

PRINCIPES

Journal of The Palm Society

October, 1981 Vol. 25, No. 4

THE PALM SOCIETY

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Contents for October

Frost Susceptibility of Palms: Experimental			
Data and Their Interpretation			
W. Larcher and A. Winter			143
Indian Ocean Odyssey: A Look at Palms	•		110
from Good Hope to Sri Lanka			
Melvin W. Sneed			153
	•	•	100
Studies on Bentinckia condapanna:			
I. The Fruit and the Seed			
D. Padmanabhan and D. Regupathy			172
A Reassessment of the Genus			
Lophospatha Burret			
J. Dransfield and J. P. Mogea			178
Distribution of the Nypa Palm in Australia			
Jeanette Covacevich			184
Regular Features			
Classified]	171,	177
Palm Literature			181
Palm Research			182
News of the Society			182
	•		188
Bookstore	•	•	189
	•	•	
Principes Endowment Fund	٠	٠	190
$\operatorname{Index}. $	•		190

Cover Picture

Pollen under SEM, from top left-clockwise Daemonorops micracantha (Griff.) Becc. ×1,650; Daemonorops grandis (Griff.) Mart. ×2,550; Calamus javensis Blume ×1,550; Korthalsia robusta Blume ×950; Korthalsia rigida Blume ×1,650; Daemonorops verticillaris Griff. Mart. ×1,600; Calamus exilis Griff. ×1,550; Korthalsia debilis Blume ×1,550; Korthalsia rostrata Blume ×1,550 in center. See p. 182.

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JOURNAL OF THE PALM SOCIETY (ISSN 0032-8480)

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

Subscription price is \$9.00 per year to libraries and institutions. Membership dues of \$15.00 per year include a subscription to the Journal. Single copies are \$5.00 each, \$20.00 a volume. Airmail delivery \$2.50 a copy or \$10.00 a volume. The business office is located at P.O. Box 368, Lawrence, Kansas 66044. Changes of address, undeliverable copies, orders for subscriptions, and membership dues are to be sent to the business office.

Second class postage paid at Lawrence, Kansas

Mailed at Lawrence, Kansas November 6, 1981 Principes, 25(4), 1981, pp. 143-152

Frost Susceptibility of Palms: Experimental Data and Their Interpretation

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The frost susceptibility of palms has been thoroughly documented on the basis of injuries observed following frost conditions. A wealth of data on this subject is to be found in Smith (1958, 1964), Barry (1961), Saakov (1963), Kellett (1969), and Campbell et al. (1977). Experimental investigations, on the other hand, have been made only on a few species (Larcher 1954, 1980, Biebl 1964). In his review on systematics and ecology of palms P. B. Tomlinson very justifiably states that "the physiological basis for the ecological preferences of palms is not understood. The needed research might well study physiological tolerances of individual palm species first in artificially controlled environments and then in field circumstances" (Tomlinson 1979, p. 97). The data presented here were obtained by experimental measurements. In their interpretation the ecological, geobotanical, and evolutionary aspects will be given priority.

Plants and Methods

Samples for the experiments were selected from the Arboretum Arco (Lake Garda Region, Northern Italy) and the Acclimatation Garden "La Orotava" at Puerto de la Cruz (Tenerife, Canary Islands). Arco (45°55′N, 112 m a.s.l.) has a southern alpine climate with strong Mediterranean influence. The annual mean temperature

is 14°C, the mean temperature of the coldest month (January) +4.1°C, and the average of annual minimum temperatures -4°C; the lowest temperatures observed are -10°C (Larcher 1979). In Arco entire five year old juvenile plants of Trachycarpus fortunei (W. J. Hook) H. Wendl., and leaves of adult Chamaerops humilis L., Washingtonia filifera (Linden) H. Wendl., and Jubaea chilensis (Molina) Boillon were sampled several times during three years.

Puerto de la Cruz (La Orotava: 28°24'N, 110 m a.s.l.) has a maritimesubtropical climate with an annual mean temperature of 19.5°C, a mean temperature of the coldest month of +16.2°C, and average annual minimum temperatures of +10.8°C. The lowest minimum temperatures are +8°C (Abreu 1977). The experiments at Puerto de la Cruz were performed in February, the coldest month of the year. Mature leaves of (a) tall adult specimens, of (j) juvenile plants before shoot extension of ca. 1 m height and of (s) seedlings with typical seedling leaves (cf. Tomlinson 1961) were taken from the following species:

CORYPHOIDEAE: (a) Livistona australis Mart., (a) Livistona chinensis (Jacq.) R. Br. ex Mart., (a) Rhapis excelsa (Thunberg) Henry, (a) Sabal minor (Jacq.) Pers., (a) Trithrinax acanthocoma Drude.

PHOENICOIDEAE: (a) Phoenix

Table 1. Freezing susceptibility of the leaves of subtropical fan palms. At the mean freezing temperature a large part of the leaves is killed

Species	First injury below °C	Mean freezing temperature (°C)
Washingtonia filifera (s)	-4	-6
Washingtonia filifera (a)	-8	-10
Livistona australis (a)	-8	-9
Livistona chinensis (a)	-9	-10.5
Rhapis excelsa (a)	-8	-10.5
Trithrinax acanthocoma (a)	-9	-10.5
Chamaerops humilis (a)	-9	-11.5
Serenoa repens (s)	-10	-12.5
Sabal minor (a)	-10.5	-13.5
Trachycarpus fortunei (s)	-9	-12
Trachycarpus fortunei (a)	-11	-14

⁽s) = seedling.

canariensis Hort. ex Chabaud, (a) Phoenix dactylifera L., (a) Phoenix reclinata Jacq., (a) Phoenix roebelenii O'Brien.

CARYOTOIDEAE: (a) Caryota urens L.

CHAMAEDOROIDEAE: (a) Chamaedorea costaricana Oersted.

ARECOIDEAE: (j) Chrysalidocarpus lutescens H. Wendl., (s) Euterpe edulis Mart., (a) Howea forsterana (C. Moore et F. Müller) Beccari.

COCOSOIDEAE: (a) Aiphanes acanthophylla (Mart.) Burret., (j) Cocos nucifera L., (j) Elaeis guineensis Jacq., (s) Jubaea chilensis (Molina) Baillon.

PHYTELEPHANTOIDEAE: (a) *Phytelephas macrocarpa* Ruiz et Pavon.

Seedlings of Trachycarpus fortunei (Hook) Wendl., Serenoa repens (Bartr.) Small, Washingtonia filifera (Linden) H. Wendl., Sabal minor (Jacq.) Pers. and Phoenix canariensis Hort. ex Chabaud were raised from seeds and kept outdoors in the Botanical Gardens of Innsbruck during summer and in a cool greenhouse in winter. Two weeks before starting the measurements seedlings of various ages (up to five

years old) were conditioned at temperatures of +5 to +10°C.

The frost susceptibility was determined by 12 hrs exposure of plant parts or entire seedlings to a series of constant test temperatures between 0°C and -20°C in research refrigerators, and by evaluation of the freezing exotherms of water saturated leaves. Tissue temperatures were monitored by copper-constantan thermocouples connected with a recorder. All data presented are average values of at least five replicates (in the case of seeds 15-20 replicates). Injury was assayed by visual change in color, by conductometric detection of electrolyte leakage from tissues, and by loss of enzymatic triphenyl tetrazolium chloride reduction. Details of the employed methods are given by Larcher (1977a, b, 1980).

Specific Freezing Limits for the Leaves of Various Species

The temperatures below which the first injuries appear and which cause severe freezing of palm leaves are listed in Tables 1 and 2. It appears that, among subtropical fan palms, *Trachy*-

⁽a) = adult plant.

Table 2. Freezing susceptibility of the leaves of feather palms

Species	First injury below °C	Mean freezing temperature (°C)
Aiphanes acanthophylla (a)	-3	-3.5
Elaeis guineensis (s)	-3	-3.5
Cocos nucifera (j)	-3	-3.8
Chrysalidocarpus lutescens (j)	-3	-4
Caryota urens (a)	-4	-5.5
Chamaedorea costaricana (a)	-4.5	-6
Euterpe edulis (s)	-5	-6.5
Howea forsterana (a)	-5.5	-6
Phytelephas macrocarpa (a)	-6	-6.5
Jubaea chilensis (s)	-7	-7.5
Jubaea chilensis (a)	-7	-9
Phoenix roebelenii (a)	-7	-8
Phoenix reclinata (a)	-7	-10.5
Phoenix dactylifera (a)	-8	-9.5
Phoenix canariensis (s)	-6	-7.5
Phoenix canariensis (a)	-9	-10.5

⁽s) = seedling.

carpus fortunei and Sabal minor are the most resistant whereas the representatives of the Livistona alliance are much more sensitive to frost temperatures. Species of Phoenix and Jubaea chilensis sustain considerably lower temperatures than the other feather palms investigated. Unfortunately it was not possible to determine the survival limits of leaves of Ceroxylon.

The experimental data correspond well with experience from occasional observations of frost damage to cultivated palms in gardens and parks (cf. Gola 1929, Odishariya 1952, Smith 1958, 1964, Barry 1961, Larcher 1963, Saakov 1963, Manley 1967, Kellett 1969, Campbell et al. 1977). There is some additional information on frost survival of particularly resistant species: Trachycarpus fortunei is successfully cultivated outdoors in several places in the British Isles (e.g. in the Botanical Gardens of Kew and of Edinburgh, where the lowest temperatures are -12.8° C and -9.4° C, respectively;

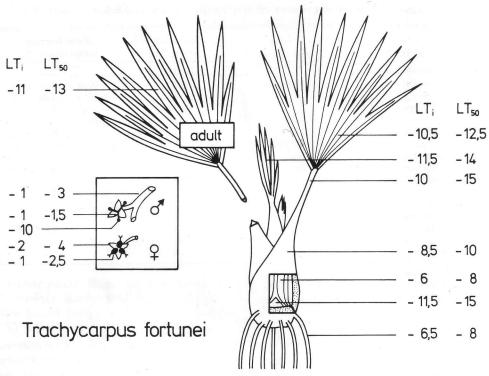
Lamb 1972). In Seattle, Washington, the leaves of adult Trachycarpus were severely damaged at -14°C, but the plant recovered (R. B. Walker, pers. comm.). Trachycarpus in the Huntington Botanical Gardens at San Marino. California, suffered leaf damage at -11°C and was defoliated at −19°C (M. Kimnach, pers. comm.). Tall specimens of Washingtonia filifera, Phoenix canariensis and Jubaea chilensis sustained temperatures of -10 to -12°C in the Lake Garda Region, at various locations of the Northern Mediterranean Regions, and at Sukhumi on the Black Sea Coast.

Frost Susceptibility of Various Vegetative Organs

Leaf damage and even complete defoliation can be, but is not necessarily, lethal for palms. Recovery of *Trachycarpus fortunei* after severe frost damage of the foliage has been repeatedly observed. In all these cases the shoot apex was still living due to better pro-

⁽j) = juvenile.

⁽a) = adult plant.



1. Frost susceptibility of various parts of juvenile and adult plants of Trachycarpus fortunei. $LT_i = Temperature$ (°C) limit for initial frost damage; $LT_{50} = Lethal$ temperature at 50% killing rate.

tection and probably also higher frost resistance. A thorough susceptibility analysis of a species can therefore not be restricted to the leaves but should include each plant organ and tissue determining survival.

Variations in the frost susceptibility of different organs and tissues of Trachycarpus fortunei are shown in Figure 1, of seedlings of Washingtonia filifera in Figure 2, and of Phoenix canariensis in Figure 3. From Figure 1 it becomes evident that the shoot apex may indeed attain higher frost resistance than the leaves, provided preceding cold weather has forced the plant to arrest its growth processes. If the plant is in the active state the shoot apex is killed together with the leaves or still earlier (Fig. 2). The most sen-

sitive parts of juvenile plants are fast growing tissues such as the intercalary elongation zone of young leaves and the succulent bases of the leaf sheaths.

The roots are very susceptible to freezing, especially the root tips. The roots are also the most vulnerable organs of palms. Parts of them are already damaged at temperatures of -1 to -2° C. Even the crown roots above the soil surface, where during a radiative frost the lowest temperatures normally occur, are more sensitive than most of the shoot tissues. As a consequence, palms are severely affected by ground frost. If only the roots have been frozen the leaves remain turgid and green for several days and there is a still longer delay before wilting oc-

curs. Because of the susceptibility of roots, if frost events are to be expected, temperature measurements should not only be made in air but also near to the ground and in the rooted soil layers. This facilitates the interpretation of subsequently appearing injuries.

Frost Susceptibility of Propagative Organs and Young Seedlings

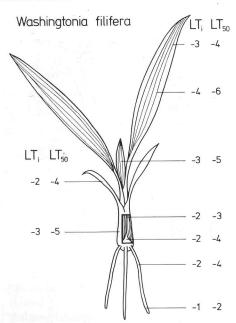
As a rule, flowers are the least resistant parts and germinating seeds and young seedlings the weakest developmental stages of a plant (Larcher 1973, Larcher and Bauer 1981). Frost therefore affects propagation at temperatures which would still be harmless to the vegetative organs of adult plants.

Flowers of Trachycarpus fortunei are damaged at -1 to -3° C; at -4.5° C they are entirely killed (see Fig. 1). In the male flowers the perianth and the filaments are the most sensitive parts; anthers and pollen remain visually unharmed until -10° C. In female flowers the ovaries are considerably more sentences.

sitive than the perianth.

Seeds are very resistant to frost. If air-dry seeds of Trachycarpus fortunei and of Washingtonia filifera were cooled to -70°C for 12 hrs, most maintained their ability to germinate. Hydrated seeds are considerably less resistant: 50% of water soaked seeds of Trachycarpus were killed after cooling to -20° C, of Washingtonia to -10° C. After cooling to -16°C, 20% of hydrated seeds of Washingtonia remained still alive. As soon as germination occurs and the primary root becomes visible, the embryo of Washingtonia is killed below -2°C, that of Trachycarpus below -10°C.

Young seedlings in the coleoptile stage and during the extension of the

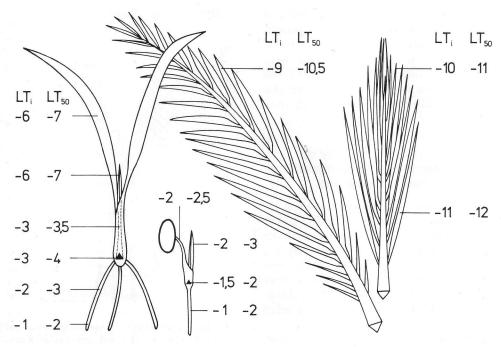


2. Frost susceptibility of various tissues of actively growing one year old seedlings of Washingtonia filifera. $LT_i = {}^{\circ}C$ causing initial injuries; $LT_{50} = {}^{\circ}C$ causing 50% injury.

primary leaf are the most sensitive steps in the life cycle (see Figs. 3 and 4). Again the roots and the elongating leaf bases are the first to be damaged by frost. With aging the susceptibility decreases rapidly in Trachycarpus fortunei and Sabal minor, more slowly in Washingtonia filifera and Phoenix canariensis. Juvenile plants of Trachycarpus attain nearly the same frost resistance as adult palms.

Seasonal and Adaptive Variations of Frost Susceptibility

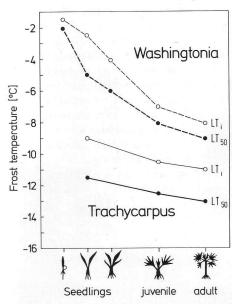
The clearly positive correlation between growth activity and frost susceptibility leads us to expect seasonal variations of the sensitivity level. Such seasonal differences can in fact be demonstrated, but only in those tis-



3. Frost susceptibility of germinating and one year old seedlings, and of still folded and mature leaves of adult plants of *Phoenix canariensis*. $LT_i = {}^{\circ}C$ causing initial injuries; $LT_{50} = {}^{\circ}C$ causing 50% injury.

sues capable of extension growth, i.e. the shoot apex and, above all, the intercalary growth zones of the leaves and leaf sheaths (Fig. 5). Fully differentiated leaves, on the other hand, show no appreciable variations throughout the year. This remarkable property is peculiar to palms. In contrast to other plant species the mature tissues exhibit approximately the same temperature limit for frost injuries in summer and winter. In palms the state of activity of individual organs and tissues apparently does not affect the rest of the vegetative plant body. This kind of autonomy of the individual parts of the organism typifies certain tropical trees, in which development is not synchronized with climatic seasonality. The analogous behavior of subtropical palms leads to the conclusion that, in contrast to woody plants that penetrate to higher latitudes, palms have not been able to evolve a complete timing of their annual pattern of growth with the increasing seasonality of climate (Larcher 1981). Nevertheless, certain processes in development are very well synchronized, as for example the process of flowering in *Trachycarpus fortunei* with photoperiod.

If mature organs exhibit only slight seasonal variability of their frost susceptibility, little effect on hardening can be expected from lowering temperatures or from other environmental stressors such as drought. Leaves of juvenile plants of *Trachycarpus fortunei* were 1–2°C less frost resistant after 10 days' exposure to 20°C as compared with cold-conditioned plants. A drought period of 10 days, during which the plants wilted to a water sat-

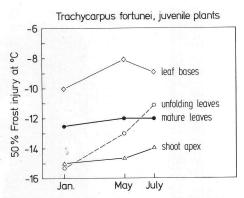


4. Effect of aging on the frost susceptibility of leaves of Washingtonia filifera and Trachycarpus fortunei. $LT_i = {}^{\circ}C$ causing initial injuries; $LT_{50} = {}^{\circ}C$ causing 50% injury.

uration deficit of 66%, also induced an increase in frost resistance of 1–2°C. Combined drought and cold treatment resulted in a shift of the injurious temperature level to -12.5°C for initial injuries, and to -14°C for 50% leaf damage. Thus, the greatest adaptation amplitude of juvenile *Trachycarpus* does not exceed 3°C. The seasonal and adaptive range of mature leaves of *Washingtonia filifera* and *Chamaerops humilis* was only 1°C or less.

Frost Susceptibility and Distribution Range of Palms

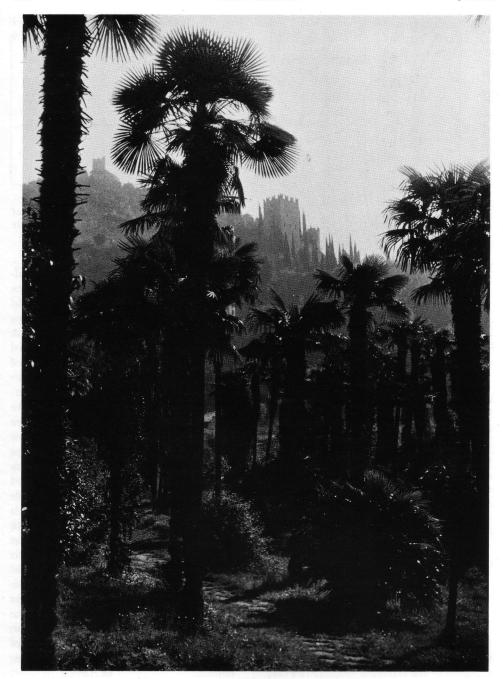
The palm family has evolved a wealth of adaptations, which accounts for their presence in widely differing environments (Read 1974). However, they have never succeeded in establishing themselves in regions with cold winter and severe frost. The Arecaceae therefore represent the classical



5. Seasonal changes in frost susceptibility of mature leaves and growing parts of juvenile plants of *Trachycarpus fortunei*.

textbook example of a plant group almost entirely confined to the tropics (Good 1974). Among the coryphoid palms, Chamaerops humilis advances as far as 40°N in Spain and Sardinia thus delimiting the extreme northward deviation of the distribution area of palms. Species of Sabal and Washingtonia in North America and of Trachycarpus in East Asia proceed up to 35°N (Moore 1973). Among the feather palms, Phoenix canariensis is native to the Canary Islands and Madeira (30°N), naturalized Phoenix dactylifera is found in Crete (35°N), and Phoenix sylvestris at 35°N in the Pandjab (Meusel 1965). In the Southern hemisphere, Jubaea chilensis delimits at 33°S the distribution area of palms in South America, Phoenix reclinata at 32°S in South Africa, and arecoid palms at 40°S in New Zealand. Altitudinal limits are 2,400 m a.s.l. for Trachycarpus species in the Himalavas (Beccari 1933) and 3,000-4,000 m a.s.l. for Ceroxylon species (Mc-Currach 1960, K. Mägdefrau pers. comm.) in the tropical Andes.

An absolute limit of distribution for both native and cultivated palms is undoubtedly the ground frost limit. Palms are unable to survive in regions



6. Trachycarpus fortunei in the Arboretum Arco, Garda Lake Region, Northern Italy.

where frost periods are of sufficient duration for negative temperatures to

develop in the soil itself.

If the natural distribution area of the most resistant palm species is compared with isotherms, good agreement appears between the northern limits for representatives of the Sabal alliance and of Trachycarpus and the average annual minimum isotherm of -10°C. It is remarkable that the -10°C isotherm is exceeded in Arkansas. It would be interesting to investigate whether the Sabal minor that pushes so far north is more resistant than experimental data suggest, or whether these dwarf palms have simply occupied favorable habitats where the temperatures are higher than those recorded in the meteorological stations. Since for naturally propagating plants the frost susceptibility of juvenile plants is decisive, the temperature limit for seedling establishment of Sabal and Trachycarpus should be at about −12°C.

In North America the distribution limits of species of the *Livistona* alliance (including *Washingtonia*) and in Southern Europe of *Chamaerops humilis* seem to correspond with the isotherm for absolute minimum temperatures of -5°C and average annual minimum temperatures of 0°C. Again a connection with survival limits of seedlings (and probably also roots) rather than adult palms appears.

Frost limitation of the natural distribution of feather palms seems to be very unlikely. *Phoenix canariensis*, which survives -10° C as an adult and -5° C as a juvenile plant, can be cultivated but does not naturally distribute at elevations much higher than 600 m a.s.l. at the Canary Islands (Santos, pers. comm.). At this altitudinal level the lowest temperatures are in the average $+6^{\circ}$ C and never lower than 0° C (Ceballos and Ortuño 1976, Abreu

1977). If the distribution areas (as presented by Moore 1973) of the other feather palms investigated are compared with isotherms below 0°C (e.g. Hoffmann 1960) no clear correlation can be recognized.

This indicates that survival limitation by low temperatures is not necessarily due to freezing. Many tropical plants suffer from chilling at temperatures between +10 and 0°C and can also be irreversibly damaged without freezing (Lyons 1973, Levitt 1980, Larcher and Bauer 1981). There is still no evidence as to whether palms are chilling sensitive. None of the species investigated showed visible damage due to acute chilling stress of 24 hrs at 0°C. However, unpublished measurements of CO2-gas exchange and of chlorophyll fluorescence transients (as an expression of photosynthetic function) revealed pathologic reactions near 0°C in seedlings of Washingtonia but not of Trachycarpus and Serenoa. The decrease in CO2-uptake at suboptimal temperatures is much steeper in Washingtonia than in Serenoa (Moraes 1980). Thus, chronic impairment of metabolic processes during long-lasting low temperatures near 0°C may result in weakening the plant and eventually lead to decay.

Acknowledgments

We are indebted to the Administrations of the "Arboretum Arco," Dr. P. Forcinella, and of the "Jardín de Aclimatación de La Orotava," Director Ing. A. A. Hodgeson and Curator Ing. J.-A. Rodriguez, for permission to take samples for the experiments. Thanks are due to the late Prof. Dr. H. E. Moore, Jr., Ithaca, N.Y., for valuable suggestions, and to Mrs. Joy Wieser for linguistic improvement of the manuscript.

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Principes, 25(4), 1981, pp. 153-171

Indian Ocean Odyssey A Look at Palms from Good Hope to Sri Lanka

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There are times when palm enthusiasts have to sit back and wonder what will happen in the sweep of world events, that might well lead to destruction of what remains of some of the world's finest flora. Little enough of it is left as it is. At this writing ominous rumblings come forth not far from places that harbor rare plants dear to collectors. The threat spews out from the highly volatile areas of S.W. Asia, fanning on down the coast of E. Africa and indeed, embracing much of the Indian Ocean area.

Interruption of travel can be threatened even though isolated palm collecting localities may not be immediately involved. There are no present barriers to travel in the Indian Ocean area. But my wife, Phyllis, and I would encourage would-be palm seekers who anticipate traveling there to go ahead with it—perhaps to be ahead of changing circumstances. Key places in the area are without parallel anywhere in the world with regard to relatively easy access to unique assemblages of palms. There are some limitations too, which might deter one's anticipation about travel into some areas. We shall mention them.

The Indian Ocean is vast and we're not about to cover all of it in this article. It fills an enormous expanse from South Africa to Australia in the south, curving northwesterly along the stretch of Indonesia to Sri Lanka (Ceylon) and

westerly to the "horn" of Africa brushing the Arabian Sea, which separates India from Saudi Arabia, Oman, and Yemen. The continental United States would fit into it with room to spare. We intend here to highlight places that could be of primary interest to palm collectors. So on with it!

After exploring the splendid palm collection in the Botanical Gardens in Rio de Janeiro we flew the long trek over the South Atlantic to Cape Town, South Africa. The Indian Ocean begins at the Cape of Good Hope, near Cape Town, which divides it from the South Atlantic.

South Africa

By design we arrived in Cape Town in October 1978, the month when much of the indigenous South African flora, sparkling with wild flowers, is at its best. The beauty of it defies description, highlighted by the tantalizingly colorful and diverse Proteaceae which include three or four genera with perhaps 250 species. Much of this can be seen at Kirstenbosch, the National Botanic Gardens of South Africa, which is devoted exclusively to the indigenous flora, some 20,000 different plants. For climatic reasons Kirstenbosch doesn't have all of them, and six regional gardens have been established in other places in South Africa.

Accordingly Kirstenbosch does not



1. Jubaeopsis caffra, Kirstenbosch Gardens, Cape Town.

boast of a palm collection, but the garden does have a few specimens including the indigenous *Jubaeopsis caf-fra* (Fig. 1). More often than not this is a trunkless palm; seed germination is poor and it is not widely cultivated. We were unable to collect seed.

Cape Town is too windy and pernaps too cool to provide a hospitable environment for many palm species, although we feel that more could be grown there if introduced. Nevertheess, splendid avenues downtown are ined with *Phoenix canariensis*, as are the beautifully landscaped grounds of the Mount Nelson Hotel, which is away from downtown with an excellent view of Table Mountain, Cape Town's pest known landmark (Fig. 2).

We flew on to Johannesburg where one sees more evidence of gold mining than palms. But from there it's only about 30 miles to Pretoria, our destination for a rendezvous with dedicated members of The Palm Society.

Amid the beauty of jacarandas in full bloom, lining the avenues of Pretoria, we were met by Dieter van Staden of the Department of Horticulture, Faculty of Agriculture, University of Pretoria, and member of The Palm



 Table Mountain backdrops Phoenix, Cape Town.

Society, who hosted our brief stay. We were privileged to visit his home, which is sited on ample grounds for his young collection of palms, and he introduced us to the Botanic Garden which has a fine collection of cycads but not many established palms. However, palms are on the way, judging from the rather extensive assemblage of seedlings and larger potted plants thriving in plant houses on the grounds.

We met Dr. Cris Scheepers, Research Officer at the laboratories, and a long-time member of The Palm Society. He has been responsible for the oncoming palm collection in the nurseries. He was enthusiastic about palms and pointed out many plants started from seed furnished by The Palm Society Seed Bank. We explored the garden, admiring the well-tended landscaping with accent on cycads (Fig. 3), and the different collections which included a large assemblage of coveted succulents indigenous to Madagascar. Also, one may see there the extraordinary Reynold's Gate at one entrance to the garden, which in the magic of its wrought iron depicts species of Aloe indigenous to South Africa.



3. Left to right: Dr. Cris Scheepers, Dieter van Staden, Phyllis Sneed and Mr. Piet Vorster, Botanic Garden, Pretoria.

Dieter and Mrs. van Staden motored us back to Johannesburg from where we went on to Durban, which is South Africa's "Miami Beach" on the shores of the Indian Ocean. Durban is subtropical, being a little more south of the Tropic of Capricorn than Miami, Florida is north of the Tropic of Cancer. We were in a world that to us was rather upside down. But Durban has palms—lots of them. We explored the area as far out as Zulu Land and environs, largely devoid of palms, but the most memorable experiences palmwise were in Durban itself, which has a very fine botanical garden dating back to 1849. It is interesting, as outlined in a small brochure we obtained that "The first curator of the Gardens was Mark J. McKen," a gardener with Kew training who had recently arrived in Natal, and who was appointed at the princely salary of fifty pounds per annum and a free hut. How McKen contrived to live is not recorded, but presumably a little money went a long way in those days, and it is apparent that he set about his duties with vigor, as in 1850 he reported having under cultivation "Bread Fruit, Ginger, Coffee, Camphor, Mangoes, Paw-paws, Cinnamon, Citrus, Tea and Pepper, and miscellaneous vegetables."

Palms were not mentioned among the early introductions, which were experimental, and no doubt possible commerical uses of palms were not thought of at the time. Later on a "Victoria Jubilee Conservatory" structure was opened in 1899, which housed a large collection of tropical plants—most of which it was discovered later could be grown and survive outdoors quite well in the Durban cli-



4. Licuala in avenue of palms, Durban Botanical Gardens, South Africa.



Hyphaene natalensis, on Natal Herbarium grounds, Durban.

mate. Palms were in the "Conservatory" assemblage and the garden now has more than 50 mature species growing in avenues and elsewhere as specimens (Fig. 4). The garden could in our judgment accommodate the introduction of many exotic palms which have not been tried there.

At the far side of the garden from the public entrance is the Botanical Research Unit, Department of Agricultural Technical Services, and the Natal Herbarium. Here we contacted Pierre du Toit of the staff who took time to show us around and inform us about palms on the grounds. Growing in front of the lab building was a specimen of the hard-to-find (for us, at least) Hyphaene natalensis, a species indigenous to South Africa (Fig. 5). Pierre du Toit gave us seeds from this tree which we mailed to Fairchild Tropical Garden in Florida, but their

germination remains doubtful. Also on the grounds there was what we were told was *Raphia australis*. We were not familiar with this species, but it was huge and handsome (Fig. 6). New leaves of this palm are said to be red and the sap makes a potent drink. We neither saw the red nor took a sip.

After visiting the sunken gardens, cycad collection and orchid house, the latter presenting the best organized display of such plants we have seen anywhere, we were satisfied and delighted with our stay in Durban. We prepared to go on to further destinations in the Indian Ocean, some of which we had visited previously and will be dealt with briefly. On 18 October 1978 we went on to Mauritius.

Mauritius

Landing here seemed like a homecoming. We had visited Mauritius almost exactly four years earlier. Not



6. Raphia, Natal Herbarium, Durban.

much had changed apparently; it's still a very much cut-over, sugar-cane exploited, little island. Yet it is one of the Mascarene Islands which before their exploitation were the source of several of the world's most coveted palms, including such favorites as Hyophorbe lagenicaulis (the bottle palm), H. verschaffeltii, three species of Latania, and Acanthophoenix, among others. We reported on our earlier visit here in Principes 20: 11–16, 1976.

We would like to remind palm lovers that Mauritius, although out of the way, is a vacation mecca for Western Europeans especially the French, for South Africans, and others. But the rock bed, ongoing attraction for palm devotees are the Royal Botanical Gardens (at) Pamplemousses, which are in the northern part of the Island, northeast of the capital Port Louis. This is some distance from the International airport at the southern end of the island.

It seems likely that the Gardens at Pamplemousses may well be the oldest established tropical botanical garden in the world. Debate arises as to definition of a botanical garden. Pamplemousses does not afford research facilities, it does not have a herbarium, and qualifies as a botanical garden only because it has a fine, longexisting collection of tropical plants, and palms in particular. The beginnings of the Garden can be traced back well over 200 years. In 1735, when Mauritius was known as "Ile de France," vegetable gardens along with a nursery were created at the present entrance to Pamplemousses.

Since our earlier visit to Mauritius, an excellent guide to the gardens has been published for the first time, and is available from offices of the Minister of Agriculture. Again, we loved exploring the gardens, which are beautifully maintained, and no one admonished us this time about collecting fallen palm seed. Supplementing our previously published pictures of the garden is a general view (Fig. 7) and an avenue of old *Hyophorbe lagenicaulis* (Fig. 8).

Again we left Mauritius very much indebted to Tony Gardner of the Forestry Service, and member of The Palm Society, who guided us into areas of the rugged southern section of the island, which still affords a look at what remains of some indigenous flora. This included *Tectiphiala ferox*, the new palm genus recently named by Dr. Moore (see *Principes* 24: 45–46, 1980). The rugged nature of the southern part of Mauritius is shown in Figure 9.

Reunion

Only a few minutes flight time from Mauritius, Reunion is the largest and most rugged of the Mascarene Islands. It is strictly French and more isolated



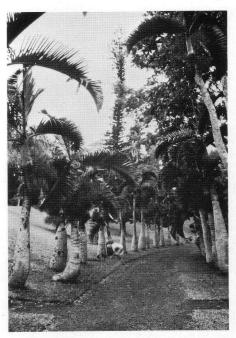
7. Palms at Pamplemousses, Mauritius.

than Mauritius. After deplaning at the very modern air terminal in Saint Denis, the capital, we rented a car and headed for St. Pierre at the lower end of the island, following the beautiful coastline most of the way. Operating out of St. Pierre, we explored the rugged interior of the island which furnished some of the most awesomely spectacular scenery one can find. The roads are well surfaced but very narrow, following contours through ravines and hugging the cliff sides. Cultivated gardens of annual flowers (chiefly plants for perfumes) made the homes attractive, for Reunion claims to be the world's largest producer of fragrance from geraniums.

As on Mauritius, much of Reunion's indigenous palm flora has been destroyed. Latania lontaroides can be found here and there, sometimes in seemingly implausible small groups

surrounded by sugar cane, or along the coast hemmed by volcanic rocks (Fig. 10). Hyophorbe indica, indigenous to Reunion, is hard to find in the wild, and Acanthophoenix is also elusive. But there's a delightful little botanic garden, which we discovered upon returning to Saint Denis, that has specimens of these palms.

On one excursion out of St. Pierre we came across a phenomenal exhibition of what one might say is "strictly for the birds." Near the road was a towering coconut palm whose leaves supported dozens of upside down birds' nests (Fig. 11). Only once before had we seen anything like it; that was near Cape Town, South Africa, where the nests were larger and appended to limbs of a massive tree quite unrelated to the palm family. There, we were told, it was the "Weaver bird." Our linguistic incapacity in French Reu-



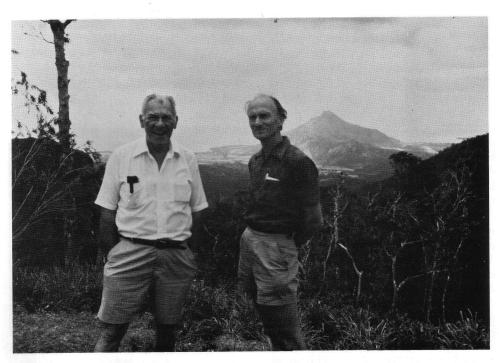
8. Avenue of older *Hyophorbe lagenicaulis*, Pamplemousses.

nion, no doubt, will give us an alibi for leaving there without obtaining proper identification of this obviously palmloving bird.

Back in Saint Denis, before going on to Madagascar, we visited Jardin Botanique, which offers specimens of Neodypsis, Livistona, Corypha, Caryota, Rhapis and others, including the indigenous Hyophorbe indica, which are more prominent in the garden than elsewhere over sections of the island we had explored. We enjoyed Reunion, fully aware that one can relax there and not be bothered very much, if at all, by huge events which might be going on elsewhere in the world.

Madagascar

On 26 October we flew on to Tananarive, the capital of Madagascar, 600 air miles west of Saint Denis. In striking contrast to the minutia that are the



9. Tony Gardner with the author in southern part of Mauritius.



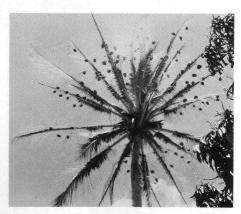
10. Latania lontaroides, Reunion.

Mascarene Islands, Madagascar is the fourth largest island in the world. It's 1,000 miles long and averages over 300 miles wide, with an area of about 228,000 square miles, lying some 200 miles off the African east coast of Mozambique. Although tropical, the island has considerable diversity of climate and topography. It is known, of course, as the source of some of the world's finest tropical flora.

But things change and one now can be "hard put" to find any of the indigenes within one's preconception of a touring radius. Madagascar's roads are poor or practically non-existent. About the only good surfaced stretches fan out of Tananarive to Majunga and Tulear. Elsewhere most of the roads are not surfaced and many are literally impassable, especially during the rainy season.

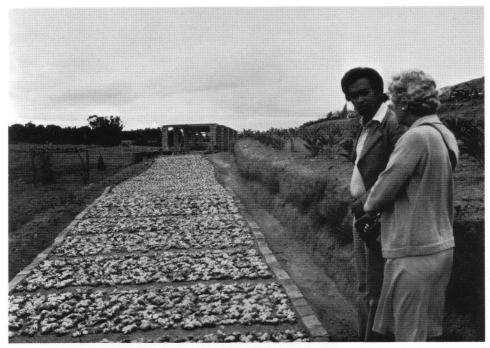
So transportation is a problem, al-

though one can fly the long distances between Tananarive and principal cities over the island. We went to Madagascar with some trepidation because of its reputation as being inhospitable



11. Bird nests compete with coconuts, Reunion.

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12. Alfred Razafindratsira and Phyllis view succulents in his nursery, near Tananarive.

to tourists. But, excepting an instance or two, we were thoroughly intrigued with the island, and certainly appreciated the splendid hospitality shown us by Palm Society member, Alfred Razafindratsira, who went out of his way to show us around. He, and his family before him, have been long identified with the cultivation of Madagascar flora.

Alfred Razafindratsira is in the process of expanding his nurseries, devoted largely to cultivation of Madagascar's famed succulents for foreign export, as shown in Figure 12. After showing us the nurseries, Alfred took us into Jardin Botanique at Tsimbazaga, which is Tananarive's botanical garden and zoo combined. It should be noted, however, that the zoo part of the combination has deteriorated, and with only a crocodile and a lonesome, but persuasive lemur remaining be-

hind bars, one can devote full attention to palms which dominate the garden. Among these were Dypsis gracilis, Neophloga lutea, Hyphaene schatan, Bismarckia nobilis, Latania, Dictyosperma, and an avenue of Chrysalidocarpus madagascariensis. Macrophloga decipiens (formerly Chrysalidocarpus decipiens) was most impressive (Fig. 13) and fruit seemed to be available, but we were not permitted to collect it. Neodypsis baroni was frequent (Fig. 14) and after a bit of searching we found Neophloga linearis growing in the shade behind the museum, which houses Madagascar's splendid butterfly collection (Fig. 15). Near here we saw the rare Neophloga lutea, but there was no seed collecting of any of these species.

One day we explored Tananarive on foot, and elected to look for some of the find handicraft items brought in by



13. Macrophloga decipiens, botanical garden, Tananarive.



14. Neodypsis baroni, botanical garden, Tananarive.



15. Neophloga linearis, botanical garden, Tananarive.



16. Neodypsis lastelliana, on residential property, Tananarive vicinity.

their creators to the Zoma Market downtown. Market holds forth one day each week when vendors spread their wares over the walkways of arcades and out into the streets. It is an occasion not to be missed, but one must guard his pockets as he elbows through the teeming throngs in the market, which stretches several blocks along Avenue de l'Independence.

We wanted to collect Neodypsis lastelliana but didn't arrange to get to places where the palm could be found in any numbers. Alfred Razafindratsira did guide us to a private property in Tananarive where we saw a most attractive young specimen (Fig. 16), but this was the only one to be seen in the area. Also, we drove some 100 miles north to the Forest Station at Manankazo where palms can be found in some quantity, mostly Macrophloga, which we had seen earlier in the



17. Macrophloga, Forest Station, Manankazo.

botanical garden. Some fine older specimens were here towering into the sky (Fig. 17), and the forest was rife with other interesting plants.

On the way to the Forest Station we passed through numerous villages, always colorful with people going about their business and often conversing in groups (Fig. 18). In rural Madagascar the group predominates—the individual is subordinate—and outsiders and their advice are not welcomed. As mentioned in a booklet we obtained, A Glance at Madagascar, "A stranger can integrate into a village or community but it takes considerable time. And it must be remembered that the village is composed of both the dead (the invisible beings) and the living (the visible); the former being the more important." It is said that ancestors "often exercise more influence dead than they did alive"! This pattern, which seems to be changing slowly, may be in part responsible for persisting agricultural practices that not only have led to denuding the landscape of indigenous flora, but also have kept it that way through periodic burning even of existing stubble for grazing purposes. One can see expansive vistas, as in Figure 19, utterly devoid of



18. Village scene, north of Tananarive.

the plant life that surely thrived there previously. Madagascar has been called the Red Island because the soil is indeed red and much of it is visible.

Alfred and Mrs. Razafindratsira had us at their home one evening for dinner, where we were privileged to meet their children and see some of the exceptionally fine plants in the nursery of the enclave surrounding their property. We were most intrigued with a potted specimen of *Dypsis hirtula* (Fig. 20), and admired this little gem with covetous eyes.

So after only 10 days in Madagascar we didn't get into the remote areas where one must go if any real collecting is to be accomplished. (For a realistic and more informative treatment of palms in Madagascar see Dr. Moore's article in *Principes* 9: 14–26, 1965.) We hadn't allowed time enough for such excursions, bearing in mind

that Madagascar is a huge territory, nor were we disposed or prepared to "rough it" sufficiently to accomplish much in the way of seed collecting. We were, after all, on only one leg of a long trip which beckoned. On 1st November we went to Mahé in the Seychelles, some 1,000 miles to the north, northeast, on farther into the reaches of the Indian Ocean.

The Seychelles

We had visited the Seychelles previously, as reported in *Principes* 20: 16–23, 1976, and were eager to return. Subsequently the Islands were granted independent status from the United Kingdom (June 1976) while retaining membership as a Commonwealth Nation. There have been some changes, subtle and otherwise, but these little islands, whose economy is almost



19. Vista, central Madagascar.

wholly dependent upon tourism, are as delightful as ever, and remain a "must-do" objective for everyone interested in palms. Not far away, though not on our itinerary, is Diego Garcia which has become an island base for the U.S. Navy.

In Victoria, the capital, we contacted Guy Lionnet, former Director of Agriculture, author of publications on the Seychelles, and a long-time member of The Palm Society. He brought us up to date regarding the status of requirements governing seed collection and forwarding them. It certainly was good to see him again. After revisiting Victoria's botanical garden and interesting curio shops, we flew the short hop to Praslin Island.

On Praslin we again rented a Mini Moke at the air strip and got established for several delightful, although partly rainy, days on this tiny island which mothers the Vallée de Mai. Six single-species genera, comprising an assemblage of some of the world's most fascinating palms are found here,



20. Dypsis hirtula, Razafindratsira nursery, Tananarive.



21. Lodoicea maldivica tops memorial to Seychelles independence on Praslin Island.

all of which are indigenous to the Seychelles.

From the air strip, the Mini Moke seemed to known where it was going, so we held on! Going along the only road available, the Mini arrived shortly at a newly created circular area where the road went left. But not the Moke, which skidded, then jerked to a halt. There at the curve was a new monument to the independence of the Sevchelles and to palms as well (Fig. 21). In its magnificant simplicity the monument announces independence for the Seychelles while acknowledging responsibilities, represented by shouldering the heavy fruit of Lodoicea maldivica (Coco de Mer), which is perhaps the world's most fascinating palm. Arching around the nut are male inflorescences. Palm lovers visiting there should be thrilled with such an introduction to Praslin Island.



22. Fruits of Lodoicea, Vallée de Mai.

The Vallée de Mai had not changed since our visit earlier, and we reveled again in its beauty and the awesomeness of its attraction. The narrow pathways are continously swept clean and as one proceeds along them, the view of the surroundings is beyond description. Supplementing earlier articles in Principes, we captured a picture of Lodoicea in fruit (Fig. 22) and saw a splendid male inflorescence on a nearby tree. Although the Vallee is overwhelmed with Lodoicea, the other five indigenous palms are there too. One never can forget an on-the-spot viewing of Deckenia nobilis, with a spathe and inflorescence close enough to touch (Fig. 23).

Again we collected seed on Praslin to send back to The Palm Society Seed Bank, after making arrangements to do so at the headquarters of the Forest Department on Praslin. We had arrived there this time with a request



23. Deckenia nobilis, Vallée de Mai.



24. Avenue of *Roystonea oleracea*, Peradeniya, Sri Lanka.

from the President of The Palm Society, Donn Carlsmith of Hawaii, to procure for him some viable seeds of Lodoicea. Thanks to the Forest Ranger and his aides on Praslin, we were privileged to acquire them and they were transported back to Mahé for forwarding to Hawaii. The four of them filled a gunny sack weighing well over 100 lbs. At the same time we acquired two additional viable seeds which were forwarded and donated to Fairchild Tropical Garden back in Miami, Florida.

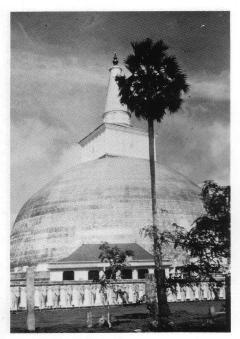
Seychelles independence, coupled with international monetary inflation, no doubt led to a price of approximately US \$60 per *Lodoicea* seed f.o.b. Praslin Island. The Seychelles government regulates the price. When we visited Praslin in 1974 before independence, the comparable price was approximately US \$6. It should be added that back on Mahé this last trip,

the going rate for a tourist's souvenir nut (dead) was US \$100.

Back on Mahé, our schedule was delayed more than a day when the plane to Colombo, capital of Sri Lanka (Ceylon), failed to arrive, but we were more than consoled with hospitality and helpfulness from friends living there who were former neighbors when we resided in Jamaica.

Sri Lanka (Ceylon)

Going from the Cape of Good Hope to Sri Lanka, just off the lower tip of India, one will have traversed the western part of the Indian Ocean. This large area is not "loaded" with palms for the would-be collector, but it has been the source of some of the world's finest palm species, which exist nowhere else. The eastern fringes of the ocean, southeasterly from Sri Lanka,



 Borassus flabellifer fronts dagaba near Anuradhapura, Sri Lanka.



 Mr. D. T. Ekanayake, Director, Royal Botanic Gardens, Peradeniya, Sri Lanka.

skirt Sumatra and drift on through the expanses of Indonesia to the western tracts of Australia. But all this southeasterly area is not usually considered Indian Ocean territory, palm-wise. It is Southeast Asia, with its profusion of palms, or Western Australia, which is not known for palms.

For palm lovers, Sri Lanka, at the northern tip of the Indian Ocean, furnishes the jewel that crowns the botanical attraction of the whole area, excepting only the Vallée de Mai, in the Seychelles. Ceylon itself is a verdant tropical gem. Palms grace the landscape, which covers about 25,000 square miles, especially in the spectacular southern half of the island, where it is mountainous and famous for its tea plantations. Palm-wise, it is renowned for the Royal Botanic Gardens at Peradeniya, which embrace

almost 150 acres of beautiful landscaping, located near Kandy, about 70 miles northeast of Colombo, the nation's capital and main port of entry. Established in 1821, the gardens have persisted and in our judgment must be ranked in the top five of the world's finest tropical botanic gardens. (Please refer to D. M. A. Jayaweera's article on the Peradeniya Gardens in *Principes* 5: 53–59, 1961, and H. E. Moore, Jr. in *Principes* 9: 28–29, 1965.)

Peradeniya has perhaps 150 species of palms. In numbers this falls far short of Miami, Florida's Fairchild Tropical Garden, which may have 400 to 500 species. But Peradeniya had a substantial collection of palms growing a century before Fairchild Tropical Garden was created. Outside the main palm collection covering about four acres in the southern part of Perade-



27. Phyllis Sneed and Stanley Keppetipola furnish scale for *Loxococcus rupicola*, Peradeniya.

niya, the garden has been noted for its palm avenues, which extend magnificently through divergent parts of the garden. There is a grand, almost unbelievable, avenue of *Roystonea oleracea* (Fig. 24). Only in Rio de Janeiro's splendid botanical garden can one see comparable avenues of this species, which is indigenous to parts of the southern Caribbean and South America. It is the tallest *Roystonea*, attaining 100 to 150 feet with no bulges in the trunk.

Borassus flabellifer, indigenous to Sri Lanka and southern India, line another avenue in Peradeniya. Often called the Palmyra Palm, this indigene has hundreds of uses, not the least of which is jaggery (brown sugar in a hard ball), vinegar and various potent "spirits," which are processed from toddy that is tapped from the palm and its inflorescences. This palm is also or-



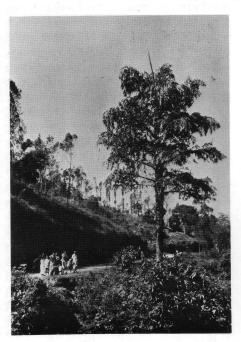
28. Vonitra thouarsiana, Peradeniya.

namental and grows well even in the northern dry areas of Sri Lanka. It can grow tall, perhaps up to 70 feet, which we guessed an old one to be that stood in the foreground of the Ruwanveliseya dagaba, with its surrounding (base) frieze of elephants, up north at Anuradhapura (Fig. 25).

Peradeniya has a fine avenue of Roystonea regia. A few years earlier it had a magnificant avenue of Corypha umbraculifera, indigenous to Sri Lanka, but the trees matured and died, and have not been restarted. The garden also affords an avenue of Lodoicea maldivica which, excepting a male specimen some 120 years old and a female over 75 years old, is comprised of relatively young trees. Due to the palm's slow growth, it will be many years hence before the avenue will appear to be complete. We are unaware of any other botanic garden that has an avenue of these rare palms. Interestingly, Peradeniya's older fruiting lodoiceas are prolific



29. Oxen and cart along roadway bordering Peradeniya's palm collection.



30. Caryota urens, south of Nuwara Eliya, Sri Lanka.



il. Areca catechu, south central Sri Lanka, high elevation in the "tea country."

enough now to furnish seed for further plantings and are being dispersed over the gardens.

Before setting out on our exploration at Peradeniya we were delighted to meet and talk about palms with D. T. Ekanayake, the current Director of the Gardens, and a member of The Palm Society (Fig. 26). We certainly appreciated the time he gave us and his assistance in approving our seed collecting mission.

Peradeniya is not unfriendly about collecting seeds as long as one identifies himself and gets permission to do so. Indeed, the garden assembles seeds of all sorts and makes them available in packets at low cost to residents and visitors. Indiscriminate collecting for obvious reasons is not permitted. The man responsible for Peradeniva's seed service is Stanley T. Keppetipola. We had met him when we first visited the gardens in 1974, corresponded with him later on, and exchanged palm seeds when we resided in Jamaica. This time he was more than helpful, as is his custom.

Away from the picturesque palm avenues, Peradeniya has many beautiful, mature palms. Stanley Keppetipola guided us back to one of them which we had admired on our earlier visit. The small *Loxococcus rupicola*,

and the barries was a second

indigenous to Sri Lanka, which we had seen earlier, had grown into a graceful and elegant specimen (see Fig. 27). And nearby were two clumps of *Vonitra thouarsiana*, a rare palm indigenous to Madagascar, and one we didn't see when we passed through there on our current odyssey (Fig. 28).

The casual, delightful, and perhaps peaceful ambience of Peradeniya may well be depicted in Figure 29, showing oxen in their unhurried progress with their cart being drawn slowly along the route adjoining the garden's palm collection.

Fanning out in any direction from Peradeniya one can see palms in Sri Lanka, like the magnificent *Caryota urens* in Figure 30, which is being approached on the left by a group of tea "pluckers" on their way to work. The betel-nut palm *Areca catechu* is everywhere (as in Fig. 31).

As noted, we have revisited some of the Indian Ocean areas, and will not pass a chance to do so again. It is certain indeed, that palm lovers will always be thrilled with even a brief glance at the Vallée de Mai or a short visit to Peradeniya. We only can hope that the palms there will ward off exploiters, survive potential destruction, and welcome all of us to their splendors in years to come.

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Principes, 25(4), 1981, pp. 172-177

Studies on Bentinckia condapanna: I. The Fruit and the Seed

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Among the native palms of south India, Bentinckia condapanna Berry is one of the rare palms occurring in the area of the Western Ghats at an altitude of 1,000-1,400 m. It is a graceful species with beautiful foliage. Large stands occur along the edge of the high-rising peaks of the Travancore hills, where wild elephants roam and feed on the soft and tender foliage. Sporadic occurrence of isolated groups of this slender palm among the vegetation of once dense sholas of the Palni hills in the northern region provides evidence for a wider distribution in the past and a history of destruction and deforestation. This rare palm is among the endangered species facing extinction due to human activities even in its native land. The inflorescence of this species, known as the "hill arecanut" and as "varikamugu" in the native Tamil language, is used for decorative purposes during ceremonial occasions.

The description of B. condapanna given in the Flora of Madras (Gamble 1935) is based on the information culled from Bourdillon's manuscript notes lodged with the Kew Herbarium. According to this description, the palm bears a slender annulate stem with a crown of pinnate leaves and inflorescences below the crown (Fig. 1). The male and female flowers are small and occur on the same spadix sunken in pits. The female flowers bear tricarpellate, but pseudomonomerous

gynoecia—with normally only one carpel fertile. The subspherical fruits develop from single carpels and the other two carpels abort. Our observations show that the fruits that may occasionally form from two or three carpels fall before the initiation of cellular endosperm. The seed is enclosed by a hard endocarp which has a basal operculum. Bourdillon's notes describe the seed as non-ruminate and sinuately grooved or ridged.

The present series is aimed at publishing studies on this rare palm and providing information useful in its conservation. The study of fruit structure presented in this paper is intended to provide a basis for extending the work to germination. At present, no published account of the details of fruit structure is available.

Materials and Methods

The fruits were collected and fixed in FAA. The materials for microtechnique were processed through the tertiary butyl alcohol series (Johansen 1940) for infiltration and embedding in paraffin wax. Sections were cut with a rotary microtome at 10–14 μ m and stained with tannic acid–ferric chloride–safranin combinations (Foster 1934).

Observations

Anatomy of the fruit and seed. The ripe fruit of Bentinckia is dark pur-



1. Bentinckia condapanna. Habit of a tree growing at Courtallam Hills, South India ×1/65.

plish in color and measures 14 mm in diameter (Fig. 2). The pericarp is differentiated into exocarp, mesocarp and endocarp. The outer epidermis is of tabloid cells with cutinized tangential walls. The exocarp also includes a few subepidermal layers and tannincontaining cells. The subepidermal layers are of thin-walled, oblong parenchymatous cells. Subjacent to this region there is a zone of tannin- or crystal-containing parenchymatous cells and fibers (40–50 μ m in diameter, Fig. 7A).

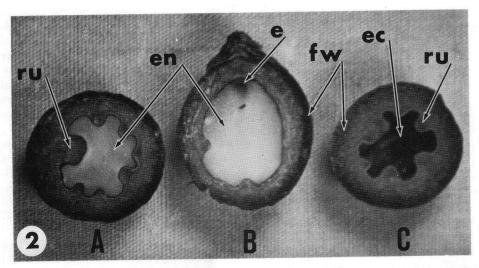
The mesocarp is made of isodiametric parenchymatous cells some of which are slightly compressed. Many of these cells show crystalline inclusions (raphides). Numerous fibers and fibrous vascular bundles (400–700 μ m in diameter) are scattered in this region (Fig. 7A).

The endocarp (100 μ m thick) is organized by the locular epidermis whose thick-walled cells form a palisade layer. Absence of vascular bundles associated with the endocarp in $B.\ condapanna$ is a noteworthy fea-

ture (Fig. 7B–D).

Development of fruit and seed. The post-fertilization ovule shows a 10–15-layered integument with a distinct outer epidermis composed of radially elongated cells. The inner epidermis of the fruit wall is composed of small rectangular cells with dense cytoplasm and prominent nuclei. The hypodermal parenchymatic layers of the fruit wall become progressively enlarged and vacuolated. The fruit, the developing seed, and the embryo sac enlarge even during the nuclear phase of the endosperm and thus push the seed coat close to the fruit wall.

The outline of the embryo sac remains even during the early post-fertilization stages and becomes progressively undulate with advancing age (Fig. 2A-C). The undulations result from localized inward growth of the parenchyma tissue in the fruit wall adjoining major vascular bundles and subjacent to the inner epidermis (Fig. 6). The pattern of growth in the tissue is interesting. Cell elongation occurs more intensely in the interior while the cells of the hypodermal layer enlarge to a limited extent but show a few divisions prior to enlargement. To keep pace with differential cell enlargement and elongation, the epidermis also undergoes divisions. As a result, the contour of the epidermis undergoes a



2. Bentinckia condapanna. Sectional views of fruits at young and mature stages ×2½. A. Cross sectional view of mature fruit showing lobed endosperm and fruit wall-seed coat complex. B. Vertical section through a mature fruit showing endosperm tissue and fruit wall-seed coat complex. C. Cross section of fruit before formation of cellular endosperm. Details: ec, central cavity of embryo sac at nuclear endosperm stage; emb, embryo; en, mature endosperm; fw, fruit wall; ru, sculpturing caused by fruit wall ingrowth.

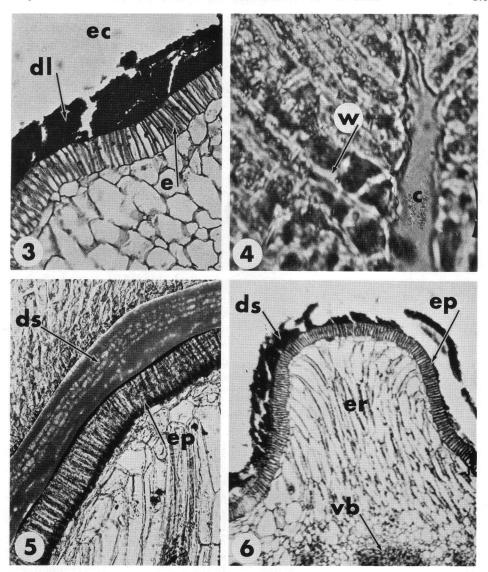
change, initiating undulations. The outer epidermis of the seed coat becomes stretched and flattened. By this time, the locular epidermal cells have elongated radially and their walls have become thickened (Figs. 3, 5, 6). At this stage, the endosperm consists of a central vacuolar cavity filled with sap (Fig. 2C) and a peripheral layer of cytoplasm with numerous free nuclei. Subsequently, cell wall formation takes place in the endosperm in a centripetal manner. With advancing development, the cells of the endosperm completely occupy the embryo sac (Fig. 2A, B) but for a narrow central cavity (Fig. 4). By this time, the reserve materials are deposited in the walls of the endosperm which, as a consequence, becomes unevenly thickened (Figs. 4, 7). Transverse sections of the fruit show that the endosperm takes the undulate outline already laid down (Fig. 2B).

The fate of the seed coat layers dur-

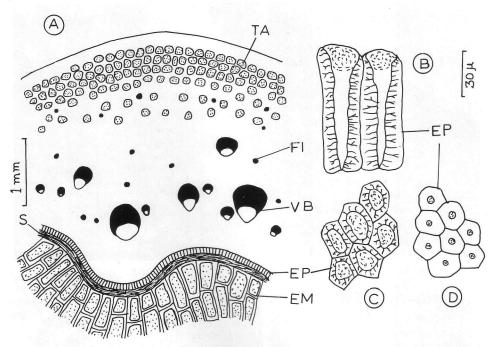
ing late ontogeny is worth mentioning. Initially, the layers of the seed coat are thin-walled. With the formation of the cellular endosperm, the inner layers begin to accumulate tanniniferous compounds (Fig. 3). The cells of the exocarp at this stage also begin to accumulate dark tanniniferous materials (Fig. 7A). The locular epidermis composed of radially elongated cells (Figs. 3, 5) becomes highly thickened and forms the endocarp. The lumen is much reduced and the wall is sculptured with ramifying pits. These thickened cells are sclereids (Fig. 7B-D).

Discussion

Development of grooved seeds in B. condapanna is in line with similar records for various arecoid palms. Grooved seeds have been recorded in Ptychococcus, Brassiophoenix, Balaka, Ptychosperma (Essig 1977) and in Physokentia (Moore 1969). The en-



3-6. Bentinckia condapanna. Photomicrographs showing internal structure of maturing fruit. Fig. 3. Part of the seed coat showing degenerating cell layers of seed coat and radially elongated cells of the endocarp ×125. Fig. 4. A part of mature endosperm tissue showing wall thickenings of the constituent cells ×270. Fig. 5. A part of the seed coat-fruit wall complex of a mature fruit ×125. Fig. 6. Details of an ingrowth of the fruit wall. Note cell elongation between vascular bundle and epidermis ×30. Details: cv, central cavity of the endosperm; dl, dark remains of the degenerated layers of the seed coat; ds, degenerating cell layers of seed coat; ec, central cavity of the embryo sac; ep, endocarp; er, elongated cells of the fruit wall causing ingrowth; w, wall thickening in mature endosperm cells; vb, vascular bundle.



7. Bentinckia condapanna. Diagrams illustrating external and internal structure of fruit and endocarp. A, cross sectional view of fruit; B, macerated endocarp cells showing highly thickened cell wall with ramifying pits and highly reduced lumen; C, outer end view of endocarp cells; D, inner end view of endocarp cells. Details: em, endosperm; ep, endocarp cells; fi, fiber; s, seed coat; ta, tannin cells; vb, fibrous vascular bundles.

docarp in palm fruits has been the subject of several investigations (Guérin 1949, Murray 1971, 1973, Essig 1977, Robertson 1977, Wessels-Boer 1968). The nature of the endocarp and its development have been taken as important criteria in attempted classifications and typifications of palm fruits (Murray 1973, Essig 1977). Accordingly, the fruit of Bentinckia could be assigned to Type I of Murray (1973).

An endocarp consisting of a single layer has been reported in caryotoid, chamaedoreoid, and pseudophoenicoid groups (Murray, 1973). The cells of this layer in *Bentinckia* are exceedingly thick-walled sclereids. The lumen is much reduced and the pits are ramifying. A similar structure was reported in *Orania aruensis* (Guerin

1949). A parallel situation apparently occurs in *Hyophorbe lagenicaulis*, a chamaedoreoid palm, and *Pseudophoenix sargentii*, a pseudophoenicoid palm (Murray, 1973). The structure of the endocarp of *Bentinckia condapanna* differs from that reported for the species of *Ptychosperma* (Essig 1977) in the absence of vascular bundles associated with it.

The occurrence of vascular and fibrous bundles in the pericarp of arecoid palms is subject to much variation. The vascular bundles occur concentrated at the inner half of the pericarp in Veitchia joannis, Carpentaria acuminata, Drymophloeus subdistichus, Balaka burretiana, Ptychosperma schefferi, and P. lauterbachii (Essig 1977). In Bentinckia, the large

bundles are distributed some distance away from the endocarp as in Normanbya normanbyi and Ptychococcus aff. elatus (Essig 1977). Even though distributed in the outer half of the pericarp, the fiber bundles in Bentinckia are not concentrated below the outer epidermis as recorded in palms of the Ptychosperma alliance described by Essig (1977). However, dense accumulation of tannin-bearing cells occurs in the hypodermal region in the fruit of B. condapanna.

The endosperm. The cellular structure of the endosperm in B. condapanna is similar to that of other investigated genera of the arecoid palms. The cell walls are highly thickened with hemicellulose deposits. The outline of the endosperm shows grooves corresponding to similar structure in the fruit wall. After the decay of the fleshy pericarp, the seed is left with large grooves on its surface. Longitudinal sections of the fruit show up the grooves as inpushings of the seed coat

and endocarp into the endosperm (cf. Moore 1969).

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Principes, 25(4), 1981, pp. 178-180

A Reassessment of the Genus Lophospatha Burret

J. DRANSFIELD AND J. P. MOGEA

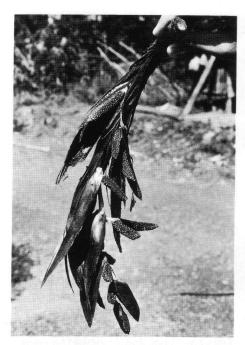
Royal Botanic Gardens, Kew, Richmond, Surrey, U. K. and Herbarium Bogoriense, LBN-LIPI, J1. Raya Juanda 22-24, Bogor, Indonesia

Abstract

New collections of Salacca clemensiana from Sabah show a close relationship but not identity with the monotypic genus Lophospatha. Examination of available herbarium material suggests the inclusion of Lophospatha in Salacca and the new combination Salacca lophospatha is published.

Lophospatha, a lepidocaryoid palm with a single species L. borneensis, was based by Burret on fragmentary material collected by the Clemens in 1931/32 at Dalas on the western slopes of Kinabalu in Sabah (Burret 1942). The collection, J. & M. S. Clemens 26380, was widely distributed but very incomplete; we assume that the holotype in Berlin is no longer extant, but isotype material in BM, BO, K, L, and SING consists of a few staminate rachillae and leaf fragments. Although the material is so incomplete, the leaflet and rachilla structure appears to approach that of Salacca, and on the basis of this similarity the genus was included, without explanation, as a synonym of Salacca by Moore (1973). In preparing a monograph of Salacca, one of us (J. P. M.) felt unable to reach any firm conclusion on the status of Lophospatha as the material was so poor. The re-finding of Lophospatha in Sabah was thus a high priority. Recently, while undertaking rattan fieldwork in Sabah, the other author (J. D.) was able to find a palm with features of the genus, albeit not in the type locality but about 30 km to the south, and so there is now material sufficient to re-examine the status of *Lophospatha*.

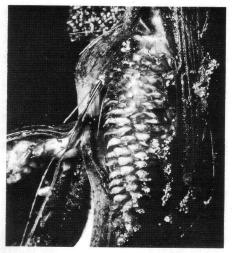
The Lophospatha-like palm was discovered beside the new road between Kota Kinabalu and Tambunan (Sinsuron Road) at an altitude of ca. 1,000 m on the northwestern slopes of the Crocker Range. A colony of about twenty plants was found growing in much disturbed forest, transitional between hill dipterocarp and lower montane forest, in a damp hollow on a steep hillslope. In habit the plants are entirely reminiscent of a Salacca; the stems are very short, subterranean or partially erect, and bear leaves to about 4 m long, the sheaths and petioles densely armed with black spines. The leaflets are strongly discolorous, dark green on the adaxial, chalkywhite on the abaxial surfaces, and the two terminal leaflets are compound, two features which are widespread in Salacca, though not diagnostic. Of even greater significance is that the inflorescences emerge from grooves in the abaxial surface of the leaf sheath, a diagnostic character of Salacca. The pistillate inflorescence of the Crocker Range plant does not differ from those of Salacca and the fruit is covered in scales with spine-like reflexed tips. The staminate inflorescence, however, is more or less pendulous and does indeed have discrete rachilla bracts,



1. Staminate inflorescence of Salacca clemensiana, Crocker Range, Sabah. (August 1979)

which, incidentally, are a clear pink at anthesis. Unfortunately some of the best material that was collected has been mislaid but we have had the opportunity to study the Sandakan and Bogor sets of the staminate plant (J. D. 5538).

Initial impressions in the field suggested that Lophospatha borneensis had indeed been refound; however comparison between the type of Lophospatha borneensis, the new Sabah collection, and the Kew material of Salacca clemensiana suggests that the new collection is Salacca clemensiana, the first record for Borneo of a palm otherwise known from Mindanao, Philippines. Sufficient differences appear to exist between L. borneensis and S. clemensiana for them to be retained as distinct species, although the material of the former is very incomplete.



2. Rachilla of Salacca clemensiana showing staminate flowers and the discrete rachilla bracts.

Burret distinguishes Lophospatha from Salacca mainly on the nature of the rachilla bracts of the staminate inflorescence which are discrete in Lophospatha but joined laterally in Salacca. Burret seemed to be quite unaware that Beccari had already described a bract type similar to that of



3. Pistillate rachilla of Salacca clemensiana showing the strongly reflexed petals, which are crimson when fresh.

- -

L. borneensis as occurring in Salacca clemensiana.

The problem of whether Lophospatha is generically distinct from Salacca can now be reassessed. As described above, the only significant difference between the two genera according to Burret is the discrete versus laterally-joined rachilla bracts. We do not believe this sufficient to separate Lophospatha, especially as in every other respect Lophospatha is a Salacca, and S. clemensiana shows this very feature. Most significantly an intermediate state occurs in the staminate inflorescence of Salacca dubia Becc. where the rachilla bracts are united by their bases but do not form horizontal rings (Beccari 1918).

As the epithet "borneensis" has already been used in the genus Salacca (Salacca borneensis Becc. = S. affinis Griff. var. borneensis (Becc.) Furtado), a new epithet is required if Lophospatha is to be included in Salacca.

Salacca lophospatha J. Dransf. & Mogea nom. nov. Type: Borneo. Sabah, J. & M.S. Clemens 26380 (holotype B(?); isotypes BM, BO, K, L, SING) Lophospatha borneensis Burret in Notizbl. Bot. Gart. Mus. Berlin-Dahlem 15: 753. 1942 (non Salacca borneensis Becc. 1886). Type: as above.

Salacca lophospatha can be distinguished from S. clemensiana as follows:

Unfortunately S. lophospatha will remain an incompletely known species until more material can be collected; it is possible that it represents a robust form of S. clemensiana.

Acknowledgments

Thanks are due to A. J. Hepburn and Mustafa bin Abdul Rahman for help in finding and collecting the palm; the loan of material from Sandakan is also gratefully acknowledged.

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MOORE, H. E., Jr. 1973. The major groups of palms and their distribution. Gentes Herb. 11: 27-140.

Erratum

Pinanga sanarani on p. 80 (Vol. 25) should read Pinanga sanarana.

Principes, 25(4), 1981, pp. 181-182

PALM LITERATURE

RATTAN: a report of a workshop held in Singapore, 4-6 June 1979. 76 pp. International Development Research Centre, Ottawa, Canada. 1980.

Rattan is a valuable forest product of Southeast Asia. Concern about overexploitation of wild stands, the major source of supply, and rapid clearing of tropical forests, led to the organization of a workshop to review the current status of rattan palms and to assess their future as economic plants.

K. D. Menon's background paper, prepared in advance, is the core of the publication. It thoroughly reviews all facets of rattans, including taxonomy, collection, processing, marketing, and research. One encouraging note is the successful plantation cultivation of *Calamus* spp., albeit at a small scale.

The report contains proposals for priority areas of research on rattans, with immediate attention directed to "conservation of existing stock; standardization of research procedures; and extension and training." As a renewable resource, rattan merits development to benefit producing countries and to provide a continuing supply of attractive furniture and baskets. This workshop is a fine beginning.

DENNIS JOHNSON University of Houston Houston, Texas

CLEMENT, CHARLES R. 1980. Bibliografia parcialmente anotado sobre Pejibaye (*Bactris gasipaes H.B.K.*) Mimeographed. pp. 1–29. Biblioteca Conmemorativa Orton, Turrialba, Costa Rica.

This is a preliminary bibliography on this important tropical American palm. Annotations are in Spanish.

Daghlian, Charles P. 1978. Coryphoid Palms from the Lower and Middle Eccene of Southeastern North America. Palaeontographia Abt B. 166: 44–82.

A beautifully illustrated account of fossil fan palms from S.E. N. America is presented, and comparisons made with extant genera and species.

Dransfield, John. 1980. Calamus sedens validated. Kew Bull. 34: 320.

nus of Palmae (Lepidocaryoideae) from Borneo. Kew Bull. 34: 529–536.

Retispatha, a new rattan genus with one species, R. dumetosa, is described and distinguished from Calamus and Daemonorops.

Lepidocaryoideae), a new genus related to *Daemonorops*. Kew Bull. 34: 761–768.

Pogonotium is described and distinguished from other rattan genera and a key to related genera provided; one species, P. ursinum, is transferred from Daemonorops and another, P. divaricatum, described as new.

Pinanga (Palmae) in Borneo. Kew Bull. 34: 769–788.

This account contains information on long established names in *Pinanga* and indicates synonymy; it also contains descriptions of new species and varieties and validates names transferred from the genus *Pseudopinanga*, which is no longer recognized as distinct.

——. 1980. Systematic notes on some Bornean palms. Bot. J. Linn. Soc. 81: 4–42.

New species in Areca, Calamus, Daemonorops, Salacca and Licuala, and a new variety of Pichisermollia insignis are described; a synopsis of Plectocomiopsis in Borneo is provided, and areas of synonymy in the above genera are indicated, all as a precursor to a palm flora of the Gunung Mulu National Park, Sarawak.

Moore, Jr., H. E. 1980. In K. H. Rechinger, Flora Iranica 146: 1-6, color pl. 1-8, map 1-2.

Nannorrhops and Phoenix are treated, the former taken to be a genus of a single species, N. ritchiana, including as synonyms N. arabica, N. naudeniana, and N. stocksiana.

Moraes, J. A. P. V. de. 1980. CO₂-gas exchange parameters of palm seedlings (*Washingtonia filifera* and *Serenoa repens*). Acta Oecologica Oeco. Plant. 1: 299–305, fig. 1–2, tab. 1.

Net photosynthesis, light and dark respiration, CO₂-transfer resistances, and water use efficiency parameters were determined.

MULLER, J. 1979. Reflections on fossil palm pollen. Proceedings of the IV International Palynological Conference, Lucknow (1976–1977) 1: 568–179.

The distribution of some characteristic fossil palm pollen grains is analyzed in relation to recent types. Lepidocaryoid, Nypoid, Caryotoid and Arecoid types can be recognized, providing evidence for origin and development of these groups. A West Gondwanaland origin for the palms as postulated by Moore is not contradicted by the fossil pollen evidence.

PALM RESEARCH

KEITH FERGUSON, Royal Botanic Gardens, Kew, Richmond, Surrey, TW9 3AB, England, has begun a survey of the comparative pollen morphology of the subfamily Lepidocarvoideae in association with Dr. J. Dransfield's taxonomic studies. Exine sculpturing and stratification are being studied with scanning and transmission electron microscopy. Madeline Harley and Phyllis Whittington-Vaughn at Kew are co-workers in the project, and Dr. G. Thanikaimoni, Institut Français de Pondichery, India, whose published data it is planned to supplement and expand, is also collaborating. So far the pollen of each of the species of Korthalsia appear to have distinct surface sculpturing. A large group of Daemonorops has diporate pollen with small apertures and a complete tectum (e.g. D. verticillaris). Many of the other Daemonorops species have diporate pollen with large apertures and a variety of surface sculpturing patterns (e.g. D. grandis and D. micracantha). Similarly there is a wide range of pollen surface sculpturing throughout the species of Calamus. Thin sections show an equally large range of variation in the wall stratification. It is hoped to investigate the pollen morphology of other subfamilies more fully later.

NEWS OF THE SOCIETY

News from California

The May meeting of the Southern California Chapter was held for the first time at San Juan Capistrano. The afternoon got under way with a visit to the R.O.P. Nursery. Tours of the nursery were conducted by Mike Bayless and Randy Albers. Many varieties of palms are being grown and someday will be used to landscape public gar-

dens in this area. Laguna Niguel Park is one such site and was our next stop.

At Laguna Niguel Park, Randy Albers introduced Gretta Lydick, President of the South Coast Garden Club. She gave a short talk on the park and about plans to develop a garden.

Last stop of the day was Walt Frey's home. His beautiful garden and a greenhouse full of rare palms was enjoyed by everyone. Many new members present were introduced by Walt. Out of town visitors introduced were Dave Best from Florida and Mark Wolf from Australia. Refreshments were served and a raffle completed our meeting.

FRANK KETCHUM

News from Texas

The Houston Area Chapter met on January 22 and on March 26 in the Rose Room at the Houston Garden Center. In January President Jim Cain reported that the "Beautify Houston" project sponsored by the Houston Chamber of Commerce had the planting of winter hardy varieties of palms as one of its four areas of emphasis. The Chapter has supported this very worthwhile project by furnishing the Chamber of Commerce with a letter stressing the enhancement provided by palm plantings around both old and new buildings. In March the project was well underway with its main goal the planting of palms at Houston Intercontinental Airport.

After a proposal by Dennis Johnson the Chapter voted to contribute \$50.00 to the Harold E. Moore, Jr. Memorial Fund.

In March 1981 the Chapter had 34 members. Seedlings of the month from January 1980 were *Licuala grandis*, but only four were alive after a year. This palm seems to be the most difficult to grow of any seedlings distrib-

uted thus far. Seedling of the Month for January was Sabal mexicana and for March Chamaerops humilis. Returning members for 1981 received a special bonus seedling of Archontophoenix cunninghamiana, and new members one of Sabal minor. The door prize a beautiful Latania was won by Ivan Britt. The annual palm show and sale will be held in late May.

The second Annual Picnic was held at the home of Bonny and Erwin Ruhland in League City where members enjoyed swimming and a garden tour. The seedlings of the month were *Pritchardia thurstonii* grown from seed collected on the Kona Coast during the Biennial Meeting in 1980.

Members are looking forward to a lecture by Professor T. Antony Davis as a special event of the September meeting.

News from Australia

The second annual meeting of the New South Wales Chapter was held in June. The following officers were elected:

President: Nicholas Heath Vice President: Eike Jacobasch Treasurer: Richard Budd

Secretary: Brian Preston

Committee members: Ken Veness, Tony Rodd

Attendance has nearly doubled since last year, most of our meetings attracting 30 to 35 members. We have upgraded our local newsletter and now feature articles submitted by members in addition to items of business and news. The topics of such articles have included growing coconuts in Sydney, cultural notes on Licuala ramsayi, uses of indigenous palms in Australia, and the world of our Banglow palm (Archontophoenix cunninghamiana). A register of palms that members are willing to swap has been initiated to complement the regular sale of seeds and seedlings at each meeting.

BRIAN PRESTON

Principes, 25(4), 1981, pp. 184-188

Distribution of the Nypa Palm in Australia

JEANETTE COVACEVICH

Queensland Museum, Brisbane, Australia

The nypa palm (Nypa fruticans Wurmb) occurs widely in southeast Asia (Ceylon, eastern India, Malaysia, Thailand, The Philippines and Indonesia), New Guinea, and northern Australia (Moore 1973, Fig. 52 and p. 105). It is known to favor coastal, particularly estuarine areas. In Australia, at the extreme southern limit of its distribution, it is known to occur in Oueensland in some estuaries of eastern Cape York Peninsula, north of the Herbert River 18°33'S, 146°17'E; and in the Northern Territory in one isolated patch on Melville Island 11°30'S. 130°30'E (Covacevich and Covacevich 1978, Wells 1979). Its occurrence in Queensland has not been mapped previously, but this is now possible, following surveys of the estuaries of eastern Cape York Peninsula.

Nypa fruticans has been observed in only nine of the 30 or so estuaries examined. These are Jardine River, Cowal Creek, Harmer Creek, Oliver River, Pascoe River, Claudie River, Lockhart River, McIvor/Morgan River and Herbert River. The location of the nine estuaries is shown in Figure 1, together with those along which there are no N. fruticans. Stands on the Olive, Claudie, and McIvor/Morgan

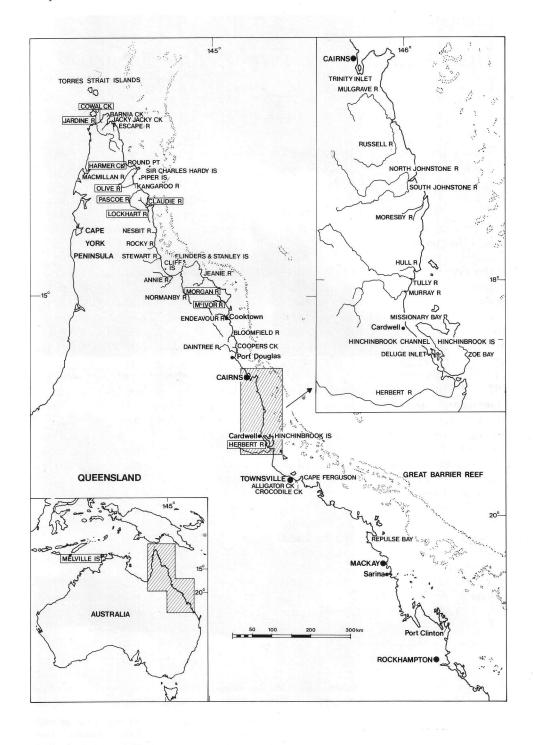
Rivers are most extensive, while trees on the Pascoe River (Cassowary Creek tributary) are most luxuriant.

The reasons for the disjunct occurrence are unclear, but it is interesting to note that all stands of Nypa palms on Cape York Peninsula are located in sandy areas (even though there are mud overlays in some situations); that they are associated with rain or wet sclerophyll forests and certain mangrove species, Sonneratia caseolaris, Rhizophora mucronata (Duke and Bunt 1979), Bruguiera sexangula, and Barringtonia racemosa; and that they are invariably concentrated near the upper reaches of brackish sections of the rivers along which they occur. Stands of N. fruticans are apparently never located in areas of continual fresh or highly saline water although they obviously tolerate both extremes during floods or very high tides.

Acknowledgment

Mr. Norman Duke (Australian Institute of Marine Science, Townsville) has provided distribution data for the more remote rivers discussed here. He also very kindly provided the figures.

Map of Nypa fruticans distribution in Australia. Locations recently visited on Cape York Peninsula
are shown and the areas of Nypa fruticans occurrence are boxed.







2. Nypa fruticans stand in the Claudie River. Note the luxuriant associated vegetation as well as some "zonal" patchiness. The species is commonly found in the back areas of river meander "growing edges" or in disconnected meanders or backwaters. 3. Nypa fruticans frontal stand in the Pascoe River.



4. Infloresence of Nypa fruticans from the Pascoe River. Note the staminate spikes and the young fruit (the central "knobby" head). 5. Inside a Nypa fruticans stand at the Pascoe River. Note the tall

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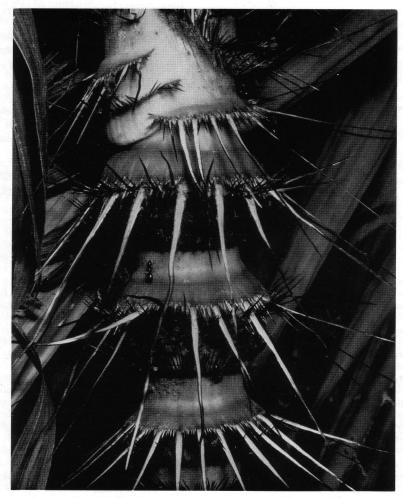
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upright 10-12 m fronds and the large aggregate fruit stalk. In this case the fruit cluster was about half a meter in diameter. 6. An uprooted Nypa fruticans seedling with the fruit still attached, from the Herbert River. Note the strong healthy root and shoot development. 7. Nypa fruticans on a washaway edge of the Pascoe River. Note the usually subterranean rhizome and roots of these obviously mature plants.

PALM PORTRAIT



 The leafsheath of Daemonorops sabut near Keningau, Sabah, East Malaysia, April 1979. Photo by J. Dransfield.

The Leafsheath of Daemonorops sabut Becc.

The sheath displays a remarkable array of spines, some upward-pointing, some reflexed; their bases are joined into circular collars. Where the spines interlock, the collars at the base form an enclosed chamber occupied by ants which also construct tunnels of debris from one gallery to the next, all the way along the stem. Near the stem tip, on the softer younger sheaths, the ants husband scale insects which provide honey-dew; on the older sheaths they make their nests. The presence of ants almost certainly helps protect the rattan apex from being destroyed by herbivores, but as yet no experimental work has been carried out to prove this. Although spines are unpleasant to handle, and the ants make this species fiendishly so, one cannot help marvelling at the beauty of the neatly interlocking spines.

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INDEX

Acanthophoenix 157, 158

Acoelorrhape 64

Acrocomia 64

Actinorhytis calapparia 4 Aiphanes acanthophylla 145

Allagoptera 59, 60; campestris 56, 59, 60

Archontophoenix alexandrae 132; cunninghamiana 89, 90, 130, 183

Areca 4, 17, 22, 23, 26, 111, 112, 113, 115; catechu 113, 170, 171; macrocalyx 14; macrocarpa 23; vestiaria 109, 111

Arecastrum 60; romanzoffianum 54, 140

Arecoideae 144

Arenga engleri 48, 49; microcarpa 16; mindorensis 80; obtusifolia 95; pinnata 80, 109, 110, 113, 124, 128; undulatifolia 115

Asterogyne 48; martiana 40, 50

Astrocaryum 104, alatum 102, 103, 104; mexicanum 104; vulgare 38

Attalea 54, 56, 58, 59, 60; borgesiana 57; concentrista 56, 59; maripa 38

Bactris 40, 47, 48, 51, 52, 64, 104; gasipaes 48, 52; longiseta 102, 103; wendlandiana 102, 103

Beach, James H. Research program 40

Beccari, Odoardo 29-35

Bentinckia 172, 176, 177; condapanna 172-177 Bismarckia nobilis 161

Bookstore 44, 88, 119, 188

Borassus 114, 116; flabellifer 124, 127, 168, 169 Brassiophoenix 174; schumannii 7, 25

Bulbil-shoot production from clonally propagated coconuts 124

Bullock, Stephen H.

Notes on the phenology of inflorescences and pollination of some rain forest palms in Costa Rica 101 Butia 54, 82, 83; archeri 57, 60, 61; ?bonnetii 54, 60; capitata 54, 81, 84, 86; hybrid 56, 58, 59; purpurascens 57, 60, 61; yatay 54

Calamus 13, 18, 23, 26, 182; exilis 141, 142; javensis 141, 142; longisetus 121

Calyptrocalyx 4, 5, 7, 9, 12, 14, 17, 18, 20, 22, 23, 26, 27

Carpentaria acuminata 176

Caryota 159; rumphiana 22, 27; urens 144, 145, 170, 171

Caryotoideae 144

Ceroxylon 145, 149

Chamaedorea 41, 45, 47, 48, 49, 50, 51, 52, 64; costaricana 144, 145; elegans 49; exorrhiza 101

Chamaedoreoideae 144

Chamaerops 81, 82, 83; humilis 81, 84, 143, 144, 149, 151, 183

Chrysalidocarpus decipiens 161; lutescens 144, 145; madagascariensis 161

Classified 43, 77, 105, 140, 171, 177

Clement, Charles R. 181

Coccothrinax 64; argentata 124, 128; readii 65, 66, 68, 70

Coconut breeding: a review of work since 1972

Cocos 54, 160; nucifera 21, 38, 54, 56, 78, 107, 124, 144, 145

Cocosoideae 144

Computer listing of palms for sale 88

Copernicia 133, 138; alba 134, 136; baileyana 134, 137, 138; burretiana 133, 134, 135; cowellii 134, 138; curtisii 134; fallaense 133; glabrescens 134, 138; hospita 134, 137, 138; macroglossa 134; prunifera 133; rigida 134, 138; × shaferi 134, 138; tectorum 133, 134,

135; × textilis 134, 136; × vespertilionum 133, 134; yarey 134, 138

Corypha 115, 159; umbraculifera 169; utan 109, 112

Coryphoideae 143

Covacevich, Jeanette

Distribution of the Nypa palm in Australia 184 Cryosophila 64, 104; albida 102, 103

Cyrtostachys 4, 6, 11, 17, 23, 26

Daemonorops 182; grandis 141, 142, 182; micracantha 141, 142, 182; sabut 189; verticillaris 141, 142, 182

Daghlian, Charles P. 181

Date 73

Davis, T. A., Sudasrip, H., & Azis, H.

Bulbil-shoot production from clonally propagated coconuts 124

Deckenia nobilis 166, 167

Desmoncus 64

Dictyosperma 161

Douglas, Richard 41 Computer listing of palms for sale 88

Dransfield, John 181

A house in Thailand 36

A manual of the Rattans of the Malay Peninsula (review) 53

and Mogea, J. P. A reassessment of the genus Lophospatha Burret 178

Drummond, Paul 190

Palm plantings by local groups on public property 39

Drymophloeus subdistichus 176 Dypsis gracilis 161; hirtula 164, 165 Elaeis guineensis 124, 127, 144, 145

Essig, Frederick B. & Young, Bradford E.

Palm collecting in Papua New Guinea II. The Sepik and the north coast 3; III. Papua 16 Euterpe 47, 48, 49, 52; edulis 144, 145; macro-

spadix 48, 49; oleracea 38

Ferguson, Keith, research program 182

Frost susceptibility of palms 143

Genera Palmarum 28

Geonoma 47, 48, 52; baculifera 38; gracilis 52; interrupta 52

Glassman, S. F., Harborne, J. B., Robertson, J., & Holloway, P. J.

Chemotaxonomic studies of selected cocosoid palms 54

Gulubia costata 7, 12, 26; crenata 14; sp. 9, 10, 14, 24, 25, 26

Haari, Niu. see Harries, Hugh 78

Harries, Hugh

Coconut breeding: a review of work since 1972 78

Heterospathe 14, 22, 26; delicatula 26

Hodel, Don, letter from 86

Hodge, W. H.

Finca Las Cruces, a Costa Rican garden 47

Howea forsterana 144, 145

Hydriastele cf. beccariana 18; microspadix 4, 5, 7, 11; sp. 23, 25, 26, 27

Hyophorbe indica 158, 159; lagenicaulis 157, 159, 176; verschaffeltii 157

Hyospathe 48, 52

Hyphaene natalensis 156; schatan 161

Invitation to contribute to Principes 15 Iriartea 47, 101; gigantea 102, 103

Jakobasch, Eike

Some notes on two native palms of southeastern Australia 130

Johnson, Dennis

An early account of palm utilization in Surinam 38

The Raposa Palm Plantation revisited 133

Review of Rattan 181

Jubaea 54; chilensis 54, 143, 144, 145, 149

Jubaeopsis 54; caffra 154

Korthalsia 182; debilis 141, 142; rigida 141, 142; robusta 141, 142; rostrata 141, 142

Larcher, W. & Winter, A.

Frost susceptibility of palms: experimental data and their interpretation 143

Latania 183; lontaroides 158, 160

Lethal yellowing disease 139

Letters 85, 139

Licuala 4, 5, 7, 9, 11, 12, 17, 25, 27, 156; grandis 183; lauterbachii 23

Livistona 14, 16, 81, 145, 151, 159; australis 130, 131, 143, 144; chinensis 143, 144; rotundifolia 110

Lodoicea 166, 167; maldivica 166, 169 Lophospatha 178, 179, 180; borneensis 178, 179,

180 Loxococcus rupicola 169, 171 Macrophloga 163; decipiens 161, 162

Manicaria saccifera 38

Mauritia flexuosa 38 Maximiliana 54

Metroxylon 91, 110, 115; sagu 15, 27, 38, 91

Microcoelum weddellianum 54

Miller, Henry L.

Palms for southeastern Virginia 81

Mogea, Johanis P.

Notes on Salacca wallichiana 120 as coauthor 178

Mohammed, Shafaat

Modernizing date production in Iraq 73
——— & Shabana, Hassan R.

Research program 40

Moore, Harold E., Jr. 28, 182

Odoardo Beccari (1843-1920) 29

memorial fund 28

Moraes, J. A. P. V. de 182

Müller, J. 182

Myers, Tamar, letter from 85

Nengella 5, 8, 11, 12, 13, 14, 17, 23, 26, 27; cf. pinangoides 23; pollen of 1

Neodypsis 159; baroni 161, 162; lastelliana 163

Neonicholsonia 48

Neophloga linearis 161, 162; lutea 161

News of the Society 41, 100, 182

Normanbya normanbyi 176

Notes on Salacca wallichiana 120

Nypa 36, 115, 184, 187, 188; fruticans 184

Oncosperma horridum 95

Opsiandra 64

Orania 5, 25; archboldiana 25, 27; aruensis 176; disticha 17, 20; gagavu 23; glauca 5, 6, 7; lauterbachiana 7, 14, 20; parva 11, 13

Orbignya 54, 56, 58, 59, 60, 64; cohune 56, 59; phalerata 56, 59

Padmanabhan, D. & Regupathy, D.

Studies on Bentinckia condapanna I. The fruit and the seed 172

Palm Briefs 130

Palm literature 181

Palm portrait 189

Palm research 182

Palms for southeastern Virginia 81

Papua New Guinea, palm collecting in 3, 16

Parajubaea cocoides 42

Paralinospadix 21, 27

Phenology and pollination of Costa Rican palms
101

Phoenix 40, 124; canariensis 143, 144, 145, 146, 147, 148, 149, 151, 154; dactylifera 128, 143, 145, 149; reclinata 143, 145, 149; roebelenii 143, 145; sylvestris 149

Phoenicoideae 144

Physokentia 174

Phytelephantoideae 144

Phytelephas macrocarpa 144, 145

Pigafetta 106, 107, 108, 110, 111, 112, 115, 116, 117, 118, 119; filaris 2, 4

Pigafetta and other palms in Sulawesi 106 Pinanga 5, 115; punicea 4, 5, 27; samarana 80

Polyandrococos 59; caudescens 56, 59 Prestoea 48, 52, 101, 103; decurrens 102, 103

Principes endowment fund 190

Pritchardia 88; lanigera 86, 87; thurstonii 140

Pseudophoenix 63, 66, 68, 71, 72; ekmanii 63; lediniana 63; sargentii 63, 65, 69, 70, 71, 72, 176; subsp. sargentii 64, 71; subsp. saonae 64; var. navassana 64; vinifera 63

Ptychococcus 7, 27, 174; archboldianus 27; elatus 27; ?elatus 7, 11, 177

Ptychosperma 5, 7, 8, 17, 19, 20, 21, 22, 23, 25, 174, 176, 177; subgenus Actinophloeus 21; burretianum 21, 23; caryotoides 18, 25; cuneatum 5, 7; elegans 19; furcatum 18; lauterbachii 7, 21, 176; lineare 25; macarthurii 16, 25; microcarpum 16, 18; mooreanum 20; pullenii 7; schefferi 4, 176; streimannii 17; vestitum 8; waiteanum 7, 8, 21, 22, 23

Putz, Francis E.

Palm literature 53

Quero, Hermilo J.

Pseudophoenix sargentii in the Yucatan Peninsula, Mexico 63

Raphia 156; australis 156; hookeri 40

Raposa palm plantation 133

Rattan: a report of a workshop reviewed 181

Rattans 110

Regupathy, D., as coauthor 172

Reinhardtia 48

Rhapidophyllum 82, 83; hystrix 81, 84, 105, 177 Rhapis 100, 140, 159, excelsa 140, 143, 144; hu-

milis 140

Rhopaloblaste 10; cf. brassii 25, 27; ledermanniana 11

Romney, David, letter from 139

Roystonea 65, 169; oleracea 38, 167, 169; regia 169

Sabal 64, 65, 81, 151; louisiana 105, 177; mexicana 183; minor 81, 84, 105, 143, 144, 147, 151, 177, 183; palmetto 16, 84, 85; umbraculifera 48

Sago palm 91

Salacca 36, 37, 120, 123, 178; affinis 120; var.
borneensis 180; beccarii 121; borneensis 180; clemensiana 178, 179, 180; dubia 180; edulis 110; lophospatha 178, 180; macrostachya 120, 121; rumphii 120, 121; sumatrana 121; wallichiana 36, 120, 121, 122, 123

Scheelea 54, 56, 57, 58, 59, 60, 65; zonensis 56

Seed Bank news 43

Seed Bank notes 80

Serenoa 151; repens 144

Sneed, Melvin W.

Indian Ocean odyssey: A look at palms from Good Hope to Sri Lanka 153

Pigafetta and other palms in Sulawesi, Indonesia 106

Socratea 47, 103, 104; durissima 102, 103

Stedman, John 38

Studies on Bentinckia condapanna 172

Syagrus 54, 58, 59, 60, 61; coronata 56, 59, 60; flexuosa 57, 59, 60; glaucescens 57, 59, 60; microphylla 57, 61; petraea 57, 60; vagans 56, 60

Synechanthus warscewiczianus 52

Tectiphiala ferox 157

Thrinax 65, 110; radiata 65, 66, 68, 70

Trachycarpus 81, 82, 83, 151; fortunei 48, 81, 84, 85, 86, 143, 144, 145, 146, 147, 148, 149, 150, 177

Trithrinax 81; acanthocoma 143, 144

Veitchia joannis 176; merrillii 140

Vonitra thouarsiana 169, 171

Washingtonia 81, 151; filifera 84, 85, 140, 143, 144, 145, 146, 147, 148, 149

Welfia georgii 101, 103

Whitten, Anthony J. & Whitten, Jane E. J.

The sago palm and its exploitation on Siberut Island, Indonesia 91

Wilson, Bob & Catherine 47

Winter, A., as coauthor 143

Wood, Gary 88