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Pollination and Evolution in Palms *)

Ilse SILBERBAUER-GOTTSBERGER **)

With 6 Figures

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Summary

SILBERBAUER-GOTTSBERGER I. 1990. Pollination and evolution in palms. – Phyton (Horn, Austria) 30 (2): 213–233, 6 figures. – English with German summary.

It is hypothesized that the original pollination mode in palms was one of general entomophily and that cantharophily is a derived mode. Many extant palm species are pollinated by more than one insect group, often with predominance of either bees, flies, or beetles. Certain morphological and physiological differentiation patterns of inflorescences and flowers are correlated with the predominance of a certain insect group, but these modifications are not so specific that they exclude other insect groups from visiting and pollinating the flowers. Furthermore, wind is a potential pollen vector. On the other hand, several species are specialized in their pollination for beetles. These cantharophilous species show different syndromes with diurnal or nocturnal attraction. Species exhibiting cantharophily belong to primitive groups as well as to more derived ones. Curculionidae and Nitidulidae are the main pollinators of cantharophilous palms, but also Scarabaeidae (Dynastinae) or Staphylinidae are involved. Pollination of palm flowers by beetles is closely related with predation. Palms offer food and mating or breeding sites for the beetles. The interrelationship palms/beetles has apparently evolved towards a balance between parasitism and successful pollination. The fact that many palms breed their own pollinators and that they additionally can be pollinated by the wind, makes them more independent from the surrounding insect fauna. Wind pollination, although derived in palms, probably was a very early event in the evolutionary history of the family and occurs today in primitive and derived species. Some small acaulescent

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*) In memory of Prof. Dr. L. VAN DER PIJL, who stimulated several of the ideas outlined in this paper.

**) Dr. Ilse SILBERBAUER-GOTTSBERGER, Botanisches Institut I der Justus Liebig-Universität, Senckenbergstraße 17–25, D-6300 Giessen, Federal Republic of Germany.

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savanna palms are derived in their habit but not necessarily in their pollination modes. In palms, the inflorescence bracts can function as protective or visually attractive organs, and further as breeding sites, pollination chambers, or in the aerodynamics of pollen capture. Nectar secretion from external nectaries in the gynoecium in species with free carpels, is supposed to be original in palms. Internal septal nectaries apparently are derived. Most cantharophilous palms do not have any nectar secretion.

Zusammenfassung

SILBERBAUER-GOTTSBERGER I. 1990. Bestäubung und Evolution der Palmen. – Phyton (Horn, Austria) 30 (2): 213–233, 6 Abbildungen. – Englisch mit deutscher Zusammenfassung.

Die lange Zeit als windblütig angesehenen Palmen werden in erster Linie von Insekten bestäubt. Es wird heute angenommen, daß die ursprünglichen Palmen als relativ kleinwüchsige Arten die tropischen Wälder besiedelten und daß sie mehrfach verzweigte Blütenstände und freikronblättrige apokarpe Zwitterblüten besaßen. Der Bestäubungsmodus dieser „Urpalmen" war wahrscheinlich eine Art von allgemeiner Entomophilie, mit Coleopteren, Dipteren und Hymenopteren als Bestäubern. Die vielen, relativ offenen Blüten sind eine wichtige Futterquelle für zahlreiche pollenfressende oder nektarsaugende Insekten, die beim Blütenbesuch teilweise auch zu Bestäubern werden können. Im Laufe ihrer Entwicklung haben sich die Palmen durch morphologische und physiologische Differenzierungen ihrer Blütenstände und Blüten mehr an die eine oder andere der besuchenden Insektengruppen angepaßt. Allerdings sind die Blüten meist auch noch für weitere Insektengruppen gut zugänglich, wodurch diese zusätzlichen Besucher ebenfalls eine Rolle als Bestäuber spielen können. Nur bei Wechselbeziehungen mit Käfern ist es anscheinend bei den Palmen zu spezialisierteren Anpassungen gekommen. Die Entwicklung exklusiv käferblütiger Palmen aus allgemein entomophilen Formen vollzog sich wahrscheinlich schon in einer frühen Differenzierungsphase. Cantharophile Palmen gibt es heute sowohl in Gruppen, die als ursprünglich, als auch in solchen, die als abgeleitet angesehen werden und zeigen Anpassungen sowohl an nacht- wie auch an tagaktive Käfer. Dabei sind Curculionidae und Nitidulidae die wichtigsten Bestäuber, es können aber auch Scarabaeidae (Dynastinae) und Staphylinidae an der Bestäubung beteiligt sein. Die Spezialisierung in der Beziehung Käfer/Palmen hat dazu geführt, daß sich etliche der bestäubenden Käferarten in den Blütenständen oder Blüten der Palmen entwickeln. Palmen sind somit teilweise, soweit sie ihre eigenen Bestäuber züchten, unabhängig von der Insektenfauna ihrer Umgebung. Windbestäubte Palmen sind zwar als abgeleitet anzusehen, das Phänomen trat aber wohl schon zu einem erdgeschichtlich frühen Zeitpunkt der Palmenentwicklung auf. Viele der rezenten, insektenbestäubten Palmen können zusätzlich durch den Wind bestäubt werden. Bei den Palmen nimmt die Bedeutung der Windbestäubung mit zunehmender Wuchshöhe und dem Auftreten in offenen Vegetationsformationen zu. Die kleinen stammlosen Savannenpalmen sind in ihrer Wuchsform zwar abgeleitet, aber nicht notwendigerweise in ihrer Bestäubung. Die Hochblätter der Blütenstände der Palmen dienen dem Knospenschutz, werden von den verschiedenen Insekten als Brutplätze benutzt, können als Bestäubungskammer funktionieren und sind auch bei der optischen Anlockung von Insekten und bei den aerodynamischen Vorgängen bei der Pollenübertragung durch den Wind von Bedeutung. Oberflächennektarien an den Außen-

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seiten apokarper Fruchtknoten sind wahrscheinlich ein ursprüngliches Merkmal der Palmen, während die daraus entstandenen Septalnektarien abgeleitet sind. Die meisten der cantharophilen Palmen zeigen keine Nektarausscheidungen. Die Entwicklung der Palmen von „Generalisten" zu spezialisierteren Käfer-, Bienen-, Fliegen- und Windbestäubten erfolgte parallel in den verschiedenen Verwandtschaftsgruppen.

1. Introduction

The idea prevailing for more than a century that wind pollination is the original and main pollination mode in palms had to be abandoned. Palms are more frequently pollinated by insects than by wind and the family seems to have originated as an entomophilous group (e. g., PORSCH 1956, EAMES 1961, VAN DER PIJL in lett. 1971, MOORE & UHL 1973, UHL & MOORE 1977, FAEGRI & VAN DER PIJL 1979). In a review, HENDERSON 1986 showed the great diversity of pollination modes in palms, though relatively few of the approximately 2500 species have been studied so far. He stated that extant species are predominantly entomophilous, and that three widespread insect mediated pollination syndromes exist, viz., beetle, bee, and fly pollination. He further speculated that beetles might have been the pollinators of ancestral palms.

This paper tries to give a new interpretation of data on pollination biology in the family. A new hypothesis on the likely pollination events in the original palms is presented. Functional aspects of inflorescence bracts, as well as the occurrence of septal nectaries are discussed. Finally, some trends in the diversification of the pollination modes are correlated with the patterns of morphological differentiation to reveal more about the supposed evolution of the family.

2. Pollination in Palms

2.1. General Entomophily (Bees, Beetles, and Flies as Pollinators)

Many palms are visited jointly by an array of insect groups, which are of varying importance in pollination. Palms apparently have not specialized much in morphology of the individual flowers, but on the other hand offer a great number of flowers in more or less large inflorescences. The flowers of palms are relatively open and easily accessible for pollen collecting and nectar sucking insects. Thus, pollination in many palms is a rather unspecialized process. However, a predominance of one pollinator or one pollinator group often occurs. The morphological or physiological adaptations for the predominant pollinator group are often not so pronounced that other insect groups are excluded from flower visitation and pollination. Therefore, palms which are pollinated jointly by bees, flies or beetles, even if one group predominates, have to be considered entomophilous in a

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general sense, rather than melittophilous, myophilous or cantharophilous. Additionally, wind is often a possibility for pollination in the entomophilous species.

2.1.1. Bees as Predominant Pollinators

Butia leiospatha (BARB. RODR.) BECC. [may be identical with *B. paraguayensis* (BARB. RODR.) BAILEY, (*Butiinae, Cocoeae*)], is mentioned as an example for this mode of pollination, and also demonstrates the diversity of insects visiting palm inflorescences and flowers, and the importance of these insects in pollination (SILBERBAUER-GOTTSBERGER 1973). As other *Cocoeae,* the medium tall *B. leiospatha* develops only one woody peduncular bract, which totally encloses the immature inflorescence. At the beginning of anthesis the bract opens in the morning, releasing the inflorescence. The numerous staminate and pistillate yellow or red purple-colored flowers are more or less laxly arranged on the branches of the inflorescences. The inflorescences are protandrous, and the staminate flowers, which emit a slight pleasant fragrance, come into anthesis 14 days before the pistillate ones. Both staminate and pistillate flowers produce nectar in septal nectaries, located in the gynoeceum of the pistillate flowers and in the pistillode of the staminate ones. Bees of the genus Trigona (Meliponinae) frequently suck nectar on both types of flowers. They also collect pollen from the staminate flowers. In the cerrado area of Botucatu, state of São Paulo, Brazil, these bees, because of their high frequency in visiting the flowers and their high capacity of pollen transportation, are the main pollinators. During anthesis various species of beetles, principally Curculionidae and Nitidulidae, as well as syrphid and muscid flies are also frequently visiting the inflorescences and flowers of both sexes and also play a role in pollination. Like in many other palms, in *Butia* different beetle species (Curculionidae and Nitidulidae) breed in different parts of inflorescences and flowers. Some of them are effective pollinators, e. g., two Anchylorhynchus (Curculionidae, Derelomini) species. Their females oviposit on the gynoeceum after having passed over the stigmas of various flowers. The larvae develop while feeding on the young seeds. The attacked flowers drop and the beetles continue to develop in the flowers on the ground. The curculionid Microstrates (Madarini), and the nitidulid Mystrops sp., are also well represented on the inflorescences and transport some pollen.

But also non-pollinating beetles breed in the closed inflorescence buds of *Butia.* Angelocentris schubarti BONDAR and Tripusus leiospathae BONDAR (Curculionidae, Madarini) perforate the spathe and lay their eggs in the inflorescence. Their larvae feed on the rachis and on staminate flowers. When the inflorescence opens, the development of the weevils is finished. The females, after mating, change to another inflorescence bud for oviposition.

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The role of Diptera in pollination of *Butia* is not yet fully understood, however, the visiting Syrphidae and Muscidae are transporting some pollen.

In addition to pollination by insects, wind pollination occurs in *B. leiospatha*. The pollen of recently opened staminate flowers, which is slightly sticky initially, becomes dry and dusty during the day.

A similar mode of pollination exists in species of various palm groups, e. g., probably in the genera, *Itaya* of the *Corypheae* (MOORE & UHL 1973), *Caryota* (SILBERBAUER-GOTTSBERGER, in prep.), and *Iriartea* of the *Caryoteae* and *Iriarteae* resp., (BULLOCK 1981, HENDERSON 1985), in *Euterpe* (HENDERSON 1985, LEÃO ALVES BOI & DA SILVA DIAS 1986) of the *Areceae*, and has also been found in many species of the *Cocoeae*, e. g., *Syagrus flexuosa* (CHAM.) GLASSM., *S. romanzoffiana* (CHAM.) BECC., and *S. coronata* (MART.) BECC., as well as in *Allagoptera campestris* (MARTIUS) KUNTZE, and *Cocos nucifera* L. (SILBERBAUER-GOTTSBERGER, in prep.). All species with this mode of pollination bear functional nectaries in the gynoecium.

A case of pollination by bees and flies is reported by ESSIG 1973 for the nectar-producing *Ptychosperma macarthurii (Ptychospermatinae, Arecoideae)*.

2.1.2. Beetles or Bees as Predominant Pollinators

In *Syagrus loefgrenii* GLASSM. *(Butiinae, Cocoeae)*, a small cerrado palm with a subterranean creeping stem, beetles or bees may be the predominant pollinators. In Botucatu, state of São Paulo, Brazil, the species was found to produce only small amounts of nectar and bees were visiting female flowers only rarely, probably in consequence of the poor nectar production. The predominant pollinators were the weevils, Hustachea aff. campestris BONDAR (Madarini), which develops in the staminate flowers, and Anchylorhynchus camposi (BONDAR) (Derelomini), which lays its eggs in the pistillate flowers. Nitidulids of the genus Mystrops seem to be pollinators, too. On the other hand, *S. loefgrenii* studied in the state of Minas Gerais, was more frequently visited by meliponid bees than by beetles. Thus, bees or beetles may be predominant pollinators of *S. loefgrenii*.

2.1.3. Flies as Predominant Pollinators

Asterogyne martiana (WENDL.) WENDL. ex HEMSELEY *(Geonomeae)* is a small understorey palm studied by SCHMID 1970, which produces androgynous spikes with the flowers arranged in pits. Staminate and pistillate flowers are whitish, fragrant and nectariferous. Anthesis is diurnal, inflorescences are protandrous, and nectar is produced in septal nectaries. Numerous flies, bees, moths and beetles approach the flowers collecting pollen and sucking nectar. Weevils also breed in the staminodial tube. The

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three fly groups Calliphoridae, Syrphidae and Drosophilidae are involved in pollination. Especially syrphids are responsible for nearly all the pollen transfer and are the main pollinators. In this species there is no indication of an additional wind pollination (SCHMID 1970).

2.2. Beetles as Exclusive Pollinators

Beetles may be additional or predominant in pollination of palms, however, in many cases they become exclusive pollinators. The majority of these cantharophilous palms do not have any nectar production, therefore their female flowers are only rarely visited by Hymenoptera and Diptera.

The staminate inflorescences of the tall *Orbignya phalerata* MART. (*Attaleinae*), the Brazilian Babassu palm, studied in the state of Maranhão (ANDERSON & al. 1988), exhale a sweet odor, and are visited by insects belonging to eleven orders. Although a diversity of Coleoptera, Diptera, Lepidoptera, and Hymenoptera were observed on the staminate or androgynous inflorescences, the night-active nitidulid beetle Mystrops mexicana was considered to be the main pollinator. Thousands of individuals of this species inhabited the inflorescences, eating pollen and breeding in the wilted staminate flowers. Also the wind was found to play a role in pollination of O. phalerata, with increasing importance in populations in more open vegetation forms. Sex distribution, phenology and pollination of *Attalea funifera* MART., studied in the Brazilian state of Bahia (VOEKS & DIAS 1985) and of *Attalea geraensis* BARB. RODR., an acaulescent palm of the cerrado in São Paulo (SILBERBAUER-GOTTSBERGER, in prep.), is similar to that of *Orbignya phalerata. Attalea geraensis* has a diurnal anthesis. The inflorescences open in the morning and exhibit cream colored flowers which exhale a strong odor, comparable to that of male *Cycas* cones. No septal nectaries are developed. The species is pollinated by Celetes and Phytotribus (Erirhininae, Curculionidae) beetles as also by Mystrops (Nitidulidae), which are found in large numbers in staminate as well as in androgynous inflorescences.

The pollination events of the mentioned *Attaleinae* species recall those of the cantharophilous *Elaeinae.* The functionally dioecious oil palms of the genus *Elaeis,* which were regarded as anemophilous for a long time, were found to be pollinated by small weevils of the tribe Derelomini in Africa as well as in America (SYED 1979, GENTY & al. 1986). In Africa, different species of Elaeidobius (Derelomini, Curculionidae) breed in different parts of the stamens of wilted flowers. They are attracted to the staminate flowers by a strong anis-like scent, promoted by the heating-up of the inflorescences (GENTY & al. 1986). The weevils feed on pollen (GENTY & al. 1986) and also visit the pistillate flowers during anthesis, attracted by a scent, which is similar to that of the male flowers, although stronger. Finding no reward on the female flowers, they return to the staminate

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inflorescences again. The phenomenon of pollination by beetles based on deceit is also known from some cycads (NORSTOG & al. 1986, TANG 1987) and, e. g., for *Myristica* (ARMSTRONG & DRUMMOND III 1986, ARMSTRONG & IRVINE 1989). Predominance of the different weevil species and their relative efficiency in pollination depend on climate and geographical region. Especially in the American species of *Elaeis*, also species of the nitidulid Mystrops breed in staminate flowers and participate in pollination.

Pollination by small beetles during the day also occurs in the monoecious, protogynous *Bactridinae Acanthococos emensis* TOLEDO var. *emensis,* a dwarf palm in the cerrados of the state of São Paulo, Brazil (SILBERBAUER-GOTTSBERGER, in prep.). The inflorescences open in the morning hours and emit a strong *Cycas*-like odor. No septal nectaries are developed. However, droplets of exudates accumulate on the stigma. During the day, small Curculionidae (Andranthobius sp., Derelomini) were seen licking at the exudates. Self-pollination, which leads to fruit formation, is possible because the anthers are open already in the bud stage.

The second mode of cantharophily in palms is also linked with a heating-up of the inflorescence and the emission of strong odors, which are described for different species as reminding of lilac, or being musty, musky or fruity. But such palms are different in having a nocturnal anthesis and a strong time-correlation of the sexual phases of anthesis and the activity of their pollinators. Two groups have to be distinguished.

In the first group the inflorescences remain enclosed in bracts during the pistillate phase. This is the case in *Cryosophila albida* BARTLETT, a representative of the most primitive tribe *Corypheae* in the most primitive subfamily *Coryphoideae,* which was studied by HENDERSON 1984 in Costa Rica. *C. albida* has hermaphrodite protogynous flowers and a nocturnal anthesis. In the evening hours, when the flowers enter the pistillate stage, the peduncular and rachis bracts open only at the apex. Heating-up and emission of a strong lilac-like scent accompany this phase. Pollination takes place at night. Small curculionids (Derelominus sp.) and nitidulids (Mystrops sp.) enter the semi-closed inflorescence in great number, and feed on bracts, inflorescence branches, and nutritious trichomes. The flowers are not harmed by the visitors. A few approaching scarabs (Cyclocephala amazona L.) are considered too large to enter the bract's opening. During the next morning the bracts drop and expose the flowers, which have now entered their male phase. In this stage, the flowers are visited by many kinds of pollen collecting insects, which are of no importance to pollination, because they do not visit the flowers in the female receptive phase. The staminate phase finishes with the abscission of the stamens during the next morning. The beetles fly away in the evening and may effect pollination when they settle on a newly opened inflorescence.

A similar kind of cantharophily is known also from the dioecious or polygamous, apocarpous *Rhapidophyllum hystrix* (PURSH) WENDL. &

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DRUDE *(Corypheae)*, studied in the south-eastern U.S.A. (SHUEY & WUNDERLIN 1973), where the female inflorescence remains permanently enclosed in bracts. A species of Notolomus (Curculionidae) is considered to be the effective pollinator. Another example is the monoecious, protogynous *Socratea exorrhiza* (MART.) WENDL. (*Arecoideae, Iriarteinae;* HENDERSON 1985), which has the inflorescences also enclosed in bracts and in the prophyll during pistillate anthesis, exhaling a musty, fruity odor. The pollinating beetles are species of Phyllotrox (Curculionidae, Derelomini) and Mystrops (Nitidulidae).

In *Manicaria (Areceae),* the entire inflorescence is enclosed in a net-like bract. Through the small interstices of the bracts, nitidulid beetles can pass (DRANSFIELD 1982).

Cantharophily also occurs in the most advanced subfamily of palms, the *Phytelephantoideae.* The dioecious *Phytelephas microcarpa* RUIZ & PAVON, studied by BARFOD & al. 1987 in Ecuador, has dimorphic inflorescences which heat-up during anthesis and emit a strong scent. The bracts of the pistillate inflorescences remain closed at anthesis. Numerous individuals of small, night-active beetles (Curculionidae, Derelomini, Phyllotrox spp.) are considered to be the most important pollinators besides other beetle groups (Staphylinidae, Nitidulidae).

In the second group the single peduncular bract opens totally at the beginning of anthesis. Some *Bactris* species studied in Costa Rica (ESSIG 1971, MORA URPI & SOLÍS 1980, MORA URPI 1982, BEACH 1984), and *Bactris maraja* MART. in the Amazonian Varzea (G. GOTTSBERGER, pers. comm.), have nocturnal anthesis, thermogenesis and emission of strong odors, which are described as musky, spicy or fruity. The pistillate flowers are already receptive at opening of the bract, 24 hours before the first staminate flowers shed their pollen. Tens of thousands of small curculionids and many dynastid beetles are active during the evening hours, passing over the pistillate flowers. They stay at the inflorescences during the next day. The staminate flowers open in the late afternoon of the second day of anthesis and pollen is released. At this time the pollen-covered beetles fly away and may cause pollination when they land on newly opened inflorescences. While MORA URPI & SOLIS 1980 in plantations of *Bactris gasipaes* found that Derelomus palmarum CHAMPION (Derelomini) was the main visitor and pollinator, BEACH 1984, in the natural habitat, found Cyclocephala amazona L. (Dynastinae, Scarabaeidae) of major importance in pollination. The sexual phases of the inflorescences seem to be better correlated with the activity of Cyclocephala than with that of the small weevils which left the inflorescences before the staminate flowers had opened. The importance of the different beetle groups for pollination of *Bactris* seems to depend on the locality of observation and may perhaps also change during the flowering season. MORA URPI & SOLÍS 1980 considered pollen transport by wind and gravity as another possibility.

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Pollination by beetles in connection with nocturnal anthesis, thermogenesis and open inflorescence bracts was also described from *Astrocaryum mexicanum* LIEBM. ex MARTIUS, another *Bactridinae* in Mexico (BURQUEZ & al. 1987), and *Astrocaryum alatum* LOOMIS in Costa Rica (BULLOCK 1981).

The protogynous inflorescences of the cantharophilous *Acrocomia aculeata* (JACQ.) LODD. ex MARTIUS *(Bactridinae),* studied in Brasília (SCARIOT 1987), generally open in the first night hours, but occasionally also during the day. The curculionid Andranthobius sp., the nitidulid Mystrops palmarum, as well as thrips (Thysanoptera), an unidentified Cyclocephala, and other beetle species are the pollinators. The wind may also cause effective pollination.

2.3. Wind Pollination

Little is known about the exclusiveness of wind pollination in palms and, looking at the palm species studied, one might doubt if exclusive wind pollination really exists. This impression may be due to the fact that so few palms have been studied and that among these only little information is available on tall ones. The middle-sized *Thrinax parviflora* SWARTZ of the primitive tribe *Corypheae*, was reported by READ 1975 to be anemophilous. The species inhabits open environments, and has hermaphrodite protandrous flowers with sepals and petals reduced, in which only one carpel is developed. These morphological characters have been interpreted as an adaptation to wind pollination (UHL & MOORE 1977). However, also small beetles and thrips were reported by READ to be present on most of the inflorescences of *T. parviflora.* In contrast to *T. parviflora, T. excelsa* LODD. ex GRISEB., which inhabits dense wet forests, has scented pink flowers, perhaps indicating entomophily (HENDERSON 1985).

The dioecious, apocarpous *Chamaerops humilis* L. *(Coryphoideae),* in Southern Spain, is wind pollinated (HERRERA 1989). But female flowers sometimes secrete nectar, and both male and female inflorescences attract weevils. HERRERA hypothesizes that being anemophilous at present, *C. humilis* bears traits of an earlier insect-pollinated condition. Perhaps the species may be considered to be ambophilous, pollinated by insects and by wind with predominance of wind pollination at the study site.

Even the classical example for a wind pollinated palm, the date palm *(Phoenix dactylifera)* is suspected to be entomophilous (HENDERSON 1986).

3. Evolutionary Trends in Palms

3.1 Habit and Habitat

From trends observed in extant palms it can be hypothesized that the earliest palms in geological history were small to medium tall plants with

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palmate leaves, growing in the understorey of tropical forests. Generally in palms, a medium tall habit and costapalmate or palmate leaves are considered to be primitive characters (MOORE & UHL 1973, UHL & DRANSFIELD 1987). The slender tall-stemmed palms *(Pigafetta, Roystonea)*, the robust-stemmed *(Washingtonia)*, the very short-stemmed or the acaulescent palms with an underground stem *(Acanthococos, Attalea geraensis)*, and the climbing palms, with up to 100 m stems *(Desmoncus, Calamus)* are derived. Like in the case of the various forms of the leaves, the derived growth forms appear to have arisen more than once in the different palm groups (UHL & DRANSFIELD 1987). The occurrence of palms in more open vegetations like savannas, or totally open places with moist or sandy ground like swamps or grasslands, and even deserts, along the shores, or on rocks, may be a derived condition.

3.2. Inflorescences, Flowers, Sex Distribution, and Breeding Systems

The primitive palm inflorescence is an axillary monopodial branching system, with many branches (UHL & DRANSFIELD 1987), which besides the prophyll(s) also has numerous peduncular, rachis and rachilla bracts. During evolution, reduction of the number of inflorescence ramifications to branching of the first order only occurred (Fig. 1). The most reduced inflorescence-type is a single spike-like inflorescence. Female and male inflorescences sometimes are dimorphic, e. g., in the *Phytelephantoideae*. This

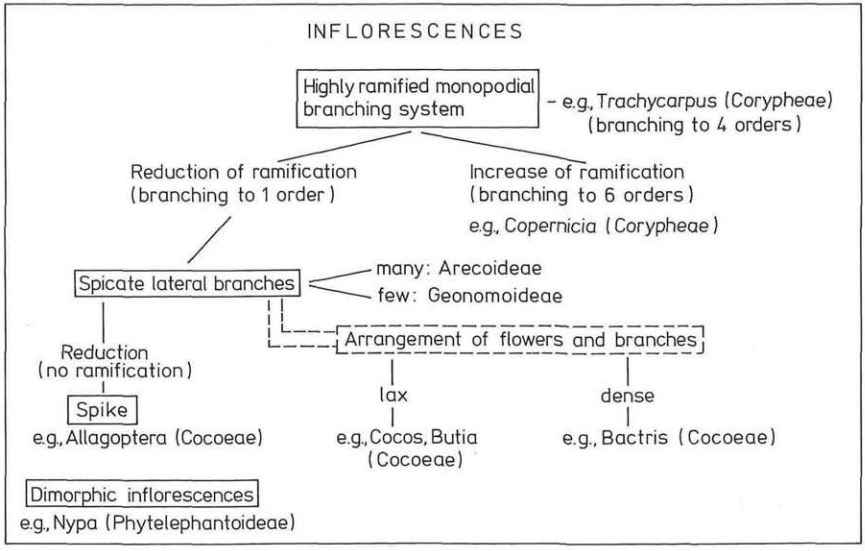

Fig. 1. Differentiation of inflorescences in regard to branching patterns and arrangement of branches and flowers.

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dimorphism apparently is not associated with any special pollination mechanism (BARFOD & al. 1987). In *Nypa,* a headlike structure bearing the pistillate flowers is surrounded by spikes composed of the staminate ones.

The arrangement of flowers on the inflorescences is quite diverse, reaching from solitary flowers to different types of flower clusters (UHL & DRANSFIELD 1987). The flowers and the branches may be arranged more densely or more laxely on the inflorescences (see Fig. 1). Apparently no association of inflorescence or flower arrangement with any pollination mode can be seen. But there seems to be a tendency that palms which are specialized for beetle pollination have more densely arranged flowers on the inflorescences.

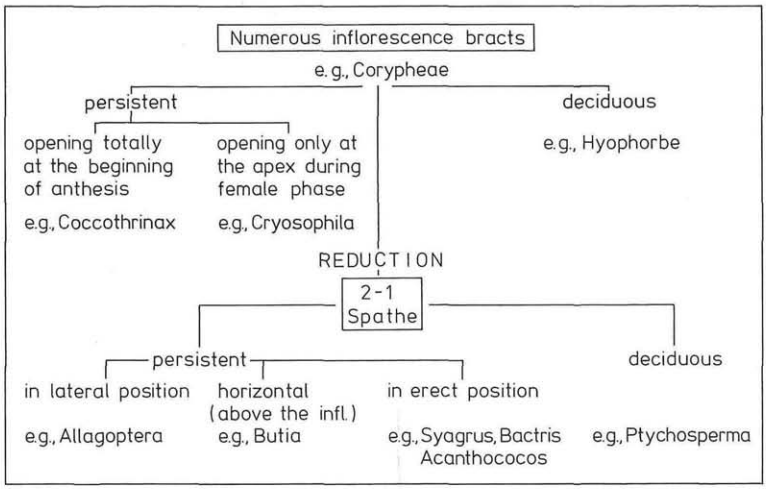

Fig. 2. Differentiation of inflorescence bracts concerning their number, persistence, and position.

During the differentiation of palms, a reduction of the number of prophylls and bracts to two or only one, often called spathe, has occurred (Fig. 2). In the *Arecoideae* the single bract is specialized, and woody. During anthesis, the bracts may persist on the inflorescences or they may be caducous. The function of the bracts is diverse (UHL & DRANSFIELD 1987). They enclose and protect the inflorescences and flowers in bud stage (Fig. 3). Opened bracts may form a kind of roof above the inflorescence, or may remain in a lateral position having apparently no function anymore. Often the bracts function in pollination. In some specialized cantharophilous species, the bracts enclose the inflorescence during the female stage of anthesis, opening only at the apex, and thus forming a kind of pollination chamber into which the pollinating beetles enter and where they remain for several hours. This pollination chamber may be considered as an analogous

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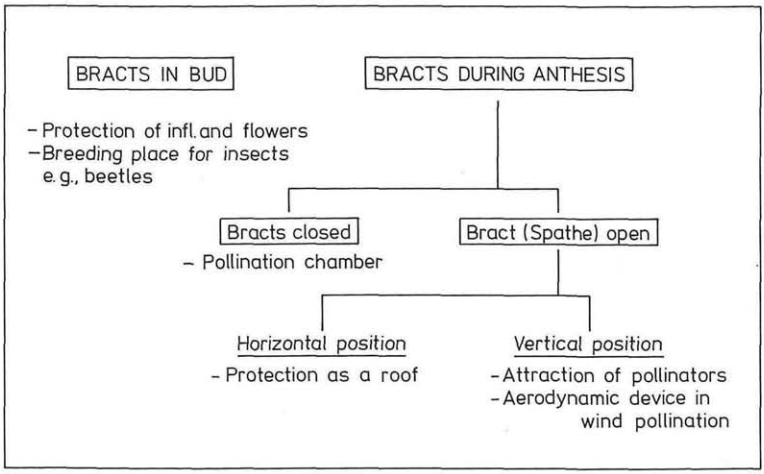

Fig. 3. Function of inflorescence bracts in bud and during anthesis.

structure to the pollination chamber formed by the petals in *Annonaceae* flowers (GOTTSBERGER 1970), or to the spathe kettle in *Araceae* inflorescences (GOTTSBERGER & AMARAL Jr. 1984). It seems that the cantharophilous palms with a pollination chamber are specialized for pollination by small beetles (Curculionidae). The small apertures of the chamber in several species, and the closed, net-like bracts of *Manicaria,* also may function as pollinator-sieves, restricting the access to flowers for small beetles only. In palms pollinated by dynastid scarab beetles, no pollination chamber is formed. Unopened inflorescence buds are used by several beetles and other insects as breeding-places. The single woody bract, in upright position when open, may have a brightly colored inner side, which, together with a showy inflorescence, perhaps functions as a visual attraction for pollinators. An erect spathe may also play a positive role as an aerodynamic device in wind pollination.

The simple pattern of a trimerous palm flower with distinct flower parts is modified in many ways (some of them are shown in Fig. 4). These modifications as, for instance, connation, and increase or loss of parts, occurs even among the least specialized coryphoid palms (UHL & DRANSFIELD 1987). An increase of number of stamens is developed already in primitive palms with hermaphrodite flowers (see Fig. 4), but is most pronounced in representatives of the advanced subfamily *Phytelephantoideae* (UHL & MOORE 1980). Such a secondary polyandry may have evolved compensating the mass of pollen-eating or -collecting insects. A reduction of the perianth occurs in association to wind pollination (e. g., *Thrinax*).

From palms with hermaphroditic flowers, species with unisexual flowers evolved. Unisexual flowers is the predominant condition in the majority

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of the extant palms (see Fig. 4). Flowers of many species bear rudiments in form of staminodes or pistillodes, but also flowers without any traces of the other sex frequently occur (UHL & DRANSFIELD 1987).

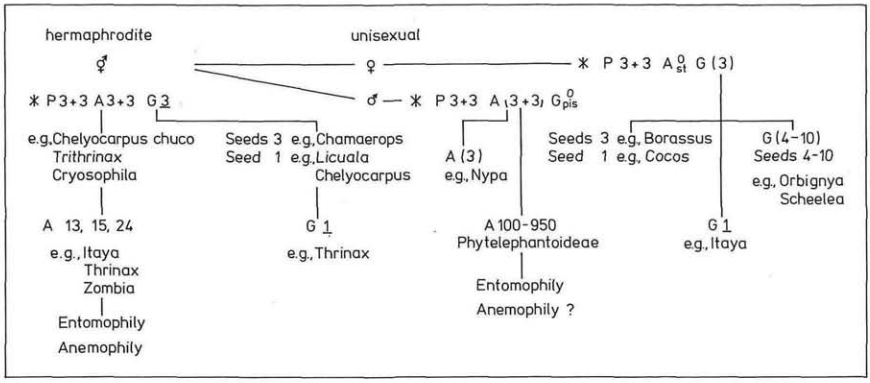

Fig. 4. Flower differentiation with some general morphological trends. Not all examples correspond in all their characters with the floral formula under which they are mentioned. For instance, the outer perianth and also the stamens are briefly connate in *Cryosophila*. The stamens are further connate in *Licuala;* the perianth is reduced in *Thrinax*. *Chamaerops* has unisexual flowers and *Nypa* has an apocarpous gynoecium. – pis = pistillode, st = staminodes, o = complete reduction.

Palms with unisexual flowers are mostly monoecious but also dioecy has evolved. In monoecious palms, staminate and pistillate flowers may be together in bisexual (= androgynous) inflorescences or they may be separate in unisexual ones.

The sex distribution in extant palms apparently does not have any direct relation with pollination. One reason for the differentiation of the unisexuality and dioecy in palms may be their breeding system. The majority of the few palms which have been tested, e. g., *Acrocomia aculeata* (SCARIOT 1987), *Thrinax parviflora* (READ 1975), *Euterpe edulis* MART. (LEÃO ALVES BOI & DA SILVA DIAS 1986), exhibit self-compatibility. One of the few exceptions found until now is *Astrocaryum mexicanum* which is self-incompatible (BURQUEZ & al. 1987). Self-compatibility seems to be the prevailing breeding system in palms, and different mechanisms to promote outcrossing are developed. In species with hermaphrodite flowers, self-pollination is avoided by a temporal separation of female and male phases, e. g., by protandry *(Thrinax)* or protogyny *(Cryosophila)*. Palms with androgynous inflorescences likewise may be protandrous (e. g., *Butia, Syagrus*), or protogynous (e. g., *Bactris, Acrocomia*). Protandry seems to be correlated with generalized entomophily and anemophily, while protogyny characterizes cantharophilous palms. Most monoecious palms have only one

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inflorescence in anthesis at one time. A spatial separation is most effective in the functional dioecious species, e. g., *Elaeis,* or in the dioecious *Phytelephantoideae.* In the self-compatible *Acanthococos emensis,* self-pollination is possible, because during the female receptive phase, the stamens in the buds are already open (SILBERBAUER-GOTTSBERGER, in prep.).

3.3. Original Pollination of Palms

Palms probably originated in the Upper Cretaceous, in the Santonian or Coniacian. No pre-Cretaceous fossils of leaves and stems can be identified with certainty as palms (UHL & DRANSFIELD 1987). The oldest unequivocal record of palm pollen *(Nypa)* is from the Maestrichtian, with an age of about 85 million years (MULLER 1984). But already at that time palms were represented by genera belonging to the *Coryphoideae,* the subfamily considered as most primitive, as well as to the *Nypoideae,* a subfamily which exhibits both primitive and advanced characters. Therefore, one must accept that palms were diversified already in the Maestrichtian.

At that time the insect fauna, which visited the flowers of the angiosperms was diverse (see CROWSON 1981, CREPET & FRIIS 1987, WILLEMSTEIN 1987). Thysanoptera are of Permian origin (WILLEMSTEIN 1987). Beetles, which probably already have been pollinators of pre-angiosperms, were diversified in the Triassic, with flower visiting Elateridae and Nitidulidae. In the Lower and Upper Cretaceous already a large variety of flower visiting beetle taxa (Curculionidae, Nitidulidae, Mordellidae, Anobiidae, Tenebrionidae) have existed. The first Chrysomelidae appeared in the Upper Cretaceous. The Diptera of the Early Cretaceous were represented by the important flower visiting Brachycera (Empididae) and, in the Upper Cretaceous, by Bibionidae and Syrphidae. Primitive pollen eating Lepidoptera, the Micropterygidae, existed since the early Cretaceous. Of the Hymenoptera, the Symphyta and the Sphecidae and Vespoidea of the Apocrita, were potential pollinators of the then existent angiosperms. Recently, even a fossil of a social Meliponinae bee was found from the Cretaceous (MICHENER & GRIMALDI 1988).

It is probable that all these insect groups visited inflorescences and flowers of ancient palms and found reward in form of pollen, nectar, floral tissues, trichomes, ovules, fruits, and seeds, as well as hiding, meeting, and breeding places. Several of these insects functioned as pollinators.

3.4. Nectar Secretion in Palms

It is quite possible that ancient palms already had some nectar production. In representatives of the primitive *Coryphoideae (Trachycarpus),* some liquid (nectar?) is produced by a superficial nectary tissue on the open ventral sutures of the incompletely closed carpels (DAUMANN 1970). In other

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primitive species, the nectar tissues are situated externally on the carpels (e. g., *Sabal,* DAUMANN 1970, UHL & MOORE 1971). In *Corypha,* nectaries are in a lateral position at the very base of the free or partly free carpels in young stages. At anthesis, carpels are connate and a short septal gland is present, which opens just below the locules (UHL & MOORE 1971). In *Livistona, Licuala, Pritchardia,* and *Serenoa (Corypheae)* the carpels are free at the base, and only the stylar region is connate. Also in these palms nectar secretion occurs from more or less external nectaries. In more derived palms with a syncarpous gynoecium the nectar is produced from septal nectaries (DAUMANN 1970, SCHMID 1983). Those nectaries are located in the spaces between the incompletely fused carpels and begin at the base of the ovary or higher as a triradiate central crater (DAUMANN 1970, SCHMID 1970, 1983, 1985, UHL & MOORE 1971, 1977, SILBERBAUER-GOTTSBERGER 1973, SMETS & CRESENS 1988). Apically, three distinct centrifugal canals separate, which open by pores or slits at different heights on the ovary. The surface of these nectaries is covered by distinct epithelial cells. The external nectar zones on carpel walls of apocarpous monocots are probably homologous to the septal nectaries in the fused carpels (VAN HEEL 1988). SMETS & CRESENS 1988 propose to call these inner and outer „septal" nectaries gynopleural nectaries.

In the gynoecium of palms stylar-canals extend from the locules to the stigmas. As far as is known, these canals never join to the septal nectaries, but are in some species revested by apparently secretory cells and seem to produce some exudates (*Geonoma, Arenga;* UHL & MOORE 1971).

Cantharophilous palms rarely have nectaries (see Fig. 5). One of the exceptions is *Salacca edulis (Calameae;* MOGEA 1978), in which the pollinating beetles lick the flower nectar. Thermogenesis seems only to occur in species without nectaries (see Fig. 5) and is probably associated with cantharophily.

3.5. Parasitism and Pollination in Palms

Entomophily in palms seems to have partly evolved in connection with parasiting insects which live on palms in multiple relationships (see LEPESME 1947), and which complete their whole life cycle or part of it in roots, stems, leaves, inflorescences, flowers, and in fruits. Palms are often damaged by the insects and their larvae. Parasitism of inflorescences and flowers by beetles probably evolved also already in the early history of palm differentiation. Some morphological characters, as the relatively hard sepals and petals, and the presence of raphids and tannins in the floral tissues, for instance in the gynoecium, might be interpreted as protective devices against parasitism, viz., adaptations compensating for the destructive life habit of the visitors (UHL & MOORE 1973, MOORE & UHL 1982, HENDERSON 1986). In many cases, such a parasitism in the floral region leads to pollination, and thus a kind of symbiosis may have evolved.

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NECTARIES	
PRESENT	ABSENT
External nectaries	
CORYPHOIDEAE	
Chamaerops	Chelyocarpus
Livistona	Cryosophila *
Licuala	Rhapidophyllum
Pritchardia	Thrinax
Corypha	
Sabal	
Septal nectaries	
CALAMOIDEAE	
Eugeissonia	
Salacca	
NYPOIDEAE	
	Nypa *
CEROXYLOIDEAE	
Pseudophoenix	
Hyophorbe	
Chamaedorea	
ARECOIDEAE	
Arenga	Attalea
Caryota	Elaeis *
Socratea	Acanthococos
Euterpe	Acrocomia
Prestoea	Astrocaryum *
Archonthophoenix	Bactris *
Ptychosperma	
Butia	
Syagrus	
Cocos	
Allagoptera	
Asterogyne	
Geonoma	
PHYTELEPHANTOIDEAE	
	Phytelephas *

Fig. 5. Some examples of genera with presence or absence of nectaries in the gynoecium. Species marked with * have thermogenesis.

Especially Coleoptera which breed in stamens or ovaries of palm flowers play a role in the pollination of many species of *Elaeis, Attalea, Orbignya, Asterogyne, Butia,* and *Syagrus*. These palms which partly breed their own pollinators, are more independent from the surrounding insect

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fauna, and perhaps therefore they can occupy more open, dry, or insect-poor habitats, without switching over to wind pollination totally. A similar symbiosis between plant and pollinator is known from the cycad *Zamia* (NORSTOG & FAWCETT 1989), in which the pollinating weevils breed in male cones and feed on them.

A picture of supposed trends in ecological differentiation and evolution of palms in respect to habitat, habit, some morphological characters and modes of pollination is shown in Figure 6.

It is presumed that the most primitive palms grew in the understorey, were medium-sized, had palmate leaves, multibranched inflorescences, and numerous prophylls and bracts, which opened totally during anthesis. More or less lax inflorescences, trimerous, hermaphrodite flowers, with free sepals and petals and an apocarpous gynoecium were further primitive characters. In the gynoecium probably some nectar secretion occurred. It is supposed that the pollination mode of the ancestral palms was a kind of unspecialized entomophily and that various insect groups existent at that time jointly visited and pollinated the palm flowers (Fig. 6 A).

From the original generalized entomophilous palms, other species evolved, in which one insect group became predominant in pollination. Certain characters of inflorescences and flowers seem to be adaptations to the predominant insect group. However, also in most extant species, the more general entomophilous characters prevail.

The predominantly bee pollinated palms (e.g., *Euterpe edulis, Cocos nucifera, Butia leiospatha,* see Fig. 6B, 6G, 6H) have lax inflorescences and colored, sweet scented flowers. Their flowers or inflorescences are protandrous and enter the sexual functional phases during the day hours. The flowers produce nectar. Pollinators belong mainly to the bee genera Trigona, Melipona, and Apis. Flies and beetles are additional pollinators. The predominantly bee pollinated species belong to primitive subfamilies as well as to more advanced ones. Many of them inhabit more open vegetation forms, or are emergent trees of forests, and are in their majority medium-tall to tall species. Only some of them are acaulescent savanna palms (*Allagoptera campestris,* see Fig. 6K). Their majority apparently may also be pollinated by the wind.

The species which are pollinated predominantly by Diptera have whitish flowers which secrete nectar (e. g. *Asterogyne martiana, Geonoma,* see Fig. 6C). Bees and beetles may function as additional pollinators. The majority of species with this mode of pollination seem to be medium-tall understorey palms.

Several palms have specialized for beetles as pollinators, some of them probably early in their evolutionary history. Cantharophilous palms belong to primitive groups, as well as to more advanced ones. Their inflorescences and flowers developed morphological and physiological modifications, which might be partly interpreted as adaptations to cantharophily. The

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more primitive species showing cantharophily are usually medium-sized understorey palms (e.g., *Cryosophila albida, Rhapidophyllum hystrix,* see Fig. 6D). They form a pollination chamber, have dense inflorescences with many bracts, are protogynous, have a nocturnal anthesis, and produce heat and strong odors. Small Curculionidae and Nitidulidae are the main pollinators.

Other cantharophilous species have evolved which do not form a pollination chamber because the inflorescence bracts open totally during anthesis. These species are also characterized by a nocturnal anthesis, thermogenesis, protogyny, production of strong musty odors, and densely crowded inflorescence branches and flowers (e.g., *Bactris maraja, B. gasipaes, Arocomia aculeata,* see Fig. 6E). Besides of the small weevils, the robust Cyclocephala species are effective pollinators. The latter belong to a more modern beetle group, the Dynastinae, which appeared only in the Tertiary (CROWSON 1981). This kind of cantharophily occurs in medium-sized to tall palms in and outside the forest.

Often cantharophily in palms is based on parasitism of the flowers by the pollinating beetles (e.g., *Elaeis guineensis, Orbignya phalerata* Fig. 6F, 6L). Such palms have day-active or night-active flowers, and in some of them thermogenesis occurs. Curculionidae and Nitidulidae are attracted by the strong odor and breed in staminate flowers. Pollination occurs by deceit. This kind of cantharophily occurs in medium to tall species in or outside the forest and probably also in some small acaulescent cerrado palms.

With increasing height and together with the radiation into more open habitats, the importance and efficiency of wind pollination increased. However, wind pollination also occurs in primitive palms (e.g., *Thrinax parviflora* Fig. 6J). Open bracts during flowering, protandry, reduction of sepals and petals, and dry pollen are linked with anemophily.

The small acaulescent savanna palms have derived and highly adapted life forms, and are diverse in respect to their pollination modes (e.g., *Syagrus loefgrenii, Allagoptera campestris, Acanthococos emensis,* see Fig. 6K, 6L).

The evolution from general entomophilous species to species which are pollinated predominantly by bees, flies, beetles or by the wind, or the differentiation of exclusively cantharophilous species, presumably occurred at different times and repeatedly in the family.

Fig. 6. Supposed trends in ecological differentiation and evolution of palms in respect to habitat, habit, anthesis, some morphological characters, flower reward (pollen, nectar), and modes of pollination. In cases with more than one possibility, the main pollinator group is underlined. – For further explanation see chapter 3.5.

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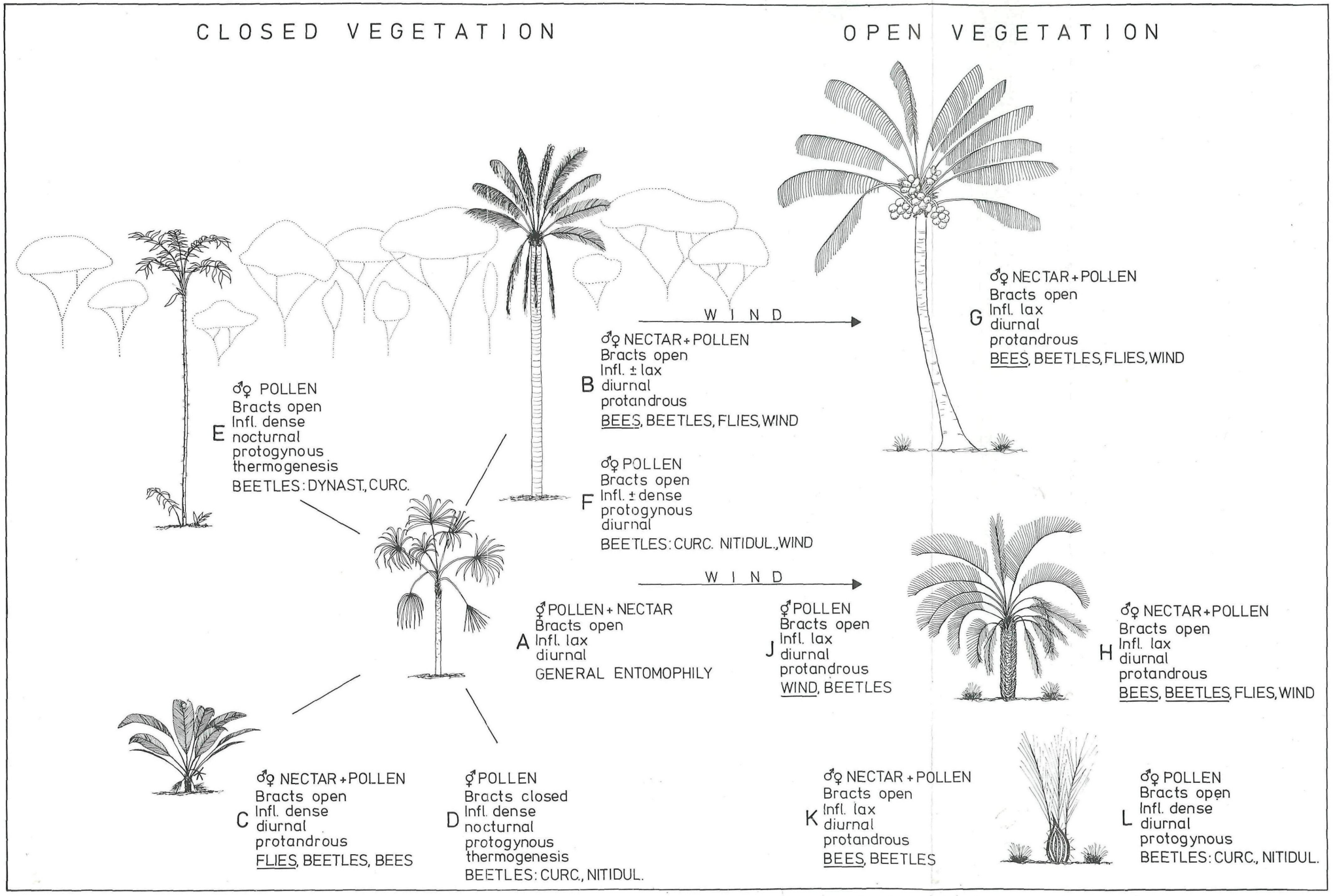

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