The palm family (Arecaceae): a microcosm of sexual system evolution

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Among the 416 angiosperm families, palms (Arecaceae) are striking in possessing almost all possible combinations of hermaphroditic and/or unisexual flowers, making them a particularly interesting subject for studies of the evolution of plant sexuality. The purpose of this review is to highlight the amazing diversity of sexual expression in palms with a view to proposing scenarios to explain the evolution of this character, drawing on the numerous advances that have been made over the last 20 years in palm systematics, ecology, developmental biology, phylogenetics and genomics. We provide an overview of the variability of sexual expression in palms, with illustrations of the associated morphological diversity and its significance to reproduction. We discuss the evolution of sexual systems using the most recent phylogenetic framework available for palms. Finally, we review advances made towards unravelling the genetic basis of sexual expression in palms. Our survey opens new perspectives for understanding how plant sexuality has evolved in angiosperms as a whole. © 2016 The Linnean Society of London, _Botanical Journal of the Linnean Society_, 2016, **182**, 376–388.

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INTRODUCTION

The diversity of reproductive structures and strategies in flowering plants has long fascinated botanists and evolutionary biologists. Reproductive systems in plants may relate to pollination, sexual expression in space and time, and mating (or breeding) systems, i.e. outcrossing vs. selfing (Barrett, 2010, 2013). The term 'sexual systems' (or sometimes sex systems) is employed to describe the spatial arrangement of sexes (both sexes in the same flower, in different flowers borne on the same plant or each sex on a different plant) (e.g. (Barrett, 1998; Charlesworth, 2006). Sexual expression in flowering plants is classically broken down into three main categories (hermaphroditism, dioecy and monoecy), with an additional minor category, often termed as

'polygamy' that defines various intermediate states between the first three groups. Hermaphroditism, in which all flowers bear functional male and female organs, is the most common situation in angiosperms. Dioecy, where male and female flowers are borne on different plants, is found in 6% of angiosperm species distributed across half of all families (Renner & Ricklefs, 1995). Monoecy, with male and female flowers borne on the same plant, has received less attention than hermaphroditism and dioecy. In a survey of various temperate and tropical floras, monoecy was estimated to occur in 3–19% of angiosperm species (de Jong, Shmida & Thuijsman, 2008). Darwin (1877) considered monoecy to be an adaptation to favour outcrossing due to greater spatial separation between pollen and stigmas, whereas dioecy guarantees that selfing will never occur. Renner & Ricklefs (1995) noted that monoecy, like dioecy, is often associated with abiotic pollination. In

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monoecious plants, outcrossing may be further favoured by temporal separation of the sexual phases, a state referred to as dichogamy.

Hermaphroditism is generally considered as the ancestral state in angiosperms, although neither the fossil record nor ancestral state reconstruction gives clear evidence for this (Endress & Doyle, 2009). Advantages of hermaphroditism include the sharing by male and female functions of costs for the production of non-sexual organs such as perianth and reward-producing structures involved in pollinator attraction, and the possibility of self-fertilization when pollen transfer is inefficient (Obbard, Harris & Pannell, 2006). Conversely, unisexual flowers allow dimorphism and consequently specialization in the number, shape, size and positioning of male and female flowers, with implications for pollination and fruiting in particular. Dioecy and monoecy are considered to be derived from hermaphroditism through pathways that may involve intermediate stages. The most likely pathway to explain the transition from hermaphroditism to monoecy is through andromonoecy (male and hermaphrodite flowers produced on the same plant) rather than gynomonoecy (female and hermaphrodite flowers produced on the same plant), as suggested by a sex allocation model (de Jong *et al.*, 2008) and corroborated by patterns of sexual systems changes in monocotyledons (Weiblen, Oyama & Donoghue, 2000). Various hypotheses have been proposed to account for the origin of dioecy in angiosperms, focusing on different drivers such as pollination mechanisms (Ashman, 2000), ecological factors (Vamosi, Otto & Barrett, 2003) and evolutionary pathways [reviewed by Barrett (2013) and Renner (2014)]. Two main evolutionary pathways have been suggested (Barrett, 2013). One involves monoecy and hypothesizes a gradual transition in the relative proportions of male and female flowers, eventually leading to sexual separation between male and female plants. Evidence for this pathway has been found in a few taxa. The other hypothetical pathway leading to dioecy in angiosperms proceeds through gynodioecy, which involves male sterility mutations, invasion of hermaphrodite populations by female individuals and further selection of the male. A phylogenetic analysis of dioecy in monocots suggested that dioecy probably evolved more often directly from hermaphroditism than from monoecy, meaning that monoecy would have evolved independently (Weiblen *et al.*, 2000).

Among the angiosperms, palms stand out as being particularly diverse in terms of sexual expression patterns in both space and time. The family comprises *c.* 2600 species (Baker & Dransfield, 2016; this issue), of which > 90% are found in tropical rainforests (Henderson, 2002; Couvreur, Forest & Baker, 2011). Palms are conspicuous, typically large-bodied organisms that often have a major ecological impact in the plant communities in which they occur (Couvreur & Baker, 2013). Although somewhat constrained by their relatively simple modular body plan, they display an impressive variability in the architectural design of their leaves, stems and floral parts (Tomlinson, 2006). In the flowers, male and female functions are often separated in various ways through space and time (Henderson, 2002), presumably to favour cross-pollination in association with the pollinating vectors (Henderson, 1986, 2002; Barfod, Hagen & Borchsenius, 2011). This variation in sexual systems, combined with the fact that there is a robust comprehensive phylogenetic framework (Baker *et al.*, 2009) available for the family, makes palms an appropriate group in which to explore hypotheses relating to the evolution of sexual strategies.

As a prelude to future research on sexual systems in palms and other angiosperms, we provide here a review of sexual expression across Arecaceae. We synthesize current knowledge of the variability of sexual expression in palms, in terms of morphology, space and time, and its developmental and genetic bases. Building on this information, we discuss putative pathways for the evolution of sexual expression in the family in its phylogenetic framework.

OVERVIEW OF SEXUAL EXPRESSION IN PALMS

SEXUAL EXPRESSION IN SPACE

In Fig. 1, we provide an overview of the proportions of the different types of sexual systems in palms. The genera considered in this study follow Palmweb (www.palmweb.org), a regularly updated online source of information on palms based largely on the universally acknowledged reference work *Genera Palmarum* (Dransfield *et al.*, 2008). The latter is therefore the backbone source of information throughout this review. The number of genera (188) has been reduced to 181 recently (Baker & Dransfield, 2016), but this difference does not significantly affect the proportions given hereafter. The number of genera and species follows Palmweb (www.palmweb.org). Hermaphroditism is found in 17% of species (16% of genera), monoecy in 52% of species (61% of genera) and dioecy in 30% of species (21% of genera). More rarely, combinations of bisexual and unisexual flowers are found on the same individual or on separate plants, a phenomenon often referred to as polygamy (Dransfield *et al.*, 2008; Kholia, 2009; Beentje, 2010). The spatial separation of male and
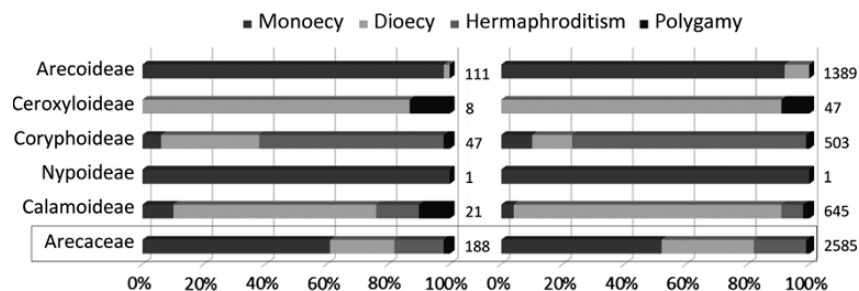
Figure 1. Genus- and species-level survey of sexual system in palms, at the family level (bottom line) and in each of the five subfamilies. Left-hand side: relative proportions of each of the four different sexual systems at the genus level, in percentages of the total number of genera. Right-hand side: relative proportions of each of the four different sexual systems at the species level, in percentages of the total number of species. Detailed numbers and proportions are given in Appendix 1.

female functions takes place at various structural levels: within flower clusters (between flowers); within inflorescences (between regions of the inflorescence); within individuals (between inflorescences) in some monoecious species; and within populations (between individuals) in dioecious species (Fig. 2).

Monoecy
The vast majority of monoecious palms occur in Arecoideae, the largest subfamily which contains more than half of all palm species. In this almost entirely monoecious clade, most species produce flowers gathered in triads or clusters derived from triads. The triad is a highly condensed sympodial flower cluster consisting of a female flower flanked by two male flowers (Fig. 2D, E) (Uhl, 1966, 1976). Male and female functions may be further separated by the production of fully developed triads at the base of the rachillae and only dyads of male flowers or single male flowers (interpreted as degenerate triads in which the female flower is lacking) present in the distal part. In large-fruited species, as found in tribe Cocoseae, this concentration of female flowers in the proximal end of the rachillae may have been selected as a cost-effective way to lend biomechanical strength to the infructescence. Outside Arecoideae, triads occur in tribe Caryoteae (subfamily Coryphoideae). In some monoecious genera, inflorescences may be unisexual by suppression of the expression of one sex in the triads, even though inflorescences of both sexes occur on the same plant [*Lepidorrhachis* (H.Wendl. & Drude) O.F.Cook, *Arenga* Labill. ex DC., *Caryota* L., *Wettinia* Poepp. ex Endl., *Marojejya* Humbert and *Elaeis* Jacq. (Baker & Hutton, 2006; Dransfield *et al.*, 2008)]. For example, in *Arenga* and *Caryota* the male flowers abort before anthesis in some inflorescences that become functionally female, whereas the female flower of the triad never develops in other inflorescences that become functionally male (Dransfield & Mogea, 1984; Basu & Basu, 1993;

Jeanson, 2011) (Fig. 2G). In *Elaeis guineensis* Jacq., these functionally unisexual inflorescences are produced in male and female cycles (Adam *et al.*, 2005). In Calamoideae, monoecy occurs only in *Raphia* P.Beauv. and *Oncocalamus* (G.Mann & H.Wendl.) H.Wendl., with both male and female flowers borne on each rachilla. In *Nypa fruticans* Wurmb, the only species in subfamily Nypoideae, the female flowers are borne on the club-shaped apex of the inflorescence and the male flowers are densely packed on rachillae borne on lateral branching systems (Fig. 2F).

Dioecy
Complete separation of sexes on different individuals is the predominant sexual system in Calamoideae and Ceroxyloideae. Remarkable arrangements occur in the ceroxyloid tribe Phytelepheae, in which four to nine male flowers are gathered in monopodial clusters densely inserted on spike-like inflorescences, and the solitary female flowers are spirally arranged on the club-shaped apex of the inflorescences (Barfod, 1991) (Fig. 2H). In the otherwise monoecious Arecoideae, tribe Chamaedoreeae is exceptional in containing the only two truly dioecious genera present in the subfamily, *Wendlandiella* Dammer and *Chamaedorea* Willd.

Hermaphroditism
Truly hermaphroditic palms are found mostly in Coryphoideae (e.g. Fig. 2A, B) and Calamoideae. *Pseudophoenix* H.Wendl. ex Sarg., the only non-dioecious genus in subfamily Ceroxyloideae, has hermaphroditic flowers on the proximal part of each rachilla. Of the three hermaphroditic genera of Calamoideae, *Eremospatha* (G.Mann & H.Wendl.) Schaedtler and *Laccosperma* (G.Mann & H.Wendl.) Druded (tribe Lepidocaryeae) bear flowers in dyads, whereas *Korthalsia* Blume (tribe Calameae) has solitary flowers.
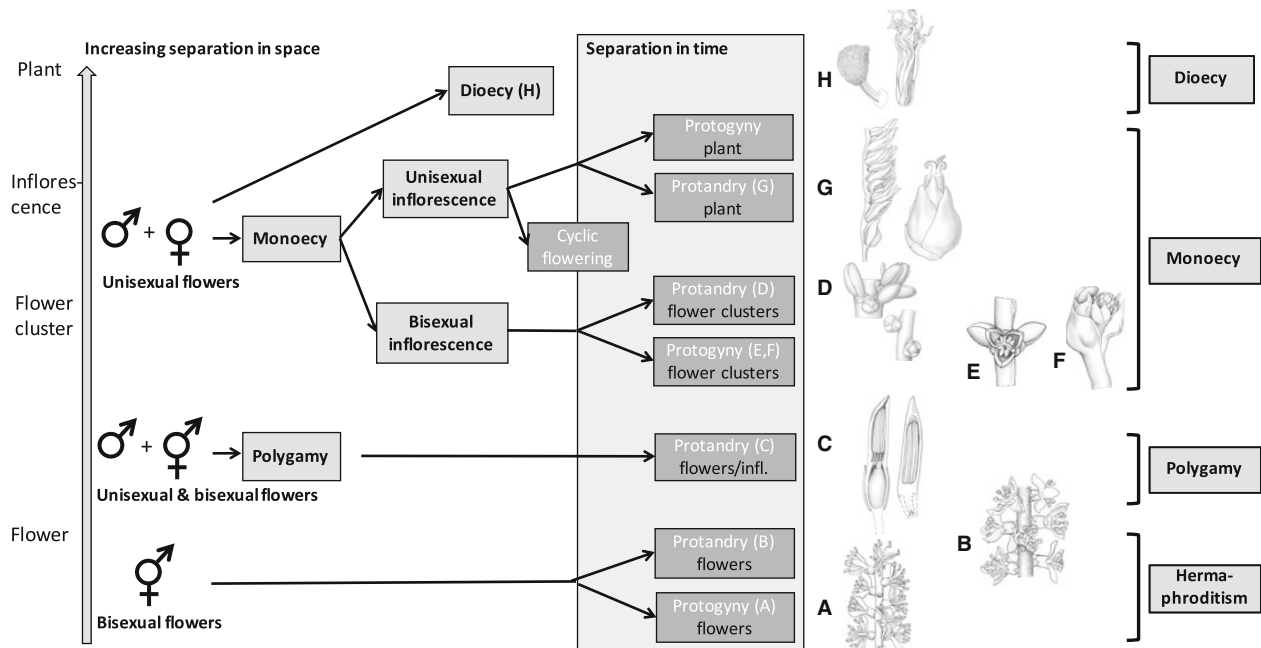
Figure 2. Diversity of sexual expression in palms. A, solitary hermaphroditic protogynous flowers of *Sabal palmetto*. B, hermaphroditic, weakly protandrous flowers of *Serenoa repens*. C, hermaphroditic (left) and male (right) flowers of *Eugeissona utilis* (andromonoecious protandrous species). D, (left) protandrous triad of two male flowers surrounding one female flower of *Dictyocaryum* sp. at male anthesis, and (right) triad of *Dictyocaryum fuscum* at female anthesis; the male flowers have fallen off. E, protogynous triad of two male flowers surrounding one female flower of *Reinhardtia simplex* at female anthesis. F, distal part of bisexual inflorescence of *Nypa fruticans* with lateral male branch on the left, next to the female head on the right. G, portions of rachillae bearing male (left) and female (right) flowers of *Attalea amygdalina*; in the congener *A. funifera* inflorescences usually bear flowers of one sex, and a shift occurs from male to female expression as the plants grow taller. H, staminate (left) and pistillate (right) inflorescences of the dioecious species *Phytelephas aequatorialis*. All the flowers in this figure are illustrated on relative scale. Artwork: Marion Ruff Sheehan. [Correction added on 25 August 2016, after first online publication on 11 June 2016: figure 2 and its legend were revised.]

Polygamy

A few unrelated palm genera, in Calamoideae and Coryphoideae (mainly in tribe Trachycarpeae), have complex combinations of bisexual and unisexual flowers, which are referred to collectively as 'polygamous' (Dransfield *et al.*, 2008). The two polygamous genera of Calamoideae, *Eugeissona* Griff. (tribe Eugeissoneae) and *Metroxylon* Rottb. (tribe Calameae), produce dyads composed of one male flower and one hermaphroditic flower, which corresponds to andromonoecy (Fig. 2C). In the otherwise dioecious genus *Rhapis* L.f. ex Aiton, a similar sexual system was found in *R. laosensis* Becc. [=*R. cochinchinensis* (Lour.) Mart.] (Giddey, Spichiger & Stauffer, 2009). Andromonoecy is not uncommon in flowering plants, occurring in *c*. 4000 species (Miller & Diggle, 2002).

PLASTICITY IN SEXUAL EXPRESSION

Little is known about sexual plasticity in angiosperms in general and palms are no exception, few detailed studies having been conducted apart from one on *Trachycarpus takil* Becc. (tribe Trachycarpeae), which revealed an unstable sexual system with age-related changes from mainly male expression to mainly female expression (Kholia, 2009). Environmentally dependent plasticity in the expression of male vs. female functions has been reported in two polygamous species of *Attalea* Kunth (tribe Cocoseae) (Voeks, 1988; Barot *et al.*, 2005). In *A. funifera* Mart., there is a shift from male to female expression as the plants grow taller and are more exposed to direct sunlight (Voeks, 1988). Changes in sexual expression are also commonly observed in the cyclical production of female and male inflorescences in African oil palm, *Elaeis guineensis* (Adam *et al.*, 2005). The length of these cycles is influenced by soil and light conditions, and consequently the female/male inflorescence ratio is a variable feature that reflects local abiotic conditions and affects yields in the plantation (Williams & Thomas, 1970; Freeman *et al.*, 1981). Male and female phases have also been recorded in *Marojejya* (Marcus, 2010), a member of tribe Areceae, like *Elaeis*.

Sexual expression in time

Temporal separation of sexual expression operates at various spatial levels: within the flower in the case of hermaphroditic species (dichogamy *sensu stricto*) (Fig. 2A–C); between flowers within flower clusters and between inflorescences within plants in the case of monoecious taxa (Fig. 2D–G); between plants; and even between populations in the case of dioecious taxa (Fig. 2H). In many palm inflorescences, sexual expression occurs in pulses or cycles, probably as an adaptation to the characteristics of the pollinating vector (Borchsenius, 1997; Henderson, 2002; Barfod, Burholt & Borchsenius, 2003). In palms bearing only hermaphroditic flowers, protandry (male organs mature before female organs) and protogyny (the opposite) can be found, protandry being more widespread (Dransfield *et al.*, 2008). The polarity of flower opening along inflorescence axes varies between species, as shown in *Licuala* Wurmb (Barfod *et al.*, 2003). In monoecious taxa, there is often a time difference in anthesis between male and female flowers within flower clusters. This applies, for example, to Arecoideae and Caryoteae, in which the majority of species have protandrous triads (Dransfield *et al.*, 2008) (Fig. 2D). This may be due to the architectural constraints of the triad, in which the female flower is last formed in the ontogenetic series, and therefore most likely to open last (Loo *et al.*, 2006). In many cases, the male and female antheses are separated by only a matter of days, whereas in others the development of the female flower is substantially delayed. In the wind-pollinated species of *Howea* Becc., an entire year elapses between male and female antheses, representing an extreme situation (Savolainen *et al.*, 2006; Babik *et al.*, 2009).

MORPHOLOGY OF SEXUAL EXPRESSION

Despite the huge variability of their sexual systems, the floral groundplan of palms contains few innovations with respect to the typical monocot groundplan. Palm flowers generally have an actinomorphic trimerous perianth, differentiated into calyx and corolla, and a superior ovary with a single ovule per locule. However, the flowers vary extensively among species in terms of size [from a few millimetres long in *Synechanthus warscewiczianus* H.Wendl. to several centimetres in *Aphandra natalia* (Balslev & A.J.Hend.) Barfod], organ numbers [from just one stamen in *Dypsis lantzeana* Baill. (Dransfield & Beentje, 1996; Rudall *et al.*, 2003) to > 1000 in *Ammandra decasperma* O.F.Cook (Barfod, 1991)] and organ fusion. Compared with other monocotyledonous taxa, the gynoecium structure is unusually variable, ranging mostly from three fused or free carpels to a single carpel (Uhl & Moore, 1971; Rudall, Ryder & Baker, 2011). In unisexual flowers non-functional reproductive organs (pistillode in male flowers and staminodes in female flowers) vary in their degree of differentiation and may sometimes be absent, this attribute having evolved repeatedly in the family. In addition to this variation, floral sexual dimorphism (referring here to the difference in appearance between male and female flowers) needs to be taken into account to fully appreciate the huge diversity of sexual expression (Fig. 3). Morphological differences between male and female flowers in palms concern size, shape and structural attributes. At one extreme, male and female flowers may be almost morphologically identical, as in some Australian species of *Livistona* R.Br. (Dowe, 2009), *Oncocalamus* and *Asterogyne* H.Wendl. ex Hook.f. (Dransfield *et al.*, 2008) (Fig. 3A, F). At the other extreme, they may be strongly dimorphic (Fig. 3D, G). In palms female flowers tend to be slightly larger than male flowers (Fig. 3B, C), but several groups display male flowers that are larger than the female ones (Fig. 3D). The most noticeable size contrast is observed in tribe Phytelepheae (Ceroxyloideae). In *Aphandra natalia*, the enormous and narrow female flowers are up to 25 cm long, whereas male flowers are ten times shorter, despite the huge number of stamens (*c.* 1000) densely packed on the enlarged floral receptacle (Barfod, 1991).

Selective pressures due to pollinator interactions may drive patterns of flower size in palms, as in other angiosperm taxa, in which differences in male and female flower sizes have been linked to attractiveness in animal-pollinated species, in relation to sexual selection theory (Willson, 1991; Kriebel, 2014). In four *Calamus* species from peninsular Thailand with presumed pollination by deceit (Boegh, 1996), a size difference between male and female flowers may have been counter-selected due to the behaviour of the pollinating bees that mainly collect pollen to nourish their brood. As these bees are attracted to inflorescences by visual cues and are able to detect and remember even minor morphological differences between male and female flowers (Barfod *et al.*, 2011), they would only visit male flowers if there was a difference in appearance. In some *Chamaedorea* species (Arecoideae), the pistillode of the male flower is larger than the gynoecium of the female flower and may play an important role in interactions with pollinating insects (Askgaard *et al.*, 2008).

A note on self-incompatibility

Palms are usually regarded as self-compatible, with no report to date of gametophytic or sporophytic
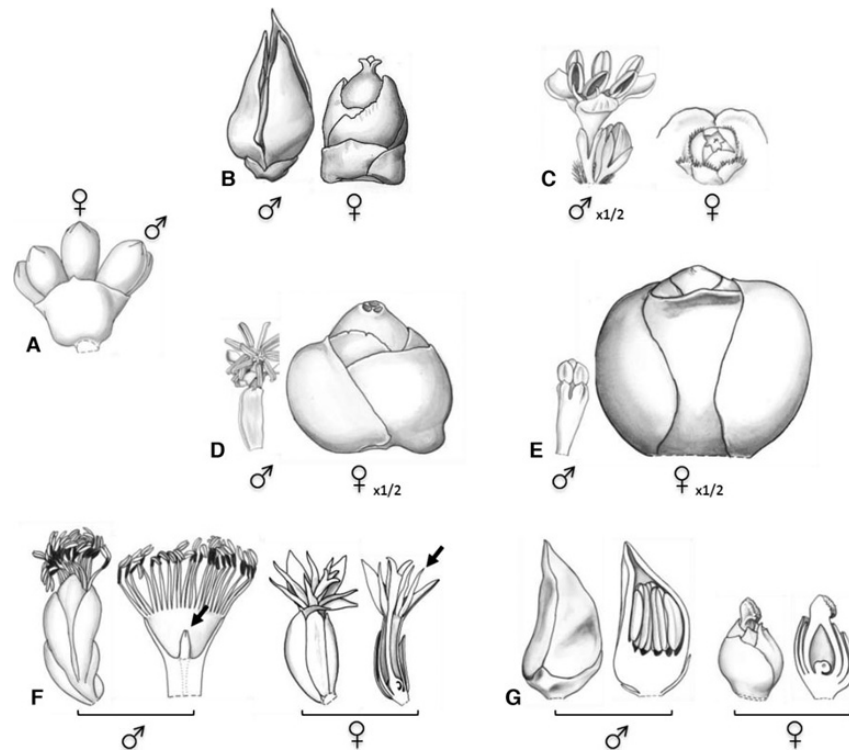
Figure 3. Illustration of the diversity of floral sexual dimorphism in palms. A, triad of *Oncocalamus macrospathus* with morphologically identical male and female (centre) flowers. B, male (left) and female (right) flowers of *Hydriastele chaunostachys*; female flowers are shorter than the male flowers. C, male (left) and female (right) flowers of *Hyphaene coriacea*; female flowers are shorter and rounder than the male flowers. D, male (left) and female (right) flowers of *Lodoicea maldivica*; female flowers are twice as long as the male flowers and rounder. E, male (left) and female (right) flowers of *Borassus aethiopum*; female flowers are four times longer than the male flowers and much rounder. F, male (left) and female (right) flowers of *Asterogyne spicata* with staminodes (arrow in female flower) similar in size (although in lower number) to stamens, and pistillode (arrow in male flower) similar in size to ovary. G, male (left) and female (right) flowers of *Pinanga coronata* with strong sexual dimorphism (no pistillode in male flowers, no staminodes in female flowers). Male and female flowers in each species are on relative scale. Artwork: Marion Ruff Sheehan.

self-incompatibility (Allen & Hiscock, 2008). However, it should be noted that few experiments have been conducted (Barfod *et al.*, 2011). Experience from horticulture indicates that hermaphroditic or monoecious palms can set fruit in cultivation, even when only single individuals are present in a particular garden. One notable exception is the Mauritian palm *Hyophorbe amaricaulis* Mart. (Maunder *et al.*, 2002), which is extinct in the wild and persists as a single individual in the botanic garden at Curepipe (Mauritius), where it fails to set viable fruit.

EVOLUTION OF SEXUAL EXPRESSION

Few hypotheses have been published that relate to the sexual system of the ancestral palm flower. It has been assumed that it is hermaphroditic (Moore & Uhl, 1982), perhaps because at the level of angiosperms as a whole monoecy and dioecy are considered as derived

conditions and end points of sexual system evolution (Barrett, 2013). There is evidence, however, that dioecy is not always an evolutionary dead-end and it can give rise to hermaphroditism (Case *et al.*, 2008). The predominance of monoecy and dioecy in palms (> 80% of the species) and the diversity of sexual systems in the early-diverging subfamilies raise questions about the ancestral sexual system of Arecaceae. Ancestral state reconstruction of this character conducted on an earlier version of the palm phylogenetic tree had resulted in an equivocal ancestral state (Weiblen *et al.*, 2000). Since then, considerable advances have been made in resolving phylogenetic relationships in the family, providing the opportunity to re-examine the evolution of sexual systems in a more detailed and robust framework. Using the comprehensive genus-level phylogenetic tree for Arecaceae (Baker *et al.*, 2009), we reconstructed the evolution of sexual systems in the family (Fig. 4A) and obtained a hypothetical evolutionary scenario for this character
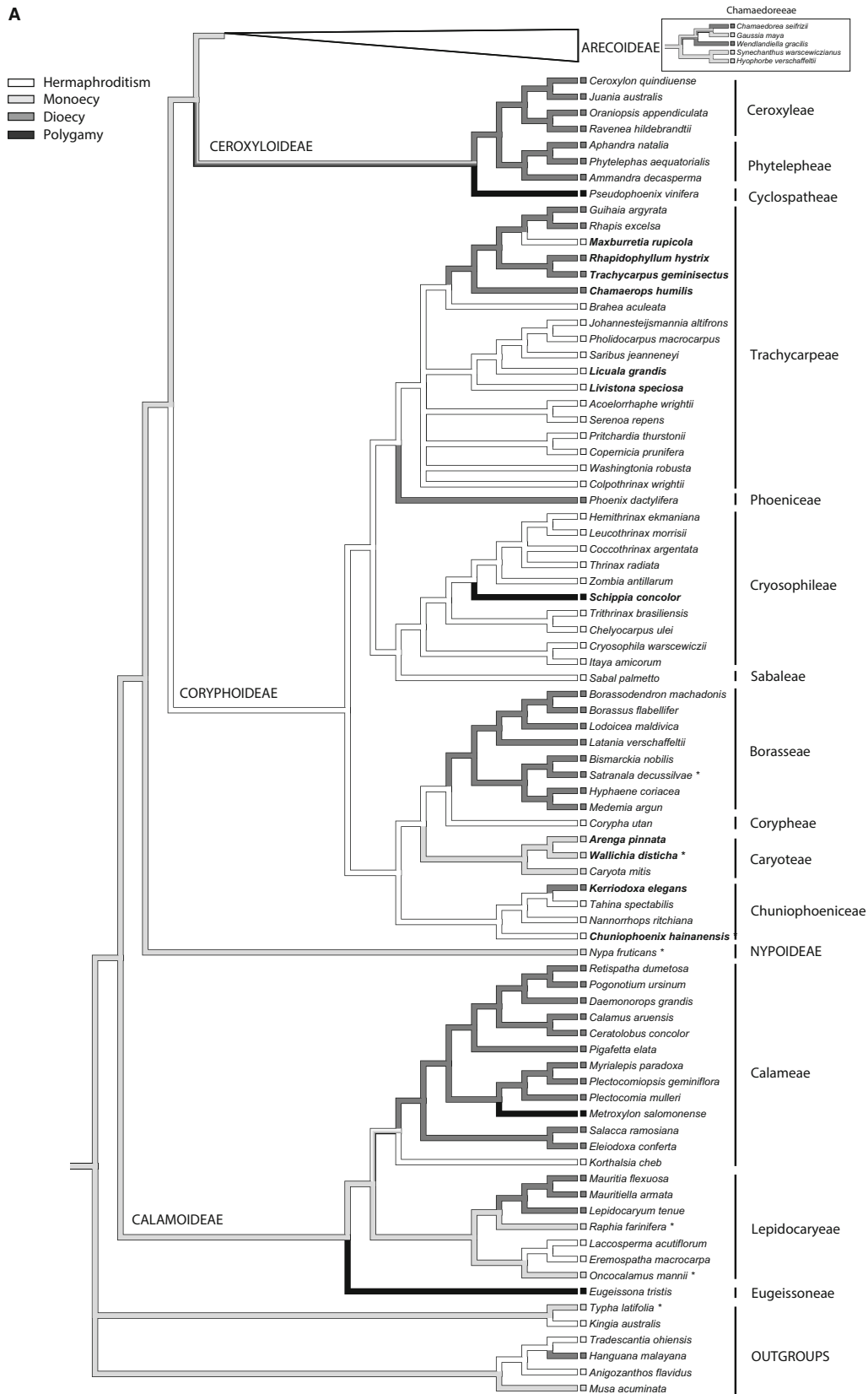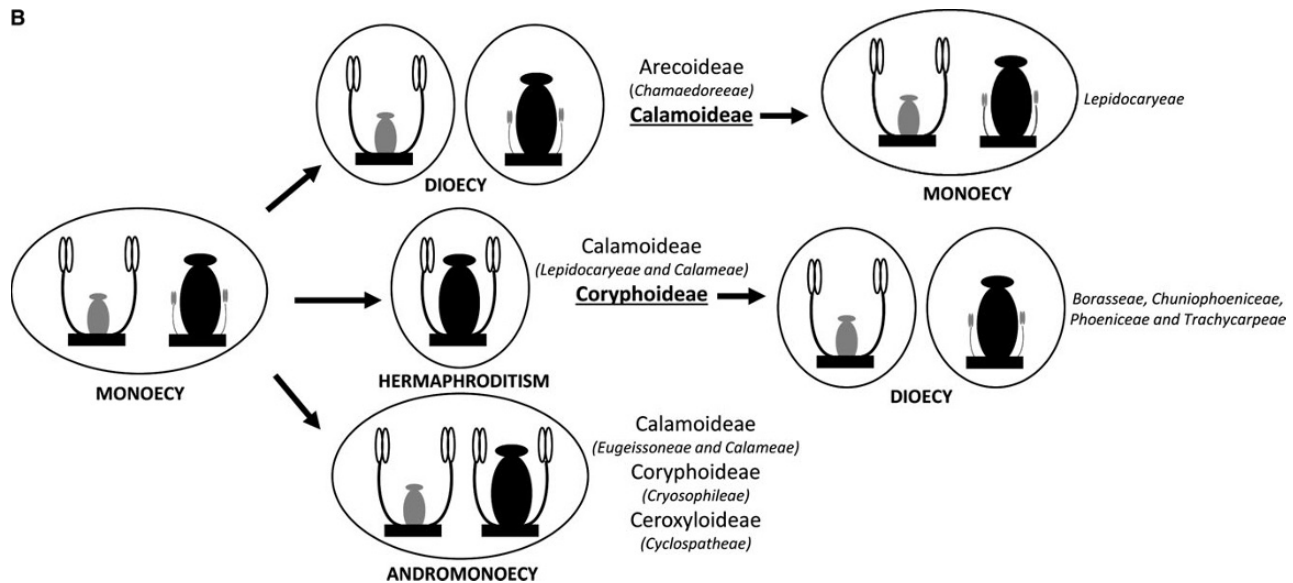
Figure 4.

B

Figure 4. Phylogenetic analysis of sexual systems evolution in palms. A, supertree from the analysis of Baker *et al.* (2009) showing the evolution of sexual systems in palms optimized using parsimony. In subfamily Arecoideae, all tribes except Chamaedoreeae are monoecious and the subfamily is therefore only represented by Chamaedoreeae in this tree. Boxes at the tips of branches are coloured according to the actual character state: white = hermaphroditism, light grey = monoecy, dark grey = dioecy, black = andromonoecy. Branch colours correspond to the inferred ancestral sate. Several colours on the same branch denote ambiguity in the ancestral state. The lack of both pistillode and staminodes is indicated by a star (in Arecoideae, this relates to three genera: *Iriartella*, *Pinanga* and *Sclerosperma*). The sexual system of the species used in the optimization is typical of the sexual system of the whole genus with exceptions, in which case the species name is in bold (in Arecoideae there is no polymorphism). Phylogenetic relationships and tribe names are according to Baker *et al.* (2009). B, scenario for the evolution of sexual systems in palms as suggested by the optimization shown in A. The tribes (italics) and subfamilies in which dioecy, hermaphroditism and andromonoecy (the most common type of polygamy) evolved are indicated on the right of each category. Subfamilies in which secondary transitions occur are underlined. Pistils are shown in black, pistillodes in grey. Stamens are shown in white, staminodes in grey.

(Fig. 4B). Both parsimony and maximum likelihood optimizations (Fig. 4A and Supporting Information, respectively; details of the methods used are given in Appendix 2) resulted in monoecy as the ancestral condition for the family, an unusual situation compared with the rest of angiosperms. From this state, dioecy and hermaphroditism were found to have evolved several times in the family, whereas polygamy evolved from dioecy, hermaphroditism or monoecy, suggesting a high degree of sexual flexibility during palm evolution. In the same scheme, dioecy was found to have evolved directly from monoecy in Arecoideae and Calamoideae and from hermaphroditism in Coryphoideae. Similarly, monoecy evolved secondarily from hermaphroditism in Coryphoideae. In Arecoideae, dioecy is found exclusively in tribe Chamaedoreeae and the strong similarities in sexual differentiation patterns between monoecious and dioecious species suggest that shared molecular mechanisms govern flower unisexuality (Castaño *et al.*, 2014). Considering the extraordinary diversity of spatial distribution

patterns seen for female and male flowers in the monoecious state, the question of whether this state is homologous between different clades of palms may be raised. Despite this apparent diversity, it should be noted that the basic unit of palm inflorescences is generally sympodial, with dyads, triads and acervuli representing different forms of cincinni (Uhl, 1988). It may actually require few evolutionary steps to switch from one form to another, supporting a homologous nature for the various forms of monoecy. The variable degree of sexual differentiation observed between male and female flowers of different clades (Fig. 3) would have been further selected in response to selection pressures related to pollination strategies (see 'Morphology of sexual expression' above).

ECOLOGICAL CORRELATES

General conclusions regarding the ecological correlates of sexual expression in palms, particularly with

respect to plant–pollinator interactions, should be drawn with caution due to the limited number of studies and the inherent complexity of plant–animal interactions (Barfod *et al.*, 2011). Only a few studies have demonstrated a link between temporal and/or spatial separation of sexual expression in palms and pollination strategies (Henderson, 2002). One example concerns the dioecious species *Phytelephas seemannii* O.F.Cook, in which sexual expression is displaced in the flowering population, typically with diurnal onset of male anthesis and nocturnal onset of female anthesis. Bernal & Ervik (1996) considered this to be an adaptation to minimize the competition for pollinators between male and female plants. Displacement of sexual expression has also been recorded on more extended time scales in the wind-pollinated monoecious palm *Howea forsteriana* (F.Muell.) Becc. In populations of this species, endemic to Lord Howe Island, the male flowering peak was found to occur 2 weeks before the peak of female receptivity (Savolainen *et al.*, 2006). This phenological difference was suggested to be linked to geology as it is not observed on all soil types (Savolainen *et al.*, 2006; Babik *et al.*, 2009).

GENETIC AND MOLECULAR BASIS OF SEXUAL SEPARATION

With regard to the temporal separation of male and female expression, no genes involved in dichogamy have as yet been identified in palms, or indeed in any angiosperms, although progress has been made in *Carya illinoinensis* (Wangenh.) K.Koch (Beedanagari *et al.*, 2005) through the identification of a genetic locus regulating this character. In the wider field of angiosperm flower and inflorescence development, much progress has been made in elucidating genetic determinants over the last two decades (Theissen & Melzer, 2007; Teo *et al.*, 2014). To date, the only member of Arecaceae for which functional studies of floral organ identity genes have been published is *Elaeis guineensis*, which appears to display a general conservation of the ABC model (Coen & Meyerowitz, 1991; Adam *et al.*, 2007). No palm sex determination genes have been reported to date, however, and even for angiosperms as a whole, this has only been achieved for monoecious *Zea mays* L. and *Cucumis melo* L. and for dioecious *Diospyros lotus* L. (Chuck *et al.*, 2007; Martin *et al.*, 2009; Akagi *et al.*, 2014). A major breakthrough was made for Arecaceae with the sequencing of the date palm (*Phoenix dactylifera* L.) genome (Al-Dous *et al.*, 2011; Al-Mssallem *et al.*, 2013). Microsatellite markers identified in the former study were tested for sex-linkage on a range of male and female palms (Cherif

et al., 2013; Zehdi-Azouzi *et al.*, 2015), allowing the characterization of three genetically linked loci that appear to be located on a Y-type sex chromosome. Further studies of the date palm genes present in this genomic region should allow identification of the molecular determinants of sex in this species. Clearly, it will be of great interest to compare data between different palm species with contrasting sexual systems, including species such as oil palm which display environmentally regulated sex determination (Adam *et al.*, 2011). In this context, the recently published oil palm genome (Singh *et al.*, 2013a, b) is an invaluable resource and has already been used to identify a genomic region of importance to sex regulation (Somyong *et al.*, 2015). The region in question contains a putative aldo-keto reductase gene that might be involved in abiotic stress response. At a physiological level, a possible role for hormones has been suggested for oil palm and date palm (e.g. Corley 1976; Masmoudi-Allouche *et al.*, 2009). These studies provide a mere hint of what may well be an important role for such molecules in palm sex determination.

SEXUAL EXPRESSION IN PALMS: IMMEDIATE AND LONG-TERM PROSPECTS

Exploring, cataloguing and understanding the great diversity of sexual expression in palms is a major challenge to researchers, but the rewards are likely to be equally great, both from a purely scientific point of view and also on account of the numerous economically important species belonging to the group. An essential prerequisite for any investigation of sexual system evolution is a deep and broad knowledge of biodiversity studied from morphological, phylogenetic and ecological perspectives. In the case of palms, this vital element is provided by the milestone work *Genera Palmarum* (Dransfield *et al.*, 2008). Molecular approaches, which have already revolutionized phylogenetic analyses of the family, are now being applied to whole genomes, and an exciting range of new tools centred around next-generation sequencing (NGS) technologies that have become available in recent years (Varshney *et al.*, 2009) are now being applied to palms (Heyduk *et al.*, 2015). The power of such approaches has already been demonstrated using oil palm, for which genes determining fruit structure and colour have been identified (Singh *et al.*, 2013a, b, 2014). To capitalize on these new technologies, it will be vital to pursue studies of flower and inflorescence diversity in the family, so as to provide a bedrock of knowledge for future evolutionary and molecular investigations.

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REFERENCES

Adam H, Collin M, Richaud F, Beulé T, Cros D, Omore A, Nodichao L, Nouy B, Tregear JW. 2011. Environmental regulation of sex determination in oil palm: current knowledge and insights from other species. *Annals of Botany* 108: 1529–1537.

Adam H, Jouannic S, Escoute J, Duval Y, Verdeil JL, Tregear JW. 2005. Reproductive developmental complexity in the African oil palm (*Elaeis guineensis*, Arecaceae). *American Journal of Botany* 92: 1836–1852.

Adam H, Jouannic S, Morcillo F, Orieux Y, Duval Y, Tregear JW. 2007. Functional characterization of MADS box genes involved in the determination of oil palm flower structure. *Journal of Experimental Botany* 58: 1245–1259.

Akagi T, Henry IM, Tao R, Comai L. 2014. A Y-chromosome-encoded small RNA acts as a sex determinant in persimmons. *Science* 346: 646–650.

Al-Dous EK, George B, Al-Mahmoud ME, Al-Jaber MY, Wang H, Salameh YM, Al-Azwani EK, Chaluvadi S, Pontaroli AC, Debarry J, Arondel V, Ohlrogge J, Saie IJ, Suliman-Elmeer KM, Bennetzen JL, Kruegger RR, Malek JA. 2011. *De novo* genome sequencing and comparative genomics of date palm (*Phoenix dactylifera*). *Nature Biotechnology* 29: 521–U584.

Allen AM, Hiscock SJ. 2008. Evolution and phylogeny of self-incompatibility systems in angiosperms. In: Franklin-Tong VE, ed. *Self-incompatibility in flowering plants – evolution, diversity, and mechanisms*. Berlin: Springer-Verlag.

Al-Mssallem IS, Hu S, Zhang X, Lin Q, Liu W, Tan J, Yu X, Liu J, Pan L, Zhang T, Yin Y, Xin C, Wu H, Zhang G, Ba Abdullah MM, Huang D, Fang Y, Alnakhli YO, Jia S, Yin A, Alhuzimi EM, Alsaihati BA, Al-Owayyed SA, Zhao D, Zhang S, Al-Otaibi NA, Sun G, Majrashi MA, Li F, Tala, Wang J, Yun Q, Alnassar NA, Wang L, Yang M, Al-Jelaify RF, Liu K, Gao S, Chen K, Alkhaldi SR, Liu G, Zhang M, Guo H, Yu J. 2013 Genome sequence of the date palm *Phoenix dactylifera* L. *Nature Communications* 4: 2274.

Ashman T-L. 2000. Pollinator selectivity and its implications for the evolution of dioecy and sexual dimorphism. *Ecology* 81: 2577–2591.

Askgaard A, Stauffer F, Hodel DFR, Barfod AS. 2008. Floral structure in the neotropical palm genus *Chamaedorea* (Arecoideae, Arecaceae). *Anales del Jardin Botanico de Madrid* 65: 197–210.

Babik W, Butlin RK, Baker WJ, Papadopulos AST, Boulesteix M, Anstett MC, Lewer C, Hutton I, Savolainen V. 2009. How sympatric is speciation in the *Howea* palms of Lord Howe Island? *Molecular Ecology* 18: 3629–3638.

Baker WJ, Dransfield J 2016. Beyond *Genera Palmarum*: progress and prospects in palm systematics. *Botanical Journal of the Linnean Society* doi: 10.1111/boj.12401.

Baker WJ, Hutton I. 2006. Lepidorrhachis. *Palms* 50: 33–38.

Baker WJ, Savolainen V, Asmussen-Lange CB, Chase MW, Dransfield J, Forest F, Harley MM, Uhl NW, Wilkinson M. 2009. Complete generic-level phylogenetic analyses of palms (Arecaceae) with comparisons of supertree and supermatrix approaches. *Systematic Biology* 58: 240–256.

Barfod AS. 1991. A monographic study of the subfamily Phytelephantoideae (Arecaceae). *Opera Botanica* 105: 5–73.

Barfod AS, Burholt T, Borchsenius F. 2003. Contrasting pollination modes in three species of *Licuala* (Arecaceae: Coryphoideae). *Telopea* 10: 207–223.

Barfod AS, Hagen M, Borchsenius F. 2011. Twenty-five years of progress in understanding pollination mechanisms in palms (Arecaceae). *Annals of Botany* 108: 1503–1516.

Barot S, Mitja D, Miranda I, Meija GD, Grimaldi M. 2005. Reproductive plasticity in an Amazonian palm. *Evolutionary Ecology Research* 7: 1051–1065.

Barrett SCH. 1998. The evolution of mating strategies in flowering plants. *Trends in Plant Science* 3: 335–341.

Barrett SCH. 2010. Understanding plant reproductive diversity. *Philosophical Transactions of the Royal Society of London Series B, Biological sciences* 365: 99–109.

Barrett SCH 2013. The evolution of plant reproductive systems: how often are transitions irreversible? *Proceedings of the Royal Society B Biological Sciences* 280: 20130913.

Basu SK, Basu P. 1993. Sex expressions in some caryotoid palms. *Journal of Economic and Taxonomic Botany* 17: 49–54.

Beedanagari SR, Dove SK, Wood BW, Conner PJ. 2005. A first linkage map of pecan cultivars based on RAPD and AFLP markers. *Theoretical and Applied Genetics* 110: 1127–1137.

Beentje H 2010. *The Kew plant glossary*. Kew: Royal Botanic Gardens.

Bernal R, Ervik F. 1996. Floral biology and pollination of the dioecious palm *Phytelephas seemannii* in Colombia: an adaptation to staphylinid beetles. *Biotropica* 28: 682–696.

Boegh A. 1996. The reproductive phenology and pollination ecology of four *Calamus* (Arecaceae) species in Thailand. *Principes* 40: 5–15.

Borchsenius F. 1997. Flowering biology of *Geonoma irena* and *G. cuneata* var. *sodiroi* (Arecaceae). *Plant Systematics and Evolution* 208: 187–196.

Case A, Graham S, Macfarlane T, Barrett S. 2008. A phylogenetic study of evolutionary transitions in sexual systems in Australasian *Wurmbea* (Colchicaceae). *International Journal of Plant Sciences* 169: 141–156.

Castaño F, Stauffer F, Marquinez X, Crèvecoeur M, Collin M, Pintaud JC, Tregear JW. 2014. Floral structure and development in the monoecious palm *Gaussia attenuata* (Arecaceae; Arecoideae). *Annals of Botany* **114:** 1483–1495.

Charlesworth D. 2006. Evolution of plant breeding systems. *Current Biology* **16:** R726–R735.

Cherif E, Zehdi S, Castillo K, Chabrillange N, Abdoulkader S, Pintaud JC, Santoni S, Salhi-Hannachi A, Glemin S, Aberlenc-Bertossi F. 2013. Male-specific DNA markers provide genetic evidence of an XY chromosome system, a recombination arrest and allow the tracing of paternal lineages in date palm. *New Phytologist* **197:** 409–415.

Chuck G, Meeley R, Irish E, Sakai H, Hake S. 2007. The maize *tasselseed4* microRNA controls sex determination and meristem cell fate by targeting *Tasselseed6/indeterminate spikelet1*. *Nature Genetics* **39:** 1517–1521.

Coen ES, Meyerowitz EM. 1991. The war of the whorls – genetic interactions controlling flower development. *Nature* **353:** 31–37.

Corley RHV. 1976. Sex differentiation in oil palm - effects of growth-regulations. *Journal of Experimental Botany* **27:** 553–558.

Couvreur T, Baker WJ. 2013. Tropical rain forest evolution: palms as a model group. *BMC Biology* **11:** 48.

Couvreur TLP, Forest F, Baker WJ. 2011. Origin and global diversification patterns of tropical rain forests: inferences from a complete genus-level phylogeny of palms. *BMC Biology* **9:** 44.

Darwin CR. 1877. *The different forms of flowers on plants of the same species*. London: John Murray.

Dowe JL. 2009. A taxonomic account of *Livistona* R. Br. (Arecaceae). *The Garden's Bulletin Singapore* **60:** 185–344.

Dransfield J, Beentje H 1996. *Lexicon palmarum*. Marly-Le-Roi: Editions Champflour in association with the Royal Botanic Gardens.

Dransfield J, Mogea JP. 1984. The flowering behaviour of *Arenga* (Palmae, Caryotoideae). *Botanical Journal of the Linnean Society* **88:** 1–10.

Dransfield J, Uhl NW, Asmussen CB, Baker WJ, Harley MM, Lewis CE. 2008. *Genera Palmarum - the evolution and classification of palms*. Kew: Kew Publishing.

Endress PK, Doyle JA. 2009. Reconstructing the ancestral angiosperm flower and its initial specializations. *American Journal of Botany* **96:** 22–66.

Freeman DC, McArthur ED, Harper KT, Blauer AC. 1981. Influence of environment on the floral sex-ratio of monoecious plants. *Evolution* **35:** 194–197.

Giddey A, Spichiger RE, Stauffer FW. 2009. Comparative floral structure and systematics in the Asian palm genus *Rhapis* (Arecaceae, Coryphoideae). *Flora* **204:** 347–357.

Henderson A. 1986. A review of pollination studies in the Palmae. *The Botanical Review* **52:** 221–259.

Henderson A. 2002. *Evolution and ecology of palms*. New York: NYBG Press.

Heyduk K, Trapnell DW, Barrett CF, Leebens-Mack J. 2015. Phylogenomic analyses of species relationships in the genus *Sabal* (Arecaceae) using targeted sequence capture. *Biological Journal of the Linnean Society* **117:** 106–120.

Jeanson M 2011. Systematics of tribe Caryoteae (Arecaceae). Thesis: Museum national d'Histoire naturelle, Paris.

de Jong TJ, Shmida A, Thuijsman F. 2008. Sex allocation in plants and the evolution of monoecy. *Evolutionary Ecology Research* **10:** 1087–1109.

Kholia BS. 2009. Gender variation in a threatened and endemic palm *Trachycarpus takil* Becc. *Current Science* **96:** 144–148.

Kriebel R. 2014. Sexual dimorphism in the flowers of *Aegiphila odontophylla* (Lamiaceae). *Systematic Botany* **39:** 1204–1207.

Loo AHB, Dransfield J, Chase MW, Baker WJ. 2006. Low-copy nuclear DNA, phylogeny and the evolution of dichogamy in the betel nut palms and their relatives (Arecinae; Arecaceae). *Molecular Phylogenetics and Evolution* **39:** 598–618.

Maddison W, Maddison D 2011. Mesquite: a modular system for evolutionary analysis. Version 3.01. Available at: http://mesquiteproject.org

Marcus J. 2010. Observations on the flowering of *Marojejya darianii*. *Palms* **54:** 189–192.

Martin A, Troadec C, Boualem A, Rajab M, Fernandez R, Morin H, Pitrat M, Dogimont C, Bendahmane A. 2009. A transposon-induced epigenetic change leads to sex determination in melon. *Nature* **461:** 1135–8113.

Masmoudi-Allouche F, Châari-Rkhis A, Kriaâ W, Gargouri-Bouzid R, Jain SM, Drira N. 2009. *In vitro* hermaphrodism induction in date palm female flower. *Plant Cell Reports* **28:** 1–10.

Maunder M, Page W, Mauremootoo J, Payendee R, Mungroo Y, Maljkovic A, Vericel C, Lyte B. 2002. The decline and conservation management of the threatened endemic palms of the Mascarene Islands. *Oryx* **36:** 56–65.

Miller JS, Diggle PK. 2002. Diversification of andromonoecy in *Solanum* section *Lasiocarpa* (Solanaceae): the roles of phenotypic plasticity and architecture. *American Journal of Botany* **90:** 707–715.

Moore HE, Uhl NW. 1982. Major trends of evolution in palms. *Botanical Review* **48:** 1–69.

Obbard DJ, Harris SA, Pannell JR. 2006. Sexual systems and population genetic structure in an annual plant: testing the metapopulation model. *The American Naturalist* **167:** 354–366.

Renner SS. 2014. The relative and absolute frequencies of angiosperm sexual systems: dioecy, monoecy, gynodioecy, and an updated online database. *American Journal of Botany* **101:** 1588–1596.

Renner SS, Ricklefs RE. 1995. Dioecy and its correlations in the flowering plants. *American Journal of Botany* **82:** 596–606.

Rudall PJ, Abranson K, Dransfield J, Baker W. 2003. Floral anatomy in *Dypsis* (Arecaceae-Areceae): a case of complex synorganization and stamen reduction. *Botanical Journal of the Linnean Society* **143:** 115–133.

Rudall PJ, Ryder RA, Baker WJ. 2011. Comparative gynoecium structure and multiple origins of apocarpy in

coryphoid palms (Arecaceae). *International Journal of Plant Sciences* **172:** 674–690.

Savolainen V, Anstett MC, Lexer C, Hutton I, Clarkson JJ, Norup MV, Powell MP, Springate D, Salamin N, Baker WJ. 2006. Sympatric speciation in palms on an oceanic island. *Nature* **441:** 210–213.

Singh R, Low E, Ooi L, Ong-Abdullah M, Ting N, Nagappan J, Nookiah R, Amiruddin M, Rosli R, Manaf M, Chan K, Halim M, Azizi N, Lakey N, Smith S, Budiman M, Hogan M, Bacher B, Brunt AV, Wang C, Ordway J, Sambanthamurthi R, Martienssen R. 2013a. The oil palm *SHELL* gene controls oil yield and encodes a homologue of SEEDSTICK. *Nature* **500:** 340–344.

Singh R, Low ET, Ooi LC, Ong-Abdullah M, Nookiah R, Ting NC, Marjuni M, Chan PL, Ithnin M, Manaf MA, Nagappan J, Chan KL, Rosli R, Halim MA, Azizi N, Budiman MA, Lakey N, Bacher B, Brunt AV, Wang C, Hogan M, He D, MacDonald JD, Smith SW, Ordway JM, Martienssen RA, Sambanthamurthi R. 2014. The oil palm *virescens* gene controls fruit colour and encodes a r2r3-myb. *Nature Communications* **5:** 4106.

Singh R, Ong-Abdullah M, Low E, Manaf M, Rosli R, Nookiah R, Ooi L, Ooi S, Chan K, Halim M, Azizi N, Nagappan J, Bacher B, Lakey N, Smith S, He D, Hogan M, Budiman M, Lee E, DeSalle R, Kudrna D, Goicoechea J, Wing R, Wilson R, Fulton R, Ordway J, Martienssen R, Sambanthamurth R. 2013b. Oil palm genome sequence reveals divergence of interfertile species in Old and New Worlds. *Nature* **500:** 335–339.

Somyong S, Poopear S, Jomchai N, Uthaipaisanwong P, Ruang-areerate P, Sangsrakru D, Sonthirod C, Ukoskit K, Tragoonrung S, Tangphatsornruang S. 2015. The AKR gene family and modifying sex ratios in palms through abiotic stress responsiveness. *Functional & Integrative Genomics* **15:** 349–362.

Teo ZWN, Song SY, Wang YQ, Liu J, Yu H. 2014. New insights into the regulation of inflorescence architecture. *Trends in Plant Science* **19:** 158–165.

Theissen G, Melzer R. 2007. Molecular mechanisms underlying origin and diversification of the angiosperm flower. *Annals of Botany* **100:** 603–619.

Tomlinson PB. 2006. The uniqueness of palms. *Botanical Journal of the Linnean Society* **151:** 5–14.

Uhl NW. 1966. Morphology and anatomy of the inflorescence axis and flowers of a new palm. *Journal of the Arnold Arboretum* **47:** 9–22.

Uhl NW. 1976. Developmental studies in *Ptychosperma* (Palmae). I. The inflorescence and the flower cluster. *American Journal of Botany* **63:** 97–109.

Uhl NW 1988. Floral organogenesis in palms. In: Leins P, Tucker SC, Endress PK, eds. *Aspects of floral development*. Berlin: J. Cramer.

Uhl NW, Moore HE. 1971. The palm gynoecium. *American Journal of Botany* **58:** 945–992.

Vamosi J, Otto S, Barrett S. 2003. Phylogenetic analysis of the ecological correlates of dioecy in angiosperms. *Journal of Evolutionary Biology* **16:** 1006–1018.

Varshney RK, Nayak SN, May GD, Jackson SA. 2009. Next-generation sequencing technologies and their implications for crop genetics and breeding. *Trends in Biotechnology* **27:** 522–530.

Voeks RA. 1988. Changing sexual expression of a Brazilian rain forest palm (*Attalea funifera* Mart.). *Biotropica* **20:** 107–113.

Weiblen GD, Oyama RK, Donoghue MJ. 2000. Phylogenetic analysis of dioecy in monocotyledons. *The American Naturalist* **155:** 46–58.

Williams CN, Thomas RL. 1970. Observations on sex differentiation in the oil palm, *Elaeis guineensis* L. *Annals of Botany* **34:** 937–963.

Willson MF. 1991. Sexual selection, sexual dimorphism and plant phylogeny. *Evolutionary Ecology* **5:** 69–87.

Zehdi-Azouzi S, Cherif E, Moussouni S, Gros-Balthazard M, Abbas Naqvi S, Ludeña B, Castillo K, Chabrillange N, Bouguedoura N, Bennaceur M, Si-Dehbi F, Abdoulkader S, Daher A, Terral J-F, Santoni S, Ballardini M, Mercuri A, Ben Salah M, Kadri K, Othmani A, Littardi C, Salhi-Hannachi A, Pintaud J-C, Aberlenc-Bertossi F. 2015. Genetic structure of the date palm (*Phoenix dactylifera*) in the Old World reveals a strong differentiation between eastern and western populations. *Annals of Botany* **116:** 101–112.

Appendix 1 Genus- and species-level survey of sexual system in palms

The first column indicates the total number of genera (bold) and species (italics). The other columns show the relative proportion of genera (bold) and species (italics) for each of the four main types of sexual system. Subfamilies are assigned according to Dransfield *et al.* (2008). Numbers of species and genera follow www.palmweb.org.

	Number of **genera**/*species*	Monoecy	Dioecy	Hermaphroditism	Polygamy
Family level					
Arecaceae	**188**/*2585*	**61%**/*52%*	**21%**/*30%*	**16%**/*17%*	**2%**/*1%*
Subfamily level					
Calamoideae	**21**/*645*	**10%**/*4%*	**66%**/*87%*	**14%**/*7%*	**10%**/*2%*

Table . *Continued*

	Number of **genera**/*species*	Monoecy	Dioecy	Hermaphroditism	Polygamy
Nypoideae	*1/1*	**100%**/*100%*	–	–	–
Coryphoideae	**47**/*503*	**6%**/*10%*	**32%**/*13%*	**60%**/*76%*	**2%**/*1%*
Ceroxyloideae	**8**/*47*	–	**87%**/*91%*	–	**13%**/*9%*
Arecoideae	**111**/*1389*	**98%**/*92%*	**2%**/*8%*	–	–

Appendix 2   Methods used for character optimization on the palm phylogenetic tree

We conducted a survey of 183 species, one for each genus included in this phylogenetic tree, which represent almost all of the recognized genera (Dransfield *et al.*, 2008; Couvreur *et al.*, 2011). We retrieved descriptions of these species from the literature and recorded the data in the database PROTEUS (see http://eflower.myspecies.info/proteus) which allows precise and complete tracking of the source information. The species vs. genus approach, called the exemplar approach, avoids the problem of coding polymorphisms whenever they occur within a genus. We used Mesquite (Maddison & Maddison, 2011) to perform parsimony (Fig. 4) and maximum likelihood optimizations (Supplementary Information) of the character 'sexual systems'. This character was coded as multistate, with four states representing hermaphroditism, monoecy, dioecy and polygamy, respectively.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Data S1. Maximum-likelihood optimization of sexual systems evolution.