PALM LITERATURE

EVOLUTION AND ECOLOGY OF PALMS. By Andrew Henderson. The New York Botanical Garden Press, Bronx, NY. 2002. SBN 0-89327-444-5. US$35.00. Paperback.259 pp., numerous halftone photos and diagrams.

Palms, the princes of the plant kingdom, command respect from many loyal subjects. Their royal heritage gives palms the freedom to make and follow their own sets of rules. Unraveling the complex linkages among palm morphology, ecology, and evolution is a major task that has preoccupied many prominent botanists, including Holttum, Corner, Tomlinson, Moore, Uhl, and Dransfield. Andrew Henderson follows this progression of big palm thinkers in this synthetic volume. The central thesis he develops in the Introduction and revisits in virtually every chapter, is that stem morphology has pervasive consequences for morphology of leaves and reproductive structures and therefore influences all aspects of vegetative and reproduction function. The evolutionary processes that have shaped the diversification of palm forms are viewed within the concept of heterochrony, the change in timing of rates of development and developmental sequences, as widely discussed by Gould in his 1997 book Ontogeny and Phylogeny. Related to these changes are allometric constraints that vary in their expression within and among evolutionary lines. Neither of these major concepts is new; heterochrony and allometry have been previously applied to particular aspects of palm morphology and evolution. But here they receive new life in the ways in Henderson's broad application and synthesis. His new vision enables linkages between vegetative and reproductive functions, and among growth rate, plant size and life history evolution.

Henderson returns to Moore's landmark 1973 publication on the Major Groups of Palms and their Distribution, leaving aside Moore's biogeographic focus in favor of a focus on morphology, life history, and ecology. He resurrects Moore's 15 major groups, abandoning the tribal classification later developed by Moore and published in Genera Palmarum by Uhl and Dransfield (1987). Henderson splits Moore's Cocosoid group into spiny and non-spiny groups for a total of 16 groups. Molecular-based phylogenetic studies suggest that 13 of these major groups are monophyletic; Coryphoids, Arecoids, and Nonspiny cocosoids are considered to be polyphyletic. A complete phylogenetic assessment of palms is not yet possible, and it is quite likely that the topography of Henderson's landscape will undergo some seismic shifts in the next decade.

Following the introduction, Henderson begins with two chapters on palm stem morphology and an analysis of size and shape of palm stems. Henderson distinguishes two types of stem morphology within the family – palms with internodal elongation and palms lacking internodal elongation. The former group shows more restricted variation of stem height and diameter ratios, whereas the latter group exhibits more variation in these ratios. To the extent that these groupings represent clades, Henderson posits that phyletic changes in stem growth rate can be related to phyletic variation in leaf morphology, reproductive structures, and the duration and timing of reproduction. He makes a convincing hypothesis that remains to be tested conclusively across the entire family.

The next chapter focuses on leaf morphology and arrangement, again emphasizing relationships between stem and leaf development. Henderson points out that leaf size and stem diameter co-vary in some palm genera, but not in others, a pattern that he later interprets within the context of beetle vs. bee/fly/wasp pollination syndromes. I found these trends to be intriguing, but a remarkably small number of palm genera are actually compared here. The discussion proceeds to inflorescence development and maturation in Chapter 5, which is followed by a chapter on reproductive duration. Phylogenetic hypotheses based on molecular data suggest that a shift from semelparity to iteroparity took place early in palm evolution in the Calamoid group, with a later reversal back to semelparity in the Coryphoid genera *Nannorrhops* and *Corypha*, associated with a reduction in growth rate and an extension of lifespan. Similarly, a reversal to semelparity took place in *Caryota* and *Wallichia* and some species of *Arenga* of the Caryotoid group, although in these cases the connection with slow growth rate and increased longevity is less universal.

In Chapter 7, Henderson extends the discussion of reproductive biology to phenology and breeding systems, leading to a detailed treatment of pollination in Chapter 8. These topics are strongly linked functionally as well as structurally. Henderson characterizes a set of traits associated with beetle pollinated species, including high synchrony and short duration of flowering, condensed inflorescences with closely-spaced flowers, rapid maturation with short, nocturnal anthesis, basipetal maturation, temperature elevation, protogyny, and lack of nectar production. In contract, species pollinated by bees,

flies, and wasps tend to have low synchrony and long duration of flowering, elongate inflorescences with loosely spaced flowers, slow maturation, long and diurnal anthesis, acropetal maturation, protandry, and production of sweet nectar. Henderson also proposes a generalized trade-off between growth and reproduction, such that internodal growth is often reduced following sexual maturity. He further points out that beetle-pollinated genera, such as *Bactris*, are strongly selected for conservatism in inflorescence size, whereas taxa pollinated by a greater variety of insects, such as *Sabal*, *Prestoea*, and *Aiphanes* lack these constraints on inflorescence size and also lack integration among inflorescence size, stem diameter, and leaf size.

Henderson describes fecundity and fruit maturation in Chapter 9, highlighting a general trend – species with larger stems produce more numerous, smaller fruits. The associations between palms and their fruit/seed dispersers and seed predators are detailed in Chapter 10. Henderson distinguishes two syndromes of seed dispersal in palms, the mammal/bruchid system and the bird/scolytid system. The former is exemplified by non-spiny Cocosoid palms, which have simultaneous fruit ripening and large, scented fruits, that tend to fall beneath the parent tree and are scatter-hoarded by various rodents. Seeds that are left behind are highly susceptible to predation by bruchid beetles. The bird/scolytid system, in contrast, applies to palms with sequential ripening and small fruits. Fruits are generally red or purplish black and have no noticeable scent. They attract a large number of birds, including toucans, parrots, and oil birds. Scolytid beetles are common seed predators of *Oenocarpus*, *Prestoea*, and *Euterpe*.

Henderson completes his work with a discussion of germination, contrasting characteristics of species with remote vs. adjacent modes. Palms with adjacent germination mode tend to have shorter, thinner stems with elongate internodes, higher growth rates, and smaller inflorescences and fruits. These species generally occur in moist forest habitats. This comparison is one of the few in the book that are based on species-level traits rather than traits at the generic or major group level.

I must admit, by the time I got to the end of the book, I was anticipating more than the one-page Epilogue. So much synthesis had been presented throughout the book's ten dense chapters that my head was reeling. I felt a need for a less-concentrated conclusion, so I had to go back through the book at my own pace, revisiting the conclusions at the end of each chapter. In this book, Henderson boldly went where no palm biologist has gone before. He chose to take a wide view and, as a result, has produced a major contribution that may well extend beyond the borders of the palm kingdom. It is laudable that, despite Henderson's extensive New World experience, the book includes many examples of Old World palms. The topics are covered in substantial detail, and are highly integrated throughout. The book illustrates the quantum leap in our understanding of palm evolution and diversification that has been enabled by molecular-based phylogenetic studies.

Henderson's orientation in this book is clearly more focused on evolution than ecology. Including a section on the geographic distribution of major taxa would have made the treatment more complete. Population and community ecology of palm species are not discussed. Palm ecology involves much more than interactions with animals and distributions across major biomes. Palms often reach high abundance in areas frequently disturbed by hurricanes or fires. Furthermore, canopy palm species can play an important role in plant and animal community structure, as keystone resources for frugivores and as agents of small-scale disturbance through leaf fall. Finally, palms also show complex meso-scale distribution patterns within tropical forests, suggesting affinities to particular soil and slope characteristics. It is important to understand the ecology of palms in their complex ecological matrix, rather than in manicured botanical gardens, where much of the research on their growth, morphology, and reproductive biology has been conducted.

Palm aficionados and scholars alike will appreciate the rich detail and broad synthesis achieved here (and, by the way, the Appendix is awesome). My copy will proudly take its place on the shelf between Corner's *Natural History of Palms* and Uhl and Dransfield's *Genera Palmarum*. Congratulations to the author and publisher on a job well done!

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