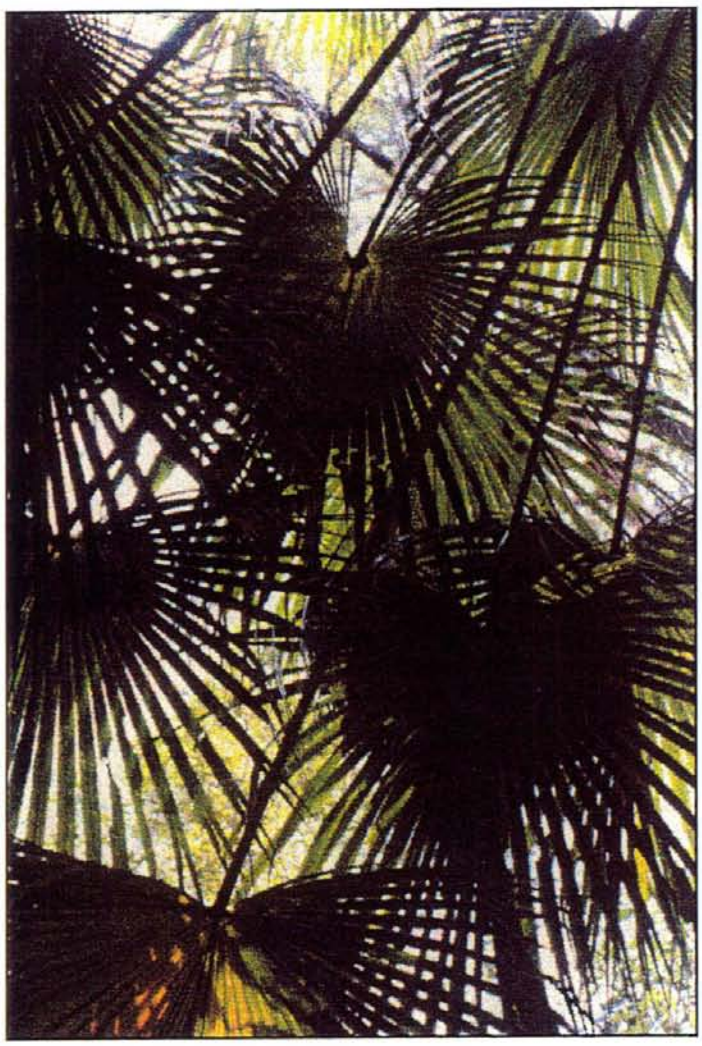
STUDIES IN THE GENUS *LIVISTONA* (CORYPHOIDEAE: ARECACEAE)



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ABSTRACT

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

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

- *exigua* lineage – small understorey palms with irregularly segmented leaves, inflorescence not basally branched
- *saribus* lineage – large canopy palms with irregularly segmented leaves, inflorescence not basally branched
- *chinensis* subclade – inflorescence not basally branched, fruit green, blue or purple, regularly segmented leaves
- *rotundifolia* subclade – inflorescence basally branched, fruit passing through orange/red to mature either orange, red or black, regularly segmented leaves
- *humilis* subclade - inflorescence not basally branched, fruit dark brown or black, regularly segmented leaves with deeply segmented lamina
- *mariae* subclade - inflorescence not basally branched, fruit dark brown or black, regularly segmented leaves with moderately segmented lamina

Although topological resolution was satisfactory, statistical support was low for the analyses and the result cannot be accepted as a reliable estimate of phylogeny.

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

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

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

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

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GLOSSARY

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

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

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

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

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

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

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

anemophily – pollination facilitated by wind or air currents

apomorphy – a derived character or character state

armed – bearing some form of spines

autapomorphy – a character state that is unique to a taxon

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

autogamy – fertilisation occurring within the same flower

bootstrapping – a statistical method to estimate confidence in a pattern

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

bracteole – a small bract borne on a flower stalk

carpel – the single unit of the gynoecium

chartaceous – paper-like, thin and stiff

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

cladistic biogeography – examination of the distribution of sister taxa of monophyletic groups, i. e. most recently evolved taxa will be the most recently vicariated

cladogram – graphic image in the form of a 'tree' depicting the phylogenetic arrangement of a group of taxa

collateral – side by side, parallel

connective – the part of a stamen that connects the anthers, usually distinct from the filament

cordate – heart shaped

costapalmate – of a palmate leaf where the petiole is extended as a midrib into the lamina

derived – in regards to evolution, the state that originates later in evolution than the ancestral state

didymous – of anthers where the connective is almost absent

dimorphic – of two forms

distal – situated farthest away from the point of attachment

endemics – species with restricted ranges, often with narrow ecological requirements and sometimes morphologically specialised

endocarp – innermost layer of the fruit wall

endosperm – the nutritive body of the seed

entomophily – pollination facilitated by insects

eophyll – the first leaf with a blade

epicarp – the outer most layer of the fruit wall

epipetalous – borne on the petals

exine – the outer surface of a pollen grain

flexuous – regularly twisted, zig-zag

foveolate – with small round depressions

geitonogamy – fertilisation between different flowers on an individual plant or clonal plants

glabrous – smooth, lacking hairs or scales

glaucous – covered with a bluish gray or greenish bloom

hastula – a flap of tissue borne at the insertion of the blade on the petiole on the upper, lower or both surfaces

homogeneous – of the seed tissue, uniform, the same throughout

homology – character states that share modifications from another condition

homoplasy – convergence, similarity without genetic relationship

hyaline – thin enough to be transparent

illegitimate – in regards to names that are nomenclaturally illegal according to the rules of the ICBN

inaperturate – in pollen, lacking any visible germination openings

interfoliar – among the leaves

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

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

isotype – a specimen that is a duplicate of the holotype

lamina – leaf blade

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

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

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

ligule – a distal projection of the leaf sheath

mesocarp – middle layer of the fruit wall

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

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

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

monosulcate – with one sulcus (see sulcus)

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

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

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

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

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

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

pedicel – a flower stalk

peduncle – the lower unbranched part of an inflorescence

perforate – pierced with holes

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

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

pleonanthic – flowering continuously over most of the life of a plant

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

polyphilic – a flower that is visited by many species of pollinator

primitive – with regards to the possession of ancestral characters

prophyll – the first bract or leaf produced on a branch

protandrous – stamens shedding pollen before the stigma is receptive

proximal – nearest to the attachment, basal

psilate – covered with small rounded protuberances

puberulous – covered with dense short hairs

rachilla – the ultimate flower-bearing axis of an inflorescence

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

relictual species – species that are persistent examples of floras now mainly vanished

rugose – wrinkled

stigmatic remains – the remnants of flower parts persistent on the fruit epicarp

subclade – portion of a major clade

subtribe – taxonomic level below tribe but above genus

subulate – awl shaped, abruptly tapered to the apex

sulcus – the furrow-like aperture of a pollen grain

suture – a scar indicative of a fold or join in the epicarp

sympatric species – related species that occur in the same geographical range

symplesiomorphy - (1) a synapomorphy of a more inclusive hierarchical level than that being considered. (2) the occurrence in two or more taxa of a monophyletic group of a plesiomorphic character or character state; that is, one that has been inherited from an ancestor more distant than the most recent common ancestor of the group.

sympodial clusters – in regards to the arrangement of flowers, where an individual flower is produced from the axil of the preceding flower's bracteole

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

tectate – of pollen grains, two-walled

testa – the outer coat of the seed

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

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

valvate – meeting exactly without overlapping

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

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

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

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

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

ABBREVIATIONS

AFLP – amplified fragment length polymorphism

Apr. – April

auct. non. – *auctorum nonnullorum*; of some authors

Aug. – August

c. – *circa* (about)

cm – centimetres

cp – chloroplast

cult. – *cultus*; cultivated

dbh – diameter at breast height; approximately 1.2 m above ground level

Dec. – December

diam. – *diametro*; diameter

DNA – deoxyribonucleic acid

E – east

EDTA – ethylenediaminetetra-acetate

Feb. – February

hort. – *hortorum*; of gardens

ICBN – International Code of Botanical Nomenclature

ined. – *ineditus*; unpublished

ITS – internal transcribed spacer

Jan. – January

Mar. – March

mm – millimetres

N – north

nom. – *nomen*; name

nom. illeg. – *nomen illegitimum*; illegitimate name

nom. inval. – *nomen invalidum*; invalid name

nom. ined. – *nomem inedit*; proposed name

nom. nud. – *nomen nudum*; name unaccompanied by a description or reference to a published description

nom. provis. – *nomen provisorius*; provisional name

nom. tant. – *nomen tantum*; name only

Nov. – November

NP – National Park

nr – nuclear ribosomal

Oct. – October

ortho. var. – orthographic variation

PAE – parsimony analysis of endemicity

PAUP – phylogenetic analysis using parsimony

PCR – polymerase chain reaction

PO – pollen:ovule ratio

RFLP – restriction fragment length polymorphism

S – south

s. n. – *sine numero*; without a number

Sept. – September

sp. – *species*; species (singular)

spp. – *species*; species (plural)

t. – *tabula*; plate

TAE – tris (hydroxymethyl) methylamine acetate ethylenediaminetetra-acetate

TBR – tree bisection and reconnection

TE – tris ethylenediaminetetra-acetate

W – west

HERBARIUM ACRONYMS

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

PERTH	Department of Conservation and Land Management, Perth, Australia
QRS	CSIRO, Atherton, Australia
S	Swedish Museum of Natural History, Stockholm, Sweden
SAR	Department of Forestry, Kuching, Sarawak, Malaysia
SING	Singapore Botanic Gardens, Singapore
UC	University of California, Berkeley, California, USA
US	United States National Herbarium, Smithsonian Institution, Washington, USA