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Cover Picture

Livistona exigua growing in heath forest in the Ulu Ingei, Brunei, June 1982.

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Livistona exigua,
A Rare Bornean Palm Refound

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In 1959, P. S. Ashton collected a dwarf fan palm from forest transitional between lowland Dipterocarp forest and heath forest ("kerangas") in the Ulu Ingei, Brunei, near the border with Sarawak. The collection was sent to Kew where eventually it was sorted and studied in detail by one of us (J.D.). Superficially like a *Licuala* in habit, the leaf splits were found to be induplicate as is usual among fan palms, rather than reduplicate as is the case in *Licuala*. Floral structure showed the palm to belong to *Livistona*. This exciting, unrecorded dimension to the genus—an undergrowth, dwarf, rain forest palm—needed recording and so the palm was duly described, as *L. exigua* (Dransfield 1977). In late 1977, when one of us (J.D.) visited the G. Mulu National Park in Sarawak, *L. exigua* was searched for but without success. Still known only from a single herbarium specimen, the chances of recollecting the palm and attempting to introduce it into cultivation seemed remote indeed.

Then the other author (P.R.M.), on forest survey work in Brunei, revisited Ashton's original collecting locality and
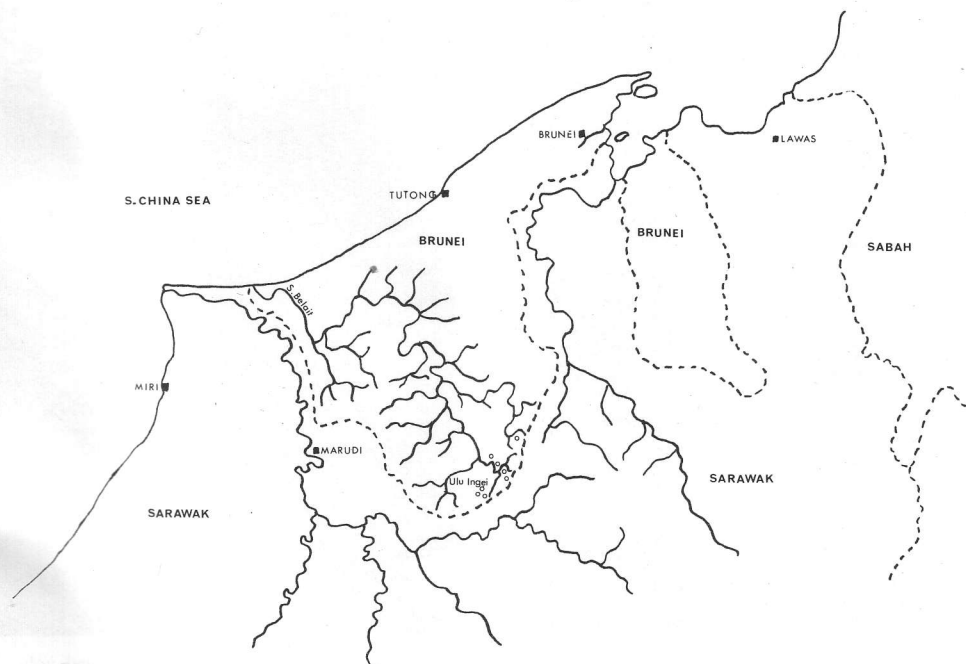
1. Map of Brunei and neighboring Sarawak; O = distribution of *Livistona exigua*.

2.   Crown of *L. exigua* showing pendulous infructescence.

3.   Close-up of pendulous infructescence.

4.   Erect infructescence in a short-stemmed individual.

5.   Seedling of *L. exigua* has very much the appearance of a species of *Licuala*.

refound the palm. Since then the palm has been found in several localities in the Belait District along the border of Brunei and Sarawak (see map). In the Ulu Ingei, it was found growing exclusively on remnant Pleistocene terraces which cap the tertiary sandstone cuestas on the rim of the Belait syncline at an altitude of 500 feet. In the Ulu Pelir Regang it occurs on very heavily eroded remnant terraces, again at 500 feet altitude. At the summit of Batu Patam and on nearby ridges it occurs up to an altitude of 865 feet. In all localities the soil is podzolized with a marked illuviated horizon of white sand. *Livistona exigua* is always confined to the top of these ridges and never grows on the side slopes. Thus its distribution is very limited and broken. Despite differences between localities, the forest in all three areas is of the general "kerangas" or heath forest type. *L. exigua* is an understory palm and when young and closely growing, it forms thickets of its elegant fan leaves. The slender trunks remain clothed in dead leaf bases and fibrous sheaths for a considerable time. Older individuals are usually to be found in more open conditions and eventually reach about 15 feet tall; in such tall individuals, the trunk becomes bare and is finely ringed with leaf scars.

Livistonia exigua was found flowering and fruiting in January and February 1982. Seed received at Kew from these collections finally germinated in June 1983. This is a very elegant palm as the figures testify. However in the experience of growers at Kew, palms from "kerangas" forest seem very difficult to cultivate.

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Nutrient Deficiency Symptoms in Five Species of Palms Grown as Foliage Plants[1]

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Proper fertilization is important for the growth of any plant, but especially in plants grown in soil-less media with little or no inherent fertility. Omission of any essential nutrient element from the fertilization regime of such plants can rapidly result in nutrient deficiency symptoms. Deficiency symptoms for most essential elements are known for most important food and fiber producing plants, but relatively little is known about specific nutritional disorders of tropical foliage plants, particularly the palms. Through the use of sand culture techniques (Hewitt 1966), it is possible to induce experimentally deficiency symptoms of most essential elements in plants, thereby relating specific symptoms to a deficiency of a single element. This has been done for palms such as coconuts (Manciot et al. 1979–1980) and oil palms (Bull 1958, Broeshart et al. 1957, Bull 1961a, Bull 1961b) which are grown as plantation crops, but limited work has been done on commercially important species grown as foliage plants (Marlatt 1978, Marlatt and McRitchie 1979). The purpose of this study was to induce experimentally and describe deficiency symptoms for all essential nutrient elements in 5 species of palms commonly used in interiorscapes.

Materials and Methods

Seedlings of *Chamaedorea elegans* Mart., *Phoenix roebelenii* O'Brien, *Caryota mitis* Lour., *Chrysalidocarpus lutescens* H. A. Wendl., and *Howea forsterana* (C. Moore & F. J. Muell.) Becc. were grown in sand culture to induce deficiency symptoms of all essential nutrient elements. Medium grade silica sand was prepared for use as a growing substrate by the following procedure:

Particulate impurities were floated off by agitation of the sand under running tap water until the effluent was clear. Twelve-liter batches of sand were placed in 15 liter capacity polypropylene containers with small drainage holes in the bottom. Each batch of sand was rinsed with 9 liters of deionized water, soaked in 1 N HCl for 30 minutes with agitation every 10 minutes, soaked in 6 N HCl with agitation for 30 minutes, rinsed with 3 liters of deionized water, soaked in 1 N HNO_3 with agitation for 30 minutes and finally, rinsed with a minimum of 10 liters of deionized water. Sand used for induction of boron deficiency was also soaked with agitation in 2 N NH_4OH. Sand used for chlorine deficiency induction was treated with 1 N and 6 N H_2SO_4 instead of HCl, while sand used to induce nitrogen deficiency was not treated with HNO_3.

Healthy 8–12-month-old palm seedlings were washed to remove all soil from

the roots and were planted in the acid-washed sand in 10-cm square polypropylene containers with polypropylene mesh placed over the drainage hole to prevent loss of sand. Five replicate plants of each species were placed in 14 separate chambers, one for each of the 13 missing elements plus a control (all essential elements provided). Plants were maintained indoors under cool white fluorescent illumination (88 $\mu E/m^2/sec$) (16 h photoperiod) at $23 \pm 2°$ C. They were irrigated once per week with one–half strength Hoagland's solution (Hoagland and Arnon 1950) for the control plants or half strength Hoagland's solution minus each of N, P, K, Ca, Mg, S, Fe, Mn, Zn, Cu, B, Mo, or Cl. Plants were also irrigated twice per week with deionized water only. Nutrient solutions were prepared using reagent grade chemicals and deionized water.

Deficiency symptoms were described as they occurred on each plant. An attempt was made to restore normal growth to the deficient palms by supplying Hoagland's solution including the deficient element. This was generally successful for N, P, Mg, and S, but with severe Ca, B, Mn, Zn, and Mo deficiencies, death of the meristem prevented recovery by the palms.

Results and Discussion

Nitrogen deficiency symptoms appeared in all five species of palms as a gradual loss of green color, first on oldest leaves, but eventually throughout the foliage. Nitrogen-deficient palms grew much more slowly, and had fewer and smaller leaves than control palms. Symptoms first appeared after about four months for *Chamaedorea*, but all species showed severe symptoms after seven months without nitrogen. After returning the deficient plants to a complete fertilizer solution, recovery was complete within four months for all species.

Growth of all 5 species of palms ceased almost immediately after they were placed in a phosphorus-free environment. Leaf color remained normal for about 7 months, but gradually faded to a light olive green color (Fig. 1). The leaves of phosphorus-deficient *Caryota* turned completely yellow after 11 months, however. Since no new leaves were produced in the absence of P, the plants eventually lost all but one or two of the newest leaves. Plants began to recover about four months after restoration of P to the fertilizer solution.

Potassium deficiency symptoms first appeared as necrotic spots or blotches on lower leaves of *Chamaedorea*, *Caryota*, and *Howea* about 9 months after starting the experiment (Fig. 2). Similar symptoms appeared on *Chrysalidocarpus* after two years. The necrosis was confined to the margins of older leaflets of potassium-deficient *Chamaedorea*, but in other species appeared within the older leaflets as streaks (*Howea* and *Caryota*) or spots (*Chrysalidocarpus*). Obvious potassium deficiency symptoms were not apparent in *Phoenix* within two years. Recovery of *Howea*, *Caryota*, and *Chrysalidocarpus* for potassium deficiency occurred within four months, but due to the severity of the symptoms the *Chamaedorea* did not recover.

Symptoms of calcium deficiency first appeared in *Chamaedorea* and *Howea* after about six months as stunted, deformed new leaves (Fig. 3). Newly emerging leaves failed to expand normally with leaflets becoming necrotic, leaving only the petiole base alive. Only necrotic petiole stubs emerged in succeeding leaves, the leaflets and most of the rachis having died before completely developing. These necrotic petiole stubs were usually water-soaked in appearance. Calcium deficiency eventually killed the meristem in these palms so that recovery was not possible. Calcium deficiency symptoms were not induced in *Caryota*, *Chrysalidocarpus*, or *Phoenix*.

Magnesium deficiency symptoms appeared first in *Chrysalidocarpus* as

1.   Phosphorus-deficient *Chamaedorea elegans* (left) showing stunted growth compared to control plant (right).

interveinal chlorosis of the oldest leaves. After nine months the oldest leaves of *Chamaedorea, Phoenix, Caryota,* and *Howea* began to yellow, progressing from the lateral margins of each leaf inward as symptoms progressed (Fig. 4). The rachis and veins of these leaves initially remained green, but under severe magnesium deficiency, the oldest leaves became completely yellow with progressively more

2.   Lower leaf of *Chamaedorea elegans* showing marginal necrosis typical of K deficiency.

3.   Calcium-deficient *Howea forsterana* showing necrotic new leaf.

green on the veins and rachis of younger leaves. Recovery from magnesium deficiency required 6–9 months after restoration of magnesium to the fertilizer solution during which time the chlorotic lower leaves were replaced by healthy leaves.

Sulfur deficiency symptoms appeared in *Chamaedorea, Howea,* and *Caryota*

4.   Magnesium-deficient *Chamaedorea elegans* with severe chlorosis on oldest leaves.

5. Sulfur-deficient *Chrysalidocarpus lutescens* (left) with uniformly yellow new foliage. Control plant on right is normal green color for this species.

palms after about one year and in *Chrysalidocarpus* after nearly two years. Symptoms were similar in these four species and appeared as uniform yellowing of the new leaves (Fig. 5). As the deficiency progressed, new leaflets often showed necrotic tips. Older leaves remained green in all but the most severely deficient plants, however. Sulfur deficiency was not induced in *Phoenix* and recovery of the other four species required about seven months.

Caryota, Phoenix, and *Chrysalidocarpus* showed iron deficiency symptoms after about one year. Symptoms were identical for these species and consisted of interveinal to general chlorosis of the newest leaves, the older leaves remaining green (Fig. 6). After two years *Chamaedorea* palms showed indistinct interveinal chlorosis of the newest leaves with some necrosis on leaflet tips. Also, newly emerging spear leaves did not open normally in this species, leaving two or three unopened leaves at the top of each plant. Recovery

of iron deficient *Phoenix* and *Chrysalidocarpus* was complete in about five months, but *Chamaedorea* and *Caryota* never recovered. *Howea* palms showed no symptoms of iron deficiency after two and one-half years in a virtually iron-free environment.

Mild manganese deficiency symptoms appeared on all but *Howea* palms after about six months without manganese. The earliest symptom was an indistinct interveinal chlorosis of the new foliage (Figs. 7,8). As the deficiency progressed, necrotic spots appeared in new foliage of *Chamaedorea, Chrysalidocarpus,* and *Caryota.* New leaves of *Chamaedorea* emerged with necrotic margins, the necrosis becoming more severe on succeeding leaves so that eventually only necrotic stubs of petioles emerged. Death of the meristem followed. In *Phoenix*, new leaves emerged chlorotic with necrotic edges, reduced in size, and did not expand normally, resulting in several partially opened leaves being present in the bud region. Manganese deficiency

6.　Chlorotic new (left) and green old (right) leaves from a single Fe deficient *Phoenix roebelenii* palm.

was not induced in *Howea* after two and one-half years. Recovery of palms deficient in manganese, as well as boron, zinc, copper, and molybdenum was not possible because such plants were severely weakened or killed by the deficiencies.

Boron deficiency symptoms appeared first on *Chamaedorea* after about seven

7.　*Chamaedorea elegans* showing symptoms typical for Zn, Mo, Mn, and Cu deficiencies in this species.

8.   *Phoenix roebelenii* showing symptoms typical for Cu, Zn, Mo, and Mn deficiencies in this species.

months. Early symptoms for *Chamaedo-rea*, as well as *Caryota* and *Phoenix* included chlorotic new leaves which were usually malformed and failed to expand normally (Fig. 9). Leaf margins were often necrotic and in severe cases, only necrotic stubs of petioles emerged with death of the meristem following. Flowers in boron-
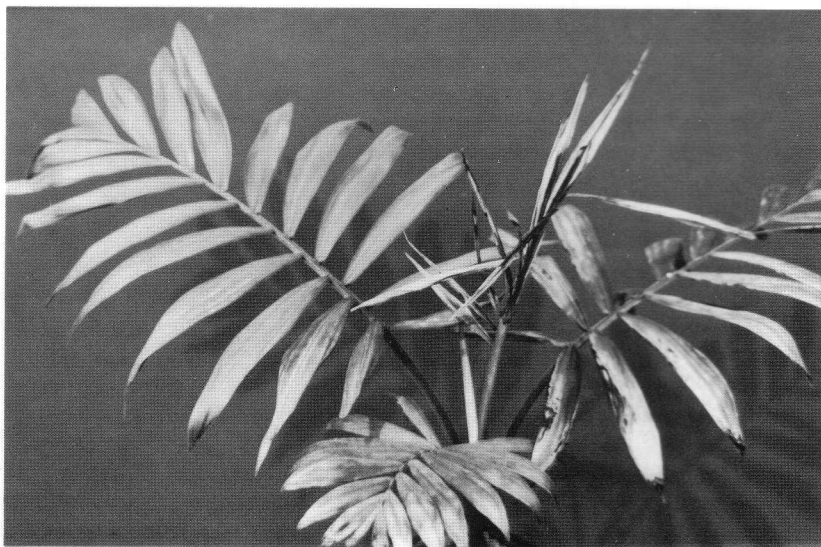
9.   Boron-deficient *Chamaedorea elegans* showing necrotic new foliage.

deficient *Chamaedorea* aborted and blackened. Symptoms were similar for *Howea*, except that no chlorosis was present and the symptoms were not expressed for two and one-half years. Boron deficiency was not induced in *Chrysalidocarpus*, but Marlatt (1978) reported transverse chlorotic streaks on new leaves which, as the deficiency progressed, coalesced and became necrotic. Death of the meristem also occurred in this species.

Zinc deficiency symptoms were induced in all but *Caryota* palms. Symptoms for *Chamaedorea* and *Phoenix* were indistinguishable from Mn deficiency, but in *Chrysalidocarpus* and *Howea* no chlorosis was present (Figs. 7,8). New leaves were reduced in size in all species and often had necrotic tips on leaflets. Zinc deficiency symptoms appeared first in *Chamaedorea* and *Chrysalidocarpus* after about nine months but *Phoenix* required about 14 months and *Howea* two and one-half years for symptoms to appear. Marlatt and McRitchie (1979) reported zinc deficiency symptoms in *Chrysalidocarpus* similar to those described here except that interveinal chlorosis was also present on the new leaves of their plants.

Copper deficiency symptoms were induced in *Chamaedorea*, *Phoenix*, and *Howea* and were similar to the zinc and manganese deficiency symptoms of those species except that chlorosis usually was not present on the new foliage (Figs. 7,8). New leaves were reduced in size, had necrotic margins, and eventually consisted solely of necrotic tipped petiole stubs. Death of the meristem occurred in *Chamaedorea* and *Howea*.

Molybdenum deficiency symptoms were induced only in *Phoenix* and *Chamaedorea* palms, requiring nine months for *Chamaedorea* and 14 months for *Phoenix* to show symptoms. In both species new growth was chlorotic, the leaves usually having large necrotic areas near the tips and margins and were deformed and reduced in size (Figs. 7,8). In *Chamaedorea*, Mo deficiency eventually resulted in only necrotic petiole stubs emerging, followed by death of the meristem as with manganese, boron, zinc, and copper deficiencies.

Chlorine deficiency was induced only in *Phoenix* and *Caryota*, the symptoms appearing after about eight months for both species. The only visible symptom in *Caryota* was a mild chlorosis of the new leaves, but in *Phoenix* chlorosis was more severe and was accompanied by incomplete separation of leaflets of new leaves such that five or six incompletely opened leaves were present on each plant (Fig. 10). These leaves had a ladder-like appearance, with leaflets being attached at the margins so securely that they could not be separated without tearing the leaflets.

In conclusion, nutrient deficiency symptoms in these five species of indoor palms are similar to those reported for larger species such as coconuts and oil palms (Bull 1958, Broeshart et al. 1957, Bull 1961a,b, Manciot et al. 1979–1980). Macronutrient deficiency symptoms were easily induced in these species of palms and were easily distinguished by their symptoms. Deficiency symptoms for these elements are similar to those described for other plant families, but this is not the case with micronutrient deficiency symptoms. Iron and chlorine deficiencies had rather distinctive symptoms, but other micronutrient deficiency symptoms were virtually indistinguishable from one another and correct diagnosis could be accomplished only by leaf elemental analysis once these symptoms were observed.

Deficiency symptoms for most elements required from 6 to 15 months or longer to be expressed in these palms. This was largely due to the slow growth rate of these palms under low light intensities, and stored nutrient reserves in the seed could also have supplied the limited amount of micronutrients required for several

10.　Chlorine-deficient *Phoenix roebelenii* with typical chlorotic, ladder-like new foliage.

months' growth. Palms recover slowly or not at all from nutrient deficiencies, particularly deficiencies of calcium and those micronutrients which cause necrosis of the new foliage. Once severe symptoms are present and the palm's only bud is damaged or killed, recovery is impossible. In this way palms differ from most other plants which have lateral meristems capable of growth following death of terminal meristems.

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Palms in Nepal Near the Top of the World

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We departed New Delhi early morning 27 November, 1978, for Kathmandu, Nepal. We had been in India two weeks, several days of which were devoted to Kashmir and trips around and out of Srinagar. We were eager to look into the enchantments and mysteries of Nepal. This sometime remote, forbidding area, famed as the fitting-out base for heroic scalers of Mt. Everest, was reached in short order by jet flight on Royal Nepal Airlines. Direct flights also are scheduled from Calcutta and Bangkok. Enroute we caught a near view of the grandeur of Everest and adjoining snow-crested sister peaks in the Himalayas.

Nepal, shrouded in age-old culture, ancient cities with their superb temples, and many, many other attractions, is a unique place for travelers. Much of the fascinating detail is beyond the scope of this brief article. But one must visit the Temple of the Living Goddess and nearby Patan, with its array of Buddhist and Hindu temples and monuments. It is highly photogenic; one can keep the camera's shutters going constantly and never capture all of it.

What generally is not recognized by many plant enthusiasts is that Nepal, more so, perhaps, than any other area of its size on earth (54,600 square miles) affords flora of all climatic zones. There are the Himalayan plants, thousands of them high in the east, temperate zone flora back west off the highlands, and subtropic and tropical plants farther west and south in the lowlands and jungles.

Kathmandu, the capital, is in a valley, a delightful area of fascinating places to visit and friendly people who can be helpful, although usually they are not conversant in English. It has a choice of good hotels, and ours sported some palms out front (Fig. 1). Not far away, across the street in fact, one could see *Livistona chinensis*, *Trachycarpus*, and towering high, a very fine *Caryota* (probably *urens*) as in Figure 2. None of these palms was indigenous to Nepal. It may be of interest to note that Kathmandu has a latitude close to that of Miami, Florida, but otherwise there is little resemblance. The Kathmandu Valley is about 4,500 feet above sea level, while Miami is zilch, and certainly there are many other outstanding differences as well. Frankly, before we got there, we hadn't expected to see much in the way of palms in Nepal. But there they were, growing in the shadow of Mt. Everest!

We indulged in a foray out of Kathmandu to Dakshinkell Hindu Temple to see sacrificial ceremonies, where the participants come in great numbers from all directions bearing sacrificial lambs, chickens, pigs, goats, dogs, and so on, to be slaughtered at the shrine. Later, after exchanging greetings the best we could, sans language ability, with a most impressive attendant at the ceremonies, we went on to the Royal Botanical Garden, located about an hour's drive out of Kathmandu.

This garden was established by the King of Nepal in 1962. It is situated at Godavari, in the southeast end of the Kathmandu Valley, surrounded by forests. In our judgement it has the potential of becoming a very fine, small garden. Approximately one-third of the 30 acre
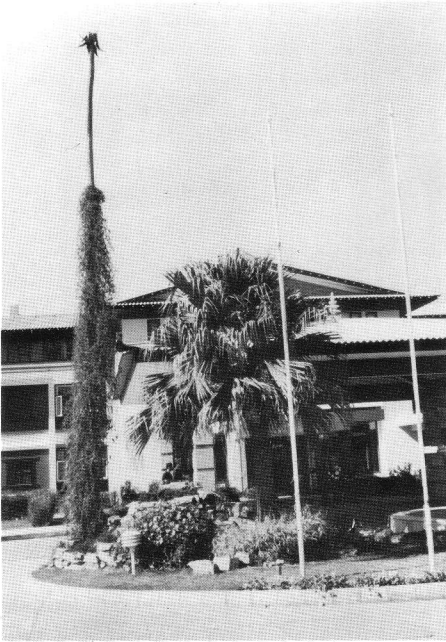
site has been developed, including a nursery, research center with laboratory and library, and palm plantings of *Areca catechu*, *Borassus* and *Caryota* (Fig. 3).

Back in Kathmandu we stripped down our gear to small over-night bags for a flight and trek to "Tiger Tops," in a jungle and former hunting reserve in the Royal Chitwan National Park. A trip to Tiger Tops is a thrill even for experienced travelers. To get there one flies, rides land rovers or elephants, and walks. Once there, the helter-skelter of everyday existence fades to a feeling of isolation.

From the aircraft landing strip at Meghauli, an open pasture amongst appropriate grazing animals, one can take the

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1. *Livistona* fronts porte-cochere, Hotel De l'Annapurna, Kathmandu. (Trunk of dead palm at left supports flowering vine.)

2. *Caryota* furnishes fine background for craft shops near Royal Palace, Kathmandu.

"elephant ride route" or the "land rover route." Both ford the wide Rapti River which in the monsoon months becomes a greatly swollen stream, unfordable at the time. This explains why one does not go to Tiger Tops from July to October each year. In fact, it is closed to visitors at that time.

Once ensconced in the tall, stilt-legged hotel accommodations, excitement mounts. At night one can look out on the trail at a baited lure for the great Bengal tiger, and by day ride the magnificant elephants (Tiger Tops maintains a fine herd of some 15) through the tall grasses in quest of the famed one-horned rhino, rare and native to Nepal (Fig. 4). We were lucky— the transport for our major trek through

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3. Young *Caryota* with Phyllis for scale, Royal Botanical Garden, Godawari, Nepal.

4. Nepal's rare, indigenous, one-horned rhino, photographed in the marshes from atop an elephant.

5. *Phoenix* juvenile transplant in landscaping at Tiger Tops, Chitwan National Park, Nepal.

the bush was a magnificent bull tusker. We were astonished at how gently and reassuringly this enormous animal trudged through deep mud in the marshes, crossed rivers, and bull-dozed through bush.

No palms were visible in the marsh and tall grass areas. Certainly the elephant carrying us was tall enough to provide a wide-ranging view. But we had seen perhaps a half dozen, small, scrubby-looking, juvenile palms that had been transplanted back in the Tiger Tops' Lodge enclave. In the heavy mist of early morning and lack of time before our expedition of the day, we paid little attention to them. We went on by boat and afoot to spend a fascinating day and night at the Tiger Tops Tented Camp, on an island in the Narayani River, at the western boundary of the National Park. Later, after returning from the camp, where we saw no palms, we began to wonder about the transplants noticed earlier. Tiger Tops does not have a large staff devoted to extraneous things, although there was a whole colony to look after the elephants (each elephant required 3 to 4 attendants). A most congenial man on the staff explained that they had simply transplanted the palm juveniles from where they were found growing naturally back up in the hills, not far from the lower hotel site.

Though we were scheduled to return to Kathmandu later in the day, going back across the rivers, etc., we felt we must explore the hill area where the palms were said to be growing. The Tiger Tops' naturalist agreed to guide us up the hill to

6. *Phoenix* sp., hill area habitat near Tiger Tops, Chitwan National Park, Nepal.

This one was quite steep, with a narrow, rocky path, but after about 20 minutes of climbing to the palm area, Phyllis and I wondered if we had staggered into an indigenous stand of a species of dwarf *Phoenix*. We couldn't identify the species, nor could we find any flowers or fruit. The palm was not particularly attractive, growing in the bush, and remarkable to us was that it existed there, in that more-or-less undisturbed area. It seemed highly unlikely that anyone deliberately planted palms in this location. We wondered whether birds, or wind, or otherwise might have accomplished it. In any case, we couldn't find out anything about the origin of the palm, much less the name of the species. But it clearly appeared to be a *Phoenix*. Phyllis gives scale for transplants in Figure 5 and the palm is shown in its habitat on hillside in Figure 6.

So palms, versatile as often they are, can be found near the top of the world. Hopefully, all of us can try to keep them growing from one end to the other of our gardens.

find them. Now, your author absolutely hates to climb hills, especially steep ones.

CLASSIFIED

Coconut and Other Palm Use in Mexico and the Philippines*

Pablo Guzmán-Rivas

The Spanish Galleons which sailed between Manila and Acapulco from 1565 to 1815 brought to Mexico merchandise and a limited number of Filipino settlers. In the Philippines, certain aspects of material culture involving palms, especially the coconut, rest in a high degree of dependence of native economies on palms for many needs, ranging from essential foods to raw materials for manufacture and household industries. This dependence is a trait which one would logically expect the Filipino immigrant to the coastlands of southwest Mexico to have brought with him and to have transmitted to local peoples.

Filipino Use of Palms

A basic group of less than two dozen species of palms provide the natives of the Philippines with foods and materials for diverse requirements of the local economy: alcohol, bags, baskets, brooms, brushes, buttons, charcoal, caulking, chairs, dyes, fertilizers, fibers, furniture, fuel, hats, mats, ornaments, raincoats, rattans, slippers, starches, structural materials, sugars, tannin, thatching, vinegars, and wines. Traditionally, the native

has exploited an abundantly distributed group of palms, a sampling of which follows:[1]

Areca caliso Becc.—alcohol; ingredient for *ikmó*.

Areca catechu L.—ingredient for *ikmó* (or *buyo*); black and red dyes; edible buds; sheathing leaves for mats, hats, slippers, etc.; source of tannin; vermifuge.

Areca ipot Becc.—ingredient of *buyo*; also an ornamental.

Arenga ambong Becc.—for its edible buds.

Arenga pinnata (Wurmb.) Merr.—the well-known *káong*; vinegar, sugar, starch; edible seeds and buds; soft fiber (*baro*); brushes, brooms, alcohol, *tubá*.

Arenga tremula (Blanco) Becc.—baskets, alcohol, *tubá*.

Calamus spp.—rattans: bent-wood, stick-reed, cane-chairs, and furniture; food and water; structural material; cordage.

Caryota cumingii Lodd. ex Mart.—the *aníbong* fish-tail palms, sources for alcohol, *barok* fiber, starches, structural materials, *tubá*.

Cocos nucifera L.—*niúg*, for baskets, brooms, brushes, coir fiber, charcoal, fertilizer, food, oil, fuel, utensils, thatching, structural material, vinegar, and wine.

Corypha elata Roxb.—alcohol, bags, baskets, beads, brooms, *burí* and *buntal* fibers, foods, mats, slippers, starches, sugars, thatching, vinegar, *tubá*.

Daemonorops spp.—rattans.

Heterospathe elata Scheff.—*buyo* ingredient, food, pith-helmets.

Livistona rotundifolia (Lam.) Mart.— (*anáhau, palma brava*), structural mate-

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rials, troughs and flues, poles, flooring, food, thatching, palm-leaf raincoats.

Livistona saribus (Lour.) Merr.—brooms.

Metroxylon sagu Rottb.—alcohol, fiber, food, mats, starches, thatching, structural materials, *tubá*.

Nypa fruticans Wurmb.—alcohol, bags, brooms, fibers, edible seeds, pith-helmets, mats, palm-leaf raincoats, sugars, thatching (perhaps the most resistant to the elements), vinegar, *tubá*.

Phoenix loureirii Kunth.—palm-leaf raincoat.

Veitchia merrillii (Becc.) Moore—the so-called *buñga de china* or *buñga de joló*, often employed as a substitute for *Areca catechu* in the preparation of *ikmó*, the universal Filipino masticatory consisting of betel pepper, lime and areca nut.

The wide availability of these and many other species of palms in limestone formations, dense humid woods in mountain slopes, in secondary forests, sylvan areas, along tidal streams, and in fresh and brackish-water swamps provided native settlements with products sufficient to support town industries. Outstanding, by far, in the historical and economic geography of many Philippine areas are *Nypa*, *Arenga*, *Calamus*, *Corypha*, and *Areca*. The primacy among palms everywhere, from coastal areas to inland elevations up to 4,500 feet, belongs to the coconut palm.[2]

Mexican Utilization of Palms

In sharp contrast, the palm family in Mexico is represented rather poorly by a relatively small number of economic species. The family is better represented in the economic flora of central and southern America. Apart from the introduced *Cocos nucifera* the most valued individuals of Palmae restricted to the southwest Mexican coastlands are some members of the genera *Sabal*, *Cryosophila*, *Brahea*, *Orbignya* and *Acrocomia*.[3] The follow-

ing is a sampling of palms of some economic value in southwest Mexico:

Sabal mexicana Mart.—*palma redonda* of Michoacán and Guerrero; *palma real* or *de micheros*, used as thatching or for chair seats; edible fruits (*micheros*).

Washingtonia robusta H. A. Wendl. *palma blanca*, *palma colorada*, *palma negra*; and *Washingtonia filifera* (Lind.) H. A. Wendl. are commonly cultivated, with some importance for thatching, baskets, cordage, food.

Cryosophila nana (H.B.K.) Bl.—*palma de escoba*, or *soyamiche* of Michoacán and Guerrero.

Brahea dulcis H.B.K.—structural material, thatching, food.

Brahea spp.—*palma blanca*, *palma negra*, *palma de Tlaco*; edible pulp and buds.

Phoenix dactylifera L.—widely cultivated. It is interesting to note that the term *dátil* is given to *Muntingia calabura* L. and more often, in northern Mexico, to *Yucca* spp. However, *dátil* in the Philippines is applied to the fruit of *Phoenix*, and appears in native dialects everywhere as such or in phonetic variants (*látires*, *rátiles*, etc.).

Calyptrogyne ghiesbreghtiana (Lind. & H. A. Wendl.) H. A. Wendl.—thatching.

Chamaedorea tepejilote Liebm. ex Mart.—edible spathes.

Orbignya cohune (Mart.) Dahlgr. ex Standley

Acrocomia mexicana Karw. ex Mart.—*coyol*, edible; also an intoxicating liquor.

Bactris spp.

In considering the list just given and that for the economically useful palms of the Philippines, some points are to be noted:

1. *Brahea dulcis* is comparable to *Corypha elata* of the Philippines in economic value. The Mexican species is found

from Nuevo León and Sinaloa in the north to Oaxaca in the south, and is known in Michoacán and Guerrero as *cocoíste, palma dulce, palma de sombrero, palma soyal,* etc. It is also often used as structural material, thatching and food. In spite of a wide geographical distribution, its usefulness is known but not exploited.

2. *Cocos nucifera* (known generally only in the *coco*-series, such as *cocotero, palma de coco, coco de agual, coco decastillo,* etc.) is cited by Standley as being put to many uses in Mexico (structural material, rafts, thatching, *tubá,* food, milk, vinegar, containers, etc.) approximately the same uses as those obtainable from *Orbignya cohune.* However, as far as one was able to observe in the *tierra caliente* of the southwest coast, most of the recorded uses for coconut could not be verified. Apart from the exploitation of the copra, other utilization was sporadic or non-existent.

3. It is evident that there is almost no correspondence between the Palmae of Mexico and those of the Philippines. A vexing puzzle is why *Arenga, Nypa, Corypha,* and *Calamus* were not introduced in southwest Mexico, in the valley of Tecomán, in San Blas and Manzanillo, and in the lowlands of the Balsas and in Guerrero, in spite of a long history of contact, through trade and migration, between the Pacific coastlands of Mexico and the Philippines.

The Coconut Palm

The Coconut in the Southwest Mexican Coastlands. The problem involving the center of origin of the coconut palm— whether in the Old World regions such as Indonesia and Malaysia, following de Candolle, or in New World tropical coasts as proposed by Cook—is a problem that enters only remotely in considering the role of the coconut palm in transplanting significant elements of southeast Asian culture in Mexico.[4] It is quite certain that

a culture complex based on the coconut palm antedated the European in the southeast Asiatic tropics. In the Pacific tropics of the New World the coconut palm was to be found in at least the coastlands from Panama to Colombia around the 1520s. Quite interestingly, it appears from Bruman's researches that the coconut was not introduced in southwest Mexico until 1539 (probably in Colima).[5] The date is significant because it shows the relative newness of the coconut palm grove as an element of the landscape and the native economy in southwest Mexico at the time of the entry of Spain in the Philippines in 1565. The early historical evidence reviewed by Bruman attesting to the presence of the coconut palm in the New World shows the lack of any definite culture complex associated with it locally, apart from the consumption of its nut. It may explain why members of López de Legazpi's expeditionary staff, who could be assumed to have had fair knowledge of the native economies in at least sections of the southwest coast of Mexico, do not appear to have been familiar nor cognizant of the uses of the palm. Their encounter in the Visayas islands with the versatile exploitation of the palm was apparently quite a revelation to them.

Forty years after the probable date of introduction into Colima, the coconut palm groves do not appear as yet to have any strong impact on the economic geography of southwest Mexico. It is definitely known that coconuts were abundant in Colima in 1587, but curiously enough, some *relaciones geográficas* touching on the coastlands either make no mention of coconuts or mention them only incidentally. The "Relación de Tancítaro", for example, goes into details about the productiveness of the *tierra caliente* and the commerce in tropical fruits, without mentioning the coconut at all. Colima "is Spanish with more then forty households . . . these Spaniards make a living from growing cacao trees and livestock raising . . . also

they plant large amounts of maize and cotton: they cannot cultivate either wheat or barley because of being in the *tierra caliente*. Colima is situated between seven and eight leagues from the ocean. Sailing by and visible from land are ships that come and go from China and some put in for provisions on that coast."[6] There is no mention of the coconut palm.

Tubá. Although the galleons were not the means through which *Cocos nucifera* was introduced into the southwest coast of Mexico, they were instrumental in bringing Filipinos to the area who acquainted natives and Spaniards alike with the economic potential of the coconut.[7] The Mexicans could have had, of course, no better masters. It is well known that the use of the palm by Filipinos is almost a complete one and, in many regions, constitutes an integral part of the total local economy. As a German traveler expressed it: "Where the coconut palm thrives, the people not only use it as a source of food and drink, but also use the wood and leaves for making their hats, tools, furniture, etc. On the beach in the poorest type of soil and without human assistance high yields are obtained. However, inland it is only with great effort that the palm will produce much fruit."[8]

When Asiatics first scattered themselves in native settlements in the *tierra caliente*, one really familiar and nostalgic landscape that must have caught their eye was that of coconut groves. It would not have taken the migrant long to see how the palm was being utilized, and to realize that he had much to contribute to the Mexican Indian's knowledge of the value of the coconut. However, the use of the sap of palms was not altogether unknown in Middle America. Use was made of the sap of *Acrocomia* spp. and *Scheelea butyracea*, a pattern limited to central American regions. The juice was not obtained from the palms in the same manner that the sap of the coconut (as well as of the *Nypa* and *Corypha* palms) is

extracted, viz. by bruising and cutting into the inflorescences. The pith of *Acrocomia* and *Scheelea* was macerated.[9]

Tubá, as a fermented beverage and also as a brandy, was introduced to the Spaniards on the occasion of Magellan's entry in the eastern central Visayan islands of the Philippines in 1521, almost simultaneously with the campaigns of conquest in the highlands of Mexico. The welcome given to Magellan and his men was in the best Filipino traditions of hospitality. The festive board placed before the Spaniards featured, among a host of items, some strips of sago palm sauteed in oil, birds, fruits, and a liquor which was said to flow from the branches of the palm trees.[10] The palm trees would not necessarily refer to the coconut palm but to any one of several species as well which also yield a sap that is generically called *tubá*, e.g., *Caryota cumingii*, *Corypha elata*, *Arenga pinnata*, *Arenga tremula*, *Nypa fruticans*, and at one time but out of favor, also from *Metroxylon sagu*.[11]

It is significant to note that the accounts dealing with López de Legazpi's first months of reconnaisance in the Visayas islands in 1565 show an apparent lack of acquaintance of the Spaniard with *tubá*. Estévan Rodríguez, relating a trip made to Binglás island (present Negros Island) to survey coastlands, reports: "We encountered an old native man and woman, along with a boy; when they saw us coming they were astonished. We told them they had nothing to fear, that we had not come to do them any harm, and that we were friends. Once they were assured of our intentions, they gave us plantains and wine of the coconut palm which was good and resembled a spurious sweet wine."[12]

The appreciation for the brandy was instantaneous, so to speak. For the return trip of the *nao capitana*, among provisions secured was an eight month's supply of what was probably palm brandy. Alfonso de Arellano claims that in Mindanao island

the natives welcome them with considerable amounts of palm wine. "They brought out large, thick bamboo stem segments filled with wine and offered some to us, but before we could drink one of them took some to show that it was good and not poisoned, we then shared drinks with them. The wine was sweet and tasted somewhat like gin; its color resembled cinnamon water, which they probably add to give it the color it has."[13]

The Spaniards gave free rein to their thirst to the degree that disciplinary measures had to be taken to ensure right conduct in the affairs of the infant settlement in Cebu, and an understanding entered into between local chieftans and López de Legazpi.[14]

After the stress and strain of pacification was almost over around the 1570s, and friendlier contact had been achieved between Spanish and native communities in central Luzon valley, in southeastern Luzon and in the coastlands of Ilocos, native drinks became better known and appreciated. Testimonies of Loarca, Ríos y Coronel and Chirino unfailingly mention palm-wine with expressions of wonder at the uses of the coconut. Loarca reports that "one Indian can in one forenoon obtain two arrobas of the sap from the palm-trees that he cultivates, that is made into brandy, vinegar, and delicious honey."[15] Chirino acutely observes that "the palms, of which there are many and varied species, are the vineyards and olive-yards of that country," and so much wine, vinegar, and oil are produced that these commodities are exported to other southeast Asiatic areas.[16] Expressing the same undercurrent of wonder at the versatility of the palms, Ríos y Coronel writes: "From this tree they obtain wine, which is the common beverage of that country; strong vinegar, which is good for the table; and milk like that of almonds, to serve with rice, and which curdles like real milk. When it is soft the fruit is like green hazel nuts in taste, and better; and there is a serum for many ills and infirmities, which is called whey, as it looks much like that of milk. It is there called tubá. They make honey from this tree; also oakum with which to caulk the ships, which lasts in the water, when that from here would rot. Likewise they make rigging, which they call cayro; and they make an excellent match for arquebuses, which, without any other attention, is never extinguished. The shoots resemble wild artichokes, while they are tender."[17]

It is not definitely known just when the tubá-industry began to be actively exploited in the coconut groves of Colima and elsewhere in the southwest coastal settlements under the guidance of Filipinos. The technique could not have taken long to disseminate among the natives. There would be needed only patience to train the inflorescences downwards, bruise and cut them, and collect the flowing sap daily. It seems that the traditional manner of producing tubá was adopted by the colimenses and used for centuries without modifications, since a visitor to the area in the 1830s describes the technique such as it was always used in Filipino areas: "To obtain this liquid, one hollows a cavity at the top of the trunk where the sap of the tree will collect. It is first of all a sweet liquid of agreeable flavor, but after a few hours of fermentation it acquires a wine-like taste and gives off carbon dioxide in large quantities."[18]

One might presume that the appeal of the tubá came when natives learned to use the sap to produce the famous arrak intoxicant. To the natives, "given to drunkenness" according to the Spaniards, the arrak was a comforting drink that rapidly spread in all the communities. The officials expressed alarm when the sales of tubá-brandy displaced current Castilian wines from the market. The government stepped in to regulate the new industry in Colima. An ordinance of 1671 brought to light by Bruman contains some interesting facets of the historical geography of tubá

fabrication in Colima.[19] In that year the residents of Colima were requesting the authorities in Mexico City to favor their community with an extension of a license to produce *tubá* which, in their opinion, was not an ordinary drink to be classified with other intoxicants. The statement in support of the request was so cleverly worded that it made the potent *tubá*-brandy appear as innocuous as orange juice.

From the text of the ordinance it appears that the cacao plantations provided until 1626 the *modus vivendi* of the Spaniards and natives of Colima. A cyclone that year caused widespread ruin of the plantations. In order to alleviate the subsequent economic dislocation in the region, the Spaniards and the natives turned to a large-scale production of *tubá* for which they were licensed for a period of ten years. The license was renewed upon request several times thereafter: 1637, 1644, 1653, 1664, and in 1668. On the occasion of renewal requested in 1637, the petitioners emphasized the medicinal properties of *tubá* and its non-intoxicating character, "medicinal and by no means noxious," after a study of the matter made by a committee.[20] Justifications for subsequent requests for extension of the license varied; in 1653, it was a ruinous fire which consumed Colima and forced her residents to leave town; in 1668, seismic disturbances created havoc in the area and it was explained further that the state benefited from taxes imposed on the industry and was also the support of chaplaincies.[21]

The rapid spread of the *tubá*-industry is confirmed by Pineda's report (1618–20) where he speaks of wine-casks mounted on burros and mules, "so great is the traffic . . . on the coast at Navidad . . . and throughout Colima that they load beasts of burden with this wine as in Spain."[22] In spite of the apparent concern of sincere officials for the health of the natives, the injunction against *tubá*

might have been largely induced by the economies of the situation. *Tubá* production struck at the heart of the trade in Spanish wines. The latter were a source for substantial returns and constituted a straightforward, unencumbered source of revenue.

In the 1830s *tubá* continued to be manufactured in Colima but the significance of it declined in view of the broadened and diversified activities of the region. The coconut groves were being exploited for the copra. Colima City at the time had a population of 15,000; another 25,000 were living in small villages within areas of intensive farming. Fossey, in 1831, found the city to be a veritable paradise of flowers and orchards and an outstanding center for agriculture.

At the present time *tubá* is almost neglected and forgotten in the *tierra caliente* of southwest Mexico except in a few towns where there still are individuals engaged in its manufacture. The people of the coastlands recognize the term *tubá*, but the toddy is found only occasionally in small shops. Very few informants in the coastal villages could give the writer a specific description of *tubá* or the manner of its extraction. The technique appears to survive only among a few peddlers in Colima and in the town of Coahuayana. *Tubá* is also known in some places in the states of Veracruz and Guerrero.

Present Status of Coconut Utilization in the Coastlands. Field work in 1956 took the writer the entire length of the coastlands from Manzanillo to the lowlands of the Balsas, and to the villages and ranchos of Cerro de Ortega, Coahuayana, El Cerrito, San Vicente, El Ticuíz, El Ranchito, San Juan de Lima, La Placita, Aquila, Maquilí, La Ticla, Ostula, Pómaro, Coíre, Caleta de Campos, Cuilala, Tizupan, La Manzanilla, Tiolán, Mexcalhuacán, Chuta, Las Peñas, Playa Azul, and Melchor Ocampo (Fig. 1). Persons encountered in the villages, many of them old men and women, were familiar with
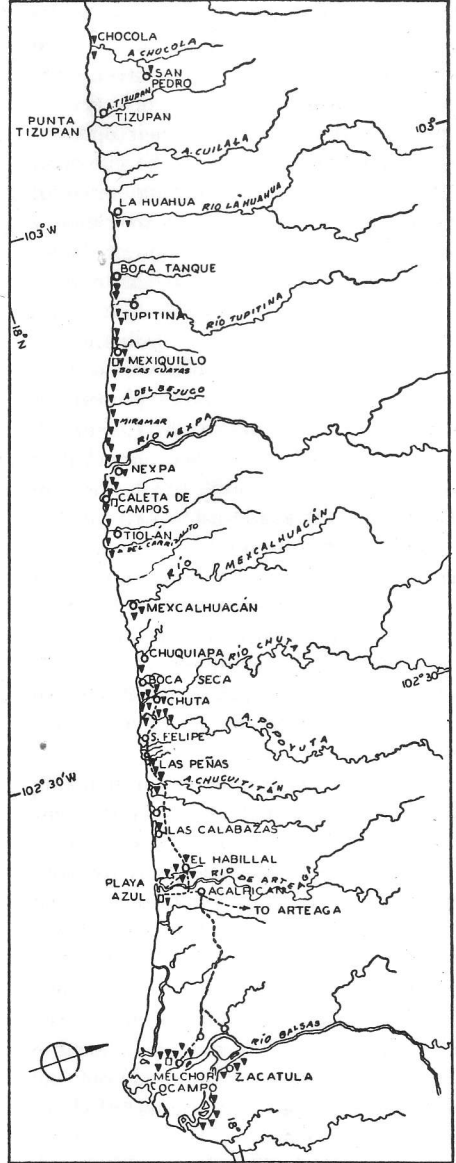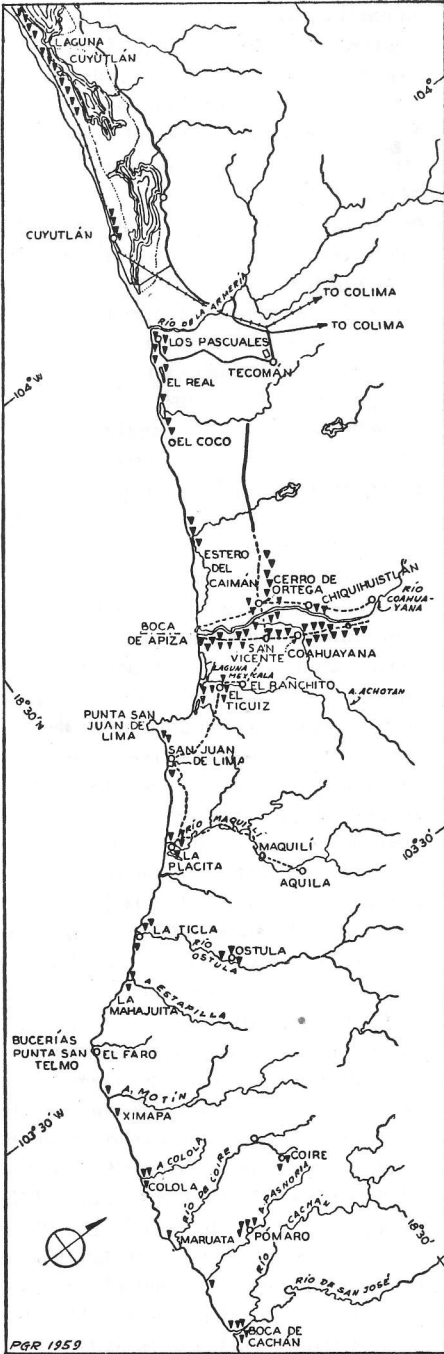
SOUTHWEST COAST OF MEXICO-
DISTRIBUTION OF THE COCONUT PALM

PALM GROVES   BRECHA

0   2   4   6   12 MI.

BASE MAP ADAPTED FROM BRAND, COASTAL STUDY, 1958

tubá but did not know of any place where it was regularly extracted. This was quite remarkable in an area where the landscape was dominated by coconut groves. Actually, few palm groves seen along the coast and strand of southwest Mexico were economically significant, evidently because of barriers of transportation. Coconut stands, large and small, some wild and untended (probably escapes), are found at the following points along the coast (Fig. 1).

Laguna de Cuyutlan: on sand and sandy loam between dunes and the lagoon are extensive plantings of coconut palms. In the middle section of the northern shore of the Laguna is an alluvial plain covered with one of the densest forest of *cayaco* palms in the Pacific coast.[23]

Real de San Pantaleón to Boca de Pascuales: extensive plantations behind a steep tidal beach and high dunes.[24]

Tecomán: some eight miles southwest of the plaza in the margin of coconut plantations against the dunes of a former barrier beach.[25]

Cerro de Ortega—Tecomán: about six miles inland; now being cleared for field crops and orchards; in 1950 the area was covered with thorny scrub vegetation.[26]

Tecomán Beach: two small plantings five miles northwest of the Boca de Apiza.

Boca de Apiza: there is an extensive reclamation of the coastal area; extensively planted to coconuts, but the groves reflect poor edaphic conditions. In 1950 a prospering grove was to be found in a sand and silt peninsula between the ocean and a brackish lagoon. By 1957, marine action had decimated the grove and only three palms remain.[27]

Coahuayana: the coconut groves are in very poor condition. The copra that is processed comes from very small nuts with scant meat. Here, however, we find one of the most active centers of copra processing in the coast, evidently favored by a seasonally reliable *brecha* through which the copra can be moved out. Interplant-

ing, a far more efficient land-use, was noticeably absent, except for occasional banana patches. A very small sale of *tubá* was seen in town, but there are no cottage industries based on the coconut palms.

El Cerrito: the groves are extensive under *ejido* (collective) management, but badly tended and overrun with brush. In 1956, the groves showed moisture-deficiency and nuts were scanty even in five and six-year old trees. Some stands are older, perhaps 12 to 15 years in age. The *ejido* is concerned only with copra. The 1955 floods ruined some areas when unconsolidated river banks collapsed, tearing chunks out of the groves. The classical Filipino "diamond" pattern of planting, considered to be the most efficient land-use was not to be seen anywhere.

El Ticuíz: fairly extensive plantings in and around the village. According to informants, 15-year old groves yield approximately 100 nuts per tree, and are collected in May and December. Trees 60 to 75 years of age are said to be giving fruit. Local varieties were denominated *nayarit* and *ticuizeño*, the former giving a sharply ovoid nut, the latter a larger, meatier one. Small young nuts were called *coquitos*, semi-mature ones *media carne*, and those fully developed for copra, *agua suelta*. Copra is sun-dried for a week; there are very limited facilities for kiln-drying.

Punta San Juan de Lima (south side): new coconut plantings, still not producing, on stretches of sand and sandy loams some 300 yards from the beach. Coconut leaves were used everywhere for *ramadas* on the beach and for temporary beach shelters occupied by stores, restaurants, and bathhouses.

La Placita: extensive mature groves in and around the village, but very sporadic utilization. Plantings are dominant in the area around the mouth of the Río Maquilí, close to a lagoon. Groves are also to be seen along the trail from La Placita to La Ticla.

Ostula river delta: the right bank is known as Palmar.

Estampilla: a handful of palm trees.

La Mahajuita: a very small stand.

Río Motín: site of extensive stands of coconuts dating back to the sixteenth century, but devastated by floods in 1932. In 1950, ten palms remained, and only seven by 1956.[28]

Arroyo de Ximapa: a small stand.

Lower Arroyo de Colola: well-drained soils and good water has started a small movement of settlers into the area.

Boca de Cachán: coconut palm stands are found on both east and west ends of the delta. Some of the groves are interplanted with maize.

Chocola: dense and compact groves.

Huahua: coconuts growing on the left bank as well as at the west end of the delta.

Tupitina to Arroyo del Bejuco and the Nexpa: extensive plantings. Connections by land and air have stimulated resettlement of areas near Boca del Tanque, Tupitina, Mexiquillo, etc. and the cultivation of coconuts. Some humid areas between the Arroyo del Morro and Boca Chica have been planted to coconuts only since 1950–51.[29]

Caleta de Campos: west beach to the Lomas de Campos.

Bocas Cuatas to Arroyo de las Salinas: coconut plantations dominate the landscape, extending through Miramar to the Arroyo de los Morritos.

Tiolán: groves border the swamps in the area.

La Majahuita—Arroyo del Carrizalito: very recent plantings.

Mexcalhuacán: "Here also was one of the earliest plantings of coconuts on the Michoacán coast, and to this day the coconuts of Mexcalhuacán are famous for their quality although there are fewer than one hundred trees in Mexcalhuacán proper."[30]

Chuquiapa: west end of the shingle and sand beach.

Río Chuta: the Chuta lowlands; groves also border the river up- and down-stream.

Río Popoyuta: groves on both banks, and up-stream.

Playa Grande: extensive coconut stands from west end (La Peñas).

Río Chucuititán: coconuts are found along the west arm of the river which parallels the beach for 1,500 yards. An extensive lagoon is bordered by coconut palms.

El Habillal—Playa Azul: scattered, dense stands.

Melchor Ocampo and Zacatula: various areas of coconut plantations in the lowlands of the Balsas River are harvested regularly. Stands are from 3 to 15 years of age. Utilization is limited to the production of copra.

Evaluation of Filipino Influences. The Filipinos who settled in southwest Mexico and introduced *tubá* and, possibly, other aspects of utilization of the coconut palm, were probably natives of the coconut-producing Philippine regions. Shipbuilding was located in areas with well developed coconut groves. Since the crews for the galleons were recruited from laborers serving the shipyards, the sailors who jumped boat in Acapulco were assuredly men very conversant with the uses of the coconut palm. What, one might ask, was the magnitude of their influence in, say Colima, Michoacán, Jalisco, and Guerrero as regards the use of coconuts other than the extraction of *tubá*? Is there any verifiable correspondence between the utilization of the coconut in southeast Asia and its utilization in the Pacific coastlands of Mexico? Such a correspondence would not, of course, argue conclusively to Filipino influence, since minor uses for the palm could have been developed independently by the Mexican native. An inquiry into the pattern of utilization in southwest Mexico brings out some striking facts:

1. Even in areas of southwest Mexico with fairly extensive coconut plantations there was apparently little involvement

with the palm in the culture of the villagers. Most of those questioned thought one coconut was like every other coconut and knew no differences in kernel characteristics, yields, uses, and values. In contrast, close and familiar contact of southeast Asiatics with the coconut palm has created in them a consciousness of differences between varieties and qualities. The native in coconut-producing areas will distinguish many varieties: those heavy in oil, a palm low in stature, which can be harvested from ground level, dwarf nuts used for ornamental objects, freak sterile nuts, nuts with soft endosperm and excellent for copra, sweet-husked nuts, decorative palamcotta, very fibrous nuts, hard-shelled nuts, the almost black nuts, and pale-brown nuts. The southwest Mexican native apparently knows only elementary differences ascribed to regions, such as *veracruzan, michoacán, nayarit, ticuizeño,* and the *mexcalhuacán* as the largest, sweetest, with the most liquor.

2. Food uses were known in a small part, such as the use of stem-tips and buds for salads, coconut milk for soups and porridges, shredded coconut meat for garnishing. Not even once, from Manzanillo to Melchor Ocampo, did the writer see the coconut actually used as a food or component of the diet.

3. The sterile, non-viable freak nut ("macapuno"), considered and prized as a delicacy in the Philippines, was unknown in the western Mexican coastlands. Market vendors had never heard of it.

4. The processing and utilization of coir fiber was unknown in the copra producing areas of southwest Mexico; husks, as far as the writer could see, were allowed to stand and rot, but in some cases were used for fuel or as re-enforcement for pole-and-mud walls.

5. No actual (or traditional) use of the coconut for folk medicine was noted.

6. Thatching with coconut fronds was used in temporary sheds; the petioles were often seen in use as fencing material.

7. There was no known instance in the coastlands of Mexico of a household craft or local industry based on raw materials from the coconut palm. Retail stores and notion counters carried no dolls, gewgaws, utensils, containers, combs, etc. made out of the husks and the hard shell of the nut.

NOTES

1. William H. Brown, Useful Plants of the Philippines, Technical Bulletin 10, (Ballarat and Melbourne, 1950) I, 207–339.
2. Juan de la Isla, Relacion de las Islas del Poniente y del camino que a ella se hizo desde la N.a. Espana, Colección de documentos inéditos relativos al descubrimiento, conquisa, y organización de las antiguas posesiones españolas de Ultramar, 2.a serie, tomo 3 (II. de las Isla Filipinas), (Madrid, 1887), 226–243.
3. Paul C. Standley, Trees and Shrubs of Mexico, Contributions from the United States National Herbarium, Vol. XXIII (Washington, 1920–26), 70. Some representatives of the *Sabal* and *Attalea* were introduced to the Philippines after 1905. (Brown, *op. cit.*, I, 212)
4. A. de Candolle, L'Origine des Plantes Cultivées, (Paris, 1883); O. F. Cook, The Origin and Distribution of the Coconut Palm in America, Contributions from the United States National Herbarium, VII, 2 (Washington, 1901), 257–293; *id.*, History of the Coconut Palm in America, *ibid.*, XIV (Washington, 1910), 271–342.
5. Henry J. Bruman, A Further Note on Coconuts in Colima, Hispanic American Historical Review, Vol. XXVII, No. 3 (Durham, 1947), 572–573.
6. Relación de Tancítaro (Arimao y Tepalcatepec), Edición y Notas por Ignacio Bernal, Tlalocan, III, 3 (Mexico, 1952), 212, 217–218.
7. Henry J. Bruman, Some Observations on the Early History of the Coconut in the New World, Acta Americana, Vol. II, No. 3 (Washington, 1944), 220–243. Bruman conjectures that by 1587, "a modest industry engaged in making drinking vessels out of coconut shells for export to Spain was already in existence in Colima" (228).
8. F. Jagor, Reisen in den Philippinen, (Berlin, 1873) 34.
9. Cook, Origin and Distribution, *op. cit.*, 287.
10. Unless one were familiar with the technique, it does appear as though the sap were flowing from the branches.
11. The technique of extraction is essentially the same in each case: inflorescences are bruised for several weeks to stimulate sap-flow. Sap is gathered often for as long as two months. Yields

are of the order of 2–20 quarts a day, depending on many factors.

12. Estévan Rodríguez, Relacion muy circunstanciada de la navegacion que hizo el Armada de S.M. a cargo del General Miguel López de Legazpi, Colección de documentos inéditos . . . Ultramar, *op. cit.*, (II de las Islas Filipinas), 373–427.

13. Alfonso de Arellano, Relacion mui singular y circunstanciada hecha por . . . capitan del patax San Lucas del Armada de General Miguel Lópes de Legazpi, *ibid.* 1–76, esp. 31–32.

14. *Ibid.*, 110–111.

15. Miguel de Loarca, Relacion de las Yslas Filipinas, Arévalo (June, 1582), BR, V, 169.

16. Pedro Chirino, S. I. Relacion de las Islas Filipinas, i de lo que en ellas antrabaiado los padres de la Compañia de Jesus, (Rome, 1604) ap. BR, XIII, 189.

17. Hernando de Los Ríos y Coronel, Reforms, BR, XVIII, 283.

18. Mathieu de Fossey, Le Mexique (Paris, 1857), 404.

19. Henry J. Bruman, Early Coconut Culture in Western Mexico, Hispanic American Historical Review, Vol. XXV (Durham, 1945), 212–223.

20. In many areas of the Philippines *tubá* is presumed to have curative properties, especially for tubercular individuals.

21. Ordinance of 1671, in Bruman, Early Coconut Culture, *op. cit.*, 221–223.

22. Captain Sebastián de Pineda, Relacion hecha por . . . en cosas tocantes a las yslas filipinas ansi de fabricar de galeones y pataches y galeras y otros pertrechos como de cosas tocantes a la guarda y conservacion de las dichas yslas, Mexico, 1619, BR, XVIII, 184–185.

23. Donald D. Brand, Coastal Study of Southwestern Mexico, II, The University of Texas (Austin, Texas, 1958), 114.

24. *Ibid.*, 11.

25. *Ibid.*, 110.

26. *Ibid.*, 109.

27. *Ibid.*, 3.

28. *Ibid.*, 45.

29. *Ibid.*, 75, 76.

30. *Ibid.*, 90.

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Formation of Plications in the Pinnate Leaves of Chrysalidocarpus lutescens and the Palmate Leaves of Rhapis excelsa

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For over 100 years plant morphologists have known that the large, dissected leaves of palms exhibit a developmental pathway which is distinctly different from that of the compound leaves of all other flowering plants. In those dicotyledons and monocotyledons having dissected leaf blades, leaflets arise as free lobes on the margin of the primordial leaf. In contrast, leaflet inception in the palms occurs by folding of the submarginal part of the lamina, followed in most groups by the secondary splitting of the blade into individual leaflets. Since this mode of leaflet origin seems to have no counterpart in other flowering plant species and is markedly complex in character, it has received a considerable amount of attention from morphologists in the last century (von Mohl 1845, Hofmeister 1868, Goebel 1884, 1926, Naumann 1887, Deinega 1898) and more recently (Yampolsky 1922, Eames 1953, Venkatanarayana 1957, Periasamy 1962, Padmanabhan 1963, 1967, Corner 1966, Padmanabhan and Veerasamy 1973). Despite the length of time that the problem has been studied and the large number of papers devoted to this subject, controversies on the mechanism of the original folding or plication remain unresolved and misinterpretations persist.

In the past there has been general agreement amongst these investigators on the general pattern of palm leaf morphogenesis. Both pinnately compound and palmately compound leaves first appear as hood-shaped protuberances which encircle the shoot apical meristem. A series of transverse to oblique folds or plications develop near the margins of the primordium (Fig. 1A); these indicate the position of the future leaf blade. A distinctive feature of these plications is that they do not extend to the leaf margin, leaving an unplicate marginal strip of tissue. During the growth of most palm leaves a localized separation of tissue results in the splitting of the lamina into individual leaflets. In some groups of palms the splitting occurs in the ridges nearest the shoot apex (Fig. 1B,C). This is the adaxial side of the leaf and because the leaf bends away from the shoot tip as it expands from the crown, the mature leaflets are trough-shaped in cross section or induplicate. In other groups of palms, the splitting occurs in the ridges farthest from the shoot apex (abaxial ridges); this results in leaflets that are ridge-shaped in cross section or reduplicate (Fig. 1D). In some palms, the location of the zones of separation does not correspond to adjacent ridges so that individual leaflets consist of a number of the original plications (Fig. 1E). The tips of the leaflets also separate from the unplicate marginal strip of tissue which is ephemeral in many groups, but which may form a pair of conspicuous reins attached to the two basal leaflets (Eames 1953).

The source of controversy in the liter-
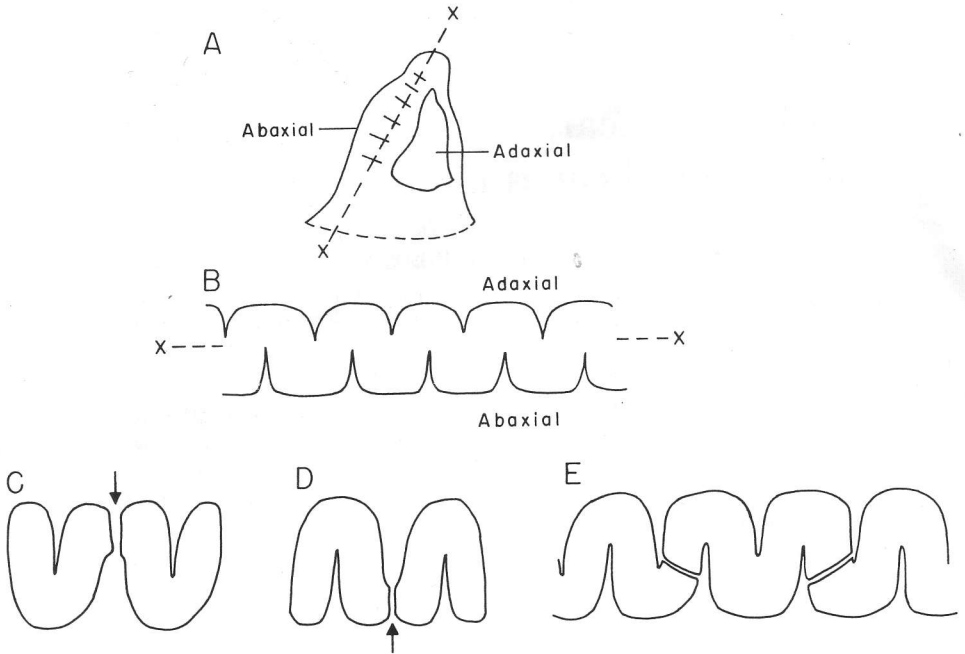
1.   Diagrams illustrating an adaxial view of a hood-shaped palm leaf primordium (A) and the appearance of a section (B) made through the submarginal plications in the plane indicated by the line (X—X). Abscission through the adaxial ridges (arrow) will result in induplicate leaflets (C); abscission through the abaxial ridges (arrow) will result in reduplicate leaflets (D); or zones of abscission in the intercostal regions may result in leaflets consisting of more than one plication (E).

ature has been over the mechanism of inception of the original folds or plications in a previously smooth lamina. The point of disagreement is whether tissue separation is involved in the initiation of the plications themselves. For example, Hofmeister (1868), Goebel (1884, 1926), Deinega (1898) and more recently Periasamy (1962) and Corner (1966) conclude that the plications are formed by a process of differential growth followed by a folding of the meristematic lamina as shown in Figure 2A–C. On the other hand, von Mohl (1845), Naumann (1887), Yampolsky (1922), Eames (1953) and Padmanabhan (1963, 1967) argue that the process of pleat formation involves not only differential growth, but also the inter-

nal separation of cells in such a way that internal schizogenous slits break through the epidermal surface on alternate sides of the leaf giving the pleated appearance (Fig. 2A,D,E). At first the differences between these alternatives might appear trivial; however, each involves quite different morphogenetic processes. If tissue separation did occur, internal cells of the ground tissue lining the schizogenous spaces and normally destined to become photosynthetic mesophyll cells would now be on the external surface of the leaf and would differentiate as the protective cells of the epidermis. In contrast, the process of differential growth only involves localized zones of growth to give rise to the adaxial and abaxial ridges of tissue with-

A
Adaxial

Abaxial

B   D

C   E
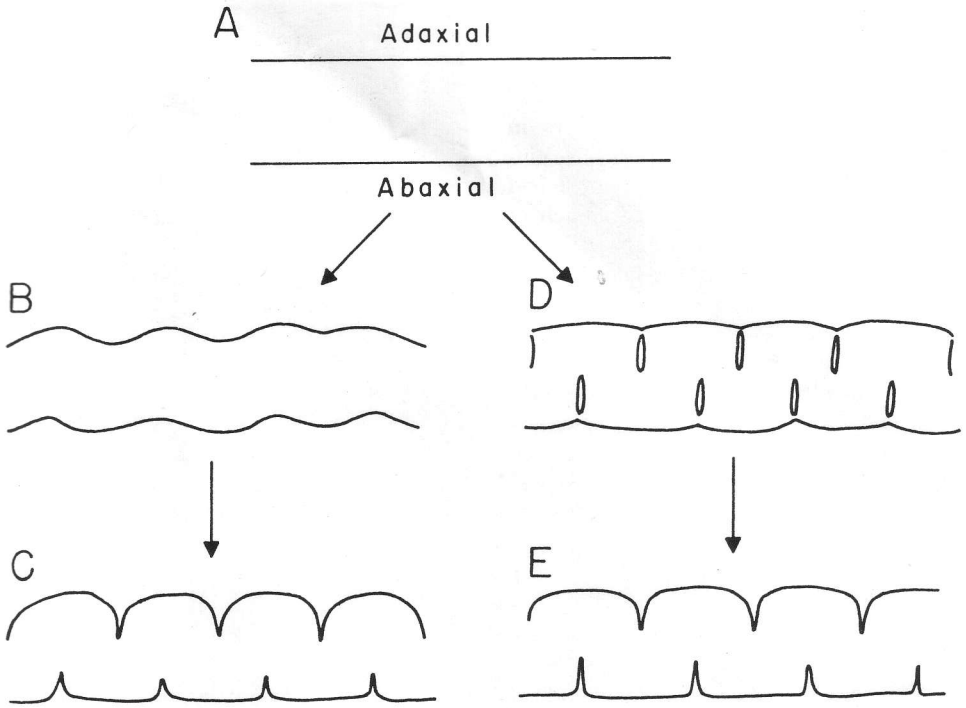
2. Diagrams illustrating the formation of alternating adaxial and abaxial ridges through differential growth (A,B,C) or through the extension of internal schizogenous slits to the surface (A,D,E).

out the complicated redifferentiation of cells.

The purpose of this study is to resolve this long standing controversy over the mechanism of plication inception and, particularly, to test the hypothesis of the schizogenous origin of the plications and subsequent redifferentiation of tissue. Since this mechanism has not been reported to occur in any other flowering plant groups, this would be a further unique feature of palm leaf development that might be of potential significance in evaluating the systematic relationships of palms, particularly with other monocotyledons having plicate leaves.

Species having the two basic types of palm leaf morphology were selected for this investigation: *Chrysalidocarpus* *lutescens* H. A. Wendl. (arecoid major group, Moore 1973) having pinnate reduplicate leaves and *Rhapis excelsa* (Thunb.) Henry (coryphoid major group, Moore 1973) having palmate induplicate leaves. Shoots of both species were collected at Fairchild Tropical Garden, Coral Gables, Florida and were shipped to the University of California, Berkeley. This investigation was carried out in conjunction with Dr. D. R. Kaplan, University of California, Berkeley, and the observations which are summarized below were reported in greater detail in three papers in the *Canadian Journal of Botany* (Kaplan *et al.* 1982a, b, Dengler *et al.* 1982). The specific methods used to study the problem of plication inception are also described in these papers.

Results

Morphogenesis in Chrysalidocarpus lu-
tescens. The mature leaf of *Chrysali-
docarpus* measures about 2 meters in
length and is differentiated into a pin-
nately compound blade, a short petiole and
a smooth, tubular base (Fig. 3). Each of
the approximately 80 leaflets has a single
major vein or rib and is reduplicate. The
leaves are arranged in either a clockwise
or counterclockwise phyllotaxis (Kaplan *et
al.* 1982*a*). The developing leaves are
tightly packed together within the apical
bud and their appearance in scanning
electron micrographs and in sectioned
material viewed in the light microscope
suggest that considerable mutual pressure
is exerted between adjacent leaves (e.g.,
Fig. 6).

Figure 4 shows a young leaf about 0.5
mm in length in which there is no external
indication of plication inception but which
clearly shows the hood-shaped lamina, and
a sheathing leaf base which encircles the
shoot apex and younger leaf primordia.
The upper limit of the sheath of the next
oldest leaf can be determined by the loca-
tion of the constriction near the base of
the leaf lamina (Fig. 4, arrow). Developing
leaves of *Chrysalidocarpus* are charac-
teristically asymmetrical. One margin of
the lamina protrudes through the sheath
of the next oldest leaf; this is the anodic
(+) margin. The other margin is appressed
against the rachis; this is the cathodic (−)
margin. The leaf illustrated in Figure 4 is
from a shoot with counterclockwise phyl-
lotaxis and therefore the right hand mar-
gin as viewed from the adaxial side is
anodic (+). Leaves from shoots with
clockwise phyllotaxis have the anodic (+)
margin on the left.

Plications first appear in leaves 0.6 to
1.0 mm in length as a series of slight
ridges and furrows having a vertical ori-
entation in the distal part of the lamina
(Fig. 5A). Formation of the ridges on the
adaxial side of the leaf is seen to precede

3

3. Mature leaf of *Chrysalidocarpus lutescens*
showing the pinnate lamina, petiole and tubular
sheathing base. Scale line equals 50 cm.

ridge formation on the abaxial side of the
anodic margin; the folding of the cathodic
margin against the rachis obscures the
ridges (Fig. 5A,B). As the leaf develops,
the abaxial surface appears flat in surface
view and the furrows between the abaxial
ridges resemble slits incised in the surface
of the lamina (Fig. 6). Plications do not
extend to the margin or apex of the leaf,
leaving an unplicate margin and a hood-
shaped leaf apex (Fig. 6). While the first
formed apical plications have a vertical
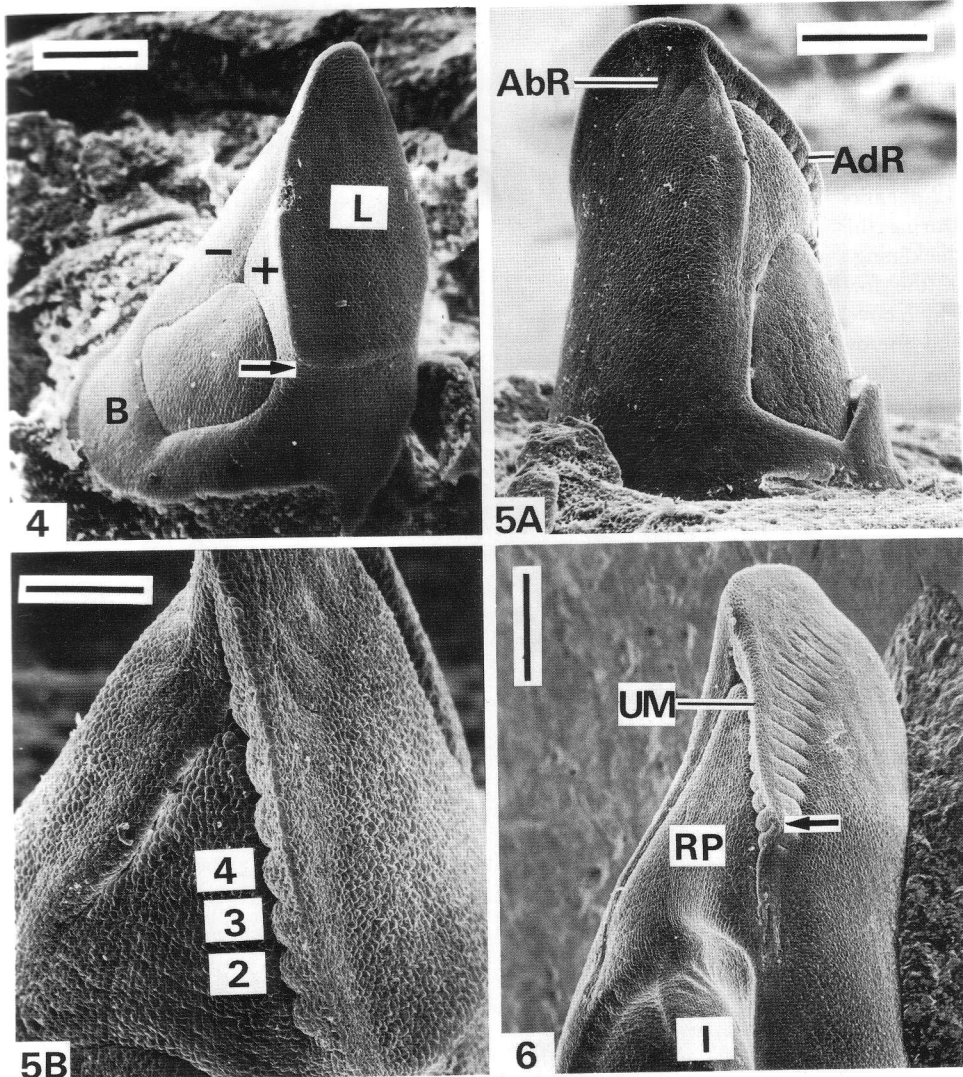
4–6.   Scanning electron micrographs of developing leaves of *Chrysalidocarpus lutescens*. Fig. 4. Leaf pri-
mordium 0.5 mm in length. Note the sheathing leaf base (B), hood shaped lamina (L) with anodic (+) and
cathodic (−) margins. The arrow indicates the constriction formed by the sheath of the next oldest leaf. Scale
line equals 200 μm. Fig. 5A. Leaf primordium about 1 mm in length. Note the vertical orientation of abaxial
ridges (AbR) on the cathodic leaf margin and the adaxial ridges (AdR) of the anodic margin. Scale line equals
200 μm. Fig. 5B. The anodic margin of the same leaf as shown in Fig. 5A and with the plications used for
histological analysis, 2, 3, 4 above the constriction, labelled. Scale line equals 100 μm. Fig. 6. Leaf 2 mm in
length in which new plications are being formed basipetally below the constriction (arrow). Note the unplicate
margin (UM), rachis protusion (RP) and impression of younger leaf on adaxial surface of sheath (I). Scale line
equals 200 μm.

orientation, later formed plications are oriented in the horizontal plane. Based on length and surface appearance, new plications appear to be added both acropetally and basipetally until the leaf reaches a length of about 5.5 mm with about 40–42 plications on each lamina half (Fig. 7). During the period of plication initiation, thickening growth of the rachis axis results in the formation of a rachis protrusion which covers the base of the adaxial ridges and furrows (Figs. 5A,6). Elongation of the leaf, particularly above the point of confluence of the margins, marked by an arrow in Figure 7, results in a gradual reorientation of the apical plications to the horizontal plane. Later in development, elongating plications come to lie in the vertical plane. This vertical packing of leaflets against the rachis can be seen in a new sword leaf as it emerges from the crown. Prior to emergence, splitting of the blade into leaflets occurs. When the leaf is fully elongated, expansion of the pulvinus at the base of each leaflet causes it to open and bend away from the rachis (Corner 1966).

Histogenesis in Chrysalidocarpus lutescens. Documentation of the early stages of leaf development using scanning electron microscopy allowed us to understand the complex three dimensional relationships of parts of the leaf during the critical stages of plication formation and to orient young leaf primordia for sectioning. Serial sections of the anodic half of the lamina just above the point of constriction (ridges 2, 3, 4 in Fig. 5B) were made from the unplicate margin through the plications to the rachis in a plane perpendicular to the axis of plication extension. These series of sections were analyzed to determine the pattern of cell growth described below; outline drawings of sections from the midregion of the plications only are illustrated in Figures 8–12.

Prior to the formation of plications the lamina of the leaf is five to seven cell layers thick and has a smooth surface (Fig. 8). The appearance of slight ridges on the adaxial side of the lamina is associated with localized areas of periclinal (parallel to the surface) and oblique divisions in middle layers of the lamina in addition to slight cell enlargement in the adaxial protodermal and subprotodermal layers (Fig. 9). Further growth of the adaxial ridges is accompanied by the development of zones of mostly anticlinal (perpendicular to the surface) divisions alternating with the ridges (Fig. 10). This pattern of growth results in an increase in surface area of the portion of the lamina undergoing plication. Since the plicated part of the lamina is bordered by the unplicate leaf margin, the leaf apex, the rachis, and the petiole (Fig. 6), and since the enlargement of these parts of the leaf does not keep pace with the plicate lamina, the comparatively rapid extension of the confined lamina is accommodated by buckling of the lamina between adaxial ridges (Fig. 10). This growth pattern brings about the appearance of abaxial ridges and furrows, and further growth in surface area results in the compression of adjacent ridges on both sides of the leaf, giving the slit-like appearance of the adaxial and abaxial furrows (Fig. 11). The plications deepen in the radial plane by further intercalary growth in the intercostal sector, causing the adaxial and abaxial ridges to be displaced from one another (Fig. 12).

All developmental stages examined in this study lacked any indication of internal slits opening to the surface to form alternating ridges and furrows, although slightly oblique sections taken near the rachis occasionally (and incorrectly) gave the impression of internal schizogenous spaces (Dengler *et al.* 1982). Analysis of serial sections also showed that the protoderm appears as a continuous layer of cells on both the adaxial and abaxial surfaces of the leaf throughout the developmental stages observed. Both of these observations support the alternative of differential
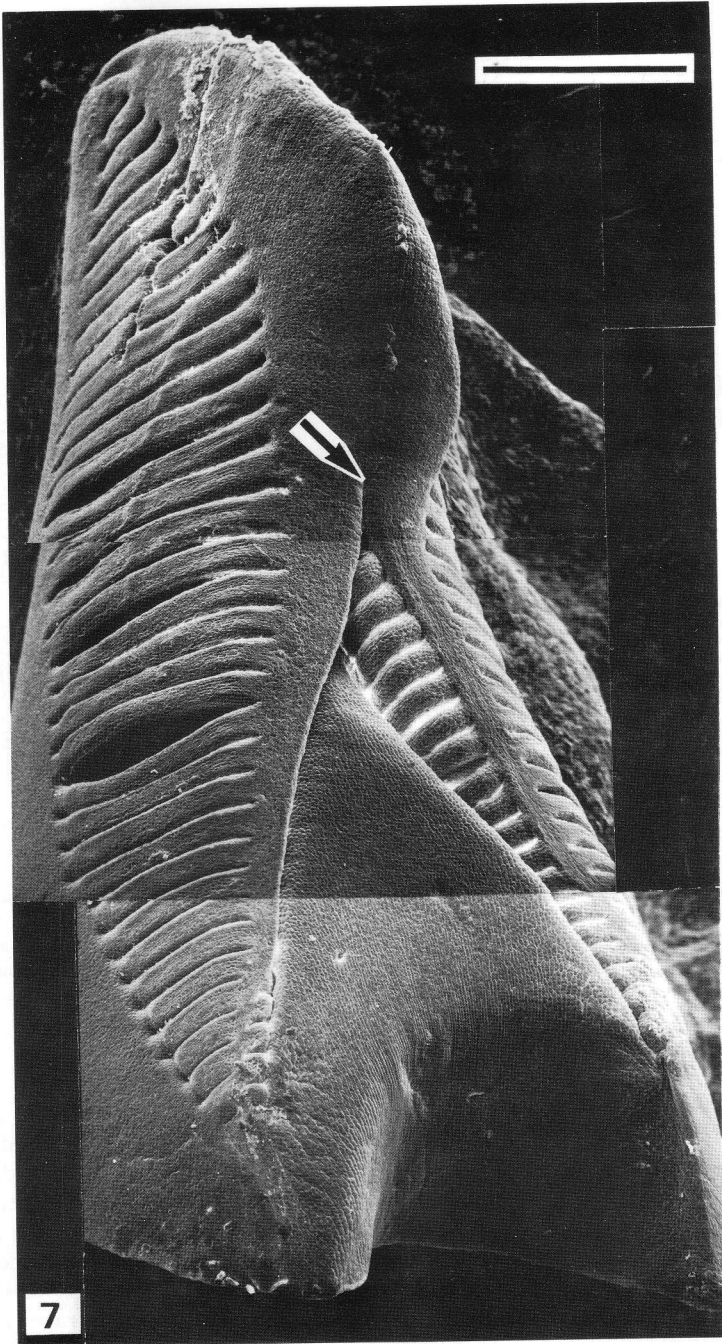
7.   Scanning electron micrograph of a leaf of *Chrysalidocarpus lutescens* 7 mm in length. Arrow indicates the point of confluence of the unplicate margins with the hood-like apex. Scale line equals 500 μm.
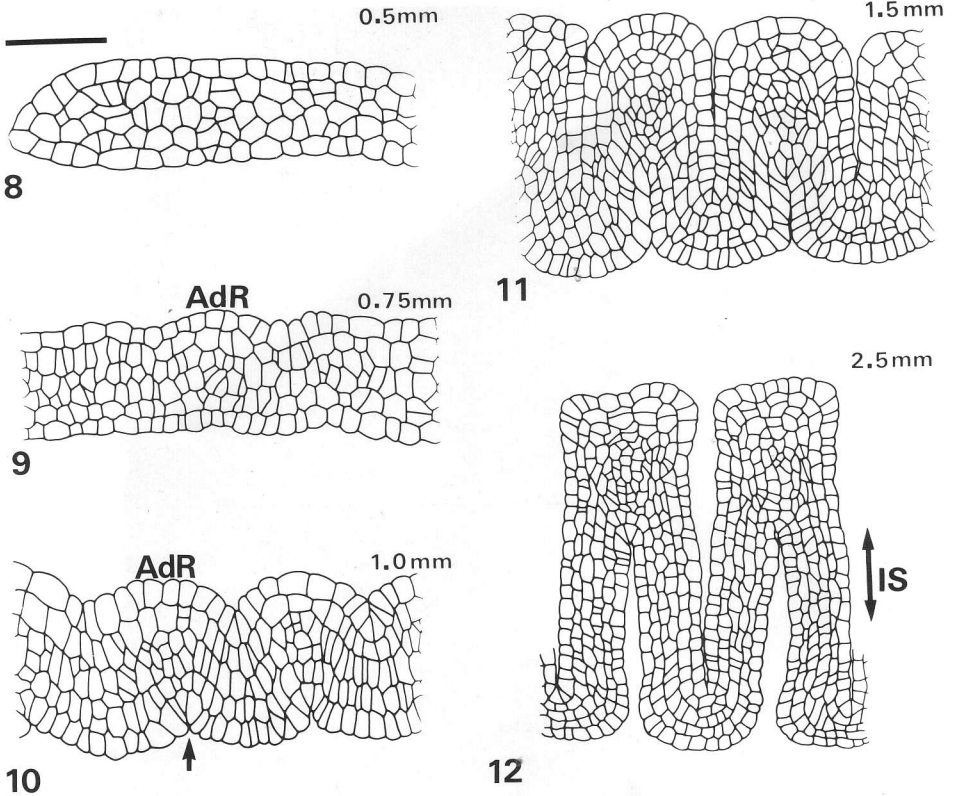
8–12. Outline drawings illustrating the midregion of plications of successively older leaves of *Chrysalidocarpus lutescens*. Sections are oriented with the adaxial surface uppermost. Scale line equals 50 μm. Fig. 8. Section of the unplicate lamina of a leaf 0.5 mm in length taken 50 μm from the margin. Fig. 9. Section of the plicate lamina of a leaf 0.75 mm in length taken 78 μm from the margin. The adaxial ridge of plication 2 above the constriction is labelled. Fig. 10. Section of a plicate lamina of a leaf about 1.0 mm in length taken 64 μm from the margin. The adaxial ridge of plication 2 is labelled. The arrow marks the position of the abaxial furrow of this plication. Fig. 11. Section of plicate lamina from a leaf 1.5 mm in length taken 84 μm from the margin. Fig. 12. Section from the plicate lamina of a leaf 2.5 mm in length taken 182 μm from the margin. Arrow shows direction of growth in intercostal sector (IS).

growth, but it can be argued that the most rigorous test of the mode of plication formation would be an analysis of the number of cell layers across the lamina. If the formation of internal schizogenous slits results in ridge and furrow inception, a decrease in the number of cell layers across the lamina at the locus of the furrows would be expected; conversely, if differential growth alone accounts for plication formation, one would expect only an increase in number of cell layers.

Counts of the number of cell layers were made at the position of the adaxial ridge (abaxial furrow); the abaxial ridge (adaxial furrow) and the intercostal sector in leaves of increasing ages as shown in Figure 13. A decrease in the number of cell layers is not observed at any stage. These comparisons clearly demonstrate a dramatic increase in the number of cell layers (from 5 to 16) in the position of the adaxial ridge (Fig. 13A); many of these cells are associated with the differentiation of the pro-
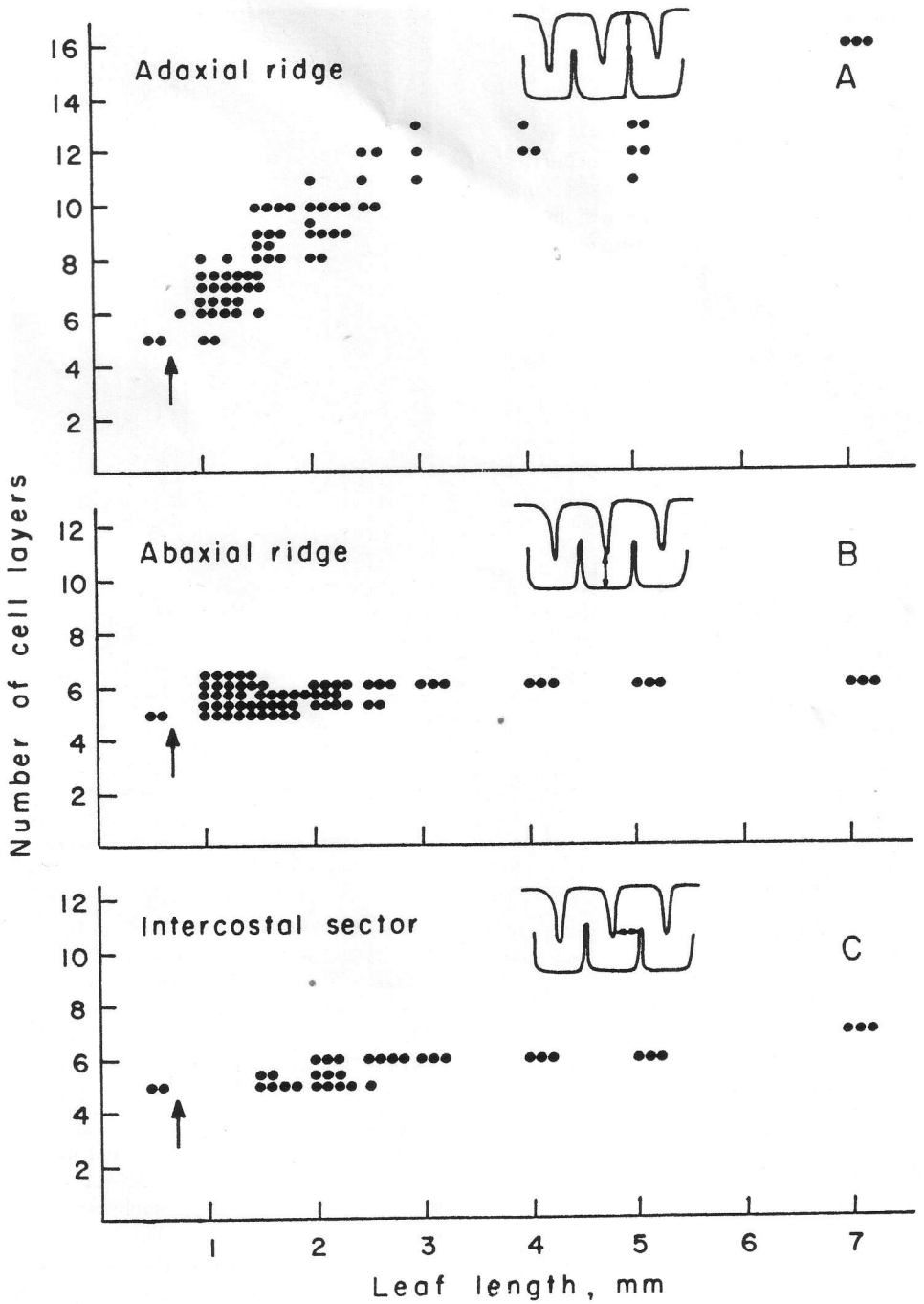
13. Scatter plots illustrating the changes in the number of cell layers in the adaxial ridge (A), abaxial ridge (B) and intercostal section (C) in the leaves of *Chrysalidocarpus lutescens* 0.5 mm to 7.0 mm in length. Arrows indicate the stage of plication inception.

cambial strand of the future leaflet mid-vein. An increase in the number of cell layers also occurs in the abaxial ridge (Fig. 13B) and the intercostal sector (Fig. 13C) although the increase is less dramatic (from 5 to 7 layers). If splitting were occurring during furrow formation and were compensated for by localized growth in the associated ridge so that the number of cell layers was not altered, one would expect to see cell wall patterns in the ridges indicative of this localized compensatory growth. Since this was not observed we conclude that all of our qualitative and quantitative histological observations are consistent with the concept of differential growth—alternating zones of the leaf lamina undergoing different growth rates resulting in plication formation.

Morphogenesis in Rhapis excelsa. The mature foliage leaf of *Rhapis* is about 0.8 meters in length and is differentiated into a palmately compound blade, a long petiole and a fibrous tubular leaf base (Fig. 14). Although the blade is divided into 10 to 12 segments, segment number does not correspond to plication number and each segment has two or more ribs along its length. A pair of small crestlike appendages called hastulae are attached at the junction of the blade and the petiole on the adaxial and abaxial sides of the leaf (Fig. 15). As in *Chrysalidocarpus*, the leaves are arranged in either a clockwise or counterclockwise spiral in the bud which imposes an asymmetry on the tightly packed developing leaf primordia (Kaplan *et al.* 1982*b*).

   Prior to the inception of plications, the young leaf primordium of *Rhapis* consists of a tubular leaf base and a hood-shaped lamina in which an anodic and a cathodic side can be distinguished (Fig. 15). The lamina differs from that of *Chrysalidocarpus* in that the apex is prolonged into a conical protuberance or "Vorläufer-spitze" characteristic of the leaves of a
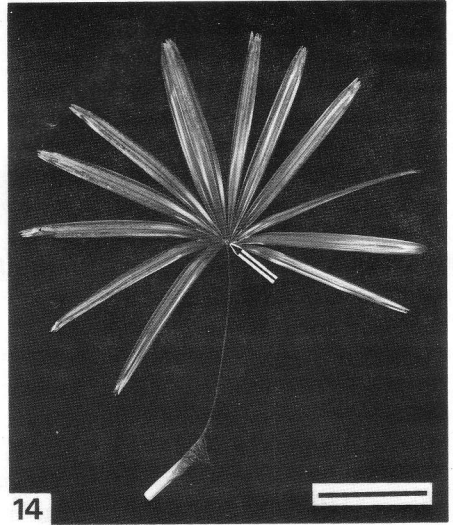
14.   Leaf of *Rhapis excelsa* showing differentiation into a palmate lamina, petiole and tubular sheathing base. Arrow indicates adaxial hastula. Scale line equals 50 cm.

number of monocotyledous species (Kaplan 1973). The concave adaxial surface of the lamina is covered by the adaxial hastula and the convex abaxial side bears the abaxial hastula. Plications are not externally visible on the abaxial side of the lamina until leaves are about 1 mm in length (Fig. 16). The first abaxial ridges appear as subtle mounds on the narrow horizontal ledge of tissue that represents the free margin of the leaf (Fig. 16). The adaxial ridges and furrows are obscured by the adaxial hastula at this stage, although sectioned leaf material reveals that the development of the adaxial ridges is actually advanced over the abaxial ridges (Kaplan *et al.* 1982*b*). As the leaf expands, the lamina becomes more vertical in orientation and the abaxial ridges become sharply demarcated from each other by slit-like grooves (Fig. 17). The first plications to be initiated are at the apex of the leaf and subsequent plication initiation occurs in a basipetal direction along both the anodic and cathodic margins. The
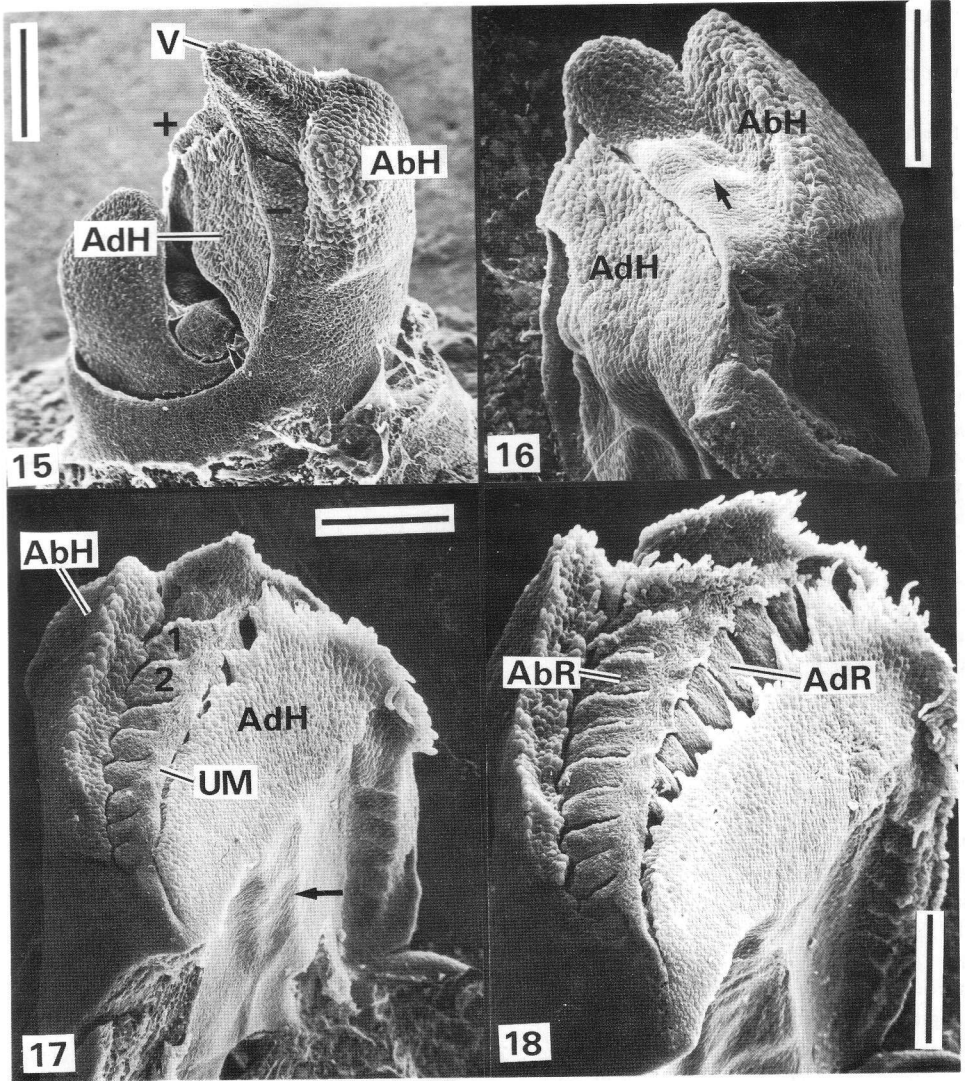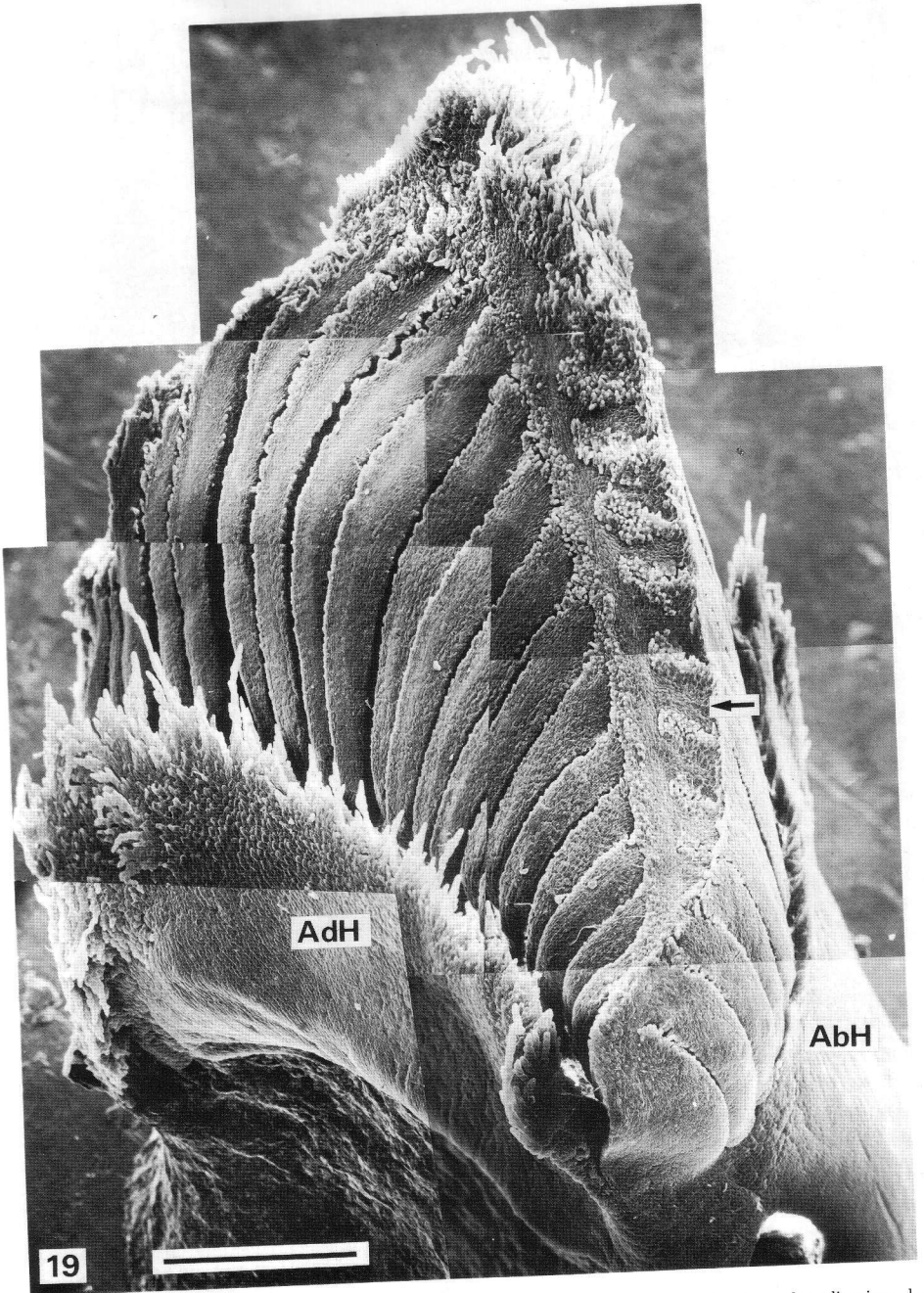
15–18.   Scanning electron micrographs of developing leaves of *Rhapis excelsa*. Fig. 15. Terminal bud showing leaves 150 μm, 400 μm and 650 μm in length. The oldest leaf exhibits an adaxial hastula (AdH), abaxial hastula (AbH), anodic (+) and cathodic (−) margins and a prominent "Vorläuferspitze" (V). Scale line equals 200 μm. Fig. 16. Leaf 1 mm in length. Slight abaxial ridges (arrow) are evident between the leaf margin and the abaxial hastula (AbH). Adaxial ridges are covered by the adaxial hastula (AdH). Scale line equals 200 μm. Fig. 17. Leaf 2 mm in length. Abaxial ridges are numbered. Note unplicate margin (UM), adaxial hastula (AdH) and abaxial hastula (AbH). Arrow indicates impression of next youngest leaf. Scale line equals 500 μm. Fig. 18. Leaf 3 mm in length. Both adaxial ridges (AdR) and abaxial ridges (AbR) are evident. Scale line equals 500 μm.

ridges and furrows of each plication clearly do not extend to the lamina margin and the crescent shaped zone of attachment of the plications to the rachis is obscured by the hastulae.

As the leaf elongates, the adaxial ridges and furrows begin to extend beyond the adaxial hastula margin (Fig. 18). The abaxial hastula elongates along with the lamina; so that while the horizontal part of the plications adjacent to the margin is exposed, the elongate, vertical portion of the abaxial ridges is protected by the hastula. The leaf illustrated in Figure 17 also shows how mutual pressures within the apical bud leave the impression of the next youngest leaf on the adaxial side of the leaf sheath (arrow). The final number of 20–24 plications is reached in leaves that are about 4.5 mm in length. Trichomes develop on the edges of the plication ridges beginning with the unplicate margin and proceeding basipetally; growth of the trichomes and margin eventually obscures the "Vorläuferspitze." Trichomes also develop on the margins of both hastulae in alignment with the plication furrows (Fig. 18). Eventually, expansion of the hastulae does not keep pace with the elongation of the plications so that both adaxial and abaxial ridges are exposed (Fig. 19). In the 6 mm leaf shown in Figure 19 the line of demarcation indicated by an arrow on the abaxial ridges delimits the original horizontal portion of the plication from the more vertically oriented part which was appressed to and covered by the abaxial hastula through much of early development. Separation of the lamina into 10 to 12 segments occurs within the intercostal zone of tissue lying between adjacent adaxial and abaxial ridges as indicated in Figure 1E. Elongation of the leaf and its segments continues until the new leaf emerges from the crown as a sword leaf. As in *Chrysalidocarpus*, expansion of the pulvinar region at the base of each segment brings about the opening of the folded segments.

Histogenesis in Rhapis excelsa. Since the orientation of the developing plications is vertical in the leaves of *Rhapis excelsa*, a histological analysis of plication inception in the leaves was based on cross sections of developing leaves. Also because of the differences in stage of development of plications of one leaf and differences along the length of each individual plication, the histological description given here will be based on cross sections from the midregion of plication 2 (Fig. 17). As in *Chrysalidocarpus*, the anodic margin of the leaf protrudes from the sheath of the next oldest leaf (Fig. 15) while the cathodic margin is somewhat compressed inside the sheath. Although this results in differences in the degrees of compression of the developing margin at early stages, plications 2 from both the anodic and cathodic margins will be used to describe histological development.

Figure 20 is a section through the anodic margin of a leaf at the stage when plication 2 first appears as a slightly convex mound which is located between the adaxially curved free margin and the adaxial ridge of plication 1. The formation of these ridges is associated with periclinal and oblique divisions in the internal cell layers (Fig. 20). At this stage the adaxial furrow between the ridges of plications 1 and 2 appears as a broad depression rather than a narrow furrow. As the leaf grows, compression of the lamina brings the ridges of adjacent plications into closer proximity, narrowing the adaxial furrow (Fig. 21). This occurs at earlier stages in plications of the cathodic margin as compared with those of the less compressed anodic margin. Internal divisions result in an increase in tissue layers at the locus of the adaxial ridge while anticlinal divisions and associated cell growth in the intercostal sector between the ridges extends the surface area of the lamina. Although extension of the plications in this palmate leaf does not occur in such a confined space as observed in *Chrysalidocarpus*, buckling of the

19.   Scanning electron micrograph of a leaf of *Rhapis excelsa* 6 mm in length when the plications have elongated well beyond the adaxial hastula (AdH) and abaxial hastula (AbH). Arrow indicates the horizontal portion of the abaxial plication ridges which are uncovered by the abaxial hastula at all stages of development. Note trichome development on leaf margin, plication ridges and margins of hastulae. Scale line equals 500 μm.
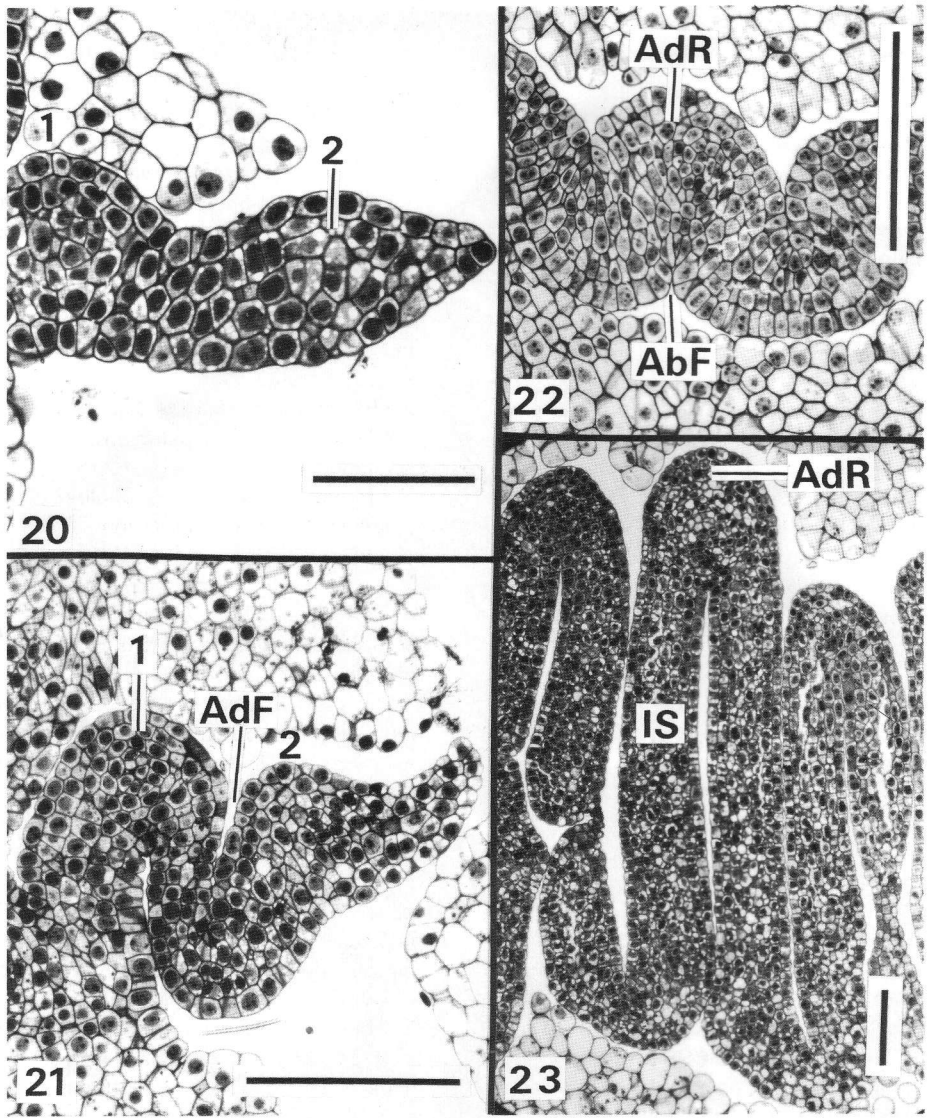
20-23. Cross sections of developing leaves of *Rhapis excelsa* showing the midregion of plication 2. Fig. 20. Section from the anodic side of a leaf 0.8 mm in length taken 187 μm from the leaf margin. The adaxial ridges of plications 1 and 2 are associated with localized periclinal and oblique divisions. Scale line equals 50 μm. Fig. 21. Section from the cathodic side of a leaf 1.0 mm in length taken 265 μm from the leaf tip. Adaxial ridges 1 and 2 are compressed so that the adaxial furrow (AdF) between them appears slit-like. Scale line equals 100 μm. Fig. 22. Section from the cathodic side of a leaf about 1.2 mm in length taken 266 μm from the tip. The adaxial ridge (AdR) and associated abaxial furrow (AbF) of plication 2 are labelled. Scale line equals 100 μm. Fig. 23. Section from the cathodic side of a leaf 2 mm in length taken 619 μm from the leaf tip. Adaxial ridge (AdR) and intercostal sector (IS) of plication 2 are labelled. Scale line equals 100 μm.

lamina also occurs and results in the formation of broadly rounded abaxial ridges and narrow abaxial furrows (Fig. 22). Intercalary growth of the intercostal sector results in the displacement of the adaxial and abaxial ridges away from each other (Fig. 23). All of these sections show a complete continuity of the protodermal layer at all stages of development.

Although this histological analysis of plication origin in *Rhapis* gave no suggestion of splitting, the same quantitative analysis of plication growth used in *Chrysalidocarpus* was carried out as an additional test of the mechanism of morphogenesis. This analysis showed that the greatest increase in number of cell layers (from 5 to 26) occurred in the adaxial ridge (Fig. 24A); as in *Chrysalidocarpus*, this is associated with the differentiation of the procambial stand of a major vascular bundle. Although the increase in the number of cell layers in the abaxial ridges (Fig. 24B) and the intercostal sectors (Fig. 24C) was less (from about 4 to about 8 cell layers), no evidence of a decrease in the number of cell layers was observed at any developmental stage.

Discussion and Conclusions

We conclude that the process of differential growth at the locus of the adaxial ridges followed by intercalary growth between ridges accounts for the original formation of plications in a submarginal position (Dengler *et al.* 1982, Kaplan *et al.* 1982b). This conclusion is based on observations of oriented serial sections through developing plications in a closely graded series of leaf lengths; our observations of sections of over 140 leaves of *Chrysalidocarpus* and 63 of *Rhapis* were consistent with this interpretation. No sections revealed the presence of internal slits developing toward the surface or any breaks in protodermal continuity which would support the hypothesis of schizogenous origin of the plications. In addition, careful counts of the numbers of cell layers across the lamina, made along the length of the plications in leaves of a range of ages, only showed an increase in the number of cell layers. One would expect a decrease in number of cell layers if splitting were occurring; the observed increase in number of cell layers supports the concept of differential growth. Perhaps the most convincing argument for our conclusion is the similarity in the histology of developing plications in a palm with pinnately compound leaves, *Chrysalidocarpus lutescens*, and a palm with palmately compound leaves, *Rhapis excelsa*. Despite the differences in the morphology of the young leaves, the orientation of the plications and the physical contraints on the developing lamina, our cross sections of developing plications of both *Rhapis* and *Chrysalidocarpus* are strikingly similar (cf., Figs. 10,22).

Our assertion that tissue separation does not play a role in the initial formation of the plications is based on an understanding of the gross morphology of the young leaves, careful control of the plane of sectioning, use of serial sections so that position within a particular plication is known, recognition of the age of the leaf under observation and examination of a large number of individual leaves. Although the earliest investigators were handicapped by the limited techniques available to them, the fact that the mechanism of this aspect of palm leaf morphogenesis has remained unresolved for over a century is largely the result of misunderstanding one or more of the factors listed above (Kaplan *et al.* 1982a).

For instance, despite Naumann's (1887) early clear statement of the problem in interpreting plication initiation, his own anatomical observations of *Phoenix* were based on cross sections of the whole leaf, an angle which would be oblique to the developing plications. Not surprisingly, he
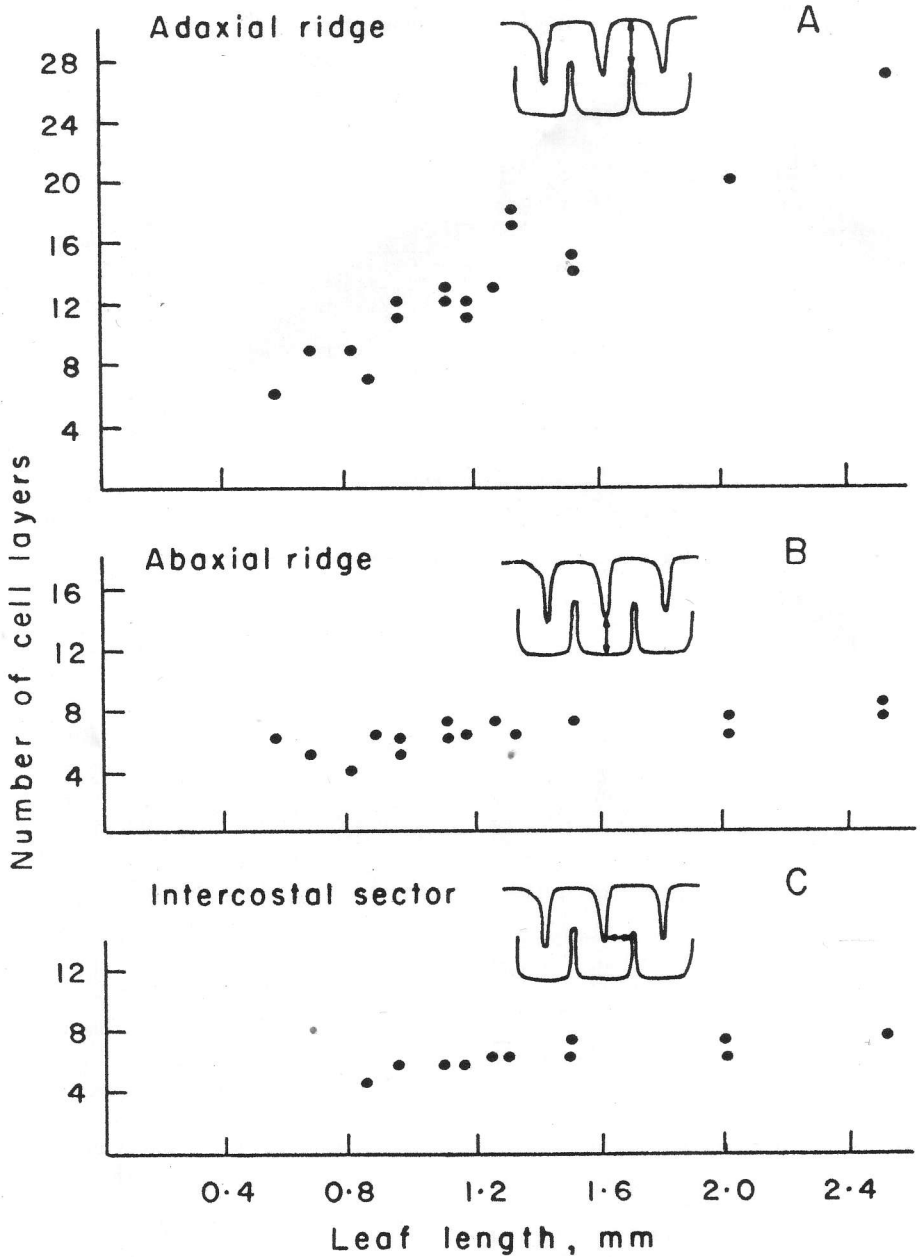
24. Scatter plots illustrating the changes in the number of cell layers in the adaxial ridge (A), abaxial ridge (B) and intercostal sector (C) in leaves of *Rhapis excelsa* from 0.5 to 2.5 mm in length.

described young plications as pouches having internal slits and deduced that they were the result of tissue separation. As another example, although Goebel (1926) took care in orienting the leaves of *Elaeis* so that sections were made tangential to the margin, some of his critical stages appear to be oblique sections made too close to the unplicate strip of marginal tissue. While he concluded that differential growth was the process resulting in the formation of plications, he failed to provide convincing evidence for the mechanism. Our own observations indicate that plication inception occurs at a relatively early state which is easily missed (by a leaf length of 5.5 mm in *Chrysalidocarpus* and a length of 4.5 mm in *Rhapis*). Venkatanarayana (1957), who attributed plication development in *Cocos* to schizogenous splitting, appears to have oriented his sections properly but to have missed the actual stage of plication inception. His figures are of a relatively late stage of plication growth and most likely represent a zone of appression of two adjacent plications similar to that shown in Figure 11 of this paper.

The major lines of evidence cited in support of the process of tissue separation are: 1) the slit-like appearance of the furrows in surface views of whole leaves and in sectional views of growing plications, and 2) the occurrence of internal slits in some sections. A primary reason that *Chrysalidocarpus* was selected to test the hypothesis of tissue separation is the narrow slit-like appearance of the furrows shortly after inception (Fig. 6). However, sections through younger plications demonstrate that the plication ridges are at first rounded with the furrows only secondarily assuming a slit-like appearance as the plications expand within a confined space (Figs. 9–11). This is more dramatically illustrated in *Rhapis*. When two adjacent plications are first initiated, they are separated by a broad shallow depression (Fig. 20); only as additional plications are initiated basipetally and all the plications extend in depth do the furrows become narrow and slit-like (Fig. 22). Some investigators have missed the stages with rounded ridges and have based interpretations on the more compressed advanced stages of plication growth. For instance Padmanabhan (1963, 1967) and Padmanabhan and Veerasamy (1973) have argued that the V-shaped grooves observed in sections of the leaves of *Cocos*, *Borassus* and *Phoenix*, as well as the zigzag appearance of the walls of the furrows, is the result of separation between the internal ground meristem cells which have an irregular alignment. Again, comparison of their illustrations with our sections indicates that the early stages of plication formation were probably missed and that the irregular appearance of some furrow surfaces may be the result of distortion of susceptible meristematic tissues caused by fixation and dehydration, a problem that also plagued many of our sections.

The appearance of internal slits in some sectional views has also provided a major source of evidence in support of tissue separation (Naumann 1887, Yampolsky 1922, Eames 1953, Padmanabhan 1963, 1967). In our material of *Rhapis* and *Chrysalidocarpus* any indication of internal slits could be shown to be the result of a somewhat oblique section taken adjacent to the rachis and the apparent internal pockets could always be shown to be continuous with the external surface of the leaf by following serial sections (Dengler *et al.* 1982, Kaplan *et al.* 1980b).

Our observations indicate that the mechanism of differential growth alone can account for the original formation of plications in the leaves of palms. In this respect palm leaf development is similar to development of compound leaves of other flowering plants in which differential growth (in the sense of localized areas of

meristematic activity) also results in the formation of leaflets from free marginal lobes. The unique aspect of palm leaf morphogenesis is the location of this localized growth in a submarginal position and the subsequent secondary separation of the plications to form individual leaflets. While our investigation led to a rejection of the hypothesis of splitting as the mechanism of plication inception, it is clear that some sort of tissue separation must occur in the abscission of leaflets from one another and from the unplicate strip of marginal tissue. Future research on palm leaf morphogenesis must test our conclusions in a wider range of palm taxa and must also examine these more complicated aspects of leaflet separation which are among the most distinctive features of morphogenesis in this unique plant group.

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NEWS OF THE SOCIETY

News from Southern California

The September Meeting

On Saturday, Sept. 10, 1983 the Southern California Chapter of The Palm Society met at the home of Pauleen Sullivan. Members were warmly greeted by Pauleen with coffee and home-made cookies provided by Mrs. Carl Dowbler.

Pauleen Sullivan's palm gardens make up one of the definitive collections of palms in the state. It is hard to select only a few of her palms to comment on but the specimens of *Cyrtostachys renda* are beautiful; the *Roystonea* is huge with over 25′ of trunk; the large *Jubaeopsis caffra* was in seed; the specimens of *Hedyscepe canterburyana* are the most beautiful I've ever seen; and many *Pytchosperma* sp., a huge clump of the ivory crowned *Pinanga*, the tallest member over 10′, were also impressive. Pauleen Sullivan's collection is outstanding and her garden is always a treat to visit.

At 2 pm John Tallman started the palm tour of the Joe Sullivan garden at Ventura College. John has worked very hard over the last few years to develop a fine palm collection at the college. A plant raffle was held in a lecture hall and a total of $290 was raised, $218 from the raffle and $72 from a plant sale held earlier. After the raffle an informal discussion was held by Walt Fey, Don Hodel, and Ross Wagner and provided an excellent opportunity to hear three experts share valuable information and to ask questions.

A Special Meeting in October

The Southern California chapter of The International Palm Society met Oct. 16, 1983 at the home of Dr. M. E. Darian in Vista, San Diego County. This meeting was held specifically to raise money for a revolving fund, the first goal of which is to finance a 600 page work "Genera Palmarum, A Classification of Palms" by Moore, Dransfield and Uhl to be published jointly by The Palm Society and the L. H. Bailey Hortorium, Cornell University.

The Darian Garden has more palm genera than any other private garden in the United States. It has some very rare palms including the famous *Lodoicia maldivica*. A specimen of *Cocos nucifera* looks healthy after several winters; there were many beautiful *Bismarckia*, a huge *Normanbya*, many huge *Roystonea*, *Neodypsis*, *Rhopalostylis*, *Howea*, *Pritchardia*, *Basselinia*, and *Caryota*, to name only a few of the many outstanding palms in the beautiful garden.

Three hundred and five people attended the meeting—55 new members joined The Society, and a total of $3,400 was raised from the admission donation and the raffle and plant sale. The highlight of the meeting, after a delicious and elegant dinner prepared for all 305 by Mrs. Darian, was a slide presentation by Dr. John Dransfield of the Royal Botanical Gardens Kew, England and Dr. Natalie Uhl of Cornell University, N.Y.

DON SANDERS

Charles Raulerson, 1916–1983

Professor Charles Raulerson, of Jacksonville Beach, Florida, died October 2, 1983 and was interred at Arlington National Cemetery on October 7th.

Professor Raulerson was a dedicated researcher in cold-hardiness in palms, although his professional training was in one of the other of his many talents. He successfully back-crossed the well-known *Butia-Arecastrum* hybrid (Raulerson and Waas 1970) with each of the parents. The F_2 hybrid he thus produced by back-crossing with *Arecastrum* is considered the most attractive specimen palm adapted to the North Florida area by those palm enthusiasts who have observed it. Since the F_1 hybrid is at least 99.9% sterile, this was extremely tedious work. Profes-

sor Raulerson was noted for his keen powers of observation, high intellect, droll sense of humor, and gentle humility.

He was born in Perry, Florida, began his military career at Fort Myer, VA, and was promoted to Lieutenant Colonel at the age of 27 during World War II.

He served on the staff of General Douglas MacArthur in Korea, Japan and the Philippines. His decorations included two Bronze Stars, five Battle Stars and the Legion of Merit.

He graduated with a Bachelor's degree in business and economics from Harvard University in 1948 and received his graduate degrees in business management at Columbia University.

Mr. Raulerson was professor of the business-management group at Jacksonville University for 25 years.

He also served as management and personnel consultant to the Southeastern regional office of State Farm Insurance Company for 22 years and conducted management seminars for the Jacksonville Chamber of Commerce for nearly two decades.

Survivors include his wife, Dr. Marian P. Raulerson of Jacksonville; his mother, Cara M. Raulerson of Jacksonville Beach; three children, Peter Raulerson of Seattle, Washington, Brent Raulerson of Jacksonville Beach and Dena Raulerson of Alameda, California, and two grandchildren.

1. RAULERSON, C. AND WAAS, W. T. II. 1970. Some notes on palms growing in the Jacksonville area of Florida. Principes 14(3):93–96.

MERRILL WILCOX

Dent Smith Honored

Dent Smith, founder of The International Palm Society, was awarded an honorary Doctor of Science degree by Florida Institute of Technology, Melbourne, Florida, at the Commencement exercises on December 10, 1983.

Dent was cited in part for his continuing efforts to create a widespread understanding and appreciation for the palm tree, as founder and first president of The International Palm Society, and for his inspiration and generosity that helped make possible the tropical landscaping of F.I.T.'s beautiful campus and the development of its botanical garden which contains one of the finest collections of palms in the nation.

The degree was conferred upon Dr. Dent Smith by Dr. Jerome P. Keuper, President of the University and a past president of The International Palm Society.

BOOKSTORE

A MANUAL OF THE RATTANS OF THE MALAY PENINSULA (J. Dransfield 1979, 270 pp.) $25.00

COCONUT PALM FROND WEAVING (Wm. H. Goodloe 1972, 132 pp.) 3.95

CULTIVATED PALMS OF VENEZUELA (A. Braun 1970, 94 pp. and 95 photographs.) 4.50

FLORA OF PANAMA (Palms) (R. E. Woodson, Jr., R. W. Schery 1943, 122 pp.) 17.00

FLORA OF PERU (Palms) (J. F. MacBride 1960, 97 pp.) 8.00

HARVEST OF THE PALM (J. J. Fox 1977, 244 pp.) 16.50

INDEX TO PRINCIPES (Vols. 1–20, 1956–1976, H. E. Moore, Jr., 68 pp.) 3.00

MAJOR TRENDS OF EVOLUTION IN PALMS (H. E. Moore, Jr., N. W. Uhl 1982, 69 pp.) 6.00

PALEM INDONESIA (in Indonesian) (Sastraprdja, Mogea, Sangat, Afriastini 1978, 52 illustrations beautifully done, 120 pp.) 5.50

PALMS (A. Blombery & T. Rodd 1982, 192 pp., 212 colored photographs) 25.00

PALMS OF BRITISH INDIA & CEYLON (Blatter 1926, reprinted in India 1978, 600 pp.) 75.00

PALMS OF THE LESSER ANTILLES (R. W. Read 1979, 48 pp.) 8.00

PALMS OF MALAYA (T. C. Whitmore 1973, 132 pp.) 16.95

PALMS OF SOUTH FLORIDA (G. B. Stevenson 1974, 251 pp.) 7.95

PALMS OF THE WORLD (J. C. McCurrach 1960, 290 pp.) 19.00

PALM SAGO (K. Ruddle, D. Johnson, P. K. Townsend, J. D. Rees 1978, 190 pp.) 7.50

SECRET OF THE ORIENT DWARF *Rhapis excelsa* (L. McKamey 1983, 51 pp.) 3.95

SUPPLEMENT TO PALMS OF THE WORLD (A. C. Langlois 1976, 252 pp.) 25.00

THE GENUS PTYCHOSPERMA LABILL. (F. B. Essig 1978, 61 pp.) 5.50

THE INDIGENOUS PALMS OF SURINAME (J. G. W. Boer 1965, Part of Flora, 172 pp.) 42.00

THE MAJOR GROUPS OF PALMS AND THEIR DISTRIBUTION (H. E. Moore, Jr., 1973, 115 pp.) 4.50
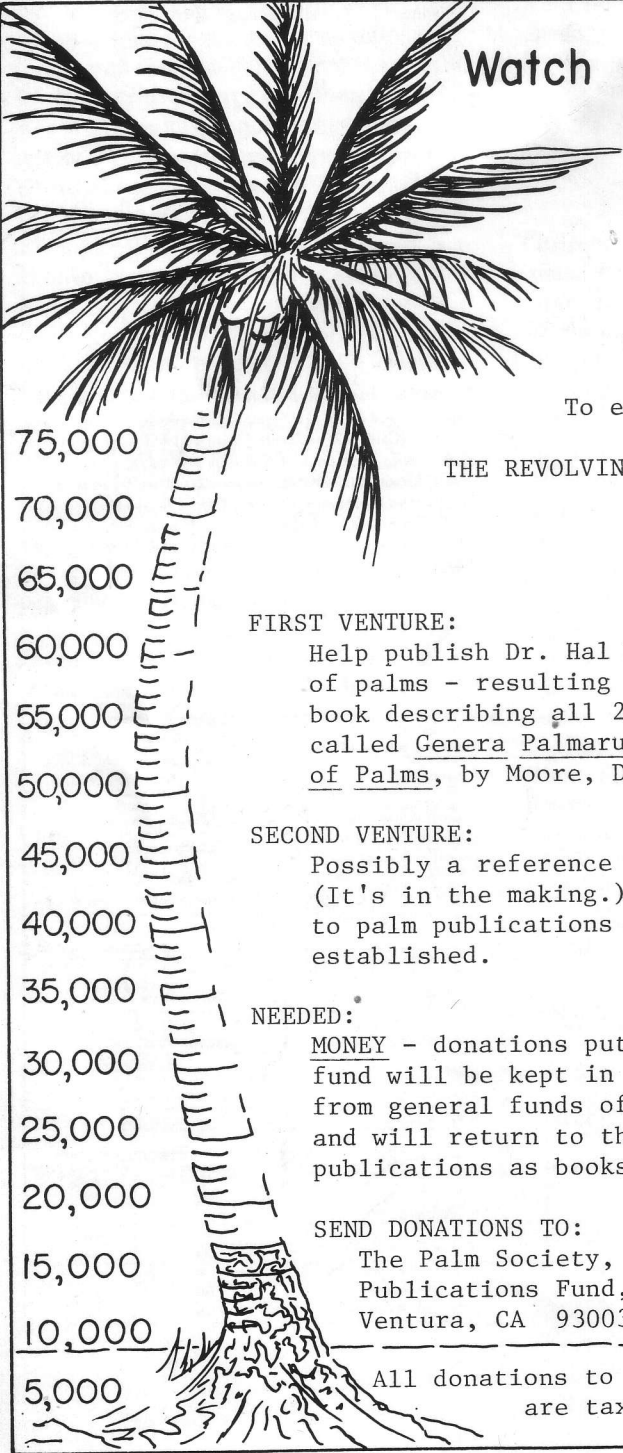
THE MINIATURE PALMS OF JAPAN (U. Okita, J. L. Hollenberg 1981, 135 pp.) 19.95

THE PALM FLORA OF NEW GUINEA (F. B. Essig, 1977, 46 pp.) 6.50

PALM PAPERS (Postage Included)

FURTHER INFORMATION ON HARDY PALMS (J. Popenoe 1973, 4 pp.) 1.25

NOTES ON PRITCHARDIA IN HAWAII (D. Hodel 1980, 16 pp.) 2.00

RARE PALMS IN ARGENTINA (reprint from *Principes*, E. J. Pingitore 1982, 9 pp., 5 beautiful drawings) 2.75

THE HARDIEST PALMS (J. Popenoe 1973, 4 pp.) 1.25

The palm books listed above may be ordered at the prices indicated plus $1.25 extra per book to cover packaging and postage. (California residents please add 6% sales tax.) Foreign checks must be in US dollars and payable on a USA bank. In some countries it is possible to send International Money Orders through the Post Office. Send check payable to The International Palm Society to Pauleen Sullivan, 3616 Mound Avenue, Ventura, CA 93003, U.S.A. ALL SALES FINAL.

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