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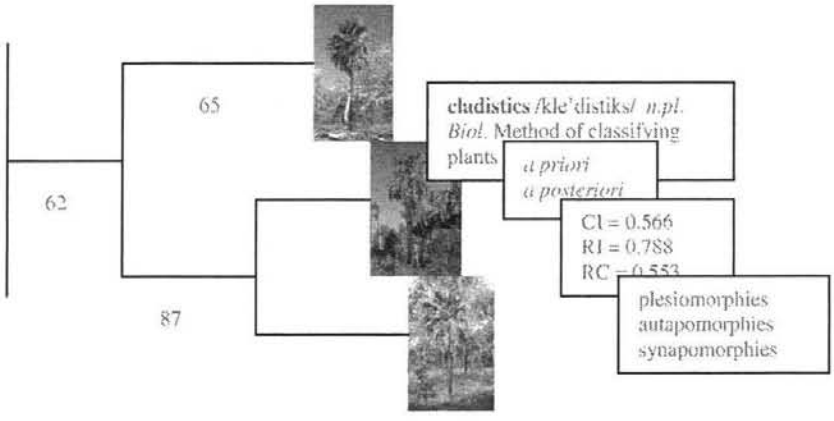
JAMES COOK UNIVERSITY AUSTRALIA

Chapter 3

Studies in the genus *Livistona* R. Br. (Coryphoideae: Arecaceae)

CLADISTIC ANALYSIS OF *LIVISTONA* BASED ON MORPHOLOGICAL CHARACTERS



3.1 Introduction

Linnaeus (1753) recognised the palms as a distinctive group based on the structure of the leaves and the sexual organs. Martius (1824) subsequently provided a hierarchical classification that aligned groups of genera based on shared characteristics that more clearly reflected 'natural' relationships. Martius placed *Livistona* within the Coryphinae, one of six 'families' designated for the palms. Martius's arrangement, with modifications, has since formed the basis of most subsequent classification systems for the family.

Hooker (1883) presented the first critical account of the palms, treated as a single family, based on an extended hierarchical system with division into tribes and subtribes. Within this system, *Livistona* was included in the tribe Corypheae, with 15 other genera, and placed between *Licuala* and *Trachycarpus*. Drude (1887) provided a modified system in which *Livistona* was placed in a tribe of 20 genera, the Sabaleae, most closely related to *Licuala* and *Erythea* (=*Brahea*). Later,

Beccari (1931) presented the first detailed treatment of *Livistona*. He related *Livistona* most closely to *Licuala*, from which it differed by leaf segmentation and corolla characters, and also *Brahea*, from which it differed in leaf venation characters, rather than more conservative fruit or flower characters. In accordance with Hooker (1883) and Drude (1887), Beccari (1921, 1931) placed *Livistona* in the tribe Corypheae, but within an extended group of 24 other genera. Beccari (1931) was the first to consider relationships among *Livistona* species, but was unable to identify any character that might be used to distinguish the Asian species from the Australian species, commenting that the Australian species were ".... not distinguishable from the Asiatic species by any remarkable character and thereby they represent a conspicuous Indo-Malayan element in the Australian flora". Subsequent classifications (Satake, 1962; Potztal, 1964) provided some minor rearrangements in suprageneric categories of the family, but the position of the Corypheae and *Livistona* has remained unchanged.

Moore (1973a) provided a detailed treatment of the palms, based on extensive field knowledge and broad-ranging morphological studies aimed at explaining the evolution of palms, and also attempting to clarify relationships between taxa more clearly than in previous systems. His system included a '*Livistona* alliance' of 13 genera (Table 3.1), arranged in ascending order of morphological specialisation, and placed *Livistona* closest to *Pholidocarpus*.

Subsequently, Tomlinson (1979), in a review of palm botany, followed Moore's informal classification, while Dransfield and Uhl (1986) applied some minor changes and provided nomenclatural formalisation of the groups that Moore had outlined. In this system, Uhl and Dransfield (1987) included *Livistona* in the Coryphoideae subfamily, tribe Corypheae and subtribe Livistoninae with a pan-tropical distribution (Table 3.2).

Table 3.1. The '*Livistona* alliance' presented by Moore (1973a).

Livistona alliance
Johannesteijsmannia unit
Johannesteijsmannia (*Teysmannia*)
Livistona unit
Wissmannia
Livistona (*Saribus*)
Pholidocarpus
Pritchardiopsis
Licuala (*Dammera*, *Pericycla*)
Pritchardia (*Eupritchardia*, *Styloma*)
Acoelorrhaphe (*Acanthosabal*, *Paurotis*)
Colpothrinax
Serenoa (*Diglossophyllum*)
Brahea (*Erythea*, *Glaucothea*)
Copernicia
Washingtonia unit
Washingtonia (*Neowashingtonia*)

Table 3.2. Genera in the Livistoninae with species numbers and distribution.
Adapted from Uhl and Dransfield (1987) and with numbers updated from recent works.

Livistona: 35 spp.; Africa, Arabia, south-eastern Asia, Malesia, Australia
Pholidocarpus: 6 spp.; south-eastern Asia, western Malesia
Johannesteijsmannia: 4 spp.; Malay Peninsula, Sumatra, western Borneo
Licuala: c. 111 spp.; south-eastern Asia, Malesia, Melanesia, northern Queensland
Pritchardiopsis: 1 sp.; New Caledonia
Pritchardia: c. 37 spp.; Hawaii, Fiji, Tonga, Danger Islands
Colpothrinax: 2 spp.; Cuba, Guatemala, Panama
Acoelorraphe: 1 sp.; southern Florida, Caribbean islands
Serenoa: 1 sp.; south-eastern United States
Brahea: 18 spp.; Baja California and off-shore islands, Mexico, Guatemala
Copernicia: 25 spp.; South America, Hispaniola, Cuba
Washingtonia: 2 spp.; south-western United States, Baja California, Sonora

Although the subtribe Livistoninae is well-characterised by a gynoecium of three carpels connate by their styles only, relationships between genera in the subtribe are not clear. Uhl and Dransfield (1987, p. 190, 192) stated that in the subtribe "....differences between the genera are mostly small....", and that *Livistona* is "....most closely related to *Licuala* and *Pholidocarpus*".

3.2 Cladistic concepts and methodologies

Cladistics is a method of analysis that is used to infer phylogenetic relationships, presented in the form of a cladogram or phylogram. A cladogram depicts a hierarchical classification system of nested clades based on common ancestry and the sharing of characters, determined by the most parsimonious arrangement of character state changes. This is achieved by the distribution of shared derived character states (i. e. synapomorphies). To construct a cladogram, observations of individual species are translated into characters and character states ("alternate forms of the same thing", Hawkins *et al.*, 1997) and arranged in a matrix in which each taxon is scored for all characters (Strong and Lipscombe, 1999).

Cladograms can be interpreted in a number of ways (Maddison and Maddison, 1992), to indicate:

- hypothesised phylogenetic history, with lines representing lineages descending through time and with branch points representing speciation events
- relative recency of common ancestry of the observed species
- hierarchical distribution of shared, homologous character states
- hierarchical distribution of shared characteristics.

Cladistic methodology, because of the inherent necessity for a comprehensive data base, obliges the researcher to focus on the selection of definable, objective characters and characters states. This method encourages an 'evenness' and comparability between species with regards to the recording and observation of their morphological characteristics, a situation that is often not required in traditional intuition-based systematic and phylogenetic analyses (Barrow, 1999).

3.2.1 *Cladistic analyses and molecular studies of palms*

In the first cladistic analysis of the palm family based on morphological and chloroplast DNA (cpDNA) restriction site data, Uhl *et al.* (1995) identified the Livistoninae as part of a clade that also included the Thrinacinae and was therefore paraphyletic (Fig. 3.1).

In this same study, a strict consensus tree based only on morphological data included *Livistona* within a group of 25 genera. Although from a tree based on molecular data only, *Livistona* was embedded in a group of seven genera, *Trachycarpus*, *Rhapidophyllum*, *Rhapis*, *Pholidocarpus*, *Brahea* and *Washingtonia*. These genera had three sister clades composed of *Acoelorraphe*/ *Serenoa*, *Johannesteijsmannia*/*Licuala* and *Colpothrinax*/*Pritchardia*/*Copernicia*.

In a study based on cpDNA sequences from the *trn*L – *trn*F region, Baker *et al.* (1999) resolved *Livistona* to be in a broadly similar phylogenetic position as that suggested by Uhl *et al.* (1995). Asmussen *et al.* (2000) (Fig. 3.2), in an analysis of

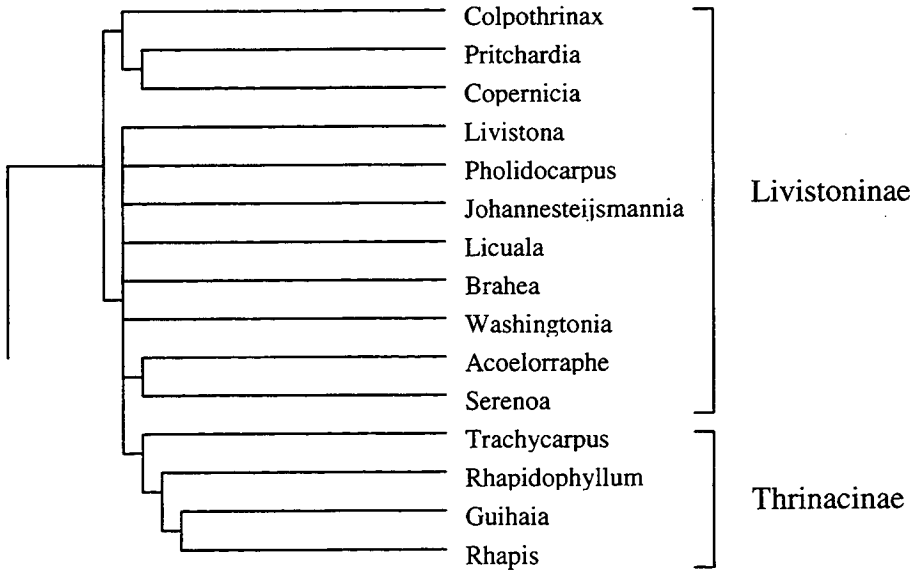


Figure 3.1. The position of Livistona as inferred from combined morphological and cpDNA data (Uhl *et al.*, 1995).

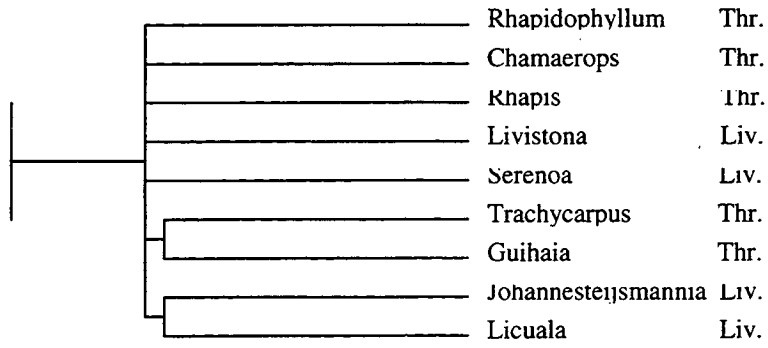


Figure 3.2. The position of *Livistona* as inferred from *rps*16 intron and *trn*L-*trn*F sequences. The clade is extracted from an analysis presented by Asmussen *et al.* (2000), of successively weighted characters of combined sequences. Genera, being in either the Livistoninae (Liv.) or the Thrinacinae (Thr.), are indicated.

*rps*16 and *trn*L-*trn*F sequences, and Asmussen and Chase (2001), in a combined analysis of *rbc*L, *rps*16 and *trn*L-*trn*F sequences, recovered a similar relationship between the Livistoninae and the Thrinacinae that was recovered by Uhl *et al.* (1995). Asmussen and Chase's (2001) conclusion was supported in an analysis of successively weighted characters, but in an analysis of equally weighted characters the relationships between genera were unresolved. It is possible that taxonomic rearrangements above the generic level are likely with further study because of the low levels of resolution and bootstrap support. Other relevant cladistic studies on Coryphoid palms include those by Evans (1995) and Zona (1990).

3.3 Relationships of *Livistona* species in Australia

Based on phenetic similarity, Rodd (1998) proposed four informal groups for the Australian species:

1. '*Mariae* group': *L. lanuginosa, L. mariae, L. nasmophila* and *L. rigida*; palms of alluvial flood-channels in semi-arid environments with large leaves having a waxy layer on the abaxial surface.
2. 'East coast group': *L. benthamii, L. drudei, L. australis, L. nitida, L. decora* and *L. fulva*; mesomorphic palms of moist habitats, with green leaves having drooping segments and globose to subpyriform black fruit.

3. 'Arafura group': *L. muelleri*, *L. humilis* and *L. eastonii*; smallish palms of monsoonal climates, with small leaves with rigid segments, and small black ellipsoid or pyriform fruit.
4. 'North-western group': *L. inermis*, *L. lorophylla*, *L. kimberleyana* [placed as a synonym of *L. lorophylla* in this thesis], *L. victoriae* and *L. alfredii*; small to moderate palms in semi-arid environments, deeply segmented leaves with a hard waxy cuticle, and short inflorescences with only a few partial inflorescences.

Rodd (1998) suggested that some apparent evolutionary convergence was possible owing to environmental conditions. The relationship of Australian species to those elsewhere has not been studied.

3.4 Evolutionary trends in palms

Based on criteria of evolutionary specialisation hypothesised in the many works of Bessey, Hutchinson and Cronquist, Moore and Uhl (1982), provided an outline of the major trends of evolution in palms. They hypothesised that palms arose in western Gondwana (South America today), and that proto-palms were small woody plants adapted to dry, cool seasonal climates. Dransfield *et al.* (1990) hypothesised that the palms with the most 'primitive' characters are in the Coryphoid subfamily and are characterised by a sympodial moderate habit, unbranched stems, palmate or costapalmate leaves, moderately branched partial inflorescences, conspicuous inflorescence bracts, bisexual trimerous flowers, six stamens, monosulcate pollen, apocarpus gynoecia, three carpels, moderate sized ovule, fleshy fruit, little differentiated endocarp, homogeneous endosperm, remote tubular germination and chromosome complement of $n = 18$ (Moore and Uhl, 1982).

3.4.1 *Character choices in the phylogeny of palms*

The choice of morphological characters used in phylogenetic studies can be controversial, and must be viewed as a compromise between theoretical and practical concerns (Wilkinson, 1995). Of primary interest is the existence of homoplasy, in which unrelated evolutionary units may have undergone convergent or parallel evolution (Sytsma and Baum, 1996). The detection and explanation of homoplasy, in a group of species, are of primary relevance in

phylogenetics. The independence of characters must also be recognised, and the conflict between independent and interdependent characters must be considered. Characters are considered interdependent if transformations in one are linked to transformations in another, or otherwise display functional integration (Pleijel, 1995). Assessments of character choice and hypotheses of evolutionary development of palms have been provided by Moore and Uhl (1982), Zona (1990), Barfod (1991), Evans (1995), Salzman and Judd (1995), Uhl *et al.*, (1995), Barrow (1999), Henderson (1999b) and Pintaud (1999).

3.4.2 *Scoring of characters states*

For analytical purposes, character states can be scored in a number of ways depending on the type of character. Qualitative characters are scored on an absence or presence basis, but the scoring of quantitative characters requires more care. For example, the retention of leaf-bases on the stem as opposed to being deciduous, a qualitative character, can be scored as an unambiguous 'absent' or 'present'. However, continuous measurements such as height, inflorescence length, fruit length etc., are difficult to code as distinct characters. The process of making continuous measurements into discrete characters is achieved by gap-coding. In this method, gaps between continuous measurements are recognised and these divisions denote the boundaries of the characters (Kitching *et al.*, 1998). Chappill (1989) concluded that continuously varying characters were useful when the number of qualitative characters was insufficient for resolution of relationships.

Not all characters are measurable or observable in all taxa; some character states may be treated as 'inapplicable' or 'unknown' during analyses. Many analyses do not differentiate between these two data types and there must be an awareness of possible conflict if matrix data contain such scores (Platnick *et al.*, 1991). Kitching *et al.* (1998) noted that the inclusion of 'inapplicable' or 'unknown' data in an analysis may increase the number of most parsimonious cladograms, and that the codes may mask the phylogenetic signal implied by the observed data.

3.4.3 *Successive weighting*

The successive weighting method is one based on the consistency of characters within an analysis (Farris, 1969). The consistency, retention and rescaled consistency indices and their implications are discussed below. Using an unweighted set of characters, an estimate of cladistic relationships for the subject taxa is achieved. Based on the result, the characters are then reweighted according to the goodness of fit to the trees obtained. Those that have a consistency index of '1' retain full weight, and those that have lower consistency indices are given reduced weights. This reduces the influence of characters with low phylogenetic signal which are introducing phylogenetic noise and obscuring relationships. Based on the new value of weight, this procedure is continued with subsequent analyses being successively weighted until the length of the trees no longer changes between analyses, or if a single tree is produced. This procedure provides characters with a weighting that is consistent with the data set, and reinforces the influence of characters that best fit the tree. The steps involved in successive weighting are:

1. perform an analysis [with characters equally weighted]
2. consider it to be a 'first guess' at cladistic relationships
3. calculate the consistencies of characters on the trees [by applying the 'reweighting character' facility in PAUP*]: this provides a measure of scoring, and the scores are used to further weight the characters
5. apply weighting and perform further analyses
6. successively repeat this process until two successive trees, or sets of trees, have the same topology and tree length.

3.4.4 *Character polarity and ordering*

Character polarity is the assignment of 'evolutionary direction' to a particular state of a character. In parsimony analysis, a root is required to allow interpretation of character evolution, and allows conversion of an unrooted tree into a rooted tree. This is achieved by the outgroup comparison method (Weston, 1994). Kitching *et al.* (1998, p. 49) defined the outgroup comparison method as: "For a given character with two or more states within a group, the state occurring in related groups is assumed to be the plesiomorphic state". The outgroup method provides

a root to a tree as it polarises characters on the assumption that the root lies outside of the ingroup in question (Kitching *et al.*, 1998).

3.5 Tree statistics

3.5.1 *Consistency index* (CI)

One method of measuring the degree to which the available data fit the trees following analysis is the consistency index (CI). It is calculated by dividing the summation of the minimum amount of change possible for the characters (M) by the actual number of changes in the characters observed on the tree (S): CI = M/S. When the CI = 1, the data fit the tree perfectly, and implies no homoplasy for that character. As the number of changes on the tree increases, the value of the consistency index reduces. Consistency indices are calculated for each character or for the tree as a whole, calculated as an average of the indices for all characters. For a tree, a high index is considered superior, and the available data, for either an individual character or for the whole tree, are regarded as being phylogenetically informative. However, the CI for a tree may correlate negatively with both the number of taxa and characters and is sensitive to uninformative characters such as autapomorphies and symplesiomorphies (Siebert, 1992).

3.5.2 *Retention index* (RI)

Another descriptor is the retention index (RI), which is a measure of the amount of synapomorphy in a data set (Farris, 1989). It is calculated by determining the amount of homoplasy as a fraction of the maximum possible homoplasy (Siebert, 1992). As with the CI, it can be applied to single characters or to the tree as a whole.

3.5.3 *Rescaled consistency index* (RC)

The rescaled consistency index (RC) combines aspects of both the CI and the RI (Farris, 1989). This index is estimated as the product of those indices, RC = CI x RI. Whereas the RC provides a scale between 0 and 1, the CI can be valued at 1 but never at 0 as it must be a fraction of the amount of change in a character. The RI is a fraction of the amount of apparent synapomorphy on a tree, which can be 0, and is therefore a relative measure of homoplasy. When CI and RI are multiplied the result may be 0, if the RI is 0. Therefore RC is an indication of the

amount of change in a character. Its relative degree of possible homoplasy and synapomorphy is compared against all other characters.

3.5.4 *Bootstrap method*

A method of estimating the degree of 'statistical confidence' in the data used in cladistic analyses is the bootstrap method. The method is used for estimating statistical error in situations when the underlying sampling distribution is unknown or difficult to derive analytically (Felsenstein, 1985). During the bootstrap analysis, characters are deleted at random with replacement until a new data set of the same size as the original set is formed. If the clades are maintained during this procedure, they then can be determined as robust, dependent upon the number of times they are retained. The result is given as a percentage of the total number of trees found in all the replicate analyses that the individual clades are retained in. A statistically valid number of replicates is 1000 or more (Kitching *et al.*, 1998). A clade that receives a bootstrap value of 100% indicates that it has been retained in all the replicates used, and that it is a reliable estimate of phylogeny - it is a feature of the taxa and character distribution, despite the random addition and deletion of characters. Conventionally, bootstrap values above 95% are considered highly reliable, although the choice of lower estimates can be arbitrary. Values below 50% indicate absence of support (Kitching *et al.*, 1998).

3.6 Aims

The aims of this study were:

- to provide a cladistic analysis of *Livistona* based on the methods previously used for palms, primarily adapted from three papers: Uhl *et al.* (1995), Evans (1995), and Zona (1990).
- to recognise those characters that are the best indicators of phylogenetic relationship in the genus *Livistona*, based on the relative scoring of tree statistics.

3.7 Materials and methods

For this analysis, 35 species of *Livistona* were recognised as operational taxonomic units (Table 3.3), based on the morphological species concept (Andersson, 1990; Stuessy, 1990). Morphological data were compiled from observations of all Australian species in the field, and many species in Papua New Guinea, Thailand, the Philippines and Indonesia. Data for other species were obtained from herbarium specimens seen at AAU, B, BM, BO, BRI, FI, K, LAE, MAK, PNH and SING, and from the literature, primarily Beccari (1931) and Rodd (1998). Supplementary observations were made on living palms in The Palmetum and Anderson Park, Townsville; Flecker Gardens, Cairns; Bogor Botanic Gardens, Indonesia; Singapore Botanic Gardens; Nong Nooch Tropical Gardens, Thailand; and Lae Botanical Gardens, Papua New Guinea. *Livistona* specimens from numerous herbaria, temporarily housed at AAU (Aarhus University, Denmark), were examined during a study visit undertaken June/July 1999.

3.7.1 *Leaf venation patterns*

Leaf venation patterns were photographed with a standard SLR camera and close-up lenses. Strong backlight was used to facilitate a high contrast between lamina and vein tissues. The area of leaf segment examined was consistent throughout, being taken from the middle area of the central segment. A standard magnification was used so that comparison could be made between specimens. Fresh leaves were used when available. In the absence of fresh leaves, dried leaves were prepared by boiling for 30 seconds in distilled water and then photographed in a moist state.

3.7.2 *Fruit epicarp features*

Epicarp surface features were examined using three scanning electron microscopes: a CamScan MaXim2040S in the Botany Department, Aarhus University, Denmark; and a JEOL JSM - 5410lv and Philips LX20 in the Microscopy Unit, James Cook University. In all cases, materials were sputter-coated with platinum. Magnifications were standardised to allow comparison between specimens. Images were reproduced on black and white film, or in some cases captured and printed digitally.

Table 3.3. Taxa used in the cladistic analysis of *Livistona*.

1. *L. alfredii* F. Muell.
2. *L. australis* (R. Br.) Mart.
3. *L. benthamii* F. M. Bailey
4. *L. boninensis* (Becc.) Nakai
5. *L. carinensis* (Chiov.) J. Dransf. and N. W. Uhl
6. *L. chinensis* (Jacq.) R. Br. ex Mart.
7. *L. chocolatina* Dowe (ined.)
8. *L. concinna* Dowe and Barfod
9. *L. decora* (Bull) Dowe (ined.)
10. *L. drudei* F. Muell. ex Drude
11. *L. eastonii* C. A. Gardner
12. *L. endauensis* J. Dransf. and K. M. Wong
13. *L. exigua* J. Dransf.
14. *L. fulva* A. N. Rodd
15. *L. halongensis* Nguyen and Kiew
16. *L. humilis* R. Br.
17. *L. inermis* R. Br.
18. *L. jenkinsiana* Griff.
19. *L. lanuginosa* A. N. Rodd
20. *L. lorophylla* Becc.
21. *L mariae* F. Muell.
22. *L. merrillii* Becc.
23. *L. muelleri* F. M. Bailey
24. *L. nasmophila* Dowe and D. L. Jones (ined.)
25. *L. nitida* A. N. Rodd
26. *L. papuana* Becc.
27. *L. rigida* Becc.
28. *L. robinsoniana* Becc.
29. *L. rotundifolia* (Lam.) Mart.
30. *L. saribus* (Lour.) Merr. ex A. Chev.
31. *L. surru* Dowe and Barfod
32. *L. tahanensis* Becc.
33. *L. tothur* Dowe and Barfod
34. *L. victoriae* A. N. Rodd
35. *L. woodfordii* Ridley

3.8 Explanation of characters used in the cladistic analysis

For qualitative characters, binary coding was applied, whereas for continuously varying quantitative characters, gap-coding was used. Although there are arguments against the inclusion of continuously varying data in cladistics, their inclusion in analyses is widely accepted (Baum, 1988; Chappill, 1989; Rae, 1998). There is also the requirement that the number of characters must exceed the number of taxa in an analysis. To achieve this, it may be necessary to use quantitative characters if the number of qualitative characters is low. For the determination of gap-coded characters, the measurements were plotted. Measurement ranges were taken from the available herbarium specimens, living plants and the literature (Appendices 3-13). The means of measurements were used to construct the scatter plots. The gaps between discrete groups were arbitrarily recognised on the plotted data where relatively large gaps occurred (Appendix 14), and three characters states were recognised. This method of gap-coding was applied to ten characters such as height, height:dbh ratio, lamina length, inflorescence length and maximum flower length, among others.

Character 1. Maximum height: < 18 m (0); 18-30 m (1); > 30 m (2). The height to which *Livistona* species grow appears independent of habitat, geographical distribution or climate type. Height is defined as from ground-level to the apex of the crown. The smallest species (5 - 7 m tall), such as *L. exigua* and *L. humilis*, occur in equatorial rainforest and seasonally dry woodland respectively, and the tallest species (30 - 40 m) such as *L. rotundifolia* and *L. australis* occur in equatorial rainforest and sclerophyll forest or rainforest respectively. A scatter plot of height measurements is included in Appendix 14.

Character 2. Ratio of height to diameter at breast height (dbh): < 93 (0); 93-138 (1); > 138 (2). Stem diameter (dbh) is usually dependent upon height, i. e. the taller the species the greater the diameter. However, correlation between height and dbh is variable across the genus. A scatter plot of height:dbh ratios is included in Appendix 14.

Character 3. Leaf-base remains: present (0); absent (1). The leaf-base in most *Livistona* species corresponds to the '*Cocos* type' as described by Tomlinson

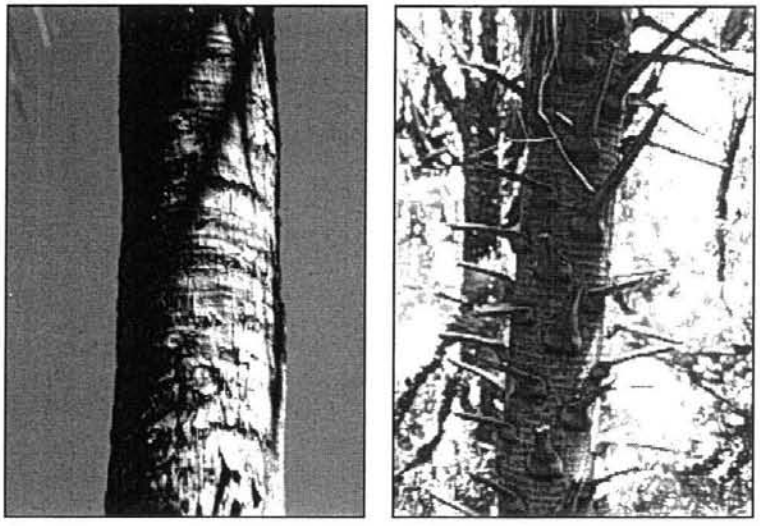


Figure 3.3. Leaf-base remains in *Livistona* (character 3). ***Left:*** Stem of *L. victoriae*, an example in which leaf-bases do not remain attached, Jasper Gorge, WA. ***Right:*** Stem of *L. benthamii*, an example in which leaf-bases remain attached, Kakadu, NT.

(1990), in which abscission of senescent leaves provides the palm with a 'clean' trunk, e. g. *L. victoriae, L. rotundifolia* etc. (Fig. 3.3). Leaf-base attachment is via a fibrous network of ventral tissues. However, in some species, the leaf-base is retained on the stem, e. g. *L. benthamii*, and has been described by Tomlinson (1990) as the '*Phoenix* type'. Although the ecological significance of the process has not been studied in detail, retained leaf-bases may offer protection to the stem during fires. Data for height, dbh, height:dbh ratio, and leaf-base retention are presented in Appendix 3.

Character 4. Lamina outline: ± circular (0); other than ± circular (1). Lamina outline (Fig. 3.4) is consistent for species, although the change in outline from juvenile to mature leaves in a single species may be considerable. Determinations were made on leaves from mature individuals. The outline was ascertained by placing the lamina on a flat surface and viewing from above. The outline may be more or less circular, or variously elliptical or oblong.

Character 5. Regular lamina segmentation: present (0); absent (1). The *Livistona* lamina is costapalmate with an unsegmented proximal portion and a segmented distal portion (Tomlinson 1990), with segments radiating from a

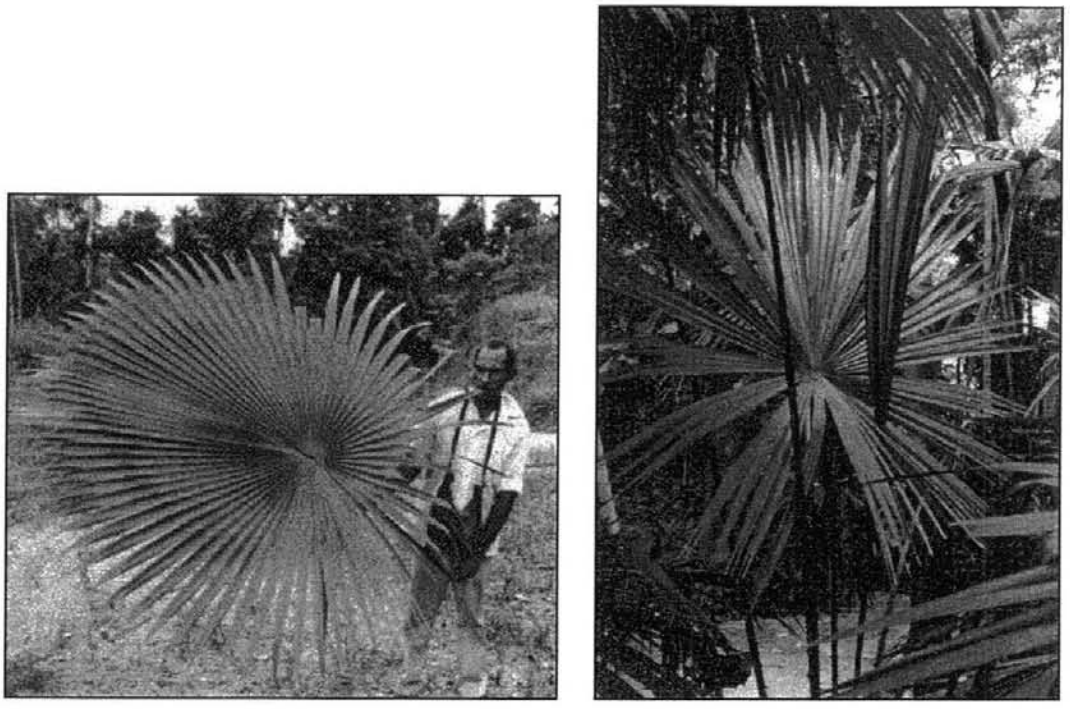


Figure 3.4. Lamina morphology in *Livistona*. ***Left:*** lamina of *L. tothur*, with a regularly segmented lamina, Papua New Guinea. ***Right:*** lamina of *L. saribus*, with an irregularly segmented lamina, cultivated plant, Townsville, Qld. Characters states determined from lamina morphology include: lamina outline (character 4) – circular or other than circular; segmentation (character 5) – regular or irregular; lamina length (character 6); and number of segments (character 7).

central point, the hastula, or congested, from along an elongate axis, the costa. Segments may be 'regular' (Fig. 3.4), of more or less uniform width and length, though usually becoming either shorter or longer but always narrower toward the margin of the leaf. This condition occurs in all but two species, *L. exigua* and *L. saribus* (Fig. 3.4), where segmentation is 'irregular', in which the lamina has two levels of division. In this type, more or less similar groups of segments with shallow divisions between them are separated from other groups of segments by relatively deep divisions that almost extend to the hastula (Fig. 3.4). Irregular segmentation also occurs in the closely related genus *Pholidocarpus*.

Character 6. Length of mid-leaf segment: < 67 cm (0); 67-125 cm (1); > 125 cm (2). The length of the mid-leaf segment is more or less constant for species in mature leaves. It is measured from the hastula to the apex of the segment (Fig. 3.5). The shortest laminae occur in *L. exigua*, c. 50 cm long, while the longest

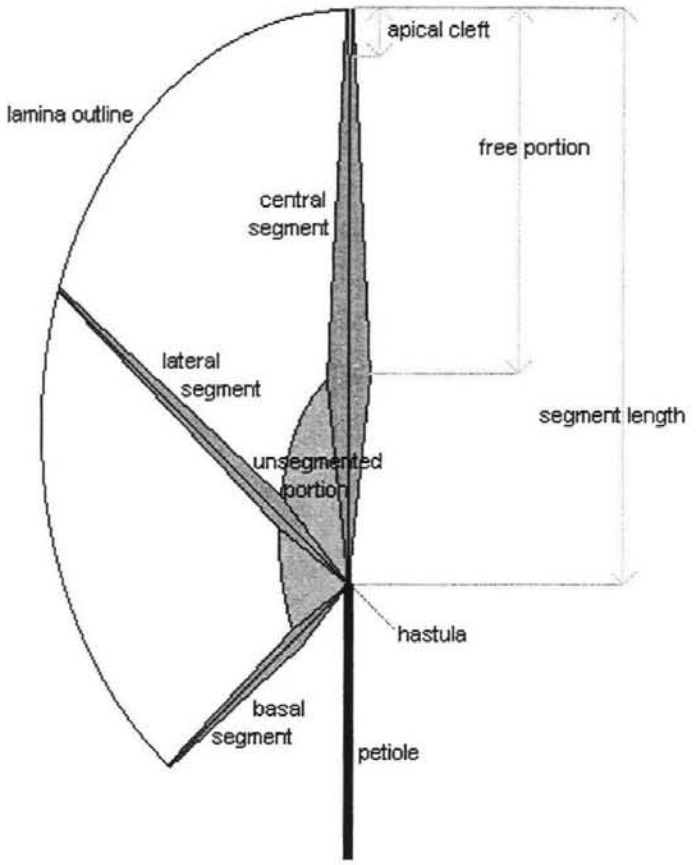


Figure 3.5. Simplified composite half-leaf of *Livistona*. Three segments are shown – central, lateral and basal - indicating from where on the central segment the length, free portion and apical cleft were measured. Both the length of the free portion (character 8) and the depth of the apical cleft (character 9) are determined, for comparative purposes, as a percentage of the length of the segment.

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occur in *L. mariae* and *L. surru*, 220-230 cm long. A scatter plot of lamina length measurements is included in Appendix 14.

Character 7. Number of segments per leaf: < 53 (0); 53-70 (1); > 70 (2).

In the leaves of mature palms, the number of segments is more or less constant for a species, although differences in a single species can reflect the ecological conditions in which the palm occurs. However, segment numbers do not necessarily correlate with leaf size, but more with segment width. For example,

both the smallest leaves and the largest leaves, in different species, have a segment range of 16-30. A scatter plot of the number of segments in a leaf is included in Appendix 14.

Character 8. Length of 'free portion' as percentage of length of leaf segment: < 58% (0); 58-74% (1); > 74% (2). The length of the separation of the segments (herein termed the 'free portion') varies considerably, but is more or less constant for a species (Fig. 3.5). In some species it is very short, e. g. *L. rotundifolia*, while in others, such as *L. inermis*, it may be for almost the entire length of the lamina. For comparison, the length of the free portion is best expressed as a percentage of the length of the segment. In this study, measurements were taken of central segments on mature leaves. The formula used was: value % = length of division / segment length x 100. A scatter plot of the length of 'free portion' of leaf segment is included in Appendix 14.

Character 9. Length of apical cleft as percentage of length of segment: < 35% (0); 35-49% (1); > 49% (2). The apex of each segment has a cleft that may be very short, as in *L. rotundifolia*, or extend to more than half the length of the segment, as in *L. inermis*. As with the length of the 'free portion' (character 8), the measurements of the length of the cleft were taken on central segments and also expressed as a percentage of the length of the segment (Fig. 3.5). The formula used was: value % = length of apical cleft / segment length x 100. Data for characters 4-9 are listed in Appendix 4. A scatter plot of the length of the apical cleft is included in Appendix 14.

Character 10. Segment apex: rigid (0); pendulous (1). The segment apex may be either rigid or pendulous (Fig. 3.6). This condition is not strictly a function of segment length, in which it would be expected that longer segments would be more prone to be pendulous than shorter ones, but it is determined by the strength of the main rib in the segment. Species with long segments may indeed have rigid apices while those with short segments may have pendulous apices.

Figure 3.6. Segment apices in *Livistona* (character 10). ***Left:*** segment apex rigid, as in *L. muelleri*, cultivated plant, Townsville, Qld. ***Right:*** segment apex pendulous, as in *L. nitida*, Dawson R., Qld.

Character 11. Adaxial surface colour: green (0); grey (1). The adaxial surface colour may be from light to dark green to various grey/greens, blue/greens and greys.

Character 12. Abaxial surface colour: green (0); grey (1); coppery or silver (2). The abaxial surface is usually different from the adaxial surface, and in many species is a lighter version compared with that found on the adaxial surface. However, various forms of tomentum may provide colours ranging from coppery to silver in various species.

Character 13. Leaf surface: non-waxy (0); waxy (1). The lamina surface may be glabrous, or covered by various forms of wax deposits. The presence or absence was recorded for both adaxial and abaxial surfaces. Data for segment and lamina characters (characters 10-13) are presented in Appendix 5.

Character 14. Number of parallel veins: < 12 (0); 12-14 (1); > 14 (2). A scatter plot of the number of parallel veins is included in Appendix 14.

Character 15. Prominent lamina venation: parallel veins most prominent (0); transverse veins most prominent (1); ± equally prominent (2). The venation of a leaf segment consists of a dominant central midrib, accompanied by a series of parallel veins of more or less equal number each side of the midrib, and transverse veins of various thickness and lengths which connect, girdle or traverse the parallel veins (Fig. 3.7). Tomlinson (1990) considered the distribution and spacing of parallel and transverse veins to be diagnostic for palm species. Barfod (1988) and Henderson (1990) have studied venation patterns in palms. Trivett and Pigg (1996) and Zona (1990) have presented reports on the correlation between climate type and venation pattern in leaves. The number of parallel veins each side of the midrib for each segment is more or less constant for each species. For consistency, middle portions of central segments were chosen for examination.

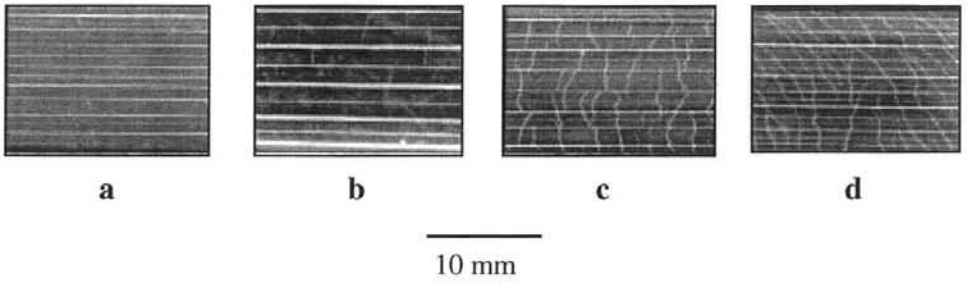


Figure 3.7. Venation patterns in *Livistona* (characters 14-18). Example of the variation for the genus present in four species. **a**. *L. carinensis* – a large number of parallel veins and very few transverse veins. **b**. *L. mariae* – a moderate number of parallel veins, though very prominent, and a moderate number of transverse veins. **c**. *L. australis* – less prominent parallel veins and prominent transverse veins. **d**. *L. chinensis* – less prominent parallel veins but numerous and prominent transverse veins.

Character 16. Transverse veins character: thin (0); very thin (1).
The average thickness of the transverse veins relative to the parallel veins is constant for species (Fig. 3.7). Therefore, the transverse veins can be characterised as thin or very thin in comparison to the parallel veins.

Character 17. Number of parallel veins crossed by transverse veins: 2 (0); 2-3 (1); 3-7 (2). The extension of the transverse veins across, or below or above, the

parallel veins is constant for each species. A single transverse vein may pass between two to seven parallel veins.

Character 18. Density of transverse veins per unit area: < 22 (0); 22-26 (1); > 26 (2). The density of transverse veins per unit area was calculated. Measurements were made of lamina areas 12.5 mm x 12.5 mm for each species. The number of parallel veins and the number of transverse veins between pairs of parallel veins were counted for ten samples per species, and a mean calculated. Data for venation characters (characters 14-18) are presented in Appendix 6. A scatter plot of the density of transverse veins per unit area is included in Appendix 14.

Character 19. Petiole cross section: channelled (0); flat (1); ridged (2). The outline of the petiole cross sections was observed in the middle portion of the petiole (Fig. 3.8). The petiole was cut at this point and the type of cross section recorded. For *Livistona*, the abaxial surface is always convex, while the adaxial surface may be convex with a moderate or pronounced ridge, flat, or shallowly or prominently concave.

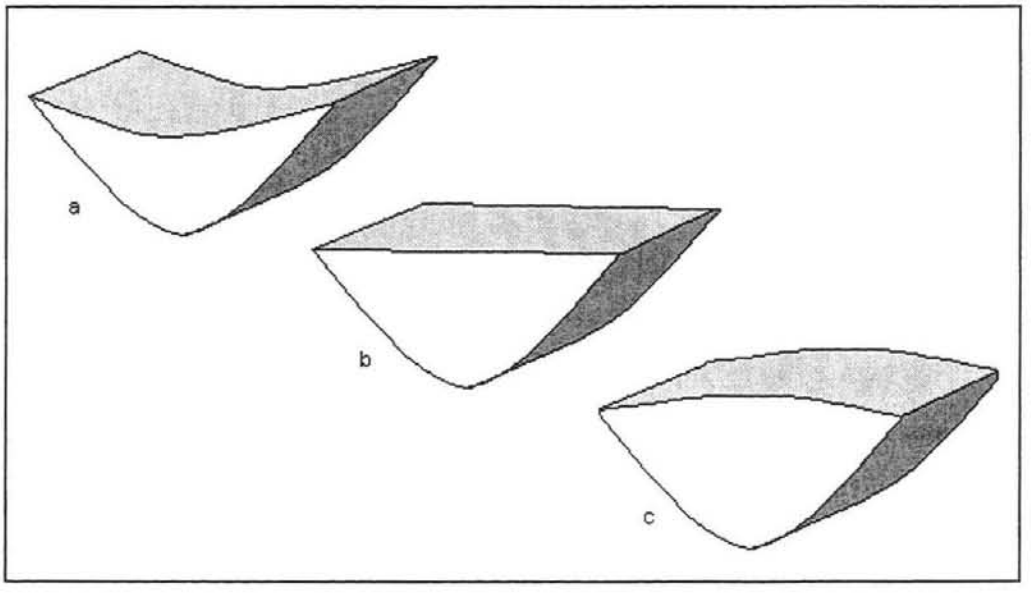


Figure 3.8. Petiole cross sections of *Livistona* (character 19). **a**. channelled: adaxial surface concave. **b**. flat: adaxial surface flat. **c**. ridged: adaxial surface convex.

Character 20. Armature: absent (0); present (1).

The petiole margins in most *Livistona* species are furnished with spines of various sizes, shapes and disposition (Fig. 3.9). Spines may be single or in pairs that are joined at the base, and either condition appears more or less constant for species.

Character 21. Spine shape: ± curved sides (0); kris-like (1).

Spines invariably have curved sides, but the sides may be either regularly convex-concave, or of a 'kris-like shape' which resembles the shape of the ceremonial daggers associated with the Thai culture (Fig. 3.10). Because of the absence of spines in *L. merrillii* and *L. papuana*, this character was denoted as 'inapplicable' in the morphological dataset (Table 3.5).

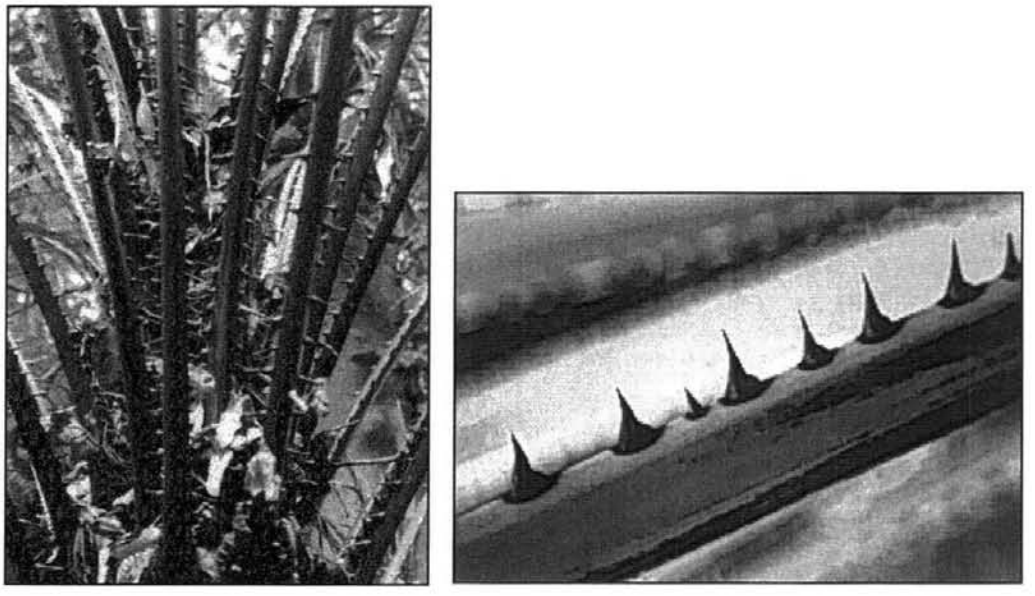
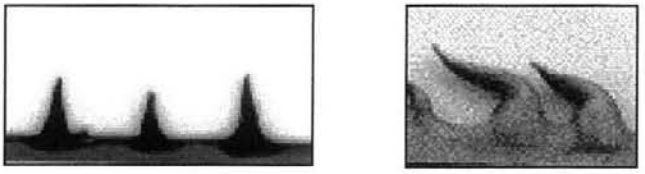


Figure 3.9. Armature in *Livistona* (characters 20-22). ***Left:*** crown of *L. saribus*. ***Right:*** petiole detail of *L. carinensis*. Armature is present in most species on the margins of the petiole, and may range from strong long spines (as here shown in *L. saribus*) to absent. When armature is present, spines may be either regularly convex-concave [sharks tooth-like], or of a kris-like shape (see Fig. 3.10). Colour is also variable, ranging from green to red, brown or black.



a b

Figure 3.10. Spine shape in *Livistona* (character 21). **a.** Spine with regularly convex-concave sides. **b.** Spine with kris-like shape.

Character 22. Spine colour: green (0); red, brown or black (1). Spine colour varies from green, red, brown or black. The colour changes according to the age of the leaf. Many species emerge with green spines that change to dark brown or black on maturity. Others emerge with the mature colour already developed. The colours used in this analysis are of the spines on mature leaves. Data for petiole and armature characters (characters 19-22) are presented in Appendix 7.

Character 23. Leaf-base fibres - prominence: not prominent (0); prominent (1); moderately or very prominent (2). The prominence of the leaf-base fibres (Fig. 3.11) was determined visually and is dependent upon the amount of fibres produced and the persistence. The fibres were designated as 'not prominent', 'prominent' or 'very prominent'.

Character 24. Leaf-base fibres - weave: fine (0); coarse (1); combined fine and coarse (2). The leaf-base fibres form a weave which is composed of either comparatively thin or thick fibres, the former classified as 'thin' and the latter as 'coarse' (Fig. 3.11). The weave is diagnostic for each species. However, a number of species, e. g. *L. rotundifolia*, *L. surru*, *L. tothur,* have the fibres in two distinct layers, one of which is thin and the other coarse.

Character 25. Leaf-base fibres - persistence: persistent (0); disintegrating (1). The leaf-base fibres may be persistent or disintegrating. This condition does not relate directly to the type of weave or the 'prominence' of fibres, but is the ability of the leaf-base fibres to withstand exposure to environmental conditions over time. Data for leaf-base fibre characters (characters 23-25) are presented in Appendix 8.

Figure 3.11. Leaf-base fibres in *Livistona*. ***Left:*** *L. australis*, an example of prominent fibres, of 'fine' weave, Seaview Range, Qld. ***Right:*** *L. drudei*, an example of very prominent fibres, of 'coarse' weave, Hen Camp Creek, Qld.

Character 26. Inflorescence with basal branching: absent (0); present (1). Two types of inflorescence structures can be recognised in *Livistona* species (Fig. 3.12). The most common is a single axis without basal branching with partial inflorescences at more or less regular intervals along the axis. The second type consists of an inflorescence that is basally branched, being either trifurcate, or infrequently bifurcate, with more or less similar axes, and with each axis otherwise conforming to the single axis type described above.

Character 27. Number of partial inflorescences: 8 or < 8 (0); > 8 (1). The inflorescence is composed of a series of 'partial inflorescences' that decrease distally in size and complexity (Fig. 3.12). The number is more or less constant for a species, and is not strictly dependent upon size of the inflorescence.

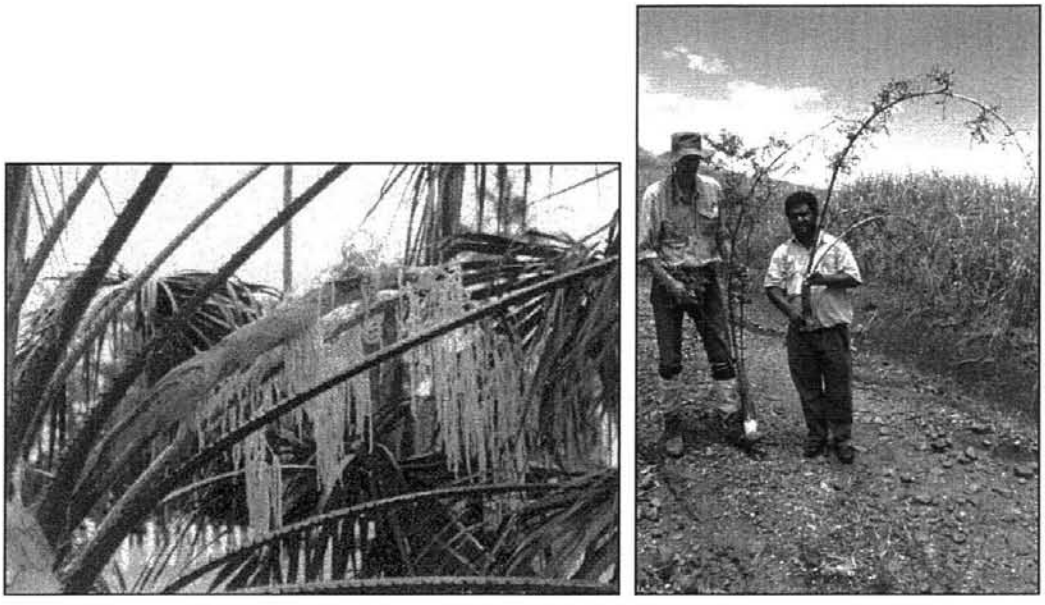


Figure 3.12. Inflorescence morphology in *Livistona*. *Left:* *L. australis*. ***Right:*** *L. chocolatina*. Two types of inflorescence structures are recognised: single axis (as here depicted in *L. australis*) or a trifurcate, or infrequently bifurcate form with each axis conforming to the single axis structure (as depicted here in *L. chocolatina*), but with a common prophyll and with each axis bearing its own peduncular bract, or rachis bract if a peduncular bract is absent. Branching units on the inflorescence are termed 'partial inflorescences'.

Character 28. Order of branching: 2 (0); 3 (1); 4 or more (2). The order of branching in the partial inflorescences is calculated with the inflorescence axis (the peduncle) as 0, with the first branch of a partial inflorescence as 1, and with subsequent branches counted to the next order.

Character 29. Inflorescence length: < 150 cm (0); 150-180 cm (1); > 180 cm (2). The length of the inflorescence is taken to include the peduncle, the rachis and up to and including the most distal partial inflorescence. A scatter plot of the measurements of inflorescence length is included in Appendix 14.

Character 30. Rachilla length: 12 or < 12 mm (0); > 12 mm (1). The rachilla is the flower-bearing axis of the inflorescence and the shortest and longest lengths are more or less constant for each species. In this analysis, only the length of the longest rachillae is used as a character. Inflorescence data (characters 26-30) are presented in Appendix 9.

Character 31. Number of peduncular bracts: 0 (0); 1 or more (1). The inflorescence is enclosed by a number of bracts that are attached at various positions on the main axis. The first bract, the prophyll, is more or less morphologically undifferentiated among species, apart from tomentum (see below). However, the subsequent bracts that enclose the peduncle and/or the partial inflorescences, vary considerably in both number and structure for certain species. Some species have bracts that enclose the peduncle, and are here termed 'peduncular bracts'. These are attached adjacent to the prophyll, and sheath the proximal portion of the peduncle below the most proximal partial inflorescence. There may be from one to many peduncular bracts. However, in some species the peduncular bract is lacking, and the first bract above the prophyll is a 'rachis bract' that encloses the lower part of the most proximal partial inflorescence. A rachis bract encloses each subsequent partial inflorescence along the main axis of the inflorescence. The number of peduncular bracts is constant for a species.

Character 32. Bract tomentum: glabrous (0); not glabrous (1). The bracts may be glabrous or covered in various forms of tomentum (Fig. 3.13). Types of tomentum are characteristic of a species.

Figure 3.13. Bract tomentum in *Livistona* (character 32). ***Left:*** *L. australis*, with moderate tomentum on the bracts, Hope Island, Qld. ***Right:*** *L. lanuginosa*, with very dense tomentum on the bracts, Glenroy Creek, Qld.

Character 33. Rachilla tomentum: glabrous (0); not glabrous (1).
The surface of the rachillae may be glabrous or covered by various tomentum. Bract and tomentum data (characters 31-33) are presented in Appendix 10.

Character 34. Number of flowers in clusters: 1 flower (0); 2-many flowers (1).
Flowers may be produced singly or in clusters of two to seven flowers (Fig. 3.14). The clusters comprise a sympodial series in which each successive flower arises in the axil of a bracteole borne on the stalk of the previous flower. The number of flowers in a cluster reduces distally on the rachilla.

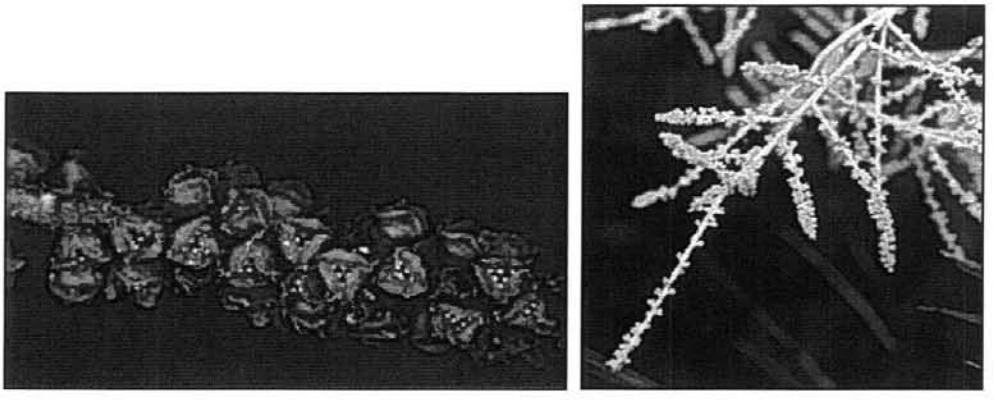


Figure 3.14. Flowers of *Livistona* (characters 34-36). ***Left:*** *L. tothur*, with solitary, small, red flowers, Oenake Mts., Papua New Guinea. ***Right:*** *L. inermis*, with flowers either solitary or in sympodial clusters (cincinni), moderate, cream-yellow, Mt. Bundey, NT.

Character 35. Flower length: 2.0 mm or < 2.0 mm (0); > 2.0 mm (1). The length of the flower is measured from its attachment to the pedicel to the apex of the petals.

Character 36. Flower colour: white, cream, yellow (0); red or maroon (1).
Petals are most commonly white, green, cream, yellow or golden yellow, but red petals occur in some species, e. g. *L. tothur* and *L. woodfordii*. The colour of the calyx can, apart from being the same colour as the petals in most species, be maroon, as in *L. muelleri* [although petals are yellow]. Floral and pollen data (characters 34-36) are presented in Appendix 11.

Character 37. Fruit shape: globose (0); ellipsoid, obovoid or other (1). Fruit shape is constant for a species, and varies from globose, subglobose, ellipsoid, obovate, pyriform and obpyriform (Fig. 3.15).

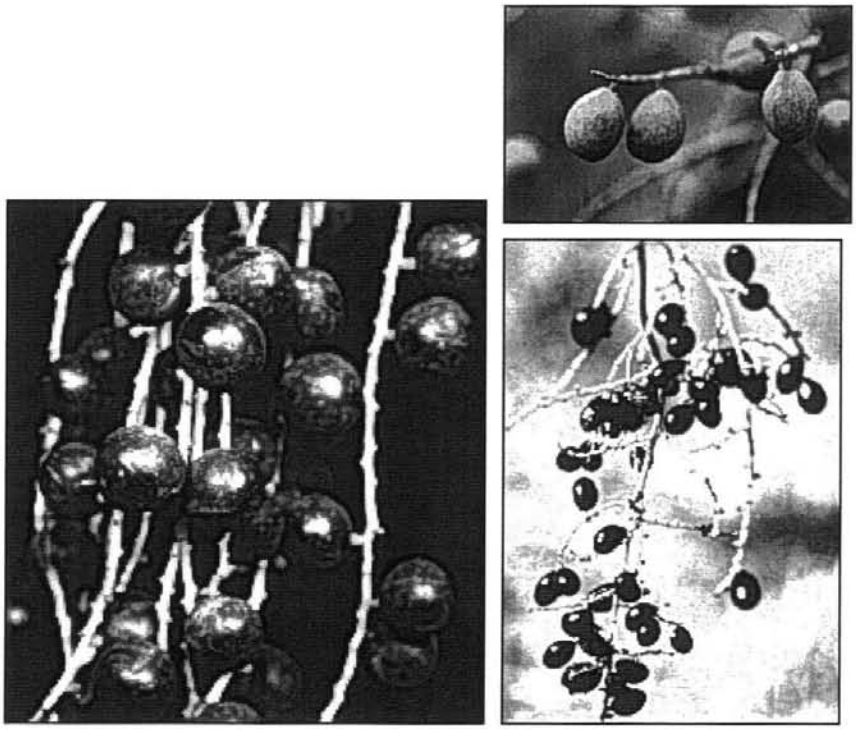


Figure 3.15. Fruit of *Livistona* (characters 37-39). ***Left:*** *L. australis*, globose fruit, Hope Island, Qld. ***Right top:*** *L. muelleri*, ellipsoid fruit, Cairns, Qld. ***Right bottom:*** *L. humilis*, pyriform/obovoid fruit, Kakadu, NT.

Character 38. Maximum fruit length: < 13 mm (0); 13-30 mm (1); > 30 mm (2). Fruit length varies within and among species, but maximum fruit length is more or less constant for a species. A scatter plot of the measurements of fruit length is included in Appendix 14.

Character 39. Fruit colour: brown, black or dark purple with no orange/red phase (0); orange/red phase maturing to orange, red or black (1); green, blue or purple with no orange/red phase (2). Fruit colours include green, blue, purple, orange, red, brown and black, and are usually constant for a species.

Character 40. Pedicel length: 2.0 mm or < 2.0 mm (0); > 2.0 mm (1). The fruit of most species is produced on a pedicel that is constant in length for a species. Fruit and pedicel character data (characters 37-40) are presented in Appendix 12.

Character 41. Epicarp 'pores': absent (0); present (1). Wax deposits of various forms cover the epicarp. The condition of the wax can be smooth or rough, with shiny fruit having erect sharp-edged wax plates and dull fruit have smooth deposits. Pores are found in many species (Fig. 3.16; Table 3.4). The pores are round, and form the apex of a 'cone shaped' surface rupture in which the wax immediately adjacent to the opening is smooth compared with the general surface. The function of the pores is not known, but their depth suggests a role in gas exchange.

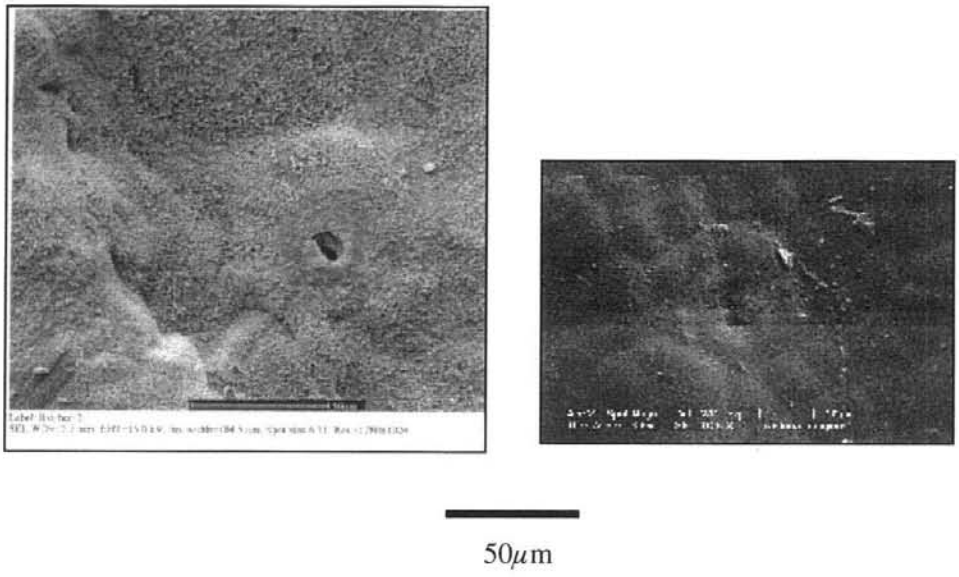


Figure 3.16. Epicarp pores in *Livistona* (character 41). The epicarp consists of a waxy coating of various forms, and may be characterised smooth, i.e. lacking pores, or by the presence of pores as depicted here in two species. ***Left:*** *L. woodfordii*. ***Right:*** *L. lanuginosa*.

Table 3.4. Specimens used in the SEM examination of epicarp features.

L. alfredii: Bromilow LA5, Fortescue River, WA
L. benthamii: Dowe 220, Koolpinyah, NT
L. chinensis: Balick 3388, cult, Florida, USA
L. chinensis: Burck 1591, Guangdong Province, China
L. chinensis: Dowe s.n., 26 July 1998, cult, Anderson Park, Qld
L. chocolatina: Ferrero 980080, Central Province, PNG, Kuriva
L. concinna: Dowe 252, Cooktown, Qld
L. decora: Corbett s.n., Apr. 2000, Magnetic Island, Mt Cook, Qld
L. decora: Furtado 30948, cult, Singapore Botanical Gardens
L. drudei: Dowe s.n., 20 May 1997, cult, Palmetum, Qld
L. drudei: Dowe s.n., 1 Aug. 1998, cult, Palmetum, Qld
L. eastonii: Hnatiuk MP28, Mitchell Plateau, WA
L. fulva: Dowe s.n., 25 Feb. 2000, cult, Flecker Gardens, Cairns, Qld
L. humilis: Munir 5590, Kakadu, NT
L. humilis: Smith 4334, Darwin, NT
L. jenkinsiana: Barfod 45208 with Pooma & Burholt, Chiang Mai, Thailand
L. jenkinsiana: Larsen *et al.* 44364, Thailand
L. jenkinsiana: Meebold 14423, Thailand
L. lanuginosa: Dowe s.n., 24 Jan. 2000, cult, Palmetum, Townsville, Qld
L. lorophylla: Beauglehole 51787, Doongan River, WA
L. mariae: Dowe s.n., 25 Jan. 2000, cult, Palmetum, Townsville, Qld
L. merrillii: Dowe s.n., 25 Feb. 2000, cult, Flecker Gardens, Cairns, Qld
L. muelleri: Brass 5950, Western Province, PNG
L. muelleri: Dowe s.n., 21 Apr. 2000, cult, Anzac Park, Townsville, Qld
L. nitida: Dowe 301, Delusion Creek, Qld
L. rigida: Dowe 212, Mataranka, NT
L. rotundifolia: Dowe s.n., 11 Feb. 2000, cult, Rosslea, Townsville, Qld
L. rotundifolia: Furtado 29393, cult, Singapore Botanical Garden
L. saribus: Dowe s.n., 24 July 1998, cult, Palmetum, Townsville, Qld
L. saribus: Dowe s.n., 21 Apr. 2000, cult, Annandale, Qld
L. saribus: Dahme s.n., Jan. 2000, cult, Florida, USA
L. saribus: Pierre 4837, Cay Ke, Vietnam
L. surru: Barfod 390, with Ferrero & Damborg, West Sepik Province, PNG
L. surru: Damborg 354 with Ferrero & Barfod, Madang Province, PNG
L. tahanensis: Nur 8006, Gunung Tahan, Malaysia
L. tothur: Damborg 418 with Barfod, West Sepik Province, PNG
L. woodfordii: Hoogland 4284, Cape Vogel, Milne Bay Province, PNG
L. woodfordii: Furtado 21175, cult, Singapore Botanical Gardens

Character 42. Embryo position: lateral (0); supra-lateral (1); sub-lateral (2). The embryo can be in either a supra-lateral, lateral or sub-lateral position in the seed relative to the longitudinal axis, and is constant for a species.

Character 43. Sexuality: hermaphroditism (0); functional dioecy (1). Sexuality is constant for a species, and is either hermaphroditic or functionally dioecious. Sexuality was not known for *L. endauensis*, *L. exigua* or *L. tahanensis*. Data for fruit, seed, eophyll and sexuality characters (characters 41-43) are presented in Appendix 13.

The 43 characters were scored in 37 taxa (35 ingroup taxa and 2 outgroup taxa) to produce the data matrix in Table 3.5. One character was deemed inapplicable and is denoted by '–' in the data matrix; this was Character 21, spine shape. In two taxa, *L. merrillii* and *L. papuana*, spines do not occur. Absent data, denoted by '?' in the data matrix (Table 3.5), are characters that are unknown for those taxa, having been unrecorded, e. g. sexuality in *L. endauensis*, *L. exigua*, *L. tahanensis*, and the absence of particular organs from the specimens examined, e. g. the inflorescence bracts in *L. tahanensis,* and the embryo position and epicarp features in *L. endauensis* and *L. exigua.*

3.9 Cladistic analyses

The cladistic analyses were performed using PAUP* version 4.0b8a written by D. L. Swofford (undated), with 35 ingroup taxa (Table 3.3) and two outgroup taxa (Table 3.5), and 43 character states (Table 3.5). Initial search parameters were set as default as recommended in the PAUP* user's manual, conducted using random addition sequences, global branch swapping and COLLAPSE and MULPARS options in effect. Characters were unordered and the search was heuristic in all analyses. Characters were polarised by outgroup comparison (Watrous and Wheeler, 1981). Two outgroup taxa, *Licuala ramsayi* and *Pholidocarpus macrocarpa*, were chosen (Table 3.5), based on estimations of their close relationship to *Livistona* in previous phylogenetic analyses (Uhl *et al.*, 1995; Baker *et al.*, 1999).

Table 3.5. Morphological dataset used in the cladistic analysis of *Livistona*, with 35 ingroup and 2 outgroup taxa, and 43 characters. '–' = inapplicable data; '?' = absent data.

character numbers	1 1111111112 2222222223 3333333334 444
	1234567890 1234567890 1234567890 1234567890 123
Licuala	0010122200 0000201011 0000000021 0001100010 000
Pholidocarpus	1010122111 0101201001 1111000021 0001100211 100
L.alfredii	0011011120 1112012011 0111000121 1111100201 111
L.australis	1010011121 0002001121 0110000221 0101100101 121
L.benthamii	1100011121 0000001021 0110000010 0111001001 001
L.boninensis	1011021101 1002002021 0001000110 1001100121 ?00
L.carinensis	2111011210 1012010011 0110001120 1001000201 ?21
L.chinensis	0011021001 1002002221 0001100100 0101101121 100
L.chocolatina	1111011000 1112002211 0001010100 1011010110 100
L.concinna	1110021111 0002002021 1121000210 0001000000 001
L.decora	1010022221 0001002111 0121101221 0001000100 111
L.drudei	1110011121 0001000021 1121000120 1111100000 001
L.eastonii	0101010120 0011002011 0121000200 1101001100 001
L.endauensis	0111011100 0000012111 1111100110 0011001121 ???
L.exigua	0210100000 0000201111 1111000000 0111010020 ???
L.fulva	0010011000 0202002021 0120000220 1111000100 101
L.halongensis	0011011011 0000012111 011100012? 1011000020 ??0
L.humilis	0100000120 0000211201 0101000120 1111001100 101
L.inermis	0111000220 1102010001 0121000100 0101101000 001
L.jenkinsiana	1011022100 0002002221 1101100101 0111101121 100
L.lanuginosa	1010022121 1112012011 0121001210 1101100100 121
L.lorophylla	0110010220 1102001011 0121000100 1101101000 101
L.mariae	1010021021 1112001021 0121001220 1101000100 121
L.merrillii	1010011000 0000011010 –122010100 1000100111 000
L.muelleri	0000011100 0002010001 0100100210 0111001000 021
L.nasmophila	1010021010 1112011011 1121001220 0001000000 121
L.nitida	1010022121 0001012021 0121101211 0101100100 101
L.papuana	2211012000 0002112210 –101110110 1011001110 1?0
L.rigida	1010021021 1111001001 0121001220 1101000000 121
L.robinsoniana	1110012001 0001102121 1121011200 0001000011 100
L.rotundifolia	2210012000 0001102221 1122011200 1001100101 100
L.saribus	2011122111 0001002001 1121000201 0001000120 100
L.surru	1111022101 0000002111 1112010101 0011010211 101
L.tahanensis	0001010100 0101002011 1110100100 ??1?0?1121 02?
L.tothur	1111021200 0111012211 0012010110 1110010211 101
L.victoriae	0011010120 1112002011 0120000200 1111000000 121
L.woodfordii	0010021000 0000002121 0121010120 0001010011 100

Two analyses were performed for comparison.

- ***Analysis 1*** – equally weighted characters. A randomly chosen tree and the strict consensus tree were chosen for discussion.
- ***Analysis 2*** – characters with successive approximations weighting (Farris, 1989), applied to the data set using the 'Reweight Characters' facility in PAUP*, until the trees in subsequent analyses began to repeat tree topology and number of steps. The options chosen in successive weighting were:
- rescaled consistency index [after Asmussen *et al.* (2000)]
- as default settings with maximum value (best fit)
- character base weight of 1.

Based on comparison of the value of the rescaled consistency indices (RC) in both analyses, the tree with the highest value was chosen for discussion.

In the analysis, characters that received high values as rescaled consistency (RC) indices were assumed to be those characters that are the best indicators of phylogenetic relationships, i. e. their distribution is more informative of relationships between taxa, than characters of lesser value. Characters that were scored '1.0' were examined in MacClade version 3 (Maddison and Maddison, 1992). The 'Character Trace' and 'Chart' facilities were used to analyse character distribution among taxa. Standard defaults, including ACCTRAN, were used in all the MacClade analyses. A bootstrap analysis was performed using 2300 replicates, the limit of available memory, with heuristic search.

3.10 Results

3.10.1 ***Analysis 1*** **– unweighted characters.** From this analysis, 75 equally most parsimonious trees were produced. The tree statistics for this analysis are presented in Table 3.6. A randomly chosen tree and the strict consensus tree are shown in Figure 3.17 and Figure 3.18 respectively.

Table 3.6. Summary of statistics for *Analysis 1* of a randomly chosen tree.

tree length	318
consistency index (CI)	0.2
homoplasy index (HI)	0.81
retention index (RI)	0.5
rescaled consistency index (RC)	0.1

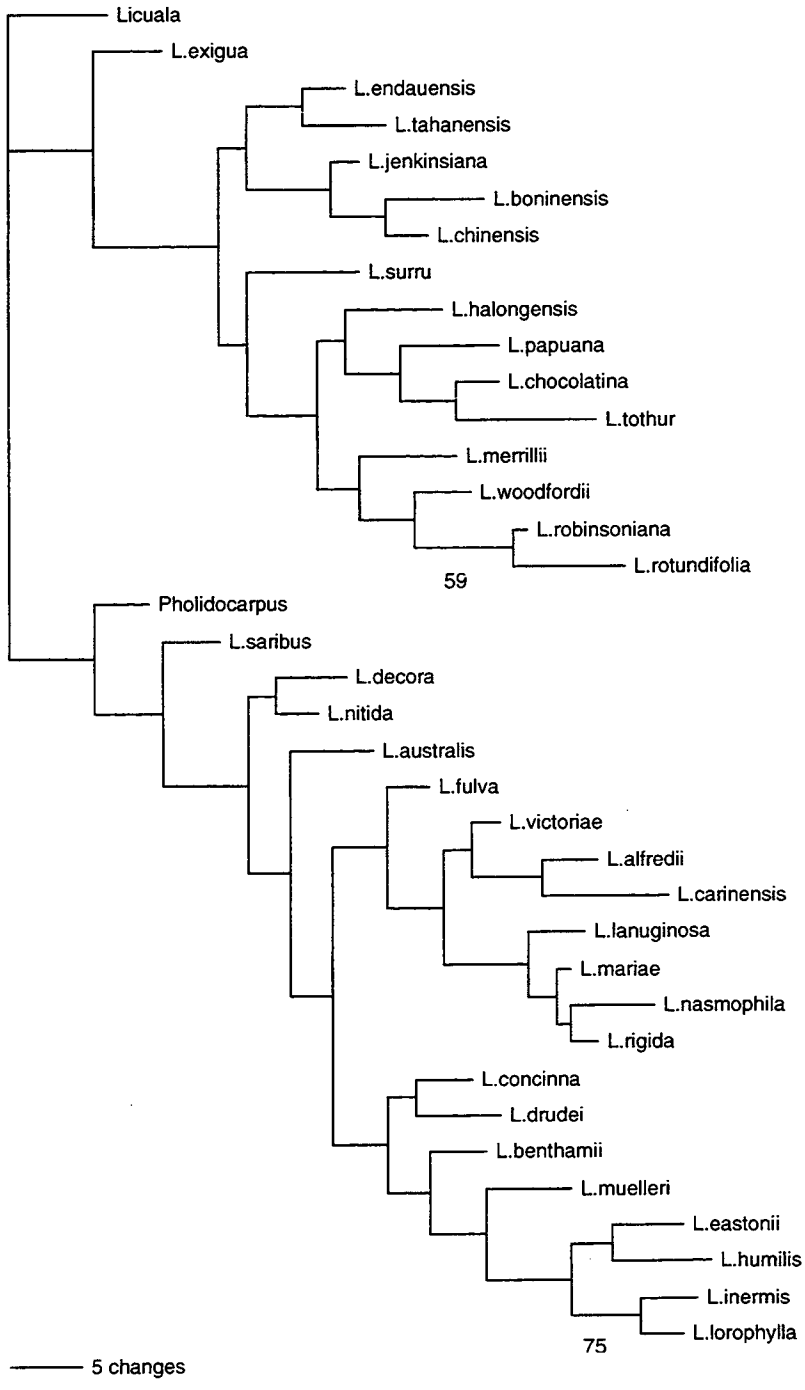


Figure 3.17. Phylogram of *Analysis 1*. A randomly chosen tree from 75 equally most parsimonious trees. Characters were unweighted, unordered and the tree search was heuristic. Tree length = 318 steps; consistency index = 0.20; homoplasy index = 0.81; retention index = 0.50; rescaled consistency index = 0.10. A bootstrap analysis was performed on this tree using 2300 replicates. As indicated on this tree, only two groups received bootstrap support greater than 50%. These included *L. robinsoniana* - *L. rotundifolia* at 59%, and *L. inermis* - *L. lorophylla* at 75%.

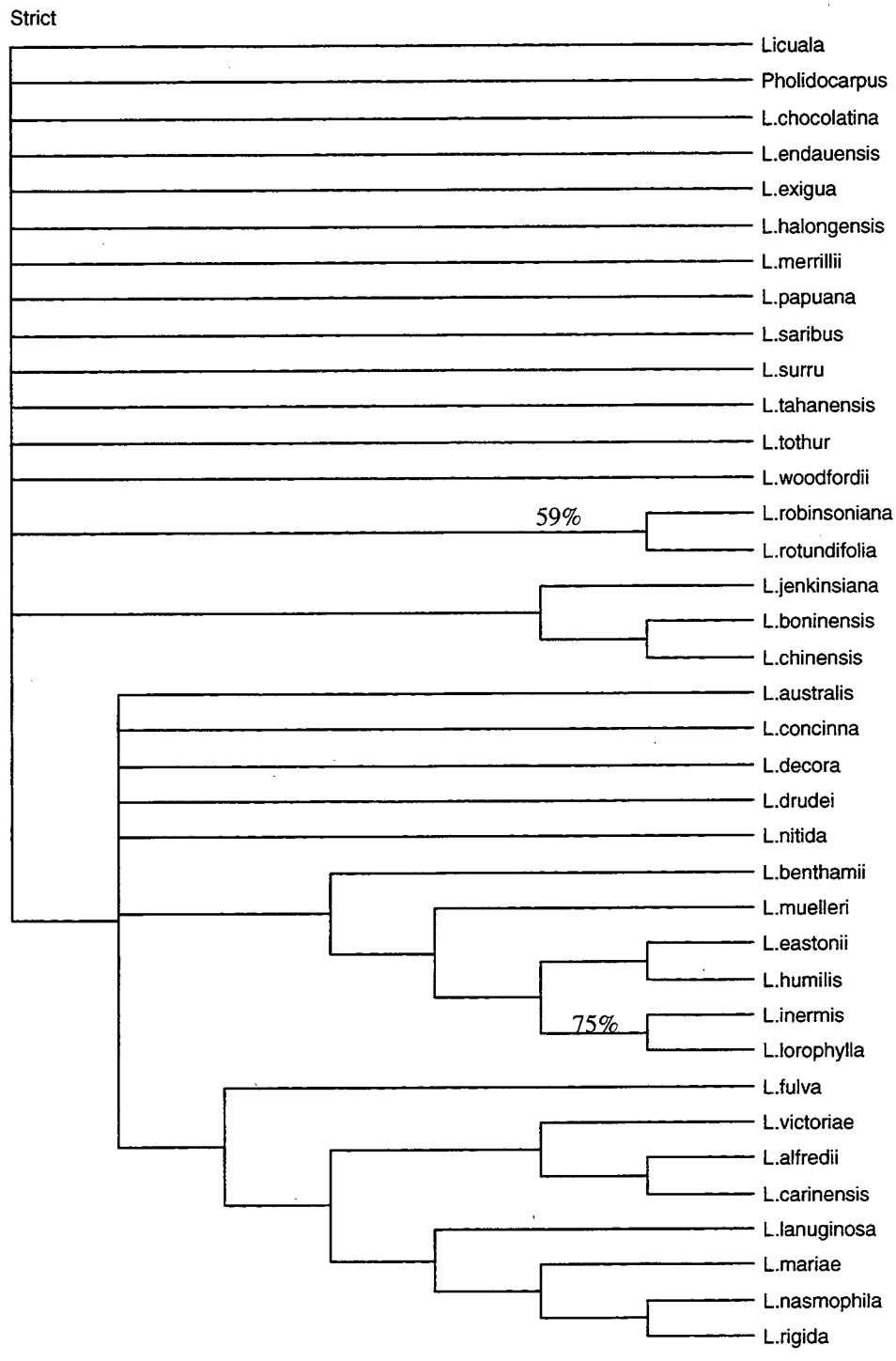


Figure 3.18. Strict consensus tree of *Analysis 1*. Strict consensus of 75 equally most parsimonious trees. Values above 50% are indicated on the tree.

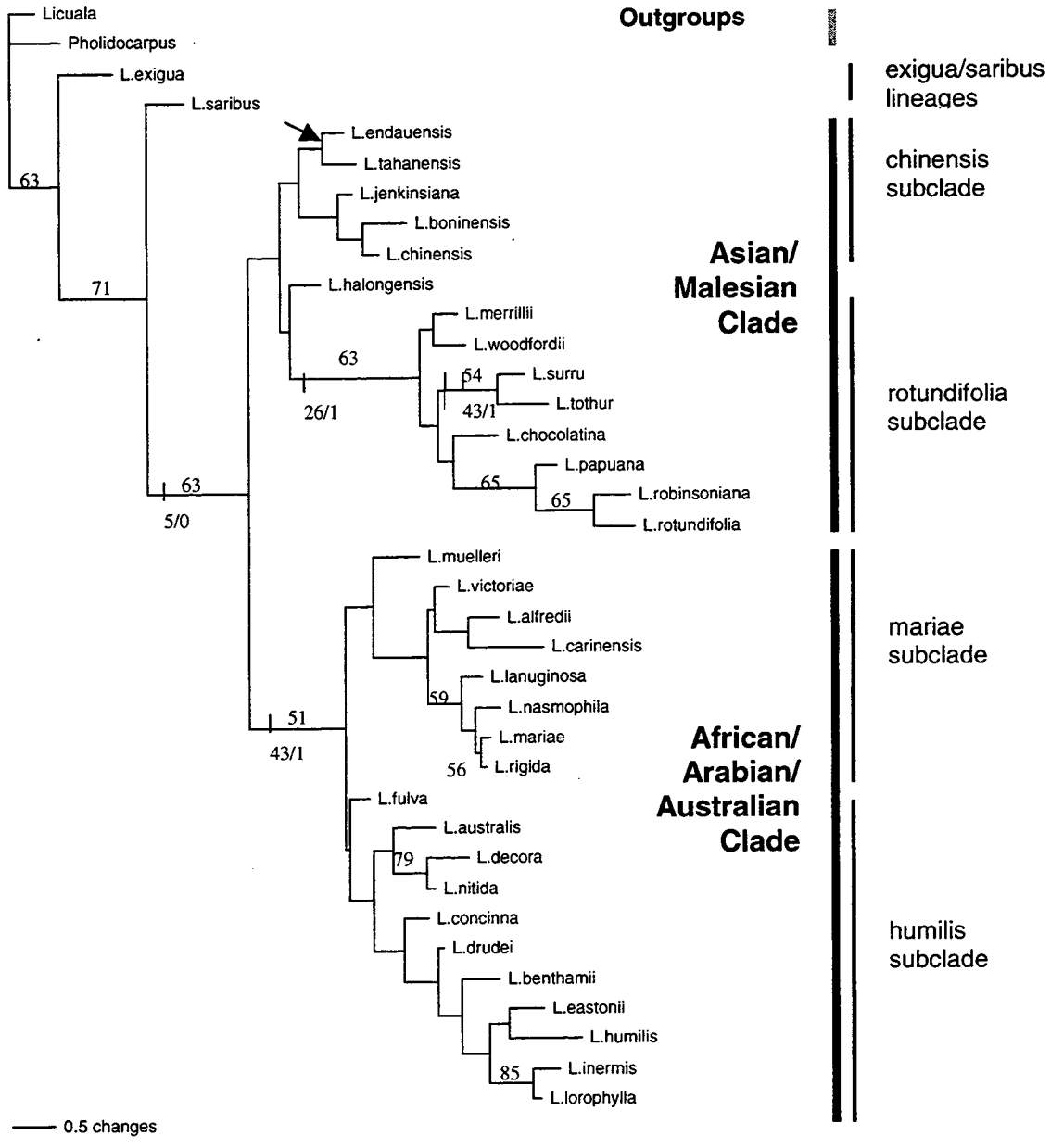


Figure 3.19. Phylogram of *Analysis 2*. One of the two equally most parsimonious trees produced in this analysis. Characters received successive weighting, unordered and with heuristic search. Tree length = 29.5 steps; consistency index = 0.31; homoplasy index = 0.69; retention index = 0.68; rescaled consistency index = 0.21. Bootstrap values and some character state changes are indicated. The arrow indicates the branch that collapsed in the strict consensus.

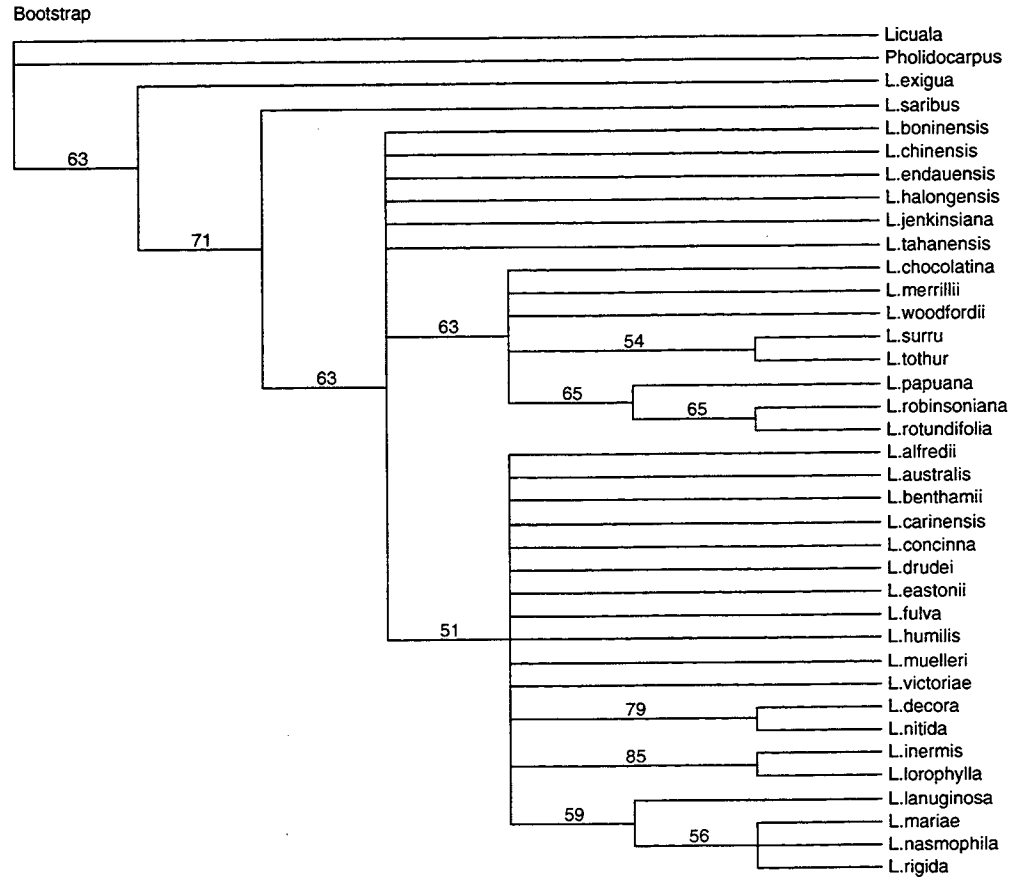


Figure 3.20. Bootstrap support values. One of two most parsimonious trees from *Analysis 2* with bootstrap support values above 50% indicated. Bootstrap analysis was performed with 2300 replicates (limit of available memory).

3.10.2 ***Analysis 2*** **– successive weighting.** Based on the same data as were used in *Analysis 1*, successive weighting was applied. For this analysis, three equally most parsimonious trees were initially produced. Weighting was applied a further three times before iteration of tree length and topology commenced with two trees. The statistics for this analysis are presented in Table 3.7. One of two final trees is presented in Figure 3.19, and the bootstrap support values are presented in Figure 3.20.

Table 3.7. Summary of statistics for *Analysis 2*.

tree length	29.5
consistency index (CI)	0.31
homoplasy index (HI)	0.69
retention index (RI)	0.68
rescaled consistency index (RC)	0.21

3.10.3 *Statistics*

For comparison between the two analyses, the tree statistics for both are presented in Table 3.8. The RC (rescaled consistency index) was taken as the marker for defining characters of higher or lesser phylogenetic relevance – the greater the value, the greater the phylogenetic relevance. Upon this basis, those characters with an RC greater than the average RC in at least one of the analyses are presented in Table 3.9. The character states (with their codes) that received

Table 3.8. Summary of statistics for both analyses.

Analysis	*1*	*2*
tree length	318	29.5
consistency index (CI)	0.2	0.31
homoplasy index (HI)	0.8	0.69
retention index (RI)	0.5	0.68
rescaled consistency index (RC)	0.1	0.21

Table 3.9: Rescaled consistency indices, measured on a randomly chosen tree, greater than the average in both analyses. These are listed in numerical order of the characters.

character	*Analysis 1*: RC=0.10	*Analysis 2*: RC=0.21
3	0.16	-
4	0.11	-
5	0.33	1.0
6	0.1	-
8	0.1	-
9	0.14	-
11	0.18	-
12	0.15	-
13	0.26	-
15	0.16	0.53
22	0.16	-
26	0.42	1.0
27	0.15	-
28	0.16	-
30	0.1	-
37	0.17	-
39	0.24	0.43
42	0.18	0.26
43	0.27	0.45

rescaled consistency indices that were greater than the average in both analyses are presented in Table 3.10. To aid in the recognition of characters that may have limited phylogenetic importance, those characters that received an RC of '0.0' in either analysis are presented in Table 3.11.

Table 3.10. Character numbers and character states (with codes) in which the rescaled consistency indices were greater than the average for both analyses.

character #	character state
5.	regular lamina segmentation: present (0); absent (1)
15.	prominent lamina venation: parallel veins most prominent (0); transverse veins most prominent (1); ± equally prominent (2)
26.	inflorescence with basal branching: absent (0); present (1)
39.	fruit colour: brown, dark purple or black, no red phase (0); orange/red phase maturing to orange, red or black (1); blue, green or purple (2)
42.	embryo position: lateral (0); supra-lateral (1); sub-lateral (2)
43.	sexuality: hermaphroditic (0); functional dioecy (1)

Table 3.11. Characters that scored a rescaled consistency index of '0.0' in both analyses.

character #	character state
20.	armature: absent (0); present (1)
34.	number of flowers in a cluster: 1 flower (0); 2-many flowers (1)

3.10.4 *Bootstrap values*

Bootstrap analyses were performed on *Analysis 1* and *Analysis 2*. The number of replicates terminated at 2300, the limit of available memory. Support for the tree from *Analysis 1* was poor, with only two groups receiving values above 50% (Fig. 3.17). These included 59% support for *L. robinsoniana* - *L. rotundifolia* and 75% support for *L. inermis* - *L. lorophylla*. Support for the tree from *Analysis 2* (Fig. 3.20) was relatively higher than for *Analysis 1*, although support values were generally low. The best supported groups included *L. inermis* - *L. lorophylla* at 85%, *L. decora* - *L. nitida* at 79%, and *L. robinsoniana* - *L. rotundifolia* at 65%.

3.10.5 *Tree description and character analysis*

The names of clades, as presented here, are based on the earliest described species name, included in the clade. They are not intended to be representative species either morphologically or phylogenetically.

The RC for *Analysis 1* was 0.1 and that for *Analysis 2* was 0.21 (Tables 3.6, 3.7). Considering the relatively higher value for the RC in *Analysis 2*, a tree produced in that analysis was chosen for further examination as it was considered to be a statistically better supported representation of phylogeny than trees produced in *Analysis 1*. The characters that scored '1.0' in *Analysis 2* are listed in Table 3.12. Utilising the trace facility in MacClade, these characters were traced onto the tree from *Analysis 2* (Figs 3.21-3.22).

Table 3.12. Characters in *Analysis 2* that scored a rescaled consistency (RC) index of '1.0'.

character #	character state
5:	lamina segmentation: regular (0); irregular (1)
26:	inflorescence branched at the base: no (0); yes (1)

In the tree from *Analysis 2* (Fig. 3.19), the first two lineages to diverge consisted of a single species each, *L. exigua* and *L. saribus*, respectively. The character state that is exclusive to the outgroups and these taxa is an irregularly segmented lamina (character 5, state 1) (Figs 3.4, 3.21). The third lineage, the Asian/Malesian clade, consists of 14 species. Within this clade there are two subclades; the *chinensis* subclade consisting of five species, and the *rotundifolia* subclade, consisting of nine species, of which most have a basally branched inflorescence (character 26, state 1) (Figs 3.12, 3.22). This character state only arises twice, at the base of this clade and also in *L. surru* and *L. tothur*.

The fourth lineage, the African/Arabian/Australian clade, consists of 19 species, of which *L. carinensis* occurs in north-eastern Africa and southern Arabia, and the remainder in Australia. Two unsupported subclades are recognised within this clade; the *mariae* subclade, with eight species, and the *humilis* subclade, with eleven species.

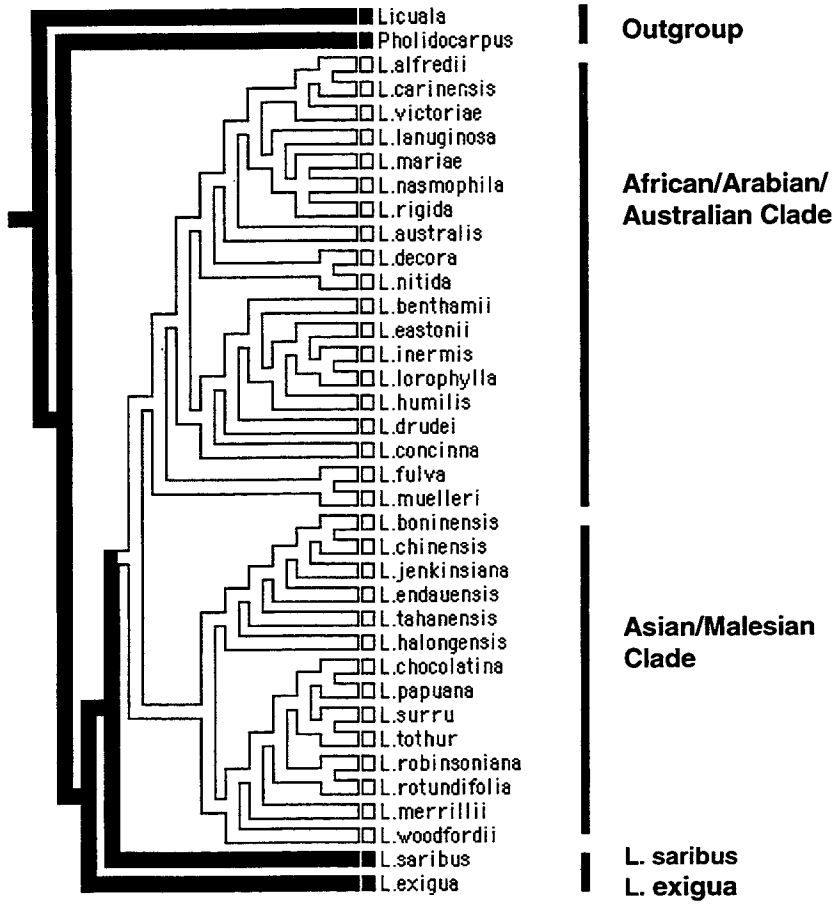


Figure 3.21. Cladogram traced with character 5 – lamina segmentation. Taxa with 'regular lamina segmentation present' (state 0) are indicated by open branches, and those with 'regular lamina segmentation absent' (state 1) are indicated by filled branches. The rescaled consistency index for this character was 1.0.

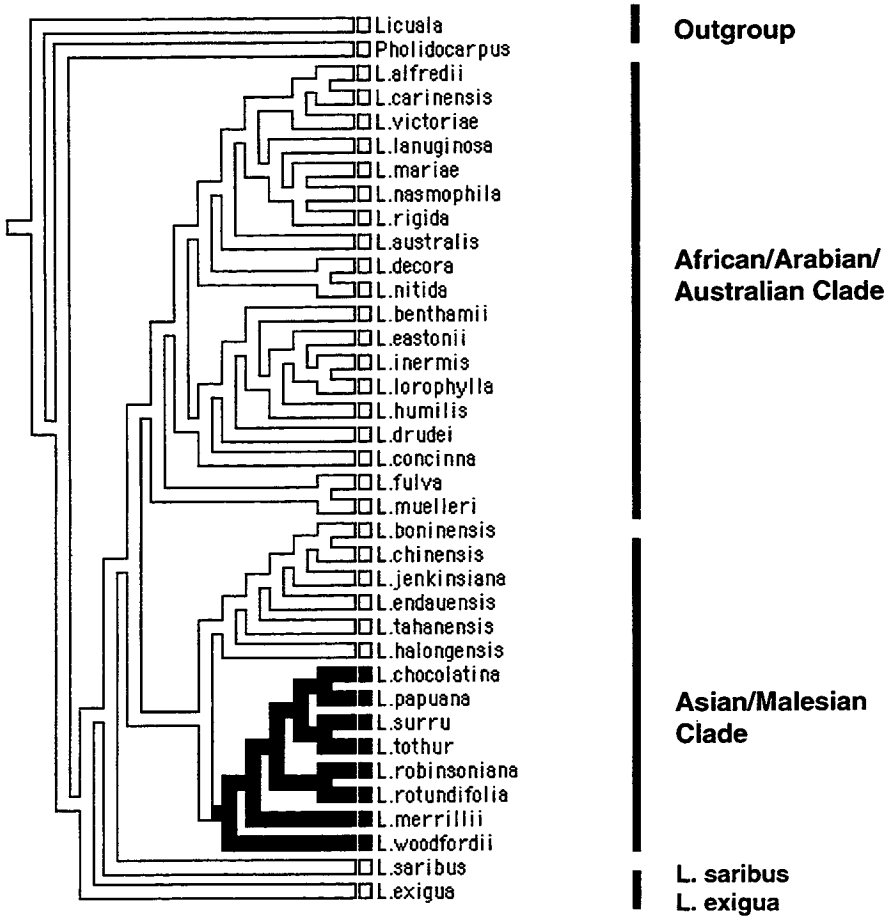


Figure 3.22. Cladogram traced with character 26 – inflorescence branching. Taxa with a basally branched inflorescence (state 1) indicated by filled branches, taxa with a basally unbranched inflorescence (state 0) indicated by open branches. The rescaled consistency index for this character was 1.0.

3.11 Discussion and conclusion

Although the topology of the randomly chosen trees in both analyses was fully resolved, the strict consensus tree in *Analysis 1* (Fig. 3.18) produced large polytomies. The randomly chosen tree was poorly supported in *Analysis 1* because of widespread and consistent homoplasy, and with low values in the consistency, retention and rescaled consistency indices (Table 3.6 and Table 3.8), and as well as low bootstrap value support (Figs 3.17, 3.18). *Analysis 2* was statistically better supported, both in the indices (Table 3.7 and Table 3.8) and bootstrap values (Fig. 3.20). The placement of taxa relative to geographical distribution was cohesive (Fig. 3.19). Considering the relative value of tree statistics (Table 3.8), resolution of tree topology and the geographical cohesion of taxa, it is reasonable to make some assumptions about phylogeny and relationships within *Livistona* based on the results of *Analysis 2*. However, the generally low statistical support for *Analysis 2* must be taken into account and the usefulness of the analysis as an indicator of phylogeny may be limited.

Four primary lineages are recognised in *Livistona* (Fig. 3.19). Two comprise a single species each, *L. exigua* and *L. saribus* respectively. Of these species, the *L. exigua* is unique within the genus as a rainforest understorey 'shrub', bearing many characters that place it close to *Licuala*. The second species is *L. saribus,* a tree palm in which the leaves are morphologically undifferentiated from those in *Pholidocarpus* species, with irregular segmentation (character 5, state 1) in which the groups of segments that have their free portions 58-74% of the length of the segment (character 8, state 1) are separated from similar groups of segments by divisions that almost reach the hastula. With the exception of *L. exigua* and *L. saribus*, other *Livistona* species have regular lamina segmentation (character 5, state 0). Despite this, these species are sufficiently similar in flower and fruit characters to include them in *Livistona*. It appears that irregular lamina segmentation has arisen a number of times within the Coryphoid palms as it also occurs in a single species in the American genus *Sabal* whose others species have regularly segmented leaves (Zona, 1990).

The third lineage includes the Asian/Malesian species (Fig. 3.19). This lineage includes the *chinensis* subclade, species with basally unbranched inflorescences

(character 26, state 0). The other subclade is the '*rotundifolia* subclade' with species occurring in the Philippines, Indonesia, New Guinea and the Solomon Islands. Most species in this subclade have, along with the outgroups, a basally branched inflorescence (character 26, state 1), and fruit passing through an orange/red phase to mature orange, red, or black (character 39, state 1).

The fourth lineage, the African/Arabian/Australian clade (Fig. 3.19), includes 19 species, of which all but one [*L. carinensis* occurs in north-eastern Africa and southern Arabia] occur in Australia. This clade has a synapomorphy that is shared with only one species outside the clade, fruit maturing brown, dark purple or black (character 39, state 0), but otherwise shares character states, such as the basally unbranched inflorescence (character 26, state 0), with other groups in other lineages. Two unsupported subclades comprise this clade; the *mariae* subclade and the *humilis* subclade. The entire clade is weakly supported with a bootstrap value of 51%.

The characters noted above had varying statistical support as indicated by the rescaled consistency indices. Characters 1 (height), 6 (length of mid-leaf segment) and 8 (length of free portion as percentage of length of leaf segment) had an RC less than the average for the tree, while character 5 (lamina segmentation), 26 (inflorescence branching) and 39 (fruit colour) had an RC greater than the average for the tree (Table 3.9). The low level of rescaled consistency indices for some characters, such as height, length of mid-leaf segment and length of free portion of segment, is suggestive of them being phylogenetically uninformative characters for this analysis. Conversely, high RC values for lamina segmentation, inflorescence branching and fruit colour, indicate that these are phylogenetically informative characters.

Considering only the Australian species of the African/Arabian/Australian clade, a comparison can be made between the results of the analyses presented here and the putative relationships of Australian species presented by Rodd (1998). Rodd's '*Mariae* group' (*L. lanuginosa*, *L. mariae*, *L. nasmophila*, *L. rigida*) formed a unit (Fig. 3.19) within the '*mariae* subclade' with a bootstrap value of 59%, thus indicating that the relationship between species in this group is not strong. The

species in Rodd's 'East coast group' (*L. australis*, *L. benthamii*, *L. concinna*, *L. decora*, *L. drudei*, *L. fulva* and *L. nitida*,) were all included in the '*humilis* subclade' (Fig. 3.19). Rodd's 'Arafura group' (*L. muelleri*, *L. humilis* and *L. eastonii*) and 'North-western group' (*L. inermis*, *L. lorophylla*, *L. kimberleyana* [placed as a synonym of *L. lorophylla* in this thesis], *L. victoriae* and *L. alfredii*) were not supported, each comprising species that were included in both subclades (Fig. 3.19).

Summary

The successively weighted cladistic analysis of *Livistona* based on morphological characters produced a fully resolved topology but had low levels of bootstrap support. Four major lineages were identified:

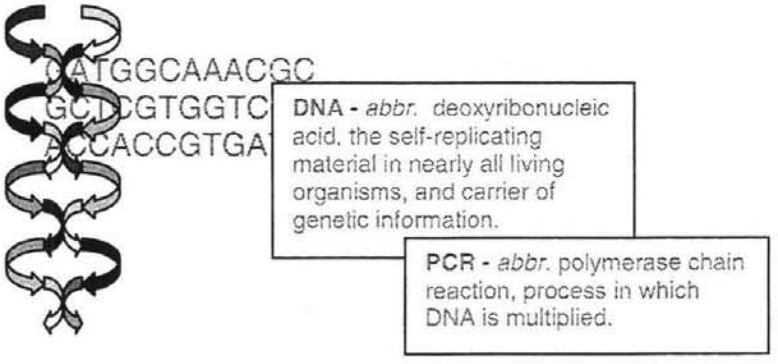
- the *L. exigua* lineage
- the *L. saribus* lineage
- the Asian/Malesian clade which includes the '*chinensis* subclade' with five species, and the '*rotundifolia* subclade' with nine species
- the African/Arabian/Australian clade which includes the *mariae* subclade with eight species, and the *humilis* subclade with eleven species.

The low levels of bootstrap support imply that this analysis is not a reliable estimate of phylogeny; however, well-resolved tree topology and geographical cohesion of species groups indicate that there may be some characters that are phylogenetically informative. It has also identified species groups that may be related and presented them in geographically cohesive units. Based on this analysis, the most phylogenetically informative characters for *Livistona* include type of lamina segmentation, type of inflorescence branching and fruit colour.

Chapter 4

Studies in the genus *Livistona* R. Br. (Coryphoideae: Arecaceae)

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



4.1 Introduction

The variation in the DNA in palms has been used in an attempt to explain the phylogeny and biogeography of the family (Table 4.1). Investigations of phylogenetic relationships have employed cpDNA restriction site data (Uhl *et al.*, 1995) that confirmed the monophyly of many higher-level taxa established in previous classifications based on morphological characters. Subsequent studies at the family level, based on sequences from the *rps*16 and *trn*L – *trn*F regions (Baker *et al.*, 1999; Asmussen *et al.* 2000) and the *rbc*L, *rps*16 and *trn*L – *trn*F regions (Asmussen and Chase, 2001), revealed some conflicts with the established classification of the family, particularly with generic level relationships. For studies at the generic level in the Calamoideae subfamily, Baker *et al.* (2000a, 2000b) provided accounts based on 5S nrDNA spacer, nrDNA ITS and cpDNA *rps*16 sequence data. These studies indicated that taxonomic changes might be appropriate for some genera in that subfamily. Asmussen (1999) provided a phylogeny for the tribe Geonomeae based on *rpl*16 sequence data. The results of that study were congruent with previous studies based on morphological characters.

The use of DNA sequence data in biogeographical studies commenced in the 1990s with a broad range of organisms under study (Sytsma, 1990; Clegg and Durbin, 1990;

van Balgooy *et al.*, 1996; Sang *et al.*, 1997; Sytsma and Hahn, 1997; Katinas and Crisci, 2000). Among the first studies to involve palms was that of Hahn and Sytsma (1999) who investigated cpDNA restriction site variation for the genus *Caryota*. That study provided a hypothesis based on phylogenetic relationships that were congruent with the early biogeographical assessments of Wallace and Huxley. Barcelos *et al.* (1999) evaluated the genetic diversity of *Elaeis* in South America and Africa using the RFLP and AFLP techniques, and established low genetic differentiation between continental populations, thus suggesting recent intercontinental dispersal for that genus.

Table 4.1. Palm studies in which molecular techniques have been used.

taxon	reference
Arecaceae (general)	Uhl *et al.* (1995)
	Anzizar *et al.* (1998)
	Baker *et al.* (1999)
	Asmussen and Chase (2001)
Calamoideae	Baker *et al.* (2000a, 2000b)
	Baker and Dransfield (2000)
Arecoideae	
Carpentaria acuminata	Shapcott (1998)
Caryota	Hahn and Sytsma (1999)
Astrocaryum	Kahn and Second (1999)
Elaeis	Barcelos *et al.* (1999)
Geonomeae	Asmussen (1999)

4.2 The internal transcribed spacer (ITS) regions

For determining phylogenies at the species level, the internal transcribed spacer (ITS) regions have been found to be useful (Baldwin *et al.*, 1995; Kim *et al.*, 1999; Hahn and Sytsma, 1999). Palm studies utilising the ITS regions include those by Baker and Dransfield (2000) and Baker *et al.* (2000a).

The ITS regions (Fig. 4.1) consist of two sequences, each of approximately 250 nucleotides, on either side of the 5.8S region and adjacent to the 18S and 26S regions

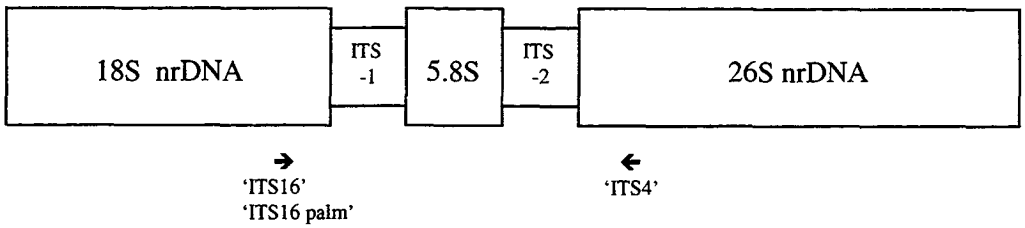


Figure 4.1 Organisation of the nrDNA region. The approximate positions of the 18S nrDNA, ITS-1, 5.8S, ITS-2 and the 26SnrDNA units are indicated. Arrows indicate orientation and approximate position of primer sites. Adapted from Baldwin (1992) and Bena *et al.* (1998).

respectively. The ITS regions provide high copy numbers, and are therefore amenable to standard laboratory techniques. Although amplification products are usually homogeneous, as reported in the Compositae (Baldwin, 1992) and in *Medicago* (Leguminosae) (Bena *et al.*, 1998), polymorphisms have been revealed in some taxa. Baker *et al.* (2000a) reported high levels of within-individual polymorphisms in the ITS regions of the palm genus *Calamus*, and subsequently adopted cloning to overcome the problem. Similarly, Denbuangboripant and Cronk (2000) also found within-individual polymorphisms, in *Aeschynanthus* (Gesneriaceae), but were still able to generate a phylogenetic tree through selective cloning. As the ITS regions contain more changes and substitutions than other regions, Baker *et al.* (2000a) proposed that the regions are evolving more rapidly and are potentially better able to resolve questions about lower level relationships than other regions. Considering the potential restrictions placed on phylogenetic interpretations brought about by the presence of polymorphisms, it was appropriate to attempt an examination of *Livistona*, to determine if this situation occurs in this genus.

4.3 Aims

The aim of this investigation was to determine if the ITS regions in *Livistona* nuclear DNA could provide sequence data for use in phylogenetic and biogeographical analyses. Although, as mentioned above, other sequences have been used for palms, the ITS regions were chosen because they have been found to be useful at lower taxonomic levels in *Calamus* (Baker *et al.*, 2000a). Logistical constraints meant that this investigation was essentially a pilot study during which molecular techniques were learnt.

4.4 Materials

Materials for the DNA investigation were obtained from both wild and cultivated sources (Table 4.2). Fresh leaf samples, cut with secateurs from the 'spear' stage of

Table 4.2 Samples used in the molecular investigations in *Livistona*. The species name, code for each species, collector and number, herbaria where specimens are deposited and origin of the collection, are indicated.

Preservation techniques: * = silica gel dried, and ** = fresh material.

species (code)	***collection number, locations of specimens, and origin***
L. alfredii (L40)	Bromilow LA1 (PERTH), wild collected WA*
L. australis 1 (P1)	Wusche s. n. (JCT), wild-collected VIC**
L. australis 2 (P2)	Craig s. n. (JCT), wild-collected NSW**
L. australis 3 (P3)	Dowe s. n. (JCT), wild-collected Qld**
L. australis 4 (P4)	Dowe s. n. (JCT), wild-collected Qld*
L. benthamii (L41)	Dowe 406 & Smith (BRI, JCT), wild-collected Qld*
L. carinensis (P5)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**
L. chinensis (P6)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**
L. chinensis (P17)	Nobe s. n. (MAK), wild-collected Japan*
L. concinna (P7)	Dowe 607 (BRI, JCT), wild-collected Qld**
L. decora (P8)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**
L. drudei (L42)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**
L. humilis (P9)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**
L. inermis (P10)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**
L. jenkinsiana (P11)	Dowe s. n. (JCT), wild-collected Thailand*
L. lanuginosa (P12)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**
L. mariae (P18)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**
L. nasmophila (P14)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**
L. nitida (P15)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**
L. saribus (P16)	Dowe s. n. (JCT), wild-collected Thailand*
L. tothur (L44)	Barfod 510 (AAU), wild collected PNG*
Licuala ramsayi (P13)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**
Pholidocarpus macrocarpa (L45)	Dowe s. n. (JCT), cultivated in Townsville Palmetum**

an emergent leaf, were either preserved using the rapid-dry silica gel method of Chase and Hills (1991), or used fresh within three hours of collection. Samples consisted of strips of lamina tissue, measuring c. 10x100 mm, from which the ribs had been removed. Materials were stored at 4°C for up to two years for some species. Some materials were obtained from seedlings grown from wild-collected seed and grown in the glass-houses at James Cook University Townsville, or from plants growing in The Palmetum, Townsville, where reliable accession data were available. For 15 of the 17 species analysed, one sample of each was examined. Four samples of *L. australis* collected from different populations, and two samples of *L. carinensis* collected from a single source, were analysed. Two outgroup taxa, *Licuala ramsayi* and *Pholidocarpus macrocarpa*, were chosen, based on their flanking positions in relation to *Livistona* in previous phylogenetic analyses (Uhl *et al.*, 1995; Baker *et al.*, 1999). The loci investigated included the ITS-1, 5.8S and ITS-2 regions (Fig. 4.1) which are positioned between the 18S and 26S regions (Baldwin *et al.*, 1995; Baker *et al.*, 2000a). The investigations were conducted in the Molecular Laboratory, School of Tropical Environmental Studies and Geography, James Cook University, Townsville.

4.5 Methods

DNA extraction

Extraction of total DNA from leaf material followed a modified PVP-SDS method developed by Waycott and Barnes (2001). The amount of leaf material used per sample was approximately 10x12 mm in area. DNA was visualised on a 1% agarose gel with ethidium bromide and viewed under ultra-violet light. Following confirmation of the presence of suitable amounts of DNA, clean up of extractions was performed using the BRESAclean™ DNA purification kit, using the manufacturer's recommended procedures. The products of the clean-up were visualised on a 1% agarose gel with ethidium bromide and viewed under ultra-violet light.

Amplification

The ITS regions were amplified from total DNA using the polymerase chain reaction (PCR). The standard profile for ITS was used with recommended times and temperatures in a MJ-PT200 PCR machine. Dilutions of template DNA, using Tris 10 mM, EDTA (Na_2)1 mM (TE) as the dilutant, ranged from 1:1 to 1:25 per sample. The PCR reactions were prepared on ice. The 25 μl of reaction mixture contained,

according to directions in the Qiagen™ Core kit, 10x PCR buffer (2.5μl), $MgCl_2$ 25 mM (0.5 μl), Q-solution (5μl), dNTP 10 mM each (0.4μl), Taq polymerase 5U/μl (0.2μl), H_20 (13.4μl), ITS 4 10 mM (1μl), ITS16/ITS16 'palm' 10 mM (1μl), and DNA (1μl). Three primers were used, ITS4, 5'-TCCTCCGCTTATTGAT ATGC-3' (White *et al.*, 1990), ITS16, 5'- CGATTGAATGGTCCGGTGAAGTGTCG-3' (Calladine, unpublished) and ITS16 'palm' 5'- CGATTGAATGGTCCGGTGA AGTGTTCG-3' (Waycott, unpublished). PCR amplification was performed using the following profile: 1 cycle of 96°C for 5 minutes; 30 cycles of 96°C for 30 seconds; 50°C for 30 seconds; 70°C for one minute; one cycle of 72°C for 10 minutes and then held at 4°C until removed from the thermal cycler. Following the PCR, using primers ITS4 and ITS16, the products were visualised on 1% agarose gel with ethidium bromide and viewed under ultra-violet light. As ITS16 produced secondary priming sites at the 18S end, the additional primer ITS16 'palm' was designed to work within the 18S region flanking ITS-1. The PCR was run again using the methods as described, but substituting ITS16 'palm' for ITS16. The products were visualised on a 1% agarose gel with ethidium bromide and viewed under ultra-violet light.

Cloning

Because PCR amplification yielded ITS products of multiple fragment lengths (presented in section 4.6 Results in Table 4.3), direct sequencing was not possible. The PCR products were run on a 40 mM Tris-acetate, 1 mM EDTA (TAE) gel, in anticipation of excision, purification and cloning. The appropriate fragment length for excision was approximately 600-700 base pairs, as determined by Baker *et al.* (2000a), and identified on the gel by comparison with molecular weight markers. Therefore, excision of the band was intended to isolate the individual section of DNA that was considered the correct molecular weight for sequencing. The appropriate bands were excised from the gel and purified using the BRESAclean™ DNA purification kit following the manufacturer's instructions. The purified products were re-amplified according to the PCR protocol outlined above. The PCR products were visualised on 1% agarose gel with ethidium bromide and viewed under ultra-violet light.

Cloning was done using the pMOS*Blue* blunt ended cloning kit RPN 5110 (Amersham, 1997) without modifications. Colonies were selected and removed with

sterile toothpicks and suspended in 30 μl of water, heated at 96°C for 2 minutes then placed on ice. Products were subjected to PCR as per the pMOS*Blue* kit colony PCR instructions using 1 μl and 2 μl of DNA template. Products were cleaned using the QIAquick PCR purification kit (Qiagen) and visualised on a 1% agarose gel with ethidium bromide and viewed under ultra-violet light.

Sequences

Purified products were cycle-sequenced using the BigDye™ kit (PE Applied Biosystems part number 403041 Rev. B) according to the manufacturer's instructions to a total of 10 μl per sample. PCR products were sequenced in both directions. Products were cleaned using Sephadex™ G-50 (Sigma S-5897) spin columns, then vacuum dried and sent for sequencing at the Molecular Analysis Facility at Griffith University, Brisbane. Sequences were edited with no ambiguities in the complementary sequences. Sequence alignments were performed using Clustal X Multiple Sequence Alignment Program version 1.81 (Jeanmougin *et al.*, 1998) (www.U.arizona.edu/~schulter/clustalW/index.html), and adjusted manually.

Analysis

Preliminary analysis of aligned sequence data was conducted using PAUP* version 4.08b. Parsimony analysis was conducted using the heuristic search, with all character sets intact, and gaps coded as missing data using the TBR [tree bisection and reconnection] branch swapping option. Settings in PAUP were otherwise set at standard default.

4.6 Results

Crude extractions of DNA and PCR products using the primers ITS4 and ITS16 were visualised on a 1% agarose gel with ethidium bromide and viewed under ultra-violet light (Figs 4.2, 4.3). As multiple bands were produced with primers ITS4 and ITS16, a second PCR was performed using ITS16 'palm'. Multiple bands were still produced despite the change in primer (Fig. 4.4). However, there was an improvement with the PCR products because there were a greater number of samples with only one band. Cloned products (Fig. 4.5) showed strong single bands but with fragment length variation. Aligned sequences of a selected group of taxa are presented in Table 4.3.

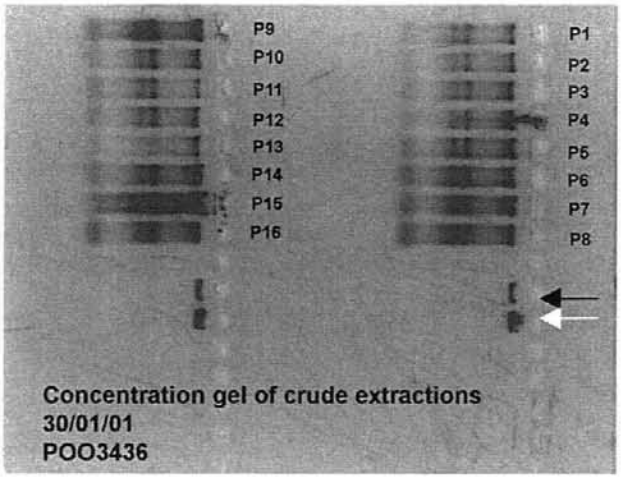


Figure 4.2. A selection of crude DNA extractions visualised by ultra-violet light on a 1% agarose gel. The primers used were ITS4 and ITS16. Lanes are orientated right to left. Standards of high molecular weight DNA, 50 ng [indicated with black arrow] and 100 ng [indicated with white arrow], are adjacent to the taxon lanes. For taxon designations see Table 4.2.

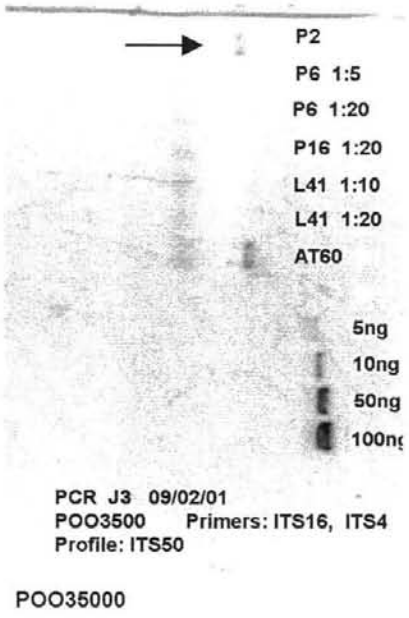


Figure 4.3 PCR products using primers ITS4 and ITS16. Lanes are orientated right to left. PCR profile ITS50 was used. Standards of molecular weights [5-100 ng] are indicated. For taxon designations see Table 4.2. Note that AT60 was a PCR control from another angiosperm family. P2, a sample with multiple bands, is indicated by an arrow.

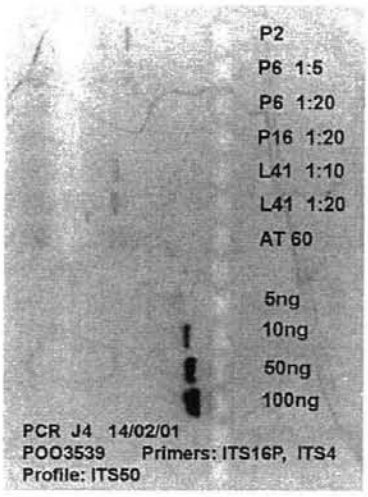


Figure 4.4 PCR products using primers ITS4 and ITS16 'palm'. Lanes are orientated right to left. Standards of molecular weights [5-100 ng] are indicated. Dilutions are indicated adjacent to the taxon codes. For taxon designations see Table 4.2. AT 60 is a control from another family.

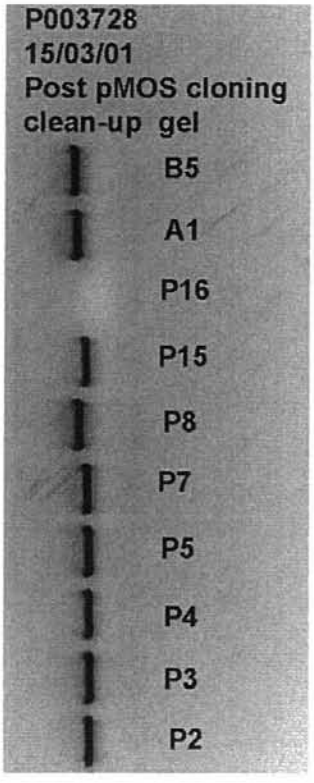


Figure 4.5 Cloned products using the pMOS*Blue* blunt ended cloning kit. Lanes are orientated right to left. Standards of molecular weights are not included on this photograph as they were removed prior to photographing. For taxon designations see Table 4.2. B5 and A1 are controls from another family.

The sequences included eight *Livistona* samples and one sequence each of *Raphia* (GenBank Accession AJ242138) and *Eugeissona* (GenBank Accession AJ242120) to verify, by comparison, that the sequences were indeed of palms and they were readily alignable with the independently obtained *Livistona* taxa. Total length of aligned sequences was 914 bp. It should be noted that in six of the eight sequences there was a large deletion corresponding to almost the entire ITS-2 region. However, this deleted portion was present in another cloned sample of *L. carinensis* (Fig. 4.6, labelled L2) that was obtained from the same DNA source. The samples of *L. carinensis* are labelled L2 and P5 and are indicated by an arrow on the preliminary PAUP analysis cladogram (Fig. 4.6).

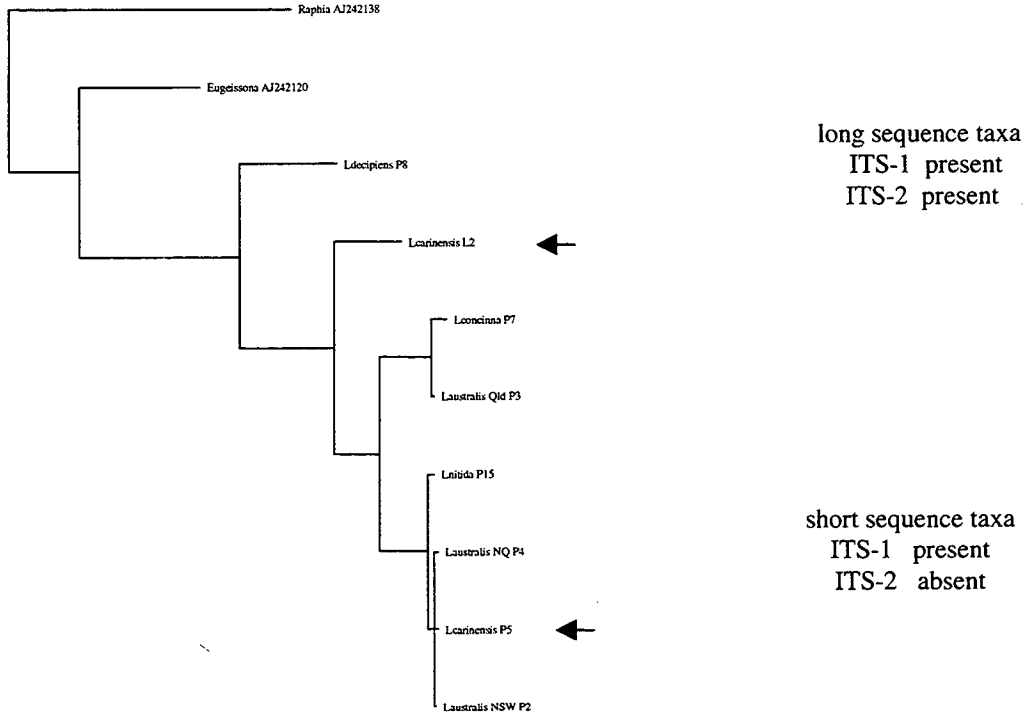


Figure 4.6 Preliminary phylogram obtained from the sequence data of eight taxa. Four basal taxa included sequence data from all three regions, ITS-1, 5.8S and ITS-2. The six taxa in the terminal clade included sequence data from only two regions, ITS-1 and 5.8S, as the ITS-2 region was deleted. The two basal taxa are GenBank accessions, with reference numbers indicated. A phylogram obtained from sequence data excluding the ITS-2 region of all ten taxa (not shown) was identical to this phylogram. Arrows indicate the replicates of *L. carinensis* L2 and *L. carinensis* P5.

Table 4.3 Aligned sequence data of selected species of *Livistona*, *Raphia* and *Eugeissona*.

```
Lnitida_P15             TCGTAACAAGGTTTCCGTAGGTGAACCTGCAGAAGGATCATTGCCGAGAC
Laustralis_NSW_P2       TCGTAACAAGGTTTCCGTAGGTGAACCTGCAGAAGGATCATTGCCGAGAC
Lcarinensis_L2          TCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGCCGAGAC
Laustralis_NQ_P4        TCGTAACAAGGTTTCCGTAGGTGAACCTGCAGAAGGATCATTGCCGAGAC
Laustralis_Qld_P3       TCGTAACAAGGTTTCCGTAGGTGAACCTGCGAAAGGATCATTGTCGAGAC
Lcarinensis_P5          NNNNNACAAGGTTTCCGTAGGTGAACCTGCAGAAGGATCATTGCCGAGAC
Lconcinna_P7            TCGTAACAAGGTTTCCGTAGGTGAACCTGCGAAAGGATCATTGTCGAGAC
Ldecora_P8               TCGTAACAAGGTTTCCGTAGGTGAACCTGCGGAAGGATCATTGTCGAGAC
Raphia_AJ242138         TCATAACAAGGTCTCT-GAGGTGAACCTATAGAAGGATCATTGTCGAGAC
Eugeissona_AJ242120     TCGTAACAAGGTTTCCATAGGTGAACCTGCGGAAGGATCATTGCCGAGAC

Lnitida_P15             GCCGACGAGGAAAAGACCCGCGAACATGTGAACGTGCTGCACAGGAGCAG
Laustralis_NSW_P2       GCCGACGAGGAAAAGACCCGCGAACATGTGAACGTGCTGCACAGGAGCAG
Lcarinensis_L2          CCCGACGAGGAAA-GACCCACGAACACGTGAACGCACCGTGCAGGAGCGG
Laustralis_NQ_P4        GCCGACGAGGAAAAGACCCGCGAACATGTGAACGTGCTGCACAGGAGCAG
Laustralis_Qld_P3       CCCGACGAGGAAAAGACCCACGAACACGTGAACGTGCTACGCAGGAGCGA
Lcarinensis_P5          GCCGACGAGGAAAAGACCCGCGAACATGTGAACGTGCTGCACAGGAGCAG
Lconcinna_P7            CCCGACGAGGAAAAGACCCACGAACACGTGAACGTGCTACGCAGGAGCGA
Ldecora_P8              CCCGATGAGGAAAAGACCAGCGAACACATGAACACGCTGTGCAAGAGCAG
Raphia_AJ242138         CC-AAGGAGG--CAGGCCCACAAACATGTGAATGCTTTTCACAT-C---G
Eugeissona_AJ242120     CT--ACGAGG--CAGACCCGTGAACATGTCAACGTGT--CA--TGCGCAG

Lnitida_P15             AAAGGCA--TGGCCGACCCGACCCTCACCCTCCCTCTCCCCCATATCGCC
Laustralis_NSW_P2       AAAGGCA--TGGCCGACCCGACCCTCACCCTCCCTC-CCCCCATATCGCC
Lcarinensis_L2          GAAGGCA--TGGCCAACCCGACCCTCGCCCTCCCTC-CCCCAATATCACC
Laustralis_NQ_P4        AAAGGCA--TGGCCGACCCGACCCTCACCCTCCCTC-CCCCCATATCGCC
Laustralis_Qld_P3       GAAGGCA--CGGCCGACCCGACCCTCGCCCTCCCTCCCCCCCCGTATCGCC
Lcarinensis_P5          AAAGGCA--TGGCCGACCCGACCCTCACCCTCCCTC-CCCCCATATCGCC
Lconcinna_P7            GAAGGCA--CGGCCGACCCGACCCTCGCCCTCCCTC-CCCCCGTATCGCC
Ldecora_P8               GAGGGCA--CGGCCGATCCGACCCTCGCCCTCCCTC-CCCTCGTATCGCC
Raphia_AJ242138         AAGCGGGGGTAGCCCCGCGGATCCACTCTGGAGGC---------ATGGCC
Eugeissona_AJ242120     A--GTGGGGTGGCCTTGCCGACCCCGCCCCGATGCC--------ATTGCC

Lnitida_P15             CACCT--------------------------CGGGGA-GT---GGGCCCT
Laustralis_NSW_P2       CACCT--------------------------CGGGGA-GT---GGGCCCT
Lcarinensis_L2          AACCT--------------------------CGGGGC-AC---GGGCCCT
Laustralis_NQ_P4        CACCT--------------------------CGGGGA-GT---GGGCCCT
Laustralis_Qld_P3       CACCT--------------------------CGGGGC-AT---GGGCCCC
Lcarinensis_P5          CACCT--------------------------CGGGGA-GT---GGGCCCT
Lconcinna_P7            CACCT--------------------------CGGGGC-AT---GGGCCCC
Ldecora_P8               CACCT-------------------------CGGGGC-AC---AGGCCCC
Raphia_AJ242138         CGACACCCTGCACTATCGAGACTGGCGGACGTGGGGTGGTGGGAGGACTG
Eugeissona_AJ242120     CAGCGCCCCGCACCATCGAGATCGGCAGACGCGGGGCAACAGGAGGACCG

Lnitida_P15             GACCCGGATGGGCACGGAGGCGCGCTCGCGGCATGCGATGCTGGGCGGTG
Laustralis_NSW_P2       GACCCGGATGGGCACGGAGGCGCGCTCGCGGCATGCGGTGCTGGGCGGTG
Lcarinensis_L2          GGCCCAGATGGGCATGGAGGCATGCCCGTGGCGTTCGGTGCTGGGCGGCA
Laustralis_NQ_P4        GACCCGGATGGGCACGGAGGCGCGCTCGCGGCATGCGGTGCTGGGCGGTG
Laustralis_Qld_P3       AACCCGAATGGGTGCAGAGGCGCGCCAACGGCATGCGGTGCTGGGCGACG
Lcarinensis_P5          GACCCGGATGGGCACGGAGGCGCGCTCGCGGCATGCGGTGCTGGGCGGTG
Lconcinna_P7            AACCCGAATGGGTGCAGAGGCGCGCCAACGGCATGCGGTGCTGGGCGACG
Ldecora_P8               AACTCGGATGGGTGCGGAGGCCCGCCCGCAGTGTGCGGTGCTGGGCAGCA
Raphia_AJ242138         CACCC---TGG-CACAGAG----------------------------
Eugeissona_AJ242120     GACC----TGG-CACGGAG----------------------------

Lnitida_P15             GGCAGACTGGACCCGGTGTGGAGGGCGCCAAGGAA---CAGGAGCATGAA
Laustralis_NSW_P2       GGCAGACTGGACCCGGTGTGGAGGGCGCTAAGGAA---TAGGAGCATGAA
Lcarinensis_L2          GGCGGACCGGACCCGACGCGGAGGGCACCAAGGAA---CAGGAGCATGAA
Laustralis_NQ_P4        GGCAGACTGGACCCGGTGTGGAGGGCGCTAAGGAA---TAGGAGCATGAA
Laustralis_Qld_P3       GGTAGATCGGACCCGGCGTGGAGGGCACCAAGGAA---CAGGAGCATGAA
Lcarinensis_P5          GGCAGACTGGACCCGGTGTGGAGGGCGCTAAGGAA---TAGGAGCATGAA
Lconcinna_P7            GGTAGATCGGACCCGGCGTGGAGGGCACCAAGGAA---CAGGAGCATGAA
Ldecora_P8               GGCAGACCAGACATGGTGCGGAGGACGCCAAAGAA---CAGGAGCATGAA
Raphia_AJ242138         --------------------GA---CACCAAGGAACCTCAAGCACAG--A
```

```
Eugeissona_AJ242120  ---------------A----G----TGCCAAGGAA--GCATGATCATGGA

Lnitida_P15          ------TGTGACGGCGCCACC----GGCAGCGGCTACCC-----------
Laustralis_NSW_P2    ------TGTGACGGCGCCACC----GGCAGCGGCTACCC-----------
Lcarinensis_L2       ------CGCGACGGCGCCACC----ACCGATGGATGCCC-----------
Laustralis_NQ_P4     ------TGTGACGGCGCCACC----GGCAGCGGCTACCC-----------
Laustralis_Qld_P3    ------TGTGACGGCACCGCT----GGCGGCGGCTGCCC-----------
Lcarinensis_P5       ------TGTGACGGCGCCACC----GGCAGCGGCTACCC-----------
Lconcinna_P7         ------TGTGACGGCACCGCT----GGCGGCGGCTGCCC-----------
Ldecora_P8           ------CACGATGATGCCGCT----GGC-AAAGCTGCCC-----------
Raphia_AJ242138      GGT----GGGCATGCGCCGTT----GCC--TGCATGACCT-CGCA-CCAA
Eugeissona_AJ242120  GGT-A-GGGGGGCGCTCCACA----GCCGACCCA-G-CCTGC--AAC-GA

Lnitida_P15          --------------------------------------------------
Laustralis_NSW_P2    --------------------------------------------------
Lcarinensis_L2       --------------------------------------------------
Laustralis_NQ_P4     --------------------------------------------------
Laustralis_Qld_P3    --------------------------------------------------
Lcarinensis_P5       --------------------------------------------------
Lconcinna_P7         --------------------------------------------------
Ldecora_P8           --------------------------------------------------
Raphia_AJ242138      ----GGTCGGGGTGGT------CAGAGGGTGTGTCGCCGTCGGGGGCATC
Eugeissona_AJ242120  GGTAGG--GGGG-G--------AAAAGGGCTCTCTAACGTTGACAGCAGC

Lnitida_P15          ---------TGCATGGTATGACTCTCGGCAATGGATATTTTGGCTCTCGC
Laustralis_NSW_P2    ---------TGCATGGTATGACTCTCGGCAATGGATATCTTGGCTCTCGC
Lcarinensis_L2       ---------CGCATGGTACGACTCTCGGCAATGGATATCTCGGCTCTCCC
Laustralis_NQ_P4     ---------TGCATGGTACGACTCTCGGCAATGGATATCTTGACTCTCGC
Laustralis_Qld_P3    ---------TGCATGGTACGACTCTCGGTAATGGATATCCCGGCTCTTGC
Lcarinensis_P5       ---------TGCATGGTATGACACTCGGCAATGGATATCTTGGCTCTCGC
Lconcinna_P7         ---------TGCATGGTACGACTCTCGGTAATGGATATCCCGGCTCCTGC
Ldecora_P8           ---------CGCATGGTATGACACTTGGTAATGGATATCTCGGCTCTCGC
Raphia_AJ242138      CTCACCGCATATGCAGTATGACTCTCGGCAATGGATATCTTGGCTCTTGC
Eugeissona_AJ242120  CTGGCC--ACACACGGTACGACCCTCGGCAACGGATATCTCGGCTCTCGC


Lnitida_P15          ATCGATGAAGAATGTAGCGAAATGCGAGATCTGGTGTGAATTGTAGAATC
Laustralis_NSW_P2    ATCGATGAAGAATGTAGCGAAATGTGATATCTGGTGTGAATTGTAGAATC
Lcarinensis_L2       ATCGATGAAGAACGTAGCGAAATGTGATACCTGGTGTGAATTGTAGAATC
Laustralis_NQ_P4     ATCGATGAAGAATGTAGCGAAATGTGATATCTGGTGTGAATTGTAGAATC
Laustralis_Qld_P3    ATCGATGAAGAACGTTGCGAAATGCGATACCTGGTGTGAATTGTAG-ATC
Lcarinensis_P5       ATCGATGAAGAATGTAGCGAAATGTGATATCTGGTGTGAATTGTAGAATC
Lconcinna_P7         ATCGATGAAGAACGTTGCGAAATGCGATACCTGGTGTGAATTGTAGA-TC
Ldecora_P8           ATCGATGAAGAATGTAGCGAAATGCGATACCCGGTGTGAATTATAGAATC
Raphia_AJ242138      ATCGATGAAGAACATAATGAAATATGATACATGGTGTGAATTGTAGAATC
Eugeissona_AJ242120  ATCAATGAAGAACGTAGTGAAATGCGATACATGGTGTGAATTGCAGAATC

Lnitida_P15          CCGCAAACCATCGAGTCTTTGAATGCAAGTTGCGCCCGAGGCCACCC-GT
Laustralis_NSW_P2    CCGCAAACCATTGAGTCTTTGAATGCAAGTTGCGCCCGAGGCCACCC-GT
Lcarinensis_L2       CCGTGAACCATCGAGTCTTTGAACGCATGTTGCGCCCAAGGTCACCCAGC
Laustralis_NQ_P4     CCGCAAACCATCGAGTCTTTGAATGCAAGTTGCGCCCGAGGCCACCC-GT
Laustralis_Qld_P3    CCACGAACCATCGAGTCTTTGAACGCAAGTTGCGCCTAAGGCCACCC-GT
Lcarinensis_P5       CCGCAAACCATCGAGTCTTTGAATGCAAGTTGCGCCCGAGGCCACCC-GT
Lconcinna_P7         CCACGAACCATCGAGTCTTTGAACGCAAGTTGCGCCTGAGGCCACCC-GT
Ldecora_P8           CCATGAACCATCGAGTCTTTGAATGCAAGTTGCACCCGAGACCACCC-G-
Raphia_AJ242138      CCATGAACCATCAAGTCTTTGAATGCAAGTTGCACCCGAGGCCATCT-G-
Eugeissona_AJ242120  CCGTGAACCATTGAGTCTTTGAACGCAAGTTGGACCTGAGACCATCC-G-

Lnitida_P15          -G-------------------------------------------------
Laustralis_NSW_P2    -G-------------------------------------------------
Lcarinensis_L2       CGAGGGCACGCCTGCCTGGGCATCATGCCAAG-------------------
Laustralis_NQ_P4     -G-------------------------------------------------
Laustralis_Qld_P3    -G-------------------------------------------------
Lcarinensis_P5       -G-------------------------------------------------
Lconcinna_P7         -G-------------------------------------------------
Ldecora_P8           -G--------CCGA---GGGCA-C--GCCTGC---TTGGGCATCACACCA
Raphia_AJ242138      -G--------CCGA---GGGCA-C--GCCTGCC-TAGG-CATCACGCCTC
```

```
Eugeissona_AJ242120  -A--------CCAA---GGGCA-C--GCCTACC-T-GGGTGTCACTCCAA

Lnitida_P15          ------------------------------------------------
Laustralis_NSW_P2    ------------------------------------------------
Lcarinensis_L2       --TGACGCTGCGGCTCCCCCGGGCCCGCGGTGGG-CCCCCAGGG-AGCC-
Laustralis_NQ_P4     ------------------------------------------------
Laustralis_Qld_P3    ------------------------------------------------
Lcarinensis_P5       ------------------------------------------------
Lconcinna_P7         ------------------------------------------------
Ldecora_P8           AGCGATGCTGCGGCTCCCCCCGGCCTGCGACGGG-CTCCT-GGGGAGCC-
Raphia_AJ242138      TCCGATGCTCC-ATCCCCCTAGGGCTCTGATGGG-CTCTGAGGG-TGG-C
Eugeissona_AJ242120  GC-GACGCTCT-GCTCCCCCGGGGCCCCAAGGGG-CTCTC-GGGGTGGGC

Lnitida_P15          ------------------------------------------------
Laustralis_NSW_P2    ------------------------------------------------
Lcarinensis_L2       ------AGACGCGGACATCAGCCTCCTTCCCCCCGATGCGGC---AGGTC
Laustralis_NQ_P4     ------------------------------------------------
Laustralis_Qld_P3    ------------------------------------------------
Lcarinensis_P5       ------------------------------------------------
Lconcinna_P7         ------------------------------------------------
Ldecora_P8           ------GGATGCAGACATCGGCCCCCCACACCCCTC-GTTGCGGTGAGTC
Raphia_AJ242138      T-----AGATGTGGACATTGGCCCCCTAT---GC-------T----TGGT
Eugeissona_AJ242120  GG----ATGCGAAAAC-T-GGCCCCCCGTGGCCC----TTGT-GCGCGGC

Lnitida_P15          ------------------------------------------------
Laustralis_NSW_P2    ------------------------------------------------
Lcarinensis_L2       C----GAGGAGCGGGCCGTCGGTGGGG---CCGG--------ACATGGTG
Laustralis_NQ_P4     ------------------------------------------------
Laustralis_Qld_P3    ------------------------------------------------
Lcarinensis_P5       ------------------------------------------------
Lconcinna_P7         ------------------------------------------------
Ldecora_P8           C----GAGGAGCGGGCCACCGATGGGG---CCGG--------ACATGGTG
Raphia_AJ242138      GTGCTGAAGCTTGGGCCGTAGT----C---AGGTCCAG----ACATGGTG
Eugeissona_AJ242120  GTGCCAAAGTTCGGGC---C-TCAGGC---GGGTCTGG----ACACGACA


Lnitida_P15          ---------------------------------ATGCC---AGACCCTAG
Laustralis_NSW_P2    ---------------------------------ATGCC---AGACCCTAG
Lcarinensis_L2       GATGGCAAACGCGCTCGTGGTCCTACCACCGTGATGCC---GGACCCCAG
Laustralis_NQ_P4     ---------------------------------ATGCC---AGACCCTAG
Laustralis_Qld_P3    ---------------------------------ATGCC---AGACCCTAG
Lcarinensis_P5       ---------------------------------ATGCC---AGACCCTAG
Lconcinna_P7         ---------------------------------ATGCC---AGACCCTAG
Ldecora_P8           GATGGCGGATGCGCTCACGGTCCTGCCACCAGGATGCT---GGACCCTAG
Raphia_AJ242138      GGTGGTGGATGCGCCTGCGATCCCATCGCC---ATGCCACTAGACCCCGA
Eugeissona_AJ242120  GTTGGTGGATGCGCCTGCGATCCCATCGCC---ATGCCCCTGGACCCTGG

Lnitida_P15          CGGCAAAGGGCCCTCGCCGGCCCC--ATTGCGTGCGGCGCCCCAGCCCCC
Laustralis_NSW_P2    CGGCAAAGGGCCCTCGCCGGCCCC--ATTGCGTGCGGCGCCCCAGCCCCC
Lcarinensis_L2       CGGCGAAGGGCCCTCGCTGCCCCC--ATCGCGTGCATCACCCCGGCCCCC
Laustralis_NQ_P4     CGGCAAAGGGCCCTCGCCGGCCCC--ATTGCGTGCGGCGCCCCAGCCCCC
Laustralis_Qld_P3    CGGCGAAGGGCCCTCGCCAGCCCC--ATTGCGTGCGGCGCCCCAGCCCCC
Lcarinensis_P5       CGGCAAAGGGCCCTCGCCGGCCCC--ATTGCGTGCGGCGCCCCAGCCCCC
Lconcinna_P7         CGGCGAAGGGCCCTCGCCAGCCCC--ATTGCGTGCGGCGCCCCAGCCCCT
Ldecora_P8           CGGCGAAGGGCCCTTGCCGCCCCC--ATCGCATGCGGGGCCCCGGCCCTC
Raphia_AJ242138      CCTGTA-GGGCCCCCTGTTGCCCCGAACCACGCATGGCACCCTGACCCCC
Eugeissona_AJ242120  GCTGCA-GGGCC-TCCTTGGC--------ACT-AG----CCCT-----TG

Lnitida_P15          GGCCGGGGCGGCACCCC-TCAGATCACGACCCCAAGTCAGGCGGGGCCAC
Laustralis_NSW_P2    GGCCGGGGCGGCACCCC-TCAGATCACGACCCCAAGTCAGGCGGGGCCAC
Lcarinensis_L2       GATCGGGGTGGCGCCCCCTCGGATCATGACCCCAGATCAGGCTGGGCCAC
Laustralis_NQ_P4     GGCCGGGGCGGCACCCC-TCAGATCACGACCCCAAGTCAGGCGGGGCCAC
Laustralis_Qld_P3    GGCCGGGGCGGCACCCC-TCAGATCACGACCCCAAGTCAGGCGGGGCCAC
Lcarinensis_P5       GGCCGGGGCGGCACCCC-TCAGATCACGACCCTAAGTCAGGCGGGGCCAC
Lconcinna_P7         GGCCGGGGCGGCCCCCCCTCGAATCGCGACCCCAAGTCAGGCAGGGCCAC
Ldecora_P8           GGCTGGGGCAGCGCCCCCTCAGATCGTGACCACAGATCAGGTGGGGCCAC
Raphia_AJ242138      GACTGGGGAAGCACCC--TCAGAATGTGACCCAGGGTCGAGTTGGCCTAC
```

```
Eugeissona_AJ242120  GGCCATGGCGGCGCCC--TCGGAACGCGACCCCAGGTCAAGGCGGGNNNN

Lnitida_P15          CCGCTAAGCTTAAGCATATCAATAAGCGGAGGA
Laustralis_NSW_P2    CCGCTAAGCTTAAGCATATCAATAAGCGGAGNN
Lcarinensis_L2       CAGCCGAGCTTAAGCATATCAATAANNNNNNNN
Laustralis_NQ_P4     CCGCTAAGCTTAAGCATATCAATAAGCGGAGGA
Laustralis_Qld_P3    CCGCTAAGCTTAAGCATATCAATAAGCGGAGGA
Lcarinensis_P5       CCGCTAAGCTTAAGCATATCAATAAGCGGAGGA
Lconcinna_P7         CCGCTGAGCTTAAGCATATCAATAAGCGGAGGA
Ldecora_P8           CCATCGAGCTTAAGCATATCAATAAGCGGAGGA
Raphia_AJ242138      CTTC-GGACTTNNNNNNNNNNNNNNNNNNNNN
Eugeissona_AJ242120  NNNNNNNNNNNNNNNNNNNNNNNNNNNNNNNN
```

4.7 Discussion

In palms, the ITS regions may contain polymorphisms that are impossible to sequence directly (Baker *et al.*, 2000a). Direct sequencing often displays the presence of several variants, some of which are possibly non-functional, although this has not been unequivocally proven. A lack of homogenisation of polymorphic and repeating DNA in some palm studies makes establishing phylogenies difficult, and cloning is necessary to isolate multiple copies and to allow analysis of sequences simultaneously (Hahn and Sytsma, 1999).

There was a high level of within-individual polymorphism in the nrDNA ITS regions of *Livistona*. Consistent multiple banding was evident at every stage of the sequencing process (e. g. Fig. 4.3). As discussed for palms by Baker *et al.* (2000a), it is most probable that the ITS regions in *Livistona* are not completely homogenised by the action of concerted evolution. It is not surprising that sequences differed because, from the outset, multiple bands were obtained. It should be noted that all alternate band lengths when sequenced possessed the same deletion in ITS-2. Support for these results, indicating that there are different copies of the ITS regions, is given by the observation of both sequenced types in the same DNA sample of *L. carinensis* as observed by the difference in cloned isolates (Fig. 4.6, samples L2 and P5).

Two types of sequences were recognised in this study. One type, designated as 'long sequence taxa' (Fig. 4.6) contained both ITS-1 and ITS-2 sequences while the other, designated as 'short sequence taxa' (Fig. 4.6) contained only ITS-1 sequences, the ITS-2 sequences having been lost. The sequences were not mutually exclusive of sample, as in *L. carinensis* both types were observed (Fig. 4.6, samples L2 and P5), and therefore the tree (Fig. 4.6) is interpreted as a gene tree and not a taxon tree.

The preliminary cladistic analysis of the sequence data (Fig. 4.6) grouped all of the shorter sequence taxa together. To confirm the preliminary results, the data were reanalysed excluding the ITS-2 region from the sequences for all taxa used. This gave a tree (not shown) of similar topology to that produced for trees generated using data of the entire sequence. Analysis of the ITS regions, using both full sequences and those that lacked the ITS-2 region, produced trees where the sequences lacking ITS-2 formed a separate clade (Fig. 4.6). This supports the idea that the two types of sequences are not homologous, as the absence of ITS-2 in one of the types may be a consequence of the excision process. However, the presence of two sequence types in *L. carinensis* supports the idea that the shortest sequences may be pseudogenes or non-functional copies.

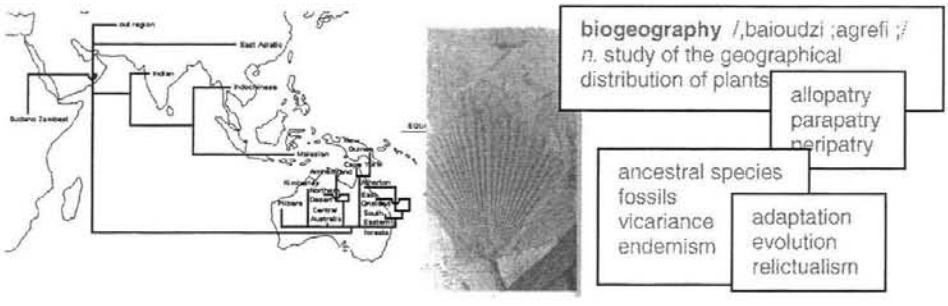
4.8 Conclusion

Using standard methods, the ITS regions appear to be of limited use as a tool for determining genetic relationships among *Livistona* species. However, with appropriately modified methods, phylogenetic and biogeographic inferences may be drawn using this region in the future. There should be more extensive testing to fully evaluate the usefulness of the ITS regions in palms. Full-length sequence copies must be obtained by more scrupulous and finer resolution of size selection of PCR products before cloning. Careful screening of sequences would avoid the inclusion of non-functional copies in analyses. It is possible that a set of full sequences for all *Livistona* species can be generated, given adequate laboratory time. Although this investigation raises questions about the genetic homogenisation and concerted evolution within *Livistona* and palms generally, it was beyond the scope of this present study to examine that question further. This is in agreement with the findings of Baker *et al.* (2000a) for *Calamus*.

Chapter 5

Studies in the genus *Livistona* R. Br. (Coryphoideae: Arecaceae)

HISTORICAL BIOGEOGRAPHY OF *LIVISTONA*



5.1 Introduction

The primary aim of biogeography is to explain the distribution of organisms throughout the biosphere. To achieve this, a range of independent disciplines including geography, geology, climatology, palaeontology and biology may be consulted in an attempt to determine how dispersion, speciation, adaptation, extinction and ecological processes have interacted through time (Morain, 1984; Myers and Giller, 1988; Humphries, 1992; Morrone and Crisci, 1995; Thorne, 1996a, 1996b; Hengeveld, 1997; Humphries and Parenti, 1999).

Biogeography is not coherent unless placed within a well-organised taxonomic and phylogenetic framework (Mickevich, 1981). It is difficult to reconstruct meaningful distribution patterns without an explicit phylogeny for the particular group under study. Many early biogeographic studies attempted to establish the 'centre of origin' or the 'centre of distribution' of a particular taxon - the dispersal method (Morronne and Crisci, 1995) - and then proceeded to describe how extant species arrived where they are today. The term 'centre of origin' is an old term which, although it does not sit easily with cladistic concepts, is useful when considering the evolution of a group or groups. It should be supported where possible with evidence from as many sources as possible.

Two processes that are intrinsic to biogeography, dispersal (Thorne, 1996a; van Balgooy et al., 1996) and vicariance (Humphries, 1981; Nelson and Platnick, 1981; Humphries and Parenti, 1999) have controlled the spread potential of ancestral species. Dispersal, as most commonly understood, involves dissemination, usually by biotic means, across either land or water. Newly founded populations may subsequently evolve into new species. Vicariance, on the other hand, is the concept that new species are created as a result of the formation of barriers, such as newly created mountains or oceans, that divide the former populations into sub-populations that may subsequently experience speciation. Much of the biogeographic literature in recent decades has included arguments concerning whether extant distribution is a result of dispersal or vicariance. Some landmasses have moved considerable distances away from each other, and those species originally established by vicariance may appear to have been established by dispersal (Thorne, 1986; Pole, 1994; Turner, 1996). In spite of the 'philosophical' arguments regarding dispersal events that are part of biogeography (as seen on the web-based TAXACOM Discussion List, April-June 2002, under the heading 'Is biogeography science?'), the distribution of species must be seen in an historical context based on monophyletic groups.

5.2 Historical biogeography

Darwin (1859), Wallace (1860) and Hooker (1860) provided some of the first biogeographic accounts based on observation and deduction. Many of the premises and ideas contained in their works remain unchallenged today. However, as more thorough data were obtained, descriptive methods were increasingly utilised (Burbidge, 1960). By the mid to late 20th Century, systematic accounts for many parts of the world had been attempted, although coverage was sporadic in some areas. It is from these accounts that the works of Croizat (1958), van Balgooy (1971) and Takhtajan (1986) were developed. They utilised complex tabulation procedures that resulted in the comparison of the distribution of taxa, and established distributional hierarchies. These provided a basis for biogeographic hypotheses.

5.2.1 *Cladistic biogeography*

In recent decades, biogeographical analytical techniques have adopted cladistic methodologies (Morrone and Crisci, 1995). The concepts and methods of cladistic biogeography were first outlined by Nelson and Platnick (1981), Humphries (1981), Mickevich (1981) and Platnick (1981). However, it was not until the work of Humphries and Parenti (1986, 1999) that a broad synthesis of concepts and applications was provided.

Cladistic biogeography is an approach that aims to extract and refine the historical patterns contained in a combination of distributional and systematic evidence. Following the completion of a cladistic analysis of the group(s) under study, cladograms of taxa that are endemic to different areas can be converted into area cladograms. Hypotheses of biogeographic relationships can be proposed by substituting the taxon labels for the area of endemism in which they occur (Mickevich, 1981; Brundin 1988; Cracraft, 1988; Humphries *et al.*, 1988; Humphries and Parenti, 1999; Vega *et al.*, 1999). Area cladograms can be interpreted to represent fragmentation of ancestral distribution by successive speciation events initiated by either dispersal or vicariant events (Page, 1988; Weston and Crisp, 1996). Studies in which cladistic techniques have been used for palms are presented in Table 5.1.

Table 5.1. Palm biogeography studies in which cladistic techniques have been used.

taxon	reference
Arecaceae (general)	Uhl *et al.* (1995)
Sabal	Zona (1990)
Cryosophila	Evans (1995)
Calamoideae	Baker and Dransfield (2000)
Caryota	Hahn and Sytsma (1999)
Iriarteeae	Henderson (1990)
Physokentia	Fuller (1999)
Drymophloeus	Zona (1999a)
Ptychospermatinae	Zona (1999b)
Archontophoencinae	Pintaud (1999)
Bactris	Salzman and Judd (1995)
Phytelephantoideae	Barfod (1991), Barfod *et al.* (1999)

5.2.2 *Parsimony Analysis of Endemicity (PAE)*

An adjunct to cladistic biogeography is the Parsimony Analysis of Endemicity (PAE) method developed by Rosen and Smith (1988). This method was adopted, with adaptations, for detecting congruence among areas of endemicity of Australian vertebrates (Cracraft, 1991), for analysing the distribution of Hawaiian Amphipoda (Myers, 1991), for identifying areas of endemism in southern Africa (Morrone, 1994), and for comparing the isolated floras of the cloud forests of Venezuela (Vega *et al.*, 1999). The PAE method groups areas (analogous to taxa) by their shared taxa (analogous to characters) according to the concept of parsimony. Data consist of area/taxon matrices and the resulting cladogram(s) represent nested sets of areas.

5.2.3 *The role of molecular data in biogeography*

The use of DNA molecular data in biogeography commenced in the 1990s with a broad range of organisms under study (Sytsma, 1990; Clegg and Durbin, 1990; van Balgooy *et al.*, 1996; Sang *et al.*, 1997; Sytsma and Hahn, 1997; Katinas and Crisci, 2000). The comparison of DNA sequences allows relationships to be estimated among organisms (Martin and Dowd, 1991). When a change in comparative sequences is shared by two or more taxa, this is considered evidence that they may be related. Molecular techniques have not yet been used extensively for palms (Lewis *et al.*, 2000). Some of the more significant studies of palms using molecular methods are presented in Table 5.2. Results of molecular studies are in most cases congruent with studies based on other methods.

Table 5.2. Palm studies in which molecular techniques have been used.

taxon	reference
Arecaceae (general)	Uhl *et al.* (1995)
	Anzizar *et al.* (1998)
	Baker *et al.* (1999)
	Asmussen *et al.* (2000)
	Asmussen and Chase (2001)
	Lewis and Doyle (2001)
Calamoideae	Baker *et al.* (2000a, 2000b)
	Baker and Dransfield (2000)
Arecoideae	Asmussen (1999)
Carpentaria acuminata	Shapcott (1998)
Caryota	Hahn and Sytsma (1999)

5.3 Regional histories

The geological history of the landmasses on which the genus *Livistona* presently occurs is very complex (Axelrod and Raven, 1978; Griffiths, 1993). Evidence suggests that two previously separated landmasses, Laurasia and Gondwana, collided and coalesced over a 100 million year period resulting in intermingling of the different biotas contained on various plates (Hall, 1998). Laurasia is hypothesised to have included present day North America, Europe and Asia, and following division of a former single landmass, Pangaea, came to occupy the Northern Hemisphere. Apart from the separation of North America, the Eurasian section of Laurasia has remained more or less stationary (Schuster, 1976). Gondwana is hypothesised to have included present-day Africa/Arabia, Madagascar, India, Australia, New Caledonia, New Zealand, South America and Antarctica, and following division of Pangaea, came to occupy the Southern Hemisphere. Following the break-up of Gondwana, the separating landmasses moved in different directions leaving Antarctica to eventually assume the most 'southern' position of the rifted fragments. The timing of the break-up of Gondwana and the rifting and drifting patterns and tracks of the component landmasses have provided geologists and biogeographers with a wealth of speculative, experimental and hypothetical scenarios (Axelrod and Raven, 1978; Barlow, 1981; Veevers, 1991; Hall, 1998; Morley, 1998; Frakes, 1999). Evidence suggests that most landmasses, of both Laurasian and Gondwanan origin, have occupied, more or less, their present positions since the early Pliocene, i. e. for at least 5 My (Hall, 1998).

The effects on plant distribution of glacial/interglacial cycles and the associated eustasy during the Quaternary, must be considered (Williams *et al.*, 1993). Australia and New Guinea would have been connected during glacial events (Doutch, 1972), and most extant Sunda and Sahul shelf islands would have been either connected or the distances between them would have been less than at present (Hall, 1998). The Horn of Africa and the southern Arabian Peninsula were part of the former Afro-Arabian Shield which was part of the larger ancestral Indian Plate (Bayer, 1984). Following separation from Gondwana in the early Tertiary, c. 60-70 Mya, the India Plate passed by 'rapidly' in its northward passage (Pilger and Rösler, 1976; Braithwaite, 1987). Schuster (1976) considered that the

paucity of the Indian flora is related to the rapid speed of the movement of the Indian Plate as it moved into different latitudes, thus wiping out biotic elements that could not adjust to changes in climate.

According to Chapman (1978), rifting in the then still intact Afro-Arabian landmass commenced in the mid- Tertiary, eventually forming the Red Sea and thus separating Arabia and Africa. In Yemen, the Hadhramawt Plateau [mentioned here in relation to the distribution of *Livistona carinensis*], is a stable area of Precambrain rocks overlaid in part by upper Cretaceous and Tertiary volcanic rocks that have not experienced marine incursions.

Within the Present stage, the impact of regionalised changes in climate patterns (Bowler *et al.*, 1976; Rull, 1998), and the effects of humans on plant dispersal must be considered (Moore, 1977; Dransfield *et al.*, 1984; Marshall, 1988; Cann and Lum, 1996; Wright and Lees, 1996).

5.3.1 *Biogeography in the South-east Asian/Australasian region*

The historical biogeography of the South-east Asian-Australasian region has been addressed by many researchers. Hooker (1860) provided the basis for subsequent studies, recognising three distinct elements in the Australasian flora: a southern element with related representatives in Africa, Australia, New Zealand and South America; a northern element with nearest relatives in south-eastern Asia; and an autochthonous element composed mainly of endemics with limited inter-regional relationships. The works of Wallace (1860, 1890, 1893) provided much of the basis for modern biogeographic interpretations of south-eastern Asia and Malesia. Wallace recognised geographical disjunctions between biological groups within this region and hypothesised that unrelated organisms occurred in adjacent regions on either side of a line running from between Bali and Lombok, between Borneo and Sulawesi and the Philippines and the Moluccas (Fig. 5.1). Wallace recognised distinct boundaries separating areas with different evolutionary histories and relationships. Although based on the fauna, 'Wallace's Line', a term first used by Huxley (van Oosterzee, 1997), can also be applied to the flora, although the demarcation is not as precise, largely because of the different reproductive and dispersal strategies adopted by plants compared to animals. The validity of

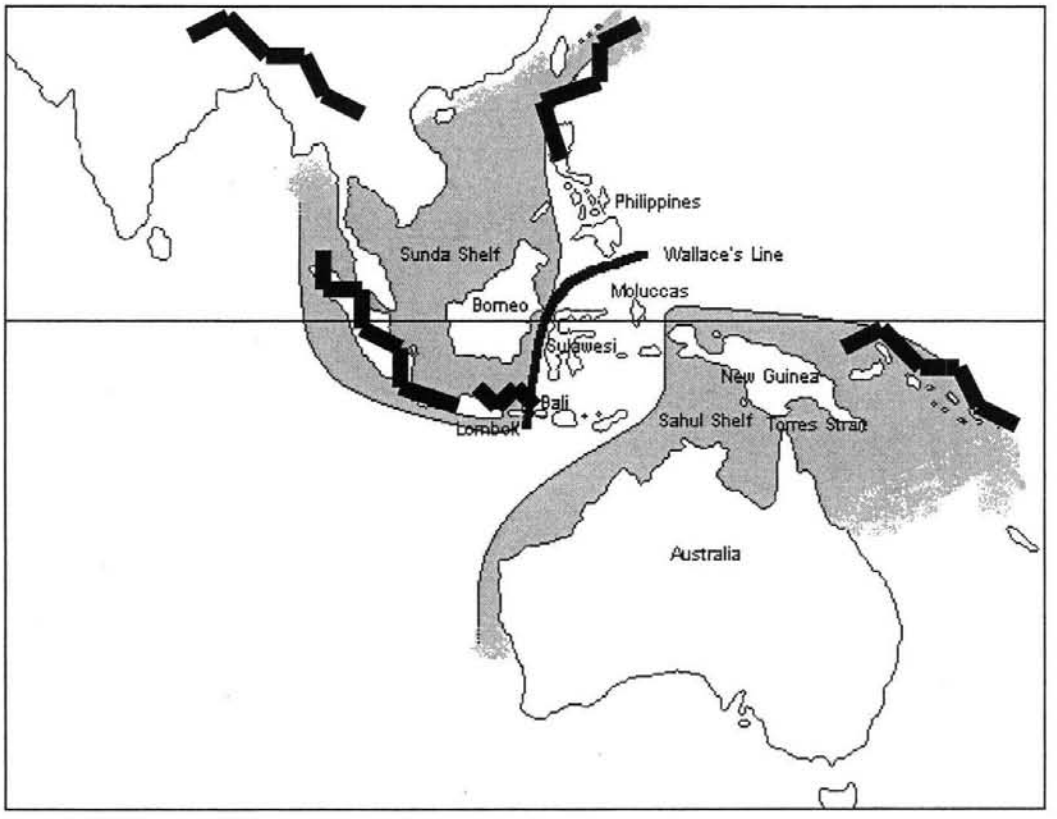


Figure 5.1. The main volcanic and mountain building areas of south-eastern Asia and Australasia. The light grey areas indicate the approximate positions of the Sunda and Sahul Shelves. A solid black line marks Wallace's Line and thick blocked lines indicate mountain building and volcanic areas. Adapted from van Oosterzee (1997).

Wallace's Line has been investigated by many researchers in recent times (Rosen, 1988). Aside from minor alterations involving areas such as Sulawesi and the southern Philippines, the biotic demarcations suggested by Wallace have generally maintained their integrity despite critical assessment (Michaux, 1991). Although the geology of the area was only recently resolved, it has been found that most biotic disjunctions correspond with geological disjunctions (Moss and Wilson, 1998).

Contemporary biogeographers have accepted the existence of biotic boundaries, in particular that of the Australian/Asian boundary, and have subsequently attempted to establish the time-frame in which dispersion, establishment and evolution of the floras have occurred (Burbidge, 1960; van Steenis, 1961, 1979; Barlow, 1981; Webb *et al.*, 1986; Truswell, 1990, 1993; Keast, 1996; Holloway and Hall, 1998;

Morley, 1998; Crisp *et al.*, 1999). Biogeographers have invoked syntheses of geology, climatology and biology in an attempt to summarise the situation in south-eastern Asia/Australia/south-western Pacific region (Keast and Miller, 1996; Holloway and Hall, 1998; Frakes, 1999). The region is best considered as a mosaic of continental fragments and volcanic intercepts, having originated from different sources and at different times. The history of biotic evolution is therefore closely related to geological and climatological processes.

Many theories have been proposed for the 'dispersability' of plant groups. Phenomena such as land-bridges (van Steenis, 1961; Smith 1963) and sunken continents (Carlquist, 1996) have been invoked to account for dispersal across large oceanic distances. For those plant groups with very limited dispersal abilities, Holloway and Hall (1998) suggested that they had been "captured by their terranes" and subsequently confined to *in situ* evolution.

It is accepted by many biogeographers that consistent biotic dispersal from Malesia into Australia began to take place during the early Miocene (c. 20 Mya), and since that time successive migrations have been periodically enhanced or curtailed by climate change and changes in sea-levels (Keast, 1996; Morley, 1998). The major line of dispersion has been through the Moluccas and New Guinea (Holloway and Hall, 1998), with an extant major demarcation across Torres Strait (Webb and Tracey, 1972; van Steenis, 1979). The dispersion has been primarily one way, as ecological factors appear to have prevented Australian elements from establishing in Malesia to the same degree that Malesian elements established in Australia (Hoogland, 1972; Keast, 1996; Morley, 1998). However, this is still open to debate.

5.3.2 *Biogeography of the Afro-Arabian area*

The biogeography of the Afro-Arabian area has not been investigated as extensively as that of the south-eastern Asian region, as evidenced by the paucity of available literature. Nevertheless, it has been hypothesised that the extant regional flora has a large number of endemics predominantly of African affinity. There is an exceptionally high number of taxa presumed to be relicts of a once more widespread flora, and a high rate of extinction occurred during the

Quaternary due to climate change (Wickens, 1977; Axelrod and Raven, 1978; Lovett, 1993).

5.4 Environmental change

It is apparent that the rates of geological processes, climate change and evolutionary processes are not in alignment (Parsons, 1988). Organisms are therefore required to constantly adapt to changing environmental conditions. In rapidly changing environments, extinctions occur faster than new species are able to evolve (Briggs, 1999). Given that organisms can only respond to changes in a more or less reactionary manner, plant dispersal and migrations are therefore influenced by land-sea relationships and climate changes (Hope, 1996). Dispersal barriers that developed in Malesia were the result of an increase in seasonal drought, a smaller total land surface due to rising sea-levels and the island nature of much of the area (van Steenis, 1979). Rising sea-levels which resulted in the separation of Australia from New Guinea, have been implicated in some vicariant events involving plants now found in both these areas (Nix and Kalma, 1972; Crisp *et al.*, 1995).

By the end of the Tertiary and the beginning of the Quaternary, most parts of the earth's crust were relatively stable but the climate was changing due to external influences such as solar orbital imbalances and global rotational oscillations (House, 1995). There is considerable evidence of climate change during the Quaternary, primarily related to glaciation/interglacial cycles and eustatic variation (Bowler *et al.*, 1976; Ladd, 1978; Loope, 1995). Based on the fossil evidence, glacial periods can be identified by an expansion of sclerophyll vegetation, and interglacials by the expansion of rainforest angiosperms (Hope, 1996). In the tropical regions of Australasia, temperatures during the Pleistocene/Holocene were cooler by up to 6-7°C at high altitude, 4-5°C in the lower montane zones, but relatively unchanged at near sea-level with an estimated decrease of no more than 1.5°C (Hope, 1996). A similar situation has been found in north-eastern Africa and southern Arabia. Fossils indicate the past occurrence of moist forest in present-day arid northern Africa (Lovett, 1993). During the Oligocene and by the mid Miocene, aridity had spread to many of the areas previously covered by lowland equatorial rainforest in Africa (Said, 1981). There

is evidence that substantial areas of gallery rainforest persisted throughout north-eastern Africa into the Holocene despite the increasing aridity and fluctuations brought by the glacial/interglacial cycles. Many present-day relictual species appear to have had their origins in these gallery forests (Wickens, 1977). In the equatorial zones of eastern Africa, temperatures and the monsoonal climate regime remained stable during the last glacial/interglacial period and low altitude forest was not substantially affected by climate change. During the last interglacial, rainfall was estimated to be 125%-135% higher than at present (Lovett, 1993).

5.5 Biogeography of palms

A summary of major biogeographic studies of palms is presented in Table 5.3. Apart from the most recent accounts, many of which have an analytical approach incorporating cladistic and molecular techniques or both, studies were based on descriptive or narrative methodologies utilising morphological investigations. Moore (1973a) hypothesised that the palms arose in west Gondwana and radiated rapidly from there to other areas. Diversity was achieved very early in the evolution of the family, although extant groups display considerable convergence and parallelism at most levels of anatomy, morphology, ecology and function (Moore and Uhl, 1982).

Table 5.3. Major biogeographic studies of palms.

taxon/area	reference
Arecaceae (general)	Moore (1973a, 1973b)
	Uhl and Dransfield (1987)
Malesia	Dransfield (1981,1987), Baker *et al.* (1998)
Madagascar	Dransfield and Beentje (1995)
Amazonia	Henderson(1995)
Iriarteinae	Henderson (1990)
Sabal	Zona (1990)
Phytelephantoideae	Barfod (1991)
Cryosophila	Evans (1995)
Greater Antillian *Bactris*	Salzman and Judd (1995)
Caryota	Hahn and Sytsma (1999)
Calamoideae	Baker and Dransfield (2000)

Fernando (1990) found that the strongest distributional relationship pattern for palms in the Philippines was for a Philippines-Sundaic-Celebes affinity. However, other levels of affinity may be construed from the same data. A reassessment of his data at the genus level (Dowe, unpublished data) indicated a strong affinity of the Philippine species of *Livistona* to those in eastern Malesia. The biota of the Philippines can be interpreted as a composite of affinities of most nearby ancestral areas, and with subsequent low endemism.

Dispersal through time has been investigated in only one species to date. The origin of northern populations of *L. chinensis* (as *L. chinensis* var. *subglobosa*), in the Ryukyu Islands and southern Japanese islands, was investigated by Yoshida *et al.* (2000). Using RAPD analysis, they concluded that the spread of ancestral populations was in a northerly direction through the Ryukyu Islands to islands near Kyushu. The value of the genetic distance they found between the most southern and most northern populations suggested an age difference between the populations of c. 1.25 million years.

5.5.1 *Palm fossils*

Determination of the affinity of palm fossils to extant species must be treated cautiously (Dransfield, 1987). Fossils, of purported affinity to *Livistona* (hereafter referred to as *Livistona*-affinity fossils) have been reported from late Cretaceous and Tertiary deposits at numerous and widespread locations in the Northern Hemisphere (Read and Hickey, 1972; Moore, 1973a; Muller, 1981; Batten, 1984; Uhl and Dransfield, 1987).

In Australia, the oldest fossil palm pollens are from late Cretaceous deposits and they have been assigned to *Nypa* or its putative progenitors (Churchill, 1973; Greenwood and Conran, 2000). *Nypa* has a distinctive globose to elliptical meridionosulcate, or alternatively termed zonasulcate (Harley and Baker, 2001), pollen distinguished by prominent pointed spines emergent from the exine (Ambwani and Kumar, 1991; Uhl and Dransfield, 1987). Pole and Macphail (1996) identified fossil fruits of *Nypa* from the Eocene deposits of western Tasmania, thus illustrating the once widespread distribution in southern Australia of this species. Numerous other pollens have been identified as palms or palm-

relatives, but very few have been assigned to extant taxa. The most common fossil palm pollens are globose to ellipsoid monosulcate forms with a reticulate exine, a type that is widespread throughout the family (Milne, 1988; Harley and Baker, 2001). In many cases it is difficult to assign pollen of extant species, let alone fossil pollen, even to the tribal level. The monosulcate pollen type to which *Livistona* conforms, occurs throughout the palm family, and pollen of most genera in the Coryphoideae is undifferentiated (Harley *et al.*, 1991). Most of the Australian fossil palm pollens are classified under the form genus *Arecipites* (Hekel, 1972). It is possible that this form includes *Livistona* and its ancestors. These pollens first appeared in the early Paleocene in Central Queensland, and the Eocene in Tasmania, Victoria and South Australia, and from that time appear more or less continuously up to the Quaternary (Lange, 1982; Truswell and Marchant, 1986; Martin, 1990; Macphail *et al.*, 1993). This indicates that palms were present in relative abundance on the ancestral Australian landmass at times prior to supposed south-east Asian contact (Greenwood and Conran, 2000). Although there are macrofossils of Arecoid palms such as *Archontophoenix* and *Linospadix* from the Eocene/Oligocene (Greenwood and Conran, 2000), there are no *Livistona*-like macrofossils yet identified from Australian, south-east Asian or Malesian sites. Leaves and associated stems of a putative *Livistona*-affinity fossil taxon designated as *Sabalites ooaraiensis* Oyama and Matsuo have been found in upper Cretaceous to Oligocene deposits in eastern China, Manchuria and Japan (Ôyama and Matsuo, 1964; Tong, 1994).

5.5.2 Some problematic distributions

Dransfield (1981) considered the distribution of palms in relationship to Wallace's Line and concluded that many genera followed the expected distribution, i. e. genera were confined to either side of the line. However, Dransfield (1981) cited a number of problematic genera, which included *Livistona,* that had more or less equal distribution either side of Wallace's Line. Corner (1966) and Dransfield (1987) suggested that *Livistona* was of Asian origin and that the diversity in Australia was due to 'recent' migration and subsequent speciation forced by climate change. A similar pattern has been suggested for some elements of the Australian palm flora (Jones, 1996; Dowe, 1995a, 1995b), although the situation with *Livistona* was inconclusive.

Uhl and Dransfield (1987) concluded that the subtribe Livistoninae had a Northern Hemisphere origin. However, they acknowledged the presence of a number of problematic distributions on isolated islands in the Southern Hemisphere, and the anomalous abundance of some genera in the Papuasian/Australian region. The disjunct distribution of *Copernicia* species in South America, a genus otherwise showing the highest diversity in the Caribbean basin but also with species in southern South America, was explained by Pleistocene climate change (Uhl and Dransfield, 1987). Considerable disjunctions also occur between closely related genera such as *Colpothrinax* in Cuba and *Pritchardia* in Hawaii and other Pacific islands to as far west as Fiji, and *Pritchardiopsis* on New Caledonia.

5.6 Aims

This chapter aims to investigate the historical patterns of distribution and radiation in *Livistona* with reference to:

- the fossil record
- distributional relationships of species occurring in the biogeographic regions outlined by Takhtajan (1986) and Cracraft (1991)
- biogeographical relationships of species inferred from cladistic analysis.

5.7 Materials and methods

5.7.1 *Distribution*

The extant distribution of *Livistona* species was determined from herbarium labels, field-work undertaken in Australia, Papua New Guinea, Thailand, Malaysia and the Philippines, and the literature, primarily Beccari (1931), Moore (1973a) and Rodd (1998). Distributional status, i.e. isolated or co-occurring, for each species was determined from the distribution data.

5.7.2 *Fossils*

The historical distribution of *Livistona* was determined from the available fossil record. Searches for fossils with possible *Livistona*-affinity were initiated at the following Australian institutions: Vertebrate Palaeontology and Palaeobotany Museum Victoria, Melbourne; School of Botany, University of Melbourne;

Clarke Geology Museum, University of Western Australia, Perth; Western Australian Museum, Perth; Australian Museum, Sydney; South Australia Museum, Adelaide; University of Adelaide, Adelaide; Department of Botany, University of Queensland, St Lucia. Other distributions were determined from the literature.

5.7.3 *Parsimony Analysis of Endemicity (PAE)*

To determine the relationships between the areas in which *Livistona* species occur, analyses based on the PAE methods of Rosen and Smith (1988) and Vega *et al.* (1999) were performed. The PAE method groups areas (analogous to taxa) by their shared taxa (analogous to characters) according to the concept of parsimony. Data are presented in matrices in Table 5.4. The analysis was performed using PAUP version 4.0b8a written by D. L. Swofford. In the PAE matrix, absence is scored as '0' and presence as '1'. Two analyses were performed:

1. utilising Takhtajan's (1986) floristic regions in which *Livistona* occurs
2. utilising Cracraft's (1991) areas of endemism for the Australian and southern New Guinea species of *Livistona*.

5.7.4 *Cladistics*

The phylogeny for *Livistona*, presented in Chapter 3, Figure 3.19, was utilised to investigate the relationships of species occurring in different areas. On the cladogram taken from Figure 3.19, distribution areas for species were aligned with the appropriate taxon. Maps are provided with the distribution of lineages and subclades.

5.7.5 *Morphological adaptation*

Aspects of adaptation such as the relationships between leaf venation patterns, stomatal morphologies and densities, and climate, were investigated as a pilot study. As these aspects did not provide a direct contribution to the development of the biogeographic hypotheses, they are not discussed here. The data are presented in Appendices15-19 as they may offer a basis for future research.

Table 5.4. Data matrices for area cladograms. **a.** Floristic regions of Takhtajan (1986) where species of *Livistona* are reported. **b.** Areas of endemism of Cracraft (1991) in Australia and southern New Guinea where species of *Livistona* are reported. 0 = absence; 1 = presence.

a.

	1 1111111112 2222222223 3333
	1234567890 1234567890 1234567890 1234
outregion	0000000000 0000000000 0000000000 0000
east Asiatic	0000101000 0000000000 0000000000 0000
Sudano-Zambesi	0000010000 0000000000 0000000000 0000
Indian	0000000000 0000001000 0000000000 0000
Indochinese	0000000000 0000001000 0000000010 0000
Malesian	0011000000 0110001100 0110010111 1101
north-east Australian	0101000111 1001110011 0011101000 0010
central Australian	1000000000 0000000000 1000001000 0010

Species identified by number on upper two lines, as follows: 1, *L. alfredii*; 2, *L. australis*; 3, *L. beccariana* (= *L. woodfordii*); 4, *L. benthamii*; 5, *L. boninensis*; 6, *L. carinensis*; 7, *L. chinensis*; 8, *L. concinna*; 9, *L. decora*; 10, *L. drudei*; 11, *L. eastonii*; 12, *L. endauensis*; 13, *L. exigua*; 14, *L. fulva*; 15, *L. humilis*; 16, *L. inermis*; 17, *L. jenkinsiana*; 18, *L. chocolatina*; 19, *L. lanuginosa*; 20, *L. lorophylla*; 21, *L. mariae*; 22, *L. merrillii*; 23, *L. muelleri*; 24, *L. nasmophila*; 25, *L. nitida*; 26, *L. papuana*; 27, *L. rigida*; 28, *L. rotundifolia*; 29, *L. saribus*; 30, *L. surru*; 31, *L. tahanensis*; 32, *L. tothur*; 33, *L. victoriae*; 34, *L. woodfordii*.

b.

	1 11111111
	1234567890 12345678
outregion	0000000000 00000000
Pilbara	1000000000 00000000
Kimberley Plateau	0000001000 01001001
Arnhemland	0010000011 00000010
northern desert	0000000001 00000010
Cape York Peninsula	0011000000 00010000
Atherton	0101010000 00010000
eastern Queensland	0100110100 10000100
south-eastern forests	0100000000 00000010
central Australia	0000000000 00100000
New Guinea	0010000000 00010000

Species identified by number on upper two lines, as follows: 1, *L. alfredii*; 2, *L. australis*; 3, *L. benthamii*; 4, *L. concinna*; 5, *L. decora*; 6, *L. drudei*; 7, *L. eastonii*; 8, *L. fulva*; 9, *L. humilis*; 10, *L. inermis*; 11, *L. lanuginosa*; 12, *L. lorophylla*; 13, *L. mariae*; 14, *L. muelleri*; 15, *L. nasmophila*; 16, *L. nitida*; 17, *L. rigida*; 18, *L. victoriae*.

5.8 Results

5.8.1 *Distribution*

The extant distribution of *Livistona* based on herbarium records and literature references is presented in Figures 5.2 and 5.7. Distribution status is presented in Table 5.5. With regards to distributional types, 19 species (54%) are isolated, i. e. there are no other species occurring within a range limit that could be expected to allow present genetic exchange. Sixteen species (46%) co-occur with one other species; of these, 12 species co-occur with more than one species.

5.8.2 *Fossil record*

Examples of fossils of *Livistona*-affinity are presented in Table 5.6 and fossil taxa putatively related to *Livistona* are presented in Table 5.7. *Livistona*-affinity fossil sites are indicated on the map in Figure 5.3. A time-scale featuring the historical biogeography of *Livistona* is presented in Figure 5.4.

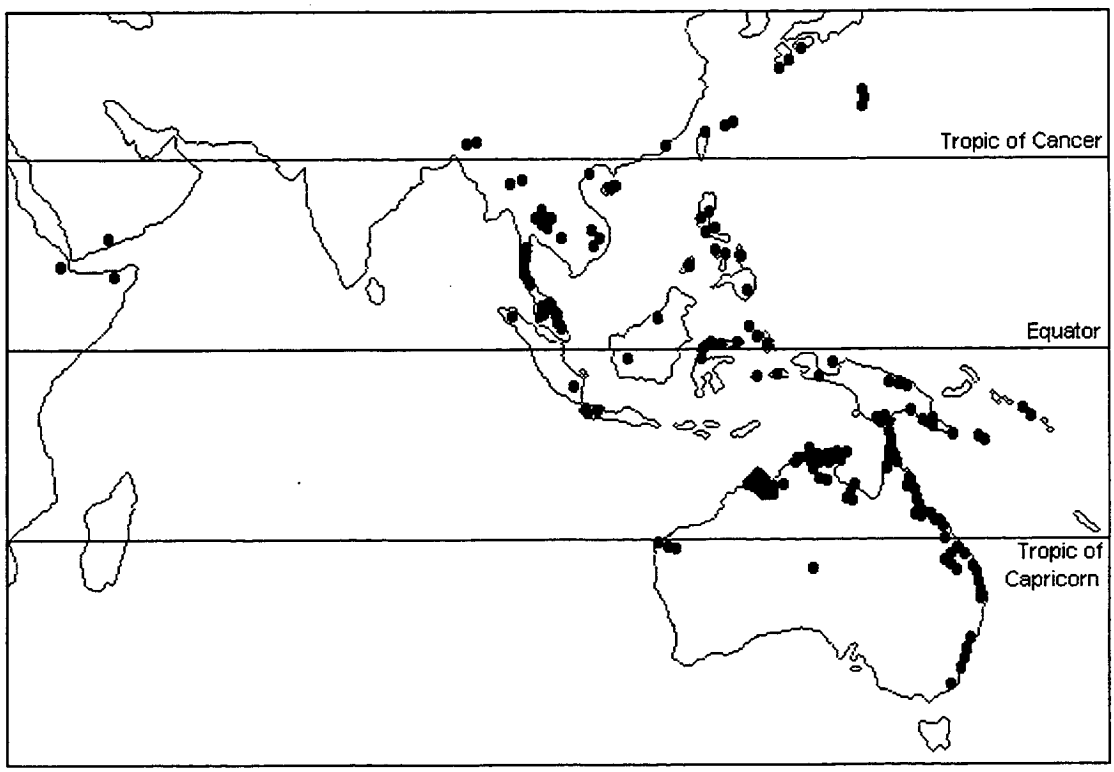


Figure 5.2. Extant distribution of *Livistona*. Distribution data are based on the citations that accompanied the c. 400 herbarium specimens that were examined as part of this thesis, and included in the 'specimens seen' section in Chapter 2.

Table 5.5. Distribution status of *Livistona* species determining isolated or co-occurring species. 'Isolated species' implies that species distribution is out of the range of potential genetic exchange of other species. 'Co-occurring species' implies that species distribution is within the range of potential genetic exchange of one or more species.

isolated species

L. alfredii
L. boninensis
L. carinensis
L. chinensis
L. chocolatina
L. endauensis
L. exigua
L. fulva
L. halongensis
L. lanuginosa
L. mariae
L. nitida
L. papuana
L. rigida
L. surru
L. tahanensis
L. tothur
L. victoriae
L. woodfordii

co-occurring species pairs

L. benthamii - L. muelleri
L. concinna - L. muelleri
L. decora – L. australis
L. drudei – L. australis
L. eastonii - L. lorophylla
L. jenkinsiana - L. saribus
L. humilis – L. inermis
L. merrillii – L. rotundifolia
L. nasmophila – L. lorophylla
L. robinsoniana – L. merrillii

co-occurrence of three species

L. australis, L. decora, L. drudei
L. benthamii, L. humilis, L. inermis
L. eastonii, L. lorophylla, L. nasmophila
L. rotundifolia, L. merrillii, L. saribus

5.8.3 *Regional distribution and area cladograms*

Biogeographic regions of Takhtajan (1986) and Cracraft (1991), in which *Livistona* species occur, and the biogeographic regions with their component species, are listed in Table 5.8 and Table 5.9 respectively. The area cladograms based on the PAE method are presented in Figure 5.5. The application of these two cladograms onto a map is presented in Figure 5.6.

5.8.4 *Cladistics*

A cladogram, derived from the cladistic analysis in Chapter 3 (Fig. 3.19), with distributional data applied, is presented in Figure 5.7. The placement of lineages and subclades on to maps is presented in Figures 5.8, 5.9, 5.10 and 5.11.

Table 5.6. Examples of fossils of *Livistona*-affinity.

fossil organs	age/epoch	locality	reference
leaf	late Cretaceous	New Jersey	Daghlian, 1978, 1981
leaf	late Cretaceous	Japan	Ôyama and Matsuo, 1964
leaf	Tertiary	Central Europe	Bruder (1890)
pollens	late Cretaceous	Canada	Janzen, 1978
fruits	Eocene	England	Reid and Chandler, 1933
			Chandler, 1964, 1978
stems	Eocene	South India	Ramanujam, 1953
			Prakash & Ambwani, 1980
stems	Quaternary?	Australia	WA Museum (WAM P90.7)
hastula/petiole	Eocene	India	Kulkarni and Patil, 1977

Table 5.7. Fossil taxa described for *Livistona* or with affinity to *Livistona*.

Livistona eocenica Ett. & Gard. (1879). Fruits from Sheppey, United Kingdom, Eocene. = *Hightea elliptica* Bowerb. (Reid and Chandler, 1933).

Livistona macrophylla Bruder (1890). Described from central Europe, Tertiary.

Livistona minima Reid and Chandler (1933). Fruits from Sheppey, United Kingdom, Eocene.

Palmoxylon arcotense Ramanujam (1953). Stem portions described from India, Tertiary (?).

Palmoxylon livistonoides Prakash and Ambwani (1980). Stem portions described from India, Eocene.

Sabalites chinensis Endô (1934). Leaf described from Manchuria, Paleogene.

Sabal nipponicus (Kryshtofovich) Endô (1934). Leaf described from Japan, Palaeogene.

Sabalites ooaraiensis Ôyama and Matsuo (1964). Leaf and petiole portions described from Japan, Paleogene.

Sabalites taishuensis Takahashi (1958). Leaf described from Japan, Palaeogene.

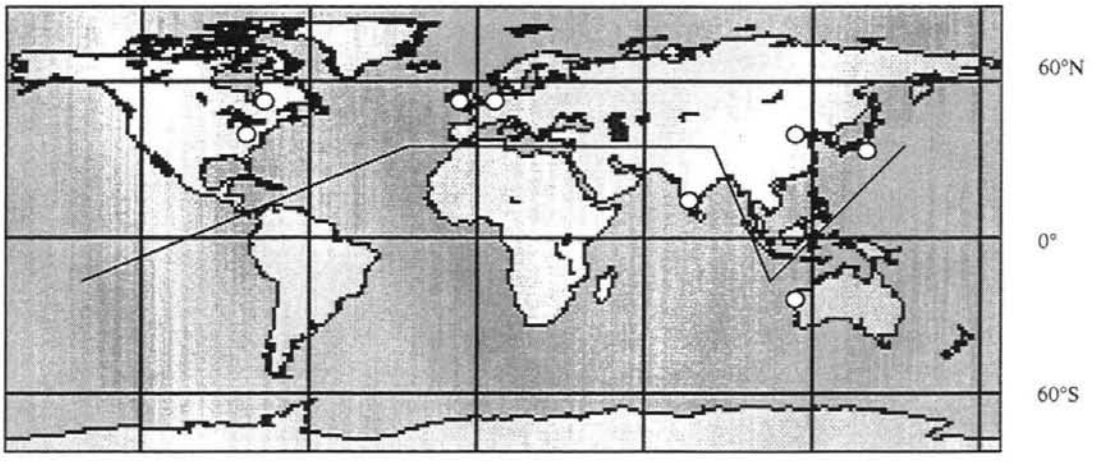


Figure 5.3. Sites of *Livistona*-affinity fossils. A white circle indicates collection sites. For details of sites refer to Tables 5.6 and 5.7. A line marks the approximate boundary between landmasses of Laurasian (north of the line) and Gondwanan origin (south of the line).

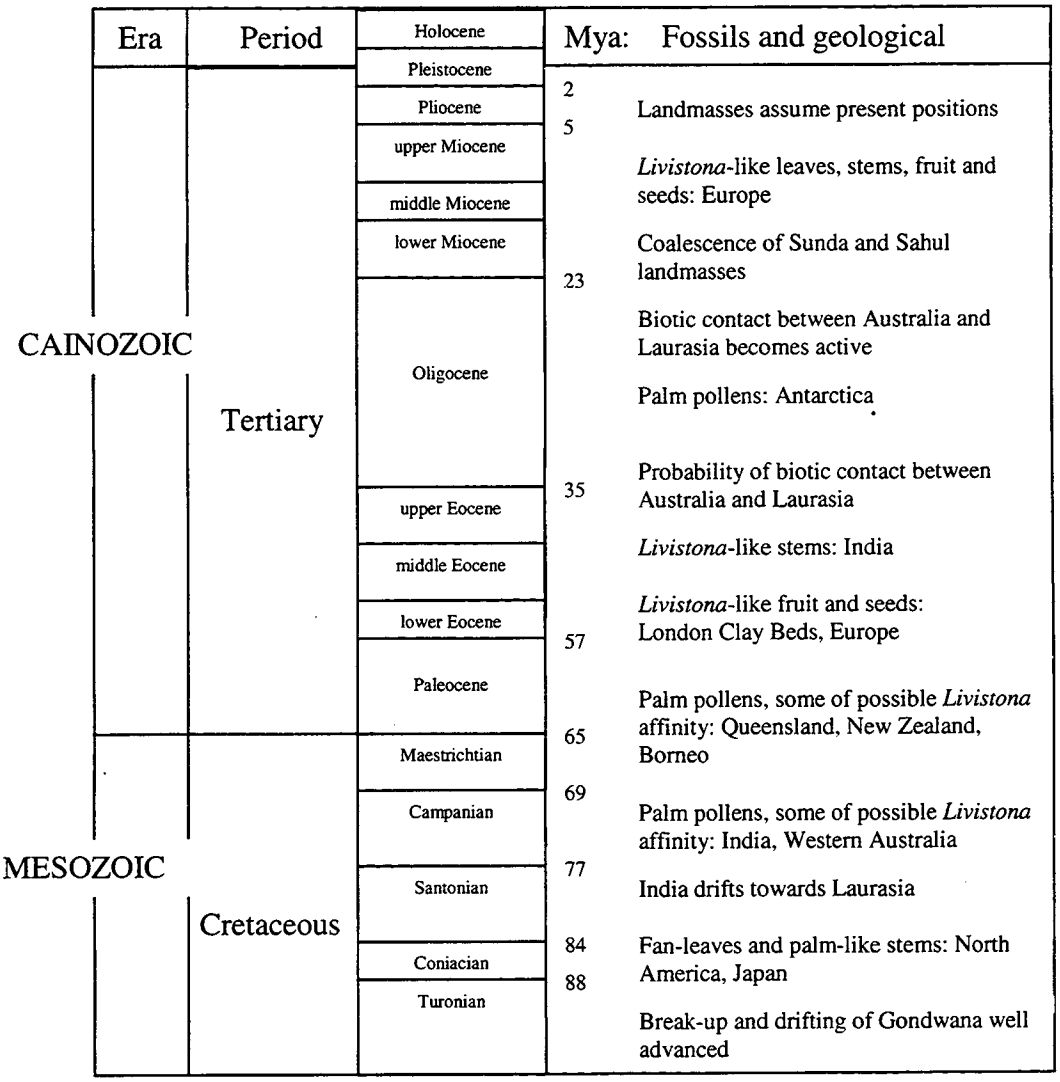


Figure 5.4. Geological timescale with fossil and geological events relevant to the historical biogeography of *Livistona*. Adapted from Holloway and Hall (1998).

Table 5.8. Biogeographic regions proposed by Takhtajan (1986), and areas of endemism by Cracraft (1991), in which *Livistona* species have been recorded.

Takhtajan	Cracraft
Eastern Asiatic region	Pilbara
Sudano-Zambesian region	Kimberley Plateau
Indian region	Arnhemland
Indochinese region	Northern desert
Malesian region	Cape York Peninsula
North-east Australian region	Atherton
Central Australian region	eastern Queensland
	south-eastern forests
	Central Australia
	New Guinea

Table 5. 9. Biogeographic regions and their component species of *Livistona*. Species that occur in more than one region are denoted by an *.

biogeographic region	**species**
(Takhtajan, 1986)	
east Asiatic	*L. boninensis*, *L. chinensis*
Sudano-Zambesi	*L. carinensis*
Indian	*L. jenkinsiana**
Indochinese	*L. jenkinsiana**, *L. halongensis*, *L. saribus**
Malesian	*L. benthamii**, *L. endauensis*, *L. exigua*, *L. jenkinsiana**, *L. chocolatina*, *L. merrillii*, *L. muelleri**, *L. papuana*, *L. robinsoniana*, *L. rotundifolia*, *L. saribus**, *L. surru*, *L. tahanensis*, *L. tother*, *L. woodfordii*
north-east Australia	*L. australis*, *L. benthamii**, *L. concinna*, *L. decora*, *L. drudei*, *L. eastonii*, *L. fulva*, *L. humilis*, *L. inermis*, *L. lanuginosa*, *L. lorophylla*, *L. muelleri**, *L. nasmophila*, *L. nitida*, *L. rigida**
Central Australian	*L. alfredii*, *L. mariae*, *L. rigida**, *L. victoriae**
Cracraft (1991)	
Pilbara	*L. alfredii*
Kimberley Plateau	*L. eastonii*, *L. lorophylla*, *L. nasmophila*, *L. victoriae*.
Arnhemland	*L. benthamii**, *L. humilis*, *L. inermis**, *L. rigida**.
Northern desert	*L. inermis**, *L. rigida**
Cape York Peninsula	*L. benthamii**, *L. concinna*, *L. muelleri**.
Atherton	*L. australis**, *L. concinna**, *L. drudei**, *L. muelleri**
eastern Queensland	*L. australis**, *L. decora*, *L. drudei**, *L. fulva*, *L. lanuginosa*, *L. nitida*
south-eastern forests	*L. australis**
central Australia	*L. mariae*
New Guinea	*L. benthamii**, *L. muelleri**

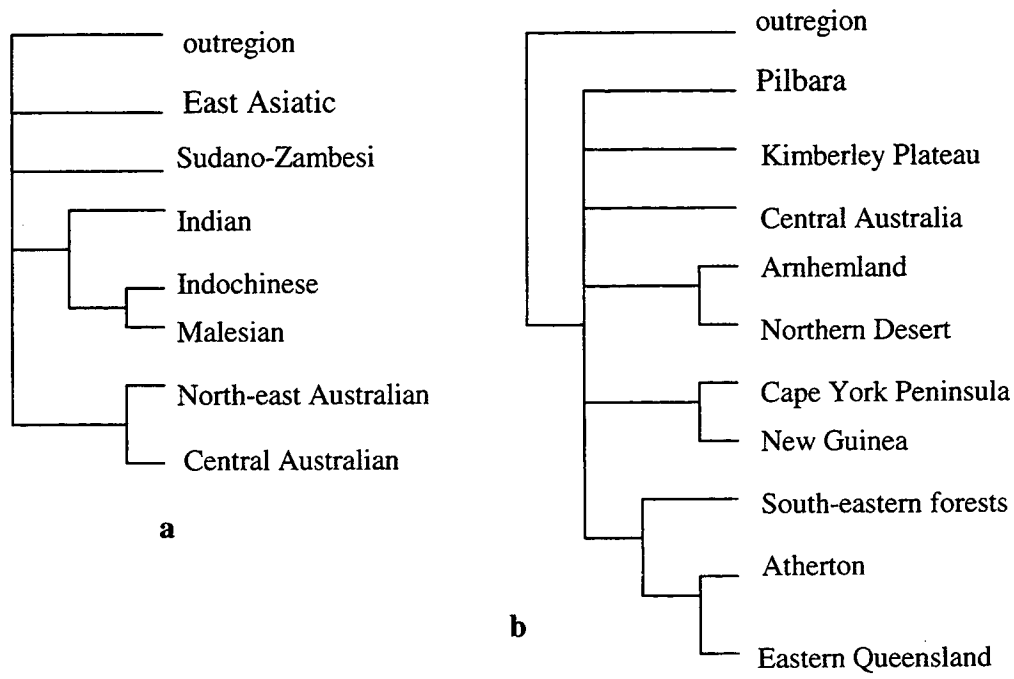


Figure 5.5. Cladograms of the distributional relationships of *Livistona* species within biogeographical areas, using the PAE method. **a**. Floristic regions of Takhtajan (1986). **b**. Areas of endemism in Australia and southern New Guinea of Cracraft (1991).

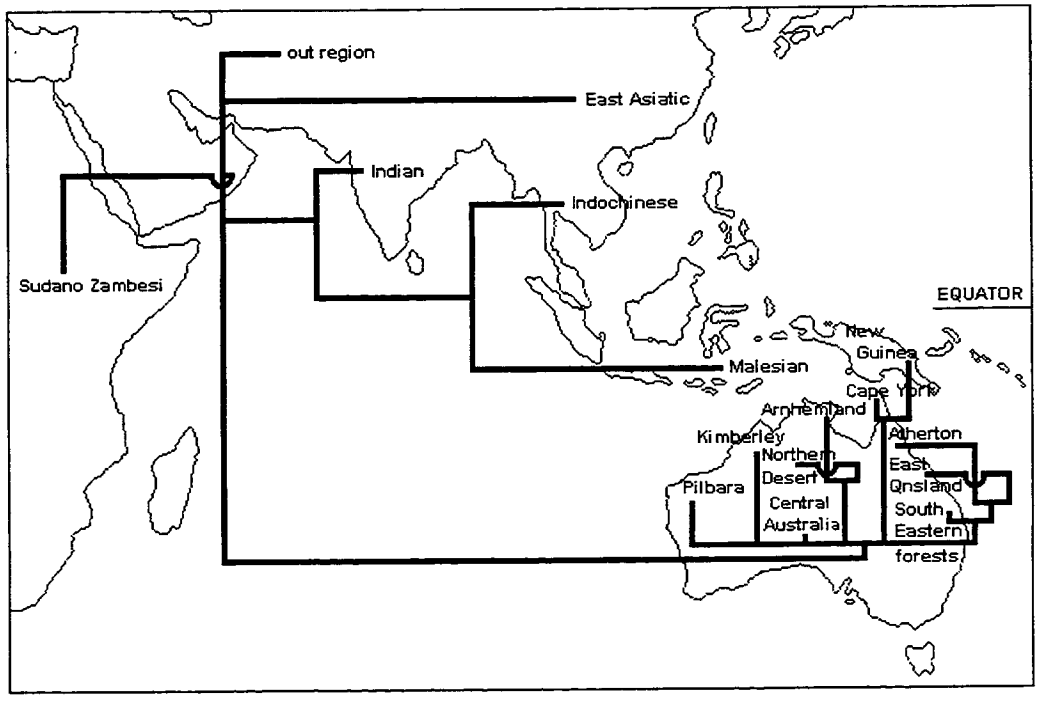


Figure 5.6. The relationships of biogeographic regions in which *Livistona* species occur. Regions are based on Takhtajan (1986) and Cracraft (1991). Takhtajan's North-east Australian and Central Australian regions (Fig. 5.5a) are replaced by Cracraft's regions (Fig. 5.5b) which give greater detail of those two regions.

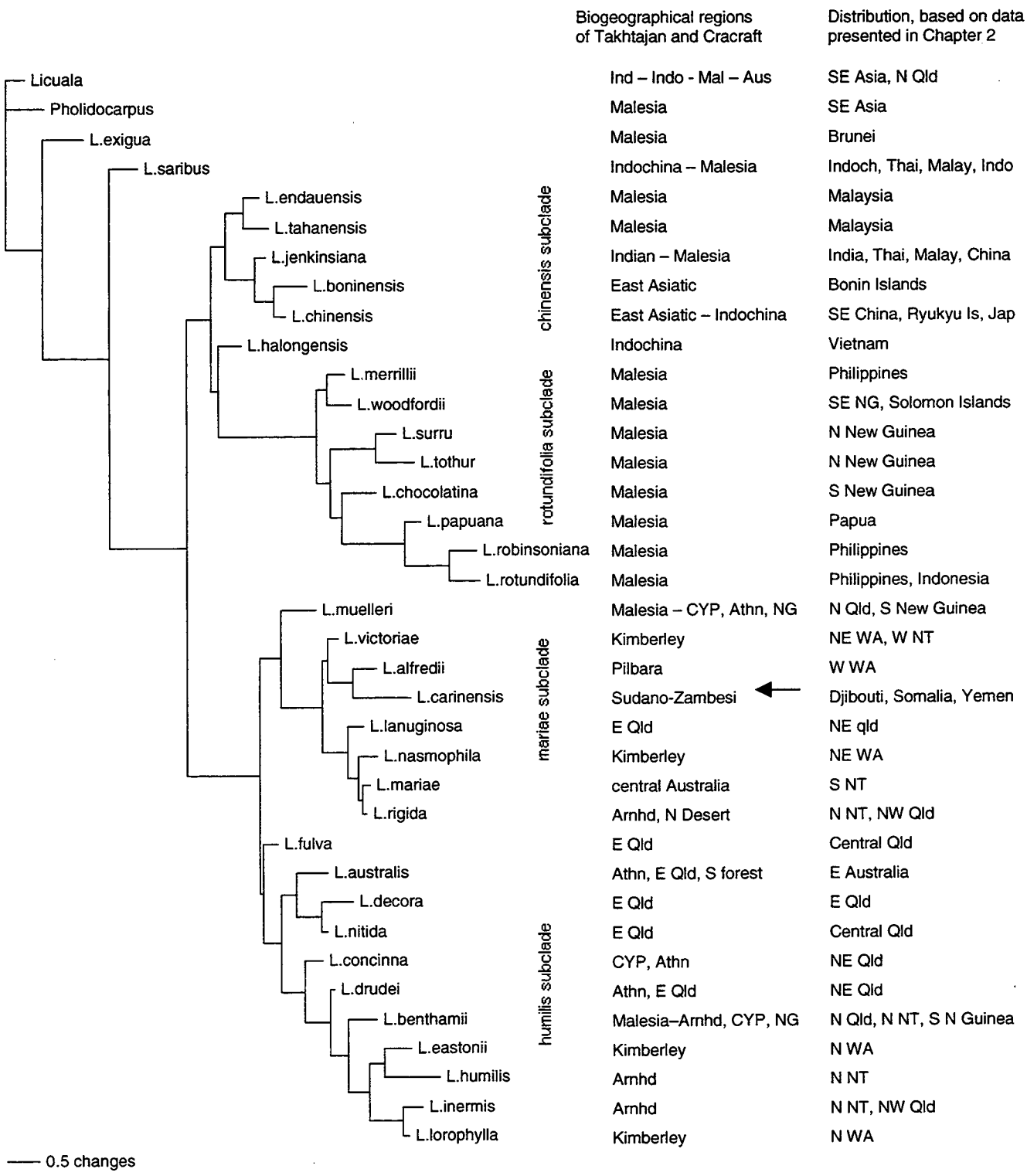


Figure 5.7. Cladogram of *Livistona* taken from cladistic analysis presented in Chapter 3, Figure 3.19. Subclades and taxon distributions are indicated. Abbreviations for biogeographical regions: Arnhd = Arnhemland; Athn = Atherton; Aus = Australian; CYP = Cape York Peninsula; E Qld = Eastern Queensland; Ind = Indian; Indo = Indochinese; Kimberley = Kimberley Plateau; Mal = Malesia; NG = New Guinea; S forest = South-eastern forests. An arrow indicates *Livistona carinensis*.

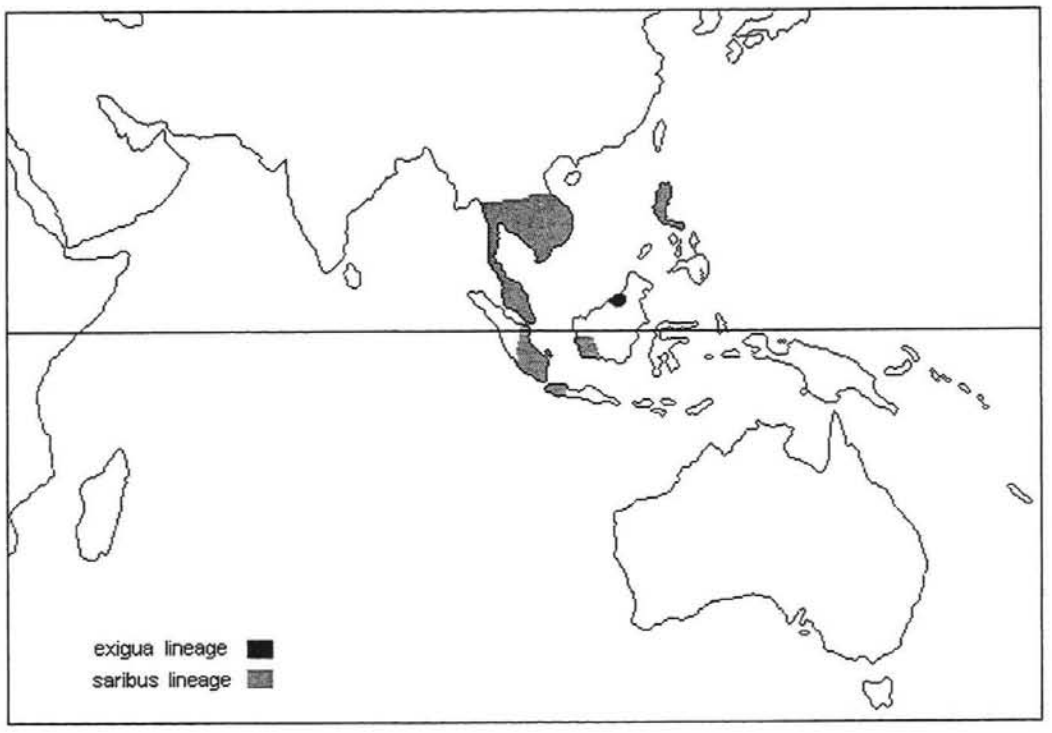


Figure 5.8. Distribution of the *exigua* and *saribus* lineages. Distributional data were taken from Figure 5.7 and Chapter 2, section 2.6.

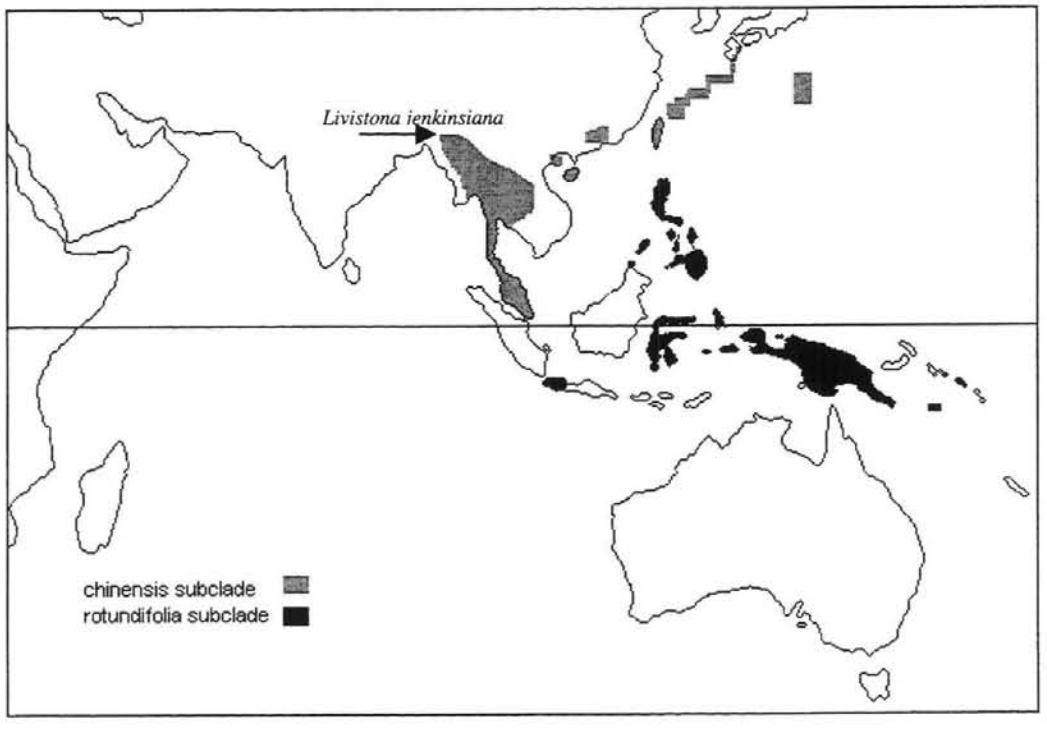


Figure 5.9. Distribution of the *chinensis* and *rotundifolia* subclades. Distributional data were taken from Figure 5.7 and Chapter 2, section 2.6. An arrow indicates the distribution of *L. jenkinsiana* in north-eastern India.

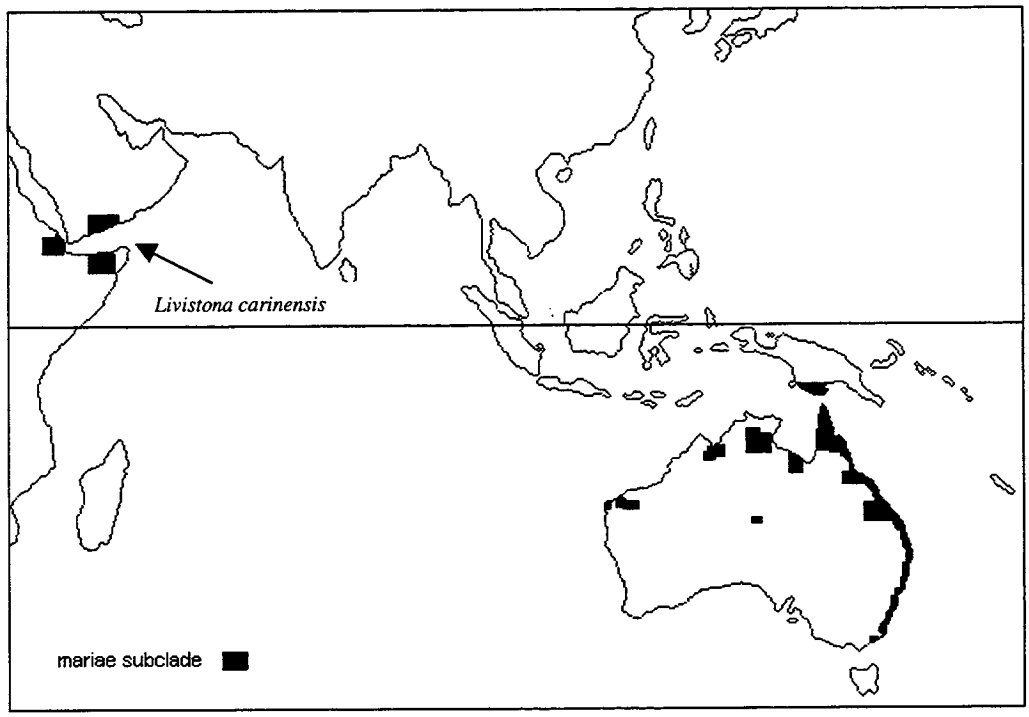


Figure 5.10. Distribution of the *mariae* subclade. Distributional data were taken from Figure 5.7 and Chapter 2, section 2.6. An arrow indicates the distribution of *L. carinensis*.

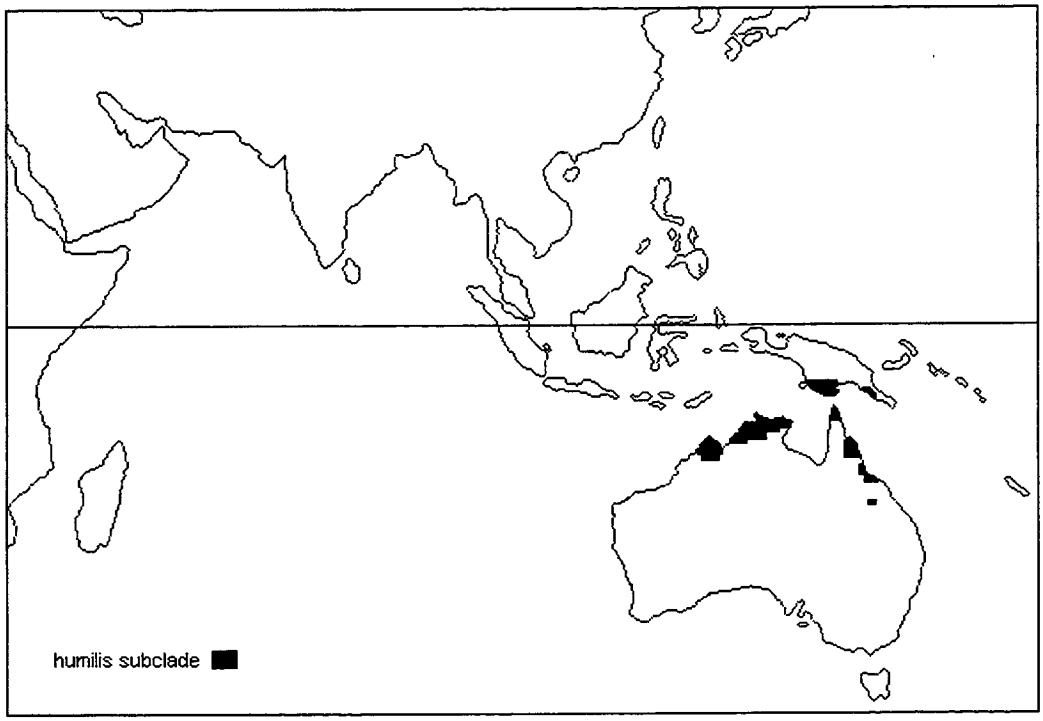


Figure 5.11. Distribution of the *humilis* subclade. Distributional data were taken from Figure 5.7 and Chapter 2, section 2.6.

5.9 Discussion

5.9.1 *Fossils*

Based on the assumption that the ecological requirements of *Livistona* species have not significantly altered over time, the disparity between the occurrence of fossil sites and the extant distribution is indicative of tectonic movements and climate change during the course of evolution of the genus (Figs 5.2, 5.3). The palaeofloras/climates to which *Livistona*-affinity fossils have been assigned [described as tropical or subtropical, or variants (Chaloner and Creber, 1990; Martin 1994; Greenwood, 1994)], generally correspond with the floristic/climatic associations in which extant species occur.

The predominance of *Livistona*-affinity fossils on terranes of Laurasian origin (Table 5.7, Fig. 5.3) supports the view that the genus may have had its rise and early development in the Northern Hemisphere, although the artefacts of biased collection intensity and fossilisation potential must not be overlooked. However, a confounding factor is the presence of *Livistona*-affinity fossils of Eocene age in India (Table 5.7, Figs 5.3, 5.4; Prakash and Ambwani, 1980). During the Eocene, the Indian Plate, a rafting fragment of Gondwana, may still have been relatively remote from Laurasia. This scenario raises a number of questions. Are the Indian fossils correctly attributed to *Livistona*? If not, then the presence of *Livistona* on terranes of Gondwanan origin may well be doubted. If these fossils are correctly attributed to *Livistona*, then *Livistona* may have been part of the Gondwanan flora, thus indicating a distribution on landmasses of both Laurasian and Gondwanan origin, and possibly an initial Pangaean distribution. A third scenario is that the estimated time of biotic exchange between India with Laurasia was earlier than the Eocene and that *Livistona* would have had time to establish on the Indian Plate, after the plate had come into biotic contact with Laurasia. The absence of Tertiary *Livistona* fossils in Australia suggests that the genus is a relatively new arrival to the region, and thus supports a Laurasian origin.

5.9.2 *Distribution and endemism*

Compared to many palm genera, *Livistona* has an extensive distribution (Fig. 5.2), and occurs within a number of distinct and otherwise floristically unrelated biogeographic regions (Table 5.9, Figs 5.5, 5.6).

The area cladogram in Figure 5.5a presents the distributional relationships of *Livistona* species within Takhtajan's biogeographical areas. The cladogram displays four branches: the East Asiatic, Sudano-Zambesi, Indian/Indochinese/ Malesian, and North-east/Central Australian. Although the PAE analysis was unable to resolve the relationships between the four branches, it indicates close affinity of the Indian, Indochinese and Malesian areas, and the North-east Australian and Central Australian regions respectively within two of the branches (Fig. 5.5a). The area cladogram in Figure 5.5b, based on Cracraft's areas of endemism in which *Livistona* species occur, shows relationships between contiguous areas. For example, Arnhemland and the Northern Desert, Cape York Peninsula and New Guinea, and Atherton and Eastern Queensland display close affinity.

5.9.3 *Relictualism*

Nineteen of the 35 species of *Livistona* exhibit isolated distribution (Table 5.5). Some species, such as *L. alfredii*, *L. carinensis*, and *L. mariae*, have very restricted distributional ranges, and are isolated from other species by 1000 km, 4500 km and 800 km respectively. Other species, such as *L. saribus*, *L. jenkinsiana* and *L. australis*, have widespread distributional ranges, and co-occur with other species.

A number of *Livistona* species have been interpreted as relictual (Menkhorst and Cowie, 1992; Morton *et al.*, 1995). In most studies, the term relictual is often not defined and its meaning is therefore open to interpretation. For the term relictual to be informative, an historical time frame must be imposed on events, such as those migrational, climatic and habitat changes that caused the taxon to become relictual, but permitted it to persist. Assume that the population size of a given species has always been small. Can the extant population be considered relictual? In many studies, being designated as relictual implies that the species was formerly widespread, and that it is a surviving element of ancient lineage persisting in a now otherwise depauerate association. For many species this can not be proven and for the present remains speculative.

Some species interpreted as relictual may indeed be recent migrants that have had sufficient time to evolve some adaptations to restricted niches. Assume that *L. mariae*, [restricted to the Finke River system in central Australia] rather than being a relict as is generally designated, is a new 'immigrant' in the process of active radiation and adaptation. Related taxa, such as *L. rigida*, *L. nasmophila* and *L. lanuginosa* may represent an 'ecological/phylogenetic lineage' in which *L. mariae* is included (Fig. 5.7). The corollary of this is that, in the absence of historical evidence such as fossils, it is difficult to differentiate between relicts and newly-arrived elements in the case of *Livistona* species.

The isolation and rarity of some Australian species such as *Livistona alfredii, L. mariae* and *L. victoriae* can be accounted for in part by assuming that they are associated with, or spread from, refugia. Their isolation from other species may be attributed to the contraction of suitable habitats due to increasing dryness of the Australian continent. There is a strong correlation between rarity of a given type of environment and rarity of species (Kruckeberg and Rabinowitz, 1985). Species that belong to either ancient or new lineages may occur in refugial environments (Coats and Kirkpatrick, 1999). In Australia, such species display considerable adaptation to xeric conditions. For example, *L. alfredii* is restricted to the semi-arid Cape Range and Fortescue River areas of Western Australia, and is considered a relict of a humid tropical palaeoclimate (Wyrwoll, 1993; Keighery and Gibson, 1993; Morton *et al.*, 1995). Similarly, *L. victoriae* is restricted to the semi-arid Bungle Bungles of Western Australia and Victoria River area of the Northern Territory, and is also considered relictual (Menkhorst and Cowie, 1992).

5.9.4 *Cladistics*

Based on the cladistic analysis presented in Chapter 3 (Fig. 3.19), and reproduced here in Figure 5.7, some comments on the comparison of distribution and inferred phylogenetic position of some *Livistona* species can be made. The clades, lineages and subclades recognised in this analysis, shown in Fig. 3.19, are:

- **Asian/Malesian clade**
  - *exigua* lineage: Borneo (Brunei)
  - *saribus* lineage: Indochina, Thailand, Malaysia, western Indonesia, the Philippines

- *chinensis* subclade: north-eastern India, Myanmar, Thailand, Malaysia, southern China, Taiwan, Ryukyu Islands, southern Japan, Bonin Islands
- *rotundifolia* subclade: the Philippines, Indonesia, New Guinea, Solomon Islands

- **African/Arabian/Australian clade**
- *mariae* subclade: Australia, southern New Guinea, Horn of Africa, Yemen
- *humilis* subclade: Australia, southern New Guinea

There is general consistency between distribution and phylogenetic position, as inferred by the cladistic analysis of *Livistona* species. For example, species in the *rotundifolia* subclade all occur in the Malesian biogeographic region [Philippines, Indonesia, New Guinea, and Solomon Islands] (Figs 5.7, 5.9), and species in the *mariae* and *humilis* subclades (Figs 5.7, 5.10, 5.11) occur generally in biogeographic regions confined to Australia and southern New Guinea. One notable inconsistency in the *mariae* subclade is *L. carinensis*, which occurs in the Sudano-Zambesi region [Djibouti, Somalia, and Yemen]. This species will be discussed in detail in Section 5.9.5. With reference to Figure 5.7, some species that display apparent inconsistency, at least based on Takhtajan's floristic regions, occur in the Australian and New Guinea regions. For example, *L. muelleri*, which occurs in monsoonal northern Queensland and southern New Guinea, is included phylogenetically in the *mariae* subclade that generally occurs in the semi-arid regions of Queensland, Northern Territory and Western Australia. This inconsistency is a consequence of the broad and imprecise boundaries of Takhtajan's floristic regions, which does not take into account the inclusion of monsoonal southern New Guinea into the Australian region (Crisp *et al.*, 1995; Brown *et al.*, 2001). A similar explanation can be provided for *L. benthamii*, a species in the *humilis* subclade (Fig. 5.7), distributed in the sub-equatorial areas in Northern Territory, northern Queensland and southern New Guinea. The occurrence of *L. muelleri* and *L. benthamii* in both southern New Guinea and northern Australia may be attributable to disjunction caused by recent marine incursion that produced Torres Strait.

5.9.5 *Distribution of Livistona carinensis*

Livistona carinensis, a component of the *mariae* subclade, occurs in north-eastern Africa and southern Arabia (Figs 5.7, 5.10), occupying irregularly flowing

seasonal watercourses in an otherwise arid environment. The species occurs about 4500 km away from the nearest *Livistona*, *L. jenkinsiana*, a component of the *chinensis* subclade, in north-eastern India (Fig. 5.9). The intervening landmasses between the ranges of *L. carinensis* and *L. jenkinsiana* do not support any species related to *Livistona*, thus making the isolation of *L. carinensis* remarkable. The floristic region in which *L. carinensis* occurs, the Sudano-Zambesi (Figs 5.5a, 5.6), generally displays only limited relatedness to the regions where other *Livistona* species occur (Takhtajan, 1986).

How can the isolation of *L. carinensis* be explained? Acknowledging that most biogeographical hypotheses cannot be disproved, and that assumptions are made with regards to historical events, a number of scenarios may be proposed to explain the distribution of *L. carinensis*. The scenarios presented are as follows:

- long-distance dispersal
- Laurasian origin
- Gondwanan origin

Long-distance dispersal

According to the cladistic analysis based on morphological characters (Figs 5.7, 5.10), the closest relatives of *L. carinensis* occur in north-western Australia, with *L. alfredii* as a sister species. Other closely related species include *L. victoriae* and others in the *L. mariae* subclade. Similar patterns of distribution (i. e. closely related organisms occur in both Australia and Africa, but are absent from intervening landmasses) have been recognised in other taxonomic groups. For example, Cranston and Hare (1995) noted the presence of Chironomids in Africa and Australia but their absence from India. Croizat (1958) had earlier recognised this distributional pattern and termed it the 'trans Indian Ocean track'.

Assuming that the cladistically inferred relationship of *L. carinensis* with species in Australia is valid (Fig. 5.7), and that present day species in the *mariae* subclade evolved from a recent common ancestor, it is expected, if dispersal did occur, that the ancestral propagating material would have moved from Australia to north-eastern Africa/southern Arabia, a relatively vast distance. Extant species have

relatively limited dispersal ability and assuming that this was also the case in the past, the long-distance dispersal scenario is regarded as implausible.

Laurasian origin

Another scenario is that ancestral Livistonas were distributed in the area of Laurasia subjected to tectonic activity that involved the collision of the Indian Plate. This scenario is based on the premise that the genus had a former distribution across an area that equates with present-day Arabia, the Himalayas and south-east Asia (southern shores of the Tethys Sea?). The intrusion of the Indian Plate, which may not have supported any elements of *Livistona* at that time, might have resulted in vicariance of the ancestral population of *Livistona*, with progenitors of *L. carinensis* becoming 'stranded' in north-eastern Africa and southern Arabia. Following the collision of the Indian plate with Laurasia, the surviving Livistonas in the west were subject to adverse climatic conditions that reduced their numbers and possibly produced extinctions, with *L. carinensis* the only eventual survivor. Those elements to the east were, conversely, able to diversify under the prevailing, presumably more favourable, environmental conditions. From there, elements radiated into eastern Asia, Malesia and Australia.

Gondwanan origin

Assuming that the phylogenetic relatedness of *L. carinensis* to species in the *mariae* subclade in Australia is valid (Fig. 5.7), a common ancestor may have occurred on the landmass that eventually was to become north-eastern Africa, southern Arabia and north-western Australia, all of which were originally part of Gondwana (Schuster, 1976). This offers support for the idea that the origin of the African/Arabian/Australian species, which includes *L. carinensis*, may have been Gondwanan and for that of the Asian/Malesian group to have been Laurasian. This scenario suggests an early Pangaean origin for the genus with the subsequent development of two centres of diversity, one in Gondwana and one in Laurasia.

5.9.6 *Diversity and distribution of Livistona*

Two lines of diversification are evident in the Asian/Malesian group (Fig. 5.7): the *chinensis* subclade (Fig. 5.9) which is confined to Malaysia, Thailand, north-

eastern India, southern China, Taiwan, and Japan and nearby archipelagoes, and the *rotundifolia* subclade (Fig. 5.9) which is confined to the Philippines, Indonesia, New Guinea and the Solomon Islands. The biogeographical relationships of *L. exigua* (Figs 5.7, 5.8), a species endemic to eastern Brunei, and *L. saribus* (Figs 5.7, 5.8), widespread in Indochina, Thailand, Malaysia, western Indonesia and the Philippines, are difficult to resolve on the available evidence.

Within Australia, two lines of diversity are evident: the *mariae* subclade (Figs 5.7, 5.10) which mostly includes the species occurring in semi-desert areas, and with some species considered to be 'relictual', and the *humilis* subclade (Figs 5.7, 5.11) which mostly includes species from monsoonal and/or moist areas. *Livistona muelleri*, from the *mariae* subclade, and *L. benthamii* from the *humilis* subclade, are essentially Australian species that co-occur in southern New Guinea and northern Australia.

5.10 Conclusion

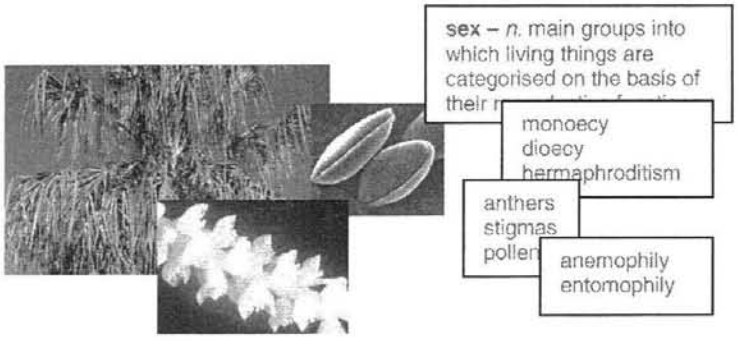
The aims of this chapter were to investigate the historical patterns of distribution and radiation in *Livistona* with reference to the fossil record, floristic regions and relationships inferred from cladistic analysis. The fossil record and the occurrence of extant species in otherwise unrelated floristic regions suggest that *Livistona* is an 'ancient' genus, and occurred in areas where it, or *proto-Livistona*, does not occur today, and may have been more widespread than at present. The marked disjunction of some species suggests former widespread distribution, which through the effects of tectonic events and/or climate change 'stranded' some taxa. The 'origin' of *Livistona* may be argued to be both Laurasian and Gondwanan, in which case a Pangaean origin of two centres of diversity can be invoked, or an origin that is strictly Laurasian, which is supported by the fossil record. For the Australian species, arguments for both a Laurasian and a Gondwanan origin have been presented (sections 5.9.1, 5.9.5). However, the most plausible scenario is that *Livistona* was a widespread Laurasian element, the ancestral population of which was 'split' by the effects of tectonic events. Following these events, elements of *Livistona* were able to persist in what is now north-eastern Africa/southern Arabia, and south-eastern Asia. An increasingly arid environment prevented

diversification of the African/Arabian elements, while conversely the eastern elements were able to diversify and produce two major lineages. The Asian/Malesian clade occurs in south-eastern and eastern Asia, and Malesia, and the African/Arabian/Australian clade, which, apart from the anomalous *L. carinensis*, occurs in Australia and southern New Guinea. The apparent close relationship between *L. carinensis* in north-eastern Africa and southern Arabia and some of the other species of the *mariae* subclade in Australia, may be an artefact of the cladistic analysis.

Chapter 6

Studies in the genus *Livistona* R. Br. (Coryphoideae: Arecaceae)

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



6.1 Introduction

Linnaeus (1753, 1754) was the first botanist to recognise the sexual traits of palms in a systematic sense, grouping genera and species based on their floral characteristics, and recognising two sexual systems: hermaphroditism and unisexuality. For further refinement of these two divisions Linnaeus used secondary characters of the androecium and gynoecium. The range of palms available to Linnaeus for study was limited, and it has only been in recent decades that a more thorough understanding of the complexity of sexual systems within the family has been possible (Moore, 1973a; Moore and Uhl, 1982; Henderson, 1986a; Tomlinson, 1990). Uhl and Dransfield (1987) recognised the same basic divisions as Linnaeus, i. e., hermaphroditism [bisexual in their terms] and unisexuality, but they provided a comprehensive summary of recent studies involving both monoecy and dioecy.

Within the palms, types of sexual expression are not confined to discrete taxonomic groups (Henderson, 1986b) (Fig. 6.1). For example, the Coryphoideae (c. 40 gen., c. 426 spp.) has both hermaphroditic and dioecious genera. The

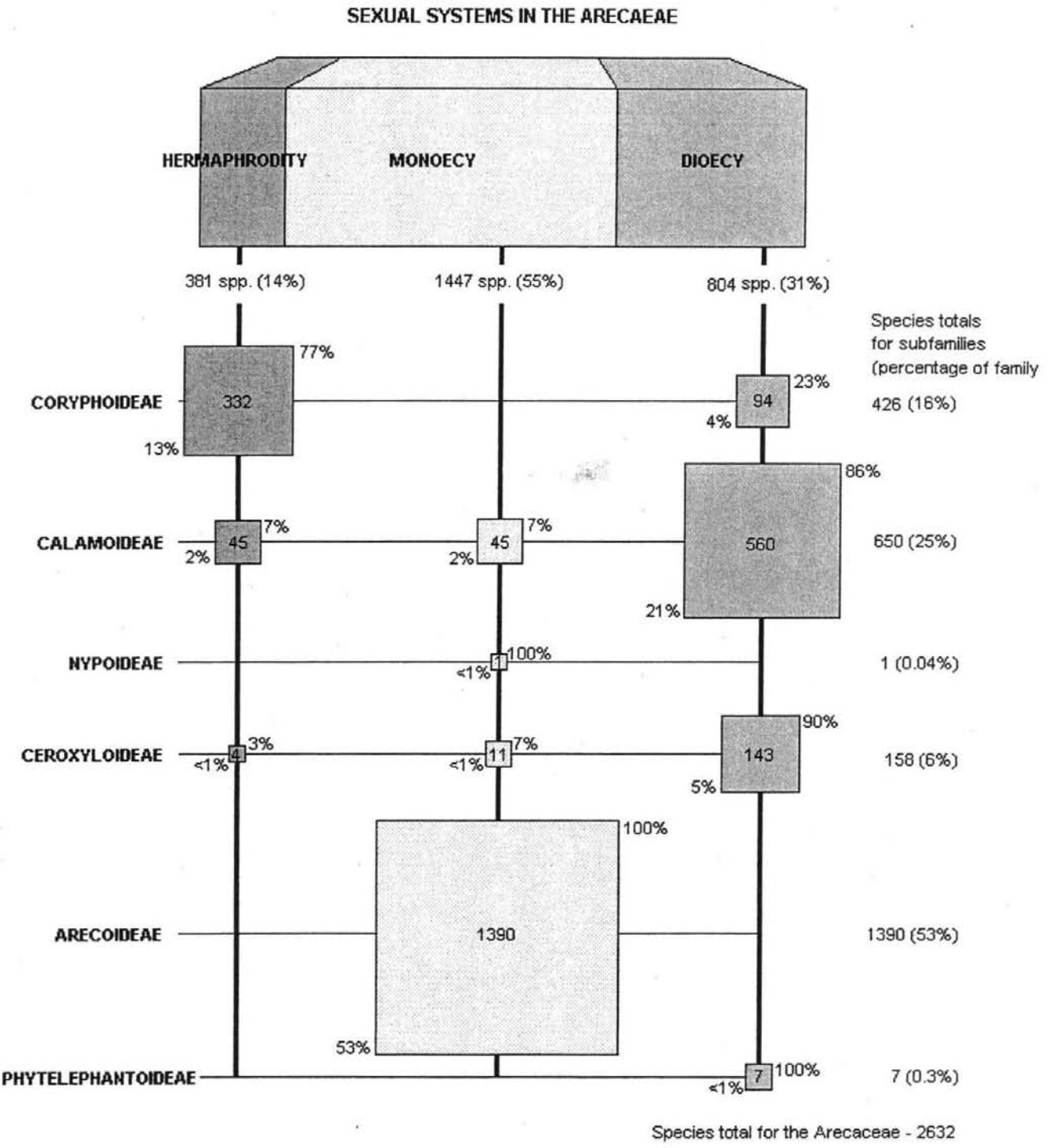


Figure 6.1. Schematic presentation of sexual expression in the Arecaceae.

The number in the box indicates the number of species within each subfamily possessing the designated sexual system. The percentage of species in the subfamily having that sexual system is indicated on the upper right hand corner of each box. The percentage of all palms belonging to the subfamily and having the designated sexual system is indicated in the lower left-hand corner. Data sourced from Uhl and Dransfield (1987), Henderson (1986a), and Tomlinson (1990).

Calamoideae (c. 22 gen., c. 650 spp.) and the Ceroxyloideae (c.11 gen., c.158 spp.) have hermaphroditic, monoecious and dioecious genera. The monotypic Nypoideae (1 gen., 1 sp.) is monoecious. The Arecoideae (c. 119 gen., c. 1390 spp.) is monoecious, while the Phytelephantoideae (c. 3 gen., c. 7 spp.) is dioecious. In a survey of dioecy in flowering plants, Renner and Ricklefs (1995) estimated that 31 genera in the Arecaceae had dioecious species, which accounts for c. 16 % of the genera in the family.

6.2 Evolution of sexual expression

The evolution of sex and the development of different breeding systems (Table 6.1) are among the major questions in botany (Darwin, 1876, 1877; Maynard Smith, 1978; Bawa, 1980; Ornduff, 1983; Thomson and Brunet, 1990). In flowering plants, hermaphroditism is considered the ancestral condition, occurring in about 72% of species (Crawley, 1997). Monoecy occurs in about 5% of species, dioecy in 4-6%, and various combinations and intermediate states such as gynomonoecy, andromonoecy, gynodioecy, androdioecy, subandroecy and trioecy make up the remainder (Richards, 1997). Bullock (1994) considered that dioecy was 'under-reported' and the percentage may be considerably higher than most estimates, possibly about 12%.

Table 6.1. Definitions of sexual systems in plants, adapted from Willson (1983), Richards (1997) and Traveset (1999).

hermaphroditism	individual plant has flowers with both male and female function
monoecy	androecia and gynoecia occur in separate flowers on one plant
gynomonoecy	a plant bears both female and hermaphroditic flowers
andromonoecy	a plant bears both male and hermaphroditic flowers
gynodioecy	female and hermaphroditic plants coexist
androdioecy	male and hermaphroditic plants coexist
subandroecy	female and plants with male and hermaphroditic flowers coexist
dioecy	plants in a population are either male or female
trioecy	female, male and hermaphroditic plants coexist in a population

Considering that hermaphroditism is regarded as the ancestral condition, and that monoecy and dioecy are regarded as progressively more derived through the pathways of gynodioecy and subandroecy (Charlesworth and Charlesworth, 1978; Greyson, 1994; Richards, 1997), questions concerning selective and adaptive constraints determining sexual expression have been posed by researchers (Uyenoyama, 1988; Lloyd, 1988; Burd, 1994; Werren and Buekeboom, 1998).

6.2.1 *Hermaphroditism to dioecy: mechanisms and consequences*

According to Renner and Ricklefs (1995), the morphological and functional characteristics most often associated with dioecious species include:

- wind (anemophily) or water pollination
- climbing habit
- perennial growth
- woodiness
- fleshy fruits
- frugivorous dispersal of fruit
- small, white to yellow or greenish flowers
- unspecialised insect pollinators
- highest frequency in the Palaeotropics

The developmental processes from hermaphroditism to dioecy are controlled by a number of factors. One of the primary selective pressures favouring dioecy appears to be the avoidance of inbreeding (Thomson and Brunet, 1990). In terms of resource allocation and genetics, it is more likely that self-compatible hermaphrodites will evolve monoecy or dioecy than develop an effective self-sterility mechanism (Longo, 1994). Physiologically, the adaptation may involve no more than an alteration of the hormone balance in the inflorescence (Cleland and Ben-Tal, 1983; Sudhersan and Abo El-Nil, 1999). It has been demonstrated that flowers on staminate plants of the dioecious *Phoenix dactylifera* L. (date palm) can be induced to develop functional pistillate organs by the application of hormones (DeMason and Tisserat, 1980), and that female sexual function is related to increased levels of naturally occurring gibberellins in individual plants (Leshem and Ophir, 1977). *Cocos nucifera* L. (coconut), an otherwise monoecious

species with unisexual flowers, may produce hermaphroditic flowers in succeeding generations through the hybridisation of certain varieties (Davis *et al.*, 1985).

If dioecy is seen as a consequence of the avoidance of self-fertilisation, then an evolutionary trend toward dioecy from a hermaphroditic origin would contribute to the limitation or prevention of deleterious conditions due to incompatibility and inbreeding (Uyenoyama, 1988). However, the adaptive and evolutionary importance of inbreeding must not be overlooked. One of the advantages of inbreeding is that it can conserve adaptive gene complexes (Shields, 1988). Ecological factors that may influence the development of dioecy and outbreeding include a potential increase in seed production to avoid seed predation (Bawa, 1980), and an increased ability to exploit a wider variety of microhabitats than hermaphroditic species (Bawa and Opler, 1975; Cox 1981; El-Keblawy and Freeman, 1999). Conversely, Pannell (1997a), in addressing the relatively small number of dioecious species of plants (c. 4-6% of the world's flora), determined that there was a selective disadvantage against evolution of unisexuality and dioecy on the grounds that hermaphrodites have an enhanced ability to maintain comparatively more stable populations.

The transition from hermaphroditism to dioecy is, at least theoretically, a simple procedure (Lloyd, 1988). Cox (1981) suggested that 'niche partitioning', in which staminate and pistillate plants occupy slightly different niches in either time or space, is the result of natural selection for decreased intersexual competition. However, such niche partitioning may impede successful reproduction, and affect the ability of either sex to succeed. Either one or both of the sexes may adopt potentially 'expensive' compensatory mechanisms.

The comparative measurement of resource expenditure by males and females during the process of reproduction is an indication of their 'fitness'. Fitness, as defined by Maclean (1987) is "the tendency of an organism and its progeny to survive, resulting from the possession of favourable genetic constitution". In hermaphrodites, maternal and paternal fitness are achieved by the same parent in different ways as it is difficult to partition structures such as petals and sepals into

unequivocal male and female contributions. In dioecy, one sex will be selected to allocate more resources into reproduction than the other sex because of competition for the same resources (Bawa and Webb, 1983). Models for predicting the relative fitness of males and females in situations of gynodioecy and dioecy were proposed by Charnov *et al.* (1976).

Male fitness is the reciprocal of the expenditure by a male per offspring fathered, and can be estimated, in part, as the degree of likelihood of a pollen grain reaching a cross-compatible stigma, successful fertilisation and seed germination (Stanton *et al.*, 1992; Kearns and Inouye, 1993). If more pollen grains are produced than necessary to fulfil this requirement, then male fitness is high. Female fitness is related to increased seed set, production of better quality seed, and the ability to nourish embryos (Bawa and Webb, 1983).

Charlesworth (1981) predicted that large fitness differences are to be expected between female and hermaphroditic individuals in a population. He estimated that seed production of females exceeds that of hermaphrodites, but he was not able to determine if this was a consequence of selfing, seed failure due to inbreeding depression, male sterility, or other factors.

6.3 Sex ratio in palms

The sex ratios [i. e. the comparative numbers of males and females in a population] of some dioecious palms have been determined.

- *Ceroxylon klopstockia* Mart. (Ceroxyleae: Ceroxyloideae) has a ratio of male to female plants of 3:2 (Braun, 1976)
- *Lodoicea maldivica* Comm. the ratio is 2:1 (Savage and Ashton, 1983)
- *Chamaedorea tepejilote* Liebm. (Hyophorbeae: Ceroxyloideae) the ratio is 5:4 (Oyama, 1990)
- *Aphandra natalia* (Phytelephantoideae) the ratio is close to 1:1 (Anders Barfod, pers. comm.).

The predominance of male plants in populations of dioecious species is thought to relate to the greater longevity of males (Richards, 1997), as well as a function of

the inverse relationship of reproductive effort and vegetative growth (Silvertown, 1987), i. e. males require less reproductive effort than females and therefore are able to increase their vegetative growth. The sex ratios of flowers in monoecious species also show a male bias. Scariot and Lleras (1991) recorded a male flower to female flower ratio of 208:1 in the inflorescences of *Acrocomia aculeata* (Cocoeae: Arecoideae); Borchsenius (1993), studying the reproductive biology of three *Aiphanes* species in Ecuador, observed ratios of male flowers to female flowers per inflorescence of 9:1, 10:1 and 20:1; and Bullock (1981) observed ratios of 2:1 for *Prestoea decurrens* (Areceae: Arecoideae), *Iriartea gigantea* and *Socratea durissima* (Iriarteeae: Arecoideae), 15:1 *for Bactris wendlandiana*, 25:1 for *Bactris longiseta*, and 27:1 for *Astrocaryum alatum* Cocoeae: Arecoideae). Similarly, male-biased pollen:ovule ratios are also recorded for palms (Tomlinson, 1990).

6.4 Rate of evolution of dioecy

Charlesworth (1981) suggested that the rate of evolution from ancestral hermaphroditism to dioecy appears to be relatively rapid. To support this claim, examples were provided in which dioecy appears to have developed in species on oceanic islands after putatively hermaphroditic or otherwise non-dioecious species formed founding populations through dispersal (Charlesworth, 1981). That speciation at least in island environments is more rapid than in continental environments is well supported (Grant, 1998). Unsaturated habitats, non-equilibrium communities and isolation from recurrent gene flow have been invoked as primary ecological conditions that may contribute to evolution on islands (Barrett, 1998).

Bawa (1980) suggested that the evolution of dioecious species on some oceanic islands was the result of selection for out-crossing in initially small colonising populations of either monoecious or hermaphroditic species. It was estimated that there is only a minor increase in dioecy on islands when comparisons are made with neighbouring mainland ancestral sources, but that there is a strong positive correlation between the prevalence of dioecy, and maximum island height and proximity to the equator (Baker and Cox, 1984; Humeau *et al.*, 1999). In contrast

to the greater rate of speciation of plants on islands, the number of pollinating insect species is significantly less than on adjacent mainland areas (Barrett, 1998).

A number of dioecious palm genera occur on isolated oceanic islands: for example, *Lodoicea* (Borasseae: Coryphoideae) on the Seychelles (with 8% of all plant species being dioecious), and *Latania* (Borasseae: Coryphoideae) on the Mascarenes (with 11-20% of all plant species being dioecious) (Baker and Cox, 1984). The closest relatives of these endemic genera occur on nearby continental Africa and Madagascar (Moore, 1973a), and are also dioecious. Hawaii, with an estimated 14.7% dioecious plant species, has a single indigenous palm genus, *Pritchardia* (Corypheae: Coryphoideae) which, however, is not dioecious but hermaphroditic, and is insect pollinated, fleshy fruited, and bird and drift distributed (Sakai *et al.*, 1995). Its closest relatives, *Washingtonia* and *Colpothrinax*, occur on mainland areas of North America, and are also hermaphroditic (Uhl and Dransfield, 1987).

6.5 Functional dioecy

Although use of the terms 'functional dioecy', 'cryptic dioecy' and 'leaky dioecy' has an inherent imprecision and different authors may apply the terms to define different systems, the breeding systems to which these refer involve plants that function as one or either sex (Meagher, 1988). Functional dioecy is most often used to describe species in which individual plants function as a single sex, despite bearing flowers that are morphologically hermaphroditic and therefore similar to each other in gross appearance (Tomlinson and Fawcett, 1972; Anderson, 1979). The term has also been used to describe situations where unisexual flowers, either functionally male or female, occur on one plant, and functional or dysfunctional hermaphrodites occur on another plant (Anderson and Symon, 1989; Schlessman *et al.*, 1990). Cryptic dioecy has been used to describe the situation when there is the retention of opposite sex structures within the flowers of each sex, and leaky dioecy when florally dimorphic dioecious species may otherwise have occasional hermaphroditic or opposite sex flowers (Humeau *et al.*, 1999). According to Richards (1997), functional dioecy may account for a phase that is intermediate between monomorphic hermaphroditism and dimorphic monoecy or dioecy in the evolution of breeding systems.

It is possible that some of the intermediate stages between hermaphroditism and dioecy, such as gynodioecy, are developmentally stable, and that further evolution toward 'full' dioecy is not possible or is otherwise unlikely (Richards, 1997). Maurice *et al.* (1994) provided a model indicating that stability of gynodioecy is possible if a nuclear-cytoplasmic interactive control of sex is invoked. Both cytoplasmic and nuclear genes are known to determine male-sterility and femaleness in gynodioecious species (Willson, 1983; Eckhart, 1992; Webb and Kelly, 1993).

Androdioecy (Table 6.1) is a rare condition that has been documented in only a few plant species (Fritsch and Rieseberg, 1992) and is considered to have evolved from dioecious rather than from hermaphroditic ancestors (Richards, 1997). However, Wallender (2001) demonstrated that androdioecy may be one of the pathways of evolution from hermaphroditism to dioecy. The apparent rarity of the condition is due to the requirement that male plants must have a high fertility rate, at least double that of the hermaphroditic plants, in order to maintain selection and 'pass their genes on' (Liston *et al.*, 1990). Whether this condition exists in palms generally, or in *Livistona* in particular, has not been fully investigated.

6.5.1 *Pollen in functionally dioecious species*

It has been observed that one of the differences between the sexes in functionally dioecious species is in their pollen morphology. In many cases, the 'male' plants have fertile pollen while the 'female' plants have infertile pollen (Haber and Bawa, 1984). Infertile pollen can be inaperturate (i. e. non-porate), is either considerably smaller or larger than fertile pollen, or is otherwise inviable and not able to germinate, or if it does germinate is unable to affect fertilisation. In some instances, anthers are sterile in 'female' plants (Tomlinson and Fawcett, 1972). Rodd (1998) reported that the anthers of the fruit-bearing plants [female] of *Livistona humilis* R. Br. lacked pollen. Inaperturate pollen has been reported in the palm genus *Pigafetta* (Calamoideae) (Furness and Rudall, 1999), though the significance of this in a dioecious genus is not known (M. Harley, pers. comm.). In *Pigafetta* the plants are strictly unisexual, with the staminate flowers occurring in pairs on the male plants, and the pistillate flowers solitary on the female plants. Although inaperturate pollen is apparently inviable in some functionally dioecious

species, it is viable in species in other sexual systems and is considered an adaptation that increases potential germination efficiency in environments where pollen is not subject to desiccation (Furness and Rudall, 1999). Haber and Bawa (1984) suggested that sterile pollen in the flowers of functionally dioecious species could be a reward retained for pollinators.

6.6 Pollination systems in palms

Sexual expression and pollination mechanisms are complexly inter-related (Bawa and Beach, 1981). Although the correlation between sexual systems and pollination mechanisms is not strict, some specific conditions in palms have been recognised. Anemophily is often associated with both hermaphroditism and dioecy (de Jong *et al.*, 1999). In monoecy, protogyny is most often associated with beetle pollination, and secondarily with fly pollination. Protandry is associated primarily with bee pollination and secondarily with fly pollination (Uhl and Moore, 1977). There are specialised relationships with pollinators such as thrips (Dransfield, 1972), wasps (Henderson, 1986b) and bats (Cunningham, 1995). There is no obvious correlation between pollination mechanisms and systematic position within the palm family (Henderson, 1985).

It is only in recent decades that the prevalence of entomophily in palms has been documented (Silberbauer-Gottsberger, 1990; Judd *et al.*, 1999). Previously, it was considered that palms were primarily anemophilous (Kerchove, 1878; Drude, 1887; Good, 1956). Although both anemophily and entomophily may be concomitant in a single species, and with each system making a contribution according to the prevailing ecological and climatic conditions (Anderson *et al.*, 1988; Herrera, 1989; Scariot and Lleras, 1991; Bovi *et al.*, 1994; Bullock, 1994; Moraes, 1996), there is often an exclusive reliance on a single system for successful reproduction. Many species appear to be highly specialised and possibly exclusively entomophilous (Brown, 1976; Beach, 1984; Moncur and Watson, 1987; Zona, 1987; Listabarth, 1992, 1994; Borchsenius, 1993; Bøgh, 1996; Ervik and Bernal, 1996; Zona, 1996). In these species, anemophily is precluded or improbable due to habitat type and physical restrictions created by inappropriate floral and pollen morphologies (Harder, 2000). Those species that are suspected to be primarily anemophilous very often possess flowers and pollen

that are morphologically and anatomically adapted for entomophily, and often present associated attractants such as scents and nectar for potential pollinators (Read, 1975; Fisher and Moore, 1977; Uhl and Moore, 1977). Faegri and van der Pijl (1979) considered such flowers to be evidence of ancestral entomophily. The presence of lipids in the pollenkitt may account for bees collecting the pollen of certain anemophilous plants (Bullock, 1994). The adoption of secondary anemophily in the palms of the hermaphroditic Thrinacinae (Corypheae: Coryphoideae) was determined to be a response to ecological conditions in which habitats changed from closed to open forest; rainfall had diminished over time, and there had been a subsequent loss of pollinators (Uhl and Moore, 1977; Henderson, 1986a). Silberbauer-Gottsberger (1990) concluded that exclusive reliance on anemophily was very doubtful for any palm species, and that both entomophily and anemophily, to various degrees, were likely to be in operation.

Read (1975) concluded that the Coryphoid genus *Thrinax* in the Caribbean was primarily anemophilous, and Shuey and Wunderlin (1977) determined that *Rhapidophyllum* was pollinated by a beetle, *Notolomus* sp. In *Rhapidophyllum* reproduction was primarily clonal, resulting from low fruit set and limited dispersability. Henderson (1984), in a study of *Cryosophila albida* Bartlett in Costa Rica, determined that the inflorescence morphology and phenology precluded self-pollination and anemophily, and that the species was primarily pollinated by curculionid beetles, *Derelominus* spp. Zona (1987) found that, in south-eastern Florida, the bee *Megachile albitarsis* was the major pollinator of *Sabal etonia* Swingle ex Nash. *Corypha*, with hermaphroditic flowers, is evidently self-compatible, as individual isolated trees set abundant fruit (Tomlinson, 1990).

Uhl and Moore (1977) hypothesised that anemophily in some genera may be derived due to the extinction of previous pollinators, and that the primitive condition could be entomophily (Silberbauer-Gottsberger, 1990; Jolivet, 1998). Conversely, Stebbins (1974) considered anemophily as the ancestral state for flowering plants. In some species, facultative entomophily may contribute to successful pollination in anemophilous species that otherwise have entomophilous characters.

Entomophilous characters include:

- colourful flowers
- possession of nectaries
- limited pollen production
- large, moist and sculptured pollen grains
- thermogenesis of inflorescences during anthesis
- strong floral odours

6.7 Seasonality

The seasonality of flowering can be an indication of breeding systems in palms. De Steven *et al.* (1987) studied palms in Panama, and concluded that flowering in most species occurs in the rainy season in concert with the seasonal increase in the activities of pollinating insects. There was also a strong flowering synchrony among and between species. Conversely, species that flower in the dry season could be expected to have a greater chance of being anemophilous, as rain can interfere with pollen dispersal and pollen viability. In seasonally deciduous communities, the open space provided by leafless trees may be an advantage for more efficient pollen dispersal by wind (Richards, 1997). In a study of 19 dioecious anemophilous species of trees in central America, Bullock (1994) reported that 14 species (74%) shed pollen in the mid-dry season or the dry-wet transition period. The prevalence of anemophily in palms that flower in the dry season may be partly explained by the semi-quiescent state that insects adopt during that season. The habit of insects moving to moister sites is dictated by food supply, advantages in predator avoidance or enhancement of mating success (Janzen and Schoener, 1968; Wolda, 1978; Delinger, 1980; Monteith, 1982; Frith and Frith, 1985; Sands and House, 1990). Aseasonality of flowering in some palm genera has been reported. Borchsenius and Bernal (1996) found that most species of *Aiphanes* [Cocoeae: Arecoideae], a genus with 22 species, produced flowers continuously throughout the year. They attributed this to the relatively constant climatic conditions that occur in most parts of the distributional range of the genus.

6.8 Pollinators and multistaminy

The specialised co-evolution of insects and palms is a factor that has contributed to an increase in the number of stamens in the flowers [i. e. multistaminy] in many species (Uhl and Moore, 1977). Concomitantly, palms that have the unspecialised six stamen condition are theoretically likely to have non-specialised pollinators. Most unisexual flowers exhibit vestigial organs of the reduced sex, ranging from minimal reduction to complete absence. Multistaminy is considered derived from trimery in palms (Moore and Uhl, 1982).

In a general context, Stebbins (1974) suggested that angiosperms evolved prior to the evolution of pollinating insects, and that early angiosperms were anemophilous. Therefore, entomophily would be the derived condition. As suggested by the fossil record, the development of some evolutionary lines in palms pre-dates the first appearance of putative pollinating insects (Proctor *et al.*, 1996). The Coryphoid line, of which *Livistona* is a component, is among those palms considered to be the most morphologically and anatomically primitive (Thorne, 1996b). Modern genera, or their ancestors, may have developed by the late Cretaceous or early Eocene (Daghlian, 1981). Some of the earliest palm fossils have been assigned to the Coryphoids (Read and Hickey, 1972).

6.9 Sexual expression in *Livistona*

Sexual expression and reproductive biology in *Livistona* have received little attention and therefore are poorly understood. Uhl and Dransfield (1987) described the genus as "....hermaphroditic (rarely dioecious)....", and "....where dioecious, anthers and ovules not developing but otherwise as in the hermaphroditic....". In a review of pollination in palms, Henderson (1986a) reported that *Livistona* flowers possessed septal nectaries, and that "....bee pollination is .... possible in *Livistona*.". Rodd (1998) stated, "....Australian species display clear signs of sexual differentiation among the palms of a population, although the nature of this sexuality is still unclear....", and "....It is possible that this is a feature of all the Australian species, or even of the genus as a whole. It remains an interesting area for further study....".

Informal observations of the sexuality of some species have been made. Rodd (1998) provided a description of *Livistona humilis* from the Northern Territory, where sexual dimorphism in inflorescence structure is clearly evident, and suggestive of a functionally dioecious condition. Rodd observed that flowers in the 'female' plants, i. e. fruit-bearing plants, had empty anther locules, and flowers on 'male' plants, i. e. nonfruit-bearing plants, had apparently morphologically complete stamens, carpels and ovules, but nevertheless did not bear fruit. The morphology of inflorescences was strikingly different between genders, with the male plants having up to five partial inflorescences, while the female possessed a single terminal partial inflorescence and many sterile bracts subtending the peduncle. Rodd (1998) also reported 'female' and 'male' plants ["some degree of functional sexual differentiation"] in *Livistona alfredii* F. Muell., *L. australis* (R. Br.) Mart., *L. eastonii* C. A. Gardner and *L. fulva* A. N. Rodd. Sexual differentiation is also suspected in *Livistona* in New Guinea (Anders Barfod, pers. comm). Apart from the dimorphic inflorescences in *L. humilis*, there are no readily observable or constant morphological differences in other *Livistona* species that differentiate functionally staminate from functionally pistillate plants.

As presently understood, there are two sexual systems that are applicable to *Livistona* (Uhl and Dransfield, 1987):

- *hermaphroditism* – describes plants in which all individual flowers have both male and female function (Richards, 1997)
- *functional (cryptic) dioecy* – describes plants in which individuals function as a single sex, despite bearing flowers that are morphologically bisexual and therefore similar to each other in gross appearance (Tomlinson and Fawcett, 1972; Anderson, 1979). As described in section 6.5, the term has been used to characterise situations where either functionally male or female flowers occur on one plant and functional or dysfunctional hermaphrodites occur on another plant. Cryptic dioecy describes the situation when opposite sex structures are retained within the flowers of each sex.

Rodd (1998) suggested that some *Livistona* species were androdioecious; however, his descriptions of these species are not consistent with his assessment.

They imply dioecy because the ovules in his 'male' plants appear morphologically complete and display no indication of reduction or loss.

6.10 Description of reproductive organs in *Livistona*

6.10.1 *Habit*

The size and habit of a plant, and its position in the environment are ultimately related to breeding systems and pollination. *Livistona* species are solitary stemmed, from 1-5 m (*L. exigua* J. Dransf.) to over 30 m tall (*L. mariae* F. Muell.), with a crown of eight (*L. humilis*) to 60 (*L. australis*) palmate leaves. Habitats include rainforest, closed to open woodlands or semi-desert, either as a component of the understorey, in the sub-canopy or as the primary canopy species. Primary specific differences occur in leaf morphology, inflorescence structure, and flower and fruit morphologies.

6.10.2 *Inflorescence*

Inflorescences are interfoliar, and in all but three species (*L. carinensis*, *L. halongensis* and *L. humilis*) do not extend beyond the leaves. Inflorescences are initiated in the axil of each leaf at the onset of reproductive maturity. Leaves and inflorescence buds are produced more or less regularly throughout the year. Leaf growth is continuous but inflorescence buds remain dormant within the leaf axil until the onset of the flowering season. With the onset of flowering, buds that were initiated the previous year develop rapidly to facilitate a more or less synchronised or closely sequential acropetal inflorescence production. From one to 15 inflorescences can be produced in a flowering event, with a period of a few weeks between maturation of the proximal and distal inflorescences. Most species flower seasonally at more or less the same time each year, although *L. australis* in southern New South Wales and Victoria flowers at an estimated 18 month interval (Orscheg and Parsons, 1996b).

The inflorescence of *Livistona* is paniculate, but differs between species in the type and order of branching, the form and number of bracts, and length relative to leaves. Two morphological types can be identified:

Type 1 (Fig. 6.2): a solitary axis with partial inflorescences arranged spirally at regular intervals and reducing in size and complexity toward the apex. Partial inflorescences are second order branch systems that terminate in flower-bearing rachillae. The proximal partial inflorescence may be subtended by a bract or bracts (termed peduncular bracts). A single bract (termed rachis bract) subtends each further partial inflorescence. In some species additional smaller bracts are present at further branching points. This type of inflorescence occurs in most species, including both hermaphroditic and putatively dioecious species, and is morphologically similar in both fruit-bearing and nonfruit-bearing plants.

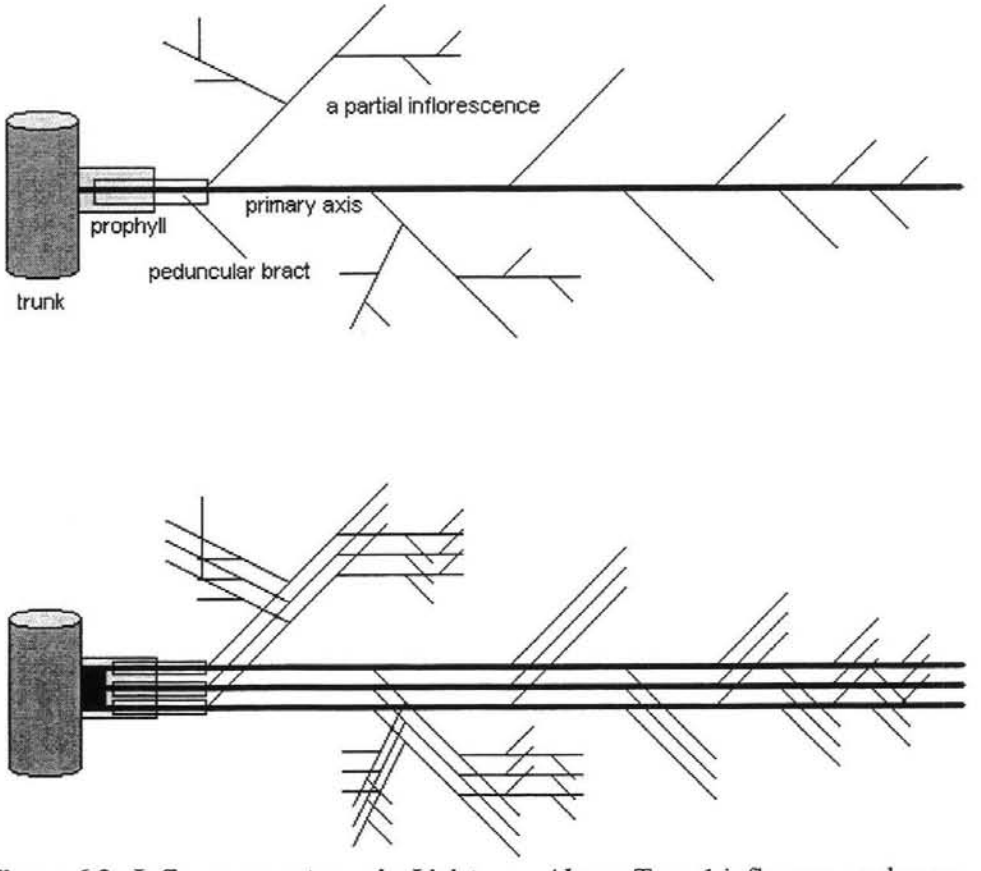


Figure 6.2. Inflorescence types in *Livistona*. *Above:* Type 1 inflorescence has an unbranched primary axis with partial inflorescences placed at ± regular intervals and reducing in size and complexity toward the distal end. ***Below:*** Type 2 inflorescence has a trifurcate or infrequently bifurcate axis with ± identical collateral axes that share a common prophyll but each axis bears an individual peduncular bract. The individual axes otherwise have a Type 1 structure.

Type 2 (Fig. 6.2): an inflorescence with collateral axes composed of two or three more or less identical structures arising at the same level at the very base of the peduncle and within a single prophyll, but with each axis bearing its own peduncular and rachis bracts, and subsequently each axis supporting a number of partial inflorescences that reduce in size and complexity toward the apex as occurs in Type 1. This type is known to occur in species distributed in the Philippines, Indonesia, New Guinea and the Solomon Islands, and has been described ontologically and morphologically by Fisher and Moore (1977).

6.10.3 *Flower morphology*

Numerous flowers are borne spirally on each rachilla. They are solitary or arranged in sympodial clusters [cincinni] of 2 to 8 flowers, widely spaced or congested, and either sessile or on pedicels. Morphologically, there are no readily apparent differences between those that function as hermaphrodites or those that function as unisexual flowers. The differences between the two flower types are primarily functional, i. e. whether the pollen is viable, inviable or absent, or whether the gynoecium is fertile or infertile. For convenience, the following floral description is of a typical functional hermaphroditic flower (Fig. 6.3).

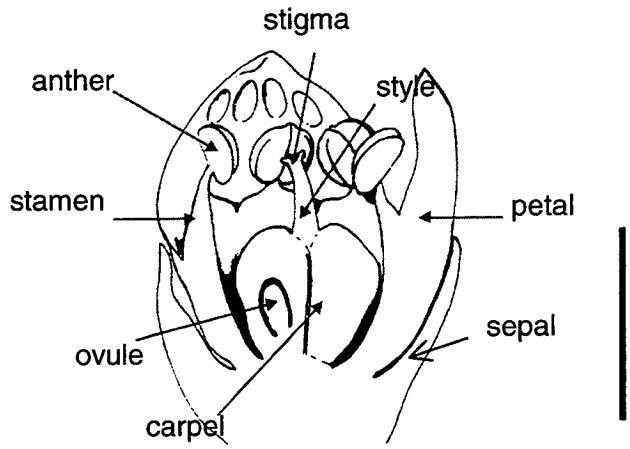


Figure 6.3. Flower of *Livistona*. Lateral view of a single flower of *Livistona chinensis*. Scale bar = 1 mm. Illustration adapted from M. Ruff Sheehan (Uhl and Dransfield, 1987).

Flowers are trimerous, 1 to 3 mm high, usually with all parts white/cream or yellow. However, in *L. muelleri* F. M. Bailey, the gynoecium and sepals are pink/mauve while in *L. tothur*, sepals, petals and gynoecium are all red. The sepals are connate for most of their length, lobed apically; petals are c. twice as long as the sepals, and triangular with acute or obtuse apices; stamens are shorter than the petals, and basally connate to form a narrow fleshy ring; filaments are 'shouldered' and narrow abruptly into the connective; anthers are non-versatile, medifixed, rounded or oblong, and latrorse [opening lateral to the filaments]; the gynoecium is tri-carpellate; carpels are wedge-shaped, basally separate, and distally connate to form a common slender style; the stigma is very small and tri-lobed; the ovule is basally attached and anatropous [bent parallel to its stalk].

Livistona flowers have no clear adaptations for insect or animal pollination, and may be relatively less efficient if entomophilous pollination is involved (Neale *et al.*, 1998). The flowers of *Livistona* provide only poor or ill adapted landing platforms, there are no apparent guiding mechanisms, and most species are usually dull coloured and with no perceptible odour.

6.10.4 *Nectaries*

Septal nectaries, also termed gynopleural nectaries (Smets *et al.*, 2000), are formed by local regions of nectariferous epidermal cells on the sides of the carpels at their base (van Heel, 1988), and are restricted to monocotyledonous families such as the Arecaceae, Iridaceae, Liliaceae and Musaceae (Fahn, 1979, 1982). They have been reported in some species of *Livistona* (Schmid, 1983). The function of nectaries in *Livistona* has not been investigated, though the secreted liquids may act as an attractant nectar for potential pollinators (Henderson, 1986a). In *Livistona humilis* (Fig. 6.4), the nectary is situated at the base of the partition between the carpels. Considering that nectaries are evidence of co-evolution between plants and insects (Cruden *et al.*, 1983), the situation with *Livistona* is that some species may be entomophilous with the nectary functioning as an attractant.

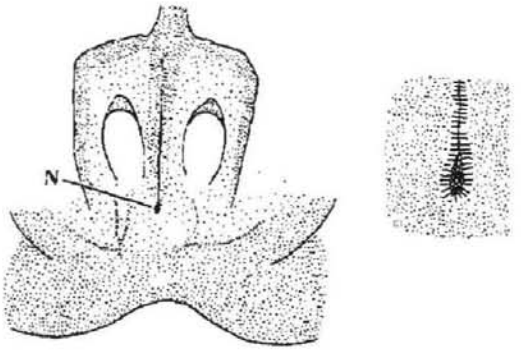


Figure 6.4. Morphology of the outer septal nectary in *Livistona humilis*.
Left: Longitudinal section through the ovary to reveal the position of the nectary (N) in the inner septum at the base of the carpels. ***Right:*** Close-up of the nectary. (From Schmid, 1983, redrawn from Brown, 1938: scale not provided).

6.10.5 *Spatial relationships of flowers*

The degree of flower density on the inflorescence, and the number of flowers that are synchronously 'active' in the flowering event, are suggestive of certain pollination systems. According to Richards (1997), those plants with many small flowers that reach anthesis and receptivity sequentially are more likely to be entomophilous, while those in which flowers have simultaneous anthesis and in which pollen is released in what has been described as a 'cloud' are more likely to be anemophilous.

6.10.6 *Anther dehiscence*

Anther dehiscence, i. e. the splitting of the anther wall to release pollen, is latrorse in *Livistona* (Uhl and Dransfield, 1987). Proctor *et al.* (1996) suggested that wind action releases, as well as disperses, the pollen in many anemophilous plants. Jackson and Lyford (1999) proposed the term 'shaker mechanism' for the degree of wind gustiness and branch flexure that is required to facilitate pollen dislodgment and release from the anthers.

6.10.7 *Stigmas*

For successful pollination, stigmas must be capable of pollen interception, i. e. be exposed, large, and either moist or sticky (Jackson and Lyford, 1999). The stigma in the flowers of *Livistona* is placed in close proximity to the anthers of the same flower. The receptive surface is small with the apex trifid, and with the lobes slightly recurved.

6.10.8 *Pollen morphology and size*

Livistona pollen is of a generalised monosulcate monocotyledonous type, but with a range of variation in the tectum between species from finely perforate to reticulate (Harley, 1990; Ferguson and Harley, 1992). Pacini and Franchi (2000) described palm pollen as 'monad pollen grouped by pollenkitt or tryphine'. Small granules have been observed in the lumina of some species (Dransfield *et al.*, 1990). Sowunmi (1972) described *L. chinensis* pollen as ellipsoidal with the long axis 18.5-27 μm. Mahabalé (1967) reported that *Livistona* pollen was binucleate at the time of shedding. In a study to determine the comparison between past and present distribution of *L. australis* in eastern Victoria, Ladd (1978) found neither surface nor sedimentary deposits of pollen, and concluded that the species was under-represented in both palaeo and extant pollen spectra. *Livistona* pollen is in the form often correlated with anemophily, both in the size range, and in having smooth exine sculpturing (Williams and Adam, 1999).

6.10.9 *Pollen:ovule ratios*

The ratio of pollen grains to ovule number [P:O] is considered to provide an indication of breeding systems and an estimate of pollination efficiency (Cruden, 1977; Cruden and Millar-Ward, 1981). As a rule, high ratios are characteristic of anemophily and low ratios of entomophily or zoophily (Richards, 1997). Cruden (1977) provided a scheme based on P:O ratios that may indicate breeding systems (Table 6.2), and also concluded that monoecious species produce fewer pollen grains than dioecious species.

Table 6.2. Reproductive characteristics and pollen:ovule (P:O) ratios as determined by Cruden (1977).

breeding system	P:O ratio
cleistogamy	4.7:1
obligate autogamy	27.7:1
facultative autogamy	168.5:1
facultative xenogamy	796.6:1
xenogamy	5859.2:1

Calculating the P:O ratios of monoecious and hermaphroditic species must be approached differently. Borchsenius (1993) calculated the P:O ratios of the palms *Aiphanes chiribogensis* Borchsenius and Balslev, *A. erinacea* (Karsten) H. Wendl. and *A. eggersii* Burret in Ecuador, to be 51.4:1, 52.7:1 and 240:1 respectively. *Aiphanes* species are monoecious and entomophilous. The P:O ratios were calculated as the male/female flower ratio on a single plant multiplied by the mean pollen content per flower and divided by the number of ovules per female flower. The calculation for hermaphroditic flowers is much simpler as the number of pollen grains per stamen and ovules in a single flower is usually representative of the population as a whole (Tomlinson, 1990).

6.10.10 *Pollination*

Bullock (1994) concluded that individuals in populations of anemophilous species were more closely aggregated in their habitats than entomophilous species, which, in some forest situations, may be many hundreds of metres apart. Jackson and Lyford (1999) stated that anemophily was most often associated with wind-adapted moderate-sized pollen, while entomophily is most often associated with small or large pollens that are suitable for biotic dispersal associated with a vector's needs. Proctor *et al.* (1996) determined that in larger pollens, $> 40\ \mu$m in length, dispersal range assuming anemophily, can be very short, while in smaller grains, $< 25\ \mu$m in length, dispersion can be inefficient because of size, shape and movement within airstreams.

Although the pollination mechanisms in *Livistona* are not fully known, pollination could occur in a number of ways (Table 6.3). With both hermaphroditism and functional dioecy potentially occurring in *Livistona*, it can be hypothesised that

Table 6.3. Pollination modes that could occur in *Livistona*. Adapted from Willson (1983), Richards (1997) and Traveset (1999).

autogamy	fertilisation occurring within the same flower
geitonogamy	fertilisation between different flowers on an individual plant or ramet, i. e. genets
xenogamy	fertilisation between pollen and ovules of different plants

the mechanisms of pollination are non-specialised and polyphilic (Richards, 1997). In hermaphroditic species, pollination could occur by any of the three mechanisms listed in Table 6.3. In functionally dioecious species, geitonogamy and xenogamy are the most likely mechanisms, although autogamy cannot be ruled out for hermaphroditic individuals.

6.11 Aims

The aims of this study were:

- to investigate the sexuality and breeding systems operating in four species of *Livistona* based on literature and observations
- to investigate whether or not, in the absence of experimental data, morphological characters could be used as predictors of sexuality and breeding conditions among species of *Livistona*.

The following questions were posed with respect to *Livistona*:

- what are the breeding systems that occur in the four species examined?
- what are the sex ratios and sexual function of plants in these species?
- are there relationships between sexuality, breeding systems and pollination mechanisms?

6.12 Materials and methods

Initial observations were made of 17 species of *Livistona* (Table 6.4) cultivated at several locations in Townsville:

- The Palmetum, Douglas
- Anderson Park Botanic Gardens, Mundingburra
- Pat Molloy Park, North Ward
- a private residence at Ross River Road, Mundingburra
- road-side planting, Ross River Road, Cranbrook

Table 6.4. Species of *Livistona* examined.

n = number of individuals; Location: P = The Palmetum,

A = Anderson Park Botanic Gardens, other = cultivated in Townsville

species	number, location
1. *L. australis*	n = 7 (P)
2. *L. benthamii*	n = 2 (P), n = 3 (A)
3. *L. chinensis*	n = 12 (P), n = 3 (A), n = 6 (other)
4. *L. concinna*	n = 1 (A)
5. *L. decora*	n = 40 (P), n = 8 (A)
6. *L. drudei*	n = 7 (P), n = 5 (A)
7. *L. fulva*	n = 2 (P)
8. *L. humilis*	n = 1 (P)
9. *L. inermis*	n = 1 (P)
10. *L. lanuginosa*	n = 12 (P), n = 3 (A), n = 16 (other)
11. *L. mariae*	n = 5 (P), n = 4 (A)
12. *L. merrillii*	n = 2 (P), n = 1 (A)
13. *L. muelleri*	n = 5 (P), n = 5 (A), n = 5 (other)
14. *L. nasmophila*	n = 5 (P)
15. *L. nitida*	n = 5 (P)
16. *L. rigida*	n = 3 (P)
17. *L. saribus*	n = 5 (P), n = 3 (A)
	Total: n = 177

All individuals (n = 177) of *Livistona* species growing in the above locations were provided with an identification code. The number of individuals studied per species ranged from 1 to 48. Observations commenced in October 1998 and continued until September 2000. Plants were examined at a maximum interval of one month and a minimum of daily observations for some species during flowering events. From the 17 species, four were chosen for detailed examination. These four species were considered to be representatives of the major ecological types in the genus.

The selection criteria included:

- *putative sexuality* – at least one of the study species to be putatively hermaphroditic and at least one of the study species to be putatively functionally dioecious based on literature or informal observations.
- *ecological type* – the following six ecological types to be represented at least once in the species to be studied: widespread or restricted distribution; continuous or disjunct distribution; and continental or insular occurrence.
- *flowering period* – at least one of the study species to flower in the dry season and at least one in the wet season.
- *numbers available* – minimum of 15 reproductively active plants from which to choose those for detailed study.
- *access to plants* – not crowded by other plants; and plants of low stature.
- *approximation of natural conditions* – the placement of plants in relation to each other to have some resemblance to natural population densities; exposure and soil drainage properties to resemble natural conditions.

The species chosen, with ecological and distribution data, were as listed below. In all cases the sexual system was putative as explained above.

- *L. chinensis* (Jacq.) R. Br. – hermaphroditic, widespread distribution in insular and moist environments; studied palms were growing in avenues of closely placed individuals; n = 21; (Fig. 6.5, top left).
- *L. decora* (Bull) Dowe – functionally dioecious, widespread and continuous continental population in seasonal environment; studied palms were growing in avenues of closely placed individuals; n = 48; (Fig. 6.5, top right).
- *L. lanuginosa* A. N. Rodd – functionally dioecious, rare species of very restricted disjunct distribution in semi-arid continental environment; studied palms were growing in a scattered irregular arrangement; n = 31; (Fig. 6.5, bottom left).
- *L. muelleri* F. M. Bailey – functionally dioecious, widespread but disjunct insular and continental distribution in strongly seasonal environment; studied palms were growing in avenues of closely placed individuals; n = 15; (Fig. 6.5, bottom right).

Figure 6.5. Habits of species of *Livistona* studied. ***Top left:*** *Livistona chinensis.* ***Top right:*** *L. decora.* ***Bottom left:*** *L. lanuginosa.* ***Bottom right:*** *L. muelleri.*

Four representative individuals were chosen from each of these species, to include two fruit-bearing and two nonfruit-bearing individuals in those species where the two types of plants occurred. Where all plants were fruit-bearing (as in *L. chinensis*), four individuals were chosen. Table 6.5 summarises the characteristics of the four species included in this study.

Table 6.5. Characteristics of species studied.

	L. chinensis	*L. decora*	*L. lanuginosa*	*L. muelleri*
natural habitat	coastal closed forest	coastal to near coastal closed forest	open forest, woodland, seasonally dry savannah	closed forest, open woodland, seasonally wet savannah
height to	15 m	18 m	18 m	12 m
# of leaves	40-60	30-60	35-45	25-35
leaf length	300-380 cm	270-360 cm	280-390 cm	130-190 cm
inflorescence length	100-120 cm	100-350 cm	140-220 cm	80-160 cm
# of partial inflorescences	c. 7	c. 10	c. 10	c. 8
branching order	3	4	4	4
sepals	cream/yellow	cream/yellow	cream/yellow	pink/maroon
petals	cream/yellow	cream/yellow	cream/yellow	yellow
anthers	cream/yellow	cream/yellow	cream/yellow	yellow
carpels	cream/yellow	cream/yellow	cream/yellow	pink/maroon
inflorescence axes colour	green	cream/green	cream/green	maroon/red
fruit shape	globose/ ellipsoidal/ pyriform	globose	globose	ellipsoid/ obovate
fruit size	15-26 x 9-18 mm	12-15 mm	25-36 mm	10-12 x 7-10 mm
fruit colour	blue green	black	brown/black	bluish/black

6.12.1 *Predicting sexuality and breeding systems*

It is impractical to perform reproductive experiments in *Livistona* because most species are over 15 m tall at maturity, flowers and pollinators are difficult to observe, and the flowers, at 1-2 mm long, are difficult to manipulate with regards to emasculation and pollen dispersal experiments. Therefore, a method with the

potential to *predict* sexuality based on readily observable morphological characteristics was investigated. In angiosperms, certain characteristics of the inflorescence, flowers, pollen, and flowering/fruiting processes may be used to predict sexuality and breeding systems (Cruden and Millar-Ward, 1981; de Jong, 1999; Traveset, 1999). From the published literature based on experimental data involving a number of angiosperm families, including small understorey species of palms, nine characters that may have 'predictive value' (Table 6.6) were chosen in order to construct an index based on the concept developed by Thórsson *et al.* (2001) in their work with morphological characters of hybrids. Following the 'scoring' of the nine characters for each species, ranking indicates the relative position of each species on a gradient between hermaphroditism and dioecy.

Table 6.6. Characters that may have 'predictive value' in sexuality and breeding systems. Based on the publications of Cruden and Millar-Ward (1981), Richards (1997), de Jong (1999) and Traveset (1999), ➪ indicates a trend to dioecy.

1. number of nonfruit-bearing individuals in population: greater # of nonfruit-bearing [i. e. male] plants ➪ dioecy
2. nonflowering period [# of months]: greater # of months ➪ dioecy
3. flowering season: dry season flowering ➪ dioecy
4. P:O ratios: more pollen per ovule ➪ dioecy
5. number of flowers in inflorescence: more flowers ➪ dioecy
6. number of flowers in one season: more flowers ➪ dioecy
7. pollen size: smaller size ➪ dioecy
8. pollen per inflorescence: greater # pollen grains ➪ dioecy
9. pollen dispersal index: greater value ➪ dioecy

6.12.2 *An index of functional gender*

Using morphological characters, a method to present ranked data, showing the degree of hermaphroditism or dioecy among a group of species, was developed, and is termed here *an index of functional gender*. The index was established by using the comparative values applied to nine sexual characters (Table 6.6) for each of the study species (Table 6.5). In the index, hermaphroditism is arbitrarily assigned a value of '0', a theoretical state having no dioecious characters, and

dioecy a value of '1', a theoretical state having no hermaphroditic characters. The method is best explained by using a hypothetical data set for one of the nine characters listed in Table 6.6. Assume that the data are for P: O ratios for four taxa. The following procedure is used:

1. Summing the observed P: O ratios of 7400, 8000, 9000 and 1280 for species 1, 2, 3 and 4 respectively gives a total of 25680
2. The value '1' is assigned to 25680 and the data for each species are re-scaled to give a set of comparative values.
3. Thus, species 1 with a P :O value of 7400, represents 7400/25680 (0.29) of the total value for the character being considered.
4. By similar reasoning, species 2 can be assigned a value of 0.31 (8000/25680), species 3 a value of 0.35 (9000/25680) and species 4 a value of 0.05 (1280/25680).
5. This procedure is applied to the remaining eight characters.
6. For each species being considered, the nine character scores are then summed, to provide an 'ultimate' score for each.
7. The ultimate scores are then used to present the relative positions of the four species on a gradient between '0' and '1', which is a schematic representation of the index of functional gender.

6.12.3 *Explanation of characters*

Characters 1-3: Percentages of nonfruit-bearing individuals in the population; flowering/fruiting period; and flowering season

The absence or presence of flowers and/or fruit was recorded for each individual. The numbers of nonfruit-bearing plants for each species were calculated. This was to provide an indication of the sexual function of individual plants, i. e. fruit-bearing plants were considered 'female' and nonfruit-bearing plants 'male'. The months in which flowering and fruiting occurred was recorded, as were the percentages of flowering/fruiting individuals for the species.

Character 4: Pollen:ovule (P:O) ratios

Five flowers were randomly chosen from a single inflorescence of each species. From these, all six anthers were removed from each flower and the 30 anthers pooled. From the pooled group, five anthers were randomly chosen. Pollen grains

were released by maceration with dissecting needles, and the pollen grains in each anther were manually counted. To obtain the aggregate for a single flower, the number in one anther was multiplied by six as there are six anthers in each flower. It was assumed that all the anthers in a single flower each contained the same number of pollen grains. The flowers of most Coryphoid palms contain one to three ovules, of which usually only one is fertile (Tomlinson, 1990). The P:O ratios were calculated as the number of pollen grains per flower to a single ovule since the number of functional ovules in *Livistona* is one. However, in many *Livistona* species flowers are produced in sympodial clusters, and in these clusters individual flowers originate in the axil of the bracteole of the more proximal flower. If one flower is successfully pollinated in a cluster, the distal flowers abort. It was observed that only one fruit was produced for each flower cluster. Some species have clusters with potentially two to seven active flowers. In effect, the pollen of all flowers in a cluster is available for only the one potentially successful ovule within a cluster. If the lowest flower is successfully pollinated then the remaining flowers will abort and the P:O ratio will be calculated for the pollen from a single flower and the single fertile ovule per flower. However, if the most distal flower in the cluster is successfully pollinated then the pollen of the preceding flowers, i. e. up to seven, must be included in the ratio. Until tested, it is assumed that the pollen in all flowers is viable. To overcome this potential conflict, the pollen from the mean number of flowers in each cluster was calculated, and used to determine the P:O ratio. Therefore, a range of P:O ratios for each species was calculated based on:

- pollen of one flower to one ovule [low range]
- pollen from the mean number of flowers per cluster to one ovule [high range]

Characters 5 and 6: Number of flowers per inflorescence; and number of flowers per season

A typical flowering inflorescence was chosen from each of the study species. Ten rachillae were randomly excised and the number of flowers counted on each, and a mean obtained. The number of rachillae on the entire inflorescence was then counted, and this number multiplied by the mean number of flowers per rachilla. Tomlinson and Soderholm (1975) found that in *Corypha utan* Lam., rachilla length and flower number per rachilla were "surprisingly uniform". The

inflorescences of *Livistona* and *Corypha* are of a similar structure, although the length of the rachillae may be relatively disparate. To calculate the number of flowers produced in a season, the number of flowers on a single inflorescence was multiplied by the number of inflorescences produced in one flowering season.

Characters 7 and 8: Pollen size and abundance

Just prior to anthesis, ten anthers were randomly chosen from an inflorescence of each species. For examination using light microscopy, the anthers were macerated with dissecting needles in a drop of distilled water on a glass slide to release the pollen. Twenty pollen grains were randomly chosen and were measured using a micrometer attached to the microscope and calibrated according to Florian (1994). Long axes (L) and short axes (l) were measured to determine mean lengths and to calculate pollen grain volumes. The formula for calculating the volume of a sphere was used - $V = \frac{4\pi r^3}{3}$, where $r = \frac{\text{long axis (L)} + \text{short axis(l)}}{4}$

In addition to light microscopy, scanning electron microscopy was also utilised. For this, pollen grains were selected in a similar manner. The fresh flowers were manoeuvred over SEM stubs that had been prepared with double-sided tape. The anthers were ruptured with a dissecting needle and the pollen dropped onto the stubs. The stubs were platinum coated in a JUC – 5000 magnetron sputtering device with ultra fine coat set to 'automatic mode' and a coating duration of 2.5 minutes. Stubs were examined in a Philips XL20 Scanning Electron Microscope with power at 15kv and spot value at 3. A uniform magnification of x2000 was used for all species. Characteristics and measurements were compared with those obtained from the light microscopy.

Character 9: Pollen dispersal

An adaptation of the pollen dispersal hypothesis of Cruden (1977) was invoked to provide an estimate of the potential effective dispersability of pollen for the four study species. The hypothesis suggests that pollen with a relatively higher dispersal index is more widely dispersed. It is therefore more likely to be indicative of dioecy as dioecious species are not usually as closely aggregated as species that are not dioecious. The index is calculated by dividing the number of pollen grains in an inflorescence by the volume of a single grain.

6.12.4 *Pollen exclusion experiments*

On six inflorescences of the fruit-bearing plants for each of the four study species, groups of rachillae on a single partial inflorescence were covered with pollen/insect exclusion bags of 20 x 16 cm size. The number of rachillae varied from four to ten, depending upon their length and degree of spread. The bags were attached prior to floral maturity and removed after four weeks. Those for *L. chinensis* and *L. decora* were placed in September, those on *L. lanuginosa* in May, and those on *L. muelleri* in February. The effectiveness of pollination, determined by fruit set, was compared in bagged/unbagged rachillae on the same inflorescence.

6.13 Results

6.13.1 *Character 1: Percentages of nonfruit-bearing individuals*

Fruit-bearing palms were defined as those bearing fruit to any degree, and nonfruit-bearing plants never bore any fruit. Some palms bore fruit in abundance on all inflorescences, with up to 13 infructescences in a season, and for the majority of flowers on an inflorescence. At the other extreme, some individuals were observed with fruit on a single inflorescence, out of a possible nine flowering inflorescences, and only on a single partial inflorescence. *Livistona chinensis* had a nonfruit set rate of 0 of 21 plants [0.0%]; *L. decora* had a rate of 12 of 45 plants [17.8%]; *L. lanuginosa* had a rate of five of 31 [17%]; and *L. muelleri* had a rate of five of 15 plants [33.3%] (Fig. 6.6).

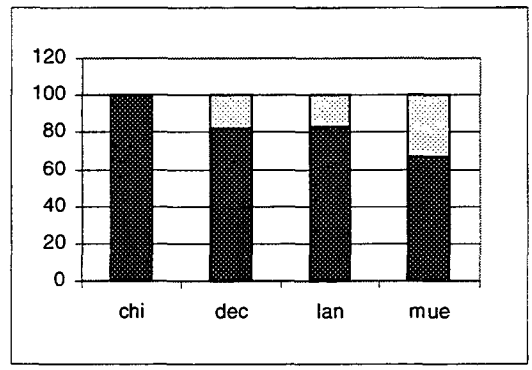


Figure 6.6. Percentages of fruit-bearing/nonfruit-bearing plants in the study populations. The fruit-bearing percentage is represented by the shaded part of the column, nonfruit-bearing percentage by the lightly-stippled portion.
chi = *L. chinensis*; dec = *L. decora*; lan = *L. lanuginosa*; mue = *L. muelleri*.

6.13.2 *Characters 2 and 3: Flowering/fruiting duration, and flowering season*

Calendars of flowering and fruiting occurrence over 15 months [July 1999 to September 2000] are presented for the four study species (Fig. 6.7). The percentage of flowering and fruiting individuals is plotted against calendar months. Over a 12 month period [July 1999 to June 2000], flowering in *L. chinensis* occurred in four months [July – October] and peaked in August, while fruit was observed in all months peaking in September-October (Fig. 6.7a). For *L. decora*, flowering was recorded in 5 months [June – October] with a peak in September, and fruiting was observed in all months with a peak in January-February (Fig. 6.7b). For *L. lanuginosa*, flowering was recorded in seven months [March – September] with an extended peak from May to August, and fruiting was observed in eight months [June – January] with a peak in October (Fig. 6.7c). For *L. muelleri*, flowering occurred in 6 months [January – June] with peaks in February and April, and fruit was observed in nine months with a peak in September-October (Fig. 6.7d). Flowering periods were determined as the months when a minimum of 50% of the population was flowering. For example, in *L. chinensis*, there were two months when flowering was occurring in 50% or more of individuals, while in *L. decora* it was three, in *L. lanuginosa* it was seven, and in *L. muelleri* it was three. This converts to *Livistona chinensis* having had ten nonflowering months; *L. decora* nine; *L. lanuginosa* five; and *L. muelleri* nine.

To calculate a score for flowering season, scores were applied to dry and/or wet season months correlated with the months of flowering for each species. Based on meteorological data for the Townsville region, the dry season months are May to December, and wet season months, January to April. Based on a 12 month cycle in *Livistona chinensis*, more than 50% of the population was in flower in two dry season months, and therefore scored 2/12 [0.16]; *L. decora* in four months, scored 4/12 [0.3]; *L. lanuginosa* in six months, scored 6/12 [0.5]; and *L. muelleri* in one month, scored 1/12 [0.08].

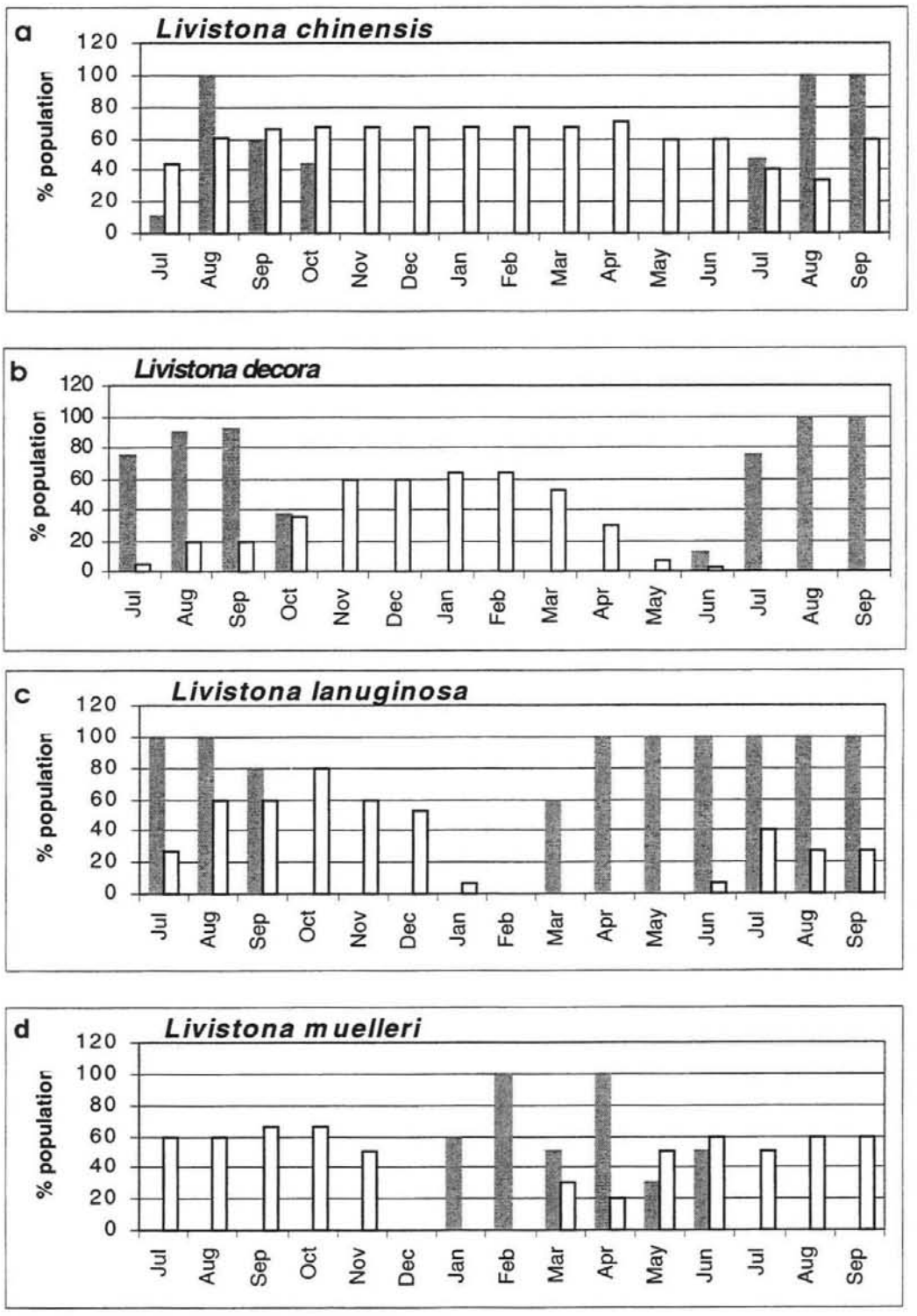


Figure 6.7 a-d. Flowering and fruiting calendars for the four study species.

Observations were made monthly from July 1999 to September 2000.

a. *Livistona chinensis* (n = 21); **b.** *Livistona decora* (n = 45); **c.** *Livistona lanuginosa* (n = 31); **d.** *Livistona muelleri* (n = 15). Percentage of flowering individuals per month = grey columns; percentage of fruiting individuals per month = clear columns. See Appendix 20 for values used.

6.13.3 *Character 4: Pollen:ovule (P:O) ratios*

The mean numbers of pollen grains per flower and P:O ratios were as follows (Fig. 6.8; Appendix 21).

	one flower	*per cluster*
• *Livistona chinensis*	3700±145.8	14800 [4 fls/cluster]
• *Livistona decora*	4000±207.9	14000 [3.5 fls/cluster]
• *Livistona lanuginosa*	4500±153.3	9000 [2 fls/cluster]
• *Livistona muelleri*	640±90.4	1920 [3 fls/cluster]

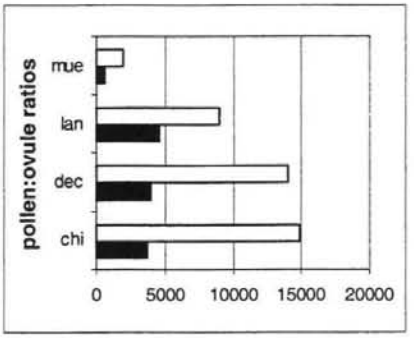


Figure 6.8. Pollen:ovule ratios in *Livistona chinensis* (chi), *L. decora* (dec), *L. lanuginosa* (lan) and *L. muelleri* (mue). The shaded bars represent the ratio in one flower, i.e. the pollen in six anthers to one ovule. The unshaded bars represent the ratio of the average number in a cluster to one ovule. The average number of flowers per cluster for each species are: *L. chinensis* - 4; *L. decora* - 3.5; *L. lanuginosa* - 2; *L. muelleri* - 3.

6.13.4 *Characters 5 and 6: Number of flowers per inflorescence; and number of flowers per season*

To estimate the number of flowers in a flowering event, the number of flowers in an inflorescence was multiplied by the number of inflorescences.

	fls/inflor	inflors/season	fls/season
• *Livistona chinensis*	66,792	13	868 x10³
• *Livistona decora*	288,610	13.5	3,824 x10³
• *Livistona lanuginosa*	500,480	14	6,005 x10³
• *Livistona muelleri*	202,335	12	2,428 x10³

6.13.5 *Character 7: Pollen size – dimensions and volume*

The mean of the long axes (L) and short axes (l), and volumes of pollen grains (n = 20) are presented for each species (Figs 6.9, 6.10; Appendix 22):

n = 20	L	SD	l	SD	volume
• *Livistona chinensis*	27.0 μm	0.70	21.6 μm	0.49	7513 μm³
• *Livistona decora*	19.6 μm	0.81	15.6 μm	0.57	2854 μm³
• *Livistona lanuginosa*	25.7 μm	1.04	16.2 μm	0.74	4814 μm³
• *Livistona muelleri*	23.4 μm	0.74	18.7 μm	0.66	4883 μm³

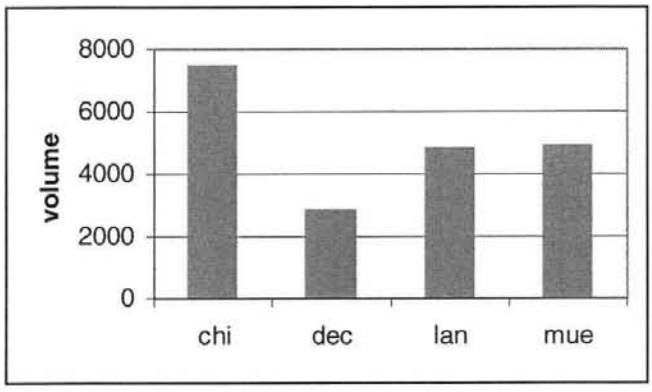


Figure 6.9. Comparison of the mean volume in μm³ of single pollen grains in *Livistona chinensis* (chi), *L. decora* (dec), *L. lanuginosa* (lan) and *L. muelleri* (mue).

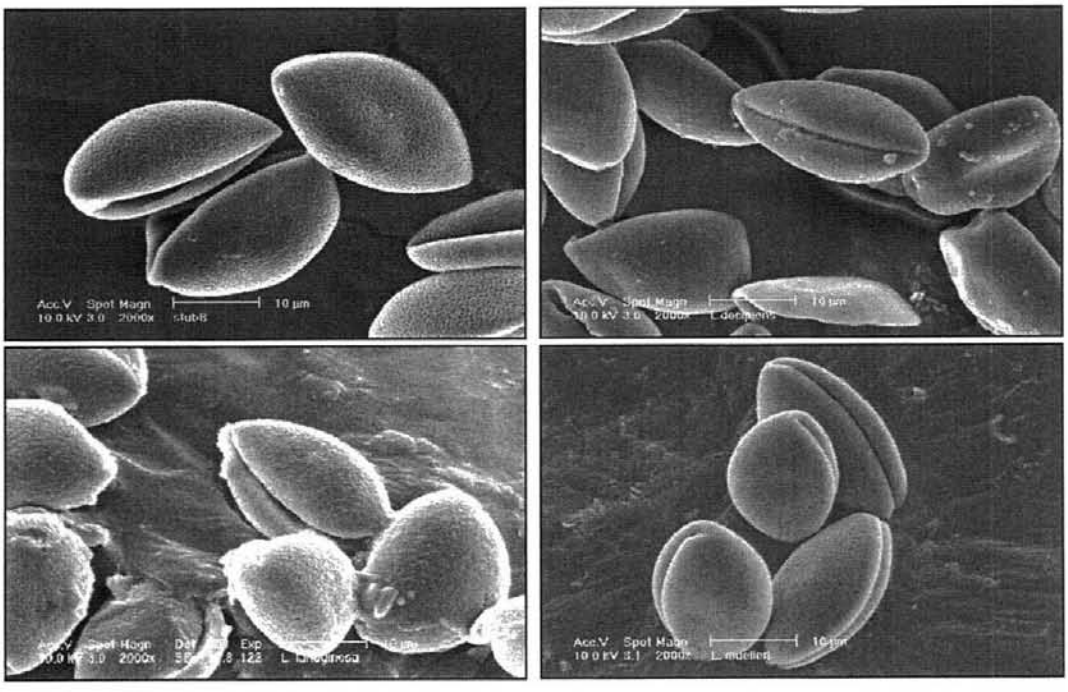


Figure 6.10. Pollen micrographs of *Livistona* species. *Top left:* *L. chinensis*. *Top right:* *L. decora*. *Bottom left:* *L. lanuginosa*. *Bottom right:* *L. muelleri*.

6.13.6 *Characters 8 and 9: Pollen abundance and pollen dispersal index*

The numbers of pollen grains in an inflorescence, and the pollen dispersal index (Cruden, 1977) calculated as a ratio of number of pollen grains to pollen volume were as follows:

	pollen grains/inflorescence	volume (μm^3)	dispersal index
• *Livistona chinensis*	247,130,400	7513	32894
• *Livistona decora*	1,154,440,000	2854	404499
• *Livistona lanuginosa*	2,252,160,000	4814	467835
• *Livistona muelleri*	129,494,400	4883	26519

6.14 Results of pollen exclusion experiments

	# pollen exclusion bags	fruit set
L. chinensis inflor. 1.	6	c. 100%
L. chinensis inflor. 2.	6	c. 100%
L. decora inflor. 1.	6	c. 100%
L. decora inflor. 2.	6	c. 100%
L. lanuginosa inflor. 1	6	nil
L. lanuginosa inflor. 2	6	nil
L. muelleri inflor. 1.	6	c. 50%
L. muelleri inflor. 2.	6	c. 50%

In *Livistona chinensis* and *L. decora*, flowers inside the pollen/insect exclusion bags were fertilised at a rate of 100%, the same rate as those that were unbagged. This suggests that flowers are either autogamous or geitonogamous within the rachillae and that insects, as pollination, vectors were most likely not involved. *Livistona lanuginosa* flowers within the pollen/insect exclusion bags failed to produce any fruit. This suggests that *L. lanuginosa* plants are xenogamous but undetermined as to whether they are anemophilous or entomophilous.

Livistona muelleri flowers within the pollen/insect exclusion bags became fertilised to a degree estimated at 50% of that of unbagged rachillae. This suggests that flowers are either autogamous and geitonogamous within the rachillae, and

that insects as pollination vectors were equally likely to effect successful pollination than abiotic means.

6.15 The *index of functional gender* - Figure 6.11

The data (Table 6.7) were treated as explained in section 6.12.1. The resulting values are listed in Table 6.8 and the index of functional gender is shown in Figure 6.11.

Table 6.7. Data for the nine predictive characters for the four study species.

	L. chinensis	*L. decora*	*L. lanuginosa*	*L. muelleri*
character	(n = 21)	(n = 45)	(n = 31)	(n = 15)
1.nonfruiting individuals	0/21 [0%]	12/45 [26.7%]	5/31 [16.1%]	5/15 [33.3%]
2.nonflowering period	10 mths	9 mths	5 mths	9 mths
3.flowering season	2 dry mths	4 dry mths	6 dry mths	1 dry mth
4.P:O ratio – one flower	3,700	4,000	4500	640
5.flowers/inflorescence	66,792	288,610	500,480	202,335
6.flowers/one season	$868x10^3$	$3,824x10^3$	$6,005x10^3$	$2,428x10^3$
7.pollen size (volume)	7513 μm^3	2854 μm^3	4814μm^3	4883 μm^3
8.pollen abundance $x10^3$	247,130	1,154,440	2,252,160	29,494
9.pollen dispersal index	32,894	404,499	467,835	26,519

Livistona chinensis had a value of 0.15, *L. decora* 0.29, *L. lanuginosa* 0.39, and *L. muelleri* 0.17. These ultimate values were used to construct the index in Figure 6.11.

Table 6.8. Values used in constructing the index of functional gender.

character	hermaphroditism	*L. chinensis*	*L. decora*	*L. lanuginosa*	*L. muelleri*	dioecy
1.	0	0	0.27	0.25	0.48	1
2.	0	0.31	0.27	0.15	0.27	1
3.	0	0.16	0.31	0.46	0.07	1
4.	0	0.29	0.31	0.35	0.05	1
5.	0	0.07	0.27	0.47	0.19	1
6.	0	0.07	0.29	0.46	0.18	1
7.	0	0.37	0.15	0.24	0.24	1
8.	0	0.07	0.31	0.61	0.01	1
9.	0	0.04	0.43	0.50	0.03	1
Subtotals:	0	1.38	2.61	3.49	1.52	9
Rescaled	**0**	**0.15**	**0.29**	**0.39**	**0.17**	**1.0**

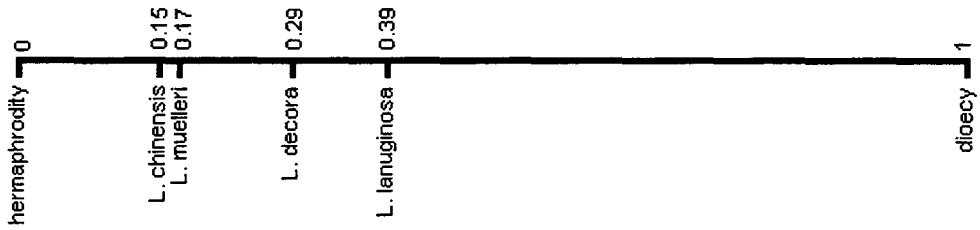


Figure 6.11. The index of functional gender, including *Livistona chinensis*, *L. decora*, *L. lanuginosa* and *L. muelleri*, plotted on a line of increasing value between hermaphroditism and dioecy. The Index was constructed from data presented in Tables 6.7 and 6.8. On the index, the higher value indicates a greater number of dioecious characters. The species are plotted along a gradient from hermaphroditism (0) to dioecy (1) with each species positioned at its relevant point.

6.16 Discussion and conclusion

There is evidence that flowering phenologies of cultivated palms are similar to those that occur in natural populations. Herrera (1989), in a study of *Chamaerops humilis* (European fan palm), noted that there was little difference between cultivated and wild plants in regards to phenology and sexuality. In a study of the flowering and fruiting of *Wodyetia bifurcata* Irvine (foxtail palm) in cultivation in The Palmetum, Townsville, Dowe (1993) found that phenology matched that of the wild populations. Reports of flowering and fruiting in natural populations of *L. chinensis* correspond with plants observed during this study (Figure 6.7). Walker (1976) and Horikawa (1972) reported *L. chinensis* flowering in April and May and fruiting in August to November, in the northern hemisphere, which seasonally adjusted for the southern hemisphere, is flowering in August and September and fruiting in January to April. As for morphology and anatomy, the study of cultivated plants is useful as a primary source of information (Tomlinson, 1990), and some palm collections in Botanical Gardens have been established and designed with research on population dynamics as primary tenets (Chakraverty and Basu, 1994; Chapin and Lorence, 2000).

For plants in cultivation, differences from natural conditions must be considered. Three of the study species, *L. decora*, *L. lanuginosa* and *L. muelleri*, occur close to the study sites in Townsville, and are subject to similar climatic and edaphic conditions as in the natural environment (Table 6.5). However, *L. chinensis* is distributed in the Ryukyu Archipelago and islands of southern Japan. This is a subtropical region with a mildly seasonal climate, so it may be that plants cultivated in Townsville will behave differently to those in nature. However, the phenological pattern, as illustrated by the data in Fig. 6.7, suggested that it was reasonable to assume that there was a similarity between cultivated and wild plants for this species.

Although there was general concordance of morphology and phenology of cultivated and wild palms in this study, there can be no direct comparison between natural and cultivated populations with respect to pollination and fertilisation success due to the potential activities of pollinators. This study aimed to analyse sexual conditions using characters that were independent of pollinator activities, as far as possible. However, interpretation of one character, whether individuals are fruit-bearing or nonfruit-bearing, may be influenced by pollinator activities. If fruit set is exclusively pollinator dependant then fruit set could be either enhanced or limited by the degree of pollinator activity in cultivation. Concomitantly, the degree of success, measured as the number of fruit set, cannot be exclusively matched to successful pollination and fertilisation, as pollinator-independent and post-fertilisation incompatibility systems will influence success rates. However, if fruit set is abiotically controlled, as in anemophily, then the rate of pollination and fertilisation success should not be influenced by whether palms are cultivated or wild, i. e., pollination and fertilisation will not be pollinator dependant.

This study has revealed that there is variability in the sexual expression in some species of *Livistona* (Fig. 6.11). Based on analysis of nine sexual and reproductive characters (Table 6.7), it was found that *L. chinensis* had the largest number of hermaphroditic characters, scoring 0.15 on the index of functional gender, and that increasing scores toward dioecy were occurring in *L. muelleri* (0.17), *L. decora* (0.29) and *L. lanuginosa* (0.39) respectively. Of the 200 genera in the palm family, about nine genera are known to have species that have different

modes of sexual expression (Uhl and Dransfield, 1987). Those genera all occur in the subfamily Coryphoideae, and some are closely related to *Livistona*.

Rodd (1998) concluded that some Australian species of *Livistona* were androdioecious. For dioecious species, it is expected that the flowers on both types of plants should be morphologically readily identifiable. In *Livistona*, flowers on both fruit-bearing (hermaphroditic) and nonfruit-bearing (putative male) individuals are morphologically similar: pollen and ovules were present in all flowers on all plants. However, due to the consistent and predictable presence of both fruit-bearing and nonfruit-bearing individuals, it was apparent that some sexual organs had lost their function. Any morphological changes related to function were not identifiable by ordinary visual means, and further investigation at microscopic level was not possible due to time constraints.

If some of the Australian species are androdioecious as suggested by Rodd (1998), [but lacking readily observable morphological variation] it would be an unusual situation. Androdioecy has been documented in only a few plant species (Fritsch and Rieseberg, 1992) and is generally considered to have evolved from dioecious rather than from hermaphroditic ancestors (Richards, 1997), although Wallender (2001) recently indicated that it may be one of the pathways from hermaphroditism to dioecy in some species. The rarity of the condition is due to the requirement that males must have an outcrossing rate at least double that of the hermaphrodites (Liston *et al.*, 1990), to maintain selection. Recent studies (Pannell, 1997b; Wallender, 2001) have found that androdioecy occurs more commonly than previously thought. It is reasonable to assume that fertilisation of hermaphroditic flowers by the pollen from male flowers could occur. Pollen/insect exclusion experiments (section 6.14) indicated those flowers on fruit-bearing plants of *L. chinensis*, *L. decora* and *L. muelleri* were self-fertile, thus limiting the dependence upon pollen from the male plants for fertilisation. However, this does not prove or disprove that fertilisation can be effected by the pollen from male plants. If there is a contribution of pollen from the male plants it, at least theoretically, must be at a very high rate if the males are to maintain genetic integrity in a population (Liston *et al.*, 1990).

In palm species, there is usually a predominance of males, both as numbers of plants in populations of dioecious species (Silvertown, 1987), and of flowers present in a population, in monoecious species (Hidajat, 1987; Borchsenius, 1993). However, in the studied species, there was a predominance of female plants, that is, a greater number of fruit-bearing plants than nonfruit-bearing plants. Is this an indication of high female fitness? Female fitness is estimated to be relatively higher in situations other than where hermaphroditism occurs (Charnov *et al.*, 1976), and is also predicted to be high in 'unstable' conditions (Burd, 1994; Richards, 1997). Could it be that some *Livistona* species are in transition from an ancestral hermaphroditic situation to dioecy as an adaptation to environmental stress, either aridity or nutrient limitation (Eckhart and Seger, 1999)?

Those species with the greater number of dioecious characters (Fig. 6.11), *L. decora* and *L. lanuginosa*, occur in environments where the climate is semi-arid to strongly seasonal (Table 6.5) and where there has been a change over time from aseasonal to seasonal, accompanied by increasing environmentally-induced stresses (Truswell, 1990). The effects of an increasingly stressful climate may produce a decrease in pollinator effectiveness, i. e., a reduction in pollinator specificity or unique symbiotic arrangements, and an increase in 'generalist' reproductive systems that are often associated with anemophily. Silberbauer-Gottsberger (1990) suggested that exclusive reliance on anemophily in palms was doubtful, and that species that were predominantly anemophilous were also entomophilous to some degree. Flower morphology and pollen characteristics (Figs 6.9, 6.10) of *L. decora* and *L. lanuginosa*, are suggestive of anemophily. Cruden (1977) and Cruden and Millar-Ward (1981) identified high pollen:ovule ratios, relatively smaller pollen and a greater pollen dispersal index as anemophilous indicators for plants. Further support for anemophily is based on the high rate of autogamy and geitonogamy in the insect/pollen exclusion experiments, as presented in section 6.14. However, this does not exclude the possibility of entomophily being a contributing factor in pollen dispersal and subsequent fertilisation, and it is possible that both anemophily and entomophily contribute to reproductive success.

It is proposed, based on inflorescence, flower and pollen morphologies (section 6.13), and the results of pollen exclusion experiments (section 6.14), that *L. chinensis* and *L. decora* are most likely primarily anemophilous, that *L. muelleri* is possibly both anemophilous and entomophilous, and that the situation with *L. lanuginosa* is unable to be determined. The data presented indicate that *L. chinensis* is predominantly autogamous, which is directly related to the hermaphroditism of that species, although geitonogamy and xenogamy may also be involved. *Livistona decora* and *L. muelleri* may exhibit autogamy (i. e., within-flower selfing), geitonogamy and xenogamy. Some flowers of these two species appear to be functionally dioecious, suggesting that in the one population there could be hermaphrodites, functional males and functional females, effectively a trioecious breeding system. *Livistona lanuginosa*, because of its apparent absence of autogamy but utilisation of geitonogamy and xenogamy, and its position on the index of functional gender (Fig. 6.11), may be described as functionally dioecious in the absence of definitively recognisable male or female plants.

Chapter 7

Studies in the genus *Livistona* R. Br. (Coryphoideae: Arecaceae)

GENERAL SUMMARY

7.1 Introduction

The primary aim of this thesis was to revise the taxonomy of the genus *Livistona* throughout its entire range. The five lines of investigation are summarised below.

7.1.1 *Systematics*

The taxonomic revision recognised 35 currently accepted taxa. 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. Some of these valid names are in synonymy, and require typification. Others are nomenclaturally invalid, and these do not require typification. Four new species, *Livistona chocolatina*, *L. concinna*, *L. surru* and *L. tothur*, were recognised as part of this treatment. Of these, the latter three have recently been formally published (Dowe and Barfod, 2001), while the first listed species will be formally published as part of the revision of *Livistona* intended for publication in the Gardens Bulletin, Singapore. Eleven names have been proposed for 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 two species: *Livistona decipiens,* which becomes *L. decora*, and *L. mariae* var. *occidentalis,* which becomes *L. nasmophila.*

7.1.2 *Cladistics*

Cladistic analyses were performed based on 43 characters and 35 taxa, and 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 trifurcate, or infrequently bifurcate, with ± identical collateral axes, fruit passing through an orange/red phase to mature either orange, red or black, regularly segmented leaves
- *humilis* subclade - inflorescence not basally branched, 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 and bootstrap support was low for the analyses and therefore the result cannot be accepted as a reliable estimate of phylogeny. However, the results, which may be used cautiously, indicate relationships between species groups.

7.1.3 *Molecular investigation*

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 that region could provide information on genetic relationships and molecular phylogeny. DNA was amplified using 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. The ITS region is potentially useful as a tool for both phylogenetic and biogeographical studies, and general aspects of homogenisation and concerted evolution may well be explained by further investigation of *Livistona* ITS DNA.

7.1.4 *Historical biogeography*

Based on three lines of investigation, the fossil record, area analysis and cladistics, biogeographical hypotheses are proposed for *Livistona*. The fossil record suggests a Laurasian origin for the genus. The analysis of area endemism, based on the

Parsimony Analysis of Endemism (PAE) method, indicates the close relationships of some contiguous areas. The cladistic analysis suggests a number of possible scenarios, including an exclusively Laurasian origin, or a number of possible 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 certain landmasses on which ancestral species occurred. Extensive speciation has since occurred in Australia and Malesia, with putative relictual species occurring in Africa and Australia. *Livistona* in Australia is most plausibly the result of migration from a northern Laurasian source rather than by autochthonous evolution.

7.1.5 *Sexuality and the index of functional gender*

The examination of morphological data among a selected group of species indicated a trend in gender function from hermaphroditism to functional dioecy. *Livistona chinensis*, *L. muelleri*, *L. decora* and *L. lanuginosa* can be ranked respectively in terms of increasing degrees of dioeciousness. It is predicted that there is a trend from autogamy/geitonogamy in *L. chinensis*, and to autogamy/geitonogamy/ xenogamy in *L. decora*, *L. lanuginosa* and *L. muelleri*. Functional dioecy in *Livistona* may be related to the evolution of species in drier, stressful environments.

7.2 Future work

Taxonomically, *Livistona* is now relatively well understood and the relationships between groups of species established. Aspects of reproductive biology require further study as do processes of adaptation and evolution. Molecular investigation of the ITS regions, or some other genes, will be appropriate to determine a detailed phylogeny for the genus, and contribute to the further development of the biogeographical hypotheses presented in this thesis.

References

Ambwani, K. and M. Kumar (1991). SEM studies of pollen in *Nypa fruticans* Wurmb. *Phytomorphology* 41: 253-255.

Amersham (1997). *pMOSBlue blunt ended cloning kit, RPN 5110.* Buckinghamshire: Amersham International.

Anderson, A. B., W. L. Overal and A. Henderson (1988). Pollination ecology of a forest-dominated palm (*Orbignya phalerata* Mart.) in northern Brazil. *Biotropica* 20: 192-205.

Anderson, G. J. (1979). Dioecious *Solanum* species of hermaphroditic origin is an example of a broad convergence. *Nature* 282: 836-838.

Anderson, G. J. and D. E. Symon (1989). Functional dioecy and andromonoecy in *Solanum*. *Evolution* 43: 204-219.

Andersson, L. (1990). The driving force: species concepts and ecology. *Taxon* 39: 375-382.

André, E. (1874). *Livistona hoogendorpii. L'illustration horticole* 21: 108.

Anzizar, I., M. Herrera, W. Rohde, A. Santos, J. L. Dowe. P. Goikoetxea and E. Ritter (1998). Studies on the suitability of RAPD and ISTR for identification of palm species (Arecaceae). *Taxon* 47: 635-645.

Asmussen, C. B. (1999). Toward a chloroplast DNA phylogeny of the tribe Geonomeae (Palmae). *Mem. New York. Bot. Gard.* 83: 121-129.

Asmussen, C. B., W. J. Baker and J. Dransfield (2000). Phylogeny of the palm family (Arecaceae) based on *rps*16 intron and *trn*L-*trn*F plastid DNA sequences. In: K. L. Wilson and D. A. Morrison (eds), *Monocots: systematics and evolution*, 525-537. Melbourne: CSIRO.

Asmussen, C. B. and M. W. Chase (2001). Coding and noncoding plastid DNA in palm systematics. *Am. J. Bot.* 88: 1103-1117.

Axelrod, D. I. and P. H. Raven (1978). Late Cretaceous and Tertiary vegetation history of Africa. In: M. J. A. Werger (ed), *Biogeography and ecology of southern Africa*, 77-130. The Hague: Junk.

Backer, C. A. and R. C. Bakhuizen van der Brink (1968). Arecaceae. *Fl. Java* 3: 165-199.

Bailey, F. M. (1898). Contributions to the Queensland Flora. Order Palmae. *Qld Agric. Journ.* 2: 129-131.

Bailey, F. M. (1902). Palmae. *Queensl. fl.* 5: 1670-1688.

Bailey, F. M. (1910). Comprehensive catalogue of Queensland plants, both indigenous and naturalised. Brisbane: Government Printer.

Bailey, L. H. (1976). *Hortus Third.* New York: Macmillan Publishing.

Baker, H. G. and P. A. Cox (1984). Further thoughts on dioecism and islands. *Ann. Missouri Bot. Gard.* 71: 244-253.

Baker, W. J., C. B. Asmussen, S. C. Barrow, J. Dransfield and T. A. Hedderson (1999). A phylogenetic study of the palm family (Palmae) based on chloroplast DNA sequences from the *trn*L-*trn*F region. *Plant Syst. Evol.* 219: 111-126.

Baker, W. J., M. J. E. Coode, J. Dransfield, S. Dransfield, M. M. Harley, P. Hoffmann and R. J. Johns (1998). Patterns of distribution of Malesian vascular plants. In: R. Hall and J. D. Holloway (eds), *Biogeography and geological evolution of SE Asia*, 243-258. Leiden: Backhuys Publishers.

Baker, W. J. and J. Dransfield (2000). Towards a biogeographic explanation of the Calamoid palms. In: K. L. Wilson and D. A. Morrison (eds), *Monocots: Systematics and evolution*, 545-553. Melbourne: CSIRO.

Baker, W. J., T. A. Hedderson and J. Dransfield (2000a). Molecular phylogenetics of subfamily Calamoideae (Palmae) based on nrDNA ITS and cpDNA *rps16* intron sequence data. *Mol. Phylogenet. Evol.* 14: 195-217.

Baker, W. J., T. A. Hedderson and J. Dransfield (2000b). Molecular phylogenetics of *Calamus* (Palmae) and related rattan genera based on 5S nrDNA spacer sequence data. *Mol. Phylogenet. Evol.* 14: 218-231.

Baldwin, B. G. (1992). Phylogenetic utility of the internal transcribed spacers of nuclear ribosomal DNA in plants: an example from the Compositae. *Mol. Phylogenet. Evol.* 1: 3-16.

Baldwin, B., M. J. Sanderson, J. M. Porter, M. F. Wojciechowski, C. S. Campbell and M. J. Donoghue (1995). The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Ann. Missouri Bot. Gard.* 82: 247-277.

Barcelos, E., G. Second, F. Kahn, P. Amblard, P. Lebrun and M. Seguin (1999). Molecular markers applied to the analysis of genetic diversity and to biogeography of *Elaeis* (Palmae). *Mem. New York Bot. Gard.* 83: 191-201.

Barfod, A. S. (1988). Leaf anatomy and its taxonomic significance in phytelephantoid palms (Arecaceae). *Nord. J. Bot.* 8: 341-348.

Barfod, A. S. (1991). A monographic study of the subfamily Phytelephantoideae (Arecaceae). *Opera Bot.* 105: 5-73.

Barfod, A. S., F. Ervik and R. Bernal (1999). Recent evidence on the evolution of Phytelephantoid palms (Palmae). *Mem. New York Bot. Gard.* 83: 265-277.

Barlow, B. A. (1981). The Australian flora: its origin and evolution. *Flora of Australia* 1: 25-75.

Barrett, S. C. H. (1998). The reproductive biology and genetics of island plants. In: P. R. Grant (ed.), *Evolution on islands*, 18-34. Oxford: Oxford University Press.

Barrow, S. (1999). Systematic studies in *Phoenix* L. (Palmae: Coryphoideae). *Mem. New York Bot. Gard.* 83: 215-223.

Basu, S. K. (1991). India: palm utilization and conservation. In: D. Johnson (ed), *Palms for human needs in Asia*, 13-35. Rotterdam: A. A. Balkema.

Basu, S. K. and R. K. Chakraverty (1994). *A manual of cultivated palms in India.* Calcutta: Botanical Survey of India.

Batten, D. J. (1984). Palynology, climate and the development of Late Cretaceous floral provinces in the Northern Hemisphere; a review. In: P. Benchly (ed), *Fossils and climate*, 127-164. Chichester: John Wiley and Sons.

Baum, B. R. (1988). A simple procedure for establishing discrete characters from measurement data, applicable to cladistics. *Taxon* 37: 63-70.

Bawa, K. S. (1980). Evolution of dioecy in flowering plants. *Ann. Rev. Ecol. Syst* 11: 15-39.

Bawa, K. S. and J. H. Beach (1981). Evolution of sexual systems in flowering plants. *Ann. Missouri Bot. Gard.* 68: 254-274.

Bawa, K.S. and P. A. Opler (1975). Dioecism in tropical forest trees. *Evolution* 29: 167-179.

Bawa, K. S. and C. J. Webb (1983). Floral variation and sexual differentiation in *Muntingia calabura* (Elaeocarpaceae), a species with hermaphrodite flowers. *Evolution* 37: 1271-1282.

Bayer, H. -J. (1984). The Arabian Shield. In: A. R. Jado and J. G. Zötl (eds), *Quaternary period in Saudi Arabia*, Vol. 2, 5-15. Wien: Springer-Verlag.

Bazara'a, M, L. Guarino, A. Miler and N. Obadi (1990). Observations on an endangered fan palm in Arabia. *Edinb. J. Bot.* 47: 375-379.

Beach J. H. (1984). The reproductive biology of the peach or "pejibayé" palm (*Bactris gasipaes*) and a wild congener (*B. porschiana*) in the Atlantic lowlands of

Costa Rica. *Principes* 28: 107-119.

Beaglehole, J. C. (1962). *The Endeavour journal of Joseph Banks 1768-1771.* Sydney: Angus & Robertson.

Beccari, O. (1877). Le specie di palme raccolte alla Nuova Guinea do O. Beccari e dal medesimo adesso desritte, con note suule species dei paesi circonvicini. *Malesia* 1: 9-102.

Beccari, O. (1886). Nuovi studi sulle palme asiatiche. *Malesia* 3: 58-149.

Beccari, O. (1904). Palmae. *Fragm. flor. Philipp.* 1: 45-48.

Beccari, O. (1905). Le Palme delle Isole Filippine. *Webbia* 1: 339-345.

Beccari, O. (1907). Notes on Philippine palms, I. *Philipp. J. Sci. C. Bot.* 2: 219-240.

Beccari, O. (1909). Notes on Philippine palms, II. *Philipp. J. Sci. C. Bot.* 4: 601-637.

Beccari, O. (1910). La "*Copernicia cerifera*" in Riviera ed una nuova specie di *Livistona. Webbia* 3: 295-305.

Beccari, O. (1911). The palms of the island of Polillo. *Philipp. J. Sci., C. Bot.* 6: 229-230.

Beccari, O. (1919a). Palms of the Philippine Islands, collected and distributed by D. E. Elmer. *Leafl. Philipp. Bot.* 8: 2997-3067.

Beccari, O. (1919b). The palms of the Philippine Islands. *Philipp. J. Sci., C. Bot.* 14: 295-362.

Beccari, O. (1921). Recensione delle Palme del vecchio mondo appartenenti alla tribu delle Corypheae, con descrizione della specie e varieta nuove che vi appartengono. *Webbia* 5: 5-70.

Beccari, O. (1931). Asiatic palms – Corypheae (ed. U. Martelli). *Ann. Roy. Bot. Gard. (Calcutta)* 13: 1-356.

Bena, G., M.-F. Jubier, I. Olivieri and B. Lejeune (1998). Ribosomal external and internal transcribed spacers: combined use in the phylogenetic analysis of *Medicago* (Leguminosae). *J. Mol. Evol.* 46: 299-306.

Bentham, G. (1878). Palmae. *Fl. austral.* 7: 132-147.

Blake, S. T. (1954). Botanical contributions of the northern Australian Regional Survey. II. Studies on miscellaneous northern Australian plants. *Austral. J. Bot.* 2: 99-140.

Blanco, M. (1837). *Flora de filipinas.* Manila.

Blatter, E. B. (1926). *The palms of British India and Ceylon*. London: Oxford University Press.

Blume, C. L. (1838). *Saribus*. *Rumphia* 2: 48-51.

Bøgh, A. (1996). The reproductive phenology and pollination biology of four *Calamus* (Arecaceae) species in Thailand. *Principes* 40: 5-15.

Borchsenius, F. (1993). Flowering biology and insect visitation of three Ecuadorean *Aiphanes* species. *Principes* 37: 139-150.

Borchsenius, F. and R. Bernal (1996). *Aiphanes* (Palmae). *Flora neotropica* 70: 1-95.

Bovi, M. L. A., M. R. do Val, G. da S. Dias and S. H. Spiering (1994). Floral biology and reproductive system of *Euterpe espiritosanensis* Fernandes. *Acta Hort.* 360: 41-56.

Bowler, J. M., G. S. Hope, J. N. Jennings, G. Singh and D. Walker (1976). Late Quaternary climates of Australia and New Guinea. *Quaternary Research* 6: 359-394.

Boyer, K. (1992). *Palms and cycads beyond the tropics*. Milton: Palm and Cycad Societies of Australia.

Braithwaite, C. J. R. (1987). Geology and palaeogeography of the Red Sea region. In: A. J. Edwards and S. M. Mead (eds), *Key environments: Red Sea*, 22-44. Oxford: Pergamon Press.

Braun, A. (1976). Various observations on *Ceroxylon klopstockia*. *Principes* 20: 158-166.

Bretschneider, E. (1898). *History of European botanical discoveries in China*. St Petersburg: Press of the Imperial Russian Academy of Sciences.

Briggs, J. C. (1999). Extinction and replacement in the Indo-west Pacific Ocean. *J. Biogeogr.* 26: 777-783.

Brown, G. K., F. Udovicic and P. Y. Ladiges (2001). Molecular phylogeny and biogeography of *Melaleuca*, *Callistemon* and related genera (Myrtaceae). *Aust. Syst. Bot.* 14: 565-585.

Brown, K. E. (1976). Ecological studies of the cabbage palm, *Sabal palmetto*. *Principes* 20: 3-10.

Brown, R. (1810). *Prodromus florae Novae Hollandiae et Insulae van-Diemen*. London: Taylor.

Brown, W. H. (1938). The bearing of nectaries on the phylogeny of flowering

plants. *Proc. Amer. Philos. Soc.* 79: 549-595.

Brummitt, R. K. and C. E. Powell (1992). *Authors of plant names*. Kew: Royal Botanic Gardens.

Brundin, L. Z. (1988). Phylogenetic biogeography. In: A. A. Myers and P. S. Giller (eds), *Analytical biogeography*, 343-369. London: Chapman & Hall.

Bull, W. (1887). *Catalogues of new beautiful and rare plants*. London.

Bullock, S. H. (1981). Notes on the phenology of inflorescences and pollination of some rain forest palms in Costa Rica. *Principes* 25: 101-105.

Bullock, S. H. (1994). Wind pollination of neotropical dioecious trees. *Biotropica* 26: 172-179.

Bureau of Meteorology (1988). *Climatic averages, Australia*. Canberra: Australian Government Publishing Service.

Burbidge, N. T. (1960). The phytogeography of the Australian region. *Austral. J. Bot.* 8: 75-212.

Burd, M. (1994). Bateman's principle and plant reproduction – the role of pollen limitation in fruit and seed set. *Bot. Rev.* 60: 83-139.

Burret, M. (1935). Neue palmen aus Neuguinea II. *Notizbl. Bot. Gart. Berlin-Dahlem* 12: 309-348.

Burret, M. (1936). Palmae chinenses. *Notizbl. Bot. Gart. Berlin-Dahlem* 13: 582-606.

Burret, M. (1939). Palmae gesammelt in Neu Guinea von L. J. Brass. *J. Arnold Arbor.* 20:187-212.

Burret, M. (1941). Bemerkungen zur Palmengattung *Livistona* R. Brown. *Notizbl. Bot. Gart. Berlin-Dahlem* 15: 319-327.

Burret, M. (1943). Die palmen Arabiens. *Bot. Jahrb. Syst.* 73: 175-190.

Cann, R. L. and J. K. Lum (1996). Mankind and Pacific biogeography. In: A. Keast and S. E. Miller (eds), *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes*, 437-443. Amsterdam: SPB Academic Publishing.

Carlquist, S. (1996). Plant dispersal and the origin of Pacific island floras. In: A. Keast and S. E. Miller (eds), *The origin and evolution of Pacific island floras, New Guinea to eastern Polynesia: patterns and processes*, 153-164. Amsterdam: SPG Academic Publishing.

Chakraverty, R. K. and S. K. Basu (1994). Conservation of palms in the Indian

Botanic Garden, Howrah: phenological observations. *Acta Hort.* 360: 57-61.

Chaloner, W. G. and G. T. Creber (1990). Do fossil plants give a climatic signal. *Journ. Geol. Soc., London* 147: 343-350.

Chandler, M. E. J. (1964). The lower Tertiary floras of southern England. 4 vols. London: British Museum of Natural History.

Chandler, M. E. J. (1978). *Supplement to the lower Tertiary floras of southern England.* Part 5. Tertiary Research Group Special Paper 4. London: Tertiary Research Group.

Chapin, M. H. and D. H. Lorence (2000). Developing a tropical botanical garden palm collection. *Palms* 44: 121-126.

Chapman, A. D. (1991). *Australian plant name index.* Canberra: AGPS Press.

Chapman, R. W. (1978). Geology. In: S. S. Al-Sayari and J. G. Zötl (eds), *Quaternary period in Saudi Arabia*, Vol. 1, 4-30. Wien: Springer-Verlag.

Chappill, J. A. (1989). Quantitative characters in phylogenetic analysis. *Cladistics* 5: 217-234.

Charlesworth, D. (1981). A further study of the problem of the maintenance of females in gynodioecious species. *Heredity* 46: 27-39.

Charlesworth, B. and D. Charlesworth (1978). A model for the evolution of dioecy and gynodioecy. *Am. Naturalist* 112: 975-997.

Charnov, E. L., J. Maynard Smith and J. J. Bull (1976). Why be an hermaphrodite? *Nature* 263: 125-126.

Chase, M. W. and H. H. Hills (1991). Silica gel: an ideal material for field preservation of leaf samples for DNA studies. *Taxon* 40: 215-220.

Chase, M. W., D. E. Solitis, P. S. Soltis, P. J. Rudall, M. F. Fay, W. H. Hahn, S. Sullivan, J. Joseph, M. Molvray, P. J. Kores, T. J. Givnish, K. J. Sytsma and J. C. Pires (2000). Higher-level systematics of the monocotyledons: an assessment of current knowledge and a new classification. In: K. L. Wilson and D. A. Morrison (eds), *Monocots: systematics and evolution*, 3-16. Melbourne: CSIRO.

Chevalier, A. (1919). *Livistona saribus* (Lour.) Merrill. *Bull. econ. l'Indochine* 22: 501-502.

Chevalier, A. (1939). La Somalie française. Sa flore et ses productions et d'agriculture tropicale. *Rev. Bot. Appl.* 217-218: 663-687.

Chiovenda, E. (1929). *Flora Somala.* Rome: Sindacato Italiano Arti Grafiche Editore.

Chippendale, G. M. (1972). Check list of Northern Territory plants. *Proc. Linn. Soc. New South Wales* 96: 207-267.

Churchill, D. M. (1973). *The ecological significance of tropical mangroves in the early Tertiary floras of southern Australia.* Geological Society of Australia Special Publication 4: 79-86.

Clegg, M. T. and M. L. Durbin (1990). Molecular approaches to the study of plant biosystematics. *Austral. Syst. Bot.* 3: 1-8.

Cleland, C. F. and Y. Ben-Tal (1983). Hormonal regulation of flowering and sex expression. In: W. J. Meudt (ed.), *Strategies of plant reproduction*, 157-180. Totowa, Allanheld, Osmun and Co.

Coats, F. and J. B. Kirkpatrick (1999). Is geographic range correlated with climatic range in Australian *Spyridium* taxa? *Austral. J. Bot.* 47: 755-767.

Corner, E. J. H. (1966). *The natural history of palms*. London: Weidenfeld and Nicolson.

Cox. P. A. (1981). Niche partitioning between sexes of dioecious plants. *Amer. Naturalist* 117: 295-307.

Cracraft, J. (1988). Deep history biogeography: retrieving the historical pattern of evolving continental biotas. *Syst. Zool.* 37: 221-236.

Cracraft, J. (1991). Patterns of diversification within continental biotas: hierarchical congruence among the areas of endemism of Australian vertebrates. *Austral. Syst. Bot.* 4: 211-217.

Cranston, P. S. and L. Hare (1995). *Conochironomus* Freeman: an Afro-Australian Chironomini genus revised (Diptera: Chironomidae). *Syts. Ent.* 20: 247-264.

Craw, R. C., J. R. Grehan and M. J. Heads (1999). *Panbiogeography: tracking the history of life*. New York: Oxford University Press.

Crawford, R. M. M. (1989). *Studies in plant survival*. Oxford: Blackwell Scientific Publications.

Crawley, M. J. (1997). Sex. In: M. J. Crawley (ed), *Plant ecology,* 2nd Edition, 156-213. Oxford: Blackwell Science.

Crisp, M. D., H. Peter Linder and P. H. Weston (1995). Cladistic biogeography of plants in Australia and New Guinea: congruent pattern reveals two endemic tropical tracks. *Syst. Biol.* 44: 457-473.

Crisp, M. D., J. G. West and H. P. Linder (1999). Biogeography of the terrestrial flora. *Flora of Australia 2nd edn*, 1: 21-367.

Croizat, L. (1958). *Panbiogeography*. Caracas.

Cruden, R. W. (1977). Pollen-ovule ratios: a conservative indicator of breeding systems in flowering plants. *Evolution* 31: 32-46.

Cruden, R. W., S. M. Hermann and S. Paterson (1983). Patterns of nectar production and plant-pollinator coevolution. In: B. Bentley and T. Elias (eds), *The biology of nectaries*, 80-125. New York: Columbia University Press.

Cruden, R. W. and S. Millar-Ward (1981). Pollen-ovule ratio, pollen size, and the ratio of stigmatic area to the pollen-bearing area of the pollinator: an hypothesis. *Evolution* 35: 964-974.

Cunningham, S. A. (1995). Ecological constraints on fruit initiation by *Calytrogyne ghiesbreghtiana* (Arecaceae): floral herbivory, pollen availability, and visitation by pollinating bats. *Amer. J. Bot.* 82: 1527-1536.

Daghlian, C. P. (1978). Coryphoid palms from the lower and middle Eocene of southeastern North America. *Palaeontographica Abt. B. Paläophytol.* 166: 44-82.

Daghlian, C. P. (1981). A review of the fossil record of monocotyledons. *Bot. Rev.* 47: 517-555.

Dale, W. L. (1974). The rainfall of Malaya. Part 1. In: J. B. Ooi and L. S. Chia (eds), *The climate of west Malaysia and Singapore*, 132-144. Singapore: Oxford University Press.

Darwin, C. (1859). *On the origin of species by means of natural selection or the preservation of favoured races in the struggle for life*. London: Murray.

Darwin, C. (1876). *The effects of cross and self fertilisation in the vegetable kingdom*. London: Murray.

Darwin, C. (1877). *The different forms of flowers on plants of the same species*. London: Murray.

Davis, T. A. (1988).*The sugar date palm (Phoenix sylvestris Roxb.)*. Nagercoil: JBS Haldane Research Centre. (Unpublished manuscript).

Davis, T. A., H. Sudasrip and S. N. Darwis (1985). *Coconut Research Institute, Manado, Indonesia: an overview of research activities*. Manado, Coconut Research Institute.

de Jong, T. J., P. G. L. Klinkhamer and M. C. J. Radamaker (1999). How geitonogamous selfing affects sex allocation in hermaphrodite plants. *J. Evol. Biol.* 12: 166-176.

Delinger, D. L. (1980). Seasonal and annual variation of insect abundance in the

Nairobi National Park, Kenya. *Biotropica* 12: 100-106.

DeMason, D. and B. Tisserat (1980). The occurrence and structure of apparently bisexual flowers in the date palm, *Phoenix dactylifera* L. (Arecaceae). *J. Linn. Soc., Bot.* 81: 283-292.

Denbuangboripant, J. and Q. C. B. Cronk (2000). High intraindividual variation in internal transcribed spacer sequences in *Aeschynanthus* (Gesneriaceae): implications for phylogenetics. *Proc. R. Soc. Lond.* B 267: 1407-1415.

de Steven, D., D. M. Windsor, F. E. Putz and B. de León (1987). Vegetative and reproductive phenologies of a palm assemblage in Panama. *Biotropica* 19: 342-356.

Devansaye, A. de la (1875). Palmiers. - Les Coryphinées. *Rev. Hort.* 47: 31-35.

Domin, K. (1915). Beiträge zur flora und pflanzengeographie Australiens. XXXI. Palmae. *Biblioth. Bot.* 85: 498-501.

Doutch, H. F. (1972). The paleogeography of northern Australia and New Guinea and its relevance to the Torres Strait area. In: D. Walker (ed), *Bridge and barrier: the natural and cultural history of Torres Strait*, 1-10. Canberra: Australian National University.

Dowe, J. (1993). Flowering behaviour and fruit development of *Wodyetia bifurcata* Irvine (the foxtail palm), in The Palmetum, Townsville, Australia. *Mooreana* 3: 6-18.

Dowe, J. L. (1995a). A preliminary review of the biogeography of Australian palms. *Mooreana* 5: 7-22.

Dowe, J. L. (1995b). Identifying east Gondwanan elements in the Australian palm flora. In: D. D. Pant (ed.), *Global environment and diversification of plants through geological time*. Allahabad: Society of Plant Taxonomists.

Dowe, J. L. and A. S. Barfod (2001). New species of *Livistona* R. Br. (Arecaceae) from north Queensland and Papua New Guinea. *Austrobaileya* 46: 165-174.

Dransfield, J. (1972). The genus *Johannesteijsmannia* H. E. Moore. *Gard. Bull., Singapore* 26: 63-83.

Dransfield, J. (1974). Notes on the palm flora of central Sumatra. *Reinwardtia* 8: 519-531.

Dransfield, J. (1977). A dwarf *Livistona* from Borneo. *Kew Bull.* 31: 759-762.

Dransfield, J. (1978). Growth forms of rain forest palms. In: P. B. Tomlinson and M. H. Zimmermann (eds), *Tropical trees as living systems*, 247-268. Cambridge: Cambridge University Press.

Dransfield, J. (1981). Palms and Wallace's Line. In: T. C. Whitmore (ed.), *Wallace's Line and plate tectonics*, 43-56. London: Oxford University Press.

Dransfield, J. (1987). Bicentric distribution in Malesia as exemplified by palms. In: T. C. Whitmore (ed.), *Biogeographical evolution of the Malay Archipelago*, 60-72. Oxford: Clarendon Press.

Dransfield, J. (1999). Species and species concepts in Old World palms. In: A. Henderson and F. Borchsenius (eds), *Evolution, variation, and classification of palms*, 5-20. Bronx: New York Botanical Garden Press.

Dransfield, J. and H. Beentje (1995). *The palms of Madagascar*. Kew: Royal Botanic Gardens Kew and the International Palm Society.

Dransfield, J., I. K. Ferguson and N. W. Uhl (1990). The coryphoid palms: patterns of variation and evolution. *Ann. Missouri Bot. Gard.* 77: 802-815.

Dransfield, J., J. R. Flenley, S. M. King, D. D. Harkness and S. Rapu (1984). A recently extinct palm from Easter Island. *Nature* 312: 750-752.

Dransfield, J. and H. E. Moore, Jr. (1982). The Martian correlation - two editions of Martius' Historia Naturalis Palmarum compared. *Kew Bull.* 37: 91-116.

Dransfield, J. and N. W. Uhl (1983a). *Wissmannia* (Palmae) reduced to *Livistona*. *Kew Bull.* 38: 199-200.

Dransfield, J. and N. W. Uhl (1983b). The transfer of *Livistona kingiana* (Palmae) to *Pholidocarpus*. *Kew Bull.* 38: 197-198.

Dransfield, J. and N. W. Uhl (1986). An outline of a classification of palms. *Principes* 30: 3-11.

Dransfield, J. and K. M. Wong (1987). A new species of *Livistona* (Palmae) from Peninsular Malaysia. *Malayan. Nat. J.* 41: 119-123.

Drude, O. (1887). Palmae. In: A. Engler and K. Prantl (eds), *Nat. Pflanzenfam.* 2(3): 1-93.

Drude, O. (1893). Uber die australischen *Livistona*-Arten. *Bot. Jahrb. Syst.* 39: 5-2.

Eckhart, V. M. (1992). The genetics of gender and the effects of gender on floral characters in gynodioecious *Phacelia linearis* (Hydrophyllaceae). *Amer. J. Bot.* 79: 792-800.

Eckhart, V. M. and J. Seger (1999). Phenological and developmental costs of male sex function in hermaphroditic plants. In: T. O. Vuorisalo and P. K. Mutikainene (eds), *Life history evolution in plants*, 195-213. Dordrecht: Kluwer

Academic Publishers.

Egge, R. G. (1979). Martius, the father of palms. *Principes* 23: 158-170.

El-Keblawy, A. and D. C. Freeman (1999). Spatial segregation by gender of the subdioecious shrub *Thymelaea hirsuta* in the Egyptian Desert. *Int. J. Plant Sci.* 160: 341-350.

Elsley, J. R. (1857). Accomplishment of the overland journey across north Australia, from the entrance of the Victoria River (N. W. Australia) to Brisbane, on the east coast. *J. Bot.* 9: 185-187.

Ervik, F. and R. Bernal (1996). Floral biology and insect visitation of the monoecious palm *Prestoea decurrens* on the Pacific coast of Colombia. *Principes* 40: 86-92.

Essig, F. B. (1977). A preliminary analysis of the palm flora of New Guinea and the Bismarck Archipelago. *PNG Bot. Bull.* 9: 1-39.

Essig, F. B. and B. E. Young (1981). Palm collecting in Papua New Guinea. II. The Sepik and the north coast. *Principes* 25: 3-15.

Evans, R. J. (1995). Systematics of *Cryosophila* (Palmae). *Syst. Bot. Monograph* 46: 1-70.

Ewart, A. J. and O. B. Davies (1917). *The flora of the Northern Territory.* Melbourne: McCarron, Bird & Co.

Faegri, K. and L. van der Pijl (1979). *The principles of pollination ecology.* 3rd revised edition. Pergamon Press: Oxford.

Fahn, A. (1979). *Secretory tissues in plants.* London: Academic Press.

Fahn, A. (1982). *Plant anatomy*, 3rd edition. Oxford: Pergamon Press.

Farris, J. S. (1969). A successive approximations approach to character weighting. *Syst. Zool.* 18: 374-385.

Farris, J. S. (1989). The retention index and the rescaled consistency index. *Cladistics* 5: 417-419.

Felsenstein, J. (1985). Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783-791.

Ferguson, I. K. and M. M. Harley (1992). The significance of new and recent work on pollen morphology in the Palmae. *Kew Bull.* 48: 205-243.

Fernando, E. S. (1990). A preliminary analysis of the palm flora of the Philippine Islands. *Principes* 34: 28-45.

Ferrero, M. D. (1997). A checklist of Palmae for New Guinea. *Palms & Cycads*

55/56: 2-39.

Fisher, J. B. and H. E. Moore, Jr. (1977). Multiple inflorescences in palms (Arecaceae): their development and significance. *Bot. Jahrb. Syst.* 98: 573-611.

Fitzgerald, W. V. (1918). The botany of the Kimberleys, north-west Australia. *J. & Proc. Roy. Soc. Western Australia.* 3: 102-224.

Florian, Z. (1994). *Microscopy*. Townsville: James Cook University of North Queensland.

Frakes, L. A. (1999). Evolution of Australian Environments. *Flora of Australia 2nd edn* 1; 163-203.

Frith, C. B. and D. W. Frith (1985). Seasonality of insect abundance in an Australian upland tropical forest. *Austral. J. Ecol.* 10: 237-248.

Fritsch, P. and L. H. Rieseberg (1992). High outcrossing rates maintain male and hermaphrodite individuals in populations of the flowering plant *Datisca glomerata*. *Nature* 359: 633-636.

Fuller, D. (1999). The lost palm of Fiji – a resolution of *Goniocladus* and a preliminary cladistic analysis of *Physokentia* (Palmae). *Mem. New York Bot. Gard.* 83: 203-213.

Furness, C. A. and P. Rudall (1999). Inaperturate pollen in monocotyledons. *Int. J. Plant Sci.* 160: 395-414.

Furtado, C. X. (1941). Palmae Malesicae IX: Two new Coryphaceous genera in Malaya. *Gards. Bull., Singapore* 11: 236-243.

Gardner, C. A. (1923). Principes. Palmae. *Forest Dept. Bull.* 32: 36-37.

Gardner, C. A. (1930). *Enumerato plantarum Australiae Occidentalis*. Perth: F. W. Simpson.

Golden, G. A. (1993). *The early European settlers of the Solomon Islands*. Melbourne: Privately published by the author.

Good, R. (1956). *Features of evolution in the flowering plants*. London: Green and Co.

Grant, P. R. (1998). Epilogue and questions. In: P. R. Grant (ed.), *Evolution on islands*, 305-319. Oxford: Oxford University Press.

Greenwood, D. R. (1994). Palaeobotanical evidence for Tertiary climates. In: R. S. Hill (ed.), *History of the Australian vegetation: Cretaceous to the Recent*, 44-59. Cambridge: Cambridge University Press.

Greenwood, D. R. and J. G. Conran (2000). The Australian Cretaceous and

Tertiary monocot fossil record. In: K. L. Wilson and D. A. Morrison (eds), *Monocots: systematics and evolution*, 52-59. Melbourne: CSIRO.

Greuter, W., J. McNeill, F. R. Barrie, H. M. Burdet, V. Demoulin, T. S. Filgueiras, D. H. Nicolson, P. C. Silva, J. E. Skog, P. Trehane, N. J. Turland, D. L. Hawksworth (2000). International Code of Botanical Nomenclature (Saint Louis Code). *Regnum Veg.* 138.

Greyson, R. I. (1994). *The development of flowers*. New York: Oxford University Press.

Griffith, W. (1844). The palms of British East India. *Calcutta J. Nat. Hist.* 5: 311-355.

Griffith, W. (1850). *Palms of British East India* arranged by John McClelland. Calcutta: Charles A. Serrao.

Griffiths, C. J. (1993). The geological evolution of east Africa. In: J. C. Lovett and S. K. Wasser (eds), *Biogeography and ecology of the rainforests of eastern Africa*, 9-21. Cambridge: Cambridge University Press.

Haber, W. A. and K. S. Bawa (1984). Evolution of dioecy in *Saurina* (Dilleniaceae). *Ann. Missouri Bot. Gard.* 71: 289-293.

Hahn, W. J. and K. J. Sytsma (1999). Molecular systematics and biogeography of the southeast Asian genus *Caryota* (Palmae). *Syst. Bot.* 24: 558-580.

Hall, R. (1998). The plate tectonics of Cenozoic SE Asia and the distribution of land and sea. In: R. Hall and J. D. Holloway (eds), *Biogeography and geological evolution of SE Asia*, 99-131. Leiden: Backhuys Publishers.

Harder, L. D. (2000). Pollen dispersal and the floral diversity of monocotyledons. In: K. L. Wilson and D. A. Morrison (eds), *Monocots: systematics and evolution*, 243-257. Melbourne: CSIRO.

Harley, M. M. (1990). Occurrence of simple, tectate, monosulcate or trichotomosulcate pollen grains within the Palmae. *Rev. Palaeobot. Palynol.* 64: 137-147.

Harley, M. M. and W. J. Baker (2001). Pollen aperture morphology in Arecaceae: application within phylogenetic analyses, and a summary of the fossil record of palm-like pollen. *Grana* 40: 45-77.

Harley, M. M., M. H. Kurman and I. K. Ferguson (1991). Systematic implications of comparative morphology in selected Tertiary and extant pollen from the Palmae and the Sapotaceae. In: S. Blackmore and S. H. Barnes (eds), *Pollen and spores:*

patterns of diversification, 225-238. Oxford: Clarendon Press.

Hasskarl, C. (1842). Plantarum rariorum. *Tijdschr. voor nat. Gesch. en Physiol.* 5: 62-63.

Hawkins, J. A., C. E. Hughes and R. W. Scotland (1997). Primary homology assessment, characters and character states. *Cladistics* 13: 275-283.

Hay, A. J. M. (1984). Palmae: In: R. J. Johns and A. J. M. Hay (eds), *A guide to the monocotyledons of Papua New Guinea, Part 3*, 195-318. Lae: Office of Forests.

Heckel, H. (1972). *Pollen and spore assemblages from Queensland Tertiary sediments.* Publication of the Geological Survey Queensland (Palaeontology Paper 30) 355: 1-33.

Hedberg, I. (1979). Possibilities and needs for conservation of plant species and vegetation in Africa. In: I. Hedberg (ed.), *Systematic botany, plant utilization and biosphere conservation*, 83-104. Stockholm: Almqvist and Wiksell International.

Hemsley, W. B. (1891). Botanical nomenclature. *Nature* 45: 169-172.

Henderson, A. (1984). Observations on pollination of *Cryosophila albida* (Palmae). *Principes* 28: 120-126.

Henderson, A. (1985). Pollination of *Socratea exorrhiza* and *Iriartea ventricosa*. *Principes* 29: 64-71.

Henderson, A. (1986a). A review of pollination studies in the Palmae. *Bot. Rev.* 52: 221-259.

Henderson, A. (1986b). *Barcella odora*. *Principes* 30: 74-76.

Henderson, A. (1990). Arecaceae. Part 1. Introduction and the Iriarteinae. *Flora Neotropica* 53: 1-100.

Henderson, A. (1995). *The palms of the Amazon.* New York: Oxford University Press.

Henderson, A. (1999a). Species, species concepts, and palm taxonomy in the New World. *Mem. New York Bot. Gard.* 83: 21-28.

Henderson, A. (1999b). A phylogenetic analysis of the Euterpeinae (Palmae; Arecoideae: Areceae) based on morphology and anatomy. *Brittonia* 51: 106-113.

Henderson, A., G. Galeano and R. Bernal (1995). *Field guide to the palms of the Americas.* New Jersey: Princeton University Press.

Hengeveld, R. (1997). Impact of biogeography on a population-biological paradigm shift. *J. Biogeogr.* 24: 541-547.

Herrera, J. (1989). On the reproductive biology of the dwarf palm, *Chamaerops*

humilis in southern Spain. *Principes* 33: 27-32.

Hidajat, E. B. (1987). Flowering behaviour in the sugar palm, *Arenga pinnata*. *Principes* 31: 78-88.

Hill, W. (1873). Report. In: G. E. Dalrymple (ed.), *Narrative and reports of the Queensland north-east coast expedition, 1873*, 48-53. Brisbane: James C. Beal, Government Printer.

Hill, W. (1875). *Catalogue of the plants in the Queensland Botanic Gardens*. Brisbane: Jame C. Beal, Government Printer.

Hnatiuk, R. J. (1977). Population structure of *Livistona eastonii* Gardn., Mitchell Plateau, Western Australia. *Austral. J. Ecol.* 2: 461-466.

Hodel, D. R. and P. Vatcharakorn (1998). The palms of Thailand. In: D. R. Hodel (ed.), *The palms and cycads of Thailand*, 1-177. Nong Nooch: Kampon Tansasha.

Holloway, J. D. and R. Hall (1998). SE Asian geology and biogeography: an introduction. In: R. Hall and J. D. Holloway (eds), *Biogeography and geological evolution of SE Asia*, 1-23. Leiden: Backhuys Publishers.

Holmgren, P. K., N. H. Holmgren, and L. C. Barnett (1990). *Index herbariorum. Part 1. The herbaria of the world*. Regnum veg. 120: 1-693.

Hoogland, R. D. (1972). Plant distribution patterns across Torres Strait. In: D. Walker (ed), *Bridge and barrier: the natural and cultural history of Torres Strait*, 131-152. Canberra: Australian National University.

Hooker, J. D. (1860). Introductory essay. *Bot. antarct. voy.* 1: I-CXXVII. London: Lovell Reeve.

Hooker, J. D. (1883). Palmae. In: G. Bentham & J. D. Hooker (eds), *Gen. pl.* 3: 870-948. London: Lovell Reeve & Co.

Hooker, J. D. (1884). *Report on the progress and condition of the Royal Gardens at Kew during the year 1882*. London: Eyre and Spottiswoode.

Hope, G. (1996). Quaternary change and the historical biogeography of Pacific islands. In: A. Keast and S. E. Miller (eds), *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes*, 165-190. Amsterdam: SPB Academic Publishing.

Horikawa, Y. (1972). *Atlas of Japanese flora*. Tokyo: Gakken.

House, M. R. (1995). Orbital forcing timescales: an introduction. In: M. R. House and A. S. Gale (eds), *Orbital forcing timescales and cyclostratigraphy*, 1-18. London; Geological Society.

Humeau, L., T. Pailler and J. D. Thompson (1999). Cryptic dioecy and leaky dioecy in endemic species of *Dombeya* (Sterculiaceae) on La Réunion. *Amer. J. Bot.* 86: 1437-1447.

Humphries, C. J. (1981). Biogeographical methods and the southern beeches (Fagaceae: *Nothofagus*). In: V. A. Funk and D. R. Brooks (eds), *Advances in cladistics*, 177-207. New York: New York Botanical Garden.

Humphries, C. J. (1992). Cladistic biogeography. In: P. L. Forey, C. J. Humphries, I. J. Kitching, R. W. Scotland, D. J. Siebert and D. W. Williams (eds), *Cladistics: a practical course in systematics*, 137-159. Oxford: Clarendon Press.

Humphries, C. J., P. Y. Ladiges, M. Roos and M. Zandee (1988). Cladistic biogeography. In: A. A. Myers and P. S. Giller (eds), *Analytical biogeography*, 371-404. London: Chapman & Hall.

Humphries, C. J. and L. R. Parenti (1986). *Cladistic biogeography*. Oxford: Clarendon Press.

Humphries, C. J. and L. R. Parenti (1999). *Cladistic biogeography*. 2nd Edition Oxford: Clarendon Press.

Humphreys, W. F., R. B. Brooks and B. Vines (1990). Rediscovery of the palm *Livistona alfredii* on the North West Cape Peninsula. *Rec. West. Austral. Mus.* 14: 647-650.

Hyam, R. and R. Pankhurst (1995). *Plants and their names: a concise dictionary*. Oxford: Oxford University Press.

Index Kewensis (1993). *Index Kewensis: on compact disc*. Oxford: Oxford University Press.

Irvine, A. K. (1984). A guide to *Livistona* in Queensland. *Palms & Cycads* 5: 2-5.

Jackson, S. T. and M. E. Lyford (1999). Pollen dispersal models in Quaternary plant ecology: assumptions, parameters, and prescriptions. *Bot. Rev.* 65: 39-75.

Jacquin, N. J. (1776). *Corypha minor*. Hort. bot. vindob. 3: 8.

Jacquin, N. J. (1801). *Latania chinensis*. *Fragm. bot.* 16.

Janzen, D. H. (1978). Some Maestrichtian palynomorphs and their phytogeographical and paleoecological implications. *Palynology* 2: 29-38.

Janzen, D.H. and T. W. Schoener (1968). Differences in insect abundance and diversity between wetter and drier sites during a tropical dry season. *Ecology* 49: 96-110.

Jeanmougin, F., J. D. Thompson, M. Gouy, D. G. Higgins and T. J. Gibson

(1998). Multiple sequence alignment with Clustal X. *Trends Biochem. Sci.* 23: 403-405.

Johnson, D. (1996). Introduction. In: D. Johnson (ed.), *Palms: their conservation and sustained utilization*, 1-6. Gland: International Union for Conservation of Nature and Natural Resources.

Johnson, R. W. (1981). The Queensland palm flora. *Qld Naturalist* 22: 10-20.

Jolivet, P. (1998). *Interrelationship between insects and plants*. Boca Raton: CRC Press.

Jones, D. L. (1995). *Palms throughout the world*. Chatswood: Reed Books.

Jones, D. L. (1996). *Palms in Australia,* 3rd Edition. Port Melbourne: Reed Books.

Judd, W. S., C. S. Campbell, E. A. Kellogg and P. F. Stevens (1999). *Plant systematics: a phylogenetic approach*. Sunderland: Sinauer Associates, Inc.

Kahn, F. and G. Second (1999). The genus *Astrocaryum* (Palmae) in Amazonia: classical taxonomy and DNA analysis (AFLP). *Mem. New York. Bot. Gard.* 83: 179-184.

Kanehira, R. (1936). *Formosan trees indigenous to the island*. Formosa: Department of Forestry.

Kanis, A., M. D. Crisp and A. E. Orchard (1999). Classification, phylogeny and the flora of Australia. *Flora of Australia*, 2nd edn, 1: 125-147.

Katinas, L. and J. V. Crisci (2000). Cladistic and biogeographic analyses of the genera *Moscharia* and *Polyachyrus* (Asteraceae: Mutisieae). *Syst. Bot.* 25: 33-46.

Kearns, C. A. and D. W. Inouye (1993). *Techniques for pollination biologists*. Niwot: University Press of Colorado.

Keast, A. (1996). Pacific biogeography: patterns and processes. In: A. Keast and S. E. Miller (eds), *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes*, 477-512. Amsterdam: SPB Academic Publishing.

Keast, A. and S. E. Miller (1996). Modern Pacific biogeography: an introduction. In: A. Keast and S. E. Miller (eds), *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes*, 1-5. Amsterdam: SPB Academic Publishing.

Keighery, G. and N. Gibson (1993). Biogeography and composition of the flora of the Cape Range peninsula. *Rec. Western Austral. Mus. Suppl.* 45: 51-86.

Kerchove, O. de Denterghem de (1878). *Les Palmiers*. Paris: J. Rothschild.

Kiew, R. (1989). Conservation status of palms in peninsular Malaysia. *Malayan nat. J.* 43: 3-15.

Kiew, R. (1991). Palm utilization and conservation in Peninsular Malaysia. In: D. Johnson (ed.), *Palms for human needs in Asia*, 75-130. Rotterdam: A. A. Balkema.

Kiew, R. and G. W. H. Davison (1989). Relations between wild palms and other plants and animals. *Malayan nat. J.* 43: 37-42.

Kim, S.-C., D. J. Crawford, M. Tadesse, M. Berbee, F. R. Ganders, M. Pirseyedi and E. J. Esselman (1999). ITS sequences and phylogenetic relationships in *Bidens* and *Coreopsis* (Asteraceae). *Syst. Bot.* 24: 480-493.

Kitching, I. J., P. L. Forey, C. J. Humphries and D. M. Williams (1998). *Cladistics, second edition: the theory and practice of parsimony analysis.* Oxford University Press, Oxford.

Kittlitz, F. H. (1844). *Vierundzwanzig vegetations – ansichten von kustenlandern und inseln des Stillen Oceans.* Siegen: B. B. H.

Kruckeberg, A. R. and D. Rabinowitz (1985). Biological aspects of endemism in higher plants. *Ann. Rev. Ecol. Syst.* 16: 447-479.

Kulkarni, A. R. and K. S. Patil (1977). *Palmocaulon costapalmatum*, a petrified palm leaf axis from the Deccan Intertrappean beds of Wardha District, Maharashtra. *Geophytology* 7: 208-213.

Kuntze, O. (1891). *Rev. Gen. Pl.*, 2. Leipzig: Arthur Felix.

Kurz, S. (1874). Enumeration of Burmese palms. J. *Asiatic Soc. Bengal* 43: 191-217.

Ladd, P. G. (1978). Vegetation history at Lake Curlip in lowland eastern Victoria, from 5200 B.P. to present. *Austral. J. Bot.* 26: 393-414.

Lamarck, J. B. A. P. M. (1786). *Coryphe. Encycl.* 2: 130-131.

Lane-Poole, C. E. (1925). *The forest resources of the Territories of Papua and New Guinea.* Melbourne: Commonwealth of Australia.

Lange, R. T. (1982). Australian Tertiary vegetation. In: J. M. B. Smith (ed), *A history of Australasian vegetation*, 44-89. Sydney: MacGraw-Hill.

Langlois, A. C. (1976). *Supplement to palms of the world.* Gainesville: University Presses of Florida.

Larcher, W. (1995). *Physiological plant ecology,* 3rd edition. Berlin: Springer-Verlag.

Latz, P. K. (1975). Notes on the relict palm *Livistona mariae* F. Muell. in central

Australia. *Trans. Roy. Soc. South Austral.* 99: 189-196.

Laumonier, Y. (1997). *The vegetation and physiography of Sumatra.* Dordrecht: Kluwer Academic Publishers.

Lawrence, G. H. M., A. F. G. Buchheim, G. S. Daniels and H. Dolezal (1968). *Botanico-periodicum-Huntianum.* Pittsburgh: Hunt Botanical Library.

Leach, G. J. (1992). *Livistona mariae* F. Muell. (Family Arecaceae). In: J. H. Leigh and J. D. Briggs (eds), *Threatened Australian plants: overview and case studies*, 24. Canberra: Commonwealth of Australia.

Leichhardt, L. (1847). *Journal of an overland expedition in Australia, from Moreton Bay to Port Essington, a distance of upwards of 3000 miles, during the years 1844-1845.* London: T. & W. Boone.

Leshem, Y. and D. Ophir (1977). Differences in endogenous levels of gibberellin activity in male and female partners of two dioecious tree species. *Ann. Bot. (London)* 41: 375-379.

Lewis, C. E., W. J. Baker and C. B. Asmussen (2000). DNA and palm evolution. *Palms* 44: 19-24.

Lewis, C. E. and J. J. Doyle (2001). Phylogenetic utility of the nuclear gene malate synthase in the palm family (Arecaceae). *Mol. Phylogenet. Evol.* 19: 409-420.

Li, H. -L. (1963). *Woody flora of Taiwan.* Narberth: Livingston Publishing Company.

Li, H. -L. (1978). Palmae. *Fl. Taiwan* 5: 784-794.

Li, H. -L. (1979). *Nan-fang ts'ao-mu chuang: a fourth century flora of southeast Asia.* Hong Kong: The Chinese University Press.

Linnaeus, C. (1753). *Species plantarum.* Stockholm: Laurentii Salvii.

Linnaeus, C. (1754). *Genera plantarum.* Stockholm: Laurentii Salvii.

Listabarth, C. (1992). A survey of pollination strategies in the Bactridinae (Palmae). *Bull. Inst. fr. études andines* 21: 699-714.

Listabarth, C. (1994). Pollination and pollinator breeding in *Desmoncus*. *Principes* 38: 13-23.

Liston, A., L. H. Rieseberg and T. S. Elias (1990). Functional androdioecy in the flowering plant *Datisca glomerata*. *Nature* 343: 641-642.

Lloyd, D. G. (1988). Benefits and costs of biparental and uniparental reproduction in plants. In: R. E. Michod and B. R. Levin (eds), *The evolution of sex: an examination of current ideas*, 233-252. Sunderland: Sinauer Associates, Inc.

Longo, C. P. (1994). Genes controlling sex expression. In: E. G. Williams, A. E. Clarke and R. B. Knox (eds), *Genetic control of self-incompatibility and reproductive development in flowering plants*, 245-265. Dordrecht: Kluwer Academic Publishers.

Lothian, T. R. N. (1959a). The Livistonas of Australia. *Principes* 2: 53-63.

Lothian, T. R. N. (1959b). Further notes concerning the central Australian cabbage palm – *Livistona mariae*. *Principes* 3: 53-63.

Loope, L. L. (1995). Climate change and island biological diversity. In: P. M. Vitousek, L. L. Loope and H. Adsersen (eds), *Islands: biological diversity and ecosystem function*, 123-132. Berlin: Springer-Verlag.

Loureiro, J. (1790). *Corypha. Fl. cochinch.* 1: 212-213.

Löve, Á. (1978). IOPB Chromosome number reports LIX. *Taxon* 27: 53-61.

Lovett, J. C. (1993). Climate history and forest distribution in eastern Africa. In: J. C. Lovett and S. K. Wasser (eds), *Biogeography and ecology of the rainforests of eastern Africa*, 23-29. Cambridge: Cambridge University Press.

Lucas, G. and H. Synge (1978). *The IUCN plant red data book.* Morges: International Union for the Conservation of Nature.

Macphail, M. K., G. J. Jordan and R. S. Hill (1993). Key periods in the evolution of the flora and vegetation in western Tasmania 1. The early-middle Pleistocene. *Austral. J. Bot.* 41: 673-707.

Maclean, N. (1987). *Macmillan dictionary of genetics and cell biology.* London, Macmillan Reference Books.

Maddison, W. P. and D. R. Maddison (1992). *MacClade: analysis of phylogeny and character evolution.* Version 3.0. Sunderland: Sinauer Associates.

Madulid, D. A. (1991). The Philippines: palm utilization and conservation. In: D. Johnson (ed), *Palms for human needs in Asia*, 181-225. Rotterdam: A. A. Balkema.

Magalon, M. (1930). *Livistona.* Contribution a l'étude des palmier l'Indochine Français, 56- 58.

Mahabalé, T. S. (1967). Pollen grains in Palmae. *Rev. Palaeobot. Palynol.* 4: 299-304.

Mahabale, T. S. and K. M. Kulkarni (1975). Studies on palms: fruits, seeds and their germination in *Livistona chinensis* R. Br. *J. Bombay Nat. Hist. Soc.* 72: 655-661.

Marshall, L. G. (1988). Extinction. In: A. A. Myers and P. S. Giller (eds),

Analytical biogeography, 219-254. London: Chapman & Hall.

Martin, H. A. (1990). Tertiary climate and phytogeography in southeastern Australia. *Rev. Palaeobot. Palynol.* 65: 47-55.

Martin, H. A. (1994). Australian Tertiary phytogeography: evidence from palynology. In: R. S. Hill (ed.), *History of the Australian vegetation: Cretaceous to the Recent*, 104-159. Cambridge: Cambridge University Press.

Martin, P. G. and J. M. Dowd (1991). Application of evidence from molecular biology to the biogeography of angiosperms. *Austral. Syst. Bot.* 4: 111-116.

Martius, C. F. P. von (1824). *Palmarum familia ejusque denuo illustrato*. Munich: Lindauer.

Martius, C. F. P. von (1838). *Livistona. Hist. nat. palm.* 1st Edition, 3(7): 238-242. Leipzig.

Martius, C. F. P. von (1849). *Livistona. Hist. nat. palm.* 2nd Edition, 3(9): 239-242, 319. Leipzig.

Maurice, S., E. Belhassen, D. Couvet and P.–H. Gouyon (1994). Evolution of dioecy: can nuclear-cytoplasmic interactions select for maleness? *Heredity* 73: 346-354.

Maynard Smith, J. (1978). *The evolution of sex*. Cambridge: Cambridge University Press.

McAlpine, J. R., G. Keig and R. Falls (1983). *Climate of Papua New Guinea*. Canberra: Australian National University Press.

McCurrach, J. C. (1960). *Palms of the world*. New York: Harper and Brothers.

Meagher, T. R. (1988). Sex determination in plants. In J. L. Doust and L. L. Doust (eds), *Plant reproductive ecology: patterns and strategies*, 125-138. New York: Oxford University Press.

Menkhorst, K. and I. Cowie (1992). Fora of the Bungle Bungle area. *West austral. CALM Research Bull.* 6: 16-52.

Merrill, E. D. (1917). *An interpretation of Rumphius's Herbarium Amboinense*. Manila: Bureau of Printing.

Merrill, E. D. (1918). *Species Blancoanae; a critical revision of the Philippine species of plants described by Blanco and Llanos*. Manila: Bureau of Printing.

Merrill, E. M. (1925). *An enumeration of Philippine flowering plants*. Manila: Bureau of Printing.

Michaux, B. (1991). Distributional patterns and tectonic development in

Indonesia: Wallace reinterpreted. *Austral. Syst. Bot.* 4: 25-36.

Mickevich, M. F. (1981). Quantitative phylogenetic biogeography. In: V. A. Funk and D. R. Brooks (eds), *Advances in cladistics*, 209-222. New York: New York Botanical Garden.

Milne, L. A. (1988). Palynology of the late Eocene lignitic sequence from the western margin of the Eucla Basin, Western Australia. *Mem. Assoc. Australas. Palaeontols.* 5: 285-310.

Miquel, F. A. W. (1855). *Licuala – Livistona*. Fl. Ned. Ind. 3: 51-60.

Miquel, F. A. W. (1868). Palmis archipelagi indici observationes novae. *Natuurk. Verh. Kon.. Akad. Deel.* 11: 1-35.

Mogea, J. P. (1991). Indonesia: palm utilization and conservation. In: D. Johnson (ed.), *Palms for human needs in Asia*, 37-73. Rotterdam: A. A. Balkema.

Moncur, M. W. and B. J. Watson (1987). Observations on the floral biology of the monoecious form of *Salacca zalacca*. *Principes* 31: 20-22.

Monod, T. (1955). Remarques sur un Palmier peu connu: *Wissmannia carinensis* (Chiov. 1929) Burret 1943. *Bulletin de l'I. F. A. N.* 17: 338-358.

Monteith, G. B. (1982). Dry season aggregations of insects in Australian monsoon forests. *Mem. Queensland Mus.* 20: 533-543.

Moore, H. E. Jr. (1963a). The types and lectotypes of some palm genera. *Gentes Herb.* 9: 245-274.

Moore, H. E. Jr. (1963b). An annotated checklist of cultivated palms. *Principes* 7: 119-182.

Moore, H. E. Jr. (1973a). The major groups of palms and their distribution. *Gentes Herb.* 11: 27-141.

Moore, H. E. Jr. (1973b). Palms in the tropical forest ecosystems of Africa and South America. In: B. J. Meggers, E. S. Ayensu and W. D. Duckworth (eds), *Tropical forest ecosystems in Africa and South America: a comparative review*. Washington: Smithsonian Institution Press.

Moore, H. E. Jr. (1977). Endangerment at the specific and generic levels in palms. In: G. T. Prance and T. S. Elias (eds), *The status of threatened and endangered plants of the Americas*, 267-283. New York: New York Botanical Garden.

Moore, H. E. Jr. (1979). Order Arecales. Fam. 39. Arecaceae, *Flora Vitiensis Nova* 1: 392-438.

Moore, H. E. Jr. (1981). Odoardo Beccari (1843-1920). *Principes* 25: 29-35.

Moore, H. E. Jr. and F. R. Fosberg (1956). The Palms of Micronesia. *Gentes Herb.* 8: 423-478.

Moore, H. E. Jr. and N. W. Uhl (1982). Major trends of evolution in palms. *Bot. Rev.* 48: 1-69.

Moraes, M. R. (1996). *Allagoptera* (Palmae). *Flora Neotropica* 73: 1-35.

Morain, S. A. (1984). *Systematic and regional biogeography.* New York: Van Nostrand Reinhold Company.

Morley, R. J. (1998). Palynological evidence for Tertiary plant dispersals in the SE Asian region in relation to plate tectonics and climate. In: R. Hall and J. D. Holloway (eds), *Biogeography and geological evolution of SE Asia*, 211-234. Leiden: Backhuys Publishers.

Morrone, J. J. (1994). On the identification of areas of endemism. *Syst. Biol.* 43: 438-441.

Morrone, J. J. and J. V. Crisci (1995). Historical biogeography. *Ann. Rev. Ecol. Syst.* 26: 373-401.

Morton, S. R., J. Short and R. D. Barker (1995). *Refugia for biological diversity in arid and semi-arid Australia.* Canberra: Department of the Environment, Sport and Territories.

Moss, S. J. and E. J. Wilson (1998). Biogeographic implications of the Tertiary palaeographic evolution of Sulawesi and Borneo. In: R. Hall and J. D. Holloway (eds), *Biogeography and geological evolution of SE Asia*, 133-163. Leiden: Backhuys Publishers.

Mueller, F. (1857). Notes made during the recent expedition across the northern portion of Australia, under the command of Mr. Surveyor Gregory. *J. Bot.* 9: 165-173.

Mueller, F. (1858). Botanical report on the north-Australian expedition, under the command of A. C. Gregory, Esq. *J. Bot. and Kew Gard. Misc.* 2: 137-163.

Mueller, F. (1874a). Palmae. *Fragm.* 8: 221-222.

Mueller, F. (1874b). *Livistona leichhardtii. Fragm.* 8: 283.

Mueller, F. (1878). Palmae. *Fragm.* 11: 54-58.

Mueller, F. (1892). Note on the West Australian fan-palm. *Victorian Naturalist* 9: 112.

Muller, J. (1981). Fossil pollen records of extant angiosperms. *Bot. Rev.* 47: 1-142.

Myers, A. A. (1991). How did Hawaii accumulate its biota? A test from the Amphipoda. *Glob. Ecol. Biogeogr. Lett.* 1: 24-29.

Myers, A. A. and P. S. Giller (1988). Process, pattern and scale in biogeography. In: A. A. Myers and P. S. Giller (eds), *Analytical biogeography*, 3-12. London: Chapman & Hall.

Nakai, T. (1928). Plants in Ogasawara Islands. *Rigakkai* 26: 1-10.

Nakai, T. (1935). Species generis Livistonae in Imperio Japonico sponte nascentes. *J. Jap. Bot.* 11: 217-224.

Nakai, T. (1936). *Corypha japonica* is not a valid name botanically. *J. Jap. Bot.* 12: 833-834.

Naves, A. and C. Fernandez-Villar (1882). *Novissima appendix*. Manilla.

Neale, P. R., A. Dafni and M. Giurfa (1998). Floral symmetry and its role in plant-pollinator systems: terminology, distribution, and hypotheses. *Ann. Rev. Ecol. Syst.* 29: 345-373.

Nelson, G. and N. Platnick (1981). *Systematics and biogeography: cladistics and vicariance*. New York: Columbia University Press.

Nguyen, T. H. and R. Kiew (2000). New and interesting plants from Ha Long Bay, Vietnam. *Gard. Bull. Singapore* 52: 185-202.

Nix, H. A. and J. D. Kalma (1972). Climate as a dominant control in the biogeography of northern Australia and New Guinea. In: D. Walker (ed), *Bridge and barrier: the natural and cultural history of Torres Strait*, 61-91. Canberra: Australian National University.

O'Brien, T. G. and M. F. Kinnaird (1996). Effect of harvesting on leaf development of the Asian palm *Livistona rotundifolia*. *Conservation Biology* 10: 53-58.

Ohwi, J. (1965). Palmae. *Flora of Japan* 253-254.

Ornduff, R. (1983). Interpretations of sex in higher plants. In W. J. Meudt (ed.), *Strategies of plant reproduction*, 21-33. Granada: Allanheld, Osmun and Co.

Orscheg, C. K. and R. F. Parsons (1996a). Ecology of *Livistona australis* (R. Br.) Martius at its southern limit, south-eastern Australia. Part 1. Distribution and genetic variation. *Mooreana* 6: 8-17.

Orscheg, C. K. and R. F. Parsons (1996b). Ecology of *Livistona australis* (R. Br.) Martius at its southern limit, south-eastern Australia. Part 2. Phenology, germination, herbivory, and regeneration and fire effects. *Mooreana* 6: 36-50.

Oyama, K. (1990). Variation in growth and reproduction in the neotropical dioecious palm *Chamaedorea tepejilote*. *J. Ecol.* 78: 648-663.

Ôyama, T. and H. Matsuo (1964). Notes on palmaean leaf from the Ôarai flora (upper Cretaceous), Ôarai Machi, Ibaraki Prefecture, Japan. *Trans. Proc. Palaeont. Soc. Japan, n. s.* 55: 241-246.

Pacini, E. and G. G. Franchi (2000). Types of pollen dispersal units in monocots. In: K. L. Wilson and D. A. Morrison (eds), *Monocots: systematics and evolution*, 295-300. Melbourne: CSIRO.

Page, R. B. M. (1988). Quantitative cladistic biogeography: constructing and comparing area cladograms. *Syst. Zool.* 37: 254-270.

Pannell, J. (1997a). The maintenance of gynodioecy and androdioecy in a metapopulation. *Evolution* 51: 10-20.

Pannell, J. (1997b). Variation in sex ratios and sex allocation in androdioecious *Mercurialis annua*. *J. Ecol.* 85: 57-69.

Parsons, P. A. (1988). Adaptation. In: A. A. Myers and P. S. Giller (eds), *Analytical biogeography*, 165-184. London: Chapman & Hall.

Pearce, K. G. (1994). The palms of Kubah National Park, Kuching Division, Sarawak. *Malayan. Nat. J.* 48: 1-36.

Pei, S., S. Chen and S. Tong (1991). *Livistona. Flora reipublicae popularis sinicae* 13: 25-29.

Pfister, R. (1892). *Livistona.* Beitr. vegl. anat. Sabaleenblatt. 50.

Pilger, A. and A. Rösler (1976). Temporal relationships in the tectonic evolution of the Afar Depression (Ethiopia) and the adjacent Afro-Arabian rift system. In A. Pilger and A. Rosler (eds), *Afar between continental and oceanic rifting*, Vol. 2, 1-25. Stuttgart: E. Schweizerbart'sche Verlagsbuchhandlung.

Pintaud, J. -C. (1999). A cladistic analysis of the Archontophoenicinae (Palmae, Areceae) based on morphological and anatomical characters. In: A. Henderson and F. Borchsenius (eds), *Evolution, variation, and classification of palms*, 279-284. New York: New York Botanical Garden Press.

Platnick, N. I. (1981). Widespread taxa and biogeographic congruence. In: V. A. Funk and D. R. Brooks (eds), *Advances in cladistics*, 177-207. New York: New York Botanical Garden.

Platnick, N. I., C. E. Griswold and J. A. Coddington (1991). On missing entries in cladistic analysis. *Cladistics* 7: 337-343.

Pleijel, F. (1995). On character coding for phylogeny reconstruction. *Cladistics* 11: 309-315.

Podzorski, A. C. (1986). *Veitchia merrillii* and its karst island home. *Principes* 30: 138-140.

Pole, M. (1994). The New Zealand flora - entirely long-distance dispersal? *J. Biogr.* 21: 625-635.

Pole, M. S. and M. K. Macphail (1996). Eocene *Nypa* from Regatta Point, Tasmania. *Rev. Palaeobot. Palynol.* 92: 55-67.

Potztal, E. (1958). Professor Dr. Max Burret. *Principes* 2: 87-91.

Potztal, E. (1964). Reihe Principes. In: H. Melchior (ed.), *A. Engler's Syllabus der Pflanzenfamilien ed. 12*, 2: 579-588. Berlin: Gebruder Borntraeger.

Prakash, U. and K. Ambwani (1980). A petrified *Livistona*-like palm stem, *Palmoxylon livistonoides* sp. nov. from the Deccan Intertrappean beds of India. *Palaeobotanist* 26: 297-306.

Proctor, M., P. Yeo and A. Lack (1996). *The natural history of pollination.* London: Harper Collins.

Rae, T. C. (1998). The logical basis for the use of continuous characters in phylogenetic systematics. *Cladistics* 14: 221-228.

Ramanujam, C. G. K. (1953). *Palmoxylon arcotense* sp. nov., a fossil palm resembling the living genus *Livistona*, from South India. *Palaeobotanist* 2: 89-91.

Read, R. W. (1965). Chromosome numbers in the Coryphoideae. *Cytologia* 30: 385-391.

Read, R. W. (1975). The genus *Thrinax* (Palmae: Coryphoideae). *Smithsonian Contr. Bot.* 19: 1-98.

Read, R. W. and L. J. Hickey (1972). A revised classification of fossil palm and palmlike leaves. *Taxon* 21: 129-137.

Read, R. W. and D. R. Hodel (1990).120. Arecaceae palm family. In: Wagner, W. L., D. R. Herbst and S. H. Sohmer (eds), *Manual of the flowering plants of Hawaii* 2: 1360-1375. Hawaii: University of Hawaii Press.

Reid, E. M. and M. E. J. Chandler (1933). *The London clay flora.* London: The British Museum (Natural History).

Renner, S. S. and R. E. Ricklefs (1995). Dioecy and its correlates in the flowering plants. *Am. J. Bot.* 82: 596-606.

Richards, A. J. (1997). *Plant breeding systems.* 2nd edition. London: Chapman

and Hall.

Ridley, H. N. (1898). New or noteworthy plants. *Gard. Chron. 3rd series* 23: 177.

Ridley, H. N. (1907). Palmae. *Mat. fl. Malay. Penins.* 2:133-221.

Ridley, H. N. (1915). The botany of Gunong Tahan, Pahang. *Journ. Fed. Malay. States Museum* 6: 127-202.

Robinson, C. B. (1911a). Philippine hats. *Philipp. J. Sci. C. Bot.* 6: 93-131.

Robinson, C. B. (1911b). Botanical notes upon the island of Polillo. *Philipp. J. Sc. C. Bot.* 6: 185-228.

Rodd, A. N. (1998). Revision of *Livistona* (Arecaceae) in Australia. *Telopea* 8: 49-153.

Rosen, B. R. (1988). From fossils to earth history: applied historical biogeography. In: A. A. Myers and P. S. Giller (eds), *Analytical biogeography*, 437-481. London: Chapman & Hall.

Rosen, B. R. and A. B. Smith (1988). Tectonics from fossils? Analysis of reef-coral and sea-urchin distributions from Late Cretaceous to Recent, using a new method. In: M. G. Audley-Charles and A. Hallam (eds), *Gondwana and Tethys*, 275-306. London: Geological Society.

Röser, M. (1993). Variation and evolution of karyotype characters in palm subfamily Coryphoideae s. l. *Bot. Acta* 106: 170-182.

Röser, M. (1994). Pathways of karyological differentiation in palms (Arecaceae). *Pl. Syst. Evol.* 189: 83-122.

Rull, V. (1998). Biogeographical and evolutionary considerations of *Mauritia* (Arecaceae), based on palynological evidence. *Rev. Palaeobot. Palynol.* 100: 109-122.

Rumphius, G. E. (1741). *Herbarium Amboinense* 1. Amsterdam: J. Burmann, Meinard Uytwerf.

Said, R. (1981). *The geological evolution of the River Nile.* New York: Springer-Verlag.

Sakai, A. K., W. L. Wagner, D. M. Ferguson and P. R. Herbst (1995). Origins of dioecy in the Hawaiian flora. *Ecology* 76: 2517-2529.

Salomon, C. (1887). *Die Palmen.* Berlin: Paul Parey.

Salzman, V. T. and W. S. Judd (1995). A revision of the Greater Antillean species of *Bactris* (Bactridinae: Arecaceae). *Brittonia* 47: 345-371.

Sands, D. and S. House (1990). Plant/insect interactions – food webs and breeding

systems. In: L. J. Webb and J. Kikkawa (eds), *Australian tropical rainforests: science – values – meaning*, 88-97. Melbourne: CSIRO.

Sang, T., D. J. Crawford and T. F. Stuessy (1997). Chloroplast DNA phylogeny, reticulate evolution, and biogeography of *Paeonia* (Paeoniaceae). *Am. J. Bot.* 84: 1120-1136.

Satake, T. (1962). A new system of the classification of Palmae. *Hikobia* 3: 112-133.

Savage, A. J. P. and P. S. Ashton (1983). The population structure of the double coconut and some other Seychelles palms. *Biotropica* 15: 15-26.

Scariot A. O. and E. Lleras (1991). Reproductive biology of the palm *Acrocomia aculeata* in central Brazil. *Biotropica* 23: 12-22.

Schlessman, M. A., P. P. Lowry and D. G. Lloyd (1990). Functional dioecism in the New Caledonian endemic *Polyscias pancheri* (Araliaceae). *Biotropica* 22: 133-139.

Schmid, R. (1983). Septal nectaries of *Asterogyne martiana* and other Palmae. *Principes* 27: 168-174.

Schultes, J. A. and J. H. Schultes (1829). *Systema Vegetabilium* 7. Stuttgart: J. G. Cottae.

Schuster, R. M. (1976). Plate tectonics and its bearing on the geographical origin and dispersal of angiosperms. In: C. B. Beck (ed.), *Origin and early evolution of angiosperms*, 48-138. New York: Columbia University Press.

Shapcott, A. (1998). The patterns of genetic diversity in *Carpentaria acuminata* (Arecaceae), and rainforest history in northern Australia. *Mol. Ecol.* 7: 833-847.

Sharma, A. K. and S. K. Sarkar (1956). Cytology of different species of palms and its bearing on the solution of the problems of phylogeny and speciation. *Genetica* 28: 361-488.

Shields, W. M. (1988). Sex and adaptation. In: R. E. Michod and B. R. Levin (eds), *The evolution of sex: an examination of current ideas*, 253-269. Sunderland: Sinauer Associates, Inc.

Shuey, A. G. and R. P. Wunderlin (1977). The needle palm: *Rhapidophyllum hystrix*. *Principes* 21: 47-59.

Siebert, D. J. (1992). Tree statistics; trees and 'confidence'; consensus trees; alternatives to parsimony; character weighting; character conflict and its resolution. In: P. L. Forey, C. J. Humphries, I. J. Kitching, R. W. Scotland, D. J. Siebert and D. M. Williams (eds), *Cladistics: a practical course in systematics*, 72-88. Oxford:

Clarendon Press.

Siebold, P. F. von (1830). Palmae. *Syn. pl. oecon. Jap.* 53. Batavia: Ter Lands Drukkerij.

Silberbauer-Gottsberger, I. (1990). Pollination and evolution in palms. *Phyton* 30: 213-233.

Silvertown, J. (1987). Possible sexual dimorphism in the double coconut: reinterpretation of the data of Savage and Ashton. *Biotropica* 19: 282-283.

Smets, E. F., L. –P. Ronse Decraene, P. Caris and P. J. Rudall (2000). Floral nectaries in monocotyledons: distribution and evolution. In: K. L. Wilson and D. A. Morrison (eds), *Monocots: systematics and evolution*, 230-240. Melbourne: CSIRO.

Smith, A. C. (1963). Summary discussion on plant distribution patterns in the tropical Pacific. In: J. L. Gressitt (ed), *Pacific basin biogeography*, 247-249. Honolulu: Bishop Museum Press.

Solander, D. (1768-1771). *Plantae novae hollandiae*. Unpublished manuscript. British Museum.

Sowunmi, M. A. (1972). Pollen morphology of the Palmae and its bearing on taxonomy. *Rev. Palaeobot. Palynol.* 13: 1-80.

Specht, R. L. and C. P. Mountford (1958). *Records of the American-Australian scientific expedition to Arnhem Land 3, botany and plant ecology*. Melbourne: Melbourne University Press.

Sprengel, C. (1825). *Systema vegetabilium* 2: 138.

Stafleu, F. A. and R. S. Cowan (1976-1988). *Taxonomic literature*. Utrecht: Bohn, Scheltema and Holkema.

Stanton, M. L., T.–L. Ashman, L. F. Galloway and H. J. Young (1992). Estimating male fitness in plants in natural populations. In: R. Wyatt (ed.), *Ecology and evolution of plant reproduction*, 62-90. New York: Chapman and Hall.

Strahler, A. H. and A. N. Strahler (1992). *Modern physical geography*, 4th Edition. New York: Wiley.

Stebbins, G. L. (1974). *Flowering plants: evolution above the species level.* Cambridge: Belknap Press of Harvard University.

Stevenson, D. W., J. I. Davis, J. V. Freudenstein, C. R. Hardy, M. P. Simmons and C. D. Specht (2000). A phylogenetic analysis of the monocotyledons based on morphological and molecular character sets, with comments on the placement of

Acorus and Hydatellaceae. In: K. L. Wilson and D. A. Morrison (eds), *Monocots: systematics and evolution*, 17-24. Melbourne: CSIRO.

Strong, E. E. and D. Lipscombe (1999). Character coding and inapplicable data. *Cladistics* 15: 363-371.

Stuessy, T. F. (1990). *Plant taxonomy: the systematic evaluation of comparative data*. New York: Columbia University Press.

Sudhersan, C. and M. Abo El-Nil (1999). Occurrence of hermaphroditism in the male date palm. *Palms* 43: 18-19, 48-50.

Suzuki, K. (1982). *Livistona chinensis* var. *subglobosa*. In: A. Miyazaki (ed.), *Flora of Japan*, 124-126. Toyko: Shibundo.

Swofford, D. L. (1993). *PAUP 3.1 user's manual*. Champaign: Illinois Natural History Survey.

Sytsma, K. J. (1990). DNA and morphology: inference of plant phylogeny. *TREE* 5: 104-110.

Sytsma, K. J. and D. A. Baum (1996). Molecular phylogenies and the diversification of the angiosperms. In: D. W. Taylor and L. J. Hickey (eds), *Flowering plant origin, evolution and phylogeny*, 314-340. New York: Chapman and Hall.

Sytsma, K. J. and W. J. Hahn (1997). Molecular systematics: 1994-1995. *Progr. Bot.* 58: 470-499.

Takhtajan, A. (1986). *Floristic regions of the world*. Berkeley: University of California Press.

Taylor, N. (1976). *Livistona. Stand. cyclop. hort.* 2: 1894-1896. New York: The Macmillan Company.

Teysmann, J. S. and S. Binnendijk (1866). *Catalogus plantarum quae in horto botanico Bogoriensi coluntur*. Batavia: Ter Lands-Drukkerij.

The Plant Names Index (1999). *International plant names index*. Published on the Internet: http://www.ipni.org [accessed 27 July 2000).

Thomson, B. H. (1889). New Guinea: narrative of an exploring expedition to the Louisiade and D'Entrecasteaux Islands. *Proc. Roy. Geogr. Soc. Lond*, new ser. 11: 524-542.

Thomson, J. D. and J. Brunet (1990). Hypotheses for the evolution of dioecy in seed plants. *TREE* 5: 11-16.

Thorne, R. F. (1986). Antarctic elements in Australian rainforests. *Telopea* 2: 611-

617.

Thorne, R. F. (1996a). Some guiding principles of biogeography. *Telopea* 6: 845-850.

Thorne, R. F. (1996b). The least specialized angiosperms. In: D. W. Taylor and L. J. Hickey (eds), *Flowering plant origin, evolution and phylogeny*, 286-313. New York: Chapman and Hall.

Thórsson, A. Th., E. Salmela and K. Anamthawat-Jónsson (2001). Morphological, cytogenetic, and molecular evidence for introgressive hybridization in Birch. *J. Hered.* 92: 404-408.

Tomlinson, P. B. (1961). *Anatomy of the monocotyledons. II. Palmae.* Oxford: Clarendon Press.

Tomlinson, P. B. (1979). Systematics and ecology of the Palmae. *Ann. Rev. Ecol. Syst.* 10: 85-107.

Tomlinson, P. B. (1990). *The structural biology of palms.* Clarendon Press: Oxford.

Tomlinson, P. B. and P. Fawcett (1972). Dioecism in *Citharexylum* (Verbenaceae). *J. Arnold Arbor.* 53: 386-389.

Tomlinson, P. B. and P. K. Soderholm (1975). The flowering and fruiting of *Corypha elata* in South Florida. *Principes* 19: 83-99.

Tong, L. (1994). Tertiary. In: Yin, H. (ed.), *The palaeobiogeography of China*, 271-292. Oxford: Clarendon Press.

Traveset, A. V. (1999). Ecology of plant reproduction: mating systems and pollination. In: F. I. Pugnaire and F. Valladares (eds), *Handbook of functional plant ecology*, 545-588. New York: Marcel Dekker, Inc.

Trivett, M. L. and K. B. Pigg (1996). A survey of reticulate venation among fossil and living land plants. In: D. W. Taylor and L. J. Hickey (eds), *Flowering plant origin, evolution and phylogeny*, 8-31. New York: Chapman and Hall.

Truswell, E. M. (1990). Australian rainforests: the 100 million year record. In: L. J. Webb and J. Kikkawa (eds), *Australian tropical rainforests: science – values - meaning*, 7-22. Melbourne: CSIRO.

Truswell, E. M. (1993). Vegetation changes in the Australian Tertiary in response to climatic and phytogeographic forcing factors. *Austral. Syst. Bot.* 6: 533-557.

Truswell, E. M. and N. G. Marchant (1986). Early Tertiary pollen of probable droseracean affinity from central Australia. *Special Pap. Palaeontology* 35: 163-

178.

Tucker, R. (1988). *Palms of subequatorial Queensland.* Milton: Palm & Cycad Societies of Australia.

Turner, H. (1996). Sapindaceae and the biogeography of eastern Australia. *Austral. Syst. Bot.* 8: 133-167.

Tuyama, T. (1972). The status of the Bonin Islands flora in the Pacific. In: A. Graham (ed), *Floristics and paleofloristics of Asia and eastern North America*, 79-81. Amsterdam: Elsevier.

Uhl, N. W. and J. Dransfield (1987). *Genera palmarum: a classification of palms based on the work of H. E. Moore, Jr.* Lawrence: Kansas: International Palm Society and L. H. Bailey Hortorium.

Uhl, N. W. and J. Dransfield (1988). *Genera palmarum*, a new classification of palms and its implications. *Adv. Econ. Bot.* 6: 1-19.

Uhl., N. W. and J. Dransfield (1999). *Genera palmarum* after ten years. *Mem. New York Bot. Gard.* 83: 245-253.

Uhl, N. W., J. Dransfield, J. I. Davis, M. A. Luckow, K. S. Hansen and J. J. Doyle (1995). Phylogenetic relationships among palms: cladistic analyses of morphological and chloroplast DNA restriction site variation. In: P. J. Rudall, P. J. Cribb, D. F. Cutler and C. J. Humphries (eds), *Monocotyledons: systematics and evolution*, 623-661. Kew: Royal Botanic Gardens.

Uhl, N. W. and H. E. Moore, Jr. (1977). Correlations of inflorescence, flower structure and floral anatomy with pollination in some palms. *Biotropica* 9: 170-190.

Uyenoyama, M. K. (1988). On the evolution of genetic incompatibility systems: incompatibility as a mechanism for the regulation of outcrossing distance. In: R. E. Michod and B. R. Levin (eds), *The evolution of sex: an examination of current ideas*, 212-232. Sunderland; Sinauer Associates, Inc.

van Balgooy, M. M. J. (1971). Plant geography of the Pacific. *Blumea Suppl.* 6: 1-222.

van Balgooy, M. M. J., P. H. Hovenkamp and P. C. van Welzen (1996). Phytogeography of the Pacific - floristic and historical distribution patterns in plants. In: A. Keast and S. E. Miller (eds), *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes*, 191-213. Amsterdam: SPB Academic Publishing.

van Heel, W. A. (1988). On the development of some gynoecia with septal

nectaries. *Blumea* 33: 477-504.

van Oosterzee, P. (1997). *Where worlds collide*. Melbourne: Reed books.

van Steenis, C. G. G. J. (1961). The land-bridge theory in botany. *Blumea* 11: 235-542.

van Steenis, C. G. G. J. (1979). Plant-geography of east Malesia. *Bot. J. Linn. Soc.* 79: 97-178.

van Steenis-Kruseman, M. J. (1950). Malaysian plant collectors and collections. *Fl. Males.* 1: 3-639.

Veevers, J. J. (1991). Phanerozoic Australia in the changing configuration of proto-Pangea through Gondwanaland and Pangea to the present dispersed continents. *Austral. Syst. Bot.* 4: 1-11.

Vega, I. L. O. A. Ayala, D. E. Organista and J. J. Morrone (1999). Historical relationships of the Mexican cloud forests: a preliminary vicariance model applying Parsimony Analysis of Endemicity to vascular plant taxa. *J. Biog.* 26: 1299-1305.

Vidal y Soler, S. (1883). *Sinopsis de familias y generos de plantas leñosas de Filipinas*. Manila.

Vidal y Soler, S. (1886). *Revision de plantas vasculares filipinas*. Manilla: M. Perez.

Vilmorin, P. L. de (1895). Gattung 1274. *Livistonea. Vilm. ill. Blumengärtn.* 1: 1149.

Wallace, A. R. (1860). On the zoological geography of the Malay Archipelago. *J. Linn. Soc.* 4: 172-184.

Wallace, A. R. (1890). *The Malay Archipelago*. London: MacMillan and Co.

Wallace, A. R. (1893). *Australasia*. London: Edward Stanford.

Wallander, E. (2001). Evolution of wind-pollination in *Fraxinus* (Oleaceae) – an ecophylogenetic approach. PhD thesis. Göteborg University, Sweden.

Walker, E. H. (1976). *Flora of Okinawa and the southern Ryukyu Islands*. Washington: Smithsonian Institution Press.

Watrous, L. E. and Q. D. Wheeler (1981). The out-group comparison method of character analysis. *Syst. Zool.* 30: 1-11.

Watson, W. (1889). Cool cultivation of tropical and sub-tropical plants. *Kew Bull.* 3: 287-306.

Waycott, M. and P. A. G. Barnes (2001). AFLP diversity within and between

populations of the Caribbean seagrass *Thalassia testudinum* (Hydrocharitaceae). *Marine Biology*. Published online Ref. DOI 10.1007/s00270100670.

WCMC (1993). *Palmae: conservation status listing of plants compiled from the WCMC plants database*. Cambridge: World Conservation Monitoring Centre.

Webb, C. J. and D. Kelly (1993). The reproductive biology of the New Zealand flora. *TREE* 8: 442-447.

Webb, L. J. and J. G. Tracey (1972). An ecological comparison of vegetation communities on each side of Torres Strait. In: D. Walker (ed), *Bridge and barrier: the natural and cultural history of Torres Strait*, 109-129. Canberra: Australian National University.

Webb, L. J., J. G. Tracey and L. W. Jessup (1986). Recent evidence for autochthony of Australian tropical and subtropical rainforest floristic elements. *Telopea* 2: 575-589.

Wei, Xing-wei and Xiao Mian-yun (1982). A new species of *Livistona* from China. *J. South China. Agri. Coll.* 3: 22-24.

Weiner, J. and R. T. Corlett (1987). Size structure of *Livistona endauensis* populations at four sites on Gunung Janing Barat, Johore, Malaysia. *Malayan. Nat. J.* 41: 297-302.

Welch, G. and H. Welch (1998). *Survey of the Bankoualé palm Livistona carinensis*. Unpublished report.

Welch, H. and G. Welch (1999). *A report on the birds of Djibouti and the Bankoualé palm Livistona carinensis*. Biodiversity Report no. 4. IUCN and Djibouti Government, Djibouti.

Wendland, H. (1862). *Pritchardia. Bonplandia* 10: 199.

Wendland, H. and O. Drude (1875). Palmae Australasicae. *Linnaea* 39: 153-238.

Werren, J. H. and L. W. Beukeboom (1998). Sex determination, sex ratios, and genetic conflicts. *Ann. Rev. Ecol. Syst.* 29: 233-261.

Weston, P. H. (1994). Methods for rooting cladistic trees. In: R. W. Scotland, D. J. Siebert and D. M. Williams (eds), *Models in phylogeny reconstruction*, 125-155. Oxford: Clarendon Press.

Weston, P. H. and M. D. Crisp (1996). Trans-Pacific biogeographic patterns in the Proteaceae. In: A. Keast and S. E. Miller (eds), *The origin and evolution of Pacific island biotas, New Guinea to Polynesia: patterns and processes*, 215-232. Amsterdam: SPB Academic Publishing.

White, T. J., T. Bruns, S. Lee and J. Taylor (1990). Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: M. A. Innis, D. H. Gelfand, J. J. Sninsky and T. J. White (eds), *PCR protocols: a guide to methods and applications*, 315-322. San Diego: Academic Press.

Wickens, G. E. (1977). Speculation on long distance dispersal and the flora of Jebel Marra, Sudan Republic. *Kew Bull.* 31: 105-150.

Wilkinson, M. (1995). A comparison of two methods of character construction. *Cladistics* 11: 297-308.

Willdenow, C. L. (1799). *Species plantarum* 2. Berlin: G. C. Nauck.

Williams, G. and P. Adam (1999). Pollen sculpture in subtropical rain forest plants: is wind pollination more common than previously suspected? *Biotropica* 31: 520-524.

Williams, M. A. J., D. L. Dunkerley, P. De Deckker, A. P. Kershaw and T. Stokes (1993). *Quaternary environments*. London: Edward Arnold.

Willson, M. F. (1983). *Plant reproductive ecology*. New York: John Wiley & Sons.

Wilson, A. J. G. (1992). Family 167 Arecaceae (Palmae). In: J. R. Wheeler (ed), *Flora of the Kimberley Region*, 1249-1250. Perth: Western Australia Herbarium.

Wilson, P. G. (1996). Myrtaceae in the Pacific, with special reference to *Metrosideros*. In: A. Keast and S. E. Miller (eds), *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes*, 233-245. Amsterdam: SPB Academic Publishing.

Wolda, H. (1978). Fluctuations in abundance of tropical insects. *Amer. Naturalist* 112: 1017-1045.

Woodford, C. M. (1890). *A naturalist among the head-hunters*. London: George Philip and Son.

Wright, S. D. and A. M. Lees (1996). Biodiversity conservation in the island Pacific. In: A. Keast and S. E. Miller (eds), *The origin and evolution of Pacific island biotas, New Guinea to eastern Polynesia: patterns and processes*, 445-461. Amsterdam: SPB Academic Publishing.

Wuschke, M. (1999). Fire resistance in a Queensland *Livistona*. *Palms* 43: 140-144.

Wyroll, K. -H. (1993). An outline of late Cenozoic palaeoclimatic events in the Cape Range region. *Rec. West. Australian Mus. Suppl.* 45: 39-50.

Yang, S. (1996). Vietnam cycad and palm expedition. *Palms & Cycads* 50: 10-19.

Yoshida, N., R. Nobe, K. Ogawa and Y. Murooka (2000). Origin of *Livistona chinensis* var. *subglobosa* (Arecaceae) on the "Islet of the Gods": Aoshima, Japan. *Am. J. Bot.* 87: 1066-1067.

Zollinger, H. (1854). *Systematisches verzeichniss*. Zurich: E. Kiesling.

Zollinger, H. (1857). Observationes botanicae novae. *Nat. tijd. Ned. Indie* 14: 145-176.

Zona, S. (1987). Phenology and pollination biology of *Sabal etonia* (Palmae) in southeastern Florida. *Principes* 31: 177-182.

Zona, S. (1990). A monograph of *Sabal* (Arecaceae: Coryphoideae). *Aliso* 12: 583-666.

Zona, S. (1996). *Roystonea* (Arecaceae: Arecoideae). *Flora Neotropica* 71: 1-36.

Zona, S. (1999a). Revision of *Drymophloeus* (Arecaceae: Arecoideae). *Blumea* 44: 1-24.

Zona, S. (1999b). New perspectives on generic limits and relationships in the Ptychospermatinae (Palmae: Arecoideae). *Mem. New York Bot. Gard.* 83: 255-263.

Appendix 1

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

1998

February. Papua New Guinea. Western Highlands, Morobe, East and West Sepik Provinces (with Michael Ferrero).

26 August. Bluewater Range (with Lucy Smith).

16-22 September. Singapore (Botanical Gardens and Herbarium), Thailand, Nong Nooch Gardens (IPS Conference).

2 October. Herveys Range.

8-22 December. Indonesia. Kebun Raya Botanical Gardens (Bogor) and Herbarium Bogoriense.

1999

7 January. Josephine Creek, Cairns (with Michael Ferrero).

24-25 March. Hen Camp Creek, Licuala State Forest, Cairns (with Chuck Hubbuch, Fairchild Tropical Gardens, Miami, USA).

26-30 March. Papua New Guinea. Lae Botanical Gardens and Herbarium (with Chuck Hubbuch, Fairchild Tropical Gardens, Miami, USA and Dale Dixon).

7-9 April. Airlie Beach, Conway Range and Long Island.

21-22 April. Mission Beach, Cairns (with Lucy Smith).

24-30 April. JCU Cairns Campus, DNA lab.

24- 31 May. Thailand (with Poonsak Vatcharakorn and Michael Ferrero).

1-6 June. United Kingdom, Royal Botanic Gardens, Kew, and Herbarium (with John Dransfield and Bill Baker).

6-20 June. Denmark, Department of Systematic Botany, Aarhus University, and Herbarium (with Anders Barfod).

21-25 June. Denmark, Botanical Library, Copenhagen University.

26 June – 3 July. Denmark, Department of Systematic Botany, Aarhus University, and Herbarium (with Anders Barfod).

17 June. Glenroy Creek, S of Ravenswood (with Neils Lunoe).

4-6 August. Hen Camp Creek, Cairns.

2 September. Mt Elliott, Cockatoo Creek (with Reni Lestari and Obed Lense).

24 September. Glenroy Creek, S. of Ravenswood (with Anders Barfod and Aniuska Kazandjian).

25 September-5 October. Cape York, via Cooktown and Iron Range (with Anders Barfod).

2000

2-20 January. Sunshine Coast, Mt Nebo, Mt Glorious, Jacobs Well and Hope Island (*Livistona australis* collections).

27 February- 14 March. Papua New Guinea. Milne Bay, Central and Gulf Provinces (with Anders Barfod, Anders Kjaer and Roy Banka).

21- 24 March. JCU Campus Cairns, DNA Lab.

17-19 October. Hen Camp Creek, Cairns, Cooktown, Barrett Creek, Chillagoe, Nolans Creek (IPS Conference, Colonial Club Resort, 'Australian Palms: history and distribution'.

23 October. Cape Cleveland, Hen Camp Creek (with Katherine Maidman, Fairchild Tropical Gardens, Miami, USA) (*Livistona drudei* and *L. decora*).

2001

13-15 May. Chillagoe, Nolans Creek (with Aniuska Kazandjian) (*Livistona muelleri* collections).

21- 29 May. Papua New Guinea, Louisiade Archipelago (with Roy Banka) (*Livistona woodfordii* collections).

10-16 June. Lawn Hill National Park (with Aniuska Kazandjian) (*Livistona rigida* collections).

23-25 August. Cairns, Flecker Gardens (with Lucy Smith and Tom Hoblyn).

2-21 December. Philippines, Polillo Island and Mt Makiling (with Domingo Madulid, Edwino Fernando and Efren Romero) (*Livistona robinsoniana* and *L. rotundifolia* var. *luzonensis* collections).

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

Explanation of headings:

ext. spec. seen: extant specimen seen. Specimens were either examined or verified by photographic or digital images.

ext. spec. not seen: extant specimens not seen. Specimens were reported to be extant by herbarium staff, but either loans or images were not available.

illustration: in the absence of an herbarium specimen, an illustration based on the specimen was chosen as the type.

not designated: most of these names are illegitimate or otherwise not valid, and associated specimens were not given in either the instance of first use or subsequent uses of the names.

lost or destroyed: specimens were cited in the prologues but were not able to be located, and presumed lost or destroyed.

New lectotypes and neotypes, chosen in this work, are indicated by ■.

species	ext. spec. seen	ext. spec. not seen	illustration	not designated	lost or destroyed
alfredii	✔				
altissima	✔ ■				
australis	✔				
beccariana	✔				
benthamii	✔				
bissula				✔	
blancoi	✔				
boninensis	✔				
brassii	✔				
carinensis	✔				
chinensis			✔		
chinensis var. subglobosa	✔				
cochinchinensis				✔	
crustacea	✔				
decora	✔				
decora var. polyantha	✔				
diepenhorstii		✔			
dournowiana				✔	
drudei	✔				

eastonii	✔				
endauensis	✔				
enervis				✔	
eocenica				✔	
erecta				✔	
exigua	✔				
fengkaiensis	✔				
filamentosa				✔	
filifera				✔	
fulva	✔				
gaudichaudii		✔			
halongensis		✔			
hasseltii					✔
holtzei		✔			
hoogendorpii	✔ ■				
humilis	✔				
humilis var. minutiflora				✔	
humilis var. novoguineensis	✔				
humilis var. sclerophylla	✔				
inaequisecta		✔			
inermis	✔				
japonica				✔	
jenkinsiana			✔ ■		
kimberleyana	✔				
kingiana		✔			
lanuginosa	✔				
leichhardtii	✔				
lorophylla	✔				
macrophylla Bruder					✔
macrophylla Roster				✔	
mariae	✔				
mariae subsp. occidentalis	✔				
mariae subsp. rigida	✔				
martii			✔		
mauritiana				✔	
melanocarpa	✔				
merrillii	✔ ■				
microcarpa	✔				
minima	✔				
mindorensis	✔				
moluccana	✔ ■				
mülleri				✔	

muelleri	✔				
nasmophila	✔				
nitida	✔				
occidentalis				✔	
okinawensis				✔	
olivaeformis	✔ ■				
ovaliformis				✔	
papuana	✔				
ramsayi	✔				
rigida	✔				
robinsoniana	✔				
rotundifolia			✔		
rotundifolia var.luzonensis	✔				
rotundifolia var. microcarpa	✔				
rotundifolia var. mindorensis	✔				
rupicola	✔				
saribus					✔
speciosa	✔				
spectabilis			✔ ■		
subglobosa	✔ ■				
tahanensis	✔				
ternatensis				✔	
tonkinensis	✔ ■				
umbraculifera				✔	
victoriae	✔				
vidalii		✔			
vogamii				✔	
whitfordii		✔			
woodfordii	✔				
zollingeri Hort. ex Devansaye	✔				
zollingeriana Blume	✔				
Totals	57	8	5	19	3

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 (-)

species	height (m)	dbh (m)	ratio	petiole base persistence
L. alfredii	12	0.32	36	-
L. australis	25	0.35	71	-
L. benthamii	18	0.13	138	+
L. boninensis	20	0.30	67	-
L. carinensis	40	0.40	100	-
L. chinensis	15	0.30	50	-
L. chocolatina	23	0.17	130	-
L. concinna	30	0.29	103	-
L. decora	18	0.25	72	-
L. drudei	20	0.18	114	-
L. eastonii	15	0.12	125	+
L. endauensis	15	0.16	94	-
L. exigua	5	0.02	250	-
L. fulva	13	0.23	58	-
L. halongensis	10	0.20	50	-
L. humilis	7	0.07	108	+
L. inermis	10	0.08	125	-
L. jenkinsiana	22	0.30	73	-
L. lanuginosa	18	0.35	50	-
L. lorophylla	15	0.15	100	-
L mariae	28	0.40	70	-
L. merrillii	20	0.30	67	-
L. muelleri	12	0.18	69	+
L. nasmophila	30	0.50	60	-
L. nitida	28	0.33	86	-
L. papuana	50	0.30	166	-
L. rigida	28	0.40	70	-
L. robinsoniana	20	0.20	100	-
L. rotundifolia	45	0.25	180	-
L. saribus	40	0.65	61	-
L. surru	20	0.22	93	-
L. tahanensis	8	0.12	67	+
L. tothur	20	0.18	114	-
L. victoriae	15	0.20	75	-
L. woodfordii	15	0.20	75	-
Licuala ramsayi	16	0.20	80	-
Pholidocarpus macrocarpus	30	0.30	90	-
Character #	(1)		(2)	(3)

Appendix 4

Leaf characters for 35 species of *Livistona* and two outgroup taxa: lamina outline, segmentation [irregular segmentation = -; regular segmentation = +], length of mid-leaf segment in cm, number of segments in a leaf, % of segment that is free (%seg free), and % of segment of the apical cleft (% apex)

species	outline	mid-leaf length	#segments	%seg free	%apex
L. alfredii	subcircular+	90-140	50-66	60-70	60-75
L. australis	circular+	100-130	80-100	49-69	50-63
L. benthamii	circular+	90-160	50-80	60-75	50-65
L. boninensis	subcircular+	120-200	50-82	45-75	20
L. carinensis	subcircular+	80-95	50-70	75-85	40-50
L. chinensis	subcircular+	120-200	50-90	45-55	13
L. chocolatina	subcircular+	100-120	45-60	44	4
L. concinna	circular+	155-165	60-78	60	41
L. decora	circular+	120-185	70-84	82-88	44-54
L. drudei	circular+	100-150	60-70	60-70	60
L. eastonii	subcircular+	60-90	40-50	50-90	49-63
L. endauensis	subcircular+	100	60-70	61	8
L. exigua	circular-	50	16-30	42	8
L. fulva	circular+	90-100	60-66	50-55	3-5
L. halongensis	subcircular	77	64	42	40
L. humilis	circular+	30-50	30-44	60-87	35-89
L. inermis	subcircular+	30-70	24-48	80-97	70-84
L. jenkinsiana	subcircular+	110-210	70-100	50-75	2-10
L. lanuginosa	circular+	130-190	80-92	60-70	50-76
L. lorophylla	circular+	60-100	34-50	85-98	55-78
L mariae	circular+	100-220	50-86	45-55	45-65
L. merrillii	circular+	100-150	70	34	6-24
L. muelleri	circular+	60-90	48-60	50-65	5-14
L. nasmophila	circular+	130-175	52-58	48	48
L. nitida	circular+	160-190	68-80	63-70	60-73
L. papuana	subcircular+	90-150	80-90	28-56	1-11
L. rigida	circular+	150-170	45-80	50-55	60-63
L. robinsoniana	circular+	75-150	60-90	38-62	4-25
L. rotundifolia	circular+	75-150	60-90	38-62	4-25
L. saribus	subcircular-	80-200	80-90	37-78	19-50
L. surru	subcircular+	180-224	70-90	45-80	6
L. tahanensis	subcircular+	57-76	49-50	58	16
L. tothur	subcircular+	150-200	60-75	62-85	1-3
L. victoriae	subcircular+	80-110	40-56	55-65	55-70
L. woodfordii	circular+	150	65-70	51	11
Licuala	circular-	120-200	70	100	2
Pholidocarpus macrocarpus	circular-	150-200	70	40-80	20-50
Character #	(4) (5)	(6)	(7)	(8)	(9)

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

species	apex	adaxial colour	abaxial colour	surface
L. alfredii	rigid	grey	grey	waxy
L. australis	pendulous	green	green	non-waxy
L. benthamii	pendulous	green	lighter green	non-waxy
L. boninensis	pendulous	grey	lighter green	non-waxy
L. carinensis	rigid	grey	lighter grey	waxy
L. chinensis	pendulous	grey	lighter green	non-waxy
L. chocolatina	rigid	grey	lighter grey	waxy
L. concinna	pendulous	green	lighter green	non-waxy
L. decora	pendulous	green	lighter green	non-waxy
L. drudei	pendulous	green	lighter green	non-waxy
L. eastonii	rigid	green	lighter green	waxy
L. endauensis	rigid	green	light green	non-waxy
L. exigua	rigid	green	lighter green	non-waxy
L. fulva	rigid	green	coppery	non-waxy
L. halongensis	pendulous	green	green	non-waxy
L. humilis	rigid	green	lighter green	non-waxy
l. inermis	rigid	grey	lighter grey	non-waxy
L. jenkinsiana	rigid	green	green	non-waxy
L. lanuginosa	pendulous	grey	lighter grey	waxy
L. lorophylla	rigid	grey	grey	non-waxy
L mariae	pendulous	grey	lighter grey	waxy
L. merrillii	rigid	green	lighter green	non-waxy
L. muelleri	rigid	green	lighter green	non-waxy
L. nasmophila	rigid	grey	lighter grey	waxy
L. nitida	pendulous	green	lighter green	non-waxy
L. papuana	rigid	green	lighter green	non-waxy
L. rigida	pendulous	grey	lighter grey	waxy
L. robinsoniana	pendulous	green	lighter green	non-waxy
L. rotundifolia	rigid	green	lighter green	non-waxy
L. saribus	pendulous	green	green	non-waxy
L. surru	pendulous	green	lighter green	non-waxy
L. tahanensis	rigid	green	grey	non-waxy
L. tothur	rigid	green	grey	waxy
L. victoriae	rigid	grey	grey	waxy
L. woodfordii	rigid	green	lighter green	non-waxy
Licuala	rigid	green	lighter green	non-waxy
Pholidocarpus macrocarpus	pendulous	green	grey	non-waxy
Character #	(10)	(11)	(12)	(13)

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

pa. = parallel; tr. = transverse. * = measured in a circular 150 mm² portion of leaf.

species	pa. veins #	pa. veins prominence	tr. veins extension	tr. vein density* # (pa. veins)
L. alfredii	14	very prominent	very thin	2-5	14 (5)
L. australis	16	most prominent	thin	2-3	23 (7)
L. benthamii	16	most prominent	thin	2-3	19 (7)
L. boninensis	11	most prominent	thin	2-5	18 (4)
L. carinensis	38	very prominent	very thin	2	5 (10)
L. chinensis	17	most prominent	thin	2-4	36 (5)
L. chocolatina	16	most prominent	thin	2-4	26
L. concinna	19	most prominent	thin	2-4	12 (5)
L. decora	13	slightly prominent	thin	2-5	23 (5)
L. drudei	14	very prominent	thin	2	14 (7)
L. eastonii	14	very prominent	thin	3-6	12 (5)
L. endauensis	9	prominent	very thin	2-4	25 (5)
L. exigua	11	+ or - = prominence	thin	2-3	25(11)
L. fulva	17	very prominent	thin	2-5	16 (7)
L. halongensis	12	prominent	very thin	2-4	25
L. humilis	12	most prominent	very thin	2-3	29 (5)
L. inermis	17	very prominent	very thin	2	11 (8)
L. jenkinsiana	19	most prominent	very thin	2-5	26 (7)
L. lanuginosa	16	very prominent	very thin	2-4	6 (4)
L. lorophylla	18	very prominent	thin	2-3	10 (6)
L. mariae	16	most prominent	thin	2-3	15 (4)
L. merrillii	11	most prominent	very thin	2-3	13 (5)
L. muelleri	16	very prominent	very thin	2	13 (8)
L. nasmophila	16	very prominent	very thin	2-3	9 (7)
L. nitida	14	most prominent	very thin	2-6	15 (5)
L. papuana	15	least prominent	very thin	2-4	26
L. rigida	12	most prominent	thin	2-3	15 (4)
L. robinsoniana	14	least prominent	thin	2-7	24
L. rotundifolia	14	least prominent	thin	2-7	30 (6)
L. saribus	13	most prominent	thin	2-5	20 (5)
L. surru	11	prominent	thin	2-6	22 (5)
L. tahanensis	13	prominent	thin	2-4	14 (5)
L. tothur	13	prominent	very thin	2-7	33 (5)
L. victoriae	20	very prominent	thin	2-4	20 (9)
L. woodfordii	11	most prominent	thin	2-5	23 (4)
Licuala	6	+ or - = prominence	thin	2-3	13 (2)
Pholidocarpus macrocarpus	15	+ or - = prominence	thin	2-3	13 (4)
Character #	(14)	(15)	(16)	(17)	(18)

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

species	petiole c/section	armature	spine shape	spine colour
L. alfredii	flat	single	curved	black
L. australis	ridged	single	curved	black
L. benthamii	ridged	single	curved	black
L. boninensis	ridged	single	curved	green
L. carinensis	flat	double	curved	black
L. chinensis	ridged	single	curved	green
L, chocolatina	flat	single	curved	green
L. concinna	ridged	single	kris-like	black
L. decora	flat	single	curved	black
L. drudei	ridged	single	kris-like	red
L. eastonii	flat	double	curved	brown
L. endauensis	flat	single	kris-like	black
L. exigua	flat	single	kris-like	brown
L. fulva	ridged	single	curved	black
L. halongensis	flat	single	curved	orange-green
L. humilis	channelled	single	curved	dark red
l. inermis	channelled	single	curved	reddish
L. jenkinsiana	ridges	double	kris-like	reddish
L. lanuginosa	flat	single	curved	black
L. lorophylla	flat	single	curved	black
L mariae	ridged	single	curved	black
L. merrillii	flat	absent	-	-
L. muelleri	channelled	single	curved	black
L. nasmophila	flat	double	kris-like	reddish
L. nitida	ridged	single	curved	dark red
L. papuana	flat	absent	-	-
L. rigida	channelled	single	curved	black
L. robinsoniana	ridged	single	kris-like	black
L. rotundifolia	ridged	single	kris-like	black
L. saribus	channelled	single	kris-like	black
L. surru	flat	paired	kris-like	black
L. tahanensis	flat	single	kris-like	brown
L. tothur	flat	single	curved	green
L. victoriae	flat	single	curved	black
L. woodfordii	ridged	single	curved	black
Licuala ramsayi	flat	single	curved	dark green
Pholidocarpus macrocarpus	channelled	single	kris-like	black
Character #	(19)	(20)	(21)	(22)

Appendix 8

Leaf-base fibre characters for 35 species of *Livistona* and two outgroup taxa: visual appearance (prominence), type of weave and persistence

species	prominence	weave	persistence
L. alfredii	prominent	coarse	persistent
L. australis	prominent	fine	persistent
L. benthamii	prominent	fine	persistent
L. boninensis	not prominent	coarse	persistent
L. carinensis	prominent	fine	persistent
L. chinensis	not prominent	coarse	disintegrating
L. chocolatina	not prominent	coarse	persistent
L. concinna	very prominent	coarse	persistent
L. decora	very prominent	coarse	disintegrating
L. drudei	very prominent	coarse	persistent
L. eastonii	very prominent	coarse	persistent
L. endauensis	prominent	coarse	disintegrating
L. exigua	prominent	coarse	persistent
L. fulva	very prominent	fine	persistent
L. halongensis	prominent	coarse	persistent
L. humilis	not prominent	coarse	persistent
l. inermis	very prominent	coarse	persistent
L. jenkinsiana	not prominent	coarse	disintegrating
L. lanuginosa	very prominent	coarse	persistent
L. lorophylla	very prominent	coarse	persistent
L mariae	very prominent	coarse	persistent
L. merrillii	very prominent	fine/coarse	persistent
L. muelleri	not prominent	fine	disintegrating
L. nasmophila	very prominent	coarse	persistent
L. nitida	very prominent	coarse	disintegrating
L. papuana	not prominent	coarse	disintegrating
L. rigida	very prominent	coarse	persistent
L. robinsoniana	very prominent	coarse	persistent
L. rotundifolia	very prominent	fine/coarse	persistent
L. saribus	prominent	coarse	persistent
L. surru	prominent	fine/coarse	persistent
L. tahanensis	prominent	fine	disintegrating
L. tothur	prominent	fine/coarse	persistent
L. victoriae	very prominent	fine	persistent
L. woodfordii	very prominent	coarse	persistent
Licuala ramsayi	not prominent	fine	persistent
Pholidocarpus macrocarpus	prominent	coarse	persistent
Character #	(23)	(24)	(25)

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

species	branching + or -	partial inflors. #	branching order #	inflor. length cm	rachilla cm
L. alfredii	-	5-7	3	180-270	13
L. australis	-	6-9	5	140-250	5-25
L. benthamii	-	7-9	2	120-210	5-12
L. boninensis	-	8	3	130-220	4-16
L. carinensis	-	6-12	3	200-240	6-10
L. chinensis	-	6-7	3	100-120	10-18
L. chocolatina	+	6-10	3	195-225	8-12
L. concinna	-	8-9	4	130(m)-205(f)	6-10
L. decora	-	8-12	4	160-250	5-20
L. drudei	-	7-8	3	160-220	1-8
L. eastonii	-	5-6	4	110-180	1-9
L. endauensis	-	8	3	150	6-10
L. exigua	-	3-4	2	15-40	6-10
L. fulva	-	7-9	4	180-230	5-16
L. halongensis	-	7	3	340	?
L. humilis	-	1 or 4-7	3	185-230	3-12
L. inermis	-	3	3	80-90	1-7
L. jenkinsiana	-	3-6	3	60-200	12-30
L. lanuginosa	-	8-12	4	140-190	3-12
L. lorophylla	-	4-8	3	80-100	1-6
L mariae	-	10-14	4	150-250	3-8
L. merrillii	+	5-10	3	100-150	4-10
L. muelleri	-	5-10	4	130-180	2-13
L. nasmophila	-	9-11	4	260-300	5-9
L. nitida	-	8-12	4	170-190	5-20
L. papuana	+	3-10	3	100-225	3-12
L. rigida	-	10-14	4	150-250	3-8
L. robinsoniana	+	10	4	90-150	3-20
L. rotundifolia	+	10	4	90-150	3-20
L. saribus	-	4-9	4	60-230	15-45
L. surru	+	5-7	3	120	14-24
L. tahanensis	-	4	3	80-91	7-10
L. tothur	+	5-6	3	125-200	6-12
L. victoriae	-	5-9	4	90-150	1-3
L. woodfordii	+	5-6	3	120-270	4-6
Licuala ramsayi	-	8	2	250	12-35
Pholidocarpus macrocarpus	-	8	2	220	15-20
Character #	(26)	(27)	(28)	(29)	(30)

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

species	peduncular bracts #	bract tomentum	rachillae tomentum
L. alfredii	1	sparse/moderate tomentum	white pruinose
L. australis	0	dense floccose scaly	glabrous
L. benthamii	0	scurfy/patchy scales/sparse	patchily pubescent
L. boninensis	1	glabrous	glabrous
L. carinensis	1	glabrous	glabrous
L. chinensis	0	sparse tomentum	glabrous
L. chocolatina	2-4	glabrous	tomentose
L. concinna	0	glabrous	glabrous
L. decora	0	glabrous	glabrous
L. drudei	1	sparse appressed scales	minutely pubescent
L. eastonii	1	sparse appressed scales	glabrous
L. endauensis	0	glabrous	scattered unbranched hairs
L. exigua	0	scurfy, sparse	dense indument, papillate
L. fulva	1	sparse tomentum	dense granular/papillose
L. halongensis	5	glabrous	velvety
L. humilis	0/5-8	sparse scurfy-pubescent	bristly-pubescent
l. inermis	0	sparse transparent hairs	glabrous
L. jenkinsiana	0	scurfy to glabrous	puberulous
L. lanuginosa	1-2	densely lanuginose	glabrous
L. lorophylla	1	sparse scurfy-tomentum	glabrous
L mariae	1	densely scaly	glabrous
L. merrillii	1	glabrous	glabrous
L. muelleri	0	sparse appressed scales	minutely papillose
L. nasmophila	0	glabrous	glabrous
L. nitida	0	densely scaly	glabrous
L. papuana	4	glabrous	finely puberulous
L. rigida	1	sparsely scaled	glabrous
L. robinsoniana	0	glabrous	glabrous
L. rotundifolia	0-1	glabrous	glabrous
L. saribus	0	glabrous	glabrous
L. surru	0	glabrous	densely pubescent
L. tahanensis	?	?	scurfy
L. tothur	1	scaly	densely pubescent
L. victoriae	1	densely woolly	minutely papillose
L. woodfordii	0	glabrous	glabrous
Licuala ramsayi	0	glabrous	glabrous
Pholidocarpus macrocarpus	0	glabrous	glabrous
Character #	(31)	(32)	(33)

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)

species	flowers/cluster #	flower length mm	colour (at maturity)	pollen size Lxl in μm
L. alfredii	1-2	2-3	yellow/white	?
L. australis	1-4	2.5-3.5	cream/yellow	?
L. benthamii	1-3	1.0-1.5	white/yellow	?
L. boninensis	5-8	2-2.8	cream	?
L. carinensis	5	2.0	yellow	23x17
L. chinensis	4-7	2.0-4	white/cream/yellow	27x22
L. chocolatina	1-4	1.2	red	?
L. concinna	1-4	1.6-2	white/cream/yellow	?
L. decora	2-6	1.5-2	yellow	20x16
L. drudei	2-5	1.7-2.2	yellow	34x23
L. eastonii	1-4	1.6-1.9	cream	27x22
L. endauensis	1-3	1.0	golden yellow	?
L. exigua	1-2	1.0	purplish	?
L. fulva	1-3	1.6-2	yellow	?
L. halongensis	2	2.0	cream/yellow	?
L. humilis	2-4	1.5-1.8	yellow	24x19
l. inermis	1-3	1.5-2.3	yellow/cream	44x37
L. jenkinsiana	1-5	3-4	greenish/yellow	37x25
L. lanuginosa	1-2	2.8-3	cream/yellow	15x10
L. lorophylla	1-4	1.2-3	cream	23x18
L mariae	3-6	1-1.8	cream/yellow	?
L. merrillii	1	3-4.5	yellow	?
L. muelleri	1-3	1.3-1.6	yellow/marron	23x19
L. nasmophila	4-6	1.4-1.5	yellow	35x27
L. nitida	1-5	2-3.2	cream/yellow	22x18
L. papuana	1-4	1-2	yellow	?
L. rigida	3-8	1.8	cream/yellow	19x9
L. robinsoniana	1-4	2.0	yellow	?
L. rotundifolia	1-4	2.0-3.0	yellow	?
L. saribus	3-5	1.5-1.7	yellow	43x25
L. surru	2-4	2	red	?
L. tahanensis	?	1-2	?	?
L. tothur	1	2	red	?
L. victoriae	1-2	1.2	cream	?
L. woodfordii	2-6	1.5	red	?
Licuala ramsayi	1-2	4-4.5	green/cream/yellow	?
Pholidocarpus macrocarpus	1-3	4	yellow	?
Character #	(34)	(35)	(36)	(not used)

Appendix 12

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

Fruit shape abbreviations: glob = globose; obo = obovoid; pyr = pyriform; ell = ellipsoid.

species	fruit shape	length mm	diameter mm	colour	pedicel length mm
L. alfredii	glo	-	36-40	brown/black	3
L. australis	glo	-	12-22	reddish brown/black	2-3
L. benthamii	obo/pyr	9-13	9-11	purple/black	2-3
L. boninensis	glo	19-30	14-18	bright green	3-4
L. carinensis	glo	-	40-50	dark brown/black	4-5
L. chinensis	glo/ell	15-26	9-18	blue-green/bright green	2.5-3
L. chocolatina	glo		25	orange-red	4-5
L. concinna	glo	-	9.0-12	shiny black	2
L. decora	glo	-	12-15	shiny black	2
L. drudei	glo	-	10-12	purple/black	1-2
L. eastonii	obo/pyr/ell	12-16	8-9	purple black	0.5-2
L. endauensis	obo/pyr	16	14	bluish green	1-2
L. exigua	glo	-	9	purplish-green	1-2
L. fulva	glo	-	12-16	black bluish pruinose	0.5-1.5
L. halongensis	glo	-	10-12	dark green	0.2-0.5
L. humilis	ell/pyr/obo	11-19	8-10	purple/glossy black	0.5-1
L. inermis	obo/pyr	0-13	6-7	glossy black	1
L. jenkinsiana	glo/ell	-	19-28	leaden blue/bluish black	4.5
L. lanuginosa	glo	-	25-35	dark brown/black	1
L. lorophylla	obo/pyr	8-14	6-9(8)	black	0.5
L mariae	glo	-	12-18	black	2
L. merrillii	glo	-	16-23	red to dark brown	2-5
L. muelleri	ell	10-12	8.5-10	bluish/black	0.5-1
L. nasmophila	glo	-	11-14	purple black	1
L. nitida	glo	-	13-18	glossy jet black	0.5
L. papuana	obo/pyr	-	10-25	orange/red	1-3
L. rigida	glo	-	12-14	black	2
L. robinsoniana	glo		11-15	red	2-3
L. rotundifolia	glo	-	11-25	vermilion red/black	2-3
L. saribus	glo	-	11-17	green/blue	1-2
L. surru	glo/obo	55-65	50-55	orange	6-12
L. tahanensis	glo/obo	-	12-14	green	2-3
L. tothur	glo	-	35-52	orange/red	2.5-5
L. victoriae	glo	-	8-11	dark brown/black	0.5-1
L. woodfordii	glo	-	6-14	orange-red	2-3
Licuala ramsayi	glo	-	8-15	red	1-2
Pholidocarpus macrocarpus	glo	-	60	red	12
Character #	(37)	(38)		(39)	(40)

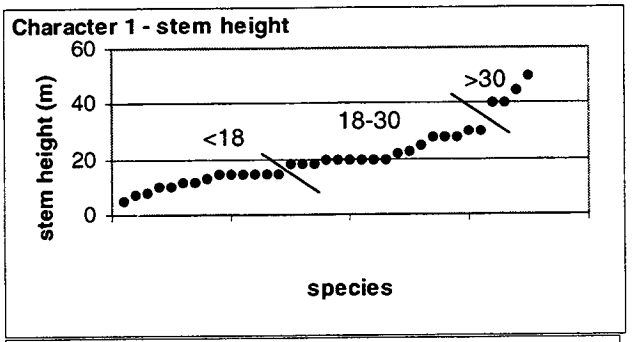
Appendix 13

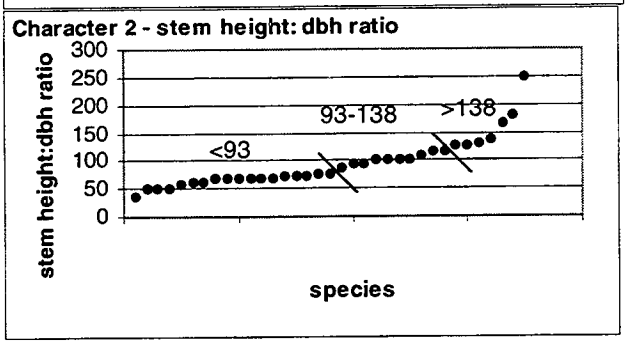
Fruit, eophyll and sexuality characters for 35 species of *Livistona* and two outgroup taxa: with or without epicarp pores (+ = present; - = not present), embryo position, number of eophyll ribs (number of samples) and sexuality

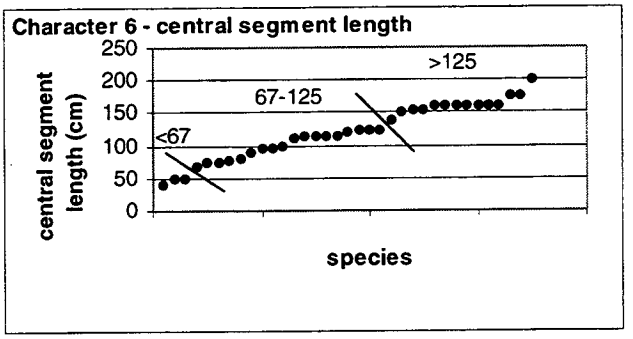
species	epicarp	embryo position	eophyll ribs	sexuality
L. alfredii	+	supra-lateral	3(11)	funct. dioecy
L. australis	+	sub-lateral	5(1)	funct. dioecy
L. benthamii	-	lateral	?	funct.dioecy
L. boninensis	?	lateral	?	hermaphroditic?
L. carinensis	?	sub-lateral	?	funct. dioecy
L. chinensis	+	lateral	7(18)	hermaphroditic
L. chocolatina	+	lateral	?	hermaphroditic
L. concinna	-	lateral	5(43)	funct.dioecy
L. decora	+	supra-lateral	5(11)	funct. dioecy
L. drudei	-	lateral	5(7),6(2)	funct. dioecy
L. eastonii	-	lateral	?	funct. dioecy
L. endauensis	?	?	5(2)	?
L. exigua	?	?	?	?
L. fulva	+	lateral	5(4), ?9(4)	funct. dioecy
L. halongensis	?	?	?	hermaphrotic
L. humilis	+	lateral	3(30)	funct. dioecy
l. inermis	-	lateral	3(10), 5(3)	funct. dioecy
L. jenkinsiana	+	lateral	7(6),8(2)	hermaphroditic
L. lanuginosa	+	sub-lateral	5(5, 5(30)	funct. dioecy
L. lorophylla	+	lateral	?	funct. dioecy
L mariae	+	sub-lateral	3(20)	funct. dioecy
L. merrillii	-	lateral	?	hermaphroditic?
L. muelleri	-	sub-lateral	3(200), 7(2)	funct. dioecy
L. nasmophila	+	sub-lateral	?	funct. dioecy
L. nitida	+	lateral	5(12)	funct. dioecy
L. papuana	+	?	?	hermaphroditic?
L. rigida	+	sub-lateral	5(4),5(120)	funct. dioecy
L. robinsoniana	+	lateral	?	hermaphroditic
L. rotundifolia	+	lateral	5	hermaphroditic?
L. saribus	+	lateral	7(29)	hermaphroditic
L. surru	+	lateral	?	funct. dioecy
L. tahanensis	-	sub-lateral	?	?
L. tothur	+	lateral	?	funct. dioecy
L. victoriae	+	sub-lateral	3(5)	funct. dioecy
L. woodfordii	+	lateral	?	hermaphroditic
Licuala ramsayi	-	lateral	?	hermaphroditic
Pholidocarpus macrocarpus	+	lateral	?	hermaphrpditic
Character #	(41)	(42)	(not used)	(43)

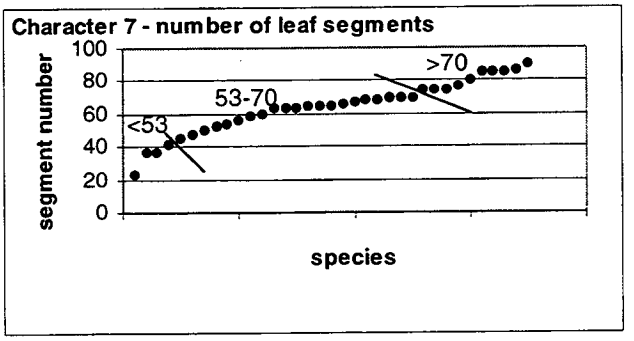
Appendix 14

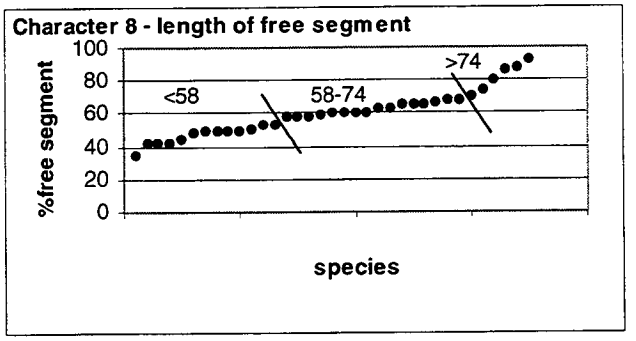
Scatter plots of continuously variable characters used in the cladistic analysis of *Livistona* and two outgroup taxa. Gap-code positions are indicated by an oblique line. *X* axis caption refers to the 35 species of *Livistona* used in this analysis. Species names are omitted due to space constraints.

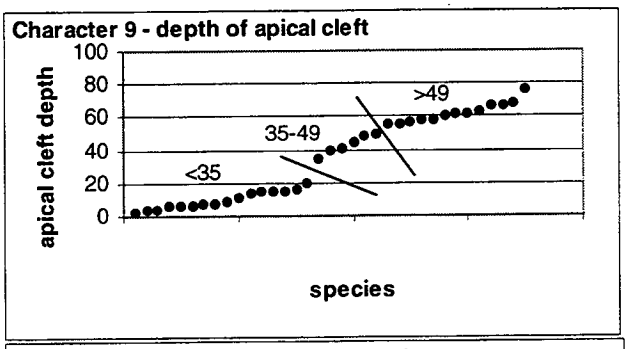











Character 9 - depth of apical cleft
apical cleft depth
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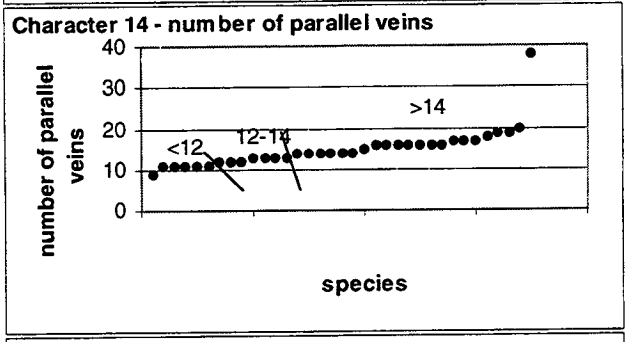
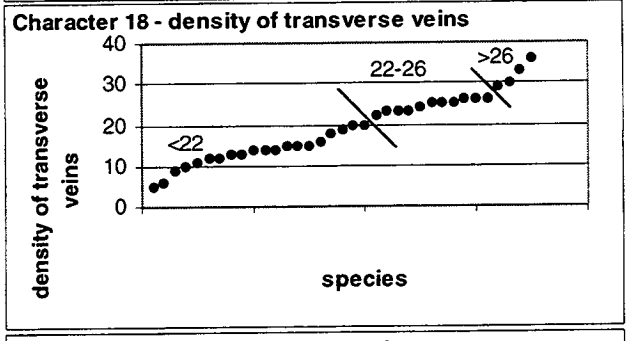
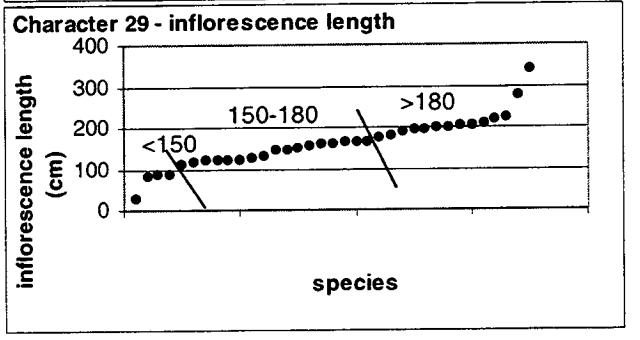
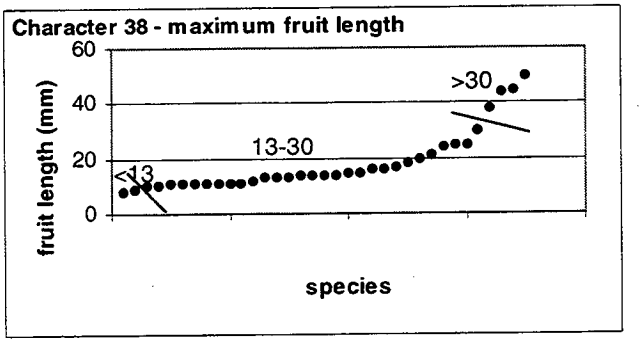
80
60
40
20
0
<35
35-49
>49
species


Character 14 - number of parallel veins
number of parallel veins
40
30
20
10
0
<12
12-14
>14
species


Character 18 - density of transverse veins
density of transverse veins
40
30
20
10
0
<22
22-26
>26
species


Character 29 - inflorescence length
inflorescence length (cm)
400
300
200
100
0
<150
150-180
>180
species


Character 38 - maximum fruit length
fruit length (mm)
60
40
20
0
<13
13-30
>30
species

Appendix 15
Altitude and rainfall data for *Livistona* species

Data obtained from Backer and Bakhuizen van der Brink, 1968; Beccari, 1931; Bureau of Meteorology, 1988; Dale, 1974; Hodel and Vatcharakorn, 1998; McAlpine *et al.*, 1983; Monod, 1955; Orscheg and Parsons, 1996; Rodd, 1998.

species	altitude range (mean) in m	rainfall range (mean) mm
L. alfredii	250-350 (300)	200-250 (225)
L. australis	0-840 (420)	850- 3500 (2175)
L. benthamii	0-100 (50)	1400-2100 (1750)
L. boninensis	25-125 (75)	1500-2000 (1750)
L. carinensis	330-975 (652)	200-400 (300)
L. chinensis	0-100 (50)	1750-3300 (2525)
L. chocolatina	250-350 (300)	1600-2000 (1800)
L. concinna	0-100 (50)	1750-1850 (1800)
L. decora	0-550 (225)	980-1450 (1215)
L. drudei	0-100 (50)	1100-2200 (1650)
L. eastonii	330-430 (380)	700-1500 (1100)
L. endauensis	100-660 (380)	3050-3550 (3300)
L. exigua	60-260 (160)	2000-4000 (3000)
L. fulva	400-660 (530)	650-750 (700)
L. halongensis	0-20 (10)	1900-2100 (2000)
L. humilis	0-240 (170)	1400-1700 (1550)
L. inermis	50-325 (187)	990-1200 (1095)
L. jenkinsiana	100-1200 (650)	2200- 2500 (2350)
L. lanuginosa	140-240 (190)	600-700 (650)
L. lorophylla	80-240 (160)	600-1500 (1050)
L. mariae	500-600 (550)	310-410 (360)
L. merrillii	60-200 (130)	1600-2000 (1800)
L. muelleri	10-250 (130)	960-2700 (1830)
L. nasmophila	100-200 (150)	730-830 (780)
L. nitida	150-800 (475)	680-700 (690)
L. papuana	0-100 (50)	2000-2200 (2100)
L. rigida	25-305 (165)	380-760 (570)
L. robinsoniana	0-450 (225)	1500-2000 (1750)
L. rotundifolia	0-300 (150)	1500-2000 (1750)
L. saribus	0-600 (300)	1800-2500 (2150)
L. surru	0-1300 (650)	2100-3500 (2800)
L. tahanensis	900-1500 (1200)	3050-3500 (3275)
L. tothur	400-600 (500)	2700-3500 (3100)
L. victoriae	80-320 (200)	600-950 (775)
L. woodfordii	0-80 (30)	3080-3180 (3130)

Appendix 16

Samples used in the SEM examination of lamina surface features for selected species of *Livistona*

The area sampled was on a mid-leaf segment, in about the middle of the segment, of a single sample per species. Magnification was standardised at x500 so that comparison between samples could be made. Samples were collected in May 2000 from palms cultivated in The Palmetum and Anderson Park Botanic Gardens, Townsville, Queensland, Australia, and are conserved in the herbarium [JCT] Botany Department, James Cook University.

L. australis: Dowe s.n., ex Bluewater Ra. cult., Palmetum

L. benthamii: Dowe s.n., ex Lockerbie Scrub, cult., Palmetum

L. carinensis: Dowe s.n., ex Yemen, cult., Palmetum

L. chinensis: Dowe, s.n., origin not known, cult., Palmetum

L. decora: Dowe s.n., origin not known, cult., Palmetum

L. fulva: Dowe s.n., ex Blackdown Tableland, cult., Palmetum

L. humilis: Dowe s.n., ex Darwin, cult., Palmetum

L. inermis: Dowe s.n., ex Darwin, cult., Palmetum

L. lanuginosa: Dowe s.n., ex Glenroy Creek, cult., Anderson Park

L. mariae: Dowe s.n., origin not known, cult., Anderson Park

L. merrillii: Dowe s.n., origin not known, cult., Palmetum

L. muelleri: Dowe s.n., ex Cairns, cult., Anderson Park

L. nitida: Dowe s.n., ex Carnarvon Gorge, cult., Palmetum

Appendix 17

Samples used in the venation pattern examination for selected species of *Livistona*

The area of leaf sampled was on a mid-leaf segment, in about the middle of the segment, of a single sample only. The areas were standardised at 12 x 10 mm. Samples were collected in May 2000 from palms cultivated in The Palmetum and Anderson Park Botanic Gardens, Townsville, Queensland, Australia, and are conserved in the herbarium [JCT] Botany Department, James Cook University.

L. australis: Dowe s.n., ex Bluewater Range, cult., Palmetum

L. benthamii: Dowe s.n., ex Lockerbie Scrub, cult., Palmetum

L. carinensis: Dowe s.n., ex Yemen, cult., Palmetum

L. chinensis: Dowe, s.n., origin not known, cult., Anderson Park

L. decora: Dowe s.n., origin not known, cult., Palmetum

L. drudei: Dowe s.n., ex Hen Camp Creek, cult., Palmetum

L. fulva: Dowe s.n., ex Blackdown Tableland, cult., Palmetum

L. humilis: Dowe s.n., ex Darwin, Palmetum

L. inermis: Dowe s.n., ex Darwin, Palmetum

L. lanuginosa: Dowe s.n., ex Glenroy Creek, cult., Anderson Park

L. mariae: Dowe s.n., origin not known, cult., Anderson Park

L. merrillii: Dowe s.n., origin not known, cult., Palmetum

L. muelleri: Dowe s.n., origin not known, cult., Anderson Park

L. nasmophila: Dowe s.n., ex Mt Gladys, WA, cult., Palmetum

L. nitida: Dowe s.n., ex Carnarvon Gorge, cult., Palmetum

L. rigida: Dowe s.n., origin not known, cult., Palmetum

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*

The table is arranged in increasing rainfall values. The results are from single samples.

species	adaxial surface	abaxial surface	ratio	rainfall (m)
L. carinensis	140	352	0.39	0.3
L. mariae	692	512	1.35	0.4
L. rigida	300	600	0.50	0.6
L. lanuginosa	472	448	0.56	0.7
L. nitida	472	829	0.57	0.7
L. nasmophila	224	392	0.57	0.8
L. inermis	240	332	0.72	1.1
L. decora	340	700	0.48	1.2
L. humilis	372	480	0.78	1.6
L. drudei	220	540	0.41	1.7
L. benthamii	48	880	0.05	1.8
L. merrillii	100	712	0.14	1.8
L. muelleri	104	520	0.20	1.8
L. chinensis	360	744	0.48	2.6

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*

The table is arranged in increasing rainfall values.

species	parallel veins	transverse veins	ratio	rainfall (m)
L. alfredii	5	4	1.25	0.2
L. carinensis	10	5	2.00	0.3
L. mariae	4	15	0.27	0.4
L. rigida	4	15	0.27	0.6
L. lanuginosa	4	6	0.60	0.7
L. nitida	5	15	0.34	0.7
L. fulva	7	16	0.44	0.7
L. victoriae	9	20	0.45	0.8
L. nasmophila	7	9	0.78	0.8
L. lorophylla	6	10	0.60	1.0
L. inermis	8	11	0.73	1.1
L. eastonii	5	12	0.42	1.1
L. decora	5	23	0.22	1.7
L. drudei	7	14	0.50	1.7
L. humilis	5	29	0.17	1.6
L. boninensis	4	18	0.20	1.8
L. rotundifolia	6	30	0.20	1.8
L. benthamii	7	19	0.37	1.8
L. benthamii	7	19	0.37	1.8
L. merrillii	5	13	0.38	1.8
L. concinna	5	12	0.42	1.8
L. kuriva	4	26	0.15	1.8
L. muelleri	8	13	0.62	1.8
L. saribus	5	20	0.25	2.2
L. australis	7	23	0.30	2.2
L. jenkinsiana	7	26	0.27	2.4
L. chinensis	5	36	0.14	2.6
L. surru	5	22	0.28	2.8
L. exigua	11	25	0.44	3.0
L. beccariana	5	33	0.15	3.4
L. tothur	5	33	0.15	3.1
L. woodfordii	4	23	0.17	3.1
L. endauensis	5	25	0.20	3.3
L. tahanensis	5	14	0.36	3.3

Appendix 20

Flowering and fruiting percentages per month for four species of *Livistona*

Palms were observed over a 15 month period from July 1999 to September 2000, of cultivated plants in the Townsville Palmetum, Anderson Park Botanic Garden and private gardens in suburban Townsville. Numbers of observed palms are indicated after the species name. The percentages are based on these numbers.

1999						2000								
Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep
L. chinensis (n = 21)														
flowering %														
11	100	60	44	0	0	0	0	0	0	0	0	47	100	100
fruiting %														
44	61	66	67	67	67	67	67	67	71	60	60	40	34	60
L. decora (n = 45)														
flowering %														
76	90	93	38	0	0	0	0	0	0	0	13	75	100	100
fruiting %														
5	20	20	35	60	60	64	64	53	30	7	2	0	0	0
L. lanuginosa (n = 31)														
flowering %														
100	100	80	0	0	0	0	0	60	100	100	100	100	100	100
fruiting %														
27	60	60	80	60	53	7	0	0	0	0	7	40	27	27
L. muelleri (n = 15)														
flowering %														
0	0	0	0	0	0	60	100	50	100	30	50	0	0	0
fruiting %														
60	60	66	66	50	0	0	0	30	20	50	60	50	60	60

Appendix 21
Pollen counts and Standard Deviation (SD)

L. chinensis
pollen/flower

	x	x^2
1.	3950	15602500
2.	3650	13322500
3.	3725	13875625
4.	3500	12250000
5.	3675	13505625
$\bar{x}$ = 3700		$\sum x^2$ = 68556250

mean of $\sum x^2$ = 13711250
— mean^2
=13690000
= $\sqrt{21250}$

mean = 3700 SD = 145.78

L. lanuginosa
pollen/flower

	x	x^2
1.	4725	22325625
2.	4600	21160000
3.	4475	20025625
4.	4425	19580625
5.	4275	18275625
$\bar{x}$ = 4500		$\sum x^2$ = 101367500

mean of $\sum x^2$ = 20273500
— mean^2
=20250000
= $\sqrt{23500}$

mean = 4500 SD = 153.29

L. decora
pollen/flower

	x	x^2
1.	4300	18490000
2.	4200	17640000
3.	3800	14440000
4.	3875	15015625
5.	3825	14630625
$\bar{x}$ = 4000		$\sum x^2$ = 80216250

mean of $\sum x^2$ = 16043250
— mean^2 =16000000
= $\sqrt{432}$

mean = 4000 SD = 207.96

L. muelleri
pollen/flower

	x	x^2
1.	520	270400
2.	790	624100
3.	590	348100
4.	625	390625
5.	675	455625
$\bar{x}$ = 640		$\sum x^2$ = 2088850

mean of $\sum x^2$ = 417770
— mean^2 =409600
= $\sqrt{8170}$

mean = 640 SD = 90.38

Appendix 22
Pollen measurements and Standard Deviation (SD)

Formula: Volume of one pollen grain = $\frac{4\pi r^3}{3}$ where $r = \frac{L+l}{4}$,

where r = long axis (L) + short axis (l)

L. chinensis
long axis (L) in μm

	x	x^2
1.	25.7	660.49
2.	28.2	795.24
3.	27.9	778.41
4.	26.9	723.61
5.	27.1	734.41
6.	25.9	670.81
7.	26.9	723.61
8.	26.9	723.61
9.	26.8	718.24
10.	27.4	750.76
11.	27.1	734.41
12.	27.3	745.29
13.	26.8	718.24
14.	26.7	712.89
15.	27.1	734.41
16.	26.8	718.24
17.	27.1	734.41
18.	27.5	756.25
19.	27.1	734.41
20.	26.5	702.25

$\bar{x} = 27$ $\sum x^2 = 14570.24$

mean of $\sum x^2 = 728.512$

— $\text{mean}^2 = 729.0$

$= \sqrt{0.488}$

mean = 27 SD = 0.7

L. chinensis
short axis (l) in μm

	x	x^2
1.	20.8	432.64
2.	21.7	470.89
3.	21.9	479.61
4.	21.4	457.96
5.	22.1	488.41
6.	20.6	424.36
7.	20.9	436.81
8.	21.6	466.56
9.	21.1	445.21
10.	21.5	462.25
11.	21.6	466.56
12.	21.7	470.89
13.	22.1	488.41
14.	21.4	457.96
15.	21.6	466.56
16.	22.1	488.41
17.	22.8	519.84
18.	21.5	462.25
19.	21.9	479.61
20.	21.7	470.89

$\bar{x} = 21.6$ $\sum x^2 = 9336.08$

mean of $\sum x^2 = 466.804$

— $\text{mean}^2 = 466.56$

$= \sqrt{0.244}$

mean = 21.6 SD = 0.49

L. decora
long axis (L) in μm

	x	x^2
1.	19.4	376.36
2.	19.3	372.49
3.	19.7	388.09
4.	21.1	445.21
5.	19.8	392.04
6.	19.6	384.16
7.	18.7	349.69
8.	19.1	364.81
9.	19.4	376.36
10.	19.8	392.04
11.	19.2	368.64
12.	19.6	384.16
13.	20.2	408.04
14.	19.2	368.64
15.	19.8	392.04
16.	18.6	345.96
17.	18.9	357.21
18.	20.2	408.04
19.	18.4	338.56
20.	22.0	484.0

$\bar{x} = 19.6$ $\sum x^2 = 7696.54$

mean of $\sum x^2 = 384.827$

— $\text{mean}^2 = 384.16$

$= \sqrt{0.667}$

mean = 19.6 SD = 0.81

L. decora
short axis (l) in μm

	x	x^2
1.	14.8	219.04
2.	14.8	219.04
3.	14.7	216.09
4.	15.7	246.49
5.	15.9	252.81
6.	16.1	259.21
7.	16.0	256.0
8.	15.5	240.25
9.	14.9	222.01
10.	15.1	228.01
11.	15.9	252.81
12.	16.2	262.44
13.	15.8	249.64
14.	15.6	243.36
15.	16.1	259.21
16.	16.2	262.44
17.	14.7	216.09
18.	15.5	240.25
19.	15.8	249.64
20.	16.7	278.89
$\bar{x}$	=15.6	$\sum x^2 = 4873.72$

mean of $\sum x^2 = 243.686$
— mean^2 =243.36
$= \sqrt{0.326}$

mean = 15.6 SD = 0.57

L. lanuginosa
long axis (L) in μm

	x	x^2
1.	25.1	630.01
2.	25.2	635.04
3.	25.2	635.04
4.	24.8	615.04
5.	26.2	686.44
6.	26.1	681.21
7.	25.7	660.49
8.	25.2	635.04
9.	27.1	734.41
10.	26.1	681.21
11.	25.1	630.01
12.	25.2	635.04
13.	26.2	686.44
14.	25.7	660.49
15.	27.1	734.41
16.	26.1	681.21
17.	25.2	635.04
18.	26.1	681.21
19.	24.8	615.04
20.	25.2	635.04
$\bar{x}$	=25.7	$\sum x^2 = 13187.86$

mean of $\sum x^2 = 659.39$
— mean^2 =660.49
$= \sqrt{1.1}$

mean = 25.7 SD = 1.04

L. lanuginosa
short axis (l) in μm

	x	x^2
1.	16.2	262.44
2.	17.1	292.41
3.	16.8	282.24
4.	15.9	252.81
5.	14.8	219.04
6.	16.3	265.69
7.	16.5	272.25
8.	16.6	275.56
9.	16.1	259.21
10.	15.1	228.01
11.	16.2	262.44
12.	16.8	282.24
13.	14.8	252.81
14.	16.5	265.69
15.	16.1	275.56
16.	16.6	272.25
17.	16.3	219.04
18.	15.9	252.81
19.	17.1	292.41
20.	16.2	262.44
$\bar{x}$	=16.2	$\sum x^2 = 5247.35$

mean of $\sum x^2 = 262.37$
— mean^2 =262.44
$= \sqrt{0.07}$

mean = 16.2 SD = 0.26

L. muelleri
long axis (L) in μm

	x	x^2
1.	22.28	492.84
2.	21.8	475.24
3.	21.9	479.61
4.	24.2	585.64
5.	23.6	556.96
6.	23.1	533.61
7.	24.1	580.81

8.	22.9	524.41
9.	22.9	524.41
10.	23.4	547.56
11.	23.1	533.61
12.	23.6	556.96
13.	23.7	561.69
14.	24.1	580.81
15.	23.8	566.44
16.	23.9	571.21
17.	23.2	538.24
18.	24.1	580.81
19.	24.0	576.0
20.	24.4	595.36

$\bar{x}$ =23.4 $\sum x^2 = 10962.22$

mean of $\sum x^2 = 548.111$

— mean^2 =547.56

$= \sqrt{0.551}$

mean = 23.4 SD = 0.74

L. muelleri

short axis (l) in μm

	x	x^2
1.	19.6	384.16
2.	18.9	357.21
3.	18.7	349.69
4.	19.4	376.36
5.	18.4	338.56
6.	19.7	388.09
7.	17.2	294.12
8.	18.2	331.24
9.	18.4	338.56
10.	18.9	357.21
11.	18.7	349.69
12.	16.9	285.61
13.	19.2	368.64
14.	19.0	361.0
15.	18.9	357.21
16.	18.8	353.44
17.	19.1	364.81
18.	18.4	338.56
19.	17.9	320.41
20.	19.7	388.09

$\bar{x}$ =18.7 $\sum x^2 = 7002.66$

mean of $\sum x^2 = 350.133$

— mean^2 =349.69

$= \sqrt{0.443}$

mean = 18.7 SD = 0.66