

A Review of Naturally Occurring Hybrids in Palms (Arecaceae)

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A review of the literature on naturally occurring hybrids in palms is presented. Approximately 114 instances of putative hybridization were found. Hybridization in palms appears to be relatively uncommon, although it may be under-reported. Within the family, there is a preponderance of records from two, taxonomically distant tribes: Trachycarpeae (Coryphoideae) and Cocoseae (Arecoideae). There does not appear to be any association between hybrids and habitat, region or morphology. Hybrids can be problematic in systematic studies, and their identification based on morphological data is challenging. There are very few polyploids in palms, and these do not appear to be a result of hybridization.

Hybrids are the result of sexual reproduction between two different taxa, usually congeneric species or subspecific taxa but sometimes between species from different genera. As such they may be isolated occurrences with no particular consequences. However, by repeated hybridization, alleles of one species may be incorporated into another (introgression). Sometimes large populations of hybrids, or hybrid zones, can form between two different, adjacent taxa. The processes of introgression and formation of hybrid zones have significant evolutionary consequences and have played a major role in the evolution of several plant families (Reiseberg & Wendel 1993).

Polyploidy, the heritable increase in genome copy number, commonly occurs in plants and may be derived from the same species (autopolyploidy), or, more often, from hybridization between different species (allopolyploidy). Wood et al. (2009) considered that most, or possibly all, plant species

ultimately had a polyploid ancestry. It is estimated that 15% of angiosperm speciation events were accompanied by ploidy increase (Soltis et al. 2007). It is also estimated that from one half to two-thirds of flowering plants are polyploids, including about 80% of the species in the grass family (Levy & Feldman, 2002, Soltis & Soltis 2009).

The goal of this paper is to review the literature on naturally occurring hybrids in palms and then to use the results to discuss several topics: the extent of hybridization in palms and the distribution of hybrids amongst subfamilies, tribes and subtribes; the association between hybrids and habitat, region or morphology; the implications of hybridization for palm systematics, both for revisionary and phylogenetic studies; and the role of hybrids in speciation of palms, particularly in ploidy levels.

Materials and Methods

A survey of the relevant literature on palms was carried out, and the results presented according to the most recent classification of the family (POWO 2022). In a few cases, personal observations from researchers were

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1. *Coccothrinax argentata* x *Leucothrinax morrisii* on Big Pine Key, Florida. Photo by Paul Craft.



2. *Coccothrinax macroglossa* x *C. pseudorigida* in Camagüey, Cuba. Photo by D.R. Hodel.



3. *Coccothrinax crinita* subsp. *brevicrinis* (left), *C. x angelae* (center) and *C. miraguama* subsp. *roseocarpa* (right). Photo by Paul Craft.

included. Numbers of species per genus and nomenclature were taken from POWO (2022) or from the most recent monographs, and distributions were taken from Dransfield et al. (2008). References to cultivated palms were omitted because there are so many of them and they are not directly related to the subject. Many of the hybrids reported here are somewhat anecdotal and based on little data and are often referred to as possible hybrids or potential hybrids. All published reports are here assumed to represent actual hybrids regardless of their level of supporting data. Genera for which no natural hybrids are known are listed in Appendix 1.

Results

CALAMOIDEAE

CALAMEAE, METROXYLINAE

The subtribe comprises one genus (*Metroxylon*, 7 species) distributed in the Asian tropics. McClatchey (1998) reported that, on Samoa, two species (*M. paulcoxii* and *M. warburgii*) were sympatric and that one specimen might be a hybrid between the two. However, the sympatry of the two species was possibly an artifact of human activity.

CALAMEAE, CALAMINAE

The subtribe comprises one genus (*Calamus*, 411 species) widely distributed throughout the

Asian tropics with one species in Africa. Henderson (2020a) reported one possible naturally occurring hybrid, involving *C. bacularis* and *C. myriacanthus*, and a few, other potential cases (*C. javensis* and *C. tenempokensis*; *C. leloi* and an unknown species; *C. insignis* and *C. longiusculus*).

CORYPHOIDEAE

SABALEAE

The tribe comprises one genus (*Sabal*, 16 species) distributed in Central America and the Caribbean. In one of the most detailed studies of hybridization in palms, Goldman et al. (2011), using molecular data (AFLPs), considered that a population of *Sabal* in Texas was a hybrid between *S. minor* and *S. palmetto* (*S. x brazoriensis*). They postulated that the initial hybridization event could have taken place thousands of years ago when the geographic distribution of the parent species was different. They considered it possible that caulescent plants of *S. minor* as well as *S. x brazoriensis* could represent an extensive regional hybrid swarm between acaulescent *S. minor* and *S. palmetto* (see also Simpson 1988). Their data also suggested that a Mexican sample of *S. minor* showed evidence of introgression with *S. mexicana*.

CRYOSOPHILEAE

The tribe comprises 11 genera (*Schippia*, 1 species; *Trithrinax*, 3 species; *Zombia*, 1 species;



4 (left). *Copernicia* × *vesperillum* in Sancti Spíritus, Cuba. 5 (right). *Copernicia* × *sueruana* in Las Tunas, Cuba. Photos by Paul Craft.

Coccothrinax, 56 species; *Hemithrinax*, 3 species; *Leucothrinax*, 1 species; *Thrinax*, 3 species; *Chelyocarpus*, 3 species; *Cryosophila*, 10 species; *Itaya*, 1 species; *Sabinaria*, 1 species) distributed throughout the Neotropics.

Naturally occurring intergeneric hybrids between *Coccothrinax* and *Thrinax* have been reported from the Florida Keys (Nauman 1989, 1990) (Fig. 1). These hybrids were found to be sterile.

In *Coccothrinax*, hybridization is common amongst cultivated species (particularly in botanical gardens), and there appear to be several naturally occurring hybrids in Cuba (Craft 2017). Craft considered that *C. orientalis* and *C. pauciramosa* could hybridize, and also *C. macroglossa* and *C. pseudorigida* (Fig. 2). Suárez Oropesa (2015), based on morphological data, described a naturally occurring hybrid from Cuba between *C. crinita* and *C. miraguama* as *C. × angela* (Fig. 3).

PHOENICEAE

The tribe comprises one genus (*Phoenix*, 13 species) widely occurring in Old World tropical and subtropical areas. The species are well-known to hybridize freely in cultivation (Dransfield et al. 2008, Gros-Balthazard 2013).

González-Peréz et al. (2004), using molecular data (RAPD markers) reported that on the Canary Islands, the naturally occurring *P. canariensis* hybridized with the introduced *P. dactylifera*. Pérez-Escobar et al. (2021) discussed the ancient hybrid origin of the date palm, *P. dactylifera*. They considered that its evolution was influenced by gene flow from two wild relatives, *P. theophrasti*, currently restricted to Crete and Turkey, and *P. sylvestris*, widespread from Bangladesh to the West Himalayas (see also Flowers et al. 2019).

TRACHYCARPEAE, LIVISTONINAE

The subtribe comprises six genera (*Livistona*, 28 species; *Licuala*, 167 species; *Lanonia* 13 species; *Johannesteijsmannia*, 4 species; *Pholidocarpus*, 6 species; *Saribus*, 9 species) distributed throughout the Asian tropics and subtropics and just reaching north-east Africa.

There are several anecdotal reports of hybridization in *Livistona* in Australia. Tucker (1975) reported a natural hybrid between *L. australis* and *L. humilis*. Dowe (2009) considered that the ranges of *L. australis* and *L. decora* overlapped in some areas and there could be hybridization between the two. Rodd (1998) mentioned possible hybrids between *L.*



6. *Copernicia* × *shaferi* in Camagüey, Cuba. Photo by D.R. Hodel.

humilis and *L. inermis* and considered it possible that *L. leichhardtii* hybridized with *L. lorophylla* and *L. mariae*. Henderson and Nguyen Quoc Dung (2019) considered that *L. jenkinsiana* and *L. saribus* formed hybrids in northern Vietnam.

Miyamoto et al. (2006) studied a population of *Licuala* at a site in lowland rainforest in Brunei, using morphological and molecular data. They considered that intermediate plants between *L. paludosa* and *L. bruneiana* could be hybrids between the two species.

Bacon et al. (2016a) found no evidence of hybridization between *Johannesteijsmannia* species, despite the species occurring in close proximity in Peninsular Malaysia.

UNPLACED GENERA OF TRACHYCARPEAE

This group comprises seven genera (*Acoelorrhapha*, 1 species; *Serenoa*, 1 species; *Brahea*, 11 species; *Colpothrinax*, 3 species; *Copernicia*, 22 species; *Pritchardia*, 29 species; *Washingtonia*, 2 species) distributed in the New World tropical and subtropical regions, with the exception of the Pacific island *Pritchardia*.

Bacon et al. (2012a) considered that there was no evidence of hybridization in *Brahea*. Ramírez-Rodríguez et al. (2011, 2012), based on morphological and molecular data, showed

evidence of hybridization between *B. dulcis* and *B. calcarea* in Mexico.

Six naturally occurring hybrids were reported in *Copernicia* from Cuba by Dahlgren and Glassman (1963): *C. × vespertilionum* (Fig. 4), *C. × sueroana* (Fig. 5), *C. × burretiana*, *C. × shaferi* (Fig. 6), *C. × textilis*, and *C. × occidentalis*. Moya López et al. (2019) accepted a seventh species, *C. × escarzana*. The widely distributed *C. hospita* is a parent of five of these hybrids. Other species such as *C. curbeloi*, *C. longiglossa* and *C. molinetii*, may also be of hybrid origin, as well as *C. oxycalyx* (Craft 2017). Craft noted that most hybrids occurred in central and eastern Cuba, where species of *Copernicia* occurred in close proximity (see also Moya López & Mayotte 1996). In some places large numbers of hybrids occurred. Verdecia Pérez (2016), based on morphological data, described a natural hybrid, *C. × dahlgreniana*, in Cuba with intermediate characteristics of *C. cowellii* and *C. macroglossa*. Most species of *Copernicia* are endemic to Cuba and the common occurrence of hybridization has been a challenge for taxonomic revisions.

For *Pritchardia*, Hodel (1980) reported that species freely hybridized in cultivation, although Hodel (2007a) did not report any naturally occurring hybrids. He noted that species seldom occurred sympatrically. Bacon

et al. (2012b) noted the difficulty of delimiting sympatric Hawaiian species because of their similarity due to recent divergence and their phenotypic plasticity. They suggested that hybridization had played an important role in the diversification of species from regions of sympatry, for example in Kauai (*P. flynnii*, *P. napaliensis*, *P. minor*, *P. waialealeana* and *P. viscosa*) and Oahu (*P. bakeri*, *P. kahukuensis* and *P. martii*).

CARYOTEAE

The tribe comprises three genera (*Arenga*, 24 species; *Caryota*, 14 species; *Wallichia*, 8 species) widely distributed in the Asian tropics.

Whitmore (1998) described “hybrid swarms” in Peninsular Malaysia between *Arenga westerhoutii* and *A. pinnata*, although he considered the latter to be introduced to the region.

Hahn (1993) suggested that *Caryota sympetala* was of hybrid origin, an idea not supported by Jeanson (2011). Hahn and Sytsma (1999) considered that there were several instances of hybridization in *Caryota*, including between sympatric species from the Philippines (*C. cumingii* and *C. rumphiana*; *C. cumingii* and *C. mitis*) and from Vietnam (*C. monostachya* and *C. maxima*).

Henderson (2007) proposed that one specimen of *Wallichia* could be a hybrid between *W. marianneae* and *W. caryotoides*, but this specimen was determined as *W. gracilis* by Jeanson (2011).

CEROXYLOIDEAE

CEROXYLEAE

The tribe comprises four genera (*Ceroxylon*, 12 species; *Juania*, 1 species; *Oraniopsis*, 1 species; *Ravena* 22 species) distributed in South America, Madagascar, Australia, and Juan Fernandez.

María José Sanín (pers. comm.) reported isolated individuals of *Ceroxylon* in Colombia being morphologically intermediate between *C. quindiuense* and *C. parvifrons*, *C. quindiuense* and *C. alpinum*, and *C. quindiuense* and *C. vogelianum*. In Peru, a population of individuals appeared intermediate between *C. peruvianum* and *C. echinulatum*.

PHYTELEPHEAE

The subtribe comprises three genera (*Ammandra*, 1 species; *Aphandra*, 1 species;

Phytelephas, 6 species) distributed in the Neotropics.

Barfod (1991) considered that *Phytelephas seemannii* subsp. *brevipes* from Panama was similar to *P. macrocarpa* subsp. *schottii* and could a hybrid between *P. seemannii* and *P. macrocarpa*.

ARECOIDEAE

IRIARTEAE

The tribe comprises five genera (*Iriartella*, 2 species; *Dictyocaryum*, 3 species; *Iriarte*, 1 species; *Socratea*, 5 species; *Wettinia*, 22 species) widely distributed in the Neotropics.

Bacon et al. (2016b) considered that in Colombia there was high potential for hybridization between the widely distributed *Wettinia kalbreyeri* and the more narrowly distributed *W. disticha*. Galeano and Bernal (2010) considered that *W. oxycarpa* could be a natural hybrid between *W. quinarina* and *W. kalbreyeri*.

CHAMAEDOREAE

The tribe comprises five genera (*Hyophorbe*, 5 species; *Wendlandiella*, 1 species; *Synechanthus*, 3 species; *Chamaedorea*, 104 species; *Gaussia*, 5 species) widely distributed in the Neotropics, with the exception of *Hyophorbe* from the Mascarene Islands. There are no records of natural hybrids in the tribe. Hybrids between species of *Hyophorbe* are common in cultivation (e.g., Hung & Pan 2014; see also Maunder et al. 2002). Hodel (1992) considered that natural hybrids probably did not occur in *Chamaedorea*, although several artificial hybrids are known from cultivation.

COCOSEAE, ATTALEINAE

The subtribe comprises 10 genera (*Beccariophoenix*, 3 species; *Jubaeopsis*, 1 species; *Voanioala*, 1 species; *Allagoptera*, 6 species; *Attalea*, 30 species; *Butia*, 22 species; *Cocos*, 1 species; *Jubaea*, 1 species; *Syagrus*, 67 species; *Parajubaea* 3 species) widely distributed in the Neotropics, southern Africa, and Madagascar.

Noblick (2017) reported a hybrid between *Butia odorata* and *Syagrus romanzoffiana*, × *Butyagrus nabonmandii*. This cross was first made from cultivated plants in Europe in the 19th century but was later found to occur naturally in Uruguay.

Moraes (1996) considered that there might be hybrids between *Allagoptera campestris* and *A.*



Fig. 7. *Attalea piassabossu* in eastern Brazil. Photo by L. Noblick.

leucocalyx in areas where the two species overlapped, and from where intermediate specimens are known.

Henderson (2020b) considered that in at least half of the 30 species of *Attalea* there was evidence of hybridization, including single instances of hybrids as well as large scale hybrid zones. Hybrids greatly complicated the taxonomy of the genus. Some of the most detailed studies of hybrids in *Attalea*, based on morphological data, were carried out by Michael Balick and colleagues (e.g., Balick et al. 1987a, 1987b; see also Anderson & Balick 1988). The following hybrids have been postulated (Henderson 2020b; see also Pinheiro 1997): *A. × minarum*, *A. × teixeriana*, *A. piassabossu* (Fig. 7), *A. × voeksii*, *A. camopiensis*, *A. degranvillei*, (*A. maripa* × ?*A. guianensis*), *A. salvadorensis*, *A. dahlgreniana*, (*A. nucifera* × *A. butyracea*) and (*A. sagotii* × *A. barreirensis*).

Gaiero et al. (2011) studied genetic diversity in four species of *Butia* in Uruguay, *B. lallemantii*, *B. paraguayensis*, *B. yatay* and *B. capitata*. They found that variability within populations was high, possibly due to gene flow, past hybridization or life history traits. In particular, they considered that current or recent hybridization between *B. lallemantii* and *B. paraguayensis* could explain the high number of admixed genotypes observed in both species. Brussa and Grela (2007) considered that *B. lallemantii* and *Syagrus romanzoffiana* formed hybrids in Uruguay. They also listed × *Butyagrus nabonandii* as occurring naturally in riverine forests and hills in eastern Uruguay. Engels et al. (2021) described a new hybrid between *B. eriospatha* and *S. romanzoffiana*, which they called × *Butyagrus paranaensis*. It occurred in forests in the central-south region of Paraná state, Brazil. Soares et al. (2014) described × *Butyagrus alegretensis* from southern Brazil, a hybrid between *B. lallemantii* and *S. romanzoffiana*. Noblick (2014) suspected hybridization between *B. paraguayensis* and *B. yatay* along the Paraná River, which defines part of the border between Paraguay and Argentina.

Hodel (2011) discussed *Syagrus* hybrids in both cultivation and the wild. Noblick (2017) recognized 14 naturally occurring hybrids in *Syagrus*, mostly from eastern Brazil. He considered that hybrids had a low frequency of occurrence and were often characterized by low fruit production, low seed germination

and by hybrid vigor, making the hybrid more robust than either of its parents. Some species were remarkably promiscuous. *Syagrus coronata* formed hybrids with several other species, including *S. vagans*, *S. microphylla*, *S. schizophylla*, *S. botryophora* and *S. romanzoffiana*. *Syagrus romanzoffiana* formed hybrids with other species including *S. coronata*, *S. flexuosa*, *S. oleracea* and *S. glaucescens*. Noblick (2017) recognized the following hybrids: *S. × lacerdamourae*, *S. × costae*, *S. × campos-portoana*, *S. × mirandana*, *S. × tostana*, *S. × matafome*, *S. × andrequeicana*, *S. × serroana*, (*S. loefgrenii* × *S. romanzoffiana*), *S. × teixeiriana*, *S. × altopalacioensis*, (*S. pleioclada* × *S. glaucescens*), *S. × cipoensis* and (*S. comosa* × *S. elata*).

COCOSEAE, BACTRIDINAE

The subtribe comprises five genera (*Acrocomia*, 9 species; *Astrocaryum*, 39 species; *Aiphanes*, 38 species; *Bactris*, 79 species; *Desmoncus*, 24 species), widely distributed throughout the Neotropics.

Wessels Boer (1971) described a hybrid, *Bactris × moorei*, between *B. acanthocarpa* and *B. oligoclada* in Venezuela. Henderson (2000) reported several hybrids in *Bactris*: (*B. mexicana* × *B. gracilior*), (*B. acanthocarpa* × unknown species), (*B. barronis* × *B. gasipaes*), (*B. brongniartii* × *B. major*), (*B. caudata* × *B. coloradonis*), (*B. corossilla* × *B. maraja*), (*B. setulosa* × *B. major*) and (*B. setiflora* × *B. corossilla*). Couvreur et al. (2006) reported possible hybrids between wild and cultivated *B. gasipaes* in western Ecuador.

Henderson (2011a) reported that several, suspected hybrids were present amongst specimens of *Desmoncus*. Most of these involved *D. polyacanthos*, the most widespread and variable species, and either *D. pumilus*, *D. mitis* or *D. horridus*. All hybrids came from the central and western Amazon region, and none occurred in other regions: (*D. polyacanthos* × *D. horridus*), (*D. leptoclonos* × unknown species), (*D. polyacanthos* × *D. mitis*), (*D. parvulus* × unknown species) and (*D. polyacanthos* × *D. pumilus*).

EUTERPEAE

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

Henderson (2004) reported that therei were hybrids between subspecies of *Hyospathe*

elegans, and a possible hybrid zone between *H. elegans* and *H. pittieri* along eastern Andean slopes.

Pereira et al. (2022) found two geographical genetic groups in *Euterpe edulis* from the Atlantic Coastal Forest of Brazil, a northern and a southern group, with a region of hybridization in the contact zone.

Balick (1991) described a hybrid between *Oenocarpus bacaba* and *O. minor*, *O. × andersonii*, from a single locality near Manaus in Brazil. Balick (1988) reported on hybrids between *O. bataua* and *O. bacaba* in Colombia, and Henderson et al. (1995) listed hybrids between *O. bataua* and *O. bacaba* and *O. bataua* and *O. mapora*.

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).

Henderson (2005) reported hybrids between *Calyptrogyne trichostachys* and *C. brachystachys*, and between *C. panamensis* and *C. fortunensis*, and a possible hybrid zone in Central America between *C. brachystachys* and *C. ghiesbreghtiana*.

There are numerous sympatric species of *Geonoma* in Neotropical forests. Knudsen (1999), Borchsenius (2002), and Borchsenius et al. (2016) have shown how differences in phenology and floral scent contribute to reproductive isolation in sympatric species or forms. Henderson (2011b) reported numerous hybrids in *Geonoma*, including three possible hybrid zones. The most convincing of these was a hybrid zone in the northeastern Amazon region involving *G. deversa* and *G. leptospadix*. He also reported numerous hybrids between subspecies within species. Henderson reported the following interspecific hybrids, four of which involved the widespread *G. deversa*: (*G. deversa* × *G. brongniartii*), (*G. deversa* × *G. leptospadix*), (*G. deversa* × *G. occidentalis*), (*G. deversa* × *G. longivaginata*), (*G. poeppigiana* × *G. brongniartii*), (*G. camana* × *G. macrostachys*), (*G. elegans* × *G. pauciflora*), (*G. orbignyana* × *G. undata*), (*G. interrupta* × *G. pinnatifrons*), (*G. poeppigiana* × unknown species), (*G. pohliana* × *G. pauciflora*), (*G. schottiana* × *G. pauciflora*) and (*G. undata* × *G. trigona*).

ARECEAE, BASSELINIINAE

The subtribe comprises six genera (*Basselinia*, 14 species; *Burretio kentia*, 5 species;

Cyphophoenix, 4 species; *Cyphosperma*, 5 species; *Lepidorrhachis*, 1 species; *Physokentia*, 7 species), distributed in New Caledonia, Vanuatu, Fiji, the Solomon Islands, and the Bismarck Archipelago.

Pintaud (2006) reported on hybrids in *Basselinia* in disturbed forests in New Caledonia between *B. pancheri* and *B. gracilis* and between *B. pancheri* and *B. deplanchei*. In some areas *B. vestita* formed hybrids with *B. gracilis* and *B. pancheri*.

ARECEAE, LINOSPADICINAE

The subtribe comprises four genera (*Calyptrocalyx*, 27 species; *Linospadix*, 7 species; *Howea*, 2 species; *Laccospadix*, 1 species) distributed in the Moluccas, New Guinea, Australia, and Lord Howe Island.

Babik et al. (2009) and Hipperson et al. (2016) reported hybrids between *Howea belmoreana* and *H. forsteriana* on Lord Howe Island (Figs. 8 & Front Cover). However, they considered that gene flow between the two species was extremely limited.

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.

Adorador and Fernando (2017) considered that a population of *Oncosperma* on Samar Island in the Philippines could be of hybrid origin, although neither of the putative parents (*O. horridum* and *O. gracilipes*) occurs on Samar.

Ludwig (2006) reported that the allopatric distribution of *Acanthophoenix* meant that the possibility of hybridization in the wild was remote. However, she reported hybrids in plantations.

UNPLACED MEMBERS OF ARECEAE

The group comprises ten genera (*Bentinckia*, 2 species; *Clinostigma*, 11 species; *Cyrtostachys*, 7 species; *Dictyosperma*, 1 species; *Dransfieldia*, 1 species; *Heterospatha*, 39 species; *Hydriastele*, 39 species; *Iguanura*, 34 species; *Loxococcus*, 1 species; *Rhopaloblaste* 6 species) widely distributed throughout the Old World tropics.

Hodel (2007b) reported that a possible hybrid between *Clinostigma samoense* and *C. warburgii* occurred on Samoa.

Discussion

There are 180 currently recognized genera of palms. Naturally occurring hybrids have been



8. *Howea belmoreana* (front left), *H forsteriana* (front right) and putative hybrid (back left) on Lord Howe Island. Photo by W. Baker.

reported in 26 of these (14% of the total). However, of the 180 genera, 54 are monospecific and about 40 have few, allopatric species. This leaves about 90 genera having two or more species some of which are distributed sympatrically in which hybrids could potentially occur. Hybrids are reported in 29% of these genera.

There are about 2,533 currently recognized species of palms, and of these 26 are hybrid species (i.e., ones that have been officially described and currently recognized). These represent <1% of the total number of recognized species. About 114 instances of naturally occurring hybridization have been reviewed here. Because several of these have the same parent, only about 156 species (6% of the total number of recognized species) are involved in hybridization.

Hybrids are not evenly distributed amongst subfamilies, tribes and subtribes. At the subfamily level, most hybrids occur in the Arecoideae (73 hybrids, 64% of the total). However, there are many more species overall in the Arecoideae, about 50% of the total number of palm species. Fewer hybrids occur in the Coryphoideae (31 hybrids, 27% of the total), and fewer still in the Calamoideae (5 hybrids, 4% of total) and Ceroxyloideae (5 hybrids, 4% of total). At the tribal level, in the

Arecoideae there are 48 hybrids reported for the Cocoseae, 16 for the Geonomateae, 4 for the Euterpeae, 4 for the Areceae, and 1 for Iriarteae. The high number for the Cocoseae is based mostly on three genera in the subtribe Attaleinae (*Attalea*, *Butia*, *Syagrus*) and two in the subtribe Bactridinae (*Bactris*, *Desmoncus*). At the tribal level in the Coryphoideae, there are 20 hybrids reported for the Trachycarpeae, 4 each for the Cryosophileae and Caryoteae and 2 for the Sabaleae. The relatively high number for Trachycarpeae is based mostly on *Livistona* and *Copernicia*. Within genera it appears that the most widespread and variable species are more likely to form hybrids. Examples are *Attalea maripa* and *A. speciosa*, *Syagrus coronata* and *S. romanzoffiana*, *Bactris acanthocarpa* and *B. major*, *Desmoncus polyacanthos*, *Oenocarpus bacaba*, *Geonoma deversa*, *Sabal palmetto*, *Livistona australis* and *Copernicia hospita*.

Hybrids do not appear to be strongly connected with any particular habitat. Using the rather broad categorization of habitats of Henderson (2002)—lowland moist forests; montane moist forests; dry forests; grasslands, savannas and shrublands; and desert and xeric shrublands—most hybrids occur in lowland moist forests (55%), followed by dry forests (21%), and grasslands, savannas and shrublands (16%). Few hybrids are found in

montane moist forests (6%) or desert and xeric shrublands (2%). These are approximately the same percentages of habitat distribution for all species of palm.

Hybrids do not appear linked to any particular continent, region, or island, although the majority (83%) are from the Neotropics. Two neotropical areas have high numbers of hybrids: Cuba and eastern Brazil.

Hybrids do not seem to be associated with any particular aspect of morphology, such as stem type, inflorescence type or germination type (Henderson 2002), nor with any particular type of pollination (although pollinators are not recorded for most parent species).

Most hybrids reviewed here are reported by systematists who are revising genera based on herbarium specimens. Different systematists have different propensities to recognize hybrids. Hybrids are anyway difficult to detect from specimens and may be under-reported. They are usually postulated based on sympatry of putative parents and morphological intermediacy of putative hybrids. Furthermore, the sample size of most species in herbaria is extremely small compared with population size, and thus few hybrid specimens may be present in samples. Hybrids appear to be a limited problem for systematists. Most reported hybrids (about 70%) appear to be isolated occurrences and may have little significance. About 20 hybrids are said to be relatively widespread, and seven hybrid zones have been reported. Some genera certainly appear to be more problematic than others for systematists, for example *Attalea*, *Syagrus* and *Copernicia*. As yet there are no studies that address the problem of palm hybrids in inferring phylogenies.

Most of the hybrids reviewed here are presumed to be contemporary or recent events, and most studies are based on morphological data. Only a few studies are based on molecular data, and of these some have addressed ancient hybrid events. Molecular data will no doubt become the norm for investigating hybrids and in studying the role of hybridization, if any, in the formation of species complexes.

Polyploidy, the duplication of whole genomes, is thought to have occurred in virtually all lineages of angiosperms (Alix et al. 2017). However, polyploidy appears to be uncommon in palms. Barrett et al. (2019) found evidence for a whole genome duplication event early in the evolution of the family. In general, they found that an ascending dysploid series of

chromosome numbers (i.e., $2n = 26, 28, 30, 32, 34, 36$) appeared to be the predominant mode of chromosomal change in palms, rather than repeated evolution of polyploidy. Dransfield et al. (2008), in a review of chromosome numbers in palms, found that only four cases of polyploidy had been reliably reported, presumably all autopolyploids, and thus not involving hybridization (compared with estimates of 60–75% polyploids in monocotyledons in general, Keeler 1998). Two of the palm polyploidys (*Arenga caudata*, *Rhapis humilis*) were tetraploids in otherwise diploid genera. The remaining two were polyploids in monotypic genera in the subtribe Attaleinae; *Jubaeopsis* from South Africa ($2n = 160–200$) and *Voanioala* from Madagascar ($2n = \text{ca. } 600$), the latter having the highest chromosome number amongst the monocotyledons. Though not a polyploid, *Beccariophoenix*, another monotypic member of the Attaleinae from Madagascar, was also distinct in having a diploid count of $2n = 36$ as opposed to $2n = 32$ in the remaining species of the Attaleinae. Gunn et al. (2015) considered that genome size in the Attaleinae suggested that polyploidy also occurred in the neotropical *Allagoptera caudescens*. The unusual chromosome numbers in the subtribe Attaleinae are concentrated in the three genera (*Beccariophoenix*, *Jubaeopsis*, *Voanioala*) that occur outside the subtribe's principal distribution in the Neotropics. The remaining neotropical genera of the subtribe produce a high number of hybrids, particularly *Attalea*, *Butia* and *Syagrus*. The significance of this is unknown.

In summary, many of the records of naturally occurring hybrids appear somewhat anecdotal, and many seem to have been as a result of human disturbance. This review gives the general impression that congeners can hybridize if brought together artificially but seldom do so naturally. However, it is certainly possible that hybrids are under-reported. Just over half of all reported hybrids are from two tribes: Trachycarpeae and Cocoseae.

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LITERATURE CITED

ADORADOR, J.T. AND E.S. FERNANDO. 2017. Palms of Samar Island, Philippines. *Palms* 61: 161–195.

- ALIX, K., P.R. GÉRARD, T. SCHWARZACHER AND J.S. HESLOP-HARRISON. 2017. Polyploidy and interspecific hybridization: partners for adaptation, speciation and evolution in plants. *Annals of Botany* 120: 183–194.
- ANDERSON, A.B. AND M.J. BALICK, M. 1988. Taxonomy of the babassu complex (*Orbignya* spp.: Palmae). *Systematic Botany* 13: 32–50.
- BABIK, W., ET AL. 2009. How sympatric is speciation in the *Howea* palms of Lord Howe Island? *Molecular Ecology* 18: 3629–3638.
- BACON, C.D., W.J. BAKER AND M.P. SIMMONS. 2012a. Miocene dispersal drives island radiations in the palm tribe Trachycarpeae (Arecaceae). *Systematic Biology*. 61: 426–442.
- BACON, C.D., M.J. MCKENNA, M.P. SIMMONS AND W.L. WAGNER. 2012b. Evaluating multiple criteria for species delimitation: an empirical example using Hawaiian palms (Arecaceae: *Pritchardia*). *BMC Evolutionary Biology* 2012: 12–23.
- BACON, C.D., ET AL. 2016a. Species limits, geographical distribution and genetic diversity in *Johannesteijsmannia* (Arecaceae). *Botanical Journal of the Linnean Society* 182: 318–347.
- BACON, C.D., ET AL. 2016b. Phylogenetics of Iriarteeae (Arecaceae), cross-Andean disjunctions and convergence of clustered infructescence morphology in *Wettinia*. *Botanical Journal of the Linnean Society* 182: 272–286.
- BALICK, M.J. 1988. *Jessenia* and *Oenocarpus*: neotropical oil palms worthy of domestication. FAO Plant Production and Protection Paper 88. Rome.
- BALICK, M.J. 1991. A new hybrid palm from Amazonian Brazil, *Oenocarpus* × *andersonii*. *Boletim do Museu Paraense Emílio Goeldi* 7: 505–509.
- BALICK, M.J., A.B. ANDERSON AND J.T. MEDEIROS-COSTA. 1987a. Hybridization in the babassu palm complex. II. *Attalea compta* × *Orbignya oleifera* (Palmae). *Brittonia* 39: 26–36.
- BALICK, M.J., C.U.B. PINHEIRO AND A.B. ANDERSON. 1987b. Hybridization in the babassu palm complex: I. *Orbignya phalerata* × *O. eichleri*. *American Journal of Botany* 74: 1013–1032.
- BARFOD, A. 1991. A monographic study of the subfamily Phytelephantoideae (Arecaceae). *Opera Botanica* 105: 1–73.
- BARRETT, C., ET AL. 2019. Ancient polyploidy and genome evolution in palms. *Genome Biology and Evolution* 11: 1501–1511.
- BORCHSENIUS, F. 2002. Staggered flowering in four sympatric varieties of *Geonoma cuneata* (Palmae). *Biotropica* 34: 603–606.
- BORCHSENIUS, F., T. LOZADA AND J.T. KNUDSEN. 2016. Reproductive isolation of sympatric forms of the understory palm *Geonoma macrostachys* in western Amazonia. *Botanical Journal of the Linnean Society* 182: 398–410.
- BRUSSA, C.A. AND I. GRELA. 2007. Flora Arbórea del Uruguay. Con énfasis en las especies de Rivera y Tacuarembó. COFUSA.
- COUVREUR, T.L.P., ET AL. 2006. Close genetic proximity between cultivated and wild *Bactris gasipaes* Kunth revealed by microsatellite markers in Western Ecuador. *Genetic Resources and Crop Evolution* 53: 1361–1373.
- CRAFT, P. 2017. The Palms of Cuba. Palm Nut Pages, Florida.
- DAHLGREN, B.E. AND S.B. GLASSMAN. 1963. A revision of the genus *Copernicia*. 2. West Indian species. *Gentes Herbarum* 9: 43–232.
- DOWE, J.L. 2009. A taxonomic account of *Livistona* R.Br. (Arecaceae). *Gardens' Bulletin Singapore* 60: 185–344.
- DRANSFIELD, J., N.W. UHL, C.B. ASMUSSEN, W.J. BAKER, M.M. HARLEY AND C.E. LEWIS. 2008. *Genera Palmarum. The Evolution and Classification of Palms*. Kew Publishing, Royal Botanic Gardens, Kew, London, U.K.
- ENGELS, M.E., T.A. MEYER AND K.P. SOARES. 2021. A new × *Butyagrus* (Arecaceae) from the Brazilian South Plateau. *Hoehnea* 48: e412020.
- FLOWERS, J.M., ET AL. 2019. Cross-species hybridization and the origin of North African date palms. *PNAS* 116: 1651–1658.
- GAIERO, P., C. MAZZELLA, G. AGOSTINI, S. BERTOLAZZI AND M. ROSSATO. 2011. Genetic diversity among endangered Uruguayan populations of *Butia* Becc. species based on ISSR. *Plant Systematics and Evolution* 292: 105–116.
- GALEANO, G. AND R. BERNAL. 2010. Palms de Colombia. Guía de campo. Universidad Nacional de Colombia, Bogotá.
- GOLDMAN, D.H., M.R. KLOOSTER, M.P. GRIFFITH, M.F. FAY AND M.W. CHASE. 2011. A

- preliminary evaluation of the ancestry of a putative *Sabal* hybrid (Arecaceae: Coryphoideae), and the description of a new nothospecies, *Sabal* × *brazoriensis*. *Phytotaxa* 27: 8–25.
- GONZÁLEZ-PERÉZ, M.A., J. CAUJAPÉ-CASTELLS AND P.A. SOSA. 2004. Allozyme variation and structure of the Canarian endemic palm tree *Phoenix canariensis* (Arecaceae): implications for conservation. *Heredity* 93: 307–315.
- GROS-BALTHAZARD, M. 2013. Hybridization in the genus *Phoenix*. *Emirates Journal of Food and Agriculture* 25: 831–842.
- GUNN, B.F., ET AL. 2015. Ploidy and domestication are associated with genome size variation in palms. *American Journal of Botany* 102: 1625–1633.
- HAHN, W.J. 1993. Biosystematics and evolution of the genus *Caryota* (Palmae: Arecoideae). Ph.D. thesis, University of Wisconsin, Madison.
- HAHN, W.J. AND K.J. SYTSA. 1999. Molecular systematics and biogeography of the southeast Asian genus *Caryota* (Palmae). *Systematic Botany* 24: 558–580.
- HENDERSON, A. 2000. *Bactris* (Palmae). *Flora Neotropica Monograph* 79: 1–181.
- HENDERSON, A. 2002. Evolution and ecology of palms. New York Botanical Garden Press.
- HENDERSON, A. 2004. A multivariate analysis of *Hyospathe* (Palmae). *American Journal of Botany* 91: 953–965.
- HENDERSON, A. 2005. A multivariate study of *Calyptragnye* (Palmae). *Systematic Botany* 30: 60–83.
- HENDERSON, A. 2007. A revision of *Wallichia* (Palmae). *Taiwania* 52: 1–11.
- HENDERSON, A. 2011a. A revision of *Desmoncus* (Arecaceae). *Phytotaxa* 35: 1–88.
- HENDERSON, A. 2011b. A revision of *Geonoma* (Arecaceae). *Phytotaxa* 17: 1–271.
- HENDERSON, A. 2020a. A revision of *Calamus* (Arecaceae, Calamoideae, Calameae, Calaminae). *Phytotaxa* 445: 1–656.
- HENDERSON, A. 2020b. A revision of *Attalea* (Arecaceae, Arecoideae, Cocoseae, Attaleinae). *Phytotaxa* 444: 1–76.
- HENDERSON, A. AND NGUYEN QUOC DUNG. 2019. Palms of Vietnam. New York Botanical Garden.
- HENDERSON, A., G. GALEANO AND R. BERNAL. 1995. *A Field Guide to the Palms of the Americas*. Princeton University Press.
- HIPPERSON, H., ET AL. 2016. Ecological speciation in sympatric palms: 2. Pre- and post-zygotic isolation. *Journal of Evolutionary Biology* 29: 2143–2156.
- HODEL, D.R. 1980. Notes on *Pritchardia*. *Principes* 24: 65–81.
- HODEL, D.R. 1992. *Chamaedorea* Palms. The International Palm Society and Allen Press, Lawrence, Kansas.
- HODEL, D.R. 2007a. A review of the genus *Pritchardia*. *Palms* 51(suppl.): 1–53.
- HODEL, D.R. 2007b. Unravelling *Clinostigma* in Samoa. *Palms* 51: 11–29.
- HODEL, D. 2011. Hybrids in the genus *Syagrus*. *Palms* 55: 141–154.
- HUNG, S.F. AND F.J. PAN. 2014. Identifying the natural hybrid between *Hyophorbe verschaffeltii* and *H. lagenicaulis* by RAPD markers. *Journal of the Experimental Forest of National Taiwan University* 28: 123–130.
- JEANSON, M. 2011. Systematique de la tribu des Caryoteae (Arecaceae). Ph.D. thesis, Muséum national d'Histoire naturelle, Paris.
- KEELER, K.H. 1998. Population biology of intraspecific polyploidy in grasses, pp. 183–206, in CHEPLIK, G.P. (ed.) *Population Biology of Grasses*. Cambridge, Cambridge University Press.
- KNUDSEN, J.T. 1999. Floral scent differentiation among coflowering, sympatric species of *Geonoma* (Arecaceae). *Plant Species Biology* 14: 137–142.
- LEVY, A.A. AND M. FELDMAN. 2002. The impact of polyploidy on grass genome evolution. *Plant Physiology* 130: 1587–1593.
- LUDWIG, N. 2006. *Acanthophoenix* in Réunion, Mascarene Islands. *Palms* 50: 82–98.
- MAUNDER, M., ET AL. 2002. The decline and conservation management of the threatened endemic palms of the Mascarene Islands. *Oryx* 36: 56–65.
- MCCLATCHY, W. 1998. A new species of *Metroxylon* from western Samoa. *Novon* 8: 252–258.
- MIYAMOTO, J., M. NAKAYAMA, N.M. WATANABE AND E. SUZUKI. 2006. Genetic and morphological variation in *Licuala paludosa* Griff. and the

- related taxa in the Tasek Merimbun Heritage Park, Borneo. *Tropics* 15: 237–243.
- MORAES R., M. 1996. *Allagoptera* (Palmae). *Flora Neotropica Monograph* 73: 1–34.
- MOYA LÓPEZ, C.E. AND P.T. MAYOTTE. 1996. “Paradiso Principium” – A palm paradise in Cuba. *Principes* 40: 152–155.
- MOYA LÓPEZ, C.E., M.T. ROSABAL AND Y.H. RIVERO. 2019. Novedades en la distribución conocida de *Copernicia* × *escazana* (Arecaceae); implicaciones para la conservación. *Monteverdia* 12: 1–8.
- NAUMAN, C. 1989. Intergeneric hybridization between *Coccothrinax* Sargent and *Thrinax* Swartz (Palmae: Coryphoideae). *American Journal of Botany* 75: 195–196.
- NAUMAN, C. 1990. Intergeneric hybridization between *Coccothrinax* and *Thrinax* (Palmae: Coryphoideae). *Principes* 34: 191–198.
- NOBLICK, L.R. 2014. *Butia*: what we think we know about the genus. *The Palm Journal* 208: 5–23.
- NOBLICK, L.R. 2017. A revision of the genus *Syagrus* (Arecaceae). *Phytotaxa* 294: 1N262.
- PEREIRA, A.G., ET AL. 2022. Patterns of genetic diversity and structure of a threatened palm species (*Euterpe edulis* Arecaceae) from the Brazilian Atlantic Forest. *Heredity* 129:161–168.
- PÉREZ-ESCOBAR, O.A., ET AL. 2021. Molecular clocks and archeogenomics of a Late Period Egyptian date palm leaf reveal introgression from wild relatives and add timestamps on the domestication. *Molecular Biology and Evolution* 38: 4475–4492.
- PINHEIRO, C.U.B. 1997. Systematic and agroecological studies in the Attaleinae (Palmae). Ph.D. Thesis, City University of New York.
- PINTAUD, J.-C. 2006. The impact of forest disturbance on the palms of New Caledonia. *Palms* 50: 123–135.
- POWO 2022. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet; <http://www.plantsoftheworldonline.org/> Retrieved 25 September 2022.
- RAMÍREZ-RODRÍGUEZ, R., E. TOVAR-SÁNCHEZ, J. RAMÍREZ, K. FLORES AND V. RODRÍGUEZ. 2011. Introgressive hybridization between *Brahea dulcis* and *Brahea nitida* (Arecaceae) in Mexico: evidence from morphological and PCR-RAPD patterns. *Botany-Botanique* 89: 545–557.
- RAMÍREZ-RODRÍGUEZ, R., P. MUSSALI-GALANTE, H. QUERO AND E. TOVAR-SÁNCHEZ. 2012. Management and its relation to hybridization, clonality and genetic structure of the Mexican palm *Brahea dulcis*. *Forest Ecology and Management* 285: 92–100.
- RIESEBERG, L.H. AND J.F. WENDEL. 1993. Introgression and its consequences in plants, pp. 70–109, in HARRISON, R.G. (ed). *Hybrid Zones and the Evolutionary Process*. Oxford University Press, UK.
- RODD, A.N. 1998. Revision of *Livistona* (Arecaceae) in Australia. *Telopea* 8: 49–153.
- SIMPSON, B.J. 1988. A field guide to Texas trees. Texas Monthly Press, Austin, Texas.
- SOARES, K.P., S.J. LONGHI, L. WITECK NETO AND L.C. ASIS. 2014. Palmeiras (Arecaceae) no Rio Grande do Sul, Brasil. *Rodriguésia* 65: 113–139.
- SOLTIS, P.S. AND D.E. SOLTIS. 2009. The role of hybridization in plant speciation. *Annual Review of Plant Biology* 60: 561–588.
- SOLTIS D.E., ET AL. 2007. Autopolyploidy in angiosperms: Have we grossly underestimated the number of species? *Taxon* 56: 13–30.
- SUÁREZ OROPESA, D. 2015. *Coccothrinax* × *angelae* (Arecaceae), nuevo híbrido natural del género para Cuba. *Revista del Jardín Botánico Nacional, Universidad de la Habana* 36: 9–14.
- TUCKER, R. 1975. Letters. *Principes* 19: 115.
- VERDECIA PÉREZ, R. 2016. *Copernicia* × *dahlgreniana*, a new natural hybrid in the savannas of Camagüey, Cuba. *Palms* 60: 85–92.
- WESSELS BOER, J. 1971. *Bactris* × *moorei*, a hybrid in palms. *Acta Botanica Neerlandica* 20: 167–172.
- WHITMORE, T.C. 1998. *Palms of Malaya*. Second edition. White Lotus Press, Bangkok, Thailand.
- WOOD, T.E., N. TAKEBAYASHI, M.S. BARKER, I. MAYROSE, P.B. GREENSPOON AND L.H. RIESEBERG. 2009. The frequency of polyploid speciation in vascular plants. *PNAS* 106: 13875–13879.

Appendix 1. Taxa for which no natural hybrids have been reported.

CALAMOIDEAE	BORASSEAE, HYPHAENINAE
EUGEISSONEAE	<i>Bismarckia</i> , 1 sp.
<i>Eugeissona</i> , 6 spp.	<i>Satranala</i> , 1 sp.
LEPIDOCARYEAE, ANCISTROPHYLLINAE	<i>Hyphaene</i> , 8 spp.
<i>Oncocalamus</i> , 4 spp.	<i>Medemia</i> , 1 sp.
<i>Eremospatha</i> , 11 spp.	BORASSEAE, LATANIINAE
<i>Laccosperma</i> , 7 spp.	<i>Latania</i> , 3 spp.
LEPIDOCARYEAE, RAPHIINAE	<i>Lodoicea</i> , 1 sp.
<i>Raphia</i> , 22 spp.	<i>Borassodendron</i> , 2 spp.
LEPIDOCARYEAE, MAURITIINAE	<i>Borassus</i> , 5 spp.
<i>Mauritia</i> , 2 spp.	CEROXYLOIDEAE
<i>Mauritiella</i> , 4 spp.	CYCLOSPATHEAE
<i>Lepidocaryum</i> , 1 sp.	<i>Pseudophoenix</i> , 4 spp.
CALAMEAE, KORTHALSIINAE	ARECOIDEAE
<i>Korthalsia</i> , 28 spp.	PODOCOCCEAE
CALAMEAE, SALACCINAE	<i>Podococcus</i> , 2 spp.
<i>Eleiodoxa</i> , 1 sp.	ORANIEAE
<i>Salacca</i> , 23 spp.	<i>Orania</i> , 30 spp.
CALAMEAE, PIGAFETTINAE	SCLEROSPERMEAE
<i>Pigafetta</i> , 2 spp.	<i>Sclerosperma</i> , 3 spp.
CALAMEAE, PLECTOCOMIINAE	ROYSTONEAE
<i>Plectocomia</i> , 14 spp.	<i>Roystonea</i> , 10 spp.
<i>Myrialepis</i> , 1 sp.	REINHARDTIEAE
<i>Plectocomiopsis</i> , 6 spp.	<i>Reinhardtia</i> , 6 spp.
NYPOIDEAE	COCOSEAE, ELAEIDINAE
<i>Nypa</i> , 1 sp.	<i>Barcella</i> , 1 sp.
CORYPHOIDEAE	<i>Elaeis</i> , 2 spp.
TRACHYCARPEAE, RHAPIDINAE	MANICARIEAE
<i>Chamaerops</i> , 1 sp.	<i>Manicaria</i> , 2 spp.
<i>Guihaia</i> , 4 spp.	LEOPOLDINIEAE
<i>Trachycarpus</i> , 10 spp.	<i>Leopoldinia</i> , 3 spp.
<i>Rhapidophyllum</i> , 1 sp.	PELAGODOXEAE
<i>Maxburretia</i> , 3 spp.	<i>Pelagodoxa</i> , 2 spp.
<i>Rhapis</i> , 11 spp.	<i>Sommieria</i> , 1 sp.
CHUNIOPHOENICEAE	ARECEAE, ARCHONTOPHOENICINAE
<i>Chuniophoenix</i> , 3 spp.	<i>Actinorhytis</i> , 1 sp.
<i>Kerriodoxa</i> , 1 sp.	<i>Archontophoenix</i> , 6 spp.
<i>Nannorrhops</i> , 1 sp.	<i>Chambeyronia</i> , 9 spp.
<i>Tahina</i> , 1 sp.	
CORYPHEAE	
<i>Corypha</i> , 5 spp.	

Appendix 1. continued.

ARECEAE, ARECINAE

Areca, 47 spp.*Nenga*, 5 spp.*Pinanga*, 143 spp.*Adonidia*, 2 spp.*Balaka*, 10 spp.*Veitchia*, 11 spp.*Carpentaria*, 1 sp.

ARECEAE, CARPOXYLINAE

Carpoxylon, 1 sp.*Satakentia*, 1 sp.*Neoveitchia*, 2 spp.*Wodyetia*, 1 sp.*Drymophloeus*, 3 spp.*Normanbya*, 1 sp.*Brassiophoenix*, 2 spp.

ARECEAE, CLINOSPERMATINAE

Cyphokentia, 2 spp.*Clinosperma*, 4 spp.*Ptychococcus*, 2 spp.*Jailoloa*, 1 sp.*Manjekia*, 1 sp.

ARECEAE, DYP SIDINAE

Chrysalidocarpus, 54 spp.*Dypsis*, 106 spp.*Lemurophoenix*, 2 spp.*Marojejya*, 2 spp.*Masoala*, 2 spp.*Vonitra*, 10 spp.*Wallaceodoxa*, 1 sp.

ARECEAE, RHOPALOSTYLIDINAE

Rhopalostylis, 2 spp.*Hedyscepe*, 1 sp.

ARECEAE, VERSCHAFFELTIINAE

Nephrosperma, 1 sp.*Phoenicophorium*, 1 sp.

ARECEAE, PTYCHOSPERMATINAE

Ptychosperma, 29 spp.*Ponapea*, 4 spp.*Roscheria*, 1 sp.*Verschaffeltia*, 1 sp.