND J.J. DOYLE. 2002. A phylogenetic analysis of tribe Areceae (Arecaceae) using two low-copy nuclear genes. *Plant Systematics and Evolution* 236: 1–17.
- LOO, A.H.B., J. DRANSFIELD, M.W. CHASE AND W.J. BAKER. 2006. Low-copy nuclear DNA, phylogeny and the evolution of dichogamy in the betel nut palms and their relatives (Arecinae; Arecaceae). *Molecular Phylogenetics and Evolution* 39: 598–618.
- MARTIUS, C.F.P. VON. 1824. *Historia Naturalis Palmarum*.
- NORUP, M.V., J. DRANSFIELD, M.W. CHASE, A.S. BARFOD, E.S. FERNANDO AND W.J. BAKER. 2006. Homoplasious character combinations and generic delimitation: a case study from the Indo-Pacific arecoid palms (Arecaceae: Arecaceae). *American Journal of Botany* 93: 1065–1080.
- PUTZ, F.E. 1979. Biology and human use of *Leopoldinia piassaba*. *Principes* 23: 149–156.
- RUDALL, P.J., K. ABRANSON, J. DRANSFIELD AND W.J. BAKER. 2003. Floral anatomy in *Dypsis* (Arecaceae - Areceae): a case of complex synorganization and stamen reduction. *Botanical Journal of the Linnean Society* 143: 115–133.
- SAKAI, W.S., M. HANSON AND R.C. JONES. 1972. Raphides with barbs and grooves in *Xanthosoma sagittifolium* (Araceae). *Science* 178: 31–315.
- STAUFFER, F.W. 2000. Contribución al estudio de las palmas (Arecaceae) del Estado Amazonas, Venezuela. *Scientiae Guaianae* 10: 197.
- STAUFFER, F.W. AND P.K. ENDRESS. 2003. Comparative morphology of female flowers and systematics in Geonomeae (Arecaceae). *Plant Systematics and Evolution* 242: 171–203.
- STAUFFER, F.W., R. RUTISHAUSER AND P.K. ENDRESS. 2002. Morphology and development of the female flowers in *Geonoma interrupta* (Arecaceae). *American Journal of Botany* 89: 220–229.
- STAUFFER, F.W., C.B. ASMUSSEN, A. HENDERSON AND P.K. ENDRESS. 2003. A revision of *Asterogyne* (Arecaceae: Arecoideae: Geonomeae). *Brittonia* 55: 326–356.
- STAUFFER, F.W., W.J. BAKER, J. DRANSFIELD AND P.K. ENDRESS. 2004. Comparative floral structure and systematics of *Pelagodoxa* and *Sommieria* (Arecaceae). *Botanical Journal of the Linnean Society* 146: 27–39.
- Uhl, N.W., J. Dransfield, J.I. Davis, M.A. Luckow, K.S. Hansen and J.J. Doyle. 1995. Phylogenetic relationships among palms: cladistic analyses of morphological and chloroplast DNA restriction site variation. Pp. 623–661 in P. RUDALL, P. J. CRIBB, D. F. CUTLER, AND C. J. HUMPHRIES (eds.), *Monocotyledons: Systematics and Evolution*. Royal Botanic Garden, Kew.
- WALLACE, A.R. 1853. *Palm Trees of the Amazon*. London: John van Voorst.
- WESSELS BOER, J.G. 1968. The Geonomoid Palms. *Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk., Tweede Sect. ser. 2*, 58: 1–202.
- WESSELS BOER, J.G. 1988. Palmas indígenas de Venezuela. *Pittieria* 17:1–332.