

PREFACE: PART OF A SPECIAL ISSUE ON PALM BIOLOGY

A family portrait: unravelling the complexities of palms

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Palms (Arecaceae) form one of the most distinctive of all plant families and are emblematic of the tropical regions of the world, in which most of their natural biodiversity is concentrated. According to the most recent estimates, the palm family contains nearly 2500 species. A large number of them are exploited in some way for human purposes; indeed, the Arecaceae have been recognized as being one of the three most important plant families in terms of human usage, along with the Poaceae and the Fabaceae (Balick and Beck, 1990; <http://www.fao.org/docrep/X0451E/X0451e04.htm>). Although a handful of species such as date palm (*Phoenix dactylifera*), oil palm (*Elaeis guineensis*) and coconut (*Cocos nucifera*) occupy a particularly high profile, due to their economic importance, many members of the Arecaceae have uses that extend far beyond their natural habitat. From an ecological point of view, palms are omnipresent in the tropical rainforests that form many of the world's biodiversity hotspots. Fossil records date their origins back as far as the early Cretaceous period and provide evidence that the basic bauplan of the Arecaceae was a successful one in evolutionary terms, corroborated by the great biodiversity of the family today.

Understanding how palms function and how their evolutionary and ecological success has been achieved remains a major challenge to researchers. Some of their typical features, such as large size, slow growth and long life cycle make them difficult subjects for studies under controlled conditions. At the same time, observations in their natural environment may be hindered by the accessibility of the terrain or by the rarity of specimens. These challenges notwithstanding, the potential rewards are great, from both a purely scientific and an applied perspective. The palm family forms, on its own, a distinct order (the Arecales) within the Commelinid clade of the monocots, along with the Poales, Dasygongonaceae, Zingiberales and Commelinales. It is of great interest to conduct comparative evo-devo studies between these well-separated and distinctive groups in order to understand how certain key characters evolved during the radiation of the monocotyledons. Similarly, much vital knowledge will be gained by tracing, through intra-family studies of the Arecaceae, the evolutionary pathways of specific traits (e.g. inflorescence and flower morphotypes) that shaped their biodiversity. A backbone for research of this type was set out in the last decade, when a solid genus-level phylogeny was established for the Arecaceae (Baker *et al.*, 2009). Another key milestone was reached in 2011 with the appearance of the first published genome sequence for a member of the Arecaceae, namely the date palm (Al-Dous *et al.*, 2011). With other palm genome sequences to follow, the coming years will

no doubt allow much progress to be made in understanding the particularities of palm genomes and their evolution with respect to other Angiosperm groups.

Progress in palm research is being made on many fronts, as revealed by the wide range of approaches used to tackle key biological questions in the articles that follow. Given their distinct characteristics, it is clear that the functioning of palms cannot be adequately understood by simple extrapolation of knowledge gained on 'model' plants. This notion is reinforced in many of the papers in this Special Issue.

The distinctly tropical character of the Arecaceae is dissected in detail in the article by Eiserhardt *et al.* (2011). In their review, the authors analyse the wide range of data obtained from studies aimed at identifying the determinants of palm spatial distributions, community composition and species richness. A range of different factors may play a role, including those of an intrinsically abiotic nature (e.g. climate and soil chemistry), those of a biotic nature (interactions with other plant species, pollinators, etc) and also dispersal-related factors. One important conclusion that emerges is that the determinants of species distribution, community composition and species richness are influenced by different factors that vary according to the spatial scale examined. Although some combinations of predictive factor and geographical scale will require further investigation in order to fill in the identified gaps, the review of Eiserhardt *et al.* provides the most complete account yet of this all-encompassing area of palm biology.

Within the field of palm phylogenetics, several articles presented in this Special Issue illustrate the continuing progress being made in tracing and understanding the family tree of the Arecaceae. The Arecoideae form the largest and most diverse of the five palm subfamilies; more than half the species of the family belong to this group, yet many questions remain to be resolved regarding their phylogeny. In their paper presented here, Baker *et al.* (2011) present results of the most densely sampled phylogenetic analysis yet of this subfamily, performed using the low-copy nuclear genes *PRK* and *RPB2*. Overall, both genes produced highly informative, well-resolved phylogenetic trees with many nodes well supported by bootstrap analyses. Of the 14 tribes and 14 sub-tribes in the classification, only five sub-tribes (from the tribe Areceae) failed to receive support. The study of Baker *et al.* therefore allows the validation of much recent data obtained in palm phylogenetics, while identifying priority areas for future studies in this important subfamily. As the authors point out, the addition of new genes to the panel of phylogenetic markers available will be essential in order to achieve the ultimate goal of a robust

family-wide palm phylogeny extending down to the species level.

The addition of novel markers for palm phylogenetic studies is a question addressed by the paper of Ludeña *et al.* (2011). In this case the Neotropical subtribe Bactridinae (Arecoideae: Cocoseae), for which some phylogenetic ambiguities remain, was used as a case study. New primers were developed for the amplification of gene sequences corresponding to palm homologues of *AGAMOUS* (a floral homeotic gene) and *PHYTOCHROME B*. The two loci studied were found to display more sequence variability than the conventionally used chloroplast loci and equal or less variability compared to the *PRK*, *RPBII* and *ITS* nuclear markers. The phylogenetic structure obtained with the *AGAMOUSI* and *PHYTOCHROME B* genes provides new insights into intergeneric relationships within the Bactridinae and highlights the existence of a monophyletic clade corresponding to the earlier recognized genus *Hexopetion*. These results illustrate the great potential offered by the inclusion of new marker genes in phylogenetic studies. This development will no doubt be facilitated by the currently emerging genomic data.

Phylogenetic studies in the palm family share similar long-term goals to those of other groups, one of the most important of which is to develop reliable, simple and low-cost protocols for species identification via DNA analysis. This objective is addressed in the study reported here by Jeanson *et al.* (2011). The authors focused on two core markers (*matK* and *rbcl*) selected by the Consortium for the Barcode of Life's Plant Working Group (CBOL-PWG) and investigated their taxonomic usefulness in the Southeast Asian tribe Caryoteae (subfamily Coryphoideae). It was found that the two core markers suggested by the CBOL-PWG gave a low species discrimination rate; however, when a third marker –*nrITS2*– was added, a species discrimination rate of 92% was obtained. This is a relatively high rate for a barcoding experiment and illustrates the importance of choosing appropriate marker genes for the group to be studied. The development of DNA barcoding approaches suitable for palms will clearly be an important focus of research in the coming years.

DNA studies of a different nature can also help to resolve questions of fundamental importance relating to the developmental biology of palms. In this issue, Jaligot *et al.* (2011) describe advances made in studies of the *mantled* epigenetic flowering abnormality observed in oil palms produced by *in vitro* micropropagation. The latter technique, based on somatic embryogenesis, shows great potential for the multiplication of high-value genotypes adapted to specific growing conditions. However, its use is hampered by the occurrence, in small but significant proportions, of the *mantled* somaclonal variant, which resembles the floral B class mutants of model plants. Abnormal palms may be sterile and therefore unproductive, thus cancelling out any potential genetic improvements made in the breeding programme from which they were obtained. Much interest therefore lies in identifying the molecular causes of the *mantled* phenotype, which has been demonstrated to be epigenetic in nature. Jaligot *et al.* review current knowledge and priorities for future research on this complex but challenging phenomenon, which will target molecular factors of particular interest such as MADS-box genes

and transposable elements, on account of their involvement in related regulatory processes in model plants.

The great potential of biotechnological approaches for maximizing the agronomic potential of cultivated palms is illustrated in the paper of Steinmacher *et al.* (2011). In this case, the peach palm *Bactris gasipaes* was studied, which provides a self-regenerating cultivated source of palm hearts thanks to its caespitose (clumping) habit. As in the case of oil palm, earlier work had revealed somatic embryogenesis to be a suitable system for micropropagation. In their study, Steinmacher *et al.* characterized the morphogenetic pathway associated with regeneration through somatic embryogenesis and devised a protocol for the establishment of cycling cultures using a temporary immersion system (TIS) for *in vitro* culture. Peach palm is one of several species from the Arecaceae for which *in vitro*-based micropropagation has been successfully applied, and the improved perspective obtained on the regeneration procedure thanks to this work will no doubt facilitate the addition of other economically important palms to the list in the future.

The evolutionary success of palms has been achieved despite certain limitations imposed by their mode of growth and development. The most notable constraint is the lack of a secondary meristem (or cambium), which means that once the stem diameter is determined, no further increase in its thickness is possible later in life, nor can any new tracheary elements be added to replace damaged ones. This character is thought to have limited the ability of palms to colonize colder environments and may in part explain their mostly tropical/subtropical distribution today (Tomlinson, 2006). Although a significant number of palm species are caespitose in habit, the canonical palm is considered to take the form of a single-stemmed plant that initiates all of its above-ground structure from a single shoot apical meristem (SAM). Understanding how the palm SAM works is fundamental to understanding how plant form is determined in the family and may help in the improvement of cultivated species. Jouannic *et al.* (2011) made important advances in this area by studying, using 2-D and 3-D microscopic approaches, the SAM of oil palm. Their work reveals that SAM structure is characterized by two contrasting phases. In the first phase, a gradually increasing single tunica-carpus structure is observed, whereas in the mature phase, corresponding to the early establishment phase of the plant, the oil palm SAM displays a stable size, a modified shape and an established histological zonation pattern. Fluctuations in SAM shape and volume occur in adult palms, probably in relation to the cycle of leaf initiation.

Another original aspect of palm structural biology that has recently been tackled is that of fruit development. In their study of eight different species representing all genera of the tribe Borasseae, Romanov *et al.* (2011) examined the morphological changes that accompany pericarp development. Data obtained allowed the histological origin of the pericarp to be monitored from the earliest stages of its differentiation and highlighted the complexity of fruit structure. This is particularly true for the mesocarp, which produces several distinct tissue layers in the fruit, including the stony pyrene. In addition to the novel insight gained into fruit development, this study is also significant in that it required the development of new histo-cytological

protocols for these very specialized plant tissues, which are generally challenging subjects to plant anatomists.

Given the great importance of flowering as a factor contributing to both to the ecological success of palms in their wild habitat and to the productivity of cultivated species exploited for their fruit, much attention continues to be focused on this area. In this issue, three different aspects of the flowering process in palms are addressed.

The paper of Barfod *et al.* (2011) reviews current knowledge of palm pollination mechanisms in the light of 25 years of research in this area, which make the Arecaceae one of the better studied of tropical angiosperm families. Available data suggest that beetles are the largest group of palm pollinators, followed by bees and flies, with more occasional contributions from mammals (e.g. bats and marsupials) and even crabs. Interactions with the visiting fauna represent a trade-off between the useful services of pollinators and the antagonistic activities of other visitors. Comparative studies of closely related palm species have suggested an important role for palm–pollinator interactions in the evolution of flowering characters such as floral structure and the timing of anthesis. Studies published to date have tended to concentrate on the South American region and on the tribe Cocoseae; it is hoped that future work will help to broaden the phylogenetic and geographical focus of research on this vital subject, which is likely to have strongly influenced evolution within the palm family as a whole.

The related subject of reproductive development is addressed in the paper of Ortega Chávez and Stauffer (2011). In their study, the authors investigate a developmental character that shows great variation in the Arecaceae, namely inflorescence structure. The tribe Chamaedoreae are an interesting case study in this context, since many species of this clade produce flowers arranged in a complex partial inflorescence called an acervulus. The latter is atypical of the subfamily Arecoideae, to which the Chamaedoreae belong, and which is typically characterized by floral triads containing a central pistillate flower flanked by two staminate flowers. New data were obtained in order to investigate the ontogenetic basis of the acervulus in *Hyophorbe lagenicaulis* and comparative studies were conducted with species from other genera of the Chamaedoreae: *Gaussia*, *Synechanthus*, *Chamaedorea* and *Wendlandiella*. The authors suggest that a cymose configuration might constitute a common denominator within the Arecoideae, although floral triads and acervuli display certain differences in their arrangements that complicate their interpretation. This study reveals the complex nature of inflorescence ontogeny in the Arecaceae and highlights the need for family-wide evo-devo studies in the future in order to fully understand this important facet of palm biodiversity.

Another striking aspect of palm reproductive development dealt with in this issue concerns the phenomenon of ‘gender plasticity’ exhibited by certain species, the best characterized of which is the African oil palm (*Elaeis guineensis*). In their paper, Adam *et al.* (2011) review current knowledge of the factors that regulate this process, which has the overall effect of promoting the production of male inflorescences in response to water deficit and other stresses, whereas female flowering is favoured when growing conditions are optimal. The slow development of the oil palm inflorescence, which usually lasts 2 to 3 years between initiation and maturity, renders studies complicated. However, the flowering response of this

species to stress provides a useful experimental system by which to study how its sex determination is regulated. Thanks to recent technological developments, functional genomic approaches are now possible. When combined with other techniques, these studies will provide new information on the fundamental processes that underlie sex determination in oil palm and help us to understand how these processes have evolved during the evolution of the Arecaceae.

The continued importance of the Arecaceae to mankind is in no doubt; neither is the fascination that palms hold to researchers, due in no small part to the distinct and often striking forms seen in the family. This issue provides a snapshot of recent and ongoing research directions and reinforces the conviction within the worldwide community that new generations of scientists will continue to be drawn to the challenge of palm biology in the years to come.

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