SYSTEMATICS AND ECOLOGY OF THE PALMAE

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INTRODUCTION

Although Linnaeus named only 10 species of true palms (31) his view of the family is still accepted. Its 2800 species are still regarded as a natural and isolated group (Palmae or Arecaceae) within its own order (Arecales). No problems exist in either ascribing a plant to the family or excluding it despite superficial similarity (to *Pandanus,* cyclanths, cycads, aroids, or Agavaceae). This review attempts to show that although they constitute one of the taxonomically best-known tropical families of flowering plants, our knowledge of the true palms is still imperfect and is not yet balanced by an equal appreciation of their ecology and physiology. In view of the obvious difficulty in collecting and studying them (1) and the small number of systematists who have investigated them it is perhaps surprising that the palms are well known taxonomically.

The palms are economically important because they include major plantation crops—e.g. oil-palm, coconut, and date-palm. Numerous species have minor economic importance as sources of oil, wax, starch, fiber, sugar, and alcohol but are of tremendous importance to local commerce as sources of food, thatch, fiber, wax, oil, timber, sugar, salt, alcoholic beverages, masticatories, and stimulants. Some are symbolic in several cultures. They have considerable aesthetic value, are used in magic and folk-medicine, and are an essential ecological associate of many primitive tribes. They have become increasingly important in commercial horticulture because of their elegant and predictable shapes.

The Botany of Palms

Most recent work on the family has been directly or indirectly influenced by H. E. Moore, Jr., of the L. H. Bailey Hortorium at Cornell University,

who has supervised the collaborative effort to apply evidence from a diversity of disciplines to the classification of the Palmae. Systematically studied topics have been elaborated and extended into related fields. Examples include (*a*) systematic vegetative anatomy (68) continued to studies of vascular construction (96-98), development, and physiology (95, 97), on the one hand, and to studies of structural and eventually ultrastructural development of the phloem, on the other hand (46, 48, 49); (*b*) comparative floral anatomy (e.g. 76–79, 82) extended to a study of floral biology (60, 80, 81); (*c*) monographic study extended to ecology (55); (*d*) comparative inflorescence morphology extended to a study of plant-animal interaction (72, 80, 81); and (*e*) study of geographic distribution applied to problems of conservation (39). All of this work must be elaborated further; future directions include systematic studies of the anatomy of palm fruits (18) and extension of the foundational work done on palm pollen (63, 65, 66), work that has only begun to use scanning-electron-microscopic (SEM) techniques extensively. A survey of tracheary elements (30) provides a background for future studies of xylem transport.

Much of this recent literature has been summarized by Moore and his associates (e.g. 37, 38, 44, 80, 81). Palms are well known morphologically even though they are difficult to study by standard methods. They are usually bulky organisms, not designed for routine herbarium procedures. One has to know the palms well in order to collect representative diagnostic samples. The few modern specialists have all been field workers, appreciative of the fact that palms can be studied best as natural populations or at least in cultivation. Moore has studied living representatives of all but 18 known genera of palms, mostly in their native environments. This has led to the appreciation of these "unruly monsters" as whole organisms. Systematically orientated field work has brought back a wealth of biological information unparalleled for any other tropical group of plants. Botanic gardens with large collections of cultivated palms have played an important role because close proximity of a diversity of living specimens facilitates the extensive comparative morphological analysis necessary in systematic work. My own interest in palms dates from an opportunity to study cultivated specimens in glasshouses at the Royal Botanic Gardens, Kew, followed by periods in the Singapore Botanic Garden, the University Botanic Garden, Legon, Ghana, and finally in Fairchild Tropical Garden, Miami, Florida, where one of the largest collections of cultivated palms has been assembled. The extensive cytological work of Read (e.g. 50–56) is based on this collection, with some counts from samples air-mailed from other sources (51, 56).

The botany of palms can certainly be said to be well understood. However, there are regrettable gaps in our knowledge, and especially between

pure and applied science. Many disease problems of economically important palms remain insoluble because of a deficiency in our understanding of the genetics, physiology, nutrition, and development of palms. Knowledge of the reproductive biology of palms is still too deficient to allow predictions about the future of the many rare species of palms threatened by destruction of their habitat (39). Knowledge of the metabolic processes in palms that lead to the accumulation of starch or oil in commercially usable quantities is very small, even though such knowledge is crucial to selective crop improvement. There is, for example, no single study of starch accumulation in the stem of *Metroxylon,* an important food source (58). We have no extensive information about translocation processes in palms, even though a recent major epidemic of lethal yellowing in coconuts (see below) is the presumed result of a phloem-borne pathogen, and even though tapping a palm inflorescence is one of the most direct sources of sugar and alcohol in the tropics (e.g. 34, 75). We have insufficient knowledge of the physical properties of coconut stems to make them an economic resource (9).

Palm Literature

The taxonomic literature on the palms is very extensive and begins with the work of C. F. P. von Martius (87a), set out sumptuously in the pages of his *Historia Naturalis Palmarum* (1849–53). This was followed by the monographic series of the Italian botanist Beccari (e.g. 4–7). The recent and excellent *Natural History of Palms* by Corner (10) is much colored by his evolutionary interpretations. Regional studies may be found in (10, 43, 90, 92). The palms include many relatively small genera that lend themselves to monographic treatment. In addition to the steady stream from the pen of H. E. Moore (e.g. 40), we have treatments of *Copernicia* (11), *Johannesteijsmannia* (12), *Maxburretia* (13), *Pseudophoenix* (54), *Ptychosperma* (17), *Thrinax* (55), and studies of the geonomoid palms (91). Moore's foundational taxonomic overview has been concisely summarized (38). We await his definitive "Genera Palmarum," which is in preparation.

However, these statements should not generate complacency. Most regions in the tropics have no specialized palm literature; in most tropical countries it is impossible to get an up-to-date statement about the systematics and nomenclature of native palms. The older taxonomic literature needs bringing up-to-date. Most genera of palms have not been monographed; this includes such familiar ones as *Arenga, Caryota, Eugeissona, Euterpe, Metroxylon.* Letouzey (32) has recently called for a monographic study of the important palm *Raphia* and has pointed out some of the existing taxonomic problems. This monographic study, he emphasizes, would require a small team of botanists working throughout Africa and making field studies of

morphological and ecological details. Moore (36) indicates that 20 years of experience went into his monograph of *Synechanthus,* a genus of 2 species!

RELATIONSHIPS OF THE PALMAE

The true palms have been related traditionally to certain other groups of woody monocotyledons, notably the Pandanaceae, Cyclanthaceae, and Araceae, largely on the basis of superficial similarity which is seen to be spurious on detailed examination. In some instances the putative similarity is based on quite elementary misconception of morphological features, as that which attempts a comparison of inflorescences in Araceae and Palmae simply because the terms "spadix" and "spathe" have been used *descriptively* for the two families.

These four groups of monocotyledons are easily distinguished by a combination of gross morphological features, substantiated by evidence from other disciplines, of which that from anatomy is still incomplete.

A Conspectus of the Palmae

Plants typically with woody self-supporting aerially unbranched trunks (rarely plagiotropic), rarely aerial branching dichotomous; if scandent, never root climbers; stem branching, if present, almost always basal and never branching distally below a terminal inflorescence. Leaves 2-, 3-, or usually many-ranked; leaf base (at least initially) a closed tubular sheath, blade well-developed, on a longer or shorter petiole (or pseudopetiole) with a single midrib or rachis; the blade plicately folded with a marginal nonplicate strip, usually split partly or completely into leaflets (pinnate leaves) or leaf segments (palmate leaves). Shoots usually pleonanthic, but hapaxanthy (sometimes leading to monocarpy) occasional. Flowers sometimes perfect, but usually diclinous by abortion and plants monoecious or dioecious. Lateral inflorescences (or first-order branches of terminal inflorescences) typically much-branched with a basal prophyll and one or more enlarged basal (but never petaloid) bracts, the distal bracts reduced. Axis rarely unbranched as a true spike (= spadix). Single inflated (sometimes woody) enveloping bract (= spathe) if present never on the trunk axis. Flowers either solitary or more usually aggregated in 2s, 3s, or more, the aggregations commonly representing condensed cincinni. Flowers usually trimerous (rarely dimerous or polymerous) with a well-developed floral envelope (the envelope rarely vestigial or absent). Flowers typically with 3, 6, or sometimes more numerous stamens, gynoecium apocarpous with 1–3 carpels or more commonly syncarpous with 3 (sometimes more) locules each with 1 functional ovule, 2 locules and ovules sometimes aborted. Fruit almost always indehiscent, baccate, or drupaceous 1–3– several-seeded, the

pericarp woody, fleshy or fibrous, the endocarp sometimes thick and woody. Endosperm abundant (usually of hemicellulose), embryo small, germination hypogeal.

Stem vascular bundles always simple, collateral with 1–2–numerous wide metaxylem vessels. Stegmata (unequally thick-walled isodiametric cells), including a spherical or hat-shaped silica body common next to fibers in all parts except roots. Latex, mucilage, trichosclereids, lysigenous air-lacunae or secretory cavities not developed.

Araceae, Cyclanthaceae, Pandanaceae

These families differ in fundamental ways, each showing a different set of diagnostic characters. The following are suggested major differences between them and palms:

Plants typically branched aerially, either as linear sympodia below terminal inflorescences (Chamberlain's model, as in many Araceae and Cyclanthaceae) or with branched sympodia (Leeuwenberg's model, Pandanaceae) or with sympodial branches on a monopodial trunk (Scarrone's and Stone's model, some Pandanaceae). Root climbers common (e.g. Araceae, Cyclanthaceae, *Freycinetia* in Pandanaceae). Leaves usually few-ranked, or spirally 3-ranked in Pandanaceae; 4-ranked in *Sararanga*. Leaf sheath apparently always an *open* tube, the blade either lanceolate, folded, and little differentiated (Pandanaceae) or if with a differentiated blade, the blade rolled in bud (Araceae), or if multi-plicate without conspicuous marginal strips and usually with 2 or more major ribs (Cyclanthaceae). Shoots most typically hapaxanthic, the terminal inflorescence unbranched and usually a true spike, with a dense aggregation of flowers (spadix) or least commonly a branched system terminating in such axes (Pandanaceae), with one or more, often petaloid, bracts on the main axis below the flower, or in the Araceae with a single often conspicuous or enveloping bract (spathe) in this position. Flowers without protective envelopes, or perianth reduced (some Araceae, Pandanaceae); flowers dimerous, trimerous, or tetramerous (as in Cyclanthaceae and some Araceae) usually with few stamens (sometimes synandrous in Araceae) or the stamens terminating branching structures (Pandanaceae) or numerous in Cyclanthaceae. Carpels various, uni- or multiovulate, gynoecium commonly syncarpous (e.g. Pandanaceae), the fruit either fleshy in various ways or apparently secondarily drupaceous in Pandanaceae, sometimes dehiscent. Seed reserve various, starchy, oily or hemicellulosic.

Stem with either simple vascular bundles (and then either collateral, with 1 or more wide metaxylem elements, or amphivasal) or frequently with compound vascular bundles resulting from a complex regular or irregular association of simple bundles. Crystals, latex, mucilaginous or secretory

lysigenous or schizogenous cavities and trichosclereids of great diversity, but siliceous stegmata not observed.

The morphological nature of the reproductive organs in the Cyclanthaceae and especially Pandanaceae has not been fully resolved so that some of my statements may be controversial. However, the principles of construction in Palmae seem different. The flowers and inflorescence of the Araceae seem relatively easy to interpret in typological terms; they differ from those of palms in never being aggregated in complex ways, and for aroids the terms "spathe" and "spadix" have the most consistent descriptive applications.

These data must be elaborated more fully because considerable morphological variation exists within each family; but the basic conclusion, that the Palmae stand apart from the other 3 families, is not likely to be challenged.

The palms thus stand in no close relation to any one group of monocotyledons, and accepting them as a monotypic order best expresses this in conventional systematics. Certain Cyclanthaceae probably approach the palms closest in details of leaf morphology but still can be distinguished (93); the similarity may reflect parallelism in view of the numerous other differences between palms and cyclanths.

With the exception of Hutchinson (29), no one has emphasized a possible systematic relation between palms and woody Liliflorae. Although there are frequent similarities (or parallels) the Agavaceae are certainly unlike the palms in their simple unplicate leaves, secondary thickening, petaloid and often tubular flowers, frequent inferior ovary, and multi-ovulate carpels. Perhaps the closest similarity could be drawn between palms and certain members of the Australian assemblage, the Xanthorrhoeaceae, an unnatural family based primarily on geographical juxtaposition of its species. *Kingia* and *Dasypogon* are quite palm-like in their anatomy but have linear or lanceolate simple leaves. The anomalous rush *Prionium* (Juncaceae) has the appearance of a diminutive palm. The Strelitziaceae have an appreciable range of habit that parallels that in palms but are very different in floral morphology. I do not wish to emphasize arborescence as a basis for phyletic reasoning but do point out that there are possible candidates for palm relatives among other groups of monocotyledons as well as the traditionally maintained palm associates like pandans, aroids, and cyclanths. It seems that these alternatives are simply less familiar.

SUBDIVISION OF THE PALMAE

Since the time of von Martius, clearly circumscribed subgroups within the Palmae have been recognized with continuous and progressive refinement by successive specialists. Hierarchical rankings have varied, but the usual

principle has been to recognize subfamilies and tribes. Currently Moore (38) recognizes 15 unranked "major groups" that are readily comparable to the taxa formally treated in earlier accounts. The essential features of these groups are set out in Table 1.

The assemblages vary in size from the monotypic nypoid group (*Nypa fruticans*), podococcoid group [*Podococcus barteri* incl. *P. acaulis* (32)], and oligotypic pseudophoenicoid to the arecoid alliance with over 700 species; the larger groups are capable of further subdivision.

The classification relies initially on gross morphological features—e.g. the orientation of the leaf plication that distinguishes induplicate ($\smile$) from reduplicate ($\frown$) groups. Small as this difference may appear, it seems to reflect the two alternative fundamental pathways in leaf development, a dichotomy even more basic than the degree of rachis extension, which produces either fan or feather leaves based on a single plan. Beyond this, characters of inflorescence, flower association, sex distribution, and flower and fruit structure are variously used.

The subdivision based on morphological evidence continues to be substantiated by evidence from other disciplines. Vegetative and floral anatomy has been particularly supportive (e.g. 38, 46, 68). Diagnostic features of leaf anatomy have been pursued even to the specific level (25, 40). Now that cumbersome and often misleading terminology of older authors has been replaced by a neutral, descriptive, and minimal set of terms (72), information of taxonomic value has been derived from a study of inflorescence morphology. Frequently the major groups have a distinctive and fairly constant kind of inflorescence morphology, an aspect revealed only by dissection of entire palms. The palm inflorescence provides material for comparative study that reveals probable phyletic trends of inflorescence elaboration, frequently paralleled in different groups (e.g. 22). Among the trends that can be recognized are: progressive reduction in number of branch orders, so that the spike or spike-like axis is a derived condition (not fundamental, as in aroids); progressive reduction in the number of large, proximal bracts, leading to inflorescences with few, 2, or even a single basal enveloping bract; and progressive sexual specialization of different parts of one inflorescence, and of different inflorescences of a single plant, and ultimately (in the dioecious state) of different plants. Aggregations of flowers on ultimate inflorescence axes are diverse and variable. Detailed studies of ultimate flower aggregations and of floral anatomy and development have provided information of taxonomic value and have led ultimately to a greater appreciation of features of pollination ecology (see below).

At the generic level there are many homogeneous and distinct genera (e. g. *Borassus, Copernicia, Metroxylon, Roystonea, Sabal*) or aggregations of genera (e.g. within the coryphoid palms), but generic limits are still

uncertain in some groups (e.g. *Syagrus, Attalea,* certain iriarteoid taxa). Future field work and more intensive morphological analysis will continue to reveal undiscovered genera (41, 42) and so will undoubtedly refine the classification of palms; the outline is certainly substantial and clear but needs extensive infilling.

Table 1 The major groups of palms and their characteristics[a, b]

Group	Geographical distribution	Sex distribution	Number of taxa (Genera/species)	Leaf morphology	Distinguishing features
Induplicate — Leaved Palms					
Coryphoid (n = 18)	Pantropical	Hermaphrodite, (monoecious) (dioecious)	32/322	Palmate (Costapalmate)	Many-bracted branched inflorescences
Phoenicoid (n = 18)	Old World (Africa–Indo-China)	Dioecious	1/17	Pinnate	Basal leaflet spines
Borassoid (n = 14, 17, 18)	Old World (Africa–New Guinea)	Dioecious	6/56	Palmate	Thick inflorescence axes
Caryotoid (n = 16, 17)	Old World; eastern tropics	Monoecious	3/35	Pinnate (Bipinnate)	Hapaxanthic basipetal flowering; toothed leaflets
Reduplicate — Leaved Palms					
Nypoid (n = 17)	Ceylon to New Guinea and Ryukyu Ist	Monoecious	1/1	Pinnate	Rhizomatous, saline estuarine swamps
Lepidocaryoid (n = 14)	Pantropical; mainly eastern tropics	Monoecious	22/664	Pinnate (rarely palmate)	Scaly fruits
Pseudophoenicoid (n = 17)	New World (Caribbean)	Hermaphrodite (polygamous)	1/4	Pinnate	Single bract pseudopedicel
Ceroxyloid (n = ?)	Disjunct (S. America, Indian Ocean)	Dioecious	4/30	Pinnate	Diverse
Chamaedoroid (n = 13, 14, 16)	Mainly New World; plus Mascarenes	Monoecious Dioecious	6/146	Pinnate	Diverse
Iriarteoid (n = ?)	New World; Tropical America	Monoecious	8/52	Pinnate	Frequently stilt-rooted
Podococcoid (n = ?)	West Africa	Monoecious	1/2	Pinnate	Leaf morphology Elongated fruit
Arecoid (n = 16, 18)	Pantropical	Monoecious	88/760	Pinnate	Crown shaft frequent
Cocosoid (n = 15, 16)	Tropical America (South Africa)[c]	Monoecious	28/583	Pinnate	Bony endocarp with 3 pores
Geonomoid (n = 14)	Tropical America	Monoecious	6/92	Pinnate	Flowers in pits
Phytelephantoid (n = 16)	Tropical America	Dioecious	4/15	Pinnate	Numerous stamens per flower, fruits in heads

[a] After (38)

[b] The characters listed are generalized and there may be exceptions. Horizontal lines suggest major discontinuities

[c] The natural range of *Cocos* into the Asian tropics is a disputed topic.

GEOGRAPHICAL DISTRIBUTION OF PALMS

Information about the geographic distribution of palms has been summarized by Moore (37). There are a few widely distributed or large genera of palms. The average number of species per genus is only 13 [2779 spp., 212 genera (38)]; 73 genera are monotypic. More than half the genera of palms have 5 or fewer species. Thus it is not surprising to find a high degree of endemism; in the South Pacific, each island or island group has its endemic species and often genera. Continental Africa is poor in palms, with about 50 species, a number much exceeded by adjacent Madagascar (115 spp.), which has 12 endemic genera. New Caledonia (30 species) represents an extraordinarily rich center of endemism; no less than 17 genera of palms are limited to the island (42).

The large size and wide distribution of a few palm genera, notably *Calamus* (370 spp.) and *Daemonorops* (115 spp.), suggests recent adaptive radiation. *Chamaedorea* (133 spp.), *Licuala* (108 spp.), and *Pinanga* (120 spp.) are also large genera, but they are exceeded in geographical range by a number of moderate-sized or even small genera like *Borassus* (7 spp.), *Hyphaene* (41 spp.), *Phoenix* (17 spp.), and *Raphia* (28 spp.). Dioecious species tend to be wide-ranging.

The otherwise generally restricted range of palms makes it relatively easy to define floristic regions and is further reflected even in the range of the major groups. There is a marked dissimilarity between the palm floras of the Old and New World. The iriarteoid, geonomoid, pseudophoenicoid, phytelephantoid, and cocosoid palms (with 3 exceptional genera in the last group) are entirely New World. The phoenicoid, caryotoid, borassoid, nypoid, and podococcoid palms are all Old World. The lepidocaryoid palms are also Old World except for *Lepidocaryum, Mauritia,* and one species of *Raphia* in the New World. Ceroxyloid and chamaedoroid palms both have a disjunct distribution in New and Old Worlds. This leaves only the coryphoid and arecoid with an essentially pan-tropical distribution. At the generic level only two palms have ranges that span the Atlantic (*Elaeis* and *Raphia*).

THE HABIT OF PALMS

Growth Limitations

Current knowledge of the growth-form of palms can be set against our recently increasing knowledge of the architectural diversity of tropical trees (27). This knowledge is often relevant to an understanding of the ecological role of palms.

Palms are growth limited (28) because they have no secondary vascular cambium and so lack any mechanism for secondary increase of vascular

tissue; they do have a limited capacity for diffuse secondary growth (68) not dependent on meristematic activity but sometimes so localized at the base of the trunk as to be mechanically useful (88). The fixed primary conducting and mechanical ability of the trunk accounts for the fixed crown size. Palms normally remain unbranched above ground simply because they either lack completely any lateral vegetative meristems or such meristems are restricted to the base of the stem. *Serenoa* is exceptional in that there are vegetative lateral meristems interspersed among the inflorescence axes along the stem, but the axes are usually creeping (23). Other irregularities of branching in palms have been described and discussed by Fisher (19–22).

In the terminology of Hallé et al (27), palms are thus precisely model-conforming. This precise growth programming suggests that they might be restricted to climatically and microclimatically predictable environments. They seem to be restricted to tropical and subtropical environments primarily because vegetative growth is essentially continuous and they lack dormancy mechanisms. Few palms can withstand extended freezing temperatures. The hardiest palm is probably *Rhapidophyllum hystrix,* ranging from central Florida to Alabama and Georgia.

Establishment Growth

The development of a massive trunk and crown from an initially narrow embryonic axis is dependent on a preliminary phase of "establishment growth" (74) in which successive internodes are progressively wider as the primary thickening meristem becomes progressively more massive. The seedling axis in palms (indeed in all monocotyledons) is thus obconical. This is evident only in stilt-palms (e.g. many iriarteoid palms) in which the seedling internodes are elongated and above ground, but supported by a series of progressively wider stilt-roots. This phase of development is evidently critical in the successful establishment of the palm, and several developmental modifications have evolved to render it more efficient. This usually results in a burying of the plumular axis, with the axis developing to its maximum diameter underground. In several genera (e.g. *Diplothemium, Rhopalostylis, Sabal*) the seedling is saxophone-shaped. The plumule initially grows obliquely downward but is reorientated quite abruptly into an erect position. The distribution of this juvenile morphology in palms is not known. The diversity of establishment processes in woody monocotyledons generally is even greater than in palms (71).

Palm Architecture

Within the considerable limits imposed by these constraints, palms achieve an appreciable diversity of growth habit. Nevertheless, only 4 of the 23 models recognized in the Hallé-Oldeman system (27) can be identified (i.e. the models of Holttum, Corner, Tomlinson, and Schoute). Holttum's model

is uncommon and refers to palms like *Corypha* and most *Metroxylon* spp., which are vegetatively unbranched and consist of one hapaxanthic axis (i.e. the vegetative axis ends in a terminal inflorescence). Corner's model is common and represents single-stemmed palms with lateral inflorescences. Both these models are distinctive among trees because the whole tree is programmed by a single vegetative shoot meristem, and reiteration does not occur. Tomlinson's model refers to multiple-stemmed palms—i.e. palms that circumvent growth restrictions by branching basally, each new trunk developing an adventitious root system. Tomlinson's model is the most versatile as well as commonest among palms. Species vary much in overall stature; axes may be partially plagiotropic or rhizomatous at the base, or scandent distally, and may or may not flower terminally. Schoute's model is rare since it includes trees with apical dichotomy of the vegetative axis, which may be erect as in species of *Hyphaene* or horizontal as in *Nypa* (70). Dichotomy here seems derived and not primitive; in *Hyphaene* the size of crowns is progressively reduced at each bifurcation so that the transport and mechanical limitations of the initial trunk axis are not exceeded; in *Nypa,* dichotomy permits proliferation of lateral-flowering plagiotropic axes that have presumably lost their ability to produce axillary vegetative meristems.

Scandent Palms

Lianescent palms have usually slender axes, with very long (up to 2 m) internodes, supported by grapnels that may be hooked extensions of the leaf rachis or inflorescence axis, the hooks either modified and backwardly directed terminal leaflets, as in *Desmoncus,* or clusters of spiny appendages like cat's claws. In most *Calamus* species, the inflorescence is reduced to a flowerless unbranched flagellum, partly adnate to distal organs (21). The scandent habit has evolved independently in the New and Old World and in different groups, chamaedoroid, cocosoid, and lepidocaryoid. These lianes are usually rhizomatous, although individual axes may be hapaxanthic. *Plectocomia* is exceptional since it is monocarpic (Holttum's model). Scandent palms represent a very successful elaboration of the palm habit; *Calamus* and *Daemonorops* are the two largest genera of palms and are associated with a number of satellite rattan genera. However, this group of palms is in need of taxonomic revision. Juvenile and adult phases are often markedly contrasted in morphology and the plants may be dioecious. Collections are often mixed, and specimens are so spiny that they are awkward to handle. This group is an important source of canes, the basis of a minor industry in Malaysia.

Ecologically rattans are weedy, often characteristic of wet and disturbed sites in the forest but readily persisting into communities with closed canopies. Do tropical vines "grow up" or are they "carried up" into the canopy?

A single rattan may well do both, developing as a juvenile plant in a gap and exploiting the enlarging canopy that closes the gap, subsequently persisting in the closed canopy by throwing up new axes from a permanent, branched rhizome system. Whether we view rattans as the curse of the forester, the pride of the cane merchant, or the puzzle of the ecologists, they certainly represent a biologically fascinating group of palms.

ECOLOGY OF PALMS

Palms occupy a diversity of habitats at different altitudes (especially in South America), are absent from truly xeric environments, and show a strong predilection for wet habitats (where they may be dominant) (37). Because some seem especially characteristic of disturbed sites, the term "weedy" may be applied—notably to *Euigeissona tristis* in Malaya, since its development inhibits forest regeneration (14). Dransfield (14) estimates that 75% of palms are rainforest species, but their great diversity of habit in the forest understorey suggests an appreciable diversity of ecological roles. The association among habit, physiology, and edaphic preference still remains virtually unexplored for palms. However, even though palms are a relatively minor component of the total forest biomass, they can be an important determining factor in forest composition because of their likely competitive interaction with canopy components when these are at sapling stages (84, 86) and can have a special influence on the soil profile (24). Bannister (2) concludes that *Euterpe globosa* (correctly *Prestoea montana*) is a normal component of "climax" forest vegetation in Puerto Rico, but the mosaic nature of succession in tropical forests suggests that palm species may have particular light-demanding attributes that make a linear "successional" concept seem too simplistic. Vandermeer et al (86) suggested that the populations of *Welfia, Socratea,* and *Iriartea* that they studied in Costa Rica have a cyclic interaction with the physical factors of their understorey forest environment. The physical environment (chiefly light patterns determined by gap size and regeneration phase) dictates the survival potential of these populations, which in turn determines the pattern of light within the environment. Somewhat similar conclusions are suggested on a more intuitive foundation in the study by de Granville (26) of the rôle of palms and other monocotyledons in the forest vegetation of French Guiana. In certain forest types he suggests that the forest understorey may become dominated by a single species—e.g. "astrocaryosed" by the dominant tendency of *Astrocaryum paramaca,* as also with *A. sciaphilum* in Suriname. Similarly, *Astrocaryum mexicanum* provides the characteristic feature of the forest understorey in Veracruz, Mexico (59). Palms thus seem a particularly representative group of organisms to study in relation to canopy-understorey interactions in tropical forests.

Palms in open sites tend to compensate for lack of species by large numbers of individuals. They frequently dominate the vegetation particularly of wet edaphically limited sites. The marked tendency of palms to make aerial root pneumatophores seems adaptive in this respect (26). Genera that characterize swamps include *Manicaria, Mauritia,* and *Raphia* in South America; *Phoenix* and *Raphia* in Africa; and *Metroxylon, Nypa,* and *Salacca* in Asia. The list of palm taxa in wetter tropical habitats is quite long (37). Palm habit in relation to habitat has been discussed most recently by Dransfield (14), and the contrasted biotope exploration of single-stemmed versus multiple-stemmed palms has been illustrated by de Granville (26). The difference in architecture between Holttum's, Corner's, and Tomlinson's model (27) in terms of overall size, root volume, detritus recycling, floral phenology, and breeding mechanism still remains unexplained. The difference between palms that do or do not sucker is usually quite clear, but the relative benefits of the two life-styles are not obvious.

Palm savannah is a common vegetation type in which the palm is the only tall tree. Examples in all three major tropical regions variously have species of such genera as *Borassus, Copernicia, Hyphaene,* and *Sabal* as the conspicuous element; but again the palms more frequently inhabit wet sites or those that are seasonally flooded. *Elaeis* is considered an aboriginal inhabitant of gallery or fringing forest in West Africa, but its range and habitat have been much broadened by human distribution (32). The most obvious feature of palm construction (the absence of secondary thickening) promotes fire-resistance and accounts for their frequent abundance in fire-climaxes (e.g. *Serenoa* associated with pines in Florida). However, the association between palms and fire has never been scrutinized very fully. Dransfield (14) cites the suggested example of *Hyphaene compressa* in East Africa; because of its branched crown (Schoute's model) it provides a nuclear site for forest regeneration in areas of savannah maintained by burning.

These brief comments about palm ecology show that the physiological basis for the ecological preferences of palms is not understood. The needed research might well study physiological tolerances of individual palm species first in artificially controlled environments and then in field circumstances.

Demography of Palms

Palms provide ideal subjects for demographic studies on woody plants because they are easily recognized and counted. Age determination is considered easy as compared with tropical trees in general because leaf scars are obvious and more or less permanent; rates of leaf production can be determined over a limited period and extrapolated to the total life span of the tree (59, 83). An estimate for the period of establishment growth is also

necessary. This can be provided by an examination of a seedling population, which in time also provides the initial entry into life tables and survivorship curves. Care is needed in applying extrapolated values since growth rates of individual palms vary enormously. And in the enthusiasm for extended analyses one must not forget the assumptions made. The extended observations of Waterhouse & Quinn (88) on *Archontophoenix* are unique in the literature on palms and provide a demonstration of the way in which diffuse secondary growth of palms can be long continued, bringing about age-dependent changes inexplicable in terms of a simple analysis of a size table (e.g. that tall trees are wider at the base, even though they have no vascular cambium, and that taller trees have longer internodes). The close dependence of morphological, demographic, and phenological analysis is well demonstrated in this study.

Sarukhán (59) has provided a population flux model for *Astrocaryum* into which data can be progressively inserted as they are accumulated. His preliminary survivorship plots show the expected concave curve, and it is suggested that older trees in a population make the greatest reproductive contribution to a population. The life span is apparently determined by accident rather than senescence. Van Valen's reconstruction of a life table for *Prestoea montana* (83) based on Bannister's observations in Puerto Rico (2) adds further assumptions but seems comparable to the results obtained for *Astrocaryum* in a number of respects. It is also interesting that the reproductive potential of *Prestoea* (Corner's model) in terms of seeds produced per individual in relation to life expectancy (a tree entering the canopy has a future life expectancy of 70 years or 350,000 seeds) is quite comparable to that of *Corypha* (Holttum's model), in which an adult palm 44 years old was estimated to have produced 250,000 seeds in its single flowering (73).

The suitability of palms for biomass measurement is also demonstrated in Van Valen's analysis. In most palms either the individual parts are few and discrete (trunks and leaves) or they are produced in conveniently sized and easily harvested units (fairly large seeds on lateral inflorescences) (87). It is estimated for *Prestoea* that reproduction uses about 5% of net photosynthesis, compared with 15–22% in *Corypha*; these values, however, are based on a population and an individual, respectively. The values, crude as they are, still suggest that Holttum's model is the more efficient producer of seed meristems. The possibility for elaborating this kind of analysis is extensive, and palms may well play a major role in developing demographic theories about tropical trees.

Palms and Predators

Because palms have little regenerative ability (in the simplest situation one vegetative meristem functions throughout the life span) they are peculiarly

vulnerable to predator attack; destruction of the one apical meristem destroys the whole tree. Uhl & Moore (80) have discussed this problem with reference to mechanisms that, directly or indirectly, protect pollen and ovules. The discussion may be extended to the ways in which the survival and reproductive potential of palms in the vegetative state may be affected by predators.

Wilson & Janzen (94) have provided information about seed mortality in *Scheelea rostrata,* where 80% of the seeds produced may be destroyed by a single species of bruchid beetle larva. This is an extreme example of the predispersal seed predation to which palms in general seem highly susceptible because of their phenology, seed size, and method of dispersal (85).

The apical meristem is protected primarily by its enclosure within the terminal crown of leaves; the youngest parts of the developing leaves are protected in the same way because they grow from basal meristems. Outer protection is provided by an enveloping series of leaf sheaths, which may become massive and woody (e.g. many coryphoid, cocosoid, and borassoid genera). The crownshaft of many arecoid palms results because most expansion is accommodated by growth; the tubular leaf base dehisces along precisely determined separation regions. In many palms the mechanical protection of the crown is frequently supplemented by prickles or similar sharp appendages.

The inflorescence is initially protected within the crown, especially by its own subtending leaf if it is lateral. It may not be exposed until this falls, as in most palms with a crownshaft. The expanding inflorescence axes, whether they protrude through the mouth of the subtending leaf, pierce its dorsal surface via a dorsal suture, or wait until the leaf falls, are themselves protected by one or more sometimes woody bracts. In the simpler situation enveloping bracts are many, the inflorescence has several orders of branching, each with associated bracts, and ultimate flower-bearing axes are unspecialized. In presumably derived inflorescences the number of bracts become few, or even one; basal bracts become large and assume the major protective function; ultimate bracts become vestigial; and the flowers are often aggregated and variously protected, as by overlapping distal bracts or by the margins of the pits into which the flowers are sunken.

Direct protection of the sex organs is provided by the floral envelope, which is rarely petaloid. Thick, hard imbricate or tightly valvate perianth segments are very important in palms, which, because of functional dioecism, retain exposed flowers of at least one sex for a considerable time. Uhl & Moore have demonstrated a diversity of structural and biochemical features likely to discourage chewing insects. There are trichomes, fibers, tannins, sclereids, raphides, and silica bodies. Carpels are protected because they mature basipetally, with many of the unpalatable structures in the apical parts (80). The same features also apply in the developing fruit, which

at maturity may be attractive to animals via a colored pericarp. A stony endocarp or bony endosperm frequently protects the small embryo.

Poisonous secondary metabolites are not usually developed in palms, wherein lies one reason for their great value to man.

POLLINATION ECOLOGY AND BREEDING MECHANISMS

The early and entirely theoretical view that palms are exclusively wind-pollinated because they have "reduced" flowers has been supplanted by field observation, which shows that although wind-pollination does occur in a diversity of palms, methods of pollen transfer involving animals are not only frequent, but diverse (60). However, few examples have yet been studied in detail, and generalizations about whether palms are primitively anemophilous or zoophilous seem premature. Uhl & Moore (81) have presented a series of case histories based on a summation of field observation and an intimate knowledge of flower structure. This sets a standard for the much needed field and laboratory examination of flower function in palms. Flower distribution in palms is diverse; dicliny is the most common arrangement, with frequent marked size differences between male and female flowers.

Dioecy

Dioecy with obligate outbreeding is found throughout the borassoid, phoenicoid, and phytelephantoid palms, in some chamaedoroid and lepidocaryoid palms, but rarely elsewhere. It may be associated with wind-pollination, as in the phoenicoid palms (in *Phoenix dactylifera,* the date palm, it has been known since pre-history). The syndrome of characters related to wind-pollination includes abundant powdery pollen and synchronous and short-term flowering of numerous and relatively well-exposed flowers. The correlation between wind-pollination and dioecy is not fixed, since *Thrinax,* with perfect flowers, is wind-pollinated (55). *Cocos* is a good example of a predominantly wind-pollinated monoecious palm; some borassoid palms, on the other hand, have septal nectaries (79).

Monoecy

Monoecism is much the commonest condition in palms, being almost universal in the arecoid line, but the distribution of male and female flowers is variable. There may be separate male and female inflorescences in a single tree, as in *Elaeis* and some other cocosoid palms; or male flowers distally and female flowers proximally on a single inflorescence, as in *Cocos;* but most commonly the two kinds of flowers are closely aggregated, as in diads, triads, cincinni, or in linear series (acervuli). Such aggregations may still

function in outbreeding because the different sexes mature at different times, often without overlap. In most coconut varieties outbreeding is virtually assured since there is usually only one inflorescence with functioning male or female flowers at one time. In caryotoid palms the separate sexual phases of one inflorescence are widely separated in time, but there may be overlap between different phases of one trunk. The existence of this chronological sexuality has to be appreciated by the collector. In multiple-stemmed palms, the advantages of sexual phases may be lost since the behavior of different trunks is nonsynchronous.

Perfect Flowers

Palms with perfect flowers are in a minority, and this condition may be associated with polygamy (e.g. *Pseudophoenix,* some coryphoid palms). Selfing is possible and indeed may be an essential feature of reproductive strategy. Thus *Corypha* has perfect flowers, but is evidently self-compatible, as indicated by the abundant fruit set of isolated cultivated individuals (73). Abundant seeding would seem to be important in this monocarpic species. Outcrossing in natural populations could then only occur between synchronously flowering individuals, but even this is minimized by the short flowering period (3 weeks). We lack detailed information about other monocarpic palms like *Raphia* and *Metroxylon.*

Breeding Mechanisms

Protogyny as an outbreeding device is known. *Nypa* is visited by a variety of insects but is said to be pollinated by drosophiloid flies that use the fleshy male axes as breeding sites (16); *Bactris* is apparently pollinated by nitidulid and curculionid beetles (15); *Hydriastele* is visited by bees, small flies, and weevils, the latter the most likely pollen visitors (16). In *Nypa* the protogyny is determined by the inflorescence structure, since the terminal aggregate of female flowers on the main axis becomes receptive before the male flowers are exposed on lateral branches. Pollen is sticky (probably related to its distinctive spinous morphology) and could not be transported by wind. *Bactris* and *Hydriastele* are protogynous because the female flowers of the triads are all receptive first. Individual flowers in *Sabal palmetto* are protogynous because stigma receptivity precedes anther dehiscence by at least 2.5 hr (8).

Protandry is recorded for *Asterogyne,* with pollination by syrphid flies (60), and is shown in *Ptychosperma,* visited by syrphid flies and *Nomia* bees. Among the insect attractants recorded for palm flowers are abundant pollen, nectar, odor (either sweet or foetid), and conspicuous aggregations of flowers, commonly against a dark background. Heat emission, which occurs in *Bactris* (61), may be an attractant. Bees are common visitors to palm

flowers, as can be seen in cultivated specimens. The need to discourage the unwanted visitor seems real enough . However, the biology of the palm inflorescence may be very complex. In *Bactris gasipaes* (peach palm) a succession of visitors occurs—beetles, drosophilid flies, bees, and moths— so that it is not clear which insect is the effective pollen vector (J. Beach, personal communication). Information of this kind is needed for other palms of potential economic importance.

ECONOMIC ASPECTS

Justification for continued and even intensified study of palms resides in their economic importance. Much still needs to be done with major crops, as is shown later, but the value of minor palm products in local economy is often underestimated. Where palms of local value enter into world trade, their products become subject to world market fluctuations, they may not compete well against plantation products with highly efficient marketing procedures, and they may not provide the stable income a grower would need if he were to exploit them effectively.

Sago

The trunk starch of *Metroxylon saga,* one source of commercial sago, illustrates the problem well (58). Palm sago from this source (mainly Sarawak) has never competed well with other sources of starch. Nevertheless this palm is locally important both as a staple for local consumption and as a trade material, particularly since it grows in large natural populations in swampy habitats otherwise unsuited to cultivated crops. However, there has been no modern revision of the genus, its reproductive biology has been little investigated, and neither its ecology nor its physiology has been explored in useful detail. All these factors would be involved in selection for yield improvement, successful plantation cultivation, or management of wild stands for sustained high yield.

Pejibaye

The edible fruit of *Bactris gasipaes* (*Guilielma gasipaes*), a food crop of growing importance, has fared somewhat better at the hands of agronomists; there is an extensive literature on this palm (G. Hartshorn, personal communication). The biggest need is a careful assessment of high-yielding varieties and likely pest problems. For this, knowledge of reproductive biology and the physiology of fruit development is needed. Part of this study should certainly involve a detailed study of the other *Bactris* species, which are frequent in tropical America and evidently diverse.

Lethal Yellowing

Of the numerous diseases of tropical crops none has more spetacular effects than lethal yellowing decline of coconuts, which will destroy a healthy palm within six months of the appearance of the first visible symptoms. This disease reached epidemic proportions in the Caribbean in the 1960s. In Jamaica, where coconuts are a major factor in the economy, losses due to lethal yellowing of up to 100,000 trees a year have been regular. An outbreak in the Miami area (where the coconut is only of ornamental value) brought it to the attention of a large urban population. The establishment of a research team by the University of Florida accelerated the rate of existing research. An International Council on Lethal Yellowing now meets on a biennial basis to report progress of the effort to combat the spread of the disease and find a cure (57).

Present knowledge implicates a phloem-inhabiting mycoplasma-like organism (MLO) as the pathogen (3, 47), but the method of spread of the disease remains unknown at the time of writing. No artificial transfer of the disease has been obtained. Remission of disease symptoms has been obtained by injecting individual palms with massive doses of antibiotics; but this is not a solution to the problem on a plantation scale and is a procedure probably detrimental to the whole research effort, since it may select resistant strains of the pathogen. The future of the coconut industry is currently dependent on the existence of varieties of coconut resistant to the disease. One aspect of research effort is a breeding program that should generate high-yielding resistant coconut varieties.

Lethal yellowing impinges on our knowledge of the taxonomy of palms. The disease is known in other species; at least other palms in infected areas die with symptoms like lethal yellowing and recognizable MLO in the phloem (67). This knowledge has been obtained in South Florida where the many species of palms in cultivation have been exposed to the disease. So far putative susceptibility has been demonstrated in 23 species representing a diversity of groups. Most of the palms are only of immediate horticultural value, but the commercial date is on the list and there is a reason to suspect cultivated *Nypa fruticans* may have succumbed to the disease.

Susceptibility to the disease thus has a peculiar taxonomic distribution. The pathogen distinguishes between different cultivars of one species, between closely related genera and species, but not between groups. The genetic basis for susceptibility or resistance is thus not clear and may depend on the behavior of an as yet unknown vector.

Current quarantine precautions are intended to contain the spread of the disease, but outbreaks in other major coconut growing areas, such as India,

the Philippines, and the South Pacific would constitute an international disaster, such is the dependence of large populations on this palm. The possibility that the disease could affect other commercial palms is alarming.

CONCLUSIONS

I have been able to present only a sampling of a rich, recent literature. There is a firm systematic foundation, surprisingly complete in view of the small number of scientists who have specialized in the group; this needs to be strengthened by continued extensive field work. In contrast, understanding of ecology and reproductive biology—to which may be added most aspects of development and physiology—remains deficient. This deficiency is serious in view of the dependence of applied research on basic knowledge.

The palms remain one of the most economically important groups of tropical plants, a major source of food and raw material that remains under-explored; they certainly increase the chances of survival for people in tropical developing countries.

Most of the fundamental research on palms has been provided by private institutions, botanic gardens, herbaria, and universities; in the United States there has been indirect governmental support, largely through the National Science Foundation. Nevertheless the gap between need and effort in the study of this important group of plants is still very evident. It should be closed, on an international cooperative basis, since the accumulation of knowledge about these plants can no longer be left to the dedication of a few, often isolated, individuals. Continuity of support and guaranteed access to the organisms over lengthy periods are needed.

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