

SYSTEMATIC STUDIES IN AFRICAN INDIGOFEREAE
(LEGUMINOSAE - PAPILIONOIDEAE)

BY

BRIAN DAVID SCHRIRE

Submitted in partial fulfilment of the requirements for the
degree of Doctor of Philosophy in the Department of Botany,
University of Natal.

Pietermaritzburg

1991

ERRATA

1. The letter **q** has been printed instead of \pm
2. Table 5.9 is on page 131a

ABSTRACT

A cladistic analysis of 51 generic and infrageneric taxa in the tribe Indigofereae (Papilionoideae) is presented, comprising 9 570 species in Africa and Madagascar. Traditionally, 4 genera have been recognized: *Phylloxylon* (9 5 species), *Rhynchotropis* (2 species), *Cyamopsis* (9 4 species) and *Indigofera* (510-520 species in Africa). 3 genera have been reinstated, i.e. *Vaughania* (11 species), *Indigastrum* (11 species) and *Microcharis* (9 26 species). *Vaughania* was previously considered to be a monotypic genus (later placed in synonymy under *Indigofera*); the others have recently been treated as subgenera of *Indigofera*. A new subgenus is described in *Indigastrum* (subgenus *Argyraeae* Schrire) as well as 17 new sections and one subsection in *Indigofera*. 18 infrageneric taxa in *Indigofera* are specified at a new rank.

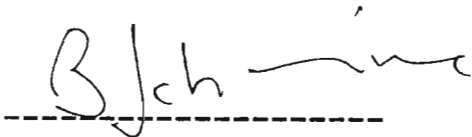
Taxonomic affinities with neighbouring tribes are discussed. A historical review is given of infrageneric subdivisions in *Indigofera* along with a newly proposed classification of infrageneric taxa in Africa. The cladogram is used to study character evolution in the tribe; from a) an ecological perspective (by identifying adaptations) and b) a phylogenetic perspective (by identifying constraining interactions between morphologies). Adaptations and critical morphologies are mapped on the cladogram to interpret developmental constraints, and the order and direction of character transformations. Key morphologies are a class of developmental constraints defined here for the first time.

The cladogram and character analyses are used to interpret a phylogenetic tree of the tribe in Africa. Major phases in the evolution of Indigofereae are hypothesized on the basis of developmental constraints, phytogeography and ecology. A taxonomic revision above the species level in Africa is presented, including keys and descriptions of genera and infrageneric taxa in *Indigofera*. Species of Indigofereae occurring in tropical Africa are listed, while a synopsis is given of southern African species with literature citations, synonymy and typification. 29 new combinations are made in *Microcharis* and *Indigastrum*.

PREFACE

The experimental work in this thesis was performed under the supervision of Dr. H.P. Linder, Dr. C.H. Stirton and Professor J. van Staden, in the Botany Department of the University of Natal, Pietermaritzburg, on a part time basis from March 1989 to March 1991.

These studies have not been submitted in any form to another University and, except where acknowledged in the text, are the results of my own work.

A handwritten signature in cursive script, appearing to read "B. D. Schrire", is written above a horizontal dashed line.

BRIAN DAVID SCHRIRE

William Harvey to George Bentham 21 November 1865.

" I am now naming Gerrards last set of Zulu Leguminosae, and may have a generic question or two to ask when I have done. I see one or two puzzles. There are many new species of *Crotalaria*, *Lotononis*, *Argyrolobium* and *Indigofera* - (endless rascal!) which will lie over for the supplement."

[ms in Royal Botanic Gardens, Kew; Bentham Letters]

ACKNOWLEDGEMENTS

I want to thank the following most sincerely for their help in putting this thesis together:

Dr Peter Linder, whose supervision was kindly offered in an external capacity, my grateful thanks for the invaluable criticism and for being so willing to take on an additional burden.

Dr Charles Stirton for much lively discussion, and supervision of the thesis during the early stages.

Professor Hannes van Staden for all the help given to ensure a smooth transition between supervisors, and for being so willing to assist whenever any problems arose.

The Director and Staff of the Botanical Research Institute, Pretoria, who provided funding for my overseas herbarium tour, for a number of plant collecting trips in South Africa and for much friendly co-operation and assistance during my period of employment. In particular my thanks go to Mrs Adela Romanowski for the photographs in the thesis; Mrs Sarie Perold and Dr Hugh Glen for their invaluable help with the electron microscopy; Mrs Estelle Potgieter for her considerable assistance in the library; Dr Roger Ellis and the staff at Velcich House (anatomical techniques) and Mr Gerrit Germishuizen for years of good legume collaboration in Wing B, PRE.

Professor Braam van Wyk for many stimulating discussions, and his considerable contribution in helping with anatomical procedures and providing facilities for light microscopy and photography.

Dr Ben-Erik van Wyk for many useful suggestions about cladistic methodology.

Dr John Rourke and the staff of the Compton Herbarium for all their assistance during two trips based in Cape Town; Mrs Pat Lorber at the Bolus Herbarium; Mrs Estelle Brink and Dr Amy Jacot Guillarmod at GRA; Miss Rosemary Williams, Mrs Helen Noble and Mr Alfred Ngwenya at NH; Mr Trevor Edwards and Mrs Jane Browning at NU and Mr Ted Oliver and Mrs Anna Fellingham at STE.

Miss Angela Beaumont and Mrs Margaret Tebbs for the black and white illustrations, and Mrs Melanie Thomas for the Latin diagnoses.

Professor Gren Lucas for kindly allowing me access to the facilities in the Herbarium and Library at the Royal Botanic Gardens, Kew, during the final six months of writing up.

Mr Jan Gillett for laying down such a sound basis for research into African Indigoferaeae, and for many helpful discussions and interesting anecdotes.

Dr Roger Polhill, Mr Gwil Lewis, Dr Lulu Rico and the staff of the Legume section at Kew for their much valued support and assistance.

Drs Matt Lavin (Bozeman, Montana); Mike Crisp (Canberra); Jenny Chappill (Perth); Peter Wilson (Sydney); Rob Geesink (Leiden); B.K. Vijay Kumar (Secunderabad, India); Alan Lievens (Baton Rouge, Louisiana); Dave Du Puy (RBG, Kew) and Jean-Noél Labat (Paris) for correspondence, collaboration and many useful ideas.

Dr Charles Nelson for the amusing excerpt from the William Harvey correspondence.

Nigel and Janet Barker for their hospitality and friendship.

Beth Gibbs Russell, Geoff Nichols, Bruce Page, Mike and Carolyn Schurr, Catherine Whitfield, Dee and Colin Paterson-Jones, Peter Phillipson, Brian and Joan Rycroft, Michael Schrire, Mary Yates, Tony and Maggie Abbott, Mark Ward and Liz MacLellan for all their help and support over the last three years.

This work is dedicated, with deepest gratitude, to

Susyn Andrews

for all her support and encouragement when it was
most needed.

TABLE OF CONTENTS

	Page
CHAPTER 1. AIMS AND OBJECTIVES	1
1.1. Introduction	1
1.2. Taxonomic problems	2
1.3. Aims of the study	3
 CHAPTER 2: CLADISTIC ANALYSIS	 7
2.1. Introduction	7
2.2. Methods	7
2.2.1. Choice of taxa	8
2.2.2. Choice of characters	10
2.2.3. Cladogram inference	11
2.3 Results	16
2.3.1. Cladogram of Cape sections of <i>Indigofera</i>	22
 CHAPTER 3: TAXONOMIC AFFINITIES	 42
3.1. Affinities with neighbouring tribes	42
3.2. Affinities in <i>Indigofera</i>	46
3.2.1. New scheme of infrageneric taxa	49
 CHAPTER 4: MORPHOLOGY: DISCUSSION OF CHARACTERS	 51
4.1 Introduction	51
4.2 Methods	51
4.2.1. Leaf clearing	51
4.2.2. Surface-scanning Electron Microscopy	52
4.3. Morphology	53
4.3.1. Habit	53
4.3.2. Stems	54
4.3.3. Trichomes and Pearl bodies	55
4.3.4. Leaves	60
4.3.5. Venation	62
4.3.6. Calcium oxalate crystals and tannin idioblasts	64
4.3.7. Stomata and epidermal morphology	65
4.3.8. Hydathodes	68
4.3.9. Petiole	69
4.3.10. Stipules and stipels	70
4.3.11. Inflorescences	71

4.3.12. Flowers	73
4.3.12.1. Calyx	76
4.3.12.2. Corolla	77
4.3.12.3. Stamens	82
4.3.12.4. Pistil	83
4.3.13. Pods	84
4.3.14. Seeds	87
4.3.15. Seedlings	88
4.3.16. Pollen	88
4.3.17. Chromosomes	90
CHAPTER 5: CHARACTER ANALYSIS: ADAPTATIONS & DEVELOPMENTAL CONSTRAINTS	106
5.1. Introduction	106
5.1.1. Guide to concepts discussed	107
5.2. Methods	108
5.2.1. Ecological analyses	109
5.2.2. Phylogenetic analyses	110
5.3. Theory	110
5.3.1. Discussion of adaptations	110
5.3.1.1. Adaptations	114
5.3.1.2. Exaptations	116
5.3.2. Discussion of developmental constraints	117
5.3.2.1. Burden	118
5.3.2.2. Canalization	119
5.3.2.3. Key morphologies	122
5.3.2.4. Heterochrony	122
5.4. Examples	132
5.4.1. Adaptations	132
1) Herbivore defences and methods of protecting resources in the Indigoferaeae	132
2) Seed dispersal mechanisms in the derived sections of <i>Indigofera</i>	138
3) Herbivore defences and methods of protecting resources in the Cape sections of <i>Indigofera</i>	142
4) Plant features attractive to pollinators in the Cape sections of <i>Indigofera</i>	144
5) Habit, seasonality and other responses to the environment in the Cape sections of <i>Indigofera</i>	147
5.4.2. Developmental constraints in the Indigoferaeae	152
5.4.2.1. Burden	152
5.4.2.2. Canalization	153
5.4.2.3. Key morphologies	154
5.4.2.4. Heterochrony	155

CHAPTER 6: PHYLOGENY AND EVOLUTION	160
6.1. Phylogeny	160
6.1.2. Methods	160
6.1.3. Cladogram vs. Phylogeny	160
6.1.4. Phylogenetic Tree: Evolutionary aspects of phytogeography and ecology	164
6.1.5. Centres of Diversity outside Africa	169
6.2. Evolution of Indigoferaeae	170
CHAPTER 7: TAXONOMY OF INDIGOFERAEAE ABOVE THE SPECIES LEVEL	172
7.1. General Literature Review	172
7.2. Generic and Infrageneric taxa of the tribe Indigoferaeae in Africa and Madagascar	177
7.2.1. Key to genera	180
1) <i>Phylloxylon</i> Baill.	183
2) <i>Vaughania</i> S.Moore	183
3) <i>Rhynchotropis</i> Harms	184
4) <i>Microcharis</i> Benth.	185
5) <i>Indigastrum</i> Jaub.& Spach	186
6) <i>Cyamopsis</i> DC.	188
7) <i>Indigofera</i> L.	189
7.2.2. Key to sections of <i>Indigofera</i>	191
7.2.2.1. Key to Group 1 sections of <i>Indigofera</i>	192
1) Section <i>Denudatae</i> Schrire sect. nov.	196
2) Section <i>Cuneifoliae</i> Schrire sect. nov.	196
3) Section <i>Stipulatae</i> Schrire sect. nov.	197
4) Section <i>Trifoliolatae</i> (E.Mey.) Schrire stat. nov.	198
5) Section <i>Distichae</i> Schrire sect. nov.	199
6) Section <i>Juncifoliae</i> (Harv.) Schrire stat. nov.	200
7) Section <i>Humifusae</i> Schrire sect. nov.	201
8) Section <i>Filicaules</i> Schrire sect. nov.	201
9) Section <i>Concavae</i> Schrire sect. nov.	202
10) Section <i>Coriaceae</i> Schrire sect. nov.	203
11) Section <i>Angustifoliolae</i> Schrire sect. nov.	204
12) Section <i>Hispidae</i> Schrire sect. nov.	205
7.2.2.2. Key to Group 2 sections of <i>Indigofera</i>	206
13) Section <i>Psiloceratiae</i> (Gillett) Schrire stat. nov.	218
14) Section <i>Tinctoriae</i> (Wight & Arn.) Schrire stat. nov.	219
15) Section <i>Subulatae</i> Schrire sect. nov.	220
16) Section <i>Hedyanthae</i> Schrire sect. nov.	221
17) Section <i>Dendroides</i> Schrire sect. nov.	222
17a) Subsection <i>Foliosae</i> Schrire subsect. nov.	223

18) Section <i>Hirsutae</i> (Rydberg) Schrire stat. nov.	224
19) Section <i>Setiflorae</i> Schrire sect. nov.	225
20) Section <i>Microcarpae</i> (Rydberg) Schrire stat. nov.	226
21) Section <i>Stenophyllae</i> (Bak.) Schrire stat. nov.	227
22) Section <i>Brevierectae</i> (Gillett) Schrire stat. nov.	228
23) Section <i>Atratae</i> (Gillett) Schrire stat. nov.	228
24) Section <i>Viscosae</i> (Rydberg) Schrire stat. nov.	229
24a) Subsection <i>Centrae</i> Gillett	230
25) Section <i>Hilares</i> Schrire sect. nov.	231
26) Section <i>Spinosa</i> (Bak.) Schrire stat. nov.	232
27) Section <i>Brevipatentes</i> (Gillett) Schrire stat. nov.	233
28) Section <i>Podophyllae</i> Schrire sect. nov.	234
29) Section <i>Pilosae</i> (Gillett) Schrire stat. nov.	235
30) Section <i>Dissitiflorae</i> (Wight & Arn.) Schrire stat. nov.	236
31) Section <i>Laxeracemosae</i> Schrire sect. nov.	237
32) Section <i>Latestipulatae</i> (Bak.f.) Gillett	238
33) Section <i>Paniculatae</i> (Bak.) Gillett	239
33a) Subsection <i>Trichopodae</i> (Bak.) Gillett	241
34) Section <i>Terminales</i> (Bak.f.) Schrire stat. nov.	241
35) Section <i>Acanthonotus</i> (Benth.) Taub.	242
36) Section <i>Ameocarpus</i> (Benth. ex Harv.) Taub.	243
37) Section <i>Demissae</i> Gillett	244
38) Section <i>Sphaeridiophora</i> (Desv.) Taub.	244
39) Section <i>Simplices-reflexae</i> (Gillett) Schrire stat. nov.	246
40) Section <i>Conjugatae</i> (Bak.) Schrire stat. nov.	247
41) Section <i>Alternifoliolae</i> (Harv.) Schrire stat. nov.	248
CHAPTER 8: SPECIES OF INDIGOFEREAE IN AFRICA	250
8.1. List of species in tropical Africa (excluding southern Africa)	250
8.2. Synopsis of southern African Indigoferae	258
8.2.1. <i>Cyamopsis</i>	258
8.2.2. <i>Microcharis</i> Benth.	259
8.2.3. <i>Indigastrum</i> Jaub. & Spach	260
8.2.3.1. Subgenus <i>Indigastrum</i>	260
8.2.3.2. Subgenus <i>Argyraeae</i> Schrire	262
8.2.4. <i>Indigofera</i>	263
8.2.4.1. Section <i>Denudatae</i> Schrire	263
8.2.4.2. Section <i>Cuneifoliae</i> Schrire	266
8.2.4.3. Section <i>Stipulatae</i> Schrire	267
8.2.4.4. Section <i>Trifoliolatae</i> (E. Mey.) Schrire	269
8.2.4.5. Section <i>Distichae</i> Schrire	275
8.2.4.6. Section <i>Juncifoliae</i> (Harv.) Schrire	276
8.2.4.7. Section <i>Humifusae</i> Schrire	277
8.2.4.8. Section <i>Filicaules</i> Schrire	279
8.2.4.9. Section <i>Concavae</i> Schrire	279

8.2.4.10.	Section <i>Coriaceae</i> Schrire	280
8.2.4.11.	Section <i>Angustifoliolae</i> Schrire	283
8.2.4.12.	Section <i>Hispidae</i> Schrire	286
8.2.4.13.	Section <i>Psiloceratiae</i> (Gillett) Schrire	287
8.2.4.14.	Section <i>Tinctoriae</i> (Wight & Arn.) Schrire	288
8.2.4.15.	Section <i>Subulatae</i> Schrire	291
8.2.4.16.	Section <i>Hedyanthae</i> Schrire	292
8.2.4.17.	Section <i>Dendroides</i> Schrire	295
8.2.4.17.1.	Subsection <i>Foliosae</i> Schrire	298
8.2.4.18.	Section <i>Hirsutae</i> (Rydberg) Schrire	301
8.2.4.19.	Section <i>Microcarpae</i> (Rydberg) Schrire	302
8.2.4.20.	Section <i>Setiflorae</i> Schrire	302
8.2.4.21.	Section <i>Viscosae</i> (Rydberg) Schrire	306
8.2.4.22.	Section <i>Hilares</i> Schrire	310
8.2.4.23.	Section <i>Spinosae</i> (Bak.) Schrire	312
8.2.4.24.	Section <i>Brevipatentes</i> (Gillett) Schrire	312
8.2.4.25.	Section <i>Podophyllae</i> Schrire	313
8.2.4.26.	Section <i>Latistipulatae</i> (Bak.f.) Gillett	313
8.2.4.27.	Section <i>Laxeracemosae</i> Schrire	314
8.2.4.28.	Section <i>Acanthonotus</i> (Benth.) Taub.	316
8.2.4.29.	Section <i>Amecarpus</i> (Benth. ex Harv.) Taub.	316
8.2.4.30.	Section <i>Demissae</i> Gillett	320
8.2.4.31.	Section <i>Sphaeridiophora</i> (Desv.) Taub.	320
8.2.4.32.	Section <i>Alternifoliolae</i> (Harv.) Schrire	321
8.3.	Economic importance of the Indigofereae	325
CHAPTER 9: CONCLUSIONS		329
REFERENCES		336

List of Tables, Figures & Plates

CHAPTER 2	Page
Table 2.1. Summary of 15 cladistic analyses	15
Table 2.2. Overall character list	17
Table 2.3. Composite cladogram of the Indigoferaeae	23
Figs. A.1. to A.17. Cladistic analyses	25
CHAPTER 3	
Fig. 3.1. Schemes of various authors for infrageneric divisions in <i>Indigofera</i>	47
Fig. 3.2. New scheme of generic and infrageneric taxa in the Indigoferaeae	48
Fig. 3.3. Generic and infrageneric relationships in the Indigoferaeae (after Gillett 1958)	50
CHAPTER 4	
Table 4.1. Taxa investigated for the presence of tannin idioblasts and calcium oxalate crystals	66
Plate 4.1. Vegetative morphology	91
Plate 4.2. SEM - Leaflet surface micromorphology. I	92
Plate 4.3. SEM - Leaflet surface micromorphology. II	93
Plate 4.4. SEM - Trichomes and glands. I	94
Plate 4.5. SEM - Trichomes and glands. II	95
Plate 4.6. SEM - Trichomes and glands. III	96
Plate 4.7. SEM - Trichomes and glands. IV	97
Plate 4.8. SEM - Trichomes and glands, V	98
Plate 4.9. Leaflet anatomy - epidermal structures, tannin sacs, areoles	99
Plate 4.10. Anatomy - Leaf venation, tracheoids, bundle sheath	100
Plate 4.11. Anatomy - Leaf venation, calcium oxalate crystals	101
Plate 4.12. Inflorescence morphology, calyces	102
Plate 4.13. Flower morphology. I	103
Plate 4.14. Flower morphology. II	104
Plate 4.15. Pod and seed morphology	105
CHAPTER 5	
Tables 5.1. to 5.9. Aptations in the Indigoferaeae	124
Fig. 5.1. Relationships between aptations and developmental constraints	113
Fig. 5.2. Conceptual model for testing adaptation	115
Fig. 5.3. Summary of ecological associations in Indigoferaeae I	157

Fig. 5.4. Summary of ecological associations in Indigofereae II	158
Fig. 5.5. Summary of ecological associations in Indigofereae III & IV	159
CHAPTER 6	
Table 6.1. Proposed phylogeny of the Indigofereae	161
Table 6.2. Phylogenetic tree of the Indigofereae in Africa	165
Fig. 6.1. Major regions of Africa	166

CHAPTER 1

AIMS AND OBJECTIVES

1.1. INTRODUCTION

Of thirty two tribes recognized by Polhill & Raven (1981) in the Papilionoideae (Leguminosae), the Indigofereae form part of an alliance with a diffuse woody base group, the Millettieae (Polhill 1981). The Indigofereae are one of the most advanced, herbaceous, predominantly Old World tropical tribes with only the large genus *Indigofera* being pantropical. The tribe is considered by Polhill (1981a) to be relatively isolated in the subfamily but evidence accumulated in this study suggests that it may be allied to the Old World *Lonchocarpus* section *Paniculati* Benth. (Polhill 1971; 1971a; Geesink 1981; 1984; Zandee & Geesink 1987).

In the last major review of the tribe (Polhill 1981), 4 genera were distinguished. *Indigofera* was broadly circumscribed to include some 700 species, while *Phylloxylon* (q 5 species), *Rhynchotropis* (2 species) and *Cyamopsis* (4 species) comprised the rest of the tribe.

In Africa, *Indigofera* is extremely diverse and forms a significant component of many vegetation types. The genus has considerable economic importance (see chapter 8) e.g. as:

- a) forage crops - many pasture species are either highly toxic or very palatable to livestock
- b) soil improvement crops - most species have root nodules and can be used for green manuring
- c) soil stabilizers - for erosion control, grazing reclamation, vegetative cover in semi-arid environments, and road or water embankments
- d) a source of chemicals - species contain a particularly wide range of compounds of interest to the pharmaceutical industry
- e) traditional medicines

- f) poisons - i.e. fish poisons or insecticides
- g) dyes - indigo
- h) seed gums - industrial thickeners, binding and flocculating agents
- i) ornamentals - for horticulture
- j) invasive weeds - agriculturally expensive

1.2. TAXONOMIC PROBLEMS

Owing to the range and diversity of *Indigofera*, and the economic potential of so many of its species, it is essential to have a stable framework of correct names for taxa. After a preliminary survey of the genus in Africa, the following taxonomic problems were identified.

- 1) No overall study has been made of generic relationships in the tribe.

Three additional genera were apparent within *Indigofera s. l.*, i.e. *Vaughania* (q 11 species), *Indigastrum* (11 species) and *Microcharis* (q 26 species). *Indigofera s. str.* is thus redefined with q 750 - 800 species (of which q 510 to 520 occur in Africa), and the other 6 genera (q 60 species) are endemic to Africa and Madagascar.

- 2) Due to the size and inherent variability of *Indigofera*, a sound classification above the species level is an essential requirement.

Although Gillett (1958) produced an admirable taxonomic account of *Indigofera s.l.* for tropical Africa, his classification above the species level was largely based on artificial groups, and he did not examine the q 280 species occurring in southern Africa.

- 3) No overall taxonomic treatment of Indigoferaceae has ever been attempted for southern Africa (*Indigofera*, 260 - 270 species; *Indigastrum*, q 10 species and a new subgenus; *Microcharis*,

4 species; *Cyamopsis*, 2 - 3 species). Previous regional revisions of *Indigofera* are listed in chapter 8.

1.3. AIMS OF THE STUDY

Four major aims have, therefore, been defined:

- 1) Delimit genera in the Indigofereae.
- 2) Establish an infrageneric classification of *Indigofera*.
- 3) Develop a model for the evolution of the tribe.
- 4) Provide a synopsis of Indigofereae in southern Africa.

To resolve the problem of relationships at the generic level, and within *Indigofera*, a cladistic approach was considered to be the only valid basis for a phylogenetic classification of the Indigofereae.

A phylogenetic approach may also be used in evolutionary and ecological research, or in agriculture (e.g. pasture management) and industry, to predict trends and interpret aspects such as the following:

- a) character evolution in the tribe (i.e. finding which neighbouring taxa should be examined to locate a character of interest, and in what context particular characters evolved or how they have been transformed).
- b) ecological adaptations (i.e. identifying functional-structural interrelationships through various aspects of:
 - i) insect-plant coevolution e.g. defenses, pollination, or seed dispersal
 - ii) breeding systems
 - iii) survival strategy i.e. responses to the environment.

- c) developmental constraints (i.e. recognizing morphologies which direct development into well defined pathways, causing various trends and patterns on the cladogram).

The cladogram of the tribe is used as a basis to explore some of these aspects (chapter 5).

The following objectives have determined the approach taken in this study.

- 1) Delimit monophyletic groups above the species level for African Indigofereae. (Seven genera, a subgenus in *Indigastrum*, and 41 African sections and 3 subsections in *Indigofera* are recognized).
- 2) Hypothesize the pattern of cladistic relationships between 51 taxa (i.e. 44 taxa in *Indigofera*, 2 in *Indigastrum* and 5 remaining genera in the tribe).
- 3) Use particular cladograms as templates on which to map various ecological associations. From an ecological perspective, characters are maintained by natural selection in their roles as aptations (adaptations and exaptations). Characters associated with a common ecological purpose e.g. protection of resources or seed dispersal are mapped on the cladogram and hypotheses are made about the direction and order of character transformations.

Examples of such ecological associations include:

- a) Defences and deterrents against predators, herbivores and pathogens (e.g. those physical structures which may abrade, puncture or impede access to movement or feeding; or chemical compounds which are toxic, repellent or anutritive, and effective by contact, inhalation or ingestion).

- b) Protection of resources (e.g. shifts in the role of protection of seeds from the pod wall to calyces, or protection of nectar from dessication).
 - c) Pollinator attraction (e.g. specific guidance, recognition or orientation cues, and floral rewards).
 - d) Various aspects of the breeding system (e.g. obligate or facultative autogamy vs. xenogamy, apomixis, cleistogamy; self compatibility vs. incompatibility, monoecism vs. dioecism, overall phenology, mass vs. extended (trap-line) flowering patterns, seed-ovule ratios and selective seed abortion).
 - e) Mechanisms promoting the transfer of the male gametophyte to the female gametophyte (e.g. tripping mechanisms, modifications in the stamens and anthers, pollen morphology and stigma and style characteristics).
 - f) Seed dispersal mechanisms (abiotic vs. biotic methods; autochory, anemochory, epizoochory and myrmecochory).
 - g) Various survival strategies in the life history (e.g. specific habitat requirements, resprouting vs. reseeding after fire, woody vs. herbaceous habit, perennial vs. annual, pyrophytic habit and possible precocious flowering, seed mimesis, specific adaptations for coping with the environment, i.e. enhanced water uptake through hairs).
- 4) Likewise, from a phylogenetic perspective, use cladograms as templates to identify particular developmental constraints (i.e. burden, canalization, key morphologies and heterochrony). These constraints arise because certain morphologies act by directing development into well defined pathways. Morphologies may either channel phenotypic change in directions set by past history and formal structure, or bias which pathway of development is adopted in evolution, or open up new areas of adaptive radiation. Such morphologies cause various trends and patterns on the cladogram.
- 5) Use the cladogram to interpret a phylogenetic tree of Indigoferaeae in Africa.

The cladistic analysis is introduced in the next chapter, firstly, to establish a working hypothesis of relationships from the large and conflicting data set, and secondly, to provide a framework for detailed analyses of characters and taxonomic affinities in later chapters.

CHAPTER 2

CLADISTIC ANALYSIS

2.1. INTRODUCTION

The cladistic method of taxonomic analysis (Hennig 1966; Eldredge & Cracraft 1980; Wiley 1981; Humphries & Funk 1984; Crisp & Weston 1987; Linder 1988) has been used relatively rarely in the Leguminosae (Crisp & Weston 1987; Lavin 1987) and some difficulty has been experienced with its application in the tribe *Millettieae* (Geesink 1984; Zandee & Geesink 1987).

In this chapter the method is applied to 51 taxa above the species level of the tribe *Indigofereae* in Africa.

2.2. METHODS

A cladogram is a rooted hierarchical diagram representing the most parsimonious solution to various possible phylogenetic trees. It is a hypothesis about a pattern of relationships based on the two main principles of monophyly and synapomorphy (Hennig 1966). Monophyletic groups are defined as having an independent history, all members have the same ancestor and they include all descendents of that ancestor (Hennig 1966). Such groups are defined by synapomorphies, which are derived characters shared uniquely by their members (Hennig 1966).

The purpose of cladistics is to investigate the phylogenetic relationships between taxa by searching for monophyletic groups on the basis of synapomorphies. The supposition that two or more species are more closely related to each other than to any other species, and that they form a monophyletic group, can only be confirmed by demonstrating their possession of common synapomorphies (Wiley 1981).

2.2.1. Choice of taxa

The tribe Indigofereae is diagnosed by the following synapomorphies:

- 1) biramous hairs
- 2) simple racemose inflorescences
- 3) caducous petals
- 4) explosive floral tripping mechanism
- 5) keel petals with lateral pockets or spurs
- 6) presence of pearl bodies

Only caducous petals are autapomorphic in the subfamily Papilionoideae, but even though the other characters appear singly or in partial combination in other tribes, they are apparently not homologous with those in the Indigofereae.

The cladistic analysis was confined to Africa for three reasons:

- 1) all genera (except *Indigofera*) are monophyletic (i.e. they have no additional species occurring outside Africa) and these include the least derived elements of the tribe.
- 2) *Indigofera* is pantropical with $\approx 750 - 800$ species, and about 510 - 520 species are found in Africa representing the major centre of variation above the species level.
- 3) It was not possible to cover all of *Indigofera* in this study because of the large number of species involved, and also it is poorly known outside Africa. It is evident that a number of non-African species cannot be placed in African groups, but a superficial survey of the former indicates that the cladistic pattern for Africa can be expected to accommodate these new infrageneric taxa.

Indigofera is defined by three synapomorphies and another character which also occurs as a parallelism in the derived genus *Cyamopsis*. These characters appear to hold for taxa found outside

Africa, suggesting that *Indigofera* is likely to be a monophyletic group, but this remains to be tested.

With the regional circumscription of this study *Indigofera* is treated as a paraphyletic group, since some infrageneric taxa only occur outside Africa while a number of others include non-African species. Examples of the latter are: *Psiloceratiae*, *Tinctoriae*, *Subulatae*, *Pilosae*, *Dissitiflorae*, *Microcarpae*, *Sphaeridiophora* and *Alternifoliolae* which comprise, among others, the basal sections of the genus. These basal groups are often widespread from Africa through India to South East Asia.

The taxa for the cladistic analysis were circumscribed as natural groups of species diagnosed by synapomorphies. Endemic African groups are clearly monophyletic because all species were examined, but monophyly had to be assumed in those groups including non-African species.

The tribe was studied in the main European herbaria (B, BM, C, E, G, K, P, S, TCD, W, Z) while the southern African species were researched in South African herbaria (BOL, GRA, NBG, NH, NU, PRE, SAM, STE) and in the field. Approximately 570 species of *Indigofera sens. lat.* (including *Indigastrum* and *Microcharis*), *Vaughania*, *Phylloxylon*, *Rhynchotropis* and *Cyamopsis* were analysed.

Owing to the logistic problems of dealing with 51 taxa in a cladistic analysis (Sanderson and Donoghue 1989), taxa which formed clear monophyletic groups were combined into larger monophyletic groups for ease of computation. The Cape groups *Juncifoliae*, *Humifusae*, *Filicaules* and *Concavae* were lumped into a supergroup *Humifusae*; and *Cuneifoliae*, *Stipulatae*, *Trifoliolatae* & *Distichae* into a larger *Trifoliolatae* group. Among the tropical taxa, *Laxeracemosae* was placed with the *Dissitiflorae*, *Brevierectae* with *Stenophyllae*; *Foliosae* with *Dendroides*; *Trichopodae* with *Paniculatae*; *Centrae* with *Viscosae* and *Indigastrum* was treated as one taxon. The number of taxa was thus reduced from 51 to 39 for the cladistic analysis.

The exclusively Madagascan genus *Phylloxylon* was an ideal outgroup for the rest of the genera in the Indigoferaeae, being anomalous in the tribe (Polhill 1981), and not sharing a number of characters synapomorphic in the other genera. The presence of bracteoles, calyces without a broad vexillary sinus, anthers lacking apiculate connective and hairs, the unspecialized pollen type and the indehiscent coriaceous pods without transverse septa and with 1 - 2 large seeds, are some of the features plesiomorphic to the rest of the tribe.

2.2.2. *Choice of characters*

Cladistics is a study of character distributions. A cladogram is a set of nested characters which if interpreted to represent patterns of common descent then becomes a phylogeny (Platnick 1979). Characters were sampled for all taxa (discussed in detail in chapter 4), and then grouped as characters and character states comparable across the tribe.

Characters are abstractions describing the relationship between various structures in different taxa. All potential character states are hypotheses of homology (Patterson 1982; Stevens 1984). Character states are postulated as being homologous on the basis of their structural, positional, ontogenetic, compositional and/or functional correspondences, and their congruence with other homologies (Patterson 1982; Humphries & Funk 1984). Such 1:1 correspondences, or similarities in the structures being compared, are the relations which characterize monophyletic groups, and the final hypotheses of homology (synapomorphies) are made after evaluating all potentially homologous characters (Stevens 1984).

Hypotheses on the polarity of character evolution were then made, establishing a hierarchical pattern of homologues, or levels of universality for each. The plesiomorphic state has a wider level of universality than the apomorph and also includes the apomorphic state. Polarity establishes the direction of character transformation (Stevens 1980; Crisci & Stuessy 1980; Stuessy &

Crisci 1984; Humphries & Funk 1984). The determination of the primitive or plesiomorphic state relative to the derived or apomorphic condition, with possible transformation of states between them, was performed by outgroup analysis (Watrous & Wheeler 1981; Donoghue & Cantino 1984; Maddison et al. 1984). Such polarities were initial hypotheses which were continually re-evaluated during subsequent analyses.

2.2.3. *Cladogram inference*

In the choice between alternative hypotheses of relationship (cladograms), parsimony is the criterion applied to find the tree that best explains a pattern of character distributions (Hennig 1966; Wiley 1981; Farris 1983; Humphries & Funk 1984). The "best" tree is considered to be the one which has the least number of character transformations from one state to another, i.e. the fewest evolutionary events (Linder 1988). Parsimony means avoiding, as much as possible, multiple origins of features (Humphries & Funk 1984). An explanation of character distribution that minimises the number of postulated events of homoplasy is preferred, i.e. *ad hoc* hypotheses of parallel evolution and reversal of characters.

In this analysis relationships were too complex to be handled by manual taxonomic methods, because of the large number of taxa involved and the relatively high levels of homoplasy in the characters. A method using a computerized Wagner parsimony programme (Kluge & Farris 1969; Funk & Stuessy 1978) was thus selected to construct the shortest tree. The programme HENNIG86 (version 1.5) by J.S.Farris (1988) was used since it provides substantial improvements over previously available programmes such as PHYLIP and PAUP (Platnick 1989).

The consistency index (Kluge & Farris 1969) is defined as the minimum number of character state changes required by a particular data set (summed over all characters) divided by the total number of state changes required to fit all of the characters most parsimoniously on to the tree (Sanderson &

Donoghue 1989). The index (ci) is used as the standard for comparison of levels of homoplasy among data sets (Kluge & Farris 1969). A character is perfectly consistent (shows no homoplasy on a cladogram) if all state changes occur only once; i.e. if homoplasy is absent the consistency index is 1.0, and ci decreases towards 0 as homoplasy increases (Sanderson & Donoghue 1989).

Sanderson & Donoghue (1989) noted that consistency indices are highly correlated with the number of taxa included in an analysis, with homoplasy increasing as the number of taxa increases. The number of taxa also influences the running time of various options; e.g. experience has shown that more than 18 taxa will effectively preclude the use of the *ie* algorithm in HENNIG86 because it becomes prohibitively time consuming. It was for these reasons that the number of taxa was reduced from 51 to 39.

Character states in the matrix are represented either as binary (0,1), or as ordinal multistate (0,1,2,3) codes (Pimental & Riggins 1987), with the latter selected to be treated additively (preserving order and direction).

The following options were considered in HENNIG86.

- 1) The approximate algorithm (options *mhennig** and *bb**) was employed when the exact method (implicit enumeration or *ie** option) became too time consuming (Platnick 1989). The approximate answer applies branch swapping to each of a number of initial trees, retaining no more than one tree for each initial one (Farris 1988). Extended branch swapping is then applied, generating all the trees it can find and retaining only the shortest ones. The exact answer generates trees certain to be of minimal length. The "*" command instructs the programme to retain all the equally most parsimonious trees in memory (rather than storing only the first 100 trees when the command is not given).

2) Diagnostic information about the character distribution in each cladogram was obtained from the interactive tree editor, Dos Equis. Selected *tsave* files (using the *tchoose* command if more than one tree was stored) were activated as procedure files, then the *xx* command displayed the tree and the states at its nodes for the first character. By analysing each character in turn, its presence or absence in the various taxa was mapped on the cladogram, and those characters diagnosing nodes could be determined. If more than one equally parsimonious tree resulted from any analysis a strict consensus tree was obtained using the *nelsen* command (Page 1989).

The eventual cladograms were obtained by the process of reciprocal illumination, by generating trees, diagnosing them (as above), and then re-evaluating presumed homologies or character polarities. This was repeated until the most congruent character distribution was achieved.

One of the major obstacles in the cladistic analysis was the problem of too many homoplastic characters obscuring the underlying pattern. To reduce homoplasy, the initial tree was studied piecemeal by performing separate analyses on component groups of clades. In dealing with a limited range of taxa, far fewer homoplastic characters were involved. Characters homoplastic at the tribal level were only retained because they were useful in resolving clades at higher levels of the analysis.

The procedure followed was one of successive resolution of each clade (from larger to smaller), as this was considered the best way to recover the most information from the data (see summary of analyses in Table 2.1). For example in the second analysis (see Fig. A.3):

1) CLADE T is a group produced by a strict consensus of 46 equally parsimonious trees.

Consensus trees have less explanatory power than any of the cladograms from which they are calculated (Carpenter 1988), but they are useful for establishing monophyletic groups of clades, which can be manipulated as follows, to resolve other clades.

2) In order to resolve CLADE A, it was necessary to reduce the level of homoplasy by treating CLADE T as a single taxon. This was done by raising the level of universality of all characters in CLADE T to those states which would only apply in the hypothetical ancestor.

3) In Fig. A.4, CLADE T (the whole of *Indigofera*) was treated as one taxon with the characters to be used in the analysis of CLADE A coded as in the hypothetical ancestor of *Indigofera*.

If a clade resolves unambiguously (as a single *ie* tree), and it has no bearing on the rest of the study group, its removal was considered justified in order to simplify subsequent analyses and to reduce the overall level of homoplasy.

4) CLADE A was removed from future analyses.

5) Again in Fig. A.3, CLADE U is a group produced by the consensus tree, and in Fig. A.5, it is coded as one taxon to help resolve relationships in the rest of *Indigofera*. In this 4th analysis, a distinct CLADE B has emerged.

6) In Fig. A.6, CLADE B was analysed by coding the rest of *Indigofera* as one taxon, and when one *ie* tree was obtained CLADE B was removed.

7) This process was continued until all clades were fully resolved.

Five successive outgroups were employed during the whole analysis (column 3 in Table 2.1) using the presumed sister group for each ingroup. Changing the outgroups was also responsible for reducing

SUMMARY OF CLADISTIC ANALYSES IN THE TRIBE INDIGOFEREAE						
ANALYSIS	(NO. OF CHARS.)	OUTGROUP	OPTIONS	TREES (NO.)	LENGTH (STEPS)	C.I.
1) Indigofereae	(56)	Phylloxylon	■* bb*	62	136	0.43
2) Indigofereae (12 characters removed - too homoplastic at tribal level)	(44)	Phylloxylon	■* bb*	46	81	0.58
3) CLADE A; CLADE T coded as one taxon	(9)	Phylloxylon	ie	1	12	0.83
4) Indigofera; CLADE U coded as one taxon; CLADE A removed	(20)	Phylloxylon	ie	1	22	0.90
5) CLADE B; Tropical sections of Indigofera coded as one taxon	(15)	Phylloxylon	ie	1	16	0.93
6) Tropical Indigofera; CLADE U coded as one taxon; CLADE B removed	(12)	Psiloceratiae (with change in character polarities)	ie	1	13	0.92
7) CLADE U; CLADE V coded as one taxon; CLADES C&D removed	(8)	Psiloceratiae	ie	1	9	1.00
8) CLADE U without Microcarpae	(21)	Hirsutae (with change in character polarities)	■*bb*	3	39	0.61
9) CLADE U without Microcarpae & Setiflorae	(22)	Setiflorae (with change in character polarities)	■*bb*	26	39	0.61
10) CLADE V;	(20)	Stenophyllae (with change in character polarities)	■*bb*	14	33	0.66
11) CLADE X; CLADE W coded as one taxon	(10)	Stenophyllae	ie	1	14	0.71
12) CLADE W; CLADE X coded as one taxon	(17)	Stenophyllae	ie	8	28	0.67
13) CLADE Y; CLADE G coded as one taxon	(20)	Stenophyllae	ie	1	33	0.68
14) CLADE H; CLADES X & G coded as one taxon	(13)	Stenophyllae	ie	1	20	0.75
15) CLADE G; CLADE Y coded as one taxon	(11)	Stenophyllae	ie	1	13	0.84

TABLE 2.1 Summary of the 15 separate cladistic analyses performed, to

the effects of homoplasy, because characters were recoded when switches in polarity occurred.

In this study 78 morphological characters were defined for 39 taxa (Table 2.2) with 22 characters (autapomorphies) not being included in the data matrix (Fig. A.1). 15 separate analyses were run on HENNIG86 to resolve this matrix, each being summarized in Table 2.1 and the results are shown at the end of the chapter (Figs. A.1 to A.16). Individual analyses were then combined in a composite cladogram of the tribe (Table 2.3). A further cladistic analysis was performed to resolve the 12 endemic Cape sections of *Indigofera* (Fig. A.17).

Table 2.3 was reconstructed from the fifteen analyses by adding back, from last to first, each fully resolved group of clades. The character distributions are a strict reflection of the patterns obtained in the individual analyses, with only the designation of synapomorphy, parallelism and reversal being adjusted to the broader level of the tribe.

Since the overall cladogram is derived from a number of separate analyses, some of which are based on consensus trees, it is unlikely to be the shortest tree available for the data set. To determine the length of the above cladogram, the topology was expressed in parenthetical notation, and used as an input tree for HENNIG86 (through a *tread* command). The *bb** algorithm was then used to find the shortest tree.

2.3 RESULTS

- 1) After removing the autapomorphies from the character list (Table 2.2), the first analysis of 56 characters (Fig. A.1) produced 62 equally parsimonious trees with a length of 136 steps and a *ci* of 0.43.

The strict consensus tree shows little resolution beyond terminal groupings because some characters are too homoplastic at the tribal level and are obscuring the underlying pattern. The most

Overall character list

- 1) BRACHYBLASTS: present = 0; absent = 1.
- 2) ABAXIAL COMMISSURE (AT BASE OF PETIOLE): present = 0; absent = 1.
- 3)* STEMS (PHYLLODENOUS): absent = 0; present = 1.
- 4)* SPINES (FROM BRANCH TIPS ONLY): absent = 0; present = 1.
- 5)* SPINES (FROM INFLORESCENCE RHACHIDES ONLY): absent = 0; present = 1.
- 6) BIRAMOUS HAIRS (ARM LENGTH): all more or less equal = 0; some markedly unequal = 1.
- 7) BIRAMOUS HAIRS (COLOUR): mixed brown (or black) and hyaline = 0; hyaline only = 1.
- 8)* BIRAMOUS HAIRS (PROMINENT BASAL CELL): absent = 0; present = 1.
- 9) BIRAMOUS HAIRS (SIZE): hairs with arms of equal length more or less the same size on the lower leaf surface = 0; such hairs of markedly different sizes on the lower leaf surface = 1.
- 10)* GLANDS (DISCOID, SESSILE): absent = 0; present over much of the plant surface = 1.
- 11) STALKED MULTICELLULAR GLAND-TIPPED HAIRS: absent = 0; present = 1.
- 12) PEARL BODIES (DENSELY SCATTERED ON STEMS): absent = 0; present = 1.
- 13) PEARL BODIES (DENSELY AGGREGATED BETWEEN LEAFLETS): absent = 0; present = 1.
- 14)* PETIOLES (PHYLLODENOUS): absent = 0; present = 1.
- 15)* LEAFLETS (DENTATE): absent = 0; present = 1.
- 16) LEAFLETS (POSITION): opposite = 0; alternate = 1.
- 17) LEAFLETS (SCLEROPHYLLOUS): absent = 0; present = 1.
- 18) LEAFLETS (CORIACEOUS WITH REFLEXED MARGINS): absent = 0; present = 1.
- 19)* LEAFLETS (SUBGLABROUS ABOVE WITH INVOLUTE MARGINS): absent = 0; present = 1.
- 20)* LEAFLETS (CRASPEDODROMOUS VENATION): absent = 0; present = 1.
- 21)* LEAFLETS (REDUCED TO TERMINAL LEAFLET ON PERSISTENT RHACHIDES): absent = 0; present = 1.
- 22)* LEAFLETS (CARTILAGENOUS MARGIN): absent = 0; present = 1.
- 23)* LEAFLETS (GLANDULAR MARGINS): absent = 0; present = 1.
- 24) STIPULES (DIMORPHIC): absent = 0; present = 1.
- 25) STIPELS: absent = 0; present = 1.
- 26) BRACTS (FOLIAR, GRADATION FROM LEAVES): absent = 0; sometimes present = 1; always present = 2.
- 27) BRACTS (TRILOBED): absent = 0; present = 1.
- 28) BRACTEOLAS: present = 0; absent = 1.
- 29) INFLORESCENCES (PANICULATE): absent = 0; present = 1.
- 30) INFLORESCENCES (SHORT, SUBTENDED BY SHORT LEAVES, WITH ERECT TO SPREADING PODS): absent = 0; present = 1.
- 31) INFLORESCENCES (SLENDER PEDUNCULATE, FEW-FLOWERED, WITH ERECT PODS): absent = 0; present = 1.
- 32) INFLORESCENCES (INCLUDING PEDUNCLE, MORE THAN 2X LENGTH OF LEAVES): absent = 0; present = 1.
- 33) PEDUNCLE (MORE THAN 2X LENGTH OF LEAVES): absent = 0; present = 1.
- 34) PEDICELS (FRUITING LENGTH): 3 mm or shorter = 0; longer than 3 mm = 1.
- 35)* PEDICELS (PATENT WITH PODS AT RIGHT ANGLES): absent = 0; present = 1.
- 36) CALYX (GLANDS ON LOBES): absent = 0; swollen-tipped = 1; capitate = 2.
- 37) CALYX (LENGTH OF LOBES): shorter than 2X length of tube = 0; longer than 2X length of tube = 1.
- 38) CALYX (LENGTH IN RELATION TO STAMINAL SHEATH): about a quarter = 0; longer than quarter = 1.
- 39) CALYX (SCARIOUS FRUITING LOBES): absent = 0; present = 1.

TABLE 2.2 Overall character list used in the cladistic analysis of the Indigofereae (autapomorphies marked *).

- 40)* CALYX (ENLARGED FRUITING LOBES): absent = 0; present = 1.
 41)* PETALS (LONGEVITY): caducous = 0; persistent = 1.
 42) STANDARD (DORSAL SURFACE): glabrous = 0; hairy = 1.
 43) STANDARD (DORSAL SURFACE VESTITURE APPRESSED BROWN STRIGOSE): absent = 0; present = 1.
 44) STANDARD (HAIRS OVER CENTRAL BLOTCH): absent = 0; sometimes present = 1.
 45) STANDARD (CENTRAL BLOTCH MERGING BROADLY ALONG VEINS TO LAMINA): absent = 0; present = 1.
 46) WING (BEARDED PROXIMAL CREST): absent = 0; present = 1.
 47) WING (DISTAL LAMINA BEARD): absent = 0; present = 1.
 48) KEEL (CYMBIFORM): absent = 0; present = 1.
 49) KEEL (PROXIMAL UPPER MARGIN FRINGE): absent = 0; present = 1.
 50)* KEEL (DISTAL UPPER MARGIN, OR APICAL, FRINGE): absent = 0; present = 1.
 51) KEEL (EXPOSURE OF UPPER PROXIMAL MARGIN ABOVE WINGS): exposed above = 0; not exposed above = 1.
 52) KEEL (LATERAL SPURS): sometimes absent = 0; always present = 1.
 53) KEEL (PROLONGED ROSTRUM): absent = 0; present = 1.
 54) ANTHERS (HAIRS): absent = 0; present = 1.
 55) ANTHERS (HAIRS SCATTERED OVER ANTHHER SURFACE): absent = 0; present = 1.
 56) ANTHERS (APICAL CONNECTIVE): absent = 0; present = 1.
 57) ANTHERS (APPENDAGES): not plumose = 0; plumose = 1; scales = 2.
 58) OVARY (LENGTH IN PROPORTION TO HORIZONTAL LENGTH OF PISTIL): longer than half = 0; about a half or less = 1.
 59)* STYLE (TWISTED AND ABRUPTLY CONSTRICTED AT THE BASE): absent = 0; present = 1.
 60) STIGMA (SHAPE): always capitate = 0; often oblique = 1.
 61) PODS (SURFACE VESTITURE): absent (glabrous) = 0; present (hairy) = 1.
 62) PODS (SURFACE VENATION PROMINENT): absent = 0; sometimes present = 1.
 63)* PODS (SPINY PROCESSES): absent = 0; present = 1.
 64)* PODS (THREE LONGITUDINAL RIDGES): absent = 0; present = 1.
 65) PODS (FLATTENED): absent = 0; present = 1.
 66) PODS (REFLEXED): absent = 0; present = 1.
 67) PODS (DRYING BLUE-BLACK): absent = 0; present = 1.
 68) ENDOCARP (TANNIN DEPOSITS): always extensive = 0; sometimes absent = 1.
 69) ENDOCARP (TANNIN DEPOSITS IN DISTINCT STRIPES): absent = 0; present = 1.
 70) SEEDS (SHAPE): subcylindrical, oblate to quadrate = 0; spherical = 1.
 71)* SEEDS (SIZE): less than 3mm wide = 0; greater than 3 mm wide = 1.
 72) SEEDS (PERSISTENT FUNICULAR REMAINS): absent = 0; sometimes present = 1.
 73) SEEDS (TUBERCULATE): absent = 0; sometimes present = 1.
 74) SEEDS (COARSELY PITTED): absent = 0; present = 1.
 75) POLLEN (MORPHOLOGY TYPE): not types 3&4 = 0; type 3 = 1; type 4 = 2.
 75a) POLLEN (MORPHOLOGY TYPE): not type 4 = 0; type 4 = 1.
 76)* POLLEN (LARGE WITH SHORT COLPI): absent = 0; present = 1.
 77) CHROMOSOMES (NUMBER): 2n=16 = 0; 2n=14 = 1.
 78)* CHROMOSOMES (NUMBER): 2n=16 = 0; 2n=12 = 1.

problematic synapomorphies were tried in various combinations, using the *ccode* command to make them active or inactive, until a much improved resolution was obtained (see below). This was not considered to be massaging the data, and it seemed the only way to resolve the cladogram any further.

- 2) In the second analysis 44 characters were used (Figs, A.2 & A.3), and this produced 46 equally parsimonious trees with 81 steps and a *ci* of 0.58.

The strict consensus tree shows a basal dichotomy with CLADE T (*Indigofera*) as a monophyletic group distinct from the other genera of the tribe in CLADE A. This dichotomy supports the decision to resurrect *Indigastrum* and *Microcharis* as distinct genera, removing them from their traditional taxonomic position as subgenera of *Indigofera* (Gillett 1958).

- 3) In the third analysis, CLADE T (the whole of *Indigofera*) was treated as one taxon to resolve CLADE A (Fig. A.4). Using *Phylloxylon* as the outgroup, the only two apomorphic states ancestral in CLADE T are for characters 28 and 56. One tree was obtained with the *ie* option. The topology of CLADE A remained the same as in the second analysis, and had a length of 12 steps and a *ci* of 0.83. CLADE A was therefore no longer considered in subsequent analyses.

This analysis gives a cladogram of all the genera in the tribe.

In the second analysis (Fig. A.3) a clear monophyletic group is evident within CLADE T, which corresponds to a grouping of the more derived herbaceous sections in the genus, CLADE U.

- 4) In the fourth analysis (Fig. A.5), CLADE U is now coded as one taxon to help resolve the pattern of relationships in the rest of *Indigofera*. One tree was produced with the *ie* option, 22 steps long, and a *ci* of 0.90.

The cladogram shows the widespread section *Psiloceratae* giving rise independantly to all the Cape sections (CLADE B) and to all the tropical sections in Africa (the rest). The fundamental divergence between the Cape and tropical sections is interesting, especially as this geographical distinction was not used as a character in the cladistic study.

5) The Cape sections (CLADE B) were then analysed on their own by coding the tropical sections of *Indigofera* as one taxon (Fig. A.6), and one *ie* tree of the same topology as above, with 16 steps and *ci* of 0.93 was obtained.

CLADE B was then removed for the sixth analysis and the outgroup was changed to the basal section *Psiloceratae* of *Indigofera*, with a consequent switch in some character polarities.

6) CLADE U was again coded as a single taxon (now polarised to the new outgroup), and one *ie* tree of 13 steps and *ci* of 0.92 resolved the basal tropical taxa into two groups: the woody *Tinctoriae* (CLADE C), and herbaceous *Hedyanthae* (CLADE D). These are linked to the rest of the more derived, herbaceous, sections of *Indigofera* (Fig. A.7).

The monophyletic CLADE U (Fig. A.3) can be seen to comprise two distinct groups of sections, CLADE V with an apomorphic Type 4 pollen, and the group arising from section *Microcarpae*.

7) In the seventh analysis (Fig. A.8), CLADES C and D were removed so *Psiloceratae* became the outgroup of CLADE U. CLADE V was then coded as one taxon. One *ie* tree 9 steps long with a *ci* of 1.00 was produced.

The resolution in this analysis supports the choice of section *Hirsutae* as an outgroup for the remaining sections of *Indigofera* (CLADE U without section *Microcarpae*) since section *Microcarpae* comprises only one species in a section of doubtful African origin.

8) The character polarities were changed accordingly, and the eighth analysis (Fig. A.9) gave 3 *bb* trees of 39 steps with a *ci* of 0.61.

Poor resolution was obtained for CLADE V in this analysis, and the character distribution indicates that better resolution would be possible using either *Setiflorae* or *Stenophyllae* as an outgroup in preference to section *Hirsutae*.

9) In the ninth analysis section *Setiflorae* was used as the outgroup (Fig. A.10) and 26 *bb* trees were obtained, each 39 steps long with a *ci* of 0.61 (the same as in the previous analysis).

The strict consensus tree, however, showed better resolution of CLADE V producing two distinct clades, CLADE W and CLADE X.

10) Section *Stenophyllae* was then coded as the outgroup of CLADE V (Fig A.11), and with the change in polarities, 14 *bb* trees, 33 steps long with a *ci* of 0.66 were produced.

The strict consensus tree highlighted the same two clades as above.

11) The eleventh analysis, again using *Stenophyllae* as outgroup, fully resolved CLADE X. CLADE W was coded as a single taxon (Fig. A.12), and this gave 1 *ie* tree of 14 steps with a *ci* of 0.71.

Two distinct clades comprising CLADE W became evident, CLADE E and the group with alternate leaflets, CLADE F.

12) CLADE W was analysed next (Fig. A.13), producing 8 *ie* trees with 28 steps and a *ci* of 0.67.

The strict consensus tree unites CLADE H and CLADE X (into CLADE Y) leaving CLADE G unresolved at the base of the tree.

- 13) CLADE Y was tested in the thirteenth analysis (Fig. A.14) with CLADE G coded as one taxon, and CLADE Y again resolved into CLADE H and CLADE X, with CLADE G at the base. One *ie* tree was obtained with 13 steps and a *ci* of 0.68.
- 14) One minimum length tree for CLADE H was obtained in the fourteenth analysis (Fig. A.15), by coding both CLADE G and CLADE X as single taxa. The *ie* tree gave a *ci* of 0.75 with 20 steps.
- 15) The final analysis (Fig. A.16) resolves CLADE G completely, with CLADE Y (CLADE H & CLADE X) coded as one taxon. A single *ie* tree was obtained, 13 steps long, with a *ci* of 0.84.

These fifteen analyses were then compiled into one composite cladogram (Table 2.3) for the tribe Indigofereae. When this topology was reconstructed and analysed, an overall length of 144 steps with a *ci* of 40 and *ri* of 68 was obtained. The *bb** algorithm was then applied to search for any shorter trees, and 62 trees, 136 steps long with a *ci* of 43 and *ri* of 71 were found. These trees showed poor resolution at the basal nodes, however, and were rejected because they did not support intuitive ideas of taxonomic relationships in the tribe. The deficiencies in the analysis, which have resulted in the admission of a cladogram 8 steps longer than the most parsimonious trees, are discussed further in chapter 6.

2.3.1. *Cladogram of Cape sections of Indigofera*

In the cladogram of the tribe (Table 2.3), closely related Cape sections were placed in larger monophyletic groups (section alliances) to reduce the number of taxa, and hence the complexity, of the overall data analysis. The cladogram of all 12 Cape sections is shown in Fig. A.17.

One tree 20 steps long, with a consistency index of 0.80, was produced by the *ie* algorithm. The outgroup, the basal section

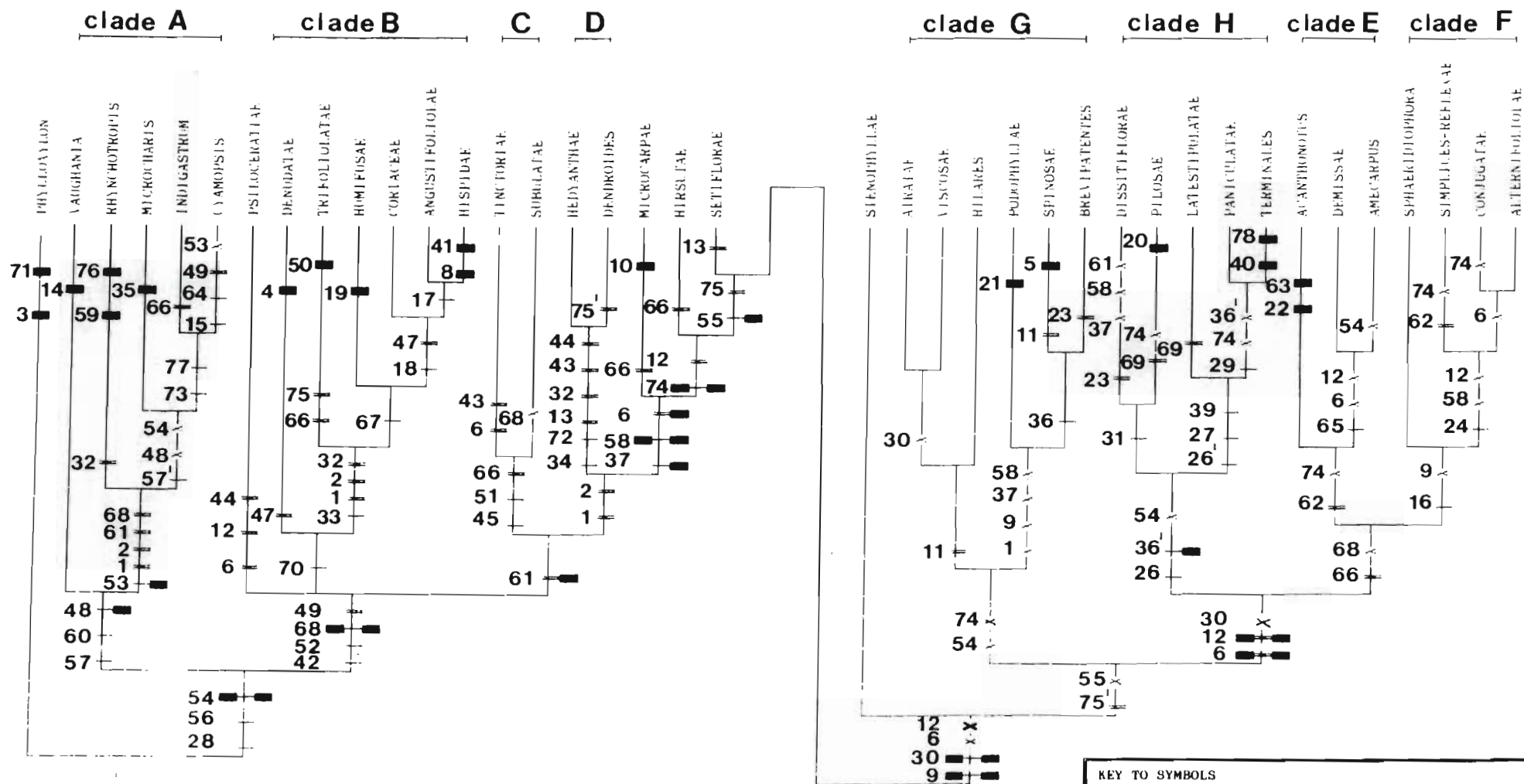
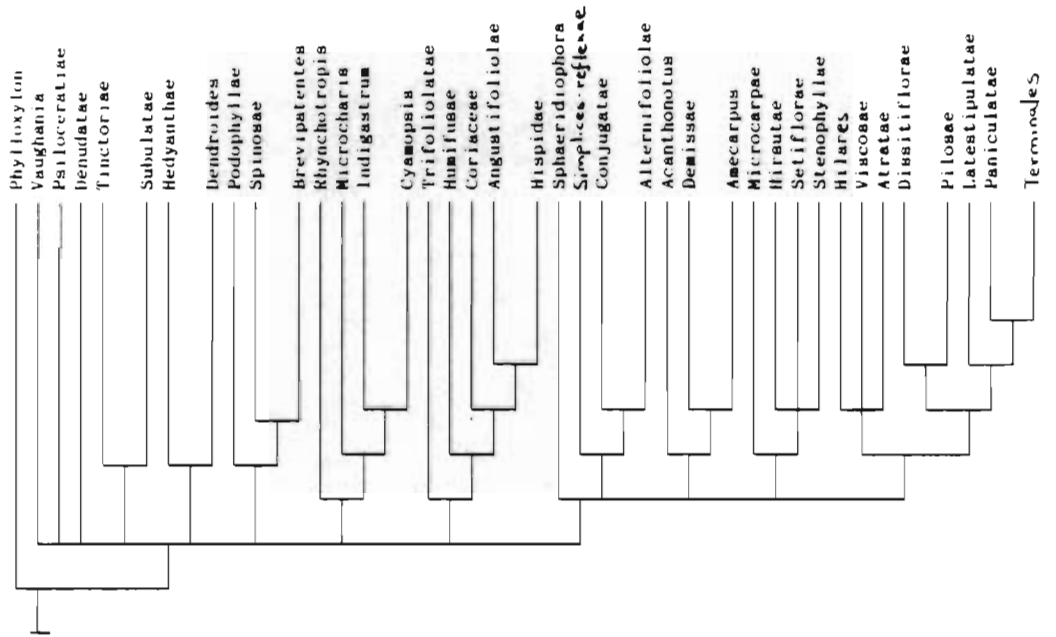


TABLE 2.3 Composite cladogram of the Indigoferae compiled from 15 cladistic analyses (summarized in Table 2.1).

KEY TO SYMBOLS	
—	= synapomorphy with no reversals higher up
- - -	= parallelism
x	= reversal
■	= autapomorphy
- ■	= synapomorphy with one reversal higher up
- ■ - ■	= synapomorphy with two reversals higher up

Psiloceratiae, was established in the tribal analysis as having given rise independently to the Cape and other tropical sections of *Indigofera*. The pattern of relationships established above is used in chapter 5 for discussing ecological associations in the Cape.



Clade 1: Taxa	Characters and character states (excluding autapomorphies)												
	12679	11111	12222	22333	33333	34444	44445	55555	55666	66666	77777	7	
			12367	84567	89012	34678	92345	67891	23456	78012	56789	02345	7
Phylloxylon	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	00000	0
Vaughania	00000	00000	00000	10000	00000	00000	00100	01101	10110	00010	00000	0	0
Rhynchosporis	11010	00000	00000	10001	00001	00000	00100	01101	10110	00010	00000	0	0
Indigastrum	11010	00000	00000	1000?	000?	00000	00000	01001	20110	01010	00100	1	0
Microcharis	11010	00000	00000	10000	00001	00000	00000	01001	20110	00010	00000	0	0
Cyamopsis	11010	00000	00000	10000	00001	00000	00010	00001	20110	00010	00100	1	0
Psiloceratae	00100	01000	00100	10000	00000	01010	10101	10101	00000	00000	00000	0	0
Denudatae	00010	00000	00000	10000	00000	01000	01010	10101	00000	00000	10000	0	0
Humifusae	11010	00000	00000	10001	10001	01000	00010	10101	00000	00100	10000	0	0
Trifoliolatae	11010	00000	00000	10001	10001	01000	00010	10101	00000	01000	10000	0	0
Coriaceae	11010	00000	10000	10001	10001	01000	01010	10101	00000	00100	10000	0	0
Angustifoliolae	11010	00001	10000	10001	10001	01000	01010	10101	00000	00100	10000	0	0
Hispidae	11010	00001	10000	1000?	00001	01000	01010	10101	00000	00000	10000	0	0
Tinctoriae	0010?	00000	00100	10000	00000	01101	00011	10101	00010	01000	00000	0	0
Subulatae	00010	00000	00100	10000	00001	01001	00011	10001	00010	01010	00000	0	0
Hedyanthae	11000	00100	00000	10001	01000	01110	10010	10101	00010	00000	01000	0	0
Dendroides	11000	00100	00000	10001	01001	01110	00010	10101	00010	00000	01001	0	0
Simplicis-reflexae	11110	00000	01000	10000	00011	01000	00010	10101	00011	01000	00001	0	0
Conjugatae	10010	00010	01100	10000	00011	01000	00010	10101	00010	01000	00001	0	0
Alternifoliolae	11010	00010	00100	10000	00011	01000	00010	10101	00010	01010	00011	0	0
Hirsutae	11100	01000	00100	10000	00011	01000	10010	10101	01010	01000	00010	0	0
Microcarpae	1111?	00000	00000	10000	00011	01000	10010	10101	01010	01000	00000	0	0
Setiflorae	11100	01100	00000	10000	00011	01000	10010	10111	01010	00000	00010	0	0
Stenophyllae	11001	00000	00000	10100	00011	01000	11010	10111	01010	00000	00010	0	0
Acanthonotus	11111	01000	00000	10000	00011	01000	10010	10101	01011	01010	00001	0	0
Sphaeridiophora	11110	00010	00000	10000	00011	01000	00010	10101	01010	00010	00011	0	0
Demissae	11011	00000	00100	10000	00011	01000	00010	10101	0101?	11010	00001	0	0
Amecarpus	11011	00000	00100	10000	00011	01000	00010	10001	01011	11010	00001	0	0
Pilosae	11001	01000	00110	10010	00211	01000	00010	1000?	01010	00001	00001	0	0
Dissitiflorae	11111	01000	00110	10010	00100	01000	00010	10001	00000	00000	00011	0	0
Latestipulatae	11111	01000	00021	10000	00211	11000	00010	10001	01010	00001	00001	?	0
Paniculatae	11101	00000	00121	11000	00011	11000	00010	10001	01010	00000	00001	0	0
Terminalis	11111	01000	00021	11000	00011	11000	00010	10001	01010	00000	00001	0	0
Atratae	11001	10000	00000	10000	00011	01100	00010	10001	01010	00000	00001	0	0
Viscosae	11011	10000	00000	10000	00011	01000	00010	10001	01010	00000	00001	0	0
Hilares	11011	10000	00000	10100	00011	01000	00010	10001	01010	00000	00001	0	0
Spinosae	01010	10000	00000	10100	0010?	01000	00010	10001	00010	00000	00001	0	0
Brevipatentes	01010	00000	00000	10100	00100	01000	00010	10001	00010	00000	00001	0	0
Podophyllae	01010	00000	00100	10100	00000	01000	00010	10001	00010	00000	00001	0	0

FIG. A.1: CLADISTIC ANALYSIS 1. INDIGOFEREAE (ALL TAXA); 56 CHARACTERS, 62 TREES.

FIG. A.2: CLADISTIC ANALYSIS 2. CHARACTER LIST AND MATRIX.

Character List Clade 2
2) ABAXIAL COMMISSURE (AT BASE OF PETIOLE): present = 0; absent = 1.
6) BIRAMOUS HAIRS (ARM LENGTH): all more or less equal = 0; some markedly unequal = 1.
11) STALKED MULTICELLULAR GLAND-TIPPED HAIRS: absent = 0; present = 1.
16) LEAFLETS (POSITION): opposite = 0; alternate = 1.
17) LEAFLETS (SCLEROPHYTIOUS): absent = 0; present = 1.
18) LEAFLETS (CORIACEOUS WITH REFLEXED MARGINS): absent = 0; present = 1.
24) STIPULES (DIMORPHIC): absent = 0; present = 1.
26) BRACTS (FOLLAR, GRADATION FROM LEAVES): absent = 0; sometimes present = 1; always present = 2.
27) BRACTS (LOBED): absent = 0; present = 1.
28) BRACTEOLAS: present = 0; absent = 1.
29) INFLORESCENCES (PANICULATE): absent = 0; present = 1.
30) INFLORESCENCES (SHORT, SUBTENED BY SHORT LEAVES, WITH ERECT TO SPREADING PODS): absent = 0; present = 1.
31) INFLORESCENCES (SLENDER PEDUNCULATE, FEW-FLOWERED, WITH ERECT PODS): absent = 0; present = 1.
32) INFLORESCENCES (INCLUDING PEDUNCLE, MORE THAN 2X LENGTH OF LEAVES): absent = 0; present = 1.
33) PEDUNCLE (MORE THAN 2X LENGTH OF LEAVES): absent = 0; present = 1.
34) PEDICELS (FRUITING LENGTH): 3 mm or shorter = 0; longer than 3 mm = 1.
36) CALYX (GLANDS ON LOBES): absent = 0; swollen-tipped = 1; capitate = 2.
37) CALYX (LENGTH OF LOBES): shorter than 2X length of tube = 0; longer than 2X length of tube = 1.
39) CALYX (SCARIOUS FRUITING LOBES): absent = 0; present = 1.
12) STANDARD (DORSAL SURFACE): glabrous = 0; hairy = 1.
43) STANDARD (DORSAL SURFACE VESTITURE APPRESSED BROWN STRIGOSE): absent = 0; present = 1.
11) STANDARD (HAIRS OVER CENTRAL BLOTCH): absent = 0; sometimes present = 1.
15) STANDARD (CENTRAL BLOTCH MERGING BROADLY ALONG VEINS TO LAMINA): absent = 0; present = 1.
48) KEEL (CYMBIFORM): absent = 0; present = 1.
19) KEEL (PROXIMAL UPPER MARGIN FRINGE): absent = 0; present = 1.
51) KEEL (EXPOSURE OF UPPER PROXIMAL MARGIN ABOVE WINGS): exposed above = 0; not exposed above = 1.
52) KEEL (LATERAL SPURS): sometimes absent = 0; always present = 1.
53) KEEL (PROLONGED ROSTRUM): absent = 0; present = 1.
54) ANTHERS (HAIRS): absent = 0; present = 1.
55) ANTHERS (HAIRS SCATTERED OVER ANTHER SURFACE): absent = 0; present = 1.
56) ANTHERS (APICAL CONNECTIVE): absent = 0; present = 1.
57) ANTHERS (APPENDAGES): not plumose = 0; plumose = 1; scales = 2.
60) STIGMA (SHAPE): always capitate = 0; often oblique = 1.
61) PODS (SURFACE VESTITURE): absent (glabrous) = 0; present (hairy) = 1.
62) PODS (SURFACE VENATION PROMINENT): absent = 0; sometimes present = 1.
65) PODS (FLATTENED): absent = 0; present = 1.
67) PODS (DRYING BLUE-BLACK): absent = 0; present = 1.
69) ENDOCAMP (TANNIN DEPOSITS IN DISTINCT STRIPES): absent = 0; present = 1.
70) SEEDS (SHAPE): subcylindrical, oblate to quadrate = 0; spherical = 1.
72) SEEDS (PERSISTENT FUNICULAR REMAINS): absent = 0; sometimes present = 1.
73) SEEDS (TUBERCULATE): absent = 0; sometimes present = 1.
74) SEEDS (COARSELY PITTED): absent = 0; present = 1.
75a) POLLEN (MORPHOLOGY TYPE): not type 4 = 0; type 4 = 1.
77) CHROMOSOMES (NUMBER): 2n=16 = 0; 2n=14 = 1.

Clade 2: Taxa	Characters and character states									
	26111	12222	23333	33334	44444	55555	55666	66677	7777	
	167	84678	90123	46792	34589	12345	67012	57902	3457	
Phylloxylon	00000	00000	00000	00000	00000	00000	00000	00000	0000	0000
Vaughania	00000	00001	00000	00000	00010	00010	111?0	00000	0000	0000
Rhynchotropis	10000	00001	00010	00000	00010	00110	11110	00000	0000	0000
Indigostrum	10000	00001	000??	00?00	00000	00100	12110	00000	1001	
Microcharis	10000	00001	0000?	00000	00000	00100	12110	00000	0000	0000
Cyamopsis	10000	00001	00000	00000	00001	00000	12110	00000	1001	
Psiloceratiae	01000	00001	00000	00001	01001	01010	10000	00000	0000	0000
Denudatae	00000	00001	00000	00001	00001	01010	10000	00010	0000	0000
Humifusae	10000	00001	00011	00001	00001	01010	10000	01010	0000	0000
Trifoliolatae	10000	00001	00011	00001	00001	01010	10000	00010	0000	0000
Coriaceae	10000	10001	00011	00?01	00001	01010	10000	01010	0000	0000
Angustifoliolatae	10001	10001	00011	00001	00001	01010	10000	01010	0000	0000
Hispidae	10001	10001	000??	00001	00001	01010	10000	0?010	0000	0000
Tinctoriae	01000	00001	00000	00001	10101	11010	10010	00000	0000	0000
Subulatae	00000	00001	00000	00001	00101	110?0	10010	00000	0000	0000
Hedyanthae	10000	00001	00010	10001	11001	01010	10010	00001	0000	0000
Dendroides	10000	00001	0001?	10001	11001	01010	10010	00001	0010	
<i>Simplicis-reflexae</i>	110?0	01001	00000	00101	00001	01010	10011	00000	0010	
Conjugatae	?0010	01001	00000	00101	00001	01010	10010	00000	0010	
Alternifoliolatae	10010	0?001	00000	00101	00001	01010	10010	00000	0110	
Hirsutae	11000	00001	00000	00101	00001	01010	10010	000?0	0100	
Microcarpae	11000	00001	00000	00101	0?001	01010	10010	000?0	0000	
Setiflorae	11000	00001	00000	00101	0?001	01011	10010	00000	0100	
Stenophyllae	10000	00001	01000	00101	00001	01011	10010	00000	0100	
Acanthonotus	11000	00001	00000	00101	00001	01010	10011	00000	0010	
Sphaeridiophora	11010	00001	00000	00101	00001	01010	10010	000?0	0110	
Demissae	10000	00001	00000	00101	00001	01010	1001?	10000	0010	
Ameocarpus	10000	00001	00000	00101	00001	01000	10011	10000	0010	
Pilosae	11000	00101	00100	02101	00001	01000	10010	00100	0?10	
Dissitiflorae	11000	00101	00100	01001	00001	01000	10000	00000	0110	
Latestipulatae	11000	00211	0000?	02111	00001	010?0	10010	00100	001?	
Paniculatae	11000	00211	10000	00111	00001	01000	10010	00000	0010	
Terminales	11000	00211	10000	00111	00001	01000	10010	00000	0010	
Atratae	10100	00001	00000	00101	10001	01000	10010	00000	0010	
Viscosae	10100	00001	00000	00101	00001	01000	10010	00000	0010	
Hilares	10100	00001	01000	00101	00001	010?0	10010	00000	0010	
Spinosae	10100	00001	01000	01001	00001	01000	10010	00000	0010	
Brevipatentes	10000	00001	01000	01001	00001	01000	10010	00000	0010	
Podophyllae	10000	00001	01000	00001	00001	01000	10010	00000	0010	

FIG. A.3: CLADISTIC ANALYSIS 2. INDIGOFEREA (ALL TAXA): 44 CHARACTERS, 46 TREES.

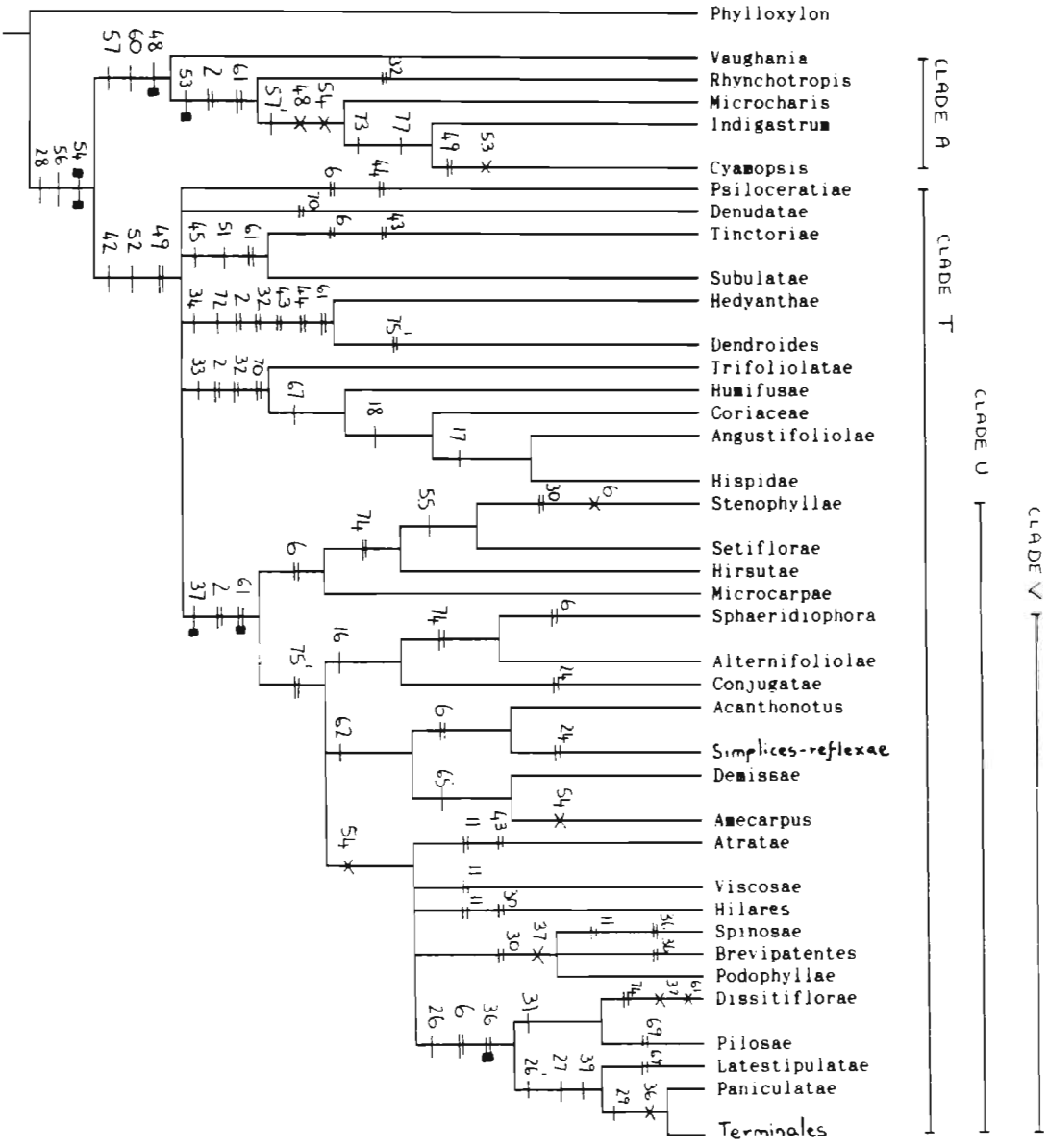


FIG. A.4: CLADISTIC ANALYSIS 3. RESOLUTION OF CLADE A; CLADE T (INDIGOFERA) CODED AS ONE TAXON; 1 TREE.

Character list Clade 3	
2) ABAXIAL COMMISSURE (AT BASE OF PETIOLE):	present = 0; absent = 1.
28) BRACTEOLES:	present = 0; absent = 1.
48) KEEL (CYMBIFORM):	absent = 0; present = 1.
53) KEEL (PROLONGED ROSTRUM):	absent = 0; present = 1.
56) ANTHERS (APICAL CONNECTIVE):	absent = 0; present = 1.
57) ANTHERS (APPENDAGES):	not plumose = 0; plumose = 1; scales = 2.
60) STIGMA (SHAPE):	always capitate = 0; often oblique = 1.
73) SEEDS (TUBERCULATE):	absent = 0; sometimes present = 1.
77) CHROMOSOMES (NUMBER):	2n=16 = 0; 2n=14 = 1.

Clade 3: Taxa	Characters
	22455 5677 8836 7037
Phylloxylon	00000 0000
Vaughania	01101 1100
Rhynchosotropis	11111 1100
Indigastrum	11011 2111
Microcharis	11011 2100
Cyamopsis	11001 2111
Clade T	11001 0000

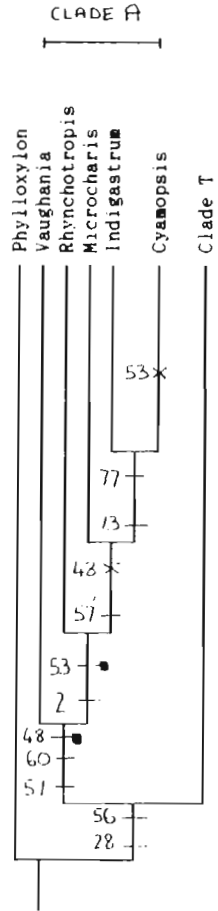


FIG. A.5: CLADISTIC ANALYSIS 4. INDIGOFERA; CLADE U CODED AS ONE TAXON; CLADE A REMOVED; 1 TREE.

Character list Clade 4	
6) BIRAMOUS HAIRS (ARM LENGTH): all more or less equal = 0; some markedly unequal = 1.	
13) PEARL BODIES (DENSELY AGGREGATED BETWEEN LEAFLETS): absent = 0; sometimes present = 1.	
17) LEAFLETS (SCLEROPHYLLOUS): absent = 0; present = 1.	
18) LEAFLETS (CORIACEOUS WITH REFLEXED MARGINS): absent = 0; present = 1.	
28) BRACTEOLES: present = 0; absent = 1.	
32) INFLORESCENCES (INCLUDING PEDUNCLE, MORE THAN 2X LENGTH OF LEAVES): absent = 0; present = 1.	
33) PEDUNCLE (MORE THAN 2X LENGTH OF LEAVES): absent = 0; present = 1.	
34) PEDICELS (FRUITING LENGTH): 3 mm or shorter = 0; longer than 3 mm = 1.	
42) STANDARD (DORSAL SURFACE): glabrous = 0; hairy = 1.	
45) STANDARD (CENTRAL BLOTCH MERGING BROADLY ALONG VEINS TO LAMINA): absent = 0; present = 1.	
47) WING (DISTAL LAMINA BEARD): absent = 0; present = 1.	
51) KEEL (EXPOSURE OF UPPER PROXIMAL MARGIN ABOVE WINGS): exposed above = 0; not exposed above = 1.	
52) KEEL (LATERAL SPURS): sometimes absent = 0; always present = 1	
54) ANTHERS (HAIRS): absent = 0; present = 1.	
56) ANTHERS (APICAL CONNECTIVE): absent = 0; present = 1.	
58) OVARY (LENGTH TO HORIZONTAL LENGTH OF PISTIL): longer than half = 0; about half or less = 1.	
61) PODS (SURFACE VESTITURE): absent (glabrous) = 0; present (hairy) = 1.	
67) PODS (DRYING BLUE-BLACK): absent = 0; present = 1.	
70) SEEDS (SHAPE): subcylindrical, oblate to quadrate = 0; spherical = 1.	
72) SEEDS (PERSISTENT FUNICULAR REMAINS): absent = 0; sometimes present = 1.	

Clade 4: Taxa	Characters			
	61112	33344	45555	56677
	3788	23425	71246	81702
Phylloxylon	00000	00000	00000	00000
Psiloceratae	?0001	00010	?0111	00000
Denudatae	00001	00010	10111	00010
Humifusae	00001	11010	00111	00110
Trifoliolatae	00001	11010	00111	00010
Coriaceae	00011	11010	10111	00110
Angustifoliolae	00111	11010	10111	00110
Hispidae	00111	?010	10111	00?10
Tinctoriae	00001	00011	01111	01000
Subulatae	00001	00011	011?1	01000
Hedyanthae	01001	10110	00111	01001
Dendroides	01001	1?110	00111	01001
Clade U	10001	00010	00111	11000

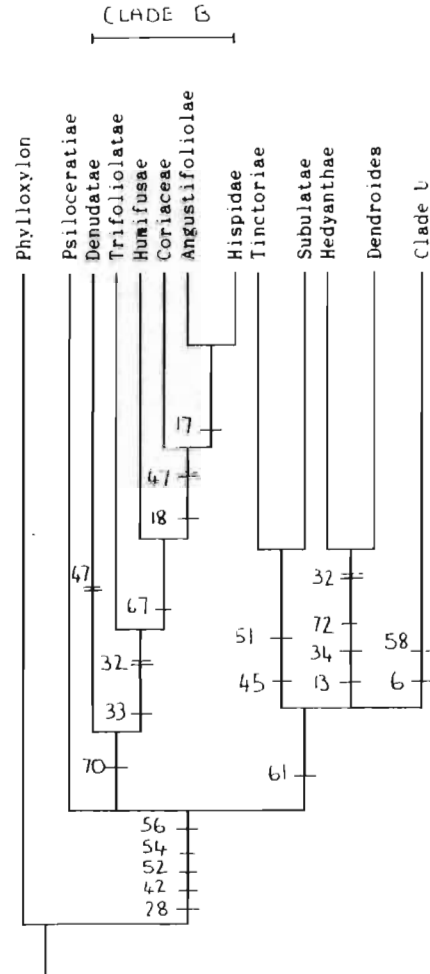


FIG. A.6: CLADISTIC ANALYSIS 5. RESOLUTION OF CLADE B; REST OF INDIGOFERA CODED AS ONE TAXON; 1 TREE.

Character list Clade 5	
1) BRACHYBLASTS:	present = 0; absent = 1.
2) ABAXIAL COMMISSURE (AT BASE OF PETIOLE):	present = 0; absent = 1.
17) LEAFLETS (SCLEROPHYLLOUS):	absent = 0; present = 1.
18) LEAFLETS (CORIACEOUS WITH REFLEXED MARGINS):	absent = 0; present = 1.
28) BRACTEOLES:	present = 0; absent = 1.
32) INFLORESCENCES (INCLUDING PEDUNCLE, MORE THAN 2X LENGTH OF LEAVES):	absent = 0; present = 1.
33) PEDUNCLE (MORE THAN 2X LENGTH OF LEAVES):	absent = 0; present = 1.
42) STANDARD (DORSAL SURFACE):	glabrous = 0; hairy = 1.
47) WING (DISTAL LAMINA BEARD):	absent = 0; present = 1.
52) KEEL (LATERAL SPURS):	sometimes absent = 0; always present = 1
54) ANTHERS (HAIRS):	absent = 0; present = 1.
56) ANTHERS (APICAL CONNECTIVE):	absent = 0; present = 1.
61) PODS (SURFACE VESTITURE):	absent (glabrous) = 0; present (hairy) = 1.
67) PODS (DRYING BLUE-BLACK):	absent = 0; present = 1.
70) SEEDS (SHAPE):	subcylindrical, oblate to quadrate = 0; spherical = 1.

Clade 5: Taxa	Characters
	12112 33445 55667 788 23272 46170
Phylloxylon	00000 00000 00000
Psiloceratiæ	00001 001?1 11000
Denudatæ	00001 00111 11001
Humifusæ	11001 11101 11011
Trifoliolatae	11001 11101 11001
Coriaceæ	11011 11111 11011
Angustifoliolæ	11111 11111 11011
Hispidæ	11111 ??111 110?1
Indigofera	00001 00101 11100

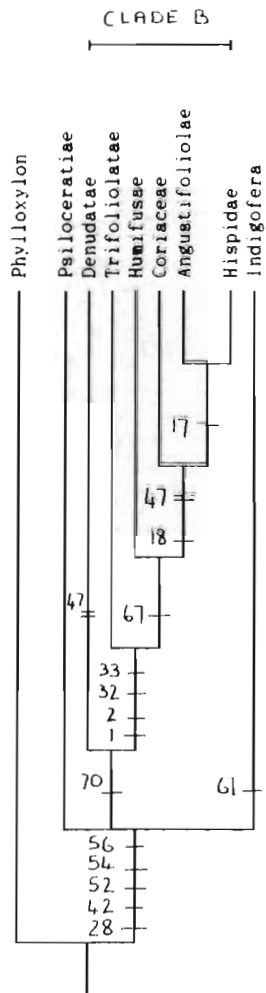


FIG. A.7: CLADISTIC ANALYSIS 6. RESOLUTION OF CLADES C & D; CLADE U CODED AS ONE TAXON; CLADE B REMOVED; 1 TREE.

Character list	Clade 6
1) BRACHYBLASTS: present = 0; absent = 1.	
2) ABAxIAL COMMISSURE (AT BASE OF PETIOLE): present = 0; absent = 1.	
13) PEARL BODIES (DENSELY AGGREGATED BETWEEN LEAFLETS): absent = 0; sometimes present = 1.	
32) INFLORESCENCES (INCLUDING PEDUNCLE, MORE THAN 2X LENGTH OF LEAVES): absent = 0; present = 1.	
34) PEDICELS (FRUITING LENGTH): 3 mm or shorter = 0; longer than 3 mm = 1.	
37) CALYX (LENGTH OF LOBES): shorter than 2x length of tube = 0; longer than 2x length of tube = 1.	
43) STANDARD (DORSAL SURFACE VESTITURE APPRESSED BROWN STRIGOSE): absent = 0; present = 1.	
45) STANDARD (CENTRAL BLOTCH MERGING BROADLY ALONG VEINS TO LAMINA): absent = 0; present = 1.	
51) KEEL (EXPOSURE OF UPPER PROXIMAL MARGIN ABOVE WINGS): exposed above = 0; not exposed above = 1.	
58) OVARY (LENGTH TO HORIZONTAL LENGTH OF PISTIL): longer than half = 0; about half or less = 1.	
61) PODS (SURFACE VESTITURE): absent (glabrous) = 0; present (hairy) = 1.	
72) SEEDS (PERSISTENT FUNICULAR REMAINS): absent = 0; sometimes present = 1.	

Clade 6: Taxa	Characters
	12133 34455 67 324 73518 12
Psiloceratae	00000 00000 00
Tinctoriae	00000 01110 10
Subulatae	00000 00110 10
Hedyanthae	11111 01000 11
Dendroides	11111 01000 11
Clade U	11000 10001 10

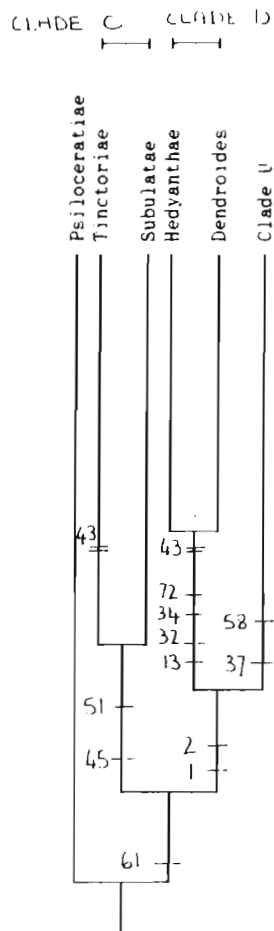
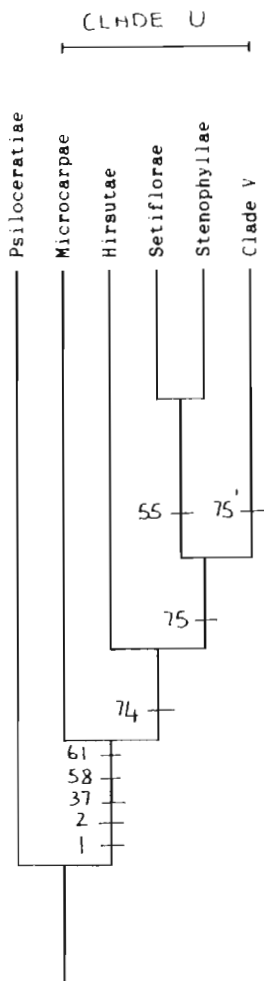


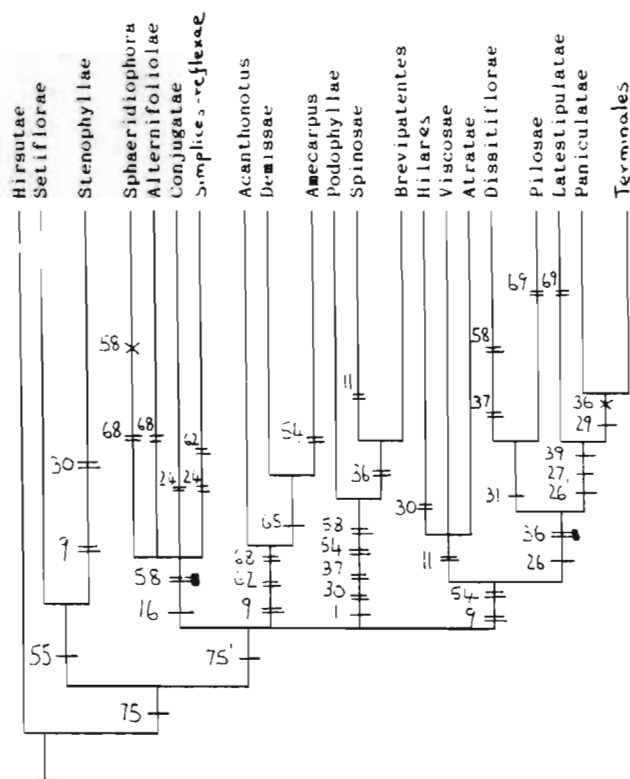
FIG. A.8: CLADISTIC ANALYSIS 7. RESOLUTION OF CLADE U; CLADE V CODED AS ONE TAXON; CLADES C & D REMOVED; 1 TREE.

Character list Clade 7	
1) BRACHYBLASTS: present = 0; absent = 1.	
2) ABAXIAL COMMISSURE (AT BASE OF PETIOLE): present = 0; absent = 1.	
37) CALYX (LENGTH OF LOBES): shorter than 2X length of tube = 0; longer than 2X length of tube = 1.	
55) ANthers (HAIRS SCATTERED OVER ANther SURFACE): absent = 0; present = 1.	
58) OVARY (LENGTH TO HORIZONTAL LENGTH OF PISTIL): longer than half = 0; about half or less = 1.	
61) PODS (SURFACE VESTITURE): absent (glabrous) = 0; present (hairy) = 1.	
74) SEEDS (COARSELY PITTED): absent = 0; present = 1.	
75) POLLEN (MORPHOLOGY TYPE): not types 3&4 = 0; type 3 = 1; type 4 = 2.	

Clade 7: Taxa	Characters
	12355 677 758 145
Psiloceratiae	00000 000
Hirsutae	11101 110
Microcarpae	11101 100
Setiflorae	11111 111
Stenophyllae	11111 111
Clade V	11101 112



Clade 8: Taxa	Characters				
	19112	22233	33355	56666	7
	164	67901	67945	82589	5
Hirsutae	00000	00000	00000	00000	0
Setiflorae	00000	00000	00001	00000	1
Stenophyllae	01000	00010	00001	00000	1
Simplices-reflexae	000?1	00000	00000	110?0	2
Conjugatae	00011	00000	00000	10000	2
Alternifoliolae	0001?	00000	00000	10010	2
Sphaeridiophora	00010	00000	000?0	00010	2
Acanthonotus	01000	00000	00000	01010	2
Demissae	01000	00000	00000	0?110	2
Ameecarpus	01000	00000	00010	01110	2
Pilosae	01000	10001	20010	00001	2
Dissitiflorae	01000	10001	11010	10000	2
Latestipulatae	01000	21000	20110	00001	2
Paniculatae	01000	21100	60110	00000	2
Terminales	01000	21100	00110	00000	2
Atratae	01100	00000	00010	00000	2
Viscosae	01100	00000	00010	00000	2
Hilares	01100	00010	000?0	00000	2
Spinosae	10100	00010	11010	10000	2
Brevipatentes	10000	00010	11010	10000	2
Podophyllae	10000	00010	01010	10000	2

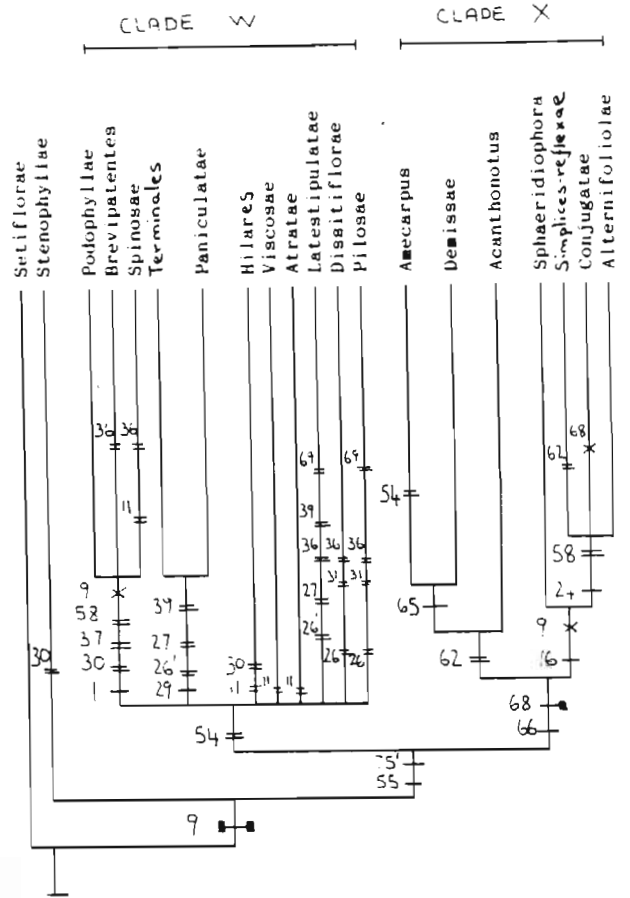


Character list Clade 8

- 1) BRACHYBLASTS: absent = 0; present = 1.
- 9) BIRAMOUS HAIRS (SIZE): hairs with arms of equal length more or less the same size on the lower leaf surface = 0; such hairs of markedly different sizes on the lower leaf surface = 1.
- 11) STALKED MULTICELLULAR GLAND-TIPPED HAIRS: absent = 0; present = 1.
- 16) LEAFLETS (POSITION): opposite = 0; alternate = 1.
- 24) STIPULES (DIMORPHIC): absent = 0; present = 1.
- 26) BRACTS (FOLIAR, GRADATION FROM LEAVES): absent = 0; sometimes present = 1; always present = 2.
- 27) BRACTS (TRILOBED): absent = 0; present = 1.
- 29) INFLORESCENCES (PANICULATE): absent = 0; present = 1.
- 30) INFLORESCENCES (SHORT, SUBTENED BY SHORT LEAVES, WITH ERECT TO SPREADING PODS): absent = 0; present = 1.
- 31) INFLORESCENCES (SLENDER PEDUNCULATE, FEW-FLOWERED, WITH ERECT PODS): absent = 0; present = 1.
- 36) CALYX (GLANDS ON LOBES): absent = 0; swollen-tipped = 1; capitate = 2.
- 37) CALYX (LENGTH OF LOBES): longer than 2X length of tube = 0; shorter than 2X length of tube = 1.
- 39) CALYX (SCARIOUS FRUITING LOBES): absent = 0; present = 1.
- 54) ANTHERS (HAIRS): present = 0; absent = 1.
- 55) ANTHERS (HAIRS SCATTERED OVER ANTHER SURFACE): absent = 0; present = 1.
- 58) OVARY (LENGTH TO HORIZONTAL LENGTH OF PISTIL): about a half or less = 0; longer than half = 1.
- 62) PODS (SURFACE VENATION PROMINENT): absent = 0; sometimes present = 1.
- 65) PODS (FLATTENED): absent = 0; present = 1.
- 68) ENDOCARP (TANNIN DEPOSITS): always extensive = 0; sometimes absent = 1.
- 69) ENDOCARP (TANNIN DEPOSITS IN DISTINCT STRIPES): absent = 0; present = 1.
- 75) POLLEN (MORPHOLOGY TYPE): not types 3&4 = 0; type 3 = 1; type 4 = 2.

FIG. A.9: CLADISTIC ANALYSIS 8. PARTIAL RESOLUTION OF CLADE U (MICROCARPAE EXCLUDED); 3 TREES.

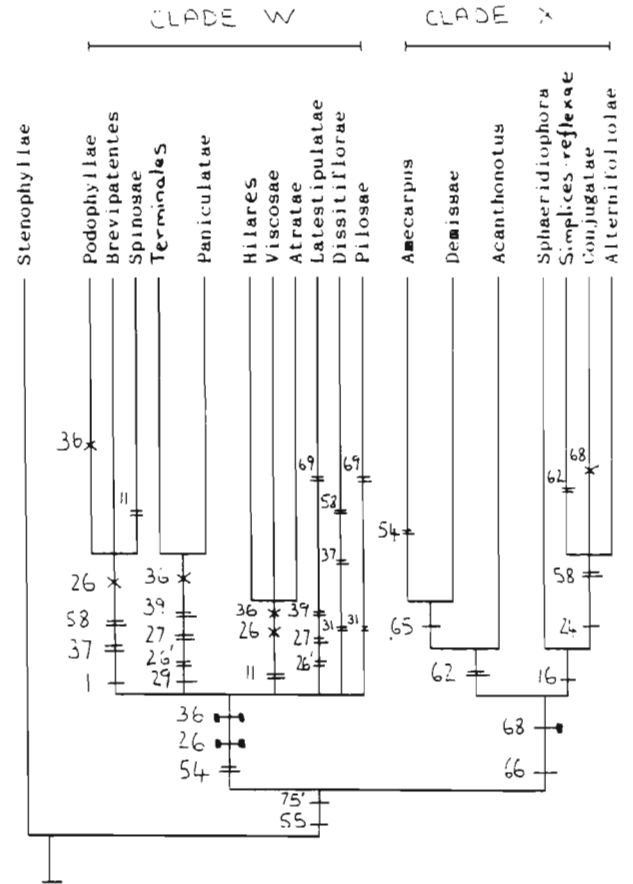
Clade 9: Taxa	Characters				
	19112	22233	33355	56666	67
	164	67901	67945	82568	95
Setiflorae	00000	00000	00001	00000	01
Stenophyllae	01000	00010	00001	00000	01
<i>Simplices-reflexae</i>	000?1	00000	00000	1101?	02
Conjugatae	00011	00000	00000	10010	02
Alternifoliolae	0001?	00000	00000	10011	02
Sphaeridiophora	00010	00000	000?0	000?1	02
Acanthonotus	01000	00000	00000	01011	02
Demissae	01000	00000	00000	0?111	02
Ameocarpus	01000	00000	00010	01111	02
Pilosae	01000	10001	20010	00000	12
Dissitiflorae	01000	10001	11010	10000	02
Latestipulatae	01000	21000	20110	00000	12
Paniculatae	01000	21100	00110	00000	02
Terminales	01000	21100	00110	00000	02
Atratae	01100	00000	00010	00000	02
Viscosae	01100	00000	00010	00000	02
Hilares	01100	00010	000?0	00000	02
Spinosae	10100	00010	11010	10000	02
Brevipatentes	10000	00010	11010	10000	02
Podophyllae	10000	00010	01010	10000	02



Character list Clade 9	
1)	BRACHYBLASTS: absent = 0; present = 1.
9)	BIRAMOUS HAIRS (SIZE): hairs with arms of equal length more or less the same size on the lower leaf surface = 0; such hairs of markedly different sizes on the lower leaf surface = 1.
11)	STALKED MULTICELLULAR GLAND-TIPPED HAIRS: absent = 0; present = 1.
16)	LEAFLETS (POSITION): opposite = 0; alternate = 1.
24)	STIPULES (DIMORPHIC): absent = 0; present = 1.
26)	BRACTS (FOLIAR, GRADATION FROM LEAVES): absent = 0; sometimes present = 1; always present = 2.
27)	BRACTS (TRILOBED): absent = 0; present = 1.
29)	INFLORESCENCES (PANICULATE): absent = 0; present = 1.
30)	INFLORESCENCES (SHORT, SUBTENDE BY SHORT LEAVES, WITH ERECT TO SPREADING PODS): absent = 0; present = 1.
31)	INFLORESCENCES (SLENDER PEDUNCULATE, FEW-FLOWERED, WITH ERECT PODS): absent = 0; present = 1.
36)	CALYX (GLANDS ON LOBES): absent = 0; swollen-tipped = 1; capitate = 2.
37)	CALYX (LENGTH OF LOBES): longer than 2X length of tube = 0; shorter than 2X length of tube.
39)	CALYX (SCARIOUS FRUITING LOBES): absent = 0; present = 1.
54)	ANTHERS (HAIRS): present = 0; absent = 1.
55)	ANTHERS (HAIRS SCATTERED OVER ANTHER SURFACE): absent = 0; present = 1.
58)	OVARY (LENGTH TO HORIZONTAL LENGTH OF PISTIL): about a half or less = 0; longer than half = 1.
62)	PODS (SURFACE VENATION PROMINENT): absent = 0; sometimes present = 1.
65)	PODS (FLATTENED): absent = 0; present = 1.
66)	PODS (REFLEXED): absent = 0; present = 1.
68)	ENDOCARP (TANNIN DEPOSITS): always extensive = 0; sometimes absent = 1.
69)	ENDOCARP (TANNIN DEPOSITS IN DISTINCT STRIPES): absent = 0; present = 1.
75)	POLLEN (MORPHOLOGY TYPE): not types 3&4 = 0; type 3 = 1; type 4 = 2.

FIG. A.10: CLADISTIC ANALYSIS 9. PARTIAL RESOLUTION OF CLADE U (WITH OUTGROUP SETIFLOAE); 26 TREES.

Clade 10: Taxa	Characters			
	11122	22333	35536	66667
	1646	79167	94582	56895
Stenophyllae	00000	00000	00100	00001
<i>Simplices-reflexae</i>	00?10	00000	00011	01?02
Conjugatae	00110	00000	00010	01002
Alternifoliolae	001?0	00000	00010	01102
Sphaeridiophora	00100	00000	0?000	0?102
Acanthonotus	00000	00000	00001	01102
Demissae	00000	00000	0000?	11102
Amecarpus	00000	00000	01001	11102
Pilosae	00001	00120	01000	00012
Dissitiflorae	00001	00111	01010	00002
Latestipulatae	00002	10020	11000	00012
Paniculatae	00002	11000	11000	00002
Terminales	00002	11000	11000	00002
Atratae	01000	00000	01000	00002
Viscosae	01000	00000	01000	00002
Hilares	01000	00000	0?000	00002
Spinosae	11000	00011	01010	00002
Brevipatentes	10000	00011	01010	00002
Podophyllae	10000	00001	01010	00002



Character list	Clade 10
1) BRACHYBLASTS: absent = 0; present = 1.	
11) STALKED MULTICELLULAR GLAND-TIPPED HAIRS: absent = 0; present = 1.	
16) LEAFLETS (POSITION): opposite = 0; alternate = 1.	
24) STIPULES (DIMORPHIC): absent = 0; present = 1.	
26) BRACTS (FOLIAR, GRADATION FROM LEAVES): absent = 0; sometimes present = 1; always present = 2.	
27) BRACTS (TRILOBED): absent = 0; present = 1.	
29) INFLORESCENCES (PANICULATE): absent = 0; present = 1.	
31) INFLORESCENCES (SLENDER PEDUNCULATE, FEW-FLOWERED, WITH ERECT PODS): absent = 0; present = 1.	
36) CALYX (GLANDS ON LOBES): absent = 0; swollen-tipped = 1; capitate = 2.	
37) CALYX (LENGTH OF LOBES): longer than 2X length of tube = 0; shorter than 2X length of tube = 1.	
39) CALYX (SCARIOUS FRUITING LOBES): absent = 0; present = 1.	
54) ANTHERS (HAIRS): present = 0; absent = 1.	
55) ANTHERS (HAIRS SCATTERED OVER ANTHER SURFACE): present = 0; absent = 1.	
58) OVARY (LENGTH TO HORIZONTAL LENGTH OF PISTIL): about a half or less = 0; longer than half = 1.	
62) PODS (SURFACE VENATION PROMINENT): absent = 0; sometimes present = 1.	
65) PODS (FLATTENED): absent = 0; present = 1.	
66) PODS (REFLEXED): absent = 0; present = 1.	
68) ENDOCARP (TANNIN DEPOSITS): always extensive = 0; sometimes absent = 1.	
69) ENDOCARP (TANNIN DEPOSITS IN DISTINCT STRIPES): present = 0; present = 1.	
75) POLLEN (MORPHOLOGY TYPE): not types 3&4 = 0; type 3 = 1; type 4 = 2.	

FIG. A.11: CLADISTIC ANALYSIS 10. PARTIAL RESOLUTION OF CLADE V; 14 TREES.

FIG. A.12: CLADISTIC ANALYSIS 11, RESOLUTION OF CLADE X; CLADE W CODED AS ONE TAXON; 1 TREE.

Character list Clade 11	
6)	BIRAMOUS HAIRS (ARM LENGTH): all more or less equal = 0; some markedly unequal = 1.
9)	BIRAMOUS HAIRS (SIZE): hairs with arms of equal length, of markedly different sizes on the lower leaf surface = 0; such hairs more or less the same size on the lower leaf surface = 1.
16)	LEAFLETS (POSITION): opposite = 0; alternate = 1.
24)	STIPULES (DIMORPHIC): absent = 0; present = 1.
58)	Ovary (LENGTH TO HORIZONTAL LENGTH OF PISTIL): about a half or less = 0; longer than half = 1.
62)	PODS (SURFACE VENATION PROMINENT): absent = 0; sometimes present = 1.
65)	PODS (FLATTENED): absent = 0; present = 1.
66)	PODS (REFLEXED): absent = 0; present = 1.
68)	ENDOCARP (TANNIN DEPOSITS): always extersive = 0; sometimes absent = 1.
75)	POLLEN (MORPHOLOGY TYPE): not types 3&4 = 0; type 3 = 1; type 4 = 2.

Clade 11: Taxa	Characters
	69125 66667 648 25685
Stenophyllae	00000 00001
Simplexes-reflexae	11?11 101?2
Conjugatae	01111 00102
Alternifoliolae	011?1 00112
Sphaeridiophora	11100 00?12
Acanthonotus	10000 10112
Demissae	00000 ?1112
Amecarpus	00000 11112
Clade W	10000 00002

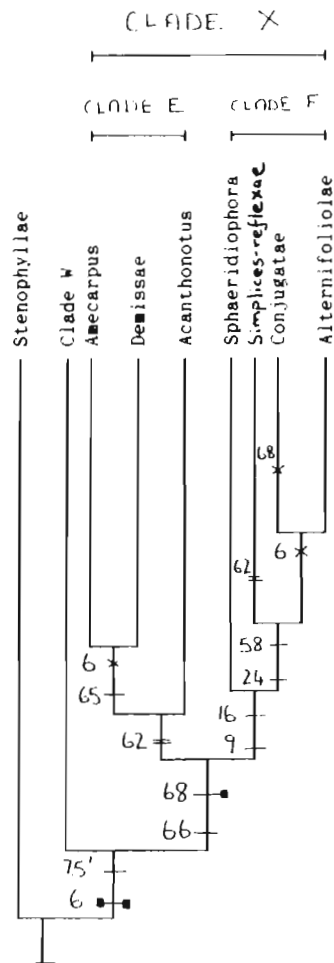


FIG. A.13: CLADISTIC ANALYSIS 12. PARTIAL RESOLUTION OF CLADE W; CLADE X
 CODED AS ONE TAXON; 8 TREES.

Character list Clade 12	
1) BRACHYBLASTS:	absent = 0; present = 1.
6) BIRAMOUS HAIRS (ARM LENGTH):	all more or less equal = 0; some markedly unequal = 1.
9) BIRAMOUS HAIRS (SIZE):	hairs with arms of equal length, of markedly different sizes on the lower leaf surface = 0; such hairs more or less the same size on the lower leaf surface = 1.
11) STALKED MULTICELLULAR GLAND-TIPPED HAIRS:	absent = 0; present = 1.
12) PEARL BODIES (DENSELY SCATTERED ON STEMS):	absent = 0; present = 1.
26) BRACTS (FOLIAR, GRADATION FROM LEAVES):	absent = 0; sometimes present = 1; always present = 2.
27) BRACTS (TRILOBED):	absent = 0; present = 1.
29) INFLORESCENCES (PANICULATE):	absent = 0; present = 1.
30) INFLORESCENCES (SHORT, SUBTENDED BY SHORT LEAVES, WITH ERECT TO SPREADING PODS):	present = 0; absent = 1.
31) INFLORESCENCES (SLENDER PEDUNCULATE, FEW-FLOWERED, WITH ERECT PODS):	absent = 0; present = 1.
36) CALYX (GLANDS ON LOBES):	absent = 0; swollen-tipped = 1; capitate = 2.
37) CALYX (LENGTH OF LOBES):	longer than 2X length of tube = 0; shorter than 2X length of tube.
39) CALYX (SCARIOUS FRUITING LOBES):	absent = 0; present = 1.
54) ANTHERS (HAIRS):	present = 0; absent = 1.
58) OVARY (LENGTH TO HORIZONTAL LENGTH OF PISTIL):	about a half or less = 0; longer than half = 1.
69) ENDOCARP (TANNIN DEPOSITS IN DISTINCT STRIPES):	absent = 0; present = 1.
75) POLLEN (MORPHOLOGY TYPE):	not types 3&4 = 0; type 3 = 1; type 4 = 2.

Clade 12: Taxa	Characters			
	16911	22233	33355	67
	12	67901	67948	95
Stenophyllae	00000	00000	00000	01
Pilosae	01001	10011	20010	12
Dissitiflorae	01001	10011	11011	02
Latestipulatae	01001	21010	20110	12
Paniculatae	0100?	21110	00110	02
Terminales	01001	21110	00110	02
Atratae	00010	00010	00010	02
Viscosae	00010	00010	00010	02
Hilares	00010	00000	000?0	02
Spinosae	10110	00000	11011	02
Brevipatentes	10100	00000	11011	02
Podophyllae	10100	00000	01011	02
Clade X	01001	00010	00000	02

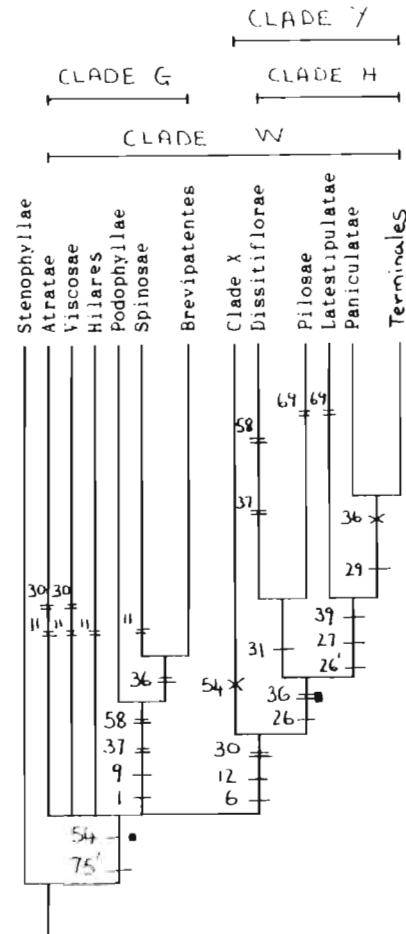


FIG. A.14: CLADISTIC ANALYSIS 13. RESOLUTION OF CLADE Y; CLADE G CODED AS ONE TAXON; 1 TREE.

Character list Clade 13	
6)	BIRAMOUS HAIRS (ARM LENGTH): all more or less equal = 0; some markedly unequal = 1.
9)	BIRAMOUS HAIRS (SIZE): hairs with arms of equal length, of markedly different sizes on the lower leaf surface = 0; such hairs more or less the same size on the lower leaf surface = 1.
12)	PEARL BODIES (DENSELY SCATTERED ON STEMS): absent = 0; present = 1.
16)	LEAFLETS (POSITION): opposite = 0; alternate = 1.
24)	STIPULES (DIMORPHIC): absent = 0; present = 1.
26)	BRACTS (FOLIAR, GRADATION FROM LEAVES): absent = 0; sometimes present = 1; always present = 2.
27)	BRACTS (TRILOBED): absent = 0; present = 1.
29)	INFLORESCENCES (PANICULATE): absent = 0; present = 1.
30)	INFLORESCENCES (SHORT, SUBTENED BY SHORT LEAVES, WITH ERECT TO SPREADING PODS): present = 0; absent = 1.
31)	INFLORESCENCES (SLENDER PEDUNCULATE, FEW-FLOWERED, WITH ERECT PODS): absent = 0; present = 1.
36)	CALYX (GLANDS ON LOBES): absent = 0; swollen-tipped = 1; capitate = 2.
39)	CALYX (SCARIOUS FRUITING LOBES): absent = 0; present = 1.
54)	ANTHERS (HAIRS): present = 0; absent = 1.
58)	Ovary (LENGTH TO HORIZONTAL LENGTH OF PISTIL): about a half or less = 0; longer than half = 1.
62)	PODS (SURFACE VENATION PROMINENT): absent = 0; sometimes present = 1.
65)	PODS (FLATTENED): absent = 0; present = 1.
66)	PODS (REFLEXED): absent = 0; present = 1.
68)	ENDOCARP (TANNIN DEPOSITS): always extensive = 0; sometimes absent = 1.
69)	ENDOCARP (TANNIN DEPOSITS IN DISTINCT STRIPES): absent = 0; present = 1.
75)	POLLEN (MORPHOLOGY TYPE): not types 3&4 = 0; type 3 = 1; type 4 = 2.

Clade 13: Taxa	Characters			
	69112	22233	33556	66667
	264	67901	69482	56895
Stenophyllae	00000	00000	00000	00001
Pilosae	10100	10011	20100	00012
Dissitiflorae	10100	10011	10110	00002
Latestipulatae	10100	21010	21100	00012
Paniculatae	10?00	21110	01100	00002
Terminales	10100	21110	01100	00002
Simplicis-reflexae	110?1	00010	00011	01?02
Conjugatae	01011	00010	00010	01002
Alternifoliolae	0101?	00010	00010	01102
Sphaeridiophora	11010	00010	00?00	0?102
Acanthonotus	10100	00010	00001	01102
Demissae	00000	00010	0000?	11102
Amecarpus	00000	00010	00101	11102
Clade G	00000	00000	00100	00002

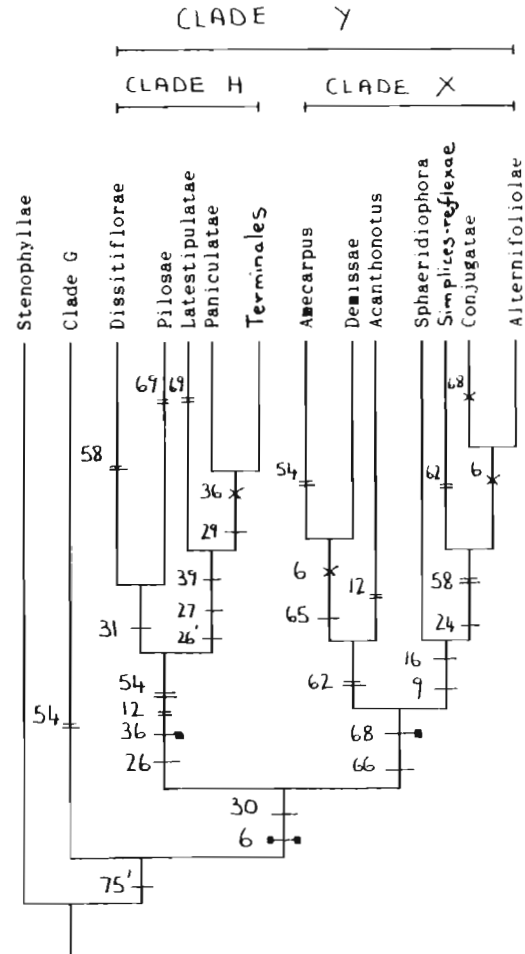


FIG. A.15: CLADISTIC ANALYSIS 14. RESOLUTION OF CLADE H; CLADES X & G CODED AS ONE TAXON; 1 TREE.

Character list Clade 14	
6)	BIRAMOUS HAIRS (ARM LENGTH): all more or less equal = 0; some markedly unequal = 1.
11)	STALKED MULTICELLULAR GLAND-TIPPED HAIRS: absent = 0; present = 1.
12)	PEARL BODIES (DENSELY SCATTERED ON STEMS): absent = 0; present = 1.
26)	BRACTS (FOLIAR, GRADATION FROM LEAVES): absent = 0; sometimes present = 1; always present = 2.
27)	BRACTS (TRILOBED): absent = 0; present = 1.
29)	INFLORESCENCES (PANICULATE): absent = 0; present = 1.
30)	INFLORESCENCES (SHORT, SUBTENDED BY SHORT LEAVES, WITH ERECT TO SPREADING PODS): present = 0; absent = 1.
31)	INFLORESCENCES (SLENDER PEDUNCULATE, FEW-FLOWERED, WITH ERECT PODS): absent = 0; present = 1.
36)	CALYX (GLANDS ON LOBES): absent = 0; swollen-tipped = 1; capitate = 2.
39)	CALYX (SCARIOUS FRUITING LOBES): absent = 0; present = 1.
54)	ANTHERS (HAIRS): present = 0; absent = 1.
69)	ENDOCARP (TANNIN DEPOSITS IN DISTINCT STRIPES): absent = 0; present = 1.
75)	POLLEN (MORPHOLOGY TYPE): not types 3&4 = 0; type 3 = 1; type 4 = 2.

Clade 14: Taxa	Characters
	61122 23333 567 1267 90169 495
Stenophyllae	00000 00000 001
Pilosae	10110 01120 112
Dissitiflorae	10110 01110 102
Latestipulatae	10121 01021 112
Paniculatae	10?21 11001 102
Terminales	10121 11001 102
Clade G	01000 00010 102
Clade X	10100 01000 002

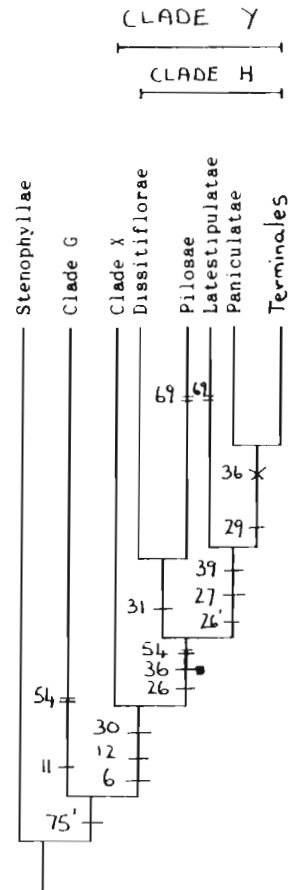


FIG. A.16: CLADISTIC ANALYSIS 15. RESOLUTION OF CLADE G; CLADE Y CODED AS ONE TAXON; 1 TREE.

Character list Clade 15	
1)	BRACHYBLASTS: absent = 0; present = 1.
6)	HIRAMOUS HAIRS (ARM LENGTH): all more or less equal = 0; some markedly unequal = 1.
9)	HIRAMOUS HAIRS (SIZE): hairs with arms of equal length, of markedly different sizes on the lower leaf surface = 0; such hairs more or less the same size on the lower leaf surface = 1.
11)	STALKED MULTICELLULAR GLAND-TIPPED HAIRS: absent = 0; present = 1.
12)	PEARL BODIES (DENSELY SCATTERED ON STEMS): absent = 0; present = 1.
30)	INFLORESCENCES (SHORT, SUBTENDED BY SHORT LEAVES, WITH ERECT TO SPREADING PODS): present = 0; absent = 1.
36)	CALYX (GLANDS ON LOBES): absent = 0; swollen-tipped = 1; capitate = 2.
37)	CALYX (LENGTH OF LOBES): longer than 2X length of tube = 0; shorter than 2X length of tube.
54)	ANTHERS (HAIRS): present = 0; absent = 1.
58)	OVARY (LENGTH TO HORIZONTAL LENGTH OF PISTIL): about a half or less = 0; longer than half = 1.
75)	POLLEN (MORPHOLOGY TYPE): not types 3&4 = 0; type 3 = 1; type 4 = 2.

Clade 15: Taxa	Characters
	16911 33355 7 12 06748 5
Stenophyllae	00000 00000 1
Atratae	00010 10010 2
Viscosae	00010 10010 2
Hilares	00010 000?0 2
Spinosae	10110 01111 2
Brevipatentes	10100 01111 2
Podophyllae	10100 00111 2
Clade Y	01001 10000 2

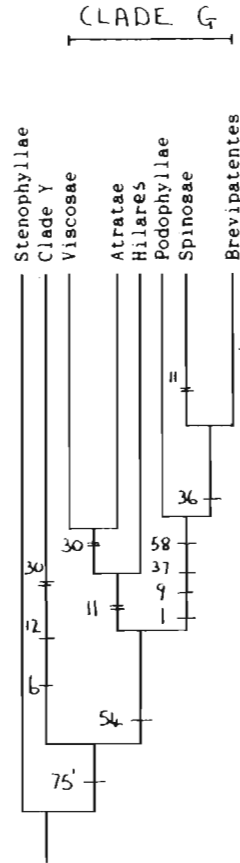
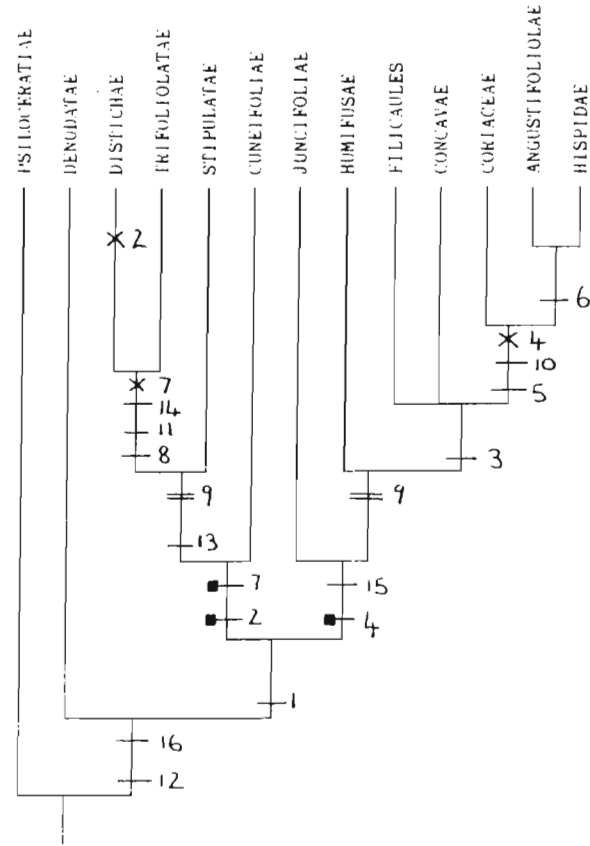


FIG. A.17: CLADISTIC ANALYSIS OF ALL CAPE SECTIONS OF INDIGOFERA: 1 TREE.

Character list (Cape Indigofera)	
1) ABAXIAL COMMISSURE (AT BASE OF PETIOLE):	present = 0; absent = 1.
2) LEAVES (TRIFOLIOLATE):	absent = 0; present = 1.
3) LEAVES (PREDOMINANTLY SUBSESSILE):	absent = 0; present = 1.
4) LEAFLETS (TENDING TO INVOLUTE MARGINS, SUBGLABROUS ABOVE):	absent = 0; present = 1.
5) LEAFLETS (CORIACEOUS, WITH REVOLUTE MARGINS):	absent = 0; present = 1.
6) LEAFLETS (SCLEROPHYLLOUS):	absent = 0; present = 1.
7) STIPULES (SHAPE):	subulate = 0; broadly ovate = 1.
8) CALCIUM OXYLATE CRYSTALS (IN LEAVES):	absent = 0; present = 1.
9) PEDUNCLE (MORE THAN 2X LENGTH OF SUBTENDING LEAVES):	absent = 0; present = 1.
10) FLOWERS (STAMINAL SHEATH LENGTH):	5 mm or longer = 0; less than 5 mm long = 1.
11) STANDARD (CENTRAL BLOTCH COLOUR IN CONTRAST TO REST OF LAMINA):	pale (hyaline) = 0; dark = 1.
12) KEEL (DARK COLOURED IN DISTAL REGION):	absent = 0; present = 1.
13) PODS (ORIENTATION):	more or less patent = 0; sharply reflexed = 1.
14) PODS (SURFACE VESTITURE):	glabrous = 0; hairy = 1.
15) PODS (DRYING BLUE-BLACK):	absent = 0; present = 1.
16) SEEDS (SHAPE):	subcylindrical = 0; spherical = 1.

Cape sections of Indigofera	
Taxa	Characters
	12345 67891 11111 1 0 12345 6
Psiloceratiae	00000 00000 00000 0
Denudatae	00000 00000 01000 1
Juncifoliae	10010 00000 01001 1
Humifusae	10010 00010 01001 1
Filicaules	10110 00010 01001 1
Concavae	10110 00020 01001 1
Cuneifoliae	11000 01000 01000 1
Stipulatae	11000 01010 11100 1
Trifoliolatae	11000 00110 11110 1
Distichae	10200 00120 11110 1
Coriaceae	10101 00011 01001 1
Angustifoliolae	10101 10011 01001 1
Hispidae	10101 10022 01021 1



CHAPTER 3

TAXONOMIC AFFINITIES

3.1. AFFINITIES WITH NEIGHBOURING TRIBES

Polhill (1981) considered the Indigofereae to be rather isolated in the subfamily. A number of suggestions have been made about affinities, i.e. the possibility of *Phylloxylon* being related to the Dalbergieae (Baker 1884; Taubert 1894; Hutchinson 1964); and the tribe in general to the Robinieae (Lavin pers. comm.), the Galegeae (de Kort & Thijssse 1984) and the Millettieae (Polhill 1981a).

The basal genus *Phylloxylon* is characterized by many plesiomorphic tribal characters (not present in the rest of the genera) as well as by highly specialized autapomorphies. Examples of the former include the habit (i.e. woody trees, which also occur in *Vaughania*); partially connate vexillary calyx lobes (separated by a broad sinus in the other genera); the presence of bracteoles (lost elsewhere); woody, few (1-2) seeded dehiscent pods (coriaceous many-seeded pods dehiscing by spirally twisting valves in the rest of the tribe); and large seeds, to more than 1 cm long occurring in a spongy endocarp (seeds rarely over 2mm long and separated by papery transverse septa in the other genera). Autapomorphies are the flattened phyllodinous stems, unique biramous hairs, ephemeral simple leaves and highly modified seedlings.

Relationships to other tribes, therefore, are likely to be seen most clearly in *Phylloxylon*.

Affinity with the Robinieae (Polhill & Sousa 1981; Lavin 1987) is considered unlikely because of the presence of the following: articulated pedicels, ebracteolate flowers, wings free from the keel, pods compartmentalized due to the adhesion of adjacent endocarp tissue, a well developed hypanthium, and an essentially

New World distribution with only the derived *Sesbania* group occurring in the Old World.

The Galegeae together with 5 other temperate tribes are marked by the presence of a rare chloroplast DNA structural mutation (Lavin & Doyle 1990). This has involved the loss of a large inverted repeat which is regarded as a derived feature of singular origin in the subfamily. The mutation was not found to occur in Indigofereae.

The Dalbergieae have a number of characters which make a close relationship with the Indigofereae improbable (Polhill 1981b). The presence of uniseriate medullary rays in wood; frequently alternate leaflets; unspecialized flowers with free, overlapping keel petals and a distinct hypanthium; indehiscent pods with specialized seed chambers containing 1 - few seeds invested in a hard endocarp; stamens often shortly and irregularly joined; various special features in the ovary (Polhill 1981b) and seeds not accumulating canavanine.

The *Lonchocarpus* group of the Millettieae, which was initially put in Dalbergieae by Bentham (1837), is somewhat transitional between the basal *Andira* group of Dalbergieae and the rest of Millettieae (Polhill 1981b). It was in the *Andira* group (near *Geoffroea*) that *Phylloxylon* was originally placed by Taubert (1894) and Hutchinson (1964).

The Indigofereae appear to be most closely allied to the Millettieae (Polhill 1981a; Geesink 1981, 1984) and perhaps more specifically to *Lonchocarpus*. The Millettieae are distinguished by pluriseriate medullary rays in the wood (also present in the *Andira* group of Dalbergieae); wing petals adhering to the keel by means of lateral folds or protuberances; ventrally connate keel petals; diadelphous or pseudo-monadelphous stamens; and predominantly dehiscent pods often with spirally twisting valves (except in *Lonchocarpus*).

The African *Lonchocarpus* section *Paniculati* is the least derived group in a broadly circumscribed genus (Geesink 1984) and the latter considers section *Paniculatae* (as a separate genus *Philenoptera* A.Rich.) to be rather central in the *Millettia* s.l., *Derris* s.l., *Lonchocarpus* s.l. complex.

In section *Paniculati* the flowers are single (not fascicled) in the axils of bracts, and are arranged in panicles (not pseudoracemes or pseudopanicles as in *Millettia*, *Derris* or the rest of *Lonchocarpus*). The panicle is considered primitive in the *Millettieae* (Geesink 1984), and since flowers are never fascicled in the *Indigoferaeae*, it appears likely that the simple raceme (so characteristic of the tribe) could have been derived from a non-fascicled inflorescence type.

Lonchocarpus cyanescens Benth. represents one species in this section known to produce commercially viable quantities of indigo, called West African or Yoruba Wild Indigo (Dalziel 1937). The presence of indigo (in the form of the glucoside indican) is also widespread in the basal groups (at least) of *Indigofera*. Kraemer (1914), however, also states that a similar principle to indican is found in *Baptisia tinctoria* (*Thermopsideae*), leaves of *Robinia pseudoacacia* (*Robinieae*) and in several species of *Psoralea* (*Psoraleeae*), and *Amorpha* and *Dalea* in the *Amorpheae*. The overall presence of indican in the subfamily, and the precise biochemistry of the various indigo compounds, needs to be examined more fully. The *Robinieae* are closely allied to the *Millettieae* (Polhill & Sousa 1981; Lavin 1987), and *Amorpheae* & *Psoraleeae* are advanced tropical tribes from the New and Old World, allied respectively to the *Robinieae* and *Millettieae* (Polhill 1981a). The *Thermopsideae* appear to have links with the base group of the subfamily, the tribe *Sophoreae*, although it is a derived temperate tribe of the Northern Hemisphere (Polhill 1981a).

Other features which are common to *Lonchocarpus* section *Paniculati* and *Indigoferaeae*, are the presence of stipels,

bracteolate flowers, partially connate vexillary calyx lobes, an intrastaminal disc and indistinct hypanthium, the standard without basal callosities, and seeds accumulating canavanine and other compounds. Section *Paniculati* stands apart from the rest of *Lonchocarpus* by the accumulation of canavanine and fairly low oxidative levels in flavonoids (Geesink 1981). Although the pods of *Lonchocarpus* are indehiscent, flat, and papery to coriaceous, *L. sericeus* in section *Lonchocarpus* has woody pods with a similar spongy endocarp to *Phylloxylon*.

Schefflerodendron, an isolated genus in Millettieae restricted to Africa, has an unusual combination of characters in the tribe. Much of the plant is covered with pearl bodies (apparently similar to those in Phaseoleae subtribe Cajaninae), and the genus has a vestiture of dark brown hairs, alternate leaflets, simple racemes, bracteoles, partially connate vexillary calyx lobes, staminal sheathes without basal fenestrae and dehiscent pods. The presence of dark brown hairs is plesiomorphic in the Indigofereae, and many of the above characters (except alternate leaflets) are found in *Phylloxylon* (where leaflets are simple). Pearl bodies occur universally in Indigofereae, and their presence in *Schefflerodendron* is rare for the Millettieae. Pearl bodies, apparently identical to those in Indigofereae, occur in the *Acosmium* and *Baphia* groups in the Sophoreae (Lewis & Stirton pers. comm.).

The Asian genus *Afgekia* in the Millettieae has tufts of hairs at each end of the anthers, a character which arises above *Phylloxylon* and defines, in part, most of the remaining genera in the Indigofereae.

The Indigofereae are also closely allied to the more advanced tropical tribes centred in the Old World, i.e. Phaseoleae, Psoraleae and Desmodieae (Polhill 1981a), but they all appear to be independently derived from the Millettieae.

The roots of *Phylloxylon* (and hence the Indigofereae) may therefore lie in the *Acosmium* or *Baphia* groups in Sophoreae that

radiated into the basal Millettieae allied to *Lonchocarpus* and *Schefflerodendron*. Putative outgroups for the tribe are *Lonchocarpus* section *Paniculati* and *Schefflerodendron*.

3.2. AFFINITIES IN INDIGOFERA

Several authors have attempted to subdivide *Indigofera* into subgenera, sections, series or "groups" (see Fig. 3.1).

The first four authors chronologically, made undesignated "groups" in the genus based principally on the number and arrangement of the leaflets. Wight & Arnott (1834) used a wider range of leaf, inflorescence, floral and fruit characters in their system.

Harvey (1862) was the first to recognize 2 subgenera in *Indigofera*, while Bentham (1865) and Baker (1871) divided the genus into 4 subgenera. Ovary and pod characters were used to define these higher order taxa while leaf characters still predominated for subgeneric "groups". Baker (1871) incorporated habit and inflorescence shape into the latter.

Taubert (1894) used similar subdivisions to Baker (1871) but he treated them as sections, series and subseries. Rydberg (1923) did not specify any infrageneric categories for his "groups", but *Ameecarpus* and *Indigastrum* were treated as synonyms of *Indigofera*. A wider range of morphological characters was used in these later systems.

Baker f. (1926), like Taubert (1894), treated the same four major subdivisions as sections, except that *Acanthonotus* was referred to *Echinatae* Wight & Arn.

Gillett (1958) produced a comprehensive infrageneric classification for the African species of *Indigofera* (see Fig. 3.2). He recognized 5 subgenera, *Acanthonotus*, *Ameecarpus*, *Indigofera*, *Indigastrum* (the latter two comprising the earlier *Euindigofera*), and *Microcharis*. The classification was based on the presence or

Willdenow (1802)	de Candolle (1825)	Wight & Arn. (1834)
foliis simplicibus foliis ternatis foliis quinatis foliis pinnatis	Simplicifoliae Oligophyllae Multijugae Brachypodae Digitatae	Echinatae Brachycarpae Monanthae Dissitiflorae Planisiliquae Laxiflorae Brachystachyae Tinctoriae Tetragonocarpae
E.Mey. (1836)	Harvey (1862)	Bentham (1865)
Unifoliatae Trifoliatae Digitatae Pinnatae-impari subsessili Pinnatae-impari petiolato Alternatim pinnatae	Subgenus Euindigofera group Juncifoliae Simplicifoliae Trifoliolatae Digitatae Pinnatae Unijugae Productae Alternifoliae Subgenus Amecarpus	Subgenus Acanthonotus Subgenus Sphaeridiophora Subgenus Euindigofera group Indigastrum Subgenus Amecarpus
Baker (1871)	Taub. (1894)	Bak.f (1926)
Subgenus Acanthonotus Subgenus Sphaeridiophora Subgenus Euindigofera group Simplicifoliae Conjugatae Capitatae Paniculatae Spinosae Trichopodae Sessiliflorae Dissitiflorae Stenophyllae Tinctoriae Subgenus Amecarpus	Section Acanthonotus Section Sphaeridiophora Section Euindigofera series Juncifoliae Simplicifoliae Conjugatae Trifoliolatae Digitatae Pinnatae subseries Spinosae Trichopodae Capitatae Sessiliflorae Dissitiflorae Stenophyllae Tinctoriae Paniculatae Section Amecarpus	Section Echinatae Section Sphaeridiophora group Eusphaeridiophora Terminales Capitatae Section Euindigofera group Juncifoliae Simplicifoliae Conjugatae Trifoliolatae Heterophyllae Spinosae Latestipulatae Opertiflorae Paniculatae Sessiliflorae Microcephalae Trichopodae Circinnatae Dissitiflorae Multijugae Alternifoliae Pinnatae Tinctoriae Stenophyllae Indigastrum Section Amecarpus
Rydberg (1923)		
Hirsutae *		
Viscosae *		
Parviflorae *		
Hendecaphyllae *		
Microcarpae *		
Lespedezoides		
Leptosepalae		
Mucronatae		
Thibaudianae		
Tinctoriae *		
Dispermae		
Platycarpae	* groups relevant to Africa	

Fig. 3.1. Schemes of various authors for infra-generic divisions in Indigofera.

Gillett (1958)	No. of species	Schrire (1991)	No. of species
Subgenus <i>Acanthonotus</i>	3	Section <i>Psiloceratiæ</i> *	21
<i>Amecarpus</i>		<i>Denudatæ</i>	8
Section <i>Amecarpus</i>	21	<i>Cuneifoliæ</i>	4
<i>Demissæ</i>	3	<i>Stipulatæ</i>	9
Subgenus <i>Indigofera</i>		<i>Trifoliolatae</i>	33
Section <i>Latestipulatæ</i>	11	<i>Distichæ</i>	5
<i>Paniculatæ</i>		<i>Juncifoliæ</i>	4
Subsect. <i>Paniculatæ</i>	18	<i>Humifusæ</i>	8
<i>Trichopodæ</i>	3	<i>Filicaulis</i>	4
Section <i>Indigofera</i>		<i>Concavæ</i>	3
Subsect. <i>Juncifoliæ</i>	1	<i>Coriaceæ</i>	8
<i>Brevierectæ</i>	15	<i>Angustifoliolæ</i>	14
<i>Anomalæ</i>	1	<i>Hispidæ</i>	7
<i>Dissitifloræ</i>	26	<i>Tinctoriæ</i> *	31
<i>Spinosæ</i>	4	<i>Subulatæ</i> *	13
<i>Brevipatentes</i>	7	<i>Hedyanthæ</i>	16
<i>Pilosæ</i>	8	<i>Dendroides</i>	15
<i>Viscosæ</i>	18	Subsect. <i>Foliosæ</i>	11
<i>Centrae</i>	12	Section <i>Hirsutæ</i>	5
<i>Atratae</i>	15	<i>Setifloræ</i>	24
<i>Psiloceratiæ</i>	11	<i>Stenophyllæ</i>	4
<i>Geanthæ</i>	2	<i>Brevierectæ</i>	4
<i>Tinctoriæ</i>	32	<i>Atratae</i>	11
<i>Hirsutæ</i>	4	<i>Viscosæ</i>	53
<i>Microcarpæ</i>	1	Subsect. <i>Centrae</i>	2
<i>Alternifoliolæ</i>	28	Section <i>Hilaris</i>	14
<i>Simplices-reflexæ</i>	4	<i>Spinosæ</i>	4
Subgenus <i>Indigastrum</i>	7	<i>Brevipatentes</i>	13
Subgenus <i>Microcharis</i>	23	<i>Podophyllæ</i>	1
		<i>Microcarpæ</i> *	1
Total <i>Indigofera</i>	278	<i>Pilosæ</i> *	13
Genus <i>Cyamopsis</i>	3	<i>Dissitifloræ</i> *	30
<i>Rhynchotropis</i>	2	<i>Laxeracemosæ</i>	6
		<i>Latestipulatæ</i>	13
Total <i>Indigoferæe</i>	283	<i>Paniculatæ</i>	16
		Subsect. <i>Trichopodæ</i>	3
		Section <i>Terminales</i>	2
		<i>Acanthonotus</i>	4
		<i>Amecarpus</i>	23
		<i>Demissæ</i>	3
		<i>Sphaeridiophora</i> *	9
		<i>Geanthæ</i>	6
		<i>Conjugatæ</i>	3
		<i>Alternifoliolæ</i> *	29
		subtotal <i>Indigofera</i>	510
		Genus <i>Microcharis</i>	26
		<i>Indigastrum</i>	11
		<i>Phylloxylon</i> [M]	5
		<i>Vaughania</i> [M]	12
		<i>Rhynchotropis</i>	2
		<i>Cyamopsis</i>	4
		Total <i>Indigoferæe</i>	570
* taxa with additional species occurring outside Africa (not including Madagascar [M])			

Fig. 3.2. The prior vs. newly proposed scheme of generic and infra-generic taxa of the *Indigoferæe* in Africa.

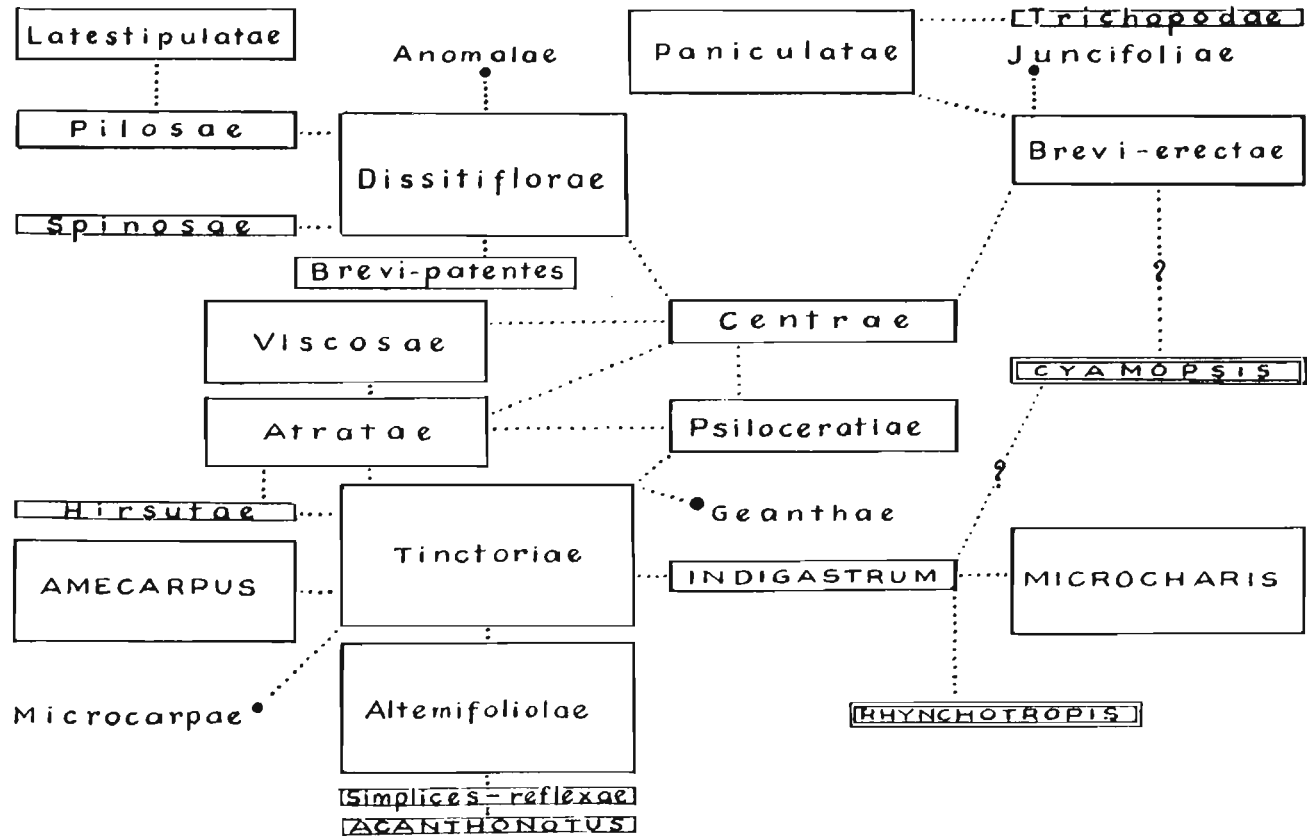
absence of an indumentum on the corolla, stamen morphology, glandulosity and the shape of the pod, and a wide range of other morphological characters. Gillett (1958) was also the first to present a diagram expressing proposed affinities of genera and infrageneric taxa in the Indigofereae (see Fig. 3.3).

Problems arising from Gillett's (1958) scheme:

- 1) The infrageneric categories are mostly artificial taxa of convenience (since the classification was principally designed for ease of use in the herbarium).
- 2) The southern African species of *Indigofera* were excluded.
- 3) The tribe Indigofereae was not examined as a whole (i.e., only *Indigofera* and closely related genera were included).
- 4) The classification was based on a relatively limited number of characters (since much more information is now available).
- 5) The diagram of affinities is not phylogenetically based.

3.2.1. New scheme of infrageneric taxa (see Fig. 3.2; taxa are described in chapter 7).

- 1) This is based on a cladistic analysis of the tribe (i.e., natural groups).
- 2) All African species of *Indigofera* and all genera in the tribe were examined.
- 3) The cladistic analysis was based on a wide range of characters including evidence from anatomy, pollen and chromosome numbers.
- 4) Relationships are indicated by a phylogentic tree based on the cladogram of the tribe (see chapter 6).



This chart is designed to express the affinities of the genera and infrageneric taxa dealt with here. It represents a cross section of an hypothetical phylogenetic 'tree'. The area devoted to each taxon is roughly proportional to the number of species involved.

FIG. 3.3 GENERIC AND INFRA-GENERIC RELATIONSHIPS IN THE INDIGOFERAEAE AFTER GILLETT (1958).

CHAPTER 4

MORPHOLOGY: DISCUSSION OF CHARACTERS

4.1 INTRODUCTION

The characters used in the cladistic analysis are grouped in broad categories (e.g. habit, inflorescences etc.), following the order in the character list (Table 2.2). The discussion is set in the context of relationships established in the cladogram, and takes into account other characters not used in the study. Many of those characters which do not fulfil the criteria of good cladistic characters were used in the analysis of adaptations and developmental constraints in chapter 5.

4.2 METHODS

Characters were assembled from all available sources. Some 570 African and Madagascan taxa in the Indigoferaceae were surveyed in the herbarium, field and in the literature, for suitable characters to use in the cladistic analysis.

Cladistic characters comprise hypotheses about polarity and homology (Linder 1988). They must be evaluated as multistate variables (binary, or with more mutually exclusive and ordered states), and they should include all homologous expressions of a feature found in the ingroup and outgroup (Pimental & Riggins 1987). Many other characters are homoplastic, too poorly known, or are phenotypically plastic.

Various methods were used to look for additional characters, or to examine others in greater detail.

4.2.1. Leaf clearing

Leaves of 82 southern African species of *Indigofera*, *Indigastrum* and *Microcharis* were cleared to test if trends in venation

patterns, tracheoid elements, calcium oxalate crystals and tannin ideoblasts yielded characters useful for the analysis at sectional level.

The methods of Klucking (1986), Lackey (1978) and Blackburn (1978) were adapted to provide reliable results with leaves of Indigofereae.

Leaves were placed in 5% NaOH for 1 to 24 hours depending on tannin content. They were then bleached and put in a saturated solution of chloral hydrate for 15 minutes to 3 hours until cleared. After going through a dehydration series to 95% alcohol, leaves were stained in 0.1M potassium permanganate for about 10 minutes. They were then removed to absolute alcohol for 4 to 5 minutes to slightly destain and to complete the dehydration series. Finally, leaves were floated in toluene and mounted on slides in Harleco coverbond. Cleared leaves were photographed with black and white film on a phase contrast light microscope.

4.2.2. *Surface-scanning Electron Microscopy (SEM).*

Samples representative of a number of characters in the tribe were taken from herbarium specimens and prepared for SEM. These included specimens of stems, leaves, calyces, petals, anthers, stigmas and pods. They were first reconstituted in boiling water and then taken through a dehydration series and dried by CO₂ in a Balzers Union critical point drier. Some 130 species had been collected in FAA preservative in the field, and samples from this material were placed directly into a dehydration series and treated as above.

Specimens were mounted on brass stubs on double sided adhesive tape, and coated with gold in a Polaron ES100 sputter coater. Samples were then studied with an ISI-SX-25 electron microscope at an accelerating voltage of 25 KV, and photographed on black and white Ilford FP4 120 roll film.

Other characters are illustrated in 5 plates of black and white line drawings.

4.3. MORPHOLOGY

4.3.1. *Habit*

The woody versus herbaceous habit in the tribe broadly agrees with the assumption that "woody equals primitive" in the subfamily (Polhill 1981a). Reversals to woodiness, however, have occurred in some highly derived groups, e.g. *Brevipatentes* - *Spinosaes* (which are often divaricately branching subshrubs of arid areas) and *Hispidae* (shrubs on nutrient poor substrates on Cape mountains).

Phylloxylon and *Vaughania* are mostly comprised of trees up to 20m in height. In *Indigofera* small trees, or shrubs with persistent above ground stems (phanerophytes), occur in *Psiloceratiae*, *Tinctoriae*, *Denudatae*, *Juncifoliae* and *Hispidae*, and with the exception of the latter, these are all the least derived sections in the genus.

The majority of species in *Indigofera* are suffrutescent perennials (chamaephytes) with new stems regenerating from a persistent woody rootstock. Further development to lignotubers occurs in some sections (e.g. *Hilares* and *Simplices-reflexae*), and the production of precocious flowering shoots (appearing before vegetative shoots) is found in *Rhynchotropis*, *Simplices-reflexae*, *I. scarceisii*, and other basal species in some advanced sections of *Indigofera*). The characteristic of "sprouting" (regeneration of stems from a woody rootstock) is plesiomorphic in the Cape taxa, and obligate "reseeders", which survive by post fire seed germination (Keeley 1977), are apomorphic.

The tribe is characterized by astragaloid root nodules (Corby 1981) which are large and frequently branched, and this type is plesiomorphic in the subfamily. Roots have a tetrarch structure (Compton 1912).

The annual habit occurs in many of the advanced taxa in tropical Africa (e.g. *Microcharis*, *Indigostrum*, *Cyamopsis*), and in the following sections of *Indigofera*:— *Paniculatae*, *Terminales*, *Ameocarpus*, *Hirsutae*, *Stenophyllae*, *Dissitiflorae*, *Viscosae* and *Sphaeridiophora*. Very few annuals appear in southern Africa, other than widespread tropical weedy species, and annuals are almost absent from the Cape region.

4.3.2. Stems

Rhizomes are found in a number of Cape sections e.g. *Juncifoliae*, *Humifusae* and *Trifoliolatae*, and in the latter a characteristic habit is to clamber through other vegetation, and flower above the canopy.

- 1) Brachyblasts (or short shoots) are distinguished by short internodes, imbricate stipules or sub-fasciculate leaves. They occur in the least derived elements of the tribe (e.g. *Phylloxylon*, *Vaughania*, and in *Psiloceratiae*, *Tinctoriae* - *Subulatae*, and *Denudatae* in *Indigofera*). The loss of brachyblasts is apomorphic with a reversal appearing in the derived *Spinosa* - *Brevipatentes* group.

- 2) An abaxial commissure at the base of the petiole is a line of demarcation between the stipules and the foliar pulvinus (Plate 4.1, fig. 1a.) The commissure has the appearance of a ledge on which the pulvinus is perched, and the stipules are attached below, to the stem. This character was noted by Polhill (1981c) as also occurring in shrubby elements in the Galegeae, and it is found only in the basal taxa of the Indigoferaceae: *Phylloxylon*, *Vaughania*, *Psiloceratiae*, *Tinctoriae* - *Subulatae* and *Denudatae*. The apomorphic condition is the absence of the commissure (Plate 4.1, fig. 1b), with the stipules being partially adnate to the base of the petiole. The loss of the commissure is irreversible, even when woodiness is secondarily derived, and it characterizes the development of the herbaceous habit.

3) Cladodes are an autapomorphy in *Phylloxylon*.

4 & 5) In the Cape section *Denudatae*, the development of spines from branch tips is an autapomorphy. Spines arise convergently in arid areas, from inflorescence rhachides in isolated species of sections *Ametarpus*, *Subulatae*, *Alternifoliolae* and *Trifoliolatae*. They characterize all species of section *Spinosa*. In Australian species, spinescence is predominantly seen in spinescent stipules, and one species has a spinescent leaf rhachis arising from modified terminal stipellae (Wilson pers. comm.).

4.3.3. *Trichomes and Pearl bodies*

The large diversity of trichomes in the tribe is discussed with reference to Solereder (1908), Theobald et al. (1979), and particularly to Vijay Kumar (1988) which contain illustrations of the following trichome types. Various ecological aspects of hairs are considered by Johnson (1975).

- a) **Uniseriate macroform biramous hairs with q equal arms.** The hairs are three celled, with a basal, stalk and biramous head cell. The encircling epidermal cells are radially arranged and are often much elongated.
 - i) T - shaped head cell with arms short to long; these are the most widespread type of trichomes, giving the characteristic strigose or silky vestiture in taxa (Plate 4.2, fig. d; Plate 4.3, fig. c).
 - ii) U - shaped head cell; common on pods in *Acanthonotus* and *Microcarpae* (Plate 4.4, fig. b).

T - shaped biramous hairs are found densely, and perpendicularly, arranged on the leaf margins in *Pilosae* and *Acanthonotus* (Plate 4.2, fig. g). Biramous hairs are caducous in many taxa, and they can be an irritant as they easily pierce the skin. These sharp rigid hairs may therefore also be a deterrent to herbivores.

Trichome orientation, whether parallel or at an angle to the midrib, appears to be a useful character at species level.

The development of biramous hairs on a young ovary is seen in Plate 4.6 (fig. b).

- b) **Uniseriate macroform biramous hairs with arms unequal**, the shorter arm less than half the longer one (Plate 4.3, fig. e). These have been called "plough-shaped" hairs by Vijay-Kumar & Ramayya (1987).
- 6) Trichomes with arms of unequal length occur occasionally in *Psiloceratiae* and *Tinctoriae* and are predominant in *Hirsutae* and many other taxa. Their presence represents a synapomorphy in the derived herbaceous sections, and accounts for the characteristic hirsute vestiture in many taxa.
- c) **Uniseriate macroform uniramous (conical) hairs**. These have a foot cell and from one to many body cells (Vijay Kumar 1988), are either straight or curved, and often taper above. Such uniramous trichomes have been noted in *Hirsutae* (Plate 4.2, figs. a & b). Vijay Kumar (1988) records them occurring in a number of Indian species.
- d) **Uniseriate cylindrical-clavate hairs** appear to be the common trichome on the stigmas of many taxa (Plate 4.5, figs. f & g).
- e) **Unicellular conical or cylindrical hairs** are found on the wing petals and anthers of many taxa (Plate 4.6, fig. a).
- 7) Many of the less derived taxa in the tribe have mixed brown (or black) and hyaline biramous hairs (type a), e.g. in *Phylloxylon*, *Vaughania*, *Psiloceratiae*, *Tinctoriae*, *Hedyanthae - Dendroides*, *Hirsutae*, *Setiflorae*, *Stenophyllae*, *Pilosae*, *Atratae* and *Paniculatae*. The significance of the character is obscure and it is unlikely to be homologous in all these taxa.

f) Epidermal "chimney-like" basal projections with apical biramous hairs (Plate 4.4, figs. c & d).

- 8) The presence of a prominent epidermal projection with an apical biramous hair is an autapomorphy in the derived Cape *Hispidae*. This is believed to be an adaptation enhancing water uptake from runoff or mist (Marloth 1903; 1910; and see chapter 5).

The vestiture of biramous hairs appears to have a multifunctional role in the tribe.

Fahn (1986) discusses the roles postulated for trichomes; e.g. they may affect transpiration by influencing the water diffusion boundary of the transpiring leaf surface; they appear to influence water economy through temperature regulation, reducing the absorption of radiant energy, and enhancing energy dissipation by the high reflectance properties of trichomes; and it is also suggested that trichomes are able to absorb water from the external environment. Alvin (1987) records a possible one-way valve allowing water into, but preventing it escaping from trichomes in *Androstachys johnsonii* (Androstachyaceae). Lysheide (1977) discusses a similar mechanism operating in biramous hairs of *Spartocytisus filipes* (Genistiae). The hairs are 3 cellular (as in Indigoferaeae), with the intermediate stalk cell surrounded by heavily cutinized cell walls. The boundary between the stalk and basal cell has fine microchannels, while that between the stalk and T-shaped head cell, is characterized by a structure of parallel cellulose microfibrils. The swelling of the hydrated wall between the head and stalk cells opens channels for water to move into the leaf, but when dehydrated, the wall collapses and water is prevented from going back into the head cell.

A similar structure of parallel microfibrils occurs in the biramous hairs of *Indigofera* (Plate 4.9, fig. f). This, together with the evidence of stalked biramous hairs appearing to enhance moisture uptake in the *Hispidae*, supports the hypothesis that biramous hairs are involved in water uptake in the tribe.

- 9) A synapomorphy in *Indigofera* is the presence of T - shaped, equal armed, biramous hairs occurring in markedly different sizes on the lower leaf surfaces (Plate 4.3, fig. c). This character may be involved with an aspect of water relations in the herbaceous sections of the genus.
- g) **Uniseriate glandular bulbous-based trichomes** have been noted in the *Setiflorae* and *Brevierectae* (Plate 4.4, figs. e & f). Almost identical trichomes were identified by Lackey (1979) in the tribe Phaseolae subtribe Cajaninae. Under SEM some of these trichomes in the *Setiflorae* show a vestigial arm at the base, and they may be modified biramous hairs.
- 10) Discoid glands on the lower leaflet surfaces were considered autapomorphic in *Microcarpae* (Plate 4.2, fig. c). They are discussed in the next section as a type of pearl body.
- h) **Multiseriate glandular capitate trichomes**, with a multicelled stalk and head (Plate 4.7, figs. a to f).
- 11) Stalked, gland-tipped, trichomes occur in *Atratae*, *Viscosae*, *Hilares* and *Spinosae*, and in many taxa they produce a sticky exudate with a strong odour. Their presence is very variable in some species, being dense in some individuals and almost absent in others. The trichomes and exudate may deter predators both physically and chemically.
- i) An unusual type of biramous hair is found on juvenile growth in some species of *Phylloxylon*, and this requires further investigation. Hairs are flattened and crinkled like cellophane strips.

Pearl bodies are single or multicelled emergences characterized by a lustrous, pearl-like appearance; a spherical or club-like shape with a basal constriction; ease of detachment from the

plant; and storage of relatively large quantities of lipid (O'Dowd 1982).

They are ubiquitous in the tribe being very variable morphologically. The author has observed aggressive ants patrolling on a number of species of *Indigofera*, and has seen the pearl bodies being harvested (presumably as ant food). This appears to be another example of reciprocal specialization in plant-ant interactions which is widespread in the Leguminosae (Janzen 1981; McKey 1989).

j) Biseriate to multiseriate clavate or cylindrical pearl bodies (O'Dowd 1982; Vijay Kumar & Ramayya 1986).

This is the common type, varying from small and clavate (with the stalk hardly visible) in *Acanthonotus* and *Sphaeridiophora* (Plate 4.8, figs. a & b); to cylindrical in *Terminales* (Plate 4.8, fig. f); broad and squat in *Laxeracemosae* (Plate 4.8, fig. e); and clearly stalked with multicellular heads in *Dendroides* (Plate 4.6, figs. f & g).

A unique development occurs in one species in *Sphaeridiophora*, where clavate pearl bodies are enclosed within a protective outer covering (Plate 4.8, figs. c & d). The species is found in arid areas.

k) Multicellular hollow-discoid pearl bodies (Vijay Kumar *et al.*, 1986), which are sessile, spherical to ovoid or disc-like and have a central cavity enclosed by a single layer of cells (Plate 4.4, fig. b; Plate 4.7, fig. h).

The discoid "glands" in character 10 of the cladistic study belong here. They are often scattered over much of the plant but are most obvious on the lower leaflet surfaces which are densely punctate-glandular. These occur in *Microcarpae* and a number of Indian species with an affinity to section *Sphaeridiophora*, e.g. *I. barberi*, *I. glandulosa*, *I. trifoliata* and *I. vestita* (Vijay Kumar 1988).

- 12) A synapomorphy in the herbaceous sections of *Indigofera*, is the significant increase in density of pearl bodies. They are scattered relatively densely over most of the plant surface (Plate 4.2, fig. a), whereas in the plesiomorphic condition they are isolated at the base of the petiole and between the leaflets.
- 13) In some sections pearl bodies have become densely aggregated in "cushion-like" clumps at the base of the petiole and between the leaflets (Plate 4.6, fig. g). This character has arisen convergently in *Setiflorae*, *Laxeracemosae* and *Hedyanthae - Dendroides*, and is an example of a character which has proved to be homoplastic at a broad level of universality, but a synapomorphy in the latter two sections.

4.3.4. Leaves

Leaves are always alternate in the tribe, and in *Indigofera*, *Indigastrum* and *Microcharis* they are imparipinnately many to few foliolate with widespread reductions to unifoliolate or simple leaves. Digitate, or predominantly trifoliolate, leaves occur in some Cape sections of *Indigofera*. Gillett (1958) notes that it seems better to use the terms "simple" and "unifoliolate" loosely as equivalents, and not in any exact sense when applied in the tribe. Leaflets are apparently simple in many species, and even in those which sometimes produce compound leaves, the simple leaves show no sign of being unifoliolate.

Leaves are simple in *Phylloxylon* (being mostly short-lived on phyllodinous stems), *Rhynchotropis*, and a number of species of *Vaughania*.

- 14) In *Vaughania*, phyllodinous petioles are autapomorphic in the genus (Plate 4.13, fig. 2a).

Indigofera amnoxylum, from the Mascarenes, also has unifoliolate phyllodinous leaves, and is an unusual species in *Psiloceratiae*,

previously placed in the monotypic genus *Bremontiera*. The occurrence of phyllodes is an interesting convergent feature in the Madagascar - Mascarenes region, and it arises in many different genera from widely divergent families (Polhill pers. comm.).

- 15) An autapomorphy in *Cyamopsis* is the presence in some species, of leaflets with dentate margins. Leaflets in the rest of the tribe all have entire margins.
- 16) In pinnate leaves, opposite leaflets are plesiomorphic, occurring widely in *Indigofera*, *Indigastrum*, *Microcharis* and *Cyamopsis*. An alternate arrangement of leaflets is a synapomorphy linking sections *Sphaeridiophora*, *Conjugatae* and *Alternifoliolae*.
- 17 & 18) The leaf morphology of the Cape sections *Coriaceae*, *Angustifoliolae* and *Hispidae* appears to have become specialized to cope with environments on nutrient poor substrates. Leaflets are coriaceous, with a unique upper surface structure (discussed below), and the margins are revolute (Plate 4.3, fig. f). In the latter two sections true sclerophylly is found with the development of narrow ericoid-type leaflets, which are densely hairy or grooved below between the margins and prominent midrib (Plate 4.1, fig. 2). The above three sections also have sessile to subsessile leaves clustered around the stems, and they are often few-foliolate on short leaf rachides.
- 19) Another possible response to the stresses associated with nutrient poor substrates may be the development of leaflets with involute margins which can be rolled up (Plate 4.1, fig 3). This character occurs to some extent in *Juncifoliae* and *Humifusae*, and markedly in *Concavae* and *Filicaules*. The leaflets are often slightly fleshy, and subglabrous above.
- 20) Leaf venation is discussed below in a more detailed analysis of leaflet anatomy.

Leaves in certain species of *Indigofera* have become highly modified. Peltate leaves are found in one precociously flowering species in East Africa (Plate 4.1, fig. 9). In *Juncifoliae* leaflets are confined to the young growth, otherwise they are reduced to scales (Plate 4.1, figs. 7 a & b), or are absent, with only the leaf rhachides persistent. In *Anomalae* the leaflets are slightly fleshy with a prominent translucent venation and a winged rhachis.

- 21) Long petioles with a distant terminal leaflet are autapomorphic in *Podophyllae*. The petiole is persistent after the leaflet drops.
- 22) The development of cartilagenous leaflet margins is an autapomorphy in *Acanthonotus*.

4.3.5. Venation

Leaf venation is predominantly campto-brochidodromous in the tribe (Freire de Carvalho & Valente 1973; Hickey 1979), but a distinct rim vein and craspedodromous venation are found in some species of *Pilosae*.

In sections *Hilares* and *Brevipatentes*, and in some species of *Viscosae* and *Latetipulatae*, the secondary veins appear to have a more acute angle of divergence from the midrib than elsewhere in the tribe (Plate 4.10, fig. a compared with b). In these sections the secondary, tertiary and some quaternary veins are also characterized by thick fibrous bundle sheaths containing many prismatic crystals (Plate 4.11, figs. b, c & e). Thick bundle sheaths (without crystals) also occur in some Cape sections of *Indigofera* and in *Microcharis*.

Areoles (or the smallest subdivisions of the mesophyll) are bounded predominantly by fifth order veins (Esau 1965; Mauseth 1988). These minor veins provide an extensive surface area in the leaf, and the ultimate branches (bundles or vein endings) usually terminate blindly in the areole. The latter contain primary xylem

in the form of annularly or spirally thickened tracheids (Mauseth 1988). The length of these ultimate veins, their degree of branching, and whether they end blindly or are continuous from one margin of the areole to the other, appear to be good characters at the species level.

In veins that end blindly, the last several tracheids are often unusual (Esau 1965), being large and irregularly shaped, and apparently used for storing water rather than distributing it (Foster 1956; Mauseth 1988). Since they differ morphologically from neighbouring tracheids (Foster 1956), and can also be found free of the veins (on the walls of the areole), they are called tracheoid idioblasts (Solereeder 1908; Metcalfe & Chalk 1950).

The free veinlet endings may correspond to conventional tracheids, being simple, undilated or tapering and devoid of tracheoids (Freire de Carvalho & Valente 1973).

Terminal tracheoid idioblasts resemble tracheary elements, but are distinct in size and shape and appear at the veinlet endings in singles, pairs or loose clusters (Rao & Bhattacharya 1981). Two types of tracheoid idioblast are common in the tribe.

a) *Brachytracheoids* are usually spheroidal, ovoid, globoid or ellipsoidal (Rao & Das 1979), and are either attached to the walls of the areola (Plate 4.10, fig. g) or are terminal to vein endings (Plate 4.9, figs. a, b & e; Plate 4.10, figs. f & g). They have differential wall thicknesses in the form of annulae or helices.

The location of tracheoids, whether associated with the vein endings or along the walls of the areole, is a useful character at species level. In xeromorphic leaves water storage tracheoids appear to be more common (Mauseth 1988).

b) *Sclerotracheoids* are ideoblasts resembling brachytracheoids in their spirally thickened walls (Plate 4.10, figs. f & g), but they differ in possessing thick sclerosed cell walls and are

relatively larger (Rao & Das 1979). These occur particularly along leaf margins and are terminal or free. The concentration of sclerotracheoids at the leaf margins of some taxa may also be a deterrent to herbivores.

No sclereids were identified in cleared leaves of the tribe (Rao & Bhupal 1973).

The actual conducting elements of xylem and phloem always have a bundle sheath of tight fitting parenchyma cells (Mauseth 1988).

Two strategies regarding water transfer and storage capabilities in leaves may be operating in the tribe, and this is reflected in the extent of bundle sheath development.

In some taxa (e.g. *Psiloceratiae* and *Denudatae*) tracheoids may be absent, the terminal veinlet has minimal branching, and the latter is completely surrounded by a bundle sheath (Plate 4.10, fig. e). More commonly one to several tracheoids occur, veinlets branch more freely and a bundle sheath is lacking (Plate 4.9, figs. b & e). Esau (1965) noted a correlation between increasing complexity of minor venation and a decreasing density of veins with bundle sheaths, i.e. the smaller the distance from vein to vein, the greater the distance between bundle sheaths.

The sclerophyllous leaves in *Hispidae* and *Angustifoliolae* have unique, elongated, thin-walled, tracheoid idioblasts densely arranged along the areole margins (Plate 4.10, fig. d).

4.3.6. *Calcium oxalate crystals and tannin idioblasts*

The presence of crystals in the Leguminosae has been reviewed by Zindler Frank (1987).

Two major types of crystals have been seen in Indigoferaeae:

- a) Twin, rod-shaped, prismatic crystals most commonly associated with the veins (Plate 4.11, figs. b, c & e), but also densely

located along the leaf margins in some *Viscosae* (Plate 4.11, fig. f), and in the radial cells surrounding the base of biramous hairs in *Subulatae* and *Distichae* (Plate 4.11, fig. a).

b) Crystal sand in the mesophyll (Plate 4.11, fig. d).

Little is known about the function of calcium oxalate crystals (Zindlar Frank 1987), but it seems from the position of some that they may be associated with anti-herbivory.

Tannin idioblasts (Foster 1956) are large spherical inclusions interspersed with smaller mesophyll cells in the leaves of many of the less derived sections of *Indigofera* (Plate 4.9, fig. c). They were observed in partially cleared leaves to be filled with tannin. Taxa without these inclusions are characterized by an even mesophyll with cells all more or less the same size (Plate 4.9, fig. d).

Table 4.1 shows the distribution of crystals and tannin idioblasts in the more advanced genera in the tribe.

Those taxa recorded as positive for both inclusions usually have one or the other in their respective species. It appears that very few of the latter possess both tannin idioblasts and crystals in the leaves.

4.3.7. *Stomata and epidermal morphology*

Leaves in *Indigoferaeae* are predominantly amphistomatic (Leelavathi *et al.* 1980) although occasionally the density of stomata on either surface may be very low. Stomata are also frequently sunken (Plate 4.3, fig. d).

It appears that the plesiomorphic state is an aogenous anomocytic stomatal arrangement (Vijay Kumar & Ramayya 1987; Karetala *et al.* 1990), and is found in *Tinctoriae*, *Dendroides* and *Alternifoliolae*. This type is characterized by the guard cells

Taxon	Tannins	Crystals
Microcharis	-	-
Indigastrum	-	+
Psiloceratiaceae	+	±
Denudatae	+	-
Trifoliolatae	+	±
Humifusae	+	-
Coriaceae	+	-
Angustifoliolae	+	-
Hispidae	+	-
Tinctoriae	+	-
Subulatae	-	+
Hedyanthae	+	±
Dendroides	-	-
Hirsutae	+	-
Setiflorae	+	-
Microcarpae	+	-
Hilares	-	+
Viscosae	-	+
Brevipatentes	-	+
Laxeracemosae	+	-
Latestipulatae	-	+
Acanthonotus	+	-
Amecarpus	-	+
Sphaeridiophora	-	+
Alternifoliolae	-	+

Table 4.1: Taxa investigated for the presence of tannin idioblasts and calcium oxalate crystals.

+ = presence, - = absence, ± = present in isolated cases

being surrounded by more than three subsidiary cells (Plate 4.3, fig. g) which are indistinguishable from other epidermal cells (Wilkinson 1979).

A number of more derived sections including *Acanthonotus*, and various Indian species, have a hemimesogenous anisocytic stomatal arrangement (Karetala et al. 1990). Guard cells are surrounded by 3 subsidiary cells (Plate 4.2, fig. h; Plate 4.3, fig. h), one of which is distinctly smaller than the others. A small percentage of stomata, in either of these predominant types, is paracytic or tetracytic (Vijay Kumar & Ramayya 1987).

Other useful epidermal features requiring investigation in a wide range of taxa are:

- a) an apapillate versus papillate epidermis, and whether papillae are present on one or both surfaces. The apapillate condition appears to be plesiomorphic, occurring in *Tinctoriae*, *Hirsutae* and *Sphaeridiophora* (Plate 4.3, figs. e & g). Papillae are common in *Viscosae* (Plate 4.3, fig. d).
- b) the shape of the anticlinal walls of epidermal cells which are either U-shaped or V-shaped wavy sinuate (e.g. in *Tinctoriae* and *Hirsutae*, Plate 4.2, fig. b) or more or less straight to curved (e.g. in *Sphaeridiophora*).
- c) the foliar costal cell pattern; regarding shape, surface, nature of anticlinal walls, their unifacial and bifacial distribution patterns, orientation and arrangement (Vijay Kumar & Ramayya 1987; Vijay Kumar 1988a).

An unusual upper leaflet morphology is found in the Cape sections *Coriaceae*, *Angustifoliolae* and *Hispidae*. The surface is smooth and shiny with no evidence of anticlinal walls, and trichomes are sunken in channels on the surface (Plate 4.3, fig. f - top left).

4.3.8. *Hydathodes*

Passive hydathodes without an epithem (Wilkinson 1979; Mauseth 1988) appear to be prevalent at vein terminations in leaf apices of most species in the tribe. Hydathodes are indicated by dense accumulations of tracheoid idioblasts in the region of the leaf apex (Plate 4.10, fig. i), particularly in the mucron (A.E. van Wyk pers. comm.). Wilkinson (1979) cites examples of this type of hydathode occurring elsewhere in the Papilionoideae, as well as in the calyx lobes in Bignoniaceae. Similar hydathodes are evident at the tooth apices of dentate leaflets in *Cyamopsis*.

Two developments towards "glandular" leaflet apices and calyx lobes have been noted in *Indigofera*.

a) In *Brevipatentes* and some species of *Spinosaes* and *Dissitiflorae*, the calyx lobes terminate in blunt, rounded apices which actively secrete a clear liquid particularly during the bud stage (Plate 4.5, figs. a & b). In *Brevipatentes* the leaflet apices are also terminated by an actively secreting "gland", and the exudate spreads along the channelled leaflet margins leaving them glistening and sticky (Plate 4.6, fig. e). An unusual parallelism occurs between two species in *Brevipatentes* and one in *Dissitiflorae*, which all have three "blister-like" glands on the leaflets, one situated terminally and one placed midway along each lateral margin (Plate 4.7, fig. g).

23) In *Dissitiflorae* many species appear to have completely glandular leaflet margins (Plate 4.2, fig. e; Plate 4.4, fig. a), but these need to be examined to see if they are homologous with the development in *Brevipatentes*. This character also possibly occurs in some species of *Laxeracemosae*.

b) In *Pilosae*, *Latetipulatae* and some species of *Dissitiflorae*, a unique development is the presence of stalked-capitate

"glands" on the tips of the leaflets, stipules and calyx lobes (Plate 4.4, figs. g & h; Plate 4.12, fig. 9). Except for the latter, these glands occur predominantly on juvenile growth.

Wilkinson (1979) notes the similarity of hydathodes to floral (and extra floral) nectaries, with the main difference being the nature of the vascular supply (phloem in nectaries and xylem in hydathodes).

Hydathodes may be multifunctional (Wilkinson 1979; Mauseth 1988), i.e. they may be involved in:

- a) actively secreting various ions, and in some cases sugars out of the leaf. An association with the latter, and ants, may have developed secondarily making this feature selective as an alternative ant-plant relationship to pearl bodies. In those taxa where this has happened, there is often a marked reduction in the density of pearl bodies on the stems and leaves. Secreting hydathodes may thus be extra floral nectaries, and their prominent position on juvenile growth, leaves and calyx lobes suggests a role in protection by attracting ants.
- b) circulating nutrients, i.e. by supplying water and nutrients to immature, expanding leaves which need a large supply of minerals, but have a poorly developed vascular system. Hydathodes also remove excess water used as a transport medium, through guttation.
- c) possibly absorbing water into the leaf where tracheoid idioblasts in the apices might play a role in water storage.

4.3.9. *Petiole*

The petiolar anatomy of two species of *Indigofera* has been investigated by de Menezes *et al.* (1986). A possible character, perhaps associated with the development of a herbaceous habit, seems to be the arrangement of vascular bundles in the pulvinus.

In *Tinctoriae* an open, U-shaped, arrangement is found whereas in *Hirsutae* the vasculature is closed, in a circular pattern. More species need to be examined to see if this character has taxonomic significance.

4.3.10. *Stipules and stipels*

Stipules are always paired and are attached, at least partly, to the base of the petiole in the herbaceous sections of *Indigofera* and in the other derived genera in the tribe. In less derived elements, the stipules are separated from the base of the petiole by an abaxial commissure.

The stipules are mostly narrowly lanceolate to subulate, becoming vestigial in many *Trifoliolatae*. They develop to being broadly lanceolate to ovate in *Pilosae - Latestipulatae* and convergently in *Cuneifoliae - Stipulatae* (Plate 4.1, figs. 5 & 6).

In *Cuneifoliae - Stipulatae* the stipules are fused around the base, leaving characteristic "collar-like" scars around the stems (Plate 4.1, fig. 5).

- 24) In *Simplices-reflexae*, *Conjugatae* and a few other precociously flowering taxa (discussed more fully in chapter 6), vestigial (stipule-like) leaves subtend the flowering shoots (Plate 4.1, fig. 4b) while "typical" stipules occur on the vegetative shoots (Plate 4.1, fig. 4a). These vestigial leaves are trilobed, scarious, broad at the base and are decurrent on the stems. The apomorphic character, therefore, is the presence of "dimorphic" stipules in these taxa.
- 25) Stipels are only present in *Indigofera*, but they have been lost in many derived sections. Stipels are not found in the Cape sections, except in *Juncifoliae* where a single stipel occurs midway between the petiolules, and in *I. cytisoides*. Otherwise they appear in *Psiloceratiae*, *Tinctoriae*, *Hirsutae*, *Viscosae - Centrae*, *Pilosae - Dissitiflorae*,

Podophyllae, *Paniculatae*, *Ameocarpus* - *Demissae* and *Conjugatae* - *Alternifoliolae*. Stipel loss has occurred a number of times.

4.3.11. *Inflorescences*

26) Bracts in the plesiomorphic state are quite distinct from the stipules and leaves, being simple, narrow or broad. A synapomorphy in *Indigofera* is a switch in shoot morphology allowing the gradual reduction of leaves to foliar bracts (Plate 4.1, fig. 8). This is apparent in only some species of *Pilosae* and *Dissitiflorae*, but the apomorphic state occurs in *Latestipulatae*, *Paniculatae* and *Terminales* where foliar bracts are present in all species.

Bracts are mostly caducous in the tribe, but are persistent in *Microcharis*, *Concavae*, *Demissae*, *Foliosae* and *Latestipulatae* - *Paniculatae* - *Terminales*.

27) The development of trilobed bracts represents the most extreme reduction of foliar bracts subtending abridged (1-3 flowered) inflorescences.

A stepwise reduction occurs from:

- a) green and leaf-like bracts (usually trifoliolate and stipulate) sometimes with vestigial simple bracts still evident at the base of each pedicel; to
- b) either, paired stipular bracts (with the rest of the foliar bract being lost), or scarious trilobed bracts (Plate 4.12, fig 3b) sometimes with vestigial stipules at the base.

28) Paired bracteoles are only present in *Phylloxylon* and their loss is a synapomorphy for the rest of the tribe. The somewhat coriaceous bracteoles occur either at the base of the calyx or on the pedicels (Plate 4.13, fig. 1f & 1g).

Inflorescences in *Phylloxylon* and *Vaughania* are generally short brachyblasts (often woody in the latter), characterized by

imbricate, broad coriaceous bracts each subtending short racemes of 1 to a few flowers (Plate 4.13, fig. 1a).

- 29) A simple axillary raceme is the characteristic inflorescence in the tribe. An apomorphy is the development of paniculate inflorescences in the *Paniculatae*.

Trends towards the paniculate condition are seen as follows:

- a) Racemes reduced to 1-3(4) flowers on very short peduncles in the axils of foliar bracts (e.g. in *Latestipulatae*; Plate 4.12, fig.1).
- b) Individual inflorescences aggregated terminally on branches as distinct co-florescences (Weberling 1965), with the foliar bracts becoming enlarged and appearing to protect the developing infructescences. These strobilate inflorescences occur in two species in *Latestipulatae* (Plate 4.12, fig. 1).
- c) Marked reduction, in *Paniculatae*, of foliar bracts to scarious trilobed bracts; abbreviation of the original raceme, often to one flower with a joint below (and sometimes a simple secondary bract at the joint indicating that the lower part represents a peduncle of a reduced raceme); contraction of flowering branches into sub-capitate heads (Plate 4.12, fig. 2), or prolongation of branches into open panicles.
- d) Dense capitate inflorescences at the ends of branches, each with an involucre of leaves passing into 5-3-1 - lobed scarious bracts, subtending reduced racemes of 1-4 flowers (Plate 4.12, fig. 3a).

The proportion of the lengths of peduncle and inflorescence rhachis to the length of the subtending leaf, the number and density of flowers, and orientation of mature pods are all useful characters for distinguishing particular types of raceme.

In *Sphaeridiophora* inflorescences are sessile, densely few to many-flowered and are shorter than to q equalling the short subtending leaves.

- 30) A synapomorphy in the sections *Brevierectae*, *Hilares* and *Spinosae - Brevipatentes* is the presence of short-pedunculate, laxly few-flowered racemes with patent to ascending pods, q equalling in length the short, few-foliolate, leaves which partially obscure the inflorescences (Plate 4.12, fig. 4).
- 31) Sections *Pilosae* and *Dissitiflorae* are characterized by relatively long, slender-pedunculate, laxly few-flowered racemes (with short flowering rhachides) and erect pods, the inflorescences q equalling in length, but not obscured by, the few to many-foliolate leaves (Plate 4.12, fig. 6).
- 32) In *Hedyanthae - Dendroides* a synapomorphy is found in the lax to dense, many-flowered, racemes with patent to erect pods, the inflorescences being more than twice the length of the subtending leaves (Plate 4.12, fig. 7).
- 33) A parallel development occurs in the Cape sections, but this is distinguished from the above by the peduncle alone, being more than twice the length of the subtending leaf (Plate 4.12, fig. 5).
- 34) Long fruiting pedicels are synapomorphic in *Hedyanthae - Dendroides*.
- 35) Pods developing at right angles to the pedicels are autapomorphic in *Microcharis* (Plate 4.15, fig.1).

4.3.12. *Flowers*

Flowers in the Indigofereae are pink to carmine red, with a greater range of colours occurring in the Cape sections, i.e. magenta, terra-cotta and coral pink.

A general trend is for larger flowers (i.e. from 7 to 18mm long) to occur in the less derived taxa in the tribe, with smaller

flowers (i.e. from 3 - 6mm long) arising in more derived groups.

The following flower types are recognized in the tribe.

Individual floral characters are discussed separately in later sections.

In *Phylloxylon* flowers are characterized by the following: bracteoles; calyx densely brown strigose, teeth shorter than the tube, vexillar teeth separated by a narrow sinus; petals glabrous, pink, keel often with an acute apex, lateral spurs mostly absent; anthers without hairs or apiculum; ovary 2 - 4 ovulate, glabrous; stigma capitate (Plate 4.13, fig. 1, a to g).

The *Vaughania* flower is ebracteolate (as in the rest of the tribe); the calyx densely brown strigose, teeth shorter than the tube, vexillar teeth separated by a broad sinus (as in the following genera); corolla pink, asymmetrical with the standard curving to one side, the wings on different planes and the keel twisted in a semi spiral (Plate 4.13, fig. 2a & b); dorsal surface of the standard mostly hyaline strigose, the rest of the corolla either glabrous or the keel having sparse hairs along the distal commissure; keel curved below, with or without lateral spurs; staminal sheath curved, stamens free distally for almost half their length (Plate 4.13, fig. 2 e & f); anthers with plumose hairs above and below, stigma capitate or oblique.

In *Rhynchotropis* (and the following genera) flowers are typically papilionoid and symmetrical. Corolla entirely glabrous, the keel L-shaped, with a prolonged rostrum distally and no lateral spurs; staminal sheath straight but curved upwards distally, stamens free for 1 to 2 mm, anthers plumose hairy above and below; style long, curved, variously flattened, twisted and constricted, stigma oblique (Plate 4.13, fig. 3, a to f).

In *Microcharis* (and the following genera) the staminal sheath is straight with stamens free only near the apex (for less than 1 mm). Corolla entirely glabrous; standard gradually tapering to a narrow base; keel without lateral spurs, prolonged rostrate

distally; anthers with basal scales (no plumose hairs); style short and thick with a somewhat discoid oblique stigma (Plate 4.14, fig. 7 a to d).

In *Indigastrum* flowers are similar to *Microcharis*, but sometimes they are more tubular, with the standard only reflexed in the distal half (Plate 4.14, fig. 6), and wings twisted outwards for half their length (Plate 4.14, fig. 10 b & c). Anther scales reduced or absent, ovary and style as in *Indigofera* (Plate 4.14, fig. 13a), stigma capitate or oblique.

An anomalous species in *Indigastrum* (*I. fastigiatum*), has flowers which are superficially actinomorphic. From the front, the three equally sized petals (the standard and two wings) curve outwards distally, with the brightly coloured keel rostrum in the middle resembling a staminode. This is superficially similar to a monocotyledonous flower, indicating perhaps, that some form of Mullerian mimicry may have occurred (Schrire 1989). This species also has a unique 1B pollen type (Ferguson & Strachan 1982).

In *Cyamopsis* flowers are superficially very much like those of *Indigofera* (Plate 4.13, fig. 4, a to d). Corolla pink, distinctly dark veined; keel with prolonged rostrum absent (as in *Indigofera*), upper margin with a sparse proximal fringe of hairs, distal commissure often strigose, lateral spurs sometimes present; staminal sheath uniquely pseudomonadelphous with the vexillary stamen loosely attached to the others, anthers with basal scales very reduced or absent; stigma oblique or capitate.

Flowers in *Indigofera* are characterized by: corolla pink or carmine, dorsal surface of standard mostly hairy; keel frequently bearded distally, upper proximal margin with a dense fringe of hairs, lateral spurs always present; anthers with or without hairs; stigma capitate (Plate 4.14, figs. 4, 5, 8, 9, 10a, 11 a-j, 12 a-b).

4.3.12.1. Calyx

The tribe is characterized by a campanulate calyx with 5 subequal lobes, the vexillary teeth the shortest and the carinal lobe the longest. This asymmetry is more marked in *Cyamopsis* than in other genera.

The calyx is bilabiate in *Phylloxylon* with the two vexillar lobes joined at the base. In the rest of the tribe a broad vexillar sinus separates the two upper calyx lobes (Plate 4.14, fig. 2).

36) A three state character is proposed for the calyx glands (discussed above as specialized hydathodes), with capitate glands being derived from blunt-tipped calyx lobes. This transformation is best seen among various species in *Dissitiflorae*.

37 & 38) The length of the calyx lobes in proportion to the tube is an important character in the tribe (discussed in detail in chapter 5.) In *Phylloxylon*, *Vaughania* and the woody elements of *Indigofera*, the lobes are deltoid and shorter than to more or less equalling the calyx tube. In some of the herbaceous sections of *Indigofera*, and in the other derived genera, calyx lobes are narrowly triangular to lanceolate, and up to twice the length of the tube on average (Plate 4.14, fig.1). A synapomorphy occurs in the more derived sections of *Indigofera* where the lobes are subulate, becoming longer than twice the length of the tube (Plate 4.14, fig. 3), and this is correlated with the development of much shorter ovaries. The proportion of calyx length to that of the staminal sheath (character 38) is merely another way of expressing character 37 and so it was not coded in the cladistic analysis.

The staminal sheath (and pistil) are always only slightly shorter than the keel except in a few species of *Phylloxylon* where the pistil is little more than half the length of the corolla.

- 39) Broader, persistent, scarious calyx lobes are synapomorphic in *Latestipulatae*, *Paniculatae* and *Terminales*. The significance of this development is discussed in chapter 5.

Completely glabrous, and somewhat glaucous calyces are characteristic of *Juncifoliae* and *Cuneifoliae* in the Cape. Calyces in *I. scarriesii* are also glabrous.

An enlarged calyx with broad, keeled lobes that are often imbricately overlapping at the base, is autapomorphic in the Cape section *Concavae* (Plate 4.12, fig. 8).

- 40) Scarious calyx lobes which become much broader after flowering (i.e. to more than 1mm wide at the base) are autapomorphic in *Terminales*, and this character is discussed in greater detail in chapter 5 (Plate 4.14, fig. 8a).

4.3.12.2. *Corolla*

In each of the flowers described above for the various genera, the particular conformation of petals is critical for the correct functioning of the tripping mechanism. The explosive release of the staminal sheath and pistil, with disorientation of the petals, is a universal character in the Indigofereae, although in *Vaughania* the mechanism appears to operate somewhat differently (Du Fuy pers. comm).

- 41) Petals which are almost immediately caducous after tripping (except the standard petal in some less derived groups) are unique in the subfamily Papilionoideae. In the derived Cape section *Hispidae*, petals are thicker textured and more durable than elsewhere, and are not caducous. They remain after individual flowers have tripped and appear to enhance the overall attractiveness of inflorescences during the relatively short flowering period. The development of persistent petals seems to have allowed the switch to a mass flowering regime in *Hispidae*, as opposed to trap-line

flowering in the rest of the tribe. These aspects are explored in greater detail in chapter 5.

The standard is usually broad, orbicular to obovate, tapering rapidly at the base to a short claw (Plate 4.14, figs. 8 & 9). Callosities and auricles are absent, although the standard is somewhat more rigid and thickened along the basal region near the claw in *Cyamopsis*. In *Microcharis* and *Indigastrum* the standard narrows at the base, tapering gradually to the claw (Plate 4.14, fig. 7 a & b). A similar development is found in the flowers of *Microcarpae*, *Acanthonotus*, *Sphaeridiophora* and some species in *Pilosae*, and also in a number of Cape sections. This character is often associated with the phenomenon, described in chapter 5 as an overlapping standard base. Flowers may be more tubular, and the base of the standard is flexed over the proximal region of the wings and keel, with the distal half of the lamina sharply reflexed over its base (Plate 4.14, fig. 6). The central blotch is not clearly visible. This character possibly has the effect of restricting access to the flower or offering greater protection to the nectary. In the plesiomorphic state, the standard is fully reflexed at the base with the central blotch clearly visible (Plate 4.14, fig. 4).

- 42) Characteristic of *Indigofera* and *Vaughania* is the presence of a dense vestiture on the dorsal surface of the standard (Plate 4.14, fig. 9). The other genera in the tribe have glabrous standards or with a few isolated hairs. A reversal to glabrous standards is found in the Cape sections *Cuneifoliae* and *Stipulatae*, and in tropical *I. scarriesii*.
- 43) The presence of a dense vestiture of appressed, dark brown, strigose hairs, on the dorsal surface of the standard, characterizes the sections *Tinctoriae*, *Hedyanthae* and *Dendroides*.
- 44) Hairs are sometimes present along the midline of the standard, in the region of the central blotch, in

Psiloceratiae, *Hedyanthae*, *Dendroides*, *Setiflorae* and *Microcarpae*.

The central blotch is either hyaline and paler than the rest of the lamina, or uniformly darker, e.g. in *Hedyanthae*, *Trifoliolatae* and *Distichae*, or speckled and often glossy. It is either evident as one region, or as two areas one on each side of the midline, which are often slightly sunken (Plate 4.14, fig. 8). The blotch is often surrounded entirely or partially by a distinct areola.

- 45) A synapomorphy in *Tinctoriae* and *Subulatae* is the presence of the pale central blotch merging broadly along the veins to the margin, breaking up the uniformity of the outer coloured part of the lamina.

Wing petals in the tribe are all characterized by a proximal crest, or ridge at the base of the limb above the claw, and ciliate margins (Plate 4.14, fig. 10a). After anthesis the contiguous crests of the paired wing bases present a flat surface below the central blotch of the standard. This together with the splayed out wing limbs offers a level platform for pollinators (Plate 4.14, fig. 5).

The proximal crests often have matching regions of minute folds which, like petal sculpturing in other tribes (Stirton 1981), appear to serve as pollinator footholds. The tripping mechanism is activated by the pollinator forcing apart the wing bases in search of nectar. The central blotch and keel provide the orientation cues for the most effective position to operate the mechanism.

- 46) Wing proximal crests are glabrous in most of the tribe, but in the following sections of *Indigofera*, the crests are moderately to densely bearded: *Psiloceratiae*, *Hedyanthae*, *Hirsutae*, *Setiflorae*, *Stenophyllae*, *Microcarpae* and *Acanthonotus* (Plate 4.14, fig. 10a).

- 47) Distal wing lamina beards occur particularly in a number of Cape sections, and in some species of *Psiloceratiae* and *Stenophyllae*.

Keel shapes are relatively variable in the tribe, but within genera the characters are very consistent (Plate 4.14, fig. 11 a-j, fig. 7d; Plate 4.13, figs. 1e, 2e & 3d).

Keel petals are connate along the lower margin in the distal half, and de Kort & Thijssse (1984) report the presence of latex containing glands on the back of the standard, on the keel petals and on the style of some Asian species of *Indigofera*. These have not been observed in African taxa.

- 48) A keel curved at the base (Plate 4.13, fig. 2e & 3d), enclosing a curved staminal sheath and pistil, is a synapomorphy in *Vaughania* and *Rhynchotropis*. In the former, the keel is twisted in a semi-spiral and the standard and wings are asymmetrically positioned. The keel, staminal sheath and pistil are straight and symmetrical in all other genera.
- 49) A dense to sparse fringe of hairs on the upper margin of the keel is characteristic of the whole of *Indigofera* (Plate 4.14, fig 11 a-j) and also occurs in *Cyamopsis*. In the former, the fringe is particularly dense in the proximal region, which is mostly clearly visible above the wing platform. The fringe is often pink-coloured and this part of the keel appears to act as a further orientation cue for pollinators.
- 50) The presence of a distal keel fringe in *Trifoliolatae*, positioned on rostrate keel apices (Plate 4.14, fig. 11d), possibly represents a different orientation cue to the above.

A unique syndrome is found in a number of Cape sections which leads to a gradual exposure of the keel over time. After anthesis

the wings are positioned close together, forming a platform above the keel. The latter is completely hidden until the wings begin to flex outwards and down along their inner margins, exposing the upper margin of the keel between them.

- 51) The upper margin of the keel is not generally exposed above the wings in *Tinctoriae* and *Subulatae*.

Flowers in the above two sections also have distinctive buds, with the apices curved upwards.

Keel beards, particularly dense on the distal third of the keel petals, occur in *Psiloceratiae*, *Denudatae*, *Coriaceae*, *Angustifoliolae*, *Hispidae*, *Tinctoriae*, *Hedyanthae*, *Dendroides*, *Stenophyllae*, *Brevierectae*, *Atratae*, *Centrae* and *Paniculatae*.

A feature common in *Indigastrum*, *Microcharis* and many species of *Indigofera* (including all Cape sections) is the possession of a region of deep red to purple colouration, usually more marked on the inside of the keel, in the position where the anthers are situated. This character is discussed in chapter 5.

- 52) Lateral spurs occur in all species of *Indigofera* (Plate 4.14, fig 11 a-j), and only in some species in the other genera of the tribe. The spurs are hollow, ascending from the lateral walls of the keel, and the rounded to pointed apices project into longitudinal folds beneath the wings. Lateral spurs provide support to the wing platform while also contributing to the tripping mechanism when the wings are pulled apart.
- 53) A prolonged keel rostrum, projecting beyond the keel apex, is a synapomorphy in *Rhynchotropis*, *Microcharis* and *Indigastrum* (Plate 4.13, fig. 3d; Plate 4.14, fig. 6).

4.3.12.3. Stamens

Stamens are diadelphous in all genera, except *Cyamopsis* which is pseudo-monadelphous (Schrire 1989). 9 stamens are connate in a gutter-like sheath around the pistil. The stamens are alternately longer and shorter and the sheath is slightly longer on the carinal side (Plate 4.14, fig. 12a).

In most genera the stamens are only free near the apex of the staminal sheath (Plate 4.14, fig. 12a), but in *Vaughania* and *Rhynchotropis* the stamens are free distally for a third to half of their length (Plate 4.13, figs. 2f & 3e).

The anthers are uniform, dorsifixed (Plate 4.5, fig. c) and all are fertile. Gillett (1958) notes that the vexillary stamen in *Microcharis* often lacks an anther.

A central feature of the tripping mechanism in Indigoferaeae is the explosive release of a dry cloud of pollen over the pollinator. One measure of the success of this mechanism is the accuracy with which pollen is expelled on the target. Anther hairs may play a role in improving this accuracy, by restricting pollen in the keel thus concentrating its effect. Anther hairs are present in all the less derived taxa (above *Phylloxylon*), which also tend to have large flowers. In many smaller flowered, derived herbaceous sections in *Indigofera* (with an advanced type-4 pollen), anther hairs have been lost.

- 54) Anther hairs are present in *Vaughania*, *Rhynchotropis* and *Indigofera*, but in the latter, the loss of such hairs is a synapomorphy in the more derived sections.

In the basal sections of *Indigofera* hairs are found above and below the anthers (Plate 4.5, fig. d; Plate 4.14, fig. 12b). Hairs occur only at the base of anthers in some of the other sections, perhaps indicating the trend towards complete loss.

- 55) Hairs are scattered all over the surface of anthers in many species of *Setiflorae* and *Stenophyllae*.
- 56) A synapomorphy for the rest of the tribe above *Phylloxylon*, is the presence of an extended apical connective on anthers (Plate. 4.6, figs. c & d). The connective is described as being gland-tipped in some species (Polhill 1981). No evidence of this, however, has been found in the African species examined so far.

This character may serve a similar function to anther hairs in concentrating pollen for expulsion.

- 57) Anther hairs are plumose in the less derived elements of the *Vaughania* alliance (*Vaughania* and *Rhynchotropis*), being extremely dense above and below the anthers. In *Microcharis*, and some species of *Indigastrum* scales develop below the anthers instead of plumose hairs (Plate 4.5, fig. e). In the rest of *Indigastrum* and in *Cyamopsis* the scales have become very reduced in size. A character transformation from plumose hairs to scales is proposed.

4.3.12.4. Pistil

The ovary gradually merges into the style, has numerous to 1 or 2 ovules, and is glabrous or hairy with the indument often developing at a later stage (Plate 4.14, fig. 13a). The style bends upwards to q erect, and is always glabrous.

- 58) A synapomorphy in the herbaceous sections of *Indigofera* is the switch over from a long ovary - short style to a short ovary - long style (Plate 4.14, fig. 13b). The significance of this character is discussed in chapter 5. Parallel developments are found in some of the herbaceous Cape sections and in *Indigastrum* subgenus *Argyraeae*.

59) The curved style in *Rhynchotropis* is variously ornamented, being twisted, dilated medially and abruptly contracted and bent below (Plate 4.13, fig. 3f).

60) Capitate stigmas are plesiomorphic in the tribe and they occur in all species of *Indigofera* (Plate 4.5, fig. f). In the *Vaughania* alliance stigmas are predominantly oblique (Plate 4.5, fig. g; Plate 4.13, figs. 3f & 4d). The oblique stigma character appears to be quite variable and a closer study of each genus may reveal distinct types. All observed stigmas in the tribe are penicillate (Plate 4.5, fig. f).

4.3.13. *Pods*

Pods are most often explosively dehiscent with two twisting coriaceous valves. They are rarely particularly coriaceous, turgid and tardily dehiscent to indehiscent, e.g. in *Phylloxylon* (Plate 4.15, fig. 2a) and *Acanthonotus* (Plate 4.15, fig. 12); or thinner walled and also tardily dehiscent, e.g. in *Terminales* (Plate 4.15, fig. 8b).

Generally, pods are linear to oblong or globose, cylindrical or tetragonal and never inflated (Plate 4.15, figs. 1, 3, 4, 6 & 7). Considerable variation in shape is found in derived members of *Tinctoriae* (pods may be moniliform, torulose, botuliform, variously curved, or globose), and in *Ameocarpus* (torulose or circinnate; Plate 4.15, fig. 11).

A unique feature of the tribe is the persistent sessile cup-like base remaining on the infructescence after the valves have fallen (Plate 4.15, fig. 6d). It is part of the ovary, and can be seen in the flower as a slightly enlarged base with two protuberences beneath the vexillary stamen. The usually glabrous cup-like structure is separated from the pod by a region of circumferent articulation. The character becomes markedly reduced or lost in *Latestipulatae*, *Paniculatae*, and *Terminales* where the pod walls become somewhat thinner than in the rest of the tribe.

Oblong to globose pods with a reduction to 1 or 2 seeds occur in *Acanthonotus*, *Demissae*, *Sphaeridiophora*, *Paniculatae*, *Terminales*, *Microcarpae* and *Tinctoriae*.

A swollen style base in the developing pod often becomes a persistent beak in many sections with long cylindrical pods (Plate 4.5, fig. h). In one species in *Tinctoriae* a distinct knob is present apically on the pod (Plate 4.15, fig. 3). The significance of this character is obscure since it is often most obvious at the developing stage, but in mature pods the beak may be involved with regulating valve dehiscence.

The pod sutures are occasionally prominent, e.g. in some Cape and other less derived sections of *Indigofera*, or often broad and pale particularly in *Dissitiflorae*, *Laxeracemosae*, *Latistipulatae*, and some *Paniculatae* and *Pilosae*. In the isolated *Indigofera ammoxylon*, from the Mascarenes, the botuliform pods break up into 4 strips, the two sutures coming away from the valves.

A papery endocarp with transverse septa between the seeds (Plate 4.15, fig 5, a & b; fig. 6b) is a synapomorphy possessed by the rest of the tribe above *Phylloxylon*.

Stipitate pods occur in *Phylloxylon* and sporadically in *Tinctoriae*, *Juncifoliae* and *Filicaules*.

- 61) Pods are glabrous in *Phylloxylon*, a few species of *Vaughania* and in the basal sections of *Indigofera*. Strigose pods characterize many sections in the tribe with parallel developments in the *Vaughania* alliance. A unique character, corresponding to the development of long calyx lobes and short ovaries, is the presence of a dense pilose, hirsute or sericeous (in *Latetipulatae*) vestiture on the pods (Plate 4.15, figs. 6a & 7a). This is often accompanied by multicellular glandular trichomes (in *Viscosae* and *Spinosaes*) or a dense covering of pearl bodies (e.g. in *Acanthonotus*, *Microcarpae* and *Sphaeridiophora*). The

character glabrous versus hairy was taken because it was difficult to determine homologies in the different vestiture types.

- 62) Pods with a prominent venation occur in *Ameocarpus*, *Acanthonotus* and *Simplices-reflexae*.
- 63) The development of spiny processes along the dorsal suture in one indehiscent species of *Acanthonotus* (*I. nummulularifolia*; Plate 4.15, fig. 12) is unique in the tribe. In an Indian species of uncertain sectional affinity (*I. glandulosa*), papery processes superficially similar to the above occur along both sutures (for illustrations see de Kort & Thijsse 1984).
- 64) Broad stramineous pods with 3 ridges on each face are an autapomorphy in *Cyamopsis* (Plate 4.15, fig. 9a).
- 65) Strongly flattened pods with eminences usually visible above the seeds (sometimes apparent as a continuous ridge along the midline of the pod), are synapomorphic for *Ameocarpus* and *Demissae*. The transverse septa are often noticeable externally.
- 66) Pod orientation is frequently a useful character at sectional level, but homoplasy is common in the tribe. Erect pods characterise *Pilosae* - *Dissitiflorae*, *Stenophyllae* - *Brevierectae*, and *Hedyanthae* - *Dendroides*. Reflexed pods arise in *Tinctoriae* - *Subulatae*, *Trifoliolatae* - *Stipulatae* - *Distichae*, *Simplices-reflexae* - *Alternifoliolatae*, *Ameocarpus*, *Hirsutae*, *Acanthonotus* - *Microcarpae* and *Indigastrum*. More or less patent pods are found in the rest of the tribe.
- 67) Glabrous black pods are characteristic of the Cape sections, *Juncifoliae*, *Concavae*, *Coriaceae* and some species in *Humifusae* and *Angustifoliolatae*.

68 & 69) The presence of tannins in the endocarp is a synapomorphy in *Indigofera*. They are apparent, in the plesiomorphic state, as irregularly scattered coarse to fine brown dots or flecks, particularly in the transverse septa (Plate 4.15, fig. 5b). A unique development occurs in the herbaceous sections coinciding with the reduction to short ovaries, where tannins appear in turgid vesicles which dry as regular large brown spots in the endocarp (Plate 4.15, fig. 6b). In *Pilosae* and *Latistipulatae* a further trend towards distinct tannin stripes is realized (Plate 4.15, fig. 7b). The tannin vesicle synapomorphy is accounted for by character 74, since the vesicles leave pitted depressions in the developing seeds which are retained in maturity (Plate 4.15, fig. 6c). Owing to homoplasy in the endocarp tannin characters, they were treated separately and not as a transformation series.

4.3.14. *Seeds*

Seeds in the Indigoferaeae have a hard osseous testa and a small oval hilum. Manning (1987) & van Staden *et al.* (1989) describe the following characters in the tribe:

- a) deltoid micropyle which is included within the funicular tissue (a derived feature in the subfamily).
- b) hyperdermal hourglass cells occurring in two rows at the hilum.
- c) epidermal cells with tannin deposition in the vacuoles, persisting to maturity.

70) Seeds are globose to cylindrical; either truncate, compressed, obloid, ellipsoid or quadrate. In the Cape sections (and in a few species in *Psiloceratiae*) seeds are characteristically spherical.

71) *Phylloxylon* has unusually large seeds for the tribe, from 4.5mm to about 15mm long. In the rest of the tribe seeds are less than 3mm long (Plate 4.15, fig. 2b).

- 72) A rudimentary rim aril is present in most taxa, but in *Hedyanthae - Dendroides* a persistent aril (possibly an elaisome) occurs on the seeds of many species (Plate 4.15, fig. 10). In the Cape sections *Cuneifoliae*, *Juncifoliae* and *Humifusae* many species have uniformly dark coloured seeds. Elsewhere seeds are usually pale brown, orange or khaki, with or without purple mottling. Many of the dark seeds have contrastingly pale, persistent, papery funicles. The function of these, if any, is obscure.
- 73) Seeds with a tuberculate testa occur in *Cyamopsis* and in isolated species in *Indigastrum* (Plate 4.15, fig. 9b).
- 74) The synapomorphy of coarsely pitted seeds from large tannin vesicles in the pod endocarp, has been discussed under character 68.

4.3.15. *Seedlings*

According to de Vogel (1979) the seedlings of *Indigofera* belong to the *Sloanea* type and subtype mode of development. Germination is phanero-epigeal, with foliar cotyledons and unifoliolate opposite eophylls (Duke & Polhill 1981). *Phylloxylon* has unique seedlings with no plumule, a root system developing for a season from cryptogeal cotyledons, and cladodes then arising from adventitious buds on the hypocotyle above a swollen foodstoring region of the root (Peltier 1971). Evidence from a preliminary comparison of *Indigofera* seedlings suggests that useful characters may be found on further study.

4.3.16. *Pollen*

A detailed study of pollen morphology in the tribe was made by Ferguson & Strachan (1982). *Phylloxylon* is characterized by a thin exine with simple stratification, small size and long colpi. The small size and thin exine distinguish the pollen from the rest of the tribe and it is scarcely different from a generalised papilionoid type.

- 75) The derived pollen Types 3 & 4 in *Indigofera* are discussed below in the context of increasing complexity of pollen morphology in the tribe.
- 76) Pollen in *Rhynchosyris* is larger than elsewhere in the tribe and together with short colpi, the type is distinct. The tectum and wall stratification, however, place it close to *Indigastrum*.

Cyamopsis has pollen slightly larger than most species of *Indigofera* with long colpi, a perforate rugulate tectum and somewhat complex exine stratification. The pollen does not readily fit into *Indigofera* Type 1 or Type 3.

Type 1A and 1B pollen distinguishes *Indigastrum* which forms a more or less distinct group with a characteristic pitted-perforate tectal surface. Type 1E pollen is found in *Microcharis* where the tectal surface is very reduced and sparsely perforate. The exine is thicker with a more complex stratification.

The basal sections of *Indigofera*, including *Psiloceratiae*, all the Cape sections (except *Trifoliolatae*), the less derived *Tinctoriae*, *Hedyanthae*, *Hirsutae* and *Microcarpae*, have Type 1C pollen with a generally perforate sculpturing and simple exine stratification.

Type 3 pollen has a finer tectal sculpturing than Type 1, but coarser than the most derived Type 4 pollen. It has characteristically uniform sculpturing over the whole surface and a more complex exine stratification, which is again transitional between Types 1 & 4. Type 3 pollen occurs in *Setiflorae*, *Trifoliolatae*, derived taxa in *Psiloceratiae* and *Tinctoriae*, *Stenophyllae* and some other Asian and North American species.

The uniform very finely microperforate tectum with complex exine stratification in Type 4 pollen, is characteristic and unique in the subfamily. Type 4A pollen, which is somewhat transitional between Type 3 and Type 4C occurs in *Simplices-reflexae*, some

Sphaeridiophora and a number of New World species. Type 4B has a coarse, striate rugulate, tectal pattern and is found in *Pilosae* and *Acanthonotus*. The most derived Type 4C pollen characterizes the rest of the more advanced herbaceous sections in the genus.

4.3.17. Chromosomes

The basic chromosome number for the tribe is $2n = 16$ (Senn 1938; Darlington & Wylie 1955; Gillett 1958) and tables of various counts of *Indigofera* species are given in Frahm-Lelieveld (1960; 1962; 1966) and Goldblatt (1981).

77) Aneuploid reductions to $2n = 14$ have occurred in *Indigastrum* and *Cyamopsis* and in a few species of *Latestipulatae* and *Paniculatae*.

78) A further reduction to $2n = 12$ is found in *Terminales*.

Hexaploids (with $2n = 48$) have occurred in a number of Himalayan and Chinese *Psiloceratiae*. Sporadic tetraploids ($2n = 32$), usually associated with high altitude or arid conditions, are found in *Psiloceratiae*, *Tinctoriae*, *Subulatae*, *Pilosae*, *Sphaeridiophora*, *Atratae*, *Brevierectae*, *Dissitiflorae* and *Alternifoliolae* as well as in various New World species.

Frahm-Lelieveld (1966) also indicates that chromosome size may be a useful character, e.g. *Hirsutae* and *Acanthonotus* are characterized by very small chromosomes.

FIGURES

- 1a) *Indigofera jucunda* Schrire (ms.) (Acocks 14025, K). Abaxial commissure at the base of the petiole, separating the leaf from the stipules. (X 2)
- 1b) *Indigofera schimperi* Jaub. & Spach var. *schimperi* (Oates 35, K). Abaxial commissure absent, the stipules attached to the base of the petiole. (X 2)
- 2) *Indigofera hispida* Eckl. & Zeyh. (Schrire 2474, K). Sclerophyllous leaflets, with revolute margins and prominent midrib below. (X 2)
- 3) *Indigofera concava* Harv. (Burchell 5931, K). Leaflets subglabrous above, with involute margins. (X 2)
- 4) *Indigofera thomsonii* Bak.f. (Bullock 3425, K).
- a) Stipules (normal) on vegetative shoots. (X 2)
- b) Stipules or vestigial leaves subtending the base of flowering shoots. (X 2)
- 5) *Indigofera cuneifolia* Eckl. & Zeyh. (Taylor 9449, K). Broad stipules leaving collar-like scars on stems when caducous. (X 1)
- 6) *Indigofera alpina* Eckl. & Zeyh. (Acocks 19961, K). Broadly ovate stipules, digitately trifoliolate leaves. (X 2)
- 7) *Indigofera filifolia* Thunb. (Burchell 6974, K).
- a) Leaflets present on juvenile growth only. (X 1)
- b) Leaflets reduced to scales, or absent, on mature growth. (X 1)
- 8) *Indigofera monantha* Bak.f. (Reekmans 10281, K). Gradual reduction of leaves to foliar bracts. (X 1)
- 9) *Indigofera peltata* Gillett (Richards 11572, K). Peltate leaves. (X 1)

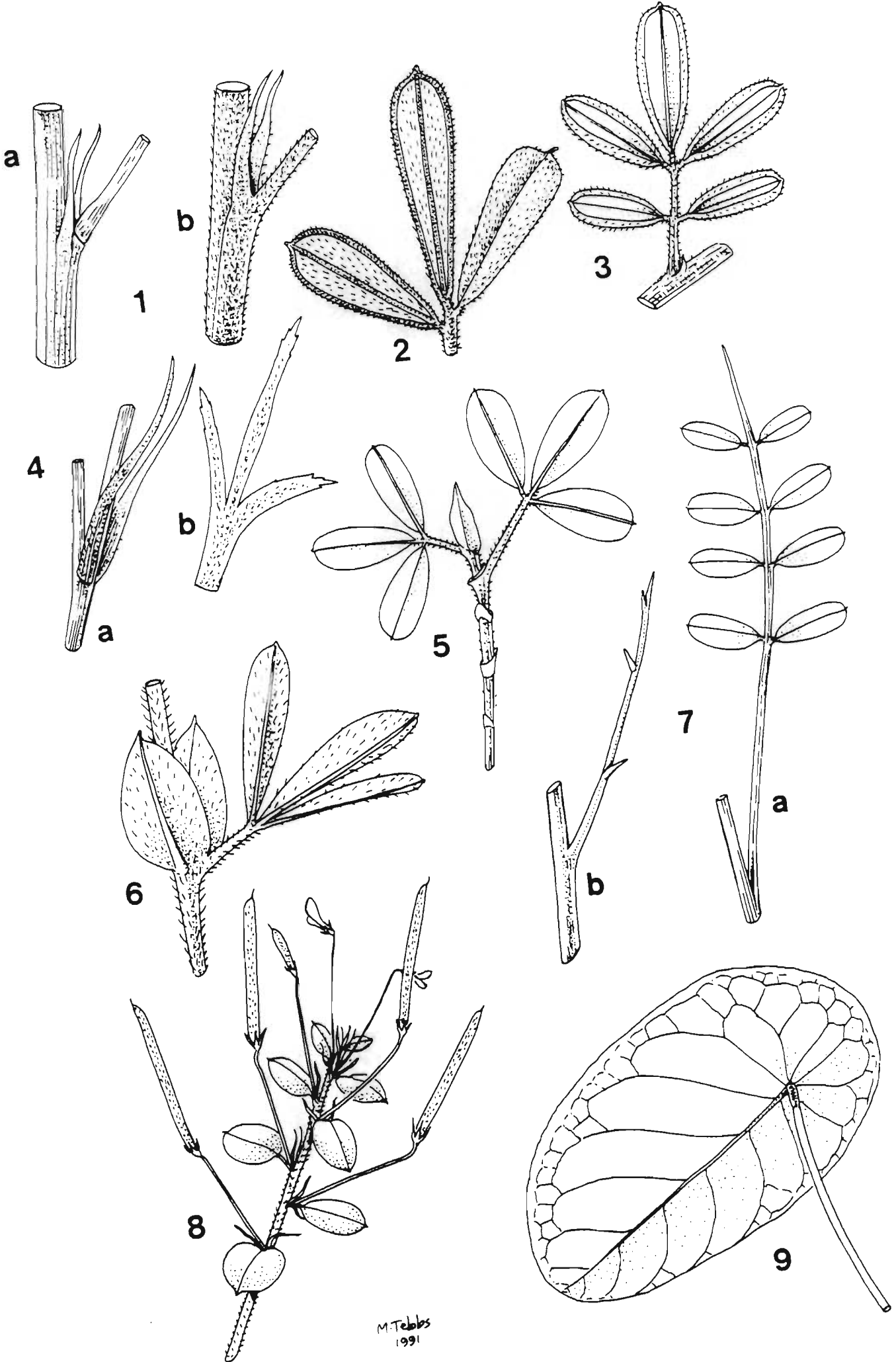


PLATE 4.2 SEM - Leaflet surface micromorphology. I

FIGURES:

- A) *Indigofera longebarbata* Engl. (Schrire 2354, K). Stems; uniramous trichomes and sessile pearl bodies. (X 48)
- B) *Indigofera longebarbata* Engl. (Schrire 2354, K). Detail of uniramous trichome base. (X 450)
- C) *Indigofera microcarpa* Desv. (Drummond 7770, PRE). Lower leaflet surface; discoid (cavitated) pearl bodies. (X 65)
- D) *Indigofera acanthoclada* Dinter (Giess & Muller 12094, PRE). Lower leaflet surface; T-shaped biramous hairs. (X 101)
- E) *Indigofera wituensis* Bak.f. (Polhill & Paulo 889, PRE). Lower leaflet surface; glandular margin. (X 97)
- F) *Indigofera macrocalyx* Guill. & Perr. (Espirito Santo 2819, PRE). Lower leaflet surface; cylindrical pearl bodies. (X 65)
- G) *Indigofera nummulariifolia* (L.) Livera ex Alston (Polhill & Paulo 2100, PRE). Lower leaflet surface; scattered pearl bodies and biramous hairs perpendicular to the margin. (X 46)
- H) *Indigofera nummulariifolia* (L.) Livera ex Alston (Polhill & Paulo 2100, PRE). Upper leaflet surface; trichome and stomata. (X 210)

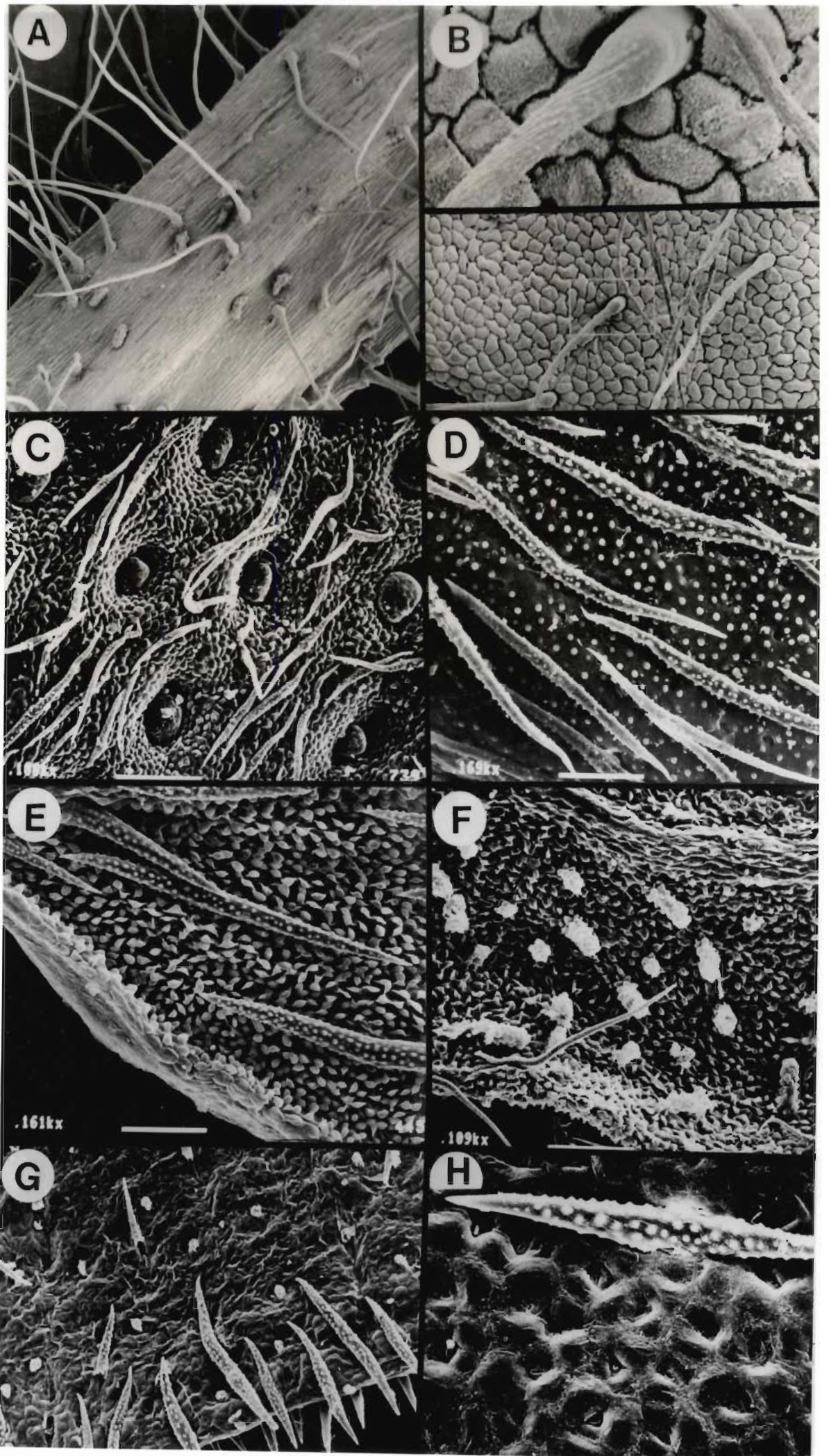


PLATE 4.3 SEM - Leaflet surface micromorphology. II

FIGURES:

- A) *Indigofera longebarbata* Engl. (Schrire 2354, K). Lower leaflet surface; uniramous hairs. (X 102)
- B) *Indigofera inhambanensis* Klotzsch (Germishuizen 3559, PRE). Upper leaflet surface; long biramous hairs giving rise to sericeous vestiture. (X 132)
- C) *Indigofera heterotricha* DC. (Schrire 2416, K). Lower leaflet surface; T-shaped biramous hairs of different sizes, multi-seriate, gland-tipped trichomes. (X 102)
- D) *Indigofera nebrowniana* Gillett (Codd 2229, PRE). Upper leaflet surface; papillate epidermis, sunken stomata. (X 480/240)
- E) *Indigofera eriocarpa* E. Mey. (Schrire 2476, K). Upper leaflet surface; biramous hairs with arms of very unequal length. (X 90)
- F) *Indigofera hispida* Eckl. & Zeyh. (Schrire 2474, K). Lower leaflet surface; sclerophyllous leaves, revolute margin (top-left, showing upper surface morphology), prominent midrib and dense vestiture. (X 42)
- G) *Indigofera verrucosa* Eckl. & Zeyh. (Schrire 2445, K). Upper leaflet surface; stomatal guard cells. (X 180)
- H) *Indigofera inhambanensis* Klotzsch (Germishuizen 3559, PRE). Upper leaflet surface, stomatal guard cells. (X 210)

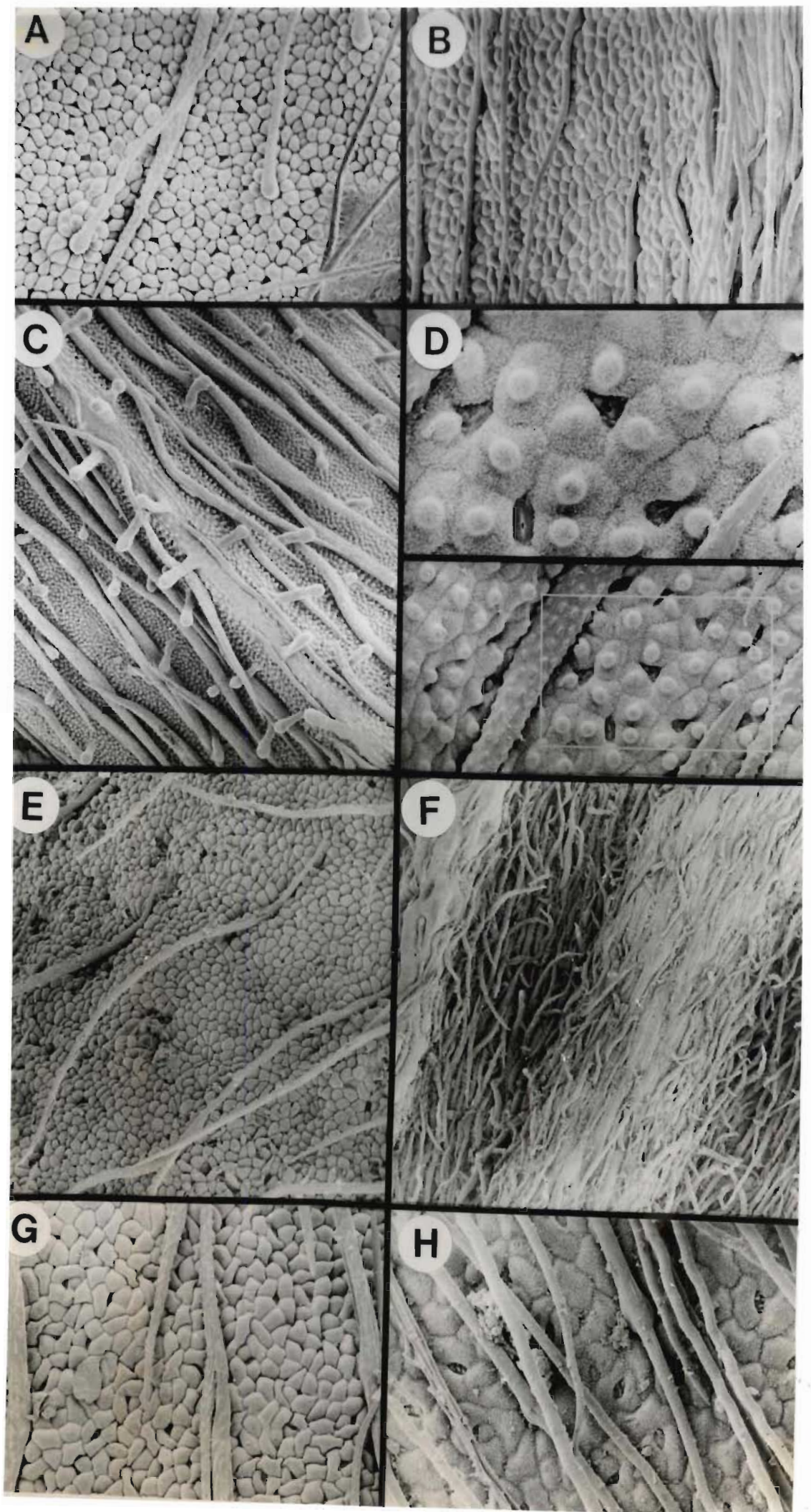


PLATE 4.4 SEM - Trichomes and glands. I (stems, leaves, calyx, pods).

FIGURES:

- A) *Indigofera wituensis* Bak.f. (Polhill & Paulo 889, PRE). Glandular leaflet margin. (X 20)
- B) *Indigofera microcarpa* Desv. (Drummond 7770, PRE). Pod surface; U-shaped biramous hairs, discoid (cavitated) pearl bodies. (X 103)
- C) *Indigofera hispida* Eckl. & Zeyh. (Schrire 2474, K). Stems; stalked biramous hairs. (X 104)
- D) *Indigofera hispida* Eckl. & Zeyh. (Schrire 2474, K). Stems; stalked biramous hair. (X 140)
- E) *Indigofera griseoides* Harms (Milne-Redhead 4342, PRE). Stems; bulbous-based trichomes. (X 100)
- F) *Indigofera griseoides* Harms (Milne-Redhead 4342, PRE). Stems; bulbous-based trichome detail, with vestigial branch at the base. (X 342).
- G) *Indigofera arenophila* Schinz (J. Boss PRE 35993, PRE). Calyx lobes; apical gland. (X 67)
- H) *Indigofera arenophila* Schinz (J. Boss PRE 35993, PRE). Calyx lobes; apical gland detail. (X 210)

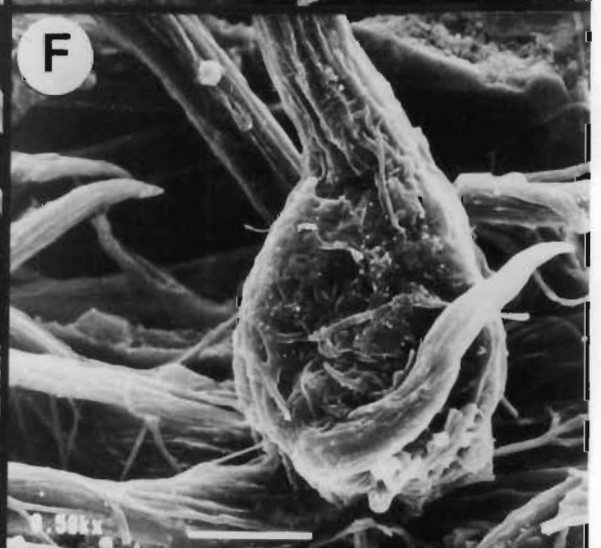
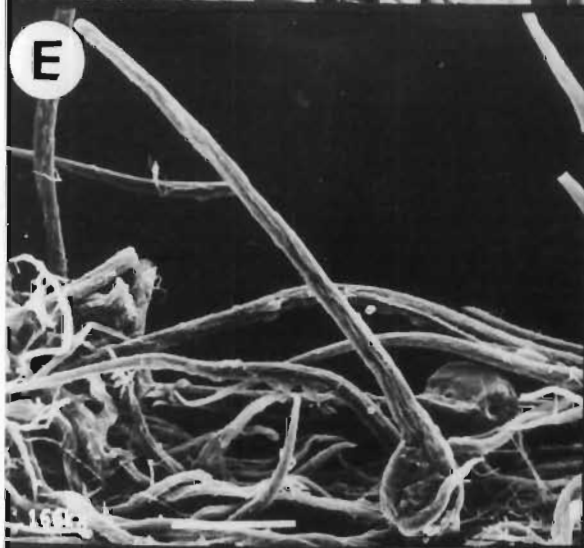
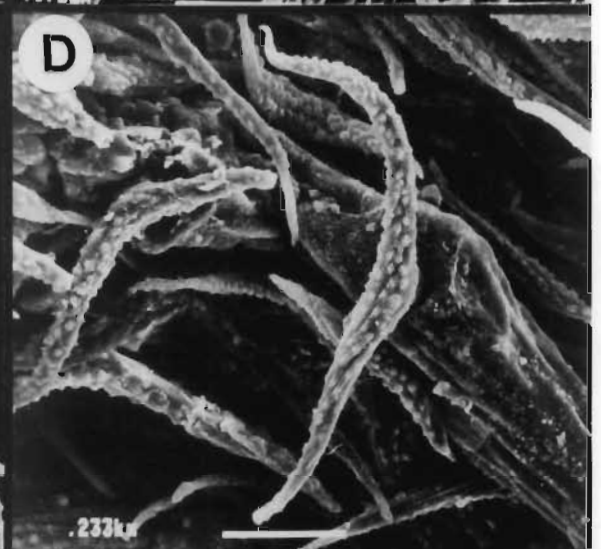
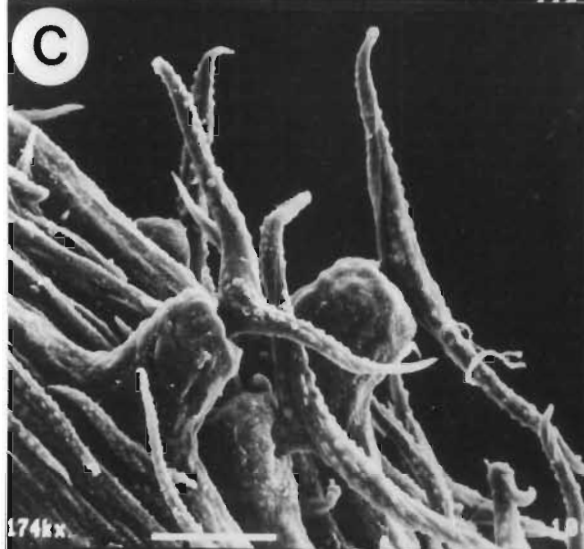
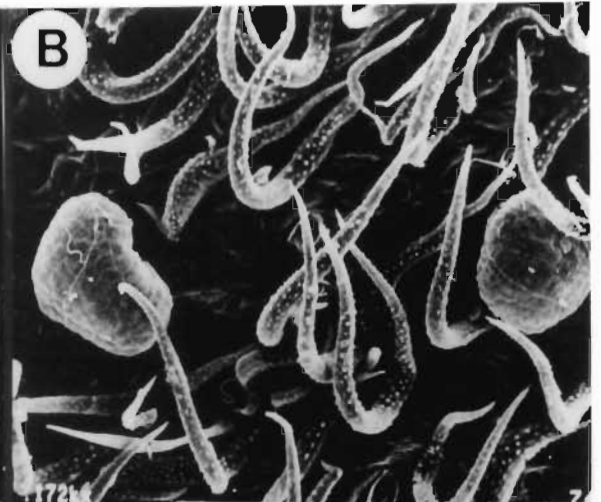
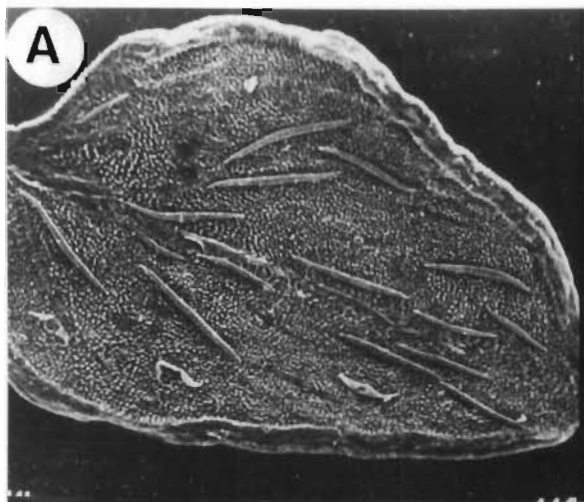


PLATE 4.5 SEM - Trichomes and glands. II (calyx, anthers, stigmas)

FIGURES:

- A) *Indigofera nebrowniana* Gillett (Codd 2229, PRE). Calyx; glandular apices. (X 35)
- B) *Indigofera nebrowniana* Gillett (Codd 2229, PRE). Calyx; glandular apex detail. (X 143)
- C) *Indigofera tristis* E. Mey. (Strey 10791, PRE). Dorsifixed anther. (X 46)
- D) *Indigofera tristis* E. Mey. (Strey 10791, PRE). Anther hairs. (X 47)
- E) *Indigastrum fastigiatum* (E. Mey.) Schrire (Hilliard & Burtt 7638, PRE). Basal anther scale. (X 64)
- F) *Indigofera tristis* E. Mey. (Strey 10791, PRE). Capitate stigma detail. (X 97)
- G) *Indigastrum fastigiatum* (E. Mey.) Schrire (Hilliard & Burtt 7638, PRE). Oblique stigma detail. (X 132)
- H) *Indigofera wituensis* Bak.f. (Polhill & Paulo 889, PRE). Persistent style base at apex of pod. (X 46)

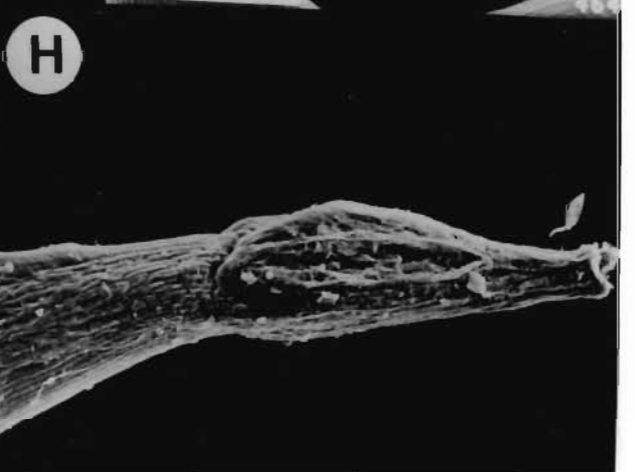
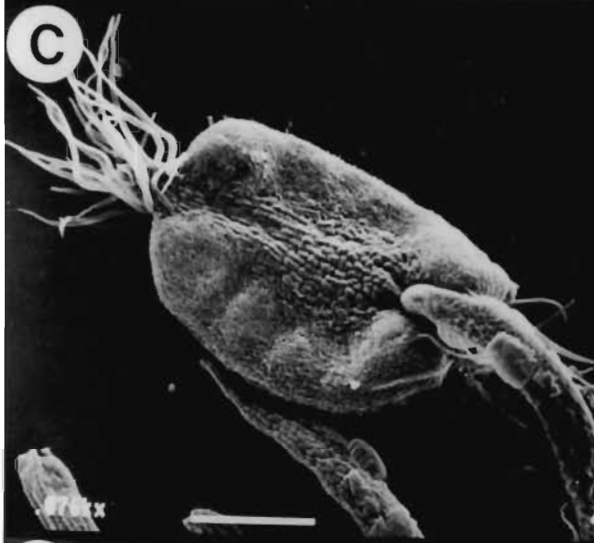


PLATE 4.6 SEM - Trichomes and glands. III (leaves, petals, anthe

FIGURES:

- A) *Indigofera schimperi* Jaub. & Spach var. *schimperi*. (Schrire 2415, K). Wing petal margin, cilia. (X 204/102)
- B) *Indigofera schimperi* Jaub. & Spach var. *schimperi*. (Schrire 2415, K). Biramous hairs developing on young ovary. (X 240)
- C) *Indigofera schimperi* Jaub. & Spach var. *schimperi*. (Schrire 2415, K). Anthers with extended apical connective. (X 48)
- D) *Indigofera schimperi* Jaub. & Spach var. *schimperi*. (Schrire 2415, K). Anther apical connective, detail. (X 480/240)
- E) *Indigofera nebrowniana* Gillett (Codd 2229, PRE). Leaflet; glandular apex. (X 30)
- F) *Indigofera herrstreyi* Schrire (Strey 7252, PRE). Pearl body on calyx lobe.
- G) *Indigofera verrucosa* Eckl. & Zeyh. (Schrire 2445, K). Clump of pearl bodies at the base of the petiole. (X 103)

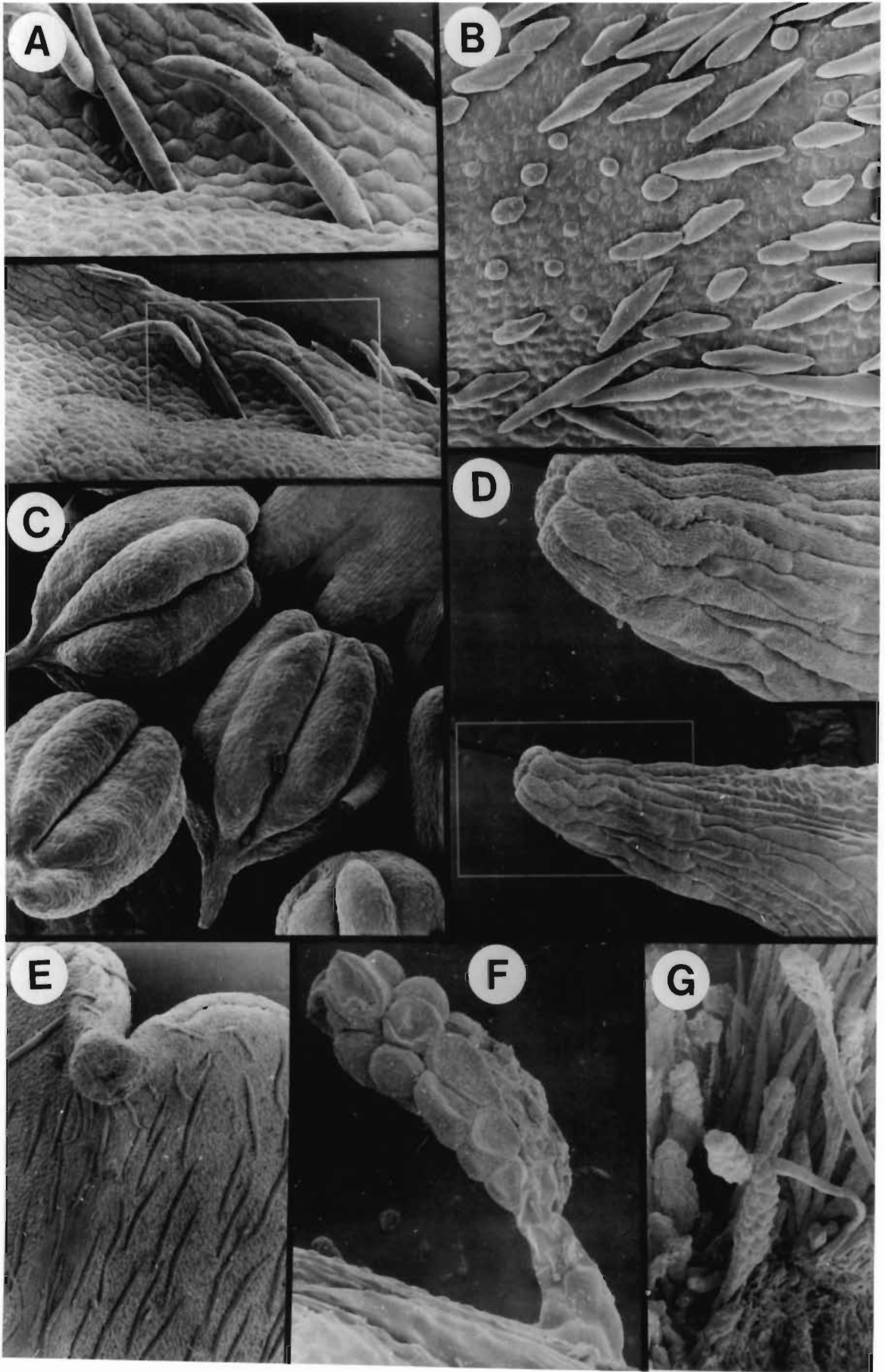


PLATE 4.7 SEM - Trichomes and glands. IV (stems, leaves).

FIGURES:

- A) *Indigofera heterotricha* DC. (Schrire 2416, K). Stem; multi-seriate gland-tipped trichomes. (X 21)
- B) *Indigofera heterotricha* DC. (Schrire 2416, K). Stem; multi-seriate gland-tipped trichomes, detail. (X 68)
- C) *Indigofera heterotricha* DC. (Schrire 2416, K). Stem; shorter multiseriate gland-tipped trichome, detail. (X 102)
- D) *Indigofera heterotricha* DC. (Schrire 2416, K). Multi-seriate gland-tipped trichome, apex detail. (X 708)
- E) *Indigofera acanthoclada* Dinter (Giess & Muller 12094, PRE). Leaflet margin, gland detail. (X 336)
- F) *Indigofera acanthoclada* Dinter (Giess & Muller 12094, PRE). Leaflet margin, glands. (X 46)
- G) *Indigofera brevicalyx* Bak.f. (Moody 7966, PRE). Lateral "blister" glands on leaflet margins. (X 33)
- H) *Indigofera microcarpa* Desv. (Drummond 7770, PRE). Lower leaflet surface; discoid (cavitated) pearl body detail. (X 330)

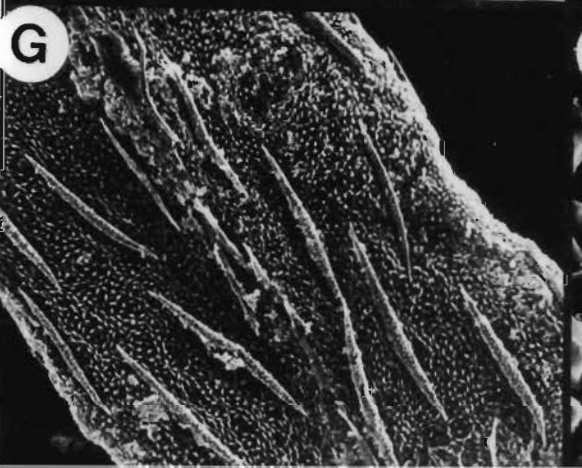
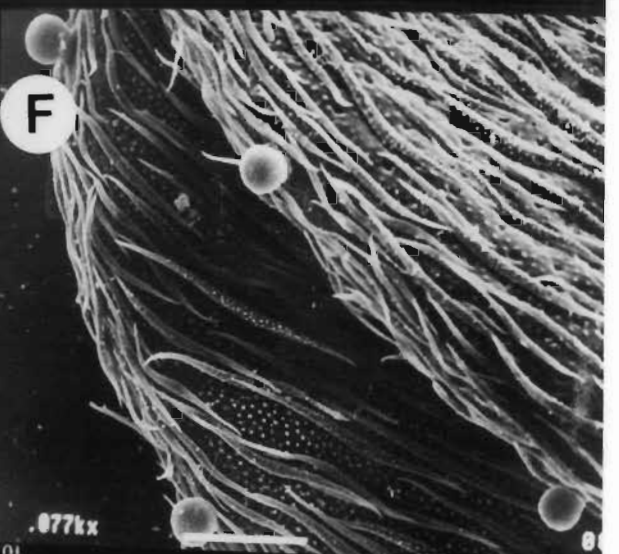
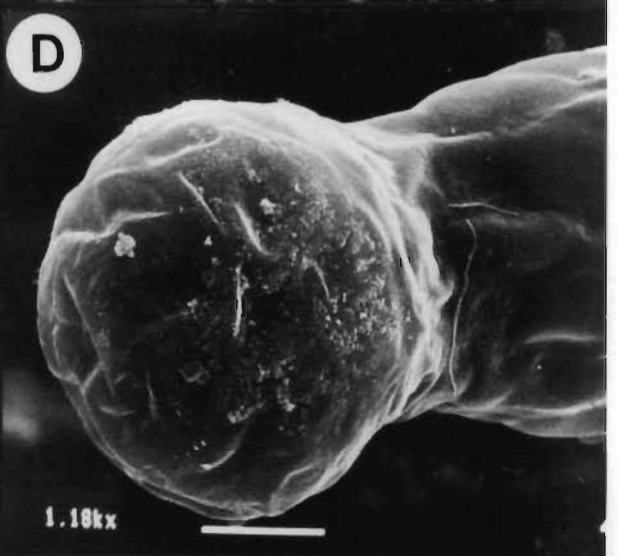
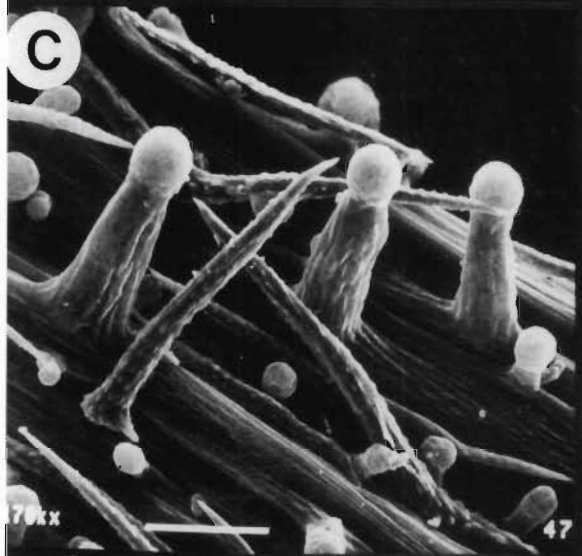
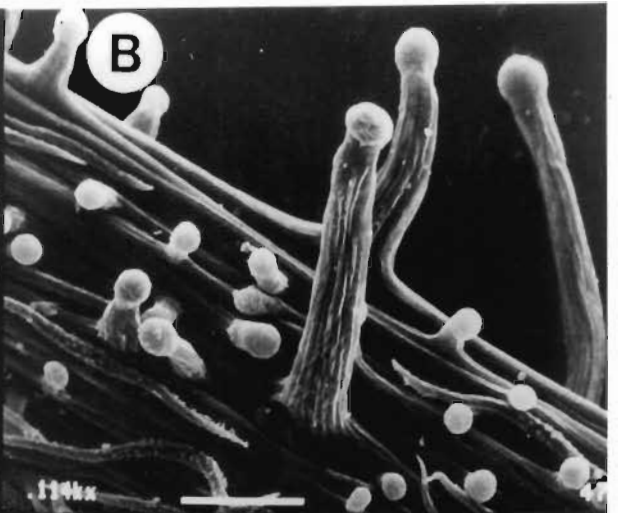
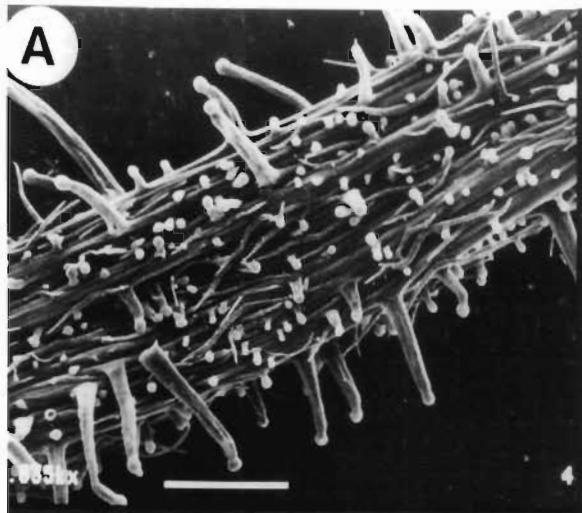


PLATE 4.8 SEM - Trichomes and glands, V (pearl bodies).

FIGURES:

- A) *Indigofera nummulariifolia* (L.) Livera ex Alston (Polhill & Paulo 2100, PRE). Lower leaflet surface; scattered pearl bodies. (X 65)
- B) *Indigofera nummulariifolia* (L.) Livera ex Alston (Polhill & Paulo 2100, PRE). Lower leaflet surface; pearl body detail. (X 648)
- C) *Indigofera anabibensis* Schreiber (Giess & Leippert 7523, PRE). Lower leaflet surface; covered pearl body. (X 480)
- D) *Indigofera anabibensis* Schreiber (Giess & Leippert 7523, PRE). Lower leaflet surface; pearl body with cover broken open. (X 504)
- E) *Indigofera vicioides* Jaub. & Spach var. *vicioides* (Miller B/1021, PRE). Pearl body, found scattered on stems. (X 450)
- F) *Indigofera macrocalyx* Guill. & Ferr. (Espírito Santo 2819, PRE). Lower leaflet surface; cylindrical pearl bodies. (X 204)

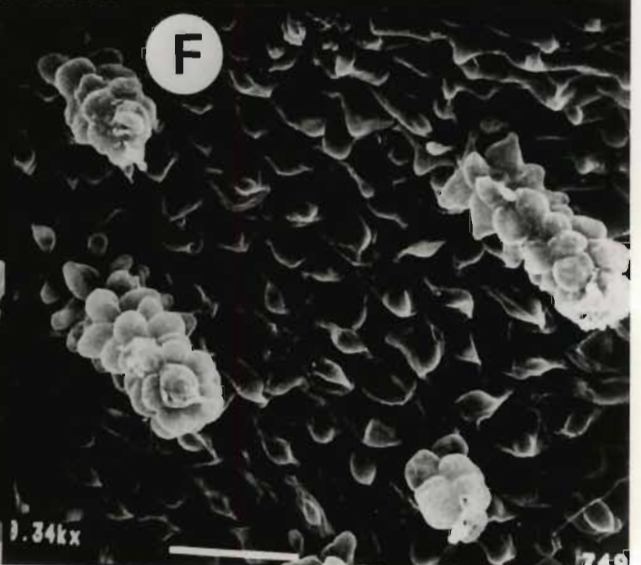
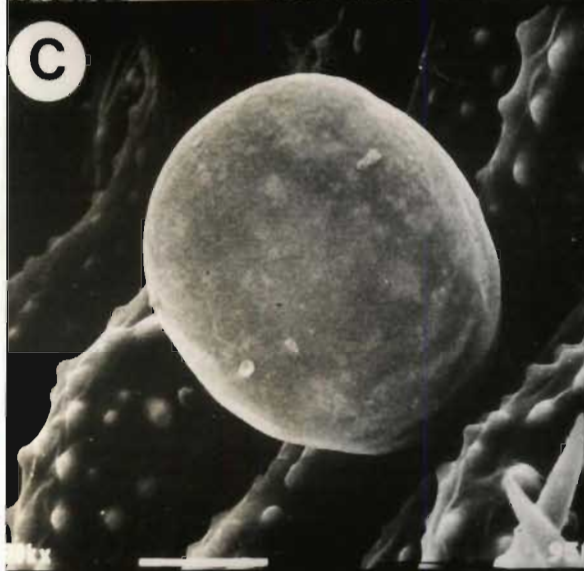
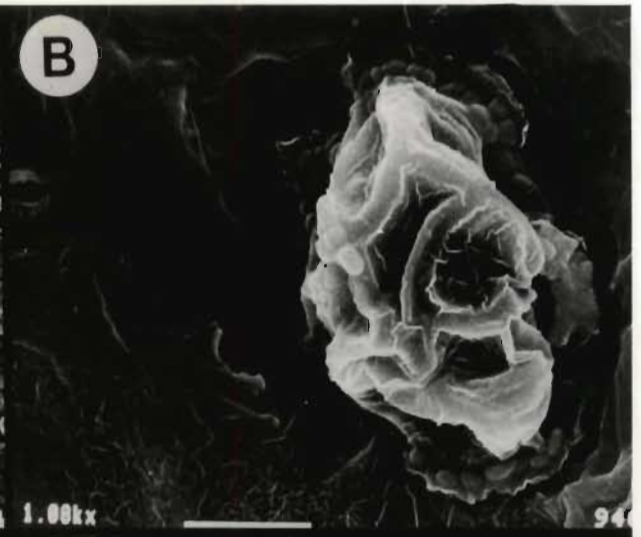
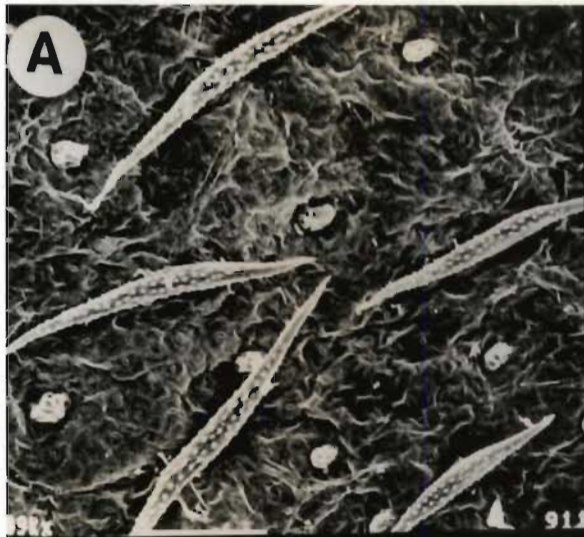


PLATE 4.9 Leaflet anatomy - epidermal structures, tannin sacs, areoles.

FIGURES:

- A) *Indigofera astragalina* DC. (Schrire 2414, K). Vein areoles, terminal veins with isolated tracheoids. (X 10)
- B) *Indigofera tristis* E. Mey. (Strey 10791, PRE). Vein areoles, terminal veins with many tracheoids. (X 10)
- C) *Indigofera evansii* Schltr. (Hilliard & Burtt 15010, PRE). Tannin sacs in mesophyll. (X 10)
- D) *Indigofera subcorymbosa* Bak. (Prosser 2028, PRE). Even mesophyll, lacking tannin sacs. (X 20)
- E) *Indigofera denudata* L.f. (Schrire 2468, PRE). Dense accumulation of tracheoids (xerophytic habit). (X 10)
- F) *Indigofera trigonelloides* Jaub. & Spach (Giess & Leippert 7337, PRE). Microfibrils below head cell in T-shaped biramous hair. (X 20)
- G) *Indigofera hispida* Eckl. & Zeyh. (Schrire 2474, K). Biramous hair base and surrounding cells. (X 40)
- H) *Indigofera astragalina* DC. (Schrire 2414, K). Biramous hairs with arms very unequal in length. (X 20)

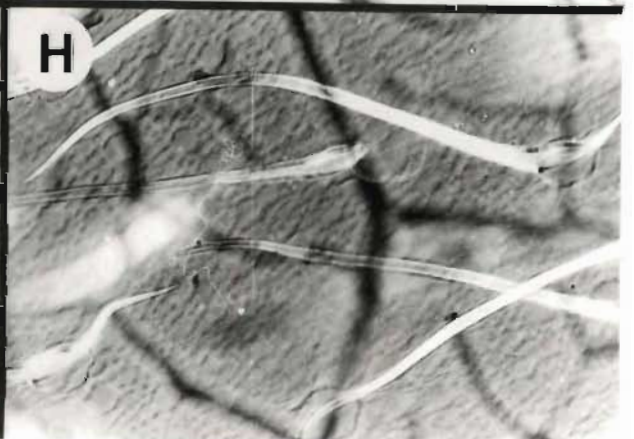
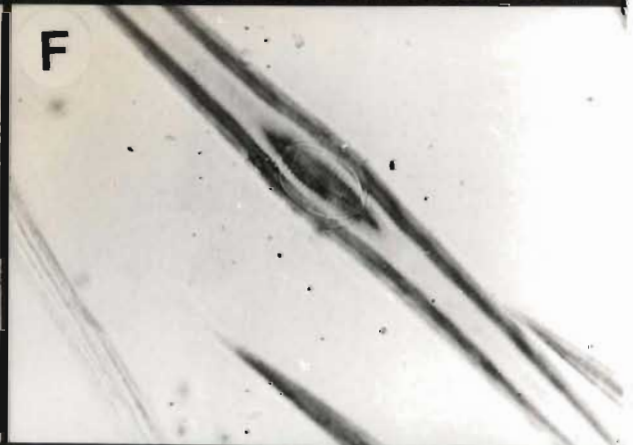
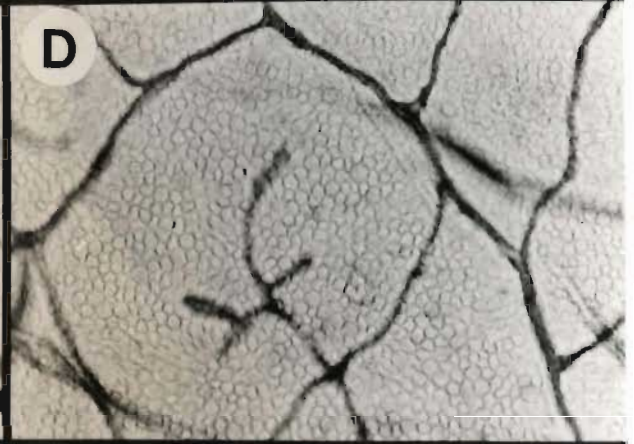
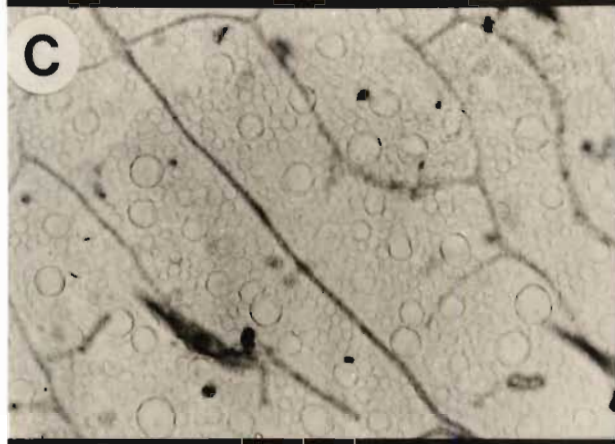
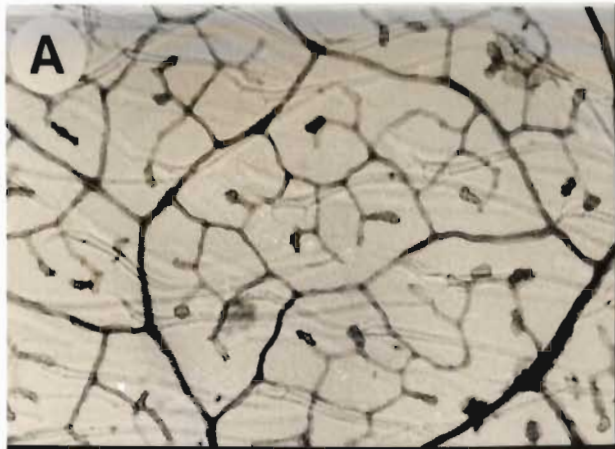


PLATE 4.10 Anatomy - Leaf venation, tracheoids, bundle sheath.

FIGURES:

- A) *Indigofera hiliaris* Eckl. & Zeyh. (Schrire 2394, K). Leaflet venation, showing thick walled tertiary and quaternary veins, and steeply ascending secondary veins. (X 3)
- B) *Indigofera tristis* E. Mey. (Strey 10791, PRE). Leaflet venation, showing no thickening of walls in tertiary and quaternary veins, and secondary veins branching at a broad angle to the midvein. (X 4)
- C) *Indigofera astragalina* DC. (Schrire 2414, K). Leaflet venation, showing no thickening of walls in tertiary and quaternary veins, and secondary veins branching at a broad angle to the midvein. (X 3)
- D) *Indigofera hispida* Eckl. & Zeyh. (Schrire 2474, K). Elongated tracheoid elements situated along the veins. (X 10)
- E) *Indigofera homblei* Bak.f. & Martin (Grobbelaar 437, PRE). Areole with terminal vein surrounded by a bundle sheath. (X 10)
- F) *Indigofera subcorymbosa* Bak. (Prosser 2028, PRE). Marginal areoles with brachytracheoids and sclerotracheoids. (X 20)
- G) *Indigofera astragalina* DC. (Schrire 2414, K). Marginal areoles with brachytracheoids and sclerotracheoids. (X 20)
- H) *Indigofera hispida* Eckl. & Zeyh. (Schrire 2474, K). Tracheoids, detail. (X 20)
- I) *Indigofera astragalina* DC. (Schrire 2414, K). Accumulation of tracheoids at the apical hydathode. (X 10)

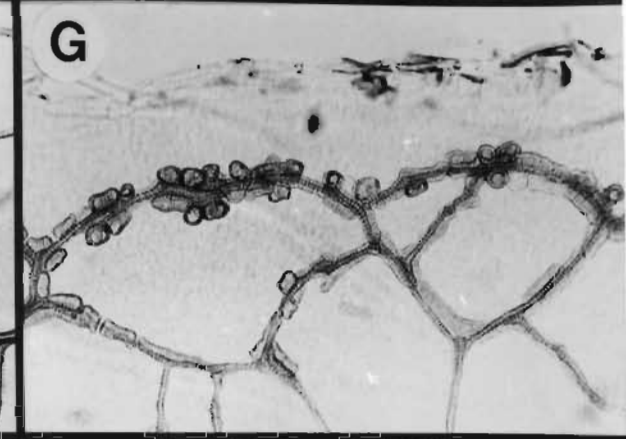
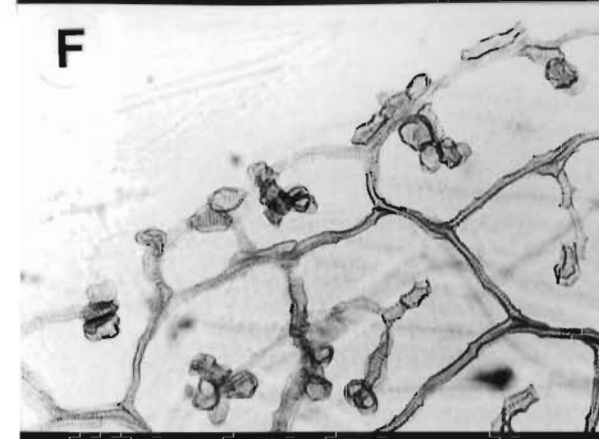
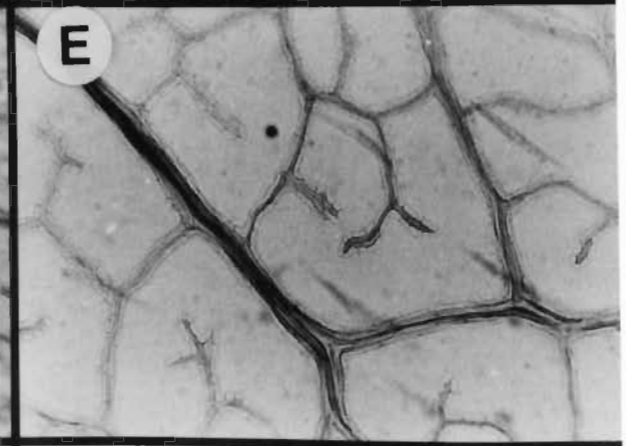
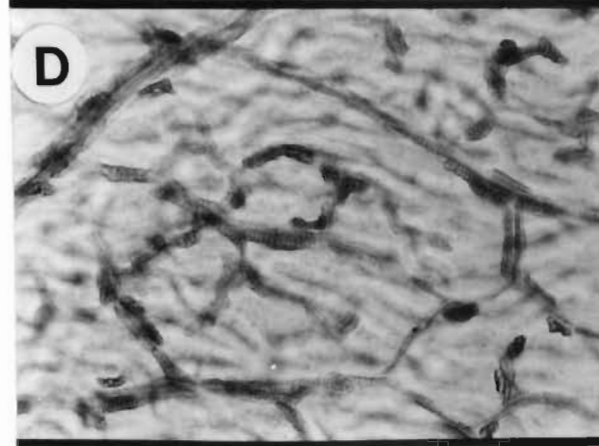
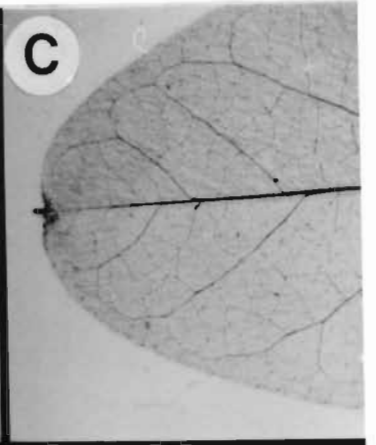
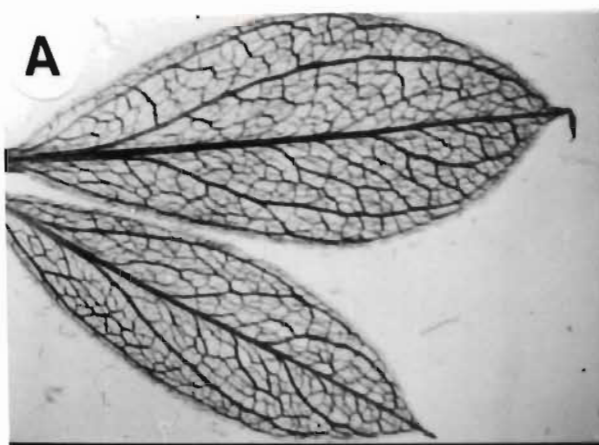


PLATE 4.11 Anatomy - Leaf venation, calcium oxalate crystals.

FIGURES:

- A) *Indigofera trita* L.f. subsp. *subulata* (Vahl ex Poir.) Ali (De Winter 3999, PRE). Prismatic crystals around the base of biramous hairs. (X 20)
- B) *Indigofera subcorymbosa* Bak. (Prosser 2028, PRE). Twin-prismatic crystals in veins. (X 20)
- C) *Indigofera nervosa* Schrire (ms.) (Schrire 2332, K). Prismatic crystals in veins. (X 20)
- D) *Indigofera bainesii* Bak. (Codd 8447, PRE). Crystal sand in mesophyll. (X 10)
- E) *Indigofera nervosa* Schrire (ms.) (Schrire 2332, K). Crystal ideoblasts in veins. (X 20)
- F) *Indigofera heterotricha* DC. (Schrire 2416, K). Crystal sand and densely packed prismatic crystals arranged perpendicularly to the margin. (X 10)
- G) *Indigofera nervosa* Schrire (ms.) (Schrire 2332, K). Leaflet venation, showing thick walled secondary and tertiary veins, and steeply ascending secondary veins. (X 3)
- H) *Indigofera pondoensis* Bak.f. ex Schrire (ms.) (Van Wyk 5349, PRE). Leaflet venation with steeply ascending secondary veins. (X 3)

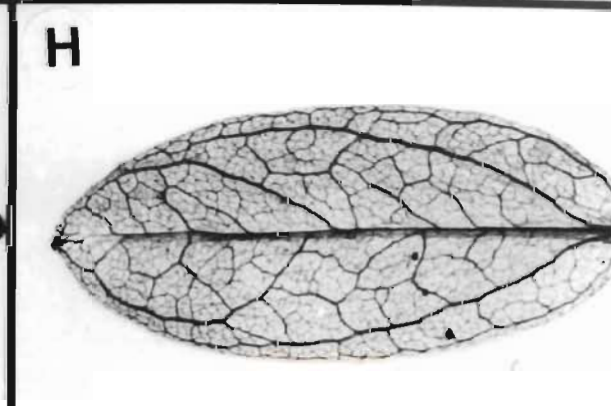
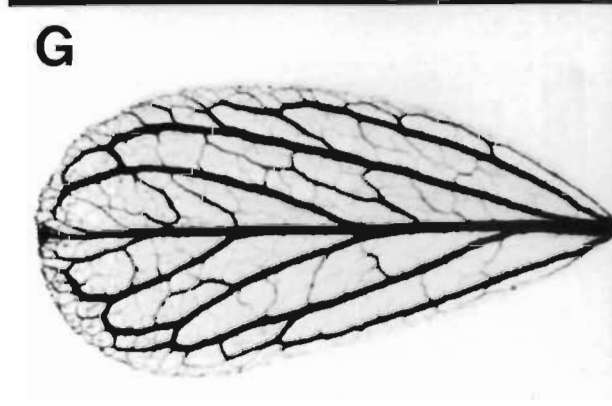
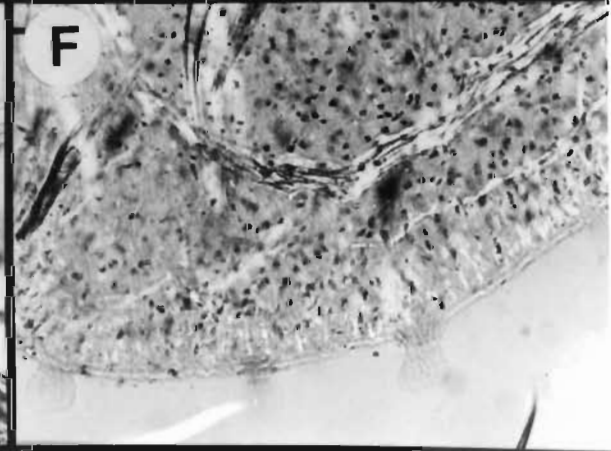
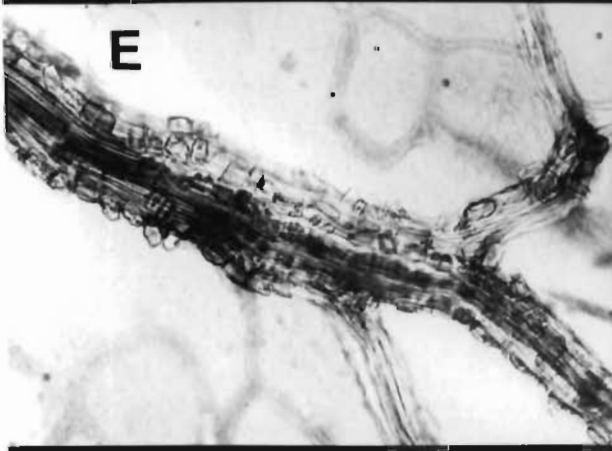
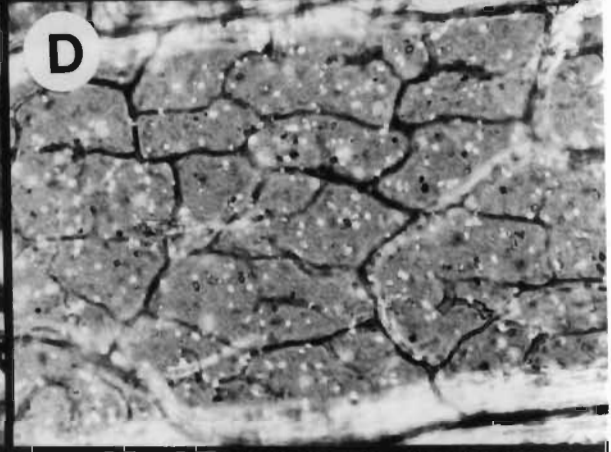
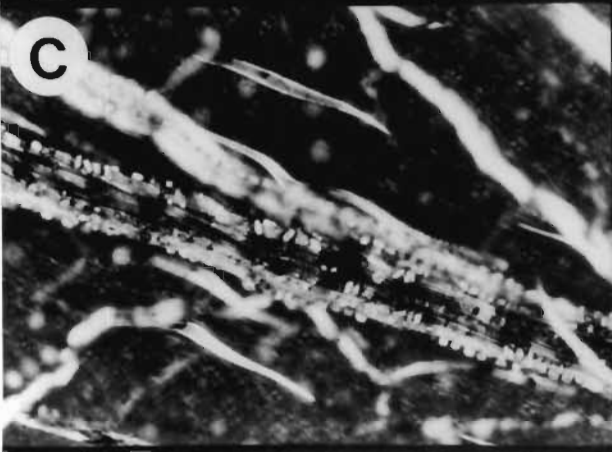
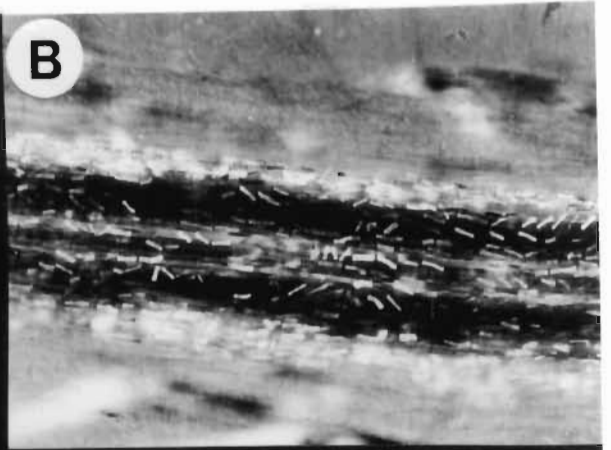
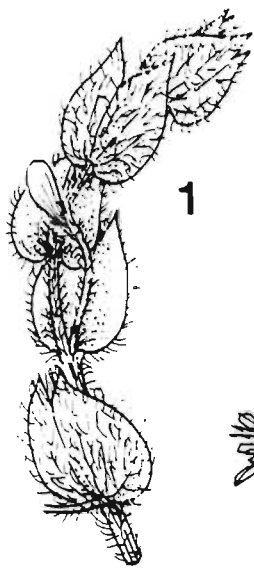


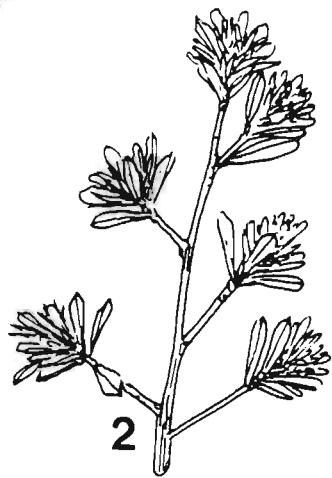
PLATE 4.12 Inflorescence morphology, calyces.

FIGURES:

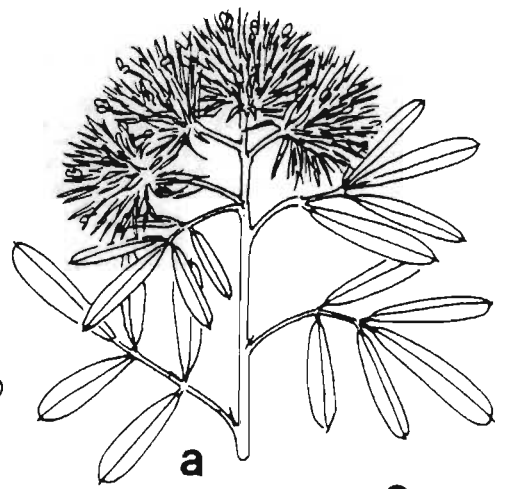
- 1) *Indigofera strobilifera* (Hochst.) Hochst. ex Bak. (Polhill & Paulo 2146, K). Broad, partially fused, bracts subtending 1-2 flowers, individual inflorescences aggregated in a distinct co-florescence or strobilus. (X 1.5)
- 2) *Indigofera pulchra* Willd. (Ern 3083, K). Individual flowering branches of reduced racemes congested into subcapitate heads, the entire syn-florescence appearing paniculate. (X 1.5)
- 3a) *Indigofera capitata* Kotschy (Forest Herbarium Ibadan 30780, K). Dense capitate syn-florescences with an involucre of leaves passing down to 5-3-1-lobed bracts subtending reduced racemes of 1-3 flowers. (X 1.5)
- 3b) *Indigofera capitata* Kotschy (Forest Herbarium Ibadan 30780, K). Single flower subtended by a scarious tri-lobed bract. (X 4)
- 4) *Indigofera nebrowniana* Gillett (Hutchinson 2938, K). Short peduncled, few-flowered, racemes more or less equalling, and partially obscured by, the leaves. (X 1.5)
- 5) *Indigofera procumbens* L. (Esterhuysen 36052, K). Inflorescences on peduncles more than twice the length of the leaves. (X 1.5)
- 6) *Indigofera tanganyikensis* Bak.f. (Gillett 20999, K). Long (slender) pedunculate, few-flowered racemes (the flowering rhachis shorter than the peduncle), more or less equalling, but not obscured by, the leaves. (X 1.5)
- 7) *Indigofera schinzii* N.E.Br. (Scheepers 137, K). Inflorescences many-flowered, peduncle and rhachis longer than twice the length of the subtending leaves. (X 1.5).
- 8) *Indigofera concava* Harv. (Burchell 5931, K). Calyx with broadly lanceolate, keeled, lobes imbricate at the base. (X 10)
- 9) *Indigofera arenophila* Schinz (J. Boss PRE 35993, PRE). Calyx with narrowly acuminate lobes, gland-tipped at the apex. (X 10)



1



2

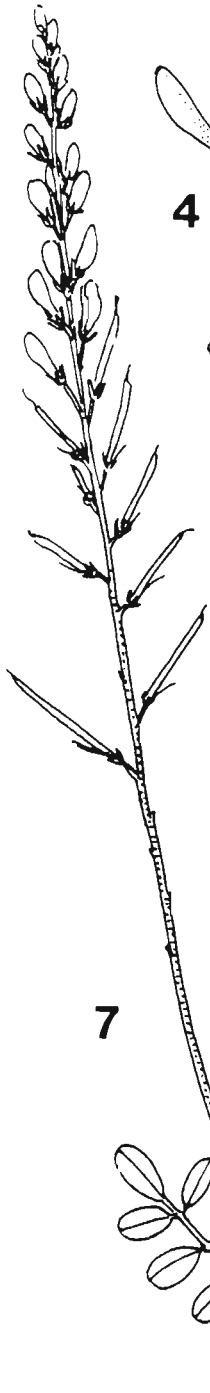


a

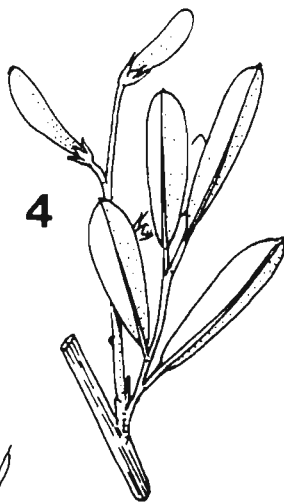
3



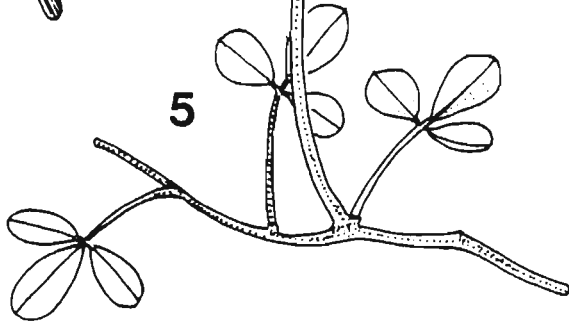
b



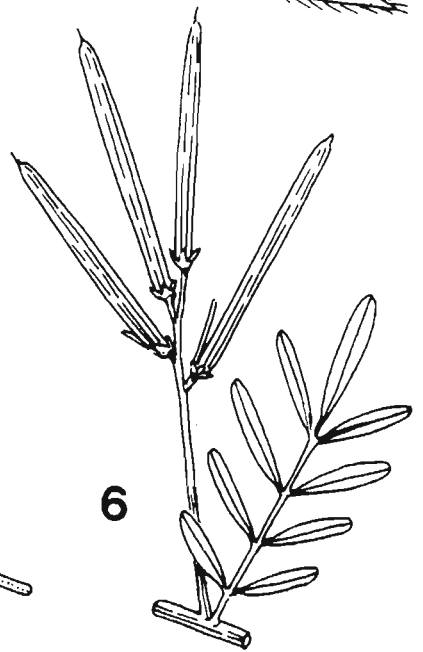
7



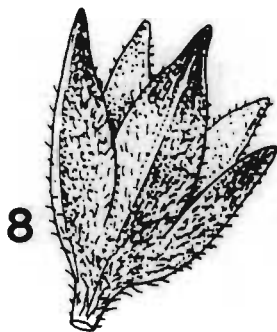
4



5



6



8



9

PLATE 4.13 Flower morphology. I (*Phylloxylon*, *Vaughania*,
Rhynchotropis & *Cyamopsis*)

FIGURES:

1) *Phylloxylon perrieri* Drake (Perrier 4851, K).

- a) Inflorescence, coriaceous bracts and paired bracteoles on the pedicels. (X 2)
- b) Flower, calyx lobes shorter than the tube. (X 4)
- c) Standard. (X 4)
- d) Wing petal. (X 4)
- e) Keel. (X 4)
- f) Staminal sheath, anthers without apiculate connective, glabrous. (X 4)
- g) Bracteoles. (X 10)

2) *Vaughania interrupta* sp. nov. (*nom. nud.*) (Du Puy M129, K).

- a) Leaves and inflorescences, phyllodenous petioles. (X 2)
- b) Asymmetrical flower; twisted keel, with one wing bent upwards, the other down. (X 4)
- c) Standard, asymmetrical. (X 4)
- d) Wing petal, (X 4)
- e) Keel, curved below. (X 4)
- f) Staminal sheath, curved; filaments free for 1-2 mm distally; anthers plumose hairy above and below. (X 6)

3) *Rhynchotropis poggei* (Taub.) Harms (Richards 10697, K).

- a) Flower. (X 4)
- b) Standard. (X 4)
- c) Wing petal. (X 4)
- d) Keel, prolonged rostrate apex. (X 4)
- e) Staminal sheath; filaments free for 1-2 mm distally; anthers plumose hairy above and below. (X 8)
- f) Style and oblique stigma. (X 8)

4) *Cyamopsis senegalensis* Guill. & Perr. (Giess et al. 5698, K).

- a) Flower. (X 4)
- b) Staminal sheath; filaments free for less than 1 mm distally, anthers glabrous. (X 10)
- c) Style, capitate stigma. (X 10)

Cyamopsis serrata Schinz (Corby 1834, K).

- d) Style, oblique stigma. (X 10)

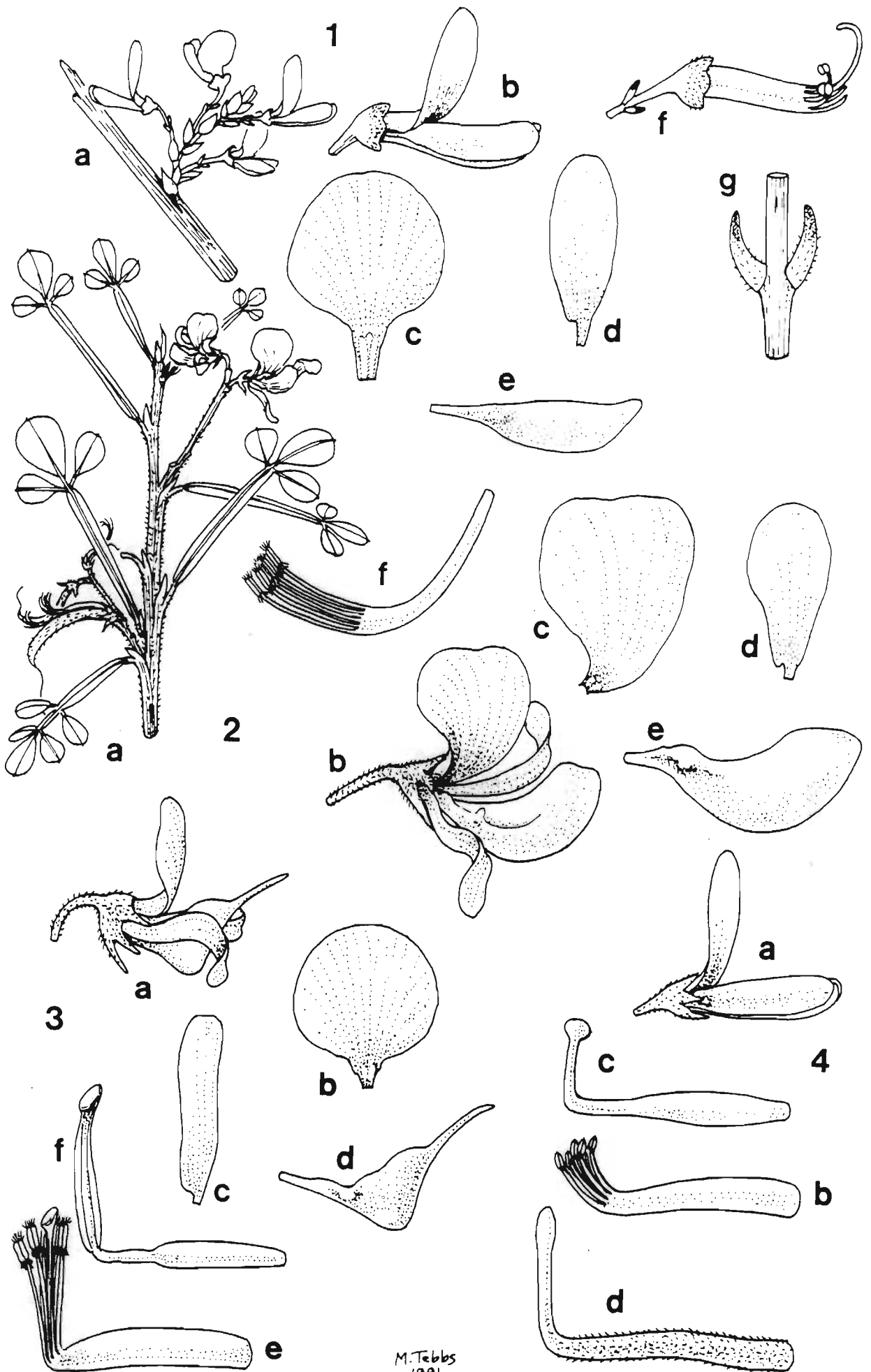


PLATE 4.14 Flower morphology. II (*Microcharis*, *Indigastrum* & *Indigofera*)

FIGURES:

- 1) *Indigofera hedyantha* Eckl. & Zeyh. (Schrire 2352; spirit colln., K). Calyx with lobes less than twice the length of the tube. (X 10) (2) Broad sinus between vexillar calyx lobes. (X 10) (3) *Indigofera longebarbata* Engl. (Schrire 2354, K). Calyx lobes more than twice the length of the tube. (X 10) (4) *Indigofera hedyantha* Eckl. & Zeyh. (Schrire 2352; spirit colln., K). Untripped flower, side view; standard fully reflexed. (X 5) (5) Untripped flower, view from above showing wing platform. (X 4) (6) *Indigastrum argyraeum* (Eckl. & Zeyh.) Schrire (Schrire 2464, spirit colln., K). Standard reflexed distally only. (X 4). (7) *Microcharis galpinii* N.E.Br. (Schrire 2427, K).
- a) Standard, dorsal view. (X 5)
 b) Standard, front view. (X 5)
 c) Pistil, style short and thick, stigma discoid. (X 5)
 d) Keel with prolonged rostrate apex. (X 7)
- (8) *Indigofera spicata* Forssk. (Schrire 2328; spirit colln., K). Standard, front view with central blotch. (X 10) (9) *Indigofera hedyantha* Eckl. & Zeyh. (Schrire 2352; spirit colln., K). Standard, dorsal view with dense, appressed, dark brown strigose vestiture. (X 3) (10) *Indigofera williamsonii* (Harv.) N.E.Br. (Schrire 2323, K). a) Wing petal showing proximal crest which is densely pilose. (X 5) *Indigastrum parviflorum* (Heyne ex Wight & Arn.) Schrire (Schrire 2399, K). b) Wing petal, outer view. (X 10) c) Wing petal, inner view. (X 10) (11) Various keel shapes, showing lateral spurs, proximal fringe of hairs along upper margin, and whether bearded distally.
- a) *Indigofera tristoides* N.E.Br. (Schrire 2378, K). (X 7)
 b) *Indigofera williamsonii* (Harv.) N.E.Br. (Schrire 2323, K). (X 7)
 c) *Indigofera denudata* L.f. (Schrire 2468, K). (X 7)
 d) *Indigofera amoena* Ait. (Schrire 2491, K). Note: the fringe of hairs along the upper margin of the keel is placed distally. (X 4)
 e) *Indigofera jucunda* Schrire (ms.) (Schrire 1410, spirit colln., K). (X 4)
 f) *Indigofera glaucescens* Eckl. & Zeyh. (Schrire 2462, K). (X 7)
 g) *Indigofera pappi* Fourc. (Schrire 2473, K). (X 7).
 h) *Indigofera herrstreyi* Schrire (ms.) (Stirton 11687; spirit colln., K). (X 7)
 i) *Indigofera arrecta* Hochst. ex A. Rich. (Schrire 2397; spirit colln., K). (X 7)
 j) *Indigofera filiformis* L.f. (Schrire 2495, K). (X 5)
- (12) *Indigofera hedyantha* Eckl. & Zeyh. (Schrire 2352; spirit colln., K).
- a) Staminal sheath; filaments free distally for less than 1 mm. (X 5)
 b) Anther; extended apical connective, hairs above and below. (X 10)

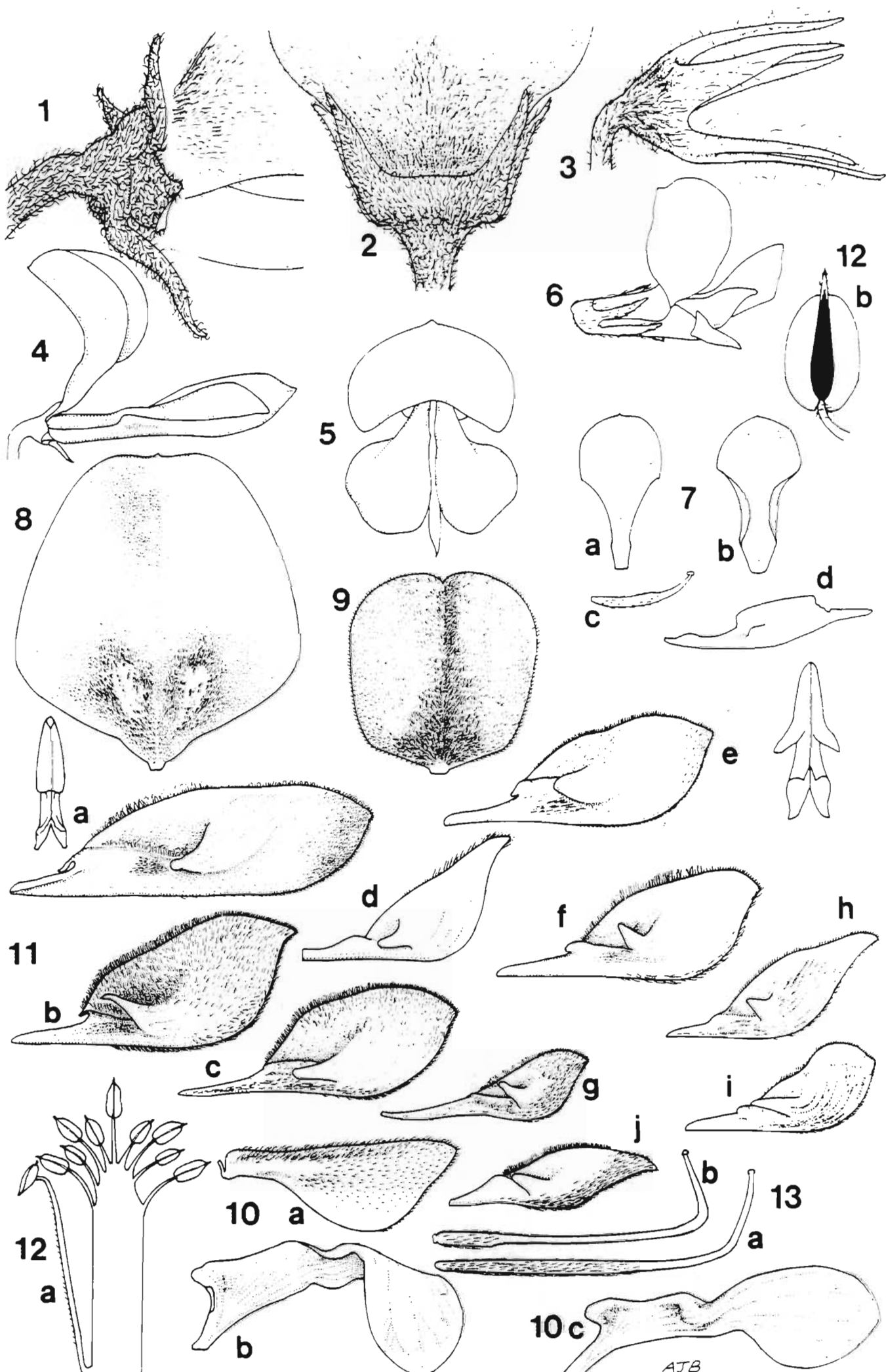
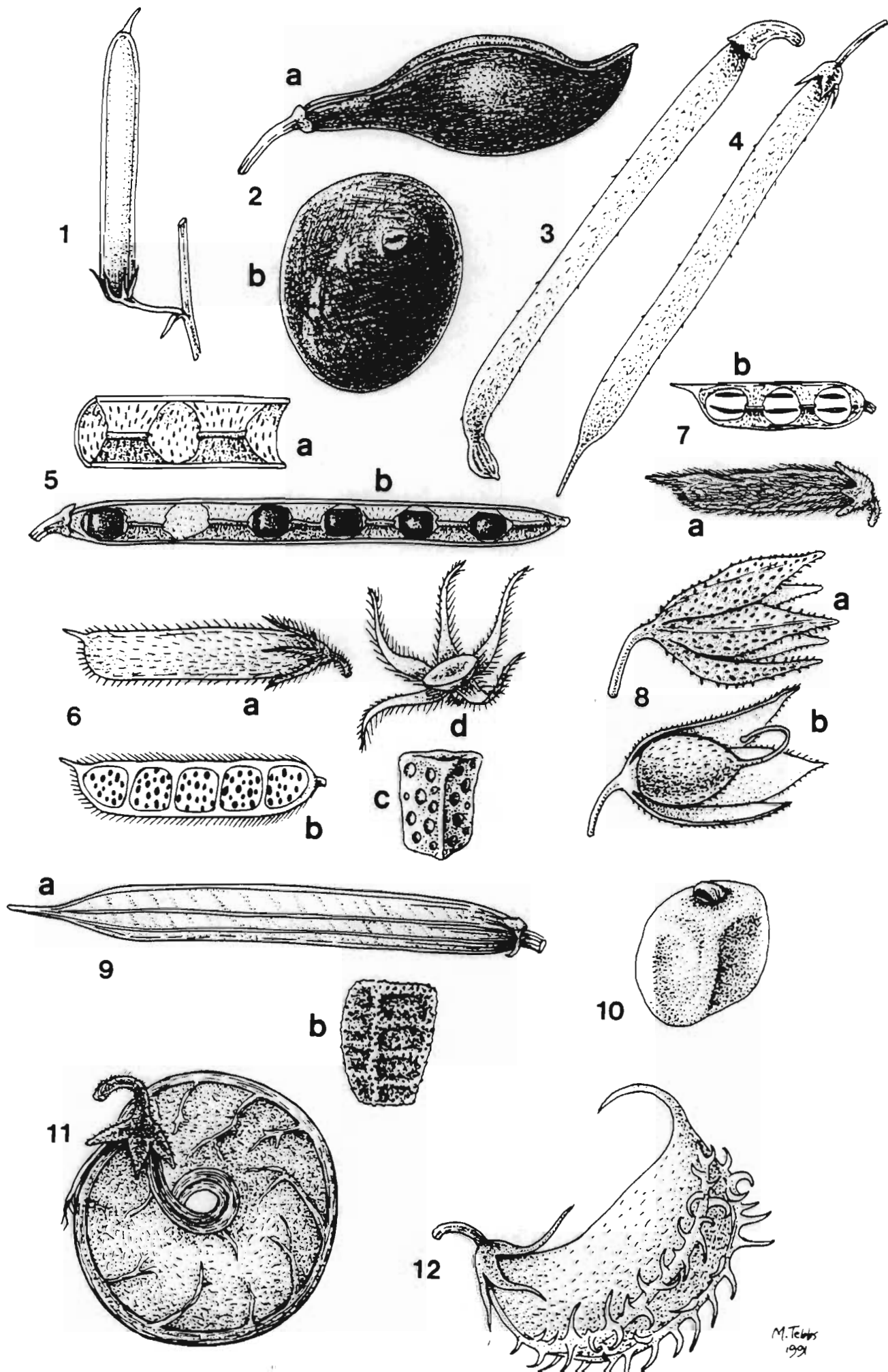


PLATE 4.15 Pod and seed morphology.

FIGURES:

- 1) *Microcharis galpinii* N.E.Br. (Corby 1299, K). Pod held at right angles to the pedicel. (X 4)
- 2) *Phylloxylon decipiens* Baill. (Du Puy M400, K).
 - a) Pod. (X 2)
 - b) Seed. (X 2)
- 3) *Indigofera rhynchocarpa* Welw. ex Bak. (Gossweiler 3842, K). Cylindrical pod with well developed style base apically. (X2)
- 4) *Indigofera tristoides* N.E.Br. (Meeuse 10319a, K). Cylindrical pod with rostrate apex. (X 2)
- 5) *Indigofera rhynchocarpa* Welw. ex Bak. (Faulkner 388, K).
 - a) Papery endocarp with tannin deposits, detail. (X 4)
 - b) Papery endocarp septa separating seeds. (X 2)
- 6) *Indigofera astragalina* DC. (Codd 5506, K).
 - a) Oblong pod with hirsute vestiture. (X 4)
 - b) Narrow endocarp septa with large tannin vesicles. (X 4)
 - c) Seed with pitted surface from tannin vesicles. (X 10)
 - d) Persistent cup-like base remaining with calyx once pod valves are caducous. (X 6).
- 7) *Indigofera inhambanensis* Klotzsch (Brenan & Vahrmeyer 14222, K).
 - a) Oblong pod with sericeous vestiture. (X 4)
 - b) Tannin stripes in papery endocarp. (X 4)
- 8) *Indigofera macrocalyx* Guill. & Ferr. (Roberty 17114, K).
 - a) Calyx with lobes enlarging in fruit, becoming broad, scarious and densely covered with pearl bodies. (X 6)
 - b) Single seeded, tardily dehiscent, pods with papery walls, pods becoming detached with the calyces. (X 6)
- 9) *Cyamopsis senegalensis* Guill. & Ferr. (Corby 1834, K).
 - a) Broad, subtetragonous, scarious pods with longitudinal ridges and rostrate apex. (X 2)
 - b) Tuberculate seeds. (X 6)
- 10) *Indigofera tristoides* N.E.Br. (Thornicroft 403, K). Persistent papery funicle remaining attached to the seed hilum. (X1)
- 11) *Indigofera circinnata* Benth. ex Harv. (Werdeman & Oberdieck 1721, K). Flattened and coiled pod. (X 4).
- 12) *Indigofera nummulariifolia* (L.) Livera ex Alston (Richards 11027, K). Single seeded, indehiscent pod with spiny processes along the dorsal sutures. (X 4)



CHAPTER 5

CHARACTER ANALYSIS: ADAPTATIONS & DEVELOPMENTAL CONSTRAINTS

5.1. INTRODUCTION

Cladistics provides a logically and empirically sound basis from which the phylogeny of a group can be inferred, and it has placed a much greater emphasis on critical selection of data and the quality of data analysis in systematics (Fink 1986). The phylogeny can serve as an independent and explanatory template for other evolutionary studies, e.g. historical biogeography, developmental biology, speciation, historical ecology, and adaptation (Coddington 1988; Donoghue 1989; Funk & Brooks 1990; Wanntorp *et al.* 1990).

Cladistic analyses add the essential historical element to fields like evolutionary biology. Cladograms help identify the context in which features evolved and they specify which organisms should be compared in evaluating the causes of character change (Donoghue 1989). When ahistorical correlations are used, they do not estimate the number of times a feature evolved and are not critical about the direction and order of character transformations (Donoghue 1989). Cladistics, therefore, provides clarification and testability for hypotheses that otherwise can only be judged by their plausibility (Coddington 1988). It is a method for discriminating among causal explanations through statements about the sequence in which features originated (Wanntorp *et al.* 1990). Cladograms, by specifying which characters were already present (and which were not) at the time a particular character arose, can help interpret this sequence.

The major aim of this chapter is to study character evolution in the African Indigoferaeae. Characters are observed from:

- 1) an ecological perspective, i.e. as products of functional-structural relationships where natural selection is responsible for maintaining their roles either as adaptations or exaptations (Gould & Vrba 1982).
- 2) a developmental or phylogenetic perspective, i.e. as morphologies directing development into well defined pathways. Morphologies may either channel phenotypic change in directions set by past history and formal structure, or influence which pathway of development is adopted in evolution; or open up new areas of adaptive radiation. Such morphologies behave as developmental constraints (i.e. through the accumulation or loss of burden, canalization and key morphologies, or by heterochrony).

5.1.1. *Guide to concepts discussed in the following sections.*

1) Structural-functional relationships:

- a) Adaptations: features arising directly from selection for a current function
- b) Exaptations: no direct origin through selection; features co-opted for a useful effect
- c) Aptations: features whose role is maintained by natural selection, i.e. combines adaptations and exaptations
- d) Non-aptations: features arising fortuitously or because of linkage to other features

2) Developmental constraints:

- a) Burden: responsibility of a feature, i.e. the number of other features dependent on an initial feature, making its subsequent modification more (or less) difficult

- b) Canalization: describes a pattern explaining pathways of evolution, i.e. as features are added (or lost) interactions become more (or less) integrated
- c) Key morphologies: features responsible for canalization, i.e. the accumulation (or loss) of key morphologies is seen by different trends and patterns of evolution
- d) Heterochrony: mechanisms of breaking constraints through changes in the timing and rates of development

5.2. METHODS

The method of comparative biology based on phylogenetic systematics (Brooks 1985; Wiley 1988; Funk & Brooks 1990) was used as modified by Linder (1991).

Funk & Brooks (1990) have evaluated two major ways of using cladograms in comparative biology:

- 1) Mapping of certain characters of interest on a cladogram to estimate both when and how many times a feature has arisen in the group being studied. This is the method used in the present study.
- 2) Comparison of more than one cladogram to see if there is evidence of processes affecting more than one lineage at a time. The following questions need to be asked:
 - a) What parts of the different cladograms agree with each other, or what parts are responsible for any ambiguity?
 - b) How does the history of one clade or a set of areas explain the history of another clade or clades?

Portions of the cladograms that are homologous are the historically determined contribution and portions that are homoplasious are not historically based.

5.2.1. *Ecological analyses*

Characters playing a role in a particular ecological association (see chapter 1), were mapped on the cladogram of the tribe. The cladogram was then used to interpret causes and consequences of character transformations in terms of adaptations (Gould & Vrba 1982; see discussion below).

The following analyses of ecological associations were made:

Adaptations in the tribe Indigoferae (Tables 5.1 & 5.2)

- 1) Herbivore defences and methods of protecting resources (Tables 5.3 & 5.4; Fig. 5.3).
- 2) Seed dispersal mechanisms in the derived sections of *Indigofera* (Table 5.5; Fig. 5.5).

Adaptations in the Cape sections of Indigofera (Table 5.6)

- 3) Herbivore defences and methods of protecting resources (Table 5.7; Fig. 5.3).
- 4) Plant features attractive to pollinators (Table 5.8; Fig. 5.4).
- 5) Habit, seasonality and other responses to the environment, e.g. survival strategies (Table 5.9; Fig. 5.5).

In each of the above analyses, the characters involved were assessed for homology, and where necessary, plesiomorphic and apomorphic conditions were established for character transformations. Morphological characters were treated as ordinal multistate variables (Pimentel & Riggins 1987) because the character states are linked in a linear sequence as part of a morphocline.

Characters were scored for presence in the taxa. The final suite of characters per taxon, for a particular ecological association, was then substituted at the terminal nodes of the cladogram. Unknown data were represented by a question mark.

All nodes were numbered on the cladogram and the most parsimonious interpretation of the character states at each internal node was obtained using the Farris optimization (Mickeyvich 1981; Mickeyvich & Weller 1990). Here the character state occurring in two of three taxa surrounding an inner node (a stem species) is assigned to that stem species (Mickeyvich 1982).

The sequence in which various character states arose can now be read from the base of the cladogram up the axes of internal (ancestral) nodes to the terminal taxa. Hypotheses about adaptations were then made (see discussion below) by examining the origin, direction and order of character transformations. The pertinent suites of adaptations were summarized and discussed for each analysis, being broadened to a suggested evolutionary scenario for the Cape sections of *Indigofera*.

5.2.2. *Phylogenetic analyses*

Examples of morphologies behaving as developmental constraints are illustrated with reference to the cladogram.

5.3. THEORY

5.3.1. *Discussion of adaptations*

Evolution can be viewed from a within-lineage or among-lineage perspective (Funk & Brooks 1990). The within-lineage patterns are the focus of population genetics or population ecology. They are the result of microevolutionary events operating on time scales less than the duration of individual species (Stebbins 1950; Dobzhansky 1970).

Evolutionary patterns among lineages are usually the focus of systematics and can be explained by reference to phylogenies. They include phenomena such as adaptations (Williams 1966; Lewontin 1978; Gould & Vrba 1982; Coddington 1988; Donoghue 1989), repeating biogeographic patterns (Nelson & Platnick 1981; Humphries & Parenti 1986; Myers & Giller 1988), and developmental or phylogenetic trends such as the gain or loss of developmental constraints (Waddington 1962; Stebbins 1974; Reidl 1978; Gould & Lewontin 1979; Alberch 1982; Maynard Smith et al. 1985; Donoghue 1989; Gould 1989). These are macroevolutionary events (Simpson 1944; Eldredge & Cracraft 1980), operating over much longer time scales than the duration of individual species. They are often manifested by persistent ancestral traits in descendent species (Funk & Brooks 1990) and they define the boundaries within which microevolution takes place.

Funk & Brooks (1990) consider two important classes of macroevolutionary processes:

- 1) Those affecting many lineages simultaneously and in the same way, i.e. correlated speciation or extinction events related to terrestrial or extraterrestrial perturbations of a periodic nature, e.g. major upheavals associated with:
 - a) climatic fluctuations (global warming or cooling, glaciation, dramatic sea level changes, changing levels of precipitation);
 - b) tectonic events (volcanic eruptions, continental rifting, isostatic uplift or subsidence, mountain building, changes in oceanographic circulation);
 - c) catastrophic asteroid impact events.

- 2) Those affecting particular lineages, i.e. developmental constraints either limit the extent and manner in which species can adapt to different selection regimes, or they establish the arena or context for evolutionary change.

Microevolution and macroevolution are parts of a more inclusive whole represented by the hierarchical nature of biological systems (Eldredge 1985; Funk & Brooks 1990). The relative contributions of these processes are based on the different rates at which they operate rather than on the ability of one process to account for everything (Funk & Brooks 1990).

Certain microevolutionary processes have among-lineage effects. Sources of characters affecting macroevolutionary patterns include biases in phenotypic frequency not directly attributable to natural selection e.g. pleiotropy, linkage, allometry, genetic drift or molecular drive (Mayr 1982; Dover 1986, Levinton 1988) and heterochrony, or changes in the timing of events during ontogeny (Alberch *et al.* 1979; Calow 1983; Funk & Brooks 1990). Some of these are discussed in the next section in terms of developmental constraints.

The origin or maintenance of characters at the macroevolutionary level (see Fig. 5.1) may or may not be influenced by natural selection (Coddington 1988).

Traits arising directly as a result of natural selection (origin), which also owe their continued existence to selection (maintenance), fulfill the criteria of being adaptations to those features responsible for their evolution (Williams 1966; Gould & Vrba 1982; Coddington 1988).

Characters are exaptations (Gould & Vrba 1982) if they arise either: i) as non-adaptations which have been co-opted by natural selection for a current use, or ii) as adaptations which have been coopted for a new use, where that use is now maintained by selection.

The term aptation (Gould & Vrba 1982) encompasses adaptations and exaptations, both of which are maintained by selection for a current use.

N A T U R A L S E L E C T I O N		NATURAL SELECTION	
		ORIGIN	NOT ORIGIN
		APTATIONS	
	MAINTENANCE	ADAPTATION	EXAPTATION
	NOT MAINTENANCE	DEVELOPMENTAL CONSTRAINTS	

Fig. 5.1 The involvement, or not, of natural selection in the origin or maintenance of traits (modified from Coddington 1988).

a) Natural selection directly involved in maintenance of traits = APTATIONS

i) Origin and maintenance = ADAPTATION

ii) Maintenance only = EXAPTATION

b) Natural selection not directly involved in the maintenance of traits = DEVELOPMENTAL CONSTRAINTS

Features not maintained by natural selection i.e. non-adaptations, or non-adaptive traits originating under selection, have usually arisen because of being closely linked with some trait strongly maintained by selection (Coddington 1988). Adaptations or non-adaptations which have become integrated into the developmental programme may act as developmental constraints (concepts discussed in section 5.3.2.).

5.3.1.1. *Adaptations*

Adaptations are genetically programmed features and behaviours that promote fitness (Maynard Smith *et al.* 1985). They are built by natural selection for a current role and are designed specifically (after a period of selection) for effectiveness in that role. This becomes expressed as a particular function (Coddington 1988; Donoghue 1989).

The cladistic viewpoint provides an operational ecological test of evolutionary adaptations.

The hypothesis (Fig. 5.2) is that the derived trait M1 arose at time *t* in the stem lineage of taxa CDE via selection for the derived function F1. The primitive trait M0, with primitive function F0, occurs in taxa A & B. The primitive trait M0 is expected to be an inferior solution to the design problem posed by F1, but it is not necessarily true that M1 is a superior solution to the design problem posed by F0 (Coddington 1988).

Adaptation is supported when the evolution of a derived morphology is strictly coincident with the origin of a derived function on a cladogram (Green 1986; Donoghue 1989).

Cladistic analysis focuses on the historical genesis of adaptation and seeks to test both its origin and maintenance by natural selection. Adaptation is not just an ahistorical interpretation of the function of a trait based on its effect on current fitness (Gould & Vrba 1982; Coddington 1988).

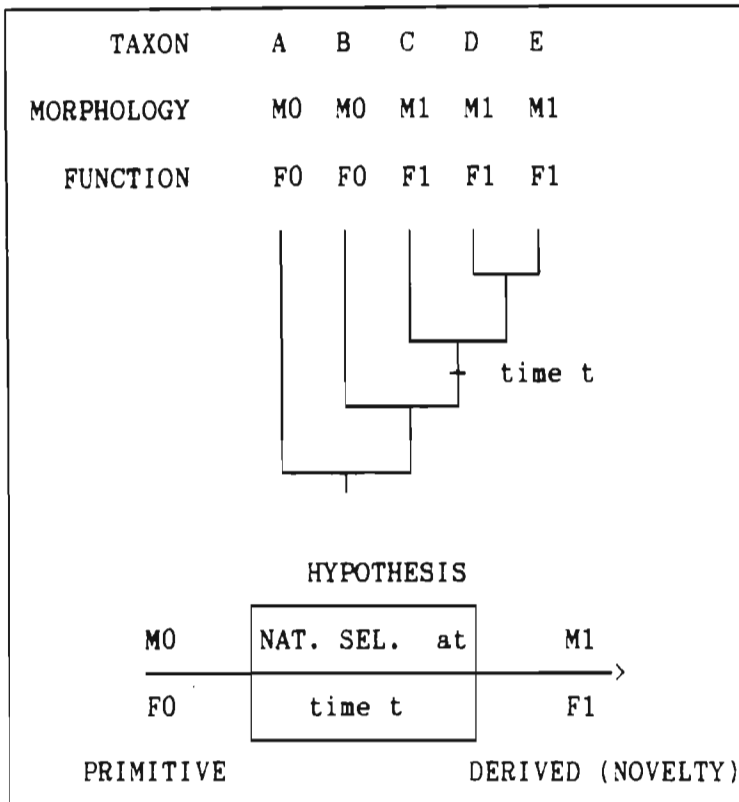


Fig. 5.2. Conceptual model for the origin via natural selection of novel morphology (M1) and function (F1) as an adaptation (after Coddington, 1988).

The testability of origin and maintenance theories derives from assuming continuity of cause from the origin of a trait to the present. Adaptation applies to homologous, apomorphic function promoted by natural selection, in contrast to plesiomorphic function. Under the hypothesis of maintenance and origin, homologous and identical function of a trait, in a number of taxa, is evidence that the original function of the trait has been conserved. If so, then conditions similar to its origin persist and they can be investigated in the present time (Coddington 1988).

Cladistic information tends to be more recoverable and comparable at lower taxonomic levels, and it is easier to establish homology of function. Adaptation can, however, provide possible selectionist explanations for synapomorphies at higher taxonomic levels.

5.3.1.2. *Exaptations*

Exaptations are useful features enhancing fitness, which are co-opted for their effects, but which are not built by natural selection for their current role (Gould & Vrba 1982). They can evolve as non-adaptations, either fortuitously or through being correlated with other characters, or they develop as other uses for existing adaptations. When a secondary utility arises, exaptations can be coopted for a current role.

For any function resulting directly from natural selection there can, at any one time, be multiple effects. Most co-opted structures will not conform precisely to their new role and this may lead to the development of secondary adaptations.

A sequential set of adaptations may result from the conversion of an initial adaptation to an exaptation with a different effect. This in turn allows the development of subsequent adaptations. The sequence in which characters arise provides an empirical basis for testing hypotheses about adaptations, exaptations and the

evolution of syndromes (Coddington 1988; Donoghue 1989). If a feature originated before the function with which it later becomes associated, it is an exaptation (Donoghue 1989).

The order in which characters are assembled in a lineage influences the evolution of functional and developmental interdependencies (see burden, discussed below). The way in which one character facilitates the evolution of other dependent characters (see canalization, discussed below) can be traced on a cladogram, and this can limit the number of possible evolutionary pathways (Donoghue 1989).

Adaptations and nonaptations can provide a large pool of variability at the phenotypic level (Gould & Vrba 1982), which is a source of material for further selection (analogous to mutations at the genetic level). The size of the pool of nonaptations, and the availability of features for cooptation to enhance fitness, may affect evolutionary flexibility.

5.3.2. *Discussion of developmental constraints*

Developmental constraints are defined as biases in the production of variant phenotypes, or limitations to phenotypic variability, caused by the structure, character, composition or dynamics of the developmental system (Gould & Lewontin 1979; Alberch 1982; Maynard Smith et al. 1985; Gould 1989; Schrire 1989).

Some constraints are direct consequences of the laws of physics or the non-variable properties of materials and complex systems, e.g. rules of symmetry, or limitations of dimension, materials and design. These are formal (or universal) constraints applying to all physical systems and to all organisms (Maynard Smith et al. 1985; Gould 1989; Schrire 1989). In contrast, historical (or local) constraints are taxon specific, and are built as particular consequences of an ancestor-descendent lineage. Both are expressed in ontogeny and can therefore be called

developmental constraints (Gould 1989). Although they mark the extremes of a crude continuum, developmental constraints refer only to historical constraints for the following discussion.

There are two levels at which constraints can be defined (Alberch 1982).

- a) The hierarchical organisation of the genome can impose limitations on the possible morphological transitions that can occur during ontogeny and phylogeny.
- b) Interactions at higher levels occur between gene products and the surrounding environment during development. These epigenetic interactions control the processes of morphogenesis and differentiation.

The two levels are not mutually exclusive, but further discussion is limited to constraints arising epigenetically.

Some adaptations have become synapomorphies at higher taxonomic levels (Coddington 1988). If adaptations and non-adaptations become integrated into both the genotype and phenotype they can act as constraints on lower levels (Wanntorp et al. 1990). The persistence of the feature is explained, therefore, not by an original function but because it is part of a co-adapted complex. Maintenance may not be due primarily to selection, but to the accumulation or loss of burden (Reidl 1978; Donoghue 1989), canalization (Waddington 1962; Stebbins 1974) and key morphologies, or to heterochrony.

5.3.2.1. *Burden*

The evolution of a feature may be traced from an initial freedom to vary (where burden is low), to later stages of constancy or fixation, where burden builds up and successful modification is less likely because of the evolution of dependent characters (Donoghue 1989). The concept of burden (Reidl 1978; Donoghue 1989) refers to the responsibility carried by a feature, i.e. the

number of subsequent events that depend on a preliminary event, or the number of features structurally and epigenetically dependent on a fundamental feature.

The hierarchical position of a feature plays a major role as an indicator of burden (Riedl 1978). Heavily burdened elements, which are often expressed earlier in development, may be expected to have larger and more pervasive effects (Riedl 1978; Donoghue 1989). Some features may remain unburdened and burden may even decrease through loss (e.g. reversal), or modification of dependent features.

The evolutionary stasis of a feature can either be due to developmental constraints limiting change, or to strong stabilizing selection (Maynard Smith *et al.* 1985). When interpreting constraints, therefore, the null hypothesis is always the likelihood that selection may be maintaining the uniformity of that feature.

5.3.2.2. *Canalization*

Developmental constraints can act by channelling phenotypic change in a direction set by past history or formal structure (Gould 1989).

The dynamics of development constrains the directionality of morphological transformation (Alberch 1982). Particular taxa tend to produce variations of a limited number and kind (Maynard Smith *et al.* 1985), with selection favouring the development of some of these, while opposing the development of others. A developmental system thus apportions variation within well defined realms by the process of canalization (Waddington 1957, 1962). This is a mechanism of self regulation in developmental pathways, producing a "standard" phenotype buffered against environmental fluctuations or underlying genetic variation.

Canalization is a directed channelling into well defined pathways of development or evolution determined by previously acquired

features, i.e. the nature of each successive change is strongly determined by changes that have occurred previously. As features are added they become dependent on existing features, because they are linked by highly co-ordinated, genetic and epigenetic interactions (Stebbins 1974). Canalization results in discrete sets of morphological states (Alberch 1982) and these potential pathways of transformation have also been called "spandrels" of developmental channels by Gould & Lewontin (1979).

Canalization can be seen on a cladogram as lineages with a canalized character sequence. Some "basic" characters remain constant with variation occurring in dependent characters.

Evolutionary canalization (Stebbins 1974) is defined as the tendency for populations to respond adaptively to new environments, in ways which are determined by characteristics acquired during previous adaptive radiations. Stebbins (1974) stated that the above depends on three other principles; i.e. selective inertia, conservation of organization and adaptive modification along lines of least resistance.

a) *Selective inertia*

The intensity of selection which is required to establish a new adaptive gene combination is many times greater than that required to maintain or modify an adaptive mechanism once it has been acquired.

b) *Conservation of organization*

Whenever a complex structure or integrated biosynthetic pathway has become an essential adaptive unit of a successful group of organisms, the essential features of this unit are conserved in all the evolutionary descendants of the group concerned. Many complex adaptive structures are likely to be retained long after the strong selective pressures required

to establish them have ceased to exist. This accounts for the persistence of useless features.

c) *Adaptive modification along lines of least resistance*

Many possible and alternative pathways exist for adaptation to a particular environmental situation. To a certain extent the particular pathway that an evolutionary line will take depends on a chance combination of genes existing in the initial population. Nevertheless an equally and perhaps even more important factor in determining the pathway of adaptation is the innate genetically controlled pattern of development that exists in the population at any stage of its evolution. This is because the direction of adaptation will often be determined according to the principle of adaptive modification along lines of least resistance (Ganong 1901).

Genetic influence and environmental stimuli have the same causal status in developmental transformation. Both play the role of evocators, and the relevant trigger can result in any one of the possible pre-existing or pre-determined developmental pathways being taken (Waddington 1975; Alberch 1982; Maynard Smith et al. 1985). In the Indigofereae, for example, a number of different developmental pathways have resulted in ant-plant associations, i.e. various types of pearl bodies and extra-floral nectaries have evolved to attract ants. Any particular adaptive shift can be accomplished in any one of several ways and many genetic or developmental pathways may thus produce the same phenotypic transformation. Vavilov (1922) in *The Law of Homologous Series* noted that similarity of developmental pathways in related species causes the appearance of similar variants.

The phylogenetic "fixation path" of a character, which becomes locked in by the evolutionary processes dependent on its existence, has been referred to as phylogenetic inertia (Cheverud et al. 1985).

5.3.2.3. *Key morphologies*

Various genetic and developmental mechanisms have evolved because of the need for lineages to manifest evolutionary plasticity if they are to survive. One factor influencing the developmental pathway actually taken is the relative ease of achieving the available alternatives (Maynard Smith *et al.*, 1985). By biasing the likelihood of entering into one pathway rather than another, a key morphology can affect the evolutionary outcome even when it does not strictly preclude an alternative.

A key morphology has an effect on one or more other morphologies by instituting, or removing, a bias which determines the pathway adopted in evolution or development. The accumulation or loss of morphologies results in switches in constraints as seen by different trends and patterns on a cladogram.

Key morphologies have the following characteristics:

- a) heavy burden
- b) they may be any form of aptation or non-aptation
- c) they can be recognized on a cladogram as being an initial feature to evolve in a canalization sequence
- d) a change in the key morphology is likely to result in the collapse of that particular canalization sequence.

5.3.2.4. *Heterochrony*

Changes in the timing and rates of development (i.e. heterochrony) are mechanisms which lead to the breaking of constraints (Alberch *et al.*, 1979; Calow 1983; Funk & Brooks 1990).

Developmental acceleration (peramorphosis, discussed in Funk & Brooks 1990) is one of a number of heterochronic events which can amplify such changes in timing to have important consequences in the organization and morphology of the adult (Calow 1983). Other examples of heterochrony which commonly occur (although not

apparently in the Indigoferaeae) are the paedomorphic events of neoteny or progenesis (Funk & Brooks 1990). The phenotypic effects that have resulted from modifications in the timing of developmental processes are subject to selection and can lead, if they are significant, to new paths of adaptive radiation and bursts of speciation (Funk & Brooks 1990).

Heterochrony may be involved if a major shift in morphologies is seen on the cladogram, thus indicating a break in previous constraints and the possible opening up of new areas of adaptive radiation. Gould (1977) would argue, however, that all change is ultimately the result of heterochrony, i.e. speciation results from variations in the rates and timing of development of different organs.

TABLE 5.1 APTATIONS IN THE INDIGOFERAE: Taxa (Part 1). Adapted from the cladogram of the tribe (Table 2.3).

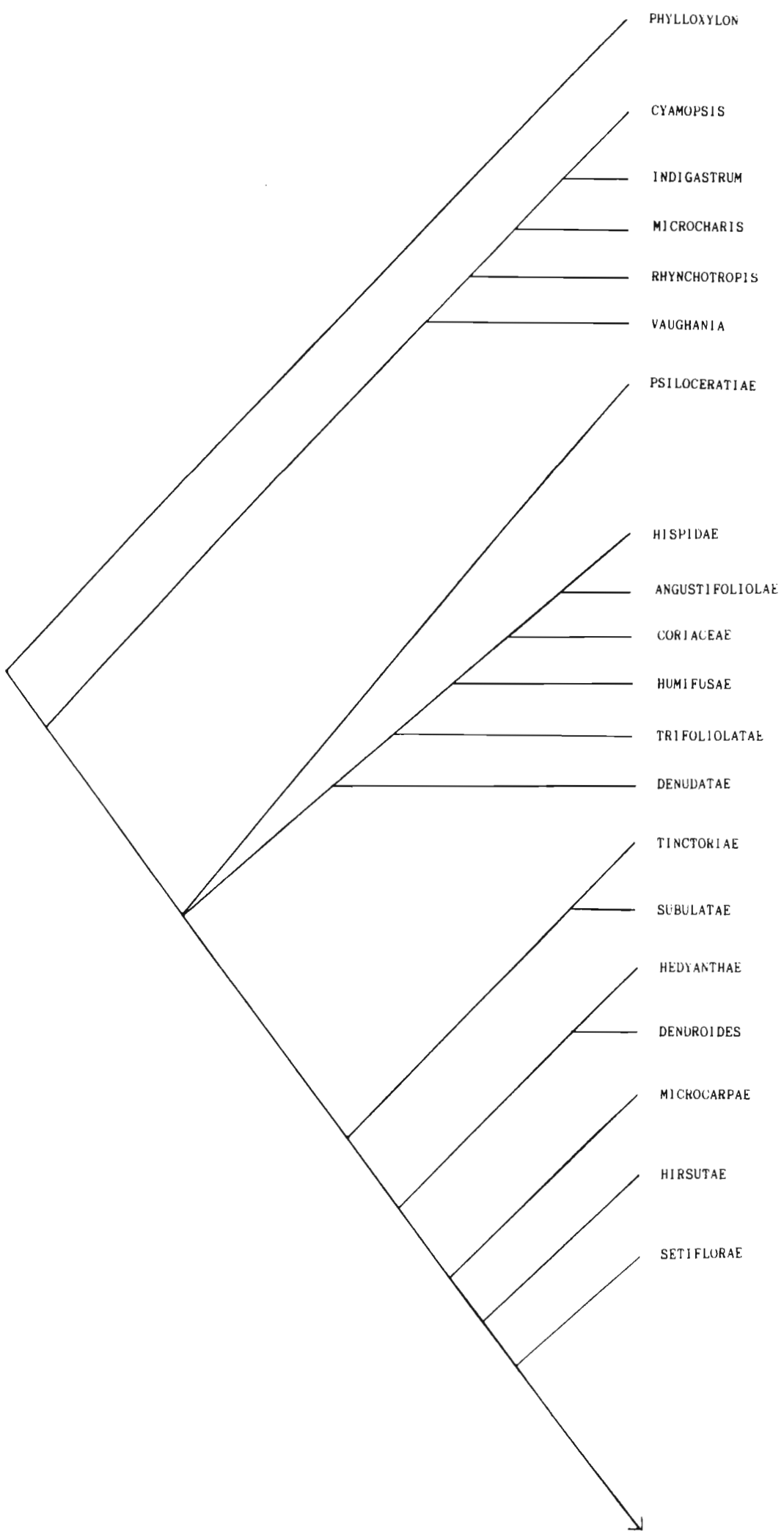
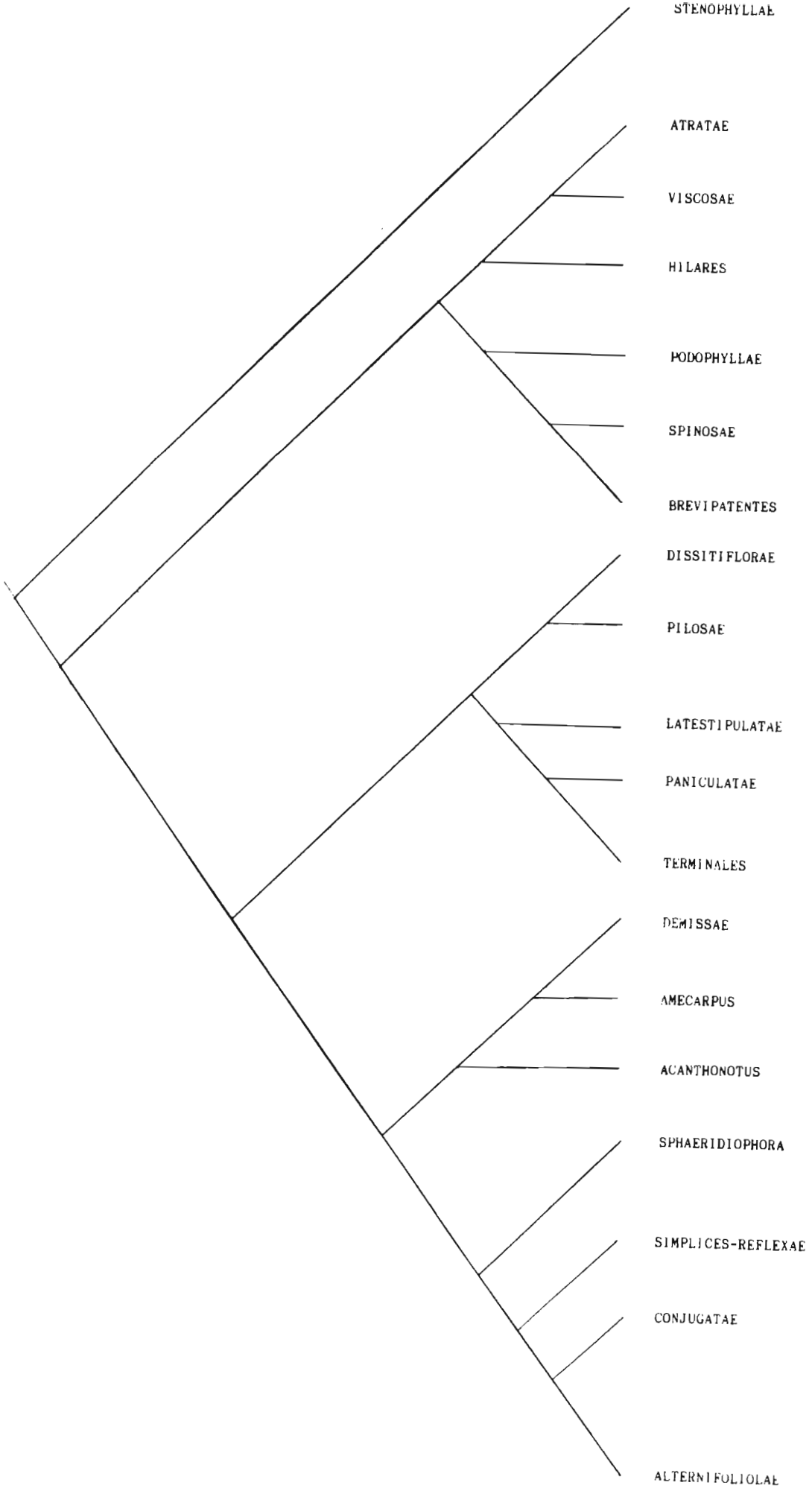


TABLE 5.2 APTATIONS IN THE INDIGOFERAE: Taxa (Part 2). Adapted from the cladogram of the tribe (Table 2.3).



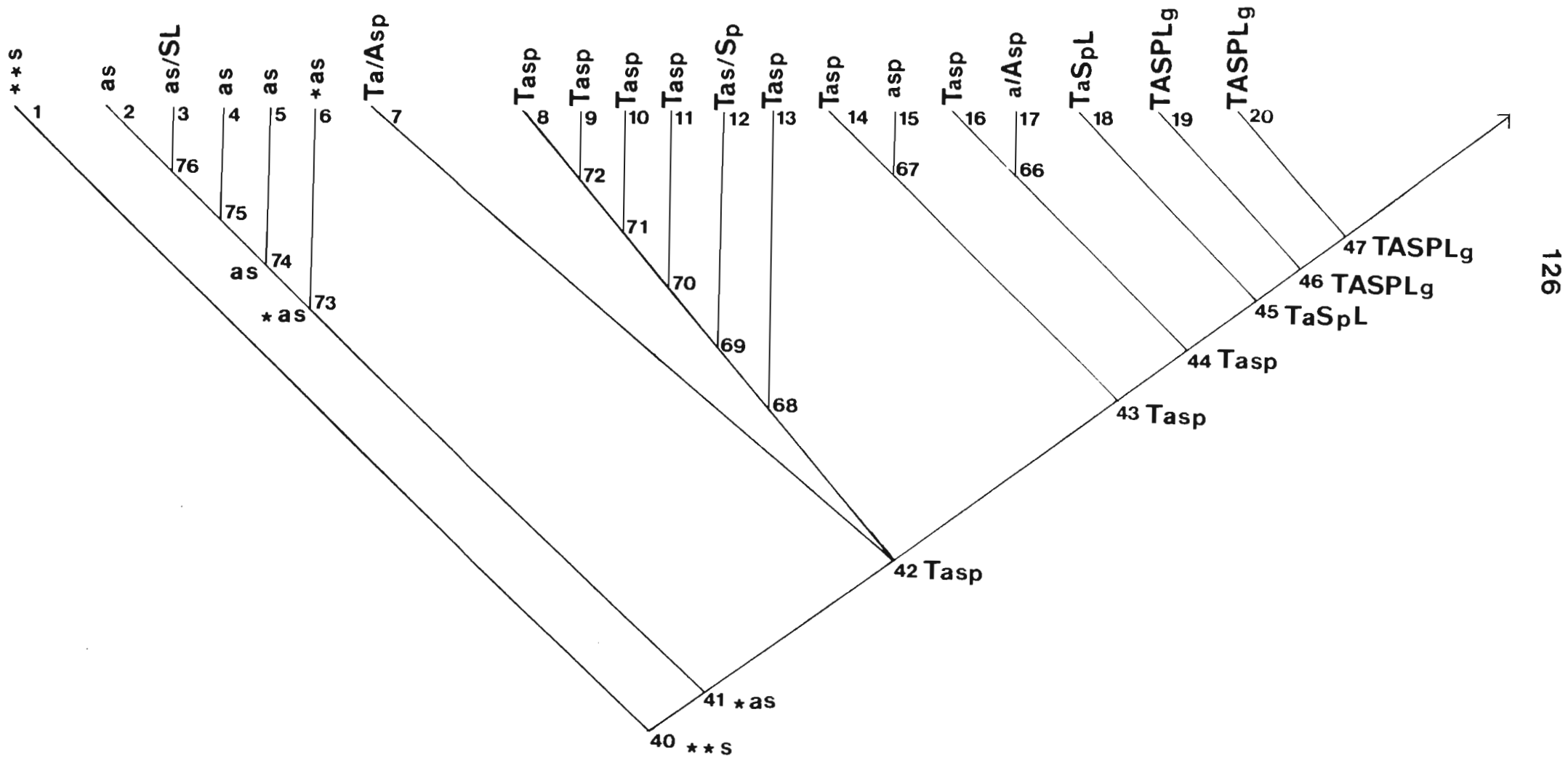


TABLE 5.3 ECOLOGICAL ASSOCIATIONS I: Herbivore defences and methods of protecting resources in the Indigoferaceae (Part 1).
 * = absence or presence of feature unknown for that taxon. Symbols explained in the text.

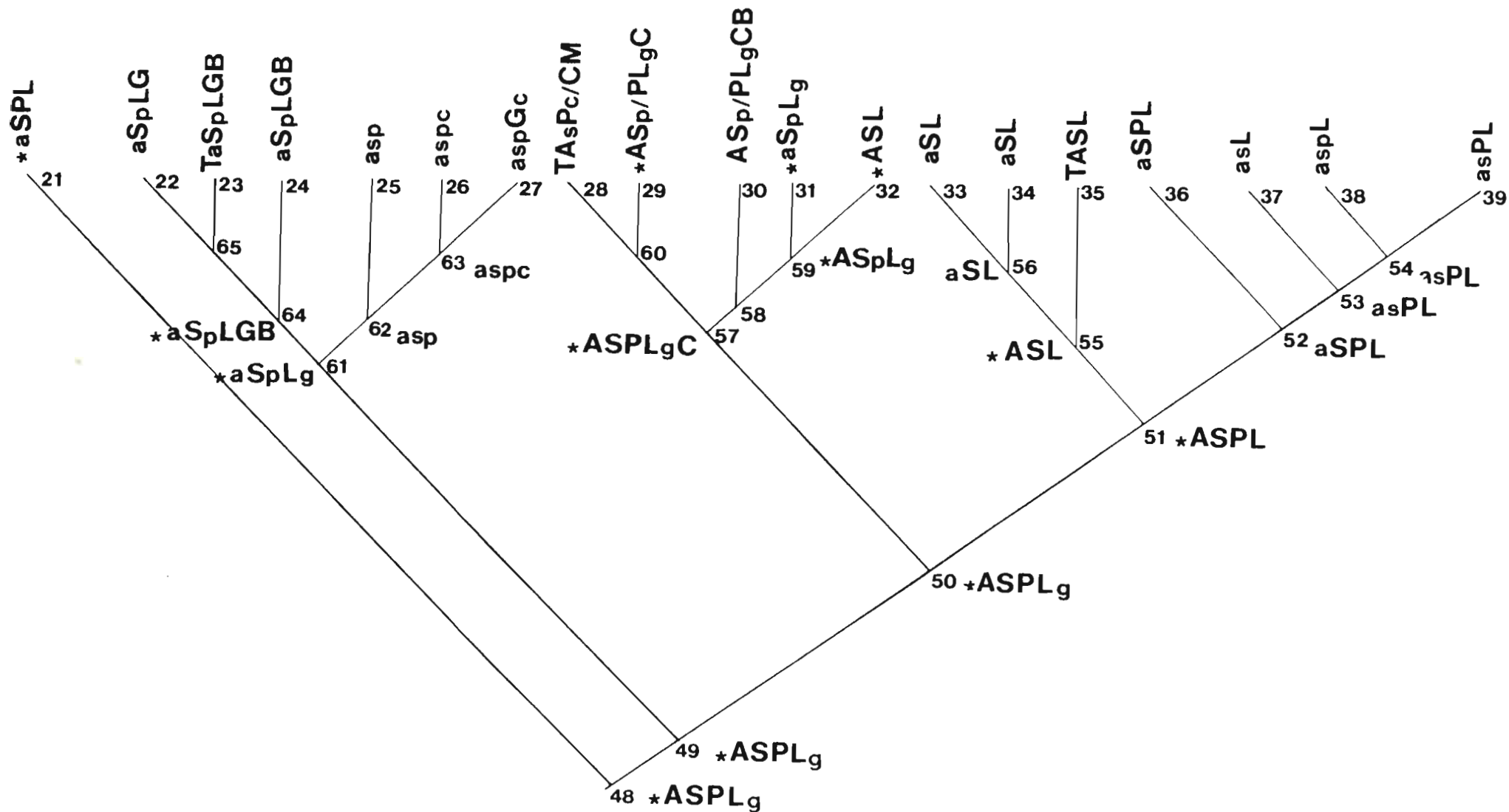


TABLE 5.4 ECOLOGICAL ASSOCIATIONS I: Herbivore defences and methods of protecting resources in the Indigoferaeae (Part 2).
 * = absence or presence of feature unknown for that taxon.
 Symbols explained in the text.

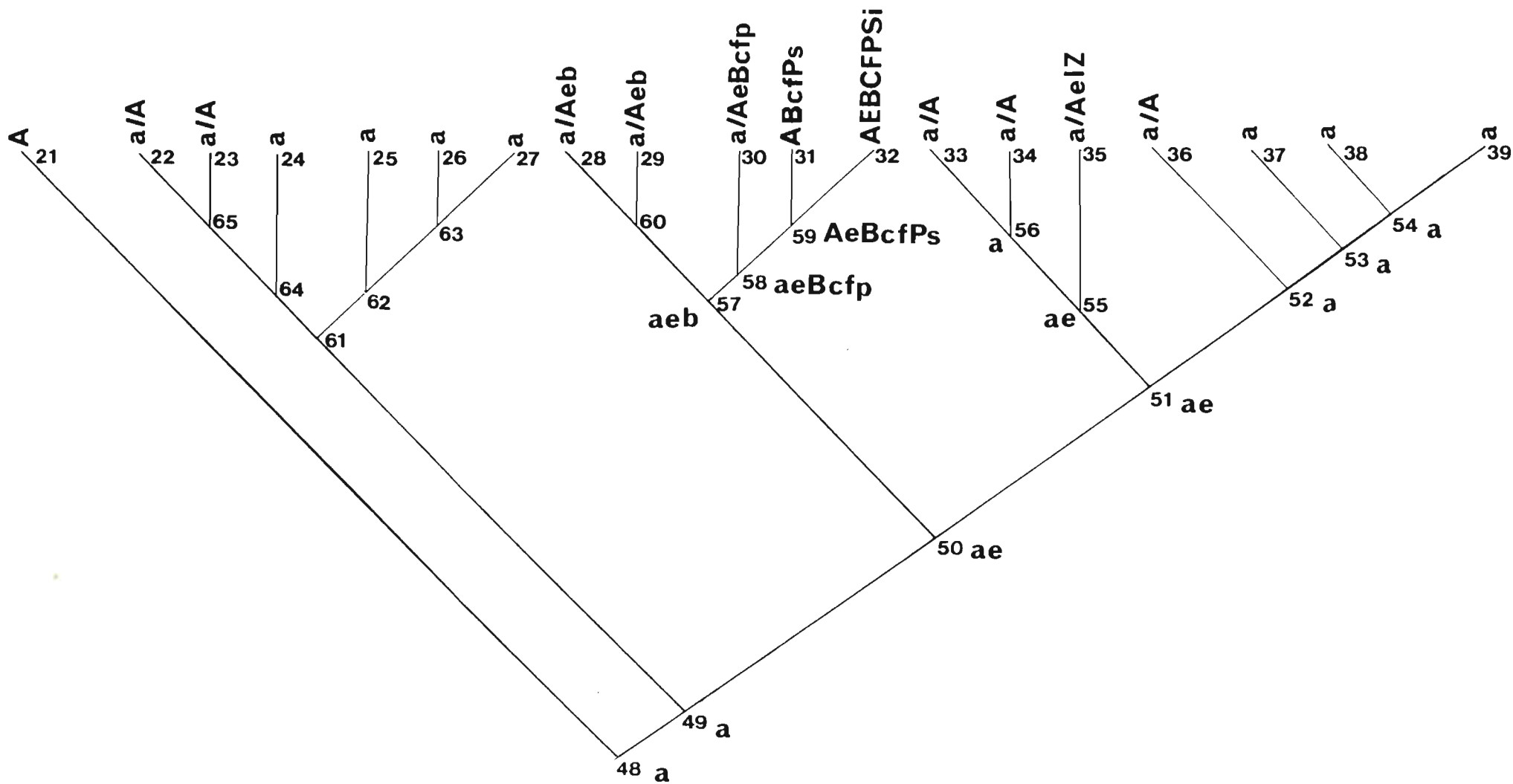


TABLE 5.5 ECOLOGICAL ASSOCIATIONS II: Seed dispersal mechanisms in the derived sections of Indigofera. Symbols explained in the text.

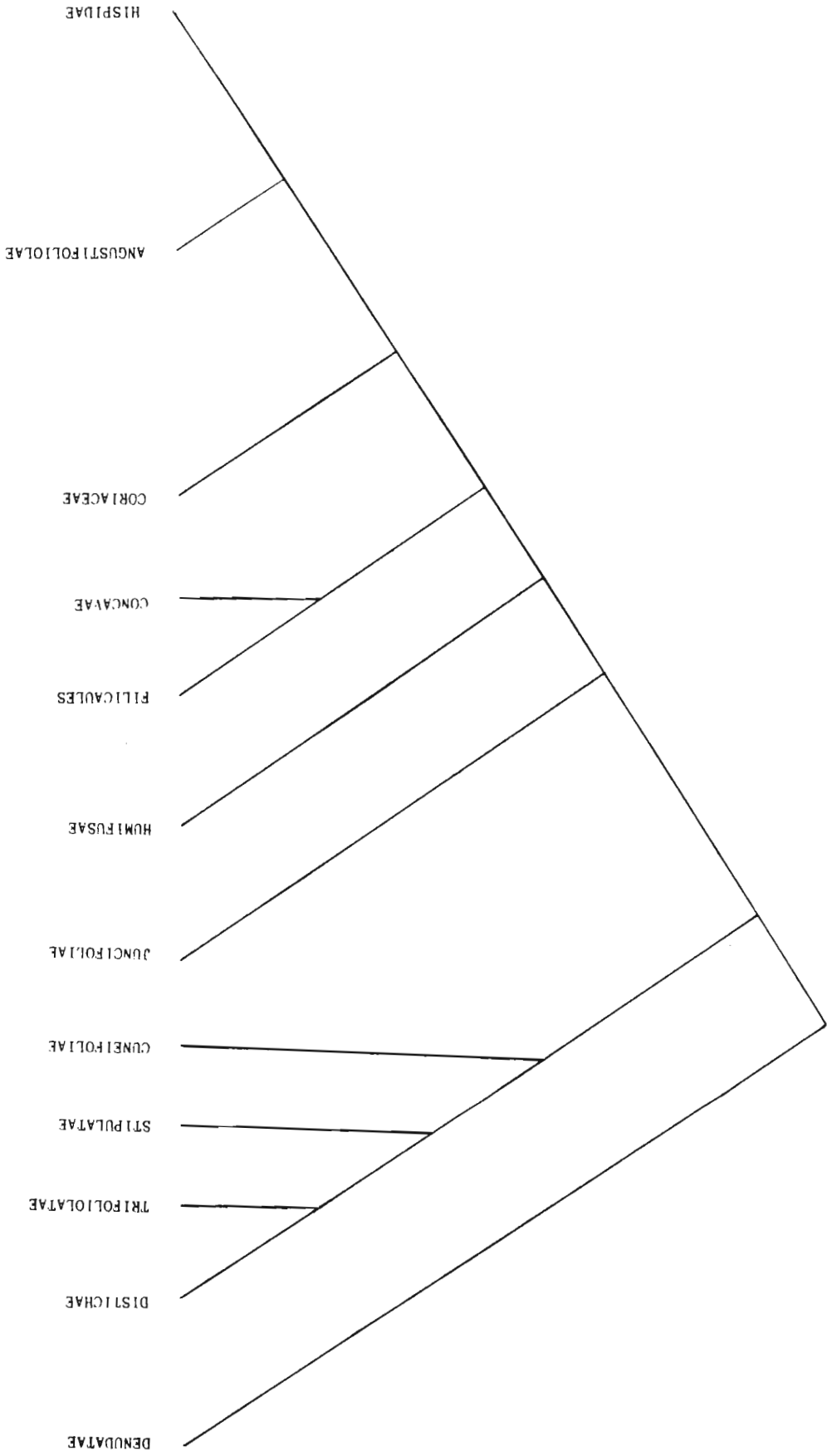


TABLE 5.6 APTATIONS IN THE CAPE SECTIONS OF INDIGOFERA: Taxa. Adapted from cladogram in the Appendix (Fig. A.17).

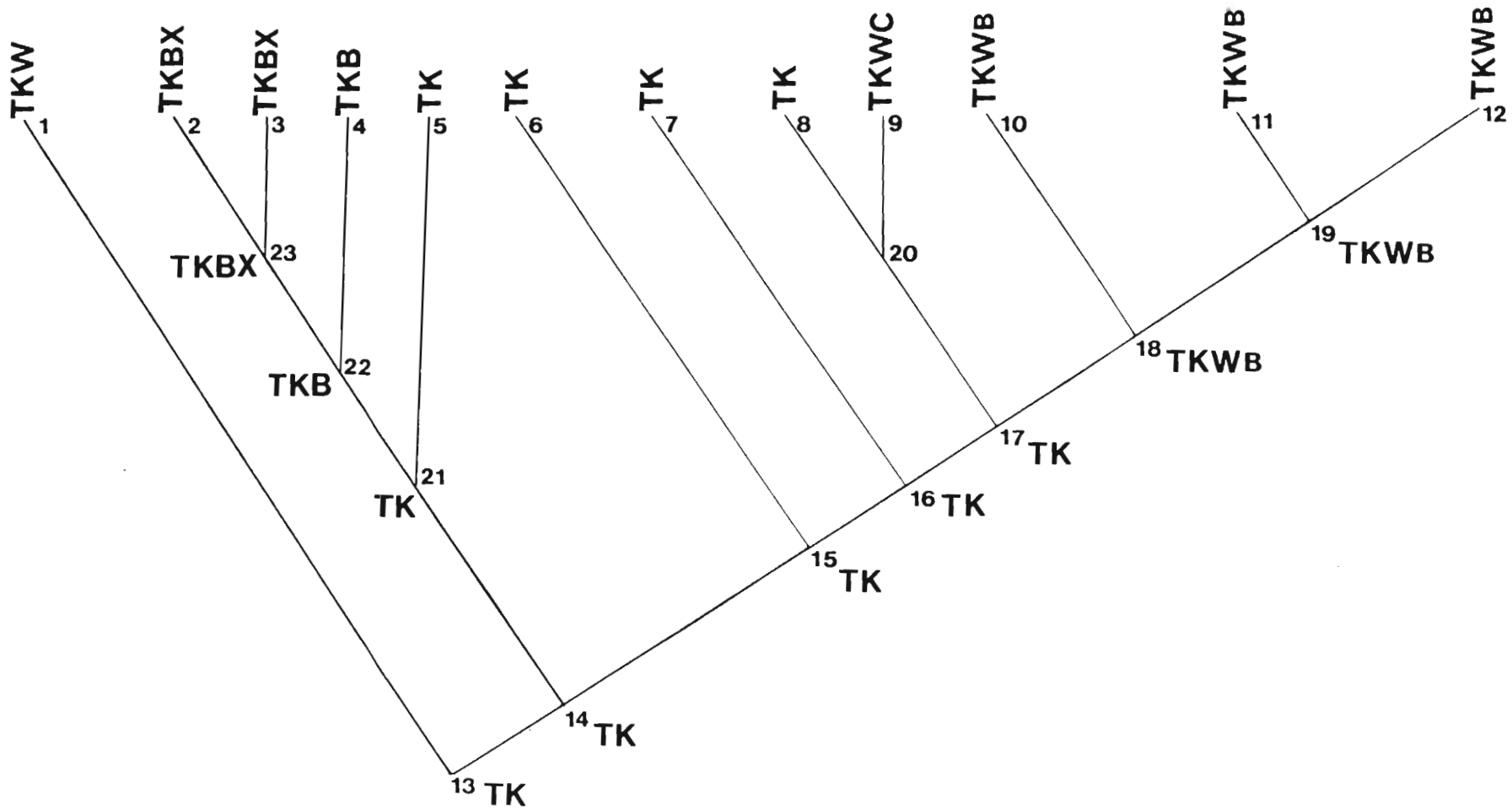


TABLE 5.7 ECOLOGICAL ASSOCIATIONS III: Herbivore defences and methods of protecting resources in the Cape sections of Indigofera. Symbols explained in the text.

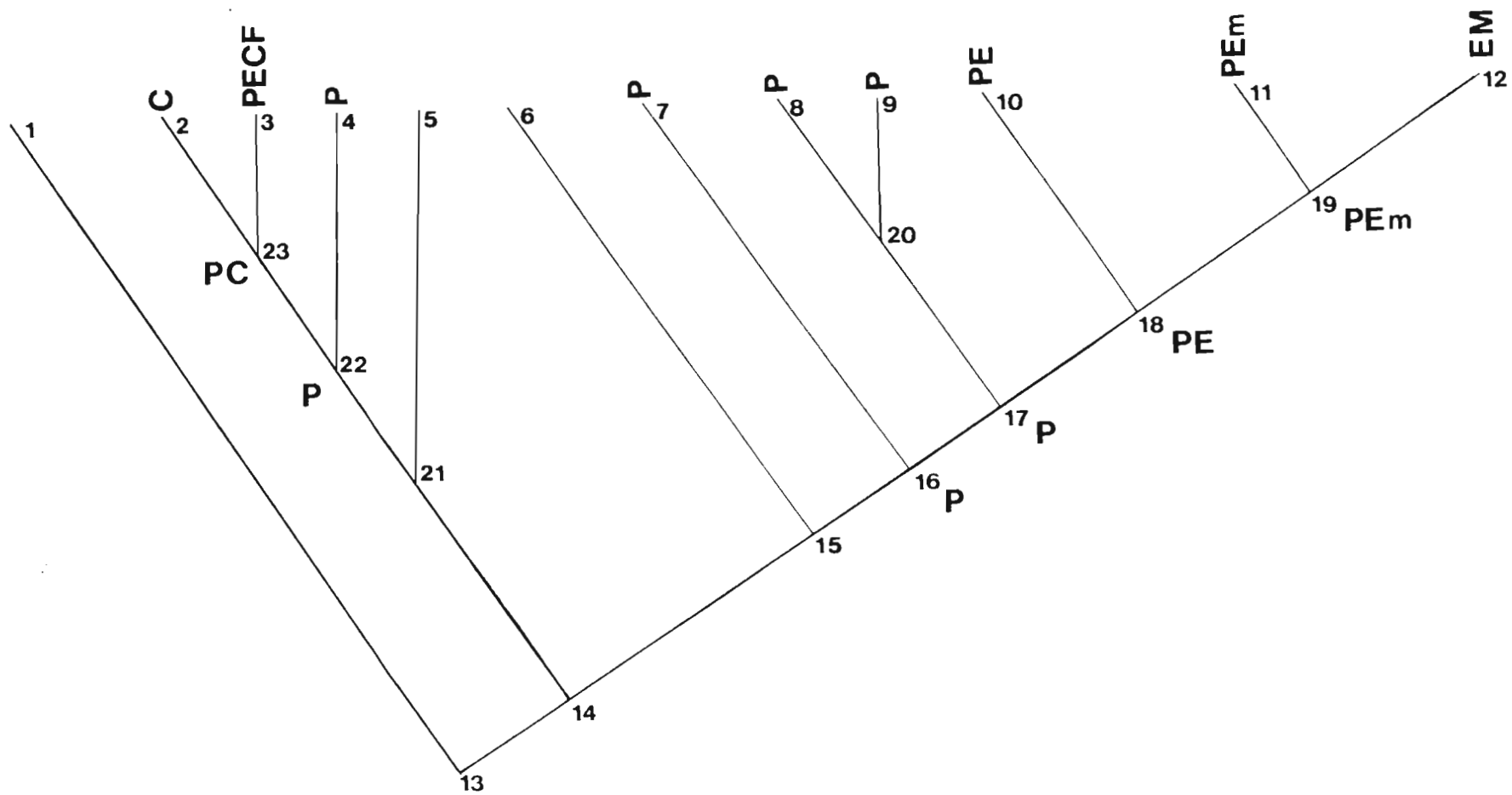


TABLE 5.8 ECOLOGICAL ASSOCIATIONS IV: Features attractive to pollinators in the Cape sections of Indigofera. Symbols explained in the text.

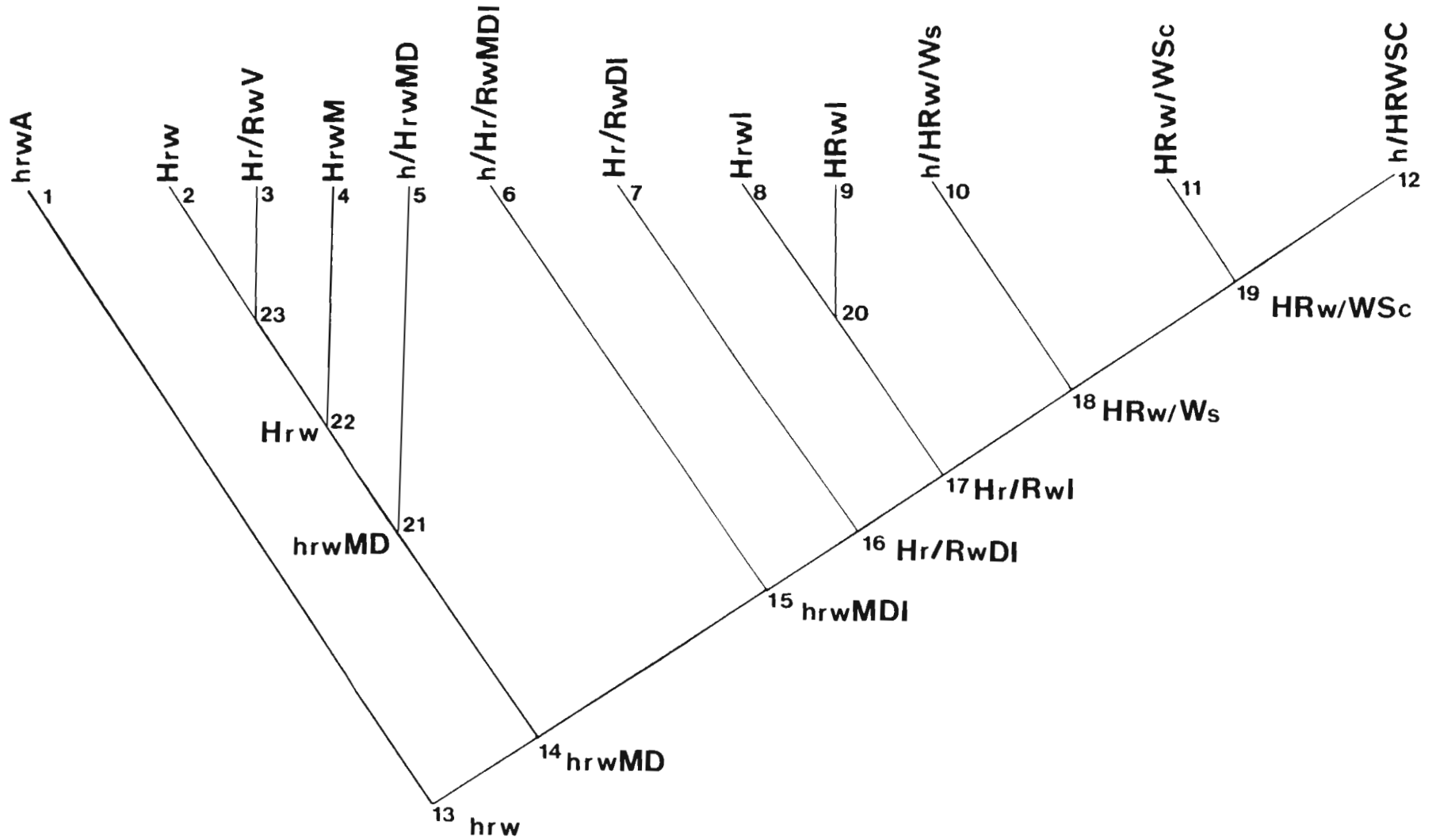


TABLE 5.9 ECOLOGICAL ASSOCIATIONS V: Habit, seasonality and responses to environment in the Cape sections of Indigofera. Symbols explained in the text.

5.4. EXAMPLES

5.4.1. Aptations

- 1) *Herbivore defences and methods of protecting resources in the Indigofereae*. See Tables 5.1 to 5.4 (Tables 5.3 & 5.4 are adapted from the tribal cladogram, Table 2.3). A summary of characters involved in this association is given in Fig. 5.3.

a) Leaf tannin ideoblasts (T = present)

A number of tropical African sections still need to be analysed but tannin idioblasts seem to be more prevalent in the less derived elements of the tribe. Complete or partial loss of tannins occurs at nodes 74, 62, 56 and 52, in those taxa found in arid areas. Tannins constitute a complex subject and their effect may depend on whether they are condensed or not. They appear to be a broad deterrent inhibiting digestion in bulk feeding herbivores, and may serve in the protection against microbial and fungal attack (Morrow *et al.* 1983; Schrire 1989).

b) Pearl Bodies:

a = isolated in leaf axils and between leaflets

A = densely scattered over stems

Isolated pearl bodies at the base of the leaves and between the leaflets characterize all taxa in the tribe, but they may be very obscure in *Phylloxylon*. At node 46, pearl bodies become much more densely scattered over the plant, particularly on the stems. Reversals to the plesiomorphic condition occur higher up at nodes 21, 61, 56 and 52. Pearl bodies have been observed to provide food for aggressive ants (O'Dowd 1982) and the plants appear to derive a measure of protection from predators (Janzen 1981).

- c) Ovary length: s = about two thirds or longer than the
 horizontal length of the style
 S = less than two thirds the horizontal
 length of the style
Calyx lobes: L = more than twice the length of the tube
 on average.

At node 45 a major shift occurs in the proportion of ovary to calyx lobe length. "Short" ovaries are half or less the horizontal length of the pistil, and the development of a short ovary with fewer seeds coincides with an increase in the length of the calyx lobes to more than twice the length of the tube (discussed in section 5.4.2.3.). The calyx lobes surround the developing pod.

The plesiomorphic state is "long" ovaries with many seeds, where ovaries are longer than half the horizontal length of the pistil, and calyx lobes are less than twice the length of the tube.

Three reversals to long ovaries are found at nodes 62, 28 and 53. At the first two nodes a reversal to short calyx lobes accompanies the ovary reversal, but at node 53 the long calyx character is retained. The close correlation in dimensions of these two characters might indicate allometric or genetic linkage (discussed in section 5.4.2.3.).

At node 52 a major evolutionary event appears to have accelerated development in ontogeny in some taxa (discussed under heterochrony in section 5.4.2.4.). Significant changes in morphology are found and these may have resulted in the disruption of any linkage between the calyx and ovary characters.

Two distinct developments are apparent.

- i) long ovaries and short calyx lobes, developing into long glabrous or strigose pods with many seeds. There may be a

possible dispersal advantage since longer valves are able to build up greater tangential stresses causing seeds to be flung further after dehiscence. Valve dehiscence may also be controlled by well developed beaks on the pod apices.

- ii) short ovaries covered by long calyx lobes, developing into short pods with relatively few seeds well protected by tannin vesicles. Pods are also often densely hirsute, silky, glandular or covered with pearl bodies. Longer pods do develop in some species, e.g. at nodes 19, 20, 21 23, 24 and 64, perhaps under selection for improved dispersal. Pods are often beaked but they rarely approach the development seen above.

A possible trade off between improved dispersal and better protected seeds might account for these lines of development. There appears to be no significant difference in the number of flowers per inflorescence in long and short podded taxa, therefore it seems unlikely that pod size is influenced by the number of flowers needed for successful pollinator attraction.

d) Endocarp tannin deposits:

- p = irregularly scattered
P = large regular tannin vesicles

Irregularly scattered tannin deposits on the endocarp is a synapomorphy at node 41. At node 46 tannins become aggregated in large turgid vesicles in the endocarp of developing pods. Mature seeds retain pitted depressions from these vesicles. At nodes 29 and 30, the vesicles aggregate as distinct stripes in the endocarp and seeds are correspondingly grooved laterally. Such dense deposits may be effective in reducing predation on developing pods thus protecting seeds. A further synapomorphy at node 41 is the presence of transverse septa between the seeds, and tannin deposits are often concentrated in these septa. Tannin vesicles are lost at nodes 61, 59, 55 and most species at node 52.

- e) Trichomes: g = subsimple to simple bristle-like hairs on stems and/or pods
 G = glandular-tipped trichomes on stems and/or pods

At the basal nodes of the tribe biramous hairs mostly occur with arms more or less equal in length. At node 45 the arms of at least some biramous hairs become very unequal, and at node 46 (with parallelisms at nodes 7 and 14) subsimple to simple bristle-like hairs appear to result from the partial or complete reduction of one branch.

The bristle-like hairs appear to be an exaptation for the development at nodes 64 and 27 of gland-tipped trichomes. The trichomes seem to be easily lost, however, and they probably arose once, at node 61, rather than in parallel in only two species at node 27. Node 61 is also characterized by the loss of pearl bodies and tannin vesicles in the pod endocarp, so loss of these defences might be correlated to the development of glandular trichomes at that node.

The gland-tipped trichomes occur most frequently on stems, are often dense, and they produce a sticky exudate with a strong odour. The trichomes and exudate may impede movement of insect predators and the secretion is possibly toxic, although no chemical analyses have been performed.

- f) Calyx lobes: c = glandular-tipped
 C = stalked-capitate glands

Gland-tipped calyx lobes occur at nodes 63 and 57. On short calyx lobes at nodes 63 and 28, the tips are swollen and glandular, secreting a sticky fluid at the bud stage. At node 57 the long calyx lobes have capitate glands at their tips, and they also occur on the apices of some stipules and leaflets at node 30, particularly on juvenile foliage. These glands appear to act as extra floral nectaries, possibly attracting ants.

- g) Leaf venation: B = thick fibrous bundle sheath around the higher order venation

Thick fibrous bundle sheaths are found around higher order veins at nodes 64, 63 and 30. This character may play a role in reducing the palatability of leaves.

- h) Leaf margins (glandular): M = present

Glandular leaf margins appear to be a unique development at node 28 and are again probably acting as extra floral nectaries attracting ants.

Discussion

Accumulations of leaf tannins, long pods (with scattered endocarp tannins in *Indigofera*) and only isolated pearl bodies attracting ants, are some of the defences in the basal genera and in the less derived groups of *Indigofera*. Other defences certainly occur (discussed in chapter 4) but their exact distribution in the tribe is still unknown. Calcium oxalate crystals appear in the leaves (and possibly other organs) in many sections; the glucoside indican occurs at nodes 42 and 43 and perhaps quite widely elsewhere; and biramous hairs and various nitrogenous toxins are also possibly broad deterrents.

A papery endocarp and transverse septa between the seeds is a synapomorphy in all taxa from node 41. Another, at node 42, is the presence of scattered endocarp tannins.

At node 45 a major shift to short ovaries and long calyx lobes is seen as a trend to fewer, better protected, seeds per pod. Biramous hairs with arms of unequal length also arise at this node, resulting in the development of a pilose, hirsute or sericeous vestiture on stems and pods.

At node 46, one synapomorphy is densely scattered pearl bodies on the stems (and sometimes pods), possibly associated with a

greater dependence on ants for protection. Another is the development of large tannin vesicles in the pod endocarp. Unequal armed biramous hairs are presumed to be plesiomorphic to subsimple to simple hairs which arise at node 46, and this in turn is considered to be an exaptation at node 61, for the adaptation to gland-tipped trichomes. The development of the latter (a novel defence in the tribe) is accompanied by a loss at node 61, of other defences such as dense pearl bodies and tannin vesicles.

A reversal at node 62 to short calyces and long ovaries, occurs with a tendency for the loss of glandular trichomes. Calyx lobe glands in a number of species at node 63 appear to be an alternative way of attracting ants in the absence of dense pearl bodies. Thick bundle sheaths characterize many species at node 61 and longer pods than usual are a trend at node 64.

From node 57 a greater reliance on ant protection than elsewhere in the tribe is indicated, because of the presence of dense pearl bodies, capitate calyx glands, short calyx lobe glands, glandular leaf margins at node 28, and the very dense covering of cylindrical pearl bodies at node 32. Tannin vesicles are lost at node 59 (see next analysis) and a reversal to long ovaries and short calyx lobes is found from node 28. This reversal appears to parallel that occurring at node 62.

Node 51 shows a marked tendency for the complete loss of leaf and endocarp tannins, dense pearl bodies and subsimple to simple bristle-like hairs, and the group occurs mostly in arid areas. Tannin vesicles are only present in isolated species at nodes 36 and 39. From node 52 an event involving developmental acceleration (heterochrony) is hypothesized, with a subsequent shift in morphological variation (see section 5.3.2.4.). A reversal to long ovaries is found at node 53 but long calyx lobes were retained contrary to trends in the rest of the tribe. Chemical defences may play a major role from node 51.

The tribe Indigofereae have a remarkable variety of different deterrent and defensive features for the protection of resources.

These, perhaps more than any other ecological association, have apparently been responsible for much of the adaptive radiation in the group. One of the major trends has been towards better seed protection. As a result a possible conflict may have arisen between requirements for improved dispersal (by means of longer pods) and the production of more and better protected seeds. This conflict seems to be evident from node 45, by the tendency of short ovaries to produce longer pods, and by the three reversals to long ovaries.

Adaptation is tested, for example, in the case of glandular trichomes. They have a historical basis, appearing to be derived from simple bristle-like hairs, and an apomorphic function which the plesiomorphic morphology is incapable of performing. Subsimple to simple bristle-like hairs are presumed to be an exaptation co-opted for protection (pilose or hirsute vestiture), which later provided the material for selection in the adaptation to glandular trichomes.

In the next example further aspects of protection are discussed with particular reference to node 57.

2) *Seed dispersal mechanisms in the derived sections of Indigofera* See Tables 5.2 & 5.5. A summary of characters involved in this association is given in Fig. 5.5.

a) Longevity: a = perennial
 A = annual

Annuals have arisen many times in the more derived and herbaceous elements of the tribe occurring in tropical Africa. In the more temperate regions of southern Africa annuals are restricted to widespread African taxa and a few endemics mostly in arid areas. In this analysis, the shift to an annual habit at node 59 is correlated with aspects of inflorescence morphology and seed dispersal.

- b) Pearl bodies: e = scattered on the stems
E = densely covering all above ground parts

The dense covering of pearl bodies on the stems at node 50 becomes particularly dense over all above ground parts at node 32. The pearl bodies are also very large at this node perhaps indicating an even greater reliance on ant defences. Dense pearl bodies are lost from node 52.

c) Shoot morphology:

- b = gradation from leaves to foliar bracts in some species
B = gradation from leaves to foliar bracts in all species

A simple axillary raceme is the basic inflorescence type occurring almost universally in the tribe. At node 57 a unique modification in shoot morphology apparently resulted in the gradation of leaves to foliar and trifid bracts. The tendency is apparent in some species at node 57, but becomes fixed in all species from node 58. Although the cause may have been a relatively minor mutation in the shoot meristem, the inclusion of this non-adaptation into the genome appears to have had a profound influence on subsequent adaptations, by breaking previous constraints on inflorescence morphology and seed dispersal (see section 5.4.2.3).

- d) Calyx lobes: c = scarious
C = scarious and enlarging in fruit

Scarious calyx lobes, which are broader than average for the tribe, occur from node 58. They appear to be an exaptation for greatly enlarged calyx lobes at node 32 which expand to more than 1 mm broad at the base after flowering. The enlarged calyces are densely covered by pearl bodies and they persist until seed maturity. The calyx is now an adaptation for wind assisted dispersal at node 32, since they become detached with the pods and can be blown along the ground.

- e) Pods: f = tendency to thin-walled pods in some species
 F = paper-thin pod walls

A tendency to thinner walled pods in some species arises at the same node as scarious calyx lobes (node 58). This may be correlated with a shift in the role of protecting developing seeds, from the pod wall to the calyx. This trend is also indicated by the loss, at node 59, of tannin vescicles or stripes in the pod endocarp. At node 32 an adaptation to paper-thin pod walls occurs together with the calyx adaptation for wind dispersal.

f) Inflorescences:

- p = racemes of 1-4 flowers on very short peduncles in
 the axils of foliar bracts.
 P = panicles

At node 58 racemes are reduced to 1-4 flowers on very short peduncles in the axils of foliar bracts. From node 59 true panicles arise by various degrees of abbreviation of the original racemes (sometimes to one flower) and by contraction of flowering branches into dense heads. The change in shoot morphology at node 57 appears to have been an exaptation for paniculate inflorescences.

- g) Seeds: s = some pods single seeded
 S = all pods single seeded

At node 59 there is a tendency for reduction to two or one seeded pods, and at node 32 the tardily dehiscent papery pods are all single seeded.

- h) Pod dehiscence: i = tendency to pod indehiscence
 I = pods indehiscent
 Dispersal mode: Z = epizoochorous

At node 35 one-seeded, indehiscent woody pods are produced which in one species have sharp recurved spines along the

dorsal suture. This appears to be an adaptation for epizoochorous dispersal, possibly on the feet of animals.

Discussion

At node 57 a unique non-adaptation in shoot morphology is hypothesized to have opened up a new channel of adaptive radiation in the breeding system, which has not been possible elsewhere in *Indigofera*. The gradation of leaves to foliar bracts appears to be an exaptation for later changes in inflorescence structure. In some species at node 58, the aggregation of racemes into strobilate co-florescences indicates the trend towards paniculate inflorescences at node 59.

The evolution of scarious calyx lobes at node 58 is correlated with a tendency to thinner walled pods in some species, in a trend where the calyx appears to be taking over the role of seed protection from the pod wall. There is no evidence from the cladogram that scarious calyx lobes had a selective origin, but they are presumed to be exaptations for two distinct trends, i.e. seed protection and for wind dispersal. These trends reach their conclusion at node 32.

At node 59 the annual habit becomes fixed together with paniculate inflorescences, indicating perhaps that panicles may be maximizing seed production in an opportunistic or r-selected life strategy (Vermeij 1978). Although annuals are found with perennials in many groups with racemose inflorescences, it appears that species with panicles are all annuals and they occur predominantly in West Africa in the arid to semi-arid Sahelian zone (Gillett 1958). The above implication requires testing in the field.

In species with paniculate inflorescences many short pods are produced, each with only one or two seeds, again perhaps maximizing the production of well protected seeds in an opportunistic situation. The pods are either thick-walled and often coarsely hispid, or thin-walled and silky to softly pilose.

A loss of distinct tannin vesicles or stripes in the endocarp of pods at node 59 may be correlated to the greater protection provided by pod vestiture, or perhaps to the reduction in seed number per pod.

At node 32 some remarkable adaptations occur partly in response to a more arid environment. Plants are very densely covered with large pearl bodies, presumably reinforcing protection by ants. The scarious calyx lobes become much broader after flowering and entirely surround the developing pods which have paper thin walls and are single seeded. No tannins are present in the endocarp and the role of seed protection appears to have switched entirely from pod wall to calyx, which is densely covered in pearl bodies. The pods are tardily dehiscent, and when mature they become detached from the plant along with the scarious calyces. This adaptation is presumed to assist in wind dispersal of seed, probably by being blown along the ground.

At node 35, an adaptation to epizoochorous dispersal is hypothesized for single seeded, indehiscent, pods with spiny processes along the margins.

3) *Herbivore defences and methods of protecting resources in the Cape sections of Indigofera.* See Tables 5.6 & 5.7. A summary of characters involved in this association is given in Fig. 5.3.

a) Leaf tannin idioblasts: T = present

Leaf tannins are evident as large tannin idioblasts in the mesophyll of all Cape sections. Tannins are a common means of deterrent in plants on nutrient-poor substrates, because carbon containing compounds are easy to accumulate while nitrogen (N) based toxins are expensive where N is limiting (Morrow *et al.* 1983).

b) Dark keel-tip colouration: K = present

Another feature common to many *Indigofera* species, but present in all Cape sections, is a region of deep red to purple colouration on the inside of the keel where the anthers are situated. The concentration of flavonoides in this area is a possible deterrent to chewing insects in the region of the anthers (Harborne 1971; Gomes *et al.* 1981).

c) Overlapping standard base: B = present

Some sections have flowers with the base of the standard flexed over the proximal region of the wings and keel, with the distal half of the lamina sharply reflexed over its base (see chapter 4). This character arose twice, at nodes 22 and 18, and may serve in protecting nectar resources from dessication. It occurs only in those groups with long peduncles where the inflorescences are particularly exposed to wind.

d) Wing and keel beards: W = present

Densely hairy beards at the distal extremities of the wings and keel may be a deterrent to chewing insects at the bud stage. The character evolved three times, at nodes 1, 9 & 18. Although tropical groups have bearded petals, these are restricted to the keel and are never as dense as in the Cape species.

e) Spiny branch tips: S = present

Spiny branch tips, together with other stress-tolerant features to be discussed later, characterize the basal group *Denudatae*.

f) Calcium oxalate crystals: X = present

Calcium oxalate crystals along the veins and in the mesophyll of leaves are common in the tropical sections but only arose once, at node 23, in those Cape sections on nutrient rich

soils. Such crystals may act as a deterrent by clogging mouthparts of chewing insects (Zindler-Frank 1987).

g) Broad and keeled calyx lobes: C = present

An enlarged calyx with broad keeled lobes imbricately overlapping at the base, arose at node 9. The feature is presumed to protect developing buds in *Concavae*.

Discussion

The standard character, dense wing and keel beards, spiny branch tips and keeled calyx lobes are adaptations restricted to the Cape sections. These characters together with the greater role played by dark keel colouration around the anthers, indicate that flowers in the Cape species are better protected than those in the tropical sections. This may be due, in part, to selection under harsh environmental conditions (nutrient poor substrates and wind), predation, and to competition in the speciose Cape flora.

The most derived sections at Node 18 are characterized by better protected flowers than elsewhere in the Cape, having petal beards and an overlapping standard base.

4) *Plant features attractive to pollinators in the Cape sections of Indigofera.* See Tables 5.6 & 5.8. A summary of characters involved in this association is given in Fig. 5.4.

a) Long peduncles: P = present

Inflorescences with very long peduncles, more than twice the length of the subtending leaves, evolved at nodes 22 and 16 and this character is unique to the Cape sections. Well exposed flowers might be advantageous in the competition for pollinators in the speciose Cape flora, resulting in better display for pollinator specialization. They form distinctive

clusters of small flowers vibrating in the wind (Whitehead *et al.* 1987).

b) Delayed keel exposure: E = present

A unique development in the Cape is a delayed exposure of the keel, perhaps enhancing flower attraction over time. After anthesis the wings are positioned close together forming a level platform above, and completely hiding, the keel. Later the wings flex outwards and down along the inner margins, exposing the upper margin, fringe and apex of the keel between them. The keel fringe and apex appear to be additional orientation cues for pollinators. This character arose twice, at nodes 3 and 18.

c) Dark coloured central blotch on standard: C = present

Most Cape species have a pale (hyaline) central blotch at the base of the standard, often completely or partially surrounded by a mauve areola. At node 23 the central blotch becomes uniformly darker than the rest of the lamina thus presenting a different nectar guide to pollinators. This may promote pollinator fidelity (Heinrich 1975).

d) Distal keel fringe: F = present

Nearly all Cape (as well as tropical) sections are characterized by the presence of a dense fringe of hairs on the upper proximal margin of the keel. The fringe is usually visible between the wings in the untripped flower and appears to act as an orientation cue and possible tactile guide to the nectary. At node 3 the keel fringe is distally placed, near the apex which is often markedly rostrate. Delayed keel exposure appears to have been an exaptation allowing the development of this different combination of orientation cues, since the cues are not visible until the keel is exposed.

- e) Mass flowering: m = persistent petals
 M = mass flowering

At node 19 the petals remain persistent after tripping, apparently enhancing the overall attraction of inflorescences. Caducous petals after tripping is almost a universal character in the genus, probably promoting pollinator efficiency by preventing wasteful revisits to a tripped flower (Schrire 1989). This appears to be an exaptation for the next character.

Mass flowering develops at node 12 and is a highly significant adaptation, apparently resulting from the evolution of persistent petals. In the rest of *Indigofera* extended flowering results from many different racemes being produced over time, each raceme having a few attractive flowers open per day. This illicit a trap-line behavioural response (Janzen 1971) by specific high-energy demanding pollinators. In mass flowering, racemes all flower more or less together with each raceme having many attractive flowers open, and the petals persist apparently to complement display after tripping. This adaptation may again be ascribed to competition for display in mountain fynbos.

There is also a greater variety of floral shapes and colours in the Cape compared with tropical sections. Bright pink, magenta, coral and terra cotta coloured flowers characterize Cape species whereas tropical sections mostly have red to carmine flowers.

Discussion

The long peduncle character which evolved at nodes 22 and 16 appears to be an exaptation for the development of delayed keel exposure and overlapping standards (Table 5.7). With increased exposure of flowers to the environment, particularly wind, a trade off is likely between selection for enhanced attraction and greater protection of resources.

Two specific attraction syndromes appear to characterize the Cape sections; a) petals remaining persistent and allowing a mass flowering regime on nutrient poor soils, and b) dark nectar guides, on nutrient rich soils, with one group possibly enhancing recognition by a distal keel fringe and rostrate keel apices.

Both syndromes appear to be further adaptations of the delayed keel exposure and long peduncle characters, although the latter is lost in mass flowering. Enhanced attraction to pollinators is likely to be adaptive for the more efficient use of available flowers in the Cape environment.

5) *Habit, seasonality and other responses to the environment in the Cape sections of Indigofera* (e.g. survival strategies). See Tables 5.6 & 5.9. A summary of some of the characters involved in this association is given in Fig. 5.5.

a) Habit: h = woody
H = herbaceous

Most Cape species are perennial suffrutices with woody shrubs characterizing the basal group at node 13. From node 14 taxa are predominantly herbaceous, with a few woody shrubs occurring at nodes 5, 6 & 12. There are no annuals in the Cape flora other than, perhaps, two isolated species at nodes 3 and 7 that are associated with seasonally waterlogged conditions.

The woody habit, often with spiny branch tips (Table 5.7), and the presence of fleshy glaucous leaflets, are some of the stress-tolerant features characterizing the basal section *Denudatae* (Vermeij 1978).

b) Moist environment requirements: M = present

Nodes 4, 5 and 6 show a preference for wet, montane, conditions. At node 15, the leaves occur at the juvenile stage or on young growth only, with leaflets later reduced to scales

on persistent photosynthetic petioles (see chapter 4). As this seems a somewhat anachronistic development in a wet adapted environment, it is suggested that these features are an adaptation to the low nutrient status of acid fynbos soils, possibly enabling the first Cape species to radiate into true fynbos. The stress tolerant features in an ancestor adapted to semi-arid conditions may have been exaptations, in a wet environment, for the development of secondary stress-tolerant features adapted to low nutrient conditions.

c) Dark coloured seeds: D = present

Uniformly dark coloured seeds are found in the basal groups at nodes 5, 6 & 7. Little information about this character can be recovered from the cladogram but it might increase fitness by reducing granivory in the soil-seed bank in a post fire situation. It is not clear, however, why the character is restricted to those basal sections mostly associated with wet-adapted environments. Many of the dark seeds have persistent papery funicles which are pale in contrast to the seed colour.

d) Leaflets with involute margins: I = present

Leaflets with involute margins that can cope with environmental stress by rolling inwards, characterize nodes 15 to 17 which comprise the *Humifusae* alliance. Leaflets are often slightly fleshy (as in the basal *Denudatae*), with an accumulation of sclero-tracheoids along the margins, but they are rarely more than sparsely to moderately hairy.

e) Response to fire: r = resprouter

R = obligate reseeder

From node 15, which contains all sections restricted to true fynbos vegetation on nutrient poor soils, there is an increase in the prevalence of obligate reseeding as a means of regeneration after fire. From node 18 all taxa are obligate reseeders. This type of regeneration is a response to the fire

regime in nutrient poor environments where fires occur at greater intervals, on average, than on nutrient rich substrates (Manders & Cunliffe 1987). The basal sections at nodes 13 and 14 are predominantly resprouters after fire, with only a few, possibly obligate, reseeder occurring at node 3.

- f) Flowering season: w = spring/summer flowering
W = autumn/winter flowering

Flowering among Cape species occurs mostly in spring through summer with some tending to flower most of the year. Autumn and winter flowering becomes progressively more prevalent at node 18, being found in some species at nodes 10 and 11 and in all species at node 12.

- g) Sclerophylly: s = coriaceous leaflets with revolute margins
S = sclerophyllous (ericoid) leaflets

Another possible response to the stresses associated with a nutrient poor substrate appears to be the development, at node 18, of coriaceous leaflets with a distinct upper leaf surface morphology and revolute margins. This is an exaptation for true sclerophylly (see chapter 4) which occurs at node 19.

- h) Stalked biramous hairs:

- c = some biramous hairs on an epidermal swelling
C = some biramous hairs stalked

At node 19 the stem biramous hairs of some species have an epidermal swelling beneath them, and this appears to be an exaptation for the development at node 12, of distinct epidermal projections with apical biramous hairs. As one of the functions hypothesized for biramous hairs is a role in water uptake (see chapter 4), it is possible that stalked biramous hairs are an adaptation enhancing water uptake from runoff or mist (Marloth 1903). This character only occurs along the southern Cape mountains, increasing markedly in density on

plants in the eastern half of this range (from Knysna to near Port Elizabeth) on the seaward slopes.

i) Clambering habit through other vegetation: V = present

A characteristic at node 3 is the habit of clambering through other plants to flower above the canopy, and many suffrutices may become quite tall and woody. This opportunistic development may be selective for enhanced display and longevity (through support and protection).

j) Fleshy leaflets: A = fleshy glaucous leaflets

k) Leaflets reduced to scales above: U = present

Discussion

After an hypothesized semi-arid origin of Cape species of *Indigofera*, as observed by the stress tolerant features in the basal section *Denudatae*, much of the further radiation appears to have occurred in forms that became adapted to wet, montane, environments. It is possible that during climatic fluctuations in the Tertiary (Deacon 1983), certain wet phases allowed taxa to invade montane areas, which later were isolated during drier periods. This possible scenario is supported by the adaptations to, or preferences for, a wet montane environment as seen in taxa at nodes 4, 5 and 6.

Evidence other than montane affinities supports a common ancestor linking *Juncifoliae* (node 6) with *Cuneifoliae* at node 5. These sections share two synapomorphies, i.e. glabrous calyces and a glabrous abaxial surface of the standard. One somewhat intermediate species, *I. fulcrata*, is restricted to wet localities and has the same broad stipules as *Cuneifoliae*. Both *Juncifoliae* and *I. fulcrata*, however, are restricted to nutrient poor substrates, and share the unusual character of a single stipel situated between the petiolules on the leaf rachis. *Cuneifoliae* is not specialized on nutrient poor soils, although

I. cuneifolia appears to tolerate them, while node 15 has become restricted to the Cape mountains. Once specialised on nutrient poor soils, taxa were apparently unable to "escape" back to nutrient rich substrates.

It is hypothesized that characters previously adapted for drought stress could now, in wet environments, become exaptations for coping with nutrient stress. These may have allowed species to radiate into the nutrient poor substrates supporting fynbos, and later, to develop adaptations for coping with this new environment.

Leaflets reduced to scales in the basal *Juncifoliae* (node 6), occurred at the same time as the development of leaves with involute margins, which characterizes the whole *Humifusae* alliance from nodes 15 to 17. This group are sparsely hairy with often slightly fleshy leaflets.

Node 18 is characterized by coriaceous or sclerophyllous ericoid-type leaves, a dense vestiture, obligate reseeding, and a tendency to winter flowering. *I. cytisoides* is an isolated taxon, distinct from the rest of the lineage at this node. Persistent petals, mass flowering and stalked biramous hairs occur from node 19.

A major radiation of Cape taxa occurs from node 22, which is only associated with nutrient rich soils. Taxa have predominantly trifoliolate leaves (with a reversal at node 2), an overlapping standard base (parallelism at node 18) and long peduncles (parallelism at node 16). From node 23, flowers are unique in having a dark central blotch, and they often have rostrate keel tips. Node 3 is characterized by a distal keel fringe, delayed keel exposure (parallelism at node 18) and frequently a clambering habit.

The 12 endemic sections of Cape *Indigofera* (comprising nearly 100 species) appear to have arisen from a tropical ancestor by progressive specialization in Cape environments. Only a very few

tropical species enter the area occupied by the Cape sections, and even then these are marginal to the Cape Floral Kingdom (Goldblatt 1978). Conversely there are also remarkably few Cape species occurring outside the range of Cape taxa.

5.4.2. *Developmental constraints in the Indigofereae* (with reference to the cladogram in Table 2.3).

Examples are given below of how developmental constraints (burden, canalization, key morphologies and heterochrony) are interpreted as operating in the tribe.

5.4.2.1. *Burden*

Throughout the Papilionoideae, the flower is remarkably consistent morphologically (an example of canalization), despite tremendous variation in the shape and size of individual parts. Floral structures in the Indigofereae carry a particular burden imposed by the explosive tripping mechanism required for pollination. The stamens and pistil are kept under tension by distinct conformations (in different genera) of the corolla, and once tripped the fertile parts are explosively released, disorientating the petals. This type of tripping mechanism has arisen independently in a number of tribes, but in Indigofereae it is unique, with petals almost immediately caducous after tripping. Structures such as the broad vexillar sinus in the calyx, proximal wing crests, level wing platform, lateral spurs or pockets on the keel, anthers with an extended apiculate connective, and anther hairs (or scales) appear to be more or less integral to the functioning of the tripping mechanism. However, they also play a direct role in pollination (Figs. 5.4. & 5.5.), and more indirectly, in various aspects of the breeding system (Fig. 5.5.). The above structures are relatively invariable in the tribe, and have become heavily burdened by the numerous attributes that are functionally dependent on them.

5.4.2.2. Canalization

Other examples (besides the typical flower shape) of canalization at the subfamily level, are the hilar groove in seeds and curved radicle in the embryo (Polhill & Raven 1981).

At the generic level canalization has occurred most obviously in the flower. The channelling into morphologically distinct flower types (see discussion in chapter 4; e.g. keel curved and twisted, with a glabrous upper margin in *Vaughania*, or keel straight with a distinct fringe of hairs along the upper margin in *Indigofera*) reflects the variety of pollination strategies and different breeding systems that have evolved in the tribe based on an explosive tripping mechanism.

In *Vaughania* and *Rhynchotropis* the following structures indicate a well defined pathway of floral development within Clade A (Table 2.3): stamens free distally for at least a third of their length; anthers plumose hairy above and below; style curved or twisted and stigma oblique.

Indigofera (inclusive of Clades B to H in Table 2.3) is the sister group of Clade A and a different pathway of floral development is indicated by the keel always having lateral spurs and a fringe of hairs along the upper margin; stamens fused into a staminal sheath for almost their entire length; anthers hairy or glabrous but not plumose; style bent upwards to erect, not curved or twisted and stigma capitate.

Canalization of floral development in the tribe has thus followed two distinct lines in the two basal sister groups in the cladogram, but in Clade A development was subsequently directed into the morphologies characteristic of *Microcharis*, *Indigastrum* and *Cyamopsis* (see chapter 4), with certain parallels arising to the *Indigofera* line (e.g. almost completely fused staminal sheath; style not curved or twisted, and stigma sometimes capitate).

5.4.2.3. *Key morphologies*

- a) From node 45 in Table 5.3 (i.e. including *Microcarpae*, *Hirsutae* and *Setiflorae* etc.) a key morphology arose, that developed into a new canalization series.

At this node a switch to a short ovary - long style morphology (ovary less than half the horizontal length of the pistil) was associated with the development of calyx lobes becoming much longer than the tube. These morphologies appear to be correlated (perhaps through allometry, pleiotropy or linkage) since reversals to a long ovary - short style morphology are nearly always accompanied by short calyx lobes.

It is hypothesized that the short ovary (key morphology) biased subsequent evolution in *Indigofera* by switching constraints to a different channel of development: i.e.

- i) relatively short few-seeded pods arose at node 45 which are densely pilose, sericeous or glandular (pods derived from long ovaries are either glabrous or sparsely to densely appressed strigose)
- ii) scattered tannin deposits in the pod endocarp developed into large tannin vesicles from node 46.

These morphologies indicate a new canalization series towards fewer, better protected seeds per pod (as discussed earlier under adaptations).

- b) The evolution of a unique shoot morphology at node 57 (in Tables 5.4 and 5.5) resulting in a gradation of leaves to foliar bracts, apparently broke previous constraints which always produced axillary racemes in the tribe.

The following new canalization sequences in inflorescence structure are hypothesized, after the evolution of foliar bracts (the key morphology). Reference is made to Tables 5.4 & 5.5 for the sequence of events; the descriptions of

characters in chapter 4; and the discussion of adaptations above):

- i) At node 58: reduction of racemes to 1-4 flowers in the leaf axils; development of strobilate co-florescences and trilobed bracts;
 At node 59: development of paniculate inflorescences; loss of tannin vesicles in the endocarp; tendency to reduction in seed number per pod (1-2 seeds); fixation of the annual habit.

The reduction of racemes and aggregation of flowering branches into panicles has apparently resulted in a maximizing of seed production in an opportunistic life strategy (with many small pods containing 1-2 seeds).

- ii) At node 58: development of scarious calyx lobes; tendency to thinner walled pods;
 At node 32: development of scarious calyx lobes enlarging in fruit; tardily dehiscent pods with paper-thin walls; reduction to single seeded pods; pods shed with enlarged calyces.

The tendency to thinner walled pods and development of broader calyx lobes indicates a shift in the role of pod wall to calyx lobes in protecting seeds; and a new seed dispersal mechanism (by wind) has evolved, with the development of calyces enlarging after flowering and becoming dispersed together with the single-seeded pods.

5.4.2.4. *Heterochrony*

The tendency towards precocious flowering from node 51 (Table 5.4) is hypothesized to have arisen because of developmental acceleration. The production of flowering shoots before leaves appears to be an adaptation to a long history of intense burning, possibly taking advantage of the immediate post fire environment.

Heterochrony resulted in the breaking of previous constraints, and a number of morphologies are lost from node 51; e.g. unequal arms in biramous hairs, different biramous hair sizes, endocarp tannins, densely scattered pearl bodies (stalked), and short ovaries.

Developmental acceleration also appears to have acted as a source of new variation rather than limiting or channelling change. New morphological characters arising in these clades include narrow standard petals tapering to the claw; prominent pod venation; flattened pods; tardily dehiscent, woody, single seeded pods sometimes with spiny processes; sessile pearl bodies most obvious in the lower leaflet surfaces and pods; type 4A pollen; dimorphic stipules and alternate leaflets.

Developmental acceleration is hypothesized, therefore, to have brought about a major shift in morphologies, and this breaking of constraints opened up new possibilities for adaptive radiation from node 51.

STEMS:	<p>Spiny branch tips Multiseriate gland-tipped trichomes Bulbous-based trichomes Pearl bodies (primary ant-plant association) Physical barrier of biramous hairs (whole plant)</p>
LEAVES:	<p>Calcium oxalate crystals (and elsewhere in the plant), along the veins, in mesophyll and on leaf margins Sclerophyllous leaflets Sclero-tracheoids along leaf margins Pearl bodies at the base of the petiole and between the leaflets (primary ant-plant association) Extra floral nectaries ("glandular" leaf apices, margins, and blister-type glands; possible secondary ant-plant association) Biramous hairs perpendicular to the leaf margin Tannins Indican (glucoside forming dye indigo) Thick fibrous bundle sheaths around veins Cyanogenesis</p>
INFLORESCENCE:	<p>Spiny inflorescence rhachides Enlarged foliar bracts around infructescences</p>
CALYX:	<p>Broad scarious calyx lobes (protecting developing pods) Extra floral nectaries on calyx lobe tips (swollen type and capitate type; possible secondary ant-plant association)</p>
FLOWERS:	<p>Strigose vestiture on dorsal surface of standard (possible protection in bud) Distal wing beards (possible protection in bud) Beard over distal third of keel (possible protection in bud) Overlapping standard base (possible protection of nectar resources) Region of dark colouration inside keel around anthers (possible accumulation of flavonoids, toxic to phytophagous insects) Hidden ovary and anthers Tapetal crystals in anthers</p>
PODS:	<p>Transverse septa between seeds Scattered tannins vs. tannin vescicles in the endocarp Hirsute, pilose or sericeous vestiture Multiseriate glandular trichomes Pearl bodies Long vs. short pods</p>
SEEDS:	<p>Hard testa Epidermal cells with tannins Canavanine, Indospicine, Karakin Pyrazine alkaloids</p>

Fig. 5.3. Summary of ecological associations in Indigoferaeae I:
Deterrent and defensive features for protection of
resources.

<p>INFLORESCENCES:</p>	<p>Many to few-flowered open racemes vs. 1-3 (4) flowers partially obscured in the axils of foliar bracts</p> <p>Extended, trap-line, flowering; (i.e. few flowers open at one time per inflorescence, the latter flowering for a relatively long period) OR mass flowering (i.e. racemes flowering for a relatively short period, each with many flowers open)</p> <p>Variety of inflorescence shapes among different species (possible recognition cues)</p> <p>Long peduncles in Cape species (possible competition for enhanced display; also vibration of small flowers in the wind and pollinator attraction)</p>
<p>FLOWERS:</p>	<p>Large variation in size - pollinated by xylocopids to smaller bees</p> <p>Variety of colours; pink, magenta, coral, terra cotta, carmine, red, orange, white</p> <p>Persistent petals (in mass flowering types, possibly complementing display after tripping; rapidly caducous petals occur in trap-line flowering types)</p> <p>Paler vs. darker central blotch, and whether an areola is present (short range orientation and recognition cues)</p> <p>Hairs on central blotch (tactile guides)</p> <p>Glabrous vs. hairy wing proximal crests (possible pollinator footholds)</p> <p>Wing inner margin ciliate (fringe complementing keel fringe described below)</p> <p>Dense, often pink to reddish, proximal or distal fringe of hairs on the upper margin of the keel - apparently a visual and tactile orientation cue</p> <p>Rostrate keel apices</p> <p>Delayed keel exposure in some Cape taxa (possibly enhancing attractiveness over time)</p> <p>Strong sweet odour produced by flowers in a number of Cape species (enhanced pollinator attraction in species-rich flora)</p>
<p>REWARDS:</p>	<p>Pollen and nectar</p>

Fig. 5.4. Summary of ecological associations in Indigoferaeae II: Guidance and recognition cues for attraction of pollinators.

Perennial vs. annual habit (k- and r- type reproductive strategies)
 Limited vegetative reproduction (new plants from rhizomes in some species)
 Resprouting vs. reseeding
 Racemose vs. paniculate inflorescences (possible association with the latter and r- type reproductive strategies)
 Hermaphrodite flowers
 Facultatively xenogamous (self compatible)
 Explosive tripping of flower (non repeatable mechanism of pollen release)
 Matinal pollination (flowers self-trip by mid morning)
 Number of morphologically different flower types in the tribe (possible pollinator specialization, e.g. asymmetrical flowers in VAUGHANIA)
 Lack of marked petal sculpturing but crude pollinator footholds present
 Lateral spurs supporting wings as a sturdy platform for pollinator landing
 Pollinators attracted to hidden rewards
 Rapidly caducous petals after tripping (possibly preventing revisits by pollinators to spent flowers)
 Explosive tripping mechanism (one of many possible functions to apparently promote pollinator movement in and between plants)
 Staminal sheath diadelphous (pseudo-monadelphous in CYAMOPSIS)
 Absence of basal fenestrae, but a rugose region may be present at the base of the vexillary stamen (possibly acting as nectar guide)
 Alternatively long and short stamens
 Apical anther connective, anther hairs and scales (possibly increasing the efficiency and accuracy of pollen transfer)
 Pollen specialization (type 4; possible association with tendency for loss of anther hairs)
 Penicillate, capitate or oblique, stigmas
 Style elaboration in RHYNCHOTROPIS (possible isolation mechanism)

Autochory by explosive dehiscence of spirally twisting valves
 Sessile cup-like base and persistent style remains at pod apices (possible control of valve dehiscence)
 Anemochory, and enlarged scarious calyces becoming detached with tardily dehiscent, one seeded, thin walled pods
 Epizoochory, and indehiscent one seeded woody pods, sometimes with spines along the dorsal suture
 Possible myrmecochory (persistent funicles or elaiosomes)
 Dark coloured seeds in some Cape groups (possible mimesis)
 Seeds with very hard testa and heat sensitive lens (Manning 1987) and extended viability through effective seed dormancy

Fig. 5.5. Summary of ecological associations in Indigoferaeae III & IV: Aspects of the breeding system & seed dispersal.

CHAPTER 6

PHYLOGENY AND EVOLUTION

6.1. PHYLOGENY

The cladogram (Table 2.3) established the basis for a working pattern of relationships in the tribe. As concepts of certain characters, i.e. hypotheses of polarity and homology are refined (e.g. during the studies in chapters 4 and 5), so the data matrix can be updated and the cladistic analysis rerun in an attempt to find a more parsimonious cladogram (see Conclusions, no. 21).

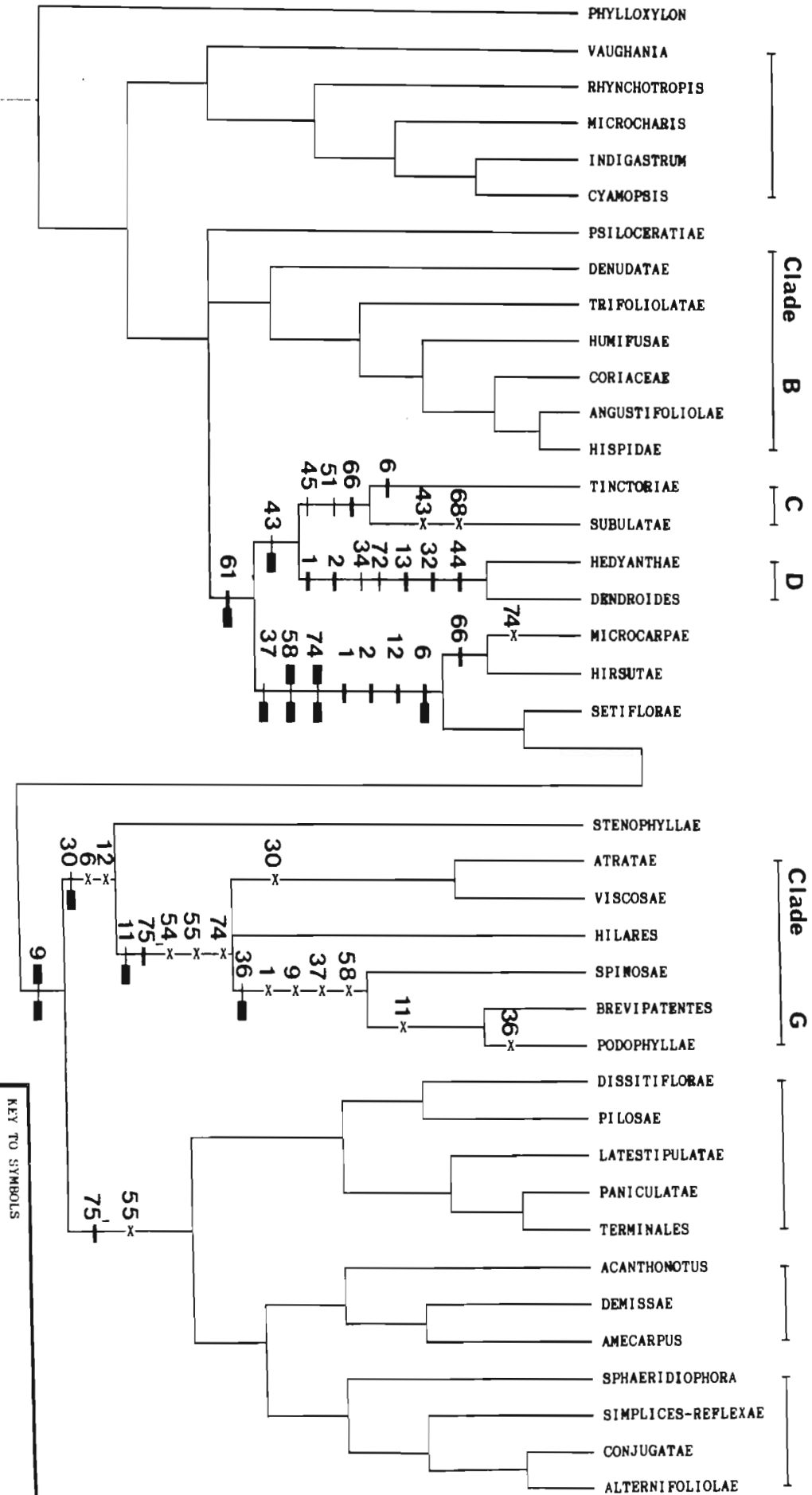
The proposed phylogeny (Table 6.1), which is based on the cladogram, is believed to reflect a pattern that may be corroborated by further cladistic analysis. Most areas of disagreement with Table 2.3 (see below) are a result of different interpretations of homoplasy, e.g. explanations of parallelisms as reversals and *vica versa*.

6.1.2. METHODS

The phylogeny (Table 6.1) is proposed on the basis of intuitive taxonomic ideas in the tribe, and the tree was constructed interactively by moving and rotating branches of the cladogram (Table 2.3) using the Dos Equis editor in HENNIG86. The tree was analysed using the full data set (Fig. A.1).

6.1.3. CLADOGRAM *vs.* PHYLOGENY

The phylogeny (Table 6.1) has a length of 147 steps, a *ci* of 39 and *ri* of 66; compared to 144 steps, a *ci* of 40 and *ri* of 68 for the cladogram. With a refined data set, however, it is hypothesized that the phylogeny might be better corroborated by a more parsimonious cladogram of the tribe than the present cladogram (Table 2.3).



KEY TO SYMBOLS

- = synapomorphy with no reversals higher up
- - - = parallelism
- x = reversal
- ▬ = autapomorphy
- ▬ = synapomorphy with one reversal higher up
- ▬ = synapomorphy with two reversals higher up

TABLE 6.1 PHYLOGENETIC TREE: Character distributions - proposed areas of divergence from the cladogram (Table 2.3).

The differences between the phylogeny and the empirically derived cladogram (Table 2.3) are discussed below.

1) In Table 6.1, Clades C & D are indicated as forming one clade, diagnosed by a synapomorphy (character 43). This character is considered more likely to have arisen once, with a later reversal in *Subulatae*, than to have developed as parallelisms in *Tinctoriae* and Clade D (as in Table 2.3). Each hypothesis involves two steps.

2) The *Hirsutae* - *Setiflorae* group (after Clade D) appears to have closer taxonomic links to the *Psiloceratiae* than to Clades C & D (as indicated in Table 2.3). In Table 6.1, the herbaceous habit (characters 1 & 2) is hypothesized to have evolved independently in the stems of Clade D and the *Hirsutae*. Two steps have been added to the overall length of the phylogeny compared with the cladogram, although both characters are linked in the one transformation to a herbaceous habit.

3) The *Microcarpae* are represented in Africa by one widespread species of probable American origin (Gillett 1958). Its precise relationships in the genus are unknown, but it appears to be derived from the *Hirsutae* rather than being less derived, as seen in Table 2.3. The closest affinities are to the *Pilosae*, in particular to the group ancestral to *Acanthonotus* and *Sphaeridiophora*.

In Table 2.3, character 66 occurs in parallel in the *Microcarpae* and *Hirsutae*, but in Table 6.1 it defines the clade linking the two sections. A reversal of character 74 in the *Microcarpae* means there is no change in the number of steps in this hypothesis.

4) Evidence seems to suggest that *Stenophyllae* are basal only to Clade G, and not also to Clades H, E and F (as in Table 2.3). The latter appear instead to be derived from *Pilosae* (in Clade H). Clade G and *Stenophyllae* form a larger clade in Table 6.1, defined by one synapomorphy (character 30) and two reversals (i.e. characters 6 & 12). In Table 2.3 characters 6 & 12 were

lost at the basal node of the second half of the cladogram and they evolved again in the stem of clades H, E & F.

The two characters which unite Clades G, H, E, & F in Table 2.3, are the advanced pollen type (character 75') and the loss of scattered anther hairs (character 55). Type 4 pollen has evolved independently in Clade D and its development appears to be correlated with the acquisition of a herbaceous habit (Ferguson & Strachan 1982). An equally likely hypothesis, therefore, may be that the advanced pollen type evolved in parallel in the two herbaceous groups, Clade G and Clades H, E & F. The restricted anther hair character is also more likely to be lost in each group. There is no change to the overall length of the phylogeny since the two additional steps above are balanced by the two steps saved in the rearrangement of characters 6 & 12.

5) Presumed taxonomic affinities in Clade G imply that Table 2.3 shows poor resolution of this group. The *Atratae - Viscosae & Hilares* sections appear to be independently derived from the basal *Stenophyllae - Brevierectae*; and *Podophyllae & Brevipatentes* are likely sister taxa arising from the *Spinosae*.

The development of glandular trichomes (character 11) is unique in the tribe and the character is believed to have evolved once, with a later reversal, and not as parallelisms as indicated in Table 2.3. This rearrangement is reflected in Table 6.1, and it supports not only the presumed basal polychotomy in Clade G (suggested above) but also the proposed sister group relations in the derived *Spinosae* alliance.

Character 36 is possibly better interpreted as a synapomorphy defining the *Spinosae* alliance, with a reversal occurring in the only species comprising the section *Podophyllae*. The reversal of character 36 makes the phylogeny one additional step longer than the cladogram.

The phylogeny is thus considered to be three steps longer than the cladogram because of:

- a) two characters which together are part of one proposed additional transformation from a woody to herbaceous habit.
- b) a third which is a secondary loss of calyx glands in a monotypic section.

6.1.4. *PHYLOGENETIC TREE: Evolutionary aspects of phytogeography and ecology*

The phylogeny (Table 6.1) is represented as a tree of relationships between taxa in Table 6.2. Individual species believed to be ancestral to infrageneric taxa have, where possible, been put at the various nodes. In most cases, however, the ancestral species is unknown and the infrageneric taxon including that species is placed at the node instead. Sister groups are either shown as diverging from a common ancestor or, in condensed form, as a linear sequence (if no conflict in relationships was evident between the cladogram and phylogeny).

The distributions of taxa on the phylogenetic tree (Table 6.2) are used for a brief discussion on the role of phytogeography and ecology in the evolution of the Indigoferaeae. The current distributions are given but too many missing areas and widespread distributions occur for them to be represented meaningfully on an area cladogram.

The major regions used for Africa (Fig. 6.1) are those delimited by Polhill (1982). These are designated on the phylogenetic tree by the following letters.

- M = Madagascar
- C = Central Africa
- E = East Africa
- W = West Africa
- N = North East Africa
- S = South Central Africa
- SA = Southern Africa

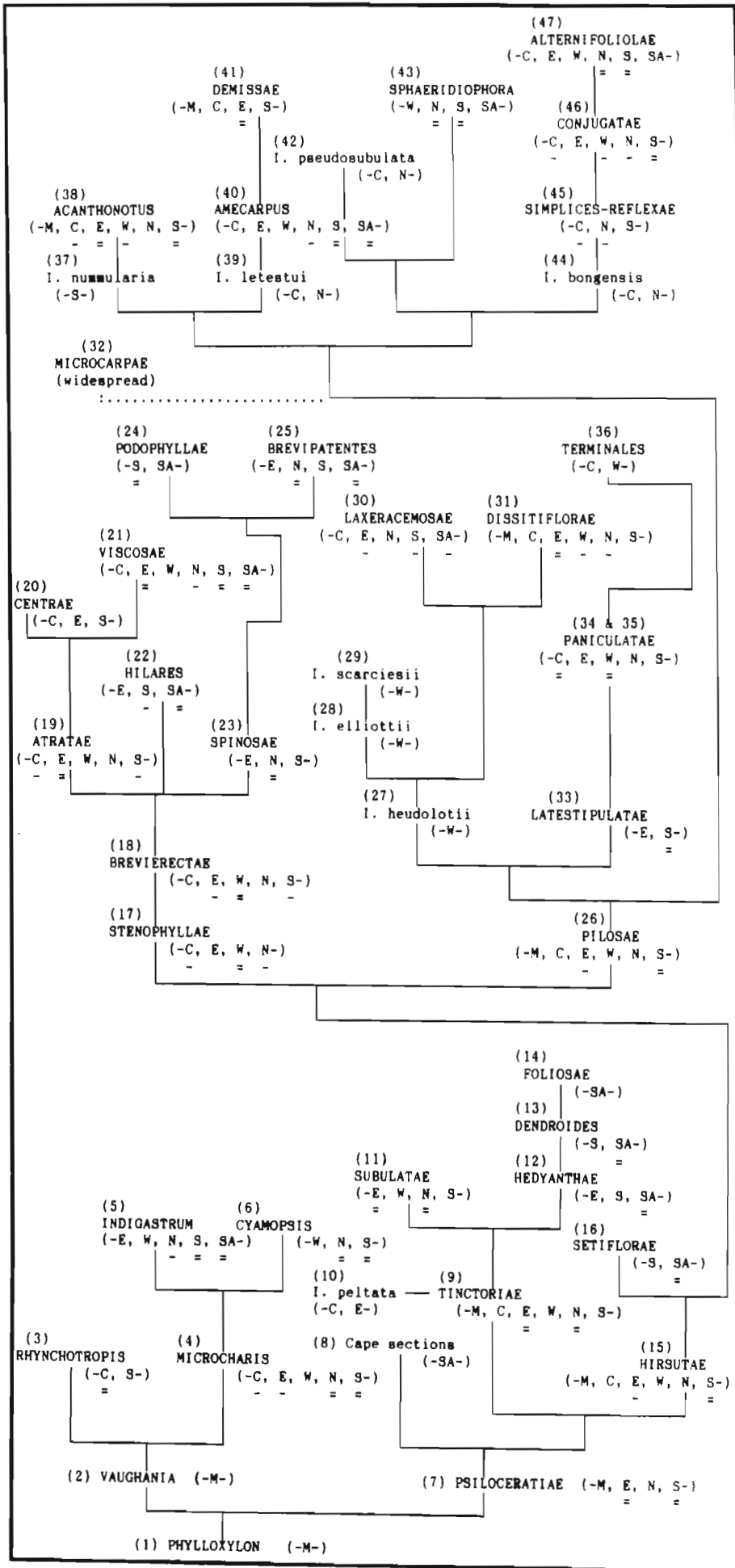


TABLE 6.2 PHYLOGENETIC TREE OF INDIGOFERAE IN AFRICA
Geographical distributions of taxa with reference to Fig. 6.1.

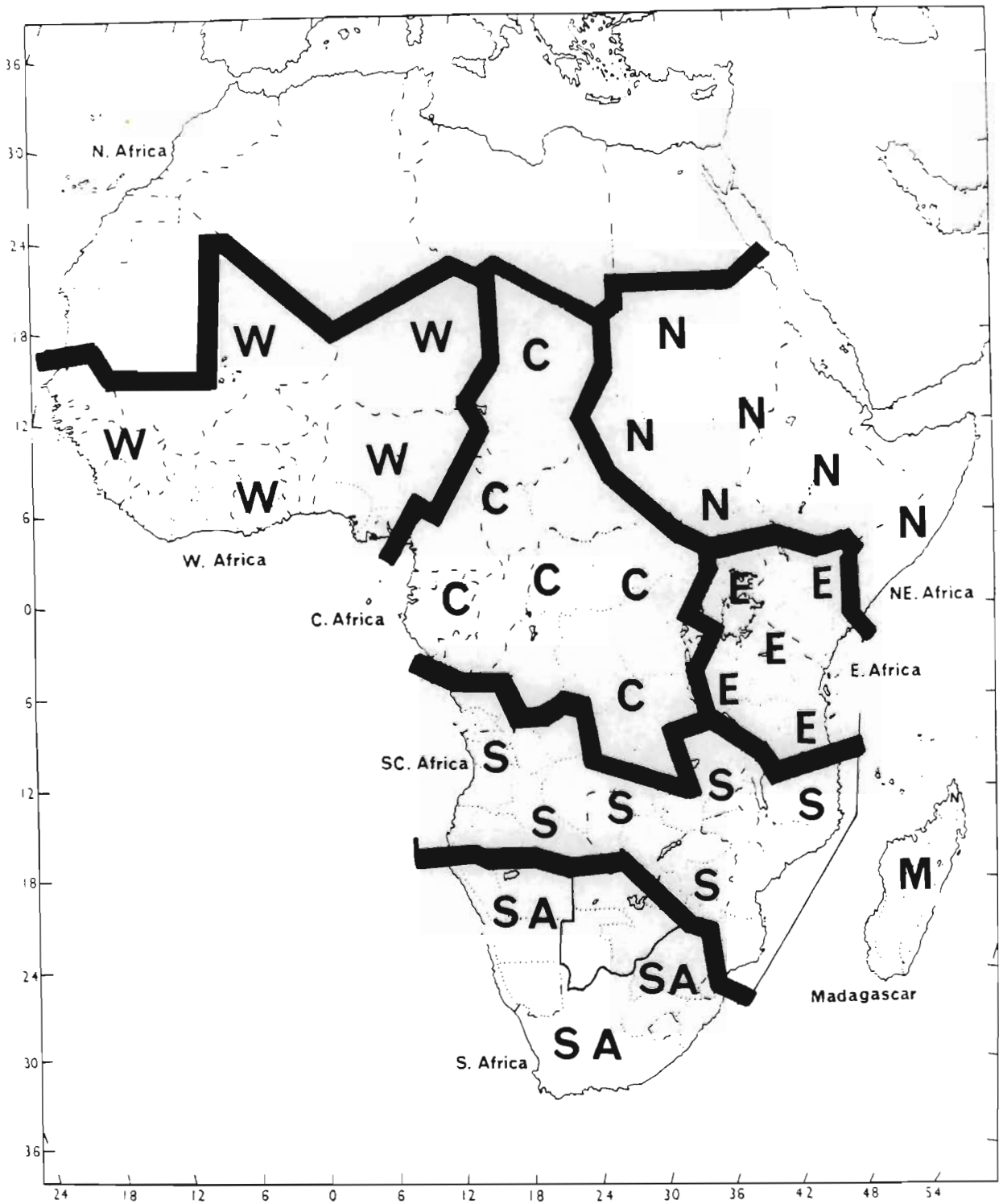


FIG. 6.1 MAJOR REGIONS OF AFRICA (After Polhill 1982): For distribution of taxa in Table 6.2. Symbols described in the text.

Single or double lines below a region indicate centres of greater species diversity for that taxon.

In Africa the tribe does not occur north of the Sahara (Fig. 6.1), perhaps indicating a post Saharan origin, at least for the more derived genera including *Indigofera*. The two basal and anomalous woody genera *Phylloxylon* and *Vaughania* are restricted to Madagascar, apparently reflecting an earlier phase of evolution which has experienced widespread extinction.

At node 7 the basal section of *Indigofera* (section *Psiloceratiae*) has an Afromontane distribution similar to that discussed by Linder (1983) for the *Disinae*. The *Psiloceratiae* also have a centre of diversity in China with a number of uniquely hexaploid species (Frahm-Leliveld 1966). The Cape sections in the south, and the node giving rise to the rest of *Indigofera*, are sister groups derived from the *Psiloceratiae*.

Two major trends are apparent within the herbaceous sections of *Indigofera* (from node 15), i.e. from West, Central and North-East Africa at node 17, and from South-Central to East Africa at node 26. These trends, however, are based on centres of present diversity and they need to be analysed more critically using biogeographical cladistic methods.

A further trend is evident in the more derived sections of the tribe, i.e. a distinct North-East to South-West (NE-SW) African distribution corresponding to the arid track proposed by De Winter (1971). This occurs from nodes 4-6, 23-25, 43 & 44-47, including the genera *Microcharis*, *Indigastrum* and *Cyamopsis*, and seven sections of *Indigofera*. A common evolutionary origin linked to the development of this arid track is hypothesized for these taxa.

A possible link might be present between two somewhat restricted areas in Africa where the development of precocious flowering has

occurred. The regions are:

- 1) Southern Zaire - Northern Zambia - Western Tanzania.
- 2) Northern Zaire - Southern Sudan - Eastern Central African Republic.

Both appear to contain highlands with old established grasslands that are subject to one annual wet season and frequent fires (White 1983; Gillett pers. comm.).

Adaptations to these conditions include the occurrence of many suffrutices with woody rootstocks producing aerial shoots after fire. Precocious flowering may allow exploitation of the immediate post fire environment by avoiding competition with subsequent grassland species. Taxa exhibiting this phenomenon are morphologically distinct, producing separate flowering and vegetative shoots, although inflorescences may develop normally in the latter. An acceleration in the timing of development appears to have occurred compared to the ancestor (discussed under heterochrony as a developmental constraint in chapter 5).

In the first region, nodes 3, 10 and a species at node 45 flower precociously and all are morphologically somewhat unusual. This event in the evolution of *Rhynchosyris* (node 3) may have given rise to the radiation of taxa from node 4. *I. peltata* (node 10) has a unique development in the form of nymphaea-like peltate leaves, the only such record in the entire Leguminosae (Gillett 1971).

In the second region, precocious flowering occurs at nodes 39, 42, 44 & 45 comprising the basal nodes of nearly the entire clade in the top third of the phylogenetic tree. A hypothesis is made that much of the radiation at the basal node of this clade may be due to speciation resulting from certain precociously flowering species.

Some of the speciation in groups from the above two areas appears to correspond with that linked to the NE-SW arid track mentioned above.

A similar example occurs in West Africa from the Loma-Man "dorsale" region in northern Sierra Leone and Guinea. The species *I. scarciensis* (at node 29) flowers precociously, is almost entirely glabrous, has winged petioles and a unique translucent venation in fleshy leaflets. This region is known for its somewhat impoverished soils and dwarf vegetation greatly affected by fire (White 1983).

Other old established grasslands maintained by natural fires occur on the high altitude Nyika plateau (Meadows 1984). Although there are no precocious flowering species of *Indigofera* in this region, such grasslands are centres of two variable pyrophytic groups of taxa from nodes 22 & 12. The section *Hilares* and *Hedyanthae* contain a number of species with large woody rootstocks from which leafy shoots emerge following fires. Such species groups are highly variable (Gillett 1958) and indeed they comprise two of the most difficult species complexes of the genus in Africa.

An unusual aspect of the phytogeography of *Indigofera* is the extent of its development in the winter rainfall area of southern Africa, and the complete absence of similar radiations into mediterranean-type climates elsewhere in the world (Gillett pers. comm.). This may reinforce the hypothesis that the genus has had a long association with Africa south of the Sahara. Only the most derived Cape sections have become adapted to a winter rainfall regime and many Cape taxa still show indications, through their flowering times, of a summer rainfall ancestry. This agrees with current ideas about the relative recency of the inception of a winter rainfall pattern in South Africa (Deacon 1983).

6.1.5. CENTRES OF DIVERSITY OUTSIDE AFRICA

One of the major centres of radiation in the genus is in the Sino-Indian region (Craib 1913; Ali 1958; 1977; Sanjappa 1985; Fang & Zheng 1989). Estimates for this area, including South East Asia (de Kort & Thijsse 1984), are from 130 - 150 species (exclusive of widespread taxa also found in Africa).

The other important region for the genus is in tropical and subtropical, North, Central and South America (Rydberg 1923; Burkart 1939). Taking the region as a whole (including the West Indies) the New World may contain 60 to 80 additional species of *Indigofera*.

In Australia, a further centre of diversity is found in *Indigofera* (Bentham 1864; Crisp 1983; Wilson 1987; Wilson pers. comm.), with an estimated 30 - 40 endemic species.

The pantropical *Indigofera* is therefore estimated to comprise 750 to 800 species overall.

6.2. EVOLUTION OF INDIGOFEREAE

The following phases of evolution and radiation are hypothesized for the tribe, based on significant switches in the pattern of morphologies on the phylogenetic tree (Table 6.2).

- 1) *Phylloxylon* and *Vaughania* are two anomalous woody genera now restricted to Madagascar. They appear to be relictual, after widespread extinction elsewhere, and may represent a phase of radiation much older than the rest of the tribe.
- 2) The woody basal section *Psiloceratae* of *Indigofera* has an Afrotropical affinity and related taxa with a similar tendency, which appear to be derived from the same phase of evolution, are the basal Cape groups (node 8), the basal *Tinctoriae* (node 9) and the *Hedyanthae* (node 12).
- 3) The fundamental shift in morphology from node 15 appears to be correlated with a widespread development of the herbaceous and annual habit, and is possibly associated with the evolution of savanna vegetation types in Africa. This phase apparently accounts for the diversification of the bulk of sections of *Indigofera*.

Speciation during this phase often appears to result from the evolution of key morphologies that have opened up new paths of adaptive radiation. Multicellular glandular trichomes (hypothesized to be exaptations from modified biramous hairs) apparently resulted in widespread speciation from node 18. Another example (already discussed in chapter 5) is the evolution of a unique shoot morphology at node 26.

- 4) In the clade including nodes 37-47 the major switch in morphology (hypothesized to be the result of heterochrony) supports the hypothesis that these nodes represent the latest major phase in the evolution of *Indigofera* above the species level.

Evidence has been led to show this phase may be linked with the development of the NE-SW arid track in Africa, and increasing aridity may have driven subsequent speciation in these new sections. Since the genera *Microcharis*, *Indigastrium* and *Cyamopsis* (nodes 4-6) and the *Spinosa* alliance (nodes 23-25) are also associated with this track, it is suggested that the same event may have resulted in the radiation of all these taxa.

CHAPTER 7

TAXONOMY OF INDIGOFEREAE ABOVE THE SPECIES LEVEL

7.1. GENERAL LITERATURE REVIEW

De Candolle (1825) placed *Indigofera* in his tribe Loteae subtribe Clitoriae (a treatment followed by E. Meyer 1836 & Walpers 1839), while *Cyamopsis* DC. was put in the preceding subtribe Trifolieae Bronn. Bentham (1837) included *Cyamopsis* in tribe Phaseoleae subtribe Glycineae Benth., and in 1839 he noted his intention of creating a subtribe "Indigoferae", but this remained invalidly published (Lievens & Urbatsch 1990). Endlicher (1840) placed *Indigofera* in tribe Loteae subtribe Galegeae Bronn, while retaining *Cyamopsis* in subtribe Glycineae. In 1859 Bentham validly published Indigoferae at tribal level in his work on Papilionaceae of Brazil, with the type genus *Indigofera* L.

Bentham was apparently not convinced by this tribal circumscription (see comments by Lievens & Urbatsch 1990) because in 1864, in *Flora Australiensis*, *Indigofera* was accommodated in the tribe Galegeae (Bronn) Torrey & Gray. In *Genera Plantarum* (1865) Bentham, again without reference to his previous treatments (1859, 1861), placed *Indigofera* and *Cyamopsis* together in subtribe Indigoferinae (Benth.) Benth. (as "Indigoferae") of tribe Galegeae. The taxon was used as a subtribe in Galegeae by Baillon (1872) and Taubert (1894), but Rydberg (1923) raised it again to tribal status. This has been followed by Hutchinson (1964), who included *Rhynchotropis* of Harms (1901), and Polhill (1981) who added *Phylloxylon* (described by Baillon 1861).

Indigofera was known as *Anil* before Linnaeus, and the eventual type species of *Indigofera* (*I. tinctoria*) was described as "*Anil sive Nil indorum color*" by Bauhin (1651) in *Historia Plantarum*. Rheede (1678) established the genus *Ameri* in *Hortus Malabaricus*. Numerous other plurinomial species were ascribed to different genera; e.g. *I. colutea* to *Colutea* (Plukenet 1691); *I.*

psoraloides to *Cytisus* (Rivinus, 1691) and to *Trifolium* (Plukenet 1696); *I. sarmentosa* to *Lotus* (Plukenet 1700); *I. cytisoides* to *Lotus* (Commelin 1701); *I. alopecuroides* to *Lotus* (Burman 1737), and *I. hirsuta* to *Astragalus* (Burman 1737).

Isnard is credited by Ludwig (1760) as having published the name *Indigo* in the *Acta Parisiensia (Memoires de l'Academie Royale des Science)*, but no trace of this was found in his publications in the above journal from 1716 to 1723 (Heller 1959). Adanson (1763) established the name *Indigo*, citing among others, *Anil* Bauhin, *Ameri* Rheede and *Indigofera* Linnaeus as synonyms. Ludwig (1737) cites the genus *Anil* March. after Marchant's description of "*Anilsive Indigo Americana, siliquis in falculae modum contortis*" in *Memoires de l'Academie Royale des Science* : 92-97 t.3 (1718). *Anil* March. was later taken up by Kuntze (1891) who latinized the name and referred to it as *Anila* Ludw. "March.". Kuntze transferred a large number of *Indigofera* species to *Anila*, making many new combinations and publishing various subspecific taxa.

Indigofera was first mentioned by Linnaeus in *Hortus Cliffortianus* (1738). He described two species, one of which was not an *Indigofera*, and the other, "*Indigofera foliis nudis*", referred again to *I. tinctoria*, the eventual type species of the genus. In 1753 *Indigofera* was published in *Species Plantarum* and according to Art 13a of the ICBN (Greuter et al. 1988), this is the limit of priority for the beginning of modern nomenclature. *Anil* Bauhin and *Ameri* Rheede thus became generic synonyms.

Three species were described by Linnaeus in 1753; *I. tinctoria*, the type species mentioned above (although it was only lectotypified by Britton & Brown 1913), *I. hirsuta*, and an Indian species *I. glabra*. He still confused *Indigofera* with other genera, however, at first describing *I. psoraloides* under *Cytisus* (1763); *I. sarmentosa* under *Ononis* (1771); *I. mauritanica* under *Lotus* (1763) and *Ononis* (1771), and *I. cytisoides* under *Psoralea* (1763). Bergius (1767) also described *I. sarmentosa* and *I. mauritanica* under *Lotus*.

Miller (1754) mentioned 3 plurinomial species under *Anil* in his fourth abridged edition of *Gardeners Dictionary*, the first major work with generic descriptions to be published after *Species Plantarum* (Stearn 1969). Although the names appeared in earlier editions (back to the first in 1731), and even though he referred *Anil* to Bauhin, *Anil* Miller became a validly published name in 1754. The two names were later declared to be nomenclaturally identical and in the eighth edition of the *Gardeners Dictionary* (1768) Miller changed *Anil* to *Indigofera*.

Desvaux (1813) described the genus *Sphaeridiophorum*, using as the type species *Hedysarum linifolium* L.f. which had already been transferred to *Indigofera* by Retzius (1786). Bentham (1865) treated it as a subgenus of *Indigofera* (as *Sphaeridiophora*) and this was followed by Baker (1871). Taubert (1894) gave *Sphaeridiophora* sectional status and this was taken up by Baker f. (1926).

The following quote about the genus *Brissonia* is made from de Kort & Thijsse (1984):

"In 1814, Desvaux validated the uninomial species name *Brissonia* of Necker (1790), as a genus with three species. He mentioned as generic synonyms *Reineria* Moench and *Tephrosia* Pers. (the latter as *Thephrosia*). In 1826 he transferred one of his original 3 species to the synonymy of *Indigofera senegalensis* [Amecarpus], and the remaining two species were later recognized as representing present *Tephrosia* [Millettieae]. Baker (1871) based his subgenus *Brissonia* of *Tephrosia* on these two species. Taubert (1894) reduced this to sectional rank, but he also mentioned *Brissonia* in the synonymy of *Indigofera*, which must have its cause in Bentham's citation (1865) of *Brissonia* Desv. (1826) in the synonymy of *Indigofera* subgenus *Amecarpus*. Bentham probably meant to cite the species which Desvaux himself already transferred to *Indigofera*. Anyway, because of Desvaux' citation of *Reineria* and *Tephrosia* as synonyms, *Brissonia* must be considered a nomenclatural synonym of *Tephrosia* (*nom. cons.*)."

Bremontiera DC. (1825a) was based on the type species *B. amoxylon* from Reunion and was placed by de Candolle (1825) in tribe Hedysareae subtribe Alhageae. A variety *burmanni* was published at the same time which has subsequently been put into the genus *Taverniera* DC. in the Hedysareae (Hutchinson 1964; Polhill 1981). The main variety was treated by Bentham (1865) and Taubert (1894) among excluded taxa with unknown affinity. *Bremontiera* was brought into synonymy under *Indigofera* by Polhill (1981).

The genus *Cordaea* was published by Sprengel (1831), based on the type of *Cyamopsis*.

G. Don (1832) described the genus *Oustropis*, with the type *O. microphyllus* based on *Lotus microphyllus* Hooker (1828). This species is a synonym of *Indigofera gracilis* Sprengel (1827) in section *Trifoliolatae*. Rafinesque (1836) used the same species, *L. microphyllus* as the type in his description of the genus *Tricoilendus*. Bentham (1865) placed *Oustropis* into synonymy under his subgenus *Euindigofera*.

Endlicher (1832) established the genus *Hemispadon* with the type species *H. pilosus* Endl. which is a synonym for *Indigofera pilosa* Poir. (1813). The genus was placed under subgenus *Euindigofera* by Bentham (1865) and this was followed by Taubert (1894).

Eilemanthus was erected as a genus by Hochstetter (1846) using the type *E. strobilifer* Hochst., and Baker (1871) made the combination into *Indigofera strobilifera*. The genus was placed into synonymy under *Indigofera* by Bentham and later authors.

The genus *Acanthonotus* was described by Bentham (1849), based on *Indigofera echinata* Willd. (now *I. nummulariifolia* (L.) Livera ex Alston), but he reduced it to subgeneric level in 1865. This was followed by Baker (1871) and Gillett (1958). Taubert (1894) treated *Acanthonotus* as one of four sections in *Indigofera* and

Baker f. (1926) placed it into synonymy of section *Echinatae* Wight & Arn. (1834).

Jaubert & Spach (1857) established the genus *Indigastrum* based on *Indigofera deflexa* Hochst. ex A.Rich. (now in synonymy under *Indigastrum parviflorum* (Heyne ex Wight & Arnot) Schrire). Bentham (1865) placed it under his subgenus *Euindigofera* and Baker f. (1926) treated *Indigastrum* as a distinct "Group" within his section *Euindigofera*. Gillett (1958) raised *Indigastrum* to a subgenus of *Indigofera*.

The genus *Phylloxylon* was published by Baillon (1861) and was thought to belong in the Euphorbiaceae. Baker (1883) described a species in the Santalaceae, *Exocarpus xylophyloides*, which pertains to *Phylloxylon* and in 1884 he created the genus *Neobaronia* which he placed in the tribe Dalbergieae. Taubert (1894) treated *Neobaronia* in the subtribe Anomalae of Dalbergieae and Hutchinson (1964), considering the genus synonymous with *Phylloxylon*, put it in the tribe Geoffroeeae allied to the Dalbergieae. The affinity of *Phylloxylon* was clarified by Polhill (1981) who placed it in the Indigoferaeae.

Harvey (1862) took up the *nom. nud.* generic name *Amecarpus* of Bentham (1846), and placed it as one of two subgenera under *Indigofera*. Bentham (1865), Baker (1871) and Gillett (1958) maintained the subgeneric rank, the latter lectotypifying it with *I. sessilifolia* DC. Taubert (1894) and Baker f. (1926) treated *Amecarpus* at sectional level.

Microcharis was described as a genus by Bentham (1865) in the tribe Galegeae subtribe "Galegeae", but a type was not designated. Two species were referred to in Benth. (1865a) but it was Gillett (1958) who lectotypified *M. tenella* Benth. (as *I. hutchinsoniana* Gillett). Taubert (1894), Baker (1871) and Baker.f. (1929) retained the generic rank for *Microcharis* (the former placing it in Galegeae subtribe Robiniinae), while Gillett (1958) treated it a subgenus of *Indigofera*.

The genus *Rhynchotropis* was described by Harms (1901) based on *Indigofera poggei* Taubert (1894). Hutchinson (1964) defined the tribe Indigofereae to include *Indigofera*, *Cyamopsis* and *Rhynchotropis*.

Moore (1920) published the monotypic Madagascan genus *Vaughania*, with the type species *V. dionaeaefolia* S.Moore, and this was transferred to *Indigofera* by Polhill (1981). Viguier (1944), in his unpublished typescript *Les Légumineuses de Madagascar*, described 13 series of Madagascan *Indigofera*, and most of series 12 refers to *Vaughania*.

7.2. GENERIC AND INFRAGENERIC TAXA OF THE TRIBE INDIGOFEREAE IN AFRICA AND MADAGASCAR

TRIBE INDIGOFEREAE

Indigofereae Benth. in C.Martius, Fl.Bras. 15(1): 5-6 (1859); Rydberg in North.Amer.Fl. 24: 137 (1923); Hutch., Gen.Fl.Pl. 1: 399 (1964); Gillett in Fl.Tr.E.Afr., Legum.- Papil. 3: 212 (1971); Polhill in Polhill & Raven, Adv. Leg. Syst. 1: 289 (1981); Lievens & Urbatsch, Taxon 39: 335-336 (1990). Type genus *Indigofera* L.

Note: Hutchinson, Gillett and Polhill wrongly ascribed Indigofereae to (Benth.) Rydberg.

Tribe **Curvembryae Diadelphae** subtribe "**Galegeae**" Bronn, Diss. Legum. 134 (1822) p.p.

Tribe **Loteae** subtribe "**Clitoriae**" DC. Prodr. 2: 216 (1825)p.p.

Tribe **Loteae** subtribe "**Trifolieae**" (Bronn) DC. Prodr. 2: 171 (1825) p.p.

Tribe **Hedysareae** subtribe **Alhageae** DC., Prodr. 2: 352 (1825)

p.p.

Tribe **Phaseoleae** subtribe "**Glycineae**" Benth. in *Annal.Wien.Mus.* 2: 112 (1837) p.p.

Tribe **Galegeae** subtribe **Indigoferinae** (Benth.) Benth. (as "Indigoferaeae") in Benth. & Hook.f., *Gen.Pl.* 1: 444 (1865); Taub. in Engl.& Prantl, *Pflanzenfam.* 3(3): 259 (1894); Viguier, *Légum. Madagasc.* (unpubl.) 302 (1944). Subtribe **Indigoferinae** Benth. in *Ann.Nat.Hist.* 3: 430-431 (1839); in Hooker, *J.Bot.* 2: 55 (1840) nom.nud.

Tribe **Loteae** subtribe "**Galegeae**" (Bronn) Endl., *Gen.Pl.* 1270 (1840) p.p.

Tribe **Loteae** subtribe "**Glycineae**" (Benth.) Endl., *Gen.Pl.* 1291 (1840) p.p.

Tribe **Galegeae** subtribe **Robinieae** Benth., in Benth.& Hook.f., *Gen.Pl.* 1: 445 (1865) p.p.

Tribe **Dalbergieae** subtribe **Anomalae** Taub. in Engl.& Prantl, *Pflanzenfam.* 3(3): 348 (1894) p.p.

Tribe **Geoffroeeae** Hutch., *Gen.Pl.Pl.* 1: 390 (1964) p.p.

Trees or most often dwarf shrubs or herbs; hairs typically biramous, dark brown coloured mixed with hyaline, or hyaline only; pearl bodies minute, scattered at the leaf bases and between the leaflets. **Leaves** pulvinate, alternate, generally imparipinnate, sometimes digitate, often reduced to 1-foliolate or simple; rarely ephemeral (*Phylloxylon*) or 0; an abaxial commissure sometimes present at the base of the petiole between the pulvinus and the stipules, or the stipules partially adnate to the base of the petiole; stipules subulate to ovate; leaflets opposite or rarely alternate, entire or toothed (in *Cyamopsis*); stipels present or absent. **Inflorescences** mostly axillary racemes (sometimes paniculate in *Indigofera*); bracteoles 0

(except *Phylloxylon*). **Flowers** pink to reddish with explosive pollen release, the lower petals (at least) soon caducous; calyx hairy (except rarely in *Indigofera*), shortly tubular with 5 subequal lobes, the lobes shorter to longer than the tube, vexillary lobes mostly separated by a broad sinus (except *Phylloxylon*). **Corolla** standard glabrous or hairy dorsally, the central blotch either paler or darker than the surrounding lamina, occasionally glossy; standard asymmetrically positioned in *Vaughania*; wings often with a conspicuous crest proximally, the petals forming a platform above the keel (except *Vaughania*; keel straight abaxially or rounded (in *Vaughania*); petals valvately connate distally, with or without lateral spurs, the upper margins of the keel usually visible between the wings with a distinct fringe of hairs proximally (in *Indigofera* and *Cyamopsis*), keel twisted in *Vaughania*. **Stamens** intrastaminal nectariferous disc present; vexillary stamen free, or lightly attached to the others (in *Cyamopsis*), staminal sheath persistent, the stamens alternately long and short distally; anthers q uniform, apiculate with expanded apical connective (except *Phylloxylon*), hairs present or absent above or below anthers; pollen tricolporate with a generally thickened endexine, columellar to granular. **Pistil** ovary longer or shorter than the horizontal length of the pistil, ovules 1 - many; stigma oblique or capitate, penicillate. **Pod** 2 - valved, septate (except *Phylloxylon*), mostly explosively dehiscent with valves twisting, or turgid and indehiscent; often with a persistent style base apically and persistent cup-like base after dehiscence; endocarp spotted with tannin deposits in *Indigofera*. **Seeds** cylindrical, globular, cuboid or rectangular; brown, yellow, orange, or khaki, often purple mottled; significantly larger in *Phylloxylon*; hilum small; cotyledons unequal; radicle oblique; endosperm usually copious. **Seedlings** mostly phaneroepigeal, usually with 1 - foliolate opposite eophylls; phyllodes adventitious from the hypocotyl in *Phylloxylon*. **Chromosomes** $2n = 14, 16, 32, 48$. **Phytochemistry** indican often present in leaves; canavanine generally found in seeds, sometimes also indospicine.

7.2.1. Key to genera

1. Branches mostly modified as **cladodes**; bracteoles present; calyx without a broad sinus between the vexillary lobes; anthers glabrous, not apiculate; pods more than 5 mm wide, with 1-2 seeds, each more than 5 mm long:
..... 1. *Phyllonxon*
1. Branches terete, angled, winged or slightly flattened; bracteoles absent; calyx with a broad sinus between the vexillary lobes; anthers apiculate or densely hairy; pods less than 5 mm wide, with 1 - many seeds, each less than 3 mm long:
2. Standard glabrous dorsally:
3. Upper margin of the keel without a proximal fringe of hairs; endocarp without tannin deposits:
4. Anthers with plumose hairs above and below; stamens free distally for at least 1 - 2 mm:
5. Petioles mostly **phyllodinous**; flowers asymmetrical with keel twisted, staminal sheath curved; keel not prolonged rostrate: 2. *Vaughania*
5. Petioles terete; flowers symmetrical with keel and staminal sheath straight; keel prolonged rostrate:
..... 3. *Rhynchotropis*
4. Anthers glabrous or with scales; stamens free distally for less than 1 mm:
6. Leaves sometimes dentate; standard broad at the base tapering suddenly to a short claw; keel not prolonged rostrate; vexillary stamen lightly attached to the

sheath; corolla veined; pods 3 - 5 mm wide,
longitudinally ridged, erect:

..... 6. *Cyamopsis*

6. Leaves never dentate; standard narrow at the base tapering gradually to the claw; keel prolonged rostrate; vexillary stamen free; corolla veins rarely apparent; pods less than 3 mm wide, never ridged, patent to reflexed:

7. Bracts persistent; inflorescence lax in bud; fruiting pedicels often over 2 mm long, φ patent, the pods often at right angles; anthers, at least those of the 4 shorter stamens, with hyaline scales at the base; style short, thick; stigma discoid:

..... 4. *Microcharis*

7. Bracts caducous; inflorescence dense in bud; fruiting pedicels rarely over 2 mm long, reflexed (as are the pods); anthers of the shorter stamens mostly with scales reduced or absent; style not short and thick; stigma oblique or capitate:

8. Inflorescences elongated, pedunculate (if sessile then leaflets 9 - 15, oblong-lanceolate, opposite); pods 10 - 20 seeded, more than 20 mm long:

..... 5a *Indigastrum* subgenus *Indigastrum*

8. Inflorescences sessile or subsessile, densely flowered in the axils of leaves; leaflets 1 - 6, obovate or cuneate, often alternate; pods 4 - 8 seeded, less than 20 mm long:

..... 5b *Indigastrum* subgenus *Argyraeae*

3. Upper margin of the keel with a proximal fringe of hairs; endocarp with tannins (except *Cyamopsis*)

9. Leaves sometimes dentate; vexillary stamen lightly attached to the sheath; corolla veined; keel glabrous or with isolated appressed hairs distally; anthers glabrous; pods 3 - 5 mm wide, longitudinally ridged:
 6. *Cyamopsis*

9. Leaves never dentate; vexillary stamen free; corolla veins rarely apparent; keel mostly bearded distally; anthers often hairy; pods less than 3 mm wide, never ridged as above:
 7. *Indigofera*

2. Standard hairy dorsally

10. Upper margin of keel with a proximal fringe of hairs; staminal sheath straight, the filaments free for less than 1 mm distally endocarp mostly with tannin deposits; keel always with lateral spurs:
 7. *Indigofera*

10. Upper margin of keel glabrous; endocarp without tannin deposits:

11. Petioles mostly phyllokinous; calyx lobes shorter than the tube; flowers asymmetrical with keel twisted (or if straight then calyx lobes equalling or longer than the tube), staminal sheath mostly curved, the filaments free for 1 - 2 mm distally; keel not prolonged rostrate, lateral spurs sometimes present:
 2. *Vaughania*

11. Petioles never phyllokinous; calyx lobes longer than the tube; keel and staminal sheath straight, the filaments free for less than 1 mm distally; keel prolonged rostrate, without lateral spurs:
 5b *Indigostrum* subgenus *Argyraeae*

- 1) *Phylloxylon* Baill., *Adansonia* 2: 54 (1861); Viguiier, *Légum. Madagasc.* 461 (1944, unpubl.); Hutch., *Gen.Fl.Pl.* 391 (1964); Polhill in Polhill & Raven, *Adv.Leg.Syst.* 1: 291 (1981).
Xylophylla ensifolia Bojer *nom. nud.* *Exocarpus xylophyloides* Bak., *Journ.Linn.Soc.* 20: 249 (1883).
Neobaronia Bak., *Journ. Linn. Soc.* 21: 336 (1884); Taub. in Engl. & Prantl, *Pflanzenfam.* 3(3): 348 (1894). Type species *Phylloxylon decipiens* Baill.

Trees to 20 m, attaining a diameter of 0.3 m, or sometimes shrubs; stems subterete, mostly widening gradually, becoming flattened, cladodes; branches entirely glabrous or closely appressed hyaline pubescent on juvenile growth, the biramous hairs uniquely flattened; branchlets occasionally spine-tipped; biramous hairs with arms always equal in length, hairs mixed dark brown and hyaline on inflorescences only; pearl bodies sparse; leaves simple (if present), mostly ephemeral or entirely absent, venation prominent; an abaxial commissure mostly present at the base of the petiole between the pulvinus and stipules; racemes subspicate, short, borne in crenations on the phyllode margins; bracts deltoid or ovate-cucullate, coriaceous; bracteoles present on the pedicels or below the calyx; flowers to 14 mm long, corolla deep rose, glabrous; calyx densely brown strigose, the teeth shorter than the tube, vexillary sinus narrow; standard with pale central blotch; keel mostly acute; staminal sheath 4 - 8 mm long (often about half the length of the flower in *P. perrieri*), straight, the filaments free distally for less than 1 mm; anthers glabrous, without apiculate expanded connective; ovary glabrous, stigma capitate; pods 1 - 2 seeded, coriaceous, turgid, tapering to the base and apex, tardily dehiscent; endocarp spongy becoming papery; seeds 5 - 15 mm wide, rounded.

- 2) *Vaughania* S.Moore, *J.Bot.* 58: 188 (1920). Type species *Vaughania dionaeaefolia* S.Moore.

Indigofera série 12 of Viguiier, *Légum. Madasc.* 347 (1944, unpubl.) p.p.

Indigofera L. p.p., Polhill in Polhill & Raven,
Adv.Leg.Syst. 1: 291 (1981).

Trees 6 - 8 m high, or shrubs; branches rigid, many, often with brachyblasts; bark coming away in strips attached to the base of broken twigs; biramous hairs with arms always *q* equal in length, hairs mixed dark brown and hyaline on inflorescences only; pearl bodies present at leaf bases and between the leaflets; leaves 9 - 5 - 1 foliolate, an abaxial commissure mostly present at the base of the petiole between the pulvinus and stipules; leaflets often on phyllodinous petioles, the latter frequently confused with simple leaves after leaflets caducous; leaflets opposite or rarely alternate, occasionally very emarginate at the apex; stipels often present; racemes densely subspicate from flowering brachyblasts; bracts deltoid or ovate-cucullate, coriaceous, imbricate; bracteoles absent; flowers to 15 mm long, corolla pink to deep rose; calyx densely brown strigose, the teeth nearly always shorter than the tube; standard with dorsal surface hyaline strigose, central blotch pale, sometimes asymmetrically positioned; wings twisting with the keel in front of standard; keel rounded below; staminal sheath distinctly curved, 6 - 14 mm long, the filaments free for 1 to 2 mm distally; anthers plumose hairy above and below; ovary mostly strigose, style curved, stigma oblique; pods 1 to many seeded, cylindrical with spirally dehiscent valves; endocarp septate, papery, without tannin deposits; seeds subcylindrical, less than 3 mm long.

- 3) *Rhynchotropis* Harms, Engl.Bot.Jahrb. 30: 86 (1901); Bak.f., Leg.Tr. Afr. 1: 166 (1926); Cronquist, Fl.Congo Belge 5: 173-174 t.9 (1954); Gillett, Kew Bull., Add. ser. 1: 136 (1958); Hutch., Gen.Fl.Pl. 400 (1964); Polhill, in Polhill & Raven, Adv.Leg.Syst. 1: 291 (1981); Lock, Legum.Afr. 333 (1989).
Type species *Rhynchotropis poggei* (Taub.) Harms.

Perennial herbs from woody rootstocks; biramous hairs with arms always *q* equal in length, hyaline only; pearl bodies restricted to the leaf bases; leaves simple, linear or narrowly

lanceolate, entire; stipules adnate to the base of the petiole, subulate; stipels absent; racemes elongate, laxly 5 - 20 flowered, axillary or subterminal on leafy shoots, sometimes on precocious flowering shoots arising from the rootstock; bracts caducous; pedicels 2 - 8 mm long, often stiffly spreading; calyx 3 - 7 mm long, more than half the length of the staminal sheath, lobes lanceolate to subulate, *q* equal or longer than the 2 - 4 mm long tube; flowers pink, petals glabrous; standard narrow at the base, tapering to the claw; keel with lateral pouches (spurs absent), apex prolonged rostrate; stamens all fertile, staminal sheath 3.5 - 6 mm long, curved upwards distally, filaments free for distal 1 - 2 mm, anthers with plumose hairs above and below; ovary linear; style abruptly constricted at the point of upward flexure, flattened and cymbiform-dilated above, then twisted below the stigma; stigma oblique, discoid; pods *q* patent, held at right angles to the pedicel when mature, 2 - 4 (6) seeded, laterally compressed or subterete, linear, straight, often shortly stipitate; endocarp without tannin deposits.

- 4) *Microcharis* Benth. in Benth. & Hook. f., Gen. Fl. 1: 501 (1865); Benth. in Trans. Linn. Soc. Lond. 25: 297 (1865a); Bak. in Oliver, Fl. Tr. Afr. 2: 132 (1871); Taub. in Engl. & Prantl, Pflanzenfam. 3(3): 277 (1894); Hutch. & Dalz., Fl. W. Tr. Afr. 1: 388 (1927); Bak. f., Leg. Tr. Afr. 2: 256 (1929). Lectotype species *Microcharis tenella* Benth. [Lectotypified in Gillett, Kew Bull., Add. ser. 1: 127 (1958)].

Indigofera subgenus *Microcharis* (Benth.) Gillett, Kew Bull., Add. ser. 1: 127 (1958); Gillett in Fl. Tr. E. Afr. Legum.-Papil. 3: 321 (1971).

Indigofera subgenus *Indigastrum* sensu Cronquist, Fl. Congo Belge 5: 124 p.p.

Indigofera L. p.p., Hutch., Gen. Fl. Pl. 1: 400 (1964); Polhill in Polhill & Raven, Adv. Leg. Syst. :291 (1981); de Kort & Thijssse in Blumea 30: 104 (1984); Thulin in Hedberg &

Edwards, Fl.Ethiopia 3: 119 (1989); Lock, Legum.Afr. :289 (1989).

Annual or perennial herbs; biramous hairs with arms always *q* equal in length, hyaline or yellowish; pearl bodies restricted to the leaf bases and between the leaflets; leaves 1 - 9 (13) foliolate or simple, leaflets opposite, entire; stipules adnate to the base of the petiole, subulate, deltoid, falcate-lanceolate or broadly cordate; stipels absent; racemes axillary or terminal, laxly 3 - 15 (30) flowered; bracts persistent; pedicels 2 - 7 mm long, often stiffly spreading; calyx *q* half or more the length of the staminal sheath, lobes *q* equal or longer than the tube; flowers pink, petals glabrous; standard narrow at the base, tapering to the claw; keel with lateral pouches (spurs absent), apex prolonged rostrate; vexillary stamen mostly sterile, staminal sheath 2 - 4 mm long; anthers glabrous, at least those of the shorter stamens with hyaline scales at the base; ovary more than half the horizontal length of the pistil, style short, thick, widened and laterally compressed at the base; stigma oblique, discoid; pods patent to erect, held at right angles to the pedicel, (5) 10 - 30 seeded, laterally compressed, linear, straight or curved; endocarp without tannin deposits; seeds quadrate.

- 5) *Indigastrum* Jaub.& Spach, Illustr. 5: 101 t 492 (1857). Type species *Indigastrum deflexum* (Hochst. ex A.Rich.) Jaub.& Spach (= *Indigastrum parviflorum* (Heyne ex Wight & Arn.) Schrire).

Indigofera subgenus *Euindigofera* Benth. in Benth.& Hook.f., Gen.Pl. 1: 494 (1865).

Indigofera "group" *Parviflorae* Rydberg, in N.Amer.Fl. 24: 140 (1923).

Indigofera "group" *Indigastrum* (Jaub.& Spach) Bak.f., Leg.Tr.Afr. 1: 161 (1926); Cronquist in Fl.Congo Belge 5: 124 (1954) p.p.

Indigofera subgenus *Indigastrum* (Jaub.& Spach) Gillett, Kew Bull., Add. ser. 1: 123 (1958); Gillett in Fl.Tr. E.Afr., Legum.-Papil. 3: 320 (1971).

Indigofera p.p., Hutch., Gen.Fl.Pl. :400 (1964); Polhill in Polhill & Raven, Adv.Leg. Syst. :291 (1981); de Kort & Thijssen in Blumea 30: 104 (1984); Thulin in Hedberg & Edwards, Fl.Ethiopia 3: 119 (1989); Lock, Legum.Afr. 289 (1989).

Annual or perennial herbs; biramous hairs with arms always q equal in length, hyaline only; pearl bodies restricted to the leaf bases and between the leaflets; leaves 1 - 17 foliolate, leaflets opposite or alternate, entire, stipules adnate to the base of the petiole, subulate or falcate-lanceolate; stipels absent; racemes axillary, many flowered, dense initially but sometimes elongating and becoming lax later; bracts caducous; pedicels 1 - 2 mm long; calyx more than half the length of the staminal sheath, lobes q equal or longer than the tube; flowers pink, petals glabrous; standard narrow at the base, tapering to the claw; keel with lateral pouches (spurs absent), apex prolonged rostrate; all stamens fertile, staminal sheath 2 - 4 mm long (to 7 mm in *I. burkeanum*); anthers glabrous, hyaline scales at the base reduced or absent (except *I. fastigiatum*); stigma oblique or capitate; pods reflexed, 4 - 20 seeded, terete or laterally compressed, linear, straight or curved; endocarp without tannin deposits; seeds quadrate.

5a) subgenus *Argyraeae* Schrire subgen. nov.

Subgenus *Argyraeae* Schrire subgenus novum a ceteris subgeneribus generis *Indigastrum* foliis 1 - 6 foliolatis vel simplicibus, foliolis plerumque alternis terminali quam lateralibus maiore, racemis in axilibus foliorum sessilibus subsessilibusve densifloris, ovario quam pistillo duplo saltem brevioris, leguminibus 4 - 8 - semina differt. Type species *Indigastrum argyraeum* (Eckl. & Zeyh.) Schrire.

Leaves 1 - 6 foliolate or simple; leaflets mostly alternate, obovate to cuneate, less than 3 times longer than wide; the terminal leaflet larger than the laterals; racemes sessile to subsessile, densely flowered in the axils of the leaves; ovary \approx half or less the horizontal length of the pistil; pods 4 - 8 seeded, less than 20 mm long, seeds sometimes tuberculate.

5b) subgenus *Indigastrum*

Leaflets opposite, more than 3 times longer than wide; racemes pedunculate, elongating and becoming lax later (except *I. deflexum*); ovary more than half the horizontal length of the pistil; pods 10 - 20 seeded, more than 20 mm long.

- 6) *Cyamopsis* DC., Prodr. 2: 215 (1825); Mem. Legum. 230 (1826); Endl., Gen.Pl. 1291 (1840); Benth. in Benth. & Hook. f., Gen. Pl. :493 (1865); Bak. in Oliver, Fl.Tr.Afr. 2: 65 (1871); Taub. in Engl. & Prantl, Pflanzenfam. 3(3): 259 (1894); Bak. f., Leg.Tr.Afr. 1: 94 (1926); Hutch. & Dalz., Fl.W.Tr. Afr. 1: 394 (1928); Viguier, Legum. Madagasc. 302 (1944, unpubl.); Gillett, Kew Bull., Add. ser. 1: 8 (1958), & in Keay (ed.2) Fl.W.Tr.Afr. 1(2): 543 (1958); Torre, in Conspect. Fl. Angol. 3: 84 (1962) Hutch., Gen.Pl.Pl. :400-401 (1964); Gillett in Fl.Tr.E.Afr., Legum.-Papil. 3: 328 (1971); Dyer, Gen.S.A.Fl.Pl. :256 (1975); Polhill in Polhill & Raven, Adv.Leg.Syst. :291 (1981); Lock, Legum.Afr. 289 (1989).
Cordaea Spreng. (ed.), Gen.Pl. 2: 581 (1831). Type species *Cyamopsis tetragonoloba* (L.) Taub.

Annual herbs; biramous hairs with arms always \approx equal in length; pearl bodies yellowish, restricted to the leaf bases and between the leaflets; leaves imparipinnate, (1) 3 - 7 foliolate, leaflets opposite, entire or dentate; stipules adnate to the base of the petiole, subulate; stipels absent; racemes axillary, 5 - 25 flowered, pedicels 1 - 2 mm long; calyx lobes \approx equal to the tube; flowers pink, petals markedly veined; standard glabrous, slightly thickened in the basal region near the claw; keel with lateral pouches, developed into

spurs in *C. serrata*, keel petals glabrous except for isolated hairs on the upper margin, and also sometimes distally along the commissure; stamens pseudo-monadelphous with the vexillary stamen lightly attached to the others, the filaments more or less the same length distally, not alternating long and short, staminal sheath 4 - 8 mm long; anthers glabrous, sometimes with reduced basal scales, apiculate connective present; ovary more than half the horizontal length of the pistil, stigma oblique (in *I. serrata*) or capitate; pods erect, 5 - 9 seeded, broad, linear, flattened to subtetragonous, with 3 longitudinal ridges on each face, apex beaked; endocarp without tannin deposits; seeds quadrate, tuberculate; $2n = 14$.

- 7) *Indigofera* L., Hort.Cliff. :487 (1738), Fl.Zeyl. :124 (1747), Gen. Pl. (ed.4) :431 (1752), Gen.Pl. (ed.5) :333 (1754), & Sp.Pl. :751 (1753); Thunb., Fl.Cap. 595 (1823); Willd., Sp. Pl. 1220 (1802); DC., Prodr. :221 (1825); Eckl. & Zeyh., Enum. 232 (1836); E.Mey., Comm. 92 (1836); Endl., Gen.Pl. 1271 (1840); Harv. in Harv. & Sond., Fl.Cap. :163 (1862); Benth. in Benth. & Hook.f., Gen.Pl. 1: 494 (1865); Bak. in Oliver, Fl.Tr.Afr. :65 (1871); Taub. in Engl. & Prantl, Pflanzenfam. 3(3): 259 (1894); Bak. f., Leg.Tr.Afr. 1: 95 (1926); Hutch. & Dalz., Fl.W.Tr.Afr. 1: 388 (1928); N.E.Br. in Burtt Davy, Man.Flor.Pl. 2: 360 (1932); Viguiier, Légum. Madagasc. 303 (1944, unpubl.); Adamson & Salter, Fl.Cap.Pen. 496 (1950); Cronquist in Fl. Congo Belge 5: 117 (1954); Gillett, Kew Bull. Add. ser. 1: 8 (1958), & in Keay (ed.2) Fl.W.Tr.Afr. 1(2): 533 (1958); Torre, Conspect. Fl. Angol. 3: 84 (1962); Hutch., Gen.Pl. Pl. :400 (1964); Gillett in Fl.Tr. E.Afr., Legum.-Papil. 3: 212 (1971); Dyer, Gen.S.A. Fl.Pl. :256 (1975); Polhill in Polhill & Raven, Adv.Leg. Syst. :291 (1981); de Kort & Thijssse in Blumea 30: 104 (1984); Thulin in Hedberg & Edwards, Fl.Ethiopia 3: 119 (1989); Lock, Legum. Afr. 289 (1989). *Anil* Bauhin, Hist.Pl. :945 (1651); March., Mem. :92 (1718); Ludw., Def.Pl. :117 (1737). *Ameri* Rheede, Hort Malab. :101 (1678). *Anil* Mill., Gard.Dict. (ed. 4) :95 (1754). *Indigo* Adans., Fam.Pl. :326 (1763). *Anila* Kuntze,

Rev.Gen.Fl. :159 (1891). Type species: *I. tinctoria* L.
[Lectotypified by Britton & Brown :371 (1913).]

Sphaeridiophorum Desv., in Journ. Bot. :125 (1813). Type
species: *Sphaeridiophorum linifolium* (L.) Desv.

Oustropis G.Don, Gen. Syst. 2: 214 (1832); *Tricoilendus*
Rafin., Fl.Tell. 2: 97 (1836) nom. superfl. Type species:
Oustropis microphyllus (Hook.) G.Don

Hemispadon Endl., Flora 15,2: 385 (1832). Type species:
Hemispadon pilosus Endl.

Eilemanthus Hochst., Flora 29: 593 (1846). Type species:
Eilemanthus strobilifera Hochst.

Acanthonotus Benth., in Benth.& Hook., Fl.Nigrit. :293
(1849). Type species: *Acanthonotus echinatus* (Willd.) Benth.

Ameocarpus Benth. ex Harv. (as subgenus), in Harv.& Sond.,
Fl.Cap. 2: 201 (1862), based on *Ameocarpus* Benth. in Lindl.,
Veg.Kingd. :554 (1846) nom.nud. Lectotype species:
Indigofera sessilifolia DC. [Lectotypified in Gillett, Kew
Bull., Add. ser. 1: 9 (1958).

Bremontiera DC., in Ann.Sci.Nat. sér. 1 4:93 (1825). Type
species: *Bremontiera amoxylum* DC.

Shrubs, dwarf shrubs, perennial or annual herbs; biramous hairs
with arms either somewhat equal or markedly unequal in length
(sometimes mixed together); uniramous gland-tipped trichomes
occasionally present; leaves pinnately many foliolate,
digitate, 3 - 1 foliolate, simple or reduced to scales;
leaflets opposite or less often alternate, entire; stipules
mostly subulate, occasionally broadly ovate, rarely vestigial;
stipels often present; inflorescences axillary racemes, or less
often open or subcapitate panicles, or flowers in axillary
clusters; standard hairy on the dorsal surface (except in

Juncifoliae, *Cuneifoliae*, *Stipulaceae*, and *I. scarriesii* in *Dissitiflorae*), mostly broad at the base, narrowing abruptly to a short claw; keel with lateral spurs, upper margin with a prominent fringe of hairs proximally (visible above the wings); staminal sheath straight, the filaments free distally for less than 1 mm; anthers often decorated with hairs; stigma terminal, capitate; pods variable in shape, either much longer than wide, many-seeded, strigose or glabrous; or relatively short, few-seeded, hirsute or sericeous; endocarp often spotted with tannin deposits.

7.2.2. Key to sections of *Indigofera*

Pods glabrous (see note a for exceptions); stipels absent (if rarely present then single between leaflets, or paired in *I. cytisoides*); flowers predominantly pink to magenta; seeds mostly *q* spherical. Endemic Cape sections (restricted to Cape and Natal Drakensberg, see note b):

..... Group 1.

Pods hairy (see note c for exceptions); stipels often present, paired; flowers mostly carmine, occasionally pink; seeds sub-cylindrical to quadrate or oblong-elliptic. Tropical African sections (widespread in Africa and summer rainfall area of South Africa):

..... Group 2.

Notes: a) Sections *Stipulatae*, *Trifoliolatae*, *Distichae*, *Hispidae* and *I. cytisoides* have hairy pods. *Stipulatae* and *Trifoliolatae* are distinguished by having peduncles much longer than twice the length of the leaves, and leaves digitately 3 (5 - 9) foliolate; *Hispidae* has sessile leaves with sclerophyllous leaflets; and *I. cytisoides* has caducous, broadly ovate, bracts. These characters do not occur in the tropical sections. *Distichae* are keyed out under both groups.

b) One widespread species in the Cape section *Stipulatae*, i.e. *I. dimidiata*, is found from the E. Cape to Transvaal and Malawi.

c) Section *Psiloceratiae* and a few species in *Laxeracemosae* and *Dissitiflorae* have glabrous pods. These sections have pinnate, many-foliolate, leaves; *Psiloceratiae* and *Dissitiflorae* are distinguished by paired stipels, and *Laxeracemosae* has relatively short pods with broad pale sutures and small flowers with staminal sheaths 3 - 4 mm long.

7.2.2.1. Key to Group 1 sections of *Indigofera*

1. Abaxial commissure present between base of petiole and the stipules; peduncles less than twice the length of the leaves; calyx lobes shorter than the tube:
 2. Branches spiny-tipped; leaves present at all stages; leaflets glaucous, slightly fleshy, stipels absent; calyx hairy:

..... 1. *Denudatae*
 2. Branches never spiny-tipped; leaves mostly present at the juvenile stage only, leaflets becoming reduced to scales later; single stipel present between leaflets; calyx glabrous:

..... 6. *Juncifoliae*
1. Abaxial commissure absent, stipules adnate to base of the petiole; peduncles mostly longer than twice the length of the leaves (except *Distichae*, *Hispidae*, *Cunifoliae* and some *Trifoliolatae*); calyx lobes more or less equalling to longer than the tube:
 3. Leaves all digitately or pinnately 3-foliolate, rarely 1-foliolate or digitately 5-9 foliolate (then leaflet margins never involute):

4. Stipules broadly ovate, often partially fused at the base leaving collar-like scars around stems; standard dorsal surface glabrous:
5. Peduncle less than twice the length of the leaves; calyx glabrous; pod glabrous, *q* patent:
 2. *Cunifoliae*
5. Peduncle more than twice the length of the leaves; calyx hairy; pods often hairy, reflexed:
 3. *Stipulatae*
4. Stipules subulate to lanceolate, not leaving collar-like scars around stems; standard dorsal surface mostly hairy, pods hairy, reflexed:
6. Peduncles less than twice the length of the leaves; leaves digitately or pinnately 1-3 (9) foliolate; calyx lobes mostly longer than twice the length of the tube; pods somewhat compressed laterally:
 5. *Distichae*
6. Peduncles more than twice the length of the leaves (for exceptions see note a); calyx lobes equalling to about twice the length of the tube; pods terete:
 4. *Trifoliolatae*
3. Leaves pinnately many to few or 1-foliolate, or digitate (with leaflet margins involute), leaflets rarely 3 in *Distichae* and *Coriaceae*:
7. Pods somewhat compressed laterally, reflexed, hairy; peduncle mostly less than twice the length of the leaves (except *I. disticha* and *I. glaucescens*); flowers carmine:
 5. *Distichae*
7. Pods terete, tetragonous or subtorulose; glabrous (except *Hispidae* and *I. cytisoides*), never reflexed; peduncle mostly

more than twice the length of the leaves (except *Juncifoliae*, *Hispidae* and *I. cytisoides*); flowers pink to magenta:

8. Leaflets subglabrous above (often paler above than below in dried specimens), margins tending to involute, never revolute:
9. Leaves petiolate (petiole longer than 3 mm), pinnate, leaflets not ericoid:
10. Leaves mostly present at the juvenile stage only, leaflets becoming reduced to scales later; single stipel present between leaflets; peduncles less than twice the length of the leaves; calyx glabrous:
..... 6. *Juncifoliae*
10. Leaves present at all stages, leaflets never reduced to scales, stipels absent; peduncles more or less twice the length of the leaves or longer; calyx hairy:
..... 7. *Humifusae*
9. Leaves sessile (petiole 3 mm long or less), pinnate or digitate, leaflets ericoid, margins strongly revolute:
11. Leaves digitate, calyx lobes subulate, keel not bearded
..... 8. *Filicaules*
11. Leaves pinnate, calyx lobes broadly lanceolate to ovate, somewhat keeled and slightly imbricate at the base; keel densely bearded for distal third of its length; pods never stipitate:
..... 9. *Concavae*
8. Leaflets hairy on both surfaces (often more so below), lower surface often paler than above in dried specimens), margins revolute; leaves sessile:

12. Leaflets coriaceous, not grooved below between the margins and midrib; petals never persistent:
13. Leaflets 25 - 50 mm long, obovate-oblong; peduncles shorter than leaves; bracts broadly ovate; pods erect, thinly canescent:
 *I. cytisoides*
13. Leaflets less than 25 mm long, often broadly obovate; peduncles longer than twice the length of the leaves; bracts subulate; pods *q* patent, glabrous:
 10. *Coriaceae*
12. Leaflets sclerophyllous, linear, oblong, elliptic to narrowly obovate, grooved below between the margins and a prominent midrib; petals sometimes persistent (always so in *Hispidae*):
14. Mostly dwarf shrubs or herbs; peduncles slender, more than twice the length of the leaves; stems without stalked biramous hairs; pods predominantly glabrous, drying black:
 11. *Angustifoliolae*
14. Mostly shrubs; peduncles robust, shorter than to equalling the leaves; stems with stalked biramous hairs; pods always hairy, not drying black:
 12. *Hispidae*

Note: a) The following species in *Trifoliolatae* have peduncles less than twice the length of the leaves: *I. obcordata* and *I. nudicaulis* (distinguished by 1 - foliolate leaves); *I. pungens* (spiny inflorescence rhachides), *I. hantamensis* (caespitose), and *I. merxmulleri* (very small 11 - 15 foliolate leaves with minute, thickened, rolled, leaflets).

1) Section *Denudatae* Schrire sect nov.

Sectio *Denudatae* ab omnibus ceteris sectionibus ramis ad apicem spiniformibus et foliolis glaucis carnosulis distinguenda. Arbores parvae vel frutices; folia pinnata; pedunculi quam folia minus quam duplo longiores; calycis lobae quam tubus breviores; alae distaliter barbatae; legumina glabra & patentia. Type species *I. denudata* L.f.

"Group" *Trifoliolatae* E.Mey. (as "*Trifoliatae*"), Comm. 93 (1836) p.p.; emend. Harv. in Harv. & Sond., Fl. Cap. 2: 164 (1862) p.p.

Series *Trifoliolatae* (E. Mey) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 261 (1894) p.p.

Small trees or shrubs; branches spine-tipped; biramous hairs with arms always & equal in length, hairs hyaline only; pearl bodies restricted to leaf bases and between the leaflets; leaves pinnately many to few-foliate, the rachis sometimes extended beyond the distal pair of leaflets; abaxial commissure present at the base of the petiole between the pulvinus and the stipules; leaflets often fleshy, glaucous; stipels absent; racemes many-flowered, peduncles not more than twice as long as the leaves; calyx much shorter than the staminal sheath, lobes shorter than the tube; corolla pink or magenta; standard dorsal surface pubescent with hyaline hairs, often persistent after other petals caducous, central blotch pale; wings bearded distally, proximal crest glabrous; keel often hyaline bearded distally; staminal sheath 6 - 14 mm long; anthers with hairs; pods & patent, many seeded, glabrous; endocarp with tannin deposits; seeds & spherical.

2) Section *Cuneifoliae* Schrire sect nov.

Sectio *Cuneifoliae* a sectione *Trifoliolatae* stipulis latis, pedunculis brevioribus, vexillo in pagina dorsali glabra, calyce glabro et leguminibus glabris patentibus distinguenda.

Frutices, suffrutices vel herbae; folia digitatim trifoliolata; stipulae late ovatae saepe ad basin connatae, cicatrices stipularum delapsarum itaque collumiformis; pedunculi quam folia minus quam duplo longiores. Type species *I. cuneifolia* Eckl. & Zeyh.

"Group" *Trifoliolatae* E.Mey. (as "*Trifoliatae*"), Comm. 93 (1836) p.p.; emend. Harv. in Harv. & Sond., Fl. Cap. 2: 164 (1862) p.p.

Series *Trifoliolatae* (E. Mey) Taub., in Engl. & Prantl, Pflanzfam. 3(3): 261 (1894) p.p.

Shrubs, dwarf shrubs or herbs; biramous hairs with arms always *q* equal in length, hairs hyaline only; pearl bodies restricted to leaf bases and between the leaflets; leaves digitately 3-foliolate; stipules broadly ovate, partially adnate to the base of the petiole, often fused at the base leaving collar-like scars on stems; leaflets glaucous; stipels absent; racemes many-flowered, peduncles not more than twice as long as the leaves; calyx glabrous, lobes more or less equal to the tube; corolla pink or magenta; standard dorsal surface glabrous, central blotch pale; wing proximal crest glabrous; keel not bearded; staminal sheath 5 - 8 mm long; anthers with hairs; pods *q* patent, many seeded, glabrous; endocarp with tannin deposits; seeds *q* spherical.

3) Section *Stipulatae* Schrire sect. nov.

Sectio *Stipulatae* a sectione *Trifoliolatae* stipulis late ovatis et vexillo in pagina dorsali glabra distinguenda. Suffrutices vel herbae; folia digitatim trifoliolatae; pedunculi quam folia plus quam duplo longiores; calyx pubescens; legumina glabra vel pubescentia, reflexa. Type species *I. dimidiata* Vogel ex Walp.

"Group" *Trifoliolatae* E.Mey. (as "*Trifoliatae*"), *Comm.* 93 (1836) p.p.; emend. Harv. in *Harv. & Sond.*, *Fl. Cap.* 2: 164 (1862) p.p.

"Group" *Trifoliolatae* (E.Mey.) Bak.f., *Leg. Tr. Afr.* 1: 108 (1926) p.p.

Dwarf shrubs or perennial herbs; biramous hairs with arms sometimes very unequal in length, hairs hyaline only; pearl bodies restricted to leaf bases and between the leaflets; leaves digitately 3-foliolate; stipules broadly ovate, partially adnate to the base of the petiole, sometimes fused at the base leaving collar-like scars on stems; stipels absent; racemes many-flowered on long peduncles (more than twice the length of the leaves); calyx hairy, lobes more or less equal to the tube; corolla pink, coral or magenta; standard dorsal surface glabrous, central blotch pale; wing proximal crest glabrous; keel not bearded; staminal sheath 5 - 8 mm long; anthers with hairs; pods reflexed, many seeded, glabrous or strigose; endocarp with tannin deposits; seeds *q* spherical.

4) Section *Trifoliolatae* (E.Mey.) Schrire *stat. nov.* Lectotype species *I. incana* Thunb.

"Group" *Trifoliolatae* E.Mey. (as "*Trifoliatae*"), *Comm.* 93 (1836) p.p.; Harv. in *Harv. & Sond.*, *Fl. Cap.* 2: 164 (1862) p.p. non Fang & Zheng, in *Acta Phyt. Sinica* 27: 168 (1989).

"Group" *Simplicifoliae* sensu Harv. in *Harv. & Sond.*, *Fl. Cap.* 2: 164 (1862) p.p. non DC.

"Group" *Digitatae* DC., *Prodr.* 2: 231 (1825) p.p.

Series *Trifoliolatae* (E. Mey) Taub., in *Engl. & Prantl*, *Pflanzenfam.* 3(3): 261 (1894) p.p.

Clambering dwarf shrubs or perennial herbs; biramous hairs with arms always *q* equal in length, hairs hyaline only; pearl bodies

restricted to leaf bases and between the leaflets; leaves pinnately or digitately 7-3-1-foliolate; stipules narrow, stipels absent; racemes many-flowered on long peduncles (more than twice the length of the leaves); calyx hairy, lobes more or less equal to the tube; corolla pink, terra cotta or magenta; standard dorsal surface hairy (rarely glabrous), central blotch dark; wing proximal crest glabrous; keel not (or hardly) bearded, fringe of hairs on upper margin usually more dense distally, apex often rostrate; staminal sheath 5 - 9 mm long; anthers with hairs; pods reflexed, many seeded, mostly strigose; endocarp with tannin deposits; seeds q spherical.

5) Section **Distichae** Schrire sect. nov.

Sectio *Distichae* a sectione *Trifoliolatae* foliis pinnatis 1-5-7-foliolatis, pedunculis brevioribus et leguminibus lateraliter compressis distinguenda. Suffrutices vel herbae; pedunculi quam folia minus quam duplo longiores; calycis lobae quam tubus plus quam duplo longiores; pagina dorsalis vexilli pubescens; legumina plerumque reflexa et aliquantum lateraliter compressa. Type species *I. disticha* Eckl. & Zeyh.

"Group" *Productae* Harv. in Harv. & Sond., Fl. Cap. 2: 166-167 (1862) p.p.

Dwarf shrubs or perennial herbs; biramous hairs with arms always q equal in length, hairs hyaline only; pearl bodies restricted to leaf bases and between the leaflets; leaves pinnately (1) 3 - 9 foliolate, rhachis sometimes not extended beyond the distal leaflet pair; stipules narrow, stipels absent; racemes many-flowered, peduncles not usually more than twice the length of the leaves; calyx hairy, lobes to more than twice as long as the tube; corolla carmine; standard dorsal surface hairy, central blotch dark; wing proximal crest glabrous; keel narrowly hyaline bearded distally; staminal sheath 5 - 8 mm long; anthers with or without hairs; ovary sometimes shorter than half the horizontal length of the pistil; pods reflexed, rarely q patent, laterally compressed

(except sometimes in *I. glaucescens*), many seeded, strigose; endocarp mostly without tannin deposits; seeds subcylindrical to quadrate.

- 6) Section **Juncifoliae** (Harv.) Schrire *stat. nov.* Lectotype species *I. filifolia* Thunb. [in Gillett, 1958]

"Group" *Simplicifoliae* DC., Prodr. 2: 222 (1825) p.p.

"Group" *Juncifoliae* Harv. in Harv. & Sond., Fl. Cap. 2: 163 (1862) p.p.

Series *Juncifoliae* (Harv.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 261 (1894).

Subsection *Juncifoliae* (Harv.) Gillett, Kew Bull., Add. ser. 1: 33 (1958) p.p.

Shrubs, dwarf shrubs or herbs; biramous hairs with arms always *q* equal in length, hairs hyaline only; pearl bodies restricted to leaf bases and between the leaflets; leaves petiolate, pinnately many to few foliolate, found at juvenile stage only, leaflets reduced to scales later; abaxial commissure present at the base of the petiole between the pulvinus and the stipules; leaflets subglabrous above, slightly fleshy, glaucous, margins tending to involute; stipules narrow (rarely broadly ovate), stipels present, single, midway between leaflets; racemes many-flowered, peduncles not more than twice as long as the leaves; calyx glabrous, lobes shorter than to equalling the tube; corolla pink or magenta; standard dorsal surface glabrous, central blotch pale; wing proximal crest glabrous; keel not (or hardly) bearded; staminal sheath 5 - 8 mm long; anthers with hairs; pods *q* patent, occasionally stipitate, many seeded, glabrous, drying black; endocarp with tannin deposits; seeds *q* spherical, black, sometimes with a persistent papery funicle.

7) Section **Humifusae** Schrire sect. nov.

Sectio *Humifusae* a sectio *Juncifoliae* foliis semper praesentibus, pedunculis longioribus et calyce pubescenti distinguenda. Frutices, suffrutices vel herbae; folia petiolata, pinnata vel raro unifoliolata; foliola in pagina superiore subglabra, glauca, marginibus plerumque involutis; pedunculi quam folia plus quam duplo longiores; calyx pubescens in sicco saepe atro; legumina glabra in sicco saepe atra. Type species *I. humifusa* Eckl. & Zeyh.

"Group" *Productae* Harv. in Harv. & Sond., Fl. Cap. 2: 166-167 (1862) p.p.

Shrubs, dwarf shrubs or herbs; biramous hairs with arms always q equal in length, hairs hyaline only; pearl bodies restricted to leaf bases and between the leaflets; stems often brittle, subsucculent; leaves petiolate, pinnately many, few to 1-foliolate; leaflets subglabrous above, slightly fleshy or coriaceous, glaucous, margins tending to involute; stipules subulate to lanceolate, often spreading; stipels absent; racemes many-flowered on long peduncles (more than twice as long as the leaves); calyx hairy, often drying black, lobes about equal to twice as long as the tube; corolla pink, terra cotta or magenta; standard dorsal surface hairy, central blotch pale; wings sometimes bearded distally, proximal crest glabrous; keel not (or hardly) bearded; staminal sheath 4 - 8 mm long; anthers with hairs; pods q patent or reflexed, many seeded, glabrous, drying black; endocarp with tannin deposits; seeds q spherical, cylindrical or quadrate, black.

8) Section **Filicaules** Schrire sect. nov.

Sectio *Filicaules* a sectione *Juncifoliae* foliis subsessilibus digitatis foliisque ericoideis margine valde involuta distiguenda. Suffrutices vel herbae; folia subsessilia digitatim 5-9-foliolata; foliola in pagina superiore subglabra, glauca; pedunculi plerumque quam folia plus quam

duplo longiora; legumina stipitata, glabra, in sicco saepe atra. Type species *I. filicaulis* Eckl. & Zeyh.

"Group" *Digitatae* sensu Harv. in Harv. & Sond., Fl. Cap. 2: 165 (1862) p.p., non DC.

Dwarf shrubs or herbs; biramous hairs with arms always \approx equal in length, hairs hyaline only; pearl bodies restricted to leaf bases and between the leaflets; leaves, subsessile, digitately 9-5-foliolate; leaflets, ericoid, subglabrous above, glaucous, margins strongly involute; stipules subulate to vestigial; stipels absent; racemes few-flowered, often on setaceous peduncles usually more than twice as long as the leaves; bracts minute, often persistent; calyx hairy, often drying black, lobes about twice as long as the tube; corolla pink or magenta; standard dorsal surface hairy, lamina becoming narrow and tapering towards the base; wing proximal crest glabrous, lamina not bearded distally; keel not (or hardly) bearded; staminal sheath 4 - 7 mm long; anthers with hairs; pods \approx patent, stipitate, often compressed with prominent sutures, few-seeded, glabrous, drying black; endocarp with tannin deposits; seeds \approx spherical, cylindrical or quadrate.

9) Section *Concavae* Schrire sect. nov.

Sectio *Concavae* ab omnibus ceteris sectionibus lobis calycis late lanceolatis carinatisque distinguenda. Suffrutices vel herbae; folia subsessilia pinnatim vel subdigitatim paucifoliolata; foliola ericoidea, in pagina superiore subglabra, glauca, margine valde involuta; pedunculi graciles, quam folia plus quam duplo longiores; lobae calycis late lanceolatae vel ovatae, saepe carinatae et ad basin leviter imbricatae; alae distaliter barbatae; legumina, glabra, in sicco atra. Type species *I. concava* Harv.

"Group" *Pinnatae* (E. Mey.) Harv. in Harv. & Sond., Fl. Cap. 2: 165 (1862) p.p.

Dwarf shrubs or herbs; biramous hairs with arms always *q* equal in length, hairs hyaline only; pearl bodies restricted to leaf bases and between the leaflets; stems often brittle, subsucculent; leaves subsessile, pinnately or subdigitately few-foliolate; leaflets ericoid, subglabrous above, glaucous, margins strongly involute; stipules subulate, minute; stipels absent; racemes many to few-flowered on slender peduncles (more than twice as long as the leaves); bracts persistent, fruiting pedicels to 3 mm long; calyx hairy, often drying black, lobes broadly lanceolate to ovate, often keeled and slightly imbricate at the base, about equal to twice as long as the tube; corolla pink or magenta; standard dorsal surface hairy, lamina narrow and tapering towards the base, central blotch pale; wings bearded distally, proximal crest glabrous; keel broadly hyaline bearded distally; staminal sheath 5 - 8 mm long; anthers with hairs; pods *q* patent, many seeded, glabrous, drying black; endocarp with tannin deposits.

10) Section *Coriaceae* Schrire sect. nov.

Sectio *Coriaceae* sectioni *Angustifoliolae* affinis sed foliis non typicis sclerophyllis differt. Suffrutices vel herbae; folia subsessilia, pinnatim paucifoliolata rhachide non ultra par distale foliolorum extensa; foliola coriacea pagina superiore sub indumento nitida et quam pagina inferiore magis atra, margine revoluta; pedunculi graciles quam folia plus quam duplo longiores; alae distaliter barbatae; legumina glabra, in sicco atra. Type species *I. alopecuroides* (Burm.f.) DC.

"Group" *Digitatae* DC., Prodr. 2: 231 (1825) p.p.

"Group" *Pinnatae* (E. Mey.) Harv. in Harv. & Sond., Fl. Cap. 2: 165 (1862) p.p.

Dwarf shrubs or herbs; biramous hairs with arms always *q* equal in length, hairs hyaline only; pearl bodies restricted to leaf bases and between the leaflets; leaves subsessile, pinnately

few-foliolate, the rhachis not extended beyond the distal leaflet pair; leaflets coriaceous, often broadly obovate, hairy above and below (upper surface glossy beneath the vestiture, and darker than the lower surface), margins revolute; stipules subulate; stipels absent; racemes many flowered, often on slender peduncles more than twice as long as the leaves; bracts caducous; calyx hairy, lobes about twice as long (or longer) than the tube; corolla pink or magenta; standard dorsal surface hairy, lamina narrow and tapering towards the base, central blotch pale; wings bearded distally, proximal crest glabrous; keel rostrate, broadly spreading hyaline bearded distally; staminal sheath 3 - 6 mm long; anthers with hairs; pods q patent, many seeded, glabrous, drying black; endocarp with tannin deposits, seeds q spherical.

11) Section **Angustifoliolae** Schrire sect. nov.

Sectio *Angustifoliolae* sectio *Hispidae* affinis sed foliolis angustioribus, pedunculis longis et leguminibus glabris differt. Suffrutices vel herbae; folia subsessilia, pinnatim pauci- vel unifoliolata, rhachide non ultra par distale foliolorum extensa; foliola sclerophylla, pagina superiore sub indumento nitida, pagina inferiore inter margines revolutas et costam prominentem sulcata; pedunculi graciles quam folia plus quam duplo longiores; alae distaliter barbatae; legumina glabra raro pubescentia, in sicco atra. Type species *I. angustifolia* L.

"Group" *Pinnatae* Harv. in Harv. & Sond., Fl. Cap. 2: 165 (1862) p.p.

Dwarf shrubs or herbs; biramous hairs with arms always q equal in length, hairs hyaline only; pearl bodies restricted to leaf bases and between the leaflets; leaves subsessile, pinnately few to 1-foliolate, the rhachis not extended beyond the distal leaflet pair; leaflets sclerophyllous, mostly linear to oblong, upper surface glossy beneath the vestiture, lower surface densely hairy, grooved between the revolute margins and

prominent midrib; stipules subulate; stipels absent; racemes mostly few-flowered, often on slender peduncles more than twice as long as the leaves; bracts occasionally persistent; calyx hairy, lobes about equal to twice as long as the tube; corolla pink or magenta, petals sometimes persistent (remaining attached to the base of the developing pod); standard dorsal surface hairy, lamina narrow and tapering towards the base, central blotch pale; wings bearded distally, proximal crest glabrous; keel apex acute to rostrate, narrowly hyaline bearded distally; staminal sheath 3 - 6 mm long; anthers with hairs; pods \varnothing patent, many seeded, glabrous or rarely strigose, drying black; endocarp with tannin deposits, seeds \varnothing spherical.

12) Section **Hispidae** Schrire sect. nov.

Sectio *Hispidae* a sectione *Angustifoliolatae* caulibus pilos biramos stipitatos ferentibus, pedunculis brevibus et leguminibus pubescentibus distinguenda. Frutices vel suffrutices; caules saepe pilos biramos stipitatos ferentes; folia sessilia, pinnatim paucifoliolata, rhachide non ultra par distale foliolorum extensa; foliola sclerophylla, pagina superiore sub indumento nitida, pagina inferiore inter margines revolutas et costam prominentem sulcata; pedunculi robusti quam folia breviores vel ea aequantes; petala persistentia ad basin leguminis evolutantis adhaerantia; alae distaliter barbatae; legumina pubescentia, in sicco non atra. Type species *I. hispida* Eckl. & Zeyh.

"Group" *Pinnatae* (E. Mey.) Harv. in Harv. & Sond., Fl. Cap. 2: 165 (1862) p.p.

Shrubs or dwarf shrubs (rarely herbs); biramous hairs with arms always \varnothing equal in length, hairs hyaline only; pearl bodies restricted to leaf bases and between the leaflets; stems often with stalked biramous hairs; leaves sessile, pinnately few foliolate, the rhachis not extended beyond the distal leaflet pair; leaflets sclerophyllous, mostly linear to oblong, upper surface glossy beneath the vestiture, lower surface densely

hairy, grooved between the revolute margins and prominent midrib; stipules subulate; stipels absent; racemes mostly few-flowered, on short peduncles more or less equalling the leaves; bracts occasionally persistent; calyx hairy, lobes about equal to twice as long as the tube; corolla pink or magenta, petals persistent (remaining attached to the base of the developing pod); standard dorsal surface hairy, lamina narrow and tapering towards the base, central blotch pale; wings bearded distally, proximal crest glabrous; keel apex acute, broadly hyaline bearded distally; staminal sheath 4 - 7 mm long; ovary sometimes shorter than half the horizontal length of the pistil; anthers with hairs; pods *q* patent, many seeded, strigose, endocarp with tannin deposits, seeds *q* spherical.

7.2.2.2. Key to Group 2 sections of *Indigofera*

1. Woody shrubs more rarely suffrutices; abaxial commissure present at the base of the petiole between the pulvinus and stipules (rarely absent in *Subulatae*); brachyblasts present:
 2. Pods glabrous (strigulose in *I. macrantha* and *I. roseo-caerulea*), *q* patent; dorsal surface of standard dense, hyaline, shortly crisped, pubescent; calyx a quarter or less the length of the staminal sheath, lobes shorter than the tube; buds not upturned distally, corolla pink, magenta or white:

..... 13. *Psiloceratiae*
 2. Pods strigose, reflexed; buds mostly upturned distally; corolla carmine:
 3. Dorsal surface of standard densely appressed dark brown strigose; calyx less than half the length of the staminal sheath, lobes shorter than to equalling the tube:

..... 14. *Tinctoriae*

3. Dorsal surface of standard appressed hyaline strigose; calyx
 q half or more the length of the staminal sheath, lobes
 twice as long or longer than the tube:
 15. *Subulatae*
1. Suffrutices or herbs; abaxial commissure absent, the stipules
 adnate to the base of the petiole (except in some *Conjugatae*);
 brachyblasts absent (except *Spinosa*, *Brevipatentes* and
Podophyllae):
4. Dorsal surface of standard densely appressed dark brown
 strigose; pedicels more than 3 mm long; pods erect to
 spreading; seeds often with a persistent papery funicle;
 biramous hairs with arms all more or less equal in length;
 leaflets often subglabrous above and pallid in dried
 specimens:
5. Staminal sheath 7 - 14 mm long, peduncles robust:
 16. *Hedyanthae*
5. Staminal sheath 4 - 7 mm long, peduncles wiry (when staminal
 sheath 7 mm long):
6. Bracts caducous, inflorescences more than twice as long as
 the leaves, laxly many-flowered; calyx less than half the
 length of the staminal sheath; keel apex not acute (except
I. amitina):
 17. *Dendroides*
6. Bracts persistent or scars conspicuous; inflorescences
 often shorter than to twice the length of the subtending
 leaves (except *I. placida*, *I. floribunda* and *I. woodii*);
 laxly 3 - 8 (20) flowered; calyx mostly from half to
 equalling the staminal sheath (except *I. verrucosa* and *I.*
stricta); keel often acute:
 17a. *Foliosae*

4. Dorsal surface of standard with hyaline hairs only, or if dark brown (or black) then hairs spreading; pedicels less than 3 mm long (except *I. heudelottii*); seeds without a persistent funicle:
7. Leaves pinnate or simple, leaflets opposite
8. Leaves distinct from bracts, calyx lobes not lanceolate or scarious; inflorescences of axillary racemes, not paniculate, or with pedicels jointed below flowers:
9. Leaflets punctate glandular below with sessile discoid pearl bodies; leaves never simple (or unifoliolate); pods tomentose, torulose, 3 - 6 seeded; endocarp spotted with tannins but without large vesicles, seeds smooth:
 20. *Microcarpae*
9. Leaflets not punctate glandular below:
10. Biramous hairs subsimple or with arms of very unequal lengths, vestiture (including pods) hirsute, pilose or sericeous, gland-tipped trichomes absent; calyces with lobes longer than twice the length of the tube (except *Dissitiflorae* and *Laxeracemosae*):
11. Dark brown (or black) biramous hairs occurring with hyaline hairs:
12. Stipules setaceous or subulate, less than 1 mm wide at the base; endocarp with large tannin vesicles, seeds pitted; anthers with hairs; leaves never simple; pods not erect:
13. Pods reflexed; pearl bodies scattered over plant, not densely aggregated as brownish clumps at the leaf bases and between the leaflets; stipels present; staminal sheaths 3 - 5 mm long:
 18. *Hirsutae*

13. Pods patent; pearl bodies densely aggregated as brownish clumps at the leaf bases and between the leaflets; stipels absent; staminal sheaths 3 - 14 mm long:

..... 19. *Setiflorae*

12. Stipules lanceolate-attenuate, more than 1-nerved, often more than 1 mm wide at the base; endocarp without large tannin vesicles (except *I. biglandulosa* which is distinguished by two stalked glands at the base of the petiole); seeds smooth (except in above species); anthers glabrous; leaves often simple; pods patent or erect:

..... 29. *Pilosae*

11. Dark brown (or black) biramous hairs absent, hyaline hairs occurring only:

14. Stipules lanceolate-attenuate, more than 1-nerved, often more than 1 mm wide at the base; stipels present (except where leaves simple); anthers glabrous; leaflets often with craspedodromous venation; pods patent or erect:

..... 29. *Pilosae*

14. Stipules triangular, subulate or falcate, less than 1 mm wide at the base:

15. Ovary longer than half the horizontal length of the pistil; calyx \leq half or less the length of the staminal sheath, lobes \leq equalling to twice the length of the tube; anthers glabrous:

16. Inflorescences laxly 1 - 5 (rarely more) flowered, on slender peduncles longer than the flowering rhachides, \leq equalling to twice the length of the subtending leaves; stipels present; pods erect,

- narrow, much longer than wide; leaf margins often viscid; staminal sheath 2 - 6 mm long:
 30. *Dissitiflorae*
16. Inflorescences laxly 5 - 15 flowered, rhachides longer than the peduncles, mostly longer than the subtending leaves; stipels absent; pods patent, less than times longer than wide, often torulose with broad pale sutures; leaf margins rarely viscid; staminal sheath 3 - 4 mm long:
 31. *Laxeracemosae*
15. Ovary $\frac{1}{2}$ half or less the horizontal length of the pistil; calyx longer than half the length of the staminal sheath, lobes twice the length or longer than the tube;
17. Staminal sheath 4.5 - 8 mm long, stems densely leafy, leaves shortly petiolate, 3 - 7 (9) foliolate, leaflets suberect; racemes 3 - 12 flowered partially obscured by and barely exceeding the leaves; pods patent to erect:
 25. *Hilares*
17. Staminal sheath 1.5 - 4 mm long, leaflets simple, asymmetrically 2 - foliolate, or rarely 3 - foliolate (in *Simplices-reflexae*):
18. Leaves always simple, leaflets with biramous hairs arranged perpendicularly along the often cartilagenous margins; pods subtriquetrous, falcate, reflexed, indehiscent, 1 - 2 seeded, sometimes with spines along the dorsal suture; anthers hairy:
 35. *Acanthonotus*

18. Leaves simple or rarely 2 - 3 foliolate; leaflets not as above; pods globose, oblong or straight, without spines, dehiscent, 1 - 10 seeded; anthers glabrous:
19. Inflorescences subsessile, clustered in the leaf axils, very densely flowered (pedunculate in *I. flavicans* which has 2 asymmetrically placed leaflets); ovary $\frac{1}{2}$ or less the horizontal length of the pistil; pods $\frac{1}{2}$ patent:
 38. *Sphaeridiophora*
19. Inflorescences elongated, laxly many-flowered, much longer than the leaves; ovary more than half the horizontal length of the pistil; pods reflexed ($\frac{1}{2}$ patent in *I. pseudosubulata* which also has 3 - foliolate leaves):
 39. *Simplices-reflexa*
10. Biramous hairs with arms all $\frac{1}{2}$ equal in length, vestiture (including pods) strigose, gland-tipped trichomes sometimes present; calyces with lobes $\frac{1}{2}$ equalling to longer than the tube:
20. Inflorescence rhachides spiny-tipped (occurring also in one or two species in *Subulatae*, *Amecarpus* and *Trifoliolatae*); gland-tipped trichomes sometimes present; pods erect to spreading (reflexed in above sections):
 26. *Spinosae*
20. Inflorescence rhachides not spiny-tipped:
21. Leaves comprising persistent filiform petioles, each with one distant terminal leaflet; branches subglabrous, virgate; stipels present; staminal sheath 3 - 4 mm long:
 28. *Podophyllae*

21. Leaves pinnate or simple, never with one distant terminal leaflet on persistent filiform petioles:
22. Stems, leaf rhachides and often the pods covered with gland-tipped trichomes (sometimes sparse in *Viscosae*):
23. Racemes 3 - 12 flowered, partially obscured by and barely exceeding the leaves; stems densely leafy; leaves shortly petiolate, (1) 3 - 7 (9) foliolate, leaflets often 3 or more times longer than wide, suberect:
 25. *Hilares*
23. Racemes densely or laxly many flowered, ascending away from the leaves; leaves simple or (5) 7 - 17 foliolate, leaflets less than 3 times longer than wide (unless simple); *q* patent:
24. Biramous hairs mixed black and hyaline; inflorescences compact, densely many-flowered:
 23. *Atratae*
24. Biramous hairs hyaline only; inflorescences elongated, laxly many flowered:
 24. *Viscosae*
22. Stems and leaves without gland-tipped trichomes.
25. Calyx more than half the length of the staminal sheath, lobes about twice as long or longer than the tube:
26. Pods laterally compressed (not tetragonous) or flat, reflexed:

27. Pods without eminences or midridge above seeds; staminal sheath 5 - 8 mm long; anthers sometimes hairy; biramous hairs of the same size on the lower leaflet surfaces; stipels absent:
..... 5. *Distichae*
27. Pods with eminences or a prominent midridge above the seeds (except *I. damarana*); staminal sheath 3 - 5.5 mm long (longer in *I. lasiantha* and *I. fanshawei*); anthers glabrous (except *Demissae*); biramous hairs of distinctly different sizes on the lower leaflet surfaces; stipels often present:
28. Bracts caducous; anthers glabrous; pods straight, curved, torulose or circinnate; inflorescences densely many-flowered:
..... 36. *Ameocarpus*
28. Bracts persistent; anthers hairy; pods straight, oval or linear; inflorescences 4 - 10 flowered, shorter than the subtending leaves:
..... 37. *Demissae*
26. Pods terete or subtetragonous:
29. Inflorescences subsessile, clustered in the leaf axils, very densely flowered, shorter than the subtending leaves; staminal sheath 1.5 - 3 mm long; ovary of half or less the horizontal length of the pistil; pods globose to linear and patent:
..... 38. *Sphaeridiophora*
29. Inflorescences not very densely flowered or clustered in leaf axils:
30. Pods tetragonous, straight or curved, reflexed; endocarp without tannin deposits; leaves

- stipellate; staminal sheath 3 - 4 mm long:
 15. *Subulatae*
30. Pods cylindrical (if winged or angular then pods erect), *q* patent or erect (reflexed in *Simplices-reflexae*); endocarp spotted with tannin deposits; stipels absent (if rarely present then staminal sheath 4.5 - 8 mm long):
31. Staminal sheath 1.5 - 4 mm long; inflorescences elongated, laxly many-flowered, much longer than the mostly simple leaves; ovary more than half the horizontal length of the pistil; pods reflexed (*q* patent in *I. pseudosubulata* where leaves 3 - foliolate):
 39. *Simplices-reflexae*
31. Staminal sheath 4 - 8 mm long; pods erect or spreading:
32. Biramous hairs mixed dark brown and hyaline; leaflets simple or 7 - 23 foliolate, racemes elongated, many-flowered, not partially obscured by leaves; leaflets *q* patent; pods over 2 mm wide, erect; endocarp with large tannin vesicles, seeds pitted:
 21. *Stenophyllae*
32. Biramous hairs hyaline only; stems densely leafy, leaves shortly petiolate, (1) 3 - 7 (9) foliolate, leaflets suberect; racemes 3 - 12 flowered partially obscured by and barely exceeding the leaves; pods less than 2 mm wide, spreading to erect; endocarp tannin spotted but without large vesicles; seeds smooth:
 25. *Hilares*

25. Calyx half or less the length of the staminal sheath, lobes about equal to twice as long as the tube:
33. Leaves always simple; racemes subsessile, 2 - 5 flowered in the leaf axils, pods erect:
 22. *Brevierectae*
33. Leaves pinnate (rarely reduced to 1 - foliolate towards the apex):
34. Inflorescences laxly 1 - 5 flowered (sometimes more in *I. elwakensis* and *I. nairobiensis*), inflorescences equalling to twice the length of the subtending leaves, sometimes obscured by leaves; calyx lobes often swollen-tipped glandular; staminal sheath 2 - 6 mm long:
35. Peduncles slender, wiry, longer than the flowering rhachides; stipels present; pods erect, glabrous or hairy; leaf margins often viscid; leaves (1) 3 - 15 foliolate:
 30. *Dissitiflorae*
35. Peduncles shorter than the flowering rhachides, inflorescences barely exceeding and often obscured by the leaves; stipels absent; pods α patent to erect, hairy; leaf margins not viscid (except in *I. nebrowniana*); leaves shortly petiolate, (1) 3 - 5 foliolate:
 27. *Brevipatentes*
34. Inflorescences laxly many flowered; ascending away from the leaves; calyx lobes without glandular apices; staminal sheath 3 - 4 mm long:

36. Pods 6 times longer than wide or less, often torulose with broad pale sutures, glabrous or hairy; pearl bodies scattered on stems:
..... 31. *Laxeracemosae*
36. Pods longer than 6 times the width, linear, cylindrical, hairy; pearl bodies restricted to leaf bases and between the leaflets:
37. Gland-tipped trichomes absent; lower 2 pairs of leaflets crowded together at the base of the leaves; keel broadly appressed hyaline bearded distally:
..... 24a. *Centrae*
37. Gland-tipped trichomes present (sometimes very sparsely, on stems or leaf rhachides); leaflets not crowded at the base; keel narrowly bearded along the distal margin of the keel:
..... 24. *Viscosae*
8. Leaves passing gradually into foliar bracts; calyx lobes mostly lanceolate and scarious; inflorescences reduced to 1 - 3 flowers in the axils of foliar bracts or paniculate with pedicels often jointed below flowers:
38. Inflorescences of 1 - 3 flowers subtended by foliar or trifid bracts (sometimes aggregated in a strobilus); stipules broadly lanceolate to ovate; vestiture sericeous; acuminate calyx lobes often gland-tipped; endocarp with tannin stripes:
..... 32. *Latetipulatae*
38. Inflorescences paniculate, sometimes condensed and sub-capituliform; stipules narrowly lanceolate to subulate; vestiture pilose; calyx lobes not gland-tipped; endocarp tannins diffuse or absent:

39. Biramous hairs mixed dark brown (or black) and hyaline; pearl bodies not densely covering stems, leaves and calyces; calyx lobes not enlarging after flowering; pods 1 - 4 seeded, dehiscent, not becoming detached with the calyces:
40. Flowers, if single, then on short jointed pedicels; inflorescences mostly condensed and subcapituliform: 33. *Paniculatae*
40. Flowers single on slender jointed pedicels 5 mm or more long: 33a. *Trichopodae*
39. Biramous hairs hyaline only; pearl bodies densely covering stems, leaves and calyces; calyx lobes expanding after flowering; pods 1-seeded, tardily dehiscent, becoming detached with the calyces: 34. *Terminales*
7. Leaflets alternate
41. Inflorescences pedunculate, elongate, many-flowered; staminal sheath 3 - 10 mm long; ovary longer than half the horizontal length of the staminal sheath; anthers with hairs;
42. Longer leaflets over 30 mm long; lower leaves 1 - 3 foliolate, upper leaves 5 - 11 foliolate, vestigial leaves sometimes present at the base of the shoots; abaxial commissure sometimes present at the base of the petiole above the stipules: 40. *Conjugatae*
42. Longer leaflets less than 30 mm long; upper and lower leaves not distinct, vestigial leaves absent (except in *I. volkensis*); abaxial commissure absent: 41. *Alternifoliolae*

41. Inflorescences subsessile, clustered in the leaf axils, very densely flowered (pedunculate in *I. flavicans* which has 2 asymmetrically placed leaflets); staminal sheath 1.5 - 3 mm long; ovary \approx half or less the length of the staminal sheath; anthers without hairs (except *I. trigonelloides*):
 38. *Sphaeridiophora*

13) Section **Psiloceratiae** (Gillett) Schrire *stat. nov.* Type species *I. sutherlandoides* Welw. ex Bak.

"Group" *Multijuga* DC., Prodr. 2: 222 (1825) p.p.

"Group" *Tinctoriae* Wight & Arn., Prod.Fl.Pen.Ind.Or. 1: 201 (1834) p.p.

"Group" *Tinctoriae* (Wight & Arn.) Bak. in Oliver, Fl.Tr.Afr. 2: 68 (1871) p.p.; emend Bak.f., Leg.Tr.Afr. 1: 139 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Tinctoriae* (Wight & Arn.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

Subsection *Psiloceratiae* Gillett, Kew Bull., Add. ser. 1: 84 (1958) p.p.

Subsection *Tinctoriae* (Wight & Arn.) Gillett, Kew Bull., Add. ser. 1: 88 (1958) p.p.

Subsection *Decorae* Fang & Zheng, in Acta Phyt. Sinica 27: 164 (1989).

Small trees or shrubs; biramous hairs sometimes with arms very unequal in length, hairs mixed dark brown and hyaline; pearl bodies often scattered on stems; leaves pinnately (5) 7 - 27 foliolate (to 3 foliolate in *I. natalensis*), the rhachis

extended beyond the distal pair of leaflets; abaxial commissure present at the base of the petiole between the pulvinus and stipules; stipels present; racemes many-flowered; calyx about a quarter the length of the staminal sheath, lobes shorter than the tube; corolla pink, rose, magenta or white; standard dorsal surface dense, hyaline, shortly crisped pubescent to strigose, often persistent after other petals caducous, central blotch pale; wing proximal crest often hairy; keel hyaline bearded distally; staminal sheath 6 - 15 mm long (4 - 5 mm in *I. micrantha*, *I. natalensis* and *I. malongensis*); anthers with hairs; pods *q* patent, many seeded, glabrous or almost so (strigulose in *I. macrantha* and *I. roseo-caerulea*); endocarp with tannin deposits; seeds *q* spherical to cylindrical.

14) Section *Tinctoriae* (Wight & Arn.) Schrire *stat. nov.*

Lectotype species *I. tinctoria* L. [Lectotypified by Britton & Brown, 371 (1913).]

"Group" *Multijuga* DC., Prodr. 2: 222 (1825) p.p.

"Group" *Tinctoriae* Wight & Arn., Prod.Fl.Pen.Ind.Or. 1: 201 (1834) p.p.

"Group" *Tinctoriae* (Wight & Arn.) Bak. in Oliver, Fl.Tr.Afr. 2: 68 (1871) p.p.; emend Bak.f., Leg.Tr.Afr. 1: 139 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Tinctoriae* (Wight & Arn.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

Subsection *Tinctoriae* (Wight & Arn.) Gillett, Kew Bull., Add. ser. 1: 88 (1958) p.p.

Shrubs or dwarf shrubs; biramous hairs with arms mostly *q* equal in length (rarely some very unequal), hairs mixed dark brown and hyaline; pearl bodies usually restricted to leaf bases and between the leaflets; leaves pinnately (3) 5 - 11 (19)

foliolate, the rachis extended beyond the distal pair of leaflets (some taxa with fewer leaflets, 20 - 50 mm long and staminal sheath 6 - 14 mm long, others with more leaflets, less than 20 mm long and staminal sheath 3 - 5 (6) mm long); abaxial commissure present at the base of the petiole between the pulvinus and stipules; stipels present; racemes many-flowered; calyx about a quarter the length of the staminal sheath, lobes shorter than the tube; flower buds often curving upwards distally; corolla pink to carmine; standard dorsal surface strigose with densely appressed dark brown hairs, wing proximal crest glabrous; keel dark brown bearded distally; staminal sheath - 14 mm long anthers with hairs (becoming glabrous in smaller flowered species); pods reflexed, many seeded, strigose, rarely stipitate; endocarp with tannin deposits; seeds cylindrical to quadrate.

15) Section **Subulatae** Schrire sect. nov.

Sectio *Subulatae* a sectione *Tinctoriae* pagina dorsali vexilli pilis hyalinis tantum ornata, et leguminibus subtetragonis distiguenda. Frutices suffrutices vel herbae pilis biramosis hyalinis tantum ornati; commisura abaxialis ad basin petioli inter pulvinum stipulasque saepe praesens; folia pinnata rhachide ultra par distalis foliolorum extensa; stipellae plerumque praesentes; alabastra in parte distali saepe sursum curvata; pagina dorsalis vexilli strigis hyalinis tantum ornata; legumina reflexa, q subtetragona. Type species *I. trita* L.f.

"Group" *Tetragonocarpae* Wight & Arn., Prod.Fl.Pen.Ind.Or. 1: 203 (1834) p.p.

"Group" *Tinctoriae* (Wight & Arn.) Bak. in Oliver, Fl.Tr.Afr. 2: 68 (1871) p.p.; emend Bak.f., Leg.Tr.Afr. 1: 139 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Tinctoriae* (Wight & Arn.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

Shrubs, dwarf shrubs or herbs; biramous hairs with arms always q equal in length, hyaline only; pearl bodies restricted to leaf bases and between the leaflets; leaves pinnately 3 - 9 (13) foliolate, the rachis extended beyond the distal pair of leaflets; abaxial commissure often present at the base of the petiole between the pulvinus and stipules (absent in *I. trita*); stipels mostly present; racemes many-flowered; calyx more than half the length of the staminal sheath, lobes to twice as long or longer than the tube; flower buds often curving upwards distally; corolla carmine; standard dorsal surface hyaline strigose; wing proximal crest glabrous; keel beard hyaline (if present); staminal sheath 3 - 5 mm long (6 - 8 mm in *I. boranica*); anthers with hairs sometimes absent; pods reflexed, straight or curved in a semicircle (*I. cliffordiana*), often sub-tetragonous rarely flattened, many seeded, strigose; endocarp with or without tannin deposits; seeds cylindrical to quadrate.

16) Section **Hedyanthae** Schrire sect. nov.

Sectio *Hedyanthae* sectionis *Dendroides* valde affinis sed floribus maioribus distiguenda. Frutices vel suffrutices, pilis biramosis mixtis fusco-brunneis hyalinisque ornati; folia pinnata, inflorescentiae (pedunculo incluso) quam folia plerumque plus quam duplo longiores; pedicelli fructiferi plus quam 3 mm longi; corolla subrosea vel rosea; pagina dorsalis vexilli dense appresse fusco-brunneo-strigosa; crista proximalis alae pubescens; vagina staminalis 7 - 14 mm longa; legumina longa, anguste cylindracea, patentia vel erecta; funiculus seminae persistens. Type species *I. hedyantha* Eckl. & Zeyh.

"Group" *Pinnatae* (E. Mey.) Harv. in Harv. & Sond, Fl. Cap. 2: 166 (1862) p.p.; Bak.f., Leg. Tr. Afr. 1: 129 (1926) p.p.

Subsection *Dissitiflorae* (Wight & Arn.) Gillett, Kew Bull.,
Add. ser. 1:40 (1958) pro min parte.

Shrubs or dwarf shrubs from woody rootstocks; biramous hairs with arms always *q* equal in length, hairs mixed dark brown and hyaline; pearl bodies restricted to leaf bases and between the leaflets, sometimes densely aggregated as brownish clumps; leaves pinnately 5 - 15 foliolate, the rhachis not usually extended beyond the distal leaflet pair, leaflets often pallid and subglabrous above (darker below) in dried specimens; stipels absent; inflorescences including the peduncle more than twice the length of the leaves, many-flowered, fruiting pedicels longer than 3 mm; calyx about a quarter the length of the staminal sheath, lobes equalling to longer than the tube; corolla pink to reddish; standard dorsal surface strigose with densely appressed dark brown hairs, central blotch dark, often hairy; wing proximal crest mostly hairy; keel dark brown bearded distally, proximal fringe well developed, pink; staminal sheath 7 - 14 mm long, anthers with hairs; pods spreading to erect, many seeded, strigose; endocarp with tannin deposits; seeds cylindrical to quadrate, funicle persistent.

17) Section **Dendroides** Schrire sect. nov.

Sectio *Dendroides*. Suffrutices vel herbae pilis biramosis mixtis fusco-brunneis hyalinisque; folia pinnata, inflorescentia (pedunculo incluso) quam folia plus quam duplo longiores; pedicelli fructiferi plus quam 3 mm longi; corolla carmina; pagina dorsalis vexilli dense appresse fusco-brunneo-strigosa; crista proximalis alae glabra; vagina staminalis 4 - 7 mm longa; legumina longa, anguste cylindracea, patentia vel erecta. Type species *I. dendroides* Jacq.

"Group" *Multijugae* DC., Prodr. 2: 224 (1825) p.p.; emend Bak.f., Leg.Tr.Afr. 1: 127 (1926) p.p.

"Group" *Dissitiflorae* (Wight & Arn.) Bak. in Oliver, Fl.Tr.Afr. 2: 67 (1871) p.p.

Subsection *Dissitiflorae* (Wight & Arn.) Gillett, Kew Bull.,
Add. ser. 1: 40 (1958) p.p.

Dwarf shrubs or herbs (few annuals); biramous hairs with arms always *q* equal in length, hairs mixed dark brown and hyaline; pearl bodies restricted to leaf bases and between the leaflets; leaves pinnately (3) 5 - 11 (17) foliolate, the rhachis mostly extended beyond the distal leaflet pair, leaflets often pallid and subglabrous above (darker below) in dried specimens; stipels absent; inflorescences including the wiry peduncle more than twice the length of the leaves, laxly many-flowered, fruiting pedicels longer than 3 mm; calyx less than half the length of the staminal sheath, lobes equal to longer than the tube; corolla pink to reddish; standard dorsal surface strigose with densely appressed dark brown hairs, central blotch dark with hyaline patches on either side of the midline; wing proximal crest glabrous (rarely hairy); keel dark brown bearded distally, proximal fringe well developed, pink; staminal sheath 4 - 7 mm long, anthers with hairs; pods spreading to erect, many seeded, strigose; endocarp with tannin deposits; seeds cylindrical to quadrate, funicle often persistent.

17a) Subsection **Foliosae** Schrire subsect. nov.

Subsectio *Foliosae* a ceteris speciebus sectionis *Dendroides* inflorescentiis brevioribus et quam foliis circiter duplo tantum longioribus et bracteis plerumque persistentibus differt. Type species *I. foliosa* E.Mey.

"Group" *Pinnatae* Harv. in Harv. & Sond, Fl. Cap. 2: 166 (1862)
p.p.

Stems reddish; pearl bodies sometimes densely aggregated at the base of the petiole or between the leaflets as brownish clumps; leaves pinnately (3) 5 - 9 (11) foliolate, leaf rhachis mostly not extended beyond the distal leaflet pair; inflorescences laxly many to few-flowered, often shorter to about twice the length of the leaves, bracts mostly persistent or scars

conspicuous; calyx from q half to equalling the length of the staminal sheath (rarely shorter), lobes equalling to q twice the length of the tube; keel apex sometimes narrowly acute.

18) Section **Hirsutae** (Rydberg) Schrire *stat. nov.* Type species *I. hirsuta* L.

"Group" *Tetragonocarpace* Wight & Arn., *Prod.Fl.Pen.Ind.Or.* 1: 203 (1834) p.p.

"Group" *Tinctoriae* (Wight & Arn.) Bak. in Oliver, *Fl.Tr.Afr.* 2: 68 (1871) p.p.; emend Bak.f., *Leg.Tr.Afr.* 1: 139 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Tinctoriae* (Wight & Arn.) Taub., in Engl. & Prantl, *Pflanzenfam.* 3(3): 262 (1894) p.p.

"Group" *Hirsutae* Rydberg, *N.Am.Fl.* 24: 140 (1923).

Subsection *Hirsutae* (Rydberg) Gillett, *Kew Bull.*, *Add. ser.* 1: 108 (1958).

Dwarf shrubs or herbs (mostly annuals); stems hirsute, biramous hairs often with arms very unequal in length, simple bristle-like hairs also present, hairs mixed dark brown and hyaline; pearl bodies often scattered on stems; leaves pinnately 5 - 9 foliolate (9 - 13 foliolate in *I. longebarbata*), the rachis extended beyond the distal pair of leaflets; stipules adnate to the base of the petiole; stipels present; racemes densely many-flowered; calyx hirsute, more than half the length of the staminal sheath, lobes more than twice as long as the tube; corolla carmine and white; standard dorsal surface with spreading hyaline and often dark brown hairs, central blotch pale; wing proximal crest hairy; keel narrowly bearded distally, occasionally with dark brown hairs; staminal sheath 3 - 5 mm long, anthers with hairs; ovary q half or less the horizontal length of the pistil; pods reflexed, at least 2 mm

wide, mostly 3 - 6 seeded, densely hirsute; endocarp with large tannin vesicles; seeds 4 spherical to quadrate, pitted.

19) Section *Setiflorae* Schrire sect. nov.

Sectio *Setiflorae* a sectione *Hirsutae* corporis perlariis ad basin foliorum et inter foliola dense aggregatis brunneisque distinguenda. Frutices, suffrutices vel herbae; brachia pilorum biramosorum saepe valde inaequalia, pilis mixtis fusco-brunneis hyalinisque; racemi dense multiflori; calyx hirsutus lobis quam tubo plus quam duplo longioribus; crista proximalis alae pubescens; antherae per totam superficiem pilis dispersis ornatae; longitudo pistilli quam ovarii plus quam bis excedens; legumina patentia, 2 - 6 - seminalia; endocarpus vesiculos tanniniferos grandis continens; semina foveolata. Type species *I. setiflora* Bak.

"Group" *Productae* Harv. in Harv. & Sond., Fl. Cap. 2: 166-167 (1862) p.p.

"Group" *Tinctoriae* (Wight & Arn.) Bak. in Oliver, Fl. Tr. Afr. 2: 68 (1871) p.p.; emend Bak. f., Leg. Tr. Afr. 1: 139 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Tinctoriae* (Wight & Arn.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

Subsection *Atratae* Gillett, Kew Bull., Add. ser. 1: 76 (1958) p.p.

Shrubs, dwarf shrubs or herbs (rarely annuals); biramous hairs often with arms very unequal in length, hairs mixed dark brown and hyaline; pearl bodies often scattered on stems, densely aggregated as brownish clumps at leaf bases and between the leaflets; leaves pinnately 7 - 17 foliolate, the rhachis extended beyond the distal pair of leaflets; stipules adnate to the base of the petiole; stipels absent; racemes densely many-

flowered; calyx hirsute, more than half the length of the staminal sheath, lobes about twice as long or longer than the tube; corolla rose-carmine to carmine; standard dorsal surface with spreading hyaline and sometimes dark brown hairs, central blotch pale; wings often sparsely bearded distally, proximal crest hairy; keel densely pilose bearded distally, hairs hyaline and often dark brown, proximal fringe along upper margin dense, pink; staminal sheath 3 - 14 mm long, anthers with hairs scattered over entire surface; ovary η half or less the horizontal length of the pistil; pods η patent, turgid, broadly subcylindrical, mostly 2 - 6 seeded, densely hirsute or pilose; endocarp with large tannin vesicles; seeds η quadrate, pitted.

20) Section **Microcarpae** (Rydberg) Schrire *stat. nov.* Lectotype species *I. domingensis* Spreng. [in Gillett, 1958]

"Group" *Microcarpae* Rydberg, N.Am.Fl. 24: 141 (1923).

Subsection *Microcarpae* (Rydberg) Gillett, Ind.Tr.Afr. 110 (1958).

Dwarf shrubs or decumbent herbs; biramous hairs sometimes with arms very unequal in length, hairs hyaline only; yellowish discoid pearl bodies scattered over stems; leaves pinnately 7 - 11 foliolate, leaflets with punctate pearl bodies beneath; stipules adnate to the base of the petiole; stipels absent; racemes densely many-flowered; calyx hirsute, more than half the length of the staminal sheath, lobes more than twice as long as the tube; corolla carmine; standard narrow at the base tapering to the claw, dorsal surface hyaline hairy; wing proximal crest sometimes hairy; keel not bearded; staminal sheath 3 - 5 mm long, anthers mostly with hairs; ovary η half or less the horizontal length of the pistil; pods reflexed, short, subtorulose, 3 - 6 seeded, tomentose; endocarp with tannin deposits; seeds η quadrate, not pitted.

- 21) Section **Stenophyllae** (Bak.) Schrire *stat. nov.* Type species
I. stenophylla Guill. & Perr.

"Group" *Stenophyllae* Bak. in Oliver, Fl.Tr.Afr. 2: 67
(1871) p.p., emend Bak.f., Leg.Tr.Afr. 1: 128 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Stenophyllae*
(Bak.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262
(1894) p.p.

"Group" *Simplicifoliae* sensu Bak.f., Leg.Tr.Afr. 1: 101
(1926) p.p., non DC.

Subsection *Brevierectae* Gillett (as *Brevi-erectae*), Kew
Bull., Add. ser. 1: 33 (1958) p.p.

Dwarf shrubs or herbs (mostly annuals); biramous hairs with arms always q equal in length, often in different sizes on the lower leaf surface, hairs mixed dark brown and hyaline; pearl bodies restricted to leaf bases and between leaflets; leaves pinnately (5) 7 - 23 foliolate or simple, the rhachis extended beyond the distal leaflet pair, leaflets linear to narrowly oblanceolate; stipules adnate to the base of the petiole, subulate; stipels mostly absent; racemes nearly sessile, lax, elongated, many-flowered; calyx with brown spreading hairs (except *I. andrewsiana*), more than half the length of the staminal sheath, lobes about twice as long or longer than the tube; corolla rose to carmine; standard dorsal surface appressed or spreading hyaline strigose; wing proximal crest hairy; keel broadly hyaline bearded distally, proximal fringe along upper margin dense, pink; staminal sheath 4 - 8 mm long, anthers with hairs scattered over entire surface, rarely glabrous; ovary q half or less the horizontal length of the pistil; pods q erect, more than 2 mm wide, subcylindrical, 3 - 15 seeded, spreading strigose; endocarp with large tannin vesicles; seeds q quadrate, pitted.

- 22) Section **Brevierectae** (Gillett) Schrire stat. nov. Type species *I. simplicifolia* Lam.

"Group" *Simplicifoliae* DC., Prodr. 2: 222 (1825) p.p.

"Group" *Simplicifoliae* (DC.) Bak. in Oliver, Fl.Tr.Afr. 2: 66 (1871) p.p.; Bak.f., Leg.Tr.Afr. 1: 101 (1926) p.p.

Subsection *Brevierectae* Gillett (as *Brevi-erectae*), Kew Bull., Add. ser. 1: 33 (1958) p.p.

Subsection *Simplicifoliae* (DC.) Fang & Zheng, in Acta Phyt. Sinica 27: 168 (1989).

Dwarf shrubs or herbs; biramous hairs with arms always *q* equal in length, often in different sizes on the lower leaf surface, hairs hyaline only; pearl bodies restricted to leaf bases and between leaflets; leaves simple, to 3 mm wide; leaflets linear to narrowly oblanceolate; stipules adnate to the base of the petiole, subulate; stipels absent; racemes nearly sessile, short, 2 - 5 flowered; calyx less than half the length of the staminal sheath, lobes about equal to twice as long as the tube; corolla pink; standard dorsal surface appressed hyaline strigose; wing proximal crest glabrous; keel broadly hyaline bearded distally, proximal fringe along upper margin dense, pink; staminal sheath 4 - 5 mm long, anthers glabrous; ovary length variable; pods erect, less than 2 mm wide, 3 - 12 seeded, strigose; endocarp with tannin deposits; seeds *q* quadrate.

- 23) Section **Atratae** (Gillett) Schrire stat. nov. Type species *I. atriceps* Hook.f.

"Group" *Tinctoriae* (Wight & Arn.) Bak. in Oliver, Fl.Tr.Afr. 2: 68 (1871) p.p.; emend Bak.f., Leg.Tr.Afr. 1: 139 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Tinctoriae* (Wight & Arn.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

"Group" *Simplicifoliae* sensu Bak.f., Leg.Tr.Afr. 1: 101 (1926) p.p., non DC.

Subsection *Atratae* Gillett, Kew Bull., Add. ser. 1: 76 (1958).

Dwarf shrubs or herbs (few annuals); biramous hairs with arms always *q* equal in length, often in different sizes on the lower leaf surface, hairs mixed dark brown (or black) and hyaline; multiseriate gland-tipped trichomes present; pearl bodies restricted to leaf bases and between leaflets; leaves pinnately (3) 5 - 15 foliolate or simple, the rhachis extended beyond the distal leaflet pair; stipules adnate to the base of the petiole, subulate; stipels absent; racemes densely many-flowered; calyx more than half the length of the staminal sheath, with brown (or black) spreading hairs, lobes about twice as long as the tube; corolla carmine; standard dorsal surface appressed hyaline strigose, black hairs sometimes present; wing proximal crest glabrous; keel broadly hyaline and black bearded distally; staminal sheath 3 - 6 mm long, anthers glabrous; ovary *q* half or less the horizontal length of the pistil; pods *q* patent, turgid, broadly subcylindrical, 2 - 6 seeded, often glandular pilose; endocarp with tannin deposits; seeds *q* quadrate to elliptic, not pitted.

24) Section *Viscosae* (Rydberg) Schrire *stat. nov.* Type species *I. colutea* (Burm.f.) Merr. (*I. viscosa* Lam.)

"Group" *Tinctoriae* (Wight & Arn.) Bak. in Oliver, Fl.Tr.Afr. 2: 68 (1871) p.p.

"Group" *Dissitiflorae* Wight & Arn., Prod.Fl.Pen.Ind.Or. 1: 200 (1834) p.p.; Bak. in Oliver, Fl.Tr.Afr. 2: 67 (1871) p.p.; Bak.f., Leg.Tr.Afr. 1: 117 (1926) p.p.

"Group" *Pinnatae* (E. Mey.) Harv. in Harv. & Sond., Fl. Cap. 2: 165 (1862) p.p.; Bak.f., Leg. Tr. Afr. 1: 129 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Dissitiflorae* (Wight & Arn.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

"Group" *Viscosae* Rydberg, N. Am. Fl. 24: 140 (1923).

Subsection *Viscosae* Gillett, Kew Bull., Add. ser. 1: 59 (1958) p.p.

Dwarf shrubs or herbs (many annuals); biramous hairs with arms always *q* equal in length (except *I. wildiana*), hairs hyaline only, in different sizes on the lower leaf surface; multiseriate gland-tipped trichomes present (sometimes very sparse); pearl bodies restricted to leaf bases and between leaflets; leaves *q* patent, pinnately (5) 7 - 17 foliolate, leaflets mostly less than 3 times as long as wide; stipules adnate to the base of the petiole, subulate; stipels rarely present; racemes elongate, often laxly many-flowered, ascending away from leaves; calyx often more than half the length of the staminal sheath, lobes about twice as long as the tube; corolla carmine; standard dorsal surface appressed hyaline strigose; wing proximal crest glabrous; keel narrowly hyaline bearded distally; staminal sheath 2 - 6 (10) mm long, anthers rarely with hairs; ovary length variable; pods *q* patent, linear, 2 - 14 seeded, sometimes glandular pilose; endocarp with tannin deposits; seeds *q* subcylindrical to elliptic, not pitted.

24a) Subsection *Centrae* Gillett, Kew Bull., Add. ser. 1: 69 (1958). Type species *I. ugandensis* Bak.f.

"Group" *Tinctoriae* (Wight & Arn.) Bak.f., Leg. Tr. Afr. 1: 139 (1926) p.p.

Multiseriate gland-tipped trichomes absent; lower two pairs of leaflets crowded together at the base of the leaves; buds

densely strigose; keel broadly hyaline bearded distally;
staminal sheath 3 - 4 mm long.

25) Section **Hilares** Schrire sect. nov.

Sectio *Hilares* ab ceteris sectionibus characteribus sequentibus distinguenda. Suffrutices vel herbae perennes caudice lignoso; trichomata multiseriata ad apicem glandulosa saepe ferentes; folia suberecta, breviter petiolata, pinnatim paucifoliolata; racemi 3 - 12 - flori folia vix excedentes et ab eis partim occulti; corolla rosea vel carmina; vagina staminalis 4 - 8 mm longa; antherae pilosae vel glabrae; legumina φ patentia vel erecta, 4 - 8 - seminalia. Type species *I. hilaris* Eckl. & Zeyh.

"Group" *Pinnatae* (E. Mey.) Harv. in Harv. & Sond., Fl. Cap. 2: 165 (1862) p.p.; Bak.f., Leg. Tr. Afr. 1: 129 (1926) p.p.

Subsection *Viscosae* Gillett, Kew Bull., Add. ser. 1: 59 (1958) p.p.

Dwarf shrubs or perennial herbs, with woody rootstocks; arms of biramous hairs mostly φ equal in length, hairs hyaline only, often in different sizes on the lower leaf surface; multiseriate gland-tipped trichomes present or absent; pearl bodies restricted to leaf bases and between leaflets; stems densely leafy, leaves suberect, shortly petiolate, pinnately 1 - 5 - 7 (15) foliolate, the rhachis mostly not extended beyond the distal leaflet pair; leaflets usually more than 3 times as long as wide, secondary venation sometimes prominent; stipules adnate to the base of the petiole, subulate; stipels rarely present; racemes 3 - 12 flowered, partially obscured by and barely exceeding the leaves; calyx more than half the length of the staminal sheath, lobes about twice as long or longer than the tube; corolla rose to carmine; standard dorsal surface appressed hyaline strigose, central blotch dark; wing proximal crest glabrous; keel narrowly hyaline bearded distally; staminal sheath 4 - 8 mm long, anthers with hairs often

present; ovary mostly more than half the horizontal length of the pistil; pods φ patent to erect, linear, 4 - 8 seeded, strigose; endocarp with tannin deposits; seeds φ quadrate not pitted.

26) Section *Spinosa* (Bak.) Schrire stat. nov. Lectotype species *I. spinosa* Forssk. [Gillett, 1958].

"Group" *Spinosa* Bak. in Oliver, Fl.Tr.Afr. 2: 67 (1871):
Bak.f., Leg.Tr.Afr. 1: 113 (1926).

Series *Pinnatae* (E. Mey.) Taub. subseries *Spinosa* (Bak.)
Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 261 (1894) p.p.

Subsection *Spinosa* (Bak.) Gillett, Kew Bull., Add. ser. 1:
50 (1958).

Shrubs or dwarf shrubs of arid areas, often divaricately branched, brachyblasts present; arms of biramous hairs always φ equal in length, hairs hyaline only; multiseriate gland-tipped trichomes rarely present; pearl bodies restricted to leaf bases and between leaflets; leaves small, shortly petiolate, pinnately (1) 3 - 7 (9) foliolate, the rachis barely extended beyond the distal leaflet pair; stipules adnate to the base of the petiole, subulate; stipels absent; racemes shortly pedunculate, 2 - 8 flowered, barely exceeding the leaves, the inflorescence rachis terminating in a spine (only at the fruiting stage in *I. longispina*); calyx about quarter the length of the staminal sheath, lobes more or less equalling to longer than the tube, sometimes swollen-tipped, glandular; corolla carmine; standard dorsal surface appressed hyaline strigose; wing proximal crest glabrous; keel narrowly hyaline bearded distally; staminal sheath 4 - 6 mm long, anthers glabrous; ovary more than half the horizontal length of the pistil; pods φ patent to erect, linear, 5 - 10 seeded, strigose; endocarp with tannin deposits; seeds φ subcylindrical to oblong or ellipsoid, not pitted.

27) Section **Brevipatentes** (Gillett) Schrire *stat. nov.* Type species *I. suaveolens* Jaub. & Spach

"Group" *Dissitiflorae* (Wight & Arn.) Bak. in Oliver, Fl.Tr.Afr. 2: 67 (1871) p.p.

"Group" *Simplicifoliae* sensu Bak.f., Leg.Tr.Afr. 1: 101 (1926) p.p., non DC.

"Group" *Trifoliolatae* sensu Bak.f., Leg.Tr.Afr. 1: 108 (1926) p.p., non E. Mey.

Series *Pinnatae* (E. Mey.) Taub. subseries *Dissitiflorae* (Wight & Arn.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

Subsection *Brevipatentes* Gillett, Kew Bull., Add. ser. 1: 52 (1958).

Shrubs or dwarf shrubs of arid areas, branches often divaricate, canescent, brachyblasts present; arms of biramous hairs always q equal in length, hairs hyaline only; multiseriate gland-tipped trichomes absent; pearl bodies restricted to leaf bases and between leaflets; leaves small, shortly petiolate, pinnately 1 - 3 - 5 (7) foliolate, rarely reduced to 1-foliolate towards the apex; the rachis sometimes not extended beyond the distal leaflet pair, leaflets rarely gland-tipped or with 2 lateral blister glands and another beneath the tip; stipules adnate to the base of the petiole, subulate or lanceolate with a broad scarious base and persistent along with petiole after the leaflets have fallen; stipels absent; racemes shortly pedunculate, 1 - 5 flowered, partially obscured by and barely exceeding the leaves; calyx about quarter the length of the staminal sheath, lobes more or less equalling to longer than the tube, often swollen-tipped, glandular; corolla carmine; standard dorsal surface appressed hyaline strigose; wing proximal crest glabrous; keel narrowly hyaline bearded distally; staminal sheath 3 - 5 mm long,

anthers glabrous; ovary more than half the horizontal length of the pistil; pods φ patent to erect, linear, 4 - 12 seeded, strigose; endocarp with tannin deposits; seeds φ quadrate to oblong or ellipsoid, not pitted.

28) Section **Podophyllae** Schrire sect nov.

Sectio *Podophyllae* ab omnibus ceteris sectionibus foliis singularissimis distinguenda. Suffrutices; rami glabrescentes virgati, brachyblastos ferentes; petioli filiforme, longi, foliolis delapsis etiam persistenti; folia unifoliolatis, foliolo distant terminalisque; racemi laxe 3 - 8 - flori; vagina staminalis 3 - 4 mm longa; anthera glabra; legumina φ patentia, linearia, 7 - 11 - seminalia. Type species *I. podophylla* Benth. ex Harv.

"Group" *Juncifoliae* Harv. in Harv. & Sond., Fl. Cap. 2: 163 (1862) p.p.

Subsection *Juncifoliae* (Harv.) Gillett, Kew Bull., Add. ser. 1: 33 (1958) p.p.

Dwarf shrubs, branches glabrescent, virgate, brachyblasts present; biramous hairs with arms always φ equal in length, hyaline only; pearl bodies restricted to leaf bases and between leaflets; petioles filiform, long, persistent after leaflets have fallen, leaves 1-foliolate, the leaflet distant and terminal; stipules adnate to the base of the petiole, subulate; stipels present; racemes laxly to densely 3 - 8 flowered, barely exceeding the petioles; calyx about half the length of the staminal sheath, lobes more or less equalling the tube; corolla carmine; standard dorsal surface appressed hyaline strigose; wing proximal crest glabrous; keel narrowly hyaline bearded distally; staminal sheath 3 - 4 mm long, anthers glabrous; ovary more than half the horizontal length of the pistil; pods φ patent to erect, linear, 7 - 11 seeded, strigose; endocarp with tannin deposits; seeds φ quadrate to oblong. not pitted.

29) Section *Pilosae* (Gillett) Schrire stat. nov. Type species *I. pilosa* Poir.

"Group" *Simplicifoliae* sensu Bak.f., Leg.Tr.Afr. 1: 101 (1926) p.p., non DC.

"Group" *Dissitiflorae* (Wight & Arn.) Bak. in Oliver, Fl.Tr.Afr. 2: 67 (1871) p.p.; Bak.f., Leg.Tr.Afr. 1: 117 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Dissitiflorae* (Wight & Arn.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

Subsection *Pilosae* Gillett, Kew Bull., Add. ser. 1: 56 (1958)

Subsection *Centrae* Gillett, Kew Bull., Add. ser. 1: 69 (1958) p.p.

Dwarf shrubs or herbs (few annuals); stems flattened, pilose; biramous hairs mixed dark brown and hyaline, some hairs with arms very unequal in length, often occurring in different sizes on the lower leaf surface; pearl bodies scattered on stems; leaves pinnately 3 - 5 (9) foliolate or simple, sometimes reduced in number towards the apex; leaflets mostly 10 - 20 mm long, biramous hairs usually arranged perpendicularly on leaf margins, venation often craspedodromous; stipules adnate to the base of the petiole, lanceolate, \approx 1 mm wide (or more) at the base; stipels present; racemes laxly 2 - 12 (20) flowered, slender pedunculate; calyx pilose, more than half the length of the staminal sheath, lobes more than twice as long as the tube, sometimes gland-tipped; corolla carmine; standard dorsal surface with spreading hyaline hairs near the apex, usually narrow and tapering towards the base; wing proximal crest glabrous or sometimes with isolated hairs; keel narrowly hyaline bearded distally; staminal sheath 2 - 5 mm long, anthers glabrous; ovary \approx half or less the horizontal length of

the pistil; pods erect or patent, 3 - 7 (11) seeded, pubescent to hirsute; endocarp with tannin deposits spotted, striped or in large vesicles; seeds *q* quadrate to ellipsoid, rarely pitted.

30) Section *Dissitiflorae* (Wight & Arn.) Schrire *stat. nov.*
Lectotype species *I. geminata* Bak. [Gillett, 1958]

"Group" *Dissitiflorae* Wight & Arn., *Prod.Fl.Pen.Ind.Or.* 1: 200 (1834) p.p.; Bak. in Oliver, *Fl.Tr.Afr.* 2: 67 (1871) p.p.; Bak.f., *Leg.Tr.Afr.* : 117 (1926) p.p.

"Group" *Trichopodae* Bak. in Oliver, *Fl.Tr.Afr.* 2: 67 (1871) p.p.; Bak.f., *Leg.Tr.Afr.* 1: 114 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Dissitiflorae* (Wight & Arn.) Taub., in Engl. & Prantl, *Pflanzenfam.* 3(3): 262 (1894) p.p.

Subsection *Dissitiflorae* (Wight & Arn.) Gillett, *Kew Bull.*, *Add. ser.* 1: 40 (1958) p.p.

Dwarf shrubs or herbs (mainly annuals); biramous hairs with arms mostly *q* equal in length, often in different sizes on the lower leaf surface, hyaline only; pearl bodies scattered on stems; leaves pinnately (1) 3 - 9 (15) foliolate, sometimes reduced in number towards the apex, rhachis extended beyond the distal leaflet pair; leaflets mostly less than 10 mm (rarely to 15 mm) long, occasionally with 2 lateral blister glands and another beneath the tip, margins often viscid; stipules adnate to the base of the petiole, subulate; stipels present; racemes laxly 1 - 5 flowered (rarely more), on slender wiry peduncles mostly longer than the rhachis, inflorescences more or less equalling to twice the length of the leaves; calyx strigose or pilose, less than half the length of the staminal sheath, lobes about equalling to twice as long as the tube, sometimes swollen-tipped, glandular; corolla carmine; standard dorsal surface hyaline pubescent; wing proximal crest glabrous; keel

narrowly hyaline bearded distally; staminal sheath 2 - 6 mm long, anthers glabrous; ovary more than half the horizontal length of the pistil; pods erect, occasionally flattened, 3 - 15 seeded, glabrous or strigose to pubescent; endocarp with tannin deposits spotted or in large vesicles; seeds *q* quadrate, sometimes pitted.

31) Section *Laxeracemosae* Schrire sect. nov.

Sectio *Laxeracemosae* a sectione *Dissitiflorae* floribus plurimis et leguminibus patentibus singularissimisque distiguenda. Herbae perennes vel annuae; caules corporibus perlariis dispersis instructi; folia pinnata; racemi laxe 5 - 15 - flori; corolla alba vel rosea; vagina staminalis 3 - 4 mm longa; antherae glabrae; legumina *q* patentia; nonnunquam torulosa, suturis latis pallidibusque; 4 - 8 - seminalia, glabra vel pubescentia; semina interdum foveolata. Type species *I. laxeracemosa* Bak.f.

"Group" *Dissitiflorae* (Wight & Arn.) Bak. in Oliver, Fl.Tr.Afr. 2: 67 (1871) p.p.; Bak.f., Leg.Tr.Afr. 1: 117 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Dissitiflorae* (Wight & Arn.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

Subsection *Centrae* Gillett, Kew Bull., Add. ser. 1: 69 (1958) p.p.

Subsection *Psiloceratiae* Gillett, Kew Bull., Add. ser. 1: 84 (1958) p.p.

Annual or perennial herbs; biramous hairs with arms either *q* equal or very unequal in length, hyaline only, occurring in different sizes on the lower leaf surface; pearl bodies scattered on stems, sometimes aggregated as brownish clumps at leaf bases and between leaflets; leaves pinnately 5 - 13

foliolate, rhachis extended beyond the distal leaflet pair, leaflets rarely with glandular apices and viscid margins; stipules adnate to the base of the petiole, triangular to subulate; stipels absent; racemes laxly 5 - 15 flowered, usually longer than the subtending leaf; calyx about half the length of the staminal sheath, lobes σ equalling to twice as long as the tube; corolla pink to white; standard dorsal surface hyaline pubescent; wing proximal crest occasionally hairy; keel not bearded distally; staminal sheath 3 - 4 mm long, anthers glabrous; ovary more than half the horizontal length of the pistil; pods σ patent, to 2 mm or more wide, somewhat torulose, relatively thin textured with broad pale sutures, 4 - 8 seeded, glabrous or pubescent; endocarp with tannin deposits spotted or in large vesicles; seeds σ quadrate, sometimes pitted.

- 32) Section **Latestipulatae** (Bak.f.) Gillett, Ind.Tr.Afr. 21 (1958). Type species *I. berhautiana* Gillett (= *I. sericea* Benth. ex Bak., in Fl.Tr.Afr. 2: 76 (1871) pro maj. parte)
- "Group" *Tinctoriae* (Wight & Arn.) Bak. in Oliver, Fl.Tr.Afr. 2: 68 (1871) p.p.
- "Group" *Paniculatae* Bak. in Oliver, Fl.Tr.Afr. 2: 67 (1871) p.p.
- "Group" *Capitatae* Bak. in Oliver, Fl.Tr.Afr. 2: 66 (1871) p.p.
- "Group" *Latestipulatae* Bak.f., Leg.Tr.Afr. 1: 112 (1926) p.p.
- "Group" *Opertiflorae* Bak.f., Leg.Tr.Afr. 1: 112 (1926) p.p.
- "Group" *Trichopodae* (Bak.) Bak.f., Leg.Tr.Afr. 1: 114 (1926) p.p.

"Group" *Dissitiflorae* (Wight & Arn.) Bak.f., Leg.Tr.Afr. 1: 117 (1926) p.p.

Dwarf shrubs or herbs (few annuals); sericeous, some biramous hairs with arms very unequal in length, hyaline only, hairs of different sizes on the lower leaf surface; pearl bodies scattered on stems; leaves pinnately 1 - 7 foliolate or simple, passing gradually into foliaceous bracts, rachis extended beyond the distal pair of leaflets; stipules adnate to the base of the petiole, asymmetrically lanceolate-acuminate to ovate, 2 - 4 mm wide at the base, sometimes gland-tipped; stipels absent; racemes 1 - 3 flowered in the axils of leafy or trilobed bracts, almost hidden, inflorescences rarely compacted within a distinct co-florescence (strobilus); calyx sericeous to pilose, more than half the length of the staminal sheath, lobes lanceolate, scarious, more than twice as long as the tube, often gland-tipped; corolla carmine; standard dorsal surface hyaline pubescent; wing proximal crest glabrous; keel not bearded distally; staminal sheath 2 - 4 mm long, anthers glabrous (rarely with isolated hairs); ovary q half or less the horizontal length of the pistil; pods erect, sometimes flattened, relatively thin textured with broad pale sutures, 2 - 4 (5) seeded, sericeous; endocarp with tannin deposits striped or in large vesicles; seeds q quadrate to ellipsoid, rarely pitted.

33) Section *Paniculatae* (Bak.) Gillett. Lectotype species *I. pulchra* Willd. [Gillett, 1958].

"Group" *Paniculatae* Bak. in Oliver, Fl.Tr.Afr. 2: 67 (1871) p.p., Bak.f., Leg.Tr.Afr. 1: 110 (1926)

"Group" *Simplicifoliae* (DC.) Bak. in Oliver, Fl.Tr.Afr. 2: 66 (1871) p.p.; Bak.f., Leg.Tr.Afr. 1: 101 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Paniculatae* (Bak.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

"Group" *Trichopodae* (Bak.) Bak.f., Leg.Tr.Afr. 1: 114
(1926) p.p.

Subsection *Paniculatae* (Bak.) Gillett, Kew Bull., Add. ser.
1: 25 (1958) p.p.

"Group" *Capitatae* Bak. in Oliver, Fl.Tr.Afr. 2: 66 (1871)
p.p.; Bak.f., Leg.Tr.Afr. 1: 97 (1926) [in section
Sphaeridiophora] p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Capitatae* (Bak.)
Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 261 (1894)
p.p.

Annual (rarely perennial) herbs, biramous hairs dark brown and hyaline, often with arms very unequal in length, hairs of different sizes on the lower leaf surface; pearl bodies restricted to leaf bases and between leaflets, rarely scattered on stems (in *I. nigricans* and *I. leptoclada*); leaves pinnately 5 - 7 (13) foliolate or simple, often becoming reduced in number above (if pinnate) and passing gradually into foliaceous or trifid bracts; stipules adnate to the base of the petiole, narrowly lanceolate to subulate; stipels sometimes present; inflorescences paniculate, sometimes condensed and subcapituliform, or less compact with some flowers single in the axils of foliar bracts, pedicels often jointed, marked by secondary bracts; calyx hyaline or brown pilose, mostly more than half the length of the staminal sheath, lobes often lanceolate, scarious, more than twice as long as the tube (except *I. paniculata*); corolla carmine; standard dorsal surface hyaline and occasionally dark brown (black) strigose; wing proximal crest glabrous; keel broadly hyaline (and black) bearded distally; staminal sheath 2 - 4 mm long, anthers glabrous; ovary q half or less the horizontal length of the pistil; pods erect or spreading, shortly cylindrical or oval, either coriaceous, terete and densely hirsute, or relatively thin textured, slightly flattened with broad pale sutures and pilose or sericeous, 1 - 2 (4) seeded; endocarp with diffuse

tannin deposits or tannins absent; seeds *q* quadrate to ellipsoid, not pitted.

- 33a) Subsection *Trichopodae* (Bak.) Gillett, Kew Bull., Add. ser. 1: 32 (1958). Lectotype species *I. trichopoda* Leprieur ex Guill. & Perr. [Gillett, 1958].

"Group" *Trichopodae* Bak. in Oliver, Fl.Tr.Afr. 2: 67 (1871) p.p., Bak.f., Leg.Tr.Afr. 1: 114 (1926) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Trichopodae* (Bak.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 261 (1894) p.p.

Lower leaves pinnate, the upper often simple, bract-like; flowers single, on slender glabrescent pedicels 5 mm or more long, pedicels jointed just below the flower; pod short with broad pale sutures.

- 34) Section *Terminales* (Bak.f.) Schrire *stat. nov.* Lectotype species *I. terminalis* Bak.

"Group" *Terminales* Bak.f., Leg.Tr.Afr. 1: 97 (1926) [in section *Sphaeridiophora*].

Subgenus *Sphaeridiophora* (Desv.) Benth. *sensu* Bak. in Oliver, Fl.Tr.Afr., 2: 66 (1871) p.p. non auct.

Subsection *Paniculatae* (Bak.) Gillett, Kew Bull., Add. ser. 1: 25 (1958) p.p.

Annual (rarely perennial) herbs, biramous hairs hyaline, often with arms very unequal in length, hairs of different sizes on the lower leaf surface; pearl bodies densely covering stems leaves and calyces; leaves pinnately 3 - 7 (13) foliolate, passing gradually into foliaceous or trifid bracts; stipules adnate to the base of the petiole, subulate; stipels absent; inflorescences paniculate, subcapituliform, secondary bracts

linear, ciliate; calyx more than half the length of the staminal sheath, lobes scarious, becoming broader after flowering, more than twice as long as the tube; corolla carmine; standard hooded with a deflexed apiculum, dorsal surface vestiture hyaline; wing proximal crest glabrous; staminal sheath 2 - 4 mm long, anthers glabrous; ovary $\frac{1}{2}$ or less the horizontal length of the pistil; pods ovoid detaching with calyces, thinly textured, tardily dehiscent, sericeous, 1 seeded; endocarp without tannin deposits; seeds not pitted.

- 35) Section **Acanthonotus** (Benth.) Taub., in Engl. & Prantl, Pflanzens-fam. 3(3): 260 (1894). Type species *I. nummulariifolia* (L.) Livera ex Alston (as *Acanthonotus echinatus* (Willd.) Benth.

Acanthonotus Benth., in Hook, Fl.Nigrit. 293 (1849) [as genus].

Subgenus *Acanthonotus* (Benth.) Benth. in Benth.& Hook.f., Gen.Fl. 1: 494 (1865); Bak. in Oliver, Fl.Tr.Afr. 2: 66 (1871); Gillett, Kew Bull., Add. ser. 1: 8 (1958).

"Group" *Echinatae* Wight & Arn., Prod.Fl.Pen.Ind.Or. 1: 198 (1834).

Section *Echinatae* (Wight & Arn.) Bak.f., Leg.Tr.Afr. 1: 96 (1926).

Annual or perennial herbs; stems flattened; some biramous hairs with arms very unequal in length, hairs often different sizes on the lower leaf surface; pearl bodies scattered on stems; leaves simple, pearl bodies present abaxially, biramous hairs usually arranged perpendiculary on cartilagenous leaf margins; stipules adnate to the base of the petiole, subulate; stipels absent; racemes 10 - 15 flowered; calyx more than half the length of the staminal sheath, lobes more than twice as long as the tube; corolla carmine; standard usually narrow and

tapering towards the base, dorsal surface hyaline hairy near the apex; wing proximal crest hairy; keel not bearded distally, apex rostrate; staminal sheath 2 - 4 mm long, anthers with hairs; ovary q half or less the horizontal length of the pistil; pods sub-triangular, falcate, indehiscent, 1 - 2 seeded, reflexed, sometimes spiny along the dorsal suture, venation prominent; endocarp tannins diffuse or absent, seeds triangular, not pitted.

- 36) Section **Amecarpus** (Benth. ex Harv.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 260 (1894). Lectotype species *I. sessilifolia* DC. [Gillett, 1958].

Amecarpus Benth., in Lindl., Veg.Kingd. 554 (1846) nom. nud. [as genus].

Subgenus *Amecarpus* Benth. ex Harv. in Harv. & Sond., Fl.Cap. 2: 201 (1862); Benth., in Benth. & Hook.f., Gen.Pl. 1: 494 (1865); Bak. in Oliver, Fl.Tr.Afr. 2: 69 (1871); Gillett, Kew Bull., Add. ser. 1: 9 (1958).

Section *Amecarpus* (Benth ex Harv.) Bak.f., Leg.Tr.Afr. 1: 163 (1926).

Dwarf shrubs or herbs (many annuals); distinct vegetative and flowering shoots found in *I. letestui*; biramous hairs with arms mostly q equal in length (except *I. circinnata* and *I. rautanenii*), hairs coarsely strigose, occurring in different sizes on the lower leaf surface; pearl bodies restricted to leaf bases and between leaflets (scattered on stems in *I. letestui* and *I. lasiantha*); leaves pinnately 3 - 5 - 7 (9) foliolate, rachis extended beyond the distal pair of leaflets; stipules adnate to the base of the petiole, subulate; stipels mostly present; racemes densely many-flowered, longer or shorter than the subtending leaves, inflorescence rachides spiny-tipped in *I. circinnata* and *I. sessilifolia*; bracts caducous; calyx more than half the length of the staminal sheath, lobes setaceous, more than twice as long as the tube

(except *I. circinnata* and *I. rautanenii*), occasionally gland-tipped in *I. lasiantha*; corolla rose, orange or carmine; standard dorsal surface hyaline strigose; wing proximal crest glabrous; keel narrowly hyaline bearded distally (broadly bearded in *I. lasiantha*); staminal sheath 3 - 5 mm long (up to 11 mm in *I. lasiantha*), anthers glabrous; ovary length variable; pods straight, curved, torulose or circinnate, flat, 2 - 8 (15) seeded, with eminences or a prominent ridge visible above the seeds (except *I. damarana*), reflexed, venation sometimes prominent; endocarp tannins absent (except *I. circinnata* and *I. rautanenii*), seeds quadrate to rounded, often dorsoventrally flattened, not pitted.

- 37) Section **Demissae** Gillett, Kew Bull., Add. ser. 1: 18 (1958).
Type species *I. demissa* Taub.

"Group" *Eusphaeridiophora* Bak.f., Leg.Tr.Afr. 1: 97 (1926)
p.p.

As in *Ameocarpus* but annual or perennial herbs only; stipels present; racemes 4 - 10 flowered, shorter than the subtending leaf rachides, bracts persistent; staminal sheath 1.5 - 4 mm long, anthers with hairs; pods flattened, reflexed or patent.

- 38) Section **Sphaeridiophora** (Desv.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 261 (1894). Type species *I. linifolia* (L.f.) Retz. (as *Sphaeridiophorum linifolium* (L.f.) Desv., based on *Hedysarum linifolium* L.f.).

Sphaeridiophorum Desv., in Journ.Bot. 3: 125, t 6 (1813)
[as genus].

Subgenus *Sphaeridiophora* (Desv.) Benth., in Benth. & Hook.f., Gen.Pl. 1: 494 (1865); Bak. in Oliver, Fl.Tr.Afr. 2: 66 (1871) p.p.

"Group" *Simplicifoliae* DC., Prodr. 2: 222 (1825) p.p.; Bak. in Oliver, Fl.Tr. Afr. 2: 66 (1871) p.p.; Bak.f., Leg.Tr.Afr. 1: 101 (1926) p.p.

"Group" *Conjugatae* Bak. in Oliver, Fl.Tr.Afr. 2: 66 (1871) p.p.; Bak.f., Leg.Tr.Afr. 1: 109 (1926) p.p.

"Group" *Sessiliflorae* Bak. in Oliver, Fl.Tr.Afr. 2: 66 (1871); Bak.f., Leg.Tr. Afr. 1: 115 (1926).

Series *Pinnatae* (E. Mey.) Taub. subseries *Sessiliflorae* (Bak.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 261 (1894).

"Group" *Eusphaeridiophora* Bak.f., Leg.Tr.Afr. 1: 97 (1926) p.p.

Subsection *Brevierectae* Gillett (as *Brevi-erectae*), Kew Bull., Add. ser. 1: 33 (1958) p.p.

Subsection *Alternifoliolae* (Harv.) Gillett, Kew Bull., Add. ser. 1: 111 (1958) *pro min parte*.

Dwarf shrubs or herbs (some annuals); biramous hairs with arms either q equal or very unequal in length; pearl bodies restricted to leaf bases and between the leaflets, or sometimes scattered on stems; leaves pinnately 3 - 7 (11) foliolate, or with 2 unequal leaflets (one terminal the other lateral), or simple, leaves often sessile; leaflets mostly alternate, pearl bodies sometimes present abaxially; stipules adnate to the base of the petiole, triangular to subulate or falcate; stipels absent; racemes mostly sessile (except *I. linnaei* and *I. flavicans*), clustered in the leaf axils, shorter than the subtending leaves, very densely 3 - 30 flowered; calyx pilose to sericeous, equalling the length of the staminal sheath, lobes more than twice as long as the tube; corolla carmine; standard usually narrow and tapering towards the base, dorsal surface hyaline hairy near the apex; wing proximal crest

glabrous; keel not bearded distally; staminal sheath 1.5 - 3 mm long, anthers glabrous (rarely with hairs); ovary $\frac{1}{2}$ or less the horizontal length of the pistil (except *I. sessiliflora*); pods globose, oblong, subtetragonous or torulose, 1 - 3 (6) seeded, patent or reflexed; endocarp tannins absent or isolated large tannin vesicles present, seeds quadrate to rounded, sometimes pitted.

39) Section **Simplices-reflexae** (Gillett) Schrire *stat. nov.* Type species *I. bongensis* Kotschy & Peyr.

Subsection *Simplices-reflexae* Gillett, Kew Bull., Add. ser. 1: 122 (1958).

Subsection *Geanthae* Gillett, Kew Bull., Add. ser. 1: 88 (1958).

"Group" *Simplicifoliae* sensu Bak. in Oliver, Fl.Tr.Afr. 2: 66 (1871) p.p.; Bak.f., Leg.Tr.Afr. 1: 101 (1926) p.p. non DC.

"Group" *Tinctoriae* (Wight & Arn.) Bak.f., Leg.Tr.Afr. 1: 139 (1926) p.p.

Dwarf shrubs or herbs, with woody rootstocks; biramous hairs with arms either $\frac{1}{2}$ equal or very unequal in length, hyaline only; pearl bodies restricted to leaf bases and between the leaflets, rarely scattered on stems; leaves sometimes vestigial at the base of shoots, the lamina reduced to a short point between decurrent stipules; foliage leaves simple or pinnately 3 - 5 foliolate; leaflets opposite; stipules adnate to the base of the petiole, lanceolate to subulate; stipels absent; racemes laxly to densely many flowered, mostly much longer than the leaves, occasionally borne in the axils of vestigial leaves below immature foliage leaves; calyx pilose to strigose, $\frac{1}{2}$ equalling the length of the staminal sheath, lobes more than twice as long as the tube; corolla carmine; standard dorsal surface hyaline hairy; staminal sheath 1.5 - 4 mm long, anthers

glabrous; ovary mostly longer than half the horizontal length of the pistil; pods linear, terete or subtetragonous, pubescent to strigose, 5 - 10 seeded, patent or reflexed; endocarp spotted with tannin deposits; seeds φ quadrate to oblong, not pitted.

40) Section **Conjugatae** (Bak.) Schrire *stat. nov.* Lectotype species *I. conjugata* Bak.

"Group" *Conjugatae* Bak. in Oliver, Fl.Tr.Afr. 2: 66 (1871) p.p.; Bak.f., Leg.Tr.Afr. 1: 109 (1926) p.p.

Series *Conjugatae* (Bak.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

"Group" *Heterophyllae* Bak.f., Leg.Tr.Afr. 1: 107 (1926) p.p.

"Group" *Alternifoliolae* (Harv.) Bak.f. (as "Alternifoliae"), Leg.Tr. Afr. 1: 133 (1926) *pro min parte*.

Subsection *Alternifoliolae* (Harv.) Gillett, Kew Bull., Add. ser. 1: 111 (1958) *pro min parte*.

Dwarf shrubs or herbs from woody rootstocks; biramous hairs with arms always φ equal in length, hyaline only; pearl bodies restricted to leaf bases and between the leaflets; leaves rarely vestigial at the base of shoots, the lamina reduced to a short point between decurrent stipules; lower leaves often simple or 1 - 3 foliolate, upper leaves 5 - 11 foliolate, the rhachis prolonged beyond the distal leaflet pair; leaflets alternate or rarely opposite, up to 60 mm long; stipules adnate to the base of the petiole, triangular to subulate; stipels absent; racemes densely many flowered, up to 150 mm long; calyx strigulose, φ equalling or slightly shorter than the staminal sheath, lobes more than twice as long as the tube; corolla pink and white; standard dorsal surface hyaline hairy; staminal sheath 3 - 7 mm long, anther hairs present; ovary longer than

half the horizontal length of the pistil; pods straight or circinnate, 5 - 8 seeded, reflexed; endocarp usually spotted with tannin deposits; seeds ϱ quadrate to oblong, not pitted.

- 41) Section **Alternifoliolae** (Harv.) Schrire stat. nov. Lectotype species *I. spicata* Forssk. [Gillett, 1958].

"Group" *Alternifoliolae* Harv. (as "*Alternifoliae*") in Harv. & Sond., Fl. Cap. 2: 167 (1862).

"Group" *Tinctoriae* (Wight & Arn.) Bak. in Oliver, Fl. Tr. Afr. 2: 68 (1871) p.p.

Series *Pinnatae* (E. Mey.) Taub. subseries *Tinctoriae* (Wight & Arn.) Taub., in Engl. & Prantl, Pflanzenfam. 3(3): 262 (1894) p.p.

"Group" *Hendecaphyllae* Rydberg, in N. Amer. Fl. 24: 141 (1923).

"Group" *Alternifoliolae* (Harv.) Bak. f. (as "*Alternifoliae*"), Leg. Tr. Afr. 1: 133 (1926) *pro maj. parte*.

Subsection *Alternifoliolae* (Harv.) Gillett, Kew Bull., Add. ser. 1: 111 (1958) p.p.

Dwarf shrubs or herbs; rootstocks woody, gnarled; biramous hairs with arms always ϱ equal in length (except *I. maritima*), hyaline or green-yellow; pearl bodies restricted to leaf bases and between the leaflets; leaves 1 - 15 foliolate; leaflets alternate; stipules adnate to the base of the petiole, triangular to lanceolate or subulate, sometimes with scarious margins; stipels occasionally present; racemes elongated, densely many flowered, on peduncles 10 - 40 mm long (except *I. circinella*); calyx more than half the length of the staminal sheath (except *I. oblongifolia* and *I. schimperi*), lobes more than twice as long as the tube; corolla pink and white, or

carmine; standard dorsal surface densely to sparsely hyaline hairy, often only distally; staminal sheath 3 - 5.5 mm long (4 - 10 mm in *I. schimperi*), anther hairs present; ovary longer than half the horizontal length of the pistil (except *I. maritima*); pods straight, falcate or circinnate; terete, tetragonous or torulose; 5 - 12 seeded, reflexed; endocarp tannins absent or isolated large tannin vesicles present, seeds q quadrate to subglobular, sometimes pitted.

CHAPTER 8

SPECIES OF INDIGOFEREAE IN AFRICA

8.1. List of species in tropical Africa (excluding southern Africa)

The tribe Indigofereae has been well revised for tropical Africa (e.g. Baker 1871; Baker f. 1926; Gillett 1958, 1971) therefore species are only listed within their respective genera and sections.

Rhynchotropis Harms

R. marginata (N.E.Br.) Gillett; *R. poggei* (Taub.) Harms

Cyamopsis DC.

C. senegalensis Guill. & Perr.; *C. serrata* Schinz; *C. tetragonoloba* (L.) Taub.

Microcharis Benth.

M. angolensis Bak.; *M. annua* (Milne-Redhead) Schrire comb. nov.; *M. asparagoides* (Taub.) Schrire comb. nov.; *M. ammophila* (Thulin) Schrire comb. nov.; *M. brevistaminea* (Gillett) Schrire comb. nov.; *M. buchneri* (Taub.) Schrire comb. nov.; *M. butayei* (De Wild.) Schrire comb. nov.; *M. cana* (Thulin) Schrire comb. nov.; *M. cufodontii* (Chiov) Schrire comb. nov.; *M. curtisiae* (Johnst.) Schrire comb. nov.; *M. disjuncta* (Gillett) Schrire comb. nov.; *M. garissaensis* (Gillett) Schrire comb. nov.; *M. gillettii* nom. nud.; *M. gyrata* (Thulin) Schrire comb. nov.; *M. kucharii* nom. nud.; *M. latifolia* Benth.; *M. longicalyx* (Gillett) Schrire comb. nov.; *M. galpinii* N.E.Br.; *M. medicaginea* (Welw. ex Bak.) Schrire comb. nov.; *M. praetermissa* (Bak.f.) Schrire comb. nov.; *M. spathulata* (Gillett) Schrire comb. nov.; *M.*

stipulosa (Chiov.) Schrire comb. nov.; *M. tenella* Benth.; *M. tisserantii* (Pellegr.) Schrire comb. nov.; *M. tritoides* (Bak.) Schrire comb. nov.; *M. wajirensis* (Gillett) Schrire comb. nov.; *M. welwitschii* (Bak.) Schrire comb. nov.

Indigastrum Jaub. & Spach

Indigastrum costatum (Guill. & Perr.) Schrire comb. nov.;
Indigastrum crotalarioides (Klotzsch) Schrire comb. nov.;
Indigastrum parviflorum (Heyne ex Wight & Arn.) Schrire comb. nov.;
Indigastrum guerranum (Torre) Schrire comb. nov.

Indigofera L.

1) Section *Psiloceratae* (Gillett) Schrire

I. baumiana Harms; *I. dekindtii* Tisserant; *I. fulgens* Bak.; *I. gloriosa* Cronquist; *I. heterocarpa* Welw. ex Bak.; *I. longiflora* Taub.; *I. longimucronata* Bak.f.; *I. lyallii* Bak.; *I. macrantha* Harms; *I. malongensis* Cronquist; *I. paucistrigosa* Gillett; *I. roseo-caerulea* Bak.f.; *I. sokotrana* Vierh.; *I. sutherlandoides* Welw. ex Bak.

2) Section *Tinctoriae* (Wight & Arn.) Schrire

I. amorphoides Jaub. & Spach; *I. arrecta* Hochst. ex A. Rich.; *I. articulata* Gouan; *I. binderi* Kotschy; *I. bogdanii* Gillett; *I. cavallii* Chiov.; *I. ciferrii* Chiov.; *I. coerulea* Roxb.; *I. corallinosperma* Torre; *I. cryptantha* Benth. ex Harv.; *I. emarginella* Steud. ex A. Rich.; *I. emarginelloides* Gillett; *I. garckeana* Vatke; *I. homblei* Bak.f. & Martin; *I. longiracemosa* Boiv. ex Baill.; *I. macrophylla* Schum.; *I. nambalensis* Harms; *I. ormocarpoides* Bak.; *I. peltata* Gillett; *I. pobeguini* Gillett; *I. podocarpa* Bak.f. & Martin; *I. repens* Cronquist; *I. rhynchocarpa* Welw. ex Bak.; *I. sedgewickiana* Vatke; *I. sparteola* Chiov.; *I.*

subcorymbosa Bak.; *I. suffruticosa* Mill.; *I. swaziensis* H. Bol.;
I. tetraptera Taub.; *I. tinctoria* L.

3) Section *Subulatae* Schrire

I. boranica Thulin; *I. cliffordiana* Gillett; *I. lupatana* Bak.f.;
I. marmorata Balf.f.; *I. omissa* Gillett; *I. spiniflora* Hochst. &
 Steud. ex Boiss.; *I. strigulosa* Bak.f.; *I. trita* L.f.

4) Section *Hedyanthae* Schrire

I. inyangana N.E.Br.; *I. tristoides* N.E.Br.; *I. goetzei* Harms

5) Section *Dendroides* Schrire

I. dendroides Jacq.; *I. filipes* Benth. ex Harv.; *I. zeyheri*
 Spreng. ex Eckl. & Zeyh.

6) Section *Hirsutae* (Rydberg) Schrire

I. astragalina DC.; *I. deightonii* Gillett; *I. hirsuta* L.; *I.*
longebarbata Engl.

7) Section *Setiflorae* Schrire

I. cecilii N.E.Br.; *I. melanadenia* Benth. ex Harv.; *I. setiflora*
 Bak.; *I. sebungweensis* Gillett; *I. williamsonii* (Harv.) N.E.Br.

8) Section *Stenophyllae* (Bak.) Schrire

I. andrewsiana Gillett; *I. lepreurii* Bak.f.; *I. prioureana*
 Guill. & Perr.; *I. stenophylla* Guill. & Perr.

9) Section *Brevierectae* (Gillett) Schrire

I. breviracemosa Torre; *I. mildbraediana* Gillett; *I. simplicifolia* Lam.; *I. tetrasperma* Vahl. ex Pers.

10) Section *Atratae* (Gillett) Schrire

I. atricephala Gillett; *I. atriceps* Hook.f.; *I. dasyantha* Bak.f.; *I. fuscosetosa* Bak.; *I. glaucifolia* Cronquist; *I. mooneyi* Thulin; *I. nyassica* Gilli; *I. paraglaucifolia* Torre; *I. schliebenii* Harms; *I. trachyphylla* Oliver; *I. ufipaensis* Gillett

11) Section *Viscosae* (Rydberg) Schrire

I. adenoides Bak.f.; *I. argentea* Burm.f.; *I. bangweolensis* R.E.Fries; *I. barteri* Hutch. & Dalziel; *I. asterocalycina* Gilli; *I. brachynema* Gillett; *I. brevifilamenta* Gillett; *I. breviviscosa* Gillett; *I. colutea* (Burm.f.) Merr.; *I. conferta* Gillett; *I. curvata* Gillett; *I. delagoaensis* Bak.f. ex Gillett; *I. dembianensis* (Chiov.) Gillett; *I. dolichothyrsa* Bak.f.; *I. dyeri* Britten; *I. heterotricha* DC.; *I. hewittii* Bak.f.; *I. livingstoniana* Gillett; *I. lydenburgensis* N.E.Br.; *I. masaiensis* Gillett; *I. mendesii* Torre; *I. mildrediana* Torre; *I. milne-redheadii* Gillett; *I. mimosoides* Bak.; *I. secundiflora* Poir.; *I. sordida* Benth. ex Harv.; *I. subargentea* De Wild.; *I. subulifera* Welw. ex Bak.; *I. viscidissima* Bak.; *I. wildiana* Gillett; *I. zenkeri* Bak.f.

Subsection *Centrae* Gillett

I. quarrei Cronquist; *I. ugandensis* Bak.f.

12) Section *Hilares* Schrire

I. griseoides Harms; *I. hilaris* Eckl. & Zeyh.; *I. microcalyx* Bak.; *I. mupensis* Torre; *I. patula* Bak.; *I. ramosissima* Gillett; *I. smutsii* Gillett

13) Section *Spinosa* (Bak.) Schrire

I. basiflora Gillett; *I. rothii* Bak.; *I. spinosa* Forssk.

14) Section *Podophyllae* Schrire

I. podophylla Benth. ex Harv.

15) Section *Brevipatentes* (Gillett) Schrire

I. desertorum Torre; *I. huillensis* Bak.f.; *I. malindiensis* Gillett; *I. pseudointricata* Gillett; *I. ogadensis* Gillett; *I. ruspolii* Bak.f.; *I. santosii* Torre; *I. suaveolens* Jaub. & Spach; *I. tanaensis* Gillett

16) Section *Pilosae* (Gillett) Schrire

I. biglandulosa Gillett; *I. erythrogramma* Welw. ex Bak.; *I. fulvopilosa* Brenan; *I. graniticola* Gillett; *I. hermannioides* Gillett; *I. pilosa* Poir.; *I. kirkii* Oliver; *I. nummularia* Welw. ex Bak.; *I. petiolata* Cronquist; *I. taylori* Gillett; *I. thikaensis* Gillett; *I. torrei* Gillett

17) Section *Dissitiflorae* (Wight & Arn.) Schrire

I. ambelacensis Schweinf.; *I. brevicalyx* Bak.f.; *I. congolensis* De Wild. & T.Durand; *I. cuneata* Bak. ex Oliver; *I. dissitiflora* Bak. ex Oliver; *I. elliottii* (Bak.f.) Gillett; *I. elwakensis* Gillett; *I. eremophila* Thulin; *I. geminata* Bak.; *I. heudelotii* Benth. ex Bak.; *I. kongwaensis* Gillett; *I. manyoniensis* Bak.f.; *I. mendoncae* Gillett; *I. micropetala* Bak.f.; *I. monantha* Bak.f.; *I. monanthoides* Gillett; *I. mwanzae* Gillett; *I. nairobiensis* Bak.f.; *I. omariana* Gillett; *I. pellucida* nom. nud.; *I. scarriesii* Scott Elliot; *I. sparsa* Bak.; *I. tanganyikensis* Bak.f.; *I. tenuis* Milne-Redhead; *I. vohemarensis* Baill.; *I. wituensis* Bak.f.; *I. zavattarii* Chiov.

18) Section *Laxeracemosae* Schrire

I. laxeracemosa Bak.f.; *I. longipedicellata* Gillett; *I. phyllanthoides* Bak.; *I. vicioides* Jaub. & Spach;

19) Section *Latestipulatae* (Bak.f.) Gillett

I. arenophila Schinz; *I. berhautiana* Gillett; *I. burttii* Bak.f.; *I. eylesiana* Gillett; *I. faulknerae* Gillett; *I. gairdnerae* Hutch. ex Bak.f.; *I. inhambanensis* Klotzsch; *I. ischnoclada* Harms; *I. kavangoensis* Schrire nom. nov.; *I. kuntzei* Harms; *I. strobilifera* (Hochst.) Hochst. ex Bak.; *I. taborensis* Gillett

20) Section *Paniculatae* (Bak.) Gillett

I. bracteolata DC.; *I. brassii* Bak.; *I. capitata* Kotschy; *I. congesta* Welw. ex Bak.; *I. dasycephala* Bak.f.; *I. leptoclada* Harms; *I. lotononoides* Bak.f.; *I. megacephala* Gillett; *I. nigricans* Vahl ex Pers.; *I. oubanguiensis* Tisserant; *I. paniculata* Vahl ex Pers.; *I. paracapitata* Gillett; *I. polysphaera*

Bak.; *I. pulchra* Willd.; *I. trialata* Chev.; *I. vanderystii*
 Gillett

Subsection *Trichopodae* (Bak.) Gillett

I. latisepala Gillett; *I. nigritana* Hook.f.; *I. trichopoda*
 Leprieur ex Guill. & Perr.

21) Section *Terminales* (Bak.f.) Schrire

I. macrocalyx Guill. & Perr.; *I. terminalis* Bak.

22) Section *Microcarpae* (Rydberg) Schrire

I. microcarpa Desv.

23) Section *Acanthonotus* (Benth.) Taub.

I. cuitoensis Bak.f.; *I. drepanocarpa* Taub.; *I. exellii* Torre; *I.*
nummulariifolia (L.) Livera ex Alston; *I. zanzibarica* Gillett

24) Section *Ameocarpus* (Benth. ex Harv.) Taub.

I. arabica Jaub. & Spach; *I. aspera* Perr. ex DC.; *I. charlieriana*
 Schinz; *I. chirensis* Cufod.; *I. circinnata* Benth. ex Harv.; *I.*
dauensis Gillett; *I. fanshawei* Gillett; *I. hochstetteri* Bak.; *I.*
holubii N.E.Br.; *I. kelleri* Bak.f.; *I. lasiantha* Desv.; *I.*
letestui Tisserant; *I. oligophylla* Klotzsch; *I. practicola*
 Bak.f.; *I. rhytidocarpa* Benth. ex Harv.; *I. senegalensis* Lam.; *I.*
sisalis Gillett

25) Section *Demissae* Gillett

I. bussei Gillett; *I. concinna* Bak.; *I. demissa* Taub.

26) Section *Sphaeridiophora* (Desv.) Taub.

I. cordifolia Heyne ex Roth.; *I. diphylla* Vent.; *I. flavicans* Bak.; *I. linifolia* (L.f.) Retz.; *I. nephrocarpa* Balf.f.; *I. sessiliflora* DC.; *I. trigonelloides* Jaub. & Spach

27) Section *Simplices-reflexae* (Gillett) Schrire

I. achyranthoides Taub.; *I. bongensis* Kotschy & Peyr.; *I. hundertii* Rossberg; *I. knoblecheri* Kotschy; *I. pseudosubulata* Bak.f.; *I. thomsonii* Bak.f.

28) Section *Conjugatae* (Bak.) Schrire

I. antunesiana Harms; *I. chevalieri* Tisserant; *I. conjugata* Bak.

29) Section *Alternifoliolae* (Harv.) Schrire

I. alternans DC.; *I. benguellensis* Bak.; *I. circinella* Bak.f.; *I. cunenensis* Torre; *I. daleoides* Benth. ex Harv.; *I. insularis* Chiov.; *I. kerstingii* Harms; *I. maritima* Bak.; *I. oblongifolia* Forssk.; *I. oxalidea* Welw. ex Bak.; *I. paraoxalidea* Torre; *I. phillipsiae* Bak.f.; *I. platyspina* nom. nud.; *I. radCIFera* Cronquist; *I. schimperii* Jaub. & Spach; *I. semitrijuga* Forssk.; *I. sesquijuga* Chiov.; *I. spicata* Forssk.; *I. taruffiana* Torre; *I. teixeirae* Torre; *I. viridiflora* Chiov.; *I. volkensii* Taub.

8.2. Synopsis of southern African Indigoferaeae

No overall revision of *Indigofera* has ever been attempted for the area covered by the Flora of Southern Africa.

The first important treatments of South African species were by Thunberg (1800, 1823), Ecklon & Zeyher (1836) and E.Meyer (1836), but Harvey (1862), in *Flora Capensis*, provided the first major revision of species in the Cape and Natal colonies. Most, but not all, the earlier published names were considered, and Harvey described many new species often using Bentham's manuscript names. The only other work on Cape species was Adamson & Salter (1950) for the Cape Peninsula.

Treatments including species from the summer rainfall region of South Africa were Baker (1871) and Baker f. (1903, 1926).

N.E.Brown (1925, 1932) revised *Indigofera* for the Transvaal, Schreiber (1970) for Namibia, and Compton (1976) for Swaziland.

In the following synopsis species are listed alphabetically in genera and sections.

8.2.1. *Cyamopsis*

Cyamopsis senegalensis Guill. & Perr., Fl. Seneg. Tent. :171, t.45 (1832); Bak., Fl. Trop. Afr. 2 :65 (1871); Bak.f., Leg. Trop. Afr. 1 :94 (1926); Hepper in Fl. W. Trop. Afr. ed. 2, 1 :543 (1958); Gillett, Kew Bull., Add. Ser. 1 :7 (1958); Schreiber in Prodr. Fl. SWA 60 :29 (1970); Gillett in Fl. Trop. E. Afr., Legum.- Papil. 1 :328 t.48 (1971); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :139 (1989). Type: Senegal, Perrottet s.n. (P, holo.).

Cyamopsis serrata Schinz, Abh. Bot. Ver. Brand. 30 :161 (1888); Bak.f., Leg. Trop. Afr. 1 :95 (1926); Gillett, Kew Bull., Add. Ser. 1 :7 (1958); Schreiber in Prodr. Fl. SWA 60 :29 (1970). Type: Namibia, Amboland, Oshiheke, Schinz s.n. (Z, holo.!).

Indigofera psammotropa Bolus, Journ. Bot. 34 :22 (1896).

Type: Cape, Hopetown distr., Muskett s.n. (BOL, holo.!).

Intermediate forms between the above species have been described as *Cyamopsis dentata* (N.E.Br.) Torre in Mem. Junta Invest. Ultram. ser. 2, 19 :49 (1960). *Indigofera dentata* N.E.Br. in Kew Bull. 1909 :102 (1909). Type: Botswana, Kwebe hills, 3400', 26.1.1898, Lugard 128 (K, lecto.!).

8.2.2.

Microcharis Benth.

Microcharis annua (Milne-Redhead) Schrire comb. nov. *Indigofera annua* Milne-Redhead in Kew Bull. 1936 :470 (1936); Gillett, Kew Bull., Add. Ser. 1 :133 (1958). Type: Zimbabwe, Wankie, April 1932, Levy 36 (PRE, holo.!.; SRGH).

Microcharis disjuncta (Gillett) Schrire comb. nov. *Indigofera disjuncta* Gillett in Kew Bull., 1955 :584 (1956); Kew Bull., Add. Ser. 1 :132 (1958); Schreiber in Prodr. Fl. SWA 60 :55 (1970). *I. acutifolia* Schinz in Abh. Bot. Ver. Brand. 30 :163 (1888) non Schlecht (1838). Type: Namibia, Kusib, 24.4.1885, H. Schinz 245 (Z, holo.!).

Microcharis galpinii N.E.Br. in Kew Bull. 1897 :258 (1897); in Burt Davy, Man. Fl. Transv. 2 :375 (1932). Type: Transvaal, nr. Barberton, summit of Saddleback Mtn., 5000', 8.3.1891. Galpin 1315 (K, holo.!.; GRA; PRE).

Indigofera pseudo-indigofera (Merxm.) Gillett, Kew Bull, Add. Ser. 1 :132 (1958). *Microcharis pseudo-indigofera* Merxm., Tr. Rhod. Sci. Ass. 43 :22 (1951). Type: Zimbabwe, Marandellas Distr., Dehn 627 (M, holo.!).

Indigofera graminea Schltr. nom. nud.

Microcharis latifolia Benth. in Trans. Linn. Soc. 25 :298 t.33 B (1865); Bak.f., Leg. Trop. Afr. :256 (1926). *Indigofera lobata*

Gillett, Kew Bull., Add. Ser. 1 :131 (1958); in Fl. Trop. E. Afr., Legum.- Papil. 1 :322 (1971). Type: Mozambique, Luabo, mouth of Zambezi, Kirk (K, holo.).

8.2.3. *Indigastrum* Jaub. & Spach

8.2.3.1. Subgenus *Indigastrum*

Indigastrum burkeanum (Benth. ex Harv.) Schrire *comb. nov.*
Indigofera burkeana Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :197 (1862); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :373 (1932); Dyer in Fl. Pl. Afr. 24, t.939 (1944); Gillett, Kew Bull., Add. Ser. 1 :125 (1958); Schreiber in Prodr. Fl. SWA 60 :52 (1970). Type: Transvaal, Magaliesberg, Dec., Zeyher 476 (K, lecto.!!; S; TCD).

Indigofera affinis Harv. in Harv. & Sond., Fl. Cap. 2 :184 (1862) *non* De Wild., Bull. J. Bot. Et. Brux. 8 :144 (1923). Type: Botswana, Lake Ngami, J. McCabe *s.n.* (K, holo.!).

Indigofera goniodes var. *damarensis* Bak.f., Leg. Trop. Afr. 1 :163 (1926). Type: Namibia, Een *s.n.* (BM, holo.).

Indigastrum costatum (Guill. & Perr.) Schrire *comb. nov.*
Indigofera costata Guill. & Perr., Fl. Seneg. :187 (1832); Bak.f., Leg. Trop. Afr. 1 :163 (1926); Gillett, Kew Bull., Add. Ser. 1 :125 (1958); in Fl. Trop. E. Afr., Legum.- Papil. 1 :320 (1971); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :137 (1989). Type: Senegal, near mouth of Senegal, Ghiandoum, Perrottet *s.n.* (P, holo.!!; BM).

subsp. *macrum* (E. Mey.) Gillett, Kew Bull., Add. Ser. 1 :125 (1958); Schreiber in Prodr. Fl. SWA 60 :53 (1970). *Indigofera macra* E. Mey., Comm. :105 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :197 (1862); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :373 (1932). Type: Cape, ad ripas fluvii Basche, 500' (V, b), 26.1.32, Drege 5419 (P, lecto.!).

Indigofera macra E. Mey. var. *aequalis* N.E.Br. in Burtt Davy, Man. Fl. Transv. 1 :44 (1926). Type: Transvaal, Zoutpansberg, Messina, Moss & Rogers 131 (K, holo.!).

var. *occidentalis* Gillett, Kew Bull. 1955 :582 (1956); Kew Bull., Add. Ser. 1 :178 (1958). Type: Senegal, Leprieur s.n. (P, holo.; BM).

Indigastrum fastigiatum (E. Mey.) Schrire comb. nov.. *Indigofera fastigiata* E. Mey., Comm. :102 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :183 (1862); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :373 (1932); Gillett, Kew Bull., Add. Ser. 1 :124 (1958). Type: Cape, inter Omsamwubo et Omsamcaba, 1200' (V, b), 2.32, Drege 5433 (P, lecto,!).

Indigofera fastigiata E. Mey. var. *angustata* Harv. in Harv. & Sond., Fl. Cap. 2 :183 (1862). Type: Cape, Zwartkops R., Zeyher 2442 (S, lecto.!).

Indigofera rostrata Conrath in Kew Bull. 1908 :223 (1908). non H. Bol. in Journ. Bot. 34 :23 (1896). Type: Transvaal, Modderfontein, 1898, P. Conrath 1196 (K, holo.!).

Indigastrum parviflorum (Heyne ex Wight & Arn.) Schrire comb. nov. *Indigofera parviflora* Heyne ex Wight & Arn., Prodr. Fl. Pen. Ind. Or. :201 (1834); Harv. in Harv. & Sond., Fl. Cap. 2 :198 (1862); Bak., Fl. Trop. Afr. 2 :83 (1871); Bak.f., Leg. Trop. Afr. 1 :162 (1926); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :367 (1932); Gillett, Kew Bull., Add. Ser. 1 :126 (1958); Schreiber in Prodr. Fl. SWA 60 :60 (1970); Gillett in Fl. Trop. E. Afr., Legum.- Papil. 1 :321 (1971); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :137 (1989). Type: India, in herbarium Wallich no. 5457, Heyne s.n. (K, holo.!).

var. *parviflorum*

Indigastrum deflexum (Hochst. ex A. Rich.) Jaub. & Spach., Ill. Pl. Or. 5, t.492 (1857). *Indigofera deflexa* Hochst. ex

A. Rich., Tent. Fl. Ab. 1 :178 (1847). Type: Ethiopia, in declivitate montium versus fluvium Tacaze prope Dscheladscheranne, 14.9.1840, *W. Schimper 1467* (P, lecto.!!; G; K; S; UPS).

B.2.3.2. Subgenus *Argyraeae* Schrire

Indigastrum argyraeum (Eckl. & Zeyh.) Schrire *comb. nov.*

Indigofera argyraea Eckl. & Zeyh., Enum. :239 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :201 (1862); Schreiber in Prodr. Fl. SWA 60 :50 (1970). Type: Cape, in locis saxosis (altit. III) laterum montium prope "Silo" ad flumen "Klipplaatrivier" tum ad "Zwartekeyrivier" (Tambukiland), Jan. - Mart., *Ecklon & Zeyher 1595* (S, lecto.!!).

Indigofera collina Eckl. & Zeyh., Enum. :239 (1836). Type: Cape, in petrosis (altit. II) collium continuorum inter flumina "Konab et Katrivier" (Ceded Territory), Fr. Jul., *Ecklon & Zeyher 1596* (S, lecto.!!).

Indigofera burchellii E. Mey. var. *paucifolia* E. Mey., Comm. :106 (1836) non DC. Type: Cape, prope Zwartbulletjie in collibus, alt. 2500' (II, d), 6.3.27, *Drege 6689* (P, lecto.!!).

I. burchellii E. Mey. var. *multifolia* E. Mey., Comm. :106 (1836) non DC. Type: Cape, in rupestribus siccis ad Groot Vischrivier, alt. 300' (V, a), 20.6.32, *Drege 3802* (P, lecto.!!).

Anila argyraea (Eckl. & Zeyh.) O. Kuntze, Rev. Gen. 3(2) :50 (1898). Type: OFS, Bloemfontein, 1560m, 15.2.1894, *O. Kuntze s.n.* (K, iso.!!).

Indigofera pseudoalternans Dinter *nom. nud.*

Indigastrum argyroides (E. Mey.) Schrire *comb. nov.* *Indigofera argyroides* E. Mey., *Comm.* :106 (1836); Harv. in Harv. & Sond., *Fl. Cap.* 2 :191 (1862); Gillett, *Kew Bull.*, *Add. Ser.* 1 :126 (1958); Schreiber in *Prodr. Fl. SWA* 60 :51 (1970). Type: Cape, ad ripas limosas fluvii Garip, 200' (III, B), 16.9.30, *Drege* 3313 (P, lecto.!).

Indigofera saxicola Engl., *Engl. Bot. Jahrb.* 10 :28 (1888) non F. Muell. (1864). *I. engleri* Bak.f. in *Journ Bot.* 41 :194 (1903); Leg. *Trop. Afr.* 1 :105 (1926). Type: Namibia, lower Swakop River, 250m, *Marloth* 1209 (SAM, lecto.!).

Indigastrum candidissimum (Dinter) Schrire *comb. nov.* *Indigofera candidissima* Dinter in *Feddes Repert.* 18 :428 (1922); in *Feddes Repert.* 30 :198 (1932); Schreiber in *Prodr. Fl. SWA* 60 :52 (1970). Type: Namibia, Rehoboth, Buellspoort, 26.3.48, *R.G. Strey* 2308 (PRE, neo.!.; NBG). The type from Kegelberg, 4.4.1911, *Dinter* 2107, was destroyed in Berlin.

Indigastrum guerranum (Torre) Schrire *comb. nov.* *Indigofera guerrana* Torre in *Mem. Junta Invest. Ultram. ser.* 2, 19 :61 t.39 (1960); Schreiber in *Prodr. Fl. SWA* 60 :57 (1970). Type: Angola, Mossamedes, entre o apeadeiro do C.F.Dois Iramacs e Virei, 9.5.1957, *B. Teixeira* 2249 (LISC, holo.; COI; LUA).

Indigastrum sp. nov. 1. aff. *I. guerranum* (Torre) Schrire.

Vouchers: *H.H.W. Pearson* 2287 (K); *W. Giess & H. Leippert* 7405 (PRE); 7419 (PRE).

B.2.4.

Indigofera

B.2.4.1. Section *Denudatae* Schrire

I. angustata E.Mey., *Comm.* :94 (1836). Type: Cape, Albany, in collibus asperis inter gramina, alt. 500 - 1000' (V, a), *Drege* 6667 (P, lecto.!).

I. stenophylla Eckl. & Zeyh., Enum. :171 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :170 (1862) non Guill. & Perr., Fl. Seneg. Tent. 1:188 t48 (1832) *nom. illegit.*. Type: Cape, in lapidosis (altit III) collium inter "Grahamstown et Vischrivier" et in Konabshoogde (Albany Ceded Territory) Aug, Oct., *Ecklon & Zeyher 1568* (S, lecto.!, K, SAM, TCD).

I. zeyheri Spreng. ex Eckl. & Zeyh. var. *trifoliolata* Eckl. & Zeyh., Enum. :241 (1836). Type: Cape, inter frutices (altit. 1) campestrium prope "Uitenhage". Mart. *Ecklon & Zeyher 1606b* (S, lecto!).

I. denudata L.f., Suppl. Fl. :334 (1781); Willd., Sp. Fl. 3(2):1226 (1802); Thunb., Fl. Cap. 597 (1823); Harv. in Harv. & Sond., Fl. Cap. 2:170 (1862). Type: Cape, in herbarium Thunberg 17330, mixed collection with *I. nigromontana* (UPS, lecto.!).

I. flexuosa Eckl. & Zeyh., Enum. :232 (1836). *I. denudata* var. *simplicifolia* Harv. in Harv. & Sond., Fl. Cap. 2 :171 (1862). Type: Cape, in solo ericeto (altit II) ad latera montis "Winterhoeks-berg" occidentem et orientem spectantia. (Uitenhage). Febr., *Ecklon & Zeyher 1562* (S, lecto.!, W).

I. arthropylla Eckl. & Zeyh., Enum. :232 (1836). Type: Cape, in solo ericeto (altit II) laterum montium in "Langekloof" (George). Dec., *Ecklon & Zeyher 1563* (S, lecto.!, SAM, TCD, W).

I. rechodes Eckl. & Zeyh., Enum. :233 (1836). Type: Cape, in collibus (altit II) prope sylvas primaevae in "Olifantshoek" ad flumen "Bosjesmansrivier" (Uitenhage). Oct., *Ecklon & Zeyher 1565* (S, lecto.!, SAM)

I. centrota Eckl. & Zeyh., Enum. :233 (1836). *I. denudata* var. *luxurians* Harv. in Harv. & Sond., Fl. Cap. 2:170 (1862). Type: Cape, in solo ericeto et limoso (altit II) laterum montium "Van Stadensriviersberg" (Uitenhage). Febr., *Ecklon & Zeyher 1566* (S, lecto.!, P, SAM).

I. dumosa E.Mey., Comm. :93 (1836). *I. denudata* var. *dumosa* Harv. in Harv. & Sond., Fl.Cap. 2:171 (1862). Type: no collector given (P, lecto!).

I. rigescens E.Mey. var. *inermis* E. Mey., Comm. :94 (1836).
I. denudata L.f. var. *inermis* (E. Mey.) Harv. in Harv. & Sond., Fl. Cap. 2: 170 (1862). Type: Cape, Zuurbergen, alt. 2000-3000' (V, a). Drege s.n. (P, lecto!).

I. kraussiana Meisn. in Hook., Lond. J .Bot. 2:83 (1843).
 Type: Cape, in solo argillaceo prope montes Winterhoek, Uitenhage (IV.C.c), March 1839., Krauss 845 (NY, holo.).

I. denudata L.f. var. *spinosa* sensu Harv. non E. Mey., in Harv. & Sond., Fl. Cap. 2 :170 (1862).

I. albanensis Bak.f. nom. nud. [Based on *T. Cooper* 1557 (BM, GRA, K).

I. frutescens L.f., Suppl.Pl. :334 (1781); Thunb., Prodr.Fl.Cap. :133 (1800); Fl.Cap. :598 (1823), Harv. in Harv. & Sond., Fl.Cap. 2 :192 (1862). Type: Cape, in herbarium Thunberg 17342 (UPS, lecto!).

I. cylindrica DC., Prodr. 2 :225 (1825) non auct. Type: Cape, in herbarium DC. 225:40, 1816, *M. Lambert* s.n. (G, holo!).

I. langebergensis L.Bol. in Ann. Bol. Herb., 1 :128 (1915). Type: Cape, SW-region, Langebergen, Riversdale Div., Garcia's Pass, alt 1500', fl. Oct. 1904, *Bolus* 11267 (BOL, lecto!).

I. nigromontana Eckl.& Zeyh., Enum. :233 (1836). Type: Cape, in "Karoo" ad montium latera inter "Zwartberge et Langekloof" (George). Dec., *Ecklon & Zeyher* 1564 (S, lecto!).

I. spinescens E. Mey., Comm. :93 (1836); Harv. in Harv.& Sond., Fl.Cap 2:169 (1862). Type: Cape, in montosis

rupestribus Leliefontein. 4600' (III, A, a), *Drege* 2061 (P, lecto.!).

I. dealbata Harv. in Harv. & Sond., Fl. Cap. 2:170 (1862).
Type: Cape, Wolwekop, *Zeyher* s.n. (K, holo.!, TCD).

I. rigescens E.Mey. var. *spinosa* E. Mey., Comm. :94 (1836).
Type: Cape, in *rupestribus* prope Zilverfontein 2000' (III, B), *Drege* 2063 (P, lecto.!).

I. sp. nov. 1. Vouchers: *P. Bond* 315 (NBG); *G. van Niekerk* 755 (BOL); *Taylor* 365 (BOL). Montagu district, Cape.

I. sp. nov. 2. "*I. salteri* Bak.f." *nom. nud.* Vouchers: *E.E. Galpin* 12889 (K, PRE); *Salter* 395/11 (K); *Schlechter* 8063 (G, GRA, K); *Salter* 1000 (BOL); *Salter* 2597 (BOL, K); *Schrire* 2490 (K). Klaver district, Namaqualand, Cape.

I. sp. nov. 3. Vouchers: *H. Bolus* 9641 (BOL, K); *Oliver, Toelken & Venter* 205 (PRE); *Oliver, Toelken & Venter* 603 (PRE); *Schrire* 2483 (K); *Jurgens* s.n. (PRE). Richtersveld region, NW Cape.

8.2.4.2. Section *Cuneifoliae* Schrire

I. cuneifolia Eckl. & Zeyh., Enum. :234 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :177 (1862). Type: Cape, inter frutices (altit. IV) laterum montis "Winterberg" prope "Philipstown" (Ceded Territory), Oct., *Ecklon & Zeyher* 1570 (S, lecto.!, K; SAM).

I. florida E. Mey., Comm. :96 (1836). Type: Cape, Katberg, in *rupestribus*, alt. 4600', (I, a), 13.11.32. *Drege* 6668 (P, lecto.!).

I. cuneifolia Eckl. & Zeyh. var. *angustifolia* Harv. in Harv. & Sond., Fl. Cap. 2 :177 (1862). Type: Cape, Grahamstown, along the rivulet, Burchell 3544 (K, lecto!).

I. monostachya Eckl. & Zeyh., Enum. :237 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :177 (1862). Type: Cape, in collibus graminosis (altit. III, IV) prope "Philipstown" (Ceded Territory). Oct., Ecklon & Zeyher 1583 (S, lecto!; K; SAM; TCD).

I. oroboides E. Mey., Comm. :94 (1836). Type: Cape, Katberg, in campsis graminosis igne combustis, alt. 3000 - 4000' (I, a), 9.11.32, Drege 3803 (P, lecto!).

I. sp. nov. 1. "*I. amatolensis* Phillipson" *nom. nud.* Vouchers: R. Story 3669 (BM, K); J.L. Sidey 3757 (K); T.R. Sim 19474 (PRE); Phillipson 427 (K); Hilliard & Burt 18886 (PRE); Schrire 2517 (K). Amatole mountains, E. Cape.

I. sp. nov. 2. Vouchers: H.T Scharf 1497 (PRE); 1579 (PRE); Macowen 32/P.M.6 (K); H.G. Fourcade 1682 (K); 2811 (K); Esterhuysen 6903 (BOL, K); 27303 (K). E. Cape, Winterhoek mountains to Kareedouw.

B.2.4.3. Section *Stipulatae* Schrire

I. alpina Eckl. & Zeyh., Enum. :236 (1836); Hilliard & Burt in Notes R. Bot. Gard. Edinb. 43 :207 (1986). Type: Cape, ad latera montis "Katriviersberg" (altit. V) supra sylvas (Kafferland). Oct., Ecklon & Zeyher 1581 (S, lecto!).

I. stipularis Link., Enum. 2 :250 (1822); Harv. in Harv. & Sond., Fl. Cap. 2 :177 (1862). Type: Cape, Bergius s.n. specimen destroyed in Berlin. Hilliard & Burt (1986) recommended abandoning this name in favour of *I. alpina*.

I. dimidiata Vogel ex Walp. in *Linnaea* 13 :523 (1839); Harv. in Harv. & Sond., Fl. Cap. 2: 176 (1862). Type: Cape, Clydesdale, moist grassy slopes, alt. 2500', 9.1885, *W. Tyson* 2588 (K, neo.!!; BOL; PRE). The original Vogel material has not been traced, and is presumed to have been destroyed in Berlin.

I. stipularis sensu Eckl. & Zeyh., Enum. :237 (1836) non Link. Type: Cape, in locis apertis et graminosis (altit. IV) inter sylvas laterum montis "Winterberg" haud procul a "Philipstown" (Ceded Territory). Oct., *Ecklon & Zeyher* 1582 (S, lecto.!).

I. dimidiata Vogel ex Walp. var. *laxior* Bak.f. in *J. Bot.* 58 :76 (1920). Type: Transvaal, Kaapshehoop, Barberton Div., Mar. 1918, *F.A. Rogers* 21076 (BM, holo.!!; K).

I. evansii Schltr. in *J. Bot.* 35 :429 (1897); Hilliard & Burtt in *Notes R. Bot. Gard. Edinb.* 43 :207 (1986). Type: Natal, Garden Castle Forest Reserve, Pillar Cave valley, alt. 6700', 5.11.1977, *Hilliard & Burtt* 10434 (E, neo.!!; K; NU; PRE). The original holotype, *Evans* 636 from Polela in Natal, was destroyed in Berlin.

I. mollis Eckl. & Zeyh., Enum. :237 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :176 (1862). Type: Cape, in locis gramine vestitis (altit V, VI) montis "Katriviersberg" supra sylvas (Kafferland) Fruct. Mart., *Ecklon & Zeyher* 1586 (S, lecto.!!; SAM).

I. mollis E. Mey., Comm. :96 (1836). Type: Locality uncertain (V, b), *Drege* 3800 (P, lecto.!).

I. pseudoevansii Hilliard & Burtt in *Notes R. Bot. Gard. Edinb.* 43 :208 (1986). Type: Natal, Mpendhle distr. 2929 AD, upper Loteni valley above Ash Cave, c1980m, 7.2.1985, *Hilliard & Burtt* 18189 (E, holo.!!; NU; PRE).

I. trifolioides Bak.f. in Rec. Albany Mus. 1 :279 (1905). Type: Transkei, Nqamakwe, 3227 BB, c3000', 12.1892, Rennie 388 (GRA, holo.).

I. corallina Hilliard & Burttt *nom. nud.*

I. sp. nov. 1. Vouchers: Hilliard & Burttt 10951 (NU, K); Phillipson 404 (K, PRE); Esterhuysen 13255 (BOL); Schrire 2520 (K). E. Cape, Hogsback area.

8.2.4.4. Section *Trifoliolatae* (E. Mey.) Schrire

I. amoena Ait., Hort. Kew 3 :68 (1789); Jacq., Hort. Schoenb. 2: 57 t.234 (1797); Willd., Sp. Pl. 3(2) :1224 (1802); Harv. in Harv. & Sond., Fl. Cap. 2 :191 (1862) *non* E. Mey. in Linnaea 7 :167 (1832) *nec* in Comm. :106 (1836). Type: Cape, hort. Kew 1782, Masson s.n. (BM, lecto.!, K).

I. bicolor (Harv.) Schrire *stat. nov.* *I. porrecta* Eckl. & Zeyh. var. *bicolor* Harv., in Harv. & Sond., Fl. Cap. 2 :174 (1862). Type: Cape, Algoa Bay, 1822, Forbes (K, lecto.!).

I. burchellii DC., Prodr. 2 :231 (1825). Type: Cape, mountains on the SW side of Graaf Reinet, 1.5.1813, Burchell 2918 (G-DC, holo.!, K).

I. bifrons E. Mey., Comm. :97 (1836) excluding var. *trifoliata* E. Mey. Comm. :97 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :179 (1862). *I. bifrons* E.Mey. var. *digitata* E. Mey., Comm. :97 (1836). Type: Cape, ad montes prope Graaf Reinet, 3000' (II, b), Drege s.n. (P, lecto.!).

I. candicans Ait., Hort. Kew 3 :67 (1789); in Curtis, Bot. Mag. 5 :198 (1792); Willd., Sp. Pl. 3(2) :1224 (1802); Harv. in Harv. & Sond., Fl. Cap. 2 :172 (1862). Type: Cape, hort. Kew 1774, Masson s.n. (BM, lecto.!, K).

I. complicata Eckl. & Zeyh., Enum. :235 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :172 (1862). Type: Cape, inter frutices (altit. II) collium Karoo similium ad flumen "Gauritzrivier" (Swellendam). Dec., *Ecklon & Zeyher 1577* (S, lecto.), TCD).

I. digitata L.f., Suppl.Pl. :335 (1781); Thunb., Prodr. Pl. Cap. :133 (1800); Fl. Cap. :598 (1823); Harv. in Harv. & Sond., Fl. Cap. 2 :179 (1862). Type: Cape, in herbarium *Thunberg 17332* (UPS, lecto.).

I. erecta Thunb., Prodr. Pl. Cap. :133 (1800); Fl. Cap. 597 (1823). Type: Cape, in herbarium *Thunberg 17337* (UPS, lecto.).

I. duthiei Bak.f. nom. nud.

I. gracilis Spreng., Syst. Veg. 4, Cur. Post. :285 (1827); Harv. in Harv. & Sond., Fl. Cap. 2 :173 - 174 (1862). *Lotus microphyllus* Hook., Bot. Mag. 55 : t.2808 (1828). Type: Cape, unknown collector (Bot. Mag. 55 : t. 2808, neo.). The original material in Sprengels herbarium was destroyed in Berlin.

I. erecta Eckl. & Zeyh., Enum. :238 (1836) non Thunb., Prodr. Pl. Cap. :133 (1800). Type: Cape, in arenoso-limoso (altit. III) laterum montium "Hottentottshollandsberge" prope J. Brinkii villam (Stellenbosch.) Jul., *Ecklon & Zeyher 1588* (S, lecto.).

I. setacea E. Mey., Comm. :95 (1836). Type: Cape, Paarlberg, inter gramina et fruticulos, 1200 - 2000' (III, A, e), *Drege 1373* (P, lecto.).

I. hantamensis Diels in Engl., Bot. Jahrb. 44 :120 (1909). Type: Cape, top of Keiskie Pass, 11.7 miles from Calvinia, 13. 6. 1955, *D.M. Commins 1177* (K, neo.), GRA, PRE). The original holotype, *Diels 736* from the Hantams-berge, was obviously destroyed in Berlin.

I. heterophylla Thunb., Prodr. Fl. Cap. :133 (1800); Fl. Cap. :597 (1823); Harv. in Harv. & Sond., Fl. Cap. 2 :172 (1862). Type: Cape; in herbarium Thunberg 17345 (UPS, lecto.!).

I. adscendens Eckl. & Zeyh., Enum. :236 (1836). Type: Cape, in collibus Karoo similibus (altit II, III) inter Hassaquaaskloof et Breederivier (Swellendam) Sept., Ecklon & Zeyher 1578 (S, lecto.!, MEL, SAM).

I. porrecta Eckl. & Zeyh. var. *montana* Eckl. & Zeyh., Enum. :235 (1836). Type: Cape, ad montium radices (altit II) prope flumen "Klynrivier" (Caledon). Sept., Ecklon & Zeyher 1572b (S, lecto.!, BOL, GRA).

I. porrecta Eckl. & Zeyh. var. *tulbaghensis* Bak.f. in Viertel. Nat. Ges. Zurich 49 :189 (1904). Type: Cape, Tulbagh, Drakenstein, A. Rehmann 2228 (Z, holo.!, BM).

I. incana Thunb., Prodr. Fl. Cap :132 (1800); Willd., Sp. Pl. 3(2) :1224 (1802); Thunb., Fl. Cap. :595 (1823); Harv. in Harv. & Sond., Fl. Cap. 2 :175 (1862). Type: Cape, in herbarium Thunberg 17348 (UPS, lecto.!).

I. intermedia Harv. in Harv. & Sond., Fl. Cap. 2 :190 (1862). *I. amoena* sensu E.Mey., Comm. :106 (1836) non Ait. nec. sensu E.Mey. in Linnaea 7 :167 (1832). Type: Cape, Ebenezer mission, Van Rhynsdorp Div., 200' (III, E, a), Drege 6674 (P, lecto.!, K).

I. denudata sensu Jacq., Hort. Schoenb. 2 :57 t.233 (1797) non L.f. Type: Cape, unknown collector in herbarium Jacquin (W, lecto.!).

I. limosa L. Bol. in Ann. S.Afr. Mus. 9(4) :255, t.VII (1915). Type: Cape, Kamiesberg, among grasses in marshy ground south west of Leliefontein, 17.1.11, 5000', Pearson 6325 (BOL, holo.!, K).

I. merxmuelleri Schreiber in Mitt. Bot. Munchen 8 :142 t.3 (1970); in Prodr. Fl. SWA 60:59 (1970). Type: Namibia, Luderitz-south, Schwarz-kalkrand, 6 miles N. of the police station at Witputz, 2.9.1963, *Merxmuellet & Giess 3445* (M, holo.; K!, PRE!, WIND).

I. meyeriana Eckl. & Zeyh., Enum. :235 (1836). *I. amoena* sensu E. Mey. in Linnaea 7 :167 (1832) *non* Ait. *nec.* sensu E. Mey., Comm. :106 (1836). Type: Cape, in Karoo prope Nieuweveld (Beaufort). Oct., *Ecklon & Zeyher 1573* (S, lecto!).

I. bifrons E. Mey. var. *trifoliata* E. Mey., Comm. :97 (1836). Type: Cape, Nieuweveldsbergen, 3500-4000' (II, d), *Drege 665* (P, lecto!).

I. cardiophylla Harv., in Harv. & Sond., Fl. Cap. 2 :175 (1862). Type: Cape, Ceres Div., Yak River, 19.7.1811, *Burchell 1245* (K, holo!).

I. nudicaulis E. Mey., Comm. :92 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :169 (1862). Type: Cape, prope Verleptpram, alt. 400' (III, B), 24.9.30., *Drege 3310* (P, lecto!).

I. obcordata Eckl. & Zeyh., Enum. :232 (1836), Harv. in Harv. & Sond., Fl. Cap. 2 :169 (1862). Type: Cape, in collibus Karro similibus (altit. II) ad flumen "Gauritzrivier" (Swellendam), Mart., *Ecklon & Zeyher 1561* (S, lecto!; SAM)

I. platypoda E. Mey., Comm. :95 (1836). Type: Locality uncertain, *Drege 6693* (P, lecto!).

I. porrecta Eckl. & Zeyh., Enum. :234 (1836) excluding var. *bicolor* Harv. Type: Cape, in campestribus ad flumina "Zwartkops et Coega rivier" in Adow (Uitenhage), (altit I) Sept., *Ecklon & Zeyher 1572* (S, lecto!, SAM).

I. procumbens L., Mant. :271 (1771); Thunb., Prodr. Fl. Cap :132 (1800); Willd., Sp. Pl. 3(2) :1225 (1802); Thunb., Fl. Cap. :597 (1823); Harv. in Harv. & Sond., Fl. Cap. 2 :174 (1862). Type: Cape, in herbarium Linnaeus 923.5 (LINN, lecto.!).

I. discolor E. Mey., Comm. :97 (1836). *I. procumbens* L. var. *discolor* (E.Mey.) Harv., in Harv. & Sond., Fl. Cap. 2 :174 (1862). Type: Cape, Laauwskloof, 400' (III, D, a), 19.2.28, Drege 6673 (P, lecto.!!; K).

I. procumbens sensu E.Mey. in Linnaea 7: 166 (1832) non L. *I. procumbens* L. var. *concolor* Harv., in Harv. & Sond., Fl. Cap. 2 :174 (1862). Type: Cape, in sabulosis (altit. I) planitiei "Tigerberg et Rietvalley" (Cap.) Sept., Ecklon & Zeyher 1571 (S, lecto.!).

I. psoraloides (L.) L., Syst. Nat. 2 :496 (1767). *Cytisus psoraloides* L., Pl. Rar. Afr. no. 33 :15 (1760); Sp. Pl. 2 :1043 (1763); Amden. Acad. 6 :93 (1763). Type: Cape, in herbarium Burman (G, lecto.!).

I. complanata Reichb. ex Spreng., Syst. IV Cur. Post. 285 (1827). Type: Cape, Ecklon 423 (W, lecto.!).

I. nitida Salter in J. S.Afr. Bot. 5 :70 (1939). Type: Cape peninsula, roadsides near Constantia Nek, Salter 7854 (BOL, holo.!).

I. pungens E.Mey., Comm. :93 (1836); Harv. in Harv. & Sond., Fl. Cap. 2: 170 (1862). Type: Cape, inter rupes prope Verleptpram, 300' (III, B), Drege 3311 (P, lecto.!).

I. racemosa L., Sp. Pl. ed.2. 2 :1062 (1763); Amden. Acad. 6 no. 37 :94 (1763). Type: Cape, in herbarium Sloan, vol. 102 f. 91 (BM, neo.!).

I. psoraloides auct. non (L.) L.; Harv. in Harv. & Sond., Fl. Cap. 2 :172 (1862) as *I. psoraleoides*; Salter in Adamson & Salter, Fl. Cap. Penin. :500 (1950).

I. thesioides J.K. Jarvie & C.H. Stirton in Bothalia, 16(2) :230 (1986). Type: Cape, Meiring's Poort, Oudtshoorn Distr. 3322 BC. 20.6.1965, *Acocks* 18288 (K, holo.), BOL, PRE).

I. tomentosa Eckl. & Zeyh., Enum. :237 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :175 (1862). Type: Cape, in dunis litoris prope "Cap Recief" et ad fluminis ostium Zwartkopsrivier (Uitenhage) Jan. Feb., *Ecklon & Zeyher* 1585 (S, lecto.), SAM).

I. incana Thunb. var. *angustistipulata* Bak.f. in Rec. Albany Mus. 1 :279 (1905). Type: Cape, Port Elizabeth, *W. Kemsley* 40 (GRA, holo.).

I. triquetra E. Mey., Comm. :95 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :173 (1862). Type: Cape, Fiquetberg, alt. 1500 - 3000' (III, A, d), *Drege s.n.* (P, lecto.).

I. venusta Eckl. & Zeyh., Enum. :235 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :171 (1862). Type: Cape, in solo limoso (altit II, III) collium prope "Brakfontein" (Clanwilliam), Sept., *Ecklon & Zeyher* 1576 (S, lecto.), K, SAM, TCD).

I. sp. nov. 1. Vouchers: W.M.Crampton (H.H.W.Pearson) 7676 (BOL, K); 7700 (BOL, K); H.H.W.Pearson 5768 (BOL, K). Kamiesberg region, NW Cape.

I. sp. nov. 2. aff. *I. gracilis*. Vouchers: *Wolley Dod* 1252 (K); 2785 (BOL, K); *Harvey* 813 (K); *Salter* 7636 (BOL); *Esterhuysen* 1287 (BOL); 21705 (BOL); *Pillans* 3430 (BOL).

I. sp. nov. 3. "*I. oxytropoides* Schltr." *nom. nud.* Vouchers: Marloth 9892 (PRE); 9908 (PRE); 9891 (PRE); 9893 (PRE). Sutherland district, W. Cape, Roggeveld mountains.

I. sp. nov. 4. Voucher: D.F. Laidler 686 (PRE). S. Cape, Gankapoort Nature Reserve (3321BC).

I. sp. nov. 5. Vouchers: Esterhuysen 22156 (BOL, K); Barker 9581 (NBG); Goldblatt 7225 (NBG). NW Cape, from Gifberg plateau.

8.2.4.5. Section *Distichae* Schrire

I. disticha Eckl. & Zeyh., Enum. :245 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :197 (1862). Type: Cape, inter frutices (altit. II) laterum montis "Bothasberg" prope "Hermanuskraal" ad flumen "Vischrivier" (Albany). Fr. Jul., Ecklon & Zeyher 1623 (S, lecto!).

I. enonensis E. Mey., Comm. :105 (1836). Type: Cape, in montibus prope Enon, alt. 1000-2000', 11.11.29, Drege 6685 (P, lecto!).

I. glaucescens Eckl. & Zeyh., Enum. :242 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :189 (1862) non R.Gra. in Wall. Cat. n. 5484 *nom. nud.* Type: Cape, in collibus arenosis (altit. I) ad flumen Zwart-kopsrivier (Uitenhage). Sept., Ecklon & Zeyher 1610 (S, lecto!; G).

I. reflexa E. Mey., Comm. :100 (1836). Type: uncertain locality, Drege s.n. (P, lecto!; K). Drege specimens in S and P, from the type locality of *I. reflexa*, do not agree with the protologue, and are identified as *I. zeyheri* Spreng. ex Eckl. & Zeyh.

Anila glaucescens (Eckl. & Zeyh.) O.Kuntze, Rev. Gen. 3(2):51 (1898).

I. harveyi Schrire *nom. nov.* *I. depressa* Harv. in Harv. & Sond., Fl. Cap. 2 :175 (1862) *non* Thunb., Prodr. Pl. Cap. :132 (1800) *nom. illegit.* Type: Cape, 1840, *Mundt & Maire s.n.* (K, lecto.!).

I. leptocarpa Eckl. & Zeyh., Enum. :236 (1836); Harv. in Harv. & Sond, Fl. Cap. 2 :173 (1862). Type: Cape, in lapidosis (altit III) laterum montium prope "Elandsrivier" (Uitenhage) Fruct. Mart., *Ecklon & Zeyher 1579* (S, lecto.!!; SAM, TCD).

I. sp. nov. 1. Vouchers: *Acocks 23086* (K, PRE); *23059* (K, PRE); *Thompson 3722* (STE); *Burchell 6331* (K); *Stirton 10264* (K). S. Cape, Riversdale to Mossel Bay.

8.2.4.6. Section *Juncifoliae* (Harv.) Schrire

I. filifolia Thunb., Prodr. Pl. Cap. :132 (1800); Fl. Cap. :595 (1823); Harv. in Harv. & Sond., Fl. Cap. 2 :168 (1862); Marloth, Fl. S.Afr. 2: t.28 (1925); Jarvie & Stirton in *Bothalia* 17 :5 (1987). Type: in collibus intra Tafelberg latere orientale, in herbarium Thunberg 17338 (UPS, lecto.!).

L. contaminata sensu Ait.f., Hort Kew 4 :261 (1812) *non* Willd. *Lebeckia contaminata* sensu Ker in Bot. Reg. 2 :104 (1816) *non* Thunb. *Indigofera filifolia* Ker in Bot. Reg. 3 notes 2 (1817). *Spartium contaminatum* sensu Ait., Hort. Kew 3 :10 (1789) *non* L. Type: Cape, *Masson s.n.* (BM, holo.!).

Lebeckia nuda Sims in Curt., Bot. Mag. 48 t.2214 (1821). *Indigofera nuda* (Sims) G.Don in Hort. Brit. :301 (1850); G.Don, Gen. Syst. 2 :209 (1832). Type: Raised from Cape seeds in 1814 by Messers Whitley, Brame & Milne at the Fulham Nursery and then sent to Sims in October 1819 as *Lebeckia contaminata* (BM, holo.)

I. aphylla Breit. ex Link., Enum. 2 :251 (1822); Breit., Hort. Breit. :209 (1817). Type: Cape, der guten Hoffnung, cultivated in the Breiter Gardens in Leipzig and later by Link in Berlin, collector unknown (B,holo., destroyed).

I. juncea DC., Prodr. 2 :225 (1825). Type: Cape, cultivated from seed sent from England, 24 Jul. 1818, *Cels s.n.* in herbarium DC. (G, holo.).

I. fulcrata Harv. in Harv. & Sond., Fl. Cap. 2 :192 (1862). Type: Cape, at the 24 rivers, Gelustwaard, fl. Dec., Zeyher 496 (K, holo.!!; S; SAM; TCD; Z).

I. gifbergensis C.H. Stirton & J.K. Jarvie in Bothalia 17 :2 (1987). Type: Cape, Pilaarsberg, north of Pakhuis Pass, 9.1967, Kerfoot 5922 (NBG, holo.!!)

I. ionii J.K. Jarvie & C.H. Stirton in Bothalia 17 :3 (1987). Type: Cape, Caledon, Vogelgat, near Hermanus, 20.11.83, *I. Williams* 3519 (K, holo.!!; NBG).

I. filifolia Thunb. var. *minor* Salter in J. S.Afr. Bot. 5 :71 (1939). Type: Cape Peninsula, marshy ground near Modderdam, 3.12.38, *Salter* 7875 (BOL, holo.!!).

8.2.4.7. Section *Humifusae* Schrire

I. capillaris Thunb., Prodr. Fl. Cap. :133 (1800); Fl. Cap. :599 (1823); Harv. in Harv. & Sond., Fl. Cap. 2 :188 (1862). Type: Cape, in herbarium Thunberg 17325 (UPS, lecto.!!).

I. tenuifolia Lam., Encycl. 3 :249 (1789). Type: Cape, *Sonnerat* in herbarium Lamarck (P, holo.).

I. declinata E. Mey., Comm. :104 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :198 (1862). Type: Cape, in montibus rupestribus

inter Keure-boomsrivier et Langekloof, alt. 3500-400' (IV, A),
13.11.31, Drege 6681 (P, lecto!).

I. pusillifolia Bak.f. *nom. nud.*

I. guthriei H. Bol. in Journ. Bot. 34 :22 (1896). Type: Cape,
Hottentot's Holland Mts. near Sir Lowry's Pass, 460m (1600'), fl.
Jan.- Feb. 1893, *F. Guthrie* sub *H. Bolus* 7509, (BOL, holo.!: GRA;
K; NH; Z).

I. humifusa Eckl. & Zeyh., Enum. :244 (1836); Harv. in Harv. &
Sond., Fl. Cap. 2 :198 (1862). Type: Cape, inter frutices (altit.
III) laterum montis "Winterhoeksberge" prope "Tulbagh". Oct.,
Ecklon & Zeyher 1622 (S, lecto!).

I. calva E.Mey., Comm. :104 (1836). Type: uncertain locality,
Drege 6680 (P, lecto!).

I. ovata L.f., Suppl. Fl. :335 (1781); Thunb., Prodr. Fl. Cap.
:132 (1800); Fl. Cap. :596 (1823); Harv. in Harv. & Sond, Fl.
Cap. 2: 168 (1862). Type: Cape, in herbarium Thunberg 17354 (UPS,
lecto.).

I. sarmentosa L.f. var. *latifolia* Eckl. & Zeyh., Enum. :238
(1836). Type: Cape, ad montes prope "Swellendam" eam Mundt
legit. Fr. Mart., *Zeyher* 2414 (S, lecto.!: K; P; W).

I. sp. nov. 1. "*I. culmenicola* Bak.f." *nom. nud.* Vouchers: *H.*
Bolus 11478 (BM, BOL, K, PRE); *H. Hall* 179
(NBG); *Compton* 16058 (NBG); *Esterhuysen* 4527
(BOL). S. Cape, Swartberg Pass to Karooport.

I. sp. nov. 2. aff *I. capillaris*. Vouchers: *Salter* 4967 (BOL);
7047 (BOL); *Esterhuysen* 34051 (BOL); 6229 (BOL);
Levyne 5320 (BOL); *H. Bolus* 4509 (BOL). Cape
Peninsula.

I. sp. nov. 3. aff *I. humifusa*. Vouchers: *Esterhuysen* 20342 (BOL); *Tyson* 681 (BOL); *Wolley Dodd* 4064 (BOL); *Schrire* 2499 (K). Hex River valley, Ceres.

8.2.4.8. Section *Filicaules* Schrire

I. dillwynioides Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :178 (1862). Type: Cape, Klipfontein, near Malmesbury, Nov. *Zeyher* 494 (K, holo.!!; PRE).

I. filicaulis Eckl. & Zeyh., Enum. :239 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :178 (1862). Type: Cape, in locis humidiusculis (altit IV) graminum ad montium latera in valle "Tulbagh" supra "Waterfall" (Worcester), Nov. Dec., *Ecklon & Zeyher* 1594 (S, lecto.!!; SAM).

I. subtilis E. Mey., Comm. :98 (1836). Type: Cape, Drakensteen-bergen, in rupestribus humidis umbrosis, 3000 - 3500', 5.10.33, *Drege* 6696 (P, lecto.!!).

I. quinquefolia E. Mey., Comm. :98 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :179 (1862). Type: Cape, in montibus apricis saxosis prope Genadendal, 3600' (IV, A), 8.10.28, *Drege* 1379 (P, lecto.!!).

8.2.4.9. Section *Concavae* Schrire

I. concava Harv. in Harv. & Sond., Fl. Cap. 2 :186 (1862). Type: Cape, on the Cradockberg near George, 11.9.1814, *Burchell* 5931 (K, lecto.!!; BOL).

I. sp. nov. 1. "*I. remota* Bak. f." *nom. nud.* Vouchers: *Esterhuysen* 35160 (BOL, K); *D.J. McDonald* 1159 (K, STE); *Burchell* 7366 (K).

I. pentaphylla sensu Burch. ex Harv. in Harv. & Sond., Fl. Cap. 2 :178 (1862) non Murr. in L., Syst. Veg. ed. 13, :564 (1774), nec Bak., Fl. Trop. Afr. 2 :182 (1871) nom. illegit.
Type: Cape, summit of a mountain peak near Swellendam, 15.1.1815, Burchell 7366 (K, holo.).

8.2.4.10. Section *Coriaceae* Schrire

I. alopecuroides (Burm.f.) DC., Prodr. 2 :231 (1825) non E.Mey.
Lotus alopecuroides Burm.f., Prodr. Fl. Cap. 23 (1768). Type: Cape, in herbarium Burman (G, lecto.).

Lotus africanus capitulis alopecuroides pediculis longis infidentibus. Burm., Cat. Pl. Af. 16 (1737).

subsp. ***alopecuroides*** Schrire

I. coriacea Ait. var. *alopecuroides* Harv. in Harv. & Sond., Fl. Cap. 2 :187 (1862). Type: Cape, in lapidosis (altit. III, IV) graminum et fruticum ad montium latera "Babylons Toorensberg" et "Klynriviersberge" (Caledon), Aug., Ecklon & Zeyher 1591 (K, lecto.!!; S; SAM; TCD).

subsp. ***minor*** (E.Mey.) Schrire stat. nov.

I. mauritanica (L.) Thunb. var. *minor* E. Mey. in Linnaea 7:167 (1832). *I. alopecuroides* (Burm.f.) DC. var. *minor* (E. Mey.) Eckl. & Zeyh., Enum. :238 (1836). *I. coriacea* Ait. var. *minor* (E.Mey.) Harv. in Harv. & Sond., Fl. Cap. 2 :187 (1862). Type: Cape, inter saxa et frutices (altit III) laterum montium Zwartberg et Klyn-riviersberge (Caledon). Aug., Ecklon & Zeyher 1591b (S, lecto.!!).

I. candolleana Meisn. in Hook., Lond. Journ.Bot. 2 :85 (1843). Type: Cape, in arenosis ad flumen Berg river, Stellenbosch. Krauss 838 (NY, holo.).

I. mauritanica (L.) Thunb. var. *erecta* Eckl. & Zeyh., Enum. :238 (1836). *I. coriacea* Ait. var. *hirta* Harv. in Harv. & Sond., Fl. Cap. 2 :187 (1862). Type: Cape, in lapidosis (altit. II) prope "Constantia" (Cap.) May., *Ecklon & Zeyher 1590b* (S, lecto.!).

I. alopecuroides sensu E. Mey., Comm. :100 (1836) *non* (Burm. f) DC.

Anila mauritanica (L.) O. Kuntze var. *oligantha* O. Kuntze, Rev. Gen. 3(2):52 (1898). Type: Cape: Muizenberg, 300m, 17.1.1894 (K, lecto.!).

I. cytisoides (L.) L., Syst. Nat. ed. 12 :496 (1767); Jacq., Hort. Schoenbr. 2: t.235 (1797); Thunb., Prodr. Fl. Cap. :132 (1800); Curt., Bot. Mag. 19: t.742 (1804); Thunb., Fl. Cap. :598 (1823); Harv. in Harv. & Sond., Fl. Cap. 2 :192 (1862); Marloth, Fl. S.Afr. 2: 60, t.28 (1925); Wijnands, The Botany of the Commelins :163 (1983). *Psoralea cytisoides* L., Sp. Pl. :1076 (1763); Burm.f., Prodr. Fl. Cap. 22 (1768). Type: Cape, in herbarium Linnaeus 923.13, *van Royen s.n.* (LINN, lecto.!).

Lotus africana frutescens Flore spicato rubicundo Moninckx, Atlas 4: t.34 (1701); Commelin, Hort. Amst. 2 :167 t.84 (1701). Type as above.

I. mucronata Lam., Encycl. 3 :247 (1789). Type: Cape, unknown collector in herbarium Lamarck (P, holo.!).

Note: *I. lotoides* Lam., Encycl. 3 :247 was not collected from the Cape as supposed by Lamark, and is a synonym of *I. oblongifolia* Forsk., Fl. Aeg. Arab. :137 (1775). It is therefore not a synonym of *I. cytisoides* (L.)L. as mentioned in Wijnands, p163 (1983).

I. filiformis L.f., Suppl. Pl. :334 (1781); Thunb., Prod. Fl. Cap. :132 (1800); Fl. Cap. :598 (1823); Harv. in Harv. & Sond.,

Fl. Cap. 2 :186 (1862). Type: Cape, in herbarium Thunberg 17339 (UPS, lecto.).

I. filiformis L.f. var. *adscendens* Eckl. & Zeyh., Enum. :239 (1836). Type: Cape, in hiatu (altit IV) montis Tafelberg ad verticem versus (Cap), Oct., *Ecklon & Zeyher 1592b* (S, lecto.; GRA).

I. filiformis L.f. var. *planifolia* E. Mey., Comm. :98 (1836). Type: Cape, ad radices montis Duivelsberg, 800' (III, D, b), 23. 7. 26, *Drege s.n.* (P, lecto.; K).

I. wynbergensis S. Moore in Journ. Bot. 16 :131 (1878). Type: Cape, in solo arenoso in fruticetis prope Wynberg, *H. Bolus 2774* (K, holo.; BOL; G).

I. candicans sensu Sieb. non Ait.

I. glomerata E. Mey. in Linnaea 7 :166 (1832); Harv. in Harv. & Sond., Fl. Cap. 2 :177 (1862). Type: Cape, Hottentotsholland Berge, Oct. 24, *Ecklon 428* (P, lecto.).

I. nivea sensu E.Mey., Comm. :96 (1836) non Willd.

I. mauritanica (L.) Thunb., Prodr. Fl. Cap. :133 (1800); Fl. Cap. :598 (1823). *Lotus mauritanicus* L., Syst. Nat. ed. 10, 2 :1179 (1759); Sp. Pl. (ed.2) :1091 (1763). *Ononis mauritanica* L., Mant. :267 (1771). Type: Cape, unknown collector in herbarium Linnaeus 931.34 (LINN, lecto.).

Lotus fruticosus Berg., Descr. Pl. Cap. :226 (1767). Type: Cape, *Lotus mihi fruticosus*, in herbarium Bergius, *Grubb s.n.* (SBT, holo.).

I. coriacea Ait., Hort. Kew 3: 68 (1789); Harv. in Harv. & Sond., Fl. Cap. 2 :187 (1862). *I. coriacea* Ait. var. *cana* Harv. in Harv. & Sond., Fl. Cap. 2 :187 (1862). Type: Cape, hort. Kew 1774 *Masson s.n.* (BM, lecto.).

I. coriacea Ait. var *major* E. Mey., *Comm.* :100 (1836). Type: Cape, kloof van Tafelberg 800', 28.7.26. *Drege* 77 (P, lecto.!).

I. superba C.H. Stirton in *Bothalia* 14 :69 (1982). Type: Cape, Caledon, near Vogelpool, Vogelgat, 9.3.78, *I. Williams* 2439 (PRE, holc.!!; NBG).

I. sp. nov. 1. aff. *I. glomerata*. Vouchers: *M.C. Gillett* 4495 (K, PRE); *Schlechter* 9659 (K, PRE); *H. Bolus* 8544 (PRE); *Acocks* 22824 (K). S. Cape, Fairfield, Elim to Napier.

8.2.4.11. Section *Angustifoliolae* Schrire

I. angustifolia L., *Mant.* :272 (1771); *Harv.* in *Harv. & Sond.*, *Fl. Cap.* 2 :186 (1862) *non* Thunb. Type: Cape, in herbarium Linnaeus 923.18, *Tulbagh s.n.* (LINN, lecto.!).

subsp. *angustifolia*

Polygala pinnata Burm. f., *Prod. Fl. Cap.* 20 (1768). Type: Cape, in herbarium Burman (G, lecto.).

subsp. *leptocaulis* (Eckl. & Zeyh.) Schrire *stat. nov.*

I. leptocaulis Eckl. & Zeyh., *Enum.* :243 (1836). Type: Cape, inter frutices (altit. III) laterum montium prope fluminis ostium "Klynrivier" (Caledon). Aug., *Ecklon & Zeyher* 1616 (S, lecto.!!; MEL).

I. strigosa Spreng., *Neue Entdeck.* 3: 54 (1822). Type: Cape, *Unknown collector* 240 (W, lecto.!).

I. tenuifolia sensu Eckl. & Zeyh. *non* Lam.

I. angustifolia L. var. *tenuifolia* (Eckl. & Zeyh.) Harv. in Harv. & Sond., Fl. Cap. 2 :186 (1862). Type: Cape, in locis arenosis umbrosis et humidiusculis (altit. I) fruticum planitie capensis, Oct., *Ecklon & Zeyher 1613* (S, lecto!).

I. grisophylla Fourcade in Transactions of the Royal Society of South Africa 21 :93 (1932). Type: Cape, Humansdorp, Otterford, 1300', Mar. 1928., *Fourcade 3669* (BOL, holo.!, K; STE).

I. mischocarpa Schltr. in Engl., Bot. Jahrb. 27 :149 (1899). Type: Cape, in clivis lapidosis montium prope Napier, in ditione Bredasdorp, alt. c. 1200', 9.12.1896, *Schlechter 9661* (Z, lecto.!, BOL, G, K).

I. mundiana Eckl. & Zeyh., Enum. :243 (1836); Harv. in Harv. & Sond. Fl. Cap. 2 :186 (1862) as *I. mundtiana*. Type: Cape, in montibus prope "Swellendam", Jan., *Ecklon & Zeyher 1617* (*Mundt legit.*) (S, lecto.!, MEL; SAM; TCD).

I. sarmentosa L.f., Suppl. Fl. :334 (1781); Thunb., Prodr. Fl. Cap. :132 (1800); Fl. Cap. :596 (1823); Harv. in Harv. & Sond, Fl. Cap. 2 :187 (1862). Type: Cape, in herbarium Thunberg 17341 (UPS, lecto.!).

Lotus africanus, tenuissimus foliis ramosissimus, floribus luteis perexiguis. Plukenet, Almagesti botanici Mantissa :119 (1700).

Lotus filiformis Berg., Descr. Pl. Cap. :227 (1767); *Ononis filiformis* L., Mant. :266 (1771). Type: Cape, *Lotus mihi filiformis* in herbarium Bergius, *Grubb s.n.* (SBT, holo.!).

I. microphylla Lam., Encycl. 3 :250 (1789). Type: Cape, unknown collector in herbarium Lamarck (P, holo.!).

I. psilocarpa Schltr. in Engl., Bot. Jahrb. 27 :148 (1899). Type: Cape, in saxosis montium supra Bainskloof, in ditione

Wellington, alt. c. 2500', 13.11.1896, *Schlechter 9151* (Z, lecto.!; BOL; G; GRA; K; P; PRE).

I. sarmentosa L.f. var. *trifoliata* E. Mey., *Comm.* :100 (1836). Type: Cape, in summo monte tabulare, 1828, *Ecklon s.n.* (P, lecto.).

I. sulcata DC., *Prodr.* 2 :231 (1825); Harv. in Harv. & Sond., *Fl. Cap.* 2 :180 (1862). Type: Cape, in herbarium DC. 231:94 (G, holo.!).

I. sp. nov. 1. "*I. potbergensis* Schrire" *nom. nud.* Vouchers: *H.C. Taylor 4332* (PRE, STE); *Acocks 23006* (PRE, STE). Potberg near Bredasdorp.

I. sp. nov. 2. "*I. calcarea* Schrire" *nom. nud.* Vouchers: *C.J. Burgers 2434* (PRE, STE); *G. van Niekerk 407* (BOL, K); *P. Bohnen 7604* (K, PRE, STE); *588/3* (PRE); *8104* (PRE); *J. Muir 1760* (PRE); *J. G. Steyn ex Galpin 5189* (PRE); *Acocks 24007* (BOL, K, PRE). Riversdale, Still Bay to Bredasdorp areas in S.Cape. Appears to be a limestone fynbos endemic.

I. sp. nov. 3. "*I. pilgeriana* Schltr." *nom. nud.* Vouchers: *Salter 1153* (BOL, K), *1012* (K); *C. M. van Wyk 559* (K, STE); *Esterhuysen 1962* (BOL, PRE); *P. Goldblatt 4718* (PRE); *N.S. Pillans 6320* (BOL); *M.R. Levyns 6431* (BOL). SW.Cape, inland on mountains, from Bainskloof, Paardeberg, Villiersdorp and Riviersonderend.

I. sp. nov. 4. "*I. swartbergensis* Schrire" *nom. nud.* Vouchers: *Hafstrom & Acocks 692* (PRE); *M.F. Thompson 2158* (PRE); *H. Bolus 11810* (BOL, K); *J.H.J. Vlok 994* (K); *Wood 3* (BOL); *E. Markotter STE 9961* (STE). S. Cape, Swartberg Mountain Pass area.

I. sp. nov. 5. Vouchers: *T.P. Stokoe* PRE 55305 (PRE); *J. Muir* 1394 (BOL, PRE); *B. Maguire* 805 (NBG). S. Cape, Cloetes Pass near Herbertsdale and Robinson Pass, Langeberg area.

I. sp. nov. 6. "*I. sclerophylla* Schrire" *nom. nud.* Vouchers: *K.A. Dahlstrand* 1418 (PRE); *J.J. Bos* 876 (K); *Fourcade* 1596 (BOL). S. Cape, Montagu Pass area near George and Knysna.

8.2.4.12. Section *Hispidae* Schrire

I. brachystachya (DC.) E. Mey. in *Linnaea* 7 :168 (1832); Harv. in Harv. & Sond., *Fl. Cap.* 2 :181 (1862). *I. angustifolia* L. var. *brachystachya* DC., *Prodr.* 2 :231 (1825). Type: Cape, in herbarium DC. 231:93, 1816, *M. Lambert s.n.* (G, holo.!).

I. angustifolia sensu Thunb., *Prod. Fl. Cap.* :133 (1800); *Fl. Cap.* :599 (1823) *non* L.

I. floribunda Schltr. *nom. nud.*

I. bisacculata Schltr. *nom. nud.*

I. flabellata Harv. in Harv. & Sond., *Fl. Cap.* 2 :180 (1862). Type: Cape, near the Keurbooms R. at Paardekraal, 27.3.1814, *Burchell* 5174 (K, lecto.!!; GRA).

I. hamulosa Schltr. in Engl., *Bot. Jahrb.* 24 :443 (1897). Type: Cape, auf steinigen Hügeln bei Elim, in 200m, 18.4.1896, *Schlechter* 7612 (Z, lecto.!!; BM; BOL; GRA; K; PRE; S; SAM).

I. hispida Eckl. & Zeyh., *Enum.* :240 (1836); Harv. in Harv. & Sond., *Fl. Cap.* 2 :180 (1862). Type: Cape, in solo ericeto (altit. II,III) laterum montium supra "Uitenhage". Febr. Mart., *Ecklon & Zeyher* 1600 (S, lecto.!!; SAM).

I. lotoides sensu E. Mey. in *Linnaea* 7 :168 (1832) *non* Lam.

I. commutata Spreng. *nom. nud.*

I. pappei Fourcade in *Transactions of the Royal Society of South Africa* 21 :94 (1932). Type: Cape, Flats, Robhoek, 650', Aug. 1921, *Fourcade* 1383 (BOL, holo.!). (K).

I. rhodantha Fourcade in *Transactions of the Royal Society of South Africa* 21 :94 (1932). Type: Cape, Knysna, Yzer Nek, 1800', Mar. 1922, *Fourcade* 2049 (BOL, holo.!.; GRA; K; STE).

I. fourcadei Schönl. *nom. nud.*

I. sp. nov. 1. Vouchers: *J. Vlok* 792 (STE); *G. Germishuizen* 4260 (NBG, PRE). S. Cape, Outeniqua Mountains near George.

8.2.4.13. Section *Psiloceratiae* (Gillett) Schrire

I. baumiana Harms in *Warburg & Baum, Kunene-Sambezi Exped.* :257 (1903); *Schreiber*, in *Prodr. Fl. SWA.* 60 :52 (1970). Type: Angola, am Habungu, Sandboden an lichten Waldstellen, 1150m, *Baum* 497 (K, iso.!.; S; Z).

I. lyallii Bak. in *J. Linn. Soc.* 20 :128 (1883); *Gillett*, *Kew Bull., Add. Ser.* 1 :86 (1958). Type: Central Madagascar, *Lyall* 241 (K, syn.!).

subsp. *lyallii*

I. obermeijerae Bremekamp in *Ann. Tv1. Mus.* :242 (1933). Type: Transvaal, Entabeni, Zoutpansberg, 12.1930, *A.A. Obermeijer* 878 (PRE, lecto.!).

Gillett (1958) described subsp. *nyassica* from Mozambique and Malaw

I. natalensis H. Bol. in Journ. Bot. 34 :23 (1896). Type: Natal, Inanda and Ismont, 1880 & 1883, *J.M. Wood* 872 (BOL, lecto.!; K; NH; SAM).

I. umbrosa Harv. *nom. nud.*

I. sylvicola Schrire *nom nov.* *I. micrantha* E. Mey., Comm. :104 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :195 (1862); Wood & Evans, Natal Plants 1:67 t.82 (1899) non Desv. in Ann. Sc. Nat. Ser. 1, 4 :410 (1826) *nec* Bunge, Enum. Fl. Chin. Bor. 16 (1833), *nom. illegit.* Type: Cape, inter Omtendo et Omsamculo, ad marginem sylvae, alt 100' (V, c), 1.3.32, *Drege* 5412 (P, lecto.!).

I. sp. nov. 1. "*I. jucunda* Schrire" *nom. nud.*

I. cylindrica auct. non DC.; E. Mey., Comm. :103 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :193 (1862); Sim, For. Fl. Cape Colony t.54 (1907).

I. sp. nov. 2. "*I. abbottii* Schrire *nom. nud.* aff. *I. sylvicola*.
Vouchers: *A. Abbott* 3052 (PRU); 3179 (NH, PRU);
A.E. van Wyk 7382 (PRU); 7412 (NH, PRU); 7416
(NH, PRU); *R. Williams* 17 (NH). Natal, Zululand,
N.Transkei coastal (& hinterland) forests.

I. sp. nov. 3. Voucher: *B. Maguire* 1474 (NBS, PRE). Transvaal,
Magoeboeskloof area.

8.2.4.14. Section *Tinctoriae* (Wight & Arn.) Schrire

I. amorphoides Jaub. & Spach, Ill. Pl. Or. t.483 (1856); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :134 (1989). Type: N. Ethiopia, *Schimper* 1474 (P, holo.!).

I. arrecta Hochst. ex A. Rich., Tent. Fl. Abyss. 1 :184 (1847); Bak., Fl. Trop. Afr. 2 :97 (1871); Wood & Evans, Natal Plants

3(2): 18 t.287 (1902); Gillett, Kew Bull., Add. Ser. 1 :105 (1958); in Fl. Trop. E. Afr., Legum.-Papil. 1 :307 (1971); Compton, Fl. Swazi. :260 (1976); de Kort & Thijssse, Blumea 30 :109 (1984); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :135 (1989) *non* Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :183 (1862). Type: Ethiopia, Adoam, Schimper 1923 (P, lecto.!; K; L).

I. cryptantha Benth. ex Harv., Fl. Cap. 2 :195 (1862) *pro min. parte, quoad pl. natalensem.*

I. cryptantha Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :195 (1862) *pro majore parte*; Bak.f., Leg. Trop. Afr. 1 :156 (1926); N.E. Brown in Burtt Davy, Man. Fl. Transv. 2 :371 (1932); Gillett, Kew Bull., Add. Ser. 1 :104 (1958); Schreiber in Prod. Fl. SWA 60 :54 (1970). Type: Transvaal, Crocodile river, Zeyher 473 (K, lecto.!; BM).

subsp. *cryptantha*

subsp. *occidentalis* (Bak.f.) B.D.Schrire *stat. nov.*

I. cryptantha Benth. ex Harv. var. *occidentalis* Bak.f. in Viertel. Nat. Ges. Zurich 49 :184 (1904). Type: Namibia, im Sande des Danob bei Rehoboth, Fleck 449 (Z, lecto.!).

I. hofmanniana Schinz in Verh. Bot. Ver. Brand. 30 :162 (1889). Type: Namibia, Omikangua in sudost. Ondonga, 2.1886, H. Schinz 242 (Z, holo.!).

I. homblei Bak.f. & Martin in Bull. Jard. Bot. Et Brux. 8 :151 (1923); Bak.f., Leg. Trop. Afr. 1 :159 (1926); Gillett, Kew Bull., Add. Ser. 1 :87 (1958). Type: Zaire, Vallee de Kapiri, Feb. 1913, *Homble' 1135* (BR, holo.).

I. ormocarpoides Bak., J. Linn. Soc. 22 :464 (1887); Gillett, Kew Bull., Add. Ser. 1 :93 (1958). Type: Madagascar, Baron 4607 (K, syn.!).

I. torulosa sensu Bak., Fl. Trop. Afr. 2 :91 (1871) non
E.Mey.

I. subcorymbosa Bak., Fl. Trop. Afr. 2 :91 (1871); Gillett, Kew Bull., Add. Ser. 1 :98 (1958); in Fl. Trop. E. Afr., Legum.-Papil. 1 :302 (1971). Type: Angola, Huila, Moro de Lopollo, *Welwitsch 2053* (K, iso.!).

I. subcorymbosa Bak. var. *eylesii* Bak.f., Leg. Trop. Afr. 1 :149 (1926). Type: Zimbabwe, Harare, 5000', 12.1919, *Eyles 1958* (K, iso.!).

I. suffruticosa Mill., Gard. Dict. ed. 8, no. 2 (1768). Type: Jamaica, unknown collector (BM, holo.!).

I. swaziensis H. Bol. in Trans. Roy. Phil. Soc. S.Afr. 16 :381 (1906); N.E. Brown in Burtt Davy, Man. Fl. Transv. 2 :371 (1932); Gillett, Kew Bull., Add. Ser. 1:97 (1958); Compton, Fl. Swazi. :264 (1976). Type: Transvaal, in graminosis pr. Crocodile River, 4800', 9.12.1893, *R. Schlechter 3908* (BOL, lecto.; BM; GRA; K; PRE).

subsp. **swaziensis**

subsp. **perplexa** (N.E.Br.) B.D.Schrire *stat. nov.*

I. perplexa N.E.Br. in Kew Bull. 1925 :154 (1925). *I. swaziensis* H. Bol. var. *perplexa* (N.E.Br.) Gillett, Kew Bull., Add. Ser. 1 :97 (1958); Compton, Fl. Swazi. :262 (1976). Type: Transvaal, Shilovane, 8.1905, *H. Junod s.n.* (K, holo.!).

I. tinctoria L., Sp.Pl. :751 (1753); DC., Prodr. 2 :224 (1825); Bak., Fl. Trop. Afr. 2 :99 (1871); Bak.f., Leg. Trop. Afr. 1 :156 (1926); Gillett, Kew Bull., Add. Ser. 1 :106 (1958); in Fl. Trop. E. Afr., Legum.-Papil. 1 :308 (1971); de Kort & Thijsse, Blumea 30 :136 (1984); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :135 (1989). Type: Sri Lanka, *Hermann* vol. 3, fol. 20 (BM, holo.!).

var. *arcuata* Gillett in Kew Bull. 24 :499 (1970). Type: Tanzania, Dodomo Distr., 60 km NW of Dodoma on rd to Manyani, Bahi 900m, 23.4.1962, Polhill & Paulo 2139 (K, holo.!; EA).

8.2.4.15. Section *Subulatae* Schrire

I. lupatana Bak.f., Leg. Trop. Afr. 1 :154 (1926); Gillett, Kew Bull., Add. Ser. 1 :98 (1958), in Fl. Trop. E. Afr., Legum.-Papil. 1 :302 (1971); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :132 (1989). Type: Mozambique, Lupata, 16 degrees 40' S, 34 degrees E., Dr. J. Kirk s.n. (K, holo.!; LISC).

I. trita L.f., Suppl. :335 (1781); Ali, Bot. Notis. 111 :553 (1958); Gillett, Kew Bull., Add. Ser. 1 :101 (1958); in Fl. Trop. E. Afr., Legum.-Papil. 1 :303 (1971); de Kort & Thijssse, Blumea 30 :139 (1984); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :133 (1989). Type: India, unknown collector in herbarium Linnaeus 923.9 (LINN, holo.).

var. *subulata* (Vahl ex Poir.) Ali in Bot. Notis. 111 :558 (1958); Schreiber in Prod. Fl. SWA 60 :61 (1970); Gillett in Fl. Trop. E. Afr., Legum.-Papil. 1 :304 (1971); de Kort & Thijssse in Blumea 30 :141 (1984). *I. subulata* Vahl ex Poir. in Lam., Encycl. Suppl. 3 :150 (1813); Bak.f., Leg. Trop. Afr. 1 :146 (1926); Gillett, Kew Bull., Add. Ser. 1 :100 (1958); Meikle, Kew Bull. 1950 :352 (1951). *I. trita* L.f. subsp. *subulata* (Vahl ex Poir.) Ali var. *subulata* in Ali, Bot. Notis. 111 :558 (1958). Type: Ghana, in herbarium de Jussieu, Thonning s.n. (P, holo.!; C; K, photo.).

I. tetragonoloba E. Mey., Comm. :106 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :190 (1862). Type: Cape, in fruticetis prope ostia fluvii Omsamculo et inter Omcomas et Port Natal, infra 100' (V, c), 22.3.32, Drege 5421 (P, lecto.!).

I. dimorphophylla Schinz in Verh. Bot. Ver. Brand. 30 :164 (1889); Bak.f., Leg. Trop. Afr. 1 :145 (1926). Type: Namibia,

Olukonda und Uukuambi, 8.1.1886, *H. Schinz* 246 (Z, holo.!: GRA; K).

I. subincana N.E.Br., *Kew Bull.* 1925 :155 (1925); in Burttt Davy, *Man. Fl. Transv.* 2 :371 (1932); Compton, *Fl. Swazi.* :263 (1976). Type: Transvaal, Messina, 2000', 2.2.1919, *F.A. Rogers* 22560 (K, holo.!: BOL; PRE).

I. rariflora Dinter *nom. nud.*

var. *scabra* (Roth) Ali in *Bot. Notis.* 111 :558 (1958). *I. scabra* Roth, *Nov. Fl. Sp.* :359 (1821). *I. subulata* Vahl ex Poir. var. *scabra* (Roth) Meikle, *Kew Bull.* 1950 :352 (1951); Gillett, *Kew Bull., Add. Ser.* 1 :100 (1958). *I. trita* L.f. subsp. *subulata* (Vahl ex Poir) Ali var. *scabra* (Roth) Ali in *Bot. Notis.* 111 :558 (1958). *I. trita* L.f. var. *scabra* (Vahl ex Poir.) Ali in Gillett, *Fl. Trop. E. Afr., Legum.- Papil.* 1 :304 (1971). Type: India, Madras, in herbarium Wallich 5475, *Heyne s.n.* (K, iso.!).

I. retroflexa Baill., *Bull. Soc. Linn. Paris* 1 :399 (1883); Bak.f., *Leg. Trop. Afr.* 1 :145 (1926). Type: Madagascar, Tulle'ar, *Grandidier s.n.* (P, holo.; K, photo.).

8.2.4.16. Section *Hedyanthae* Schrire

I. densa N.E.Br. in *Kew Bull.* 1925 :152 (1925); in Burttt Davy, *Man. Fl. Transv.* 2 : 369 (1932); Compton, *Fl. Swazi.* :261 (1976). Type: Transvaal, Barberton Distr., nr. Barberton, 1.1907, *Thorncroft* 2974 (K, holo.!: PRE).

I. dregeana E. Mey., *Comm.* :100 (1836); Harv. in *Harv. & Sond., Fl. Cap.* 2 :182 (1862). Type: Natal, inter Umkomaas et Port Natal, alt 300' (V, c), 22.3.32, *Drege* 5434 (P, lecto.!).

I. gerrardiana Harv. in Harv. & Sond., Fl. Cap. 2 :595 (1862). Type: Natal, Bushmans River, March 1861, *Gerrard & McKen 431* (TCD, holo!).

This taxon should not to be confused with *I. gerardiana* Wall. ex Bak. in Hoof.f., Fl. Brit.Ind. 2 :100 (1876) which is a synonym of *I. heterantha* Wall. ex Brandis, For. Fl. N.W. & C.Ind. :135 (1874). The plant is a cultivated ornamental in Europe and South Africa, originally from the Himalayas.

I. frondosa N.E.Br. in Kew Bull. 1925 :156 (1925); in Burtt Davy, Man. Fl. Transv. 2 :372 (1932). Type: Transvaal, Lydenburg Distr., hills near Belfast, 6500', *H. Bolus 11815* (K, holo!).

I. hedyantha Eckl. & Zeyh., Enum. :243 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :188 (1862); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :372 (1932); Compton, Fl. Swazi. :261 (1976). Type: Cape, in collibus (altit. III) prope "Philipstown" (Ceded Territory), Oct., *Ecklon & Zeyher 1614* (S, lecto.!, K; PRE; SAM).

I. secunda E. Mey., Comm. :102 (1836). Type: Cape, in graminosis inter Klipplaatrivier et Zwartkey, alt. 3800' (I, a), 16.11.32, *Drege 5427* (P, lecto!).

Anila hedyantha (Eckl. & Zeyh.) O.Kuntze, Rev. Gen. 3(2) :51 (1898). Type: Cape, Cathcart, *O. Kuntze s.n.* (K, iso!).

I. inyangana N.E.Br. in Kew Bull. 1906 :102 (1906). Type: Zimbabwe, Manika, Inyanga Mts., Dec. 1899, *E. Cecil 174* (K, holo!).

I. hedyantha sensu Gillett, Kew Bull., Add Ser. 1 :50 (1958) pro parte.

I. brevifolia N.E.Br. in Kew Bull. 1925 :155 (1925); in Burtt Davy, Man. Fl. Transv. 2 :372 (1932). Type: Transvaal, Lydenburg Distr., Graskop nr. Pilgrims Rest, 29.1.1906, *J. Burtt Davy in Government Herbarium 1475* (K, holo.!, PRE).

I. ripae N.E.Br. in Kew Bull. 1925 :157 (1925); Man. Fl. Transv. 2 :372 (1932). Type: Transvaal, Lydenburg Distr., banks of river near Lydenburg, *F. Wilms* 301 (K, holo.!; BM; G; P; Z).

Doubtfully distinct from *I. tristoides* N.E.Br.

I. rostrata H. Bol. in Journ. Bot. 34 :23 (1896); N.E.Br. in Burt Davy, Man. Fl. Transv. 2 :372 (1932); Compton, Fl. Swazi. :263 (1976) non Conrath in Kew Bull. 1908 :223 (1908). Type: Cape, grassy hills near Komgha, fl. March, alt. 1800', *H.G. Flanagan* 509 (BOL, holo.!; K; PRE; SAM; Z).

Anila zeyheri (Spreng. ex Eckl. & Zeyh.) O.Kuntze var. *macrophylla* O.Kuntze, Rev. Gen. 3(2) :52 (1893). Type: Natal, Charlestown, 22.3.1894, 1800m, *O. Kuntze s.n.* (K, iso!).

I. tristis E. Mey., Comm. :101 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :182 (1862). Type: Cape, in graminosis inter Umzavubu et Umsikaba, alt. 1000 - 2000' (V, b), 18.2.32, *Drege* 5431 (P, lecto!).

I. corniculata E. Mey., Comm. :101 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :184 (1862). Type: Cape, inter Umtata et Umzavubu, alt. 1800' (V, b), 5.33, *Drege* 5425 (P, lecto!).

I. tristoides N.E.Br. in Kew Bull. 1925 :150 (1925); Man. Fl. Transv. 2 :368 (1932); Compton, Fl. Swazi. :264 (1976). Type: Transvaal, Lydenburg district, by river near town, 12.1894, *F. Wilms* 322 (K, holo.!; BM; NU; PRE).

I. sp. nov. 1. Voucher *J.M. Wood* 7894 (NH, K). Natal, Clairmont, near Durban.

I. sp. nov. 2. aff *I. tristoides* and *I. hedyantha*. Vouchers: *C.J. Ward* 1757 (GRA, K, PRE); 2617 (NU, PRE); *E.S. Pooley* 1777 (K, NU); *G. Germishuizen* 3167 (K, PRE), *M.J. Wells* 2075 (K, PRE); *B.D. Schrire* 359 (NH). Natal, Zululand.

I. sp. nov. 3. aff. *I. hedyantha*. Vouchers: *K.J. Bloem* 70 (PRE); *E.E. Galpin* 13117 (K); 13118 (K, PRE); *Smuts & Gillett* 2424 (PRE); *Codd* 8210 (K, PRE); *O.M. Hilliard* 2961 (NU). Transvaal, Steenkampsberg W. of Lydenburg, Mt. Anderson nr. Pilgrims Rest, and Suikerboskop nr. Dullstroom.

I. sp. nov. 4. Vouchers *B. van Ginke* 519 (PRE); *F. Wilms* 6460 (PRE). Transvaal, near Bethal and Lydenburg.

8.2.4.17. Section *Dendroides* Schrire

I. amitina N.E.Br. in *Kew Bull.* 1925 :158 (1925); in *Burt Davy, Man. Fl. Transv.* 2 :373 (1932). Type: Transvaal, nr. Waterval Boven, 2.1915, *F.A. Rogers* 14440 (K, hol.; PRE).

I. evansiana *Burt Davy* in *Kew Bull.* 1921 :278 (1921). Type: Transvaal, Wakkerstroom Distr., Amersfoort, circa 5500', in and around the Agric. Show Ground, 15.3.1917 (in fruit), *Burt Davy* 17345 (BOL, hol.; K).

I. pauxilla N.E.Br. in *Kew Bull.* 1925 :155 (1925); *Man. Fl. Transv.* 2 :xiv & 2 :370. Type: Transvaal, bei der stad Lydenburg, 1.1885, *F. Wilms* 314 (K, hol.; BM; G; P; PRE, photo.).

I. filipes *Benth. ex Harv.* in *Harv. & Sond., Fl. Cap.* 2 :198 (1862); *Bak.f., Leg. Trop. Afr.* 1 :122 (1926); N.E.Br. in *Burt Davy, Man. Fl. Transv.* 2 :367 (1932); *Gillett, Kew Bull., Add. Ser.* 1 :43 (1958). Type: OFS, Caledon River, fl. Jan., *Zeyher* 472 (K, lect.; G; S; SAM; TCD).

I. galpinii N.E.Br. in *Kew Bull.* 1925 :158 (1925); in *Burt Davy, Man. Fl. Transv.* 2 :373 (1932); *Compton, Fl. Swazi.* :261 (1976). Type: Transvaal, Berea Ridge, Barbeton, 3000', 2.1891, *E.E. Galpin* 1299 (K, hol.; BOL; GRA; NH; PRE; SAM; Z).

- I. lepida* N.E.Br. in Kew Bull. 1925 :157 (1925); in Burt Davy, Man. Fl. Transv. 2 :372 (1932). Type: Transvaal, nr. Barberton, alt. 3000', 1.2.1890, *G. Thorncroft* 266 (K, holo.!).
- I. masonae* N.E.Br. in Kew Bull. 1925 :157 (1925); in Burt Davy, Man. Fl. Transv. 2 :372 (1932). Type: *E. Mason* 29 Transvaal, Waterval Boven, 1922 (K, holo.!).
- I. ovina* Harv. in Harv. & Sond., Fl. Cap. 2 :189 (1862). Type: Cape, summits of rocky hills in Queenstown and Cradock Districts, *F.W. Barber* 61 (TCD, holo.!).
- I. schinzii* N.E.Br. in Burt Davy, Man. Fl. Transv. 1 :44 (1926) & in 2 :xiv & 2 :372 (1932). Type: Transvaal, in fruticet mont. Houtbosch-berg, 5500', 7.2.1894, *R. Schlechter* 4409 (Z, holo.!). BOL; K; PRE; UPS).
- I. tenuissima* E. Mey., Comm. :94 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :171 (1862). Type: Natal, Port Natal in vallibus graminosis, infra 100' (V, c), 25.3.32, *Drege* 5422 (P. lecto.!).
- I. longipes* N.E.Br. ex Bak.f. in Viertel. Nat. Ges. Zurich 22 :180 (1904). Type: Natal, Ladysmith Distr., near Acton Homes, 13.1.86, *J.M. Wood* 3525 (K, lecto.!). BM; BOL; NH).
- I. longipes* N.E.Br. in Kew Bull. 1906 :19 (1906). Type: Natal, stony hillside nr. Ladysmith, 4.2.1895, 3400', *J.M. Wood* 5727 (K, holo.!). NH).
- Anila tenuifolia* (Lam.) O.Kuntze var. *filifolia* O.Kuntze, Rev. Gen. 3(2) :52 (1898). Type: Natal, Colenso, 1050m, 17.3.1894, *O. Kuntze* (K, iso!).
- I. zeyheri* Spreng. ex Eckl. & Zeyh., Enum. :241 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :185 (1862). Type: Cape, in locis apertis et gramine vestitis (altit I) nemorum ad flumen "Zwartkopsrivier" (Uitenhage), Jan., *Ecklon & Zeyher* 1606 (S, lecto.!). SAM).

- I. cinerascens* Eckl. & Zeyh., Enum. :241 (1836). Type: Cape, inter frutices (altit III) ante nemora in "Adow" (Uitenhage), Oct. 29, Ecklon & Zeyher 1607 (S, lecto!).
- I. nana* Eckl. & Zeyh., Enum. :242 (1836). Type: Cape, in collibus arenosis (altit I) ad flumen "Zwartkopsrivier" (Uitenhage), Aug. 29, Ecklon & Zeyher 1611 (S, lecto!; MEL).
- I. stricta* L.f. var. *pedunculata* Eckl. & Zeyh., Enum. :240 (1836). Type: Cape, in collibus inter flumina "Krum et Camtoursrivier" (Uitenhage), Dec., Ecklon & Zeyher 1602b (S, lecto.).
- I. viminea* E. Mey., Comm. :102 (1836). Type: Cape, Klein Bruin-tjieshoogte in collinis, alt. 2800' (V, a), 21.10.29, Drege 5423 (P, lecto!).
- I. acutisepala* Conrath ex Bak.f. in H. Schinz, Mitt. Bot. Mus. Univ. Zurich 22 :179 (1904); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :372 (1932). Type: Transvaal, Modderfontein, 12.1897, P. Conrath 215 (Z, lecto!; K; PRE).
- Anila zeyheri* Kuntze var. *normalis* Kuntze, Rev. Gen. 3(2) :52 (1893). Type: Natal, Krantzklouf, O. Kuntze s.n. (K, lecto.).
- I. sp. nov.* 1. aff. *I. zeyheri*. Vouchers: Stirton 8918 (NH, PRE); Acocks 13954 (K, PRE); Hilliard & Burtt 5939 (K); Gerrard 1071 (K); K.L. Tinley 740 (NU). Natal, Ngome Forest area.
- I. sp. nov.* 2. "*I. inandensis* Bak.f." nom. nud. Vouchers: J.M. Wood 435 (BOL, K); 11409 (K); M.J. Wells 1108 (NU, PRE); J.M. Wood 855 (GRA); Hilliard & Burtt 676 (NU). Natal, Nagle Dam, Inanda and Sydenham areas around Durban.

I. sp. nov. 3. Vouchers: A.O.D. Mogg 6596 (PRE); Barrett 259 (PRE). Natal, Allerton (3030DA) and Swaziland, Usutu Forest, (2631CA).

8.2.4.17.1. Subsection *Foliosae* Schrire

I. floribunda N.E.Br. in Kew Bull. 1925 :159 (1925), and in Burt Davy, Man. Fl. Transv. 2 :373 (1932). Type: Transvaal, Mac Mac, 7. 1884, C. Mudd s.n. (K, holotype; PRE).

I. foliosa E. Mey., Comm. :102 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :181 (1862) *non* Willd. in Rottl., Ges. Naturf. Fr. Neue Schr. 4 :217 (1803) *nom.nud.* Type: Cape, inter Umzimvubu et Umsikaba, in valle inter gramina altiora, alt. 800' (V, b), 18.2.32, Drege 5436 (P, lectotype!).

I. vestita Harv. in Harv. & Sond., Fl. Cap. 2 :182 (1862) *non* Bak. in Hook.f., Fl. Brit. Ind. 2 :96 (1876). Type: Natal, coastland to 1000', lat. 30 degrees S., Feb. to April 1855, Sutherland s.n. (K, holotype!).

I. alopecurus Schltr. in Engl., Bot. Jahrb. 40 :93 (1907). Type: Natal auf lehmigen Aekern bei Dalton, am Noodsberg, Pietermaritzburg district, c1000', Sept. 1904, H. Rudatis 11 (B, destroyed).

I. glencoensis (O. Kuntze) Schrire *stat. nov.* *Anila rupestris* (Eckl. & Zeyh.) O.Kuntze var. *glencoensis* O.Kuntze, Rev. Gen. 3(2) :52 (1898). Type: Natal, Glencoe, 1450m, 21.3.1894, O. Kuntze s.n. (K, holotype!).

I. krookii Schltr. ex A. Zahlbr. in Ann. Nat. Hofmus. Wien 20 :24 (1905). Type: Natal, Pietermaritzburg, in convalle fluminis Mooiriver, 23.2.1895, Krook 2624 (W, holotype; BM).

I. woodii H. Bol. var. *parvifolia* H. Bol. in Journ. Bot. 34 :24 (1896). Type: Natal, Griqualand East, summit of Mt.

Currie, alt. 7300', fl. Feb. 1884, *W. Tyson 1758* (BOL, holo. !; PRE).

I. obscura N.E.Br. in Kew Bull. 1925 :156 (1925) and in Burt Davy, Man. Fl. Transv. 2 :372 (1932). Type: Transvaal, Ermelo Distr., near Ermelo, *R. Leendertz 3121* (K, holo. !; PRE).

I. placida N.E.Br. in Kew Bull. 1925 :149 (1925), and in Burt Davy, Man. Fl. Transv. 2 :368 (1932). Type: Transvaal, Ermelo Distr., Spitzkop, 12.1915, *Pott 5083* (K, holo. !; PRE).

I. rufescens E. Mey., Comm. :103 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :193 (1862) *non* Poir., Encycl. Suppl. 3 :148 (1813), *nom. illegit.*. Type: Natal, between Umzimkulu and Umkomaas rivers, under 500' (V, c), *Drege 5414* (P, lecto.!).

I. stricta L.f., Suppl. Fl.: 334 (1781); Thunb., Prodr. Fl. Cap. :133 (1800); Fl. Cap. :599 (1893); Eckl. & Zeyh., Enum. :240 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :181 (1862). Type Cape, Krumrivier prope rivos, fl. Jan., in herbarium Thunberg 17364, *Thunberg s.n.* (UPS, lecto.!).

I. angustifolia sensu Curt., Bot. Mag. 13: t.465 (1799) *non* L.

I. pauciflora E. Mey., Comm. :99 (1836) *non* Eckl. & Zeyh. Type: Cape, ad margines sylvorum prope Georg, alt 500' (IV,C,b), 1.9.31, *Drege 6676* (P, lecto.!).

I. notata N.E.Br. in Kew Bull. 1906 :102 (1906). Type: Cape, East London Div., Quigney, 60m, 26.9.1899, in herbarium Galpin 2793, *C. Schonberg* (K, holo. !; GRA; FRE).

I. verrucosa Eckl. & Zeyh., Enum. :242 (1836) *non* R. Gra. in Wallich herbarium 5469 *nom. nud.* Type: Cape, in collibus (altit I-III) ad flumen "Zwartkopsrivier" et in "Adow" (Uitenhage), Oct. 29, *Ecklon & Zeyher 1608* (S, lecto. !; SAM).

I. punctata Thunb., Prodr. Fl. Cap. :133 (1800); Fl. Cap. :599 (1823) *non* Eckl. & Zeyh. Type: Cape, in herbarium Thunberg 17360 [left-hand specimen] (UPS, lecto.!).

I. leptophylla E. Mey., Comm. :99 (1836). *I. zeyheri* Spreng. ex Eckl. & Zeyh. var. *leptophylla* (E.Mey.) Harv. in Harv. & Sond., Fl. Cap. 2 :185 (1862). Type: Cape, Drege 6682 (P, lecto.!).

I. stricta L.f. var. *acuta* Harv. in Harv. & Sond., Fl. Cap. 2 :181 (1862). Type: Cape, Bathurst Div., between Blue Krantz & Kaffir Drift Military Post, 21.9.1813, Burchell 3706 (K, holo.!).

I. glabella Fourcade in Transactions of the Royal Society of South Africa 21 :93 (1932). Type: Cape, Humansdorp Div: Geelhoul(t) River, 400', July 1922, Fourcade 2220 (BOL, holo.!!; K).

I. woodii H. Bol. in Journ. Bot. 34 :24 (1896). *I. woodii* H. Bol. var. *intermedia* H. Bol. in Journ. Bot. 34 :24 (1896). Type: Natal, Griqualand East, Mts. near Clydsdale, 900m, March 1886, W. Tyson 1267 (BOL, lecto.!!; K; SAM).

var. *laxa* H. Bol. in Journ. Bot. 34 :25 (1896). Type: Natal, Inanda, grassy hill, 1800', Jan. 1880, J.M. Wood 974 (BOL, lecto.!!; GRA; K; NH; PRE; SAM).

I. sp. nov. 1. aff *I. verrucosa* and *I. zeyheri*. Vouchers: L.E. Codd 9272 (K, PRE); H. Bolus 8870 (K); H.G. Flanagan 2615 (PRE); van Breda 869 (PRE); Burt & Hilliard 3725 (NU). Transkei, from Mqanduli, Idutywa and Umtata districts.

I. sp. nov. 2. "*I. herrstreyi* Schrire *nom. nud.* Vouchers: A.E. van Wyk 5337 (PRE, FRU); R.G. Strey 7252 (NH, PRE), L. du Toit 114 (NH, PRE); C.H. Stirton 8071 (NH, PRE).

I. sp. nov. 3. "*I. gleichenoides* Schrire" *nom. nud.* Vouchers:
P.B. Phillipson 403 (K); *Dahlstrand* 1528 (GRA);
P. Macowan 1523 (GRA); *S.M. Johnson* 1180 (GRA);
Esterhuysen 14553 (BOL); *Schrire* 2519 (K).

8.2.4.18. Section *Hirsutae* (Rydberg) Schrire

I. astragalina DC., *Prodr.* 2 :228 (1825); N.E.Br. in *Burt Davy*, *Man. Fl. Transv.* 2 :371 (1932); *Gillett*, *Kew Bull.*, *Add. Ser.* 1 :110 (1958); in *Kew Bull.* 14 :290 (1960); in *Kew Bull.* 24 :500 (1970); in *Fl. Trop. E. Afr.*, *Legum.- Papil.* 1 :310 t.45 (1971); *Ali*, *Fl. W. Pak.* 100 :79 (1977); *Thulin* in *Hedberg & Edwards*, *Fl. Ethiopia* 3 :135 (1989). Type: Senegal, 15.1.1825 in herbarium DC. 228:66, *Perrottet* 143 (G, holo.!).

I. giesii Schreiber in *Mitt. Bot. Munchen* 8: 140 t.2 (1970); in *Prodr. Fl. SWA* 60:57 (1970), Type: Namibia, Ovamboland, 4.6 m SE. of Oshandi, 15.2.1959, *de Winter & Giess* 7022 (M, holo.).

I. hirsuta L., *Sp.Fl.* 751 (1753); *Bak.f.*, *Leg. Trop. Afr.* 1 :146 (1926); *Ali* in *Bot. Notis* 3 :559 (1958); *Gillett*, in *Kew Bull.*, *Add. Ser.* 1 :109 (1958); in *Kew Bull.* 14 :290 (1960); in *Kew Bull.* 24: 500 (1970); in *Fl. Trop. E. Afr.*, *Legum.- Papil.* 1 :310 t.45 (1971); *Verdc.*, *Man. New Guinea Legum.* :351 (1979); *de Kort & Thijssse*, *Blumea* 30 :120 (1984); *Thulin* in *Hedberg & Edwards*, *Fl. Ethiopia* 3 :135 (1989). *non* Harv., in *Harv. & Sond.*, *Fl. Cap.* 2 :194 (1862). Type: Sri Lanka, *Hermann* 172 vol. 1, fol. 60 (BM, holo.!).

I. longebarbata Engl., *Hochgebirgsflora Afrikas* :257 (1892); *Bak.f.*, *Leg. Trop. Afr.* 1 :147 (1926); *Gillett*, *Kew Bull.*, *Add. Ser.* 1 :109 (1958); in *Fl. Trop. E. Afr.*, *Legum.- Papil.* 1 :309 (1971); *Compton*, *Fl. Swazi.* :262 (1976); *Thulin* in *Hedberg & Edwards*, *Fl. Ethiopia* 3 :135 (1989). Type: N. Ethiopia, nr. Debra Tabor, 2300m, 15.7.1863, *W. Schimper* 1389 (K, iso.!: 2).

I. hirsuta sensu Harv. in Harv. & Sond., Fl. Cap. 2 :194
(1862) non L.

I. schlechteri Bak.f., Viertel. Nat. Ges. Zurich 49 :192
(1904); N.E.Br. in Burt Davy, Man. Fl. Transv. 2 :371
(1932). *I. griquana* Schltr. ex A.Zahlbr., Ann. Nat. Hof. Mus.
Wien 20 :23 (1905). Type: Natal, in graminosis mont. Insiswa,
2200m, *R. Schlechter* 6499 (Z, lecto.!; GRA).

8.2.4.19. Section *Microcarpae* (Rydberg) Schrire

I. microcarpa Desv., Journ de Bot. ser. 2, 3 :79 (1814); Gillett,
Kew Bull., Add. Ser. 1 :110 (1958); in Fl. Trop. E. Afr., Legum.-
Papil. 1 :312 (1971); Thulin in Hedberg & Edwards, Fl. Ethiopia 3
:135 (1989). Type: Brazil, unknown collector (P, holo.).

8.2.4.20. Section *Setiflorae* Schrire

I. atrata N.E.Br. in Burt Davy, Man. Fl. Transv. 2 :xxiii & :369
(1932). Type: Transvaal, in graminosis pr. Bergendale, 6200',
20.12.1893, *R. Schlechter* 4007 (K, holo.!; BM; GRA; PRE; Z).

I. cecili N.E.Br. in Kew Bull. 1906 :101 (1906); Gillett, Kew
Bull., Add. Ser. 1 :83 (1958). Type: Zimbabwe, Manika, Inyanga
Mts., 6000-7000', Dec. 1899, *E. Cecil* 186 (K, holo.).

I. commixta N.E.Br. in Kew Bull. 1925 :152 (1925); in Burt Davy,
Man. Fl. Transv. 2 :369 (1932). Type: Transvaal, Bloemhof Distr.,
on top of a kopje on the farm Kaffraria nr. Christiana, 13.3
1912, *J. Burt Davy* 13228 (PRE, holo.).

I. comosa N.E.Br. in Kew Bull. 1925 :153 (1925); in Burt Davy,
Man. Fl. Transv. 2 :370 (1932); Compton, Fl. Swazi. :260 (1976).
Type: Transvaal, Pretoria Distr., colles supra Aapiesriver, *A.
Rehmann* 4397 (K, holo.!; Z).

I. malacostachys Benth. ex Harv. var. *seminuda* N.E.Br. in Burt Davy, Man. Fl. Transv. 1 :44 (1926). Type: Transvaal, Pretoria, 19.11.1901, *J.W.E. Kirk 14* (K, holo.).

I. confusa Prain & Bak.f., J. Bot. 40 :143 (1902). *I. arrecta* Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :183 (1862). Type: Transvaal, Pretoria, Distr., Mooi River, Dec., *Zeyher 474* (K, holo.; S; SAM).

I. pretoriana Harms in O. Kuntze, Rev. Gen. 3(2) :52 (1898). Type: Transvaal, Pretoria, 1500m, 17.2.1894. 1500m, O. Kuntze s.n. (K, iso.,PRE).

I. egens N.E.Br. in Burt Davy, Man. Fl. Transv. 2 :xiv & :369 (1932). Type: Transvaal, Boshveld, Pienaarsrivier, *A. Rehmann 4798* (K, holo.; Z).

I. eriocarpa E. Mey., Comm. :103 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :194 (1862). Type: Natal, in collinis dumosis prope Port Natal, alt. 400' (V, c), 26.3.32, *Drege 5424* (P, lecto.).

Anila eriocarpa (E. Mey.) O. Kuntze, Rev. Gen. 3(2) :51 (1898). Type: Natal, Clairmont, Krantzklouf, O. Kuntze s.n. (K, iso.).

I. melanadenia Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :195 (1862); Gillett, Kew Bull., Add. Ser. 1 :83 (1958). Type: OFS, Doornkop, April, *Zeyher 481* (K, holo.; S; SAM).

I. malacostachys Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :184 (1862); N.E.Br. in Burt Davy, Man. Fl. Transv. 2 :370 (1932); Compton, Fl. Swazi. :262 (1976). Type: Transvaal, Magaliesberg, Nov. *Zeyher 478* (K, holo.; S; SAM).

I. malacostachys Benth. ex Harv. var. *macrura* Conrath ex Bak.f. in Viertel. Nat. Ges. Zurich 49 :188 (1904). Type: Transvaal, Irene bei Pretoria, 1.1898, *P. Conrath 223* (Z, holo.; K).

I. mollicoma N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :xiv & :370 (1932); Compton, Fl. Swazi. :262 (1976). *I. nelsonii* N.E.Br. in Kew Bull. 1925 :154 (1925) *non* Rydberg in N. Amer. Fl. 24 :150 (1923), *nom. illegit.* Type: Transvaal, Waterberg Distr., Nylstroom at Sandfontein, Aug. 1880, *W. Nelson* 292 (K, holo.).

I. oxytropis Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :193 (1862); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :370 (1932). Type: Transvaal, Magaliesberg, Nov., *Zeyher* 477 (K, holo.; S; SAM).

I. pongolana N.E.Br. in Kew Bull. 1925 :154 (1925); in Burtt Davy, Man. Fl. Transv. 2 :371 (1932). Type: Transvaal, Waterberg Distr., in drainage basin of Pongola River, Dec. 1919, *J. Burtt Davy* 18235 (K, holo.).

I. reducta N.E.Br. in Burtt Davy, Man. Fl. Transv. 1 :44 (1926). *I. atrinota* N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :xxiii & :369 (1932). Type: Transvaal, in saxosis mont. Houtboschberg (2329DD), 5800', 7.2.1894, *R. Schlechter* 4412 (K, holo.; BOL; GRA; PRE).

I. rehmannii Bak.f. in Viertel. Nat. Ges. Zurich 49:190 (1904); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :371 (1932). Type: Transvaal, Houtbosch, *A. Rehmann* 6224 (Z, holo.; K, photo.).

I. sanguinea N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :xiv. & :370 (1932); Compton, Fl. Swazi. :263 (1976). Type: Transvaal, bei der stadt Lydenburg, Sept. 1895, *F. Wilms* 345 (K, holo.; BM; NU; PRE; W; Z).

I. setiflora Bak. in Fl. Trop. Afr. 2 :90 (1871); Bak.f., Leg. Trop. Afr. 1 :146 (1926); Gillett, Kew Bull., Add. Ser. 1 :82 (1958); in Fl. Tr. E. Afr., Legum.- Papil. 1 :286 (1971). Type: Angola, Huilla, Benguela, *Welwitsch* 2020 (K, iso.).

I. accepta N.E.Br. in Kew Bull. 1925 :153 (1925); in Burtt Davy, Man. Fl. Transv. 2 :370 (1932). Type: Transvaal, The

Downs, Pietersburg Div., 12.1917, *F.A. Rogers* 21995 (K, holo.!; BOL; PRE).

I. velutina E. Mey., *Comm.* :104 (1836); Harv. in Harv. & Sond., *Fl. Cap. 2* :194 (1862). Type: Cape, ad fluvium quendam minorum haud procul ab Omsamcaba, alt. 800' (V, b), 20.2.32, *Drege* 5430 (P, lecto!).

I. williamsonii (Harv.) N.E.Br. in Burt Davy, *Man. Fl. Transv.*, 1 :45 (1926); Gillett, *Kew Bull., Add. Ser.* 1 :83 (1958) pro parte. *I. eriocarpa* E.Mey. var. *williamsonii* Harv. in Harv. & Sond., *Fl. Cap. 2* :194 (1862). Type: Natal, Port Natal, *I. Williamson s.n.* (TCD, holo.!; K).

I. sp. nov. 1. aff. *I. egens*. Vouchers: *Acocks* 23599 (PRE); *J. van Son Herb.Tvl.* 30441 (K); *R.H. Westfall* 868 (K, PRE). Transvaal, Thabazimbi, Kransberg and Rankins Pass area of the Waterberg.

I. sp. nov. 2. aff. *I. reducta*. Vouchers: *G.K. Theron* 3498 (PRE); *N. Jacobsen* 1522 (PRE); *H.S. Mathews* 847 (PRE). Transvaal, Ohrigstad Nature Reserve (2430DC).

I. sp. nov. 3. Vouchers: *R.A. Dyer & L.E. Codd* 9048 (K, PRE); *H.J. Schlieben* 7527 (K); *E. Esterhuysen* 21450 (BOL, K); *Strey & Schlieben* 8491 (K); *R.H. Archer* 375 (PRE); *H.P. van der Schijff* 5343 (PRE). Transvaal, Blaauw-berg area W. of Zoutpansberg.

I. sp. nov. 4. Vouchers: *H.J. Schlieben* 7324 (K); *J.B. Gillett* 2879 (K). Transvaal, east of Louis Trichardt and around Wylies Poort in the Zoutpansberg.

I. sp. nov. 5. aff *I. melanadenia* and *I. comosa*. Vouchers: *E.E. Galpin* 4463 (K); *L. Coetzer* 142 (K); *G. Germishuizen* 169 (K, PRE); *J.P. Kluge* 2142 (PRE); *C.H. Stirton* 1822 (K); *P.J. Muller & J.C.*

Scheepers 188 (K, PRE); *F. Venter* 1148 (K, PRE).
E. Transvaal from the Pilgrims Rest to Letaba
Districts,

I. sp. nov. 6. "*I. gogosa* Schrire" *nom. nud.*. Vouchers: *Abbott*
3335 (NH, PRU); *O.M. Hilliard* 1138 (NH); *Schrire*
2344 (K).

8.2.4.21. Section *Viscosae* (Rydberg) Schrire

I. adenocarpa E. Mey., *Comm.* :105 (1836); *Harv.* in *Harv. & Sond.*,
Fl. Cap. 2 :196 (1862); *Schreiber* in *Prod. Fl. SWA* 60 :49 (1970)
pro parte. Type: Cape, in collibus ad Garip, alt. 300' (III, B),
16.9.30, *Drege* 3312 (P, lecto!).

I. adenoides Bak.f. in *Viertel. Nat. Ges. Zurich* 49 :182 (1904);
N.E.Br. in *Burt Davy, Man. Fl. Transv.* 2 :368 (1932). Type:
Transvaal, Houtbosch, *A. Rehmann* 6217 (BM, holo.!; K; Z; PRE,
photo.).

I. aquae-nitentis Bremekamp in *Ann. Tvl. Mus.* 15 :241 (1933).
Type: Transvaal, Blinkwater (Pietersburg), 20.1.1931, *Bremekamp*
178 (PRE, holo!).

Doubtfully distinct from *I. dolichothyrsa* Bak.f.

I. colutea (Burm.f.) Merr. in *Philip. J. Sci.* 19 :355 (1921);
Gillett, Kew Bull., Add. Ser. 1 :65 (1958); *Schreiber* in *Prod.*
Fl. SWA 60 :53 (1970); *Gillett* in *Fl. Trop. E. Afr., Legum.-*
Papil. 1 :266 (1971); *de Kort & Thijssse, Blumea* 30:115 (1984);
Thulin in *Hedberg & Edwards, Fl. Ethiopia* 3 :127 (1989). *Colutea*
siliquosa enneaphyllos Indiae orientalis, siliquis & foliis
aversa parte pubescentibus Pluk., *Phytographia* t.166 f.3 (1691).
Galega colutea Burm.f., *Fl. Ind.* :172 (1768) *non* Willd., *Sp. Pl.*
3 :1246 (1802). *I. viscosa* Lam., *Encycl.* 3 :247 (1789). Type:
India, in herbarium Sloane vol. 95, fol. 185 (BM!).

I. seticulosa Harv. in Harv. & Sond., Fl. Cap. 2 :196 (1862).
Type: Australia, N.Territory, Port Essington, 1839, A.
Armstrong 385 (K, holo.). Harvey thought the type was from
South Africa.

I. junodii N.E.Br., Kew Bull. 1925 :147 (1925); in Burt Davy,
Man. Fl. Transv. 2 :367 (1932). Type: Transvaal, Shilovane,
Sept., *H.A. Junod* 645 (K, holo.; BM; Z).

I. delagoaensis Bak.f. ex Gillett, Kew Bull., Add. Ser. 1 :67
(1958). Type: Mozambique, Lourenco Marques Distr., 100',
30.11.1897, *R. Schlechter* 11532 (K!, holo., BM!, iso.).

I. dolichothyrsa Bak.f., Leg. Trop. Afr. 1 :130 (1926). Type:
Angola, open bush near km. 108.5 on the Mossamedes Railway,
2.5.1909, *H.H.W. Pearson* 2812 (K, lecto.).

I. ecklonii (Harv.) Schrire stat. nov. *I. heterotricha* DC. var.
ecklonii Harv. in Harv. & Sond., Fl. Cap. 2 :190 (1862). Type:
Cape, in collibus arenosis (altit. II) inter flumina "Konab et
Kat" rivers (Ceded Territory), Fr. Jun., *Ecklon & Zeyher* 1619 (S,
lecto.; MEL; SAM; TCD).

I. enormis N.E.Br. in Kew Bull. 1925 :148 (1925); in Burt Davy,
Man. Fl. Transv. 2 :367 (1932). Type: Transvaal, Waterberg
Distr., nr. Potgietersrust, 1.1909, *R. Leendertz* 1948 (K,
holo.; PRE).

I. grata E. Mey., Comm.: 103 (1836); Harv. in Harv. & Sond., Fl.
Cap. 2 :194 (1862). Type: Natal, ad ostia fluvii Omsamculo, (V,
c), 4.3.32, *Drege* 5416 (P, lecto.).

I. heterotricha DC., Prodr. 2 :227 (1825); Harv. in Harv. &
Sond., Fl. Cap. 2 :189 (1862) non var. *ecklonii* Harv.; N.E.Br. in
Burt Davy, Man. Fl. Transv. 2 :368 (1932); Gillett, Kew Bull.,
Add. Ser. 1 :63 (1958); Schreiber in Prod. Fl. SWA 60 :57
(1970). Type: Cape, at Klipfontein, Griqualand West Div.,

29.12.1812, in herbarium DC. 227:61, *Burchell* 2635 (G, holo.!, K).

I. rudis N.E.Br. in Kew Bull. 1925 :149 (1925); . Type: Transvaal, Zoutpansberg Distr., Messina, 1917, *F.A. Rogers* 19485 (PRE, holo.; BOL; K).

I. ingrata N.E.Br. in Kew Bull. 1925 :150 (1925); in Burtt Davy, Man. Fl. Transv. 2 :368 (1932). Type: Transvaal, Lilliput, Zoutpansburg Distr., 1950', 2.2.1919, *F.A. Rogers* 22535 (K!).

I. lydenburgensis N.E.Br. in Kew Bull. 1925 :149 (1925); in Burtt Davy, Man. Fl. Transv. 2 :368 (1932); Gillett, Kew Bull., Add. Ser. 1 :63 (1958). Type: Transvaal, bei der stadt Lydenburg, 10.1894, *Wilms* 310 (K, holo.!, BM; G; P).

I. mimosoides Bak. in Fl. Trop. Afr. 2 :90 (1971); Gillett in Fl. W. Trop. Afr., ed. 2, 1 :540 (1958); in Kew Bull., Add. Ser. 1 :63 (1958); in Fl. Trop. E. Afr., Legum.- Papil. 1 :262 (1971). Type: Angola, Huila, *Welwitsch* 2045 (LISU, lecto.; BM).

var. *mimosoides*

I. pauciflora Eckl. & Zeyh., Enum :244 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :196 (1862). Type: Cape, inter frutices (altit. IV) montium prope flumen "Elandsrivier" (Uitenhage), Mart., *Ecklon & Zeyher* 1618 (S, lecto.!, MEL).

I. elliptica E. Mey., Comm. :99 (1836) non Roxb., Fl. Ind. 3 :380 (1832). Type: Unknown locality, *Drege* 6686 (P, lecto.!).

I. pearsonii Bak.f., Leg. Trop. Afr. 1 :132 (1926). Type: Namibia, bed of Tsondab River above Abbabies, 30.12.1915, *H.H.W. Pearson* 9121 (K!, holo.!).

Doubtfully distinct from *I. dolichothyrsa* Bak.f.

I. pechuelii O. Kuntze in Berlin Jahrb. K. Bot. Gart. :263 (1886). Type: Namibia, Tsachab River, O. Kuntze (?NY, holo.).

I. fleckii Bak.f. in Viertel. Naturf. Ges. Zurich 49 :185 (1904); Schreiber in Prod. Fl. SWA 60 :56 (1970). Type: Cape, Great Namaqualand, Orange River, *Fleck 611* (Z, lecto!).

Doubtfully distinct from *I. heterotricha* DC.

I. poliotes Eckl. & Zeyh., Enum. :242 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :185 (1862). Type: Cape, inter frutices (Altit. III) collium in "Adow" (Uitenhage), Sept., *Ecklon & Zeyher 1609* (S, lecto!; SAM; TCD).

I. rupestris Eckl. & Zeyh., Enum. :241 (1836). Type: Cape, inter saxa (altit. V) laterum montis "Winterberg" (Kafferland), frut. Jan., *Ecklon & Zeyher 1603* (S, lecto!).

I. punctata sensu Eckl. & Zeyh., Enum. :241 (1836) non Thunb.

I. adonensis E. Mey. Comm. :99 (1836). Type: Cape, Ado, in graminosis, alt. 1200' (V, a), 5.12.29, *Drege s.n.* (P, lecto!).

I. setosa N.E.Br., Kew Bull. 1912 :274 (1912). *I. seticulosa* Harv. var. *luxurians* H. Bol. in Journ. Bot. 34:24 (1896). Type: Natal, Inanda, on a grassy hill at Umhloti, 2.2.1882, *J.M. Wood 1602* (K, holo!; NH; PRE).

I. sordida Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :190 (1862); N.E.Br., in Burt Davy, Man. Fl. Transv. 2 :368 (1932); Gillett, Kew Bull., Add. Ser. 1 :62 (1958). Type: Transvaal, Aapies River, Oct., *Zeyher 480* (K, holo!; G; SAM; TCD).

I. sordida Benth. ex Harv. var. *eglandulosa* N.E.Br. nom. nud.

I. graniticola Dinter nom. nud.

- I. sp. nov.* 1. Voucher: *D. van Druten s.n.* (K, PRE), Transvaal, Rust de Winter and Skilpadfontein.
- I. sp. nov.* 2. aff *I. adenoides*. Vouchers: *A. Balsinhas 3592* (K, PRE); *L.E. Codd 4171* (K, PRE); *H.J. Schlieben 7422* (K); *Rogers 21851* (GRA). Transvaal, Zoutpansberg W of Louis Trichardt.
- I. sp. nov.* 3. Voucher: *P.M. Croeser 41* (PRE). Transvaal, Olifants River Bridge on the Tzaneen/Hoedspruit road.
- I. sp. nov.* 4. aff. *I. heterotricha* and *I. dolichothyrsa*. Voucher: *Acocks 13485* (PRE). Natal, near Muden.
- I. sp. nov.* 5. Vouchers: *Schlieben 9003* (PRE); *H.H.W. Pearson 3599* (K); *H.C. Taylor 8424* (K); *Dinter 5134* (K). Namibia, Wortel to Pofadder (Namiesberge) and Warmbad; N.Cape, Kenhardt district
- I. sp. nov.* 6. Vouchers: *Burchell 1939* (K); *Acocks & Hafstrom 1526* (PRE); *A. Brueckner 484* (K, PRE); *Campbell 1476* (K).

8.2.4.22. Section *Hilares* Schrire

- I. buchananii* Burtt Davy in Kew Bull. 1921 :49 (1921); N.E.Br in Burtt Davy, Man. Fl. Transv. 2 :367 (1932); Compton, Fl. Swazi. :260 (1976). Type: Transvaal, Ermelo dist., Lion's Glen near Amsterdam, 27.1.1909, *J.B. Buchanan T.D.A.Herb. 4779* (BOL, holo.!; K; PRE).
- I. crebra* N.E.Br. in Kew Bull. 1925 :150 (1925); in Burtt Davy, Man. Fl. Transv. 2 :368 (1932); Compton, Fl. Swazi. :260 (1976). Type: Swaziland, Hlatikulu, Jan. 1911, *M.M. Stewart 26* (K, holo.!).

I. hilaris Eckl. & Zeyh., Enum. :241 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :188 (1862); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :368 (1932); van Druten in Fl. Fl. Afr. 32, t.1247 (1957); Gillett, Kew Bull., Add. Ser. 1 :61 (1958); Compton, Fl. Swazi. :261 (1976). Type: Cape, in declivitatibus graminosis (altit IV) montis "Winterberg" ad "Philipstown" (Ceded Territory), Oct., *Ecklon & Zeyher 1605* (S, lecto.!).

I. hirta E. Mey., Comm. :101 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :182 (1862). Type: Cape, in graminosis inter Umtata et Umzavubu, alt. 1500-2000' (V, b), 2.32, *Drege 5429* (F, lecto.!).

Anila hilaris (Eckl. & Zeyh.) O. Kuntze, Rev. Gen. 3(2) :51 (1898). Type: Natal, Clairmont, *O. Kuntze s.n.* (?NY, holo.).

I. hilaris Eckl. & Zeyh. var. *drakensbergensis* Bak.f. in Viertel. Nat. Ges. Zurich 49 :186 (1904). Type: OFS, Hochebene W of van Reenen's Pass, Drakensberg, 29.12.1886, *A. Schenck 725* (Z, holo.!!; K).

I. compacta N.E.Br., Kew Bull. 1925 :151 (1925); in Burtt Davy, Man. Fl. Transv. 2 :368 (1932). Type: Transvaal, Barberton Div., Abbots Hill, 3500', 27.8.1890, *E.E. Galpin 1039* (K, holo.!!; NH; PRE; Z).

I. leipzigiae Brem. in Ann. Tvl. Mus. 15 :241 (1933). Type: Transvaal, Leipzig, at the foot of the Blaauwberg, Zoutpansberg, 17.1.31, *Bremekamp & Schweickerdt 102* (PRE, holo.!).

I. hybrida N.E.Br. in Kew Bull. 1925 :152 (1925); in Burtt Davy, Man. Fl. Transv. 2 :369 (1932); Compton, Fl. Swazi. :261 (1976). Type: Transvaal, Ermelo Distr., Spitskop, Dec. 1915, *R. Pott 5079* (PRE, holo.!!; K).

I. rubroglandulosa Germishuizen in *Bothalia* 17(1) :33 (1987).
 Type: Natal, Margate (3030CD), grassland, 25.6.1972, R.G. Strey
 10990 (PRE, holo.!, NH; K).

Doubtfully distinct from *I. crebra* N.E.Br.

I. sp. nov. 1. "*I. pondoensis* Bak.f." *nom. nud.* Vouchers: F.
 Bachmann 634 (K, Z); H. Rudatis 823 (K, Z); N.
 Grobbelaar 63 (PRE); A.E. van Wyk 5349 (PRE);
 J.L. Sidey 4187 (PRE); A.O.D. Mogg 12752 (PRE);
 Schrire 2342 (K).

I. mildrediana sensu A. Torre *non* R.Torre in Mem. Junta
 Invest. Ultram., Lisboa Ser. 2 no. 19 :52 (1960).

8.2.4.23. Section *Spinosa* (Bak.) Schrire

I. acanthoclada Dinter in Fedde Rep. 18 :427 (1922). *I.*
longispina Bak.f. ex Gillett, Kew Bull., Add. Ser. 1 :52 (1958);
 Schreiber in Prodr. Fl. SWA 60 :59 (1970). Type: Namibia, E.
 Karasberg, sandy plains NE. of Narudas sud., 1320m, 28.12.1912,
 H.H.W. Pearson 8149 (K, neo.!, GRA, SAM).

The original type, Dinter 3048, appears to have been destroyed in
 Berlin. The taxon is neotypified with the type of *I. longispina*
 Bak.f. ex Gillett.

8.2.4.24. Section *Brevipatentes* (Gillett) Schrire

I. bainesii Bak., Fl. Trop. Afr. 2 :71 (1871); Bak.f., Leg. Trop.
 Afr. 1 :102 (1926); Gillett, Kew Bull., Add. Ser. 1 :55 (1958);
 Schreiber in Prodr. Fl. SWA 60 :52 (1970). Type: Botswana, S. of
 lake Ngami, Oct.- Nov. 1861, T. Baines s.n. (K, holo.!).

I. variabilis N.E.Br. in Journ. Bot. 41 :192 (1903); in Kew
 Bull. 1909 :103 (1909); Bak.f., Leg. Trop. Afr. 1 :119

(1926); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :367 (1932) pro min parte; non De Wild. (1904). Type: Botswana, Kwebe Hills, 3400', 20.1.1898, E.J. Lugard 119 (K, lecto.!; GRA).

I. simplicifolia sensu Bremekamp & Obermeyer, Ann. Tv1. Mus. 16: 419 (1935) non Lam.

I. nebrowniana Gillett, Kew Bull., Add. Ser. 1 :54 (1958). Type: Transvaal, in saxosis mont. Magaliesbergen, 5000', 6.11.1893, Schlechter 3646 (K, holo.!; BM; GRA; Z).

I. variabilis N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :367 (1932) pro maj. parte; non N.E.Br. (1903; 1909).

I. sp. nov. 1. "*I. nervosa* Schrire nom. nud.. Vouchers:

A.J.Phelan 649 (NU); M.D.S. Nel 251 (PRE); H.J. Schlieben 10167 (PRE); B. Downing 614 (NH); Schrire 2332 (NH); J. Gerstner 2805 (K). Natal, W. Zululand.

I. sp. nov. 2. aff. *I. ruspolii* Bak.f. Vouchers : P.S. Goodman

851 (NU); K.L. Tinely 850 (NU); J.H. Ross 2231 (K, NH, PRE); N. Grobbelaar 1820 (K, PRE); M.J. Wells 2221 (PRE).

8.2.4.25. Section *Podophyllae* Schrire

I. podophylla Benth. ex Harv. in Harv. & Sond, Fl. Cap. 2 :168 (1862); in Hook.f., Icon. Pl. 18, t.1800 (1888); Gillett, Kew Bull., Add. Ser. 1 :33 (1958). Type: Mozambique, Delagoa Bay, Forbes s.n. (K, holo.!).

8.2.4.26. Section *Latistipulatae* (Bak.f.) Gillett

I. arenophila Schinz in Bull. Herb. Boiss. 6 :524 (1898); Bak.f., Leg. Trop. Afr. 1 :119 (1926); Gillett, Kew Bull., Add. Ser. 1

:22 (1958); Schreiber in Prodr. Fl. SWA 60 :50 (1970). Type: Namibia, Amboland, Oshiheke bei Olukonda, 15.3.1894, *Rautanen 215* (K, iso.).

I. antennulifera L. Bol. in Ann. Bot. Herb. 1 :188 (1915). Type: Zimbabwe, nr. Victoria Falls, *Flanagan 3089* (BOL, holo.).

I. gairdnerae Hutch. ex Bak.f., Leg. Trop. Afr. 1 :115 (1926); Gillett, Kew Bull., Add. Ser. 1 :22 (1958); Schreiber in Prodr. Fl. SWA 60 :57 (1970); Gillett in Fl. Trop. E. Afr., Legum.-Papil. 1 :227 (1971). Type: Zambia, Sesheke, island in the flooded Zambezi, April, *A.E. Gairdner 510* (K, holo.).

I. inhambanensis Klotzsch in Peters, Reise Mossamb., Bot. :48 (1861); Bak.f., Leg. Trop. Afr. 1 :120 (1926); Gillett, Kew Bull., Add. Ser. 1 :24 (1958); Schreiber in Prodr. Fl. SWA 60 :58 (1970). Type: Mozambique, Lourenço Marques, entre a Costa do Sol e Marracuene, Muntanhane, 15.11.1960, *A. Balsinhas 268* (K, neo.). The original Peters material was destroyed in Berlin.

I. polycarpa Benth ex Harv. in Harv. & Sond., Fl. Cap. 2 :191 (1862) *non* Willd. ex Spreng. (1826). Type: Mozambique, Delagoa Bay, *Forbes s.n.* (K, holo.).

I. kavangoensis Schrire *nom. nov.* *I. procumbens* Torre in Mem. Junta Invest. Ultram. ser. 2, 19 :50 t.30 (1960) *non* L. (*nom. illegit.*). Type: Angola, Bié, rio Cuito, 3.1906, *Gossweiler 3782* (COI, holo.; BM; LISJC).

8.2.4.27. Section *Laxeracemosae* Schrire

I. laxeracemosa Bak.f. in J. Bot. 41 :241 (1903); Leg. Trop. Afr. 1 :126 (1926); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :368 (1932); Gillett, Kew Bull., Add. Ser. 1: 85 (1958); in Fl. Trop. E. Afr., Legum.-Papil. 1 :287 (1971). Syntypes: *Lieut. Speke 14* Mozambique, Delagoa Bay, 1860 (K!); *W.L. Scott s.n.* Delagoa Bay,

8.1887 (K!); *Dr. J.Kirk s.n.* Kongone, mouth of Zambezi, 29.1.1861 (K!).

I. bolusiana Schltr. *nom. nud.*

I. transvaalensis Bak.f. in Mitt. Bot. Mus. Univ. Zurich 22 :193 (1904); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :367 (1932). Type: Transvaal, in arenosis pr. Zwartkopies, Pretoria, 1560m, 15.1.1894, *R. Schlechter* 4176 (BM, holo.!; BOL; GRA; K; PRE; Z).

Doubtfully distinct from *I. vicioides*.

I. vicioides Jaub. & Spach, Illustr. Fl. Orient. 5: t.481 (1856); Bak., Fl. Trop. Afr. 2 :81 (1871); Bak.f., Leg. Trop. Afr. 1 :122 (1926); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :367 (1932); Gillett, Kew Bull., Add. Ser. 1 :73 (1958); Schreiber, in Prodr. Fl. SWA. 60 :62 (1970); Gillett in Fl. Trop. E. Afr., Legum.-Papil. 1 :277 (1971); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :130 (1989). Type: N Ethiopia, Dscha Dscha, 8.7.1853, *W. Schimper* 1216 (P, holo.!).

var. *vicioides*

var. *rogersii* R.E.Fries; Gillett, Kew Bull., Add. Ser. 1 :73 (1958). *I. rogersii* R.E. Fries, Wiss. Ergeb. Schwed. Rhod. Kongo Exp. 1911-12 1 :80 (1914). Type: Zambia, *R.E. Fries* 235 (UPS, holo.).

I. varia E. Mey., Comm. :104 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :195 (1862). Type: Cape, ad ripas praeruptas fluvii Basche, alt. 500' (V, b), 28.1.32, *Drege* 5418 (P, lecto.!).

I. cognata N.E.Br. in Kew Bull. 1925 :147 (1925); in Burtt Davy, Man. Fl. Transv. 2 :367 (1932). Type: Transvaal, Nelspruit, 4.1920, *F.A. Rogers* 23929 (K, holo.!; BOL; PRE).

I. dissimilis N.E.Br. in Kew Bull. 1925 :151 (1925); in Burt Davy, Man. Fl. Transv. 2 :368 (1932). Type: *F.A. Rogers 23923 bis*. Transvaal, "probably from Barberton" (K, holo.).

I. sp. nov. 1. Vouchers: *J. Boss Herb.Tvl. 35013* (PRE), *W. Giess 10157* (PRE); *B. deWinter 2804* (K, PRE). Namibia, Waterberg Plateau in the Otjiwarongo district.

8.2.4.28. Section *Acanthonotus* (Benth.) Taub.

I. nummulariifolia (L.) Livera ex Alston in Trim., Handb. Fl. Ceylon 6, Suppl. :72 (1931); Gillett, Kew Bull., Add. Ser. 1 :8 (1958); Torre in Consp. Fl. Angol. 3 :100 (1962); Schreiber in Prodr. Fl. SWA 60 :59 (1979); Gillett in Fl. Trop. E. Afr., Legum.- Papil. 1 :217 (1971). *Hedysarum nummularifolium* L., Sp. Pl. :746 (1753). Type: Sri Lanka, *Hermann s.n.* (BM, holo.).

I. echinata Willd., Sp. Pl. 3 :1222 (1802); Bak., Fl. Trop. Afr. 2 :69 (1871); Bak.f., Leg. Trop. Afr. 1 :96 (1926). Type: India, Madras, Tranquebar, in herbarium Willdenow 13882 (B, holo.).

8.2.4.29. Section *Ameocarpus* (Benth. ex Harv.) Taub.

I. charlieriana Schinz in Verh. Bot. Ver. Brand. 30 :165 (1889); Gillett, Kew Bull., Add. Ser. 1 :17 (1958); Schreiber in Prodr. Fl. SWA 60 :52 (1970); Gillett in Fl. Trop. E. Afr., Legum.- Papil. 1 :224 (1971). Type: Namibia, Olukonda, Feb. 1886, *H. Schinz 244* (Z, holo.!!; GRA; K).

I. aspera auct. non Ferr. ex DC.

var. *charlieriana*

var. **scaberrima** (Schinz) Gillett, Kew Bull., Add. Ser. 1 :17 (1958). *I. scaberrima* Schinz in Verh. Bot. Ver. Brand. 30 :163 (1889). Type: Namibia, Dombale, *H. Schinz* 232 (Z, holo.!!; K).

I. relaxata N.E.Br. in Kew Bull., 1925 :148 (1925); in Burt Davy, Man. Fl. Transv. 2 :367 (1932). Type: Transvaal, Warmbaths, Jan. 1909, *R. Leendertz* 2094 (K, holo.!!; PRE).

var. **lata** Gillett, Kew Bull., Add. Ser. 1 :17 (1958). Type: Namibia, Klein Karas, 800m, 15.9.31, *I. Ortendahl* 273 (UPS, holo.!!; K, photo.).

I. circinnata Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2: 202 (1862); N.E.Br. in Burt Davy, Man. Fl. Transv. 2 :367 (1932); Gillett, Kew Bull., Add. Ser. 1 :11 (1958). Type: Transvaal, Magaliesberg, Oct., *Burke* 355 (K, lecto.!!; PRE; SAM; TCD).

I. damarana Merxm. & Schreiber in Bull. Jard. Bot. Brux. 27 :274 t.9 (1957); Schreiber in Prod. Fl. SWA 60 :55 (1970). Type: Namibia, Rehoboth, Gravenstein, 22.2.1956, *Volk* 11568 (M, holo.).

I. wilmaniae Bak.f. ex Gillett, Kew Bull., Add. Ser. 1 :15 (1958). Type: N.Cape, Hay Div., Niekerks Hoop, red sand, frequent, Mar. 1921, *M. Wilman* 1384 (K, holo.!!; BOL; BM).

I. hochstetteri Bak., Fl. Trop. Afr. 2 :101 (1871); Gillett, Kew Bull., Add. Ser. 1 :13 (1958); in Fl. Trop. E. Afr., Legum.-Papil. 1 :223 (1971); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :122 (1989). Type: N. Ethiopia, *W. Schimper* (P, holo.).

subsp. **streyana** (Merxm.) Schreiber in Mitt. Bot. Munchen 2 :293 (1957); in Prod. Fl. SWA 60 :58 (1970). *I. streyana* Merxm. in Mitt. Bot. Munchen 1 :89 (1951). Type: Namibia, Bullspoor, 24.6.1950, *R.G. Strey* 2630 (M, holo.; K; PRE).

I. hochstetteri Bak. subsp. *hochstetteri* auct. non Bak.

I. holubii N.E.Br. in Kew Bull. 1925 :148 (1925); in Burt Davy, Man. Fl. Transv. 2 :367 (1932); Gillett, Kew Bull., Add. Ser. 1 :12 (1958); Schreiber in Prod. Fl. SWA 60 :58 (1970). Type: Transvaal, in Marico Distr., *Dr. Em. Holub s.n.* (K, lecto!).

I. leendertziae N.E.Br. in Burt Davy, Man. Fl. Transv. 2 :xxiv & :367 (1932); Gillett, Kew Bull., Add. Ser. 1 :12 (1958). *I. torulosa* E. Mey. var. *praecalva* N.E.Br. in Burt Davy, Man. Fl. Transv. 1 :45 (1926). Type: Transvaal, Waterberg Distr. Potgietersrust, Jan. 1909, *R. Leendertz 1942* (K, holo!).

Possibly not distinct from *I. torulosa* E. Mey.

I. praticola Bak.f. in Viertel. Nat. Ges. Zurich 70 :218 (1925); Gillett in Kew Bull., Add. Ser. 1 :14 (1958); in Fl. Trop. E. Afr., Legum.-Papil. 1 :223 (1971). Type: Zimbabwe, Panda ma, Tenka, 1887, *Holub s.n.* (Z, holo.; BM!).

I. rautanenii Bak.f. in Viertel. Nat. Ges. Zurich 49 :189 (1904); Gillett, Kew Bull., Add. Ser. 1 :12 (1958); Schreiber in Prod. Fl. SWA 60 :60 (1970). Type: Namibia, Otjikango, 30.1.1903, *Rautanen 464* (Z, holo.!, G; K; PRE, photo.).

I. rhytidocarpa Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :202 (1862); Gillett in Kew Bull., Add. Ser. 1:12 (1958). Type: OFS, Thabanchu, Feb. & Vet River, Mar., *Burke & Zeyher s.n.* (K, holo!).

subsp. rhytidocarpa

I. sessilifolia DC., Prodr. 2 :231 (1825); Harv. in Harv. & Sond., Fl. Cap. 2 :202 (1865); Gillett, Kew Bull., Add. Ser. 1 :11 (1958); Schreiber in Prod. Fl. SWA 60 :61 (1970). Type: N.Cape, Griqualand West, Hay Div., on the Asbestos Mtns. at the Kloof village. 16.2.1812, in herbarium DC. 231:102, *Burchell 2039* (G, lecto.!, K).

I. patens Eckl. & Zeyh., Enum. :236 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :201 (1862). Type: Cape, in lapidosis (altit. III, IV) prope "Silo" ad flumen "Klipplaatrivier" (Tambukiland), Nov., *Ecklon & Zeyher 1580* (S, lecto!).

I. hedranophylla Eckl. & Zeyh., Enum. :232 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :201 (1862). Type: Cape, in frutices (altit. II) ad "Konabshoogde" et prope "Fort Beaufort" (Ceded Territory). Fr. Jul., *Ecklon & Zeyher 1560* (S, lecto!; SAM).

I. falcata E. Mey, Comm :93 (1836) var. *glaberrima* E. Mey.; Harv. in Harv. & Sond., Fl. Cap. 2 :201 (1862). Type: Cape, in collibus saxosis siccis prope Flatdrift, 2400' (II, d), 16.3.27, *Drege 904* (P, lecto!).

I. falcata E. Mey, Comm :93 (1836) var. *pubescens* E. Mey., Comm. :94 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :201 (1862). Type: Cape, prope Bitterwater, 2300' (II, d), 23.3.27 *Drege s.n.* (P, lecto!).

I. meloloboides Benth. *nom. nud.*

I. torulosa E. Mey., Comm. :105 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :202 (1862); N.E.Br in Burt Davy, Man. Fl. Transv. 2 :367 (1932); Gillett, Kew Bull., Add. Ser. 1 :12 (1958). Types: Cape, ad ripas praeruptas fluvii Basche, alt. 500' (V, b), 26.1.32, *Drege 5417* (P, lecto!).

var. *torulosa*

var. *angustiloba* (Bak.f.) Gillett, Kew Bull., Add. Ser. 1 :12 (1958); N.E.Br. in Burt Davy, Man. Transv. 2 :367 (1932). *I. angustiloba* Bak.f., Viertel. Nat. Ges. Zurich. 49 :183 (1904). Type: Transvaal, Lydenburg Distr., bei der stadt Lydenburg, Nov. 1889, fl. & fr., *F. Wilms 321* (BM, holo!; K; Z).

I. sp. nov. 1. aff. *I. rautanenii*. Vouchers: *H. Merxmüller* & *W. Giess* 30635 (K); *W. Giess* 8984 (PRE); *de Winter* & *Leistner* 5757 (K); 5830 (K). Namibia, Outjo and Kaokoveld areas.

8.2.4.30. Section *Demissae* Gillett

I. demissa Taub. in Engl., Pflwelt. O. Afr. C :209 (1895); Bak.f., Leg. Trop. Afr. 1 :98 (1926); Gillett, Kew Bull., Add. Ser. 1 :18 (1958); in Fl. Trop. Afr., Legum.- Papil. 1 :225 (1971). Type: Malawi, *Buchanan* 1163 (K, lecto!).

8.2.4.31. Section *Sphaeridiophora* (Desv.) Taub.

I. anabibensis Schreiber in Mitt. Bot. München 8 :137 t.1 (1970), in Prodr. Fl. SWA 60 :50 (1970). Type: Namibia, Kaokoveld, 6 m S. of Orupembe, 10.6.1963 (M, holo.; WIND).

I. flavicans Bak., Fl. Trop. Afr. 2 :73 (1871); N.E.Br. in Kew Bull. 1909 :102 (1909); Bak.f., Leg. Trop. Afr. 1 :110 (1926); N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :371 (1932); Gillett, Kew Bull., Add. Ser. 1 :116 (1958); Schreiber in Prodr. Fl. SWA 60 :56 (1970). Type: Botswana, SW. of Lake Ngami, Oct.- Nov. 1861, *T. Baines s.n.* (K, holo!).

I. trigonelloides Jaub. & Spach, Ill. Fl. Or. 5, t.482 (1856); Bak., Fl. Trop. Afr. 2 :79 (1871); Bak.f., Leg. Trop. Afr. 1 :116 (1926); Gillett, Kew Bull., Add. Ser. 1 :35 (1958); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :123 (1989). Type: Ethiopia, Gageros, ad flumen Tecase, 3000 - 4000', 1.9.1853, *H. Schimper* 1523 (P, holo!).

I. sp. nov. 1. aff *I. trigonelloides*. Voucher: *R. Seydel* 273 (PRE). Namibia, Naibriver area.

8.2.4.32. Section *Alternifoliolae* (Harv.) Schrire

I. alternans DC., Prodr. 2 :229 (1925); Harv. in Harv. & Sond., Fl. Cap. 2 :199 (1862); N.E.Br. in Burt Davy, Man. Fl. Transv. 2 :372 (1932); Gillett, Kew Bull., Add. Ser. 1 :120 (1958); Schreiber in Prodr. Fl. SWA 60 :50 (1970) *non* E. Mey., Comm. :107 (1836). Type: N.Cape, Griqualand West, plains at the foot of the Asbestos Mtns., between the Kloof Village and Witte Water, 17.2.1812, in herbarium DC. 229:73, *Burchell 2079* (G, holo.); K).

var. *alternans*

I. effusa E. Mey., Comm. :107 (1836). Type: Cape, in planitie sicca prope Colesberg, 4200' (I, b), 25.2.33, *Drege 690* (P, lecto.).

Anila alternans (DC.) O. Kuntze, Rev. Gen., 3(2) :50 (1898). Type: Cape, Cradock, Modderivier, Middelburg rd., 940m, 12.2.1894, *O. Kuntze s.n.* (K, iso.).

I. enneaphylla sensu Eckl. & Zeyh., Enum. :244 (1836) *non* L., Mant. 2 :272 (1771) *nec* Bak., Fl. Trop. Afr. 2 :95 (1871).

I. auricoma E. Mey., Comm. :107 (1836); Harv. in Harv. & Sond., Fl. Cap. 2 :200 (1862); Gillett, Kew Bull., Add. Ser. 1 :121 (1958); Schreiber in Prodr. Fl. SWA 60 :51 (1970). Type: Cape, in collibus saxosis prope Verleptpram, 500' (III, B), 20.9.30, *Drege s.n.* (P, lecto.).

I. auricoma E. Mey. var. *cuneata* Bak.f. in Viertel. Nat. Ges. Zurich 49 :184 (1904); Leg. Trop. Afr. 1 :137 (1926). Type: Namibia, *Nels 263* (Z, holo.).

I. cunenensis Torre in Mem. Junta Invest. Ultramar. Ser. 2, 19 :58 t.38 (1960); Schreiber in Prodr. Fl. SWA 60 :59 (1970). Type: Angola, Mossamedes, foz do rio Cunene, 15.1.56, *Mendes 1295* (LISC, holo.).

Doubtfully distinct from *I. benguellensis* Bak., Fl. Trop. Afr. 2 :87 (1871). Type: Angola, Mossamedes, *Welwitsch 2061* (BM, holo.!; K).

I. daleoides Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :200 (1862); Bak.f., Leg. Trop. Afr. 1 :137 (1926); N.E.Br. in Burt Davy, Man. Fl. Transv. 2 :370 (1932); Gillett, Kew Bull., Add. Ser. 1 :117 (1958); Schreiber in Prodr. Fl. SWA 60 :55 (1970). Type: Transvaal, Magaliesberg, *Zeyher 479* (K, lecto.!; BOL; G; S; SAM).

var. *daleoides*

I. daleoides var. *dammarensis* Bak.f. in Journ. Bot. :327 (1903). Type: Namibia, Damaraland, *T.G. Een s.n.* (BM, holo.).

var. *gossweileri* Bak.f., Leg. Trop. Afr. 1 :138 (1926); Gillett, Kew Bull., Add. Ser. 1 :118 (1958). Type: Angola, Benguella, *Gossweiler 4944* (K, holo.).

I. hololeuca Benth. ex Harv. var. *angolensis* Bak.f., Leg. Trop. Afr. 1 :137 (1926). Type: Angola, *Pearson 2354* (K, holo.).

I. exigua Eckl. & Zeyh, Enum. :244 (1836) non E. Mey., Comm. :108 (1836). Type: Cape, in solo limoso (altit. II) collium prope flumen "Olifantsrivier" (Clanwilliam), Oct., *Ecklon & Zeyher 1620* (S, lecto.).

I. arenaria E. Mey., Comm. :107 (1836). Type: Cape, in collibus arenosis prope Ebenezer, 300' (III, E, a), 6.11.33, *Drege 6688* (P, lecto.).

I. hololeuca Benth. ex Harv. in Harv. & Sond., Fl. Cap. 2 :200 (1862); Gillett, Kew Bull., Add. Ser. 1 :121 (1958). *I. alternans* sensu E. Mey., Comm. :107 (1836) non DC. Type: Cape, Gariep, near Verleptpram, 300', 17.9.30, *Drege s.n.* (K, holo.!; G; P).

I. maritima Bak., Fl. Trop. Afr. 2 :89 (1871); Bak.f., Leg. Trop. Afr. 1 :136 (1926); Gillett, Kew Bull., Add. Ser. 1 :118 (1958); Schreiber in Prodr. Fl. SWA 60 :59 (1970). Type: Angola, Mossamedes, Benguela, sandy sea shore, *Welwitsch 2061b* (K, Piso.!).

I. neglecta N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :xxiv & :371 (1932). Type: Transvaal, Crocodile river, Oct., *Burke s.n.* (K, holo.!).

I. oxalidea Welw. ex. Bak., Fl. Trop. Afr. 2 :86 (1871); Bak.f., Leg. Trop. Afr. 1 :134 (1926); Gillett, Kew Bull., Add. Ser. 1 :120 (1958). Type: Angola, Huilla, Benguela, *Welwitsch 2023* (BM, holo.!!; K).

I. supralevis N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :xxv & :371 (1932). Type: Transvaal, Lydenburg, bei der stadt, Dec.1895, *F. Wilms 287* (K, holo.!).

I. radicifera Cronquist in Bull. J. Bot. Et. Brux. 22 :223 (1952); Gillett, Kew Bull., Add. Ser. 1 :120 (1958); in Fl. Trop. E. Afr., Legum.- Papil. 1 :318 (1971). Type: Tanzania, Ufipa Distr., shore of Lake Tanganyika, Msamba, *van Meel 1212* (BR, holo.).

I. schimperi Jaub. & Spach, Ill. Pl. Or. 5, t.484 (1856), Bak.f., Leg. Trop. Afr. 1 :138 (1926); Gillett, Kew Bull., Add. Ser. 1 :116 (1958); Schreiber in Prodr. Fl. SWA 60 :60 (1970); Gillett in Fl. Trop. E. Afr., Legum.- Papil. 1 :313 (1971); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :136 (1989). Type: Ethiopia, ad montes prope Dscha-Dscha, alt. 5500', Jul. 1852, *W. Schimper 1218* (P, holo.!).

I. tettensis Klotzch in Peters, Reise Mossamb., Bot. 1 :51 (1861); Bak.f., Leg. Trop. Afr. 1 :138 (1926) pro maj. parte; N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :371 (1932). Type: Mozambique, Tete, *Peters s.n.* (B, destroyed).

var. *schimperi*

var. *baukeana* (Vatke) Gillett, Kew Bull., Add. Ser. 1 :116 (1958); in Fl. Trop. E. Afr., Legum.-Papil. 1 :314 (1971). *I. baukeana* Vatke in Dester. Bot. Zeitschr. 29 :220 (1879). Type: Kenya, Kitui, *Hildebrandt* 2787 (P, lecto.!, K).

I. spicata Forssk., Fl. Aegypt. -Arab. :138 (1775); Gillett, Kew Bull., Add. Ser. 1 :119 (1958); in Fl. Trop. E. Afr., Legum.-Papil. 1 :317 (1971); Thulin in Hedberg & Edwards, Fl. Ethiopia 3 :136 (1989). Type: Yemen, *Bolgose, Forsskal s.n.* (C, holo.!).

I. hendecaphylla Jacq., Coll. Bot. 2 :358 (1789) & Ic. Pl. Rar., 3, t.570 (1788-89). "*I. endecaphylla* Jacq." sensu Poir. in Lam., Encycl. Suppl. 3 :147 (1813); Harv. in Harv. & Sond., Fl. Cap. 2 :199 (1862); Bak.f., Leg. Trop. Afr. 1 :134 (1926). Type: Guinea, unknown collector (W, holo.!).

I. anceps Vahl ex Poir. in Lam., Encycl. Suppl. 3 :147 (1813). Type: Ghana, in herbarium de Jussieu, *Thonning s.n.* (P, holo.!).

I. endecaphylla Jacq. var. *angustata* Harv. in Harv. & Sond., Fl. Cap. 2 :199 (1862). Type: Port Natal, *Gueinzus 195* (K, lecto.!, W).

I. bolusii N.E.Br. in Burtt Davy, Man. Fl. Transv. 2 :xxiv & :371 (1932). Type: Transvaal, *Barberton, juxta ripas flum, Kaap, 1200', 9.1886, H. Bolus 7722* (K, holo.!, BOL).

I. teixeirae Torre in Mem. Junta Invest. Ultram. ser. 2, 19 :59 t.29 (1960); Schreiber in Prodr. Fl. SWA 60 : 61 (1970). Type: Angola, *Mossamedes a 40 km do a peadeiro do C.F. Dois Irmaos, Caracul, estrada do Virei, 9.5.1957, B. Teixeira 2363* (LISC, holo.; COI).

SPECIES DUBIA

I. aristata Spreng., Syst. Veg. 3:274 (1826).

I. sieberiana Scheele in Linnaea 17: 337-338 (1843).

I. bijuga Vogel ex Walp., in Linnaea 13 :523-524 (1834) based on a collection by Krebs.

8.3. Economic importance of the Indigoferaeae

The Indigoferaeae contains a considerable number of economically important plants, as illustrated below.

Many species are heavily utilised by animals, e.g. *I. ovina* (*Hedyanthae*) is relished by cattle, sheep and goats in the Cape (Allen & Allen 1981), and many others are used as fodder crops (de Kort & Thijsse 1984). As yet little research has been done into the overall forage value of *Indigofera* species. *Cyamopsis tetragonoloba*, the Calcutta lucerne or guar bean, has long been cultivated in Asia for cattle fodder and guar gum. The latter is obtained from the water soluble fraction of ground seed endosperms, and it has 5-8 times the thickening power of starch (Allen & Allen 1981). This is used in the food industry as a protective colloid and thickener, in the pharmaceutical industry as a stabiliser and binding agent, and in the mining industry as a flocculating agent. It is also used in the paper, cosmetics and explosive industries, and consumption of guar gum in the United States exceeds 6,800 metric tons annually. Seed gums also occur in *Indigofera* (Bailey 1971).

Many species of *Indigofera* contain toxic compounds (Watt & Breyer-Brandwijk 1962). Duke (1981) recorded toxic organic nitro compounds in 26 species, some containing cyanides, others being severe irritants to animal's hooves, and still others causing specific diseases in certain animals. *I. burchellii* (*Trifoliolatae*) gave positive results in the Feigl-Anger

cyanogenesis test, out of 47 southern African species analysed by R.-E. van Wyk (pers.comm.).

Diploid and tetraploid forms of *I. spicata* (*Alternifoliolae*) have been found to differ in containing a hepatotoxic aminoacid, indospicine, that interferes with the synthesis and utilisation of arginine (Bell 1972; 1978; de Kort & Thijsse 1984). The problem of some forms of *I. spicata* being a valuable fodder while others are toxic, is discussed by Dalziel (1937) and Gillett (1958). The toxic element also appears to cause abortion in cattle and death in sheep and rabbits (Gillett, 1958). Gillett (1958) also lists a number of species that are definitely toxic even in relatively small amounts.

Research into the specific toxicities of *Indigofera* is very important since the genus is a major component of most pasture systems in Africa. Van der Walt & Steyn (1939) reported that test sheep died from tympanites (bloating) when they ate large quantities of the fodder *I. sessilifolia* (*Amecarpus*). The roots of some species contain fish poisons, arrow poisons and insecticides (Allen & Allen 1981). Other toxins include a rich variety of flavonoids (Gomes *et al* 1981), canavanine (Bell 1981; Bell *et al.* 1978) and a toxic nitro-compound, karakin (Harborne 1971). Smith (1966) cites the common name of *Indigofera buchananii* (*Hilares*) as "gifbossie", or poison bush.

Historically, *Indigofera* was most important for the production of dyes (see Bentley & Trimen 1880; Allen & Allen 1981), and *I. arrecta* (*Tinctoriae*) is a Natal species which was used commercially to produce indigo (Wood 1902; Watt & Breyer-Brandwijk 1962). Many other species contain the glucoside indican although in smaller amounts. Burkill (1935) describes in detail the early history and method of manufacturing the dye. Indican is derived from indole, a benzpyrrol, which is a precursor of one of the growth hormones, indole acetic acid. The production of indican, forming a glucoside with the addition of glucose to indole, may act like other known glucosides (e.g. digitalin) in being herbivore deterrents. Yoshida & Hasegawa (1977) report the

presence of the pyrazine base alkaloid *stizolomine* in the *Psiloceratiae* and *Tinctoriae*.

de Kort & Thijssse (1984) mention that flowers and occasionally the seeds of certain *Indigofera* species are eaten by humans, and Allen & Allen (1981) note that *Cyamopsis* is used as a vegetable. Many species (of both genera) are suitable as soil covers and soil improvement crops, i.e. as green manure and as stabilisers (Burkill 1935; Gillett 1958; Allen & Allen 1981; de Kort & Thijssse 1984). More research is needed into using these for maintaining a vegetative cover in semi-arid environments, for controlling erosion, for cost-effective cover of road and water embankments, and in veld reclamation. *I. argyraea* (*Indigastrum*) is cited on *Codd 2465* (PRE) as having soil binding properties. This species grows well in semi-arid areas.

Medicinally, plant-part decoctions have been used as anthelmintics, febrifuges and treatments for skin diseases and heart trouble (Watt 1890; Burkill 1935; Dalziel 1937; Watt & Breyer-Brandwijk 1962; Dastur 1977; Drury 1978; de Kort & Thijssse 1984). A specimen *C.A. Smith 4323* (PRE) states that the root of *I. argyraea* is excessively bitter, and a decoction of the root is said to be used for sore eyes. Its common name is the "seer oog bossie". Indigo, itself, has been used as a remedial agent in epilepsy, infantile convulsions, chorea, hysteria and amenorrhoea (Bently & Trimen 1880).

Branches and twigs of one species of *Indigofera* are recorded by de Kort & Thijssse (1984) as being used in basket work.

A number of African species have great potential in the horticultural trade as ornamentals. *I. jucunda* Schrire (= *I. cylindrica* auct. non DC.; *Psiloceratiae*) is an attractive shrub commonly used in gardens in coastal Natal and the Highveld in South Africa, where it flowers for a considerable period of time. The woody Cape species *I. frutescens* and *I. langebergensis* (both in *Denudatae*), *I. cytisoides* (*Coriaceae*), and *I. filifolia* (*Juncifoliae*) are very striking in botanic gardens. Tropical

southern African species in the *Hedyanthae* (e.g. *I. rostrata*) and *I. podophylla* (*Podophyllae*) would also make promising subjects. Asian species are common ornamentals in Europe, and two of these, *I. heterantha* Wall. and *I. decora* Lindl. (both from China), have been cultivated very successfully in higher altitude gardens in South Africa.

Some species are weeds (Wells et al. 1986), generally with the undesirable characteristics of being competitive for space, light, water and nutrients, or occasionally they are seed contaminants. *I. heterotricha* (*Viscosae*) is recorded as replacing preferred grass vegetation, while species like *I. filipes* (*Dendroides*) are non invasive ruderals.

CHAPTER 9

CONCLUSIONS

- 1) In this study 7 genera are recognized in the Indigoferaeae compared with 4 in the last review of the tribe (Polhill 1981).
- 2) The Indigoferaeae are a monophyletic group diagnosed by a number of synapomorphies. *Indigofera* was treated as a paraphyletic group because of the regional circumscription of the study, but a survey of extra-African taxa indicates that the genus is probably monophyletic.
- 3) To reduce the very high level of homoplasy in the analysis, it was decided to study the initial tree piecemeal, by performing separate analyses on component groups of clades. The procedure involved successive resolution of each clade (from larger to smaller) as this was considered the best way to recover the most information from the data. A composite cladogram was obtained by recombining the separate analyses, i.e. by adding back, from last to first, each fully resolved group of clades.
- 4) The cladistic analyses were applied to 4570 species in 51 generic and infrageneric taxa in the Indigoferaeae (reduced to 39 taxa by combining some into larger monophyletic groups for ease of computation by the parsimony programme HENNIG86), and as a result two major levels of magnitude of variation became apparent, i.e. between:
 - i) accepted genera in the tribe
 - ii) infrageneric divisions in *Indigofera*.Accordingly:
 - a) *Vaughania* is upheld as a genus comprising some 11 species restricted to Madagascar. Previously it was only treated as a monotypic genus (Moore 1920), later put into synonymy under *Indigofera* by Polhill (1981).

- b) *Indigastrum* and *Microcharis* are treated as genera, although traditionally they have been regarded as subgenera in a more broadly circumscribed *Indigofera sens. lat.* (Gillett 1958, 1971). *Vaughania*, *Indigastrum* & *Microcharis* are closely related to *Rhynchotropis* and *Cyamopsis*.
- c) 44 infrageneric taxa in *Indigofera* are treated at more or less the same rank (i.e. 41 sections and 3 subsections), rather than as a combination of subgenera and sections as in previous treatments. 18 infrageneric taxa are newly described and a further 18 are given new combinations.
- 5) *Indigastrum* comprises two subgenera (with subgenus *Argyraeae* Schrire, being newly described here).
- 6) *Phylloxylon* is considered basal in the tribe because it does not share a number of characters synapomorphic in the other genera. Relationships to other tribes are likely, therefore, to be most apparent in *Phylloxylon*.
- 7) The roots of the Indigoferaeae are hypothesized to lie in the *Acosmium* or *Baphia* groups in Sophoreae, but the tribe is believed to be most closely allied to *Lonchocarpus* section *Paniculatae* and *Schefflerodendron*, in the Millettieae. The former is possibly the sister group of the tribe.
- 8) Cladistics provides a logically and empirically sound basis from which the phylogeny of a group can be inferred. The phylogeny can serve as an independent and explanatory template for other evolutionary studies since a cladogram adds the essential historical element to help identify the context in which features evolved. The number of times a feature appeared can be estimated as well as the direction and order of character transformations. Cladistics is a method for discriminating among causal explanations through statements about the sequence in which features originated, i.e. this sequence can be interpreted by specifying which

characters were already present (and which were not) at the time a particular character arose.

- 9) Aptations that characterize a particular ecological association (i.e. a set of functional-structural relationships maintained by natural selection), or morphological features giving rise to developmental constraints, can be mapped on the cladogram. Hypotheses can then be made about their evolution by examining the origin, direction and order of character transformations.
- 10) Cladistic analysis can focus on the historical genesis of adaptation, to test both its origin and maintenance by natural selection. Adaptation is not just an ahistorical interpretation of the function of a character based on its effect on current fitness. It is only supported when the evolution of a derived morphology is strictly co-incident on the cladogram with the origin of a derived function.
- 11) Exaptations are useful features enhancing fitness but they are not built by natural selection for their current role. They can evolve as non-aptations or as other uses for existing adaptations. When a utility arises exaptations can be co-opted for a current role, i.e. if a feature originates on a cladogram before the function with which it later becomes associated, it is an exaptation.
- 12) The order in which characters are assembled in a lineage bears on the evolution of functional and developmental interdependencies. Some aptations and non-aptations have become synapomorphies at higher taxonomic levels, and if these have become integrated in the genotype and phenotype they can act as constraints on the lower levels. The persistence of the feature (morphology) is explained, therefore, not by an original function but because it is part of a co-adapted complex. Its maintenance may not be due primarily to selection but to developmental constraints (i.e. the

accumulation of burden, canalization and key morphologies, or to heterochrony).

- 13) Burden refers to the responsibility carried by a feature, i.e. the number of features structurally or epigenetically dependent on an initial feature. As burden builds up, the evolution of a feature may be traced on a cladogram, from an initial freedom to vary, to later stages of constancy or fixation.
- 14) Developmental constraints can act by channelling phenotypic change in a direction set by past history or formal structure. Canalization may be followed cladistically, as a directed apportioning of variation into well defined pathways of evolution determined by previously acquired features, i.e. the nature of each successive change is strongly determined by earlier changes. As features are added (or lost) interactions become more (or less) integrated.
- 15) Various genetic and developmental mechanisms have evolved because of the need for lineages to manifest evolutionary plasticity if they are to survive. Any number of possible pre-existing developmental pathways may be adopted, and one factor influencing the pathway actually taken is the relative ease of achieving the available alternatives.
- 16) Key morphologies are a particular class of developmental constraints defined here for the first time. A key morphology has an effect on one or more other morphologies by instituting, or removing, a bias which determines the pathway adopted in evolution or development. The accumulation or loss of key morphologies results in switches in constraints as seen by changing trends and patterns on a cladogram. Cladistics provides an explicit view of key morphologies causing switches in constraints.
- 17) Developmental constraints are not just limits imposed on selection by channelling change in certain directions; they

can also open up new areas of adaptive radiation, e.g. through heterochrony.

- 18) The importance of making explicit references to the cladogram when drawing up evolutionary explanations is illustrated by many examples in the text. Without a historical basis it is impossible to estimate the number of times a trait evolved or to know about the direction and order of character transformations. Cladistics provides clarity and testability for evolutionary hypotheses that otherwise can only be judged by their plausibility.
- 19) Much interest has recently been shown in applying the cladistic method more widely in comparative biology. The identification of particular adaptations or developmental constraints significantly increases the level of information that can be gathered from studies of complex natural systems, and they may also indicate the need to explore relationships that initially were not apparent. Application of this method could also avoid the apparently similar problems of mosaic evolution (Stebbins 1984) and heterobathmy (Stevens 1986).
- 20) A phylogenetic tree is proposed which is based on the cladogram, but it attempts to reflect a pattern which may be corroborated later by further cladistic analysis. The differences between the phylogeny and the empirically derived cladogram are justified in terms of contrasting interpretations of homoplasy.
- 21) The deficiencies in the original analysis, which resulted in the admission of a cladogram 8 steps longer than the most parsimonious trees, can be ascribed to the following:
 - a) the overall aim of the cladistic analysis was to present a working pattern of relationships in the tribe, which was otherwise obscured by large numbers of taxa, and relatively high levels of homoplasy in the characters. As such, this was an attempt to show how the preliminary phase of a

cladistic analysis was achieved, a process mostly overlooked when only the most parsimonious cladogram is presented.

- b) the cladogram provided a yardstick for critically examining intuitive taxonomic ideas (especially during the character analyses in chapters 4 & 5), thus making it possible to reconsider some of the synapomorphies and character transformations used in the original cladogram. A number of characters, therefore, need to be re-evaluated and the data matrix modified accordingly.

This process of refining characters (i.e. hypotheses of polarity and homology) is still continuing, with the eventual aim of obtaining a more parsimonious cladogram than Table 2.3.

- 22) Four major phases of evolution and radiation are hypothesized for the tribe in Africa and Madagascar, based on studies of developmental constraints, phytogeography and ecology.
- 23) In the species treatment of the tribe, tropical African species are listed under their respective genera and infrageneric taxa, while a synopsis (with literature citations, synonymy and typification) is given for the lesser known southern African species. In southern Africa 4 genera are recognized, i.e. *Cyamopsis* (2 species), *Microcharis* (4 species), *Indigastrum* (8 species) and *Indigofera* (261 species in 33 infrageneric taxa). 29 new combinations are made in the endemic African genera *Microcharis* and *Indigastrum*.
- 24) With the increasing amount of cladistic information becoming available in plant systematics, there is a growing need to find unifying theories to explain common evolutionary patterns. Major shifts in morphology can highlight periods of significant evolutionary change in a group of taxa. Aspects of historical ecology can build on phylogenetic studies of biogeography and speciation in an attempt to provide evolutionary explanations that take many causal agents into

account. Such explanations need to be resolved for a number of unrelated taxonomic groups, and correlated with common speciation events related to major environmental perturbations.

- 25) An exciting goal for future systematic research is the idea of a general theory that might account for the evolution of plant biota in Africa. It now seems possible to achieve this by applying comparative cladistic methods to a number of existing taxonomic works, and using a multidisciplinary approach that involves all the relevant earth and life sciences.

REFERENCES

- ADAMSON, R.S. & SALTER, T.M. 1950. *Flora of the Cape Peninsula*. :496 -501. Juta, Capetown.
- ADANSON, M. 1763. *Familles des plantes* 2:326, 566. Paris.
- AITON, W. 1789. *Hortus kewensis* 3: 67-69. London.
- ALBERCH, P. 1982. Developmental constraints in evolutionary processes. In J.T. Bonner (ed.), *Evolution and development* :313-332. Springer Verlag, New York.
- ALBERCH, P., GOULD, S.J., OSTER, G.F. & WAKE, D.B. 1979. Size and shape in ontogeny and phylogeny. *Paleobiology* 5: 296-315.
- ALI, S.I. 1958. Revision of the genus *Indigofera* L. from W. Pakistan and NW. Himalayas. *Botaniska Notiser* 3(3): 543-577.
- ALI, S.I. 1977. Papilionaceae. In E. Nasir & S.I. Ali (eds.), *Flora of West Pakistan* No. 100. University of Karachi.
- ALLEN, O.H. & ALLEN, E.K. 1981. *The Leguminosae: A Source Book of Characteristics, Uses and Nodulation*. Macmillan, London & Basingstoke.
- ALSTON, A.H.G. 1931. *Indigofera nummulariifolia*. In H. Trimen, *A hand-book to the flora of Ceylon* 6(suppl.): 72.
- ALVIN, K.L. 1987. Leaf anatomy of *Androstachys johnsonii* Frain and its functional significance. *Annals of Botany*. 59: 579-591.
- BAILEY, R.W. 1971. Polysaccharides in the Leguminosae. In J.B. Harborne, D. Boulter & B.L. Turner (eds.), *Chemotaxonomy of the Leguminosae* :503-541. Academic Press, London.

- BAILLON, H.E. 1861. Species Euphorbiacearum. A. Euphorbiacees Africaines. Deuxieme Partie. *Adansonia* 2: 27-55.
- BAILLON, H.E. 1872. *The Natural History of Plants* Vol.2. English translation by M.M. Hartog. L. Reeve and Co., London.
- BAILLON, H.E. 1883. *Indigofera retroflexa*. *Bulletin mensuel de la Societe Linneenne de Paris* 1: 399. Paris.
- BAKER, E.G. 1903. The Indigoferas of tropical Africa. *Journal of Botany* 41: 185-194, 234-245, 260-267, 323-334.
- BAKER, E.G. 1905. Indigoferaeae. In H.Schinz, Beitrage zur Kenntniss der Afrikanischen Flora 17. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zurich* 49: 179-194.
- BAKER, E.G. 1905a. Report on some South African species of *Indigofera* in the Albany Museum Herbarium. *Records of the Albany Museum*. 1: 279-281.
- BAKER, E.G. 1920. In S.Le M.Moore, Plantae Rogersianae. *Journal of Botany* 58: 76.
- BAKER, E.G. 1925. *Indigofera praticola*. In H.Schinz, Beitrage zur Kenntnis der Afrikanischen Flora 32. *Vierteljahrsschrift der Naturforschenden Gesellschaft in Zurich* 70: 218.
- BAKER, E.G. 1926. *The Leguminosae of Tropical Africa* 1: 95-166. Gent.
- BAKER, E.G. & MARTIN. 1923. *Indigofera homblei*. In E.G.Baker & E.de Wildman, Sur quelques *Indigofera* du Congo Belge. *Bulletin du Jardin botanique de L'Etat, a Bruxelles* 7: 143-159.
- BAKER, J.G. 1883. Contributions to the Flora of Madagascar - Part 1. Polypetalae. *The Journal of the Linnean Society. Botany* 20: 126-127.

- BAKER, J.G. 1884. Further contributions to the Flora of Central Madagascar. *Journal of the Linnean Society, Botany* 21: 336.
- BAKER, J.G. 1887. Further contributions to the Flora of Madagascar. *The Journal of the Linnean Society, Botany* 22:463-464.
- BAKER, J.G. 1871. Papilionaceae. In D.Oliver, *Flora of Tropical Africa* 2: 65-103. Reeve, London.
- BAUHIN, J. 1651. *Historia plantarum* 2: 945-946. Yverdon.
- BELL, E.A. 1972. Toxic amino acids in the Leguminosae. In J.B. Harborne (ed.), *Phytochemical Ecology* :163-177. Academic Press, London.
- BELL, E.A. 1978. Toxins in seeds. In J.B.Harborne (ed.), *Biochemical Aspects of Plant and Animal Coevolution* :143-161. Academic Press, London.
- BELL, E.A., LACKEY, J.A. & POLHILL, R.M. 1978. Systematic significance of canavanine in the Papilionoideae (Faboideae). *Biochemical Systematics and Ecology* 6: 201-212.
- BELL, E.A. 1981. Non-Protein Amino Acids in the Leguminosae. In R.M. Polhill & P.H. Raven eds., *Advances in legume systematics* 2: 489-499. Royal Botanic Gardens, Kew.
- BENTHAM, G. 1837. *Commentationes de leguminosarum generibus*. Vienna.
- BENTHAM, G. 1846. In J. Lindley, *The vegetable kingdom* :554. London.
- BENTHAM, G. 1849. In W.J. Hooker, *Niger Flora* : 293. London.
- BENTHAM, G. 1859. Papilionaceae. Columns 1-216. In C.F.P. de Martius (ed.), *Flora Brasiliensis* 15(1): 5-6. Monachii.

- BENTHAM, G. 1861. *Flora Hongkongensis: A description of the flowering plants and ferns of the island of Honkong*. L. Reeve and Co., London.
- BENTHAM, G. 1864. *Flora australiensis* 2: 194-201. Lovell Reeve & Co., London.
- BENTHAM, G. 1865. Leguminosae. In G. Bentham & J.D. Hooker, *Genera Plantarum* 1: 494, 501. Reeve, London.
- BENTHAM, G. 1865a. Description of some new genera and species of tropical Leguminosae. *Transactions of the Linnean Society, London* 25: 297-298.
- BENTLEY, R. & TRIMEN, H. 1880. *Medicinal Plants* 2: 72. J. & A. Churchill, London.
- BERGIUS, P.J. 1767. *Descriptiones plantarum ex Capite Bonae Spei* 226-228. Stockholm.
- BERTOLONI, A. 1832. *Dissertatio de quibusdam novis plantarum speciebus et de bysso antiquorum, Bononia* 1: 3-6, t.1.
- BLACKBURN, D.T. 1978. A colorfast stain for polyester-embedded ligneous tissues. *Stain technology* 53: 356-358.
- BOLUS, H. 1896. Contributions to the Flora of South Africa. *Journal of Botany* 34: 22-25.
- BOLUS, H. 1906. Contributions to the African Flora. *Transactions of the South African Philosophical Society* 16: 26-27.
- BOLUS, L. 1915. Leguminosae. In, List of the Plants collected in the Percy Sladen Memorial Expeditions, 1908-9, 1910-11. *Annals of the South African Museum* 9,4: 253-256.
- BOLUS, L. 1915a. Novitates Africanæ. *Annals of the Bolus Herbarium* 1: 128-129.

BREITER, C.A. 1817. *I. aphylla*. *Hortus Breiterianus* :209.
Leipzig.

BREMEKAMP, C.E.B. 1933. New or otherwise noteworthy plants from the Northern Transvaal. *Annals of the Transvaal Museum* 15: 241-242.

BRITTON, N.L. & BROWN, A. 1913. *An Illustrated Flora of the Northern United States, Canada and the British Possessions* ed.2, 2: 371-372. Charles Scribner & Sons. New York.

BRONN, H.G. 1822. *De formis plantarum leguminosarum primitivis et derivatis*. :134. Heidelberg.

BROOKS, D.R. 1985. Historical Ecology: A new approach to studying the evolution of ecological associations. *Annals of the Missouri Botanical Garden* 72: 660-680.

BROWN, N.E. 1897. In *Diagnoses Africanæ X*. *Kew Bulletin* 1897: 258.

BROWN, N.E. 1906. In *Diagnoses Africanæ XVI*. *Kew Bulletin* 1906: 101-102.

BROWN, N.E. 1909. List of plants collected in Ngamiland and the northern part of the Kala hari Desert. *Kew Bulletin* 1909: 101-103.

BROWN, N.E. 1912. *Indigofera setosa*. In *Diagnoses Africanæ XLIX*. *Kew Bulletin* 1912: 274.

BROWN, N.E. 1925. New species of *Indigofera* from the Transvaal and Swaziland. *Kew Bulletin* 1925: 142-159.

BROWN, N.E. 1926. *Indigofera*. In J. Burtt Davy, *A Manual of Flowering Plants and Ferns of the Transvaal with Swaziland* 1: 44-45.

- BROWN, N.E. 1932. *Indigofera*. In J. Burtt Davy, *A Manual of Flowering Plants and Ferns of the Transvaal with Swaziland* 2: xxiii-xxv, 360-373. Longmans, London.
- BURKART, A. 1952. *Las Leguminosas Argentinas* ed. 2. ACME, Buenos Aires.
- BURKILL, I.H. 1935. *Dictionary of the economic products of the Malay Peninsula*. London.
- BURMAN, J. 1737. *Thesaurus zeylanicus. Catalogi duo plantarum africanorum* :16. Amsterdam.
- BURMAN, N.L. 1768. *Flora indica* :172, & *Prodromus florae capensis* : 20, 23. Leiden.
- BURTT DAVY, J. 1921. New or noteworthy South African Plants I. *Kew Bulletin* 1921: 49.
- BURTT DAVY, J. 1921a. New or noteworthy South African Plants III. *Kew Bulletin* 1921: 278-279.
- CALOW, P. 1983. *Evolutionary Principles*. Blackie, Glasgow & London.
- CANDOLLE, A.P. de, 1825. *Prodromus systematis naturalis regni vegetabilis* 2: 221-233. Paris.
- CANDOLLE, A.P. de, 1825a. *Bremontiera*. In *Annales des Sciences Naturelles* sér. 1, 4: 93.
- CANDOLLE, A.P. de, 1826. *Memoires sur la famille des Légumineuses* :230. Paris.
- CARPENTER, J.M. 1988. Choosing among multiple equally parsimonious trees. *Cladistics* 4: 291-296.

- CHEVERUD, J.M., DOW, M.M. & LEUTENEGER, 1985. The quantitative assessment of phylogenetic constraints in comparative analyses: Sexual dimorphism in body weight among primates. *Evolution* 39: 1335-1351.
- CODDINGTON, J.A. 1988. Cladistic tests of adaptational hypotheses. *Cladistics* 4: 3-22.
- COMPTON, R.H. 1976. The Flora of Swaziland. *Journal of South African Botany* Suppl. Vol. 11: 259-264.
- COMMELIN, J. 1701. *Horti medici amstelodamensis* 2 :167 t.84. Amsterdam.
- COMPTON, R.H. 1912. An investigation of the seedling structure of the Leguminosae. *Journal of the Linnean Society. Botany.* 41: 1-122.
- CONRATH, P. 1908. In *Diagnoses Africanarum*: XXII. *Kew Bulletin* 1908: 223.
- CORBY, H.D.L. 1981. The systematic value of Leguminous root nodules. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 2: 657-670. Royal Botanic Gardens, Kew.
- CRAIB, W.G. 1913. The Indigoferas of China. *Notes from the Royal Botanic Garden Edinburgh* 36: 47-77.
- CRISCI, J.V. & STUESSY, T.F. 1980. Determining primitive character states for phylogenetic reconstruction. *Systematic Botany* 5: 112-135.
- CRISP, M.D. 1983. Papilionoideae. In B.D. Morley & H.R. Toelken (eds.), *Flowering Plants in Australia.* :151-164. Rigby, Adelaide.
- CRISP, M.D. & WESTON, P.H. 1987. Cladistics and legume systematics, with an analysis of the Bossiaeeae, Brongniartieae

and Mirbelieae. In C.H. Stirton (ed.), *Advances in legume systematics* 3: 65-130. Royal Botanic Gardens, Kew.

CRONQUIST, A. 1952. New species and varieties of Papilionaceae from the Belgian Congo. *Bulletin du Jardin Botanique de L'Etat Bruxelles* 22: 219-227.

CRONQUIST, A. 1954. Galegeae. In *Flora du Congo Belge et du Ruanda-Urundi* 5: 117-175. Brussels.

CURTIS, W. 1799. *I. angustifolia*. *Botanical Magazine* t.465.

DALLWITZ, M.J. & FAINE, T.A. 1986. Users Guide to the DELTA System. ed.3. *Division of Entomology report no. 13*. CSIR. Canberra.

DALZIEL, J.M. 1937. The useful plants of West tropical Africa. Appendix to J. Hutchinson & J.M. Dalziel (eds.), *Flora of West Tropical Africa* : 243-250. Crown Agents, London.

DARLINGTON, C.D. & WYLIE, A.P. 1955. *Chromosome atlas of flowering plants*. George Allen & Unwin, London.

DASTUR, J.F. 1977. *Medicinal Plants of India and Pakistan* 4th reprint. D.B.Taraporevala, Bombay.

DEACON, H.J. 1983. Comparative evolution of mediterranean type ecosystems: a southern perspective. In. F.J. Kruger, D.T. Mitchell & J.U.M. Jarvis (eds.), *Mediterranean type ecosystems: the role of nutrients*. Springer-Verlag. Berlin.

DE KORT, I. & THIJSSSE, G. 1984. A Revision of the genus *Indigofera* (Leguminosae-Papilionoideae) in Southeast Asia. *Blumea* 30: 89-151.

DE VOGEL, E.F. 1979. *Seedlings of Dicotyledons*. PUDOC, Wageningen.

- DE WILDEMAN, E. 1923. In E.G. Baker & E. De Wildeman, Sur quelques *Indigofera* du Congo Belge. *Bulletin du Jardin Botanique de l'etat a Bruxelles* 8: 143-159.
- DE WINTER, B. 1971. Floristic relationships between the northern and southern arid areas in Africa. *Mitteilungen der Botanischen Staatssammlung Munchen* 10: 424-437.
- DESVAUX, N.A. 1813. *Journal de Botanique, appliquee* 1: 125. Paris.
- DESVAUX, N.A. 1814. *Journal de Botanique, appliquee* 3: 78-80. Paris.
- DESVAUX, N.A. 1826. Observations sur la famille des Legumineuses. *Annales des sciences naturelles Ser.1* 9:411.
- DIELS, L. 1909. Formationen und Florenelementa im nordwestlichen Kapland. In A. Engler, *Botanische Jahrbuch* 44: 120. Leipzig.
- DINTER, K. 1922. Pflanzenarten aus Deutsch-Sudwestafrika. *Repertorium specierum novarum regni vegetabilis* 18: 427-429.
- DINTER, K. 1932. Diagnosen neuer sudwestafrikanischer Pflanzen. *Repertorium specierum novarum regni vegetabilis* 30: 198-199.
- DOBZHANSKY, T. 1970. *Genetics of the evolutionary process*. Columbia University Press, New York.
- DON, G. 1832. *A general system of gardening and botany* 2 :214. Rivington, London.
- DONOGHUE, M.J. 1989. Phylogenies and the analysis of evolutionary sequences, with examples from seed plants. *Evolution* 43(6): 1137-1156.

DONOGHUE, M.J. & CANTINO, P.D. 1984. The logic and limitations of the Outgroup Substitution Approach to Cladistic Analysis. *Systematic Botany* 9(2): 192-202.

DOVER, G.A. 1986. The spread and success of non-Darwinian novelties. In S. Karlin & E. Nevo (eds.), *Evolutionary Processes and Theory* :199 -237. Academic Press, New York.

DRURY, H. 1978. *The useful plants of India* ed. 2. pp. 253-257. W.H. Allen, London.

DUKE, J.A. 1981. *Handbook of legumes of the world of economic importance*: 94-101. Plenum, London & New York.

DUKE, J.A. & POLHILL, R.M. 1981. Seedlings of the leguminosae. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 2: 941-949. Royal Botanic Gardens, Kew.

DYER, R.A. 1975. *The genera of southern African flowering plants*. 1: 256. Department of Agricultural Technical Services. Pretoria.

ECKLON, C.F. & ZEYHER, C. 1836 (Jan.). *Enumeratio plantarum africae australis extratropicae* 2: 232-245. Hamburg.

ELDREDGE, N. 1985. *The Unfinished Synthesis*. Columbia University Press, New York.

ELDREDGE, N. & CRACRAFT, J. 1980. *Phylogenetic patterns and the evolutionary process*. Columbia University Press, New York.

ENDLICHER, S.L. 1832. *Stirpium pemptas, iconibus et descriptionibus illustrata*. *Flora* 15, 2: 385, t.1.

ENDLICHER, S.L. 1840. *Genera Plantarum* 2: 1291. Vienna.

ENGLER, H.G.A. 1888. *Plantae Marlothianae*. *Botanische Jahrbucher* 10: 28.

- ESAU, K. 1965. *Plant Anatomy* ed.2. Wiley, New York.
- ENGLER, H.G.A. 1892. *Indigofera longebarbata*. In, *Über die Hochgebirgsflora Afrikas*, pp. 257-258. Berlin.
- FAHN, A. 1986. Structural and functional properties of trichomes of xeromorphic leaves. *Annals of Botany* 57: 631-637.
- FANG, Y. & Zheng, C. 1989. A study on the genus *Indigofera* Linn. from China. *Acta Phytotaxonomica Sinica* 27(3): 161-177.
- FARRIS, J.S. 1970. Methods for computing Wagner trees. *Systematic Zoology* 19: 83-92.
- FARRIS, J.S. 1983. The logical basis of phylogenetic analysis. In N.I. Platnick & V.A. Funk (eds.), *Advances in cladistics*, vol. 2, chp. 1. Columbia University Press, New York.
- FARRIS, J.S. 1988. Hennig 86 version 1.5, reference manual.
- FERGUSON, I.K. & SKVARLA, J.J. 1981. The pollen morphology of the subfamily Papilionoideae (Leguminosae). In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 2: 859-896. Royal Botanic Gardens, Kew.
- FERGUSON, I.K. & STRACHAN, R. 1982. Pollen morphology and taxonomy of the tribe Indigoferaeae (Leguminosae: Papilionoideae). *Pollen et Spores* 24(2): 171-210.
- FINK, W.L. 1986. Microcomputers and phylogenetic analysis. *Science* 234: 1135-1139.
- FORSSKAL, P. 1775. *Indigofera*. *Flora aegyptiaca-arabica* : 137-138. Copenhagen.
- FOSTER, A.S. 1956. Plant idioblasts: Remarkable examples of cell specialization. *Protoplasma* 26: 184-193.

FOURCADE, H.G. 1932. Contributions to the flora of the Knysna and neighbouring divisions. *Transactions of the Royal Society of South Africa* 21: 93-95.

FRAHM-LELIVELD, J.A. 1960. Observations on chromosomes in the genus *Indigofera*. *Acta Botanica Neerlandica* 9: 286-293.

FRAHM-LELIVELD, J.A. 1962. Further observations on chromosomes in the genus *Indigofera*. *Acta Botanica Neerlandica* 11: 201-208.

FRAHM-LELIVELD, J.A. 1966. Cytotaxonomic notes on the genera *Indigofera* L. and *Cyamopsis* DC. *Genetica* 37: 403-426.

FREIRE DE CARVALHO, L. d'A. & VALENTE, M. DA C. 1973. Contribuição ao estudo da nervação foliar das Leguminosas dos Cerrados. IV - Faboideae. *Revista Brasileira de Biologia* 33(4): 457-472.

FRIES, R.E. 1914. *Indigofera rogersii*. In *Wissenschaftliche Ergebnisse der Schwedischen Rhodesia-Kongo-Expedition, 1911-12* 1: 80.

FUNK, V.A. & STUESSY T.F., 1978. Cladistics for the practising plant taxonomist. *Systematic Botany* 3: 159-178.

FUNK, V.A. & BROOKS, D.R. 1990. Phylogenetic systematics as the basis of comparative biology. *Smithsonian Contributions to Botany*. 73: 1-45. Washington.

GANONG, W.F. 1901. The cardinal principles of morphology. *Botanical Gazette* 31: 426-434.

GEESINK, R. 1981. Tephrosieae. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 1: 245-260. Royal Botanic Gardens, Kew.

GEESINK, R. 1984. *Scala Millettiearum*. Leiden Botanical Series 8, 1-131. E.J.Brill/ Leiden University Press, Leiden.

- GERMISHUIZEN, G. 1987. A new species of *Indigofera* from Natal and Transkei. *Bothalia* 17(1): 33-34.
- GILLETT, J.B. 1956. *Indigofera*. New species, varieties and names from West Tropical Africa. *Kew Bulletin* 1955: 573-585.
- GILLETT, J.B. 1958. *Indigofera* (*Microcharis*) in tropical Africa with the related genera *Cyamopsis* and *Rhynchotropis*. *Kew Bull.*, Add. Ser. 1: 1-166.
- GILLETT, J.B. 1958a. *Indigofera*. In J. Hutchinson & J.M. Dalziel (ed. 2 revised by R.W.J. Keay), *Flora of West Tropical Africa* 1(2): 533-543. Crown Agents for the Colonies, London.
- GILLETT, J.B. 1970. Additions to our knowledge of *Indigofera* in East Tropical Africa. *Kew Bulletin* 24(3): 465-506.
- GILLETT, J.B. 1971. Indigoferaceae. In E. Milne-Redhead & R.M. Polhill (eds.), *Flora of Tropical East Africa*, Legum.- Papil. 1: 212-330. Crown Agents for the Colonies, London.
- GOLDBLATT, P. 1978. An analysis of the flora of southern Africa: its characteristics, relationships, and origins. *Annals of Missouri Botanical Garden* 65: 369-436.
- GOLDBLATT, P. 1981. Cytology and the phylogeny of Leguminosae. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 2: 427-464. Royal Botanic Gardens, Kew.
- GOMES, C.M.R., GOTTLIEB, O.R., GOTTLIEB, R.G. & SALATINO, A. 1981. Phytochemistry in perspective: Chemosystematics of the Papilio-noideae. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 2: 465-488. Royal Botanic Gardens, Kew.
- GOULD, S.J. 1977. *Ontogeny and Phylogeny*. Belknap Press of Harvard University Press, Cambridge, Mass.

- GOULD, S.J. 1989. A developmental constraint in *Cerion*, with comments on the definition and interpretation of constraint in evolution. *Evolution* 43(3): 516-539.
- GOULD, S.J. & LEWONTIN, R.C. 1979. The spandrels of San Marco, or a critique of the adaptationist programme. *Proceedings of the Royal Society, London B205*: 581-598.
- GOULD, S.J. & VRBA, E.S. 1982. Exaptation - a missing term in the science of form. *Paleobiology* 8(1): 4-15.
- GREEN, H.W. 1986. Diet and arboreality in the emerald monitor, *Varanus prasinus*, with comments on the study of adaptation. *Fieldiana Zoology*: 31: 1-12.
- GREUTER, W., ed. 1988. International Code of Botanical Nomenclature. *Regnum Vegetabile* 118.
- GUILLEMIN, J.A. & PERROTTET, G.S. 1832. Indigofera. In *Florae Senegambiae tentamen* 5: 172-189.
- GUTHRIE, L., PILLANS, N.S. & SALTER, T.M. 1939. Plantae Novae Africae. *Journal of South African Botany* 5: 70-71.
- HARBORNE, J.B. 1971. Terpenoid and other low molecular weight substances of systematic interest in the Leguminosae. In J.B. Harborne, D. Boulter & B.L. Turner (eds.), *Chemotaxonomy of the Leguminosae* :279. Academic Press, London.
- HARMS, H. 1898. In O. Kuntze, *Revisio generum plantarum* 3,2: 52. Leipzig.
- HARMS, H. 1901. Leguminosae africanae II. *Botanische Jahrbucher* 30: 75-94.
- HARMS, H. 1903. *Indigofera baumiana*. In O. Warburg, *Kunene-Sambesi Expedition, H. Baum 1903* :257. Berlin.

- HARVEY, W.H. 1862. Leguminosae. In W.H. Harvey & D.W. Sonder, *Flora Capensis* 2: 163-203. Hodges, Smith & Co., Dublin.
- HEINRICH, B. 1975. Energetics of pollination. *Annual Review of Ecological Systematics* 6: 139-170.
- HELLER, J.L. 1959. Index auctorum et librorum a Linnaeo (Species Plantarum, 1753) citatorum. In J.L.Heller & W.T.Stearn, *An Appendix to the Species Plantarum of Carl Linnaeus* (In the facsimile reprint of Species Plantarum) 2: 42-44. Ray Society, London.
- HENNIG, W. 1966. *Phylogenetic Systematics*. Translated by D.D.Davis & R.Zangerl. University of Illinois Press, Urbana.
- HEPPER, F.N. 1958, *Papilionaceae*. In J. Hutchinson & J.M. Dalziel (ed. 2 revised by R.W.J. Keay), *Flora of West Tropical Africa* 1(2): 543. Crown Agents for the Colonies, London.
- HICKEY, L.J. 1979. A revised classification of the architecture of Dicotyledonous leaves. In C.R. Metcalfe & L. Chalk (eds.), *Anatomy of the Dicotyledons* ed.2. 1: 25-39. Clarendon Press, Oxford.
- HILLIARD, D.M. & BURTT, B.L. 1986. Notes on some plants of southern Africa XII. *Notes from the Royal Botanical Garden Edinburgh* 43: 207-210.
- HOCHSTETTER, C.F. 1846. Nova Genera Plantarum Africa proponit et describit. *Flora* 29: 593.
- HOOKER, J.D. 1888. *Indigofera podophylla*. *Icones Plantarum*
- HOOKER, W.J. 1828. *Lotus microphyllus*. *Botanical Magazine* 55: t.2808.

- HUMPHRIES, C.J. & FUNK, V.A. 1984. Cladistic Methodology. In V.H. Heywood & D.M. Moore (eds.), *Current Concepts in Plant Taxonomy*. pp. 323-362. Academic Press, London & Orlando.
- HUMPHRIES, C.J. & PARENTI, L. 1986. *Cladistic Biogeography*. Clarendon Press, Oxford.
- HUTCHINSON, J. 1964. Papilionaceae. In *Genera of Flowering Plants* Vol. 1. Oxford.
- HUTCHINSON, J. & DALZIEL, J.M. 1928. *Papilionaceae*. In *Flora of West Tropical Africa* 1(2): 388-394. Crown Agents for the Colonies, London.
- JACQUIN, N.J. 1789. *Collectanea ad botanicam* 2: 358. Vienna.
- JACQUIN, N.J. 1797. *Plantarum rariorum horti caesarei schoenbrunnensis* 2: t233-t236.
- JANZEN, D.H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* 171: 203-205.
- JANZEN, D.H. 1981. The defences of Legumes against herbivores. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 2: 951-977. Royal Botanic Gardens, Kew.
- JARVIE, J.K. & STIRTON, C.H. 1986. A new species of *Indigofera* from the southern Cape. *Bothalia* 16,2: 230-231.
- JARVIE, J.K. & STIRTON, C.H. 1987. The *Indigofera filifolia* complex (Fabaceae) in southern Africa. *Bothalia* 17(1): 1-6.
- JAUBERT, H.-F. & SPACH, E. 1857. *Illustrationes plantarum orientalium* 5: 101 t.481-482 and t.492-493 (1857). Paris.
- JOHNSON, H.B. 1975. Plant pubescence: an ecological perspective. *The Botanical Review* 41(3): 233-258.

- KARETALA, Y.Y., HUSSAIN, H.S.N. & NURANI, M.A. 1990. Observations on the cuticular features and stomatal ontogeny in the leaves of some Papilionaceae from Nigeria. *Fedded Repertorium* 101: 183-188.
- KEELEY, J.E. 1977. Seed production, seed populations in soil, and seedling production after fire for two congeneric pairs of sprouting and non-sprouting chaparral shrubs. *Ecology* 58: 820-829.
- KER, J.B. 1816. *Lebeckia contaminata*. *Botanical Register* 2: 104.
- KER, J.B. 1817. *I. filifolia*. *Botanical Register* 3: notes 2.
- KLOTZSCH, J.F. 1861. Botanik Leguminosae. In W.C.H. Peters, *Reise nach Mossambique* 1: 48-52. Berlin.
- KLUCKING, E.P. 1986. *Leaf venation patterns*. Vol. 1. Annonaceae. : 12-15. J. Cramer, Berlin.
- KLUGE, A.G. & FARRIS, J.S. 1969. Quantitative phyletics and the evolution of anurans. *Systematic Zoology* 18: 1-32.
- KRAEMER, H. 1914. *Applied and Economic Botany* : 573-574. Philadelphia.
- KUNTZE, C.E.O. 1886. *Plantae Pechuellanae Hereroenses*. *Jarbuch des Koniglichen Botanischen Gartens und des Botanischen Museums zu Berlin* 4: 263.
- KUNTZE, C.E.O. 1891. *Revisio generum plantarum* 1:159, 2:938-940, 3(2) :50-52. Leipzig.
- LACKEY, J.A. 1978. Leaflet anatomy of the Phaseoleae and its relation to taxonomy. *Botanical Gazette* 139: 436-446.
- LACKEY, J.A. 1979. Leaflet hairs of *Adenodolichos* (Leguminosae - Papilionoideae). *Iselya* 1(2): 81-85.

- LAMARCK, J.B.A.P.M.de, 1789. *Encyclopedie methodique. Botanique.* 3: 244-252. Paris.
- LAVIN, M. 1987. A cladistic analysis of the tribe Robinieae (Papilionoideae), Leguminosae. In C.H. Stirton (ed.), *Advances in legume systematics* 3: 31-64. Royal Botanic Gardens, Kew.
- LAVIN, M. & DOYLE, J.J. 1990. Evolutionary significance of the loss of the chloroplast-DNA inverted repeat in the Leguminosae subfamily Papilionoideae. *Evolution* 44(2): 390-402.
- LEELAVATHI, P., RAMAYYA, N & PRABHAKAR, M. 1980. Foliar stomatal distribution patterns Leguminosae and their taxonomic significance. *Phytomorphology* 30: 195-204.
- LEVINTON, J. 1988. *Genetics, Paleontology and Macroevolution.* Cambridge University Press, Cambridge.
- LEWONTIN, R.C. 1978. Adaptation. *Scientific American*. 239: 156-169.
- LIEVENS, A.W. & URBATSCH, L.E. 1990. Correct author citation for the tribal name Indigoferae (Fabaceae: Faboideae). *Taxon* 39: 335-337.
- LINDER, H.P. 1983. The historical phytogeography of the *Disinae* (Orchidaceae). *Bothalia* 14: 565-570.
- LINDER, H.P. 1988. A review of cladistics for botanists. *South African Journal of Botany* 54 (3): 208-220.
- LINDER, H.P. 1991. A review of the African Restionaceae. *Contributions from the Bolus Herbarium*. In press.
- LINK, H.F. 1822. *Enumeratio plantarum horti regii botanici berolin-ensis altera* 2: 250-251. Berlin.
- LINNAEUS, C. 1738. *Hortus cliffortianus* :487. Amsterdam.

- LINNAEUS, C. 1753. *Species plantarum*. (Facsimile edition, 1959) 2:751. London.
- LINNAEUS, C. 1760. *Plantae rariores Africanæ* :15 (no. 37). Stockholm.
- LINNAEUS, C. 1763. *Amoenitates academicae* 6: 93-94 (no.33 & 37). Stockholm.
- LINNAEUS, C. 1763a. *Species plantarum* ed.2 2: 1062, 1076, 1091. Stockholm.
- LINNAEUS, C. 1767. *Systema naturae* ed.12 2: 496. Stockholm.
- LINNAEUS, C. 1771. *Mantissa plantarum altera* : 266-267, 271-273. Stockholm.
- LINNAEUS, C. filius. 1781. *Supplementum plantarum* : 334-335. Braunschweig.
- LOCK, J.M. 1989. *Legumes of Africa: a checklist*. Royal Botanic Gardens, Kew.
- LUDWIG, C.G. 1737. *Definitiones plantarum* : 117. Leipzig.
- LUDWIG, C.G. 1760. *Definitiones generum plantarum* ed. 3: 261-262. Leipzig.
- LYSHEDE, O.B. 1977. Structure and function of trichomes in *Spartocytisus filipes*. *Botaniska Notiser* 129: 395-404.
- MAUSETH, J.D. 1988. *Plant Anatomy* The Benjamin/Cummings Publishing Company, Menlo Park, California.
- MADDISON, W.P., DONOGHUE, M.J. & MADDISON, D.R. 1984. Outgroup analysis and parsimony. *Systematic Zoology* 33: 83-103.

- MANDERS, P.T. & CUMLIFFE, R.N. 1987. Fynbos plant life histories, population dynamics and species interactions in relation to fire: an overview. *South African National Scientific Programmes Report No. 135*. CSIR, Pretoria.
- MANNING, J.C. 1987. *The legume seed as a multifunctional organism (with particular reference to the Papilionoideae)*. Ph.D. thesis. University of Natal, Pietermaritzburg.
- MARCHANT, M. 1718. Description de l'Indigotier. *Memoires de l'Academie Royale des Sciences*. pp. 92-97.
- MARLOTH, R. 1903. Results of experiments on Table Mountain for ascertaining the amount of moisture deposited from the south-east clouds. *Transactions of the South African Philosophical Society* 14(4): 403-408.
- MARLOTH, R. 1910. On the absorption of water by aerial organs of plants. *Transactions of the Royal Society of South Africa* 1(2): 429-433.
- MAYNARD SMITH, J., BURIAN, J.R., KAUFFMAN, S. ALBERCH, P, CABBELL, J., GOODWIN, B., LANDE, R., RAUP, D. & WOLPERT L. 1985. Developmental constraints and evolution. *The Quarterly Review of Biology* 60(3): 265-287.
- MAYR, E. 1982. Adaptation and selection. *Biologisches Zentralblatt* 101: 161-174.
- McKEY, D. 1989. Interactions between ants and leguminous plants. In C.H. Stirton & J.L. Zarucchi (eds.), *Advances in Legume Biology* :673-718. Missouri Botanical Garden monograph no. 29. St Louis, Missouri.
- MEADOWS, M.E. 1984. Late Quaternary vegetation history of the Nyika Plateau, Malawi. *Journal of Biogeography* 11: 209-222.

- MEIKLE, R.D. 1951. Tropical African plants XXI. *Kew Bulletin* 1950: 352.
- MEISNER, C.F. 1843. Contributions towards a Flora of South Africa. In W.J. Hooker, *The London Journal of Botany* 2: 83-86. London.
- MENEZES, E.M., RAFFAELLI, D.L. & HAKIME, M.I. 1986. Aspectos morfológicos e anatómicos de órgãos vegetativos de duas espécies de *Indigofera* L. (Leguminosae- Papilionoideae). *Garcia de Orta, Sér. Bot.*, Lisboa, 8: 3-8.
- MERRILL, E.D. 1921. A review of the new species of plants by N.L. Burman in his Flora Indica. *Philippine Journal of Science* 19(3): 355.
- MERXMULLER, H. 1951. In K.Suessenguth & H.Merxmuller, Species et varietates novae vel rariae in Africa australi et centrali lectae. *Mitteilungen der Botanischen Staatssammlung Munchen* 1(heft 3): 89-90.
- MERXMULLER, H. 1951a. *Microcharis pseudo-indigofera*. 7In *Proceedings and Transactions of the Rhodesia Scientific Association* 43: 22.
- MERXMULLER, H. & SCHREIBER, A. 1957. Einige neue Leguminosen aus Sudwestafrika. *Bulletin du Jardin Botanique de L'Etat Bruxelles* 27: 274-276 t.9.
- METCALFE, C.R. & CHALK, L. 1950. *Anatomy of the Dicotyledons* 1: 502-535. Clarendon Press, Oxford.
- MEYER, E.H.F. 1832. *Indigofera*. *Linnaea* 7: 166-169.
- MEYER, E.H.F. 1836 (Feb.). *Commentariorum de plantis Africae australis* : 92-108. Leipzig.

- MICKEVICH, M.F. 1981. Quantitative phylogenetic biogeography. In V.A. Funk & D.R. Brooks (eds.), *Advances in Cladistics* :209-222. Proceedings of the Willi Hennig Society, New York: Botanical Garden.
- MICKEVICH, M.F. 1982. Transformation series analysis. *Systematic Zoology* 31: 461-478.
- MICKEVICH, M.F. & WELLER, S.J. 1990. Evolutionary character analysis: tracing character change on a cladogram. *Cladistics* 6: 137-170.
- MILLER, P. 1731. *The gardeners dictionary* ed. 1. London.
- MILLER, P. 1754. *The gardeners dictionary*. Abridged ed. 4 :54. London.
- MILLER, P. 1768. *The gardeners dictionary* ed. 8 no. 2. London.
- MILNE REDHEAD, E.W.B.H. 1936. Tropical African Plants: XIV. *Kew Bulletin* 1936: 470.
- MOORE, S.le M. 1878. *Alabastra diversa*. *Journal of Botany* 16: 131.
- MOORE, S. 1920. *Plantarum Mascarensim pugillus*. *Journal of Botany* 58: 188.
- MORROW, P.A., DAY, J.A. FOPX, M.D., FROST, P.G.H., JARVIS, J.U.M., MILEWSKI, A.V. & NORTON, P.M. 1983. Interaction between plants and animals. In J.A. Day (ed.), *Mineral nutrients in mediterranean ecosystems*. *South African National Scientific Programmes Report No. 71*. CSIR, Pretoria.
- MYERS, A.A. & GILLER, P.S. 1988. *Analytical Biogeography*. Chapman & Hall, London.
- NECKER, N.J.de 1790. *Elementa botanica* 3: 36. Neuwied.

- NELSON, G. & PLATNICK, N. 1981. *Systematics and Biogeography: cladistics and vicariance*. Columbia University Press, New York.
- NIXON, K.C. & WHEELER, Q.D. 1990. An amplification of the phylogenetic species concept. *Cladistics* 6: 211-223.
- O'DOWD, D.J. 1982. Pearl bodies as ant food: an ecological role for some leaf emergences of tropical plants. *Biotropica* 14(1): 40-49.
- OLIVER, D. 1888. *Indigofera podophylla*. In J.D.Hooker, *Icones Plantarum* 18: t.1800.
- PAGE, R.D.M. 1989. Comments on Component-compatibility in Historical Biogeography. *Cladistics* 5(2) :167-182.
- PATTERSON, C. 1982. Morphological characters and homology. In K.A. Joysey and A.E. Friday (eds.), *Problems in phylogenetic reconstruction*. :21-74. Academic Press, London.
- PELTIER, M. 1971. Singularités de la graine et de la plantule chez *Phylloxylon ensifolium* Baill. (Papilionacées). *Adansonia* ser. 2, 10: 533-535.
- PIMENTAL, R.A. & RIGGINS, R. 1987. The nature of cladistic data. *Cladistics* 3 (3): 201-209.
- PLATNICK, N.I. 1979. Philosophy and the transformation of cladistics. *Systematic Zoology* 28: 537-546.
- PLATNICK, N.I. 1989. An empirical comparison of microcomputer parsimony programs II. *Cladistics* 5: 145-161.
- PLUKENET, L. 1691. *Phytographia* t.166 f.3. London.
- PLUKENET, L. 1696. *Almagestum botanicum* :320 f.3. London.
- PLUKENET, L. 1700. *Almagesti botanici mantissa* :119. London.

- POIRET, J.L.M. 1813. *Encyclopedie methodique, Botanique*. Suppl. 3: 145-151. Paris.
- POLHILL, R.M. 1971. Some observations on generic limits in Dalbergieae-Lonchocarpaceae. *Kew Bulletin* 25: 259-273.
- POLHILL, R.M. 1971a. Dalbergieae. In E. Milne Redhead & R.M. Polhill (eds.), *Flora of Tropical East Africa, Legum.- Papil.* 1: 65-73. Crown Agents, London.
- POLHILL, R.M. 1981. Indigofereae. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 1: 289-291. Royal Botanic Gardens, Kew.
- POLHILL, R.M. 1981a. Papilionoideae. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 1: 191-208. Royal Botanic Gardens, Kew.
- POLHILL, R.M. 1981b. Dalbergieae. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 1: 233-242. Royal Botanic Gardens, Kew.
- POLHILL, R.M. 1981c. Galegeae. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 1: 357-363. Royal Botanic Gardens, Kew.
- POLHILL, R.M. 1982. *Crotalaria in Africa & Madagascar*. A.A. Balkema, Rotterdam.
- POLHILL, R.M. & RAVEN, P.H. (eds.). 1981. *Advances in legume systematics* 2 vols. Royal Botanic Gardens, Kew.
- POLHILL, R.M. & SOUSA, M. 1981. Robinieae. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 1: 283-288. Royal Botanic Gardens, Kew.
- PRAIN, D. & BAKER, E.G. 1902. Notes on Indigofera. *Journal of Botany* 40: 60-67, 136-144.

- RAFINESQUE, C.S. 1836. *Synoptical Flora Telluriana* 2: 97. Philadelphia.
- RAO, T.A. & BHATTACHARYA, J. 1981. Comparative morphology of foliar sclereids in *Boronia* Sm. (Rutaceae). *Proceedings of the Indian Academy of Science* 90(1): 9-29.
- RAO, T.A. & BHUPAL, D.P. 1973. Typology of sclereids. *Proceedings of the Indian Academy of Science* B77: 41-55
- RAO, T.A. & DAS, S. 1979. Typology of foliar tracheoids in angiosperms. *Proceedings of the Indian Academy of Science* B88: 331-345.
- REIDL, R. 1978. *Order in living organisms. A systems analysis of evolution*. John Wiley & Sons, New York.
- RETZIUS, A.J. 1786. *Observationes botanicae* 4: 29. Leipzig.
- RHEEDE, H.A. van. 1678. *Hortus indicus malabaricus* 1: 101-102, t.34. Amsterdam.
- RICHARD, A. 1847. Leguminosae. In *Tentamen florae abyssinicae* 1: 178-185. Paris.
- RIVINUS, A.G. 1691. *Ordo plantarum quae sunt flore irregulari tetra-petalo* :71 f.135. Leipzig.
- ROTH, A.G. 1821. *Indigofera scabra*. In *Novae plantarum species*. : 359. Halberstad.
- RUTHERFORD, M.C. & WESTFALL, R.H. 1986. Biomes of southern Africa - an objective categorization. *Memoirs of the Botanical Survey of South Africa* 54. Botanical Research Institute, Pretoria.
- RYDBERG, P.A. 1923. Indigoferaeae. In *North American Flora* 24: 137-153.

- SALTER, T.M. 1939. *Plantae Novae Africanae*. *Journal of South African Botany* 5: 70-71.
- SANDERSON, M.J. & DONOGHUE, M.J. 1989. Patterns of variation in levels of homoplasy. *Evolution* 43(8): 1781-1795.
- SANJAPPA, M. 1985. The genus *Indigofera* L. (Fabaceae - Papilionoideae) in Burma. *Reinwardtia* 10(2): 211-244.
- SCHEELE, A. 1843. *Botanische Beitrage*. *Linnaea* 17: 337-338.
- SCHINZ, H. 1888. *Beitrage zur Kenntnis der Flora von Deutsch-Sudwest Afrika 2. Verhandlungen des Botanischen Vereins der Provinz Brandenburg* 30: 161-165.
- SCHINZ, H. 1898. *Beitrage zur Kenntnis der Afrikanischen Flora 7. Bulletin de L'Herbier Boissier* 6: 524-525.
- SCHLECHTER, R. 1897. *Decades plantarum novarum Austro-Africanarum*. *Journal of Botany* 35: 429.
- SCHLECHTER, R. 1897a. *Plantae Schlechterianae novae vel minus cognitae describuntur I*. In A. Engler, *Botanische Jahrbucher* 24: 443. Leipzig.
- SCHLECHTER, R. 1899. *Plantae Schlechterianae novae vel minus cognitae describuntur II*. In A.Engler, *Botanische Jahrbucher* 27: 148-149. Leipzig.
- SCHLECHTER, R. 1905. *Indigofera griquana & I. krookii*. In A. Zahlbruckner, *Plantae Pentherianae 3. Annalen des Naturhistorischen Hofmuseum in Wien* 20(1): 22-24.
- SCHLECHTER, R. 1907. *Beitrage zur Kenntnis der Flora von Natal*. In A. Engler, *Botanische Jahrbucher* 40: 93. Leipzig.

- SCHREIBER, A. 1957. Beitrage zur Kenntnis der Leguminosen Sudwest-Afrika. *Mitteilungen der Botanischen Staatssammlung Munchen* 2(heft 16): 291-295.
- SCHREIBER, A. 1970. Fabaceae. In H. Merxmuller ed., *Prodromus einer Flora von Sudwest Afrika* 60: 38-63. Cramer. Lehre.
- SCHREIBER, A. 1970a. Einige neue Fabaceen aus Sudwestafrika. *Mitteilungen der Botanischen Staatssammlung Munchen* 8: 137-144, t.1.
- SCHRIRE, B.D. 1989. A multidisciplinary approach to pollination biology in the Leguminosae. In C.H. Stirton & J.L. Zarucchi (eds.), *Advances in Legume Biology* :183-242. Missouri Botanical Garden monograph no. 29. St. Louis, Missouri.
- SENN, H. 1938. Chromosome number relationships in the Leguminosae. *Bibliographia Genetica* 12: 175-336.
- SIMPSON, G.G. 1944. *Tempo and mode in evolution*. Columbia University Press, New York.
- SIMS, J. 1821. *Lebeckia nuda*, in W.Curtis, *Botanical Magazine* t.2214.
- SMITH, C.A. 1966. *Common Names of South African Plants*. Agricultural Technical Services. Pretoria.
- SOLEREDER, H. 1908. *Systematic anatomy of the Dicotyledons*. Translated by L.A. Boodle & F.E. Fritsch. Vol. 1: 253-281. Oxford.
- SPRENGEL, K.P.J. 1822. *Neue Entdeckungen im ganzen Umfang der Pflanzenkunde* 3: 54. Leipzig.
- SPRENGEL, K.P.J. 1826. *Caroli Linnaei....Systema vegetabilium* 3: 272-279. Gottingen.

- SPRENGEL, K.P.J. 1827. *Caroli Linnaei....Systema vegetabilium* 4(2) Curae posteriores : 284-286. Gottingen.
- SPRENGEL, K.P.J. 1831. *Caroli Linnaei....Genera Plantarum* ed. 9, 2: 581. Gottingen.
- STEARNS, W.T. 1969. Introduction to P. Miller, *The gardeners dictionary*. Abridged ed.4 (facsimile reprint). London.
- STEBBINS, G.L. 1950. *Variation and evolution in plants*. Columbia University Press, New York.
- STEBBINS, G.L. 1974. *Flowering plants, evolution above the species level*. Edward Arnold, London.
- STEBBINS, G.L. 1984. Mosaic evolution, mosaic selection and angiosperm phylogeny. *The Botanical Journal of the Linnean Society* 88: 149-164.
- STEVENS, P.F. 1980. Evolutionary polarity of character states. *Annual Review of Ecology & Systematics* 11: 333-358.
- STEVENS, P.F. 1984. Homology and Phylogeny: Morphology and Systematics. *Systematic Botany* 9 (4): 395-409.
- STEVENS, P.F. 1986. Evolutionary classification in Botany, 1960 - 1985. *Journal of the Arnold Arboretum* 67: 313-339.
- STIRTON, C.H. 1981. Petal sculpturing in Papilionoid legumes. In R.M. Polhill & P.H. Raven (eds.), *Advances in legume systematics* 2: 771-788. Royal Botanic Gardens, Kew.
- STIRTON, C.H. 1982. A new species of *Indigofera* from the south-west Cape. *Bothalia* 14: 69-82.
- STIRTON, C.H. & JARVIE, J.K. 1987. *Indigofera gifbergensis*. In J.K. Jarvie & C.H. Stirton, *The Indigofera filifolia complex (Fabaceae) in southern Africa*. *Bothalia* 17(1): 2-3.

- STUESSY, T.F. & CRISCI, J.V. 1984. Problems in the determination of evolutionary directionality of character state change for phylogenetic reconstruction. In T. Duncan & T.F. Stuessy (eds.), *Cladistics: perspectives on the reconstruction of evolutionary history*, Chp. 5. Columbia University Press, New York.
- TAUBERT, P. 1894. Leguminosae. In A. Engler & K. Prantl (eds.), *Die natürlichen Pflanzenfamilien* ed.1. 3(3): 184-384. Berlin.
- TAUBERT, P. 1895. *Indigofera demissa*. In A.Engler, *Die Pflanzenwelt Ost-Afrikas* C: 209-211.
- THEOBALD, W.L., KRAHULIK, J.L. & ROLLINS, R.C. 1979. Trichome description and classification. In C.R. Metcalfe & L. Chalk (eds.), *Anatomy of the Dicotyledons* ed.2. 1: 40-53. Clarendon Press, Oxford.
- THULIN, M. 1989. *Indigofera*. In I. Hedberg & S. Edwards (eds.), *Flora of Ethiopia* 3: 119-138. Addis Ababa.
- THUNBERG, C. 1800. *Prodromus plantarum capensium* 2: 132-133. Uppsala.
- THUNBERG, C. 1823. *Flora capensis* :595-599. Stuttgart.
- TORRE, A.R. 1960. Taxa angolensia nova vel minus cognita - 1. In *Memorias da Junta de investigacoes do ultramar* ser. 2, no. 19: 50-62, t29-39.
- TORRE, A.R. 1966. Indigofereae. In A.W. Exell & A. Fernandes (eds.), *Conspectus Florae Angolensis* 3: 84-140. Lisbon.
- VAN DER WALT, E. & STEYN, D.G. 1939. Test sheep die from Tympanites (bloating). *Onderstepoort Journal of Veterinary Science*. 12: 335-366.
- VAN STADEN, J., MANNING, J.C. & KELLY, K.M. 1989. Legume seeds -- the structure: function equation. In C.H. Stirton & J.L. Zarucchi

- (eds.), *Advances in Legume Biology* :417-450. Missouri Botanical Garden monograph no. 29. St. Louis, Missouri.
- VATKE, W. 1879. Plantas in itinere africano ab J.M.Hildebrandt collectas. in *Osterreichische botanische Zeitschrift* 29: 220-221.
- VAVILOV, N.I. 1922. The Law of Homologous series in the inheritance of variability. Translated and published in 1951. *Chronica Botanica* 13: 55-94.
- VERMEIJ, G.J. 1978. *Biogeography and adaptation*. Harvard University Press, Cambridge.
- VIGUIER, R. 1944. *Les Légumineuses de Madagascar*. Archives de Botanique, Caen. (unpublished.)
- VIGUIER, R. 1949. Leguminosae madagascarienses novae. *Notulae Systematicae* 13: 333-369.
- VIJAY KUMAR, B.K. 1988. Structure, distribution and classification of plant trichomes in relation to taxonomy in *Indigofera* L. (Fabaceae). *Indian Journal of Forestry* 11(2) 120-130.
- VIJAY KUMAR, B.K. 1988a. Foliar epidermal characters in relation to taxonomy of some *Indigofera* L. *Journal of the Swamy Botanical Club* 5(2): 67-72.
- VIJAY KUMAR, B.K. & RAMAYYA, N. 1986. Structure, distribution and ontogeny of multiseriate cylindrical hairs in *Indigofera* L. (Fabaceae). *Journal of the Swamy Botanical Club* 3(4): 175-177.
- VIJAY KUMAR, B.K. & RAMAYYA, N. 1987. Foliar dermatypes of some endemic taxa of *Indigofera* L. (Fabaceae) and their taxonomic significance. *Indian Journal of Botany* 10: 113-120.
- VIJAY KUMAR, B.K., PRABHAKAR, M., RAMAYYA, N. & LEELAVATHI, P. 1986. Structure, distribution and development of cavitated

- trichomes in *Indigofera* L. (Fabaceae). *Geophytology* 16(2): 227-231.
- WADDINGTON, C.H. 1957. *The strategy of the genes*. Allen & Unwin, London.
- WADDINGTON, C.H. 1962. *New Patterns in Genetics and Development*. Columbia University Press, New York.
- WADDINGTON, C.H. 1975. *The Evolution of an evolutionist*. Edinburgh University Press, Edinburgh.
- WALPERS, W.G. 1839. Animadversiones criticae in Leguminosas Capensis. *Linnaea* 13: 519-526.
- WALPERS, W.G. 1842. Papilionaceae. *Repertorium botanices systematicae* 1: 660-671.
- WANNTORP, H.-E., BROOKS, D.R., NILSSON, T., NYLIN, S., RONQUIST, F., STEARNS, S.C. & WEDELL, N. 1990. Phylogenetic approaches in ecology. *Oikos* 57: 119-132.
- WATROUS, L.E. & WHEELER, Q.D. 1981. The outgroup comparison method of character analysis. *Systematic Zoology* 30: 1-11.
- WATT, G. 1890. *A dictionary of the economic plants of India* 4: 383-369. Calcutta.
- WATT, J.M. & BREYER-BRANDWIJK, M.G. 1962. *The Medicinal and poisonous plants of southern and eastern Africa*. ed.2. Livingstone, Edinburgh & London.
- WEBERLING, F. 1965. Typology of inflorescences. *Journal of the Linnean Society. Botany*. 59: 215-221.
- WELLS, M.J. et al. 1986. A catalogue of problem plants in southern Africa. *Memoirs of the Botanical Survey of southern Africa* 53. Botanical Research Institute, Pretoria.

- WHITE, F. 1983. *The vegetation of Africa*. UNESCO, Paris.
- WHITEHEAD, V.A., GILIOME, J., & REBELLO, A.G. 1987. Insect pollination in the Cape flora. In A.G. Rebello (ed.), A preliminary synthesis of pollination biology in the fynbos biome. *South African National Scientific Report No. 141*. CSIR, Pretoria.
- WIGHT, R. & ARNOTT, G.A.W. 1834. *Prodromus florae peninsulae Indiae orientalis* : 201. London.
- WILEY, E.O. 1981. *Phylogenetics: The theory and Practice of Phylogenetic Systematics*. John Wiley & Sons, New York.
- WILEY, E.O. 1988. Vicariance Biogeography. *Annual Review of Systematics and Ecology* 19: 513-542.
- WILKINSON, H.F. 1979. The plant surface (mainly leaf). In C.R. Metcalfe & L. Chalk (eds.), *Anatomy of the Dicotyledons* ed.2. 1: 97-165. Clarendon Press, Oxford.
- WILLDENOW, C.L. (ed.) 1802. *Linné, Species Plantarum* ed. 4, 3(2): 1220-1239. Berlin.
- WILLIAMS, G.C. 1966. *Adaptation and natural selection*. Princeton University Press, New Jersey.
- WILSON, P.G. 1987. Taxonomic notes on some Australian species of *Indigofera* (Fabaceae, Faboideae). *Journal of the Adelaide Botanic Gardens* 10(1): 119-126.
- WOOD, J.M. 1902. *Natal Plants* 3: t.287. Bennet & Davis. Durban.
- YOSHIDA, T. & HASEGAWA, M. 1977. Distribution of stizolamine in some leguminous plants. *Phytochemistry* 16: 131-132.
- ZANDEE, M. & GEESINK, R. 1987. Phylogenetics and legumes: a desire for the impossible? In C.H. Stirton (ed.), *Advances in legume systematics* 3: 131-167. Royal Botanic Gardens, Kew.

ZINDLER-FRANK, E. 1987. Calcium oxalate crystals in legumes. In C.H. Stirton (ed.), *Advances in legume systematics* 3: 279-316. Royal Botanic Gardens, Kew.