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THE INTERNATIONAL PALM SOCIETY

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PRINCIPES

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Cover Picture

The endemic *Roystonea violacea* with its violet-brown trunk near Río Maya, Maisí, eastern Cuba. Photo by Scott Zona. See p. 225.

PRINCIPES

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Editorial

Don Hodel brings to a close the series of articles on the taxonomy of *Chamaedorea* in which he validates the names of new species and clarifies past confusions. This is, of course, as a precursor to his magnum opus, the *Chamaedorea* Book. By validating new species in *Principes*, he has saved us all having to read Latin in his book.

Two articles in this issue deal with pests and diseases of palms. The first is concerned with the cane weevil borer, a pest of sugar cane in Queensland. This beetle has begun to affect palms in Queensland and the effects can be quite serious; palms may be severely disfigured or even die as a result of infestations. Ironically, the pest was not nearly so serious when cane farmers burnt their fields prior to harvesting. The current practice of not burning has allowed the pest population to increase and the dramatic increase of palm cultivation has provided hosts for the weevil. The other article deals with that most serious of palm diseases, lethal yellowing. Colleagues from Mexico provide an overview of the physiology and biochemistry of the disease; this is complex and should emphasize just how difficult it may be to control the disease.

From Mexico we have an article by Hermilo Quero on a new species of *Sabal* from Yucatan. Although the genus has recently been monographed, this novelty has been discovered, illustrating that even in well known genera, new taxa may be discovered during careful field work.

Perhaps most exciting for the grower is Scott Zona's account of *Roystonea* in Cuba. The front cover, illustrating *R. violacea*, provides evidence of the majesty of these spectacular palms.

Sadly we record by obituary the deaths of two long serving members. Ruth Schatz, a founder member, will be remembered for her long service to the Society. T. A. Davis was a tireless worker on the economically important palms of southern India who contributed many articles to *Principes*.

JOHN DRANSFIELD
NATALIE W. UHL

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The Cultivated Species of *Chamaedorea* with Cespitose Habit and Pinnate Leaves

DONALD R. HODEL

University of California, 2615 S. Grand Ave., Suite 400, Los Angeles, CA 90007

The cultivated *Chamaedorea* with cespitose habit (multiple or clustered stems) and pinnate leaves are among the most handsome, useful, and widely grown species of the genus. They are found in four of the eight subgenera that comprise *Chamaedorea*. This paper features those in subgenus *Chamaedoropsis* since they are widely cultivated but often misidentified. In addition, a name for a new species with cespitose habit and pinnate leaves, but in subgenus *Chamaedorea*, is proposed here since the new species is very similar in habit to and easily confused with those species in subgenus *Chamaedoropsis*. A combination of characters, including solitary inflorescences, solitary, regularly spaced staminate flowers with apically free petals, and black fruits, distinguish subgenus *Chamaedoropsis* from other subgenera in *Chamaedorea*. Staminate flowers with the petals connate apically and there adnate to the pistillode and the corolla opening by lateral apertures distinguish subgenus *Chamaedorea*.

There are other cultivated species with cespitose habit and pinnate leaves but I touch on these other species only briefly though, since they have vegetative characters that readily distinguish them from those species featured here. In addition, several of the other species are in different subgenera and thus also differ substantially in their flowers. These other species include *C. microspadix*, *C. cataractarum*, and some forms of *C. elatior* and *C. tepejilote*. Another *Chamaedorea* with cespitose habit and pinnate leaves, *C. graminifolia*, is not

cultivated, at least in its pure form. Cespitose stems spreading by rhizomes and forming loose clusters with finely textured leaves, numerous, narrowly linear, straight pinnae, and a glaucous covering on the stem and apical portion of the leaf sheath distinguish *C. graminifolia*. *C. schippii* is a synonym of *C. graminifolia* and growers and collectors frequently but erroneously apply the name *C. schippii* in cultivation to material of a hybrid between *C. graminifolia* and *C. pochutlensis*.

Chamaedorea graminifolia, like the new species proposed here and the highly variable *C. elatior*, is in subgenus *Chamaedorea*; thus, it has staminate flowers with the petals connate apically and the corolla opening by lateral apertures. *C. elatior* is very distinctive due to its vining, climbing habit and strongly reflexed, hooklike terminal pinnae. Actually, solitary-stemmed forms of *C. elatior* are more common but occasionally one encounters cespitose forms. In addition to shoots originating from the base of the plant, new branches on the cespitose forms of *C. elatior* may arise a meter or more above the ground.

Staminate flowers clustered in groups and with free, apically spreading petals and red fruits easily distinguish *C. microspadix*. I discussed *C. cataractarum* and *C. tepejilote*, members of subgenus *Stephanostachys*, in an earlier paper (Hodel 1990). Densely packed staminate flowers contiguous even in bud set subgenus *Stephanostachys* well apart from subgenus *Chamaedoropsis*. Other distinguishing

characters of *C. cataractarum* and *C. tepejilote* include the acaulescent habit with creeping, dichotomously branched stems of the former and the pinnae of the latter that dry leaving keeled, shining yellow, prominent nerves. Like *C. elatior*, there are solitary-stemmed or cespitose forms of *C. tepejilote*.

Here I provide a key to all the cultivated species of *Chamaedorea* with cespitose habit and pinnate leaves although I discuss only those in subgenus *Chamaedoropsis* and the newly named species in subgenus *Chamaedorea*. I include *C. graminifolia* in the key even though it is not cultivated since a synonym, *C. schippii*, is of common usage in horticulture and the hybrids existing between *C. graminifolia* and *C. pochutlensis* are often the source of confusion. Expanded descriptions of all taxa will appear in my forthcoming treatment of *Chamaedorea* that the International Palm Society will publish in 1991.

Key to the Cultivated Species of *Chamaedorea* with Cespitose Habit and Pinnate Leaves

1. Plants appearing acaulescent but with very short, creeping, dichotomously branched stems; pinnae briefly decurrent on rachis. *C. cataractarum*
1. Plants with visible, elongated stems not dichotomously branched or creeping; pinnae not decurrent. 2
2. Plants climbing, vinelike; terminal pinnae reflexed, hooklike. *C. elatior*
2. Plants with erect or leaning stems, not climbing or vinelike; terminal pinnae forward-pointing. 3
3. Fruits red; staminate flowers greenish, clustered in groups of 3-4. *C. microspadix*
3. Fruits black; staminate flowers yellowish, not clustered in groups. 4
4. Pinnae with 5-12 primary nerves above; staminate flowers contiguous in bud. *C. tepejilote*
4. Pinnae with dominant midrib and 1-2 less prominent nerves on each side of this above; staminate flowers solitary. 5
5. Leaves with less than 16 pinnae on each side of rachis. *C. seifrizii*

5. Leaves with 20 or more pinnae on each side of rachis. 6
6. Apex of leaf sheath with ligules. 7
6. Apex of leaf sheath lacking ligules. 8
7. Ligules long-lanceolate, to 5 cm long or more, brownish and fibrous. *C. quezalteca*
7. Ligules short, triangular, less than 2 cm long, green with only a brown margin. *C. costaricana*
8. Pinnae narrowly linear; stems widespreading by rhizomes, forming loose colonies. *C. graminifolia*
8. Pinnae lanceolate; stems tightly clustering. 9
9. Leaf sheaths fibrous, grayish, persistent near top of stem, new shoots emerging from bases of bare stems; petals of staminate flowers spreading apically. *C. pochutlensis*
8. Leaf sheaths thick, durable, \pm woody, brown, persistent throughout stem, new shoots emerging from tops of basal sheaths; petals of staminate flowers connate apically. *C. hooperiana*

Chamaedorea costaricana Oerst.,

Vidensk. Meddel. Dansk. Naturhist. Foren. Kjoebenhavn 1858: 19, 1859 ("costaricanas"). Type: Costa Rica, Turrialba, Oersted 6543 (holotype C).

Nunnezharia costaricana (Oerst.) O. Kuntze, Revisio Generum Plantarum 2: 730, 1891.

Chamaedorea biolleyi Guillaum., Bull. Mus. Hist. Nat. (Paris) 28: 543, 1922. Type: Cult., *Biolley s. n* (holotype P).

Chamaedorea linearia L. H. Bailey, Genes Herb. 6: 249, Fig. 131, 1943. Type: Panamá, El Boquete, Pittier 2922 (holotype US).

Chamaedorea seibertii L. H. Bailey, Genes Herb. 6: 238, 1943. Type: Panamá, Chiriquí, Seibert 218 (holotype MO).

Omanthe costaricana O. F. Cook, Science 90: 298-299, 1939, name of no botanical standing.

Stems 3-8(15) m tall (Figs. 1-3), 2-8 cm diam., erect but often leaning with age on adjacent vegetation, internodes 5-40 cm long, forming fairly dense or \pm open clumps several meters across. Leaves 4-7, 1-2 m long; sheath 20-60 cm long or more with a ligule on each side of petiole at apex, these initially lanceolate and mem-



1. A large clump of *Chamaedorea costaricana* grows in a ravine near Monteverde, Costa Rica, *D. & M. Hodel* 693. 2. This handsome clump of *Chamaedorea costaricana* is in the San Diego Zoo, California. 3. The main stems of *Chamaedorea costaricana* have short, horizontal, lateral stems at the base from which the new side shoots arise.

branous and later deciduous or rotting away to leave a triangular base 1–2 cm long (Fig. 4); petiole to 35 cm long; rachis to 100 cm long with a pale band extending onto sheath; pinnae 20–27 on each side of rachis, 25–60 × 2.5–4 cm, long linear-lanceolate to lanceolate, slightly sigmoid or ± straight and slightly falcate, a whitish midrib prominent above with 2 prominent primary nerves on each side of this. Inflorescences infrafoliar (Fig. 5), 30–60 cm long; peduncles 20–50 cm long; rachises 10–30 cm long; staminate with 15–50 rachillae, these 20–30 cm long, ± pendulous or drooping; pistillate with 10–30 rachillae, these 20–35 cm long, red-orange in fruit. Fruits globose, black, 6–10 mm diam.

Distribution: PANAMA. COSTA RICA. NICARAGUA. HONDURAS. Dense, moist to wet forest on both the Atlantic and Pacific slopes, 700–2,000 m elevation.

Specimens Examined: PANAMÁ. Coclé: El Valle, *D. & M. Hodel* 747 (BH, PMA). Veraguas: Bajo Chitra, *de Nevers & McPherson* 6793 (MO); S. Azuero Peninsula, *Hammel* 5374 (MO). Herrera: Las Minas, Chepo, *McPherson* 10938 (MO); Cerro Alto Higo, *Hammel* 4038 (MO). Los Santos: Río Pedregal, *Lewis et al.* 2927 (BH). Bocas del Toro: Cerro Bonyic, *Kirkbride & Duke* 604 (MO). Chiriquí: no specific locality, *Wagner* 476 (GOET); Volcán de Chiriquí, *Seibert* 218 (holotype of *C. seibertii*, MO); *Woodson & Schery* 502 (MO); *Woodson et al.* 948 (MO); *Hammel*

1565 (MO); Cerro Punta, *D. & M. Hodel* 732, 736A, 736B (BH, PMA); *Folsom et al.* 2080 (MO); *Hammel* 1528 (MO); *Croat* 26272 (MO); Cerro Pate Macho, *de Nevers & Charnley* 6688 (MO); Volcán Barú, *de Nevers & Charnley* 5995 (MO); Boquete, *Pittier* 2922 (holotype of *C. linearia*, US); *D. & M. Hodel* 731A, 731B (BH, PMA); *de Nevers & McPherson* 6809; Cerro Pelota, *Knapp* 1492, 1514 (MO); Cerro Horqueta, *C. & W. von Hagen* 2100 (MO); Planes de Chiriquí, *Croat* 48840 (MO); Los Llanos, *McPherson* 9261 (MO). COSTA RICA. Cartago: Turrialba, *Oersted* 6543 (holotype C); *Wendland* 24 (GOET); Río Pacuare, *Hodel & Grayum* 978 (BH, CR); Tapantí, *Hodel & Grayum* 698A, 698B (BH, CR); San José: Quebrado Tablazo, *Grayum & Schatz* 5138 (MO); above San Isidro, *Moore & McAlpin* 10151 (BH). Heredia: Volcán Barva, *Burger & Burger* 7687 (F). Puntarenas: Río Cotón, *Davidse* 24478 (MO); Sabalito, *Moore & Parthasarathy* 9436, 9437 (BH); hills above Palmar Norte, *Moore* 6549 (BH); Río Buru, *Gómez et al.* 21564, 21565, 21566 (MO); Monteverde, *D. & M. Hodel* 693A, 693B (BH, CR); *Moore* 10182 (BH); *Hammel & Haber* 13942 (MO); *Hammel & Trainer* 13810 (MO); *Haber & Bello* 6026, 5966 (MO). Guanacaste: Quebrada Zopilote, *Grayum et al.* 6214 (MO); Guayabo de Bagaces, *Gómez et al.* 24515 (MO); Rincón de la Vieja, *Garwood et al.* 680 (F, BM); Volcán Miravalles, *Burger* 9110 (F). Alajuela: Zarcero, *Croat* 24515 (MO); Santa María National Park, *Liesner* 4758 (MO). NICARAGUA. Chontales: Santo Domingo, *Bunting & Licht* 1194 (F). Granada: Volcán Mombacho, *Baker* 195 (RSA, CAS). Matagalpa: Santa María de Ostuma, *Williams et al.* 29201, 27673 (F); Cerro Picacho, *Williams et al.* 29201 (F); El Arenal, *Molina* 31600 (F). Jinotega: Jinotega, *Bunting & Licht* 966 (F). Madriz: S. Somoto, *Williams & Molina* 20275 (F). HONDURAS. El Paraíso: Volcanitos, *Pastor* 102 (UNAH). Ocote-

peque: San Marcos, *Nelson* 7985 (UNAH). CULTIVATED. Costa Rica: Puntarenas, San Vito, Jardín Botánico Robert y Catherine Wilson, *D. & M. Hodel* 709A, 709B (BH), originally from Las Alturas de Cotón; *D. & M. Hodel* 710A, 710B (BH), originally from Volcán Barva; Turrialba, C.A.T.I.E., *Croat* 575 (MO); San Jose, Ciudad Colón Hacienda Universidad Para La Paz, *Zamora & Chavarria* 1515 (MO). United States: Florida, Fairchild Tropical Garden 3017A, *Read* 1492 (BH). France: Paris, *Biolley s. n.* (holotype of *C. biolleyi*, P).

Oersted described and named *C. costaricana* from material he collected in mountain forests about 1,000–1,500 meters elevation near Turrialba, Costa Rica during his travels in Central America in the middle of the 19th century. Today, the native forest in this area is virtually gone, having been destroyed long ago for agricultural purposes. A few stands of *C. costaricana* still exist near the type locality, though, not far from Turrialba in forest remnants on the slope of Volcán Barva.

Chamaedorea costaricana is a most variable species throughout its rather wide range. Different species have been proposed based principally on size and number of parts and prominence of nerves of the pinnae. I have examined the type of *C. costaricana* and those of the other species I include in synonymy here; I can find no good differences to distinguish them.

Generally, there seems to be a relationship between altitude and rainfall and size of plants. It seems that smaller forms occur in lower altitudes with lower and perhaps more seasonal rainfall while larger forms occur at higher altitudes where rainfall is greater and less seasonal and evaporation less. Bailey's *C. linearia* is near the large end of the spectrum with plants being larger in every part. At the small end is Bailey's *C. seibertii*. The typical *C. costaricana* that Oersted described represents the middle of the spectrum. In a few instances at high or wet locations, such as Cerro Punta

in Panamá and Tapantí in Costa Rica, *C. costaricana* attains rather large size. At Cerro Punta, we collected material with stems to 15 meters in height and nearly 8 cm diam. Botanists and horticulturists have confused these large forms of *C. costaricana* with *C. woodsoniana*. The solitary habit with even more robust stems, lack of persistent ligules at the apex of the leaf sheath, heavily nerved, straight pinnae, larger inflorescences with longer peduncles, and elongated fruits distinguish *C. woodsoniana*.

The presence of the two ligules at the apex of the leaf sheath is a diagnostic character unifying these forms. These appendages are lanceolate and membranous and more or less deciduous, at least in their upper portion. The lower or basal portion is not as membranous and is often persistent as a triangular tooth or auricle (Fig. 4) long after the upper portion has fallen or rotted away. Since the upper portion is membranous and rots away rather rapidly, the overall visibility of this appendage is much reduced with time. Therefore, it is best viewed on leaf sheaths on the apical portions of stems near new, emerging leaves.

Chamaedorea costaricana has been cultivated for ornament in San José, Costa Rica at least since the late 1800s and probably earlier, the forested slopes of Volcán Barva serving as a ready and accessible source of plants and seeds. Today, handsome clumps are found throughout the city. It is also commonly found in towns and villages to the north of San José along National Route 9 that winds past Volcán Barva to the Atlantic lowlands. Here, such as at the towns of Heredia and Barva, it is seen as a large hedge, screen, or single specimens in many of the yards and residences. From Costa Rica, it has spread throughout the horticultural world and is one of the more widespread members of the genus in cultivation, being found in gardens and collections in California, Florida, Hawaii, Australia, and elsewhere.

Surprisingly, much, if not most, of the material in California cultivated as *C. costaricana* is actually *C. pochutlensis*. In addition, material in California and Hawaii grown as *C. woodsoniana* is actually *C. costaricana*.

Chamaedorea hooperiana D. R. Hodel
sp. nov. (Figs. 6–8).

Subgenus *Chamaedoreae* Mart. ex H. A. Wendl. inflorescentiis masculis solitariis, floribus masculis solitariis petalis connatis apicaliter corollis aperturis lateralibus. *C. graminifoliae* H. A. Wendl. et *C. pochutlensi* Liebm. affinis sed surculis basilibus propullanibus erectis post vaginas infuscatas persistentes crassas induratas subligneas, foliis crassis induratas differt. Typus: Cult., D. R. Hodel 772 (holotypus BH; isotypi CR, HNT, K, MEXU, MO, NY).

Cespitose, new lateral shoots emerging from tops of old dried persistent basal sheaths (Fig. 8), forming fairly dense clumps to 3–4 m across, erect, leaning with age, to 4–5 m tall, stems 2–2.5 cm diam., green, ringed, often covered with old leaf bases, internodes to 15 cm long. Leaves 5–7, erect-spreading, pinnate; sheath to 40–50 cm long, tightly clasping, obliquely open apically and there splitting deeply opposite petiole with age, rough-brown-margined, below this whitish and longitudinally striate-nerved, old sheaths persistent, drying brown, hard, durable, ± woody; petiole to 20–35 cm long, lime-green and grooved especially near the base adaxially, rounded and pale abaxially; rachis to 0.8–1 m long, lime-green and sharply angled adaxially, rounded abaxially with a green or yellowish band extending onto sheath, attenuate apically; 20–26 pinnae on each side of rachis (Fig. 7), these regularly arranged, opposite to subopposite, flat off rachis, elongate-lanceolate, lower and middle ones longest, these to 40 × 1.8 cm, becoming progressively shorter toward apex of rachis,



4. The short ligule at the apex of the leaf sheath is a diagnostic feature of *Chamaedorea costaricana*. Compare it with that of *Chamaedorea quezalteca* in Figure 12. 5. The infructescence of *Chamaedorea costaricana* is held below the leaves. 6. A large clump of *Chamaedorea hooperiana* grows at Ingwersen Nursery in Oceanside, California. 7. Leaf and pistillate inflorescence of *Chamaedorea hooperiana* were taken from a plant cultivated in the garden of P. Sullivan in Ventura, California, Hodel 804.

± straight, only slightly falcate, long-acuminate, slightly contracted at base, ± thick, durable, a prominent pale midrib sharply angled adaxially and 2 much less prominent primary nerves on each side of this, secondaries and tertiaries faint and inconspicuous, midrib prominent abaxially, apical pair of pinnae slightly wider.

Inflorescences infrafoliar, emerging from tops of dried persistent sheaths, erect. Sta-

minate with peduncle to 30 cm long, 1.5 cm wide at base, erect-spreading, pale green where exposed; bracts 5-6, tubular, tightly sheathing, obliquely open apically and there bifid except largest which is long-acuminate and greatly exceeds peduncle and often conceals 1 or 2 smaller ones, longitudinally striate-nerved, drying brown at anthesis; rachis 20 cm long, light green; 40-45 rachillae, these to 25 cm long,

spreading-drooping, light green, 1.75–2 mm diam. Pistillate (Fig. 7) with peduncle to 50 cm long, 1.5 cm wide at base, erect, pale or greenish in flower where exposed, reddish orange in fruit; bracts 6, similar to those of staminate inflorescence, brown and persistent in fruit; rachis to 22 cm long, green-yellow at anthesis, reddish orange in fruit; 40 rachillae, lower ones longest, these to 22 cm long, apical ones to 10 cm long, spreading slightly, \pm stiff, yellow-green at anthesis, reddish orange in fruit.

Staminate flowers spirally arranged, 3–3.5 mm distant, subglobose, 3–3.5 \times 3–4 mm, highly aromatic, slightly sunken in elliptic depressions; calyx cupular, 1 \times 2 mm, membranous, light green, shallowly 3-lobed, lobes broadly rounded, sepals connate nearly to top; petals valvate, connate apically and there adnate to pistillode and corolla opening by lateral slits, petals later apically spreading slightly? but remaining inwardly curved, yellow, 3.5 \times 3 mm, broadly acute, reflexed only slightly at tip, margins \pm thickened; stamens 2.5 mm tall, filaments 1–1.5 mm long, very pale green, nearly clear-colored, anthers 1 mm long, yellow changing to white; pistillode columnar, 2.75 mm tall, light green, darkened and narrowed apically. Pistillate flowers in rather remote spirals, 8 mm distant, globose, 3 \times 3 mm, slightly immersed in elliptic depressions; calyx very light green or nearly yellow, 1–1.5 \times 3 mm, prominently 3-lobed, lobes broadly rounded, sepals connate and/or lightly imbricate basally; petals tightly imbricate, opening only briefly apically, light greenish yellow, 2.5–2.75 \times 3 mm, acute; pistil globose, light green, 3 \times 3 mm, styles lacking, stigma lobes distinct but low, rounded. Fruits black, oblong-globose, 7–8 mm diam.

Distribution: MÉXICO. Veracruz. Dense, wet forest, 1,000–1,500 m elevation.

Specimens Examined: MÉXICO. Veracruz: Catemaco, *D. & R. Hodel 922* (BH, MEXU); *Dressler & Jones 91* (GH).

CULTIVATED. California: La Habra, garden of Lou Hooper, *Hodel 772* (holotype BH; isotypes CR, HNT, K, MEXU, MO, NY); Ventura, garden of Pauleen Sullivan, *Hodel 804* (BH); San Marino, Huntington Botanical Gardens 43001, *Hodel 690* (BH).

The epithet honors Lou Hooper of La Habra, California in whose garden I collected the type specimen.

Chamaedorea hooperiana exists in only a few collections in southern California. Pauleen Sullivan in Ventura, Louis Hooper in La Habra, Jack Ingwersen in Oceanside (Fig. 6), and the Huntington Botanical Gardens in San Marino have mature plants in their gardens. For years these plants were unidentified and their origin uncertain. The common story was that the existing plants originated from one introduction by an unknown seaman who collected seeds in a port of call in Central American and brought them to Southern California.

In December, 1989, during field work in México, we found it in the wild in the Catemaco region of Veracruz, enabling us to provide a known locality for it. Sullivan has plants of both sexes and produces seeds regularly that she has distributed to local palm collectors and hobbyists. I originally thought that this species was *C. karwinskyana* and plants of *C. hooperiana* may have been distributed as such. However, I have since examined the type of *C. karwinskyana* and realize that it can be included with *C. pochutlensis*.

Similar florally to *C. graminifolia* and vegetatively to *C. pochutlensis*, *C. hooperiana* can be distinguished in the manner in which it sends forth new shoots from the base of the plant. These emerge from the tops of the persistent, nearly woody, basal leaf sheaths (Fig. 8). In addition, *C. hooperiana* has thicker, durable, nearly plasticlike leaves. Rhizomatous stems emerging some distance from the parent plant and soft, thin, narrowly linear pinnae also distinguish *C. graminifolia*. Other distinguishing characters of *C. pochutlensis*

include the staminate flowers with apically spreading petals and broader, softer pinnae.

A handsome species of easy culture, *C. hooperiana* is a vigorous and relatively fast grower. Its eventual size should be considered when placing it in the landscape. With age, it will form rather dense clumps several meters across. Stems toward the perimeter of the clump tend to lean outward gracefully, occupying even more space. It is more resistant to infestations of mites than *C. costaricana* and *C. pochutlensis* and is much superior as an indoor plant. In fact, it holds great promise for use in interior situations due to its tolerance of low light and low humidity and resistance to pests. Collectors in southern California have made hybrids between *C. hooperiana* and *C. pochutlensis*.

Chamaedorea pochutlensis Liebm. in Mart., *Historia Naturalis Palmarum* 3: 308, 1849. Type: México, Oaxaca, Liebmann 6579 (holotype C, isotype MO).

Chamaedorea karwinskyana H. A. Wendl., *Allg. Gartenzeitung* 21: 179, 1853b. Type: Cult., *Wendland s. n.* (holotype GOET).

Nunnezharia pochutlensis (Liebm. in Mart.) O. Kuntze, *Revisio Generum Plantarum* 2: 730, 1891.

Nunnezharia karwinskyana (H. A. Wendl.) O. Kuntze, *Revisio Generum Plantarum* 2: 730, 1891.

Chamaedorea elatior Hort. (non Mart.).

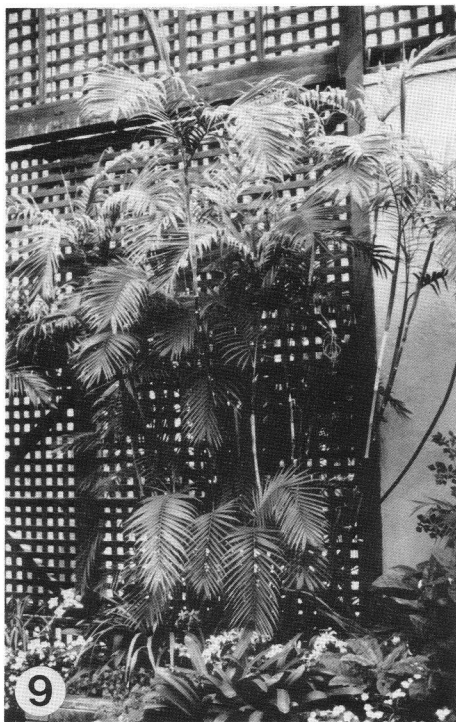
Chamaedorea robusta Hort.

Stems to 3–5 m tall or more (Figs. 9, 10), 2–3 cm diam., internodes 10–25 cm long, forming dense clumps eventually reaching 2–3 m across. Leaves 3–5, to 2 m long; sheath to 30 cm long, green but drying pale or whitish and persisting on stem; petiole to 30 cm long; rachis to 1 m long or more with a pale or light green band extending onto sheath, petiole and sheath \pm slightly glaucous; pinnae 20–33

on each side of rachis, regularly arranged, elongate-lanceolate, to 40 \times 2–3 cm, a prominent pale midrib and 2 submarginal primary nerves, secondaries and tertiaries inconspicuous. Inflorescences infrafoliar, erect-spreading; peduncles 30–40 cm long; rachises 10 cm long; staminate with 12–25 rachillae, these 15–20 cm long, slender \pm drooping, green; pistillate with 12–18 rachillae, these 15 cm long, slender, spreading and \pm stiff but becoming \pm drooping and reddish orange in fruit. Staminate flowers strongly aromatic. Fruits black with glaucous bloom, globose-ellipsoid, 12–13 \times 8–10 mm.

Distribution: MÉXICO. Moist forest on the Pacific slope, 50–2,000 m elevation.

Specimens Examined: MÉXICO. Oaxaca: inland from Puerto Ángel, Moore 8238 (BH); in hills behind Pochutla, Liebmann 6579 (holotype C, isotype MO); D. & R. Hodel 940 (BH, MEXU); in hills behind Puerto Escondido, D. & R. Hodel 934A, 934B (BH, MEXU). Guerrero: road from Acapulco to Acahuizotla, Moore 6202 (BH). Michoacán: near Atenga on road to Playa Azul, Moore 8789 (BH); near Uruapan, Moore et al. 5755 (BH); Apatzinga, Aguillilla, Hinton et al. 15984. Jalisco: Colima, Rancho El Jabali, Sanders et al. 8146 (RSA); Estación Biología Las Joyas. Cochrane & Judziewicz 10647 (RSA); road from Autlán to Barra de Navidad, Moore & Bunting 8743 (BH); Sierra de Parnaso, Boutin & Kinnach 3113 (HNT); Sierra de Manantlán, Cerro La Piedra Bola, Iltis & Guzman 29106, 29107 (WIS); La Manzanilla, McVaugh 25051 (MICH). Nayarit: road from Tepic to Jalcocotán, Moore & Bunting 8693 (BH); Boutin 2090 (HNT). Sinaloa: Sierra Tacuichamona, Capadero, Gentry 5605 (GH); Sierra Surotato, La Jolla, Gentry 7281 (RSA). Durango: below Los Molinos, Kinnach & Sanchez-Mejorada 1781 (HNT); El Palmito, Kinnach & Sanchez-Mejorada 1689 (HNT). CULTIVATED. México: Guadalajara, Iltis & Nee 1667 (WIS); Cuernavaca, in park by Palacio Cortes,



Moore 6207. United States: California, Los Angeles, Vavra Estate, *Moore 6419, 6462* (BH); San Marino, Huntington Botanical Gardens 36339, *Hodel 788* (BH), originally from Durango; Huntington Botanical Gardens 25010, *Hodel 789* (BH), originally from Nayarit; New York, Ithaca, L. H. Bailey Hortorium, *Moore 8173 bis* (BH), originally from Michoacán. Germany: Hannover, *Wendland s. n.* (holotype of *C. karwinskyana*, GOET), originally collected by Karwinski in México; Munich, Botanische Garten, *Moore 7383* (BH).

Liebmann described and named *C. pochutlensis* from material that he collected near Pochutla in Oaxaca (Martius 1849). It is a variable species and occurs over a rather wide range of nearly 2,000 km (1,300 miles) in western México. It is not a common plant throughout its range and is usually found as isolated clumps on cliff sides in ravines and canyons.

Other than its original description and a few other short botanical accounts, mention of *C. pochutlensis* is lacking in the literature. It has been cultivated in California since the early 1900s, most of the plants there probably originating from collections made in México by Edward Howard for the Doheny Estate in Los Angeles. Plants probably of the same origin were at the Vavra Estate (formerly property of the University of California at Los Angeles) in the 1960s and some still exist at the Huntington Botanical Gardens in San Marino. The Huntington has added to its holdings of *C. pochutlensis* with recent collections from Durango and Jalisco in México.

Wendland described and named *C. karwinskyana* from material cultivated at

Herrenhausen and originally collected in México. Wendland obtained his material from Baron von Karwinski who introduced the species to Europe and who cultivated it at his garden in Munich.

Chamaedorea karwinskyana is mentioned frequently in horticultural accounts and was apparently cultivated as early as the 1840s in European greenhouses and Mediterranean gardens under the name *Chamaedorea elatior* (Wendland 1853a, Guillaumin 1923). Wendland (1853a) pointed out that this occurred when Martius (1837) confused *C. elatior* (which Martius himself had named in 1830) with another species recently introduced to European gardens from México. In his 1837 work, Martius erroneously illustrated this other species as *C. elatior*. Wendland (1853b) recognized this error and named this other species *C. karwinskyana*. According to Burret (1935) material referable to *C. karwinskyana* was still cultivated in European collections as *C. elatior* as recently as the 1930s.

Surprisingly, most plants of *C. pochutlensis* in California are misidentified as *C. costaricana*. The two are similar in their long-pinnate leaves but the ligules at the apex of the leaf sheath of *C. costaricana* easily distinguish it from *C. pochutlensis*. Hertrich (1951) discussed and Muirhead (1961) illustrated *C. pochutlensis* at the Huntington Botanical Gardens in San Marino, California erroneously as *Collinia elegans*.

Collectors have made a hybrid in California and perhaps elsewhere reportedly between *C. schippii* (= *C. graminifolia*) and *C. costaricana*. However, it is not *C. costaricana* but *C. pochutlensis* that was utilized as one of the parents with *C. schip-*

←

8. New side shoots of *Chamaedorea hooperiana* arise in a characteristically vertical fashion from behind persistent, woody leaf bases. 9-10. *Chamaedorea pochutlensis* forms handsome clumps in the conservatory at Balboa Park in San Diego, California. 11. A particularly striking clump of *Chamaedorea quezalteca* is in the garden of R. Palmer in Whittier, California.

pii (= *C. graminifolia*). Since *C. graminifolia* in cultivation is already hybridized and, therefore, not pure, the resulting offspring are in reality backcrosses with *C. pochutlensis*.

Chamaedorea quezalteca Standl. & Steyerl., Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 204, 1947. Type: Guatemala, Quezaltenango, *Standley 87159* (holotype F).

Legnea lacinata O. F. Cook, Nat. Hort. Mag. 22: 134, 1943b, name of no botanical standing.

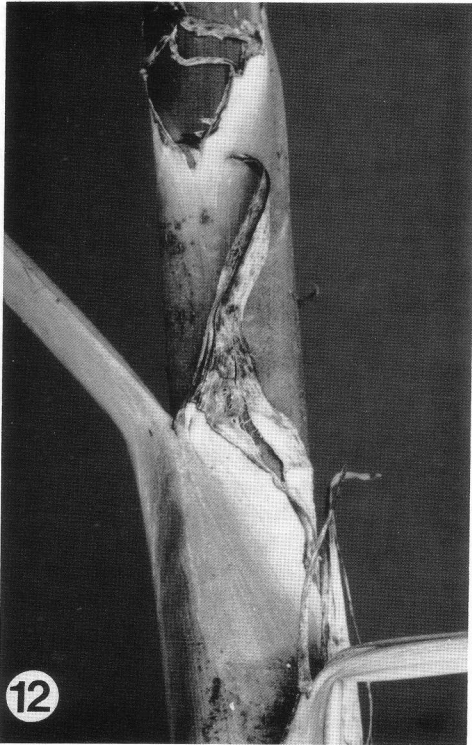
Stems sometimes with branches in place of inflorescences, to 4 m tall or more (Fig. 11), 1–3 cm diam., internodes to 20 cm long. Leaves 3–5, spreading; sheath 17–40 cm long, becoming dry and grayish and then persistent and durable, prominent ligules on either side of petiole at apex, these fibrous (Fig. 12), 4.5–10 cm long, becoming tattered; petiole 20–30 cm long; rachis to 1 m long with a pale band below extending onto sheath; up to 20 pinnae on each side of rachis, lanceolate, falcately acuminate, 30–45 × 3–5 cm, a midrib and 2 primary nerves on each side of this prominent above, secondaries slender, numerous, inconspicuous. Inflorescences infrafoliar, emerging through or from behind old sheaths at the nodes; peduncles slender, 30–45 cm long; staminate with rachis 10–15 cm long; rachillae 15–25, these 15–20 cm long, slender, spreading to pendulous; pistillate with rachis to 5 cm long; rachillae 6–10, these to 15–20 cm long, red-orange in fruit. Fruits black, globose, to 1 cm diam.

Distribution: GUATEMALA. MÉXICO. EL SALVADOR. HONDURAS. Dense, moist or wet forest on the Pacific and Atlantic slopes, 1,000–2,000 m elevation.

Specimens Examined: HONDURAS. Morazán: Cerro de Uyuca, *Moore 6754* (BH); *Glassman 2037* (GH). Comayagua: above Siguatepeque near El Achote,

Yuncker et al. 6184 (GH, MICH, U). EL SALVADOR. Ahuachapán: Sierra de Apaneca, *Standley 20137* (F). GUATEMALA. Quezaltenango: Volcán de Zunil, *Standley 65423* (F); *Wendland 6* (GOET); Volcán de Santa María, *Standley 68331* (F); *Standley 87159* (holotype F); *Hodel & Castillo 901* (BH, AGUAT); Mazatenango, *Bunting & Licht 356* (F). San Marcos: San Marcos, *Hodel & Castillo 997* (BH, AGUAT); Aldea Fraternidad, *Williams et al. 26216, 26218* (F). Alta Verapaz: Cobán, *Moore 8224* (BH, F); *Hodel & Castillo 895* (BH, AGUAT). Huehuetenango: on Cerro Negro near Aguacate, *Hodel & Castillo 998* (BH, AGUAT). MÉXICO. Chiapas: Motozintla, *Breedlove 41701, 42826, 69095* (CAS); Ángel Albino Corzo, *Breedlove & Bourell 67428* (CAS); Rizo de Oro, Cintalapa, *Breedlove & Smith 21785, 31337* (CAS); La Independencia, *Breedlove 33617* (CAS). CULTIVATED. Guatemala: Universidad de San Carlos, *Hodel & Castillo 867* (BH, AGUAT); Huehuetenango, Hotel Zaculeu, *Iltis & Lind G-102* (WIS). México: Chiapas, San Cristobal de las Casas, *Breedlove & McClintock 23671* (CAS). United States: New York, Ithaca, Bailey Hortorium, *Moore 8224 bis* (BH), originally from Alta Verapaz, Guatemala; California, Whittier, garden of R. Palmer, *Hodel 783* (BH); Huntington Beach, garden of L. Rossten, *Hodel 800* (BH); both collections from California originally from Cerro Volcán Verde, El Salvador.

A handsome species with long-pinnate, flat leaves and clustering, smooth, green, canelike stems, Standley and Steyermark described and named *C. quezalteca* from a pistillate collection from the lower slope of Volcán de Santa María in Quezaltenango, Guatemala. We found it near the type locality on the Pacific slope and also near Cobán on the Atlantic slope. For such an obscure name, the plant is surprisingly widely cultivated in Guatemala, appearing in parks and plazas of many cities. Exceptionally fine specimens can be seen in the



12. The ligule at the apex of the leaf sheath of *Chamaedorea quezalteca* is long and fibrous. 13. *Chamaedorea seifrizii* with a typically tight cluster of numerous stems is at Waimea Falls Park and Arboretum in Hawaii.

Botanical Gardens in Guatemala City. In Quezaltenango, local residents sell the cut leaves for use in flower arrangements and bouquets.

Chamaedorea quezalteca is close to *C. costaricana* but can be distinguished by the nature of the ligules at the apex of the leaf sheath. In the former, these are fibrous and persistent (Fig. 12), attaining a length of up to 10 cm while in the latter they are membranous with the upper portion rotting or weathering away to leave a persistent triangular base only about 1–2 cm high.

Chamaedorea quezalteca is rare in cultivation outside of its native range, the only plants recorded occur in a few collections in southern California and in the greenhouse at the L. H. Bailey Hortorium at Cornell University, Ithaca, New York

where they are labeled *C. pulchra*. The plants in California were grown from seeds that Alan Bredeson of Lemon Grove collected from cultivated plants near Cerro Volcán Verde in El Salvador in 1976. Lois Rossten of Huntington Beach has a staminate plant and Richard Palmer of Whittier and Alan Bredeson have pistillate plants. We have successfully hand-pollinated Palmer's plant with pollen from Rossten's and fruits have been set and matured. The few plants, none mature, in the greenhouse at Cornell University in New York were grown from seeds collected by the late H. E. Moore, Jr. in Alta Verapaz, Guatemala. In addition, we distributed seeds in 1989 from Guatemala (Hodel & Castillo 867). *C. quezalteca* is susceptible to infestations of mites.

Chamaedorea seifrizii Burret, Notizbl.

Bot. Gart. Berlin-Dahlem 14: 268, 1938. Type: México, Yucatán, Chichén Itzá, *Seifriz s. n.* (holotype B, destroyed).

Chamaedorea erumpens H. E. Moore, Gentes Herb. 8: 232, figs. 96–97Aa, 1951. Type: Cult., *Moore 5830* (holotype BH).

Chamaedorea erumpens 'Fairchild' H. E. Moore, Gentes Herb. 8: 233, fig. 97B, 1951. Type: Cult., *Moore 5832* (holotype BH).

Meiota campechana O. F. Cook, Nat. Hort. Mag. 12: 138, 1943, name of no botanical standing.

Stems to 40 or more in fairly dense and tight clump (Fig. 13), to 3 m tall, 1–2 cm diam., white-spotted, ageing with a thin glaucous covering, internodes 5–20 cm long. Leaves 4–5, gray-green or green, ± stiff or drooping; sheath to 30 cm long, persistent; petiole to 10 cm long; rachis 30–45 cm long with very faint light green band extending onto sheath; pinnae 13–18 on each side of rachis, terminal ones 2–3 nerved, remainder 1-nerved with conspicuous midrib and numerous closely spaced and fine secondaries on each side of this, midrib prominent below, or 5–6 pinnae on each side of rachis with terminal pair 9-nerved, lanceolate or linear, straight, median ones largest, these to 20–35 × 0.8–3 cm, basal ones smaller, these 14–20 × 0.5–1.8 cm, subapical ones 10–15 × 1–1.5 cm, apical pair 8–15 × 2.5–3 or to 9 cm wide. Inflorescences infrafoliar, erumpent at base of old sheaths, short, stiff; staminate with peduncle 3.5–5.5 cm long; rachillae 5–12, these 7.5–15 cm long, stiff, erect; pistillate up to 7 per stem in flower and fruit at once; peduncle 3.5–8.8 cm long, erect; rachis 1–3 cm long; rachillae 4–6, these to 10 cm long, stiff, erect, orange in fruit. Staminate flowers aromatic. Fruits black, globose, 8 mm diam.

Distribution: MEXICO. BELIZE. GUATEMALA. HONDURAS. Open or dense, moist or wet woodland or forest on

the Atlantic slope, to 500 m elevation, often on limestone.

Specimens Examined: HONDURAS. Islas de Bahía: Roatán Island, *Molina 20715* (F). GUATEMALA. Petén: Tikal, *Hodel 847, 850* (BH). BELIZE. Orange Walk: August Pine Ridge, *Davidse & Brant 32751* (CAS); Yo Creek, *Hodel & Thomas 1131A, 1131B* (BH). Corozal: between Sarteneja and Chunox, *Davidse & Brant 32605* (CAS). MÉXICO. Campeche: east of Francisco Escarcega, *Reznicek et al. 222* (MICH). Quintana Roo: Xel-Ha, *Tillez 3557* (CAS). Yucatán: Chichén Itzá, *Moore 8096* (BH). CULTIVATED. United States: Florida, Fairchild Tropical Garden, *Moore 5830* (holotype of *C. erumpens*, BH), *5829* (BH); *Moore 5832* (holotype of *C. erumpens* 'Fairchild,' BH); *Moore 5831* (BH); cultivated collections from Florida originally from Belize; California, Whittier, garden of R. Palmer, *Hodel 794A, 794B, 795, 821* (BH). Belize: Cayo, Teakettle, *Hodel & Thomas 1133A, 1133B* (BH), originally collected at Beaver Dam, Mile 34, Western Highway, Belize.

Burret described and named *C. seifrizii* from material that William Seifriz collected near the Mayan ruins at Chichén Itzá in the state of Yucatán in México. Mayans cultivated it around their villages and temples as ornament and possibly for religious purposes. The Mayan names *xiat* and *chiat* mean near the edge of water, in apparent allusion to the habitat. I have observed *C. seifrizii* in Petén in northern Guatemala in low, seasonally swampy or boggy situations. In fact, local people state that it is mainly confined to "baja tierra" or low land. Although not named until 1938, others, like Millspaugh (1898) and Standley (1930), encountered it at an earlier date but listed it under other names.

As interpreted here, *C. seifrizii* displays a tremendous amount of foliar variation in the wild although the flowers are essentially the same in the various types and forms. Burret's *C. seifrizii* is typified by stiff leaves

with narrow, linear, and upright pinnae. Moore described and named *C. erumpens* from plants cultivated at Fairchild Tropical Garden in Miami, Florida. These plants had apparently been brought in from Belize or grown from seeds that William Schipp sent and by 1950 had become quite popular in south Florida and were used extensively as an indoor decorative as well as in the exterior landscape. Moore noted two leaf forms in *C. erumpens*. That with the pinnae regularly arranged he selected as the type. The other, with the terminal ones united and much broader, he designated as a horticultural variety honoring Dr. David Fairchild. Both types were growing together at Fairchild Tropical Garden and presumably had come from the same lot of seeds. Moore stated that he found no differences other than in the foliage.

Moore (1951) continued in his discussion and stated that *C. erumpens* was similar in floral morphology with its close relative *C. seifrizii* and the differences were mainly in the shape and nervation of the pinnae. *C. erumpens* had lanceolate rather than linear pinnae that were at least twice as broad as those of *C. seifrizii*. In addition, he noted *C. seifrizii* as being a scrambling palm. When considered over its entire range, the shape and size of pinnae are a variable character and of dubious merit in distinguishing between these two taxa. In fact, there is less foliar variation between Burret's typical *C. seifrizii* and Moore's typical *C. erumpens* than between the latter and its horticultural variety 'Fairchild.' In Belize, I have observed leaves of both extreme types of pinnae (*seifrizii* and *erumpens*) on the same plant. The scrambling nature of certain forms is probably not a reliable character either. Rather, it seems to be a function of age and of the amount of light; older plants in lower light seem to lean and scramble more while those in higher light are more compact, stiff, and upright. The amount of light also affects the stiffness of the leaves. Those in higher light have stiff, somewhat v-shaped, upright

pinnae while those in lower light have drooping, flat, softer pinnae.

Not abundant in the wild, *C. seifrizii* occurs as scattered clumps in disturbed woodland or forest. In Orange Walk, Belize, it grows in disturbed forest or woodland remnants on the margins of sugarcane fields where it is subjected to exceedingly dry conditions for several months each year. *C. seifrizii* is very widely cultivated and appears in gardens and collections in California, Hawaii, Florida, Europe, Australia, the Far East, and elsewhere. In fact, it is highly likely that more plants are in cultivation than in the wild. Often occurring naturally on limestone outcroppings in its native habitat, *C. seifrizii* is well adapted to culture in south Florida where extensive plantings now exist.

The commercial industry recognizes two forms of *C. seifrizii*. One, the most popular, more or less corresponds to Burret's type with stiff leaves and narrow, linear, upright pinnae while the other falls into Moore's type with softer leaves and broader, flat pinnae. Extensive plantings of both forms have existed in south Florida for years and have served as a source of breeding stock for commercial seed production. Much hybridizing has occurred between the two and this, coupled with the natural variation within the species, has resulted in innumerable variants or breeding lines in the trade. In fact, most of the material produced commercially in Florida is called, for lack of a better term, Florida Hybrid.

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Lois Rossten, Pauleen Sullivan, Louis Thomas, and the Jardín Botánico Robert y Catherine allowed me to collect material in their gardens.

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(Continued on p. 218)

Cane Weevil Borer, *Rhabdoscelus obscurus* (Coleoptera: Curculionidae), a Pest of Palms in Northern Queensland, Australia

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ABSTRACT

In recent years the cultivation of ornamental palms (Arecaceae) has increased markedly in northern Queensland. Consequently, several insects have become important pests, particularly *Rhabdoscelus obscurus* (Boisduval), the cane weevil borer. The larvae of this beetle feed on various species of palms, making the plants unsaleable. Death or lodging of the trees may also result. This paper documents its pest status, derived from information in the literature and from consultation with local growers.

Although *Rhabdoscelus obscurus* (Boisduval), the cane weevil borer, was originally described from New Ireland the original range of the species is unknown. Zimmerman (1968) believed that *R. obscurus* was probably native to the Papuan area, and has since spread, its current distribution ranging from the Celebes in Indonesia through New Guinea, south and east to Queensland, Polynesia, and Micronesia and north to Hawaii. Its spread is almost certainly associated with the transport of sugar cane by man.

Mungomery (1953) was of the opinion that *R. obscurus* first entered Queensland in infested sugar cane directly from New Guinea about 1896. Jarvis (1927) stated that it was first noticed in the Mossman and Johnstone River districts in 1907, spreading rapidly as far south as Mackay through unrestricted movement of seed cane between mill areas. By the mid 1930's *R. obscurus* was second only to cane beetle (Scarabaeidae: *Lepidiota* spp. and other genera) as a pest of sugar cane in Queens-

land. Some badly infested fields in the South Johnstone district had one in three stalks affected, with populations of over 250,000 larvae per hectare (Mungomery 1953). Mungomery (1953) believed that *R. obscurus* only reached its current negligible pest status in the sugar industry when preharvest burning of the crop became almost universal. This practice destroyed most emerging adults and milling killed most larvae and pupae.

The first enquiry we received about *R. obscurus* as a pest of palms in northern Queensland was related to an attack on coconut palm in Cairns in 1977. Since that time reports have gradually increased, with a large number being received over the last two years. Although this undoubtedly reflects an increased interest in growing palms in the area, long term enthusiasts interviewed believed that there was a definite increase in weevil activity over the last 2 to 3 years. The purpose of this paper is to provide an information base on this weevil and its importance to northern Queensland palm growers and to discuss the need or otherwise for further studies.

Life History

Most literature on the life history of *R. obscurus* relates to sugar cane, especially from Hawaii where the weevil is still a major pest. The following information is largely from Napompeth et al. (1972). The adult female chews a cavity about 3 mm

deep in the sugar cane stalk, usually in adult feeding scars or cracks, sometimes at internodes or in leaf sheaths. A single egg is then laid, which hatches in 3–7 days (mean 4.6). The developing larva (Fig. 2) feeds on the pith (not the fibers), tunnelling up and down the stalk, occasionally breaking through to the surface leaving characteristic windows. The larval stage, which has about 6 instars, lasts from 45–61 days (mean 54.3). It then enters a prepupal stage of about 7 days, finally pupating in a cocoon made of a spirally woven mass of fibers and frass. After 17–25 days (mean 21) the adults emerge. Adult beetles (Fig. 1) are variable in color, with about 6 distinct patterns of light and dark markings. Each adult weevil is 10.0 ± 3.0 mm in length and 3.5 ± 1.1 mm in width, while weight varies from 21.3–118.2 mg (mean 66.1 in males, 67.8 in females). Adults are long lived, surviving up to 70 months in captivity, but probably less in the wild. Beetles fly infrequently and are most active around dawn and especially dusk. Van Zwaluwenburg and Rosa (1940) found that *R. obscurus* can move considerable distances (mainly by flight), marked and released specimens being taken up to 0.5 km from release sites. They concluded that wind was probably the main environmental influence on field movement and that most infestations in new fields came from adjacent fields, rather than carrying over from crop to crop. One female can lay up to 176 eggs, 90% of which are laid in the first 25 weeks (laboratory conditions). Eggs are not laid continuously but in short periods of activity.

Dharmaraju et al. (1979) discussed the weevil's life history in coconut palms. Eggs are laid in the epidermis of 4–6 year old trees. Up to several hundred larvae were found developing within the trunk of a single tree. Pink sap which exudes from wounds attracts other adults. Cocoons are found inside the trunk, the weevils leaving exit holes as they emerge. Heavy infestations weaken the trunk and the tree may

fall over and die. Damage mostly occurs up to 1 meter above the ground.

Overseas Hosts

R. obscurus is considered to be primarily a pest of sugar cane, although Muir and Swezey (1916) believed that the original hosts were likely to have been palms and bananas. Napompeth et al. (1972) listed corn, papaya, *Ravenala madagascariensis* J. F. Gmel. (traveller's tree) and *Strelitzia reginae* Banks (Birds-of-paradise) as alternate hosts and Zimmerman (1968) listed maize and other grasses, *Erianthus* spp. and *Inocarpus fagifer* (Parkinson) Fosb. (as *edulis* J. R. & G. Forster).

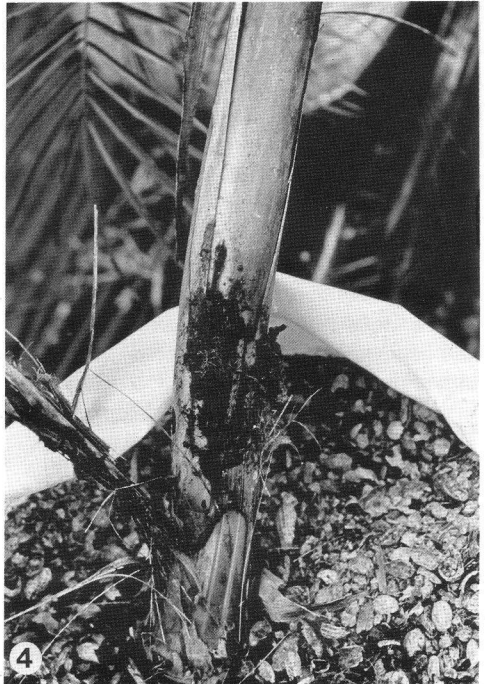
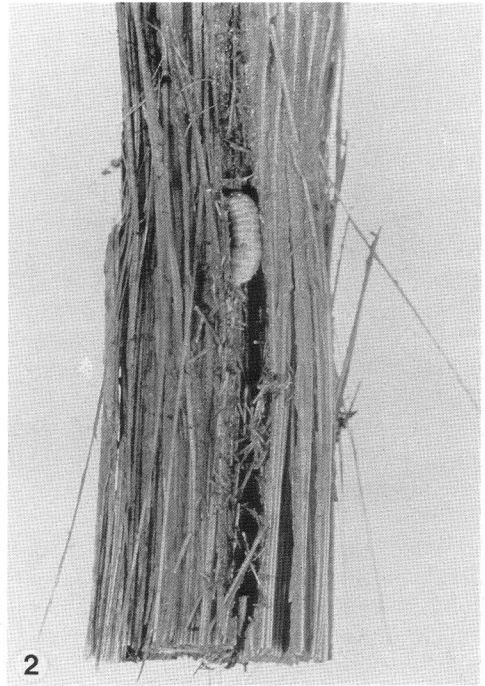
Napompeth et al. (1972) listed the following palms as hosts: *Archontophoenix alexandrae*—alexandra palm; *Areca catechu*—betel-nut palm; *Caryota urens* L.—wine palm; *Cocos nucifera*—coconut palm; *Metroxylon sagu* Rottboel—sago palm; *Pritchardia martii* (Gaud.) H. A. Wendl.—loulou palm; *Ptychosperma elegans*—solitaire palm; *Roystonea elata* (Bart.) Harper—royal palm; *Sabal palmetto* (Walter) Lodd. ex J. A. & J. H. Schultes—cabbage palm. Lever (1969) also listed *Cocos nucifera*, *Areca catechu* and *Metroxylon* spp. as hosts.

Australian Hosts

The majority of available records in Australia are for sugar cane. Mungomery (1937) stated that he knew of no authentic record of *R. obscurus* feeding on bananas in Queensland. He did record *Archontophoenix alexandrae* as a host, the cocoons being present in felled wild trees.

Natural Enemies

A tachinid parasite of *R. obscurus*, *Lixophaga sphenophori* (Villeneuve) was successfully introduced from Papua New Guinea by Jarvis, working with the Hawaiians, Muir and Kershaw, in 1910. By 1918



1. Adult *Rhabdoscelus obscurus*. 2. Mature larva of *R. obscurus* in trunk of young *Archontophoenix alexandrae*. 3. Damaged trunk of *Archontophoenix alexandrae*. Note jelly-like exudate from *R. obscurus* feeding hole. 4. Damage to potted *Archontophoenix alexandrae* by *R. obscurus*.

it was well established in the Mossman area and was then reared in numbers at the Meringa laboratories of the Bureau of Sugar Experiment Stations and widely released between Proserpine and Cairns. Although it was still present as late as 1952, Montgomery (1952) stated that parasitism rates rarely exceeded 5% which he attributed to the removal of available hosts by the yearly harvest. Wilson (1960) however, noted that *L. sphenophori* did exercise a high degree of control of *R. obscurus* where conditions were favorable, such as the Tully-Mossman area.

In addition to *L. sphenophori*, Muir & Swezey (1916) (except where indicated) listed the following as natural enemies of *R. obscurus*:

Plaesius javanus Erichson (HISTERIDAE)—Larvae and adults of this large beetle live inside weevil infested palms and bananas, feeding on weevil adults and larvae, especially on *Cosmopolites* and *Sphenophorus* (other weevil genera related to *R. obscurus*) in bananas. *P. javanus* was released in Cooran, southeast Queensland to control *Cosmopolites sordidus* (Germar), the banana weevil borer, in 1928 (Weddell 1932). One *Plaesius* larva can consume up to 34 weevil larvae per day, an adult averaging 8 per day. Waterhouse and Norris (1987) stated that despite several attempts to introduce this species into southeast Queensland and New South Wales from both Java and Fiji (where it had been successfully introduced), it failed to become established.

Platysoma abruptum Erichson (HISTERIDAE)—This species is similar to *P. javanus* but smaller.

Simodactylus sp. (ELATERIDAE)—Larvae feed on *R. obscurus* in palms, especially the pupal stage.

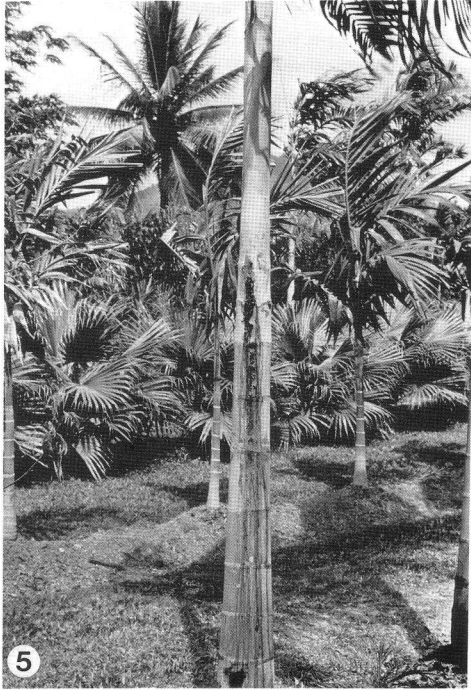
Chrysopilus sp. (RHAGIONIDAE)—Larvae of these flies feed on beetle and other fly larvae in palms and bananas. Waterhouse and Norris (1987) noted the introduction into Australia in 1928 of *Chrysopilus ferruginosus* Wiedemann

against *C. sordidus*. Like the histerid *Plaesius javanus* it failed to establish. Zimmerman (1968) lists the elaterid, *Conoderus exul* (Sharp) and "various ants, mites, fungi and some other predators and parasites" as affecting *R. obscurus* numbers.

Other agents are also recorded as parasites or predators of *R. obscurus*, including rats which will eat the cocoons and *Bufo marinus* L., the cane toad, which commonly preys on *R. obscurus* adults (Wilson 1960). Wilson (1960) also reported that the green muscardine fungus *Metarrhizium anisopliae* attacks *R. obscurus* in Queensland and that the species was considered for biological control in 1923–24. He also reported the introduction of an unspecified entomogenous fungus from the Philippines in 1928. It was then cultured on media and transmitted to *R. obscurus*, but no further information is available on its success or otherwise.

The Current Survey

Twenty-two growers were interviewed and their nurseries examined in late 1989 with regard to *R. obscurus*. For each nursery, notes were taken on size of plantings, establishment dates, range of palm species grown, and microhabitat. With respect to *R. obscurus*, data were obtained on amount and type of damage, palm species affected, age and situation (potted or field planted) of palms attacked, weather or seasonal effects noted by grower, and any control measures employed. These growers ranged from enthusiasts with an interest in palms, to commercial seedlings suppliers and producers of larger plants for landscaping. Large scale growers had trees in pots or in the field numbering several hundred thousand plants. The area covered extends from Cape Tribulation (100 km north of Cairns) south to Bramston Beach on the coast, plus Kuranda and Julatten at higher altitudes (300–400 m) on the Atherton Tableland. (see Fig. 7). All but five of these



5. Damage by *R. obscurus* to trunk of *Wodyetia bifurcata*. Note cracking. 6. Damage to trunk of *Chrysalidocarpus madagascariensis* by *R. obscurus*. Note exudate from feeding hole and subsequent staining.

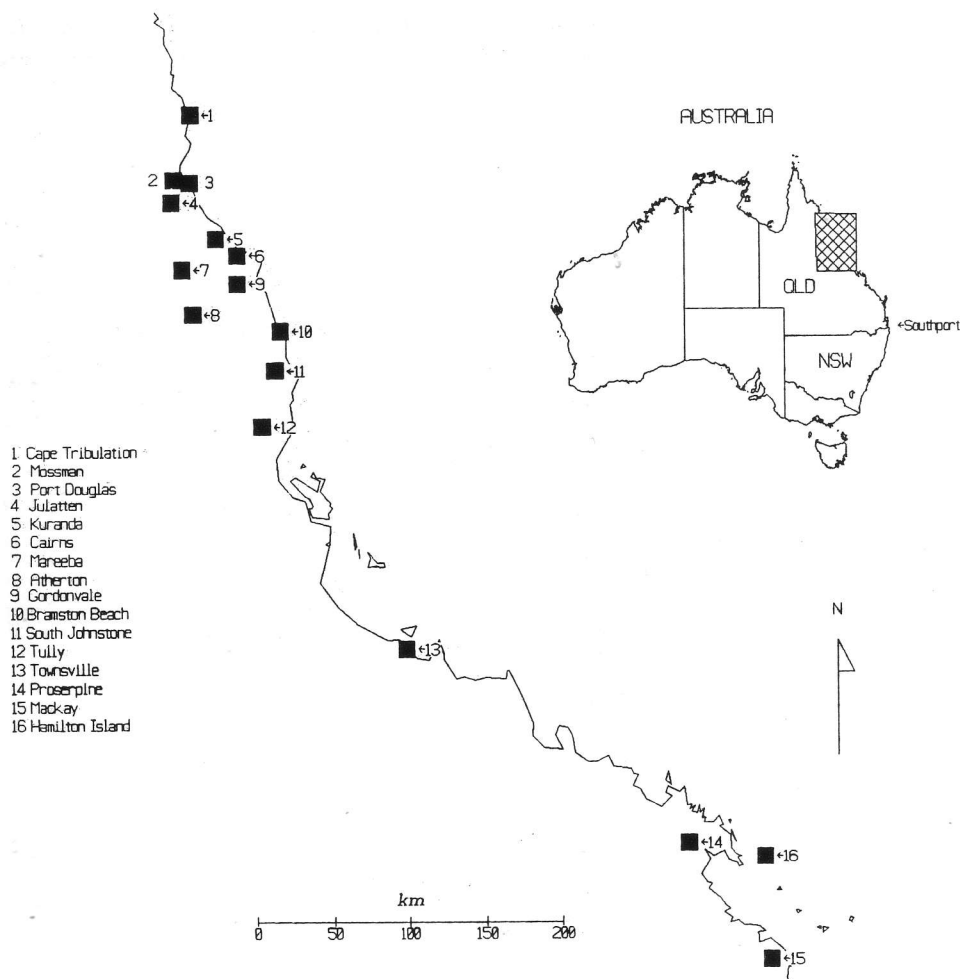
had weevil problems ranging from mild to severe. The five negative cases included some very recently established plots or those using heavy chemical control programs which apparently kept the weevils in check. The climate is tropical monsoonal with hot wet summers and warm dry winters.

Palm plantations are grown in a variety of habitat types ranging from rainforest to *Melaleuca* or *Eucalyptus* open forest, with several on former sugar cane land. There appears to be no correlation between weevil activity and habitat type, all areas being equally susceptible.

R. obscurus is active throughout the year in the region, although several growers believed there was increased activity in the wetter summer months. Others also believed there was an increase in activity in the dry late winter/early spring period.

This could indicate that there are two generations per year and this possibility was supported by larval sizes encountered during the survey—either large or very small, with no intermediates. The dry season peak also coincides with the period of sugar cane harvest in northern Queensland, and beetles could be moving into palms as this host disappears. Growers believed that beetle activity was not influenced by short term weather patterns, but long term effects such as a series of wet or dry years could be expected to affect weevil numbers.

Table 1 lists the species of palms found to be hosts of *R. obscurus* at the time of the survey. Although most records were confirmed by the senior author, a few are species noted by growers as susceptible to attack. However, as adult and larval stages of the insect and its damage are quite distinctive, the grower records are accepted



7. Map of study area with place names used in text.

as valid. The most susceptible hosts are *Carpentaria*, *Chrysalidocarpus*, *Roystonea* and *Wodyetia*. However, this could reflect the palms most popular with growers. One long-term palm grower was of the opinion that there were few palms that *R. obscurus* would not attack.

The tachinid parasite *Lixophaga sphenophori* was found to be active at two coastal sites, one at Port Douglas and the other at Cape Tribulation. Adult flies emerged from *R. obscurus* pupal cells in *Carpentaria*, *Chrysalidocarpus* and

Metroxylon. At the Port Douglas site, 36 weevil pupal cells were closely examined for fly pupae. Of these, 21 were found to be parasitized, each weevil pupal cell containing 1–7 fly pupae, with a mean of 2.4 fly pupae per parasitized weevil pupa. This high parasitism rate contrasts with the situation in weevil infested sugar cane where the parasite is rarely encountered, possibly due to low host numbers and the unsuitability of sugar cane fields for survival and development of the fly (K. Chandler, pers. comm.). The beetles *Dactylosternum*

Table 1. Palm hosts of *Rhabdoscelus obscurus* (Boisduval) in northern Queensland.

Species	Common name	Native (N) or Exotic (E)
Coryphoideae		
<i>Licuala</i> spp.	Licuala Palms	E
<i>Phoenix canariensis</i> Hort. ex Chabaud	Canary Island Date Palm	E
Calamoideae		
* <i>Metroxylon salomonense</i> (Warb.) Becc.	Solomon Sago Palm	E
* <i>Pigafetta filaris</i> (Giseke) Becc.	Pigafetta Palm	E
Ceroxyloideae		
* <i>Hyophorbe lagenicaulis</i> (L. H. Bailey) H. E. Moore	Bottle Palm	E
Arecoideae		
<i>Caryota mitis</i> Lour.	Clustered Fishtail Palm	E
* <i>Chrysalidocarpus madagascariensis</i> Becc.	Green Cane Palm	E
* <i>Chrysalidocarpus lutescens</i> H. A. Wendl.	Golden Cane Palm	E
* <i>Neodypsis decaryi</i> H. Jumelle	Triangle Palm	E
<i>Phloga nodifera</i> Noronha ex. Salomon	—	E
<i>Dypsis</i> sp.	Dypsis Palms	E
<i>Euterpe</i> spp.	Assari Palms	E
* <i>Roystonea regia</i> (Kunth) O. F. Cook	Cuban Royal Palm	E
* <i>Archontophoenix alexandrae</i> (F. v. Mueller) H. A. Wendl. & Drude	Alexandra Palm	N
* <i>Archontophoenix cunninghamiana</i> (H. A. Wendl.) H. A. Wendl. & Drude	Bangalow Palm	N
* <i>Carpentaria acuminata</i> (H. A. Wendl. & Drude) Becc.	Capentaria Palm	N
* <i>Normanbya normanbyi</i> (W. Hill) L. H. Bailey	Black Palm	N
* <i>Wodyetia bifurcata</i> A. K. Irvine	Foxtail Palm	N
* <i>Ptychosperma elegans</i> (R. Br.) Blume	Solitaire Palm	N
* <i>Areca catechu</i> Ln.	Betel-nut Palm	E
* <i>Dictyosperma album</i> (Bory) H. A. Wendl. & Drude ex Scheff.	Princess Palm	E
* <i>Cocos nucifera</i> L.	Coconut Palm	E
* <i>Syagrus romanzoffiana</i> (Chamisso) Glassman	Queen Palm	E
* <i>Aiphanes caryotifolia</i> (Kunth) H. A. Wendl.	Coyure Palm	E
<i>Bactris gasipaes</i> Kunth	Peach Palm	E

* Either adults, larvae or damage of *R. obscurus* seen by K.H.H. Palm classification after Uhl and Dransfield (1987).

abdominale (Fabricius) (Hydrophilidae) and *Platysoma* sp. (Histeridae) were found in weevil infested *Metroxylon* at Cape Tribulation, but it is not known if these were actually preying on *R. obscurus* larvae.

Damage (Figs 3-6)

Adult *R. obscurus* were found sheltering under leaf bases e.g., on *Wodyetia*,

and at the base of inflorescences. Adults were not observed causing damage in the palms, although R. Goebel (pers. comm.) reported numbers damaging the flowers of coconut. Adult feeding scars are recorded on sugar cane. It is not known where the eggs are laid although it is suspected that they are mostly deposited in the leaf bases.

Larval damage has been observed from just above and adjacent to the root mass to two meters or more above the ground.

In younger palms the larvae mine the central portion of the stem, completely destroying the plant. Damage extends up and down the stem for a number of centimeters from the initial point of entry. In older palms larvae mine the thicker leaf bases, e.g., *Metroxylon* and *Pigafetta*, as well as extending for a short distance into the trunk. Splitting occurred in specimens of *Wodyetia* with a trunk diameter of about 100 millimeters.

The obvious external symptoms of larval feeding in palms are listed below. The "windowing" which occurs in sugar cane was not observed.

- (i) A jelly-like exudate from holes in leaf bases and/or stems (Fig. 3)
- (ii) Splitting of the trunk at or near the base and further up the trunk (Figs. 4,5)
- (iii) Staining of the trunk, especially if the palm sustains a high population of larvae (Fig. 6)

In young palms and older individuals of some species, e.g., *Neodypsis decaryi* and *Chrysalidocarpus madagascariensis*, the internal mining by larvae can cause death of the plant. Quite often a large area at the base of some species will be destroyed leaving the palm susceptible to lodging. Holes and splitting of the trunk cause disfigurement in older plants making them unsuitable for sale.

Pupation occurs in a case of spirally woven fibers. In some species, e.g., *Chrysalidocarpus lutescens* and *Carpentaria acuminata*, large numbers of pupal cases were observed protruding through splits in the trunk. These splits were presumed to be caused by extensive larval feeding. Pupal cases were also found at ground level within the remains of the trunks of dead plants.

Discussion

R. obscurus is a member of the weevil subfamily Rhynchophorinae which includes many genera of economic importance, including the well known stored products

pest *Sitophilus*, and the banana pests *Cosmopolites* and *Polytus*. Several other genera are important palm pests including the large *Rhynchophorus* spp. (up to 55 mm in length) and the smaller *Diocalandra* spp. (6–8 mm). Although the asiatic palm weevil *Rhynchophorus ferrugineus* (Olivier) has not yet been found in Australia, the four-spotted coconut weevil, *Diocalandra frumenti* (Fabricius) is occasionally taken in coconuts in northern Queensland where it seems to be secondary to *R. obscurus*. Hill (1983) stated that the pest status of *D. frumenti* was open to dispute.

It appears, from comments made by growers interviewed and by the numbers of enquiries received, that the incidence of *R. obscurus* in palms in northern Queensland is increasing. There would seem to be two factors contributing to this—the dramatic increase in number and size of plantings of palms for the nursery trade, and the trend back to green cane harvest in the sugar cane industry. Although there is no direct evidence, we believe that *R. obscurus* infestations in newly established nurseries primarily come from infested plants received from older established nurseries. Indeed this is backed up by recent outbreaks in southern areas (Hamilton Island and Southport in Queensland and even into New South Wales) where *R. obscurus* has not previously been known to occur. Once established in a nursery, populations build up giving the impression that the problem is increasing. The long term effect of the sugar cane industry returning to green harvest is not known. Although unburnt fields favor weevil development, modern cane varieties are much harder than those used earlier in the century and are much less susceptible to *R. obscurus* attack (K. Chandler, pers. comm.).

To control the weevil, most growers undertake routine crop hygiene, e.g., removal and destruction of dead fronds and infested material. Chemical control measures are not yet approved by the Depart-

ment of Primary Industries in Queensland but would undoubtedly have a place in a well managed nursery. Zimmerman (1968) believed that satisfactory biocontrol of *R. obscurus* would be exceedingly difficult. The tachinid *L. sphenophori* has been established in the area for 79 years and is unlikely to become more important than at present. Previous attempts (at least 5 between 1921-28) to introduce the histerid *P. javanus* have failed and it is unlikely that regulations now in force would allow importation into Australia of such a general predator as a biocontrol agent.

Further work on the problem should involve studies on the biology of *R. obscurus* in palm hosts, including egg laying sites and host susceptibility (Zimmerman 1968) felt that sick or injured palms were more prone to weevil attack). Trials of chemical control measures, their usefulness, best formulations and application techniques and timing would also be of benefit to the palm nursery industry.

Acknowledgments

Thanks go to Maria Walford-Huggins, Keith Chandler and Roger Goebel for advice on palms, weevils and the sugar industry. Karen Koch provided the photograph for Figure 1. Neil Gough and Brian Cantrell read and commented on the manuscript. This paper would not have been possible without the cooperation of the many palm growers interviewed.

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Physiology and Biochemistry of Lethal Yellowing in *Cocos nucifera*

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The coconut is the main source of oil in the tropics. These areas provide the most favorable conditions for the germination and growth of coconut trees where other oil seeds cannot succeed. Approximately 30% of the fruit can be converted to copra (Harries 1971) which, in turn, has 60-64% oil (Grimwood 1975).

The yearly world copra production in 1982 was 4.9 million tons. The main producers were The Philippines and Indonesia. Mexico supplied 2.9% of the world production (FIRA 1985).

The coconut crops in Mexico and Central America are presently threatened by a disease called lethal yellowing (LY). To date, millions of palms have died in Jamaica, Cuba, Florida and Mexico due to this disease, for which there are no adequate control measures yet.

Other reviews have focused on the etiology and epidemiology of LY (Tsai 1980, McCoy 1983). However, our present knowledge on the physiological and biochemical mechanisms involved in the host-pathogen relationship is still limited. The present paper reviews most of the physiological and biochemical studies carried out so far, and proposes an experimental model of the various alterations that take place during the disease development.

Lethal Yellowing

Since its appearance in the last century, LY has killed millions of palms in Jamaica

(Romney 1972), Florida (Fisher 1975), Tanzania (Schuiling and Mpunami 1990), and more recently, the Yucatan Peninsula (McCoy et al. 1983; Villanueva et al. 1987).

Mycoplasmalike organisms (MLO) were pointed out as causal agents of the disease based on two lines of evidence: a) cross-sections of sieve tube elements observed under the electron microscope revealed the presence of bodies with tripartite membranes and an approximate diameter of 0.3 μm (Beakbane et al. 1972, Plavsic-Banjac et al. 1972, Thomas 1979); and b) treatment of diseased palms with tetracycline, but not penicillin, stopped the development of the disease (McCoy 1973). Since MLO were first pointed out as the causal agents, other studies have documented MLO traversing cell walls (Beakbane et al. 1975) and sieve plate pores (Parthasarathy 1974) in diseased palms, suggesting how the microorganism may move to adjacent cells. A number of attempts have been made to isolate and cultivate these microorganisms from LY-affected palms. Eden-Green and Tully (1979) isolated 35 species of *Acholeplasma* from phloem sap and decaying tissue of diseased palms. These isolates were immunologically related to either *A. axanthum* or *A. oculi*. After unsuccessfully carrying out pathogenicity and transmission tests with these isolates, Eden-Green et al. (1985) concluded that these microorganisms were not the etiological agents of LY

but rather epiphytes or saprophytes of the decaying tissue. In a different study, Eden-Green and Waters (1981) isolated and characterized a *Spiroplasma* from diseased palm tissue which was different from *S. citri* or corn stunt *Spiroplasma*. Failure to repeat the obtention of these isolates in subsequent experiments, and their inability to infect susceptible palm species, suggested that these were not the causal agents of the disease (Eden-Green et al. 1983). It appears therefore, that the causal agent is very susceptible to manipulation and thus, its isolation is a difficult task that has not been accomplished. This may also be the reason why the MLO needs a vector to infect the palm.

Studies carried out in Fort Lauderdale, Florida by F. W. Howard and co-workers (1983) pointed towards the cixiid *Myndus crudus* Van Duzee as the vector for the MLO that causes LY. This insect feeds on the phloem of leaves and presumably introduces the MLO through this mechanism. The MLO can then manage to establish themselves within areas with high nutrient demand such as apical meristem, roots and inflorescences as indicated by the localization of MLO by electron microscopy in these tissues (Thomas and Norris 1980).

Lethal yellowing has been shown to require an incubation period of 4 to 9 months before visible symptoms appear (Dabek 1974, 1975). These visible symptoms have been used to grade the severity of the disease (McCoy 1973). First, the nuts fall off the tree regardless of their size, then the inflorescences become necrotic even before they open. This is followed by yellowing of the leaves from the lower to the higher fronds. At this stage the flag and spear leaves may also be yellow or dead. Finally, the whole crown falls off the tree leaving a naked trunk. This final stage is known as "telephone pole" due to its appearance. In juvenile trees, the symptoms include a yellowish discoloration from the distal ends of the fronds, followed by the total yellowing and decay

of the spear leaves and meristem (Tsai 1980). Symptoms in roots have also been reported. Eden-Green (1976, 1982) found that induced adventitious roots become increasingly necrotic as yellowing of leaves progresses. In mature palms, death occurs 3-6 months after the appearance of the first visible symptom (Grylls and Hunt 1971).

Physiological and Biochemical Alterations Caused by LY

Several physiological and biochemical modifications associated with LY have been documented. Alterations in both phloem and xylem fluxes, nutrient supply, stomatal behavior, enzyme levels, electrophoretic patterns and growth regulators, have been detected in diseased palms when compared to healthy ones.

Phloem Transport. MLO have been found confined to sieve tubes in diseased plants (Howard et al. 1983, 1984; Parthasarathy 1974; Thomas 1979). The presence of MLO in the sieve tubes has been associated with phloem malfunctions (Eden-Green and Waters 1982). Although the exudation rate increased in palms at the first stages of the disease (stage 2), in severely affected palms (stage 4-7), this rate was drastically reduced (from 15 ml/hour to less than 5 ml/hour). This phenomenon could be explained as it has been proposed by Kollar et al. (1989) for the infection of apple by MLO. When the MLO population is low, there is impairment of the sieve tube sealing mechanism. As the MLO titer increases, the tubes can become obstructed reducing phloem flux. This obstruction could be the result of necrosis, callose deposition, or even the MLO themselves occluding the sieve pores. In *Cocos nucifera*, callose deposition at early stages of the disease has been reported (Nienhaus et al. 1982). There is some electron (Beakbane et al. 1972) and fluorescence (Cardena-López et al. 1989) microscopic evidence that MLO may be blocking the sieve

tubes. However, an actual physical blockage of the flow in the sieve tubes of LY-infected *Cocos nucifera* plants remains to be demonstrated.

Xylem Transport. As opposed to phloem, there is no evidence of the presence of MLO in the tracheids or evidence of any physical obstruction of tracheary elements on LY diseased palms (Dabek 1973). However, there is enough evidence that water transport through xylem is reduced as a result of LY (Carter 1965, Dabek 1973, Eskafi et al. 1986). Using ^{32}P , Eskafi et al. (1986), showed that xylem transport was reduced 75% in LY diseased palms when ^{32}P was applied at the base of the petiole, and 100% when applied through either stem or roots. After studying root uptake capacity and water flow in excised roots and petioles, respectively, they suggested that although malfunction of root and petiole may limit water movement in LY affected palms to a certain extent, the limiting factor is closure of stomata. However, since they did not study transport through excised stems, reduced water transport at this level cannot be ruled out.

Stomatal Behavior. Healthy palms show a typical diurnal fluctuation in xylem pressure, from -1 bar at night to -10 bars at midday. In LY diseased palms, however, these normal fluctuations did not occur showing xylem pressures of around -4 bars during most of the day (McDonough and Zimmermann 1979). This results from the fact that stomata remain closed at midday in LY affected palms (Eskafi et al. 1986, Leon et al. 1989). In fact, Leon et al. (1989) showed that stomatal diffusive conductance of LY diseased palms remained as low as 0.01 cm/s during most of the day, whereas healthy palms showed a fluctuation from 0.01 to 0.2 cm/s.

Stomatal closure has also been associated with other diseases caused by MLO in species as varied as *Catharanthus roseus*, *Ulmus americana*, *Fraxinus americana*, *Prunus virginiana* and *Zea*

mays (Matteoni and Sinclair 1983). This suggests that stomatal closure may be a common mechanism of response to invasion by most MLO in plants. This stomatal closure may be explained by hormonal imbalances (see below). However, it can also be caused by other compounds like toxins (Ayres 1981), phenols (Plumbe and Willmer 1986a), and phytoalexins (Plumbe and Willmer 1986b), as found in other plant systems. Therefore, the possible role of these substances in the LY-induced stomatal closure should be studied.

In LY-affected plants of *Cocos nucifera*, stomatal closure has been detected 2 weeks before the appearance of any other LY symptoms (McDonough and Zimmermann 1979, Eskafi et al. 1986). For this reason, it has been suggested that stomatal closure might be a useful parameter for the detection of the disease at a relatively early stage.

Nutrients. Dabek and Hunt (1976) reported the effect of exogenous application of various compounds including some nutrients such as copper and zinc on diseased fronds of *Cocos nucifera*. The application of both copper and zinc to yellow leaves of LY affected palms resulted in their re-greening. This might suggest that the yellowing that LY diseased plants experience is the result of micronutrient deficiency, perhaps associated with the lack of water flow through xylem reported before (McDonough and Zimmermann 1979). However, Stemmer et al. (1982) studied the trunk phloem sap content of healthy and diseased palms and they did not find significant differences in the amounts of Cu, Zn, K, N, Mg, Ca and Fe. This discrepancy could be due to the different tissues analyzed.

Photosynthetic Rates. With stomata closure affecting CO_2 uptake in palms with LY, photosynthetic rates should be expected to be reduced. We have found that palms at early stages of the disease (partial stomatal closure) have similar photosynthetic rates to those of healthy palms,

but in severely LY affected palms (fully closed stomata) photosynthetic rates are greatly reduced (Santamaría J.M., unpublished). However, stomatal closure is not necessarily the only cause of reduction in photosynthesis. Leaf chlorophyll content is steadily reduced as the disease progresses (Sanchez et al. 1989). Additionally, we have observed a decrease in a polypeptide of Mr = 55,000, which suggests a reduction in the large subunit of ribulose bisphosphate carboxylase (RUBISCO) in leaf extracts of severely LY affected palms when analyzed by sodium dodecyl sulfate polyacrylamide gel electrophoresis (SDS-PAGE) (Villanueva M.A., unpublished). Certainly, more detailed studies using antibodies and studies on enzyme activity are required to define the role of RUBISCO on photosynthesis decay in LY affected palms.

Photosynthesis in diseased plants can also be altered by modifications of its end-products as occurs in various diseases caused by virus, bacteria or fungi (Buchanan et al. 1981). These modifications include the utilization of sugars produced in photosynthesis to produce amino acids. Whether this is the case in LY affected *C. nucifera* palms and whether this may contribute to the increased arginine content found in these palms (Sanchez et al. 1989) remains to be defined.

Plant Growth Regulators. Although systematic studies on plant growth regulators (PGR) in LY affected palms have not been reported so far, Dabek and Hunt (1976) made a series of observations which indirectly suggest changes in PGR availability in LY affected tissue. They studied the effect of exogenous applications of gibberellic acid (GA), kinetin and indoleacetic acid (IAA) on longevity of healthy and diseased *C. nucifera* detached pinnae. Treatment with GA caused an increase in the longevity of both healthy and diseased pinnae as well as re-greening of initially yellow areas of diseased pinnae. Kinetin and IAA did not have any effect on the longevity of either healthy or diseased pin-

nae. Regarding re-greening of yellow diseased pinnae, the effect of kinetin was only partial, whereas combined with IAA it was more effective. The authors suggested that this could be indicative of a disturbance of the hormonal balance in coconut palms affected with LY.

One of the alterations of LY is stomatal closure (Eskafi et al. 1986). Abscisic acid (ABA) has been demonstrated to control stomatal closure in several species (Zhang et al. 1987). An increase in ABA may be responsible for stomatal closure in LY affected pinnae. So far no attempts have been made to test this idea. Alternatively, a reduced supply of cytokinins might also result in stomata closure (Reid and Bradford 1984). Therefore, stomata closure in LY affected palms could also result from a reduced supply of cytokinins particularly since both phloem and xylem transport are impaired. Moreover, evidence exists that roots are damaged in LY affected palms (Eskafi et al. 1986), so that cytokinin synthesis in this tissue may be affected. It is likely that both ABA and cytokinins are involved in the stomatal closure in LY infected palms.

Some of the visible symptoms of LY include premature abscission of fruits and leaf senescence. Ethylene has been involved in both fruit abscission (Sexton et al. 1985) and leaf senescence (Roberts et al. 1985) in several species and may also be related to these processes in LY. If this was the case, an accumulation of ethylene should be expected in LY diseased palms. As far as we know, no direct measurements of ethylene have been made in LY diseased tissues. However, Dabek and Hunt (1976) tested the capacity of healthy and diseased pinnae to promote ripening of bananas. They found that healthy pinnae promoted a faster ripening than diseased pinnae which they believe may be related to a lower production of ethylene in diseased tissue. However, in the whole plant, synthesis of ethylene may also take place in the roots and the capacity for ethylene evolution of

detached pinnae may not necessarily reflect the ethylene production capacity of the whole LY affected plant.

In order to clarify whether or not changes in PGR concentrations take place in LY and if they have a causal relationship with the development of symptoms, more detailed studies on endogenous PGR concentrations of diseased tissue are required.

Enzyme Activities and Protein Electrophoretic Patterns. The response of a plant to pathogens can be varied. The most characterized responses include changes in enzyme levels such as peroxidases (Agrios 1969, Kanazawa et al. 1965, Solymosy et al. 1967). Dabek (1974) found no differences in peroxidase activity from either healthy or LY affected palms. However, in diseased palms there was a negative relationship between the polyphenolic compound content and the peroxidase activity. This relationship was not observed in healthy palms. He suggested that once well characterized and standardized, this relationship could be used as an early symptom diagnostic test for LY since the phenomenon appeared before visual symptoms occurred. Nevertheless, no further reports have been made.

In another study, catalase activity, which is involved in polyphenol metabolism, was found to increase in early stages of the disease (i.e. before the first visual symptoms) (Dabek 1974). The activity of the enzyme decreased as the disease progressed, until it was reduced to 50% of the activity found in healthy palms (Dabek and Hunt 1976). These authors suggested that this decrease was a consequence of the damage to the pathway of protein biosynthesis and was not an exclusive symptom of LY.

Other studies have focused on changes in enzyme activities from extracts analyzed by SDS-PAGE. Among the detected enzymes in both healthy and diseased palms were three peroxidases, five esterases, a ribonuclease and an alkaline phosphatase (McCoy 1983). However, no variations in

the pattern from healthy compared to diseased tissue were observed.

The determinations of protein changes in diseased palms have been analyzed by raising antibodies against diseased palms and by sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) of extracts from phloem and petiole base tissue. Charudattan and McCoy (1975) reported that the binding of antibodies raised against phloem exudate filtrates of diseased palms was specific for LY affected palms but not for healthy palms of *Cocos nucifera* and *Veitchia merrillii*. However, no further reports of the antigenic nature of the molecule(s) recognized by the antibodies exist, nor have these antibodies been applied for diagnostic tests. In a separate study McCoy (1983) found a low molecular weight protein in extracts of bud tissue from diseased *V. merrillii* palms analyzed by SDS-PAGE, which was not present in the healthy counterpart. In contrast, in LY affected *C. nucifera* plants, this protein was not observed and the SDS-PAGE patterns were identical for both healthy and diseased palms whether bud tissue (McCoy 1983) or phloem exudate extracts (Stemmer et al. 1982) were analyzed.

It would be interesting to know if the antibodies raised against phloem exudate filtrates from diseased palms bind the low molecular weight protein found in *V. merrillii*. It would also be worthwhile to purify this low molecular weight protein for raising antibodies against it to be used in further studies or as a diagnostic test provided the antigen is present in the pre-symptomatic stage.

Arginine Content. If the MLO that causes LY is similar to those species of *Mycoplasma* that require arginine, it would be expected that high levels of arginine in host tissues favoured infection, whereas low levels of this amino acid would not. Barcelon and co-workers (1983) tested this idea and analyzed the arginine content in the leaves of several palm species with different degrees of susceptibility to LY.

They found that those species with higher levels of arginine were more susceptible than those with lower levels. This could be very useful as a criterion for selection of tolerant individuals.

The content of arginine in LY affected palms has been measured by Stemmer et al. (1982). The arginine content in the phloem sap of diseased leaves was about 66% greater than in that of healthy leaves. The difference was not statistically significant; however, it may be indicative of an actual difference. In fact, we have found a four- to five-fold increase in arginine content in severely affected leaves (Sanchez et al. 1989) which suggests a higher proteolysis in severely affected palms. Analysis of the proteins from the nuts of healthy palms (Hagenmaier et al. 1974, 1975) has shown arginine to be the second most abundant amino acid. If this is also true for the proteins in other plant parts (e.g. leaves), an increased availability of arginine would be expected in infected palms. This would favor the survival of arginine-utilizing MLO. In addition, preliminary results in our laboratory show a positive correlation between degradation of proteins and disease severity, as shown by the analysis of protein extracts from pinnae from intermediate leaves by SDS-PAGE (Villanueva, M.A., unpublished). Alternatively, the increased arginine content may result from an increased synthesis either as a plant response, or induced by the MLO. The latter could be brought about via transformation since MLO has been shown to contain plasmids (Sears et al. 1989, Davis et al. 1988).

Experimental Model

In an attempt to integrate the information described above, we present the following experimental model (Fig. 1).

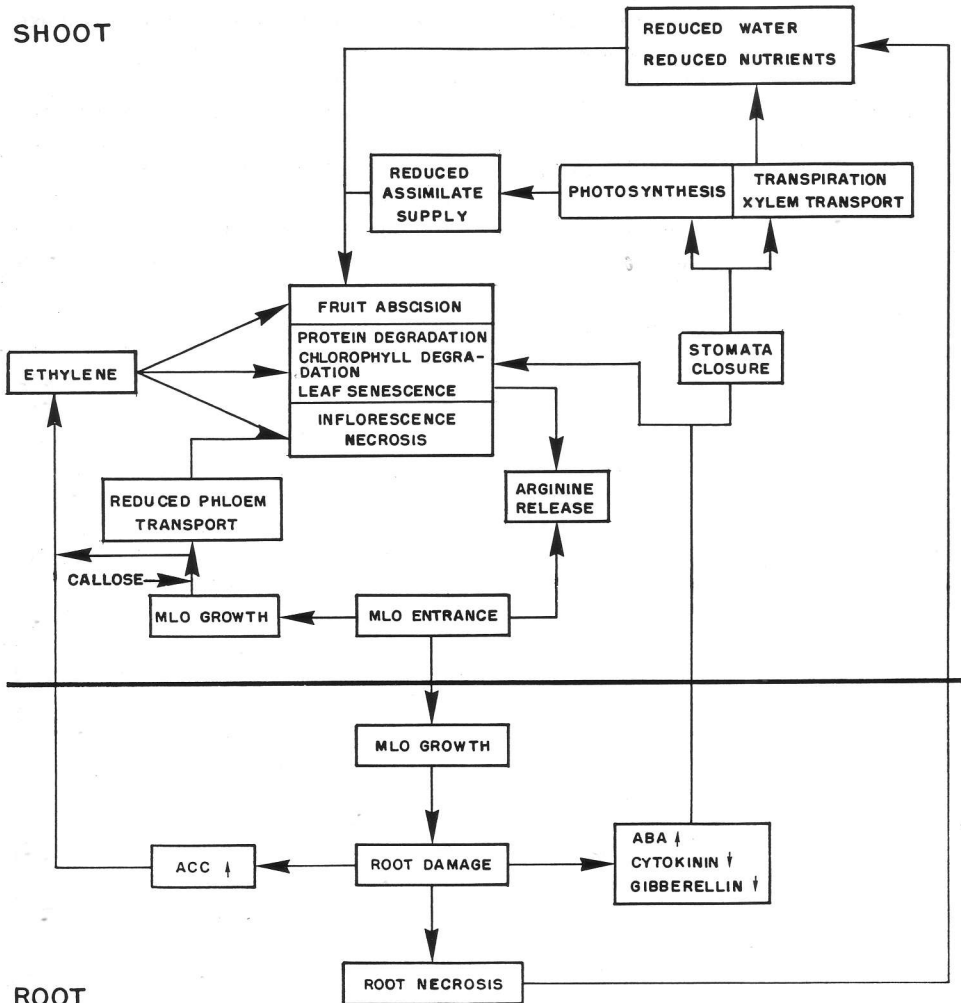
Pre-symptomatic Stage. Once the MLO are introduced to the phloem by the vector, it may be transported by mass flow to actively-growing plant parts (e.g. young

leaves and roots, developing inflorescences and vegetative meristems). There, they can be provided with an adequate supply of nutrients including arginine, which could be particularly important if MLO associated with LY requires this amino acid for its growth. In such a case, the demand of this amino acid at the beginning of the infection may be expected to be satisfied by the free arginine content within the plant.

During this stage, which takes about four to nine months (Dabek 1974, 1975), the MLO population is presumed to grow and initiate physiological and biochemical changes. Only a few of these, such as alterations in polyphenol levels and peroxidase and catalase activities, have already been documented (Dabek 1974). However, other changes can also occur in both roots and aerial parts such as production of callose, further growth of the MLO, or production of MLO substances for the alteration of the plant metabolism. These alterations may cause a general disruption of plant performance such as early root damage. This could precede the root necrosis reported in the symptomatic stage (Eskafi et al. 1986). If this is the case, root malfunction could lead to hormonal imbalance, as has been reported for flooding (Reid and Bradford 1984) and water stress (Davies et al. 1981).

Symptomatic Stage. The earliest symptom which can be detected is stomata closure (Eskafi et al. 1986). This can be reflecting changes in PGR balance. Both increases in ABA content (Davies et al. 1981) and decreases in cytokinin and gibberellin contents have been shown to promote stomata closure (Jackson and Campbell 1979). Both changes in leaf PGR contents can originate in other plant parts. Zimmermann proposed as early as 1979 that in LY affected plants a metabolite moving from the roots or stem to the leaves was responsible for stomata closure. More recently, stomata closure in water stressed plants has been shown to be mediated by

SHOOT



ROOT

1. Proposed experimental model which integrates the sequence of physiological and biochemical alterations that lead to the appearance of symptoms of lethal yellowing in palms.

ABA which is apparently synthesised in the stressed roots and then mobilized to the leaves (Zhang et al. 1987). Plants under flooding also show stomata closure which has been associated with a reduced synthesis of cytokinins and gibberellins as roots are damaged (Reid and Bradford 1984). In the case of LY roots are affected; therefore stomatal closure could be the result of an altered PGR balance. This idea is consistent with the results obtained by Dabek and Hunt (1976) suggesting that

in LY infected coconut palms, cytokinin and gibberellin contents are reduced.

A sustained stomatal closure can lead to dramatic changes in the performance of the palm, for instance, reduced rates of photosynthesis due to a shortage of carbon dioxide uptake. Additionally, it could indirectly cause a reduction in the supply of water and nutrients as transpirational driving force decreases. This reduced nutrient supply may cause fruit abscission as it has been proposed by Zimmermann (1979).

Since several other types of stress have been shown to cause ethylene evolution (Jackson and Campbell 1975, Jaffe and Telewski 1984), an increased ethylene content could also be involved in promoting early fruit abscission. An increase in ethylene synthesis in aerial parts could be favored by increased 1-aminocyclopropane-1-carboxylic acid (ACC) synthesis in damaged roots as reported in the case of flooding (Reid and Bradford 1984).

In addition, the presence of MLO in the phloem vessels has been associated with callose deposition (Nienhaus et al. 1982) which, in turn, could lead to ethylene evolution. This is supported by the fact that ethylene evolution in the case of thigmomorphogenesis has been demonstrated to follow callose deposition and to keep a causal relationship with the development of symptoms (Jaffe and Telewski 1984).

As the disease develops, pronounced leaf yellowing appears. This also could be the result of a reduced nutrient supply and hormonal changes such as increases in ethylene content and decreases in cytokinins and gibberellins leading to leaf senescence. Further damage in roots could, in turn, be favored by reduced assimilate supply from senescing leaves. In this way the apical meristem and younger leaves would also suffer from reduced nutrients and assimilate supply, eventually leading to necrosis in the apical meristem and favoring senescence of younger leaves.

At later stages when the MLO population has grown, the arginine demand should be expected to be great if the microorganism depends on this amino acid. If regular levels of free arginine are not enough, then MLO would require additional sources of arginine, for instance, arginine-rich proteins from which arginine could be released by hydrolysis in senescing leaves. The possibility that the extra arginine resulted from a shift in the end products of photosynthesis, as occurs in other diseases, cannot be discarded. Alternatively, arginine *de novo* synthesis could be occurring and

maybe controlled by MLO. MLO from other diseases have been shown to contain plasmids (Davis et al. 1988, Sears et al. 1989). Therefore, the mode of action of the LY-MLO via transformation cannot be ruled out.

Conclusions

The present knowledge on physiological and biochemical aspects of lethal yellowing is in general inconclusive, since it is mostly based on indirect evidence. Therefore, it is important to extend our understanding of the alterations caused by LY, in particular during the presymptomatic stage, since several events occurring in the symptomatic stage should result from changes occurring earlier. It is difficult to study these early events since we lack both early diagnostic methods and a reliable transmission system. Some of the possible alternatives to develop the former are: a) the production of antibodies which react against antigens of both presymptomatic and symptomatic stages; b) the systematic monitoring of physiological and biochemical alterations (photosynthetic rates, enzyme activities, electrophoretic patterns, etc.) in healthy palms of infected areas until they start developing symptoms; and c) the obtention of DNA probes to identify MLO DNA in infected palms.

Other areas which require further study are: a) the culture (possibly via organ culture) and ultimate identification of the causal agent of LY, b) mechanisms of MLO dissemination, c) MLO-palm arginine relations, d) changes on the balance of growth regulators.

The integration of this knowledge might lead to the development of selection criteria for coconut palms resistant to lethal yellowing and the establishment of adequate ways to control the disease.

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Sabal gretheriae, a New Species of Palm from the Yucatan Peninsula, Mexico

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Sabal is a New World genus, ranging in the Northern Hemisphere from the Caribbean Islands and Southeastern United States, through Mexico and Central America, to Venezuela (Bailey 1944).

Mexico has the greatest diversity of *Sabal* with 7 of the 15 known species (Zona 1990). The Yucatan Peninsula comprises the states of Campeche, Quintana Roo and Yucatan, where 3 wild species of *Sabal* occur, *S. mauritiiformis* (Karsten) Grisebach & H. A. Wendland, *S. mexicana* Martius and *S. yapa* Wright ex Becari (Quero 1989).

I conducted a recent survey on the "Palmas de la Peninsula de Yucatán" comprising intensive field work in order to verify distribution ranges of some of the species, as well as to confirm the identity of some palms for which I had not enough material. Collecting flowers and fruits from a *Sabal* population growing in the north-eastern portion of the Peninsula, I noticed that these palms, while having a strong similarity to *Sabal mexicana*, did not correspond with the latter species nor with the other taxa commonly occurring in the Yucatan Peninsula. Because this geographic region is located close to Cuba, I assumed that it could be a Cuban species, such as *Sabal maritima* (Kunth) Burret or *S. palmetto* (Walt.) Loddiges ex J. A. & J. H. Schultes (sensu Zona 1990). In order to clarify the situation, I examined herbarium and living wild specimens in Cuba.

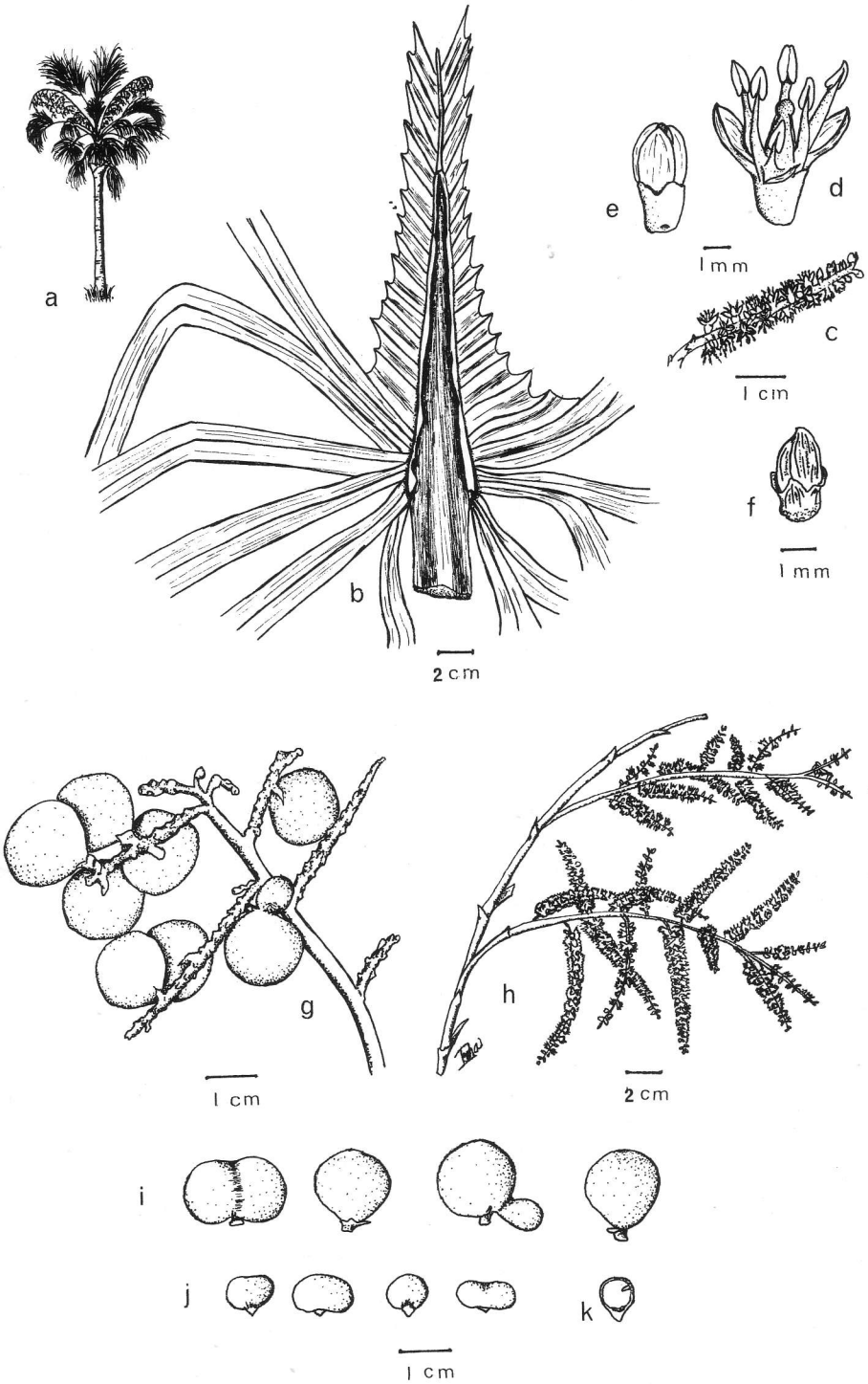
After studying the Cuban materials, I

concluded that there are remarkable differences between those *Sabal* species from Cuba and those of Yucatan, sufficient for those from the Chiquila region in Quintana Roo to be considered as belonging to a new species.

Sabal gretheriae Quero, sp. nov.

(figs. 1-6).

Palma mediocris usque ad 8 m alta, trunco 20-30 cm diametro. Folia magna, lamina ca. 2 m lata, petiolis apice 3-4 cm latis, glabris, hastula longe acuminata, glabra, marginibus incurvatis, 13-22 cm longa, segmentis numerosis, unicostatis, costa media prominente, venis transversalibus conspicuis uterque paginis, segmentis centralibus usque ad 1.30 m longis, 7 cm latis, apice bifurcatis, palman longitudine $\frac{1}{3}$ laminae, sinibus filiferis. Inflorescentiae ascendentes, folias non excedentes, 1.80-2.00 m longae, ramosissimae. Flores albi, fragrantés, calyce costato, urceolato vel cupulato, ca. 1.5 mm longo, petalis spatulatis siccatis costatis, 5 mm longis, filamentis ca. 5 mm longis, antheris 1.2-1.5 mm longis, pistillo conico ca. 4 mm longo, apice papilloso. Fructus subglobosi vel pyriformes, nigri, 16-20 mm lati, 16-18 mm alti. Semina subglobosa vel ovata-depressa, base plerunq; manifeste apiculata; micropyle supraequatoriali. Typus: Mexico, Quintana Roo, 4 km S of Chiquila on road to Kantunilkin, Quero 3592 (Holotypus MEXU; isotypi CICY, NY, UAMIZ, US).



Medium-sized palm to ca. 8 m tall; trunk 20–30 cm diam., with persistent petiole bases only near the crown. Leaf large, with blade more than 2 m diam.; petioles 1.20–1.40 m long, 5–6 cm wide in the middle and 3–4 cm wide at the apex; hastula narrowly triangular to acuminate, 15–22 cm long, glabrous, never lepidote, with incurved to erect margin, never flat; segments 100–120, robust, the middle ones 1.10–1.30 m long, 6–7 cm wide, with a prominent midvein and very conspicuous transverse veinlets on both surfaces, segment apices bifid for 30–40 cm, generally breaking at the apex; palman 40–50 cm long, filiferous at the sinuses at least in the smaller segments, the blade from the larger segments frequently marginally broken above the sinus in a narrow strip 5–11 mm wide. Inflorescence appressed-ascending with 3 orders of branching, not exceeding the leaves, 1.80–2.0 m long, with 25–28 primary branches; rachillae 9–11 cm long, 1–1.2 mm diam. in the lowermost primary branches. Flowers white, fragrant, 4–4.5 mm long; calyx urceolate to cupulate, trilobed, 1.5–2 mm long, strongly costate when dry; petals spathulate, narrow ca. 4 mm long, 1.5 mm wide, ascending to spreading at anthesis, strongly costate when dry; filaments ca. 5 mm long, anthers 1.2–1.5 mm long, pistil conical ca. 4 mm long, with papillose apex, ovary 1.2–1.5 mm high. Fruit globular to globular-pyriform, 16–20 mm diam., 16–18 mm high, black at maturity, epicarp smooth, mesocarp fleshy to 4 mm thick. Seed subglobose to irregularly depressed ovoid, not concave, 9.5–12.2 mm diam., 6–9 mm high, frequently strongly apiculate at the base by the funicular remnant, to 2.2 mm high; embryo supraequatorial.

Specimens examined: MEXICO: Quin-



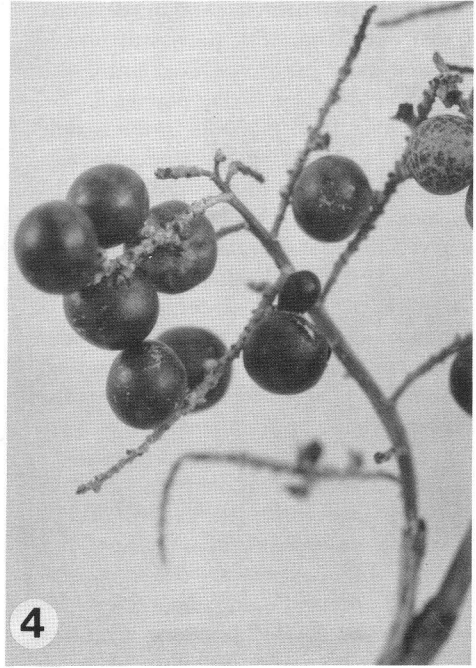
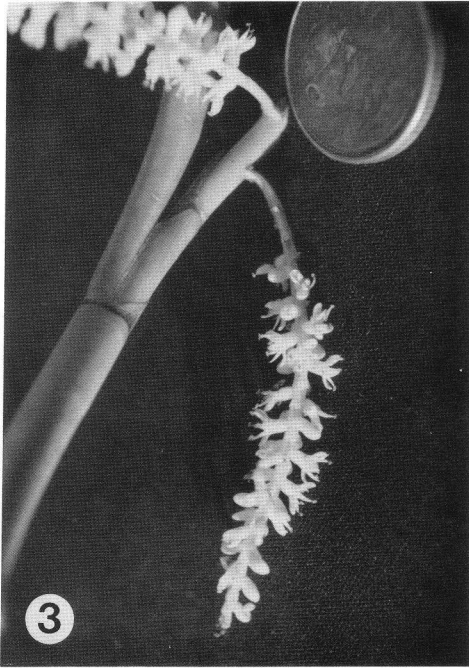
2. Habit of *Sabal gretheriae* in the type locality.

tana Roo: 4 km S. of Chiquilá on the road to Kantunilkin, *Quero* 3592 (Holotype MEXU, isotypes CICY, NY, UAMIZ, US); 2 km S of Chiquilá on the road to Kantunilkin, *Orellana* 831; 3 km S of Chiquilá on the road to Kantunilkin, *Orellana* 837; 4 km S of Chiquilá on the road to Kantunilkin, *Quero* 3588; 3.5 km S of Chiquilá on the road to Kantunilkin, *Quero* 3591; 2.5 km S of Chiquilá on the road to Kantunilkin, *Quero* 3596 (all CICY).

In addition, numerous measurements were made from randomly distributed plants in the population.

This species is named in honor of Rosaura Grether of the Department of Botany, Universidad Autónoma Metropol-

1. *Sabal gretheriae*. a) general appearance of the palm; b) part of the leaf; c) rachilla with flowers; d) open flower; e) flower bud; f) dried flower; g) fruiting branches; h) flowering branches; i) fruits; j) seeds; k) cross section of seed.



3. Close-up of a rachilla with open flowers. 4. Primary branch with fruits.

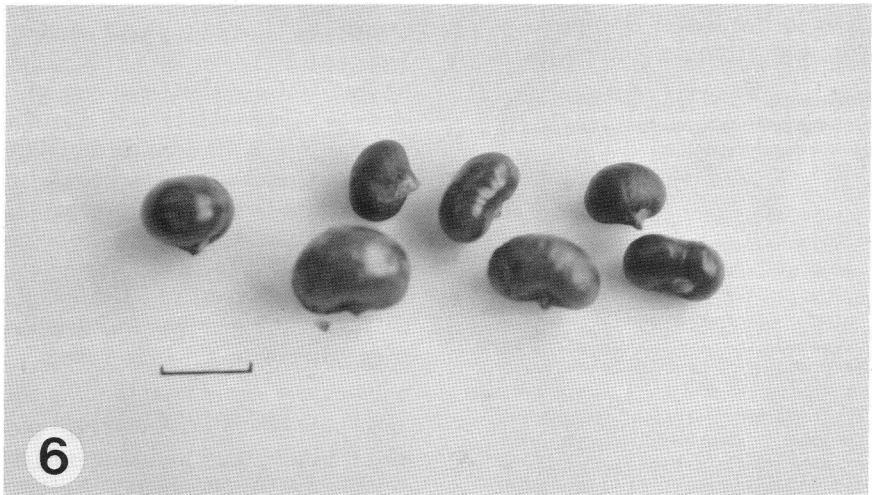
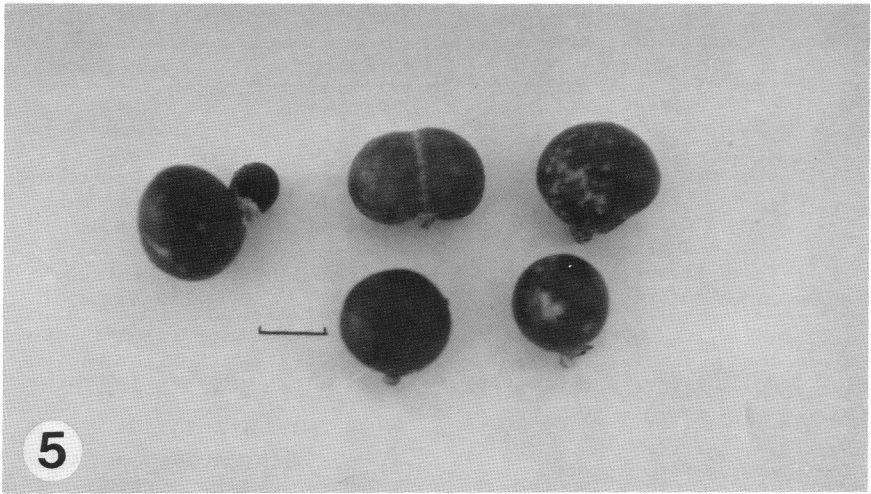
tana-Iztapalapa, who collected palms with the author for many years.

Distribution: The new species is only known to date in the vicinity of Chiquilá, Quintana Roo, a small coastal town located in front of Holbox Island at the northeasternmost point of the Yucatan Peninsula.

This palm is abundant in this restricted area, growing under disturbed conditions, on sandy-loam plane soils. At the limit of its distribution, it grows in association with *Sabal yapa* and *Acrocomia mexicana* Karw. ex Martius.

Sabal gretheriae can be confused in the Yucatan Peninsula with *S. mexicana* because of the unicastate segments, large fruits and petals costate when dry. However, both species can readily be distinguished because the former has the broadest leaf segments 6–7 cm, appressed-ascending inflorescences, spatulate petals, and spheroidal depressed not concave

seeds, 7–9 mm high with an irregular outline, while *S. mexicana* has segments 3.2–5.3 cm wide, an arcuate inflorescence, obovate to oblong petals, and obloid concave seeds, 5.7–7.4 mm high. In addition, some anatomical differences exist between them, both in type and distribution of the bundle sheath extensions and the small adaxial vascular bundles; *S. mexicana* has no extensions of the major vascular bundles and also has 3–7 small vascular bundles between the major ones; *S. gretheriae* has extensions in the major vascular bundles and 7–9 small vascular bundles. The karyotype of the new species comprises 14 metacentric pairs, 8 of them with satellites and 4 submetacentric pairs, 1 of them with satellites, while *S. mexicana* has 14 metacentric pairs, 4 of them with satellites and 4 submetacentric pairs (Palomino, personal communication). Furthermore, *S. mexicana* grows only in the southwestern portion of the Peninsula, in the state of



5. Variation in fruit shape (bar indicates 1 cm). 6. Variation in seed shape (bar indicates 1 cm).

Campeche, and flowering from January to April, while *S. gretheriae* grows only in the northeast, in the state of Quintana Roo, and flowers from May to August.

The new species can be distinguished

from the two apparently more related Cuban species by the petals costate when dry. Other differences between them are as follows:

Table. Comparison of the new species with two others.

	<i>Sabal gretheriae</i>	<i>Sabal maritima</i>	<i>Sabal palmetto</i>
Segments	6-7 cm wide	2.4-5.3 cm	2.5-4.2 cm
Hastula	glabrous	lepidote	lepidote or glabrescent
Calyx	1.2-1.5 mm long	1.5-2.2 mm	1.3-2.4 mm
Petals	spathulate, costate	obovate, non-costate	spathulate non-costate
Fruit	16-20 mm diam. 14-16 mm high	8.5-14.2 mm diam. 8.4-12.6 mm high	8.1-13.9 mm diam. 8-13.8 mm high
Seed	spheroid depressed 9.5-12 mm diam. 6-9 mm high	obloid concave 6.5-9.7 mm diam. 4.5-6.2 mm high	obloid concave 5.4-9.7 mm diam. 4-7 mm high

Also, it should be noted that the new species can be distinguished from *S. palmetto* by the widely spaced nerves and its very prominent transverse veinlets.

depressed, not concave, 6-9 mm high
..... *S. gretheriae*

Key to the *Sabal* Species from the Yucatan Peninsula

- 1. Leaf segments with 3 prominent nerves, the central one more prominent than the lateral; petals not costate when dry
 - 2. Leaves with a small costa, and short palman the segments thus drooping; segments soft and silvery beneath; inflorescence with 4 orders of branching *S. mauritiformis*
 - 2. Leaves with a large costa, strongly curved with long palman; segments hard and green beneath; inflorescence with 3 orders of branching *S. yapa*
- 1. Leaf segments with 1 prominent central nerve; petals costate when dry
 - 3. Trunk with persistent petiole bases in at least the upper 1/3; largest leaf segments 3-5.5 cm wide; inflorescence arcuate; petals obovate to oblong; seeds obloid, concave 5-7.4 mm high *S. mexicana*
 - 3. Trunk with persistent petiole bases only at the top; largest leaf segments 6-7 cm wide; inflorescence appressed-ascending; petals spathulate; seeds spheroidal to ovoid

Acknowledgments

I wish to express my appreciation to the Centro de Investigación Científica de Yucatan (CICY) and to CONACyT (grant: A128CCOE891345(B1-2)), both of them made possible a sabbatical period at Merida, Yucatan, which was essential for this work. I wish to express a special acknowledgment to Dr. Roger Orellana, researcher at CICY for his assistance during the realization of this work, Dr. Fernando Chiang for his assistance with the Latin description, and Dr. Robert Bye and Biol. José Arellano for critically reviewing the manuscript.

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Notes on Roystonea in Cuba

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The *Roystonea* palms of Cuba are one of the most conspicuous elements of that flora, yet surprisingly (or perhaps not surprisingly given their size and bulk), they have received little detailed study. In an early revision of the genus, L. H. Bailey (1935) described two taxa from eastern Cuba and brought to three the number of taxa of *Roystonea* known from that island. Bailey's work, however, merely scratched the surface of the floristic richness of Cuba. Shortly thereafter, León (1943) described three species, all from eastern Cuba, and raised the total number of indigenous *Roystonea* to six. León's work brought recognition to the astonishing diversity of royal palms in the remote eastern province of Cuba, then known as Oriente and now known as Guantánamo.

In mid-September of 1990, I traveled to Cuba to spend three weeks studying the common *Roystonea regia* and the poorly known species of Guantánamo which had not been collected since León's original work nearly a half a century ago.

My first stop in Cuba was the Jardín Botánico Nacional, whose director, Dr. Angela Leiva, is actively conducting research in Cuban palms and has supervised the growth of the palm collection at JBN. The collection is extensive, although Angela laments that she still does not have all the native species of palms in cultivation. The only species of royal palm growing at JBN is *R. regia*, which is proving to be something of a weed. I also met with Dr. Miguel Rodríguez Hernández, who helped arrange my itinerary, and Dr. Vladimir Moreno, a specialist in forestry and

conservation, who was to accompany me to Guantánamo.

Toward the end of my stay in Havana, I had the great pleasure of spending a morning with Onaney Muñoz, who was well known to me as the author of many new species of *Coccothrinax*. His 1982 catalog of the palms of Cuba, co-authored with Atilla Borhidi, was my guide book to much of the fascinating palm flora of that island. We discussed the status of palm research in the Caribbean, problems in conservation, and causes of diversity in the Cuban flora. His generosity in sharing his ideas on biogeography is much appreciated.

The palm specialist O. F. Cook (1900) created the genus *Roystonea* to accommodate the Cuban royal palm, *R. regia*, first collected by the famed explorers Alexander von Humboldt and Aimé Bonpland around 1800. Carl Kunth, a German botanist working with Humboldt and Bonpland's collections, had placed the species in the genus *Oreodoxa*, a genus now known to be a rejected synonym of *Prestoea*. Cook recognized the Cuban royal's distinctiveness and placed it in *Roystonea*, a genus he named in honor of General Roy Stone, a U.S. Army engineer who served in Puerto Rico. Bailey took up the genus in 1935 and recognized 12 taxa, including two varieties of *R. regia* that he described from Cuba. He again published a revision of the genus in 1949, in which he incorporated the Cuban species described by León just six years earlier, and recognized a total of 17 taxa from South America and the islands of the Caribbean. Allen (1952) added two more taxa to the genus and



1. *Roystonea regia* var. *regia* on a hillside in the Municipio de Yateras, Guantánamo.

extended its range to include Central America. At present, the genus includes approximately 12 taxa, with the center of diversity in the province of Guantánamo in eastern Cuba.

Roystonea regia* (Kunth) Cook var. *regia

The most abundant and one of the most useful palms in Cuba is the “palma real” or “palma criolla,” the royal palm (Fig. 1). It is the national tree of Cuba, and its likeness appears in official seals and crests as well as in folk art. It grows in fertile, well drained soil throughout the island up to elevations of approximately 1000 m. It is immediately recognizable by its concrete

white trunk, which is usually ventricose (slightly swollen) in the middle, but it may be irregularly swollen or constricted anywhere along its length. It bears a full crown of leaves above a green crownshaft, and produces several infructescences throughout the year.

Roystonea regia var. *regia*, as well as other *Roystonea* species, is most commonly used in two non-destructive ways in Cuba: fruits (“palmiche”) are used to feed hogs, and leafbases (“yaguas”) are used as a waterproof covering for bales of tobacco. Both uses are current in Cuba today and are not dying out or being replaced with other materials. Another common but destructive use of *Roystonea* is for timber. Planks are cut from the trunk



2. Destructive uses of *Roystonea*. A. Wood planks cut from *Roystonea* sp. and used for rural home construction, Vega Larga, near Baracoa. Thatch is coconut, *Cocos nucifera*. B. Furniture at the Jardín Botánico Nacional made from the trunks of *R. regia* var. *regia*. Note the royal palm motif.

and used for siding in rural houses (Fig. 2a). Furniture is also made from the wood (Fig. 2b).

Modern statistics for the use of yaguas are lacking, but La Rosa (1974) reported that in the province of Las Villas alone (now the provinces of Sancti Spiritus, Villa Clara, Cienfuegos, and part of Matanzas) nearly 2.1 million yaguas were used to wrap bales of tobacco. Four yaguas are required to cover one bale. Although 2.1 million may seem incredible, Ruebens (1968) estimated that there are more than 11 million individuals of *R. regia* var. *regia* on the island of Cuba!

Palmiche is a valuable commodity all over Cuba. It is the preferred foodstuff for fattening hogs. Ideally, a hog enclosure includes one or more royal palms so that the hogs can feed on the fruits as they drop to the ground throughout the year. If the hog enclosure does not include royal palms, skilled climbers, called *desmochadores* (Fig. 3), cut infructescences while the fruits are still red (i.e., before they turn purple-black and drop off), and the fruits are allowed to ripen in a shaded place before feeding to the hogs. Alternatively, the fruits are allowed to ferment, and the fermented fruits are fed to the hogs as silage.

Palmiche is rich in oil. Ruebens (1968) found that on average, fresh palmiche mesocarp is 10.7% oil and that fresh seeds are 21% oil. Unlike most oils derived from palms, palmiche oil is unusually high in unsaturated fatty acids, the more desirable fatty acids for edible oils. Stillman and Reed (1934) found that the fatty acid composition of palmiche kernel oil is as follows: 16.0% myristic acid, 7.5% palmitic acid, 1.0% stearic acid, 32.0% lauric acid, 28.5% oleic acid, 9.5% linoleic acid, and 5.0% capric acid. By comparison, oleic acid, an unsaturated fatty acid, comprises 13.0–24.4% of the oil of *Bactris gasipaes* kernels and only 10.5–18.5% of the oil from *Elaeis guineensis* kernels (Lleras and Coradin 1988).

According to the Food and Agriculture Organization of the United Nations, Cuba imports virtually all of its vegetable oils, including 400 MT of olive oil and 95,000 MT of sunflower oil annually (FAO 1987). On several occasions, palmiche oil extraction facilities have operated in Cuba to take advantage of this abundant natural resource. Ruebens (1968) provided a detailed description of an extraction facility near Remédios, Villa Clara, which had the capacity to produce 5.8 MT/day of palmiche oil for industrial use. The plant, however, is no longer operational. I suspect that the difficulties in harvesting palmiche and providing the quantity of fruit needed by the plant made the facility economically unfeasible. However, economic conditions in Cuba's future may once again make palmiche oil a profitable proposition.

Onaney Muñoz related to me an interesting anecdote that during the Prohibition Era, the notorious Chicago gangster Al Capone operated a facility in Havana for making laundry soap with palmiche oil. The facility was merely a front for his illegal rum running business, and after Prohibition was repealed, he sold the soap factory. Onaney mentioned that although the soap was of excellent quality, the factory soon went bankrupt without the clandestine support from the rum business.

Roystonea regia var. **maisiana** Bailey and var. **pinguis** Bailey

Bailey described these varieties to accommodate plants that he felt were only slightly different from the common *R. regia* var. *regia*. *Roystonea regia* var. *maisiana* (Fig. 4), endemic to Maisí, where it is abundant, is much more slender and less ventricose than the typical variety. I measured a population of *R. regia* var. *maisiana* and found that the trunk diameter at breast height averaged 36.5 cm (N = 11), compared with an average of 46.9 cm (N = 25) for a population of *R. regia* var. *regia*. This species would be an elegant



3. Julio Escalante, a skilled *desmuchador*, climbing *Roystonea regia* var. *regia* near Baracoa.



palm for cultivation, but virtually nothing is known of its horticultural requirements.

In contrast, *R. regia* var. *pinguis* is, according to Bailey (1935), a more robust palm, described from the Imías River region of the southern coast of Guantánamo. I found the *Roystonea* palms at the type locality to fit the description of *R. lenis* (see below) and suspect that the two taxa may be conspecific.

Roystonea lenis León

This palm is known by the common name "palma de seda," which translates to "silk palm." Some palms, subsequently identified as *R. lenis*, were called "palma conga" and "palma india." The reasons behind these common names were not known to the climbers or to the rural people that I interviewed. In overall appearance, *R. lenis* is very difficult to distinguish from *R. regia*. *Roystonea lenis* differs from *R. regia* by the shape of the sepals of the staminate flowers and by the large, nearly spherical fruits with hard, durable endocarps. The latter characteristic became abundantly clear as we spent many hours cleaning seeds prior to bringing them into the United States.

This species was described from a small village named Vega Larga, southeast of the city of Baracoa on the north coast of Guantánamo province; however, we also collected *R. lenis* in the region of Imías on the southern coast, the type locality for Bailey's *R. regia* var. *pinguis*. The Imías palms have large fruits and reniform sepals and thus answer to the description of *R. lenis*. The palm is apparently abundant in both localities and has been less affected by land clearing since it occurs in more mountainous areas west of the Meseta de Maisí.

Roystonea violacea León

"Palma morada," "palma criolla azul," or "palma roja" is still abundant in the region of the Río Maya in Maisí. Having never before seen this species, we passed by several individuals before noticing that the color of their trunks was not the customary concrete white of *R. regia*, but nor was it the "violet" of León's description. With a covering of algae and lichens, the trunk of *R. violacea* at first does not warrant much attention, but when seen growing adjacent to a specimen of *R. regia*, the difference is immediately apparent. The color is almost a milk chocolate brown with just the hint of violet or mauve (See Front Cover); however, older palms seem to fade or age to a more typical pale gray color. The young palms, with only 3–4 m of clean trunk, are the most colorful. One local coffee grower asserted that "palma criolla azul" is merely the juvenile condition of *R. regia*, but there are technical differences other than color that separate the two species.

The flowers of *R. violacea* are also more colorful than those of other species. The staminate flowers are purple at the base of the petals, filaments, and pistillodes. The staminate flowers open before the pistillate flowers and attract numerous bees of the families Apidae and Halictidae. No floral fragrance was detected.

Although certainly a palm of great ornamental value, nothing is known of its horticultural requirements.

Roystonea stellata León

This species is one of the most intriguing in the genus. León was so struck by its star-shaped stigmatic scar that he placed *R. stellata* ("palma blanca") in its own section, *Roystonea* section *Astrophora*. I

←

4. *Roystonea regia* var. *maisiana* and the author, Puriales Abajo, Maisí. Photo by V. Moreno.

was especially hopeful to find this species, but extensive searches of the type locality and vicinity, as well as interviews with climbers and coffee growers, brought forth no specimens. One older grower recalled seeing a fruit with a star-shaped stigmatic scar but could not remember when or from what tree he had seen such a fruit. The type locality, the vicinity of La Yagruma and Pueblo Viejo, was cleared for coffee plantations shortly after the revolution of 1959. Older residents of the area recalled vast stands of palms in Maisí but admit that now all the palms are gone.

Whether *R. stellata* still exists in some small, isolated population or is already extinct is difficult to say, but in either case, the loss of this species is directly attributable to loss of habitat. Borhidi and Muñiz (1983) listed this species as "rare," but I would say it is probably extinct or in immediate danger of extinction in its native habitat. *Roystonea stellata* may be in cultivation at the Botanical Garden of Cienfuegos (formerly operated by Harvard University). Cultivated individuals, if they exist, may represent the only hope for this little known royal palm.

The IUCN conservation statuses of the royal palms endemic to eastern Cuba were given by Dransfield et al. (1988) as "not threatened" (for *R. lenis*), "rare" (*R. regia* var. *pinguis*), and "indeterminate" (*R. violacea* and *R. stellata*). *Roystonea regia* var. *maisiana* was not included in their report. Although *R. lenis* seems less threatened because it occurs in areas less favorable for agriculture, *R. violacea*, *R. regia* var. *maisiana*, and *R. stellata* occupy restricted ranges, and their habitats have been seriously disturbed. Moreover, seedlings and juveniles of these taxa are not common, so even though adult plants may be abundant, they are apparently not reproducing. On area farms, the seeds of those adult palms which have been spared the axe are often harvested for pig feed, thus effectively preventing any natural reproduction. With the exception of

R. stellata which is already endangered or extinct and *R. lenis* which is rare, the *Roystonea* endemic to Maisí might best be classified as vulnerable, "taxa believed likely to move into the endangered category in the near future if the causal factors continue operating" (Dransfield et al. 1988).

Seeds of the Cuban royal palms have been distributed to the Jardín Botánico Nacional, Fairchild Tropical Garden, and the Seed Bank of the International Palm Society. Widespread habitat destruction in Maisí means that cultivation may be the best way of ensuring the continued survival of these species and underscores the important role botanical gardens and the IPS play in palm conservation.

The most interesting question about the Cuban *Roystonea* remains: how did so many species evolve in such a small area, eastern Guantánamo, without any geographical isolation from one another? Despite claims, as yet unsubstantiated, that *Roystonea* taxa hybridize, no hybridization is obvious among the taxa in Guantánamo. The geological history of the area does not suggest that separate land masses (and hence, separate floras) combined to create Guantánamo and the Meseta de Maisí we see today. Did the species evolve elsewhere and somehow migrate to eastern Guantánamo? How do these species maintain their genetic integrity when growing in close proximity? As I continue with my studies of the genus *Roystonea*, I hope to propose answers to these questions.

Acknowledgments

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greatly appreciate the field assistance of Dr. Vladimir Moreno, without whom I would still be wandering around Guantánamo. Lastly, I salute the climbers, José Manuel Leiva and Julio Escalante.

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Obituary: T. A. Davis

T. A. Davis was a familiar name within the scientific community for more than four decades, during which he published over two hundred articles in national and international journals on a variety of natural science subjects. Among them were: abnormalities in the coconut and other palms; behavioral studies of the coconut robber crab; the nesting habit of the baya weaver bird; hatching technique of the Australian thermometer birds; a mathematical solution to the structure of the sunflower head; biometric analyses of fruit production in coconut and arecanut palms based on their phyllotaxy; and studies of the manifestation of the Fibonacci numerical sequence in the morphology of plants as well as in animals.

The sudden death of T. A. Davis on 10 November 1989 was a great loss to science. Dr. Davis's approach to studying the plants and animals which he found around him was, to some, unconventional for this day and age because he always tried to

see nature in its totality, but the results he achieved made important contributions.

Trupapur Antony Davis was born on 9 February 1923 to a Christian family in Nagercoil, Tamilnadu, near the southern tip of India. According to family tradition, one son was to become a priest. Since his elder brother had opted for the priesthood, Antony went to study agriculture. After graduation from Madras University in 1944, he pursued graduate study in crop physiology at Madras Agricultural Research Institute in Coimbatore, graduating with the equivalent of a M.Sc. degree. Antony began his professional career in 1947 as a research scientist at the then Sugarcane Research Station, at Karnal, Punjab, in northern India. A man born and raised in a palm-tree environment his interests naturally turned toward the coconut palm. In 1952, Antony left Karnal and moved south to join the newly-established Coconut Research Station at Kyangulum, Kerala, as a coconut physiologist. Some of his outstanding research findings on the physiology and morphology of coconut palms were published while at Kyangulum.

It was during that period that he met J. B. S. Haldane, the famous naturalist, mathematician and philosopher. Impressed with Davis, Haldane later invited him to join the Indian Statistical Institute in Calcutta, as his research collaborator.

In 1960, Antony joined I.S.I. as associate professor in the Crop Science Division. He later was promoted to the rank of Professor in the Natural Science Division. From 1960 to 1977, Davis created within I.S.I. a school of palm studies and encouraged many young botanists to take up research on palms, a subject which had been neglected in India up to that time. In 1972, he completed a Ph.D. in biometry at I.S.I. with a study of the coconut and other crop plants.

I first met Antony Davis in 1963 when I was curator of the Indian Botanic Garden's palm collection. Davis was a frequent visitor, collecting palm specimens and studying in detail the biology of the garden's large living collection of palms.

In mid 1977, Davis left I.S.I. to join FAO as a coconut specialist and spent the major part of the succeeding years at the Coconut Research Institute, Manado, Indonesia (see Davis et al. 1985). Finally in early 1985 he returned to India and put his heart and boundless energies into developing the Haldane Research Centre at Nagercoil, which he had founded in 1982 in honor of his friend and mentor. In early 1985 I had the opportunity to spend a few days at the HRC and there met Dennis Johnson who was collaborating with Antony on a study of the utilization and development of the palmyra palm in southern India (see Davis and Johnson 1987). I recall the great enthusiasm with which Antony showed me his research plots, coconut orchards and rich collection of reference books and journals.

Near the end of 1988, Antony Davis came to Calcutta and expressed the desire to form a palm society in India which would work in collaboration with the International Palm Society. Davis believed that a

national organization would encourage young palm scientists in their studies of palms as well as serve to promote palm growing in India. The Palm Society of India was registered in June 1989 under the presidency of Mr. Shri Dhar, and in August Dr. Davis travelled to Calcutta to attend the first meeting. Davis designed the logo for the society which depicts the native palmyra palm and suggested the name "Palmyra" for the newsletter. Little did we know that that first meeting of the society would be Davis's last.

Among his numerous publications, the last and most important was a book entitled *The Sugar Date Palm* (Phoenix sylvestris), unpublished at this writing. Davis was a member of the Board of Directors of the International Palm Society (1984–1988), and was a regular contributor to *Principes*.

T. A. Davis is survived by three sons: Bernard, a statistician; Basil, a priest and Jerome, an engineer. His widow Eunice Davis is now the guiding force behind the Haldane Research Centre.

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Obituary: Ruth Shatz

The International Palm Society has lost another of its Charter Members. Ruth Shatz of Coral Gables, Florida, passed away peacefully in her home on April 21, 1991. She was 86 years old.

Ruth was born in New York City. After her marriage she moved to Carmel, New

York, where she and her husband raised three children and operated a model dairy, poultry and fruit farm. In 1956 they moved to Coral Gables where she continued to live after her husband's death in 1966. She was an ardent gardener and became interested in the many tropical plants in her new home, particularly the palms. She had a small but charming garden containing a surprisingly large collection of palms.

She was elected to the Board of The Palm Society (before the name was changed) in 1978 and served as Treasurer from that time until 1984. During her term in office she instituted new fiscal procedures and was an invaluable member of the Board. Her clear thinking and strict adherence to the rules governing various aspects of the Society were in the tradition of excellence as exemplified by our Editors, whose policies were established by the late Dr. H. E. Moore. We are indeed an example of a well-run, successful horticultural society and Ruth Shatz was a strong contributor toward making us so. She will be missed.

She attended all Biennial Meetings until the last few, and the Post-Biennial Trips, including the one around the world in 1968. She often traveled with Lucita Wait and they contacted members in any location in which they found themselves, thus cementing friendships and contacts in many places.

Her family has asked those wishing to make a donation in her memory to send it to the Endowment Fund of the IPS, a fund she helped set up and was created to ensure the continued publication of *Principes* and to perpetuate the IPS.

TEDDIE BUHLER

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PALM CONSERVATION

A new palm conservation project has been initiated to produce a Global Action

Plan for Palms. The IUCN/Species Survival Commission, Peter Scott Action Plan Fund, has awarded a grant to complete the research. Work began in July 1991 and is expected to take at least one year. The study will be published by IUCN in their Action Plan Series.

The action plan will be an activity of the Palm Specialist Group, one of 90 such groups constituting the Species Survival Commission. The Group was formed in 1985; currently it is made up of 14 members: Michael J. Balick, Chairman (USA), Dennis V. Johnson, Deputy-Chairman (USA), S. K. Basu (India), Rodrigo G. Bernal (Colombia), John Dransfield (UK), Tony Irvine (Australia), Salar Khan (Bangladesh), Ruth Kiew (Malaysia), Jean Yves Lesouef (France), Domingo A. Madulid (Philippines), Johans P. Moga (Indonesia), Monica Morais R. (Bolivia), Voara Randrianasolo (Madagascar) and Robert W. Read (USA).

Since its establishment, the Palm Group has undertaken two major projects aimed at generating essential palm conservation and utilization data. The first, WWF3322, began in 1986 with support from WWF-US, and examined palm conservation and utilization in Latin America and the Caribbean. Follow-up work continues. The second, WWF3325, with support from WWF-International, ran from 1987 to 1989 and investigated palm utilization and conservation in four Asian countries: India, Indonesia, Malaysia, and the Philippines. The final project report will be published as a book entitled *Palms for Human Needs in Asia* (1991).

An action plan for the palm family is urgently needed. Forest clearing and degradation pose serious threats to the maintenance of palm biodiversity, especially in tropical rainforests where so many species occur. The conservation status of many palm species in the wild still is unclear because of inadequate field studies; taxonomic revision of a number of genera is also required. In both instances, on a world

scale, we must have a better idea of the current situation and where conservation work should be done first.

Palm utilization is equally important. The Palmae provides a broad spectrum of subsistence items on which local populations depend. Natural palm populations also are exploited for a number of economically important food and industrial products supplying national and international markets. The improved management of natural palm populations has the potential to assure sustainable supplies of these products for commercial purposes, and to encourage keeping the forest intact. Protection of wild palm genetic resources is also of importance to major domesticated species, such as the African oil, coconut and date palms, for their maintenance and further improvement through plant breeding. In addition, a number of semidomesticated palms (e.g., palmyra palm and several rattans) have the potential for full domestication.

The action plan will set forth the priority actions needed to assure the maintenance of maximum palm biodiversity as well as to identify the key utilization issues which impact negatively on wild populations and the sustainable harvest of palm products for subsistence and commercial purposes. In more detail, the action plan will: (1) ascertain the current *in situ* (in the wild)

and *ex situ* (under cultivation) status of threatened species; (2) propose courses of action to maintain maximum palm biodiversity of both economic and (currently) noneconomic species; (3) identify key research issues needing attention; (4) suggest ways to promote sustainable utilization of palm products by means of palm management and/or domestication. The action plan will be organized according to major geographic regions: Asia; Australia; Oceania; Africa; Madagascar; and Latin America and the Caribbean. The overriding objective is to compile an action plan with priorities which strike a balance between palm conservation and palm utilization.

I invite all Palm Society members to participate in the process of compiling the Global Action Plan for Palms, by sharing their information, insights and concerns. Correspondence should be sent to the address listed below. Over the past 35 years, our Society has made an outstanding contribution to the scientific knowledge of palms and has enhanced the appreciation of this beautiful and useful plant group. A committed effort is now essential to keep the Palm family intact for the next generation.

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Borassodendron borneense in primary lowland rain forest, Brunei (Photo: J. Dransfield)

