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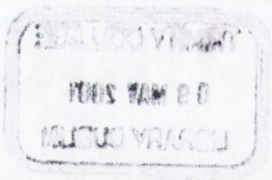
A Systematic Revision of the *Uvaria* L. group (Annonaceae) in Continental Asia.

A thesis submitted to the University of Dublin, Trinity College for the Degree of Doctor of Philosophy.

August 11th, 2000

Conor V. Meade B.Sc.



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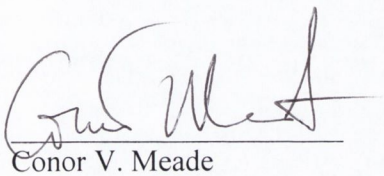

Conor V. Meade

SUMMARY

The goal of this research project has been to complete a taxonomic revision of *Uvaria* L. (Annonaceae) and its affiliates in Continental Asia. Research was based primarily at the Trinity College Herbarium. Research visits were also made to the Royal Botanic Gardens, Kew, London, The Natural History Museum, London, The Rijksherbarium, Leiden, The Herbarium of Utrecht University, Utrecht and the herbarium of the Museum Nationale D'Histoire Naturelle, Paris. A three month field expedition was made to Thailand, Vietnam and Singapore in 1998, and included field collecting and visits to all the main herbaria of each country. A research collection was assembled at TCD based on material from the Trinity College herbarium and material received on loan from institutes in Europe, North America and Asia.

The first task of the work was to determine which genera could usefully be included in the revision, and this was done through a combination of literature research and consultation with established Annonaceae taxonomists. Revision work began with a survey and description of type material. This was followed by a more comprehensive description of each species which encompassed the full extent of morphological variation evident in the research collection. A full taxonomic history of each taxon in the group was documented from the scientific literature. Early printed books were consulted at the Trinity College Library, the Library of the Natural History Museum, London and the Library of Kew Gardens, London.

Phylogenetic relationships within the *Uvaria* group were assessed based on morphological and DNA sequence data. Morphological data was generated from a survey of material at TCD and various other institutes. DNA was extracted from field-collected material preserved in silica gel and from herbarium material. Sequence data was generated from the ITS region of nuclear ribosomal DNA using the Polymerase Chain Reaction and cycle sequencing, both of which were completed by the author at the Plant Molecular Systematics Laboratory, TCD. Data analysis was carried out using a variety of phylogenetic methods, including maximum parsimony, maximum likelihood and distance techniques. These analyses were carried out using PAUP 4.0 (David Swafford, 2000) running on an Apple Macintosh G3 PowerPC.

Analysis of morphometric variation within the *Uvaria* group was based on measurements of herbarium material for each taxon. Patterns of variation were assessed using Principal Components Analysis, Discriminant Analysis and independent t-Tests. These analyses were carried out using SPSS 8.0 (SPSS Inc., 1998) running on an IBM PC (Fujitsu 450 MHz, Pentium III).

The main results of all aspects of the research are expressed within the framework of the taxonomic account for the *Uvaria* group presented in Chapter 4. The main findings are as follows. (a) the *Uvaria* group comprises two main lineages, one including *Uvaria* L. and *Cyathostemma* Griff., as currently defined, and a second including *Ellipeia* Hook. f. & Thoms., *Ellipeiopsis* R.E. Fries and *Rauwenhoffia* Scheff. All the *Cyathostemma* species occurring in Continental Asia have been subsumed into *Uvaria*. (b) A new monotypic genus, *Nervopetalum*, has been created to accommodate *Uvaria hahnii* (Finet & Gagnep.), which emerges in the *Ellipeia* lineage. (c) *Ellipeia* now includes the monotypic genus *Anomianthus* Zoll. and *Uvaria pauciovulata* Hook. f. & Thoms. The generic boundaries of all the above genera have been refined, and in the case of *Uvaria sens. auct.* they have been significantly broadened. In terms of phylogenetically informative characters, stamen and carpel structure have been found to be more reliable than petal structure. Fruit structure is also informative, however much of the detectable variation is autapomorphic. Leaf structure was found to be a useful guide to taxon identity, however it is largely unreliable/ homoplasic when incorporated into phylogenetic analysis.

All line drawings, maps and illustrations have been produced by the author, except in the case of Xerox copies – in which the source material is indicated.

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First and foremost I would like to thank my Supervisor, John Parnell, for all his help and advice over the course of this research project, and for his assistance with the 1998 field trip to Southeast Asia. I would also like to thank Trevor Hodkinson for his assistance with the molecular aspects of the project. My sincerest thanks also to Mark Chase for making available the sequencing facility at the Jodrell Laboratory. David Simpson and Madeline Harley deserve particular mention for their advice at crucial stages in the progress of the revision – my sincerest thanks to them. I would also like to thank Professor David Jeffrey, head of the Botany Department, the technical staff (especially Siobhán on the day of submission) and the Executive Officer, Mary Foody.

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Thanks to Mum and Dad for bringing me into existence and for putting up with me thereafter. Thanks to the bruds, to Corm and Niamh, and as I said at UCD, 'thanks to Bran, wherever you are'.

For Emer

They heard somewhere in that tenantless night a bell that tolled and ceased where no bell was and they rode out on the round dais of the earth which alone was dark and no light to it and which carried their figures and bore them up into the swarming stars so that they rode not under but among them and they rode at once jaunty and circumspect, like thieves newly loosed in that dark electric, like young thieves in a glowing orchard, loosely jacketed against the cold and ten thousand worlds for the choosing.

Cormac McCarthy, *All the Pretty Horses*.

Table of Contents

List of Tables ....

List of Figures ....

Preamble 1

CHAPTER 1 - INTRODUCTION **3**

Taxonomy and Systematics of *Uvaria* and the Annonaceae **4**

Uvaria L. - an Overview 4

The Origin of _Uvaria_ L. in the Modern Scientific Literature 5

The Annonaceae - Family Characteristics 5

The Development of Angiosperm Classification 8

The Origin of the Angiosperms 13

Evolutionary Trends in the Annonaceae 16

Delimiting the _Uvaria_ Group 26

Ecology, Utility and Biogeography of _Uvaria_ and the Annonaceae **31**

Ecology of the Annonaceae 31

Origin and Radiation of the Annonaceae 32

Contemporary Habitat Preferences of the Annonaceae in Continental Asia 35

Current Distribution 35

Climate of Continental Asia 38

Indian Subcontinent 38

Indo-Chinese Region 40

Forest Vegetation Types 42

Evergreen Forests 42

Deciduous Forests 44

Secondary Formations 46

Floristic Divisions 46

Utility of the Annonaceae 47

CHAPTER 2 - PHYLOGENETIC ANALYSIS OF THE *UVARIA* GROUP 49

Introduction 50

Phylogenetic Analysis - Problems with Molecular and Morphological data 50

Data Analysis 53

Distance Methods 53

Maximum Parsimony 54

Search Algorithms 55

Maximum Parsimony Optimality Criteria 56

Statistical Testing of Inferred Phylogenies 57

Maximum Likelihood 59

Consistency of Distance and Optimality Criteria Methods 60

Selection of Analysis Techniques 60

Analysis of Molecular Data 63

Target Sequence – ITS 63

Structure 63

Evolutionary Constraints 64

Amplification Considerations 65

Paralogues 65

Secondary Structures 65

Materials and Methods 66

DNA Extraction 66

PCR Amplification 67

Sequencing 69

Results 71

Raw Data 71

Amplification and Sequencing 71

Sequence Scoring and Alignment 71

Sequence Content 71

Phylogenetic Analysis 73

Dataset 73

Parsimony Analysis 73

Maximum Likelihood Analysis 77
Distance Analysis 77

Analysis of Morphological Data 81
Character Scoring 81
Matrix Assembly 83
Results 85
Maximum Parsimony 85
Distance Analysis using Neighbour Joining 88

Combined Analysis 91
Assessment of Similarity between Datasets 91
Analysis of Combined Dataset 93

Discussion 95
Molecular Data 95
Nucleotide Content 95
Phylogenetic Analysis 96
Morphological Data 98
Conclusions 99

CHAPTER 3 - MORPHOMETRIC ANALYSIS OF THE *UVARIA* GROUP 100

Introduction 101
Inflorescence and Fruit Character Variability in a Sample of All Uvaria Group Taxa 102
The Use of Leaf-Shape Characters for Discriminating Between Uvaria Group taxa 102
Difficult Taxonomic Groups 103
The Uvaria narum Complex 103
Uvaria cordata and U. microcarpa 103

Materials and Methods 104
Specimen Measurement and Construction of Dataset 104
Analysis Techniques 104
Statistical Analysis 109
Inflorescence and Fruit Character Variability in a Sample of All Uvaria Group Taxa 109
The Use of Leaf-Shape Characters for Discriminating Between Uvaria Group taxa 109
Difficult Taxonomic Groups 109
The Uvaria narum Complex 109
Uvaria cordata and U. microcarpa 110

Results 111
Inflorescence and Fruit Character Variability in a Sample of All Uvaria Group Taxa 111
The Use of Leaf-Shape Characters for Discriminating Between Uvaria Group taxa 117
Difficult Taxonomic Groups 125
The Uvaria narum Complex 125
Uvaria cordata and U. microcarpa 134

Discussion 137
Inflorescence and Fruit Character Variability in a Sample of All Uvaria Group Taxa 137
The Use of Leaf-Shape Characters for Discriminating Between Uvaria Group taxa 138
Difficult Taxonomic Groups 140
The Uvaria narum Complex 140
Uvaria cordata and U. microcarpa 142

CHAPTER 4 - TAXONOMIC REVISION OF THE *UVARIA* GROUP IN CONTINENTAL ASIA **143**

Introduction 144

Changes to Existing Classifications 144

Keys 147

Figures 147

Leaf Outlines 147

Notation for Material Examined 150

Notation for Type Material 150

Sources for Referenced Literature 151

Research Collection 151

Keys and Taxonomic Accounts 152

Ellipeiopsis 159

Uvaria 165

Rauwenhoffia 273

Ellipeia 278

Nervopetalum 288

Distribution Maps 293

CHAPTER 5 - DISCUSSION **302**

Biogeographic and Ecological Patterns 303

Results of Morphological and Molecular Analyses 310

REFERENCES ....

APPENDICES ....

1. Facsimile of Original Account of *Uvaria zeylanica* L. ....

2.1. Aligned ITS Matrix ....

2.2. Character Scores for Tree in Figure 2.7 ....

3.1. Material Examined for Morphometric Analysis ....

3.2. Morphometric Data Matrix ....

3.3. Summary Leaf Outlines for Each Taxon (Reduced Scale) ....

4.1-14 Photographic Images of Annonaceae and *Uvaria* ....

4.15 Leaf Venation Terminology ....

4.16 Indument Terminology ....

4.17 Administrative Boundaries for India ....

4.18 Administrative Boundaries for Sri Lanka ....

4.19 Administrative Boundaries for China ....

4.20 Floristic Provinces of Cambodia, Laos and Vietnam ....

4.21 Floristic Provinces of Thailand ....

List of Tables

1.1 Annonaceae: summary of major systematic classifications 19
1.2 Composistion of the *Uvaria* group 30

2.1 PCR reaction mix components and thermal cycling protocol 68
2.2 Sequencing reaction mix components and thermal cycling protocol 69
2.3 Samples used for molecular analysis 72
2.4 Nucleotide content data for ITS-1 and ITS-2 in final matrix 74
2.5 Descriptive statistics for maximum parsimony trees 1 & 2 76
2.6 Character scoring for morphological data matrix 82
2.7 Morphological data matrix 84
2.8 Descriptive statistics for maximum parsimony tree generated from morphological dataset 85
2.9 Size and percentage G-C content of the ITS region in Uvarieae (Annonaceae) and selected angiosperm families 95

3.1 Character measurements used in multivariate analysis 106
3.2 Comparison of grouping effectiveness of stepwise and simultaneous addition methods from Discriminant Analysis 110
3.3 Principal components analysis of log normalised flower measurements for total dataset 113
3.4 Principal components analysis of log normalised fruit measurements for total dataset 113
3.5 Discriminant analysis of log-normalised flower measurements for total dataset 115
3.6 Discriminant analysis of log-normalised fruit measurements for total Dataset 115
3.7 Principal components analysis of leaf ratio measurements for total dataset 117
3.8 Discriminant analysis of leaf ratio measurements for total dataset 118
3.9 Principal components analysis of mean leaf ratio measurements for each taxon 119

3.10 Principal components analysis of fruit sctructure in the *Uvaria narum* complex 126
3.11 Principal components analysis of flower structure in the *Uvaria narum* complex 126
3.12 Discriminant analysis of leaf ratio and log-normalised fruit measurements for *Uvaria narum* complex 126
3.13 Discriminant analysis of leaf ratio and log-normalised flower measurements for *Uvaria narum* complex 131
3.14 Discriminant analysis classification results for the *Uvaria narum* complex 132
3.15 Independent samples t-test for *Uvaria microcarpa* and *U. cordata*: summary of characters whose means differ significantly at $p < .01$ between the two species 135

4.1 Summary of nomenclature changes proposed for revision of *Uvaria* group in Continental Asia (a): accepted names and proposed new names and combinations 145
4.2 Summary of nomenclature changes proposed for revision of *Uvaria* group in Continental Asia (b): *synonyma nova* 146

List of Figures

1.1 Distribution of *Uvaria* 6
1.2 A facsimile copy of 'Narum Panel' from Rheede's *Hortus malabaricus* ... 7
1.3 A monochasial rhipidium, based on growth patterns observed in various *Uvaria* species 9
1.4 *Artabotrys hexapetalus* (L. f) & *Orophea corymbosa* (Baill.) Miq. 10
1.5 *Annona muricata* L. 11
1.6 *Uvaria grandiflora* Roxb. ex Hornem & *Polyalthia longifolia* Benth. & Hook. f. ex Hook. f. & Thoms. 20
1.7 *Xylopia aethiopica* (Dunal) A. Rich & *Miliusa indica* Leschen ex A. DC. 21
1.8 Gynoecium and androecium structure in various Annonaceae 22
1.9 South and Southeast Continental Asia - Political Boundaries 36
1.10 Monsoon weather systems in South and Southeast Continental Asia 37
1.11 Physical features of South and Southeast Continental Asia 39

2.1 Structure of nrDNA repeats in plants 71
2.2 Histogram of character changes at each nucleotide site in the ITS region based on the topology of MP tree no. 1 75
2.3 Two most parsimonious trees generated from ITS dataset 78
2.4 Maximum likelihood tree generated from ITS dataset 79
2.5 Neighbour-Joining tree generated from ITS dataset 79
2.6 Unrooted phylogram based on ML tree in Figure 2.5 80
2.7 Single most parsimonious tree generated from morphological dataset 89
2.8 Neighbour-Joining tree generated from morphological dataset 90
2.9 Combined representation of MP consensus trees from morphological and molecular datasets 92
2.10 Strict consensus tree of 2 most parsimonious trees generated from combined datset 93

3.1 Radian measurements for sampling of leaf shape 107
3.2 Calculation of Leaf Radian Ratios 108

List of Tables

1.1 Annonaceae: summary of major systematic classifications 19
1.2 Composistion of the *Uvaria* group 30

2.1 PCR reaction mix components and thermal cycling protocol 68
2.2 Sequencing reaction mix components and thermal cycling protocol 69
2.3 Samples used for molecular analysis 72
2.4 Nucleotide content data for ITS-1 and ITS-2 in final matrix 74
2.5 Descriptive statistics for maximum parsimony trees 1 & 2 76
2.6 Character scoring for morphological data matrix 82
2.7 Morphological data matrix 84
2.8 Descriptive statistics for maximum parsimony tree generated from morphological dataset 85
2.9 Size and percentage G-C content of the ITS region in Uvarieae (Annonaceae) and selected angiosperm families 95

3.1 Character measurements used in multivariate analysis 106
3.2 Comparison of grouping effectiveness of stepwise and simultaneous addition methods from Discriminant Analysis 110
3.3 Principal components analysis of log normalised flower measurements for total dataset 113
3.4 Principal components analysis of log normalised fruit measurements for total dataset 113
3.5 Discriminant analysis of log-normalised flower measurements for total dataset 115
3.6 Discriminant analysis of log-normalised fruit measurements for total Dataset 115
3.7 Principal components analysis of leaf ratio measurements for total dataset 117
3.8 Discriminant analysis of leaf ratio measurements for total dataset 118
3.9 Principal components analysis of mean leaf ratio measurements for each taxon 119

3.10 Principal components analysis of fruit sctructure in the *Uvaria narum* complex 126
3.11 Principal components analysis of flower structure in the *Uvaria narum* complex 126
3.12 Discriminant analysis of leaf ratio and log-normalised fruit measurements for *Uvaria narum* complex 126
3.13 Discriminant analysis of leaf ratio and log-normalised flower measurements for *Uvaria narum* complex 131
3.14 Discriminant analysis classification results for the *Uvaria narum* complex 132
3.15 Independent samples t-test for *Uvaria microcarpa* and *U. cordata*: summary of characters whose means differ significantly at $p < .01$ between the two species 135

4.1 Summary of nomenclature changes proposed for revision of *Uvaria* group in Continental Asia (a): accepted names and proposed new names and combinations 145
4.2 Summary of nomenclature changes proposed for revision of *Uvaria* group in Continental Asia (b): *synonyma nova* 146

List of Figures

1.1 Distribution of *Uvaria* 6
1.2 A facsimile copy of 'Narum Panel' from Rheede's *Hortus malabaricus* ... 7
1.3 A monochasial rhipidium, based on growth patterns observed in various *Uvaria* species 9
1.4 *Artabotrys hexapetalus* (L. f) & *Orophea corymbosa* (Baill.) Miq. 10
1.5 *Annona muricata* L. 11
1.6 *Uvaria grandiflora* Roxb. ex Hornem & *Polyalthia longifolia* Benth. & Hook. f. ex Hook. f. & Thoms. 20
1.7 *Xylopia aethiopica* (Dunal) A. Rich & *Miliusa indica* Leschen ex A. DC. 21
1.8 Gynoecium and androecium structure in various Annonaceae 22
1.9 South and Southeast Continental Asia - Political Boundaries 36
1.10 Monsoon weather systems in South and Southeast Continental Asia 37
1.11 Physical features of South and Southeast Continental Asia 39

2.1 Structure of nrDNA repeats in plants 71
2.2 Histogram of character changes at each nucleotide site in the ITS region based on the topology of MP tree no. 1 75
2.3 Two most parsimonious trees generated from ITS dataset 78
2.4 Maximum likelihood tree generated from ITS dataset 79
2.5 Neighbour-Joining tree generated from ITS dataset 79
2.6 Unrooted phylogram based on ML tree in Figure 2.5 80
2.7 Single most parsimonious tree generated from morphological dataset 89
2.8 Neighbour-Joining tree generated from morphological dataset 90
2.9 Combined representation of MP consensus trees from morphological and molecular datasets 92
2.10 Strict consensus tree of 2 most parsimonious trees generated from combined datset 93

3.1 Radian measurements for sampling of leaf shape 107
3.2 Calculation of Leaf Radian Ratios 108

3.3 Principal components analysis of log-normalised floral measurements for complete dataset: plot of taxon scores for components 1 & 2 114
3.4 Discriminant analysis of log-normalised floral measurements for complete dataset: plot of case scores for discriminant functions 1 & 2 116
3.5 Discriminant analysis of leaf ratio measurements for complete dataset: plot of case scores for discriminant functions 1 & 2 120
3.6 Discriminant analysis of leaf ratio measurements for complete dataset: plot of group centroid scores for discriminant functions 1 & 2 121
3.7 Principal components analysis of mean leaf ratios: plot of taxa scores for components 1 & 2 122
3.8 Plot of taxon scores for L/L_1 and C/L_1 123
3.9 Plot of taxon scores for the characters L/L_1 and P/L_2 124
3.10 Principal components analysis of fruit structure in the *Uvaria narum* complex: plot of case scores for components 1 & 2 127
3.11 Principal components analysis of flower structure in the *Uvaria narum* complex: plot of case scores for components 1 & 2 128
3.12 Discriminant analysis of leaf and floral characters (A) and leaf and fruit characters (B) in *U. lurida*, *U. macropoda* and *Uvaria narum* 133
3.13 A selection of characters whose means differ significantly between *Uvaria cordata* and *U. microcarpa* 136

4.1 A & B. Stamen and Carpel type in *Ellipeia* and *Uvaria* clades. C. Leaf venation terminology 148
4.2 Indument Terminology 149
4.3 *Ellipeiopsis ferruginea* var. *ferruginea* leaf shape 162
4.4 *Ellipeiopsis ferruginea* var. *cherrevensis* leaf shape 164
4.5 *Uvaria lamponga* leaf shape 173
4.6 *Uvaria lurida* leaf shape 177
4.7 *Uvaria macropoda* leaf shape 180
4.8 *Uvaria grandiflora* leaf shape 187
4.9 *Uvaria curtisii* leaf shape 190
4.10 *Uvaria dac* leaf shape 193
4.11 *Uvaria hamiltonii* leaf shape 198
4.12 *Uvaria maclurei* leaf shape 201

4.13 *Uvaria calamistrata* leaf shape 204
4.14 *Uvaria zeylanica* leaf shape 206
4.15 *Uvaria sphenocarpa* leaf shape 209
4.16 *Uvaria semicarpifolia* leaf shape 212
4.17 *Uvaria cordata* leaf shape 217
4.18 *Uvaria microcarpa* leaf shape 222
4.19 *Uvaria rufa* var. *rufa* leaf shape 230
4.20 *Uvaria rufa* var. *timoriensis* leaf shape 231
4.21 *Uvaria lobbiana* leaf shape 235
4.22 *Uvaria narum* leaf shape..... 240
4.23 *Uvaria tonkinensis* leaf shape 243
4.24 *Uvaria boniana* leaf shape 246
4.25 *Uvaria orientalis* leaf shape 248
4.26 *Uvaria pierrei* leaf shape 251
4.27 *Uvaria micrantha* leaf shape 256
4.28 *Uvaria kerrii* line drawing 260
4.29 *Uvaria kerrii* leaf shape 261
4.30 *Uvaria wrayii* leaf shape 263
4.31 *Uvaria wrayii* line drawing 264
4.32 *Uvaria argentea* var. *bracteata* leaf shape 268
4.33 *Uvaria vietnamensis* leaf shape 271
4.34 *Uvaria vietnamensis* line drawing 272
4.35 *Rauwenhoffia siamensis* leaf shape 275
4.36 *Ellipeia dulcis* leaf shape 283
4.37 *Ellipeia pauciovulata* leaf shape 286
4.38 *Nervopetalum hahnii* leaf shape 291
4.39 Distribution map – *Ellipeiopsis ferruginea* 293
4.40 Distribution map – *Rauwenhoffia siamensis* & *U. lamponga* 293
4.41 Distribution map – *Ellipeia dulcis* & *E. pauciovulata* 294
4.42 Distribution map – *Nervopetalum hahnii* 294
4.43 Distribution map – *Uvaria lurida* & *U. macropoda* 295
4.44 Distribution map – *Uvaria grandiflora* 295
4.45 Distribution map – *Uvaria curtisii* & *U. dac* 296
4.46 Distribution map – *Uvaria hamiltonii* 296

4.47 Distribution map – *Uvaria maclurei* & *Uvaria zeylanica* 297
4.48 Distribution map – *U. calamistrata* & *U. cordata* 297
4.49 Distribution map – *Uvaria sphenocarpa* & *U. microcarpa* 298
4.50 Distribution map – *Uvaria semicarpifolia* & *U. rufa* 298
4.51 Distribution map – *Uvaria narum* & *U. lobbiana* 299
4.52 Distribution map – *Uvaria wrayii*, *U. kerrii*, *U. tonkinensis* & *U. orientalis* 299
4.53 Distribution map – *Uvaria pierrei* & *U. boniana* 300
4.54 Distribution map – *Uvaria micrantha* & *U. bracteata* 300
4.55 Distribution map – *Uvaria vietnamensis* 301

5.1 Distribution patterns of selected *Uvaria* group taxa whose distributions are confined to Continental Asia 305
5.2 Distribution patterns of selected *Uvaria* group taxa whose distributions Extend into Malesia 306
5.3 Distribution of *Uvaria* group in Continental Asia 308
5.3 Distribution of *Uvaria* group in Continental Asia relative to rainfall patterns 309

Preamble

This work forms part of a larger effort to analyse the diversity and systematics of the Annonaceae (Maas, 1984; Mennega, 1989; van Heusden, 1992; van Setten & Koek-Noorman, 1992; Kessler, 1993; Maas *et al.*, 1994; Kessler *et al.*, 1996), and to complete tribal accounts for the regional floras of tropical Asia. In both cases this is the first attempt to tackle one of the four large palaeotropical genera (*Polyalthia*, *Artabotrys*, *Xylopia*, *Uvaria*) which constitute the taxonomic core of the family in Asia and Africa. The goal of this work is to begin the revision of *Uvaria* by focusing on the genus in continental Asia. The geographic range of the genus includes all of continental Asia between the Gulf of Cambay in western India, Guandong in southern China and the Isthmus of Kra in southern Thailand. It also occurs on Sri Lanka, the Andaman-Nicobar Islands and Hainan. The isthmus of Kra is regarded as the floristic boundary between Indochina and Malesia, while the Gulf of Cambay and Guandong represent the western and eastern extremities of the Asian wet-tropical zone. 26° N represents the approximate northern limit of *Uvaria* records in the region.

The taxonomic scope of the project has been determined following interpretation and analysis of existing classifications of the family. A '*Uvaria* group' has been selected for revision in order to better delimitate generic boundaries within *Uvaria* and its closest relatives. This group can be equated with a revised Uvarieae tribe, however several prominent authorities have advised against the use of the tribal system in the Annonaceae.

The revision of *Uvaria* and its affiliates in continental Asia can be subdivided into two principal avenues of investigation. The first relates to resolving the identity and proper name for each taxon that is included in the analysis, and this has been done using the established practice of type comparisons and historical literature research.

The second avenue of research involves the analysis of these taxa using phylogenetic and phenetic techniques. In practice there is a dynamic interplay between taxonomic, phylogenetic and phenetic investigations. The first product of these combined analyses is a hypothetical classification model, however as more data is analysed

using each technique, the model is progressively modified to incorporate the sum-total of evidence which has been acquired. In this way the incomplete hypotheses of the past are modified to produce a new model which is statistically and phylogenetically robust and taxonomically well-informed.

Chapter 1 places this work in context and is divided into two sections. The first section, Taxonomy and Systematics of *Uvaria* and the Annonaceae, begins with a short overview of *Uvaria.* This is followed by a more general discussion of the Annonaceae and the way in which attitudes have changed over time regarding the position of the family (and other Magnoliales families) within the angiosperms. The internal classification of the family is also discussed, and this sets the stage for a formal delimitation of the '*Uvaria* group' - the focus of the revision. The second section of Chapter 1 provides an overview of the biogeography, human uses and ecology of *Uvaria* and the Annonaceae. Most of this second section is of specific relevence to later Chapters of the thesis, particularly the notes which accompany the taxonomic accounts in Chapter 4, however some additional information is included in order to outline the importance of the family in spheres other than systematics and taxonomy.

The results of this work are presented in their final format, and the results of earlier superseded analyses are not discussed. Phylogenetic and phenetic results are presented in chapters 2 and 3 respectively. The final product of all analyses, the formal revision, is presented in chapter 4. The identity of taxa in chapters 2 and 3 conforms with currently accepted names, however many of these are changed as part of the taxonomic treatment in chapter 4.

In many ways chapter 4 should be presented as the concluding chapter. However, some discussion of results is required and it seems impractical to include this *before* the formal taxonomic revision given that the inferences of this work are important to the discussion. The introduction to chapter 4 does include reference to the two preceding chapters where the results of these analyses have a bearing on the taxonomic classification.

CHAPTER 1 - INTRODUCTION

Taxonomy and Systematics of *Uvaria* and the Annonaceae

Uvaria L. - an Overview

The currently estimated number of species for *Uvaria* is approximately 150, making it the second largest genus in the family (the largest being the neotropical genus *Duguetia*, with 250 species). Uvarias occur in the moist tropical regions of Africa, Madagascar, Continental Asia, Malesia, Northern Australia and the Bouganville-Solomon Island chain (Figure 1.1). All species are climbers or scandent/scrambling shrubs, and grow by means of twining branchlets. Some lowland rainforest species can grow to heights of 30 m or more, often with a single 8-10 cm diameter main stem, however the more usual habit is a many-branched climber in disturbed or marginal riverine vegetation (Appendix 4.5A & B).

The predominant leaf shape is obovate, however elliptical and narrowly ovate leaves are also common. Most species have a tomentose indument with a characteristic ferruginous hue, especially in the juvenile stages. Many species lose this indument, sometimes very rapidly, while others retain a prominent hirsute tomentum into maturity. In all species the hairs are stellate, with 2 – 25+ branches. The inflorescence can be leaf-opposed or axillary, and in rare cases is cauliflorous. Flowers range in number from one to five or six per inflorescence, with usually a maximum of two-three open at any one time.

The petals are imbricate, six in number and membranous or coriaceous, however some Asian and many African species have fleshy petals. In some species the petals remain erect, but mostly they are reflexed at maturity (Appendix 4.1A). Colours range from yellow-white to purple-brown. The stamens are laminar or cuneate and the stamen apex may be flattened or obtuse. Most species have glabrous stamens, however a few have hairs on the locules or the connective. The ovaries are hairy and the stigmas are U-shaped and glabrous. Ovule number ranges from 2 to 30, with most species having between four and ten. Monocarps are normally stipitate, however in a few species they are sessile or nearly so (Appendix 4.1B). The pericarp can be thin or thick and fleshy. The flesh is usually white in colour and where edible is bittersweet.

The origin of *Uvaria* L. in modern scientific literature

The first modern scientific description of a *Uvaria* was made by Rheede in his *Hortus indicus malabaricus* (1679). He made descriptions of many Annonaceae including 'Corinti-Panel', 'Kasjou-Panel', 'Kal Tsjerou-Panel' and 'Narum-Panel', all of which were derived from colloquial names in Sinhalese.

Figure 1.2 shows a facsimile copy (courtesy of the TCD Library) of the illustration for 'Narum-Panel' in *Hortus malabaricus*. Although lacking in detail, it provides a clear representation of the main characters which |Linnaeus would later use to delimit the genus. The leaves are alternate, exstipulate, pinnately-veined and entire. The flowers are solitary or few in number, mounted on an axillary or leaf-opposed pedicel. There are six membranous petals which expand and reflex at maturity and are often persist into the fruiting stage as a loose basally-connate ring on the pedicel. The floral head has numerous stamens in several whorls and a central gynoecium of numerous free carpels. The fruits are fleshy, apocarpous and mounted on an elongate stipe. The description accompanying the plate provides an extended account of the form and structure of the plant, particularly the seeds (several seeds oriented horizontally and separated by a thin membrane, with a smooth testa carrying sub-cuticular transverse striations). These descriptions provided |Linnaeus (1748, 1753) with more than enough detail on which to base his new *Uvaria* (a facsimile copy of the *Species Plantarum* account for *Uvaria zeylanica* shown in Appendix 1).

The Annonaceae - Family Characteristics

The Annonaceae are a natural, easily-identified family of c. 2,300 species and 130 genera (Heywood, 1978, Kessler, 1993). The family has a pantropical distribution, with two genera extending into the temperate zone of North America. All species are woody, growing as shrubs, climbers or trees. The leaves are entire, exstipulate and pinnately veined, and contain characteristic ethereal oil cells. The bark is usually grey-black-brown in colour, finely grooved, and often with ubiquitous lozenge-shaped lenticels over the surface. The inflorescence is a terminal, supra-axillary or rarely

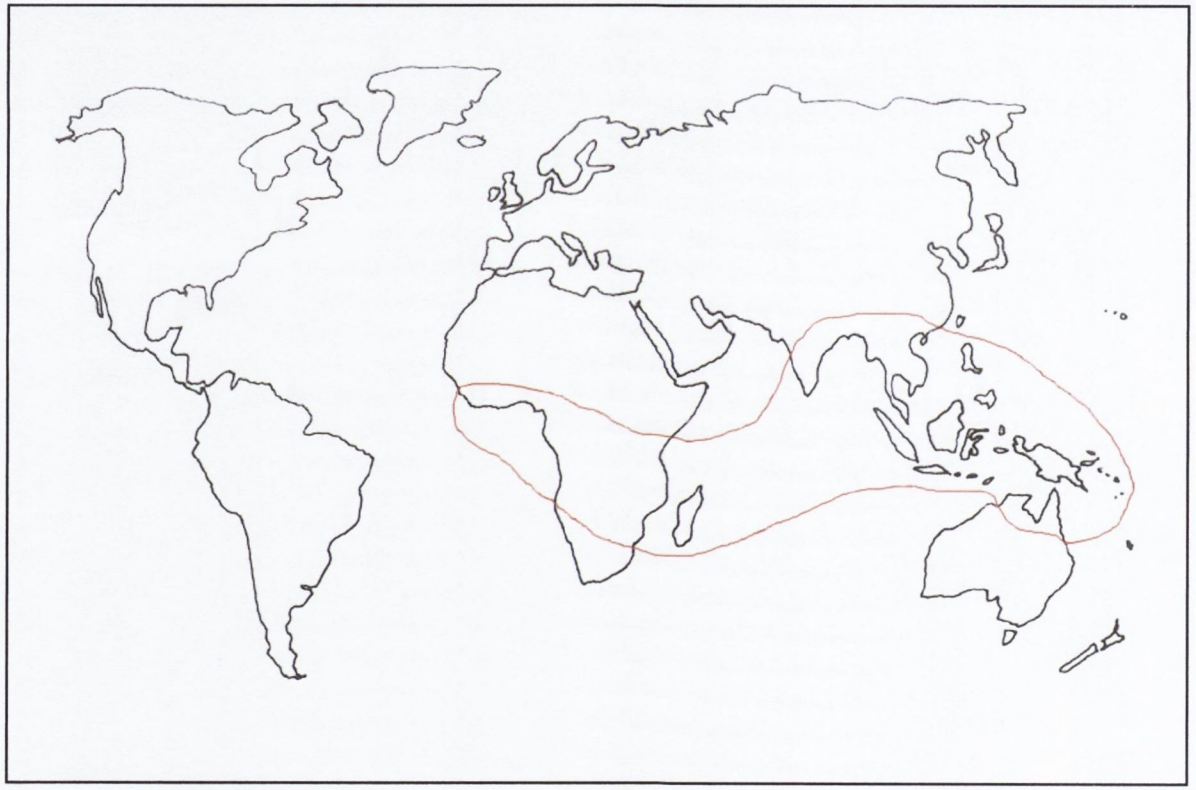


Figure 1.1. The distribution of *Uvaria* L. in Africa, Asia and Malesia.



Figure 1.2. A facsimile copy of 'Narum-Panel', Fig. 10 in Volume 1 of Rheede's *Hortus malabaricus*.

axillary cyme, most often in a monochasial rhipidium (Figure 1.3). Flowers can be numerous or solitary. The flowers usually have three sepals and two whorls of three petals, which may be membranous or fleshy. There is a large diversity in sepal and petal shape, and while fusion and reduction is common, the vast majority of species retain a full set of nine clearly distinct tepals. The inner whorl of petals is the most variable, forming, for example, the characteristic Annonaceous 'pollination chamber' in many genera, or the clawed 'mitreform' obovate petals seen in certain Asian genera (Fig. 1.4, Appendix 4.2B & 4.3).

The stamens have two pairs of lateral or extrorse locules but lack a well-developed filament. A characteristically enlarged connective obscures the locules from above, although in certain cases the stamens can be laminar and the connective elongate and flattened. Pollen is uni-, tri- or inaperturate, occurring in monads or tetrads. The carpels are normally free, however in certain groups there is a tendency towards aggregation, either in pseudosyncarpy, as in *Annona* (Figure 1.5, Appendix 4.4A), or paracarpy, in *Monodora* and *Isolona* (Fig. 1.8). Ovule number ranges from 1-30, in one or two lateral or basal rows. The receptive apparatus of the carpel is not differentiated into stigma and style, however many taxa show a narrowing or neck below the stigmatic surface. This neck, as in many primitive families of the Magnoliids, is not fully closed, and the abaxial side of most ovaries also has a longitudinal groove which is believed to represent the fusion line between the two lobes of the ancestral proto-carpel. The fruits may form an aggregate, or, as in most cases, may mature as stipitate monocarps. Most fruits are indehiscent, however *Xylopia* and *Anaxagorea* have dehiscent fruits.

The Development of Angiosperm Classification

Through the course of the twentieth century there has been a consolidation of scientific thinking regarding the origin and radiation of the Angiosperms. The last 25-30 years in particular have seen considerable progress in the development of a satisfactory hypothesis. These recent advances have in many ways come at the crest of a wave. Subsequent to the publication of *The Origin of Species* in 1859, plant

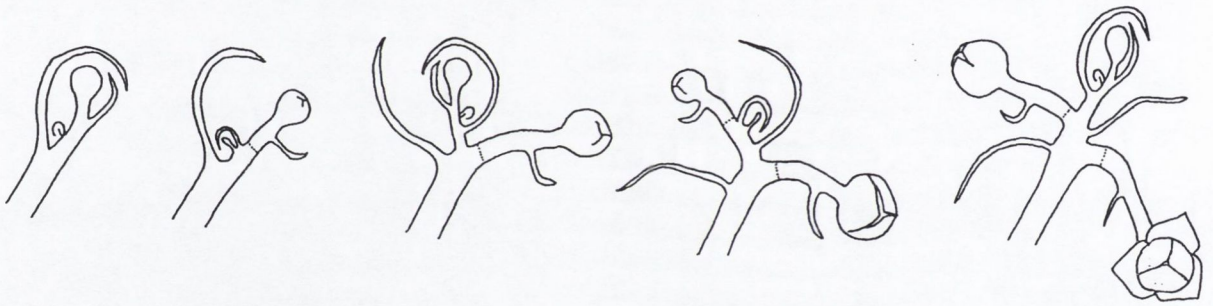


Figure 1.3. A *monochasial rhipidium,* the cymulose inflorescence type typical of Annonaceae. Drawing based on growth patterns observed in various *Uvaria* species. Each pedicel and bud is sheathed by a basal and medial bract. The basal bract opens first and the medial bract then opens to reveal the floral bud. Secondary buds emerge in the axil of the basal bract.

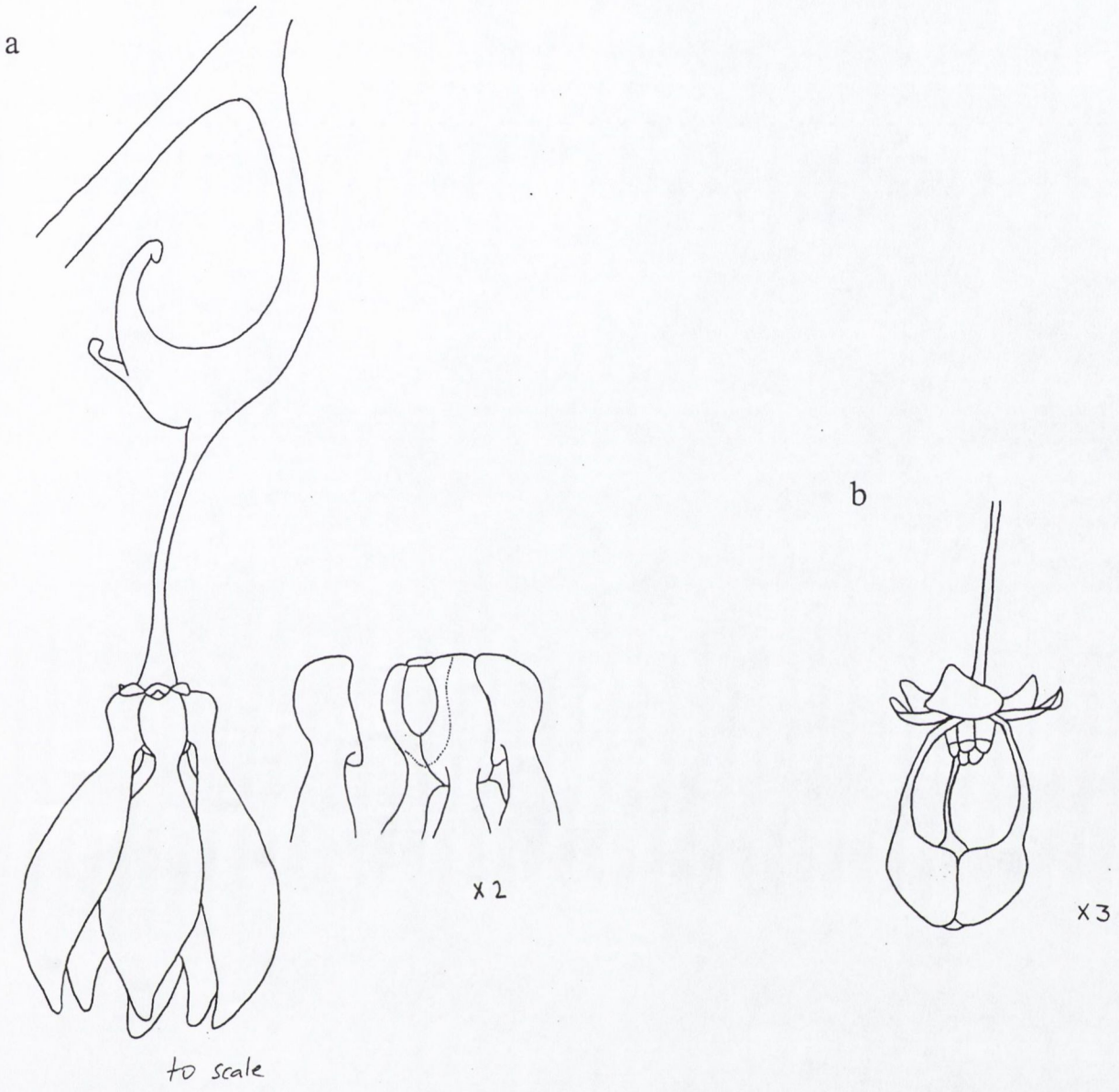


Figure 1.4. (a) *Artabotrys hexapetalus* (L. f.) Bhandari (drawing pers. obs., Thailand). Detail showing entrance to pollination chaber at the base of two inner whorl petals. (b) *Orophea corymbosa* (Baill.) Miq. (drawing after Baillon, 1868) showing the floral dome characteristic of many Annonaceae, particularly the 'Mitrephorm' genera of Asia.

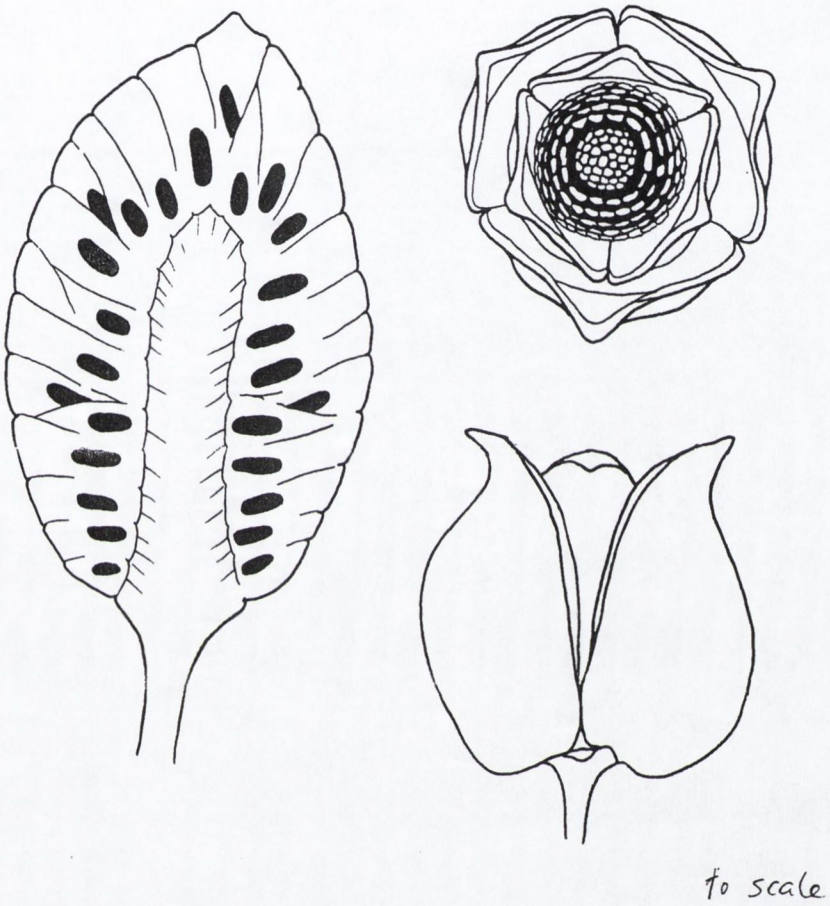


Figure 1.5. *Annona muricata* L. showing pseudosyncarpous fruits. Each monocarp contains a single seed with basal placentation. (Drawing after pers. obs., Singapore)

classification regimes were very slow to incorporate the evolutionary precepts which Darwin had proposed.

A critical factor in this 'delay' might be attributed to Bentham and Hooker's seminal *Genera Plantarum,* which although published in 1862, was pre-Darwinian in construction and a direct descendent of De Candolle's *Systema* (1817) and *Prodromus* (1824). However, it is clear in hindsight that a revised version of the *Prodromus* was needed before any realistic assessment of evolutionary patterns in the plant kingdom could be attempted. Species new to science were at that time emerging from all parts of the world in unprecedented numbers, and the botanical landscape of 1859 was a good deal more complex than it had been in 1824. In many ways, therefore, *Genera Plantarum* provided a summary of current botanical knowledge which, when combined with the theoretical aspects of *The Origin of Species*, set the stage for a new classification of the green plants.

However, even though the new evolutionary interpretation had an immediate impact on the way in which nature was perceived, many of the groups first espoused by De Candolle and then enlarged and/or revised by Bentham and Hooker survived the turmoil of the Darwinian revolution and, indeed, are still acceptable today. In many ways this can be put down to the intuitive and dexterous manner in which these authors organised the plant kingdom as they knew it. Indeed, Darwin felt that the classifications of De Candolle and his successors were unknowingly framing the patterns of evolution. He remarks in Chapter 14 of *The Origin of Species*,

> ... the characters which naturalists consider as showing an affinity between two or more species, are those which have been inherited from a common parent, [and] all true classification being genealogical ... community of descent is the hidden bond which naturalists have unconsciously been seeking.

Given that Darwin saw such a congruence between the emergence of distinct taxonomic patterns in nature and the processes of natural selection, and recognised that these patterns were clearly evident in existing biological works, it is not surprising that taxonomic works such as the *Prodromus* and *Genera Plantarum* have been so amenable to the evolutionary paradigm. De Candolle (1813) did see a

hierarchy of organisation in nature, and although he was certainly aware of the idea of descent with modification (Lamark and St. Hilaire were his Parisian contemporaries) he never explicitly outlined a theory of evolution to justify his classifications. Hooker was of course well aware of Darwin's theories, and regularly corresponded and talked with him in the years prior to the publication of *The Origin of Species*. He was nonetheless slow to interpret his own work in light of Darwin's theory (Burrow, 1968), possibly because his classifications were intended as a functional guide to plant diversity, rather than an interpretation of it. Notwithstanding the attempts of Engler & Prantl (1891) and others to interpret existing classifications in light of the evolutionary theory, it would be almost 50 years after the publication of *Genera Plantarum* that the first truly evolutionary interpretation of flowering plants would be presented. Bessey's 'Phylogenetic taxonomy of flowering plants' (1915) was the pivotal moment when angiosperm classification was deconstructed and genuinely re-assessed according to the logic set out in Darwin's theories.

The Origin of the Angiosperms

The changing interpretation of what constitutes the basal angiosperm group has been of critical importance to the development of Angiosperm classification. Engler and Prantl (1891) judged the *apetalae* to be the ancestral angiosperm group. In this system, the catkin-bearing Hamamelidae and apetaloid monocots were the basal groups of the dicotyledons and monocotyledons respectively from which evolved the more 'complex' entemophilous flowering systems. This hypothesis seemed to be well supported by the fact that the putative ancestors of the angiosperms, the gymnosperms, were thought to be dependent on wind pollination.

Bessey (1915) identified the 'ranalean' or 'magnoliid' complex as the basal group of angiosperms from which the other dicots were derived. He also laid down a set of *Dicta* to support his classification, identifying clear avenues of evolution across a whole array of morphological and anatomical characters. In this scenario, the entemophilous flowers of the Magnoliaceae are identified as the ancestral form from which all others derived and the apetaloid groups are regarded as having abandoned insect and animal pollen-vectors and *reverted* to wind-pollination. Cronquist (1968),

Takhtajan (1969), and Heywood (1978) have presented classifications based on overall morphological evidence which support the hypothesis of Bessey. These conclusions are also supported by analysis of palynological evidence. Comparing extant and fossil pollen, Walker and Doyle (1975), Doyle (1978) and Walker & Walker (1984) all suggest that the magnoliid hypothesis on the origin of Angiosperms is probably correct, however the latter suggest that while the Magnoliaceae are the most primitive family in the larger dicot lineage, a separate basal lineage supports the Nympheaceae and all the monocots.

Taylor & Hickey (1992) argued that the true ancestors of the angiosperms were related to a palaeoherb complex centred on the palaeoherb group which Donoghue & Doyle's palynological analysis (1989) had identified as the basal angiosperms. This complex is centred on the Nymphaceae, however latterly has been expanded into a 'eoangiosperm' group including the Chloranthaceae, Cabombaceae, Ceratophyllaceae, and Piperaceae among others (Taylor & Hickey, 1996). This group is hypothesised to be basal both to the remainder of the dicots and all of the monocots, and infers that the woody habit in flowering plants is derived from the herbaceous one.

In Cronquist's (1968) interpretation, the major primitive magnoliid families are all woody and include the Magnoliaceae, Winteraceae, Annonaceae, Myristicaceae and Lauraceae - all grouped into order Magnoliales and sub-class Magnoliidae. Other families in the sub-class include the Piperaceae, Ranunculaceae and Nymphaceae. Derived from the Magnoliidae are all the other groups of dicots - the Dilleniidae (centered around and derived from the Delliniaceae), Rosidae (Rosaceae) and Caryophyllidae (Caryophyllaceae), with the Asteridae (Asteraceae) derived from within the Rosidae.

The Magnoliidae (*sensu* Cronquist) are woody, have uni- or triaperturate pollen, and mostly occur in equable, tropical or warm-temperate regions. Several of the smaller families within the order have unusually primitive characters. The Degeneraceae and Himantandraceae, with laminar unmodified stamens and partly or completely unsealed carpels, the Australobaileyaceae, with laminar unmodified stamens and the Winteraceae and Amborellaceae, with no wood vessels, all show characters which are

believed to reflect the ancestral angiospermous condition. Among the larger families there is generally a more orthodox structure in vegetative and reproductive organs, however we see considerable variation in the arrangement of the floral head. The Magnoliaceae have an undifferentiated perianth with numerous, spirally arranged carpels and stamens on an elongated receptacle. The Annonaceae, showing a slightly more complex level of floral organisation, have a reduced (fixed) number of perianth segments and a compact receptacle carrying few or many spirally-inserted stamens and carpels. The Lauraceae also exhibit a fixed perianth organisation, with a reduced and fixed number of stamens and a solitary carpel.

The character evidence contained in Cronquist's Magnoliidae point toward a hypothetical angiosperm ancestor which was woody and had an inflorescence composed of unsealed proto-carpels and flattened proto-stamens spirally arranged about a compressed shoot. The palaeoherb model suggests that the ancestral angiosperm was herbaceous and possibly rhizomatous, the leaf bases were flattened and sheath-like, the floral organs were reduced in number and occurred in cymose/ racemose inflorescences and the pollen was monosulcate.

More recent analysis of molecular data (Soltis *et al.*, 1999; Qiu *et al.*, 1999) has suggested an intermediate hypothesis. Evidence from analysis of nuclear and chloroplast DNA sequences suggests that a subset of the Magnoliales (*sensu* Cronquist) are the sister group of all angiosperms. This group includes, at it's base, the Amborellaceae, followed by the Nymphaceae, Schisandraceae, Illiceaece and Austrobaileyaceae. All other angiosperms, including the monocots and the remaining dicots (eudicots) and Magnoliales, are contained in a single monophyletic group. Although there is strong support for these latter three groups being part of a single clade, their relationship to one another is less clear. Soltis *et al.* found that the Magnoliales and the monocots are sister to the eudicots, whereas Qiu *et al.* found that the Magnoliales and the eudicots were grouped together with the monocots as a sister group.

This scenario appears to match well with hypotheses suggesting a semi-aquatic herbaceous origin for the angiosperms where vessels were absent and, indeed, unnecessary. This hypothetical ancestor would have given rise to two separate

lineages which became the monocots and the woody dicots. However, while the Nymphaceae/ palaeoherbs and monocots may have shared this aquatic origin, the majority of the early angiosperm group are woody. This conflict gives added support to Cronquist's (1968) assertion there may be several parallel lineages which arose from a common ancestor or closely related group of ancestors.

In terms of the position of the Annonaceae, although the family is undoubtedly of ancient origin, it appears to be less uniquely 'primitive' than earlier workers (e.g. Bessey, 1915; Cronquist, 1968; Takhtajan, 1969) may have thought. However, the immediate familial relationships of the Annonaceae remain much as these authors have suggested, with the family firmly nested within the woody Magnoliid complex which includes the Magnoliaceae, Degeneraceae, Eupomatiaceae and Myristicaceae.

Furthermore, it seems clear that the evolutionary patterns (e.g. floral reduction and fixation of perianth number) which are evident in this complex should be regarded as autapomorphies within the group. In other words, the Annonaceae and Myristicaceae are not intermediates between, for example, the Magnoliaceae and the more advanced groups of angiosperms, but are terminal branches in a separate Magnoliid radiation. Equally, the monocots, Magnoliids and the Amborelleaceae-Nymphaceae-Shisandraceae group may yet emerge as a single clade, with the remainder of the dicots, the eudicots, forming a separate radiation altogether.

Evolutionary Trends in the Annonaceae

The data of Soltis *et al.* (1999) and Qiu *et al.* (1999) provide an interesting insight into relationships amongst the Magnoliales. The sister group of the Annonaceae in both analyses is the Eupomatiaceae, with the Degeneraceae and Magnoliaceae slightly more distant. As hypothesised by Takhtajan and Cronquist, the Lauraceae are separate from all the above taxa, however the Winteraceae, considered by both authors to be close to Magnoliaceae-Annonaceae, are aligned with the Piperaceae at the margins of the Magnoliales-Piperales clade. A phylogenetic analysis of molecular data based on

the Annonaceae alone also finds *Eupomatia* as a sister group, with the Magnoliaceae, Degeneraceae and Winteraceae more distant (Bygrave and Chase, *in press*).

The suggestion of a close relationship between the Eupomatiaceae and the Annonaceae is not new. Bentham and Hooker (1862) first placed *Eupomatia* within the Annonaceous tribe Miliuseae, and Hutchinson (1964, 1969) elevated the Annonaceae and Eupomatiaceae to a separate order, the Annonales. Walker, (1976) also concluded the two were closely related, suggesting a sub-order Annoninaceae within the Magnoliales. If Cronquist (1968) did not suggest such a relationship, he accounted for his caution when he pointed out,

> We have ... a heterogeneous group of relic families, some of them consisting of only one or a few species. Each of these families has evolved slowly, independently of the others, and now presents a mixture of primitive and more advanced characters. Much of the evolution has evidently been parallel in different groups, reflecting the independent realisation of initially similar evolutionary potentialities. The sharing of advanced characters is therefore no guarantee of close relationship. (p. 136)

Considering this insight, if the molecular data are showing the true relationships of the group, we should not expect it to be immediately obvious from morphological data. Indeed, in an ancient group such as the Magnoliales, it is highly probable that large gaps in morphological data will have accrued. Aside from partially erasing the traces of true relationships in the group these gaps can also suggest positively misleading affinities. This is particularly true in the smaller families where primitive taxa containing critical information have (presumably) been lost. This is the case with many of the Pacific island families such as the Amborelleaceae, Degeneraceae, Eupomatiaceae and Austrobaileyaceae, which may once have had extensive distributions across many continents, but today form part of relic floras in isolated tropical islands and refugia.

The problem of limited data is not so acute in the Annonaceae. The family is large, with c. 2300 species and 130 genera, and has a pantropical distribution. These taxa are ecologically successful and often constitute a significant proportion of the vegetation

wherever they are found. However, the great age and speciation of the Annonaceae has led to taxonomic problems of the other extreme. The taxonomic affinities of the family, particularly in relation to floral morphology, are notoriously convoluted (Sinclair 1955; Fries 1959; van Heusden, 1992; Kessler, 1993). Reticulate distribution of apparently homologous characters is commonplace, and often where one set of characters suggests a clear affinity between species or genera, another set will suggest a completely different affinity.

There are six sub-familial/tribal groupings which have featured in most classifications of the Annonaceae since Bentham and Hooker's (1862) treatment. Hutchinson (1923, 1964) divided the family into two sub-families, the Annonoideae (including the apocarpous and pseudosyncarpous genera) and the Monodoroideae (including the parasyncarpous genera) (Table 1.1). The Uvarieae (Figure 1.6a, Appendix 4.1), based around *Uvaria*, has included genera with (mostly) valvate sepals and imbricate expanding petals in two subequal whorls. The second and usually largest group is the pantropical Unoneae (Figure 1.6b, Appendix 4.2A), based around the now much reduced genus *Unona*. The Unoneae are characterised by valvate sepals and valvate expanding petals, again in two subequal whorls. The third group, the Mitrephoreae, (Figure 1.4b, Appendix 4.2B) contains largely Asian genera which have a very characteristic floral dome formed by a connivance of the distinctly obovate inner petals. Petals on the outer whorl can be larger or smaller than the inner whorl and are usually erect. The Xylopieae (Figure 1.4a & 1.7a, Appendix 4.3), centred on the pantropical *Xylopia*, have ovate-lanceolate, usually fleshy petals, the outer whorl mostly larger than the inner, remaining erect or spreading, with the inner petals usually remaining connivent along their margins. The second last group, the Miliuseae, share the reduced outer whorl of petals typical of *Miliusa* (Figure 1.7b). The outer whorl is often identical to the sepals, while the inner whorl is often basally connate. The final group in the Annonoideae is the Annonineae, centred around *Annona*, and the main delimiting feature of the group is their pseudosyncarpous fruits (Figure 1.5, Appendix 4.4A). Many species also have a characteristic pollination chamber formed by a connivance of the inner petals. An illustration of the parasyncarpous gynoecium of the Monodoroideae is shown in Figure

Table 1.1. Annonaceae: summary of major systematic classifications. See text for discussion.

Fries (1959)	Hutchinson (1923, 1964)	Sinclair (1955)
Annonoideae	Annonoideae	Annonoideae
Uvarieae	Uvarieae	Uvarieae
Uvaria-gruppe	Miliuseae	Miliuseae
Duguetia-gruppe		
Asimina-gruppe		
Hexalobus-gruppe		
Guatteria-gruppe		
Unoneae	Unoneae	Unoneae
Desmos-gruppe	Xylopineae	Xylopieae
Polyalthia-gruppe	Annoninae	Mitrephoreae
Unonopsis-gruppe		Annonineae
Xylopia-gruppe		
Artabotrys-gruppe		
Orphea-gruppe		
Annona-gruppe		
Trigynaea-gruppe		
Monanthotaxis-gruppe		
Tetramerantheae		
Monodoroideae	Monodoroideae	Monodoroideae

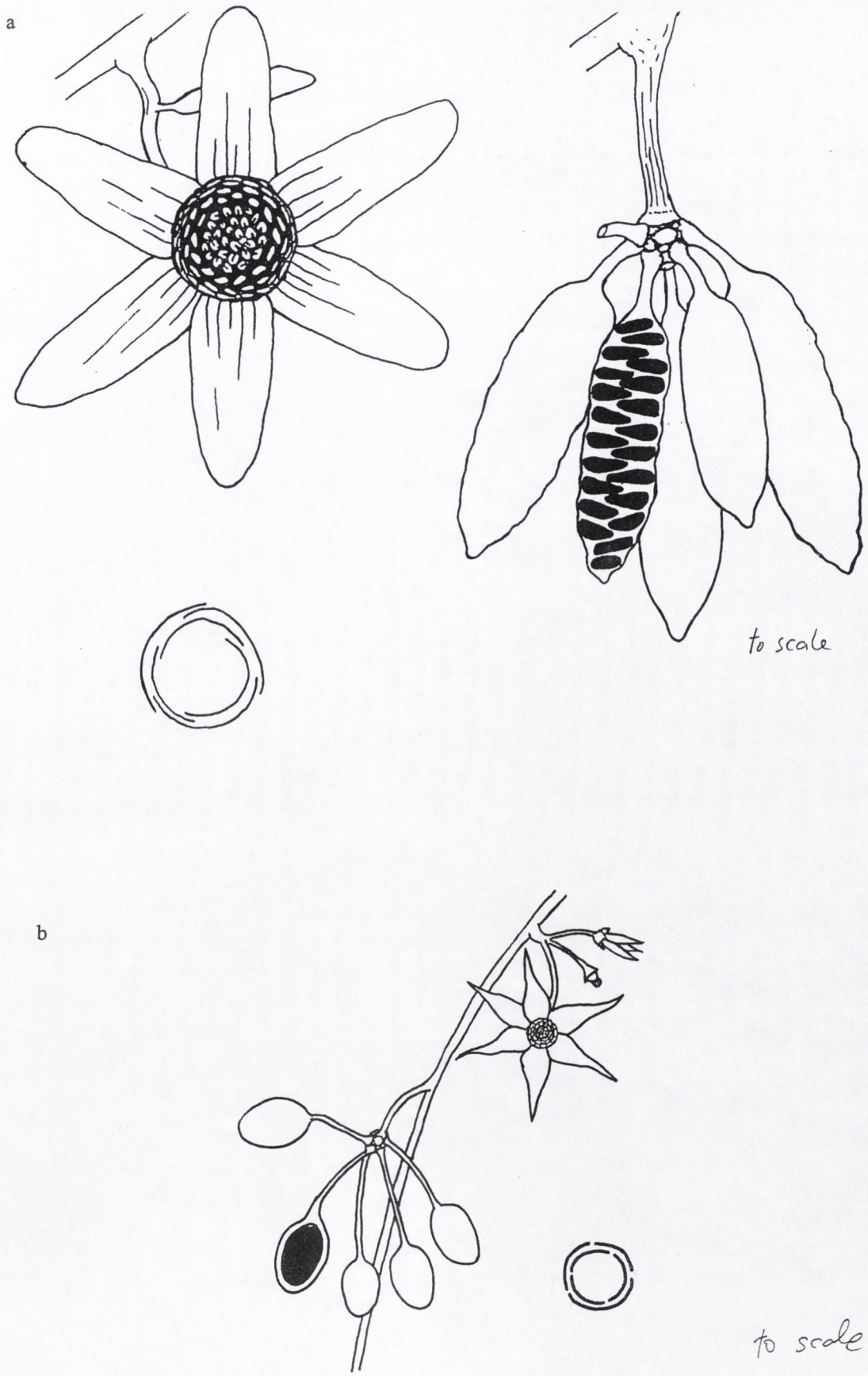


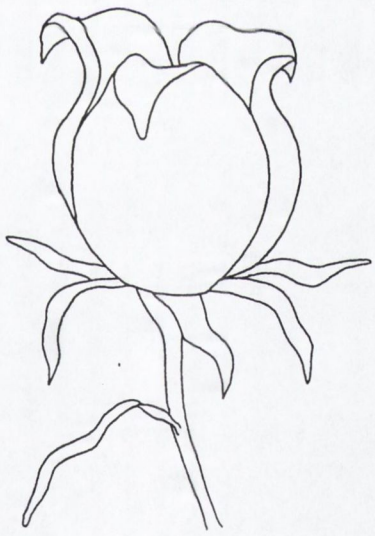
Figure 1.6. (a) *Uvaria grandiflora* Roxb. ex Hornem. with imbricate aestivation of petals in bud. (b) *Polyalthia longifolia* Benth. & H. f. ex H. f. with valvate aestivation of petals in bud. (Both drawings based on personal observation in the field and at TCD).

a



to scale

b



to scale

Figure 1.7. (a) *Xylopia aethiopica* (Dunal) A. Rich (drawing after Verdcourt, 1971). Both whorls of petals erect basally, apices variously spreading. Inner petals remain connivent along the supra-basal margins. Monocarps are dehiscent. (b) *Miliusa indica* Leschen ex A. DC. Outer whorl of petals are much-reduced and sepal-like (Drawing after Baillon, 1868).

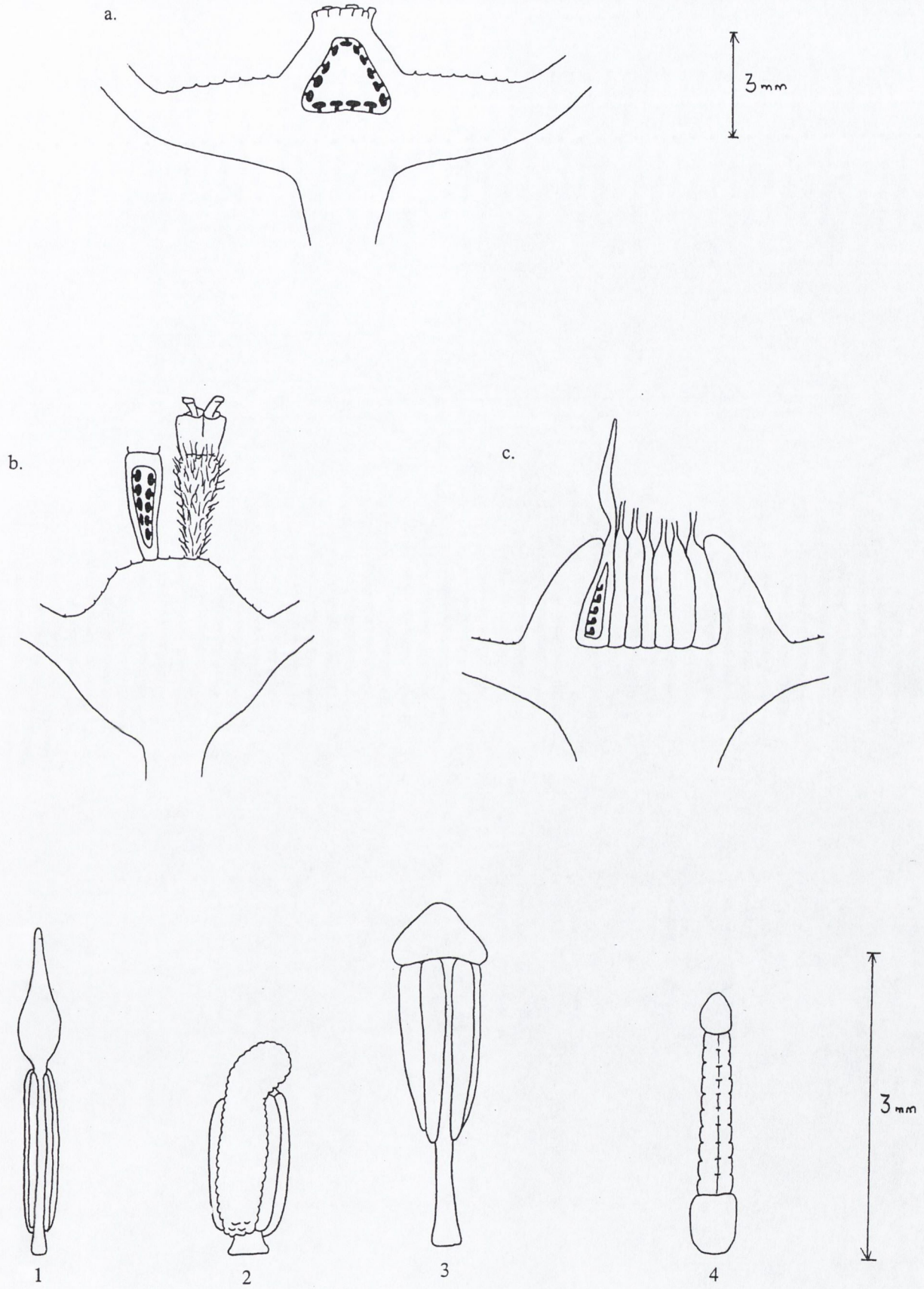


Figure 1.8. Gynoecium and androecium structure in various Annonaceae. (a) Parasyncarpous gynoecium of *Monodora angolensis* Diels formed by reduction and fusion of carpels. Stigmatic surface retains lobes of individual carpels. (b) Free carpels mounted on dome-shaped receptacle in *Asteranthe asterias* Engl. & Diels showing the gynoecial structure typical of the the majority of Annonaceae. (c) Free carpels mounted in a depressed receptacle in *Xylopia aethiopica* (Dunal) A. Rich. (d) A variety of stamen forms from various genera - 1. *Cananga odorata* (Lam.) H. f. & Th. 2. *Monanthotaxis fornicata* (Baill.) Verd. 3. *Asimina triloba* Dunal. 4. *Xylopia aethiopica* (A. Rich) Benth. Drawings after Verdcourt, 1971, and Baillon, 1868.

Sinclair (1955) and Fries (1959) both retained an element of these divisions in their respective treatments of the Annonaceae. Even though Sinclair was revising just a fraction of the family (perhaps 40% of the species known at the time) he made it clear that any classification of the family had to be flexible,

> The classification of the Annonaceae into tribes is a difficult problem and I do not think there can ever be a satisfactory division in spite of some admirable attempts. The present one should not therefore be regarded as final. (p. 170)

Fries' monograph of the entire family was of course more ambitious, however much of the insightful work in the monograph is focused on Africa and to a lesser extent South America (his two areas of regional specialisation) rather than a truly unified pantropical assessment. Much of his Asian data are derived from Sinclair. He recognised the two sub-families of Hutchinson; the Monodoroideae, incorporating the African genera *Monodora* and *Isolona*, both having a single ovary made up of several entirely fused carpels, and the Annonoideae, containing the remainder of the family. He named just two tribes, the Uvarieae (imbricate petals) and the Unoneae (valvate petals). These were divided into a total of 14 'gruppen' - five in the Uvarieae and nine in the Unoneae. These groups were more sharply defined than Bentham and Hooker's, however unlike Sinclair, Fries ended up with stark geographic anomalies in certain groups. His predominantly palaeotropical *Uvaria gruppe* included, for example, *Sapranthus* and *Stenanona* from Central America. The predominantly American *Asimina gruppe* included *Cyathostemma*, *Stelechocarpus* and *Enicosanthum*, all from tropical Asia. There were also several morphological anomalies; climbing genera were often grouped within predominantly arborescent groups, and taxa with stellate and simple hairs were grouped together. While the overall monograph provided a very useful account of diversity in the family as a whole, subsequent workers found many problems in the classification system which Fries had used.

Van Heusden (1992) reinterpreted Fries classification in a study of floral diversity in the family. She retained only three of Fries' groups, identifying the over-reliance on homoplasic floral characters as the source of instability in his system. She concluded that carpel and stigma structure, ovule placentation and stamen shape are all characters which have previously been ignored but can provide reliable data for future

classifications. Utilising these characters she was able to establish 19 informal groups which were relatively robust when tested against the available evidence from palynological and karyological studies. A summary of stamen and carpel structure in the family is provided in Figure 1.8.

The apparent unreliability of many floral characters at the supra-generic and tribal level is fortunately not repeated in pollen and fruit characters. A number of palynological studies in the 1970s and 1980s shed new light on phylogenetic relationships within the Magnoliales and the Annonaceae (e.g. Doyle, 1978; Le Thomas, 1980, 1981; Le Thomas & Lugardon, 1976; Walker 1974a,b). A consensus emerged that the primitive Magnoliales/Annonaceae pollen type was one with an amorphous/granular exine, but opinion differed as to the hypothetical structure of the sulcus and aperture.

Doyle and Le Thomas (1994, 1996) have produced a cladistic analysis of these pollen data combined with data from morphological studies. Their main conclusion is that the Asiatic-American genus *Anaxagorea* with granular monosulcate pollen is basal in the family. In this new arrangement, the remainder of the family is divided into three main clades. The first contains genera with mono- and disulcate columellar pollen, including e.g. *Malmea* and *Miliusa*. The second group includes genera with granular inaperturate pollen which is formed in monads, including *Uvaria* and the African climbing genus *Monanthotaxis*. The final, largest clade contains genera with granular inaperturate pollen which is formed in tetrads, including *Xylopia*, *Duguetia* and *Annona*.

Several trends in morphological characters are evident based on this phylogeny. The ancestral fruit type is a stipitate monocarp, which in *Anaxagorea* and *Xylopia* is also dehiscent. Pseudosyncarpy, or the basal fusion of carpels, has originated twice within the family, once in the *Annona* group and once in the *Fusaea-Duguetia* group. Parasyncarpy, the almost complete fusion of carpels into a unilocular gynoecium, has originated just once, in *Monodora* and *Isolona*. Reduction and increase in the number of ovules from the 3-4 seen in *Anaxagorea* appears to have occurred several times, however there is a parallel maintenance of overall ovule number per inflorescence. Stigma shape is conservative, with elongate stigmas arising twice from a basal sessile

type. Stamen morphology is also a relatively reliable character, with the laminar, unmodified stamen of *Anaxagorea* basal to a major group having broadened or capped stamens (e.g. *Uvaria*) and two smaller groups with prolonged or pointed apices (e.g. *Cananga*). Sepal characters are much more conservative and reliable than petal characters, with imbricate sepals being characteristic of the basal genera, and valvate sepals (with occasional reversions to imbricate) being characteristic of the rest of the family. The range of petal characters which have up to now been preferred by taxonomists are seen to be highly homoplasic and misleading.

Fruit structure in the Annonaceae has been examined in detail by van Setten & Koek-Noorman (1992). Their informal taxonomic groupings are often completely at odds with those of Fries, but emerged intact from the broad-based cladistic analyses of Doyle and Le Thomas (above) – confirming the usefulness of fruit structure for taxonomic and systematic studies of the Annonaceae.

The molecular analyses of Bygrave & Chase (in press) provide an interesting comparison with the data of Doyle and Le Thomas. In most respects the two alternative phylogenies agree. *Anaxagorea* is basal in both groups, with two sub-basal clades encompassing *Tetrameranthus-Cleistopholis-Ambavia* and *Malmea-Sapranthus* emerging just above *Anaxagorea*. *Uvaria*, *Annona*, *Hexalobus*, *Monodora* and *Isolona* are grouped together in a terminal clade in both treatments. *Xylopia* and *Artobotrys* emerge somewhat differently on the two trees, being nested in the *Uvaria* – *Monodora* terminal clade in Doyle and Le Thomas, but emerging in a medial clade with *Fusea* and *Duguetia* below *Uvaria* in the molecular data tree.

The basal position of Anaxagorea in both the palynological and molecular analyses of the Annonaceae provides an interesting link to Eupomatia (Eupomatiaceae), the closest relative of the Annonaceae according to the molecular studies of Soltis *et al.* (1999) and Qui *et al.* (1999). Both *Eupomatia* and *Anaxagorea* have an internal whorl of elongate staminodes which separate the stamens and carpels (*Xylopia* is the only other Annonaceous genus showing this character) (van Heusden, 1992). Endress (1984) reports that these inner staminodes are also sectretory in both *Anaxagorea* and *Eupomatia*, as well as in some taxa in the Himantandraceae and Degeneraceae.

Delimitating the *Uvaria* group

Early classifications of the family (e.g. De Candolle, 1824; Hooker & Thomson, 1855) placed *Uvaria* at the beginning of the phenetic treatment, where its numerous free carpels with many ovules, and spreading, *Clematis*-like petals seemed to represent the most 'simple' floral arrangement in the family. The later phylogenetic interpretations of Sinclair (1955) on the Malaysian Annonaceae, and Fries (1959) on the entire family also placed *Uvaria* in a primitive complex, Sinclair commenting,

> There is a tendency to proceed from simplicity to complexity, e.g. from simple petals with no distinction between blade and claw, to the complex dome-shaped petals of the Mitrephorae ... (p. 169).

This pattern of thinking has led to a variety of genera being associated with *Uvaria* at various times. Only a small subset of these are, in fact, closely related to *Uvaria,* and in the context of this work are referred to as the '*Uvaria* group'. The generic boundaries between this core group and *Uvaria* are ill-defined, and in order to revise *Uvaria* in Continental Asia it is necessary to establish which genera should be included within the core *Uvaria* group. As a starting premise, the *Uvaria* group could be described as;

> The group which includes *Uvaria* and it's closest affiliated genera in a single monophyletic group. The affiliated genera should share most of the more distinctive characters of *Uvaria* such as a climbing habit, stellate hairs, imbricate petals and inaperturate monadal pollen.

Five broadly-based morphological accounts dealing with the Annonaceae were selected as starting point for determining the make-up of the *Uvaria* group; Sinclair (1955), Fries (1959), van Heusden (1992), Kessler (1993) and van Setten & Koek-Noorman (1993). There is considerable variation amongst the various authors as to which genera should be placed within the *Uvaria* group. Sinclair (1955) was concerned only with the Malaysian Annonaceae, and ascribed 9 genera to the group. Fries (1959) attributed 10 genera and c.188 species to the group, van Heudsen (1992) attributed seven genera and c.169 species, whilst van Setten and Koek-Noorman

(1992) placed just six genera and c.165 species. While four genera were included in all the latter three groupings, a later classification by Kessler (1993) included a much greater number, covering 17 genera and c. 204 species. This latter classification, while based on a wider field of taxonomic data, also introduced to the group a number of anomalies. It includes three neotropical genera which might have been excluded from the group on the basis that *Uvaria*, and consequently its closest relatives, was strictly a paleotropical genus (Hutchinson 1964, Cronquist 1982).

Kessler (1993) identified a small number of characters which could be used to distinguish the *Uvaria* group genera from other genera in the Annonaceae. These are: (i) flowers leaf opposed, sometimes terminal; (ii) petals imbricate; (iii) ovules several, lateral; (iv) stellate hairs often present. However he also noted that the enormous amount of reticulate distribution of primitive and advanced characters and paralellelism makes it very difficult to assess evolutionary relationships and establish monophyletic tribes within the Annonaceae. He further states that 'it seems much better to arrange the genera only in informal groups than in formalised supra generic taxa', echoing the views of Sinclair. This approach was also adopted by van Heudsen (1992) and van Setten and Koek-Noorman (1993). However, despite this unity of thinking, the practical application of these ideas varied greatly between the authors; for example, genera from no less than 9 of van Heusden's Annonaceae groups are included in the Kessler *Uvaria* group.

It seems clear that some of the genera listed by the above authors (Table 1.2) appear to have weaker morphological affinities for the *Uvaria* group than others. In *Hexalobus*, for instance, the petals are transversely folded in the bud. *Tetrameranthus* has a spiral phyllotaxy (unique in the family) and a 4-merous perianth while *Toussaintia* has 6-20 petals in 2-3 series and a prominently elongate torus. Ovule number and placentation and seed structure show considerable variation also. *Anomianthus*, *Balonga*, *Cyathostemma*, *Ellipeia*, *Melodorum*, *Rauwenhoffia*, *Tetrapetalum* and *Uvaria* all have several ovules inserted in two lateral rows, and a smooth testa on the mature seed. *Ellipeiopsis* shares this seed structure, however the single ovule is apically inserted - a rare feature in the family. *Hexalobus*, *Sagaraea*, *Sapranthus*, *Stelechocarpus*, *Stenanona*, *Afroguatteria* and *Enicosanthum* all have a transversely striate testa, and in *Enicosanthum* the single ovule is basally inserted.

Stamens and carpels are typically very numerous in the group, but *Dasoclema* (G_1), *Hexalobus* (G_{3-12}), *Dendrokingstonia* (G_1, A_{9-12}) and *Sagaraea* (G_{2-10}) are all characterised by a reduction/limitation in carpel (and stamen) number. At a superficial level it seems that morphological anomalies are just as common as morphological similarities within the pooled *Uvaria* group of the various authors.

Recent family-wide work on pollen ultrastructure (Doyle & Le Thomas, 1994, 1996) and rbcL sequence data (Bygrave and Chase, unpubl.) provides convincing evidence that many of the apparent affinities which unite the pooled *Uvaria* group are misleading. In particular it indicates that *Uvaria* is not a basal member of the Annonaceae, but belongs to a more derived lineage. In this revised scenario, the floral and fruit characteristics of the genus could still be regarded as being 'primitive', however Doyle and Le Thomas (1996) indicate that there are clear morphological patterns associated with pollen type. Examination of these trends makes it clear that morphological features which were once thought of as primitive in *Uvaria* are in fact derived.

Significantly, both sets of analyses also provide strong evidence that the *Uvaria* groups of Kessler and Fries are polyphyletic and involve the grouping of genera which are similar by convergence rather than uniquely shared ancestry. The groups of van Setten and Koek-Noorman (based on fruit structure) and van Heusden (based on floral structure) are better supported, particularly by the molecular data.

In the molecular study of Bygrave and Chase the terminal clade which contains *Uvaria* includes 15 taxa not included in the analysis of Doyle and Le Thomas, and with a few exceptions, all are African/Asian climbing genera. In terms of the present work, the most significant result of the rbcL analysis is that *Uvaria* emerges within a well-supported clade that includes *Melodorum*, *Cyathostemma*, *Anomianthus* and *Ellipeiopsis*. All these genera have stellate hairs and biseriate placentation. *Ellipeiopsis*, *Melodorum* and *Cyathostemma* (*sensu stricto*) have partially imbricate petals, while in *Uvaria* (*s.s.*) the petals can be either fully or partially imbricate. The sister group of this *Uvaria* clade includes the Paleotropical climber genus *Friesodielsia*, the Asiatic climbers *Dasymaschalon* and *Desmos*, and the African

climber *Monanthotaxis*. All the taxa of this sister group have valvate, membranous petals, simple hairs and uniseriate placentation.

Monanthotaxis is the only genus from this large terminal clade which is also included in the surveys of Doyle and Le Thomas. Significantly, in their combined analysis of pollen and morphological data, *Monanthotaxis* emerges as the sister group of *Uvaria*. Given that none of the other genera in the terminal clades of Bygrave and Chase are included in the palynological analysis, the clustering of *Uvaria* and *Monanthotaxis* matches the pattern seen in the molecular results.

In summary, when all the evidence is accounted for from van Heusden (1992), van Setten & Koek-Noorman (1993), Doyle and Le Thomas (1994, 1996) and Bygrave & Chase (unpubl.), and these data are assessed according to the starting precept stated above, the core *Uvaria* group includes the following genera; *Uvaria*, *Anomianthus*, *Afroguatteria*, *Balonga*, *Cyathostemma, Ellipeia, Ellipeiopsis*, *Rauwenhoffia* and *Tetrapetalum. Melodorum* is somewhat more distantly related.

For the purposes of this revision, only the genera of the core *Uvaria* group occurring in Continental Asia are being considered, ie. *Anomianthus*, *Cyathostemma*, *Ellipeia*, *Ellipeiopsis*, *Rauwenhoffia* and *Uvaria*. Excluded from consideration on the basis of geographic distribution are *Afroguatteria* and *Balonga* (African genera) and *Tetrapetalum* (restricted to the Sunda Islands). *Melodorum* is excluded because it is not part of the core group.

Table 1.2. Composition of *Uvaria* Group (excluding *Uvaria* L.) according to various authors based on morphological, pollen and rbcL data

Genus Name		Geographic. Region	Morphological Group[1]	Uvarioid Pollen[2]	*Uvaria* clade rbcL[3]	No. of species
Tetrapetalum Miq.	§	SE Asia	a,b,c,d	-	-	2
Ellipeia Hook f & Thomas	§	SE Asia	a,b,c,d,e	-	-	5
Ellipeiopsis R.E.Fries	§	SE Asia	a,b,c,d	-	yes	2
Anomianthus Zoll.	§	SE Asia	a,c,d	-	yes	1
Cyathostemma Griffith	§	SE Asia	c,d,e	-	yes	8 (5)
Rauwenhoffia Lour.	§	SE Asia	b,d,e	-	-	3 (1)
Balonga Le Thomas	§*	Africa	c,d,e	-	-	1
Afroguatteria Bout.	§*	Africa	a,b	yes	-	1
Melodorum Lour.	†	SE Asia	c	-	yes	5
Dasoclema Sincl.		SE Asia	c	-	-	1
Sagaraea Dalz.		SE Asia	b,e	-	-	9
Stelechocarpus (Bl.) Hook. f. & Thoms.		Asia	b,e	-	no	5
Enicosanthellum Ban.		Asia	b	-	-	2
Enicosanthum Becc.		Asia	b,e	-	no	16
Cleistophilis Pierre ex. Engl.		Africa	b	no	no	4
Greenwayodendron Verdc.		Africa	b	no	no	2
Toussaintia Boutique		Africa	a,b	-	no	3
Mkilua Verdc.		Africa	b	no	no	1
Dendrokingstonia (H. f & Th.) Raus.		Africa	b,e	-	-	1
Hexalobus A.DC.		Africa	b	no	no	5
Sapranthus Boutique		S. America	a,b	no	no	10
Stenanona Stanley		S. America	a,b	-	-	2
Tetrameranthus R.E. Fries		S. America	b	no	no	2
Desmopsis Safford		C. America	a	-	-	16
Mischogyne Excell		Africa	a	-	-	

Key: § retained as members of '*Uvaria* group' in this thesis; * African *Uvaria* group; † Asian affiliate of *Uvaria* group; Group[1] a - Fries (1959), b - Keßler (1993), c - Van Setten & Koek Noorman (1993), d - Van Heusden (1992), e - Sinclair (1955). Uvarioid Pollen[2] from Doyle & Le Thomas (1996); *Uvaria* clade rbcL[3] from Bygrave & Chase (in press).

Ecology, Utility and Biogeography of *Uvaria* and the Annonaceae

Ecology of the Annonaceae

The Annonaceae are almost exclusively a lowland tropical family, the one exception being the North American Genus *Asimina* which extends as far north as the Great Lakes. All members of the family are evergreen and woody, however in certain genera (e.g. *Ellipeiopsis*) an annual shrubby growth habit is observed. In tropical America the family is common in wet closed-canopy forests and open dry savannah (Reiner, 1998), while in Africa and Asia it is mostly restricted to wetter closed-canopy forests (Le Thomas, *pers. comm.* & *pers. obs.*). In some areas taxa are recorded from higher altitudes, for example *Annona cherimola,* which occurs at elevation up to 2,600 m in the northern Andes (Maas, 1998), and *Phoenicanthus coriaceae* which grows at altitudes up to 1,800 m in Sri Lanka (Huber, 1985). The largest tree in the family is probably *Mezzetia leptopoda*, which reaches a height of 40 m in the lowland forests of Peninsular Malaysia. *Polyalthia*, *Xylopia*, *Goniothalamus*, *Cyathocalyx* and *Alphonsea* (among others) have many arborescent species reaching over 20 m in height. Erect shrubs are common throughout the family's range, however scandent shrubs and climbers are mostly palaeotropical. The family contributes significantly to overall species abundance in lowland rainforest ecosystems, particularly in the middle strata (Boutique, 1951; Le Thomas, 1969; Foster, 1990; Kessler & van Heusden, 1993), however in other tropical ecosystems they are much less prominent.

Annonaceae fruits are staple for many frugivorous mammals and birds (Van Roosmalen, 1985), while the flowering cycle of many species is closely correlated with the reproductive behaviour of Coleoptera (Gottsberger, 1977, 1988). Most flowers are sweet-smelling, however many also smell of decaying flesh and fodder. In most genera some form of pollination chamber is created by a connivance of the inner whorl of petals (Fig. 1.4) and the rigidity of the petal alignment and/or the narrowness of the aperture between the inner petal bases plays a key role in selecting the size of beetles and/or other insects which can enter the chamber. Many genera also exhibit

more open or spreading petals where the physical selection barrier is not present. Pollinator reward is offered mostly in the form of soft, sugar-rich and lipid-rich tissue at the petal bases, particularly on the inner whorl. These tissues are normally browsed upon by beetles with large, chewing mouthparts. Cockroaches and Drosophilid flies have been recorded as the main pollinators of certain *Uvaria* species (Nagamitsu & Inoue, 1997), feeding on stigmatic exudates and pollen. Gottsberger *et al.* (1998) suggest that tissues with high lipid and sugar content also play a part in nocturnal thermogenesis which enhances odour release and attracts thermophilic insects. In genera with membranous petals (particularly) the petal bases also appear to be secretory. Certain genera, including *Uvaria*, do not appear to have secretory or fleshy petals and offer reward to pollinators in the form of edible pollen and nectar.

Endress (1994) records that most Annonaceae are self-compatible and protogynous with a distinct neutral phase between the female (first) and male phase. In tropical species of *Asimina* the female phase lasts between two and six days, the male phase lasts just one day and there is a neutral phase (one day) in between (Norman & Clayton, 1986). In *Cananga odorata* the flowering cycle is much more compressed. Floral scents are released 24 hours before the onset of the female phase at sunset, however by sunset the following evening the cycle is complete and anthesis occurs (Deroin, 1988). Field and herbarium observations undertaken for this research suggest that Uvaria and its relatives are also protogynous (*Rauwenhoffia siamensis* has clear female and male phases), however no records have been made on self-compatibility or the timing of the flowering cycle.

Origin and Radiation of the Annonaceae

Data derived from studies of palynological (Walker, 1971; Le Thomas, 1981; Walker & Walker 1984) and paleontological (Raven & Alexrod, 1974; Schuster, 1976) data appear to suggest that West Africa-Amazonia is the most probable locus of origin for the Annonaceae, possibly while the two continents were still joined as West-Gondwanaland (before c. 100 m.y. BP). Geographical radiation of the family from this locus has probably followed several different routes and taken place over several

distinct periods of time, giving rise to regional Annonaceous floras which constitute elements from a variety of disparate migrations.

For example, the North American Annonaceae appear to constitute two distinct elements; a tropical one which spread from South America from the late Eocene onwards, and a temperate one (including *Asimina* and *Deeringothamnus*) which has an African affiliation (Walker 1971, 1972). Raven & Axelrod (1974) suggest that these temperate elements reached North America via Europe before the Eocene, when Africa and Eurasia were closely aligned about 20° north of the equator.

Raven (1979) has hypothesised that the proximity of Northern Africa and Southern Europe facilitated a prolonged period of biotic migration between the two continents for much of the Paleocene. This Africa-Europe migration pathway is believed to have introduced many formerly West-Gondwanic elements to Eurasia (Raven & Axelrod, 1974). Much of the southern coastline of Eurasia experienced a moist equable climate during this period, and this might explain how the Annonaceae came to be quite diverse in tropical Eurasia (from England eastward) by the Eocene , c. 55 m.y. B.P. (Chandler, 1964).

However, a second great migration from Africa to Asia is believed to have taken place with the collision of India into southern Asia c. 45-55 m.y. BP (Patriat & Achache, 1984; Morley 1999). This 'rafting' of biota across the Indian Ocean brought a large number of African-Indian taxa that had hitherto been absent from Asia. These predominantly tropical taxa spread and diversified through the Asian landmass and became prominent features of the Southeast Asian and Sunda Islands floras (Morley, 1998). However, climate changes over the last 1-5 million years has resulted in many of these taxa, for example *Durio* (Bombacaeae) and *Eugeissonia* (Arecaceae), being reduced or eliminated from India (Baker *et al.*, 1998; Holloway & Hall, 1998; Morley, 1998).

A hypothetical example of Indian immigrant taxa shifting eastward to Indochina and Malesia is provided Ridder-Numan (1995, 1998). She has hypothesised that the climbing genus *Spatholobus* (Leguminosae-Papilionoideae) and its ancestors arrived in Southern and Southeast Asia via India, and later spread to Malesia. Once in

Malesia, successive periods of sea level and climatic change resulted in the rapid radiation of the genus throughout the archipelago. Today there are relatively few representatives of the genus in India, however the Southeast Asian and Malesian taxa are much more diverse. A major pillar of this hypothesis is the fact that fossil Leguminosae only appeared in East Asia in the Eocene, whereas they are clearly evident before this time in the fossil record of India. The Dipterocarpaceae show a similar fossil pattern (Morley, 1998).

Morley (1999) reports that Annonaceous-type pollen is evident in India from the Paleocene (c. 60 m.y. B. P.), before its collision with mainland Asia. This would suggest a dual migration route for the family from Africa into Asia, via the North Africa - Southern Europe route and via the the Africa - India route. However, present understanding of the distribution and ecological preferences of the Annonaceae suggests that whatever the composition of the Annonaceae in India prior to the late Tertiary, it seems probable that much of the family disappeared from the subcontinent during the drying events of the Quaternary - and this makes it more difficult to determine the true affiliations of the surviving Indian Annonaceae.

In general, the Annonaceae are much less diverse in India than in Southeast Asia. There are no Annonaceous genera endemic to India, and many smaller Southeast Asian genera are completely absent from the subcontinent (for example *Phaeanthus*, *Ellipeia*, *Dasoclema*, *Disepalum*). There are no known Annonaceae species or genera which are present in Africa and India but not in Southeast Asia/ Malesia, whereas several large genera exhibit an Africa-India-Indochina-Malesia distribution (e.g. *Uvaria*, *Artabotrys*, *Polyalthia*). Unfortunately, these patterns make it difficult to unravel the history of the family beyond its arrival in Asia from Africa. All that can be concluded is that the Asian Annonaceae may be derived from two separate migration events.

Contemporary Habitat Preferences of the Annonaceae in Tropical Asia

Current Distribution

The present distribution of *Uvaria* in Continental Asia closely follows that of the Annonaceae as a whole. The range of the genus includes the entire areas of Thailand, Cambodia, Laos, Vietnam and Myanmar, and the provinces of Yunnan, Kweichow, Guandong, Guangxi and Hainan in China (Figure 1.1). The genus also occurs in the tropical areas of India, including the Andaman and Nicobar Islands, from the Gulf of Cambay in the west to Assam in the east. *Uvaria* is absent from the semi-desert region in Northwest India (Rajastan) and the montane Himalayan areas in Assam, Sikkhim, the Punjab and Kashmir. The southernmost distribution of the genus in the region is in Sri Lanka, 6° North of the equator. The political divisions of the region are shown in Figure 1.9.

The current distribution of the Annonaceae (and other moisture-loving tropical taxa) in Continental Asia is overwhelmingly influenced by the monsoonal climate systems which dominate the region (Figure 1.10) (Lauer, 1989). The family is almost entirely restricted to lowland areas of high rainfall where there is no period of prolonged drought (i.e. greater than 5-6 months per year). Unlike their relatives in Africa and South America, the Annonaceae of Asia are not characterised by an ability to cope with water stress and only a few species, such as *Polyalthia cerasoides* (deciduous tree) and *Ellipeiopsis ferruginea* (annual or perennial shrub) show any real resilience under water-stress conditions.

The real measure of drought/ water deficit is most accurately defined in terms of soil moisture, for both high and low rainfall areas can contain dry and wet soils respectively. For example, Annonaceae are often found in gallery forests of the river valleys which cut west-east across the dry eastern half of the Deccan Peninsula – despite their complete absence from the arid hinterland (Saldhana & Nicholson, 1976; Matthew, 1983). Equally, shallow free-draining soils in Indochina are unlikely to support any Annonaceae in all but the highest rainfall areas (*pers. obs.*).

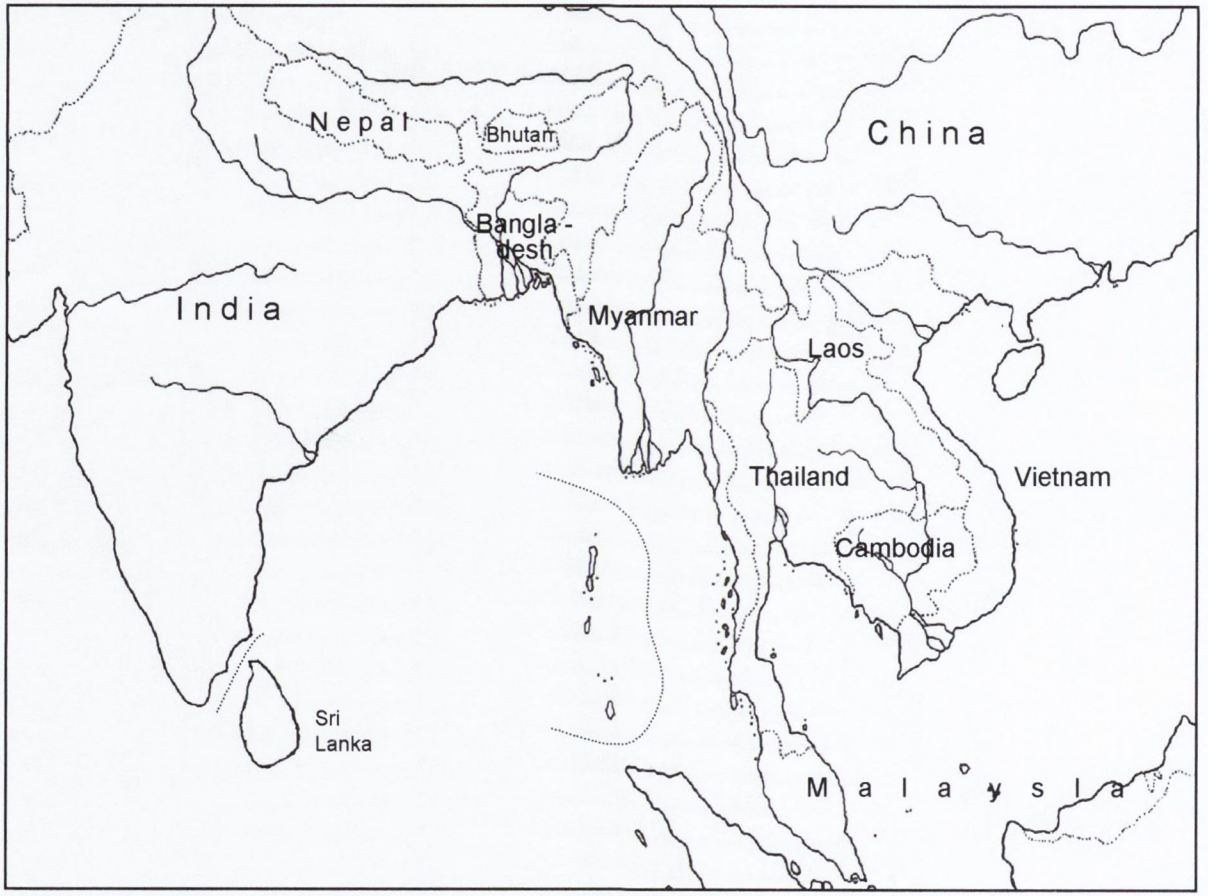


Figure 1.9. South and Southeast Continental Asia - Political Boundaries.

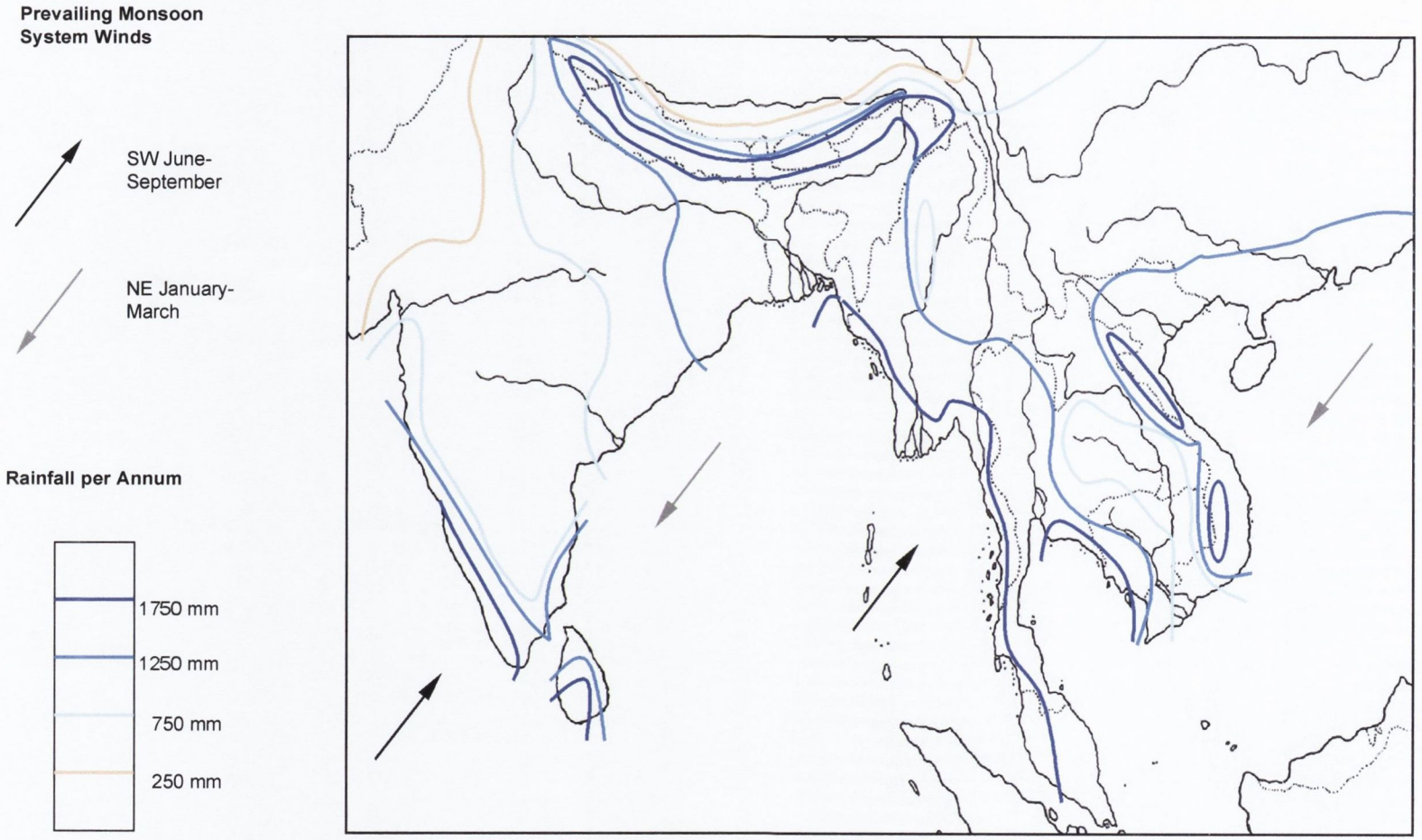


Figure 1.10. Monsoon weather systems and mean annual rainfall in South and Southeast Asia.

Climate of Continental Asia

The moist tropical climatic zone extends to 26° N in Continental Asia, farther north than anywhere else in the Northern Hemisphere (Lauer, 1989). There are two main factors causing this phenomenon. Firstly, there are two monsoons per year, a south-west (summer) monsoon in June-September, and a north-east (winter) monsoon in January-March (Vidal, 1979; Lauer, 1989; Sumithraarachchi, 1989). The summer monsoon blows in from the Indian Ocean and carries large volumes of rain over the Indian subcontinent and Southeast Asia. The winter monsoon is less moist, gathering moisture from the Bay of Bengal and the South China Sea, however it ensures winter rainfall for many areas on the eastern coast of India, Sri Lanka, the upper Malay penninsula, Indochina and in southern China (Figure 1.10). The second factor contributing to the enlarged wet-tropical zone is the Himalayan Massif, which extends from North West India and Pakistan to Assam, with splinter chains spreading east and south from here into Southern China and Southeast Asia (Figure 1.11). These ranges precipitate most of the moisture contained in westerly, southerly and easterly aircurrents, ensuring that moist soil conditions prevail throughout the region for much of the year.

As a result of these moisture patterns, the characteristic arid deserts which lie north and south of the wet tropical belt in Africa, America and Australia are much reduced along these same latitudes in East Asia. Indeed in Rajastan, northwest India, there is a clear north-south boundary between a typical hot desert system (the Persian arid zone) and the wet tropical system prevalent over India and Southeast Asia. In the east there is a near-continuous gradation from a wet tropical climate in Southern China through to subtropical and temperate climate zones farther to the north. North of the Himalayas we see a different climatic boundary, with a sharp transition into cold rain-shadow desert on the Tibetan plateau.

Indian Subcontinent

The extremes of wet and dry are more intense in the Indian subcontinent than in Southeast Asia. In Sikkhim, Bhutan and Assam rainfall can be as high as 8000 mm

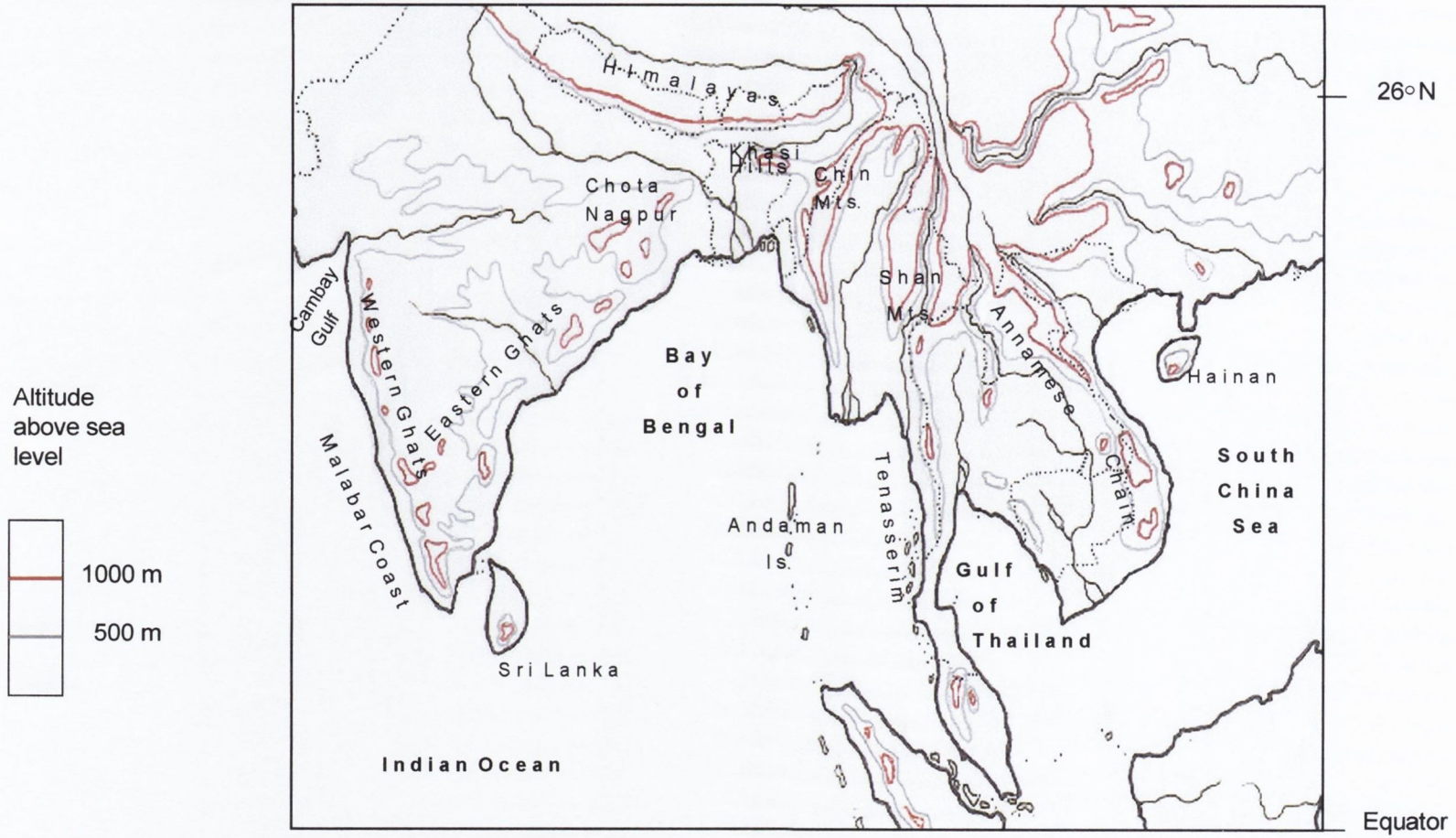


Figure 1.11. Physical features of South and Southeast Continental Asia.

per annum (Lauer, 1989; Walsh, 1996). Alternately, in regions such as western Madhya Pradesh and central Maharashtra and Karnataka, there is a distinct winter dry season and annual precipitation can be as low as 300-500 mm (Saldhana & Nicholson, 1976). This reduced rainfall is caused by a rain-shadow in both monsoons. In the summer monsoon, the Western Ghats along the Malabar coast intercept most of the rainfall, whereas in the winter monsoon, the few clouds that do move in from the Bay of Bengal are intercepted by the Eastern Ghats in Andhra Pradesh and the Chota Nagpur plateau in Bihar (Hooker & Thomson, 1855). The more elevated regions of the central peninsula such as Bihar, Orissa, and eastern Madhya Pradesh are more moist, while the western Malabar coast is extremely wet, receiving between 3000 and 5000 mm of rainfall annually (Hooker & Thomson, 1855; Brandis, 1921; Lauer, 1989). The Gangeatic plain is also very moist, receiving heavy rains in the summer monsoon and extensive runoff from the Himalayas throughout the rest of the year.

Sri Lanka is more open than the Peninsula to both the Indian Ocean and the Bay of Bengal and receives continuous rainfall for most of the year. The low-lying northern plains are the driest, receiving between 800 and 1000 mm of rainfall per annum, however the central mountains and southwest coast receive between 2500 and 4000 mm (Sumithraarachchi, 1989). Rajastan, in Northeast India, is the driest part of the subcontinent, receiving less than 250 mm of precipitation per year, all of it during the summer monsoon (Hooker & Thomson, 1855; Brandis, 1921).

Indo-Chinese Region

The climate of Indochina is dominated by the same summer and winter monsoons as India. There are three belts of lowland in the region where rainfall is plentiful for 9-10 months of the year (Jovet-Ast, 1942; Vidal, 1979; Rundel & Boonpragob, 1995). The first extends from Chittagong in Bangladesh along the west coast of Myanmar as far as Taninthari (Tenasserim), and continues south through Thailand to Ranong and Satun. The second comprises the mountain system which extends from Chanthaburi in Southeast Thailand to Pursat in Western Cambodia. Both of these belts receive substantial rainfall throughout the summer monsoon with only one or two months of dry weather in January-February. Mean annual precipitation in the west Myanmar and

Chanthaburi-Pursat belts is greater than 3,000 mm per year, with some parts of Taninthari and Trat receiving over 4,000 mm. The third area of high precipitation is the mountainous region of Annam in central Vietnam where rainfall averages 2,500-3,000 mm per year. The North-East winter monsoon predominantes in this system, with heavy rainfall coming inland from the Gulf of Tonkin and the South China Sea between September and February. Lower rainfall also occurs in the June-September monsoon.

Moderate rainfall (c. 1500 - 2000 mm per annum, Vidal, 1979) occurs across the mountainous belt that extends from eastern Myanmar through Yunnan, Northern Thailand, Laos, and Northern Vietnam (Figure 1.11). The massif is cut at regular intervals by large north-south flowing rivers, including the Sulween (Myanmar), the Mekong (Yunnan-Laos) and the Da (Vietnam). The plateau is highest in northeast Yunnan (highest peaks 5,500 m) and becomes gradually lower through Myanmar (4,500m), Vietnam (3,143 m), Laos (2,817 m) and Thailand (2,560 m). Much of this region has a sub-alpine or temperate climate, however the slopes and valleys below 1,250 m grade quickly into sub-tropical and tropical forest systems.

There are two distinctly dry areas in the region. The largest extends from northeast Thailand through the southern tip of Laos, central Cambodia and into southernmost Vietnam. A smaller isolated dry region occurs in central Myanmar between the Chin and Shan mountains (Vidal, 1979; Rundel & Boonpragob, 1995). As in the Deccan province of India, the dry climate of these regions is caused by rain shadow during both monsoons. In Indochina, the Chanthaburi-Pursat chain absorbs most of the rain coming in from the Southwest monsoon, whereas in winter the Annamite and Laotian mountains receive nearly all the moisture coming in from the South China Sea. In central Myanmar the Chin mountains intercept most of the rainfall coming with the summer monsoon, and the northeast winds in winter bring only dry air from continental China. In both these dry areas rainfall is in the region of 750 to 1,250 mm per year. Most of this comes in the summer monsoon, with less than 100 mm falling the five months between November and April.

Forest Vegetation Types

Tropical vegetation structure and composition is strongly influenced both by the mean annual amount of rainfall and the seasonality of this rainfall (Lauer, 1989), and these rainfall patterns, in combination with varying soil conditions, result in the development of many different tropical forest types. The perhumid climatic regime (producing year-round rainfall/ soil-water availability) which gives rise to humid lowland rainforests generally occurs in the regions immediately north and south of the equator, however the presence of favourable climatic elements allows lowland rainforest vegetation to extend up to and occasionally beyond the tropics of Cancer and Capricorn (Whitmore, 1984, 1989; Lauer, 1989; Walsh, 1996). Adjoining these areas of lowland rainforest are evergreen and seasonally dry forest areas which experience either a lower level of overall rainfall/ soil water-availability or a marked seasonality in rainfall/ soil-water availability compared with rainforest areas (Vidal, 1979; Whitmore, 1984; Rundel & Boonpragob, 1995). The causes of these variations in rainfall and soil-water availability are diverse, and involve a combination of prevailing climatic conditions, topographic influences, soil type and groundwater availability (Brinkmann, 1989; Lauer, 1989; Sanchez, 1989; Rundel & Boonpragob, 1995).

Evergreen forests

With the exception of Southwestern Sri Lanka, lower Peninsular Thailand and Annam, which experience more or less perhumid climatic conditions, most of the areas in Continental Asia which are covered with lowland tropical rainforest experience some form of dry season with a reduced level of rainfall (Hooker & Thomson, 1855; Kurz, 1877; Vidal, 1979; Sumithraarachchi, 1989; Rundel & Boonpragob, 1995) - however rainforest vegetation persists in these areas because the annual dry period is never sufficiently long or arid enough to result in a significant drying of the soil. Lowland rainforests occur from sea-level up to 200 m and typically experience 1500 mm+ rainfall per annum (Whitmore, 1984, 1989; Walsh, 1996).

Lowland rainforests in Asia are characterised by a closed canopy between 30 and 45 m high which is overtopped by a scattered emergent layer 40 - 55 m high (Vidal,

1979; Whitmore, 1984; Kira & Yoda, 1989; Richards, 1996). Beneath the closed canopy is a multi-stratified sub-canopy layer composed of juvenile canopy and emergent species and mature sub-canopy species. Lianas, palms and epiphytes are also abundant in this layer. The ground flora is relatively poor and is dominated by shade-tolerant Zingiberaceae, Araceae, Orchidaceae and shrubby Arecaceae. The canopy layers contain a diverse array of evergreen tree species, including Dipterocarpaceae, Myristicaceae, Lythraceae, Lamiaceae, Myrtaceae, Anacardiaceae, Sapotaceae, Moraceae, Leguminosae, Euphorbiaceae and Sterculiaceae (among others) (Hooker & Thomson, 1855; Kurz, 1877; Brandis, 1921; Parkinson 1923; Vidal, 1979; Whitmore, 1984; Takhtajan, 1986; Sumithraarachchi, 1989).

The Annonaceae are most abundant and diverse in this habitat. In Sri Lanka, for example, 19 (or 56%) of the 34 native species of Annonaceae are confined to this habitat, while a further 5 species (or 15%) extend into other forest types (Huber, 1985). Common Annonaceae trees in lowland rainforests of Continental Asia include *Polyalthia*, *Mezzetia*, *Xylopia*, *Miliusa*, *Goniothalamus*, *Mitrephora*, *Pseuduvaria* and *Orophea*. Common climbers include *Uvaria*, *Cyathostemma*, *Dasymaschalon*, *Desmos*, *Fissistigma* and *Artabotrys*, while several *Polyalthia* species form part of the scant shrub layer.

Dry evergreen forest occurs in moist, deep soils of the lower hills from 200 to 500 m altitude and along many watercourses in the drier lowlands (Rundel & Boonpragob, 1995). The canopy is usually dominated by evergreen species, with *Hopea* and *Dipterocarpus* spp. being the most important, however deciduous species can also be present on drier sites. As in lowland rainforest, the understory is well-developed with an abundant growth of lianas, palms and epiphytes. Shade tolerant monocots predominate in the sparse ground flora, with orchids, zingibers, shrubby palms and bamboos all relatively common. Common Annonaceae trees include *Polyalthia*, *Cyathocalyx*, *Xylopia*, *Miliusa*, *Orophea* and *Pseuduvaria* spp. Common lianas include *Anomianthus*, *Artabotrys*, *Cyathostemma*, *Desmos*, *Dasymaschalon*, *Fissistigma*, *Melodorum*, *Rauwenhoffia* and *Uvaria* spp. Rainfall in these forests is typically 1200-1500 mm per annum, however unlike deciduous forests, this rainfall is spread more or less evenly throughout the year (Vidal, 1979; Rundel & Boonpragob, 1995).

In many areas dry evergreen forests intergrade with mixed deciduous forests and hill evergreen forests, and this association can result in very high amounts of overall species diversity on hillsides between 300 and 1,000 m (e.g. Elliot *et al.*, 1989). The extent of the dry season has a great influence on the distribution of species within these forests, and the increase in precipitation associated with increase in altitude means that moisture-loving species often appear on lower mountain slopes and valleys when they are absent from the plains below (*pers. obs.* at Thung-Yai Naresuwan, Doi Suthep, Doi Inthanon).

Hill evergreen and montane forests occur at elevations above 1,000 m, and are characterised by the presence of many holarctic/ temperate elements. Tropical groups are largely absent from these forests - most noticably the Dipterocarpaceae, but also absent are, for example, the Moraceae and Annonaceae. Magnoliaceae, Fagaceae, Podocarpaceae and Pinaceae become progressively more dominant with increasing altitude (T. Santisuk, *pers. comm.*; Vidal, 1979; Rundel & Boonpragob, 1995). Above 2,000 m these forests are almost entirely temperate in character, with a deciduous canopy and an abundant ground flora composed of ferns, mosses, orchids, grasses and sedges (*pers. obs.* at Doi Inthanon and BaVi).

Deciduous Forests

Most parts of tropical Continental Asia experience a dry season which results in a partial drying of the soil, and forests in these areas are characterised by the presence of deciduous canopy species, particularly *Shorea*, *Hopea* and *Dipterocarpus* spp. (Dipterocarpaceae). Other widespread tree species include *Tectona grandis* and *Vitex* spp. (Verbenaceae), *Garcinia* spp. (Clusiaceae), *Myristica* spp. (Myristicaceae), *Diospyros* spp. (Ebenaceae), *Lagerstroemia* spp. (Lythraceae), *Terminalia* spp. (Combretaceae), and *Afzelia*, *Xylia* and *Pterocarpus* spp. (Leguminosae) (Saldhana & Nicholson, 1976; Vidal, 1979; Bunyavejchewin, 1983; Sumithraarachchi, 1989; Rundel & Boonpragob, 1995; Parthasarathy & Sethi, 1997).

There are several forms of deciduous forest. The most floristically diverse of these is the 'mixed deciduous' type, characterised by a diverse evergreen element in the forest canopy. These forests occur in areas with a mean annual rainfall of 1400-1800 mm, with 5-6 dry months (Rundel & Boonpragob, 1995). The canopy of mixed forests can reach 35 m in height, and on wetter sites there are well-developed understory and shrub layers, the latter usually dominated by various bamboo species and shrubby palms (*pers. obs.*; Vidal, 1979; Bunyavejchewin, 1983; Rundel & Boonpragob, 1995). Annonaceae are reasonably common in mixed forests that adjoin evergreen gallery forest, however the overall abundance and diversity of the family is lower in this vegetation type than in evergreen forest. *Polyalthia* and *Cyathocalyx* spp. are the only trees of note, while *Uvaria*, *Desmos*, *Fissistigma*, *Artabotrys*, *Rauwenhoffia* and *Anomianthus* are the most common lianas. *Ellipeiopsis ferruginea* and a few *Polyalthia* spp. are common shrubs.

In areas where the dry season extends beyond 6 months of the year, deciduous Dipterocarp species become progressively more dominant in the canopy and sub-canopy layers. These Dipterocarp-dominated forests are highly variable in structure, and range from the 'deciduous Dipterocarp' forest type characterised by a closed canopy and a sparse understory, to the 'open' or 'dry' Dipterocarp forest type, characterised by scattered stunted canopy trees and a diverse shrub understory (*pers. obs.*; Vidal, 1979; Bunyavejchewin, 1983; Rundel & Boonpragob, 1995). Fire is a major influence on vegetation structure in these forests, and the ground flora of the open/ dry forest types is dominated by fire-tolerant shrubs and annuals. In the driest parts of tropical Continental Asia, for example the Deccan plateau, north-central Myanmar and central Indochina, the drier deciduous forests grade into dry thorn scrub and open savanna (Salandha & Nicolson, 1976; Vidal, 1979; Bunyavejchewin, 1983; Rundel & Boonpragob, 1995). The only Annonaceous species of note in these forests are *Ellipeiopsis ferruginea*, a common shrub in deciduous Dipterocarp forests in Indochina and *Polyalthia cerasoides*, a deciduous tree which occurs in similar habitats in India.

Secondary Formations

Throughout most of Continental Asia the various forms of tropical forest form a complex mosaic of vegetation, with one form grading into another as a result of differences in rainfall, drainage and fire conditions. However, human disturbance over the last 75 years has meant that much of the remaining forests are typically a mosaic of isolated undisturbed patches and more extensive tracts of degraded open/dry dipterocarp forest adjoining agricultural land (*pers. obs.*; S. Suddee *pers. comm.*; Sternstein, 1976; Vidal, 1979; Rundel & Boonpragob, 1995). The distribution of many Annonaceae species has been reduced as a result of anthropogenic disturbance, particularly those species which are characteristic of understory vegetation in evergreen forests. However, Annonaceae species which are typical of disturbed secondary forest formations have become more common, particularly in the case of opportunistic liana species of *Uvaria*, *Artabotrys*, *Fissistigma* and *Desmos* (*pers. obs.*; Huber, 1985).

Floristic Divisions

The wet-tropical region of Continental Asia can be divided into two distinct floristic regions – a western region comprising the Deccan Peninsula, Sri Lanka, Bengal and Assam ('Indian Subcontinent'); and an eastern region comprising Myanmar, the Andaman Islands, Indochina and Southern China ('Indochinese region') (Takhtajan, 1986). The Rajastan Desert and Himalayan Massif constitute clear phytogeographic borders on the western and northern extremities of the Indian floristic region. Takhtajan (1986) identifies the Chin-Manipur range on the India-Myanmar border as the boundary between the Indian and Indochinese Regions. Van Steenis (1950) identified the Isthmus of Kra as the floristic division between Indochina and Malesia, however in reality there is a gradation between the two which begins in Narathiwat - Satun in the south and ends in Kanchanaburi – Tavoy in the North. For the purposes of this work, the Thai-Malay border is being used as the southern boundary for the Indochinese Region. In southern China there is a gradation from lowland moist-tropical forest to lowland moist-temperate forest on the northern borders of Guandong and Yunnan Provinces, and in the central parts of Kweichow Province (Whitmore,

1987; *pers. obs.* herbarium labels). The northern borders of these Provinces are selected in this work as convenient boundaries for the wet-tropical zone.

Utility of Annonaceae

The only Annonaceae which are widely exploited commercially are the Annonas, collectively referred to as Cherimoyai and Guanbanai in South America (where they originate) and 'custard apples' in the English-speaking horticulture trade. Their aggregate fruits are common in marketplaces throughout the tropics and they have been cultivated the Palaeotropics for over 300 years (as recorded in Burmann's 1737 *Thesaurus Zeylanicus*). In most parts of Africa and Asia Annonas have derived colloquial names containing the stem 'non'. *A. suamosa* (sweetsop, custard apple), *A. muricata* (soursop), *A. reticulata* (bullock's heart, sugar apple) and *A. cherimola* (cherimoya, custard apple) are the most widely planted species (Morton, 1981; Mabberly, 1997) with *A. cherimola* cultivated as far north as coastal Andalusia in Spain. Breeding experiments are under way in many locations to modify the texture, flavour and shelf life of these fruits in order to facilitate wider commercial exploitation. *Rollinia*, a sister genus to *Annona* with the same aggregate fruits is also cultivated in the neotropics.

Annonaceae are extensively used in traditional medicine, and the efficacy of many herbal preparations has stimulated extensive pharmacological investigations of the ethereal oils contained in root, bark and leaf extracts. In recent years more than 250 constituents have been identified in the essential oils of Annonaceae, and dozens more are added each year – many of them unique to the family and to individual species. Benzoic acids and a wide variety of acetogenins are the most frequently identified active compounds in the various tissue extracts.

Leaf, root and bark extracts from *Uvaria* species have been shown to demonstrate significant anti-malarial activity (Nkunya *et al.*, 1991), anti-bacterial and anti-fungal activity (Padmaja *et al.*, 1993), anti-herpes simplex activity (Silva *et al.*, 1997), anti-house dust mite activity (Raynaud *et al.*, 2000) and anti-tumour activity (Yu, 1999). Acetogenins from other genera in the family have shown promising cytotoxic and

anticancer properties, and a very specific antiprotozoal action against the Leishmania and Trypanosoma species responsible for the widespread Leishmaniasis and Chagas diseases (Chatrou *et al.* 1997).

Other recorded uses for Annonaceae in traditional medicine include treatments against fevers, dysentery, worms, venereal diseases, tuberculosis, epilepsy, and rheumatism. They are also used as antitussives, liver protectives, antalgics, spasmolytics, and for their contraceptive and hormonal activities (e.g. Morton, 1981).

Annonaceaous wood is not generally exploited commercially, but is often valued for firewood and is used for poles, canoes, and bridges. The only species commercially exploited are *Oxandra lanceolata* (Lancewood) in the West Indies, and some related species of *Oxandra* in the Amazon basin and in Panama. The sapwood is commercially desirable, and used for special items such as bobbins, fishing rods, organ-building, billiard cues, textile machinery, and articles of turnery (Chatrou *et al* 1997).

In South-east Asia flowers of two native subspecies of *Cananga odorata* develop an attractive fragrance, and *Cananga odorata* var. *longifolia* is widely cultivated as an ornamental. The essentials oil, '*Cananga* oil' or 'ylang-ylang', has been collected since the end of the 19th century and are extensively used in the perfume and cosmetics industry (Klein, 1975). 'Mkilua' is a floral extract of the East African native *Mkilua fragrans* and is widely used by Swahili and Arab women. The seeds of *Monodora myristica* ('calabash nutmeg') and *Xylopia aethiopica* (used as 'pepper' in Europe before *Piper nigrum*) are used worldwide as spices, and the indigenous people of Central America use the flowers of *Cymbopetalum penduliflorum* with vanilla to flavour chocolate. *Polyalthia longifolia* is widely planted as an ornamental in India, Myanmar, Thailand and Vietnam. *Artabotrys hexapetalus* is commonly used as a trellis-climber to cover e.g. bus shelters and outdoor assembly areas in Thailand and *Uvaria grandiflora* is cultivated as an ornamental in Sri Lanka, Bangladesh and West Bengal.

CHAPTER 2 - PHYLOGENETIC ANALYSIS OF THE *UVARIA* GROUP

Introduction

Phylogenetic Analysis - Problems with Molecular and Morphological Data

Within the evolutionary paradigm we assume that phylogenetic relatedness can be determined by examining similarities in characteristics between organisms - whether they be at the molecular, cellular, organ or whole organism level. There is also a requirement that in order for these characteristics to have a phylogenetic significance they must have a heritable genetic basis (Hillis, 1987).

In this context the advantage of discrete molecular datasets over morphological datasets is obvious – we are putatively dealing with the smallest units of evolutionary change. However, estimation of phylogeny based on sequence divergence between taxa is not as straightforward as might first appear – increased understanding of molecular evolution has identified a number of unexpected complications which can be pitfalls as well as opportunities. For example, the relationship between mutation rate, time and evolutionary distance is complex (Hillis *et al.*, 1996). Numerous studies have shown that while there is a definite correlation between time and mutation rate, these mutation rates can vary between different genes and different taxa (Li & Tanimura, 1987; Avise, 1994). This rate heterogeneity makes phylogenetic estimation more difficult, and causes a variety of problems depending on the analysis method being used. However, the heterogeneity phenomenon also allows flexibility, particularly in relation to studying relationships at different phylogenetic levels, such as at familial, generic, or infra-specific ranks. This flexibility (combined with the availability of computer-based analysis techniques) has been the basis for the rapid growth in molecular systematic research (Soltis & Soltis, 1995; Moritz & Hillis, 1996).

Selection of an appropriate DNA sequence for each phylogenetic study is dependent on a number of factors. Firstly it is critical that the sequence concerned has the potential to identify relationships at a level/ rank appropriate to the study. In functional terms this potential can be equated with the level of evolutionary constraint that is acting on a sequence region. For example, the more important a particular

protein-coding sequence is to an organism, the more important it is that the sequence be inherited unchanged through each successive generation. By extension, if the gene is of crucial importance to cellular functions, it is probable that the sequences will change only negligibly over long periods of evolutionary time. As a result these coding regions are useful for examining relatedness amongst lineages which have been separated for a very long time, such as those representing families or orders of angiosperms (e.g. Chase *et al.* 1993, Soltis *et al.* 1997).

On the other hand, if the sequence is a non-coding region, mutations in the DNA sequence will not (in most cases) effect specific organic processes, and as a result the evolutionary constraints acting on that sequence will be relatively lax. In this case we can examine relationships of much more closely related taxa, such as those at the tribal or generic level (Baldwin *et al.*, 1992; Olmstead *et al.* 1999). Using direct base-pair sequencing technology, the spectrum of DNA sequence types that exist between these two extremes can be targeted according to their potential to reveal phylogenetic relationships at a given level.

However, this flexibility is tempered by a number of phenomena that can undermine the efficacy of the technique. Several workers have pointed out that DNA sequencing can inadvertently focus on gene evolution rather than organismal evolution (Ohta, 1991; Brower *et al.*, 1996; Moritz & Hillis, 1996). This can arise as a result of two distinct processes - lineage sorting and horizontal transfer/ hybridisation (de Quiroz *et al.*, 1995). In both cases, sampling of a single gene region which has been subject to unorthodox inheritance patterns results in the production of misleading hypotheses, and without a broader sampling of other gene regions the problem can go unnoticed.

Lineage sorting is instigated by gene duplication events, where duplicate polymorphisms emerge within a sequentially diverging lineage and are then distributed between the new lineages in an unusual way. While gene duplication can, as in this case, result in the formation of new alleles, it can also occur without the generation of any polymorphism at all. Here, multiple copies of the gene emerge because of a high demand for a particular gene product within a cell. As such, a selective requirement for this kind of duplication is that particular gene copies retain their functionality. Maintenance of this functionality is achieved by so-called

'concerted' evolution (e.g. Hillis *et al.*, 1991), which ensures an active homogenisation of all gene duplicates within the genome.

There is an additional concern over duplication events with regard to so-called 'pseudo-genes'. In this case a gene duplicate suffers a critical mutation which renders it non-functional, however it is retained in the genome and inherited in the normal way. As a result, although the gross structure of the pseudogene resembles that of its parental type, it begins to evolve in a more or less selection-free environment and accumulates mutations at a rate much higher than would apply were it still involved in protein production. Pseudogenes may inadvertently be sequenced instead of the original parental gene, leading to the inferral of cryptic phylogenetic scenarios. It is therefore important to distinguish between paralogues (pseudogenes) and orthologous regions and only use the latter for phylogenetic reconstruction. In practice this is often difficult.

These dangers are often compounded by the selective nature of sampling. Because molecular techniques are not cheap, and usually require a deliberate new sampling of fresh material for most studies, severe limitations are often placed on the extent and appropriateness of sampling which can be carried out, and also on the number of gene regions which can be sequenced.

Generation of morphological data is not quite as prone to the above limitations because a whole-organism sample is normally made which generates a more comprehensive sample of phylogenetic information. Furthermore, because it is relatively easy to gather morphological data from museum specimens it is possible to generate a much larger sample size for each taxon than is often possible with molecular studies (Hillis, 1987; Patterson *et al.*, 1993). However, because morphological data is frequently prone to errors of interpretation, access to a wide sample is no guarantee that a particular study will yield a reliable phylogenetic hypothesis. In addition, morphological analyses are just as susceptible as molecular analyses to the distorting effects of hybridisation (Wendel & Doyle, 1999).

Early differences between workers over whether molecular or morphological data offered the best potential for assessment of phylogeny have gradually been replaced by a consensus that it is desirable to have the maximum amount of phylogenetic information, from whatever source. The most important consideration is that the data be reliable.

Data Analysis

The practical analysis of phylogeny assumes that ancestral characteristics are inherited, and that the evolutionary history of a group of taxa can be defined by examining changes in these characteristics (Zimmerman, 1934; Hennig, 1950, 1965). However, given that all character change datasets are incomplete due to factors such as extinction or selective sampling, it is only possible to *estimate* the actual phylogeny of any given group. Estimation of phylogeny is currently achieved by one of two techniques, either; (i) using an algorithm to generate a single hypothetical tree; or (ii) generating a large number of hypothetical trees using a search algorithm and then selecting the 'best-fit' trees according to specific optimality criteria (Swofford *et al.*, 1996).

A variety of dedicated phylogenetic software packages such as PHYLIP (Felsenstein, 1993), Hennig 86 (Farris, 1986) and PAUP (Swofford, 2000) are available, and all offer a range of techniques for the purpose of tree generation.

Distance Methods

The first estimation technique described above encompasses what are known as 'distance methods', including UPGMA (unweighted pair group method using arithmetic averages; Sneath & Sokal, 1973) and Neighbor-Joining [NJ] (Saitou & Nei, 1987). In these techniques the overall distance or difference between taxa is calculated according to various formulae and then the taxa are linked together, based on their (dis)similarity, to construct a single hypothetical tree. Because they are not shackled with a requirement to compare a large number of trees, these techniques tend to be

computationally fast. On the other hand, because they make little reference to the form of phylogenetic signal which is contained in a dataset, i.e. a form determined by evolution, they can be unsuited to phylogenetic inference in groups where evolutionary distances might be great, although the level of divergence between taxa in a dataset depends as much on the type of characters being analysed as the on the actual evolutionary distance between the taxa. UPGMA is particularly limited in this context because it assumes the data are ultrametric, i.e. that rates of change are equal between all taxa on a tree, or in the case of nucleotide data, that a molecular clock is in operation (e.g. Li, 1997, p. 132; Hillis *et al.,* 1994). Neighbour-Joining does not assume data are ultrametric and so is more sensitive to evolution rate heterogeneity (Hillis *et al.*, 1994).

Maximum Parsimony

The second major group of techniques, using optimality criteria [OC], are often regarded as being most suited to phylogenetic studies in the sense that they incorporate assumptions either about the way in which evolution proceeds or the way in which it can best be traced (Swofford *et al.*, 1996). The most widely used optimality criteria method, parsimony, is based on an assumption that the most plausible hypothetical trees are those which require the minimum possible amount of evolutionary change between all the taxa in the tree. Initially known as the 'minimum net evolution' method (Edwards & Cavalli-Sforza 1963; 1964) the term 'parsimony' was widely adopted after Camin & Sokal (1965) used it when applying the minimum net evolution method to discretely coded morphological characters. The inference is to the parsimony method of Okham, or 'Occam's Razor' (Wiley, 1981), where the simplest plausible explanation for any natural phenomenon is accepted because there is no evidence to suggest that nature is unnecessarily complicated. Whether such a supposition can be made about tracing paths of evolution is debatable (Felsenstein, 1988), however several authors take the position that phylogenetic parsimony merely resembles Occam's Razor out of coincidence, and that the technique has merits based solely on the processes of evolution as we understand them (Swofford *et al.* 1996). Perhaps the most valued aspect of parsimony analysis is that it maximises character

congruence, i.e. it preferentially maintains relationships that are supported by character agreement between taxa.

The probability of generating a correct estimate (according to the, in this case, parsimony criteria) is directly related to two characteristics of the dataset. Firstly there is a positive correlation between the number of informative characters, i.e. characters which reveal dis/similarity between taxa, and the probability of generating a close estimate of the true phylogeny (Felsenstein, 1988). Secondly, every taxon in the matrix must exhibit some level of congruence (similarity) with at least one other taxon, otherwise the analysis will be unable to resolve its position within the phylogeny.

Once a reliable dataset has been assembled, the process of tree generation can begin. As mentioned earlier, the process of finding the best tree according to the OC (in this case maximum parsimony [MP]) can be divided into two distinct phases (i) a search for an initial shortest tree and (ii) the testing/ retesting of this tree according to the MP criterion.

Search Algorithms

A variety of search algorithms can be used to generate hypothetical trees, including e.g. Heuristic, Branch and Bound and Exhaustive searches. In the case of the latter two, a complete survey of the treespace (i.e. the space which contains all possible trees that can be constructed from a dataset) is carried out to ensure that the best-fit/ most parsimonious tree has been found in the search. However, because both these methods are computationally intense, particularly when the number of taxa is high, the more rapid heuristic-type searches are often favoured.

There are several kinds of heuristic searches, all of which traverse the treespace in an incomplete manner and use 'prepping' to enhance the quality of the trees produced in each search. This procedure is carried out repeatedly until there is reasonable confidence that the most parsimonious tree has been found.

'Stepwise-Addition' and 'Star-Decomposition' heuristic searches are regarded as 'greedy' algorithms as they tend to analyse only the trees which are similar to the first tree they generate in each particular search. As a result, if the optimal tree is distant from those generated in the first search, neither of these techniques are likely to find it. A further option in heuristic searches is 'Branch-Swapping', where an initial optimal tree is variously dismembered and rebuilt according to one of three main methods; Nearest Neighbour Interchange, Subtree Pruning, and Tree Bisection and Reconnection. In each case the dismembering/ rebuilding continues as long as progressively better/ shorter trees are found. Because these processes constitute a more radical rearrangement pattern than either Star-Decomposition or Stepwise-Addition, there is a higher probability that Branch-Swapping will find an optimal tree. All of these search methods are discussed in Swofford *et al.* (1996).

Maximum Parsimony Optimality Criteria

Determining which are the shortest, minimum change, trees out of the sample that is generated using the search algorithm depends largely on how individual characters are treated within the optimality criteria. Directionality and constraint are the two principal concerns in this regard. The directionality of a character refers to its supposed change over evolutionary time from a primitive/ ancestral/ plesiomorphic state to a more derived/ evolved/ apomorphic state, and determining the direction of these changes is critical to the application of the shared derived character rule of Hennig. The outgroup analysis method is the most commonly used for resolving directionality (e.g. Hennig, 1950, 1965; Maddison *et al.*, 1984; Hillis, 1987). It determines primitive character states within a monophyletic group (the ingroup) by identifying which of them are also evident in a sample taxon from a sister monophyletic group (the outgroup), thereby identifying the character states which existed in the common ancestor of both groups. Character states which differ from this ancestral state are thus regarded as being derived.

Ontogenetic analysis has also been suggested as a reliable method for inferring directionality (e.g. Kluge & Strauss, 1985). It has an advantage over the outgroup method in that developmental states can be observed directly, and as a consequence

resolving character directionality does require any *a priori* assumptions about relationships between ingroup and outgroup. However, it can be difficult and time-consuming to acquire ontogenetic data, and even where it is available many systematists still favour the outgroup method (Hillis, 1987).

By determining the direction of character change it is possible to select certain character changes as being plausible/ acceptable or implausible/ unacceptable and impose *constraints* on the structure of the phylogenetic tree. The simplest parsimony criteria are those which impose no constraints ('Fitch parsimony', Fitch, 1971) or minimal constraints ('Wagner parsimony', Kluge and Farris, 1969) on permissible character-state changes. Dollo (Farris, 1977) and Camin-Sokal (1965) parsimony are much more restrictive, requiring that acceptable character changes be uniquely derived or irreversible respectively. In all cases, the parsimony criteria requires that the favoured phylogeny be the shortest possible tree which adheres to the constraints imposed.

Statistical Testing of Inferred Phylogenies

Once a search has generated a final shortest tree or trees, based on the optimality criteria, there are a suite of methods which can be used to assess the reliability of branching patterns and characters within the tree(s). Branch reliability can be assessed by secondary analyses such as Bootstrap (Felsenstein, 1985) and Jacknife (Mueller & Ayala, 1982) resampling, and the Support method (Bremer, 1994). Although widely used in phylogenetic studies, all three techniques have shortcomings in terms of their reliability (reviewed by Swofford *et al.*, 1996), however in the absence of more accurate measures it is widely accepted that using one or more of the techniques will provide an insight into the reliability of the tree topology. A further tool for summarising branch relationships is the consensus tree (reviewed by e.g. Wiley *et al.*, 1991, p.71-90). Here the topologies of the most parsimonious trees are compared and then summarised according to various protocols. A 'strict' consensus tree will retain only those branches and nodes which appear in all the trees, with all non-universal branches represented as polytomies (multiple branches from the same node). The 'majority-rule' consensus retains branches which appear in a minimum number of

trees, usually 50% or more. Support values are attributed to each branch in the majority-rule consensus tree and indicate the percentage of most parsimonious trees which support each particular branch.

Character reliability within a tree can be assessed using three descriptive statistics (the consistency index [CI], the retention index [RI] and the product of the two, the rescaled consistency index [RC]) which examine the behaviour of each specific character on a particular tree topology. Essentially these indices measure the probable homoplasy of a character (i.e. its reliability relative to the surrounding data matrix), with low values suggesting that it is either being incorrectly read, and so represents a parallelism or convergence, or that it is not being supported by other characters because those characters are somehow missing from the dataset. In practice a low index score is simply taken to mean that the character is adding to tree length without providing strong support for any of the branches. These indices are useful for (i) ensuring morphological characters are being properly scored, (ii) as a means of identifying unreliable molecular characters, and (iii) as a means for assigning weights to characters for subsequent parsimony analyses through successive/ iterative weighting (Farris, 1969).

In the latter case, successive weighting, characters are re-assigned a weight proportional to their CI, RI or RC score in an initial heuristic search. With these new weights applied, the matrix is re-sampled using the search algorithm to generate a new tree or trees. These new trees are then re-scored for their character index values. A new weight is applied to each character according to this latest index value, and another search begins. The process is repeated until each successive sampling produces the same identical tree(s). In a successively weighted tree the more heavily weighted characters, i.e. those with high index values in the first sample, will change less often than lightly weighed characters, thus adding a limited evolutionary assumption to the analysis, i.e. that certain characters are more phylogenetically informative than others. In this way the successive weighting technique diminishes the impact of unstable homoplasic characters. It can be particularly useful in extracting trees from datasets with high homoplasy 'noise' levels.

Maximum Likelihood

A second form of optimality-criteria search methods is Maximum Likelihood [ML] (Cavalli-Sforza & Edwards, 1967; Felsenstein 1981). In this technique, computation is focused on finding the tree which is most likely to generate an observed dataset. Several aspects of the technique distinguish it from the parsimony approach, however two of the most important are that branch length has an important influence on node identity in the tree topology, and that an evolutionary model is explicitly part of the optimality criteria. One of the principal advantages of ML over MP is apparent when data we are working with is in the 'Felsenstein Zone'. This refers to scenarios where there is significant evolutionary rate heterogeneity evident in different taxa within a single matrix. Felsenstein (1978) showed that in unmodified MP analysis, taxa with an increased rate of evolution in the sampled gene regions are more likely to be paired together than with taxa showing more conservative rates of evolution in these regions ('long branch attraction', Hendy & Penny, 1989), irrespective of their true evolutionary relationship. Felsenstein (1988) argued that because Maximum Likelihood includes a consideration of branch lengths, and thus the possibility of rate heterogeneity, it involves a more realistic consideration of actual evolutionary processes than MP analysis.

However, the perceived accuracy and flexibility of ML comes at a cost; namely that derivation of ML trees is so computationally intense that only a limited number of taxa can be analysed at any one time (more than c. 11 taxa causes a dramatic increase in computation time, Lewis, 1999). However, computation times are highly dependent of the number of parameters which are known versus the number which need to be estimated for the evolutionary model used in each analysis. The parameters refer to the patterns of sequence evolution which are likely to have been acting on a gene region, and include (among others) consideration of the transition to transversion ratio, the evolutionary rates for nucleotide sites in the sequence, the frequency of the four bases in the matrix and whether or not a molecular clock is operating. The more of these parameters that are known prior to the beginning of a ML analysis, the more rapidly the search will generate the maximum likelihood tree (Lewis, 1999). PAUP 4.0 provides a facility to study the structure of the matrix so that many of these parameters can be fixed prior to analysis.

As with Maximum Parsimony Analysis, the Bootstrap and Jacknife resampling methods can be used to measure branch reliability. However, unlike MP analysis, the requirement for a detailed molecular evolution model in ML analysis means that morphological data and some forms of molecular data are not amenable to the technique.

Consistency of Distance and Optimality Criteria Methods

An important consideration for all phylogenetic analyses is consistency. A given statistical technique is consistent if its estimate of a target value converges on that true value with an increasing sample size. The intuitive assumption that consistency should apply across the range of phylogenetic analysis techniques is not supported in all cases. A series of modelling experiments with molecular data have indicated that while ML and to a lesser extent NJ are largely consistent irrespective of the behaviour of data, MP can become inconsistent under certain circumstances, principally when there are varying rates of evolution between taxa (Saitou & Imanishi, 1989; Kuhner & Felsenstein, 1994) and between characters (Tateno *et al.*, 1994). Where evolutionary rates are reasonably constant in a matrix, unweighted MP performs very well, and this performance can be maintained for matrices with unequal rates of evolution by weighting character behaviour according to a variety of evolutionary models (Hillis *et al.*, 1994). In all tests, UPGMA emerges as the least satisfactory method, and this seems largely due to its inability to deal with any form of rate heterogeneity. Despite the fact that these modelling experiments highlighted the weaknesses of MP relative to rate heterogeneity (Saitou & Imanishi, 1989; Kuhner & Felsenstein, 1994, Tateno *et al.*, 1994) the same experiments also revealed its reliability at very low sample sizes, where it outperformed NJ and often ML in estimating true phylogeny.

Selection of Analysis Techniques

From a Hennigian perspective it is difficult to imagine NJ as an appropriate technique for reconstructing phylogeny because it makes no assumptions about character change behaviour on a tree. However, modelling experiments have shown that with modifications, the technique makes accurate estimates of *overall* phylogeny, without

perhaps the close scrutiny which MP pays to particular character state changes. As a result, while a NJ-inferred phylogeny may suggest unsatisfactory relationships in portions of the tree topology (which MP would not allow), it would appear that the overall NJ phylogeny estimate is often quite robust. Furthermore, because tree construction is based on branch-lengths, the technique copes very well with rate heterogeneity in molecular data.

Unlike NJ, MP analysis stems directly from Hennigian precepts and so generates tree topologies which are easily interpreted from a phylogenetic perspective. However, from a statistical standpoint the technique does have weaknesses related to rate heterogeneity, and for molecular data at least, there is sometimes support for the use of unevenly weighted Fitch constraints where rate heterogeneity is an obvious feature of a data matrix.

ML copes well with rate heterogeneity in molecular datasets. However, computation times for this technique are extremely long, and the need for a complex evolutionary model means that morphological data cannot be considered.

As well as the relative performance of each method, it is also important to consider the best ways to compare and analyse data from different sources, which in the case of this study involves molecular and morphological data. This can be done in two ways, either by combining the data into a single matrix before analysis to produce a 'combined data' tree, or by summarising the data from the trees in each separate analysis in a consensus tree. In terms of pooling datasets into a single matrix, it may initially seem inappropriate to make a single nucleotide character score equivalent in weight to the score attributed to, for example, a floral organ. One could argue that the genetic template which underpins the formation of a floral organ includes several genes, and as a result contains vastly more information than a single nucleotide site. However, the underlying concern in all phylogenetic analysis relates to the signal contained in any character. If morphological and molecular data produce trees which agree with one-another, then the signal is the same in both sets of characters (de Quiroz *et al.*, 1995). Where this kind of harmony exists, the source of the character score is relatively unimportant and there are no empirical reasons why the datasets should not be combined.

However, where there is incongruence between datasets, and this can occur between plastid and nuclear sequence datasets as much as morphological and molecular datasets, there is strong support for the idea that datasets should not be combined (Bull *et al.*, 1993). There are as yet no statistical methods for determining critical levels of incongruence between datasets, however there is a general guideline available (Bull *et al.*, 1993, summarised by de Quiroz *et al.*, 1995). Under the criteria of Bull, if the divergence between trees from two separate datasets is greater than that which might be expected due to sampling error (i.e. there are major differences in tree topology from the two datasets which are well-supported by bootstrapping/ jacknifing), and so is due either to divergent evolutionary patterns or the fact that one dataset is fundamentally unreliable, then the level of incongruence is significant and the datasets should be kept separate. If, on the other hand, sampling error can reasonably account for the incongruence (i.e. differences in topology have weak bootstrap/ jacknife support), then the incongruence should not be regarded as significant and the data should be joined. Indeed in this latter case, combining the datasets will bring the phylogeny estimate significantly closer to the true phylogeny simply by increasing the sample size.

Despite the case made in favour of automatic data pooling on the basis that total evidence must always be considered (e.g. Kluge & Wolf, 1993), it seems wise to be as cautious in combining datsets as one would be in selecting characters in the first instance. In fact, just as incongruence between morphological characters often leads to a fruitful re-appraisal of character scoring, incongruence between datasets may provoke a reassessment of data which ultimately leads to a more robust overall analysis. Equally, accepting a 'disfigured' topology simply because it comprises the total evidence may hide the fact that one or more of the original datasets produced a very accurate estimate on its own.

Analysis of Molecular Data

Target Sequence - the ITS Region of Nuclear Ribisomal DNA

Structure

Nuclear ribosomal DNA (nrDNA) codes for the production of ribosomes and in most organisms there are thousands of repeats within a single genome, with the majority being located around the nucleolar organising region (Appels & Dvorak, 1982; Appels & Honeycutt, 1986; Jorgensen & Cluster, 1988; Soltis & Soltis, 1999). Each repeat (Figure 2.1) consists of a transcribed region that comprises an external transcribed spacer (ETS), followed by the 18S gene, an internal transcriber spacer (ITS-1), the 5.8S gene, a second internal transcribed spacer (ITS-2) and finally the 26S gene. Each repeat is a single transcriptional unit, however copies of the spacer regions are not incorporated into mature ribosomes.

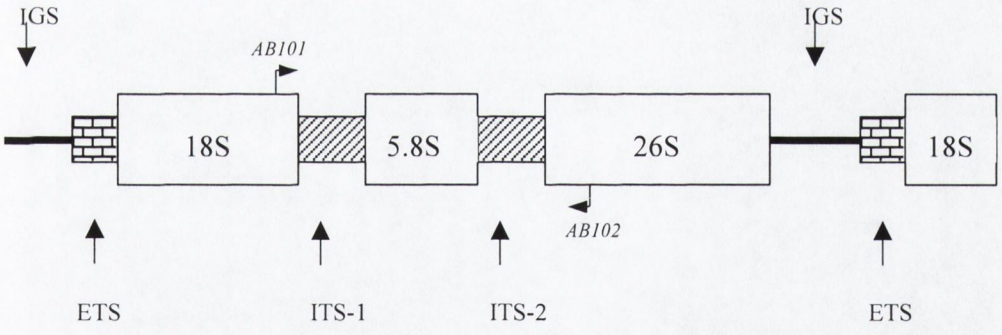


Figure 2.1. Diagram illustrating structure of nrDNA repeat in plants. IGS is the intergenic spacer. ITS-1 and ITS-2 are the internal transcribed spacers; ETS is the external transcribed spacer. 18S, 5.8S and 26S represent the ribosomal rRNA genes. AB101 and AB102 refer to the forward and reverse primers respectively for the ITS region. (After Baldwin *et al.*, 1995 and Soltis & Soltis 1999).

The length and composition of the 18S gene (c. 1,800 bp, Nickrent & Soltis, 1995), the 5.8S gene (c. 160 bp, Takaiwa *et al.,* 1985) and the 26S gene (c. 3,300 bp, Bult *et al.* 1995) are similar in all plants, however the spacer regions are more variable (Jorgensen & Cluster, 1988; Baldwin *et al.*, 1995).

Evolutionary constraints

The ITS-1 and –2 regions are not prone to the same evolutionary constraints as the ribosomal genes which they adjoin, however unlike the IGS they do appear to be under some selective pressure, probably as a result of their influence on the formation of large and small subunit rRNAs (van der Sande *et al.*, 1992). The level of involvement of different portions of the ITS region in the formation of these subunits appears to vary, suggesting that different portions are under different, and in certain cases negligible levels of conservative pressure.

ITS repeats are sometimes heterogeneous. However, where there has been experimental observation of ITS evolution in vertebrates, there is strong evidence to show that parallel or concerted evolution via unequal crossing-over and gene conversion homogenises copy type by the assertion of one repeat type over all others. (Hillis *et al.*, 1991). The prevalence of this concerted evolution means that even though there is a high copy number of nrDNA in the genome it is possible to amplify and directly sequence the ITS region (often without the need to choose individual repeat types).

While a similar study has yet to be carried out for higher plants, existing plant data suggests that the restraints on repeat divergence within individuals appear to vary from one group to next. It has already been documented that, for example, the Portulacaceae exhibit an enormously variable family of ITS repeats within the same species and even the same individuals, making phylogenetic inference extremely difficult (Soltis & Soltis, 1999). In addition to multiple functional ITS repeats, both non-functional ITS and recombinants may also be present in individual plants (Buckler *et al.*, 1997), and this can disrupt the analysis process.

However, while these particular limitations will apply to certain plant groups, in general it appears that ITS divergence between taxa over time seems stable enough to facilitate assessment of phylogenetic relationships. In the first broad survey of the ITS region in angiosperm families, Baldwin *et al.* (1995) found that ITS-1 varied in size from e.g. 189 bp in the Scrophulariaceae to 287 bp in the Malvaceae, with G+C content varying from 42% to 58% respectively in the same groups. ITS-2 varied in size from 187 bp in the Polemoniaceae to 252bp in the Cucurbitaceae, with G+C content varying from 48% to 60% respectively in the same families. Compared to the very limited bp sequence divergence seen in the ribosome genes, which have been used by Soltis *et al.* (1997) to infer deep phylogenetic relationships within the angiosperms, this kind of base variation the ITS region is ideally suited to assessing relationships of closely related taxa.

Amplification considerations

Paralogues

It is possible that divergent evolution may have been acting within nrDNA repeats, meaning that PCR amplification may identify incongruent ITS paralogues within in the same individual. Cloning procedures can be used to establish the identity of the various paralogues, however where they are very divergent the probability of generating useful phylogenetic information decreases dramatically (Baldwin *et al.* 1995). Paralogues which differ in length can be identified on a single forward or reverse strand chromatogram where the indel location is followed by an unreadable banding pattern (caused by the detection of more than one base at each band).

Secondary structures

The high G-C content of most ITS sequences mean that single-strand templates and transcript copies are prone to forming secondary structures by Watson-Crick intrastrand base-pairing (Baldwin *et al.* 1995; Hillis & Hillis, 1999) and this can inhibit both amplification and strand mobility in the sequencing gel. In addition, non-functional ITS single strand copies have lower secondary structure stability than functional ITS copies, meaning that they can be preferentially amplified where no

measures are taken to inhibit secondary structure formation in the functional ITS copies. Buckler *et al.* (1997) suggest that highly denaturing PCR conditions be used (e.g. the addition of Dimethyl Sulphoxide – DMSO) to prevent preferential amplification of non-functional ITS.

Materials and Methods

DNA Extraction

DNA extraction, purification, amplification and cycle sequencing was carried out by the author at the molecular systematics laboratory at TCD. Sequencing on the ABI Prism automated sequencer was carried out by technical staff at the Jodrell Laboratory, Kew Gardens, London. DNA was extracted from 22 specimens (Table 2.3) using a hot-CTAB protocol (adapted from Doyle & Doyle, 1987). Leaf material was cut into small pieces and ground in a CTAB-based buffer (at 65°C) using a pestle and mortar. CTAB (hexadecyltrimethylammonium bromide) is a detergent which performs a critical function in the extraction buffer, solubilising plant membranes and forming complexes with the DNA. Other components of the extraction buffer include EDTA (ethylenediaminetetaacetate – inhibits metal dependent enzymes), 2-mercaptoethanol (protects DNA from quinines, disulphides, peroxidases and polyphenoloxidases) and PVP (polyvinylpyrrolidone – reduces the effect of polyphenols, quinines and tannins) The pH of the CTAB buffer was optimised at 8.0 – 9.0 using 100mM Tris-HCl so as to inhibit the action of degrading enzymes such as DNAases (optimal pH of c. 7.0) and lipolytic /lipoxygenases (optimal pH of 5.0-6.0). Later, CI (24:1 chloroform: isoamyl alcohol – which helps separate the aqueous DNA–containing phase from the solution) was added and the solution was mixed for 30 minutes and centrifuged at 4000rpm. After spinning the aqueous phase was removed to a clean test tube, and an equal volume of 100% isopropanol was added to precipitate the DNA. After being stored at -20°C for 1-4 weeks (to further precipitate the DNA), the extracted DNA solution was washed using 70% ethanol and spun in a centrifuge. After decanting the DNA was air-dried and resuspended in TE buffer (10 mM Tris HCl pH 8.0, 1mM EDTA).

PCR amplification can be inhibited where there is a significant phenolic component in the cytoplasm, and it is well documented that the Annonaceae have a large diversity of phenolic compounds. Phenolics and other contaminants were removed from the extraction mix using the CONCERT™ purification system (Life Technologies, 1999). Here, DNA is adsorbed to a silica membrane using a binding solution ('H1'), and the remaining cellular material is washed away using a wash buffer ('H2'). The DNA is then resuspended in warm TE buffer, as before.

PCR amplification

The polymerase chain reaction ('PCR', Mullis & Faloona 1987) was used to amplify the targeted ITS sequences in the DNA template using a Perkin Elmer DNA Thermal Cycler 480. The ITS region was primed for amplification using the primer sequences of Baldwin (1992) and Sun *et al.* (1994) (forward ACGAATTCATGGTCCGGTG-AAGTGTTC; reverse AGAATTCCCCGGTTCGCTCGCCGTTA). Two different amplification mixes were used over the course of the research work and these are detailed in Table 2.1. Successful amplification depends on the various components of the amplification mix interacting in a specific manner, and there are many factors which determine whether or not this takes place. The PCR cycle (Table 2.1) has three distinct phases. The denaturing phase (at 97°C) causes the two-stranded DNA template to separate. This is followed by the annealing phase (at c. 52°C) where the AB101-102 primers attach to the target sequences, and this in turn is followed by the extension phase (at c. 72°C) where *Taq*-polymerase (© Promega Inc.) generates a transcribed copy of the DNA template in the 5' – 3' direction. Mg^{++} is a cofactor of *Taq*-polymerase and encourages the binding of the primers to the DNA template, while the dNTPs act as a source for construction of the transcribed DNA copies. In the second cycle, both the original template and its copies act as templates for transcription, and as each cycle is repeated (from the second cycle onwards) there is an exponential increase of copies of the targeted DNA.

If amplification is not working efficiently then a number of modifications can be made to the protocol. Where there are concerns over primer activity, as when e.g. the sequence of the target primer site is marginally different from the primers, the annealing temperature can be lowered so as to reduce the specificity of the primers,

although this can result in the amplification of non-target sequences. The number of cycles can be increased so as to give more time for the 'pick-up' of successful early transcriptions. The make-up of the amplification mix can also be modified by increasing the quantity of template or Mg^{++}, although there are problems associated with both of these changes. If the quantity of DNA template solution is increased too much, there is the potential for altering the pH or molarity of the reaction mix. Increasing the amount of Mg^{++} can have a similar effect to lowering the annealing temperature in that non-target sequences can be primed. The problems associated with secondary structures can be partly overcome by the addition of detergents to the PCR mix such as DMSO, betaine, or, as was used in this work, QIAGEN Q-solution.

Table 2.1. PCR reaction mix components and thermal cycling protocol.

PCR Reaction Mix

	Mix 1		Mix 2	
	Volume (µl)	**Concentration**	**Volume (µl)**	**Concentration**
Component				
QUAIGEN Q-solution	-	-	20.0	
Sterile ultrapure H_2O	69.5 – 73.5		64.0	
Buffer (10x)	10.0	1x	10.0	1x
DNTPs (10mM)	2.0	0.1mM	2.0	0.1mM
AB101 (forward primer) 100ng/ul	1.0	100ng	1.0	100ng
AB102 (reverse primer) 100ng/ul	1.0	100ng	1.0	100ng
$MgCl_2$ 25mM	10.0	2.5mM	-	-
Promega *Taq* polymerase (5 units/ul)	0.5	2.5 units	0.5	2.5 units
Template DNA (c. 50ng/ul)	2.0 – 6.0	100-300ng	1.5	75ng
Total volume	100.0		100.0	

PCR Thermal Cycling Protocol

	Cycle Phase	**Temperature (°C)**	**Duration (minutes)**
Standard cycle	1. Denaturing	97	1
(29-39 Cycles)	2. Annealing	48-52	1
	3. Extension	72	3
Final cycle	1. Denaturing	97	1
	2. Annealing	48-52	1
	3. Extension	72	7
	4. Soak	4	∞

Successful amplification was confirmed by running an electrophoretic 1.2% agarose gel using a 5µl test aliquot from the post-PCR reaction mix. Each aliquot is mixed with 1µl of Promega loading dye, loaded into a lane on the gel and run for c. 20 minutes at 125 volts. A positive sample of a successfully amplified ITS region is also included. As in all electrophoretic gels, same-length DNA strands migrate at the same rate from the negative to the positive anodes in the gel rig. The appearance in a test lane of a strong single band which is parallel to the band in the positive ITS lane indicates that amplification has been successful.

Sequencing

Cycle sequencing reactions (Sanger *et al.* 1977; Hillis *et al.* 1995) were carried out on the amplified DNA using fluorescently-labelled dye terminators. In cycle sequencing the copies are preferentially generated from the template and not from other copies, so it is not a chain reaction. Details of the sequencing reaction mix and thermal cycle protocol are shown in Table 2.2. Forward and reverse strands were sequenced in separate reactions. An MJ Research PTC-200 DNA Engine was used for the cycle sequencing reactions.

When an aliquot from a completed sequencing reaction mix is run on a sequencing gel, we should see a continuous stream of progressively longer (by one base) fragments pass through the gel, although in reality there will be numerous copies of each specific fragment moving along the gel at any one time. Because the dye terminators also fluoresce light at a wavelength specific to each of the four bases, as each progressively longer set of fragments pass through a light sensor at the end of the gel the dye terminators identify which of the four bases has been added at the end of the fragment over and above the (one base shorter) fragments which have just passed through the sensor. In this way a sequential banding pattern is produced which can be read as a single 'copy' of the original target ITS template.

Before a sequencing reaction mix can be run on a sequencing gel it needs to be purified to remove excess dye terminators. This was achieved by adding each 10ul

reaction mix to 52ul of cleanup mix (50 ul of 100% ethanol, 2ul of sodium acetate) in a 1.5ml tube. After being left at room temperature and then on ice, in each case for 5 minutes, the mixture was spun at 13,000 rpm for 25 minutes. After decanting, the remaining DNA was washed in 70% ethanol and spun at 13,000 rpm for 5 minutes. After decanting, this last procedure was repeated again. Finally the 1.5ml tube was air dried for 24 hours, at which time it is ready for sequencing.

Sequencing of all samples in this project were done using an ABI Prism© 377 DNA Sequencer at the Jodrell laboratory, Royal Botanic Gardens, Kew, England.

Table 2.2. Sequencing Reaction Mix Components and Thermal Cycling protocol.

Sequencing Reaction Mix

Component	Volume (µl)	Concentration
SDD H_20	1.8	
Sequencing Buffer	3.5	
AB101 or AB102 (5ng/ul)	0.7	3.5ng
Dye Terminator/ Taq/ dNTP 'Pink' mix	1.0	0.1 mM
DNA template* (c. 500ng/ul)	3.0	1500ng
Total Volume	10.0	

*Containing successfully amplified ITS sequences

Sequencing Reaction Thermal Cycling Protocol

	Cycle Phase	Temperature (°C)	Duration (min:sec)
Standard Cycle* (24 Cycles)	1. Denaturing	96	0:10
	2. Annealing	50	0:05
	3. Extension	60	4:00
Final Cycle* (1 cycle)	1. Denaturing	96	0:10
	2. Annealing	50	0:05
	3. Extension	60	4:00
	4. Soak	4	∞

*Temperature change between cycle phases was set to 1°C per second.

Results

Raw data

Amplification and Sequencing

The 22 specimens from which DNA was extracted are listed in Table 2.3. Not all of the extracted DNA was successfully amplified. In the case of *Cyathostemma argenteum* this was probably due to DNA degradation related to the age and/or the preservation method of the herbarium sheet. Two African *Uvaria* species, *U. faulkneri* and *U. chamae* were successfully amplified from herbarium sheets. Two specimens (*Uvaria grandiflora* 2 and *U. cordata* 2) were successfully amplified but could not be incorporated into the phylogenetic analysis because of the high level of incongruence between various repeats in the genome. The ITS of a third specimen, *Magnolia* sp., which was being sampled as a potential outgroup for the analysis, was too divergent from the ingroup to be of any use in this regard.

Sequence Scoring and Alignment

Sequences were returned from Kew via email to the TCD molecular systematics lab. Confirmation of base scoring and assembly of forward and reverse strands into 'contigs' was done using the SEQUENCHER software package (© Gene Codes Corporation, 1998). Alignment of contigs was done manually in a Nexus file matrix edited using the PAUP 4.0b software package (© David Swofford, 2000) and the Se-Al alignment package (© Andrew Rambaut, 1999). The final aligned matrix is shown in Appendix 2.1.

Sequence Content

The 18S, 5.8S and 26S gene sequences stand out clearly in the matrix, with little divergence between the taxa. The small amount of diversity which is evident is probably due to experimental error, although certain changes, such as at position 27 in the 18S gene appear to be phylogenetically informative. The exact location of the 5.8S

Table 2.3. Samples used for molecular analysis. *Amplification was incomplete or failed to generate usable data.

	Taxon name on specimen	Leaf preservation method	Voucher specimen	Herbarium	Location	Amplification successful
1.	*Ellipeiopsis cherrevensis*	Silica gel	*S. Suddee 839*	TCD	Thailand	Yes
2.	*Uvaria hahnii*	Silica gel	*P. Chalermglin 21-7-99*	TCD	Thailand	Yes
3.	*Anomianthus dulcis*	Silica gel	*P. Chalermglin 23-7-99*	TCD	Thailand	Yes
4.	*Rauwenhoffia siamensis*	Silica gel	*C. Meade 76*	TCD	Thailand	Yes
5.	*Melodorum fruticosum*	Silica gel	*P. Chalermglin 7-7-99*	TCD	Thailand	Yes
6.	*Uvaria rufa* var. *rufa*	Silica gel	*C. Meade 98-10-16-06*	TCD	Thailand	Yes
7.	*Uvaria pierrei*	Silica gel	*C. Meade 98-10-17-01*	TCD	Thailand	Yes
8.	*Uvaria micrantha*	Silica gel	*C. Meade 98-10-18-03*	TCD	Thailand	Yes
9.	*Uvaria viet namensis*	Silica gel	*C. Meade 98-10-16-03*	TCD	Thailand	Yes
10.	*Uvaria hamiltonii* var. *hamiltonii*	Silica gel	*C. Meade 84*	TCD	Thailand	Yes
11.	*Uvaria grandiflora* 1	Silica gel	*C. Meade 98-10-18-04*	TCD	Thailand	Yes
12.	*Uvaria cordata* 1	Silica gel	*C. Meade 98-10-17-02*	TCD	Thailand	Yes
13.	*Uvaria macropoda*	Silica gel	*Weerasooriya & Meegaskumbra 6225*	PDA	Sri Lanka	Yes
14.	*Uvaria microcarpa*	Silica gel	*C.L. Law 18/5/99 s.n.*	HKU	China	Yes
15.	*Uvaria chamae*	Herbarium	*Warnecke 148*	HAM	Togo	Yes
16.	*Uvaria faulkneri*	Herbarium	*Vollesen 4667*	C	Tanzania	Yes
17.	*Dasymaschalon blumei*	Silica gel	*C. Meade 79*	QBG	Thailand	Yes
18.	*Artabotrys odorotissimum*	Silica gel	*C. Meade 87*	TCD	Vietnam	Yes
19.	*Cyathostemma argenteum*	Herbarium	*Burley et al. 2558*	L	Kalimantan	No
20.	*Magnolia sp.*	Fresh	*C. Meade 100*	TCD	Ireland	Yes*
21.	*Uvaria grandiflora* 2	Silica gel	*C. L. Law 18/5/99 s.n.*	HKU	China	Yes*
22.	*Uvaria cordata* 2	Silica gel	*C. Meade 98-10-17-03*	TCD	Thailand	Yes*

gene was confirmed using a comparative alignment of a *Magnolia* sp. (C. Meade 100) ITS sequence with the existing Matrix. As reported by other workers (e.g. Baldwin 1992, Baldwin *et al.* 1995) the length of the 5.8S region was 160 ±1 bp.

Nucleotide content data for the sampled taxa are summarised in Table 2.4. The mean total length of the ITS region between the forward and reverse primer sites, excluding 5.8S, is c. 491 bp. The mean length of ITS-1 is c. 272 bp long, and ITS-2 is c. 219 bp. These measures exclude gaps created for alignment of the matrix. ITS-1 contains two large indels. The first, at positions 91-102 is caused by a single, c. 11 bp insertion in the outgroup species *Dasymaschalon blumei*. The second is at positions 405-429 (c. 36 bp) in *Rauwenhoffia siamensis*. ITS-2 does not exhibit any large indels.

Figure 2.2 illustrates the varying rate of changes at each nucleotide site in the ITS region as measured on tree no. 1 from the MP analysis. In ITS-1 there are two major areas of instability; between bases 205-225 and 390-440. ITS-2 exhibits more changes than ITS-1, however here they are quite evenly spread throughout the spacer. ITS-1 and ITS-2 both exhibit conserved regions in their central portions, at bases 247-375 and 778-828 respectively. In the latter case, although there are a number of base changes evident between the taxa at this region, the number of indels is significantly lower than in the the remainder of the matrix.

Phylogenetic analysis

Datset

ITS-1 & 2 were united for the purposes of phylogenetic analysis as recommended by Baldwin *et al.* (1995).

Parsimony Analysis

Parsimony analysis of the final matrix using heuristic search options in PAUP 4.0 yielded two most parsimonious trees and these are illustrated in Figure 2.3. Heuristic

Table 2.4. Nucleotide content data for ITS-1 and ITS-2 in final matrix. See text for discussion.

Sequence Length

Mean length (bp) and gap data for ITS-1 and ITS-2

Region	*Mean length*
ITS-1	272
ITS-2	219
ITS-1 & ITS-2	491

A, C, G, T Content

Mean and range of frequencies across all taxa for ITS 1 & ITS 2

		Missing data and gaps included		Missing data and gaps excluded	
	Base	*Mean*	*Range*	*Mean*	*Range*
ITS-1	A	0.149	0.131 – 0.185	0.191	0.176 – 0.233
	C	0.254	0.191 – 0.268	0.325	0.289 – 0.346
	G	0.320	0.251 – 0.339	0.410	0.379 – 0.429
	T	0.057	0.040 – 0.088	0.073	0.051 – 0.101
ITS-2	A	0.091	0.061 – 0.106	0.116	0.106 – 0.132
	C	0.293	0.201 – 0.324	0.375	0.355 – 0.403
	G	0.303	0.195 – 0.341	0.387	0.360 – 0.405
	T	0.094	0.075 – 0.119	0.121	0.103 – 0.145
ITS-1 & ITS-2	A	0.126	0.105 – 0.162	0.161	0.148 – 0.210
	C	0.271	0.232 – 0.291	0.348	0.320 – 0.369
	G	0.307	0.253 – 0.334	0.393	0.328 – 0.408
	T	0.076	0.062 – 0.110	0.098	0.080 – 0.142
5.8S	A	0.223	0.217 – 0.229	0.223	0.217 – 0.234
	C	0.297	0.280 – 0.299	0.298	0.280 – 0.301
	G	0.290	0.274 – 0.293	0.290	0.279 – 0.293
	T	0.188	0.185 – 0.210	0.189	0.185 – 0.210

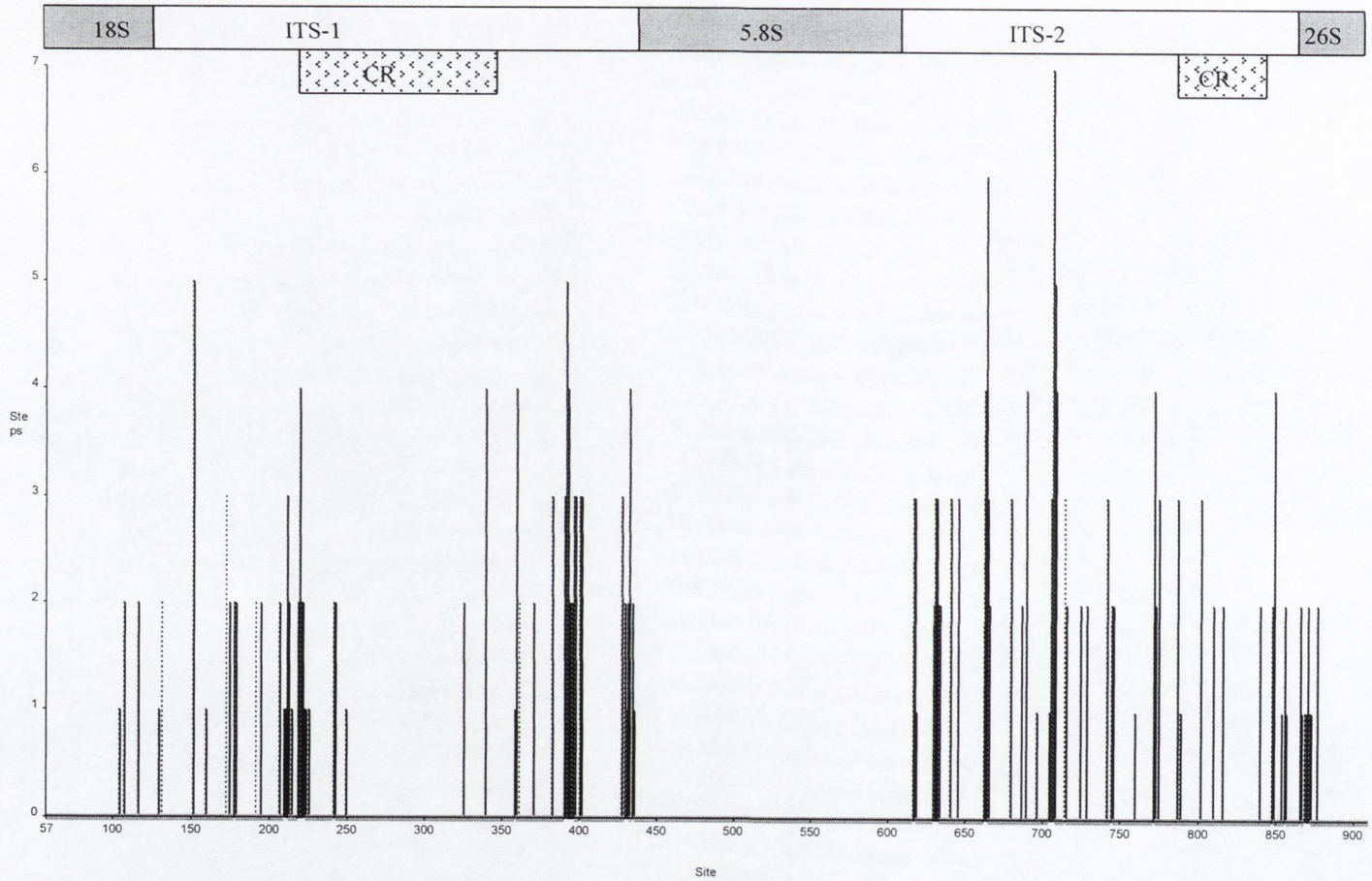


Figure 2.2. Histogram detailing the number of character changes (= steps) at each nucleotide site in the ITS region based on the topology of MP Tree no. 1 generated from the molecular dataset. Spacer and coding regions are indicated above the histogram, cross-hatched sections indicate conserved regions [CR] in ITS-1 and ITS-2.

tree searches were carried out over 100 repetitions using random stepwise addition and the TBR branch-swapping algorithm. Bootstrap resampling was carried out over 1000 replicates using both TBR and NNI branch-swapping.

Descriptive statistics of the two trees are summarised in table 2.5. Two major lineages are evident in both trees; a *Uvaria-Cyathostemma* clade, including *Cyathostemma micranthum* and all the Asian and African species of *Uvaria*; and an *Ellipeia* clade, including *Anomianthus dulcis*, *Uvaria hahnii*, *Rauwenhoffia siamensis* and *Ellipeiopsis cherrevensis* –all close relatives of *Ellipeia* (an additional genus sampled for morphological analysis – see next section). One difference between the two trees is in the position of *Uvaria cordata.* In tree no. 1 *U. cordata* is nested at the base of a *U. grandiflora* clade which forms a sister group to all the other Asian species of *Uvaria*. The two African species, *U. chamae* and *U. faulkneri,* form a sister group to the Asian clade. In tree no. 2 the Asian species also form a single clade, however this time they are grouped into a 'phylocline', with several smaller groups branching away at intervals along the clade. Three terminal pairings from tree 1, *U. grandiflora – U. macropoda*, *U. rufa – U. hamiltonii* and *U. pierrei – U. micrantha* are maintained in tree 2, with *U. vietnamensis*, *U. microcarpa* and *U. cordata* forming single terminal branches between these groups. *Melodorum fruticosum* represents a sister group to the *Ellipeia* and *Uvaria* clades and occupies a basal position in the tree next to the outgroup taxon *Dasymaschalon blumei*.

Table 2.5. *Descriptive statistics for maximum parsimony trees 1 & 2.*

Length	420
Consistency Index (CI)	0.800
Retention Index (RI)	0.604
Rescaled Consistency Index (RC)	0.483

Maximum Likelihood Analysis

The single tree generated from ML analysis is shown in Figure 2.4.The tree was generated using heuristic search settings in Paup 4.0 (100 repetitions using random stepwise addition and TBR). For the maximum likelihood (evolutionary model) settings, base frequencies and the transition/transversion rate were estimated from the matrix. The proportion of variable sites was set according to the gamma distribution (shape parameter 0.4464, estimated from the matrix) and a molecular clock was not enforced. Bootstrapping was carried out over 100 replicates using NNI, and the ML model parameters were those developed during the initial heuristic ML search. The structure of the final ML tree is identical to tree no. 1 generated in the MP search. One difference between the ML tree and MP tree no. 1 is the length of the basal branches, with *M. fruticosum* emerging more distant from *D. blumei* in the ML tree than in the MP trees. The branches supporting the *Uvaria-Cyathostemma* clade and the *Ellipeia* clade are shorter in the ML tree than in the MP tree. An alternative representation of the ML tree topology is shown in Figure 2.6.

Distance Analysis

The single tree generated using the mean character difference + minimum evolution NJ settings in PAUP 4.0 is shown in Figure 2.5. Bootstrap values were calculated over 1000 repetitions using TBR. The basal branches of the tree are the same as those seen in the MP and ML trees, however the structure of the *Ellipeia* group differs between the NJ and the MP + ML trees. Many of the *Uvaria* terminal pair groups seen in the MP and ML trees are also maintained in the NJ tree, i.e. *U. grandiflora – U. macropoda*, *U. pierrei – C. micranthum,* and *U. chamae – U. faulkneri*. However, *U. vietnamensis* and *U. cordata* are paired together at the base of the *U. grandiflora*, *U. macropoda* and *U. microcarpa* clade, a topology not seen in any of the other trees.

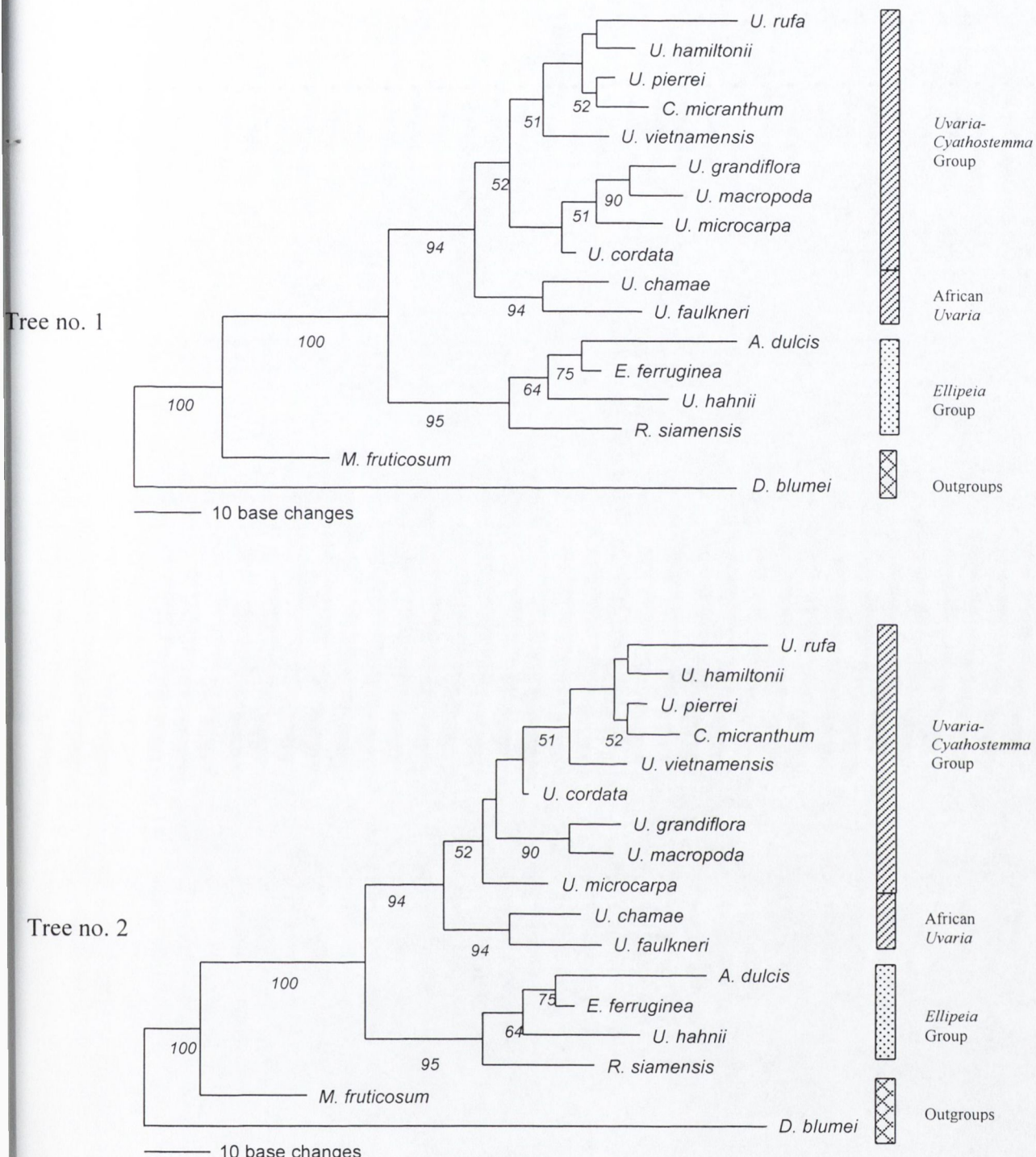


Figure 2.3. Two most parsimonious trees generated from ITS dataset in using Maximum Parsimony [MP] with heuristic search options. Bootstrap values are shown below branches. See text for discussion.

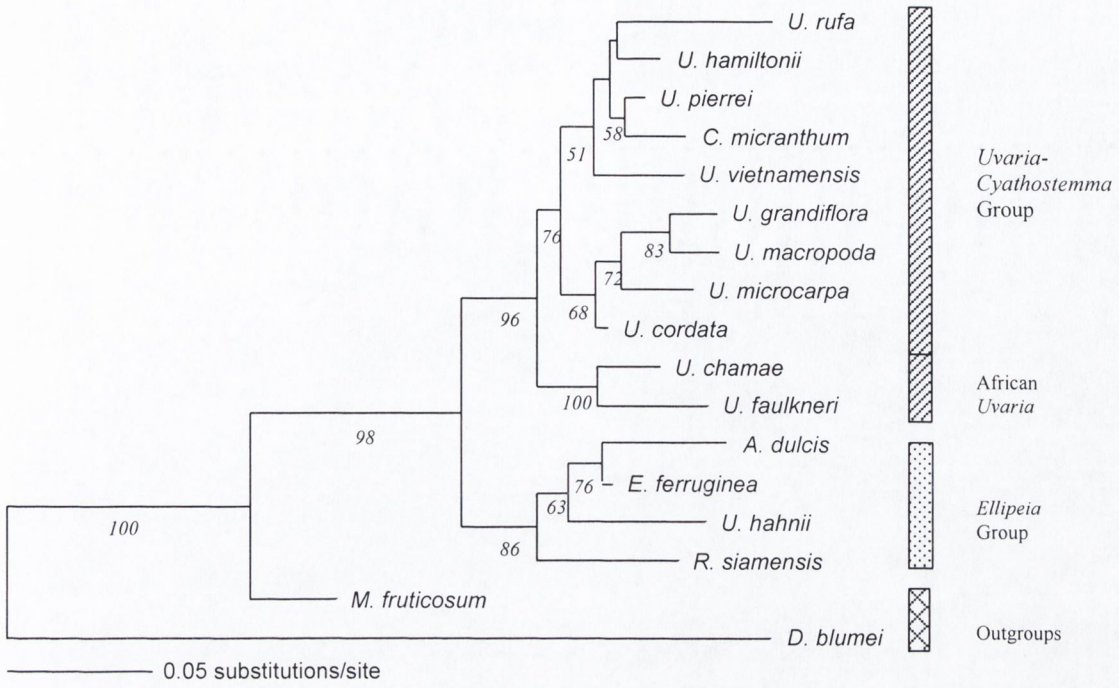


Figure 2.4. Maximum likelihood [ML] tree generated from ITS dataset. Bootstrap values are shown below branches. See text for discussion.

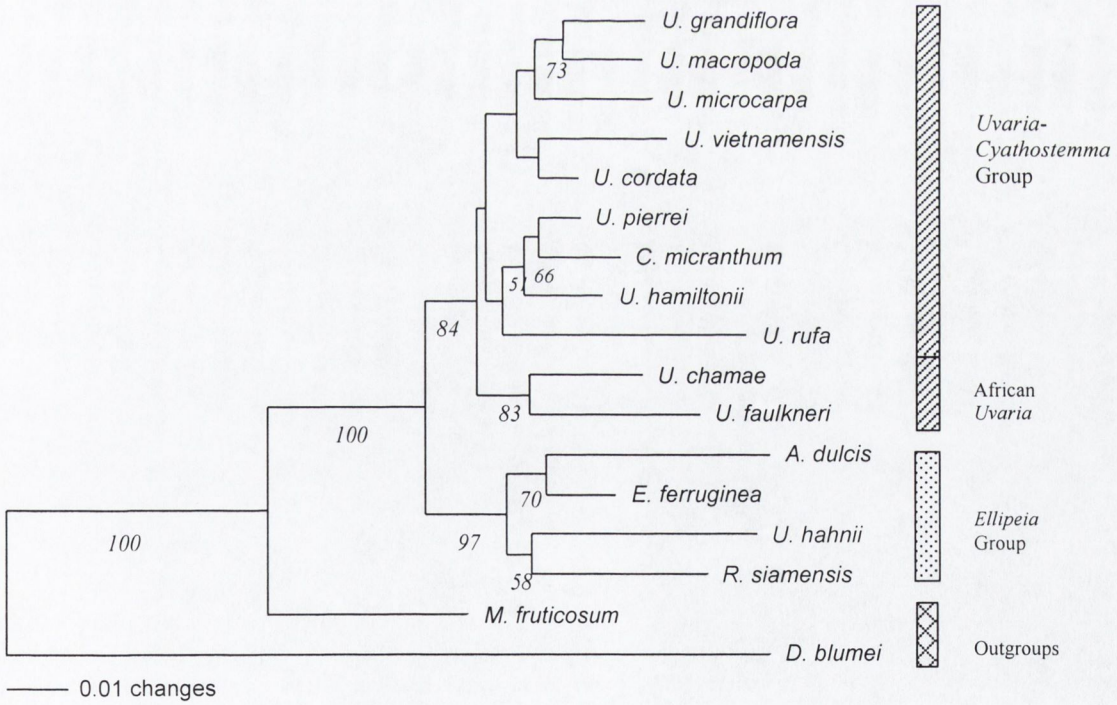


Figure 2.5. Neighbour-Joining [NJ] Tree generated from ITS dataset. Bootstrap values are shown below branches. See text for discussion.

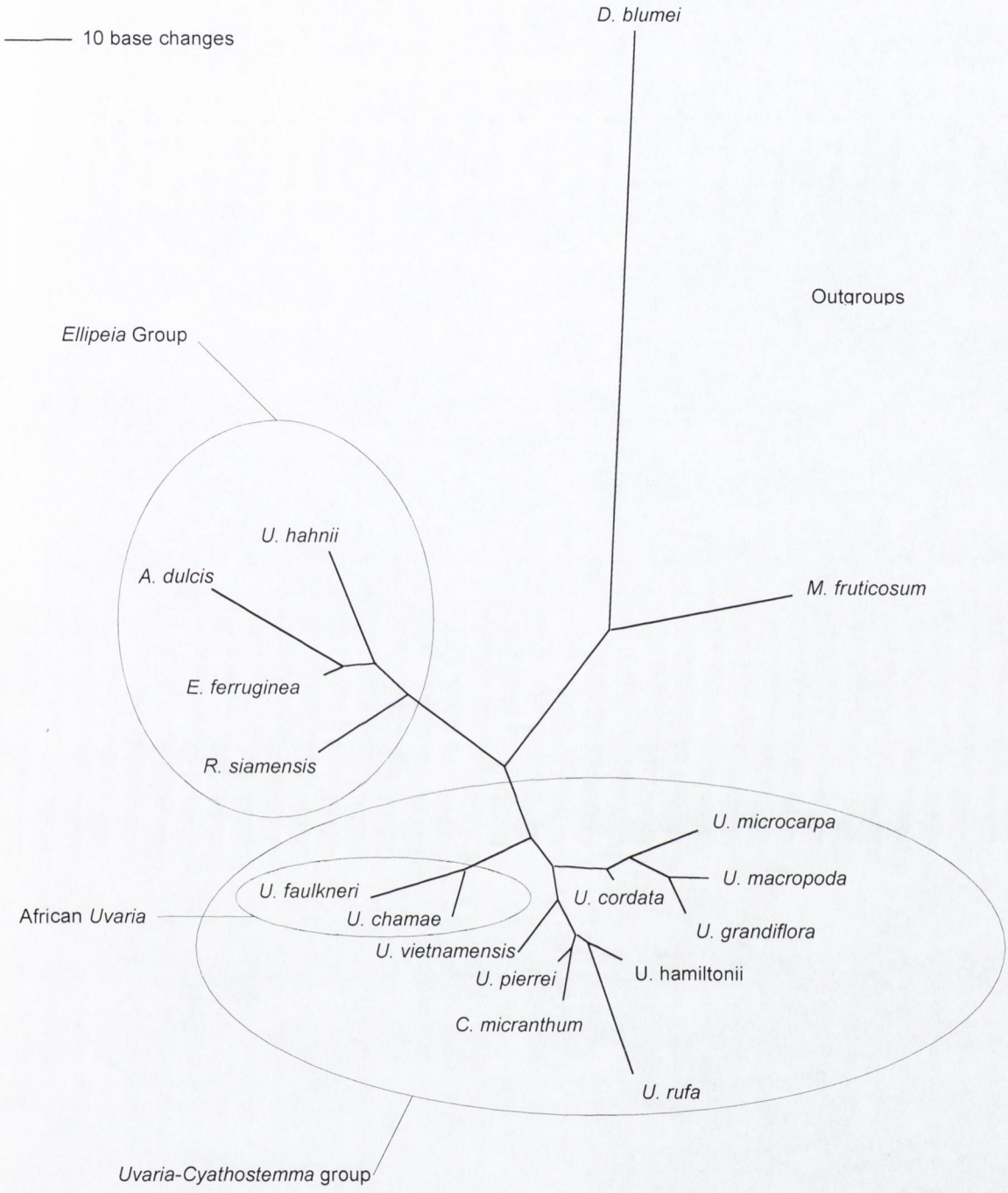


Figure 2.6. An unrooted phylogram based on the ML tree (Figure 2.4 above) with main clades identified. Branch lengths are measured by the number of base changes between taxa.

Analysis of Morphological data

Character Scoring

Phylogenetic analysis of taxonomic groups based on morphological data is difficult and prone to error. The main source of instability in the technique is incorrect scoring of characters, either because they are interpreted incorrectly and/or because they are essentially uninformative. Both problems stem from the subjective nature of character assessment, however with the application of a few basic rules it is possible to minimise the disruption caused by these problems.

The first task is to select homologous rather than analogous characters for analysis. Inclusion of analogous characters (i.e. structures which are deemed similar across a number of taxa because of mis-scoring) as a single homologous character can be highly disruptive to the analysis. Discerning between homologous and analogous structures can best be done by examining them through the various phases of development in each taxon under study. Analogous characters are not without value, for once they have been identified some of them may provide useful data for the matrix in the sense that they may be present in one subset of taxa, but absent from the other.

The second task is to distinguish between size change and shape change. As several workers have pointed out, discrete changes in shape constitute a much greater amount of evolutionary change than changes in size (Alberch *et al.*, 1979), and as such are more informative for phylogenetic analysis. Nonetheless there is some phylogenetic information contained in 'continuous' characters which differ only in terms of size. However, the use of arbitrary size intervals to generate binary scores for particular characters can distort the phylogenetic information that may be contained in these size differences. Genuine polarised size differences can be identified by plotting character measurements - taxon scores which lie near or outside the standard deviation for the entire sample can be viewed as divergent and given a different binary score to the remainder of the sample. However, the point at which divergence from the mean should be interpreted as phylogenetically informative is a subjective matter. A more

objective method is to make size change relative, that is, to correlate it with a second character using e.g. ratio or regression. These correlations can then be plotted as a single numerical value for each taxon on a histogram with a normal distribution curve, or each taxon can be scored on a plot with the two correlation factors as axes. This approach has the added benefit in that it reduces the impact of absolute size in favour of a more shape-change oriented analysis, increasing the probability that it will capture phylogenetically informative data.

In total 49 characters were scored for the matrix (listed in Table 2.6). Six characters were scored on the basis of continuous measurements, the remaining 43 on the basis of discrete presence/absence character states.

Table 2.6. Character scoring for morphological data matrix. See text for discussion.

Character		0	1	2	3
1	Shoot indument	≤ 1mm	≥1mm		
2	Leaf L/W Ratio	≤2.07	2.08-2.44	2.45-3.07	≥3.07
3	Upper blade glabrous	no	yes		
4	Upper blade scabrous	no	yes		
5	Secondary veins	complete	incomplete		
6	Leaves	coriaceous	membranous		
7	Inflorescence	sub-terminal	terminal		
8	Pedicel TS	circular	flattened		
9	Receptacle diameter	≤ 5 mm	>5 mm		
10	Receptacle	raised	flat		
11	Calyx connate	no	yes		
12	Calyx valvate	no	yes		
13	Calyx calyptrate	no	yes		
14	Sepals	flat	concave		
15	Calyx	smooth	tuberculate		
16	Calyx with apicule	no	yes		
17	Calyx splitting	evenly	unevenly		
18	Petals variable in no.	no	yes		
19	Petals membranous	no	yes		
20	Petals thickened	no	yes		
21	Whorls	equal	outer > inner		
22	Inner whorl base	unchanged	glabrous		
23	Inner whorl base	obtuse	narrowed		
24	Inner petals	reflexed	erect	closed	connivent

Table 2.6. *Continued.*

Character		0	1	2	3
25	Marginal glands	absent	present		
26	Petal colour	red/purple	yellow/white		
27	Petal base at maturity	free	connate		
28	Stigma	short	elongate		
29	Stigma	conical	not so		
30	Stigma lobes	narrow	broad		
31	Stigma	glabrous	hairy		
32	Neck at apex of ovary	no	yes		
33	Neck at base of stigma	no	yes		
34	Stamens all fertile	no	yes		
35	Sub-staminodes	absent	present		
36	Locules	glabrous	hairy		
37	Connective apex	papillate	smooth		
38	Connective apex humped	no	yes		
39	Locules stipitate	no	yes		
40	Carpel length	< stamen	= stamen	> stamen	
41	Fruit stipe length	sessile	$1 \leq x \leq 30$ mm	$30 < x \leq 55$ mm	>55 mm
42	Stipe thickened	no	yes		
43	Fruit L/W ratio	$x < 1$	$1 \leq x < 2$	$2 \leq x < 3$	$x = 3+$
44	Ridge or keel present	no	yes		
45	Apicule present	no	yes		
46	Seed no.	1	2-16	16+	
47	Pericarp (dried)	tight	loose	thick	
48	Aril	triangular	lobed		
49	Seed Orientation	perpendicular	angled		

Matrix Assembly

A total of 33 taxa were used to construct the matrix (Table 2.7) including a hitherto undescribed species from the tribe, listed as 'Sp. nov.'. *Melodorum leichardtii* was selected as the outgroup and no *a priori* character weighting was used. With the exception of the African taxa *Uvaria lucida* and *U. chamae,* all the taxa sampled occur in or are restricted to the Continental Asia region.

Table 2.7. Morphological data matrix used for Maximum Parsimony and Neighbour-Joining phylogenetic analysis. The column on the left lists taxon names, the top two rows indicate character number. * indicates missing data. # not used in the final analysis of morphological data due to low level of character congruence with remainder of matrix [which increases the overall number of most parsimonious trees that can be generated from the dataset], but incorporated into combined DNA-Morphological analysis based on the higher levels of overall congruence.

	1 2 3 4 5 6 7 8 9	1 0	1 1 1 2 3 4 5 6 7 8	1 9	2 0	2 1 2 3 4 5 6 7 8	2 9	3 0	3 1 2 3 4 5 6 7 8	3 9	4 0	4 1 2 3 4 5 6 7 8	4 9
U.lamponga	0 2 0 0 0 0 0 0 1	0 0	0 1 0 1 1 * *	0	0 0 0 0 0 0 0 0	1	0 0 1 0 1 1 1 0	1	0 0 0 0 1	1 1 1	* * 1 2 0 1
A.dulcis	0 1 0 0 0 0 1 0 0	0 0	1 0 1 0 0 0 0 0	0	0 0 0 0 0 0 0 0	1	1 1 1 1 1 1 0 0	0	1 1 0 1 0 1 1 1	1 2	1 0 1 0 0 1 0 1 0
U.boniana	0 2 1 0 1 1 0 0 0	0 0	1 0 1 0 0 0 0 0	1	1 1 1 1 1 0 0 1	1	1 1 0 0 1 1 1 0	1	0 0 1 2	1 0 1 0 0 1 0 0 1
U.calamistrata	0 1 0 0 0 0 0 0 0	1 0 0	1 1 0 1 0 0 0 0	0	0 0 0 0 0 0 1 0	1	1 0 0 1 0 1 1 1	0	1 0 0 0 1	1 1 1 0 0 1 2 0 1
U.chamae	0 1 1 0 0 0 0 0 0	0 1 0	0 1 0 0 0 0 1 0	0	0 0 0 0 0 0 * 1	0	0 1 0 1 1 1 0 1	0	0 0 0 1	1 1 2 1 0 1 2 0 1
E.ferruginea	0 0 0 0 0 0 0 0 0	0 1 1	0 1 0 0 0 0 0 1	1	1 1 1 1 1 1 1 1	0	0 0 1 1 0 1 0 1	1	1 1 1 2	1 0 1 0 0 0 1 0 0
E.cuneifolia	0 1 0 0 0 0 1 0 0	0 0 1	0 1 0 0 0 0 0 0	0	1 1 2 0 1 1 0 0	0	1 1 0 1 0 1 1 1	1 2	1 0 0 0 1	0 0 0 0
U.curtisii	1 2 0 0 0 0 0 0 1	0 0 0	1 0 0 1 0 0 0 0	0	0 0 0 0 0 0 0 1	1	0 0 1 0 1 1 1 0	1	0 0 0 1	2 1 2 1 0 1 2 0 1
U.dac	0 2 0 0 0 0 0 0 1	0 0 0	1 0 0 1 1 0 0 0	0	0 0 0 0 0 0 0 1	1	0 0 1 0 0 1 1 0	1	0 0 0 0	1 1 2 1 0 1 2 0 1
U.vietnamensis#	1 2 0 0 0 0 * 0 *	* * * * * * * *	* * * * * * * *	*	* * * * * * * *	*	* * * * * * * *	*	* * * *	2 1 1 0 0 1 2 0 1
U.grandiflora	0 1 0 0 0 0 0 0 1	0 0 0 1 0 0 1 0	0 0 0 0 0 0 0 0	0	0 0 0 0 0 1 0 0	0	0 1 1 1 0 0 0 0	0	0 0	2 1 3 1 0 2 2 0 1
U.hahnii	0 2 0 0 0 0 0 0 0	0 0 0 1 0 0 0 0	0 0 0 0 0 0 1 1	1	1 1 1 1 1 1 0 0	0	1 1 0 1 0 1 1 1	1 1	1 0 1 0 0 1 1 1	1 1
U.hamiltonii	1 1 0 0 0 0 0 0 1	0 0 0 1 0 0 1 0	0 0 0 0 0 0 0 0	0	0 0 0 0 0 1 0 0	0	1 1 1 0 1 0 0 0	0	2 1 1 0 0 1 2 0 1
U.lobbiana	0 1 0 0 0 0 0 0 0	1 0 1 0 1 0 0 0	0 0 0 0 0 0 0 0	0	0 0 0 0 0 1 0 0	0	1 1 0 0 1 0 0 0	1	2 1 1 1 0 1 2 0 1
U.lucida	0 0 1 0 0 0 1 0 0	1 1 0 0 1 0 0 0	0 1 0 0 0 0 0 0	0	0 0 0 0 0 * 1 0	0	1 0 1 1 1 0 1 0	0	0 1	1 1 2 0 0 1 2 0 1
U.lurida	0 2 1 0 1 0 0 0 1	0 0 0 1 0 1 1 1	1 0 0 0 0 0 0 0	0	0 0 0 0 0 0 0 1	0	1 1 1 0 1 0 0 0	2	3 1 1 1 0 1 2 0 1
U.macropoda	0 2 1 0 1 0 0 0 1	0 0 0 1 0 1 1 1	1 0 0 0 0 0 0 0	0	0 0 0 0 0 0 0 1	0	1 1 1 0 1 0 0 0	2	3 1 3 1 0 1 2 0 1
U.cordata	0 0 0 0 0 0 0 1 0	0 1 0 0 1 0 0 0	0 0 0 0 0 0 0 0	0	0 0 0 0 0 1 0 0	0	1 1 1 1 1 0 0 0	0	1 1 1 0 0 1 2 0 1
U.mclurei	0 1 0 0 0 0 0 0 0	1 0 0 1 0 0 0 0	0 1 0 0 0 0 0 0	0	0 0 0 0 0 1 0 0	0	1 1 1 0 1 0 0 0	0	1 1 1 0 0 1 2 0 1
M.leichardtii	0 3 0 0 1 1 1 0 0	1 0 1 0 1 0 0 0	0 0 0 1 1 1 1 3	0	* 1 0 0 0 0 1 1	1	0 1 1 1 1 2 1 0	3	0 1 1 0 0 0
C.micranthum	0 2 1 0 1 1 0 0 0	0 0 0 1 0 1 0 0	0 0 0 1 1 1 1 1	0	1 1 0 1 1 0 0 0	0	1 1 1 0 1 0 0 0	1	1 0 1 0 0 1 0 0 1
U.microcarpa	0 0 0 0 0 0 0 0 0	0 1 0 0 1 0 0 0	0 0 0 0 0 0 0 0	0	0 0 0 0 0 1 0 0	0	0 1 1 1 1 1 0 0	0	0 0	1 1 1 0 0 1 2 0 1
U.narum	0 2 1 0 1 0 0 0 1	0 0 0 1 0 0 0 1	0 0 0 0 0 0 0 0	0	0 0 0 0 0 0 0 0	0	1 1 1 0 1 0 0 0	2	2 1 1 0 0 1 2 0 1
U.pauciovulata	0 0 0 0 0 0 1 0 1	0 0 1 0 1 0 0 0	0 0 0 0 0 0 1 1	1	0 1 1 0 0 0 1 1	0	1 0 1 0 1 1 1 1	2	1 0 0 0 1 1 0 0 0
U.pierrei	0 2 0 0 1 1 0 0 0	1 0 1 0 1 0 0 0	0 0 0 1 1 1 1 1	0	0 1 1 1 0 0 1 1	1	0 1 0 1 0 0 1 2	1	0 1 0 0 1 0 0 0
U.rufa	0 1 0 1 0 0 0 0 0	1 0 1 0 1 0 0 0	0 1 0 0 0 0 0 0	0	1 0 0 0 0 0 0 1	0	0 1 0 0 1 0 0 0	1	2 1 1 0 0 2 2 0 1
U.semicarpifolia	0 0 0 0 0 0 0 1 1	0 1 0 0 1 0 0 0	0 0 0 0 0 0 0 1	3	0 1 1 0 0 0 0 1	1	1 0 1 0 0 0 2	1	0 1 0 0 1 2 0 1
R.siamensis	0 3 0 0 1 1 0 0 0	0 0 0 1 0 1 0 0	0 0 0 1 1 1 1 1	0	1 1 1 0 0 1 1 0	1	0 1 0 1 1 1 1 2	1	0 1 0 0 1 1 0 1
U.sphenocarpa	0 2 0 0 0 0 0 0 0	1 1 0 0 1 0 0 0	0 * 0 0 0 0 0 0	1	1 0 0 1 0 1 1 1	0	1 0 0 0 1	0	1 1 0 0 1 2 0 1
Sp.nov	0 2 0 0 1 1 0 0 0	1 0 1 0 1 0 0 0	0 0 0 0 0 0 0 1	0	* 1 1 1 0 0 1 1	1	0 1 1 0 0 1	*	* * * * * * * 0 *
C.wrayi	0 1 0 0 1 1 0 0 0	* 0 1 0 1 0 0 0 0	0 0 0 1 1 1 1 0	1	1 1 1 1 0 0 1 1	1	0 1 0 1 0 0 2	1	0 1 0 0 1 0 0 0
U.zeylanica	0 2 1 0 1 1 0 0 0	0 0 0 1 0 0 0 0	0 1 0 0 0 0 0 0	0	1 0 0 1 0 1 1 1	0	1 1 0 0 2	1	0 1 0 0 1 1 0 1
C.longipes	0 2 0 0 0 1 0 0 0	0 0 0 1 0 1 0 0	0 0 0 1 1 1 1 1	1	0 0 1 1 1 0 0 1	1	1 0 1 1 0 1 1 0	2	* * * * * * 1 * * *
C.argenteum	0 1 0 0 1 1 0 0 0	0 0 0 1 0 1 0 0	0 0 0 0 1 1 0 0	1	0 1 0 1 1 1 0 1	0	1 1 1 0 1 0 0 0	2	* * * * * 1 * * 0

Results

Maximum Parsimony

Maximum parsimony heuristic searches were carried out using PAUP 4.0. Tree construction was done using random stepwise addition and TBR. Successive weighting using 'mean RC' values for all 49 characters yielded a single tree after one cycle (Figure 2.7). As can be seen from Table 2.8, the Consistency Index [CI] score of 0.38 (with character weights reset to 1 for the purposes of tree interpretation) indicate that there is a large amount of homoplasy in the data matrix. However, the Retention Index [RI] score is high, indicating that although there are a large number of character changes in the tree, the number of changes observed is considerably less than the total number that are possible. This can be explained by the fact that characters with a low CI score often have more than 2 possible states or, where there are just two states, have a more or less equal number of taxa exhibiting the two states. An example of the former is character 2 (leaf L:W ratio), and an example of the latter is character 17 (calyx splitting evenly/unevenly).

Table 2.8. Descriptive statistics for Tree generated in Successively Weighted Maximum Parsimony heuristic search. Unmodified statistics are given to the right, while statistics for the adjusted tree length (based on resetting character weights to 1 after final SW tree has been generated) are shown at left.

	Character weights reset to 1	SW character weights
Length	157	
Consistency Index [CI]	0.379	0.584
Retention Index [RI]	0.703	0.860
Rescaled Consistency Index [RC]	0.266	0.502

While several of these low CI characters, particularly the ones relating to leaf structure, are simply homoplasic, there are a number with high RI values (between 0.8 and 1.0, for example) which are useful for delimiting groups on the tree. Characters 14-16 (calyx structure) are a typical example. Three major groupings within the

Uvaria-Cyathostemma clade can be delimited using this floral character; the terminal *U. grandiflora* clade (calyx calyptrate – character 16), the terminal *U. cordata* clade (calyx connate – character 14) and the basal clade beginning with *C. micranthum* and ending with *U. rufa* (calyx valvate – character 15). However these clades are not well supported by bootstrapping and so are not identified on the tree.

The most informative characters are those indicated on the basal branch of the *Uvaria-Cyathostemma* clade and the *Ellipeia* clade (characters 31, 33, 38, and 39). The latter clade is distinguished by a hairy stigma with a distinct basal neck and stamens with stipitate locules and a humped, waxy connective. The larger *Uvaria* clade is distinguished by a glabrous stigma without a prominent basal neck and stamens with sessile locules and a papillate connective. Both these branches have high bootstrap support. The division clearly separates *Uvaria pauciovulata* and *U. hahnii* (which are firmly nested in the *Ellipeia* clade) from the remainder of the genus.

Within the *Uvaria* clade the distinction between *Uvaria* and *Cyathostemma* is not clear. *Cyathostemma argenteum* and an undescribed species, *Sp. nov.*, both show characters which are intermediate between *Cyathostemma* and *Uvaria* as currently described, and both emerge in an intermediate position in this tree. *Uvaria zeylanica* shows a number of affinities with *Cyathostemma*, principally in leaf and indument type, and it emerges next to *Sp. nov* in the tree.

Uvaria boniana and *U. pierrei* emerge nested in a small clade at the base of the *Cyathostemma* group, and are well separated from the remainder of the genus above and including *U. zeylanica*. While there is reasonably strong bootstrap support (73%) for the separation of *Cyathostemma* (below *sp. nov.*) from *Uvaria* (above *U. zeylanica*), the relationship is clearly paraphyletic. *Cyathostemma* alone is also paraphyletic, with no clearly defined clades that retain strong bootstrap support. The only conservative character that changes between the basal *Cyathostemma* group and the remainder of the *Uvaria* clade is character 24 (inner petals erect to reflexing, *C.I.* 0.6) between *Sp. nov.* and *U. zeylanica*.

Significantly, there are two important character changes between the basal *Cyathostemma* group and *C. argenteum*; character 29 (stigma conical to U-shaped)

and character 22 (inner petal bases glabrous to hairy). The latter state for both these characters is typical of all the Uvarias above *C. argenteum*.

In the *Ellipeia* clade there is strong bootstrap support (93%) for a terminal group including *Ellipeia cuneifolia*, *Uvaria pauciovulata* and *Anomianthus dulcis*. These three taxa have a terminal inflorescence, obovate, membranous petals and 1-3 seeded fruits with a smooth thin pericarp and a small pointed apicule. Below this is *U. hahnii*, which differs in having solitary, leaf-oppose flowers, elongate lanceolate petals and a distinctive, 8-14 seeded fruit with a thickened, verrucose pericarp. *Ellipeiopsis ferruginea,* which emerges below *U. hahnii*, is distinctive in that it is the only species in the tribe which never exhibits a climbing habit, growing as an annual or perennial shrub with a horizontal, creeping stem. It also differs in having a single, sub-apically inserted seed in the mature fruit. The basal taxon in the clade, *Rauwenhoffia siamensis,* has similar fruits to *U. hahnii*, but its flowers are similar to *Melodorum leichardtii*, the outgroup taxon.

Melodorum leichardtii exhibits two important characters which are shared by taxa elsewhere in the family. The first are the reduplicate-valvate petals with a connivent inner whorl, a character typical of many groups in the family but absent from the other Uvarieae except for the unusual case in *Uvaria* of the connivent inner whorl in *U. semicarpifolia*. The second is the moniliform fruit with 2-4 segments each containing a single seed, which is also characteristic of *Desmos*, a climbing genus in Southeast Asia. When 1-seeded the fruits of *M. leichardtii* superficially look like single-seeded fruits of *A. dulcis* or *C. wrayii*. Rooting the tree with *M. leichardtii* as an outgroup has a readily identifiable impact on its structure. It has membranous, glabrous leaves, thickened petals, and a *U. boniana*-like carpel and stamen, explaining why the *Cyathostemma* group is drawn towards the base of the *Uvaria-Cyathostemma* clade, and why *E. ferruginea* and *R. siamensis* are drawn to the base of the *Ellipeia* clade. Appendix 2.2 gives a full account of the CI, RI and RC scores for all characters as mapped onto the Maximum Parsimony trees.

Distance Analysis using Neighbour-Joining

A single NJ tree was generated from the morphological data matrix using both *mean character* and *total character* difference settings under the 'minimum evolution' objective function in PAUP 4.0 (Figure 2.8). Bootstrap values were generated over 1000 replicates using random stepwise addition and TBR. There are some interesting differences between this tree and the Maximum Parsimony tree shown in Figure 2.7.

In terms of overall structure, the basal dichotomy in the MP tree between the *Uvaria-Cyathostemma* clade and the *Ellipeia* clade is maintained in the NJ tree, as is the paraphyletic relationship between *Cyathostemma* and *Uvaria*. Within the terminal *Uvaria* groups, the *U. grandiflora* clade is also the same in both trees. However, there are some small differences in the position of certain taxa in the tree. In the NJ tree, *Uvaria narum* joins *U. rufa* and *U. lobbiana* in a single clade, *U. semicarpifolia* emerges at the base of the terminal group just above *U. zeylanica*, and *Cyathostemma micranthum* joins the base of the *C. wrayii – U. boniana* clade.

In the *Ellipeia* clade there is a dichotomy between the *Ellipeia cuneifolia* clade (including *Anomianthus dulcis* and *U. pauciovulata*) and the remaining taxa.
In general the bootstrap support for all branches in the NJ tree is low, and even the basal dichotomy in the tree is not well supported.

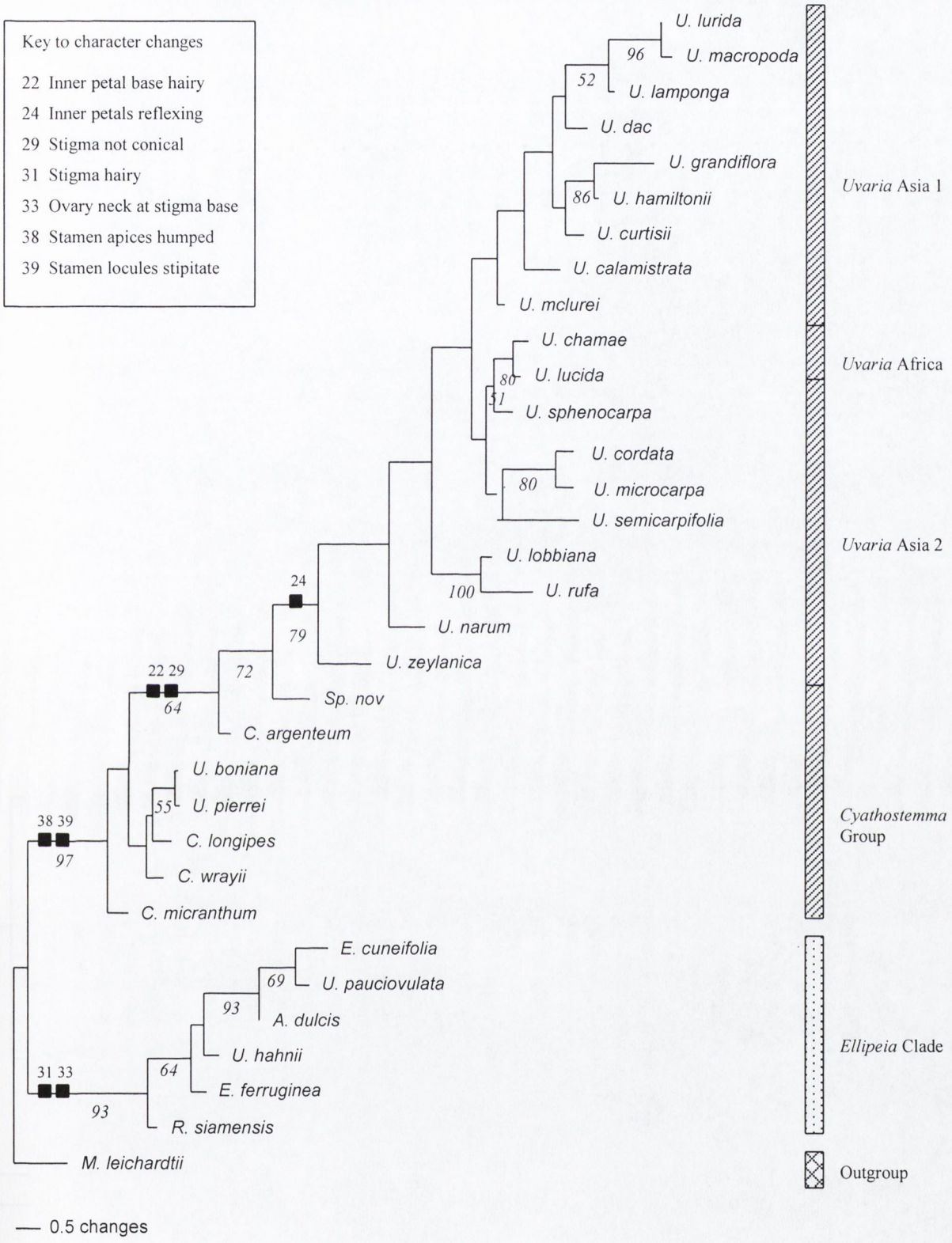


Figure 2.7. Single most parsimonious tree generated from the morphological dataset using mean RC successive weighting. Numbers below the branches indicate bootstrap values. Black pegs indicate important characters that change between various sections of the tree. The bars to the right of the tree indicate the major groups and clades in the tree. See text for discussion.

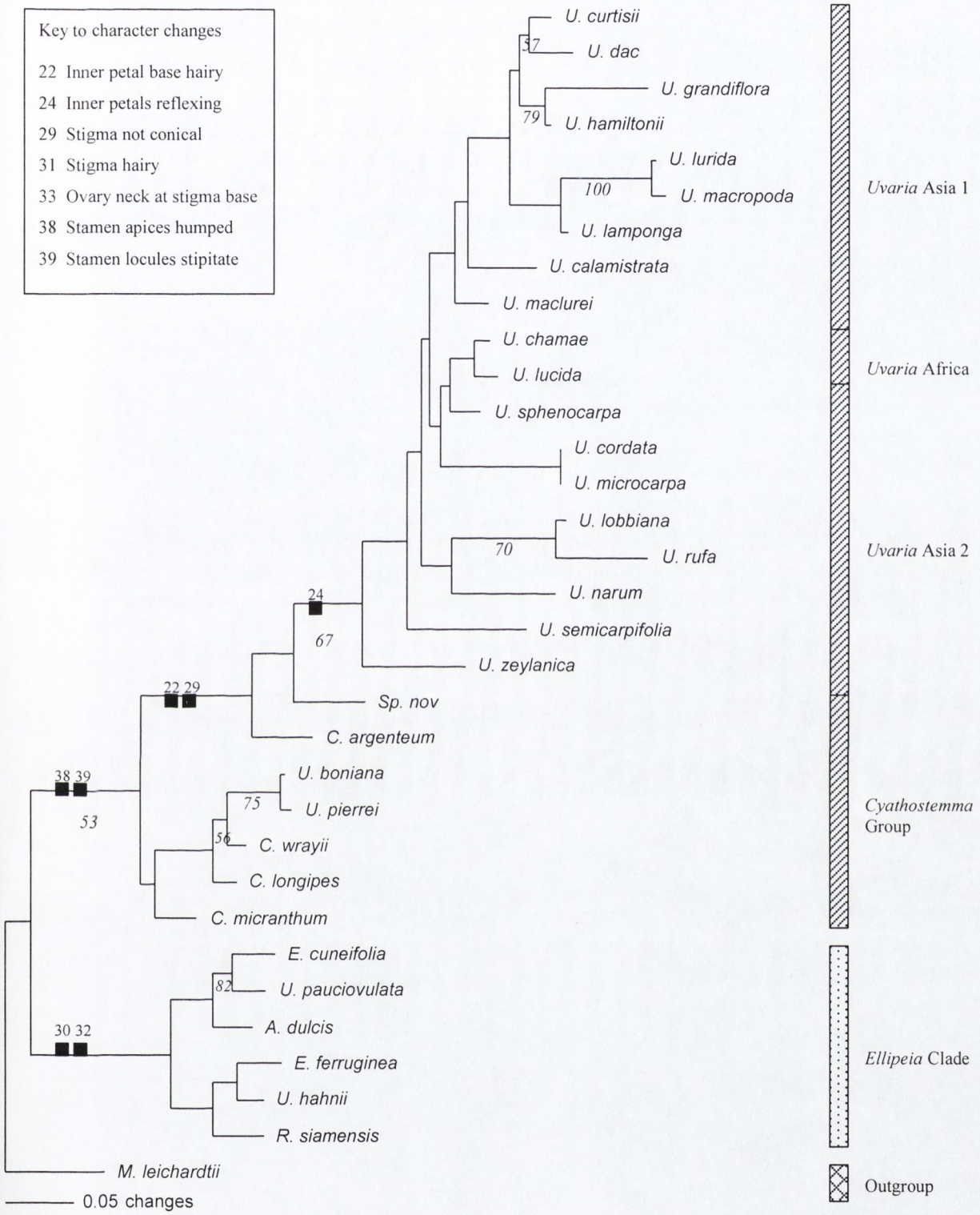


Figure 2.8. Neighbour-Joining tree generated from morphological dataset using mean and total character difference with the minimum evolution objective function. Numbers below the branches indicate bootstrap values. Black pegs indicate important characters that change between various sections of the tree. The bars to the right of the tree indicate the major groups and clades in the tree. See text for discussion.

Combined analysis

Assessment of Similarity Between Datasets

In order to determine the similarity between molecular and morphological datasets it was necessary to remove 20 of the 35 taxa used in the morphological analysis. A MP analysis of this reduced group yielded 3 most parsimonious trees, which were then combined into a strict consensus tree and compared with a consensus tree of the two most parsimonious trees generated from the molecular dataset (Figure 2.7). Bootstrap values for this reduced matrix morphological data tree were calculated over 1000 repetitions using random addition and TBR branch swapping.

Aligning the trees in this way reveals that they agree in terms of the principal dichotomy between the *Uvaria-Cyathostemma* clade and the *Ellipeia* clade. However, the internal makeup of the *Uvaria-Cyathostemma* group is different between the two trees. In the morphological tree (to the left in Figure 2.9), *C. micranthum* and *U. pierrei* are basal within the clade, however in the molecular tree (to the right) these taxa are nested firmly within the clade. To a lesser extent *U. rufa* exhibits the same behaviour between the two trees, emerging in a basal position in the morphological tree but coming out at a terminal node in the molecular tree. The remaining taxa are more or less similarly placed in both trees. In the *Ellipeia* clade, *R. siamensis* is basal in both trees, however the relationships between *U. hahnii*, *A. dulcis* and *E. ferruginea* differ, with the molecular tree placing the latter two as sister taxa, while the morphological tree makes *U. hahnii* the sister taxon to *A. dulcis*. The significant difference observed between the two datasets in terms of the position of *C. micranthum* and *U. pierrei* is mitigated somewhat by the bootstrap values retrieved for both tree topologies. In particular the low values seen for the *C. micranthum* - *U. pierrei* branch in the molecular tree suggest that their location in that tree is equivocal. In other words while the two topologies do disagree there is weak statistical support for this disagreement. As a result it seems there is potential to resolve the instability by combining the datasets.

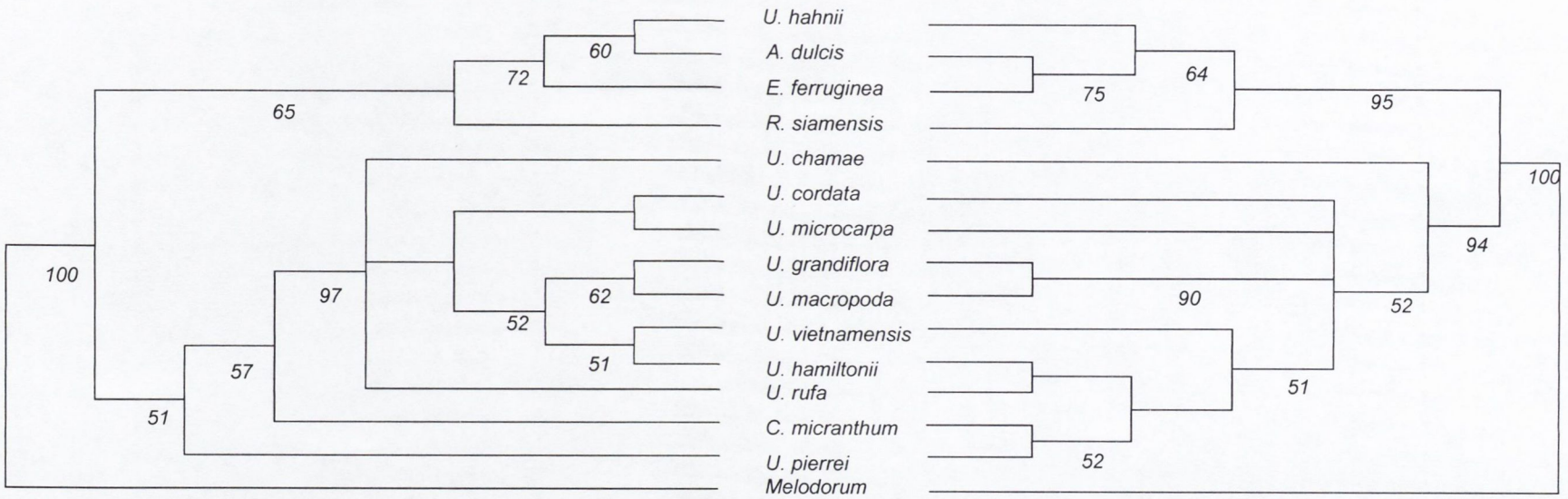


Figure 2.9. A combined representation of MP consensus trees from the morphological (at left) and molecular (at right) datasets. The morphological data consensus tree was derived from a strict consensus of 3 most parsimonious trees generated over 1000 repetitions using random stepwise addition and TBR branch swapping from the reduced matrix of 15 taxa and 51 characters. Index scores for tree: CI = 0.64, RI = 0.75, RC = 0.48. The molecular data consensus tree was generated from a strict consensus of the two most parsimonious trees described in Figure 2.4. Values below the branches indicate bootstrap values calculated for the two datasets over 1000 repetitions using the stepwise addition and TBR settings in PAUP 4.0.

Analysis of Combined Dataset

A PAUP Nexus file was created which combined molecular and morphological data into a single matrix with 15 species common to both datasets included. Characters were given equal Fitch weighting, and a heuristic MP search using random addition and TBR branch swapping yielded 2 most parsimonious trees. A strict consensus of these trees is shown in Figure 2.10. Bootstrap values were calculated over 1000 repetitions using random addition and TBR branch-swapping. The basal dichotomy seen in all molecular and morphological trees between the *Uvaria-Cyathostemma* and *Ellipeia* clades is maintained. Bootstrap support for the *Uvaria-Cyathostemma* branch, at 97%, is higher than that seen in either the molecular or the morphological trees in Figure 2.9. At 92%, support for the *Ellipeia* clade is slightly lower than that retrieved for the molecular tree (95%), but it is considerably higher than the support in the morphological tree (65%). Most significantly however is the emergence of *U. pierrei* and *C. micranthum* as sisters to the *Uvaria* clade, with 90% bootstrap support for a monophyletic *Uvaria* clade that includes all the remaining Asian and African Uvarias.

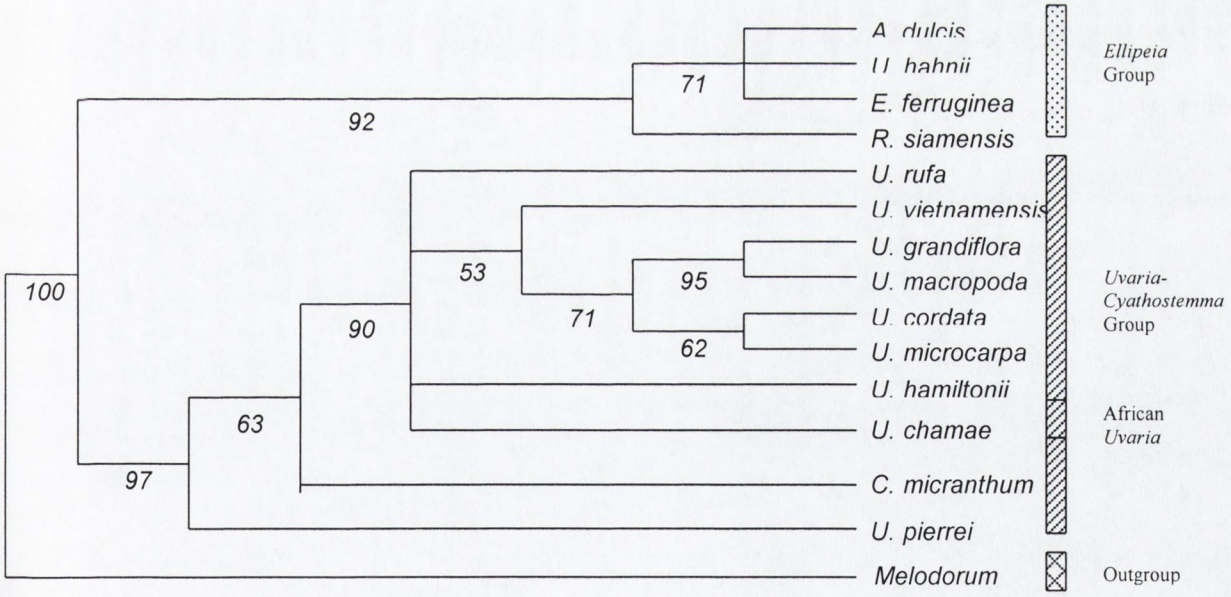


Figure 2.10. Strict consensus tree of 2 most parsimonious trees generated from the combined dataset. Values above the branches indicate bootstrap scores. Bars to the right of the tree indicate the major groups and clades in the tree. Treelength = 389, CI = .715, RI = .625, RC = .447. See text for discussion.

Discussion

Molecular Data

Nucleotide content

Table 2.4 highlights the difference in nucleotide content between ITS-1 & 2 and the 5.8S gene, with the ITS regions showing a much higher G-C content than 5.8S. This pattern is by no means typical of the angiosperms, and as Baldwin *et al.* (1995) point out, G-C content varies considerably between and even within families (see Table 2.9 below). The ITS G-C content of the *Uvarieae* is quite high compared to that seen in members of most of the families in this survey, however the Poaceae show similarly high G-C values.

Table 2.9. Size and percentage G-C content in Uvarieae (Annonaceae) and selected angiosperm families. Additional data from Baldwin *et al.* 1995.

Family	ITS-1		ITS-2	
	Size	% G & C	Size	% G & C
Annonaceae (Uvarieae)	272	67-77	219	71-81
Asteraceae (Madiinae)	254-261	48-51	216-223	50-53
Fabaceae (Galegeae)	221-231	55-60	207-217	50-54
Malvaceae	277-298	49-53	240	57
Poaceae (*Oryza*)	194	73	233	77
Scrophulariaceae (*Mimulus*)	189-214	44-49	203-225	45-48

The existence of conserved regions in both ITS-1 and –2 suggests some level of increased evolutionary constraint and as such correlate well with the existence of a central 'helix-V' region of *Saccharomyces* ITS which Van der Sande *et al.* (1992) identified as being of critical functional importance in the formation of large and

small subunit rRNAs after the transcription of the entire nrDNA region. It is also interesting to note that the 3' end of ITS-1 is highly unstable, indicating relatively lax evolutionary constraint. Van der Sande *et al.* (1992) found that equivalent areas in *Saccharomyces* were of low importance in the formation of subunit rRNAs, and this lack of function would suggest that they could also be under low evolutionary constraint.

One impact of high G-C content is an increased probability of secondary structure formation in transcript copies during PCR. This may partly explain the difficulty experienced in amplifying many of the taxa used in this study.

Phylogenetic Analysis

The basal dichotomy in the MP, ML and NJ trees is well supported by Bootstrap resampling. These branches give rise to two separate clades; an *Ellipeia* clade, containing *Uvaria hahnii*, *Anomianthus dulcis*, *Ellipeiopsis ferruginea* and *Rauwenhoffia siamensis*, and a *Uvaria* clade, containing all the remaining Asian species of *Uvaria*, the two African species of *Uvaria*, and *Cyathostemma micranthum*. Significantly, *Melodorum fruticosum* emerges as a clear sister taxon to these clades.

Two important conclusions can be drawn from the molecular results. The first is that the two African Uvarias, *U. chamae* and *U. faulknerii*, form a strongly supported monophyletic group. Secondly, *Cyathostemma micranthum* emerges nested within the main Asian *Uvaria* clade and suggests that *Cyathostemma*, or part of it, may be derived from within *Uvaria.* Additional support for this scenario is provided by the emergence of *U. pierrei* as a sister to *C. micranthum*, a relationship which is also supported by morphological data. The only major grouping in the Asian *Uvaria* clade which is strongly supported is the twinning of *U. grandiflora* with *U. macropoda* (bootstrap support 90% in the MP tree, 83% in the ML tree and 73% in the NJ tree).

In general, the branches with high bootstrap support in the MP trees are also present in the NJ and ML trees. The topologies of the ML tree (Figure 2.4) and MP tree no. 1 (Figure 2.3) are identical, however MP tree no. 2 (Figure 2.3) differs from these two

trees in relation to the position of *U. cordata* in the terminal *Uvaria* clade. The topology of the NJ tree shows a similar relationship, agreeing with the two MP trees and the ML tree regarding the basal dichotomy and the position of the African Uvarias, but differing in relation to the position of *U. cordata* in the terminal clade.

While groups within the *Ellipeia* clade are well resolved with reasonably robust bootstrap values, the *Uvaria* clade is more unstable. There are several factors which might explain this. The first may be related to differences in speciation rate in the two clades. While total branch length for each taxon is similar between the two clades, there are considerably more species in the *Uvaria* clade than the *Ellipeia* clade. Existing taxonomic knowledge suggests that the sampled ratio of 4:11 is equivalent to the actual species diversity of the two clades in continental Asia, however when Malesia and Africa are taken into account, the *Uvaria* clade is possibly 10 times as large as *Ellipeia*. If we assume that nucleotide evolutionary rates are more or less equal between the two clades then this would account for the relatively lower resolution power of the 600 bp sequence for the Uvarias relative to the Ellipeias.

The strong agreement between the MP, ML and NJ trees and the relatively strong bootstrap support and index support (the MP trees have a CI of 0.80) for these tree topologies suggests that a majority of the variable sites are carrying the same phylogenetic signal. However, certain regions do show higher rates of homoplasy. This can be attributed to the effect of multiple substitutions and/or substitution rate heterogeneity at particular sites. Furthermore, both ITS-1 and to a lesser extent ITS-2 exhibit regions with significant length heterogeneity. These trends suggest that the evolutionary rate is so rapid in the ITS region that relationships at an interspecific level can quickly become obscured. As a result, it seems reasonable to assume that existing homoplasy will be resolved by a greater sampling of taxa in both branches of the ingroup

One additional result is unequivocal from the molecular trees, and that is that *Melodorum* is a sister group to the *Ellipiea-Uvaria* clade.

Morphological Data

As with the trees generated from the molecular dataset, the principal dichotomy in the MP morphological data tree is between *Ellipeia* and *Uvaria-Cyathostemma* clades. Bootstrap support for the clades at 93 and 97% respectively, is quite high compared to values attained for similar phylogenetic analyses of other Annonaceous genera (e.g. van Zuilen, 1996). However, the absence of >50% bootstrapping support for many of the branches indicates that they are supported by characters with a less than optimal mean RC score. Examination of the scoring indices in Appendix 2.2 confirms this, with the characters scoring CI, RI and RC values of 1.0 usually changing unambiguously on the branches with high bootstrap scores.

The main inferences from the MP tree are as follows; (i) a single well-defined *Uvaria* group forms a terminal clade in the *Uvaria-Cyathostemma* branch, (ii) *Cyathostemma* is a paraphyletic intermediate group between the terminal *Uvaria* group and the remainder of the tribe, and this group also includes several taxa currently ascribed to *Uvaria*, and (iii) the *Ellipeia* clade includes *Ellipeia, Rauwenhoffia*, *Ellipeiopsis* and *Anomianthus*, as well as *Uvaria pauciovulata* and *U. hahnii*.

These groups are well defined by floral and fruit characters. The terminal *Uvaria* group, including *U. zeylanica* and *U. narum*, is united in having membranous or coriaceous petals which partially or fully reflex at maturity, U-shaped, usually broad stigmas, and 4-many seeded fruits with a thickened or fleshy pericarp. The intermediate *Cyathostemma* group has erect, usually thickened petals with the inner whorl usually reduced in size, an elongate, glabrous stigma, and usually a sub-glabrous indument at maturity. The *Ellipeia* clade is defined by elongate, hairy stigmas with a distinct basal neck, stamens with stipitate anther locules and a humped connective apex, and fleshy or coriaceous petals with a glabrous base and often a pair of lateral glands on the inner whorl.

In broad terms these relationships are also supported by the NJ tree, the only difference being the emergence of a poorly supported dichotomy at the base of the *Ellipeia* clade. The low bootstrap support seen throughout the NJ tree highlights the influence of successive weighting on the MP tree. When the mean RC weighting is

removed from the characters in the MP analysis, bootstrap support drops to similar levels seen in the NJ tree.

Conclusions

It is clear from both the molecular and morphological trees and the tree generated from the combined dataset that the *Uvaria* group is divided into two distinct clades, one consisting of *Anomianthus*, *Ellipeia*, *Ellipeiopsis*, *Rauwenhoffia*, *Uvaria hahnii* and *U. pauciovulata*, and a second consisting of *Cyathostemma* and the remaining species of *Uvaria*, including the African species *Uvaria chamae* and *U. lucida*.

Erect, thickened petals with a pronounced difference in size between the inner and outer whorls is characteristic of *Melodorum*, *Rauwenhoffia*, *Ellipeiopsis* and *Cyathostemma* and so appears to be plesiomorphic within the group. By extension, and irrespective of where the tree is rooted, there has been a separate origin of coriaceous petals in the terminal *Ellipeia* taxa and in the terminal *Uvaria* group.

Melodorum shares similar stamen structure with the *Ellipeia* clade and similar carpel structure with the *Uvaria-Cyathostemma* clade, suggesting that these respective characters are also plesiomorphic.

CHAPTER 3 – MORPHOMETRIC ANALYSIS OF THE *UVARIA* GROUP

Introduction

The goal of the work included in this chapter has been to identify patterns of morphological variation amongst the *Uvaria* group in continental Asia. This is distinct from the phylogenetic analysis outlined in Chapter 2 in that the goal is to describe phenetic differences between taxa independent from consideration of evolutionary relationships. Furthermore, the emphasis here is on the measurement of continuous characters (i.e. characters which change in size between taxa) rather than the discrete characters (i.e. characters which have different states or shapes in different taxa) used in Chapter 2.

The multivariate phenetic analyses used in this chapter rely on the generation of summary functions to discriminate between taxa. These functions summarise the variability present in all the characters that have been sampled, however different methods emphasise different characteristics of the character data. Principal Components Analysis [PCA] summarises the overall variability of characters, and plots constructed using PCA component axes show if there is any difference between samples/ taxa when each individual sample is treated as a single group. PCA also provides detailed information on the characters which have the most variability and by extension make the greatest contribution to separating the individual samples in the analysis.

Discriminant Analysis [DA] extracts a different kind of information from the character data. Here the emphasis is on discriminating between groups in the sample, so unlike PCA, each individual sample is assigned to an *a-priori* group. DA constructs a series of functions which discriminate between the various *a-priori* groups based on the measurement data provided in each character. This generates information on how robust the group is, and, by plotting the samples using the DA functions, whether certain samples assigned to the group are very similar or very different to other members of the group. If a sample is inputted with no *a-priori* group affiliation, DA will identify which of the groups it should be assigned to. As such the character information generated by DA relates not to the overall variability of each character but rather its usefulness in discriminating between the *a-priori* groups.

These two techniques generate an enormous amount of information about the characters and taxa which have been sampled and provide a powerful mechanism for examining taxonomic relationships – particularly where they are used to resolve taxonomic relationships which are unclear from the sampling of discrete morphological characters. Three separate investigations were completed using these analyses of measurement data: (i) an assessment of inflorescence and fruit character variability in a sample of all *Uvaria* group taxa; (ii) an examination of the usefulness of leaf-shape characters for discriminating between *Uvaria* group taxa; and (iii) an examination of character variability in two difficult taxonomic groups.

Inflorescence and fruit character variability in a sample of all Uvaria group taxa

The principal task for this analysis is to establish whether there are any inflorescence or fruit characters that are universally useful for discriminating between taxa. This can be achieved by analysing two datasets: one that includes all the inflorescence measurements from the complete sample of taxa; and a second which includes all the fruit measurements from the complete sample of taxa. An important distinction will be made between the overall variability of a character (as identified using PCA) and the discriminating variability of a character (as identified using DA).

The use of leaf-shape characters for discriminating between Uvaria group taxa

A problem encountered in the identification of most taxa in the group is the large number of duplicate (sterile) sheets that are created for each flowering or fruiting specimen. In the absence of adequate labelling, as is the case where these duplicate sheets are deposited in secondary herbaria, most of these specimens cannot be identified. Having examined specimens from each taxon it became clear to me that while there were not enough discrete characters to discriminate between the leaves of all the taxa in the *Uvaria* group, there were definite shape patterns associated with the leaves of each taxon. However, these leaf-shape patterns have never been statistically analysed, and so I set about devising a way to do this. Because multivariate analysis has the capacity to compare composite taxon models (i.e. their sum-total character data), I designed a novel centroid-radian technique (see Figures 3.1 and 3.2 and Table

3.1) to see if taxa in the *Uvaria* group can be discriminated from one another on the basis of their leaf *bauplan.*

Difficult taxonomic groups

The Uvaria narum complex

It is clear from the phylogenetic analysis of the *Uvaria* group in Chapter 2 that most taxa can be readily distinguished on the basis of discrete characters. However, there are a number of cases where discrete characters do not adequately distinguish between taxa. This is particularly true for the *Uvaria narum* complex, which includes (under currently accepted names) *U. narum* (Dunal) Bl., *U. lurida* Hook. f. & Thoms., *U. lurida* var. *sikkimensis* King, *U. hookeri* King, *U. macropoda* Hook. f. & Thoms. and *U. eucincta* Beddome ex Dunn (all in India), and *U. concava* Tiejsm. & Binn. and *U. leytensis* (Elmer) Merr. in Malesia. Researchers have been confused as to the correct identity of these taxa from the moment they were first described, and indeed neither Hooker & Thomson (1855, 1872) nor King (1893) had the time or material to fully resolve the relationships of the group in India. Even more recent publications (e.g. Mitra, 1993) fail to make a clear differentiation between the taxa. A crude examination of flowering type material makes it possible to distinguish three groups within the complex based on discrete sepal and petal characters; (i) *Uvaria narum*, (ii) *U. macropoda* and (iii) *U. lurida*, *U. eucincta* and *U. concava.* It is much more difficult to identify taxa based on the commonly used fruit characters - only *U. macropoda* is identifiable with any degree of certainty. The goal of the phenetic analyses of this group is to (a) determine the actual number of taxa in the complex and (b) to identify the characters which best distinguish between them.

Uvaria cordata and U. microcarpa

Another problem group includes *Uvaria cordata* (Dunal) Alston and *U. microcarpa* Champ. ex Benth. The two species share very similar leaves, flowers and fruits, and while certain authors have sought to unite the taxa, (e.g. *U. macrophylla* var. *microcarpa*, Finet & Gagnep., 1906), more recent work (e.g. Phạm-hoàng Hộ, 1991) makes very little distinction between the two species. Statistical analysis of character variance has been employed to determine (a) whether the two taxa are distinct and (b) the characters which best discriminate between them.

Materials and Methods

Specimen Measurement and Construction of Dataset

All the analyses presented in this chapter are based on the complete dataset shown in Appendix 3.1. Table 3.1 provides a key to the 43 morphological characters scored for each sample case.17 characters were derived from leaf radian measurements based on the radian overlay sheet shown in Figure 3.1. Two additional leaf characters (18 and 19 in Table 3.1) were also measured. Of the remainder, 17 were based on length measurements of various inflorescence structures, and seven were based on measurements of fruit structure.

A total of 364 herbarium specimens from 31 taxa were sampled (Appendix 3.2). Where multiple measurements were possible for certain characters on selected sheets, the values were averaged before being recorded to the complete dataset spreadsheet. In the case of leaf radian measurements, every effort was made to ensure that the leaf sampled from each sheet was mature and entire and did not show any asymmetry or distortion caused by stress, infection or herbivory. Again, where multiple measurements were possible, the data was averaged before being entered into the spreadsheet.

Analysis Techniques

Data-normalisation was achieved either by conversion of measurements into ratios (in the case of leaf-radians) or replacement of measurements with their Log_{10} value (in the case of all other characters). These transformations are listed in the right-hand column of Table 3.1. Figure 3.2 shows how the leaf ratio values were calculated and what they were designed to represent.

Principal Components Analysis [PCA], Discriminant Analysis [DA] and the Independent Samples t-Test were used to analyse the dataset using SPSS 8.0® (© 1997, SPSS Inc.). The procedures involved in using these techniques, including the

functioning of the various analysis settings, are discussed in Norušis/ SPSS (1994) and SPSS (1998).

For PCA, cases with missing values were excluded casewise. Jackson (1993) showed that the broken-stick method (Frontier, 1976) was generally the most accurate test of component significance across a range of data matrix types, particularly where correlation was not significant between characters in the matrix. However, the same work also demonstrated that where there is a strong correlation between characters in the matrix, such as is often encountered in morphometric analyses, the Kaiser-Guttman $\lambda > 1$ stopping rule is also accurate at determining the significance of components. A Pearson correlation test on the matrices used in the analyses presented here showed a significant correlation between characters. As a result, components with a $\lambda > 1$ were regarded as significant for all the analyses presented in this chapter. For the DA analyses, prior probabilities for group membership were computed from group sizes. Characters were added in each analysis either stepwise or simultaneously.

Table 3.1. Character measurements used in multivariate analysis. Mode of transformation from sampled distributions to normal distribution indicated in right hand column. [# Log transformations are Log_{10}]. A-Q and L1 and L2 represent leaf radians. Figures 3.1 and 3.2 show how the leaf radians were measured and then converted into ratios that summarise leaf shape.

Number	Abbreviation	Measurement	Normal Transformation#
Leaf			
1.	L	Overall length of leaf	L/L1
2.	L1	Length from base of midrib to widest point	Log_{10} $(L1)^2$
3.	L2	Length from widest point to midrib apex	Log_{10} $(L2)^2$
4.	M	Width of leaf at widest point	Log_{10} $(M)^2$, L/M
5.	A	Length of radian A	A/L1
6.	B	Length of radian B	B/L1
7.	C	Length of radian C	C/L1
8.	D	Length of radian D	D/L1
9.	E	Length of radian E	E/L1
10	F	Length of radian F	F/L1
11.	G	Length of radian G	G/L1
12.	H	Length of radian H	H/L1
13.	K	Length of radian K	K/L2
14.	N	Length of radian N	N/L2
15.	O	Length of radian O	O/L2
16.	P	Length of radian P	P/L2
17.	Q	Length of radian Q	Q/L2
18.	PET	Length of petiole	Log_{10} (PET)
19.	V.NO	Number of Veins	Log_{10} $(V.NO)^2$
Inflorescence			
20.	PED.C	Pedicel length	Log_{10} (PED.C)
21.	PED.W	Pedicel width	Log_{10} (PED.W)
22.	PED.N	Peduncle length	Log_{10} $(PED.N)^2$
23.	Br.W	Lower bract width	Log_{10} $(Br.W)^2$
24.	Br.L	Lower bract length	Log_{10} $(Br.L)^2$
25.	SEP.L	Sepal length	Log_{10} (SEP.L)
26.	SEP.W	Sepal width	Log_{10} (SEP.W)
27.	i.PETW	Inner petal width	Log_{10} (i.PETW)
28.	i.PETL	Inner petal length	Log_{10} (i.PETW)
29.	i.PETM	Distance of widest point from petal base	Log_{10} (i.PETM)
30.	REC	Width of receptacle	Log_{10} (REC)
31.	CAR	Length of carpel	Log_{10} (CAR)
32.	STG.W	Width of stigma	Log_{10} $(STG.W)^1$
33.	STG.L	Length of stigma	Log_{10} (STG.L)
34.	STM	Length of stamen	Log_{10} (STM)
35.	LOC	Length of stamen locule	Log_{10} (LOC)
36.	STW	Width of stamen	Log_{10} $(STW)^1$
Fruit			
37.	STIP	Length of stipe	Log_{10} (STIP)
38.	STIP.M	Width of stipe – middle	Log_{10} $(STIP.M)^{1,2}$
39.	STIP.APX	Width of stipe – apex	Log_{10} $(STIP.X)^{1,2}$
40.	FR.W	Width of monocarp	Log_{10} (FR.W)
41.	FR.L	Length of monocarp	Log_{10} (FR.L)
42.	N.SD	Number of seeds	Log_{10} $(N.SD)^{1,2}$
43.	APIC	Length of apicule	Log_{10} $(APIC)^1$

Key: [1] only used in analysis of *U. narum – U. lurida – U. macropoda*. [2] only used in analysis of *U. cordata – U. microcarpa*.

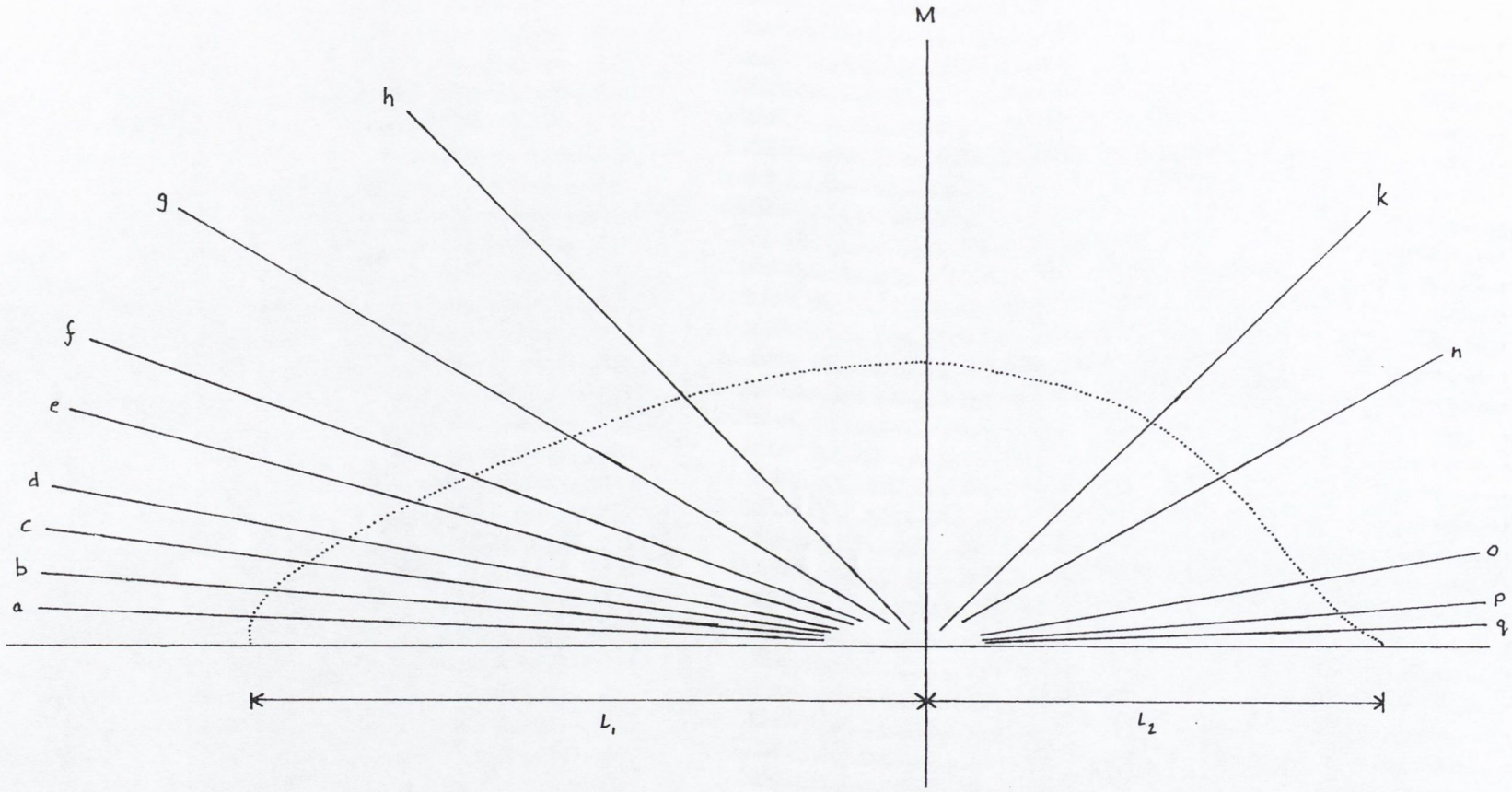


Figure 3.1. Radian measurements for sampling leaf shape. A-K, M and N-Q represent external points on the leaf margin. L1 represents the distance from the leaf base to the widest point of the leaf as measured along the midrib to line M. L2 measures the distance from the line M to the apex. Radians were drawn onto a tracing paper overlay sheet which was centered over each leaf by aligning L1 - L2 along the leaf midrib and M with the widest point.

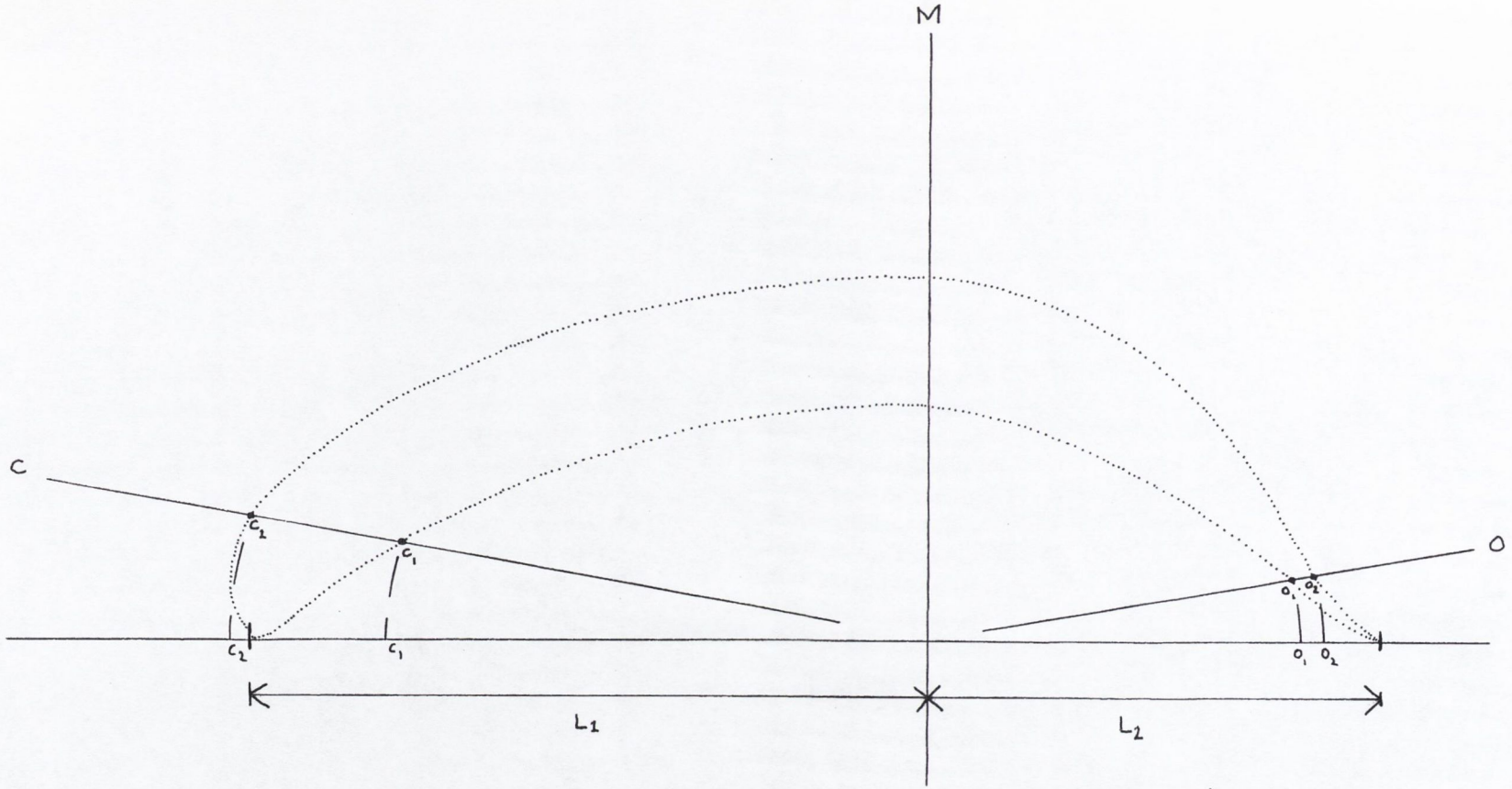


Figure 3.2. Calculation of leaf radian ratios. Two leaf types (1 and 2) are superimposed onto the main axes described in Figure 3.1. The interception points between Radians C and O (designed to measure leaf base and leaf apex shape respectively) and these leaf outlines are indicated. In order to convert the measurements C1 and C2 into ratios, these values are divided by L1. The distance from the origin (intercept of L1-L2 and M) to C2 is greater than L1, so when C2 is divided by L1, the value prodiuced is greater than 1.0. Similarly, C1 is less than L1, producing a value less than 1.0. In this way, leaf types with a cordate base typically produce C ratio values around 1.0 and leaf types with a cuneate or retuse base have much lower C ratio values. Radian O measures apex shape. Leaf types with a narrow or acuminate apex (such as leaf type 1, above) generally have lower O values (O/L2) than leaf types with a broad or obtuse apex (leaf type 2, above).

Statistical Analysis

Inflorescence and fruit character variability in a sample of all Uvaria group taxa

Because nearly all species in the group flower and fruit only once a year it is normal that herbarium material exhibits *either* flowers *or* fruits, but usually not the two together. As a result, examining the relative importance of each character required that floral and fruit characters be analysed separately. Principal Components Analysis was carried out on the floral and fruit datasets to establish which were the most variable characters. Discriminant Analysis of the datasets was then carried out to establish which characters best discriminate between taxa in the group. For DA, simultaneous entry resulted in higher correct classification rates than the stepwise technique for the floral dataset, however there was no difference between simultaneous and stepwise entry scores for the fruit dataset (Table 3.2).

The use of leaf-shape characters for discriminating between Uvaria group taxa

The analysis of variance in leaf shape within the entire group was approached in two ways. In the first approach, all cases in the complete dataset were entered, meaning that each taxon had between 1 and 25 entries, depending on sampling frequency. In the second approach mean ratio values were calculated for each taxon so that only 31 values (i.e. for 31 taxa) were used. Both PCA and DA were used to analyse the first sample, however only PCA was used for the second. PCA settings were identical to those in the analyses in Section 1. For the Discriminant Analysis, simultaneous addition of character variables again generated the most accurate classification rates across all taxa (Table 3.2).

Difficult taxonomic groups

The Uvaria narum complex

For the analysis of the *U. narum* complex two initial sub-samples of data from the relevant taxa were made (floral and fruit characters) and these were analysed using PCA to determine if any general clustering patterns were evident in the principal component plots. Leaf data was excluded from these PCA analyses because it obscured the variability present in the floral and fruit characters. Discriminant Analysis was then carried out on leaf & flower and leaf & fruit data. For the flowering

specimens, taxon identity (and DA group membership) was assigned based on the presence of discrete characters. For the fruiting specimens, taxon identity was assigned based on the cluster-group that each specimen belonged to in the PCA plot of fruit measurement data. In the case of material identified on the label as *U. eucincta*, *U. concave, U. leytensis* or *U. hookeri*, group membership was not determined prior to the Discriminant Analysis. Stepwise entry of character variables for DA using Wilks' Lambda (minimisation of Wilks' Lambda/ maximisation of *F* statistic) proved the most powerful entry method for both the leaf-flower and leaf-fruit datasets (Table 3.2).

Uvaria cordata and U. microcarpa

For the analysis of differences between *Uvaria cordata* and *U. microcarpa*, an Independent t-Test was carried out on all characters shared by the two species. Identification of significant differences in mean character values at $P < .01$ was preceded by a test of equality of variance in the two groups using Levene's test (Manly, 1986). Where the two groups showed different amounts of variance in a particular character, a separate-variance t-Test was used. Where variance was not significantly different, the pooled-variance t-Test was used.

Table 3.2. Comparison of grouping effectiveness of stepwise and simultaneous addition methods for Discriminant Analysis of datasets in each section : % of cases assigned to correct taxon group. Stepwise addition scores are for Wilks' Lambda method.

		% of cases assigned to correct taxon group	
		Stepwise addition	Simultaneous addition
Dataset sub-sample		%	%
Total dataset – floral characters	(Section 1)	89.5	96.9
Total dataset – fruit characters	(Section 1)	80.2	80.2
Total dataset – leaves only	(Section 2)	43.2	60.3
U. narum complex – leaves and flowers	(Section 3)	100.0	81.3
U. narum complex – leaves and fruits	(Section 3)	100.0	53.3

Results

Inflorescence and fruit character variability in a sample of all Uvaria group taxa

Table 3.3 details the results of the Principal Components Analysis of the floral dataset, and identifies the characters with the most overall variability. Carpel length has the highest Component 1 factor loading, and so is the most variable character, however the first seven characters in the table all show a high factor loading for this component. Pedicel length shows the highest factor loading (in this case negative) for Component 2, while stigma length has the highest factor loading for Component 3. The latter two characters also show a relatively low factor loading for Component 1. Stigma width has the highest factor loading Component 4, however this component is not significant.

A scatter plot generated using Principal Component 1 & 2 scores for each valid case in the flower dataset is shown in Figure 3.3. *Uvaria grandiflora* has by far the largest carpels in the group and also has a high Component 1 score on the plot, whereas the taxon with the smallest carpels, *Cyathostemma micranthum*, has the lowest Component 1 score. The position of these two taxa is indicative of a general trend in the plot, with smaller-flowered species having generally low Component 1 scores, and large-flowered species having high scores. For Component 2, species with broad stigmas and stamens such as *U. microcarpa*, *U. cordata* and *U. rufa* tend to have high positive scores, whereas those with long pedicels, such as *U. narum* and *U. hamiltonii* tend to have negative scores. This accurately reflects the factor loadings for these characters.

Table 3.4 details PCA results for the fruit dataset. Only 4 characters were sampled in this analysis and only the first principal component was found to be significant using the Kaiser-Guttman test. Monocarp length has the highest factor loading for component 1, however monocarp width and seed number are also strongly correlated with this factor.

Table 3.5 (DA) identifies the floral characters that best discriminate between taxa in the group. Stamen locule length, sepal length and petal length are the most significant

characters in this regard, emerging with the highest correlation scores for Discriminant Functions 1, 2 and 3 respectively. Stigma length (highest score for Discriminant Function 4) and pedicel length (highest score for Discriminant Function 5) are also important.

A scatter plot generated using Discriminant Function 1 & 2 scores for each valid case is shown in Figure 3.4. While there is a strong similarity between the relative positions of many taxa in this plot and the PCA plot, for example the triangular relationship between *U. grandiflora, U. microcarpa* and *Cyathostemma micranthum*, each taxon is much more clearly grouped into a cluster. Many of these clusters are distinct from the general swarm of data points, for example *Uvaria hahnii*, *Uvaria boniana* and *Uvaria zeylanica*. Significantly, there are already differences evident between a number of the difficult taxa which are examined separately later in this chapter (the *U. narum* complex and *U. cordata* - *U. microcarpa*).

Table 3.6 details the results of the Discriminant Analysis of fruit measurement data. There is a greater level of agreement between the PCA and DA results for fruit structure (Tables 3.4 and 3.6 respectively) than is seen for floral structure, however this is probably due to the fact that a significantly smaller sample of characters was taken from fruits than from flowers. One clear difference between the PCA and DA analyses of fruit structure is the importance of stipe length. This character emerges with the lowest factor loading for Principal Component 1 yet has the highest correlation with Discriminant Function 1, indicating that while the overall variability of the character is lower than for other characters, this variability contains a strong discriminating power.

Table 3.3. Principal Components Analysis of log-normalised flower measurements for total dataset: eigenvalue scores, % of variance and character correlation coefficients for first 4 component axes. Characters ordered on the basis of Factor Loadings. Character coefficients less than ± 0.1 are left blank. Significant components (based on Kaiser-Gutman criteria) indicated by *.

	Component 1*	2*	3*	4
Eigenvalue	7.474	1.279	1.216	.801
% of variance	57.489	9.841	9.354	6.160
Cumulative %	57.489	67.331	76.685	82.845
Character				
Carpel length	.910	.106	.230	
Sepal width	.853		-.311	-.106
Stamen locule length	.852	.368	.102	-.176
Petal length	.851	-.394		.160
Stamen length	.849	.356	.211	-.167
Petal width	.848	-.338		
Petal midpoint	.847	-.362		.152
Pedicel width	.769	.129	-.211	-.317
Sepal length	.734		-.542	
Stamen width	.682	.406	.140	
Pedicel length	.539	-.512	.254	
Stigma length	.492		.702	.252
Stigma width	.426	.394	-.294	.717

Table 3.4. Principal Components Analysis of log-normalised fruit measurements for total dataset: Eigenvalue scores, % of variance and character correlation coefficients for 2 component axes extracted in analysis. Characters ordered on the basis of Factor Loadings. Significant components (based on Kaiser-Gutman criteria) indicated by *. Character coefficients less than ± 0.1 are left blank.

	Component 1*	2
Eigenvalue	2.702	.803
% of variance	67.543	20.079
Cumulative %	67.543	87.622
Character		
Monocarp length	.944	
Monocarp width	.870	-.231
Number of seeds	.867	-.226
Stipe length	.549	.833

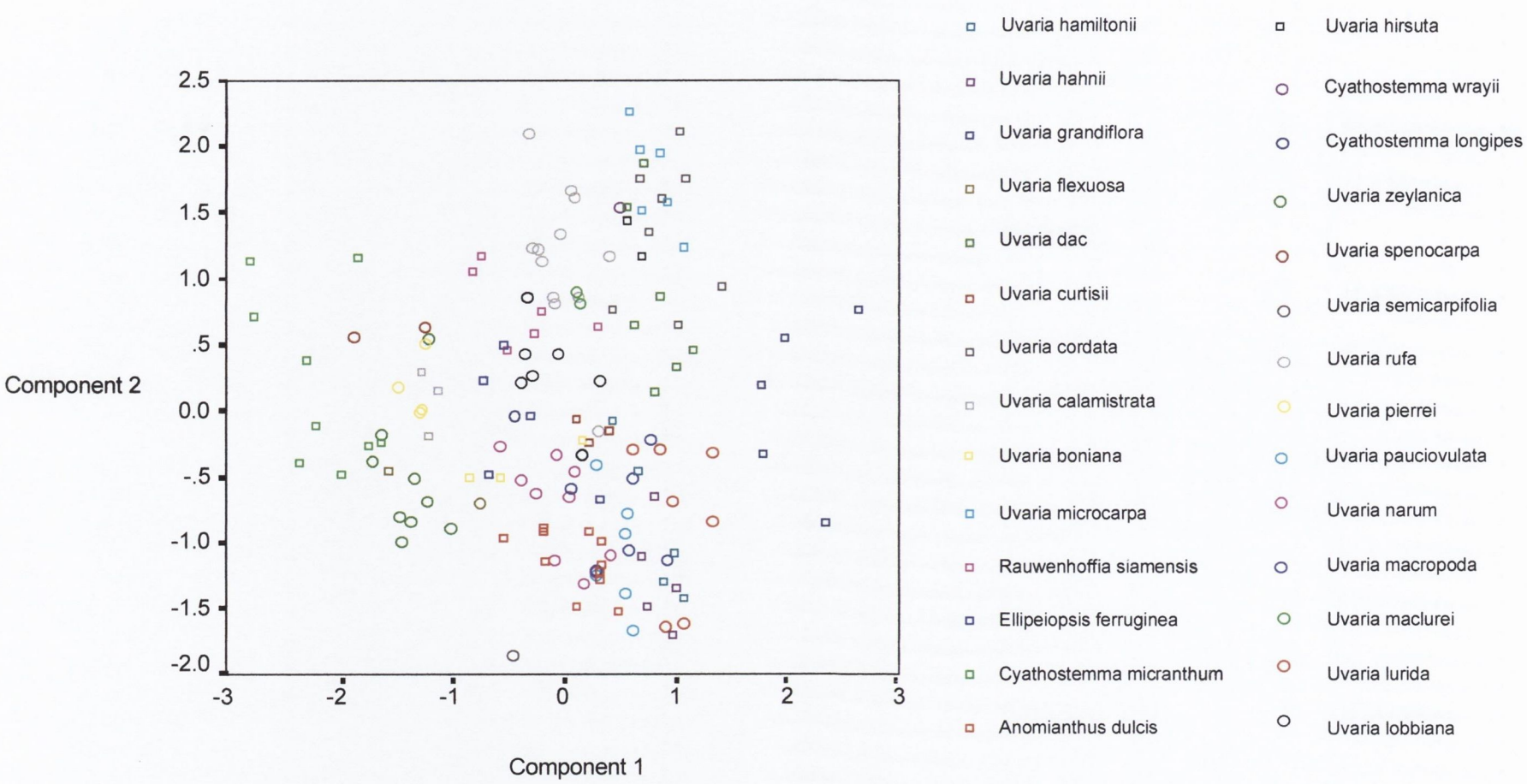


Figure 3.3. Principal Components Analysis of log-normalised floral measurements for complete dataset: plot of individual scores for components 1 and 2.

Table 3.5. Discriminant Analysis of log-normalised flower measurements for total dataset: Eigenvalues, % of total variance, Canonical correlation and pooled within-groups correlations for first 5 standardized canonical Discriminant functions. Characters ordered by absolute size of correlation within each function, beginning with function 1.

	Function 1	2	3	4	5
Eigenvalue	21.636	9.300	7.007	3.429	2.711
% of variance	43.3	18.6	14.0	6.9	5.4
Cumulative %	43.3	61.9	75.9	82.8	88.2
Canonical Correlation	.978	.950	.935	.880	.855
Character					
Stamen locule length	.821	.280	-.203	-.275	.127
Stamen length	.768	.374	-.180	.120	.068
Carpel length	.520	.264	.226	.200	.323
Sepal width	.486	-.120	.296	-.193	.003
Sepal length	.498	-.558	.418	-.106	.156
Petal length	.387	-.003	.681	.088	.019
Petal width	.387	.229	.650	-.309	-.253
Pedicel length	.135	.251	.353	-.282	.634
Stamen width	.263	.075	-.021	.104	.059
Stigma width	.138	-.085	-.008	-.112	.096
Pedicel width	.318	.008	.081	-.146	-.236
Petal midpoint	.315	.089	.490	.044	-.029
Stigma length	.150	.295	.184	.462	.036

Table 3.6. Discriminant Analysis of log-normalised fruit measurements for total dataset: Eigenvalues, % of total variance, Canonical correlation and pooled within-groups correlations for first 4 standardized canonical Discriminant functions. Characters ordered by absolute size of correlation within each function, beginning with function 1.

	Function 1	2	3	4
Eigenvalue	13.132	3.810	3.214	2.030
% of variance	59.2	17.2	14.5	9.1
Cumulative %	59.2	76.4	90.9	100.0
Canonical Correlation	.964	.890	.873	.818
Character				
Stipe length	.918	-.383	-.060	-.079
Monocarp length	.424	.858	-.265	-.119
Monocarp width	.314	.812	.486	-.078
Number of seeds	.280	.657	-.128	.689

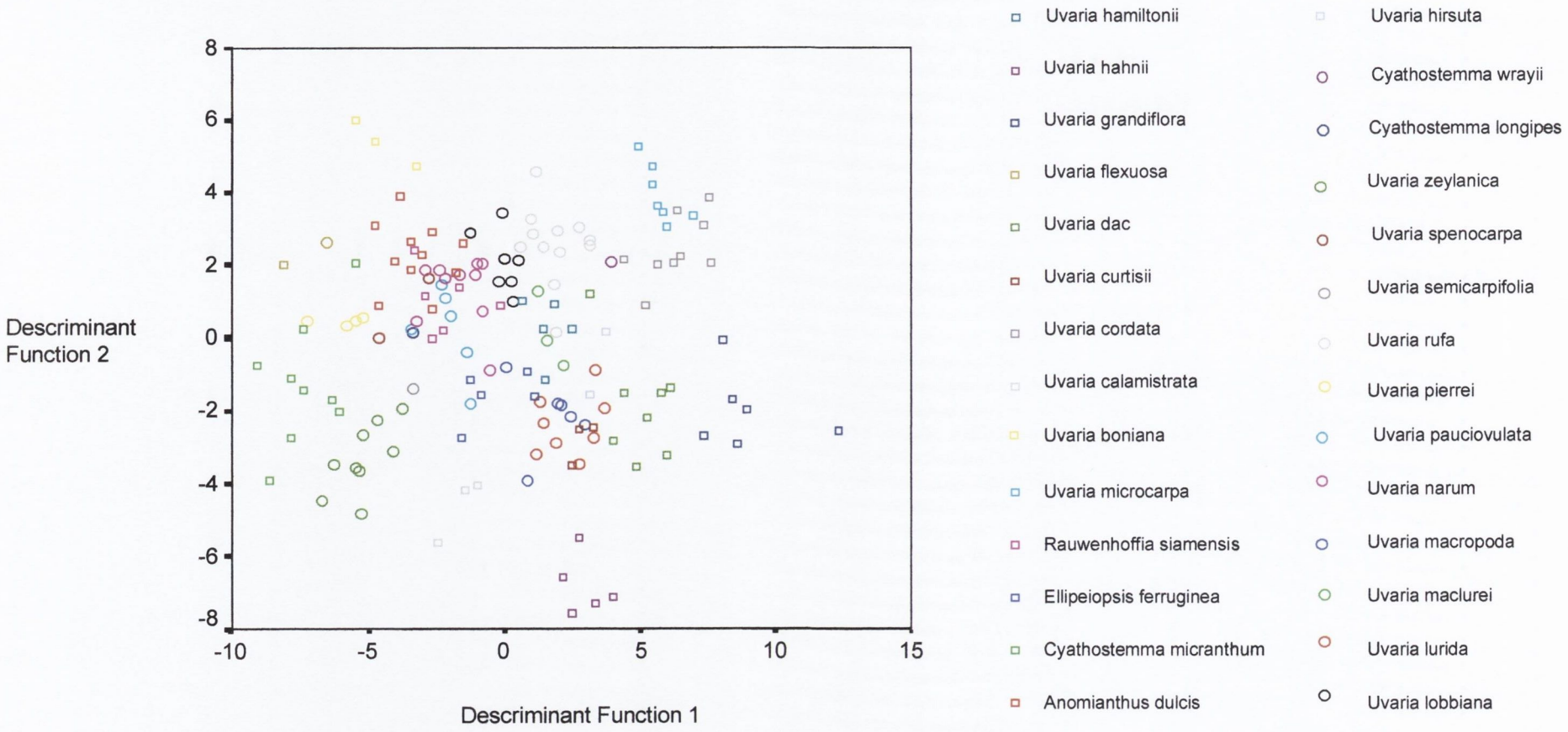


Figure 3.4. Descriminant Analysis of log-normalised floral measurements for complete datatset: Plot of individual scores for Discriminant Functions 1 and 2.

The use of leaf-shape characters for discriminating between Uvaria group taxa

PCA results for sampling approach 1 (all cases in the dataset entered with no *a-priori* grouping) are shown in Table 3.7. DA results for sampling approach 1 (all cases in the dataset entered with *a-priori* grouping) are shown in Table 3.8. In both the PCA and DA analysis, leaf character C/L_1 emerges as highly correlated with the major summary axis (Component 1 in Table 3.7 and Function 1 in Table 3.8 respectively). A scatter plot generated using Discriminant Function 1 & 2 scores for each valid case is shown in Figure 3.5. A second plot from the same discriminant analysis, this time using only the group centroid scores, is shown in Figure 3.6. Taxa with cordate leaf bases tend to score highly on Function 1, reflecting a C/L_1 score close to 1.0 (see Figure 3.2), while those with cuneate or narrowly retuse bases and C/L_1 scores much less than 1.0 tend to have low scores. Taxa whose leaves are relatively broad score highly on Function 2, whereas those with long narrow leaves tend to have low scores.

Table 3.7. Principal Components Analysis of leaf ratio measurements for total dataset: Eigenvalue scores, % of variance and character correlation coefficients for first 4 component axes. Characters ordered on the basis of Factor Loading. Scores less than ± 0.1 are left blank. Significant components (based on Kaiser-Gutman criteria) indicated by *. A-Q and L_1 and L_2 represent leaf radian measurements. Figures 3.1 and 3.2 show how the leaf radians were measured and then converted into ratios that summarise leaf shape.

	Component 1*	2*	3*	4*
Eigenvalue	8.829	3.451	1.237	1.059
% of total variance	55.183	21.566	7.730	6.621
Cumulative %	55.183	76.749	84.479	91.100
Character				
E/L1	.907	.351	.102	
D/L1	.907	.346		.114
C/L1	.899	.299	-.168	.191
F/L1	.892	.367	.159	-.104
G/L1	.869	.371	.208	-.193
L/M	-.837	.135		.358
B/L1	.826	.269	-.313	.341
H/L1	.799	.344	.283	-.232
K/L2	.757	-.520	-.115	-.232
N/L2	.756	-.575		-.158
O/L2	.675	-.656	.170	.131
A/L1	.669	.191	-.468	.471
L/L1		.835	.414	
P/L2	.596	-.674	.283	.240
Q/L2	.495	-.633	.379	.297

Table 3.8. Discriminant Analysis of leaf ratio measurements for total dataset: Eigenvalue, % of variance, Canonical Correlation and pooled within-groups character correlations for first 5 standardized canonical Discriminant functions. Characters ordered by absolute size of correlation within each function beginning with function 1. A-Q and L_1 and L_2 represent leaf radian measurements. Figures 3.1 and 3.2 show how the leaf radians were measured and then converted into ratios that summarise leaf shape.

	Function 1	2	3	4	5
Eigenvalue	3.195	1.782	1.017	.809	.477
% of Variance	35.6	19.9	11.3	9.0	5.3
Cumulative %	35.6	55.5	66.8	75.8	81.1
Canonical Correlation	.873	.800	.710	.669	.568
Character					
C/L1	.619	.048	-.227	.453	-.125
B/L1	.617	-.129	-.412	.432	-.024
K/L2	.591	.042	.237	.005	-.329
N/L2	.586	-.046	.374	.039	-.422
A/L1	.583	-.311	-.516	.208	-.014
L/M	-.552	-.282	.031	-.012	.356
D/L1	.544	.173	-.177	.481	-.082
P/L2	.358	-.306	.475	.357	-.052
O/L2	.440	-.259	.468	.234	-.199
G/L1	.480	.470	-.118	.578	-.124
F/L1	.481	.383	-.098	.560	-.101
E/L1	.515	.324	-.105	.539	-.151
H/L1	.375	.371	-.115	.488	-.015
PET	.507	.219	.235	-.442	.517
L/L1	-.191	.272	-.373	.453	.067
Q/L2	.228	-.217	.347	.362	.002

Table 3.9 details PCA results for sampling approach 2 (mean taxon ratio values derived from *a-priori* single-taxon groups). Figure 3.7 shows a scatter plot generated using principal component 1 and 2 scores for each taxon. Figure 3.8 shows a scatter plot generated using mean taxon scores for C/L_1 and L/L_1, the characters most closely associated with principal components 1 and 2 respectively. In order to show variability in leaf apex shape relative to L/L_1 (C/L_1 summarises leaf base shape) Figure 3.9 has been included showing a scatter plot generated using mean taxon scores for P/L_2 and L/L_1. Both of these graphs also contain mean leaf outlines for species with extreme values on the character axes. As in the previous two analyses, C/L_1 emerges in this PCA analysis as the most highly correlated character with Component 1 (Table 3.9). However, both PCA analyses differ from the DA analysis in relation to the most important character uncorrelated with C/L_1. The former both clearly identify this character to be L/L_1 (which summarises whether a leaf is ovate, elliptical or obovate), while DA identifies G/L_1 (an intermediate measure of leaf base shape and length to width ratio). As a general guide, Appendix 3.3 shows leaf bauplan outlines for all taxa in miniature form.

Table 3.9. Principal Components Analysis of mean leaf ratio measurements for each taxon: Eigenvalue scores, % of variance and character correlation coefficients for first 3 component axes. Characters ordered on the basis of Factor Loading. Scores less than ± 0.1 are left blank. Significant components (based on Kaiser-Gutman criteria) indicated by *. A-Q and L1 and L2 represent leaf radian measurements. Figures 3.1 and 3.2 show how the leaf radians were measured and then converted into ratios that summarise leaf shape.

	Component		
	1*	2*	3
Eigenvalue	10.088	2.766	.998
% of variance	67.252	18.442	6.656
Cumulative %	67.252	85.694	92.350
Character			
C/L1	.956	.155	
D/L1	.939	.276	
E/L1	.919	.367	
B/L1	.898		-.108
L/M	-.890		.273
F/L1	.890	.421	
K/L2	.869	-.338	-.223
N/L2	.866	-.401	-.165
G/L1	.862	.458	
H/L1	.834	.460	.161
O/L2	.796	-.554	.193
A/L1	.762	-.113	-.268
P/L2	.708	-.582	.387
Q/L2	.611	-.510	.584
L/L1	-.155	.854	.440

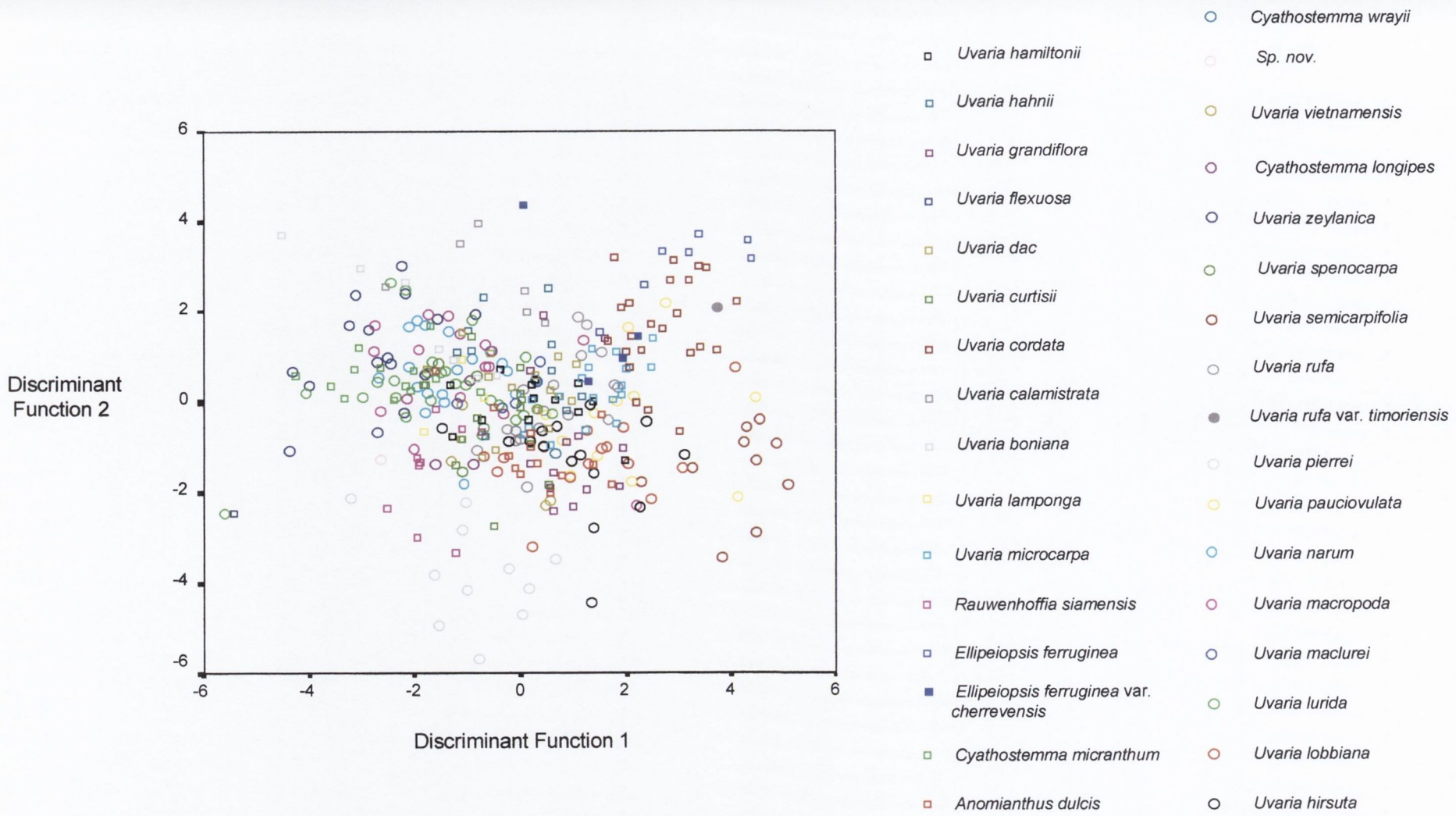
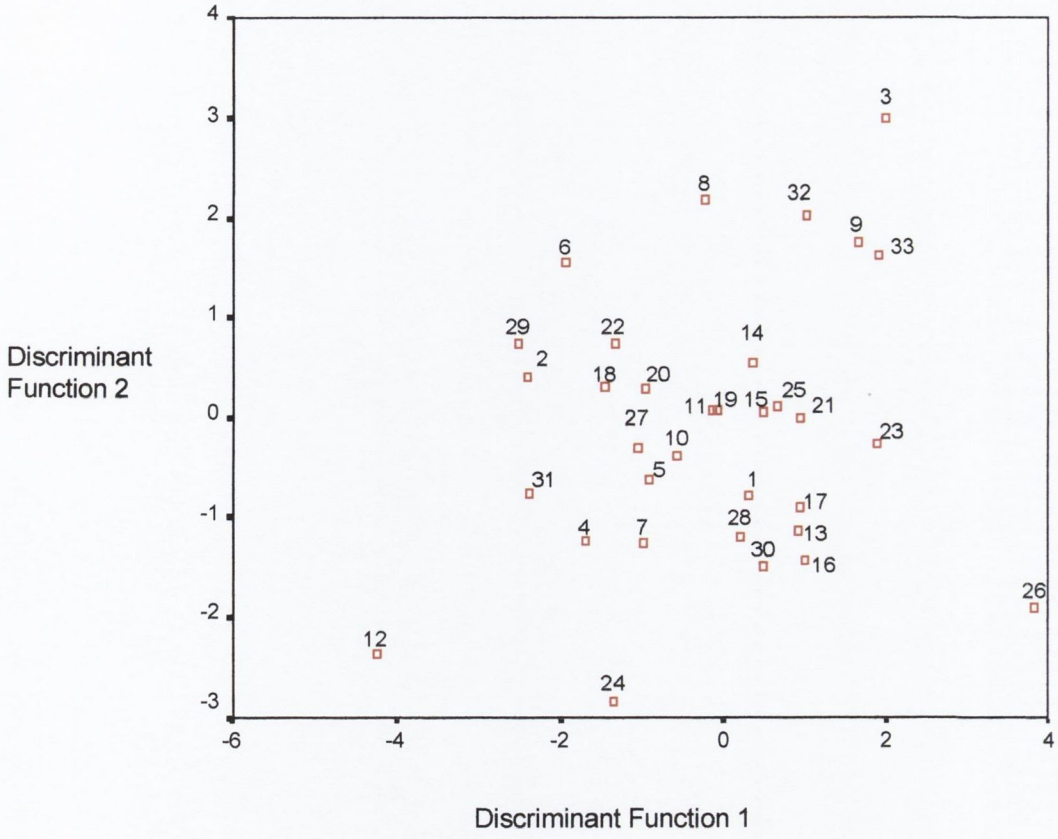
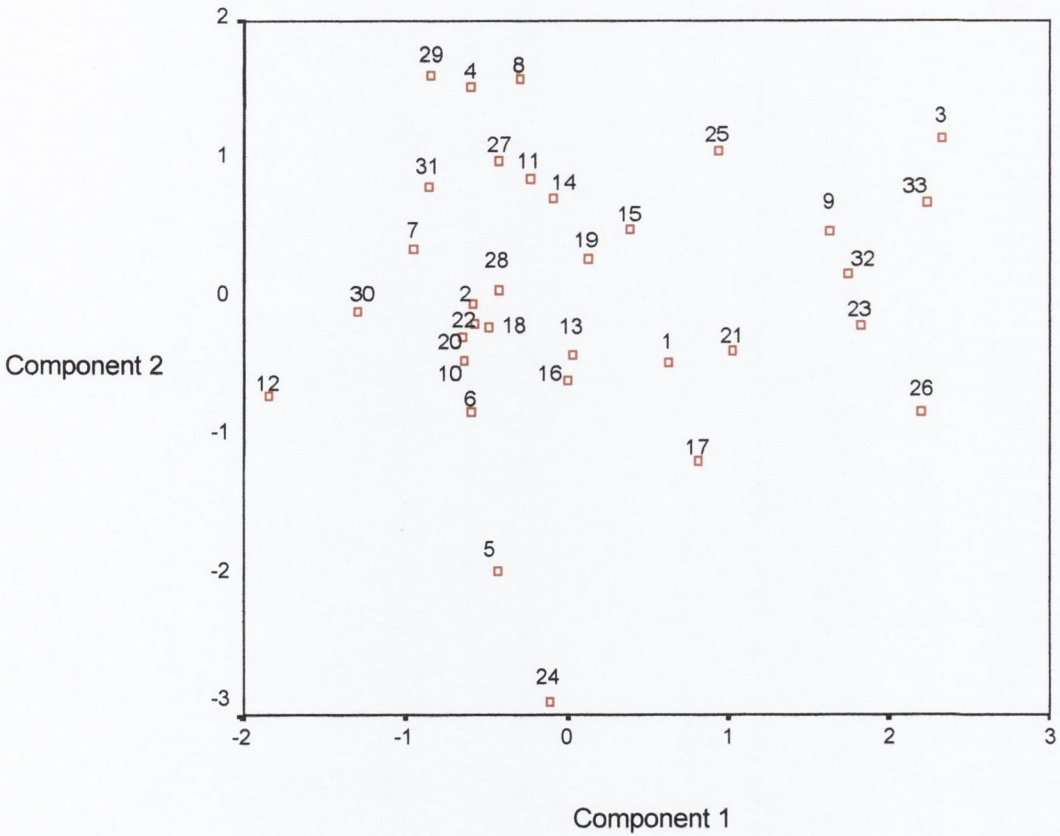


Figure 3.5. Discriminant Analysis of leaf ratio measurements for complete datatset: Plot of individual scores for Discriminant Functions 1 and 2.



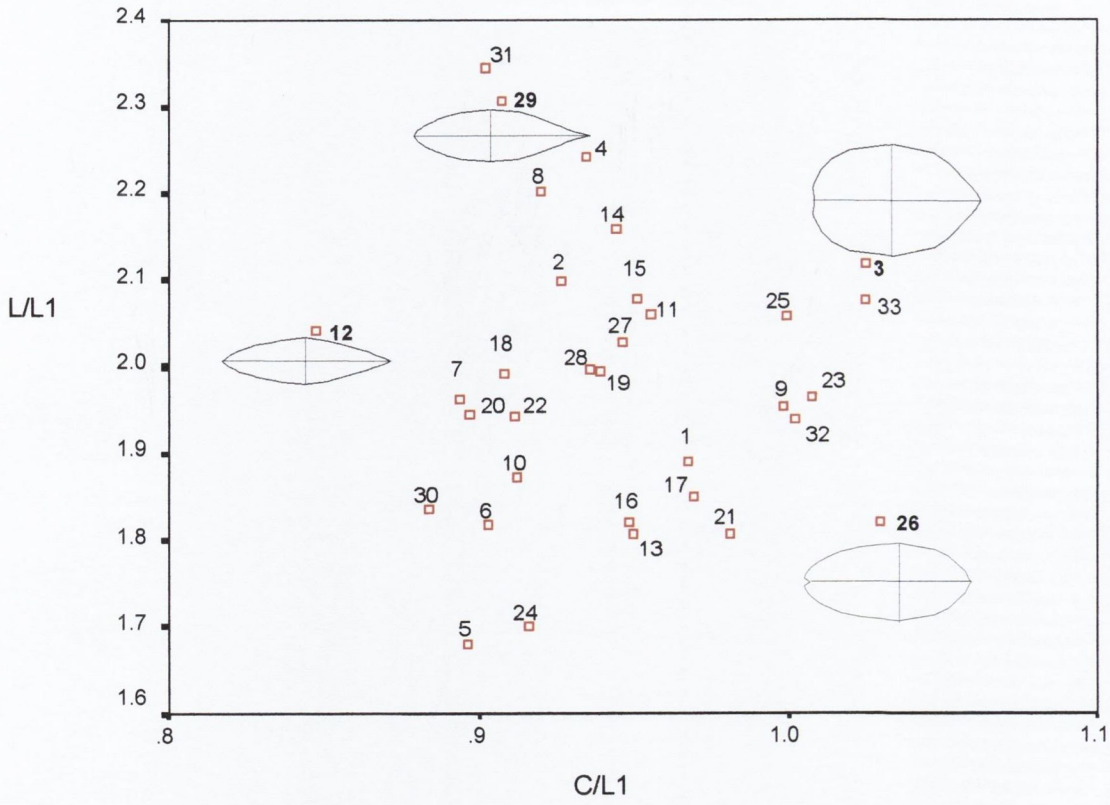
1. *Anomianthus dulcis*
2. *Rauwenhoffia siamensis*
3. *Ellipeiopsis ferruginea* var. *cherrevensis*
4. *Cyathostemma micranthum*
5. *Cyathostemma wrayii*
6. *Cyathostemma longipes*
7. *Uvaria boniana*
8. *Uvaria calamistrata*
9. *Uvaria cordata*
10. *Uvaria curtisii*
11. *Uvaria dac*
12. *Uvaria flexuosa*
13. *Uvaria grandiflora*
14. *Uvaria hahnii*
15. *Uvaria hamiltonii*
16. *Uvaria hirsuta*
17. *Uvaria lobbiana*
18. *Uvaria lurida*
19. *Uvaria maclurei*
20. *Uvaria macropoda*
21. *Uvaria microcarpa*
22. *Uvaria narum*
23. *Uvaria pauciovulata*
24. *Uvaria pierrei*
25. *Uvaria rufa* var. *rufa*
26. *Uvaria semicarpifolia*
27. *Uvaria sphenocarpa*
28. *Uvaria vietnamensis*
29. *Uvaria zeylanica*
30. *Uvaria lamponga*
31. *Sp. Nov.*
32. *Ellipeiopsis ferruginea* var. *ferruginea*
33. *Uvaria rufa* var. *timoriensis*

Figure 3.6. Discriminant Analysis of leaf ratios for complete dataset: plot of group centroid scores for each taxon for Discriminant Functions 1 and 2. Taxon number identifications at right.



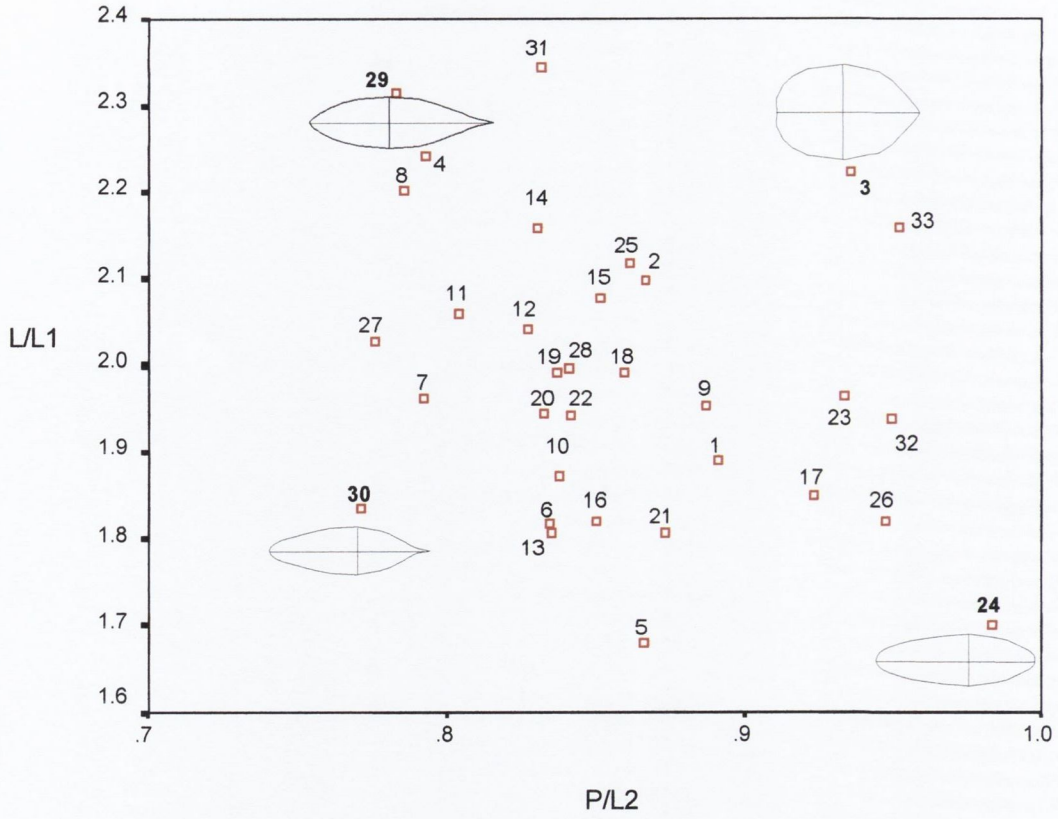
1. *Anomianthus dulcis*
2. *Rauwenhoffia siamensis*
3. *Ellipeiopsis ferruginea* var. *cherrevensis*
4. *Cyathostemma micranthum*
5. *Cyathostemma wrayii*
6. *Cyathostemma longipes*
7. *Uvaria boniana*
8. *Uvaria calamistrata*
9. *Uvaria cordata*
10. *Uvaria curtisii*
11. *Uvaria dac*
12. *Uvaria flexuosa*
13. *Uvaria grandiflora*
14. *Uvaria hahnii*
15. *Uvaria hamiltonii*
16. *Uvaria hirsuta*
17. *Uvaria lobbiana*
18. *Uvaria lurida*
19. *Uvaria maclurei*
20. *Uvaria macropoda*
21. *Uvaria microcarpa*
22. *Uvaria narum*
23. *Uvaria pauciovulata*
24. *Uvaria pierrei*
25. *Uvaria rufa* var. *rufa*
26. *Uvaria semicarpifolia*
27. *Uvaria sphenocarpa*
28. *Uvaria vietnamensis*
29. *Uvaria zeylanica*
30. *Uvaria lamponga*
31. *Sp. Nov.*
32. *Ellipeiopsis ferruginea* var. *ferruginea*
33. *Uvaria rufa* var. *timoriensis*

Figure 3.7. Principal Components Analysis of mean leaf ratios: plot of taxa scores for Components 1 and 2. Taxa names and plot identification numbers listed on the right.



1. *Anomianthus dulcis*
2. *Rauwenhoffia siamensis*
3. *Ellipeiopsis ferruginea* var. *cherrevensis*
4. *Cyathostemma micranthum*
5. *Cyathostemma wrayii*
6. *Cyathostemma longipes*
7. *Uvaria boniana*
8. *Uvaria calamistrata*
9. *Uvaria cordata*
10. *Uvaria curtisii*
11. *Uvaria dac*
12. *Uvaria flexuosa*
13. *Uvaria grandiflora*
14. *Uvaria hahnii*
15. *Uvaria hamiltonii*
16. *Uvaria hirsuta*
17. *Uvaria lobbiana*
18. *Uvaria lurida*
19. *Uvaria maclurei*
20. *Uvaria macropoda*
21. *Uvaria microcarpa*
22. *Uvaria narum*
23. *Uvaria pauciovulata*
24. *Uvaria pierrei*
25. *Uvaria rufa* var. *rufa*
26. *Uvaria semicarpifolia*
27. *Uvaria sphenocarpa*
28. *Uvaria vietnamensis*
29. *Uvaria zeylanica*
30. *Uvaria lamponga*
31. *Sp. Nov.*
32. *Ellipeiopsis ferruginea* var. *ferruginea*
33. *Uvaria rufa* var. *timoriensis*

Figure 3.8. Taxon scores for the characters most closely associated with components 1 (C/L1) and 2 (L/L1) in Principal Components Analysis of mean leaf ratio values. L/L1 represents the position of the widest point of the leaf along the midrib, distinguishing ovate leaves (towards the top of the plot) from obovate leaves (towards the bottom). C/L1 represents the extent to which the leaf base is cuneate (to the left), retuse (centre) or cordate (to the right). Leaf outlines represent the mean shape (independent of size) for the adjacent taxon in bold. Identification numbers for taxa at right.



1. *Anomianthus dulcis*
2. *Rauwenhoffia siamensis*
3. *Ellipeiopsis ferruginea* var. *cherrevensis*
4. *Cyathostemma micranthum*
5. *Cyathostemma wrayii*
6. *Cyathostemma longipes*
7. *Uvaria boniana*
8. *Uvaria calamistrata*
9. *Uvaria cordata*
10. *Uvaria curtisii*
11. *Uvaria dac*
12. *Uvaria flexuosa*
13. *Uvaria grandiflora*
14. *Uvaria hahnii*
15. *Uvaria hamiltonii*
16. *Uvaria hirsuta*
17. *Uvaria lobbiana*
18. *Uvaria lurida*
19. *Uvaria maclurei*
20. *Uvaria macropoda*
21. *Uvaria microcarpa*
22. *Uvaria narum*
23. *Uvaria pauciovulata*
24. *Uvaria pierrei*
25. *Uvaria rufa* var. *rufa*
26. *Uvaria semicarpifolia*
27. *Uvaria sphenocarpa*
28. *Uvaria vietnamensis*
29. *Uvaria zeylanica*
30. *Uvaria lamponga*
31. *Sp. Nov.*
32. *Ellipeiopsis ferruginea* var. *ferruginea*
33. *Uvaria rufa* var. *timoriensis*

Figure 3.9. Taxon scores for characters L/L1 and P/L2. L/L1 represents the position of the widest point of the leaf along the midrib, distinguishing ovate leaves (towards the top of the plot) from obovate leaves (towards the bottom). P/L2 represents the extent to which the leaf apex is acuminate (to the left), acute (centre) or obtuse (to the right). Leaf outlines represent the mean shape (independent of size) for the adjacent taxon in bold. Identification numbers for taxa at right.

Difficult taxonomic groups

The Uvaria narum complex

PCA results for the fruit-only dataset are detailed in Table 3.10 and Figure 3.10 shows a plot of case scores for Components 1 and 2 from this analysis. This plot clearly identifies three groups of fruiting types, labelled α, β and γ. If we examine the location of type material on the plot, we see that the type material for *U. macropoda*, *U. narum* (sensu Wallich) and *U. lurida* are placed in groups α, β and γ respectively.

Component 1 is strongly correlated with stipe apex width, monocarp length and stipe length. This clearly separates the β-*narum* group from the α-*macropoda* and γ-*lurida* groups. Component 2 separates the latter two groups on the basis of apicule length, the α-*macropoda* specimens being characterised by a large prominent apicule. The β-*narum* specimens have a small apicule, while in the γ-*lurida* specimens it is rudimentary. Monocarp width has a strong negative factor loading for Component 2, and this contributes to the separation of the β-*narum* and α-*macropoda* groups (with narrow monocarps) from the γ-*lurida* group (with broad monocarps).

Table 3.11 shows PCA results for the flower-only dataset and Figure 3.11 shows a plot of case scores for Components 1 and 2. This analysis does not produce the same strong clustering patterns seen in the PCA of fruit data, despite the fact that non-type specimen identity has been established using discrete characters. While the type material of *U. macropoda*, *U. narum* (sensu Wallich) and *U. lurida* are reasonably well separated on the plot in Figure 3.11, the boundaries between each taxon cluster are unclear. Component 1 in Table 3.10 and Figure 3.11 is strongly correlated with stamen length and pedicel width, while Component 2 is strongly correlated with stigma width (negatively) and receptacle diameter. Component 1 separates *U. narum* from *U. lurida* (though not completely), while Componenet 2 separates *U. macropoda* from the latter two. The type material of *Uvaria eucincta* emerges quite close to the type material for *U. lurida*.

Table 3.10. Principal Components Analysis of fruit structure in the *Uvaria narum* complex: Eigenvalues, % of variance and character correlation scores for Components 1 and 2. Characters ordered on the basis of Factor Loading. Scores less than ± 0.1 are left blank. Significant components (based on Kaiser-Gutman criteria) indicated by *.

	Component 1*	2*
Eigenvalue	4.532	1.035
% of Variance	75.540	17.242
Cumulative %	75.540	92.782
Character		
Width of stipe – apex	.970	
Monocarp length	.961	.164
Length of stipe	.937	.126
Width of stipe – middle	.897	-.341
Monocarp width	.775	-.559
Length of apicule	.620	.750

Table 3.11. Principal Component Analysis of log-normalised flower measurements for *Uvaria narum* complex: Eigenvalues, % of variance and character correlation scores for Components 1 and 2. Characters ordered on the basis of Factor Loading. Scores less than ± 0.1 are left blank. Significant components (based on Kaiser-Gutman criteria) indicated by *.

	Function 1*	2*
Eigenvalue	6.109	2.269
% of Variance	43.637	16.207
Cumulative %	43.637	59.844
Character		
Stamen length	.926	
Pedicel width	.918	
Sepal length	.882	
Stamen locule length	.872	-.180
Carpel length	.849	-.200
Sepal width	.778	.173
Petal length	.774	
Petal midpoint	.670	
Stigma width	.115	-.868
Receptacle diameter		.820
Stamen width	-.357	-.544
Petal width	.505	.541
Pedicel length	-.244	.163
Stigma length	-.181	.320

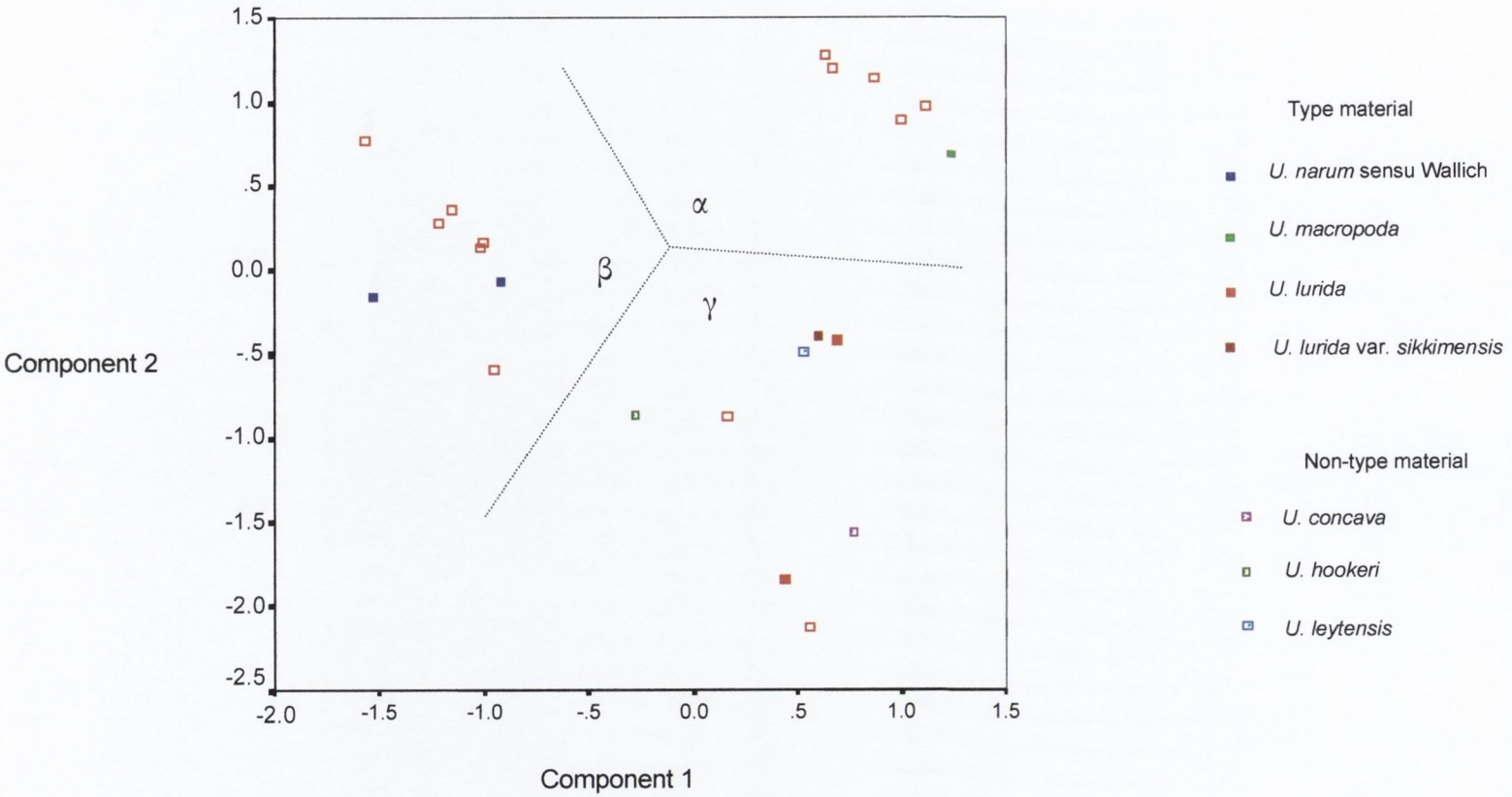


Figure 3.10. Principal components analysis of fruit characters in the *Uvaria narum* complex: plot of case scores for components 1 and 2. Component 1 is positively correlated with stipe length, width of stipe apex and length of monocarp. Component 2 is positively correlated with apicule length and negatively correlated with monocarp width. Broken line represents a division between the three main types of fruit in the complex -α , β and γ . The location of type material and selected non-type material within these groups is also indicated.

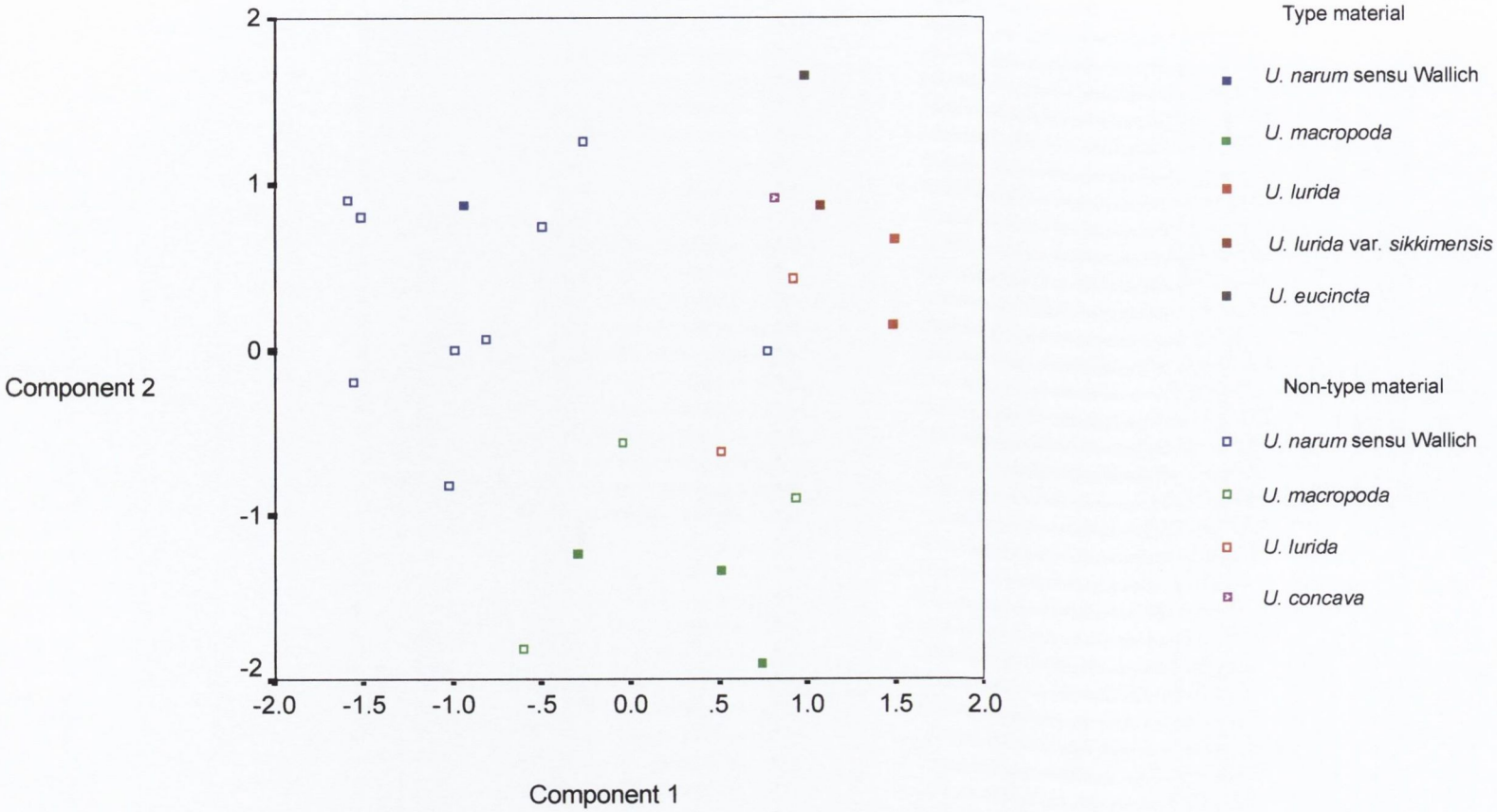


Figure 3.11. Principal components analysis of floral characters in the *Uvaria narum* complex: plot of case scores for components 1 and 2. Component 1 is positively correlated with stamen length, pedicel width and sepal length. Component 2 is positively correlated with receptacel diameter and negatively correlated with stigma width. The location of type material is indicated.

Discriminant Analysis of fruit structure in the *U. narum* complex (Table 3.12) identified apical and medial stipe width as the two most important discriminating characters, with fruit length (positive) and apicule length (negative) the next most highly correlated characters with Functions 1 and 2 respectively. Apical stipe width and fruit length (Function 1) discriminate between all three groups (Figure 3.12B). The negative correlation of apicule length with Function 2 results in the *U. macropoda* group (with long apicules) scoring negatively on this axis. The positive correlation of medial stipe width with Function 2 results in *U. narum* group (with narrow stipes) also scoring negatively on this axis. The DA classification (Table 3.14) places *Uvaria lurida* var. *sikkimensis, U. hookeri, U. concava* and *U. leytensis* within the *U. lurida* group, and this result is clear from the plot in Figure 3.12B.

For DA of the leaf-flower dataset (Table 3.13 and Figure 3.12A), the most important discriminating characters are sepal length (positively correlated with Function 1) and stigma width (negatively correlated with Function 2). The generally larger flowers and stout pedicels of *U. lurida* and *U. macropoda* causes them to emerge with higher scores in Function 1 than the smaller-flowered *U. narum* (Figure 3.12A). The large, broad stigmas of *U. macropoda* have a strong influence on the negative Function 2 scores seen for this taxon, whereas *U. narum* and *U. lurida*, with narrow stigmas, have mostly positive scores. The DA classification (Table 3.14) places *Uvaria eucincta, Uvaria concava* and *U. lurida* var. *sikkimensis* within the *U. lurida* group, and this result is clear from the plot in Figure 3.12A.

Table 3.12. Discriminant Analysis of leaf ratio and log-normalised fruit measurements for *Uvaria narum* complex: Eigenvalues, % of total variance and pooled within-groups correlations for first 2 standardized canonical Discriminant functions. Characters ordered by absolute size of correlation with first function. A-Q and L1 and L2 represent leaf radian measurements. Figures 3.1 and 3.2 show how the leaf radians were measured and then converted into ratios that summarise leaf shape.

	Function 1	2
Eigenvalue	72.708	13.173
% of Variance	84.7	15.3
Cumulative %	84.7	100.0
Canonical Correlation	.993	.964
Character		
Width of stipe – apex	.426	.231
Q/L2	-.342	.178
Monocarp length	.342	.064
Monocarp width	.304	.173
C/L1	-.258	.075
N/L2	-.198	.005
B/L1	-.145	.114
H/L1	-.129	.091
Petiole length	-.028	-.025
Width of stipe – middle	.205	.365
L/M	.150	-.277
Length of apicule	.204	-.274
P/L2	.082	.212
O/L2	.077	.211
L/L1	.166	-.204
A/L1	-.036	.169
K/L2	-.116	.163
D/L1	-.006	.129
E/L1	-.058	.093
G/L1	-.021	.076
Number of seeds	-.042	.046
F/L1	.015	.034

Table 3.13. Discriminant Analysis of leaf ratio and log-normalised flower measurements for *Uvaria narum* complex: Eigenvalues, % of total variance, Canonical correlation and pooled within-groups correlations for first 2 standardized canonical Discriminant functions. Characters ordered by absolute size of correlation with first function. A-Q and L1 and L2 represent leaf radian measurements. Figures 3.1 and 3.2 show how the leaf radians were measured and then converted into ratios that summarise leaf shape.

	Function 1	2
Eigenvalue	12.481	4.589
% of Variance	73.1	26.9
Cumulative %	73.1	100.0
Canonical correlation	.962	.906
Character		
Sepal length	.697	-.126
Pedicel width	.516	-.015
Carpel length	.507	-.061
L/M	.326	-.300
Stamen length	.297	.166
Stamen width	-.280	-.172
Petiole length	.254	.062
Sepal width	.230	-.199
Stamen locule length	.225	.053
Pedicel length	-.097	-.070
Petal length	.026	.002
Stigma width	.041	-.530
A/L1	-.198	.456
C/L1	-.084	.444
E/L1	-.065	.434
B/L1	-.103	.429
D/L1	.034	.414
N/L2	-.010	.387
F/L1	-.072	.384
Petal width	.146	.365
G/L1	-.089	.360
K/L2	-.213	.328
Receptacle diameter	.298	.310
Stigma length	.007	.280
H/L1	-.123	.266
L/L1	.031	-.239
Q/L2	.116	.180
P/L2	.111	.150
Petal midpoint	.021	.127
O/L2	-.020	.105

Table 3.14. Discriminant analysis classification results for the *Uvaria narum* complex based on inflorescence and fruit structure. 100.0% of original grouped cases were correctly classified. See text for discussion.

	Predicted Group Membership		
Taxon	*U. lurida*	*U. macropoda*	*U. narum*
Floral Data			
U. lurida	6	0	0
U. macropoda	0	7	0
U. narum	0	0	8
U. concava	1	0	0
U. eucincta	1	0	0
Fruit Data			
U. lurida	5	0	0
U. macropoda	0	6	0
U. narum	0	0	8
U. concava	1	0	0
U. leytensis	1	0	0
U. hookeri	1	0	0

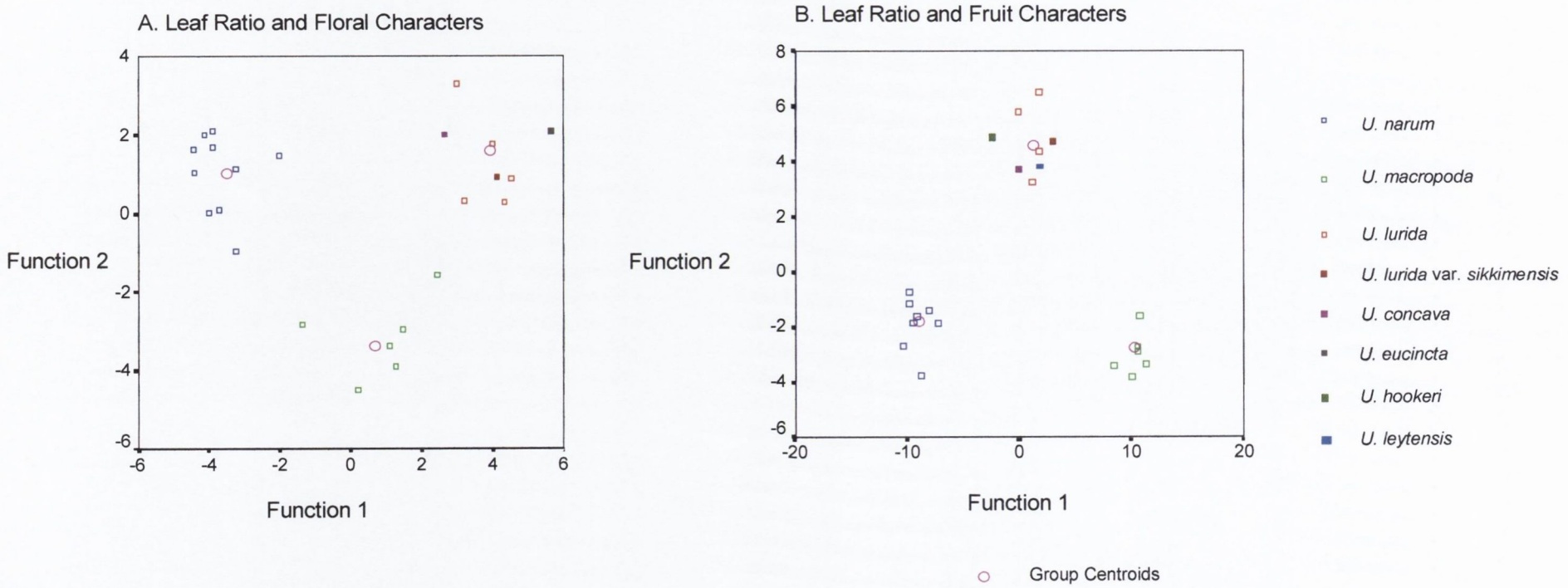


Figure 3.12. Discriminant Analysis of leaf and floral characters (plot A, at left) and leaf and fruit characters (plot B, at right) in *Uvaria lurida*, *U. macropoda* and *U. narum*. In both plots horizontal axes represent Discriminant Function 1, vertical axes discriminant Function 2. Characters most closely associated with Functions 1 and 2 in plot A are sepal length and stigma width respectively. Characters most closely associated with Functions 1 and 2 in plot B are Width of stipe – apex and width of stipe – middle respectively.

Uvaria cordata and U. microcarpa

The mean values for all characters were compared between *U. cordata* and *U. microcarpa* using the Independent t-Test procedure. Table 3.15 lists the characters which differed at a significance level of $P < .01$. Several characters also differed at a significance level of $P < .001$. Some of the most informative characters include leaf width (M), position of the widest point along the midrib (L_1), fruit length and width, petiole length, vein number, bract width, stipe width and compound peduncle length. Figure 3.11 shows four scatter plots (A-D), each generated using two characters which can be used to differentiate between the two species, based on their significance scores in the t-Test. One character not included is leaf width as this is highly correlated with L_1. A better spread of points is achieved by plotting L_1 against G/L_1, which is an intermediate measure of leaf base shape and leaf length to width ratio. From these plots we can see a varying amount of separation between the two species. In terms of leaf structure, petiole length and vein number (Figure 3.13C) discriminate well between the two, while L_1 and G/L_1 (Figure 3.13D) are less clear. Bract width and compound peduncle length provide a slightly better separation (Figure 3.13A), however the best characters are clearly fruit length and width (Figure 3.13B).

Table 3.15. Independent Samples t- for *Uvaria microcarpa* and *Uvaria cordata*: summary of characters whose means differ significantly at P<.01 between the two species. Analysis carried out using SPSS 8.0 (© SPSS Inc., 1998)

Character	Species	N	Mean	Std. Deviation	Std. Error Mean	Equal variances assumed based on Levine's test	t-test for Equality of Means		
							t	df	Sig. (2-tailed)
Compound peduncle length	*U. microcarpa*	8	.7191	.3416	.1208	Yes	-6.723	19	.000
	U. cordata	13	2.0577	.4927	.1367				
Petiole length	*U. microcarpa*	17	1.5550	.2358	.0572	Yes	-6.676	37	.000
	U. cordata	22	2.2243	.3570	.0761				
Leaf vein number	*U. microcarpa*	17	2.3300	.1252	.0303	No	-4.338	29.917	.000
	U. cordata	22	2.6311	.2927	.0624				
Bract width	*U. microcarpa*	8	.8812	.2522	.0891	Yes	-6.018	18	.000
	U. cordata	12	1.7587	.3557	.1027				
Fruit width	*U. microcarpa*	10	2.2178	.1242	.0392	Yes	-6.161	18	.000
	U. cordata	10	2.6962	.2118	.0669				
Fruit length	*U. microcarpa*	10	2.6808	.1757	.0555	No	-4.578	13.224	.000
	U. cordata	10	3.2502	.3519	.1113				
Stipe width midpoint	*U. microcarpa*	11	.3006	.1986	.0598	Yes	-7.953	17	.000
	U. cordata	8	1.1581	.2728	.0964				
Stipe width apex	*U. microcarpa*	11	.6296	.1611	.0485	Yes	-7.858	17	.000
	U. cordata	8	1.3800	.2559	.0904				
G/L1	*U. microcarpa*	18	.7023	.0974	.0229	Yes	-3.468	39	.001
	U. cordata	23	.7902	.0645	.0134				
H/L1	*U. microcarpa*	18	.5746	.0952	.0224	Yes	-3.472	39	.001
	U. cordata	23	.6656	.0726	.0151				
M	*U. microcarpa*	18	3.3213	.3333	.0785	Yes	-7.130	39	.000
	U. cordata	23	3.9821	.2606	.0543				
L1	*U. microcarpa*	18	4.1115	.3733	.0879	Yes	-4.773	39	.000
	U. cordata	23	4.6066	.2914	.0607				

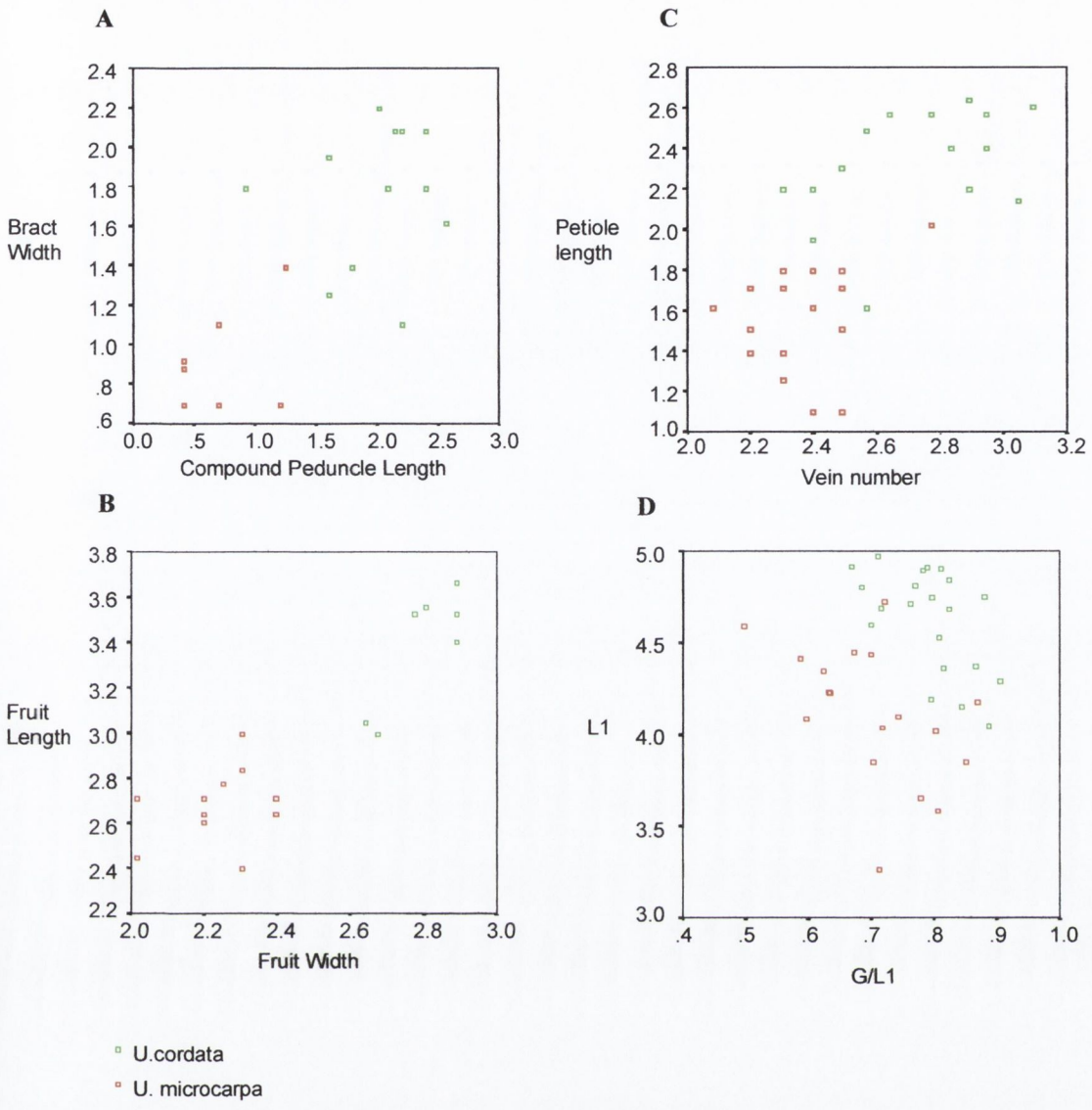


Figure 3.13. A Selection of characters whose means differ significantly between *Uvaria cordata* and *Uvaria microcarpa.* All values are log-normalised with the exception of the G/L1 ratio. Plot A ; bract width v. compound peduncle length, Plot B; fruit length v. fruit width, Plot C; petiole length v. vein number, Plot D; L1 v. G/L1.

Discussion

Inflorescence and fruit character variability in a sample of all Uvaria group taxa

There are some interesting patterns evident in the PCA and DA results for the floral character analysis (Table 3.3 and 3.5 respectively). The characters with the highest factor loadings for PCA Components 1-3 in Table 3.3 are different to those with the highest correlations for DA Functions 1-3 in Table 3.5. The inference here is that the characters with highest overall variability are not necessarily the best characters for discriminating between taxa. Carpel length and pedicel length (the characters with the highest factor loadings for PCA axes 1 and 2 respectively in Table 3.3 and Figure 3.3) are good examples of this pattern. Much of the variability evident in the dataset for these characters is generated by a few exceptional taxa. *Uvaria grandiflora* has carpels that are between twice and six times as long as the other taxa in the matrix. Similarly, *Uvaria boniana* and *Uvaria maclurei* have pedicels that are between four and eight times as long as taxa with the shortest pedicels. The latter character emerges with the highest correlation for Function 4 in the DA table, while carpel length is not strongly correlated with any of the DA Functions. This can be accounted for by the fact that while there is a large absolute variation in pedicel length between taxa, this variation is much more restricted within each taxon. Carpel length, on the other hand, is very similar for a large number of taxa (reducing its discriminating value) and also within *U. grandiflora* there are length differences of up to 30%.

The best character for discriminating between taxa (as identified by the highest correlation with DA Factor 1) is stamen locule length, this emerges with the third highest factor loading for Component 1 in Table 3.3, indicating that the overall variation (as well as the discriminating variation) of this character is quite high. This is a useful quality for the purposes of taxonomic discrimination in the sense that it may lessen the amount of effort required to identify size differences between taxa in this character. This finding would also appear to support the strong emphasis placed on stamen structure by Hooker & Thomson (1855, 1872), Finet & Gagnepain (1906) and Ridley (1922) in their taxonomic treatments of the group. The emergence of sepal length as a significant discriminating character is also very useful. Most previous workers have focused on petal size to a much greater degree than sepal size, and this

result indicates that the character could play a more important role in taxonomic identification.

Stipe length and monocarp length emerge as the most variable characters and the best discriminating characters (Tables 3.4 and 3.6). This matches well with existing classifications that emphasise these two characters as well as pericarp indument (which was not measured in these analyses due to the deciduous nature of fruit hairs). It is interesting to note that seed number does not appear as variable as monocarp length. Although there is a strong correlation between these two characters (Table 3.4), the difference between the two may be attributable to the compression, in certain taxa, of the two seed rows into a single row as the fruit matures, causing the monocarp to lengthen. This would offset any linear relationship that might otherwise exist between seed number and monocarp length.

The use of leaf-shape characters for discriminating between Uvaria group taxa

In both the PCA and DA analysis of leaf characters for the total dataset, character C/L_1 emerges as highly correlated with the major summary axis (Component 1 in Table 3.7 and Function 1 in Table 3.8 respectively). Furthermore, C/ L_1 also emerges in the PCA results for the mean ratio dataset as the most highly correlated character with Component 1 (Table 3.9). The first six leaf ratios (A-F/ L_1, including C/ L_1) were designed to summarise the shape of the leaf base in each sample, and these results indicate that C/ L_1 contains the greatest variation of values and carries the greatest discriminating power of these leaf-base values. B/ L_1, D/ L_1 and E/ L_1 are all correlated to varying degrees with C/ L_1 in each of the three sets of results, and this combined result provides very clear support for the use of leaf base shape as a taxonomic character.

The three analyses differ over which character has the highest correlation for summary function 2. Principal Components Analysis of the complete and mean value datasets both clearly identify this character to be L/ L_1, which summarises whether a leaf is ovate, elliptical or obovate. DA identifies G/ L_1, an intermediate measure of leaf base shape and length to width ratio. Interestingly, G/ L_1 emerges with the second

highest positive correlation for Component 2 in both of the PCA results. L/ L_1 does not have a significant positive or negative correlation with any of the five major functions in the Discriminant Analysis. The inference here is that while G/ L_1 accounts for a significant amount of variation uncorrelated with C/ L_1, it also has a significant discriminating power. L/ L_1, on the other hand, accounts for a larger proportion of the variation uncorrelated with C/L1, but it has a weaker discriminating power.

The plots in Figures 3.6 (DA) and 3.7 (PCA, mean taxon values) separate the sampled taxa in a more or less similar manner. In both cases we see a clear separation of taxa that can be directly related to variation in leaf shape. The lower ('x') axis of both plots is correlated with leaf base shape. As a result, cordate leaf types appear with high values on this axis in both plots, e.g. *U. semicarpifolia* (no. 26) and *U. cordata* (no. 9), while on the left we see narrowly retuse or cuneate leaf types such as *U. flexuosa* (no. 12) and *U. zeylanica* (no. 29). The vertical ('y') axis differs between the two plots, with the PCA results placing ovate leaf types towards the top, e.g. *C. micranthum* (no. 4) and obovate leaf types towards the bottom, e.g. *U. wrayii* (no. 5) and *U. pierrei* (no. 24). The DA results place broadly elliptical-cordate leaf types such as *Ellipeiopsis ferruginea* (no. 3) and *U. calamistrata* (no. 8) towards the top of the plot, with narrowly-elliptical leaf types coming out towards the bottom, e.g. *U. pierrei* (no. 24) and *U. flexuosa* (no. 12). Though both plots produce a similar spread of data points, with extreme leaf types at the margins and a cluster of more similar leaf types towards the centre, the PCA plot provides a slightly clearer separation of taxa than the DA plot.

A significant finding of these analyses is that the varieties of *U. rufa* and *Ellipeiopsis ferruginea* which I identified solely on the base of leaf shape differences are clearly distinct in both the DA and PCA plots, providing strong support for the formal establishment of these varieties.

Figure 3.8 shows a plot generated with the characters most closely associated with Components 1 and 2 in the PCA results for the mean dataset (C/ L_1 and L/ L_1 respectively – see Figure 3.2 for explanation of values). Superimposed onto this are outlines of mean leaf shapes for the taxa at the margins of the plot, providing a visual

key to the changing leaf shapes across the plot. Figure 3.9 presents a similar plot, this time with P/ L_2 and L/ L_1, the former being a measure of leaf apex shape. Again, mean leaf outlines are included as a visual guide.

Based on these results it is clear that taxa can be separated based on the leaf radian measurements used in this analysis. With additional work, this technique promises to provide a valuable aid for identifying the many sterile specimens which exist in herbaria.

In addition, each taxonomic account in Chapter 4 includes an outline of the mean leaf shape for each species as recorded in the dataset. As far as possible the leaf shape outlines are size-independent, with the midrib axis of each leaf containing a scale measure. These outlines provide an accurate representation of the typical 'bauplan' leaf type encountered in the majority of specimens of each taxon. Obviously there are deviations, particularly in the smaller leaf types which are harder to measure and the taxa with a lower sample size, however in general terms they serve as a reliable key to leaf shape for each species. As a quick reference guide, these leaf outlines are also shown in Appendix 3.3 (6 outlines per page).

Difficult taxonomic groups

The Uvaria narum complex

The first goal of this analysis was to examine variation in fruit structure as a means of delimiting the taxa in the complex irrespective of the taxonomic group that each particular specimen has been ascribed to. PCA was selected for this analysis because it summarises the variation in several characters without consideration of group membership. Table 3.10 and Figure 3.10 detail the preliminary PCA fruit data results. The PCA results presented here indicate that fruit character measurements can provide a reliable method for discriminating between taxa. Stipe apex width, monocarp length, stipe length and apicule length are all reliable characters. Figure 3.10 clearly identifies three groups of fruiting types, labelled α, β and γ, each of which are clustered around the type material for *U. macropoda*, *U. narum* (sensu Wallich) and *U. lurida* respectively.

Uvaria hookeri is also placed in group γ with *U. lurida* in Figure 3.10. This confirms a number of trends which are evident from visual examination of the herbarium specimens. Throughout the tribe there is a tendency for species with elongate stipes to show a rapid extension of the stipe prior to growth and expansion of the monocarp. It seems clear from the type material of *U. hookeri* that the fruits are not a distinctive form, but rather the juvenile fruits of *U. lurida*. The emergence of *U. hookeri* in the *U. lurida* group suggests that this is indeed the case.

As regards the status of *U. lurida* var *sikkimensis* (characterised by King in the original description as having an elongate stipe relative to type material for the species), this emerges within the γ-*lurida* group alongside a specimen of *U. concava* from the Philippines. Comparison of type material between *U. lurida*, *U. lurida* var. *sikkimensis* and *U. concava* indicates that these taxa may all be regional forms of the same species, with the westernmost Indian Peninsula populations having a shortened stipe, and the Assam-Sikkim and Malesian populations having a relatively longer stipe.

Principal Components Analysis of floral variation in the *U. narum* complex (Table 3.10, Figure 3.11) does not produce the same strong clustering patterns seen in the PCA of fruit data, despite the fact that non-type specimen identity has been established using discrete characters.

Discriminant Analysis of fruit structure (Table 3.12) places *Uvaria lurida* var. *sikkimensis, U. hookeri* and *U. concava* within the *U. lurida* group (Table 3.14), and this result is clear from the plot in Figure 3.12B. For DA of the leaf-flower dataset (Table 3.13 and Figure 3.12A), places *Uvaria eucincta*, *Uvaria concava* and *U. lurida* var. *sikkimensis* within the *U. lurida* group (Table 3.14) and this result is also clear from the plot in Figure 3.12A.

In conclusion, these data suggest that the *U. narum* complex has just three species and not the six species and one variety currently described. *Uvaria hookeri* King, *U. eucincta* Bedd., *U. concava* Teijsm. & Binn. and *U. lurida* var. *sikkimensis* King all belong under *U. lurida* Hook. f. & Thoms., while *U. narum* (Dunal) Bl. and *U.*

macropoda Hook. f. & Thoms. are distinct species which can be clearly identified using the characters analysed in this study.

Uvaria cordata and *U. microcarpa*

Analysis of *U. cordata* and *U. microcarpa* was based on an Independent t-Test of mean values for each character shared by the two taxa, and as such it is a departure from the multivariate analyses in the preceding studies. Leaf, fruit and sepal-petal structure in the two taxa can be very similar indeed, and it was hoped that aside from delimitating the variation in these characters for both taxa, several other characters would emerge which could also be used for this purpose. Table 3.15 lists the characters which differed between the two taxa at a significance level of $P < .01$, and several of these also differed at a significance level of $P < .001$.

Figure 3.13 shows a series of plots generated using a selection of these significant characters. These plots show a varying amount of separation between the two species. In terms of leaf structure, petiole length and vein number (Figure 3.13C) discriminate well between the two, while L1 and G/L_1 (Figure 3.13D) are less clear. Bract width and compound peduncle length provide a slightly better separation (Figure 3.13A), however the best characters are clearly fruit length and width (Figure 3.13B). These results support the retention of *U. cordata* and *U. microcarpa* as distinct species and provide reliable array of characters for distinguishing between them.

CHAPTER 4 - TAXONOMIC REVISION OF THE *UVARIA* GROUP IN CONTINENTAL ASIA

Introduction

Changes to Existing Classifications

This taxonomic treatment has been based on a combination of phylogenetic, phenetic and taxonomic data. Phylogenetic analysis of molecular and morphological data in Chapter 2 identified two major clades within the *Uvaria* group - the *Ellipeia* clade, comprising *Anomianthus*, *Ellipeia*, *Uvaria pauciovulata*, *Ellipeiopsis*, *Uvaria hahnii* and *Rauwenhoffia* (all characterised by a hairy stigma and stipitate stamens - Figure 4.1.A), and the *Uvaria-Cyathostemma* clade (characterised by glabrous stigmas and sessile stamens Figure 4.1.B), comprising all the remaining Asian Uvarias, two African Uvarias and all the Asian members of *Cyathostemma*.

Close scrutiny of these results suggests a number of changes should be made to existing taxonomic classifications. The first change is that *Anomianthus* and *Uvaria pauciovulata* are more properly accommodated within *Ellipeia*. The second change relates to *Uvaria hahnii,* which is sufficiently different from all the other genera in the *Ellipiea* clade to warrant the creation of a new genus, *Nervopetalum*. In terms of the *Uvaria-Cyathostemma* clade, the analysis failed to identify a clear boundary between the two genera, and so it is proposed here to subsume all of the studied *Cyathostemma* species into *Uvaria* section *micrantha*. The remainder of the *Uvaria* genus is accommodated within section *micrantha* and section *grandiflora*. In addition to these changes, phylogentic data provides strong evidence that *Rauwenhoffia* should be maintained as a distinct genus and not subsumed into *Melodorum* as Tien Ban (1974) has suggested.

Table 4.1 contains the list of accepted names, new names and new combinations proposed for the revision of the *Uvaria* group in Continental Asia. Table 4.2 contains a list of *Synonyma nova* contained in the revision.

Taxonomic differentiation between taxa in the *Uvaria narum* complex (*U. narum*, *U. lurida* and *U. macropoda*) is based upon many of the findings outlined in Section 3 of Chapter 3. Similarly, distinction between *Uvaria cordata* and *U. microcarpa* is based on the important discriminating characters identified in Section 4 of Chapter 3.

Table 4.1. Summary of nomenclature changes proposed for revision of *Uvaria* group in Continental Asia (a): accepted names and proposed new names and combinations.

Ellipeia dulcis (Dunal) C. Meade	*comb. nov.*
E. pauciovulata (Hook. f. & Thoms.) C. Meade	*comb. nov.*
var. *scortechinii* (King) C. Meade	*comb. et stat. nov.*
Ellipeiopsis ferruginea (Buch.- Ham. ex Hook. f. & Thoms.) R.E. Fr.	*comb. et stat. nov.*
var. *cherrevensis* (Pierre ex. Finet & Gagnep.) C. Meade	
	gen. nov.
Nervopetalum C. Meade	*comb. nov.*
N. hahnii (Finet & Gagnep.) C. Meade	
Rauwenhoffia siamensis Scheff.	
Uvaria* section *grandiflora	
U. calamistrata Hance	
U. cordata (Dunal) Alston	
U. curtisii King	
U. dac Pierre ex Finet & Gagnep.	
U. grandiflora Roxb. ex Hornem.	
var. *flava* (Teijsm. & Binn.) Sincl.	
U. hamiltonii Hook. f. & Thoms.	
var. *kurzii* King	
U. lamponga Scheff.	
U. lobbiana Hook. f. & Thoms.	
var. *ptychocalyx* (Miq.) C. Meade	*comb. et stat. nov.*
U. lurida Hook. f. & Thoms.	
U. maclurei Diels	
U. macropoda Hook. f. & Thoms.	
U. microcarpa Champ. ex Benth.	
U. narum (Dunal) Bl.	
var. *macraeii* C. Meade	*var. nov.*
U. rufa (Dunal) C. Meade	*comb. nov.*
var. *timoriensis* (Bl.) C. Meade	*comb. et stat. nov.*
U. semicarpifolia Hook. f. & Thoms.	
U. sphenocarpa Hook. f. & Thoms.	
U. zeylanica L.	
Uvaria* section *micrantha	
U. argentea Bl.	
U. boniana Finet & Gagnep.	
U. kerrii C. Meade	*sp. nov.*
U. micrantha (A.DC) Hook. f. & Thoms.	
var. *elongata* C. Meade	*var. nov.*
U. orientalis (Jovet-Ast) C. Meade	*nom. nov.*
U. pierrei Finet & Gagnep.	
U. tonkinensis Finet & Gagnep.	
U. vietnamensis Jovet-Ast ex C. Meade	*sp. nov.*
U. wrayii (King) C. Meade	*comb. nov.*

Table 4.2. Summary of nomenclature changes proposed for revision of *Uvaria* group in Continental Asia (b): *synonyma nova*.

Name	Proposed synonymy
Ellipeia Hook. f. & Thoms.	*Anomianthus* Zoll.
Uvaria lamponga Scheff.	*Uvaria andamanica* King
Uvaria lurida Hook. f. & Thoms.	*Uvaria lurida* var. *sikkimensis* King *Uvaria concava* Teijsm. & Binn. *Uvaria hookeri* King *Uvaria eucincta* Bedd. Ex. Dunn. *Unona leytensis* Elmer
Uvaria grandiflora Roxb. ex Hornem.	*Uvaria purpurea* var. tuberculata King *Uvaria rubra* Robinson *Uvaria rhodonta* Hance
Uvaria dac Pierre ex Finet & Gagnep.	*Uvaria varaigneana* Pierre ex Finet & Gagnep.
Uvaria maclurei Diels	*Uvaria kweichowensis* P-T Li
Uvaria cordata (Dunal) Alston	*Unona littoralis* Bl. *Uvaria ovalifolia* Bl. *Uvaria gamopetala* Zoll.
Uvaria rufa (Dunal) C. Meade *comb. nov.*	*Uvaria rufa* Bl. *Uvaria hamiltonii* Hook. f. & Thoms. var. *fauveliana* Finet & Gagnep.
Uvaria rufa (Dunal) C. Meade var. *timoriensis* (Bl.) C. Meade *comb. et stat. nov.*	*Uvaria branderhorstii* Burck
Uvaria narum (Dunal) Bl.	*Uvaria narum* (Dunal) Wall Cat. 6473 *Uvaria narum* Wall. ex Wight & Arnott *Uvaria flexuosa* Heyne ex Wall. Cat. 6473b *Guatteria malabarica* Dunal *Guatteria montana* A.DC *Uvaria malabarica* Oken
Uvaria tonkinensis Finet & Gagnep.	*Melodorum vietnamense* var. *calcareum* Tien Ban *Uvaria tonkinensis* var. *subglabra* Finet & Gagnep. *Cyathostemma longipes* Craib *Uvaria subglabra* Merr. & Mete (*nom. ined.*)
Uvaria orientalis (Jovet-Ast) C. Meade *nom. nov.*	*Uvaria flexuosa* Jovet - Ast. *(nom. illegit.)*
Ellipeia dulcis (Dunal) C. Meade *comb. nov.*	*Uvaria pachychila* Merr. ex Phạm-hoàng Hộ

Keys

For the fruiting key it has proven impractical to try and key the genera according to fruit structure, so taxa are identified directly to species. The reader is then referred to the number of each taxon according to their position in the generic accounts which follow. The key for flowering material identifies to genus level first, then to species and variety. Certain species for which the flowers or fruit are not known are excluded from the flowering or fruiting keys respectively - these include *Uvaria vietnamensis* (fruit only known), and *U. orientalis* and *U. argentea* (flowers only known).

Figures

Figures 4.1.C and 4.2 provide a visual guide to the terminology used for describing leaf structure and indument type resepectively. Line drawings (where included) are indicated at the end of each taxonomic description. Appendix 4 includes a series of photographs of members of the Annonaceae and the *Uvaria* group. The relevent distribution map is indicated at the end of the Ecology and Distribution section for each account, and all maps are located at the end of the Chapter. The maps contain taxon distributions for Continental Asia only. A guide to the administrative boundaries for states, provinces and districts of India, Sri Lanka, China, Thailand, Cambodia, Laos and Vietnam are provided in Appendices 4.15-4.19.

Leaf Outlines

Each taxonomic account is accompanied by a composite drawing of leaf shape based on the measurements included in the dataset in Chapter 2. The drawings are made using the polar plot option in SigmaPlot 5.0 (SPSS, 1999) with radians as the plotting axes. As far as possible the leaf shape outlines are size-independent, with the midrib axis of each leaf containing a scale measure. These shape outlines are based on the mean vlues recorded for each species and provide an accurate representation of the typical 'bauplan' leaf type encountered in the majority of specimens of each taxon. Obviously there are deviations, particularly in the smaller leaf types which are harder to measure and the taxa with a lower sample size, however in general terms they serve as a reliable guide to leaf shape for each species.

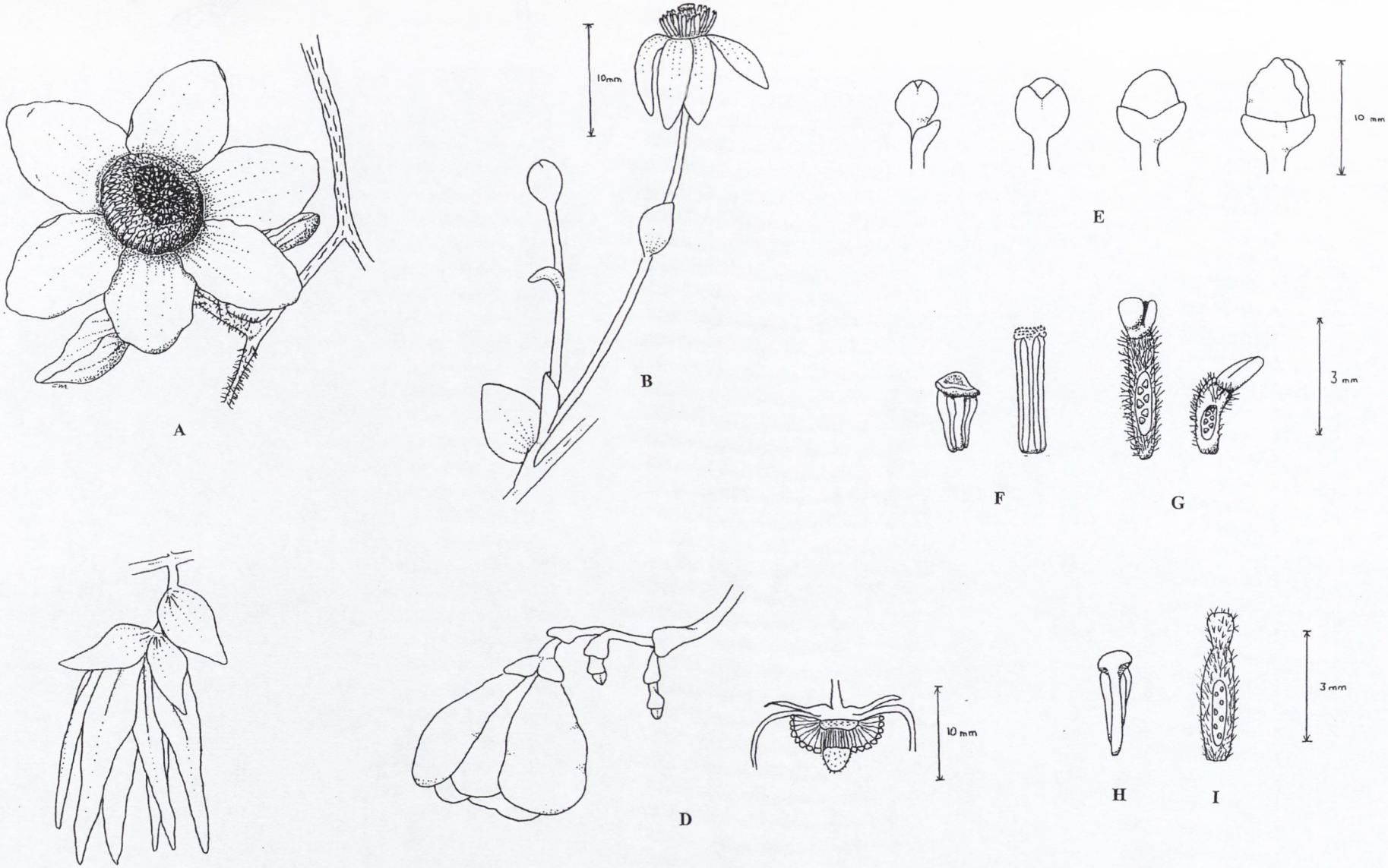


Figure 4.1. Main inflorescence features of the *Uvaria* group. **A**. *Uvaria grandiflora*, a typical example of the *Uvaria* section *grandiflora* flower type. **B**. *Uvaria maclurei*, showing prominent basal and medail bracts and an elongate pedicel. **C**. Pendulous flower of *Nervopetalum hahnii* (Finet & Gagnep.) C. Meade *comb. nov.*, showing sepals and petals with prominent venation. **D**. *Ellipeia pauciovulata* (H. f. & Th.) C. Meade *comb. nov.*, showing pundulous inflorescence with prominent wrapping bracts and a section through the receptacle showing the dome-shaped gynoecium with scattered stigmatic hairs. **E**. Development of the cup-shaped calyx tyoical of many *Uvaria* species as seen in *Uvaria semicarpifolia*. **F**. Stamen types typical of *Uvaria*. **G**. Carpel types typical of *Uvaria*. **H**. Stamen type typical of *Ellipeia* clade. **I**. Carpel type typical of *Ellipeia* clade. All drawings to scale unless otherwise indicated.

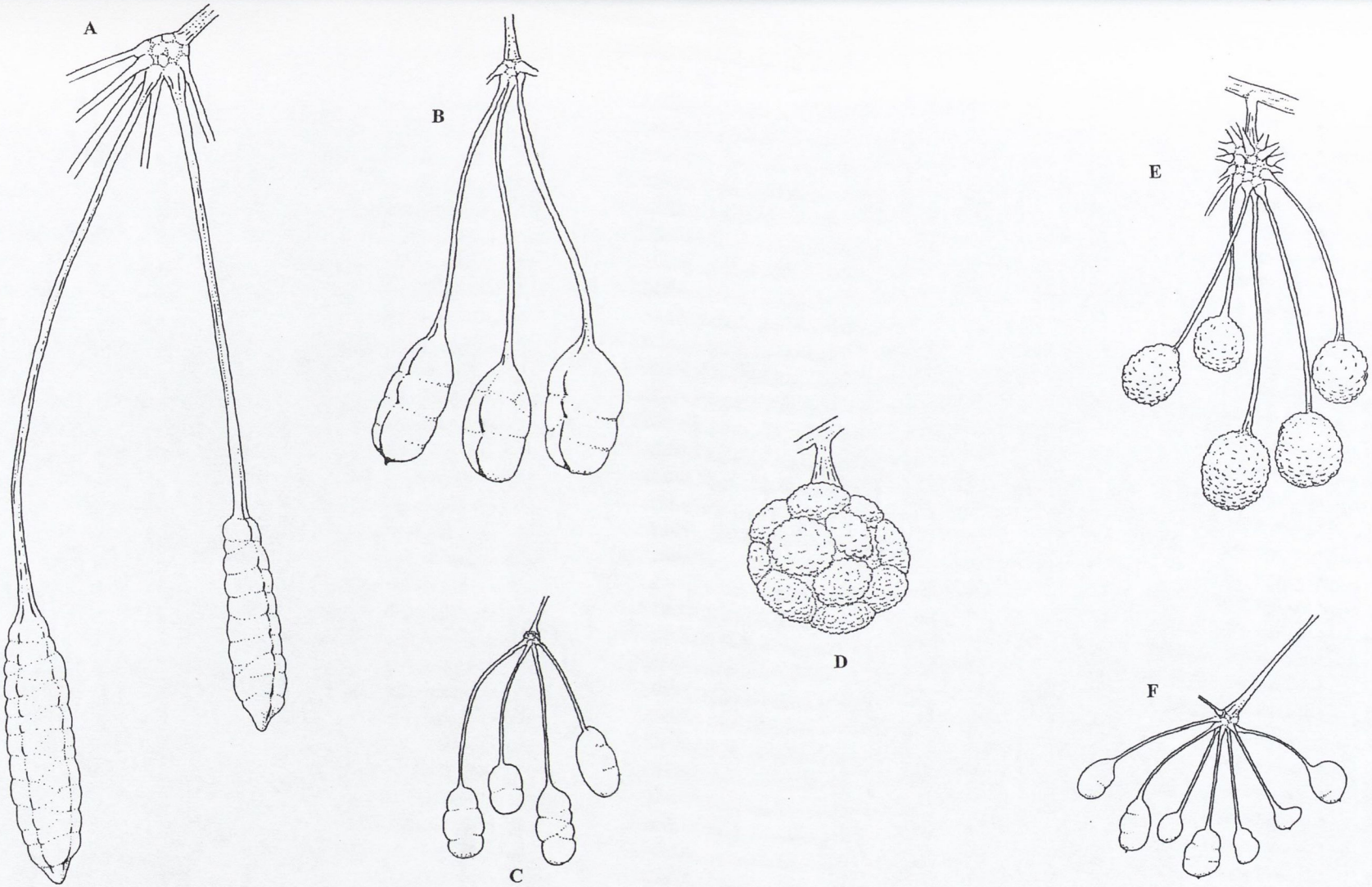


Figure 4.2. Fruit Types in the *Uvaria* group. **A**. *Uvaria macropoda*. **B**. *Uvaria lurida*. **C**. *Uvaria narum*. **D**. *Uvaria sphenocarpa*. **E**. *Uvaria lobbiana*. **F**. *Uvaria micrantha*. All drawings to scale.

Notation for Material Examined

A specific format has been used for listing the material examined for each taxon. Specimens with flowers or fruit are listed as (fl.) or (fr.) respectively, or, where both are present, as (fl., fr.). Provinces in Thailand and Indochina are listed according to the *Flora of Thailand* and *Flore du Cambodge, du Laos et du Vietnam* respectively. For the latter, the codes are listed as (Country – Province No. – CLV). For example, Pursat (Pouthisat) Province in Cambodia is listed as (C – 10 – CLV). For Thailand, the codes are listed as (Province No. – Floristic Region No.), e.g. Surat Thani Province (61 – Pen). For India, locations are given for the state only, i.e. Maharashtra. For Sri Lanka, the floristic divisions are based on the map which accompanies the *Revised Handbook to the Flora of Ceylon*. Chinese locations are listed according to Province, however locality descriptions are often in Chinese script and so have been illegible to this author. For Myanmar (Burma), Provinces are listed according to modern names, so Tenasserim is called Taninthari, Pegu becomes Bago etc. Peninsular Malaysian collections are listed under the State, e.g. Kedah. Material from the Malesian Islands is normally assigned to the island locality on the label, however where possible local district divisions are given for the Philippines and also for Sumatra, Java and Borneo.

Notation for Type Material

Type specimens are listed according to country. For many older specimens parentheses have been used to indicate the exact notation on the specimen label, particularly where no collection number is indicated. In certain cases it has not been possible to identify the collector and/ or exact collecting location for each specimen. Notable collections in this regard are those of Wallich, King and Thwaites, though in each of these cases the vast majority of collections are well annotated. In general the specimens of Roxburgh do not have a collection location on the label, an exception being the ones that Wallich incorporated into the East India Company herbarium.

Sources for Referenced Literature

All the accounts presented in this revision are original, and no part of the text (save herbarium label details) has been copied from any other source. All reference material quoted in the taxonomic accounts was seen in its original printed form or in facsimile. Plates and descriptions from early printed books were viewed at the old Library, TCD and at the libraries of BM and K. The Wallich, Jussieu and De Candolle catalogues were seen at K, P and G respectively. Hermann's *Museum Zeylanicus* was seen at BM.

Research Collection

Loans were received from the following institutions over the course of the study; A, AAU, ABD, BKF, BM, BR, C, E, G, HAM, K, L, LIV, LISU, NY, P, Sing, U, US. Material was viewed *in situ* at BK (Bangkok Agricultural Herbarium), BKF, BM, CMU (Chiang Mai University), K, L, P, HCMC (Ho Chi Minh City - Saigon), HN (Hanoi), HNU (University of Hanoi) and Sing. Extensive use was made of the Annonaceae material at TCD, particularly the collections of Hooker & Thomson, Thwaites, Wallich and Kerr. Several new collections were also made by the author and Dr. Piya Chalermglin in Thailand, and by the author and Mr. Somran Suddee in Vietnam. Approximately 1,300 specimens were examined in total.

The *Uvaria* Group

Sarmentose or erect shrubs or climbers with stellate hairs; sepals valvate; petals imbricate or partially imbricate, free or basally connate at maturity; fruits apocarpous, monocarps stipitate or rarely sessile; seeds 1-30, laterally or sub-apically inserted in one or two rows.

Key for Flowering Material

1a. Annual or perennial shrub with shortened horizontal stem .... **1. *Ellipeiopsis***

1b. Sarmentose or erect shrub, or climber 2

2a. Stigma hairy 3

2b. Stigma glabrous ..... ***2. Uvaria***

3a. Petals fleshy, to 8 x 10 mm .... **3. *Rauwenhoffia***

3b. Petals membranous or coriaceous, to 40 x 25 mm 4

4a. Sepals small, ovate, concave, 4-8 x 3-8 mm, sepals and petals without distinct venation ..... **4. *Ellipeia***

4b. Sepals large and leaf-like with prominent central vein, flat or convex, up to 15 x 10 mm, petals with prominent palmate venation .... **5. *Nervopetalum***

Key for fruiting material

Numbers after taxa refer to their position in the generic keys which follow.

1a. Annual or perennial shrub with shortened horizontal stem and erect branches; monocarps red, ellipsoidal, c. 10-15 mm long x 8-10 mm wide, fleshy, shortly stipitate, single seed with apical placentation ..... ***Ellipeiopsis ferruginea* (1a &1b)**

Myanmar-Thailand-Indochina

1b. Scandent shrub or climber with vertical stem; monocarps red or green, placentation lateral or sub-basal, seeds 1-many 2

2a. Monocarps numerous, c. 10 - 30+ at maturity, 1-4 seeded, globose, ovoid or transversely ovoid; pericarp thin; stipes typically long and narrow, never wider than 2 mm 3

2b. Monocarps 2-20 in number, but usually less than 10, 4-30 seeded, globose, ovoid or oblong; pericarp thickened or rarely thin, fleshy; stipes typically short and thickened or long with with deep striations 9

3a. Fruit transversely ovoid with prominent apicule, densesly tomentose; pericarp thin, seeds 1-2(-3) ..... ***Ellipeia pauciovulata* (1)**

Malay Peninsula south of the Isthmus of Kra

3b. Monocarps largely glabrous, apicule when present small and/or blunt, seeds 1-4 4

4a. Leaves elliptic - broadly elliptic - shortly obovate, base retuse-shortly cordate, apex acute, membraneous; veins 15-18, sub-parallel, frequently branching basally and medially; indument tomentose on younger shoots, on abaxial blade sparse becoming sub-glabrous, over midrib hairs erect, tomentose, c. 1 mm long, adaxial blade hairs sub-tomentose, on veins and midrib hairs ferruginous, stocky, tomentose towards petiole ..... ***Ellipeia dulcis* (2)**

Thailand and Southern Indochina, Java – Lesser Sunda Is

4b. Leaves narrowly ovate - elliptic - obovate, base cuneate to retuse, apex bluntly acute to acuminate, membraneous, usually waxy; veins 8-14(-16), rarely branching basally or medially; indument occasionally persistent over midrib, elsewhere hairs sparse, more often glabrous or sub-glabrous, hairs less than 0.5 mm long 5

5a. Leaves 100-250 mm long, broadly elliptical to obovate, base broadly retuse to narrowly cordate, apex often with prominent acuminum 6

5b. Leaves 50-150 mm long, narrowly ovate-elliptical-obovate or narrowly oblong, base cuneate or narrowly retuse, apex acute 7

6a. Leaves elliptical-narrowly obovate, base retuse, apex acuminate or rarely acute, c. 130-170 x 50-60 mm, thinly coriaceous, waxy above, veins 9-11... ..... ***Uvaria tonkinensis* (18)**

Northern Indochina and Hainan

6b. Leaves obovate, less often oblong, base retuse, apex acute-aciminate, to 250 x 95 mm, membraneous, veins 12-15 .... ***U. wrayii* (24)**

Isthmus of Kra to Sumatra

7a. Leaves distinctively narrow-oblong, base retuse, apex obtuse or retuse, leaf margin turned downward .... ***U. pierrei* (21)**

Mekong basin below Loei

7b. Leaves ovate-elliptical, base cuneate, apex acute to narrowly acute, leaf margin flattened 8

8a. Monocarps 10 - 20, green turning yellow, globose to shortly oblong, c. 9.5 x 8 mm at maturity, no apicule present; pericarp fleshy, becoming thin and black after drying, glabrous, smooth; stipe c. 14-20-(-23) mm, glabrous, smooth, seeds 1-2(-3) ..... ***U. micrantha* (22)**

Myanmar – Indochina – Andamans – Malesia

8b. Monocarps 25-45+, green turning red/purple at maturity, ovoid, ellipsoid or shortly cylindric, c. 15-17(-20) x 11(-13) mm, occasionally with a prominent apicule; pericarp c. 2 mm thick, soft and juicy when ripe, drying brown/black,

surface somewhat warty with short scattered stellate hairs; stipe c. 35-45 mm long, 1 mm in diameter, striate with scattered short c. 0.75-1 mm diameter stellate hairs seeds 4-6 ..... ***U. boniana*** **(19)**

Northeast Vietnam and Southern China

9a. Monocarps sessile, gathered into pseudo syn-carpous conglomerate, individual monocarps cuneate-obovoidal, sides flattened against adjacent monocarps .... ***U. sphenocarpa*** **(11)**

Endemic to Sri Lanka

9b. Monocarps clearly stipitate, or if in dense cluster then narrowed stipe clearly visible at monocarp base, sides not flattened against adjacent monocarps ... 10

10a. Monocarp with dense covering of epidermal outgrowths 12

10b. Monocarp smooth, striate or tubercled, but without epidermal outgrowths .. 13

12a. Moncarps 20+, spheroidal, 20 - 30 mm in diameter, with dense beard of long hairs, each carrying a tomentum of rufous stellate hairs; pericarp red, flesh white; stipe to 45 mm long x 2 mm diameter .... ***U. vietnamensis*** **(26)**

Central Indochina

12b. Monocarps 2-12, spheroidal-oblongoidal, c. 30 x 20 mm, initially covered with prominent beard of 5-8 mm long membraneous bluntly triangular outgrowths, later tuberculate with scattered remnants of outgrowths over surface; stipe short, 3-5mm x 2.5-3mm .... ***U. calamistrata*** **(9)**

Guangxi, Hainan & Northeastern Vietnam

13a. Monocarp basally or sub-basally attached; pericarp thick, epidermis deeply grooved and warted; stipe 2-5 mm wide , 5-10 mm long, deeply striate 14

13b. Monocarp basally attached, smooth, glabrous, sparse or tomentose or where tubercled stipe much greater than 10 mm long 15

14a. Monocarps 1-8(-10), sub-basally attached, c. 45 x 25 mm diam., oblongoid; pericarp thickened, epidermis warted with fine tomentose indument, mature fruits green with brown tint; stipe 5-10 x 2.5-3 mm, thickly striate, tomentose; seeds 6-12 in 2 rows; leaves narrowly elliptic-obovate, acute-distinctly acuminate, base retuse, c. 180-190 x 60-80 mm; veins 11-13 ..... ***U. dac* (6)**

Southern Indochina

14b. Monocarps 1-4, basally attached, 40-45 x 30-35mm, ovoid-ellipsoidal; pericarp thick, tuberculate, sub-sessile; stipe c. 6 x 5 mm, striate; seeds 6-10; leaves elliptical-narrowly obovate, apex acute, shortly acuminate or rarely obtuse, base cuneate-retuse, c. 110-160 x 40-60 mm, coriaceous; veins (9-)10-12 ..... ***U. maclurei* (8)**

Yunnan, Kweichow, Guangzhow & Hainan

15a. Stipe short, c. 2-4 mm x 2 mm; monocarps oblong, pale yellow or cream in colour at maturity, minutely tomentose, c. 4-12 in number 16

15b. Stipe c. 5-50 x 1.5-4 mm; monocarps green, red or purple at maturity, glabrous or hairy 17

16a. Leaves broadly elliptic to narrowly obovate ..... ***Nervopetalum hahnii***

Indochina and Myanmar

16b. Leaves bluntly lanceolate/ elliptical or ovate-elliptic-oblanceolate 26

17a. Stipe elongate, c. 50-150 x 2-3 mm, striate 18

17b. Stipe 5-40 mm long, smooth or shallowly striate 20

18a. Monocarp globose or ovoid, c. 16-18 x 20-25 mm, prominently tubercled; seeds 4-6 ..... ***U. lobbiana* (16)**

Southern Myanmar to Borneo and Java

18b. Monocarp oblong or cylindrical, c. 35-70 x 20-30 mm, smooth or somewhat tubercled; seeds 2-16 19

19a. Monocarp narrowly cylindrical with prominent tapering apicule c. 5-10 mm long; seeds 10-16 ..... ***U. macropoda* (3)**

Endemic to Sri Lanka

19b. Monocarp shortly oblong to oblong, apicule when present c. 1-2 mm long; seeds 2-10 ..... ***U. lurida* (2)**

India – Southeast Asia – Malesia

20a. Monocarp oblong, glabrous to sub-glabrous 21

20b. Monocarp broadly ellipsoidal to oblong, ferrugino-tomentose until maturity 23

21a. Stipe narrow, c. 10-35 x 1-2 mm; moncarps 4-20+, oblong, smooth, c. 10-20 x 6-10 mm; pericarp fleshy at maturity, drying thin 22

21b. Stipe short, thick, 2-10 x 2-4 mm; monocarps 10-20, oblong, to c. 30 x 16.5 mm; pericarp thick and soft at maturity ..... ***U. cordata* (13)**

Sri Lanka, Bangladesh – Indochina – Malesia

22a. Monocarps 4–8+, green turning yellow then dark purple at maturity, ovoid to shortly oblongoidal, c. 20 x 10 mm; stipe c. 10-15 x 1-2 mm, shortly tomentose; seeds c. 6-8; leaves elliptic-broadly obovate, c. 80-150 x 40-80 mm, thickly coriaceous, apex acute-rounded, base cordate or broadly retuse, frequently oblique, blade often undulate at margin; veins 9-11(-12) ..... ***U. microcarpa* (14)**

Southern China & Northeast Indochina

22b. Monocarps 5-20+, green turning orange then red, globose to oblong, 10-15 x 6-8 mm; stipe narrow, c. 25-35 x 1 mm diam.; seeds 2-6; leaves oblong-elliptical-oblanceolate, up to 145 x 45 mm, sub-coriaceous, waxy, base cuneate, apex acute-acuminate, acuminum to 15 mm; veins c. 10-11 ..... ***U. narum* (17)**

Sri Lanka and Oceanic Southwest India

23a. Monocarps oblong-cylindrical, 50-75 x 10 -20 mm; stipe c. 20-30 x 4 mm, deeply striate; seeds 16-30 ..... ***U. grandiflora* (4)**

Bangladesh – Southern China - Southeast Asia - Malesia

23b. Monocarps globose, shortly oblong or broadly ellipsoid, to c. 30 x 20 mm; seeds 5-20 24

24a. Stipe 10-15 x 3 mm; leaves broadly obovate 160-400 mm long, thickly coriaceous, glabrous above at maturity ..... ***U. semicarpifolia* (12)**

Endemic to Sri Lanka

24b. Stipe 25-35 mm long; leaves obovate, 100-200 mm long, coriaceous, upper surfaces scabrous to sparse at maturity 25

25a. Monocarps c. 10-14, globose to oblong, c. 20 x 15 mm, green turning red; pericarp fleshy or thin, outer surface ferrugino- tomentose, often lumpy-tomentose; seeds 6-12 ..... ***U. hamiltonii* (7)**

Assam – Myanmar – Northern Indochina - Hong Kong

25b. Monocarps 4-8(-20), cylindrical, c. 25-35 x 14-21 mm, young fruits green with rufous tint, pericarp thick and hard; mature fruits bright red in colour, flesh soft, pericarp wall sub-glabrous, thin and easily torn; seeds 5-20+ ..... ***U. rufa* (15)**

Southern Indochina – Malay Peninsula – Andaman Islands – Western Malesia

26a. Leaves bluntly lanceolate/ elliptical, base retuse, apex bluntly acute, c. 90-150 x 30-40 mm, thinly coriaceous, veins 8-11(-14) ..... ***Rauwenhoffia siamensis***

Southern Indochina

26b. Leaves ovate-elliptic-oblanceolate, base cuneate, apex acute-acuminate, c. 55-70(-95) x 20-28(-35) mm, membranous, veins c. 8-12 ..... ***U. zeylanica* (10)**

Sri Lanka & Southernmost India

1. *ELLIPEIOPSIS* R.E. Fries

Ark. Bot. 3:41 (1955), type *E. ferruginea* (Buch.-Ham. ex Hook. f. & Thoms.) R.E. Fries.

Annual or perennial shrubs with stellate hairs, stems horizontal, young shoots smooth, tomentose, later becoming striate, hairs persistent in grooves only, ***leaves*** coriaceous, ovate-obovate, cordate, acute, veins sub-parallel, prominent, both surfaces tomentose with pale to ferruginous stellate hairs; ***inflorescence*** flowers yellow or white, solitary, leaf-opposed; ***calyx*** sepals basally connate, valvate at tips, petals imbricate, valvate basally, remaining erect; ***corolla*** inner petals carrying a pair of supra-basal lateral glands; ***stigma*** elongate, hairy, hairs cuneate, locules stipitate, ***monocarps*** 1-seeded, placentation apical or sub-apical, pericarp green and hard, maturing red, flesh pale, juicy.

Key to species occurring in Continental Asia

1a. Leaves ovate-oblong ..... **1a. *E. ferruginea* var. *ferruginea*** *Myanmar*

1b. Leaves obovate ..... **1b. *E. ferruginea* var. *cherrevensis*** *Thailand-Indochina*

1a. *Ellipeiopsis ferruginea* (Buch.-Ham. ex Hook. f. & Thoms.) R.E. Fries

Ark. Bot. 3:41 (1955); *Uvaria ferruginea* Hamilton-Buchanan ex Hook. f. & Thoms. Fl. Ind 1:96 (1855), Type; Myanmar, 'Meaday, Tenasserim, Hamilton-Buchanan s.n.' (BM!); Kurz Forest Flora of British Burma 1:29 (1877); King Ann. Roy. Bot. Gard. Calcutta, 4:24 t. 15 (1893); Brandis D., Indian Trees, 4th ed. 17-18 (1921); *Ellipeia ferruginea* (Hamilton-Buchanan ex Hook. f. & Thoms. Fl.) Hook. f. & Thoms. Fl. Br. Ind. 1:52 (1875).

Habit a small shrub with a single or branched horizontal stem producing erect c. 1 m high branchlets. ***Young shoots*** densely ferrugino-tomentose, becoming striate and

sparse to sub-glabrous with age. ***Leaves*** coriaceous, broadly elliptical-oblong, base cordate, apex obtuse, cuspidate or acute, 120-150 x 50-80 mm, *veins* 11-12(-14), parallel, sunken above, strongly emergent below, trailing traces strong, forming sub-marginal vein, interprimaries rare, secondary veins kinked, tertiary venation reticulate; *indument* abaxial blade sub-tomentose, hairs erect, 1-3 branched, pale, becoming sparse to sub-glabrous with age, midrib and primary vein bases tomentose, hairs erect, c. 2-5 branched; adaxial blade hairs sub-tomentose, c. 6-10+ branched, spreading, rufous, hairs tomentose over midrib and all vein traces generating distinctive sand-coloured downy appearance. ***Petiole*** c. 8-10 x 2 mm, ferrugino-tomentose. *Inflorescence* leaf-opposed, flowers solitary, peduncle much reduced, pedicel c. 8-12(-20) x 1 mm, tomentose, medial bract narrowly elliptical, 8-15 x 2-3 mm, pale green, tomentose on both surfaces, venation not prominent. ***Calyx*** sepals 3, basally connate, tips valvate, ovate-acute, c. 5-6 x 8 mm, concave, recurving basally at maturity, outer surface densely tomentose, inner surface warty and sparse basally, tomentose elsewhere. ***Corolla*** petals 6, yellow-white in colour, imbricate, outer whorl larger than inner, outer petals broadly ovate, c. 12-14 x 10-12 mm, apex bluntly acute, base constricted to c. 3.25 mm wide, outer surface tomentose, inner surface tomentose along margins and at apex, glabrous at base, inner petals narrowly ovate, c. 12-14 x 7-8 mm, outer surface tomentose, inner surface basally glabrous, base more constricted than outer whorl, c. 2.25-2.5 mm wide, with 2 conspicuous marginal glands present, tissue contiguous to glabrous base of inner surface. ***Stamens*** numerous, c. 1.8-2 mm, cuneate, connective apex glabrous, rusty in colour, shiny, often extending as ridge down external side, locules stipitate. ***Carpels*** c. 25-30, 2.5-3 mm long, ovary tomentose, hairs fine, many-branched, forming even surface, stigma elongate, c. 0.8-1 mm long, glabrous, U-shaped with lateral groove, ovule 1, placentation apical or sub-apical. ***Fruit*** monocarps 5-20, c. 10 x 4.5 mm, red in colour with conspicuous black apicule, pericarp fleshy, smooth, sparse to sub-glabrous, becoming black, thin and undulate upon drying, one seed, basally attached, ellipsoidal. Leaf shape shown in Figure 4.3. Appendix 4.6A.

1b. var. *cherrevensis* (Pierre ex Finet & Gagnep.) C. Meade *comb. et stat. nov.*

Ellipeiopsis cherrevensis (Pierre ex. Finet & Gagnep.) R. E. Fries Ark. Bot. 3:41 (1955); *Ellipeia cherrevensis* Pierre ex. Finet & Gagnep. Bull. Soc. Bot. France 52, Mém.4(2):76 (1906) *et* Flore Générale de L'Indo-Chine 1:58 pl. 5b (1907), Type; Cambodia 'Cherreo Mts, 4/1870, Pierre 1790' (Holo- P! Iso - A! C! L! NY!); Craib Fl. Siam. Enum. 1:32 (1931); Jovet-Ast, Supplément a la Flore Générale de L'Indochine, 1:64, F. Gagnepain ed. (1938)

Leaves broadly obovate.

Ecology and distribution *E. ferruginea* is an ecological anomoly within the *Uvarieae*. The climbing stem has become modified so that the plant now creeps directly over the soil, with successive branchlets growing upward from the slow-growing apical meristem. The leaves are fleshy and thick-veined and the species appears well adapted to the dryer forest habitats of Southeast Asia, particularly open Dipterocarp forest. Other habitats recorded include rice-paddy levées, sand dunes and pine forest scrub. Although the species occurs in visibly greater numbers where the soil is well watered and/or a degree of cover is provided by canopy trees, it is much less common in the evergreen vegetation favoured by other members of the tribe, and is unrecorded from most of the evergreen forests in southern Indochina and Peninsular and Southeast Thailand. It also appears absent from the dryest regions of Northeast Thailand. The species was reported (by Hooker and Thomson) to be common in Pegu and the Irawaddy floodplain, although only a few collections from Myanmar have been located. The single record from Bangladesh, if genuine, represents the most westerly distribution for the species. Distribution is shown in Figure 4.39.

Notes When Fries established the genus *Ellipeiopsis* he maintained the distinction between var. *ferruginea* and var. *cherrevensis* at the species level. The only difference between the two is in leaf shape, with var. *ferruginea* having elliptical obovate leaves and var. *cherrevensis* having ovate-elliptical leaves, a distinction not warranting separate species status for the two taxa. The two do maintain distinct distributions; var. *cherrevensis* throughout much of Southern Indochina and Thailand, and var.

ferruginea east of the Thai-Myanmar mountain border, and for this reason it seems wise to retain them as varieties of the same species.

Vern. *Thailand*; Ubon Ratchatani; Thai: 'Phee Puan Noi' (Suddee 797)

Ellipeiopsis ferruginea* var. *ferruginea

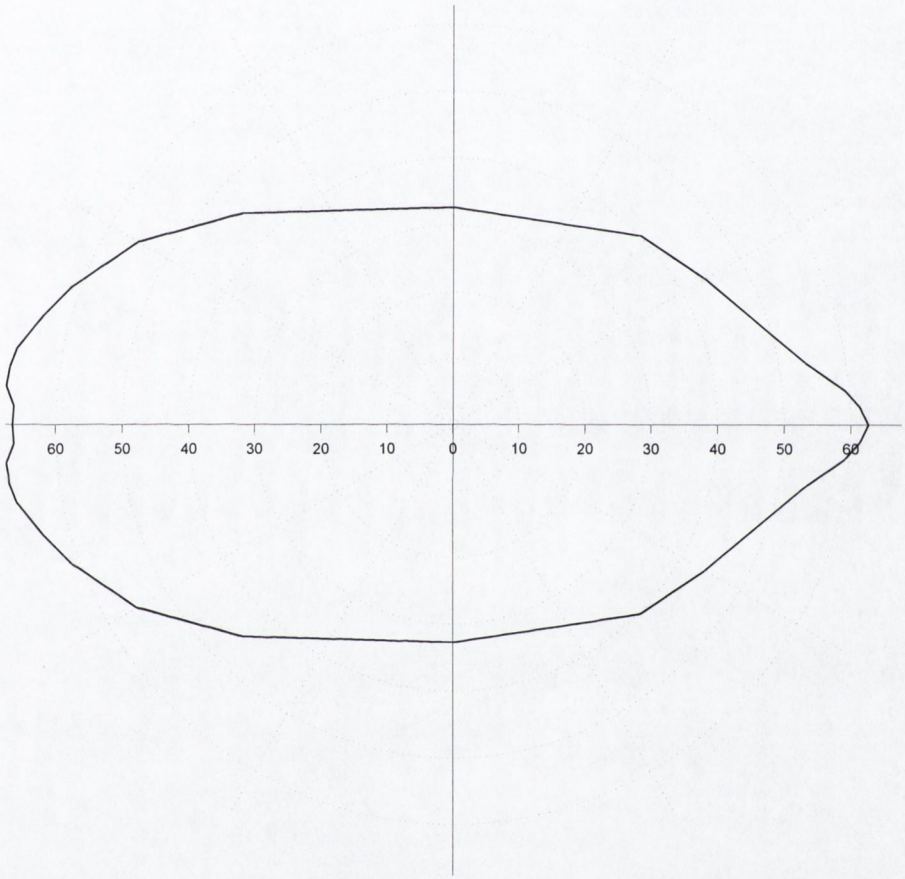


Figure 4.3. Mean leaf outline for *E. ferruginea* var. *ferruginea* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Material Examined

Bangladesh Conulla Teela 15/9/1871 Clarke 14227A (fl., fr.) (K); Conulla Teela 15/9/1871 Clarke 14227B (fl., fr.) (BM)

Myanmar *Taninthari* (Tenasserim); Meaday, Buchanan-Hamilton s.n. (fl.) (BM); *Mandalay*; near Pyinmana, 09/06/27, Parkinson 6141 (fl.) (K).

Var. *cherrevensis*

Cambodia Preah Viheear Province (CLV - 6 - C); Cherreo Mts, 4/1870, Pierre 1790 (fl.) (A, C, L, NY, P).

Thailand *Mae Hong Son Province* (1 – N); Mae Sa Liang, Ban Mae Hang (Mong Village) 300m, 12/6/94, Palee 193 (CMU); *Chiang Mai Province* (2 - N); Awp Luang Gorge, off the Hod-Mae Rd., 29/09/89, Maxwell 89-1124 (fr.) (A); near Bo Luang, 400m, 12/06/73, Geesink et al. 5835 (fl.) (L); Doi Inthanon, E. side, near Sop Aep, 800m, 12/12/69, van Buesekom & Phengkhlai 2054 (fr.) (L); Doi Inthanon, Mae Klang waterfall, interior of Chom Thong, 30/09/71, Murata et al. T-15397 (fr.) (L); Doi Inthanon, along Me Klang River (RS-3), 30/07/88, Koyama T-61621 (fr.) (A); Doi Inthanon, Nam Tok Mai Klang, 8/11/65, Sangkhachand 11 (BK); Doi Saget, southern part, Huay Hang Cry area, Bah Kiang Subdistrict, 450m 13/06/90, Maxwell 90-625 (fl.) (A); Doi Suthep, E. side, Wang Bua Bahn area, 500m, 22/08/87, Maxwell 87-861 (fr.) (L); Doi Suthep, NW slope, Mae-Rim Samoeng Road, 13/09/97, Suddee 839 (fr.) (TCD); Doi Suthep, 30/08/21, Kerr 340 (fl.) (TCD); Doi Suthep, 06/05/09, Kerr 636 (fl.) (BM, K, L, TCD); *Chiang Rai Province* (3 - N); Muang Payoa, 11/07/31, Put 3952 (BM, BK); *Tak Province* (10 - N) along road 75km N of Tak, Northern District, 08/06/68, van Buesekom & Phengkhlai 1063 (fl., fr.) (AAU, L); Doi Car, a hill c. 40 cm W of Tak, 700m, 22/07/73 Murata et al. T - 16804 (fl.) (L); Lansang National Park, 400m, 22/07/73, Murata et al. T-16681 (fr.) (L); *Sukothai Province* (11 – N) Sah Wahng Ah Rome Temple area, Muang Gow District, 9/6/72, Maxwell 72-295 (BK); *Nakhon Phanom Province* (22 - NE); 01/05/32 Kerr 21443 (fl.) (TCD); *Chaiyapum Province* (25 - E); Chum Pae, 3-400m, 11/08/72, Larsen 31688 (L); *Nakhon Ratchasima Province* (26 - E); Ban Chum Seng, 26/5/29, Nai Noe 289 (BK); Ban Chum Seng, 21/3/30 Put 3068 (BK); Khao Yai N.P, E. part, Pak Thong Chai, 11/08/68, Larsen 3336 (AAU); Pirmai, 5/8/63, Pradit 810 (BK); Sakaerat

ERS along Huai Krae stream, Pak Thong Chai, , 400m, 01/11/69, van Buesekom & Charoenpol 2003 (fr.) (L); Sakaerat ERS, 07/12/83, Fukuoka & Ito T-34886 (fr.) (L); Sakaerat ERS, along main road to compound, 14.29 N 101.55 E, 18/10/98, Meade 98-10-18-02 (fr.) (TCD); *Buriram Province* (27 – E); Amphoe Maung, 22/6/84, Sahol et al 6058 (BM); *Roi Et Province* (29 –E); Kaset Wisai, Ban Nam Om, 9/6/82, Paisooksantivatana y-1029-82 (BK); *Ubon Ratchathani Province* (32 - E); Ban Sang Muang, Po Sai District, 07/09/97, Suddee 797 (fr.) (TCD); *Kanchanaburi Province* (34 - SW); Erawan, 1-300m, 02/07/74, Larsen 34015 (fr.) (L); Thung Yai NP, hills above ranger station, 14.19 N 99.12 E, 29/9/98 (-) (TCD); *Phetchaburi Province* (39 – SW); Cha-am, Paisooksantivatana y-2375-89 (BK); *Locality Unknown*; 01/05/29 Noe 289 (fl.) (TCD, L).

Ellipeiopsis ferruginea* var. *cherrevensis

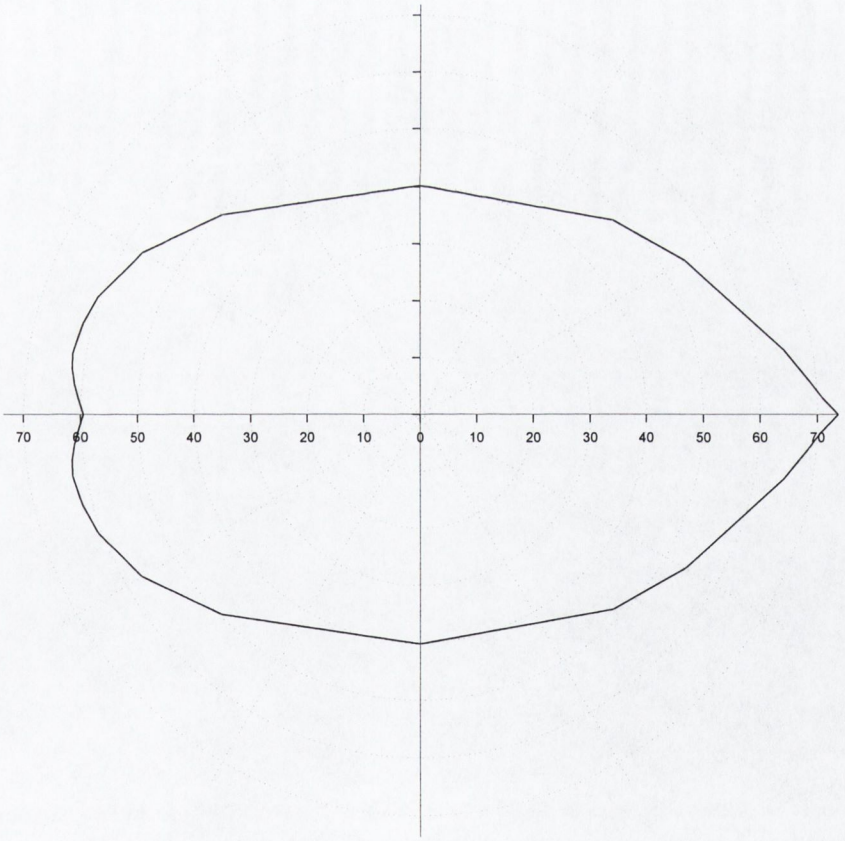


Figure 4.4. Mean leaf outline for *E. ferruginea* var. *cherrevensis* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

2. *UVARIA* L.

Sp. Pl.:536 (1753) *et* Gen. Pl. ed.5:140 (1754), type *U. zeylanica* L.; Dunal, Anon. 88 (1817); A. DC., Syst. 1:481 (1817) *et* Prodr.1:88 (1824); Bl., Fl. Javae 1:11 (1830); Hook. f. & Thoms., Fl. Ind. 1:95 (1855) *et* Fl. Br. Ind. 1:47 (1872); Miq., Fl. Ned. Ind. 1(2):22 (1858); Thw., Enum. Pl. Zeyl. 6 (1858); Benth. & Hook. f., Gen. Pl. 1:23 (1863); King, J. As. Soc. Beng. 61(2)1:19 (1893) *et* Ann. Bot. Gard. Calcutta 4:14 (1893); Ridley, Fl. Mal. Pen. 1:28 (1922); Sincl., Gard. Bull. Sing. 14(2):206 (1955); R. E. Fr. *in* Die Natur. Pflanz. Band 17aII 45 (1959); Hutchinson, Gen. Fl. Pl. 1:82 (1964); Huber, Rev. Handb. Fl. Ceylon 5:11 (1985). *Porcelia* Ruiz & Pavon (1794). *Pyragma* Norunha *in* Verh. Batav. Gen. 5 ed. 1, Art. IV:3 (1790). *Marenteria* Du Petit-Thouars, Gen. Nov. Madagasc. 18 (1806). *Armenteria* Du Petit-Thouars ex Baillon *in* Bull. Soc. Linn. Paris 1:338 (1882). *Uvariella* Ridley, Fl. Mal. Pen. 1:35 (1922).

Pre-Linnean accounts: *Uva* Burm. *Thes. Zeyl.* 231 (1737). *Narum* Adans. *Fam. Pl.* 2:365 (1763).

Habit climbers or sarmentose shrubs with often prominent ferruginous stellate indument; ***Leaves*** membranous or coriaceous, obovate or less often elliptic or ovate, base cordate, retuse or cuneate, apex acute, acuminate or obtuse, veins 6-25+, sub-parallel or convergent, secondary veins complete and kinked or incomplete, indument (sub-)tomentose and ferruginous on both surfaces of young leaves, in mature leaves abaxial surface sparse or glabrous, hairs erect when persistent, rarely scabrous, adaxial surface tomentose to sub-glabrous, hairs spreading; ***Petiole*** with abaxial canal, adaxial surface often transversely foliated, tomentose to sub-glabrous; ***Inflorescence*** a monochasial or rarely branched rhipidium of 1-5 flowers, typically on younger shoots, rarely cauliflorous, secondary buds arising from prophyll in axil of bract just below articulation of pedicel, bract also present midway along pedicel, bracts ovate or obovate, membranous or coriaceous, clasping or free, sometimes large and leaf-like, often wanting, peduncle, pedicel and calyx with identical indument, hairs tomentose or rarely sparse, fine or warted; ***Calyx*** valvate, basally connate or calyptrate, sepals 3, rarely 2 or 4, membranous and spreading or fleshy and concave; ***Corolla*** imbricate, petals 6 or rarely 4-8, erect, reflexed or partially reflexed at maturity, fleshy or

membranous, ovate, oblong or obovate, red, purple, yellow or white, apex obtuse, acute or bluntly acute; ***Stamens*** laminar or rarely cuneate, locules sessile or nearly so, apex papillate or smooth, convex, often elongate, rarely globose, all fertile or with outer whorl of (sub-)staminodes; ***Carpels*** hairy, stigmas glabrous, elongate or broad, lobes U-shaped; ***Fruit*** monocarps globose, oblong or cylindrical, stipitate or rarely sessile, flesh soft at maturity, pericarp smooth, warted, bearded or with longitudinal ridges; Seeds 2-30, lateral in 2 rows, testa brown, smooth, ruminations visible, aril circular or triangular.

A. Petals broadly ovate-acute, concave, erect, occasionally spreading but never reflexed, fleshy, never membranous, stigma elongate or conical ....***Uvaria* section *micrantha***

B. Petals ovate, elliptical, oblong or obovate, acute or obtuse, spreading, often reflexed, membranous or fleshy, stigma with broad U-shaped lobes .... ***Uvaria* section *grandiflora***

Uvaria* section *grandiflora

1a. Calyx calyptrate in bud 2

1b. Calyx valvate or connate (cup-shaped) in bud 13

2a. Pedicel and calyx warty with dense indument of many-branched thickly set hairs 3

2b. Pedicel and calyx with uniform often hirsute indument of ferruginous stellate hairs 5

3a. Inflorescence of 2-5 flowers, leaves 150-250 mm long, veins 13-23 .... **1. *U. lamponga*** *Andaman Islands, Sumatra, Java*

3b. Flowers solitary or rarely 2-3, leaves 80-150 mm long, veins 8-14 4

4a. Petals 4-6, red throughout, obovate, apex obtuse, concave .... **2. *U. lurida*** *India – Southeast Asia – Malesia*

4b. Petals 6-8, red with yellow base, elliptical, apex bluntly acute, flattened .....

..... **3. *U. macropoda*** *Endemic to Sri Lanka*

5a. Mature petals 20-50 mm long, carpels 5-8 mm long 6

5b. Mature petals < 22 mm long, carpels < 5 mm long 7

6a. Petals red, sub-coriaceous, elliptical or oblong, c. 30-50 x 12-20 mm .....
..... **4a. *U. grandiflora* var. *grandiflora***
Bangladesh – Southern China - Southeast Asia - Malesia

6b. Petals red or white, fleshy, broadly ovate-elliptical, c. 20-40 x 15-25 mm .....
..... **4b. *U. grandiflora* var. *flava***
Southeast Thailand – Malay Peninsula – West Malesia

7a. Flowers 30-45 mm diameter, buds up to 15 mm diameter before opening 8

7b. Flowers < 30 mm diameter, buds 5-7.5 mm diameter before opening 11

8a. Young shoots, leaves, pedicel and outer surface of calyx with c. 0.5 – 1.0 mm long, 1-3 branched, persistent ferruginous hairs, ...
..... **5. *U. curtisii*** *Malay Peninsula south of Ranong*

8b. Young shoots, leaves, pedicel and outer surface of calyx sub-tomentose at first with c. 0.25-0.4 mm long deciduous ferruginous hairs, at maturity sparse or sub-glabrous 9

9a. Bracts broadly obovate to circular-ovate, often wrapping around pedicel, c. 10 x 10 mm, persistent, calyx splitting evenly into 3 sepals, leaves broadly obovate, apex acute 10

9b. Bracts narrowly ovate-acute, c. 4-10 x 1.25-2 mm, often wanting, calyx splitting unevenly into 2-4 sepals, leaves obovate, apex cuspidate or acuminate
..... **6. *U. dac*** *Southern Indochina*

10a. Leaf veins 14-25, narrowly spaced, parallel, petals red, distinctly obovate and concave, apex obtuse, 15-20 x 9-11 mm, ...
..... **7a. *U. hamiltonii* var. *hamiltonii***
Assam – Myanmar – Northern Indochina - Hong Kong

10b. Leaf veins 10-13, sub-parallel, petals white or yellow, elliptical-oblong, apex obtuse or rarely concave 10-15 x 8-10 mm .... **7b. *U. hamiltonii* var. *kurzii***

Indochina – Southern China

11a. Pedicel c. 30-40 mm long with prominent broadly ovate basal and medial bracts ..... **8. *U. maclurei***

Yunnan, Kwaichow, Guangzhow & Hainan

11b. Pedicel 5-10 mm long, bracts not prominent 12

12a. Petals yellow, oblong, apex obtuse, usually erect or partially recurved at maturity, never reflexed .... **9. *U. calamistrata***

Guangzhow, Hainan & Northeastern Vietnam

12b. Petals red, elliptical, apex acute, membranous, fully reflexed at maturity .... **10. *U. zeylanica*** *Sri Lanka & Southernmost India*

13a. Calyx splitting apically in early bud to form 3-pointed connate ring around base of unopened corolla, splitting again into 3 subequal ovate-acute sepals with expansion of corolla 14

13b. Calyx valvate in bud 17

14a. Stamens all fertile 15

14b. Outer whorl of staminodes or sub-staminodes present 16

15a. Inner petals opening with outer petals, never connivent, leaves 70 - 200 mm long, base retuse or shortly cordate, veins 9-10 .... **11. *U. sphenocarpa*** *Endemic to Sri Lanka*

15b. Inner petals connivent, forming dome above receptacle, opening before senescence, leaves 160 - 450 mm long, base cordate, veins 16-20 .... **12. *U. semicarpifolia*** *Endemic to Sri Lanka*

16a. Inflorescence of 2-5 buds in tightly-packed rhipidium, up to 3 open at any time, pedicels broad and flattened with abaxial groove, bracts broadly obovate, clasping, coriaceous, petals very broadly elliptical, acute or obtuse, concave, membranous or coriaceous, up to c. 15 x 12 mm, apices usually remaining infolded ..... **13. *U. cordata***

Sri Lanka, Bangladesh – Indochina – Malesia

16b. Inflorescence of 1-2, rarely 3 buds, peduncle and pedicel not flattened, both c. 5-15 mm long, bracts elliptic-oblong, free, wavy, petals broadly elliptical to narrowly ovate, flat or somewhat concave, coriaceous-fleshy, to c. 14 x 10 mm partially reflexed at maturity ..... **14. *U. microcarpa***

Southern China & Northeast Indochina

17a. Pedicel and calyx covered with warty tomentum of blunt, many-branched ferruginous hairs, outer whorl of staminodes 18

17b. Pedicel and calyx with sparse, many-branched fine hairs, petals basally connate, staminodes not present 20

18a. Leaves distinctly scabrid on abaxial surface ..... **15. *U. rufa***

Southern Indochina – Malay Peninsula – Andaman Islands – Western Malesia

18b. Leaves often smooth and waxy, sub-glabrous to glabrous on abaxial surface 19

19a. Young shoots with scattered hairs, leaves elliptic – narrowly obovate, veins 8-14 ..... **16a. *U. lobbiana* var. *lobbiana***

Western Malesia from Isthmus of Kra to Borneo and Java

19b. Young shoots with dense warted indument of blunt, tufted hairs, leaves distinctly obovate, veins 12-20, narrowly spaced ..... **16b. *U. lobbiana* var. *ptychocalyx***

Southern Myanmar, Malay Peninsula and Sumatra

20a. Petals 6, red, obovate, apex obtuse-acute, concave, inner and outer whorls distinct ..... **17a. *U. narum* var. *narum***

Sri Lanka and Oceanic Southwest India

20b. Petals 6-9, red, elliptical, apex bluntly acute, rarely concave, tomentose, outer and inner whorls not distinct ..... **17b. *U. narum* var. *macraei***

Endemic to Sri Lanka

Uvaria* section *micrantha

1a. Pedicel elongate, c. 35-90 mm long 2

1b. Pedicel < 30 mm long 4

2a. Pedicel 35-90 mm long, 2 mm wide, flattened, outer petals broadly ovate, 8-15 mm wide x 9-15 mm long, inner petals narrowly ovate, 6-10 mm long x 4-8 mm wide ..... **18. *U. tonkinensis***

Northern Indochina and Hainan

2b. Pedicel 30-50 mm long, ≤1 mm wide at base and apex and 0.5 mm wide medially 3

3a. Pedicel 30-50 mm long, 1 mm wide at base and apex and 0.5 mm wide medially, outer petals 8 mm long x 7 mm wide, inner petals narrowly ovate, 8 mm long x 5 mm wide ..... **19. *U. boniana***

Northeast Vietnam and Southern China

3b. Pedicel 30 mm long, 0.35-0.45 mm wide, outer petals 4.5 mm long x 3 mm wide, inner petals 5 mm long x 2.5 mm wide ..... **20. *U. orientalis***

Quang Tri Province, Central Vietnam

4a. Leaves distinctly oblong, 45-90 x 17-35 mm, base and apex retuse-obtuse ..... **21. *U. pierrei*** *Mekong basin below Loei*

4b. Leaves obovate, elliptical or lanceolate, base cuneate or retuse 5

5a. Leaves elliptical, lanceolate or narrowly ovate, 70-150 x 20-50 mm 6

5b. Leaves broadly obovate, 150-250 x 65-95 mm 7

6a. Leaf base cuneate, outer petals c. 3.25 mm long x 2.5 mm wide, inner petals c. 3.35 mm long x 2 mm wide, stigma with broadened U-shaped lobes .... **22. *U. micrantha***

Myanmar – Indochina – Andamans – Malesia

6b. Leaf base retuse, outer petals to 9 mm long x 7mm wide, inner petals to 8.5 mm long x 6.5 mm wide, stigma lobes narrow, elongate .... **23. *U. kerrii***

Mountains of Southwestern Thailand - Myanmar

7a. Inflorescence from younger shoots, petals coriaceous, margin prominently tomentose, outer petals 5-6 mm long x 4.5-5.5 mm wide, inner petals 4-5 mm long x 3.5-4 mm wide, erect, not spreading at maturity .... **25. *U. bracteata***

Northern Indochina, Taninthari and Chonburi

7b. Inflorescence from mature shoots or older wood, petals fleshy, margin not tomentose, both whorls up to 9 mm long x 6 mm wide, erect, often spreading at maturity ..... **24. *U. wrayii*** *Isthmus of Kra to Sumatra*

1. *Uvaria lamponga* Scheff.

Natuurk. Tijdschr. Ned.-Indi 31:2 (1870), Type; 'Sumatra, Lampongs' Teijsmann s.n. (BO, n.v.); Backer & Brink, Fl. Java 1:103 (1963).

Syn. nov. *U. andamanica* King, J. As. Soc. Beng. 61(2)1:21 (1892) et Ann. Roy. Bot. Gard. Calcutta, 4:29 t. 25 (1893), Syntypes: India, South Andaman Island, King's collector s.n. (BM!, K); Parkinson, For. Fl. Andaman Is. p. 79 (1923); Mitra, Flora of India 1:289 (1993); Srivastava & Kumur, J. Bomb. Nat. Hist. Soc. 89(3):389-391 (1992).

Habit climber. ***Young shoots*** stout, sub-tomentose or floccose, becoming sub-glabrous and striate, bark black, hairs many-branched, rufous. ***Leaves*** narrowly obovate to oblanceolate, base retuse, apex acuminate, 150-250 x 60-80 mm, acuminum to 15 mm, *veins* 13-23, traces fine, not forming distinct sub-marginal vein, emergent below, short inter-primaries occasionally present, secondary veins incomplete or strongly kinked, tertiary venation reticulate, midrib sunken above, emergent below, primary veins feint above distinct below, tertiary venation distinct below, *indument* variable, glabrous on upper blade, sparse erect ferruginous hairs over midrib and primary veins, hairs on lower surface many-branched, ferruginous, floccose over blade and venation in younger leaves, later becoming sub-tomentose to sparse over veins and sub-glabrous on blade. ***Petiole*** 5-6 x 2 mm, tomentose-floccose. ***Inflorescence*** leaf-opposed, flowers 2-3, or up to 5 in a branching rhipidium, peduncle 2-5 mm long, pedicel 4-10 mm long, basal and medial bracts ovate, 4-5 x 4-5 mm, peduncle, pedicel and bracts with floccose indument, hairs as for lower surface of leaves. ***Calyx*** calyptrate in bud, sepals 3 broadly ovate, 7-8 x 4 mm, basally connate, outer surface as for pedicel, inner surface hairs fine, combed. ***Corolla*** petals 6, red in colour, coriaceous, broadly ovate, apices incurved, c. 10 x 6 mm. ***Stamens*** numerous, 3-4 mm long, apex flattened. ***Carpels*** numerous, 3-4 mm long, ovary tomentose, stigma glabrous, U-shaped, ovules 4-6. ***Fruit*** monocarps 5-30, ovoid to oblongoid, c. 18 x 25 mm, pericarp thick, epidermis warted, hairs many-branched, spreading, deciduous, stipe c. 10 x 3-4 mm, seeds 1-6, compressed-ellipsoid, c. 12 x 10 x 5 mm. Leaf shape described in Figure 4.5.

Ecology and Distribution *U. lamponga* is a very rare species, with only isolated collections from mixed monsoon forest in Java, Sumatra and the Andamans. Distribution is shown in Figure 4.40.

Notes *U. lamponga* is a close relative of *U. lurida* and *U. macropoda*, however the shorter stipe and floccose indument on the underside of the leaves should make it easily distinguishable from these species. The indument is similar to *U. lobbiana* var *ptychocalyx* - but this latter species has valvate sepals, an outer whorl of staminodes and a 35-70 mm long stipe. A recent collection from the Andamans by Srivastava and

Kumur is the first from those islands for over 100 years - they report that the fine twigs are used by islanders as 'Datun' for brushing teeth.

Material Examined

India *Andaman Islands*; 1884, Dr. Kings Collector 209 (BM); 1884, Dr. King's Collector s.n. (fl.) (BM, G).

Indonesia *Java*; Bogor, plot XIV E, 19, November 1902, Merrill s.n. (fl.) (NY).

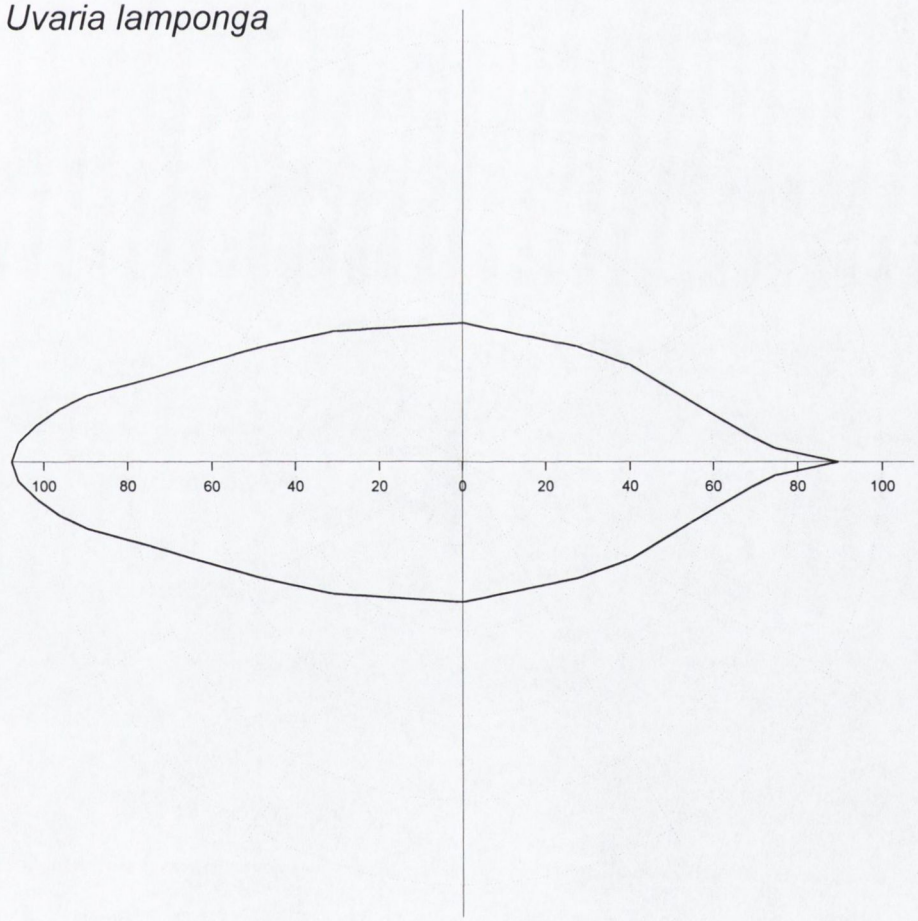


Figure 4.5. Mean leaf outline for *U. lamponga* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

2. *Uvaria lurida* Hook. f. & Thoms.

Fl. Ind. 1:101 (1855) *et* Fl. Br. Ind. 1:50 (1873), type: India, 'Khasia Hills, 2,000ft, Hook. f. & Thoms.' (K! holotype, *designated here*) (BM! E! K! TCD! syntypes); King, Ann. Bot. Gard. Calcutta, 4:28 t. 23 (1893); Finet & Gagnep., Bull. Soc. Bot. France 52, Mém. 4 (2):68 (1906) *et* Flore Générale de L'Indo-Chine 1:53 (1907); Brandis, Indian Trees 4th ed. 17 (1921); Grierson & Long., Fl. Bhut. 1(2):238 (1984); Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):306 (1991). Mitra, Flora of India 1:291 (1993).

Syn. nov. *U. concava* Teijsm. & Binn., Nederl. Kruidk. Arch. 3:406 (1855). *Uvaria hookeri* King, Ann. Bot. Gard. Calcutta 4:28 t. 22 (1893); Cooke, Fl. Pres. Bombay 1:9 (1903); Haines, Bot. B. & O. 2:10 (1921); Mitra, Flora of India 1:291 (1993); *U. narum* Wall ex. Hook. f. & Thoms. var. *macrophylla* Hook. f. & Thoms. Fl. Br. Ind. 1:50 (1872). *U. eucincta* Bedd. Ex Dunn, Bull. Misc. Inf. 182 (1914), type; India; 'Ruschamdah hills, 12/12/1885 Beddome 50' (BM!). *U. leytensis* (Elmer) Merr., Philipp. J. Sci. 10:230 (1915). *Unona leytensis* Elmer, Leafl. Philipp. Bot. 5:1744 (1913), type: Philippines, 'Leyte, Palo, Jan. 1906, Elmer 7365' (NY!).

Habit large woody climber. ***Young shoots*** tomentose, becoming sparse very quickly, hairs ferruginous, many-branched. ***Leaves*** elliptic-oblong to narrowly obovate, c. 130-150 x 40-50 mm, base retuse, apex acute or less often acuminate, coriaceous; *veins* c. 10-12, gradually inarching, interarching irregular, inter-primary veins frequent, microvenation almost completly reticulate with occasional short secondary veins; *indument* abaxial surface entirely glabrous, shiny, adaxial surface indument sparse, hairs many-branched, blunt. ***Petiole*** c. 7-10 x 1.25 mm, hairs sparse, blunt, many-branched, abaxial groove deep, often overtopped by margins, transverse foliations distinct, warty. ***Inflorescence*** terminal or leaf-opposed by apposition, flowers solitary or with dormant secondary bud, pedicel c. 10-20(-50) x 2.5 mm, tuberculate, tomentum of large many-branched, blocky rufous hairs, peduncle sometimes evident to 5 mm at base with small dormant floral bud, peduncle-pedicel often distinctly broader than supporting shoot, buds globose to conical with prominent apicule. ***Calyx*** calyptrate, sepals 2-4 but typically 3, basally connnate, c. 11 x 10 mm, ovate-acute, concave, outer surface with same indument as pedicel, inner surface with sub-tomentose indument of fine, few-branched straggling hairs, becoming sub-glabrous basally. ***Corolla*** petals 6, rarely 4, dark pink or red in colour, basally connate, very broadly obovate with much narrowed base, apex obtuse, c. 20 x 15 mm, outer surface densely tomentose with many-branched pale to rufous hairs, not

as tuberculate as calyx and pedicel, inner surface with sub-tomentose indument as for inner surface of calyx, but more dense, petals detaching from receptacle as connate ring. ***Stamens*** numerous, c 3.5 mm long, glabrous, connective apex flattened or shallowly truncate, locules full length. ***Carpels*** numerous, c. 3.5 mm long, ovary with flattened, many-branched spreading hairs, stigma short, U-shaped, not distinctly lobed, ovules 8-10 in two rows. ***Fruit*** monocarps c. 5 to many, green turning orange-yellow at maturity, smooth, globular-oblongoidal, c. 15-30 x 10-17 mm, often with 1 or more longitudinal ridges, small apicule often present, occasional constrictions between seeds, pericarp soft, fleshy at maturity, stipe long, c. 50-100(-120) x 2-4 mm, typically flattened, often with prominent longitudinal ridges/striations, young stipe and monocarp with sparse indument, later sub-glabrous; *seeds* c. 2-10 in two closely-packed rows, ovoid- compressed ovoid, 8-11 x 6-9 x 3-5 mm, smooth, aril and raphe not prominent. Appendix 4.7A & B. Leaf shape shown in Figure 4.6.

Ecology and Distribution This is the most widely distributed *Uvaria* species in Asia, covering almost the entire distribution of the genus. It's westernmost distribution is the Southern Deccan peninsula, and with the exception of Sri Lanka and the Andaman/ Nicobar Islands, it occurs right across Bengal, Indochina and Malesia. In India, Borneo and the Phillipines it seems to be quite common, elsewhere it is less frequently collected. Distribution is shown in Figure 4.43.

Notes King elevated the *U. narum* var. *macrophylla* of Hooker and Thomson to *U. hookeri*. They all distinguished this taxon by the co-occurrence of long, thick stipes and small, monocarps with seeds in two rows. However, visual examination of specimens of *U. hookeri* suggest they are merely young fruiting specimens of *U. lurida*, and the statistical analyses in Section 3 of Chapter 3 support this conclusion. As for the two rows of seeds, in many Uvarias there is a progressive compression of the two rows of fertilised ovules in the young carpel into what appears one row in the mature fruit. The analyses in Chapter 3 also established that *U. concava*, *U. eucincta* and *U. lurida* var. *sikkimensis* are all properly placed under *U. lurida*. The most variable characters in *U. lurida* seem to be fruit size and pedicel length. Plants from the wetter, more equatorial habitats produce typically larger fruits than elsewhere, while some of the Philippine specimens exhibit much longer pedicels than normal. However, the tuberculate inflorescence, unevenly-splitting calyx and connate corolla

are distinctive characters througout the range, and none of the variation seen in this study is distinctive or consistent enough to warrant the formal designation of varieties. That said, this is a species with a very broad geographical range, and sampling of herbarium material here has been focused on only one half of that range - continental Asia. As a result, one or more regional varieties may have been overlooked during the selective sampling of Malesian material. In terms of distinguishing fruiting material of this species from *U. narum*, the thickened stipe and larger monocarps of *U.lurida* should make it easy to identify.

Vern. Often referred to as a lotus-like flower, India; Oriya: 'Gaichiria' (Mitra 1993); Thailand; Chonburi, 'Bua Bok' Eng. 'terrestrial lotus flower' (Din 238); Chantaburi, 'Kluai Aai Phon' (Bunnak 2).

Material Examined

India *Andhra Pradesh*; Salem District, off Nagalur, Periakalrayans, 1150m, 05/07/79, Matthew 23587 (fr.) (US); *Assam*; Gelaghat District, June 1891, Mann s.n. (fl.) (BM); Khasia hills, 2000 ft., regio subtropico, Hook. f. & Thoms.s.n. (fl.) (BM, E, K, TCD); *Bihar & Orissa* Ayatpur, Puri District, 16/04/17, Haines 3707 (fl.)(ABD, K) (fl.); *Karnataka*; Hassan District, Yethinalla, Shiradi Ghat, 28/05/69, Saldanha 13640 (fl.) (US); Hassan District, near Hettur, 21/08/69, Saldanha 14566 (fr.) (US); Hassan District, Road to Malgod, 13/03/70, Saldanha 16583 (fl.) (US); *Maharashtra*; N. W. Ghats, Matquon Rai, 5/1881, Young s.n. (fr.) (BM); Southern Concan, Law s.n. (K); *Sikkim*; 800ft Mongpur Peak, 11/8/1881, King s.n. (fr.) (G); Mongpur Peak, 3000ft 1/12/1887, Gamble 28025 (fr.) (K); 1500ft, 2/10/1877, King 4935 (fl.) (BM, G, K); *Tamilnadu*; Ganjam District, Kuncholy, 2000 ft., 5/4/09, Dawkins 14218 (K); Goomsah hills, Beddome 49 (fl.) (BM); Goomsah hills, Tamilnadu 12/12/1885 Beddome 52 (fl.) (BM); Kodaikanal District, Dindigul, Ganesapuram-Palani Road, Palni Hills, 800m, 22/03/87, Matthew 48691 (fr.) (AAU); Kodaikanal District, Dindigul, Thadiankudisai - Adalur Road, top, 04/08/88, Matthew 53326 (fr.) (K); Ruschamdah hills, above Kunadah, 3/6/1879 Beddome 51 (fl.) (BM); Ruschamdah hills, 12/12/1885 Beddome 50 (fl.) (BM).

Thailand *Chonburi Province* (55 – SE); Ban Buang, 68m, 18/07/66, Phengkhlai 1273 (fl.) (BKF); Sriracha, Pan sa-det, c. 50m, 17/11/46 Din 238 (fl.) (BKF); *Chanthaburi Province* (57 – SE); Khao Soi Dao, c. 730m, 10/06/60, Bunnak 2 BKF no.202 (fl.) (BKF).

Malaysia *Sabah*; Sandakan Sept.-Dec. 1920 Ramos 1667 (fr.) (A); *Sarawak*; S. side of Gunung Sibis, Miri District, 29/11/66 Tan & Wright S.27533 (fr.) (NY); Siargao 01/04/28, Wenzel 3208 (fr.) (NY).

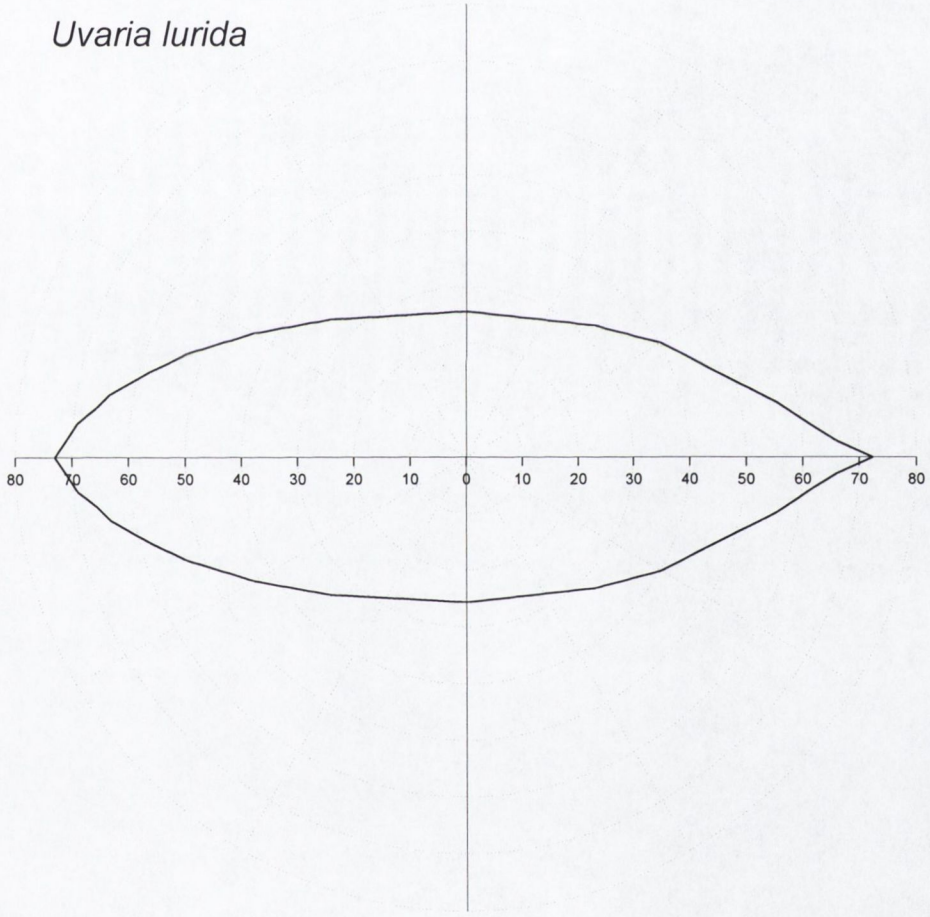


Figure 4.6. Mean leaf outline for *U. lurida* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Indonesia *Java*; Peutjang Island 27/03/64 Kostermans 35A (fr.) (G) coral habitat 5m altitude, climber (fr.); Udjung Kulon Reserve, Peutjang Island, 20/12/61, Soepadmo 304 (fl.) (C); *Flores*; Mbengen, S.E. region of Western Province 10/05/65 Kostermans 22116 (fl.) (A, AAU, K, L).

Philippines *Luzon*; Bataan Province; Lamao River, Mt. Marivelos, Oct. 1903 Merrill 3301 (fr.) (NY); Benguet Subprovince, 01/05/14, Merrill 9666 (fl.) (NY); Isabela Province, San Mariano, Feb.-Mar. 1926 Ramos & Edano 46784 (fr.) (NY); Laguno Province, Nov. 1915 Ramos 24059 (fr.) (NY); *Leyte*; Palo, Jan. 1906, Elmer 7365 (fr.) (NY); *Mindanao*; Siargao, Apr. 1919, Ramos & Pascasio 34447 (fl.) (NY).

3. *U. macropoda* Hook. f. & Thoms.

Fl. Ind. 1:101 (1855) *et* Fl. Br. Ind. 1:50 (1872), lectotype (*designated here*): Sri Lanka; *'s.coll.* C.P. 2544' (BM!); isotypes: Ceylon, *'s.coll.* C.P. 2544' (G! K! TCD!); Walker s.n. (K!); Thw., Enum. Pl. Zeyl. 6 (1858); Bedd., Ic. Pl. Ind. Or. 16, t. 79 (1874); King, Ann. Bot. Gard. Calcutta 4:27 t. 20 (1893); Trimen, Handb. Fl. Ceylon 1:19 (1893); Alston, Kandy Fl. 1 (1931); Huber, Rev. Handb. Fl. Ceylon 5:19 (1985).

Habit climber up to 35 m tall. ***Young shoots*** sub-tomentose with blunt rufous hairs, quickly becoming deeply striate and grey in colour with prominent lenticels. ***Leaves*** elliptical-obovate, base narrowly retuse to cuneate, apex obtuse to shortly acute/ acuminate, 80-130(-150) x 30-50(-60) mm, coriaceous, waxy; *veins* c. 8-12(-14), indistinct, sub-parallel, interarching pattern irregular, not forming sub-margin, inter-primary veins frequent, microvenation reticulate, secondary veins indistinct, midrib slightly depressed abaxially, emergent adaxially, other venation indistinct on both surfaces; *indument* abaxial blade completely glabrous, adaxial blade and midrib sub-glabrous with very rare rufous c. 10+ branched hairs. ***Petiole*** c. 5-6(-8) x 1 mm, indument sparse, hairs blunt, more dense than on lower midrib and blade. ***Infloresence*** terminal or (sub-) opposed by apposition, flowers solitary, pedicel c. 15-20 x 1-1.5(-2) mm diam., peduncle-pedicel distinctly broader than young shoots,

narrowing at base, bracts usually wanting, buds spherical-conical with prominent apicule, pedicel and bud covered with thickened, many-branched hairs giving coarsly tuberculate appearance. ***Calyx*** calyptrate, splitting irregularly into (2-)3(-4) unevenly sized sepals, to c. 10 x 9 mm, ovate, acute, often one larger sepal carrying apicule, outer surface indument as for pedicel, inner surface hairs smaller and finer, surface smooth, not tuberculate. ***Corolla*** petals 6-8, red with yellow base, basally connate, elliptical-oblong, acute, c. 18 x 8 mm, petal bases fused for 1-4 mm, petal apices often concave but not distincly obovate, indument on outer surface densely tomentose with pale, many-branched fine hairs, overlain by scattered large rufous hairs as found on calyx and pedicel, more dense along central axis and towards base, especially on outer whorl, inner surface densely and shortly tomentose with no large rufous hairs. ***Stamens*** numerous, c. 2.25 - 3 mm long, glabrous, connective apex broad, convex or flattened or rarely shallowly truncate, shortly papillate, locules full length. ***Carpels*** c. 30, 3 – 3.75 mm long, ovaries tomentose with flattened spreading hairs, stigmas U-shaped with very large, broad lobes c. 1-1.25 mm wide, raised distinctly above stamens, some occlusion of stigma on external side, ovules 12-16. ***Fruit*** monocarps c. 10-16, 50-70 x 10-15 mm, narrowly cylindrical and angular with 4 distinct longitudinal ridges, apicule usually thickened and prominent, c. 5-10 mm long, pericarp thick but outline of seeds usually visible, indument sparse, stipes distinctly elongate, 65-150 mm+, thickened at base, broadening and becoming angular towards monocarp, deeply striate; *seeds* 10-16, in two rows closely packed together to seem like one row, oval, c. 7 x 5 x 4 mm, smooth, aril and raphe not well developed. Leaf shape shown in Figure 4.7.

Ecology and Distribution Endemic to Sri Lanka. Widely distributed in the island NE of Kurunugella-Badulla Districts in the dry and moist climatic zones up to 700m. Occasional in disturbed forest of the wetter SW hills, absent from the the S and SW lowlands. Distribution is shown in Figure 4.43.

Notes *U. macropoda* is intermediate between *U. lurida* and *U. narum*, easily distinguished from these two species by its few carpels with very large, broad stigmas and its distinctive fruits with a large, tapering apicule. Huber (1985) reports that in Ceylon *U. narum* and *U. macropoda* are ecologically distinct, with *U. narum* being restricted to the wetter S and SW of the island.

Vern. *Sri Lanka*; Sinhalese; 'Attu-muddah' (Huber 1985).

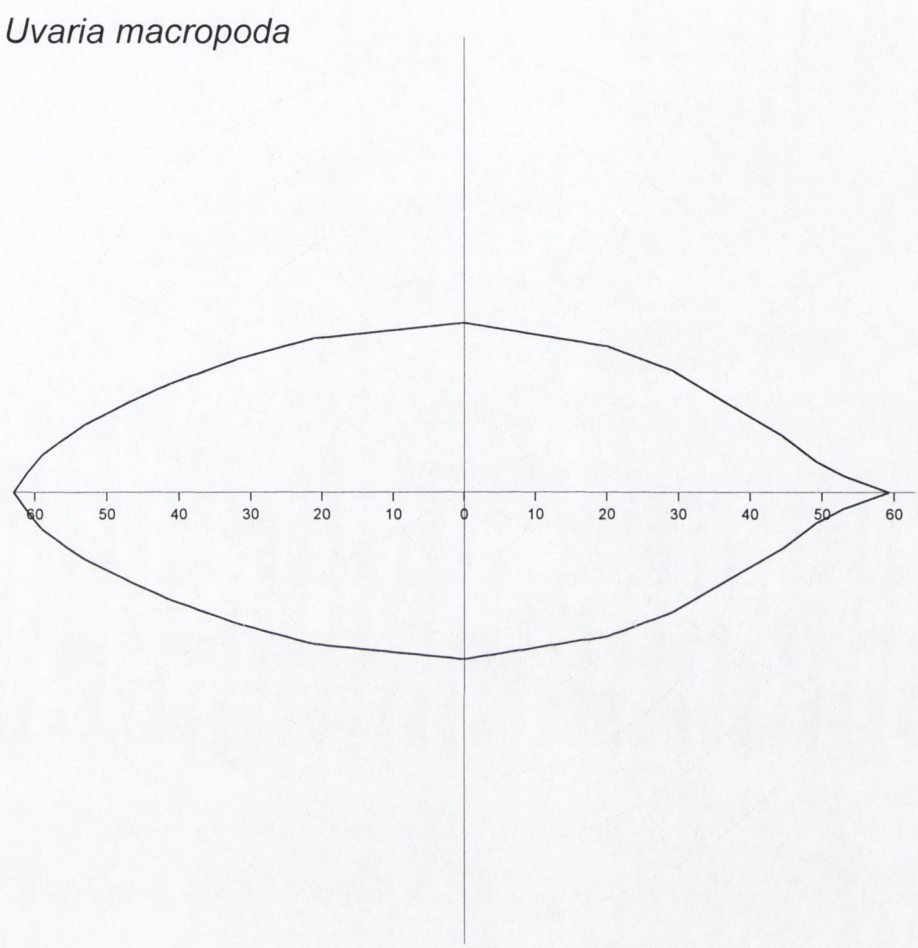


Figure 4.7. Mean leaf outline for *U. macropoda* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Material Examined

Sri Lanka *Amparai District*; E. of Maha-Oya, 07/05/75 Jayasuriya 2110 (fl.) (K, L, US); *Anuradhapura District*; Ritigala Strict Natural Reserve, 1940ft. Weweltenna plain, freq. 30/09/72, Jayasuriya 881 (-) (US); Ritigala Strict Natural Reserve, 1100

ft., E. slope, 21/01/73, Jayasuriya 1077 (fr.) (US); Ritigala Strict Natural Reserve, Anuradhapura Distr. 1400 ft., W. slope 08/08/73 Jayasuriya 1274 (fl.) (K, US); *Badulla District*; Diyaluma Falls, 520m, 16/11/77, Huber 632 (US); Meda Oya, low altitude, near the flow of Hepala Oya into river Mahaweli; 29/10/71, Jayasuriya 396 (fl., fr.) (K, NY, US); *Kandy District*; Gannurowa Hill, Peradeniya Forest, 09/07/78, Meijer 1704 (fr.) (L); *Kurunegala District*; Arankale, 21/10/73 Waas 228 (fl.) (K); Doluwa Kanda, 7.37.N 80.25.E, 14/02/75, Sumithraarachchi DBS 645 (fl.) (US); *Matale District*; Diokandahena, near Dambulla, 250m, 15/10/77, Huber 458 (fl.) (US); west side of Dambulla Hill, 17/06/32, Simpson 9783 (fl.) (BM); *Polonnaruwa District*; N. bank of Amban Ganga, Ambamedilla, 60m 11/10/77 Huber 435 (fl.) (L); Banks of Mahaweli Ganga, Thunmodera, 07/06/74, Waas 582 (fl.) (US); *Ratnapura District*; Kalanne, 12th mile post on Embilipitiya-Rakwana Road, 17/10/71, Balakrishnan NBK 908 (fr.) (US); Kalanne, 12th mile post on Embilipitiya-Rakwana Road, 17/10/71, Balakrishnan NBK 906 (fl.) (US); *Locality Unknown*; *s.coll.* CP. 2544 (fl., fr.) (BM, G, K, TCD); Ceylon 1600ft., Walker 160 (fl.) (K).

4a. *U. grandiflora* Roxb. ex Hornem.

Hort. Haffnensis Suppl. 140 (1819), holotype: India, 'April 1818 *HBC, Uvaria grandiflora* Roxb. Ex. Ind. Orient.' (C!);Roxb., Hort. Bengal. (1814) 43 *nom. nud.*, *et in* Fl. Ind. (2nd ed.) 3:665 (1832); Wall., Pl. As. Rar. 2:21 t. 121 (1830); Sincl., Gard. Bull. Sing. 14(2):202, t. 6 (1955); Tsiang Ying & P-T Li *in* Fl. Rep. Pop. Sin. 30(2):26, t. 10 (1979); Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):305 (1991). *U. purpurea* Bl., Bijdr. 11 (1825) *et* Fl. Jav. (Anonaceae)1:13, t.1 *et* t. 13a (1830), syntypus 'Java, Blume s.n., ex Herb. Bl.' (NY!); Hook. f. & Thoms., Fl. Ind. 1:95 (1855) *et* Fl. Br. Ind 1:47 (1872); Miq., Fl. Ned. Ind. 1:22 (1859); Benth., Fl. Hongkongensis 9 (1861); King, J. As. Soc. Beng. 61(2)1:15 (1892) *et* Ann. Roy. Bot. Gard. Calc. 4:21, t. 12 (1893); Ridley, Fl. Mal. Pen. 1:31 (1922); Merr., Lignan Sci. Journ. 5:77 (1927); *U. platypetala* Champ. ex Benth., Kew Journ Bot. 3:257 (1851), Holotype: 'Hong Kong, 1850 Champion 38' (K!); *Unona grandiflora* DC., Prod. 1:90 (1824).

Syn. nov.; *U. purpurea* var. *tuberculata* King, J. As. Soc. Beng. 61(2)1:15 (1892); *Uvaria rubra* Robinson, Bull. Torrey Bot. L. 35:68 (1908), Holotypus: Phillipines, 'Santa Cruz, Davao Province, Mindanao, 29/6/05, Williams 3042' (NY!). *U. rhodonta* Hance *in* Walp. Ann. 2:19 (1851).

Habit shrub to 3m or large woody climber. ***Young shoots*** densely tomentose, becoming striate and somewhat glabrous later, initially flexuous, straightening later. ***Leaves*** elliptic-obovate, base subcordate/ very shortly retuse, apex obtuse-acute, 130-190(-250) x 50-75(-100) mm; *veins* 11-14(-16), sub-coriaceous to coriaceous, secondary veins kinked, apices interarching c. 10 mm from margin, trailing trace often strong leading to formation of sub-marginal vein, all venation depressed above and emergent below; *indument* abaxial surface sparse to sub-glabrous, hairs stellate and simple, dense over midrib and vein junctions, occasional elsewhere on veins and blade, adaxial blade tomentose to rarely sparse, hairs all stellate, c. 10 branched, 0.3-0.5 mm diam., less dense on midrib than on blade. ***Petiole*** short, 5-6 x 2 mm, thicker than midrib, sparsely tomentose, warted and transversely foliated, black. ***Inflorescence*** leaf-opposed or sub-opposed, solitary or rarely with second dormant bud, or cauliflorous with elongate, often many-branched cyme of 3 to many pedicels, 1 or 2 bearing mature flowers, pedicel 10-15 x 2 mm, or up to 60 x 2 mm, ferrugino-tomentose, hairs to 0.5 mm diam., surface smooth, often striate towards receptacle, basally and medially bracteate, bracts large, ovate-elliptical, 10-33 x 5-20 mm, leafy, veins palmate, prominent, indument densely tomentose to tomentose, hairs longer and darker on adaxial veins surfaces. ***Calyx*** calyptrate in bud, later forming 3 (rarely 2 or 4) ovate-acute, 15-25 x 9-18 mm sepals, indument densely ferrugino-tomentose, very short and paler on inside, longer on outside, sepals conspicuous, green, reflexing at maturity. ***Corolla*** petals 6, whorls subequal, 20-45 x 8-15 mm, elliptical-oblong to rarely very narrowly obovate, base narrow, apex obtuse or very bluntly acute, sparse stellate indument on inner surface of both whorls, more dense on outer surface, petals very large and showy, deep red to purple, oblong, margins often turned downward in fully expanded specimens. ***Stamens*** numerous, large, 6-8 x 1.25 mm, connective head shortly papillate, flattened, dorsal ridge often prominent, stellate indument running length of connective, locules full length, glabrous. ***Carpels*** numerous, 8.0 - 8.5 x 1.5 mm, ovary shortly and densely tomentose, stigma U-shaped, glabrous, somewhat lobed, 2 x 1-2 mm wide, usually producing copious amounts of nectar when ripe causing gynoecium to fuse in dried specimens, ovules 24-36. ***Fruit*** monocarps 6-12(-20), receptacle very much enlarged, to c. 25 mm in diam., stamen abscission scars forming prominent ring at base, stipes to 30 x 4 mm, thickened toward base and apex, smooth to (thickly) striate, shortly and densely tomentose; monocarps 50-75 x 10-20

mm, cylindrical, apex globose to conical, smooth or often with longitudinal and/or lateral ridges present, constrictions between seeds often present, seeds 16-30, hemi-ellipsoidal to ovoid, often dorso-ventrally flattened, to 7 x 5 x 2 mm, smooth, ruminations visible. Appendix 4.8 A & B. Leaf outline shown in Figure 4.8.

4b. var. *flava* (Teijsm. & Binn.) Sincl.

Gar. Bull. Sing. 14(1):44 (1953). *U. flava* Teijsm. & Binn., Natuurk. Tijdschr. Ned.-Indie 25:419 (1863); Miq., Ann. Mus. Bot. Lugd. Bat. 2:6, t. 1 (1865); *U. purpurea* var. *flava* (Teijsm. & Binn.) Scheff., Natuurk. Tijdschr. Ned.-Indie 31:4 (1869), type: Indonesia, cult. Hort. Bog., Teijsmann s.n. (BO-holo *n.v.*). *U. purpurea* var. *alba* (Miq.) Scheff., Natuurk. Tijdschr. Ned-Ind 31:4 (1869), type: Philippines, Luzon, prov. Bataan, Lamao River, 11/8/1903, Barnes 50, (destr.).

Differs from the typical form of the species in having thick, fleshy, usually broadly and bluntly ovate petals which can be either red or yellow-white in colour and bruise easily. Appendix 4.8C.

Ecology and Distribution *U. grandiflora* is found mostly in evergreen forest but there are occasional records from semi-deciduous dipterocarp forest. Although a widespread species, it has been collected most frequently in Hongkong, Hainan and Southeast Thailand. It also appears very common in the middle and lower Malay Peninsula, and there are several records from around Songkhla. Several early collections from Tenasserim (now Taninthari) suggest it is a common species there too, but no recent material is available from this region. The plant is absent from the Indian subcontinent, but there have been some collections made in Sri Lanka. However, the plant is most probably introduced on the island. *U. grandiflora* also occurs in Malesia as far east as the Phillipines and New Guinea. Distribution is shown in Figure 4.44.

Notes The flowers of *U. grandiflora* are not particularly variable, however the fruit can vary considerably. The monocarp can be wholly tubular or constricted between the seeds and the surface can be either smooth, striate or tuberculate. As the fruit matures the pericarp softens, causing the outline of seeds within the monocarp to

become more sharply defined. In most respects *U. grandiflora* lives up to it's name, producing the largest bracts, sepals, petals, stamens and carpels of any *Uvaria* species in Asia, and the fruit also produces the most seeds per carpel (up to 30). The large solitary flowers are instantly recognisable at all stages of development. Where the inflorescence produces more than one flower the dimensions of all organs are reduced, and this can lead to confusion with large-flowered specimens of *U. microcarpa*. However, *U. microcarpa* has an outer whorl of staminodes which should instantly differentiate it from *U. grandiflora*. Infertile specimens are most likely to be confused with *U. cordata*, *U. microcarpa* and *U. dac*. The retuse leaf base of *U. grandiflora* is usually enough to distinguish it from the two former species (which have cordate bases) although there are rare specimens of *U. microcarpa* which are retuse. *U. grandiflora* also tends to retain its leaf indument to a much greater extent than these two species. The leaves of *U. dac* are smaller, have fewer veins and are much more acuminate than than those of *U. grandiflora*. The only variety recognised in continental Asia is var. *flava*, which is restricted to the wetter habitats of Southeast and Peninsular Thailand. Cauliflorous inflorescences are seen in both varieties, and probably arise as a result of year-round production of flowers which then fail to achieve fertilisation. This is suggested by the fact that fruiting receptacles, where present, are always terminal in cauliflorous specimens. The fruits of *U. grandiflora* are edible, but are not as highly regarded as those of *U. rufa*. However, the year-round production of large, fragrant flowers make it a popular feature of tropical Asian botanic gardens. In Hainan the leaves are used in the making of cakes and rice whiskey.

Vern. *Thailand*; Trat Province "kluey pang-pon" "epiphyte squirrel banana" (Dee 191), Surat Thani Province "klui mu sang" (Kerr 13319), Trang Province"Yan nom kwai" (Bunnab 284); *Vietnam*; Quangtri Province "Bu tu Bo" (Poilane 31254); *China*; Hainan; "Sait'ang Chau Kung", "Tai T'ang Chau Kung", "Tai Kok Lok Tszt'aing" (McClure 8944).

Material Examined

Sri Lanka Botanic Garden Peradeniya, 01/12/78, Kostermans 27199 (fl.) (G, L);

Locality unknown; 23/01/09, Fraser 116 (fl.) (BM, US).

Myanmar *Taninthari*; Tavoy, "Hindoostan" 18/9/1827 Wallich 260/ 6485 (fl.) (BM); Tavoy, Wallich 6485b (BM); Tavoy, Wallich 6485c; *Locality unknown*; April 1818 HBL s.n. (fl., fr.) (C); (BM); Wallich s.n. (fl.) (BM).

China *Hong Kong*; N of Mt. Gough, Hong Kong 7/6/1873, Lamont 8 (fl.) (BM); 31/5/1894 , Bodinier 828 (fl.) (E); 24/01/09 Champion 38 (fl., fr.) (BM, K) (fl., fr.); 4/1852 , Hance 933 (fl., fr.) (BM); 12/9/1898 Henry s.n. (fr.) (NY) (fr.); 31/5/1884 , Sampson s.n. (fl.) (BM); *Hainan Province*; Kochow District 05/05/29, Tsiang Ying 2110 (fl.) (NY); Lam Ko District, Lin Fa Shan, 08/08/27, Tsang 399 (fr.) (E, NY, US); Ling Shui District, near Po T'eng (Bodeng), 01/04/32, Liang 61556 (fl., fr.) (NY); Ling Shui District, Po-T'eng (Bodeng), 300m 01/06/35, How 72850 (fl.) (BM, A); Ling Shui District, Po T'eng Shi (Bodeng), 29/05/32, Fung 20029 (fl.) (BM, E, NY, US); Man Ch'eung District, 13/04/32, McClure 20011 (fl.) (NY); Tingshuan, 24/08/30, Liou 7940 (fl.) (PE); Yaichow, 16/07/33 How 71035 (fl.) (NY); 18/12/34, Liang 66428 (fl.) (NY); 60m 10/04/22 , McClure 8944 (fl.) (NY); *Province unknown*; 18/06/36 Lau 27189 (fl.) (PE); Kouang-Teheou-Wan 21/10/08 , Robert s.n. (fl.) (NY, P).

Laos *Louang Namtha Province* (L - 2 - CLV); Mong Hsing, Haut, 01/05/29, Ward 8928 (-) (NY).

Vietnam *Quangtri Province* (V - 25 - CLV); Col d'Ailao, Poilane s.n. (HCMC); Pio, 18/06/24 Poilane 11049 (fl.) (HCMC); Salung Pro, 31/12/40, Poilane 31254 (fr.) (P).

Thailand *Nong Khai Province* (20 - NE); Bang Yai, Phonpisai, 8-6-1963, Adisai 488 (fl.) (BKF); *Chaiyaphum Province* (25 – E); Phu Khieo W.S., 14-6-94, Th. S et al (BKF); *Ubon Ratchatani Province* (32 – E); Ubon Ratchatani, NE Botanic Gardens, cultivated, 17/10/98 , Chalermglin & Meade 98-10-17-3 (-) (TCD); *Prachuap Khiri Khan Province* (37 - SW); Huai Yang Waterfall, S of Prachuap, 11.4N 99.5E, low altitude, 10/02/70 van Beusekom 2765 (fl.) (BKF, L); *Krung Thep Maha Nakhon Province* (49 – C); private horticultural plot, 10k N of Don Muang Airport 18/10/98, Meade & Chalermglin 98-10-17-4 (-) (TCD); *Chanthaburi Province* (57 – SE); Khao

Soi dao, 13.0N 102.15E, 250-300m 18/12/74 Geesink 7896 (fl.) (BKF); Khao Soi Dao, Chanthaburi Province, c. 400m, 13.00N 102.15E 10/11/69 , van Buesekom & Smitinand 2096 (fl.) (BKF, L); *Trat Province* (58 – SE); Kao Saming, 24/01/27 Put 543 (fl., fr.) (BM); Kao Saming, 29-1-1927, Put 584 (fl.) (BK); Kao Saming, 29/01/27 Put 586 (fl.) (BM); Salak Koh, Koh Chang, 12.0N 102.4E, 50m, 08/05/74, Geesink 6620 (fl.) (L); *Surat Thani Province* (61 – Pen.); Ban Kawp Kep, c. 10m, 13-4-1927, Allan/ Kerr 13319 (fl.) (BK, BM); Kao Noi, Ko Samui, 28-6-1966, Sakol 1147 (fl.) (BK): Kao Song, Ta Chana, Surat, 8-7-1966, Sakol 1248 (fl.) (BK); *Krabi Province* (64 - Pen); Nong Khon, 15/08/64 Sangkhachand 1026 (fl.) (BKF, L); *Trang Province* (67 - Pen); Khao Chong, 82m, 08/01/66, Bunnnab 284 (fl.) (BKF); Khao Chong, 20/12/65, Bunnab & Sukkri 239 (fl.) (BKF, E); Khao Chong, 15k E of Trang, 99.45E 7.3N, 2m, 13/11/90, Larsen 41299 (fl., fr.) (AAU, BKF, PSU); Khao Chong, 02/02/69, Phusomaeng & Punin 48 (fl.) (BKF, C, L); Khao Chong, 02/02/69, Samrong 48 (fl.) (BKF); *Songkhla Province* (69 - Pen); Hat Yai, Dec 26th 1927, Kerr 13661 (fl.) (BK, BM); Khao Kho Hong, Hat Yai, 100.2E 7.0N, 250m, 30/10/90, Larsen 40936 (fl., fr.) (AAU, BKF, PSU); Khao Noi, Songkhla, 25-40m 23/04/79, Congdon 389 (fr.) (BKF); Songkhla 09/01/66, Smitinand 11862 (fl.) (BKF); Ton Nga Chang, Songkhla Province, 1-200m, 100.10E 7.00N 04/10/91, Larsen *et al.* 42126 (fl.) (AAU, BKF, PSU); Niyomdham 94649 (BKF); *Province unknown*; Khao Phut Thong Arboretum, 50m, 12/1991, Santisuk s.n. (fl.) (BKF); *s.coll.* BKF 5302 (fl.) (BKF); *s.coll.* BKF 52461 (fl.) (BKF).

Peninsular Malaysia *Kedah*; E of Kuah, Palau Langkawi, 18/12/74, van Balgooy 2236 (fl.) (L); *Kelantan*; Wray 3352, 2-1889 (Sing.); 27-10-87 T&P 1147 (Sing.); *Malacca*; Brisu, Malacca, sea level, 6/1888, Derry 50 (fl.) (BM); Malacca, Griffith s.n. (fl.) (NY); 12/1889, Henry 326 (Sing.); Malacca 12/1830, Walker (fl.) (BM); *Pahang*; Kuala Takam 01/06/17, Evans s.n. (fl.) (K); Taman Negara N.P., Track from Kenyam to caves, 27/04/75, van Balgooy 2547 (fl.) (L); *Penang*; Penang 6/1890, Curtis 234 (fl.) (AAU); Curtis sn, Penang 5-1892 (Sing.); Penang, Porter s.n. (fl.) (BM); *Perak*; Kuala Kangsa, 1892, Ridley s.n. (Sing.); Perak; Larut, 8/1883, King 4786 (fr.) (K, G) Locality unknown; Ridley 12-1895; Wallich s.n. (fl.) (BM); *Negeri Sembilan*; Jelebu District, Pasoh Forest, 80-120m 21/05/96 Gardette 1866 (-) (K, KEP, L, Sing.); Tanjong Sena, Rembau N.S. 25/04/63, Kasim Bin Rajab 520 (fl.) (K).

Indonesia *Sumatra*; Kota Pinang, subdivision Laboehan Batoe 25/05/33, Toroes 4334 (fl.) (NY, MICH); Silo Maradja, Asahan, East Coast 01/06/27, Bartlett 8413 (fl.) (MICH, NY, US); East Coast, Yates 1379 (fl.) (NY); East Coast 23/07/32, Toroes 3250 (fr.) (NY, MICH); *Java* Jawa Barat; Bogor 01/06/04 Backer s.n. (fl., fr.) (U); Bogor, Cult. in Botanic Gardens [XVI.E.5], 24/11/80 , Okada 3368 (fl.) (NY); Bogor, Cult. in Botanic Gardens, 1886/87, Warburg 1805 (fl.) (NY); Jampang Kulon, S. of Sakabumi, W. Java, 400m, 16/09/85, van Balgooy 5147 (fl.) (L, U); *Locality unknown*; Blume s.n. (fl.) (NY).

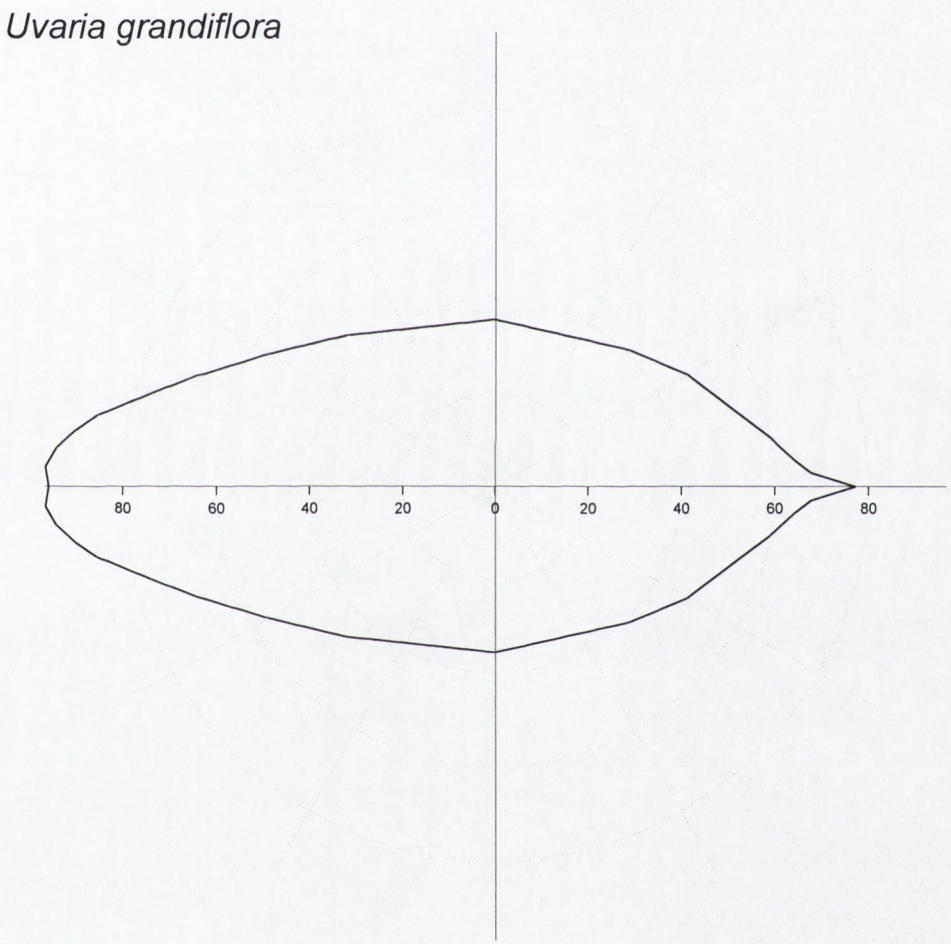


Figure 4.8. Mean leaf outline for *U. grandiflora* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Phillipines *Luzon*; Rizal Province, Bosobo, 01/06/06, Ramos 980 (fl.) (NY); *Mindanao*; Surigao Province, Mt. Cantigao, low altitude, 20/03/31, Convocar 130 (fl.) (NY); Misamis Province, Mt. Malidang, 01/05/06, Mearns 4777 (fl.) (NY); *Palawan*; 31/05/06 , Foxworthy 42885 (fl.) (NY); *Panay* Island; SW range of Mt. Baloy, Laggit, 2-3k SE of Lublub, 122.06E 11.03N, 200m, 08/08/87, Varadarajan 1571 (fr.) (NY).

var. *flava*

Thailand *Chonburi Province* (55 – SE); Nong Khum, Siracha tasert, 25m, 10-11-1927, Collins 1680 (fl.) (BK); Toong Brong, Sattahip District, 4-12-1971, Maxwell 71-765 (fl. petals white) (AAU, BK). *Chanthaburi Province* (57 – SE); N. Soy Mtn, Bong Nam Rawn district, 250m, 5-5-1975, Maxwell 75-489 (fl.) (AAU, BK); *Trat Province* (58 – SE); Dong Ta Beng, Khao Sameng, 21/10/46 Dee 191 (fl., petals white) (BKF); *Songkhla Province* (69 – Pen.); Suan Dtoon falls, Muang District, 25m, 11/10/84 Maxwell 84-312 (fl.) (BKF, PSU).

Java *Jawa Barat*; Cult in Hort. Bog. XI-A-20, Scheff 206 (fl.) (L).

5. *Uvaria curtisii* King

J. As. Soc. Beng. 61(2)1:19 (1893) *et* Ann. Roy. Bot. Gard. Calc. 4 (1893) 23 Pl. 24A, lectotype (*designated here*): Malaysia, 'Penang, Government Hill, 2000 ft., 5/1893, Curtis 1415' (Sing.!); syntypes: Malaysia, 'Penang, Government Hill, 2000 ft., 5/1892, Curtis 1415' (BM!, K!) *et* 'Perak, Ulu Bubong, King's Collector 8543' (C!); Ridley, F.M.P. 1 (1922) 32; Sinclair, Gard. Bull. Sing. 14(2):206 (1955).

Habit shrub or large climber with distinctive hirsute indument. ***Young branchlets*** sub-tomentose, hairs ferruginous, hirsute, becoming sparse with age. ***Leaves*** sub-coriaceous, elliptical to narrowly obovate, acute or shortly acuminate, base retuse, c. 210-250 x 60-70 mm; *veins* 10-12+, up to 30 mm apart, sub-parallel, branching angle often shallow, c. 40-50 deg., trailing apices fine, indistinct; *indument* hairs

ferruginous, hirsute, c. 0.5–1 mm long, on abaxial surface erect and emergent over midrib depression, less prominent over secondary veins, very sparse over blade with mixed simple and stellate hairs on younger leaves, simple hairs persistent into maturity, on adaxial surface hairs all stellate, sparse and long on midrib and lateral veins, sub-tomentose to sparse on blade, hairs somewhat shorter and more spreading on blade than on midrib and veins, hairs prominent at margin generating ferruginous tint. ***Petiole*** c. 8 x 3 mm, wider than midrib, especially in older leaves, ferrugino-tomentose with long stellate hairs 0.6 - 1.0mm long. ***Inflorescence*** leaf-opposed, flowers 2, secondary bud normally dormant, peduncle 1.5 - 12 mm, pedicels long and thin, to c. 20-30 x 1 mm, basal bract narrowly elliptical, c. 8 x 2 mm, often clasping, medial bract ovate to broadly elliptical, c. 4-5 x 2.5-3 mm., indument ferrugino-hirsute on peduncle, pedicel, bracts and early bud. ***Calyx*** calyptrate in bud, sepals 3, c. 10 x 6 mm, ovate, acute to narrowly acute, apices sometimes reflexed at maturity, inner surface hairs fine, pale, sub-tomentose. ***Corolla*** petals 6, white or greenish yellow, subequal, elliptic-acute, c. 13 x 6.5 mm, membranous, spreading, hairs sub-tomentose, short, and pale on both surfaces, with scattered ferruginous hairs on outer surface, inner surface carrying prominent indents from stamen connectives. ***Stamens*** numerous, 3 mm long, glabrous, connectives papillate, truncate or somewhat flat and elongate in marginal stamens, ridge sometimes present on adaxial surface, locules full length. ***Carpels*** numerous, 3 mm long, ovary with dense combed-tomentose indument, stigma U-shaped, lobes not broadened, ovules c. 20 in 2 lateral rows. ***Fruit*** monocarps 10-30, cylindrical/ oblongoidal, c. 65 x 25 mm, tomentose, stipe 10-40 x 2-3 mm, *seeds* c. 16, flattened ellipsoidal. Leaf outline shown in Figure 4.9.

Ecology and Distribution. A rare species limited to rainforests in the western and southern Malay Peninsula. A new record for Thailand. Distribution shown in Figure 4.45.

Notes. A very close relative of *U. hirsuta*, but can be distinguished from that species by its smaller yellow/white petals (vs. the red petals of *U. hirsuta*), its shorter, less hirsute indument and its peculiar leaves, which have distinctly fewer, more narrowly-angled veins than *U. hirsuta*. The Collection of Geesink and Santisuk at Ranong is a new record for Thailand.

Uvaria curtisii

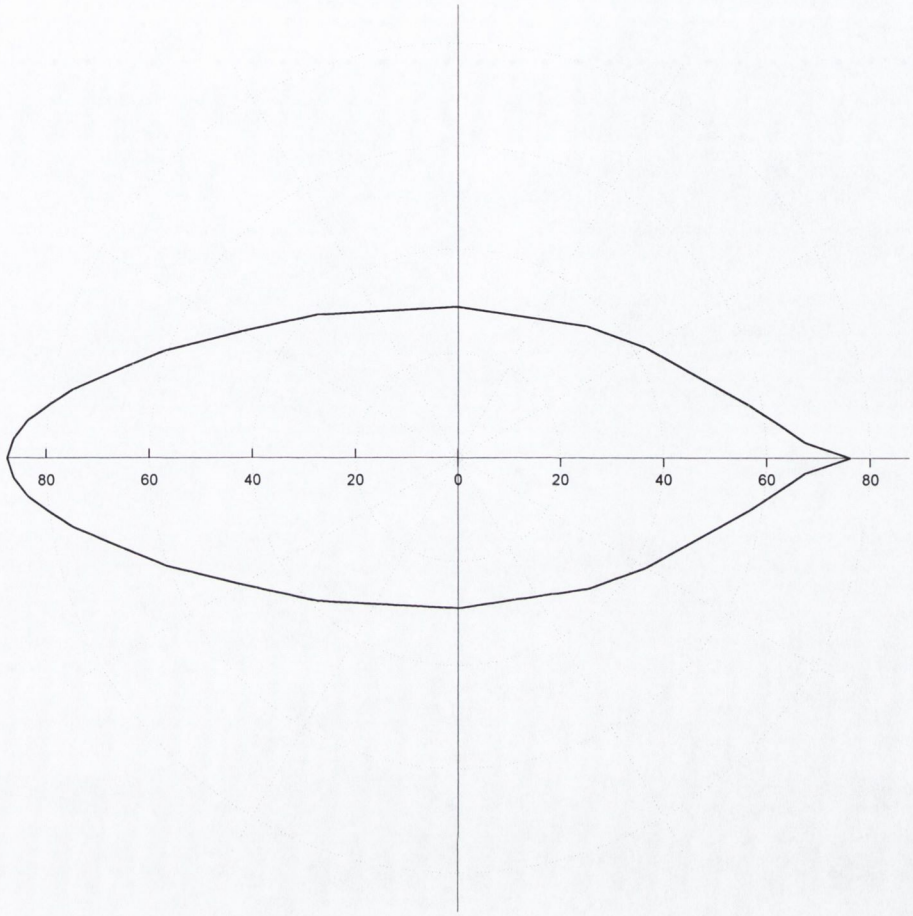


Figure 4.9. Mean leaf outline for *U. curtisii* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Material Examined

Thailand; *Ranong province* (60 – Pen.); Khlong Kam Puan, 9.15N 98.20E, 100m, 01/05/73, Geesink and Santisuk 5104 (fl.) (BKF, C, E, L, P).

Malay Peninsula; *Jahore*; Muar at Biawak, 4/1901, Curtis 3623 (K, Sing); *Pahang*; Jerantut, 24/11/24., Burkhill and Hainff 16071 (Sing.); Ulu S. Kerau, Central Pahang, top of ridge, c. 300m, 11/07/67, Whitmore FRI 3998 (fr.) (L); *Penang*; Government

Hill, 2000ft., 5/1892 Curtis 1415 (BM, K, Sing.); Government Hill, 2000ft., 6/1888, Curtis 1415 (K).

Singapore Bukit Timah FR., Kruing Path, 27/5/53 Sinclair 39652 (K, L, Sing.).

6. *Uvaria dac* Pierre ex Finet & Gagnep.

Bull. Soc. Bot. France 52, Mém.4(2):65 (1906) *et* Flore Générale de L'Indo-Chine 1:49 (1907), lectotype (*designated here*): Cambodia, 'prov. de Samrong-tong, monts cherreo, avril 1870, Pierre no. 748' (K!); syntypes: Cambodia, 'prov. de Samrong-tong, monts cherreo, avril 1870, Pierre no. 748' (P!), 'prov. de Thepong, monts Tamir, mai 1870, Pierre no. 748' (K!, P!) *et* 'prov. de Kampot, monts de Kam-Chay, mai 1874, Pierre no. 1459' (A! HCMC! K! P!); Jovet-Ast, Supplément a la Flore Générale de L'Indochine, 1:63 (1938); Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):304 (1991).

Syn nov.: *U. varaigneana* Pierre ex Finet & Gagnep., Bull. Soc. Bot. France 52, Mém. 4(2):64 (1906) *et in* Flore Générale de L'Indo-Chine 1:48 (1907), type: Vietnam, 'Cochinchine, prov. de Bien-hoa, pres Chiao-shan, 1875-77, Pierre 1785' (P-holo!); Jovet-Ast, Supplément a la Flore Générale de L'Indochine, 1:63 (1938).

Habit climber or sarmentose shrub. ***Young branchlets*** ferrugino-tomentose, hairs quickly becoming blunt and sparse, wood pale in colour, striate, lenticels not prominent. ***Leaves*** narrowly elliptic-obovate, acute-distinctly acuminate, base retuse, c. 180-190 x 60-80 mm; *veins* 11-13, up to 30 mm apart in central part of midrib, trailing trace faint, not forming distinct sub-margin, secondary veins kinked, midrib and primary veins shallowly depressed above, emergent below, microvenation visible but not distinct above, distinct below; *indument* abaxial surface with erect-tomentose hairs along midrib, becoming sub-glabrous at maturity, mixed 1-4+ branced hairs on blade, sparse becoming glabrous, adaxial hairs 10 branched, sparse on midrib, sub-tomentose on blade, becoming sub-glabrous. ***Petiole*** c. 5-7 x 2 mm, tomentose becoming sparse. ***Inflorescence*** leaf-opposed, flowers solitary or rarely 2-3, pedicel 8-15(-25) mm, often flattened to c. 2 mm broad, otherwise c. 1.25 mm, bracts ovate-acute, c. 4-7(-10) x 1.25–2 mm, often wanting, pedicel and bract densely ferrugino-

tomentose. ***Calyx*** calyptrate in bud, splitting into 2-4 often unevenly sized ovate-acute sepals, each (7-)10 x (8-)10 mm, at length spreading, outer indument tomentose to sparsely tomentose, hairs c. 10-branched, short and rufous, inner surface sub-tomentose. ***Corolla*** petals 6, elliptic, obtuse-acute, spreading, c. 15-20 x 8-10 mm, inner and outer surfaces sparsely tomentose, stamen indents sometimes prominent, whorls subequal, yellow or rarely red. ***Stamens*** numerous, c. 4.5 mm long, glabrous, connective truncate, adaxial ridge often present, locules full length, staminodes not present. ***Carpels*** c. 10-15, c. 3.5 mm long, ovary densely ferrugino-tomentose, stout in appearance, apex narrowed into distinctive neck, stigma glabrous with conspicuously broad U-shaped lobes, partly occluded by extension of ovary wall above neck, ovules c. 16 in 2 lateral rows. ***Fruit*** monocarps 1-8(-10), sub-basally attached, c. 45 x 25 mm diam., oblongoid, pericarp thickened, epidermis warted with fine tomentose indument, mature fruits green with brown tint, stipe 5-10 x 2.5-3 mm, thickly striate, tomentose, seeds 6-12 in 2 rows, c. 10 x 6 x 4 mm, hemi-ellipsoidal. Appendix 4.9A. Leaf outline shown in Figure 4.10.

Ecology and Distribution *Uvaria dac* shows a typical Indochinese distribution centred in the low valleys and plains of Southern Vietnam, Southern Laos, Cambodia and Northeastern Thailand, with an isolated record from BaVi mountain in North Vietnam. Distribution is shown in Figure 4.45.

Notes *Uvaria varaigneana* was described with *U. dac* by Finet and Gagnepain from Pierre's MSS, however it now seems that it and *U. dac* were merely flowering and fruiting specimens respectively of the same species. *Uvaria dac* is the name in more common usage, so it is being conserved here. The plant shows little phenotypic variation, save the occasional occurrence of red rather than yellow petals, and the presence of persistently tomentose leaves in some specimens from central Vietnam. The fruit seems unusual in retaining a green colour up to maturity. The dense cluster of unripened fruits is often used by (rather agressive) ants as a platform for nest-building.

Vern. *Cambodia*; Khmer: 'pudac' or 'phle dac' (Pierre 748, 1459).

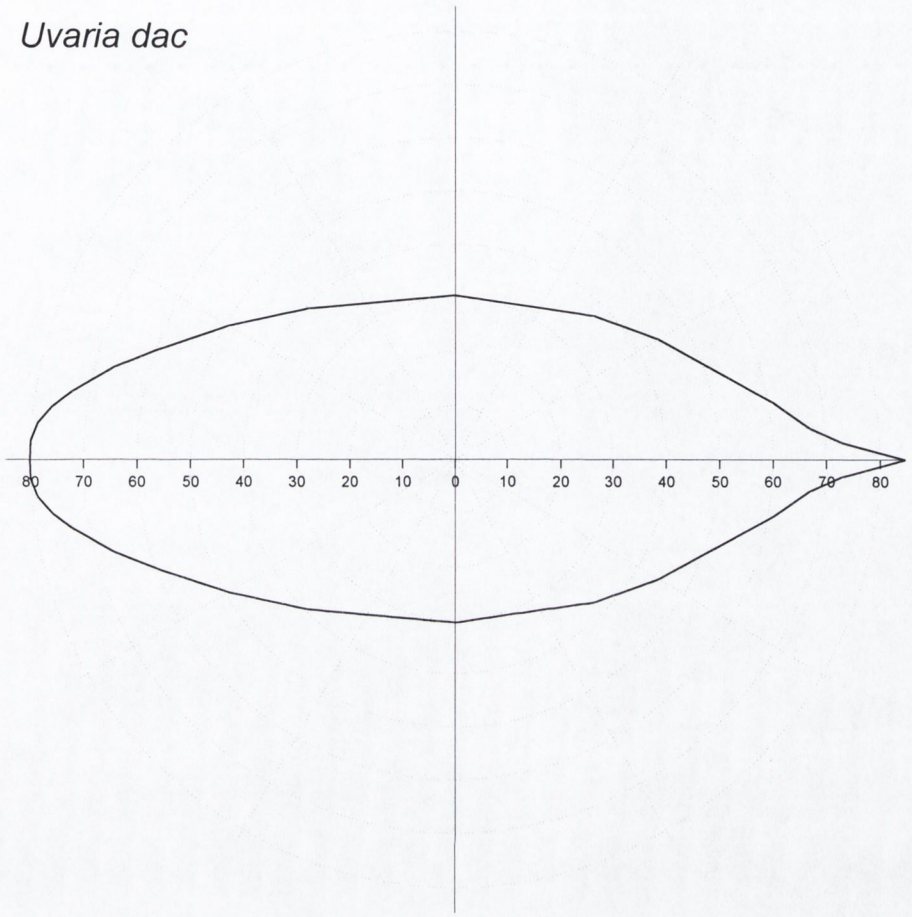


Figure 4.10. Mean leaf outline for *U. dac* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Material Examined

Vietnam *HayTay Province* (V – 13 – CLV); Foret humide, Tu Phap, BaVi, 18-5-1940, Petelot 2645 (fl.) (HNIP, HNU, P); *Kontum Province* (V – 30 – CLV); Moray Sathay, Ha Thi Dung 321 (HN, HCMC); Gialai Kontum, Ha Thi, Dung 312 (HN); Galai Kontum, Juc 8 (HN); Moray Dakto Kontum, 4-4-78, Dao 212 (HN, HCMC); Moray Dakto, 4-4-78, Phiong 458 (HN); Moray Dakto, Phiong 453 (HN, HCMC); Dak Mon, Dak Loley, 28-3-78, Ban 214 (HCMC, HN); Daklong, Dakglei, Nhan 269 (HN); T.D. Ly 488 (HCMC, HN); *Dong Nai Province* (V - 40 - CLV); near Chiao-

shan, Bien-Hoa, 1875-1877, Pierre 1785 (fl.) (K, P). *Locality Unknown*; T.D. Ly 461; Ha Thi Dung 300.

Laos *Saravane Province* (C – 13 – CLV); Road between Lao-Lao and Saravane, 17/04/27, Poilane 13254 (fl.) (P, HCMC); Pa Toi Dong, 10/04/27, Poilane 13723 (fl.) (P).

Cambodia *Siem Reap Province* (L - 7 - CLV); Angkor, 6/1866, Thorel s.n (fr.) (P); *Kompong Speu Province* (C - 17 - CLV); Hills near Chambok, 300m, 08/06/30, Poilane 17489 (fl., fr.) (HCMC, K, P); *Koh Kong Province* (C - 18 - CLV); Chereer Mountain, 4/1870, Pierre 748 (fl., fr.) (K, P); Tamire Mountain, 800m 5/1870, Pierre 748 (fl.) (K, P); *Kampot Province* (C - 19 -CLV); Camchay Mountains, 400m, 5/1874, Pierre 1459 (fl.) (A, K, HCMC, P).

Thailand *Nong Khai Province* (19 – NE); Nong Khai, banks of Mekong, 1866-1868, Thorel 9179 (fl., fr.) (P); *Chaiyaphum Province* (25 - NE); Dat Don near Chaiyaphum, 15.57N 102.02E, 300-400m 13/08/72, Larsen 31809 (-) (L, AAU); *Nakhon Ratchasima Province* (26 – E); Kaogai, 600-800m, 18-3-1965, Kasem 438 (fl.) (BK); *Saraburi Province* (44 – C); Muang district, Sam Lahn forest, 100m, 18-5-1974, Maxwell 74-509 (fr.) (AAU, BK); Muang District, Sahm Lahn Forest, 125m, 30-3-1974, Maxwell 74-218 (fl.) (AAU, BK, BKF); Sam Lahn, 14.3N 101.10E, 100m 18/05/74, Geesink 6777 (fr.) (L).

7a. *Uvaria hamiltonii* Hook. f. & Thoms.

Fl. Ind. 96 (1855) *et* Fl. Brit. Ind. 1:48 (1875), lectotype (*designated here*): India, Bihar State, hills near Monghir, '26/5/1811, Buchanan-Hamilton s.n.' Wallich Cat. 6485 E (*Herb. Wall.* K!), isotype: Wallich Cat. 6485E *pro parte* (BM!); King, J. As. Soc. Beng. 61(2)1:13 *et* Ann. Bot. Gard. Calcutta, 4:17, t. 6 (1893); Finet & Gagnep. Bull. Soc. Bot. France 52, Mém. 4(2):68 (1906); Brandis, Indian Trees, 4th ed., 17 (1921); Haines, Bot. B. & O. 2:10 (1921); Craib, Fl. Siam. Enum. 1:30 (1931); Whitmore, Enum. F. Pl. Nep. 2:27 (1979); Grierson & Long, Fl. Bhut. 1(2):238 (1984); Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):306 (1991); Mitra, Flora of India 1:293 (1993).

Habit A large climber to 30 m, or a scrambling, rarely upright, shrub. ***Young branchlets*** ferrugino-hirsute, becoming shortly tomentose then sub-glabrous and distinctly striate. ***Leaves*** (elliptic-)obovate, base sub-cordate to retuse, apex acute-acuminate, 115-175(-205) x 60-85 mm, membranous; *veins* 14-25, narrowly spaced, parallel, sometimes branching basally or medially, leading and trailing trace fine, inter-primary veins frequent, secondary veins kinked, not prominent, midrib sunken above, emergent below, primary veins slightly sunken above, emergent below, secondary and tertiary venation visible but not prominent on both surfaces; *indument* abaxial blade sub-tomentose with simple-sellate hairs, denser on midrib and at vein bases, adaxial surface hairs stellate only, sub-tomentose on blade, sparse on midrib and larger veins, prominent at margin. ***Petiole*** short, c. 4 x 2 mm, not much thicker than midrib, warty, tomentose to sub-tomentose. ***Inflorescence*** flowers 1 or 2 or rarely 3, leaf-opposed or sub-opposed, peduncle c. 5mm, pedicel c. 35 x 2 mm, bracts broadly obovate to circular-ovate, often wrapping around pedicel, c. 10 x 10 mm, veins prominent adaxially, peduncle, pedicel and bracts shortly ferrugino-tomentose, indument often lumpy or warted. ***Calyx*** calyptrate in bud, sepals 3 or very rarely 4, spreading, partially recurved, connate at base, triangular to very broadly ovate, bluntly acute, 7 x 10 mm, tomentose or lumpy-tomentose on outer surface, venation faintly visible. ***Corolla*** petals 6, red, subequal, distinctly obovate, apex broadly concave-rounded, c. 10-22 x 10-14 mm, densely and shortly tomentose on both surfaces. ***Stamens*** numerous, 2.5-3 mm long, connective apex short, papillae often prominent, locules sometimes stipitate. ***Carpels*** numerous, c. 2 mm long, ovary densely tomentose, stigma glabrous, U-shaped, ovules 10-12. ***Fruits*** monocarps c. 10-14, globose to oblong, c. 20 x 15 mm, green turning red, pericarp fleshy or thin, flesh pale white in colour, edible, bittersweet to taste, outer surface ferrugino-tomentose, often lumpy-tomentose, stipe c. 25-35 x 1.25-2.25 mm, striate, especially when thick, tomentose, monocarp attachment basal or sub-basal; *seeds* 6-12, c. 11 x 4 x 2 mm, ellipsoidal, laterally compressed, smooth, brown, ruminate. Leaf outline shown in Figure 4.11. Appendix 4.1A & B.

7b. var *kurzii* King

J. As. Soc. Beng. 61(2)1:11 *et in* Ann. Bot. Gard. Calcutta, 4:30 t. 27a (1893), syntypes: South Andamans, Kurz s.n. (fl.) (CAL n.v.); South Andamans, King s.n. (fl.) (CAL n.v.); Parkinson, For. Fl. Andaman Is. p. 79 (1923); Kumar & Sinha, J. Bom. Nat. Hist. Soc. 91:340-341 (1994); *Uvaria kurzii* (King) P-T Li, Acta. Phytotax. Sinica. 14:106 (1976).

Differs from the typical form of the species in having smaller leaves with 10-13 sub-parallel veins and a white-yellow corolla with coriaceous, elliptical-oblong, obtuse, 10-15 x 8-10 mm petals.

Ecology and Distribution *Uvaria hamiltonii* has a northerly distribution relative to most other species of the genus, extending from the Himalayan foothills of Eastern Nepal through Sikkhim, Bhutan, Bangladesh, Assam and Myanmar, and then on through Thailand, Laos, and Northern Vietnam to Southern China. It also occurs in an arc extending south along the Eastern Ghats from the type location in Bihar State as far as Tamil Nadu. Plants originally from Assam have been cultivated since the early 1800s at Peradeniya Gardens in Sri Lanka (where it has become naturalised) and also at Bogor Gardens in Java. Like most Uvarias in mountain or disturbed habitats, the species is often found in gullies and along watercourses where the soil is deep and damp. At the northernmost latitudes the plant has not been collected above 650 m, and so is still essentially a lowland tropical species. Var. *kurzii* has so far been found in the Andamans, Thailand and Southern China. Distribution shown in Figure 4.46.

Notes Although *U. hamiltonii* shares characters with many different species there are a few characters by which it can readily be identified; (i) the 2-3 thick, elongate pedicels, (ii) the basally free, obovate, concave petals and (iii) the partially lumpy ferruginous indument present on the pedicel and calyx and the stipe and monocarp of ripening fruits. The distinctive venation of the leaves also makes it one of the easier species to identify from sterile specimens. The petals of var. *kurzii* can be similar to those of *U. dac*, and in specimens which lack fruits the lumpy-tomentose calyx and larger, more tomentose leaves of var. *kurzii* should make it possible to distinguish the two.

Vern. *Thailand*; Chiang Mai Province "nom khwai" (Meade 85); Lampang Province, "nom meo pa" (Winit 1733); Ranong Province "nom maeo paa" (Smitinand, p. 340); Trat Province "Kluai phangphon" (Smitinand p. 340); *India*; Bihar & Orissa "Selaluli", "Lakankuli" (Haines, Fl. Bih. Or.), "Lakantinli" (Mitra, Fl. Ind.), Bengal "Laktean" (Mitra, Fl. Ind.).

Material Examined

Nepal Chule Chuli, 26.48N 81.42E, 1000 ft. 28/05/69, Williams 249 (fl.) (BM); Ramnagou, Chilwan, 500m, 01/06/94, Wesche 11209 (fl.) (BM, K); Soktim T.E. (Mai Khola) 26.48N 87.55E, 1500ft 19/04/71, Stainton 6792 (fl.) (BM); Mai Khola (below Ilam) East Nepal, in Schima forest, 26.50N, 87.56E, 200 ft, 19/5/71, Stainton 6860(fl.) (BM).

India *West Bengal*; Cultivated in Calcutta Botanic Gardens, 1863, Pierre 3679 (fl.) (C, L, P); Kurz s.n. (fl.) (US); West Duars, Bengal, Tondu, 5/1869, Haines 628 (fl.) (K); Athmallik; Andharikhol, 22/06/37, Mooney 479 (fl.) (K); *Tamil Nadu*, Goonsam Hills near Kurching, 28/02/09 Beddome 46, 47 (fl.) (BM, Sing.); Kuicholy, 2000 ft., Dawkins 14219 (fl.) (K), *Sikkim*; Langkok, Mungpo, 2/6/1903 Prain s.n. (fl.) (US); Tani, Beddome 48 (fl.) (K); Terai, Hooker, f. 118 (fl.) (K); 1200ft., 8/10/1875, King 2350 (fr.) (L); *Bihar & Orissa*; mountains near Monghir/Munger, 26/5/1811, Herb. Wallich 6485E (fl.) (BM); Rajgoon, Angel District, 03/06/17, Haines 3709 (fl.) (K).

Bangladesh Dhaka, sea level, 25/4/1869, Clarke 8438 (fl.) (K); Dhaka, 20/5/1873, Clark 20094 (fl.) (BM).

Myanmar *Bago*; Karen Chang Waterfalls, Taungoo District, 400ft. 24/05/25, Dawkins 1112 (fl.) (K); *Mandalay*; Road to Meiktila, 03/03/09 Prazer s.n (fl.) (G); Sakangyi Reserve, near Maymyo Plateau, 3,500 ft. 25/08/12 Lace 5920 (fr.) (E, K); Shan Hills, Terai, 2000 ft. 6/1888 Collett 832 (fl.) (K).

China Hong Kong 1860-64, Pierre s.n. (fl.) (BM, K, L, NY, P).

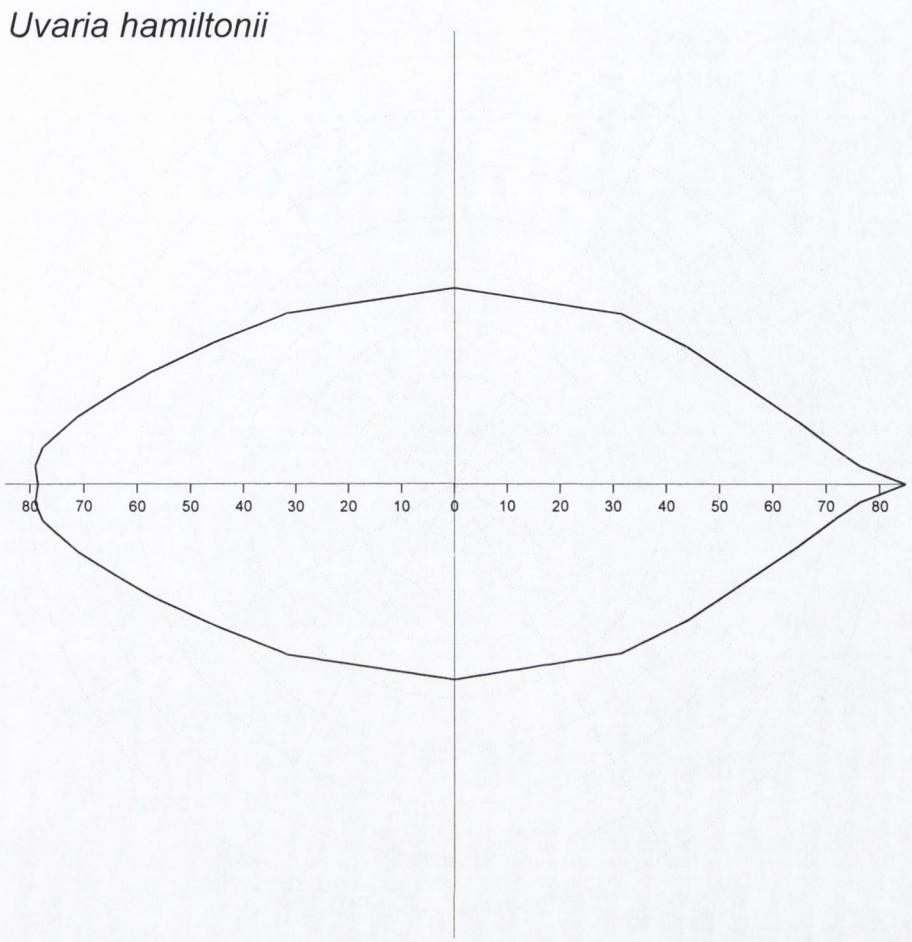


Figure 4.11. Mean leaf outline for *U. hamiltonii* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Laos *Province Unknown;* Mong Hsing, Haut, 5/1929, Ward 8928 (fl.) (NY).

Vietnam *Ha Tay Province* (V-13 - CLV); Phap, near S'on Tay, 18/5/40 Petelot 2645 (HCMC); Mt. BaVi, Ban Dao Khoi, 21/4/76, Tien Ban s.n. Fl. Vietnamica 19 (fl.) (HN); Mt. BaVi, 23/11/76, Ly s.n. Fl. Vietnamica 146 (HN); *Hoa Binh Province* (V – 14 – CLV); Lac Thuy, June/64, s.n. (HN); *Quang Nam – Da Nang Province* (V – 27 - CLV); Hoi Na, 17/8/20, Poilane 1745 (fr.) (P); *Province unknown*; 25/5/81, *s.coll.* T. 895 (HN); Sa Van, 25/5/62, *s.coll.* (HN); Ho Na, 17/5/64, *s.coll.* (HN); Chilang-Langson, 22/6/63, Sô 1 (HN); Ding s.n. Fl. Vietnamica 245 (HN); *s.coll.* Fl. Vietnmanica 1792 (HN).

Thailand *Chiang Mai Province* (2 – N), Doi Chiang Dao, southern foothills, near Ranger Station, Doi Chiang Dao W.S., c. 300m, 20/10/98, Meade 85 (fr.) (TCD).

Java Cult. Hort. Bot. Bog. Java, plots XVI E & XI A.56, 16 11/1902 Merrill s.n. (-) (NY).

Var. *kurzii*

Thailand *Lampang Province* (7 - N); MaeSung, 170m, 16/06/26, Winit 1733 (fl.) (BK, BKF); *Petchaboon Province* (16 - NE); Lom Kao, Nam Nao, 600m, 25/05/51, Smitinand 560 (fl.) (BKF); *Locality unknown*; Mi Song, 700 ft., 3/5/12, L.V.Phrao 309 - Fl.Siam 5142. (fl.) (BKF).

8. *Uvaria maclurei* Diels

Notzibl. Bot. Gart. Berl: 73 (1931), lectotype (*designated here*): China, 'Hainan, Tik Tsok Mau, 18/5/22, McClure 9697' (E!), isotypes: China, 'Hainan, Tik Tsok Mau, 18/5/22, McClure 9697' (A! BM! C! G! N! P!); Tsiang Ying & P-T Li, Fl. Rep. Pop. Sin. 30(2):20, t. 8 (1979).

Syn. nov.; *U. kweichowensis* P-T Li, Acta. Phytotax. Sinica. 14:107 (1976), holotype: China, Kweichow, 8/8/59, *coll.* 739 (fr.) (PE!).

Habit climber or scandent shrub. ***Young shoots*** sub-tomentose with short 10+ branched ferruginous hairs. ***Leaves*** elliptical-narrowly obovate, apex acute, shortly acuminate or rarely obtuse, base cuneate-retuse, c. 110-160 x 40-60 mm, coriaceous; *veins* (9-)10-12, gradually inarching, trailing trace not strong, rare, secondary veins kinked, tertiary venation reticulate, microvenation visible but not prominent above or below; *indument* abaxial surface completely glabrous, shiny, adaxial blade sub-glabrous, on midrib and lateral veins hairs c. 4-6 branched, fine, becoming glabrous at maturity. ***Petiole*** 3.5-5.5 x 1.5-1.75 mm, thicker than midrib, sub-tomentose

becoming sparse over warty black epidermis. ***Inflorescence*** flowers 1-2, peduncle sub-sessile, 1-2 mm, pedicel c. 30-40 mm, basal and medial bracts ovate, c. 5.5 x 4 mm with prominent veins, often persistent, peduncle, pedicel and bracts sub-tomentose as for young shoots, pedicel often tomentose towards receptacle. ***Calyx*** calyptrate in bud, sepals 3, c. 5-5.25 x 4-4.5 mm, thin and leafy, hairs sparse on inner surface, sparse to sub-tomentose on outer surface, at length reflexed. ***Corolla*** petals 6, purple, elliptical-acute, c. 10-12 x 4-5.5 mm, tomentose on outer surface, sparse on inner surface, hairs 3-5 branched, at length spreading and reflexing. ***Stamens*** <50, c. 3.5 mm, locules full-length, connective apex flattened, somewhat elongate, papillate, prominent dorsal ridge running to base. ***Carpels*** c.12-15, 3 mm long, ovary tomentose with flattened spreading hairs, stigma flat and glabrous, U-shaped, ovules 8-10. ***Fruit*** monocarps ovoid-ellipsoidal, 40-45 x 30-35mm, tuberculate, pericarp thick, seeds 6-10, sub-sessile, stipe c. 6 x 5 mm, striate. Leaf outline shown in Figure 4.12.

Ecology and distibution This appears to be a rare species, occurring in Hainan, Yunnan and Kweichow Provinces, and although no collection has been seen from Guandong, it is probable that it occurs in this province also. Distribution is shown in Figure 4.47.

Notes The stamens, carpels and petals of *U. maclurei* are similar to *U. rufa*, however the calyx, pedicel and fruit are closer to the *U. grandiflora* group. The species most likely to be confused with *U. maclurei* is *U. dac*, particularly in relation to the fruits; however, in *U. dac* the flowers are much larger, the stamens more numerous and the pedicels much shorter.

Material Examined

China *Hainan Province*; Yik Tsok Mau, 18/5/22, McClure 9697 (fl.) (E, A, BM, C, G, NY, P); *Yunnan Province*; Szemar, Tu Zey Mountains, Mengsi and locality, Red River Valley near Vietnam border, Henry 12148 (fl.) (NY); *Guizhou Province*; Libo County, Southeast Guizhou, 660m, 26/5/83, Song Xianghou 897 (fl.) (PE); 8/8/59, *coll.* 739 (fr.) (PE).

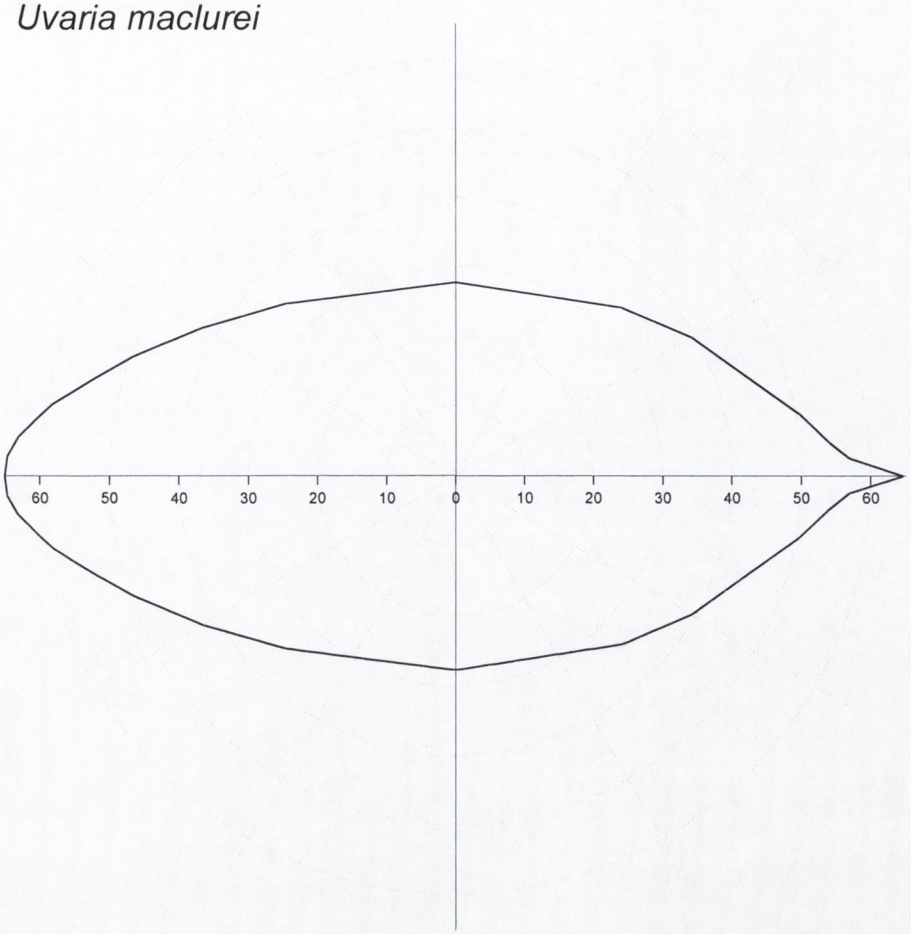


Figure 4.12. Mean leaf outline for *U. hamiltonii* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

9. *Uvaria calamistrata* Hance

J. Bot., London, 20:77 (1882), lectotype (*designated here*): China, 'Hong Kong, Aug 1861, Hance 7436' (K!), isotypes: China, 'Hong Kong, 10/8/1881', Ford s.n. (K!) & 'Hong Kong, Aug. 1861', Hance 7436 (BM!); Forbes & Hemsley, J. Linn. Soc. 23:25 (1886); Finet & Gagnep., Bull. Soc. Bot. France 52, Mém. 4(2):69 (1906) *et* Flore Générale de L'Indo-Chine 1:53 (1907); Tsiang Ying & P-T Li, Fl. Rep. Pop. Sin. 30(2):26, t. 10 (1979); Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):304 (1991).

Habit climber or scandent shrub, often scrambling over semi-wooded rocky slopes.

Young shoots tomentose, becoming mostly glabrous, bark striate with pale auricles.

Leaves broadly elliptic, 70-120mm x 35-45mm, apex acute-acuminate-cuspidate, base retuse-cuneate; *veins* 8-11, trailing trace weak, inter-primary veins rare, secondary crossing veins kinked, midrib and primary venation depressed above, emergent below; *indument* abaxial blade of young leaves with sparse pale hairs, becoming glabrous and shiny with maturity, hairs sub-tomentose over midrib and bases of primary veins, becoming sub-glabrous, adaxial surface tomentose to sub-tomentose, later sparse, hairs stellate, pale, with occasional more conspicuously branched and prominent rufous hairs, especially on veins and midrib. ***Petiole*** 5-8mm long, tomentose. ***Inflorescence*** flowers solitary, 2 or rarely 3, sub-opposed, peduncle 2-3 mm, pedicel c. 5-10 mm long, densely tomentose, basally and medially bracteate, one or both bracts often wanting, bracts ovate-obovate-oblanceolate, c. 2 x 1 mm, outer surface tomentose, inner surface sub-tomentose, veins not prominent. ***Calyx*** calyptrate in bud with apicule, sepals 3, basally connate, triangular-ovate, apex acute to bluntly acute, to 5-6 x 4 mm, membranous, concave, remaining incurved, tomentose on outer surface, sparse on inner surface, often persistent into fruiting stage. ***Petals*** 6, yellow in colour, ovate-oblong, 6-10 x 3-3.5 mm, apex rounded, whorls subequal, partially recurved at maturity, inner and outer surfaces of both whorls tomentose, hairs finer, shorter and more evenly distributed than on inner surface of sepals. ***Stamens*** numerous, 1.5-1.8 mm long, connective apex truncate, often obscuring locules completely, papillate, with prominent ridge on external surface, locules full length, staminodes absent. ***Carpels*** c. 20-40, 1.5 mm long, ovary tomentose apically and on sides exposed at margin of gynoecium, other surfaces glabrous with scattered stellate hairs c. 0.5 mm in diameter, stigma U-shaped with elongate lateral slit, 0.2-0.4 mm long x 0.4-0.65 mm wide, ovules 10-12. ***Fruit*** monocarps 2-12, c. 30 x 20 mm, spheroidal-oblongoidal, initially covered with prominent beard of 5-8 mm long membranous bluntly triangular outgrowths, later tuberculate with scattered remnants of outgrowths over surface, stipe short, 3-5mm x 2.5-3mm; *seeds* 1-12, c. 12 x 6 x 4mm, ellipsoid, to hemi-ellipsoidal, smooth, ruminations faint, hilum 5 x 4 mm, ovate. Leaf shape is shown Figure 4.13.

Ecology and Distribution Hong Kong and Hainan Provinces in China, Vinh Phu Province in Northern Vietnam. *U. calamistrata* ccupies a similar range of habitats to *Uvaria boniana*, particularly in Hainan, where many specimens have been collected scrambling over rocky scrub on steep hillsides. Distribution shown in Figure 4.48.

Notes The bearded juvenile fruit of *U. calamistrata* is amongst the most distinctive in the genus. The beard is very different from that seen in *Uvaria vietnamensis*, where the outgrowths are distincly hair like, and covered with smaller branches which carry numerous small ferruginous hairs. The outgrowths in *U. calamistrata* are glabrous and impersistent.

Vern. *China*; Hainan 'Mo Lai Chi T'ang' (Tsang 339).

Material Examined

China *Hainan Province*; Ching Mai District, Pak Shik Ling and vicinity, Ku Tung village, 26/07/33, Lei 888 (fr.) (NY); Lam Ko District, Lin Fa Shan and vicinity, 05/08/27, Tsang 339 (fr.) (PE, BM, E, L, NY, US); Ngai District; Fung Leng, 03/09/32, Lau 468 (fr.) (E, NY, BM); Wen-ch'ang District, Tung Koo Shan and vicinity, near Shan Hoi village, 25/08/32, Fung 20430 (fr.) (NY); Yaichow, 7/33, How 71043 (fr.) (E, P); Locality unknown; 18/07/33, Liang 62151 (fr.) (E, NY); 11/08/33 Wang 33631 (fr.) (NY); 08/10/33, Wang 34503 (fr.) (NY). *Hong Kong;* Hong Kong Island, Wangchuck-Hang, 08/05/41 Taam 2056 (fl.) (G, US); Hong Kong Island, Lamont s.n. (fr.) (BM); Hong Kong Island, 8/186, Hance 7436 (fr.) (BM, K); Locality unknown; 10/8/1881, C. Ford s.n. (fl.) (K); 23/5/1894, Bodinier 989 (fl.) (E, P); Hong Kong, 9/1874, Lamont 12a (fr.) (BM); 9/6/1893, C. Ford s.n., (fl.) (P).

Vietnam *Vinh Phu Province* (CLV –12 –V); Song Hoa, 02/11/05, Castellini 60, (fl.) (P); Locality unknown; 29-3-1980, Ban 94 (HN).

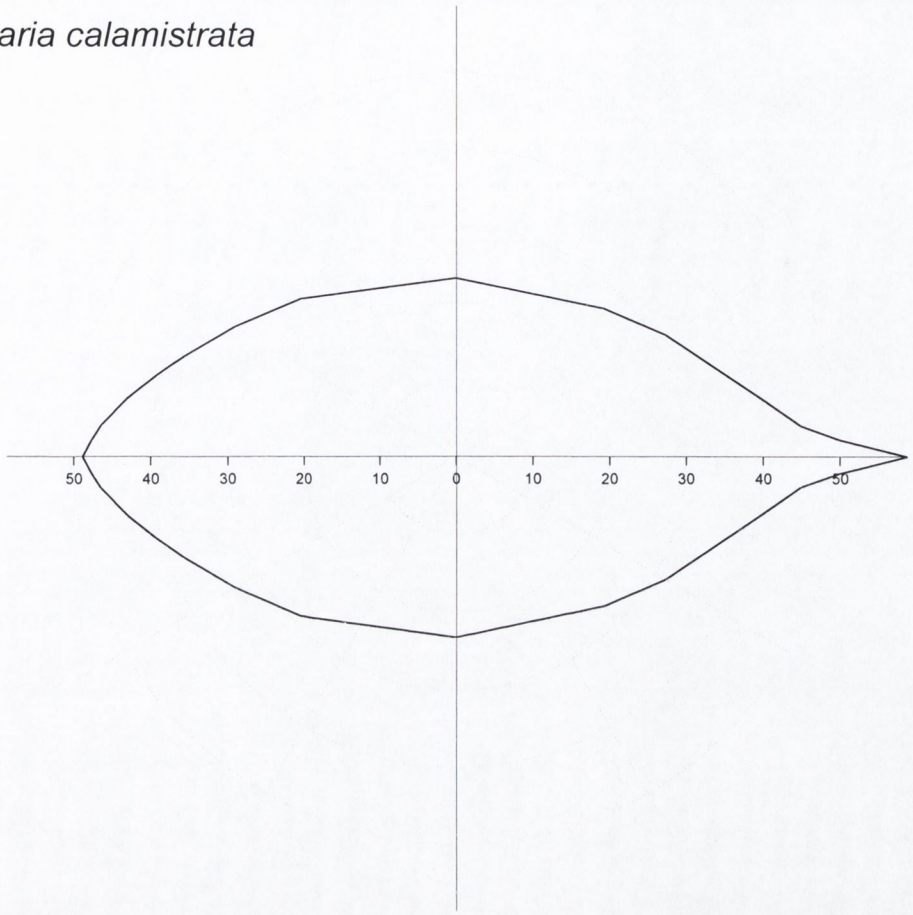


Figure 4.13. Mean leaf outline for *U. calamistrata* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

10. *Uvaria zeylanica* L.

Sp. Pl. 536. (1753) excl. syn. "*narum-panel*" Rheede, lectotype (*Kessler des.*): Herb. Herm. 5:163 (t. 224), syntypes: Herb. Herm. 2:80, 3:12; Don, Gen. Syst. 1:92 (1831); Dunal, Anon. 88 (1817); Hook. f. & Thoms., Fl. Ind. 1:102 (1855) *et* Fl. Br. Ind. 1:51 (1872); Thw., Enum. Pl. Zeyl. 6 (1858); King, Ann. Bot. Gard. Calcutta, 4:30 t. 27a (1893); Trimen, Handb. Fl. Ceylon 1:20 (1893); Huber, Rev. Handb. Fl. Ceylon 5:16 (1985); Mitra, Fl. India 1:295 (1993). *U. coriacea* Vahl, Symb. 3:72 (1794). *U. heyneana* W. & A., Prodr. 8 (1834) (not of Wall.). *U. lutea* Wall., Cat. 6462 (not of Roxb.) *nom. nud.* Wall. Cat. 6462ab (*Herb. Wall.* K. !).

Non est U. zeylanica Lam., Encycl. 1:596 (1785); *U. zeylanica* DC., Syst. 1:481 *et* Prodr. 1:88 (1824).

Pre-Linnean accounts; *Kasjou-panel* Rheed. Hort. Mal. 5:35 t. 18 (1679).

Habit climber or sarmentose shrub 1-2 m high. ***Young shoots*** sub-tomentose, smooth, quickly becoming striate and sub-glabrous. ***Leaves*** ovate-elliptic-oblanceolate, base cuneate, apex acute-acuminate, c. 55-70(-95) x 20-28(-35) mm, membranous, waxy; *veins* c. 8-12, interarching half way between midrib and margin, leading and trailing traces ± equally prominent, secondary venation poorly developed, tertiary venation reticulate, midrib narrow, shallowly depressed above, prominent below; *indument* young leaves glabrous on abaxial blade, sparse 2-4 branched hairs over midrib, mature leaves completely glabrous, adaxial blade glabrous, isolated 5-10 branched hairs on midrib and base of primary veins, more frequent towards base of leaf. *Petiole* c. 2-3 x 1 mm, tomentose when young, sparse when mature, hairs ferruginous, surface black, waxy. ***Inflorescence*** terminal or leaf-opposed by apposition, flowers solitary or less often 2-3, peduncle 1.5-2 mm pedicel c. 4-7 mm, average 5 mm, densely tomentose hairs pale or ferruginous, bracts narrowly ovate-elliptical, membranous, sparse to sub-tomentose on outer surface, sub-glabrous inside. ***Calyx*** calyptrate in bud, tearing into 3 sub-equal ovate-acute to broadly lanceolate membranous sepals, outer surface tomentose at first, later sparse, inner surface sub-glabrous, parallel veins prominent on both surfaces, sepals often persistent to fruiting stage. ***Corolla*** petals 6, dark red-purple in colour, narrowly elliptical-oblong, apex acute or less often narrowly obtuse, c. 10 x 3 mm, membranous, somewhat warty, inner surface sub-glabrous, outer surface sparse to sub-tomentose with 1-5 branched straggling pale hairs, margins and apex tomentose, both surfaces. ***Stamens*** numerous, c. 1 mm long, cuneate, locules full-length, connective glabrous, broadly concave, undulating. ***Carpels*** c. 20, 1 mm long, cuneate, ovary hairy, stigma glabrous, U-shaped, lobes broad, c. 0.6 mm diam., ovules c. 6. ***Fruit*** monocarps 6-12, shortly oblong, apex and base rounded, c. 12 x 8.5 mm, densely and shortly tomentose, hairs ferruginous, blunt, pericarp thin in young fruits, later thickening, becoming fleshy, edible, stipe short, c. 3 x 1.25 mm; *seeds* c. 6 in 2 rows, hemispheroidal or flattened hemi-ellipsoidal, c. 4 x 3 x 2 mm, testa brown, smooth and shiny, ruminations visible, raphe distinct but not raised, aril oval-ellipsoid, hilum heart-shaped to oval, to .5 x 1.5mm. Leaf shape shown in Figure 4.14.

Ecology and Distribution Confined to Sri Lanka and Southern Tip of Deccan Peninsula (Tamil Nadu, Kerala). In Sri Lanka the plant usually grows as a scrambling shrub in dry regions and as a medium to large climber in the wetter forested regions,

usually in secondary vegetation. Huber (1985) notes the plant is most common near the coast, often on sand-dunes. In southern India the plant is confined to moist lower hill forests. Distribution is shown in Figure 4.47.

Notes. *U. zeylanica* is the type species for the genus. Linnaeus confused it with the 'narum-panel' of Rheede (later *Unona narum* Dunal) from the Malabar coast, though the specimens and plate which he described from Hermann's *Mus. Zeyl.* are of *U. zeylanica* only. Kessler has lectotypified a *U. zeylanica* plate from this collection, however this includes the fruit only.

Vern. *Sri Lanka*; Sinhalese: 'Palukan', 'Palanga' (Herb. Hermann), 'Karu-veppal' (Tamil – Huber, 1985).

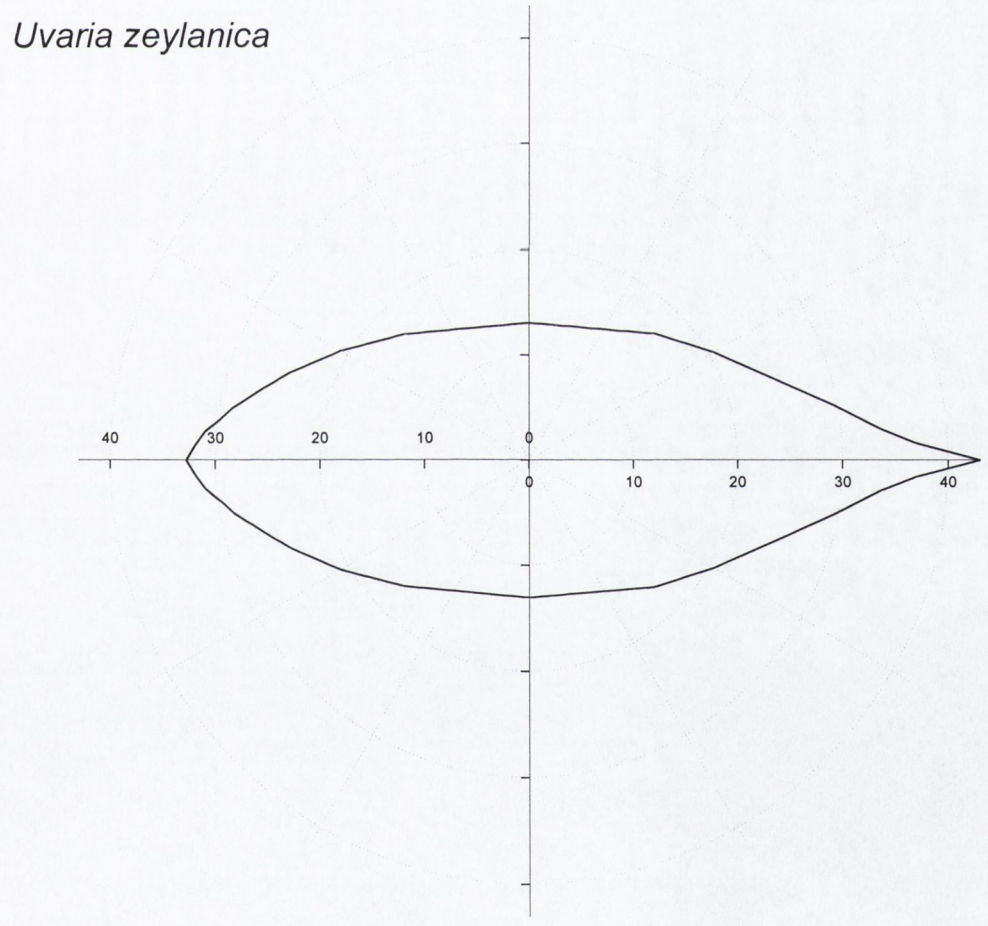


Figure 4.14. Mean leaf outline for *U. zeylanica* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Material Examined

Sri Lanka *Anuradhapura District*; Ritigala, 13/07/74 Waas 366 (fl.) (US); *Colombo District*; Welisara, 27/11/31, Simpson 8935 (fl., fr.) (BM); *Galle* District; Bona Vista near Galle, 10m 06/11/77, Huber 571 (fl.) (HBG); near Weligama, 01/01/80, Kostermans 28043 (fr.) (L); *Jaffna District*; Vaddakkachchi, Paranthan-Mullaitivu Road, 17/11/70, Kundu & Balakrishnan 705 (fl., fr.) (US); *Kalutara* District; Kalutara, Macrae 216 (fl.) (NY); Velikanda, 80.0 E 6.37N, 27/10/79, Klackenberg 239 (fl.) (NY); Yagirala, Kalutara, 100m, 29/06/75 Waas 1303 (fl.) (US); *Puttalam District*; Daluwa Village west of Puttalam Lagoon, 08/06/72 Maxwell & Jayasuriya 823 (fl.) (NY); *Locality Unknown*; Wallich 6462a,b (fl.) (K, BM); 25/01/09, Fraser 179 (fl.) (BM, TCD); *s.coll.* C.P. 1030 (fl., fr.) (BM, K, TCD, US); Joinville s.n. (fl.) (BM).

India *Kerala*; Kotta Hill, Trirandrum, 18/03/34 Erlanson 5578 (fl.) (NY).

11. *U. sphenocarpa* Hook. f. & Thoms.

Fl. Ind. 1:99 (1855) *et* Fl. Br. Ind. 1:48 (1872), lectotype (*designated here*): Ceylon, *s. coll.* C.P. 1045 (BM!), syntypes: Ceylon, Walker s.n. (K! TCD!), Champion s.n. (K!) and *s. coll.* C.P. 1045 (G! K! P! TCD! US!); Thw., Enum. Pl. Zeyl. 6 (1858); Bedd., Ic. Pl. Ind. Or. 17, t. 82 (1870); King, Ann. Bot. Gard. Calcutta 4:20 t. 11 (1893); Trimen, Handb. Fl. Ceylon 1:19 (1893); Huber, Rev. Handb. Fl. Ceylon 5:14 (1985).

Habit climber or sarmentose shrub. ***Young shoots*** ferrugino-tomentose, becoming sparse, bark black, smooth at first, later grey-black and striate, hairs persistent in grooves. ***Leaves*** 70-140(-200) x 25-40(-70) mm, elliptic - narrowly obovate, base retuse to shortly cordate, apex acuminate, acuminum to 30 mm, sub-coriaceous; *veins* c. 9-10, inarching gradually, usually not parallel, occasional inter-primary veins present to 0.5 length of primary veins, secondaries not well developed, tertiary venation reticulate, midrib and primary venation slightly sunken above, emergent

below; *indument* stellate with occasional simple hairs on abaxial surface; upper blade hairs 1-8 branched, sparse, becoming sub-glabrous, on herbarium specimens hairs blunted or worn away, lower blade sub-tomentose to sparse, hairs larger, more rufous than above, 4-10 branched, forming distinctly tomentose indument on basal portions of midrib and veins, elsewhere finer, less prominent. ***Petiole*** c. 4-5 x 1.5-2 mm, appearing much thicker than midrib base, sub-tomentose to sparse with large ferruginous hairs. ***Inflorescence*** leaf-opposed, flowers solitary or in short 2-3 flowered cyme, usually only one bud in flower at any one time, peduncle sub-sessile, pedicel c. 3-4 mm, bracts clasping, ovate, c. 4 x 2 mm, pedicel and bracts with dense ferrugino-tomentose indument. ***Calyx*** sepals 3, basally connate, opening early, c. 4.5 x 2.5 mm, broadly ovate, indument ferrugino-tomentose on outer surface, sparse at margin, on inner surface glabrous at base, sparse elsewhere. ***Corolla*** petals 6, pale yellow in colour, elliptical-obovate, obtuse/ bluntly acute, c. 6-6.5 x 4-4.5 mm, spreading, tomentose on outer surface, sub-tomentose on inner surface. ***Stamens*** c. 50+, 2 mm long, all fertile, connective head broad and flat, somewhat T-shaped, very shortly papillate, dorsal ridge prominent, locules full length. ***Carpels*** c. 50, 2 mm long, .5 mm wide, ovary tomentose, stigma U-shaped, lobes large, copious nectar often present, ovules c. 4. ***Fruit*** monocarps sesseile, c. 10-16, yellowish, gathered into pseudo syn-carpous conglomerate, individual monocarps cuneate-obovoidal, 18-25 x 15-20 mm, sides flattened against adjacent monocarps, all surfaces densely tomentose, apical surface coarsly warted; *seeds* c. 4, 10 x 5 x 3 mm, smooth, brown. Leaf shape is shown in Figure 4.15.

Distribution and Ecology Endemic to Sri Lanka, occuring in wet and dry zones from sea level to c. 700 m. Huber (1985) notes it has become more common due to disturbance of primary forest. One collection has been seen from a cultivated specimen at Bogar Gardens in Java. Distribution is shown in Figure 4.49.

Notes The flowers and leaves of *U. calamistrata* (China and Vietnam) can be similar to *U. sphenocarpa*.

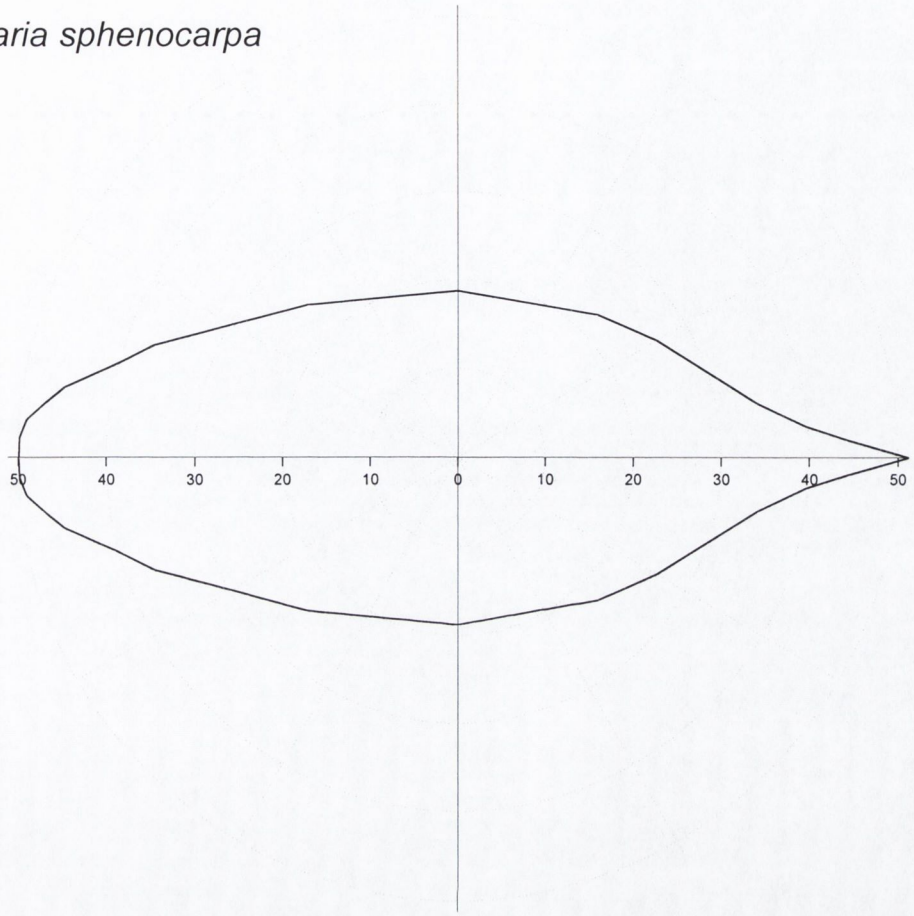


Figure 4.15. Mean leaf outline for *U. sphenocarpa* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Material Examined

Sri Lanka *Anuradhapura District*; Ritigala Strict Natural Reserve, E. slope of Andikana, 375m, 21/01/73, Jayasuriya 1066 (fl.) (US); Ritigala Strict Natural Reserve, on ridge S. of Na-Ulpota, W. side 08/08/73, Jayasuriya 1277 (fr.) (US); *Galle District*; riverbank opposite Kitugalle, 600m 24/04/80, Kostermans 28356 (fl.) (L); Sinharaja Forest, near Weddegalle, 150m Dec./78, Kostermans 27109 (fl.) (L); *Matara District*; between Deniyaya and Kotapola, 11/11/77, Huber 597 (fl.) (US); *Puttalam District*; Wilapattu N.P., Dangaha Urinaya, Plot 32, sand dunes, 11/07/69, Wirawam w32-20 (fl.) (US); *Vavuniya District*; Mullaitivu-Mankulam Road, ca. 3km from Mullaitivu, 24/06/75, Sumithraarachchi DBS 805 (fr.) (US); *Locality*

unknown; ex Hook. f. & Thoms. *s. coll.* (fl.) (L); Champion s.n. (K); *s. coll.* C.P. 1045 (fl., fr.) (BM, G, K, P, TCD, US); Walker s.n. (fl.) (K, TCD).

Java Cult. in Hort. Bog., *s. coll.* (fl.) (L).

12. *U. semicarpifolia* Hook. f. & Thoms.

Fl. Ind. 1:97 (1855) *et* Fl. Br. Ind. 1:49 (1872), lectotype (*designated here*): Ceylon, Thwaites C.P. 244 (BM!), syntypes: Ceylon, Walker s.n. (K), Thwaites C.P. 244 (G! K! L! P! TCD!) and Griffith s.n. (K!); Thw., Enum. Pl. Zeyl. 6. (1858); Bedd., Ic. Pl. Ind. Or. 17, t. 82 (1870); King, Ann. Bot. Gard. Calcutta 4:20, t. 11 (1893); Trimen, Handb. Fl. Ceylon 1: 19 (1893); Huber, Rev. Handb. Fl. Ceylon 5:14 (1985).

Habit a very large climber up to 30 m tall. ***Young shoots*** densely tomentose, shoots becoming woody and ridged quickly, indument retained in grooves, glabrous on ridges, lenticels large and numerous. ***Leaves*** elliptic-oblong, base cordate, apex obtuse to cuspidate, 160-230(-450) x 90-110(-120) mm, coriaceous; *veins* c. 16-20(-25), prominent, often perpendicular to midrib at base then arching at c. 60-70 deg. toward margin, veins sub-parallel, leading and trailing trace strong, forming distinct sub-margin, secondary veins prominent, kinked, complete toward margin, tertiary venation sub-reticulate, inter-primary veins rare, midrib and primary veins depressed abaxially, prominent and emergent adaxially, tertiary venation visible but not distinct; *indument* abaxial blade completely glabrous and shiny, hairs on midrib erect, tomentose, 1-4 branched, up to 1 mm long, hairs sparse on vein bases, glabrous towards margin, adaxial blade sparse to sub-tomentose, hairs 3-8 branched, midrib and veins sparsely tomentose with straggling 5-10 branched hairs, becoming tomentose towards petiole. ***Petiole*** thick, 7-10 x 3-4 mm, ferrugino-tomentose, warted along transverse foliations. ***Inflorescence*** leaf-opposed, flowers 2-3, peduncle c. 6-7 x 3 mm, flattened in TS, pedicels c. 10 mm with basal 3 mm adnate to sympodial axis, densely tomentose, bracts broadly obovate, to c. 4 x 6.5 mm, densely tomentose outside, glabrous within, often wanting. ***Calyx*** connate, splitting apically in early bud

at c. 5-6 mm diam., later forming connate ring, finally splitting into 3 sepals prior to opening of corolla, sepals ovate-acute, c. 8 x 4 mm, fleshy, shortly ferrugino-tomentose outside, glabrous within. ***Corolla*** petals 6, green, maturing yellow then brown, outer whorl spreading, c. 9 x 7 mm, broadly ovate, outer surface shortly and densely tomentose, hairs finer than on calyx, inner petals connivent, obovate, basally constricted/ shortly clawed, c. 8 x 6 mm, indument as for outer whorl. ***Stamens*** numerous, 1.5 – 2 mm, tubular, connective concave, prominently papillate, locules full length. ***Carpels*** c. 20 - 25, 2.5mm long, ovary tomentose, somewhat flattened apically, stigma U-shaped, glabrous, ovules c. 8. ***Fruit*** monocarps c. 10-20, broadly ellipsoidal to obovoid, c. 30-40 x 20-30 mm, shortly and densely tomentose, surface tubercled/ undulating, pericarp c. 4 mm thick in unripe specimens, stipe c. 3 x 10-15 mm; *seeds* c. 8., to 12 x 10 x 6 mm. Leaf shape shown in Figure 4.16.

Ecology and Distribution Endemic to lowland rainforest in the wetter parts of SW Sri Lanka. Distribution is shown in Figure 4.49.

Notes *U. semicarpifolia* can be distinguished from *U. cordata* by its tomentose fruits, more oblong leaves with c. 20 parallel veins and its juvenile yellow flowers.

Material Examined

Sri Lanka *Galle District*; Kannelliya forest near Hiniduma, 400m, 01/09/74, Kostermans 25493 (fl., fr.) (G, L, P, US); Karunagala District; Weudakanda, 12/8/74, Waas 776 (fl.) (L); *Matara District*; river valley immediately North of Diyadawa Forest Reserve, 410m 11/11/77, Huber 602 (fl.) (L, US) *Ratnapura District;* Forest South of Veddagala, Sinharaja, 04/11/77, Huber 556 (fl., fr.) (HBG, L, P); 3/1846 Thwaites C.P. 244 (K); *Locality Unknown*; Thwaites C.P. 244 (fl., fr.) (BM, G, L, P, TCD); Walker 165 (fl.) (G); Walker s.n. (K).

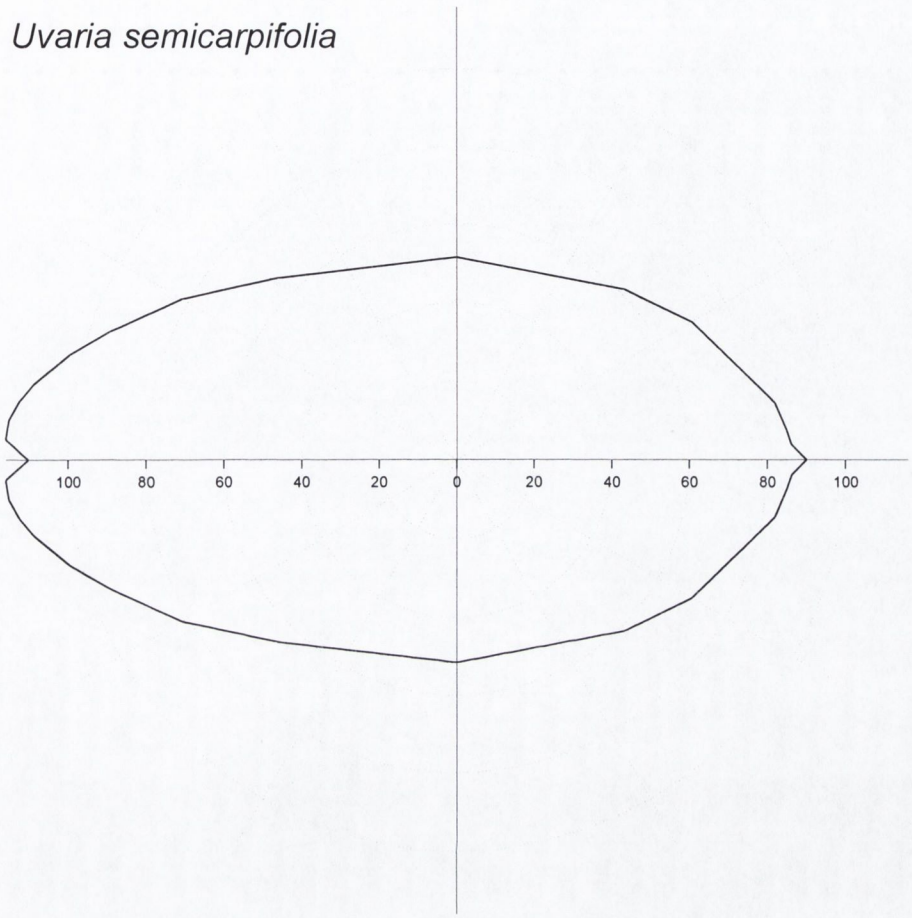


Figure 4.16. Mean leaf outline for *U. semicarpifolia* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

13. *Uvaria cordata* (Dunal) Alston

Handb. Fl. Ceylon 6 (Suppl.):4 (1931); Sinclair, Gard. Bull. Sing. 14(2):206 (1955); Huber, Rev. Handb. Fl. Ceylon 5:14 (1985); Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):304 (1991); Mitra, Flora of India 1:289 (1993). *Guatteria cordata* Dunal, Monogr. Anon. p. 129, tab. 29 (1817), type: Monogr. Anon. p. 129, tab. 29; DC. Prodr. 1:93 (1824). *U. macrophylla* Roxb., Hort. Beng. p. 91 (1814) *nom. nud*; *U. macrophylla* Roxb. ex Wall., Pl. As. Rar. 2:22, t. 122 (1831). *Uvaria cordata* Wall., Cat. 6486 (1832) *nom. nud.*. *U. macrophylla* Wall., Cat. 6487 excl. e, f (1832) *nom. nud. U. macrophylla* Roxb., Fl. Ind. ii 2:663 (1832); Hook. f. & Thoms., Fl. Ind. 1:97 (1855) *et* Fl. Br. Ind 1:49 (1872); Kurz, Fl. Br. Burma 1:28 (1877); King, Mat. F.M.P. 1(4):265 (1892) 265 *et* Ann. Roy. Bot. Gard. Calc. 4:19, t. 10 (1893); Finet & Gagnep., Bull. Soc. Bot. France 52, Mém.4(2):67 (1906) *et* Flore Générale de

L'Indo-Chine 1:50 (1907); Ridley, F.M.P. 1:30 (1922); Craib, Fl. Siam. Enum. 1:30 (1931); Jovet-Ast, Supplément a la Flore Générale de L'Indochine, 1:64(1938).

Syn. nov.: *Uvaria littoralis* (Bl.) Bl., Fl. Javae (Anonaceae) 1:26, t. 7 (1830); *U. ovalifolia* Bl., Fl. Javae (Anonaceae) 1:27, t. 8 *et* 14a (1830); King, Ann. Roy. Bot. Gard. Calc. 4:29 t. 13 (1893); *U. gamopetala* Zoll., Linnaea 29:310 (1857-58).

Epitypes (*designated here*); t. 122, Pl. As. Rar. (1831); Wall. Cat. 6487 A *H.B.C.* (*Herb. Wall.* K!).

Habit large climber, reaching 30 m. ***Young shoots*** densely ferrugino-tomentose, becoming striate, glabrous. ***Leaves*** broadly ovate-oblong(-obovate), base cordate-subcordate, apex obtuse or shortly acuminate, rarely obcordate, c. 200-300 x 150-180(-200) mm, coriaceous; *veins* 5-25+, gradually inarching, sub-parallel and often basally branched or merging, leading and trailing trace strong, forming distinct sub-margin, secondary crossing veins frequent, kinked, midrib and primary venation depressed above, strongly prominent beneath, *indument*; abaxial blade sub-glabrous becoming glabrous at maturity except over trace depressions, here hairs sub-tomentose, midrib and main vein traces densely tomentose, adaxial blade usually sub-tomentose, tomentose towards base, younger leaves ferrugino-tomentose on venation and blade, hairs easily worn away from all surfaces on dried specimens but especially from adaxial vein traces. ***Petiole*** c. 10 x 3.5 mm, ferrugino-tomentose, not obviously thicker than midrib base, adaxial groove deep. ***Inflorescence*** 2-5+ buds in tightly-packed rhipidium, up to 3 open at any time, compound peduncle 5-10(-15) mm long, 2-3 mm diam., flattened in TS, densely ferrugino-tomentose, pedicel 3-10 mm x 2-2.5 mm, flattened with shallow groove on inner surface, basally and medially bracteate, bracts broadly obovate, rarely ovate, fleshy, to 5 x 7 mm diam., remaining concave and wrapping around pedicel, often enclosing younger buds, ferrugino-tomentose. ***Calyx*** connate in early bud then splitting apically to form a basally connate three-pointed ring around bud, ring later splitting into 3 ovate-acute sepals, 4 – 6 x 6 – 8 mm wide. ***Corolla*** petals fleshy, basally connate, ovate–acute, usually distinctly concave, expanding to 15-18 x 10-12 mm, reflexing at maturity, outer surface shortly tomentose, hairs paler than on calyx and pedicel, inner surface warty, indument short, sub-tomentose, villose. ***Stamens*** numerous, 5-6 mm long, connective apex elongate, 5-sided in central whorls, flat in outer whorls, minutely pappilate, locules not

stipitate, decreasing in size to staminodal outermost whorl. ***Carpels*** 20-25, 4-4.25 mm long, indument stellate, short and somewhat combed, stigma short, glabrous, U-shaped, base narrowed and sub-tomentose, ovules 12-14. ***Fruit*** monocarps 10-20, spherical-ovoid-oblong, younger fruits bright green, sub-glabrous, often with contrictions between seeds, mature fruits c. 30 x 16.5 mm, usually glabrous, orange-yellow turning maroon red, ripening black with soft pericarp, stipe 2-5 x 2-3 mm, seeds 10-14, hemi-ellipsoidal, 10 x 7 x 3 mm. Leaf shape shown in Figure 4.17. Appendix 4.10 A & B.

Distribution and Ecology This is a variable species, found mainly in mixed and evergreen forests below 300m, but also surviving well in fire-prone or disturbed deciduous Dipterocarp forest. It is distributed from New Guinea through Malesia into Southeast Asia, Myanmar and Bangladesh with an outlying population in Sri Lanka. The species exhibits a wide range of phenotypic diversity, particularly in the shape and indument of the leaves. Distribution is shown in Figure 4.48.

Notes The type material which Dunal mentions in the original description ('Uvaria zeylanica Herb. Deless.') appears to be lost or destroyed. There are *'Uvaria zeylanica'* specimens in Herb. Deless. in Geneva, but these are annotated by Dunal as types for *U. dulcis* and *U. javana*. As a result, the plate accompanying the description is the sole type material remaining. However it is not possible to identify *Guatteria cordata* from the plate (a problem with most of Dunal's plates). Consequently, Wallich's clear, full colour illustration of *U. macrophylla* Roxb (*Pl. As. Rariores*) has been selected as an epitype (in keeping with article 9.7 of the St. Louis Code). Wallich directed that the drawing be made from a living specimen in Calcutta which had been collected by Roxburgh in Tennasserim, and Wallich's collection from that same plant, Wall. Cat. 6487A *H.B.C.* (K) is also designated as an epitype.

Vern. *Laos*; Laotian: 'May Kang' (Poilane 11878); *Myanmar*; Burmese: 'Thwa-bwot-nway' (Kurz 1877); *Singapore*; Malay: 'Pisang-Pisang' (Ridley s.n. 1890). *Thailand*; Thai: Trang Province 'Kluai muu sang' (Smitinand p. 340); Chumphon Province 'Kaa liap', 'Nom maeo yai' (Smitinand p. 340); Nakhon Si Thammarat 'Nom khwaai' (Smitinand p. 340); Surat Thai 'Nom wua' (Smitinand p. 340); *Thailand*;

Karen: Chiang Mai Province; Mae Hong Son "Chuu-biang" (Smitinand p. 340); *Thailand*; Malay: Narathiwat 'Laa-koh' (Smitinand p. 340).

Material examined

Sri Lanka *Location unknown*; *s.coll.* C.P. 3527 (fl.) (BM, K, TCD); Champion s.n. (fl.) (K).

India Calcutta Botanic Gardens, cultivated, Wallich 6487a *HBC* (fl., fr.) (K).

Myanmar *Taninthari (Tenasserim);* Tavoy district, Banks of the Banchuang Road 2 miles S of Paungdaw village, 14.0N 98.3E 275m, 22/08/62, Keenan 1162 (fl.) (E, K); E Bank of the Banchaung R., 2 miles N of Paungdaw village, Tavoy District, Tenasserim, c.14N 98.30E, 800ft 01/08/61 Keenan 1256 (fl.) (E); Tavoy, Roxburgh 110 (fl.) (BM); Tavoy, W. Gomez, Wall. Cat. 6487d (fl.) (K); Tenasserim 11/01/09 Helfer 438 (fl.) (K); Wallich 987 21/9/1815 (fl.) (BM); Roxburgh s.n. (fl.) (BM); *Bago*; Toungoo, Donzayit, east bank of Sittang, 150ft. 04/08/11 Lace 5386 (fl.) (K, E); Yowah, Kurz 58 (fr.) (K); *Yangon*; Nuigaladou, Rangoon 04/09/32 Parkinson 14965 (fl.) (K); Rangoon, 1826, Wall. Cat. 6487c, Wallich, (fl.) (K); 1826, Wall. Cat. 6487b (fl.) (K).

Vietnam *Dong Nai Province* (V - 40 - CLV); at Bao Chiang, near Bien Hoa, 8/1865, Pierre 178 (-) (BM, C, K, P); *Lam Dong Province* (V – 33 – CLV): Dalat, Poilane 30328 (HCMC). *Province unknown*: Poilane 215911 (fr.) (K, P).

Thailand *Mae Hong Son Province* (1 - N); Mae Sarieng, 9-7-1966, Prayad 362 (BK); 20k W of Mae Saering, 18.45N 98.0E, 400m, 13/06/73, Geesink 5926 (fl.) (AAU, C); Khun Yuam, 18.15N 98.0E, 6-700m, 06/09/74, Larsen 34209 (-) (AAU, L, P); Mae Sariang district, Mae Salah (Karen) Village, 20-11-94. Maxwell 94-1228, (BKF, CMU); *Chiang Mai Province* (2 -N); 10km W of Fang, 19.57N 99.11E 600m 23/07/68 Larsen 2600 (fl.) (AAU, C); Doi Chiang Dao, SW foothills near Ban Yang Pong Luang, Chiang Mai Province (2 - N) 525m 29/10/89 Maxwell 89-1324 (fr.) (E);

Doi Chiang Dao, SW foothills near Ranger Station, Chiang Mai Province (2 - N) 250m 24/10/98 Meade 84 (fr.) (TCD); *Chiang Rai Province* (3 – N); 450m, 16-9-22, Winit 774 (BK); *Phayao Province* (4 – N), Muang District, 19.08 N 99.45 E, Doi Luang NP, S. Side, Doi Nok/ Doi Luang Mtn., E end of Huai Fat Valley, 29-12-98, P. Sidisunthorn & S. Gardner 9031 (CMU); *Nan Province* (5 - N); Muang Pua, c. 300m, 01/03/21 Kerr 4965 (fr.) (BK, BM); Muang Pua (Nan), 300m, 1-3-1921, Kerr 4965 (BK); *Lampang Province* (7 – N); Hang Mat District, Doi Kuhn Dahn N. P., SE side, Mae Pry Station, 29-7-94, Maxwell 94-817 (CMU); *Tak Province* (10 - N); Khao Pha wo, c. 70k W of Tak, 700m, 23/07/73, Murata T-16889 (fl.) (L, KYOTO); *Khampaeng Phet Province* (N - 13); Khlong Lan NP, track E of Waterfall, 16.6N 99.23E, 250m, 21/08/95, Parnell et al. 95-352 (fl.) (TCD); *Maha Sarakham Province* (23 - NE); Ban Wan, 17/06/32 Lakshnakara 958 (herb. Kerr) (fl.) (BM); *Chaiyaphum Province* (25 - E), Nam Phoeom, near weir, 16.2N 101.45E, 600m, 19/10/71, van Buesekom 4432 (fr.) (L); Phu Kieo Wildlife Sanctuary, 1-6-1995, Santisuk s.n. (BKF); Phu Kieo Wildlife Sanctuary, 8-1-1996. Wangprasert s.n (BKF); *Nakhon Rachasima Province* (26 - E), Khao Yai N. P., along Huyta Kon River, 6-800m, 19/07/73, Murata T - 16329 (fl.) (L, KYOTO); Khao Yai National Park, 20/12/62, Phengkhlai 601 (fr.) (L); Khao Yai National Park, Khao Kieo (mtn.), 14.45N 102E, 5-600m, 31/10/69, van Buesekom 1950 (fr.) (L); *Krung Thep Maha Nakhon Province* (49 - C) Bankeng, Krabin, 25m 09/11/30 Marcan 2565 (fr.) (BM); *Chonburi Province* (55 – SE); Siricha district, Kow Kieo, 100m, 17-5-1975, Maxwell 75-520 (BK); *Trat Province* (58 - SE), Ko Chang, 12.0N 102.4E, 50m, 08/05/74 Geesink 6621 (fl.) (L); *Chumpon Province* (59 - P); Siepyuan, 07/09/27, Put 985 (fl.) (BM, L); Sripzaan, 05/09/27, Put 938 (fl.) (BM, L); Siepyuan, 7-9-1927, Put 985 (BK); *Surat Thani Province* (61 - P) Klawng Nam Wing, 1.100m 06/03/27 Kerr 12241 (fr.) (L, BM); *Phuket Province* (63 - P), Ton Sai Wildlife Sanctuary, 300m, 04/07/79, Niyomdham 177 (fl.) (BKF, C L); *Trang Province* (67 - P); Kao pad pa near Pathalung, 7.40N 99.45E, 200m, 15/06/74, Geesink 7263 (fl.) (L); *Satun Province* (68 - P); Thon Pliew, c.25k N of Satun, 100m, 100.09E 6.54N, 28/10/93 Larsen 44107 (fr.) (AAU); Tarutao Island, , 20-5-1969, Chermsirivantha & Kasem 1423 (BK); *Location Unknown*; TS 8462 (BKF); Sanan 487 (BKF); Ban Wan Maddaham, 17-6-32, Lakshnakara 958 (BK).

Peninsular Malaysia *Malacca*; Griffiths s.n. (fl.) (BM); *Penang*; Batu Fessinghi, 01/05/66, Stone 6298 (fl.) (L); Porter s.n. (fl.) (BM); Wallich 6486 (fl.) (BM, K); *Perak*; Larut, 300-400ft 4/1884 King 5776 (fl.) (BM); *Location unknown*; Maingay 24, 1031 A (fl., fr.) (BM).

Singapore Bukit Timah, 1898, Ridley s.n. (Sing.); Changi, 21-2-1891, Ridley s.n. (Sing.); Chan Chu Kang, 11-1-1894, Ridley s.n. (Sing.); Chan Chu Kang, 1892, Ridley s.n. (Sing.); Changi, 1-11-1890, Ridley s.n. (Sing.); Gardens Jungle 22/03/09 Ridley s.n. (fl.) (BM); Juroak, 1893, Ridley s.n, (Sing.); McRitchie Jogging Trail, 22/10/96, Lai LJ84 (Sing.); McRitchie Reservoir, South side, 18/11/59, Sinclair 10151 (Sing.); Selitar, 29-10-1889, Ridley s.n. (Sing.); Selitan 04/03/09 Ridley s.n. (fl.) (BM); Tampenis Road, 17-6-1890, Ridley s.n (Sing.); *Location unknown*; Ridley s.n. 1895 (Sing.).

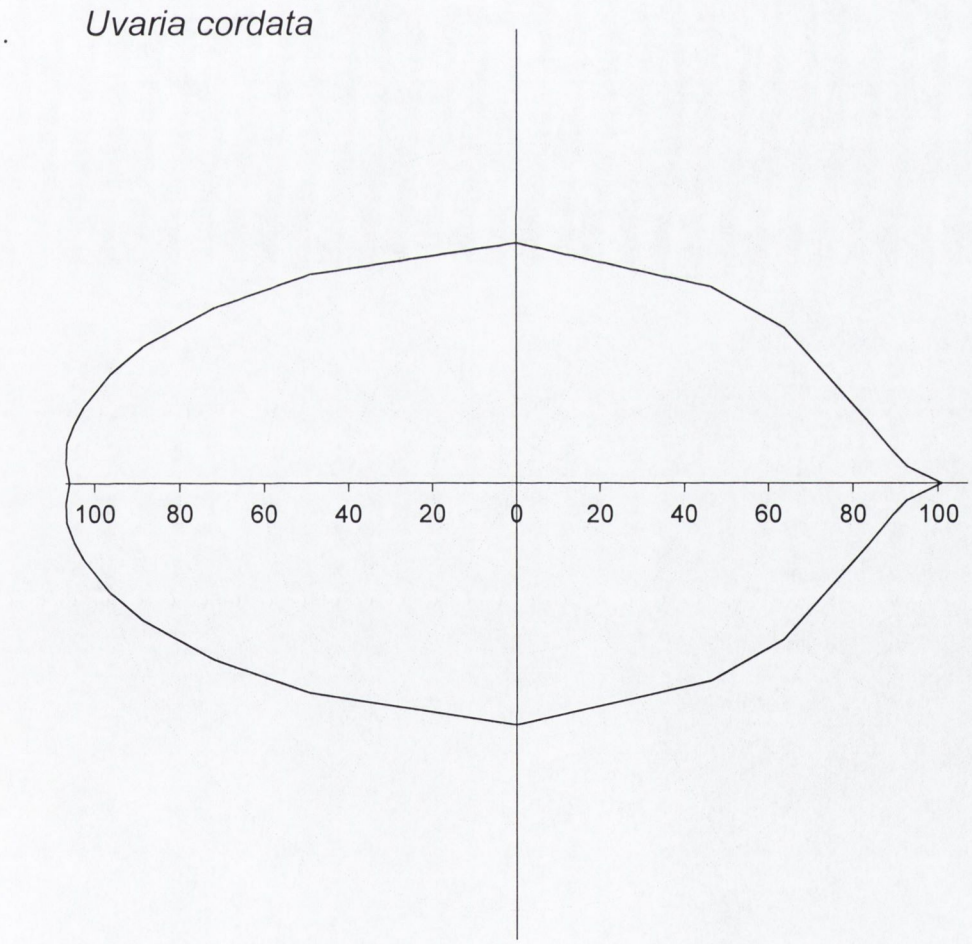


Figure 4.17. Mean leaf outline for *U. cordata* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Java *Locality Unknown*; *s. coll. 'Uvaria littoralis* Bl.' Bl. det, ex Herb. Bog. (fl.) (U).

Borneo *Locality Unknown*; *'Uvaria ovalifolia* Bl.' Teijsmann s.n. ex Herb. Lugd. Bat. (fl.) (U); *'Uvaria littoralis* Bl.' Teijsmann s.n. ex. Herb. Lugd. Bat. (fl.) (U)

Sulawesi Salager, 20/5/13, van Leeuwen 1690 (fl.) (U).

Papua New Guinea *Bougainville*, 16/10/30, Kajewski 2257 (Sing.); Lolorua, 30m, 24/2/35, Carr 11497 (fl.) (NY)

14. *U. microcarpa* Champ. ex Benth

Hook. J. Bot. & Kew Gard. Misc. 3:257 (1851), lectotype (*designated here*): China, 'Hong Kong, 1850, Champion 39' (ex. *Herb. Benth.* K!), isotype: China, 'Hong Kong, Champion s.n.' (ex. *Herb. Hook.* K!); Benth., Fl. Hongkong 10 (1861); Li, Acta. Phytotax. Sin. 14:106 (1976); Tsiang Ying & P-T Li, Fl. Rep. Pop. Sin. 30(2):22 (1979); Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):307 (1991). *U. badiiflora* Hance, Walp. Ann. 3:119 (1851). *U. macrophylla* Roxb. ex. Wall. var. *microcarpa* (Champ.) Finet & Gagnep., Bull. Soc. Bot. France 52, Mém. 4(2):67 (1906) *et* Flore Générale de L'Indo-Chine 1:67 (1907). *U. obovatifolia* Hayata, Icon. Pl. Form. 3:11 (1913).

Habit scandent shrub or climber. ***Young shoots*** ferrugino-tomentose, becoming striate and glabrous, sometimes flattened and broad. ***Leaves*** c. 80-150 x 40-80 mm, elliptic-broadly obovate, thickly coriaceous, apex acute-rounded, base cordate or broadly retuse, frequently oblique, blade often undulate at margin, *veins* 9-11(-12), parallel, trailing trace strong, forming distinct sub-margin, short interprimaries common, secondary veins strongly kinked, midrib and primary veins sunken on abaxial surface, emergent and strongly defined on adaxial surface, *indument* hairs tomentose-erect on on abaxial surface of midrib, sparse to sub-glabrous on veins, blade sub-glabrous to glabrous, hairs on adaxial surface 5-10+ branched, fine, straggling, hairs sparse on blade, more dense on midrib and veins, tomentose at base only. ***Petiole*** short and thickened, 5-6 x 2 mm, shortly and sparsely ferrugino-tomentose, black warty underneath. ***Inflorescence*** leaf-opposed, flowers 1-2(-3),

peduncle 1.5–3.5(-10) mm, pedicel c. 10-15 x 1.4-1.8 mm, both sometimes flattened in TS, bracts elliptic-oblong, 3-5 x 2-3 mm, veins prominent, peduncle, pedicel and bracts all shortly ferrugino-tomentose. ***Calyx*** connate in early bud then splitting apically to form a basally connate three-pointed ring around bud, ring later splitting into 3 triangular/ broadly ovate c. 5-7 x 5-10 mm sepals, remaining concave, sometimes reflexed, often persistent as connate ring, ferrugino-tomentose on outer surface, slightly less dense on inner surface. ***Corolla*** petals 6, brown-red, ovate-broadly elliptical, obtuse-bluntly acute, apex often incurved, inner whorl c. 10-12 x 7-8 mm, outer whorl c. 10-12 x 8-9 mm, fleshy, erect at first, later recurved, surface warty becoming smoother at maturity, densely and shortly tomentose on both surfaces, inner surface distincly marked by stamen apices. ***Stamens*** numerous, c. 4.5-6 mm long, glabrous, locules full-length, connective apex pappillate, flattened, becoming progressively longer and broader toward external whorl, outer whorl semi-staminodal with small basal locules c. 0.5-1 mm long. ***Carpels*** numerous, c. 4 mm long, in dense, tight whorl at centre of receptacle, ovary ferrugino-tomentose, stigma c. 1 x 0.5 mm, glabrous, U-shaped, lobes somewhat broadened, ovules c. 6-8 in two rows. ***Fruit*** monocarps 4 – 8+, green turning yellow then dark purple at maturity, c. 20 x 10 mm, ovoid to shortly oblongoidal, pericarp thin after drying, stipe c. 10-15 x 1-2 mm, shortly tomentose; *seeds* c. 6-8, flattened-ovoid, c. 8 x 8 x 2 mm, dark brown, smooth, shiny, ruminations visible, aril c. 4 x 2 mm, hilum circular-ellipsoid c. 1 mm diam. Leaf shape shown in Figure 4.18.

Ecology and Distribution *U. microcarpa* shows a typical Indochinese-South China distribution, extending from Quang-Tri in Central Vietnam to the Lianhua Shan range in Guandong Province. It is often found as a scandent or erect shrub in open vegation. However it is most common growing as a climber in areas of (semi-) intact forest, usually near watercourses or on hillsides. In the Lianhua Shan Range (22.5 N) it is found at altitudes of up to 1500m. Distribution is shown in Figure 4.49.

Notes This species and *U. cordata* are very closely related, however there are several characters which can be used to tell them apart. The inflorescence structure is the most obvious difference, with *U. microcarpa* having one or two flowers mounted on a narrow elongate pedicel with small elliptical bracts. The peduncle, where developed, is narrow and circular in TS. In *U. cordata* the flowers are mounted on a

closely-packed cyme of 2-5+ pedicels. The peduncle and pedicel are short and broad, usually having a prominent abaxial groove, with very prominent obovate clasping bracts. Important differences are also evident in the flowers. While the petals of *U. cordata* are typically concave-acute and bright red in colour, those of *U. microcarpa* are flat/ spreading, broadly elliptical and red-brown in colour. The outermost whorl of stamens in both species are sub-staminodal with a pair of small locules at each side of the stamen base. While these locules are rudimentary in *U. cordata*, in *U. microcarpa* they can be up to half the length of the stamen. In specimens with young fruits it can be extremely difficult to tell the two apart, although, as the species epithet suggests, the fruits of *U. microcarpa* are considerably smaller and carry less seeds than those of *U. cordata*. Statistical analysis in Section 4 of Chapter 3 established that differences in monocarp size and stipe width are significant between the two taxa. These analyses also showed a significant difference in leaf size and leaf vein number. *U. microcarpa* tends to have smaller leaves and although this is a useful spot-character in reasonably leafy specimens, flowering shoots of *U. cordata* can have leaves of the same size and shape. The presence of any large leaves is usually a good indication that the plant is *U. cordata*. The two species occupy different geographic ranges; *U. cordata* west and south of the Mekong and *U. microcarpa* north and east of it. *U. cordata* is present in the Mekong Delta and probably also in Cambodia. The most southerly record for *U. microcarpa* is in Dac Lac Province, inland from Da Lat.

Vern. *China*; Cantonese: Guandong Province 'Kai Kung Shwe' (Sin Lu Nin 125); 'T'ang Lang' (McClure 638); 'Chow Beong Ip T'ang' Lao 20206. McClure (638) reports the leaves are used to make yeast cakes ('Tsau peng').

Material Examined

Hainan Province *Ching Mai District*; Pak Shik Ling and vacinity, Ku Tung Village, 07/04/33, Lei 510 (fl.) (NY); *Lam Ko District*, Na Chong Yuen village, 16/12/32, Lei 298 (fr.) (L, NY, Sing., US); *Lam Ko-Chung Mai Districts*, Paak Shek Shan, 12/06/28, Tsang 659 (fl.) (NY); *District Unclear*; Dung Ka, 1700ft, 17/04/09, N.K. Chun 43384 (fl.) (NY); Tun Shan Lim, Mangun, 05/04/32, S.P. Ko 52124 (fl.) (NY); Yaichow, 06/07/33, How 70957 (fl.) (NY, US); Yaichow, Liang 62133 (fr.) (NY);

Locality Unknown; 1600ft, 17/04/09, F.C. How & N.K. Chun 70111 (fr.) (NY); 12/01/34, C. Wang 36481 (fr.) (NY); 22/07/33, C. Wang 33223 (fl.) (NY); 11/1889, Henry 8012 (fl.) (E).

Guandong Province *Canton (Guangzhou);* Canton vicinity, 02/10/17, Levine 362 (fr.) (US); Canton vicinity, 05/12/17, Levine 894 (fl.) (US); Guangzhou, 03/07/81, Yip 383 (fr.) (L); Canton, Hooker s.n. (fl.) (E); Canton and surrounds, Millet s.n. (fl., fr.) (TCD); Canton, Reeves s.n. (fl.) (NY); *Kao-Yao District*; Ting, 08/04/22, McClure 8922 (fl.) (E); Tingwu Shan, 04/05/28, W.Y. Chun 6259 (fl.) (E); Tingwu Shan, 29/07/32, S.Y. Lau 20206 (fl.) (K, NY); Tingwu Shan, 07/05/28, W.Y. Chun 6486 (fl.) (E); *Lim Kong District*, Tse Shaan near Tse Haai Tsuen, 05/01/32, McClure 638 (fr.) (NY); *Pok Lo District*, Loh-Fu Shan, 4,000 ft., 31/4/1932, Tsui 54 (fr.) (NY); Loh-Fu Shan, 100m 20/04/78 K'tung 5724 (-) (L); *District Unclear*; Chung Shan, Ooi Tung, 26/4/31, Tsang 39 (fl.) (NY); Kochow, Tai-tseh-weh, Sing Tong, 700m, 5/5/29 (fl.) (NY); Kochow, on the way to Kwang Tan, 12/08/28, Tsiang Ying 908 (fr.) (E); Sie-lung, Loting, 14/09/28, Tsiang Ying 1161 (fr.) (E); Sui Kai, Machung, 14/6/35, Siu Lu Nin 125, (fl., fr.) (NY); Wu-King-Fu, 60m W of Swatow, foothills of Lianhua Shan, 24.25N 115.0E, 9/1899, Dalziel s.n. (fl., fr.) (E).

Hong Kong *Hong Hong Island*; Mount Victoria, 5/1874 s.coll. 9, 898. 63-431-L (fl.) (L); 1850, Champion 39 (fl.) (K); Champion s.n. (fl.) (K); 5/1853, Hance 932 (fl.) (BM); 16/06/28, Tsiang Ying 608 (fr.) (E, NY); 1853-56, Wright s.n. (fl., fr.) (L, NY); Ford s.n. (fr.) (NY); 23/5/1894, Thadinier 890 (fl.) (E); *Lantau Island*; Tungchung-hang, 30/09/40, Y.W. Taam 1826 (fr.) (NY); Tai-O, 17/08/29, Tsiang Ying 3087 (fl.) (K, NY, PE); Tai-O, 17/08/29, W.Y. Chun 3087 (fl.) (NY); 25/12/27, W.T. Tsang 16578 (fr.) (NY); *New Territories*; Clear Water Bay, Tai-po-tsai, 31/05/70, Shiu Ying Hu 10312 (fl.) (K); Ma On Shan, near village, 11/05/68, Ying Hu 7288 (fl.) (PE).

Guangxi Province *District Unclear*; Shap Man Taai Shan, Nam She Village, SE of Shang-sze (now Cenxi/Censheng), Guandong Border, 31/10/34, Tsang 24537 (fr.) (NY); She-feng DaShan, c. 30k S. of Nanning, 2000ft, 22/10/28, Ching 8146 (fr.) (L, NY, US).

Vietnam *Bac Thai Province* (V – 8 – CLV); Phan Me, Petelot 2678 (fr.) (HCMC); *Hoa Binh Province* (V - 9 - CLV); Haie d'un village entre Hudong et Hoa Binh, 01/05/36, Petelot 5800 (fl.) (US, P); *Quang Ninh Province* (V – 10 – CLV); Dam-ha, 05/07/40, W.T. Tsang 29821 (fl.) (L, Sing.); Dam-ha, 09/09/40, W.T. Tsang 30247 (fr.) (C, E); *Vinh Phu Province* (V – 12 – CLV); Thuy dumg, Phu-toc, 12/8/79, Tram Lii-Sanh 129 (fl.) (HN); *Ha Tay Province* (V – 13 – CLV); Mt. Bavi, Son T'ay, 4/6/40, Petelot 2641 (fl.) (HCMC); *Quang Tri Province* (V - 25 - CLV); Trieu Hai,06/04/09, Pirey 64 (fl.) (P); *Dac Lac Province* (V – 32 – CLV); Chuan An, Dac Mil (On Lao Border), Phuong 973 (HCMC); *Province Unknown*; Ankhi-kmhinang, 10/5/81, Flora Vietnamica 465 (fl.) (HN) 'Tonkin' Bon 5604 (fl.) (P); 'Annam', Poilane 13415 (HCMC); *Locality Unknown*; Petelot 5800 (fl.) (HCMC); Poilane 21521 (fl.) (K, P); Flora vietnamica 8089 (fr.) (HN); Flora vietnamica 5856 (HN); Flora vietnamica 2165 (HN).

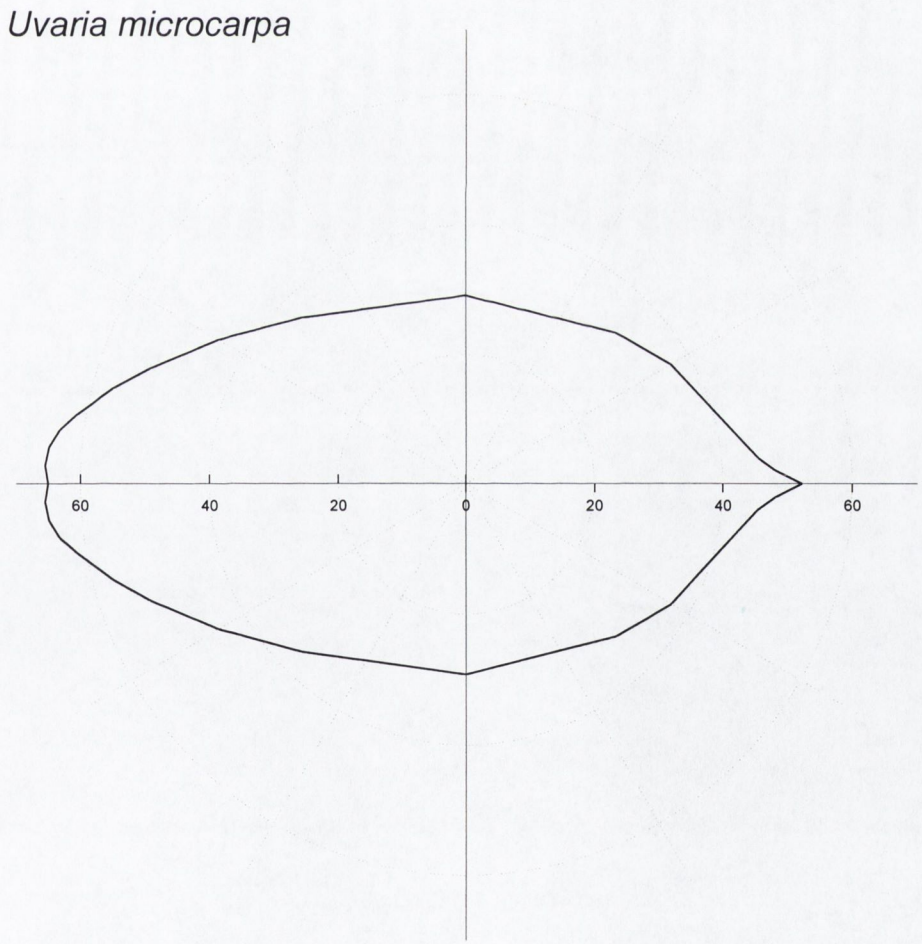


Figure 4.18. Mean leaf outline for *U. microcarpa* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Laos *Savannakhet Province* (L – 12 – CLV); kilo 20 de la route a Guang Zu, 09/01/25, Poilane 11844 (fr.) (P); kilo 22 de la route a Guang Zu, 30/01/25 Poilane 11878 (fr.) (HCMC, P); on road from Savannakhet to Quangtri, Poilane 12077 (fr.) (P).

15. *Uvaria rufa* (Dunal) C. Meade *comb. nov.*

Guatteria rufa Dunal, Anon. p. 129, t. 29 (1817), lectotype (*designated here*): Java, 'Annona (Uvaria) Tomentosa, herbier de l'Inde de M. Poivre – Java, Jussieu Cat No. 10,795 + B, ab Uvaria tomentosa Roxb t.35, differ follis basi subcordati.' (*Herb. Juss.*, P!), syntypes: Java, 'Cananga? tomentosa D. C., Uvaria tomentosa occurit in fallor antea sub numonae Annona tomentosa, indie – apprite par M. Lahaye, Herb. Juss. Cat. 10,795 + A' (*Herb. Juss.*, P!) *et* Timor,'Guatteria rufa, isle de Timor, Riedlé, voyage Captain Boudin.' (P!, G); DC., Syst. 1:504 (1817) *et* Prodr. 1:93 (1824), Miq., Fl. Ned. Ind. 1:48 (1859). *Uvaria rufa* Bl., Fl. Javae (Anonaceae)1:19 t. 4, 13C (1830), type: Java, '*Uvaria rufa* Bl., Java, Bl' (K! L! P!); Finet & Gagnep., Bull. Soc. Bot. France 52, Mém. 4:67 (1906) *et* Flore Générale de L'Indo-Chine 1:51 (1907); Merrill, Enum. Phillip. Pl. 2:156 (1923); Craib, Fl. Siam. Enum. 1:31 (1931); Jovet-Ast, Supplément a la Flore Générale de L'Indochine, 1:64 (1938); Sinclair, Gard. Bull. Sing. 14(2):211 (1955); Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):305 (1991); Mitra, Flora of India 1:293 (1993). *U. astrosticta* Miq. *in* Fl. Ind. Bat. Suppl. 1:370 (1861) *et* Ann. Mus. Bot. Lugd.-Bat. 2:8 (1865), lectotype (*designated here*): Sumatra, 'Sumatra Austr., Lampang, Tarabangie, 4261 H.B.' Teijsmann (U!), syntype: Sumatra, 'Sumatra Austr., Bepisang, Tigo nemrin, Lamp, 4338 H.B.' Teijsmann (U!); King, J. As. Soc. Beng. 61(2)1:23 (1892) *et* Ann. Bot. Gard. Calcutta, 4:30 t. 27a (1893); Ridley, F.M.P. 1:34 (1922). *U. ridleyi* King, J. As. Soc. Beng. 61(2)1:19 *et* Ann. Roy. Bot. Gard. Calc. 4:23 t. 24b (1893), lectotype (*designated here*): Malaysia, 'Pahang, Ridley' (K!); Ridley, F.M.P. 1:32 (1922); *U. hamiltonii* Hook. f. & Thoms. var. *fauveliana* Finet & Gagnep., Bull. Soc. Bot. France 53 Mém. 4:68 (1906) *et* Flore Générale de L'Indo-Chine 1:52 (1907), type; Vietnam, 'Insulae île de Phu Quoc, hab in montibus, Raong Chiao, 3/1874, Pierre 1787' (BM!, K!, P-holo.!); *U. fauveliana* (Finet & Gagnep.) Pierre ex Jovet-Ast, Notul. Syst. (Paris) 9:87 (1940) (*pro parte*).

Habit shrub or large woody climber. ***Young shoots*** ferrugino-tomentose, hairs becoming blunt and sparse, bark smooth, becoming striate with prominent lenticels. ***Leaves*** elliptic-narrowly obovate, base retuse to sub-cordate, apex acute, 100-175 x 35-75 mm, blade rigid, sub-coriaceous; *veins* 10-13, sub-parallel, evenly spaced, trailing trace fine, not forming distinct sub-margin, inter-primaries rare, secondaries

kinked, bifurcation sometimes basal or medial, midrib depressed above emergent below, primaries flat or slightly raised above, emergent below, microvenation indistinct above, emergent below, *indument* abaxial blade sparse, hairs 2-5 branched, erect, scabrid, longer over midrib and veins forming prominent ferrugino-tomentose ridge, adaxial blade hairs 9-12 branched, sub-tomentose, blunt on midrib and veins. ***Petiole*** thicker than midrib, c. 4-5 x 1.5 mm, ferrugino-tomentose. ***Inflorescence*** leaf-opposed, cymose with up to 4 peduncles each bearing a single floral bud with only the oldest 1 or 2 bearing mature flowers at any one time, peduncle c. 3 x 1.5 mm, pedicels c. 8-10 mm, bracts c. 6 x 4.5 mm, ovate, apex acute-rounded, palmate veins visible on outer surface, peduncle and pedicel with ferrugino-tomentose hairs, hairs sparse and shorter on bracts. ***Calyx*** sepals 3, valvate at apex, connate basally, broadly triangular, c. 6 x 3 mm, apex acute-obtuse, indument ferruginous on inner and outer surfaces, forming distinct ridge at margin, often persistent, forming detached ring at base of fruiting receptacle. ***Corolla*** petals 6, red or dark purple in colour, broadly elliptic-oblong, apex rounded, c. 12-14 x 5-6 mm, whorls subequal, fully reflexed at maturity, indument sparse, fine and shaggy. ***Stamens*** c. 30-40, 3-3.5(-4) long x .5 mm wide, glabrous, flattened, connective cap to 1 mm long, papillate, locules full length, latrorse/extrorse, staminodes present, broadly obovate and flattened, c. 14 in number, 3 mm long x 1.5-2 mm wide, sub-marginal whorl of stamens broad and flat and staminode-like with much-reduced locules. ***Carpels*** c. 20 or less, 3.75 x 0.75 mm., ovary tomentose, hairs many-branched, flattened, stigma U-shaped and glabrous but occluded on three sides by extension of ovary wall above a distinctly narrowed neck, ovules c. 24 in two lateral rows. ***Fruit*** monocarps 4-8(-20), c. 25-35 x 14-21 mm, cylindrical, young fruits green with rufous tint, pericarp thick and hard, mature fruits bright red in colour, flesh white, juicy, pericarp wall sub-glabrous, thin and easily torn, stipe ridged, elongate, c. 25-30 x 1-2 mm, indument sparse, hairs spreading; *seeds* 5-14(-20+), c. 6 x 4 x 2 mm, compressed-ellipsoidal, ruminations visible, in two rows, occasionally compressed into what appears to be one row. Leaf shape shown in Figure 4.19. Appendix 4.11A & B.

var. *timoriensis* (Bl.) C. Meade *comb. et stat. nov.*

Uvaria timoriensis Bl., Fl. Javae (Anonaceae)1:21 (1828), type: Timor, 'Timor, Reinwardt.' (L!). *Uvaria scabra* Miq., Ann. Mus. Bot. Lugd.-Bat. 2:3 (1865), type: Ceram, 'Insula Molucca Klein Ceram: Forsten' (L!). *U. branderhorstii* Burck, *in* Lorenz, Nova Guinea 8:427 (1911), type: New Guinea 'New Guinea, 19/12/06, Branderhorst 200'(L!)'

Distinguished by a large, cordate, ovate, membranous leaf type, a longer pedicel and a larger basal bract than seen in the typical *U. rufa* variety. Leaf shape shown in Figure 4.20.

Distribution and ecology Probably the most common species of *Uvaria* in Continental Asia. Although it is found in most forested habitats (though only occasionally in thickets in open dipterocarp forest) it is most common in dry evergreen and mixed deciduous types, and survives well in remnant vegetation. Mature plants can be up to 25m high with dozens of lofty branches spreading through the canopy of the supporting tree. It occurs throughout Indochina and from Peninsular Malaysia to New Guinea, but curiously no specimens have been recorded from Borneo. The *timoriensis* variety is the predominant form of the species in the islands east of Java. Distribution is shown in Figure 4.50.

Notes *U. rufa* is most easily distinguished by the rough texture of the abaxial leaf surface and the outer whorl of broad and flat staminodes. The sweet tangy fruit is valued throughout much of Indochina and although it is not actively cultivated, individual wild plants are often well known to local communities. The plant is also valuable to traditional medicine, particularly in the treatment of stomach cramp and period pain. Vernacular names are recorded for the plant in most parts of Southeast Asia, although in Thailand it and *U. hamiltonii* are often called by the same name, probably due to the similarity of their fruits.

This plant has been commonly known as *U. rufa* Blume, but although Blume did make a full description of the plant in his *Flora Javae* (1830), Dunal had already described it as *Guatteria rufa* in his Annonaceae *Monograph* (1817). Blume makes

reference to the latter in his description of *Uvaria rufa*, but does not specifically mention it as a synonym, as he does with *Uvaria javana*, for example. For this reason the original Dunal description takes priority, with Blume's name reduced to a later homonym.

Blume correctly spotted that there are differences between the typical form and the Timor variety, which he called *U. timoriensis*. However, I have not seen any discrete difference between the two and so have reduced *U. timori*ensis to a variety of *U. rufa*. Dunal also included the two varieties under the same species, as the Paris and Geneva type specimens for *Guatteria rufa* include the typical form (Poivre and Lahaie collections from Java) and the Timor variety also (Riedlé collections from Timor).

Vern. *Laos*; Lao: 'Khua phi pho naw' (Vidal 588). *Thailand*; Thai : 'Nom Ngua' Chiang Mai (Soradet 475, Kerr 18833), Chumpon (Khantachai 1023), 'Nom Kwai' Phetchaburi (Kerr 5719), Pattani (Kerr 7728), 'Nom meo' Bangkok (Kerr 6959), 'See muon' Chaiyaphum (BKF no. 51506), 'Pee puan' Saraburi (Maxwell 74-639); Krabi Province 'Nom wua' (Smitinand p.340). *Timor*; Dawan: 'Kok laba' (Kooy 329).

Material Examined

var. *rufa*

India *Nicobar Islands*, Mus, Car Nicobar, sea level, 8/6/74, Nair 1557 (fl.) (L).

Cambodia *Pursat Province* (C - 10 - CLV); Sre Ambel, 11/05/28 Poilane 15282 (fl.) (HCMC); Trassay, 12/04/28, Poilane 15067 (fl.) (NY, HCMC); 27/06/30, Poilane 17794 (HCMC); *Kampong-Chuang Province* (C - 11 - CLV); Monts Kampong-Chuang, Godefroy 184 (fl.) (P); *Kampong Cham Province* (C - 12 - CLV); North of Nimot, 26/06/28, Poilane 15356 (fl.) (HCMC); *Kampot Province* (C - 19 - CLV); Geoffray 392 (fl.) (P); 21/08/19, Poilane s.n. (fl.) (HCMC); *Locality unknown*; 1/1869 Pierre 655 (fl.) (P); 5/1870 Pierre 655 (BKF); Pierre 655 (fl.) (HCMC); 6/6/1878 Harmand 178 (fl.) (P); 02/06/30 Poilane 17416 (fl.) (HCMC).

Laos *Viang Chaen Province*(L - 9 – CLV); North of Nam Ngum Rreservoir, 29/05/55, Talbot de Malahide 15 (fl.) (BM); Vientaine, 31/05/48, Vidal 588 (fl.) (HCMC); *Province unclear*; Hung Kong, Thorel s.n. (fl.) (P) ; Kok Kheo, Phonthane, Spire 287 (fl.) (P).

Vietnam *Kontum Province* (V - 30 - CLV); 24/04/78 Phuong 604 (HCMC); *Gialai Province* (V – 31 – CLV); Song Long Dakchat, 24/04/78, Ban 604 (fl.) (HN); *Tay Ninh Province* (V - 39 - CLV); Cay Cong, 1/1867, Pierre 120 (fl.) (BM, C HCMC, P); Tay Ninh, mountains, 22/02/39 Muller 904 (fl.) (P, HCMC); *Dong Nai Province* (V - 40 - CLV); Boa Chiang, 7/1877 Pierre 1874 (fl.) (BM); Song Dinh, near Bien Hoa, 30/06/19 Poilane 161 (fl.) (NY, HCMC); *Kien Giang Province* (V - 52 - CLV); Phu Quoc Island, Raong Chiao, 3/1874, Pierre 1787 (BM, K, P holo); Phu Quoc Island, 2/1874, Pierre 655 (fl.) (P); *Province unclear*; 'Cochinchine' c. 1863 Thorel 897 (fl.) (P); Quang Phu, Dec Nong, 15/05/79 Ban 282 (fl.) (HN).

Thailand *Chiang Mai Province* (2 – N); Chiangmai, 29/4/66, Chersmirivathana 534 (BK); Doi Suthep; 300m, 30/05/09, Kerr 660 (fl.) (BM, TCD); Doi Suthep, 03/05/34, Kerr 18833 (BK); Doi Suthep, south side, west of Mae Heeyah Nai Village, 18/06/89, Maxwell 89-777 (fl.) (E); Doi Suthep, 1100m, 09/06/49, Soradet 475 (fl.) (BKF); Doi Suthep, 1100m, 10/06/53, Soradet 475 (BKF); Muang District, Chiang Mai University, opposite Engineering Building, 20/08/98, Rattanayun & Santanachote 5 (fl.) (CMU); Muang District, Wat U-Mong, 06/08/99, Tumersnis 14 (CMU); Muang Petchabun, c. 100m 30/03/22, Kerr 5719 (fl.) (BM); Muang Sam Sak, 200m, 05/04/22, Kerr 5741 (fl.) (BK, BM, K, TCD); *Udon Thani Province* (19 - NE); Kud em, Phonpisai, Nong Khai 04/06/67, Adisai 456 (BK); Non Sang 20/05/68 Bunchuai 1638 (fl.) (L); *Chaiyaphum Province* (25 – E); BKF no. 51506 (fl.) (BKF); *Nakhon Ratchasima Province* (26 - E); Bam Chung Seng, 24/05/33, Mai Hoe 222 (BK); Ban Chum Seng, 23/05/29 Nai Noe 222 (fl.) (BM); *Buriram Province* (27 - E), Huan Bak Dang, 20/05/70, BKF 51506/ coll. 126 (fl.) (BKF); *Surin Province* (28 – E); Ban Jan Gual, Eastern district, beside temple, Hurlburt 3 (fr.) (BKF); *Roi Et Province* (29 – E); 150m, 22/06/69, Smitinand 10758 (fl, fr.) (L, BKF); *Ubon Ratchatani Province* (32 – E); Ubon Ratchatani, c. 200m, 02/03/24 Kerr 8591 (fl.) (BM, BKF, C; *Uthai Thani Province* (33 - SW); Ban Rai, 18/07/64, Sangkachand 983 (fl.) (BKF, L); *Si Sa Ket Province* (34 - E), Kanthararun District, Chia Village, 27/03/49, Ploenchit 1571

(fl.) (BKF); Kantralak district, 13/04/70, Sangkhachand 247 (fl.) (BK); *Phetchaburi Province* (36 – SW), 31/03/26 Kerr 5719 (BK); 15/01/89 Nanakorn 88216 (fl.) (U); *Prachaup Khiri Khan Province* (37 – SW), Huey Hang Forest Reserve, 169-188m 22/04/01 Laudxay 40-107 (fl.) (KKU); Huoy Wa Toon, 10m, 29/06/24 Winit 661 (fl.) (BKF); *Saraburi Province* (47 – C); Sahm Lahn Forest, Muang District, 300m 01/04/74 Maxwell 74-254 (fl.) (AAU, BK, BKF); Sahm Lahn Forest, Muang District, 100m 30/06/74 Maxwell 74-639 (fl, fr.) (AAU, BK, L); *Krung Thep Maha Nakhon Province* (49 – C); Bangkok, Pekret, canal bank, 16/04/22, Marcan 729 (fl.) (BM); Vanpruk 49 (fl.) (BKF); 01/07/26, Marcan 2119 (fl.) (BM); 22/04/23 Kerr 6959 (fl.) (BM, BK); *Prachaburi Province* (53 – SE); Kabin District, 02/03/99, Phengklai 6826 (fl, fr.) (BKF); *Chon Buri Province* (55 – SE); Siracha, Nawng Kaw , 30/03/23 Kerr 6776 (fl.) (BM, BK); Siracha west, 30/05/30, Collins 1253 (BK); Siracha, 10/05/20 Kerr s.n. BKF no. 13945 (fl.) (BKF); Siracha, Collins 105a (BM); *Chanthaburi Province* (57 – SE); Khao Phra Bat, 27/08/72, Larsen 32134 (fr.) (L); Makham 09/04/59, Smitinand 5777 (fl.) (BKF); Makham, 50-100m, 09/04/59, Sorensen et al. 7233 (fl.) (BKF, C); Muang District, c.7km west of Chanthaburi, 04/04/71, Maxwell 71-282 (fl.) (BK, L); 13/ 4/25, Nai Noe 59, (fl.) (BK, BM); Pong Nam Ron 06/09/56, Smitinand 3499 (fr.) (BKF); Pong Nam Ron Pailin, West of Khao Soi Dao Tai, 28/08/72, Larsen 32164 (fr.) (AAU, L); Khao Soi Dao Tai, 12/06/59, Sangkhachand 7 (fl.) (BKF, L); *Chumphon Province* (59 – Pen.); Kapora waterfall, Tha Sae, 27/05/73, Faray 71 (fl.) (BK); Nam-Tok-Yai-Thai, 30/04/63, Khantachai 1023 (fl.) (BKF); *Surat Thani Province* (61 – Pen.); Bang Yai River, 04/06/70, Sakol 1004 (BK); Bangbao, 100m, 8/8/55, Smitinand 2901 (fr.) (BKF); *Krabi Province* (64 – Pen.); Tambon Kao Panom, 02/04/30 Kerr 18833 (fl.) (BM, C; *Trang Province* (67 – Pen.); Trang, 02/04/19, Vanpruh 620 (BKF); Trang, 30/09/24, D. Bourke s.n (fl.) (BK); on the Trang-Krabi Road, 19/05/84, W.N. 516 (fl.) (BKF); *Satun Province* (68 – Pen.); Amphoe Muang, 19/04/73, Kasem 1389 (BK); *Songkhla Province* (69 – Pen.); Bantom Island, Lake Songkhla, Satingpra, 26/5/84, Siriirugsa 817 (fl.) (BKF); Had Yai District, Ban Klang, 06/06/85, Maxwell 85-577 (fl.) (BKF, NY); Haad Yai District, base of Ko Nong, 10m, 12/08/88, Maxwell 84-21 (fr.) (BKF); *Pattani Province* (70 – Pen.); Nong Chick, 21/07/90, Santisuk s.n. (fl, fr.) (BKF); Yala Pattani, 50m, 05/09/27 Kerr 7728 (fl., fr.) (BK, BM); *Narathiwat Province* (72 – Pen.); Bacho, 10/5/61 Sangkachand 135 (BKF); Su Ngai Kolok, 10/09/85, Niyomdham et al. 952 (fl.) (AAU, C); *Province not known*; Santisuk BKF no. 95594.

(BKF); Southeast Thailand, Dee 1192 (BKF); 01/04/25 Noe 59 (C); Collins 197 (BM); *s.coll.* BKF 1192 (fl.) (BKF); Sakol 6070 (BK); Nom Maell, 18/05/59, Umpai 87 (BK); Huan nam wing, Bua rai, 17/04/67, Larsen 285 (fl.) (BK).

Peninsular Malaysia *Kuala Trengganu*; Kuala Berok, Sungei Nerus, 18/09/55 S.F. 40879 (-) (Sing.); *Pahang*; 8/1884 Ridley s.n. (fl.) (BM); *Perak*; Scortechini 1216 (fl.) (BM); *Setul*; near Batu Buuga, 01/03/10, Ridley 15001 (BM).

Singapore *Botanic Garden* 13/04/09, Clemens 22457 (fl.) (NY).

Sumatra *Lampung Province*: Bepisang, Tiga Nemin, 4338 H.B. (fl.) (U); Larap, Tarabangie, 4261 H.B. (fl.) (U); *Province unclear*; Teysmann s.n. (fl.) (K); Sumatra occidental, Miquel herb. s.n. (fl.) (U).

Java *Batavia*; 01/11/04 Backer s.n. (fl.) (U); *Brambesnan* 1/12/1900 Jensen s.n. (C; *Surabaya* 10/1793 - 8/1794 Lahaie 1772 (fl.) (P); *Locailty unknown*; Blume s.n. (fr.) (K, L, P); 01/04/20 *Bakhuizen* s.n. (fl.) (U); Poivre s.n. (fl.) (herb. Juss. P); Lahaye s.n. (fl.) (herb. Juss. P).

var. *timoriensis*

Flores 5/1966, Verheijen 2271 (fl.) (L).

Ceram Klein Ceram, Forsten (fl.) (L, U).

Sulawesi Salya Island, Weber s.n. (fl.) (L).

Timor Insula Timor, 4/1803, Brown s.n. (fl.) (BM); 1808, Riedlé s.n. (fl.) (BM, G, P); de Castro s.n. (fl.) (LISU); 2/2/66, Kooy 329 (fl.) (L); ex herb. Paris (fl.) (C, L, TCD); Teijsmann & Binnendijk s.n. (fl.) (U); Teijsmann s.n. (fl.) (U).

Philippines *Luzon*; Rizal Province; 01/08/11, Ramos 1048 (fr.) (U); Rizal Province, Montalban, 01/03/17 Elmer 17418 (fl.) (C); Rizal Province, Malapadnabato,

22/03/09, no. 2735 (fl.) (P); Rizal Province, Manila, 1845-1847 Didricliseau 3138 (C); Rizal Province, Manila, Leg Vidal no. 6 (ex MA) (fl.) (AAU); May, June 1905, Ahern 31999 (fl.) (P); Pangasinan Province, Umingan, 01/05/14, Merrill 'Species Blancoanae' no.199 (fl.) (L, P); *Mindanao*; Davao Province; Santa Cruz, Marinchique, May 1884, Vidal no. 6 (AAU); Davao Province; Tibanban, Eda–o 11348 (BK); *Locality unknown*; Ins Philippinis, Cuming s.n. (C).

New Guinea 19/12/06, Branderhorst 200 (fl.) (L, U).

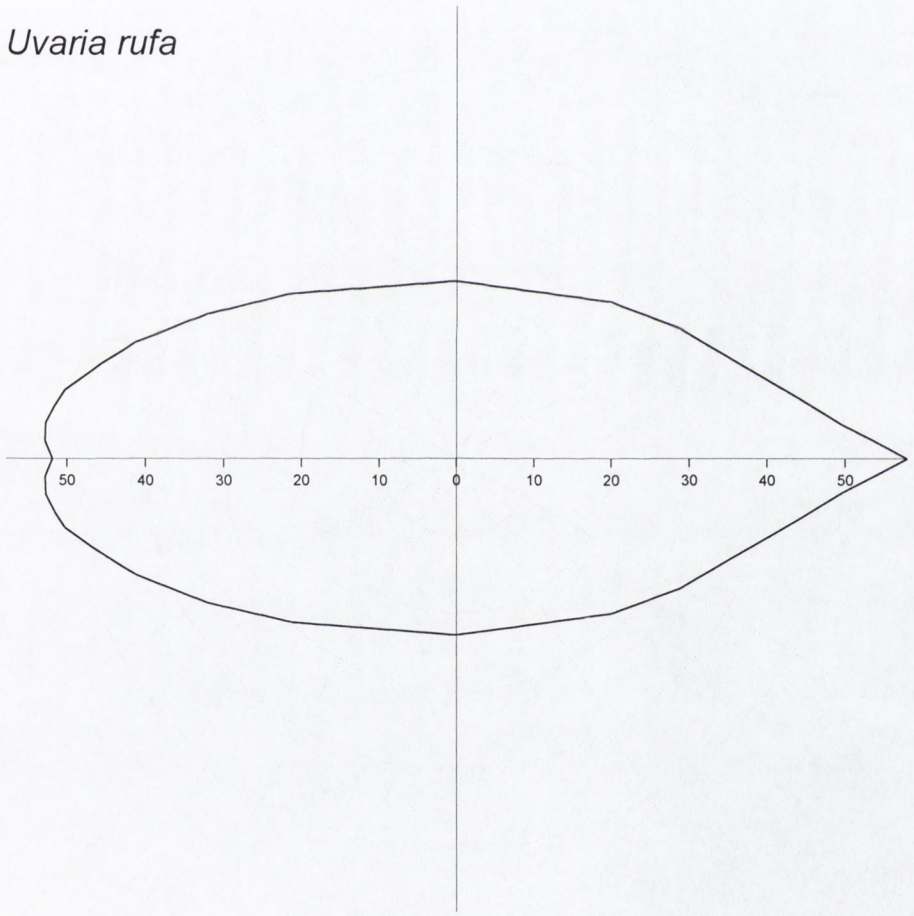


Figure 4.19. Mean leaf outline for *U. rufa* var. *rufa* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Uvaria rufa var. *timoriensis*

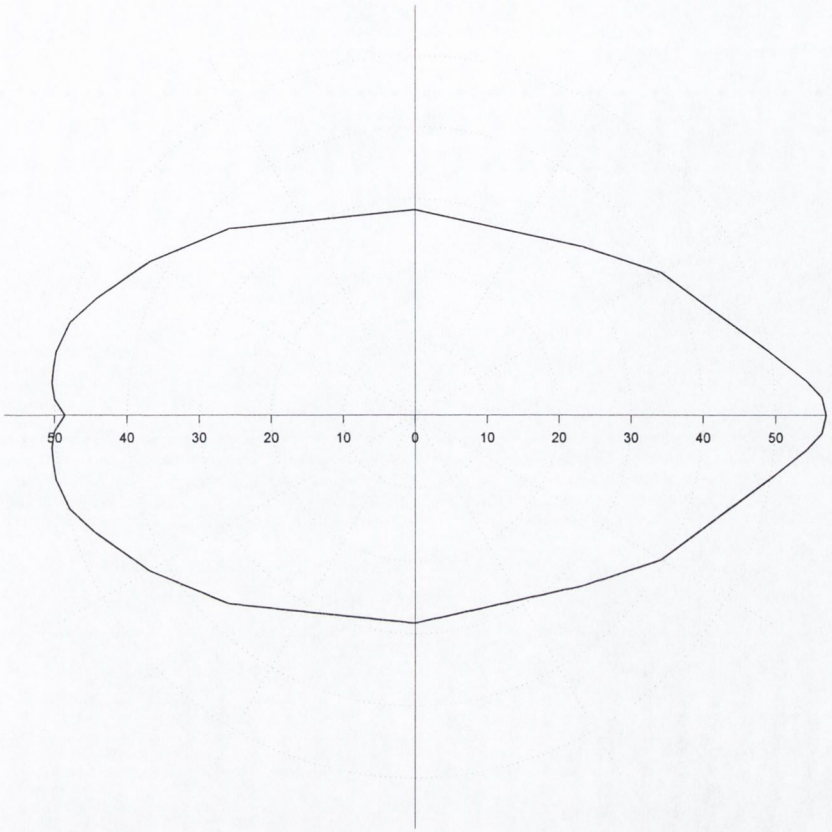


Figure 4.20. Mean leaf outline for *U. rufa* var. *timoriensis* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

16a. *Uvaria lobbiana* Hook. f. & Thoms.

Fl. Ind. 1:100 (1855) *et* Fl. Br. Ind. 1:49 (1872), lectotype (*designated here*): Malaysia, 'Malacca, Griffith 1845' (*ex Herb. Hook.* K!); syntypes: Malaysia, 'Malacca, Griffith' (BM! K! P! TCD!), Griffith s.n. 'E.Ind.Comp. No. 434, 435' (fl.) (*ex Herb. Hook.* K!), Lobb s.n. Singapore (*ex Herb. Hook.* K!); King, J. As. Soc. Beng. 61(2)1:15 *et* Ann. Bot. Gard. Calcutta, 4:19 t. 9 (1893); Ridley, F.M.P. 1:30 (1922); Sinclair, Gard. Bull. Sing. 14(1):44 (1953); Sinclair, Gard. Bull. Sing. 14(2):208 (1955). *U. sub-repanda* Wall., Cat. 6483 *nom. nud.* (K!)

Habit a large climber to 30m. ***Young shoots*** smooth, hairs sparse, many-branched, becoming sub-glabrous, striate, often with prominent lenticels in older shoots. ***Leaves*** elliptic-narrowly obovate, base shortly cordate, apex acute-cuspidate, 100-175(-200) x 40-75(-85) mm, coriaceous; *veins* 8-14, basally parallel and then gradually inarching, trailing trace fine, not forming distinct sub-margin, secondaries kinked, microvenation reticulate, indistinct above, visible below especially toward margin, midrib shallowly depressed above, emergent below, *indument* abaxial blade sub-glabrous to glabrous, hairs c. 20-branched, rubbing off easily, midrib sub-tomentose, hairs erect or spreading, adaxial surface sparse to sub-glabrous, hairs on midrib and sub-tomentose. ***Petiole*** 3-4 x 1.25-2 mm, appearing much broader than midrib base, sparse to sub-tomentose, transverse foliations prominent. ***Inflorescence*** supra-axillary or rarely leaf-opposed, flowers 1-2(-4), peduncle c. 2-5 x 1.5 mm, pedicel 5-10(-14) x 1.5 mm, both usually flattened in TS and densely tomentose with large rufous hairs, bracts broadly ovate, c. 6-10 x 6-10 mm, membranous, sparse to sub-tomentose with tomentose margin, veins prominent. ***Calyx*** sepals 3, undulate and imbricate in bud, ovate, 7 x 3.5 mm long, recurving at tips, outer and inner surface indument more dense than on bracts. ***Corolla*** petals 6, usually yellow but often turning pink or red, inner whorl c. 10 x 8 mm, outer whorl 11 x 8 mm, shortly and broadly ovate, less often elliptical, apex obtuse or bluntly acute, inner surface undulate, tomentose, outer surface often with transverse ridges of large blunt stellate hairs. ***Stamens*** numerous, 2.25-2.5(-3) mm, locules full length, connective flattened and shortly elongate with prominent papillae, outer whorl of staminodes. ***Carpels*** numerous, 2.25-2.5(-3) mm, ovary densely tomentose with ring of elongate hairs c. 0.25 mm long beneath stigma, stigma U-shaped with prominent lateral slit, glabrous, ovules c. 6-8(-10). ***Fruit*** monocarps ovoid or globose, c. 16-18 x 20-25 mm, prominently tubercled, sub-

tomentose, stipe 35-55(-70) x 1.5-2 mm, finely striate, indument sparse; *seeds* 4-6, c. 12 x 10 x 4.5 mm, smooth, raphe prominent but not raised. Leaf shape shown in Figure 4.20.

16b. var. *ptychocalyx* (Miq.) C.Meade *comb. et stat. nov.*

Uvaria ptychocalyx Miq., Ann. Mus. Bot. Lugd.-Bat. 2:4 (1865), type: Borneo 'Korthals legit, Borneo Australis, ad Sakoembang in Poeloe Lampei' (L!); Hook. f & Thoms., Fl. Br. Ind. 1:49 (1872); Kurz, Fl. Br. Burma 1:28 (1877).

Differs from the typical form of the species in having a dense tuberculate indument over the young shoots and a distinctive obovate leaf form. ***Young shoots*** indument densely tuberculate, hairs many-branched, blunt. ***Leaves*** distinctly obovate, c.(120-) 150-215 x 75-95(-100) mm, *veins*; 12-20, parallel, progressively inarching only towards the leaf apex, *indument*; abaxial blade sparse with semi-persistent 1-3 branched erect hairs, where present rough to the touch, hairs tomentose and erect over midrib and primary veins, becoming sub-glabrous with age and toward leaf margins, adaxial surface with sparse to sub-tomentose many-branched hairs, midrib and veins usually sub-tomentose, becoming more tomentose and tuberculate towards base of midrib.

Distribution and Ecology a common species in lowland rainforests of Taninthari, Peninsular Thailand, the Malay Peninsula, Sumatra and Borneo, and there is one collection from the Andaman Islands. Var. *ptycocalyx* is restricted to the wet coastal strip running from Bago through Taninthari to Surat Thani and Phuket. Distribution is shown in Figure 4.51.

Notes *U. lobbiana* seems closely related to *U. rufa* and *U. leptopoda* (Lower Malay Peninsuala). The densely tomentose broadly ovate petals and prominently tuberculate fruits of *U. lobbiana* should distinguish it from both these species. The petals of *U. leptopoda* are glabrous on the inner surface and the fruits, though mounted on a long stipe, are smooth and tomentose. The fruits of *U. rufa* have a short c. 25-30 mm long

stipe and c. 5-14(-20+) seeds, and the stamens are much reduced in number with an outer whorl of c. 14 – 20 broadened staminodes. The staminodes of *U. lobbiana* are the same width as the outermost whorl of fertile stamens and 30 – 40 in number.

Vern. *Myanmar*; Burmese: 'Thwa-Botnway' (Kurtz 1877); *Thailand*; Thai: 'Thao Tan Lued', Surat Thani (Put 59); 'Kluai moo-sang' Ranong (Sangkachand 1128); *Borneo*; Central Kalimantan, local name 'Akam itam' (Endert 2333).

Material Examined

India *Andamans*; 1884, King's coll. 338 (fl.) (K).

Thailand *Chumpon Province* (59 – Pen.); Langsuan, c. 90m, Feb 14, 1927, Kerr 11943 (BK); Ban Ha, Sept. 1927, s.coll. 9 (BK); *Trang Province* (67 - Pen); Ampo Kao Kao, 05/08/29, Rabil 377 (fl.) (BM); *Narathiwat Province* (72 - Pen.); Bacho, 21/04/61, Sangkhachand 76 (fl.) (BKF, C, K, L, P).

Malaysia *Johore*; Gunong Pulai F.R., 800ft., 23/09/70, Chan FRI 17536 (fr.) (L); Palau Tioman 1300ft, 7/5/27, Now 1876 (Sing.); *Kedah*; Gunong Jerai, Kedah Peak, 1200ft., 14/05/69, Stone 8542 (fl.) (L); *Melaka*; 19/01/09, Griffith s.n. (BM, K, P, TCD); Griffith s.n. E.Ind.Comp. No. 434, 435 (fl.) (K); Maingay 1026 (fl., fr.) (K); 20/5/1866 Maingay 27=1027 and1463 (fl.) (K, L); Bukit Bruang, April 1890, Derry 429 (L, Sing.); Sept.1887, Curtis 1234 (Sing.); *Negeri Sembilan*; Pasoh FR, Jelebu District, 80-120m, 09/05/96, Gardette 1831 (fl.) (Sing); *Pahang*; Taman Nagara NP, c. 100m, 27/04/75, v. Balgooy 2554 (fl.) (AAU, L); *Penang*; Palau Penang, foot of hill, 1898, Curtis s.n. (BM); Penang, Curtis 841 (fl.) (AAU, K, Sing.); Moniat Road East, 18/10/1951, Sinclair 39351 (Sing.); govt. Hill Penang, 1000ft. May 1896, Curtis s.n. (Sing.); Apr. 1888, Curtis 1408 (Sing.); *Perak*; Larut, 8/1883, King 4787 (fl., fr.) (BM, K, L, Sing.); *Selangor*; Dec. 1896. Ridley 8217 (Sing); *Terengganu*; Ulu S. Trengan, near K. Petang, Ulu Terengganu 900ft, 3/6/68, Cockburn FRI 8439 (K, L, Sing.) *Location Unknown*; Maingay 30 pro pars (fl., fr.) (K).

Singapore Garden's Jungle, Ridley 9211 (fl.) (BM, Sing.); Lobb s.n. (fl.) (K).

Indonesia *Sumatra* Atjeh; Gunung Leuser Reserve, 3.0N 97.5E, 50-125m, 16/07/79, de Wilde 18767 (fr.) (L); Asahan, Silo Maradja, Jun. 1927, Bartlett 8725 (fl.) (NY); Batong Singterry, Korthals s.n. (fl.) (L); Laboehan Batoe, Kota Pinang District, Si Mandi Angin, 16/5/33, Toceos 4137 (fl.) (NY); Lampung; Korthals s.n. (fr.) (L); Location Unclear; Korthals s.n. (fl.) (L, NY); *Kalimantan*; East Kutai R, near Sengata and Mentoko Rivers, E. Kalimantan, 0.3N 117.2E, alt. < 300m, 03/07/89, Leighton 723 (fl.) (L); West Koetai, no. 12, near Liham Batoe Beng. Central E. Kalimantan, 40m, 31/07/25 Endert 2333 (fl., fr.) (L).

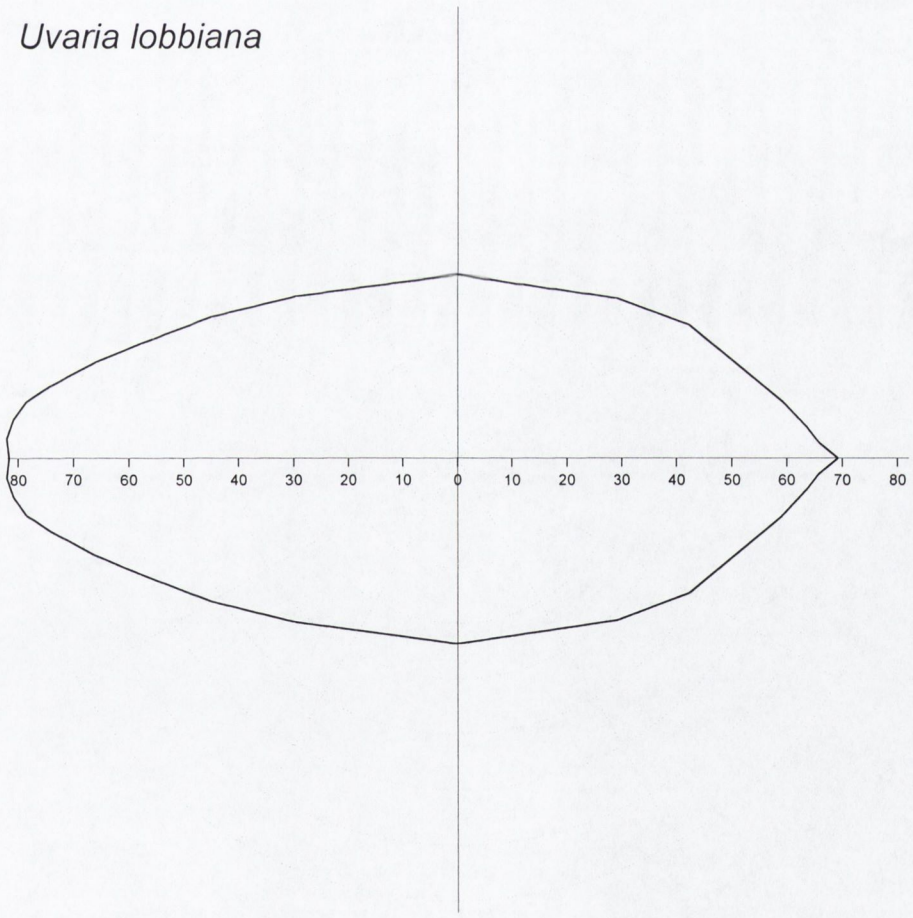


Figure 4.21. Mean leaf outline for *U. lobbiana* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Var. *ptychocalyx*

Myanmar *Taninthari (Tenasserim)*; Mergui, Herb. Helfer/ E.Ind.Comp. No. 440 (fl.) (K, P); *Bago*; Yomah, Kurz 64 (fr.) (K); Rangoon, 26/1/1853, McCalland s.n. (fl.) (K); Rangoon (1867-1868) Maingay 28 (fl.) (K); *Locality Unknown*; 1827, Wallich 6487e (-) (BM, K).

Thailand *Ranong Province* (60 - Pen.); Kapoe, 15/11/65 Sangkhachand 1128 (fl.) (BKF, C, P); *Surat Thani Province* (61 - Pen.); Nong Som, Ban Na, 09/09/27, Put 59 (fl.) (BM); 02/03/74, Nimanong 10 (fr.) (BKF, C, P); 18/08/75, Prapat 45 (fl.) (AAU, C, L, P). *Phuket Province* (63 - Pen.); Khao Pra Taeo WRC, 29/12/83 Fukuoka T-35641 (fr.) (BKF).

Indonesia *Kalimantan;* Sakoembang in Poeloe Lampei, Korthals s.n. (fl.) (L); *Java;* Bogor, cult in Bot. Bog., 1886/7, Warburg 1803 (fl.) (NY)

17a. *Uvaria narum* (Dunal) Bl.

Fl. Javae Anon. 5 (1830). *Unona narum* Dunal, Anon. 99 (1817) excl. syn. Rumph., type: Rheede, Hort. Mal. t. 10 (1679); DC., Syst. 1:481 (1817) *et* Prodr. 1:88 (1824); Don, Gen. Syst. 1:93 (1831). *Uvaria zeylanica* L. *sensu* Lam., Encycl. 1:596 (1785). *Uvaria zeylanica* L. *sensu* DC., Syst. 1:481 (1817) [*pro parte*].

Syn. nov.: *Uvaria narum* (Dunal) Wall., Cat. 6473 (1832) *nom nud.*; *U. narum* Wall. ex Wight & Arnott, Prodr. 9 (1834); Hook. f. & Thoms., Fl. Ind. 1:102 (1855) *et* Fl. Br. Ind. 1:50 (1872) excl. var. b; Thw., Enum. Pl. Zeyl. 6 (1858); King, Ann. Bot. Gard. Calcutta 4:20 t. 21 (1893); Trimen, Handb. Fl. Ceylon 1:19 (1893); Cooke, Fl. Pres. Bombay 1:15 (1903); Brandis, Indian Trees, 4th ed. 17 t. 6 (1921); Alston, Kandy Fl. 2 (1931); Gandhi, Fl. Hassan Distr. (Karnataka) 39 (1976); Huber, Rev. Handb. Fl. Ceylon 5:18 (1985); Mitra, Flora of India 1:291 (1993). *Uvaria flexuosa* Heyne ex Wall., Cat. 6473b (1830) *nom. nud. Guatteria malabarica* Dunal, Anon. 134 (1817); *G. montana* DC., Prodr. 1:94 (1824); *Uvaria malabarica* Oken, Allg. Naturge Sch. 3(2):1254 (1841).

Epitype (*designated here*): Ceylon, 'Uvaria zeylanica enc. No. 3, Narum-panel Rheed. Mal. 2 t. 10' (*Herb. Juss.* P!).

Pre-Linnean accounts; *Narum-panel* Rheede, Hort. Mal. 2:11 t. 10 (1679); *Kal tsjerou-panel* Rheede, Hort. Mal. 5:33 t. 17 (1679); *Frutex baccifer, fructu ad singulos flores multiplici* Rai., Hist. 1636 (1693).

Habit sarmentose shrub or climber. ***Young shoots*** black, very finely striate, sparse or sub-glabrous becoming glabrous very quickly, hairs small, c. 0.2 mm diam. ***Leaves*** oblong-elliptical-oblanceolate, base cuneate, apex acute-acuminate, c. 145 x 45 mm, acuminum to 15 mm, sub-coriaceous, waxy; *veins* c. 10-11, fine, distinct, sub-parallel, trailing trace forming fine sub-margin, inter-primary veins frequent, secondary veins indistinct, tertiary venation reticulate; *indument* rare spreading hairs on very young leaves, quickly becoming glabrous above and below; ***Petiole*** c. 4-5 x 1 mm, glabrous, transverse foliations prominent, minutely tubercled. ***Inflorescence*** terminal or leaf opposed, flowers solitary, buds globose, peduncle c. 4 mm long, pedicel c. 20-30 mm, 0.75 - 0.85 mm diam., broadening at receptacle, indument sparse to sub-tomentose, hairs rufous, fine, many-branched, bracts membranous, ovate-elliptical, c. 3 x 1.5 mm, sub-glabrous to sparse. ***Calyx*** valvate, sepals 3, broadly ovate, c. 6-8 x 3.5-4.5 mm, concave, reflexing at maturity, outer surface sub-glabrous and minutely tuberculate with ferrugino-tomentose margin and apex, inner surface densely and shortly tomentose with pale shaggy stellate hairs. ***Corolla*** petals 6, blood-red in colour, membranous, basally connate, outer whorl 10-12 x 9-11 mm, inner whorl 8-11 x 7-9 mm, all petals initially broadly ovate-acute, maturing obovate, obtuse-acute, concave, reflexed at maturity, shed as a ring, both surfaces of both whorls shortly tomentose with fine, somewhat straggling pale hairs, c. 0.2 mm diam. ***Stamens*** numerous, c. 1.75 mm long, locules full-length, connective apex globose, very shortly papillate, staminodes not present. ***Carpels*** numerous, c. 2 mm long, ovary hairy, stigma U-shaped, not lobed, glabrous, black, often covered with exudate, ovules 6. ***Fruits*** numerous, green turning orange then red, monocarps globose to oblong, 10-15 x 6-8 mm, surface sub-glabrous to glabrous, granular or minutely tuberculate, at maturity pericarp drying thin, stipe narrow, c. 25-35 x 1 mm diam., sub-glabrous with scattered pale stellate hairs c. 0.2 mm diameter; *seeds* 2-6, c. 5.5 x 4 x 3 mm, compressed ovoid, ruminations visible, raphe darker than remainder of testa, aril not prominent, 2 rows packed closely together. Leaf shape shown in Figure 4.22.

17b. var. *macraeii* C. Meade *var. nov.*

Holotype: Sri Lanka, 'Macrae 77' (BM!); isotype: Sri Lanka; 'Macrae 88' (BM!)

A varietas typicus corolla uni-seriatus basi-connatus petalis complanatus ellipticus sub-acutus differt.

Distinguished from the typical form of the species by having elliptical-acute flattened petals which are fused basally for 2-4 mm and not differentiated into an inner and outer whorl.

Distribution and Ecology a common species near watercourses on the wet coastal plains and hills of SW Sri Lanka and the Malabar coast. Var. *macraeii* is restricted to Sri Lanka. Distribution is shown in Figure 4.51.

Notes *U. narum* was the first *Uvaria* to receive attention from European botanists, most notably by Rheede who described it (with the addition of a good plate) as 'Narum-panel' in his *Hortus Malabaricus*. When Linneaus established the genus with his description of *U. zeylanica* he listed Rheede's 'Narum-panel' as a synonym of the new species. Later Dunal differentiated between Rheede's 'Narum-panel' and *U. zeylanica* L., renaming the former under the binomial *Unona narum*. He also including Lamarck's description of '*U. zeylanica* L.' as a synonym of *Unona narum*. The material upon which Lamarck based his '*U. zeylanica*' description survives in Paris, and has been selected here as an epitype for *U. narum.*

This species is often confused with *U. lurida*, and to a lesser extent *U. macropoda*. The two best characters for quickly differentiating between the species are calyx and fruit structure. While *U. lurida* and *U. macropoda* have a strongly tuberculate calyptrate calyx with a prominent apicule, the calyx of *U. narum* is valvate and covered with a short sub-tomentose indument of fine rufous hairs. Section 3 of Chapter 3 established important differences in fruit structure between the three species. The mature monocarps of *U. narum* and *U. lurida* are both oblongoidal and sub-glabrous, however those of *U. narum* are much smaller, have a pericarp which

becomes very thin upon drying, and are mounted on a short narrow stipe. The fruits of *U. lurida* are variously thick-walled, usually large, carrying one or more longitudinal ridges on the monocarp surface, and mounted on a long, thickened stipe. The monocarps of *U. macropoda* are narrowly cylindrical, tomentose, have a thick apicule and are mounted on stipes upt twice as long and broad as those of *U. lurida.*

Vern. *Sri Lanka*; Sinhalese: 'Pangan', (Huber, 1985); *India*; Kannada: 'Kariballi' (Mitra, 1993); Malayalam: 'Narumpannal' (Mitra, 1993); Tamil: 'Puliccan', 'Tiger's eyes', 'Manikolinjan' (Matthew 1993).

Material examined

Sri Lanka *Ratnapura District*; Ballancoda, Walker 175 (K); *Location unknown*; *s.coll.* C.P. 1032 (fl.) *pro pars* (K, NY, TCD).

India *Goa*; Chapora, 20/11/1896 Lapes 37 (fl.) (LISU); *Karnataka*; near Mangalore, 21/01/09, Hohenhacker 332 (K); Mysore, Buchanan s.n. (fl.) (BM); *Kerala*; Calicut (Kozhikode), 01/02/05, Meebold 721 (fl.) (G); Calicut (Kozhikode), 1/1843, Perrottet s.n. (fr.) (P); Suckidy Coatay, near Calicut, 4/1846, Wight 18 (fr.) (K); Cranganore, Trarancore,, 9/1884, Gamble 14841 (fl.) (K); Travancore, sea level, 01/01/33, Yeshoda 425 (fl.) (NY); Nilghiri Hills, 1837-1838 Perrottet 40 (fl.) (G); Nilghiri Hills, Perrottet 17 (fl., fr.) (TCD); Nilghiri Hills, Johnson s.n. (fl., fr.) (TCD); *Maharashtra*; Chandawar, Pai 582 (fl.) (AAU); Dhareshurar, Pai 615 (fl., fr.) (AAU); Southern Concan, Dalzell s.n. (K); Chola Ghat, Concan, Stocks s.n. (fl., fr.) (K); *Tamilnadu*; Dindigul, Wight s.n. in Wallich 6473 a,b (fr.) (BM, K); Wamdory, Beddome 53 (fl.) (BM); Tamilnadu, Nagalur forests, Periakalarayans, 900m, 11/04/80, Matthew 27464 (-) (L).

Var. *macraeii*

Sri Lanka *Galle District*; Kannelliya forest near Hiniduma, 08/05/73, Kostermans 24753 (fl.) (L); Kannelliya forest near Hiniduma, 400m, 07/11/77, Huber 588 (fl.)

(US); *Kalutara District*; Pelawatte, sea level, 21/01/70, Cramer 2811 (fl.) (US); *Location unkown*; Macrae 77, 88 (fl.) (BM); *s.coll.* C.P. 1032 *pro pars* (fl.) (BM, NY).

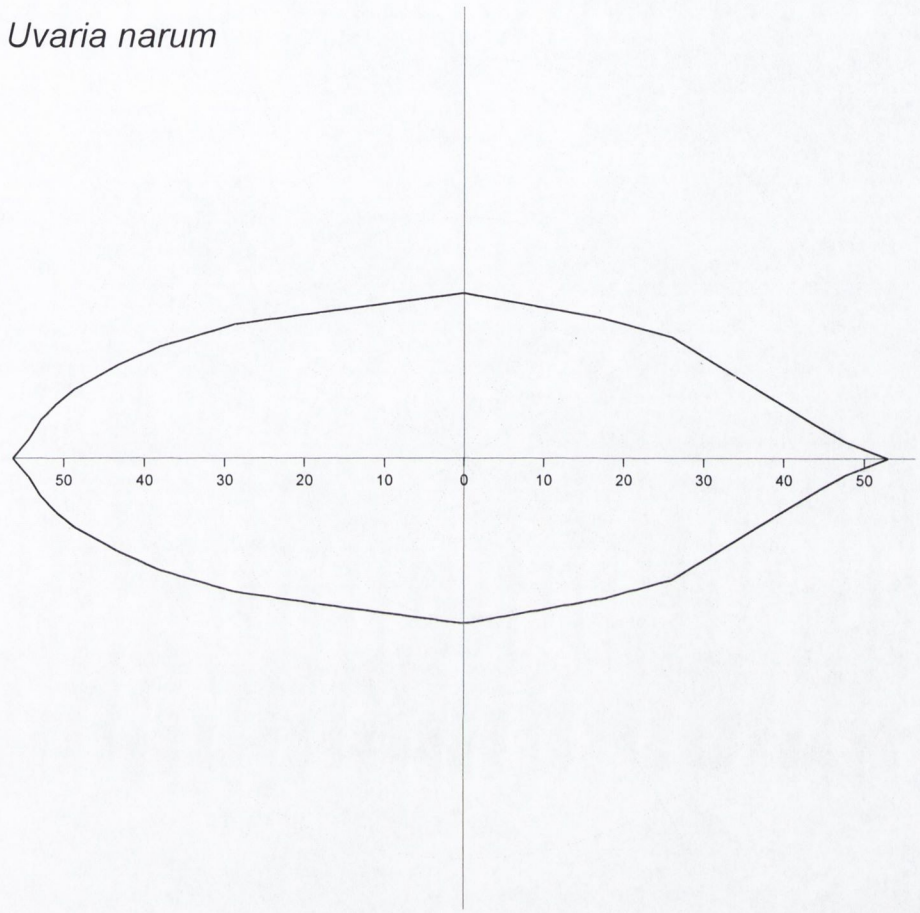


Figure 4.22. Mean leaf outline for *U. narum* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

18. *Uvaria tonkinensis* Finet & Gagnep.

Bull. Soc. Bot. France 53 Mém. 4:74 (1906) *et* Flore Générale de L'Indo-Chine 1:57 t. 9 (1907), type: Vietnam, Mt. Thinh Chan, Ninh Binh, Tonkin, 28/4/1884, Bon 2566 (P-lecto!); *Melodorum vietnamense* Tien Ban, Bot Zhurn. 59:242 (1974).

Syn. nov.; *Uvaria tonkinensis* var. *subglabra* Finet & Gagnep., Bull. Soc. Bot. France 53 Mém. 4:74 (1906) *et* Flore Générale de L'Indo-Chine 1:57 (1907), synypes: Vietnam, Tonkin, 7/12/1883, Bon

s.n.; Vietnam, Tonkin, Mt. But-son, 19/11/1883 & 21/10/1888, s.n. (P n.v.). *Melodorum vietnamense* var. *calcareum* Tien Ban, Bot. Zhurn. 59:242 (1974), type: Vietnam, Cho Ganh, Tonkin, June 1923, Petelot 906 (A-iso, BM, P-holo, US). *Cyathostemma longipes* Craib., Bull. Misc. Inf. (1925), type: Thailand, Ubon Ratchatani Province (Udawn), Pu, 4/3/1924, Kerr 8607 (BM!, K-holo!, P-iso!). *Uvaria subglabra* Merr. & Mete *nom. ined.*, type: China, Hainan, Tsat Cha Ling, Ch'ang-kiang District, 16/5/1933, Lau 1751 (NY-iso!).

Habit climber or scrambling shrub. ***Young shoots*** sparsely tomentose, hairs ferruginous, fine, straggling, 5-10 branched, bark black, striate. ***Leaves*** elliptical-obovate, base retuse, apex acuminate or rarely acute, c. 130-170 x 50-60 mm, thinly coriaceous, waxy; *veins* 9-11, trailing traces fine, not forming distinct sub-marginal vein, interprimaries uncommon, secondary veins short, incomplete, tertiary venation reticulate, fine, dense, visible on both surfaces, midrib depressed abaxially, emergent adaxially, primary veins indistinct or somewhat depressed on abaxial surface, emergent on adaxial surface; *indument* mature leaves completely glabrous above, abaxial venation and blade with sparse indument becoming sub-glabrous or glabrous, hairs fine, 3-10 branched, rufous, 0.6 mm diameter. ***Petiole*** 5-7 x 1.5 mm, black, abaxial groove deep, adaxial surface with prominent transverse foliations, hairs sub-tomentose, becoming sparse, rufous, fine, straggling. ***Inflorescence*** leaf-opposed or sub-opposed, flowers solitary or rarely two or three from young shoots, peduncle 3-5 x 1 mm, pedicel elongate, 35-90 x 1.5-2 mm, flattened medially, striate, sub-glabrous, hairs spreading, 5-10 branched, 0.5 mm, basal bract to 11 x 3 mm with prominent central vein, sub-tomentose to sparse above and below, medial bract very small, c. 1 x 1 mm, ovate acute, tomentose, both bracts usually wanting. ***Calyx*** sepals 3, valvate, free, opening early, remaining small, c. 4.5 mm wide x 2 mm long, surface warted, outer surface with sparse indument, tomentose at margins, inner surface glabrous. ***Corolla*** petals 6, imbricate, yellow-green in colour, erect, concave, outer whorl larger than inner, outer petals c. 8-15 mm wide x 9-15 mm long, broadly ovate, apex bluntly acute to obtuse, base narrowed, inner petals 4-8 mm wide x 6-10 mm long, narrowly ovate acute, base of both whorls fleshy, apex and margins membranous, both surfaces of outer petals tomentose at margins and apex, glabrous at base, outer surface of inner petals tomentose, inner surface basally glabrous, apex tomentose, hairs on all petals ferruginous, very short, almost papillate. ***Stamens*** numerous, c. 2 x 0.4 mm, apex tomentose, locules sessile. ***Carpels*** 3 mm long, stigma elongate, 1 mm long, glabrous, ovary tomentose, hairs ferruginous, 5 - branched, 0.5 mm diameter,

ovules 2. ***Fruit*** monocarps numerous 15-30, green turning red, transversely ovate to glabrous, to c. 9 x 7 mm (1-seeded), 10 x 9 mm (2-seeded), pericarp thin, flaking easily after drying, stipe c. 25-40 x 1.25 mm, finely striate with isolated spreading rufous hairs, seeds 1-2, to c. 9x7x4.5 mm, hilum A-shaped, 1.5 x 1.5 mm. Leaf shape shown in Figure 4.23.

Ecology and Distribution This species appears to be ecologically flexible, growing in dry disturbed forest vegetation as well as in evergreen forest. Distributed from Hainan (no records from mainland China) through northern Vietnam into Laos and Northeast Thailand. Distribution is shown in Figure 4.52.

Notes Examination of the type material for *U. longipes* confirms it is the same taxon as *Uvaria tonkinensis*. Leaf characters have been used to distinguish the varieties *U. tonkinensis* var. *calcareum* and *Melodorum vietnamense* var. *subglabra*, however in both cases these characteristics are not sufficiently distinctive to warrant varietal status. There is considerable variation in pedicel length between various specimens, however this variation does not appear to be correlated with any other character differences nor with a particular geographic distribution.

Material Examined

China *Hainan*; Tsat Cha Ling, Ch'ang-kiang District, Lau 1751, 15/05/29 (fl.) (P, NY); Yaichow, How 71129, Jun-29, (fr., fl.) (NY); 700ft., How 70607, June 1929, (fl.) (NY); *locality unclear*; Wang 33476, 01/08/29 (fr.) (NY); Liang 62397, 04/08/29 (fr.) (NY).

Vietnam *Son La Province* (V - 3 - CLV); Montains Thinh - Chau (H.N.), Bon 2566, 28/4/1884 (fl., fr.) (P); *Langson Province* (V - 9 - CLV); near Thanh Nai, Petelot 6421, 11/05/34 (fl.) (P, NY); *Province unclear*; Tonkin, Cho Ganh, Petelot 906, 31/05/19, "bateaux calcaeris" (fl.) (P).

Laos *Vieng Chang Province* (L - 9 - CLV); Kam Yuak, c. 300m, Kerr 21257 , 24/04/28, (fl.) (L, P).

Thailand *Ubon Ratchatani Province* (35 - E); Pu, Kerr s.n. & 8607, 04/03/20, (fl.) (BM, K, P).

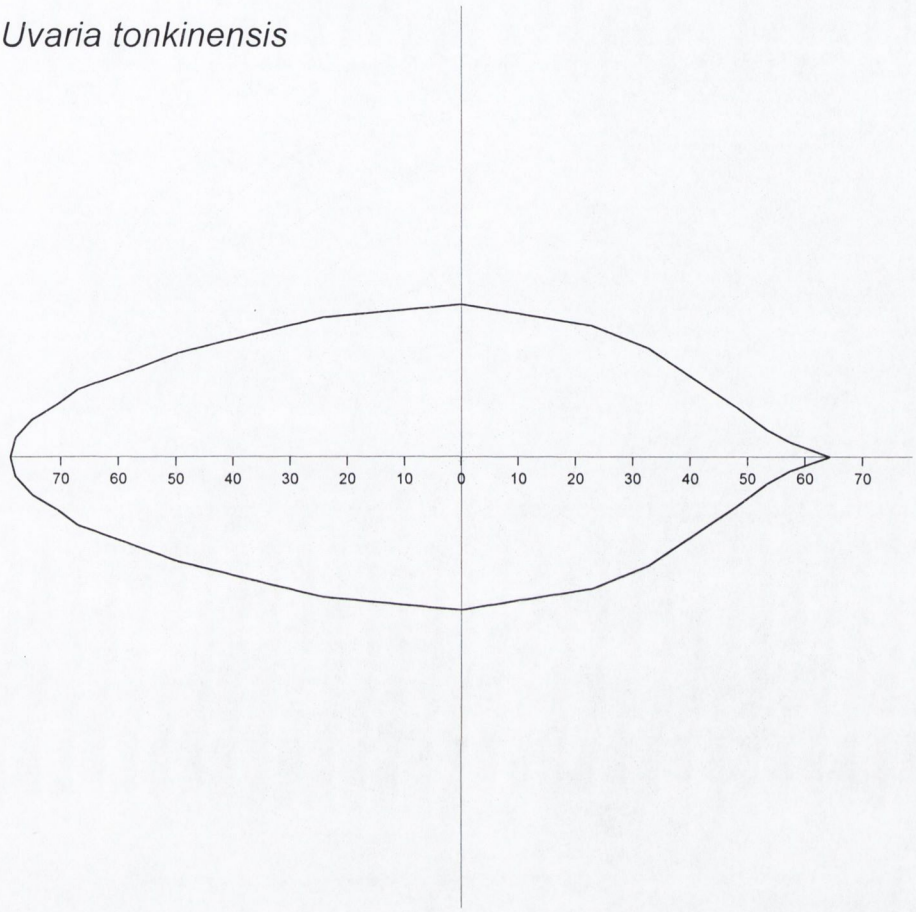


Figure 4.23. Mean leaf outline for *U. tonkinensis* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

19. *Uvaria boniana* Pierre ex Finet & Gagnep.

Bull. Soc. Bot. France 4:71 (1906), lectotype (*designated here*): Vietnam, 'Ha-Tay Province, Nin-thai, 17/9/1888' *Bon* 3956, (P!, G!), syntypes: Vietnam, 21/5/1889 *Bon* s. n. (P!), Quang Ninh Province, Quang-Yen, 5/1886 *Balansa* 4185, (K!, P!); Jovet-Ast, Supplément a la Flore Générale de L'Indochine 1:39 (1938), Gagnepain, F. ed. Li P-T, Acta Phytotax. Sinica. 14:106 (1976).

Habit sarmentose shrub to 2.5 m or woody climber to 20 m, crown a dense network of twining branchlets, the latter particularly evident in open thickets. ***Young shoots*** sub-glabrous to glabrous with occasional c. 1 mm diameter pale stellate hairs, bark black, striate, shiny. ***Leaves*** elliptic-obovate, (50-)80-110 x (20-)35-40 mm, apex narrowly acute-acuminate, base cuneate, membranous, both surfaces shiny; veins c. 8-10, bifurcation often at mid-point between midrib and margin, leading and trailing traces equal or leading trace somewhat stronger, tertiary venation reticulate, midrib somewhat depressed above, emergent below, primary veins and microvenation somewhat raised above and below, clearly visible on both surfaces; *indument* leaf blade glabrous on both surfaces, abaxial midrib with sparse 2-5 branched hairs, adaxial midrib sub-glabrous. ***Petiole*** 4-5 x 1 mm, glabrous except for sparse hairs along abaxial groove. ***Inflorescence*** flowers 1(-2), leaf-opposed; pedicel c. 40 mm long, diam. c. 1 mm at base and apex, 0.5 mm or less medially, surface black, shiny and striate with scattered pale stellate hairs, bracts small and indistinct, to c. 2 x 1 mm, ovate, usually wanting. ***Calyx*** sepals 3, valvate, connate at base, broadly ovate to triangular, apex rounded, c. 2.5 x 3.5 mm, reflexed basally, apex remaining incurved, inner and outer surfaces red-green drying black, glabrous centrally with ferrugino-tomentose margins especially prominent on inner surface, often persistent. ***Corolla*** petals 6, red drying black, thickened centrally and basally, thinner toward margins; outer whorl c. 8 x 7 mm, 1.5-2 mm thick, ovate, rounded apically, concave, inner whorl c. 8 x 5 mm, 1-1.5 mm thick, obovate, apex bluntly acute to rounded, concave, base more constricted and narrower than outer whorl; both whorls ± glabrous and leathery on external surface, short stellate indument on margins and towards apex, inner surface with short ferrugino-tomentose indument most dense at apex and margins, sparse towards centre and glabrous at base, imprint of connectives and stigmas often prominent in indument of central basal area, both whorls remaining erect and incurved. ***Stamens*** numerous, c. 1.5-1.7 mm long, connective cap flat/discoid/convex, indument dense, blunt, sometimes present on external ridge of connective, locules full length, staminodes not present, outermost whorls of stamens reduced in size to c. 1.2–1.5 mm with connective cap extending as ridge on external side. ***Carpels*** numerous, c. 3 mm long, ± erect at centre of gynoecium, incurved toward margin, ovary with dense indument of combed stellate hairs, stigma to 0.75

mm long, glabrous, U-shaped in section, lobes narrow, ovules 6-8 in 2 rows. ***Fruit*** monocarps 25-45+, ovoid, ellipsoid or shortly cylindric, c. 15-17(-20) x 11(-13) mm, ± basally attached, occasionally with a prominent apicule, green turning red/purple at maturity, drying brown/black, surface somewhat warty with short, scattered, stellate hairs, pericarp c. 2 mm thick, soft and juicy when ripe, stipe c. 35-45 mm long, 1 mm in diameter, surface black/brown, striate with scattered short c. 0.75-1mm diameter stellate hairs as for pedicel; *seeds* 4-6, 10 x 7 x 4 mm, laterally attached in 2 rows, aril thickened above the raphe on one side, hilum v-shaped, testa brown, shining, ruminations visible. Leaf shape shown in Figure 4.24.

Ecology and Distribution Confined to northeast Vietnam and Gaundong, Guangxi and Hainan Provinces of Southern China. *Uvaria boniana* is typically found in evergreen and semi-deciduous forest and scrub from sea-level to 850 m. In forest habitats it can grow to 20 m, reaching well into the canopy, and unusually for the Uvarieae, has been collected several times scrambling over rocks in scrub vegetation on steep open hillsides. Distribution is shown in Figure 4.53.

Notes The dense twining habit of crown branchlets is distinctive, as are the waxy and almost entirely glabrous leaves. This species is a close relative *of Uvaria tonkinenis* but distinguished from this species by its much shorter, narrower pedicels, smaller, less broadly ovate petals and smaller, more delicate leaves. The two are also separated geographically, with *U. tonkinensis* extending from north central Vietnam through Indochina to western Thailand. *Uvaria orientalis* is very similar to *U. boniana*, exhibiting all the floral characters of the latter, but in miniature.

Vern. Vietnam, 'trong tua' (Bon 3956); Hainan 'pat kok shue' (Tsang 815).

Material Examined

China *Hainan*; Shek Mang Tai Shan, 02/08/33, Tso 23506 (fr.) (NY); Taam-chau District, Tiu Lung Shan, 11/09/27, Tsang 815 (fl.) (NY); Wontungshan, 07/08/30, Chun 21983 (fr.) (NY); Yaichow, 21/08/33, Liang 62759 (fl.) (K, NY); 10/10/33,

Liang 63446 (fl.) (NY); 13/06/58, *Wei* 20501 (fr.) (PK); 02/08/33, Wang 33547 (fl.) (NY, P, PK); *Guandong*; Luo-fu Shan, 23/09/78, K'tung 78 (fl.) (L); Shap Man Taai Shan, Tang Lung Village, SE. of Shang-sze-Kwangtung border (Shang-sze District), 10/08/34, Tsang 23995 (fr.) (NY), 30/07/34, Tsang 23823 (fl.) (NY); Ting Wu Shan, 26/09/63, Ting 1039(fl.) (L); Wan Tong Shan, Ying Tak District, 24/06/32, Tsui 387 (fr.) (K, NY, US); Tsang 14467 (fl.) (NY); *Guangxi*; Me-Kon, She-Feng Dar Shan, S. Nanning, 05/11/28, Ching 8440, (fr.) (NY).

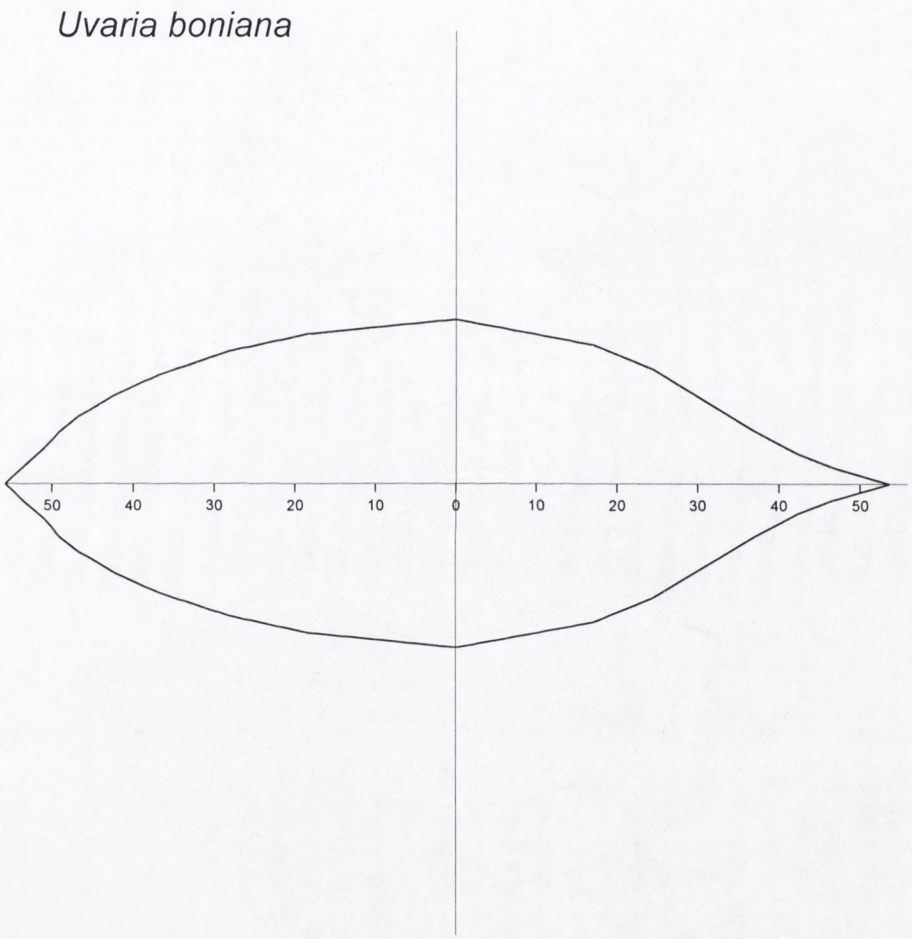


Figure 4.24. Mean leaf outline for *U. boniana* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Vietnam *Ha-Tay Province* (CLV-13-V); Ninh-Thai, 17/9/1888, Bon 3956 (fl.) (P, G); Ninh-Thai, 11/8/1889, Bon s.n. (fl.) (P); *Quang Ninh Province* (CLV-10-V); near Quang-Yen, 5/1886, Balansa 4185 (fr.) (P, K); *Location unknown*; Petelot 6057 (fr.) (P); Ban 45 (fl.) (HN); Ban 116 (fr.) (HN).

20. *Uvaria orientalis* (Jovet-Ast) C. Meade *nom. nov.*

Uvaria flexuosa Jovet-Ast, Supplément a la Flore Générale de L'Indochine, 1:64 *et* Notul. Syst. (Paris) 9:73 (1940), type 'Annam, Massif de la Mere et L'Enfant 5/1923, Poilane 6781' (holo P!, iso HCMC!) *nom. illegit.*

Non est Uvaria flexuosa Heyne ex Wallich *nom nud.*

Habit climber with small leaves, crown a dense network of twining branchlets. ***Young branchlets*** sparse indument of c. 12+ branched rufous hairs, becoming glabrous, surface black, foliated, smooth and shiny. ***Leaves*** narrowly elliptical to lanceolate, base cuneate, apex narrow, tapering, acute-acuminate, c. 70-75 x 20 mm; *veins* c. 10-13, branching early, trailing trace fine, hardly distinct from reticulate tertiary venation, secondary veins present but never complete, midrib triangular in TS, somewhat depressed above, not curving inward at contact with blade below; *indument* abaxial surface glabrous except for tomentose hairs over midrib and sparse ring of hairs on margin, adaxial surface glabrous except for sparse 6-10 branched c. 0.25-0.35 mm diam. spreading hairs on midrib. ***Petiole*** 2-6 x 0.75 mm, sub-tomentose to sparse, hairs rufous, c. 12+ branched, 0.5 mm diam., becoming sub-glabrous, shiny, black, transversely foliated. ***Inflorescence*** flowers solitary, leaf-opposed or supra axillary, peduncle sub-sessile, c. 1-2 mm long, pedicel c. 30 mm long, very narrow, c. 0.35-0.45 mm diam., smooth and shiny, black with sparse rufous hairs as for shoots pedicel with single basal obovate to round c. 3 x 3 mm bract with hairs on margin and midrib, venation prominent. ***Calyx*** sepals 3, valvate, broadly ovate, c.1 x 1 mm, tubercled, with sparse 10+ branched spreading rufous hairs, dense at margin. ***Corolla*** petals 6, inner whorl narrower than outer, outer whorl ovate, 4.5 mm long x 3 mm wide, inner whorl obovate with narrowed base, 5 mm long x 2.5 mm wide, inner and outer surface of both whorls basally sub-glabrous with tomentose margin and apex. ***Stamens*** numerous, c. 1.2 mm long, connective apex enlarged, club-shaped, broad, papillate, locules stipitate. ***Carpels*** numerous, c. 2 mm long, ovaries hairy on ridges and apex, stigmas glabrous, U-shaped, elongate, ovules 6. ***Fruit*** not known. Leaf shape shown in Figure 4.25.

Notes The name chosen by Jovet-Ast (1940, above) for this taxon, *Uvaria flexuosa*, had already been validly published as part of Wallich's Catalogue in 1832. The new epithet '*orientalis*' derives from the collecting locality, on the eastern coast of Indochina. This species is known only from the type collection. There is little discrete character difference between this specimen and *Uvaria boniana* other than the much smaller size of all organs in *U. orientalis*. However, it is very unusual in the Uvaria group to see both young leaves and young flowers growing together on the same new shoots. It must be assumed therefore that the smaller leaves of *U. orientalis* are not a juvenile form, but are distinctive for the species. For this reason it seems wise to retain *U. orientalis* until more material becomes available. Distribution is shown in Figure 4.52.

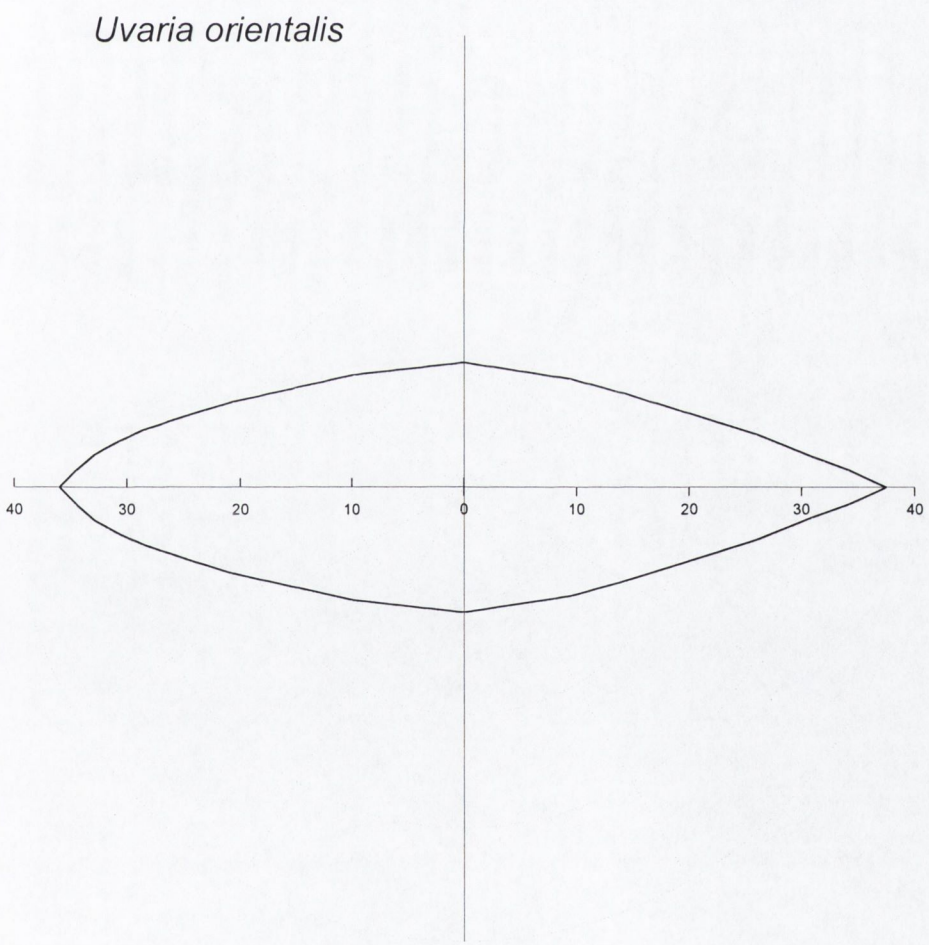


Figure 4.25. Mean leaf outline for *U. orientalis* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Material Examined

Vietnam *Quang Tri Province* (V–25-CLV); Massif de la Mere et L'Enfant 5/1923, Poilane 6781 (fl.) (HCMC, P).

21. *Uvaria pierrei* Finet & Gagnep.

Bull. Soc. Bot. France 52, Mém.4(2):64 (1906) *et* Flore Générale de L'Indo-Chine 1:56 t. 8 (1907), lectotype (*designated here*): Cambodia, 'Harmand, s. n., bords de la riviere Pursat, 6/1876' (P!); syntypes: Cambodia; 'Godefroy 48 Pnom-penh, Cambodge 29 Mai 1878' (P!, HCMC!), Vietnam: 'Pierre 1789. mont Dinhs, prov. de baria, Cocochine, 6/1871' (A!, BM!, HCMC!, K!, P!); Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):308 (1991).

Habit Scandent shrub or climber. ***Young shoots*** sub-tomentose, hairs c. 10- branched, becoming sub-glabrous and striate with distinct white lenticels. ***Leaves*** distinctively narrow-oblong, base retuse, apex obtuse or retuse, c. 45-90 x 17-35 mm, coriaceous, often shiny, leaf margin turned downward; *veins* c. 12-14, short, interarching midway between midrib and margin, indistinct, inter-primaries frequent, secondary veins indistinct from reticulate tertiary venation; *indument* adult leaves almost completely glabrous; abaxial midrib with sparse erect stellate hairs near base, midrib apex and blade glabrous, hairs on adaxial midrib and veins sparse to sub-glabrous, blade glabrous. ***Petiole*** c. 3-4.5 x 1.25 mm, distinctly broader than midrib, indument sparse. ***Inflorescence*** leaf-opposed or sub-opposed, flowers 2, often with one bud dormant, peduncle c. 3-4 mm, tomentose to sub-tomentose, pedicels c. 10mm, often transversely flattened with longitudinal groove, broadly ovate-acute, c. 2.5 x 4 mm diam., clasping, outer surface sub-tomentose, inner surface sub-glabrous. ***Calyx*** sepals 3, valvate, opening early, sepals broadly ovate, acute, c. 2.25 x 4.5 mm, sometimes reflexing at maturity, remaining concave, outer surface tomentose at base with thick ferruginous hairs, becoming sparse towards apex, at margin tomentose with fine, paler-coloured hairs, inner surface glabrous except for tomentose margin. ***Corolla*** petals 6, purple, narrowly ovate to broadly elliptical, base constricted, apex

obtuse or very bluntly acute, c. 4.5-5.25 x 4-4.5 mm, fleshy, thickened basally, inner whorl somewhat smaller than outer, both whorls remaining erect, hardly expanding, often infolding along longitudinal axis upon drying, indument sparse on both surfaces of both whorls, becoming more tomentose at margin, hairs fine, spreading. ***Stamens*** numerous, c. 1 mm long, connective apex flat, angle with main axis varying, locules full length. ***Carpels*** c. 40, 1.75 mm long, ovaries 5-sided, ridges and neck hairy, stigma large, c. 0.6 x 0.4 mm, broad and elongate, U-shaped, glabrous, with prominent longitudinal slit, ovules 4-6 in 2 rows. ***Fruit*** monocarps c. 5 – 15, green maturing yellow then purple, globose or ovoid, c. 17.5 x 12.5 mm, sub-glabrous, smooth or very finely tuberculate, pericarp fleshy, stipe c. 7 – 12 mm, somewhat striate, sub glabrous, seeds 2-4, up to c. 12 x 9 x 4 mm at maturity, aligned longitudinally within monocarp. Leaf shape is shown in Figure 4.26. Appendix 4.12A & B.

Ecology and distribution Confined to the Mekong basin below Loei. Often observed as a shrub. Distribution is shown in Figure 4.53.

Notes The peculiar oblong leaves of this species make it instantly recognisable. The only species in Continental Asia whose leaves resemble it in any way is *Rauwenhoffia siamensis*, however this species can be distinguished from *U. pierrei* by its large yellow flowers and sub-sessile fruits. The longitudinal alignment of seeds in the mature monocarp appears to arise as a result of the non-expansion of tissue between seed attachments after fertilisation, causing the seeds to rotate within the monocarp as they grow. *Uvaria goloensis* Merr. from the Philippines is very similar morphologically.

Vern. *Thailand*; Loei; Thai: 'Phee Phuan' (Smitinand p. 101); *Laos*; Champasak Province; Lao: 'Ngaw keuah' (Maxwell 98-946).

Material Examined

Vietnam *Baria-Vung Tau Province* (V – 41 – CLV); Mont Dinh, Baria, Jun. 1866, Pierre 1789 (fl.) (A, BM, K, P).

Laos *Champasak Province* (L – 15 – CLV); summit of Hang Kohn Hill, S. tip Khong Island, Khong District, 14-9-98, Maxwell 98-946 (fr.) (CMU).

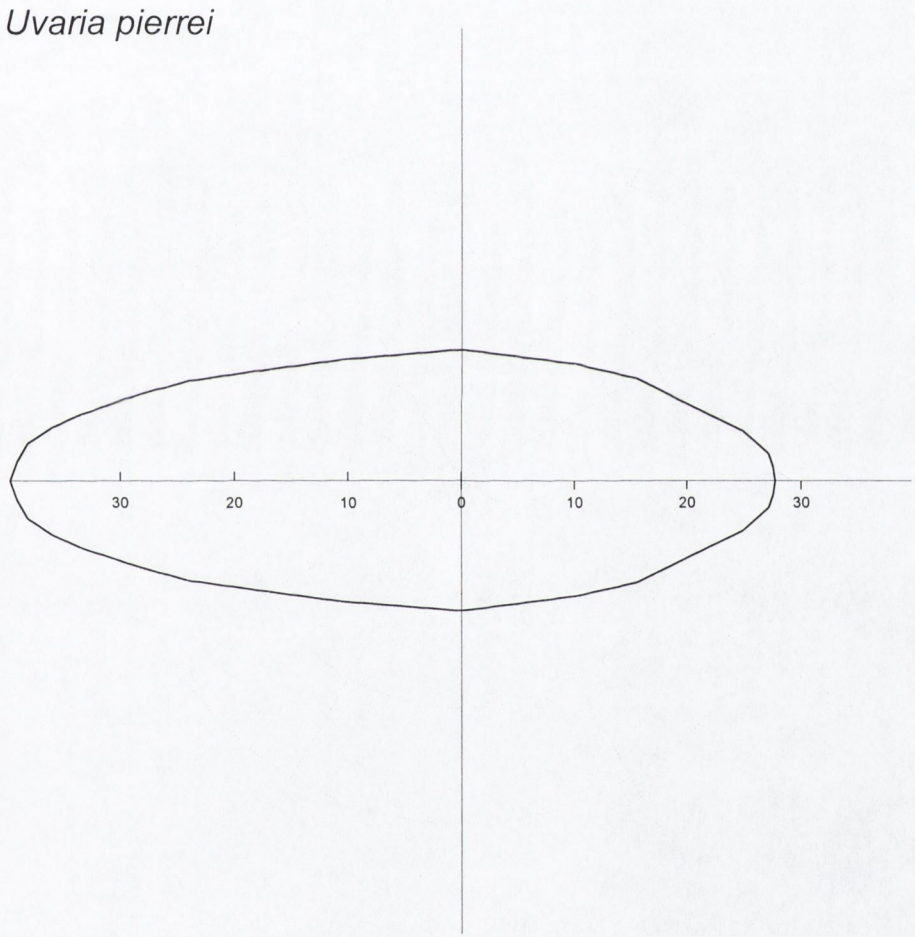


Figure 4.26. Mean leaf outline for *U. pierrei* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Cambodia *Pursat Province* (C – 10 – CLV); 'Coastal forest, Pursat', Jun. 1876, Harmand s.n. (fl.) (P); Pursat, Jun. 1878, Godefroy s.n., (fl.) (K, P); *Kampong Cham Province* (C – 12 – CLV); Campong Long, 1866-68, Thorel 2063 (fl.) (P); *Kandal Province* (C – 15 – CLV); Pnam Penh, 24/5/1878, Godefroy 48 (fl.) (P); *Location unknown;* Mangen s.n. (fl.) (P).

Thailand *Ubon Ratchatani Province* (32 – E); in cultivation, NE Botanic Garden, Ubon Ratchatani, 17/10/98, Meade 98-10-17 (fr.) (TCD); *Locality Unknown*; BKF 5260 (fl.) (BKF).

22. *Uvaria micrantha* (A.DC) Hook. f. & Thoms.

Fl. Ind. 1:103 (1855) *et* Fl. Br. Ind. 1:51 (1872); Miq., Fl. Ned. Ind. 1:22 (1859); Kurz, Forest Fl. Br. Burma 1:29 (1877); King, J. As. Soc. Beng. 61(2)1:21 (1893) *et* Ann. Roy. Bot. Gard. Calc. 4:26, t. 18 (1893); Finet & Gagnep. *in* Bull. Soc. Bot. France 52, Mém. 4 (2):70 (1906) *et* Flore Générale de L'Indo-Chine 1:54 (1907); Merr., Philipp. J. Sci., C 10:230 (1915) *et* Enum. Philipp. Pl. 2:155 (1923); Ridley, Fl. Mal. Pen. 1:33 (1922); Craib, Fl. Siam. Enum. 1:30 (1931). *Guatteria? micrantha* A. DC. Mem. Anon. 5 (1832), type: 'Wallich Cat. 6449 ad Amhearst, Burma' (holo- *Herb. Wall.* K!, Iso- BM!). *Cyathostemma micranthum* (A.DC) Sincl., Gard. Bull. Sing. 14(2):225 (1955). *Polyalthia fruticans* A.DC., Mem. Anon. 42 (1832), type: Myanmar, 'Gomez, Wall Cat. 6430, Burma, Tavoy 1827' (*Herb. Wall.* K!, BM!). *Anaxagorea sumatrana* Miq., Fl. Ned. Ind. Bat. (suppl.) 382 (1861), type: Sumatra, 'Sumatra austr. in Lampong prope Tega-nennin, leg. Teijsmann' (L!). *Uvaria sumatrana* (Miq.) Hook. f. & Thoms., Fl. Br. Ind. 1:51 (1872). *Cyathostemma sumatrana* (Miq.) Boerl., Icon. Bogor. 1:42 (1899). *Popowia nitida* King, J. As. Soc. Beng. 61(2)1:92 (1893), type: Andaman Is., 'Kurz, S. Andamans, Hobdaypur, 4/7/1891' (G!).

Habit climber or scrambling shrub with narrow tangling branches forming dense thicket. ***Young shoots*** sub-tomentose, hairs 5-6 branched, striations appearing early. ***Leaves*** elliptical to shortly lanceolate to narrowly obovate, base cuneate, apex acuminate-acute, c. 70-120 x 20-40 mm, thinly coriaceous, waxy, drying dark brown above and below; *veins* 9-12 (or up to 16 with long acuminum), trailing trace fine, not forming distinct sub-margin, inter-primaries frequent, prominent, secondary venation

poorly developed, tertiary venation reticulate, indistinct above, distinct but not emergent below; *indument* blade glabrous above and below, abaxial midrib initially with erect 2-3 branched subtomentose hairs, becoming sparse towards apex and with age, lower side with isolated c. 1-2 branched hairs clinging to midrib, always aligned toward leaf apex. ***Petiole*** 2-3(-4) x .75 mm, hairs sub-tomentose ferruginous, 3-6 branched. ***Inflorescence*** leaf-opposed, floral buds 1-3, often only the primary flower opened, the others enclosed by bracts, peduncle sub-sessile, c. 1.5(-2) mm x .075 mm diam., pedicel c. 2-4(-5) x 0.5 mm, basal bract ovate, 4-6 x 1-2(-4) mm, medial bract smaller, ovate-acute, to 1.5 x 2 mm, peduncle and pedicel flattened with prominent ridges, ferrugino-tomentose, hairs 5+ branched, basal bracts tomentose on outer surface when young, becoming sparse centrally, inner surface glabrous except for sparse indument at margins. ***Calyx*** sepals 3, valvate, broadly ovate-acute, c. 2 x 2.75 mm, concave, outer surface tomentose, becoming sparse at maturity, hairs pale, 3-5 branched, margin tomentose, inner surface glabrous and warty around base and central area, hairs tomentose toward margin. ***Corolla*** petals 6, green-yellow to maroon in colour, outer whorl larger than inner, outer petals ovate-oblong, apex bluntly acute to narrowly obtuse, c. 3.25 x 2.5 mm, inner petals broadly elliptical with distinctly constricted base, c. 3.35 x 2 mm, apex as for outer petals, both whorls thick and fleshy, concave, reflexing at maturity to clearly expose stamens and carpels. ***Stamens*** numerous, c. 0.6-1 mm long, connective flat, cap-like, angle to main axis variable, papillate, locules full length. ***Carpels*** c. 20, 0.8-1.5 mm long, erect or bent inward at margin of gynoecium, ovaries angular/ridged due to compression in gynoecium, hairy along ridges and just beneath stigma, hairs fine, many-branched, stigma U-shaped, glabrous, somewhat elongate, ovules 2(-4). ***Fruit*** monocarps 10 - 20, green turning yellow, globose to shortly oblong, c. 9.5 x 8 mm at maturity, pericarp fleshy, becoming thin and black after drying, stipe c. 14-20-(-23) mm, glabrous, smooth, *seeds* 1-2(-3), c. 7 x 4 x 4 mm when in single-seeded monocarp, to 7 x 4 x 2 mm when 2-3 seeded, aril 2.5 x 1.75mm, triangular, hilum A-shaped. Leaf shape shown in Figure 4.27. Appendix 4.13A.

var. *elongata* C.Meade *var. nov.*

Type: 'E. Kalimantan, KPC coal mining company, Sangatta, 20m, 14/04/95, Kessler 1180' (Holo- TCD! Iso- L!).

A varietas typicus pediceliis elongatis differt. Differs from the typical variety of the species in having a distinctly elongate pedicel and different flowering pattern.

Inflorescence floral buds opening in close succession, often with 2 open together, peduncle c. 5 mm long, pedicel (5-)10-12mm long, narrower and not as flattened as the typical variety.

Distribution and Ecology *Uvaria micrantha* has a wide distribution from Northern Vietnam through Indochina and Malesia (including the Andamans) to New Guinea. Var. *elongata* is predominant from Borneo eastwards, with both varieties occurring in Sumatra and Peninsular Malaysia. Although there are some records from open dipterocarp forests in central Thailand, this species is usually found in wetter habitats near watercourses or in wet evergreen forests. Distribution is shown in Figure 4.54.

Notes Sinclair (1955) transferred *U. micrantha* to *Cyathostemma* on the basis of its petal aestivation. Close examination of living specimens makes it clear that the petals of *C. micranthum* are imbricate along the entire margin and become reflexed at maturity, which is very different from the basally valvate, unopening corolla typical of *Cyathostemma* as originally described by Griffith (1854).

Vern. *Laos*; Savannakhet, Lao: 'Tinh Thang'; Khmer: 'Phka Ousel' (both Poilane 16375); *Thailand*; Prachaup Khiri Khan 'Nom maeo' (Smitinand p. 101), Prachin Buri 'Namtao noi' (Smitinand p. 101).

Material Examined

India *Andaman Islands*; South Islands, Kurz s.n. (fl.) (G, P); Helfer 433 (fl.) (A, P).

Myanmar *Taninthari* (Tennasserim); Amhearst, 01/01/09, Wall Herb. Cat. 6449 (fl.) (BR, K); Tavoy, 01/01/09, Wall. Cat. 6430, W. Gomez (fl.) (BM, Herb. Wall. K); Singkon, Mergui, 50m, 3/6/32, Kerr 21660 (BK).

Vietnam *Thua Thien Hue Province* (V – 26 – CLV); Hue, Aug. 1887 Harmand in Pierre 1837 (P); *Ninh Thuan Province* (V - 36 - CLV); Cana, 24/10/25, Poilane 12426 (fl.) (A, HCMC); *Dong Nai Province* (V – 40 – CLV); Nui Chua Chan, 23/8/31, Poilane 19371, Poilane 19373 (HCMC); Nui Chua Chan, 22/8/31, Poilane 19368 (HCMC); Boa Chang, near Bien Hoa, Sept. 1867, Pierre 209 (P); *Baria-Vung Tau Province* (V – 41 – CLV); 1866, Pierre 209 (HCMC); *Ho Chi Minh City* (V – 42 – CLV); Aug. 1864, Lefevre 332 (P); *An Giang Province* (V - 47 - CLV); Chao Doc, August 1867, Pierre 209 (fl.) (A, NY); *Location Unknown*; Fl. Vietnamica 592, 2/7/89; Bo Hong Phuc in Fl. Vietnamica 280 21/8/87 (HN).

Laos *Champasak Province* (L – 15 – CLV), Khong District, Sahong Island, E. side, along banks of Mekong River 15/10/97, Maxwell 97-1184 (fl.) (CMU); *Savannakhet Province* (L – 12 – CLV); Ban That, 19 km from Savannakhet, 3/7/29, Poilane 16375 (A, P).

Cambodia *Siem Reap Province* (C – 7 – CLV); Pnom Bakheng, 06/06/38, Poilane 27210 (A, HCMC, P); Angkor, c. 1866, Thorel 989 (P); *Kampong Cham Province* (CLV - 12 - C); Vo Kra Van, north of Memot, 28/06/28, Poilane 15367 (fl.) (A, HCMC); *Kampong Speu Province* (CLV - 17 - C); 08/06/30, Poilane 17488 (fl.) (A, NY); *Kampot Province* (C – 19 – CLV) Kampot, Mar. 1874, Pierre 209 (P).

Thailand *Uttaradit Province* (9 - N); Nakawn Dai, 200m, 17/04/22, Kerr 5862 (fl.) (BK, TCD); *Nakhon Ratchasima Province* (26 – E) Bua Kao, Korat, 7/11/31, Put 4316 (BK); *Sisaket Province* (31 – E); Kantaralak District, Dongrak range, Chong Bat Lak, 600m, 18/8/76, Maxwell 76-540, (fl., fr.) (BK); *Phetchaburi Province* (36 - SW) Kaeng Krachen NP, track to Thorthip Waterfall, 500m, 26/08/95, Parnell et al. 95-467 (fr.) (TCD); *Prachuap Khiri Khan Province* (40 - SW); Bangsaphan, 11.10N 99.4E, 29/12/27 Put 1421 (fl.) (BK); Hua Hin, 01/10/27, Collins 1582 (fr.) (US); Huai Yang, 2/10/30, Put 3173 (BK); *Chonburi province* (55 – SE); Siricha District, Kew

Kiee, 150m, 9/5/75, Maxwell 75-396 (fl.) (BK); Sriracha, 01/04/20, Kerr 4151 (fl.) (BK, TCD); Siricha District, Khao Khieo, 200m, 12/6/76, Maxwell 76-390 (BK); Sattahip District, Toong Brong, 50m, 10-6-71 Maxwell 71-425 (fl.) (BK); *Sa Kaeo Province* (56 – SE); Aran Pratet, 15/9/30, Put 3137 (fr.) (BK, TCD); *Chanthaburi Province* (57 – SE); Bong Nam Rawn District, North Khao Soi Dow, 200m, 6/5/75, Maxwell (fl.) (BK); *Surat Thani Province* (61 – Pen.); Kaw Lao, 20/7/27; Kerr 12966 (fl.) (BK, TCD); Ban Ha, 7/9/27, Yuang 23 (BK); *Nakhon Si Thammarat Province* (65 - Pen); Khoa Luang N. P., Ka Rom waterfall, Lau Saka, 05/12/72, Santisuk 303 (fr.) (BKF); Ko Tao, 15/04/27, Kerr 12761 (-) (BK, L); *Songkhla Province* (69 - Pen); Lem Son, alt <50m, 10/4/28, Kerr 15133, (fl.) (BK, L, TCD); *Pattani Province* (70 – Pen.); evergreen forest, 50m, Kerr 7843 (fl.) (BK); *Yala Province* (71 – Pen.); Banang Sata, 200m, 31/7/28, Kerr 7419 (BK).

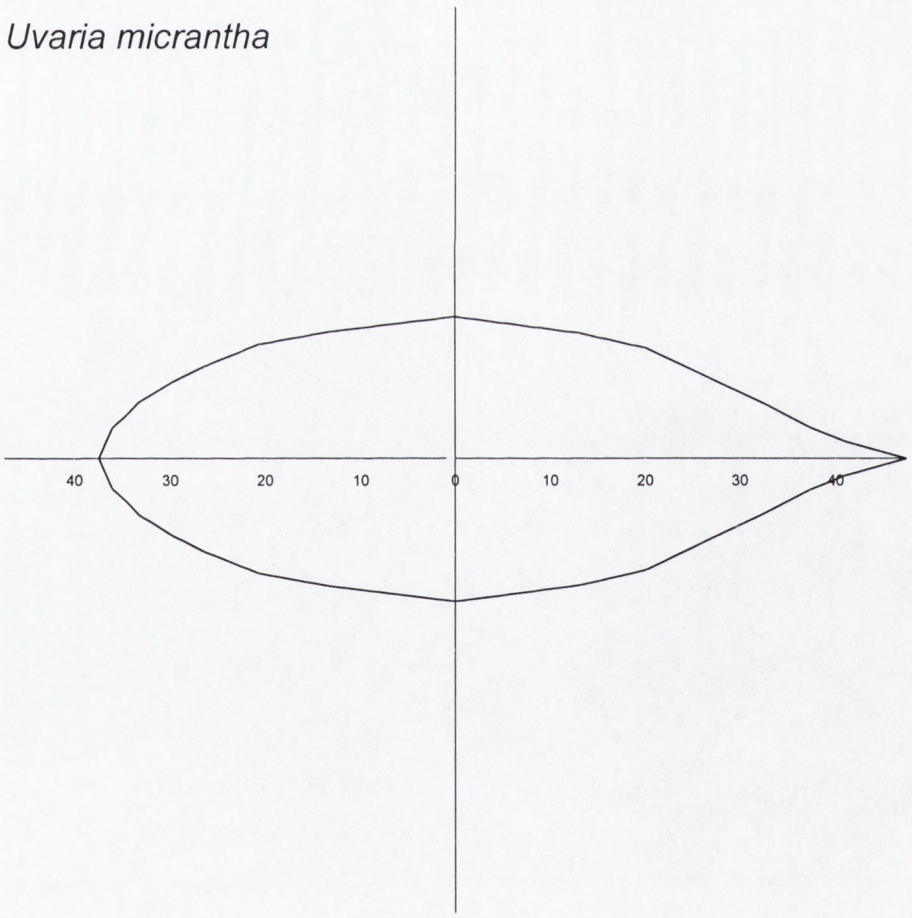


Figure 4.27. Mean leaf outline for *U. micrantha* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Var. *elongata*

Malaysia *Sarawak*; 01/11/20, Agama 1081 (A).

Indonesia *Bali*; Tirladjaja Kusuma, 30/05/64, Diling 1034 (fl.) (A); *Kalimantan*; E. Kalimantan, KPC coal mining company, Sangatta, 20m, 14/04/95, Kessler 1180 (fl.) (TCD, L); *Sumatra*; Lampang , Teijsmann 4383 (fl.) (A).

Phillipines *Busuanga*; 01/09/22, Ramos 41225 (A, BK); *Luzon*; 01/09/16, Elmer 14397 (-) (A, NY); *Palawan*; Bataraza Municipality, at Gamayon, on Tuba - Sumbling road, 24/06/94, Soejarto et al. 8551 (fl.) (A); Ibangley, Brookside Hill, Pagdanan Range, 40m 24/04/84 Podzorski SMHI 978 (fr.) (A); Takdua Zigzag, 35-40km from Puerto Princesa, 30/07/88 Soejarto & Reynoso 6242 (fr.) (A); Tatanoram, base of Mt. Beaufort, Irawan river valley, Puerto Princesa municipality 04/04/89 Soejarto *et al.* 6407 (fl.) (A, L, NY); Tatanoram, base of Mt. Beaufort, Irawan river valley, Puerto Princesa municipality 04/04/89, Podorski SMHI 2171, SMHI 1866 (fl.) (L); TayTay, 01/05/13, Merrill 9271 (fl.) (A, NY); *Tawitawi*; Sulu Province, 01/08/24, Ramos & Edano 44124 (fr.) (A, NY).

Papua New Guinea Kangsia, Papua, 0m, 02/02/35, Carr 11088 (fl.) (L, NY).

23. *Uvaria kerrii* C. Meade *sp. nov.*

Uvaria a folia anguste-ovata ad elliptica, basi retusa, apice acuta, c. 150 x 50 mm, inflorescentia ramosa, cauliflorum, multiflora, pedunculus curtus, pedicellus elongatus, tomentotus et bibracteatus, bractea basalis ovatis, persistens, c. 4 x 3 mm, amplectens, bractea medianus deciduus, sepala concava, ovata, cuspidata, coriacea, c. 5 x 7 mm, petala concava, ovata, acutiusucula, coriacea, petala externa c. 9 x 7 mm, interna c. 8.5 x 6.5 mm, stamina numerosa, glabra, c. 5 mm longa, carpella c. 50, ovaria tomentosa, c. 4 mm longa, stigmata elongata, angustata, glabra, c. 1 mm longa, ovula circiter 16.

Uvaria having narrowly ovate to elliptical c. 150 mm long x 50 mm wide leaves with retuse base and acute apex; inflorescence branched, cauliflorous, many-flowered, peduncle short; pedicel elongate, tomentose and with two bracts, basal bract ovate, persistent, c. 4 mm long x 3 mm wide, clasping, medial bract deciduous; sepals concave, ovate, cuspidate, coriaceous, c. 5 mm long x 7 mm wide; petals concave, ovate, broadly acute, coriaceous, external petals c. 9 mm long x 7 mm wide, internal petals c. 8.5 x 6.5 mm; stamens numerous, glabrous, c. 5 mm long; carpels c. 50, ovaries tomentose, c. 4 mm long, stigmas elongate, narrowed, glabrous, 1 mm long, ovules about 16.

Holotypus: Thailand, Prachuap Khiri Khan, Khao Luang, c. 400m, 4/7/1926, Kerr 10814 (K!); isotypus: Thailand, Kanchanaburi, Three Pagodas Pass, 14-5/5/1946 Kostermans 428 (L, K)

Habit woody climber. ***Leaves*** elliptical, base retuse to broadly cuneate, apex acute to acuminate, to 150 x 50 mm, sub-coriaceous; *veins* 8-10, strongly incurved, trailing trace fine, not forming distinct sub-marginal vein, secondary veins fine, kinked or incomplete, tertiary venation reticulate, very fine; *indument* abaxial surface entirely glabrous at maturity, blunt hairs occasionally persistent along midrib depression, adaxial blade glabrous with isolated hairs alongside midrib, midrib with scattered 2-5 branched hairs, branches oriented towards leaf apex, isolated hairs also present on primary veins. ***Petiole*** c. 6 x 1 mm, smooth, indument sparse to sub-glabrous, more dense in abaxial groove. ***Young shoots*** shortly tomentose, quickly becoming smooth and striate. ***Inflorescence*** cauliflorous, dichasial, peduncles short and closely packed, c. 1 mm long x 2 mm wide, pedicel to 22 x 1 mm, basal bract triangular, clasping to pedicel, c. 4 x 3 mm, medial bract wanting, pedicel flattened with 2-3 shallow longitudinal grooves, indument tomentose on bracts, tomentose to sub-tomentose on peduncle and pedicel, up to 5 mature flowers at a time, receptacle flat, c. 3 mm diameter. ***Calyx*** sepals 3, valvate, basally connate, ovate, to c. 7 mm wide x 5 mm long, sub-tomentose on both surfaces. ***Corolla*** petals 6, imbricate along entire margin, outer petals ovate, bluntly acute, concave, coriaceous, to 9 mm long x 7 mm wide, inner whorl narrowly ovate, bluntly acute, concave, coriaceous, to 8.5 mm long x 6.5 mm wide, bases of both whorls somewhat thickened, inner and outer indument shortly tomentose. ***Stamens*** numerous but reduced to 3 or 4 whorls, c. 5 x 1 mm, glabrous, connective with prominent extrorse ridge, apex flattened, bluntly acute,

papillate, locules full length. ***Carpels*** c. 50, c. 5 x 1 mm, ovary tomentose, stigma narrow, 1mm long, U -shaped, glabrous, ovules c. 16. ***Fruit*** unknown. Line drawing Figure 4.28. Leaf shape shown in Figure 4.29.

Ecology and Distribution *Uvaria kerrii* is restricted to the dry evergreen forests of southwestern Thailand. Distribution is shown in Figure 4.52.

Notes this species is intermediate between *Cyathostemma* s.s. and *Uvaria*. The narrow, elongate stigma and cauliflorous inflorescence is characteristic of many *Cyathostemma* species which have been moved in this revision to *Uvaria*. However, the petals are not unlike those of *Uvaria cordata* and *U. microcarpa*, and are distinctly imbricate in bud, and the c. 16 ovules remind of *Uvaria grandiflora* or *U. rufa*. The elongate, laminar stamens with full-length locules and the sub-glabrous, waxy leaves with kinked or incomplete secondary veins are characteristic of species in both *Cyathostemma* and *Uvaria*.

Vern. Thailand, 'Too wan ret', Kerr 10814.

Material Examined

Thailand *Kanchanaburi Province* (SW – 34); Three Pagodas Pass, Kostermans 428, 14-5/5/1946 (fl.) (L, K). *Prachuap Khiri Khan Province* (SW – 37); Khao Luang, c. 400m, 4/7/1926, Kerr 10814 (fl.) (K).



Figure 4.28 *Uvaria kerrii* C. Meade *sp. nov.* (a) Leaf and shoot, to scale. (b) Inflorescence, x 2. (c) Stamen and carpel structure, scale indicated. (d) section through inflorescence, scale indicated.

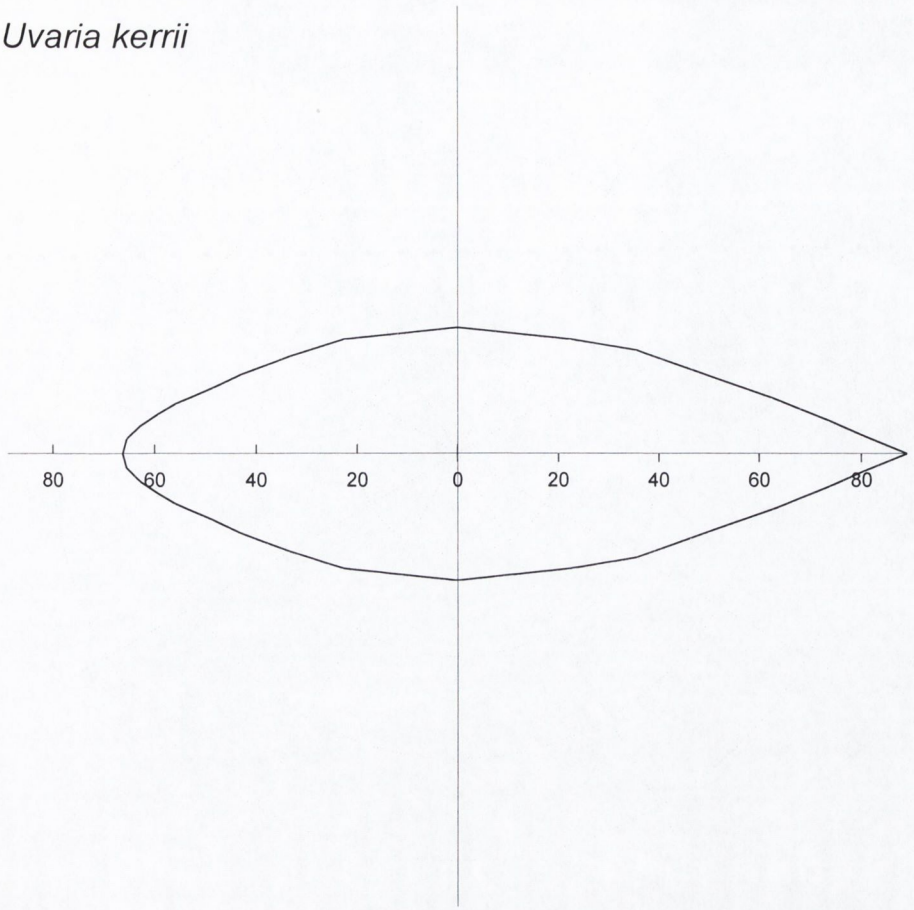


Figure 4.29. Mean leaf outline for *U. kerrii* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

24. *Uvaria wrayii* (King) C. Meade *comb. nov.*

Cyathostemma wrayii King, J. As. Soc. Beng. 61(2)1:9 (1892) *et* Ann. Roy. Bot. Gard. Calcutta, 4:12 (1893); lectotype (*designated here*): Malaysia, Perak, Scortecnhini 131b (K!), syntypes: Malaysia, Larut, King 4207 (Sing!, Cal.) *et* Malaysia, Perak, Taiping, Waterfall, 300ft., 10/1888, Wray 3283 (Sing!); Sinclair, Gard. Bull. Sing. 14(2):224 (1955).

Habit small shrub or climber. ***Young shoots*** sparsely tomentose with scattered dense patches (particularly near petioles), distinctive light-ferruginous hue of fine hairs over black bark, hairs persistant, becoming short, striations becoming prominent later. ***Leaves*** obovate, less often oblong, base retuse, apex acute-aciminate, to 250 x 95 mm, membranous, *veins* 12 - 15, widely spaced, inarching gradually, trailing trace fine, not

forming distinct sub-marginal vein, occasional inter-primary veins, secondary veins short, incomplete except towards leaf margin, tertiary venation densely reticulate, midrib depressed above, emergent below, microvenation visible above and below; *indument* hairs erect and shortly-tomentose over midrib, sparse and spreading over veins, becoming glabrous, blade sub-glabrous becoming glabrous; adaxial blade sub-glabrous with occasional hairs on tertiary venation, midrib very sparse, hairs spreading, often short, otherwise straggling. ***Petiole*** sparse to sparsely tomentose, hairs fine, straggling, more dense than on midrib, on younger leaves ferrugino-tomentose. ***Inflorescence*** axillary or supra-axillary, often cauliflorous, flowers 2-5, peduncle to 3 mm, pedicels 2 to 8 mm long, bracteate with 2 almost laminar acute bracts, enlarging to 4 x 2 mm, narrowly ovate-acute, ferrugino-tomentose becoming sparse with larger size. ***Calyx*** sepals 3, free, opening early and reflexing, remaining small, concave, broadly ovate-acute, coriaceous, to 4 mm wide x 3 mm long, indument sparsely tomentose, hairs fine, ferruginous. ***Corolla*** petals 6, green-yellow in colour, free, imbricate at tips, broadly ovate in bud, becoming narrowly ovate, bluntly acute to obtuse, thickly coriaceous to fleshy, up to c. 9 mm long x 6 mm wide, whorls subequal, often opening but not reflexing, indument sub-tomentose to sparse, hairs becoming short, blunt, almost papillate, glabrous basally on inner side. ***Stamens*** numerous, c.1.4 mm long, glabrous, connective flattened, distinctly papillate, locules full length. ***Carpels*** numerous, c. 2 mm long, neck of longer hairs at apex of ovary, below glabrous except on ridges, arched inwards at outer whorls, straight towards centre, stigma glabrous, elongate, ovules 2-3, lateral. ***Fruit*** monocarps numerous, ovoid, c. 9-13 x 6-9 mm, stipe 15 - 20 mm, narrow, pericarp thin, flaking off easily when dry, thickened apicule often present, seeds 1-2, c. 9 x 8 x 4 mm, single seeds ellipsoidal or proncouncedly hemi-ellipsoidal when two seeds present, hilum A-shaped, c. 1.5 x 1.5 mm. Leaf shape shown in Figure 4.30. Line drawing Figure 4.31. Appendix 4.13B.

Ecology and Distribution A fairly common species occurring in evergreen forests up to c. 400m from the Isthmus of Kra south to Sumatra. Distribution is shown in Figure 4.52.

Notes The large obovate membranous leaves of this species make it one of the more easily recognised from sterile specimens. An early identification of van Buesekom

and Phengkhlai 564 as a possible new *Uvaria* species was the first indication in the course of this project that a taxonomic distinction between *Cyathostemma* and *Uvaria* might be untenable. The Thai collections represent new records for the taxon in the Kingdom.

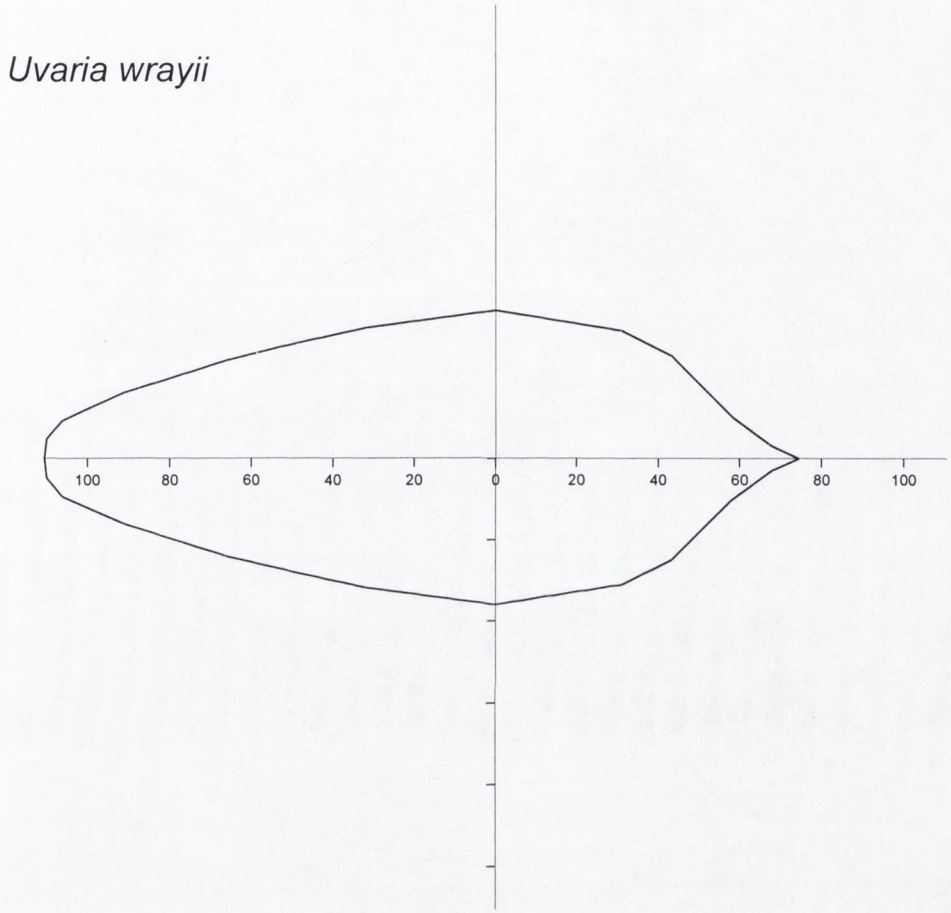


Figure 4.30. Mean leaf outline for *U. wrayii* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Material Examined

Thailand *Chumpon Province* (59 - Pen); Tako, near Langsuan, 19/06/24, Put 1748 (fl.) (K, L); *Ranong Province* (60 - Pen); Khao Saideng, 400m, 03/05/64, van Beusekom & Phengkhlai 564 (fl.) (L); *Phangnga Province* (62 - Pen); Khlong Nang Yon, 9.15N 98.20E, 100m, 30/4/1973, Geesink & Santisuk 5062, (fl.) (BKF); N. of

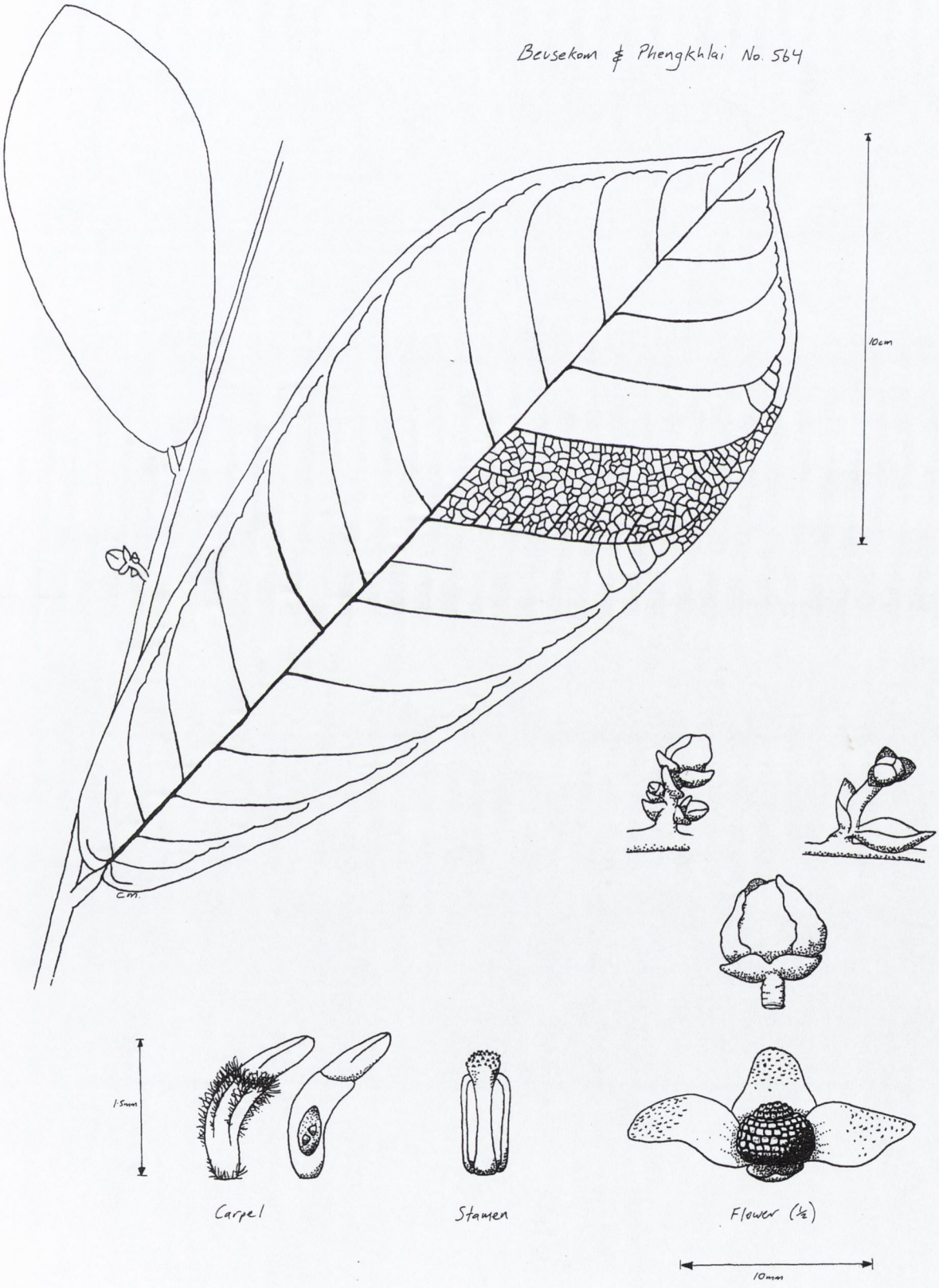


Figure 4.31 *Uvaria wrayii* (King) C. Meade *comb. nov.*

Thung Maphrao, 50-100m, 8.33N 98.14E, 18/07/68, Larsen 31150 (fl.) (AAU); *Phatthalung Province* (66 - Pen); 100m 100.05 E 7.20 N, 23/10/89, Larsen 43944 (fl.) (AAU); *Songkhla Province* (69 - Pen); Boripat Falls National Park, Rattapoom, 100m, 23/10/81, Maxwell 85-1001 (fl., fr.) (A).

Peninsular Malaysia *Pahang*; Jerantut, 11/03/92, David 105 (fl.) (P); *Penang*; 16/10/47, Sinclair S.F. 39341, (-) (Sing); *Perak*; Larut, 100m ,5/1883, King 4207 (P); 100m, 10/1888, Wray 3283 (fl.) (Sing); 23/09/20, Hanif 14189 (fl.)(Sing).

Indonensia *Sumatra*; East Coast, Mebang Moeda, Koealoe, 07/09/24, Toreos 1288 (fl.) (NY).

25. *Uvaria argentea* Bl.

Fl. Jav. (Anonaceae)1:24, t. 6 & 13d (1830); Miq., Fl. Ned. Ind. 1:25 (1859). *Cyathostemma argenteum* (Bl.) Sincl., Sarawak Mus. Journ. 5(3):599 (1951) *et* Gard. Bull. Sing. 14:220 (1955).

Habit much-branched climber with distinctive wrapping branchlets. ***Leaves*** elliptic or oblong, less often obovate, 50-100(-180) x 30-50(-65) mm, obtuse, acute or shortly acuminate, narrowly retuse, membranous; *veins* (9) 10 - 12 (13), fine, gradually inarching, trailing traces fine, not forming distinct sub-marginal vein, secondary veins kinked or incomplete, tertiary venation very fine, dense, reticulate, midrib shallowly depressed above, emergent below, primary veins marginally raised above, distinct below, microvenation visible above and below; *indument* upper blade glabrous, sparse stellate erect hairs over midrib, sparse spreading hairs over primary veins, lower surface sparse hairs on midrib and veins, blade glabrous. ***Petiole*** 4-7 x 1.5 mm, tomentose becoming sub-glabrous, adaxial surface prominently warted and transversely foliated. ***Young shoots*** tomentose becoming sub-glabrous and prominently striate early. ***Inflorescence*** flowers solitary or occasionally 2-4, peduncle 2 mm long, pedicel to 7 mm, basal bract 7-9 mm long x 5-6 mm wide, membranous, medial bract c. 5 x 3.5 mm, obovate, often wrapping over floral bud, indument dense over peduncle, pedicel and bracts, becoming less dense as bracts expand. ***Calyx*** sepals

3, free, valvate, broadly ovate, apex obtuse-cuspidate, to 4.5 mm wide x 3 mm long, often reflexed at maturity, indument tomentose on both surfaces, outer surface hairs somewhat rufous, on inner surface hairs straggling, fine, often sub-glabrous basally. ***Corolla*** petals 6, red in colour, drying dark green to black, whorls unequal, remaining erect, outer petals ovate-oblong, acute, concave, 5-6 mm long x 4.5-5.5 mm wide, inner whorl narrowly ovate, acute, strongly concave, 4-5 mm long x 3.5-4 mm wide, outer surface of both whorls warty, indument sparse, tomentose at margin, hairs straggling, straw-coloured, inner surface hairs fine, straggling, combed, glabrous medially on outer petals, glabrous basally on inner petals, with prominent stamen indents in both whorls. ***Stamens*** numerous, 2 mm long, connective with short, blunt tomentum, apex 0 .75 mm long, oblongoidal or globose, locules full length, glabrous. ***Carpels*** c. 30, 3.5 mm long, S-shaped, ovaries hairy, stigma U-shaped, elongate, 1-1.25 mm long, glabrous, ovules 4-10. ***Fruit*** not seen. Leaf shape shown in Figure 4.32.

Var. ***bracteata*** (Roxb.) C. Meade *comb. et stat. nov.*

Uvaria bracteata Roxb., Fl. Ind. 3:660 (1832); lectotype (*designated here*): India, Roxb. s.n. (BM!); Wall., Cat. 6468 (1832) *nom. nud.*; Hook. f. & Thoms., Fl. Ind. 1:100 (1855) *et* Fl. Br. Ind. 1:49 (1872), Kurz, Fl. Br. Burma 1:28 (1877). *U. gomeziana* A.DC., Mém. Anon. 27, Mém. Soc. Phys. Genève 5:203 (1832), type: Myanmar, Tavoy, W. Gomez in Wall. Cat. 6459 (BM!, G!, K-W!). *Cyathostemma yunnanense* Hu, Bull. Fan. Mem. Inst. Biol. 10:121 (1940); Tsiang & P. T. Li, Fl. Rep. Pop. Sin. 30:28, t. 11 (1979), type: China, Yunnan Province, Fo Hai, Wang 74789, (PE Holo, NY Iso!).

Epitypes (*designated here*): India, Sylhet, Wallich Cat. 6468 (BM!, P!, K!, K-W!, G!) & Roxb. Icon no. 2290 (K!).

Differs from the type variety in having white or yellow-green petals, and the leaves are usually larger and almost exclusively obovate.

Distribution and Ecology *Uvaria argentea* var *argentea* occurs in lower Peninsular Malayisa, Java and Borneo. Var. *bracteata* occurs in well-watered mountain foothills in Northern Indochina, Taninthari and Chonburi up to c. 1100 m. Distribution is shown in Figure 4.54.

Notes *Uvaria argentea* is recognised from herbarium specimens by its membranous leaves and grey-green to black petals with a pale tomentose indument on the margins. Sinclair (1951) listed *U. bracteata* Roxb. under *Cyathostemma argenteum* (Bl.) Sinclair. However, the petals of Roxburgh's taxon are always green-yellow or grey, as opposed to deep red or purple for Blume's species, and there also is a marked disjunction in the distributions of the two. For these reasons it seems wise to retain Roxburgh's *U. bracteata* as a variety of *U. argentea* rather than reduce it to a synonym. The type of *Cyathostemma yunnanense* Hu (Wang 74789) matches the Roxburgh lectotype. Roxburgh (1832) describes the fruits in *Fl. Indica*, [2nd ed., p.661,]; ' [fruits] ... few, pendulous, of the size of a small pillets egg, from oval to oblong, obtuse at both ends, smooth, when ripe of a rich yellow, seeds, a few, oval, compressed, smooth.' Sealy (1956) and Forman (1997) provide notes relating to the names and type material of Roxburgh's *Flora Indica*. This is a new record for Thailand.

Vern. *India/Bangladesh* at Sylhet, 'Jupa bun kula', Roxburgh. Fl. Ind. 2:220 (1832).

Material Examined

Bangladesh/ India *Silhet*; Roxburgh s.n. (fl.) (BM); F. Da Silva in Wall Herb. Cat. 6468 (fl.) (BM, G, K, K-W, P).

China *Yunnan*; Fo-Hai, 1090m, May 1932 Wang 74879 (fl.) (A).

Myanmar *Taninthari* (Tennasserim); Tavoy, W. Gomez in Wall Herb. Cat. 6459 (fl.) (K, G).

Thailand *Chiang Mai Province* (2 – N); Doi Chiang Dao, Chiang Mai, 700m, 19.20N 98.50E, 02/06/69, Geesink *et al.* 5662 (fl.), (AAU, BKF, C, E, L); *Chonburi Province* (55 – SE), Ang Chang Nam, Kow Kieo Park, Bahn Bueng District, 300m, 25/06/71, Maxwell 75-658 (fl.) (L); *Locality unclear*; 1956/2498?, BKF SN 004083/ Roy. For. Dept. Herb. No. 12878 (fl.) (BKF).

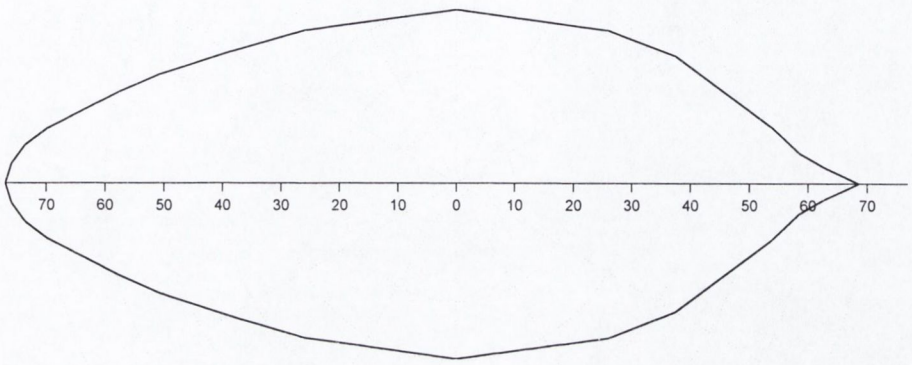


Figure 4.32. Mean leaf outline for *U.argentea var. bracteata* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

26. ***Uvaria vietnamensis*** Jovet-Ast ex C. Meade *sp. nov.*

Uvaria fauveliana Pierre *sensu* Jovet-Ast Supplément a la Flore Générale de L'Indochine, 1:64 (1938) *et* Notul. Syst. (Paris) 9:87 (1940) [*pro pars*].

non est Uvaria hamiltonii Hook. f. & Thoms. var. *fauveliana* Finet & Gagnep., Bull. Soc. Bot. France 53 Mém. 4:68 (1906) *et* Flore Générale de L'Indo-Chine 1:52 (1907).

Uvaria fructus ruber globosus barbatus 20-30 mm diam. 4-8 seminalis stipitatus, ramulis et foliis ferrugino-hirsutus scabridus. Uvaria with red, bearded, 20-30 mm diam., 4-8 seeded, stipitate fruits and ferrugino-hirsute somewhat scabrous branchlets and leaves.

Holotypus: Vietnam, Quang Tri Province, 'Annam, Massif de la mere et l'Enfant, 24/05/23, Poilane 6699' (P!), *isotypus*: Vietnam, Quang Nam Province; 'Ba Na, 25 km NW of Dà Năng, 24/07/23, Poilane 7326' (E! P!); Vietnam, Quang Nam Province; 'May-July /27, J & M. S. Clemens 3827' (BM! NY! P! U!).

Habit climber or scrambling shrub. ***Young shoots*** sub-tomentose, hairs ferruginous with 2-5 c. 1 mm long multi-cellular branches, bark smooth becoming striate and sparse with occasional persistent larger hairs. ***Leaves*** elliptic to narrowly obovate, (70-)90-225 x (35-)40-75mm, apex acuminate/ acute, base narrowly cordate, sub-coriaceous; *veins* 14-16, trailing trace fine, interprimary veins rare, secondary veins kinked, midrib and veins somewhat sunken on abaxial surface, prominent on adaxial surface, microvenation indistinct above, visible below; *indument* abaxial blade surface sparse to sub-tomentose, hairs simple, occasionally 2 branched, c. 1 mm long, midrib densely tomentose with erect 1 or 2+ branched hairs 0.75 – 1 mm long; adaxial midrib and blade sub-tomentose to sparse with 4-8 branched, c. 0.6-0.85 mm long stellate hairs. ***Petiole*** 3-5 x 1.5-2 mm, indument sub-tomentose, stellate, hairs fine and pale coloured or more thickly set and ferruginous. ***Inflorescence*** not known. ***Fruit*** monocarps c. 20+, spheroidal, diameter c. 20 - 30 mm, covered with distinctive 3+ branched c. 5 mm long outgrowths, each covered with ferrugino-tomentose branches, pericarp red at maturity, flesh pale white, bittersweet to taste, stipes to 45 x 2mm, striate with sub-tomentose indument, *seeds* 4-8, shortly hemi-ellipsoidal, c. 11 x 5.25-7 x 2-3 mm, aril priminent, 4 x 2.5 - 3 x 3mm, surface leathery, brown, ruminations visible. Leaf shape shown in Figure 4. 33. Line drawing Figure 4.34. Appendix 4.9B.

Ecology and Distribution A rare plant, occuring from central Vietnam through Southern Laos into northeastern Thailand in mixed deciduous or dry evergreen forest habitats above 100m altitude. Distribution is shown in Figure 4.55.

Notes *U. vietnamensis* is described from a fruiting specimen collected by Poilane and subsequently listed as *U. fauveliana* Pierre by Jovet-Ast in the Supplement to Fl. de l'As. Or. However, Pierre's *U. fauveliana* type specimen, which had no fruit, is in fact *Uvaria rufa*. Poilane's specimen, which has fruit but no flowers, is definitely not *U. rufa* or any other known *Uvaria*. With luck a flowering specimen will be found in the

near future. The flesh of *U. vietnamensis* fruit is sweet and edible at maturity, and ripens in a very similar way to that of *U. hamiltonii.* However, the distinctive bearded epidermis of *U. vietnamensis* fruits is instantly recognisable and looks similar to that of the rambutan (*Nephelium lappaceum*, Sapindaceae). The *Uvaria* species most similar to *U. vietnamensis* are *U. hirsuta* and *U. hamiltonii*. All three exhibit a long ferruginous indument and have similar shaped leaves. However, aside from being restricted to the Malay Peninsula in continental Asia, *U. hirsuta* can be distinguished from *U. vietnamensis* by it's oblong, 20+ seeded beardless fruit (vs. the globose 4-8 seeded bearded fruit in *U. vietnamensis*) and by the longer, finer and softer indument over the vegetative organs (the hairs of *U. vietnamense* are rough and almost scabrid to the touch). *U. hamiltonii* also differs in having a finer and more sparse leaf and shoot indument, and its fruit - though similar in shape to *U. vietnamensis* - has a sub-tomentose indument rather than the rambutan-like beard.

***Vern**. Laos*; Mây khe cân (Poilane 11721), Ngaw keuah (Maxwell 98-1053); *Vietnam*; Dây cham cham (Poilane 7326).

Material Examined

Vietnam *Quang Nam Province* (CLV - 27 - V); Ba Na, 25 km NW of Dà Năng, 24/07/23, Poilane 7326 (fr.) (E, P); May-July /27, J & M. S. Clemens 3827 (fr.) (BM, NY, P, U) (CLV - 27 - V); *Quang Tri Province* (CLV – 25 - V); Massif de la mere et l'Enfant, 24/05/23, Poilane 6699 (fr.) (P).

Laos *Savannakhet Province* (CLV - 12 - L); Kilo 20 on the road from Savannakhet to Quang Fri, 21/01/25, Poilane 11721 (fr.) (E, P) *Champasak Province* (CLV - 15 - L); summit of Hang Kohn Hill, southern tip of Khong island, Khong District, 20-9-98, Maxwell 98-1053 (fr.) (CMU).

Thailand *Ubon Ratchatani Province* (NE – 26); Soi Sawan Waterfall, 16/10/98, Chalermglin & Meade 98-10-16-03 (-) (TCD).

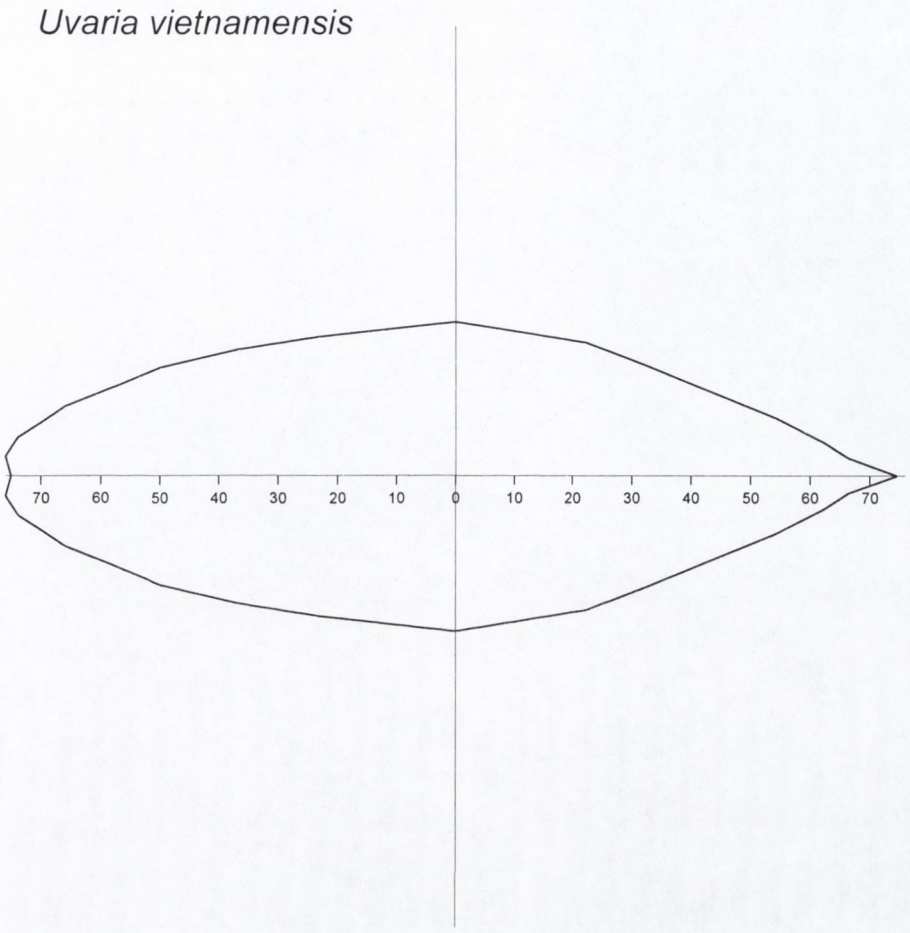


Figure 4.33. Mean leaf outline for *U. vietnamensis* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.



Figure 4.34 *Uvaria vietnamensis* Jovet-Ast ex C. Meade *sp. nov.* (a) Leaf and shoot with fruiting receptacle. (b) monocarp structure. (c) tomentose outgrowth from monocarp epidermis.

3. *RAUWENHOFFIA* Scheff.

Ann. Jard. Buit. 2:21 (1885), type *R. siamensis* Scheff.; Sincl., Gard. Bull. Sing. 14(2):228 (1955); Hutchinson, Gen. Fl. Pl. 1:93 (1964).

Climbers or erect shrubs with stellate hairs; ***inflorescence*** leaf-opposed, flowers 1-3 in short rhipidium, ***calyx*** valvate, sepals 3, concave, acute, coriaceous, ***corolla*** petals pale green or yellow, broadly ovate, apex narrowly obtuse or bluntly acute, valvate at base, imbricate at tips, fleshy, remaining erect; ***stamens*** cuneate, locules stipitate, connective apex globose, finely papillate, bright orange; ***stigma*** elongate, hairy, forming prominent dome above gynoecium; ***fruit*** monocarps 1-6 seeded, stipe c. 10mm, pericarp fleshy, green turning yellow, minutely ridged.

... **R. siamensis** *Southern Indochina*

1. *Rauwenhoffia siamensis* Scheffer

Ann. Jard. Buitenzorg 2:23 (1885), type, Thailand 'Cultiv. in Bot. Gard. (from Siam), Teijsmann Hb. BO No. 17785' (Holo- BO, n.v.); Boerl., Icon. Bog. 1(2):197 t. 70 (1899); Ridley, Fl. Mal. Pen. 1:89 (1922); Craib, Fl. Siam Enum. 1:45 (1925); Jovet-Ast, Supplément a la Flore Générale de L'Indochine 1:104 (1938); Sinclair, Gard. Bull. Singapore 14:228 (1955); Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):303 (1991). *Uvaria godefroyana* Finet & Gagnep., Bull. Soc. Bot. France 52, Mém. 4(2):71 (1906) et Flore Générale de L'Indo-Chine 1:55 pl. 7 (1907), syntypes: Cambodia 'Angkor, 1875, Harmand 612, 621' (P!); 'Pursat, 11/6/1875, Harmand 298' (P!). *Melodorum schefferi* Pierre ex Finet & Gagnep., Bull. Soc. Bot. France 52, Mém. 4(2):134 pl. 19a (1906) *et* Flore Générale de L'Indo-Chine 1:99 (1907). *Melodorum siamensis* (Scheffer) Tien Ban, Bot. Zhurn. 59:241 (1974)

Habit shrub or climber. ***Young shoots*** tomentose with large many-branched ferruginous hairs scattered over smaller, finer, less pigmented hairs, not quite obscuring bark, but nearly so, older wood becoming striate with prominent lenticels, later sub-glabrous. ***Leaves*** (bluntly) lanceolate/ elliptical, base retuse, apex narrowly to bluntly acute, c. 90-150 x 30-40 mm, thinly coriaceous, waxy texture above; *veins* 8-11(-14), trailing trace fine, not forming distinct sub-margin, interprimaries frequent, secondary veins kinked or incomplete, tertiary venation reticulate; *indument* sub-

tomentose adaxially with underlying layer of fine, c. 6-8 branched hairs overlain with scattered, thickened, many-branched hairs especially on midrib and midrib base, glabrous above except for sparse spreading stellate hairs on upper midrib. ***Petiole*** tomentose, c. 3.5 x 1.25 mm. ***Inflorescence*** leaf-opposed or sub-opposed, flowers solitary or rarely 2-3, peduncle sub-sessile, c. 1.5 x 1.25 mm, pedicel c. 8 x 1.25 mm, shortly and densely tomentose, hairs pale, overlain by scattered larger rufous hairs, deeply grooved/ striate, basal and medial bracts ovate-acute, c. 2-5 x 1-2 mm, sub-tomentose, deciduous, usually wanting. ***Calyx*** sepals 3, valvate, opening early, very broadly ovate-acute, c. 3 x 6 mm, thickened and remaining incurved, base concave, outer surface indument as for pedicel, inner surface glabrous. ***Corolla*** petals 6, yellow-white in colour, valvate basally, imbricate at tips, outer whorl larger than inner, outer petals broadly ovate, c. 8 x 8 mm, inner petals broadly elliptical with constricted base, c. 8 x 5.5 mm, outer surface of both whorls densely tomentose, hairs fine, pale, inner surface of outer whorl tomentose at apex and on margins of base, central basal area glabrous, inner whorl completely glabrous at base, apex tomentose. ***Stamens*** numerous, c. 1.5 mm long, cuneate, apex flat or shallowly globose, obscuring locules, rusty brown or orange in colour with waxy texture, covered with tiny blunt papillae, locules stipitate. ***Carpels*** c. 10, 3 mm long, ovaries covered with blunt stallate hair-scales giving very finely warted appearance, neck present between ovary and stigma covered with long stellate hairs; stigmas prominent, lobed, U-shaped, c. 1 mm long, forming distinct dome above stamens, secreting copious amounts of nectar, ovules c. 4-8. ***Fruit*** monocarps 2-10 (usually 3-6), globose or shortly oblong, c. 10-12 x 8-9 mm, very minutely tubercled with sub-tomentose indument of blunt stellate scales, outline of seeds often clear within pericarp, stipe sub-sessile, c. 3 x 1 mm, striate, seeds c.2-4(-6), compressed hemi-ellipsoidal, c. 7 x 4 x 3 mm. Leaf shape shown in Figure 4.35. Appendix 4.6B.

Ecology and Distribution A common species in Thailand except in the Northern Region, extending into Cambodia, Southern Vietnam and Tenasserim (Taninthari) in Myanmar. It is probable that the species also occurs in the Northern Malay States of Kelantan, Perlis and Kedah. Approximately 50% of collections record *R. siamensis* as a shrub or small tree, most often occurring in disturbed or marginal forest vegetation, particularly bamboo scrub/forest. Distribution is shown in Figure 4.40.

Notes *Rauwenhoffia siamensis* is probably the closest living relative of *Ellipeiopsis ferruginea*. The two have similar flowers, but the fruit, leaf and growth habits are very different. It is also a close relative of *Nervopetalum hahnii*, with the two species sharing fruit and leaf characters. Tien Ban's decision to move it to *Melodorum* is unsupported by the majority of important characters, particularly petal aestivation, and stamen and carpel structure, and so it seems wise to retain it as a separate genus.

Vern. *Thailand*; Krung Thep, Thai: 'Nom meo' (Kerr); Khon Kaen, Thai; 'Nom maeo' (Playarat).

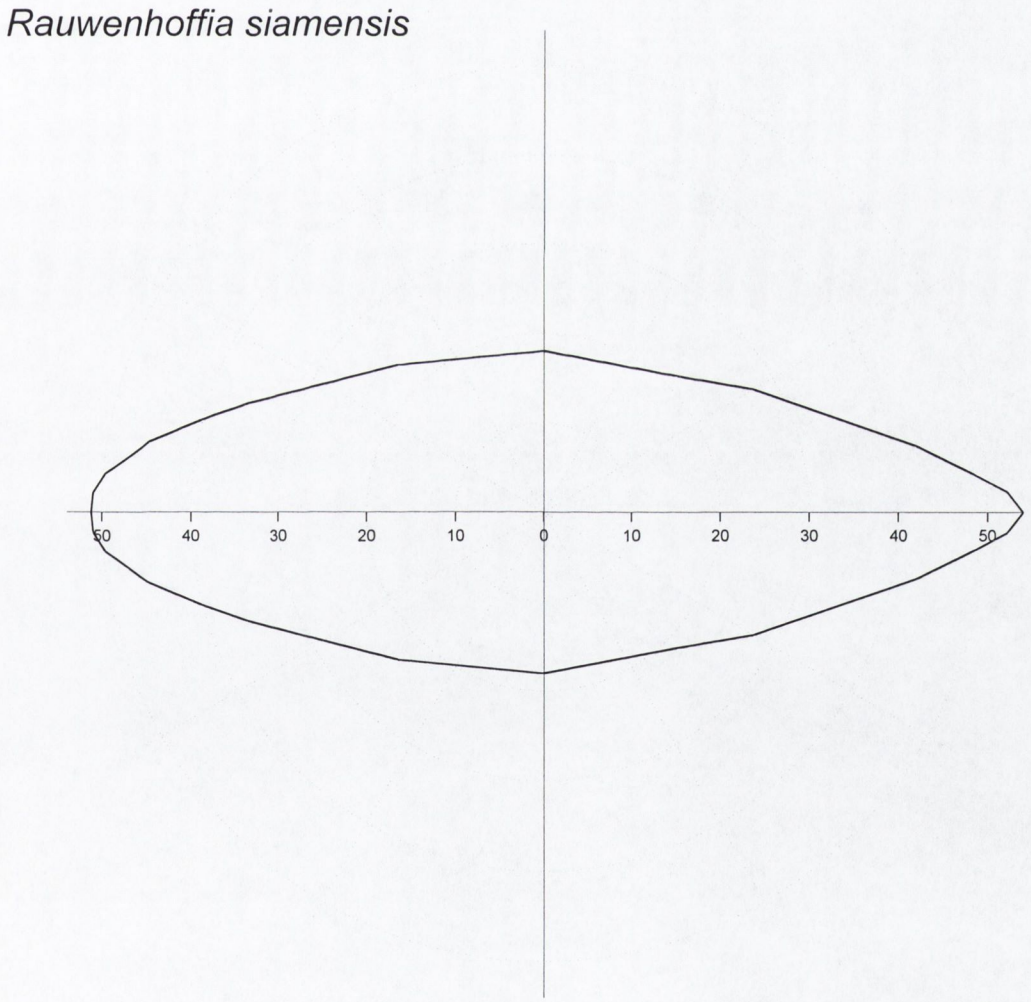


Figure 4.35. Mean leaf outline for *R. siamensis* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Material Examined

Myanmar *Taninthari*; Eastern Mergui, 150m, Kerr 21608 (BK).

Vietnam *Thua Thien-Hue Province* (V - 26 - CLV); Da Nang, May - Jul. 1927, Clemens 3131 (fl.) (NY); Da Nang, May - Jul. 1927, Clemens 3447 (fl.) (NY); Hue, 29/9/21, McClure 793 (fl.) (A); *Kanh Hoa Province* (V – 35 – CLV); Nha Thrang, 4-5 Feb. 1914, Chevalier 30452 (fl., fr.) (P); Nha Trang, 11/05/29, Neilsen 606 (C).

Cambodia *Siem Reap Province* (C – 7 – CLV); Angkor, 1875, Harmand 612, 621(fl.) (P); *Pursat Province* (C – 10 – CLV); Pursat, 11/6/1875, Harmand 298' (fl., fr) (P).

Thailand *Maha Sarakham Province* (23 - NE); Kosum Phisai, 150m, 01/05/68, Smitinand 10445 (BKF, L); *Khon Kaen Province* (24 – NE); Khon Kaen, Playarat s.n. 7-91 (KKU); *Surin Province* (28 – E); Tatoom, Ponkrok District, 7-6-82, Paisooksantivatna & Sutheesorn 906-82 (fr.) (BK); *Prachuap Khiri Khan Province* (37 – SW); Khao Luang, c. 300m, 3/7/24, Kerr 10797 (fl.) (BK); Prachuap, 90m, 13/7/21, Winit 615 (BK); Prachuap, 120m, 7/7/21 Winit 667 (BK); Khao Luang, c. 300m, 6/7/26, Kerr 10874 (fl.) (BK); *Anthong Province* (42 - C); Wat Glang, Muang District, Angthong, 14/08/71, Maxwell 71-479 (fr.) (AAU, BK); Wat Glahng, Howa Pie, Muang District, 02/04/72 Maxwell 72-175 (AAU, BK); Wat Glahng, Hoa Pie, Muang District, 25m, 31/05/75, Maxwell 75-571 (AAU); *Saraburi Province* (44 – C); Munam Sak, 40m, 1/6/23, Kerr 7033 (fl.) (BK, TCD); Ban Nwang Bua. 1/10/27, Put 1110 (BK); *Krung Thep Province* (49 - C); outside front door of BKF, cultivated, Chatuchack, 08/10/98, Meade 76 (fl.) (BKF, TCD); Kasetstart University, cultivated, Maxwell 71-754 (BK); Put s.n. Bangkok 15/2/32 (BK); Pknet, near Bangkok, 14/10/23, Kerr s.n. (fl.) (BK); Near Bangkok, Smyth 647 (BK); *Chonburi Province* (55 - SE); Sriracha, 27/06/20; Kerr 4308 (TCD); *Chanthaburi province* (57 – SE); Bong Nam Rawn District, N. Khao Soy Dow, 250m, 6/5/75, Maxwell 75-496; *Krabi Province* (64 – Pen.); Aranga, c. 50m, 12/5/30, Kerr 19313 (BK); *Nakhon Si Thammarat Province* (65 – Pen.); Ban Bua Put, Ko Samui, 14/5/28, Kerr 15727 (fl.) (BK, TCD); *Songkhla Province* (69 - Pen); Bantom Island, Lake Songkhla, 0m, 26/05/84, Sirirugsa 818 (A); Khao Kho Hang, 06/10/88, Larsen 40277 (AAU);

Pattani Province (70 – Pen.), Kok Po, <50m, 05/04/18, Kerr 15067 (BK, K); *Narathiwat Province* (72 – Pen.); Nikhomwang, 7-5-1968, Prayed 1367 (BK); Amphoe Baco, 31/12/68, Prayed 1638 (fr.) (BK).

4. *ELLIPEIA* Hook. f. & Thoms.

Fl. Ind. 1:104 (1855) *et* Fl. Br. Ind. 1:52 (1872), type *E. cuneifolia* Hook. f. & Thoms.; Benth. & Hook. f., Gen. Pl. 1:23 (1863); King, J. As. Soc. Beng. 61(2)1:124 (1892) *et* Ann. Roy. Bot. Gard. Calc. 4:32 (1893); Ridley, Fl. Mal. Pen. 1:35 (1922); Sincl., Gard. Bull. Sing. 14(2):230 (1955); Hutchinson, Gen. Fl. Pl. 1:83 (1965).

Syn. nov.; *Anomianthus* Zoll. Linnaea 29:324 (1857-8), type; *A. dulcis* (Dunal) Sincl. (*A. heterocarpus* Zoll.).

Climbers or scrambling shrubs with stellate hairs; ***inflorescence*** a pendulous terminal rhipidium of 1-5 flowers; ***calyx*** valvate, opening early; ***corolla*** petals white, yellow or orange, membranous or coriaceous, imbricate, obovate, basally constricted, inner surfaces variously glabrous from base toward apex; ***stamens*** cuneate, locules stipitate, connective apices globular, glabrous or papillate; ***stigmas*** hairy, forming prominent dome above gynoecium; ***fruit*** monocarps 1-3 seeded, placentation lateral, pericarp thin, carrying prominent apicule.

Key to species occurring in Continental Asia

1a. Petals white or yellow-pink, inner petals with lateral supra-basal orange glands, ovules 1-8 .....**1. *E. dulcis***

Thailand and Southern Indochina, Java – Lesser Sunda Is

1b. Petals white or cream, inner petals without glands, ovules 1-2 .... **2. *E. pauciovulata***

Malay Peninsula south of the Isthmus of Kra

1. *Ellipeia dulcis* (Dunal) C. Meade *comb. nov.*

Uvaria dulcis Dunal Mon. Anon. 90 t.13 (1817), lectotype (*designated here*); 'Uvaria dulcis, [*Uvaria zeylanica*], Java, hb. Ventenat' (*Herb. Deless.* G!); DC., Syst. 1:483 (1817) *et* Prodr. 1:88 (1824); Don, Syst. 1:92 (1831); *non sensu. auct. in e.g.* ; Hook. f & Thoms., Fl. Ind. 1:98 (1855) *et* Fl. Br. Ind. 1:48 (1877); Miq., Fl. Ned. Ind. 1:23 (1859); King, J. As. Soc. Beng. 61(2)1:14 *et* Ann. Roy. Bot. Gard.

Calcutta, 4:18 t. 8 (1893); Ridley, F.M.P. 1:30 (1922). *Anomianthus dulcis* (Dunal) Sincl., Gard. Bull. Singapore 14:217 (1955); Backer & van den Brink, Fl. Java 1:105 (1963); Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):302 (1991). *U. javana* Dunal, Mon. Anon. 91, t. 14, lectotype (*designated here*) 'Uvaria javana, [*Uvaria tomentosa* ? Roxb. t. 35 perquam affinis], Java, Lahaye, hb. Ventenat' (*Herb. Deless.* G!). *Uvaria aurita* Bl., Fl. Jav. Anon. 15 t. 2 (1828); Miq., Fl. Ned. Ind. 1:24 (1859). *Anomianthus auritus* (Bl.) Backer, Schoolfl. Java 23 (1911). *Uvaria heterocarpa* Bl., Fl. Jav. Anon. 41 (1828); *Anomianthus heterocarpus* Zoll., Linnaea 29:324 (1857-58); Boerl., Icon. Bogor. 2:96 t. 28 (1899); Finet & Gagnep., Bull. Soc. Bot. France 52, Mém.4(2):60 (1906) *et* Flore Générale de L'Indo-Chine 1:46 (1907); Craib, Fl. Siam. Enum. 1:54 (1931). *Uvaria pachychila* Merr. ex Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):307 (1991), type, Vietnam, Dalat, 1/4/32, Squires 905 (NY!).

non est Uvaria javana Dunal *sensu auct.*

Habit sarmentose shrub or climber, reaching lengths of 30 m or more. ***Young shoots*** tomentose to sub-tomentose, becoming glabrous and striate with distinctive pale lenticels. ***Leaves*** elliptic - broadly elliptic - shortly obovate, apex acute, base retuse-shortly cordate, c. 100-140 x 45-60 mm, membranous; *veins* 15-18, sub-parallel, frequently branching basally and medially, trailing trace fine, not forming distinct sub-margin, interprimaries frequent, well developed, secondaries kinked, tertiaries reticulate, midrib depressed above, emergent below, primary veins visible but scarcely depressed above, distinct below, microvenation visible below only; *indument* abaxial blade hairs 1-4+ branched, sparse becoming sub-glabrous, over midrib hairs erect, tomentose, c. 1 mm long, adaxial blade hairs 5+ branched, sub-tomentose, on veins and midrib hairs c. 10 branched, ferruginous, stocky, tomentose towards petiole. ***Petiole*** tomentose, c 3.5-5 x 1 mm. ***Inflorescence*** terminal, flowers 1 to many, usually 2-3, peduncle c. 5–10 mm, pedicel c. 12-25 mm, both ferrugino-tomentose, bracts broadly ovate, sub-tomentose, c. 2-3 x 3.5-4.5 mm, deciduous, often wanting. ***Calyx*** sepals 3, valvate, connate at base, c. 3.25 x 4.5 mm, ovate-acute, outer surface ferrugino-tomentose, inner surface sub-tomentose, hairs finer. ***Corolla*** petals 6, white or yellow-pink in colour, broadly elliptical-acute at first, expanding to obovate-acute at maturity, outer whorl slightly larger than inner whorl, outer petals c. 21.5 x 11.5 mm, indument on outer surface mixed, underlying tomentum of fine pale hairs overlain by scattered larger rufous hairs usually gathered into distinct trace along central axis, inner surface basally glabrous, at apex hairs as for underlying tomentum on outer surface, inner petals c. 20.5 x 10.5 mm, outer surface tomentose, rufous hairs

present but less numerous than on outer whorl, inner surface basally glabrous with two lateral orange-coloured glands inserted above the base. ***Stamens*** numerous, c. 1.5 mm long, connective broad and flattened, often forming lip on abaxial side, papillate, glabrous, locules stipitate. ***Carpels*** c. 25, 2.5 mm long, hairy usually below stigma neck and along lateral ridges, stigma long and hairy with distinct neck, U-shaped, gynoecium forming distinct dome above stamens, ovules c. 14-16. ***Fruit*** monocarps c. 10+, oblong/ shortly cylindrical, c. 10 x 6.5 mm, glabrous, green turning orange, then red, pericarp hard at first, juicy when ripe, becoming thin and flaky upon drying, particularly in mature fruits, stipe c. 5-10 mm, seeds 1-8, c. 5 x 4 x 4 mm, compressed-ovoid, raphe distinct, aril transversely compressed. Leaf shape shown in Figure 4.36.

Ecology and Distribution *Ellipeia dulcis* has a disjunct distribution, being relatively common in Thailand and southern Indochina and in Java. There are also records from the lesser Sunda Islands and the Moluccas. The species is often found in scrub vegetation, however it is most commonly found in disturbed moist forest where it can form large localised populations. Unlike many of the *Uvaria* group, it seems well adapted to drier environments, and is common in the low-rainfall zones of northeastern Thailand and central Java. Distribution is shown in Figure 4.41.

Notes The membranous obovate petals with conspicuous lateral glands on the inner whorl should be enough to distinguish this plant from it's closest relatives. Examination of the type material of *U. dulcis* and *U. javana* at Geneva reveals that they are in fact the same species, explaining why Dunal's original descriptions of the two are almost identical. The common application of *U. javana* is based on Blume's interpretation in *Flora Javae* (1830), however the latter is a distinct species and needs to be conserved or renamed.

Vern. *Thailand*; Chon Buri Province; Thai: 'Nom Noo' (Collins 1581); 'Nom Myow' (Collins 903, 1254); Chiang Mai Province; 'Nom Ngua' (Kerr 5402); Sakon Nakhon Province; 'Sai Liew' (Lakshnakara 1078); 'Nom Woa' (Chermairivathana 530); Ubon Ratchatani Province; 'Tob hu' 'Tein tang' (Lakshnakara 884); Nakhon Pathom Province; 'tin tang noi' (Kerr 21459).

Material Examined

Cambodia *Pursat Province* (C – 10 - CLV); Massif Pursat, between Ko Virk and La Kiang Chon, 09/05/28 Poilane 15260 (fr.) (HCMC, US); Kom Nom, on road to Trassay, 26/4/28, Poilane 15125 (HCMC); Kaoh Kong Province (C – 18 – CLV); Sre Ambel, Poilane 17410 (HCMC); *Locality Unknown*; 31/7/29, Béjeaud 47 (HCMC).

Laos *Viengchiang Province* (L – 9 – CLV); Viengchiang, 6/7/48, Vidal 584 (HCMC). *Savanakhet Province* (L – 12 – CLV); between LaoBao and Tchepon, 28/5/27, Poilane 13360 (HCMC).

Vietnam *Kontum Province* (V – 30 – CLV); Dak Gley Village, on slopes of Dak Poko River, 600m, 29/03/95, Averyanov et al. VN 985 (fl.) (HN); *Dac Lac Province* (V – 31 – CLV); Easup, Krong Na, Buon Don, 16/4/87, Nguyen Tien Hiep 405 (HN); *Lam Dong Province* (V - 33 - CLV); Dalat, 01/04/32, Squires 905 (fl.) (NY); *Khanh Hoa Province* (V - 35 CLV); Nhatrang, 09/05/22, Poilane 3193 (fl.) (Ham, HCMC, P); Ninh Hoa, 4/5/22, Poilane 3172 (HCMC); Ninh Hoa, 13/11/22, Poilane 5175 (HCMC); Ninh Hoa, 9/6/23, Poliane 6832 (HCMC); North of Ninh Hoa, 10/6/23, 6838 (HCMC); *Ninh Thuan Province* (V - 36 – CLV); Ba Kan, 28/2/24, Poilane 9789 (HCMC, P); CaNa, 26/12/23, Poilane 9342 (HCMC); Phan Rang, 26/06/19, Poilane 108 (fl.) (Ham, HCMC, P); *Dong Nai Province* (V - 40 - CLV); Bao Chiang near Bien Hoa, Jul. 1877, Pierre 1873 (BM, P); Bien Hoa, 24/8/31, Poilane 19396 (HCMC, P); *Province Unknown*; Honguan, 11/05/30, Poilane 17377 (fl.) (US); Snoi Dan, Southern Vietnam 26/07/61, Schmid s.n. (fl., fr.) (P); Pierre 6/1864, Pierre 385 (fl., fr.) (L, P, US).

Thailand *Mae Hong Son Province* (1 - N); Ban Huai Sai, 12km S of Mae Sariang, 18.06N 97.55 E, 12/07/68, Larsen 2381 (fr.) (L); Maesariang, 8-7-1966, Prayad 359, (fl., fr.) (BK); *Chiang Mai Province* (2- N); Bun Hay Hin Dahm area, Na Kau Ruah Subdistrict, 19/5/92, Maxwell 92-225 (CMU); Doi Suthep, 300m, Kerr 12 (fl.) (TCD); Doi Suthep, 300m 26/05/09, Kerr 607 (fl.) (TCD); Doi Suthep, 04/05/66, Sukkri 12 (fl.) (L); Doi Suthep, 27/4/66, Chermairivathana 530, Nom WO l.n. (fr.) (BK); Doi Suthep, 27/4/66, Chermairivathana 537 (fr.) (BK); Doi Suthep, southern tip, Mae Heeyah Nai Village, Muang District, 400m 23/05/88, Maxwell 88-509 (fl.) (L); Huay

Din Dahm, Nahm Prae Subdistrict, Hahng Dong, 400m, 29/08/87, Maxwell 87-899 (fr.) (L); Mae Rim to Sameng highway, km 2, just N of Doi Suthep- Pui NP, 375m 07/09/89, Maxwell 89-1044 (fl.) (L); Maerim-Samung Road, 7/9/89, Pooma 326 (CMU); Mae Rim, beside stream, 15k N of Chiang Mai, 18.55N 98.54E, 450m, 15/07/68, Larsen 2477 (fr.) (L); Mi Chim, Chiangmai, 600m, 9-5-1921, Kerr 5402 (BK); Ob Luang NP, Chiang Hawt District, South side of gorge at park HQ, near Mae Jam river, 14/7/96, Maxwell 96-948 (CMU); Sahn Kahm Village, Chom Tong, 300m 09/10/89 Kertkusol 15 (fr.) (L); Wieng Hang, near Wat Glawng Lohm, 2k west of Wieng Hang Toan, near Mae Haht (Karen) Village, Maxwell 95-335 (CMU); *Chiang Rai Province* (3 -N); Ban Mai Pattana, Namng Bah Gaw subdistrict, 450m, 28/07/88, Maxwell 88-926 (fr.) (L); *Lamphun Province* (6 - N); 27k N of Li, 78k S of Lamphun, 410m, 05/06/63, Merrill 5457 (fl.) (L); *Sukothai Province* (11 – N), Muang Gow District, near PraTahDueNahmDokSoGachana Temle, 6/11/71, Maxwell71-746 (fl.) (BK); *Sakon Nakhon Province* (20 – NE); Phuphan NP, 300m, 8-5-97, Pooma 1628 (CMU); Punna Ni kom, 28/6/32, Lakshnakara 1078 (BK); *Chaiyaphum Province* (25 – E); Ban Lui Lai, 700m, 15.40N 102.0E, 25/05/74, Geesink *et al.* 6940 (fl.) (L); Kang Keo, 28/10/65, Sakol Suthisorn 676 (BK); *Surin Province* (28 - E); Kao Sawai, 18/5/65, Sakol 251 (fl.) (BK); *Sisaket Province* (31 – E); Kantralak district, 14/4/66, Prayad Sangkhashand 250 (fl.) (BK); Kantralak district 28/4/66, Prayad Sangkhachand 285 (BK); *Ubon Ratchathani Province* (32 – E); Ubon Ratchathani, 10/6/32, Lakshnakara 884, (BK); *Prachaup Khiri Khan Province* (37 – SW); Pran, 50m, 15/7/26, Kerr 10990 (fl.) (BK); Awng Kau, 1/10/27, D.Collins 1581 (fr.) (BK); *Nakhon Pathom Province* (46 – C); Mak Daahan, Lakawn Pasam, c. 100m, 14/5/32 Kerr 21459 (BK); *Nakhon Nayok Province* (45 – C); Nang Tae-Keai, 25/3/75, Sakol Sutheesorn 3240 (BK); *Saraburi Province* (47 - C); Sahm Lahn, 125m 14/04/74 Maxwell 74-285 (fl.) (BK, L); Sahm Lahm Forest, 200m, 14/07/74, Maxwell 74-715 (fr.) (BK, L); Sahm Lahn Forest, 125m 26/07/75 Maxwell 75-718 (fr.) (BK, L); *Chon Buri Province* (55 - SE); Sattahip district, Toong Brong, near sea level, 7/10/72, Maxwell 72-430 (fl.) (BK); Sattahip district, Toong Brong, near sea level, 23/6/74, Maxwell 72-626 (fl.) (BK); Sattahip District, Toong Brong, 23/06/74, Maxwell 74-626 (fr.) (L); (BK); Sriracha, 21/05/26, Collins 1254 (fl., fr.) (BK, US); Sriracha, 13/05/27, Collins 1508 (fl., fr.) (BK, US); Sriracha District, Khao Kieo, 200m, 7/4/75, Maxwell 75-378 (BK); Sriracha district, Khao Kieo, 350m, 31/8/75, Maxwell 75-952 (fr.) (BK); Hoop farang, near Sriracha, 1/7/23, Collins 903 (BK); Wang Kenai, 10m,

16/05/27, Marcan 2214 (fl.) (BM, TCD); *Province Unknown*; Doi Wang National Park, E. side, Mae Dtawn Nai Village area, 550m, 19/6/97, Maxwell 97-678 (CMU); *Locality Unknown*; 01/07/24, Marcan 1798 (TCD).

Indonesia *Java* Preanger sur Kadipateau, 10/11/04, Hochreutiner 2516 (fl.) (L); Samoeng, 11/11/11, Leeunen 364a (fl.) (L); Surabaya, 01/01/24, Rant s.n (fl.) (L); Surabaya, 06/03/19, Backer 26572 (fl.) (L); Java c.1796 Lahaie s.n. (fl.) (G); "Uvaria javana DC", Leschenault s.n. (fl., fr.) (P); Java 1816 *s.coll.* (fl.) (TCD); *Madura*; Bangkalan, 10-50m 21/02/15, Backer 18936 (fr.) (L); North Coast, Hilly country, common, 10 - 150m, 08/03/15, Backer 19942 (fr.) (L); *Bali;* Penginuman near Gilimanuk, W. Bali, 5m, 14/10/85, van Balgooy 5268 (fl.) (L); *Sumbawa Nusa Tenggara*; 5km S of Bima, near Dessa, 70-80m, 20/02/39, Bloembergen 3155 (fr.) (L); *Buru*; Insula Bourou Sept. 1844, Laballadière s.n. (fl.) (TCD).

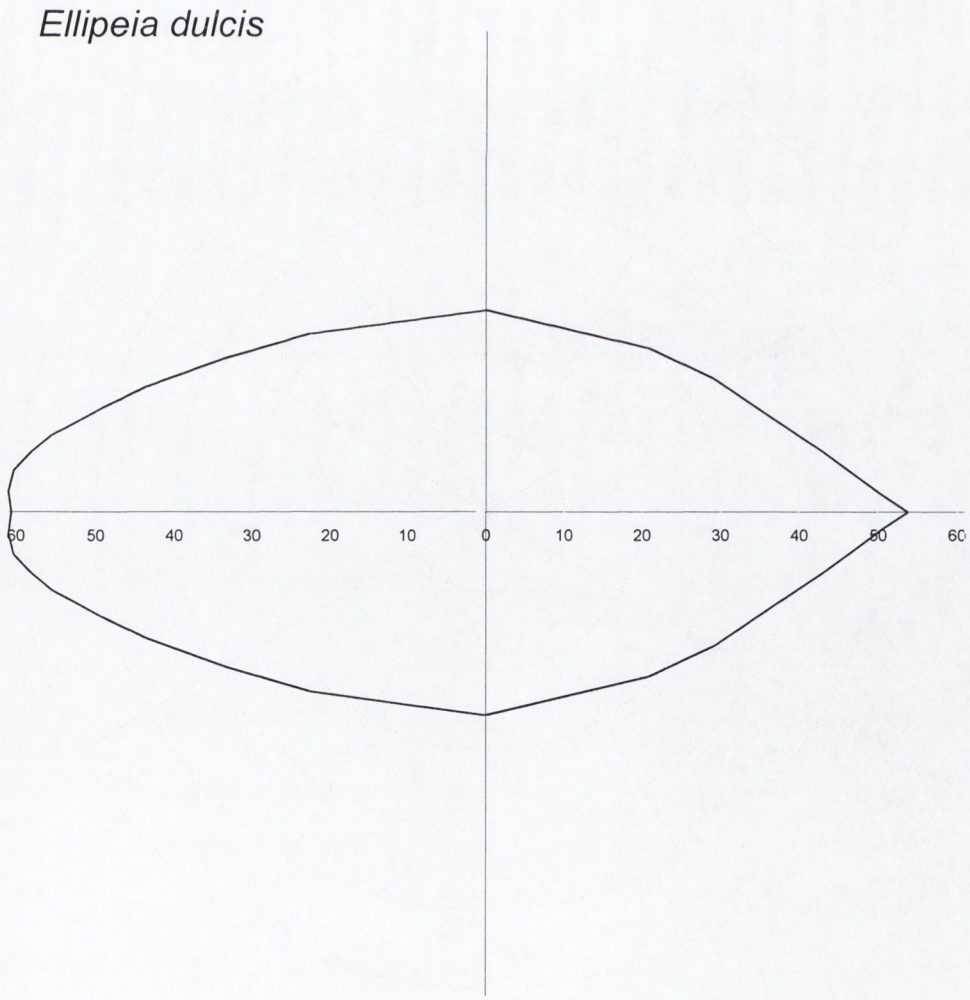


Figure 4.36. Mean leaf outline for *E. dulcis* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

2. ***Ellipeia pauciovulata*** (Hook. f. & Thoms.) C. Meade *comb. nov.*

Uvaria pauciovulata Hook. f. & Thoms., Fl. Br. Ind. 1:51 (1872), lectotype (*designated here*); Maingay 104 (K!), syntypes (K! Sing!); King, J. As. Soc. Beng. 61(2)1:20 *et* Ann. Bot. Gard. Calcutta, 4:25 t. 16 (1893); Sinclair, Gard. Bull. Sing. 14(2):217 t. 9 (1955).

Habit scandent shrub or woody climber. ***Young shoots*** tomentose, hairs ferruginous, stout, c. 20+ branched, quickly becoming sparse, bark black, striate. ***Leaves*** (ovate-) elliptic-narrowly obovate, base shortly cordate/retuse, apex acute, 95-140 x 50-60 mm, coriaceaous; *veins* 9-12(-14) sub-parallel, almost perpendicular to midrib at base then arching gradually, trailing trace usually fine, sometimes forming distinct sub-marginal vein on lower surface, inter-primaries occasional, secondary veins complete, slightly kinked, midrib and primary veins sunken above, emergent below, microvenation indistinct above, prominent below; *indument* hairs many-branched, ferruginous, young leaves with sparse hairs on both surfaces, at maturity abaxial surface glabrous, adaxial blade sub-glabrous becoming sparse to tomentose on vein bases and midrib. ***Petiole*** c. 4-5 x 1.5 mm, sparse to sub-tomentose, warty. ***Inflorescence*** terminal, cymulose, flowers 1 or 2, rarely 3, peduncle 2-7 mm long, pedicel c. 8-10 x 2.5 mm, broad and flattened, sub-tomentose to tomentose, hairs stocky, c. 20+ branched, ferruginous, bracts ovate, clasping, often enclosing floral buds, persistent, c. 9 x 5 mm, prominent central vein often visible, indument as for pedicel. ***Calyx*** sepals 3, basally connate, ovate-triangular, acute, c. 7-8 x 6-7 mm, somewhat thickened/ coriaceous, often persistent, outer surface ferrugino-tomentose as for pedicel and bracts, inner surface glabrous basally, surface black, shiny, warted, elsewhere sub-tomentose, hairs 1-5 branched, downy, combed. ***Corolla*** petals 6, white or cream in colour, large and showy, incurved, coriaceous, white or yellow, whorls unequal, outer whorl broadly obovate, c. 15-20 x 12-14 mm, base 3.5 mm, coriaceous, undulating, inner whorl narrowly obovate, c. 15-20 x 11-13 mm, base appearing much narrower, c. 2.5 mm, indument on outer surface of both whorls as for pedicel and bracts, central vein trace often covered with ferruginous hairs, inner surface of outer whorl sub-tomentose, hairs downy, straggling, 3-8 branched, petal base glabrous, black, inner surface of inner whorl almost completely glabrous except for downy indument at apex and around margins, both whorls remaining incurved. ***Stamens*** numerous, 1.25-1.5 mm, cuneate, locules uneven in length, stipitate, connective apex

globose or flattened, smooth. ***Carpels*** numerous, c. 2.5-2.75 mm, ovaries tomentose, hairs flattened and spreading, stigmas elongate with sparse stellate hairs over surface, c. 1 mm long, U-shaped with prominent longitudinal slit, ovules 1-2(-3), gynoecium dome-shaped, raised. ***Fruit*** monocarps numerous, spheroidal/ shortly oblongoidal, c. 8-23 x 9 mm diam. (length directly related to number of seeds), pericarp thin with prominent apicule, monocarps basally or sub-basally attached, stipe c. 10-15 mm x 1 mm, striate, monocarp and stipe densely and shortly tomentose. Seeds 1-2 or very rarely 3, smooth, wrapped tightly by monocarp tissue, ruminations not visible beneath surface, raphe dark, prominent. Leaf shape shown in Figure 4.37.

Var. scortechinii (King) C. Meade *comb. et stat nov.*

U. scortechinii King, J. As. Soc. Beng. 61(2)1:20 *et* Ann. Bot. Gard. Calcutta, 4:25 t. 17 (1893), types; Malaysia; 'Perak, Scortechini 1990' (A!, K! - holo); 'Perak, Scortechini s.n.' (BM!); Sinclair, Gard. Bull. Sing. 14(2):218 (1955).

Differs from the typical variety of the species in having broadly ovate-elliptical leaves with prominent, thickened venation.

Ecology and Distribution confined to lowland rainforest on the Malay Peninsula South of the Isthmus of Kra. Smitinand 10916 is a new record for Thailand. Distribution is shown in Figure 4.41.

Notes The inflorescence structure, petals, stamens, carpels and fruits of this species are closer to those of *Ellipeia cuneifolia* than to any *Uvaria* species. The major difference between it and *E. cuneifolia* is that the inner petals remain closed and imbricate over the gynoecium in *E. cuneifolia* whereas they open in *E. pauciovulata*. The single seed of *E. cuneifolia* has been looked upon as a defining character of the genus, however close examination of the fruits of *E. pauciovulata* reveal that they differ from the former only in the number of seeds present. The shape, indument and venation of the leaves in the the two species are also different. Variety *scortechinii* has identical flowers to the typical variety of the species, however the leaves are distinct. It is known only from the type specimens collected in Perak.

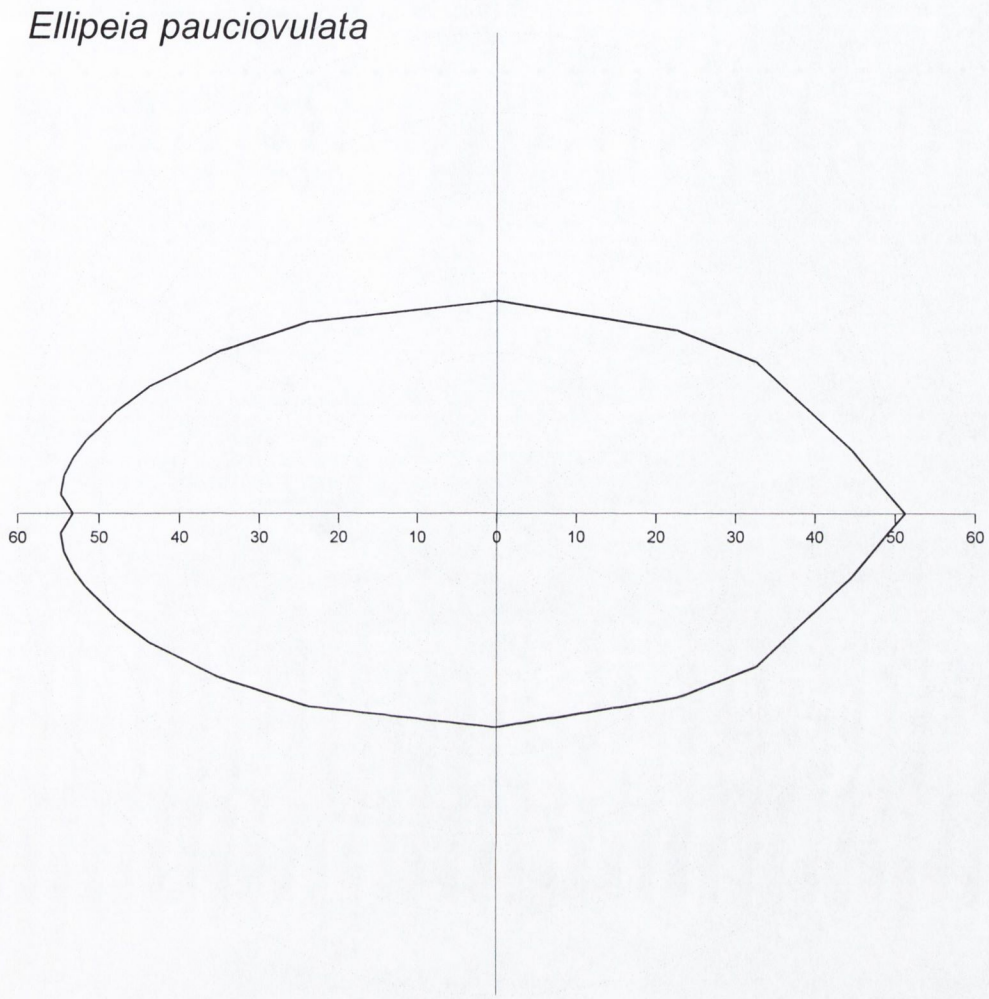


Figure 4.36. Mean leaf outline for *E. pauciovulata* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Material Examined

Thailand (new record) *Narathiwat Province* (72 - Pen.); Waeng, 13/06/70, Smitinand 10916 (fl.) (BKF).

Malaysia *Johore*; Sungkai Kayn, East Johore, 19/10/36, Kiah Sing Field No. 32128 (BM, Sing.); *Kedah*; Gunung Peali, below lower woods. Dec 1904, Ridley 12178, (Sing.); *Penang*; highlands, May 1886, Curtis 825 (-) (Sing.); *Perak*; Larut, 500-1000ft., 10/1884, King 6748 (fl., fr.) (BM); *Malacca*; 14/6/1865, Maingay 1023 (fl.)

(K); 27/5/1868 Maingay 3392 (fl.) (K); *Selangor*, Suryei Buloh, 10-5-1930, Foxworthy 17051, (Sing.); *Locality Unknown*; Maingay 1023A (fl., fr.) (K).

Singapore Bukit Timah FR, tree no. 347, 01/06/39, Ngadiman Sing. Field No. 36432 (BM, K, Sing.); Bukit Timah FR, 2/5/1953, Sinclair 39578 (-) (Sing.); Sungkai Morai, 19/12/53, Sinclair Sing. Field No. 40179 (BM); Lai LJ74 15-10-96, Mandai Forest, Opp Jalan Lada Hitan, Lianes near water-edge. (-) (Sing.).

Var. *scortechinii*

Malaysia *Perak*; Scortechini 1990 (fl.) (A, K); Scortechini s.n (fl.) (BM).

5. NERVOPETALUM C. Meade *gen. nov.*

Uvariae affinis, frutex sarmentosus, pilis stellatis, folia elliptica vel obovata angustata, acuta vel acuminata, basi retuse, supra et subter tomentosa vel sub-glabra, inflorescentia solitaria, oppositifolia, brevipedicellata, sepala valvata, ovata-lanceolata, c. 15 x 20 mm, membranacea, nervia, sub-tomentosa, petala basi valvata, apice imbricata, nervia, angustata-ovata vel lanceolata, coriacea, basi intra glabri cum duo glandibus lateralis, monocarpia cum pericarpium verrucosum, semina 10-14.

Uvaria-like climbers or scrambling shrubs with stellate hairs, leaves elliptic to narrowly obovate, acute or acuminate, retuse, above and below tomentose to sub-glabrous, flowers solitary, leaf-opposed, pedicel short, sepals valvate, ovate-lanceolate, c. 15 x 20 mm, membranous, with prominent longitudinal veins, sub-tomentose, petals basally valvate, apically imbricate, with prominent longitudinal veins, very narrowly ovate to lanceolate, coriaceous, basally glabrous on inner surface with two c. 3 mm long marginal glands present, monocarps 10-14 seeded, pericarp verrucose.

Key to species occurring in Continental Asia

1a. Leaves membranous to coriaceous, sub-glabrous above, sub-tomentose below, apex acute – acuminate, petals c. ≥ 35 mm long .... **1a. *N. hahnii* var. *hahnii*** *Indochina and Myanmar*

1b. Leaves coriaceous, sparse above, tomentose below, apex usually acuminate, petals ≤ 30 mm long, inner petals ≤ 25 mm long .... **1b. *N. hahnii* var. *kontumiense*** *Kontum Province, Vietnam*

1a. *Nervopetalum hahnii* (Finet & Gagnep.) C.Meade *comb. nov.*

Unona hahnii Finet & Gagnep. Bull. Soc. Bot. France 52, Mém.4(2):78 (1906) et Flore Générale de L'Indo-Chine 1:59 (1907); Lectotype (*designated here*) Cambodia; 'Kampot, 13/5/04, Geoffray 385' (P!); Isotypes; 'Kampot, 3/1874, Pierre 1786=746' (P!); 'Kamchay Mts., Kampot, 26/6/1896 Hahn s.n.' (P!); *Desmos hahnii* (Finet & Gagnep.) Merr. Philipp. J. Sci. 10:235 (1915). *Uvaria hahnii* (Finet & Gagnep.) Sincl. Gard. Bull. Sing. XIV. 40 (1955). *Melodorum hahnii* (Finet & Gagnep.) Tien Ban Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):334 (1991).

Habit Scandent shrub or woody climber. ***Young shoots*** sub-tomentose, becoming glabrous, bark black with deep striations. ***Leaves*** elliptic to narrowly obovate, sub-coriaceous, apex acute-acuminate, base retuse, c. 100-160 x 40-65 mm, *veins* 9-12 (-14), gradually inarching, not always parallel, spacing varying, inter-primaries rare, secondaries kinked, tertiary venation reticulate, midrib depressed above, emergent below, microvenation flat or somewhat raised above, emergent below; *indument* abaxial blade sparse becoming glabrous, hairs 3-5 branched, fine, spreading, midrib hairs erect, c. 5+ branched, sub-tomentose becoming sparse, adaxial blade hairs mixed, smaller fine hairs 4-6 branched, sparse at first, becoming glabrous, larger ferruginous hairs erect, rare on blade, sub-tomentose on veins and midrib. ***Petiole*** c. 7 x 1 mm, black and warty, tomentose becoming sparse or sub-glabrous. ***Inflorescence*** flowers solitary, leaf-opposed, peduncle 1-3.5 mm long, pedicel c. 9-10 mm long, prominently striate, broadening to c. 2 mm diam. near receptacle, hairs tomentose, many-branched, ferruginous, bracts ovate-acute, c. 15-20 x 10-15 mm, leaf-like with prominent palmate veins, outer surface indument sparse, hairs c. 5+ branched, stocky, becoming sub-tomentose along central vein, hairs on inner surface finer, evenly spread over surface. ***Calyx*** sepals 3, valvate, ovate-lanceolate, c. 15 x 10 mm, large and leaf-like with prominent central vein, flat or convex, reflexed at maturity, inner and outer indument as for bracts. ***Corolla*** petals 6, creamy-white or yellow in colour, lanceolate-acute with prominent longitudinal veins, outer petals c. 35-45 x 10 mm, base narrowed to c. 2 mm , inner petals c. 35-45 x 6-7 mm, base narrowed to c. 1.5 mm with two c. 3 mm long marginal glands present, indument on outer surface of both whorls mixed, underlying tomentum of fine pale hairs overlain basally and along central axis by scattered 5+ branched erect ferruginous hairs, inner surface of both whorls tomentose, hairs fine, base somewhat glabrous on outer whorl, distinctly

glabrous on inner whorl. ***Stamens*** numerous, c. 2.5 mm long, cuneate, connective apex convex, humped, bright orange in colour and distinctly pappillate, locules raised, varying in length. ***Carpels*** c. 20, c. 3.5 mm long, ovary tomentose, narrowed into distinct neck below stigma, stigma c. 1 mm long, U-shaped, hairy, ovaries c. 14 in 2 rows. ***Fruits*** monocarps c. 4-8, ovoid-oblong, c. 16-10 x 9-10.5 mm, minutely striate, tomentose, pericarp thick and soft at maturity, stipe short, c. 8 mm long, seeds 10-14 in 2 rows, c. 7 x 4 x 2 mm, compressed ovoid, smooth, aril 3 x 2 mm, often transversely compressed. Leaf shape shown in Figure 4.38. Appendix 4.14A & B.

1b. Var. *kontumiense* (Tien Ban ex Phạm-hoàng Hộ) C.Meade *comb. et stat nov.*

Melodorum kontumiense Tien Ban ex Phạm-hoàng Hộ, Câycỏ Việtnam 1(1):334 (1991).

Differs from the typical variety of the species in having shorter, equally broad petals, and narrowly obovate acuminate leaves with a sub-tomentose indument on both surfaces.

Ecology and Distribution *N. hahnii* is centred in eastern Thailand and southern Indochina and is most common in the Chonburi – Pursat massif area. There is an outlying collection from Madalay in Myanmar. The species has been recorded from dryer forest habitats, but most collections are from disturbed lowland evergreen forest. Var. *kontumiense* has so far been collected only in Kontum Province (Vietnam). Distribution is shown in Figure 4.42.

Notes The narrow elongate petals and large wavy sepals and bracts of *N. hahnii* should make it easy to distinguish from *E. dulcis*, it's most similar-looking relative. Authors have differed over which is the proper genus for the plant, placing it successively in *Unona* (Finet & Gagnep.), *Desmos* (Merrill), *Uvaria* (Sinclair) and *Melodorum* (Tien Ban). There is no doubt that it shares characters with all these groups, however in each case it has been an anomoly in the host genus. The closest relatives of *N. hahnii* are the Ellipeias and *Rauwenhoffia*, and indeed the most

important floral and fruit characters place it almost exactly midway between these two genera. However, given the not inconsiderable differences between *Ellipeia* and *Rauwenhoffia* the most appropriate course of action is to place this taxon in a new genus.

Vern. *Cambodia*; Kampong Spoe Province; Khmer: 'Vo Tril' (Poilane 15169); Pursat Province; Khmer: 'Tril Sia' (Martin 246).

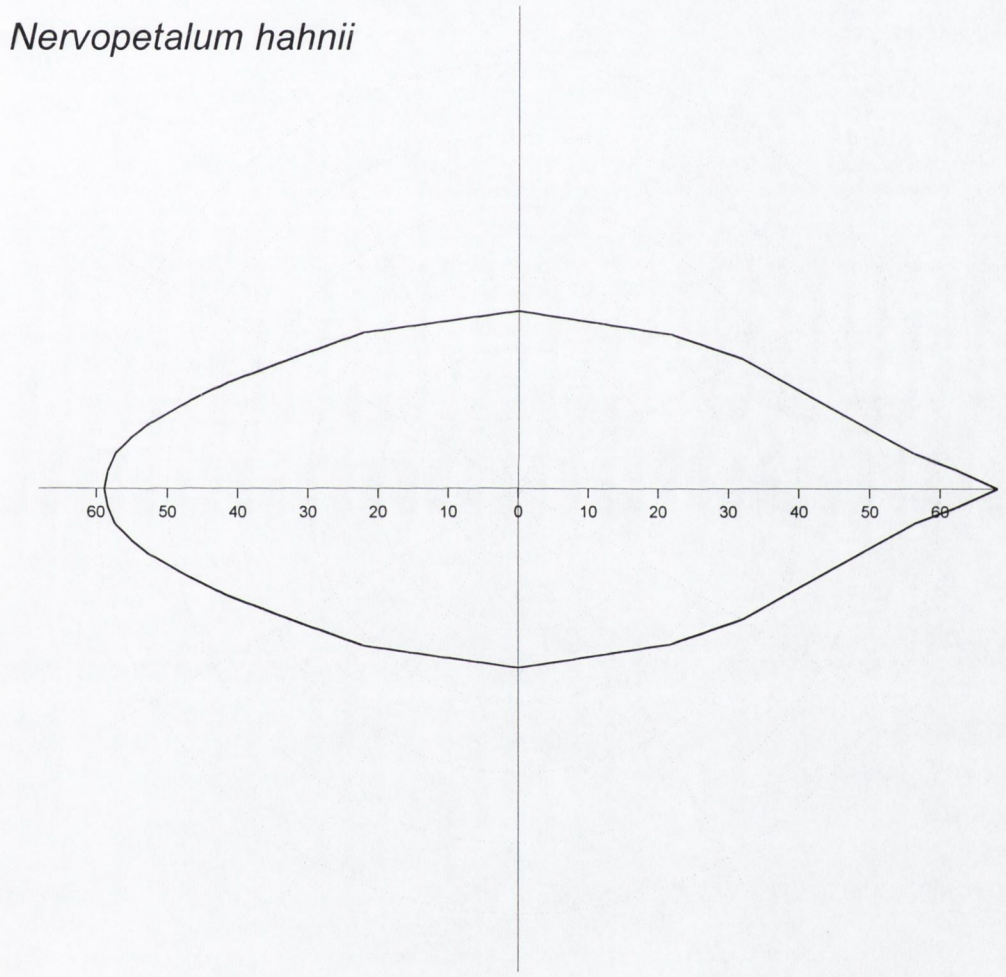


Figure 4.38. Mean leaf outline for *N. hahnii* material examined in this study. Numbers on the horizontal axis indicate distance in mm from widest point of leaf projected onto midrib.

Material Examined

Myanmar *Mandalay*; Mayniyo Plateau, 01/08/13, English 39 (fr.) (K).

Cambodia *Siem Reap* Province (C – 7 – CLV); Angkor, 1866-1868, Thorel 2102 (fl.) (P); *Pursat Province* (C - 10 - CLV); Svay Pak, 06/07/65, Martin 246 (fr.) (P); *Kampong Spoe Province* (C - 17 - CLV); Pnom Tho ma So, near Ko Virk village, 02/05/28, Poilane 15169 (fl.) (P); *Kampot Province* (C - 19 - CLV); Kamchay Mts, 26/2/1896, Hahn s.n. (fl., fr.) (P); Kampot, 3/1874, Pierre 1786 (fl.) (P); Kampot, 13/04/04, Geoffray 385 (fl.) (P); *Locality Unknown*; Pierre s.n. ex Herb. Hance no. 20172 (fl.) (BM).

Laos *Savannakhet Province* (L - 12 - CLV); Between Savannakhet and Bouthat, 27/06/29, Poilane 16333 (fr.) (P); Bouthat, 30/6/29, Poilane 16351 (fl.) (Sing.)

Thailand *Nong Kkai Province* (19 - NE); Chaiyaburi, 01/05/32, Kerr 21326 (fl.) (BM); *Nakhon Phanom Province* (21 - NE); Pu Wat, c. 300m, 16/05/32, Kerr 21498 (fl.) (BK, BM); *Sisaket Province* (31 - E); Chong Bat Lak, Kantaralak District, 14.30N 104.0E, 670m, 11/04/76, Maxwell 76-200 (fl.) (AAU, BK, L); *Saraburi Province* (44 - C); Sahm Lahn, 150m, 30/03/74, Maxwell 74-224, (fl.) (AAU, BK); *Chonburi Province* (55 - SE); Sattahip District, Toong Brong, 07/05/72, Maxwell 72-219 (fl.) (AAU, BK); Sriricha District, Khao Kieo, 350m, 07/04/75, Maxwell 75-366 (fl.) (AAU, BK, L); Sriracha District, Khao Kieo, 13.16N 101.5E, 400m, 18/04/76, Maxwell 76-245 (fl.) (AAU, BK); Sriracha, Nong Nam Kro, 100 m, 05/04/20, Kerr 4171 (fl.) (AAU, BK, BM, K); *Rayong Province* (56 - SE); Ban Pe, 19/02/30, Put 2707 (fl.) (BK, E, K, TCD); *Chanthaburi Province* (57 - SE); Khao Phra Bat, N. of Chanthaburi, 12.52N 102.10E, 100m 27/08/72, Larsen et al. 32104 (fr.) (AAU); *Trat Province* (58 - SE), Khao Saming, 01/04/25, Noe 53 (fl.) (BK, E, K, TCD);

Var. *kontumiense*

Vietnam Kontum Province (V – 30 – CLV); Kon plong, 16/4/78, K.Dao 258 (fl.) (HCMC); Moray Dak To, 3/4/78, Ly 430 (fl.) (HCMC); Moray Dak To, 4/4/78, K.Dao 215 (fl.) (HCMC).

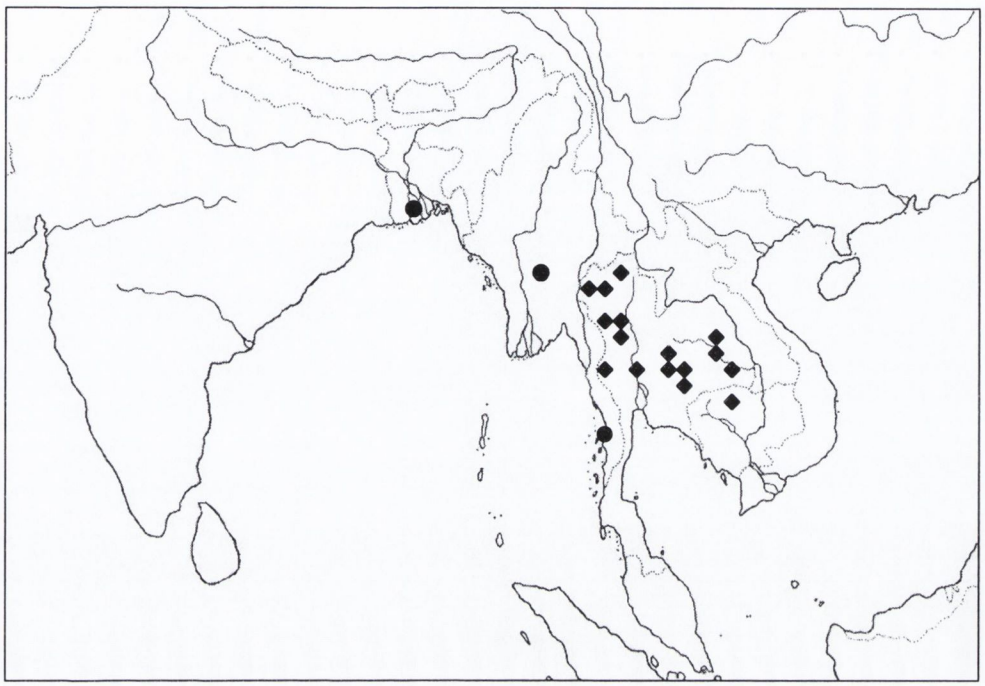


Figure 4.38.. *Ellipeiopsis ferruginea* (Buch-Ham. ex Hook. f. & Thoms.) R. E. Fr. ◆ var. *ferruginea* ● var. *cherrevensis*

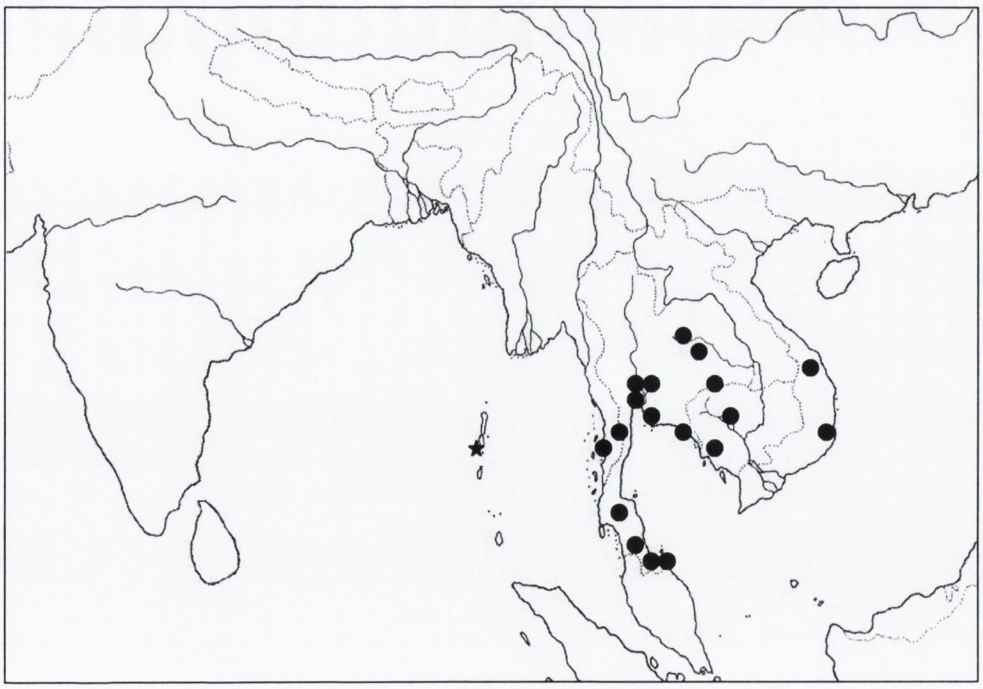


Figure 4.39. ● *Rauwenhoffia siamensis* Scheff. ★ *Uvaria lamponga* Scheff.

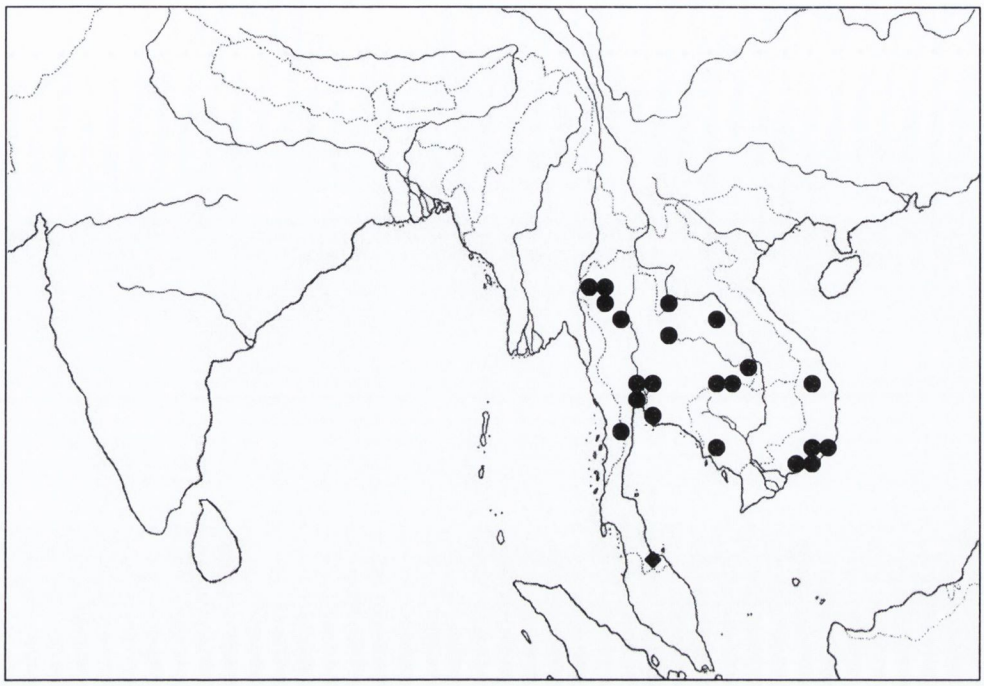


Figure 4.40. ● *Ellipeia dulcis* (Dunal) C. Meade *comb. nov.* ◆ *E. pauciovulata* (Hook. f. & Thoms.) C. Meade *comb. nov.*

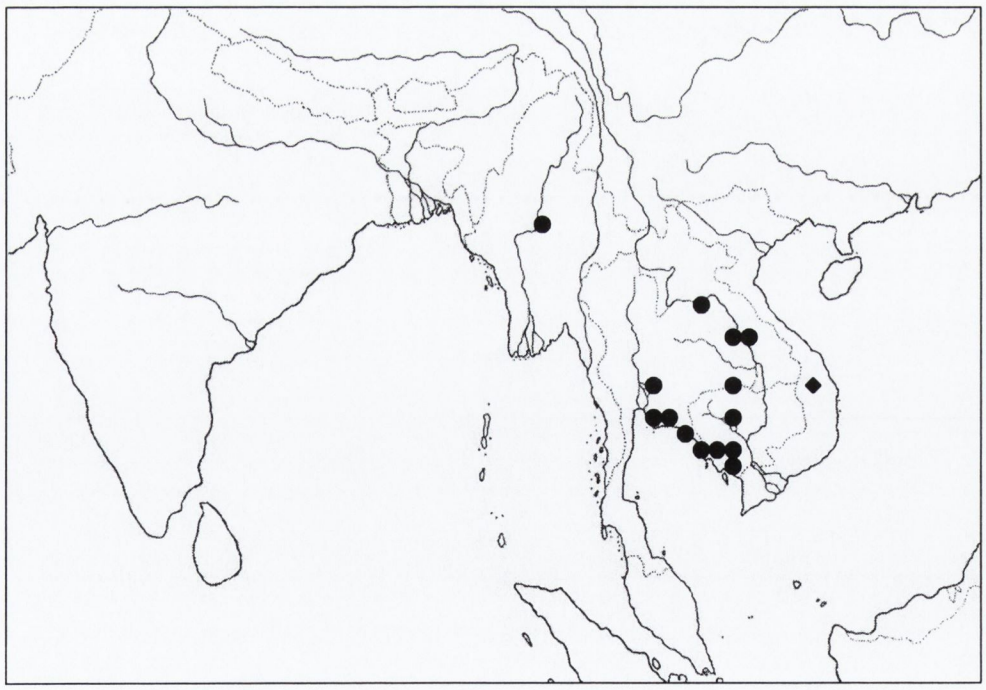


Figure 4.41. *Nervopetalum hahnii* (Finet & Gagnep.) C. Meade *comb. nov.* ● var. *hahnii* ◆ var. *kontumiense* Tien Ban ex. C. Meade *comb. nov.*

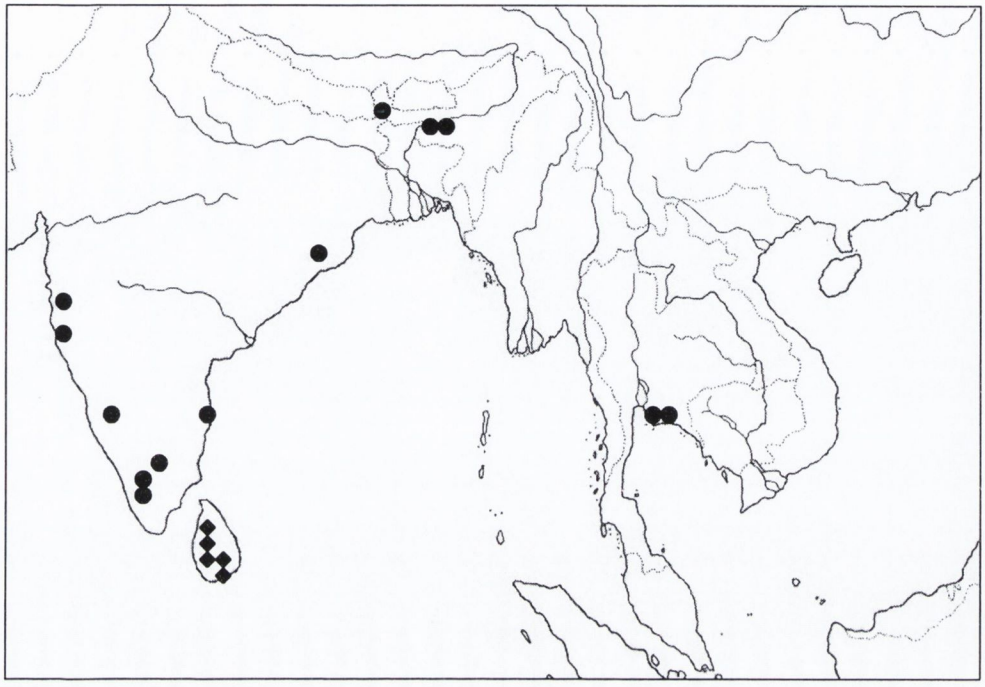


Figure 4.42. ● *Uvaria lurida* Hook. f. & Thoms. ◆ *U. macropoda* Hook. f. & Thoms.

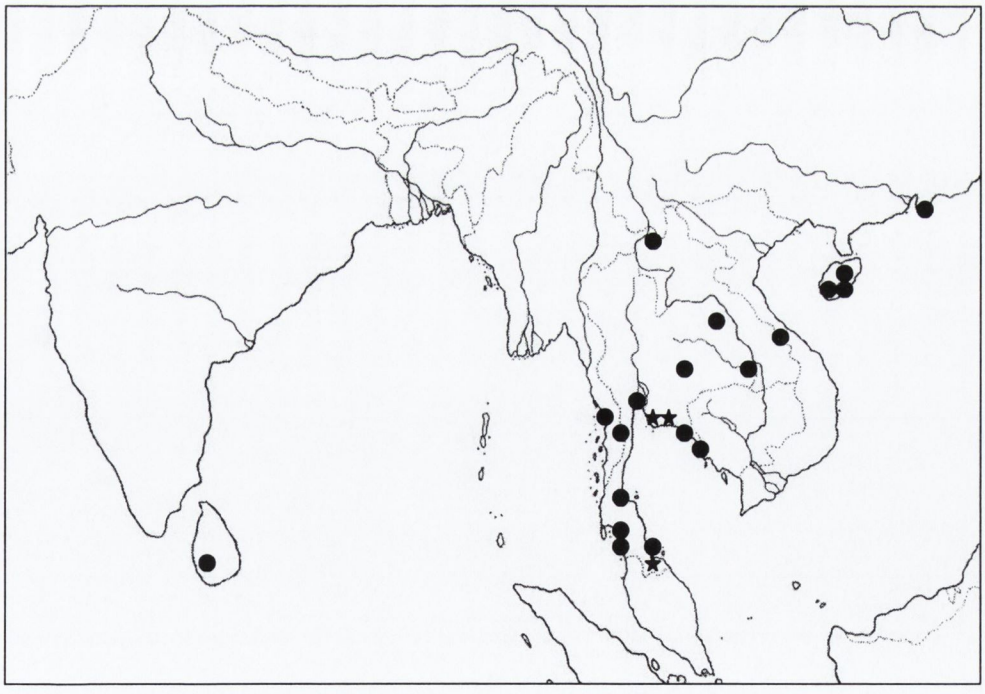


Figure 4.43. *Uvaria grandiflora* Roxb. Ex Hornem. ● var. *grandiflora* ★ var. *flava*

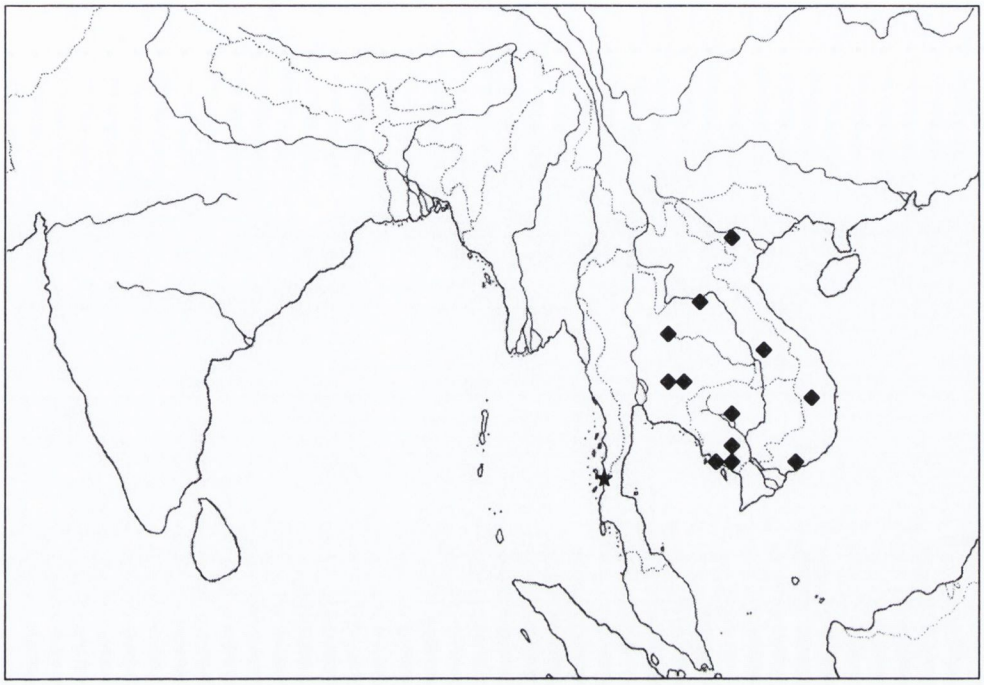


Figure 4.44. ★ *Uvaria curtisii* King ◆ *U. dac* Pierre ex. Finet & Gagnep.

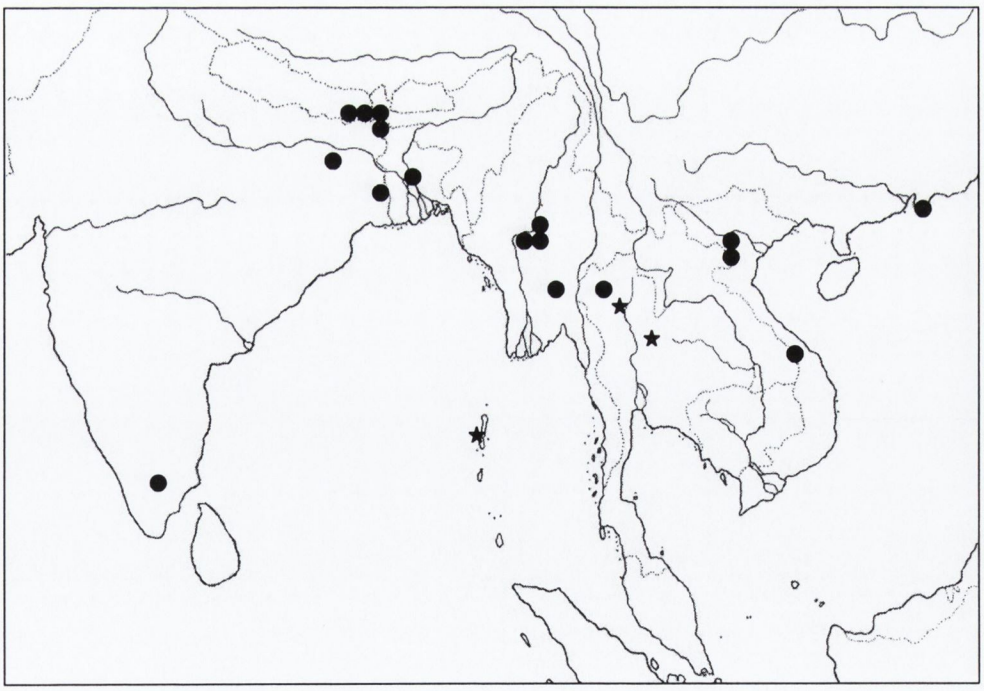


Figure 4.45. *Uvaria hamiltonii* Hook. f. & Thoms. ● var. *hamiltonii*
★ var. *kurzii*

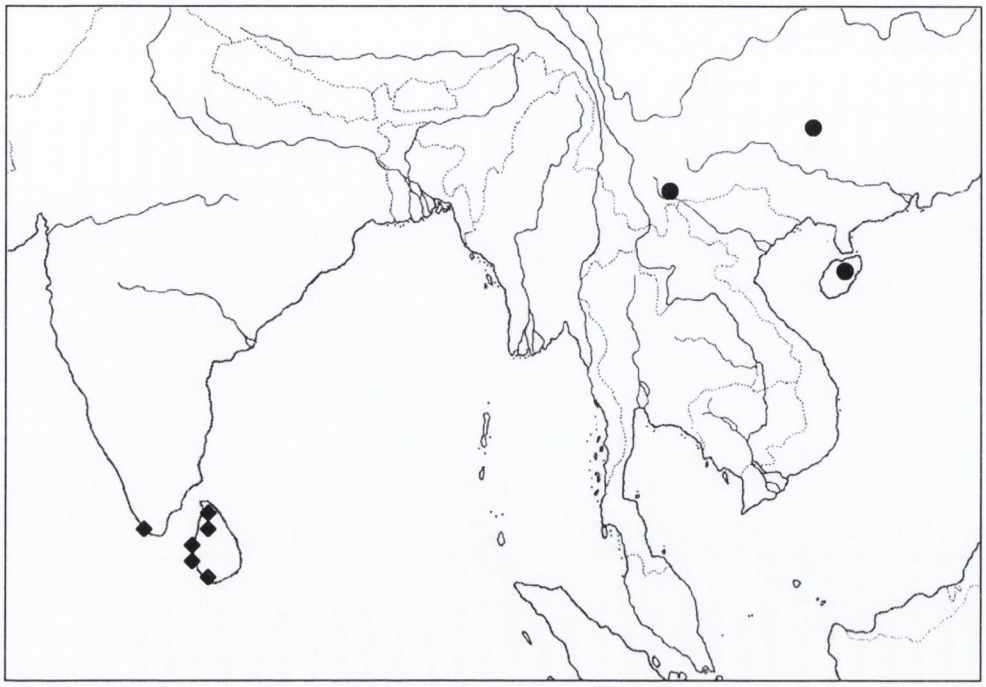


Figure 4.46. ● *Uvaria maclurei* Diels ◆ *Uvaria zeylanica* L.

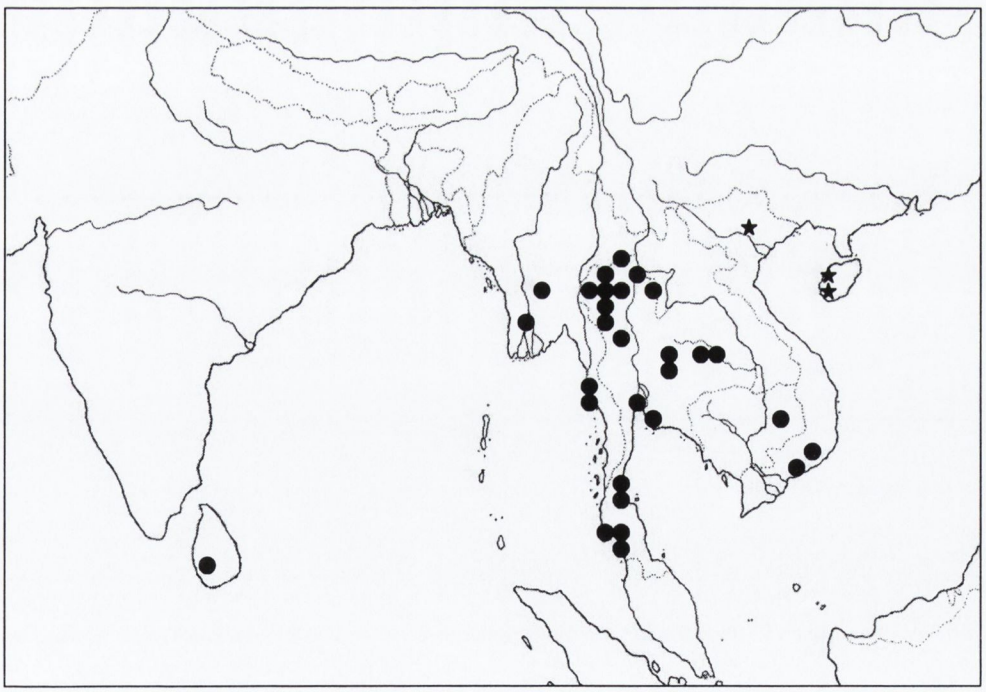


Figure 4.47. ★ *Uvaria calamistrata* Hance ● *U. cordata* (Dunal) Alston

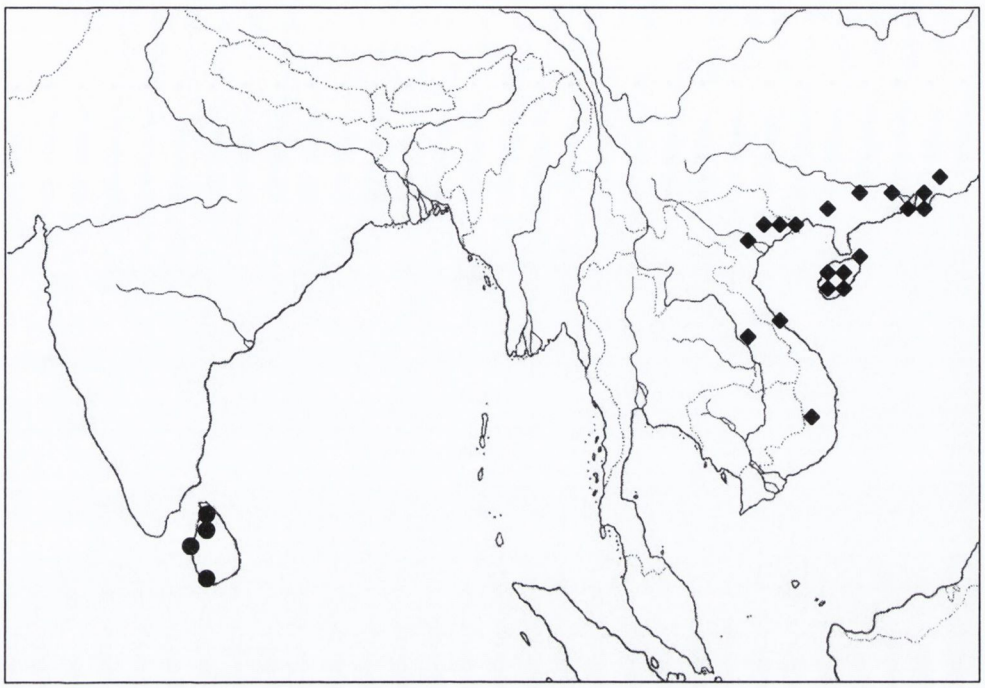


Figure 4.48. ● *Uvaria sphenocarpa* Hook. f. & Thoms. ◆*U. microcarpa* Champ. ex Benth

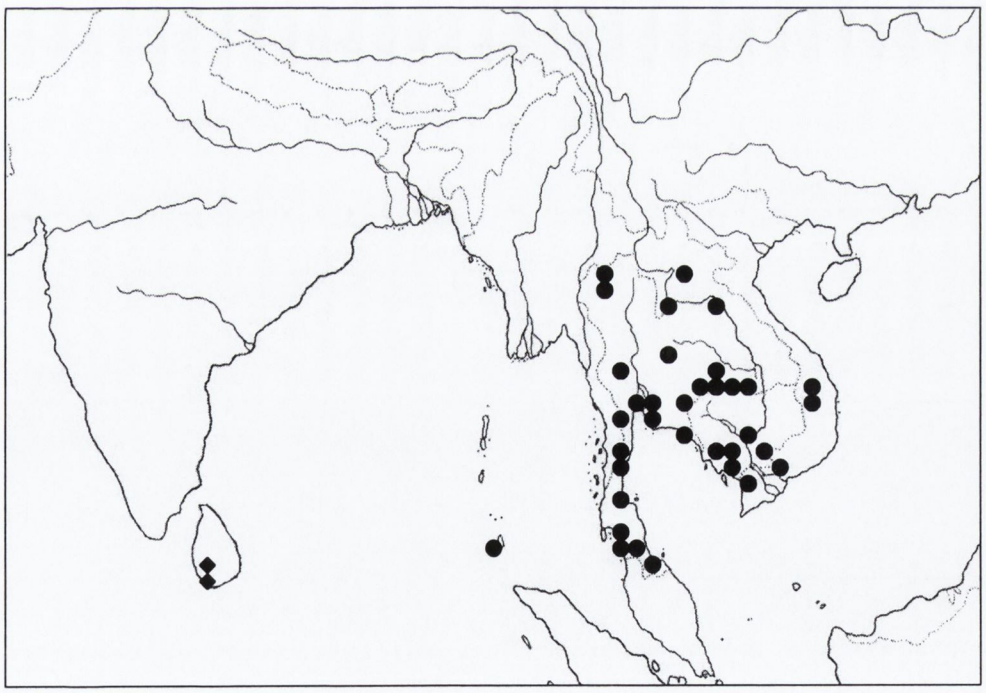


Figure 4.49. ◆ *Uvaria semicarpifolia* Hook. f. & Thoms. ● *U. rufa* (Dunal) C. Meade *comb. nov.*

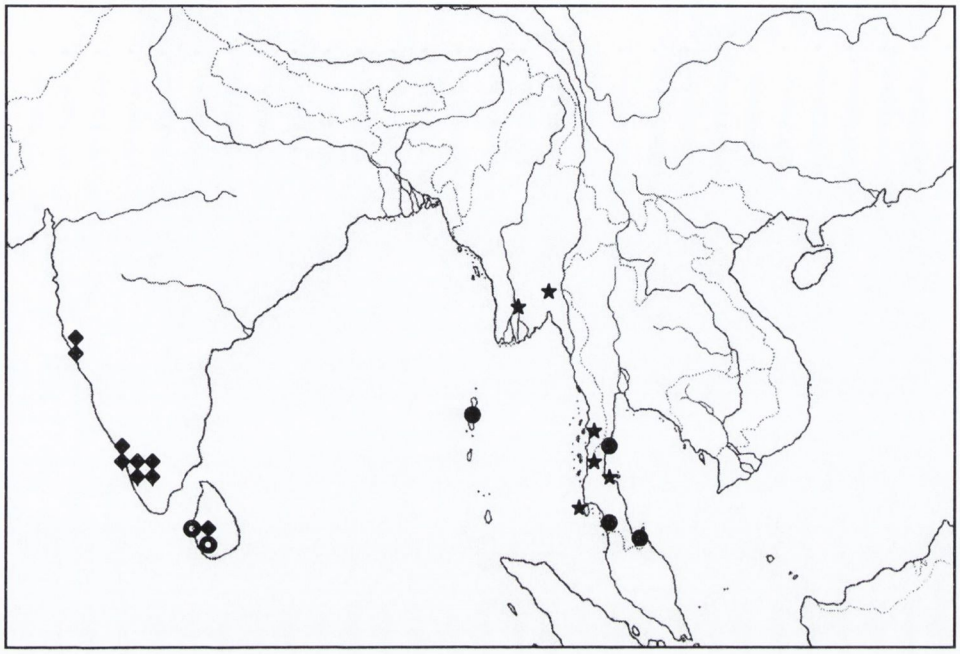


Figure 4.50. *Uvaria narum* (Dunal) Bl. ◆ var. *narum* ⊙ var. *macraei* C. Meade *var. nov.* *U. lobbiana* Hook. f. & Thoms. ● var. *lobbiana* ★ var. *ptychocalyx* (Miq.) C. Meade *comb.* et *stat. nov.*

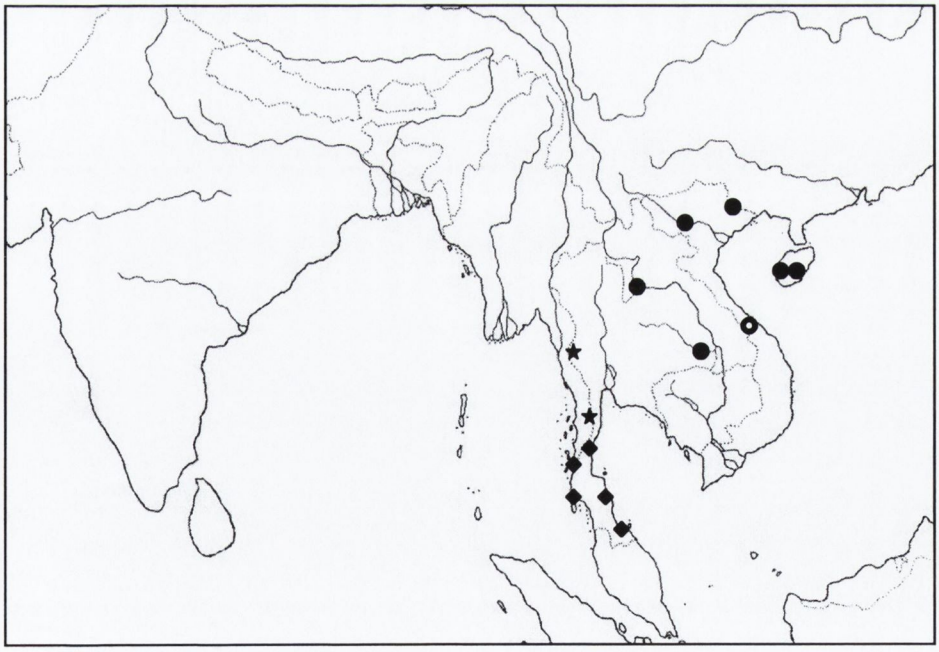


Figure 4.51. ◆ *Uvaria wrayii* (King) C. Meade *comb. nov.* ★ *U. kerrii* C. Meade *sp. nov.* ● *U. tonkinensis* Finet & Gagnep. ⊙ *U. orientalis* (Jovet-Ast.) C. Meade *nom. nov.*

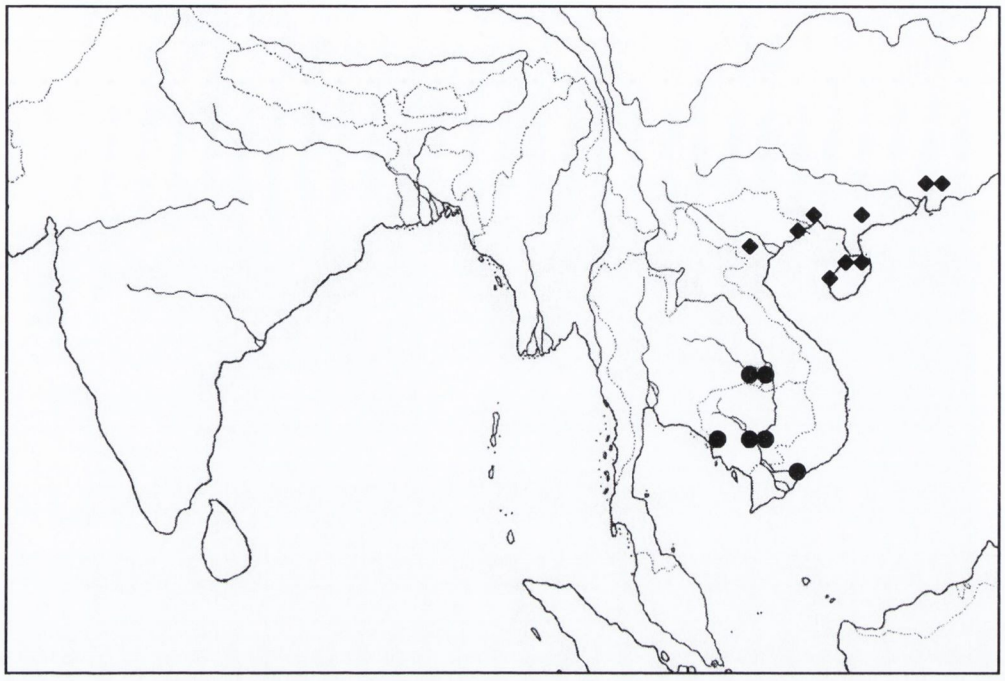


Figure 4.52. ● *Uvaria pierrei* Finet & Gagnep. ◆ *U. boniana* Pierre ex Finet & Gagnep.

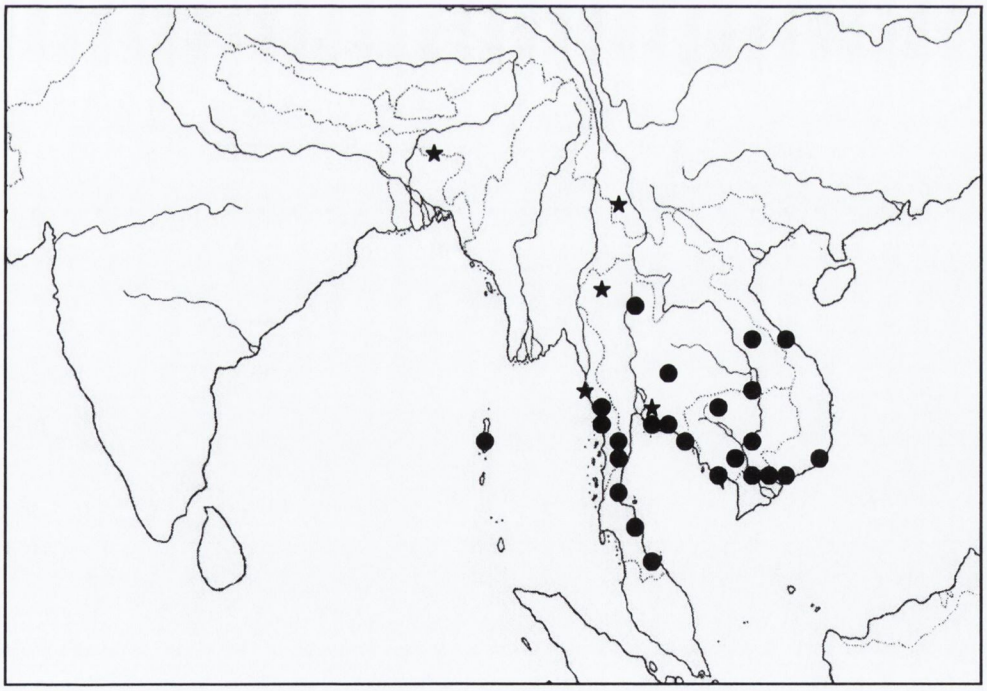


Figure 4.53. ● *Uvaria mictrantha* (A. DC.) Hook. f. & Thoms. ★ *U. argentea Bl.* var. *bracteata* (Roxb.) C. Meade *comb. et stat. nov.*

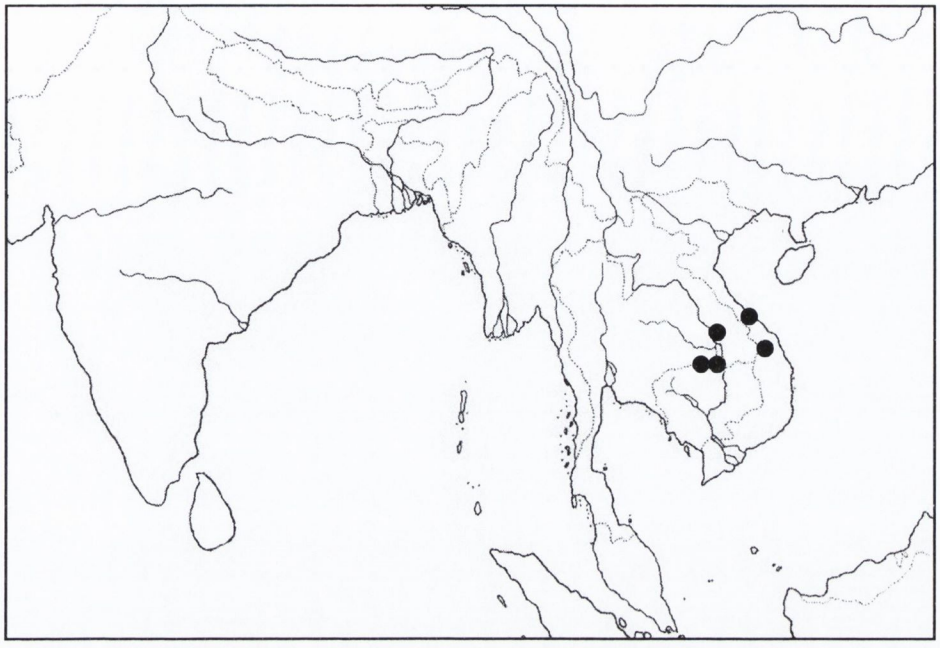


Figure 4.53. ● *Uvaria vietnamensis* Jovet-Ast ex C. Meade *sp. nov.*

CHAPTER 5 - DISCUSSION

Biogeographic and Ecological Patterns

Prior to this revision one of the main questions relating to the biogeography of *Uvaria* and its allies was whether or not the group as a whole was divided into distinct African and Asian elements. In other words, were *Uvaria* and its affiliates in Asia derived from a single radiation on the continent, or did the various groups have distinct phylogenetic origins which preceeded the current geographical disjunction of *Uvaria* between Asia and Africa. One of the most significant findings of the combined phylogenetic analysis in Chapter 2 is that the African and Asian elements of *Uvaria* emerge in a single monophyletic group, quite apart from the *Ellipeia* clade. The inference of this result is that *Uvaria* has evolved in Africa and Asia subsequent to separation from its Asian affiliates.

What remains unanswered is whether the genus originated in Asia or Africa. The fact that the African element is nested within a larger Asian *Uvaria* group suggests that the genus first emerged in Asia and then spread to Africa. How might this have happened? The hypothetical centre of origin for the family as a whole is Amazonia-West Africa (Raven & Axelrod, 1974; Le Thomas, 1982). This would imply the movement of a proto-Uvarian ancestor into Asia, followed by a recolonisation of Africa after the lineage separated from the remainder of the *Uvaria* group.

Raven (1979) has outlined the possibility of extensive migrations between Eurasia and Africa across an intermittent link between North Africa and Southern Europe in the Eocene (c. 35 million years BP), when both areas were characterised by a moist tropical climate. Chandler (1964) has confirmed the presence of Annonaceae pollen in Europe at this time, and this suggests the possibility that return migration by Annonaceae was possible from Eurasia back to Africa. This scenario would facilitate the type of migration involved in an Asia-based hypothesis on the origin of *Uvaria*.

If *Uvaria* originated in Africa, then it is reasonable to assume that the *Ellipeia* lineage emerged there also and spread to Asia in a separate migration from that of *Uvaria*. Again, the proximity of Africa and Eurasia during the Eocene may have facilitated this parallel migration pattern.

The final possibility is that the *Uvaria* and *Ellipeia* clades spread between Africa and Asia via India. This scenario allows for the possibility that after India separated from Africa and Madagascar some 70 million years BP either (a) the two lineages arose from a common ancestor in India or (b) they arrived in India by separate migrations from Africa. The results of this research are inconclusive on this matter. Future work could address this question directly by trying to identify the sister clade to the *Uvaria* group.

The Indian subcontinent and Indochina both contain centres of endemism for the *Uvaria* group. In Sri Lanka and the Malabar Coast (Regions 1 and 1a in Figure 5.1) there are seven *Uvaria* species in total, and of these five are endemic. In Indochina there are two areas with a distinct pattern of endemism (Regions 2 and 3 in Figure 5.1), and these contain 8 endemic species in total. Region 4 in Figure 5.1 represents a centre of endemism which extends into Peninsular Malaysia but not onto the Sunda islands. Three species are endemic to this region in Thailand, however up to four more share this distribution in Peninsular Malaysia (*U. leptopoda* King, *Cyathostemma viridiflorum* Griffith, *Cyathostemma hookeri* King, *Cyathostemma acuminatum* King). Three species are endemic to the broader Indochina region (Region 5 in Figure 5.1), while a fourth, *Ellipeia dulcis* is found in this region and in the lesser Sunda Islands, but is absent from Peninsular Malaysia, Borneo and Sumatra.

Most species in the group which occur in Continental Asia and Malesia display a similar distribution pattern in Indochina, being largely absent from Northern Indochina (Figure 5.2). However, in India *Uvaria lurida* and *U. cordata* show completely different distributions, the former extending throughout the Deccan Peninsula from Sikkim to Karnataka, while the latter is found only in Sri Lanka. With regard to the floristic regions of Takhtajan (1986), there are 5 species endemic to the Indian Region and 11 endemic to the Indochinese Region. In general the distribution patterns of the *Uvaria* group mirror those outlined by Baker *et al.* (1998), Morley (1988) and Ridder Numan (1995, 1998), which show a much reduced taxonomic diversity for a variety of Asian groups in India relative to Southeast Asia.

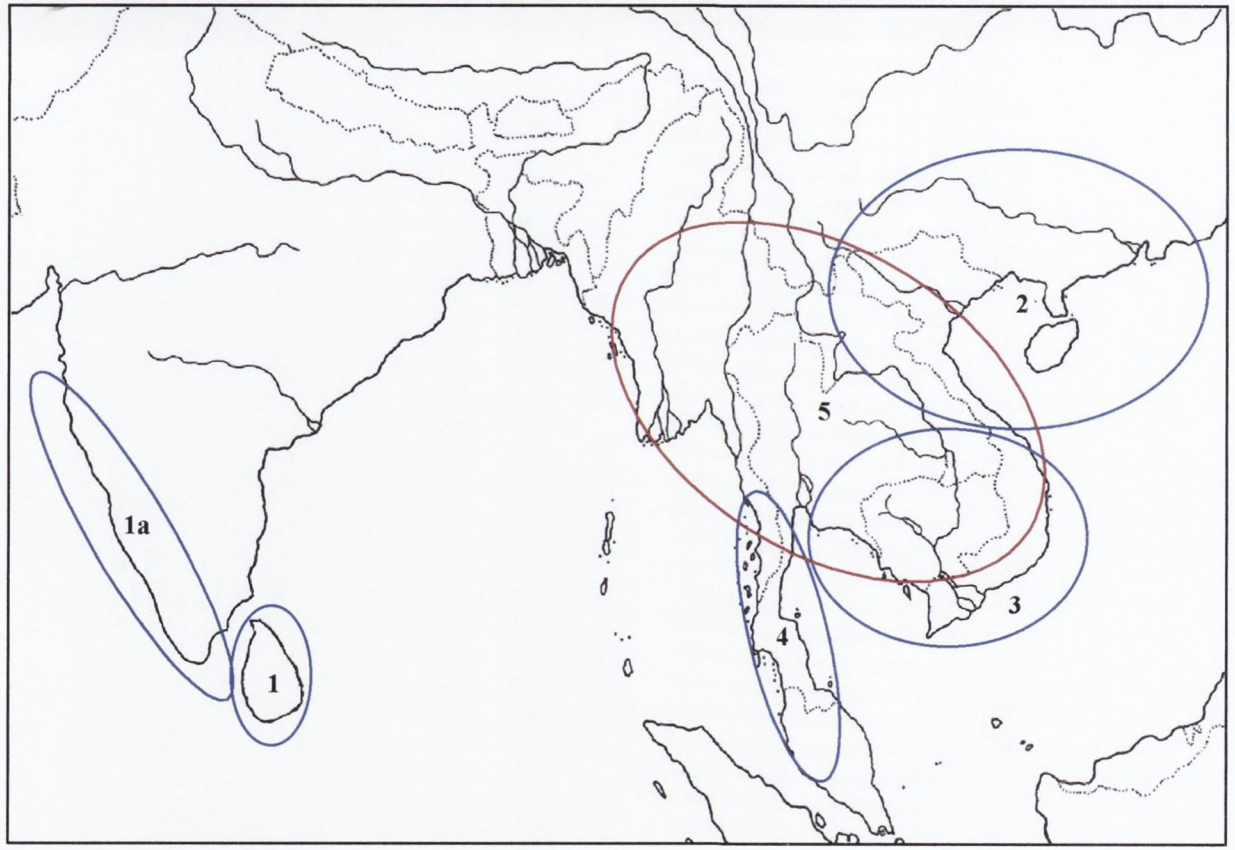


Figure 5.1. Distribution patterns for selected *Uvaria* group taxa whose distributions are confined to Continental Asia. **1.** Sri Lanka. *U. sphenocarpa*, *U. semicarpifolia*, *U. macropoda*. **1a**. Sri Lanka and the Malabar Coast. *U. zeylanica*, *U. narum*. **2.** Northern Indochina. *U. maclurei*, *U. calamistrata*, *U. microcarpa*, *U. tonkinensis*, *U. boniana*, *U. orientalis*. **3**. Southern Indochina. *U. pierrei*, *U. vietnamensis*. **4**. Peninsular Thailand. *U. wrayi*, *U. curtisii*, *Ellipeia pauciovulata*. **5**. Indochina. *U. dac, Ellipeopsis ferruginea*, *Nervopetalum hahnii*.

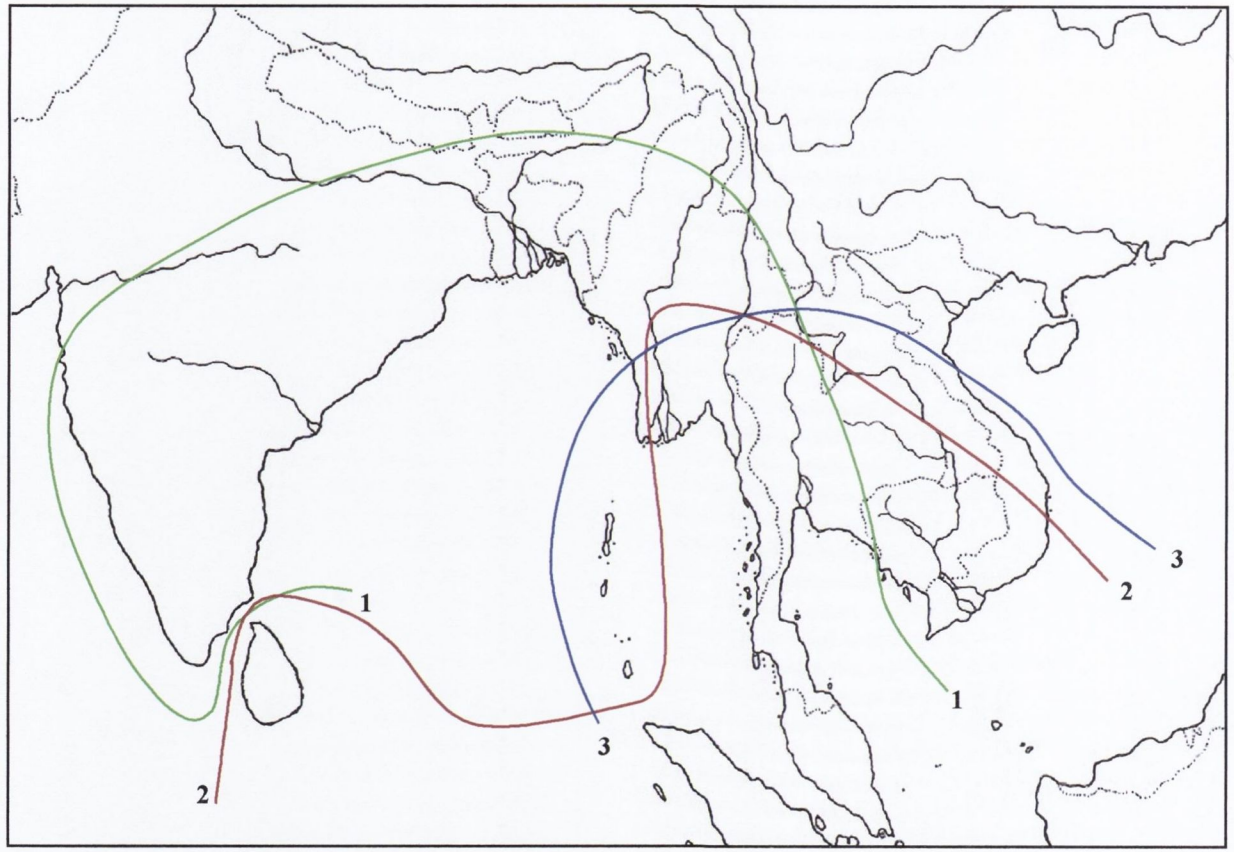


Figure 5.2. Distribution patterns for selected *Uvaria* group taxa whose distributions extend into Malesia.

— *1. Uvaria lurida*

— *2. U. cordata*

— *3. U. rufa, U. micrantha*

Over the course of this revision, Malesian material has been examined extensively, partly because type material is often Malesian, and partly because many Malesian taxa share a very close relationship with just three species - *U. rufa*, *U. grandiflora* and *U. cordata,* all of which are common in Indochina. Many Malesian taxa appear to be only marginally different from these three species, and the flora as a whole does not exhibit the variety of form seen in the Continental element. However, it is probable that the overall species diversity of Uvarias in Malesia is higher than in Continental Asia, and Borneo in particular seems certain to contain many more species than are currently documented.

This study has confirmed that *Uvaria* group taxa are overwhelmingly restricted to well-watered soils. There is also an interesting relationship between rainfall patterns and the distribution of the group (Figures 5.3 and 5.4), with the apparent distribution in Southern China and India - Sri Lanka showing a remarkable correlation with wetter climate areas. The wetter parts of Indochina (Peninsular Thailand - Myanamar and Southeast Thailand - Northwest Cambodia) are also characterised by a large number of collections, whereas the drier central parts (with the exception of the Mekong floodplain) show a lower level of collections. Central and Northern Thailand have yielded a large number of collections, and this is a function both of the higher intensity of botanical collecting, and the widespread occurrence of mixed deciduous and dry evergreen forests in these areas.

Only one taxon in the Asian *Uvaria* group, *Ellipeiopsis ferruginea*, is common in dryer Dipterocarp forest types, however it is absent from the open Dipterocarp forest typical of dryer, freely-draining soils. *Ellipeia dulcis* has an unusual distribtion - it is common in mixed deciduous forests of central and southern Thailand- Indochina and the same habitats in Java and Timor, but is absent from the more well-watered lowland forests of the Peninsular Thailand and Malaysia.

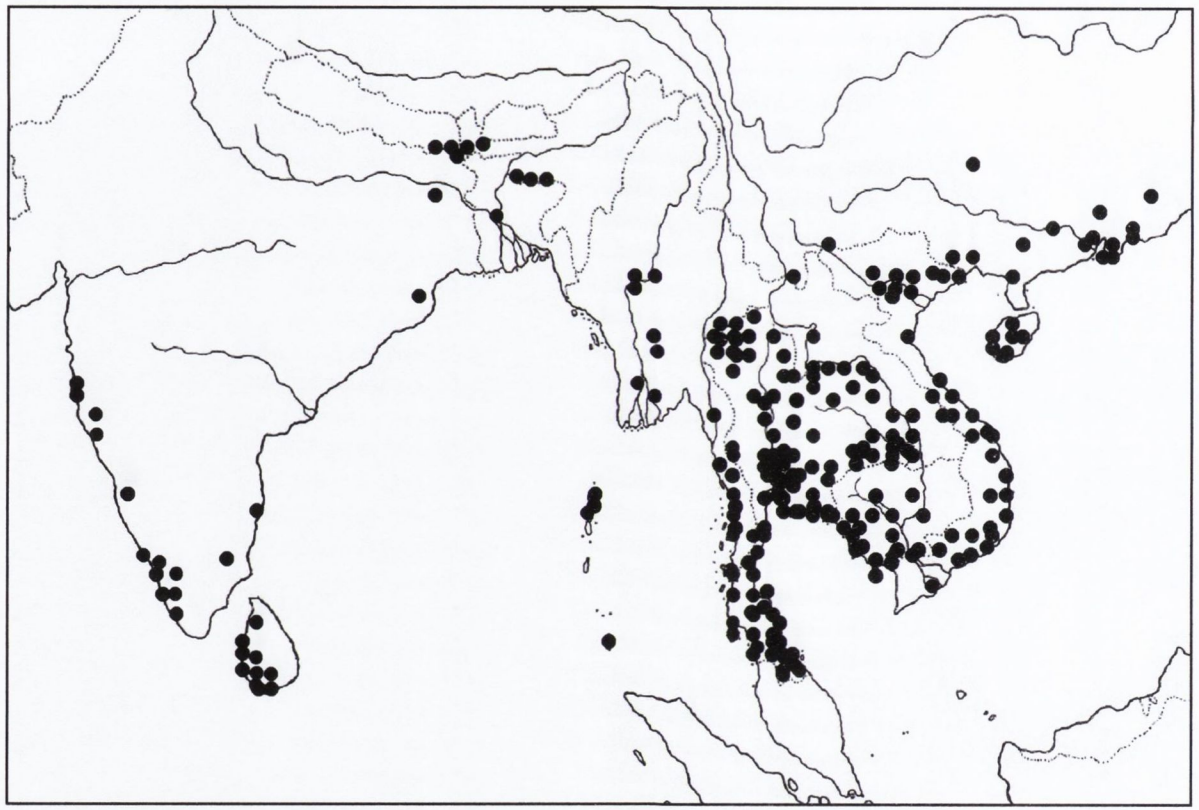


Figure 5.3. Distribution of *Uvaria* group in Continental Asia. Each dot represents a collection locality. (Certain localities have been collected several times.)

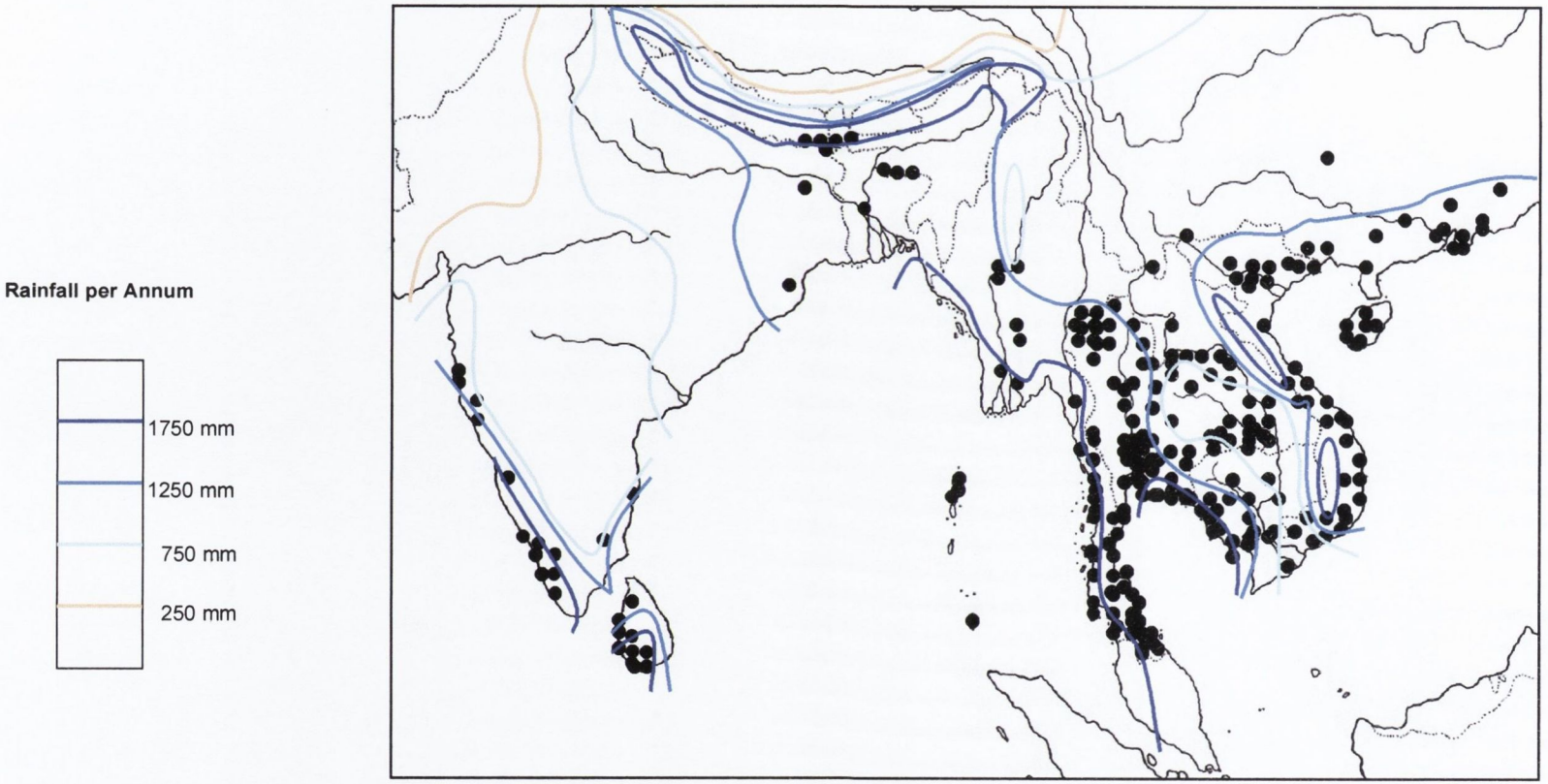


Figure 5.4. Distribution of *Uvaria* group in Continental Asia relative to mean annual rainfall patterns.

The most common habitat for *Uvaria* in Asia is lowland evergreen forest, and the forests of Peninsular Thailand - Taninthari and Southeast Thailand - Northwest Cambodia contain the greatest overall diversity of species in the region. Of the widespread species, *U. rufa* and *U. cordata* are the most vigorous, being common wherever mixed and evergreen lowland forest has been disturbed. Several species are typically found in elevated forests, including *U. hamiltonii*, *U. grandiflora* and *U. argentea var. bracteata*. *Uvaria boniana* and *U. calamistrata* are common in disturbed hillside forests in China, particularly where there are residues of deeper alluvial soil. *Uvaria pierrei* shows an interesting distribution, being centered along the banks and tributaries of the lower Mekong. *Uvaria orientalis* and *U. kerrii* are the rarest species in the region, with one and two collections each, however both come from areas where botanical collecting appears to have been quite limited.

Results of Morphological and Molecular Analyses

The phylogenetic investigations detailed in Chapter 2 have been largely successful in addressing the main questions of interest in this revision. Clear patterns of character evolution have been established and this will, it must be hoped, revive some level of confidence in the utility of morphological characters for phylogenetic analysis in the Annonaceae. One finding which should be of interest to other workers in this regard is the importance of stamen and carpel structure. These characters proved to be more reliable and informative than any characters based on the shape, aestivation or texture of the sepals and petals. In addition, stigma structure emerged as being more important than ovule number for determining basal divisions in the group.

However, while the outcome of this particular analysis has been successful, it would be unwise to infer that floral characters can be useful at all levels of investigation (other workers have clearly shown that this is not the case). A more realistic assessment would be to say that where characters are properly studied, they can be informative. However, in the absence of other phylogentic data (anatomical, palynological, molecular sequence data etc.) the task of interpreting floral homology above the 'tribal' level is extremely difficult.

In terms of the molecular data, time constraints meant that the sample size was slightly smaller than would have been preferred. Equally, it would have been preferable to have sequenced the trnL-F region as well as the ITS region. However, although these disappointments limited the scope of what could be done, they did not undermine the analysis which was actually completed.

Phenetic analysis of morphological variance proved to be very effective in delimiting taxonomic divisions in the absence of discrete characters. For both the *Uvaria narum* complex and *Uvaria cordata* - *U. microcarpa*, a suite of characters were identified which, when used together, can unambiguously identify the taxa concerned. Analysis of leaf variation was also successful in identifying patterns, albeit in a more subtle context. The composite leaf shapes generated for each taxon bear a remarkable similarity to the 'bauplan' which one (subconsciously) looks for when trying to confirm the identity of a particular species, without ever *exactly* resembling the leaves of any particular sample. To see this numerical representation of what is normally identified intuitively is a pleasant outcome, not least because it provides a small nugget of evidence to justify our faith in the great botanists of the past who simply *saw* the patterns in nature, and organised it accordingly.

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Appendices

Laurus tulipifera, baccis calyculatis. *Raj. hist.* 1690.

fœtida. β. Magnolia foliis ovato-oblongis subtus viridibus. *Anon.*
Magnolia altissima, flore ingenti candido. *Catesb. car.* 2. *p.* 61. *t.* 61. *Ehret. pict.*
Magnolia amplissimo folio, fructu cæruleo. *Plum. gen.* 38.
Magnolia flore maximo albo fœtido, foliis deciduis amplis, florum ad ramulorum seriem sphærice cingentibus, fructu majori. *Gron. virg.* 61.

grisea. γ. Magnolia foliis ovato-oblongis subtus griseis. *Anon.*
Laurus tulipifera, foliis subtus ex cinereo aut argenteo purpurascentibus. *Raj. hist.* 1718.

tripetala. δ. Magnolia amplissimo flore albo, fructu coccineo. *Catesb. car.* 2. *p.* 80. *t.* 80.

acuminata. ε. Magnolia flore albo, folio majore acumniato haud albicante. *Catesb. car.* 2. *p.* 15. *t.* 15. *Gron. virg.* 61.
Habitat in Virginia, Carolina. ♄
Utrum hæ: α. β. γ. δ. ε. sint distinctæ, determinent autoptæ in solo naturali? harum.
δ. Petalis tribus exterioribus reflexis.
ε. Foliis ovatis acuminatis.
β. Flore maximo & longiore in diametro quam foliorum longitudo & Foliis subtus griseis.

MICHELIA.

Champaca. 1. MICHELIA. *Fl. zeyl.* 144.
Champacam. *Rheed. mal.* 1. *p.* 31. *t.* 19. *Raj. hist.* 1641.
Habitat in India. ♄

UVARIA.

zeylanica. 1. UVARIA foliis integerrimis.
Uvaria. *Fl. zeyl.* 224. *
Narum-panel. *Rheed. mal.* 2. *p.* 11. *t.* 9. *Raj. hist.* 1636.
Habitat in India. ♄

japonica. 2. UVARIA foliis serratis.
Frutex viscosus procumbens, folio telephii vulgaris æmulo, fructu racemoso. *Kæmpf. amœn.* 476. *t.* 477.
Habitat in Japonia. ♄

ANNONA.

muricata. 1. ANNONA foliis ovali-lanceolatis glabris nitidis planis, pomis muricatis. *Hort. cliff.* 222. * *Gron. virg.* 61. *Roy. lugdb.* 491.

Anno-

Appendix 1. A facsimile copy of the original account of *Uvaria zeylanica* by Linneaus in *Species Plantarum* (1753).

Appendix 2.1. Aligned Molecular Data Matrix.

Input data matrix (continued)

```
            1111111111111111111111111111111111111111111111111111111111111111
            2333333333344444444445555555555666666666677777777778888888888999
Node        9012345678901234567890123456789012345678901234567890123456789012
-------------------------------------------------------------------------------
melofrut    GCGTGAC-----TCGAACGGACACGGAGGGGGGGGGACGCTGCCCCCGCCGCGGCACCGGCGGGA
anomdulcB   CCGTGACCC-GATCGAACGGATGGGGGGGTGGGGGACTCTGCCCCCTGCGGGGCACCGGCGCGA
uvarhahnB   CCGTCACCCGGAT------GATGGGGG--TGGGGG-CGCTGCGCCCGCCGCGGCACCGGCGCGA
elischerr   CCGTGACCC-GATCGAACGGATGGGGG--TGGGG-ACGCTGCGCCCGCCGCGGCACCGGCGCGA
rauwsiam    CCGTTACCC-GATCG----GATGGGGG--TGGG--ACGCTGCGCCCGCCGCGGCACCGGCTTGA
uvarrufa    CCGTGACCCCGATCGAACGGAG-----GGGGGGGGACGCT-CGCACGTCGCGGCACCGGCACGA
uvarpier    CCGTGACCC-GATCGAACGGAG-----GGGGGGGGACGCTGCGCACGTGGCGGCACCGGCGCGA
uvarmicra   CCGTGACCC-GATCGAACGGAA------GGGGGGGACGCTGCGCACGTGGCGGCACCGGCGCGA
uvarfauv    CCGTGACCCCGATCGAACGGGG-------G----GACGCTGCGCACGTGGCGGCACCGGCGCGA
uvarhami    CCGTGACCCCGATCGAACGGAG-------GGGGGGACGCTGCGCACGTGGCGGCACCGGCGCGA
uvargran    CCGTGACCC-GATCGAAGGGAG------GGGGGGGACGCTGCGCCCGCCGCGGCACCGGCGCKA
uvarmacr    CCGTGACCC-GATCGGACGGAG-------GGGGGG-CGCTGCGCCCGCCGCGGCACCGGCGCGA
uvamphyll   CCGTGACCC-GATCGAACGGAG------GGGGGGGACGCTGCGCCCGCCGCGGCACCGGCGCGA
uvarmicr    CCGTGACCC-GATCGAACGGAG------GGGGGGGACGCTGCGCCCGCCGCGGCACCGGCGCGA
uvarcham    TTGTGACCC-GATCGAACGGAG------GGGGGGGACGCTGCACTCGCCGCGGCACCGGCGCGA
uvarfaulk   CTGTGACCC-GATCGAACGGAA-----GGGGGGGGACGCTGCGCTCGCCGCGGCACCGGCGCGA
dasyblum    ATGTGAC-----TAGAACG-AA-----------------TGGC-----------------GGA
```

Input data matrix (continued)

```
            1111111222222222222222222222222222222222222222222222222222222222
            9999990000000000111111111122222222223333333333444444444445555555
Node        3456789012345678901234567890123456789012345678901234567890123456
-------------------------------------------------------------------------------
melofrut    TGCCGGGCGCGGTGCGG--------AGGCGGCGATC------CTTT-----CCCGCCGCGGCAC
anomdulcB   GGCCGCGC---GTGGG------CGCTCTCG--GATC------CTCTCTACTCTCGCCGCGGCAC
uvarhahnB   GGCCGGGC---GTGGG------CGCGGCCGGCGATC------CTCT--GCTCCCGCCGCGGCAC
elischerr   GGCCGGGC---GTGGG------CGCGGTCGGCGATC------CTCT--ACTCCCGCCGCGGCAC
rauwsiam    GGCCGGGC---GTGGG------CGTGGTCGGCGATC------CT-----CTCCCGCCGCGGCAC
uvarrufa    GGCC-GGC---GTGGCGAAC------------GATCCGA---CTCTCCC---------------
uvarpier    -GCCGGGC---GTGGCGC-----GGCCGGC--GATC------CTCTCC------GCCG-GGCAC
uvarmicra   GGCCGGGC---GTGGCGCA----GGCCGGC--GATC------CTCTCCC-----GCCGCGGCAC
uvarfauv    GGCCGGGC---GTGGCGC-----GGCCGGC--GATCCC----CTCTCC------GCCGCGGCAC
uvarhami    GGCCGGGC---GCGGCGC-----GGTCGGC--GATCCC----CTCTCC------GCCGCGGCAC
uvargran    GGCCGGGC---GTGGCACGAGG-GGCCGGCGAGATCCTACTACTCTCCC-----GCCGCGGCAC
uvarmacr    GGCCGGGC---GTGGCAGGAGG-GGCCGGCGAGATC------CTCTCTCCCC--GCCGCGGCAC
uvamphyll   GGCCGGGC---GTGGCGGCACGCGGCCGGC--GATC------CTCTCCC-----GCCGCGGCAC
uvarmicr    GGCCGGGC------GCGGCACGGGGCCGGC--GATC------CTCTCCC-----GCCGCGGCAC
uvarcham    TGCCGGGCACGGCGG------GCGGCCGGC--GATC------CTCTCCC-----GTCGCGGCAC
uvarfaulk   GGCCGGGCGCGGC--------GCGGCCGGC--GATC------CTCTCCC-----GTCGCGGCAC
dasyblum    TGGGGGGC-----------------AG-------TCCCTTTCCTCTCCC--GCCACCGCTGGAC
```

Input data matrix (continued)

```
            2222222222222222222222222222222222222222233333333333333333333
            5556666666666777777777788888888899999999990000000000111111111112
Node        7890123456789012345678901234567890123456789012345678901234567890
-------------------------------------------------------------------------------
melofrut    CGGCGCGAGGCCGGGCGCGGCGAACGATCGACCCAACCCA--CGGCGCGAGTGGCGCCAAGGAC
anomdulcB   CGGCGCGAGGCCGGGCGCT--GAACAACCGACG-CACACA--CGGC--GAGTGGGGCCAA-GAC
uvarhahnB   CGGCGTGAGGCCGGGCGCGGCGAACGACCGACG-CACCCA--CGGCGCGAGTGGCGCCAA-GAC
elischerr   CGGCGCGAGGCCGGGCGCGGCGAACGACCGACG-CACCCA--CGGCGCGAGTGGCGCCAAGGAC
rauwsiam    CGGCGCGAGGCCGGGCGCGGCGAACGACCGACG-CACCCA--CGGCGCGAGTGGCGCCAAGGAC
uvarrufa    ------------------------------GYG------ACA-----CGAGTGGCGCCAAGGAC
uvarpier    CGGCGCGAGGCCGGGCG-GGCGAACGAC-GA-G-CACCCA--CGGCGCGAGTGGCGCCAAGGAC
uvarmicra   CGGCGCGAGGCCGGGCGCGGCGAACGACCGACG-CACCCACACGGCGCGAGTGGCGCCAAGGAC
uvarfauv    CGGCGCGAGGCCGGGCGCGGCGAACGACCGACG-CACCCA--CGGCGCGAGTGGCGCCAAGGAC
uvarhami    CGGCGCGAGGCCGGGCGCGGCGAACGACCGACG-CACCCA--CGGCGCGAGTGGCGCCAAGGAC
uvargran    CGGCGCGAGGCCGGGCGCGGCGAACGAC-CACG-CACCCACACGGCGCGAGTGGCGCCAAGGAC
uvarmacr    CGGCGCGAGGCCGGGCGCGGCGAACGAC-GACG-CACCCACACGGCGCGAGTGGCGCCAAGGAC
uvamphyll   CGGCGCGAGGCCGGGCGCGGCGAACGAC-GACG-CACCCACACGGCGCGAGTGGCGCCAAGGAC
uvarmicr    CGGCGCGAGGCCGGGCGCGGCGAACGAC-GACA-CACCCACACGGCGCGAGTGGCGCCAAGGAC
uvarcham    CGGCGCGAGGCCGGGCGCGGCGAACGACCGACG-CACCCA--CGGCGCGAGTGGCGCCAAGGAC
uvarfaulk   CGGCGCGAGGCCGGGCGCGGCGAACGACAGACG-CACCCA--CGGCGCGAGTGGCGCCAAGGAC
dasyblum    TGGCGCGAGGTCGGGCGTGGCGAACGACCGAC-CCAT-AA---GGCGCGAGTGGCACCAAGGAC
```

Input data matrix (continued)

```
            3333333333333333333333333333333333333333333333333333333333333333
            2222222223333333333444444444455555555556666666666777777777788888
Node        1234567890123456789012345678901234567890123456789012345678901234
-------------------------------------------------------------------------------
melofrut    CCC-AAGAGGATCGCGGGGGAGGAGG---------ACGGCCGTCCCCTCCGCCGC----GAGAG
anomdulcB   CCCGAAGAGGAGCGCGTGGGAGGAGGGCGGGCGC-AATGCCGTCCCCTCCGCCGC----GAGAG
uvarhahnB   CCCGAAGAGGA-CGCGGGGGAAGA-GGCGGGCGC-AAGGACGTCCCCTCCGCCGC----GGGAG
elischerr   CCCGAAGAGGAGCGTGGGGGAGGAGGGCGGGCGC-AATGCCGTCCCCTCCGCCGC----GAGAG
rauwsiam    CCCGAAGAGGAGCGCGGGGGAGGAGGGCGGGCGC-AATGCCGTCCCCTCCGTCGTCGC-GAGAG
uvarrufa    CCCAAAGAGGAGCGCGGGGGAGGAGGGCGGGCGC-AACGCCGTCCC-TTCGCCGC----KAGAG
uvarpier    CCCGAAGAGGAGCCC--GGGAGGAGG-CGGGCGC-AACGCCGTCCCCTCCGCCGC----GAGAG
uvarmicra   CCCGAAGAGGAGCGCGGGGGAGGAGGGCGGGCGC-AAYGCCGTCCCCTCCGCCGC----GAGAG
uvarfauv    CCCGAAGAGGAGCGCGGAGGAGGAGGGCGGGCGC-AACGCCGTCCCCTCCGCCGC----GAGAG
uvarhami    CCCGAAGAGGAGCGCGGTGGAGGAGGGCGGGCGC-AACGCCGTCCCCTCCGCCGC----GAGAG
uvargran    CCCGAAGAGGAGCGCGGGGGAGGAGGGCGGGCGC-AATGCCGTCCCCTCCGCCGC----GGGAG
uvarmacr    CCCGAAGAGGAGCGCGGGGGAGGAGGGCGGGCGC-AATGCCGTCCCCTCCGCCGC----GGGAG
uvamphyll   CCCGAAGAGGAGCGCGGAGGAGGAGGGCGGGCGC-AAYGCCGTCCCCTCCGCCGC----GAGAG
uvarmicr    CCCGAAGAGGAGCGCGGGGGAGGAGGGCGGGCGC-AATGCCGTCCCCTCCGCCGC----GAGAG
uvarcham    CCCAAAGAGGAGCGCGGGGGAGGAGGGCGGGCGC-AACGACGTCCCCTTCGCCGC----GAGAG
uvarfaulk   CCCGTAGAGGAGCGCGGGGGAGGAGGGCGGGCGC-AATGCCGTCCCCTYCGCCGC----GGGAG
dasyblum    CCC-AAGATGAGCGCAGCCGGGGAGAGGAGGACAGGCGTCACCTCCCCCATACCGC---GAGAG
```

Input data matrix (continued)

```
            3333333333333344444444444444444444444444444444444444444444444444
            8888899999999900000000001111111112222222223333333333444444444
Node        5678901234567890123456789012345678901234567890123456789012345678
------------------------------------------------------------------------------
melofrut    GGAATCGA-----------------------------------ATGTCGGACGACTCTCGGCA
anomdulcB   GGAAATATATACAGA-----------------------------GTT-C-GACGACTCTCGGCA
uvarhahnB   GGAATAGATAGAAA-----------------------------GTCTTTGACGACTCTCGGCA
elischerr   GGAATACATACACATGTGT-----------------------AGTCTTTGACGACTCTCGGCA
rauwsiam    GGAATCGAATGTGCTGTGTTGAAATAAACACTACACGCAAAAAAGAGTCGGACGACTCTCGGCA
uvarrufa    GGAATCGAATGAAATATGACTTGAAA---------------TATGACT-GGACGACTCTCGGCA
uvarpier    GGAATCGAAT-------------------------GAGATAC--GAGTCGGACGACTCTCGGCA
uvarmicra   GGAATCGAATGAAAAT---------------------GATAC--GAGTCGGACGACTCTCGGCA
uvarfauv    GGAAAA-------------------------------------TATGAGTCGGACGACTCTCGGCA
uvarhami    GGAATCGAATGAAA-------------------------TAC--GAGTCGGACGACTCTCGGCA
uvargran    GGAAAAAT--GATAA------------------------TAC--GAGTCGGACGACTCTCGGCA
uvarmacr    GGAAAATA--GTAAA------------------------TAC--GAGTCGGACGACTCTCGGCA
uvamphyll   GGAAAAT-----------------------------GATACATGAGTCGGACGACTCTCGGCA
uvarmicr    GGAAAAT-----------------------------GATAC--GAGTCGGACGACTCTCGGCA
uvarcham    GGAATCGAATGAAATA--------------------------GAGTCGGACGACTCTCGGCA
uvarfaulk   GGAATGGAATGAAATA--------------------------GAGTCGGACGACTCTCGGCA
dasyblum    GGAATCG--TCAAATTCT-----------------------CATCTCGGACGACTCTCGGCA
```

Input data matrix (continued)

```
            4444444444444444444444444444444444444444444444444445555555555555
            4555555555566666666667777777778888888888999999999900000000000111
Node        9012345678901234567890123456789012345678901234567890123456789012
------------------------------------------------------------------------------
melofrut    ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
anomdulcB   ACGGATATATCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
uvarhahnB   ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
elischerr   ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
rauwsiam    ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
uvarrufa    ACGGATATCTC-GCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATT--
uvarpier    ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
uvarmicra   ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
uvarfauv    ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
uvarhami    ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
uvargran    ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
uvarmacr    ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
uvamphyll   ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
uvarmicr    ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
uvarcham    ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
uvarfaulk   ACGGATATCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
dasyblum    ACGGATGTCTCGGCTCTCGCATCGATGAAGAACGTAGCGAAATGCGATACTTGGTGTGAATTGC
```

Input data matrix (continued)

```
            5555555555555555555555555555555555555555555555555555555555555555555
            1111111222222222233333333334444444444555555555566666666667777777
Node        3456789012345678901234567890123456789012345678901234567890123456
-------------------------------------------------------------------------------
melofrut    AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCTCCCGGCCGAGGGCA
anomdulcB   AGAATCCCGCGAACCCTCGAGTCTTTGAACGCAAGTTGCGCCCHARGCCACCCGGGCGAAGGGA
uvarhahnB   AGAATCCCCCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCACCCGGGCGAAGGCA
elischerr   AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCTCCCGGCCGAGGGCA
rauwsiam    AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCTCCCGGCCGAGGGCA
uvarrufa    AGAATCCTGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCAAGGCCACCCGGCCGAGGGCA
uvarpier    AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCACCCGGCCGAGGGCA
uvarmicra   AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCACCCGGCCGAGGGCA
uvarfauv    AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCACCCGGCCGA-GGCA
uvarhami    AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCACCCGGCCGAGGGCA
uvargran    AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCACCCGGCCGAGGGCA
uvarmacr    AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCTCCCGGCCGAGGGCA
uvamphyll   AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCACCCGGCCGAGGGCA
uvarmicr    AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCACCCGGCCGAGGGCA
uvarcham    AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCACCCGGCCGAGGGCA
uvarfaulk   AGAATCCCGCGAACCATCGAGTCTTTGAACGCAAGTTGCGCCCGAGGCCACCCGGCCGAGGGCA
dasyblum    AGAATCCTGCGAACCATCAAGTCTTTGAACGCAAGTTGCGCTCAAGGCCACCCGGCGGACGGCA
```

Input data matrix (continued)

```
            5555555555555555555555666666666666666666666666666666666666666666666
            7778888888888999999999900000000001111111111222222222233333333334
Node        7890123456789012345678901234567890123456789012345678901234567890
-------------------------------------------------------------------------------
melofrut    CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCACCCGGCCC----GGGTCGCT---GGCGG
anomdulcB   CCCCTGCCTGGGCGTCACGCA-CCGCGCTGGCCCCACCCCCCCCGACGGGGGG-CGACGGGCGG
uvarhahnB   CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCACGACCCCCGACGGGG---CTGCCGGCCG
elischerr   CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCA-CCCCCCCGACGGGGG--CGACGGGCGG
rauwsiam    CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCA---CCCCCGACGGGG-TTTGACGGGCGG
uvarrufa    CGCCTGCCTGGGCGTCAC-CA-CCGCGCTGCCCGCACCATCCCTGATGGGGCTG---CGAGCGG
uvarpier    CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCACCGCCCCCGACGGGGCTG---CGGGCGG
uvarmicra   CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCACCGT-CCCGACGGGGCTA---CGGGCGG
uvarfauv    CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCACCGCCCCCGACGGGGCCTG--CGGGCCG
uvarhami    CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCACCGCCCCCGACGGGGCTG---CGGGCGG
uvargran    CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCA----CCCCGACGGGGCC--GACGGGCGG
uvarmacr    CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCA----CCCCGACGGGGC---GACGGGCGG
uvamphyll   CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCACCGCCCCCGACGGGGCCTG--CGGGCGG
uvarmicr    CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCACCG----GGACGGGGC---GACGGGCGG
uvarcham    CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCA----CCCCGACGGGGC---GACGGGCGG
uvarfaulk   CGCCTGCCTGGGCGTCACGCA-CCGCGCTGCCCGCA----CCCCGACGGGGC---GACGGGCGG
dasyblum    CGCTTGCCTGGGCTTCACG-ACCTGCGATGCCTGCACCCGGCCCCC--GGGT---GACTGGCAG
```

Input data matrix (continued)

```
            7777777777777777777777777777788888888888888888888888888888888
            6777777777788888888899999999990000000000111111111122222222233333
Node        9012345678901234567890123456789012345678901234567890123456789012
-----------------------------------------------------------------------------
melofrut    CCC----GGGGAGCCGGTGC--GAT-CGGA-CGCCGCGCGCGCCGCCCGCTCCGAGGGGA---C
anomdulcB   CCC------GGAGCCGCTCC--GAT-CGGA-CGCCGCGCGCGCCGCCCGCTCCGAGGGGA---C
uvarhahnB   CCC------GGAGCCGTTCC--GAT-CGGA-CGCCGCGCGCGCCGCCCGCTCCGAGGGGA---C
elischerr   CGC------GGAGCCGCTCC--GAT-CGGA-CGCCGCGCGCGCCGCCCGCTCCGAGGGGA---C
rauwsiam    CCCCCGGAGGGAGCCGCTCC--GAT-CGGA-CGCCGCGCGCGCCGGCCGCTCCGAGGGGA---C
uvarrufa    CCT------AGAGCCGCTCC--GAT-CGGA-GGCCGCGCTCGCTGGCCGCTCCGAGGGCA---C
uvarpier    CCC------GGAGCCGCTCC--GAT-CGGA-CGCCGCGCGCGCCGCCCGCTCCGAGGGGA---C
uvarmicra   CCCCGGA--GGAGCCGCTCC--GAT-CGGA-CGCCGCGCGCGCCGCCCGCTCCGAGGGGA---C
uvarfauv    CCC------GGAACCGGT-----------------------------------------------
uvarhami    CCC------GGAGCCGCTCC--GAT-CGGA-CGCCGCGCTCGCCGCCCGCTCCGAGGGGACGAC
uvargran    CCC------GGAGCCGCTCC--GAT-CGGA-CGCCGCGCGCGCCGCCCGCTCCGAGGGGA---C
uvarmacr    CGCCGC---TGAGCCGCTCC--GAT-CGGA-CGCCGCGCACGCCGCCCGCTCCGAGGGGA---C
uvamphyll   CCC------GGAGCCGCTCC--GAT-CGGA-CGCCGCGC-CGCCGCCCGCTCCGAGGGG----C
uvarmicr    CTCCC--GGGGAGCCGCTCC--GAT-CGGA-CGCCGCGCGCGCCGCCCGCTCCGAGGGGA---C
uvarcham    CAC------GGAGCCGCTCC--GAT-CGGACAGCCGCGCGCGCCGCCCGCTCTGAGGGGA---C
uvarfaulk   CAC------GGAGCCGCTCT--GATATGGACAGCCGCGCGCGCCGCCCGCTCAGAGGGGA---C
dasyblum    CCTCTTAGAGGAGCCACTGC--GAT-CATA-TGTTGCGCGCGTCGCCCGCTCCAAGGGGA---C
```

Input data matrix (continued)

```
            8888888888888888888888888888888888888888888888888888888888888888
            3333333444444444455555555556666666666777777777888888888899999999
Node        3456789012345678901234567890123456789012345678901234567890123456
-----------------------------------------------------------------------------
melofrut    GT----AGGCGCCCTCCC-----------------GGACTGCGTCGCGACCCCAGGTCAGGCG
anomdulcB   GT----AGGCGCCTTCC------------------TCTCTGCGTCGCGACCCCAGGTCAGGCG
uvarhahnB   GT----AGGCGCCTTCCCCCC----------GCGGGACTCTGCGTCGCGAC-------------
elischerr   GT----AGGCGCCTTCC------------------TCTCTGCGTCGCGACCCCAGGTCAGGCG
rauwsiam    GTAGT-AGGCGCCTCCCCACC----------GCGGGACTCTGCGTCGCGACCCCAGGTCAGGCG
uvarrufa    GT---CAGGCGCCTCCCCCACC--------------GGACTGTGTCGCGACCCCAGGTCAGGCG
uvarpier    GT---GAGGCGCCTCCCCCACC--------------GGACTGCGTCGCGACCCCAGGTCAGGCG
uvarmicra   GT---GAGGCGCCTCCCCCACC-------GGTCGTGGGACTGCGTCGCGACCCCAGGTCAGGCG
uvarfauv    -----------------------------------------------------------------
uvarhami    GT---CAGGCGCCTCCCCCACC--------------GGACTGCGTCGCGACCCCAGGTCAGGCG
uvargran    GT---GAGGCGCCTCCCCCACCACA--TGTAATGTTGGACTGCGTCGCGACCCCAGGTCAGGCG
uvarmacr    GT---CAGGCGCCTCCCCCACCA----TGTGTTGTTGGACTGCGTCGCGACCCCAGGTCAGGCG
uvamphyll   GA---CAGGCGCCTCCCCCACC--------------GGACTGCGTCGCGACCCCAGGTCAGGCG
uvarmicr    GT----AGGCGCCCTCCC-----------------------------------------------
uvarcham    GT----ACGCGCC-TCCCCC-ACC------------GGACTGCGTCGCGACCCCAGGTCAGGCG
uvarfaulk   GT----TGGCGCCYTCCCCCCACC------------GGACTGCGTCGCGACCCCAGGTCAGGCG
dasyblum    GT----AGGCGCCTCCCCCCCTCGA------------GACTATGTCGCGACCCCAAGTCAGGCT
```

Input data matrix (continued)

```
                888899999999999999999999999999999999999999999999999999999999999999
                999000000000011111111112222222223333333333444444444455555555556
Node            789012345678901234567890123456789012345678901234567890123456789012
--------------------------------------------------------------------------------
melofrut        GGGCCACCCGCCGAGTTTAAGCATATAAATAAGCGGAGGAAAAGCAACTTACCAGGATTCT---
anomdulcB       GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGGAGGAAAA--------------------
uvarhahnB       ----------------------------------------------------------------
elischerr       GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGGAGG------------------------
rauwsiam        GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGGAGGAAAAGAAACTAAGCAGGATT-----
uvarrufa        GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGGAGGAAAAGAAACTCA-------------
uvarpier        GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGGAGGAAAAGAAACTTACCAGGATTCCCCT
uvarmicra       GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGCAGG-AAAGAAACTTACCAGGATTCCCCT
uvarfauv        ----------------------------------------------------------------
uvarhami        GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGGAGGAAAAGAAACTTACCAGGATTCCCCT
uvargran        GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGGAGGAAAAGAAACTTACCAGGATT----A
uvarmacr        GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGGAGAAAAAAG--CTTGCAA--ATTC--AA
uvamphyll       GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGGAGGAAAAGAAA-TTACCAGGATTCCCAA
uvarmicr        ----------------------------------------------------------------
uvarcham        GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGGAGGAAAAGAAACTTA-CAGGATTCCCAA
uvarfaulk       GGGACACCCGCCGAGTTTAAGCATATAAATAAGCGGAGAAAAAGAATTTTA-------------
dasyblum        GGGCCACCGCCCGAGTTTAAGCATATTAATAA--------------------------------
```

Input data matrix (continued)

```
                9999999999
                6666666667
Node            1234567890
----------------------------
melofrut        ----------
anomdulcB       ----------
uvarhahnB       ----------
elischerr       ----------
rauwsiam        ----------
uvarrufa        ----------
uvarpier        A---------
uvarmicra       AG--------
uvarfauv        ----------
uvarhami        A-GGAGATCA
uvargran        ----------
uvarmacr        GG-TTAA---
uvamphyll       G---------
uvarmicr        ----------
uvarcham        ----------
uvarfaulk       ----------
dasyblum        ----------
```

Appendix 2.2. Character Indices for MP tree in Figure 2.7.

Appendix 2.2. Character indices for MP tree in Figure 2.7.

Unrooted tree(s) rooted using outgroup method
Optimality criterion = maximum parsimony

Character diagnostics:

Character	Range	Min steps	Tree steps	Max steps	CI	RI	RC	HI	G-fit
1	1	1	2	2	0.500	0.000	0.000	0.500	0.750
2	3	3	13	19	0.231	0.375	0.087	0.769	0.231
3	1	1	5	16	0.200	0.733	0.147	0.800	0.429
4	1	1	1	1	1.000	0/0	0/0	0.000	1.000
5	1	1	4	12	0.250	0.727	0.182	0.750	0.500
6	1	1	2	10	0.500	0.889	0.444	0.500	0.750
7	1	1	3	5	0.333	0.500	0.167	0.667	0.600
8	1	1	2	2	0.500	0.000	0.000	0.500	0.750
9	1	1	4	10	0.250	0.667	0.167	0.750	0.500
10	1	1	7	9	0.143	0.250	0.036	0.857	0.333
11	1	1	2	7	0.500	0.833	0.417	0.500	0.750
12	1	1	2	16	0.500	0.933	0.467	0.500	0.750
13	1	1	2	10	0.500	0.889	0.444	0.500	0.750
14	1	1	4	10	0.250	0.667	0.167	0.750	0.500
15	1	1	1	3	1.000	1.000	1.000	0.000	1.000
16	1	1	1	8	1.000	1.000	1.000	0.000	1.000
17	1	1	1	3	1.000	1.000	1.000	0.000	1.000
18	1	1	2	3	0.500	0.500	0.250	0.500	0.750
19	1	1	5	6	0.200	0.200	0.040	0.800	0.429
20	1	1	3	8	0.333	0.714	0.238	0.667	0.600
21	1	1	2	10	0.500	0.889	0.444	0.500	0.750
22	1	1	1	12	1.000	1.000	1.000	0.000	1.000
23	1	1	2	13	0.500	0.917	0.458	0.500	0.750
24	3	3	5	16	0.600	0.846	0.508	0.400	0.600
25	1	1	2	3	0.500	0.500	0.250	0.500	0.750
26	1	1	7	14	0.143	0.538	0.077	0.857	0.333
27	1	1	2	3	0.500	0.500	0.250	0.500	0.750
28	1	1	2	6	0.500	0.800	0.400	0.500	0.750
29	1	1	2	5	0.500	0.750	0.375	0.500	0.750
30	1	1	6	12	0.167	0.545	0.091	0.833	0.375
31	1	1	1	6	1.000	1.000	1.000	0.000	1.000
32	1	1	2	2	0.500	0.000	0.000	0.500	0.750
33	1	1	1	6	1.000	1.000	1.000	0.000	1.000
34	1	1	1	2	1.000	1.000	1.000	0.000	1.000
35	1	1	1	2	1.000	1.000	1.000	0.000	1.000
36	1	1	1	1	1.000	0/0	0/0	0.000	1.000
37	1	1	4	10	0.250	0.667	0.167	0.750	0.500
38	1	1	1	7	1.000	1.000	1.000	0.000	1.000
39	1	1	2	9	0.500	0.875	0.438	0.500	0.750
40	1	1	3	5	0.333	0.500	0.167	0.667	0.600
41	3	3	5	9	0.600	0.667	0.400	0.400	0.600
42	1	1	2	13	0.500	0.917	0.458	0.500	0.750
43	3	3	7	9	0.429	0.333	0.143	0.571	0.429
44	1	1	4	7	0.250	0.500	0.125	0.750	0.500
45	1	1	2	3	0.500	0.500	0.250	0.500	0.750
46	2	2	4	4	0.500	0.000	0.000	0.500	0.600
47	2	2	4	12	0.500	0.800	0.400	0.500	0.600
48	1	1	2	2	0.500	0.000	0.000	0.500	0.750
49	1	1	5	8	0.200	0.429	0.086	0.800	0.429

Appendix 3.1

Material Examined for Morphometric Analysis

Anomianthus

A. dulcis (Dunal) Sinclair

Vietnam *Lam Dong Province* (V - 33 - CLV); Dalat, 01/04/32, Squires 905 (fl.) (NY); *Khanh Hoa Province* (V - 35 CLV); Nhatrang, 09/05/22, Poilane 3193 (fl.) (Ham); *Province Unknown*; Snoi Dan, Southern Vietnam 26/07/61, Schmid s.n. (fl., fr.) (P); Pierre 6/1864, Pierre 385 (fl., fr.) (L). **Thailand** *Chiang Mai Province* (2- N); Doi Suthep, 300m, Kerr 12 (fl.) (TCD); Doi Suthep, 300m 26/05/09, Kerr 607 (fl.) (TCD); *Lamphun Province* (6 - N); 27k N of Li, 78k S of Lamphun, 410m, 05/06/63, Merrill 5457 (fl.) (L); *Saraburi Province* (47 - C); Sahm Lahn Forest, 125m 26/07/75 Maxwell 75-718 (fr.) (BK, L); *Chon Buri Province* (55 - SE); Sriracha, 21/05/26, Collins 1254 (fl., fr.) (US). **Indonesia** *Java* c.1796, Lahaie s.n. 'Uvaria javana, [*Uvaria tomentosa* ? Roxb. t. 35 perquam affinis], Java, Lahaye, hb. Ventenat' (fl.) (Holo – *Herb. Deless.* G); Samoeng, 11/11/11, Leeunen 364a (fl.) (L); Surabaya, 01/01/24, Rant s.n (fl.) (L); Surabaya, 06/03/19, Backer 26572 (fl.) (L); "Uvaria javana DC", Leschenault s.n. (fl., fr.) (P).

Cyathostemma

C. argenteum

Bangladesh/ India *Silhet*; Roxburgh s.n. (fl.) (BM); F. Da Silva in Wall Herb. Cat. 6468 (fl.) (K). **Thailand** *Chiang Mai Province* (2 – N); Doi Chiang Dao, Chiang Mai, 700m, 19.20N 98.50E, 02/06/69, Geesink et al. 5662 (fl.), (AAU); *Chonburi Province* (55 – SE), Ang Chang Nam, Kow Kieo Park, Bahn Bueng District, 300m, 25/06/71, Maxwell 75-658 (fl.) (L).

C. micranthum (H.f. & Th.) Sinclair

India *Andaman Islands*; South Islands, Helfer 433 (fl.) (A, P). **Vietnam** *Dong Nai Province* (V – 40 – CLV); Boa Chang, near Bien Hoa, Sept. 1867, Pierre 209 (P). **Thailand** *Uttaradit Province* (9 - N); Nakawn Dai, 200m, 17/4 or 17/11/22, Kerr 5862 (fl.) (BK, TCD); *Prachuap Khiri Khan Province* (37 – SW); Hua Hin, 01/10/27, Collins 1582 (fr.) (US); *Nakhon Si Thammarat Province* (69 - Pen);Ka Rom waterfall, Lau Saka (?) 05/12/72, Santisuk 303 (fr.) (BKF); *Songkhla Province* (73 - Pen); Lem San, San Mala?, alt <50m, 10/4/28, Kerr 15133 (fl.) (BK, L, TCD).

var. *elongata*

Indonesia *Kalimantan*; E. Kalimantan, KPC coal mining company, Sangatta, 20m, 14/04/95, Kessler 1180 (fl.) (TCD, L). **Phillipines** *Palawan*; Tatanoram, base of Mt. Beaufort, Irawan river valley, Puerto

Princesa municipality 04/04/89 Soejarto et al. 6407 (fl.) (A, L, NY); TayTay, 01/05/13, Merrill 9271 (fl.) (A, NY); *Tawitawi*; Sulu Province, 01/08/24, Ramos & Edano 44124 (fr.) (A, NY).

C. wrayii

Thailand Ranong Province (60 – Pen.); Khao Saidangm 400m, 4/5/68, van Beusekom & Phengkhlai 564 (fl.) (AAU, BKF, C, E, K, KYO, P).

C. longipes Craib

Vietnam *Langson Province* (V - 9 - CLV); near Thanh Nai, Petelot 6421, 11/05/34 (fl.) (P, NY). **Laos** *Vieng Chang Province* (L - 9 - CLV); Kam Yuak, c. 300m, Kerr 21257 , 24/04/28, (fl.) (L, P). **Thailand** *Ubon Ratchatani Province* (35 - E); Pu, Kerr s.n. & 8607, 04/03/20, (fl.) (BM, K, P).

sp. nov. Aff. *Cyathostemma*

Thailand Prachaup Khiri Khan (37 – SW); Khao Luang, c. 400m, 4/7/1926, Kerr 19814 (fl.) (P).

Ellipeiopsis

E. ferruginea (Buch-Ham ex H.f.& Th.) R.E. Fries

Bangladesh Conulla Teela 15/9/1871 Clarke 14227B (fl., fr.) (BM); **Myanmar** *Taninthari* (Tenasserim); Meaday, Buchanan-Hamilton s.n. (fl.) (BM);*Mandalay*; near Pyinmana, 09/06/27, Parkinson 6141 (fl.) (K).

var. *cherrevensis*

Thailand *Chiang Mai Province* (2 - N); near Bo Luang, 400m, 12/06/73, Geesink et al. 5835 (fl.) (L); Doi Inthanon, along Me Klang River (RS-3), 30/07/88, Koyama T-61621 (fr.) (A); Doi Saget, southern part, Huay Hang Cry area, Bah Kiang Subdistrict, 450m 13/06/90, Maxwell 90-625 (fl.) (A); Doi Suthep, 30/08/21, Kerr 340 (fl.) (TCD); Doi Suthep, 06/05/09, Kerr 636 (fl.) (K); *Tak Province* (10 - N) along road 75km N of Tak, Northern District, 08/06/68, van Buesekom & Phengkhlai 1063 (fl., fr.) (AAU).

Rauwenhoffia

R. siamensis Scheff.

Cambodia *Pursat Province* (C – 10 – CLV); Pursat, 12/4/09, Poilane 15067 (fl.) (NY). **Thailand** *Anthong Province* (42 - C); Wat Glang, Muang District, Angthong, 14/08/71, Maxwell 71-479 (fr.) (AAU, BK); Wat Glahng, Howa Pie, Muang District, 02/04/72 Maxwell 72-175 (AAU, BK); Wat Glahng, Hoa Pie, Muang District, 25m, 31/05/75, Maxwell 75-571 (AAU); *Krung Thep Province* (49 - C); outside front door of BKF, cultivated, Chatuchack, 08/10/98, Meade 76 (fl.) (TCD); *Chonburi Province* (55 - SE); Sriracha, 27/06/20; Kerr 4308 (TCD); *Nakhon Si Thammarat Province* (65 – Pen.); Ban Bua Put, Ko Samui, 14/5/28, Kerr 15727 (fl.) (BK, TCD); *Songkhla Province* (69 - Pen); Bantom Island, Lake Songkhla, 0m, 26/05/84, Sirirugsa 818 (A); Khao Kho Hang, 06/10/88, Larsen 40277 (AAU); *Pattani Province* (70 – Pen.), Kok Po, <50m, 05/04/18, Kerr 15067 (BK, K).

Uvaria

U. boniana Finet & Gagnep.

China *Hainan* 02/08/33, Wang 33547 (fl.) (NY). **Vietnam** *Ha-Tay Province* (CLV-13-V); Ninh-Thai, 17/9/1888, Bon 3956 (fl.) (P); Ninh-Thai, 11/8/1889, Bon s.n. (fl.) (P); *Quang Ninh Province* (CLV-10-V); near Quang-Yen, 5/1886, Balansa 4185 (fr.) (P, K); *Location unknown*; Petelot 6057 (fr.) (P).

U. calamistrata Hance

China *Hainan Province*; Ngai District; Fung Leng, 03/09/32, Lau 468 (fr.) (E,); Locality unknown; 08/10/33, Wang 34503 (fr.) (NY). *Hong Kong;* Hong Kong Island, 8/186, Hance 7436 (fr.) (BM); Hong Kong, 9/1874, Lamont 12a (fr.) (BM). **Vietnam** *Vinh Phu Province* (CLV –12 –V); Song Hoa, 02/11/05, Castellini 60, (fl.) (P).

U. cordata (Dunal) Alston

Sri Lanka; *Location unknown*; *s.coll.* C.P. 3527 (fl.) (TCD). **India**; Calcutta Botanic Gardens, cultivated, Wallich 6487a *HBC* (fl., fr.) (BM). **Myanmar**; *Taninthari (Tenasserim);* Tavoy district, E Bank of the Banchaung R., 2 miles N of Paungdaw village, Tavoy District, Tenasserim, c.14N 98.30E, 800ft 01/08/61 Keenan 1256 (fl.) (E); Tavoy, Roxburgh 110 (fl.) (BM); Wallich 987 21/9/1815 (fl.) (BM); Roxburgh s.n. (fl.) (BM); *Pegu*; Toungoo, Donzayit, east bank of Sittang, 150ft. 04/08/11 Lace 5386 (fl.) (E); *Yangon*; Rangoon, 1826, Wall. Cat. 6487c, Wallich, (fl.) (K). **Thailand**; *Chiang Mai Province* (2 -N); 10km W of Fang, 19.57N 99.11E 600m 23/07/68 Larsen 2600 (fl.) (Cop); Doi Chiang

Dao, SW foothills near Ban Yang Pong Luang, Chiang Mai Province (2 - N) 525m 29/10/89 Maxwell 89-1324 (fr.) (E); Doi Chiang Dao, SW foothills near Ranger Station, Chiang Mai Province (2 - N) 250m 24/10/98 Meade 84 (fr.) (TCD); *Khampaeng Phet Province* (N - 13); Khlong Lan NP, track E of Waterfall, 16.6N 99.23E, 250m, 21/08/95, Parnell et al. 95-352 (fl.) (TCD); *Chaiyaphum Province* (25 - E), Nam Phoeom, near weir, 16.2N 101.45E, 600m, 19/10/71, van Buesekom 4432 (fr.) (L); *Nakhon Rachasima Province* (26 - E), Khao Yai National Park, Khao Kieo (mtn.), 14.45N 102E, 5-600m, 31/10/69, van Buesekom 1950 (fr.) (L); *Surat Thani Province* (61 - P) Klawng Nam Wing, 1.100m 06/03/27 Kerr 12241 (fr.) (BM); *Phuket Province* (63 - P), Ton Sai Wildlife Sanctuary, 300m, 04/07/79, Niyomdham 177 (fl.) (C); *Satun Province* (68 - P); Thon Pliew, c.25k N of Satun, 100m, 100.09E 6.54N, 28/10/93 Larsen 44107 (fr.) (AAU). **Peninsular Malaysia**; *Perak*; Larut, 300-400ft 4/1884 King 5776 (fl.) (BM); *Location unknown*; Maingay 24, 1031 A (fl., fr.) (BM).

U. curtisii King

Thailand; *Ranong province* (60 – Pen.); Khlong Kam Puan, 9.15N 98.20E, 100m, 01/05/73, Geesink and Santisuk 5104 (fl.) (C, E, L). **Malay Peninsula**; *Jahore*; Muar at Biawak, 4/1901, Curtis 3623 (K); *Pahang*; Ulu S. Kerau, Central Pahang, top of ridge, c. 300m, 11/07/67, Whitmore FRI 3998 (fr.) (L); *Penang*; Government Hill, 2000ft., 5/1892 Curtis 1415 (BM, K); Government Hill, 2000ft., 6/1888, Curtis 1415 (K). **Singapore** Bukit Timah FR., Kruing Path, 27/5/53 Sinclair 39652 (K).

U. dac Finet & Gagnep.

Vietnam; *Dong Nai Province* (V - 40 - CLV); near Chiao-shan, Bien-Hoa, 1875-1877, Pierre 1785 (fl.) (P). **Cambodia**; *Siem Reap Province* (L - 7 - CLV); Angkor, 6/1866, Thorel s.n (fr.) (P); *Kompong Speu Province* (C - 17 - CLV); Hills near Chambok, 300m, 08/06/30, Poilane 17489 (fl., fr.) (K, P); *Koh Kong Province* (C - 18 - CLV); Chereer Mountain, 4/1870, Pierre 748 (fl., fr.) (K, P); Tamire Mountain, 800m 5/1870, Pierre 748 (fl.) (P); *Kampot Province* (C - 19 -CLV); Camchay Mountains, 400m, 5/1874, Pierre 1459 (fl.) (A, K, P). **Laos**; *Saravane Province* (C – 13 – CLV); Road between Lao-Lao and Saravane, 17/04/27, Poilane 13254 (fl.) (P). **Thailand**; *Nong Khai Province* (19 – NE); Nong Khai, banks of Mekong, 1866-1868, Thorel 9179 (fl., fr.) (P).

U. flexuosa Jovet-Ast.

Vietnam *Quang Tri Province* (CLV–25-V); Massif de la Mere et L'Enfant 5/1923, Poilane 6781 (fl.) (HCMC, P).

U. grandiflora Roxb. Ex Hornem.

China *Hong Kong*; N of Mt. Gough, Hong Kong 7/6/1873, Lamont 8 (fl.) (BM); 24/01/09 Champion 38 (fl., fr.) (BM, K); 12/9/1898 Henry s.n. (fr.) (NY). **Vietnam** *Quangtri Province* (V - 25 - CLV); Salung Pro, 31/12/40, Poilane 31254 (fr.) (P). **Thailand** *Chanthaburi Province* (57 – SE); Khao Soi dao, 13.0N 102.15E, 250-300m 18/12/74 Geesink 7896 (fl.) (BKF); *Trat Province* Salak Koh, Koh Chang, 12.0N 102.4E, 50m, 08/05/74, Geesink 6620 (fl.) (L); *Songkhla Province* (69 - P); Khao Kho Hong, Hat Yai, 100.2E 7.0N, 250m, 30/10/90, Larsen 40936 (fl., fr.) (AAU). **Peninsualar Malaysia** *Perak*; Larut, 8/1883, King 4786 (fr.) (K). **Indonesia** *Java* Jawa Barat; Bogor 01/06/04 Backer s.n. (fl., fr.) (U); Jampang Kulon, S. of Sakabumi, W. Java, 400m, 16/09/85, van Balgooy 5147 (fl.) (U).

var. *flava* (Teijsm. & Binn.) Sincl.

Thailand *Chonburi Province* (55 – SE); Toong Brong, Sattahip District, 4-12-1971, Maxwell 71-765 (fl) (AAU); *Trat Province* (58 – SE); Dong Ta Beng, Khao Sameng, 21/10/46 Dee 191 (fl.) (BKF).

U. hahnii (Finet & Gegnep.) Sincl.

Cambodia *Kampong Spoe Province* (C - 17 - CLV); Pnom Tho ma So, near Ko Virk village, 02/05/28, Poilane 15169 (fl.) (P); *Kampot Province* (C - 19 - CLV); Kamchay Mts, 26/2/1896, Hahn s.n. (fl., fr.) (P); Kampot, 3/1874, Pierre 1786 (fl.) (P); Kampot, 13/04/04, Geoffray 385 (fl.) (P). **Thailand** *Saraburi Province* (44 - C); Sahm Lahn, 150m, 30/03/74, Maxwell 74-224, (fl.) (AAU); *Chonburi Province* (55 - SE); Sriricha District, Khao Kieo, 350m, 07/04/75, Maxwell 75-366 (fl.) (AAU); Sriracha, Nong Nam Kro, 100 m, 05/04/20, Kerr 4171 (fl.) (K); *Rayong Province* (56 - SE); Ban Pe, 19/02/30, Put 2707 (fl.) (TCD); *Chanthaburi Province* (57 - SE); Khao Phra Bat, N. of Chanthaburi, 12.52N 102.10E, 100m 27/08/72, Larsen et al. 32104 (fr.) (AAU).

U. hamiltonii Hook. f. & Thoms.

Nepal Ramnagou, Chilwan, 500m, 01/06/94, Wesche 11209 (fl.) (BM). **India** *Bihar & Orissa*; mountains near Monghir/Munger, 26/5/1811, Herb. Wallich 6485E (fl.) (BM); *Tamil Nadu*, Goonsam Hills near Kurching, 28/02/09 Beddome 46 (fl.) (BM). **Myanmar** *Mandalay* Sakangyi Reserve, near Maymyo Plateau, 3,500 ft. 25/08/12 Lace 5920 (fr.) (E, K).**China** Hong Kong 1860-64, Pierre s.n. (fl.) (K). **Thailand** *Chiang Mai Province* (2 – N), Doi Chiang Dao, southern foothills, near Ranger Station, Doi Chiang Dao W.S., c. 300m, 20/10/98, Meade 85 (fr.) (TCD).

var. *kurzii* King

Thailand *Lampang Province* (7 - N); MaeSung, 170m, 16/06/26, Winit 1733 (fl.) (BKF); *Petchaboon Province* (16 - NE); Lom Kao, Nam Nao, 600m, 25/05/51, Smitinand 560 (fl.) (BKF).

U. lobbiana Hook. f. & Thoms.

Thailand *Narathiwat Province* (72 - Pen.); Bacho, 21/04/61, Sangkhachand 76 (fl.) (BKF, C, K, L, P). **Malaysia** *Kedah*; Gunong Jerai, Kedah Peak, 1200ft., 14/05/69, Stone 8542 (fl.) (L); *Melaka*; Griffith s.n. E.Ind.Comp. No. 434, 435 (fl.) (K); *Perak*; Larut, 8/1883, King 4787 (fl., fr.) (BM, K, L, Sing.); *Selangor*; Dec. 1896. Ridley 8217 (Sing); *Location Unknown*; Maingay 30 pro pars (fl., fr.) (K). **Indonesia** *Sumatra* Atjeh; Gunung Leuser Reserve, 3.0N 97.5E, 50-125m, 16/07/79, de Wilde 18767 (fr.) (L).

var. *ptychocalyx* (Miq.) C. Meade

Myanmar *Taninthari (Tenasserim)*; Mergui, Herb. Helfer/ E.Ind.Comp. No. 440 (fl.) (K). **Thailand** *Ranong Province* (60 - Pen.); Kapoe, 15/11/65 Sangkhachand 1128 (fl.) (C); *Surat Thani Province* (61 - Pen.); 18/08/75, Prapat 45 (fl.) (P). *Phuket Province* (63 - Pen.); Khao Pra Taeo WRC, 29/12/83 Fukuoka T-35641 (fr.) (BKF). **Indonesia** *Kalimantan;* Sakoembang in Poeloe Lampei, Korthals s.n. (fl.) (L).

U. lamponga Scheff.

India *Andaman Islands*; 1884, Dr. Kings Collector 209 (BM); 1884, Dr. King's Collector s.n. (fl.) (BM, G).

U. lurida Hook. f. & Thoms.

India *Assam*; Khasia hills, 2000 ft., regio subtropico, H.f. & Th.s.n. (fl.) (BM, K, TCD); *Bihar & Orissa* Ayatpur, Puri District, 16/04/17, Haines 3707 (fl.)(K) (fl.); *Karnataka*; Hassan District, near Hettur, 21/08/69, Saldanha 14566 (fr.) (US); *Maharashtra*; N. W. Ghats, Matquon Rai, 5/1881, Young s.n. (fr.) (BM); Southern Concan, Law s.n. (K); *Sikkim*; 800ft Mongpur Peak, 11/8/1881, King s.n. (fr.) (G); Mongpur Peak, 3000ft 1/12/1887, Gamble 28025 (fr.) (K); 1500ft, 2/10/1877, King 4935 (fl.) (BM); *Tamilnadu*; Ganjam District, Kuncholy, 2000 ft., 5/4/09, Dawkins 14218 (K); Goomsah hills, Beddome 49 (fl.) (BM); Kodaikanal District, Dindigul, Ganesapuram-Palani Road, Palni Hills, 800m, 22/03/87, Matthew 48691 (fr.) (AAU); Kodaikanal District, Dindigul, Kodaikanal District, Dindigul, Thadiankudisai - Adalur Road, top, 04/08/88, Matthew 53326 (fr.) (K); Ruschamdah hills, 12/12/1885 Beddome 50 (fl.) (BM). **Thailand** *Chonburi Province* (55 – SE); Ban Buang, 68m, 18/07/66, Phengkhlai 1273 (fl.) (BKF); Sriracha, Pan sa-det, c. 50m, 17/11/46 Din 238 (fl.) (BKF). **Indonesia** *Java*; Peutjang Island 27/03/64 Kostermans 35A (fr.) (G). **Philippines** *Leyte*; Palo, Jan. 1906, Elmer 7365 (fr.) (NY).

U. maclurei Diels

China *Hainan Province*; Yik Tsok Mau, 18/5/22, McClure 9697 (fl.) (BM, G); *Yunnan Province*; Szemar, Tu Zey Mountains Henry 12148 (fl.) (NY); *Guizhou Province*; Libo County, Southeast Guizhou, 660m, 26/5/83, Song Xianghou 897 (fl.) (PE); 8/8/59, *coll.* 739 (fr.) (PE).

U. macropoda Hook. f. & Thoms.

Sri Lanka *Anuradhapura District*; Ritigala Strict Natural Reserve, 1100 ft., E. slope, 21/01/73, Jayasuriya 1077 (fr.) (US); Ritigala Strict Natural Reserve, Anuradhapura Distr. 1400 ft., W. slope 08/08/73 Jayasuriya 1274 (fl.) (US); *Badulla District*; Meda Oya, low altitude, near the flow of Hepala Oya into river Mahaweli; 29/10/71, Jayasuriya 396 (fl., fr.) (US); *Kandy District*; Gannurowa Hill, Peradeniya Forest, 09/07/78, Meijer 1704 (fr.) (L); *Matale District*; Diokandahena, near Dambulla, 250m, 15/10/77, Huber 458 (fl.) (US); *Polonnaruwa District*; Banks of Mahaweli Ganga, Thunmodera, 07/06/74, Waas 582 (fl.) (US); *Ratnapura District*; Kalanne, 12th mile post on Embilipitiya-Rakwana Road, 17/10/71, Balakrishnan NBK 908 (fr.) (US); *Locality Unknown*; Ceylon 1600ft., Walker 160 (fl.) (K); *s.coll.* CP. 2544 (fl., fr.) (BM, TCD); C.P. 1032 (fl.) *pro pars* (NY, K).

U. narum (Dunal) Bl.

Sri Lanka *Ratnapura District*; Ballancoda, Walker 175 (K); *Location unknown*; *s.coll.* C.P. 1032 (fl.) *pro pars* (TCD). **India** *Goa*; Chapora, 20/11/1896 Lapes 37 (fl.) (LISU); *Karnataka*; near Mangalore, 21/01/09, Hohenhacker 332 (K); Mysore, Buchanan s.n. (fl.) (BM); *Kerala*; Calicut (Kozhikode), 01/02/05, Meebold 721 (fl.) (G); Calicut (Kozhikode), 1/1843, Perrottet s.n. (fr.) (P); Suckidy Coatay, near Calicut, 4/1846, Wight 18 (fr.) (K); Cranganore, Trarancore,, 9/1884, Gamble 14841 (fl.) (K); Nilghiri Hills, 1837-1838 Perrottet 40 (fl.) (G); Nilghiri Hills, Perrottet 17 (fl., fr.) (TCD); Nilghiri Hills, Johnson s.n. (fl., fr.) (TCD); *Maharashtra*; Southern Concan, Dalzell s.n. (K); *Tamilnadu*; Dindigul, Wight s.n. in Wallich 6473b (fr.) (BM); Wight s.n. in Wallich 6473a (fr.) (K).

var. *macraeii* C. Meade

Sri Lanka *Location unkown*; Macrae 77, 88 (fl.) (BM).

U. microcarpa Champ. ex Benth.

China *Hainan Province;* District Unclear; Yaichow, 06/07/33, How 70957 (fl.) (NY, US); Yaichow, Liang 62133 (fr.) (NY). *Guandong Province* Canton (Guangzhou); Canton vicinity, 02/10/17, Levine 362 (fr.) (US); Canton vicinity, 05/12/17, Levine 894 (fl.) (US); Canton, Hooker s.n. (fl.) (E); Canton and surrounds, Millet s.n. (fl., fr.) (TCD); *District Unclear*; Kochow, on the way to Kwang Tan, 12/08/28, Tsiang Ying 908 (fr.) (E); Sie-lung, Loting, 14/09/28, Tsiang Ying 1161 (fr.) (E); Wu-King-Fu, 60m W of Swatow, foothills of Lianhua Shan, 24.25N 115.0E, 9/1899, Dalziel s.n. (fl., fr.) (E).

Hong Kong; Hong Hong Island; Ford s.n. (fr.) (NY); New Territories; Ma On Shan, near village, 11/05/68, Ying Hu 7288 (fl.) (PE). *Guangxi Province*; District Unclear; Shap Man Taai Shan, Nam She Village, SE of Shang-sze (now Cenxi/Censheng), Guandong Border, 31/10/34, Tsang 24537 (fr.) (NY). **Vietnam** *Hoa Binh Province* (V - 9 - CLV); Haie d'un village entre Hudong et Hoa Binh, 01/05/36, Petelot 5800 (fl.) (US); *Quang Ninh Province* (V – 10 – CLV); Dam-ha, 09/09/40, W.T. Tsang 30247 (fr.) (E).

U. pauciovulata Hook. f. & Thoms.

Thailand *Narathiwat Province* (72 - Pen.); Waeng, 13/06/70, Smitinand 10916 (fl.) (BKF). **Malaysia** *Malacca*; 14/6/1865, Maingay 1023 (fl.) (K); 27/5/1868 Maingay 3392 (fl.) (K); *Locality Unknown*; Maingay 1023A (fl., fr.) (K). **Singapore** Bukit Timah FR, tree no. 347, 01/06/39, Ngadiman Sing. Field No. 36432 (BM, K, Sing.).

var. *scortechinii* (King) C. Meade

Malaysia *Perak*; Scortechini 1990 (fl.) (A, K).

U. rufa (Dunal) C. Meade

Cambodia; *Pursat Province* (C - 10 - CLV); Trassay, 12/04/28, Poilane 15067 (fl.) (NY). **Vietnam**; *Tay Ninh Province* (V - 39 - CLV); Cay Cong, 1/1867, Pierre 120 (fl.) (BM); *Kien Giang Province* (V - 52 - CLV); Phu Quoc Island, Raong Chiao, 3/1874, Pierre 1787 (K, P). **Thailand**; *Chiang Mai Province* (2 – N); Doi Suthep; 300m, 30/05/09, Kerr 660 (fl.) (BM); Doi Suthep, south side, west of Mae Heeyah Nai Village, 18/06/89, Maxwell 89-777 (fl.) (E); *Roi Et Province* (29 – E); 150m, 22/06/69, Smitinand 10758 (fl, fr.) (BKF); *Saraburi Province* (47 – C); Sahm Lahn Forest, Muang District, 300m 01/04/74 Maxwell 74-254 (fl.) (AAU); Sahm Lahn Forest, Muang District, 100m 30/06/74 Maxwell 74-639 (fl, fr.) (L); *Chanthaburi Province* (57 – SE); Pong Nam Ron Pailin, West of Khao Soi Dao Tai, 28/08/72, Larsen 32164 (fr.) (AAU, L); *Trang Province* (67 – Pen.); on the Trang-Krabi Road, 19/05/84, W.N. 516 (fl.) (BKF); *Songkhla Province* (69 – Pen.); Had Yai District, Ban Klang, 06/06/85, Maxwell 85-577 (fl.) (NY); *Pattani Province* (70 – Pen.); Yala Pattani, 50m, 05/09/27 Kerr 7728 (fl., fr.) (BM). **Indonesia** *Java;* Surabaya 10/1793 - 8/1794 Lahaie 1772 (fl.) (P). **Singapore** Botanic Garden 13/04/09, Clemens 22457 (fl.) (NY).

var. *timoriensis* (Bl.) C. Meade

Timor 1808, Riedlé s.n. (fl.) (P). **Philippines** *Luzon*; Pangasinan Province, Umingan, 01/05/14, Merrill 'Species Blancoanae' no.199 (fl.) (L, P); *Mindanao*; Davao Province; Santa Cruz, Marinchique, May 1884, Vidal no. 6 (AAU).

U. semicarpifolia Hook. f. & Thoms.

Sri Lanka *Galli District*, Kannelliya forest near Hiniduma, 400m, 01/09/74, Kostermans 25493 (fl., fr.) (US); *Matara District*; river valley immediately North of Diyadawa Forest Reserve, 410m 11/11/77, Huber 602 (fl.) (US); *Ratnapura District,* Forest South of Veddagala, Sinharaja, 04/11/77, Huber 556 (fl., fr.) (HBG); 3/1846 Thwaites C.P. 244 (K); *Locality Unknown*; Thwaites C.P. 244 (fl., fr.) (BM, G, TCD); Walker 165 (fl.) (G); Walker s.n. (K).

U. sphenocarpa Hook. f. & Thoms.

Sri Lanka *Vavuniya District*; Mullaitivu-Mankulam Road, ca. 3km from Mullaitivu, 24/06/75, Sumithraarachchi DBS 805 (fr.) (US); *Locality unknown*; *s. coll.* C.P. 1045 (fl., fr.) (BM, K); Walker s.n. (fl.) (K).

U. vietnamensis C. Meade

Vietnam *Quang Nam Province* (CLV - 27 - V); Ba Na, 25 km NW of Dà Năng, 24/07/23, Poilane 7326 (fr.) (E, P); May-July /27, J & M. S. Clemens 3827 (fr.) (P) (CLV - 27 - V). **Thailand** *Ubon Ratchatani Province* (NE – 26); Soi Sawan Waterfall, 16/10/98, Chalermglin & Meade 98-10-16-03 (-) (TCD).

U. zeylanica L.

Sri Lanka *Anuradhapura District*; Ritigala, 13/07/74 Waas 366 (fl.) (US); *Colombo District*; Welisara, 27/11/31, Simpson 8935 (fl., fr.) (BM); *Galle* District; Bona Vista near Galle, 10m 06/11/77, Huber 571 (fl.) (HBG); near Weligama, 01/01/80, Kostermans 28043 (fr.) (L); *Jaffna District*; Vaddakkachchi, Paranthan-Mullaitivu Road, 17/11/70, Kundu & Balakrishnan 705 (fl., fr.) (US); *Kalutara* District; Kalutara, Macrae 216 (fl.) (NY); Velikanda, 80.0 E 6.37N, 27/10/79, Klackenberg 239 (fl.) (NY); Yagirala, Kalutara, 100m, 29/06/75 Waas 1303 (fl.) (US); *Puttalam District*; Daluwa Village west of Puttalam Lagoon, 08/06/72 Maxwell & Jayasuriya 823 (fl.) (NY); *Locality Unknown*; 25/01/09, Fraser 179 (fl.) (BM, TCD); *s.coll.* C.P. 1030 (fl., fr.) (BM, TCD, US). **India** *Travancore*; Kotta Hill, Trirandrum, 18/03/34 Erlanson 5578 (fl.) (NY).

Appendix 3.2 - Morphological Data Matrix

Specimen no.	Collector no.	L	M	L1	L2	a	b	c	d	e	f	g	h	k	n	o	p	q	pel	v.no	v.an	ind	pedc	pedW	pedn	br.w	br.L	sp.W	sp.L	i.ptW	i.ptL	i.ptM	o.ptW	o.ptL	o.ptM	rec	car	stgW	stgL	stm	loc	stW	loc.b	stip	fr.W	fr.L	n.sd	hilW	hilL
A. dulcis	Lahaie Java SYNTYPUS G	127	28.5	65	62	64.5	63.5	61	59	53	48	41.5	35.5	31	35.5	48	54	58	4	12	49	39.7	20	0.8	0	3	5	4.5	4	10.5	24	13	11	24	10	2.5	3	0.4	1	2.2	1.3	0.4	0.25						
A. dulcis	Poilane 3193 Ham	140	35	73	67	73.5	72.5	72	70	65.5	61	51.5	43.5	41	46.5	59	63	65	6.5	16	50	20.3	22	0.8	0 *	*		5	4	14	25	10	12.5	25	12	2.5	2.5	0.4	0.8	2	1.4	0.4	0.1						
A. dulcis	Pierre 385 L	87.5	22.5	44.5	43	44.5	45	44.5	43.5	40	37.5	32	27.5	25.5	29	36.5	39	40.5	3	14	40	36.5	11	0.9	0	2	3.5	4	2.5	12	16	9	13	15	8.5	2	2	0.3	0.7	1.7	1.1	0.55	0.1						
A. dulcis	Merrill 5457 L	94.5	28	42	52.5	41	40.5	38.5	37.5	34.5	32.5	29	25.5	27.5	32.5	42	47	51	3	11	39	27.5	15	0.7	0	2	3.5	4	3	11	30	21	12	25	11	1.75	3.3	0.7	1	2	1.2	0.5	0.2						
A. dulcis	Squires 905 NYBG	105	22.5	60	45	60.5	57.5	53	50	44.5	41	34.5	28.5	26	30	39.5	42	43.5	4.5	16	52	29.5	29	1.1	0	4	4	5	4	15	24	13	18	23	13.5	2	3	0.4	1	1.8	1	0.4	0.2						
A. dulcis	Leeunen 364a L	150	30	77.5	72.5	77.5	78	76	72	64	58	48	39.5	36.5	41	55	61	65.5	4.5	12	46	20.3	13.5	0.7	0 *	*		3	3	6.5	15.5	7	6	40.5	5	1.6	2	0.25	0.7	1.5	0.8	0.25	0.15						
A. dulcis	Rant Jan 1924 L	124	27	62	61.5	63	63.5	62	60	53.5	49	41.5	34	30.5	35.5	47.5	53	56	3.5	14	50.5	24.3	11	0.8	0	2	4	4	3	9	20	11.5	10	15	6	2.5	2.1	0.4	0.7	1.7	1	0.6	0.2						
A. dulcis	Kerr 12 TCD	74	17	36.5	37.5	36.5	36.5	35.5	34	31	27.5	23.5	20	19.5	22.5	29.5	33	35	3	15	39	45	18.5	0.8	0	2.5	4	4.5	3.5	11.5	21	14	13.5	19	8	1.5	2.5	0.7	0.9	1.5	1	0.55	0.2	4	9	8	3		
A. dulcis	Schmid s.n. P	107	23	58.5	48.5	60	61	59.5	57.5	52	46	39	32	26.5	31	40	44	46.5	5	13	41	18	12	1.2	0 *	*		4.5	3	10	20	15	10	20	6	2	3.5	0.5	1	1.5	1	0.7	0.15	7	6	8.5	2	1	0.5
A. dulcis	Collins 1254 S	94.5	21.5	54.5	40	54	54.5	54	52	47.5	43	34	27	24.5	28	35.5	37.5	38.5	5	12	44	31	18	0.8	0	3	5	4	2.5	9	16	8	12	16	8	2.1	3	0.3	1	1.4	0.8	0.5	0.2	7	6	11	6		
A. dulcis	Leschenault Java P	109	20	57	52	59.5	59	57.5	55.5	49	44.5	35	27.5	25	29	37.5	41.5	44.5	3.5	12	46	40.7	22.5	1.2	0	4	8	7	4.5	9	17	12	11	14	9	2	3	0.3	1	1.5	1	0.5	0.15	5	4	5	1		
A. dulcis	Backer 18936 L	130	29.5	69.5	60	71.5	71	69	66.5	61	56.5	48	38.5	36.5	41.5	51	55.5	58	4	12	35	39.3																							10	7	14.5	7		
A. dulcis	Maxwell 75-718 L	146	28	87.5	58	87	84	79	75	66.5	59	47	36	32	36.5	47.5	52.5	54.5	5	15	42.5	17																							9	8	13	7	1.5	2
A. dulcis	**Arerage**	**114**	**26**	**61**	**54**	**61**	**61**	**59**	**56**	**51**	**46**	**39**	**32**	**29**	**34**	**44**	**48**	**51**	**4.2**	**13**	**44**	**30**	**####**	**18**	**0.9**	**0**	**2.8**	**4.6**	**4.5**	**3.4**	**11**	**21**	**12**	**12**	**22**	**8.8**	**2**	**2.7**	**0.4**	**0.9**	**1.7**	**1.1**	**0.5**	**0.2**	**###**	**7**	**6.7**	**10**	**4.3**	**1.3**	**1.3**
C.micranthum	Helfer 433 Harv	81.3	13.5	32.3	49	31.8	31.5	30.5	29.5	27.5	25	21	17	17.5	22	34	39.5	43	2.75	12	57 *		3.5	0.6	1	3	3	2.5	1.5	2.5	3.2	2	2.7	3	1.8	1.5	1.5	0.25	0.4	1.8	0.65	0.3	0						
C.micranthum	Pierre 209 NY	116	20	48.3	67.5	47.5	46.5	45	44	40	37.5	32.5	26	25.5	31.5	46.5	51.5	56.5	4.5	10	49																							17	5	8	1		
C.micranthum	Ramos & Adano 4424 NY	99	17	43	56	43	42.5	40.5	39.5	35.5	33.5	28.5	22.5	22.5	27.5	39.5	44.5	49.3	2.5	10	54																							15.5	8	10	2		
C.micranthum	Merrill 9271 Harv	90.5	13	40.5	50	39.7	38.5	36.5	34.5	31.5	27	22.5	17	17.5	22	34	39	45	2	10	41		10.5	0.7	1.9	2.5	4.5	3.5	3	2.5	4	1.5	3	3.5	1	1.75	1	0.3	0.25	1	0.7	0.3	0						
C.micranthum	Kerr 15133 TCD	73.7	14.5	32.7	41	32.5	32	31	29.7	27.7	25.5	21.5	17	17	20	28	31.5	34.5	2	9	53		3	0.5	1	3.5	4	3	1.9	2	3	1.3	2.9	3	1	1.5	1.1	0.4	0.3	0.7	0.6	0.3	0						
C.micranthum	Kerr 5862 TCD	78.5	15.5	37	41.5	36.7	36	34.5	33.7	30.7	28	24	19.5	18.5	21.5	30	34.5	38	3	10	56		6.5	0.7	0.8	4	4	3.5	2.5	2	5	3	4	5	1.5	1.8	1.5	0.4	0.35	0.8	0.6	0.2						
C.micranthum	PK 1180 TCD	71	11.7	31	40	30	29.3	27.5	26.5	24	22.2	18.7	15	14.5	17.5	26.7	31	34.5	1.5	10	47		12	0.4	1	2	3.5	2.5	2	1.5	3.5	1.5	1.8	3.5	1.5	1.5	1	0.35	0.3	0.8	0.6	0.25						
C.micranthum	Santisuk 307 BKF	108	20.5	57	51	56	55.5	54.5	53.5	48.7	44	36.5	28.5	25.5	29.7	39.7	44.5	47.5	4	12	56																							22	8.5	10	3		
C.micranthum	Pierre s.n. Harv	69	12.5	26	43	25.5	25.5	25	24.5	22.7	21.3	18.7	16	17	21.5	30.5	32.5	36.5	1.5	10	51		1.5	0.5	0.7	2.75	2.5	2.2	2	1.4	1.7	0.8	1.7	2	0.5	1.6	1	0.25	0.25	0.7	0.55	0.3						
C.micranthum	Pierre 209 Harv	68	11	23	45	22.7	22.5	22	21.7	20.5	19	16.5	14	15	19.5	28	32.5	35	2	10	56		2	0.6	0.5	2	3	2	1.5	1.9	2	0.9	2	2	0.9	1.4	0.8	0.3	0.3	0.6	0.5	0.2						
C.micranthum	Collins 1582 Smith	83	16.5	43	40	41.5	40.5	39	37.5	34.5	30.7	25.7	21.5	19.5	23.5	30.7	33.5	36.5	3	11	60																							10	8	10	2		
C.micranthum	Chalermglin & Meade 98-10-18-03	84.5	14.7	34.5	50	34	33.7	32.7	31.7	29	27	23.5	13.5	13.5	22.7	32.5	38	41	2.5	10	68		2.1	0.6	1	1.1	1.2	2.1	2.8	2.1	3.5	2	2.2	3.5	1	1.6	1	0.4	0.2	0.65	0.4	0.25						
C.micranthum	Soejarto et el. 6407 Harv	80.5	13.5	38.5	42	37	36	33.5	32.5	28.7	25.7	21	17	18.7	22.5	29.3	33	36	2	10	60		10	0.6	1.5	1.5	4.5	3.5	2	2.5	3.75	1.5	3	3.75	1.5	1.8	0.9	0.2	0.15	1	0.6	0.25						
C.micranthum	**Arerage**	**85**	**15**	**37**	**47**	**37**	**36**	**35**	**34**	**31**	**28**	**24**	**19**	**19**	**23**	**33**	**37**	**41**	**2.6**	**10**	**54**	**####**	**####**	**5.7**	**0.6**	**1**	**2.5**	**3.4**	**2.8**	**2.1**	**2**	**3.3**	**1.6**	**2.6**	**3.3**	**1.2**	**1.6**	**1.1**	**0.3**	**0.3**	**0.9**	**0.6**	**0.3**	**0**	**###**	**15**	**7.9**	**9.3**	**2.3**		
E'sis ferruginea	Clarke 14227 K	120	26.5	62.5	57	57	62	62	61	59.5	56.5	53	44.5	36.5	33.5	40.5	52.5	56	5	10	36		6	1.2	0			6	4.5	4	9	2	10	9	2	2.5	1.9	0.3	0.4	1.5	1.2	0.7	0.1						
E'sis ferruginea	Kerr 340 TCD	148	40.5	56.5	91	57.5	58	59	59.5	60	59.5	56	50	51	62	78.7	83.5	86.5	10	9 *			6	1	0			6	5	5.5	10	3	9	11	3	3	1.7	0.5	0.5	1.4	0.8	0.7	0.15						
E'sis ferruginea	Buch-Hamilton Typus BM Burma	122	34.5	63.7	58	63.7	63.7	64	63.5	61.5	58.7	52	43.5	39.5	45.5	53	55.5	56.7	7	10	55																							1.5	5	10	1		
E'sis ferruginea	Parkinson 6141 K Burma	150	36	72.5	77	73	73	72.5	72	63.7	65.2	58	46.7	46.5	54.5	69.5	73.5	75.5	6.5	11	52		5.5	1.5	0	3.5	10	7	6.5	6	10	3	9	12	5.5	3	2.3	0.5	1	1.4	0.8	0.6	0.1						
E'sis ferruginea	Hamilton-Buch S.n. BM Burma	130	33.7	71	58.5	71.5	71.7	71	70.7	67	64	57	45	38.5	42.7	53	56	57.5	6	12	61		15	1.5	0	4	12	8	8	9	15	9	12.5	15	9									1.5	5	7.5	1		
E'sis ferruginea	**Arerage**	**134**	**34**	**65**	**68**	**65**	**66**	**66**	**65**	**62**	**61**	**55**	**46**	**42**	**48**	**59**	**64**	**66**	**6.9**	**10**	**51**		**8.1**	**1.3**	**0**	**3.8**	**11**	**6.8**	**6**	**6.1**	**11**	**4.3**	**10**	**12**	**4.9**	**2.8**	**2**	**0.4**	**0.6**	**1.4**	**0.9**	**0.7**	**0.1**		**1.5**	**5**	**8.8**	**1**		
E'sis ferr. var cherr	Maxwell 90625 Harv	129	40	65.5	63.5	67	69	70	70.7	70.2	68.5	61.7	51.5	42.2	46.7	55	58.5	61.2	16	11	42		4	1.7	0			6.5	5.2	6	7	2	10	8	2	2.7	2	0.3	0.4	1.8	1.2	0.8	0.2						
E'sis ferr. var cherr	Koyama T-61621 Harv	139	44	69	70	70.2	71.5	72.7	73	71.7	70.5	65	55.5	55	54.2	61.5	65.2	68	12	12	57																							2	4	10	1		
E'sis ferr. var cherr	Geesink et al. 5835 L	142	44.7	59	82.5	59	60.5	61.5	62.5	62.2	61.5	59.5	53	53.5	61.5	75.5	79.7	81	12	11	44		14	1.5	0	3	14	8	9	8	12	8	11	14	6	2.5	2.5	0.3	1	1.75	1.2	0.8	0.15						
E'sis ferr. var cherr	Kerr 636 K	127	32.3	53.5	73.5	54.2	54.5	54	53.5	51.7	50.3	47	40.5	39.5	46.5	63	67.5	70	6	9	48																							2	4	7.5	1		
E'sis ferr. var cherr	c. Buesekom & Phengklai 1063 AAU	127	37.5	62	64.5	63	63	63.5	63.5	62.5	61	56	48	45	50.5	56	58	59.5	5	10	52																							2	5	8	1		
E'sis ferr. var cherr	Pierre s.n. Harv TYPUS	121	42.5	50.5	70.5	51	52	52.5	52.7	53	52.3	52	48.5	51.5	56.5	66	68.5	69.5	6	10	51																												
E'sis ferr. var cherr	**Arerage**	**131**	**40**	**60**	**71**	**61**	**62**	**62**	**63**	**62**	**61**	**57**	**50**	**48**	**53**	**63**	**66**	**68**	**9.5**	**11**	**49**	**#### ####**	**9**	**1.6**	**0**	**3**	**14**	**7.3**	**7.1**	**7**	**9.5**	**5**	**11**	**11**	**4**	**2.6**	**2.3**	**0.3**	**0.7**	**1.8**	**1.2**	**0.8**	**0.2**	**###**	**2**	**4.3**	**8.5**	**1**		
R. siamensis	Maxwell 75-571 AAU	101	15.5	43	58	43.5	43	41.5	40.5	38	35.5	30.5	24	22.5	28	43	50	55	2.5	10	44	44.5	7	0.7	0.5			5	2	4	6	3.1	6.5	5	2	2	2.5	0.7	1.5	1.5	1	0.7			3	7.5	7.5	4	1	1
R. siamensis	Meade 76 TCD	87	15	39	48	39	38.5	38	37	35	32	26.5	21	20.5	25.5	38	43	46	3.2	9	45	50.7	6.5	1	0.5			5	2.5	4	6	2.5	7.5	7	2	2	2.5	1.2	1.5	1.5	1	0.7							
R. siamensis	Maxwell 72-125 AAU	103	15	52.5	50	52	50.5	47.5	45.5	39.5	35	27.5	31.5	19.5	25.5	39	43	46	2.5	10	44	46	11	0.95	1	1	2	6	4	6	8	3	8.5	9	2	2.5	3.2	0.5	1	1.9	1.2	0.7							
R. siamensis	Larsen 40297 AAU	89	14	43	46	42.5	41	39	37.5	33.5	30	24	19	18.5	23	35	41	44	3.5	9	44	18.7	16	1.25	2	2	3	8	4																					
R. siamensis	Kerr 15067 K	91	14	40.5	50.5	40.5	39.5	37.5	36	31.5	27.5	23	18	18.5	23	36.5	41.5	45	3	11	58	0	16.5	1.25	1	1.5	2	6	2.5	5	6	2.5	7.5	6	2	2.25				1.5	1	0.6		3.5	10	10.5	8	1.5	1
R. siamensis	Kerr 15724 TCD	127	18	70	57	69.5	68	62.5	58.5	49	41	32	24	23.5	30.5	46.5	52.5	56	4.5	12	45	1.67	11	1.1	2	2	2.5	7	4	8	12	6	12	11	4	3.5	4	1.1	1.4	2.5	1.7	0.9							
R. siamensis	Maxwell 71-479 AAU	89.5	14	34.5	55	35	34.5	34	33.5	30.5	28	23.5	29	18	24.5	40	46	50	2.5	10	53	46.5	9	1	1	2.5	3	5	3	5	9	6	8	9	2	2.5	3.2	1.5	1.5	1.9	1.3	0.7		2.5	8	12	6.5		
R. siamensis	Sirirugsa 818 Harv	128	18	66	62	65.5	63.5	60.5	57.5	50	44.5	35.5	27	25	31	44.5	50	53	6	10	54	17	10	1	2	1	2	6.5	4	5.5	7.5	3	11.5	10	3.5	3				2.2	1.7	0.8							
R. siamensis	Kerr 4308 TCD	151	20.5	72	79	71.5	69.5	66	62.5	53.5	46.5	35.5	26	27	35.5	62	71	75.5	4	13	53.5	9	9.5	1	1.5	1	2	5	3	4	7	5	7.5	9	3	2.5	3.1	0.6	0.7	1.6	1.1	0.7							
R. siamensis	**Arerage**	**107**	**16**	**51**	**56**	**51**	**50**	**47**	**45**	**40**	**36**	**29**	**24**	**21**	**27**	**43**	**49**	**52**	**3.5**	**10**	**49**	**26**	**####**	**11**	**1**	**1.3**	**1.6**	**2.4**	**5.9**	**3.2**	**5.2**	**7.7**	**3.9**	**8.6**	**8.3**	**2.6**	**2.5**	**3.1**	**0.9**	**1.3**	**1.8**	**1.3**	**0.7**	**#### ###**	**3**	**8.5**	**10**	**6.2**	**1.3**	**1**
U. lamponga	King 209 1884 HOLO? K	222	40.5	121	101	121	116	109	114	91	81.5	66.5	52	41	53	68	75	80.5	7	23	40.5	3	5	1.5	3.5	*	*	*	*	*	*	*	*			*	*	*	*	*	*	*							
U. lamponga	King's collector s.n. G	137	19.5	75.5	61.5	73.5	69.5	63.5	58.5	49	41.3	33	25	23.5	28.5	42.5	48.5	52.5	5.5	15	41	2																							12	14	26	10		
U. lamponga	King's coll. s.n. BM	233	39.5	126	107	124	120	113	107	91.5	80.5	66	53	49.5	57.5	75	84	91	6	21	48	4.25																												
U. lamponga	**Arerage**	**197**	**33**	**108**	**90**	**106**	**102**	**95**	**93**	**77**	**68**	**55**	**43**	**38**	**46**	**62**	**69**	**75**	**6.2**	**20**	**43**	**3.1**	**####**	**5**	**1.5**	**3.5**	**#### ####**	**#### ####**	**#### ####

Specimen no.	Collector no.	L	M	L1	L2	a	b	c	d	e	f	g	h	k	n	o	p	q	pet	v.no	v.an	ind	pedc	pedW	pedn	br.w	br.L	sp.W	sp.L	i.ptW	i.ptL	i.ptM	o.ptW	o.ptL	o.ptM	rec	car	stgW	stgL	stm	loc	stW	loc.b	stip	fr.W	fr.L	n.sd	hilW	hilL
C. argenteum	Wall Cat. 6468 K	118	25.5	68.3	50	67	64.5	60.8	56.3	50	46	37.5	31	30.5	35.3	42	45	46.5	3																																
C. argenteum	Maxwell 75-658 L	184	33.8	103	81	102	99.5	93	86	75	65.8	53	42.5	40.5	47.5	61.3	65.5	71	4																																
C. argenteum	Geesink et al. 5662 L	150	34	76	74	74.7	71.3	69.5	66.5	61.5	56.5	48	40.3	43.5	52	65	69	72	5																																
C. argenteum	Roxburgh s.n. BM	130	25.3	60.5	69.5	60.5	60	58.8	56.8	52.5	48	40.5	33.5	33	38.5	50.5	55.5	61.5	4																																
C. argenteum	**Average**	**146**	**30**	**77**	**69**	**76**	**74**	**71**	**66**	**60**	**54**	**45**	**37**	**37**	**43**	**55**	**59**	**63**	**4**																																
U. calamistrata	Hance 7436 K SYN	108	21.5	50.5	57.5	49.5	48	46	44.5	41	37.5	32	27	24.5	27.5	35.5	41.5	50	7	9	44	118	5	0.8	3	2	5.5	3.5	4	2	8	5	4	9	6	1.7	1.2	0.5	0.25	1.5	1.15	0.4		5	16	21	8		
U. calamistrata	Castellini 60 P	77	20.5	39	38	38.5	37.5	36.5	35.5	33	31.5	28.5	25.5	22.5	24.5	30	32.5	34.5	4.5	7	46.5	115	3	1	3.5	2	4.5	5.5	5	2.75	5.75	3	2.75	5.75	3	2.5	1.5	0.4	0.2	1.5	1.1	0.4							
U. calamistrata	Lau 468 E	104	24.5	47.5	56	47	46.5	44.5	43.5	41	38.5	35	30	28.5	33.5	41	46	50.5	6	8	50	119																						4	12	16	6		
U. calamistrata	Hance 7436 BM SYN	119	22.5	54	64.5	51	49.5	47	45	41.5	38.5	33	28.5	26.5	32	44.5	49.5	54.5	5	9	44	118	3	0.7	2	2	2.5	4.5	5.5	2.5	5	3					2	1.5	0.65	0.4	1.2	1	0.5		3	11	14	4		
U. calamistrata	Lamont 12A BM	115	26.5	52.5	62.5	51.5	51	50	48.5	45.5	42	37.5	32.5	31.5	36.5	49	54	58	8	8	49	61.3																						3.5	22	32	10		
U. calamistrata	Wang 34503 NY	123	23.5	49.5	73.5	48	47	45.5	44.5	41.5	39.5	35.5	30	29.5	35	45.5	53	58.5	8.5	10	45	123																						5	15	27	8		
U. calamistrata	**Average**	**108**	**23**	**49**	**59**	**48**	**47**	**45**	**44**	**41**	**38**	**34**	**29**	**27**	**32**	**41**	**46**	**51**	**6.5**	**8.5**	**46**	**109**	**####**	**3.7**	**0.8**	**2.8**	**2**	**4.2**	**4.5**	**4.8**	**2.4**	**6.3**	**3.7**	**3.4**	**7.4**	**4.5**	**2.1**	**1.4**	**0.5**	**0.3**	**1.4**	**1.1**	**0.4**	**####**	**###**	**4.1**	**15**	**22**	**7.2**		
U. cordata	Miyomdham 177 Cop	200	55	93	107	93.5	93	91.5	90	87	83.5	75	65.5	61	67	77.5	88	96	9	10	57	6	5.5	2.1	8	6	2	8	5	8	14	10	12	17	4	2	5	1	1.5	7	4.5	1.5	0.15							
U. cordata	Ridley s.n. BM	129	37.5	63.5	65.5	65.5	67	66.8	65.5	62.5	59.5	53.5	46	45.5	52.5	62	63.5	64	5	8	43	42.5	4	1.5	5	7	4	7	4.5	8	13	10	9	11	6	2	4	1	1	6	4	1	0						
U. cordata	Wallich 6487a BM	261	70.5	127	134	129	131	132	131	125	119	105	82.5	87.5	102	120	124	126	11	19	57	0	10	2.5	13	5	5	6.5	4	8	14	9	9.5	11	6	2.5	4	0.6	1	6	4	1	0	2	14	21	6		
U. cordata	Wallich 6487c BM	253	54	136	117	137	136	132	129	119	112	91	72	54	67.5	78.5	94.5	101	13	29	48	0																												
U. cordata	Lace 5386 E	233	74.5	135	98	136	136	135	134	128	122	109	91	83.5	87	89.5	91	92	11	17	46	6	17	2.5	11	8	6	8	6	12	18	16	12	15	9	3	4.5	0.7	1	6.5	5	1.1	0						
U. cordata	Keenan 1256 E	227	68	108	119	108	107	106	105	100	97.5	89	79	79.5	90	105	107	109	13.5	22	54	16.8	16	2.5	7.5	9	5	9	7	8	10	6	12	13	7	*	*	*	*	6	*	1	0						
U. cordata	Wallich 987 BM	226	60	115	111	116	117	117	117	114	108	91.5	77	70.5	80.5	94.5	99.5	104	14	18	55	29.5	13.5	1.5	6	4	5	6	6	7	12	8	8.5	13	8	2	3	*	*	5	3	0.75	0						
U. cordata	Thwaites CP 3527 TCD	110	37	57	52.5	57.5	57.5	57.5	57.3	56.5	54.5	50.5	44.5	41.5	43	46	48	50	6	10	53	21	12	2	9	3	3.5	6	5	11	13.5	10	10	13	3	2	5	*	1	*	*	0						
U. cordata	Roxburgh s.n. BM	275	66.5	116	159	120	121	121	120	118	115	102	84.5	80.5	97	125	134	137	9	18	53	22.3	8	2	5	3.5	4	7	4	*	*	*	*	*	1.5	4	0.3	1	*	*	0						
U. cordata	Roxburgh 110 Tavoy BM	176	49.5	73	103	75	76	76	76	74	71.5	66	58.5	61.5	70.5	83.5	89.5	95.5	5	13	54	16.8	9	2	9	8	6	6.5	6	8	12	8	9	12	7	2	4	0.6	0.8	6.5	3	1.1	0						
U. cordata	Larsen 2600 Cop	266	68	124	142	125	126	124	121	114	108	95	80.5	81.5	93	115	121	126	8.5	21	59	14	10	1.5	11	6	5.5	7.5	6	12	20	11	13	20	12	2	4	0.5	0.5	7	4	1.2	0						
U. cordata	Parnell 95-352 TCD	197	60.5	111	86	112	113	111	109	105	98	84.5	70.5	69.5	75	79	80	81	11	17	52	28.8	11	2	2.5	6	4	6	4.5	7.5	11	7.5	8	13	9	1.5	3	0.3	0.4	4.5	3	1	0						
U. cordata	King 5776 BM	200	50	109	90.5	110	110	108	105	97.5	92	78	64.5	59.5	70.5	81	86.5	88	9	11	53	19.3	8.5	2.1	8.5	8	5	10	4	10	14	10	11	14	6	1.5	4	0.3	1	7	5.5	1.5	0						
U. cordata	Maxwell 89 1324 E	243	67.5	133	110	134	134	132	129	122	116	104	86.5	81.5	84.5	89	93.5	98.5	13	16	48	13.8			17																				1.5	18	39	20		
U. cordata	Larsen 44107 AAU	242	59	122	120	121	119	115	112	114	96	83.5	68.5	72.5	84.5	103	107	111	11	17	55	6																						1.9	18	30	14		
U. cordata	Buesekom 4432 L	114	32.5	66	47.5	66.5	66.5	66.5	65.5	62.5	60	52.5	42.5	36	38.5	44.5	45.5	46.5	4.5	12	44.5	16.5																						1.5	16	34	16		
U. cordata	Buesekom 1950 L	156	42	78.5	77.5	78.5	78	77.5	76.5	74	71	64	54.5	51.5	61	71	73	73	10	12	52	24.3																						2	14	21	8		
U. cordata	Meade 84 TCD	251	74.5	136	115	137	138	138	135	129	122	107	90.5	77	79	86.5	94.5	101	13	14	66	14.3																						4	18	34	14		
U. cordata	Maingay 1031A/24 BM	145	47	79.3	65.5	80.3	80.3	79.8	79.5	77.5	74	68.5	61.3	54	55.5	58	61	63.5	6	10																								17	16.5	35	7		
U. cordata	Pahang Ridley s.n.	169	44.5	99.5	69	101	99.5	96.5	93.5	87.5	82	69.5	56	48	52.5	61.5	64	65.5	7	11	59	8.75	10	2	*	*	*	7	4	10	14	8	12.5	14	8	2	4.5	0.4	1	*	*	*							
U. cordata	Kerr 12241 BM	275	73.5	145	130	145	144	141	137	129	121	103	86	82	92.8	110	115	121	12	13																								5.5	14.5	20	5		
U. cordata	**Average**	**207**	**57**	**106**	**101**	**107**	**107**	**106**	**104**	**100**	**94**	**83**	**70**	**66**	**74**	**85**	**90**	**93**	**9.6**	**15**	**53**	**16**	**####**	**10**	**2**	**8.7**	**6.1**	**4.6**	**7.3**	**5.1**	**9.1**	**14**	**9.5**	**11**	**14**	**7.1**	**2**	**4.1**	**0.6**	**0.9**	**6.2**	**4**	**1.1**	**0**	**###**	**4.4**	**16**	**29**	**11**	**####**	**####**
U. curtisii	Whitmore FRI 2998	195	36	105	90	101	96.5	91.5	86.5	74.5	67	56	46	42	49	60	67.5	71	7	13	40	18.2																									27	65			
U. curtisii	Whitmore FRI 2998	189	32.5	99	90	98.5	95.5	91.5	86.5	77	69.5	56	44.5	39.5	46.5	64	70	74	7.5	11	40	18.2																													
U. curtisii	Sinclair Sing. 39652	151	27	81	70	80.5	78	73	68.5	57	50	42	34	35	42	56	62	63.5	8	12	50	10																													
U. curtisii	Sinclair Sing. 39652	178	31.5	92.5	85	91.5	90	86	82	74	66	54	42	39	44	63	70	74	7	10	50	10																													
U. curtisii	Geesink & Santisuk 5104 L	89.5	14	45.5	44	44	43	41.5	39.5	36	32.5	26.5	20.5	19.5	22.5	33.5	36	38.5	4	10	30	24.7	18	2	1	1.75	4.5	7.5	9.5	6.5	11	5.25	6.5	10	5	2.5	3	0.6	0.2	3	2.7	0.7							
U. curtisii	Geesink & Santisuk 5104 Cop.	123	26	65	58	64	63	62.5	61	56	51	43	35	31	32	45	49.5	52	5	14	40	17.7	16	1	1	2	4	8	9	6	11.5	5.25	6.5	10	5	2.5	3	0.6	0.2	3	2.7	0.7							
U. curtisii	Geesink & Santisuk 5104 E	97	15	48	49	47	46	44	42	38	36	27	22	19.5	24	34	37.5	41	5.5	11	40	19.3	10	1	1	1.5	5	5	7.5	5	9					4	2			2.5									
U. curtisii	Curtis 1415 BM	195	36	105	90	105	103	99	95	85	79	64.5	50.5	43	53	75	78	81	6	13	40	11.7	21	1	1	1.5	4.5	10	10																				
U. curtisii	Curtis 1415 BM	154	27	90	64	90	87	82.5	79	71	63	48	30.5	32	40	56	62	64	4.5	13	35	7.67	21	1	1	1.5	4.5	10	10																				
U. curtisii	Curtis 1415 K 1888	262	39	141	121	138	133	125	118	101	88	64	55	48	60	88	102	109	7.5	12	35	5	18.5	1	1	2.5	6.5	8	7	5	11					5	2			2.2									
U. curtisii	Curtis 1415 K 1892	202	33	103	99	102	99	94	88.5	76	67.5	53	41	41	49	67.5	78	84	5	14	40	5.67	27	1.5	0.8	2	5	8	8	5.5	11																		
U. curtisii	Curtis 1415 K	133	23	70.5	62	69.5	68.5	64	61.5	55	50	40.5	31.5	31.5	38	47.5	55	60	5	12	35	5.67	18.3	1.25	0.83	1.75	4	8	8	4	12	5	5	11	5.25	2.25	2.3	0.75	0.4	2.5	2.3	0.55						
U. curtisii	Curtis 3623 K	161	36	92	69	90	87	82.5	79	72	66	56	46	42.5	49	60	63	65.5	5.5	13	40	24.3	10	1	1.2	1.5	2	8	9																				
U. curtisii	**Average**	**164**	**29**	**87**	**76**	**86**	**84**	**80**	**76**	**67**	**60**	**49**	**39**	**36**	**42**	**58**	**64**	**68**	**6**	**12**	**40**	**14**	**####**	**18**	**1.2**	**1**	**1.8**	**4.4**	**8.1**	**3.7**	**5.3**	**11**	**5.2**	**6**	**10**	**5.1**	**3.3**	**2.5**	**0.7**	**0.3**	**2.6**	**2.6**	**0.7**	**####**	**###**	**####**	**27**	**65**	**####**	**####**
U. dac	Poilane 17489 P	118	19.5	44	74	44.5	43.5	42.5	41.5	38.5	35.5	30	24.5	24	30.5	44.5	51	57	5	11	50	25.7	18	2	2.5	2	12	9	7	7.5	18	11	7	16	8	3.25	4	*	*	4	*								
U. dac	Poilane 17489 P	106	20	55	50.5	55.5	54.5	53	51	46	40.5	37	23	20	24.5	34	38.5	40.5	5.5	10	50	25.7	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*							
U. dac	Poilane 1459 ISO Harv	132	34	64.5	67	64.5	64.5	63.5	61.5	57.5	54	47	40.5	41.5	47	54	57.5	60.5	5	11	50	34	10	1.5	2	*	*	10	8	10	15	8.5					*	*	*	*	4.2	3.3	*							
U. dac	Pierre 1785 HOLO P	125	24	67	58	66	65	62.5	60	55	49.5	40.5	32	28	33	43	47	51	5	11	50	31.6	*	*	*	*	*	*	*	*	*	*	*	*	*	*	2.5	0.75	0.38	2.38	1.81	*		*	*	*	10		
U. dac	Poilane 17490 P	149	20	73.5	75	74	73.5	69.5	66	59	53.5	41.5	31.5	32	38	53.5	60	65	5.5	11	43	23.8	25	1.5	4	*	*	5	5	7	18	6	8	17	8	*	4	1.2	0.75	4.3	3	0.6		10	19.5	32.5	12		
U. dac	Pierre 748 SYN P	262	44	122	140	121	119	115	109	95	83	66	54.5	57.5	70	102	111	123	5	15	45	20.5	14	1.25	2	*	*	9	12	7.5	15	9				*	3.5	1.25	0.5	4	3.5	*							
U. dac	Pierre 1459 SYN P	137	27	68	69	68.5	68	65.5	63.5	57.5	51.5	43.5	35.5	34	41	53.5	58	63	5.5	12	48	22.7	11.5	1.75	1.5	4.5	1.15	13	13	9	18	8.25	9	18	8.25	*	4	1.8	1	4	3.5	*							
U. dac	Pierre 748 SYN P	246	38.5	141	105	137	131	123	106	90.5	68	51.5	43	44.5	51	67	76	85	6	14	43	21.6	8	1.25	4.5	4.5	1.2	9	9	9	13	*				*	3.5	1.25	0.75	4	3.5	*							
U. dac	Pierre 1459 SYN K	197	41	108	89	108	107	104	101	92.5	84.5	70	55	48.5	56.5	71	78	85	6	10	45	22.6	13	1.75	2	4	1.5	11	8	6	14	8	9	14	6	3.5	3.5	1.5	0.75	4.5	3.75	0.75							
U. dac	Pierre 748 SYN K	178	36.5	82.5	95	83	82.5	81.5	80.5	76	70	60	50	46	56	74.5	83	89	5	13	50	23	10	1.5	1.5	6	2	8	8	6.5	11	4.5				*	3.5	1	5	3.5	3.1			8	21.5	29	6		
U. dac	Poilane 17489 8/6/1930	117	20.5	46.5	70	47.5	46.5	45.5	44.5	41	38	32	26	25	30.5	44	51	57	5	11	49	37.3	17	1.5	2	10	2	10	10	8	17	10				*	3.5	1.3	0.75	4.5	3.75	*							
U. dac	Poilane 13254	183	22.5	68	115	67.5	65.5	63.5	60	52.5	47	38	29	27	37	64	77	87	7	13	35	51.3	15	1.5	4	5	2	11	12	*	*	*				*	*	*	*	*	*	*							
U. dac	Thorel s.n. 6/1866 Angkhor P	115	26	59	56	58.5	58.5	57.5	56.5	52	48.5	41.5	33	32.5	33	51	54.5	56	5.5	9	40	30.7	22	*	*	3.5	7	2	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*	*		7	11	16			
U. dac	Thorel 9179 P	171	29	74	96.5	75	74.5	73	72	66.5	61	52	42	40	49	70	82	94	5	10	45	39	8	2	2	4	1	8	9	6	9	4.5				5	3.5	1	1	4	3.5	*		8	19.5	30	10		
U. dac	Meade 98-10-18-1 dupl.3 TCD	224	43	119	105	120	118	115	111	101	92	76	58.5	51	57.5	77	87	93	6.5	12	50	14.8																						14	23.5	45	12		
U. dac	Meade 98-10-18-1 dupl.2 TCD	180	41	90	90	91	90.5	89.5	87	82	76.5	64.5	53	49	57	72	78	81	5	13	50	23.5																						15	24.5	47.5	13		
U. dac	**Average**	**165**	**30**	**80**	**85**	**80**	**79**	**76**	**73**	**66**	**60**	**49**	**39**	**38**	**44**	**61**	**68**	**74**	**5.5**	**12**	**46**	**28**	**####**	**14**	**1.6**	**2.6**	**5.2**	**2.8**	**9.4**	**9.2**	**7.7**	**15**	**7.8**	**8.3**	**16**	**7.6**	**3.9**	**3.6**	**1.2**	**1.2**	**3.9**	**3.3**	**0.7**	**####**	**###**	**10**	**20**	**33**	**11**		
U. flexuosa	Poilane 6781 Holo P	73.5	10.5	36	37.5	34.5	33	30.5	29	25	22.5	17.5	14.5	13.5	16.5	26.5	31	34.8	2	9	54	5.33	29	0.5	1	3	3.5	2.5	1.5	2.5	5	3	3	4.5	1.5	1.6	1.7	0.25	0.3	1	0.7	0.35	0.1						
U. grandiflora	Champion 38 Typus K	143	27.5	81	62	83	82.5	79	75.5	66.5	58.5	47.5	37.5	33.5	39.5	50	54	56.5	4.5	11	45	21.8	15	2.5	1	8	11	12	13	11	22	12	17	22	8	*	*	0.75	*	5.8	5	1.2	0						
U. grandiflora	Wallich s.n. Typus BM	156	36	85.5	70.5	86.5	86	83	80	72.5	64.5	54.5	44.5	44	48	58	61.5	65	4.5	16	46	34	20	2.1	5	12	18	21	17	13	22	14	14	21	11	5	6	1.1	1.1	6.5	5.6	1	0						
U. grandiflora	King 4786 Typus K	190	35	99.5	90.5	101	99.5	97.5	94	84	75.5	60	47.7	45	51.5	72.5	79.5	83	6	16	43.5	21.5																						16	13	58							
U. grandiflora	Henry 12-9-1898 NY	159	31.5	78	81	81	79.5	76.5	73.5	66.5	61	51	41	39.5	47	63.5	69.5	73.5	9	12	31.5	40.7																						25	16.5	75						
U. grandiflora	Lamont 8 BM	158	25.5	82	75.5	83	81.5	76	70	58	50.5	41	33	31.5	36.5	50	55	60	6.5	14	38.5	16	17	2.2	3	18	28	15	14	19	16	11	13	16	7	5.5	5	*	*	7	5.5	1	0						
U. grandiflora	Maxwell 71-765 AAU	165	40	99.5	65	101	99.5	94.5	90	79.5	73	61.5	50.5	42.5	53	62	60.5	61	7	11	51	15.5	19	3	5	28	37	18	25	18	34	25	36	40	22	6	8	0.75	1	11.5	10	2.5	0.25						
U. grandiflora	Poilane 31254 P	236	43	131	105	133	131	125	118	100	88	70.5	55.5	42.5	54.5	71	79.5	85.5	9	12	47	17.5																						20	18	78	24		
U. grandiflora	Geesink 6620 L	207	41	105	102	105	104	101	97	89	82	67	54	45	50.5	59.5	66	71	7	15	55	20	13	2.8	32	2.2	14	17	17	16	28	15	20	24	16	4	5	0.5	0.5	5	4	0.9	0.1						
U. grandiflora	Geesink 7896 BKF	254	62.5	155	99	152	147	139	133	117	108	90.5	74.5	67.5	73.5	81	83.5	87.5	12	18	54	10.5	32	3.1	55	5	16	16	22	18.5	45	27.5	18.5	45	27.5	6	6	1	0.6	6	5	1.3	0.2						
U. grandiflora	Dee 191 BKF	138	28.5	87	51	87	85.5	80.5	77	65	55.5	44.5	35.5	31.5	34.5	41.5	45.5	48	5	12	41	9.75	17	3.5	4	*	*	*	*	20	32	15	22	37	20	9	7	1.2	0.5	11.5	9	1.5	0.4						
U. grandiflora	Backer s.n. U	198	40	109	89	110	108	104	97.5	84	74.5	61.5	49.5	49.5	58	73.5	79	82.5	6.5	12	38.5	6.75	31.5	2.5	4	13.5	9	16	15	*	*	*	*	*	6.5	7	1	1	7	6	1.5	0.1		44	15	45	22		
U. grandiflora	Balgooy 5147 U	113	23	63	50	64	63	61	59	53	47	37.5	30.5	27.5	33.5	43.5	46.5	48	4.5	12	40	13.3	21	1.4	4.5	5	12	16	16	15	25	13	19	28	7	5	5	0.8	0.7	7	6	1	0.15						
U. grandiflora	Larsen 40936 AAU	134	28	70	63.5	70.5	63	65.5	63.5	58.5	52.5	44.5	36.5	33	39	53.5	58	60.5	5	13	52	17.5	17	1.2	4.5	20	33	14	15	13	25	18	16.5	25	11	5	*	*	*	7	5.7	1.5	0.1		14	11.5	40			
U.grandiflora	**Average**	**173**	**36**	**96**	**77**	**97**	**95**	**91**	**87**	**76**	**68**	**56**	**45**	**41**	**48**	**60**	**64**	**68**	**6.7**	**13**	**45**	**18**	**####**	**20**	**4.4**	**12**	**12**	**20**	**16**	**17**	**16**	**28**	**17**	**20**	**29**	**14**	**5.8**	**6.1**	**0.9**	**0.8**	**7.4**	**6.2**	**1.3**	**0.1**	**###**	**24**	**15**	**59**	**23**		

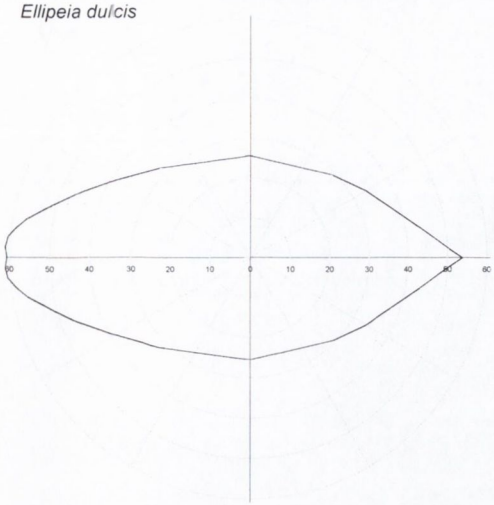
Specimen no.	Collector no.	M	L1	L2	a	b	c	d	e	f	g	h	k	n	o	p	q	pel	v.no	v.an	ind	pedc	pedW	pedn	br.w	br.L	sp.W	sp.L	i.ptW	i.ptL	i.ptM	o.ptW	o.ptL	o.ptM	rec	car	stgW	stgL	stm	loc	stW	loc.b	stip	fr.W	fr.L	n.sd	hilW	hilL
U. hahnii	Maxwell 75-366 AAU	159	32.5	75	83.5	75.5	74	71.5	69	61.5	56	45.5	37	40	47.5	63	69	73.5	10	12	43	40.8		11	1.2	0	6	10	10	14	7.5	24	10	10	25	7	3	4	0.8	1	2.5	1.5	0.7	0.5							
U. hahnii	Maxwell 74-224 AAU	145	30.5	73	72	73.5	72.5	69.5	66	60.5	55.5	45.5	37.5	36.5	41	50.5	56	62	7	11	39	29.8		10	1.5	1	14.5	15	12.5	15	7	36	18	10.5	35	6	3	4	0.75	1	2	1.2	0.8	0.35							
U. hahnii	Larsen et al. 32104 AAU	134	27.3	67.5	66	68	67	64.5	62	55	50	42.5	34.5	34	39	50	55	59	8.5	14	50	38.7																					3	9	16	12			
U. hahnii	Hahn, s.n. Lecto P	100	23.8	52.5	47.5	51.5	51	49.5	49	45	40.5	35	28.5	29.5	36.5	54.5	62.5	69	7	10	44	43.5		10	1	3.5	10	21	10	17	8	34	12	10	32	4	2.5				2.75	1.4	0.8	0.7							
U. hahnii	Geoffray 385 Avril 1904 P	135	26.5	58.5	76	58	58	56	54.5	49.5	45.5	38	31.5	29	35	50	59	67	6	12	43	21.7		10	1.1	3	11	17.5	10	18	7	44	23	10.5	45	22	2	3.5	0.7	0.5	2.6	1.6	0.7	0.7							
U. hahnii	Pierre 1786-746 Para P	142	25.3	54.5	87	54.5	54	52.5	51	46.5	43.5	38.5	32.5	33	40.5	58	66.5	79	7	10	47.5	41.5				2	12	13	9	12	7.5	41	23	11	40	8	2.5				2.5	1.5	0.6	0.4							
U. hahnii	Kerr 4171 K	112	22.5	44	68	43.5	42.5	41	40.5	37	35	31.5	26	29	35.5	49	54	56.5	5	9	36.5	49.3		11	1	0	10	16	10	16	4.5	30	16	8	43	13	3	3		0.5	2.75	1.8	1	0.5							
U. hahnii	Put, Feb 19, 1930 K	110	22.5	55.5	54.5	53.5	51.5	49.5	44	40.5	34.5	27.5	31.5	27	31.5	41	46	50	6	11	44	37		8	2	1	8	12	11	15	7.5	40	15	11	43	13	3			0.5	2.55	1.4	0.9	0.6							
U. hahnii	Ker 2707 TCD	119	19.8	58.5	60	57	55.5	53	51	46	42	34.5	27	25	30	41.5	47	50.5	6	11	47.5	48.3																			2.8	1.6	0.9	0.6							
U. hahnii	Poilane 15169 P	116	22	49	66.5	49	49	48	46	42	38.5	33	27	26.5	32.5	44.5	50.5	56	9.5	10	40.5	63		6	1	2	13	17	11	16	6.5	38	18	10	35	3	4	3.5	0.6	0.7	2.2	1.1	0.5	2.5		7	10.5	19	12	0.5	0.5
U. hahnii	Average	127	25	59	68	58	58	56	53	48	44	37	31	31	37	50	57	62	7.2	11	44	41	####	9.4	1.3	1.6	11	15	10	15	7.2	36	17	10	38	9.6	2.9	3.6	0.7	0.7	2.5	1.5	0.8	0.8	###	5	9.8	18	12	0.5	0.5
U. hamiltonii	Wallich 6485E Type BM	180	45	89.5	90.5	90.5	88.5	85.5	83	78	72.5	63.5	54.5	52.5	59.5	77	81.5	85.5	4.5	22	59	11	*	*	*	*	*	*	*	*	11.5	19	13	12	20	10	4.5	*		0.8	0.5	*	*	*							
U. hamiltonii	Smitinand 560 BKF var. kurzii	131	34	60	71	60	60.5	59	58	54.5	51.5	45	40	40	45	59.5	63.5	66	4	15	54	21.5		22	2	4	6.5	8	10	7	10	15	7	10	19	6	*	*	*	*	*	*	*							
U. hamiltonii	Wirat 1733 BKF var. kurzii	190	42.5	87	103	88	88	86.5	84.5	78	72.5	62.5	52.5	52	61.5	77.5	84.5	91	4	12	46	8		36	1.5	4.5	6.5	8.5	10	7	9	13	6.5	9.5	14	6	3	3.5	0.5	0.5	2.7	2	1	0							
U. hamiltonii	Wang 7864b Beij	220	44	117	103	116	110	102	97	85	77	65.5	54.5	54.5	62.5	80.5	88.5	92.5	4.5	17	57	10.5																					23	20	29	4			
U. hamiltonii	Clarke 20094 BM	103	24.5	52.5	50	51.5	51	48	46.5	42.5	39.5	35	30.5	28.5	33	40.5	43.5	46.5	2.5	15	53.5	8.5		32.5	1.5	2	9	13.5	7.5	6	10.5	31.5	14	11.5	20	11.5	4	3.5	0.6	0.5	2.7	1.8	1	0							
U. hamiltonii	Phrae 309 BKF	155	46.5	76	79	77	77	76	73.5	68	63.5	56.5	50.5	51	57.5	70	73.5	71	4.5	17	61	*		33	1.5	4	8	15	12	10	12	15	8	12	15	5	4	*	*	*	*	*	*	*							
U. hamiltonii	King 2350 L	174	37.5	70.5	103	72	72.5	69.5	67.5	61.5	56	49.5	41	47	54.5	73.5	84.5	90	7	16	50.5	9.25																					32	13.5	19	8			
U. hamiltonii	Lace 5920 E	174	41.5	102	72	103	101	97.5	93.5	84	76	65	54	43.5	47.5	58.5	63.5	67.5	6.5	16	45	15.3																					30	18	24	10			
U. hamiltonii	Stainton 6860 BM	190	38.5	75.5	114	76	75.5	73	70	64.5	59.5	51.5	43.5	49.5	58	77.5	89.5	96	6.5	15	48.5	12.8		27	1.5	3.5	*	*	*	*	14.5	27	18	13	23.5	12	4.75	3.5	1.1	0.4	3	2	0.8	0							
U. hamiltonii	Wesche 71209 BM	176	32.5	92	84	91.5	88.5	84	80.5	72	65	53	41.5	39	46.5	64.5	72.5	78	3.5	14	66	12.3		35	1.1	3	5	8	11	10	12	26	17	13.5	25	13	4	3	0.9	0.8	3	1.8	0.75	0.2							
U. hamiltonii	Beddome 46 BM	119	32	47.5	71	48.5	49	49	48	46	44.5	39.5	36	37.5	44	57	61.5	64	4.5	14	50.5	27		31	1.8	2	8.5	8.5	8.5	8.5	10.5	21.5	16	11	21.5	9.5	3.5	3	0.8	0.6	3	2	0.7	0.2							
U. hamiltonii	Meade 85	231	51.5	113	118	112	109	103	98	88.5	81.5	68.5	60	60.5	63.7	87.2	94.5	104	6	18	46.5																					40	20	26	6			
U. hamiltonii	Pierre s.n. 5/1864 K	87	21.5	42.5	44.5	43	42.5	41	39	36	33.5	28.5	25	25	27.5	34.5	38	41	3.5	14	53.5	15																											
U.hamiltonii	Average	164	38	79	85	79	78	75	72	66	61	53	45	45	51	66	72	76	4.7	16	53	14	####	29	1.6	3.1	7.1	10	9.7	7.8	11	20	12	11	19	8.7	3.8	3.3	0.8	0.6	2.9	1.9	0.8	0.1	###	31	18	25	7		
U. hirsuta	Poilane 11721 E Laos	132	28	56.5	75	59	59.5	57.5	56	53	49	42.5	35	34	43	61	67	70	5	14	40	10.5																											
U. hirsuta	van Helidinfen 17 U Java	230	39	143	87	147	142	134	124	99	82.5	64	44.5	42	51	70.5	79.5	81	7	12	55	24		36	1	0.8	9	4	9.25	11	8.5	16					3.75	0.5	1	3.5	3.1				22	14.3	29.8	22		
U. hirsuta	Curtis 4/1890 BM Penang	236	40	118	118	119	117	112	107	94	84	67	52	50	60	81	90	95	5	17	55	3.8		20	2	0.7	5	2	6	6	6	10	4	6	9	4	2.5	4	0.8	1	4	3.4							
U. hirsuta	Ridley 1907 BM Sing	158	27	82.5	75	85	82	76	71	61.5	54.5	43.5	33.5	32	37	47.5	52.5	56	6	13	70	3.8		30	3	1	5.5	1.75	7	9								4											
U. hirsuta	King 8350 BM Sing	155	37	85.5	69	90.5	89	86.5	83.5	76	69	59	47	41	46	57.5	61	65	7.5	13	50	2.4		30	1	1	9	3	9	11	6	13.5		6	13.5			4			5	4.7							
U. hirsuta	Haniff 225 Cop Penang	208	39	118	90	119	115	107	101	90	81	65.5	51	48	54	66.5	76	82.5	6	13	60	2.2		30	1	1.2			7	8	6	11		6	11			3	0.6	0.7	3.2	3							
U. hirsuta	King 3890 U Larut Perak	161	33.5	86.5	74	88	87	85	83	75	69	57	45	38	45	57	64	68	5	13	60	2.6		20	2	1.1	4.5	2	7	8	6	11	5	4	9	5	2.7				4	3.8							
U. hirsuta	Maingay 2710 K Sing	138	26	67	71	68	68.5	67	66	57	52	43.5	38.5	31.5	39	53	58.5	63.5	5	13	43	1.4		16.7	2.5	1	5.5	1.75	10	8	5.5	10	4	6.25	10	3	2.25	4	0.5	0.5	4	3.7							
U. hirsuta	Wallich 6458b BM/K Penang	162	35.5	86.5	75	88	88	86	84	77.5	71	61	42.5	42	48	60	65	68	5	12	50	3		24	2.5	1			9	8	6	12		6	12			3	0.4	0.5	3.2	3				32	11.5	23	24		
U. hirsuta	M. Shah 1704 K Jahore	215	37	126	89	127	123	114	106	95	83	66	51	53	64	80.5	86.5	88	8	16	60	3.83																					27.8	11.5	35.3	24		
U. hirsuta	Wallich 6458a K Penang	90	22.5	45	45	47.5	45	45	41.5	39	42	36	28	29.5	33.5	40	42	43	5	11	58	3.33		18	1.5	1.2	5	2	7	7																			
U. hirsuta	U.168165B Sumatra Teijs?	87.5	20	52.5	35	55	55.3	52.5	51	45.5	42	34	27	23	24	29	32	33.5	5	10	50	3.83		10	2.5	1																							
U. hirsuta	U.168164B Bangka	101	21	50.5	50	52	52	50.5	48.5	43.5	39	32.5	26	25.5	30	38.5	41	44	4.5	12	48	6																											
U. hirsuta	U.212963B Java	218	27.5	141	77	137	128	116	107	86.5	72	52.5	39	32.5	39	54	60	65	8	15	49	2.67																											
U. hirsuta	Ridley Feb. 1917 BM Kelantan	112	26	62	50	63.5	64	62.5	60	55	51	42	33	22	31	40	43	46	6	13	55	2.17																											
U. hirsuta	Average	160	31	88	72	90	88	83	79	70	63	51	40	36	43	56	61	65	5.9	13	54	3.6	####	23	1.9	1	6.2	2.4	7.9	8.4	6.3	12	4.3	5.7	11	4	2.5	3.7	0.6	0.7	3.8	3.5	####	####	###	29	13	33	23		
U. lobbiana	Bartlett 6873 L	138	31.5	70.5	67	73	73.5	71.5	68.5	63.5	54.5	50	40.5	40.5	48.5	58	61.5	63.5	6	11	53	81																					34	21	25	10			
U. lobbiana	Fukuoka T.35641 BKF	144	37	83.5	60.5	84.5	84	81	77.5	69.5	62.5	52.5	43	43	48	54.5	57	59.5	6	12	49	3																					68	19	22.5	6			
U. lobbiana	deWilde 18767 L	127	28.5	67.5	59.5	68	67	65	63	57.5	53	45	36.5	36.5	43	53.5	56	56.5	7	13	56	5																					38	18	26	6			
U. lobbiana	Sangkhachand 76 L	205	45	118	87	117	114	118	102	89.5	82.5	68	55	55.5	63.5	76	79	81	7	12	44	1.67		8	0.7	2	9.5	10	6	3	6.5	8	3.5	6.5	8	3.5	2.5	2.8	0.8	0.7	3	1.5	0.4	0.4							
U. lobbiana	Helfer 440 K	162	35.5	94.5	67	93.5	92.5	88	84.5	74	66.5	55	44	46	54	61.5	64	65	5.5	18	46.5	9.25		11	1.2	8.5	7	6	6.5	4	6.5	7	4	6.5	10	3.5	2.5	2	0.5	0.3	2.6	1.9	0.6	0.1							
U. lobbiana	Prapat 45 P	139	40.5	95.5	43	97.5	98	98.5	97	90.5	83.5	71.5	55	37.5	36.5	37.5	40.5	41.5	7	14	51	20.3		7	2	1.6	10	5	8	4	11	12	6	8	12	6	3	3	0.5	0.8	2.3	1.5	0.4	0.1							
U. lobbiana	Balgooy 2554 AAU	153	27	77	75.5	78.5	76	73	70.5	62	53.5	43.5	33.5	36.5	46.5	66.5	71.5	73	4.5	14	46	3.75		2	0.8	4.5	8	5	8	4	10	15	9	9	16	6	2.5	*	*	*	*	2.5	1.8	0.5	0.2							
U. lobbiana	Wimanong 10 Cop	215	55	108	107	110	109	106	103	95.5	89	76	63.5	67.5	83.5	93	99.5	101	7	17	43	11																					44	16.5	24	4			
U. lobbiana	King 4787 K	164	29.5	82	81.5	81	79.5	76.5	72.5	64	57	47	38	38	47.5	65	70.5	74.5	4.5	14	52	3		11	1	2	4	5	8.5	2	4.5	10	5	7	8.5	4.5	3	2.2	0.5	0.6	2	1.2	0.5	0.05							
U. lobbiana	Maingay 30 TYPUS K	178	28	98.5	79.5	98	94	88	83.5	72.5	62.5	49.5	38.5	36	43.5	63	70.5	75	6.5	13	57.5	*																					52	15.5	17	4			
U. lobbiana	Griffith Malacca K	119	29.5	67	51.5	67	67	65.5	63	58	52.5	44.5	37	36.5	41	46.5	48.5	49.5	4.5	13	57.5	10.7		5	2	4	7	8	8	3.5	7	9.5	5	8	11	4	2.6	2.5	0.5	0.4	2.8	1.3	0.6	0.1							
U. lobbiana	Sangkhachand 1128 Cop	96	24.5	45	51	45	45	44.5	43.5	41	36.5	31.5	27.5	32	38.5	47.5	50	50.5	5	13	57	22		9	2.1	11.5	4.5	3	*	*	8	9.2	5	8	10.5	4	3	*	0.6	0.4	2.5	1.7	0.7	0.15							
U. lobbiana	Stone 8542 L	121	23.5	57.5	63.5	57.5	57	55.5	53.5	49.5	45	37.5	30.5	30.5	37	52.5	57.5	60	4	14	51	2		4	1.5	4	5	4	5	3	7	8.5	6	6.5	9	3.75	2	2.2	0.6	0.3	2.4	1.8	0.6	0.1							
U. lobbiana	Korthals s.n. TYPUS Ptychoc. L	155	35.5	79	76	79.5	79	77	75	67.5	62.5	54.5	44.5	44	52.5	66.5	69	70.5	6	18	53.5	17.3		14.5	1.5	1.5	9	6	8	3.5	11	10	6.5	10	12.5	5	2	2.3	0.5	0.4	2.35	1.7	0.9	0.1							
U. lobbiana	Average	151	34	82	69	82	81	79	75	68	62	52	42	41	49	60	64	66	5.8	14	51	15	####	7.9	1.4	6	7.1	5.8	7.3	3.4	7.9	9.9	5.6	7.7	11	4.5	2.6	2.4	0.6	0.5	2.5	1.6	0.6	0.1	###	49	18	22	5.8		
U. lurida	H.f. & Th. s.n. Type TCD	91.5	14	51.5	40	49	48	46	44	39	35	26	19	17.5	21.5	32	34.5	37	5.5	8	27.5	7		17	2.3	0			11	12	15	20	12			4.5	3.8	0.9	0.8	3.5	3.1	0.6						8	
U.lurida	Din 238 BKF	107	22.5	60	47	58.5	57.5	56	53.5	49	44.5	36.5	30	29	33	41	42	43	5	7	42	5		16	2	0			10	11	17	22	13			5	2.5	0.5	0.3	2.4	2	0.7							
U. lurida	Saladanha 14566 S	91.5	19.5	41.5	50	40	39.5	38	37.5	35.5	34	30.5	26	24.5	30.5	41.5	44.5	46	5.5	10	66	0																					52	20.5	27	8			
U. lurida	Kostermans 35A G	148	32	87	60.5	85.5	84	81.5	80	72	65.5	52	42	38	44	52	53	54	3	10	40	2																					115	18	45	14			
U. lurida	King 4935 G	117	18	61.5	55.5	57	55.5	51.5	49.5	44.5	40	32.5	26	27.5	33	47	50.5	52	4	9	42	3.5		8	1.5	0			12	10	11	14	6.5			3	3	0.7	0.5	2.5	2.2	0.6							
U. lurida	King s.n. G	146	22	62	84	57	50	52	46	40	32	26	28	27.5	39	50.5	77.5	3.5	10	38	4.25																					92	13	27	12			
U. lurida	Beddome 49 BM	136	27	74	52	73.5	73.5	70.5	70	64	59	48.5	38.5	36	43.5	54.5	57.5	60	7	13	40	8		10	2.5	0			11	14	13	16	10			6	3.5	0.5	0.5	2.5	2	0.4							
U. lurida	Beddome 50 BM	178	30.5	81	97	78.5	77	75	72.5	66	60.5	51.5	41	42	52.5	77.5	86.5	91.5	6	14	40.5	7.25		8.5	2.5	0																							
U. lurida	King 4935 BM	183	31.5	86	97	83	81	78	75.5	69.5	64.5	54.5	43	41.5	51.5	76.5	83	88	5	8	44	4		10	2	0			12	11	10	17	8			4	3.5	0.5	0.5	3	2.2	0.5							
U. lurida	King s.n. BM	127	22.5	71	56	67.5	66	62.5	60	53.5	49	40	31	28.5	34.5	45.5	49	52	6	9	42	3		17	1.9	0			16	14	20	18	10			4.8	3.5	0.8	0.3	2.2	1.8	0.5							
U. lurida	Haines 3707 K	191	29	81	110	79	77.5	74	71	62.5	57.5	46.5	37.5	38.5	49.5	78.5	90.5	95	0.5	11	38	5.25		16	2	0			11	11.5	13	13	6.5			5	2.3	0.7	0.4										
U. lurida	Phengklai 1273 BKF	112	21	60	52	57.5	56.5	53.5	52	48	43.5	37.5	30	28.5	35.5	44.5	47.5	49	4	8	42	2.25		20	1.8	0						19	24.5	16		4				3	2.7	0.6							
U. lurida	10Ne 2503 BKF	64	15	33	31	31.5	31	30.5	30	28.5	27	23	19	19	23.5	29	30	36	3	7	33	6.25		10	1.9	0						20	23	16.5		4	3	0.5	0.3	2.4	2.1	0.5							
U. lurida	H.f. & Th. s.n. Type BM	114	22.5	68.5	45	66	64	61	59	53	48.5	40	30.5	21.5	29.5	31	39	41	3.5	9	34	4.5		14	1.7	0			10	9	11	12	5			3	3.3	0.7										
U. lurida	H.f. & Th. S.n. Type K	107	20.5	61	46	60.5	59	57	55	50.5	44	36	28	26.5	30	37	39	40.5	5	8	37.5	2.75		16	2	0			10	10.5	17	24	19			4	3.7	0.5	0.6	3.5	2.8	0.6						8	
U. lurida	Law s.n. (HH) Concan K	204	33.5	96.5	107	95	93	88	86.5	79.5	72	59	45.5	42.5	53.5	82.5	93.5	102	4.75	12	46	0		15	1.1	2	*	*	6	7	9	14	11	12.5	13.5	11.5	*	*	*	*	*	*	*						8	
U. lurida	E. Dawkins 14218 Madras K	197	27.5	87.5	109	83	80	77	73.5	66.5	59.5	47	36	36.5	49	83	93	97.5	7	12	52	0		11	2.9	2	*	*	11.5	11.5	11.5	14	10	12	14	10	*	*	*	*	*	*	*							
U. lurida	King 4935 Sikkim K	155	23.5	77	77.5	73.5	70.5	67	63	55.5	49.5	40	30.5	29.5	36.5	55.5	62.5	67.5	5	9	47	0		6	1.5	1	*	*	8	10	12	12.5	7	12	12.5	7	*	*	*	*	*	*	*							
U. lurida	Col. Jenkins s.n. (HH) Assam K	188	34.5	106	82.5	104	100	95.5	91	80.5	72.5	59	45.5	43	51	67.5	72.5	75.5	5	11	43	0		24	2.5	1	*	*	13	14	12.5	14	12.5	15	17	13	4.5	2.8	*	*	2	1.8	0.65							
U. lurida	Matthew 53326 Madras K	130	24.5	68.5	61.5	68	67.5	65.5	63.5	59.5	54	43.5	33.5	30	36	49	55.5	59	5.5	9	40	0																					64	18	28	9			
U. lurida	Gamble 28.25 K	136	24	68.5	67	65	62	59	56.5	51	46.5	39.5	32.5	27	31	44	50.5	54.5	5.5	11	51	6.75		10	2	0																	110	12.5	30	9			
U. lurida	Young SN BM	199	38	97	102	96	94	92	89	82.2	76	63	49	49	61	81.5	90	94.5	5	14	58	0.25																											
U. lurida	Matthew 23587 S	164	22.5	67	97	66	65	63	60	55	51	41.5	32	30	39	62	72	80	3	13	38.5	0.5																					30	19	26	8	1.7	2.5

Specimen no.	Collector no.	L	M	L1	L2	a	b	c	d	e	f	g	h	k	n	o	p	q	pel	v.no	v.an	ind	pedc	pedW	pedn	br.w	br.L	sp.W	sp.L	i.ptW	i.ptL	i.ptM	o.ptW	o.ptL	o.ptM	rec	car	stgW	stgL	stm	loc	stW	loc.b	slip	fr.W	fr.L	n.sd	hilW	hilL
U. macrurei	Xianghou 897 (Kweichow) K	134	30.8	63.5	70	63.5	62.5	60.5	58.5	54.5	50.8	45	37.5	37.5	44.5	56	60.5	63	4.5	11	56	4.25	22.5	1.2	1.5	3.25	6	4	5								2	3											
U. macrurei	PE 739	150	33	74	76	73.5	72	70	68	63	59.5	51.5	42.5	42.5	50.5	61	65.5	68	5.5	10	45	21.7																						11	32	42	*		
U. macrurei	McClure 9697 ISO BM	126	21	64	62	63.5	61.5	58.5	56.5	50	45	36.5	28.5	21	32.5	43.5	47.5	50.5	5.5	11	42	7	37	1.4	2.5	4.4	6	4	4	4.5	11	4	5.5	10	5	1.8	3.5	0.3	0.8	3	2.4	0.75	0.1						
U. macrurei	Henry 12148 E	127	29	64.5	62	64.8	63.8	62	60	55	50	42.5	35.5	34.5	40	49.5	52.5	56.5	3.5	12	57	14	37.5	0.8	1.5	5.5	5.5	6	7	5.25	12	6	6.5	10	5	2.25	3.5	*	*	3	2.5	0.6	0.3						
U. macrurei	McClure 9697 ISO G	113	24.8	59.5	53.5	58.5	57	54.5	52	47	43	36	30	29.5	35	42.5	45.5	47	4.5	9	35	5	36	1.2	2	4	5	4.5	5.5	4	8	4	4.5	8.5	4.5	2	3.65	1	0.75	3.2	2.3	0.6	0.1						
U. macrurei	**Average**	**130**	**28**	**65**	**65**	**65**	**63**	**61**	**59**	**54**	**50**	**42**	**35**	**33**	**41**	**51**	**54**	**57**	**4.7**	**11**	**47**	**10**	**####**	**33**	**1.2**	**1.9**	**4.3**	**5.6**	**4.6**	**5.4**	**4.6**	**10**	**4.7**	**5.5**	**9.5**	**4.8**	**2**	**3.4**	**0.7**	**0.8**	**3.1**	**2.4**	**0.7**	**0.2**	**###**	**11**	**32**	**42**			
U. macropoda	Jayasuriya 396 S	131	23.5	78	53	76.5	74	70	67	58.5	52.5	42.5	33.5	28	33	41.5	46.5	52	4.5	11	51	0.75	21.5	2	0			12	10	11.5	19	10				3	3.5	1.2	0.3	2.5	2.1	0.5				12		
U. macropoda	Jayasuriya 1077 S	126	26.8	63.5	62	62	60	58	55.5	50	45.5	39	32	30.5	35	44.5	48	50.5	5	9	52	2.25																						105	10	31	12		
U. macropoda	Jayasuriya 1274 S	127	26	60	67	58.5	57.5	55	53.5	49	45	40	32.5	30	31.5	49	52.5	55	4.5	9	40	0.5	12.5	1.7	0	1	1.5	9	8	8	17	10				4.5													
U. macropoda	S Waas 582 S	96.5	15	49	47.5	46.5	44	41	36.5	33	26.5	20.5	19.5	22.5	32	35	37	46	4.5	8	43	0																						75	9.5	45	12		
U. macropoda	Huber 458	107	16.5	48.5	58	47.5	45.5	43	41	37	33.5	28	22.5	21.5	27	42	47	50	4	10	46	5	15	1.5	0					9	14	6				3.5	3	1.4	0.3	2	1.7	0.6							
U. macropoda	Balakrishnan NBK 908	131	27	63.5	67	62.5	61	59	56.5	52	47.5	39.5	33.5	31	36.5	50.5	55	60	6	14	62	4.5																							18	80	14			
U. macropoda	Thwaites CP 2544 TCD	80	15	36	44	35	34	33.5	32.5	30	27.5	24	20	18	22.5	29.5	33.5	36	3.5	8	38	3.25	18	2.2	0			10	10	8	14	5				3.5	4	1	0.2	2.5	2.2	0.7							
U. macropoda	Jayasuriya 396 NY	94	19	48	46	45	44	42	40	37	34.5	29	24	23	28	37	41	43	5	9	45	0.75																						70	10	55	12	1.2	2
U. macropoda	Thwaites CP 2544 BM	88.5	18	45.5	43	44	42.5	41	38.5	34.5	31	26	21	22	21	35.5	38	39	2.5	8	37	1.67	12	1.75	0			10	8	8.5	18	10				3.5	4	1	0.1	2.6	2.3	0.9				140	15	65	12		
U. macropoda	Jayasuriya 396 K	112	24.5	61	50.5	64	62	59	56.5	50	45.5	38	31	30.5	35	42.5	46	47.5	6	11	40	0																						70	11	41	8		
U. macropoda	Jayasuriya 1274 K	136	29	74	62	73	71.5	67	64	56.5	51.5	43.5	36.5	33	39.5	50.5	53.5	57	5.5	9	50	0	12	1	1	*	*	6.5	5	7	14	9				3	2.2	1.3	0.5	2	1.8	0.7							
U. macropoda	Col. Walker 1160 (HH) SYN K	114	22	63	51	61	60	58	56	49.8	45	37.5	29	27	31.5	39.5	41.5	44.5	6	8	44	0	13.5	1.6	2	*	*	9	10	8	15	7.5				5	*	*	*	*	*	*							
U. macropoda	Thwaites CP 1032=2544 SYN K	130	22.8	66	63.5	61.5	59.5	56.5	54.5	49.5	45	37	30	28.5	35	48	53.5	57.5	5	10	41	0	18	1	1	*	*	8	9	6	19	10				3.5	2.2	1	0.4	2	1.8	0.7				135	14	58	8		
U. macropoda	Chatterjee BM	106	20	51.5	54	51	50	48	46	42	38.5	32.5	25.5	24.5	30	42	46	52	6	9	50	1.75	15	1.5	0			10	10	5.5	16	7				5				1.8	1.6	0.5							
U. macropoda	Thwaites CP 1032 NYBG	180	26	90.5	89.5	86.5	82.5	77.5	72.5	63	56	45.5	36	36	44	66	75	80	4	11	52	0.2	17	1.7	2	0		9	11	10	13	7				5	4	0.8	0.3	3.25	2.9	0.5							
U. macropoda	Meijer 1704	200	43	109	91	104	99	94.5	91	83	76.5	65.5	53.5	49.5	56	69.5	76	79	5	9																						140	13	57	10		
U. macropoda	**Average**	**122**	**23**	**63**	**59**	**61**	**59**	**56**	**54**	**48**	**44**	**37**	**30**	**28**	**34**	**45**	**49**	**53**	**4.8**	**9.6**	**46**	**1.4**	**15**	**1.6**	**0.6**	**0.5**	**1.5**	**9.3**	**9**	**8.2**	**16**	**8.2**	**####**	**####**	**####**	**4**	**3.3**	**1.1**	**0.3**	**2.3**	**2.1**	**0.6**	**###**	**105**	**13**	**54**	**11**	**1.2**	**2**
U. microcarpa	Ying Hu 7288 Beijing	101	23	59.5	41	59.5	59.5	57	54.5	48	43	35.5	29	24.5	27.5	33	35.5	38	4.5	12	47	7.25	11	1.2	1.5	2.4	3	9	5	13	17	9	12	17	4	1.2	4	0.4	1	7	5	1	0.15						
U. microcarpa	Ching 8146 Smith	147	39	84.5	62	85.5	86	83.5	80.5	75	69.5	59	47	41.5	44.5	48	52.5	58	6	11	50	12.8																						8	10	11	4		
U. microcarpa	Levine 899 Smith	121	27	68.8	52.5	69.5	69.5	68.5	66.5	61.5	54.5	43.5	34.5	31.5	35.5	41.5	44	46	5	11	43	5	12	2	2	3	3.5	6	3	8	12.5	9	7.5	11	6.5	2.5	5	0.6	1	6.5	4.75	1.2	0.1						
U. microcarpa	Levine 362 Smith	81.5	20.5	38.5	43	39.5	39.5	39.5	39	37.5	35.5	30	25	26.5	30	36	38.5	39.5	5	8	47	14																						10	10	20	9		
U. microcarpa	Petelot 5800 Smith	121	26	68.5	52	69	67.5	65.5	62.5	56.5	51.5	43.5	34	31.5	34.5	39.5	42	44.5	3	11	38	20.3	11	1.2	1.5	2	4	*	*	6	11	8	9	11	4	*	4	0.6	1	6	4.5	1.2	0						
U. microcarpa	Millet s.n. TCD	107	28	47	60	47.5	49	49.5	49.5	48	45	40	33	33.5	39.5	49	52.5	55	4.5	9	47	6	10	2	3.5	4	3.5	5	4	7	9	5	8	9.5	4.5	2.5	4.5	0.6	1	6	4.5	0.8	0	*		7.5	15	4		
U. microcarpa	Champion 39 K	136	41	65	70.5	66	67.5	68.5	68.5	67	64.5	56.5	48	49.5	54	65.5	67.5	68.5	5.5	10	56	6.25	16.2	1.2	3.33	2	3.5	6.5	5	8	13.5	9	10	12	7.5	2.5	5	0.5	1	7	5	1	0						
U. microcarpa	Hance 932 BM	83	21.5	47	36	47.5	47	47	45.5	42.5	39	33	27	24.5	27	31	32.5	34.5	4	10	53	4	16	1.5	1.5	2.5	3	7	3	8.5	12	8	8.5	12	5	*	3.5	*	*	6	4.5	1	0	6.5	*	*		8	
U. microcarpa	Taam 1826 NYBG	52.5	11.5	26	26.5	26	26	25.5	24.5	23	21.5	18.5	15	13.5	16	21.3	23.5	24	3.5	10	51	9.67																						20	10	17	7		
U. microcarpa	Hooker s.n. E	73	21.5	36	37	36	36	36	35.5	33.5	32	29	26	26	29.5	34.5	35	35	5.5	9	47.5	7.67	11.5	1.9	2	2	2	10	3.5	7.5	10	4.5	8.5	10	3.5	3	3.5	0.5	1.5	5	3.8	0.75	0						
U. microcarpa	How 70957 NYBG	102	26.5	56.5	45	57	56.5	55.5	53.5	49	46	40.5	33.5	29.5	31.5	39	41	42.5	6	11	43	19.3	10	1.5	2	2	1	8	4	8.5	11	8	10	12.5	6.5	3	3.5	0.5	0.75	6	4.5	0.8	0						
U. microcarpa	Lau 20206 NY	123	29	77	45.7	77.7	77	74.5	72	65	57	48	38	31.5	33.7	38.7	40.5	42.5	5.5	9																						9	7.5	11.5	3		
U. microcarpa	Ford s.n. NY	153	33.5	85.3	67.5	86.5	85.5	82	73.5	69	63.5	57.3	43.5	33	43	50	53	60	5.5	12																						17.5	9	14	4		
U. microcarpa	Tsang 30247 E	169	30.5	98.5	70.5	97.5	94	89.5	84	71.5	61.5	49	39	38.5	44.5	52.5	58.5	63	6	10																						12	11	15	3		
U. microcarpa	Tsiang-Ying 908 NY	107	28.5	55.5	51.3	56.5	56.3	55.7	55	53	50.5	44.5	36.5	34.5	38.5	44.8	47.7	49.5	3	12																						8	9	13.5	4		
U. microcarpa	Tsiang-Ying 1161	132	30	82.5	49	81.5	79.8	77.3	74.3	68	61.5	48.5	38.5	32.5	36.5	40.8	42.8	45	6	12																						14	9	15	5		
U. microcarpa	Dalziell s. n. E	101	30.5	60	41	60	60.3	59	57.5	54.5	50.8	44.5	36.5	32.3	34.8	37.5	38.5	39.3	4	9																						6.5	9.5	16	5		
U. microcarpa	Tsang 24537 NY Guandong	203	57	113	90	115	114	112	109	101	94	81	69	60.5	64	69	75.5	81.5	7.5	16	52.5	11.3																						15	11	14	*		
U. microcarpa	**Average**	**117**	**29**	**65**	**52**	**65**	**65**	**64**	**61**	**57**	**52**	**45**	**36**	**33**	**37**	**43**	**46**	**48**	**5**	**11**	**48**	**10**	**####**	**12**	**1.6**	**2.2**	**2.5**	**2.9**	**7.4**	**3.9**	**8.3**	**12**	**7.6**	**9.2**	**12**	**5.2**	**2.5**	**4.1**	**0.5**	**1**	**6.2**	**4.6**	**1**	**0**	**###**	**12**	**9.4**	**15**	**5.1**		
U. narum	Meebold 721 G	80	15.5	44	36	43	41.5	40.5	39	37	35	30	24	21	24	31.5	34	35	4.5	12	65	0	18.5	1	0	2	3	7	4	10	10	3				5.5	2	0.5	0.5	1.5	1.3	0.7							
U. narum	Meebold 721 G	87.5	16.5	46.5	41	45	43.5	42	41	37.5	35	28	22	20.5	25	31	35	40	4.5	11	56	0	10	0.8	0	2	3	5.5	3	9	11	5				4.5	2.1	0.7	0.5	1.5	1.3	0.7							
U. narum	Meebold 721 G	93	21	50	43	49.5	49	47.5	46	43	41	34.5	22.5	22	31	36	38.5	40	6	9	48	0	31	0.8	0			7.5	5	11	9	5				4.5	2	0.5	0.5	1.5	1.3	0.7							
U. narum	Macrae 88	130	23	70.5	59	67	65	61.5	58.5	52	46	37.5	30.5	29	37	49	52	54.5	6	12	63	1.5	24	1	0			6.5	5	6	15	6				5	2.2	0.7	0.6	1.8	1.7	0.65							
U. narum	Perrottet 40	90.5	29.5	46	44.5	44	43.5	43	41.5	38	35	29	23	23	27	36	38.5	40	3	11	71	0	16	0.7	0	1.5	2.5	5	4	6.5	8	3				3	2	0.4	0.6	1.5	1.2	*						6	
U. narum	Johnson TCD	99	19	57	42	55	54.5	53.5	52.5	48	42.5	34	27	24.5	27	32	36	39	4	10	62	0	14	1	0	2.5	3	8	4	11	11	6				5	2.4	0.7	0.5	2	1.7	0.8			20	4	10	5	
U. narum	Gamble 14841 K	136	18	63.5	72	61	59	55.5	53	46	41	33	25	25	32	49	57	63	5	12	41	0	*	1	0			7	3.5	9	10	5				5	2	0.4	0.4	2.5	1.3	0.6							
U. narum	Thwaites CP 1032 TCD	82.5	19.5	44.5	38	42	41	40	38	35	31	25	20	16.5	20	28	33	36	4.5	8	50.5	0	18	1	0			8	4	12	17	10				5	2.5	0.5	0.3	2	1.8	0.4							
U. narum	Wallich 6473B BM	124	21.5	74	50	70.5	67	63.5	61	55.5	49.5	39.5	30	29.5	34	42	45	46	9	8	50.5	0	45	0.8	0					10	13	8				5	2.4	0.5	0.3	1.9	1.7	0.6			22.5	10	14.5	4	1.5	1.5
U. narum	Buchanan s.n. BM	89	19	45	44	43.5	42	41	38	35	31	25	23	26	33	38.5	42	43	3	12	62	0	*	0.85	0			5	5	8.5	10	6				4.5	2.5	0.4	0.35	1.8	1.5	0.5							
U. narum	Perrottet 17 TCD	84	13	41	43	39.5	39	38	36	31	26.5	20.5	15	16	20	29	31	33	5	12	60	0	16	0.9	0					6.5	9.5	6				5	2.5	0.5	0.6	1.8	1.4	0.35			20	7	13	5		
U. narum	Lapas 37 LISU	160	24.5	82	78	80	77	72.5	69.5	62.5	57	45	32.5	32	39	56	65	69	6	14	57	0	20	1.55	0			8	5	10	12	9				4.5	2.1	0.5	0.2	1.9	1.6	0.5							
U. narum	Perrottet s.n. P	122	21.5	62	60	61	60	59	57	52	47	38	29	25	28	40	43.5	51	3	11	51	0																						15	8	13	5	1.4	1.4
U. narum	Walker 175 (HH) K	95	21.8	55	40	52.5	52	51	50	45	40.5	33.5	27	21	28.5	35	37.5	38.5	8	9	50	0.5	8.5	1.5	2.5	*	*	5	4	15	20	17				4	3	0.8	0.4	2	1.6	0.8	0						
U. narum	Wight 18 (HH) K	172	28.5	75	97	73.5	72.5	70	66	59	54	46	33	37	46.5	62.5	77	85	5	10	6	0																						23	8	14	6		
U. narum	Wall. Cat. 6473a (HH) K	131	23.5	62	69	60.5	60	59	57.8	52.5	47.5	40.5	31	30	36.5	50.5	56.5	60	6	10	47	0																						22	8	15	5		
U. narum	Hohenhacker 332 (HH) K	82.5	13.8	41	41.5	38.5	37.5	36	35	32	28.5	22.5	18	18	23.5	33.5	37.5	39	7	7	58	0	19	0.8	1	*	*	5	4	10	9.5	5.5				3	3	0.8	0.5	1.9	1.7	0.6							
U. narum	Dalziell s.n. K	117	22.3	56	61	54.3	53.5	51.8	50.5	46.5	43	36.5	29	27.5	32.5	43.5	47.7	50.3	4.5	10																						33.5	7	12.5	6		
U. narum	Wallich 6473a	103	19.3	55.5	47.5	52	51	50	48	42.5	39	32.5	25	24	28	35.5	40.5	43.8	5	11																						17	6	9	3		
U. narum	**Average**	**109**	**21**	**56**	**53**	**54**	**53**	**51**	**49**	**45**	**41**	**33**	**26**	**25**	**30**	**40**	**45**	**48**	**5.2**	**10**	**53**	**0.1**	**20**	**1**	**0.3**	**2**	**2.9**	**6.5**	**4.2**	**9.6**	**12**	**6.8**	**####**	**####**	**####**	**4.5**	**2.3**	**0.6**	**0.4**	**1.8**	**1.5**	**0.6**	**0**	**22**	**7.3**	**13**	**5**	**1.5**	**1.5**
U. pauciorulata	Ngadiman Sing F.no. 36432 K	74	15	39	35	41	40.5	40	39	37	33	27	20	19	22	29	32	33.5	5	14	45	23.3	9.3	3.67	2.5	8	3	7	5	12.6	16.5	13				4.5	2.5	0.4	1	1.5	1								
U. pauciorulata	Maingay 3392 K Malacca T	96	22.5	46	50	47	47	46	45.5	44.5	42	36	29.5	29	35	44.5	47	48	5	11	40	7.43	8.33	3.33	3	7.5	5	7	6	11.5	19	13				4				1.5	1								
U. pauciorulata	Maingay 1023A K Malacca T	82	19	39	43	39	39	38.5	38.5	37	35.5	30	24	23.5	29	40	43	44	5.5	14	44	11.2	10	2.25	2	9	5	6	4.5	12	13	7				4.5	3	0.4	1.2	1.5	1				15	9.5	8.88	1.57	1	1
U. pauciorulata	Maingay 1023A June 14 K T	70	13.5	31	39	32.5	32	31.5	30.5	28.5	26	22.5	18.5	17	22.5	31	33.5	37	4	10	40	25	10.5	3	2.5	10	6	7	5	13.5	16.5	10.5				5	3	0.4	1.2	1.5	1								
U. pauciorulata	Ngadiman Sing F.no. 36432 BM	146	28	83	62.5	85.5	84.5	82	79.5	71	66	52.5	38	34	40	51.5	57	61	5	13	35	9.67																												
U. pauciorulata	Smitinand 10916 BKF47576SN4077	106	30	57.5	48	58	58	57.5	56.5	53	50	43.5	37	35	40.5	43	46	47	5	10	45	18	12	2.5	2.25	14	8	8.75	7.5	16	19	11				4	2.5	0.4	1										
U. pauciorulata	Smitinand 10916 BKF47576SN4079	93	28	43	50	44	45	45	44	42.5	40.5	38.5	37	32	36	39	42	44.5	5	14	48	19.6	10.5	2	2.25	9	5	7	7	18	19	11				4	2.5	0.4	1										
U. pauciorulata	Ngadiman Sing F.no. 3432 sh.2 BM	63.5	14.5	33.5	30	34.5	34	33.5	32.7	30	28	23.5	18.5	17.5	20.5	25	28	29	4.5	15	54	23	10	4	2.5	10	4	7	5	13	18.5	15				3	2.5	0.5	1.1	1.1	0.8								
U. pauciorulata	Scortechini 1990 Arnold	136	45	67	68.5	70	70	70	68.5	67	65	61	55	56.5	64.5	71	70	69.5	6	13	45	44	8	1.9	1.8	8	5	5	6	11	19	14	10	17	8	2	2.6	0.3	0.7	1.5	1	0.5						2	
U. pauciorulata	Haniff s.n. SING	102	23.5	54	48	54.5	53.7	52	50.2	46	42.3	36.5	30.3	28	32.5	40.5	42.8	44.5	8.5	10	*	*	8	2	2	7.5	5	*	*	10	13	10	14	15	9.5	1.8	2.6	0.4	0.8	1.2	0.8	0.35						
U. pauciorulata	Penemot 4311 P	131	34.5	62.8	68	63.3	63.5	62.8	61.5	58.8	56	49.5	41.5	40	45.5	55.3	59	62	8.5	12	*	*	10	2.4	1.2	10	8	8	8	14	25	13	18	21	12	2.1	2.2	0.4	1	1.3	1	0.35							
U. pauciorulata	Scortechini 1990 K	156	44	83	73	87.5	87	84.5	82	78	73	64	55	55	65	74	74	73	7	13	35	44																												
U. pauciorulata	**Average**	**104**	**26**	**53**	**51**	**55**	**55**	**54**	**52**	**49**	**46**	**40**	**34**	**32**	**38**	**45**	**48**	**49**	**5.8**	**12**	**43**	**23**	**####**	**9.7**	**2.7**	**2.2**	**9.3**	**5.4**	**7**	**6**	**13**	**18**	**12**	**14**	**18**	**9.8**	**3.5**	**2.6**	**0.4**	**1**	**1.4**	**1**	**0.4**	**####**	**###**	**15**	**9.5**	**8.9**	**1.8**		

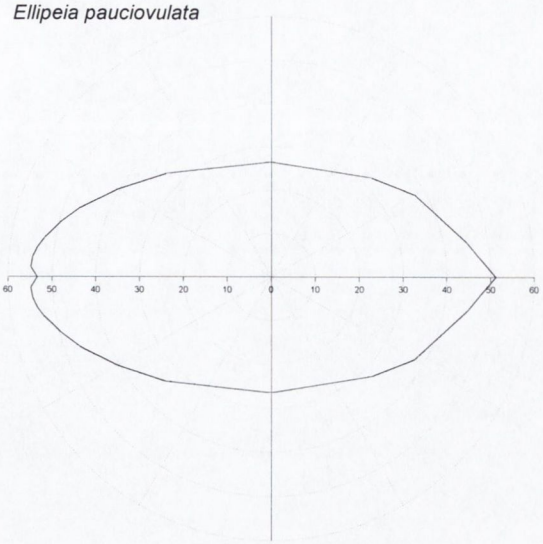
Specimen no.	Collector no.	L	M	L1	L2	a	b	c	d	e	f	g	h	k	n	o	p	q	pet	v.no	v.an	ind	pedc	pedW	pedn	br.w	br.L	sp.W	sp.L	i.ptW	i.ptL	i.ptM	o.ptW	o.ptL	o.ptM	rec	car	stgW	stgL	stm	loc	stW	loc.b	stip	fr.W	fr.L	n.sd	hilW	hilL
U. pierrei	BKF 5260	52.5	8.5	37	15.5	36	35	33	30.5	24.5	21	15	11	10	12	14.5	15.5	15.5	2	9	55	2.5	6	1	1	5	2	4	2.25	4	6	3.5	5	5	2	1.5	1.7	0.3	1 *	*	*							
U. pierrei	"	60	9	39	21	38.5	37	34.5	30	26	22	15.5	11.5	12	15	20.5	21	21	3	9	60	3.8	7	1.1	1	5	3	6	2	5	5	2	5	5	1.7	1.5	2	0.3	1 *	*	*							
U. pierrei	Harmand 48 P. SYN	74	10.5	37	37	36.5	36	34	31.5	27	24	19	15.5	15.5	20	33	36.5	37	4.5	9	55	11	6.5	1.5	1.5	4.5	2	5	2	4	5	3	3.75	5	2.2	2 *	*	*	*	*	*	*							
U. pierrei	Harmand 6/76 P SYN	47	14	29	18	26.5	25.5	23.5	21.5	18.5	16.5	13	9.5	10	12	17	18	18	3	9	45	12.5	6	1.1	2	4	3	5	2	3.5	5	2	3.5	4	2	2.5	1.5	0.4	0.7	1	0.8	3*							
U. pierrei	Pierre 1789 P SYN	91.5	14	57.5	34	57.5	57	54	51	44	38	28	20	19	22	31	33	33.5	4.7	14	75	18	4	1	1.5	4	2	3.5	2	5	3.5	2.5				2	1.5	0.4	0.5	0.75	0.7	2*							
U. pierrei	Godefroy 28/6/78 K	62.5	8.5	34.5	28	34	32.5	31.5	30	25	21.5	16	12	11.5	15	25	27	27.5	4	8	40	5.75	8.5	1.5	2.5	4	2.5	4.25	2.5	4	6	2.5	4	5	1.9	2.75	1.75	0.6	0.4 *	*	*							
U. pierrei	Herb Forest Cambodge P	66.5	13.5	34.5	32	34	33.5	32	31	28.5	26	21	12	17	21	30.5	32	32.5	3.5	9	50	7.5	5	1	1.25	3	1.75	4.5	2.25	4.25	5	2.5				2	1.7	0.5	0.3	1	0.8	25*							
U. pierrei	Meade & Chalermglin 98-10-17-01	79.7	13.2	47.5	32.2	47	46.5	44.7	42.5	36.7	31.5	24.2	47.5	17.5	23	30.2	31.7	32	4.5	9	65																							9	12	18	3		
U. pierrei	Meade & Chalermglin 98-10-17-01	82.3	13.5	52.2	30.1	51.5	50.2	47.7	44.2	37.5	32	24	12.5	18.5	22.7	24	30	30	5	11	53																							8.5	12	17	3		
U. pierrei	Meade & Chalermglin 98-10-17-01	66.4	10.7	34.2	32.2	33.7	33.5	32.2	30.7	27.7	25	20	15	14.2	19	30	31.2	32	4	9	58																							8	12.5	18	4		
U. pierrei	Herb Forest Cambodge P	58.5	10.7	33.5	25	34	33.5	32	30.5	27	24	19	13.5	13	16	22.5	24	24.5	3	8	48	5.5	5	1	2	3	1.75	4	2.15	4	5	3				2	1.7	0.5	0.3	1	0.8	0.3							
U. pierrei	**Average**	**67**	**11**	**40**	**28**	**38**	**36**	**34**	**29**	**26**	**20**	**16**	**14**	**18**	**25**	**27**	**28**	**3.7**	**9.5**	**55**	**8.3**	####	**6**	**1.2**	**1.6**	**4.1**	**2.3**	**4.5**	**2.1**	**4.2**	**5.1**	**2.6**	**4.3**	**4.8**	**2**	**2**	**1.7**	**0.4**	**0.6**	**0.9**	**0.8**	**0.3**	####	###	**8.5**	**12**	**18**	**3.3**		
U. rufa	Kerr 660 BM	91	19.5	44	47	45	45	44.5	43.5	34.5	37	31.5	25.5	25	29.5	37.5	40.5	43.5	4	12	53	38	10	1.5	5	5	8	6	3	5	8	4.5	5	9	4.5	2	3.6	5	7	4	2.5	0.7	0.3							
U. rufa	Maxwell 74.639 L	112	27.5	65	46.5	66.5	66	64	62	57.5	53	45	36	29.5	32.5	39.5	42	44.5	5	13	57	35.3	5	1	3	3.5	3.5	5	3	4.5	8	6	5.5	8	5	2.5	3	0.4	0.5	3.5	2	0.75	0		28	14	27	20		
U. rufa	Larsen 32164 L	99	18.5	56	43	57	56	54	51.5	43.5	38	30.5	23.5	22	25	32.5	36.5	40	4	12	56	40.5																							20	19	35	18		
U. rufa	S.Vidal (Lep) AAU	86	13.3	43.5	42.5	43.5	44.5	44	43.5	40.5	37	30.5	24.5	21	23.5	32.5	37.5	39.5	5	10	54.5	42	14	1.5	1.5	5.5	4 *	*		5	9	5	6	10	4 *	*		0.7 *		3.5	2	0.7	0							
U. rufa	Maxwell 74.254 AAU	69.5	21	36.5	33	36.5	37	37	37	36.5	35	31	25.5	21	23	28.5	30.5	32	4	12	62	19.5	7	1.5	1.5	8	10	9	6	8	13.5	7.5	9	15	7	3	3	0.5	0.4	3	1.5	0.75	0.25							
U. rufa	Maxwell 89.777 E	115	22	53	62	53.5	54	53	51.5	46.5	42	35.5	28.5	26.5	31.5	44.5	50.5	54	4	11	56.5	35.3	11	1	6	5	7	5	3	5.5	13	7	7	17	9	2.5	4	0.5	0.75	3.5	2	0.75	0.1							
U. rufa	Pierre 120 BM	151	36.3	65	85.5	67	67.5	67.5	67	65	61.5	54	44	47	56	71.5	78	81	5.5	11	58	23.8	11	1	2	4	5	4.5	3	4.8	8	5	5	8	5	2	3	0.5	0.6	3.5	2.1	0.8	0.2							
U. rufa	Smitinand 10758 BKF	101	26	42.5	58	43.5	44	44	44	43	41.5	37.5	33.5	31.5	36	46	51	54.5	4.5	11	53	24																							27	14	26	16		
U. rufa	BKF 25151	108	22	46.5	61	47.5	47.3	47	46.5	43.5	40.5	34.5	28	27.5	33	48.5	55	58	4.5	14	64	26.7	7	1	3	4	3.5	4.5	2	5	6.5	3	5	6.5	3.5	2.5	4	0.4	1	3.5	2	0.6	0.15							
U. rufa	Riedle s.n. Timor P	106	28.5	48.5	57	50	50.5	50.5	50.5	49.5	47	42.5	36.5	33	39.5	50	54.5	56.5	4	10	48.5	23.5	7	1.5	1	9	10.5	5	3	5.5	9	6	6	10	4	3	3.5	0.6	0.5	3	1.6	0.8	0.1							
U. rufa	Labate s.n. Java P	150	24.5	65	85	66.5	67	66.5	65.5	61.5	55	43	34	32.5	40.5	60.5	70	79	5	13	56	29.3	7	1.5	1.5	4.5	5	6	3	5	7.5	5	4.5	7	5.5	2.5	4.5	0.4	0.8	3.5	2	0.7	0.1							
U. rufa	Blancoanae 199 P	105	24	36	69	37.5	38.5	39.5	40	39.5	38.5	35	30.5	30.5	36.5	55.5	61.5	64.5	5	12	57	80	11.5	1.5	1.5	5	6	4.5	5	3.5	5	2	3.5	6	6	2.5	2 *	*	*	*	*	*							
U. rufa	Maxwell 85.577 NY	101	19.7	52.5	48	53	54	52	50	47	44	37.5	28.5	24	27	35	39	43	7	13	58	64.3	6	1.5	5	1.5	4	6	2.5	5	12.5	4				3.5	3	0.5	0.5	3.5	2.6	*							
U. rufa	Poilane 15067 NY	97	19	58	39	58	57	54	52	47	42	32	24.5	22	25	31	35	39	3.5	9	35	47	8	2	1	2	3	7	3	6	12	8				2.25	3.5	0.5	0.5	4.2	3 *								
U. rufa	WN 516 BKF	99	20	50	49	51.5	51	50	49.5	45.5	42	34.5	27	25	30	37.5	41	43.5	5	11	50	48	8.5	1.5	2	6	5	5	2.5	5.5	8	3.5				3.5	3	0.4	0.5	3	2 *								
U. rufa	Kerr 7728 BM	130	21	64	66	65	63.5	61	59	52	46	37	24	30	38	48.5	53.5	57.5	5	12	35	65.3	9	2	1	3	3	4	2.5	5	10	7				2	3	0.7	0.4	3	2 *		35	20	27	20		
U. rufa	Pierre 1787 ISOT K	127	23	53	74	54.5	54.5	54	53	49	44.5	38	31.5	30.5	36	53	59	66	6	16	45	11.5	6	1	1			5	3.5	7	9					4	2			2									
U. rufa	Pierre 1787 ISOT P	132	23.5	54	77.5	54.5	55	54	52	48	44.5	38	31.5	30.5	38	55	63	70	6	14	50	4	7	1	1			5	3.5	5.5	9					4	2			2									
U. rufa	**Average**	**110**	**23**	**52**	**58**	**53**	**53**	**52**	**51**	**47**	**44**	**37**	**30**	**28**	**33**	**45**	**50**	**54**	**4.8**	**12**	**53**	**37**	####	**8.4**	**1.4**	**2.5**	**4.8**	**5.4**	**5.5**	**3.1**	**5.5**	**9.1**	**5.4**	**5.9**	**9.7**	**5**	**2.8**	**3.2**	**0.9**	**1.1**	**3.2**	**2.1**	**0.7**	**0.1**	###	**28**	**17**	**29**	**19**		
U. semicarpifolia	CP 244 Thwaites P	216	42.5	118	98.5	129	121	119	115	108	97	78	62	64	75	95	97	97	7	17	46	16.6	12	2	2	10	4	9	5	7	10	5				3.5	1.2	0.3	0.2	1	0.7	0.22			12	12	14			
U. semicarpifolia	Huber 556 Hamb	190	56	100	90	109	108	106	104	99	94	83.5	67.5	63.5	73.5	88	90	91	8	19	53	36.3																							9	27	36	8	1	1.2
U. semicarpifolia	Kostermans 25493 S	189	50	102	87	109	109	107	105	99.5	93.5	80	62	60	68	78	79	80	10.5	19	50	44.3																							15	21	26			
U. semicarpifolia	Huber 602 S	165	46	73	92	78.5	78.5	79	78	76	72	63	54	57.5	67.5	82	85	85.5	7.5	20	65	34																													
U. semicarpifolia	CP 244 Thwaites BM	228	59	118	110	121	121	118	114	106	98	83	69	66	79	102	105	107	7	18	55	20.5	11	1.5	7	7	5	9	4	7	7	2																	
U. semicarpifolia	CP 244 Thwaites TCD	226	59	109	117	120	120	118	114	105	100	86	73	68.5	80	102	107	108	7	19	62	17.6	7	1.2	3	6	2.5	8	3	6	6	2.5																	
U. semicarpifolia	Thwaites CP 244 SYN K	169	40	113	56.5	115	113	111	107	97	87	71.5	54	46.5	50.5	55	56	56.5	7.5	19	49 *																							8	18	22	8		
U. semicarpifolia	Thwaites CP 244 G	263	64.5	143	120	152	152	149	145	135	126	116	83	79.5	92.5	110	112	114	7.5	20	54 *																													
U. semicarpifolia	Walker 165 G	177	48	95.5	81.5	102	101	99.5	98	92	81	75	63.5	59	67	76.5	78	78.5	6	17	56 *		10	1.2	3	4	4	10	4	10	7	4																				
U. semicarpifolia	Col. Walker s.n. SYN K	179	50.5	131	48.5	134	133	128	124	113	103	82	65	49	47.5	44.5	45.5	46.5	9	20	47 *		6	1.2	7	5.5	4	6.5	3	5.5	8	5	7	8	3.5	*	*	*	*	*	*	*							
U. semicarpifolia	**Average**	**200**	**52**	**110**	**90**	**117**	**116**	**113**	**110**	**103**	**95**	**82**	**65**	**61**	**70**	**83**	**85**	**86**	**7.7**	**19**	**54**	**28**	####	**9.2**	**1.4**	**4.4**	**6.5**	**3.9**	**8.5**	**3.8**	**7.1**	**7.6**	**3.7**	**7**	**8**	**3.5**	**3.5**	**1.2**	**0.3**	**0.2**	**1**	**0.7**	**0.2**	####	###	**11**	**20**	**25**	**8**		
U. sphenocarpa	Thwaites CP 1045 (HH) SYN K	92.5	17.5	47.5	45	47.5	46.5	44	42.5	38	34	28.5	23	21	23.5	30	35	39	4	7	42 *																							1	20	22 *			
U. sphenocarpa	Col. Walker s.n. (HH) SYN K	124	23.5	61.5	62	62.5	62	59.5	56.5	49	48	35.5	29	28	32.5	44.5	51	57.5	4	12	56 *		2	1	8 *	*		4	1.5	2.5	4	2																				
U. sphenocarpa	Thwaites CP 1045 SYN BM	109	19.5	56	53	55	53.5	51.5	49.5	43.5	39.5	31.5	25.5	23.5	27.3	36.5	39.5	44	4.5	10	47.5	24	4	1	1.5	2	3.5	3.5	2	4.5	5	2.75				2.2	1.3	0.85	0.25	1.8	1.4	0.45	0.1		1	13	14	4		
U. sphenocarpa	DBS 805 Smith	79.5	14.5	34.5	45	34.5	34.5	33.8	33	30.5	27.5	23.5	19.5	18	21.5	27.5	33.5	37	2	9	45	6.67																							0.5	16	19.5	4		
U. sphenocarpa	**Average**	**101**	**19**	**50**	**51**	**50**	**49**	**47**	**45**	**40**	**37**	**30**	**24**	**23**	**26**	**35**	**40**	**44**	**3.6**	**9.5**	**48**	**15**	####	**3**	**1**	**4.8**	**2**	**3.5**	**3.8**	**1.8**	**3.5**	**4.5**	**2.4**	####	####	####	**1.6**	**1.2**	**0.7**	**0.2**	**1.4**	**1.2**	**0.3**	**0.1**	###	**0.8**	**16**	**19**	**4**		
U. vietnamensis	Clemens 3827 P	132	22.5	65.5	66	67	65.5	63	60.5	54	48.5	38.5	30	28	33.5	47	52.5	56	6.5	14	40	21.2																							35	11	15			
U. vietnamensis	Poilane 7326 P	109	18	49	60	49	49	48	47.5	44	41.5	32.5	25.5	25	30.5	46	51	56	5	16	50	23.6																							43	9	11			
U. vietnamensis	Poilane 7326 E	120	24	62.5	57	63.5	62	59.5	58	53	48	40	32	29	34	50	56	57	5	15	45	18.8																							50	10	13			
U. vietnamensis	Clemens 3827 BM	161	27	76	85	76.5	74	68	65	54.5	48.5	38	30.5	30	37	55	65	70.5	5.5	15	50	28																							57	16	20			
U. vietnamensis	Meade TCD 98-10-16-03 Ubon	227	38	122	105	124	120	113	104	89	79	63	47	46	51	78	89	93	7	18	60	51.7																													
U. vietnamensis	**Average**	**150**	**26**	**75**	**75**	**76**	**74**	**70**	**67**	**59**	**53**	**42**	**33**	**32**	**37**	**55**	**63**	**67**	**5.8**	**16**	**49**	**19**	####	####	####	####	####	####	####	####	####	####	####	####	####	####	####	####	####	####	####	####	####	####	####	####	####	###	**46**	**12**	**15**	####		
U. zeylanica	Kostermans 28043 L	82	15	39	43	38	37.5	36	34.5	33	30	26	20.5	18	22	31	35	39.5	4	11	60	0																							1.5	12	18	7	0.5	1.5
U. zeylanica	Kundu & Balakrishnan 705 Smith	57	8	23	34	22.5	21.5	20.5	19.5	18	16	13	10.5	10	12.5	21.5	25	28	2	7	45	2.4	6	1	1			2.5	4	3	8	4				1	1	0.75	0.5	0.7	0.75	0.5							
U. zeylanica	Waas 366 Smith	74.5	12.5	35.5	39	34.5	33	31	30	27.5	25.5	22	18	16.5	20	27	30	32.5	2.5	8	47.5	4	5.5	0.75	1.5	0.75	0.75																							
U. zeylanica	Thwaites CP 1030 Smith	78.5	15.5	32	46.5	30	29	28	27	24.5	23	21	18	20.5	25	35.5	39.5	43.5	3.5	7	55	1.25																							2	4.5	6	6		
U. zeylanica	Waas 1303 Smith	121	20	50	71	48.5	46.5	45	43.5	40.5	37.5	32.5	26.5	26.5	33	47.5	53	58	4.5	9	50	0.5	3.5	0.75	1	0.5	0.5	2	4	4	5	2.5				1.5	1	0.75	0.5	0.9	0.75	0.5							
U. zeylanica	Thwaites CP 1030 BM*	76	14	34	42	33.5	33	32	31.5	29.5	28	24.5	20	17.5	22	31.5	36	39	2	11	55	3.25	4.5	1.2	2	1.75	2.5	3.5	3.5	3	5	2.5				1	1.5	0.5	0.5	1.2	1	0.5			2	12	16	8	0.5	1
U. zeylanica	Simpson 8935 BM*	81.5	13	32	49.5	31.5	31	29.5	28.5	26	24	18.5	16	17	19.5	29.5	33	37	4	9	55	2.25	5	0.6	2	1.75	1.5	2.75	3.5	4	8	4				1	1	0.5	0.2	1.1	0.85	0.5			1	8	10	7	0.5	1
U. zeylanica	Macrae 216 NY	67	13.5	23.5	43.5	22.5	22	21.5	21	20	19	17	15	16.5	20	29	33	35.5	5	8	60	0	3.5	0.7	1.3			2	4	4	10	5				1.5	1.8	0.6	0.2	1.2	0.9	0.5							
U. zeylanica	Erlanson 5578 NY	79.5	12.5	35	44.5	34	33.5	32.5	31.5	28.5	25.5	20	15.5	16	21	33.5	38	41.5	3.5	10	52.5	1	4	1	1	1	1	3	3.75	3	5	2				1	0.8	0.5	0.2	1	0.8	0.5							
U. zeylanica	Erlanson 5578 NY	64	11.5	30	34	29.5	29	27.5	27	25	23	20	15.5	15	18	25.5	29	31	3	8	48	1																													
U. zeylanica	Fagerlind & Klac. 239 NY	59	10	24.5	34.5	23.5	23	22	21	19	18	15	12	12	15	21	24	26	3	7	32.5	1.25	3	1	1	3		4.5	4	3	8	4.5				4.5	1	0.5	0.2											
U. zeylanica	Thwaites CP 1030 TCD	66.5	12	30.5	36	30	29	28	27	25	23.5	20	16.5	16.5	20	26	28.5	31	2	8	58	2	4	1	1	1	1.5	3.5	5	4	8	3.5				1.5	1.6	0.7	0.2											
U. zeylanica	Fraser 179 TCD	93.5	20	40	53.5	39.5	39	37.5	36.5	33	31	28	24	28.5	27.5	37	44	49.5	4	8	57	0	5.5	1	2	1	1.2	4	5	3	7	4				1.5				1	0.7	0.5								
U. zeylanica	Huber 571 HBG*	78.5	12.5	32.5	46	32.5	32	30	29	27	25	22	17.5	18	23	32.5	37	39	2	10	40	2.2	4.5	1	1	2	2.5	4	4.5	5.67	8.17	3.58				1.5	1.5	0.7	0.2	1.1	0.85	0.5			1	7	10	5	0.5	0.8
U. zeylanica	Wallich 6462 BM	61	9	30	31	30	28	26.5	25	21	19	15	11	11	13	20	23	26	1	9	25	0	5	1	1.5	1.5	1.9	4	4	3	6	3				1.2	1.2	0.5	0.2	1.1	0.8	0.5							
U. zeylanica	Maxwell & Jayasuriya 823 NY	73.5	10	32.5	41	31	30	28	26.5	23.5	21	18	14	13	16	27	31.5	35	2	8	38	5.25	5	0.8	1	1.1	2.2	3.5	5	3.5	9	1.5				1	1	0.5	0.2	1	0.8	4.5							
U. zeylanica	**Average**	**76**	**13**	**33**	**43**	**32**	**31**	**30**	**29**	**26**	**24**	**21**	**17**	**17**	**20**	**30**	**34**	**37**	**3**	**8.6**	**49**	**1.6**	####	**4.5**	**0.9**	**1.5**	**1.2**	**1.6**	**3.3**	**4.2**	**3.6**	**7.3**	**3.3**	####	####	####	**1.5**	**1.2**	**0.6**	**0.3**	**1**	**0.8**	**0.9**	####	###	**1.5**	**8.7**	**12**	**6.6**	**0.5**	**1.1**

Appendix 3.3. Summary leaf outlines for each taxon (50% of actual size). All measurements are in mm.

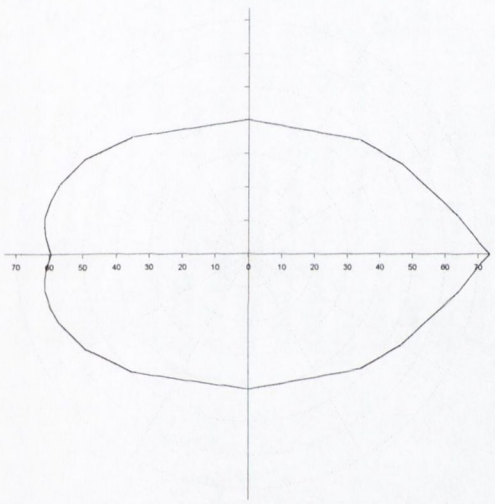
Ellipeia dulcis



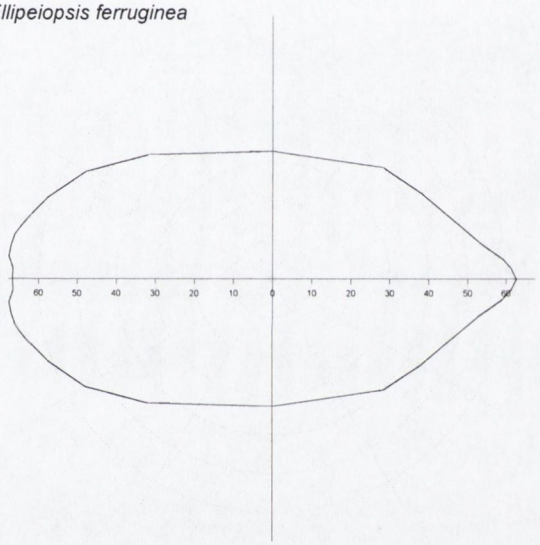
Ellipeia pauciovulata



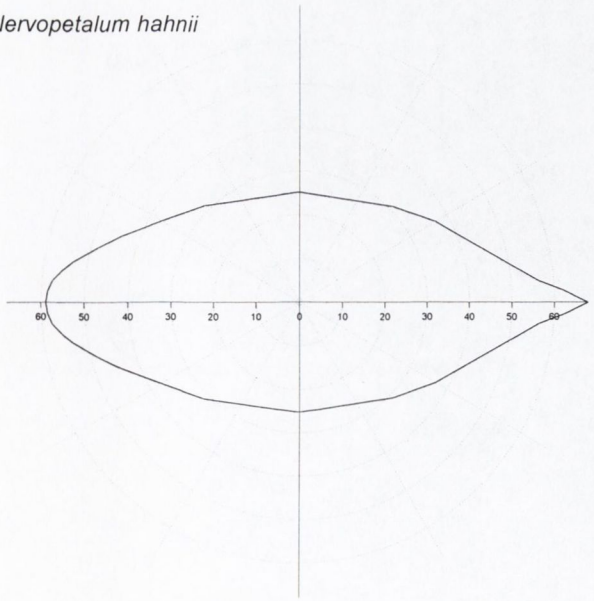
Ellipeiopsis ferruginea var. *cherrevensis*



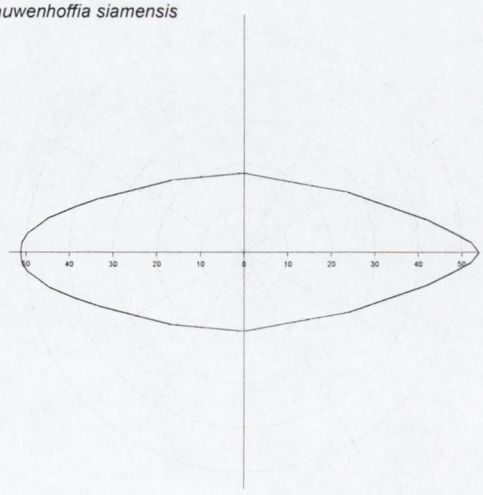
Ellipeiopsis ferruginea



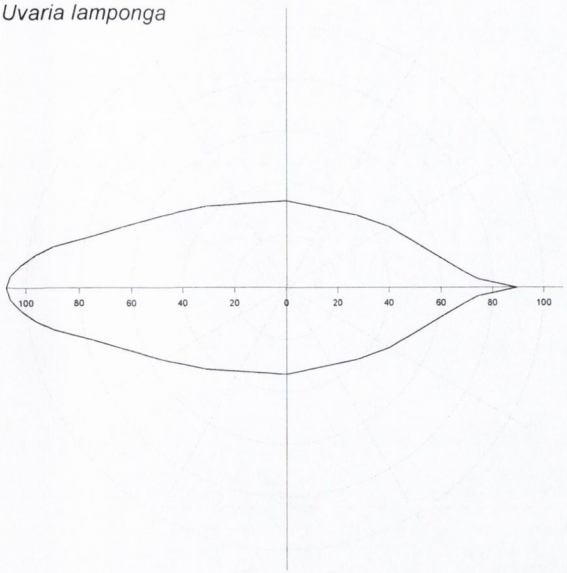
Nervopetalum hahnii



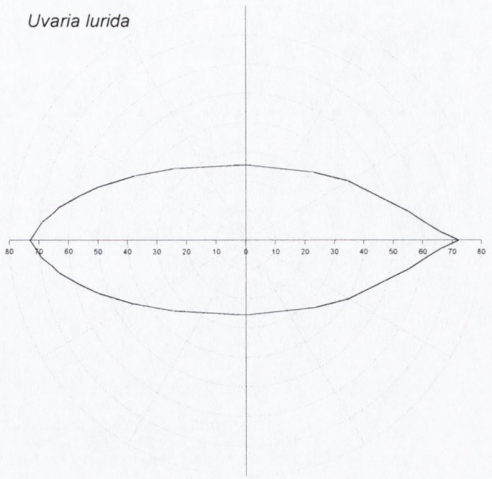
Rauwenhoffia siamensis



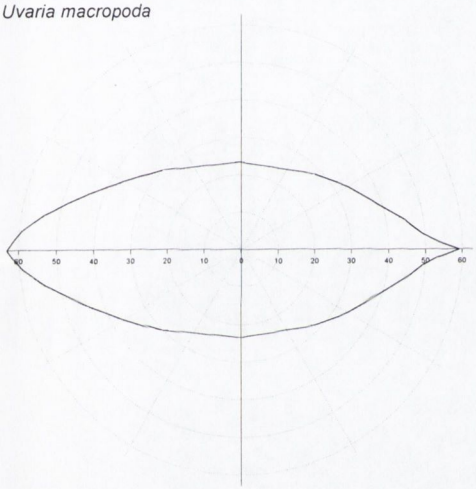
Uvaria lamponga



Uvaria lurida



Uvaria macropoda



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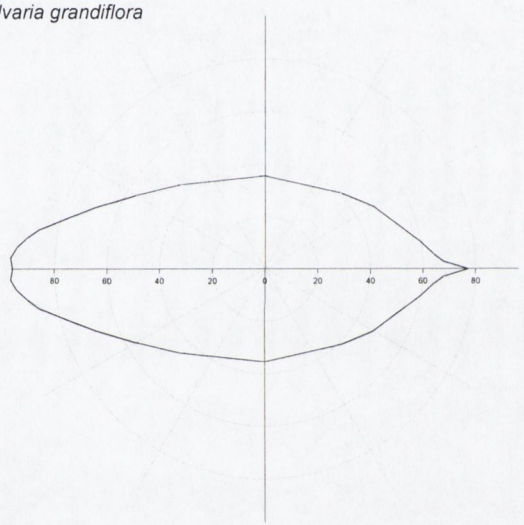
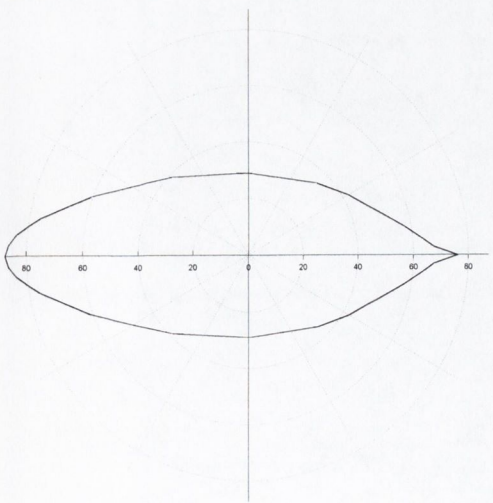
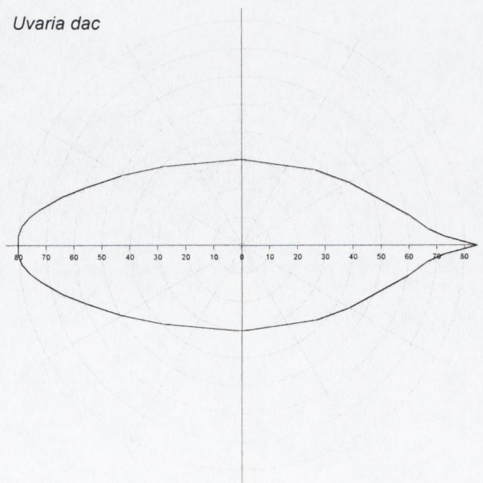


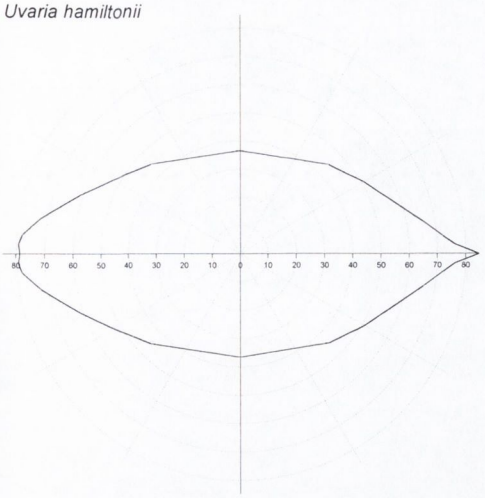
Uvaria curtisii



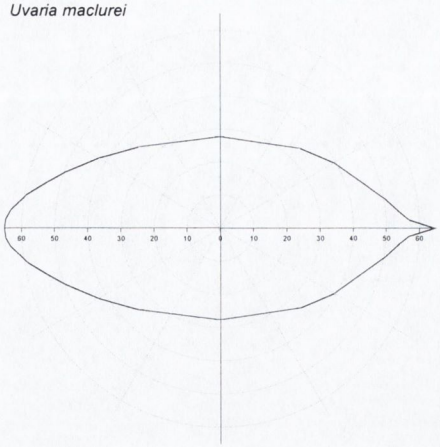
Uvaria dac



Uvaria hamiltonii



Uvaria maclurei



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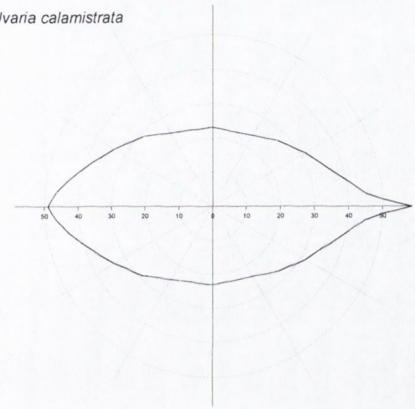
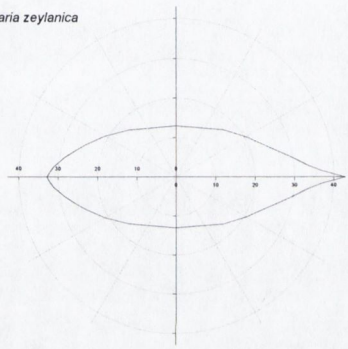
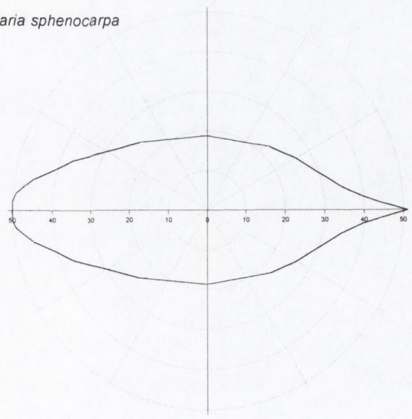


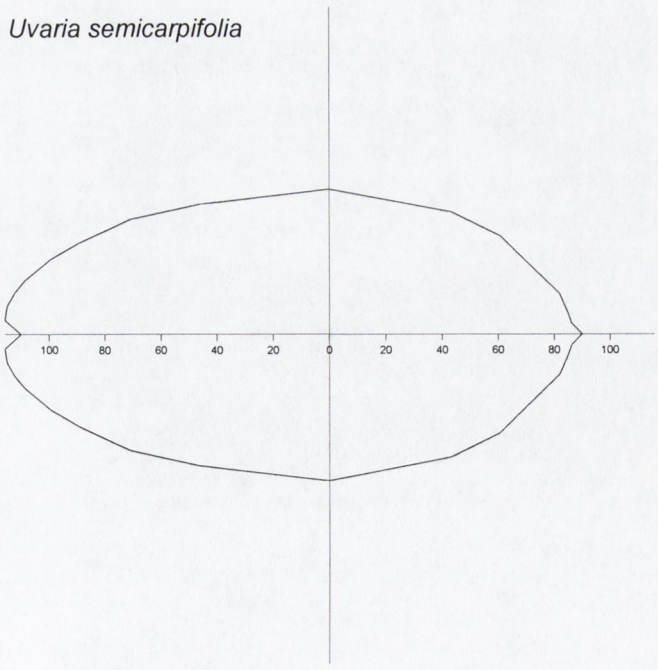
Uvaria zeylanica



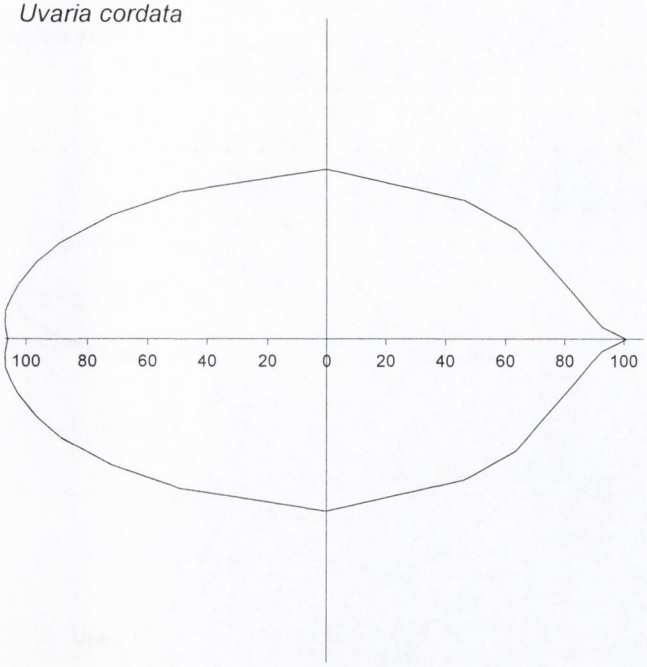
Uvaria sphenocarpa



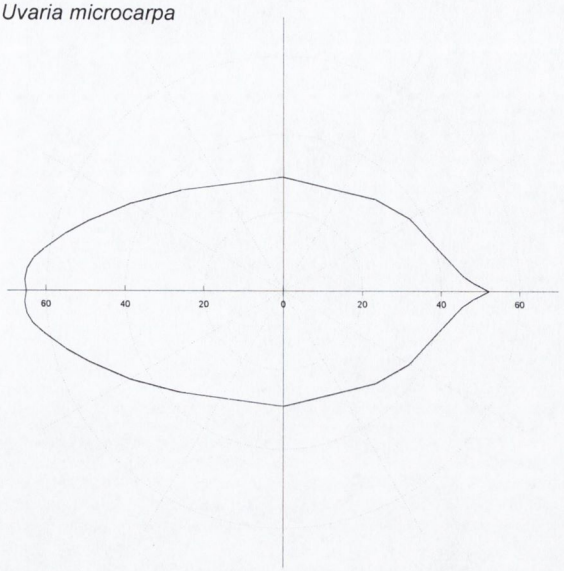
Uvaria semicarpifolia



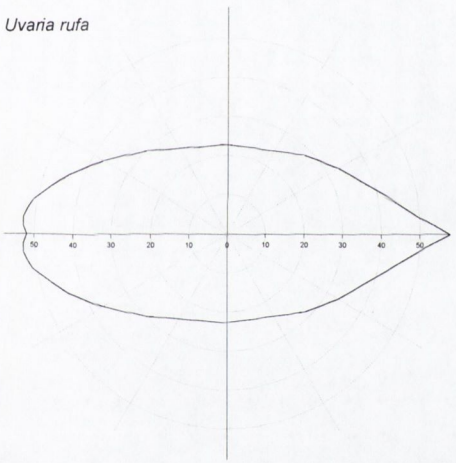
Uvaria cordata



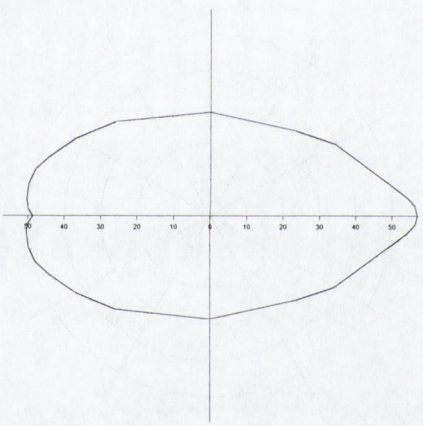
Uvaria microcarpa



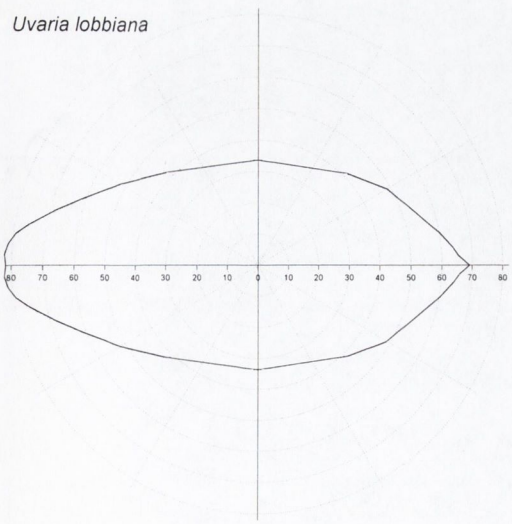
Uvaria rufa



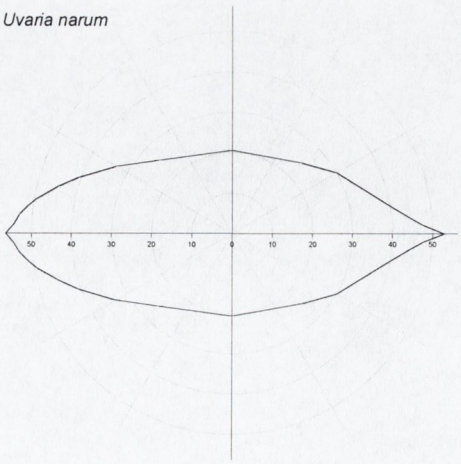
Uvaria rufa var. *timoriensis*



Uvaria lobbiana



Uvaria narum



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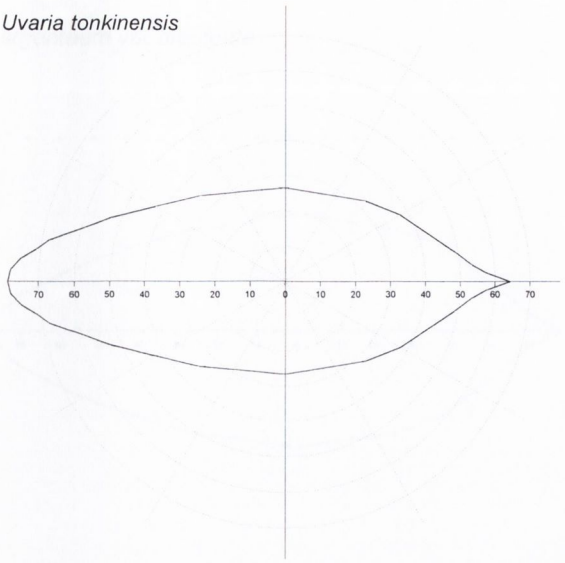

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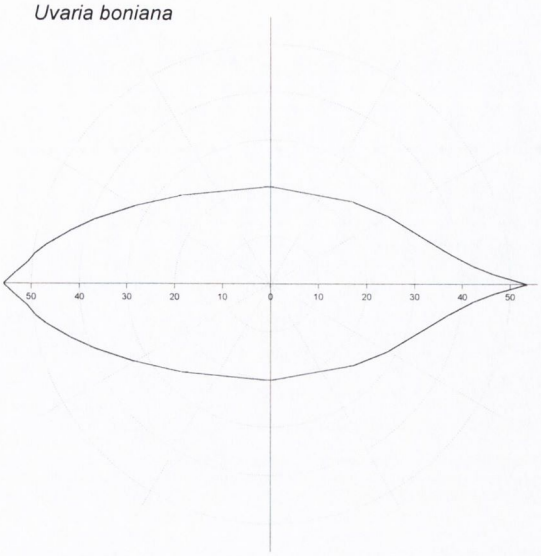

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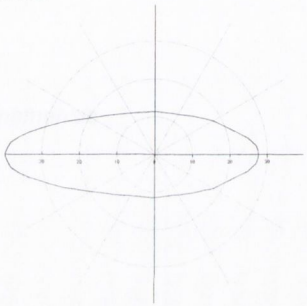

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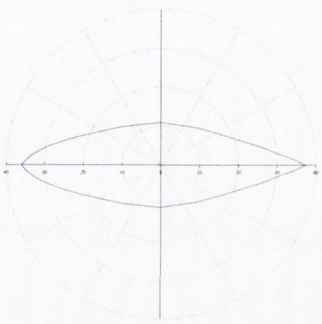
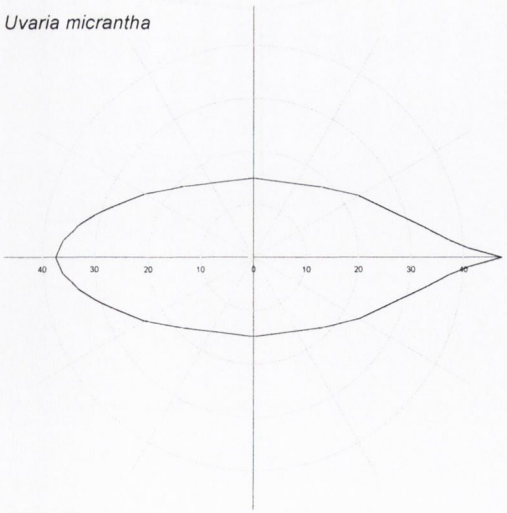
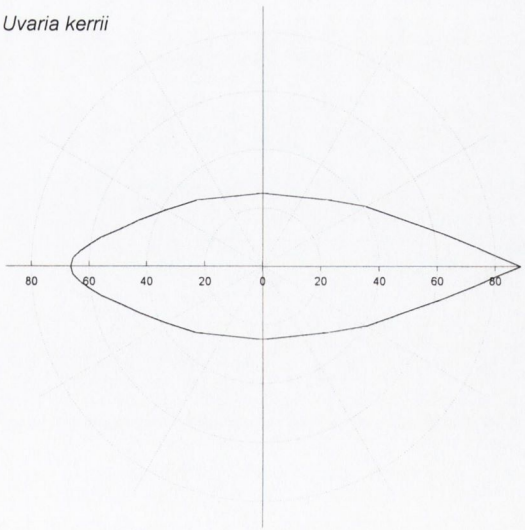


Uvaria micrantha



Uvaria kerrii



Appendix 4.1



A. *Uvaria hamiltonii* Hook. f. & Thoms.,
Chiang Mai Province, Northern Thailand (PC)

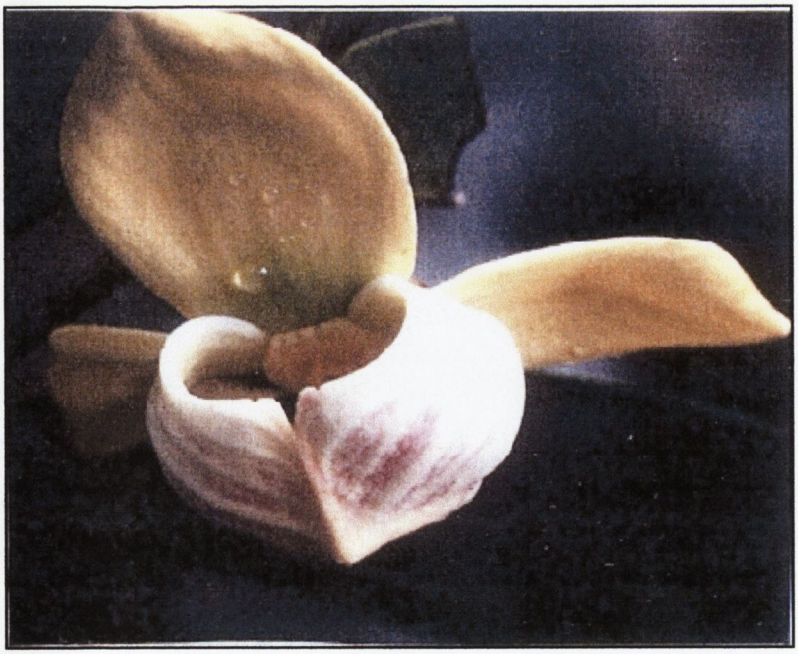


B. *Uvaria hamiltonii* Hook. f. & Thoms.,
Doi Chaing Dao, Chiang Mai Province, Northern Thailand (CM)

Appendix 4.2



A. *Alphonsea* sp., Peninsular Thailand (SS)
(Unoneae)



B. *Mitrephora* sp., Southeast Thailand (PC)
(Mitrephoreae)

Appendix 4.3



Artabotrys hexapetalus (L. f.) Bhandari,
Northeast Thailand, (PC)
(Xylopieae)



Artabotrys hexapetalus (L. f.) Bhandari,
Khon Kaen University, Northeast Thailand (CM)
(Xylopieae)

Appendix 4.4



A. *Annona squamosa* L. (Annoneae)



B. *Ellipeia dulcis* (Dunal) C. Meade *comb. nov.*
Eastern Thailand (PC).

Appendix 4.5



A. *Ellipeia dulcis* (Dunal) C. Meade *comb. nov.*

(white arrows) Typical climbing habit, disturbed mixed deciduous forest, c. 500 m altitude, Doi Suthep, Chiang Mai Province, Northern Thailand (CM).



B. *Uvaria vietnamensis* Jovet-Ast ex C. Meade *sp. nov.*

Typical scandent habit on alluvial soil near Soi Sawan waterfall, c. 300 m altitude, Ubon Ratchatani Province, E. Thailand (CM)

Appendix 4.6



A. *Ellipeiopsis ferruginea* (Buch.-Ham. ex Hook. f. & Thoms.) R.E. Fries
var. *cherrevensis* (Pierre ex Finet & Gagnep.) C. Meade *comb. nov.*
Sakaerat Env. Research Station, Nakhon Ratchasima Province, Eastern Thailand (CM)



B. *Rauwenhoffia siamensis* Scheff.
Cultivated opposite entrance to BKF herbarium, Chatuchak,
Krung Thep, Central Thailand (CM).

Appendix 4.7



A. *Uvaria lurida* Hook. f. & Thoms. Southeast Thailand (PC)



B. *Uvaria lurida* Hook. f. & Thoms. Southeast Thailand (PC)

Appendix 4.8



A. *Uvaria grandiflora* Roxb. ex. Hornem.,
Singapore Botanic Gardens (CM)



B.*Uvaria grandiflora* Roxb. ex. Hornem.,
Central Thailand (PC)





C. *Uvaria grandiflora* Roxb. ex. Hornem. var. *flava* (Teijsm. & Binn.) Sincl.,
red and white flowered varieties, Southeast Thailand (PC)

Appendix 4.9



A. *Uvaria dac* Pierre ex Finet & Gagnep.
Sakaerat Env. Research Station, Nakhon Ratchasima Province,
Eastern Thailand (CM)



B. *Uvaria vietnamensis* Jovet-Ast ex C. Meade *comb. nov.*
Eastern Thailand (PC).

Appendix 4.10



A. *Uvaria cordata* (Dunal) Alston,
Ubon Ratchatani Botanic Garden, Eastern Thailand (CM).



B. *Uvaria cordata* (Dunal) Alston,
Doi Chiang Dao, Chiang Mai Province, Northern Thailand (PC)

Appendix 4.11



A. *Uvaria rufa* (Dunal) C. Meade *comb. nov.* (PC)



B. *Uvaria rufa* (Dunal) C. Meade *comb. nov.* (PC)

Appendix 4.12



A. *Uvaria pierrei* Finet & Gagnep.,
Ubon Ratchatani Botanic garden, Eastern Thailand (PC)



B. *Uvaria pierrei* Finet & Gagnep.,
Ubon Ratchatani Botanic garden, Eastern Thailand (PC)

Appendix 4.13



A. *Uvaria micrantha* (A. DC.) Hook. f. & Thoms.
Sakaerat Env. Research Station, Nakhon Ratchasima Province, Eastern Thailand (CM)



B. *Uvaria wrayii* (King) C. Meade *comb. nov.*
Peninsular Thailand (PC)

Appendix 4.14

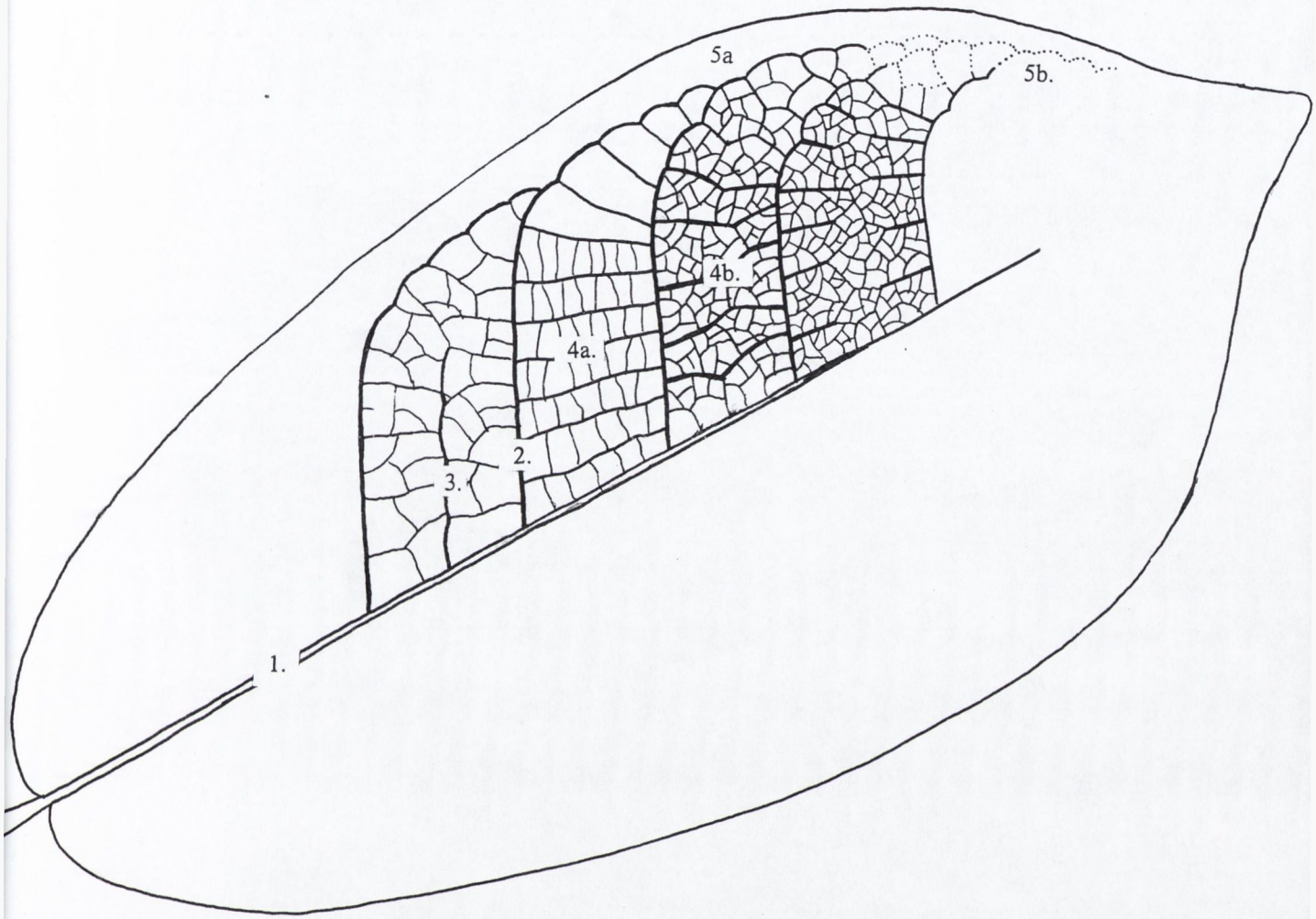


A. *Nervopetalum hahnii* (Finet & Gagnep.) C. Meade *comb. nov.* var. *hahnii*
Eastern Thailand (PC)



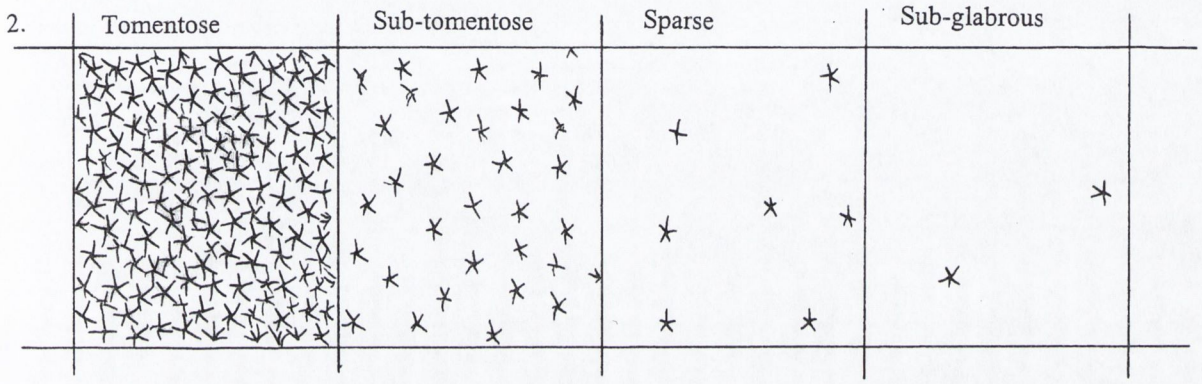
B. *Nervopetalum hahnii* (Finet & Gagnep.) C. Meade *comb. nov.* var. *hahnii*
Eastern Thailand (PC)

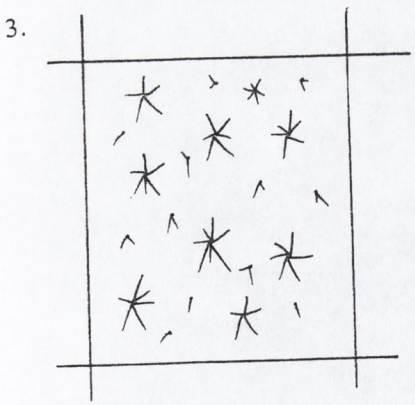
Appendix 4.15-4.16. Leaf and Indument Structure.

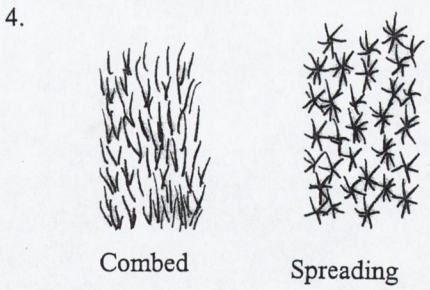


Appendix 4.15. Leaf venation terminology. 1. midrib. 2. Primary vein. 3. Inter-primary vein. 4a-c. Secondary veins. a parallel. 4b kinked. 4c incomplete. 5a-b. Trailing trace. 5a forming distinct sub-marginal vein. 5b fine, not forming distinct sub-marginal vein.



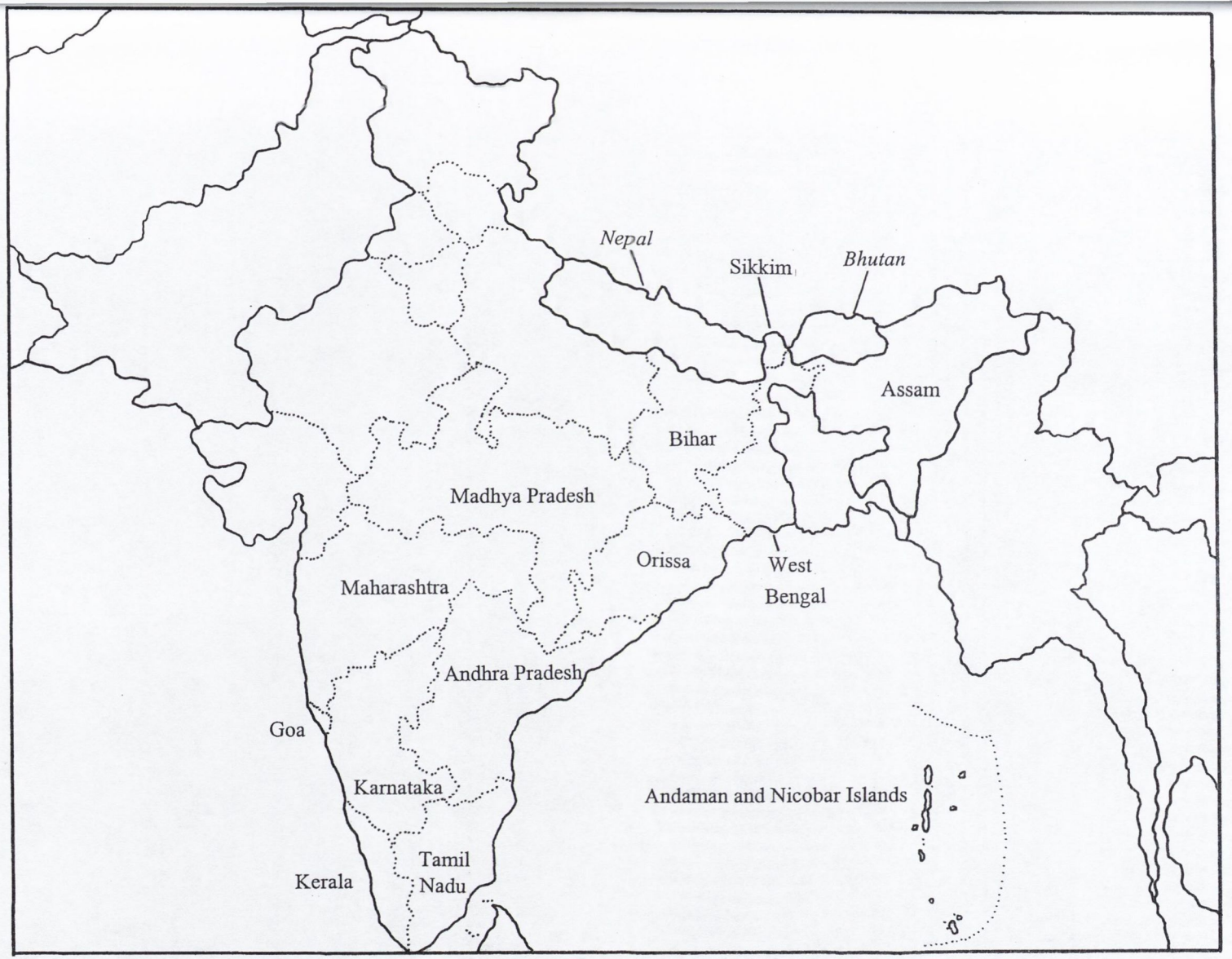




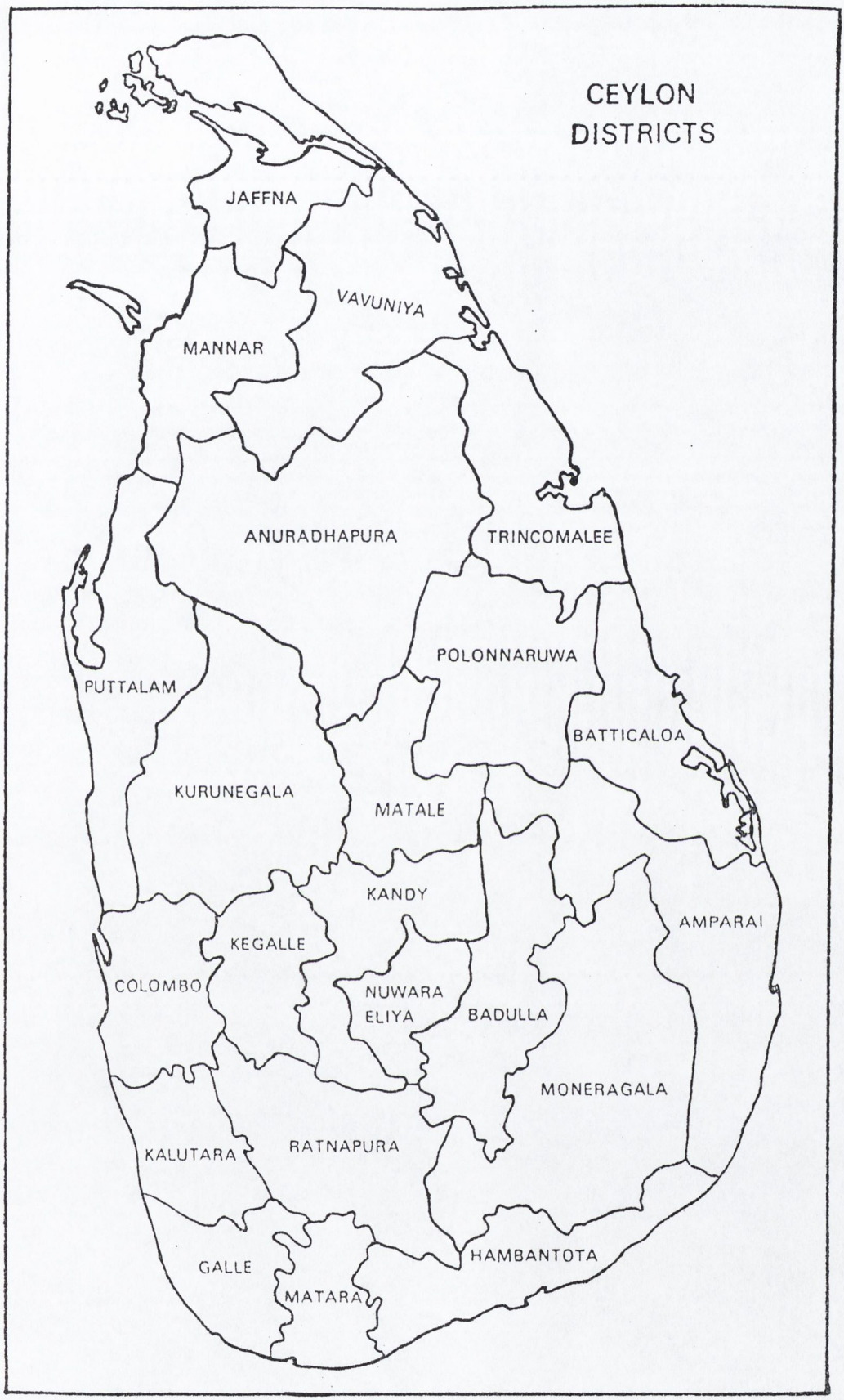


Appendix 4.16. Indument terminology. 1. Stellate hair types. 2. Hair density. 3. Example of mixed indument of simple and stellate hairs. 4. Different kinds of ovary indument.

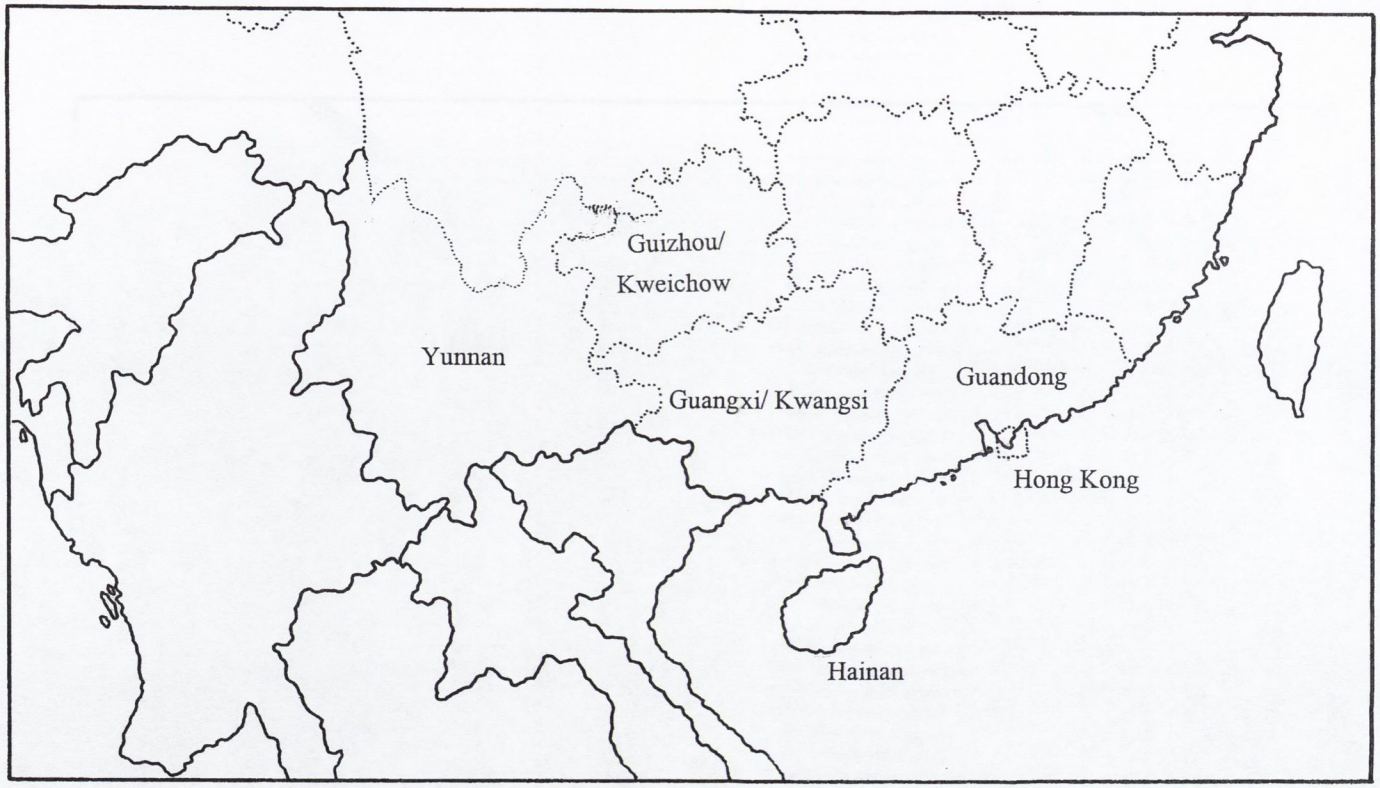
Appendix 4.17-4.21. Administrative Boundaries.



Appendix 4.17. Nepal, Bhutan and States in the wet tropical region of India.

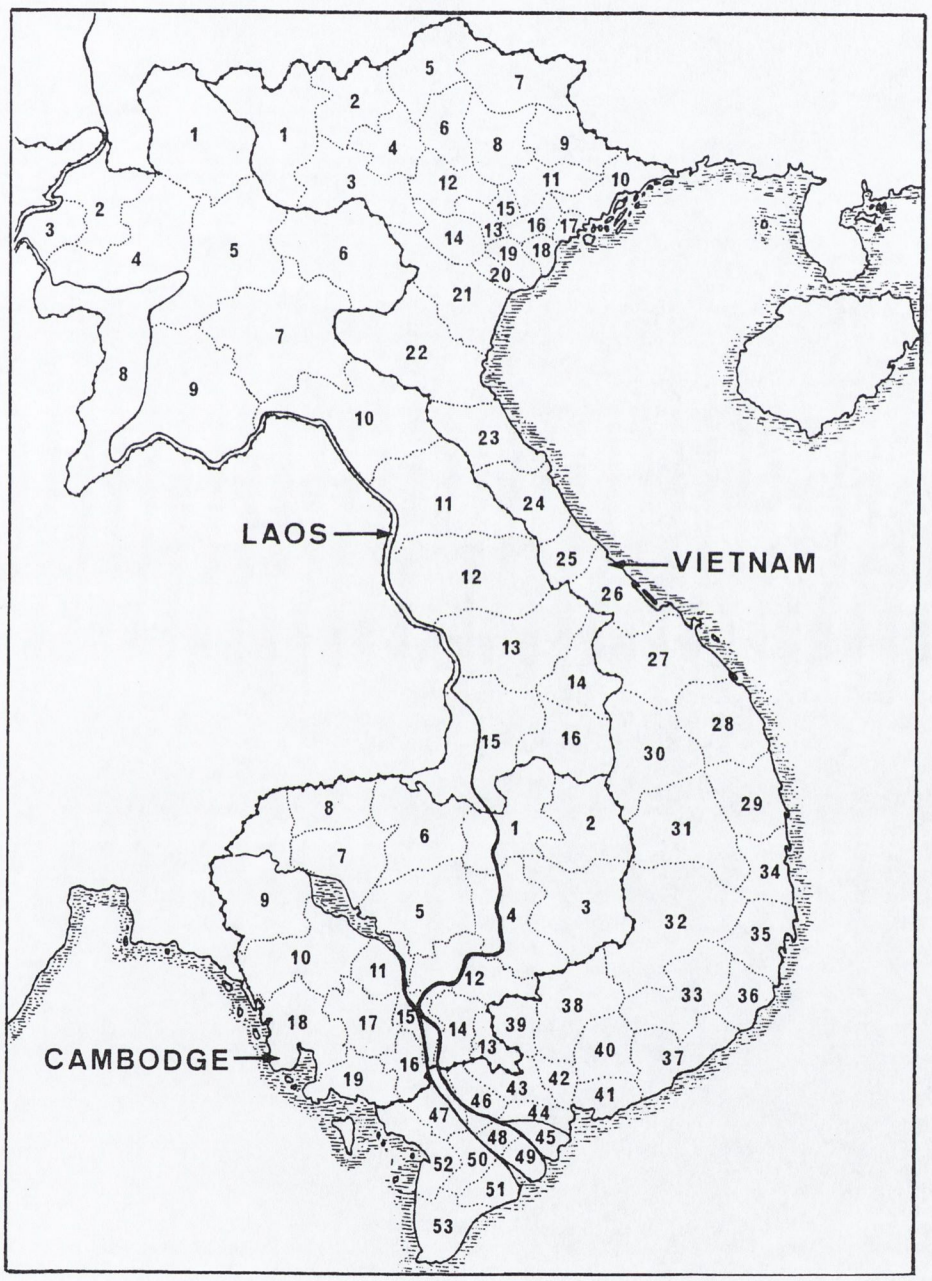


Appendix 4.18. Administrative divisions of Sri Lanka (from the *Revised Handbook to the Flora of Ceylon*).



Appendix 4.19. Provinces in the wet tropical region of Southern China.

CARTE DES PROVINCES



Appendix 4.20. Floristic divisions of Vietnam, Cambodia and Laos (from the *Flore du Cambodge, du Laos et du Vietnam*).

LISTE NUMÉRIQUE DES PROVINCES

Les nombres indiquent la situation sur la carte et l'ordre de citation dans le texte relatif au matériel étudié.

CAMBODGE

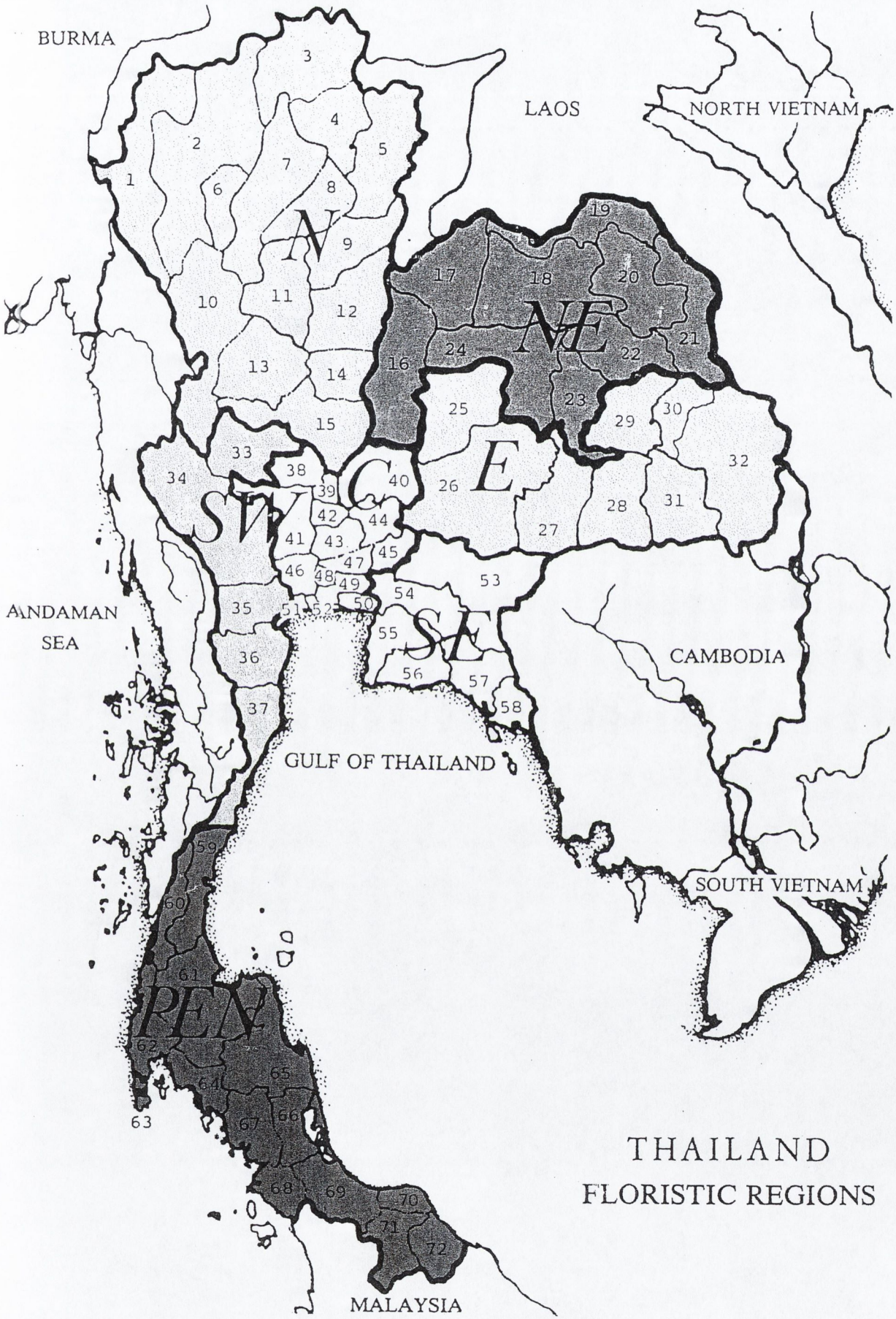
1. Stung Treng
2. Ratanakiri
3. Mondulkiri
4. Kratie
5. Kompong Thom
6. Preah Vihear
7. Siem Reap
8. Oddor Meanchey
9. Battambang
10. Pursat
11. Kompong Chhnang
12. Kompong Cham
13. Svay Rieng
14. Prey Veng
15. Kandal
16. Takeo
17. Kompong Speu
18. Koh Kong
19. Kampot

LAOS

1. Phong Sali
2. Louang Namtha
3. Bokeo
4. Oudomsai
5. Louang Prabang
6. Houa Phan
7. Xieng Khouang
8. Sayabouri
9. Vientiane
10. Bolikhamsai
11. Khammouane
12. Savannakhet
13. Saravane
14. Sekong
15. Champassak
16. Attopeu

VIÊTNAM

1. Lai Châu
2. Lào Cai
3. Son La
4. Yên Bai
5. Hà Giang
6. Tuyên Quang
7. Cao Bang
8. Bac Thai
9. Lang Son
10. Quang Ninh
11. Hà Bac
12. Vinh Phu
13. Hà Tây
14. Hoa Binh
15. Ha Nôi
16. Hai Hung
17. Hai Phong
18. Thai Binh
19. Nam Hà
20. Ninh Binh
21. Thanh Hoa
22. Nghê An
23. Hà Tinh
24. Quang Binh
25. Quang Tri
26. Thua Thiên-Huê
27. Quang Nam-Dà Nang
28. Quang Ngai
29. Binh Dinh
30. Kon Tum
31. Gia Lai
32. Dac Lac
33. Lâm Dông
34. Phu Yên
35. Khanh Hoa
36. Ninh Thuân
37. Binh Thuân
38. Sông Bé
39. Tây Ninh
40. Dông Nai
41. Bà Ria-Vung Tàu
42. Hô Chi Minh Ville
43. Long An
44. Tiên Giang
45. Bên Tre
46. Dông Thap
47. An Giang
48. Vinh Long
49. Trà Vinh
50. Cân Tho
51. Soc Trang
52. Kiên Giang
53. Minh Hai



Appendix 4.21. Provinces of Thailand (from the *Flora of Thailand*).

FLORISTIC REGIONS AND PROVINCES OF THAILAND

I. *N* (NORTHERN)
- 1 Mae Hong Son
- 2 Chiang Mai
- 3 Chiang Rai
- 4 Phayao
- 5 Nan
- 6 Lamphun
- 7 Lampang
- 8 Phrae
- 9 Uttaradit
- 10 Tak
- 11 Sukhothai
- 12 Phitsanulok
- 13 Kamphaeng Phet
- 14 Phichit
- 15 Nakhon Sawan

II. *NE* (NORTH-EASTERN)
- 16 Phetchabun
- 17 Loei
- 18 Udon Thani
- 19 Nong Khai
- 20 Sakon Nakhon
- 21 Nakhon Phanom
- 22 Kalasin
- 23 Maha Sarakham
- 24 Khon Kaen

III. *E* (EASTERN)
- 25 Chaiyaphum
- 26 Nakhon Ratchasima
- 27 Buri Ram
- 28 Surin
- 29 Roi Et
- 30 Yasothon
- 31 Si Sa Ket
- 32 Ubon Ratchathani

IV. *SW* (SOUTH-WESTERN)
- 33 Uthai Thani
- 34 Kanchanaburi
- 35 Ratchaburi
- 36 Phetchaburi
- 37 Prachuap Khiri Khan

V. *C* (CENTRAL)
- 38 Chai Nat
- 39 Sing Buri
- 40 Lop Buri
- 41 Suphan Buri
- 42 Ang Thong
- 43 Phra Nakhon Si Ayutthaya
- 44 Saraburi
- 45 Nakhon Nayok
- 46 Nakhon Pathom
- 47 Pathum Thani
- 48 Nonthaburi
- 49 Krung Thep Maha Nakhon (Bangkok)
- 50 Samut Prakan
- 51 Samut Songkhram
- 52 Samut Sakhon

VI. *SE* (SOUTH-EASTERN)
- 53 Prachin Buri
- 54 Chachoengsao
- 55 Chon Buri
- 56 Rayong
- 57 Chanthaburi
- 58 Trat

VII. *PEN* (PENINSULAR)
- 59 Chumphon
- 60 Ranong
- 61 Surat Thani
- 62 Phangnga
- 63 Phuket
- 64 Krabi
- 65 Nakhon Si Thammarat
- 66 Phatthalung
- 67 Trang
- 68 Satun
- 69 Songkhla
- 70 Pattani
- 71 Yala
- 72 Narathiwat