

Comparative floral structure and systematics in the Asian palm genus *Rhapis* (Arecaceae, Coryphoideae)

Anne Giddey, Rodolphe E. Spichiger, Fred W. Stauffer*

Conservatoire et Jardin botaniques de la Ville de Genève, CP 60, CH-1292 Chambésy/GE, Switzerland

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Abstract

A comparative study of the floral structure in the species of the genus *Rhapis* (Arecaceae, Coryphoideae, Rhipidinae) is presented. Flowers are mainly unisexual, with three sepals, three petals, 6 stamens or staminodes and three carpels or carpelodes. Some evidences of basal congenital and apical postgenital fusion of the carpels, first time reported in the genus, were observed in the gynoecium. Ovules are basally attached and crassinucellate; they appear to be slightly anatropous. The morphology of the filaments suggests a division of the species into two groups: *Rhapis excelsa* and *R. subtilis* exhibit thick and keeled filaments, whereas *R. gracilis*, *R. humilis*, *R. laosensis*, *R. micrantha* and *R. multifida* have slender, non-keeled filaments. Relationships of *Rhapis* with the rest of the genera of Rhipidinae are inferred on the light of floral structure.

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Introduction

The genus *Rhapis* (Arecaceae, Coryphoideae) consists of clustering unarmed palms, commonly known as Lady Palms. Moderate in size, these familiar ornamental plants have a long history of cultivation. Despite the fact that some species of *Rhapis* are well represented in horticulture and may be considered as ideal subjects for research, few studies have been carried out to date regarding their floral structure. The genus is composed of nine currently valid species. Eight taxa were accepted by Hastings (2003) and Govaerts and Dransfield (2005). However, the recent discovery of *Rhapis vidalii* Aver., H.T. Nguyen & L.K. Phan (Averyanov et al., 2006) in Vietnam shows that the genus may contain more

species. The species of *Rhapis* are distributed from southern China southwards through Indochina to peninsular Thailand and northern Sumatra (Dransfield and Uhl, 1998). *Rhapis* is represented by small undergrowth palms of tropical evergreen, lowland forest (Averyanov et al., 2006; Hastings, 2003; Uhl and Dransfield, 1987).

The genus was traditionally placed within subfamily Coryphoideae, tribe Corypheae, subtribe Thrinacinae. The character that places *Rhapis* into Corypheae is the combination of its palmate, induplicate leaves and usually unisexual, only slightly dimorphic flowers. Corypheae appear to be the least specialized of the three coryphoid tribes, and the 31 genera included in the tribe Corypheae are systematically of primary importance (Dransfield and Uhl, 1998; Uhl and Dransfield, 1987). The four subtribes of Corypheae are defined on the basis of their gynoecium structure (Dransfield and

*Corresponding author.

E-mail address: fred.stauffer@ville-ge.ch (F.W. Stauffer).

Uhl, 1998; Dransfield et al., 1990; Uhl and Dransfield, 1987): distinct carpels, usually three, are characteristic of Thrinacinae (14 genera). Two main lines of evolution were traditionally distinguished in this subtribe on the basis of distinct evolutionary trends (Dransfield and Uhl, 1998; Hastings, 2003; Uhl and Dransfield, 1987). Eight genera, restricted to the New World, are characterized by the reduction of the carpels to one and the reduction of the perianth to a single cupule (Uhl and Dransfield, 1987). The six remaining genera are mainly restricted to the Old World (with the exception of *Rhapidophyllum*) and tend towards dioecy and also elaboration and fusion of the perianth organs. These two evolutionary groups are redistributed within distinct tribes in the new palm classification (Dransfield et al., 2005). In this recent classification, the entirely New World line of Thrinacinae represents the tribe Cryosophileae and the second line, which includes *Rhapis*, is in tribe Livistoneae, representative of the subtribe Rhapsidineae. Except for *Rhapidophyllum* (in North America), the new subtribe Rhapsidineae strictly belongs to the Old World. Tribe Cryosophileae and subtribe Rhapsidineae, respectively, representing New World and Old World genera of the former subtribe Thrinacinae, are strongly supported and unrelated clades (Asmussen and Chase, 2001; Asmussen et al., 2006; Hahn, 2002; Uhl et al., 1995), but can be scarcely distinguished morphologically (Dransfield et al., 2005).

The recent work of Asmussen et al. (2006) has shown that the phylogenetic relationships in selected groups of Coryphoid genera are rather well resolved, and there are high bootstrap values for many of the subclades. Monophyly has been confirmed for the tribes Borasseae and Phoenixaceae, whereas Corypheae, to which *Rhapis* has been traditionally assigned, is not monophyletic. The relationships of *Rhapis* with other genera of the subtribe Thrinacinae have not yet been clearly established. They were inferred for the first time by Asmussen and Chase (2001) using *rbcL*, *rps16*, *trnL-trnF* sequences. In this study, *Rhapis* (only represented by *R. excelsa*) forms a sister relationship with *Rhapidophyllum*, but only weak support (59% bootstrap) was provided. The *Rhapis/Rhapidophyllum* clade is part of an unresolved polytomy also containing *Trachycarpus* and *Guihaia*. Using *atpB*, *rbcL* and 18S nrDNA sequences, Hahn (2002) found that *Rhapis* (represented by *R. subtilis*) was sister to a clade formed by *Chamaerops* and *Trachycarpus*, but this relationship was rather weakly supported. More recently Asmussen et al. (2006) suggested a sister relationship between *Rhapis* (represented by *R. excelsa*) and *Maxburretia*, but only weakly supported (bootstrap % ≤ 50). The *Rhapis/Maxburretia* clade is sister to *Rhapidophyllum*, but also in this case there is weak statistical support.

The aims of the present study are to provide basic information on the floral structure of the species

currently recognized for the genus *Rhapis* and to analyze this data in the context of the systematics of the group.

Materials and methods

Plant material

The morphological and anatomical study was based on dried flowers sampled from the collections of the following herbaria: A, AAU, BM, G, K, LE (photo) and P. Liquid-fixed flowers were sampled from pickled collections at AAU and K; fresh flowers were obtained from living collections at the Conservatoire & Jardin botaniques de la Ville de Genève, the Royal Botanic Gardens of Kew and the Fairchild Tropical Botanic Garden of Florida (Table 1).

Scanning electron microscopy and serial microtome sectioning

Flowers were dissected for morphological study under a stereomicroscope (Wild M3B) and some parts of the dissected specimens were chosen for scanning electron microscopy. They were dehydrated, critical-point-dried and sputter-coated with gold. Micrographs were obtained using a Zeiss DSM 940A scanning electron microscope (Orion 6.60 Imaging System). For the anatomical investigations, flowers at or close to anthesis were chosen and the priority was given to species where both male and female flowers were available. Sepals were removed from all flowers investigated and petals were partially removed in some cases. Petals were only partially removed in order to avoid damaging filaments of the stamens or staminodes. The flowers were then dehydrated and embedded in Technovit 7100 (2-hydroxyethyl methacrylate) and sectioning was carried out using a rotary microtome (Leitz 1512) at 5–10 μ m thickness. The sections were stained with toluidine blue and red ruthenium, then mounted in Assistant-Histokitt mounting medium. Photos of the anatomical sections were obtained using a microscope Leica DMIRE2 and a camera Leica DC 300F.

Results

Shared floral characters in *Rhapis*

Inflorescence and flower arrangement

The species of *Rhapis* are dioecious to polygamodioecious. Staminate and pistillate inflorescences are superficially similar, interfoliar, branching to 1–3 orders. In *R. laosensis* the rachillae are strongly sinuous and twisted. Rachillae bear solitary, rarely paired flowers.

Table 1. Specimens studied.

Species	Collector(s)	Number of collection or plot ^a	Institution
<i>Rhapis excelsa</i> (Thunb.) Henry	N/A	N/A	Living collection G
	N/A	1975-4105	Living collection K
	N/A	1983-4887	Living collection K
	N/A	1987-2572	Living collection K
	H.H. Chung	2709	Herbarium BM
	A. Schinini	5840	Herbarium G
	Not indicated	K number 51382	Spirit collection K
<i>Rhapis gracilis</i> Burret	El. Colani	s.n.	Herbarium collection P
<i>Rhapis humilis</i> Blume	W.J. Baker with J. Dransfield, P. Rudall & D. Cooke	1151	Herbarium K
	W.J. Baker with J. Dransfield, P. Rudall & D. Cooke	1151	Spirit collection K
	J. Dransfield	923	Spirit collection K
	L. Fitt	31	Herbarium K
	D.K. Harder, P.K. Loc, N.T. Hiep & N.Q. Binh	4132	Herbarium K
	H. Zollinger	646	Herbarium P
	A. Chevalier	32535	Herbarium P
<i>Rhapis laosensis</i> Becc.	T. Evans with J. Dransfield	TDE34	Spirit collection K
	T. Evans with J. Dransfield	TDE35	Herbarium K
	A.F.G. Kerr	20762	Herbaria K, BM
	Dr. Thorel	3154	Herbarium P
<i>Rhapis micrantha</i> Becc.	R.P. Bon	2545	Herbarium P
	R.P. Bon	2045	Herbarium P
<i>Rhapis multifida</i> Burret	N/A	N/A	Living collection G
	S.K. Lau	2864	Herbarium A
<i>Rhapis subtilis</i> Becc.	N/A	71239P	Living collection FTG
	Not indicated	Not indicated	Herbarium K
	A.S. Barfod, W. Ueachirakan, T. Burholt & S. Barrow	45205	Herbarium K
	A.F.G. Kerr	8148	Herbaria K, BM
	A.F.G. Kerr	10896	Herbarium BM
	A.F.G. Kerr	15354	Herbarium BM
	A.F.G. Kerr	19291	Herbarium BM
	O. Maessen	s.n.	Herbarium K
	A. Marcan	2634	Herbarium BM
	G. Smith & W. Sumawong	GC85	Herbarium and spirit collection K
	G. Smith & W. Sumawong	GC93	Herbarium and spirit collection K
	G. Smith & W. Sumawong	GC110	Herbarium and spirit collection K
	G. Smith & W. Sumawong	GC145	Spirit collection K
	W. Sumawong	s.n.	Spirit collection K
	W. Sumawong	6	Herbarium K
	Harder, Hiep, Averyanov et al. (photo)	DKH 8123	Herbarium LE

Two spirit specimens (K), collected in Thailand, were not determined (*Rhapis* sp., Kew numbers 62011 and 47990). Two spirit specimens (AAU), collected in Thailand and labelled as *Rhapis excelsa*, were considered as doubtful (Barfod & Ueachirakan 41289 and Larsen et al. 42134).

^aPlot number is given for living plants.

Paired flowers were observed in an infructescence of *R. humilis* (Zollinger 646, P). Each flower is preceded by one or two small bracts; however, three preceding bracts were present in the case of paired flowers. Flowers are

spirally arranged in a clockwise ascending way. The distance of insertion between flowers is not constant along the rachilla. Each rachilla ends with a flower in terminal or sub-terminal position. A lateral prolongation

of the apex of the rachilla is usually present, sometimes associated with a bract (some specimens of *R. laosensis*: Chevalier 32535, P; Thorel 3154, P). Male flowers are usually more densely packed on the rachillae than the female ones.

Flowers

Flowers are usually unisexual, with three sepals, three petals, six stamens or staminodes, and three carpels or carpelodes (when a pistillode is clearly differentiated). Flowers range from approximately 2.5 to 6 mm in length for male flowers, particularly elongate in the case of *R. humilis* (to 7.2 mm), and about 2.5–5 mm in length for female flowers. The floral plan is rather simple, although a considerable degree of connation in the perianth and fusion of the filaments to the petals for almost all their length can be observed. Only the very tip of the filaments and the anthers are not fused to the inner surface of the petals. Female flowers studied were superficially globose, whereas male flowers were elongate, either clavate, obovoid or obconical. *R. subtilis* represents an exception among the species of *Rhapis* studied, exhibiting superficially similar male and female flowers, both with a more or less ovoid shape. Hermaphrodite flowers were only observed in *R. laosensis* (Evans & Dransfield TDE34, spirit collection K). In this case, polygamous inflorescences bear hermaphrodite and male flowers. All flowers developing on the polygamous inflorescences are morphologically similar and not distinguishable from each other without dissection. However, male flowers borne on polygamous inflorescences are relatively larger and show some morphological differences compared to the male flowers developing on strictly staminate inflorescences. These two types of male flowers observed in *R. laosensis* are hereafter referred to as “type I” (male flowers from staminate inflorescences) and “type II” (male flowers from polygamous inflorescences). *R. vidalii* exhibits pedicellate flowers with a particularly long stalk-like base (based on photos of the herbarium specimen Harder et al. DKH 8123, LE).

Perianth

When fresh material was studied, the perianth of *Rhapis* flowers at anthesis was yellowish or greenish. This concerns *R. excelsa* (male and female flowers), *R. multifida* (male flowers) and *R. subtilis* (male and female flowers). In *R. subtilis*, patches of dark pigment (perhaps, tanniferous tissue) are present on rachillae and also on flowers (sepals, petals, connectives of the anthers and carpels). Petals alternate with the sepals and carpels are antisepalous (alternating with the petals). Sepals and petals are, respectively, connate for $\frac{1}{3}$ to $\frac{3}{4}$ of their length. The flower base, above the level of attachment of sepals and petals, is usually developed into a \pm long androgynophore. The calyx is cup-shaped, 3-lobed distally.

The corolla is basally tubular, topped by three triangular lobes which are rather tough and often thick at their tips. The lobes are specially short in male flowers that exhibit petals usually connate for $\frac{3}{4}$ of their length. Free lobes of the petals are either directly valvate or first briefly imbricate and then valvate. In the imbricate cases, lateral margins of lobes extend under neighbouring lobes. Two different imbricate patterns of petals were observed in *Rhapis* flowers. One pattern consists of one petal lobe completely outside, one completely inside and the third one in between. This pattern was observed in *R. excelsa* (some female flowers), *R. multifida* (male flowers), *R. subtilis* (male and female flowers). In the second pattern observed, each petal lobe has one covering and one covered flank. It is therefore comparable to the pentamerous contort pattern as described in Endress (1994). This pattern was observed in some female flowers of *R. excelsa*. Some staminate specimens of *R. excelsa* (plant 1987–2572, living collection K; Kew number 51382, spirit collection K) exhibit flowers with a groove between the petals, which are therefore incompletely connate. Some male flowers of *R. humilis* exhibit also a well marked groove between two of their three petals. This groove may extend over almost all the length of the petals. Tanniferous idioblasts are usually abundant and vascular bundles are spread throughout the tissues of the perianth.

Androecium, fertile stamens

Fertile stamens are inserted in two whorls; three longer stamens alternate with three shorter ones. The longer set alternates with the petals and is therefore visible between the corolla lobes. In the male flowers selected for SEM observations (*R. excelsa* and *R. subtilis*; Fig. 1), the two sets of stamens were, respectively, at different stages of development. Dehiscence was already present in the shorter set of stamens but not in the longer set. Filaments are fused to the corolla, only free at their very tips. They exhibit two different trends in the genus: filaments are usually linear, rather slender and terete in some species (*R. gracilis*, *R. humilis*, *R. laosensis* type I, *R. micrantha* and *R. multifida*), whereas they are thick and keeled in others (*R. excelsa*, *R. laosensis* type II and *R. subtilis*). Stamens of *R. excelsa* present thick filaments gradually enlarged upwards before narrowing at the level of the connective. The filaments are gibbous with several keels. In *R. subtilis*, the stamens exhibit large keeled filaments. The two lateral keels decrease at the apex and filaments are thus narrowed when reaching the connective. Fertile anthers in all species are basifixed, rounded to cordate, latrorse, with dark tannin-containing connectives.

In the flowers investigated, anther walls exhibit only two layers of cells corresponding to the epidermis and the endothecium (Fig. 2b). In addition, the septum

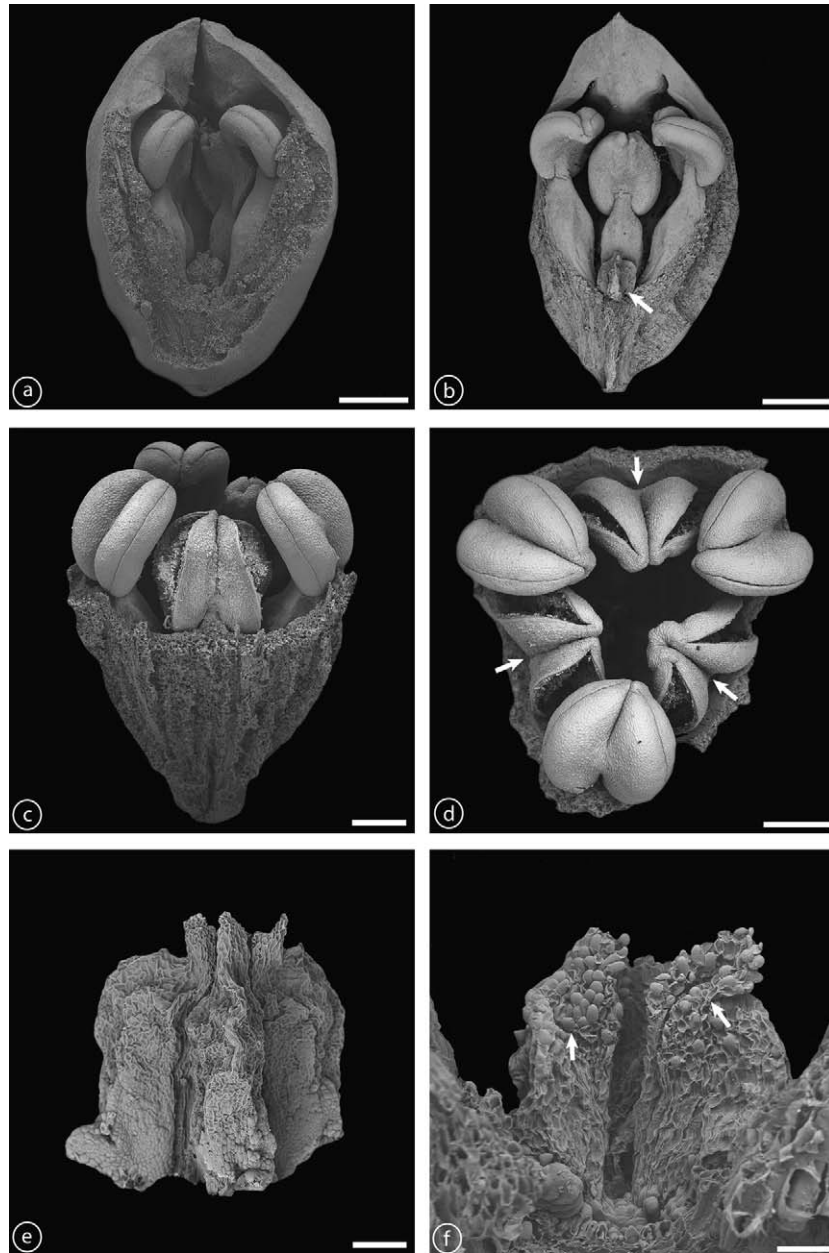


Fig. 1. SEM micrographs of the *Rhapis* androecium. (a) *Rhapis subtilis*: one petal removed (scale bar 800 µm), (b) inner view of one petal with three stamens, arrow pointing to the pistillode (scale bar 800 µm), (c) lateral view of the androecium (scale bar 400 µm), (d) upper view of the androecium, arrow pointing to the anthetic set of anthers (scale bar 400 µm), (e) pistillode (scale bar 100 µm), (f) *Rhapis excelsa*: detail of pistillode, arrows pointing to the papillate surface (scale bar 50 µm).

between the pollen sacs appears to be degraded. Tanniferous idioblasts surround the vascular bundles of the filaments in *R. excelsa* and *R. subtilis*, whereas they are rather concentrated in the epidermis for *R. laosensis* (hermaphrodite flowers). Each fertile stamen is served by one vascular bundle.

Androecium, staminodes

Staminodes are usually also in two whorls, all six well developed, at least externally similar to the fertile stamens. The staminodes of the set opposite to the

carpels are located in their dorsal grooves. With the development of the carpels, staminodes tend to be compressed between carpel walls and petals. The filaments of the staminodes are thus more flat than the filaments of the fertile stamens. Abortive anthers of staminodes are also flattened and do not contain pollen. The sterile anthers are usually cordate with dark connectives.

The vascular bundle of the filaments is surrounded by tanniferous idioblasts (based on *R. subtilis*, Fig. 2a). Anthers of staminodes have also tanniferous connectives, but with empty thecal structures: two loops

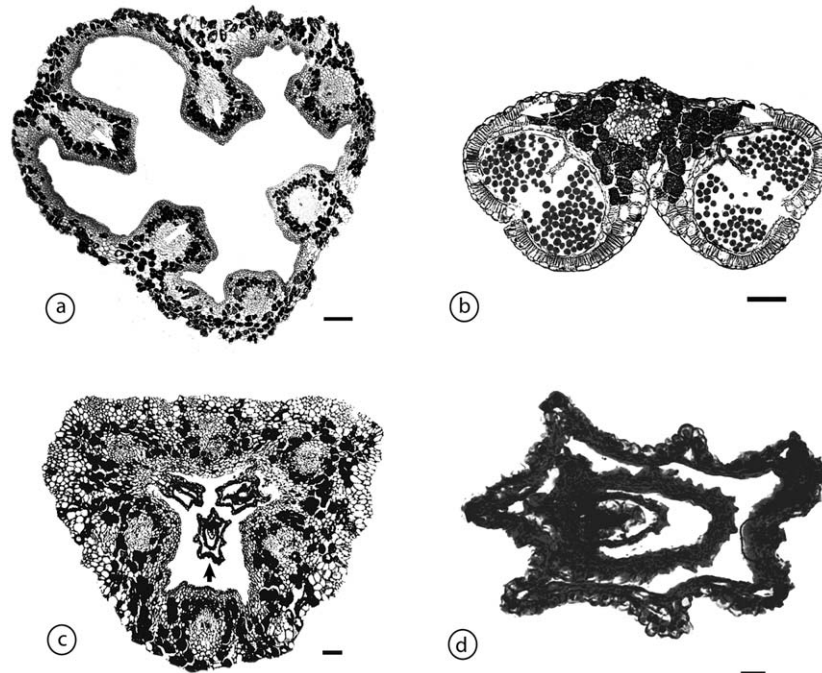


Fig. 2. Anatomical cross sections of the *Rhapis* androecium. (a) *Rhapis subtilis*: arrows pointing to the tanniferous base of the filaments (scale bar 200 µm), (b) *Rhapis subtilis*: one isolated anther, arrows pointing to the well differentiated endothecium (scale bar 100 µm), (c) *Rhapis subtilis*: arrow pointing to the tricarpellate sterile gynoeceum (scale bar 100 µm), (d) *Rhapis subtilis*: one isolated carpellode (scale bar 20 µm).

on each side apparently correspond to vestigial pollen sacs.

Gynoeceum, fertile carpels

The gynoeceum (Figs. 3 and 4) is composed of three uniovulate carpels, free or united to different degrees. Carpels are in all cases basally congenitally fused for a very short distance. In addition to this fusion, evidence of postgenital fusion appeared during this study. Postgenital fusion was observed at the apex of the gynoeceum in female flowers of *R. laosensis*, *R. micrantha* and *R. subtilis*, and in hermaphrodite flowers of *R. laosensis*. In the female and hermaphrodite flowers of *R. laosensis*, a free space is present in the center of the gynoeceum along almost all its length, except at the apex where the carpels are connate. A female specimen of *R. subtilis* (plant 71239P, living collection FTG) exhibited flowers with distinctive carpel features (type II flowers). Among the species with female flowers available, only *R. excelsa* exhibited flowers with completely free carpels. The carpels in *Rhapis* are sac-like, with a flat ventral side and a bulged dorsal side. The carpels of the type II flowers of *R. subtilis* are more elongate (strongly longer than broad) than the other carpels studied. The ventral slit was observed not to be completely closed in the upper part of the carpels at least in the hermaphrodite flowers of *R. laosensis*. A deep

groove is present in the dorsal side of the carpels. The three staminodes opposite the carpels take place in the dorsal grooves. Fertile female organs and abortive male organs are therefore in close contact. The carpels of the hermaphrodite flowers of *R. laosensis* lack dorsal grooves. In the hermaphrodite flowers, anthers are inserted above the carpels and do not touch them. In female flowers, sterile anthers of the staminodes opposite the carpels take place in the deep upper part of their dorsal groove. Carpels of hermaphrodite flowers are well developed, however to a lesser degree than the carpels of the female flowers. In hermaphrodite flowers, anthers fill more space inside the flower above the carpels. As a consequence, carpels are limited in their development. The styler region in *Rhapis* consists of a very short neck, ventrally situated, or is nearly absent, then the stigmas appear sessile. Particularly in *R. excelsa*, the styles are drastically reduced. In the flowers of type II in *R. subtilis*, the styles are the longest observed in the genus, consisting of an obvious neck topped with the stigma.

Carpels appear to exhibit separate styler canals, even when they are fused at the apex. In the type II flowers of *R. subtilis*, the carpels are basally congenitally fused for a relatively long distance compared to the other flowers studied. The fused central part of the gynoeceum is narrowed towards the apex and carpels are then

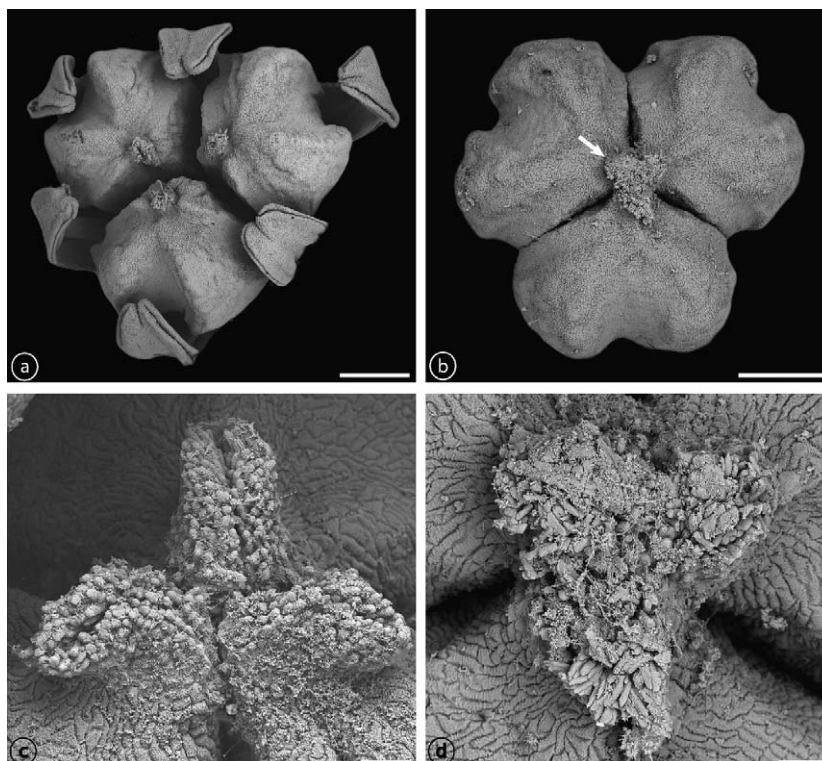


Fig. 3. SEM micrographs of the *Rhapis* gynoecium. (a) *Rhapis excelsa*: carpels and staminodes (scale bar 400 μm), (b) *Rhapis subtilis*: carpels, arrow pointing to the postgenitally united region of the stigmas (scale bar 400 μm), (c) *Rhapis subtilis*: stigmas (scale bar 50 μm), (d) *Rhapis subtilis*: detail of postgenitally united stigmas (scale bar 50 μm).

separate from approximately the mid-height of the ovaries. At least in the hermaphrodite flowers of *R. laosensis*, the ventral slit of the carpels do not appear completely closed in the upper part. A slit seems to be present from the locule, and also from the locular or stylar canal, towards the center of the gynoecium. Protection of the ovules is provided by various histological devices. Raphide idioblasts are particularly present in the ovary at the level of the ovules. In almost all the species studied the tanniferous idioblasts are common throughout the carpels, particularly abundant in the dorsal and apical regions of the ovary. In the hermaphrodite flowers of *R. laosensis*, the tanniferous idioblasts are small compared to the other species investigated. They are widespread throughout the reproductive parts of the flowers (carpels, ovules and stamens) and are particularly concentrated in the epidermal and subepidermal layers. In the type I flowers of *R. subtilis*, tanniferous idioblasts are also observed in the ovules, where they may form a compact layer in the chalaza and funiculus. The outer mesophyll of the carpels in *Rhapis* (hypodermis) is composed of a sclerified tissue. In comparison with the other flowers investigated, tissues of the type II flowers of *R. subtilis* show a higher concentration of histological devices for protection of the ovules. Raphide idioblasts are parti-

cularly abundant and a subepidermal unicellular layer of lignified cells is additionally present on the dorsal sides of the locules.

The ovules in *Rhapis* are basally attached, crassinucellate. They appear to be slightly anatropous and bitegmic. The two integuments are difficult to distinguish in the ovules of the available material. A large funicular aril was observed in the hermaphrodite flowers of *R. laosensis*. The ovule is served by the ventral vascular bundles of the carpel. These vascular bundles are especially well differentiated in the flowers of type II in *R. subtilis*. At the mid-height of the ovary, one dorsal, seven lateral and one to two ventral bundles at each side of the ventral slit are observed.

Gynoecium, pistillode

A reduced gynoecium is usually present in male flowers and consists of three tiny separate carpelodes or sometimes simply a rudimentary structure without specific shape. It is rarely completely absent. Carpelodes show various levels of differentiation. They may be sac-like, superficially resembling minute carpels, or flat triangle-shaped. A neck, in the extension of the ventral side, may be present or absent. It corresponds to a rudimentary style-stigma structure. In the male flowers, the pistillode is composed of three separate

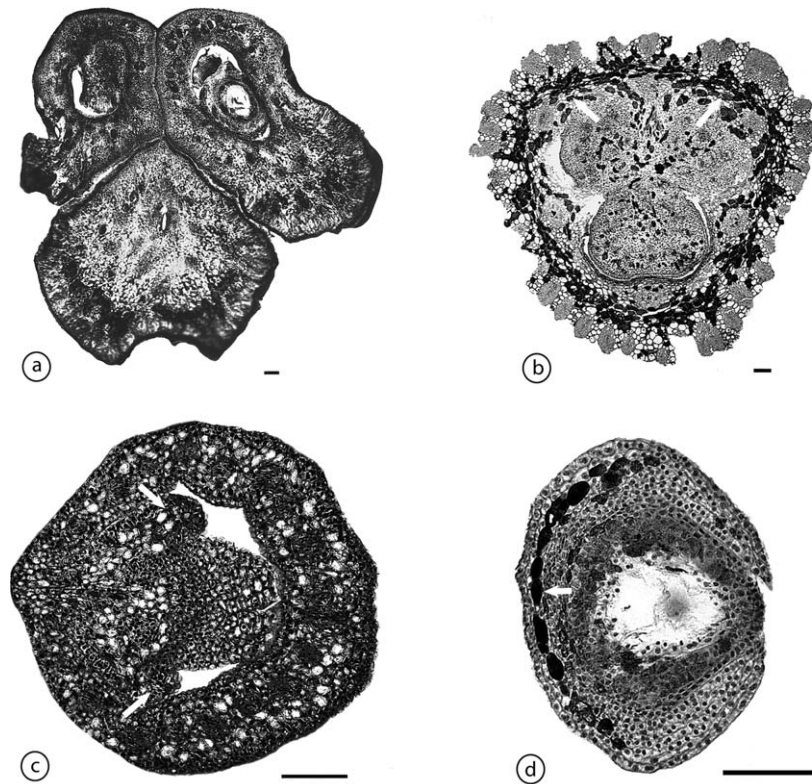


Fig. 4. Anatomical cross sections of the *Rhapis* gynoecium. (a) *Rhapis excelsa*: carpels of a female flower (scale bar 100 μ m), (b) *Rhapis subtilis*: basal level of the carpels in a female flower, arrow pointing to the heavily tanniferous base of the perianth (scale bar 100 μ m), (c) *Rhapis laosensis*: isolated carpel of a hermaphrodite flower, arrow pointing to the aril of the ovule, lateral to the funiculus (scale bar 100 μ m), (d) *Rhapis subtilis*: isolated ovule of a female flower, arrow pointing to the tanniferous region of the chalaza (scale bar 100 μ m).

carpellodes with one abortive ovule per carpellode. Carpellodes appear to differentiate ventral slits, with possible production of secretions in the sterile stigmatic branches. Tanniferous idioblasts are abundant at the top of the carpellodes.

Discussion

Morphological features in the flowers of *Rhapis*

Morphological data from the previous treatments (Beccari, 1931; Hastings, 2003; Uhl et al., 1969) are globally congruent with the results of the present study. Slight differences sometimes appeared regarding the general shape of the flowers or the presence/absence of a stalk-like base. These divergences probably reflect different stages of development in the flowers studied.

Hermaphrodite flowers were observed only for *R. laosensis*, as previously pointed out by Hastings (2003). The polygamous inflorescences of *R. laosensis* included male and hermaphrodite flowers, both superficially similar. Polygamous inflorescences with superficially similar female and hermaphrodite flowers were

previously described for *R. excelsa* (Tomlinson and Zimmermann, 1968; Uhl et al., 1969).

Perianth

The main peculiarity observed in the perianth of *Rhapis* is that the lobes of the petals can be briefly imbricate. In all flowers studied, the corolla was connate at the base and the free lobes were usually valvate. In some cases, they were basally briefly imbricate and only apically valvate. Lobes briefly imbricate were observed in *R. excelsa* (female flowers only), *R. multifida* (male flowers, female not seen) and *R. subtilis* (both male and female flowers). This character was previously mentioned for female flowers of *R. excelsa* by Uhl et al. (1969) and also in the general description of the genus *Rhapis* (Uhl and Dransfield, 1987).

Androecium

It is remarkable that the arrangement of the stamens in male and hermaphrodite flowers of *Rhapis* allows an optimal filling of the inner space. Due to the difference of length in filaments of the two stamen whorls, anthers develop alternatively at different heights in the inner space of the flower. Additionally, in the male flowers

observed with the SEM (*R. excelsa* and *R. subtilis*), the two whorls of stamens were not at the same stage of development. The shorter whorl was at an older stage.

In the immature male flowers studied (*R. excelsa* and *R. multifida*), anthers were close to their final size, whereas the filaments were still very short. The filaments elongate with the corolla tube when approaching maturity. For *R. multifida*, the observation of the flowers throughout all their development shows that the filaments, as well as the corolla tube, elongate rapidly close to anthesis. The early differentiation of anthers is due to the complicated histological development of the pollen sacs. The histological structure of the filaments (usually simply parenchyma, with one central vascular bundle) allows them elongating within a short time (Endress, 1994).

Gynoecium

The gynoecium of *Rhapis* flowers shows different degrees of fusion, at least in some species. Carpels are postgenitally connate at the apex (female and hermaphrodite flowers of *R. laosensis*, female flowers of *R. micrantha* and female flowers of type I in *R. subtilis*) or basally congenitally fused for a relatively long distance (female flowers of type II in *R. subtilis*). For the female flowers of *R. laosensis* and *R. micrantha*, the fusion of the carpels was observed on rehydrated herbarium specimens that were examined with a stereomicroscope. For the hermaphrodite flowers of *R. laosensis* and the female flowers of *R. subtilis*, the fusion of the carpels was obvious on the anatomical sections. Only one species (*R. excelsa*) was found with completely separate carpels. The observation of separate carpels in this particular species is congruent with the results of Uhl et al. (1969), who anatomically investigated the flowers of *R. excelsa*. The fact that the carpels in the genus *Rhapis* can be congenitally fused at the base and postgenitally fused towards the apex is remarkable and relatively unknown for the rest of the palm flowers anatomically studied so far. The formation of a compitum in the postgenitally united carpels, as described in several Geonomateae (Stauffer and Endress, 2003; Stauffer et al., 2002) may be also possible in the genus *Rhapis*, but this requires of further developmental studies.

Uhl et al. (1969) described the ventral slits of the carpels as completely closed in *R. excelsa*. In the present work, the ventral slits were also observed to be completely closed in *R. excelsa*, but appeared to be slightly open in the upper part of the carpels at least in the hermaphrodite flowers of *R. laosensis*. For *R. subtilis*, we found a slit from the locule and from the locular or stylar canal towards the center of the gynoecium, but it appeared to be discontinued. The ventral slit of the carpels in *Rhapis* seems therefore, in some cases, incompletely closed to different degrees.

Additional material and species should be investigated for determining if the completely closed ventral slits are distinctive of *R. excelsa*.

Carpels were, in general terms, similarly structured in the flowers studied (see general description of the gynoecium). The exceptional features identified concern the carpels of *R. laosensis* (hermaphrodite flowers) and *R. subtilis* (type II female flowers). The peculiarity of the carpels in hermaphrodite flowers of *R. laosensis* was the lack of a dorsal groove. The position of the anthers in the hermaphrodite flowers was not the same as in the female ones. In the hermaphrodite flowers, fertile anthers are situated above the carpels, without touching them. In the female flowers, sterile flattened anthers are in contact with the carpels, placed in their dorsal groove. The structure of the carpels in female flowers reflects therefore their close contact with the staminodes. The second exception in the carpel structure was observed in female flowers of *R. subtilis* (type II). These flowers exhibited elongate carpels, with relatively long styles. Some evidences of postgenital fusion and abundant histological devices for protection of the ovules suggest that these flowers were at or close to anthesis. This particular structure of the carpels was therefore not related to a young stage of development. In addition, clearly immature flowers of *R. micrantha* did not exhibit elongate carpels. This character may therefore be distinctive of *R. subtilis*.

Species grouping on the basis of the characters studied

In the present research, a thorough comparative approach was mainly possible for male flowers. The most conspicuous difference found in this kind of flowers within the genus concerns the stamen filaments. On this basis, species of *Rhapis* can be divided into two groups: *R. excelsa* and *R. subtilis* exhibit thick and keeled filaments, whereas *R. gracilis*, *R. humilis*, *R. laosensis*, *R. micrantha* and *R. multifida* show slender and linear filaments, appearing terete or elliptic in cross section. Concerning *R. laosensis*, this description of filaments refers only to the male flowers of type I (flowers borne on strictly staminate inflorescences). Polygamous inflorescences appeared to be rare in the genus, suggesting that male flowers of *R. laosensis* borne on polygamous inflorescences (referred to as type II in the text) are relatively exceptional. These flowers exhibited intermediate filaments: they were keeled, but distinctly less thick than those of *R. excelsa* and *R. subtilis*.

During this work it was not possible to study male flowers of two species: *R. robusta* and *R. vidalii*. According to the characters employed in the key to species of *Rhapis* published by Hastings (2003),

R. robusta is included in the group with terete filaments. According to Averyanov et al. (2006), the androecium of *R. vidalii* is characterized by three antipetalous stamens with thick filaments, whereas the three stamens alternating with the petals are subsessile and exhibit very short filaments. In this species, the longer set of stamens is therefore opposite to petals. All other species of *Rhapis* have the longer set alternating with the petals. The thick filaments could stress some relationship of *R. vidalii* with *R. excelsa* and *R. subtilis*, but the position of the longer set and the presence of subsessile stamens are not observed elsewhere in the genus.

Comparison of *Rhapis* with the other genera of Rhipidinae

When comparing *Rhapis* with the other genera of the subtribe Rhipidinae (*Chamaerops*, *Guihaia*, *Maxburretia*, *Rhapidophyllum* and *Trachycarpus* as described by Dransfield and Uhl, 1998; Uhl, 1978; Uhl and Dransfield, 1987), the following distinctive floral characters can be pointed out: male and female flowers of *Rhapis* are usually relatively dissimilar, sepals and petals are both, respectively, connate for a relatively long distance, an andro-gynophore was usually present. Among the species studied, *R. subtilis* appeared to be an exception concerning the dissimilarity between the male and female flowers. In this species, flowers of both sexes were superficially similar with an ovoid shape.

Based on our results, *Guihaia* and *Maxburretia* appear to be the closest genera related to *Rhapis*. Similarly to the *Rhapis* flowers, the flowers of *Guihaia* and *Maxburretia* have petals basally connate (for a shorter distance than those of *Rhapis*) and filaments fused to the petals. Regarding *Guihaia*, other similarities are the slightly rounded shape of the anthers and the presence of staminodes borne directly on the petals. This character was observed in female flowers of *R. micrantha*. *Guihaia* differs from *Rhapis* in having sepals distinct except at the very base, basally imbricate, and the absence of a pistillode in the male flowers. Regarding *Maxburretia*, the petals exhibit some additional similarities with *Rhapis*: they are connate at the base, somewhat imbricate at mid-length, and then valvate. They are also thickened at their tips. Ovules with basal arils are also present in both genera. *Maxburretia* differs from *Rhapis* in having sepals distinct, imbricate, and filaments forming a staminal cupule in some species. The other genera of the Rhipidinae differ from *Rhapis* in having flowers in clusters (*Rhapidophyllum* and *Trachycarpus*), petals distinct and imbricate (*Rhapidophyllum* and *Trachycarpus*), filaments not fused to the petals (*Chamaerops*, *Rhapidophyllum* and *Trachycarpus*), and fused into a staminal ring (*Chamaerops*). It has to be pointed out that flowers of some genera have been only poorly

investigated to date and critical data are therefore lacking for a more detailed comparison.

Although *Rhapis* was previously studied (Hastings, 2003; Uhl et al., 1969), a comparative floral approach of all the species within the genus was not carried out and anatomical investigations were also lacking. The material available for our study did not allow a complete investigation of all species; however, it provides new insights that should be further explored. Our results on the comparative approach suggest a possible division of the species into two groups based on the structure of the filaments. Some features newly observed in *Rhapis*, like the partial fusion of the carpels, may suggest an intermediate position of the genus among the Coryphoideae. Collection of additional specimens of *Rhapis* in the wild, especially of female flowers, would be necessary for better understanding the delimitation of the species. Developmental studies should be also carried out to guarantee a careful comparative approach of the reproductive organs.

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