



PRINCIPES

Journal of The Palm Society

July, 1971
Vol. 15, No. 3

THE PALM SOCIETY

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PRINCIPES

JOURNAL OF THE PALM SOCIETY

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Cover Picture

The Twice-pinnate leaves of Caryota mitis make an interesting pattern against the sky. Photo by M. V. Parthasarathy.

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JOURNAL OF THE PALM SOCIETY

An illustrated quarterly devoted to information about palms and published in January, April, July and October by The Palm Society, Inc.

Subscription price is \$6.00 per year to libraries and institutions. Membership dues of \$10.00 per year include a subscription to the Journal. Single copies are \$1.50 each. The business office is located at 7229 S.W. 54th Avenue, Miami, Florida 33143. Changes of address, undeliverable copies, orders for subscriptions, and membership dues are to be sent to the business office.

Application to mail at second class postage rates is pending at Miami, Florida 33143 and at Lawrence, Kansas 66044.

Mailed at Lawrence, Kansas
JULY 12, 1971

A New Palm Hybrid from the Fairchild Tropical Garden*

S. F. GLASSMAN

Research Associate, Field Museum, and Professor, Biological Sciences,
University of Illinois, Chicago Circle

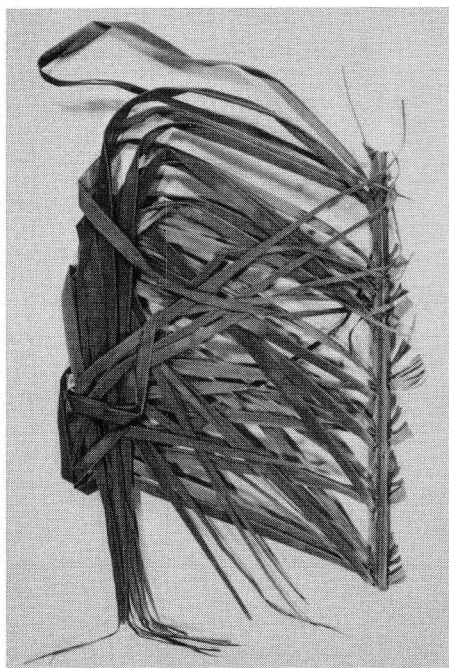
In preparing a taxonomic revision of the palm genus *Syagrus* Mart., I have recognized a total of five hybrids between species in this genus (Glassman,

* This work has been supported by National Science Foundation Grant GB-6899.

1963, 1968a, 1968b, 1970b). *Syagrus coronata* (Mart.) Becc. appears to be one of the parents in four of these hybrids, *S.* × *Camposportoana* (Bondar) Glassman, *S.* × *Matafome* (Bondar) Glassman, *S.* × *Tostana* (Bondar) Glassman, and *S.* × *Costae* Glassman; whereas,



1. *Syagrus Romanzoffiana* N. of Bragança, Minas Gerais, Brazil. Note trunk without persistent petiole bases.



2. *Syagrus Romanzoffiana*. Portion of leaf rachis showing clustered pinnae. From Glassman & Gomes 8000 (CHI).



3. *Syagrus Romanzoffiana*. Sheathing leaf base (right) and adjoining petiole parts showing soft fibrous or smooth margins. From Glassman & Gomes 8000 (CHI).

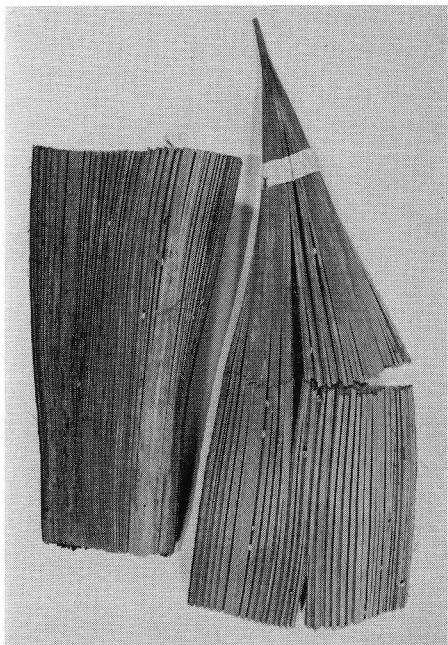
S. Romanzoffiana (Chamisso) Glassman, 1968a (formerly placed in the genus *Arecastrum* by Beccari, 1916) is involved in the hybridization of *S.* × *Camposportoana* and *S.* × *Teixeiriana* Glassman.

Hybridization between *S. Romanzoffiana* and *S. capitata* (Mart.) Glassman, 1970a, (formerly placed in the genus *Butia* by Beccari, 1916) and its varieties has been reported in the literature by Barbosa Rodrigues (1903), Beccari (1916), Bailey (1936) and Burret (1940); but according to descriptions, illustrations and specimens cited in these articles I am unable to find evidence of a clear-cut hybrid between these two taxa.

Barbosa Rodrigues described his hybrid under the following name: *Cocos Romanzoffiana-pulposa* Barb. Rodr. (1903). This palm was reported as

growing wild in Uruguay, but no specimens were cited. There is insufficient information in the description, however, to warrant recognition of this taxon as a hybrid.

Another hybrid, designated by Beccari as *Arecastrum Romanzoffianum* × *Butia*, was published in *L'Agricoltura Coloniale* 10: 462-464, 1916. The following collection, which I have seen, was cited in the paper: Cultivated, Villa St. Louis, near the boundary of Ventimiglia, Italy, *Berger s.n.* (FI, holotype). The type specimens, consisting of five herbarium sheets, have spadices (branched part) up to 60 cm. long, male flowers 8 mm. long, female flowers 5.5-6.0 mm. long and 4.5 mm. wide, petiole margins with very short spines (Beccari described them as *not* spiny), none of the pinnae are clustered along the rachis, and the



4. *Syagrus Romanzoffiana*. Expanded part of spathe showing deeply plicate-sulcate exterior. From *Glassman & Costa 8742* (CHI).



5. *Syagrus Romanzoffiana*. Cross-sections (extreme left and right) and longitudinal sections (central) showing the very irregular gibbous seeds enclosed in the very irregular endocarp cavities. From *Glassman & Gomes 8000* (CHI).

middle ones are up to 104 cm. long and 2.5 cm. wide, with oblique, split tips. The above information fits the general description of *S. capitata* and there seems to be very little to indicate hybridization with *S. Romanzoffiana*. Beccari, however, did describe the spathes as being plicate-sulcate (in *S. capitata* they are almost smooth), but spathes were not among the type specimens sent from the herbarium at Firenze, Italy. Furthermore, no fruits were described by Beccari in this article. Even though there is some evidence for hybridization (i.e., plicate-sulcate spathes), it is insufficient to recognize *Berger s.n.* as a distinct hybrid between *S. Romanzoffiana* and *S. capitata*.

Bailey mentioned a putative hybrid between the two taxa mentioned above in *Gentes Herbarum* (1936). The tree was growing in the Royal Palm Nur-

series at Oneco, Florida, but he did not see flowers or fruits and no specimens were cited. Although, there are indications of hybridization, such as spiny petioles and plicate-sulcate spathes, the evidence is inconclusive because of the lack of flowers and fruits.

Burret (1940) reported a hybrid between the two species in question in *Rodriguesia*, but he did not give it a formal description. The illustrations show two photos of trees and detailed drawings of the male and female flowers and external views of the fruit. Petioles appear to be non-spiny and the pinnae are not clustered. No specimens were cited. Photos were sent to Burret by Urbano Key from Porto Alegre, Rio Grande do Sul, Brazil, where the plant is thought to be indigenous.

On a recent trip to the Fairchild Tropical Garden, Miami, Florida, I was shown three mature trees labelled "*Butia* × *Arecastrum* hybrid" and was told that these grew much faster than other trees labelled "*Butia capitata*" in the same plot. The hybrid trees were planted in 1960 and were about 6–7 meters tall, whereas, one of the other trees ("*Butia capitata*") was planted in 1938 and was only about 5 meters tall. Superficially, the hybrid trees resemble *Syagrus capitata* because the petiole margins are spiny, the petiole bases are persistent on the



6. *Syagrus* × *fairchildensis*. Trees from which holotype (left foreground) and paratype (middle foreground) specimens were described. Note trunks with persistent petiole bases.

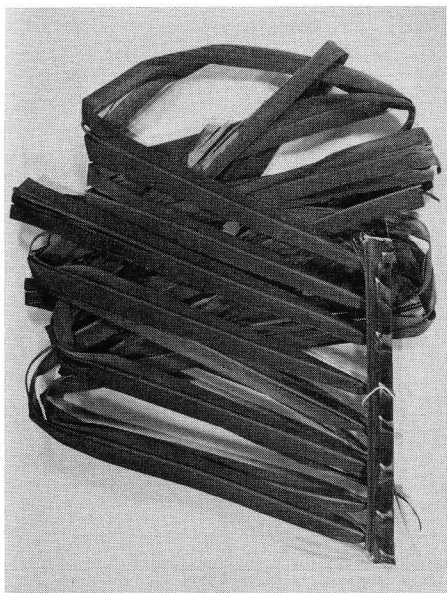
trunk, and the pinnae are not clustered; however, closer inspection revealed that the spathes are plicate-sulcate and the fruits have a thick endocarp and an irregular endocarp cavity characteristic of *S. Romanzoffiana*. At this point I was convinced that I had seen enough material to recognize these trees as clear-cut hybrids. Subsequently, complete collections of leaves, inflorescences and infructescences were made from two trees.

Since previous descriptions of hybrids between *S. capitata* and *S. Romanzoffiana* have been incomplete and inconclusive, I am describing a hybrid between these two species as new, naming it after the

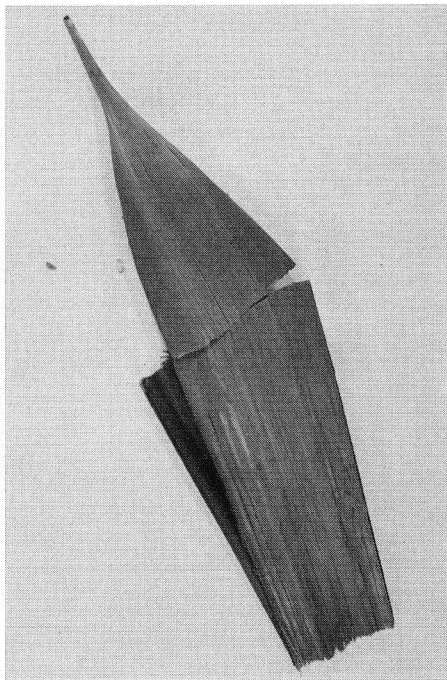
Fairchild Tropical Garden where many fine specimens of palms and other plants are cultivated.

Syagrus* × *fairchildensis Glassman,
hybr. nov.

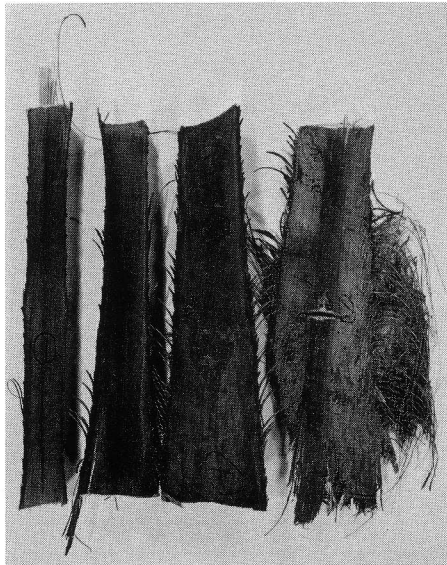
Palma hybrida 6–7 m. alta. Folia aequaliter pinnatisecta petiolo dentato rhachidi 253–293 cm. longa pinnis utrinque 105–113. Spathae pars inflata plicato-sulcata 121–156 cm. longa 14.5–17.0 cm. lata. Flores masculi inferiores 10–13 mm. longi superiores 6–9 mm. longi; flores foeminei 5–7 mm. longi 4.0–4.5 mm. lati. Fructus 1.5–2.1 cm. longus 1.3–1.6 cm. in diam. cavitate endocarpi asymetrica.



7. *Syagrus* × *fairchildensis*. Portion of leaf rachis showing regularly arranged pinnae. From *Glassman 8765* (CHI).

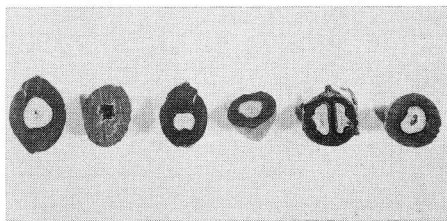


9. *Syagrus* × *fairchildensis*. Expanded part of spathe showing grooves of variable depth on exterior. From *Glassman 8764* (CHI).

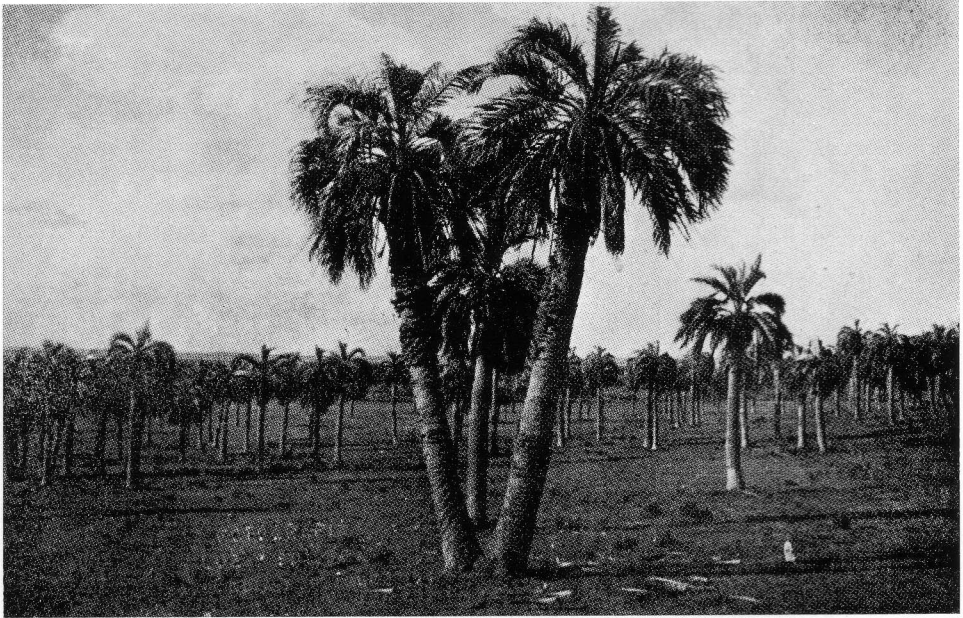


8. *Syagrus* × *fairchildensis*. Sheathing leaf base (far right) showing mixture of soft fibers and stiff fibers on margins, and petiole parts showing stiff fibers on margins (central ones) and short teeth on margins (far left). From *Glassman 8764* (CHI).

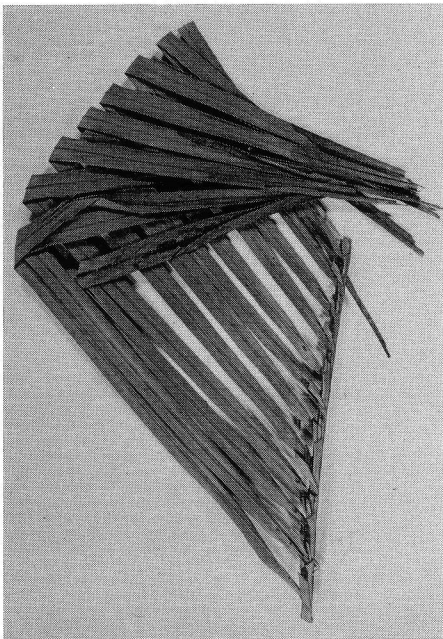
Hybrid palm 6–7 m. tall; sheathing bases and petiole bases persistent along most of the length of the trunk; dividing line between sheathing base and petiole often indistinct; sheathing base up to 27



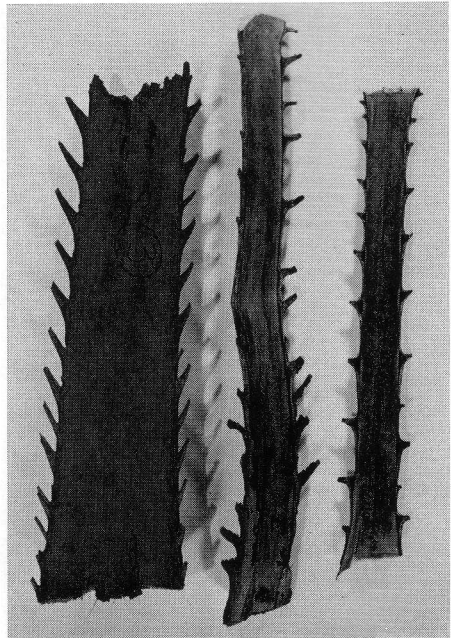
10. *Syagrus* × *fairchildensis*. Cross-sections (third from right and extreme right) and longitudinal sections of fruits showing slightly irregular to very irregular seeds enclosed in the irregular endocarp cavities. Note fruit (second from right) with two irregular seeds in the irregular endocarp cavities. From *Glassman 8765* (CHI).



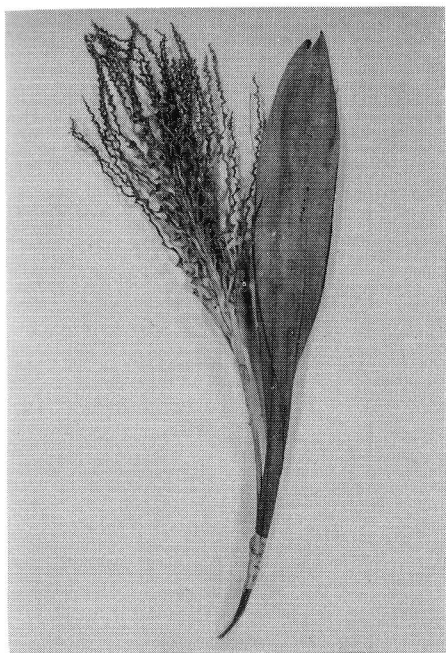
11. *Syagrus capitata*. Stand of trees in Uruguay. After Herter (1930).



12. *Syagrus capitata*. Portion of leaf rachis from tree cultivated at Fairchild Tropical Garden showing regularly arranged pinnae. From Glassman 8766 (CHI).

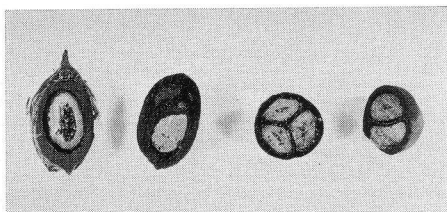


13. *Syagrus capitata*. Petiole parts showing coarse teeth on lower part (far left) and progressively shorter teeth on upper part (far right). From Glassman 8766 (CHI).



14. *Syagrus capitata*. Relatively smooth spathe (without grooves), and spadix. From *Glassman 8746* (CHI).

cm. long and 17 cm. wide, margins armed with soft fibers only or soft fibers intermixed with stiff, spine-like fibers; petiole up to 108 cm. long, about 8 cm. wide near base and 2.5–3.0 cm. near apex, margins with spine-like fibers near base, these fibers gradually becoming smaller and dentate up to apex; rachis of leaf 253–293 cm. long; pinnae 105–113 pairs, mostly not clustered, slightly glaucous on both surfaces, middle ones up to 106 cm. long and 2.5 cm. wide, mostly with oblique tips; expanded part of spathe 121–156 cm. long, 14.5–17.0 cm. wide and 2–3 mm. thick, plicate-sulcate but depth of grooves variable; branched part of spadix 94–151 cm. long, peduncular part up to 82 cm. long; branches up to 127 or more in number, the lowermost one 67–77 cm. long; male flowers 10–13 mm. long on lower spadix branches, 6–9 mm. long on upper spadix branches;



15. *Syagrus capitata*. Longitudinal sections (left) of fruits showing a single chamber with a single seed, and cross-sections (right) showing three chambers with three seeds, and two chambers with two seeds. From *Glassman 8766* (CHI).

female flowers 5–7 mm. long, 4.0–4.5 mm. wide; fruit broadly ovoid, 1.5–2.1 cm. long and 1.3–1.6 cm. in diameter, with very short beak, endocarp 2–6 mm. thick, mostly with one chamber, cavity slightly irregular to very irregular in shape, trivittate within, when two-chambered, cavities irregular, apparently not trivittate within; seed usually one, conforming to shape of endocarp cavity, easily separating from cavity, ovoid and slightly irregular to very irregular and uncinata in shape, 0.4–0.9 cm. long and 0.6–0.8 cm. in diameter, seeds when two irregular in shape, up to 0.9 cm. long and 0.2–0.4 cm. in diameter; endosperm homogeneous.

Specimens Cited: Fairchild Tropical Garden, Miami, Florida, cultivated tree about 7 m. tall, plot 111, no. FG-60-754A, March 25, 1970, *Glassman 8764* (CHI, holotype); same data except tree about 6 m. tall, no. FG-60-754B, *Glassman 8765* (CHI, paratype).

Both plants cited above came from the Florida Nursery and Landscape Co., Leesburg, Florida, and were planted in the Fairchild Tropical Garden during November, 1960, when they were about 1.5 m. tall.

Seeds of *S. × fairchildensis* are apparently sterile because no developed embryos could be found when several sectioned fruits were examined. Inspection of 5,000 pollen grains from ten different

TABLE 1.

	<i>S. Romanzoffiana</i> (Figs. 1-5)	<i>S. × fairchildensis</i> (Figs. 6-10)	<i>S. capitata</i> (Figs. 11-15)
Height of tree.	Up to 15 (20) m.	6-7 m.	Up to 5 m. or more.
Persistence of sheathing bases and adjoining petiole bases.	Usually dehiscent from trunk for most of its length.	Persistent on trunk for most of its length.	Usually persistent at least on upper half of the trunk.
LEAF			
Sheathing base and petiole margins.	Soft fibrous toward base, becoming smooth toward apex.	Soft fibrous and stiff fibrous toward base, becoming dentate toward apex.	Fibrous and coarsely spiny toward base, becoming coarsely or finely dentate toward apex.
Rachis length.	Up to 320 cm.	253-293 cm.	Up to 183 cm.
Number of pinnae per leaf.	Up to 165 pairs.	105-113 pairs.	Up to 63 pairs.
Clustering of pinnae.	Tight clusters of 2-5.	Mostly not clustered.	Mostly not clustered.
Pinnae tips.	Mostly acuminate.	Mostly oblique.	Mostly oblique.
Length and width of middle pinnae.	Up to 85 cm. by 2-3 (3.8) cm.	Up to 106 cm. by 2.5 cm.	60-75 cm. by 1.5-2.0 (2.7) cm.
EXPANDED PART OF SPATHE			
Length and width.	Up to 150 cm by 21 cm.	121-156 cm. by 14.5-17.0 cm.	40-100 cm. by 4.0-8.5 cm.
Thickness.	5-7 mm.	2-3 mm.	Mostly 0.5-2.0 mm., Occasionally 3-5 mm.
Texture.	Usually tough, woody-fibrous.	More or less brittle, or woody-fibrous.	Mostly brittle, occasionally woody-fibrous.
Grooving.	Deeply plicate-sulcate.	Plicate-sulcate but depth of grooves variable.	Mostly smooth, frequently with shallow grooves.
BRANCHED PART OF SPADIX			
Length.	Up to 125 cm.	94-151 cm.	Up to 94 cm.
Number of spadix branches.	Up to 196.	127 or more.	40-60.
Length of lowest spadix branch.	Up to 62 cm.	67-77 cm.	Up to 69 cm.
Length of male flowers (lower and upper branches).	11-16 and 4-10 mm.	10-13 and 6-9 mm.	7-10 and 4-7 mm.
Length and width of female flowers.	4.5-6.0 mm. by 4-6 mm.	5-7 mm. by 4.0-4.5 mm.	4-8 mm. by 4-6 mm.

TABLE 1. (Continued)

	<i>S. Romanzoffiana</i> (Figs. 1-5)	<i>S. × fairchildensis</i> (Figs. 6-10)	<i>S. capitata</i> (Figs. 11-15)
MATURE FRUIT			
Length and diameter.	2.0-2.6 (3.0) cm. by 1.2-1.7 (2.4) cm.	1.5-2.1 cm. by 1.3-1.6 cm.	1.8-2.6 cm. by 1.5-2.2 cm.
Number of chambers.	1.	1-2.	1-3.
Thickness of endocarp (along sides).	2-7 mm.	2-6 mm.	1-3 mm.
Shape of endocarp cavity.	Very irregular.	Slightly irregular to very irregular.	Regular.
SEEDS			
Length and diameter.	0.8-1.2 cm. × 0.6 cm.	0.4-0.9 cm. × 0.6-0.8 cm.	1.8-2.4 cm. × 1.0-1.4 cm.
Shape.	Gibbous-uncinate.	Ovoid and slightly irregular to very irregular and uncinata.	Ovoid or triangular.
Separation from endocarp cavity.	Not separating.	Readily separating.	Readily separating.
GEOGRAPHIC DISTRIBUTION			
	Brazil: Bahia, Minas Gerais, Goiás, Mato Grosso, São Paulo, Guanabara, Paraná, Santa Catarina, Rio Grande do Sul; Bolivia?, Paraguay; Argentina; Uruguay.	Only known from cultivation.	Brazil: Minas Gerais, Goiás, São Paulo, Paraná, Santa Catarina, Rio Grande do Sul; Uruguay.

male flowers revealed that less than five percent were fertile. The fertility was tested by staining pollen with aniline blue powder dissolved in lactophenol.

The above chart (Table 1) shows similarities and differences between the hybrid and its two parent species. It is not known for certain whether *S. capitata* and *S. Romanzoffiana* hybridize in nature, but such a union is possible where the ranges of the two species overlap (see Table 1).

When Table 1 is analyzed, it shows that *S. × fairchildensis* is similar to *S. capitata* in the persistent petiole bases on

the trunk, the toothed petiole margins, the regularly arranged pinnae with oblique, split tips and the seeds which easily separate from the endocarp cavity; and it resembles *S. Romanzoffiana* in the plicate-sulcate spathes which are approximately the same size, and in the irregular endocarp cavity and irregularly shaped seeds. The hybrid is more or less intermediate between the two parent species in the relatively narrow spine-like fibers on the sheathing base, the relatively smaller teeth on the petiole margins, size of rachis, number of pinnae per leaf, texture, thickness and grooving of the

spathe, number of spadix branches, length of male flowers, and shape of both the endocarp cavity and seeds. *Syagrus* × *fairchildensis* differs from either parent in the longer pinnae, longer spadices, and smaller fruits. Greater dimensions in the first two characters probably could be attributed to conditions of cultivation, whereas, fruit size can be explained by the fact that measurements for the hybrid were made from old fruits in which the exocarp and mesocarp had fallen off.

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EDITOR'S CORNER

Erratum

The name of the palm in the first line on page 35 of this volume should have been set in italic rather than boldface since the citation is for a synonym, not an accepted name, thus:

? *P. cycadifolia* Hort. Athen ex E.

H.E.M.

Editor returns

Dr. Moore will return shortly from a highly successful palm-collecting journey around the world. Material collected on this trip of rare and little-known palms will fill in some of the major gaps in our understanding of the palm genera and their interrelationships. Beginning with the next issue of PRINCIPES, Dr. Moore will give a full account of his latest adventures and discoveries.

F.B.E.

The Fate of *Scheelea rostrata* Fruits Beneath the Parent Tree: Predispersal Attack by Bruchids

DANIEL H. JANZEN

Department of Biology, University of Chicago

Scheelea palms are common in some Central American lowland forests with a mild dry season, and occasionally are common in swamps and riparian sites experiencing a severe dry season. In Costa Rica, the seeds of these large trees are subject to intense predation by two species of bruchid beetles and several species of terrestrial rodents. Predation beneath the parent tree by bruchids is described here as the first step in an examination of the effect of seed predation on the population dynamics of *Scheelea rostrata* (Fig. 1a).

General Interaction

An individual tree of *Scheelea rostrata* usually produces one or none (maximum of two) fruit-bearing inflorescences (Fig. 1a) each year. Fruit maturation requires at least six months and about 1400 large yellow fruits fall from one inflorescence over a month-long period. In moderately undisturbed forests, terrestrial rodents then chew the rind and mildly sweet pulp (exocarp and mesocarp) from the fruit, leaving the bony endocarp which is indehiscent and contains one to four seeds. Newly cleaned endocarps are often discarded within 3 m. of the tree trunk. Some intact fruits and clean endocarps are carried away by rodents and scatter- or cache-hoarded. Since individual clean endocarps that have been dispersed by rodents probably have a much lower probability of being found by bruchids than those clumped beneath the tree, they are probably es-

sential to the survival of the *S. rostrata* population. The fate of such dispersed endocarps is the subject of a study in progress (Janzen and Wilson, 1971).

Endocarps remaining beneath the tree are highly susceptible to oviposition by bruchids almost immediately after being partially cleaned of pulp. Since very newly cleaned endocarps have only one egg on them, a bruchid probably lays only one egg (Fig. 1b) per endocarp per encounter. However, there are enough encounters so that most endocarps receive two to five eggs (Fig. 1c) with extremes at 15 to 20 eggs. Endocarps are susceptible to oviposition for at least one month, or at least until the taste and odor of fermentation are gone from their surface. Oviposition occurs even when the endocarp is covered by the light litter of fruit rinds, old flowers, and frond fragments beneath the parent palm.

The first instar bruchid larva bores directly through the endocarp into the endosperm of the seed. More than one larva usually enters the endosperm, but only one matures, probably because the largest larva cannibalizes the smaller ones. There may be up to three seeds per endocarp and very rarely four, and occasionally a bruchid matures in each; more usually, one larva eats all the seeds in an endocarp. A larva consumes all of each seed available to it. Just before pupating (Fig. 1d), the larva cuts an exit tunnel almost all the way through

TABLE 1. Percent of seed mortality in 10,925 endocarps collected below 118 *Scheelea rostrata* in different habitats and at different endocarp ages in five Costa Rican sites. Approximately 100 endocarps were collected from beneath each of the parent palms. Status of endocarp determined by dissection, and at this level of discrimination, all seeds in an attacked endocarp are regarded as dead.

	Percent apparently viable	Percent containing bruchid larvae	Percent dead for unknown reasons	Examined:	
				Total endocarps	Total trees
<i>Forest</i>					
Newly fallen endocarps	89.6	9.7	0.7	888	9
Medium age endocarps	14.9	77.0	8.1	6219	67
Old and rotting endocarps	10.2	18.1	70.7	1056	12
<i>Pasture</i>					
Medium age, all endocarps	63.9	19.3	16.8	2707	30
Stream or pond edge only	4.0	65.1	30.9	571	7
Open grass only	81.3	7.0	11.7	2136	23

the endocarp wall; the emerging adult finishes the job (Fig. 1e).

No arthropod parasites of the bruchid have been found in the 10,925 endocarps opened in this study (Table 1). However, an unidentified microbial disease kills a highly variable number of pupae, full-sized larvae, and adults before they complete development. The litter beneath the parent palm is probably thoroughly contaminated by this pathogen, owing to the disintegration of endocarps containing the remains of diseased bruchids.

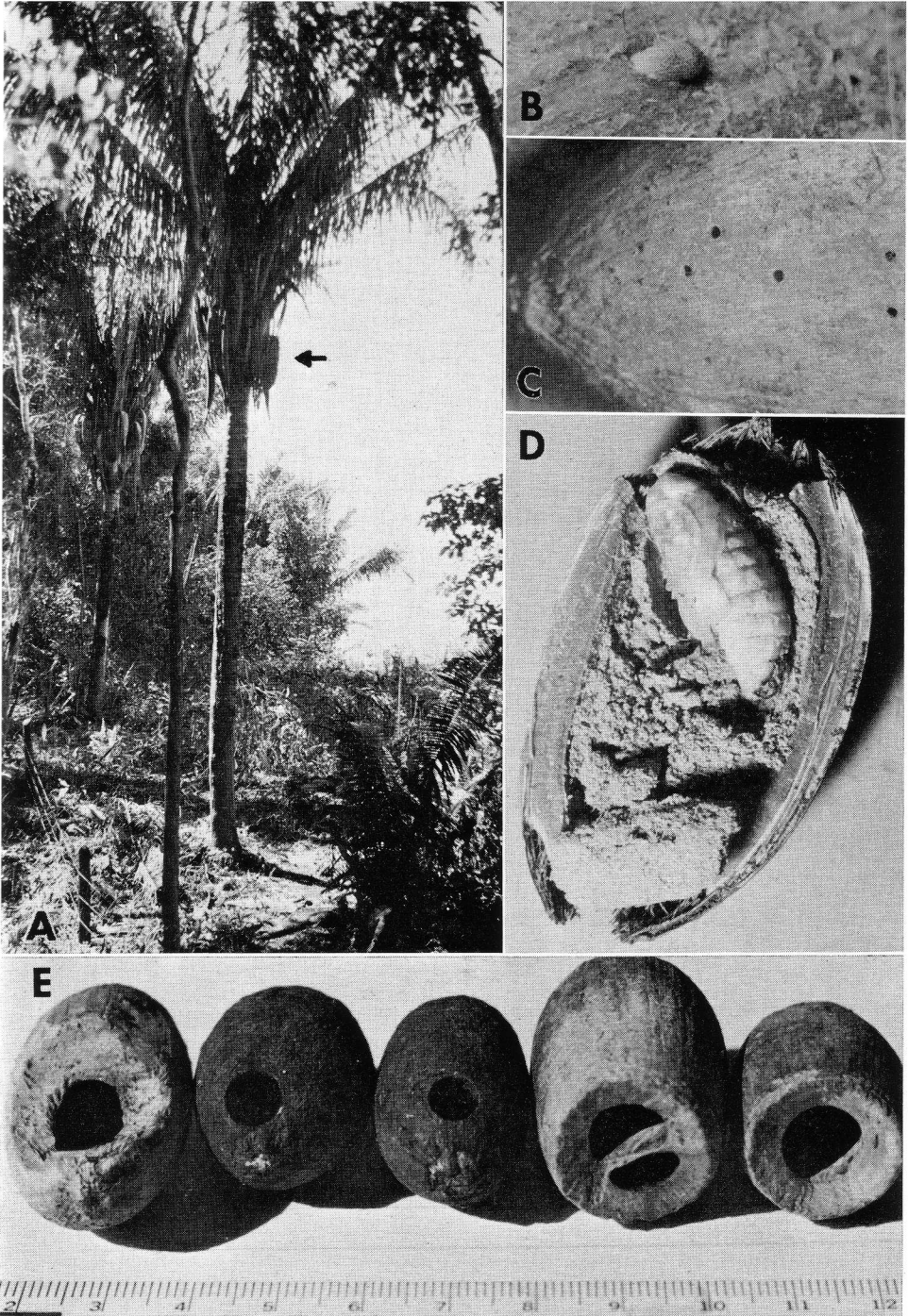
The moderate synchrony of fruit fall from one palm results in some synchrony of the bruchid life stages under a given adult tree. However, in any local palm population, fruit crops of all ages are present (though their relative frequency varies). Bruchids of all ages are there-

fore present in a pooled sample of endocarps from below several trees; susceptible endocarps are oviposited on at all times of year.

At unknown times of year (neither mid rainy season—September, nor mid dry season—February, March), at least two species of terrestrial rodents chew open large numbers of medium aged endocarps (Fig. 1e) beneath the parent tree. They are in search of either mature bruchid larvae or palm seeds. The hypothesis that the rodents are in search of bruchid larvae is supported by the observation that the rodent only chews until the cavity containing the seed is opened (Fig. 1e); through this small access hole the bruchid larva could be removed but the tight-fitting, intact seed could not be pulled or chewed out. In

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1. Bruchid predation in *Scheelea rostrata*. a, Reproductive adult *Scheelea rostrata*, Barranca Site, February, 1970. Note cluster of fruits at arrow. b, Freshly laid egg of *Caryobruchus buscki* (1.8 mm long). c, Entrance holes of first instar larvae of *C. buscki* in endocarp. d, Pupa of *C. buscki* with head in exit tunnel through stony endocarp; entire endosperm replaced by powdery frass from feeding by bruchid larva. e, Left to right: endocarp chewed open laterally by rodent, apparently to prey on bruchid larva; two endocarps with *C. buscki* exit holes; double-seeded endocarps with end cut off by rodent, apparently to eat bruchid larvae; ditto, single-seeded endocarp.



addition, most superficially intact endocarps at this time in the history of the crop are medium-aged and contain bruchid larvae (Table 1, column 2). Further, it is probable that the metabolically active larva contains a wider variety of nutrients than the oil-rich endosperm and quiescent embryo.

The few unattacked seeds beneath the parent germinate at least during the first four months of the rainy season (May–September). Whether the young plants survive the following dry season appears related to factors such as herbivore damage, moistness of the site, and the amount of sunlight received during the year. Beneath adult *S. rostrata* that are left in pastures after clearing the forest, there is no seedling survival.

Materials and Methods

This report is restricted to five somewhat separate populations of *S. rostrata* in the northwestern part of Costa Rica.

1) Barranca site—intensive endocarp collecting (February, July, September, 1970) was done in the local population on the hills and bottom-lands of the small river drainage that crosses the Pan-American highway, 5.6 to 8.5 miles northwest of the turn-off into the city of Puntarenas from this same highway. This site is centered on Orian's (1969) "Barranca site." The original areal extent of this population is unknown owing to extensive clearing, but the absence of *S. rostrata* in riparian vegetation to the north and south of the Barranca site suggests that it was not continuous with any of the other local populations in the dry northwestern lowlands of Costa Rica. I estimate that there are at least 1000, and not over 2000, adult *S. rostrata* growing in habitats where they can reproduce at the Barranca site.

2) Taboga site—intensive sampling (July, September, 1970) was done in

the river bottoms along the Rio Higuef6n on Finca Taboga (south of Cañas, Guanacaste Province) in the southeastern portion of the Costa Rican M.A.G. Field Station. The reproducing portion of this very local population is now restricted to the narrow strip of forest remaining along the river ("Area III" in Janzen and Schoener, 1968) and the contiguous palm forest (*palmar*) of about 10 acres extent that is occasionally flooded. A few adult trees remain in the pastures cleared in 1963–1965 on the flood plain of the Rio Higuef6n. I estimate that there are about 200 reproducing adult *S. rostrata* at the Taboga site.

3) Colorado site—a few collections were made from the 13 adult *S. rostrata* remaining in pastures along the creek network about halfway between the Barranca and Taboga sites (6.6 miles from the Pan-American highway on the road from that highway to Colorado on the Gulf of Nicoya; September, 1970). Since there is total seedling mortality during the dry season in the pastures around these palms, they are only a small and non-reproducing remnant of what probably was a population equivalent to that at the Barranca or Taboga sites; they appear to be the only adult *S. rostrata* between the two sites.

4) Esparta site—the palms (September, 1970) are scattered among hillside pastures and clumped in some creek bottoms from about 50 to 200 m. elevation along the Puntarenas—San Ramon highway (Puntarenas Province, 3 to 6 miles northeast of Esparta). This population, containing at least a thousand widely spaced adults, probably represents what used to be the northernmost extension of the large *S. rostrata* population that currently extends along the Pacific coastal foothills south of Puntarenas at least as far south as Palmar Sur and the Golfito region of Costa Rica.

The Esparta population might at one time have been continuous with the Barranca population, but the pastures and deciduous forest between them now give no hint of it.

5) Peñas Blancas site—separated from the Taboga site by at least 90 miles of forest subjected to a very severe dry season, this population extends along the Pan American highway from the Costa Rican—Nicaraguan border to 10 miles south (September, 1970); this population extends north into Nicaragua for an unknown distance along rivers draining into Lake Nicaragua. At present, it probably contains less than 200 adults in habitats where they can reproduce south of the Nicaraguan border. This population may, however, extend eastward and thus be continuous with a large population on the Atlantic coastal plain.

The taxonomy of the genus *Scheelea* is somewhat muddled, but two things are clear. There is no indication that the large palm at the five sites listed above represents more than one morphospecies; *coyol* (*Acrocomia vinifera* Oerst.) is the only other large palm in the vicinity of the five sites, and it reproduces in drier sites than *S. rostrata*. The three species of *Scheelea* listed by Standley (1937) for this part of Costa Rica [*S. costaricensis* Burret, *S. gomphococca* (Mart.) Burret, *S. rostrata* (Oerst.) Burret] are either described from one of the five populations listed above or were described from cultivated plants (Moore, pers. comm.); Standley's claim that *Scheelea* is widespread in the lowlands of northwestern Costa Rica was not based on personal observation and is unlikely ever to have been true under contemporary weather regimes. I have applied the name *S. rostrata* (cf. Burret, 1929) to the palms examined in this study on the advice of Dr. H. E. Moore, Jr.

Caryobruchus buscki Bridwell is one of the world's largest bruchids (Bridwell 1929) and ranges from Costa Rica to Venezuela (Kingsolver, in lit.). It is responsible for almost all the mortality by bruchids at the four southernmost sites (1–4). The slightly smaller *Pachymerus cardo* (Fahraeus) (Kingsolver, in lit.) had only occasionally been encountered there. At the Peñas Blancas site, *P. cardo* appears to be responsible for as high as 50 percent of the bruchid predation on some seeds. The damage by these two beetles has not been recorded separately in this study, but differences between them are probably responsible for a small amount of the intercrop and inter-habitat variance in seed mortality recorded in Table 1. Numerous other species of palm bruchids are briefly discussed by Bridwell (1929) and Paxson (1961).

In the endocarp samples recorded in Table 1, only superficially intact endocarps were collected. Samples of about 100 endocarps each were collected from beneath the following number of palms at each site: Barranca 88, Taboga 23, Peñas Blancas 4, Colorado 2, Esparta 1. Endocarps chewed upon by rodents, endocarps with bruchid exit holes, and endocarps with germinating pores rotted open were not included. When encountered, endocarps with germinated seeds were also discarded, but this did not normally enter into the decision-making process as the actual number of living and newly germinated seedlings below most forest palms sampled was far less than 1 percent of the total number of intact endocarps. The age of the endocarps beneath the tree was subjectively estimated, based on such things as their degree of decomposition and amount and age of litter that had fallen on them. The total number of endocarps of all ages beneath a palm usually ranged from 1000 to 5000 (e.g., Table 2). Endocarps

TABLE 2. *Fate of seeds in 1385 endocarps of all ages (about ¼ of total) below a large adult S. rostrata (forest, Barranca site, 12 September 1970).*

Percent endocarps with at least one viable seed	1.8
percent of these endocarps double-seeded with one seed dead, and dead bruchid larva in other seed	36.0
Percent endocarps with all seeds killed by bruchid	80.4
Percent of these with:	
one seed, killed by now dead larva	46.8
two seeds, both killed by now dead larva	7.3
one seed, dead pupa	0.4
two seeds, dead adult and dead larva	0.1
one seed, dead adult	2.3
one seed, live larva	16.8
two seeds, live larvae	0.8
one seed, live pupa	0.1
adult burchid exits (17% of these had 2 exits)	25.1
Percent endocarps with only aborted seeds or other non-predator mortality	7.5
Percent endocarps killed by rodent chewing in the middle	10.2

were inspected by breaking them with a hammer.

Seed Mortality

The variation in seed mortality beneath the parent tree can be most profitably discussed in the context of the age of the endocarp after falling, the fate of the bruchid and palm seeds in the endocarp, and the habitat of the parent palm. This should be regarded as pre-dispersal mortality (Janzen, 1970) for the following reason. Judging from the enclosure of the well-armed seed(s) in the sweet exocarp, release of the fruit by the parent (so-called "gravity dispersal") should be regarded as a behavioral trait analogous to the various morphological traits of many tropical plants that increase fruit availability to the dispersal agents. In this case, then, the drupe is not dispersed until it has been carried away from beneath the

parent plant (*cf.* Janzen and Wilson, 1971).

Age of drupes and degree of predation by bruchids.

As an endocarp ages, it becomes increasingly difficult to ascertain exactly why its seed(s) died. Further, a live seed in an old endocarp has a very different probability of being killed by a bruchid than one in an endocarp newly cleaned of exocarp and mesocarp. For these reasons, seed mortality is discussed separately for different age classes whenever possible.

Newly fallen endocarps. Endocarps newly cleaned of exocarp and mesocarp characteristically have a low percent of infestation by bruchids and a high percent of apparently viable seeds (Table 1) (Jordan, 1970, records 61 percent germination for seeds in endocarps of this age from a Peruvian *Scheelea*,

though the reason for failure of 39 percent was not given). Such endocarps have been on the ground up to a month, are beige to white, are extremely hard, have the fibrous cap over the germinating pores firmly in place, have numerous pulp fibers attached to the surface, often smell or taste slightly fermented, and often have the remains of bruchid eggs cemented firmly to their upper surface. These endocarps often have new fruit rinds prominently mixed with them and are quite distinct from older endocarps from previous inflorescences. First or second (or rarely third) instar bruchid larvae are found in the seeds in freshly cleaned endocarps; these young larvae have usually eaten up to 30 percent of the endosperm. By the time the larva has reached the second instar, it has almost always eaten the embryo. It should be noted that first instar larvae and small second instar larvae are difficult to locate in the remains of a seed after smashing the bony endocarp open, and despite careful searching for larvae, the figure of 89.6 percent seed viability in Table 1 is probably a five to ten percent over-estimate. For the purposes of this sample, if at least one seed is attacked by a bruchid, it is considered that all seeds in that endocarp will die (see later discussion of multiple-seeded endocarps).

When the endocarps have been on the ground beneath the parent palm one to four months, the highest percent mortality unquestionably due to bruchids is recorded (Table 1). Of the 67 crops examined, 64 percent had bruchids in more than 85 percent of their superficially intact endocarps beneath the parent. That only 77 percent of the total endocarps examined in this age class had bruchids is partly due to the presence of a number of endocarp crops of about one month age. Characteristically, only 40 to 70 percent of these

endocarps contain bruchid larvae since bruchid attack of the crop is not yet complete. There are also some crops in this sample that are old enough that 10 to 30 percent of the bruchids have died in the endocarp, causing it to be classified as "dead for unknown reasons." Microhabitat differences within the forest also lead to lower percentages of unquestionable seed mortality by bruchids, and will be discussed in a later section.

Medium aged endocarps. Endocarps of this age are beige to dark brown, are moderately hard, have a distintegrating fibrous cap over the germinating pores, have no remains of pulp fibers, smell and taste like litter composed of leaves and branches, and are often partially or totally buried in litter. If washed, these endocarps display various numbers of 0.4 mm. diameter entrance holes made by first instar bruchid larvae. The fourth and last instar bruchid larvae have usually eaten all of one or more seeds in the endocarp and have sometimes cut the first part of an exit hole. Occasionally, larvae or pupae killed by disease are encountered in medium-aged endocarps. This is the age at which endocarps are normally chewed open by rodents.

Old endocarps. Once the endocarp crop has been on the ground more than about five months, the percent bruchid infestation of superficially intact endocarps is again low (forest palms, Table 1). This is due for the most part to two causes. 1) Part of the endocarps have bruchid exit holes or have been chewed open by a rodent (Fig. 1e). The opened endocarps are not included in the sample. 2) Part of the bruchids have died of disease and the endocarps containing these are pooled under "dead for unknown reasons." Since it is very difficult to determine the upper age limit of old endocarps, these samples very likely contain endocarps from two or three

inflorescences, and these endocarps range from five to eighteen months in age. Bruchids appear to have a short life span in the endocarp as compared to live seeds, which can live at least one year. Therefore, the percent viability of seeds in old endocarps is probably biased upwards and the percent of endocarps with bruchids biased downwards, if the data from forest palms in Table 1 are treated as representative of a crop from one palm, followed through time. On the other hand, some viable seeds will also have germinated; this will bias the percent of viable seeds slightly downwards.

Characteristically, old endocarps are very dark brown, weigh less than younger ones, have a surface easily gouged with the thumbnail, are easily broken with a hammer, and have the germinating pores partially exposed. The few bruchids found in these endocarps are full grown larvae, pupae or adults. Many are dead from disease, their bodies turgid with milky fluid. At a slightly later stage, only the bruchid's body fragments remain. When care is taken to distinguish seeds that rotted internally from those with endosperm eaten by a bruchid which later died, it is clear that 80 percent or better of the seeds in the "dead for unknown reasons" endocarps in Table 1 were killed by bruchid larvae (and see later detailed crop analysis in Table 2). Further, it is impossible to know what percent of apparently rotted seeds were killed by a first instar larva that died after entering the seed endosperm.

In summary, as a given crop of endocarps ages on the ground below forest palms, the number of endocarps containing viable seeds declines rapidly, and after about one month reaches a low level of 5 to 20 percent which then continues to gradually decline. The percent of superficially intact endocarps

containing live bruchids climbs rapidly during the first month, and then slowly declines. The percent of endocarps "dead for unknown reasons" remains small until the crop is three to five months old. After this, bruchids begin to die or emerge.

These changes with age of the endocarp crop are also reflected in the content of a sample of endocarps of all ages collected below one parent tree (Table 2). All endocarps were gathered from approximately one quarter of the area within 2 m. of the base of a fully reproductive *S. rostrata* (12 September 1970, Barranca site). This tree was in old secondary forest and evidence of rodent activity was less than usual near its base. The endocarps below the tree ranged from medium-aged (fallen two to three months before) to an age where the endocarp was beginning to disintegrate; endocarps so old that they could be broken between the fingers were not collected. There was the exceptional number of about 200, two- to five-month-old seedlings beneath the palm (about 50 in the area from which drupes were collected). The exceptional number of seedlings beneath this palm was probably due to the unusual dryness (for *Scheelea* habitat) of this hilltop forest being inimical to the bruchid population. Taking these seedlings into account, and adding in the endocarps probably removed by rodents, there appears to have been the remains of the endocarps from four to five inflorescences beneath the tree. In this sample, care was taken to distinguish between those seeds killed by bruchids that later died in the endocarp, and those that aborted or rotted following germination; the high figure of bruchid mortality (46.8%, Table 2) shows clearly that the high percent of "dead from unknown causes" (70.7%) recorded in Table 1 is primarily due to bruchids.

Fate of the Bruchid and the Palm Seed

To this point, I have treated the endocarp as though its seed was either killed or not. About two out of every five trees, however, have a high frequency of endocarps with two or more seeds (Fig. 2e; seven trees were encountered with a high frequency of triple-seeded endocarps and one with quadruple-seeded endocarps). When multiple-seeded endocarps are subject to a low frequency of oviposition, medium-aged endocarps commonly have a large larva in one or two of the seeds, with the second or third seed still viable. Events may take several courses from this point. Most commonly, a larva chews through the 0.5- to 1 mm.-thick partition between the embryos and eats the other larva or the remaining viable seed. That a larva may eat one to three seeds is probably the proximal cause of the greater than two-fold variation in body weight of newly emerged adults.

Occasionally the larva dies before it cuts into the second seed. The germinating pore of the destroyed seed eventually rots open, admitting the litter fauna and flora. These organisms quickly puncture the thin wall between the seeds and kill the viable seed. In Table 2, 36 percent of the viable seeds were in double-seeded endocarps, each of which contained one bruchid larva that had recently died. These seeds had a much lower chance of producing viable seedlings than did the viable seeds in single-seeded endocarps.

The bruchid may emerge without having chewed into the second seed (or larva). For example, of the 280 endocarps with exit holes in the crop recorded in Table 2, 17 percent had two exit holes. Of the 232 endocarps with single exit holes, 12 percent had been double-seeded endocarps but in no case had the

other seed survived; it was either eaten or rotted.

The death of at least one seed in the endocarp is not insured by a single oviposition on the endocarp. Preliminary surveys of larval success in endocarps newly cleaned of pulp indicate that at least one half of the first instar larvae die while boring through the hard endocarp, or shortly after entering the seed. Their penetration of the endocarp neither leads to germination of the seed nor its immediate death. Fungus or bacterial damage to the seed, however, sometimes begins at this point. If the seed is damaged and then the bruchid larva dies, the endosperm begins to distintegrate quickly in the area of the cavity eaten by the larva. It is likely that bacterial and fungal spores are carried into the seed by the first instar larva, which becomes contaminated when it chews through the egg wall and the outer surface of the endocarp.

A healthy bruchid larva kills the palm seed very quickly. While feeding is initially peripheral, the larva quickly bores into the center of the endosperm. By the third instar it has usually eaten the embryo. Growing larvae that die of disease usually appear to do so after they are full-sized and have consumed all of the seed. I have found only three dead medium-aged larvae among several thousand larvae examined.

Just as oviposition on the endocarp does not guarantee loss of the seed within, the presence of a large larva in a medium-aged endocarp does not insure the production of an adult bruchid. While the frequency of disease was not determined in most samples, diseased larvae were found beneath almost all trees sampled. From the data in Table 2, a rough estimate can be obtained of the number of larval, pupal and adult bruchids that may die of disease. A minimum of 962 bruchids grew to an

age where they either emerged or died in the endocarp; of these bruchids, only 34 percent emerged as adults.

Habitat of the parent palm.

The habitat immediately surrounding the parent palm strongly influences the fate of the endocarp beneath the parent. This is most striking when comparing grassy pasture with adjacent forest (Table 1). A palm need be only a few meters into a grassy pasture for the frequency of bruchids to be drastically reduced. For example, two adults at the Taboga site were 10 and 15 m. from the forest edge, and only 17 and 24 percent of their medium-aged endocarps contained bruchid larvae. This pasture was cleared of forest in 1967. About 2 m. into the adjacent forest, and 20 to 30 m. from the pasture trees, the only other two *S. rostrata* in the area had 72 and 87 percent of their medium-aged endocarps with bruchids in them. If a palm is several hundred meters from forest or a brush-filled watercourse, it usually has no evidence of bruchid damage to endocarps of any age.

Within the grassland there is a significant difference between attack of endocarps under trees in open pasture and those growing within about 5 m. of watercourses (Table 1). The high bruchid damage to *S. rostrata* near watercourses in pastures is probably due to the presence of wet hiding sites for adults during the dry season, rather than due to the brushy vegetation that often grows near water in pastures; palms in pastures on level ground, and accompanied by low brush, have little or no bruchid damage to their endocarps.

S. rostrata in pastures have greatly reduced rodent activity at their bases. The rind and mesocarp of most fruits rot off in about a month and there is no evidence of rodents chewing into the endocarp. Endocarps with the rinds rotted off are

susceptible to bruchid oviposition. On rare occasions forest fruit crops are free of rodent activity but are heavily attacked by bruchids once the endocarp is exposed.

Despite freedom from bruchid and rodent predation on endocarps, *S. rostrata* in pastures do not reproduce themselves. By the end of the rainy season as many as 500 young seedlings may be found within 3 m. of a pasture tree, provided that cattle have not badly trampled the site. However, these seedlings do not survive the dry season, since seedlings more than a year old are never encountered in pastures in the general study area. Since adult *S. rostrata* are sometimes left standing when the forest is cleared, there is a small fraction of the adult population that appears to be surviving in a pasture habitat. In fact, these trees are as removed from the local gene pool as if they had been cut with the forest, unless they pollinate forest palms or rodents carry their fruits to the forest. However, in southern Costa Rica, where the dry season is less severe (Palmar Sur region, cf. Janzen, 1967), *S. rostrata* seedlings do survive the dry season in pastures.

Within the forest there is one easily recognized large source of variation in seed mortality by bruchids. *S. rostrata* growing such that their endocarps fall where they will be regularly washed well downstream, tend to have substantially reduced bruchid damage. Since no adult bruchids can be emerging from endocarps below such a tree, the low level of infestation is probably due to low rates of movement of adult bruchids between palms. For example, only 1.0, 5.2 and 6.1 percent of the drupes below three palms in stream bottoms at the Barranca site were attacked. There were heavily infested crops within 15 m. of these palms. Interestingly, this low infestation rate is also probably representa-

tive of endocarps from the first inflorescence produced by a palm upon attaining adulthood.

Discussion

These data and anecdotal life histories do not allow a definitive statement as to the impact of the bruchids and rodents on the population dynamics of *S. rostrata*. However, they do suggest a number of readily testable hypotheses that are currently the basis for field experiments in Costa Rica; the hypotheses are outlined here with the hope that they will be applied elsewhere by other workers.

1) If rodents are prevented from removing the endocarps of *S. rostrata* from beneath the parent palm or chewing into the endocarps (in a moderately undisturbed forest), the bruchids should achieve 100 percent predation of the palm seeds. A corollary is that in areas where dispersal agents remove all the palm endocarps rather than discard them beneath the parent, or remove the fruits directly from the parent tree, palm bruchids will not exist.

2) The farther a freshly cleaned palm endocarp is placed from a fruiting parent, the lower will be the probability of the endocarp being attacked by a bruchid.

3) The larger the pile of freshly cleaned endocarps at a site where there is no parent, the more likely that it will be found by bruchids (this experiment mimics the effect of cache-hoarding by rodents).

4) Any distance effects discovered in 2) and 3) above will not be influenced by the proximity of adult *S. rostrata* that have not borne fruit for many years.

The data in this paper, and the apparently very low dispersal ability of the bruchids, suggest an interesting reproductive phenomenon for the palm. For example, let us estimate that a

newly reproductive adult *S. rostrata* palm produces two consecutive inflorescences a year, each bearing 1400 fruits. Assume the bruchids kill 90 percent of each fruit crop left below the parent, once a bruchid sub-population has become established below the palm. If we also assume that the bruchid infestation rate doubles with each inflorescence after the first, and starts at 1.5 percent with the first inflorescence, then the usual high infestation will not be reached until the seventh inflorescence. This means that the first six inflorescences borne by the newly reproductive palm could produce 7187 endocarps free of bruchid attack. It would then take another 25.5 years (51 inflorescences) to subsequently produce as many viable endocarps. Dispersal agents are likely to carry off as many endocarps that have fallen from an inflorescence during the first years as during later years. The palm therefore has a much greater apparent reproductive ability per inflorescence during its first years than during later years. One consequence of this lag in bruchid predation should be strong selection favoring delay of reproduction until the palm has grown to an age when it can produce full-sized inflorescences as rapidly as can an old adult.

If in fact there is a very low infestation rate of the endocarps from the first inflorescences produced, there is also strong selection pressure favoring a phenotype that delays fruit production until the bruchids from the endocarps from the previous inflorescence have emerged and died or immigrated. This directional selection is of course countered by the failure of such a palm phenotype to 1) provide food for the local rodents, and 2) place seeds in the habitat while "waiting" for its local bruchid sub-population to decline. Of the total adult-sized palms at the study

sites, those that produce fruits do so almost continually.

If the low infestation of endocarps beneath palms on pasture edges and forest creek-bottoms is due to the bruchids' low dispersal ability between palms, as suggested above, then inter-palm distances probably play a strong role in the variation observed in bruchid infestation in forested sites, where infestation of a particular crop ranges from 60 to 100 percent.

At the study sites, not all adult *S. rostrata* produce large numbers of fruits. The consequence is that some trees are effectively males, while others are male and female. From the bruchid's viewpoint, then, there are fruiting palms (females) and non-fruiting palms (males). If these differences in sexuality are genetically based, and if inter-female distances are correlated with the percent predation on the endocarps below the parent, the bruchids may play an important role in the evolution of the palm's sexuality. A palm genotype that produces only female trees will lower her own reproductive success slightly if she produces an offspring close enough to raise the bruchid infestation of her own future crops. Likewise, she lowers the reproductive success of that offspring by providing a close source of bruchids. A genotype that produces male and female offspring can add one or more male palms in her immediate vicinity without lowering her reproductive output or that of the male. Further, if the female tree produces a reduced number of male flowers (relying on adjacent males for pollination), her total fruit output may be even higher. The outcome of competition between the all female genotype and the male-female genotype should be a progressively more dioecious population the more intensive the bruchid predation. Further, the shift from the first to the second genotype should result in the

total palm density at a site that is progressively closer to the maximum possible were there no drupe predation at all and the palm population density were set by competition alone (*cf.* Janzen, 1970).

The role of the bruchid's disease in this system has not been discussed. It is likely that the pathogenicity of the litter below the palm builds up gradually during the first few years of fruit production. The disease then probably kills a relatively constant percent of each bruchid generation. This constant mortality effectively lowers the carrying capacity of the habitat for bruchids, and should lead to a higher proximity in time and space of the palms than would otherwise be the case. However, it is unlikely that the pathogenicity of the site below the tree is sensitive to slight differences in bruchid density below each palm that may result from differences in distance between adult palms. The disease is therefore likely to influence only the mean density of palms at the site, and not the detailed spatial relationships of the plants.

At the five sites examined in this study, the bruchid-*Scheelea*-rodent interaction is rapidly becoming a historical event. At all sites, more mature forest is being converted to brushy pastures and then to pure grass pasture. Some adult *S. rostrata* are left standing when the forest is cut and it is easy to conclude that they are part of the pasture flora (*e.g.*, Standley, 1937), when in fact they are reproductively dead. One must also be careful not to regard the absence of bruchids in the pasture as normal; the breakdown of the bruchid-palm interaction spells a loud warning to studies attempting to understand the evolution and operation of complex tropical ecosystems in the face of omnipresent agricultural activity.

The large *coyol* palm (*Acrocomia*

vinifera) that replaces *S. rostrata* when the forest is cleared in the vicinity of the five study sites is instructive on this point. *Acrocomia vinifera* is very common and reproduces very well; its fruits are eaten by cattle and the drupes deposited throughout the pasture. In old brushy pastures, there are *A. vinifera* of all ages. It is tempting to regard *coyol* as a native wild palm. However, I have not found any adults in forests more than about 30 years old and they do not occur in natural disturbance sites such as river banks and creek bottoms. *Acrocomia vinifera* also differs from *S. rostrata* in that it has endocarps with single seeds, endocarps about one-third the volume of those of *S. rostrata*, very strongly synchronized fruit maturation (January), two or three synchronized inflorescences per tree, no accumulation of endocarps beneath the tree (owing to cattle eating the fruits), and less than one percent infestation by bruchids. As with any plant that has suddenly become very abundant in a new environment, understanding the evolution and adaptive significance of these traits will be extremely difficult unless its original habitat still exists and can be located.

Acknowledgments

I deeply thank A. B. Weder and C. S. Vaughan for spending the better part of a summer examining endocarps at the Barranca site. D. E. Wilson aided tremendously in collection and analysis of the endocarps from all sites in the September samples. Further information was gathered by N. J. Scott as part of field activities of a course entitled

"Fundamentals of tropical biology: an ecological approach" and taught under the auspices of The Organization for Tropical Studies (July, 1970). The system was first encountered while I was teaching in Scott's course in February, 1970. This study was substantially supported by NSF grants GB-7805 and GB-25189. R. Schmid, C. E. Schnell, D. E. Wilson, H. G. Baker, D. Bradford, and H. E. Moore, Jr. offered invaluable comments on the manuscript.

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Additions and Corrections to “An Annotated Checklist of Cultivated Palms”

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An annotated checklist of cultivated palms was published in *Principes* 7: 119–182, 1963. It was noted then that certain problems had not been resolved and that errors would certainly be present. Studies undertaken between 1963 and the present suggest certain changes in taxonomy as in *Elaeis*, *Laccospadix*, *Sabal*. Other changes correct errors in nomenclature as in *Vonitra fibrosa* or citation as in *Areca triandra*. An asterisk preceding the name indicates a comment on the reason for change and the whole is to be used in conjunction with the checklist previously published. Names accepted as correct are printed in boldface; synonyms are italicized.

It will be noted that changes have not been made to conform with recent studies of S. F. Glassman (see *Palm Literature*, p. 19) who has included a series of genera—*Arecastrum*, *Arikuryroba*, *Barbosa*, *Butia*, *Chrysallidosperma*, *Lytocaryum*, *Microcoelum*, *Rhyticocos*—in *Syagrus*.

Taxonomists should agree on the correct name for a plant in any particular genus but they may not always agree on the limits of the genus nor on the species to be included. I am not yet convinced that the submergence of these several genera is useful either to the systematist who wishes to recognize evolutionary end-points or departures from the basic pattern—as most of these seem to be departures from the basic pattern of *Syagrus*—or to the user of plant names.

Most particularly, I cannot agree that *Butia* can be associated with *Syagrus*. That the peduncular bract or spathe may become wrinkled in age does not negate a rather fundamental difference between the bracts of *Butia*, *Cocos*, *Jubaea*, *Jubaeopsis*, and those of *Syagrus* and its allies at the time when the presence or absence of plications may serve some function. There are differences in gynoeceum and in fruit that also separate *Butia*. The fact that sterile or essentially sterile hybrids may be obtained in cultivation or even occasionally in nature does not disguise the normal distinctness of these kinds of palms. Sterile intergeneric hybrids are known elsewhere. They may illuminate generic relationships but not necessarily call for the union of genera. I therefore continue to accept *Butia* etc. until such time as my understanding of evolution among the cocosoid palms may change.

Acrocomia crispa: **Gastrococos crispa**

Acanthosabal: **Acoelorrhaphe**

ACOELORRHAPHE: add as synonym

Acanthosabal Proschowsky, Gard. Chron. ser. 3, 77: 91. 7 Feb. 1925.

Acoelorrhaphe Wrightii: add as synonym

Acanthosabal caespitosa Proschowsky, Gard. Chron. ser. 3, 77: 91. 1925.

Actinorhytis Calapparia: change reference for synonym to

Areca Calapparia Blume, Rumphia
2: 68, pl. 100, f. 2. 1838-39.

***Areca triandra** Roxburgh in Buchanan-Hamilton, Memoirs of the Wernerian Society 5: 310. 1826 ('1824').

* This is an earlier publication of the name than that given in the checklist (p. 126). It appeared at the same time as *Areca laxa* Buchanan-Hamilton (*op. cit.* p. 309) which was considered a variety of *A. triandra* by Beccari in a posthumous paper edited by Martelli (*Atti Soc. Tosc. Pisa Mem.* 44: 116. 1934). Thus when the two are united, the name *Areca triandra* should be used under provisions of Article 57, *International Code of Botanical Nomenclature* (1966) not *A. laxa* as was done by Burret (*Notizbl. Berlin* 12: 602. 1935) on the assumption that there was a difference in dates of publication.

Butia Gaertneri: **Syagrus coronata**

Calyptrocalyx australasicus: **Laccospadix australasicus**

Copernicia prunifera: change citation of synonyms as follows:

Copernicia cerifera (Arruda da Camara) Martius, *Hist. Nat. Palm.* 3: 242 [ed. 1]. 1839.

Corypha cerifera Arruda da Camara, *Discurso Util. Inst. Jard.* 1810.

Corozo: **Elaeis**

Corozo oleifera*: **Elaeis oleifera

***DAEMONOROPS**: read **Daemonorhops**

* The spelling *Daemonorhops* is orthographically correct according to Dr. W. J. Dress.

Dictyosperma fibrosum: **Vonitra fibrosa**

Diplothemium: change entry as follows:

D. maritimum: **A. arenaria**.

ELAEIS: add generic synonym and entry as follows

Corozo N. J. Jacquin ex Giseke, *Prael.* 42, 92. 1792.

***E. oleifera** (Humboldt, Bonpland, et Kunth) Cortés, *Flora Colombiana* 1: 203. 1897.

Alfonsia oleifera Humboldt, Bonpland et Kunth, *Nov. Gen. Sp.* 1: 307 [fol. 246]. 1816.

Corozo oleifera (Humboldt, Bonpland et Kunth) L. H. Bailey, *Gent. Herb.* 3: 59. 1933.

Elaeis melanococca of authors not of J. Gaertner.

* The distinctions between *Elaeis guineensis* and *E. oleifera* appear to be at the specific level rather than at the generic level when the two are compared carefully.

GASTROCOCOS S. A. Morales, *Rep. Fis. Nat. Cuba* 1: 57. 1865.

***G. crispa** (Humboldt, Bonpland et Kunth) H. E. Moore, *Principes* 11: 121. 1968 ('1967')

Cocos crispa, *Acrocomia crispa*, *Gastrococos armentalis*, *Acrocomia armentalis* (see p. 124 of checklist under *Acrocomia crispa*).

* Reasons for this change were noted in *Principes* 11: 114-121. 1967

Geonoma: add

see: Wessels Boer, The geonomoid palms. *Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen, afdeling Naturkunde*, ser. 2, 58(1): 1-202. 1968.

G. binervia: **G. interrupta**.

G. deversa (Poiteau) Kunth, *Enum. Pl.* 3: 231. 1841.

Gynestum deversum Poiteau, *Mémoires du Muséum d'Histoire Naturelle*, Paris 9: 390. 1822.

Geonoma longepetiolata Oersted, Vid. Medd. Kjoebenh. 1858: 36. 1859.

G. dicranospadix Burret, Bot. Jahrb. 63. 169. 1930.

G. longepedunculata Burret, Notizbl. Berlin 11: 8. 1930

***G. interrupta** (Ruiz et Pavon) Martius, Hist. Nat. Palm. 2: 8. 1823.

Martinezia interrupta Ruiz et Pavon, Syst. 296. 1798.

G. binervia Oersted, Vid. Medd. Kjoebenh. 1858: 33. 1859.

* Wessels Boer referred *G. binervia* to *G. oxycarpa* in 1968 but earlier united it with *G. interrupta* (*Flora of Suriname* 5: 27. 1965). The last seems a more satisfactory solution as noted by Moore in *Taxon* 18: 231. 1969.

G. Lindeniana H. Wendland, Linnaea 28: 337. 1856.

G. pumila Linden et H. Wendland, Linnaea 28: 338. 1856.

G. longepedunculata: **G. dicranospadix**

G. longepetiolata: **G. deversa**.

G. pumila: **G. Lindeniana**.

***LACCOSPADIX** H. Wendland et Drude, Linnaea 39: 206. 1875.

* *Laccospadix* was referred to *Calyptrocalyx* earlier on the strength of Bentham's treatment in *Flora Australiensis*. Experience with the genus in the field shows it to be amply distinct from *Calyptrocalyx*.

L. australasica H. Wendland et Drude, Linnaea 39: 206. 1875 ('australasica').

Calyptrocalyx australasicus (H. Wendland et Drude) J. D. Hooker in Bentham et J. D. Hooker, Gen. Pl. 3: 903. 1883.

Latania: add the following synonymy

L. lontaroides

Latania rubra N. J. Jacquin, Fragmenta Botanica 13. 1801.

L. rubra: **L. lontaroides**.

Licuala: substitute the following earlier description

L. peltata Roxburgh ex Buchanan-Hamilton, Memoirs of the Wernerian Society 5: 313. 1826 ('1824').

Mauritia aculeata: native in Colombia and Venezuela not Brazil according to A. Dugand. (Personal communication)

Mauritia elegans: native in Colombia, not Venezuela according to A. Dugand (personal communication)

Nephrosperma Vanhoutteanum: combining authority should read I. B. Balfour

***Paralinospadix Petrickiana** Burret, Notizbl. Berlin 13: 471. 1937.

('Petrickianus'). New Britain?

Linospadix Petrickiana Hort. Sander, Gard. Chron. ser. 3, 24: 298, fig. 87, 1898, provisional name.

* It was previously noted that this palm had not been described but a description was provided by Burret in 1937 based on plants cultivated at Singapore Botanical Gardens. The earlier name *Linospadix Petrickiana* was clearly specified as provisional hence was not validly published. Moreover, it was used for a juvenile plant impossible to place botanically.

Phoenix acaulis Roxburgh, Plants of the coast of Coromandel 3: 69, pl. 273. 1819.

Phoenix canariensis: the following changes are required. See *Principes* 15: 33-35. 1971.

P. canariensis Hortorum ex Chabaud,
La Provence Agricole et Horticole
Illustrée 19: 263, fig. 66-68.
1882.

?*P. cycadifolia* Hort. Athen ex E.
Regel, Gartenfl. 28: 131, pl. 974.
1879.

P. cycadifolia: ?**P. canariensis**

Pinanga coronata (Blume ex Martius)
Blume, Rumphia 2: 83. 1838-39
(‘1836’).

Areca coronata Blume ex Martius,
Hist. Nat. Palm. 3: 179. 1837.

SABAL

The following changes are explained in
a separate article entitled “Notes on
Sabal in cultivation.”

S. Beccariana: **S. princeps**.

S. Blackburniana Glazebrook ex J.
A. & J. H. Schultes, Syst. Veg.
7(2): 1488. 1830 (*‘Blackburniana-
num’*).

S. Blackburnia Glazebrook in Lou-
don, The Gardener’s Magazine and
Register of Rural and Domestic
Improvement 5: 52, 1829, pro-
visional name.

S. exul: **S. mexicana**.

S. glaucescens: **S. mauritiiformis**

S. guatemalensis: **S. mexicana**

S. mauritiiformis (H. Karsten) Gri-
sebach et H. Wendland in Gri-
sebach, Fl. Brit. W. Ind. 514.
1864.

Trithrinax mauritiiformis H. Karsten,
Linnaea 28: 244. 1864 (*‘mauritiiae-
formis’*).

S. glaucescens Loddiges ex H. E.
Moore, Gent. Herb. 9: 287. 1963.

S. nematoclada Burret, Repert. Sp.
Nov. 48: 256. 1940.

S. mayarum: **S. Yapa**.

S. mexicana Martius, Hist. Nat. Palm.
3: 246 [ed. 1]. 1839.

S. guatemalensis Beccari, Webbia 2:
68. 1907.

S. texana (O. F. Cook) Beccari,
Webbia 2: 78. 1907.

Inodes texana O. F. Cook, Bull.
Torrey Club 28: 534. 1901.

Inodes exul O. F. Cook, United States
Department of Agriculture, Bureau
of Plant Industry Circular 113:
14. 1913.

Sabal exul (O. F. Cook) L. H. Bailey,
Rhodora 18: 155. 1916.

S. nematoclada: **S. mauritiiformis**.

S. Palmetto: add as synonym

S. viatoris L. H. Bailey, Gent. Herb.
6: 403. 1944.

S. peregrina: **S. Yapa**.

S. princeps Hortorum ex Beccari,
Webbia 2: 59. 1907. Cultivated
in Italy.

S. Beccariana L. H. Bailey, Gent.
Herb. 4: 397. 1940.

S. texana: **S. mexicana**.

S. umbraculifera: **S. domingensis** as
to much material in cultivation, **S.
Blackburniana** as to name. See
previous annotations.

S. viatoris: **S. Palmetto**.

S. Yapa C. Wright ex Beccari, Webbia
2: 64. 1907.

S. mayarum H. H. Bartlett, Carnegie
Inst. Publ. 461: 35. 1935.

S. peregrina L. H. Bailey, Gent. Herb.
6: 400. 1944.

Scheelea Humboldtiana: native in Ven-
ezuela not Colombia according to
A. Dugand (Personal communica-
tion).

Syagrus coronata: add

Butia Gaertneri Hort. and *Cocos Gaertneri* Hort., names only, according to Barbosa Rodrigues, Pl. Nov. Cult. Rio de Janeiro 1: 12. 1891.

Syagrus orinocensis: grows in Colombia according to Dugand (personal communication).

**Vonitra fibrosa* (C. H. Wright) Becc., Agric. Colon. 5: 322. 1911.

Dictyosperma fibrosum C. H. Wright, Kew Bull. 1894 (94): 359. Oct. 1894.

Dypsis Thouarsiana Baillon, Bull. Mens. Soc. Linn. Paris 2 (147): 1163. post 7 Nov. 1894.

Vonitra Thouarsiana (Baillon) Becc., Bot. Jahrb. 33, Beiblatt 87: 18. 1906.

* This represents a change over the listing on p. 170 of the checklist which was accepted on the basis of Jumelle and Perrier de la Bathie's work in *Flore de Madagascar, 30^e Famille* (1945). Both epithets for the species were published in 1894 but *Dictyosperma fibrosum* appeared in October while *Dypsis Thouarsiana* was proposed at the meeting of the Société Linnéenne de Paris on November 7, 1894, and must have been published after that date. When the two species are united, priority requires the use of the epithet *fibrosa*.

PALM BRIEFS

Palms can be painfully slow about reaching flowering age, as anyone who has grown them from seed will attest, but occasionally we are startled by an inflorescence appearing from the juvenile leaves of a palm seedling. The *Chrysalidocarpus lutescens* pictured at right flowered about 20 months after planting. Such an event is rare, but probably caused by some small environmental stimulus or internal imbalance of growth substances. It suggests that the state of flowering is separated from the state of non-flowering by only a thin line, even in seedlings. What a bonanza would be opened up to geneticists and plant breeders if we could learn to cross that line at will!

FRED B. ESSIG



NEWS OF THE SOCIETY

Key to Brazilian Palms

One of the Society's members in Brazil, Dr. J. T. de Medeiros Costa, has published a very comprehensive key to the palms of that huge country in the *Annals of the Twentieth National Botanical Congress*, January 1969. Dr. Costa is a professor in the Department of Ecology of the Federal University of Pernambuco. This key attempts to bring up to date those previously published by earlier authors such as Drude (1883), Löfgren (1917) and Beccari & Pichi-Sermolli (1956). It lists the five sub-families, twenty-seven genera and 450 species of palms native to Brazil. Unfortunately, most of us are not familiar enough with the Portuguese language to read this paper with ease.

Palm Is National Tree of Colombia

Professor Armando Dugand has sent the Society an article written by him which appeared in the *Magazine Dominical* of November 22, 1970. In it he reviews the nomenclatural history of the genus *Ceroxylon*. Of the eleven species native to Colombia, Professor Dugand considers *C. quindiuense* the most beautiful. It is also outstanding because of its great height, reaching 50-60 meters (150 to 180 feet), and its habitat in the Central Andes at elevations between 1700 and 3400 meters (5000 to 10,000 feet) above sea level.

On the 27th of July, 1949 Prof.

Dugand proposed this palm as the national tree of Colombia before the Institute of Natural Sciences of the National University, Bogota. The "wax palm" was so named by the members of the Institute. Some of these palms were planted in the Parque de la Independencia in Bogota in 1910, to celebrate the first 100 years of Colombia's independence.

Out-of-print Numbers of Principes

Members who wish to complete their sets of PRINCIPES may now order Xerox reproductions of out-of-print numbers from University Microfilms, A Xerox Company, 300 North Zeeb Road, Ann Arbor, Mich. 48106. The cost is 8¢ per page, with a minimum of \$3.00 per issue.

California Native Palms

Anyone who wants to visit the scattered groves of *Washingtonias* in the California desert would find useful a column written by Paul Wilhelm in the *Daily News of Indio, Calif.*, Saturday, Feb. 20, 1971. This column, sent to us by one of our California members, pinpoints the locations of many out-of-the-way groves and gives some interesting facts about these "solitary dwellers of the silent places."

LUCITA H. WAIT

PHOTO GALLERY



The rainforests of the Osa Peninsula in Costa Rica are a treasure-trove of palms. Look for *Asterogyne*, *Bactris*, *Cryosophila*, *Geonoma* and *Iriartea* in this picture. Photo by Fred B. Essig.