Review

POLLINATION SYSTEMS OF PALMS (ARECACEAE)

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Abstract—A review is given of pollination systems in the palm family (Arecaceae). Pollination studies of 149 species (6% of the total number) in 60 genera (33% of the total number) are reviewed. The majority of these studies (75%) are of Neotropical palms. In the sample of 149 species, approximately 52% are beetle-pollinated, 27% bee-pollinated, 7% fly-pollinated, 5% thrips pollinated, 5% wind pollinated, 3% moth-pollinated, and 1% mammal-pollinated. A few other species may be bird-pollinated. Adaptations of inflorescences and flowers to pollinators are not readily apparent except for a general tendency for bee-/fly-pollinated species to have longer, open inflorescences and beetle-pollinated species to have shorter, condensed inflorescences. Classical pollination syndromes are not useful in describing, classifying, or predicting palm pollination systems because of numerous exceptions. The degree to which palm pollination systems may be considered specialized or generalized is unclear. There appear to have been numerous, bidirectional shifts in palms between beetle pollination and bee/fly pollination, and less often shifts to other pollinators. Beetle-pollinated inflorescences are usually visited by bees, and bee-pollinated inflorescences are usually visited by beetles. It seems likely that many species of palm, irrespective of pollinator, have their inflorescences used as brood-sites by beetles.

Keywords—Palmae, pollination syndromes, Curculionidae, Nitidulidae, bees.

INTRODUCTION

The palm family (Arecaceae) comprises a total of 182 genera and approximately 2,460 species. These are unevenly divided among the Neotropics (ca. 770 species), Africa, including southern Europe (ca. 70 species), and the Asian tropics, including the Indian and Pacific Ocean islands (ca. 1,620 species). The family is distributed throughout tropical and subtropical areas of the world, rarely entering temperate regions, but is most diverse, abundant, and conspicuous in lowland tropical forests (Dransfield et al. 2008, POWO 2023).

The first, modern pollination study of a naturally occurring palm was Schmid's (1970a, b) study of *Asterogyne*. Since then, there have been numerous studies of palm pollination. These have been reviewed by Henderson (1986), Uhl & Dransfield (1987), Silberbauer-Gottsberger (1990), Tomlinson (1990), Howard et al. (2001), Henderson (2002), Dransfield et al. (2008), and Barfod et al. (2011). There have been more than 50 important studies of palm pollination published since 2011, particularly detailed studies of palms from Colombia and Brazil. Review of these new studies, together with earlier ones, show the extraordinary complexity of the interaction between palm inflorescences and their pollinators, and also show the limited extent of our knowledge of pollination in the family. Results of the review are discussed in terms of the extent of floral and inflorescence adaptation to pollinators in palms, the usefulness of pollination syndromes in the family, the degree of generalization versus specialization in pollination systems, and shifts in pollination systems.

MATERIALS AND METHODS

An extensive literature search on palm pollination was carried out using both printed and online resources. Google Scholar was used to search for online publications using the various palm genera followed by "pollination", using the "Any time" filter. Less emphasis was placed on studies from cultivated plants, especially crops such as coconut, date, betel nut, and oil palms. A brief summary of each study is given, emphasizing phenology, inflorescence development, and pollinators. Where there are numerous studies of different species within a genus, or the same species at different sites, then the data are tabulated. These summaries necessarily omit a large amount of detail, but their aim is to give a comparative overview of phenology, inflorescence development, and insect visitors in all palms that have been studied. A brief summary of each subfamily and tribe is also given.

Results are ordered according to the classification scheme of genera given in Dransfield et al. (2008), with a few modifications. Notes on inflorescence morphology are also taken from Dransfield et al. (2008). Number of species per genus is taken from POWO (2023, hybrid species excluded), again with a few modifications. Authors of the names of palm taxa will be found in POWO, and authors of insect taxa in the various cited publications. The species-level phylogeny of the palm family (Ferreira et al. in prep.) is referred to in order to make preliminary inferences about shifts from one inflorescence type or pollination system to another. The studies reviewed here are extremely variable in the rigor of the methodology used to establish pollination effectiveness. Conclusions reached here might change as more is learned about pollination of these and many understudied species.

This is a review of pollination in palms, rather than reproductive biology of palms, and thus there are several topics that are not reviewed here (e.g., predation by insects, compatibility systems, etc.). There are several family-level reviews of some of these topics, such as sexual systems (Nadot et al. 2016), pollen type and pollinators (Feldman 1990, Sannier et al. 2009), early insect pollination (Feldman 1990), protection of pollen and ovules (Uhl & Moore 1973), raphides in anthers (Henderson & Rodriguez 1999), and insects on palms (Lepesme 1947, Howard et al. 2001).

Some of the terms used in this review are defined here. Pollination is a process whereby pollen from anthers is transported to stigmas, and the process can be viewed as a system. A pollination system is defined as a combination of the traits (colour, shape, scent, development, etc.) of the flower or inflorescence and the agents that transport the pollen (Ollerton 2021). Thus, a pollination system is an attribute of a particular species, or even of a population within a species, whereas a pollination syndrome is a general summary of similar floral traits found within various different plant species. In contrast to the flowers of many plant families, those of palms are not particularly diverse morphologically. With few exceptions, individual flowers are often rather small and nondescript. However, they are aggregated in large numbers on inflorescences. The inflorescence is here considered to be the unit of pollinator attraction and reward in palms, rather than the individual flower.

The sexual systems of palms are referred to as hermaphrodite, monoecious, dioecious, or polygamous. Hermaphrodite refers to flowers in which stamens and pistils occur together in the same flower (often referred to as a bisexual flower). Plants with such flowers may also be referred to as hermaphrodite. Monoecious refers to plants that bear unisexual flowers, staminate and pistillate, on the same plant. Monoecious plants may have inflorescences with staminate and pistillate flowers, or may have unisexual inflorescences that can be either staminate or pistillate. Dioecious refers to plants that bear either staminate or pistillate flowers. Less commonly, combinations of hermaphrodite and unisexual flowers are found on the same individual or on separate plants, a state referred to as polygamous. For all palm species, 17% are hermaphrodite, 52% monoecious, 30% dioecious, and 1% polygamous (Nadot et al. 2016).

Anthesis can refer to either inflorescences or flowers. Staminate anthesis is when anthers are shedding pollen, and pistillate anthesis is when stigmas are receptive. Generally, within an inflorescence with both staminate or pistillate flowers, or within a hermaphrodite flower, anthesis of one sex occurs before the other. This is referred to as dichogamy. When staminate flowers (or stamens in a hermaphrodite flower) are at anthesis before pistillate flowers, it is referred to as protandry (flowers or inflorescences are protandrous). When pistillate flowers are at anthesis first, it is referred to as protogyny (flowers or inflorescences are protogynous).

A few species of palm are semelparous. In these the period of reproduction is condensed into a single episode, followed by death of the individual. All other species are iteroparous. In these there are multiple reproductive episodes over the lifetime before death.

RESULTS

CALAMOIDEAE

Calamoideae, *Eugeissoneae*

The tribe comprises one genus (*Eugeissona*, 6 species) distributed in Peninsular Thailand, Peninsular Malaysia, and Borneo. One species has been studied.

Eugeissona

Eugeissona is semelparous and polygamous. Inflorescences are erect amongst (Fig. 1A) or above the leaves. Flowers are large and are borne in a cupule of bracts, in tight pairs of a staminate flower and a hermaphrodite flower. The petals end in extended sharp points. Pollination of *Eugeissona tristis* has been studied by Wiens et al. (2008) in Peninsular Malaysia. Plants produced inflorescences throughout the year. Flower buds produced nectar for 38 days (all numbers are medians) before they opened, and this nectar leaked out from the buds through gaps between the petals. The nectar contained 3.8% alcohol concentration. Flowers were able to produce this alcoholic nectar because they harboured several species of fermenting yeast. Wiens et al. suspected that inoculation of the nectar with yeast started very soon after the nectar was exuded, and that insect visitors, such as drosophilid flies, nitidulid beetles, and various bees, transported the yeast.

Figure 1. A. Infructescence of *Eugeissona tristis* (image by J. Dransfield). B. Staminate inflorescence of *Mauritia flexuosa*. C. Partial staminate inflorescence of *Calamus peregrinus*. D. Inflorescence of *Calamus melanochaetes*, covered by semi-persistent bracts at anthesis.

During this time, flowers produced a strong alcoholic scent. Staminate flowers opened first for one night and produced pollen. This was followed by a period of 42 days with no production of pollen or nectar, followed by 51 days of nectar production. This was followed by two nights of staminate anthesis, and then a period of 21 days of little nectar production followed by pistillate anthesis. Inflorescences attracted up to seven species of small, non-flying mammal, but the nocturnal pentailed treeshrew (*Ptilocercus lowii*, Ptilocercidae) was the most frequent visitor. The treeshrews moved up and down the inflorescence, consuming nectar (in relative amounts that would intoxicate a human), but it appeared to have no effect on the treeshrews. *Eugeissona tristis* grows in dense groves, and the treeshrews moved from palm to palm, thus pollinating the flowers.

Compared to other palms and their pollinators, *Eugeissona* seems an extreme example of specialized pollination, especially in terms of its reward for pollinators. It is unusual in other respects. It is sister genus to all other genera of the Calamoideae, and this subfamily is sister to all other palm subfamilies (Ferreira et al. in prep.). It is semelparous. It has an unusual flower arrangement (dyads of one staminate and one hermaphrodite flower), and unusual flowers with long, woody, spiny petals, amongst the largest in the family. Stauffer et al. (2016) described a unique type of nectary from *E. tristis*. As outlined above, it has unique inflorescence development, with anthesis taking place over more than 100 days, and unique pollinators. It has a long fossil record (Dransfield et al. 2008). The main pollinator is the pentailed treeshrew. This also has a long evolutionary history and presumably a long interaction with *Eugeissona*. Wiens et al. (2008) wrote: "The pentailed treeshrew is considered a living model for extinct mammals representing the stock from which all extinct and living treeshrews and primates radiated."

It is curious that inflorescences develop from pre-anthesis nectar production to pistillate anthesis over more than 150 days, and yet there are apparently only three days of staminate anthesis.

Calamoideae, Lepidocaryeae, Ancistrophyllinae

The subtribe comprises three genera (*Oncocalamus,* 4 species; *Eremospatha,* 11 species; *Laccosperma,* 7 species) distributed in Africa. No genera have been studied.

Calamoideae, Lepidocaryeae, Raphiinae

The subtribe comprises one genus (*Raphia,* 22 species) distributed in Africa with one species in the Neotropics. No species have been studied.

Calamoideae, Lepidocaryeae, Mauritiinae

The subtribe comprises three genera (*Mauritia,* 2 species; *Mauritiella,* 5 species; *Lepidocaryum*, 1 species) distributed in the Neotropics. Two genera have been studied.

Mauritia

Mauritia is dioecious with large, much branched inflorescences. Staminate rachillae bear paired or solitary flowers (Fig. 1B), those of pistillate bear solitary flowers. Pollination of *M. flexuosa* has been studied at six different sites (Table 1).

Flowering was reported to be throughout the year at one site, but at other sites there was a 3–7-month flowering season, and this could be at different times of the year. For example, Mendes et al. (2017) recorded a peak in flowering from August to October during the dry season, while Abreu (2001) recorded a peak from March to April during the rainy season.

On staminate inflorescences anthesis usually lasted about a week, sometimes longer. Flowers usually opened in flushes during the late afternoon, from 15.00 onwards, and lasted about 24 hours. They were bright orange in colour and sweetly scented but did not produce nectar. At two sites, staminate inflorescences were reported to heat up, at one site not. Pollen was reported to be sticky by two studies and powdery by one study (the one that reported wind pollination).

On pistillate inflorescences, anthesis lasted 6–15 days. Flowers usually opened during the late afternoon, from 16.00 onwards, and lasted 48–96 hours. Flowers were bright orange in colour and sweetly scented. Two studies reported that they produced nectar (although it was not clear is this was nectar or stigmatic exudate), and two that they did not. At two sites, pistillate inflorescences were reported to heat up, and at one site that they did not.

Table 1. Pollination of *Mauritia flexuosa*.

Site	Ecuador, Napo	Colombia, Casanare	Brazil, Roraima	Brazil, Amazonas	Brazil, Maranhão	Brazil, Minas Gerais
Flowering season (months), peak	November to January, peak in December	throughout the year, peak June to September	September to November	February to August, peak in April	peak August to October	November to April, peak in March to April
Duration of ♂ anthesis on an inflorescence (days)	ca. 6	to 30	<7	7–15	7–9	8–12
Start of ♂ anthesis (time)	17.00	16.00	irregular	16.00	15.00	18.00
Duration of ♂ anthesis in a flower (hours)	ca. 12	to 20	-	24	ca. 24	24–48
♂ scent	sweet scent	strong, sweet scent	sweet scent	strong scent	strong, sweet scent	sweet scent
♂ temperature elevation	-	-	none	-	1°C above ambient	2.9°C above ambient
♂ nectar	-	none	none	-	-	none
Duration of ♀ anthesis on an inflorescence (days)	ca. 6	6–15	<7	5	-	-
Start of ♀ anthesis (time)	17.00	16.00	irregular	16.00	16.00	17.00
Duration of ♀ anthesis in a flower (hours)	ca. 96	48	-	to 96	to 72	48
♀ scent	sweet scent	strong, sweet scent	sweet scent	strong scent	strong, sweet scent	sweet scent
♀ temperature elevation	-	-	none	-	5°C above ambient	2.9°C above ambient
♀ nectar	-	present	none	-	none	present
Number of insect visitors (species)	at least 10	♂ 61, ♀ 16	♂ 20, ♀ 13	at least 25	♂ 65, ♀ 41	12
Most effective pollinators	Alticinae sp. (Chrysomelidae)	*Mystrops* sp. (Nitidulidae)	wind	Nitidulidae, Curculionidae, Cucujidae	*Grasidius* sp. (Curculionidae)	*Trigona* (Apidae)
Reference	Ervik (1993)	Núñez & Carreño-Barrera (2013)	Khorsand Rosa & Koptur (2013)	Storti (1993)	Mendes et al. (2017)	Abreu (2001)

Large numbers of different species of insect visited inflorescences, from at least 10 to 65, more on staminate than on pistillate. Each of the six studies postulated different pollinators. Ervik (1993) considered a chrysomelid beetle in the Alticinae was the most likely pollinator. Núñez & Carreño-Barrera (2013) found that a nitidulid beetle, *Mystrops dalmasi* was the most effective pollinator. They stated that wind pollination did not occur at their site. Khorsand Rosa & Koptur (2013) considered that wind was the primary pollen vector. They did not record any temperature elevation nor any nectar production in pistillate flowers. Interestingly, nor did they record late afternoon opening of flowers, rather staminate and pistillate flowers opened irregularly. They also recorded a low diversity of insect visitors to flowers and stated that these visitors were not pollinators. Storti (1993) considered pollination was by beetles in the families Nitidulidae, Curculionidae, and Cucujidae. She considered that wind pollination did not occur at her site. Mendes et al. (2017) found that flowers did not produce nectar but exhibited temperature elevation during anthesis. They considered that curculionid beetles in the genus *Grasidius* were the most likely pollinators, although wind could contribute to the pollination but in a relatively minor way. Finally, Abreu (2001) recorded that pistillate flowers produced nectar, and bees (*Trigona* sp.) were common visitors to both staminate and pistillate flowers, collecting pollen and nectar respectively, and were probably the most effective pollinators.

Núñez & Carreño-Barrera (2013) considered that the nitidulid pollinators were attracted to staminate inflorescences by scent and were rewarded with pollen and were attracted to reward-less pistillate inflorescences by scent ("chemical mimicry"). Núñez & Carreño-Barrera (2013) and Knudsen et al. (2001) found that *M. flexuosa* inflorescences gave off scents dominated by tridecane, and that scent from staminate and pistillate inflorescences were 95% similar. Mendes et al. (2017) considered that the weevil pollinators were attracted to staminate inflorescences by scent and were rewarded with pollen, but were attracted to pistillate inflorescences by scent but were rewarded with stigmatic exudate.

Núñez & Carreño-Barrera (2016) carried out a survey of insect visitors to *M. flexuosa* inflorescences in seven sites in Colombia; four in the Amazon region (Amazonas, Caquetá, Guaviare, and Putumayo) and three in the Orinoco region (Arauca, Casanare, and Meta). They found a total of 104 species of insect visiting inflorescences and between 50% and 75% of the species were found at all sites. They found that the composition and abundance of the insect fauna differed among sites. Despite these differences in the overall fauna, they considered that a smaller group of insects were the most effective pollinators at all sites, and this group contained *Grasidius* spp., *Phytotribus* sp., *Phyllotrox* sp., and *Celetes* sp. (Curculionidae), *Mystrops dalmasi* (Nitidulidae), and *Trigona amalthea* (Apidae). Thus, insect visitors to *Mauritia* inflorescences could be divided into generalists (which varied in composition and abundance from site to site) and specialists (weevils, nitidulids, bees) that did not vary from site to site. These specialists not only pollinated the palms but also, in the case of the beetles, oviposited and bred on inflorescences and thus depended on the palms for their life cycle (i.e., brood-site pollinators). Thus, a mutual dependence between palms and beetles existed. Of the six studies in Table 1, only two gave detailed lists of pollinators, Núñez & Carreño-Barrera (2013) and Mendes et al. (2017). Interestingly, these two studies, from almost opposite sides of the geographic range of *M. flexuosa*, list almost the same pollinators as Núñez & Carreño-Barrera (2016), namely curculionids (*Grasidius*, *Phytotribus*, and *Celetes*), nitidulids (*Mystrops*), and bees (*Trigona*).

One other study is relevant here. Reina Vivas & Bravo Gomez (2021) also analyzed geographic variation in the composition of inflorescence-visiting weevils. They studied five populations of *M. flexuosa* in Colombia and concluded that there was low geographic variation in the community of weevils associated with inflorescences. They wrote: "Based on the similarity of the results in composition, richness, abundance and diversity, it is concluded that there is a low spatial variation in the community of weevils associated with inflorescences of *M. flexuosa*. This can be explained by the strong dependence and specificity that many of the community weevils present with the palm, demonstrating a mutualism where the palm receives the benefit of pollination and the weevils a source of both refuge and food to carry out their life cycle."

Mauritia flexuosa is one of the most widespread of palms in South America, occurring from Trinidad and northern Venezuela all the way through the Amazon region to Bolivia and central Brazil. It is also one of the most abundant species, occurring in large stands in wet, swampy places, in both forested and savanna regions. It is not considered to be particularly variable morphologically (and has very few synonyms for such a widespread species). The six study sites (Table 1) span almost the entire geographic range and habitat type of *M. flexuosa*. The westernmost study site is in lowland rainforest in Napo, Ecuador (Ervik 1993) and is almost 4,000 km from the easternmost study site in open, coastal areas in Maranhão, Brazil (Mendes et al. 2017). The northernmost study site is in gallery forest in savannas in Casanare, Colombia (Núñez & Carreño-Barrera 2013) and is almost 4,000 km from the southernmost study site in swampy areas in the cerrado of Minas Gerais, Brazil (Abreu 2001). At first sight, the studies in Table 1 might suggest that *M. flexuosa* has different phenology, inflorescence development, and insect visitors at different sites, and different pollinators, including beetles, bees, and wind. The contribution of different pollinators seems to vary by season and by geography, possibly linked to climatic and environmental variables. This could be viewed as an example of incipient speciation whereby populations become reproductively isolated through different pollinators in different environments (pollination ecotypes, Van der Niet et al. 2014). However, studies by Núñez & Carreño-Barrera (2013, 2016), Mendes et al. (2017), and Reina Vivas & Bravo Gomez (2021) suggest there may be a widespread group of specialist pollinators of *M. flexuosa* comprising small curculionid and nitidulid beetles. These feed, mate, and oviposit on staminate inflorescences, where their larvae develop, and visit pistillate inflorescences because they are deceived by scent, which is similar to that of staminate inflorescences, or to feed on the stigmatic exudate of the pistillate flowers. All six studies listed in Table 1 included curculionids and nitidulids as insect visitors to inflorescences. Given the wide range of *M. flexuosa*, and the vast stands in which it occurs in some areas (Goulding & Smith 2007), there could be astronomical numbers of individual beetles associated with its inflorescences.

Mauritiella

Mauritiella is dioecious. Staminate plants produce inflorescences bearing paired or solitary flowers. Pistillate plants produce inflorescences with solitary flowers. *Mauritiella aculeata* has been studied by Listabarth (1999b) in Venezuela. Flowering season was only one month and there was high synchrony between staminate and pistillate flowering. Staminate anthesis on an inflorescence lasted 4–7 days. Staminate flowers opened from 06.00–07.00 and lasted one day. They were green in colour and produced a fir-like scent. Pistillate anthesis on an inflorescence lasted 3–7 days. Pistillate flowers opened during the mornings and lasted about 24 hours. They were green in colour and produced a fir-like scent. At least seven species of insect, all diurnal, visited inflorescences and the most effective pollinators were considered to be bees, *Trigona* spp. (Apidae).

Mauritiella aculeata has a much narrower range than *Mauritia flexuosa*, and a more specialized habitat. It has a considerably shorter flowering season, and morning rather than late afternoon or evening anthesis. It is interesting that no curculionid or nitidulid beetles were recorded from inflorescences.

Calamoideae, *Calameae*, *Korthalsiinae*

The subtribe comprises one genus (*Korthalsia,* 28 species) distributed in the Asian tropics. No species have been studied.

Calamoideae, *Calameae*, *Salaccinae*

The subtribe comprises two genera (*Eleiodoxa,* 1 species; *Salacca,* 23 species) distributed in the Asian tropics. One genus has been studied.

Salacca

Salacca is dioecious and has inflorescences borne near ground level. Staminate flowers are borne in pairs and are closely spaced on the rachillae. Pistillate inflorescences are condensed with closely spaced flowers borne in pairs of a pistillate flower and a sterile staminate flower. Mogea (1978) studied pollination of cultivated plants of *S. zalacca* (as *S. edulis*) in Indonesia. Anthesis on staminate inflorescences lasted three days, and flowers secreted nectar. Anthesis on pistillate inflorescences started at 18.00. Flowers were at anthesis for about 12 hours. A nectar-like secretion was produced by the pistillate petals, and flowers gave off a ginger scent. Inflorescences were reported to be visited by four species of insect. The most abundant was a curculionid weevil and this was considered to be the pollinator. The weevils fed on a nectar-like secretion from the pistillate petals, and oviposited there.

Atmowidi et al. (2021) reported that nine species of insect visited inflorescences of cultivated *S. zalacca* in Indonesia, and that three of these were potential pollinators—the derelomine weevil *Nodocnemus* sp. and the bees *Apis cerana* and

Tetragonula laeviceps. It seems likely that the unidentified weevils cited by Mogea (1978) are also *Nodocnemus*.

Calamoideae, Calameae, Metroxylinae

The subtribe comprises one genus (*Metroxylon,* 5 species) distributed in the Asian tropics. *Metroxylon* is semelparous (except for one species) and polygamous. In semelparous species, numerous inflorescences are produced together at the same time and these project above the leaves in a large compound structure. Flowers are borne in pairs of a staminate flower and a hermaphrodite flower. No species have been studied in their natural habitat, but Jong (1995) studied pollination of cultivated plants of *M. sagu* in Sarawak, Malaysia. Total anthesis on an inflorescence (this is assumed here to include all inflorescences on a stem) lasted 50–100 days. Flowers were borne in pairs although it was common that one or other flower bud of the pair aborted during development. Staminate flowers opened first and inflorescences were at staminate anthesis for 21–28 days. Individual staminate flowers opened at around 10.30 and lasted approximately one day. Flowers produced nectar. There was sometimes a slight overlap between staminate anthesis and anthesis of hermaphrodite flowers. Anthesis of hermaphrodite flowers lasted about 14 days. Flowers opened from 07.00 and produced nectar. It was not clear if staminate and pistillate anthesis of hermaphrodite flowers overlapped. Large numbers of stingless bees (*Trigona* spp.) visited inflorescences at anthesis of both staminate and pistillate flowers.

Utama (1986) has also given a few notes on pollination of *M. sagu* in Java.

Calamoideae, Calameae, Pigafettinae

The subtribe comprises one genus (*Pigafetta,* 2 species) distributed from Sulawesi to New Guinea. No species have been studied.

Calamoideae, Calameae, Plectocomiinae

The subtribe comprises three genera (*Plectocomia,* 14 species; *Myrialepis,* 1 species; *Plectocomiopsis,* 6 species) distributed in the Asian tropics. No genera have been studied. There is one brief mention of insect pollination in *Plectocomia* (Madulid 1980).

Calamoideae, Calameae, Calaminae

The subtribe comprises one genus (*Calamus,* 411 species) widely distributed throughout the Asian tropics with one species in Africa. *Calamus* is dioecious. Inflorescence of staminate plants contain closely spaced staminate flowers, alternately and distichously arranged along the rachillae (Fig. 1C). Inflorescences of pistillate plants contain dyads of one pistillate flower paired with a neuter flower (a flower that is similar to a staminate flower but does not produce pollen). The dyads are alternately and distichously arranged along the rachillae. Ten species have been studied (Table 2).

Flowering seasons were generally rather short. In Bøgh's (1996) site in Thailand, different species had different peak months for flowering, and in some species staminate plants began flowering before pistillate plants.

For staminate inflorescences, anthesis lasted 5–150 days, and there was a particularly wide range in *C. castaneus*. In three species (*C. caesius, C. moseleyanus,* and *C. manan*), anthesis began early in the evening. In six species (*C. hookerianus, C. longisetus, C. peregrinus, C. rudentum, C. smitinandii,* and *C. thwaitesii*) it began later in the evening, usually around midnight, and in one species, *C. castaneus*, it began early in the morning. Flowers opened in flushes each day, were short-lived, and produced nectar and a sweet scent.

For pistillate inflorescences, anthesis lasted 7–31 days. Anthesis was nocturnal in all species except *C. castaneus,* where it began early in the morning. Duration of anthesis of flowers was 24–96 hours, but considerably longer in *C. castaneus*. Neuter flowers on pistillate inflorescences produced nectar and presumably the sweet scent.

Lee et al. (1995) considered that nocturnal, nectar-feeding moths in the families Pyralidae and Noctuidae were the most effective pollinators of *C. caesius* and *C. moseleyanus,* and Alloysius (1999) also indicated moths as pollinators of *C. manan*. These three species are closely related and are characterized by their leaves with cirri and relatively short inflorescences (Henderson 2020a). On the other hand, *C. longisetus, C. peregrinus, C. rudentum,* and *C. smitinandii* have leaves with flagella and tend to have longer inflorescences.

Table 2. Pollination of *Calamus* spp. (1/2, continued next page)

	C. caesius Borneo	*C. moseleyanus* (as *C. subinermis*) Borneo	*C. manan* Borneo	*C. hookerianus* India	*C. thwaitesii* India
Flowering season (months), peak	-	-	October to December	peak May to August	peak May to August
Duration of ♂ anthesis on an inflorescence (days)	-	10–15	41	12	>15
Start of ♂ anthesis (time)	18.00	18.00	18.00	23.00	01.00
Duration of ♂ anthesis in a flower (hours)	6–12	6–12	10	12–18	12–18
♂ scent	-	scent	strong scent	strong, sweet scent	strong, sweet scent
♂ temperature elevation	-	-	-	-	-
♂ nectar	-	present	present	present	present
Duration of ♀ anthesis on an inflorescence (days)	20–30	10–15	25	12–15	12–15
Start of ♀ anthesis (time)	-	nocturnal	mostly nocturnal	01.00	01.00
Duration of ♀ anthesis in a flower (hours)	96	48	24–48	ca. 12	ca. 12
♀ scent	scent	scent	-	scent	scent
♀ temperature elevation	-	-	-	-	-
♀ nectar	present	present	present, from neuter flowers	-	-
Number of insect visitors (species)	31 (♂), 24 (♀)	41 (♂), 64 (♀)	77 (♂), 16 (♀)	-	-
Most effective pollinators	Pyralidae, Noctuidae	Pyralidae, Noctuidae	Pyralidae, Noctuidae, *Trigona* spp. (Apidae)	-	-
Reference	Lee & Jong (1995), Lee et al. (1995)	Lee & Jong (1995), Lee et al. (1995)	Alloysius (1999)	Sulekha (2003)	Sulekha (2003)

Bøgh (1996) found that these were visited by a variety of insects (but not moths) and that diurnal bees (*Trigona* spp.) were the most probable pollinators. He was puzzled by the fact that staminate flowers opened and released nectar well before dawn, but no moths were found on flowers during the night. Sulekha (2003) did not give any information on pollinators, but the inflorescence development of the two species studied, *C. hookerianus* and *C. thwaitesii,* was similar to that of other flagellate species. The other species, *C. castaneus,* is in neither the cirrate nor the flagellate group of species, but in the *Calamus albidus* group of species (Henderson 2020a). It has diurnal anthesis and pollination by trigonid bees. One notable feature of the insect visitors to *Calamus* inflorescences is the complete lack of Nitidulidae and scarcity of Curculionidae. *Calamus moselyanus*

Table 2. Pollination of *Calamus* spp. (2/2)

	C. longisetus Thailand	*C. peregrinus* Thailand	*C. rudentum* Thailand	*C. smitinandii* (as *C. sp.*) Thailand	*C. castaneus* Thailand
Flowering season (months), peak	-	November to April	at least June to August	September to April	July to September
Duration of ♂ anthesis on an inflorescence (days)	-	30–60	-	45–150	5–65
Start of ♂ anthesis (time)	22.00	22.00	22.00	22.00	06.00
Duration of ♂ anthesis in a flower (hours)	ca. 12	ca. 12	ca. 12	ca. 12	2–9
♂ scent	sweet scent	sweet scent	sweet scent	-	sweet, musky scent
♂ temperature elevation	-	-	-	-	-
♂ nectar	present	present	present	present	present
Duration of ♀ anthesis on an inflorescence (days)	at least 7	at least 7	few days	at least 7	11–31
Start of ♀ anthesis (time)	18.00	18.00	18.00	18.00	before 06.00
Duration of ♀ anthesis in a flower (hours)	ca. 48	ca. 48	ca. 48	ca. 48	24–240
♀ scent	sweet scent	sweet scent	sweet scent	-	sweet scent
♀ temperature elevation	-	-	-	-	-
♀ nectar	present, from neuter flowers	present, from neuter flowers	present, from neuter flowers	present, from neuter flowers	present, from neuter flowers
Number of insect visitors (species)	4	12	23	12	>23
Most effective pollinators	*Trigona* spp. (Apidae)	*Trigona* spp. (Apidae)	*Trigona* spp. (Apidae)	*Trigona* spp. (Apidae)	*Trigona* spp. (Apidae)
Reference	Bøgh (1996)	Bøgh (1996)	Bøgh (1996)	Bøgh (1996)	Kidyoo & McKey (2012)

is unusual in having a higher number of insect visitors to pistillate, rather than staminate inflorescences.

There are two other brief studies of *Calamus viminalis* (as *C. siamensis*) in cultivation (Pattanavibool & Sornsathapornkul 2001, Sornsathapornkul & Pattanavibool 2000). Plants flowered throughout the year. Staminate flowers were scented and produced nectar. Pistillate anthesis lasted 24 hours. Bees, *Apis* sp. and *Trigona* sp., were considered the most effective pollinators.

The function of the neuter flowers is of interest. Both Bøgh (1996) and Kidyoo & McKey (2012) considered that these flowers, similar in appearance to staminate flowers, attracted pollinators to pistillate inflorescences by their production of nectar and scent, and in doing so placed them in contact with stigmas of the adjacent pistillate flower.

All the species discussed above have open inflorescences. However, there are some *Calamus* species (previously included in *Daemonorops*) that have condensed inflorescences with closely spaced flowers. In *C. calicarpus* and *C. melanochaetes* (Fig. 1D) the inflorescences are greatly contracted and covered by semi-persistent bracts at anthesis with the rachillae and flowers crowded together. At anthesis the bracts surrounding the inflorescence split laterally to reveal the flowers. Unfortunately, there are no studies of pollination of these species, but they appear to be beetle-pollinated (Dransfield 1979a). In a few other species of *Calamus* (formerly included in *Ceratolobus*) the prophyll completely encloses the inflorescence during and after anthesis, and opens only by two, small lateral splits near the apex. The prophyll may split later as fruits develop, but at anthesis the only way for insects to reach the flowers is by crawling inside the prophyll through the minute apical split. Dransfield (1979b) reported that staminate and pistillate inflorescences produced a musty scent. Although there was no direct evidence of insect pollination, the presence of numerous insects, particularly staphylinids in both staminate and pistillate inflorescences, seemed to indicate beetle pollination. Species of *Calamus* formerly included in *Calospatha, Retispatha*, and *Pogonotium* also have condensed inflorescences, as well as a few other species such as *C. sedens*.

Summary for Calamoideae

Of the 549 species (almost a quarter of all palm species) and 17 genera of Calamoideae, pollination of only 15 species in six genera has been studied.

Eugeissona is extraordinary by almost any measure, particularly in inflorescence development, and such development has not been reported in any other palm. The only other hermaphrodite palm studied, *Metroxylon*, appears to be pollinated by bees. Both these palms have unusually long periods of anthesis on an inflorescence, 100 days or more, although in *Metroxylon* this includes all inflorescences on a single stem.

Two genera and two species have been studied in the subtribe Mauritiinae. *Mauritia flexuosa* is a good example of the complexities of pollination—the more data available, the more complex and variable the pollination system appears. Depending on locality, *Mauritia* could be considered to be beetle-pollinated, bee-pollinated, or wind-pollinated.

Salacca is remarkable in that it is one of the few, perhaps the only beetle-pollinated palm in which pistillate flowers produce nectar, or at least a nectar-like secretion.

Bøgh (1996) wrote: "At present, no clue can be given to a link between the pollinators and the morphological and phenological variation in *Calamus* flower presentation." However, there seems a potential link between nocturnal anthesis in both staminate and pistillate inflorescences with sweet scent and nectar production, and moth pollination. All species studied but one (*C. castaneus*) have this kind of inflorescence development.

In *Calamus* in general, there may have been at least six independent shifts from relatively open inflorescences to more condensed, closed inflorescences (e.g., *C. calospathus, C. dumetosus, C. melanochaetes, C. pogonotium* and related species, *C. sedens, C. subangulatus* and related species) (Ferreira et al. in prep.). The condensed, closed inflorescences may be beetle pollinated, although this has yet to be studied in any detail. It is interesting that *Calamus*, by far the largest genus of palms, is dioecious; dioecy is often associated with clades of lower species richness (Heilbuth 2000).

NYPOIDEAE

The subfamily comprises one genus, *Nypa*, with one species, *N. fruticans*. This is widely distributed in the Asian tropics from Sri Lanka and eastern India through Indochina, Malaysia, Indonesia, the Philippines, and New Guinea, and reaching eastern Australia, the Solomon Islands, and the Ryukyu Islands.

Nypa

Nypa is monoecious. Inflorescences have unusual morphology. Initially they are tightly covered with bracts. Pistillate flowers are borne in a dense, globose head that terminates the inflorescence axis. Lateral branches bear short rachillae with densely arranged staminate flowers (Fig. 2A). *Nypa fruticans* has been studied in five localities (Table 3).

Plants flowered throughout the year, with peaks at various times of the year. Inflorescences were protogynous. Pistillate anthesis lasted 1–5 days, and all flowers opened together early in the morning. However, there was some doubt that

Figure 2. A. Inflorescence of *Nypa fruticans*, the central pistillate with developing fruits, the lateral staminate past anthesis. B. Flowers of *Sabal etonia* (image by S. Zona). C. Open, elongate inflorescence of *Coccothrinax argentata* (image by R. Duno de Stefano). D. Condensed inflorescence of *Cryosophila warscewiczii* after pistillate anthesis and before staminate anthesis.

pistillate flowers were at anthesis for more than two days because of the difficulty of determining if their stigmas were receptive or not. Flowers produced stigmatic exudate, accompanied by temperature elevation. One study reported a strong, sweet scent and another reported no scent. Staminate anthesis began the day after the first day of pistillate anthesis. There seemed to be someoverlap between the end of pistillate anthesis and the start of staminate anthesis. Staminate anthesis lasted 10–40 days, with flushes of flowers opening each day in the morning. Staminate anthesis was accompanied by a strong scent and temperature elevation. Staminate flowers were bright orange and produced sticky pollen, but did not produce nectar.

The number of different species of insect visiting inflorescences was relatively low. Pollination was reported to be by drosophilid flies and nitidulid and curculionid beetles. Drosophilid flies were reported to feed and breed on pistillate and staminate flowers, and complete their life cycle on the inflorescences (Essig 1973). Such is the length of anthesis on an inflorescence that the offspring of the flies could themselves become pollinators. Nitidulid and curculionid beetles ate pollen, mated, and oviposited on inflorescences. The persistent staminate flowers may be a site for developing insect larvae.

Table 3. Pollination of *Nypa fruticans*.

	New Guinea	Peninsular Malaysia	Thailand*	Thailand	Philippines
Flowering season (months), peak	-	throughout the year, peak October to February	-	peak from December to February	throughout the year
Duration of ♀ anthesis on an inflorescence (days)	-	4–5	-	2(–3)	1
Start of ♀ anthesis (time)	-	ca. 06.00	-	03.00	-
Duration of ♀ anthesis in a flower (hours)	-	-	-	48	-
♀ scent	-	strong, sweet scent	-	none	-
♀ temperature elevation	-	present	6°C above ambient	present	-
♀ nectar	none	-	-	-	-
Inter-anthesis (days)	-	-	-	-	-
Duration of ♂ anthesis on an inflorescence (days)	-	30–40	-	10–14	13–14
Start of ♂ anthesis (time)	ca. 09.30	ca. 07.00	-	-	-
Duration of ♂ anthesis in a flower (hours)	-	ca. 5	-	-	-
♂ scent	-	strong scent	coumarin scent	strong, coumarin scent	-
♂ temperature elevation	-	present	-	-	-
♂ nectar	none	-	-	-	-
Number of insect visitors (species)	at least 3	9	10	6	15
Most effective pollinators	*Drosophila* sp.	*Drosophila* spp.	*Epuraea* sp. (Nitidulidae), Curculionidae spp.	"beetles", "large flies"	*Drosophila* sp., *Epuraea* sp. (Nitidulidae),
Reference	Essig (1973)	Fong (1986, 1987)	Staarup et al. (2018)	Hoppe (2004)	Mantiquilla et al. (2013, 2016)

*Study carried out in a botanical garden.

Inflorescences may attract more insects than indicated in Table 3. Panabang et al. (2017), in a detailed study of visitors to *Nypa* inflorescences in the Philippines, recorded 26 species of insect visitors. They found that *Epuraea* sp. and *Haptorcus* sp. (Nitidulidae), Rhynchoporini sp. and Apionini sp. (Curculionidae), and *Drosophila* spp. (Drosophilidae) were the main insect visitors and likely pollinators. On the other hand, Nguyen (2008) recorded only six species of insect visiting *Nypa* inflorescences in Vietnam, and these were all bees, flies, or, more rarely, wasps. Azuma et al. (2002) found more than 25 chemical compounds in the floral scent of *Nypa*, dominated by carotenoid derivatives.

Summary for Nypoideae

Despite its extraordinary inflorescence morphology, *N. fruticans* appears to be pollinated by insects that are relatively common as palm pollinators, drosophilid flies and nitidulid beetles. Development of inflorescences, with protogyny, short pistillate anthesis, temperature elevation, and scent, fits a beetle pollination syndrome, but *N. fruticans* is pollinated by insects from two orders, Diptera and Coleoptera.

CORYPHOIDEAE

Coryphoideae, Sabaleae

The tribe comprises one genus (*Sabal*, 15 species) distributed in Central America and the Caribbean.

Sabal

Sabal produces elongate, much-branched inflorescences with numerous, solitary, hermaphrodite flowers (Fig. 2B). Four species have been studied (Table 4).

Flowering seasons appeared to be relatively short, at least in the more northerly occurring species. In *S. palmetto* there was an increase in the length of flowering season from north to south of its range.

Anthesis on an inflorescence lasted 5–20 days. All species had diurnal anthesis with flushes of flowers opening each day, and flowers produced nectar and scent. Two species, *S. minor* and *S. palmetto,* exhibited random/basipetal direction of development of flowers on an inflorescence and basipetal development within flowers, hence protogyny. The other two species, *S. etonia* and *S. mauritiiformis,* exhibited acropetal development of flowers on an inflorescence and acropetal development within flowers, hence protandry. The significance, if any, of this is unclear. Henderson (2002) considered that it could be related to basipetal foraging of wasps and acropetal foraging of bees on inflorescences. *Sabal minor* and *S. palmetto* are closely related (Ferreira et al. in prep.), *S. etonia* and *S. mauritiiformis* not so closely.

There were large numbers of different species of insect visiting inflorescences. Bees and wasps were the most effective pollinators. Koptur & Khorsand Rosa (2018) recorded 22 insect species visiting inflorescences of *S. palmetto*. Many of these were the same as visitors to two other sympatric palms, *Serenoa repens* and *Coccothrinax argentata*.

Brieva-Oviedo & Núñez (2020) noted several contrasting aspects of *S. mauritiiformis* pollination; high intensity of flowering and high numbers of flowers per inflorescence but low level of reproductive efficiency (7.6%), high numbers of insect visitors but few individuals of each visitor, and beetles (including *Phyllotrox*) the most diverse

Table 4. Pollination of *Sabal* spp.

	S. etonia USA	*S. mauritiiformis* Colombia	*S. minor* USA	*S. palmetto* USA
Flowering season (months), peak	May to July	April to November, peak June to August	June to July	April to August
Dichogamy, direction of anthesis	weakly protandrous, acropetal	protandrous, acropetal	protogynous, random/ basipetal*	protogynous, random/ basipetal*
Duration of anthesis on an inflorescence (days)	5–7	10–20	10–17	7–14
Start of ♂ anthesis (time)	07.20	06.30	10.00	07.30
Start of ♀ anthesis (time)	-	10.00	06.00	05.00
Scent	strong, pungent scent	scent	scent	sweet scent
Temperature elevation	-	-	-	-
Nectar	present	present	present	present
Number of insect visitors (species)	30	65	40	65
Most effective pollinators	bees (Megachilidae, Halictidae)	*Nannotrigona* sp., *Scaptotrigona* sp. (Meliponidae)	*Ampelopsis* sp. (Vespidae)	bees (Halictidae, Apidae)
Reference	Zona (1987)	Brieva-Oviedo & Núñez (2020)	Ramp (1989)	Brown (1973, 1976)

* data from Brieva-Oviedo & Núñez (2020).

group of insect visitor but bees the most abundant and most effective pollinators.

Coryphoideae, *Cryosophileae*

The tribe comprises 11 genera (*Schippia,* 1 species; *Trithrinax,* 3 species; *Zombia,* 1 species; *Coccothrinax,* 39 species; *Hemithrinax,* 3 species; *Leucothrinax,* 1 species; *Thrinax,* 3 species; *Chelyocarpus,* 4 species; *Cryosophila,* 10 species; *Itaya,* 1 species; *Sabinaria,* 1 species) distributed throughout the Neotropics. Three genera have been studied.

Coccothrinax

Coccothrinax has inflorescences with solitary, hermaphrodite flowers (Fig. 2C). These lack well-developed sepals and petals. Pollination of *C. argentata* has been studied in Florida by Khorsand Rosa & Koptur (2009) and Koptur & Khorsand Rosa (2018). Plants flowered from February to May. All flowers on an inflorescence opened together very quickly before 08.00 and produced a strong, sweet scent but did not produce nectar. Whether the flowers were protandrous or protogynous was not reported. Flowers were at anthesis for less than one week. Five different species of insect visited inflorescences, three species of bee, one fly, and one ant. The three bee species were considered the most effective pollinators. Khorsand Rosa & Koptur (2009) considered that bees and wind could contribute to pollination, while Koptur & Khorsand Rosa (2018) emphasized the role of the carpenter bee, *Xylocopa micans,* in pollination.

Coccothrinax argentata is unusual in that it does not produce nectar, all flowers of an inflorescence open together at the same time, and few different species of insect visit inflorescences.

Thrinax

Thrinax has inflorescences with solitary, hermaphrodite flowers. These lack well-developed sepals and petals. Read (1975) studied pollination of *T. parviflora* in Jamaica. Individual plants could produce 4–10 inflorescences at one time, and all inflorescences flowered at the same time. Flowers opened at dawn and were at staminate anthesis immediately following exertion from the rachis bracts. Pollen was powdery and produced in large quantities. At this time stigmas were compressed. The following morning, stigmas expanded and were funnel-like. No scent, nectar, or insect visitors were reported. Plants were presumed to be wind-pollinated, although self-pollination seemed likely. However, Read (cited in Uhl & Moore 1977) found "small pollen-eating beetles and thrips-like insects present in profusion on most inflorescences."

Campos-Navarrete et al. (2013) listed megachilid bees (*Megachile* spp.) as pollinators of *T. radiata* at a site in coastal Mexico.

Cryosophila

Cryosophila has inflorescences with solitary, hermaphrodite flowers (Fig. 2D). Henderson (1984) studied pollination of *C. warscewiczii* (as *C. albida*) in Costa Rica. Plants flowered for at least three months, from June to August. Inflorescences were protogynous. Pistillate anthesis took place for at least 36 hours before the enclosing rachis bracts opened. In the hours prior to bract opening, inflorescences heated up to 2.2–3.2°C above ambient. At the same time a strong, musty scent was produced. The enclosing rachis bracts opened around dawn, and at this time temperature of the bud rose steeply to 7.6°C above ambient. As soon as the stigmas were visible, they were found to be past anthesis. During the same morning staminate anthesis began and continued until the following morning. Thirteen species of insect visited inflorescences. The most effective pollinators were considered to be curculionid (*Derelominus* sp.) and nitidulid (*Mystrops* sp.) beetles. These beetles arrived on the inflorescence during the morning of the opening of the rachis bracts, and left after staminate anthesis.

Summary for Cryosophileae

Of the 11 genera and 67 species of the tribe, only three species in three genera have been studied. In Ferreira et al. (in prep.), five genera (*Chelyocarpus, Cryosophila, Itaya, Trithrinax, Sabinaria*) are basal in the Cryosophileae clade. These have more or less condensed inflorescences and closely spaced flowers, and may all be beetle-pollinated based on the similarity of the inflorescences of *Chelyocarpus, Itaya, Trithrinax*, and *Sabinaria* to those of *Cryosophila*. Franz & Valente (2005) considered that the derelomine weevil *Celetes trithrinacis* reproduced on *Trithrinax campestris*, and Bernal (2014) considered mystropine beetles to be the probable pollinators of *Sabinaria*. The more derived genera in the phylogeny (*Coccothrinax, Hemithrinax, Leucothrinax, Schippia, Thrinax, Zombia*) exhibit a possible shift to more open inflorescences. *Leucothrinax* may be wind-pollinated, based on the similarity of its inflorescences to those of *Thrinax*, although the role of insects in *Thrinax* pollination is unclear. The other four genera are all possibly pollinated by diurnal insects, especially bees. However, within *Hemithrinax* there is the same marked contrast in inflorescence length between the elongate inflorescences of *H. ekmaniana* and the condensed inflorescences of *H. compacta* (Henderson 2023), and there may be bee and beetle pollination, respectively, here.

Coryphoideae, *Phoeniceae*

The tribe comprises one genus (*Phoenix*, 13 species) widely occurring in Old World tropical and subtropical areas, and just reaching the Mediterranean. All species are dioecious. No species has been studied in naturally occurring populations. *Phoenix dactylifera*, the date palm, has been studied but always in cultivation. Purseglove (1973) described the short-lived anthesis of staminate and pistillate flowers of *P. dactylifera*, and this, and the condensed inflorescences with closely spaced flowers, are certainly indicative of beetle pollination. There are several other reports that point to widespread beetle pollination in the genus, and that weevils and nitidulids co-occur on inflorescences. The persistent peduncular bract may also play a role in pollination.

A new species of *Derelomus* has recently been described from *P. dactylifera* in Cyprus (Alziar 2007; see also Ponel & Lemaire 2012). Meekijjaroenroj & Anstett (2003) reported that they found numerous small derelomine weevils (*Neoderelomus piriformis*) on inflorescences of cultivated plants of *P. canariensis* in southern France. They considered that these weevils pollinated the palms, and that they also occurred in the Canary Islands (the natural habitat of *P. canariensis*). On the other hand, Sosa et al. (2021) considered that *P. canariensis* was mainly wind-pollinated in the Canary Islands. Meekijjaroenroj & Anstett (2003) noted that derelomine weevils had been found on inflorescences of *P. loureiroi* (Fig. 3A) in Thailand, and they raised the possibility that all species of *Phoenix* could be weevil-pollinated. Audisio et al. (2014) reported a nitidulid beetle, *Kabakovia*, from *P. loureiroi*. Sabatelli et al. (2020) recently described two new species of *Meligethinus* (Nitidulidae) from staminate inflorescences of *P. reclinata* in Mozambique, and found a total of six species of *Meligethinus* on *P. reclinata* inflorescences. Haran et al. (2022) reported six, related species of *Derelomus* weevils as brood-site pollinators on inflorescences of *P. reclinata.* Thus *P. reclinata* inflorescences appear to host a diverse assemblage of both nitidulid beetles and weevils.

Coryphoideae, *Trachycarpeae*, *Rhapidinae*

The subtribe comprises six genera (*Chamaerops,* 1 species; *Guihaia,* 4 species; *Trachycarpus,* 10 species; *Rhapidophyllum,* 1 species; *Maxburretia,* 3 species; *Rhapis,* 11 species) distributed, with the exception of the Neotropical *Rhapidophyllum*, in subtropical and tropical areas of the Old World (and temperate areas in the case of the western Mediterranean *Chamaerops*). Two genera have been studied.

Chamaerops

Chamaerops is dioecious with short, condensed inflorescences (Fig. 3B). Herrera (1989) studied pollination of *C. humilis* in Spain. Plants flowered from April to May. Staminate plants tended to flower earlier, but there were more pistillate plants than staminate. Staminate inflorescences were at anthesis for about seven days. Staminate flowers were yellow, produced a faint scent, no nectar, and powdery pollen. Pistillate inflorescences were at anthesis for 7–15 days. Flowers opened in a basipetal direction, were yellow, and sometimes produced nectar. Inflorescences attracted a variety of insects but the most frequent was a curculionid beetle, *Derelomus chamaeropis*. However, Herrera considered that plants were mostly wind-pollinated.

Anstett (1999) described the life cycle of *Derelomus chamaeropis.* The weevils occurred only on *C. humilis* inflorescences and carried pollen, and Anstett considered that they were the most likely pollinators. Weevils ate pollen and laid eggs on staminate inflorescences, and larvae bored into and developed only on staminate inflorescences. They remained in the rachises of the old inflorescences throughout the winter months, pupating and emerging in the spring. Weevils fed on but rarely oviposited on pistillate

Figure 3. A. Condensed, pistillate inflorescences of *Phoenix loureiroi*. B. Condensed, staminate inflorescences of *Chamaerops humilis*. C. Elongate, open inflorescences of *Licuala peltata*. D. Condensed, hermaphrodite inflorescence of *Johannesteijsmannia altifrons* (image by P. Vatcharakorn).

inflorescences. Dufaÿ & Anstett (2004) and Dufaÿ (2010) found that, on average, staminate plants had more inflorescences and were at anthesis earlier and for a longer time than pistillate plants. Weevils laid eggs on pistillate inflorescences, but eggs and larvae did not develop. Pistillate inflorescences appeared to prevent the development of weevil eggs, thus protecting themselves from predation. However, Jácome-Flores et al. (2018) found that although staminate plants hosted higher numbers of weevil larvae, about 30% of pistillate plants also hosted larvae. But these pistillate plants had a low mean proportion of fruit-set or were without fruits.

Dufaÿ et al. (2003) discovered that *Derelomus chamaeropis* weevils were not attracted to the palms by the faint scent given off by the inflorescences, but rather by a much stronger scent given off by the leaves. Scent was produced by the sinuses of the leaves. The sinus is situated at the base of the split between adjacent leaf segments, on the adaxial surface of the leaf. This scent was produced only during anthesis of inflorescences. Caissard et al. (2004) showed that the scent was actually produced by the whole leaf and not just the sinus. Scents were predominantly terpenoids and benzenoids, typical of floral scents. Dufaÿ et al. (2004) studied the scent produced by the leaves. They found that scent production reached a maximum at the time pollinator visits were required. Staminate plants produced higher levels of scent than pistillate, but scent composition did not differ between staminate and pistillate plants.

Armbruster (2011), in discussing brood-site pollination, wrote: "In those plant species that experience active pollination (minimally figs, yuccas, senita cacti) and those that lack co-pollinators (minimally figs, yuccas, *Chamaerops*, *Trollius*) we see the most specialized plant-pollinator relationships ever described." However, a second pollinator of *C. humilis* has recently been reported, the nitidulid *Meligethinus pallidulus* (Muñoz-Gallego et al. 2022, García et al. 2018; see also Ponel & Lemaire 2012). *Chamaerops humilis* may thus be an example of a brood-site pollination system comprising a sympatric assemblage of multiple species on the same host plant (Haran et al. 2022).

Rhapidophyllum

Rhapidophyllum is dioecious, less often polygamous or monoecious. Inflorescences are condensed and do not project much from the leaf bases, and flowers are closely spaced. Shuey & Wunderlin (1977) studied pollination of *R. hystrix* in the southern United States. Flowering occurred from February to November, mostly from March to August. Flowers were yellow, orange, or purple. In a population, staminate inflorescences were more numerous and projected more above the leaf bases. Staminate inflorescences produced a musty scent. Pistillate inflorescences produced a similar, weaker scent during the evening hours. Large numbers of a curculionid weevil, *Notolomus* sp., visited inflorescences and were considered to be the most effective pollinator.

Coryphoideae, *Trachycarpeae*, *Livistoninae*

The subtribe comprises seven genera (*Livistona,* 28 species; *Licuala,* 174 species; *Lanonia* 19 species; *Johannesteijsmannia,* 4 species; *Pholidocarpus,* 6 species; *Saribus,* 9 species; *Acoelorraphe,* 1 species) distributed, with the exception of the Caribbean *Acoelorraphe,* throughout the Asian tropics and subtropics and just reaching east Africa. Two genera, *Licuala* and *Johannesteijsmannia,* have been studied.

Licuala

Licuala has open, elongate inflorescences with hermaphrodite flowers (Fig. 3C). Barfod et al. (2003) studied three species in Thailand (Table 5).

The flowering season of *L. spinosa* lasted only three months. Inflorescences were at anthesis for approximately 30 days in *L. spinosa*, but only 4–5 days in *L. peltata*. Flushes of flowers opened each day. Flowers were protandrous. Flowers were at staminate anthesis from approximately 06.00 to early afternoon. Flowers were sweetly scented and produced small amounts of nectar. Stigmas were receptive the same day at approximately 18.00 until the afternoon of the following day.

About 20 different species of insects visited the inflorescences. The most effective pollinators of *L. spinosa* were considered to be flies in the families Calliphoridae and Tachinidae, and of *L. distans* and *L. peltata*, *Trigona* spp.

Table 5. Pollination of *Licuala* spp.

	L. distans Thailand	*L. peltata* Thailand	*L. spinosa* Thailand
Flowering season (months), peak	-	-	September to November
Dichogamy	protandrous	protandrous	protandrous
Duration of anthesis on an inflorescence (days)	-	4–5	ca. 30
Start of ♂ anthesis (time)	-	-	06.00
Start of ♀ anthesis (time)	-	-	18.00
Scent	sweet, honey-like scent	sweet, honey-like scent	sweet, honey-like scent
Temperature elevation	-	-	-
Nectar	present	present	present
Number of insect visitors (species)	-	-	20
Most effective pollinators	*Trigona* spp. (Apidae)	*Trigona* spp. (Apidae)	Calliphoridae sp., Tachinidae sp.
Reference	Barfod et al. (2003)	Barfod et al. (2003)	Barfod et al. (2003)

Table 6. Pollination of *Johannesteijsmannia* spp.

	J. altifrons Malaysia	*J. lanceolata* Malaysia	*J. magnifica* Malaysia	*J. perakensis* Malaysia
Flowering season (months), peak	-	October to July	March	March-April, October-December
Dichogamy	?	protandrous	?	-
Duration of anthesis on an inflorescence (days)	7–10	7 (–14)	7–12	-
Start of ♂ anthesis (time)	05.00	07.00	07.00	-
Start of ♀ anthesis (time)	05.00	08.30 or 09.00	07.00	-
Scent	sweet/sour scent	sweet/sour scent	sweet/sour scent	sour scent
Temperature elevation	-	-	-	-
Nectar	none	none	none	none
Number of insect visitors (species)	13	13	10	-
Most effective pollinators	*Trigona* spp.	flies (Phoridae, Cecidomyiidae), stingless bees (*Trigona*)	*Trigona* spp.	*Trigona* spp.
Reference	Chan & Saw (2011)	Chan (2009), Chan et al. (2011)	Chan & Saw (2011)	Chan & Saw (2011)

Barfod et al. (2011) noted large differences in the composition of the visiting fauna to inflorescences of *L. spinosa* in Peninsular Thailand. Inflorescences of forest-growing palms were visited by 18 insect species of which calliphorid and tachinid flies and a halictid bee carried the largest pollen loads, whereas palms growing in open areas were visited by five kinds of insects of which only two species of calliphorid fly carried large pollen loads. Floral scent chemistry of four *Licuala* species (including *L. spinosa*) has been studied by Meekijjaroenroj et al. (2007).

Johannesteijsmannia

Johannesteijsmannia inflorescences are condensed and bear closely spaced, hermaphrodite flowers (Fig. 3D). Four species have been studied (Table 6).

There did not appear to be any particular pattern for flowering seasons, and they varied from one month to 10 months. Anthesis on an inflorescence lasted 7–12 days. Flushes of flowers opened each day, and direction of anthesis on a rachilla was acropetal or random. Dichogamy of flowers was unclear. It appeared that staminate anthesis took place before pistillate anthesis in *J. lanceolata* (although Chan (2009) reported that the start of stigma receptivity could not be ascertained), possibly at the same time in other species. Flower scent was recorded as sweet or sour. No nectar was produced.

Relatively few species of insect visited inflorescences, and the most effective pollinators were considered to be stingless bees (*Trigona* spp.) or flies.

Inflorescences of *Johannesteijsmannia* are condensed with short rachillae and closely-spaced flowers and thus might appear to be beetle-pollinated. Both Chan & Saw (2011) and Dransfield (1970) noted that inflorescences were borne at ground level and were often covered by leaf debris. Dransfield noted that flowers smelled of sour milk and sewage and observed: "…beetle larvae, nitidulid beetle adults and ants are abundant in inflorescences…" Rozainah & Sinniah (2006) also noted that inflorescences of *J. lanceolata* were covered with debris and that nitidulid and staphylinid beetles were potential pollinators. However, flowers have diurnal anthesis, sweet or sour scent, and are reported to be bee-pollinated. Chan & Saw (2011) recorded beetles in *J. altifrons* and *J. magnifica*, but not in *J. lanceolata*. They wrote: "The role of beetles as potential pollinators of

Johannesteijsmannia remains to be tested since we did not examine them for pollen loads."

Chan & Saw (2011) reported that the mean number of pollen grains per anther in *J. magnifica* was 79 and in *J. lanceolata* it was 45. These are extremely low numbers; palm anthers usually contain tens of thousands of pollen grains (e.g., 10,000 pollen grains per anther in *Calamus manan,* Alloysius 1999; 20,451 pollen grains per anther in *Attalea allenii,* Núñez et al. 2005). Anthers of *Johannesteijsmannia* are described as "minute" by Dransfield et al. (2008). These small, introrse anthers with few pollen grains, as well as the apparent lack of dichogamy in some species and close juxtaposition of the anthers and stigmas, raise the question of whether all or some species are all or partly self-pollinated. Chan & Saw (2011) reported the breeding system of *J. lanceolata* and *J. magnifica* to be "facultatively selfing".

Unplaced genera of Trachycarpeae

This group comprises six genera (*Serenoa,* 1 species; *Brahea,* 11 species; *Colpothrinax,* 3 species; *Copernicia,* 15 species; *Pritchardia,* 29 species; *Washingtonia,* 1 species) distributed in the Neotropical tropical and subtropical regions, with the exception of the Pacific Island *Pritchardia*. One genus has been studied.

Serenoa

Serenoa is hermaphrodite and the relatively large, much-branched inflorescences produce high numbers of flowers. Pollination has been studied by Carrington et al. (2003) and Koptur & Khorsand Rosa (2018). Plants flowered in April and May (Hilmon 1969). Flowers opened asynchronously on an inflorescence over a 30-day period. Anthesis proceeded in an acropetal direction. Flowers opened from 02.00 to 14.00, opening at a faster rate after 07.00. Nectar was produced as soon as the flowers opened. Flowers were protandrous. Anther dehiscence began at 08.00 and continued until about 11.00. Stigmas were receptive mostly on the following day. Inflorescences were visited by 34 species of insect. The most effective pollinators were considered to be four bee species: *Colletes* sp., *Augochloropsis metallica*, Halictidae sp., and *Apis mellifera*.

There are two other relevant reports. Caissard et al. (2004) noted that *Serenoa* leaves and flowers produced scent (as in *Chamaerops*), and Deyrup & Deyrup (2012) reported that 311 species of insect visited flowers of *S. repens*.

Colpothrinax and Pritchardia

Although there are no detailed studies of these two genera, they are of particular interest in terms of pollination. Both have similar hermaphrodite flowers with the filament bases connate into a cupule. The Cuban *Colpothrinax wrightii* has the petals forming a fleshy, deciduous cap over the stamens. Dalsgaard et al. (2016) listed the Yellow-faced Grassquit (*Tiaris olivaceus*) as pollinator of *C. wrightii*. Petals of the Central American *C. aphanopetala* do not form a cap, and this species may be pollinated by syrphid flies (Evans 2001).

In the Hawaiian *Pritchardia* the corolla lobes also form a cap which is deciduous at anthesis and the filament bases are connate to form a conspicuous tube, and this tube fills with nectar (Vaughan 1918, St. John 1932). *Pritchardia* has also been postulated to be bird-pollinated, possibly by Hawaiian honeycreepers (Beccari & Rock 1921, Porsch 1930). Many species have elongated inflorescences arching out from the leaves, and this may be significant in terms of bird pollinators.

Summary for Trachycarpeae

The subtribe Rhapidinae comprises six genera and 30 species. Only two species in two genera (*Chamaerops, Rhapidophyllum*) have been studied, and they are both pollinated by derelomine weevils. The production of scent by the leaves of *Chamaerops* is remarkable, and the phenomenon is likely to occur in other genera. It is also remarkable that a derelomine weevil and nitidulid beetle occur together on *Chamaerops*, mirroring the association almost invariably found in Neotropical, beetle-pollinated palms. There is considerable variation in sexual systems in the subtribe. Kholia (2009) showed that gender expression in *Trachycarpus takil* was not stable. He found a tendency for young plants to behave as male and these could subsequently change sex from male to bisexual and to female on ageing (see also Jousson et al. 2023). In Ferreira et al. (in prep.), the two beetle-pollinated genera are basal in the Rhapidinae clade. The other four genera (*Guihaia, Trachycarpus, Maxburretia,* and *Rhapis*) appear to have more open inflorescences, although nothing is known of their pollination systems.

The subtribe Livistoninae comprises seven genera and 241 species, but there are very few studies. The two genera studied, *Licuala* and *Johannesteijsmannia,* are sister genera (Ferreira et al. in prep.). There is a striking contrast between the elongate, open inflorescences of *Licuala* and the condensed, closed inflorescences of *Johannesteijsmannia.* Nevertheless, both appear to have diurnal anthesis and fly or bee pollination, although the role of beetles in *Johannesteijsmannia* pollination is unclear.

Of the six unplaced genera of the Trachycarpeae, only *Serenoa* has been studied in detail and that appears to have a typical bee pollination system. In Ferreira et al. (in prep.), *Serenoa* is sister genus to *Acoelorraphe* (here included in subtribe Livistoninae), and that genus is also likely to be bee-pollinated. The possibility of bird pollination in *Colpothrinax* and *Pritchardia* is notable. If confirmed, this would considerably broaden the phylogenetic diversity of both palm pollinators and bird pollination systems. It also raises the question about why the presumably insect-pollinated ancestors of these palms would switch to birds as pollen vectors (Ollerton 2024).

Coryphoideae, *Chuniophoeniceae*

The tribe comprises four genera (*Chuniophoenix,* 3 species; *Kerriodoxa,* 1 species; *Nannorrhops,* 1 species; *Tahina,* 1 species) with a disjunct distribution in Old World tropical and subtropical areas. No genera have been studied. The same contrast is found in this tribe as in others, from open, elongate inflorescences (e.g., *Tahina*) to condensed, closed inflorescences (e.g., *Kerriodoxa*).

Coryphoideae, *Caryoteae*

The tribe comprises two genera (*Caryota,* 13 species; *Arenga,* 24 species) widely distributed in the Asian tropics. Both genera have been studied.

Caryota

Caryota is semelparous (except one species). Stems of *C. urens* are solitary and inflorescences develop in a basipetal direction (i.e., the first inflorescences to open are at the top of the stem). Plants are monoecious with unisexual flowers in triads. Ratnayake et al. (1991) and Ratnayake (unpublished report) gave some notes on the pollination of *C. urens* in Sri Lanka. Plants flowered throughout the year. Inflorescences were protandrous. Staminate anthesis on an inflorescence lasted 15–21 days. Flowers opened between 19.30 and 24.00, with a peak from 21.30 to 22.00. Individual flowers lasted 12–15 hours. There was an inter-anthesis period of 14–21 days. Pistillate anthesis lasted 8–14 days. Flowers opened throughout the day. Individual flowers lasted 24–48 hours. Inflorescences were visited by at least seven species of insect in the orders Coleoptera, Hymenoptera, and Diptera. The most likely pollinator was considered to be a species of stingless bee.

Arenga

Arenga is semelparous (except three species, including *A. obtusifolia*). Zakaria et al. (1999) studied pollination of *A. obtusifolia* and *A. westerhoutii* in Peninsular Malaysia (Table 7).

Inflorescences of both species were described as unisexual, although plants of *A. westerhoutii* were said to be protogynous. Although the triad is the basic unit of flower arrangement in *Arenga,* staminate inflorescences occurred by abortion of the pistillate flowers, and pistillate inflorescences occurred by abortion of staminate flowers. Plants of both species produced inflorescences throughout the year.

Staminate anthesis on an inflorescence continued for 3–8 days. Flowers opened in flushes each day, early in the morning, and produced a sweet scent. Flowers were short-lived and soon fell from the inflorescence.

Pistillate anthesis on an inflorescence lasted 10–20 days. Flowers of *A. obtusifolia* produced a sweet scent, fainter than staminate flowers. Flowers of *A. westerhoutii* did not produce any scent.

No insect visitors were observed on inflorescences during the evening and night. Inflorescences at staminate anthesis were visited during the day by at least seven species of insect, including large numbers of bees and drosophilid flies. Fewer insects visited pistillate inflorescences. The most effective pollinators were considered to be the bees, *Trigona spp.* and *Apis* sp., and a curculionid beetle.

Audisio et al. (2014) gave a list of host plants of the genera of the nitidulid subfamily Meligethinae and included *Cryptarchopria* found on *Arenga*

Table 7. Pollination of *Arenga* spp.

	A. obtusifolia Malaysia	*A. westerhoutii* Malaysia
Flowering season (months), peak	throughout the year	throughout the year
Duration of ♂ anthesis on an inflorescence (days)	5–8	3–4
Start of ♂ anthesis (time)	early morning	early morning
Duration of ♂ anthesis on a flower (hours)	-	-
♂ scent	sweet scent	sweet scent
♂ temperature elevation	-	-
♂ nectar	-	-
Inter-anthesis (days)	-	-
Duration of ♀ anthesis on an inflorescence (days)	10–20	10–20
Start of ♀ anthesis (time)	-	-
Duration of ♀ anthesis on a flower (hours)	-	-
♀ scent	sweet scent	none
♀ temperature elevation	-	-
♀ nectar	-	-
Number of insect visitors (species)	at least 7	at least 10
Most effective pollinators	*Trigona* spp., Curculionidae sp.	*Trigona* sp., *Apis* sp., Curculionidae sp.
Reference	Zakaria et al. (1999)	Zakaria et al. (1999)

inflorescences. The role of *Cryptarchopria* and other beetles in pollination of *Arenga,* or the rest of the tribe, is unknown. Jeanson et al. (in prep.) reported that several species of *Arenga* had strongly scented staminate flowers.

Summary for Caryoteae

Of the two genera and 37 species, only one *Caryota* and two *Arenga* species have been studied. These have been reported to be bee-pollinated. In this scenario, the nocturnal staminate anthesis of *C. urens* is anomalous, and the role of beetles in both genera is unclear. In *Arenga,* the considerably longer period of pistillate anthesis compared with staminate anthesis is unusual—the reverse is usually the case.

Species of *Caryota* and *Arenga* are known to have complex patterns of morphology, parity, and inflorescence development (Jeanson et al. in prep.). For example, *A. westerhoutii* has solitary stems and is semelparous with basipetal inflorescence development. On the other hand, *A. obtusifolia* has clustered stems and is iteroparous with acropetal inflorescence development. Nevertheless, inflorescence development and pollinators appear to be similar in both species.

Coryphoideae, Corypheae

The tribe comprises a single genus (*Corypha,* 5 species) widely distributed from southern India to northern Australia. No species have been studied.

Coryphoideae, Borasseae, Hyphaeninae

The subtribe comprises four genera (*Bismarckia,* 1 species; *Satranala,* 1 species; *Hyphaene,* 8 species; *Medemia* 1 species) distributed in Africa, Madagascar, Arabia, and India. No genera have been studied. Fanshawe (1966) considered *Hyphaene thebaica* to be wind-pollinated, although "insect activity has been noted on the flowers."

Coryphoideae, Borasseae, Lataniinae

The subtribe comprises four genera (*Latania,* 3 species; *Lodoicea,* 1 species; *Borassodendron,* 2 species; *Borassus,* 5 species) widely distributed in Africa, Madagascar, the Seychelles, the Mascarene Islands, and through the Asian tropics to New Guinea. Two genera have been studied.

Lodoicea

Lodoicea is dioecious. Staminate flowers are arranged in cincinni of 60–70 flowers, with each cincinnus in a pit in the rachilla. A cincinnus is a flower cluster wherein each successive flower arises in the axil of a bracteole borne on the stalk of the previous flower (Dransfield et al. 2008). Flowers are exserted one by one in succession from the mouth of the pit. Pistillate flowers are unusually large, with leathery sepals and petals. Gerlach (2003) and Blackmore et al. (2012) studied pollination of *L. maldivica* in the Seychelles. Plants flowered throughout the year with a peak of staminate inflorescences in November.

Few data on inflorescence and flower development were given in either study. Flowers on staminate inflorescences produced large amounts of sticky pollen. They also produced copious nectar, and according to Gerlach (2003) the nectaries are on the margins of the bracts surrounding flowers. Flowers produced a strong, musty, sweet scent.

On pistillate inflorescences, only one flower was at anthesis at any one time, and this for only few hours of the day. Pistillate flowers produced nectar and scent although to a lesser extent than staminate flowers.

Copious nectar production by staminate inflorescences attracted numerous insects, slugs, and geckos. Gerlach (2003) considered the most effective pollinators to be flies, particularly the dolichopodid fly *Ethiosciapus* sp. Gerlach reported that *Ethiosciapus* sp. had been collected on pistillate flowers carrying *Lodoicea* pollen. On the other hand, Blackmore et al. (2012) considered bees (*Trigona* sp.) to be the most effective pollinators. Although Blackmore et al. found dolichopodid flies (*Cyrturella*) on inflorescences, they noted that these flies were carnivorous by nature and did not carry pollen on their bodies, and that they were unlikely to act as pollinators. Blackmore et al. noted that *Cyrturella* was similar to those flies identified by Gerlach as *Ethiosciapus.*

Borassus

Borassus is dioecious. Staminate flowers are arranged in cincinni of about 30 flowers, with each cincinnus in a pit in the rachilla. Flowers are exserted one by one in succession from the mouth of the pit. Pistillate flowers are solitary, unusually large, and have leathery sepals and petals. Two species have been studied (Table 8).

Table 8. Pollination of *Borassus* spp.

	B. flabellifer India	*B. aethiopum* Senegal
Flowering season (months), peak	August to January	July to March, peak in August to November
Duration of ♂ anthesis on an inflorescence (days)	65–94	-
Start of ♂ anthesis (time)	08.00	day and night
Duration of ♂ anthesis in a flower (hours)	-	about 6
♂ scent	-	scent
♂ temperature elevation	-	-
♂ nectar	-	-
Duration of ♀ anthesis on an inflorescence (days)	20–30	-
Start of ♀ anthesis (time)	-	-
Duration of ♀ anthesis in a flower (hours)	48–96	about 96
♀ scent	-	strong scent
♀ temperature elevation	-	-
♀ nectar	present	present
Number of insect visitors (species)	-	34
Most effective pollinators	-	*Apis mellifera* (Apidae), *Nomia* sp., *Nomiodes* spp. (Halictidae), *Rhinia apicalis* (Diptera, Rhiniidae), *Chrysomia* sp. (Calliphoridae)
Reference	Chathukutty Nambiar (1954)	Thione (2000)

Plants flowered for 6–9 months. Staminate inflorescences of *B. flabellifer* were at anthesis for 65–94 days. Individual flowers opened in flushes each day around 08.00 and were at anthesis for about 6 hours. Staminate flowers were scented in *B. aethiopum.*

Pistillate inflorescences of *B. flabellifer* were at anthesis for 20–30 days. Individual flowers were at anthesis for 48–96 hours and produced nectar, and they were strongly scented in *B. aethiopum*.

At least 34 species of insect visited inflorescences of *B. aethiopum*. The most effective pollinators were considered to be bees and flies: *Apis mellifera* (Apidae), *Nomia* sp., *Nomiodes* spp. (Halictidae), *Rhinia apicalis* (Diptera, Rhiniidae), and *Chrysomia* sp. (Calliphoridae).

Bayton et al. (2003) reported that the only insects visiting staminate inflorescences of *B. madagascariensis* were honeybees, *Apis mellifera*.

Summary for Borasseae

There are four genera and 11 species in subtribe Hyphaeninae. There are no studies of pollination except for anecdotal records of wind pollination in *Hyphaene* (Fanshawe 1966). However, pistillate flowers of *Hyphaene* and *Bismarckia* have nectaries, and at least these may be insect-pollinated.

Of the four genera and 11 species in the subtribe Lataniinae, only two species in two genera, *Lodoicea* and *Borassus*, have been studied. Genera in the Lataniinae are notable for their elaborate and unusual staminate flower arrangement and morphology, and large pistillate flowers with leathery sepals and petals. Nevertheless, pollination appears to be by entirely ordinary means of bees and flies. It is possible that bee pollination is widespread in the subtribe. At least *Borassus* and *Lodoicea* flowers produce nectar, and Ferguson et al. (1987) reported *Trigona* visiting flowers of *Borassodendron* and *Hyphaene.* However, *Borassodendron borneensis* appears to have condensed inflorescences, at least compared to those of *B. machadonis*.

Lodoicea is an example of how two different investigators, studying the same species in the same place, can consider two different insects to be pollinators.

Although there are rather few data for the tribe, all the indications are that species exhibit diurnal anthesis, scented staminate flowers, scented and nectariferous pistillate flowers, and are bee- or fly-pollinated. No derelomine weevils or nitidulid beetles were recorded from any species of Borasseae.

CEROXYLOIDEAE

Ceroxyloideae, Cyclospatheae

The tribe comprises a single genus (*Pseudophoenix,* 4 species) distributed in the Caribbean region. No species have been studied in detail. Campos-Navarrete et al. (2013) listed a halictid bee (*Augochlorella pomoniella*) and a wasp (Vespidae sp.) as pollinators of *P. sargentii* at a site in coastal Mexico.

Ceroxyloideae, Ceroxyleae

The tribe comprises four genera (*Ceroxylon,* 13 species; *Juania,* 1 species; *Oraniopsis,* 1 species; *Ravenea,* 22 species) distributed in South America, the Juan Fernandez islands, Australia, and Madagascar. Bernardello et al. (2001) suggested that *Juania* was wind pollinated. One genus has been studied in detail.

Ceroxylon

Ceroxylon is dioecious with much branched inflorescences and numerous small flowers. Four species have been studied (Table 9).

Ceroxylon sasaimae flowered throughout the year, but the three sympatric species (*C. parvifrons, C. ventricosum,* and *C. vogelianum*) had asynchronous seasonal peaks such that there was at least one species in flower throughout the year.

Inflorescences on staminate plants were at anthesis for 1–8 days. Staminate flowers were at anthesis in the morning and lasted six hours. Staminate flowers produced a sweet scent, dominated by alkenes in *C. sasaimae*. No nectar production nor temperature elevation was reported in either staminate or pistillate flowers.

Inflorescences on pistillate plants were at anthesis for 3–15 days. Pistillate flowers were at anthesis in the morning or afternoon and lasted 24–96 hours. Pistillate flowers produced a sweet scent, in *C. sasaimae* similar in chemical composition to that of staminate flowers.

Table 9. Pollination of *Ceroxylon* spp.

	C. parvifrons Colombia	*C. sasaimae* Colombia	*C. ventricosum* Colombia	*C. vogelianum* Colombia
Flowering season (months), peak	March to May	throughout the year, peak in May and June	January to May	June to December
Duration of ♂ anthesis on an inflorescence (days)	1	6	1	8
Start of ♂ anthesis (time)	morning	morning	morning	morning
Duration of ♂ anthesis in a flower (hours)	6	6	6	6
♂ scent	sweet scent	sweet scent	sweet scent	sweet scent
♂ temperature elevation	-	-	-	-
♂ nectar	-	none	-	-
Duration of ♀ anthesis on an inflorescence (days)	4	3	15	6
Start of ♀ anthesis (time)	afternoon	morning	afternoon	afternoon
Duration of ♀ anthesis in a flower (hours)	24	24	96	24
♀ scent	sweet scent	sweet scent	sweet scent	sweet scent
♀ temperature elevation	-	-	-	-
♀ nectar	-	none	-	-
Number of insect visitors (species)	37	39	40	37
Most effective pollinators	*Mystrops rotundula* (Nitidulidae)	*Mystrops pulchra* (Nitidulidae)	*Mystrops rotundula* (Nitidulidae)	*Mystrops rotundula* (Nitidulidae)
Reference	Carreño-Barrera et al. (2020)	Núñez (2014)	Carreño-Barrera et al. (2020)	Carreño-Barrera et al. (2020)

A large number of different species of insect visited inflorescences, 37–40. The most effective pollinators were considered to be *Mystrops* (Nitidulidae), *M. pulchra* in *C. sasaimae* and *M. rotundula* in the three sympatric species (*C. parvifrons, C. ventricosum,* and *C. vogelianum*). Other species of *Mystrops* were present in all species but there were far fewer individuals. These beetles fed on pollen, mated, and oviposited on the peduncles, peduncular bracts, and rachillae of staminate inflorescences. Carreño-Barrera et al. (2020) estimated a median abundance of over 42,000 individuals of *Mystrops rotundula* on staminate inflorescences of *C. ventricosum*. They wrote: "The pollination success of the studied species of *Ceroxylon* can be explained by the adopted strategy of maintaining a large pollen supply for the large swarms of *Mystrops rotundula,* which are strictly dependent on this resource, whereas also conning them into visiting the rewardless pistillate inflorescences."

There are other relevant studies on another species of *Ceroxylon*. Martínez et al. (2021) found that *C. quindiuense* flowered sequentially along an altitudinal gradient, thus providing a constant food source, in the form of staminate inflorescences, to pollinating insects. Kirejtshuk & Couturier (2009) collected five species of *Mystrops* from a single staminate inflorescence of *C. quindiuense* in Peru, four of them undescribed species. Martínez et al. (2018) noted sex change in plants of *C. quindiuense* in Colombia.

Ravenea

Although there are no detailed studies, species of *Ravenea* from Madagascar may be both beetle-pollinated and bee-pollinated. Dransfield & Beentje (1995) noted that the condensed inflorescences of *R. louvelii* and *R. dransfieldii* heated up before anthesis and produced a strong, musty scent. Inflorescences were visited by curculionid and nitidulid beetles and these could have been pollinators. On the other hand, species such as *R. sambiranensis* and *R. madagascariensis* have lax, spreading inflorescences and were possibly bee-pollinated. *Ravenea* appears to be an example of a genus having both condensed and open inflorescences. According to the Ferreira et al. (in prep.), some *Ravenea* species with condensed inflorescences are basal in the genus, and those with lax, spreading inflorescences are derived. However, at least one species with condensed inflorescences, *R. nana*, is in a more derived position in the clade, suggesting more than one shift in pollination.

Ceroxyloideae, *Phytelepheae*

The tribe comprises three genera (*Ammandra,* 1 species; *Aphandra,* 1 species; *Phytelephas,* 4 species) distributed in the Neotropics. Two genera have been studied.

Aphandra

Aphandra is dioecious with strongly dimorphic inflorescences. Staminate inflorescences are fleshy and elongate with numerous groups of flowers borne on short pedicels (Fig. 4A). Staminate flowers have up to 650 stamens. Pistillate inflorescences are condensed, with few, large flowers (Fig. 4B). Pollination of *A. natalia* was studied by Ervik (1993) and Ervik et al. (1999) in Ecuador. Plants flowered throughout the year.

Figure 4. A. Staminate inflorescence of *Aphandra natalia*. B. Pistillate inflorescence of *Aphandra natalia*. C. Staminate inflorescence of *Phytelephas macrocarpa*. D. Pistillate inflorescence of *Phytelephas macrocarpa*.

Staminate inflorescence buds heated up before opening, reaching 10°C above ambient, and rapidly decreased in temperature after opening. Inflorescences opened during the day and rapidly elongated for about 48 hours, shedding pollen by friction or by insect activity. Inflorescences produced a strong, unpleasant scent, based on pyrazine compounds. Pistillate inflorescence buds also heated up, reaching 19°C above ambient before opening, and then slowly decreasing. Pistillate flowers were receptive for about 48 hours. Inflorescences were visited by 28 species of insect. Most visitors arrived during the day time. The most effective pollinators were considered to be weevils in the Baridinae and staphylinid beetles in the Aleocharinae.

There are several interesting aspects of pollination in *A. natalia*, especially compared to the two other genera of the tribe, *Ammandra* and *Phytelephas*. Ervik et al. (1999) noted the remarkable absence of the beetles *Mystrops* (Nitidulidae) and Derelomini (Curculionidae) from inflorescences of *A. natalia*. These two groups of beetles are found on inflorescences of almost all other Neotropical, beetle-pollinated palms, including *Phytelephas*. Furthermore, *A. natalia* was visited and pollinated by weevils in the Baridinae, and these were not found on *Ammandra* and *Phytelephas.* Ervik et al. considered that the absence of *Mystrops* and Derelomini from *A. natalia*, and presence of Baridinae, may be explained in part by the pyrazine scent produced by *A. natalia*, different from the scents produced by *Ammandra* and *Phytelephas*. Also of interest is that the Baridinae weevils apparently preferred to oviposit on pistillate inflorescences, rather than staminate. Barfod & Uhl (2001) found that the pedicels of the staminate flower groups of *A. natalia* produced a great number of raphide idioblasts (cells containing bundles of raphides) at anthesis. These were the same size as pollen grains and mixed with the pollen on the inflorescences. Barfod & Uhl hypothesized that these idioblasts deterred insect larvae from feeding on staminate inflorescences.

Phytelephas

Phytelephas is dioecious with strongly dimorphic inflorescences. Staminate inflorescences are fleshy and elongate with numerous groups of flowers borne on short pedicels (Fig. 4C). Staminate flowers have up to 950 stamens. Pistillate inflorescences are condensed, with few, large flowers (Fig. 4D). Two species have been studied (Table 10).

Flowering seasons were relatively short, of 2–4 months duration. Staminate inflorescences heated up before anthesis, reaching 8–12.1°C above ambient. Anthesis of staminate inflorescences began during the day in *P. aequatorialis* and *P. macrocarpa* (Colombia) and during the night in *P. macrocarpa* (Ecuador). Anthesis began immediately after bract opening as inflorescences elongated, and lasted one day or less. Inflorescences shed pollen during the period of elongation, for 12–48 hours. Flowers produced a strong scent, based on methyl anisol. Pistillate inflorescences heated up before anthesis, reaching 5.2–14.7°C above ambient. Pistillate inflorescences opened during the night in all three species. Pistillate flowers were at anthesis immediately after bract opening and continued at anthesis for 24–48 hours. Flowers produced a similar but weaker scent to that of staminate flowers.

Numerous species of insect visited inflorescences, 29–59, and some were present in large numbers. Bernal & Ervik (1996) estimated that 20,000 individuals of *Amazoncharis* spp. visited staminate inflorescences of *P. seemannii.* The most effective pollinators were considered to be *Phyllotrox* spp. (Curculionidae), *Mystrops* spp. (Nitidulidae), and *Amazoncharis* spp. and *Xanthopygus* sp. (Staphylinidae). These beetles ate pollen, mated, and oviposited on inflorescences. Bernal & Ervik (1996) reported that in *P. macrocarpa*, the staphylinid beetles *Amazoncharis* constructed egg chambers in the fleshy pedicels of the staminate flowers. Bernal & Ervik considered that this reproductive behavior was similar to the behavior of a related subtribe of staphylinids, Gyrophaenina. Species in this subtribe oviposit in fleshy mushrooms, whose spores they eat. Bernal & Ervik also noted that the staphylinid *Xanthopygus* was considered a predator of *Amazoncharis.* Pérez & Núñez (2018) have given a general survey of staphylinid beetles associated with palm inflorescences in the Chocó region of Colombia.

Auffray et al. (2023) carried out a detailed analysis of the insect visitors to inflorescences of *P.*

Table 10. Pollination of *Phytelephas* spp.

	P. aequatorialis Ecuador	*P. macrocarpa* Ecuador	*P. macrocarpa* (as *P. seemannii*) Colombia
Flowering season (months), peak	October to November	May to July	February to May, peak in March
Duration of ♂ anthesis on an inflorescence (days)	-	<1	1
Start of ♂ anthesis (time)	during the day	during the night	mostly during the day
Duration of ♂ anthesis in a flower (hours)	-	ca. 12	-
♂ scent	scent	strong sweet/unpleasant	strong scent
♂ temperature elevation	10°C above ambient	10.4°C above ambient	12.1°C above ambient
♂ nectar	-	-	none
Duration of ♀ anthesis on an inflorescence (days)	-	-	ca. 2
Start of ♀ anthesis (time)	during the night	during the night	mostly during the night
Duration of ♀ anthesis in a flower (hours)	ca. 48	24–48	ca. 48
♀ scent	scent	strong sweet/unpleasant	strong scent
♀ temperature elevation	-	14.7°C above ambient	8.5°C above ambient
♀ nectar	-	-	none
Number of insect visitors (species)	53	29	59
Most effective pollinators	*Phyllotrox* spp. (Curculionidae), *Mystrops* (Nitidulidae), *Xanthopygus* (Staphylinidae)	*Phyllotrox* spp. (Curculionidae), *Mystrops* (Nitidulidae), *Amazoncharis* spp., *Xanthopygus* sp. (Staphylinidae)	*Amazoncharis* spp., *Xanthopygus* sp. (Staphylinidae)
Reference	Ervik et al. (1999)	Barfod et al. (1987, as *P. microcarpa*), Ervik et al. (1999)	Bernal & Ervik (1996)

aequatorialis. They reported 59 morphospecies of arthropod, although the most numerous visitors were beetles in the families Staphylinidae, Nitidulidae, and Curculionidae. More beetles visited staminate inflorescences than pistillate. They identified 16 potential pollinator species, nine of which visited both staminate and pistillate inflorescences synchronously at dusk or during the night, and seven of which visited inflorescences asynchronously during the day.

There are several interesting aspects of pollination in *Phytelephas*, especially compared to the related genera *Ammandra* and *Aphandra*. All three genera have distinct floral scents, sesquiterpenes in *Ammandra*, butylpyrazine in *Aphandra*, and methyl anisol in *Phytelephas*, while staminate and pistillate inflorescences of the same genus produce very similar scents. Ervik et al. (1999) considered that these specific scents of the three genera were responsible for attracting specific pollinators, and that the similarity between staminate and pistillate scents was responsible for attracting insects from staminate inflorescences to otherwise reward-less pistillate inflorescences. They called this process "deceptive attraction by odour automimicry". Auffray et al. (2023) considered that: "…pollinator attraction relies on a high chemical resemblance between male and female inflorescences (i.e., intersexual chemical mimicry) and that this similarity prevents the dusk- and night-active pollinators to discriminate among floral sexes, allowing female inflorescences to receive visits." Possibly the nocturnal opening of pistillate inflorescences in *Phytelephas* is also significant here, in that they would not compete with staminate inflorescences, which are losing scent during the night. The production of scent has been associated with temperature increase in inflorescences, and temperature increase may be responsible for volatilizing the chemical compounds in scents (Ervik & Barfod 1999, Pincebourde et al. 2016).

Summary for Ceroxyloideae

Of the three tribes of the Ceroxyloideae, there are no studies of the Cyclospathae, but some quite detailed studies of the dioecious Ceroxyleae and Phytelepheae.

Of the four genera of the Ceroxyleae, only *Ceroxylon* has been studied in detail. It is notable that beetles of a single genus, *Mystrops* (Nitidulidae), were considered the most effective pollinators, and the three sympatric species of *Ceroxylon* (*C. parvifrons, C. ventricosum,* and *C. vogelianum*) were pollinated by the same species of *Mystrops*. *Ravenea* may be a genus with both beetle and bee pollination.

In the Phytelepheae, staminate and pistillate inflorescences are quite different morphologically and present perhaps the most extreme example of sexual dimorphism in the palms. In fact, it was only recently, with the use of molecular data, that the Phytelepheae were found to be related to the Ceroxyleae and placed in the same subfamily (Dransfield et al. 2008).

There are several remarkable features of *Ceroxylon* and *Phytelephas*. They are closely related and yet their inflorescence morphology is totally dissimilar. Despite this, they are both beetle pollinated with a brood-site pollination system involving, amongst others, the nitidulid *Mystrops*. There is marked similarity between the two genera in inflorescence development. Staminate anthesis on an inflorescence lasts only one or a few days, staminate flowers are at anthesis for only a few hours, inflorescences are strongly scented, pistillate inflorescences are at anthesis for only a few days and pistillate flowers are at anthesis for one or a few days. No nectar is produced, and there is temperature elevation (not recorded in *Ceroxylon*). Large numbers of insect species visit inflorescences and pollinators are beetles whose life cycles depend on the palms.

ARECOIDEAE

Arecoideae, Iriarteeae

The tribe comprises five genera (*Iriartella,* 1 species; *Dictyocaryum,* 3 species; *Iriartea,* 1 species; *Socratea,* 5 species; *Wettinia,* 22 species) widely distributed in the Neotropics. Four genera have been studied.

Iriartella

Plants are monoecious with unisexual flowers in triads. Henderson (1990) studied *I. setigera* in the Amazon region of Brazil and in southern Venezuela. Plants flowered from February to November. Flowers continued developing for about three weeks after the peduncular bracts opened. Inflorescences were protogynous. Pistillate flowers had receptive stigmas during the morning and were sweetly scented. An inter-anthesis period was not recorded. Staminate anthesis was also diurnal, at least from 10.00–14.00, and staminate flowers also produced a sweet scent. Only three species of insect visited inflorescences. Two species of *Phyllotrox* (Curculionidae) visited inflorescences at both pistillate and staminate anthesis, as well as a few *Trigona*. The most effective pollinators were considered to be *Phyllotrox* spp.

Küchmeister (1997) studied *I. setigera* at or near the same Brazilian site as Henderson (1990). Plants flowered from May to June, and fewer plants flowered from September to October. Inflorescences were protogynous. Pistillate flowers were receptive during the day and were very sweetly scented but did not produce nectar. There was no inter-anthesis period, and sometimes pistillate and staminate anthesis overlapped. Staminate anthesis was also diurnal, flowers were sweetly scented but did not produce nectar. Only five species of insect visited inflorescences and the most effective pollinators were considered to be two weevils, *Phyllotrox* sp. and Derelomini sp. (Curculionidae). Küchmeister also noted that weevils could have been attracted by fulgorid exudates (hemipteran insects whose nymphs produce honeydew).

Listabarth (1999a) studied *I. setigera* in southern Venezuela. Plants flowered from September to December. Inflorescences were protandrous. Staminate anthesis lasted about 10 days, and staminate flowers opened during the morning and fell from the inflorescence during the afternoon of the same day. Staminate anthesis was followed by an inter-anthesis period of seven days. Pistillate anthesis lasted about seven days. Pistillate flowers were at anthesis for two days, and produced small amounts of stigmatic exudate. Neither flowers at staminate anthesis nor pistillate anthesis produced any scent. Inflorescences were visited by few species of insect, and *Trigona* bees were considered the most effective pollinators.

It seems unlikely that *I. setigera* could exhibit both protogyny, sweet scent, no inter-anthesis period, and beetle pollination (Henderson 1990, Küchmeister 1997) as well protandry, no scent, an inter-anthesis period, and bee pollination (Listabarth 1999a). Examination of herbarium specimens from both southern Venezuela and Brazil seems to confirm protogyny, or at least overlap between staminate and pistillate anthesis. Küchmeister also illustrated a rachilla of *I. setigera* showing a pistillate flower at anthesis surrounded by closed staminate flowers. On the other hand, Moore (1963) considered *I. setigera* to be protandrous. The matter is unresolved.

Iriartea

Plants are monoecious and the large, open inflorescences bear unisexual flowers in triads (Fig. 5B). Henderson (1985) studied pollination of *I. deltoidea* (as *I. ventricosa*) in southern Venezuela. Inflorescences were protandrous. Staminate anthesis lasted approximately 10 days. Individual staminate flowers were short-lived and produced a sweet scent. Pollen was shed in sticky masses. Pistillate anthesis took place after staminate anthesis and continued for at least five days. Inflorescences were visited by bees, wasps, and flies. *Trigona* spp. were considered to be the most effective pollinators.

Bullock (1981) gave some notes on pollination of *I. deltoidea* (as *I. gigantea*) in Costa Rica. Staminate anthesis lasted 10–14 days. Staminate flowers opened in flushes each morning and abscised in the afternoon. There was an inter-anthesis period of two days, followed by 3–4 days of pistillate anthesis. Pollinators were considered to be six species of *Trigona*.

Núñez (2014) recorded six different species of Curculionidae from three genera (*Celetes, Derelomus, Andranthobius*) visiting inflorescences and acting as casual pollinators of *I. deltoidea* in Colombia, and eight species of meliponid bees from five genera (*Nannotrigona, Partamona, Scapotrigona, Tetragona, Trigona*). The nitidulid *Mystrops* was also given as a principal pollinator of *Iriartea*.

Socratea

Plants are monoecious with relatively short inflorescences bearing unisexual flowers in triads (Fig. 5C). Henderson (1985) studied pollination of *S. exorrhiza* in southern Venezuela. Inflorescence buds opened during the night. Inflorescences were protogynous. Pistillate flowers were at anthesis at or before the bract opening, and produced a musty, fruity scent. Pistillate anthesis lasted approximately 12 hours. During the following night, staminate anthesis took place, and staminate flowers fell from the inflorescence the following morning. Large numbers of *Phyllotrox* sp. (Curculionidae) and *Mystrops* sp. (Nitidulidae) visited inflorescences during the night of pistillate anthesis and left the inflorescence at the following staminate anthesis. They were considered to be the most effective pollinators.

Núñez (2014) recorded two different species of *Andranthobius* (Curculionidae) visiting inflorescences and acting as casual pollinators of *S. exorrhiza* in southern Colombia.

Wettinia

Wettinia is monoecious. Inflorescences are usually multiple at a node, and then the central inflorescence, which is often pistillate, develops before the lateral, often staminate ones (Fig. 5D). Flowers are unisexual and are often crowded on the rachillae. Two species have been studied (Table 11).

Plants flowered throughout the year. Pistillate inflorescences developed before staminate. Pistillate anthesis took place during the night, and anthesis on an inflorescence lasted six days. Flowers were at anthesis for less than 24 hours and

Figure 5. A. Elongate, open inflorescence of *Dictyocaryum lamarckianum*. B. Elongate, open inflorescence of *Iriartea deltoidea.* C. Inflorescence of *Socratea exorrhiza*, past staminate anthesis (image by R. Bernal) D. Condensed, staminate inflorescence of *Wettinia quinaria*.

produced a strong scent and temperature elevation. No nectar was produced.

On staminate inflorescences, anthesis took place during the day or night and lasted three days. Flowers were at anthesis for less than 24 hours and produced a strong scent and temperature elevation. No nectar was produced.

Inflorescences were visited by large numbers of species of insect, 38–52. *Mystrops* spp. and *Phyllotrox* sp. were considered the most effective pollinators. These beetles ate pollen, mated, oviposited, and left the inflorescences when the staminate flowers began to fall.

Núñez et al. (2005) suggested that *Mystrops* sp. had a specific relationship with *W. quinaria* and was attracted by its unique floral scent. Núñez et al. hypothesized that the diurnal anthesis of *W. quinaria* and the diurnal activity of its nitidulid pollinators coevolved as a response to the high, predominantly nocturnal rainfall in the Chocó region of Colombia.

Restrepo et al. (2016) sampled *Mystrops* from inflorescences of eight different species of *Wettinia* in Colombia. They found 17 different *Mystrops* morphospecies. Although there was some sharing of *Mystrops* morphospecies amongst species, they found high specificity between *Mystrops* assemblages and *Wettinia* species, and in general one primary *Mystrops* visitor per *Wettinia* species.

Lara et al. (2017) studied flowering phenology and flower visitors of *W. kalbreyeri* in Colombia. They found that plants flowered throughout the

Table 11. Pollination of *Wettinia* spp.

	W. maynensis Ecuador	*W. quinaria* Colombia
Flowering season (months), peak	throughout the year	throughout the year
Duration of ♀ anthesis on an inflorescence (days)	6	-
Start of ♀ anthesis (time)	-	18.00
Duration of ♀ anthesis in a flower (hours)	<24	-
♀ scent	strong scent	strong scent
♀ temperature elevation	2.7°C above ambient	3.2°C above ambient
♀ nectar	none	-
Duration of ♂ anthesis on an inflorescence (days)	3	-
Start of ♂ anthesis (time)	during the day	18:00
Duration of ♂ anthesis in a flower (hours)	<24	-
♂ scent	strong scent	strong scent
♂ temperature elevation	10°c above ambient	2.2°C above ambient
♂ nectar	none	none
Number of insect visitors (species)	38	52
Most effective pollinators	*Mystrops* sp. (Nitidulidae) *Phyllotrox* sp. (Curculionidae)	*Mystrops* sp. (Nitidulidae)
Reference	Rodriguez & Balslev, unpublished data	Núñez et al. (2005)

year, and there were many more staminate inflorescences than pistillate. Even though they found different assemblages of insect visitors on staminate and pistillate inflorescences, with many more individual insects on staminate inflorescences, they considered that the abundance of *Mystrops* spp. in these assemblages indicated that these were the most important pollinators. They concluded that the higher number of staminate inflorescences and their availability throughout the year could be an adaptation to support a permanent community of pollinators. In a study of *W. maynensis* in Ecuador, Peñuela et al. (2019) found that plants also flowered throughout the year, although they did not find many more staminate inflorescences than pistillate inflorescences. They considered that climatic factors such as temperature and relative humidity influenced production of staminate inflorescences.

Summary for Iriarteeae

Of the five genera and 32 species in the Iriarteeae, five species in four genera have been studied.

Little is known of pollination in *Dictyocaryum* (Fig. 5A) and *Iriartea*, but both have open, elongate inflorescences and may be bee-pollinated (summarized in Henderson 1990). *Socratea* appears to be beetle-pollinated. There is more information on *Wettinia*. This genus has diverse inflorescences and flowers. Despite this, pollination of the species that have been studied appears to be predominantly by *Mystrops,* and the study of Restrepo et al. (2016) suggests that all species of *Wettinia* may be *Mystrops*-pollinated.

Ferreira et al. (in prep.) resolved *Iriartea* and *Dictyocaryum* as basal in the Iriarteeae clade. *Iriartella* forms the third branch and is sister to the two remaining genera, *Socratea* and *Wettinia*. The pollination studies of *Iriartella* are inconclusive, but *Socratea* and *Wettinia* are clearly beetle-pollinated, and thus there has been a marked shift from *Iriartea* and *Dictyocaryum* with their elongate, protandrous, bee-pollinated inflorescences to *Socratea* and *Wettinia* with their condensed, protogynous, beetle-pollinated inflorescences.

Arecoideae, *Chamaedoreeae*

The tribe comprises five genera (*Hyophorbe,* 5 species; *Wendlandiella,* 1 species; *Synechanthus,* 3 species; *Chamaedorea,* 106 species; *Gaussia,* 5 species) widely distributed in the Neotropics, with the exception of *Hyophorbe* from the Mascarene Islands. Three genera have been studied.

Wendlandiella

Wendlandiella is dioecious. Flowers are arranged in acervuli (a group of flowers borne in a short row). Acervuli are arranged in an alternate and opposite manner along the rachillae. Listabarth (1993a) studied *W. gracilis* (as *W.* sp.) in Amazonian Peru. Plants flowered from July to October. Inflorescences of staminate plants remained at anthesis for up to 70 days. Individual flowers were at anthesis around 08.00, and abscised on the afternoon of the same day. Inflorescences of pistillate plants remained at anthesis for up to 15 days. Individual flowers were at anthesis for up to five days. Neither staminate nor pistillate flowers produced any scent. There were no insect visitors to inflorescences. Wind was considered to be the most effective pollinator.

Wendlandiella is notable for the extremely long duration of staminate anthesis on an inflorescence, 70 days, one of the longest of any palm reviewed here. Listabarth (1993a) reported that fruit set in *Wendlandiella* was rare, and Stauffer et al. (2019) considered that it could be an example of a palm that relies on vegetative reproduction.

Synechanthus

Synechanthus is monoecious. Inflorescences bear numerous rachillae. Flowers are arranged in acervuli, a group of flowers borne in a row, the proximal 1–2 of which are pistillate, the rest staminate (Fig. 6A). Acervuli are arranged in

Figure 6. A. Acervuli of *Synechanthus warscewiczianus*, each with one, proximal pistillate flower (arrowed) and one of the distal, staminate flowers at anthesis (image by R. Bernal). B. Staminate inflorescence of *Chamaedorea ernestii-augustii* (image by D. Hodel). C. Staminate inflorescences of *Chamaedorea tepejilote* (image by D. Hodel). D. Inflorescence of *Sclerosperma mannii*, covered by persistent bracts.

alternate and opposite rows along the rachillae. *Synechanthus warscewiczianus* has been studied on the Pacific coast of Colombia by Siefke & Bernal (2004). Plants flowered at least in July and August, probably throughout the year. Inflorescences were protandrous. Staminate anthesis on an inflorescence continued for 18–25 days. Staminate flowers opened in flushes each day, proceeding in a basipetal direction along the rachillae. Staminate flowers opened between 06.00 and 13.00 and produced small amounts of nectar but no scent. They were at anthesis for a few hours only and fell from the inflorescence on the afternoon of the same day. There was an inter-anthesis period of 3–5 days. Pistillate anthesis on an inflorescence lasted 5–9 days. Pistillate flowers opened between 06.00 and 18.00 and were at anthesis for 2–3 days. At least 64 species of insect visited inflorescences at anthesis. The most effective pollinators were considered to be flies from five families: Syrphidae (*Copestylum* sp.), Simulidae (1 sp.), Sciaridae (1 sp.), Empididae (1 sp.), and Muscidae (1 sp.).

Chamaedorea

All species are dioecious. Inflorescences are solitary or sometimes clustered at a node, and may be spicate or more often branched (Fig. 6B, 6C). Flowers are spirally arranged along the rachillae and are usually solitary, and may be densely to distantly arranged. They are sessile or sometimes sunken in pits. Nine species have been studied (Table 12).

Flowering seasons were a mean of six months, but most species had shorter peaks of flowering, usually of 1–2 months duration. The four sympatric species (*C. ernestii-augustii, C. neurochlamys, C. oblongata, C. tepejilote*) at the Belize site all flowered at the same time during the dry season, and the three sympatric species (*C. costaricana, C. macrospadix, C. tepejilote*) at the Costa Rica site also appeared to flower in the dry season.

On staminate inflorescences, anthesis lasted 1–7 days, apart for an exceptionally long time of 31 days in *C. radicalis*. There are only two records for the start of staminate anthesis, both from *C. pinnatifrons*, one at 06.00 and the other at 18.00. Flowers were at anthesis for 48–120 hours. Flowers produced nectar and were scented, although two species (*C. alternans, C. radicalis*) did not produce either. There was no temperature elevation in staminate or pistillate inflorescences. Pollen, when described, was powdery except for one species, *C. ernestii-augustii*, which was reported to be sticky.

On pistillate inflorescences, anthesis lasted 5–11 days, and on a flower for 48–144 hours, apart from an exceptionally long time in *C. tepejilote*, 168–216 hours. Flowers produced nectar and were scented, although two species (*C. alternans, C. pinnatifrons*) did not produce either and one species (*C. radicalis*) produced only nectar.

The number of species of insect visiting inflorescences was relatively low, with a mean of seven. However, lists of insect visitors were seldom given. Pollination in two species (*C. alternans, C. radicalis*) was reported to be by wind. The other seven species (*C. costaricana, C. ernestii-augustii, C. macrospadix, C. neurochlamys, C. oblongata, C. pinnatifrons, C. tepejilote*) studied, from two different sites (Belize and Costa Rica) were reported to be pollinated by the same species of thrips, *Brooksithrips chamaedoreae*. In South America, *C. pinnatifrons* was said to be pollinated by thrips and wind in Peru, and by *Sanariana* sp. (Chrysomelidae) and wind in Venezuela.

There are various somewhat anecdotal records of wind pollination in *Chamaedorea* (e.g., Bawa et al. 1985 for *C. tepejilote*, as *C. exorrhiza*). These records should be treated with caution given the results of studies in Belize and Costa Rica. Even for the two records of wind pollination, Otero-Arnaiz & Oyama (2001) reported that thrips visited staminate inflorescences of *C. alternans*, and Berry & Gorchov (2004) did not discount insect pollination, especially given the nectariferous pistillate flowers of *C. radicalis.*

Based on her observations, Porter Morgan (2007) wrote of the life cycle of the thrips: "When the life cycle of the pollinating thrips, *Brooksithrips chamaedoreae*, is examined in the context of the reproductive activities of the *Chamaedorea* species involved in this study, it becomes clear that these thrips and *Chamaedorea* are involved in a highly specialized dependent mutualism. Based on my observations the life cycle of *Brooksithrips chamaedoreae* occurs as follows. Adult female thrips lay eggs inside of staminate *Chamaedorea* flowers and, after hatching, the larvae feed on the drying flowers and rachillae. Next, larvae probably pass through at least one more larval stage before they either drop to ground of their own accord, or fall

Table 12. Pollination of *Chamaedorea* spp. (1/3)

	C. alternans Mexico	*C. costaricana* Costa Rica	*C. ernestii-augustii* Belize	*C. macrospadix* Costa Rica
Flowering season (months), peak	October to January, peak in November	-	January to May, peak in March	-
Duration of ♂ anthesis on an inflorescence (days)	ca. 3	-	4–7	-
Start of ♂ anthesis (time)	-	-	-	-
Duration of ♂ anthesis in a flower (hours)	-	-	72–120	-
♂ scent	none	-	sweet scent	-
♂ temperature elevation	-		none	
♂ nectar	none	-	present	-
Duration of ♀ anthesis on an inflorescence (days)	ca. 8	-	7	-
Start of ♀ anthesis (time)	-	-	-	-
Duration of ♀ anthesis in a flower (hours)	-	-	72–120	-
♀ scent	none	-	strong, sweet scent	-
♀ temperature elevation	-	-	none	-
♀ nectar	none	-	present	-
Number of insect visitors (species)	1 on ♂, 0 on ♀	ca. 7	-	ca. 7
Most effective pollinators	wind	*Brooksithrips chamaedoreae* (Thripidae), wind	*Brooksithrips chamaedoreae* (Thripidae)	*Brooksithrips chamaedoreae* (Thripidae), wind
Reference	Otero-Arnaiz & Oyama (2001)	Ríos et al. (2014)	Porter Morgan (2007)	Ríos et al. (2014)

with the senescing flowers. There is probably one generation each year. The thrips remain in the soil, usually within the top 30 cm, for the duration of the rainy season. Pupae are cued to complete their development and become adult thrips by the rising temperature and reduction of rains that signals the beginning of the warm, dry season. The adult thrips emerge from the soil, where they have spent the cool and rainy 'winter' months and seek out *Chamaedorea* flowers. Due to the clustered distribution of the palms, as well as the fact that the larvae fall to the ground under their parent plants, *Chamaedorea* flowers tend to be located easily. Also, the phenology of these *Chamaedorea* species is such that they flower soon after the rainy season ends. Thus, the flowers become available at approximately the same time as the adult thrips are emerging.

Male thrips visit staminate inflorescences primarily for pollen and other nutritional rewards, while they visit pistillate inflorescences primarily to entice females for mating activity. On the other hand, female thrips visit staminate inflorescences for both nutritional rewards, specifically pollen, and to utilize staminate flowers as a brood site. Female thrips are attracted to pistillate

Table 12. Pollination of *Chamaedorea* spp. (2/3)

	C. neurochlamys Belize	*C. oblongata* Belize	*C. pinnatifrons* Costa Rica	*C. pinnatifrons* Peru
Flowering season (months), peak	January to May, peak in March	October to August, peak in March and April	February to June	June to August, peak in June and July
Duration of ♂ anthesis on an inflorescence (days)	4–7	4–7	-	<1
Start of ♂ anthesis (time)	-	-	-	18.00
Duration of ♂ anthesis in a flower (hours)	48–72	-	-	ca. 12
♂ scent	fruity scent	sweet, musty scent	-	sweet scent
♂ temperature elevation	none	none	-	-
♂ nectar	-	present	-	-
Duration of ♀ anthesis on an inflorescence (days)	10	7	-	ca. 5
Start of ♀ anthesis (time)	-	-	-	-
Duration of ♀ anthesis in a flower (hours)	-	ca. 96	-	48
♀ scent	sweet, fruity scent	sweet, musty scent	-	none
♀ temperature elevation	none	none	-	-
♀ nectar	-	-	-	none
Number of insect visitors (species)	ca. 10	ca. 10	ca. 7	ca. 5
Most effective pollinators	*Brooksithrips chamaedoreae* (Thripidae)	*Brooksithrips chamaedoreae* (Thripidae)	*Brooksithrips chamaedoreae* (Thripidae), wind	thrips, wind
Reference	Porter Morgan (2007)	Porter Morgan (2007)	Ríos et al. (2014)	Listabarth (1993a)

inflorescences primarily by the male-produced sex pheromone during the peak hours of activity for mating opportunities, rather than by the fragrance produced by the pistillate inflorescences. As pollen has been cited as a food that provides the necessary energy for thrips mating, the majority of the thrips arriving at the pistillate inflorescence of *Chamaedorea* for copulation may have previously visited staminate flowers and therefore be carrying *Chamaedorea* pollen.

It is important to note that female thrips must oviposit in staminate flowers that have not yet undergone anthesis, because the hatching of eggs and development of larvae to a stage where they are able to leave the inflorescence and pupate requires approximately 8 days, and the flowers are at anthesis for 4 to 6 days. Therefore, eggs must be laid prior to anthesis to ensure the proper amount of development time. This requirement is not problematic for thrips, as they tend to oviposit in small, closed locations, where their bodies are in maximum contact with the surrounding floral tissues. The opening flowers of *Chamaedorea* provide enclosed floral chambers, which thrips utilize as areas in which to lay their eggs. Also by entering the flowers and ovipositing prior to

Table 12. Pollination of *Chamaedorea* spp. (3/3)

	C. pinnatifrons Venezuela	*C. radicalis* Mexico	*C. tepejilote* Belize	*C. tepejilote* Costa Rica
Flowering season (months), peak	-	all year, peak in March to June	January to May, peak in March	-
Duration of ♂ anthesis on an inflorescence (days)	-	31	4–7	-
Start of ♂ anthesis (time)	06.00	-	-	-
Duration of ♂ anthesis in a flower (hours)	48	ca. 72	-	-
♂ scent	-	none	sweet, fruity scent	-
♂ temperature elevation	-	-	none	-
♂ nectar	-	none	present	-
Duration of ♀ anthesis on an inflorescence (days)	-	11	7–9	-
Start of ♀ anthesis (time)	-	-	-	-
Duration of ♀ anthesis in a flower (hours)	96	144	168–216	-
♀ scent	-	none	sweet, fruity scent	-
♀ temperature elevation	-	-	none	-
♀ nectar	-	present	present	-
Number of insect visitors (species)	7	ca. 3	ca. 8	ca. 7
Most effective pollinators	*Sanariana* sp. (Chrysomelidae), wind	wind	*Brooksithrips chamaedoreae* (Thripidae), Staphylinidae	*Brooksithrips chamaedoreae* (Thripidae), wind
Reference	Seres & Ramírez (1995)	Berry & Gorchov (2004)	Porter Morgan (2007)	Ríos et al. (2014)

anthesis, thrips allow their eggs the time necessary for development. Therefore, the timing of oviposition and the timing of floral anthesis are closely linked.”

Porter Morgan (2007) considered that there was probably only one thrips generation per year. However, Sakai (2002) wrote, of thrips in general: “An outstanding characteristic of thrips is their high rate of reproduction. They can grow from an egg to adult in 1–2 weeks, and produce several generations within a single flowering season. As a result, large numbers of individuals are produced and can function as pollinators even if the original pollinator populations were small.”

Ríos et al. (2014) used cluster analysis on 18 floral traits (e.g., flower and pollen morphology) from 52 *Chamaedorea* species. They found that species clustered into five groups. They wrote: “None of the groups were entirely described by anemophilous or entomophilous traits alone; instead, most species possessed a combination of inflorescence and flower characteristics adapted for wind as well as insect pollination……..Floral trait analyses suggest that pollination mechanisms within the dioecious palm genus *Chamaedorea* do not constitute a dichotomy between entomophilous and anemophilous species, since most species exhibit a combination of floral traits for both insect and wind pollination. While some *Chamaedorea* species may be completely entomophilous or anemophilous, most analyzed species have floral traits that simultaneously allow for the transport of pollen by both vectors, a system termed 'ambophily'... These results suggest that based on morphological traits, a large number of species may be ambophilous. This type of mixed pollination should be explicitly considered in future experiments of pollination biology in *Chamaedorea*."

There is exceptional diversity in inflorescence and flower morphology in *Chamaedorea* (Hodel 1992, Askgaard et al. 2008). Hodel recognized seven different subgenera in the genus, and these were distinguished mostly by floral morphology. The seven thrips-pollinated species (*C. costaricana, C. ernestii-augustii, C. macrospadix, C. neurochlamys, C. oblongata, C. pinnatifrons, C. tepejilote*) belong to three different subgenera. Notably, *C. ernestii-augustii,* in subgenus *Eleutheropetalum*, has bright orange pistillate flowers, and *C. tepejilote*, in subgenus *Stephanostachys*, has densely spaced staminate flowers. The relationship between floral morphology and pollinators is therefore obscure. Askgaard et al. (2008) wrote: "Thus based on a rather incomplete sampling of the species diversity within *Chamaedorea* it can be concluded that the link between floral anatomical features and pollination mechanism remains unclear."

Summary for Chamaedoreeae

Of the five genera and 120 species of the tribe, there are studies of 11 species in three genera.

There is a marked contrast between the dioecious *Wendlandiella* and the monoecious *Synechanthus*. The former may be wind-pollinated (if it is pollinated at all) and has an exceptionally long period of staminate anthesis, and the latter appears to be fly pollinated.

Chamaedorea is a large, widespread genus with numerous species and diverse inflorescence and floral morphology. Despite this, the evidence so far suggests that species could be pollinated almost exclusively by thrips and wind, although the relative importance of either is still unclear. In the case of the thrips, this appears to be an example of a brood site pollination mutualism. The mechanism by which sympatric, thrips-pollinated species that flower at the same time avoid pollen from heterospecific species is unknown.

Arecoideae, Podococceae

The tribe comprises one genus (*Podococcus*, 2 species) distributed in Africa. No species have been studied.

Arecoideae, Truongsonieae

The tribe comprises one genus (*Truongsonia*, 1 species) distributed in Vietnam. The species has not been studied.

Arecoideae, Oranieae

The tribe comprises one genus (*Orania*, 30 species) distributed in Malesia and Madagascar. No species have been studied.

Arecoideae, Sclerospermeae

The tribe comprises one genus (*Sclerosperma*, 3 species) distributed in Africa. No species have been studied in detail. This genus is one in which the short, spicate inflorescence is covered by a bract at anthesis, at least initially (Fig. 6D). According to van Valkenburg et al. (2008) the bract of *Sclerosperma mannii* has a distal opening. During pistillate anthesis the inflorescence had an elevated temperature and is "… filled with a transparent liquid at the base." Inflorescences were visited by numerous nitidulid beetles. *Sclerosperma* and *Podococcus* are closely related (Ferreira et al. in prep.) and there is an interesting contrast between the condensed, bract-enclosed inflorescences of the former and the elongate, open inflorescences of the latter.

Arecoideae, Roystoneeae

The tribe comprises one genus (*Roystonea*, 10 species) distributed in the Caribbean region. No species have been studied. Bruno de Medeiros (pers. comm.) reported a species of weevil (*Notolomus* sp.) on inflorescences of cultivated plants in Panama, and considered that bees were the most probable pollinator.

Arecoideae, Reinhardtieae

The tribe comprises one genus (*Reinhardtia*, 6 species) distributed in Central America and the Caribbean. No species have been studied.

Arecoideae, *Cocoseae*, *Attaleinae*

The subtribe comprises 10 genera (*Beccariophoenix,* 3 species; *Jubaeopsis,* 1 species; *Voanioala,* 1 species; *Allagoptera,* 6 species; *Attalea,* 30 species; *Butia,* 23 species; *Cocos,* 1 species; *Jubaea,* 1 species; *Syagrus,* 56 species; *Parajubaea* 3 species) widely distributed in Madagascar, southern Africa, and the Neotropics. Five genera have been studied.

Allagoptera

Allagoptera is monoecious. Inflorescences are spicate and bear closely spaced, unisexual flowers arranged in triads, with staminate flowers only on distal part of the inflorescence (Fig. 7A). Sometimes, especially on younger plants, the pistillate flowers do not develop, giving all staminate inflorescences. Pollination of *A. arenaria* has been studied by Leite (1990) in eastern Brazil.

Plants flowered throughout the year with a peak in June and July. Inflorescences opened at any time of day but usually early in the morning. Prior to opening, inflorescences heated up to 2°C above ambient. Inflorescences were protandrous. Soon after bract opening all staminate flowers were at anthesis. Staminate anthesis lasted about 3 days and the flowers then began to fall from the inflorescence. Flowers produced a strong, musky scent. There was an inter-anthesis period of nine days. Pistillate flowers opened slowly but synchronously over a period of 3–5 days, and were then all at anthesis for 24 hours. Pistillate flowers produced a similar but weaker scent to that of the staminate flowers. They also produced nectar.

Figure 7. A. Inflorescence of *Allagoptera arenaria* at pistillate anthesis. B. Staminate inflorescence of *Attalea funifera* C. Inflorescence of *Butia catarinensis* D. Inflorescence of *Syagrus orinocensis* (image by R. Bernal).

Inflorescences were visited by about 13 species of insect. The most effective pollinators were considered to be *Mystrops* spp. (Nitidulidae) and *Derelomus* spp. (Curculionidae). The beetles fed on pollen, mated, and oviposited on staminate flowers, and eggs and larvae continued their development on the ground after the staminate flowers had fallen. Leite noted the high degree of synchrony between the development of the staminate flowers and that of the beetles. Bees, butterflies, and wind could also contribute to pollination.

Allagoptera arenaria is unusual in that it is beetle-pollinated and yet has several features usually associated with bee pollination—protandry, diurnal staminate anthesis, a several day inter-anthesis period, and pistillate flowers with nectar. On the other hand, temperature elevation, musky scent, and synchronous, relatively short-lived staminate and pistillate anthesis is usually associated with beetle pollination.

On another species of *Allagoptera*, *A. caudescens* (previously *Diplothemium caudescens* and *Polyandrococos caudescens*), Bondar (1941a) recorded the derelomine weevil *Derelomus sternicornis* (now *Diplothemiobus*) from inflorescences.

Attalea

Attalea is monoecious. Inflorescences are large and bear unisexual flowers in triads (Fig. 7B). However, sexual expression is quite complex. Sometimes the pistillate flowers of an inflorescence do not develop, giving all staminate inflorescences, and sometimes staminate flowers do not develop, giving all pistillate inflorescences. Less common are inflorescences with both staminate and pistillate flowers, but even here staminate flowers sometimes produce sterile pollen, and so the inflorescence is then functionally pistillate. Individual plants can produce all of these different kinds of inflorescence; usually younger plants tend to produce more staminate inflorescences and older more pistillate. Staminate flowers are notable for their diverse morphology. In fact, previously four or five different genera were recognized based on staminate flower morphology. The genus is also notable for its propensity to hybridize (Henderson 2020b). Nine species have been studied (Table 13). The data in Table 13 refer to unisexual inflorescences, so there is no inter-anthesis period.

Plants flowered throughout the year although there were usually annual peaks of 2–6 months duration. *Attalea sagotii* and *A. guianensis* had shorter flowering seasons of six months.

Anthesis on a staminate inflorescence lasted 2–4 days. Staminate flowers were at anthesis usually in the morning, although in *Attalea sagotii* and *A. guianensis* they opened in the evening. All flowers were at anthesis immediately on bract opening, at least in *A. allenii*, although in *A. sagotii* they were reported to open in flushes over 2–3 days. Individual flowers were at anthesis for 12 hours or less. Inflorescences heated up at anthesis, from 4.5–10°C above ambient, and produced a sweet or fruity scent. Flowers did not produce nectar.

Anthesis on a pistillate inflorescence lasted 3–5 days. Pistillate flowers opened during the day although in *Attalea sagotii* and *A. guianensis* they opened in the evening. Individual flowers were at anthesis for 48–72 hours, much longer in *A. funifera*, 120–168 hours. Inflorescences heated up at anthesis, from 4–8°C above ambient, and produced a sweet or fruity scent (the only exception was *A. speciosa*, whose pistillate inflorescences did not produce a scent at anthesis nor did they heat up). Flowers did not produce nectar.

Inflorescences were visited by large numbers of different species of insect, from 17–49. The most effective pollinators were *Mystrops* (Nitidulidae) and sometimes other Curculionidae and Staphylinidae. Insects visited staminate inflorescences in large numbers. For example, Núñez (2014) reported that staminate inflorescences of *A. maripa* were visited by an average of 65,700 individual insects, the most abundant of which were *Mystrops*. Beetles ate pollen, mated, and oviposited on staminate inflorescences. Insects visited pistillate inflorescences in much lower numbers, and *Mystrops* and other pollinators were considered to be deceived into visiting pistillate inflorescences by their visual and olfactory similarity to staminate inflorescences.

There is some evidence that *Attalea* species are pollinated by specific species of *Mystrops*. Of the three *Attalea* species he studied, Núñez (2014) wrote: "The evaluated variables, which included

Table 13. Pollination of *Attalea* spp. (1/2)

	A. allenii Colombia	*A. butyracea* Colombia	*A. funifera* Brazil	*A. guianeneis* (as *A. attaleoides*) Brazil	*A. insignis* Colombia
Flowering season (months), peak	throughout the year	throughout the year, peak from June to October	throughout the year, peak from December to April	August to January	throughout the year, peak from March to June
Duration of ♂ anthesis on an inflorescence (days)	ca. 3	4	ca. 2	2-3	2
Start of ♂ anthesis (time)	06:00	during the day	-	18.00	during the day
Duration of ♂ anthesis on a flower (hours)	-	-	few	ca. 12	-
♂ scent	scent	scent	sweet scent	scent	scent
♂ temperature elevation	5.4°c above ambient	4.5°c above ambient	-	6°c	7.5°c above ambient
♂ nectar	none	-	-	-	-
Duration of ♀ anthesis on an inflorescence (days)	-	-	-	2-3	-
Start of ♀ anthesis (time)	06:00	during the day	-	17.00	during the day
Duration of ♀ anthesis on a flower (hours)	72	72	120–168	-	72
♀ scent	scent	scent	scent	scent	scent
♀ temperature elevation	7°c above ambient	4.5°C above ambient	-	4°C	5.5°C above ambient
♀ nectar	none	-	-	-	-
Number of insect visitors (species)	21	ca. 40	17	24	ca. 36
Most effective pollinators	*Mystrops* sp. (Nitidulidae)	*Mystrops* spp. (Nitidulidae)	*Mystrops* sp. (Nitidulidae), *Phyllotrox* sp. (Curculionidae)	*Mystrops* sp. (Nitidulidae), Staphylinidae spp., *Groatus* sp., *Phytotribus* sp., *Belopoeus* sp. (Curculionidae)	*Mystrops* spp. (Nitidulidae)
Reference	Núñez et al. (2005)	Núñez (2014)	Voeks (2002)	Küchmeister (1997)	Núñez (2014)

Table 13. Pollination of *Attalea* spp. (2/2)

	A. maripa - Colombia	*A. phalerata* - Brazil	*A. sagotii*[1] - Brazil	*A. speciosa* (as *Orbignya phalerata*) - Brazil
Flowering season (months), peak	throughout the year, peak from October to March	throughout the year, peak from September to October	March, July to November	throughout the year, peak from January to May
Duration of ♂ anthesis on an inflorescence (days)	3	3	2–3	2
Start of ♂ anthesis (time)	during the day	09.00	18.00	-
Duration of ♂ anthesis on a flower (hours)	-	-	ca. 12	several
♂ scent	scent	sweet scent	fruity scent	sweet scent
♂ temperature elevation	5°C above ambient	present	10°C above ambient	none
♂ nectar	-	none	-	-
Duration of ♀ anthesis on an inflorescence (days)	3	-	2–3	-
Start of ♀ anthesis (time)	during the day	during the day	17.00	-
Duration of ♀ anthesis on a flower (hours)	72	-	-	48
♀ scent	scent	weaker sweet scent	weaker fruity scent	none
♀ temperature elevation	4°C above ambient	none	8°C above ambient	none
♀ nectar	-	none	-	none
Number of insect visitors (species)	ca. 49	23	30	24
Most effective pollinators	*Mystrops* sp. (Nitidulidae)	*Mystrops* sp. (Nitidulidae), Madarini (Curculionidae)	*Mystrops* sp. (Nitidulidae), Curculionidae, Staphylinidae	*Mystrops* sp. (Nitidulidae)
Reference	Núñez (2014)	Fava et al. (2011)	Küchmeister (1997), Küchmeister et al. (1993)	Anderson et al. (1988)

[1] Identified as *Attalea microcarpa* in Küchmeister (1997) and as *Orbignya spectabilis* in Küchmeister et al. (1993).

abundance, frequency, pollen loads, behavior and temporal variation, determined that the main pollinators of the three different species of palms were *Mystrops* (Nitidulidae: Coleoptera): *A. butyracea* was pollinated by *Mystrops* sp.1, *Mystrops* sp.2 and *Mystrops* sp.3; *A. insignis* was pollinated by *Mystrops* sp.4 and *Mystrops* sp.5; and *Mystrops* sp.6 pollinated *A. maripa.*"

Núñez et al (2005) wrote of *A. allenii*: "*Mystrops* sp. nov. B uses the staminate inflorescences as an aggregation site for mating, ovipositing and finding protection. The heating of the staminate inflorescences coincides with the duration of the larval phase of this species, and it probably accelerates its development in the early stages, as temperature is an important factor in controlling development during the first hours of life in insects…"

There are a few other less detailed studies of *Attalea* and most of these confirm the general pattern described above: Lopera Blair et al. (2007) for *A. amygdalina* in Colombia; Silberbauer-Gottsberger (1990) for *A. geraensis* in Brazil; and Moraes et al. (1996) for *A. phalerata* in Bolivia. On the other hand, Feil (1995) considered that *A. colenda* in Ecuador was pollinated by bees and wind, although Balslev & Henderson (1987) reported finding thousands of *Mystrops* on a staminate inflorescence of *A. colenda*. Storti & Storti (2002) studied insect visitors to *A. maripa* inflorescences in Brazil. They found a peak of flowering from July to November and considered a scarab beetle, *Cyclocephala* sp., to be the most effective pollinator. They did not record any Nitidulidae from inflorescences. Tucker Lima (2009) and Tucker Lima et al. (2021) reported on flower colour variation in *A. phalerata*. Floral scent of four of the species in Table 13 was studied, and each found to be different (Núñez 2014, Núñez et al. 2005). For three of these species, scents of staminate and pistillate inflorescences were over 90% similar, as is usually found in palms, but in the fourth species, *A. allenii*, staminate and pistillate scent similarity was only 47%.

Many of the beetles associated with *Attalea* (and *Syagrus*) inflorescences were first described by Bondar (e.g., Bondar, 1940a, 1940b, 1941a, 1941b). Although he was not particularly concerned with pollination, Bondar, working mostly in eastern Brazil, was one of the first entomologists to describe beetles and their behavior on palm inflorescences. Bondar (1964) wrote: "Cada gênero e, às vêzes, cada espécie de palmeiras nativas têm sua própria fauna entolomológica e, pelos insetos colhidos, pode-se determinar o gênero e a espécie de palmeira." (Each genus of native palms, and at times, each species, has its own entomological fauna, and by means of the insects collected, one can determine the genus and species of the palm).

Butia

Butia is monoecious. Inflorescences bear unisexual flowers in triads (Fig. 7C). Pollination has been studied in three species (Table 14).

Butia catarinensis flowered for eight months, *B. odorata* for six, and *B. paraguayensis* for at least 10 months. Inflorescences were protandrous. Staminate anthesis on an inflorescence lasted 5–15 days. Flowers opened in the morning and flushes of flowers opened each day. Individual flowers were at anthesis for 12–48 hours. Flowers were scented and produced nectar.

There was in inter-anthesis period of 1–15 days. Pistillate anthesis continued for 2–8 days and individual flowers were at anthesis for 24–48 hours. Flowers were scented and produced nectar.

Large numbers of different species of insect visited inflorescences. The most effective pollinators were considered to be bees, especially *Thectochlora alaris* and *Trigona* spp. Bees collected pollen from staminate flowers, and fed on nectar from staminate and pistillate flowers.

Haran et al. (2023a) considered that Rosa (2000) had overlooked weevils on *B. catarinensis* inflorescences, by only collecting insects during the day, and that hundreds of individuals of *Anchylorhynchus eriospathae* occurred on inflorescences, and these weevils bred on pistillate flowers. Silberbauer-Gottsberger et al. (2013) noted that a large number of different species of insect visited the inflorescences of *B. paraguayensis*. They divided these insects into three groups; 1) a group of parasitic beetles that oviposited on bracts and flowers; 2) a group including both parasites and pollinators, for example curculionids (e.g., *Anchylorhynchus*) and nitidulids (e.g., *Mystrops*); and 3) a group comprising pollinators such as bees and some flies that feed on pollen and nectar. A fourth, non-pollinating group visited only staminate flowers and consumed pollen and

Table 14. Pollination of *Butia* spp.

	B. catarinensis (as *B. capitata* var. *odorata*) - Brazil	*B. odorata* - Brazil & Uruguay	*B. paraguayensis*[2] - Brazil
Flowering season (months), peak	July to February, peak in November and December	September to February, peak in November and December (Morel 2006)	at least May to February
Duration of ♂ anthesis on an inflorescence (days)	5–10	6–11	ca. 15
Start of ♂ anthesis (time)	08.00	-	morning
Duration of ♂ anthesis on a flower (hours)	ca. 12	ca. 12	24–48
♂ scent	sweet scent	-	sweet scent
♂ temperature elevation	-	-	-
♂ nectar	present	present	present
Inter-anthesis (days)	2–6	1–5	10–15
Duration of ♀ anthesis on an inflorescence (days)	2–8	4–6	2–3
Start of ♀ anthesis (time)	08.00	-	-
Duration of ♀ anthesis on a flower (hours)	48	-	24–48
♀ scent	sweet scent	-	sweet scent
♀ temperature elevation	-	-	-
♀ nectar	present	present	present
Number of insect visitors (species)	28 (bees only)	42	at least 45
Most effective pollinators	*Thectochlora alaris*, *Dialictus* spp. (Halictidae)	Tiphidae, Apidae (Hymenoptera)	*Trigona* spp. (Meliponinae), Halictidae spp., Apinae spp.
Reference	Rosa et al. (1998), Rosa (2000)	da Fonseca (2014)	Silberbauer-Gottsberger (1973), Silberbauer-Gottsberger et al. (2013)

[2] Identified as *B. leiospatha* by Silberbauer-Gottsberger (1973) and as *B. paraguayensis* by Silberbauer-Gottsberger et al. (2013).

nectar, for example some weevils. Silberbauer-Gottsberger et al. reported that 30–50% of pistillate flower buds were parasitized by *Anchylorhynchus*, and that these buds fell to the ground where the weevil larvae continued to develop.

Morel (2006) studied *B. odorata* in Uruguay. She noted that neither staminate nor pistillate flowers produced scent during anthesis, and that beetle larvae developed in both staminate and pistillate flowers and destroyed developing fruits. Mercadante-Simöes et al. (2006) briefly described inflorescence development of *B. capitata* in Brazil, and Dias et al. (2022) studied reproductive biology of cultivated plants of the same species.

Cocos

Cocos is monoecious and inflorescences bear unisexual flowers in triads There are various studies of the coconut, *C. nucifera,* all from cultivated plants (reviewed in Thomas & Josephrajkumar 2022). It appears to have fairly typical inflorescence development, with protandry, a relatively long, diurnal staminate anthesis with nectar production, a short inter-anthesis period, and a relatively short, diurnal pistillate anthesis with sweet scent and nectar production. Bee pollination was considered most likely (e.g., Hedström 1986). However, Cock (1985) reported that a derelomine weevil, *Derelomorphus eburneus,* was host specific on *C. nucifera* in Malaysia and bred on its inflorescences and could be a pollinator; Thomas & Josephrajkumar (2022) reported that a weevil, *Amorphoidea coimbatorensis*, was also a potential pollinator in India; and Chakravarthy & Thyagaraj (2012) reported squirrels as pollinators in India.

Syagrus

Syagrus is monoecious. Inflorescences bear unisexual flowers in triads (Fig. 7D), although occasionally all staminate inflorescences are produced. Pollination has been studied in five species (Table 15).

Plants flowered throughout the year in all but one species, *Syagrus inajai*, although most species had peaks of flowering. All species were protandrous. Staminate anthesis lasted 5–15 days on an inflorescence. Anthesis appeared to be diurnal in *S. coronata, S. orinocensis*, and *S. loefgrenii*[3], and nocturnal in *S. inajai* and *S. smithii*. Individual flowers were at anthesis for 12–48 hours. Staminate inflorescences were reported to produce a sweet scent and no temperature elevation (with the exception of *S. inajai*). Nectar production was recorded in only one species, *S. loefgrenii*.

There was an inter-anthesis period of 5–15 days, followed by 2–15 days of pistillate anthesis. Pistillate anthesis appeared to be diurnal in *S. orinocensis* and nocturnal in *S. smithii*. Individual flowers were at anthesis for 24–96 hours. Pistillate inflorescences produced nectar in some cases and a mostly sweet scent.

There were large numbers of different species of insect visiting inflorescences, 30–55, except for *S. inajai*. The most effective pollinators were usually reported to be curculionid and nitidulid beetles. The beetles ate pollen, mated, and oviposited in flowers or in the peduncular bracts (i.e., brood-site pollinators). One species, *S. orinocensis*, was pollinated by stingless bees.

Table 15. Pollination of *Syagrus* spp. (1/2)

	S. coronata Pernambuco, Brazil	*S. coronata* Bahia, Brazil	*S. inajai*, Brazil
Flowering season (months), peak	throughout the year, peak in November	throughout the year	March to July
Duration of ♂ anthesis on an inflorescence (days)	7–10	5–6	several days
Start of ♂ anthesis (time)	-	day	evening
Duration of ♂ anthesis on a flower (hours)	-	-	-
♂ scent	vanilla scent	-	-
♂ temperature elevation	none	none	6°C above ambient
♂ nectar	-	-	-
Inter-anthesis (days)	15	5–8	several days
Duration of ♀ anthesis on an inflorescence (days)	10–15	3–6	several days
Start of ♀ anthesis (time)	-	day and night	-
Duration of ♀ anthesis on a flower (hours)	-	48–96	-
♀ scent	vanilla scent	-	-
♀ temperature elevation	none	none	6°C above ambient
♀ nectar	-	present	-
Number of insect visitors (species)	40	55	8
Most effective pollinators	*Anchylorhynchus* sp., *Andranthobius* sp. (Curculionidae), Nitidulidae sp., *Trigona spinipes* (Apidae)	*Anchylorhynchus* sp. (Curculionidae)	Curculionidae, Nitidulidae, Staphylinidae, Scarabaeidae, Apidae
Reference	Barbosa et al. (2021)	de Medeiros et al. (2019)	Küchmeister (1997)

Table 15. Pollination of *Syagrus* spp. (2/2)

	S. orinocensis Colombia	*S. loefgrenii*[3] Brazil	*S. smithii* Colombia
Flowering season (months), peak	throughout the year, peak May to September	throughout the year	throughout the year, peak July to December
Duration of ♂ anthesis on an inflorescence (days)	8–16	ca. 15	14
Start of ♂ anthesis (time)	ca. 06.30	morning	late afternoon
Duration of ♂ anthesis on a flower (hours)	-	24–48	12
♂ scent	sweet scent	straw-like scent	sweet scent
♂ temperature elevation	none	-	-
♂ nectar	-	present	-
Inter-anthesis (days)	8	10–15	10
Duration of ♀ anthesis on an inflorescence (days)	2–3	5–7	4
Start of ♀ anthesis (time)	ca. 06.30	-	late afternoon
Duration of ♀ anthesis on a flower (hours)	-	24–48	-
♀ scent	sweet scent	straw-like scent	sweet scent
♀ temperature elevation	none	-	-
♀ nectar	present, small amount	present	-
Number of insect visitors (species)	43 to ♂, 20 to ♀	ca. 30	37
Most effective pollinators	stingless bees (Apidae, Meliponini)	*Anchylorhynchus* sp., *Microstrates* sp., *Hustachea* sp., *Phytotribus* spp. (Curculionidae), *Mystrops* (Nitidulidae), *Silvanus* sp. (Silvanidae)	*Mystrops* spp. (Nitidulidae)
Reference	Nuñez & Carreño-Barrera (2017)	Silberbauer-Gottsberger et al. (2013)	Guerrero-Olaya & Núñez (2017)

[3] Identified as *Syagrus petraea* by Silberbauer-Gottsberger et al. (2013), but more likely to be *S. loefgrenii* (Bruno de Medeiros, pers. comm.).

Barbosa et al. (2021) analyzed scents from inflorescences of *S. coronata*. They found 23 volatile compounds in the scent emitted by the flowers, and these did not differ between staminate and pistillate phases, and also that peduncular bracts produced scent with a single volatile compound, this not found in inflorescences.

Syagrus species exhibit protandry, long-lasting staminate anthesis, a several day inter-anthesis period, and a generally shorter period of pistillate anthesis. However, there appear to be both beetle-pollinated and bee-pollinated species. Four species, *S. coronata, S. inajai, S. loefgrenii*, and *S. smithii*, are recorded as beetle-pollinated, while *S. orinocensis* is bee-pollinated. There are several other studies that stress bee pollination. For example, Siqueira (1989) considered cultivated plants of *S. romanzoffiana* to be pollinated by bees, *Trigona* sp. and *Tetragonisca* sp. (Apidae, Meliponini). Rocha (2009) considered that a stingless bee, *Trigona spinipes* was the main pollinator of *S. coronata*. On the other hand, Guerrero-Olaya et al. (2018) recorded 17 species of weevils from staminate inflorescences and nine species from pistillate inflorescences of *S. sancona* in Colombia. The authors considered that *Anchylorhynchus* spp., *Phyllotrox* sp., and *Derelomus* sp. had a mutualistic association with the palm. In general, it seems that inflorescences of *Syagrus* are visited by a great diversity of potential pollinators, particularly bees and beetles. In some species stingless bees are considered more important pollinators (e.g., Núñez & Carreño-Barrera 2017) and in others beetles (e.g., Guerrero-Olaya & Núñez 2017).

de Medeiros et al. (2019) examined insect visitors in detail, showing the great complexity of the interactions between the palm and insects. They showed how *S. coronata* is pollinated by both generalist insects, mostly bees, as well as specialist beetles that breed on inflorescences. Of these latter, the weevil *Anchylorhynchus trapezicollis* was considered to be both an important pollinator and a seed predator. Adults visited staminate and pistillate flowers in large numbers, adult females oviposited between the petals of the pistillate flowers, and later instars consumed the developing fruits (as well as other conspecific larvae). Interestingly, although *Mystrops* sp. were present on inflorescences of *S. coronata,* they were not considered pollinators. Further complexity of the interaction was demonstrated by de Medeiros & Farrell (2020). They studied weevil visitors to inflorescences of *S. coronata* and *S. botryophora* in eastern Brazil. Based on molecular data, they found that what appeared to be nine different weevil morphospecies actually comprised 14 different cryptic species. One morphospecies, *Anchylorhynchus trapezicollis,* pollinator of both species of *Syagrus,* was found to comprise three cryptic species. These three were sympatric; the first occurred on both *Syagrus* species, the second only on *S. coronata,* and the third only on a southern population of *S. botryophora.*

Syagrus may be one of the few examples where the shift between bee and beetle pollination has occurred within the same genus, a shift usually found between genera. This can be seen by comparing two species, *S. orinocensis* (Nuñez & Carreño-Barrera 2017) and *S. smithii* (Guerrero-Olaya & Núñez 2017). Both species occur in eastern Colombia and are very similar to one another in inflorescence and flower morphology. Their inflorescence development is almost identical. *Syagrus orinocensis* has 8–16 days of staminate anthesis, an eight day inter-anthesis period, and 2–3 days of pistillate anthesis; *S. smithii* has 14 days, 10 days, and four days, respectively. However, there is one significant difference. Flowers of *S. orinocensis* open early in the morning and so have diurnal anthesis, those of *S. smithii* open in the late afternoon and so have nocturnal anthesis. Given the similarity in insect visitors to the two species, especially Curculionidae, Nitidulidae, and Hymenoptera, and the difference in anthesis, it is inevitable that *S. orinocensis* is pollinated predominantly by bees and *S. smithii* by beetles. Nuñez & Carreño-Barrera (2017) designated the 43 species of insect visitors to *S. orinocensis* inflorescences into groups based on their behaviour. Twelve species of meliponid bees were designated as principal or co-pollinators and five species of Curculionidae were designated co-pollinators. For *S. smithii,* of the 37 species of insect visitor, two species of Nitidulidae (*Mystrops* spp.) were designated as principal pollinators, but not any Hymenoptera.

Syagrus inajai, S. orinocensis, S. sancona, and *S. smithii* are all in the same clade (Ferreira et al. in prep.). If the basal species in this clade, *S. sancona,* is presumed to be beetle-pollinated (Guerrero-Olaya et al. 2018), then at least one shift can be inferred from beetle pollination to bee pollination. This shift in pollinators is associated with a change in the time of anthesis, from diurnal to nocturnal. Diurnal anthesis is often associated with nectar production (as in pistillate flowers of *S. orinocensis*) and nocturnal anthesis associated with no nectar production and temperature elevation (as in *S. inajai*).

Arecoideae, *Cocoseae*, *Bactridinae*

The subtribe comprises five genera (*Acrocomia,* 8 species; *Aiphanes,* 37 species; *Astrocaryum,* 39 species; *Desmoncus,* 24 species*; Bactris,* 79 species), widely distributed throughout the Neotropics. All genera have been studied.

Acrocomia

Acrocomia is monoecious. Inflorescences bear unisexual flowers (Fig. 8A). There are 1–few rather distantly spaced triads at the base of each rachilla and closely spaced staminate flowers only distally. Pollination of *A. aculeata* has been studied in three localities (Table 16).

Flowering seasons were of 4–6 months duration. The peak of the flowering season at the northern site, in Casanare, Colombia was in the dry season, whereas the peak flowering season at the two southern sites in the Brazilian cerrado was in the rainy season. The two Brazilian sites are about 700 km apart and the palms at each site had slightly different flowering seasons.

Inflorescences were protogynous. Peduncular bracts opened in the evening, less often during the night, to reveal the pistillate flowers already at

Figure 8. A. Inflorescence of *Acrocomia aculeata*. B. Inflorescence of *Aiphanes horrida* (image by R. Bernal). C. Inflorescence of *Astrocaryum alatum* (image by R. Aguilar). D. Inflorescence of *Bactris killipii*.

anthesis. Pistillate anthesis continued for less than one day. A strong scent was given off at this time, but there were no records of temperature elevation. There was no inter-anthesis period, and some overlap on an inflorescence between pistillate and staminate anthesis.

Staminate anthesis began approximately 24 hours after bract opening and continued for 4–5days. Sometimes flushes of flowers opened each day in a basipetal direction along the rachillae, and at other times all staminate flowers appeared to be at anthesis together. Individual flowers were at anthesis for 24 hours. Scent was also given off at this time, but there were no records of temperature elevation during staminate anthesis.

A large number of different species of insect visitors to inflorescences were reported at the Casanare site, fewer at other sites. In all three sites, the most effective pollinators were considered to be *Andranthobius* sp. (Curculionidae) and *Mystrops* sp. (Nitidulidae), as well as *Cyclocephala* sp. (Scarabaeidae) at the Distrito Federal site. Thousands of these small beetles arrived at newly opened inflorescences in the evening, presumably attracted by the strong scent as the peduncular bract opened, and contacted stigmas of pistillate flowers and, if they came from other inflorescences at staminate anthesis, deposited pollen. During staminate anthesis, beetles ate and became covered in pollen, mated, and oviposited on staminate flowers. At the end of or during staminate anthesis the beetles departed for another inflorescence at pistillate anthesis.

Table 16. Pollination of *Acrocomia aculeata*.

	Casanare, Colombia	Distrito Federal, Brazil	Minas Gerais, Brazil
Flowering season (months), peak	December to May, peak in March and April	August to December, peak in October and November	November to February
Duration of ♀ anthesis on an inflorescence (days)	<1	1	<1
Start of ♀ anthesis (time)	17.00	18.00	19.00
Duration of ♀ anthesis on a flower (hours)	<24	24	<24
♀ scent	scent	strong, pungent scent	strong scent
♀ temperature elevation	-	-	-
♀ nectar	-	-	-
Inter-anthesis (days)	-	0 (overlap)	0
Duration of ♂ anthesis on an inflorescence (days)	4–5	5	5
Start of ♂ anthesis (time)	17.00	18.00	-
Duration of ♂ anthesis on a flower (hours)	24	-	-
♂ scent	-	scent	-
♂ temperature elevation	-	-	-
♂ nectar	-	-	-
Number of insect visitors (species)	48	11 species of beetle	11
Most effective pollinators	*Andranthobius* sp. (Curculionidae), *Mystrops* sp. (Nitidulidae)	*Andranthobius* sp. (Curculionidae), *Mystrops* sp. (Nitidulidae), *Cyclocephala* sp. (Scarabaeidae)	*Andranthobius* sp., *Phyllotrox* sp. (Curculionidae), *Mystrops* spp. (Nitidulidae)
Reference	Carreño-Barrera et al. (2021)	Scariot et al. (1991)	Brito (2013)

Carreño-Barrera et al. (2021) wrote: "there is one particular aspect of the reproductive ecology of *A. aculeata* in our studied population that stands out. There are two subsets of effective pollinators of *A. aculeata*, largely determined by their relative abundances and contribution to cross-pollination constituted by a set of main pollinators (*Andranthobius* sp.1 and *Mystrops* sp.1) and a set of accessory pollinators (*Andranthobius* sp.2, *Grasidius* sp.1, *Phyllotrox* sp.1, *Andranthobius* sp.3, *Mystrops* sp.2, and *Cyclocephala forsteri*). The main pollinators, *Andranthobius* sp. and *Mystrops* sp., also dominate the flower-visiting insect fauna associated with *A. aculeata* elsewhere throughout its natural distribution in Colombia…… and in Brazil. Co-pollination thus becomes a highly specialized strategy in *A. aculeata*."

Although there were no records of temperature elevation in *Acrocomia* inflorescences (Table 16), there are some historical records, reviewed in Ervik & Barfod (1999).

Aiphanes

Aiphanes is monoecious and inflorescences bear unisexual flowers in triads (Fig. 8B). These are borne superficially and somewhat distantly along the rachis, and distal parts of the rachillae tend to have staminate flowers only. Four species have been studied (Table 17).

There are few data on flowering seasons. *Aiphanes horrida* flowered for five months.

All species were protandrous. Staminate anthesis on an inflorescence lasted 8–50 days and was apparently mostly diurnal. Flushes of flowers opened each day, and individual flowers were at anthesis for less than one day. Staminate flowers produced nectar in small amounts and were not scented.

Table 17. Pollination of *Aiphanes* spp.

	A. horrida (as *A. aculeata*), Peru	*A. chiribogensis*, Ecuador	*A. eggersii*, Ecuador	*A. erinacea*, Ecuador
Flowering season (months)	February to June	-	-	-
Duration of ♂anthesis on an inflorescence (days)	15–20	40–50	8–10	17–23
Start of ♂ anthesis (time)	morning	all hours	-	peak before 09.00
Duration of ♂ anthesis on a flower (hours)	few	<24	<24	<24
♂ scent	-	none	none	none
♂ temperature elevation	-	-	-	-
♂ nectar	-	present	present	present
Inter-anthesis (days)	2–4	>15	ca. 8	4–8
Duration of ♀ anthesis on an inflorescence (days)	2–3	>10	ca. 8	7–9
Start of ♀ anthesis (time)	-	-	-	-
Duration of ♀ flower anthesis on a flower (hours)	24–48	96–168	96–168	96–168
♀ scent	-	none	none	none
♀ temperature elevation	-	-	-	-
♀ nectar	-	present	present	present
Number of insect visitors	-	22	2	>50
Effective pollinators	wind? insects?	Lauxaniidae sp., micro-moths	*Apis* (Apidae)	Drosophilidae sp., *Copestylum* sp. (Syrphidae)
Reference	Listabarth (1992)	Borchsenius (1993)	Borchsenius (1993)	Borchsenius (1993)

There was an inter-anthesis period of 2–15 days, followed by a shorter period of pistillate anthesis of 2–10 days. Individual pistillate flowers were at anthesis for 24–168 hours. Flowers produced nectar but no scent.

Large numbers of different species of insect visited two of the species, *A. chiribogensis* and *A. erinacea*, although in *A. eggersii* only two species were recorded. Pollinators were reported to be flies, bees, or wind. Listabarth (1992) considered that the role of insects and wind in pollination of *A. horrida* could not be assessed. However, Núñez (2014) reported that several weevil genera (*Andranthobius, Derelomus, Hustachea, Odontoderes, Palmocentrinus*) visited inflorescences of *A. horrida* in Colombia and that a species of *Derelomus* was the principal pollinator. In this context, it may be significant that *A. horrida* has the shortest period of pistillate anthesis, with all pistillate flowers opening together.

Notable in *Aiphanes* are the staminate and pistillate flowers of *A. chiribogensis* and *A. erinacea* with spreading petals, which are reddish-violet in *A. chiribogensis*. These are quite different from those of other genera in the Bactridinae, with nonspreading, mostly white or cream petals, and may be associated with bee and fly visitation.

Borchsenius & Bernal (1996) wrote of *Aiphanes*: "The observations suggest that a series of related pollination mechanisms occur in the genus and that these are due to differences in speed of inflorescence development and flower morphology. The combination of relatively large staminate flowers with linear anthers and rapid inflorescence development (less than one month total anthesis time) appears to be associated with pollination by bees, sometimes with participation of beetles (Coleoptera), bugs (Hemiptera), and wind [e.g., *A. aculeata* (=*A. horrida*), *A. eggersii*], whereas the combination of small staminate flowers with minute oval anthers and slower inflorescence development [e.g., *A. chiribogensis, A. erinacea*] appears to be associated with pollination by flies. The colour of the flowers may also be related to pollination system. Large staminate flowers are generally cream or yellow, whereas small staminate flowers often are more or less purple. Finally, a more specific plant-pollinator relationship, involving weevils mimicking staminate flower buds, may occur in *A. simplex*."

Astrocaryum

Astrocaryum is monoecious. Inflorescences bear unisexual flowers (Fig. 8C). There are 1–few rather distantly spaced triads at the base of each rachilla, with large pistillate flowers, and closely spaced, smaller staminate flowers only distally. Five species have been studied (Table 18).

Flowering seasons appear to be relatively short, of only 3–5 months duration. Inflorescences were protogynous. When the peduncular bract opened, all pistillate flowers were at anthesis immediately or soon afterwards. In *A. acaule, A. gynacanthum,* and *A. gratum* anthesis took place in the afternoon or early evening, whereas in *A. mexicanum* and *A. vulgare* it took place early in the morning. Duration of pistillate anthesis was about one day. Inflorescences produced a sweet or musky scent and temperature elevation. *Astrocaryum mexicanum* and *A. vulgare* had notably higher temperature elevation.

Staminate anthesis took place in the afternoon or early evening of the day following pistillate anthesis in all species except *A. vulgare*. Here, staminate anthesis took place in the early morning, but since pistillate anthesis was also early in the morning, there was still an approximate 24 hour period between the two. Duration of staminate anthesis was 1–2 days. Inflorescences produced scent and lower temperature elevation than pistillate inflorescences.

There were relatively few species of insect visitors to inflorescences, although these were seldom completely enumerated (see below). In most cases the most effective pollinators were Nitidulidae, often *Mystrops* spp. These were sometimes present in large numbers (up to 30,000 individuals per inflorescence in *A. vulgare*, Consiglio & Bourne 2001). There is an interesting contrast between nocturnal anthesis and weevil/scarab pollination in *A. gynacanthum*, and diurnal anthesis and nitidulid pollination in *A. vulgare*.

Aguirre & Dirzo (2008) carried out a detailed study of the insect visitors to inflorescences of *A. mexicanum* at the same locality where Búrquez et al. (1987) studied pollination, Los Tuxtlas in Veracruz, Mexico. Aguirre & Dirzo reported that they collected 60 species of arthropod on inflorescences of *A. mexicanum*. They wrote: "Using a median value of 2.0 inflorescences per reproductive palm, the abundance of arthropods associated to the inflorescences of *A. mexicanum* in Los Tuxtlas is an astonishing number of 1.596 million arthropods ha^{1}." More than 50% of these species were beetles. Among these, four species of Nitidulidae were identified as the most important pollinators, *Mystrops mexicanus, Mystrops sp., Colopterus aberrans,* and *Eumystrops centralis*. Considering these figures, there could be a fantastic number of nitidulids living on *A. mexicanum*.

There are a few other records of interest. Aguirre et al. (2011) and Dáttilo et al. (2015) studied the effect of forest fragmentation on pollinators and pollination of *A. mexicanum*. Listabarth (1992) noted that *A. jauari* had a short flowering season of three months in Venezuela. Inflorescences were protogynous and at anthesis for 3–4 days. Oliveira et al. (2003) studied pollination of cultivated plants of *A. vulgare* in Brazil. They considered that two species of *Mystrops* and the derelomine weevil *Terires minusculus* were the most effective pollinators. Bullock (1981) gave some notes on *A. alatum* in

Table 18. Pollination of *Astrocaryum* spp.

	A. acaule Brazil	*A. gynacanthum* Brazil	*A. gratum* Peru	*A. mexicanum* Mexico	*A. vulgare* Guyana
Flowering season (months), peak	-	-	October to December	March to May	April to August
Duration of ♀ anthesis on an inflorescence (days)	ca. 1	ca. 1	<1	<1	<1
Start of ♀ anthesis (time)	evening	after 14.00	after 15.30	04.00	04.00
Duration of ♀ anthesis on a flower (hours)	ca. 24	ca. 24	<24	16	24
♀ scent	sweet scent	-	sweet, yeast scent	weak nutty to yeasty scent	weak, musky scent
♀ temperature elevation	ca. 3.0°C above ambient	6.8°C above ambient	6°C above ambient	13.8°C above ambient	13.6°C above ambient
♀ nectar	-	-	-	none	-
Inter-anthesis (days)	0	0	0	0 (overlap)	0
Duration of ♂ anthesis on an inflorescence (days)	ca. 2	ca. 2	<1	ca. 1	ca. 1
Start of ♂ anthesis (time)	18.00	18.00	15.00	20.30	03.00
Duration of ♂ anthesis on a flower (hours)	ca. 48	ca. 48	ca. 24	36	24
♂ scent	-	-	sweet, yeast scent	-	-
♂ temperature elevation	ca. 3°C above ambient	-	-	-	2.9°C above ambient
♂ nectar	-	-	-	none	-
Number of insect visitors (species)	at least 5	at least 5	at least 12	32	11
Most effective pollinators	*Mystrops* spp. (Nitidulidae), *Chlorota* sp. (Scarabaeidae), *Phytotribus* (Curculionidae)	*Chlorota* sp. (Scarabaeidae), Baridinae spp. (Curculionidae)	*Mystrops* spp. (Nitidulidae), Notarinae spp. (Curculionidae)	*Mystrops*, *Colopterus* (Nitidulidae)	Nitidulidae spp.
Reference	Küchmeister et al. (1998)	Küchmeister et al. (1998)	Listabarth (1992)	Búrquez et al. (1987)	Consiglio & Bourne (2001)

Costa Rica. Pistillate anthesis was short-lived and took place at night. Staminate anthesis occurred the following night and lasted less than 12 hours. Pollination was considered to be by beetles.

Desmoncus

Desmoncus is monoecious. Inflorescences bear unisexual flowers in triads. Two species have been studied (Table 19).

Plants flowered from December to February, and in *D. mitis* somewhat irregularly at other times of year. Inflorescences were protogynous. The peduncular bract opened early in the evening at about 18.00. All pistillate flowers were at anthesis immediately after the opening of the bract, and remained so for 10–12 hours. Inflorescences heated up and gave off a sweet scent. Nectar production was not recorded from pistillate or staminate

Table 19. Pollination of *Desmoncus* spp.

	D. mitis, Peru	*D. polyacanthos*, Peru
Flowering season (months), peak	December to February (July, October)	December to January
Duration of ♀ anthesis on an inflorescence (days)	<1	<1
Start of ♀ anthesis (time)	18.00	ca. 18.00
Duration of ♀ anthesis on a flower (hours)	10–12	10–12
♀ scent	scent	strong, sweet scent
♀ temperature elevation	1.7°c above ambient	3.1°C above ambient
♀ nectar	-	-
Inter-anthesis (days)	<1	<1
Duration of ♂ anthesis on an inflorescence (days)	<1	<1
Start of ♂ anthesis (time)	16.30	16.30
Duration of ♂ anthesis on a flower (hours)	3	4
♂ scent	scent	fainter, sweet scent
♂ temperature elevation	1.2°C above ambient	3°C above ambient
♂ nectar	-	-
Number of insect visitors (species)	7	10
Most effective pollinators	*Phyllotrox* sp. (Curculionidae)	*Epuraea* sp.[4] (Nitidulidae), *Phyllotrox* sp. (Curculionidae)
Reference	Listabarth (1994)	Listabarth (1994)

[4] This may be a misidentification, see Cline (2005), and it is possibly *Mystrops*.

flowers. There was an inter-anthesis period of about 12 hours.

Staminate flowers were at anthesis simultaneously at about 16.30 on the following day. Individual flowers were at anthesis for a short period of usually 3–4 hours duration and then fell from the inflorescence. Inflorescences at staminate anthesis heated up and gave off a sweet scent, although less so than pistillate flowers.

There were relatively few species of insect visitors to inflorescences, 7–10. In both *Desmoncus* species the most effective pollinators were considered to be small beetles. *Desmoncus mitis* was pollinated by a curculionid (*Phyllotrox* sp.), and *D. polyacanthos* was pollinated by curculionids (*Phyllotrox* sp.) and nitidulids (possibly *Mystrops* sp.). These beetles arrived at inflorescences in large numbers at the beginning of pistillate anthesis. They came into contact with stigmas as they fed on flower tissue, mated, and oviposited on staminate flower buds. They left the inflorescence, covered in pollen, immediately after staminate flower abscission. Their larvae developed in the fallen staminate flowers on the ground. Adults emerged after 10–14 days.

Bactris

Bactris is monoecious. Inflorescences bear unisexual flowers in triads (Fig. 8D). Twenty taxa have been studied (Table 20).

Flowering seasons were relatively short, with a mean of four months duration. At their study site in Amazon Brazil, Henderson et al. (2000b) found that most taxa flowered in the rainy season and early dry season. Individuals within a taxon flowered synchronously and had a short duration of initiation (number of months between first and last individuals initiating flowering within a year). Overall at the site, the various taxa of *Bactris* flowered over a 10–month period.

Inflorescences were protogynous. Pistillate flowers were at anthesis immediately after the opening of the peduncular bract. This took place in the late afternoon or early evening, usually between 16.00 and 18.00, rarely earlier in the day.

Since all pistillate flowers appeared to be at anthesis at the same time, duration of anthesis of a flower is the same as duration of anthesis in an inflorescence. This varied from 4–24 hours, rarely more, but was seldom precisely documented. Inflorescences at pistillate anthesis heated up before and at anthesis (with one exception), and the temperature elevation tended to be greater than that at staminate anthesis. Inflorescences gave off a scent at this time, described as sweet, yeasty, balsamic, or musky. Nectar production was not recorded from pistillate or staminate flowers.

Staminate flowers were at anthesis approximately 24 hours after the beginning of pistillate anthesis. Individual flowers were at anthesis for a short period, usually 1–3 hours, seldom more, and then fell from the inflorescence.

Table 20. Pollination of *Bactris* spp. (1/5)

	B. acanthocarpa var. exscapa, Brazil	*B. acanthocarpa var. intermedia*, Brazil	*B. acanthocarpa var. trailiana*, Brazil	*B. acanthocarpoides*, Brazil	*B. bidentula*, Bolivia
Flowering season (months), peak	irregular, peak in January	irregular	April to September, peak in April-May	March	October to February
Duration of ♀ anthesis on an inflorescence (days)	1	1	1	-	-
Start of ♀ anthesis (time)	16.00	16.30	17.00	during the day	05.30
Duration of ♀ anthesis on a flower (hours)	24	24	24	-	-
♀ scent	weak, sweet scent	weak scent	strong to weak scent	scent	sweet scent
♀ temperature elevation	4.7°C above ambient	7.5°C above ambient	7.2°C above ambient	7°C above ambient	-
♀ nectar	-	-	-	-	-
Inter-anthesis (days)	0	0	0	-	-
Duration of ♂ anthesis on an inflorescence (days)	ca. 1	-	<1	-	<1
Start of ♂ anthesis (time)	night	16.30	16.35	evening	17.00
Duration of ♂ anthesis on a flower (hours)	<24	-	ca. 2	-	1.5
♂ scent	-	-	-	-	-
♂ temperature elevation	3.9°C above ambient	2.6°C above ambient	2.6°C above ambient	7°C above ambient	-
♂ nectar	-	-	-	-	-
Number of insect visitors (species)	23	14	11	5	at least 6
Most effective pollinators	*Colopterus* sp. (Nitidulidae), *Phyllotrox*, (Curculionidae)	*Colopterus* sp. (Nitidulidae), *Phyllotrox*, (Curculionidae)	*Phyllotrox* sp. (Curculionidae)	Nitidulidae sp., *Phyllotrox* sp., *Celetes* sp., *Palmocentrinus* sp. (Curculionidae)	*Phyllotrox* spp., *Phytotribus* sp. (Curculionidae)
Reference	Henderson et al. (2000a)	Henderson et al. (2000a)	Henderson et al. (2000a)	Küchmeister (1997)	Moraes & Sarmiento (1992)

Table 20. Pollination of *Bactris* spp. (2/5)

	B. bifida, Peru	*B. coloradonis (as B. porschiana),* Costa Rica	*B. gasipaes* Costa, Rica	*B. gastoniana,* Brazil	*B. glaucescens,* Brazil
Flowering season (months), peak	April to May, October to November	August to September	-	January to July, peak in April and May	October to April, peak in October and November
Duration of ♀ anthesis on an inflorescence (days)	<1	ca. 1	<1	>1	1
Start of ♀ anthesis (time)	15.45	16.00	16.00	18.20	17.00
Duration of ♀ anthesis on a flower (hours)	8	24	24	32	24
♀ scent	yeasty scent	musky scent	musky scent	-	scent
♀ temperature elevation	6.3°C above ambient	several ° above ambient	several ° above ambient	2.5°C above ambient	none
♀ nectar	-	none	none	-	none
Inter-anthesis (days)	0	0	0	0	0
Duration of ♂ anthesis on an inflorescence (days)	<1	<1	<1	-	<1
Start of ♂ anthesis (time)	13.30	16.30	16.30	ca. 02.00	17.30
Duration of ♂ anthesis on a flower (hours)	ca. 6	ca. 2	<1	-	ca. 14
♂ scent	scent	-	-	-	scent
♂ temperature elevation	5.0°c above ambient	-	-	3.7°C above ambient	none
♂ nectar	-	none	none	-	-
Number of insect visitors (species)	at least 12	9	at least 6	10	6
Most effective pollinators	*Epuraea* sp.[5] (Nitidulidae); *Phyllotrox* spp. (Curculionidae)	*Grasidius* sp., *Phyllotrox* sp. (Curculionidae) *Cyclocephala* sp., *Mimeoma* sp. (Scarabeidae)	*Phyllotrox* sp. (Curculionidae) *Cyclocephala* sp., (Scarabeidae)	*Colopterus* sp. (Nitidulidae), *Phyllotrox* sp. (Curculionidae)	*Derelomus* sp. (Curculionidae)
Reference	Listabarth (1996)	Beach (1984)	Beach (1984)	Henderson et al. (2000a)	Fava et al. (2011)

[5] This may be a misidentification, see Cline (2005), and it is possibly *Mystrops*.

Table 20. Pollination of *Bactris* spp. (3/5)

	B. guineensis, Costa Rica	*B. guineensis*, Colombia	*B. hirta*, Brazil	*B. hirta* var. *spruceana*, Brazil	*B. killipii*, Brazil
Flowering season (months), peak	-	March to December, peak in June and July	December to January	irregular, peak in December to January	January to April, peak in January
Duration of ♀ anthesis on an inflorescence (days)	<1	<1	<1	ca. 1	ca. 1
Start of ♀ anthesis (time)	18.30	18.00	17.00	ca. 17.15	17.00
Duration of ♀ anthesis on a flower (hours)	ca. 12	ca. 4	-	24	ca. 24
♀ scent	-	balsamic scent	strong scent	scent	strong, musty scent
♀ temperature elevation	-	12°c above ambient	2°c above ambient	2.3°c above ambient	3.0°c above ambient
♀ nectar	-	-	-	-	-
Inter-anthesis (days)	-	0	-	0	0
Duration of ♂ anthesis on an inflorescence (days)	<1	<1	<1	-	<1
Start of ♂ anthesis (time)	16.15	18.00	17.00	ca. 17.00	17.20
Duration of ♂ anthesis on a flower (hours)	ca. 2	2	2–3	-	1
♂ scent	musky scent	balsamic scent	scent	-	-
♂ temperature elevation	-	10°c above ambient	4°c above ambient	2.1°c above ambient	2.7°c above ambient
♂ nectar	-	-	-	-	-
Number of insect visitors (species)	at least 7	27	8	13	11
Most effective pollinators	*Mystrops* sp. (Nitidulidae), *Phyllotrox* sp., *Grasidius* sp. (Curculionidae)	*Mystrops* sp. (Nitidulidae), *Andranthobius* sp., *Phyllotrox* sp., *Grasidius* sp. (Curculionidae)	*Nitidulidae* sp., *Phyllotrox* spp., *Palmocentrinus* sp. (Curculionidae)	*Colopterus* sp. (Nitidulidae), *Phyllotrox* sp. (Curculionidae)	*Phyllotrox* sp. (Curculionidae)
Reference	Essig (1971a, b)	Brieva-Oviedo et al. (2020)	Küchmeister (1997)	Henderson et al. (2000a)	Henderson et al. (2000a)

Table 20. Pollination of *Bactris* spp. (4/5)

	B. major, Costa Rica	*B. maraja*, Brazil	*B. maraja*, Peru	*B. maraja* var. *trichospatha*, Brazil	*B. oligocarpa*, Brazil
Flowering season (months), peak	-	October to November	October to November	peak in December	-
Duration of ♀ anthesis on an inflorescence (days)	<1	<1	<1	-	1
Start of ♀ anthesis (time)	18.30	ca. 12.00	18.00	-	ca. 05.00
Duration of ♀ anthesis on a flower (hours)	ca. 24	ca. 6	5	-	24
♀ scent	-	scent	yeasty scent	-	-
♀ temperature elevation	-	3°c above ambient	8.2°c above ambient	-	3.3°C above ambient
♀ nectar	-	-	-	-	-
Inter-anthesis (days)	0	-	-	-	0
Duration of ♂ anthesis on an inflorescence (days)	<1	<1	<1	-	-
Start of ♂ anthesis (time)	16.15	dusk	16.45	-	05.20
Duration of ♂ anthesis on a flower (hours)	ca. 2	2-3	ca. 3	-	-
♂ scent	musky scent	scent	yeasty scent	-	-
♂ temperature elevation	-	1.2°C above ambient	9.7°C above ambient	-	3.8°C above ambient
♂ nectar	-	-	-	-	-
Number of insect visitors (species)	at least 7	8	at least 17	16	3
Most effective pollinators	*Mystrops* sp. (Nitidulidae), *Phyllotrox* sp., *Grasidius* sp. (Curculionidae)	Nitidulidae sp., *Phyllotrox* sp. Curculionidae spp., Staphylinidae sp.	*Epuraea* sp. (Nitidulidae), *Phyllotrox* spp. (Curculionidae)	*Phyllotrox* sp. (Curculionidae)	*Colopterus* sp. (Nitidulidae), *Phyllotrox* sp. (Curculionidae)
Reference	Essig (1971a, b)	Küchmeister (1997)	Listabarth (1996)	Henderson et al. (2000a)	Henderson et al. (2000a)

Table 20. Pollination of *Bactris* spp. (5/5)

	B. simplicifrons, Brazil	*B. simplicifrons*, Brazil	*B. tomentosa*, Brazil
Flowering season (months), peak	irregular	March to April	December to April, peak in January
Duration of ♀ anthesis on an inflorescence (days)	1	<1	1
Start of ♀ anthesis (time)	ca. 17.00	16.30	17.00
Duration of ♀ anthesis on a flower (hours)	24	ca. 20	24
♀ scent	-	fruit scent	weak scent
♀ temperature elevation	3.3°C above ambient	8.6°C above ambient	3.3°C above ambient
♀ nectar	-	-	-
Inter-anthesis (days)	0	-	
Duration of ♂ anthesis on an inflorescence (days)	-	<1	<1
Start of ♂ anthesis (time)	16.20	16.00	16.30
Duration of ♂ anthesis on a flower (hours)		2–3	ca. 1
♂ scent	-	fruit scent	-
♂ temperature elevation	2.9°C above ambient	7.4°C above ambient	2.4°C above ambient
♂ nectar	-	-	-
Number of insect visitors (species)	6	5	15
Most effective pollinators	*Phyllotrox* sp. (Curculionidae)	Nitidulidae sp., *Phyllotrox* sp. (Curculionidae)	*Phyllotrox* sp. (Curculionidae)
Reference	Henderson et al. (2000a)	Küchmeister (1997)	Henderson et al. (2000a)

Remarkably, in *B. tomentosa*, a sudden movement of the rachilla caused all staminate flowers to fall from the inflorescence soon after anthesis. Inflorescences at staminate anthesis heated up before and at anthesis, although usually less than pistillate inflorescences, and gave of a similar scent to that at pistillate anthesis, but often described as weaker.

In general, there were rather few species of insect visitors to inflorescences, ranging from 3–27, with a mean of 10 species. In all cases the most effective pollinators were considered to be curculionid (*Andranthobius, Grasidius, Phyllotrox, Phytrotribus*) and nitidulid (*Colopterus, Mystrops*) beetles (given that *Mystrops* have been recorded from other *Bactris* species, it seems possible that Henderson et al. (2000a) misidentified the nitidulids, and they are *Mystrops*, not *Colopterus*). These beetles arrived at inflorescences, sometimes in large numbers, at or before the splitting of the peduncular bract. They fed on the stigmatic exudate of pistillate flowers and on the petals of staminate flowers, mated, and oviposited on staminate flowers. Listabarth (1996) reported that beetle larvae developed rapidly in the fallen staminate flowers. Larvae fed on the flowers and mature larvae left the flowers after 2–4 days. They then completed metamorphosis in 12–14 days. Henderson et al. (2000a) considered that the internal surface of the peduncular bract may also be an attractant for insects.

Brieva-Oviedo et al. (2020) quantified pollinators of *B. guineensis*. For each inflorescence visitor, its relative abundance (RA) on pistillate inflorescences was multiplied by its pollen transport efficiency (PE). Thus pollinator importance (PI) = RA × PE. The PI was then used to calculate each visitor's relative importance value (RIV) (RIV = Σ PI × 100). Visitors were then classified as main pollinators (RIV >10% - *Andranthobius, Grasidius, Mystrops*), accessory pollinators (RIV 1–9.9% - *Phyllotrox*), and non-pollinators (RIV < 1%). *Andranthobius* sp. had by far the highest RIV value (65%).

Most *Bactris* taxa had a 24-hour cycle of anthesis, with a few exceptions. *Bactris bidentula* bracts opened early in the morning and there was approximately 36 hours between staminate and pistillate anthesis. The bract of *B. gastoniana* opened at 18.20, but pistillate anthesis did not take place until 32 hours later, at 02.00. The bract of *B. oligocarpa* opened early in the morning at 05.00 and staminate anthesis took place almost exactly 24 hours later. *Bactris gastoniana* and *B. oligocarpa* shared other anomalies. They had higher temperature elevation at staminate anthesis rather than at pistillate anthesis, rachillae had no trichomes at pistillate anthesis, and staminate flowers persisted on the rachillae rather than falling. Pollinators appeared to be nitidulids rather than curculionids. These two species are related, both in the *Pyrenoglyphis* group (Henderson 2000). *Bactris major*, also in the *Pyrenoglyphis* group, also had persistent staminate flowers, although the significance of this is unclear. In two species, *B. acanthocarpoides* and *B. maraja*, anthesis of both pistillate and staminate flowers took place within the same day (Küchmeister 1997).

The role of scarab beetles in *Bactris* pollination is unclear. They have been recorded as inflorescence visitors to only two of the species listed in Table 20, *B. coloradonis* and *B. gasipaes*, both from La Selva in Costa Rica. Bullock (1981) also reported scarab beetles visiting inflorescences of *B. longiseta* and *B. obovata* (as *B. wendlandiana*) at La Selva. In a study of the pollination of the cultivated *B. gasipaes* at La Selva, Beach (1984) considered that scarab beetles and weevils were pollinators. On the other hand, Urpí & Solís (1980) studied pollination of *B. gasipaes* at two other sites in Costa Rica. At the wetter of the two sites, near La Selva, they found similar insect visitors as did Beach, but at the dryer site they did not find any scarabs, and thus did not consider scarab beetles to be as important as weevils as pollinators (see also Urpí 1982). It appears that the presence of scarab beetles may be related to locality rather than species of palm. However, Atencio-Valdespino et al. (2023) found a few scarabs on inflorescences of *B. gasipaes* in Panama. Núñez (2014) found scarab visitors to inflorescences in 40 out of 58 species of Colombian palms. Despite their common occurrence, he considered that scarab beetles played a minimal role in palm pollination, with the exception of *Acrocomia aculeata*.

Henderson et al. (2000a) reported that rachillae of most of the taxa studied were covered with easily removed trichomes, although they did not report that insects ate the trichomes. However, Rickson et al. (1990) reported that scarab beetles ate the trichomes on *B. gasipaes* inflorescences, and since the trichomes contained on nutritional value, they hypothesized that they acted as gastroliths in the beetles' digestive tract.

Arecoideae, *Cocoseae*, *Elaeidinae*

The subtribe comprises two genera (*Barcella,* 1 species; *Elaeis,* 2 species) occurring in the Neotropics and Africa. One genus has been studied.

Elaeis

Elaeis is monoecious with separate staminate and pistillate inflorescences (Fig. 9B). Both kinds of inflorescence can be produced on the same plant but they occur in alternating cycles. Inflorescences are condensed with closely spaced flowers, and the pistillate inflorescences are partially covered by fibrous bracts at anthesis.

Inflorescence development of *E. guineensis* has been described by Purseglove (1973) and Auffray et al. (2017). Flowers on staminate inflorescences opened around 08.00. All flowers opened within two days and anthesis lasted 2–4 days on an inflorescence. Flowers were anise scented. On pistillate inflorescences flowers also opened at 08.00. All flowers opened within 24 hours and were receptive for 36–48 hours. In Ecuador, Auffray (2017) reported that both staminate and pistillate inflorescences heated up just before and during anthesis, with several peaks of up to 7°C above ambient temperature in staminate and pistillate inflorescences.

Syed (1979) reported on insect visitors to *E. guineensis* inflorescences in West Africa. He found large numbers of visitors on staminate inflorescences and fewer on pistillate inflorescences. The most abundant of these on staminate inflorescences were several species of derelomine weevils, *Elaeidobius* spp. and a staphylinid beetle, *Atheta*, and the most abundant on pistillate inflorescences were other derelomine weevils, *Prosoestus* spp. Syed found that staminate inflorescences produced scent continuously but pistillate inflorescences produced it in short pulses during anthesis. These pulses of scent attracted

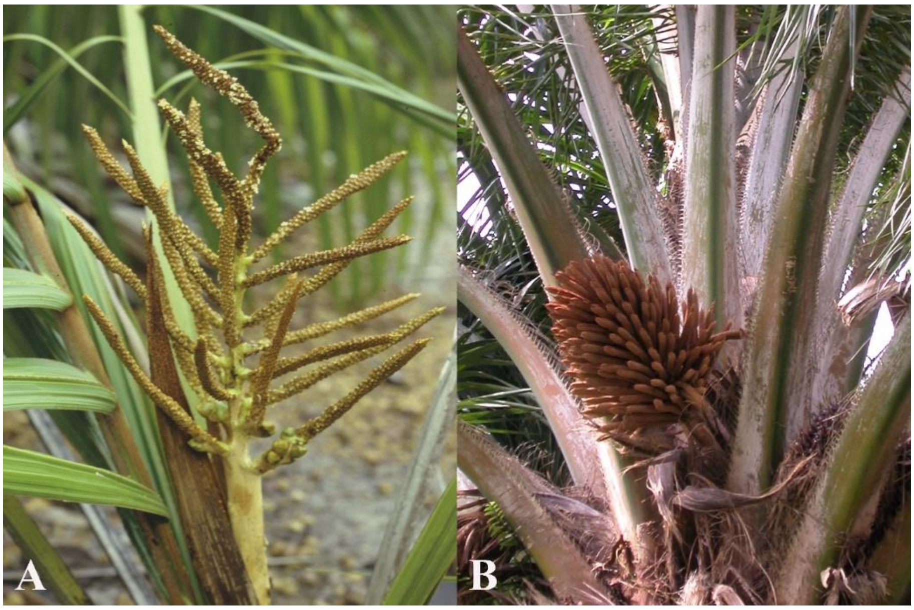

Figure 9. A. Open, bisexual inflorescence of *Barcella odora*. B. Condensed, staminate inflorescence of *Elaeis guineensis*.

thousands of *Elaeidobius* spp. from staminate to pistillate inflorescences, and they were carrying pollen. They returned to staminate inflorescences when they found no reward on pistillate inflorescences.

Haran et al. (2020) revised *Elaeidobius*. They recognized eight species, all of which could be present on the same *Elaeis* inflorescence. Haran et al. (2021) considered that the two weevil genera, *Elaeidobius* and *Prosoestus*, were specialized brood-site pollinators, and the larvae of *Elaeidobius* species developed in staminate flowers of *Elaeis*, while *Prosoestus* larvae developed in pistillate inflorescences. In a phylogenetic analysis of the derelomine weevils of *E. guineensis*, Haran et al. (2021) discovered that the 7–10 species of *Elaeidobius* and *Prosoestus* that pollinate the oil palms in West Africa formed a monophyletic group. They wrote: "To our knowledge, this radiation of 7 to 10 phylogenetically closely related species associated with a single host–plant constitutes a unique case among plant-pollinator mutualistic systems, including derelomine weevils…" Even more remarkable, Haran et al. found that the derelomine pollinators of *E. guineensis* are more closely related to other Old World genera, rather than to the weevil pollinators of the Neotropical *E. oleifera*. In other words, the two *Elaeis* species had independent colonization of derelomine weevils.

Nitidulids have also been reported from *E. guineensis* inflorescences but their role in pollination is unclear. Endrödy-Younga (1978) reported *Palmopria* spp. from inflorescences in Ghana, and Jelínek (1992) reported *Epuraea* spp. and *Meligethinus* spp. in Rwanda. It is remarkable that the same two groups of insects, derelomine weevils and nitidulid beetles, that so often pollinate Neotropical palms, are also present on inflorescences of African palms.

The second *Elaeis* species is the Neotropical *E. oleifera*, occurring in Central America and the Amazon region. There have been few studies of pollination of this species. In Ecuador, Auffray (2017) reported that anthesis on both staminate and pistillate inflorescences began around sunset, and continued for approximately five days. Both heated up just before and during anthesis, with a peak of up to 10°C in staminate inflorescences, and several peaks of up to 4°C in pistillate inflorescences. Pollinators were considered to be the derelomine *Grasidius hybridus*. This weevil was highly specific to *Elaeis oleifera*, and its visits coincided exactly with staminate and pistillate anthesis. On the other hand, Bruno de Medeiros (pers. comm.) did not find weevils on *E. oleifera* in Panama and considered that it was probably pollinated by *Mystrops* (likely *M. costaricensis*).

It is interesting that anthesis of *E. guineensis* was reported to be during the morning and thus diurnal, while anthesis of staminate and pistillate inflorescences of *E. oleifera* was reported to be during the evening, thus nocturnal. It is unclear if *E. oleifera* has only a single pollinating weevil, or if there are several species involved, as in *E. guineensis*.

Summary for Cocoseae

Of the 10 genera and 125 species of the subtribe Attaleinae, five genera and 18 species have been reasonably well studied. *Allagoptera* and *Attalea* have a similar pollination system, with short periods of staminate and pistillate anthesis and beetles, primarily *Mystrops*, as pollinators. *Butia* and *Syagrus* have longer periods of staminate and pistillate anthesis, and are pollinated by both bees and/or beetles. However, as noted above, *Syagrus* may have both beetle- and bee-pollinated species (few genera have both, the only other example is *Hydriastele*). *Butia* and *Syagrus* are at least partially pollinated by the weevil *Anchylorhynchus*, which oviposits on pistillate flowers and can cause up to 50% of them to abort.

Because pollination in five out of the 10 genera in the subtribe has not been studied, consideration of shifts between pollination systems inferred from a phylogeny (Ferreira et al. in prep.) is somewhat tentative. Furthermore, it is not always obvious how to assign pollination systems to genera. While *Allagoptera* and *Attalea* can be considered beetle-pollinated, both bee- and beetle-pollination occur within *Syagrus*. Nevertheless, some shifts are apparent. *Cocos* is placed at the base of the *Attalea* clade, implying a shift from a protandrous, open, possibly bee-pollinated inflorescence to closed, beetle-pollinated inflorescences.

Of the five genera and 187 species of the subtribe Bactridinae, all genera and 27 species have been studied. Flowering seasons of the four beetle-pollinated genera (*Acrocomia, Desmoncus, Astrocaryum, Bactris*) were relatively short, usually about 3–6 months duration. The flowering season of only one species of *Aiphanes* was recorded, five months, but Borchsenius & Bernal (1996) considered that most *Aiphanes* species flowered throughout the year. *Acrocomia, Desmoncus, Astrocaryum,* and *Bactris* are protogynous. *Bactris* and *Desmoncus* have a similar pollination system, with short pistillate and staminate anthesis, both lasting less than 24 hours, with staminate anthesis lasting only 3.5–4 hours. It is perhaps significant that the weevil *Phyllotrox* is pollinator of many species in these two genera. *Astrocaryum* is somewhat similar but has slightly longer staminate anthesis and seems mostly nitidulid-pollinated. *Acrocomia* is unusual in that while it has a short pistillate anthesis, staminate anthesis can continue for several days with flushes of flowers each day, unlike the short, synchronous, few hours of staminate anthesis found in *Astrocaryum, Bactris*, and *Desmoncus*. On the other hand, *Aiphanes* is quite different. It is protandrous and has much longer duration of staminate and pistillate anthesis and a much longer inter-anthesis period, and is pollinated by bees, flies, or wind. However, the situation in *Aiphanes* may be more complex. While Borchsenius (1993) recorded bee or fly pollination in some species, there is evidence that other species may be beetle pollinated (Núñez 2014). *Aiphanes* may be a genus, like *Syagrus*, where both bee/fly and beetle pollination occur.

In Ferreira et al. (in prep.), *Astrocaryum* is basal in the Bactridinae, followed by *Aiphanes,* and then *Acrocomia* is sister to the remaining two genera, *Desmoncus* and *Bactris*. These relationships imply marked shifts in inflorescence morphology and development from the beetle-pollinated *Astrocaryum* to the bee/fly-pollinated *Aiphanes* with its elongate, slowly developing inflorescences, to the beetle-pollinated *Acrocomia, Desmoncus*, and *Bactris*, with their condensed, rapidly developing inflorescences. Despite the apparent similarity of their pollinators, *Acrocomia, Desmoncus, Astrocaryum,* and *Bactris* show quite marked morphological diversity in their inflorescences.

The subtribe Elaeidinae contains two genera, *Barcella* with open, elongate, bisexual inflorescences (Fig. 9A) and *Elaeis* with closed, condensed, unisexual inflorescences (Fig. 9B). The economic importance of the oil palm, *E. guineensis*, means that there have been numerous studies of its reproductive biology. These studies have revealed the extraordinary complexity of the sexual system of the palm itself, and of the interactions between the palm and its pollinators.

In most genera of the Cocoseae, with the possible exception of *Aiphanes*, the peduncular bract seems to play a role in pollination, either in attracting pollinators, or in scent production, or as a brood site.

Arecoideae, Manicarieae

The tribe comprises one genus (*Manicaria,* 2 species) distributed in South America. One species has been studied.

Manicaria

Manicaria is monoecious and inflorescences bear unisexual flowers in triads. Inflorescences at anthesis are covered by the fibrous prophyll and peduncular bract which keeps the rachillae closely bunched. Pollination of *M. saccifera* has been studied in Colombia by Copete et al. (2018). Plants flowered throughout the year with a peak in May. Inflorescences were protogynous. All pistillate flowers were at anthesis simultaneously during the day and lasted one day. Inflorescences at pistillate anthesis produced scent and heated up, with an increase in temperature of 4°C above ambient. Staminate anthesis [assumed here to take place the day following pistillate anthesis] was diurnal lasted two days. There was an increase in temperature of 4.7°C above ambient. Inflorescences were visited by eight species of insect. The most effective pollinators were considered to be a species of *Mystrops* (Nitidulidae). This was the only visitor small enough to pass through the fibrous peduncular bract during pistillate anthesis, and to access the pistillate flowers through the small opening of the petals.

Copete et al. (2018) emphasized the two barriers that prevented access by all but one species of insect to stigmas, the fibrous peduncular bracts and the pistillate flowers. The petals of the pistillate flowers did not open completely at anthesis, and the stigmas could only be accessed through two small, 1–2 mm spaces between the petals.

Apart from *Manicaria*, a few other palms have their inflorescences covered by bracts at anthesis. These include *Calamus* spp., *Pholidostachys* spp., *Sclerosperma* spp., and *Pinanga* spp. Copete et al. (2018) were the first to show how one of these, *Manicaria*, is pollinated. It is an extraordinary system, where all insects but the single pollinator species are excluded at anthesis.

Arecoideae, Euterpeae

The tribe comprises five genera (*Hyospathe,* 6 species; *Euterpe,* 7 species; *Prestoea,* 10 species; *Neonicholsonia,* 1 species; *Oenocarpus,* 9 species), all Neotropical. Four genera have been studied.

Hyospathe

Hyospathe is monoecious and inflorescences bear unisexual flowers in triads (Fig. 10A). Listabarth (2001) studied pollination of *H. elegans* in Huánuco, Peru. Plants flowered from March to June, with a peak in April and May (wet-dry season transition). Inflorescences were protandrous. Staminate anthesis on an inflorescence lasted 10–14 days, with flushes of flowers opening each day. Individual staminate flowers opened from 06.00 and anthers dehisced from 07.00–10.00. Flowers fell from the inflorescence in the late afternoon or early evening of the same day. Flowers produced an intense, sweet scent and nectar. After an inter-anthesis period of 2–6 days, pistillate anthesis lasted 4–7 days. Pistillate flowers were at anthesis at all times of day with the majority at anthesis in the early morning. Pistillate flowers were receptive for 48 hours. Flowers produced a less intense sweet scent and nectar. Sixty species of insect visited the inflorescences. From their abundance and behavior on inflorescences at pistillate anthesis, it appeared that bees (*Trigona* spp., *Plebeia* sp.) as well as blow and fruit flies (Calliphoridae, Drosophilidae) were the most effective pollinators.

Küchmeister (1997) reported five species of insect visiting inflorescences of *H. elegans* in Brazil, and that blow flies and hover flies (Calliphoridae, Syrphidae) were pollinators.

Euterpe

Euterpe is monoecious with open inflorescences bearing unisexual flowers in triads (Fig. 10B). Four species have been studied (Table 21).

Flowering was seasonal in *E. edulis*, lasting from 4–8 months. Plants flowered during the wet season at three sites, but in the dry season at the Espírito Santo site. *Euterpe precatoria* and *E. espiritosantensis* were also seasonal but *E. oleracea* flowered throughout the year.

Inflorescences were protandrous. Staminate anthesis on an inflorescence lasted 7–18 days. Anthesis usually began early in the morning, and flushes of flowers opened each day and fell from the inflorescence after 4–24 hours. Staminate flowers produced a sweet scent and nectar.

There was a short inter-anthesis period of 1–6 days. Pistillate anthesis on an inflorescence lasted 3–14 days. Anthesis began during the morning, with individual flowers lasting 24–120 hours. Pistillate flowers produced a sweet scent and nectar.

Flowers, particularly staminate flowers, were visited by large numbers of different species of insect. The most effective pollinators of *E. edulis* were reported to be meliponid bees, particularly *Trigona* spp. and *Plebeia* spp. Santos et al. (2018) listed *Apis mellifera*, *Plebeia* sp., and an euglossine bee as pollinators of *E. edulis*. *Euterpe oleracea* and *E. espiritosantensis* were also said to be pollinated by bees, flies, and weevils. *Euterpe precatoria* was somewhat different and was reported to be pollinated by an assemblage of curculionid, chrysomelid, and staphylinid beetles, and halictid bees. Some authors considered that wind pollination took place, some not. Zamudio et al. (2021) found a prevalence of wind pollination. They wrote: "In short, the contribution of wind versus insect pollination to seed production in *E. edulis* may vary in time, space, and between different sized palms and be closely linked to both climatic and environmental conditions."

Campbell et al. (2018) carried out a detailed analysis of visitors to *E. oleracea* inflorescences, and recorded 194 insect taxa. This number included species of bees, flies, wasps, ants, and beetles. *Trigona* spp. (Apidae, Meliponini) were the most abundant visitors and beetles the most diverse, with 51 taxa. Staminate inflorescences attracted a higher number of visitor taxa than pistillate inflorescences. Campbell et al. divided the 51 taxa of beetles into two groups, 14 taxa of curculionids that they termed specialized pollinators, and 37 taxa of non-curculionids that they termed non-specialized. They wrote: "In summary, pollinator diversity and specialized curculionid beetles underpinned pollination services in açaí [*E. oleracea*]." Da Costa (2019) also recorded a high

Figure 10. A. Open inflorescence of *Hyospathe elegans*. B. Open inflorescences of *Euterpe oleracea*. C. Open inflorescence of *Prestoea decurrens* (image by R. Bernal). D. Condensed inflorescence of *Oenocarpus mapora*.

Table 21. Pollination of *Euterpe* spp. (1/3)

	E. edulis Espírito Santo, Brazil	*E. edulis* São Paulo, Brazil	*E. edulis* Santa Catarina, Brazil	*E. edulis* Santa Catarina, Brazil	*E. edulis* Misiones, Argentina
Flowering season (months), peak	April to November, peak in July	September to December, peak in October	September to February	November to February	September to January
Duration of ♂ anthesis on an inflorescence (days)	ca. 18	ca. 15	7–9	5–7	7–17
Start of ♂ anthesis (time)	07.00	06.00	07.00	06.00	-
Duration of ♂ anthesis on a flower (hours)	-	-	-	12	24
♂ scent	sweet scent	scent	sweet scent	sweet scent	sweet scent
♂ nectar	present	present	present	present	present
Inter-anthesis (days)	ca. 6	-	-	-	6
Start of ♀ anthesis (time)	07.00	morning	-	05.00	-
Duration of ♀ anthesis on an inflorescence (days)	-	-	-	-	-
Duration of ♀ anthesis on a flower (hours)	72	-	24	48	72
♀ scent	sweet scent	-	sweet scent	sweet scent	sweet scent
♀ nectar	present	present	present	present	present
Number of insect visitors (species)	-	15	-	-	147 species or morphospecies
Most effective pollinators	*Trigona* sp., *Nannotrigona* sp., *Oxytrigona* sp., *Apis* sp. (Apidae)	*Trigona* sp. (Apidae)	*Plebeia* spp. (Apidae)	Coleoptera, Hymenoptera	*Plebeia* spp., *Trigona* sp., *Leurotrigona* sp. (Apidae), wind
Reference	Wendt et al. (2011)	Reis et al. (1993)	Dorneles et al. (2013)	Mantovani & Morellato (2000)	Zamudio et al. (2021)

Table 21. Pollination of *Euterpe* spp. (2/3)

	E. oleracea Pará, Brazil	*E. oleracea* Pará, Brazil	*E. oleracea* Pará, Brazil	*E. oleracea* Pará, Brazil	*E. precatoria,* Brazil
Flowering season (months), peak	throughout the year, peak from December to April	-	throughout the year, peak from February to May	throughout the year, peak December to February	October to March, peak December to February
Duration of ♂ anthesis on an inflorescence (days)	10–14	13	10–12	10–25	17
Start of ♂ anthesis (time)	-	09.00	-	08.30	06.00
Duration of ♂ anthesis on a flower (hours)	-	4	-	6	6.5
♂ scent	-	-	none	sweet scent	sweet scent
♂ nectar	present	present	-	-	present
Inter-anthesis (days)	1–2	-	-	2	6
Duration of ♀ anthesis on an inflorescence (days)	3–5	3	4	6–14	3
Start of ♀ anthesis (time)	-	10.00	-	08.00	07.00
Duration of ♀ anthesis on a flower (hours)	24	120	96	48	24–48
♀ scent	-	-	sweet scent	sweet scent	sweet scent
♀ nectar	present	present	-	-	present
Number of insect visitors (species)	74 (?)	-	20	9	at least 36
Most effective pollinators	*Trigona* spp. (Apidae), *Augochloropsis* sp., *Dialictus* sp. (Halictidae)	*Melipona* spp. (Apidae)	Curculionidae	Coleoptera, Hymenoptera	Curculionidae spp. (including *Phyllotrox*), Chrysomelidae spp., Staphylinidae sp., Halictidae sp.
Reference	Bezerra et al. (2020)	Venturieri (2008)	Jardim (1991)	Oliveira (2002)	Küchmeister et al. (1997)

Table 21. Pollination of *Euterpe* spp. (3/3)

	E. espiritosantensis Espírito Santo, Brazil	*E. espiritosantensis* São Paulo, Brazil
Flowering season (months), peak	April to November, peak in September	January to May
Duration of ♂ anthesis on an inflorescence (days)	18	6–23
Start of ♂ anthesis (time)	07.00	08.00
Duration of ♂ anthesis on a flower (hours)	24	24
♂ scent	sweet scent	faint scent
♂ nectar	present	present
Inter-anthesis (days)	6	5–6
Duration of ♀ anthesis on an inflorescence (days)	9	3–8
Start of ♀ anthesis (time)	07.00	-
Duration of ♀ anthesis on a flower (hours)	72	48
♀ scent	sweet scent	-
♀ nectar	present	-
Number of insect visitors (species)	at least 10	15
Most effective pollinators	*Trigona* sp., Nanotrigona sp., *Oxitrigona* sp., *Apis* sp. (Apidae)	Apidae spp., Syrphidae sp.
Reference	Wendt et al. (2011)	Bovi et al. (1994)

diversity of insects visiting inflorescences of *E. oleracea*, 61 species and 28 morphospecies. Guimarães (2009) also noted the importance of curculionids in pollination of *E. longibracteata*, recording 23 species visiting inflorescences. He considered that five of these, *Phyllotrox* spp., *Bondariella* sp. and Erirhininae spp. were the most abundant and most likely pollinators of *E. longibracteata.*

Prestoea

Prestoea is monoecious with open inflorescences bearing unisexual flowers in triads (Fig. 10C). Two species have been studied (Table 22).

Plants flowered throughout the year. Inflorescences were protandrous. Staminate anthesis on an inflorescence lasted 14–19 days. It began in the morning, and flushes of flowers opened each day and fell from the inflorescence later the same day. Individual flowers lasted 6–9 hours. Flowers produced no scent or a sweet scent, and nectar. No temperature elevation was recorded, in either staminate or pistillate inflorescences.

There was an inter-anthesis period of 2–8 days. Pistillate anthesis on an inflorescence lasted 1–7 days. Anthesis began during the morning, and individual flowers lasted 24–48 hours. Pistillate flowers produced no scent or a sweet scent, and nectar.

Inflorescences were visited by a large number of different species of insect. The most effective pollinators of *P. schultzeana* were reported to be syrphid flies, and of *P. decurrens* apid and halictid bees. It is curious that *P. decurrens* flowers did not produce any scent.

Knudsen (1995) gave some notes on the pollination of *P. acuminata* in Ecuador. Plants were protandrous. Staminate anthesis lasted ten days, and flowers had a weak, sweet scent. Twenty species of insect were found on inflorescences, 13 Coleoptera (including weevils and *Mystrops* spp.), six Diptera, and one Hymenoptera. Flies or weevils were possible pollinators. Bannister (1970) also gave some notes on pollination of *P. acuminata* (as *Euterpe globosa*) in Puerto Rico. Plants flowered throughout the year with a peak from June to September. Staminate anthesis lasted 7–14 days. Honeybees and small flies were considered to be pollinators.

Table 22. Pollination of *Prestoea* spp.

	P. decurrens, Costa Rica	*P. decurrens*, Colombia	*P. schultzeana*, Ecuador
Flowering season (months), peak	-	throughout the year	throughout the year, peak from December to June
Duration of ♂ anthesis on an inflorescence (days)	14	18	19
Start of ♂ anthesis (time)	9.30	09.00	06.00
Duration of ♂ anthesis on a flower (hours)	-	ca. 6	ca. 9
♂ scent	-	none	sweet scent
♂ temperature elevation	-	-	none
♂ nectar	-	present	present
Inter-anthesis (days)	2	2	4–8
Duration of ♀ anthesis on an inflorescence (days)	4	7	1–7
Start of ♀ anthesis (time)	-	09.00	morning
Duration of ♀ anthesis on a flower (hours)	-	48	24–48
♀ scent	-	none	sweet scent
♀ temperature elevation	-	-	none
♀ nectar	-	present	present
Number of insect visitors (species)	-	26	33
Most effective pollinators	*Trigona* spp. (Apidae), *Neocorynura* sp., *Lasioglossum* sp. (Halictidae)	*Dialictus*, *Neocorynura* (Halictidae)	*Copestylum* (Syrphidae)
Reference	Bullock (1981	Ervik & Bernal (1996)	Ervik & Feil (1997)

Ayala González et al. (2024) studied insect visitors to *P. acuminata* and *P. schultzeana* in Ecuador. They found 82 insect morphospecies visiting inflorescences of *P. acuminata* and 42 morphospecies for *P. schultzeana*. Based on the abundance and frequency of these insects on both staminate and pistillate inflorescences, they considered that *P. acuminata* was pollinated by six species of Coleoptera (two Chrysomelidae, three Curculionidae, one Nitidulidae), and *P. schultzeana* was pollinated by three species of Coleoptera (two Chrysomelidae, one Curculionidae) and two Diptera (one Ceratopogonidae, one Drosophilidae). Although these two *Prestoea* are sympatric in some parts of Ecuador, few species of insect were found on inflorescences of both species.

Oenocarpus

Oenocarpus is monoecious with the condensed inflorescences bearing unisexual flowers in triads (Fig. 10D). Pollination has been studied in four species (Table 23).

Flowering was throughout the year in most species except *O. bacaba*. Inflorescences were protandrous. Staminate anthesis on an inflorescence lasted 7–24 days. This was shorter in *O. mapora*, 9–10 days, and longer in *O. bataua*, 14–24 days. Anthesis began in the late afternoon or early evening, and flushes of flowers opened each evening. Individual flowers were at anthesis for 8–24 hours. Flowers produced a strong scent and no nectar. Inflorescences heated up during anthesis, with *O. bacaba* having a higher temperature than other species.

There was a short inter-anthesis period of 2–10 days. Pistillate anthesis on an inflorescence lasted 1–7 days. Anthesis began in the late afternoon or early evening. Anthesis was shorter in *O. mapora*, 1–4 days, and longer in *O. bataua*, 1–7 days. Individual flowers were at anthesis for 24-72 hours. Flowers produced a strong scent and no

Table 23. Pollination of *Oenocarpus* spp. (1/3)

	O. bacaba, Brazil	*O. balickii*, Colombia	*O. bataua*, Antioquia, Colombia	*O. bataua*, Antioquia, Colombia
Flowering season (months), peak	March to September	throughout the year	throughout the year, peak from December to February	throughout the year
Duration of ♂ anthesis on an inflorescence (days)	14	14	13–15	15
Start of ♂ anthesis (time)	18.30	late afternoon	18.30	late afternoon
Duration of ♂ anthesis on a flower (hours)	-	8–12	12–24	8–12
♂ scent	strong fruity scent	strong scent	strong scent	strong scent
♂ temperature elevation	13.2°C above ambient	4.8°C above ambient	5.8°C above ambient	5.2°C above ambient
♂ nectar	-	none	-	-
Inter-anthesis (days)	7–10	5–8	7–9	5–8
Duration of ♀ anthesis on an inflorescence (days)	4–5	1–4	5–7	1–4
Start of ♀ anthesis (time)	18.30	18.30	18.30	18.30
Duration of ♀ anthesis on a flower (hours)	-	48	24	48
♀ scent	strong fruity scent	strong scent	strong scent	strong scent
♀ temperature elevation	10.7°C above ambient	5.5°C above ambient	4.5°C above ambient	4°C above ambient
♀ nectar	-	none	-	-
Number of insect visitors (species)	at least 50	33	81	63
Most effective pollinators	Curculionidae, Nitidulidae, Staphylinidae, Scarabaeidae, Chrysomelidae	*Derelomus*, *Phyllotrox*, *Anchylorhynchus*, *Andranthobius*, *Terires*, *Baridinae* spp., (Curculionidae), *Mystrops* (Nitidulidae)	Baridinae sp., *Phyllotrox* sp., (Curculionidae)	*Derelomus*, *Phyllotrox*, *Anchylorhynchus*, *Andranthobius*, *Terires*, *Baridinae* spp., (Curculionidae), *Mystrops* (Nitidulidae)
Reference	Küchmeister et al. (1998)	Núñez et al. (2015)	Núñez & Rojas-Robles (2008)	Núñez et al. (2015)

Table 23. Pollination of *Oenocarpus* spp. (2/3)

	O. bataua Chocó, Colombia	*O. bataua* Amazonas, Brazil	*O. bataua* Napo, Ecuador	*O. mapora* (as *O. minor*) Amazonas, Colombia
Flowering season (months), peak	-	-	throughout the year, peak from February to April	throughout the year
Duration of ♂ anthesis on an inflorescence (days)	21	14	21–24	9–10
Start of ♂ anthesis (time)	-	19.00	-	late afternoon
Duration of ♂ anthesis on a flower (hours)		-	-	8–12
♂ scent	-	strong scent	scent	strong scent
♂ temperature elevation	-	6.6°C above ambient	-	6.2°C above ambient
♂ nectar	-	-	none	-
Inter-anthesis (days)	-	7–10	5–12	5–8
Duration of ♀ anthesis on an inflorescence (days)	7	4–5	4–6	1–4
Start of ♀ anthesis (time)	-	18.30	16.00	18.30
Duration of ♀ anthesis on a flower (hours)		-	72	48
♀ scent	-	strong scent	scent	strong scent
♀ temperature elevation	-	6.3°C above ambient	5°c above ambient	7°C above ambient
♀ nectar	-	-	none	-
Number of insect visitors (species)	9	at least 30	36	33
Most effective pollinators	*Omophoita* sp. (Chrysomelidae)	Curculionidae, Nitidulidae, Staphylinidae, Scarabaeidae, Chrysomelidae	*Derelomini* spp. (including *Phyllotrox* sp.) (Curculionidae) *Mystrops* sp. (Nitidulidae)	*Derelomus*, *Phyllotrox*, *Anchylorhynchus*, *Andranthobius*, *Terires*, *Baridinae* spp., (Curculionidae) *Mystrops* (Nitidulidae)
Reference	Collazos & Mejía (1988)	Küchmeister et al. (1998)	García (1988)	Núñez et al. (2015)

Table 23. Pollination of *Oenocarpus* spp. (3/3)

	O. mapora (as *O. minor*) Amazonas, Brazil	*O. mapora* Panama
Flowering season (months), peak	-	-
Duration of ♂ anthesis on an inflorescence (days)	7–10	7–10
Start of ♂ anthesis (time)	18.30	ca. 18.00
Duration of ♂ anthesis on a flower (hours)	-	ca. 12
♂ scent	raw vegetable scent	-
♂ temperature elevation	9.2°C above ambient	-
♂ nectar	-	-
Inter-anthesis (days)	7–10	ca. 7
Duration of ♀ anthesis on an inflorescence (days)	3	ca. 7
Start of ♀ anthesis (time)	17.30	-
Duration of ♀ anthesis on a flower (hours)	-	few nights
♀ scent	raw vegetable scent	-
♀ temperature elevation	8.9°C above ambient	-
♀ nectar	-	-
Number of insect visitors (species)	at least 20	-
Most effective pollinators	Curculionidae, Nitidulidae, Staphylinidae, Scarabaeidae, Chrysomelidae	*Anchylorhynchus bicarinatus* (Curculionidae)
Reference	Küchmeister et al. (1998)	de Medeiros (in press)

nectar. Inflorescences heated up during anthesis, with *O. bacaba* again having a higher temperature than other species. Both Núñez et al. (2015) and de Medeiros (in press) noted stigmatic exudate from pistillate flowers of *O. mapora*.

Inflorescences, particularly during staminate anthesis, were visited by a large number of different species of insect. The most effective pollinators were curculionid (especially *Phyllotrox*) and nitidulid (especially *Mystrops*) beetles. These fed on pollen, mated, and oviposited on staminate flowers. de Medeiros (in press) studied insect visitors to *O. mapora* inflorescences in detail. He showed that the most important pollinator was a derelomine weevil, *Anchylorhynchus bicarinatus.* Adult weevils oviposited between the sepals of pistillate flowers. However, the larvae could not grow in flowers that were developing into fruits, and only grew in naturally aborted flowers. This is a much less antagonistic interaction than that found in other palms pollinated by *Anchylorhynchus.* For example, in *Butia* and *Syagrus,* different pollinating species of *Anchylorhynchus* can cause up to 50% of pistillate flowers to abort.

Oenocarpus is unusual in being protandrous and beetle-pollinated (like some species of *Syagrus*). The four species (*O. bacaba, O. balickii, O. bataua, O. mapora*) have similar inflorescence development and pollinators (and very similar inflorescences). Núñez et al. (2015) considered that the sympatric *O. balickii, O. bataua,* and *O. mapora* had some specificity of pollinators, and Núñez & Rojas-Robles (2008) suggested the existence of an intimate association and a high degree of specialization between the beetles and inflorescences of *O. bataua*.

Summary for Euterpeae

The tribe comprises five genera and 33 species, of which four genera and 11 species have been studied. There is thus quite good knowledge of pollination in the tribe, particularly since there are several detailed studies. Núñez et al. (2015) may be the first example of a bipartite network in a palm pollination study.

All four genera have similar inflorescence development with relatively long staminate anthesis, an inter-anthesis period, and a shorter pistillate anthesis. Flushes of short-lived flowers open each day. The only exception is *Oenocarpus*, which has nocturnal rather than diurnal anthesis. Unlike other genera, *Oenocarpus* inflorescences do not produce nectar and exhibit temperature elevation.

The number of insect species visiting inflorescences was relatively high, with a mean of 40. Pollination of *Hyospathe, Euterpe*, and *Prestoea* appears similar, with mixed species groups of pollen/nectar feeding, diurnal insects as pollinators, mostly from the orders Hymenoptera and Diptera. As pointed out by Listabarth (2001) and Ervik & Feil (1997), in many cases different species in these three genera shared the same species of pollinators. Within widespread species, such as *E. edulis*, occurring in different habitats and with different flowering seasons, the relative proportions of the constituent species of the pollinator group varied such that one particular species or group of species appeared to be the most effective pollinator in one particular habitat. The role of beetles in pollination of both *Euterpe* and *Prestoea* is unclear. *Euterpe precatoria* and possibly some populations of *E. oleracea* appear to be beetle-pollinated, as does *P. acuminata*. This is unusual because these species exhibit diurnal anthesis and sweetly scented, nectariferous flowers.

Pollinators of *Oenocarpus* were mostly curculionid and nitidulid beetles that fed, mated, and oviposited on inflorescences (i.e., brood-site pollinators). Nevertheless, the bee and fly pollinators of *Hyospathe, Euterpe*, and *Prestoea* were found on *Oenocarpus* inflorescences, and the beetle pollinators of *Oenocarpus* were found on *Hyospathe, Euterpe*, and *Prestoea* inflorescences. There may be one, significant exception to this. While weevils, particularly Derelomini, were reported as visitors for all species in all four genera, and are often considered co-pollinators, nitidulids were seldom reported as visitors to *Hyospathe, Euterpe*, and *Prestoea*, and yet were reported as principal pollinators in all *Oenocarpus* species. Here they could occur in large numbers. García (1988) reported from 4,000 to 18,000 individual *Mystrops* per inflorescence of *O. bataua*.

Unlike the Cocoseae, the peduncular bract does not appears to play any role in pollination, and in most species, it falls from the inflorescence before anthesis.

In Ferreira et al. (in prep.) *Hyospathe* is resolved as sister to all other genera, and these form two main clades. In one clade *Neonicholsonia* is sister to *Prestoea*, and in the other *Euterpe* is sister to *Oenocarpus*. These relationships suggest a marked shift from diurnal anthesis, nectar production, and bee/fly pollination in *Hyospathe, Prestoea*, and *Euterpe* to nocturnal anthesis, temperature elevation, and beetle pollination in *Oenocarpus*.

Arecoideae, *Geonomateae*

The tribe comprises six, Neotropical genera (*Welfia,* 2 species; *Pholidostachys,* 8 species; *Calyptrogyne,* 18 species; *Calyptronoma,* 3 species; *Asterogyne,* 5 species; *Geonoma,* 68 species). Four genera have been studied.

Welfia

Welfia is monoecious. Inflorescences are branched with a few, stout rachillae (Fig. 11A). Unisexual flowers are arranged in triads and these are sunken in pits in the rachillae. Bullock (1981) and Vandermeer (1983) gave brief notes on pollination of *Welfia regia* (as *W. georgii*) in Costa Rica. Inflorescences were protandrous. Staminate anthesis lasted 10–15 days with flushes of flowers opening each day. Anthesis was diurnal and individual flowers lasted one day. There was an inter-anthesis period of 1–2 days. All pistillate flowers were then at anthesis simultaneously for 1–2 days. Bullock (1981) reported that flowers were visited by six species of *Trigona*. Vandermeer (1983) reported a large number of different species of insect visiting inflorescences but the most common were *Trigona* bees and small curculionid beetles. He considered that bees were attracted to pistillate flowers by the prominent, spreading staminodes that mimicked the stamens of staminate flowers. He also considered that long-distance dispersal of *W. regia* pollen could be accomplished by beetles.

Núñez (2014) recorded six species of stingless bees visiting *W. regia* inflorescences in Colombia. *Welfia regia* is notable for its large flowers, the staminate with numerous (33–43) stamens (Henderson & Villalba 2013), short period of pistillate anthesis, and the possible mimicry of pistillate flowers.

Calyptrogyne

Calyptrogyne is monoecious. Inflorescences are usually elongate and spicate (Fig. 11B). Unisexual flowers are arranged in triads and these are sunken in pits in the rachillae. Staminate flowers have the filaments united into a fleshy tube, and pistillate flowers have a fleshy staminodial tube with a deciduous, cap-like apex that covers the stigmas before anthesis. Pistillate flowers cannot be pollinated unless an inflorescence visitor removes the cap-like apex of the staminodial tube. One species has been studied. Beach (1986), Cunningham (1995, 1996, 2000), and Tschapka (2003) reported on *C. ghiesbreghtiana* in Costa Rica. Plants flowered throughout the year with a peak between July and November. Inflorescences were protandrous. Staminate anthesis on an inflorescence lasted 3–7 days. Staminate flowers were at anthesis from 16.00 to 24.00 and each flower lasted only one night. Staminate flowers produced a garlic scent. There was an inter-anthesis period of 3–7 days. Pistillate anthesis lasted 1–2 days. Flowers were at anthesis from 20.00 to 24.00 and produced a garlic scent. Two kinds of bats visited inflorescences, frugivorous bats that perched on the inflorescence and nectariferous bats that hovered over the inflorescence. Both kinds of bat ate the fleshy filament tubes from staminate flowers, thus picking up pollen, and the fleshy staminodial tubes of the pistillate flowers, thus contacting

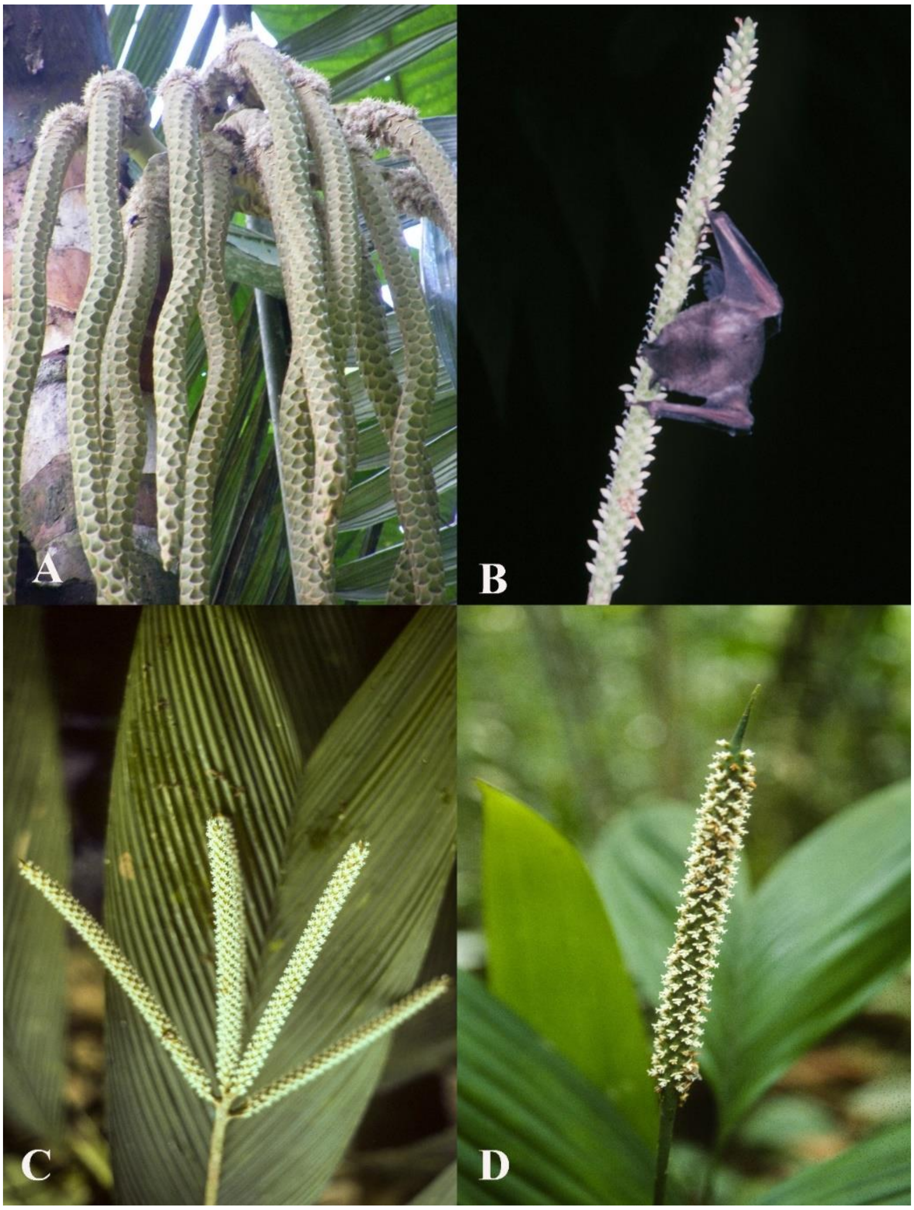

Figure 11. A. Inflorescence of *Welfia regia* (image by R. Bernal). B. Inflorescence of *Calyptrogyne ghiesbreghtiana*, visited by *Carollia* sp. (image by M. Tschapka). C. Inflorescence of *Asterogyne martiana* at pistillate anthesis. D. Inflorescence of *Geonoma macrostachys* at pistillate anthesis.

stigmas. Although no nectar was produced by the flowers, the filament tubes and staminodial tubes were reported to be sweet-tasting. Frugivorous bats were considered the most effective pollinators, although Cunningham (1995) wrote: "Pollen transfer by bats, the pollinators of *C. ghiesbreghtiana,* is extremely unreliable." A few insects visited inflorescences, including katydids, scarab beetles, weevils, ants, and *Trigona* sp., but were not considered pollinators. Sperr et al. (2009) reported that the Mexican mouse opossum (*Marmosa mexicana*) visited flowers of *C. ghiesbreghtiana*.

Knudsen (1999a) reported that floral scent of *C. ghiesbreghtiana* was dominated by sulphur compounds, and these are common in bat-pollinated plants. Interestingly, she sampled a second species, *C. costatifrons*, which had a different floral scent dominated by fatty acid derivatives.

Asterogyne

Asterogyne is monoecious. Inflorescences are elongate and spicate or branched with a few rachillae (Fig. 11C). Unisexual flowers are arranged in triads and these are sunken in pits in the rachillae. One species has been studied. Schmid (1970a, b) reported on *A. martiana* in Costa Rica. He considered that plants probably flowered throughout the year. Inflorescences were protandrous. Staminate anthesis on an inflorescence lasted up to five days. Pulses of flowers opened in a basipetal direction each day. Flowers opened at 05.00 and fell from the inflorescence around noon. They produced sticky pollen, a strong, sweet scent, and copious nectar. There was an inter-anthesis period of 1–2 days. Pistillate anthesis lasted 1(–2) days. Flowers opened at 05.00 and were at anthesis for less than one day. They produced a strong, sweet scent and copious nectar. Inflorescences were visited by approximately 48 species of insect. Derelomine weevils were abundant but nitidulids absent. Syrphid flies were considered the most effective pollinators. They foraged for nectar and ate pollen from staminate flowers, thus becoming covered in pollen, and foraged for nectar on pistillate flowers, thus contacting stigmas.

Knudsen (1999a) reported that floral scent of *A. martiana* was dominated by monoterpene linalool and linalool-derived compounds.

Geonoma

Geonoma is monoecious. Inflorescences are either spicate (Fig. 11D) or branched. Unisexual flowers are arranged in triads and these are sunken in pits in the rachillae. Twenty-two taxa have been studied (included in this number are various subspecies or morphotypes from different localities) (Table 24).

Taxa of *Geonoma* have long flowering seasons. Seven taxa were recorded to flower throughout the year, and others had a 4–9-month flowering season. Some taxa were recorded to have peaks of flowering and these could be in either wet or dry seasons. In places where sympatric taxa were studied, they had overlapping anthesis (e.g., Borchsenius 1997) or staggered anthesis (Borchsenius 2002), or seasonal peaks of anthesis (Listabarth 1993b, see also Henderson et al. 2000b).

All taxa were protandrous. Staminate anthesis on an inflorescence lasted a relatively short time (4–7 days) in three taxa and a relatively long time (7–32 days) in 13 taxa. There were two records of exceptional times, 90 days in *G. cuneata* subsp. *irena* and 75–180 days in *G. epetiolata*. Within taxa, the duration of staminate anthesis on an inflorescence was always longer than the duration of pistillate anthesis. Staminate flowers opened between 06.00 and 09.30 in most taxa, with only one exceptional record, 04.00 in *G. macrostachys*. Staminate flowers opened in flushes each day and the direction of anthesis on an inflorescence was either basipetal or acropetal, or without any particular direction. Individual staminate flowers remained at anthesis for less than one day, falling from the inflorescence after 1–12 hours. Staminate flowers were usually scented (except *G. deversa*) but seldom produced nectar. Pollen was reported to be sticky in three taxa and powdery in one taxon. Temperature elevation was not recorded.

There was a relatively short inter-anthesis period of 1–6 days in most taxa. There were three exceptional taxa. In *G. pohliana* subsp. *weddelliana* there was an inter-anthesis period of 15 days. In *G. interrupta* and *G. cuneata* subsp. *irena* there was no such period and staminate and pistillate anthesis overlapped on an inflorescence.

Table 24. Pollination of *Geonoma* spp. (1/5)

	G. aspidiifolia, Brazil	*G. brongniartii*, Peru	*G. cuneata* subsp. *Irena*, Ecuador	*G. cuneata* subsp. *Sodiroi*, Ecuador	*G. deversa*, Venezuela
Flowering season (months), peak	October to March	August to December	throughout the year	December to April, peak in January	throughout the year
Duration of ♂ anthesis on an inflorescence (days)	14	18–32	90	(4–)6	13–21
Start of ♂ anthesis (time)	06.00	06.30	09.00	06.00	-
Duration of ♂ anthesis on a flower (hours)	ca. 10	ca. 5	ca. 4	1–2	-
♂ scent	fruity scent	slight, fruity scent	slight metallic scent	strong, organic scent	none
♂ temperature elevation	-	-	-	-	-
♂ nectar	present	none	none	-	-
Inter-anthesis (days)	14	1–6	0, overlap	1–2	-
Duration of ♀ anthesis on an inflorescence (days)	7–14	3–5	28–56	1(–2)	4–7
Start of ♀ anthesis (time)	06.00	-	08.30	-	-
Duration of ♀ anthesis on a flower (hours)	24–48	24–48	24	ca. 10	48
♀ scent	fruity scent	weaker fruity scent	-	weaker organic scent	none
♀ temperature elevation	-	-	-	-	-
♀ nectar	present	none	present, small amount	-	-
Number of insect visitors (species)	10	14	7	12	7
Most effective pollinators	Calliphoridae sp.	wind	*Trigona* sp., *Scapotrigona* sp. (Apidae), Halictidae sp.	Drosophilidae spp., Sphaeroceridae sp.	*Derelomini* sp. (Curculionidae)
Reference	Küchmeister (1997)	Listabarth (1993b)	Borchsenius (1997)	Borchsenius (1997)	Listabarth (1999a)

Table 24. Pollination of *Geonoma* spp. (2/5)

	G. epetiolata, Costa Rica	*G. interrupta*, Peru	*G. interrupta*, Mexico	*G. macrostachys*, Ecuador	*G. macrostachys*, Peru
Flowering season (months), peak	throughout the year	June to October, peak in August to September	at least January to March	-	December to July, peak in March to June
Duration of ♂ anthesis on an inflorescence (days)	75–180	-	-	at least 4	11–20(–26)
Start of ♂ anthesis (time)	06.00	-	-	09.00	09.30
Duration of ♂ anthesis on a flower (hours)	ca. 12	-	-	ca. 5	-
♂scent	-	faint, fruit scent	scent	strong, sweet scent	sweet, spicy scent
♂ temperature elevation	-	-	-	-	-
♂nectar	none	present?	-	none	none
Inter-anthesis (days)	1–5	0, overlap	overlap	1	1–2
Duration of ♀ anthesis on an inflorescence (days)	13–28	-	-	at least 3	1–3
Start of ♀ anthesis (time)	-	-	-	08.30	08.30
Duration of ♀ anthesis on a flower (hours)	192	24–48	-	ca. 24	ca. 8
♀ scent	-	faint, fruit scent	scent	fainter, sweet scent	sweet, spicy scent
♀ temperature elevation	none	-	-	-	
♀ nectar	none	present?	-	none	none
Number of insect visitors (species)	4	25	49 (species & morphospecies)	21	22
Effective pollinators	small bees? weevils? flies?	*Melipona* sp., *Trigona* sp., *Plebeia* spp., (Apidae), Vespidae spp., Muscidae spp.	bees	*Trigona* sp. (Trigonidae), Drosophilidae sp.	*Trigona* sp., *Plebeia* spp., *Euglossa* spp. (Apidae), Syrphidae spp.
Reference	Martén & Quesada (2001)	Listabarth (1993b)	Cerón-Martínez (2019)	Olesen & Balslev (1990)	Listabarth (1993b)

Table 24. Pollination of *Geonoma* spp. (3/5)

	G. macrostachys, Colombia	*G. macrostachys* 'small form', Ecuador	*G. macrostachys* 'large form', Ecuador	*G. macrostachys* '*acaulis*', Peru	*G. macrostachys* '*acaulis*', Colombia
Flowering season (months)	throughout the year	-	-	September to February, peak from November to January	throughout the year
Duration of ♂ anthesis on an inflorescence (days)	13	10–16	7–12	12–18	13
Start of ♂anthesis (time)	04.00	06.30	08.30	07.00	09.30
Duration of ♂ anthesis on a flower (hours)	ca. 7	3.5	6.5	4	4
♂ scent	-	fruity scent	fruity scent	spicy nutmeg scent	-
♂ temperature elevation	-	-	-	-	-
♂ nectar	-	-	-	-	-
Inter-anthesis (days)	2	1–2	1–2	1–2	2
Duration of ♀ anthesis on an inflorescence (days)	3	1–3	1–3	1–2	3
Start of ♀ anthesis (time)	05.00	6.30	09.00	07.00	07.30
Duration of ♀ anthesis on a flower (hours)	ca. 13	ca. 24	ca. 24	-	10
♀ scent	-	fruity scent	fruity scent	spicy, nutmeg scent	-
♀ temperature elevation	-	-	-	-	-
♀ nectar	-	-	-	-	-
Number of insect visitors (species)	15	19	24	3	9
Effective pollinators	*Oxytrigona* sp., *Euglossa* sp., *Partamona* sp., (Apidae)	beetles?	bees, wasps	Derelomini sp. (Curculionidae)	*Oxytrigona* sp., *Euglossa* sp., *Partamona* sp., *Plebeia* sp. (Apidae)
Reference	Tunaroza (2015)	Borchsenius et al. (2016)	Borchsenius et al. (2016)	Listabarth (1993b)	Tunaroza (2015)

Table 24. Pollination of *Geonoma* spp. (4/5)

	G. maxima subsp. *chelidonura* (as *G. juruana*), Brazil	*G. maxima* subsp. *maxima* (as *G. maxima*), Brazil	*G. maxima* subsp. *spixiana* (as *G. spixiana*), Brazil	*G. maxima* subsp. *Maxima*, Venezuela	*G. oligoclonal*, Colombia
Flowering season (months)	January to February, September to October	March to November	May to June, October to November	August to February	throughout the year
Duration of ♂ anthesis on an inflorescence (days)	14	14–20	15–30	10–16	7
Start of ♂anthesis (time)	06.45	09.00	05.30	-	06.00
Duration of ♂ anthesis on a flower (hours)	ca. 8	ca. 6	ca. 10	-	8.5
♂ scent	fruity scent	fruity scent	fruity scent	strong, perfume-like	-
♂ temperature elevation	-	-	-	-	-
♂ nectar	present, small amount	present	present, small amount	-	-
Inter-anthesis (days)	6	6–12	10	2–3	2
Duration of ♀ anthesis on an inflorescence (days)	8	8–10	7	3–5	3
Start of ♀ anthesis (time)	06.00	09.30	07.30	-	07.00
Duration of ♀ anthesis on a flower (hours)	48	48	-	48–72	10
♀ scent	fruity scent	fruity scent	fruit scent	strong, perfume-like	-
♀ temperature elevation	-	-	-	-	-
♀ nectar	present, small amount	present	present, small amount	-	-
Number of insect visitors (species)	16	14	8	11	20
Effective pollinators	*Euglossa* sp., cf. *Eufriesea* sp., *Plebeia* sp., *Partamona* sp. (Apidae)	*Euglossa* sp., *Plebeia* sp., (Apidae), Halictidae spp., Syrphidae sp.	*Euglossa* sp., cf. *Eufriesea* sp. (Apidae), Halictidae sp., Syrphidae sp.	*Trigona* sp. (Apidae)	Drosophilidae spp., Syrphidae spp.
Reference	Küchmeister (1997)	Küchmeister (1997)	Küchmeister (1997)	Listabarth (1999a)	Tunaroza (2015)

Table 24. Pollination of *Geonoma* spp. (5/5)

	G. pohliana subsp. *weddelliana* (as *G. brevispatha*), Brazil	*G. simplicifrons*, Venezuela	*G. tenuis*, Venezuela
Flowering season (months)	throughout the year, peak from April to August	-	-
Duration of ♂ anthesis on an inflorescence (days)	-	-	-
Start of ♂anthesis (time)	08.00	05.00	06.30
Duration of ♂ anthesis on a flower (hours)	-	10	12
♂ scent	sweet scent	-	-
♂ temperature elevation	-	-	-
♂ nectar	none	-	-
Inter-anthesis (days)	15	-	-
Duration of ♀ anthesis on an inflorescence (days)	-	-	-
Start of ♀ anthesis (time)	08.00	06.00	06.00
Duration of ♀ anthesis on a flower (hours)	48–96	192	192
♀ scent	sweet scent, fainter than staminate	-	-
♀ temperature elevation	-	-	-
♀ nectar	present, small amount	-	-
Number of insect visitors (species)	18	10	4
Effective pollinators	Muscidae spp., Sarcophagidae sp.	Chrysomelidae, Curculionidae, Diptera	Curculionidae, Diptera
Reference	Ostrorog & Barbosa (2009)	Seres & Ramirez (1995)	Seres & Ramirez (1995)

Pistillate anthesis on an inflorescence lasted 1–14 days in most taxa. There were two records of exceptional time periods (as in staminate anthesis), 28–56 days in *G. cuneata* subsp. *irena* and 13–28 days in *G. epetiolata*. Pistillate flowers opened between 06.00 and 09.30 in most taxa, with only one exceptional record, 05.00 in *G. macrostachys*. Flowers opened in flushes each day and the direction of anthesis on an inflorescence was acropetal, although this was seldom recorded. Pistillate flowers remained at anthesis for 24–48 hours, seldom more or less, exceptionally for 192 hours in *G. epetiolata*. Pistillate flowers were scented, and several authors noted that this was weaker than in staminate flowers. There were a few records of nectar production, and then in small amounts.

There were relatively few species of insect visitors to inflorescences, with a mean of only 16 species per taxon. Pollination was considered to be by wind in one species (*G. brongniartii*), and this species was also reported to have powdery pollen and to have slight scent (Listabarth 1993b) or no scent (Knudsen 1999a). Pollinators were unknown in *G. epetiolata*. Effective pollinators in the other taxa were reported to be derelomine weevils in two taxa, and bees and flies in other taxa. Fly pollinated taxa tended to have shorter inflorescence development. Pollinating insects were reported to collect pollen from staminate flowers and visit pistillate flowers by deceit. *Geonoma* taxa appear to be pollinated by various combinations of species of diurnal, flying insects, especially bees and flies, or occasionally by wind. It is interesting that the nitidulid *Mystrops* has been recorded from *Geonoma* inflorescences, but seldom as pollinator.

The high diversity and often elaborate patterns of inflorescence development amongst *Geonoma* taxa and the relatively low number of insect visitors indicate a distinct pollination system for each taxon. This is supported by the findings of Knudsen (1999a) who studied floral scent chemistry of 15 taxa of *Geonoma*. She considered that each taxon had a distinct floral scent. Similarly, Knudsen (1999b) studied floral scent chemistry of eight sympatric, co-flowering taxa of *Geonoma* in an Ecuadorean forest. She concluded that each had a characteristic, distinct floral scent and this contributed to reproductive isolation amongst species.

Two of the species included in Table 24, *G. maxima* and *G. macrostachys*, were reported to be visited by, and possibly pollinated by, euglossine bees. These bees collected scent from staminate and pistillate flowers, and thus effected pollination. Bacon et al. (2021) also found *Euglossa* sp. (and *Oxytrigona* sp.) as principal pollinators of two morphotypes of *G. macrostachys*. Knudsen (1999a) reported that *G. maxima* and *G. macrostachys* had floral scents dominated by monoterpenes and sesquiterpenes, and these included compounds associated with euglossine bee pollination in other plants. It may be coincidental, but both these species have pistillate flowers with digitately lobed staminodial tubes.

One interesting result of this review of pollination in *Geonoma* taxa concerns species complexes and morphotypes. Henderson (2011) considered that several species of *Geonoma* were widespread and variable, and he termed them species complexes. These species complexes were sometimes divided into subspecies (e.g., *G. maxima*) or sometimes into morphotypes rather than formal taxa (e.g., *G. macrostachys*). However, the studies reviewed here (Table 24) suggest that both allopatric populations of the same subspecies or morphotype, and sympatric populations of different subspecies or morphotypes, can have distinct pollination systems. For example, the two '*acaulis*' morphotypes of *G. macrostachys*, one from Peru and the other from Colombia, differ in their effective pollinators, derelomine weevils in Peru and meliponid and euglossine bees in Colombia. The two allopatric populations of *G. maxima* subsp. *maxima*, one from Venezuela and one from Brazil, also differ in their development and pollinators. Borchsenius et al. (2016) studied two sympatric morphotypes of *G. macrostachys* in Ecuador and found that they differed morphologically and genetically and in their habitat preference, and also in their inflorescence development. Although the spectrum of insect visitors was similar, floral scent differed such that the two morphotypes were reproductively isolated. Sometimes two sympatric populations have been regarded by taxonomists, based on herbarium specimens, as belonging to the same species, whereas study of their inflorescence development and pollinators shows them to be distinct taxa. The most extreme example of this is found in *G. cuneata*. Borchsenius (1997) showed that the inflorescence development of *G. irena* and *G. cuneata* var. *sodiroi* could hardly be more different from each other, and yet these had been treated as either the same species, or as subspecies of *G. cuneata*. If a biological species concept was applied to these *Geonoma* subspecies/morphotypes such as proposed by Listabarth (1999c), there clearly would be many more species of *Geonoma*. However, it should be pointed out that there are some counter-examples. The three sympatric subspecies of *G. maxima* in Brazil, subspp. *maxima*, *chelidoneura*, and *spixiana* have similar inflorescence development and pollinators.

Summary for Geonomateae

Of the six genera and 104 species in the tribe, four genera and 15 species have been studied. These show a great diversity of inflorescence development and pollinators.

There are no studies of *Pholidostachys*, although this is an interesting genus from a pollination point of view. Ferreira et al. (in prep) resolved two clades within *Pholidostachys*. One of these has two species, *P. sanluisensis* and *P. synanthera* (Fig. 12A), with elongate, open inflorescences free of bracts at anthesis, and the other clade has three species, *P. dactyloides* (Fig. 12B), *P. panamensis,* and *P. pulchra*, with condensed, closed inflorescences covered by fibrous bracts at anthesis. Nothing is known of pollination, although Knudsen (1999a) considered that *P. synanthera* may be fly-pollinated, based on the similarity of its floral scent to that of *Asterogyne martiana*. There appears to have been a major shift in inflorescence morphology and pollinators within *Pholidostachys*.

Calyptrogyne ghiesbreghtiana can be seen as an extreme example of specialization in palm pollination, especially in terms of the reward offered to pollinators, sweet-tasting flower tissues (like the other mammal-pollinated palm,

Figure 12. A. Open inflorescence of *Pholidostachys synanthera*. B. Closed inflorescence of *Pholidostachys dactyloides* covered by persistent bracts.

Eugeissona tristis, which offers alcoholic nectar as a reward to treeshrews). *Calyptrogyne anomala*, which has short, branched inflorescences borne near ground level, may be pollinated by non-flying mammals (de Nevers & Henderson 1988). There are no studies of *Calyptronoma* (sister to *Calyptrogyne*), but there is a striking contrast between the condensed, branched inflorescences of *Calyptronoma* and the elongate, spicate inflorescences of most species of *Calyptrogyne.* Scott Zona (pers. comm.) notes that *Calyptronoma dulcis* (now *C. plumeriana*) was named for its sweet-tasting staminal and staminodial tubes.

Geonoma is interesting in that it exhibits a basic pattern of inflorescence development (relatively long, diurnal staminate anthesis followed by relatively short, diurnal pistillate anthesis), but from this basic pattern a whole series of different development patterns and pollination systems has evolved involving numerous different pollinators. There is a huge range in inflorescence development, from the rapidly developing *G. cuneata* subsp. *sodiroi* with a total anthesis of up to 10 days to the slowly developing *G. epetiolata* with a total anthesis of up to 213 days.

Unlike the Cocoseae, the peduncular bract does not appear to play any role in pollination, and in most species (with the exception of some species of *Pholidostachys*) it falls from the inflorescence before anthesis.

Ferreira et al. (in prep.) resolved *Pholidostachys* as basal in the Geonomateae clade, followed by *Welfia,* then *Asterogyne,* then *Calyptronoma* and *Calyptrogyne* as sister to *Geonoma.* This suggests several major shifts within and amongst genera in inflorescence morphology, particularly within *Pholidostachys* and from the bee/fly-pollinated *Asterogyne* and *Welfia* to the bat-pollinated *Calyptrogyne*.

Arecoideae, *Leopoldinieae*

The tribe comprises one genus (*Leopoldinia,* 3 species) distributed in South America. *Leopoldinia* is monoecious with large, much-branched inflorescences and flowers in triads. Inflorescences may be unisexual by abortion of staminate or pistillate flowers. Two species have been studied.

Leopoldinia piassaba was studied by Guánchez (1997) in Amazonas, Venezuela. Plants flowered once a year during October and November. They produced either staminate or pistillate inflorescences, but an individual plant could produce staminate one year and pistillate another. In general, older, taller plants produced more pistillate inflorescences. Anthesis of an individual inflorescence lasted 6–10 days. Staminate flowers produced a sweet scent. Numerous insects visited inflorescences, more on staminate than on pistillate, with a peak of insect activity between 7.00 and 10.00 am. Guánchez considered that the most important pollinator was "…un Hymenoptera del género *Parisoschoenus* sp." However, *Parisoschoenus* is a genus of weevils, and it is unclear if Guánchez considered a Hymenoptera or a Coleoptera was the most important pollinator.

Guánchez (1997) studied *L. pulchra* in Amazonas, Venezuela. Plants flowered during all months of the year. They produced either staminate or pistillate inflorescences or inflorescences with staminate and pistillate flowers. Anthesis on an inflorescence lasted 6–10 days. No detectable scent was produced. Numerous insects visited inflorescences, more on staminate than on pistillate, with a peak of insect activity between 7.00 and 10.00 am. It is unclear if Guánchez considered a Hymenoptera or a Coleoptera was the most important pollinator.

Listabarth (1999b) studied *L. pulchra* at a different site in Amazonas, Venezuela. Plants flowered during October and November. Inflorescences contained staminate and pistillate flowers. On an inflorescence, staminate anthesis lasted approximately 21 days followed by approximately seven days of pistillate anthesis. Staminate anthesis began at 9.00 am and individual flowers fell from the inflorescence during the afternoon. No detectable scent nor nectar was produced. Pistillate anthesis began at 8.00 am and individual flowers were at anthesis for 36–48 hours. No detectable scent or nectar was produced. Numerous insects visited inflorescences. The most likely pollinators were bees in the genus *Trigona*.

There is conflicting information on the phenology, inflorescence development, and pollination of *L. pulchra*, doubts about the pollination of *L. piassaba*, and no information on the third species, *L. major*.

Arecoideae, Pelagodoxeae

The tribe comprises two genera (*Pelagodoxa,* 2 species; *Sommieria,* 1 species) occurring in the Pacific islands and New Guinea. No genera have been studied.

Arecoideae, Areceae, Archontophoenicinae

The subtribe comprises three genera (*Actinorhytis,* 1 species; *Archontophoenix,* 6 species; *Chambeyronia,* 9 species) occurring in New Guinea, Australia, and New Caledonia. No genera have been studied in their natural habitat. Skutch (1932) described inflorescence development of cultivated plants of *Archontophoenix cunninghamiana* in Panama. Inflorescences were protandrous. Staminate anthesis lasted 12–14 days. Individual flowers opened during the morning and abscised a few hours later. Flowers had a sweet scent. An inter-anthesis period was not recorded. Pistillate anthesis lasted 5–6 days.

Arecoideae, Areceae, Arecinae

The subtribe comprises three genera (*Areca,* 47 species; *Nenga,* 5 species; *Pinanga,* 144 species), widely distributed in the Asian tropics. No genus has been studied in detail except for the cultivated *Areca catechu*. Apparently, this has a typical bee pollination system. Plants are monoecious with unisexual flowers in triads. Purseglove (1973) described inflorescence development. Plants were protandrous. Staminate flowers opened between 09.00 and 12.00 and were sweetly scented. Staminate anthesis continued for 14–28 days. Pistillate anthesis lasted 3–4 days.

Dransfield et al. (2008) considered *Areca* and *Nenga* to be protandrous and *Pinanga* to be protogynous. Essig (1977) considered that some species of *Areca* from New Guinea might be protogynous, but this was queried by Dransfield et al. (2008). *Areca furcata* is the only species of palm with poricidal anthers, and may be buzz-pollinated. Ferguson et al. (1983) briefly described pollination of cultivated *Pinanga coronata* and suggested that all species of *Pinanga* might be beetle-pollinated. Two species, *P. cleistantha* and *P. simplicifrons,* have inflorescences that are enclosed by the prophyll at anthesis (Dransfield 1982).

Arecoideae, Areceae, Basseliniinae

The subtribe comprises six genera (*Basselinia,* 14 species; *Burretiokentia,* 5 species; *Cyphophoenix,* 4 species; *Cyphosperma,* 5 species; *Lepidorrhachis,* 1 species; *Physokentia,* 7 species), distributed in New Caledonia, Lord Howe Island, Vanuatu, Fiji, the Solomon Islands, and the Bismarck Archipelago. No genera have been studied.

Arecoideae, Areceae, Carpoxylinae

The subtribe comprises three genera (*Carpoxylon,* 1 species; *Satakentia,* 1 species; *Neoveitchia,* 2 species) distributed in the western Pacific Ocean on Fiji, Vanuatu, and the Ryukyu Islands. No genera have been studied in detail. Dowe et al. (1997) noted that *Carpoxylon* *macrospermum* was protandrous. Staminate anthesis began immediately after bract fall and lasted for weeks. There was a short inter-anthesis period, followed by a few days of pistillate anthesis. Potential pollinators were bees, wasps, and flies.

Arecoideae, Areceae, Clinospermatinae

The subtribe comprises two genera (*Cyphokentia,* 2 species; *Clinosperma,* 4 species) confined to New Caledonia. No genera have been studied.

Arecoideae, Areceae, Dypsidinae

The subtribe comprises six genera (*Dypsis,* 106 species; *Lemurophoenix,* 2 species; *Marojejya,* 2 species; *Masoala,* 2 species; *Vonitra,* 10 species, *Chrysalidocarpus,* 54 species) all confined to Madagascar and just reaching the Comores and Pemba. Dransfield & Beentje (1995) considered that bee and fly pollination was probably common in the Dypsidinae. They noted that some species, such as *D. pachyramea* and *D. remotiflora,* had exceptionally small flowers, scarcely 1 mm diameter, in which the petals hardly opened. They considered that *Marojejya,* with its condensed inflorescences, could be beetle-pollinated. Rudall et al. (2003) noted the presence of septal nectaries in most species of *Dypsis* (in the broad sense) and considered them likely to be pollinated by small insects. Only one genus has been studied.

Dypsis

Dypsis is monoecious with unisexual flowers in triads. Ratsirarson & Silander (1996) studied pollination of *D. decaryi* (as *Neodypsis decaryi*) in Madagascar. Plants flowered throughout the year with a peak between August and January. Inflorescences were protandrous. Staminate anthesis took place 60 days after the peduncular bract opened. Inflorescences were at staminate anthesis from 14 to over 35 days. Individual staminate flowers were at anthesis for less than one day. Staminate flowers produced a sweet scent and nectar. Pistillate anthesis took place after all staminate flowers had fallen. Individual pistillate flowers were at anthesis for two days. Pistillate flowers produced a sweet scent and nectar. At least five species of insect visited inflorescences. The most effective pollinators were considered to be honey bees.

Arecoideae, Areceae, Laccospadicinae

The subtribe comprises four genera (*Calyptrocalyx,* 28 species; *Linospadix,* 7 species; *Howea,* 2 species; *Laccospadix,* 1 species) distributed in the Moluccas, New Guinea, Australia, and Lord Howe Island. Williams (2021) considered that thrips were potential pollinators of *Linospadix* in Australia. Only one genus has been studied.

Howea

Howea is monoecious. Inflorescences are spicate and solitary or multiple per node. Flowers are unisexual and borne in triads. Savolainen et al. (2006) and Babik et al. (2009) reported on the two species of *Howea* occurring sympatrically on Lord Howe Island. For populations of the two species, peaks of anthesis were separated by about six weeks. For *H. forsteriana,* staminate anthesis peaked two weeks before pistillate anthesis. For *H. belmoreana,* there was overlap in staminate and pistillate anthesis. In both species, inflorescences were at staminate anthesis first. There was then a one-year inter-anthesis period, after which pistillate anthesis took place. Exclusion experiments indicated that both species were wind-pollinated.

The two species of *Howea* have remarkably high numbers of stamens, 30–70 per flower.

Arecoideae, Areceae, Oncospermatinae

The subtribe comprises four genera (*Oncosperma,* 5 species; *Deckenia,* 1 species; *Acanthophoenix,* 3 species; *Tectiphiala,* 1 species) widely distributed in the Asian tropics and Indian Ocean islands. No genera have been studied.

Arecoideae, Areceae, Ptychospermatinae

The subtribe comprises 14 genera (*Ptychosperma,* 29 species; *Ponapea,* 4 species; *Adonidia,* 2 species; *Balaka,* 11 species; *Veitchia,* 11 species; *Carpentaria,* 1 species; *Wodyetia,* 1 species; *Drymophloeus,* 3 species; *Normanbya,* 1 species; *Brassiophoenix,* 2 species; *Ptychococcus,* 2 species, *Jailoloa,* 1 species, *Manjekia,* 1 species; *Wallaceodoxa,* 1 species) widely distributed in the Old World tropics.

Two genera have been studied in cultivation, and some notes given on one other genus in its natural habitat. Essig (1973) reported on inflorescence development of cultivated plants of *Ptychosperma macarthurii* in Papua New Guinea.

After the fall of the peduncular bract and exposure of rachillae, flowers remained in bud for 90 days before anthesis. Inflorescences were protandrous. Flushes of staminate flowers opened each day for 14 days. Flowers opened at dawn and abscised by noon. A large drop of nectar was produced at the apex of the pistillode. There was possibly a 3–4 day inter-anthesis period. Pistillate flowers were at anthesis for at least two days and secreted nectar. A halictid bee, *Nomia* sp., was considered the most likely pollinator.

Dowe (1993) reported on pollination of cultivated plants of *Wodyetia bifurcata* in Australia. After the fall of the peduncular bract and exposure of rachillae, flowers remained in bud for 70–90 days before anthesis. Inflorescences were protandrous. Flushes of staminate flowers opened each day for 40–50 days. Flowers opened before sunrise and shed pollen by late morning. They fell from the inflorescence about six hours later. Flowers produced a sweet scent and a large drop of nectar at the apex of the pistillode. There was a three-day inter-anthesis period. Pistillate anthesis lasted 9–11 days with flushes of flowers opening each day. Individual flowers appeared receptive for 3–4 days. They produced a sweet scent, milder than the staminate flowers, and nectar accumulated along the petal margins, as well as stigmatic exudate. Eleven species of insect were collected from inflorescences and the most effective pollinators were considered to be halictid bees.

Inkrot et al. (2007) gave some notes on the flowering of *Normanbya normanbyi* in its native habitat in Australia. Plants flowered all the year round with a peak from March to September. Inflorescences were protandrous. Flushes of staminate flowers opened each day for about 40 days. Individual flowers opened early in the morning and lasted about 24 hours. There was an inter-anthesis period of nine days. Pistillate anthesis lasted about 14 days. Individual flowers were at anthesis for about seven days and produced nectar. No data on pollinators were given.

The three genera, *Ptychosperma, Wodyetia,* and *Normanbya*, are protandrous and have similar inflorescence development, although *Ptychosperma* has a much shorter period of total anthesis, 19–20 days versus 52–63 days in the other two genera. Notable is the extended period of flower bud exposure after the peduncular bract has fallen and before anthesis, 70–90 days in *Ptychosperma* and *Wodyetia*. One other interesting feature of these genera, found in most other Ptychospermatinae, is the prominent, nectar-producing pistillode in the staminate flowers.

Arecoideae, Areceae, Rhopalostylidinae

The subtribe comprises two genera (*Rhopalostylis,* 2 species; *Hedyscepe,* 1 species) distributed in Lord Howe Island, New Zealand, Chatham Islands, Norfolk Island and Kermadec Islands. One genus has been studied.

Rhopalostylis

Rhopalostylis is monoecious and inflorescences bear unisexual flowers in triads. Esler (1969) and Waite (2012) have studied pollination of *R. sapida* in New Zealand. Plants flowered from November to May. Inflorescences were protandrous, and anthesis began immediately after the peduncular bract opened. Staminate anthesis lasted seven days. Flowers produced stigmatic exudate from the pistillode and had a strong, fruity scent. Several days, possibly seven, after the finish of staminate anthesis, pistillate flowers were at anthesis. Numerous insects, birds, and geckos visited inflorescences at anthesis. Pollination was probably by insects, particularly small flies, but the actual pollinators were unknown, possibly because of the large number of introduced insects, particularly *Vespula* wasps, that visited inflorescences.

Arecoideae, Areceae, Verschaffeltiinae

The subtribe comprises four genera (*Nephrosperma,* 1 species; *Phoenicophorium,* 1 species; *Roscheria,* 1 species; *Verschaffeltia,* 1 species) distributed on the Seychelles islands. No genera have been studied.

Unplaced members of Areceae

This group comprises 10 genera (*Bentinckia,* 2 species; *Clinostigma,* 11 species; *Cyrtostachys,* 7 species; *Dictyosperma,* 1 species; *Dransfieldia,* 1 species; *Heterospathe,* 39 species; *Hydriastele,* 39 species; *Iguanura,* 34 species; *Loxococcus,* 1 species; *Rhopaloblaste* 6 species) widely distributed throughout the Old World tropics. One genus has been studied.

Hydriastele

Hydriastele is monoecious and inflorescences bear unisexual flowers in triads. Essig (1973) studied pollination of *H. wendlandiana* (as *H. microspadix*) in New Guinea. Inflorescences were protogynous. All pistillate flowers of an inflorescence were at anthesis before dawn, as soon as the peduncular bract opened. Pistillate anthesis lasted a few hours. Inflorescences gave off a musty scent but did not produce any nectar. All staminate flowers were at anthesis the next day, 24 hours after bract opening. Pollen was shed between dawn and 08.00, and staminate flowers fell from the inflorescence after that time. Inflorescences were visited by bees, flies, and weevils. Derelomine weevils (*Nodocnemus* sp.) were considered to be the most effective pollinators.

Hydriastele is of interest because it is the only genus of palms to exhibit both protandry and protogyny (with the possible exception of *Areca*). One group of species (formerly included in *Gronophyllum, Nengella,* and *Siphokentia*) has protandrous inflorescences, and the other group of species (including those formerly included in *Gulubia*) has protogynous inflorescences. *Hydriastele wendlandiella* is in this second group, and, as discussed above, has typical beetle pollination. Remarkably, there appears to be little difference in inflorescence morphology between the protandrous and protogynous species, although there are differences in pistillate flowers. The protandrous species have pistillate flowers with large triangular petals that cover the stigmas before anthesis, whereas the protogynous species have pistillate flowers with rounded petals which do not cover the stigmas. Even more remarkable is the rapid development of inflorescences of the protandrous species. Essig & Young (1985) described the protandrous species of *Hydriastele* (as *Gronophyllum* and *Nengella*) as having the staminate flowers at anthesis as soon as the peduncular bract fell, and by the second day all staminate flowers had fallen and the pistillate flowers were at anthesis. This rapid development is more like that found in protogynous palms and no other protandrous palm reviewed here has such rapid inflorescence development. This rapid, diurnal anthesis has been confirmed by Yudaputra et al. (2017) who studied inflorescence development of cultivated plants of the protandrous *H. beguinii*.

In a phylogenetic study of *Hydriastele*, Loo et al. (2006) suggested that protogyny may have arisen from one to five times, with as many as four reversals to protandry.

Summary for Areceae

The Areceae comprises 61 genera and 700 species, all of which are Old World in their distribution. Plants are monoecious and have inflorescences with unisexual flowers in triads, although *Lepidorrachis* is reported to have unisexual inflorescences (Baker & Hutton 2006). Only four genera (*Chrysalidocarpus, Howea, Hydriastele, Rhopalostylis*) and four species in the tribe have been studied (three other genera, *Archontophoenix, Ptychosperma,* and *Wodyetia*, have been studied in cultivation). Despite this, there are some interesting aspects of pollination in the tribe.

Genera in the Ptychospermatinae have remarkably long periods of bud exposure after the peduncular bract has fallen and before staminate anthesis, 70–90 days. This long exposure has also been noted in *Dypsis decaryi* but not in other genera in the Areceae, where anthesis occurs immediately after bract fall (e.g., *Archontophoenix, Carpoxylon, Hydriastele, Rhopalostylis*). The inter-anthesis period of 365 days in *Howea* is extraordinary, especially when compared with the one-day period in *Hydriastele*. This latter genus is also interesting for the numerous shifts between protandry and protogyny.

Despite these few studies, there are no reasons to think that the distribution of pollination systems in the tribe will be any different from the rest of the family. There are indications of widespread beetle pollination in *Pinanga* and widespread bee or fly pollination in *Dypsis* and *Chrysalidocarpus* and in the Ptychospermatinae. With the possible exceptions of *Pinanga* and *Hydriastele*, the peduncular bract does not appear to play any role in pollination in the tribe, and is usually deciduous before anthesis.

THE MAIN INSECT POLLINATORS OF PALMS

Some notes are given here on the main insect pollinators of palms—Nitidulidae, Curculionidae, and bees.

Nitidulidae

The family Nitidulidae comprises 10 subfamilies, approximately 351 genera, and nearly 4,500 species (Jelínek et al. 2010). These small beetles are often referred to as sap beetles and are distributed throughout the world. They are associated with a wide variety of substrates, although the vast majority feed on fresh or decaying plant tissues or on fungi occurring on decaying organic matter (Jelínek et al. 2010).

The Neotropical tribe Mystropini of the subfamily Nitidulinae comprises about eight genera and 50 species (Kirejtshuk & Couturier 2010). Members of the tribe are anthophilous (Audisio 1993) and are associated with palm inflorescences or with inflorescences of other monocotyledons. The genus *Mystrops* is the most important palm pollinator, and almost all Neotropical, beetle-pollinated genera reviewed here have *Mystrops* as pollinator. The genus comprises about 33 species (Kirejtshuk & Couturier 2010), but many more appear to be undescribed. For example, Núñez (2014) recorded 74 species of *Mystrops* in Colombia. Apparently both adults and larvae feed exclusively on palm inflorescences. In the studies reviewed here, *Mystrops* spp. have been identified as pollinators or co-pollinators of some or all species of the following genera: *Acrocomia, Allagoptera, Astrocaryum, Attalea, Bactris, Ceroxylon, Cryosophila, Desmoncus, Manicaria, Mauritia, Oenocarpus, Phytelephas, Socratea, Syagrus,* and *Wettinia.* In some of these genera there is evidence of host specificity, for example in *Attalea* (Núñez 2014) and *Wettinia* (Restrepo et al. 2016).

The other Nitidulidae subfamily of interest is the Old World Meligethinae. These are commonly referred to as pollen beetles. This subfamily of little less than 50 genera and 700 described species is closely related to the Nitidulinae (Audisio et al. 2014 and unpublished data). Jelínek (1992) considered that Neotropical *Mystrops* and Old World Meligethinae showed remarkable parallel evolution of sexual dimorphism. However, he considered that few Meligethinae showed the same host specificity as *Mystrops.* Additional data collected more recently by Audisio et al. (2014 and unpublished) clearly suggest that most palm-associated Meligethinae species also exhibit a high degree of host-specificity. It is remarkable that the ubiquitous association between Derelomini weevils and Mystropini nitidulids in the Neotropics is mirrored in the Old World with Derelomini weevils and Meligethinae nitidulids (Jelínek 2000).

Audisio et al. (2014) gave a list of host plants of Meligethinae genera. Several genera were associated with palm inflorescences—*Cryptarchopria* on *Areca*, *Arenga*, and *Caryota; Kabakovia* on *Phoenix; Meligethinus* on *Chamaerops*, *Nannorrhops*, *Elaeis*, and *Raphia*; and *Microporodes* and *Palmopria* on *Elaeis*. More recently, *Meligethinus* has been recorded on *Phoenix* inflorescences (Sabatelli et al. 2020). It is unclear if any or all of these are pollinators but it seems likely. In particular, *Meligethinus* is quite commonly reported from palm inflorescences (*Chamaerops, Elaeis*, *Phoenix*). Sabatelli et al. (2020) reported that the genus comprised about 20 species and that both larvae and adults fed on palm inflorescences. A revision of *Meligethinus*, including the descriptions of a few new Afrotropical species, is almost ready to be published (Sabatelli et al. unpublished data).

There are two other nitidulid subfamilies of interest, Epuraeinae, with *Epuraea* as pollinator of *Nypa,* and Cillaeinae, with *Colopterus* as pollinator of *Astrocaryum* and *Bactris*.

It is unclear if *Mystrops* or other nitidulid genera form multispecies assemblages of brood-site pollination mutualisms on the same host, as described below for weevils. However, there is one interesting aspect of nitidulids as pollinators, especially in relation to weevils. The palms they pollinate often have diurnal rather than nocturnal anthesis. In the present review, diurnal anthesis and nitidulid pollination has been recorded in *Nypa, Ceroxylon, Wettinia, Allagoptera, Attalea, Astrocaryum*, and *Manicaria*. On the other hand, weevil pollination appears to be often associated with nocturnal anthesis.

Curculionidae

The family Curculionidae comprises at least 10 subfamilies, 4,600 genera, and 51,000 described species (Oberprieler 2014). Commonly known as weevils, they are distributed throughout the world. Adults and larvae feed on many different plants and tissues.

The subfamily Curculioninae comprises approximately 34 tribes, 350 genera, and 4,500 species (Caldara et al. 2014). These are commonly known as flower weevils and their larvae develop predominantly in flowers, fruits, and seeds. Palm pollinators have traditionally been placed in one tribe of the Curculioninae, the Derelomini. This tribe comprises about 40 genera and 265 species, and members are commonly known as palm flower weevils (Franz 2006).

Franz (2006), in a phylogenetic study of the Derelomini, proposed a revised classification of the tribe. He recognized five subtribes. The Derelomina comprised nine genera (*Anchylorhynchus, Celetes, Derelomus, Elaeidobius, Grasidius, Lomederus*, *Phytotribus, Prosoestus,* and *Terires*), all from South America or Africa. All genera and species are pollinators of palms and are often referred to in the present review. The Acalyptina comprised 10 genera, distributed in tropical Asia and Australia. They were said to be pollinators, predominantly of palms. Only one genus of Acalyptina, *Nodocnemus*, is referred to as pollinator in the present review (*Salacca* in Indonesia and *Hydriastele* in Papua New Guinea), although these few records may reflect the lack of knowledge of pollination in Asian palms. Subtribe Notolomina contained four genera (*Andranthobius, Derelominus, Diplothemiobus,* and *Notolomus*). All are Neotropical, and all have been referred to here as palm pollinators, or at least as visitors to palm inflorescences. Subtribe Phyllotrogina contained 11 genera. This subtribe is mostly Neotropical and some are palm pollinators. However, some genera have transitioned to non-palm hosts such as Cyclanthaceae. Franz considered one genus in the subtribe, *Phyllotrox* to be particularly problematic taxonomically. Although the genus has been cited frequently as a palm pollinator in the present review, some species may have transitioned to other host plants. The fourth subtribe, Staminodeina contained two genera, neither of which are associated with palms. Franz wrote: "Although their relative degrees of host specificity vary, as a whole derelomines may have shaped the evolution of palms more than any other insect taxon."

Most recently, Haran et al. (2023b), in studying phylogenetic relationships within the subfamily Curculioninae, have shown that the Derelomini is not monophyletic but comprises four, unrelated lineages. Three of these lineages correspond to the subtribes recognized by Franz (2006)—Derelomina, Notolomina, and Phyllotrogina.

Knowledge of one genus of subtribe Derelomina, *Anchylorhynchus*, is relatively detailed and shows the complexity of the interactions between these weevils and palms. Twenty-five species of *Anchylorhynchus* are recognized based on morphological data, but many of these represent complexes of cryptic species that can only be recognized with molecular data (de Medeiros & Vanin 2020). One such complex of three cryptic species, based on *A. trapezicollis*, can occur on the same or different species of *Syagrus* (de Medeiros & Farrell 2020). The original host palm of *Anchylorhynchus* may have been *Syagrus* and species have transitioned to other genera such as *Butia*, *Oenocarpus*, and *Euterpe*, and some species may have transitioned back to *Syagrus* (de Medeiros & Vanin 2020). *Anchylorhynchus* species are commonly found on three different palm genera (*Syagrus*, *Butia*, *Oenocarpus*), but as pollinators they can range from important to unimportant (de Medeiros in press.). Adults oviposit on pistillate flowers and developing larvae may destroy developing fruits, or developing fruit may deter larval development, and larvae may cannibalize conspecific larvae (de Medeiros et al. 2014). In the present review, *Anchylorhynchus* is reported to be the most effective pollinator of two species of *Syagrus* and three of *Oenocarpus* (all of which are protandrous).

One other genus of subtribe Derelomina, *Celetes*, has been revised (Franz & Valente 2005). All of the approximately 40 species are Neotropical, and all are found only on palms. Their life histories are fairly uniform. Adults feed on pollen or tissue from petals or peduncles, and females oviposit on the internal surface of the peduncular bracts. Their life cycle lasts 3–4 months, about the same time as fruit development (and about the same time as peduncular bracts persists on the infructescence). *Celetes* species usually have only one palm host species. Franz & Valente postulated a series of host shifts from an ancestral association with *Attalea* and *Syagrus* to other hosts such as *Astrocaryum, Allagoptera, Euterpe,* and *Mauritia.* In the present review, *Celetes* is reported to be the most effective pollinator of

Mauritia. Haran et al. (2023a) showed how different genera of weevils oviposited on different parts of palm inflorescences, where their larvae developed, for example *Andranthobius* and *Phyllotrox* on staminate flowers, *Celetes* and *Phytotribus* on bracts, and *Terires* and *Anchylorhynchus* on pistillate flowers.

Haran et al. (2022) studied the phylogeny of tropical African derelomine weevils. Results indicated that there was an early association between weevils and palms, followed by transitions to other host plants, particularly in the Ebenaceae. In discussing brood-site pollination mutualisms of derelomine weevils and palms, Haran et al. noted a range of reciprocal adaptations. Adult weevils are attracted to inflorescences by specific floral or leaf scents, and some inflorescences heated up which enhances scent production and weevil larvae development. Some species of weevil have long hairs on their bodies which may facilitate pollen transport, and most weevils appear to mimic inflorescences in their body colour. As a reward for pollination, palm inflorescences provide a mating site and source of food for adults, and a site for larval development. Haran et al. noted another interesting feature of brood-site pollination mutualisms—the weevils often form sympatric assemblages of multiple species on the same host. Examples are the approximately ten, closely related species of weevil found on *Elaeis guineensis* inflorescences, and the more or less closely related lineages of six *Derelomus* species found on *Phoenix reclinata*. Haran et al. wrote: "The origin, evolutionary significance and reciprocal benefit of these assemblages of what appear to be functionally redundant species remain unclear and constitute a stimulating research prospect on brood-site mutualism."

A second subfamily of the Curculionidae, the Baridinae, also contains palm pollinators. There are up to 550 genera and 4,300 species (Morimoto & Yoshihara 1996). Although Baridinae species have been considered as pollinators in several of the studies reviewed here, they have seldom been identified to genus. They have been considered the most effective pollinators of *Aphandra* and species of *Oenocarpus*. Haran et al. (2023a) listed several Baridinae in their list of brood-site pollination mutualisms. They wrote of the Baridinae: "Due to their unresolved phylogeny, complex taxonomy and very high number of undescribed taxa… they are rarely identified beyond the subfamily or tribe level in pollination studies, preventing accumulation of knowledge. A great diversity of baridine pollinators, with or without brood sites as rewards, remains to be discovered." Valente (1997) revised the Baridinae genus *Microstrates*. She recognized 11 species and considered them associated only with the palm genera *Syagrus* and *Butia*. Adult females oviposited in staminate flowers, where larvae developed. Each species of *Microstrates* was associated with only one species of palm.

There appears to be a high degree of host specificity in derelomine and baridine weevils. Núñez (2014) studied the association between weevils and inflorescences of 20 different species of palms in Colombia. He found 114 species of weevil on these palms, most of which were from the Derelomini or Baridinae. The number of weevil species per palm species ranged from 2–26, with an average of 12. Núñez found a high level of specificity, and 85% of the weevil species were considered specific to a particular palm. Haran et al. (2023a) wrote: "The vast majority of weevils engaged in brood-site pollination appear to be strictly monophagous as larvae. Such a level of specialization is rare for weevils and phytophagous insects in general, even when considering other groups of endophagous feeders, which are known to be generally highly specialized……. One of the most striking cases reflecting this host specificity is the pollination ecology of sympatric palms belonging to the genus *Oenocarpus* in the Amazon……. The three species studied have a very similar floral structure and phenology, but each has a specific assemblage of weevil pollinators, only a few of which are able to visit several *Oenocarpus* species. … All detailed studies of host plant associations using molecular data have found a higher than previously thought weevil diversity and a very high degree of specialization on their hosts…".

As noted above, weevils often co-occur with nitidulid beetles on palm inflorescences, and both are brood-site pollinators. The interaction between the two groups has not been studied. Both feed on pollen. As far as is known, *Mystrops* oviposit on or in staminate flowers, particularly on stamens, where their larvae develop. Weevils usually use their rostrum to drill an oviposition site inside different parts of the inflorescence, in bracts, rachillae, staminate flowers, or pistillate flowers. One potential difference between the two families, in terms of palm pollination, is that weevils are often associated with nocturnal anthesis and nitidulids with diurnal anthesis.

Two studies have quantified the number of palm taxa associated with weevils. Franz & Valente (2005) gave a list of host associations of derelomine flower weevils, based on published records, specimen labels, or their own observations. For palms, they listed 38 genera and almost 100 species. Haran et al. (2023a) gave a literature review of weevils involved in brood site pollination mutualisms. For palms, they included 34 genera and 113 species. The vast majority of these were reported to be pollinated by weevils belonging to the Derelomini, together with a few Baridinae and other groups. While the lists of Franz & Valente (2005) and Haran et al. (2023a) are not directly comparable, they do indicate a widespread association between weevils and palms, regardless of whether the weevils are pollinators or not. As seen repeatedly in the present review, bee-pollinated palm inflorescences are almost always visited by beetles (and the converse is true), particularly weevils and nitidulid beetles. It is somewhat difficult to make lists of palms involved in brood-site pollination mutualisms with weevils. Some genera, such as *Attalea* and *Wettinia*, are considered to be mostly pollinated by nitidulid beetles even though weevils are reported as visitors and possibly co-pollinators. Nevertheless, there are certainly a high number of genera and species of palms that exhibit weevil/palm brood-site pollination mutualisms. As seen in the present review, Derelomini have been identified as pollinators or co-pollinators of about 60 species in the following 22 genera: *Acrocomia, Allagoptera, Aphandra, Astrocaryum, Attalea, Bactris, Chamaerops, Cryosophila, Desmoncus, Elaeis, Euterpe, Geonoma, Hydriastele, Iriartella, Mauritia, Oenocarpus, Phytelephas, Rhapidophyllum, Salacca, Socratea, Syagrus,* and *Wettinia.* It seems possible, at least in the neotropics, that most palm inflorescences are used as brood-sites by beetles.

Bees

Bee pollinators of palms come mostly from two families, the Halictidae (sweat bees) and the Apidae. This latter family includes, amongst others, carpenter bees (*Xylocopa*), euglossine bees (Euglossini), stingless bees (Meliponini, including *Trigona*), and honey bees (*Apis*) (Michener 2000).

As reviewed here, bees (often *Trigona*) are pollinators or co-pollinators of some or all of the species of the following genera: *Aiphanes, Arenga, Borassus, Butia, Calamus, Chrysalidocarpus, Euterpe, Geonoma, Hyospathe, Iriartea, Johannesteijsmannia, Licuala, Lodoicea, Mauritia, Mauritiella, Metroxylon, Prestoea, Sabal, Serenoa*, and *Syagrus*. Almost all these genera have nectariferous pistillate flowers (except *Johannesteijsmannia* and possibly *Mauritia*; not reported for *Arenga* and *Iriartea*). Bees visit staminate flowers to collect pollen and sometimes nectar, and pistillate flowers to take nectar. Bees are almost always visitors to non-bee-pollinated palms.

Núñez (2014) reviewed the role of stingless bees in the pollination of Colombian palms. From 81 species of palm he recorded 97 species of bee in 13 genera, with 1–15 species of bee per palm. The highest number of bee species per palm genus was in *Wettinia* (32 bee species) followed by *Attalea* (28 species), *Astrocaryum* (20 species), and *Bactris* (16 species) (all beetle-pollinated palms). Bee activity was diurnal and mostly occurred at staminate anthesis when bees collected pollen. Núñez found a strong association between bees and palms. He considered that palms were important in the survival of bees, but bees played a relatively minor role in palm pollination. One of the reasons for this was because bees mostly visited inflorescences at staminate anthesis. He found bees to be efficient pollinators of species of *Geonoma, Prestoea, Sabal,* and *Syagrus*, secondary pollinators of species of *Attalea, Astrocaryum, Euterpe,* and *Mauritia*, and to have no role in the pollination of species of *Aiphanes, Manicaria,* and *Oenocarpus*.

Núñez's (2014) results imply a somewhat limited role for bees in palm pollination. His results are not directly comparable to the results of the present review because he included only stingless bees and Colombian palms. In the studies reviewed here, for South American palms only, approximately 12% of species are considered to be pollinated by stingless bees, and for all species and all bees, approximately 27% are reported to be bee-pollinated. This latter figure is similar to the 26% given by Barfod et al. (2011).

DISCUSSION

There are a total of 182 genera and approximately 2,460 species of palm. Pollination studies of 60 genera (33% of the total) and 149 species (6% of the total) are reviewed here. Of these 149 species, 109 (75%) are Neotropical. Old World palms are thus a particularly big gap in our knowledge of palm pollination, especially considering there are more than twice as many Old World species as Neotropical. The discussion in the following paragraphs is based on this small sample of mostly Neotropical palms.

In general, studies of pollination of palms have lagged far behind those of other plant families. Most of the early descriptive, and much of the recent experimental work on pollination of flowering plants has been based on small, herbaceous plants from temperate regions with one or a few flowers per plant, and these visited by relatively few insects, most of which are Hymenoptera or Lepidoptera. Palms are more difficult to study. Consider, for example, *Oenocarpus bataua*. It occurs in Neotropical rainforests, its inflorescences are situated on a woody stem up to 20 m above ground level and are up to two meters long with over 100,000 flowers, anthesis is nocturnal, and there are more than 80 species of arthropod visitors, many of which are Coleoptera and some of which may be present in tens of thousands of individuals (Núñez & Rojas-Robles 2008).

ADAPTATION TO POLLINATORS IN PALM FLOWERS AND INFLORESCENCES

In flowering plants in general, the remarkable diversity of reproductive structures is usually considered to be at least in part a consequence of selective pressures exerted by pollinators. There are an estimated 352,000 species of flowering plants, the vast majority of which are pollinated by animals (Ollerton 2021). These pollinators include an equally diverse and numerous arrays of invertebrates (mostly Lepidoptera, Coleoptera, Hymenoptera, and Diptera) as well as birds, bats, lizards, and non-flying mammals (Ollerton 2017). Thus, floral and inflorescence morphology and development, especially traits such as flower shape, colour, nectar production, and scent, have evolved to a great extent through pollinator-mediated selection.

In several places in this review, authors have expressed doubts over the adaptive significance of inflorescence morphology (e.g., Bøgh 1996) or flower anatomy (e.g., Askgaard et al. 2008). For pollen morphology, Sannier et al. (2009) found no correlation between the diverse ornamentation of palm pollen and pollinators. They wrote: “However, there is a possibility that our results indeed reflect the reality and that pollen ornamentation is not involved in the pollination syndrome in palms…… Palm flowers are relatively poorly diversified in morphology when compared to the spectacular flowers of other groups…… The lack of correlation between pollen ornamentation and pollinators may be accounted for by a weak degree of specialization in the pollination system.” On the other hand, Uhl & Moore (1977) found correlations between floral anatomy and pollination in various genera of palms.

Based on the studies reviewed here, it is usually difficult to infer if some morphological feature of flowers or inflorescences has been selected by pollinators. It can be inferred, based on knowledge of pollination systems, that certain features are associated with pollinators. For example, there is a general tendency in palms for elongate, open inflorescences to be associated with bee or fly pollination, and shorter, condensed inflorescences to be associated with beetle pollination. Nectariferous flowers are usually associated with bee pollination, and heat production with beetle pollination. For *Calyptrogyne ghiesbreghtiana*, inflorescence and floral morphology appear clearly adapted to bat-pollination. On the other hand, the dioecious *Chamaedorea* is a large genus with diverse inflorescence and floral morphology (and with differences between staminate and pistillate inflorescences within species), but with apparently uniform pollinators (thrips and wind). Considering that pollinators are just one small subset of the organisms that live on and interact with palms, and are potentially selective agents, not only on inflorescences but on roots, stems, and leaves, it is perhaps not surprising that there is little obvious evidence of morphological adaptation to pollinators. The general impression from this review is that there are few apparent morphological adaptations in palms, which is not to say that no such adaptations exist. What does seem more adaptive is inflorescence development, with relatively long-lasting anthesis in bee-pollinated palms and relatively brief anthesis in beetle-pollinated ones. The mean length of anthesis of an inflorescence for bee-pollinated palms is 30 days, whereas for beetle-pollinated palms it is 12 days. It appears that it is the developmental sequence of the inflorescence, including nectar, heat, and scent production, rather than morphology, that has evolved independently in the different taxa of palms.

POLLINATION SYNDROMES

The concept of pollination syndromes was originally based on the common observation that unrelated species of plants had evolved similar flower traits, and this convergent evolution was assumed to be a result of selection driven by similar pollinators. This concept was codified by Faegri and van der Pijl (1979) who defined the various syndromes. In flowering plants in general, there have been extensive discussions of the usefulness and degree of predictability of pollination syndromes (e.g., Rosas-Guerrero et al. 2014, Armbruster et al. 2000, Fenster et al. 2004, Ollerton 2021). One of the main criticisms has been that the use of pollination syndromes over-simplifies what are extremely complex interactions between plants and their pollinators (Ollerton et al. 2009, Dellinger 2020).

Henderson (1986), following Faegri & van der Pijl (1979), used the concept of pollination syndromes to classify the various palm pollination systems he reviewed. He recognized four different syndromes in the family—beetle pollination (cantharophily), bee pollination (mellitophily), fly pollination (myiophily), and wind pollination (anemophily). The beetle pollination syndrome was based on protogyny, ivory- or cream-coloured inflorescences, small, crowded flowers mature at bract fall, numerous stamens, short-lived, nocturnal anthesis, temperature elevation, musty scent, and absence of nectaries. From the present review it is apparent that there are many beetle-pollinated palms that do not fit this syndrome. For example, pistillate flowers of *Salacca zalacca* produce nectar; *Oenocarpus* spp. inflorescences are protandrous and have relatively long periods of anthesis and large flowers that are not mature at bract fall; and some species of *Ceroxylon* have diurnal anthesis and sweet-scented inflorescences. There are similar exceptions for the bee pollination syndrome. This was based on protandry, coloured flowers developing after bract fall, fewer stamens, long-lived, diurnal anthesis, no temperature elevation, sweet scent, and nectaries (Henderson 1986). Again it is apparent that there are many bee-pollinated palms that do not fit this syndrome. It does not apply to the bee-pollinated species of *Calamus* with nocturnal anthesis, nor to other bee-pollinated palms such as *Coccothrinax argentata* and *Johannesteijsmannia* spp. that do not have nectariferous pistillate flowers. Furthermore, there is no apparent association between pollination syndrome and number of stamens. Similar arguments could be used against recognizing fly-pollination and wind-pollination syndromes. One syndrome not mentioned by Henderson (1986), ambophily, has also been suggested for palms, as noted for *Chamaedorea*. Abrahamczyk et al. (2023) list several other palm genera (*Astrocaryum, Attalea (as Orbignya), Cocos, Elaeis, Euterpe*) as ambophilous, but in most of these, wind pollination seems incidental rather than part of the pollination system.

Clearly pollination syndromes have a limited use in describing, classifying, or predicting pollination systems in palms. Listabarth (2001) doubted the validity of mellitophily and myiophily, based on his observation of low pollinator specificity, although he stated that: "in palms a cantharophilous pollination syndrome definitely exists." On the other hand, Consiglio & Bourne (2001) doubted the predictive value of the beetle-pollination syndrome. Barfod et al. (2011) also questioned the validity of syndromes, and considered that they were too simplistic to reflect diverse palm pollination systems. How, then, can pollination systems in palms be classified? In general, systems are too diverse and complex to classify into any particular scheme. They vary amongst and sometimes within genera, and within species they can vary from place to place and from season to season. Nevertheless, it is still useful to say that a palm is beetle-pollinated or bee-pollinated without ascribing any particular pollination syndrome.

GENERALIZATION VERSUS SPECIALIZATION IN PALM POLLINATION SYSTEMS

Another criticism of the pollination syndrome concept is that it tends to focus on specialized pollination systems, here understood to mean ecological specialization (Armbruster 2017). A specialized plant/pollinator interaction is one in which one visitor pollinates one particular plant. On the other hand, a generalist interaction is one in which many visitors may pollinate one plant. This implies that the fewer the number of visitors to flowers, the more specialized the system. Much of the earlier literature on pollination biology emphasized specialized pollination systems, as if they were the norm. More recently it has become apparent that many supposedly specialized systems are more complex and may involve several pollinator species rather than a single one (Waser et al. 1996). There has been much discussion in pollination studies on the extent to which pollination systems may be considered specialized or generalized, or where they might lie along a continuum from extreme specialization to extreme generalization (e.g., Johnson & Steiner 2000). In palms, these questions have seldom been addressed in any detail, except for a general tendency to regard bee and fly pollination systems as generalized and beetle pollination systems as specialized.

What is the extent to which palm pollination systems can be regarded as specialized or generalized? If a specialized pollination system is defined as one in which there is only a single pollinator, then there are few such systems in palms. The only example appears to be *Manicaria* (unless one considers wind pollination, and then the wind-pollinated species would have the most specialized systems). Even in the cases of the two mammal-pollinated palms, the treeshrew-pollinated *Eugeissona* and the bat-pollinated *Calyptrogyne*, both have several different mammal pollinators. If numbers of different species of pollinators on inflorescences is the only way to quantify a pollination system and place it along a specialized/generalized gradient, then there is still not enough data for palms.

The other way to describe pollination systems in terms of specialization and generalization is a subjective assessment. So, for example, *Euterpe* is reported to have a generalized pollination system (e.g., Küchmeister et al. 1997) while *Oenocarpus* is reported to have a specialized pollination system (e.g., Núñez & Rojas-Robles 2008), which is essentially saying that bee pollination is generalized and beetle pollination is specialized. However, this may not be the case. *Sabal mauritiiformis*, for example, might be considered to have a typical, generalized pollination system. It has large, open inflorescences with diurnal anthesis and hermaphrodite, nectariferous, scented flowers visited by 65 different species of insect. However, only one insect pollinator had a Relative Importance Value (RIV) of over 10%, the bee *Nannotrigona mellaria*, with a RIV of 84% (Brieva-Oviedo & Núñez 2020). Based on the few other studies where pollinators have been quantified, using a RIV for each pollinating insect (Núñez & Rojas-Robles 2008, Núñez 2014, Guerrero-Olaya & Núñez 2017, Nuñez & Carreño-Barrera 2017, Brieva-Oviedo et al. 2020, Carreño-Barrera et al. 2021), there is usually only one pollinator, rarely 2–4, that has the highest RIV, usually by a wide margin, in both bee- and beetle-pollinated palms. Further evidence for specialization in palm pollination systems comes from the high levels of host specificity, especially in beetle pollinated palms, for example *Attalea* (Núñez 2014) and *Wettinia* (Restrepo et al. 2016). And, as described by Haran et al. (2022), there is now evidence of another feature of weevil brood-site pollination mutualisms—the weevils often form sympatric assemblages of multiple species on the same host. All this leads to the conclusion that, despite numerous visitors to inflorescences, most pollination systems in palms are specialized. How this degree of specialization is measured, or even if it can be measured at all, is unclear.

SHIFTS IN PALM POLLINATION SYSTEMS

There have been no studies of pollinator-driven speciation at the microevolutionary level in palms. There are some species whose pollination systems may be examples of microevolutionary processes, particularly widespread species having populations with different pollinators in different habitats (e.g., *Mauritia flexuosa, Euterpe* spp.). These populations may be considered examples of pollination ecotypes, and the species is undergoing incipient speciation whereby isolated populations undergo selection by pollinators and eventual reproductive isolation between populations (Van der Niet et al. 2014). However, even with lack of knowledge of microevolutionary processes, shifts in pollination between taxa can be inferred from phylogenies (Van der Niet & Johnson 2012). There have been great advances in knowledge of the phylogeny of the palm family recently (e.g., Ferreira et al. in prep.), and these allow the investigation of macroevolutionary patterns and shifts between one pollination system and another.

About 86% of palms in the sample here are pollinated either by beetles, bees, or flies. There are about half-a-dozen relatively well-documented examples of shifts from bee/fly pollination to beetle pollination (e.g., *Euterpe* to *Oenocarpus*) and a similar number of shifts from beetle pollination to bee/fly pollination (e.g., *Allagoptera* to *Syagrus*). In palms in general, based solely on elongate/open inflorescences and shorter/condensed inflorescences, without any knowledge of pollination but assuming the former to be bee-pollinated and the latter beetle-pollinated, there appear to be numerous other examples of shifts, in both directions. In one sense, all shifts between sister genera involve some change in inflorescence or flower morphology, and such shifts may be associated with pollination. Within the palms there appear to be numerous, bidirectional shifts between closed inflorescences and beetle pollination and open inflorescences and bee/fly pollination, and shifts to other pollinators, and the number of shifts may be equivalent to the number of genera. However, whatever the number, it is certainly far less than the potential number (i.e., one less than the total number of palm species). There appear to be some additional shifts within genera, such as *Calamus* and *Pholidostachys*, and shifts within genera without any apparent changes in floral morphology, such as *Syagrus*. Van der Niet & Johnson (2012) found that, in a sample of 3,500 flowering plants, approximately 25% of divergence events in clades were characterized by pollinator shifts.

After such shifts, there may be many species in a genus that differ from one another in inflorescence and floral morphology, but still have the same general pollination system. For example, in the Euterpeae, a tribe with 33 species, there has been only one shift from bee/fly-pollinated, open inflorescences in *Hyospathe, Prestoea*, and *Euterpe* to beetle-pollinated, closed inflorescences in *Oenocarpus*. The nine species of *Oenocarpus* differ from one another in details of inflorescence and floral morphology, yet are all pollinated by similar beetles. Similarly, in the Bactridinae, there has been a shift from the bee/fly-pollinated *Aiphanes* to the beetle-pollinated *Acrocomia, Desmoncus*, and *Bactris*. These three genera have diverse inflorescence and floral morphology but all of the ca. 140 species are probably pollinated by similar beetles, often nitidulids. After shifts between sister genera, speciation and changes in inflorescence and floral morphology may not be associated with selection by pollinators. For example, Henderson (2002) considered that changes in inflorescence size within *Oenocarpus* were associated with changes in stem size, culminating in the slender-stemmed *O. simplex* with spicate inflorescences.

It is unclear if these shifts are pollinator mediated, and how such shifts would take place. As seen in the present review, palm inflorescences attract many insect visitors, and bee/fly-pollinated inflorescences also attract beetles, and *vice versa*. Presumably the beetle visitors to bee-pollinated palms also use the inflorescences as brood sites, as in beetle-pollinated palms. These shifts are often associated with various aspects of inflorescences, in particular from nectar production (bees/flies) to heat production (beetles). Indeed, nectar production and heat production appear closely related and mutually exclusive phenomena in palms. These shifts are usually also associated with changes in inflorescence development, with bee/fly-pollinated inflorescences developing more slowly (based on the sample here, a mean inflorescence anthesis of 30 days) and beetle-pollinated inflorescences developing more rapidly (mean anthesis 12 days). Nevertheless, despite these few, presumably, pollinator-mediated shifts, there must have been many more speciation events that did not involve pollination.

For pollination, palms seem to have tried just about everything—bats (*Calyptrogyne*), bees (many genera), birds (?*Pritchardia*), butterflies (*Allagoptera*), buzz-pollination (?*Areca*), chrysomelids (*Oenocarpus*), euglossines (*Geonoma*), flies (*Prestoea*), moths (*Calamus*), nitidulids (many genera), non-flying mammals (*Eugeissona*), scarabs (*Bactris*), self-pollination (?*Johannesteijsmannia*), staphylinids (*Phytelephas*), thrips (*Chamaedorea*), wasps (*Sabal*), weevils (many genera), and wind

(*Howea*). However, about 86% of the sample of palms reviewed here have either bee/fly or beetle pollination, and there appear to have been constant bidirectional shifts between the two. In summary, pollination in palms is extremely complex and we still know little about it.

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The data used to write this article are available on Zenodo (https://zenodo.org).

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