This file is part of the following reference:


Access to this file is available from:

http://eprints.jcu.edu.au/24103/

The author has certified to JCU that they have made a reasonable effort to gain permission and acknowledge the owner of any third party copyright material included in this document. If you believe that this is not the case, please contact ResearchOnline@jcu.edu.au and quote http://eprints.jcu.edu.au/24103/
STUDIES IN THE GENUS *LIVISTONA*
(CORYPHOIDEAE: ARECACEAE)

Thesis submitted by
John Leslie DOWE BSc (Hons 1) James Cook
in October 2001

for the degree of Doctor of Philosophy
in Tropical Plant Sciences
within the School of Tropical Biology
James Cook University.
STATEMENT OF ACCESS

I, the undersigned, the author of this thesis, understand that James Cook University will make it available for use within the University Library and, by microfilm or other means, allow access to users in other approved libraries. All users consulting this thesis will have to sign the following statement:

In consulting this thesis I agree not to copy or closely paraphrase it in whole or in part without the written consent of the author; and to make proper public written acknowledgment for any assistance that I have obtained from it.

Beyond this, I do not wish to place any restriction on access to this thesis.

(Name) (Date) 2 October 2001
STATEMENT OF SOURCES

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references given.

2 October 2001

(Name) (Date)
ABSTRACT

This thesis provides new insights into the genus Livistona based on taxonomy, cladistic analyses, molecular investigation, historical biogeography, and gender function. The taxonomic treatment recognises 35 currently accepted taxa. Four new species, Livistona chocolatina, L. concinna, L. surru and L. tothur, are described as part of this treatment. They will be formally published elsewhere. Literature research revealed that 92 names have used Livistona as part of the binomial. Of these, 68 are typified by extant herbarium specimens. Five names are typified by illustrations. Of the remaining 19 names, types were never designated. It is proposed that eleven names require typification, including Livistona saribus, Chamaerops biroo, Corypha decora, Corypha minor, Livistona altissima, Livistona hoogendorpii, Livistona jenkinsiana, Livistona spectabilis, Livistona tonkinensis, Saribus olivaeformis and Saribus subglobosus. New names are proposed for L. decipiens, which becomes L. decora, and L. mariae var. occidentalis, which becomes L. nasmophila.

Phylogenetic relationships were examined using cladistic analyses based on morphological characters. Forty-three characters and 35 taxa were investigated with two character weighting options: unweighted and successive weighting. In the most robust analysis, the following major lineages were evident:

- **exigua** lineage – small understorey palms with irregularly segmented leaves, inflorescence not basally branched
- **saribus** lineage – large canopy palms with irregularly segmented leaves, inflorescence not basally branched
- **chinensis** subclade – inflorescence not basally branched, fruit green, blue or purple, regularly segmented leaves
- **rotundifolia** subclade – inflorescence basally branched, fruit passing through orange/red to mature either orange, red or black, regularly segmented leaves
- **humilis** subclade - inflorescence not basally branched, fruit dark brown or black, regularly segmented leaves with deeply segmented lamina
- **mariae** subclade - inflorescence not basally branched, fruit dark brown or black, regularly segmented leaves with moderately segmented lamina
Although topological resolution was satisfactory, statistical support was low for the analyses and the result cannot be accepted as a reliable estimate of phylogeny.

The internal transcribed spacer (ITS) regions of nrDNA and the intervening 5.8S region of a group of Livistona species were investigated to determine if a useful phylogeny could be inferred from that region. DNA was amplified via polymerase chain reaction (PCR) using three primers. Multiple (polymorphic) bands were produced consistently for most species and some sequences had lost the entire ITS2 portion. The results indicate that a Livistona-specific primer will need to be designed and that more refined screening of products will be necessary if full length and non-polymorphic sequences are to be obtained.

Hypotheses of historical biogeography were developed utilising three lines of investigation. Firstly, the fossil record suggests a Laurasian origin for the genus. Secondly, an analysis of area endemism, based on the Parsimony Analysis of Endemism (PAE) method, indicates a close relationship of some contiguous areas in which Livistona species occur. Thirdly, a cladistic analysis suggests a number of possible scenarios, including an exclusively Laurasian origin, or combinations of both Laurasian and Gondwanan origin. The distribution of species in otherwise floristically unrelated regions suggests that the genus is ‘ancient’, and that initial radiation may have occurred prior to tectonic events that isolated the landmasses on which ancestral species occurred. Extensive speciation has since occurred in Australia and Malesia, with putatively relictual species occurring in Africa and Australia. The occurrence of Livistona in Australia is most plausibly the result of migration from a Laurasian source, rather than being an autochthonous element.

Morphological aspects of a group of representative species were investigated to determine if there were any trends in gender function from hermaphroditism to functional dioecy. Based on predictive morphological criteria, a trend from hermaphroditism to dioecy was indicated in the four species that were studied, and Livistona chinensis, L. muelleri, L. decora and L. lanuginosa can be ranked in increasing degrees of dioeciousness respectively. Functional dioecy in Livistona may be related to the evolution of species in drier, stressful environments.
Acknowledgments

I would like to offer sincere thanks to my supervisors, Associate Professor Betsy Jackes, Dr Leone Bielig and Professor Anders Barfod who guided, advised and corrected me during every phase of this thesis. For support with advice and guidance with laboratory techniques and valuable discussion here at James Cook University I would like to acknowledge Dr Dale Dixon, Dr Paul Gadek, Dr Karen Edwards, Associate Professor David Blair, Dr Michelle Waycott and Ainsley Calladine. Aniuska Kazandjian, one of my fellow PhD students, is especially thanked for her *joie de vivre*, smile, support and encouragement, and for making my days in Tropical Biology thoroughly enjoyable. Lucy Smith is also especially thanked for providing the illustrations of new species, for essential encouragement and concern, and elevating me to a level of observation that would otherwise not have been possible. I offer a very special thanks to Andi Cairns for her perceptive insights, generous support, unfailing tolerance and friendship. My beloved sons Ashton, Jaydyn and Calem Dowe are thanked for tolerating my many absences during field-work.

For supply of information and materials in regards to many aspects of *Livistona* in Australia, I thank Stephen van Leeuwen and Peter Kendrick [CALM, WA]; George Kendrick [WA Museum], David Greenwood [Victoria University of Technology], John Conran [University of Adelaide], Nick Carlile [University of NSW], Heather Craig [JCU, Townsville], Arden Dearden [Cairns], Dr Gordon Guymer, Paul Forster and Rod Henderson [BRI], and Tony Irvine [CSIRO, Atherton].

In Denmark whilst on study excursion at Aarhus University, I received considerable help and friendship from Professor Anders and Denise Barfod, Annie Sloth [SEM assistance], and Jørn Madsen and Charlotte Muuksgaard in Copenhagen.

For general herbarium, literature or materials assistance I thank Dr M. Pignal at Paris Herbarium; Johannes Mogea, Dr Irawati and Kartini Kramadibrata at Herbarium Bogoriense, Indonesia; Dr Piero Cuccuini and Marcello Tardelli at the
Botanical Museum, Florence, Italy; Dr Hiroshi Ehara, Rika Nobe, Hideto Kato, Dr Mikio Ono and Naoto Yoshida in Japan; Tobias Spanner in Germany; Shri Dhar in India; Gregori and Indrah Hambali in Bogor, Indonesia; Rudi Maturbongs at Manokwari Herbarium, Indonesia; Lim Chong Keat and Dr Leng Guan Saw in Malaysia; Dr. M. Thijisse at Rijksherbarium, Leiden, in the Netherlands; Dr. Chrissen Gemmill in New Zealand; Dr. Domingo Madulid and Mr Efren Romero of the Philippines National Herbarium, and Dr. Edwino Fernando of the University of the Philippines, Los Baños; Ivan Schanzen in Russia; Dr John Dransfield, Dr Bill Baker and Dr Madeline Harley at the Royal Botanical Gardens, Kew, United Kingdom; Hilary and Geoff Welch, and Martin Gibbons in United Kingdom; John Bishock, Mike Dahme, Gary Dahme, Dan Harder, John Ingwerson and Sam Sweet in the United States; Michael Ferrero, Kampon Tansasha and Poonsak Vatcharakorn at Nong Nooch Tropical Gardens, Thailand; Dr Osia Gideon, Roy Banka, Anders Kjaer, Laurie Martin, Walter Benko, Jamie White, Tanya Zeriga and Luke Moimoi in Papua New Guinea; Dr Nguyễn Tien Hiếp in the Hanoi, Herbarium, Vietnam; and Dr Ruth Kiew in the Singapore Herbarium.

Generous funding, essential to the completion of this thesis, was provided by the Australian Biological Resources Study, Canberra, the Australia Pacific Science Foundation, and the Pacific Biological Foundation. Grants were received from James Cook University through the Doctoral Merit Research Scheme and the Internal Research Supplementary funding scheme. Liz Visher of ABRS and Dr Barry Filshie of the Pacific Biological Foundation are especially thanked for their assistance regarding grant matters.

I must also thank a multitude of persons—library technicians, field assistants, government department officials and land custodians—whom I am unable to name but who have contributed in many ways to this thesis.

Photograph credits: Figure 2.4, W. J. Baker; Figure 2.5, S. Zona; Figure 2.11, R. Kiew; Figure 2.12, G. Dahme; Figure 2.13, H. Kato; Figure 2.14, H. Ehara; Figure 2.16, J. Dransfield; Figure 2.25, H. Welch. All other photographs by the author.
# Table of Contents

Statement of access ................................................................. ii
Statement of sources - Declaration ........................................... iii
Abstract ............................................................................. iv
Acknowledgments................................................................. vi
Table of contents ................................................................. viii
Chapters and sections ......................................................... ix
List of Figures ..................................................................... xv
List of Tables ....................................................................... xviii
Glossary ............................................................................... xx
Abbreviations ...................................................................... xxv
Herbarium acronyms ............................................................ xxvii
Chapter 1 GENERAL INTRODUCTION

1.1 Introduction ........................................................................................................... 1
1.2 Palm classification ................................................................................................. 2
1.3 The genus Livistona R. Br. .................................................................................. 3
1.4 Taxonomic history ................................................................................................. 5
1.5 Biology, ecology and other studies of Livistona .................................................. 14
1.6 Conservation ......................................................................................................... 14
1.7 Scope, outline and aims of the thesis ..................................................................... 14

Chapter 2 SYSTEMATIC TREATMENT OF LIVISTONA

2.1 Introduction ............................................................................................................ 17
2.2 Materials and methods ......................................................................................... 19
2.3 Results ................................................................................................................... 20
   2.3.1 Taxonomic resolution of closely related species ............................................ 20
   2.3.2 Typification summary .................................................................................... 23
2.4 Taxonomy .............................................................................................................. 26
2.5 Key to species of Livistona .................................................................................. 28
2.6 Descriptions of species ......................................................................................... 33
2.7 Excluded and uncertain names ............................................................................ 155

Chapter 3 CLADISTIC ANALYSIS OF LIVISTONA BASED ON MORPHOLOGICAL CHARACTERS

3.1 Introduction .......................................................................................................... 159
3.2 Cladistic concepts and methodologies ................................................................. 162
   3.2.1 Cladistic analyses and molecular studies of palms .................................... 163
3.3 Relationships of Livistona species in Australia ................................................... 164
3.4 Evolutionary trends in palms ............................................................................... 165
   3.4.1 Character choices in the phylogeny of palms .............................................. 165
   3.4.2 Scoring of character states .......................................................................... 166
   3.4.3 Successive weighting .................................................................................... 167
   3.4.4 Character polarity and ordering .................................................................. 167
3.5 Tree statistics ....................................................................................................... 168
   3.5.1 Consistency index (CI) ................................................................................ 168
   3.5.2 Retention index (RI) .................................................................................... 168
3.5.3 Rescaled consistency index (RC) .............................................. 168
3.5.4 Bootstrap method ..................................................................... 169

3.6 Aims ............................................................................................ 169

3.7 Materials and methods ................................................................. 170
  3.7.1 Leaf venation patterns .............................................................. 170
  3.7.2 Fruit epicarp features .............................................................. 170

3.8 Explanation of characters used in the cladistic analysis ............... 172

3.9 Cladistic analyses ........................................................................ 189

3.10 Results ....................................................................................... 191
  3.10.1 Analysis 1 — unweighted characters ........................................ 191
  3.10.2 Analysis 2 — successive weighting ............................................ 195
  3.10.3 Statistics .............................................................................. 196
  3.10.4 Bootstrap values ................................................................... 197
  3.10.5 Tree descriptions and character analysis .................................. 198

3.11 Discussion and conclusion ............................................................ 201

Chapter 4  AN INVESTIGATION OF THE INTERNAL TRANSCRIBED SPACER (ITS) REGIONS IN nrDNA OF LIVISTONA SPECIES

4.1 Introduction .................................................................................. 204

4.2 The internal transcribed spacer (ITS) regions ................................ 205

4.3 Aims ............................................................................................. 206

4.4 Materials ....................................................................................... 207

4.5 Methods ....................................................................................... 208

4.6 Results .......................................................................................... 210

4.7 Discussion ..................................................................................... 217

4.8 Conclusion .................................................................................... 218

Chapter 5  HISTORICAL BIOGEOGRAPHY OF LIVISTONA

5.1 Introduction .................................................................................. 219

5.2 Historical biogeography ............................................................... 220
  5.2.1 Cladistic biogeography ............................................................ 221
  5.2.2 Parsimony analysis of endemicity (PAE) .................................... 222
  5.2.3 The role of molecular data in biogeography ................................. 222
5.3 Regional histories
  5.3.1 Biogeography in the South-east Asian/Australasian region
  5.3.2 Biogeography of the Afro-Arabian area
5.4 Environmental change
5.5 Biogeography of palms
  5.5.1 Palm fossils
  5.5.2 Some problematic distributions
5.6 Aims
5.7 Materials and methods
  5.7.1 Distribution
  5.7.2 Fossils
  5.7.3 Parsimony analysis of endemicity (PAE)
  5.7.4 Cladistics
  5.7.5 Morphological adaptation
5.8 Results
  5.8.1 Distribution
  5.8.2 Fossil record
  5.8.3 Regional distribution and area cladograms
  5.8.4 Cladistics
5.9 Discussion
  5.9.1 Fossils
  5.9.2 Distribution and endemism
  5.9.3 Relictualism
  5.9.4 Cladistics
  5.9.5 Distribution of Livistona carinensis
  5.9.6 Diversity and distribution of Livistona
5.10 Conclusion
Chapter 6 DEVELOPMENT OF A MORPHOLOGICALLY BASED METHOD TO PREDICT SEXUALITY IN LIVISTONA
6.1 Introduction
6.2 Evolution of sexual expression
  6.2.1 Hermaphroditism to dioecy: mechanisms and consequences
6.3 Sex ratio in palms
Chapter 7 GENERAL SUMMARY

7.1 Introduction ............................................................................................................. 294
  7.1.1 Systematics ......................................................................................................... 294
  7.1.2 Cladistics ........................................................................................................... 294
  7.1.3 Molecular investigation ..................................................................................... 295
  7.1.4 Historical biogeography ..................................................................................... 296
  7.1.5 Sexuality and the Index of functional gender ..................................................... 296

7.2 Future work ............................................................................................................. 296

References ...................................................................................................................... 297

Appendices .................................................................................................................... 334

Appendix 1. Time-table for field-trips and excursions during which Livistona specimens were collected, examined and studied, for the duration of the PhD

Appendix 2. Typification of names associated with Livistona, with reference to c. 400 herbarium specimens and the taxonomic literature

Appendix 3. Stem characters for 35 species of Livistona and two outgroup taxa: height (maximum recorded), dbh, height:dbh ratio, and whether petiole bases are persistent on the stem (+) or deciduous leaving a smooth stem (-)

Appendix 4. Leaf characters for 35 species of Livistona and two outgroup taxa: lamina outline, segmentation, lamina length, number of segments, % of free segment and % of segment of the apical cleft

Appendix 5. Leaf characters for 35 species of Livistona and two outgroup taxa: condition of the segment apex, adaxial colour, abaxial colour, and leaf surface

Appendix 6. Venation characters for 35 species of Livistona and two outgroup taxa: mean number of parallel ribs in a single segment, character of parallel ribs, character of transverse veins, the number of parallel veins that are crossed by the transverse veins, and the mean density of transverse veins per unit area, with the number of parallel veins that are crossed in parentheses

Appendix 7. Petiole and armature characters for 35 species of Livistona and two outgroup taxa: profile of petiole cross section, armature (i.e., single or double spines), spine shape (with curved sides or kris-shaped), and spine colour

Appendix 8. Leaf-base fibre characters for 35 species of Livistona and two outgroup taxa: visual appearance (prominence), type of weave and persistence
Appendix 9. Inflorescence characters for 35 species of Livistona and two outgroup taxa: branching condition, average number of partial inflorescences, maximum order of branching of partial inflorescence, range of inflorescence length, and rachillae length

Appendix 10. Inflorescence bract characters for 35 species of Livistona and two outgroup taxa: number of peduncular bracts, and types of bract and rachillae tomentum

Appendix 11. Flower and pollen characters for 35 species of Livistona and two outgroup taxa: number of flowers in a cluster, flower length, colour, pollen dimensions (L = long axis; l = short axis)

Appendix 12. Fruit and pedicel characters for 35 species of Livistona and two outgroup taxa: fruit shape, length, diameter, colour, and pedicel length

Appendix 13. Fruit, eophyll and sexuality characters for 35 species of Livistona and two outgroup taxa: with or without epicarp pores (+ = present; - = not present), embryo position, number of eophyll ribs (number of samples) and sexuality

Appendix 14. Scatter plots of continuously variable characters used in the cladistic analysis of Livistona and two outgroup taxa

Appendix 15. Altitude and rainfall data for Livistona species

Appendix 16. Samples used in the SEM examination of lamina surface features for selected species of Livistona

Appendix 17. Samples used in the venation pattern examination for selected species of Livistona

Appendix 18. Stomatal densities on adaxial and abaxial surfaces per unit area of 1.0 mm², the ratio of adaxial:abaxial densities, and annual rainfall in metres for selected species of Livistona

Appendix 19. Venation patterns of Livistona species in a unit area of 12 x 10 mm, number of parallel veins and transverse veins, ratio of parallel veins: transverse veins, and annual rainfall in metres for species of Livistona

Appendix 20. Flowering and fruiting percentages per month for four species of Livistona

Appendix 21. Pollen counts and Standard Deviation (SD)

Appendix 22. Pollen measurements and Standard Deviation (SD)
LIST OF FIGURES

Figure 1.1 Distribution of Livistona ................................................................................. 4
Figure 1.2 Portrait of Robert Brown, Livistona humilis in habitat and the type specimen of Livistona humilis ................................................................. 6
Figure 1.3 Protologue of Livistona .................................................................................. 7
Figure 1.4 Portraits of prominent Livistona taxonomists .............................................. 9
Figure 1.5 Time-lines of the taxonomy of Livistona ..................................................... 10
Figure 2.1 Livistona rotundifolia. .................................................................................... 35
Figure 2.2 Livistona robinsoniana. .................................................................................. 40
Figure 2.3 Livistona merrillii. ......................................................................................... 45
Figure 2.4 Livistona papuana. ......................................................................................... 49
Figure 2.5 Livistona woodfordii. ..................................................................................... 52
Figure 2.6 Livistona chocolatina. .................................................................................... 56
Figure 2.7 Livistona tothur. ............................................................................................ 59
Figure 2.8 Livistona surru. ............................................................................................... 63
Figure 2.9 Livistona jenkinsiana. ................................................................................... 66
Figure 2.10 Livistona endauensis. ................................................................................... 70
Figure 2.11 Livistona tahanensis. ................................................................................... 73
Figure 2.12 Livistona halongensis. .................................................................................. 75
Figure 2.13 Livistona boninensis. .................................................................................... 78
Figure 2.14 Livistona chinensis. ....................................................................................... 82
Figure 2.15 Livistona saribus. ......................................................................................... 88
Figure 2.16 Livistona exigua. .......................................................................................... 93
Figure 2.17 Livistona muelleri. ....................................................................................... 95
Figure 2.18 Livistona nasmophila. .................................................................................. 99
Figure 2.19 Livistona decora. ......................................................................................... 102
Figure 2.20 Livistona inermis. ....................................................................................... 106
Figure 2.21 Livistona benthamii. ..................................................................................... 110
Figure 2.22 Livistona concinna. ..................................................................................... 114
Figure 2.23 Livistona nitida. .......................................................................................... 117
Figure 2.24 Livistona australis. ...................................................................................... 119
Figure 2.25 Livistona carinensis. ................................................................................... 123
Figure 2.26 Livistona alfredii. ......................................................................................... 127
Figure 2.27 Livistona humilis. ....................................................................................... 130
Figure 2.28 *Livistona fulva* ................................................................. 134
Figure 2.29 *Livistona eastonii* ............................................................ 136
Figure 2.30 *Livistona victoriae* ........................................................... 138
Figure 2.31 *Livistona drudei* ............................................................... 141
Figure 2.32 *Livistona lorophylla* ......................................................... 144
Figure 2.33 *Livistona lanuginosa* ......................................................... 148
Figure 2.34 *Livistona mariae* ............................................................... 151
Figure 2.35 *Livistona rigida* ................................................................. 154
Figure 3.1 The position of *Livistona* as inferred from combined morphological and cpDNA data ................................................................. 163
Figure 3.2 The position of *Livistona* as inferred from rps16 intron and trnL-trnF sequences ................................................................. 164
Figure 3.3 Leaf-base remains in *Livistona* ............................................. 173
Figure 3.4 Lamina morphology in *Livistona* .......................................... 174
Figure 3.5 Simplified composite half-leaf of *Livistona* ............................ 175
Figure 3.6 Segment apices in *Livistona* ............................................... 177
Figure 3.7 Venation patterns in *Livistona* ............................................. 178
Figure 3.8 Petiole cross sections of *Livistona* ....................................... 179
Figure 3.9 Armature in *Livistona* ......................................................... 180
Figure 3.10 Spine shape in *Livistona* .................................................... 181
Figure 3.11 Leaf-base fibres in *Livistona* .............................................. 182
Figure 3.12 Inflorescence morphology in *Livistona* ............................... 183
Figure 3.13 Bract tomentum in *Livistona* ............................................. 184
Figure 3.14 Flowers of *Livistona* .......................................................... 185
Figure 3.15 Fruit of *Livistona* .............................................................. 186
Figure 3.16 Epicarp pores in *Livistona* .................................................. 187
Figure 3.17 Phylogram of Analysis 1 ....................................................... 192
Figure 3.18 Strict consensus tree of Analysis 1 ........................................ 193
Figure 3.19 Phylogram of Analysis 2 ....................................................... 194
Figure 3.20 Bootstrap support values ...................................................... 195
Figure 3.21 Cladogram traced with character 5 – lamina segmentation ........ 199
Figure 3.22 Cladogram traced with character 26 – inflorescence branching ... 200
Figure 4.1 Organisation of the nrDNA region ......................................... 206
Figure 4.2 A selection of crude DNA extractions visualised on agarose gel .... 211
Figure 4.3  PCR products using primers ITS4 and ITS16.  ............................................. 211
Figure 4.4  PCR products using primers ITS4 and ITS16 ‘palm’. ................................. 212
Figure 4.5  Cloned products using the pMOSBlue blunt ended cloning kit.................. 212
Figure 4.6  Preliminary phylogram obtained from the sequence data .................... 213
Figure 5.1  The main volcanic and mountain building areas of south-eastern Asia and Australasia.  ............................................................................................................. 225
Figure 5.2  Extant distribution of Livistona. ................................................................. 234
Figure 5.3  Sites of Livistona-affinity fossils. ................................................................. 237
Figure 5.4  Geological timescale with fossil and geological events. ......................... 238
Figure 5.5  Cladograms of the distributional relationships of Livistona species within biogeographical areas, using the PAE method.  ........................................... 240
Figure 5.6  The relationships of biogeographic regions ............................................. 240
Figure 5.7  Cladogram of Livistona taken from cladistic analysis in Chapter 3 ....... 241
Figure 5.8  Distribution of the exigua and saribus lineages ....................................... 242
Figure 5.9  Distribution of the chinensis and rotundifolia subclades .......................... 242
Figure 5.10  Distribution of the mariae subclade ......................................................... 243
Figure 5.11  Distribution of the humilis subclade ....................................................... 243
Figure 6.1  Schematic presentation of sexual expression in the Arecaceae ................. 253
Figure 6.2  Inflorescence types in Livistona ............................................................... 267
Figure 6.3  Flower of Livistona .................................................................................... 268
Figure 6.4  Morphology of the outer septal nectary in Livistona humilis .................. 270
Figure 6.5  Habits of species of Livistona studied ...................................................... 276
Figure 6.6  Percentages of fruit-bearing/nonfruit-bearing plants ................................ 282
Figure 6.7  Flowering and fruiting calendars for the four study species ................... 284
Figure 6.8  Pollen:ovule ratios ................................................................................... 285
Figure 6.9  Comparison of the mean volumes of single pollen grains .................... 286
Figure 6.10  Pollen micrographs of Livistona species .............................................. 286
Figure 6.11  The index of functional gender ............................................................. 289
LIST OF TABLES

Table 1.1  Names applied to Livistona ................................................................. 11
Table 1.2  Summary of some studies involving Livistona ...................................... 15
Table 2.1  Comparison of morphological characteristics of Livistona inermis and
L. lorophylla ........................................................................................................... 21
Table 2.2  Comparison of morphological characteristics of Livistona beccariana
and L. woodfordii .................................................................................................. 22
Table 2.3  Summary of typification for names in Livistona ..................................... 23
Table 2.4  List of currently accepted taxa recognised in this account .................... 24
Table 2.5  Taxa for which neotypes and lectotypes need to be chosen ................... 25
Table 3.1  The Livistona alliance presented by Moore ........................................... 161
Table 3.2  Genera in the Livistoniinae with species numbers and distribution ....... 161
Table 3.3  Taxa used in the cladistic analysis of Livistona ....................................... 171
Table 3.4  Specimens used in the SEM examination of epicarp features ............... 188
Table 3.5  Morphological dataset used in the cladistic analysis ............................. 190
Table 3.6  Summary of statistics for Analysis 1 ...................................................... 191
Table 3.7  Summary of statistics for Analysis 2 ...................................................... 195
Table 3.8  Summary of statistics for both analyses ............................................... 196
Table 3.9  Rescaled consistency indices greater than the average in both analyses ... 196
Table 3.10 Character number and character states in which rescaled consistency
index was greater than the average ........................................................................ 197
Table 3.11 Characters that scored a rescaled consistency index of ‘0.0’ ................... 197
Table 3.12 Characters that scored a rescaled consistency index of ‘1.0’ ................... 198
Table 4.1  Palm studies in which molecular techniques have been used ............... 205
Table 4.2  Samples used in the molecular investigations in Livistona ................... 207
Table 4.3  Aligned sequence data of Livistona, Raphia and Eugeissona ................. 214
Table 5.1  Palm studies in which cladistic techniques have been used .................. 221
Table 5.2  Palm studies in which molecular techniques have been used ................ 222
Table 5.3  Major biogeographic studies of palms ............................................... 228
Table 5.4  Data matrices for area cladograms ....................................................... 233
Table 5.5  Distribution status of Livistona species ............................................... 235
Table 5.6  Examples of fossils of Livistona-affinity ............................................... 236
Table 5.7  Fossil taxa described for Livistona ....................................................... 237
Table 5.8  Biogeographic regions proposed by Takhtajan and Cracraft ................. 239
Table 5.9 Biogeographic regions and their component species of *Livistona* .... 239
Table 6.1 Definitions of sexual systems in plants. ........................................... 254
Table 6.2 Reproductive characteristics and pollen:ovule (PO) ratios. ............ 272
Table 6.3 Pollination modes that could occur in *Livistona*. .......................... 273
Table 6.4 Species of *Livistona* examined. ..................................................... 274
Table 6.5 Characteristics of species studied.................................................... 277
Table 6.6 Characters that may have predictive value in sexuality. .................. 278
Table 6.7 Data for the nine predictive characters.......................................... 288
Table 6.8 Values used in constructing the index of functional gender. .......... 288
GLOSSARY

*abaxial* – the side of an organ that faces away from the axis that bears it, e.g. the under surface of a leaf

*adaptation* – process of evolutionary modification which results in improved survival and reproduction efficiency; any heritable character, morphological, physiological or developmental, that enhances survival or reproductive success

*adaxial* – the side of an organ that faces toward the axis that bears it, e.g. the upper side of a leaf

*advanced* – in regards to evolution, the character state that originates later in evolution than the ancestral state

*allopatric species* – a species that has evolved in different and disjunct areas from a sister species

*anatropous* – describing the orientation of an ovule, being bent parallel to its stalk so that the micropyle is adjacent to the hilum

*ancestral* – with regards to the possession of primitive characters by organisms

*anemophily* – pollination facilitated by wind or air currents

*apomorphy* – a derived character or character state

*armed* – bearing some form of spines

*autapomorphy* – a character state that is unique to a taxon

*autochthonous* – being the original inhabitants of an area: having evolved *in situ*

*autogamy* – fertilisation occurring within the same flower

*bootstrapping* – a statistical method to estimate confidence in a pattern

*bootstrap value* – the proportion of times a pattern is repeated in a bootstrapping procedure

*bracteole* – a small bract borne on a flower stalk

*carpel* – the single unit of the gynoecium

*chartaceous* – paper-like, thin and stiff

*clade* – a branch of an evolutionary tree representing descendants from a common ancestor

*cladistic biogeography* – examination of the distribution of sister taxa of monophyletic groups, i.e. most recently evolved taxa will be the most recently vicariated
cladogram — graphic image in the form of a ‘tree’ depicting the phylogenetic arrangement of a group of taxa
collateral — side by side, parallel
connective — the part of a stamen that connects the anthers, usually distinct from the filament
cordate — heart shaped
costapalmate — of a palmate leaf where the petiole is extended as a midrib into the lamina
derived — in regards to evolution, the state that originates later in evolution than the ancestral state
didymous — of anthers where the connective is almost absent
dimorphic — of two forms
distal — situated farthest away from the point of attachment
endemics — species with restricted ranges, often with narrow ecological requirements and sometimes morphologically specialised
endocarp — innermost layer of the fruit wall
endosperm — the nutritive body of the seed
entomophily — pollination facilitated by insects
eophyll — the first leaf with a blade
epicarp — the outer most layer of the fruit wall
epipetalous — borne on the petals
exine — the outer surface of a pollen grain
flexuous — regularly twisted, zig-zag
foveolate — with small round depressions
geitonogamy — fertilisation between different flowers on an individual plant or clonal plants
glabrous — smooth, lacking hairs or scales
glaucous — covered with a bluish gray or greenish bloom
hastula — a flap of tissue borne at the insertion of the blade on the petiole on the upper, lower or both surfaces
homogeneous — of the seed tissue, uniform, the same throughout
homology — character states that share modifications from another condition
homoplasy — convergence, similarity without genetic relationship
hyaline — thin enough to be transparent
illegitimate – in regards to names that are nomenclaturally illegal according to the rules of the ICBN

inaperturate – in pollen, lacking any visible germination openings

interfoliar – among the leaves

internode – part of a stem between the attachment of two leaves

inviable – in regards to pollen or fruit, unable to germinate

isotype – a specimen that is a duplicate of the holotype

lamina – leaf blade

lanceolate – of leaf segments, narrow, tapering to both ends

latrorse – of anthers, opening sideways, lateral to the filament

lectotype – a specimen that serves in place of a lost or unplaced holotype

ligule – a distal projection of the leaf sheath

mesocarp – middle layer of the fruit wall

monocolpate – a pollen grain with a single aperture extending the length of the grain

mononomic – describing pre-Linnaean names that consist of a single word

monophyletic group – a group of organisms that contains the most recent ancestor plus all and only all its descendants

monosulcate – with one sulcus (see sulcus)

neotype – a specimen selected in place of a holotype in the absence of original material

node – the area of stem where the leaf is (was) attached

outgroup – a taxon used in a cladistic analysis for comparative purposes, usually with respect to character polarity determination

paraphyletic – being a group of organisms that includes their most recent common ancestor and some but not all of its descendants

parsimony – the general scientific criterion for choosing among competing hypotheses that explains the data most simply and efficiently

partial inflorescence – with regards to the structure of the inflorescence of Coryphoid palms, a single unit of the iterative branching system that makes up the inflorescence

pedicel – a flower stalk

peduncle – the lower unbranched part of an inflorescence

perforate – pierced with holes
**phylogenetic systematics** - a method of classification that utilises hypotheses of character transformation to group taxa hierarchically into nested sets and then interprets these relationships as a phylogenetic tree

**plesiomorphic** - a state that arose earlier in the evolution of a group of taxa than its alternative state

**pleonanthic** - flowering continuously over most of the life of a plant

**plicate** - pleated, as in the folds developed in newly emerging spear leaves in palms

**polyphilic** - a flower that is visited by many species of pollinator

**primitive** - with regards to the possession of ancestral characters

**prophyll** - the first bract or leaf produced on a branch

**protandrous** - stamens shedding pollen before the stigma is receptive

**proximal** - nearest to the attachment, basal

**psilate** - covered with small rounded protuberances

**puberulous** - covered with dense short hairs

**rachilla** - the ultimate flower-bearing axis of an inflorescence

**rachis** - the axis of an inflorescence beyond the first branches, i.e., beyond the peduncle

**relictual species** - species that are persistent examples of floras now mainly vanished

**rugose** - wrinkled

**stigmatic remains** - the remnants of flower parts persistent on the fruit epicarp

**subclade** - portion of a major clade

**subtribe** - taxonomic level below tribe but above genus

**subulate** - awl shaped, abruptly tapered to the apex

**sulcus** - the furrow-like aperture of a pollen grain

**suture** - a scar indicative of a fold or join in the epicarp

**sympatric species** - related species that occur in the same geographical range

**sympleisiomorphy** - (1) a synapomorphy of a more inclusive hierarchical level than that being considered. (2) the occurrence in two or more taxa of a monophyletic group of a plesiomorphic character or character state; that is, one that has been inherited from an ancestor more distant than the most recent common ancestor of the group.
**sympodial clusters** – in regards to the arrangement of flowers, where an individual flower is produced from the axil of the preceding flower’s bracteole

**synapomorphy** – an apomorphy that unites two or more taxa into a monophyletic group

**tectate** – of pollen grains, two-walled

**testa** – the outer coat of the seed

**tomentum** – covering of short hairs, scales, wool or down

**type specimen** – a specimen upon which the name was established and to which it is forever bound

**valvate** – meeting exactly without overlapping

**versatile** – of anthers, freely swinging about the point of attachment to the filament

**vicariance** – the process whereby an ancestral species splits as a result of the imposition of a barrier(s) within the original population

**vicariant species** – closely related and ecologically equivalent species that tend to be mutually exclusive occupying disjunct geographical areas

**Wallace’s Line** – the boundary that marks unrelated biological realms east and west of a line drawn approximately through central Malesia; Huxley first coined the term based on the work of Alfred R. Wallace.

**xenogamy** – fertilisation between pollen and ovules of different plants or genets
ABBREVIATIONS

AFLP – amplified fragment length polymorphism
Apr. – April
auct. non. – auctorum nonnullorum; of some authors
Aug. – August
c. – circa (about)
cm – centimetres
cp – chloroplast
cult. – cultus; cultivated
dbh – diameter at breast height; approximately 1.2 m above ground level
Dec. – December
diam. – diametro; diameter
DNA – deoxyribonucleic acid
E – east
EDTA – ethylenediaminetetra-acetate
Feb. – February
hort. – hortorum; of gardens
ICBN – International Code of Botanical Nomenclature
ined. – ineditus; unpublished
ITS – internal transcribed spacer
Jan. – January
Mar. – March
mm – millimetres
N – north
nom. – nomen; name
nom. illeg. – nomen illegitimum; illegitimate name
nom. inval. – nomen invalidum; invalid name
nom. ined. – nomen inedit; proposed name
nom. nud. – nomen nudum; name unaccompanied by a description or reference to a published description
nom. provis. – nomen provisorius; provisional name
nom. tant. – nomen tantum; name only
Nov. – November
NP – National Park

nr – nuclear ribosomal

Oct. – October

ortho. var. – orthographic variation

PAE – parsimony analysis of endemicity

PAUP – phylogenetic analysis using parsimony

PCR – polymerase chain reaction

PO – pollen:ovule ratio

RFLP – restriction fragment length polymorphism

S – south

s. n. – sine numero; without a number

Sept. – September

sp. – species; species (singular)

spp. – species; species (plural)

t. – tabula; plate

TAE – tris (hydroxymethyl) methylamine acetate ethylenediaminetetra-acetate

TBR – tree bisection and reconnection

TE – tris ethylenediaminetetra-acetate

W – west
## HERBARIUM ACRONYMS

<table>
<thead>
<tr>
<th>Acronym</th>
<th>Institution Name and Location</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>Harvard University, Harvard, USA</td>
</tr>
<tr>
<td>AAU</td>
<td>Department of Systematic Botany, Aarhus University, Denmark</td>
</tr>
<tr>
<td>B</td>
<td>Botanischer Garten und Botanisches Museum, Berlin, Germany</td>
</tr>
<tr>
<td>BKF</td>
<td>Royal Forest Department, Bangkok, Thailand</td>
</tr>
<tr>
<td>BH</td>
<td>Bailey Hortorium, Cornell University, Ithaca, USA</td>
</tr>
<tr>
<td>BM</td>
<td>Natural History Museum, London, United Kingdom</td>
</tr>
<tr>
<td>BO</td>
<td>Herbarium Bogoriense, Bogor, Indonesia</td>
</tr>
<tr>
<td>BR</td>
<td>Jardin Botanique National de Belgique, Meise, Belgium</td>
</tr>
<tr>
<td>BRI</td>
<td>Queensland Herbarium, Mt Coot-tha, Brisbane, Australia</td>
</tr>
<tr>
<td>BSIP</td>
<td>Department of Forest Herbarium, Honiara, Solomon Islands</td>
</tr>
<tr>
<td>CAHUP</td>
<td>Museum of Natural History, University of the Philippines at Los Baños</td>
</tr>
<tr>
<td>CANB</td>
<td>Australian National Herbarium, Canberra, Australia</td>
</tr>
<tr>
<td>CANT</td>
<td>South China Agricultural University, Canton, China</td>
</tr>
<tr>
<td>DNA</td>
<td>Conservation Commission, Darwin, Australia</td>
</tr>
<tr>
<td>FI</td>
<td>University of Florence, Italy</td>
</tr>
<tr>
<td>FT</td>
<td>Tropical Herbarium of Florence, Italy</td>
</tr>
<tr>
<td>FTG</td>
<td>Fairchild Tropical Garden, Miami, USA</td>
</tr>
<tr>
<td>JCT</td>
<td>Tropical Plant Sciences, James Cook University, Townsville, Australia</td>
</tr>
<tr>
<td>K</td>
<td>Royal Botanic Gardens, Kew, United Kingdom</td>
</tr>
<tr>
<td>KEP</td>
<td>Forest Research Institute of Malaysia, Kepong, Malaysia</td>
</tr>
<tr>
<td>L</td>
<td>Rijksherbarium, Leiden, Netherlands</td>
</tr>
<tr>
<td>LAE</td>
<td>Forest Research Institute, Lae, Papua New Guinea</td>
</tr>
<tr>
<td>LBC</td>
<td>Forestry Herbarium, Museum of Natural History, University of the Philippines at Los Baños</td>
</tr>
<tr>
<td>M</td>
<td>Botanische Staatssammlung, Munich, Germany</td>
</tr>
<tr>
<td>MAK</td>
<td>Tokyo Metropolitan University, Japan</td>
</tr>
<tr>
<td>MAN</td>
<td>Forestry Division, Manokwari, Indonesia</td>
</tr>
<tr>
<td>MEL</td>
<td>National Herbarium of Victoria, Melbourne, Australia</td>
</tr>
<tr>
<td>NSW</td>
<td>National Herbarium of New South Wales, Sydney, Australia</td>
</tr>
<tr>
<td>NY</td>
<td>New York Botanical Garden, New York, USA</td>
</tr>
<tr>
<td>P</td>
<td>Muséum National d'Histoire Naturelle, Paris, France</td>
</tr>
<tr>
<td>PNH</td>
<td>Philippine National Herbarium, Manila, Philippines</td>
</tr>
</tbody>
</table>
PERTH  Department of Conservation and Land Management, Perth, Australia
QRS  CSIRO, Atherton, Australia
S  Swedish Museum of Natural History, Stockholm, Sweden
SAR  Department of Forestry, Kuching, Sarawak, Malaysia
SING  Singapore Botanic Gardens, Singapore
UC  University of California, Berkeley, California, USA
US  United States National Herbarium, Smithsonian Institution,
    Washington, USA