

Palms

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FRONT COVER

Rhapis humilis. RBG Kew, accession no. 1973-12600. (Photo: A. McRobb, RBG Kew). See article by L. Hastings, p. 62.

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BACK COVER

Cluster of mature *Pseudophoenix sargentii* palms tagged for monitoring in "Upper Class." See article by A. James, p. 57.



NEWS FROM THE WORLD OF PALMS

The photograph at right was supplied by IPS Member \$\$\$ Bear and represents a new kind of palm for the digital age. Utilities companies in California and elsewhere are disguising cellular telephone relay stations as trees, including this *faux Phoenix*. It is a convincing imitation but no match for the real thing.

This photograph was taken in \$\$\$\$, California, USA.

THE EDITORS



Pseudophoenix sargentii in Dominica

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1. Mature buccaneer palm (*Pseudophoenix sargentii*) with bulge, constricted stem, and three inflorescences

This article provides an account of the buccaneer palm, *Pseudophoenix sargentii*, on the island of Dominica, where until recently its status was poorly known.

It was August 2001 and Ms. Dena Garvue, conservation assistant with The Nature Conservancy, was nearing the end of her assignment with the Forestry, Wildlife & Parks Division (FWPD) on the Eastern Caribbean island

of Dominica. Before the end of her tour of duty, and together with two staff members of the Division and an intern, Ms. Garvue embarked upon an important field visit to the north and west coasts of the island. The purpose of that visit

was to investigate the status of a local population of buccaneer palm (*Pseudophoenix sargentii*) (Fig. 1) that had first been reported for the island in 1969, by R. W. Read in Principes. She immediately reported back to the Division that a population of the palm did in fact exist above the village of Mero, about 11 miles north of the island's capital. The FWPD was also informed that the palm is currently classified as threatened or as endangered in other parts of its range and that the Dominican population was the only one that exists outside of the Northern Caribbean. Suffice it to say, at the time none of the officers at the FWPD was familiar with that species of palm.

Not much has been written about the Dominican population of the buccaneer palm. Notable references, however, are Read's article "Some notes on *Pseudophoenix* and a key to the species," which was published in 1969, "Trees of Puerto Rico and the Virgin Islands" (Little et al. 1974), and "Flora of the Lesser Antilles: Leeward and Windward Islands" by R. A. Howard (1979). Since then, no further mention was made of the palm on the island until the 2002 issue of PALMS, and the Caribbean Palms Symposium hosted by the Fairchild Tropical Garden in Florida, USA, in May 2002.

It must be noted that although generally unknown to the botanical community, the buccaneer palm was well known to local inhabitants who, until the late 1960s, regularly harvested the spear leaves of the juvenile of this palm. A small group of women

from the nearby villages of Mero and St. Joseph harvested the leaves, shredded them, put them to dry, plaited the material, then sold it in bundles to a handicraft outlet in the capital for making ladies' hats.

Facing Up to the Challenge

Following a reconnaissance of the site in the hills above Mero, near Dominica's west coast (Fig. 2), a 3-man team from the FWPD set out to work in earnest on 6 September 2001. The aim of this ambitious exercise was to gather as much information as possible on the size and characteristics of the population of buccaneer palm on Dominica.

The scorching heat of two short dry spells that interrupted the 2001 official rainy season, the relatively steep slopes – which are more suited for mountain goats than foresters – combined with the thorns from six different plants were not enough to dampen our enthusiasm. We spent many long weekdays and Saturdays, sometimes literally in the blazing sun, in the rain and even during a thunderstorm, measuring stem heights and girths of the palms. We also counted leaf scars, measured the lengths of the longest leaves on younger palms and recorded the status of flowering and fruiting of mature palms.

Our 15-minute lunch breaks were sometimes spent in the cool of a small cave that we had stumbled upon accidentally in the "Upper Class," the highest sub-population of the palm on Dominica.



2. Mero-St. Joseph area along Dominica's west coast, where the buccaneer palm population occurs.



3. Growth of this juvenile palm in Samdi Gwa was interrupted, producing an ornate-looking stem.

With mature palms located at up to 173 m above sea level in "Upper Class," Dominica's population of *Pseudophoenix sargentii* is not only the most southerly and easterly in the species' range, but may possibly be the highest above sea level (Back Cover).

There were days when, past 6:00 p.m., and while ending a long day's work, we would stop to admire the sun setting over the canopy of tree crowns and palm fronds or to watch the reflection of the sun on the calm waters of the Caribbean Sea only a few hundred meters away.

We had tripped and fallen on several occasions while working on the clayey slopes, and often got scratched, cut or tangled among the vines while we documented over 3,340 palms of various sizes and ages, distributed in ten sub-populations over an area of about 25 acres. However, only about 2% of the current population of buccaneer palm on Dominica is reproductively mature.

The Sub-populations

We also assigned descriptive names to the other sub-populations of the palm, which are contained within two small watersheds. "The Hilltop" is located at the top of a small hill; a brush fire in 2001 had taken its toll on some of the palms in

"Fireball;" currently there are three large houses in "The Mansions," while the remains of a concrete house stand above the palms in "The Ruins." Three of the other sub-populations were named "The Corner," "Two Roads" and "The Valley." Also, we had worked all day on the Saturday before Mardi Gras at "Samdi Gwa," while the most southerly and challenging of the sub-populations was appropriately named "Southern Blues" (Fig. 3).

Dominica's population of *Pseudophoenix sargentii* grows amongst dry to semi-deciduous forest, with tree species such as *Plumeria alba*, *Bursera simaruba*, *Clusia mangle*, *Tabebuia heterophylla*, *Manilkara bidentata* and *Sabinea carinalis* – the island's national flower.

Standing Above The Others

Among the ten sub-populations of the buccaneer palm on Dominica, three stand above the rest. The Hilltop has the highest proportion of reproductively mature palms (RMP), with approximately 35.6% of the population of palms at that site having borne flowers by 2002. However, even with its large "mature adult" population, the Hilltop site hardly has any regeneration or saplings to show, except for a light scattering of "newly" germinated seedlings.

Hilltop also hosts the palm with the largest diameter (29.6 cm at breast height) and the palm with the largest bulge (31.2 cm diameter). Also, approximately 40% of the palms in that sub-population have bulges and/or constrictions on the stem; bulging is rarely encountered in the other sub-populations except at Upper Class.

Southern Blues has the largest sub-population, although two brush fires at the end of May and early June 2002 claimed at least eleven palms and injured over thirty others from the previous population of 1,005. Possibly the oldest palm in the Dominica population, with 113 scars, a stem height of 3.20 m and a diameter of 15.3 cm in 2002, is located in that sub-population and was affectionately named "Pampo." At the age of 127 years in 2002, Ms. Elizabeth "Pampo" Israel is possibly the world's oldest living person and resides in Portsmouth, Dominica's second town. Only eight of the palms in Southern Blues are reproductively mature, but this particular sub-population has a dearth of young seedlings; it also supports a large number of juveniles and sub-adults.

Upper Class, on the other hand, has only 22 palms that had borne flowers by August 2002. The mature palms in that sub-population are relatively tall, with stem height averaging 3.28 m, and



4. Fruits are eaten by birds before fully ripe, February 2002.

internodes of up to 18 cm. In fact, because of the height of the tallest trees in that sub-population, coupled with the closeness of the younger scars, we resorted to using binoculars in order to count the upper scars on the taller trees. That sub-population also has very few juveniles but a surprisingly large number of young seedlings (with no rings and leaf-lengths averaging less than 0.5 m in 2002). There is an even larger number of younger seedlings that have only eophylls and the first set of lanceolate leaves. It is estimated that that sub-population may have as many as 1,500 very young seedlings scattered around and among the handful of "giants." It is possible that some episodic events occurred in Southern Blues and Upper Class which resulted in the unusual structure of these two sub-populations.

The tallest palm in the Dominica population is located in The Valley – which has only 72 palms with pinnate leaves. In early 2002 this palm had a stem height of 4.49 m, a diameter of 20.1 cm and only 50 scars. This palm was jokingly assigned the name, "Overgrown," as it only reached reproductive maturity in August 2002.

Harvest of the Cherry-like Fruits

At the beginning of 2002, only ten of the palms in the Dominican population of buccaneer palms had mature fruit. The fruits on nine of these trees

ripened between the end of January and the middle of February, while the infructescence on the other tree ripened in June.

The year 2003, however, is expected to bring forth a "bumper harvest." The small yellow flowers began to appear in June 2002, providing nectar and pollen for the honeybees and bumblebees, and at least 75 trees are expected to produce the next batch of cherry-like fruits from the population.

Agents of Dispersal

After first suspecting fruit-eating bats to be the main agents of dispersal of the seeds of the buccaneer palm in Dominica, we had the opportunity to witness a Lesser Antillean saltator (*Saltator albicollis*), while feeding on the fruits on one of the palms in Upper Class, chase away a Lesser Antillean bullfinch (*Loxigilla noctis*) that had come to partake of the "harvest" (Fig. 4).

We found a feeding perch used by the saltators in Upper Class, but it appears that a secondary agent of dispersal may be involved in moving the seeds. Several pieces of pericarp of the ripe palm fruits were found scattered over a small area near the perch, but barely any seeds were found. This would suggest that either the Dominican ground lizard (*Ameiva fuscata*), or possibly rats, or crabs

(*Gecarcinus ruricola* and *Coenobita clypeatus*) may be carrying away seeds that have been dropped by the saltators and the bullfinches while feeding.

The Future of Dominica's Population of *Pseudophoenix*

Dominica's (and the Eastern Caribbean's) only population of the buccaneer palm faces a wide range of threats. These include the general lack of knowledge about the palm in Dominica, the annual brush fires, housing development and the land-ownership situation in the area where the palms occur. Brush fires may be resulting in some mortality or causing injury to several palms annually. To these threats may be added the erosion from runoff on the steeper slopes and habitat degradation from the invasion of the Mulch or Lemon Grass (*Cymbopogon citratus*) into the areas where the palms occur.

Currently, the Forestry, Wildlife & Parks Division is attempting to propagate the buccaneer palm. The Division is also in the process of developing a Plan-of-Action for the protection, conservation and increasing public awareness of the buccaneer palm on Dominica. The Division also proposes to launch a campaign to raise sufficient funds to enable the Government of Dominica to acquire some of the lands where *Pseudophoenix sargentii* (and the endemic *Sabinea carinalis*) occur. This is in order to afford some protection to the palm

population in the wild, as well as to conserve part of the habitat of this species.

Acknowledgments

I would like to acknowledge the invaluable assistance and support provided in the field by Alvin Dejean and Stephen Toussaint, two drivers at the Forestry, Wildlife & Parks Division in Dominica. The assistance and support provided by the then acting Director and other members of staff of the Division on other occasions, as well as the support provided by Dr. Scott Zona and Ms. Dena Garvue are also gratefully acknowledged.

LITERATURE CITED

- HOWARD, R.A. 1979. Flora of the Lesser Antilles: Leeward and Windward Islands – Monocotyledoneae. Arnold Arboretum, Harvard University, Jamaica Plain, Massachusetts.
- JAMES, A. 2002. Buccaneer palm rediscovered on Dominica... So what! Prepared for the Caribbean Palms Symposium, Fairchild Tropical Garden, 18 May 2002 (Unpub.).
- LITTLE, E.L. JR, R.O. WOODBURY AND F.H. WADSWORTH. 1974. Trees of Puerto Rico and the Virgin Islands. U.S. Department of Agriculture Forest Service, Washington, D.C.
- READ, R.W. 1969. Some notes on *Pseudophoenix* and a key to the species. *Principes* 13: 77–79.
- ZONA, S. 2002. A revision of *Pseudophoenix*. *PALMS* 46: 19–38.

Seed dispersal and predation by Peccaries and Suidae, A call for personal field observations.

There is a dearth of information on seed dispersal and predation by Neotropical Peccaries and Paleotropical Suidae. Many "anecdotal" field observations are not published but would provide crucial ecological information. I am currently preparing a review on the seed dispersal and predation by Peccaries and Suidae. If you are willing to share your observation in particular if seeds were crushed, spit out, swallowed or germinated after passing through the animal, then please contact me. All observations will be cited as "personal communications."

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A Revision of *Rhapis*, the Lady Palms

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1. *Rhapis excelsa* canes from the Economic Botany Collections, Royal Botanic Gardens, Kew. From left to right: unfinished sunshade handle, EBC 37520; walking stick, EBC 37462; walking cane, EBC 37506; sunshade handle, EBC 37553; walking stick, EBC 37500; sunshade handle, EBC 37577; ladies umbrella handle stained green, EBC 37577. (Photo: A. McRobb, RBG Kew.)



The Lady Palms are among the most familiar and widely grown of all ornamental palms, yet, surprisingly, the taxonomy of the genus has often been confused and several species remain poorly known. In this account of *Rhapis*, eight species are recognized, and the complex nomenclatural history of the genus is discussed.

Rhapis, a genus of clustering palms commonly known as Lady Palms, belongs to subfamily Coryphoideae, tribe Corypheae, subtribe Thrinacinae. It is characterized by slender stems, palmate leaves, divided regularly into many-folded segments with truncate or oblique apices; the divisions into segments unusually occurs between the folds, rather than along the folds, a situation known elsewhere only in *Rhapidophyllum*. The

flowers are fleshy with sepals and petals united basally, and the six stamens are free but epipetalous. Its palmate, induplicate leaves, and solitary, only slightly dimorphic flowers, are characters that put *Rhapis* into subfamily Coryphoideae, tribe Corypheae, and the presence of free carpels places it in subtribe Thrinacinae. This subtribe shows two main lines of evolution that have produced two distinct groups. One is

entirely New World, the other, which includes *Rhapis*, is mainly Old World and tends towards dioecy and elaboration and fusion of the perianth segments. The genera most closely related to *Rhapis* are *Maxburretia* and *Guihaia*. *Rhapis* differs from these in always having an erect stem, leaf sheaths that never develop into spines, leaf segments usually with many folds, conspicuous veinlets, splits between leaf segments being between folds and the larger fleshy slightly stalked flowers with the sepals and petals united basally with separate epipetalous filaments. The name *Rhapis* comes from the Greek word *rhapis* (rod), alluding to the rod-like canes or stems (Beeler 1960).

The elegant appearance of *Rhapis* along with its modest proportions and ease of cultivation make it horticulturally desirable and it has been widely cultivated and traded since the 17th Century. Yet despite this long history of cultivation, *Rhapis* taxonomy is in confusion and due to its horticultural importance a revised taxonomy is much needed.

Although distinct species can be recognized within *Rhapis* they tend to be separated by few characters. In the past there has been a tendency to use leaf blade dissection to delimit species but this is very variable between populations and with age, and therefore not a reliable character at species level.

Taxonomic history

The genus *Rhapis* has had a complex taxonomic history. It was first described by Linnaeus f. in Aiton's *Hortus Kewensis* (1789) and included just one species, *R. flabelliformis* L'Hérit ex Aiton (a synonym of *R. excelsa*). This species of *Rhapis* has been extensively cultivated since the mid 1600s with many cultivars selected and registered by Japanese horticulturists, including dwarf and variegated forms (McKamey 1985).

Three further species of *Rhapis* were published by Blume in 1836, *R. humilis*, *R. major* and *R. javanica*. Like *R. excelsa*, *R. humilis* has also been in cultivation since the 17th Century, again with variegated forms developed and registered in Japan (McKamey 1985).

In 1910 three additional species of *Rhapis* were published by Beccari (*R. micrantha*, *R. laosensis* and *R. subtilis*).

In 1930 Burret published an eighth species of *Rhapis*, *R. gracilis*. Also in this year Alfred Rehder published the new combination *R. excelsa* for *R. flabelliformis*, since the taxon was found to have been wrongly placed in *Chamaerops* and have been described as *Chamaerops excelsa* by Thunberg in

1784, predating *R. flabelliformis* by five years (see Rehder 1930).

A revision of *Rhapis* by Odoardo Beccari was published posthumously by Ugolino Martelli in 1931. It included five accepted species, *R. flabelliformis* (synonym of *R. excelsa*), *R. humilis*, *R. micrantha*, *R. laosensis* and *R. subtilis* and listed eleven doubtful ones. Blume's *R. major* and *R. javanica* were placed in synonymy of *R. flabelliformis*. The work seems to have overlooked Rehder's new combination for *R. flabelliformis* and Burret's *R. gracilis* of 1930.

Six years after Beccari's revision, six more species were added to *Rhapis*, three by Burret (*R. multifida*, *R. robusta* and *R. filiformis*) and three by Gagnepain (*R. grossefibrosa*, *R. divaricata* and *R. macrantha*). Eight years after the revision (in 1939) Bailey produced a synopsis of *Rhapis*; he included nine species (*R. excelsa*, *R. humilis*, *R. micrantha*, *R. laosensis*, *R. subtilis*, *R. gracilis*, *R. robusta*, *R. filiformis* and *R. macrantha*) and added his own observations on the two species then in cultivation, *R. excelsa* and *R. humilis*.

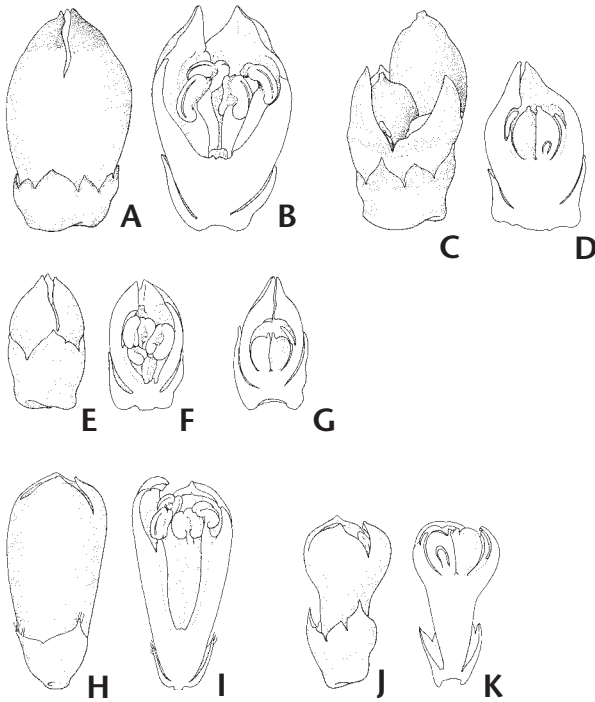
A number of combinations published under *Rhapis* have been transferred to *Sabal minor* (Jacq.) Pers. These include *R. arundinacea* Aiton (1789, see Moore 1975), *R. acaulis* Willd. (1806, see Moore 1963) and *R. caroliniana* Hort. ex Kunth (1841, see Shuey & Wunderlin 1977). Beccari (1931) had previously given *R. arundinacea* and *R. caroliniana* as synonyms of *Rhapidophyllum hystrix* (Pursh) H.Wendl. & Drude.

More recently Dransfield et al. (1985) transferred *R. grossefibrosa* to a new genus *Guihaia*, as *G. grossefibrosa* (Gagnep.) J. Dransf., Lee & Wei, and in 1997 Wei placed *R. filiformis* Burret in synonymy with *G. grossefibrosa*. The most recent species to be described, *R. siamensis* Hodel (1997), is considered in this revision to be a synonym of *R. subtilis*. The present author accepts eight species.

Materials and Methods

The following account is based primarily on the examination of herbarium specimens. In addition a small number of living collections of *R. excelsa* and *R. humilis* were seen at the Royal Botanic Gardens, Kew.

Throughout, all the specimens cited have been seen unless otherwise indicated. Those cited for FI have been critically examined by J. Dransfield (pers. comm.). The sex of the specimens has been recorded where possible. Petiole width is measured at 1 cm below the petiole apex and the inflorescence rachis is measured just below the first branching point. The overall measurement



2. Flowers of *Rhapis*. *Rhapis subtilis*. **A** Staminate flower $\times 8$; **B** Staminate flower in longitudinal section $\times 8$; **C** Pistillate flower $\times 8$; **D** Pistillate flower in longitudinal section $\times 8$. *Rhapis excelsa*. **E** Staminate flower $\times 8$; **F** Staminate flower in longitudinal section $\times 8$; **G** Pistillate flower in longitudinal section $\times 8$. *Rhapis humilis*. **H** Staminate flower $\times 8$; **I** Staminate flower in longitudinal section $\times 8$; **J** Pistillate flower $\times 8$; **K** Pistillate flower in longitudinal section $\times 8$. **A, B** from McKamey *s.n.*, **C, D** from Dransfield & Bhoonab 5488, **E, G** from Rehder *s.n.* in 1886, **H, I** from Temperate House, Kew, **J, K** from Chow 6249. Drawn by Lucy T. Smith.

of the rachis length includes the rachillae. The term receptacular-stalk refers to the base of the receptacle and corolla when they are elongated. Fruit is described only if it is available. Fruit colour is taken from herbarium label data or photographs. Author names are abbreviated according to Brummitt and Powell (1992).

This study was limited by the small number of specimens available, of which a high proportion are from cultivated material, and the fact that none of the species has been seen in the wild by the author. Despite being a small palm *Rhapis* are large and fibrous enough to make their collection, and the preparation of specimens from them difficult, and as a result many older herbarium specimens of *Rhapis* are incomplete, often with no stem material. *Rhapis* is distributed in areas which have been politically unstable, with no opportunity until recently for observation in the wild or for re-collection. Therefore, excepting specimens from Thailand, North Sumatra, Vietnam and Laos, no recent wild collections were available for this study. Species habitat in lowland tropical forest makes them particularly vulnerable to deforestation, which may have reduced populations considerably since herbarium collections were made in the late 18th and early 19th Centuries. The species are poorly represented in cultivation; the most commonly cultivated are *R. excelsa*, *R. humilis* and *R. subtilis*. Furthermore

R. humilis and *R. excelsa* are represented in herbaria by a very small proportion of wild-collected specimens. *Rhapis laosensis*, *R. multifida*, *R. gracilis* and *R. robusta* are less commonly cultivated, but the author has seen only wild material of these.

Taxonomic Treatment

Rhapis L. f. ex Aiton, Hortus Kewensis 3: 473. 1789. Lectotype: *R. flabelliformis* L'Hérit. ex Aiton (illegitimate name) = *R. excelsa* (Thunb.) A. Henry ex Rehder. Mart., Hist. Nat. Palm 3: 253. 1838; Kunth, Enum. 1, Pl. 3: 251. 1841; Benth. et Hook. f., Gen. Pl. 3 (2): 930. 1883.

Small, clustering, pleonanthic, unarmed dioecious or rarely hermaphrodite palms. Stems slender, erect, covered with persistent leaf sheaths, eventually becoming bare. Leaves induplicate, palmate, marcescent; sheaths sparsely tomentose when young, pale brown to dark brown; petiole elongate, slender, elliptic in cross-section, margins smooth or minutely scabrid and brown papillate; adaxial hastula small, more or less triangular, sometimes tomentose, abaxial hastula absent; mature blade glabrous, divided between folds into several-ribbed segments with minutely scabrid margins, major splits from between 1/3 radius to near the base, apices divided along and between the folds to form secondary splits. Inflorescences interfoliar, male, female and hermaphrodite sexes superficially similar, branching to 1–3 orders;

prophyll tubular, 2-keeled, usually sheathing, splitting along the abaxial midline; peduncle usually entirely enclosed in leaf sheath, peduncular bracts absent; rachis usually longer than the peduncle, bearing 1–3(4), large, sheathing, single-keeled bracts subtending first order branches, distal rachis bracts smaller, split to the base, small narrow triangular bracts subtending second order branches; rachillae formed from secondary and tertiary branches; rachis and rachillae glabrous or tomentose; rachillae lax, spreading, male sometimes more crowded than the female, bearing spirally arranged solitary, or rarely paired flowers in the axils of minute apiculate bracts. Flowers: male, female and hermaphrodite symmetrical, sexes superficially similar, size increasing with maturity; calyx cup-shaped, 3-lobed, lobes sometimes irregular; corolla fleshy, tubular, 3-lobed, usually with a stalk-like base comprising extended receptacle and corolla (receptacular-stalk), lobes triangular, valvate; stamens and staminodes 6, biseriate, the taller row in-between the corolla lobes. Male flowers with filaments \pm adnate along the entire length of the corolla tube, free at their tips, anthers basifixed, short, rounded; pollen elliptic, monosulcate, with finely reticulate, tectate exine (Uhl & Dransfield 1987); pistillode minute, 3-lobed. Female flowers with staminodes, carpels 3, distinctly wedge-shaped, each with a short apical style and cylindrical stigma; ovules 1 per carpel, basally attached, hemianatropous, with a basal fleshy aril. Fruit developing from one carpel, sometimes 2 or 3 carpels developing, stalked or sessile (stalk appearing to develop from the receptacular-stalk of the flower), stigmatic remnants persist at apex, epicarp papillose, mesocarp fibrous, endocarp thin, brittle. Seed with short lateral raphe; endosperm homogeneous, laterally penetrated by the seed coat, embryo sub-basal or lateral (Uhl & Dransfield 1987). Germination remote-tubular; eophyll entire slender, strap-shaped, plicate (Uhl & Dransfield 1987).

Distribution. South China (5 species.), Japan (2 spp. possibly originating from the wild), Laos (3 spp.), Vietnam (2 spp.), central and southern Thailand and northern Sumatra (1 sp.). The recorded distribution suggests that *Rhapis* is likely to occur in Myanmar (Burma), but the author has not seen any collections from there.

Habitat. Undergrowth palms of tropical evergreen, lowland forest. In Thailand and Sumatra *R. subtilis* is confined to limestone hills. Where *R. subtilis* occurs in North Sumatra at Lho'Nga, North Aceh, the limestone forms a characteristic landscape called cockpit (or labyrinth) karst which has regular series of conical or hemispherical hills and

hollows with moderately steep sides (30–40°, Whitten et al. 1987). In Laos *R. laosensis* occurs on alluvial river levées over underlying sandstone (J. Dransfield, pers. comm.).

Anatomy. *Rhapis* is anatomically the best-known palm; it has been chosen for studies because of its moderate size and wide availability. Detailed anatomical studies have been undertaken on leaf (Tomlinson 1961, Kaplan et al. 1982), stem (Zimmermann & Tomlinson 1965) and flowers (Uhl et al. 1969). For discussion of these studies see Uhl and Dransfield (1987).

Genetics. *Rhapis excelsa* and *R. humilis* are the only two species to have been investigated and as they are often mislabelled as each other, the results must be viewed with caution. Both species are reported to have a gametic chromosome number $n=18$ (Read 1966, Sharma & Sarkar 1957). This is at the upper limit of the range of chromosome numbers for Palms ($n = 13–18$ excluding polyploids) and is a characteristic of most members of the Coryphoideae, which is congruent with the view that they may be one of the oldest palm groups (Uhl & Dransfield 1987). Sharma and Sarkar (1957) also concluded that, due to a similarity in karyotypes indicating an origin from a common ancestor, *Rhapis* and *Corypha* could be grouped together as members of a similar evolutionary line. *Rhapis flabelliformis* (= *R. excelsa*) and *R. humilis* are reported sometimes to show polyploidy in cultivation with $n = 36$ (Sharma & Sarkar 1957).

Conservation status. *Rhapis divaricata* (= *R. excelsa*) is listed as rare in Vietnam (Walter & Gillett 1998 citing Nguyen Nghia Thin 1991). Despite their being widely cultivated there is no other published information on the status of species in the wild. *Rhapis laosensis* is abundant in Laos, but *R. subtilis* in Sumatra is virtually extinct (J. Dransfield, pers. comm. 2001).

Uses. The main use of *Rhapis* is as ornamental plants. According to Burkill (1935), Kaempfer saw *R. flabelliformis* (synonym of *R. excelsa*) in cultivation in Japan during his voyages in 1690–92. In 1774, James Gordon introduced male plants into Europe, probably by seed. Commonly known as Lady Palms, *R. excelsa*, *R. humilis* and *R. subtilis* are now widely grown in the USA and elsewhere as ornamentals, highly prized and of significant economic importance (Jones 1994). Good illustrations of the dwarf and variegated varieties of *R. excelsa* and *R. humilis* developed in Japan can be seen in Ellison and Ellison (2001). *Rhapis subtilis* and *R. laosensis* were brought into cultivation in the 1960s (McKamey 1989). *Rhapis laosensis* and *R. gracilis* are essentially collectors'

items. *Rhapis robusta* is cultivated only in China, and *R. multifida* has become well established in cultivation (Jones 1994).

Rhapis laosensis shoots are edible; the leaf sheaths are peeled away to reveal the shoots which are sold for food in local markets in Laos (J. Dransfield & Evans, pers. comm.). In Chinese medicine the petiole, leaf sheath and fruits are used to stop bleeding and the root to treat rheumatism and stimulate blood circulation (Chin & Keng 1992). Herbarium specimen labels record *Rhapis excelsa* being used as chopsticks and bowstrings and its stems being used for sticks and canes, including in the construction of sedan chairs. Examples of *R. excelsa* canes imported from China for sunshade and umbrella handles and walking sticks, can be found in the walking stick collection of the Economic Botany Collections (EBC) at Kew (Fig. 1). They form part of the 'Partridge Canes' of 19th Century commerce and have handles fashioned from the stem-base and roots. One sunshade has an elaborately curved handle with an extra piece of cane twisted into it and one walking stick has a patterned top section studded with mother of pearl. Despite their narrow diameter these canes are solid and very strong.

Key to Species of *Rhapis*

- 1. Mature flowers up to 6.1 × 4 mm, rachis glabrous; male ovoid, female cylindrical, both coriaceous; calyx margins irregular, usually with darkly pigmented bands *R. subtilis*
 Mature flowers usually smaller, if as large, then rachis not glabrous; flowers obovoid, obtriangular or clavate, fleshy; calyx margins regular or irregular, evenly pigmented 2.
- 2. Inflorescence with large conspicuous, usually coriaceous, boat-shaped, almost entirely overlapping bracts, not sheathing the rachis; leaf segment tips distinctly cuculate
 *R. laosensis*
 Inflorescence with less conspicuous papyraceous, tubular, rarely overlapping bracts, sheathing the rachis; leaf segment tips sometimes cuculate 3.
- 3. Leaf segments with all primary splits reaching very close to the blade base, within 3–5 mm when viewed from below 4.
 Leaf segments with at least some primary splits not reaching 3–5 mm from the blade base when viewed from below 5.
- 4. Leaf segments 5–7 *R. micrantha*
 Leaf segments 2–4 *R. gracilis*

- 5. Segments up to 375 mm long with relatively straight sides, apices usually truncate with regular dentate secondary splitting; inflorescence with rachis pale brown, glabrous; filaments keeled *R. excelsa*
 Segments up to 450 mm long with slightly curved sides, apices usually oblique, secondary splitting with irregular appearance; inflorescence with rachis pale or dark brown, glabrous or tomentose; filaments terete 6.
- 6. Leaf segments 5–20; inflorescence greatly exceeding the bracts 7.
 Leaf segments 2–4; inflorescence not greatly exceeding the bracts 8.
- 7. Leaf sheath with coarse outer fibers and fine inner ones; inflorescence branching to 2 orders; bracts large thick, dark brown; rachis pale brown with pale brown tomentum; flowers with calyx irregularly lobed; fruit receptacular-stalk to 5 mm *R. multifida*
 Leaf sheath with outer and inner fibers similar in thickness; inflorescence branching to 3(–4) orders; bracts of relatively medium thickness, pale brown with darker patches; rachis dark brown and bearing rusty brown tomentum; flowers with calyx regularly lobed; (fruit not seen) *R. humilis*
- 8. Inflorescence with bracts distant, not overlapping, very thin-textured; rachis tomentose; flowers small 1.8 × 1 mm; corolla with a receptacular-stalk to half the flower length *R. robusta*
 Inflorescence with bracts close, the tips of one overlapping the base of the next; rachis usually glabrous; flowers to 3.1–4.3 × 2.1–2.2 mm; corolla with a short receptacular-stalk less than one quarter the flower length; calyx lobes acute *R. gracilis*

1. *Rhapis excelsa* (Thunb.) A. Henry in Rehder, J. Arnold Arb. 11: 153. 1930. *Chamaerops excelsa* Thunb. Fl. Jap. 130. 1784. *Trachycarpus excelsus* (Thunb.) H. Wendl., in J. Gay, Bull. Soc. Bot. France 8: 429–430. 1861. Non *C. excelsa* Mart., Lectotype (chosen here): *C.P. Thunberg*, sheet no. 24386 (UPS, photo K).

Rhapis flabelliformis L'Hérit ex Aiton, Hortus Kewensis 3: 473. 1789; Mart., Hist. Nat. Palm. 3: 253, 254. 1838; Becc., Ann. Roy. Bot. Gard., Calcutta 13: 244. 1931. Superfluous illegitimate name. Lectotype: *C.P. Thunberg*, sheet no. 24386 (UPS, photo K).

Rhapis major Blume, Rumphia 2: 55–56. 1836. Type: *Blume s.n.* no date (L).

Rhapis Kwamwonzick Siebold (*Chamaerops Kwanwortzick* Hort.), in Linden, Illustration Horticole 34: 39. 1887.

Rhapis divaricata Gagnep., in Humbert, Not. Syst. 6(3): 158. 1937, Indo-China (Vietnam); in Lecomte, Fl. Gén. Indo-Chine, 6(8): 996. 1937. Type: *Chevalier 37823* (P).

Stems to 2.5 m tall, with sheaths 15–21 mm diam., without sheaths 8–12 mm. Leaf sheath loosely sheathing the stem, usually with outer and inner fibers of similar thickness, producing a squared mesh, some young sheaths with flatter, coarser outer fibers and tomentum, ligule not remaining intact at maturity; petiole to 4 mm wide, margin often smooth, rarely minutely scabrid, often bearing brown papillae; blade with V-shaped or semi-circular outline, variable in size, often with a conspicuous palman, segments (1)4–13, folds 11–25, to 375 mm long, broad, relatively straight-sided, narrowing slightly at base and apex, apices sometimes cuculate, usually truncate, with regular dentate secondary splitting, primary splits to within 2.5–61 mm of the blade base, sometimes with brown papillae at the base and along the ribs, sometimes scabrid along the adaxial ribs, thick in texture, adaxial and abaxial surfaces similar in colour, often with a yellow tinge, adaxial occasionally darker, transverse veinlets conspicuous. Inflorescence, male and female similar in general appearance, branching to 2 or 3 orders; prophyll tubular, overlapping the base of the first rachis bract, relatively thin in texture, reddish brown, sometimes darker at the base, inner surface smooth, outer surface with tomentum often only at the distal end; rachis bracts 2(–3), sometimes with a distal incomplete rachis bract, similar in appearance to prophyll; rachis overall length to 260 mm, 4–8 mm diam., rachillae 7.5–110 mm long, 0.8–1.9 mm diam., usually glabrous, pale brown, sometimes with small patches of caducous tomentum. Flowers densely packed on the rachillae. Male flowers globose when young, elongating when mature to 5.2 × 3.8 mm; calyx to 2.8 mm, lobes to 2 mm, usually with a regular margin; corolla sometimes narrowed into a short receptacular-stalk to 1 mm; filaments, shorter row to 2.2 mm, longer row to 2.5 mm, broad, to 0.4 mm, with adaxial keel, triangular in cross section; pistillode sometimes present. Female flowers to 3.6 × 3.2 mm; calyx to 2.3 mm; corolla with a receptacular-stalk to 1.1 mm; staminodes present. Fruit sometimes with 3 carpels developing, often only one reaching maturity, to 8–10 × 8 mm, borne on a short receptacular-stalk to 2 mm, epicarp shiny translucent, minutely papillose, with conspicuous black lenticels. (Fig. 2 E–G).

Distribution. China, Yunnan; South Central China, Hainan; South East China, Guangdong, Fujian, Hongkong; Japan.

Habitat. woods, 3080 ft (939 m); river valley; wooded mountain side.

Representative specimens. CHINA: Herb Forsyth *s.n.* 1835 male (K); Yunnan, *Henry 10173* (K); SOUTH CENTRAL CHINA: Hainan, *I.P. Yuk Shing L.U. 18346* (K); SOUTH EAST CHINA: Guangdong, *T.M. Tsui 249* immature probably male (A, K); Fujian (Nantai Island) *Tang Chung-Chang 4258* male (A); Hongkong *Urquhart sn 1861* (K), Happy Valley woods, *Wilford 1301* female (in fruit) (K, A) JAPAN: Nagasaki *Lgt Fakmouti s.n.* 1928 male (L); *C.P. Thunberg sheet 24386* (UPS, photo K). CULTIVATED: *Blume s.n.* no date (type of *R. major* Bl.) (L); Australia, Queensland, Brisbane Botanic Garden, *M. Strong Clemens 42997* male (A); *N. Goom s.n.* 1844 (L.); Bermuda, Pembroke, *E.A. Manuel 973* (A); France, Jardin de Cels *s.n.* 1819 male, *s.n.* 1821 male (K); Germany, Frankfurt, *A.S. Rehder s.n.* 1886 male and female with well developed anthers (A); Hongkong Botanic Garden, *C. Ford 566* male (K); *s.n.* 1895 female in fruit (K), *Shiu Ying Hu, 12934* 1973 female in fruit (K); India, Chitpur, Adzar *J.S. Gamble 17612* male (K), Herb. Hort. Bot. Calc. *s.n.* 1891 male (K), Madras *A.G. Bourne s.n.* 1900 (K); North Vietnam, Son Tay, *Aug. Chevalier 37823* female (P), Hanoi Botanic Garden, *herb. Ch. d'Alleizette 7706* 1909 male (L); Malay Peninsula, plant house in a tub *s.n.* 1929 female or hermaphrodite (K); South East China, Fujian, (Nantai Island) *H.H. Chung 2709* male (A, K); Sri Lanka, Bot. Gard., Peradeniya, *S. Rutherford & M.M.P. Bandard R-75* (K); Taiwan, *Jih-ching Liao 10637* (L); UK, Herb J. Gay, Dr Gordon *s.n.* 1776 (BM), Kew, Royal Botanic Gardens, Kew *s.n.* 1856 male and female or hermaphrodite (K), Acc. no. 1987-2573, *s.n.* 1998 (K).

Two specimens [Malay Peninsula, plant house in a tub *s.n.* 1929 (K) and Kew, Royal Botanic Gardens, Kew *s.n.* 1856 (K)] have flowers that appear female but have well developed anthers and may be hermaphrodite.

Rhapis excelsa differs from *R. humilis* in having outer leaf sheaths loosely sheathing the stem, ligule not remaining intact at maturity producing many detached fibers; blade varying from both semi-circular to V-shaped in outline, thicker in texture and a paler, more yellow-green in colour in dried specimens, often with fewer segments, segments straighter sided with truncate apices and more regular dentate secondary splitting, palman less conspicuous. While individual differences in the vegetative characters are difficult to pinpoint between *R. excelsa* and *R. humilis*, when all the vegetative characters are taken as a whole the

leaves can be distinguished easily. Inflorescence characters are more noticeably different. *Rhapis excelsa* differs in having glabrous rachis and rachillae at maturity, tomentum often present on the bracts and stamens with broader keeled filaments; not more than three rachis bracts were recorded, while four were recorded for *R. humilis*.

Rhapis excelsa may be of Chinese and Japanese origin, as suggested by the herbarium specimens, or from China introduced to Japan and from there to the West. The long history of cultivation probably accounts for the selection of many variants within the species including dwarfism and variegation.

A short description is given for the name *Rhapis flabelliformis* L'Hérit ex Aiton in Aiton, Hort. Kew 1(3): 473. 1789. It includes a reference to a plate of the species: L' Hérít., Stirp. nov., 2. Plate 100, which has not been located, despite thorough searching through the copies of L' Hérítier's *Stirpes Novae* in the libraries at Kew (K), the Linnean Society (LINN), the Natural History Museum, London (BM) and the New York Botanic Garden (NY). In each of the copies in these libraries plate 100 is *Solanum xanthocarpum*, and *R. flabelliformis* does not appear in the book. In the BM copy of *Hortus Kewensis* "[ined]" has been added next to the *R. flabelliformis* reference, and it could be that the author in Aiton was basing his statement on unpublished material that was later not included (Judith Magee, librarian, pers. comm.). L' Hérítier did not finish *Stirpes Novae* due to misfortune during the French Revolution; he had planned to issue two volumes (Bucheim 1966). The author of *Rhapis flabelliformis* in Aiton (1789) may have seen the unpublished plate which subsequently may have been separated from the other loose plates (later some of these were collected together) during the distribution of L' Hérítier's estate after he was murdered in 1800 (Stafleu & Cowan 1981).

Aiton's *Hortus Kewensis* (1789) was written by Solander and continued by Dryander, both scholar librarians employed by Joseph Banks (Stearn W. T. pers. comm.; Carter 1988). The Solander boxes at BM contain the detailed descriptions of all the species described in Aiton (W. T. Stearn pers. comm.). Solander's description of *R. flabelliformis* (Pages 317–321, Solander boxes BM) was located and when translated from the Latin indicates that the specimen on which *R. flabelliformis* was based was collected from a plant growing in Dr. James Gordon's garden at Mile End, London, in 1776. This specimen is at the Natural History Museum (BM) and has been identified by the author as *R. excelsa*.

The nomenclatural and taxonomic history of *R. excelsa* is inextricably linked with that of *R. humilis* and so these aspects of the two species are discussed together here. The type specimen of *R. excelsa* is Thunberg's *Chamaerops excelsa* which comprises two sheets in the Thunberg collection at Upsala, Sweden – collection number 24385, consisting of a leaf and partial inflorescence, and 24386, comprising a single leaf. Good close-up photographs enabled the author critically to examine the type. The type is a mixed collection and thus lectotypification is necessary. Sheet 24385 matches the widely accepted application of the name *R. humilis*, while 24386 matches *R. excelsa*. In order to maintain nomenclatural stability for these two very widely grown horticultural plants, I have selected Thunberg sheet number 24386 (U) to represent the type of *R. excelsa*. This mixed collection type specimen has bedevilled the taxonomy from the very beginning (Beccari referred to "Un grande imbroglio di nomenclatura") and has been responsible for much of the past confusion between these two species.

A short description is given for the name *Rhapis flabelliformis* L'Hérit ex Aiton in Aiton, Hort. Kew 1(3): 473. 1789. It includes the name *Chamaerops excelsa* Thunb. in synonymy, which was published five years earlier and following modern nomenclatural rules the correct name for the taxon is therefore *Rhapis excelsa* (Thunb.) A. Henry, resulting in the name *Rhapis flabelliformis* being superfluous and the type specimen for it being Thunberg sheet number 24386 (U), the type of *Rhapis excelsa*. For full details of *Rhapis flabelliformis* L'Hérit ex Aiton see Text Box.

The species epithet for *Rhapis Kwamwonzick* Siebold has several different spellings in the literature but *Kwamwonzick* is the only one that is validly published. It does not appear to be represented by a type specimen; however, the description and illustration match *R. excelsa*.

2. *Rhapis micrantha* Becc., Webbia 3: 220. 1910; and 5 (1a): 60. 1920; Becc., Bull. Mus. Hist. Nat. Paris, 17(3): 157. 1911; Becc., Ann. Roy. Bot. Gard., Calcutta 13, 249. 1931; Gagnep., in Lecomte, Fl. Gén. Indo-Chine 6(8): 996. 1937. Lectotype (chosen here): Vietnam, Dong Ban mountains, Kien Khe, *R.P. Bon 2345*, staminate component (P, FI isolectotype).

Stems to 1–2 m tall, with sheaths 17–18 mm diam., without sheaths 8–9 mm. Leaf sheath tightly sheathing the stem producing a neatly flattened appearance with coarse flattened outer fibers and finer inner ones at maturity, producing a diagonal lined mesh, ligule not remaining intact at

maturity; petiole to 2.5 mm wide, margin smooth or sometimes minutely scabrid; blade with wide V-shaped almost semicircular outline, without a conspicuous palman, segments 5–7, folds 17–21, to 220 mm long, sides curved, tapering slightly towards base and apex, apices sometimes cucullate, usually oblique, with regular secondary splitting, primary splits to within 3–5 mm of the blade base, adaxial ribs smooth, abaxial surface of blade noticeably paler than adaxial. Inflorescence, male branching to 2 orders, female to 3; prophyll similar to rachis bracts; rachis bracts 3, sometimes with a distal incomplete rachis bract, bracts tubular more expanded in male than in female, overlapping the base of the next bract, reddish brown, darker at the base, in the male with tomentum on the outer surface, in the female with tomentum on the outer surface at the distal end only; rachis overall length to 190 mm, 4–5 mm diam., rachillae 16–60 mm long, 0.5–0.8 mm diam., in the male with tomentum, sparser on the rachillae, in the female glabrous. Male flowers to 3.8 × 2.4 mm; calyx to 1.6 mm, lobes to 0.8 mm, margin regular or irregular; corolla sometimes without a receptacular-stalk or with a short receptacular-stalk to 0.8 mm; filaments, shorter row to 1.6 mm, longer row to 2 mm, to 0.2 mm diam.; pistillode present. Female flowers, only immature available, small, globose to 2.2 × 2.3 mm; calyx to 1.5 mm, lobes to 1 mm, margin regular; corolla with a receptacular-stalk to 0.9 mm; staminodes present. Fruit not seen.

Distribution. Laos, Vietnam.

Habitat. Mountainous regions.

Representative specimens. LAOS: *Dr. M. Spire 5929* male (P). VIETNAM: Dong Ban Mountains, Kien Kha, *R.P. Bon 2045* (P), *2345* male (P, FI), *U. Martelli* photo probably of *2345* (Ann. Roy. Bot. Gard., Calcutta 13 plate 55), *2545* (P, FI).

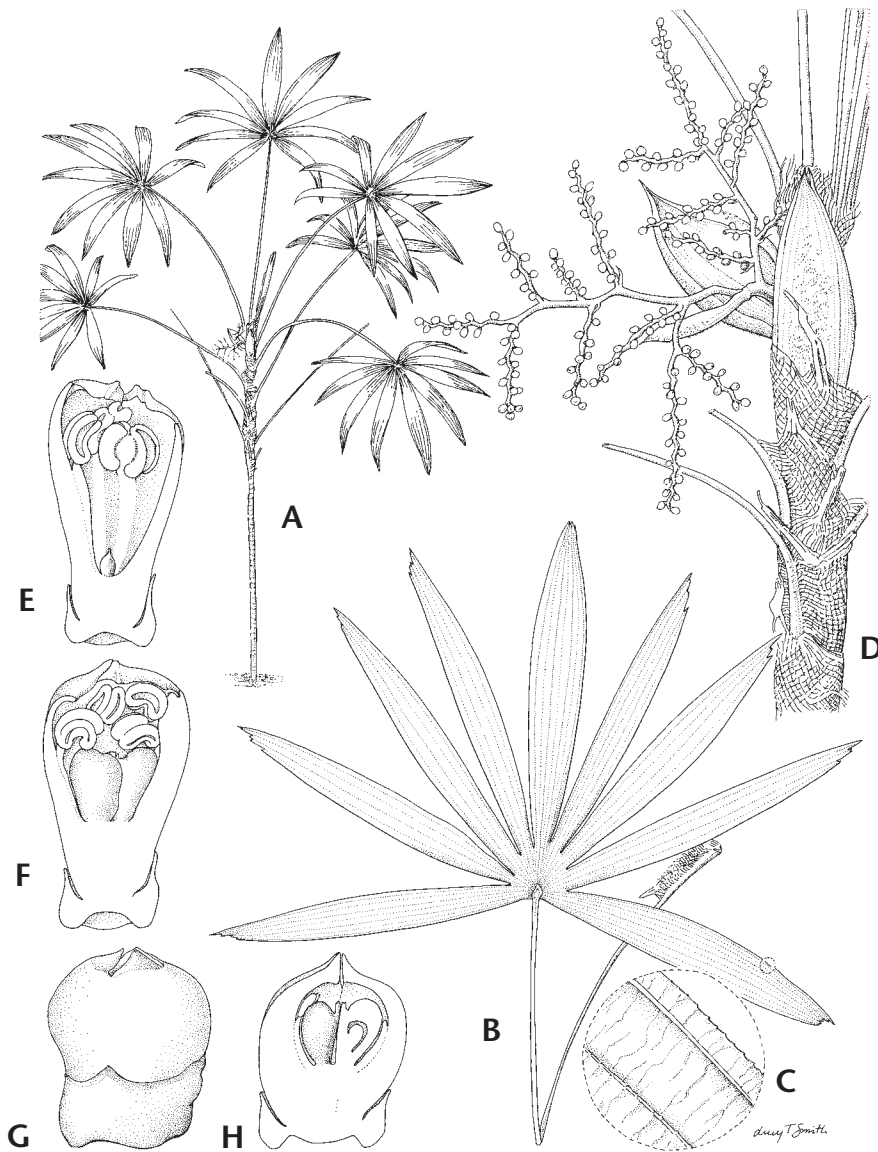
This species can be recognized by the few segments that split close to the blade base and the inflorescence bracts and rachis on the male specimens with tomentum, contrasting with the glabrous rachis and almost completely glabrous bracts on the female inflorescence. Fruit is said to be white when fresh (Beccari 1910). The male inflorescences examined had more rachillae than the female ones giving a more dense appearance. This species most closely resembles *R. excelsa*; it differs from it in having a neat leaf sheath, tightly sheathing the stem, with coarse outer, slightly flattened fibers and finer inner ones at maturity, smooth adaxial segment ribs, not being brown papillate, segments tapering at both ends, all segments splitting closer to the blade base, male rachis and bracts with much tomentum and

stamens being broad but not keeled. There were no mature female flowers or fruits available for study, but those on *Bon 2345* (FI) are described by Beccari (1910, 1931) as “flowers prolonged at the base [drawing (1931) indicates 5 mm long and 2 mm wide], into a long columnar solid base, upon which rest the carpels” with fruit 8–9 mm diam. This long receptacular-stalk contrasts with the short receptacular-stalk (to 2 mm) of *R. excelsa*. An illustration of the flowers of *R. P. Bon 2345* (P) and a photograph of the whole specimen were published in Beccari (1931), and so this specimen was chosen by the author as lectotype. Recollection of this species from Vietnam and Laos, especially of female plants, is necessary to gain a better understanding of its delimitation.

3. *Rhapis humilis* Blume, *Rumphia*, 2: 54. 1836; Mart., *Hist. Nat. Palm*, 3: 254. 1850; Becc., *Ann. Roy. Bot. Gard.*, Calcutta 13: 247. 1931. Type: Japan *C.P. Thunberg s.n.* (L).

Rhapis javanica Blume, *Rumphia* 2: 56. 1836. Type: Java *Blume s.n.* no date (L).

Stems to 6 m tall, with sheaths 18–40 mm diam., without 15–28 mm. Leaf sheath closely sheathing the stem, fibers narrow, outer and inner fibers of similar thickness, producing a squared mesh, ligule remaining intact at maturity; petiole to 4 mm wide, sometimes minutely scabrid; blade with semi-circular to lunulate outline, with a conspicuous palman, segments 7–20, folds 16–36, to 440 mm long, sides slightly curved, apices oblique with irregular secondary splitting, primary splits to within 19–105 mm of the blade base, with tomentum at the base, brown papillae along the ribs, mostly adaxially, ribs scabrid, thick in texture, adaxial and abaxial surfaces similar in colour. Inflorescence, male and female similar in appearance, branching to 3 orders; prophyll tubular, overlapping the base of the first rachis bract, medium thickness, pale brown with areas of greenish brown, mostly glabrous with patches of tomentum on the outer surface edges; rachis bracts 3(–4), sometimes with a distal incomplete rachis bract, similar in appearance to the prophyll, overlapping the base of the next bract; rachis overall length to 410 mm, to 10 mm diam., rachillae 8–165 mm long, slender 0.2–1.2 mm diam., dark brown with rusty tomentum. Flowers 1.0–3.5 mm apart, large. Male flowers sometimes paired, long, obtriangular to 6.6 × 2.8 mm; calyx to 1.8 mm, minutely papillate usually with tomentum on the apices of the lobes, lobes shallow to 0.5 mm with regular margins; corolla narrowing gradually into a receptacular-stalk to 1.9 mm; filaments, shorter row to 3.2 mm, longer to 3.8 mm, to 0.4 mm diam. Female flowers to 4.4



3. *Rhapis laosensis*.
A Habit; **B** Leaf
 $\times 1/4$; **C** Leaf detail
 $\times 3$; **D** Portion of
 stem with
 inflorescences,
 showing bracts
 $\times 2/3$; **E** Staminate
 flower in
 longitudinal
 section $\times 11$; **F**
 Hermaphroditic
 flower in
 longitudinal
 section $\times 11$; **G**
 Pistillate flower
 $\times 11$; **H** Pistillate
 flower in
 longitudinal
 section $\times 11$. **A–D**,
G, **H** from *T. Evans*
et al. 35, **E**, **F** from
T. Evans et al. 34.
 Drawn by Lucy T.
 Smith.

$\times 2.5$ mm; calyx to 2.3 mm, tomentose, lobes to 1 mm with regular margin and acute apices; corolla clavate, distinctly narrowed to 1.5 mm in diam., with a receptacular-stalk to 2.5 mm; staminodes present. Fruit unavailable. (Fig. 2 H–K, 3)

Distribution. South China, Sichuan; South Japan, South Kyushu Island.

Habitat. Forest, 100–1000 m.

Representative specimens. SOUTH CHINA: Guangxi, Lungchow, *HB Morse* 380 (K); Sichuan, Mt. Omei, *C.L. Chow* 6249 female (A); *W.P. Fang* 12533 (A). JAPAN: *C.P. Thunberg* s.n. (L); South Kyushu, Kirishma-Omuta National Park, *E.H. Wilson* s.n.

1917 (A); *C.P. Thunberg* sheet number 24385 (U, photo). CULTIVATED: Java, *Blume* s.n. no date (L); UK, Kew, Royal Botanic Gardens, Kew, s.n. 1884 male (K), s.n. 1858 male (K), *L.H. Fitt* 31 male (K), *W. Baker et al.* 1151 male (K).

In his revision of *Rhapis*, Beccari (1931) based his description of the flowers of this species on an old collection (s.n. 1884) taken from a clump at Kew; thus he must have considered it to be typical *R. humilis*. This clump is still extant at Kew (accession no 1973–12600) (Front Cover).

Rhapis humilis can be distinguished from *R. excelsa* by the leaf sheaths with intact ligule and neat fibers, closely sheathing the stem; blade semi-

circular in outline, segments tapering at the apex with less regular secondary splitting, palman more conspicuous; inflorescence with rachis bracts usually glabrous and rachis with tomentum; calyx usually with tomentum and stamens with more slender filaments. Four rachis bracts were recorded in one specimen. Mt Omei is a Buddhist retreat, and so the specimens from this locality may have been cultivated.

See under *R. excelsa* for comments on nomenclature.

4. *Rhapis multifida* Burret, Notizbl. Bot. Gart. Mus. Berlin. 13: 588. 1937. Type: China, Guangxi, Chen Bien, *S.P. Ko* 56092 (holotype probably SYS or IBSC, not seen).

Stems recorded to 2.5 m tall, diam. not recorded. Leaf sheath fibers close together with coarse outer fibers partially obscuring finer inner ones, producing a diagonal-lined mesh, ligule often remaining intact at maturity; petiole to 4 mm wide, margin smooth; blade large, with conspicuous palman, segments 14, folds 30, the longest segments to 450 mm, narrow (1 or 2 folds), tapering, apices pointed with secondary splitting, primary splits to within 23–66 mm of the blade base, thick in texture. Inflorescence, male not seen, female branching to 2 orders; prophyll similar in appearance to rachis bracts; rachis bracts 3 or 4, large, tubular, overlapping the base of the next rachis bract, relatively thick in texture, dark brown, lacking tomentum, sometimes also a distal incomplete rachis bract present; rachis greatly exceeding the bracts, overall length to 560 mm, broad 8–10 mm diam., rachillae densely packed on the rachis, those of the second order held at right angles to those of the first order, relatively short and narrow, pale brown with pale rusty brown tomentum. Male flowers unavailable. Female flowers 3–5 mm apart, to 4.5 × 3.0 mm; calyx to 2 mm, tomentose, lobes to 0.8 mm with pale edged irregular margin; corolla darkly pigmented, with a long receptacular-stalk to 2.5 mm; staminodes present. Fruit to 8 mm diam., borne on a receptacular-stalk to 5 mm long; epicarp shiny translucent papillose, apical region with conspicuous lenticels.

Distribution. South China, West Guangxi, South East Guangdong.

Habitat. 1000–1500 m, shrub in mixed forest on rocky slopes.

Representative specimens. SOUTH CHINA: Guangxi, *S.K. Lau* 38648 female post-fruit (A); *A.N. Steward* & *H.C. Cheo* 158 female (A); Guangdong, *K.M. Feng* 13462 female (in fruit) (A). CULTIVATED: Japan: Honshu, Izu, *M. Mizushima* 874 (A).

The specimens seen indicate that this is probably the largest and most robust species of *Rhapis*. Complete stem width, blade shape and colour of abaxial surface were not available from the specimens or recorded on the notes on the sheets. All the specimens seen with inflorescence were female; one was in flower and the others were in fruit. The fruit is yellow according to *Feng* 13462. The distinctive large number of segments which do not split close to the blade base produce a conspicuous palman. A notable characteristic of this species is the relatively long receptacular-stalk of the fruit.

5. *Rhapis laosensis* Becc., *Webbia* 3: 225. 1910; Becc., *Bull. Mus. Hist. Nat. Paris*, 17(3): 157. 1911; Becc., *Ann. Bot. Gard., Calcutta* 13: 248. 1931; Gagnep., in *Lecomte, Fl. Gén. Indo-Chine*, 6(8): 997. 1937; Gagnep., in *Humbert, Not. Syst.*, 6(3): 160. 1937. Lectotype (chosen here): Laos, Saraburi, *Dr Thorell* 3154 (P, FI isolectotype).

Rhapis macrantha Gagnep., in *Humbert, Not. Syst.* 6(3): 160. 1937; Gagnep., in *Lecomte Fl. Gén. Indo-Chine* 6(8): 995. 1937. Type: North Annam, Vinh, *Chevalier* 32535 (P).

Stems to 3 m tall, with sheaths, 11–30 mm diam., without sheaths 5–11 mm. Leaf sheath with outer and inner fibers close, fine, producing a squared mesh, ligule sometimes remaining intact at maturity; petiole to 2.5(4.5) mm wide, with a few brown papillae along the margin at the base and apex; blade with V-shaped or semi-circular to lunulate outline, with a conspicuous palman, segments 3–9(12), folds 15–27, to 340 mm long, sides curved, apices distinctly cucullate, oblique, with irregular dentate secondary splitting, primary splits to within 10–87 mm of the blade base, margins scabrid, thick texture, adaxial surface glossier than abaxial and slightly darker, transverse veinlets conspicuous. Inflorescence, the male and female similar in general appearance, branching to 2 orders; prophyll, large boat-shaped, usually completely overlapping the first rachis bract, thick and woody in texture, pale brown, tomentose, rachis bracts 1(–2), first bract, reddish brown, large, boat-shaped, thick in texture, either keeled or with up to 3 distinct ribs, inner surface shiny, outer surface tomentose, not sheathing the rachis, a second incomplete rachis bract present in some specimens, similar to the first bract but thinner in texture; rachis overall length to 90(140) mm, to 5 mm diam., rachillae short 15–45 mm, covered with minute rusty brown papillae. Flowers, male more densely packed on the rachillae than female, similar in size. Male flowers, obtriangular to 3.5 × 2.6 mm; calyx to 1.3 mm, lobes to 0.8 mm with regular margin; corolla, narrowing towards the

base, lacking a receptacular-stalk; filaments, shorter row to 1.8 mm, longer to 2 mm, narrow, to 0.2–3.5 mm diam.; pistillode minute. Female flowers, globose to 3.4 × 2.8 mm; calyx to 1.2 mm, lobes to 0.5 mm; corolla with a receptacular-stalk to 1.8 mm; staminodes present. Fruit with three carpels developing, borne on a short receptacular-stalk to 0.5 mm. Mature fruit not seen. Hermaphrodite inflorescence with male and hermaphrodite flowers to 4.2 × 2.5 mm; calyx to 1.5 mm; corolla with a receptacular-stalk to 1.4 mm; hermaphrodite flower carpels to 1.2 mm. (Figs. 3, 4, 5).

Distribution. Laos; Vietnam.

Habitat. Alluvial river levée, sandstone soil 200 to 530 m, evergreen and degraded semi-evergreen forest.

Representative specimens. LAOS: Saraburi, *Thorell 3154* male, female and possible hermaphrodite or well developed staminodes (P, FI); La-Khon, Mekong valley, *Dr Thorell, s.n.* 1866–1868 (P, FI) Xieng khouang, *Spire 568* (P); Borikhana, Wieng Chan, *A.F.G. Kerr 20762* male (P, K); Savannaket, *Poilane 12005* (P), Nakai, *Evans TDE 34* male and hermaphrodite, *35* female, Khamkheut, *Evans TDE 38*, Pakkading *Evans TDE 61* male (K). VIETNAM: North Annam, Vinh, *Chevalier 32535*, (P).

The large thick overlapping prophyll and first rachis bract, shiny adaxial leaf surface which usually has a pinkish tinge when dried and distinctly cuculate leaf segment tips are characteristic of this species. One inflorescence seen was hermaphrodite with larger male and hermaphrodite flowers to 4.2 × 2.5 mm. Specimen labels give the flower colour as greenish cream (female) and bright yellow (male). Photographs of the male inflorescence of *TDE 34* (Fig. 4 - whole specimen, Fig. 5 - close up of inflorescence) show greenish creamy yellow flowers. Beccari (1931) illustrated the specimen *Dr Thorell 3154* (P), so this specimen was chosen as the lectotype.

6. *Rhapis robusta* Burret, Notizibl. Bot. Gart. Mus. Berlin. 13: 587. 1937. Type: China, Guanxi, Lungchow, *S.P. Ko 55429* (holotype SYS or IBSC, not seen; isotype IBSC).

Stem height not recorded, with sheaths to 11 mm diam., without to 6 mm. Leaf sheath fibers close together with outer coarse fibers, obscuring finer inner ones, producing a diagonal-lined mesh, ligule remaining intact at maturity; petiole to 1.2 mm wide, smooth; blade, with conspicuous palman, segments 4, folds 17–19, the longest to 218 mm, broad, sides curved, tapering at base and apex, apices oblique, with shallow secondary splitting, primary splits to within 16–37 mm of the

blade base. Inflorescence, male unavailable, female branching to 2 orders; prophyll unavailable, rachis bracts 2, sometimes with a distal incomplete rachis bract, tubular, not overlapping the base of the next bract, relatively thin (papery), reddish brown, darker at the base, glabrous, tightly sheathing the rachis; rachis overall length to 220 mm, narrow, 2 mm diam., rachillae few, narrow to 0.5 mm diam., occasionally with sparse rusty tomentum. Flowers, male unavailable, female small to 1.8 × 1 mm; corolla tightly closed with a long receptacular-stalk to 0.9 mm; carpel to 1 mm long. Fruit unavailable.

Distribution. South China, Guangxi.

Habitat. Forest undergrowth.

Representative specimens. SOUTH CHINA: Guanxi, *S.P. Ko 55429* female (IBSC)

Only one specimen of this species was available for study; more specimens are needed in order to gain a more complete picture. A notable characteristic of this specimen is that the apices of the bracts do not overlap with the base of the bract distal to them. The height was not recorded on the specimen label, but it is likely from the other measurements taken that this species is smaller than the other species and the specimen seen was more slender than any of the other specimens of the genus. According to the specimen label, the flowers are light green and the fruit is green.

7. *Rhapis gracilis* Burret, Notizibl. Bot. Gart. Mus. Berlin. 10: 883–884. 1930. Type: China, Guangdong, Win Foo, *S.S. Sin 5338* (holotype SYS or IBSC, not seen; isotype IBSC).

Stem height not recorded, with sheaths 6–8 mm diam. without sheaths 3–5 mm. Leaf sheath with very fine, wavy fibers with a square mesh, ligule sometimes remaining intact at maturity; petiole to 1.8 mm wide, margin usually smooth sometimes bearing minute brown papillae; blade small, with V-shaped outline, without a palman, segments 2–4, folds 11–15, longest to 180 mm, apices oblique with secondary splitting, primary splits to within 3–15 mm of the blade base, both surfaces similar in colour, green with white tinge, transverse veinlets very conspicuous. Inflorescence, the male and female similar in general appearance with few rachillae, branching to 2 orders; prophyll and 2 rachis bracts similar in appearance, tubular, overlapping the base of the next bract, medium thickness, reddish brown, inner surface shiny, outer dull, lacking tomentum; rachis overall length to 200 mm, narrow, to 2 mm diam., few rachillae, occasionally with sparse tomentum where the rachis is adnate to the

peduncle, medium brown. Flowers, 2–3 mm apart. Male flowers obovoid, to 4.3 × 2.2 mm; calyx to 2 mm, lobes acute to 1.1 mm with regular margin; corolla with a receptacular-stalk to 1 mm; filaments, shorter row to 1.2 mm, longer to 1.6 mm, to 0.3 mm diam. Female flowers only immature seen, to 3.1 × 2.1 mm; calyx to 2.6 mm, margin regular, lobes acute to 1.1 mm; corolla with a receptacular-stalk to 0.2 mm. Fruit to 8 mm diam., borne on a receptacular-stalk to 2.5 mm; epicarp dull, papillose.

Distribution. South China, Guangdong; Laos.

Habitat. 160 m at the foot of limestone hills.

Representative specimens. SOUTH CHINA: Guangdong, S.S. Sin, 5338 female (IBSC). LAOS: Cammon (northern part is now Bolikhamsay, southern part is Khammuane) *El Colani s.n.* 1930 male (P).

This species is similar vegetatively to *Rhapis subtilis* but differs in the flowers, notably in possessing acute calyx lobes. Burret recorded a fruit receptacular-stalk to 5 mm, a character which also distinguishes it from *R. subtilis*. Only two herbarium specimens were available for study, including an isotype. The heights of the specimens were not recorded on the labels; however, it is likely from the other measurements taken that this is smaller than *Rhapis subtilis*. According to specimen label data the fruit is green-blue.

8. *Rhapis subtilis* Becc., *Webbia* 3: 227. 1910; Becc., *Bull. Mus. Hist. Nat. Paris*, 17(3): 157. 1911; Gagnep., in Lecomte *Fl. Gén. Indo-Chine*, 6(8): 997. 1937. Type: Laos, Lakon, Mekong valley, *Thorell 3099* (holotype P).

Rhapis siamensis Hodel, *Palm J.* 136: 19–20. 1997. Type: Thailand, Phattalung, *Hodel & Vatcharakorn 1652* (holotype BK, not seen).

Stems to 3 m tall, with sheaths (6)8–20 (25) mm diam., without (3)4–15 mm. Leaf sheath often with coarse, flattened outer immature fibers obscuring finer inner ones producing a diagonal-lined mesh, mature inner and outer fibers of similar thickness producing a squared open, often fine mesh, ligule sometimes remaining intact at maturity; petiole to 0.9–3 mm wide, often bearing minute brown papillae along the margin, sometimes only at the base or apex; blade with V-shaped or semi-circular outline, variable in size, sometimes with a conspicuous palman, segments 2–11, folds 7–25, to 380 mm long, sides curved, apices sometimes cucullate, oblique, sometimes truncate, with dentate secondary splitting, primary splits to within 1.5–168 mm of the blade base, brown papillae along the ribs, mostly adaxially and at the base, rather thin-textured, abaxial and

adaxial surfaces similar in colour, pale green, transverse veinlets very conspicuous. Inflorescence, the male and female similar in general appearance, branching to 1 or 2 orders; peduncle relatively long, to 220 mm, glabrous; prophyll tubular, overlapping the first rachis bract, relatively thin-textured, pale-brown to reddish-brown, inner surface usually dull, occasionally shiny (*Thorell 30599*), outer surfaces dull, mostly glabrous, tomentose sometimes on edges and keels; rachis bracts 1–2, similar in appearance to the prophyll, overlapping the base of the next bract; rachis overall length 65–280(340) mm, ca. 2.3 mm diam., increasing up to 4 mm; rachillae few, to 34–238 mm long, 0.5–1.6 mm diam., male rachillae shorter than female, glabrous, pale brown. Flowers, relatively well spaced on the rachillae, large, coriaceous. Male flowers ovoid to 6.1 × 4.0 mm; calyx to 2.5 mm, lobes to 0.7 mm with irregular margin, sometimes darkly pigmented; corolla marked with faint vertical lines of darker pigment, with acute lobes, narrowed into a receptacular-stalk to 1.8 mm; filaments, shorter row to 1.5 mm, longer row to 2.0 mm, broad, to 0.5 mm diam., keeled; pistillode present. Female flowers, cylindrical to 5.5 × 3.2 mm, often conspicuously banded; calyx to 2.2 mm with a pale basal rim, lobes to 0.9 mm with a dark, irregular margin; corolla with vertical markings sometimes less distinct than in the male, with acute triangular, black or black-based beak like lobes, with a receptacular-stalk to 2 mm, 3 carpels developing; staminodes present. Fruit to 9.5 × 9.5 mm, 1–3 borne on a short receptacular-stalk to 2 mm, epicarp shiny translucent, minutely papillose, with conspicuous black lentils. (Fig. 2 A–D).

Distribution. Thailand, Laos, Sumatra.

Habitat. Limestone slopes, evergreen forest, 40–200m.

Representative specimens. THAILAND: Nakhon Ratachasi, *Kerr 8148* male, female (BM, K); Trang, Huay Nod, Khao Nam Prai, *J. Dransfield JD 5447* male (K), *J. Dransfield & C. Bhoonab JD 5448* female (K), Nam Tai Ch. *Charoenphol, K. Larsen & E. Warncke 3663* (K); Huay Nod. *G. Smith & W. Sumawong GC 85* male (K); Phattalung, *D.R. Hodel & P. & R. Vatcharakorn 1652* (BK, not seen), *Kerr 15354* female, *19291* male, female (BM, K); Prachuap, *Kerr 10896* female (BM, K), *T. Smitland 8519* (K, L); Songkhla, Hat Yai, *G. Smith & W. Sumawong GC 110* (K) male, *GC 145* male (K); Pran, Ban Pak Tawan, *A. Marcan 2634* female (BM, K). Chantaburi, Kao Wong, *W. Sumawong 15797-2* female (K), Phetchaburi, Kaeng Krachan, *A.S. Barford, W. Ueachirakan, T. Burholt, S. Barrow 45205* female (K), *Parnell, Pendry, Jebb & Thirawat Boonthavikoon 95-498* female (K). LAOS: Mekong



4. *Rhapis laosensis*, Evans TDE 34, Laos. (Photo: J. Dransfield)



5. *Rhapis laosensis*, male inflorescence, Evans TDE 34, Laos. (Photo: J. Dransfield)

valley, Thakhek (Lakon), *Dr. Thorel 3099* (P holotype, FI isotype). SUMATRA: Aceh, Lhok'nga, *D. Agranoff & W. Fickling s.n.* 1984 (K), *O. Maessen s.n.* 1986 female (K). CULTIVATED: Hongkong, *N.J. Brigham s.n.* (no date but before 1927 - det label) (A); Thailand, Trang, Muang, Khao Chong Botanic Garden (from Kao Nam Prai), *G. Smith & W. Sumawong GC 93* female (K), *G. Dear 13/86* (K); USA, California, Pine Island Nursery, *L. McKamey s.n.* male, female 1984 (K).

This species of *Rhapis* has a relatively fine leaf sheath and prominent cross veins on the leaf segments, and rachis bracts usually with little or no tomentum. The flowers are well spaced on few pale coloured, smooth textured rachillae. It differs from other species in only having first or second order branching in the inflorescence, large coriaceous flowers conspicuously banded with pigment when mature, with vertical lines of pigment on the corolla producing a ribbed appearance and irregularly toothed calyx. The fruit is described as white or whitish on specimen labels. The conspicuous black lenticels on the fruit are often concentrated in the apical half, this is very obvious in *L. McKamey s.n.* 1984 (K).

The large number of specimens seen enabled assessment of the variation in size within this species, from specimens with 2–4, short segments through to specimens with up to 11, relatively long segments. This variation was found to be continuous without distinct subgroups. The largest specimens occur in the peninsular of Thailand and include *D.R. Hodel & P. & R. Vatcharakorn* 1652, described as a new species in 1997 but which in fact represents the extreme end of the range of variation of *R. subtilis*. The smallest specimens come from Northeast Thailand and just over the boarder in Laos. The Sumatran specimens overlap with the smaller ones from Peninsula Thailand.

Index to accepted names, synonyms and excluded names of *Rhapis*

Chamaerops excelsa Thunb. synonym of ***Rhapis excelsa*** (Thunb.) A. Henry

Rhapis acaulis Willd., Sp. Pl. 4(2): 1093. 1806 = ***Sabal minor*** (Jacq.) Pers., see Moore (1963).

Rhapis arundinacea Aiton Hort. Kew. 474. 1789 = ***Sabal minor*** (Jacq.) Pers., see Moore (1975).

Rhapis aspera Hort ex Baxter, Loud. Hort. Brit. Suppl. 3: 624 1850 4th edition. Based on *Chamaerops aspera* Siebold. This is a name without a description and thus with no botanical standing – *nomen nudum*.

Rhapis cochinchinensis Mart., Hist. Nat. Palm. 3: 254. 1838; Becc., Webbia 3: 245. 1910. From

Vietnam. According to the description this species has petioles with short upright spines, so this is not *Rhapis*. It has dioecious flowers, so it is unlikely to be *Licuala* which is predominantly hermaphrodite. According to Beccari (1910) it is possible that the species has been classified from a mixed specimen with the flowers of a *Rhapis* and the young leaves of *Livistona saribus*.

Rhapis caroliniana Hort. ex Kunth, En. Pl. 3 in index (non p. 246) 1841 = *Rhapidophyllum hystrix* H. Wendl. & Drude. ex Ind. Kew. (Becc 1931) = ***Sabal minor*** (Jacq.) Pers., see Shuey & Wunderlin (1977).

Rhapis cordata Hort ex Baxter, Loud Hort. Brit. Suppl. 3: 624 1850 4th edition. This is a name without a description – *nomen nudum*.

Rhapis divaricata Gagnep. synonym of ***Rhapis excelsa*** (Thunb.) A. Henry

Rhapis excelsa (Thunb.) A. Henry

Rhapis filiformis Burret, Notizbl. Bot. Gart. Mus. Berlin. 13: 586. 1937 = ***Guihaia grossefibrosa*** (Gagnep.) J. Dransf. Lee & Wei, see Wei (1997).

Rhapis flabelliformis L'Hérit ex Aiton synonym of ***Rhapis excelsa*** (Thunb.) A. Henry

Rhapis gracilis Burret

Rhapis grossefibrosa Gagnep., in Lecomte, Fl Gén. IndoChine 6(8): 994. 1937 = ***Guihaia grossefibrosa*** (Gagnep.) J. Dransf., Lee & Wei.

Rhapis humilis Blume

Rhapis javanica Blume synonym of ***Rhapis humilis*** Blume

Rhapis Kwamwonzick Siebold synonym of ***Rhapis excelsa*** (Thunb.) A. Henry

Rhapis Kwannontsik pictured in Dai 1895. This is a name without a description and thus with no botanical standing – *nomen nudum*.

Rhapis Kwanwon Siebold, listed in the Von Siebold and Company Catalogue 7. 1856. This is a name without a description and thus with no botanical standing – *nomen nudum*.

Rhapis kwanwortsik H. Wendl., Ind. Palm 34. 1854; Seeman 416. 1857; Becc., Webbia 60, 61. 1921. Reported to be based on *Chamaerops kwanwortsik* Siebold; Beccari (1921 & 1931) cited it as a synonym or a doubtful species. This is a name without a description and thus with no botanical standing – *nomen nudum*.

Rhapis laosensis Becc.

Rhapis macrantha Gagnep., synonym of ***Rhapis laosensis*** Becc.

Rhapis major Blume, synonym of **Rhapis excelsa** (Thunb.) A. Henry

Rhapis micrantha Becc.

Rhapis multifida Burret

Rhapis robusta Burret

Rhapis siamensis Hodel, synonym of **Rhapis subtilis** Becc.

Rhapis sirotsik Hort. ex H. Wendl., Kerch. Palm 255. 1878, listed as *R. humilis*. Becc., Ann. Roy. Bot. Gard., Calcutta 13, 244. 1931, listed as *R. humilis*. Based on *Chamaerops sirotsik* Siebold, Wendl., Ind. Palm 34. 1854. No type specimen; unclear drawing. This is a name without a description and thus with no botanical standing – *nomen nudum*.

Rhapis subtilis Becc.

Trachycarpus excelsus Thunb. synonym of **Rhapis excelsa** (Thunb.) A. Henry

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LITERATURE CITED

- AITON, W. 1789. Hortus Kewensis. 3: 473–474. G. Nicol, London.
- BAILEY, L.H. 1939. Article 11. Species of *Rhapis* in cultivation. – The Lady Palms. Gentes Herbarum 4: 199–208.
- BEELER, B.H. 1960. What's in a name? Principes 4: 144.
- BECCARI, O. 1910. Palme dell'Indo-China. Webbia 3: 220–228, 245.
- BECCARI, O. 1921. Recensione delle palme del vecchio mondo: appartenenti alla tribu delle Corypheeae. Webbia 5(1a): 1–70.
- BECCARI, O. 1911. Classification des palmiers d'Indo-Chine. Bull. Mus. Hist. Nat. de Paris 17: 157.
- BECCARI, O. 1931. Asiatic palms – Corypheeae (ed. U. Martelli). Ann. Roy. Bot. Gard. (Calcutta) 13: 1–356. Plate 1, 55.
- BUCHHEIM, G. 1966. A bibliographical account of L'Héritier's "Stirpes novae." Huntia 2:29–58.
- BLUME, C.L. 1836. Rumphia. Vol 2. Lugduni Batavorum, Amsterdam.
- BRUMMITT, R.K. AND C.E. POWELL (eds). 1992. Authors of plant names. A list of authors of scientific names of plants, with recommended standard forms of their names, including abbreviations. Royal Botanic Gardens, Kew, Kew.
- BURKILL, I.H. 1935. A dictionary of the economic products of the Malay Peninsula Vol 2. Crown agents for the colonies, London.
- BURRET, M. 1930. *In* Diels, L. (ed.). Miscellanea sinensia 3. Notizbl Bot. Gart. Mus. Berlin. 10(99): 883–884.
- BURRET, M. 1937. Palmae chinenses. Notizbl Bot. Gart. Mus. Berlin. 13(120): 586–589.
- CARTER, H.B. 1988. Sir Joseph Banks 1743–1820. British Museum (Natural History), London. p 251.
- CHIN, W.Y. AND H. KENG. 1992. Illustrated dictionary of Chinese medicinal herbs. CRCS Publications, Sebastopol, CA.
- DAI, N.N. 1895. Useful plants of Japan described and illustrated Vol 3 of plates: 713. Agricultural society of Japan, Tokyo.
- DRANSFIELD, J., S.K LEE AND F.N. WEI. 1985. *Guihaia*, a new coryphoid genus from China and Vietnam. Principes 29: 3–12.
- ELLISON, D. AND A. ELLISON. 2001. Cultivated palms of the world. University of New South Wales Press, Sydney.
- GAGNEPAIN, F. 1937. Palmiers d'Indochine Nouveaux de litigieux. Not. Syst. 6: 149–160.
- GAGNEPAIN, F. 1937 *Rhapis*: 993–998 *In* Lecomte, H. Flore Générale L'Indo-Chine. 6(8): 993–998. Masson et Cie, Paris.
- HODEL, D.R. 1997. New species of palms from Thailand, part 2. Palm J. 136: 7–20.
- HOOKER, J.D. 1883. Palmae. *In* G. Bentham and J. D. Hooker (eds). Genera Plantarum 3(2) 870–948. L. Reeve & Co., London.

- JONES, D.L. 1994. Palms throughout the world. Reed New Holland, Sydney, London.
- KAPLAN, D.R., N.G. DENGLER AND R.E. DENGLER. 1982. The mechanism of plication inception in palm leaves: histogenetic observations on the palmate leaf of *Rhapis excelsa*. Can.J. Bot. 60: 2999–3016.
- KERCHOVE DE DENTERGHEM, O. 1878. Les palmiers; histoire iconographique. J. Rothschild, Paris.
- KUNTH, C.S. 1841. Enumeratio plantarum 3. J. G. Cott, Stuttgart and Tubingen.
- L'HÉRITIER DE BRUTELLE, C-L. 1786. Stirpes novae aut minus cognitae. Fascle 2. Tab. 100 (Fasc. 8&9, after August 1805). Paris.
- LINDEN, J. 1887. Pl 10. *Rhapis kwamwonzick* Sieb. L'illustration Horticole 34: 39.
- MARTIUS, C.P.F. VON. 1838. Historia Naturalis Palmarum 3. Munich.
- MCKAMEY, L. 1985. *Rhapis subtilis*. Palms & Cycads 6: 1–4.
- MCKAMEY, L. 1989. *Rhapis* palms – cultivated species and varieties: culture and care of the ladies. Principes 33: 129–139
- MOORE, H.E., JR. 1963. An annotated checklist of cultivated palms. Principes 7: 119–182.
- MOORE, H.E., JR. 1975. The identity of *Rhapis arundinacea*. Principes 19: 151.
- READ, R.W. 1966. New chromosome counts in the Palmae. Principes 10: 55–61.
- REHDER, A. 1930. New species varieties and combinations from the herbarium and the collections of the Arnold Arboretum. Journal of the Arnold Arboretum 11: 153–154.
- SEEMAN, B. 1857. Botany of the voyage of H.M.S. Herald. Lovell Reeve, London.
- SHARMA, A.K. AND S.K. SARKAR. 1957. Cytology of different species of palms and its bearing on the solution of the problems of phylogeny and speciation. Genetica 28: 361–488.
- SHUEY, A.G. AND R.P. WUNDERLIN. 1977. The needle palm: *Rhapidophyllum hystrix*. Principes 21: 47–59.
- SIEBOLD, P.F., VON. 1856. Catalogue raisonné. Prix-courant des plantes et graines du Japon cultivées dans l'établissement de von Siebold & Comp. Henry & Cohen, Leide, Bonn.
- STAFLEU, F.A. AND R.S. COWAN. 1981. Taxonomic literature, ed.2. 3. Lh-O: 1-2. A selective guide to botanical publications and collections with dates, commentaries and types. Bonhn, Scheltema & Holkema, Utrecht.
- THUNBERG, C.P. 1784. Flora Japonica. In Bibliopolio I. G. Mulleriano, Leipzig.
- TOMLINSON, P.B. 1961. Palmae. In C.R. METCALFE (ed.). Anatomy of the Monocotyledons 2. Clarendon Press, Oxford.
- UHL, N.W., L.O. MORROW AND H.E. MOORE JR. 1969. Anatomy of the palm *Rhapis excelsa*, 7. Flowers. J. Arnold Arbor. 50: 138–152.
- UHL, N.W. AND J. DRANSFIELD. 1987. Genera Palmarum: A classification based on the work of H.E. Moore Jr. L: H. Bailey Hortorium and International Palm Society. Allen Press. Lawrence, Kansas. pp. 610
- WALTER, K.S. 1998. 1997 IUCN Red Data List of Threatened Plants. Compiled by the World Conservation Monitoring Centre. IUCN – The World Conservation Union, Gland, Switzerland and Cambridge, UK.
- WEI, F. 1997. A taxonomic study on palm family from Guangxi. Guihaia 17: 193–205.
- WENDLAND, H. 1854. Index palmarum, cyclantheorum, pandanearum, cycadearum, quae in hortis europaeis coluntur. Aulica Hahn, Hannover.
- WENDLAND, H. 1861. In Gay, M. Le *Chamaerops excelsa* Thunb., post-scriptum. Bull. Soc. Bot. France 428–430.
- WHITTEN, A.J., S.J. DAMANSK, J.N. ANWAR AND HISYAM. 1987. The ecology of Sumatra, ed. 2. Gadjah Mada University Press, Yogyakarta, Indonesia.
- WILLDENOW, C. L. 1806. Species plantarum 4(2): 1093.
- ZIMMERMANN, M.H. AND P.B. TOMLINSON. 1965. Anatomy of the palm *Rhapis excelsa*, 1. Mature vegetative axis. J. Arnold Arbor. 46: 160–178.

Seed Biology of Palms: A Review

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Seeds are a very important component of the life cycle of plants. They not only carry the necessary genetic variation required for evolutionary change, but they are quite often the only means of long-distance dispersal and long-term dormancy (Silander 1985). On the other hand, seeds are a valuable resource for the propagation and conservation of germplasm. Hence, the study of palm seeds remains a priority for future research.

The palm family (Arecaceae) comprises between 2200 (Johnson 1996) and 2600 (Jones 1995) species distributed throughout tropical and subtropical areas. Very little is known about the seed biology of most of these species. Scientific research has been carried out on a small number of species, mostly of economic value. Based on the reviews by Corner (1966), Tomlinson (1979), Moore and Uhl (1982), Uhl and Dransfield (1987) and others, our purpose is to summarize the most distinctive characteristics of seed biology of palms.

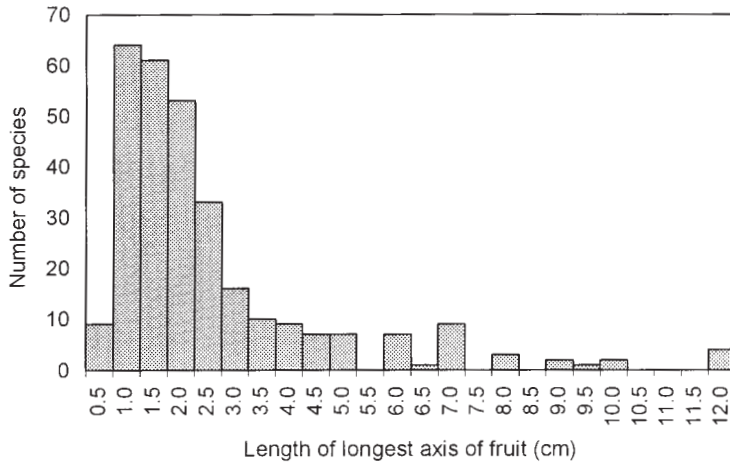
Palms are one of the most peculiar life forms among higher plants. These arboreal monocots share an assemblage of reproductive traits that are unique in many ways. Their propagules – nuts or seeds – are possibly the most characteristic feature, always containing part of the fruit (pericarp, exocarp, mesocarp and endocarp) (Corner 1966). Size of palm seeds ranges from the gigantic *Lodoicea maldivica* seeds (each weighs more than 20 kg and is about 50 cm long) to the very small seeds of *Roscheria melanochaetes* and *Chamaedorea elegans*, which are about 7 mm and 5 mm long, respectively (Sneed 1976, Moore & Uhl 1982, Jones 1995). The most common seed sizes in palms are between 1 and 12 cm (Fig. 1) (Jones 1995).

Morphology and anatomy

Anatomy and morphology of palm seeds have been useful bases for the definition of trends in

the evolution of the family Arecaceae. Generally, the gynoeceum develops only one seed (primitive character in palms) due to either the fact that only one of the three carpels is fertile, or that all three carpels are fertile, but two of them abort during fruit or seed development (Robertson 1977, Davis 1978, Padmanabhan & Regupathy 1981). Alternatively, all carpels that develop produce a seed surrounded by an endocarp (Siddiqi et al. 1991). Polyembryony – several embryos surrounded by the same endocarp – (Davis 1978, May et al. 1985, Clancy & Sullivan 1988), and parthenocarpic production of seeds (Shukr et al. 1988, Rohani et al. 1997) are also known among palms. Some species such as *Attalea phalerata* (as *Scheelea leandroana*), produce a single seed per fruit or multiseeded fruits with a variable number of seeds among fruits (Koebernik 1971, Moore & Uhl 1982). This fact has an ecological significance in palms like *Attalea butyracea* (as *Scheelea rostrata*); predators prefer fruits with a single mature seed, producing a negative selective pressure upon individual with this character (Bradford & Smith 1977).

Mesocarp and endocarp are commonly the most important structures remaining from the fruit. The mesocarp may vary from fleshy to very fibrous, whilst the endocarp may be differentiated into a hard stony structure as in *Cocos nucifera* and *Jubaeopsis caffra* (Murray 1973, Robertson 1977, Moore & Uhl 1982), or it may be papery or



1. Frequency distribution of palm fruit size (N = 298). The longest axis of the fruit was considered as the fruit size. This figure does not include species with the largest seed size, such as *Cocos nucifera*, whose fruit length is 22.5 cm (Zizumbo-Villarreal 1997) and *Lodoicea maldivica* whose fruit length is 50 cm (Uhl & Dransfield 1987).

an undifferentiated line of cells, as in *Caryota mitis* and *Mauritia flexuosa* (Murray 1973). Generally, the endocarp cannot be separated from the seed coat, which is poorly developed. At the time of dissemination, the endosperm may be solid, creamy, liquid or a combination of the three consistencies, as for example, in *Cocos nucifera*, *Jubaeopsis caffra* and *Attalea speciosa* (as *Orbignya martiana*) (Robertson 1977, May et al. 1985). Endosperm consistency also changes during the seed maturation process (Corner 1966). Endocarp classification can be found in Murray (1973).

Palm seeds contain small embryos relative to the seed size and a large amount of endosperm. In many cases, the different seed components are not completely developed at the time of dissemination. In several species such as *Cocos*

nucifera, the embryo initially consists of a simple disk of cells located near the operculum of a very large seed (Ginieis 1957, Corner 1966). Later, the cotyledon is differentiated into a tubular base, the petiole and the distal haustorium (Tomlinson 1990). The haustorium absorbs and assimilates nutrients from the endosperm, and during this process both the cotyledon and the embryo grow until they fill the entire nut cavity (DeMason 1985). However, the process of embryo development has been studied in detail for few palms, the best example being the date palm, *Phoenix dactylifera* (Lloyd 1910, DeMason 1984, DeMason et al. 1989).

In palms, the main storage resources for embryo development are lipids and insoluble polysaccharides (DeMason 1986, Chandra &

Table 1. Characteristics and adaptations of palm germination according to Rees (1960a) and Tomlinson (1960).

Type	Embryo	Plumule and radicle	Petiole and petiole	Ecological adaptation to the environment	Species-type
A	Straight	Along its main axis. Persistent radicle	Elongates, eligulate	dry	Phoenix-type
B	Straight	Obliquely to its long axis. Persistent radicle	Elongates, ligulate	dry	Washingtonia-type
C	Curved	Oblique. Non-persistent radicle	Scarcely elongates, ligulate	shaded and moist	Archontophoenix-type

DeMason 1988, DeMason et al. 1989). Many palm seeds contain very large amounts of lipids, e.g. the endosperm of the oil palm *Elaeis guineensis* contains 47% lipids and 36% insoluble carbohydrates in the form of galactomannan. During the early stages of germination, carbohydrates are metabolized more rapidly than lipids, but during seedling development the haustorium (cotyledon) actively converts triglycerides to carbohydrates (Alang et al. 1988). In other cases, the endosperm itself digests stored reserves, which are then subsequently absorbed by the haustorium, as in *Phoenix dactylifera* and *Washingtonia filifera* (DeMason et al. 1985).

Embryology

Differences are found in the form of the embryo, being either straight or curved. Germination is hypogeal (cotyledon below or on the soil surface) and cryptocotylar (cotyledon remains enclosed in the nut) (Pammel & King 1930). Nevertheless, there are four distinct variations in plantlet development in relation to the position of the plumule and radicle (oblique or along the main axis), persistence or loss of the radicle, degree of elongation of the cotyledon petiole, and presence or absence of a ligule (Tomlinson 1960). These differences have been related to establishment in

Table 2. Dispersal mechanisms among palms.

	Species	Dispersal agents	References
Primary dispersal	<i>Bactris baculifera</i>	birds	Bannister 1970; Trejo-Pérez 1976; Brown 1976a; Guix & Ruiz 1995; Matos & Watkinson 1998
	<i>Chamaedorea tepejilote</i>		
	<i>Euterpe edulis</i>		
	<i>E. globosa</i>		
	<i>Sabal palmetto</i>		
	<i>Syagrus romanzoffiana</i>		
Primary dispersal	<i>Acrocomia aculeata</i>	bats	Gardner 1977
	<i>Bactris</i> spp.		
	<i>Dypsis lutescens</i>		
	<i>Iriarteia exorrhiza</i>		
	<i>Livistona chinensis</i>		
Secondary dispersal	<i>Astrocaryum standleyanum</i>	monkeys	Oppenheimer, 1982
	<i>Bactris</i> spp.		
	<i>Desmoncus orthacanthos</i>		
	<i>Oenocarpus panamanus</i>		
	<i>Attalea butyracea</i>		
	<i>Socratea exorrhiza</i>		
Secondary dispersal	<i>Cocos nucifera</i>	water	Harries 1978; Smith et al. 1990; Matos & Watkinson 1998
	<i>Euterpe edulis</i>		
	<i>Attalea speciosa</i>		May et al. 1985
	<i>Euterpe globosa</i>		Bannister 1970
	<i>Astrocaryum</i> spp.	vertebrates (including rodents)	Glanz et al. 1982; Smythe et al. 1982; May et al. 1985; Eguiarte et al. 1993; Lott et al. 1995; Huch & Adler 1997; Brewer 2001
	<i>Normanbya normanbyi</i>		
	<i>Attalea speciosa</i>		
	<i>Bactris</i> spp.	ungulates	Bodmer 1991
	<i>Oenocarpus bataua</i>		
	<i>Mauritia flexuosa</i>		
<i>Syagrus romanzoffiana</i>	fish	Gottsberger 1978; de Souza-Steveaux et al. 1994	
<i>Astrocaryum jauari</i>			

moist or in dry environments. In *Sabal* and other palms of dry environments the cotyledon stalk develops into a tubular structure (remote ligular), which pushes the seedling below the soil surface protecting it from dehydration and giving ecological significance (Tomlinson 1960). In palms from shaded and moist habitats as *Archontophoenix* this characteristic is of no ecological advantage. A summary of the variations in embryo development and of the possible ecological constraints is shown in Table 1 (Tomlinson 1960, Rees 1960a).

Seed dispersal

Among palms hydrochory, barochory and zoochory are common, but anemochory is extremely rare. However, gravity is the most common dispersal mechanism of large and heavy seeds. Due to their size and to the fact that seeds in some species remain attached to the rachilla for a long time, other mechanisms are necessary for primary and secondary seed dispersal. For example, in *Cocos nucifera* (Harries 1978), and in *Reinhardtia gracilis* var. *gracilior* (Mendoza 1994) the action of strong winds plays an important role in seed dissemination (Brown 1976a). When mature seeds are not abscised or are trapped among leaf bases, they can germinate on the tree, but the seedling dies (Harries 1978, Clancy & Sullivan 1988).

Primary dispersal by different species of animals, mainly birds, has been reported in a review by Zona and Henderson (1989) for several palm species. Canopy characteristics of tropical forests and the behavior of animal dispersers can strongly influence seedling recruitment of some palms (Svenning 2001). Secondary dispersal is carried out by other mechanisms, such as water, and/or by vertebrates including rodents, ungulates and fishes (Table 2). Seawater dispersal of *Sabal palmetto* and *Cocos nucifera* requires the embryo to be tolerant to the dehydrating effect of salty water; this tolerance can be distributed differentially among cultivars and the natural population (Brown 1976a, Karunaratne et al. 1991).

Barochorous dispersal produces a clustered distribution of seedlings which leads to high seedling mortality. Only those seeds that are far away and isolated can survive; therefore, a random distribution among adults could occur (Sterner et al. 1986, Barot et al. 1999). This pattern does not differ from that proposed by Connell (1970) and Janzen (1970) for tropical species. In other cases, high seed mortality occurs below the parent plant due to predation, which is density-dependent (Janzen 1970). Seeds of *Attalea butyracea* (as *Scheelea rostrata*), *Euterpe globosa* and *Chamaedorea*

tepejilote are heavily predated by beetles on the soil; however, seeds removed rapidly by mammals could avoid predation, and germinate when they are forgotten in their burrows (Janzen 1971, 1972, Oyama 1991).

During dispersal fruit coats covering the seed have an important role to protect the embryo for a long time, while seeds are floating in water (as coconut and *Nypa*). Fibrous bundles of lignin in the mesocarp and/or the endocarp may also be a defense against seed predators, favouring dispersal by birds and mammals (Stocker & Irvine 1983, Bodmer 1991, Fragoso 1997). In contrast, predators damage seeds that do not have hard structures to protect the embryo, as in *Astrocaryum paramaca*. However, some of these seeds can survive, and thus predators can act as reliable dispersers (Forget 1991).

The coconut embryo develops in a way that presents a fascinating combination of adaptive traits for long distance sea water dispersal, germination and establishment in harsh environments on tropical sandy beaches (Edmonson 1941, Sento 1974, Sugimura & Murakami 1990). The fibrous mesocarp and stony endocarp allow flotation in salty water for long periods of time, thus preserving the viability of the seed. Embryo development remains practically isolated from any damaging effect of the external environment for several months, allowing long distance movement of the propagule. When the coconut arrives on a sandy beach, the heat of the sand accelerates the development of the embryo, and the plumule protrudes through the germinative pore. The plumule achieves photosynthesis, which allows the seedling to develop inside the coconut a strong rooting structure that escapes from the harsh conditions of the soil surface (Foale 1968).

Seed germination

Palms show an amazing diversity of developmental processes, timing and requirements for germination (Corner 1966). Protrusion of the embryo may take place as a result of the development of either the radicle or the plumule. Mechanisms of seed germination and dormancy are poorly understood processes for most palms. However, it is known that many species show rapid germination, such as *Jubaea chilensis* and *Sabal causiarum* that require only 13–20 and 12–22 days, respectively for full germination (Wagner 1982, Carpenter 1989), while others take more than five years to start germinating (e.g. *Chamaedorea seifrizii*) (Wagner 1982).

According to Tomlinson (1971) *Nypa fruticans* shows vivipary, an extreme case of palm seed

germination in which seeds germinate on the mother plant. This probably occurs as in other viviparous species because seeds do not dehydrate during seed maturation (Kermode 1995, Vertucci & Farrant 1995). Seeds have enough water to germinate on the tree and do not show a clear period of quiescence or dormancy; therefore, embryo development is continuous. However, *Nypa* can be dispersed ungerminated in the fruit. When mature fruits are collected from the tree and the seeds are extracted, seed germination begins 4–5 days after sowing in a moist substrate and is completed by 22 days, showing a brief period of rest, the duration of which is widely spread among the seed population (Siddiqi et al. 1991).

There is also wide variation in germination time among palms (Koebernik 1971, Basu & Mukherjee 1972, Wagner 1982, Endt 1996), including those from the same environment (Braun 1968, Jordan 1970). In a seed cohort, synchrony of seed germination can be from immediate and almost simultaneous to very delayed and/or sporadic. Seeds of *Metroxylon warburgii* and *M. vitiense* germinated almost simultaneously after falling to the ground (Doren 1997), while in *Ceroxylon ceriferum* (as *C. klopstockia*), *Chamaedorea elegans*, *Elaeis guineensis*, *Gronophyllum ramsayi* and *Pelagodoxa henryana*, germination is erratic, and several years may be required for all seeds to germinate (Hussey 1958, Poole & Conover 1974, Braun 1976, Wagner 1982, Braun 1984, Clarke 1988, Phillips 1996). This delayed or sporadic germination has been linked with different factors such as seedling escape from predation (Braun 1968). It has also been related to the extent of the period of dryness in savannas and forests. Different germination peaks from the same seed cohort could occur in several subsequent years during each wet season (Rees 1962, Carvalho et al. 1988, Ataroff & Schwarzkopf 1992, Harms & Dalling 1995, Olvera 1997).

Germination rates and germination capacity among seeds from different populations (cohorts and individuals of the same species) may differ considerably, as has been demonstrated for coconut and other species. These differences are mainly due to environmental and genetic factors in natural populations and/or to selection during domestication, or different handling techniques in cultivated species (Whitehead 1965, Robertson 1977, Al-Madeni & Tisserat 1986, Broschat & Donselman 1986, Clement & Dudley 1995, Rohani et al. 1997, Zizumbo-Villarreal & Arellano-Marín 1998).

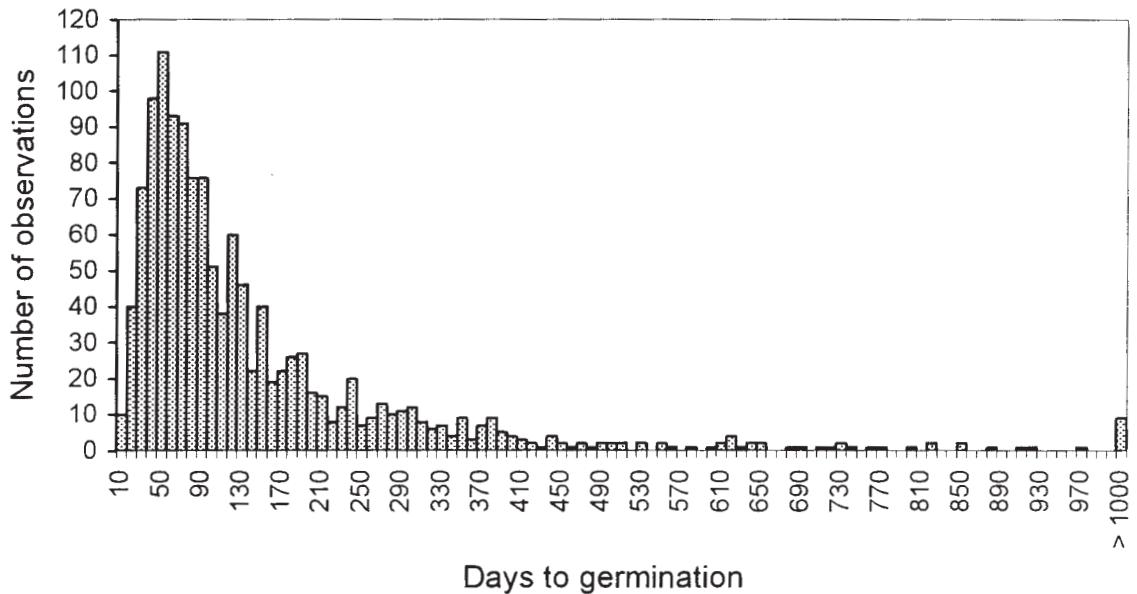
Variation in germination rates and germination capacity has also been related to different degrees

of maturation among seeds. Immature fruits of apparently full size could remain on the tree for a long time (Tomlinson & Soderholm 1975); therefore, occasionally it is difficult to identify seed maturation from the external appearance of the fruit (Holmquist & Popenoe 1967, Manokaran 1978, Broschat & Donselman 1988, Kheong 1992, Phillips 1996). It is necessary to identify maternal effects that could induce different degrees of maturation in the same infructescence during palm seed development. In Asteraceae and other flowering plants the position of seeds in the infructescence can produce polymorphism in seed requirements for germination (Baskin & Baskin 1998). This type of maternal effect could be related to erratic germination e.g. seeds from the same infructescence of *Arenga engleri* can germinate over a period of 515 days (Koebernik 1971). Maternal effects could also explain differences in germination requirements among batches, individuals, populations or years of seed production.

Several studies summarize germination data on palms (e.g. Braun 1968, Koebernik 1971, Basu & Mukherjee 1972), but the information is not uniform, and data about treatments are not always included. The criterion to define time for germination is also expressed in several ways, producing misunderstanding of the information: i) time to start germination, ii) time for full germination, iii) time for 50% of germination, iv) the interval between the start and the end of germination. The distribution of "time for germination" of 457 species is shown in Figure 2, which was taken from 1281 published records. From all the data reviewed it is possible to show that it is common for palms to begin germination within 120 days after planting. However, due to the heterogeneity of information it is difficult to conclude anything with certainty about the time necessary for completion of germination, especially for species that show delayed and/or sporadic seed germination.

Seed dormancy and germination requirements

According to the most widely accepted concept of germination – defined as the moment when the embryo protrudes through the seed covers – palm seeds do show a period of quiescence or dormancy. Some authors state that dormancy does not exist in palms because in most cases the embryo is immature at the time of dispersal and keeps developing while germination is arrested (Corner 1966). This is common among dormant seeds of flowering plants. Consequently, morphological dormancy related to anatomical features of embryo, and/or physical dormancy related to



2. Frequency distribution of "time for germination" of 457 species taken from 1281 published records. Data taken from the last twelve observations show that time for germination in some species took from 1021 to 1941 days.

features of the surrounding structures (coat, endosperm, etc.) have been proposed for palms that show delayed germination (Baskin & Baskin 1998). Germination delay after dissemination may have different causes among palms, varying from seed dormancy to unsuitable environmental factors for germination and/or the interaction between them.

Anatomical embryo immaturity is frequent in palms, but very little is known about other causes of morphological dormancy. Sometimes embryos in culture are capable of growing immediately, but germination of nuts is delayed because of a hormonal imbalance (physiological dormancy) (Hussey 1958, Robertson & Small 1977, Yuri 1987). Therefore, treatments with gibberellins and other hormones may promote germination percentage or increase germination rate in dormant seeds of several species (Nagao et al. 1980, Odetola 1987, Chin et al. 1988).

Moisture. Moisture balance between seeds and the surrounding environment determine the progress of germination. Conditions such as radiation, soil moisture and atmospheric humidity may affect this balance (Hussey 1958, Robertson & Small

1977, Ferreira & Santos 1992). Seeds gaining moisture will germinate faster than those that take up little or no water at all. Contrary, excess of moisture may also become an obstacle to germination due to improper ventilation for the physiological process of germination, or because it can promote the development of pathogenic fungi (Rees 1960a, b, 1963, Robertson & Small 1977, Fullington 1978).

From the physiological point of view it has not been demonstrated that lack of oxygen induces dormancy (Bradbeer 1988). Nevertheless, it has been proposed that oxygen is required to break chemical dormancy caused by substances in the endocarp that inhibit or delay seed germination (Hussey 1958, Robertson & Small 1977). In order to remove chemical inhibitors in palm seeds, the most common treatment is to soak the seeds for a period of 12–72 hours or more. However, prolonged soaking could be required only to break down the hard seed covers or to increase water uptake making germination more uniform and/or faster (Kheong 1992, Chalita et al. 1996, Davies & Pritchard 1998a, Doughty 1988, Moussa et al. 1998), as occurs in the field during flooding (Kitzke

1958). Due to the general practice of removing the fleshy parts of the fruits and washing the seeds before germination (Yocum 1961, Rees 1963), and in the absence of adequate experimental procedures to test the presence of chemical inhibitors, there have been few studies of the effects of soaking on germination that have been sufficiently documented (Kitzke 1958, Robertson & Small 1977, Ehara et al. 2001).

Seed covers. Dormancy has been attributed to a hard or water-impermeable seed cover (physical dormancy, Baskin et al. 2000), such as a fibrous mesocarp and/or a stony endocarp, which are very common among palms (Holmquist & Popenoe 1967, Robertson & Small 1977, Daquinta et al. 1996). In fact the hardness of many palm nuts has prompted their use for handicrafts (Bernal 1988, Doren 1997). However, in species such as *Jubaeopsis caffra* it has been demonstrated that parts of the seed (stony endocarp and hard endosperm) are permeable to water and oxygen (Robertson & Small 1977). After removing the hard shell of *Acrocomia aculeata* (as *A. mexicana*) and *A. sclerocarpa*, germination time was reduced from 440 and 878 days to 138 and 373 days, respectively (Koebernik 1971). Also, the endosperm by itself could be a barrier for germination that may delay germination for more than 150 days (Koebernik 1971, Murray 1973).

An extreme case of dormancy imposed by a hard coat has been described for *Chamaerops humilis* from the Mediterranean area; germination takes about a month to initiate, but a treatment of 4.5–7 hours of concentrated sulphuric acid to weaken the coat, allows germination after only 7 instead of 35 days (Merlo et al. 1993). It should be emphasized that seed covers only delay water absorption and probably oxygen diffusion (Robertson & Small 1977). Then, sooner or later the embryo itself will break the seed covers when it becomes more vigorous and/or when the germination process is initiated after imbibition (Baskin & Baskin 1998). Seed covers in palms act mainly as a mechanical obstacle for germination contrary to the impermeable hard coat of legume seeds (Vázquez-Yanes & Orozco-Segovia 1994).

Temperature. Most palm seeds are thermophilous, since optimal temperatures for germination are between 30–40°C (Odetola 1987, Addae-Kagyah et al. 1988, Carpenter 1988, Muñoz et al. 1992, Broschat 1998, Ehara et al. 1998). Soil temperatures above 38°C, but below 42°C can reduce the time required for germination of seeds of *Elaeis guineensis* from years to weeks (Rees 1960b, 1962). However, some species from subtropical areas do not require such high

temperatures, and a few even require a period of cool temperature (cold stratification at 5°C) to reach the highest germination percentage. For example, several cold-tolerant *Sabal* species and *Rhapidophyllum hystrix* require cold stratification and have their optimal temperatures for germination in a temperature range that is relatively low for most palms (21–25°C, Clancy & Sullivan 1988, Carpenter 1989). *Sabal palmetto* additionally requires daily fluctuating temperatures to reach high germination percentages, while constant temperatures are suboptimal for germination (Brown 1976b).

Heating at 38–40°C for several days is a common practice to induce germination of palm seeds (Addae-Kagyah et al. 1988). However, knowledge of the morpho-physiological role of high temperature on dormancy and seed germination is based on only few rigorous studies carried out on *Elaeis guineensis* (Hussey 1958, Rees 1962). The time of exposure to high temperatures required to induce germination can be as long as two months or more. This can be considered as a stratification treatment because high temperatures are necessary to break dormancy, but not necessarily needed for germination. The effect of this treatment is retained during seed storage.

In other plant families an optimal warm stratification commonly occurs at lower temperatures than in palm seeds (25–30°C), accelerating the growth rate of embryos (e.g. *Jeffersonia diphylla*, Podophyllaceae, Baskin & Baskin 1989, 1998). Nevertheless, in *E. guineensis* the effect of warm stratification has not been directly related to the embryo growth rate, but it has been reported that gibberellic acid can substitute the effect of heat in accelerating seed germination (Nagao et al. 1980). In this species high temperature seems to be related to: 1) changes in the physiological ability of the embryo to modify the characteristics of the abscission layer of the operculum, promoting its rupture, 2) changes in the characteristics of the endosperm reducing the constraint to the embryo growth, 3) modifications of the embryo, which can make efficient use of the endosperm. In fact, the main problem for germination of *E. guineensis* seeds is the presence of the operculum; once it is abscised, the embryo germinates (Hussey, 1958).

Germinating palms at constant high temperatures is not always adequate. In some cases this treatment induces germination as in *Coccothrinax argentata* and *Acoelorrhapha wrightii* (Carpenter 1988). Nevertheless, these temperatures are deleterious for other species, and germination percentages are higher when high daily

temperatures are followed by a period of relatively low temperature, e.g. in coastal dunes, deserts and other sunny environments (Rees 1962). On the other hand, non-dormant seeds of species that can germinate at relatively low constant temperature (25°C) can also germinate at fluctuating temperatures that include high temperatures during the diurnal period (e.g. 25–35°C, Carpenter 1989). It has been shown that germination temperatures are related to the lipids melting point. This relationship is crucial to understand adaptive evolution and biogeographic distribution of angiosperms (Linder 2000). Then, future research is necessary to understand the effect of high temperature on the liquefaction of lipids in the seeds and its relation to palm seed germination.

Light. It has been documented that light may act as a germination inhibitor in *Sabal palmetto* (negative photoblastism, Brown 1976b). Germination of seeds covered by soil suggests that most seed palm species are indifferent to light, although the effects of light on germination have not been properly studied. For example, in *Calamus manan*, Aminuddin and Siti (1990) tested seed germination in the open and beneath the canopy, but not in the darkness. To identify positive or negative photoblastism or indifference to light it is necessary to test seed response to darkness, white light and far red light, either beneath the canopy, or using special filters. Some positively photoblastic seeds germinate in far red light but not in darkness (Smith 1982).

Biotic interactions. In some cases primary and secondary animal dispersers promote germination

as in *Pinanga insignis*, *Caryota rumphiana* and *Attalea speciosa* (as *Orbignya martiana*) (May et al. 1985). Sometimes transit through the guts of birds and mammals removes the sarcotesta and/or the mesocarp, which accelerates germination of species like *Attalea speciosa* (as *Orbignya martiana*) and *Washingtonia filifera* (Bullock 1980, Stocker & Irvine 1983, May et al. 1985). In other cases, seeds are deposited in safe sites that correlate with the best conditions for germination and establishment, as *Astrocaryum mexicanum* and *A. murumuru* (Cintra & Horna 1997, Martínez-Ramos & Samper 1998).

Handling. Palm seeds collected and transported to places away from sites of production are often very difficult to germinate. Part of the problem may be partial dehydration during handling. In seeds of *Chamaedorea alternans*, even a small degree of desiccation induces hysteresis and rehydration is not completed; therefore, germination is inhibited (Rodríguez et al. 2000). On the other hand, there are palm seeds in which germination is improved by partial dehydration at the end of seed maturation. This partial dehydration may take place before or during dissemination (Robertson & Small 1977, Kheong 1992, Daquinta et al. 1996, Zizumbo-Villareal 1997).

Field germination. Several studies have documented conditions for germination in the field (Fullington 1978, Velez 1992), e.g. for *Caryota mitis* and *Prestoea acuminata* (as *P. trichoclada*) (Raich & Gong 1990, Bonilla & Feil 1995, Bonadio 1998, Matos & Watkinson 1998). However, there is a deficiency of experimental studies designed to document

Table 3. Types of storage behavior among palms.

Species	Seed moisture content (%)	Habitat	Storage behavior	References
<i>Bactris gasipaes</i>	-			Ferreira & Santos 1992, 1993; Hong et al. 1997; Andrade 2001
<i>Calamus manan</i>	67	tropical	recalcitrant	
<i>Chamaedorea tepejilote</i>	40	humid		
<i>Euterpe precatoria</i>	-			
<i>Euterpe edulis</i>	-			
<i>Mauritia flexuosa</i>	-			
<i>Coccothrinax argentata</i>	-			
<i>Phoenix dactylifera</i>	34	dry	orthodox	Hong et al. 1997
<i>Sabal mexicana</i>	12–13			
<i>Washingtonia filifera</i>	-			
<i>Acoelorrhaphe wrightii</i>	-	tropical		Rees 1960b; Grout et al. 1983; Chin et al. 1984; Hong et al. 1997
<i>Attalea crassispata</i>	57	brackish		
<i>Roystonea regia</i>	50	swamps	intermediate	
<i>Adonidia merrillii</i>	45	or seasonal		
<i>Elaeis guineensis</i>	21–30	areas		

field germination. It is necessary therefore, to carry out laboratory and field experiments to provide more information about the factors that break dormancy and/or induce germination, and to improve techniques for propagation of palms from seeds. Currently there is much useful anecdotal information, but it contributes little to the biological knowledge of palm seed germination. Many manuals and papers directed to horticulturists working on palm propagation in nurseries or botanical gardens describe a variety of treatments for germination. However, these treatments cannot be applied as a rule for all the species; seed characteristics and the habitat of each species need to be taken into account (Rees 1963, Doughty et al. 1986, Hodel 1992).

Seed longevity

One of the first classifications of palm seed longevity was that of De Leon (1961), who was able to test viability of seeds coming from all over the world at the Fairchild Tropical Garden. He classified them in three groups: a) short lived seeds, which lose viability after only 2 or 3 weeks of storage – most of these were species from tropical humid origin; b) an intermediate group with viability of 4 to 6 weeks, also of tropical origin; and, c) long-lived seeds characteristic of species of subtropical and/or very seasonal climates with viability of two to three or more months. Hong et al. (1997) questioned the validity of this classification. These authors based their classification on the initial seed moisture content, tolerance to dehydration and low temperatures, while De Leon's classification ignores storage and handling conditions.

Seed longevity and storage behavior are closely related. Therefore, any discussion about this subject should be based on Hong & Ellis (1996). Seeds with low moisture content that are tolerant to low temperatures (below 0°C) and have a long viability are classified as orthodox; those with high moisture content, no tolerance to dehydration or to temperatures are classified as recalcitrant; these seeds have a short viability. Finally, those seeds that are tolerant to dehydration, but not to low temperatures (0°C and -20°C) were classified as intermediate. The viability of these seeds can be prolonged by dehydration.

Generally, palm seeds have high seed moisture content at the time of dissemination; however, even within a genus, species can differ in their storage behavior (Hong et al. 1997). As expected some palm seeds from tropical humid environments are classified as "recalcitrant" due to their high moisture content (Table 3). Nevertheless, other palms from tropical humid,

brackish swamps or more seasonal areas are intermediate, while others from seasonally dry climates or dry environments show the orthodox storage behavior and can be maintained viable in cold dry storage (Table 3).

On the other hand, lack of information about seed physiology could lead to a wrong classification of storage behavior. *Elaeis guineensis* has been classified as recalcitrant due to its high moisture content, later was classified as orthodox due to its favorable seed response to cryopreservation, and finally as intermediate after more detailed studies (Grout et al. 1983, Chin et al. 1984, Hong et al. 1997). This could explain why 30% of its seeds remained viable after 33 months when kept under bare soil in natural conditions (Galt 1956, cited in Rees 1960b).

Cryopreservation. According to the definition, intermediate and recalcitrant seeds cannot survive cryogenic storage. However, it has been possible to keep frozen seeds or embryos of *Elaeis guineensis* (intermediate), *Calamus manan* and *Cocos nucifera* (recalcitrant) viable for a considerable period of time (>15 months) (Grout et al. 1983, Chin et al. 1989, Engelmann et al. 1995, Hong et al. 1997). Amazingly, tropical seeds of *Ptychosperma macarthurii* and other species germinated after 1 hour in liquid nitrogen (Al-Madeni & Tisserat 1986). Cryopreservation of the excised embryos, either by encapsulation or vitrification may solve the difficulties of germplasm conservation of palms in the future. More research on palm tissue culture should be performed.

Handling. Responses of palm seeds to dryness may cause confusion with regard to how long they can be stored. In some cases, dryness may induce a long lasting dormancy that might be misinterpreted as loss of viability; germination might be delayed for such a long time that seeds have been declared dead too soon (De Leon 1958, Kitzke 1958, Rees 1962). After dissemination, seeds of *Geonoma membranacea* and *Acoelorrhaphe wrightii* normally germinate within 48 and 90 days, respectively. However, previously dehydrated seeds developed a very retarded and erratic germination pattern (up to three and fifteen months, respectively) (Koebernik 1971, Dickie et al. 1993). On the other hand, chemical treatments (benomyl, methomyl, etc.) used for seed disinfections, and applied before germination tests, can cause an important germination reduction as in *Bactris gasipaes* (Coates-Beckford & Chung 1987). At the moment, storage behavior and seed viability of most palm species is uncertain or ought to be confirmed taking into account handling and storage of seeds from collection

(Hong et al. 1997, Davies & Pritchard 1998a, b). Several techniques to prolong viability of entire recalcitrant seeds have been developed, including suitable handling, transportation, the use of fungicides, keeping seeds in moisture and warm storage, etc. A temperature of 23°C has been shown to be suitable for *Dypsis lutescens* (as *Chrysalidocarpus lutescens*) (Broschat & Donselman 1986).

Ecological longevity. Longevity of palm seeds may differ considerably between field and controlled storage conditions. Recalcitrant seeds of *Attalea speciosa* (as *Orbignya phalerata*) survived for 9 months in the field, but less than 3 months in controlled conditions (Carvalho et al. 1988). In spite of expecting rapid germination from recalcitrant seeds, it has been reported that seeds of *Chamaedorea alternans* survived in the natural soil seed bank for 290 days (Moreno-Casasola 1976). Seeds of this species may require a long time to germinate under controlled conditions (Rodríguez et al. 2000), unlike other recalcitrant or short-lived seeds, which germinate quite quickly (Jordan 1970, Manokaran 1979, Hong et al. 1997). Thus, a relatively long viability in the moist soil of the forest might be favorable for those seeds requiring after-ripening. However, very little information is available on this subject.

Because palms are an important component of tropical and subtropical forests, are the world's third most useful plant family (Johnson 1996), and generate great interest among collectors, fans, horticulturists and scientists, we urge to make a greater effort to increase our knowledge on the biology of these species. Any contribution will enhance our ability to propagate, use, manage, and preserve this extraordinary and important plant family.

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LITERATURE CITED

- ADDAE-KAGYAH, K.A., D.M. OSAFO, N.S. OLYMPIO AND O.K. ATUBRA. 1988. Effect of seed storage, heat pretreatment and its duration on germination and growth of nursery stock of the idolatrica palm, *Elaeis guineensis* var *idolatraca* (Chevalier). *Tropical Agriculture* 65: 77–83.
- AMINUDDIN B.M. AND H.M. SITI. 1990. Influence of light on seed germination of *Calamus manan*. *Pertanika* 13: 327–330.
- ALANG, Z.C., G.F.J. MOIR AND L.H. JONES. 1988. Composition, degradation and utilization of endosperm during germination in the oil palm (*Elaeis guineensis*). *Annals of Botany* 61: 261–268.
- AL-MADENI, M.A. AND B. TISSERAT. 1986. Survival of palm seeds under cryogenic conditions. *Seed Science and Technology* 14: 79–85.
- ANDRADE, A.C.S. 2001. The effect of moisture content and temperature on the longevity of heart of palm seeds (*Euterpe edulis*). *Seed Science and Technology* 29: 171–182.
- ATAROFF, M. AND T. SCHWARZKOPF. 1992. Leaf production, reproductive patterns, field germination and seedling survival in *Chamaedorea bartlingiana*, a dioecious understory palm. *Oecologia* 92: 250–256.
- BANNISTER, B.A. 1970. Ecological life cycle of *Euterpe globosa* Gaert. In: ODUM, H.T. AND R.F. PIGEON (eds). *A tropical rain forest*, pp. 299–314. Oak Ridge Tenn. U.S. Atomic Energy Commission.
- BASKIN, J.M. AND C.C. BASKIN. 1989. Seed germination ecophysiology of *Jeffersonia diphylla*, a perennial herb of mesic deciduous forests. *American Journal of Botany* 76: 1073–1080.
- BASKIN, C.C. AND J.M. BASKIN. 1998. *Seeds: ecology, biogeography, and evolution of dormancy and germination*. Academic Press, San Diego, California, USA. 665 p.
- BASKIN, J.M., C.C. BASKIN AND L. XIAOJIE. 2000. Taxonomy, anatomy and evolution of physical dormancy in seeds. *Plant Species Biology* 15: 139–152.
- BASU, S.K. AND D.P. MUKHERJEE. 1972. Notes on culture - studies on the germination of palm seeds. *Principes* 16: 136–137.
- BAROT, S., J. GIGNOUX AND J.C. MENAUT. 1999. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. *Ecology* 80: 1987–2005.
- BERNAL, R. 1988. Demography of the vegetable ivory palm *Phytelephas seemannii* in Colombia, and the impact of seed harvesting. *Journal of Applied Ecology* 35: 64–74.
- BODMER, R.E. 1991. Strategies of seed dispersal and seed predation in Amazonian ungulates. *Biotropica* 23: 255–261.

- BONADIO, W.A. 1998. The ecology of *Roystonea oleraceae* palm swamp forest in the Nariva Swamp (Trinidad). *Wetlands* 18: 249–255.
- BONILLA, D. AND J.P. FEIL. 1995. Production of ramets and germination of *Prestoea trichoclada* (Arecaceae) – a source of palm heart in Ecuador. *Principes* 39: 210–214.
- BRADBEER, J.W. 1988. Seed dormancy and germination. Blackie A & P, Glasgow. 146p.
- BRADFORD, D.F. AND C.C. SMITH. 1977. Seed predation and seed number in *Scheelea* palm fruits. *Ecology* 58: 667–673.
- BRAUN, A. 1968. Cultivated palms of Venezuela. *Principes* 12: 39–60.
- BRAUN, A. 1976. Various observations on *Ceroxylon klopstockia*. *Principes* 20: 158–166.
- BRAUN, A. 1984. More Venezuelan palms. *Principes* 28: 73–84.
- BREWER, S.W. 2001. Predation and dispersal of large and small seeds of a tropical palm. *Oikos* 92: 245–255.
- BROSCHAT, T.K. 1998. Endocarp removal enhances *Butia capitata* (Mart.) Becc. (pindo palm) seed germination. *HortTechnology* 8: 586–587.
- BROSCHAT, T.K. AND H. DONSELMAN. 1986. Factors affecting storage and germination of *Chrysalidocarpus lutescens* seeds. *Journal of the American Society of Horticultural Science* 111: 872–877.
- BROSCHAT, T.K. AND H. DONSELMAN. 1988. Palm seed storage and germination. *Principes* 32: 3–12.
- BROWN, K.E. 1976a. Ecological studies of the cabbage palm, *Sabal palmetto*. II. Dispersal, predation, and escape of seeds. *Principes* 20: 49–56.
- BROWN, K.E. 1976b. Ecological studies of the cabbage palm, *Sabal palmetto*. III. Seed germination and seedling establishment. *Principes* 20: 98–115.
- BULLOCK, S.H. 1980. Dispersal of a desert palm by opportunistic frugivores. *Principes* 24: 29–32.
- CARPENTER, W.J. 1988. Temperature affects seed germination of four Florida palm species. *HortScience* 23: 336, 337.
- CARPENTER, W.J. 1989. Influence of temperature on germination of *Sabal causiarum* seed. *Principes* 33: 191–194.
- CARVALHO, J.H., F.G. ALCOFORADO AND L.D. MORAES. 1988. Effects of different conditions and duration of storage on the germination of Babassu seeds (*Orbignya phalerata*). *Principes* 32: 55–58.
- CHALITA MARTINS, C., W. RODRÍGUEZ DA SILVA AND M. LEAO ALVES BOVI. 1996. IV. Tecnologia de sementes e de fibras: tratamentos pré-germinativos de sementes da palmeira inajá. *Bragantia* 55: 123–128.
- CHANDRA SEKSHAR, K.N. AND D. DEMASON. 1988. Quantitative ultrastructure and protein composition of date palm (*Phoenix dactylifera*) seeds: a comparative study of endosperm vs. embryo. *American Journal of Botany* 75: 323–329.
- CHIN, H.F., Y.L. HOR AND M.B. MOHD LASSIM. 1984. Identification of recalcitrant seeds. *Seed Science and Technology* 12: 429–436.
- CHIN, H.F., B. KRISHNAPILLAY AND Z.C. ALANG. 1988. Breaking dormancy in *Kentia* palm seeds by infusion technique. *Pertanika* 1: 137–141.
- CHIN, H.F., B. KRISHNAPILLAY AND Y.L. HOR. 1989. A note on the cryopreservation of embryos from young coconuts (*Cocos nucifera* var. MAWA). *Pertanika* 12: 183–186.
- CINTRA, R. AND V. HORNA. 1997. Seed and seedling survival of the palm *Astrocaryum murumuru* and the legume tree *Dipteryx micrantha* in gaps in Amazonian forest. *Journal of Tropical Ecology* 13: 257–277.
- CLANCY, K.E. AND J.M. SULLIVAN. 1988. Some observations on seed germination, the seedling, and polyembryony in the needle palm *Rhapidophyllum hystrix*. *Principes* 32: 18–25.
- CLARKE, P.J. 1988. Letters to Principes. *Principes* 32: 86, 87.
- CLEMENT, C.R. AND N.S. DUDLEY. 1995. Effect of bottom heat and substrate on seed germination of pejibaye (*Bactris gasipaes*) in Hawaii. *Principes* 39: 21–24.
- COATES-BECKFORD, P.L. AND P.C. CHUNG. 1987. A study of the germination, disease symptoms and fungi associated with pejibaye seeds. *Seed Science and Technology* 15: 205–218.
- CONNELL, J.H. 1970. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: DEN BOER P.J. AND G.R. GRADWELL (eds). *Dynamics of numbers in populations*, pp. 298–312. *Proceedings of the Advanced Study Institute, Centre for Agricultural Publications and Documentation, Wageningen, Netherlands.*
- CORNER, E.J.H. 1966. *The natural history of palms.* University of California Press, Berkeley and Los Angeles. 393 p.

- DAQUINTA, M.O.C., I. CAPOTE, I. COBO, M. ESCALONA AND C. BORROTO. 1996. *In vitro* germination of *Chamaedora seifrizii*. *Principes* 40: 112, 113.
- DAVIES, R.I. AND H.W. PRITCHARD. 1998a. Seed storage and germination of the palms *Hyphaene thebaica*, *H. petersiana* and *Medemia argun*. *Seed Science and Technology* 26: 823–828.
- DAVIES, R.I. AND H.W. PRITCHARD. 1998b. Seed conservation of dry land palms of Africa and Madagascar: needs and prospects, pp. 37–43. *Forest Genetic Resources No. 26*. FAO, Rome, Italy.
- DAVIS, T.A. 1978. Some unusual formations in palms. *Principes* 23: 80–83.
- DE LEON, N.T. 1958. Viability of palm seeds. *Principes* 2: 96–102.
- DE LEON, N.T. 1961. Viability of palm seeds. *American Horticultural Magazine* 40: 131–132.
- DEMASON, D.A. 1984. Growth parameters in the cotyledon of date seedlings. *Botanical Gazette* 145: 176–183.
- DEMASON, D.A. 1985. Histochemical and ultrastructural changes in the haustorium of date (*Phoenix dactylifera* L.). *Protoplasma* 126: 168–177.
- DEMASON, D.A. 1986. Endosperm structure and storage reserve histochemistry in the palm, *Washingtonia filifera*. *American Journal of Botany* 73: 1332–1340.
- DEMASON, D.A. AND J.I. STILLMAN AND G.S. ELLMORE. 1989. Acid phosphatase localization in seedling tissues of the palms, *Phoenix dactylifera* and *Washingtonia filifera*, and its relevance to controls of germination. *Canadian Journal of Botany* 67: 1103–1110.
- DE SOUZA-STEVEAUX, M.C., R.R.B. NEGRELLE AND V. CITADINI-ZANETTE. 1994. Seed dispersal by the fish *Pterodoras granulosus* in the Paraná River Basin, Brazil. *Journal of Tropical Ecology* 10: 621–626.
- DICKIE, J.B., M.J. BALICK AND I.M. LININGTON. 1993. Studies on the practicality of *ex situ* preservation of palm seeds. *Principes* 37: 94–98.
- DOREN, E.T. 1997. Vegetable ivory and other palm nuts/seeds as an art/craft medium. *Principes* 41(4): 184–189.
- DOUGHTY, S.C. 1988. Growing palms in the New Orleans area. *Principes* 32: 96–100.
- DOUGHTY, S.C., E.N. O'ROURKE AND E..P. BARRIOS. 1986. Germination induction of pygmy date palm seed. *Principes* 30: 85–87.
- EDMONSON, C.H. 1941. Viability of coconut seeds after floating in sea. *Occasional Papers of Bernice P. Bishop Museum*. Honolulu, Hawaii 16: 293–304.
- EGUIARTE, L.E., A. BÚRQUEZ, J. RODRÍGUEZ, M. MARTÍNEZ-RAMOS, J. SARUKHÁN AND D. PIÑERO. 1993. Direct and indirect estimates of neighbourhood and effective population size in a tropical palm, *Astrocaryum mexicanum*. *Evolution* 47: 75–87.
- EHARA, H., C. KOMADA AND O. MORITA. 1998. Germination characteristics of Sago palm seeds and spine emergence in seedling produced from spineless palm seeds. *Principes* 42: 212–217.
- EHARA, H., O. MORITA, C. KOMADA AND M. GOTO. 2001. Effect of physical treatment and presence of the pericarp and sarcotesta on seed germination in sago palm (*Metroxylon sagu* Rottb.). *Seed Science and Technology* 29: 83–90.
- ENDT, D. 1996. Some observations on the growing of the chonta palm *Juania australis*. *Principes* 40: 27–30.
- ENGELMANN, F., N. CHABRILLANGE, S. DUSSERT AND Y. DUVAL. 1995. Cryopreservation of zygotic embryos and kernels of oil palm (*Elaeis guineensis* Jacq.). *Seed Science Research* 5: 81–86.
- FERREIRA, S.A. DO N. AND L.A. SANTOS. 1992. Viabilidade de sementes de pupunha (*Bactris gasipaes* Kunth). *Acta Amazonica* 22: 303–307.
- FERREIRA, S.A. DO N. AND L.A. SANTOS. 1993. Efeito da velocidade de secagem sobre a emergencia e vigor de sementes de pupunha (*Bactris gasipaes* Kunth). *Acta Amazonica* 23: 3–8.
- FOALE, M.A. 1968. Growth of the young coconut palm. *Australian Journal of Agricultural Research* 19: 781–799.
- FORGET, P.M. 1991. Scatterboarding of *Astrocaryum paramaca* by *Proechimys* in French Guiana: comparisons with *Myoprocta exilis*. *Tropical Ecology* 32: 155–167.
- FRAGOSO, J.M.V. 1997. Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *Journal of Ecology* 85: 519–529.
- FULLINGTON, J.G. 1978. Notes on Culture. *Principes* 22: 63.
- GALT, R. 1956. Studies on the germination of oil palm seed. WAIFOR report (unpublished).
- GARDNER, A.L. 1977. Feeding habits. In: BAKER, R.J., J.K. JONES JR. AND D.C. CARTER, (eds.) *Biology of Bats of the New World*. Family Phyllostomatidae. Part II, pp. 293–350. Special Publications Museum, Texas Tech University.

- GINIEIS, C. 1957. Étude morphologique et anatomique des embryons de quelques espèces du genre *Phoenix*. Bulletin de Muséum 29: 439–445.
- GLANZ, W.E., R.W. THORINGTON, JR., J. GIACALONE-MADDEN AND L.R. HEANEY. 1982. Seasonal food use and demographic trends in *Sciurus granatensis*. In: LEIGH, E.G., A.S. RAND AND D.M. WINDSOR (eds). The ecology of a tropical forest: seasonal rhythms and long term changes, pp. 239–252. Smithsonian Institution Press, Washington, D. C.
- GOTTSBERGER, G. 1978. Seed dispersal by fish in the inundated regions of Humaita, Amazonia. Biotropica 10: 170–183.
- GROUT, B.W.W., K. SHELTON AND H.W. PRITCHARD. 1983. Orthodox behavior of oil palm seed and cryopreservation of the excised embryo for genetic conservation. Annals of Botany 52: 381–384.
- GUIX, J.C. AND X. RUIZ. 1995. Toucans and thrushes as potential dispersers of seed-predatory weevil larvae in southeastern Brazil. Canadian Journal of Zoology 73: 745–748.
- HARMS, K.E. AND J.W. DALLING. 1995. Observations on the seasonal consistency in germination timing for *Scheelea zonensis*. Principes 39: 104–106.
- HARRIES, H.C. 1978. The evolution, dissemination and classification of *Cocos nucifera* L. The Botanical Review 44: 265–320.
- HOCH, G.A. AND G.H. ADLER. 1997. Removal of black palm (*Astrocaryum standleyanum*) seeds by spiny rats (*Proechimys semispinosus*). Journal of Tropical Ecology 13: 51–58.
- HODEL, D.R. 1992. *Chamaedorea* palms. Allen Press, Lawrence, Kansas. 338 p.
- HOLMQUIST, J.D. AND J. POPENOE. 1967. The effect of scarification on the germination of seed of *Acrocomia crispa* and *Arenga engleri*. Principes 11: 23–25.
- HONG, T.D. AND R.H. ELLIS. 1996. A protocol to determine seed storage behavior. In: ENGELS, J.M.M. AND J. TOLL (eds). IPGRI. Technical Bulletin No. 1. International Plant Genetic Resources Institute, Rome, Italy. 63 p.
- HONG, T.D., S. LINNINGTON AND R.H. ELLIS. 1997. Seed storage behavior: a compendium. IPGRI. Handbooks for Genebanks. No. 4, pp. 501–515. International Plant Genetic Resources Institute. Rome, Italy. 656 p.
- HUSSEY, G. 1958. An analysis of the factors controlling the germination of the seed of the oil palm, *Elaeis guineensis* (Jacq.). Annals of Botany 22: 259–286.
- JANZEN, D.H. 1970. Herbivores and the number of trees species in tropical forests. American Naturalist 104: 501–528.
- JANZEN, D.H. 1971. The fate of *Scheelea rostrata* fruits beneath the parent tree: predispersal attack by bruchids. Principes 15: 89–101.
- JANZEN, D.H. 1972. Association of a rainforest palm and seed-eating beetles in Puerto Rico. Ecology 53: 258–261.
- JOHNSON, D. (ed) AND IUCN/SSC PALM SPECIALIST GROUP. 1996. Palms: Their Conservation and Sustainable Utilization. Status Survey and Conservation Action Plan. IUCN, Gland, Switzerland and Cambridge, UK. 116 + viii pp.
- JONES, D.L. 1995. Palms throughout the world. Smithsonian Institution Press. Washington D.C. 410 p.
- JORDAN, C.B. 1970. A study of germination and use in twelve palms of Northeastern Peru. Principes 14: 26–32.
- KARUNARATNE, S., S. SANTHA AND A. KOVOOR. 1991. An *in vitro* assay for drought-tolerant coconut germplasm. Euphytica 53: 25–30.
- KERMODE, A.R. 1995. Regulatory mechanisms in the transition from seed development to germination: interactions between the embryo and the seed environment. In: KIGEL, J. AND G. GALILI (eds). Seed development and germination, pp. 273–332. New York, Marcel Dekker.
- KHEONG, Y.S. 1992. Aspects of seed technology of rattans. In: RAZALI, W., J. DRANSFIELD AND N. MANOKARAN (eds). A guide to the cultivation of rattan, pp. 143–148. Forest Research Institute Malaysian K.L. Malaysian Forest Record No.35.
- KITZKE, E.D. 1958. A method for germinating *Copernicia* palm seeds. Principes 2: 5–8.
- KOEBERNIK, J. 1971. Germination of palm seed. Principes 15: 134–137.
- LINDER, C.R. 2000. Adaptive evolution of seed oils in plants: Accounting for the biogeographic distribution of saturated and unsaturated fatty acids in seed oils. The American Naturalist 156: 442–458.
- LOTT, R.H., G.N. HARRINGTON, A.K. IRVINE AND S. MCINTYRE. 1995. Density-dependent seed predation and plant dispersion of the tropical palm *Normanbya normanbyi*. Biotropica 27: 87–95.
- LLOYD, F.E. 1910. Development and nutrition of the embryo, seed and carpel in the date, *Phoenix*

- dactylifera* L. Annals of the Missouri Botanical Garden 21: 103–164.
- MANOKARAN, N. 1978. Germination of fresh seeds of Malaysian rattans. The Malaysian Forester 41: 319–324.
- MANOKARAN, N. 1979. Age of the bertam palm, *Eugeissona tristis* Griff., at the tenth leaf stage. The Malaysian Forester 42: 125–129.
- MARTÍNEZ-RAMOS, M. AND C. SAMPER. 1998. Tree life history patterns and forest dynamics: a conceptual model for the study of plant demography in patchy environments. Journal of Sustainable Forestry 6: 85–125.
- MATOS, D.M.S. AND A.R. WATKINSON. 1998. The fecundity, seed, and seedling ecology of the edible palm *Euterpe edulis* in southeastern Brazil. Biotropica 30: 595–603.
- MAY, P.H., A.B. ANDERSON, M.J. BALICK AND J.M.F. FRAZAO. 1985. Subsistence benefits from the babassu palm (*Orbignya martiana*). Economic Botany 39: 113–129.
- MENDOZA OCHOA, A.E. 1994. Demografía e integración clonal en *Reinhardtia gracilis*, una palma tropical. Tesis Doctoral. Instituto de Ecología. Universidad Nacional Autónoma de México. México. 156 p.
- MERLO, M.E., M.M. ALEMÁN, J. CABELLO AND J. PEÑAS. 1993. On the Mediterranean fan palm (*Chamaerops humilis*). Principes 37: 151–158.
- MOORE, H.E., JR. AND N.W. UHL. 1982. Major trends of evolution in palms. The Botanical Review 48: 1–69.
- MORENO-CASASOLA, P. 1976. Latencia y viabilidad de semillas de vegetación primaria. In: GOMÉZ-POMPA, A., C. VÁZQUEZ-YANES, S. DEL AMO-RODRÍGUEZ AND A. BUTANDA-CERVERA (eds). Investigaciones sobre la regeneración de selvas altas en Veracruz, México, pp. 527–548. Compañía Editorial Continental, S.A., México.
- MOUSSA, H., H.A. MARGOLIS, P.A. DUBE AND J. ODONGO. 1998. Factors affecting the germination of doum palm (*Hyphaene thebaica* Mart.) seeds from the semi-arid zone of Niger, West Africa. Forest Ecology and Management 104: 27–41.
- MUÑOZ, B., R. ORTA AND E. MEDERO. 1992. Algunos aspectos de la germinación de semillas de *Roystonea regia* (H. B. K.) O.F. Cook 1. c. var. *regia*. Ciencias Biológicas 24: 119–123.
- MURRAY, S.G. 1973. The formation of endocarp in palm fruits. Principes 17: 91–102.
- NAGAO, M.A., K. KANEGAWA AND W.S. SAKAI. 1980. Accelerating palm seed germination with gibberellic acid, scarification, and bottom heat. HortScience 15: 200–201.
- ODETOLA, J.A. 1987. Studies on seed dormancy, viability, and germination in ornamental palms. Principes 31: 24–30.
- OLVERA, S. 1997. *Sabal mexicana* (palma apachite). In: GONZÁLEZ-SORIANO, E., R. DIRZO AND R.C. VOGT (eds). Historia natural de Los Tuxtlas, pp.150–153. Universidad Nacional Autónoma de México. México.
- OPPENHEIMER, J.R. 1982. *Cebus capucinos*: home range, population dynamics, and interspecific relationships. In: LEIGH, E.G., A.S. RAND AND D.M. WINDSOR (eds). The ecology of a tropical forest: seasonal rhythms and long term changes, pp. 253–272. Smithsonian Institution Press, Washington, D. C.
- OYAMA, K. 1991. Seed predation by a curculionid beetle on the dioecious palm *Chamaedorea tepejilote*. Principes 35: 156–160.
- PADMANABHAN, D. AND D. REGUPATHY. 1981. Studies on *Bentinckia condapanna*: I. The fruit and the seed. Principes 25: 172–177.
- PAMMEL, L.H. AND C.M. KING. 1930. Germination and seedling forms of some woody plants. Proceedings of the Iowa Academy of Science 37: 131–141.
- PHILLIPS, R.H. 1996. *Pelagodoxa henryana* in Fiji. Principes 40: 148–151.
- POOLE, R.T. AND C.A. CONOVER. 1974. Germination of *Neanthe bella* palm seed. Proceedings of the Florida State Horticulture Society 87: 429–430.
- RAICH, J.W. AND W.K. GONG. 1990. Effects of canopy openings on tree seed germination in a Malaysian dipterocarp forest. Journal of Tropical Ecology 6: 203–217.
- REES, A.R. 1960a. Early development of the oil palm seedling. Principes 4: 148–150.
- REES, A.R. 1960b. The germination of oil palm seeds: a review. Journal of the West African Science Association 6: 55–62.
- REES, A.R. 1962. High-temperature pre-treatment and the germination of seed of the oil palm, *Elaeis guineensis*. Annals of Botany 26: 569–581.
- REES, A.R. 1963. Germination of palm seeds using a method developed for the oil palm. Principes 7: 27–30.
- ROBERTSON, B.L. 1977. Morphology and development of the fruit and seed of *Jubaeopsis caffra* Becc. Principes 21: 23–30.
- ROBERTSON, B.L. AND J.G.C. SMALL. 1977. Germination of *Jubaeopsis caffra* seeds. Principes 21: 114–122.

- RODRÍGUEZ, M., A. OROZCO-SEGOVIA, M.E. SÁNCHEZ-CORONADO AND C. VÁZQUEZ-YANES. 2000. Seed germination of six mature neotropical rain forest species in response to dehydration. *Tree Physiology* 20: 693–699.
- ROHANI, O., N. RAJANAIDU AND S. JALANI. 1997. Seed characteristics of African accessions of oil palm (*Elaeis guineensis*). *Principes* 41: 5–11.
- SENTO, T. 1974. Studies on the seed germination of palms VI. On *Cocos nucifera* L., *Phoenix humilis* Royle var. *hanceana* Becc. and *Phoenix sylvestris* Roxb. *Journal of the Japanese Society of Horticultural Science* 42: 380–388.
- SHUKR, M.M., M.A. CLOR, AND T.A. AL-ANI. 1988. Seed and fruit development of *Phoenix dactylifera* as influenced by type of pollination and some growth substances. *Principes* 32: 160–164.
- SIDDIQI, N.A., M. SHAHIDULLAH AND M.A.H. SHAHJALAL. 1991. Studies on seeds, germination success and raised seedlings of *Nypa fruticans*. *Indian Forester* 117: 553–559.
- SILANDER, Jr., J.A. 1985. Microevolution in clonal plants. In: JACKSON, J.B.C., L. W. BUSS AND R.E. COOK (eds). *Population biology and evolution in clonal organisms*, pp.107–152. Yale University Press, New Haven.
- SMITH, H. 1982. Light quality photoperception and plant strategy. *Annual Review of Plant Physiology* 33: 481–518.
- SMITH, J.M.B., H. HEATWOLE, M. JONES AND B.M. WATERHOUSE. 1990. Drift disseminules on cays of the Swain Reefs, Great Barrier Reef, Australia. *Journal of Biogeography* 17: 5–17.
- SMYTHE, N., W.E. GLANZ AND E.G. LEIGH, JR. 1982. Population regulation in some terrestrial frugivores. In: LEIGH, E.G., A.S. RAND AND D.M. WINDSOR (eds). *The ecology of a tropical forest: seasonal rhythms and long term changes*, pp. 227–238. Smithsonian Institution Press, Washington, D. C.
- SNEED, M.W. 1976. In quest of the big seed (with observations along the way). *Principes* 20: 11–23.
- STERNER, R.W., C.A. RIBIC AND G.E. SCHATZ. 1986. Testing for life historical changes in spatial patterns of four tropical tree species. *Journal of Ecology* 74: 621–633.
- STOCKER, G.C. AND A.K. IRVINE. 1983. Seed dispersal by cassowaries (*Casuaris casuaris*) in North Queensland's rainforests. *Biotropica* 15: 170–176.
- SUGIMURA, Y. AND T. MURAKAMI. 1990. Structure and function of the haustorium in germinating coconut palm seed. *Japan Agricultural Research Quarterly* 24: 1–14.
- SVENNING, J.-C. 2001. On the role of microenvironmental heterogeneity in the ecology and diversification of Neotropical rain-forest palms (Arecaceae). *The Botanical Review* 67: 1–53.
- TOMLINSON, P.B. 1960. Essays on the morphology of palms. *Principes* 4: 6–61.
- TOMLINSON, P.B. 1971. The shoot apex and its dichotomous branching in the *Nypa* palm. *Annals of Botany* 35: 865–879.
- TOMLINSON, P.B. 1979. Systematics and ecology of the Palmae. *Annual Review of Ecology and Systematics* 10: 85–107.
- TOMLINSON, P.B. 1990. *The structural biology of palms*. Clarendon Press, Oxford. 477 p.
- TOMLINSON, P.B. AND P. K. SODERHOLM. 1975. The flowering and fruiting of *Corypha elata* in South Florida. *Principes* 19: 83–99.
- TREJO-PÉREZ, L. 1976. Diseminación de semillas por aves en "Los Tuxtlas", Veracruz. In: GOMÉZ-POMPA, A., C. VÁZQUEZ-YANES, S. DEL AMOR-RODRÍGUEZ AND A. BUTANDA-CERVERA (eds). *Investigaciones sobre la regeneración de selvas altas en Veracruz, México*, pp. 447–465. Compañía Editorial Continental, S.A., México.
- UHL, N.W. AND J. DRANSFIELD. 1987. *Genera Palmarum. A classification of palms based on the work of Harold E. Moore Jr. L.H. Bailey Hortorium & International Palm Society*, Allen Press, Kansas. pp 610.
- VÁZQUEZ-YANES, C. AND A. OROZCO-SEGOVIA. 1994. Signals for seeds to sense and respond to gaps. In: CALDWELL, M. M. AND R. W. PEARCY (eds). *Exploitation of environmental heterogeneity by plants: ecophysiological processes above and belowground*, pp. 209–236. Academic Press, Inc. San Diego, California, 429 p.
- VELEZ, R. 1992. *Ptychosperma elegans* regenerating in Southern California. *Principes* 36: 35.
- VERTUCCI, C.W. AND J.M. FARRANT. 1995. Acquisition and loss of desiccation tolerance. In: KIGEL, J. AND G. GALILI (eds). *Seed development and germination*, pp. 237–271. Marcel Dekker, New York.
- WAGNER, R.I. 1982. Raising ornamental palms. *Principes* 26: 86–101.
- WHITEHEAD, R.A. 1965. Speed of germination, a characteristic of possible taxonomic significance in *Cocos nucifera* Linn. *Trop. Agriculture, Trin.* 42: 369–372.

- YOCUM, H.G. 1961. A method for germinating palm seeds. *Principes* 5: 31, 32.
- YURI, J.A. 1987. Propagation of Chilean wine palm (*Jubaea chilensis*) by means of *in vitro* embryo culture. *Principes* 31: 183–186.
- ZIZUMBO-VILLARREAL, D. 1997. El cocotero en México: historia, variación morfofisiológica y diversidad genética. Tesis Doctoral. Instituto de Ecología. UACPyP/CCH. Universidad Nacional Autónoma de México. México. 183 p.
- ZIZUMBO-VILLARREAL, D. AND J. ARELLANO-MARÍN. 1998. Germination patterns in coconut populations (*Cocos nucifera* L.) in Mexico. *Genetic Resources and Crop Evolution*. 45: 465–473.
- ZONA, S. AND A. HENDERSON. 1989. A review of animal-mediated seed dispersal of palms. *Selbyana* 11: 6–20.

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Pollination Biology of Saw Palmetto (*Serenoa repens*) in Southwestern Florida

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1. Saw palmetto (*Serenoa repens*) with one inflorescence.

The saw palmetto is a familiar and important component of vegetation in southeastern USA where it is also of economic significance. This paper describes its pollination biology.

Saw palmetto (*Serenoa repens* (Bartr.) Small), a prostrate palm endemic to the southeastern coastal plain of the United States, is common in a variety of habitats from seasonally flooded pine forests to xeric coastal dunes and inland scrub (Tanner et al. 1996). Saw palmetto flower and fruit production is important both ecologically and commercially in the region. Over 300 species of insects have been observed visiting saw palmetto flowers (M. Deyrup, Archbold Biological Station, pers. comm.); some of these flower visitors collect nectar and/or pollen, while others find mates or prey near or on the flowers. Where present, European honeybees (*Apis mellifera*) are prominent flower visitors that produce commercial "saw palmetto honey." Saw palmetto fruits are eaten by many species of wildlife, including black bear (*Ursus americanus*), white-tailed deer (*Odocoileus virginianus*), raccoon (*Procyon lotor*), wild turkey (*Meleagris gallopavo*), northern bob-white (*Colinus virginianus*), gray fox (*Urocyon cinereoargenteus*) and gopher tortoise (*Gopherus polyphemus*; Maehr & Layne 1996). In addition, fruit demand for medicinal use has increased because saw palmetto fruit is used to treat benign prostatic hyperplasia (enlarged prostate; Berry et al. 1984). Since 1996, annual harvests of saw palmetto fruits in Florida have totalled at least 7,000,000 kg (M. Huffman, Plantation Medicinals Inc., pers. comm.).

Saw palmetto flowers are borne on densely-branched, interfoliar inflorescences, 0.5–0.75 m long (Fig. 1). Saw palmettos can produce over five inflorescences at one time, but commonly produce one to three. Each inflorescence contains several thousand individual flowers (Fig. 2). The bisexual flowers are 5–6 mm long, with three white, partially connate petals that are reflexed at anthesis (Fig. 3). Each flower has six stamens and one pistil, with a 3-ovulate, superior ovary. Usually only one ovule matures into a seed (Godfrey 1988).

Although seasonality of saw palmetto flowering and fruiting has been described (Hilmon 1968), very little is known about pollination biology. Knowledge of pollination biology should help land managers maintain biodiversity and natural functioning of ecosystems in which saw palmetto is prominent, while making informed decisions concerning management for wild fruit harvesting. In this study we (1) documented timing of flower bud opening, anther dehiscence, stigma receptivity and nectar production, (2) observed insect visitors to flowers and (3) experimentally characterized some aspects of the breeding system. Saw palmetto exhibits several characteristics consistent with biotic pollination (Faegri & van der Pijl 1979), such as a conspicuous floral display,

sticky pollen, floral fragrance and nectar production. Since biotic pollination is usually associated with outcrossing (Proctor 1978), we expected that the breeding system would include at least some outcrossing. This study addressed the following specific questions: 1. How long do flowers function? 2. When is pollination likely to occur? 3. Are insect pollinators required for seed set?

Materials and Methods

Phenology. We conducted all fieldwork at the University of Florida Southwest Florida Research and Education Center, in Collier County, Florida. To characterize timing of bud opening, we observed a total of 16 inflorescences on February 10 and 13, 1998 and March 3 and May 18, 1999. During the afternoon before each observation, we marked mature buds by tying nylon sewing thread around the base of each bud. On observation dates, we checked each marked bud every 20 min from 02:00 to 14:00. We recorded bud opening, presence of nectar in flowers, anther dehiscence and insect visitors to inflorescences. We attempted to collect insect visitors, and sampled pollen loads on collected insects using fuchsin glycerine jelly (Beattie 1971). We also observed insect visitors to five additional inflorescences during March and April 1998. For these inflorescences, we recorded insect visitors for 10 min out of every 30 min, from 09:00 to 16:00.

On February 13, 1998 and May 26–28, 1999 we collected and characterized 1- and 2-day-old flowers. We defined 1-day-old flowers as those that had opened earlier (either pre- or post-dawn) on the collection date, and 2-day-old flowers as those that had opened the day before the collection date. On each date we collected 10, 1-day-old and 10, 2-day-old flowers at 10:30 and 13:30. We observed each of the 160 flowers under a dissecting microscope, and recorded anther dehiscence, presence of pollen in anthers, presence of moisture and/or pollen on the stigma and presence of nectar in the flower. For the 120 flowers collected in 1999 we determined stigma receptivity by applying 3% hydrogen peroxide to the stigmas and watching for bubbling (indicating peroxidase activity and stigma receptivity) under a dissecting microscope (Kearns & Inouye 1993). On May 26, 27 and 28, 1999, we also collected and characterized 3-, 4- and 5-day-old flowers, respectively. We collected 10 flowers at 10:30 and 10 flowers at 13:30 on each of the three days, and recorded the same information that we recorded for 1- and 2-day-old flowers in 1999.

Breeding System. Saw palmetto is a clonal species with branching, prostrate stems and a spreading

Table 1. Insect visitors to saw palmetto (*Serenoa repens*) flowers, activity of visitors, and presence of pollen on bodies of visitors. Insects were observed and collected from five inflorescences in Collier County, Florida during March and April 1998.

Insect Visitors	on rachis	on flowers	nectaring	pollen on body
Orthoptera				
Blattidae 1 sp. indet.		X		
Thysanoptera				
Heterothripidae 1 sp. indet.	X			
Hemiptera				
<i>Largus succinctus</i>		X		
Homoptera				
Flatidae 2 sp. indet.	X			
Coleoptera				
Coccinellidae 1 sp. indet.	X	X	X	
<i>Notolomus basalis</i>	X			X ^a
Diptera				
<i>Plecia nearctica</i>	X	X	X	X ^b
Stratiomyidae 1 sp. indet.		X	X	
Bombyliidae 1 sp. indet.		X		
Dolichopodidae 1 sp. indet.	X			
<i>Ornidia obesa</i>		X		
Syrphidae 2 sp. indet.		X	X	
<i>Physoconops</i> sp.		X		
Muscidae 2 sp. indet.	X	X	X	
Hymenoptera				
<i>Dasymutilla</i> sp.		X		
<i>Camponotus</i> sp.	X	X	X	
Formicidae 3 sp. indet.	X	X	X	X ^a
Formicidae 5 sp. indet.	X			
<i>Polistes metricus</i>		X	X	
<i>Polistes exclamans</i>		X	X	
<i>Mesochyttarus cubicola floridana</i>		X	X	
<i>Colletes</i> sp.		X	X	X
<i>Augochloropsis metallica</i>		X	X	X
Halictidae 1 sp. indet.		X	X	X
<i>Apis mellifera</i>		X	X	X

^afewer than 100 grains of pollen present.

^bpollen amounts varied, but usually fewer than 100 grains present.

growth habit similar to tillering in grasses. At the terminal end of each stem branch is a meristem with a rosette of leaves, hereafter called a ramet. On February 22, 1999 we located 25 saw palmetto ramets of similar height and width that had initiated inflorescences. We verified that each ramet originated from a separate stem, and thus were reasonably confident that the ramets were from different genetic individuals. To characterize the breeding system, we used an experimental

design consisting of five treatments: (1) emasculated and open-pollinated (allowed xenogamy, geitonogamy), (2) caged and hand (self)-pollinated (tested for geitonogamy), (3) emasculated and caged (allowed agamospermy, possible geitonogamy), (4) caged (tested for self-pollination without flower visitors), and (5) non-manipulated (hereafter these treatments will be referred to as (1) – (5)). We did not include a caged, cross-pollinated treatment, because we assumed

Table 2. Numbers of fruits and percent fruit set of saw palmetto (*Serenoa repens*) flowers subjected to five treatments to characterize the breeding system (see Methods and Materials for descriptions of treatments). Each of five treatment replicates consisted of 20 flowers within an inflorescence of an individual saw palmetto ramet. # = number of fruits. % = percent fruit set.

Replicate (N=20 flowers)	Treatment									
	Emasculated, Open-pollinated (1)		Caged, Hand (self)-pollinated (2)		Caged, Emasculated (3)		Caged (4)		Non-manipulated (5)	
	#	%	#	%	#	%	#	%	#	%
1	3	15	1	5	0	0	0	0	5	25
2	1	5	1	5	0	0	1	5	3	15
3	2	10	2	10	2	10	0	0	4	20
4	4	20	1	5	0	0	0	0	5	25
5	3	15	1	5	0	0	0	0	4	20

that the emasculated, open-pollinated and non-manipulated treatments included xenogamy. We marked 5 ramets for each of the 5 treatments, and marked 20 buds on one inflorescence of each ramet by gently tying nylon sewing thread below the base of each bud, for a total of 100 buds per treatment.

For the caged treatments, we placed cylinders (16 cm diameter) constructed from chicken wire and wrapped twice with white bridal veil (mesh <3 mm diameter) on inflorescences before anthesis began. To help exclude pollinators, we used metal wire to fasten excess bridal veil material on the bottom of each cage around the inflorescence rachis, and applied Tanglefoot (The Tanglefoot Co., Grand Rapids, MI), a sticky material that excludes or traps crawling insects, around the base of the rachis. Each cage covered approximately

half of an inflorescence, consisting of 800–1000 buds.

For the hand-pollinated treatments, we monitored buds daily until they opened. Between 08:00 and 10:00 on the day of bud opening, we carefully removed cages and obtained stamens from other flowers on the same ramet with dehisced anthers containing pollen. We then rubbed these anthers over the stigmatic surface of each treated flower until we observed pollen on the stigma using a hand lens. We completed this treatment during the same time period that the emasculaton treatment was completed.

We monitored marked flowers until they either fell off or produced fruit. We removed cages and counted all fruits on May 13, 1999, after all fruits began to develop. We recorded fruit set when a



2. Saw palmetto inflorescence containing thousands of flowers.

flower's style and stigma had withered but the flower remained attached to the rachilla, and the ovary wall had turned green. We used a Kruskal-Wallis test to test for differences in numbers of fruit set among treatments and performed two planned comparisons. First, to determine if cross-pollination increased fruit set, we compared treatments (4) and (5). Second, to determine if geitonogamy increased fruit set, we compared treatments (2) and (3).

Results

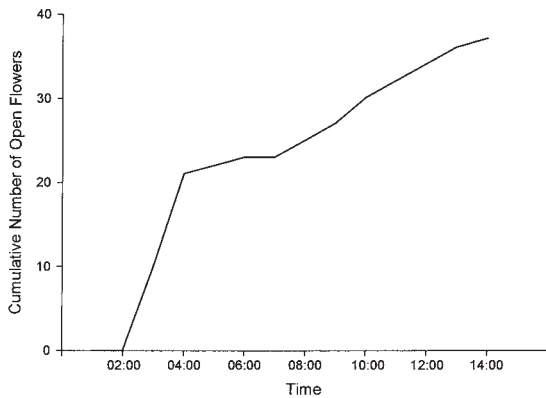
Phenology: Flowers opened asynchronously within an inflorescence over a period of approximately 1 month, with anthesis progressing from the base to the top of the inflorescence. During the 1998 and 1999 12-hr observation periods, a total of 37 marked buds opened. Over half of the buds opened from 02:00 to 04:00. Very few buds opened between 04:00 and 07:00. Buds opened at a faster rate after 07:00, with approximately 40% of buds opening between 07:00 and 14:00 (Fig. 4). Nectar was visible at the base of the gynoecium as soon as buds opened. Anther dehiscence began at 8:00, with the number of flowers with dehiscing anthers increasing rapidly until 11:00 (Fig. 5). Anthers of

shaded flowers and later-opening flowers dehiscence somewhat later than flowers in the sun or flowers that opened earlier. Median time between dehiscence of the first anther in a flower and dehiscence of all anthers was 2 hrs (range = 40 min–5 hr). Of 26 flowers for which we quantified anther dehiscence, 11 had all anthers dehiscence by 14:00.

Flowers collected 1, 2 and 3 days after opening of buds showed similar timing for anther dehiscence. Virtually all anthers of collected flowers had dehiscence during the first day of anthesis. Maximum amounts of pollen were available on anthers immediately after dehiscence, also during the first day of anthesis. Stigma receptivity, however, occurred somewhat later than anther dehiscence, indicating that saw palmetto flowers are weakly protandrous. During the first day of anthesis, stigmas were receptive in only 14% of flowers collected. By the morning of the second day of anthesis, however, over 80% of flowers had receptive stigmas. Proportions of flowers with receptive stigmas continued to be high (70-100%) through the morning of the fourth day of anthesis (Fig. 6). The three-lobed stigma appeared open and moist in receptive stigmas. The lobed stigma



3. Saw palmetto flower buds and open flowers.

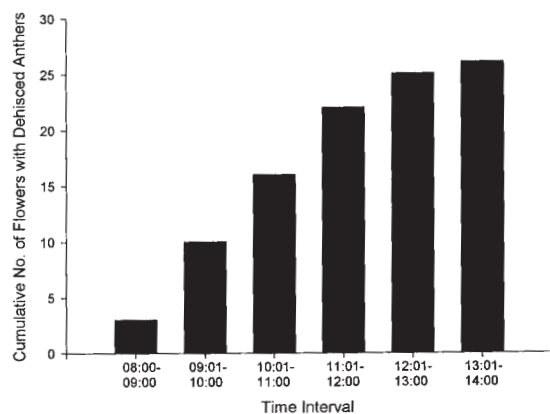


4. Cumulative numbers of saw palmetto (*Serenoa repens*) flowers open over 12-hr time period. Data were pooled from observations of marked buds on 16 inflorescences on February 10 and 13, 1998 and March 3 and May 18, 1999, in Collier County, Florida.

in non-receptive flowers was closed, with one lobe appearing as a hood over the stigmatic surface. Nectar was consistently present in flowers through the second day of anthesis and sporadically present through the fourth day of anthesis. After the fourth day of anthesis, styles, stigmas and petals browned and withered.

Insect Visitors: We observed 34 insect species on saw palmetto inflorescences, representing 7 orders: Orthoptera, Thysanoptera, Hemiptera, Homoptera, Coleoptera, Diptera and Hymenoptera (Table 1). Approximately 80% of the species were in the orders Diptera and Hymenoptera.

5. Cumulative numbers of saw palmetto (*Serenoa repens*) flowers with anthers dehisced from 08:00 to 14:00 during the first day of anthesis. Data were pooled from observations of marked flowers on 16 inflorescences on February 10 and 13, 1998 and March 3 and May 18, 1999, in Collier County, Florida.



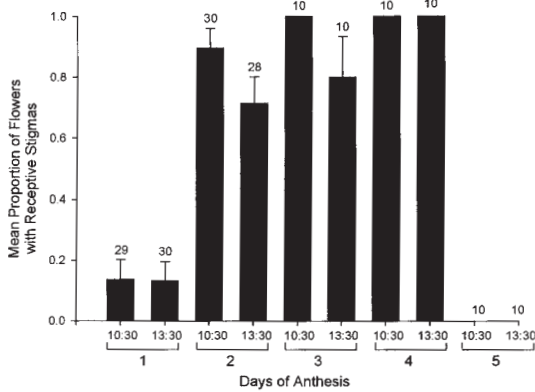
Diptera were common flower visitors, but usually carried no pollen (Table 1). Syrphid flies (Syrphidae) were represented by three species, *Ornidia obesa* and two unidentified species. These flies tended to visit single flowers and obtain nectar quickly while hovering. One of the unidentified species was a common visitor that we observed at four of the five inflorescences. It visited an inflorescence only once or twice during the day, usually during the morning. Muscid flies (Muscidae) were represented by two species. These flies obtained nectar while crawling from flower to flower and usually stayed on inflorescences for several minutes per visit.

Two Diptera species carried pollen on their bodies (Table 1). The first, *Plecia nearctica* (Bibionidae; lovebug) was a very common visitor. Single or coupled individuals actively foraged for nectar, crawled over numerous flowers, or simply lay on inflorescences, sometimes remaining for hours. Lovebugs usually carried pollen (typically <100 grains) on various parts of their bodies. *Physoconops* sp. (Conopidae) also carried pollen. Two individuals were observed with pollen on the ventral surface of their abdomens.

Other Diptera observed and collected were one species each in the families Stratiomyidae, Bombyliidae and Dolichopodidae. Species in Stratiomyidae and Bombyliidae were observed on only one occasion. The Dolichopodidae species was a very common visitor to inflorescences but presumably visited flowers as an insect predator.

Hymenoptera contained the most species of insect visitors, the most numerous visitors, and virtually all of the presumed pollinator species (Fig. 7). The most common insect visitors were ants (Formicidae), represented by *Camponotus* sp. and eight unidentified species. Three out of four species that we observed nectaring carried pollen (typically < 100 grains) on their bodies (Table 1).

Vespidae was represented by three species: *Polistes metricus*, *Polistes exclamans* and *Mesochocyttarus cubicola floridana*. These common visitors obtained nectar and crawled over numerous flowers, but carried no pollen on their bodies (Table 1). However, four bee species – *Colletes* sp. (Colletidae), *Augochloropsis metallica* and an unidentified species in Halictidae, and *Apis mellifera* (Apidae) – were potential pollinators. All of these species carried large loads (> 100 grains) of *Serenoa* pollen (Table 1). *Apis mellifera* visited most frequently, approximately every 30 min to 1 hr at all five inflorescences. *Colletes* sp. and the halictid species were observed regularly at two inflorescences.



6. Mean proportions of saw palmetto (*Serenoa repens*) flowers with receptive stigmas. Flowers were collected May 26–28, 1999. Error bars represent standard errors of means. Numbers above histogram bars indicate sample sizes of flowers collected. Flowers were collected at 10:30 and 13:30 on days 1–5 of anthesis, as noted below histogram bars.

Other species that we observed visiting flowers were a cockroach (Orthoptera: Blattidae), a true bug (Hemiptera: Largidae: *Largus succinctus*) and a beetle (Coleoptera: Coccinellidae); none of these species carried pollen (Table 1). We observed the cockroach at night on one occasion. A thrips species (Thysanoptera: Heterothripidae) and two planthopper species (Homoptera: Flatidae) were common at inflorescences but were not observed visiting flowers. *Notolomus basalis* (Coleoptera: Curculionidae) was common on inflorescence branches. Although we did not observe it visiting flowers, a collected individual had fewer than 100 grains of *Serenoa* pollen on its body (Table 1).

Breeding System. Median fruit set ranged from 0 in treatment (4) to 20% in treatment (5) (Table 2). A Kruskal-Wallis test showed differences in number of fruits produced among treatments ($\chi^2_4=18.58$, $p < 0.001$). Treatment (5), with cross pollination, had higher fruit set than treatment (1), without cross pollination ($0.01 < p < 0.025$). Although no difference in fruit set was detected between treatments (2), with 100% hand pollination (geitonogamy) and (3), without hand pollination ($p > 0.1$), failure to detect a difference may have been due to small sample size.

Discussion

Phenology of anthesis, behavior of insect visitors and results of experimental manipulation of flowers indicated that *Serenoa* has a facultatively xenogamous breeding system. Because *Serenoa* is a clonal species, however, apparent xenogamy may in fact be pollination from genetically

identical ramets. Whereas addition of a hand-cross-pollination treatment may have helped distinguish between xenogamy and geitonogamy, much more work would be required to characterize genotypes of ramets.

Anthesis lasted approximately 4 d, with weak protandry promoting xenogamy or geitonogamy. Although pollination is possible throughout anthesis, probability is highest on the second day. At this time stigmas are most likely to be receptive, and nectar is most likely to be present as an attractant for potential pollinators.

Although *Serenoa* flowers were visited by a wide variety of dipterans and hymenopterans, the primary pollinators appeared to be bees. Bees carrying large loads (> 100 grains) of *Serenoa* pollen regularly visited flowers of every inflorescence observed. In addition to carrying large pollen loads, bees promoted xenogamy by visiting inflorescences of many different *Serenoa* ramets, and by crawling over numerous flowers of each inflorescence. Through this activity, bees not only may pollinate two-day-old flowers while obtaining nectar, but also may pollinate older flowers with receptive stigmas, but without nectar. This behavior is equally likely to result in geitonogamy and self-pollination.

The most prominent insect in this study was the European honeybee (*Apis mellifera*), a likely function of nearby (< 1 km) apiaries. Where honeybees are sparse or absent, native bees are likely the primary pollinators (M. Deyrup, Archbold Biological Station, personal communication). Although we observed little or no pollen on bodies of most flies and wasps, they may cross-pollinate *Serenoa* flowers. Behavior of other insects that remain primarily on one inflorescence (e.g., lovebugs, ants) occasionally may result in geitonogamy or self-pollination.

We conclude from the results of experimental manipulation of flowers that while both geitonogamy and xenogamy are possible, insects are required for effective pollination of *Serenoa* flowers. Treatments (2), (3) and (4) showed that geitonogamy is possible but results in low or only occasional fruit set. The comparison between treatments (1) and (5) demonstrated that xenogamy increased fruit set to normal levels. Three possible explanations for fruit set in treatment (4) are apomixis, pollination of flowers by thrips, and geitonogamy *via* gravity or wind. A caged treatment using insecticide to exclude thrips would help to clarify the mechanism (Baker & Cruden 1991, Kearns & Inouye 1993).



7. Hymenopteran visiting saw palmetto flowers.

Subtle differences in breeding systems exist between *Serenoa* and related, co-occurring palm species. *Sabal etonia* Swingle ex Nash has weakly protandrous, primarily bee-pollinated flowers similar to those of *Serenoa*. Timing of flower opening and anther dehiscence also were similar, but unlike *Serenoa*, anthesis in *Sabal etonia* lasted only 1 day (Zona 1987). *Sabal palmetto* (Walter) Lodd. ex Schult. also has primarily bee-pollinated flowers, but the flowers are protogynous and function only for 1 day (Brown 1976). *Sabal minor* (Jacq.) Pers. has weakly protogynous, primarily wasp-pollinated flowers that function for 1 d (Ramp 1989). *Rhapidophyllum hystrix* H. Wendl. & Drude is usually dioecious, has self-compatible flowers, and is reportedly pollinated by a species of *Notolomus* (Shuey & Wunderlin 1977).

Percentage fruit set for *Serenoa* in this study is low when compared to other palm species (Brown 1973, Ramp 1989), but is comparable to natural *Serenoa* fruit set from other sites. Fruit set from six ramets monitored in two other southwestern Florida sites during a concurrent study ranged

from 2-39%, and averaged 18% (M. Carrington, University of Florida, unpublished data). *Serenoa*'s low fruit set may be the result of a preponderance of pollination by geitonogamy among different genetically identical ramets.

Because *Serenoa* shares pollinating species (notably *Apis mellifera*) with at least the two other bee-pollinated palms, competition for pollinators could occur. However, *Serenoa* has a longer flowering season than either *Sabal etonia* or *Sabal palmetto* (personal observation), its inflorescences are longer-lived (Zona 1987, personal observation), and its flowers are longer-lived (Brown 1976, Zona 1987). All of these characteristics should increase the likelihood that *Serenoa* flowers will receive intraspecific pollen. In addition, we identified only *Serenoa* pollen on insects visiting *Serenoa* flowers, suggesting that constancy of flower visitors was high.

As a result of demand for saw palmetto fruits for medicinal use, interest in fruit harvesting and in establishing commercial plantations has increased.

Results from this study indicate that insect pollination of flowers is an essential component of managing saw palmetto for fruit production. To encourage insect visitation to flowers, land managers should not use insecticides in managed areas during flowering and should reduce or suspend insecticide use in areas adjacent to saw palmettos. Although placing apiaries in or near saw palmetto areas during flowering may increase fruit set, introduced honeybees may out-compete native bee species, thus reducing rates of pollination for other native plant species (Corbet 1991).

Establishment of plantations has been virtually non-existent in the United States, and probably is not needed in the Southeast where extensive areas of wild saw palmettos occur. Where saw palmetto is cultivated in greenhouses, nurseries or plantations, however, this study has shown that opportunities may exist for self- or cross-pollination of flowers *via* hand-pollination.

Annual saw palmetto flowering and fruiting are significant ecological events that attract hundreds of insect species, and provide food for bird and mammal species, most notably the rare Florida black bear. Land managers will face increasing challenges to provide human benefits (i.e., wild fruit picking, enlarged prostate treatment) while conserving biodiversity and ecological phenomena. This study, through reporting on the natural history of flowering and pollination, is a contribution toward this end.

LITERATURE CITED

- BAKER, J.D., AND R.W. CRUDEN. 1991. Thrips-mediated self-pollination of two facultatively xenogamous wetland species. *American Journal of Botany* 78: 959–963.
- BEATTIE, A.J. 1971. A technique for the study of insect-borne pollen. *Pan-Pacific Entomologist* 47: 82.
- BERRY, S.L., D.S. COFFEY, P.C. WALSH AND L.L. EWING. 1984. The development of human benign prostatic hyperplasia with age. *Journal of Urology* 132: 474–479.
- BROWN, K.E. 1976. Ecological life history and geographical distribution of the cabbage palm, *Sabal palmetto*. Ph.D. Dissertation, North Carolina State University, Raleigh, NC, USA.
- BROWN, K.E. 1976. Ecological studies of the cabbage palm, *Sabal palmetto*. *Principes* 20: 3–10.
- CORBET, S.A. 1991. Applied pollination ecology. *Trends in Ecology and Evolution* 6: 3–4.
- FAEGRI, K., AND L. VAN DER PIJL. 1979. The principles of pollination ecology, ed 3. Pergamon Press, Oxford, UK.
- GODFREY, R.K. 1988. Trees, shrubs, and woody vines of northern Florida and adjacent Georgia and Alabama. University of Georgia Press, Athens, GA, USA.
- HILMON, J.B. 1968. Autecology of saw-palmetto (*Serenoa repens* (Bartr.) Small). Ph.D. Dissertation, Duke University, Raleigh, NC, USA.
- KEARNS, C.A. AND D.W. INOUE. 1993. Techniques for pollination biologists. University Press of Colorado, Niwot, CO, USA.
- MAEHR, D.S. AND J.N. LAYNE. 1996. Florida's all-purpose plant, the saw palmetto. *Palmetto* (Fall 1996): 16–10, 15, 21.
- PROCTOR, M.C.F. 1978. Insect pollination syndromes in an evolutionary and ecosystemic context. In A.J. RICHARDS [ed.], *The pollination of flowers by insects*, 105–166. Academic Press, New York, USA.
- RAMP, P.F. 1989. Natural history of *Sabal minor*: demography, population genetics and reproductive ecology. Ph.D. Dissertation, Tulane University, New Orleans, LA, USA.
- SHUEY, A.G. AND R.P. WUNDERLIN. 1977. The needle palm: *Rhapidophyllum hystrix*. *Principes* 21: 47–59.
- TANNER, G., J.J. MULLAHEY AND D. MAEHR. 1996. Saw-palmetto: an ecologically and economically important native palm. IFAS Circular WEC-109, University of Florida, Gainesville, FL, USA.
- ZONA, S. 1987. Phenology and pollination biology of *Sabal etonia* (Palmae) in southeastern Florida. *Principes* 31: 177–182.

Relationship Between *Mauritia flexuosa* and *Eupalamides cyparissias* in the Peruvian Amazon

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In this paper the relationship between *Mauritia flexuosa* and an important moth pest is described.

Mauritia flexuosa L.f., commonly known in Peru as *aguaje*, is widely distributed in the north of South America, principally in the Amazon basin, in an area comprising Peru, Bolivia Colombia, Ecuador, Venezuela, Brazil, the Guayanas, and north to Trinidad and Panama (Henderson et al. 1995).

Eupalamides cyparissias Fab. (Lepidoptera: Castniidae) (also referred to as *Castnia daedalus*, *Eupalamides daedalus* and *Lapaeumides daedalus* (Howard et al. 2001)) is a moth native to South America. It is widely distributed in the entire Amazon basin including Peru, Colombia, Ecuador, Venezuela, Brazil, the Guayanas and north to Panama. In South America the species is known to be a major pest to the economically important palms *Cocos nucifera* L. and *Elaeis guineensis* Jacq. Here we report evidence of four new host palms native to Amazonia – *Mauritia carana* Wallace,

Mauritiella peruviana (Becc.) Burret, *Astrocaryum murumuru* Mart. and *A. javarense* Trail ex Drude. We report on damage caused by *E. cyparissias* to the economically important palm *M. flexuosa* (dwarf ecotype) and suggest natural factors that control the population levels of the larvae in this species.

The present work was carried out between December 2000 and September 2001 in the Peruvian Amazon near the municipalities of Iquitos, Pevás and Mazán in the State of Loreto. Field observations were made on the development stages of the nocturnal lepidopteran, *E. cyparissias* and its activity level at different times of the day, and on damage to one of its host palms, *Mauritia flexuosa*. To determine the infestation rate and patterns on the host plant we examined a total of 21 inflorescences on 16 individuals of the dwarf type of *M. flexuosa* at the three localities. Using a

bisturi and metal screen we identified and recorded the number of infestations present in the basal, middle and apical regions of inflorescences.

The host plant

Mauritia flexuosa grows naturally in swamp areas on poorly drained soils flooded by rains. It forms very dense populations in its natural habitat called *aguajales* and is often planted in agricultural production systems. The palm generally fruits at 7–8 years of age, or when the stem reaches 6–7 meters in height and the internodes measure at least 12 cm (pers. obs.).

In lowland Peruvian Amazon we have observed an ecotype of *M. flexuosa* that starts fruiting at five years, even before the stem has developed or has reached 1 m in height and the internodes are less than 6 cm. These dwarf *aguajes*, known by the Bora Indians as *shapishico aguaje*, grow on upland soils (*tierra firme*) free from the periodic or seasonal flooding characteristic of the *aguajales*. They are always found as solitary individuals and in open areas relatively free of shrubs and trees. The dwarf *aguaje* palm has between 16 and 25 fronds and flowers annually producing from four to seven inflorescences. Each inflorescence produces an average of 442 (s.d. 14.7) ovoid fruits.

Both types of the *aguaje* palm are of major socio-economic importance to the Peruvian Amazon people. The fruits are marketed and consumed directly or as pulp in drinks, popsicles and ice cream. The petiole is used in craft-making, the mat for walls and ceilings in traditional houses, and the stem hosts larvae of the *Rynchophorus palmarum* (Insecta: Curculionidae), commonly known in the region as *suri* and consumed by local people (Padoch 1986, Mejia 1986).

The pest *E. cyparissias* is reportedly found on alternative host palms including *Syagrus romanzoffiana* (Cham.) Glassman, *S. schizophylla* (Mart.) Glassman, *Hyphaene thebaica* (L.) Mart., *Livistona* sp., *L. chinensis* (Jacq.) R. Brown, *Nephrosperma* sp., *Phoenix dactylifera* L., *P. rupicola* T. Anderson, *Pritchardia pacifica* Seemann & H. Wendl., *Sabal* sp., *S. blackburniana* Glazebrook ex Schultes, *S. mexicana* Mart. and *Washingtonia filifera* (Linden) H. Wendl. (Reyne in Schuilting and Van Dinther 1980), *Attalea maripa* (Aubl.) Mart. and *Roystonea regia* (Kunth) O.F. Cook (Van Dinther in Schuilting and Van Dinther 1980), *Mauritiella peruviana* (Becc.) Burret, *Astrocaryum murumuru* Martius and *A. javarense* Trail ex Drude.

The pest

The adult of *E. cyparissias* is a nocturnal lepidopteran with a robust body measuring

140–180 mm in wingspan. Its flight activity was observed to occur between 5:30 and 6:30 in the morning and 5:30 to 7:00 in the evening. The eggs are gray, oval, with deep furrows, and measure 5–6 mm in length. The larva is 110–130 mm in length, and in its primary stages feeds on the surface of petiole, scratching the epidermis and then perforating the interior. The pupa measures 64–95 mm in length and is contained in a compact cocoon formed of fibers of the palm itself (Mariau 2000). On the dwarf *aguaje*, the pupal stage is found at the base of the petiole. The larvae of *E. cyparissias* damage the peduncle, rachis, rachillae, petiole and, rarely, the stem of the *aguaje* palm. Larval activity can be recognized externally by the presence of excrement near the feeding tunnels and by the gummy secretions emitted by the plant as a physiological response to herbivory. The larvae produce sinuous tunnels up to 2.5 m in length and 3.5 cm in diameter with irregular borders. The tunnels interrupt the flow of water and nutrients in the plant, thus causing premature senescence of the flowers or fruits whose fall is aided by light winds. When the infestation occurs at early stages of raceme development all flowers or fruits are lost. At advanced stages of development, however, fruit loss is only partial.

Of the 21 racemes observed in the three regions, 19 (90.5%) hosted the *E. cyparissias* larva. When we compare the infestation rate on racemes from the three areas we find the highest in Pevas at 100%, followed by Iquitos at 90% and Mazan at 83%. These results show that the insect pest is widely distributed and well represented in the areas studied. The small differences in infestation rate between areas sampled, none statistically different (Chi-squared = 1.76; 2 d.f.), may correspond to the behavior of *E. cyparissias* and may be an artefact of having sampled the areas during different seasons.

The distribution of damage by *E. cyparissias* along the length of the inflorescence is not significantly different (Chi-square = 1.97; 2 d.f.), although the highest rate was found in the basal region (39.7%), followed by the middle (34.9%) and apical (25.4%) regions. There is a marked preference (although not tested) for the initiation of attack at the base of the inflorescence; from there, as the larva develops, it migrates towards the inflorescence apex, even when there is enough food nearby.

Population regulation of *Eupalamides cyparissias*

In a single inflorescence several adults may oviposit at different times. Although an inflorescence may host up to eight larvae at different development stages, we suggest that only

one of these will complete its development to adulthood. While the average diameter of an *aguaje* inflorescence is greater than 10 cm, the maximum width of the feeding tunnel was only 3.5 cm. The average length of an inflorescence is 3.2 m and a single larva can burrow tunnels of up to 2.5 m in length in one year (average duration of the larval stage). When these measurements are considered, there should be a sufficient food supply in a single inflorescence for several larvae to develop to adulthood. However, we never found this to be the case; all inflorescences observed hosted only one larva. We observed that when two or more tunnels meet in the inflorescence the larva at a more advanced stage predated the smaller one. This phenomenon suggests that larval cannibalism is one factor that regulates population levels in the *aguaje* raceme. This finding is in contrast to the physical-chemical factors found at the adult level in other insect groups where, using neurophysiological mechanisms, the female chooses an adequate location for oviposition and the development of the larva (e.g., Wildermuth 1993).

These observations lead us to suggest that space, or food availability, is the limiting factor for the growth and development of multiple larvae in a single inflorescence. During this study we encountered no natural enemies associated with any developmental stage of the *aguaje* pest *E. cyparissias*; thus, natural predators and parasites do not have a major role in its population regulation. However, in plantations of *Elaeis guineensis* and *Cocos nucifera*, the wasp *Ooencyrtus* (Hymenoptera: Encyrtidae) and the ants *Odontomachus*, *Pheidole* and *Iridomyrmex* (Hymenoptera: Formicidae) were reported to parasitize and predate the eggs of *E. cyparissias* (Mariau 2000)

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LITERATURE CITED

- HENDERSON, A., G. GALEANO AND R. BERNAL. 1995. Field Guide of the Palms of the Americas. Princeton University Press, New Jersey, USA, 352 pp.
- HOWARD, F.W., D. MOORE, R.M., GIBLIN-DAVIS AND R.G. ABAD. 2001. Insects of palms. CAB International, Wallingford, 400 pp.
- MARIAU, D. 2000. La faune du palmier à huile et du cocotier. 1. Les lépidoptères et les hémiptères ainsi que leurs ennemis naturels. Montpellier, France, CIRAD-cp, 97 pp
- MEJIA, K. 1986. Utilization of Palms in Eleven Mestizo Villages of the Peruvian Amazon (Ucayali River, Department of Loreto). Advances in Economic Botany 6: 130–136.
- PADOCH, C. 1986. Aguaje (*Mauritia flexuosa* L.f) in the Economy of Iquitos, Perú. Advances in Economic Botany 6: 214–224.
- SCHUILING, M. AND J.B.M. VAN DINTHER. 1980. Ecology and control of *Castnia daedalus*, a major pest of oilpalm in Brazil. Sonderdruck Band 9: 161–174.
- WILDERMUTH, H. 1993. Habitat selection and oviposition site recognition by the dragonfly *Aeshna junea* (L): an experimental approach in natural habitats (Anisoptera: Aeshnidae). Odonatologica 22: 27–44.

Pritchardia *pacifica* Crown Droop

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1. *Pritchardia pacifica* with crown droop (NTBG # 860148.002).

Crown droop in *Pritchardia pacifica* is a puzzling phenomenon without obvious cause.

The National Tropical Botanical Garden (NTBG) has an extensive *Pritchardia* conservation collection as a core element of its conservation, science and educational goals (Chapin & Lorence 2000, Chapin et al. 2001). This developing collection endeavors to capture the genetic diversity of wild Hawaiian and Pacific sources by representing as many individuals and populations as possible (Chapin et al. in press).

In September 2001, we noticed a *Pritchardia pacifica* with its crown drooping. This became a cause of great concern because of the possibility that it might be caused by a disease or pest that could spread to the extensive *Pritchardia* conservation collections in the garden. With the use of a cherry picker, the area horticulturalist, Mark Chaffee, examined the crown. We fully expected a report requiring removal of the tree. Instead, Mark described all of the leaves as being green with no browning of the leaf edges. A leaf sample was taken for analysis. With regular visits to monitor its progress or decline, the authors noticed none of the flowers or fruits aborting, no leaf die back occurring, leaf color remaining green; apart from facing downward, it was an apparently healthy crown (Fig 1). We made inquiries with the North American Palm Curatorial Group (NAPCG) (Chapin et al. 2002a), and discovered that only three people in Hawaii had observed crown droop before, once on "Restaurant Row" in Honolulu, and currently at a car dealership in Lihue, Kauai. Inquiries with the car dealership's manager revealed that no known treatment was given to the trees. The drooping crowns of the trees in Lihue by the car dealership righted themselves within nine months. In Restaurant Row, Mr. Desmond Ogata of the University of Hawaii, Agricultural Diagnostics Service Center (ADSC), ran a series of tests to identify a disease agent but was unsuccessful. The ADSC insect clinic



2. Close up of the crown of the same palm shown in Fig. 1.

was also unable to identify any insects, specifically mites, that could have caused the damage. These trees also righted themselves after an unspecified amount of time. We also heard that individuals of both *P. pacifica* and *P. thurstonii* had developed crown droop in a hotel landscape in Hawaii, and the trees were cut down.

Our tree was injected with 20 ml of potassium phosphite (H₃PO₃; Formula 1, Magna-Gro Corp, Carson City, NV). A 60 ml eccentric tip disposable plastic syringe modified to maintain a slight pressure on the solution was filled with potassium phosphite inserted into a tight fitting hole about 5 cm deep, drilled at a slight downward angle about waist height on the trunk and pressurized.

Table 1. Nutritional analysis of two seedlings, one healthy tree, and the same tree with "crown droop" during and after recovery.

Habit & Health	Origin	Date Analyzed	P	K	Ca	Mg
Healthy Seedling	NTBG Nursery 1 (000504)	05 Sep. 2001	0.28	2.50	0.28	0.26
Healthy Seedling	NTBG Nursery 2 (000504)	05 Sep. 2001	0.27	3.02	0.29	0.27
Healthy tree	NTBG Lawai (860148.001)	05 Sep. 2001	0.32	2.13	0.21	0.28
Tree with crown droop (during droop)	NTBG Lawai (860148.002)	05 Sep. 2001	0.33	2.32	0.23	0.29
Tree with crown droop (after recovery)	NTBG Lawai (860148.002)	08 Oct. 2002	0.22	1.98	0.30	0.43

The solution was taken up by the tree in about 20 minutes. One of us (JO) has adapted this technique for preventing *Phytophthora* heart rot of coconut caused by *Phytophthora katsurae*. This technique is widely used to control *Phytophthora* root rot of avocado (Coffey 1987, Darvas et al. 1984).

Samples of the afflicted tree, a neighboring tree of the same seed source but healthy, and leaf samples from two young seedling *P. pacifica* palms from the NTBG nursery were sent to the ADSC. The only detectable possibility was a boron deficiency, which is consistent with descriptions and illustrations in Broschat and Meerow (2000). Another suggestion was pesticide overspray but this could not be confirmed. No pests, parasitic bacteria, fungi or diseases were detected by the ADSC.

The NTBG tree corrected itself and returned to a healthy appearance after one year. Another leaf sample was taken from a newer but developed leaf in the crown and sent to ADSC for analysis. The results from the initial samples and the recent sample are shown in Table 1.

The etiology of this condition remains unknown. It is also unknown if other palm species or genera are similarly afflicted. The authors seek accounts of observations similar to this and the causative agents.

Acknowledgments

We thank Mark Chaffee for collecting leaf samples and Mike Maunder for his guidance as we

examined this tree and for discussions on the implications of crown droop.

LITERATURE CITED

- BROSCHAT, T.K. AND A.W. MEEROW. 2000. Ornamental palm horticulture. University Press of Florida, 256 pp.
- CHAPIN, M.H. AND D.H. LORENCE. 2000. Developing a tropical botanical garden palm collection. PALMS 44: 121–126.
- CHAPIN, M.H., D.H. LORENCE, S. PERLMAN AND K.R. WOOD. 2001. Support for the conservation of endemic Pacific palms through ex situ collections at the National Tropical Botanical Garden, Hawaii, USA. Botanic Gardens Conservation News 3(6): 46–48.
- CHAPIN, M. H., M. MAUNDER AND P. ALLENSTEIN. 2002a. Conservation value and status of *ex situ* palm collections in North American botanical gardens. AABGA Meeting 2002.
- CHAPIN, M.H., K.R. WOOD, S.P. PERLMAN AND M. MAUNDER. in press. The conservation status of the endemic *Pritchardia* (Arecaceae) palms of Hawaii. Oryx.
- COFFEY, M. D. 1987. *Phytophthora* root rot of avocado – an integrated approach to control in California. Plant Dis. 71: 1046–1052.
- DARVAS, J.M., J.C. TOERIEN AND D.L. MILNE. 1984. Control of avocado root rot by trunk injection with phosethyl-Al. Plant Dis. 68: 691–693.

Table 1., continued.

Na	Mn	Fe	Zn	Cu	B
0.16	104	56	11	15 1	6
0.14	157	57	11	17	13
0.22	22	35	12	19	13
0.13	17	34	13	21	13
0.11	27	85	7	8	20

PALM LITERATURE

PALMS WON'T GROW HERE AND OTHER MYTHS: WARM-CLIMATE PLANTS FOR COOLER AREAS. By David A. Francko. Timber Press, Portland, Oregon. 2003. ISBN: 0-88192-575-6. US\$27.95, hard bound. pp. 267.

Author David A. Francko's obsession is beyond therapy. By his own admission, all hope of recovery vanished when he saw a specimen of *Rhapidophyllum hystrix* growing in Cincinnati, Ohio, in the early 1990s. Since then, he has been obsessed with growing southern plants in his decidedly northern landscape. His mad pursuit is given full rein in his book with the attention-grabbing title "Palms Won't Grow Here and Other Myths: Warm-Growing Plants for Cooler Areas."

The book includes four chapters on basic garden design, plant hardiness, zone maps, and microclimate. It is a very personal account of his gardening successes, written in a friendly, accessible style. Chapter 5 is "Cold Hardy Palms." Chapter 6 discusses broadleaf evergreens. Chapter 7 is given over to deciduous trees and shrubs, while the final chapter is devoted to bamboos, bananas, yuccas, agaves and a few miscellaneous plants. Seventy nine color plates are grouped together after Chapter 2, but halftone illustrations occur throughout the book. The photos are not up to Timber Press' usually high standards.

IPS members in the cooler areas or those in areas subjected to rare but devastating cold spells will want to take note of Francko's strategies for "winter care" (Chapter 4). These can be elaborate – wrapping plants with water-proofed batting, building temporary wind breaks and covering them with mulch – or they can be as simple as throwing a blanket over a tender specimen. They are useful techniques for protecting valuable specimens during cold weather.

Francko's discussion of hardy palms (Chapter 5) rounds up the usual suspects for growing in the temperate zone. His most novel idea is the use of palms as "die-back perennial shrubs." *Livistona chinensis* is said to perform admirably in this respect. *Livistona chinensis* as a shrub? I could not help but wonder whether palms that are killed back to the bud year after punishing year will grow back every summer. Is this method truly sustainable? Is it a realistic way of using palms as herbaceous perennials? Time – and adventurous palm growers – will tell. He recommends *L. chinensis*, *Phoenix roebelinii* and *Chamaedorea radicalis* for the die-back regime, but I still suspect that plants growing under such taxing conditions would never look their best.

My biggest complaint with the book is the lack of a clear definition for his "North-by-South" landscaping concept. He says it is about growing southern plants in northern landscapes, but as we all have plants from other latitudes growing in our gardens, this distinction seems trivial. He claims that he is not specifically aiming for a tropical style of landscape design, and his inclusion of temperate oaks, cherries and hydrangeas backs up that claim, but again and again, he extolls the tropical look and feel of palms, bananas and bamboos. He really seems to want a tropical garden in Ohio. I read the book, took careful note of his recommended species, and still I do not know what a "North-by-South" landscape is or how it differs from other landscapes. Not until p. 165 did I learn that one of the goals of the "North-by-South" landscape is to have flowers throughout the year. The definition seems as elusive to the author as it is to the reader.

I caught myself grumbling at minor errors of fact in the book: There are not just ten USDA hardiness zones in North America (his own map shows eleven). Ammonium is not the preferred form of nitrogen for most plants (plants absorb nitrate nitrogen). There is not just one species of *Passiflora* native to the USA (seven are native to Florida). Minor errors like these detract from the authoritativeness of the book. There are a couple of instances where Francko uses scientific names that have no botanical standing, so readers looking for those plants by those names will draw blank looks from nurserymen. Despite Francko's introductory admonitions that hardiness is a difficult issue to quantify, he routinely falls into the trap of saying that this species or that is hardy to X°F, when he knows full well that hardiness depends on microclimate, cold duration, plant condition, genetic background and other factors. Hardiness cannot be simplified to a minimum temperature on a thermometer somewhere in the vicinity of the plant. His claim that he uses a scientific approach to cold hardiness is simply not justified.

In the end, I sympathize with Dr. Francko. I would willingly give certain expendable body parts to grow tulips, irises, and delphiniums here in Zone 10. Gardeners in every USDA Hardiness Zone long for the unusual, the exotic, be it "North-by-South" or "South-by-North." For anyone living in a cold climate and wanting to grow palms, this book may awaken an obsession that no therapist can touch.

SCOTT ZONA
FAIRCHILD TROPICAL GARDEN

***Borassus heiniana* from the Sepik Region of Papua New Guinea**

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1. A 30 m tall individual of *Borassus heiniana* towering over the village of Maramba: notice the villagers at the foot. The palm was grown from a seed planted about 60 years ago as a symbol of the ties between the old settlement, Kamangauwi Village, near the main population of *Borassus heiniana*, and the new settlement in Maramba Village.



Every palm collector knows, that when he stumbles across a rare population of palms, he must take action immediately – tomorrow the chance of collecting may have passed. But it is not always enough to put your own sweat, blood and money into the work; sometimes you also have to overcome the malevolent spirit that seems to follow the palm and bring bad luck to the collector.



2. Close-up of the *Borassus heiniana* palm in Fig. 1, with several immature infructescences.

My story takes its beginning in a village named Maramba. It is remotely situated in a vast, swampy blackwater area, south of the Middle Sepik River in Papua New Guinea. It was one of the numerous localities I visited in my pursuit of data for my Masters thesis on the sago palm, *Metroxylon sagu*.

Already before my arrival at the village, my interest in palms was obvious, and my local companions had urged me to see a single palm individual, which grew in the centre of the village. The first couple of days my sago project kept me busy, but on the third day we ventured out to see the fantastic palm, which in the meanwhile had

grown to monstrous dimensions in the stories of the village people. Working in PNG had taught me to hold my horses and not expect too much, so I was ready for disappointment.

To my great joy and amazement, a majestic fan-leaved palm towered over the low stilt huts (Figs 1, 2). It stood more than 30 meters tall on a trunk with a diameter of about 45 cm. My first impulse was that I had encountered a species of *Livistona* far away from home. But on better inspection, the deeply split petioles revealed that I had an individual of the rare, but famous *Borassus heiniana* on my hands.

The palm held a number of apparently immature infructescences. The villagers told me that these fruits would fall off when they were still green and chicken egg-sized, and that all germination attempts had failed. Half joking, I suggested that we should cut it down for collection. Judging from the faces of the people, this was *not* a joking matter. They told me the story of the palm, which left me breathless.

About 60 years ago a couple of clans from a distant village decided to settle down in the swamps. With them they brought a single palm seed, which was planted in the middle of the settlement. The palm held great significance as a monument of the ties between the new and the old villages. When a new spirit house was recently built (the old one had been burnt down by missionaries), it was decided to use leaves of *Borassus* palms as thatch and wall material (Fig. 3). Further reading will reveal that the journey to the mother population is long and laborious. Nonetheless, more than 20 canoe loads of *Borassus* leaves were brought down the stream.

I organised an expedition to take me to the distant palm population the following day. Starting before sunrise, we had the obligatory one hour's waiting for everybody to get ready. One and a half hour's

motor canoe ride brought us to our landing site on the northern banks of the huge main river. Ahead of us lay 15 km of walking through wide stretches of flat Kunai grassland with thick forest and sago swamps in the waterlogged depressions. The first 10 km of wandering in the merciless tropical sun put the sweat glands of my poor white skin on extra duty. The entry in a patch of forest brought shade and great relief to everybody. During a short rest, a few individuals of *Arenga microcarpa* were cut, and the palm hearts were devoured with great pleasure. Apart from a multitude of this often-collected palm, only a few other palms had found their way through the grassland to this patch of forest. A number of *Gulubia costata*, *Ptychosperma* sp., and a single individual of *Licuala lauterbachii* were observed – and, of course, thousands of individuals of the king of the swamps, the sago palm. This spiny and colossal palm completely dominates the wettest depressions and makes passage a nightmare.

A stretch of about 200 meters went through a swamp that was so deep that it was impossible to wade to the other side, but fortunately a large number of smaller and larger trunks had been laid out as bridges. Some of the trunks would stay on

3. The "Spirit House" in Maramba Village. More than 20 canoe loads of *Borassus* leaves were brought the long way down the Sepik River to built the house in the traditional ways of the ancestors. Large parts of the roof and the pale parts of the walls was constructed with *Borassus* leaves, and for the rest, sago leaves were used.





4. Field assistant David Hambut with a leaf and an infructescence of *Borassus heiniana*.

the surface when trodden on. Others would sink in the water until they reached support in the mud. Almost safely arrived on the other side I slipped and landed with a leg on each side of a slippery log. My first alarming thought was: NOTEBOOK !!, and within a split second I was on my feet again, fumbling in my pocket for the precious book. Luckily I had thought of putting it in a plastic bag and it was safe, a destiny unfortunately not shared by my now dripping cigarettes.

Soon we arrived at the village of Kamangauwi and hundreds of people gathered to see the white "Masta," who was in town. After a short intro-

duction we were allowed to search the lands and collect any number of palms we wished. Going west of the village, we soon encountered the first juveniles of the stand. Scattered with distances of 25–50 meters, we found a number of half-grown and full-grown individuals, but none in flower or fruit. The large group of young men, who followed us, had spread out in all directions looking for flowering material. Judging from my own walking distance and the distant negative reports from searching villagers, I estimated the size of the stand to be about 300 × 300 meters.

A positive report brought us to an individual with ripe fruits. It stood 12.5 meters tall measured to

the base of the crown, which consisted of 20 bluish green leaves. Making scientific collections proved to be hard work, especially in liberating the infructescences, which were covered at the base by the leaf sheaths. The leaf sheaths did not form a crown shaft, but were split 50 cm along the backside. From the base to the end of the brown, fibrous petiole edges, the sheaths measured 1.3 m. Ignoring the warnings, I soon found myself with a blood dripping hand, caused by the very sharp edges of the 1.5–1.8 m long petioles.

Head-shaking, I looked at the 3 enormous leaf sheaths I had decided to collect, but ventured on with the collection of the even larger leaf blades. Measured from petiole to tip, the blade was 2.3 m long, of which the costa occupied 40 cm. The blade measured 3.2 m across, and consisted of a total of 78 segments. Between each segment were deep incisions and at the tips were short incisions (Fig. 4).

Turning to the infructescences, I realised what a task I had taken on my shoulders. The crown bore three infructescences, ranging from ping-pong ball sized green, immature fruits to ripe, black fruits, which were 11 cm long and 9 cm wide. The slightly triangular fruits contained 3 seeds (in some 1–2 seeds were aborted), which were contained in whitish husk, covered by a shiny, black skin. Each of the infructescences bore 30–40 fruits and had a rachis length of 50 cm and a peduncle length of 80 cm. All in all the collection of this one individual filled up 4 large plastic bags and weighed around 20 kg.

This could have been the happy end of a successful collection, but still many hours of travelling lay between me and my base in the National Herbarium in Lae. As mentioned already, this palm was apparently protected by a malevolent spirit, causing bad luck to its enemies. I had already cut my hand on the sharp petioles, and on our way back I did not manage to pass the deep swamp unscathed, but took a muddy and smelly dive from a rolling trunk. As I knew that I would soon enough dry in the burning sun in the grassland, I took it with a smile. Only I was not the only one to enjoy the sun on the dirt track, and only a quick performance of my later so famous “there

is a two meter long snake between my legs dance” saved me from a poisonous bite.

When we arrived safely at the riverbank, our boat driver informed us that he had bought sufficient fuel for the five hour canoe ride to the district capital, Angoram. But after a few hours ride, the sound of a dying engine told me that the gallons you buy in that place apparently were much smaller than normal gallons. Left with only the weak current as drive, we spent the whole night drifting through the millions of mosquitoes that feasted on our blood. In Angoram, I was presented with the next challenge; palms of this size does not fit very well into standard newspaper sheets. Two hours were spent trying to make the various palm parts stay inside the sheets long enough for me to place them in plastic bags with methylated alcohol. The four-hour car ride on stony roads to the provincial capital, Wewak was strenuous but without major event. The arrival at this civilised town might again have brought an end to this story, but the malevolent spirit was still on my tail.

As my luggage already consisted of my field gear and three big bags of palm material, I had to make arrangements for some of the bags to be forwarded to Lae by air freight. Not very confident about this, I flew to Lae. The following day I received the depressing news that the aviation authorities had closed Wewak Airport for jet-size air-planes, and only small carriers were permitted to land during repair work to the runway. Now 300 km of tropical country separated me and my palm collection. Not until the next day, I had a new receipt for the airfreight of the package and a promise of arrival the following morning. Unfortunately the collection had to change air-plane midway, but I was confident that I had managed to shake off the malevolent spirit. I could not be more wrong, as the palm *did* disappear. After radioing five different airports, the official finally found it in the Highlands town Goroka. Two more days in anxiety went by, and the precious collection finally arrived in Lae. To dry the large fruits, I had to drill holes in each seed, but still it took a full week. The malevolent spirit finally seemed to have lost his breath.

Anomalous Crown Growth in *Pritchardia* *napaliensis*

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1. Wild *Pritchardia napaliensis* growing in the largest population in Hoolulu Valley, Kauai, Hawaii. Photo: Steve Perlman.

An unusual crown growth of *Pritchardia napaliensis* is described and documented from ex situ collections at the National Tropical Botanical Garden. The cause is unknown. Greenhouse experiments where the growing meristem has been mechanically and chemically treated have been set up in an attempt to reproduce the anomaly. The authors having not seen this in the wild or in cultivation seek responses from readers who have observed this same phenomenon.

There are thought to be 22 species of *Pritchardia* endemic to Hawaii and each species is confined to a single island (Beccari & Rock 1921). St. John described *Pritchardia napaliensis* based upon a specimen collected by Charles Christensen on Kauai in 1976. He named this plant for the Na Pali Coast of Kauai where it was first collected (St. John 1981). *Pritchardia napaliensis* is a small palm with about 20 leaves and an open crown. It belongs to the *P. remota* complex which Read and Hodel (1990) define as only distinguishable from each other with difficulty, and they include four species in this complex. *Pritchardia napaliensis* typically grows in habitats ranging from mesic forests to montane wet forests from 150 to about 1,160 m (500 to about 3,800 ft) elevation. The largest population in Hoolulu Valley contains between 60 and 80 plants and the two other populations, Pohakuao and Hanakoa each contain three or fewer plants, giving a total of fewer than 90 known wild individuals. It is ranked as endangered by the USFWS (Wagner et al. 1999).

The National Tropical Botanical Garden (NTBG) has 36 plants of *P. napaliensis* from a seed collected by Steve Perlman in 1990 from the wild population in Hoolulu Valley, Kauai, Hawaii (Fig. 1) and planted in 1993 in a garden site within the McBryde Garden of NTBG.

2. *Pritchardia napaliensis* exhibiting a multiple crowned growth habit in NTBG's *ex situ* collections. Photo: M.H. Chapin.



Of these 36 trees, 31 have anomalous crown growth that appears to be a form of leaf suckering from the growing tip (Fig. 2). Five palms do not have the suckering crown habit. The solitary stem is still developing normally. In addition, a nearby *Pritchardia munroi*, planted in the same year, also has a suckering crown, which is equally unusual (Wood et al. 2001). This crown growth anomaly has never been seen or documented in wild *P. napaliensis* or any of the Hawaiian *Pritchardia* species or in *ex situ* palm collections.

It is unclear what caused this unusual crown growth. The authors considered physical damage either by insects or gardening tools, or chemical damage such as herbicide overspray. In an effort to understand better what caused this and to attempt to induce the same suckering crown development, 25 seedlings of *P. pacifica* and *P. arecina* were selected. They have been included in a greenhouse experiment and subjected to two treatments. Five seedlings of each taxon have had their growing tip sliced vertically with a razor, and the area treated with fungicide. Five seedlings of *P. pacifica* were sprayed with 2,4-Dichlorophenoxyacetic Acid (2,4-D). Five seedlings of each species are being used as controls. It may take several years to see the results.

We welcome new information or similar observations from our readers and we will continue to monitor this unusual growth habit in *Pritchardia*.

LITERATURE CITED

- BECCARI, O. AND J.F. ROCK. 1921. A monographic study of the genus *Pritchardia*. Memoirs Bernice P. Bishop Museum 8: 1-77.
- READ, R. AND D. HODEL. 1990. *In*: WAGNER, W. L., D. R. HERBST, AND S. H. SOHMER. 1990. Manual of the flowering plants of Hawaii. Vol. 1-2. Bishop Museum Press, Honolulu, Hawaii 83: 45-114.
- ST. JOHN, H. 1981. New species from Kauai. Hawaiian plant studies 97. Pacific Science 35: 97-103.
- WAGNER, W.L., M.M. BRUEGMANN, D.M. HERBST AND J.Q.C. LAU. 1999. Hawaiian vascular plants at risk: 1999. Bishop Museum Occasional Papers. Bishop Museum Press, Honolulu. No. 60, 58 pp.
- WOOD, K.R., S. PERLMAN, M.H. CHAPIN AND M. MAUNDER. 2001. Critically Endangered Hawaiian Plant Taxa & Conservation Collections within the Genetic Safety Net (GSN). Interim Report on Field Research Conducted Under USFWS Grant No. 122000G001.

OBITUARY

KENNETH (KEN) C. FOSTER

Ken Foster, 73, died Friday morning December 13th, 2002, at St. Francis Medical Center in Honolulu, Hawai'i, after a lengthy battle with cancer and heart problems.

Ken, who was born in Massachusetts, had been very active within the IPS, as well as with local chapters in Southern California, Florida and Hawai'i for most of his adult life. His IPS involvement included two years as President in the 1970s. Ken and Don Hodel made a number of collecting trips in the late 1970s, primarily to islands in the southwest Pacific. Thanks to their efforts we now have many unusual and mature palms from Fiji, New Caledonia, Papua New Guinea and other islands here in Hawai'i. For the last twelve years or so, Ken lived on the island of Hawai'i. He was a very active member of Hawai'i Island Palm Society (HIPS) and served as Vice President from 1999 to 2001. His knowledge about palms was extensive, and he was often asked to act as guide on various garden tours.

I first met Ken in 1994 on one of my visits to the Big Island of Hawai'i. At the time I lived in Poway, California, and was planning to move to the Hilo side of the Big Island. Ken, and his wife, Ruth, lived in Kalapana, about a half mile away from the Pacific Ocean. Ken had an incredible collection of about 800, mostly unusual, palms in containers up to 25 gallon size. He was meticulously taking care of his collection in anticipation of being able to buy a couple of acres at a higher elevation, and plant them. My wife, Karolyn, and I made the move to Hawai'i in late 1995, and settled in Leilani Estates, about 6 miles from Kalapana, around the 750 foot elevation. Shortly after we had finished building our house, Ken and Ruth bought a house on two heavily wooded acres, also in Leilani Estates. Ken was thrilled at the prospect of finally being able to put his collection in the ground. We now lived about a mile apart, and I had the opportunity to talk palms with Ken several times a week.

A few years later, Ken underwent heart surgery. Unfortunately, for all practical purposes, this also meant an end to his palm planting days. He was able to continue with his seed business – collecting, cleaning and selling palms seeds – and this kept him active, despite his health problems. In 2001, however, he accepted his limitations, and he and Ruth decided to sell the property. Jerry and Cindy Andersen from San Clemente, California, bought the property, and the fact that another “palm person” bought it was a source of great satisfaction to Ken.

Because of Ken's increasingly frail health, he spent close to a year in Houston, Texas, where he was close to his son, Will, and had access to excellent medical facilities at the Veterans Administration hospital. He was determined to return to Hawai'i, however, and came back in September 2002. His intention was to live on the island of O'ahu, in order to be close to Tripler Army Hospital, but he also visited the island of Hawai'i a few times in September and October 2002. I flew over from Hilo to Honolulu on November 15th and spent half a day with Ken. By sheer coincidence, he had been released from the hospital the day before, so we were able to drive around to a couple of his favorite places. Ken had lost a lot of weight, and was very weak, but certainly hadn't lost his interest in palms. He commented on a number of palms we saw, including some that had mature fruit, that was obviously just going to fall to the ground and go to waste. In Ken's eyes, this was the ultimate form of waste! Within a week of my trip over there, he was back in the hospital, and his condition quickly deteriorated to the point that he couldn't even speak on the telephone. Four weeks after I saw him, he quietly passed away.

Ken's love and enthusiasm for, knowledge of, and dedication to palms was unique and he will be truly missed by all those who were fortunate to know him and spend time with him.

BO-GÖRAN LUNDKVIST
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Editors' Note: A remembrance of Ken Foster by Don Hodel will appear in the next issue of PALMS.

OBITUARY

U.A. YOUNG

Ulysses Alexander Young IV (81 years old), one of the founding members of the International Palm Society and a past president, died on Thursday April 10, 2003. He was a native of Lubbock County, Texas, who moved to Tampa in 1954 and started gardening right away. His garden was full of more typical common landscape plants in the beginning, but on completion of his garden, the Youngs visited Fairchild Tropical Garden in Miami. He was so inspired that when he came home he made plans for the removal of his common landscape plants to make room for the rare palms that he had seen at Fairchild Tropical Garden. While he did buy a few palms for his collection, he grew most from seed. The Youngs travelled the world and collected many of the treasures in their garden. All have a story behind them. Many people from all over would come to see their garden of palms and cycads. Their garden was a home owner's version of Fairchild Tropical Garden in miniature, but the Youngs were lucky to have four city lots. In fact when they moved into their home there were dirt roads and few of the houses that now exist in the up-scale neighborhood.

Another hobby of Dr. U.A. Young was wood-turning. He would create some of the most exotic pieces from rare woods collected around the world. He would often enter his pieces in the Florida State Fair.

U.A. Young was one of the kindest, most generous people that one could meet. Several years back

before his health started to decline he would give tours to anyone who wanted one or anyone who showed up on his doorstep. He would give most people some of his surplus plants and spread his enthusiasm to countless other people. Many doctors around town collect palms and cycads because of his influence. One thing that always amazed me was that Dr. Young never spoke a bad word about anyone. He chose to talk only about the good – a most admirable trait.

I can remember the first time that I really had a chance to look at all of the plants more closely in his garden was after the 1983 freeze. His garden was devastated by this and the following freeze the next winter, but I saw what had survived and was greatly impressed. His garden was a good learning tool for me and many others in Central Florida. I began working for Dr. U.A. Young around 1986 and continued for more than 14 years. I never lost the respect and admiration that I had for him from the start.

He had to be careful with his hands since he was an orthopaedic surgeon. But he retired about this time and began to relax and enjoy his well earned retirement and garden. Within a couple of months of working with him I had his garden in good shape and was grateful that Dr. Young would come out and work with me on occasion. He really enjoyed his palms; they were his first love. He will be missed by many.

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