



Beyond *Genera Palmarum*: progress and prospects in palm systematics

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The systematic biology of the palm family (Arecaceae) is probably better known than that of any other tropical plant family of comparable size. As a result, the palms are now regarded as a model group for tropical rain forest research. Ten years ago, the first phylogenetic classification of palms was established as a foundation for the second edition of the palm systematic synthesis, *Genera Palmarum* (GP2), which was published in 2008. Here, we review progress in palm systematics since GP2, summarizing the latest developments in an updated palm classification and schematic phylogenetic tree. To date, the palms comprise 181 genera and *c.* 2600 species. In just 8 years, six new genera and 200 new species have been described, whereas eight genera have been sunk into synonymy. This reflects the highly dynamic nature of systematic discovery of palms at both forest and phylogenetic frontiers. Palm phylogenetics is a vibrant field, with new trees being generated and utilized in increasingly innovative and ambitious ways. Existing understanding of relationships among the five subfamilies has been confirmed and deep nodes in the subfamilies are crystallizing, especially in subfamilies Arecoideae and Coryphoideae. We conclude that palm systematic knowledge is far from complete and that tools, such as GP2, only stimulate further scientific research and discovery. Despite recent advances, however, many aspects of the palm Tree of Life still remain scarcely known. The vast datasets that the phylogenomic revolution is now bringing to bear on palms promise to elucidate many of these unknowns. The ultimate goal, a species-level phylogenetic tree for palms, is now coming within reach. © 2016 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2016, **182**, 207–233

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INTRODUCTION

Systematics advances in increments, with each step intended as a successive approximation towards the optimal solution. Palms (Arecaceae) are no exception to this trend. Such has been the success of the palm systematic endeavour that few, if any, tropical plant families of comparable size rival palms in terms of fundamental systematic resources (Govaerts & Dransfield, 2005; Dransfield *et al.*, 2008b; Baker *et al.*, 2009; Baker & Couvreur, 2013a; Govaerts *et al.*, 2015). As a result, palms are now widely regarded as a model group for tropical plant research (Eiserhardt *et al.*, 2011b; Couvreur & Baker, 2013). How have palms, which are notoriously difficult to study, become so well known? Put simply, over decades and centuries, palms have attracted specialists who are drawn to their economic importance (Balick

& Beck, 1990), their keystone role in ecosystems (Eiserhardt *et al.*, 2011b; ter Steege *et al.*, 2013) or perhaps merely to their charisma and the scientific challenge that they present. The work of generations of such palm specialists has laid the foundations of palm biology today.

A BRIEF HISTORY OF *GENERA PALMARUM*

Following the remarkable contributions of 19th and early 20th century innovators, such as Martius, Griffith, Blume, J. D. Hooker, Beccari and Burret (summarized in Dransfield *et al.*, 2008b), the modern palm systematic era dawned with the work of Harold E. Moore Jr. (1917–1980). From his base in the L. H. Bailey Hortorium at Cornell University, Moore became the leading light in palm research from the 1950s to the 1970s. An avid fieldworker, he explored for palms across the globe, studying all but 12 of the

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palm genera known at the time in the wild. Building on his taxonomic experience and his collaborations with Cornell anatomist Natalie Uhl, Moore aimed to understand the evolution of palms (Moore & Uhl, 1973, 1982) and to complete an account of all palm genera, a *Genera Palmarum*. In 1973, Moore published the 'Major Groups' paper (Moore, 1973), in which he proposed an informal classification comprising 15 groups in five major lines of evolution, based on explicit interpretations of morpho-anatomical specialization. This paper has since served as an important baseline for a truly phylogenetic classification of palms.

In 1980, Moore died unexpectedly, leaving many materials for his *Genera Palmarum*, especially illustrations, but the book itself remained essentially unwritten. The task passed to Natalie Uhl and John Dransfield, who critically reassessed Moore's groupings, formalizing a new classification of six subfamilies, 14 tribes and 36 subtribes, based on evolutionary concepts of the time (Dransfield & Uhl, 1986). This formed the foundation of *Genera Palmarum, a classification of palms based on the work of Harold E. Moore Jr.* (Uhl & Dransfield, 1987), or GP1, for short. The title defers to Moore's contribution, but it should be stressed that this 610-page book was an entirely new work, with original descriptions of all 200 genera accepted at the time, introductory chapters and other materials produced by Uhl and Dransfield. At the time, no comparably detailed or complete work for palms had been published since the legendary three-volume *Historia Naturalis Palmarum* of Martius (von Martius, 1823–1850). Its influence is clear from the amount of palm research that it spawned, as indicated by the c. 800 citations of GP1 recorded by Google Scholar today.

In a sense, GP1 became a victim of its own success. With the mass of new information about palms arising from research inspired by GP1, a complete revision became necessary (Uhl & Dransfield, 1999). A version of the GP1 classification, with updated generic taxonomy, was published in *Families and Genera of Vascular Plants* (Dransfield & Uhl, 1998), but the rapid rise of molecular phylogenetics pointed to the need for a much more radical revision (Uhl *et al.*, 1995; Baker *et al.*, 1999a; Asmussen, Baker & Dransfield, 2000; Asmussen & Chase, 2001). In the early 2000s, a project to produce a new *Genera Palmarum* took shape during a succession of meetings hosted by the Montgomery Botanical Center. Recognizing the opportunity to build a classification around a formal phylogenetic framework, Dransfield and Uhl drew in new collaborators, especially those active in the field of palm phylogenetics (Conny Asmussen-Lange, William Baker, Madeline Harley and Carl Lewis). At a summit in

Cornell University in 2004, the authors constructed a new classification of palms as a foundation for the new *Genera Palmarum*, drawing on all available phylogenetic evidence, which was published the following year (Dransfield *et al.*, 2005). The resulting book, *Genera Palmarum – the Evolution and Classification of Palms* (Dransfield *et al.*, 2008b), now known widely as GP2, is not simply a revised edition of GP1, but a completely new account of the palms. At 744 pages, GP2 contains c. 40% more content than GP1, including rewritten treatments for the 183 accepted genera, significant additions on phylogeny, biogeography, the fossil record and pollen, and expanded illustrations, photographs, maps and glossary.

The phylogenetic classification of GP2 employs monophyly as the primary criterion for the delimitation of taxa and topological evidence to determine a logical linear taxonomic sequence. As a result, the classification is substantially different from that of GP1. Major realignments were made in the five subfamilies of the new classification (Asmussen *et al.*, 2006). Coryphoideae was expanded to include Caryoteae (formerly in Arecoideae), and Chamaedoreae (formerly in Ceroxyloideae under the name Hyophorbeae) was moved to Arecoideae. Ceroxyloideae was re-delimited to include Phytelephantoideae of GP1 (as Phytelephea) with tribes Cyclospatheae and Ceroxyleae. Significant changes were made at tribal and subtribal levels, such as the re-delimitation of Areceae and the subtribes within it. Further details of the correspondence between the classifications of GP2, GP1 and earlier schemes can be found in Chapter 9 of GP2.

Ten years on, it is time to reflect on the classification underpinning GP2 and the developments that have taken place in palm systematics since its first publication (Dransfield *et al.*, 2005), as Uhl and Dransfield did 10 years after GP1 (Uhl & Dransfield, 1999). Having set the scene, in the remainder of this paper we review developments in two main areas, (1) palm classification and (2) phylogenetics, providing an extensive bibliography of the latest palm research and concluding with a discussion of future prospects for palm systematics.

PALM CLASSIFICATION

The delimitation of the five subfamilies, 28 tribes and 27 subtribes recognized in the GP2 classification has, so far, been robust to new phylogenetic findings and, to date, no amendments to the higher level classification have been proposed [with the exception of the correction of the subtribe name *Linospadicinae* to *Laccospadicinae* (Dransfield *et al.*, 2011); Table 1].

Table 1. Summary of change in taxon numbers in the classification of palms. Column 2 indicates the taxa recognized in the first publication of the phylogenetic classification of palms (Dransfield *et al.*, 2005), updated and refined in *Genera Palmarum* (GP2; Dransfield *et al.*, 2008b). Column 3 reflects the status of palm classification in October 2015 (see text). Species numbers derived from Govaerts *et al.* (2015).

	2008	2015
Subfamilies	5	5
Tribes	28	28
Subtribes	27	27
Genera	183	181
Unplaced genera	17	17
Species	c. 2400	c. 2600

Although modifications in the future cannot be ruled out, the GP2 suprageneric classification appears to be meeting its stated goals of being phylogenetically informative and stable.

At the genus level, however, there has been considerable change. Currently, 181 genera are accepted, a net decrease of only two from the 183 recognized by Dransfield *et al.* (2008b), but this conceals the fact that six additional genera are now accepted, whereas eight have been placed in synonymy (Table 2). The recognition of six new genera in the 8 years since the publication of GP2 in 2008 is striking, given that only seven genera were added in the 21 years between the publication of GP1 and GP2: *Voanioala* J.Dransf. (Dransfield, 1989), *Aphandra* Barfod (Barfod, 1991), *Lemurophoenix* J.Dransf. (Dransfield, 1991), *Satranala* J.Dransf. & Beentje (Dransfield & Beentje, 1995b), *Dransfieldia* W.J.Baker & Zona (Baker *et al.*, 2006), *Leucothrinax* C.Lewis & Zona (Lewis & Zona, 2008) and *Tahina* J.Dransf. & Rakotoarin. (Dransfield *et al.*, 2008a). The additional

Table 2. Changes in accepted palm genera since the publication of *Genera Palmarum* (GP2; Dransfield *et al.*, 2008b)

Subfamily	Genera gained	Genera lost
Calamoideae		<i>Ceratolobus</i> <i>Daemonorops</i> <i>Pogonotium</i> <i>Retispatha</i>
Coryphoideae	<i>Lanonia</i> <i>Saribus</i> <i>Sabinaria</i>	<i>Pritchardiopsis</i> <i>Wallichia</i>
Arecoideae	<i>Jailoloa</i> <i>Manjekia</i> <i>Wallaceodoxa</i>	<i>Lytocaryum</i> <i>Solfia</i>

genera have resulted from novel discoveries in the field, phylogenetic evidence or a combination of both. In contrast, the sinking of genera has been driven purely by phylogenetics and findings of non-monophyly. The overwhelming majority of the generic gains and losses are in palms of the Asian Pacific, reflecting the relative intensity of systematic research on palms in this region. A full classification of palms is presented here (Table 3), updated to account for all changes to date.

GENERA GAINED SINCE GP2

The generic treatments provided here are structured to be consistent with the generic treatments in GP2, with some abbreviations. A ‘fossil record’ section is excluded as fossils have not been linked to any of the new genera at this time.

Sabinaria R.Bernal & Galeano, *Phytotaxa* 144: 28 (2013). Type: *Sabinaria magnifica* Galeano & R.Bernal (Fig. 1).

Etymology: Named after the daughter of the authors, Sabina Bernal Galeano.

Taxonomic account and description: Galeano & Bernal (2013).

Distribution and ecology: One species known only from the Serranía del Darién in north-western Colombia, but probably also occurring in neighbouring areas of Panama. Primary, tropical rain forest between 100 m and 250 m.

Anatomy: Pollen (Bogotá-A *et al.*, 2015).

Relationships: *Sabinaria* belongs to Cryosophileae (Coryphoideae). It is well supported as sister to *Itaya* H.E.Moore (A. Cano, unpubl. data).

Common names and uses: *Girasol* (sunflower in Spanish). Leaves used occasionally for umbrellas or thatch.

Notes: Known only from a small, isolated area in the Darién Gap, *Sabinaria* is probably the most spectacular of the new genera discovered since GP2 (Galeano & Bernal, 2013; Bernal, 2014). Colombia has been rather well explored for palms in recent decades on account of the scientific leadership of two of South America’s most prolific palm biologists, Rodrigo Bernal and Gloria Galeano. Thus, the discovery by Norman Echavarría and Saúl Hoyos, botanical collaborators of Bernal and Galeano, of such a conspicuous and unusual new genus was highly surprising. The spectacular leaves of *Sabinaria* are its most distinctive character, being divided almost in half by a deep median, abaxial split (in common with other Cryosophileae, such as *Cryosophila* Blume or *Chelyocarpus* Dammer), whereas the remainder of the lamina margin is almost

Table 3. Revised classification of Arecaceae, updated to incorporate changes made since *Genera Palmarum* (GP2; Dransfield *et al.*, 2008b). In the interests of stability, the linear sequence of genera has not been revised here because of the large amount of palm phylogenetic research in progress at the moment, and is consistent with the prevailing accounts (Dransfield *et al.*, 2005, 2008b; Trias-Blasi *et al.*, 2015). Changes are indicated with superscript letters and summarized as follows. ^A*Calamus*, expanded to include *Ceratolobus*, *Daemonorops*, *Pogonotium* and *Retispatha* (Baker, 2015; Henderson & Floda, 2015). ^B*Sabinaria*, new genus (Galeano & Bernal, 2013). ^C*Livistona*, re-delimited, species transferred to *Saribus* (Bacon & Baker, 2011). ^D*Licuala*, re-delimited, species transferred to *Lanonia* (Henderson & Bacon, 2011). ^E*Saribus*, resurrected and re-delimited to include part of *Livistona* and monotypic *Pritchardiopsis* (Bacon & Baker, 2011). ^F*Lanonia*, new genus (Henderson & Bacon, 2011). ^G*Arenga*, expanded to include *Wallichia* (Jeanson, 2011). ^H*Syagrus*, expanded to include *Lytocaryum* (Noblick & Meerow, 2015). ^ILaccospadicinae, subtribal name corrected from Linospadicinae (Dransfield *et al.*, 2011). ^J*Ponapea*, expanded to include part of *Drymophloeus* (Zona *et al.*, 2011). ^K*Balaka*, expanded to include *Solfia* (Zona & Baker, 2014). ^L*Veitchia*, expanded to include part of *Drymophloeus* (Zona *et al.*, 2011). ^M*Drymophloeus*, re-delimited, species transferred to *Ponapea* and *Veitchia* (Zona *et al.*, 2011). ^{N-P}*Jailoloa*, *Manjekia*, *Wallaceodoxa*, new genera (Heatubun *et al.*, 2014b).

SUBFAMILY**Tribe**

Subtribe	Genus
CALAMOIDEAE	
Eugeissoneae	1. <i>Eugeissona</i> Griff.
Lepidocaryeae	
Ancistrophyllinae	2. <i>Oncocalamus</i> (G.Mann & H.Wendl.) H.Wendl. 3. <i>Eremospatha</i> (G.Mann & H.Wendl.) Schaedtler 4. <i>Laccosperma</i> (G.Mann & H.Wendl.) Drude
Raphiinae	5. <i>Raphia</i> P.Beauv.
Mauritiinae	6. <i>Lepidocaryum</i> Mart. 7. <i>Mauritia</i> L.f. 8. <i>Mauritiella</i> Burret
Calameae	
Korthalsiinae	9. <i>Korthalsia</i> Blume
Salaccinae	10. <i>Eleiodoxa</i> (Becc.) Burret 11. <i>Salacca</i> Reinw.
Metroxylinae	12. <i>Metroxylon</i> Rottb.
Pigafettinae	13. <i>Pigafetta</i> (Blume) Becc.
Plectocomiinae	14. <i>Plectocomia</i> Mart. & Blume 15. <i>Myrialepis</i> Becc. 16. <i>Plectocomiopsis</i> Becc.
Calaminae	17. <i>Calamus</i> L. ^A
NYPOIDEAE	18. <i>Nypa</i> Steck
CORYPHOIDEAE	
Sabaleae	19. <i>Sabal</i> Adans.
Cryosophileae	20. <i>Schippia</i> Burret 21. <i>Trithrinax</i> Mart. 22. <i>Zombia</i> L.H.Bailey 23. <i>Coccothrinax</i> Sarg. 24. <i>Hemithrinax</i> Hook.f. 25. <i>Leucothrinax</i> C.Lewis & Zona 26. <i>Thrinax</i> L.f. ex Sw. 27. <i>Chelyocarpus</i> Dammer 28. <i>Cryosophila</i> Blume 29. <i>Itaya</i> H.E.Moore 30. <i>Sabinaria</i> R.Bernal & Galeano ^B

Table 3. *Continued*

SUBFAMILY		
Tribe		Genus
Subtribe		
Phoeniceae		31. <i>Phoenix</i> L.
Trachycarpeae		
Rhapidinae		32. <i>Chamaerops</i> L. 33. <i>Guihaia</i> J.Dransf., S.K.Lee & F.N.Wei 34. <i>Trachycarpus</i> H.Wendl. 35. <i>Rhapidophyllum</i> H.Wendl. & Drude 36. <i>Maxburretia</i> Furtado 37. <i>Rhapis</i> L.f. ex Aiton
Livistoninae		38. <i>Livistona</i> R.Br. ^C 39. <i>Licuala</i> Wurmbr. ^D 40. <i>Johannesteijsmannia</i> H.E.Moore 41. <i>Pholidocarpus</i> Blume 42. <i>Saribus</i> Blume ^E 43. <i>Lanonia</i> A.J.Hend. & C.D.Bacon ^F
Unplaced Trachycarpeae		44. <i>Acoelorrhaphe</i> H.Wendl. 45. <i>Serenoa</i> Hook.f. 46. <i>Brahea</i> Mart. 47. <i>Colpothrinax</i> Schaedtler 48. <i>Copernicia</i> Mart. ex Endl. 49. <i>Pritchardia</i> Seem. & H.Wendl. 50. <i>Washingtonia</i> H.Wendl.
Chuniophoeniceae		51. <i>Chuniophoenix</i> Burret 52. <i>Kerriodoxa</i> J.Dransf. 53. <i>Nannorrhops</i> H.Wendl. 54. <i>Tahina</i> J.Dransf. & Rakotoarin.
Caryoteae		55. <i>Caryota</i> L. 56. <i>Arenga</i> Labill. ex DC. ^G
Coryphea		57. <i>Corypha</i> L.
Borasseae		
Hyphaeninae		58. <i>Bismarckia</i> Hildebr. & H.Wendl. 59. <i>Satranala</i> J.Dransf. & Beentje 60. <i>Hyphaene</i> Gaertn. 61. <i>Medemia</i> Württemb. ex H.Wendl.
Lataniinae		62. <i>Latania</i> Comm. ex Juss. 63. <i>Lodoicea</i> Comm. ex DC. 64. <i>Borassodendron</i> Becc. 65. <i>Borassus</i> L.
CEROXYLOIDEAE		
Cyclospatheae		66. <i>Pseudophoenix</i> H.Wendl. ex Sarg.
Ceroxyleae		67. <i>Ceroxylon</i> Bonpl. ex DC. 68. <i>Juania</i> Drude 69. <i>Oraniopsis</i> (Becc.) J.Dransf., A.K.Irvine & N.W.Uhl 70. <i>Ravenea</i> H.Wendl. ex C.D.Bouché
Phytelephea		71. <i>Ammandra</i> O.F.Cook 72. <i>Aphandra</i> Barfod 73. <i>Phytelephas</i> Ruiz & Pav.

Table 3. *Continued*

SUBFAMILY	
Tribe	Genus
Subtribe	
ARECOIDEAE	
Iriarteeae	74. <i>Iriartella</i> H.Wendl. 75. <i>Dictyocaryum</i> H.Wendl. 76. <i>Iriartea</i> Ruiz & Pav. 77. <i>Socratea</i> H.Karst. 78. <i>Wettinia</i> Poepp. ex Endl.
Chamaedoreae	79. <i>Hyophorbe</i> Gaertn. 80. <i>Wendlandiella</i> Dammer 81. <i>Synechanthus</i> H.Wendl. 82. <i>Chamaedorea</i> Willd. 83. <i>Gaussia</i> H.Wendl.
Podococceae	84. <i>Podococcus</i> G.Mann & H.Wendl.
Oranieae	85. <i>Orania</i> Zipp.
Sclerospermeae	86. <i>Sclerosperma</i> G.Mann & H.Wendl.
Roystoneae	87. <i>Roystonea</i> O.F.Cook
Reinhardtiae	88. <i>Reinhardtia</i> Liebm.
Cocoseae	
Attaleinae	89. <i>Beccariophoenix</i> Jum. & H.Perrier 90. <i>Jubaeopsis</i> Becc. 91. <i>Voanioala</i> J.Dransf. 92. <i>Allagoptera</i> Nees in M.A.P.zu Wied-Neuwied 93. <i>Attalea</i> Kunth 94. <i>Butia</i> (Becc.) Becc. 95. <i>Cocos</i> L. 96. <i>Jubaea</i> Kunth 97. <i>Syagrus</i> Mart. ^H 98. <i>Parajubaea</i> Burret
Bactridinae	99. <i>Acrocomia</i> Mart. 100. <i>Astrocaryum</i> G.Mey. 101. <i>Aiphanes</i> Willd. 102. <i>Bactris</i> Jacq. ex Scop. 103. <i>Desmoncus</i> Mart.
Elaeidinae	104. <i>Barcella</i> (Trail) Drude 105. <i>Elaeis</i> Jacq.
Manicarieae	106. <i>Manicaria</i> Gaertn.
Euterpeae	107. <i>Hyospathe</i> Mart. 108. <i>Euterpe</i> Mart. 109. <i>Prestoea</i> Hook.f. 110. <i>Neonicholsonia</i> Dammer 111. <i>Oenocarpus</i> Mart.
Geonomateae	112. <i>Welfia</i> H.Wendl. 113. <i>Pholidostachys</i> H.Wendl. ex Hook.f. 114. <i>Calyptrogyne</i> H.Wendl. 115. <i>Calyptronoma</i> Griseb. 116. <i>Asterogyne</i> H.Wendl. ex Hook.f. 117. <i>Geonoma</i> Willd.

Table 3. Continued

SUBFAMILY

Tribe

Subtribe	Genus
Leopoldinieae	118. <i>Leopoldinia</i> Mart.
Pelagodoxeae	119. <i>Pelagodoxa</i> Becc. 120. <i>Sommieria</i> Becc.
Areceae	
Archontophoenicinae	121. <i>Actinorhytis</i> H.Wendl. & Drude 122. <i>Archontophoenix</i> H.Wendl. & Drude 123. <i>Actinokentia</i> Dammer 124. <i>Chambeyronia</i> Vieill. 125. <i>Kentiopsis</i> Brongn.
Arecinae	126. <i>Areca</i> L. 127. <i>Nenga</i> H.Wendl. & Drude
Basseliinae	128. <i>Pinanga</i> Blume 129. <i>Basselinia</i> Vieill. 130. <i>Burretiokentia</i> Pic.Serm. 131. <i>Cyphophoenix</i> H.Wendl. ex Hook.f 132. <i>Cyphosperma</i> H.Wendl. ex Hook.f 133. <i>Lepidorrhachis</i> (H.Wendl. & Drude) O.F.Cook 134. <i>Physokentia</i> Becc.
Carpoxylinae	135. <i>Carpoxylon</i> H.Wendl. & Drude 136. <i>Satakentia</i> H.E.Moore 137. <i>Neoveitchia</i> Becc.
Clinospermatinae	138. <i>Cyphokentia</i> Brongn. 139. <i>Clinosperma</i> Becc.
Dypsidinae	140. <i>Dypsis</i> Noronha ex Mart. 141. <i>Lemurophoenix</i> J.Dransf. 142. <i>Marojejya</i> Humbert 143. <i>Masoala</i> Jum.
Laccospadicinae ^I	144. <i>Calyptrocalyx</i> Blume 145. <i>Linospadix</i> H.Wendl. 146. <i>Howea</i> Becc. 147. <i>Laccospadix</i> H.Wendl. & Drude
Oncospermatinae	148. <i>Oncosperma</i> Blume 149. <i>Deckenia</i> H.Wendl. ex Seem. 150. <i>Acanthophoenix</i> H.Wendl. 151. <i>Tectiphiala</i> H.E.Moore
Ptychospermatinae	152. <i>Ptychosperma</i> Labill. 153. <i>Ponapea</i> Becc. ^J 154. <i>Adonidia</i> Becc. 155. <i>Balaka</i> Becc. ^K 156. <i>Veitchia</i> H.Wendl. ^L 157. <i>Carpentaria</i> Becc. 158. <i>Wodyetia</i> A.K.Irvine 159. <i>Drymophloeus</i> Zipp. ^M 160. <i>Normanbya</i> F.Muell. ex Becc. 161. <i>Brassiophoenix</i> Burret 162. <i>Ptychococcus</i> Becc. 163. <i>Jailoloa</i> Heatubun & W.J.Baker ^N 164. <i>Manjekia</i> W.J.Baker & Heatubun ^O 165. <i>Wallaceodoxa</i> Heatubun & W.J.Baker ^P

Table 3. Continued

SUBFAMILY

Tribe

Subtribe	Genus
Rhopalostylidinae	166. <i>Rhopalostylis</i> H.Wendl. & Drude 167. <i>Hedyscepe</i> H.Wendl. & Drude
Verschaffeltiinae	168. <i>Nephrosperma</i> Balf.f. 169. <i>Phoenicophorium</i> H.Wendl. 170. <i>Roscheria</i> H.Wendl. ex Balf.f. 171. <i>Verschaffeltia</i> H.Wendl.
Unplaced Areceae	172. <i>Bentinckia</i> Berry ex Roxb. 173. <i>Clinostigma</i> H.Wendl. 174. <i>Cyrtostachys</i> Blume 175. <i>Dictyosperma</i> H.Wendl. & Drude 176. <i>Dransfieldia</i> W.J.Baker & Zona 177. <i>Heterospatha</i> Scheff. 178. <i>Hydriastele</i> H.Wendl. & Drude 179. <i>Iguanura</i> Blume 180. <i>Loxococcus</i> H.Wendl. & Drude 181. <i>Rhopaloblaste</i> Scheff.



Figure 1. *Sabinaria magnifica*, Serranía del Darién, Colombia. A, Habit, with the eponymous Sabina Bernal Galeano providing scale. B, Infructescence, rachis bracts parted to reveal fruits. Photographs: W. J. Baker.



Figure 2. *Lanonia gracilis*, cultivated, Kebun Raya, Bogor, Indonesia. A, Habit. B, Inflorescence. Photographs: W. J. Baker.

entire, being only shallowly lobed by short splits. In addition, the lamina is glossy green above, but silver-white below.

Sabinaria most closely resembles its sister genus *Itaya* as they both bear a biseriate perianth, gynoecea comprising a single carpel and androecea with numerous stamens. *Sabinaria* is, however, distinguished from *Itaya* by its unisexual flowers, the pistillate flowers being located at the base of the lower rachillae only, and the persistent rachis bracts that enclose the rachillae (especially at the base) and tightly ensheath the developing fruit. In contrast, *Itaya* has hermaphroditic flowers and deciduous rachis bracts. The flowers of *Sabinaria* are also unique in Cryosophyleae in that the two whorls of the perianth, although distinct, are connate at a single point of contact.

Lanonia A.J.Hend. & C.D.Bacon, Syst. Bot. 36: 887 (2011). Type: *Lanonia acaulis* (A.J.Hend., N.K.Ban & N.Q.Dung) A.J.Hend. & C.D.Bacon (basionym: *Licuala acaulis* A.J.Hend., N.K.Ban & N.Q.Dung) (Fig. 2).

Etymology: Based on a Vietnamese local name *la non*, meaning hat palm, referring to its use in the manufacture of the typical conical hats of the region.

Taxonomic account and description: Henderson & Bacon (2011).

Distribution and ecology: Eight species, six from Vietnam, two of which reach into adjacent Laos and China, respectively, one from Hainan and one from Java. Primary, tropical rain forest from low elevation to 1700 m.

Anatomy: Not studied.

Relationships: *Lanonia* belongs to Livistoninae (Coryphoideae: Trachycarpeae). It is strongly supported as a monophyletic genus that is moderately to strongly supported as sister to *Johannesteijsmannia* H.E.Moore (Henderson & Bacon, 2011; Bacon, Baker & Simmons, 2012a; Bacon *et al.*, 2013a).

Common names and uses: Hat palm or *la non* (Vietnam). At least one species [*L. centralis* (A.J.Hend., N.K.Ban & N.Q.Dung) A.J.Hend. & C.D.Bacon] used for making conical hats in Vietnam. For further details on common names and uses, see Henderson & Bacon (2011).

Notes: *Lanonia* was described as a segregate of the Asia-Pacific genus *Licuala* Wurm. by Andrew Henderson and Christine Bacon (2011). Comprehensive phylogenetic research on Trachycarpeae (Henderson & Bacon, 2011; Bacon *et al.*, 2012a, 2013a) revealed that a group of species described in *Licuala* is in fact



Figure 3. *Saribus*. A, *S. merrillii*, habit, cultivated. B, *S. rotundifolius*, trifurcate inflorescence base, cultivated, Kebun Raya, Bogor, Indonesia. Photographs: C. E. Lewis and W. J. Baker.

more closely related to *Johannesteijsmannia* than it is to *Licuala*, and required recognition at generic rank. This was surprising because it showed that the unique *Licuala*-type leaf is not restricted to a single genus as previously thought, but shared among two monophyletic lineages that are not sister taxa, i.e. *Lanonia* and *Licuala* s.s. *Licuala*-type leaves are, in essence, typical induplicately divided, palmate coryphoid leaves that are further subdivided to the base into wedge-shaped segments by a number of deep, secondary, splits along abaxial folds (Dransfield *et al.*, 2008b). The leaves of *Lanonia* are further characterized by the central segment being split to the apex of a short costa, which bears a pulvinus-like structure on its abaxial surface.

A number of reproductive characters further distinguish *Lanonia* from the superficially similar *Licuala* and its sister genus *Johannesteijsmannia*. *Lanonia* is typically dioecious, often with sexually dimorphic inflorescences, and bears staminate flowers in pairs or clusters and solitary pistillate flowers. The staminate flowers contain dorsifixed, non-versatile anthers, whereas the perianth of the pistillate flowers reflexes in fruit, the calyx splitting into six lobes after anthesis. Although half of the included species are based on taxa described in the 19th and

early 20th centuries, remarkably, the remaining four are recent discoveries described since 2007.

Saribus Blume, *Rumphia* 2: 48 (1838). Lectotype: *Saribus rotundifolius* (Lam.) Blume (basonym: *Corypha rotundifolia* Lam.) (Fig. 3).

Pritchardiopsis Becc., *Webbia* 3: 131 (1910). Type: *Pritchardiopsis jeanneneyi* Becc. [= *Saribus jeanneneyi* (Becc.) C.D. Bacon & W.J.Baker].

Etymology: Latinization of a Moluccan plant name, *saribu*.

Taxonomic account and description: Eight species treated in a monograph of *Livistona* R.Br. (Dowe, 2009) and a ninth in *Pritchardiopsis* (Hodel & Pin-taud, 1998). A description of the genus is not currently available.

Distribution and ecology: Nine species, six endemic to Papuasia (New Guinea and Solomon Islands), one endemic to the Philippines, one endemic to New Caledonia and one species that is widespread in central Malesia (Philippines to Raja Ampat). Various kinds of tropical, ever-wet forest from lowlands to 1300 m.

Anatomy: Leaf (Tomlinson, Horn & Fisher, 2011).

Relationships: *Saribus* belongs to Livistoninae (Coryphoideae: Trachycarpeae). It is strongly supported as a monophyletic genus and is resolved as



Figure 4. *Jailoloa halmaherensis*, Halmahera, Indonesia. A, Habit. B, Fruit. Photographs: C. D. Heatubun.

sister to *Pholidocarpus* Blume, although with only weak support (Bacon & Baker, 2011; Bacon *et al.*, 2012a, 2013a).

Common names and uses: Numerous local names reported by Dowe (2009). Uses include leaves for thatch and edible palm hearts. *Saribus rotundifolius* is an important ornamental in the tropics.

Notes: Although the generic name *Saribus* is far from new (Blume, 1838), the concept of this resurrected genus, as proposed by Christine Bacon and William Baker (Bacon & Baker, 2011), is significantly different from any used previously. As with *Lanonia*, the evidence for the addition of a further coryphoid genus in Livistoninae stemmed from phylogenetic studies of Trachycarpeae (Bacon *et al.*, 2012a, 2013a), which showed that *Livistona* (*sensu* Dransfield *et al.*, 2008b; and Dowe, 2009) was not monophyletic, but divided into two separate clades. The first clade comprised the majority of *Livistona* as sister to all other genera of Livistoninae. The remaining *Livistona* spp. formed the second, smaller clade, which was resolved as sister to *Pholidocarpus*. This segregate group, in which the New Caledonian monotypic genus *Pritchardiopsis* was also nested, was thus delimited as a new generic concept for which two genus names already existed: *Saribus*, typified on *S. rotundifolius* (Lam.) Blume, and *Pritchardiopsis*, the former, older name

taking priority. It should be noted that, in the most recent monograph of *Livistona* (Dowe, 2009), the species now included in *Saribus* were highlighted as a distinct group of close relatives, although a connection to *Pritchardiopsis* was not made.

The group is unique among other genera of Livistoninae in its trifurcate inflorescences, which comprise three (sometimes two) equal primary axes within a common prophyll (in contrast with the single axis of all other Livistoninae). In addition, the mature fruits of *Saribus* spp. are orange, orange-brown or red, whereas *Livistona* fruits are green, blue, purple, brown or black. A number of leaf anatomical characters have also been identified for *Saribus* (Tomlinson *et al.*, 2011).

The removal of *Saribus* accentuates the disjunct distribution of *Livistona* s.s., which occurs in South-East Asia only west of Wallace's Line, Australia, the horn of Africa and the Arabian Peninsula (Bacon & Baker, 2011).

Jailoloa Heatubun & W.J.Baker, Kew Bull. 69 (9525): 5 (2014). Type: *Jailoloa halmaherensis* (Heatubun) Heatubun & W.J.Baker (basonym: *Ptychosperma halmaherense* Heatubun) (Fig. 4).

Etymology: Refers to Jailolo, an earlier name for the island of Halmahera.



Figure 5. *Manjekia maturbongsii*, Biak, Indonesia. A, Habit. B, Inflorescence. Photographs: W. J. Baker.

Taxonomic account and description: Heatubun, Zona & Baker (2014b).

Distribution and ecology: One species from Halmahera. Heath forest on ultramafic rocks at c. 550 m.

Anatomy: Not studied.

Relationships: *Jailoloa* belongs to Ptychospermatinae (Arecoideae: Areceae). It is moderately supported as sister to *Manjekia* W.J.Baker & Heatubun (Alapetite, Baker & Nadot, 2014).

Common names and uses: None recorded.

Notes: The publication of any new palm genus is a significant event, but the simultaneous description of three new genera is unprecedented in recent decades (Heatubun *et al.*, 2014b, c). *Jailoloa*, *Manjekia* and *Wallaceodoxa* Heatubun & W.J.Baker were described as a result of fieldwork in eastern Indonesia led by Charlie Heatubun and William Baker to smaller islands to the north and west of the western end of New Guinea. The first two genera were initially described in *Ptychosperma* Labill. and *Adonidia* Becc., respectively, based on morphological and DNA evidence (Heatubun, 2011a; Zona *et al.*, 2011; Baker & Heatubun, 2012). These decisions were reconsidered as a result of subsequent work on the molecular phylogenetics of Ptychospermatinae, which placed the three taxa with *Adonidia* in a paraphyletic group at the base of a clade also con-

taining the sister genera *Veitchia* H.Wendl. and *Balaka* Becc. (Alapetite *et al.*, 2014). The three new genera reflect this phylogenetic topology and morphological disparities, whilst maintaining taxonomic stability of existing genera (Heatubun *et al.*, 2014b). The three new genera are similar to *Adonidia* in their endocarp and seed characters (terete seed with straw-coloured fibres adhering to the endocarp), which have been considered to be systematically useful (Zona, 1999), but they are abundantly distinct in other respects.

Jailoloa is a slender palm of ultramafic heath forest, known only from one site in a nickel mining concession in Halmahera. It is distinguished from other genera of Ptychospermatinae by its recurved leaves with leathery ascending leaflets, purple inflorescence axes and flower and orange–yellow fruit. *Ptychosperma*, the most superficially similar genus, does not have ascending leaflets or the same combination of inflorescence and fruit colours, and usually has ridged endocarps and seeds.

Manjekia W.J.Baker & Heatubun, Kew Bull. 69 (9525): 9 (2014). Type: *Manjekia maturbongsii* (W.J.Baker & Heatubun) W.J.Baker & Heatubun (basonym: *Adonidia maturbongsii* W.J.Baker & Heatubun) (Fig. 5).



Figure 6. *Wallaceodoxa raja-ampat*, Waigeo, Indonesia. A, Habit. B, Inflorescence. Photographs: C. D. Heatubun.

Etymology: Based on a local name *Manjek* (Biak dialect).

Taxonomic account and description: Heatubun *et al.* (2014b).

Distribution and ecology: One species from Biak Island. Lowland rain forest on limestone up to 170 m.

Anatomy: Not studied.

Relationships: *Manjekia* belongs to subtribe Ptychospermatinae (Arecoideae: Areceae). It is moderately supported as sister to *Jailoloa* (Alapetite *et al.*, 2014).

Common names and uses: *Manjek* (Biak dialect). The stems are used in building construction.

Notes: *Manjekia* is a moderately robust, solitary palm that is recorded from several lowland rainforest localities on limestone in Biak Island. Its arching leaves bear broadly lanceolate, pendulous, praemorse leaflets with concave, praemorse apices and its inflorescence axes are white or greenish white. *Manjekia* bears some similarities to *Adonidia*, in which it was originally described, such as the white inflorescences branched up to four orders, the red fruit and similar seed and endocarp morphology, but its leaves do not resemble those of *Adonidia*, which have ascending, narrow leaflets in slightly different planes that are less conspicuously praemorse and fewer stamens in the staminate flowers (30–32, instead of 45–50 in *Adonidia*). See also notes under *Jailoloa*.

Wallaceodoxa Heatubun & W.J.Baker, Kew Bull. 69 (9525): 9 (2014). Type: *Wallaceodoxa raja-ampat* Heatubun & W.J.Baker (Fig. 6).

Etymology: The name commemorates Alfred Russel Wallace (1823–1913), renowned British naturalist, explorer of the Malay Archipelago and Amazon, co-discoverer of the theory of evolution by natural selection and author of the first field guide to palms (Wallace, 1853). Suffix *-odoxa* means ‘glory’.

Taxonomic account and description: Heatubun *et al.* (2014b).

Distribution and ecology: One species from the Raja Ampat Islands (known only from Gag and Waigeo). Lowland rainforest on limestone up to 50 m.

Anatomy: Not studied.

Relationships: *Wallaceodoxa* belongs to Ptychospermatinae (Arecoideae: Areceae). It is moderately supported as sister to *Adonidia* (Alapetite *et al.*, 2014).

Common names and uses: *Gulbotom* (Wayaf or Gebe dialect). The stem is used in building construction and the seed is consumed as a betel nut substitute.

Notes: *Wallaceodoxa* is a rare palm of the Raja Ampat Islands (Heatubun, Lekitoo & Matani, 2014a). Fewer than 40 adults have been recorded from the islands of Gag and Waigeo, to which it appears to be restricted. It is a moderately robust, solitary palm bearing arching leaves with narrow,

pendulous leaflets that are obliquely praemorse at their apices. A pronounced layer of thick, white and brown–black indumentum covers the leaf sheath, petiole and rachis. The inflorescences are greenish white with thick rachillae and relatively crowded floral triads. The staminate flower contains a short, ellipsoid pistillode, rather than the elongate, bottle-shaped pistillode that is typical of many Ptychospermatinae. With the exception of seed and endocarp characters, *Wallaceodoxa* does not obviously resemble its sister genus *Adonidia*, or indeed any other genus in the subtribe. See also notes under *Jailoloa*.

GENERA LOST SINCE GP2

CERATOLOBUS, *DAEMONOROPS*, *POGONOTIUM* AND
RETISPATHA (CALAMOIDEAE: CALAMEAE: CALAMINAE).

The non-monophyly of the rattan genus *Calamus* L. has been revealed in multiple phylogenetic studies (Baker *et al.*, 1999b; Baker, Dransfield & Hedderson, 2000a; Baker, Hedderson & Dransfield, 2000b, c; Baker *et al.*, 2009; W. J. Baker, unpubl. data), all of which indicate that the remaining genera of Calaminae are variously nested in *Calamus*. In GP2, Dransfield *et al.* (2008b) were reluctant to address this problem taxonomically, following earlier authors (Baker *et al.*, 2000b) who preferred to wait for further data before proposing an alternative classification. Notwithstanding this, a process of reduction in genera of Calaminae had already started, first with the sinking of *Calospatha* Becc. into *Calamus* in preparation for GP2 (Baker & Dransfield, 2008), more recently followed by *Retispatha* J.Dransf. (Henderson & Floda, 2015). Baker (2015) completed this process by sinking the remaining three genera of Calaminae (*Ceratolobus* Blume, *Daemonorops* Blume ex Schult.f. and *Pogonotium* J.Dransf.) into *Calamus*, thereby expanding the largest genus of palms from > 400 to c. 520 species.

The re-delimited, broad concept of *Calamus* has several advantages. First, it is a stable, pragmatic solution to the *Calamus* problem that is likely to be robust to any future phylogenetic findings. Second, it ensures that the largest genus of palms is in fact monophyletic and phylogenetically sound. Third, it is more easily identified, compared with the ambiguously defined and polymorphic *Calamus* s.s. and the multiple genera nested in it. *Calamus* is now defined as a genus of dioecious, pleoanthic rattan species, usually with a swollen knee-like structure on the leaf sheath at the petiole base, with inflorescences adnate to the internode and leaf sheath above the axil of origin, and with floral clusters almost always comprising a functional pistillate flower and a sterile staminate flower in the female plant and a solitary staminate flower in the male plant. The genus also

appears to be supported by anatomical evidence (Seubert, 1996; Fisher, Tan & Toh, 2002; Tomlinson & Spangler, 2002; Tomlinson *et al.*, 2011).

PRITCHARDIOPSIS (CORYPHOIDEAE: TRACHYCARPEAE:
LIVISTONINAE).

Saribus includes the sole species of the monotypic *Pritchardiopsis* (Bacon & Baker, 2011; Bacon *et al.*, 2012a). As *Saribus* is an earlier generic name, *Pritchardiopsis* has therefore been placed in synonymy. For further discussion, see the treatment of *Saribus* above.

WALLICHIA (CORYPHOIDEAE: CARYOTEAE).

Jeanson (2011) completed a monographic study of tribe Caryoteae that points to the sinking of *Wallichia* Roxb., as a result of it being embedded in a paraphyletic *Arenga* Labill., although formal synonymy has not yet been published. Dransfield *et al.* (2008a, b) acknowledged that the differences between the two genera are small, the only unambiguous character being the sepals of the staminate flower being connate in a tube, rather than free and imbricate (as in *Arenga*). Therefore, this taxonomic change is unsurprising.

LYTOCARYUM (ARECOIDEAE: COCOSEAE: ATTALEINAE).

In GP2, the small genus *Lytocaryum* Toledo is distinguished from other species of Attaleinae by its fruit with its epicarp and mesocarp splitting at maturity and its thin endocarp, by its narrow, closely spaced leaflets with pale indumentum abaxially and its versatile anthers. In a recent paper (Noblick & Meerow, 2015), a strong case is made for reducing *Lytocaryum* into *Syagrus* Mart., as proposed by earlier workers (e.g. Glassman, 1965). There is much phylogenetic evidence for the close relationship between *Lytocaryum* and *Syagrus* (Hahn, 2002b; Gunn, 2004; Baker *et al.*, 2009), with the most recent studies (Meerow *et al.*, 2009, 2015) suggesting that *Lytocaryum* may in fact be nested in *Syagrus*. Noblick & Meerow (2015) also demonstrated that all distinguishing characters of *Lytocaryum* are found, at least to some extent, in *Syagrus*.

SOLFIA (ARECOIDEAE: ARECEAE: PTYCHOSPERMATINAE).

The Samoan, monotypic *Solfia* Rechner was resurrected from synonymy in *Drymophloeus* Zipp. on morphological grounds (Zona, 1999) and included as an accepted genus in GP2. Multiple molecular phylogenetic studies have indicated that it is closely related to *Balaka* from Fiji and Samoa (Norup *et al.*,

2006; Baker *et al.*, 2009, 2011; Zona *et al.*, 2011). However, a recent study of Ptychospermatinae with near-complete taxon sampling (Alapetite *et al.*, 2014) placed *Solfia* in *Balaka*. Consequently, *Solfia* was placed in synonymy (Zona & Baker, 2014), resulting in a monophyletic if somewhat heterogeneous *Balaka* (e.g. in relation to endocarp morphology), which is consistent with the rather challenging nature of generic delimitation across the subtribe.

THE CASE OF *HEXOPETION* (ARECOIDEAE: COCOSEAE: BACTRIDINAE).

Hexopetion Burret, originally described by Burret (1934), was resurrected and expanded by Pintaud, Millán & Kahn (2008) as a segregate of two species from *Astrocaryum* G.Mey. The characters presented to distinguish *Hexopetion* were multifold lateral leaflets in adults, the lack of a sterile portion of the rachilla between the basal pistillate flower and distal staminate flowers, white, woolly indumentum on the rachilla between the flowers, stigmas much shorter than the ovary and leaf vascular anatomical features. Phylogenetic evidence to support the segregation of *Hexopetion* was not presented at that time. Dransfield *et al.* (2008b) considered that insufficient justification had been provided for *Hexopetion* to be accepted in GP2.

Several molecular phylogenetic studies have now clarified that the two *Astrocaryum* spp. included in *Hexopetion* by Pintaud *et al.* (*A. alatum* H.F.Loomis and *A. mexicanum* Liebm. ex Mart.) form a monophyletic group that is sister to a clade comprising all remaining *Astrocaryum* spp. (Eiserhardt *et al.*, 2011a; Ludena *et al.*, 2011; Roncal *et al.*, 2013, 2015; Meerow *et al.*, 2015). Thus, the argument for accepting *Hexopetion* or not is equivocal from a phylogenetic standpoint because *Astrocaryum* is monophyletic whether or not the *Hexopetion* spp. are included. Eiserhardt *et al.* (2011a) emphasized this point, but drew attention to the split between *Hexopetion* spp. and the remainder of *Astrocaryum*, which is deeper than any other in *Astrocaryum* (although it is younger than any other genus-level split in the subtribe), and the biogeographical disjunction between Central American *Hexopetion* and the mostly Amazonian remainder of *Astrocaryum*. Primarily, however, the case for recognizing *Hexopetion* rests on a subjective judgement on the sufficiency of its morphological distinctness.

Some authors have taken up *Hexopetion* (e.g. Roncal *et al.*, 2013, 2015), whereas others prefer the broad sense *Astrocaryum* (e.g. Eiserhardt *et al.*, 2011a; Meerow *et al.*, 2015). We concur with Meerow *et al.* (2015) that *Hexopetion* would be better recog-

nized at subgeneric level in *Astrocaryum* than as a genus.

SPECIES-LEVEL TAXONOMY

Although the focus of this paper is palm systematics at the genus level and above, a note on species-level taxonomy is merited. Since the publication of GP2, > 200 new palm species have been described (IPNI, 2015), with > 320 names published in total, if new combinations and replacement names are also considered. Genera that have been revised entirely (or at regional or infrageneric level) since GP2 include *Basselinia* Vieill. (in part; Pintaud & Stauffer, 2011), *Ceroxylon* Bonpl. (Sanín & Galeano, 2011), *Chunio-phoenix* Burret (Henderson, 2015), *Cyrtostachys* Blume (Heatubun *et al.*, 2009), *Desmoncus* Mart. (Henderson, 2011a), East Malesian *Areca* L. (Heatubun *et al.*, 2012), *Eremospatha* (G.Mann & H.Wendl.) Schaedtler, *Laccosperma* (G.Mann & H.Wendl.) Drude and *Oncocalamus* Mann & H. Wendl. (Sunderland, 2012), *Geonoma* Willd. (Henderson, 2011b), *Leopoldinia* Mart. (Henderson, 2011c), Bornean *Licuala* (Saw, 2012), *Livistona* (including most of *Saribus*; Dowe, 2009), *Lytocaryum* (now included in *Syagrus*; Noblick & Lorenzi, 2010), *Orania* Zipp. (Keim & Dransfield, 2012), *Pholidostachys* H.Wendl. ex Benth. & Hook.f. (Henderson, 2012), *Trithrinax* Mart. (Cano, Perret & Stauffer, 2013) and *Welfia* H.Wendl. (Henderson & Villalba, 2013). In addition, many new species have been published in non-monographic studies, e.g. in *Areca* (e.g. Heatubun, 2011b; Heatubun, Iwanggin & Simbiak, 2013), *Calamus* (e.g. Henderson & Nguyen Quoc, 2013; Baker & Dransfield, 2014), *Dyopsis* Noroha ex Thou. (e.g. Rakotoarinivo, Trudgen & Baker, 2009; Rakotoarinivo & Dransfield, 2010) and *Syagrus* (e.g. Noblick, Lorenzi & Souza, 2014). These publications indicate that there is still much alpha taxonomic research and species discovery to be accomplished in the palm family.

The biodiversity informatics portal *Palmweb* (Palmweb, 2015) has grown to become an important internet resource for palm systematics, providing complete taxonomy and distribution information for all genera and species, based on the *World Checklist of Palms* (Govaerts *et al.*, 2015) and additional rich content (e.g. descriptions, images) for c. 1500 species (Baker *et al.*, 2015). *Palmweb* data have also been provided to larger biodiversity informatics portals, such as *eMonocot* (Gardiner, Bone & Kilgallen, 2013). Content from *Palmweb* has also been repurposed in an application for mobile devices, *Palmworld*, which brings technical taxonomic con-

tent to a broader audience through a more accessible interface (Palmworld, 2015).

PALM PHYLOGENETICS

Palm phylogenetic research from its inception to 2008 was extensively reviewed in GP2, which also summarized phylogenetic evidence for each taxon from genus to subfamily. Forty-six phylogenetic papers were reported in GP2, more than one-half of which included morphological data (either exclusively or in combination with DNA data). A much smaller subset of these papers, based primarily on DNA, and with broad taxon sampling at the higher level, were of particular importance to the formulation of the new classification (Baker *et al.*, 2000a, c; Lewis & Doyle, 2001, 2002; Hahn, 2002a, b; Asmusen *et al.*, 2006; Norup *et al.*, 2006; Savolainen *et al.*, 2006; Trénel *et al.*, 2007; and some unpublished research cited in GP2 as Baker *et al.*, in review and in prep., now published as Baker *et al.*, 2009; Baker *et al.*, 2011, respectively).

Here, we provide a synthesis of palm phylogenetic developments since GP2, focusing primarily on the phylogenetics of higher level groups. The most strongly supported phylogenetic relationships among the subfamilies and tribes of palms are summarized in Figure 7.

PALM FAMILY-WIDE PHYLOGENETICS

The most prominent contribution to family-wide phylogenetics since GP2 was published by Baker *et al.* (2009), who generated the first complete genus-level phylogenetic analysis of palms. This study brought together all available major phylogenetic datasets into a supermatrix comprising 14 DNA sequence data partitions, a DNA restriction fragment length polymorphism dataset and a morphological dataset covering all palm genera. These data were analysed with a variety of supermatrix and supertree methods, resulting in a range of alternative topologies that arbitrated objectively between hypotheses obtained from subsets of the 16 partitions. The taxonomic congruence between the alternative topologies was formally evaluated to achieve a 'best estimate' of the most consistently recovered relationships. Importantly, the resulting trees were much more highly resolved than other comprehensive palm phylogenetic trees available at the time (Asmusen *et al.*, 2006).

The results of Baker *et al.* (2009) were used heavily as evidence to underpin the GP2 classification, even though they were published after GP2. Since that time, the 'palm supertree' of Baker *et al.*, as it

is often called, has been a springboard for many important comparative studies addressing biogeography and diversification (Baker & Couvreur, 2012, 2013a, b; Kissling *et al.*, 2012; Eiserhardt *et al.*, 2013a), biome origins (Couvreur, Forest & Baker, 2011; Couvreur & Baker, 2013), community assembly (Eiserhardt *et al.*, 2013b) and the evolution of floral (Sannier *et al.*, 2009; Nadot *et al.*, 2011; Rudall, Ryder & Baker, 2011), vegetative (Couvreur *et al.*, 2015; Thomas & Boura, 2015) and chemical (Siles, Cela & Munné-Bosch, 2013) traits.

Despite the wide uptake of the Baker *et al.* (2009) 'palm supertree', its potential for use in macroevolutionary research is limited by its lack of species-level detail. Some studies have identified expedient workarounds to overcome this problem (Couvreur *et al.*, 2011, 2015; Kissling *et al.*, 2012; Eiserhardt *et al.*, 2013b), but, recently, a more comprehensive solution has been sought in the construction of a complete species-level phylogenetic analysis of palms (Faurby *et al.*, in press). Faurby *et al.* assembled all publicly available DNA data for palms, covering all genera and 901 species, adding morphological data that increased the number of species for which at least one data type was available to 1255 species, representing c. 50% of the family. The complete species-level phylogenetic tree was constructed using a novel Bayesian approach with the placement of the remaining 50% of unsampled species informed by taxonomic information.

The value of the phylogenetic analysis of Faurby *et al.* lies primarily in its potential as a tool for evolutionary, ecological and biogeographical research that requires a complete tree, rather than as a truly accurate reconstruction of palm species-level relationships for systematic purposes. However, in constructing the backbone of their phylogenetic tree, Faurby *et al.* revisited the supermatrix of Baker *et al.* (2009), reanalysing it with Bayesian methods, in contrast with the parsimony-based 'total evidence' and supertree analyses that Baker *et al.* had used. A surprising number of conflicting relationships between the two studies were revealed, the more highly supported disagreements being concentrated in Calamoideae, Coryphoideae, Ceroxyleae, Cocoseae and Areceae. This serves as an important reminder that different analytical approaches should, where possible, be utilized in parallel to gain a rounded picture of the phylogenetic signal within datasets. It also further highlights areas of poor data sampling in the Baker *et al.* supermatrix, some of which have been addressed in subsequent studies. Fortunately, the tree of Faurby *et al.* did not call into question the GP2 classification, beyond those issues that were already discussed by Baker *et al.* (2009).

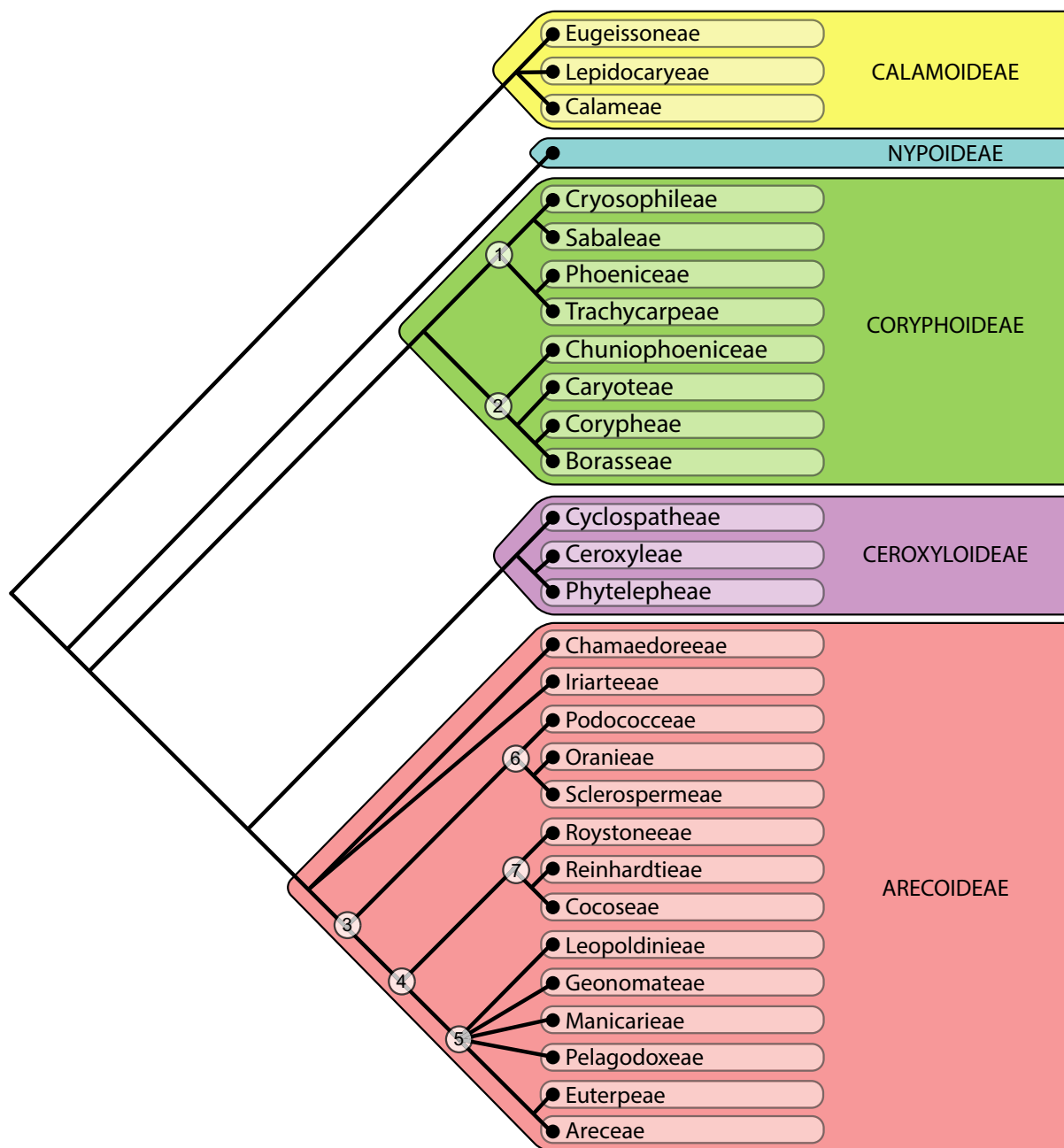


Figure 7. Schematic tree synthesizing the phylogenetic relationships among palms (redrawn and updated from Dransfield *et al.*, 2008b; fig. 6.1, p. 98). All nodes are strongly supported in at least one of the most comprehensive phylogenetic studies of palms (strong support = $\geq 90\%$ bootstrap or jackknife support for maximum parsimony or likelihood analyses, ≥ 0.9 posterior support for Bayesian analyses, or supported by ≥ 5 input trees for supertree analyses). No strongly supported conflicting relationships were identified. Relationships among subfamilies are well established (Asmussen *et al.*, 2006; Baker *et al.*, 2009, 2011; Barrett *et al.*, 2016; Faurby *et al.*, in press). Evidence for numbered nodes is as follows. Node 1. CSPT clade – Barrett *et al.* (2016), Faurby *et al.* (in press); lower support: Baker *et al.* (2009), Bacon *et al.* (2012a). Node 2. Syncarpous clade – Asmussen *et al.* (2006), Baker *et al.* (2009), Bacon *et al.* (2012a), Barrett *et al.* (2016), Faurby *et al.* (in press). Node 3. Comer *et al.* (2015, 2016), Faurby *et al.* (in press); lower support: Baker *et al.* (2009). Node 4. Comer *et al.* (2015, 2016). Node 5. Core arecoid clade – Baker *et al.* (2009, 2011), Comer *et al.* (2015, 2016), Faurby *et al.* (in press). Node 6. POS clade – Baker *et al.* (2009, 2011), Comer *et al.* (2015, 2016), Faurby *et al.* (in press). Node 7. RRC clade – Baker *et al.* (2011), Comer *et al.* (2015, 2016), Faurby *et al.* (in press); lower support: Baker *et al.* (2009). For evidence for remaining nodes, see text.

The impact of the next-generation sequencing revolution (Pyron, 2015) is now being felt in palm phylogenetics (Comer *et al.*, 2015, 2016; Barrett *et al.*, 2016, in press; Heyduk *et al.*, 2016). Two of these studies (Comer *et al.*, 2015; Barrett *et al.*, 2016), focusing on the whole family and Arecoideae, respectively, have already included complete or near-complete plastid genome data for 62 genera of palms. These studies provide strong support for the GP2 classification and relationships among the five subfamilies (Fig. 7) that have been established in earlier studies (e.g. Asmussen *et al.*, 2006; Baker *et al.*, 2009, 2011). In addition, Barrett *et al.* (2016) illustrated, for the first time with genomic data, the exceptionally slow rate of plastid DNA evolutionary change that has dogged all plastid phylogenetic studies of palms (Baker *et al.*, 1999a; Asmussen *et al.*, 2000, 2006; Asmussen & Chase, 2001; Scarcelli *et al.*, 2011).

PHYLOGENETICS OF CALAMOIDEAE

Little additional research on calamoid phylogenetics has been published since GP2, although several studies are currently in progress. The summary relationships among tribes presented in GP2 as (Eugeissoneae (Lepidocaryeae, Calameae)) have, however, been challenged. Baker *et al.* (2009) found support for this pattern from supertree analyses, but their supermatrix analysis resolved a paraphyletic Lepidocaryeae with Eugeissoneae embedded in it as sister to *Raphia* P.Beauv. However, these relationships are poorly supported. Others have also found different relationships (Barrett *et al.*, 2016; Faurby *et al.*, in press), including a paraphyletic Lepidocaryeae and a sister relationship between Eugeissoneae and Calameae. These findings reflect ambiguity regarding the placement of Eugeissoneae and the monophyly of Lepidocaryeae that were already prevalent in the earliest studies of the subfamily (Baker *et al.*, 2000a, c; Fig. 7). These uncertainties may be a result of the intrinsic properties of calamoids, such as their great age (*c.* 80 Mya) and the relatively rapid succession of divergences at their base (Baker & Couvreur, 2013a), or long branch artefacts in species-poor lineages, such as Eugeissoneae. However, the available evidence for Calamoideae is based on rather limited data sampling and, where deep character sampling has been achieved (Barrett *et al.*, 2016), taxon sampling was limited. On balance, the deep relationships in Calamoideae remain an open question.

At a lower taxonomic level, two phylogenetic studies of Ancistrophyllinae (Lepidocaryeae) have confirmed the monophyly of the three genera accepted in the subtribe (Faye *et al.*, 2014; Faye, 2015). The latter study strongly resolved the relationships

among the genera, placing *Laccosperma* as sister to *Eremospatha*.

PHYLOGENETICS OF CORYPHOIDEAE

Significant clarification of the relationships among the tribes of Coryphoideae has been achieved with the publication of highly congruent phylogenetic topologies of the subfamily since GP2 (Baker *et al.*, 2009; Bacon *et al.*, 2012a; Barrett *et al.*, 2016; Faurby *et al.*, in press). We can now be confident that the subfamily is divided into two major clades (Fig. 7): the CSPT and the syncarpous clades. The CSPT clade, coined here, is divided into two subclades, one comprising the New World thatch palm clade (sister tribes Cryosophileae and Sabaleae; recovered by the above authors, except Faurby *et al.*, in press) and the other containing Phoeniceae as sister to Trachycarpeae. Evidence for the subclades of the CSPT clade has been found previously (e.g. Uhl *et al.*, 1995; Asmussen *et al.*, 2006), but robust support for their sister relationship has appeared only in more recent studies. It should be noted that, although the supertree analysis of Baker *et al.* (2009) resolved the relationships described above, their supermatrix analysis placed Phoeniceae sister to all remaining CSPT members, but without bootstrap support. The syncarpous clade contains four tribes, which resolve as (Chuniophoeniceae (Caryoteae (Corypheae, Borasseae))), as indicated in earlier studies (Bayton, 2005; Asmussen *et al.*, 2006). The supermatrix analysis of Baker *et al.* switches the placement of tribes Caryoteae and Corypheae, but without support.

In the GP2 classification, Dransfield *et al.* (2008a, b) were unable to erect a complete classification in tribe Trachycarpeae as a result of inadequate phylogenetic resolution, and therefore placed only some of the 17 genera in the two subtribes Rhipidinae and Livistoninae, leaving seven genera [six from the Americas, one (*Pritchardia* Seem & H.Wendl.) from the Pacific] unplaced to subtribe. We now have a much clearer understanding of the relationships among the genera of Trachycarpeae (Henderson & Bacon, 2011; Bacon *et al.*, 2012a, b, 2013a, b; Barrett *et al.*, 2016) that supports the monophyly of the two subtribes, placing *Brahea* Mart. sister to Rhipidinae, and a clade of *Acoelorrhaphe* H.Wendl. and *Serenoa* Hook.f. as the sister group of Livistoninae. The best evidence (Bacon *et al.*, 2012a) suggests that *Copernicia* Mart. ex Endl., *Pritchardia* and *Washingtonia* H.Wendl. fall outside this group as a monophyletic or paraphyletic group, with the placement of *Colpotherinax* Schaedtler remaining ambiguous. The relationships of the unplaced genera of Trachycarpeae do not lend themselves readily to classifica-

tion without recognizing several small subtribes that cannot be easily distinguished morphologically. For the time being, the unplaced Trachycarpeae remains a useful and practical concept.

The comprehensive tribe-wide research on Trachycarpeae (Bacon *et al.*, 2012a) has been complemented by a series of focused studies with dense species sampling aimed at taxon delimitation (Bacon & Baker, 2011; Henderson & Bacon, 2011; Bacon *et al.*, 2012b), and the biogeography of Wallace's Line (Bacon *et al.*, 2013a), Australia (Crisp *et al.*, 2010) and the Isthmus of Panama (Bacon *et al.*, 2013b). Consequently, Trachycarpeae now ranks as one of the best known groups of palms from a systematic and macroevolutionary perspective. Beyond Trachycarpeae, Pintaud *et al.* (2010) used simple sequence repeats to explore species limits in *Phoenix* L., which confirmed the prevailing taxonomy, without inferring phylogenetic relationships because of the limitations of the markers used. Heyduk *et al.* (2016) have recently published a comprehensive phylogenetic analysis of *Sabal* Adans. in a paper that established invaluable new tools for next-generation sequencing in palms (see below).

PHYLOGENETICS OF CEROXYLOIDEAE

When preparing the GP2 classification, all evidence converged on the same relationships among the three tribes of Ceroxyloideae, placing Cyclospatheae sister to a clade of Ceroxyleae and Phytelepaeae (Hahn, 2002b; Asmussen *et al.*, 2006; Trénel *et al.*, 2007; Fig. 7). Subsequent studies confirmed these results (Baker *et al.*, 2009, 2011; Faurby *et al.*, in press). Recently, however, plastid phylogenomic analyses have proposed an alternative topology, placing Cyclospatheae sister to Phytelepaeae (Barrett *et al.*, 2016). Although substantial data underpin this contrasting topology, we note that this node is one of only a few with a bootstrap percentage < 100% (although the values are still high, mostly > 95%), indicating lower confidence than most other relationships recovered in the study. The low taxon sampling (one species per tribe) is also potentially problematic because long branch artefacts may be an issue in this group (Asmussen *et al.*, 2006). Further taxon sampling would mitigate this risk. In addition to higher phylogenetic research on Ceroxyloideae, species-level phylogenetic analyses have been conducted for Phytelepaeae (Barfod, Trénel & Borchsenius, 2010) and *Ceroxylon* (M. Sanín, unpubl. data).

PHYLOGENETICS OF ARECOIDEAE

Phylogenetic research since GP2 on Arecoideae (Baker *et al.*, 2009, 2011; Comer *et al.*, 2015, 2016;

Faurby *et al.*, in press) has provided strong support for several major clades in the subfamily (Fig. 7): (1) the POS clade (Podococceae, Oranieae, Sclerospermeae); (2) the RRC clade (Roystoneaeae, Reinhardtiaeae, Cocoseae); and (3) the core arecoid clade (Areceae, Euterpeae, Geonomateae, Leopoldinieae, Manicarieae, Pelagodoxeae). These studies do not provide consistent accounts of the relationship among and within these groups. However, by weighing up the strongly supported relationships against the weaker hypotheses, especially from recent plastid and nuclear phylogenomic research, a clearer picture emerges (Fig. 7). Most studies identify Iriarteae and Chamaedoreae as the earliest branching lineages in Arecoideae, although all possible alternative arrangements are recovered, i.e. the two tribes as sisters (Comer *et al.*, 2016) or the two as a paraphyletic group with Iriarteae (Asmussen *et al.*, 2006; Baker *et al.*, 2009; Comer *et al.*, 2016; Faurby *et al.*, in press) or Chamaedoreae (Comer *et al.*, 2015) as sister to all remaining arecoids. The POS clade is most strongly supported as sister to an RRC + core arecoid clade (Comer *et al.*, 2015, 2016), although moderate support has also been recovered for a topology in which the positions of the RRC and POS clades are switched (Baker *et al.*, 2009; Faurby *et al.*, in press). In the POS clade, strong evidence points to Oranieae being sister to Sclerospermeae (Baker *et al.*, 2009, 2011; Comer *et al.*, 2015, 2016). In the RRC clade, Reinhardtiae is most closely related to Cocoseae (Baker *et al.*, 2009, 2011; Comer *et al.*, 2015, 2016; Faurby *et al.*, in press).

The relationships among the core arecoids remain elusive, but recent phylogenomic data point to at least one strongly supported node, placing Areceae as sister to Euterpeae (Comer *et al.*, 2015, 2016). Other proposed relationships, such as Leopoldinieae sister to all other core arecoid tribes (Comer *et al.*, 2016) or a corky-warted fruit clade (Manicarieae + Pelagodoxeae; Comer *et al.*, 2016), remain doubtful because of low support values and conflict. The higher level relationships of Arecoideae, although better known now than previously, remain a potentially fruitful focus of future research.

The phylogenetics of several arecoid tribes have been studied in depth since GP2. There is much conflict between phylogenetic hypotheses for intergeneric relationships in Chamaedoreae (Asmussen *et al.*, 2006; Thomas *et al.*, 2006; Cuenca & Asmussen-Lange, 2007; Cuenca, Asmussen-Lange & Borchsenius, 2008; Baker *et al.*, 2009, 2011; Cuenca, Dransfield & Asmussen-Lange, 2009). However, the studies with the densest data and taxon sampling offer moderate to strong support for a clade comprising *Chamaedorea* Willd., *Gaussia* H.Wendl. and *Synechanthus* H.Wendl., which is sis-

ter to *Wendlandiella* Dammer, with *Hyophorbe* Gaertn. sister to all remaining Chamaedoreae (Cuenca *et al.*, 2008, 2009; Baker *et al.*, 2011). A recent study of tribe Iriarteae confirms the monophyly of all five accepted genera, and finds strong support for a clade of *Iriartea* Ruiz & Pav. and *Dicthyocaryum* H.Wendl. resolving as sister to a second clade comprising the remaining three genera (Bacon *et al.*, in press).

Cocoseae has been intensively studied since the publication of GP2, with papers focusing on higher relationships in the tribe (Meerow *et al.*, 2009, 2015; Eiserhardt *et al.*, 2011a), providing further support to the well-established sister group relationship between Bactridinae and Elaeidinae that has been reported frequently elsewhere (Hahn, 2002b; Asmusen *et al.*, 2006; Baker *et al.*, 2009, 2011; Comer *et al.*, 2015, 2016). Highly incongruent relationships have been found among Bactridinae in the studies that have sampled all genera (Baker *et al.*, 2009; Eiserhardt *et al.*, 2011a; Meerow *et al.*, 2015), although support is highest and most widespread in the study of Eiserhardt *et al.*, which is based on five plastid DNA regions and three nuclear regions. Several papers have focused on the phylogenetics of the complex genus *Astrocaryum* and its implication for Neotropical biogeography (Ludena *et al.*, 2011; Roncal *et al.*, 2013, 2015). Considerable ambiguity also remains in the intergeneric relationships of Attaleinae, although the best sampled studies all point to the American taxa forming a clade and the African (*Jubaeopsis* Becc.) and Madagascan (*Beccariophoenix* Jum. & H.Perrier, *Voanioala*) coming together in a sister clade or paraphyletic group (Baker *et al.*, 2009; Meerow *et al.*, 2009, 2015; Eiserhardt *et al.*, 2011a). *Attalea* Kunth has recently been the focus of species-level phylogenetic research (C. Freitas, unpubl. research).

Multiple studies converge on a common set of relationships among genera of Geonomateae (sister relationship between *Welfia* and *Pholidostachys*, *Calyptrogyne* H.Wendl. embedded in a paraphyletic *Calyptronoma* Griseb.), albeit with patchy support and questions over the placement of *Asterogyne* H.Wendl. ex Hook.f. (Roncal *et al.*, 2005, 2010, 2011; Baker *et al.*, 2009, 2011). The addition of new nuclear data, however, places *Pholidostachys* as sister to all remaining Geonomateae, followed by *Welfia*, and *Asterogyne* as sister to the *Calyptrogyne/Calyptronoma* clade (Roncal *et al.*, 2012).

The relationships in Areceae, the largest tribe of all palms, remain poorly understood, to the extent that relations among subtribes are scarcely established (with the exception of a weakly supported western Pacific clade) and the monophyly of some subtribes remains questionable (e.g. Basseliniinae,

Laccospadicinae, Rhopalostylidinae; Baker *et al.*, 2009, 2011). The relationships of the ten genera that were not placed to subtribe in the GP2 classification of Areceae remain obscure. Two subtribes have become better known through focused studies. An extensive plastid DNA study has illuminated the relationships among the species and genera of Archontophoenicinae, although questioning the placement of *Actinorhytis* H.Wendl. & Drude in this group (Domenech *et al.*, 2014). Two papers on Ptychospermatinae have substantially improved the understanding of the generic limits and relationships of this difficult subtribe, resulting in substantial generic change (Zona *et al.*, 2011; Alapetite *et al.*, 2014), including the movement of species of *Drymophloeus* to expanded *Veitchia* and *Ponapea* Becc., the sinking of *Solfia* into *Balaka* and the establishment of the new genera *Jailoloa*, *Manjekia* and *Wallaceodoxa* (Heatubun *et al.*, 2014b; Zona & Baker, 2014).

PROSPECTS

Global knowledge of higher level palm systematics is in excellent shape. GP2 provides a robust baseline, reflecting the achievements of the strong, collaborative research community working on palm biology, which is fuelled by regular interactions through the European Network of Palm Scientists, 5-yearly World Palm Symposia and other co-operations, such as the European Union-funded Palms project (Balslev, Macia & Navarrete, 2015). Like GP1, GP2 has been a springboard for the many new developments in palm taxonomy and phylogenetics that have been synthesized here. However, numerous aspects of palm systematics are still unknown and palm researchers must grasp new opportunities to address these, so that the full potential of the palms as a model group for tropical plant research can be achieved (Couvreur & Baker, 2013). We conclude here with some perspectives on how the next steps in palm systematics may be taken.

IN PALM TAXONOMY, EXPECT THE UNEXPECTED

Palm species continue to be discovered at a startling rate. Even well-studied areas become hotspots for new discoveries because enhanced knowledge of a region facilitates the identification of further novelties. For example, the completion of baseline tools for the palms of Madagascar (Dransfield & Beentje, 1995a; Dransfield *et al.*, 2006) has unlocked our ability to detect yet more new taxa. The combination of field and phylogenetic exploration has also been productive at the genus level. The description of six new genera so soon after GP2 was highly unexpected and

the location of further new genera cannot be ruled out. In summary, it is far too early to consider palm taxonomy as adequately understood. We must take all opportunities to explore palm taxonomic frontiers in the field and herbarium and embrace the insights from the molecular characterization of species (Buerki & Baker, 2016). Without knowing our species, we are poorly equipped to study them, and even less able to protect them from extinction.

THE PALM TREE OF LIFE IS NOT COMPLETELY KNOWN

No larger family of tropical plants is probably better known phylogenetically than the palms. The palm community has established a complete genus-level framework (Baker *et al.*, 2009) and a synthetic species-level framework (Faurby *et al.*, in press), each building on numerous in-depth case studies, and is now moving into the genomic era (Barrett *et al.*, in press). However, although we have reason to be confident in many critical relationships, there are numerous areas of significant ambiguity in some of the most diverse and important groups of palms, such as in Arecoideae and Calamoideae, and species-level phylogenetics are incompletely known. Understanding the relationships of such ecologically and economically important plants is of fundamental scientific importance and must remain a high priority.

PHYLOGENOMICS WILL REVOLUTIONIZE PALM RESEARCH

Next-generation sequencing methods are now becoming routinely used in phylogenetics. The impact of these methods is now being felt in palms as plastid and nuclear datasets of unprecedented scale are being brought to bear on palm phylogenetics from the species to the family level (Barrett *et al.*, in press). The sequence capture methods recently published by Heyduk *et al.* (2016) are particularly promising as they are ambitious and informative, yet tractable. The potential of this scale of DNA sequence data to inform or even overturn palm systematics is immense. Next-generation sequencing methods also have the potential to unlock herbaria as a source of samples for sequencing, because they are much more tolerant of degraded DNA than traditional Sanger sequencing methods (Buerki & Baker, 2016). A caveat should be added here that these approaches may not be a panacea and some relationships may ultimately prove to be insoluble for real biological reasons. We have already seen, for example, that rates of discordance among gene trees can be extremely high, undermining confidence in resolved relationships (Heyduk *et al.*, 2016; Comer *et al.*, 2016). This should not be an obstacle to exploiting the new

tools to the full, but suggests that optimism should be tempered with realism.

A SPECIES-LEVEL PHYLOGENY OF PALMS IS WITHIN REACH

Species-level phylogenetic trees are in great demand for evolutionary and ecological research, and palms are no exception. In palms, researchers needing a complete species tree have resorted to simulating the branches into the genus-level supertree of Baker *et al.* (2009) or assembling larger trees from publicly available data (Couvreur *et al.*, 2011; Kissling *et al.*, 2012; Eiserhardt *et al.*, 2013b; Couvreur *et al.*, 2015; Faurby *et al.*, in press). However, we are now poised to build a species-level phylogenetic tree, not based on interpolating branches, but on real data. The scientific need for complete species-level phylogenetic research is evident, to produce fundamental biodiversity knowledge for pure and applied comparative research and to reinforce palms as a model group for tropical research. The data underpinning such an endeavour would also yield an authoritative genomic resource for palms, providing molecular tools in support of identification and other applied uses. New phylogenomic tools now make a species-level phylogenetic tree for palms a tractable objective, but it can only be achieved within a collaborative framework, in which researchers share material from the field, cultivation, DNA banks and herbaria, working together on complementary protocols and sharing data freely and fairly. These are the principles of the Palm Phylogeny Working Group, established at the World Palm Symposium in Montenegro, Colombia in July 2015. The road ahead for palm systematic research has never been more exciting.

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DEDICATION

This paper is dedicated to French palm expert Jean-Christophe Pintaud. News of Jean-Christophe's unexpected death just days after the 2015 World Palm Symposium that he co-organized brought not only immense sadness, but also many reflections on wonderful times spent studying, debating and travelling for palms with him. Jean-Christophe was an extraordinary and generous individual, a selfless and open collaborator in a time when science is becoming only more competitive and self-centred. He was a brilliant palm biologist, able to move fluidly from the finest detail to the biggest of 'big picture' ideas. As an incisive critic, his views were argued meticulously, but also shared kindly. Jean-Christophe gave his time, ideas and resources freely to all around him, seniors, peers and those fortunate enough to come under his wing. The palm community has lost a great friend who has made an indelible mark on our field.

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