

# ResearchOnline@JCU

This file is part of the following reference:

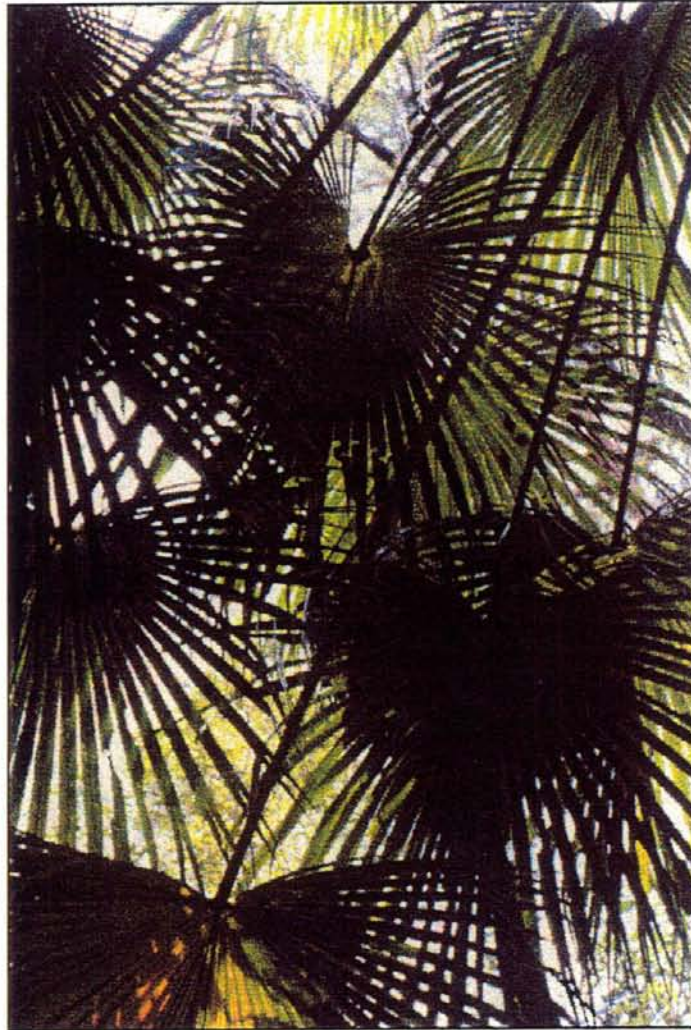
**Dowe, John Leslie (2001) *Studies in the genus Livistona* (Coryphoideae: Arecaceae). PhD thesis, James Cook University.**

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](mailto: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)

*2 October 2001*

(Date)

## 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 Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references given.

(Name)

*2 October 2001*  
.....

(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 Mogeia, 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. Thijssse 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 Tiên Hiệp 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 <i>Livistona</i> R. Br. ....	3
1.4	Taxonomic history.....	5
1.5	Biology, ecology and other studies of <i>Livistona</i> .....	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 <i>Livistona</i> . ....	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 <i>Livistona</i> 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 endemism (PAE)	222
5.2.3	The role of molecular data in biogeography	222

5.3	Regional histories.....	223
5.3.1	Biogeography in the South-east Asian/Australasian region.....	224
5.3.2	Biogeography of the Afro-Arabian area.....	226
5.4	Environmental change.....	227
5.5	Biogeography of palms.....	228
5.5.1	Palm fossils.....	229
5.5.2	Some problematic distributions.....	230
5.6	Aims.....	231
5.7	Materials and methods.....	231
5.7.1	Distribution.....	231
5.7.2	Fossils.....	231
5.7.3	Parsimony analysis of endemism (PAE).....	232
5.7.4	Cladistics.....	232
5.7.5	Morphological adaptation.....	232
5.8	Results.....	234
5.8.1	Distribution.....	234
5.8.2	Fossil record.....	234
5.8.3	Regional distribution and area cladograms.....	236
5.8.4	Cladistics.....	236
5.9	Discussion.....	244
5.9.1	Fossils.....	244
5.9.2	Distribution and endemism.....	244
5.9.3	Relictualism.....	245
5.9.4	Cladistics.....	246
5.9.5	Distribution of <i>Livistona carinensis</i> .....	247
5.9.6	Diversity and distribution of <i>Livistona</i> .....	249
5.10	Conclusion.....	250

**Chapter 6 DEVELOPMENT OF A MORPHOLOGICALLY BASED  
METHOD TO PREDICT SEXUALITY IN *LIVISTONA***

6.1	Introduction.....	252
6.2	Evolution of sexual expression.....	254
6.2.1	Hermaphroditism to dioecy: mechanisms and consequences.....	255
6.3	Sex ratio in palms.....	257

6.4	Rate of evolution of dioecy .....	258
6.5	Functional dioecy .....	259
6.5.1	Pollen in functionally dioecious species .....	260
6.6	Pollination systems in palms. ....	261
6.7	Seasonality.....	263
6.8	Pollinators and multistaminy.....	264
6.9	Sexual expression in <i>Livistona</i> .....	264
6.10	Description of reproductive organs in <i>Livistona</i> . ....	266
6.10.1	Habit .....	266
6.10.2	Inflorescence .....	266
6.10.3	Flower morphology .....	268
6.10.4	Nectaries.....	269
6.10.5	Spatial relationships of flowers .....	270
6.10.6	Anther dehiscence. ....	270
6.10.7	Stigmas .....	271
6.10.8	Pollen morphology and size .....	271
6.10.9	Pollen:ovule ratios.....	271
6.10.10	Pollination .....	272
6.11	Aims .....	273
6.12	Materials and methods.....	273
6.12.1	Predicting sexuality and breeding systems.....	277
6.12.2	An index of functional gender.....	278
6.12.3	Explanation of characters .....	279
6.12.4	Pollen exclusion experiments.....	282
6.13	Results .....	282
6.13.1	Character 1: Percentages of nonfruit-bearing individuals.....	282
6.13.2	Characters 2, 3: Flowering/fruiting duration, flowering season.....	283
6.13.3	Character 4: Pollen:ovule (P:O) ratios .....	285
6.13.4	Characters 5, 6: Number of flowers per inflorescence, season .....	285
6.13.5	Character 7: Pollen size – dimensions and volume.....	286
6.13.6	Character 8, 9: Pollen abundance, pollen dispersal index.....	287
6.14	Results of pollen exclusion experiments .....	287
6.15	The index of functional gender .....	288
6.16	Discussion and conclusion. ....	289

## 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

<b>References</b> .....	297
-------------------------	-----

<b>Appendices</b> .....	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 mm<sup>2</sup>, 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

<b>Figure 1.1</b>	Distribution of <i>Livistona</i> .....	4
<b>Figure 1.2</b>	Portrait of Robert Brown, <i>Livistona humilis</i> in habitat and the type specimen of <i>Livistona humilis</i> .....	6
<b>Figure 1.3</b>	Protologue of <i>Livistona</i> .....	7
<b>Figure 1.4</b>	Portraits of prominent <i>Livistona</i> taxonomists.....	9
<b>Figure 1.5</b>	Time-lines of the taxonomy of <i>Livistona</i> .....	10
<b>Figure 2.1</b>	<i>Livistona rotundifolia</i> . ....	35
<b>Figure 2.2</b>	<i>Livistona robinsoniana</i> . ....	40
<b>Figure 2.3</b>	<i>Livistona merrillii</i> . ....	45
<b>Figure 2.4</b>	<i>Livistona papuana</i> .....	49
<b>Figure 2.5</b>	<i>Livistona woodfordii</i> .....	52
<b>Figure 2.6</b>	<i>Livistona chocolatina</i> .....	56
<b>Figure 2.7</b>	<i>Livistona tothur</i> .....	59
<b>Figure 2.8</b>	<i>Livistona surru</i> .....	63
<b>Figure 2.9</b>	<i>Livistona jenkinsiana</i> . ....	66
<b>Figure 2.10</b>	<i>Livistona endauensis</i> .....	70
<b>Figure 2.11</b>	<i>Livistona tahanensis</i> . ....	73
<b>Figure 2.12</b>	<i>Livistona halongensis</i> . ....	75
<b>Figure 2.13</b>	<i>Livistona boninensis</i> . ....	78
<b>Figure 2.14</b>	<i>Livistona chinensis</i> .....	82
<b>Figure 2.15</b>	<i>Livistona saribus</i> .....	88
<b>Figure 2.16</b>	<i>Livistona exigua</i> .....	93
<b>Figure 2.17</b>	<i>Livistona muelleri</i> . ....	95
<b>Figure 2.18</b>	<i>Livistona nasmophila</i> .....	99
<b>Figure 2.19</b>	<i>Livistona decora</i> . ....	102
<b>Figure 2.20</b>	<i>Livistona inermis</i> .....	106
<b>Figure 2.21</b>	<i>Livistona benthamii</i> .....	110
<b>Figure 2.22</b>	<i>Livistona concinna</i> .....	114
<b>Figure 2.23</b>	<i>Livistona nitida</i> . ....	117
<b>Figure 2.24</b>	<i>Livistona australis</i> .....	119
<b>Figure 2.25</b>	<i>Livistona carinensis</i> . ....	123
<b>Figure 2.26</b>	<i>Livistona alfredii</i> .....	127
<b>Figure 2.27</b>	<i>Livistona humilis</i> .....	130



<b>Figure 2.28</b> <i>Livistona fulva</i> .....	134
<b>Figure 2.29</b> <i>Livistona eastonii</i> .....	136
<b>Figure 2.30</b> <i>Livistona victoriae</i> . ....	138
<b>Figure 2.31</b> <i>Livistona drudei</i> . ....	141
<b>Figure 2.32</b> <i>Livistona lorophylla</i> .....	144
<b>Figure 2.33</b> <i>Livistona lanuginosa</i> .....	148
<b>Figure 2.34</b> <i>Livistona mariae</i> . ....	151
<b>Figure 2.35</b> <i>Livistona rigida</i> .....	154
<b>Figure 3.1</b> The position of <i>Livistona</i> as inferred from combined morphological and cpDNA data.....	163
<b>Figure 3.2</b> The position of <i>Livistona</i> as inferred from <i>rps16</i> intron and <i>trnL-trnF</i> sequences.....	164
<b>Figure 3.3</b> Leaf-base remains in <i>Livistona</i> . ....	173
<b>Figure 3.4</b> Lamina morphology in <i>Livistona</i> .....	174
<b>Figure 3.5</b> Simplified composite half-leaf of <i>Livistona</i> . ....	175
<b>Figure 3.6</b> Segment apices in <i>Livistona</i> . ....	177
<b>Figure 3.7</b> Venation patterns in <i>Livistona</i> . ....	178
<b>Figure 3.8</b> Petiole cross sections of <i>Livistona</i> . ....	179
<b>Figure 3.9</b> Armature in <i>Livistona</i> . ....	180
<b>Figure 3.10</b> Spine shape in <i>Livistona</i> . ....	181
<b>Figure 3.11</b> Leaf-base fibres in <i>Livistona</i> .....	182
<b>Figure 3.12</b> Inflorescence morphology in <i>Livistona</i> . ....	183
<b>Figure 3.13</b> Bract tomentum in <i>Livistona</i> .....	184
<b>Figure 3.14</b> Flowers of <i>Livistona</i> . ....	185
<b>Figure 3.15</b> Fruit of <i>Livistona</i> . ....	186
<b>Figure 3.16</b> Epicarp pores in <i>Livistona</i> . ....	187
<b>Figure 3.17</b> Phylogram of Analysis 1.....	192
<b>Figure 3.18</b> Strict consensus tree of Analysis 1. ....	193
<b>Figure 3.19</b> Phylogram of Analysis 2.....	194
<b>Figure 3.20</b> Bootstrap support values.....	195
<b>Figure 3.21</b> Cladogram traced with character 5 – lamina segmentation. ....	199
<b>Figure 3.22</b> Cladogram traced with character 26 – inflorescence branching.....	200
<b>Figure 4.1</b> Organisation of the nrDNA region .....	206
<b>Figure 4.2</b> A selection of crude DNA extractions visualised on agarose gel.....	211

<b>Figure 4.3</b> PCR products using primers ITS4 and ITS16. ....	211
<b>Figure 4.4</b> PCR products using primers ITS4 and ITS16 ‘palm’ .....	212
<b>Figure 4.5</b> Cloned products using the pMOS <i>Blue</i> blunt ended cloning kit.....	212
<b>Figure 4.6</b> Preliminary phylogram obtained from the sequence data .....	213
<b>Figure 5.1</b> The main volcanic and mountain building areas of south-eastern Asia and Australasia. ....	225
<b>Figure 5.2</b> Extant distribution of <i>Livistona</i> . ....	234
<b>Figure 5.3</b> Sites of <i>Livistona</i> -affinity fossils. ....	237
<b>Figure 5.4</b> Geological timescale with fossil and geological events. ....	238
<b>Figure 5.5</b> Cladograms of the distributional relationships of <i>Livistona</i> species within biogeographical areas, using the PAE method. ....	240
<b>Figure 5.6</b> The relationships of biogeographic regions.....	240
<b>Figure 5.7</b> Cladogram of <i>Livistona</i> taken from cladistic analysis in Chapter 3 ....	241
<b>Figure 5.8</b> Distribution of the <i>exigua</i> and <i>saribus</i> lineages.....	242
<b>Figure 5.9</b> Distribution of the <i>chinensis</i> and <i>rotundifolia</i> subclades.....	242
<b>Figure 5.10</b> Distribution of the <i>mariae</i> subclade.....	243
<b>Figure 5.11</b> Distribution of the <i>humilis</i> subclade. ....	243
<b>Figure 6.1</b> Schematic presentation of sexual expression in the Areaceae. ....	253
<b>Figure 6.2</b> Inflorescence types in <i>Livistona</i> . ....	267
<b>Figure 6.3</b> Flower of <i>Livistona</i> . ....	268
<b>Figure 6.4</b> Morphology of the outer septal nectary in <i>Livistona humilis</i> . ....	270
<b>Figure 6.5</b> Habits of species of <i>Livistona</i> studied. ....	276
<b>Figure 6.6</b> Percentages of fruit-bearing/nonfruit-bearing plants. ....	282
<b>Figure 6.7</b> Flowering and fruiting calendars for the four study species.....	284
<b>Figure 6.8</b> Pollen:ovule ratios.. ....	285
<b>Figure 6.9</b> Comparison of the mean volumes of single pollen grains.....	286
<b>Figure 6.10</b> Pollen micrographs of <i>Livistona</i> species. ....	286
<b>Figure 6.11</b> The index of functional gender.....	289

## LIST OF TABLES

<b>Table 1.1</b>	Names applied to <i>Livistona</i> .....	11
<b>Table 1.2</b>	Summary of some studies involving <i>Livistona</i> .....	15
<b>Table 2.1</b>	Comparison of morphological characteristics of <i>Livistona inermis</i> and <i>L. lorophylla</i> .....	21
<b>Table 2.2</b>	Comparison of morphological characteristics of <i>Livistona beccariana</i> and <i>L. woodfordii</i> .....	22
<b>Table 2.3</b>	Summary of typification for names in <i>Livistona</i> .....	23
<b>Table 2.4</b>	List of currently accepted taxa recognised in this account.....	24
<b>Table 2.5</b>	Taxa for which neotypes and lectotypes need to be chosen.....	25
<b>Table 3.1</b>	The <i>Livistona</i> alliance presented by Moore.....	161
<b>Table 3.2</b>	Genera in the Livistoninae with species numbers and distribution.....	161
<b>Table 3.3</b>	Taxa used in the cladistic analysis of <i>Livistona</i> .....	171
<b>Table 3.4</b>	Specimens used in the SEM examination of epicarp features.....	188
<b>Table 3.5</b>	Morphological dataset used in the cladistic analysis.....	190
<b>Table 3.6</b>	Summary of statistics for Analysis 1.....	191
<b>Table 3.7</b>	Summary of statistics for Analysis 2.....	195
<b>Table 3.8</b>	Summary of statistics for both analyses.....	196
<b>Table 3.9</b>	Rescaled consistency indices greater than the average in both analyses.	196
<b>Table 3.10</b>	Character number and character states in which rescaled consistency index was greater than the average.....	197
<b>Table 3.11</b>	Characters that scored a rescaled consistency index of '0.0'.....	197
<b>Table 3.12</b>	Characters that scored a rescaled consistency index of '1.0'.....	198
<b>Table 4.1</b>	Palm studies in which molecular techniques have been used.....	205
<b>Table 4.2</b>	Samples used in the molecular investigations in <i>Livistona</i> .....	207
<b>Table 4.3</b>	Aligned sequence data of <i>Livistona</i> , <i>Raphia</i> and <i>Eugeissona</i> .....	214
<b>Table 5.1</b>	Palm studies in which cladistic techniques have been used.....	221
<b>Table 5.2</b>	Palm studies in which molecular techniques have been used.....	222
<b>Table 5.3</b>	Major biogeographic studies of palms.....	228
<b>Table 5.4</b>	Data matrices for area cladograms.....	233
<b>Table 5.5</b>	Distribution status of <i>Livistona</i> species.....	235
<b>Table 5.6</b>	Examples of fossils of <i>Livistona</i> -affinity.....	236
<b>Table 5.7</b>	Fossil taxa described for <i>Livistona</i> .....	237
<b>Table 5.8</b>	Biogeographic regions proposed by Takhtajan and Cracraft.....	239

<b>Table 5.9</b>	Biogeographic regions and their component species of <i>Livistona</i> . .....	239
<b>Table 6.1</b>	Definitions of sexual systems in plants. ....	254
<b>Table 6.2</b>	Reproductive characteristics and pollen:ovule (PO) ratios. ....	272
<b>Table 6.3</b>	Pollination modes that could occur in <i>Livistona</i> . ....	273
<b>Table 6.4</b>	Species of <i>Livistona</i> examined. ....	274
<b>Table 6.5</b>	Characteristics of species studied. ....	277
<b>Table 6.6</b>	Characters that may have predictive value in sexuality. ....	278
<b>Table 6.7</b>	Data for the nine predictive characters. ....	288
<b>Table 6.8</b>	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

*monomial* – 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

***pleoanthic*** – 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

***symplesiomorphy*** - (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.** – *nomem 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 endemism  
**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

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

**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