A Reappraisal of the Generic Limits and Subdivision of *Barleria* L. (Acanthaceae)

submitted by

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DECLARATION

I declare that this dissertation is my own original work. It is being submitted for the degree of Doctor of Philosophy in the Faculty of Science, University of the Witwatersrand, Johannesburg. It has not been submitted before for any other degree in any other University.

The following was contributed by other people:

- analysis of flavonoid extracts: Professor B-E. van Wyk

Where the research findings of other workers are referred to it is duly acknowledged in the text.

M.-J. Balkwill

Mandy-Jane Balkwill

TO MY HUSBAND, KEVIN

ABSTRACT

In this dissertation the circumscription and subdivision of *Barleria* L. (Acanthaceae) is investigated.

Barleria is a large, polymorphic genus of herbs and shrubs, the delimitation and subdivision of which has long been subject to question. Approximately 300 species are known in the genus, occurring mainly in Africa and south-eastern Asia, particularly in tropical and sub-tropical zones. Previous studies of *Barleria* have followed two divergent approaches: those that result in a broad circumscription of the genus (e.g. Bentham, 1876), and those that recognise numerous, small segregate genera (e.g. Oersted, 1854). The only world-wide accounts of *Barleria* to date are those of Nees (1847), Bentham (1876) and Lindau (1895). All more recent accounts have been undertaken as parts of floras for particular geographic or floristic regions. Despite the publication of seven such accounts between 1895 and 1967 (the most recent), the problem of satisfactory subdivision of the genus, as perceived by Bentham (1876), still remained and provided one of the main motivations for embarking on the current research.

The aims of this research were to: i) re-assess the circumscription and sub-division of *Barleria*;

ii) provide a modern classification of the genus on a global scale, and iii) assess evolutionary relationships and lineages within the genus. The approach adopted was a multidisciplinary one, combining research in the laboratory, herbarium and field wherever possible. Careful sampling of a wide range of species was necessary in order to cover the morphological variability and geographic distribution of the genus as thoroughly as possible. Approximately 240 of the 300 described species were studied. Emphasis was placed on various aspects of morphology, anatomy of fruits and phytogeography, with particular attention paid to the accurate determination of characters and character-states, assessment of their evolutionary polarity and distribution within the genus. In the search for reliable characters, a number of new and previously neglected characters were found, and the homology of previously misunderstood characters (e.g. spine systems) was established. A wide range of characters was investigated, but only ten of these were selected for use in the cladistic analyses. These characters were those

for which evolutionary polarity and homology could be determined with a high degree of confidence and included: basic configuration of the corolla lobes; structure of the stigma; the presence of hollow or solid beaks on the capsules; the number of seeds in the mature capsule; anatomy of the septum (three characters); composition of the androecium; the nature of the hygroscopic hairs on the seeds and the structure of the fruit wall. Data was analysed using an iterative approach to cladistics in order to establish a sound empirical basis for a new classification. *Crabbea* Harv. was used as the outgroup in the cladistic analyses. The generic concept adopted here is a phylogenetic one based on monophyly.

The overall conclusion of the research is that *Barleria* is a single, though polymorphic, genus considered to represent a true monophyletic unit clearly delimited by the consistent co-occurrence of three characters: globose, honeycombed pollen; predominance of double cystoliths and a 4-partite calyx arranged as two inner and two outer sepals. A new classification is proposed — it is the first to cover the genus on a global scale since 1895. Two subgenera (*Barleria* and *Prionitis*) and seven sections are described. Two of the sections (*Somalia* and *Prionitis*) are retained as previously circumscribed, although new characters are used to delimit them; two of the taxa (Sections *Barlerites* and *Stellatohirtae*) are recognised for the first time at the sectional level; one of the sections (*Barleria*) is retained partially as circumscribed in earlier accounts, but with two previously included groups removed and elevated to sectional status; two of the sections (*Barleriopsis* and *Barlerianthus*) are described here for the first time.

As a result of the research findings reported here, a number of directions for future research have been identified. These include: i) A full taxonomic revision of *Barleria*; ii) In-group analyses of the sections proposed here in order to clarify relationships within each section and to facilitate the description of sub-groups within the sections; iii) Detailed investigation of biogeographical trends within *Barleria*, and iv) broad-scale investigations of characters across the Acanthaceae in order to assess the reliability of characters as markers for generic and supra-generic groups.

TABLE OF CONTENTS

ABSTRACT iv

CHAPTER 1: General Introduction 1

1.1. Introduction 1

1.2. Objectives of the research 2

1.3. Approach 3

1.4. Structure of the dissertation 4

CHAPTER 2: Generic Delimitation 6

2.1. Introduction 6

2.2. The changing generic concept of *Barleria* 9

2.3. Characters used in the delimitation of *Barleria* 11

2.4. Conclusions 15

CHAPTER 3: The placement of *Barleria* in the Acanthaceae 17

3.1. Introduction 17

3.2. The placement of *Barleria* in the Acanthaceae 17

3.3. Conclusions 28

CHAPTER 4: Previous Infra-generic classifications of *Barleria* 30

4.1. Introduction 30

4.2. The classifications 30

4.3. General Conclusions 37

CHAPTER 5: Variation in Characters and character states 39

5.1. General Introduction 39

5.2. Materials and methods 40

5.3. Characters and character states in *Barleria* 43

5.3.1. Vegetative Morphology 43

a. Habit 44

b. Morphology of leaves 50

c. Pubescence 53

5.3.2 Spine Systems 59

5.3.3. Inflorescences 62

a. Classification of inflorescence structure in *Barleria* 64

b. Evolutionary trends in inflorescence

structure 68
5.3.4. Bracts and Bracteoles 75
5.3.5. Floral Morphology 80
5.3.5.1. Calyx 80
5.3.5.2. Corolla 82
a. Morphology 82
b. Pigmentation 90
5.3.5.3. Androecium 93
5.3.5.4. Gynoecium 94
5.3.6. Capsules and Seeds 96
a. Morphology of the fruit 96
b. Composition of the septum 101
c. Seeds 102
5.4. General Conclusions 104
CHAPTER 6: Phylogenetic Relationships 107
6.1. General Introduction 107
6.2. Selection of Taxa 110
6.3. Selection and coding of characters 111
6.4. Cladistic Analyses 112
6.5. General discussion and conclusions 122
CHAPTER 7: FORMAL TAXONOMY 129
Generic Description 129
Discussion 131
i) Distributions and numbers of species 132
ii) Infra-generic taxa 140
Key to the infra-generic taxa of *Barleria* 141
Enumeration of the Taxa 143
Subgenus I: Barleria 143
Section I: *Barleria* 144
Section II: *Barleriopsis* 153
Subgenus II: Prionitis 162
Section III: *Prionitis* 162

Section IV: *Somalia* 170
Section V: *Barlerianthus* 117
Section VI: *Barlerites* 182
Section VII: *Stellatohirtae* 186
Taxa of Unknown Affinity 189
CHAPTER 8: General Conclusions 190
Introduction 190
Conclusions, contributions and limitations 190
Future Directions 193
REFERENCES 196
APPENDIX 1 205
APPENDIX 2 227
APPENDIX 3 250

LIST OF TABLES

Table 2.1:	Species described in *Barleria* by Linnaeus in *Species Plantarum* (1753)	10
Table 2.2:	Summary of main characters used in previous generic descriptions of *Barleria*	12
Table 2.3:	Past accounts of *Barleria*	13
Table 4.1:	Infra-generic classification of *Barleria sensu* Nees (1847)	31
Table 4.2:	Infra-generic classification of *Barleria sensu* Clarke (1885)	32
Table 4.3:	Infra-generic classification of *Barleria sensu* Lindau (1895)	33
Table 4.4:	Infra-generic classification of *Barleria sensu* Clarke (1899)	34
Table 4.5:	Infra-generic classification of *Barleria sensu* Clarke (1901)	35
Table 4.6a:	Infra-generic classification of *Barleria sensu* Obermeijer (1933)	36
Table 4.6b:	Characters used to sub-divide Section *Barleria sensu* Obermeijer (1933).	36
Table 5.1:	Taxa sampled for analysis of flavonoids, source of material and voucher specimens	42
Table 6.1:	Summary of the cladistic analyses conducted to determine phylogenetic relationships within *Barleria*	113
Table 6.2:	Character set and polarisations used in cladistic analyses	114
Table 6.3.	Additional characters not used in the cladistic analyses	115
Table 7.1:	Total numbers of species, number of endemics and number of representatives from each Section in each major area in which *Barleria* occurs	133
Table 7.2:	Symbols used to denote major areas of the world in which *Barleria* occurs	135

Table 7.3: Matrix of Sorensen's Indices showing similarity (as a percentage) between different areas in terms of species of *Barleria* present 136

LIST OF FIGURES

Figure 3.1: Summary of the Classification of the Acanthaceae proposed by Nees (1847), showing the position of *Barleria* and allied genera 19

Figure 3.2: Summary of the classification of the Acanthaceae proposed by Anderson (1864), showing the position of *Barleria* and allied genera 20

Figure 3.3: Summary of the classification of the Acanthaceae proposed by Bentham (1876), showing the position of *Barleria* and allied genera 21

Figure 3.4: Summary of the classification proposed by Lindau (1895), showing the position of *Barleria* and allied genera 23

Figure 3.5: Summary of the classification of the Acanthaceae proposed by Burkill & Clarke (1899), showing the position of *Barleria* and allied genera 24

Figure 3.6: Summary of the classification of the Acanthaceae proposed by Bremekamp (1965), showing the position of *Barleria* 25

Figure 5.1: Variation in leaf morphology in *Barleria* 52

Figure 5.2: Types of trichomes found in *Barleria* 55

Figure 5.3: Variation in the morphology of spinous bracteoles in selected species of *Barleria* 63

Figure 5.4: Diagrammatic representation of the structure of inflorescence units showing dichasial branching only 67

Figure 5.5: Diagrammatic representation of the structure of inflorescence units showing dichasial and monochasial branching 69

Figure 5.6: Diagrammatic representation of the structure of inflorescence units showing monochasial growth only 70

Figure 5.7: Inflorescence units exhibiting unusual structure 71

Figure 5.8: Putative evolutionary trends in the structure of

inflorescence units in *Barleria* 73
Figure 5.9: Possible routes along which formation of terminal synflorescences may proceed 74
Figure 5.10: Variation in the morphology of modified floral bracts in *Barleria* 76
Figure 5.11: Variation in the morphology of bracteoles in selected species of *Barleria* 78
Figure 5.12: Calyx morphology in *Barleria* 79
Figure 5.13: Variation in the morphology of the anticous and posticous calyx lobes in selected representatives of *Barleria* 81
Figure 5.14: Diagrammatic summary of variation in corolla morphology in *Barleria* 84
Figure 5.15: Variation in the composition of the androecium in selected representatives of *Barleria*. 92
Figure 5.16: Morphology of the stigma in *Barleria* 95
Figure 5.17: Variation in the morphology of the capsule in *Barleria* 97
Figure 5.18: Comparison of dehisced acanthaceous capsule with elastic placental bases and a dehisced capsule of *B. scindens* 99
Figure 5.19: Variation in the composition of the septum in *Barleria* 100
Figure 5.20: Variation in seed morphology in selected representatives of *Barleria* 103
Figure 6.1: Estimates of phylogenetic relationships in the genus *Barleria* as obtained in Analysis 1 116
Figure 6.2: Estimates of phylogenetic relationships in the genus *Barleria* as obtained in Analyses 2, 3 and 4 119
Figure 6.3: Estimates of phylogenetic relationships in the genus *Barleria* as obtained in Analyses 5 and 6, and chosen cladogram for the genus 121
Figure 6.4: Branching diagram representing the classification of *Barleria* proposed by Clarke (1899) 126
Figure 6.5: Branching diagram representing the classification of *Barleria* proposed by Obermeijer (1933) 127

Figure 7.1: Map showing global distribution of *Barleria* and the numbers of species occurring in different regions of the world 134
Figure 7.2: Variation in the morphology of the leaves, corollas, bracteoles and calyces of selected representatives of Section *Barleria* 145
Figure 7.3: Global distribution of members of Section *Barleria* 146
Figure 7.4: Variation in the morphology of the leaves, corollas, bracteoles, bracts and calyces in selected representatives of Section *Barleriopsis* 154
Figure 7.5: Global distribution of members of Section *Barleriopsis* 155
Figure 7.6: Variation in the morphology of the leaves, corollas, bracteoles, bracts and calyces of selected representatives of Section *Prionitis* 164
Figure 7.7: Global distribution of members of Section *Prionitis* 165
Figure 7.8: Variation in the morphology of the leaves, corollas, bracteoles and calyces of selected representatives of Section *Somalia* 172
Figure 7.9: Global distribution of members of Section *Somalia* 173
Figure 7.10: Variation in the morphology of leaves, corollas, bracteoles and calyces of Sections *Barlerianthus* and *Barlerites* 178
Figure 7.11: Global distribution of members of Section *Barlerianthus* 179
Figure 7.12: Global distribution of members of Section *Barlerites* 184
Figure 7.13: Variation in the morphology of the leaves, corollas, bracteoles, bracts and calyces of selected representatives of Section *Stellatohirtae* 187
Figure 7.14: Global distribution of members of Section *Stellatohirtae* 188

LIST OF PLATES

Plate 5.1: Habit of selected species of *Barleria* 47

Plate 5.2: Habit of *B. scindens* Oberm. 48

Plate 5.3: Habit of selected species of *Barleria* 49

Plate 5.4: Sunken glands on the leaves of *B. rotundifolia* (Section *Prionitis*), as viewed with a light microscope 57

Plate 5.5: Axillary spine systems in Section *Prionitis* and Section *Barleria* 60

Plate 5.6: Corolla morphology of selected species of Sections *Barleria* and *Barleriopsis* 85

Plate 5.7: Variation in corolla morphology in selected representatives of Section *Barleria* 86

Plate 5.8: Corolla morphology in selected representatives of Section *Somalia* 87

Plate 5.9: Corolla morphology in selected representatives of Sections *Somalia, Stellatohirtae* and *Prionitis* 89

Plate 7.1: Selected representatives of Section *Barleria* 149

Plate 7.2: Selected representatives of Sections *Barleria* and *Barleriopsis* 150

Plate 7.3: Selected representatives of Section *Barleriopsis* 158

Plate 7.4: Selected representatives of Section *Prionitis* 167

Plate 7.5: Selected representatives of Sections *Prionitis* and *Somalia* 168

Plate 7.6: Selected representatives of Section *Somalia* 174

Plate 7.7: Selected representatives of Section *Barlerianthus* 180

Plate 7.8: Selected representatives of Section *Barlerianthus*, showing the morphology of the capsules and glabrous seeds 181

Plate 7.9: Selected representatives of Sections *Stellatohirtae* and *Barlerites* 185

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CHAPTER 1

General Introduction

1.1. Rationale for the study

Barleria L. (Acanthaceae) is a large, pantropical genus of herbs and shrubs comprising, at a conservative estimate, some 300 species world-wide (see Appendix 1). Its greatest representation is in Africa and Asia, with the greatest centre of diversity (approximately 77 species) in east tropical Africa. As with other large, variable acanthaceous genera of Linnaean origin such as *Justicia* L. (Graham, 1988) and *Ruellia* L. (Cadman, 1987), studies of *Barleria* have followed two divergent approaches: those resulting in a broad circumscription of the genus and those that recognise numerous small, segregate genera. Probably the most extreme example of the latter approach is that of Oersted (1854) who split the 28 species he saw into 10 segregate genera. Although his treatment has never been seriously followed, it is perhaps indicative of the level of variability present in the genus. Bentham (1876) adopted a broad definition of *Barleria*, as he felt that the genus could be relatively easily defined, although it was clearly polymorphic. The problem that Bentham perceived was not one of generic delimitation, but rather that of the satisfactory sub-division of this variable assemblage of species into natural groups (Bentham, 1876).

The only accounts of *Barleria* that have been undertaken on a world-wide basis are those of Nees (1847), Bentham (1876) and Lindau (1895). All more recent accounts have been undertaken as parts of floras for particular geographic or floristic regions. Despite the publication of no less than seven regional revisions of *Barleria*, the problem of satisfactory sub-division of the genus still exists, especially if the genus is considered on a monographic scale. Almost every character in *Barleria* is highly variable, the degree of variation in any particular character (e.g. the composition of the androecium) being almost as great within the genus as it is across the entire family (Balkwill & Getliffe Norris, 1988). Not all combinations of characters are represented in any one geographic area. The regional nature of most of the studies of *Barleria* (Clarke 1885, 1899, 1901; Ridley, 1923; Hutchinson & Dalziel, 1931; Obermeijer, 1933; Benoist, 1967) has

meant that successful keys to species have been produced for particular regions. However, in terms of infra-generic classification on a global scale, the regional accounts have lead to some confusion. Classifications have been proposed in several of the regional accounts (*l.c.*) but, as may be expected, none of them fully accommodates species from out of its geographic area. Furthermore, some of these classifications do not accommodate all species now known to occur within the areas for which the accounts were written. If *Barleria* is a single genus, then it should be possible to produce a single infra-generic classification for it. I concur with Graham (1988), that a stable infra-generic classification is highly desirable, not only from a theoretical standpoint, but also in terms of producing a consistent treatment that can be adopted in the various floristic works that are being produced in different geographic areas.

Existing classifications of *Barleria* have emphasised different characters, with most attention paid to spi[illegible]ence, morphology of inflorescences, colour and form of flowers, overall morphology of the fruit and the number of seeds. Although the variation in these features initially seems to be very useful, it is extremely difficult to obtain correlation between different characters or character-states. An important aspect of the research undertaken for this thesis was the search for reliable characters on which to base a classification of the entire genus.

1.2. Objectives of the research

The initial aim of this research was to re-assess the generic limits of *Barleria*, such that a new classification could be produced for the southern African species. An initial survey of southern African material showed that several of the species exhibited combinations of characters that could not be accommodated in the classifications of Clarke (1899, 1901) or Obermeijer (1933). After a preliminary survey of some tropical African species (those of which material was available in local herbaria), it became apparent that to undertake a study of this nature, it would be necessary to sample the entire genus on a world-wide basis. It was also thought more desirable, both philosophically and practically, to make the overall aim of the research the production of a classification for *Barleria* on a world-wide scale.

The objectives of the research were:

1. To re-assess the delimitation of *Barleria*.
2. To provide a modern infra-generic classification of the genus on a world-wide basis.
3. To assess evolutionary relationships and lineages within the genus.

1.3. Approach

As the number of species in *Barleria* is rather high, it would have been impossible to study every one in detail in a limited period of time. Thus, careful sampling of a wide range of species was necessary to cover the morphological variability and geographic distribution of the genus. Southern Africa represents the second highest centre of diversity in *Barleria*. It was thought, therefore, that it would be satisfactory to initiate the study using mainly southern African species (of which there are about 70), as it was easy to conduct extensive field studies and obtain herbarium material. During this initial phase of the research, as much herbarium material of tropical African species as was available from the National Herbarium of South Africa (PRE) and the National Herbarium of Zimbabwe (SRGH) was also studied. Based on this material, initial working hypotheses were formulated regarding character variability and possible infra-generic groupings. These working hypotheses were then tested and modified by investigation of as many of the other species in the genus as possible. Material was obtained on loan from E, EA, FT, K and MO. In addition, five weeks were spent working through the holdings of *Barleria* in the herbaria of the Royal Botanic Gardens at Kew (K) and Edinburgh (E). The entire collection of *Barleria* at the Herbarium of the British Museum of Natural History (BM) was also studied. Initial surveys of the material concentrated on scoring species for the presence or absence of certain key characters. A selection of these taxa was then studied in detail. Each of these selected taxa was studied across its entire geographic range, in order to take in as much of the range of variation as possible. Approximately 240 of the 300 described species of *Barleria* were ultimately studied as well as material of numerous undescribed species. Appendix 1 is a list of all described species of *Barleria*, including known synonymy, and Appendix 2 is a list of selected voucher specimens of the species studied. It was not possible to trace material of certain names and the validity of some of these taxa is

unclear. The full extent of synonymy in the genus is also not known as it is in sore need of a full taxonomic revision. Appendix 1 also includes a list of those names of which material was not seen.

In this study a multidisciplinary approach combining work in the herbarium, laboratory and field (where possible) was adopted. Emphasis was placed on various aspects of morphology, anatomy of the fruits and phytogeography. Data was analysed using an iterative approach to cladistics in order to establish a sound empirical basis on which to establish a new classification. This study placed most emphasis on the accurate description of characters and character-states and their distribution within the genus, and less emphasis on taxonomic differences at the species level.

1.4. Structure of the dissertation

Details of the methods used to study particular features or to analyse data are included in the chapters in which they are relevant. Chapter 2 includes a discussion of the criteria used for generic delimitation, both in a general theoretical context and in terms of the taxonomic history of *Barleria*. Previous attempts to split the genus are also discussed in Chapter 2. Chapter 3 considers the placement of *Barleria* within the Acanthaceae, as this had important bearing on the selection of an outgroup for the genus, and on the types of characters selected for use in this study. Previous infra-generic classifications and the characters on which these works were based are discussed in Chapter 4. Characters and character states are described and discussed in detail in the fifth chapter of the dissertation. Chapter 5 also includes a discussion of the distribution of character states within the genus and in related genera, where appropriate. The determination of polarities and homologies and evolutionary trends within certain characters are explained, and the criteria for selection of particular characters for inclusion in the cladistic analyses are provided in Chapter 5. The phylogenetic relationships based on the results of cladistic analyses are presented in Chapter 6. The strengths and weaknesses of each of the cladograms obtained are evaluated in this chapter and the most plausible evolutionary lineages that can be inferred from the cladograms are discussed. Sub-genera and sections are formally described in Chapter 7 (Formal Taxonomy). This chapter includes a key to the infra-generic groups as well as lists of taxa included within each group. Smaller groups within some of the sections are described informally and the characters

on which these sub-groups are based are discussed. The number of species within each group, the probable centre of diversity and the geographic distribution of each group is discussed. Chapter 8 contains concluding remarks; in this chapter the contribution that this thesis makes to the state of knowledge in this field is assessed; furthermore, the findings of this research are placed in the context of current and future research in *Barleria* and the Acanthaceae as a whole. Areas of research that are particularly worthy of future investigation are highlighted.

CHAPTER 2

Generic Delimitation

2.1. Introduction

There is a vast body of literature in which theoretical discourse regarding the nature of species and species concepts can be found (see Mayr, 1992 for a recent review). However, much less has been written, at least directly so, on the nature of genera and generic concepts. The concept of rank is inevitably linked to the assigning of names (Clayton, 1983). What the name of an organism is would not matter very much if it were a name and nothing more. The generic name, however, is also an expression of relationship between species (Camp, 1940). Much of the available literature on generic concepts concentrates on the historical shift from viewing genera mainly as cataloguing devices, to viewing them as biological units (or "natural groups") that have some objective reality in nature (Clayton, 1983). Associated with this is discussion of the problems relating to marrying the two concepts successfully without too much disruption of long-accepted nomenclature (Anderson, 1940; Bartlett, 1940; Camp, 1940; Greenman, 1940; Sherff, 1940; Walters, 1961; Clayton 1972, 1983; Stevens, 1984a, 1985; Funk, 1985).

The scientific concept of "genus" had its origins in pre-Linnaean folk concepts (Bartlett, 1940; Clayton, 1983). The generic concept in folk botany arose from the grouping together of similar looking organisms under generic names, primarily as a matter of linguistic necessity (Bartlett, 1940). Many of the genera recognised today were taken over, with little change, from traditional folk taxonomies (Bartlett, 1940; Clayton, 1983). These genera are thus a natural product of European thought of the 17th and 18th centuries (Walters, 1961), a time when many authors still believed in the concept of "Special Creation". Genera were thought of more as "facts" than as "concepts" (Camp, 1940).

Linnaeus (1753) generally accepted the genera established by Tournefort and Plumier

who preceded him (Bartlett, 1940). Although it is not possible to define clearly what is meant by the Linnaean concept of genera (Sherff, 1940), he evidently regarded his genera as "entities of nature". Wiley (1981) has provided a detailed discussion of natural groups, but there are very few explicit statements in the primary literature regarding the properties or contents of such natural groups (Stevens, 1984a). Linnaeus regarded his genera as natural but did not necessarily have any particular defining characters for these natural groups (Stevens, 1984a). The members of his genera usually had a number of features in common that tended to co-vary, but membership of a particular species in a genus depended not so much on possession of these characters, but on whether or not Linnaeus thought the species belonged to that genus (Stevens, 1984a). Such genera could be considered "natural" in the sense of Aristotlean naturalness (Wiley, 1981). Few of Linnaeus' genera were particularly large at the time he described them (Walters, 1961); for example, *Barleria* contained only 5 species. Large Linnaean genera can be seen to have arisen through the "historical accidents of Linnaean description" (Walters, 1961). It probably did not seem necessary to Linnaeus in grouping the species known to him, to make the generic descriptions any more exclusive than he did. These "permissive" generic descriptions have allowed for the inclusion of a very wide variety of species into the Linnaean genera (Walters, 1961) - this has certainly been the case with large acanthaceous genera such as *Justicia*, *Ruellia* and *Barleria*, as will be demonstrated later in this chapter.

The publication of the *Origin of Species* (Darwin, 1859), did not change the way in which taxonomists constructed their classifications or formed groups, but only the way they explained what they thought these represented (Bartlett, 1940; Stevens, 1984a, 1985). Increasingly, classifications and the groups they contained were to represent phylogeny as well as fulfilling the roles of information retrieval and predictivity as they had done previously (Stevens, 1984a). With respect to the circumscription of genera, as with other ranks, the main change since the time of Linnaeus has been to formulate groups that show "natural affinity by descent." Such groups are "natural" in a phylogenetic context; the members of such a group share a common ancestor that is not ancestral to any other group. Such groups are thought to exist in nature and are the products of natural processes. Our classification of such groups should, therefore, be consistent with such natural processes (Wiley, 1981). Relatively recent articles by Clayton (1972, 1983) and Stevens (1984a, 1985) provide a convenient summary of

generic delimitation as frequently practised by modern botanists. In these publications the reasons for recognising genera are discussed and the criteria used in their circumscription are given. Funk (1985) has provided a concise account of the application of cladistic principles in the delimitation of genera in the Compositae.

Clayton's discussions (1972, 1983) are based on the principle that the genus is a composite idea and a subjective approach to a natural phenomenon. The formal definition of a genus is given by Clayton (1983) as an "arbitrary and abstract level of morphological difference". The rank of species was originally also conceived as an arbitrary and abstract level of morphological difference (Clayton, 1972), but biologists gradually realised that it corresponded with a definite biological phenomenon - the closed breeding system (Clayton, 1972, 1983). Although Clayton concedes that genera do seem to have an objective reality of some sort, no distinct relationship of the genus with a biological phenomenon has been found. Our concept of genera then, remains, for Clayton at least, a simplifying abstraction called forth by our need to catalogue, remember and communicate (Clayton, 1983). The relationship of such genera to phylogeny is only very tenuous. Stevens (1985), suggests that the answer to the problems outlined by Clayton, is to reject the notion of the genus as a composite idea. Genera can and should be based phylogenetically. If this is done, then we should be able to produce a phylogenetic classification in which the groups we define are "natural" (share a common evolutionary fate through time) and the classification fulfils the roles of predictivity and mnemonic utility insisted upon by Clayton (1983).

Two issues that have dominated the literature on generic concepts are: (i) the fear that defining genera on a phylogenetic basis will lead to nomenclatural instability, and (ii) the ways in which regional versus monographic work affect our generic concepts. Most early authors (Bartlett, 1940; Camp, 1940; Greenman, 1940; Sherff, 1940; Walters, 1961) made a plea for adopting a conservative concept of genera in order to preserve nomenclatural stability. Some of these authors (Camp, 1940; Sherff, 1940) added the cautionary note that biologists, whilst trying to maintain stability, should not be bound by a nomenclatural system so rigid that it could not serve to express both the rank and the degree of relationship between organisms. Clayton (1983) has largely echoed the views of the earlier authors, stating that the criterion of convenience should not override evidence of relationship, but that it should strongly influence the translation of such

evidence into a system of discretely defined genera. Following this approach, fine details of "phylogenetic supposition" need only be expressed in some form of dendrogram (Clayton, 1983). Stevens (1985), with whom I concur, has effectively pointed out that defining genera on a phylogenetic basis (and, thus producing a phylogenetic classification) need not result in great nomenclatural instability or change. The limits of genera can be adjusted such that a monophyletic assemblage includes a particular name, is of a "reasonable" size or is separated by a clear morphological gap (Stevens, 1985). The number of hierarchical levels in phylogenetic classifications can be reduced by various stratagems. Furthermore, Funk (1985) has effectively demonstrated in the Compositae that application of cladistic principles does not automatically lead to splitting of previously recognised groups. Many of the problems foreseen by Clayton (1983) and others before him can be effectively avoided if we: reject the notion of genera as a composite idea; remember that all taxa are hypotheses and that what we aim at producing in our classifications is our best estimate of phylogeny and that, in all cases, detailed justification for the circumscription of our taxa should be given (Stevens, 1985). The question also should not be one of "large" or "small", but whether or not the groups we recognise are monophyletic (Funk, 1985).

Our concept of genera is sensitive to the sample of species available for study. There is thus the danger, especially with widespread taxa, that divergent treatments in local floras will lead to the description of segregate genera in certain areas because the authors are unaware of the full range of variation (Willdenow, 1811; Anderson, 1940; Camp, 1940; Greenman, 1940; Sherff, 1940; Clayton 1972, 1983; Stevens, 1985). This has certainly been the case in *Justicia* (Graham, 1988), *Ruellia* (Cadman, 1987) and, to a much lesser extent, in *Barleria*. This has lead to a call by authors on this topic for more monographic work so that stable generic limits can be set within the framework of which local floras can be produced (Graham, 1988).

2.2 The changing generic concept of *Barleria*

Barleria L. has long been recognised as a taxonomically difficult genus. Although it has not suffered as many attempts to split it into segregate genera as have *Ruellia* and *Justicia*, its circumscription has often been subject to question. Much of the difficulty

associated with *Barleria*, as with genera like *Ruellia* (Long, 1973), arises from its remarkable phenotypic plasticity. Linnaeus established *Barleria* in 1753 for a group of five species, three of which were from India and two from central and South America (see Table 2.1). One of these, *B. solanifolia* L., has since been transferred to another genus, *Barleriola* Oerst., and *B. coccinea* has been placed in synonymy with *Ruellia coccinea* Vahl.

Table 2.1: Species described in *Barleria* by Linnaeus in *Species Plantarum* (1753).

Species	Place of origin
B. buxifolia	India
B. cristata	India
B. prionitis	India
B. coccinea	Central America
B. solanifolia	South America

The Linnaean concept of *Barleria* included herbaceous plants having a persistent 4-partite calyx with large outer lobes and smaller inner lobes; a sympetalous, funnel-shaped corolla with an unequally 5-fid limb; a bifid stigma and an acute, compressed, quadrangular capsule containing 2 seeds (see Table 2.2). This concept was largely retained and expanded by later authors such as de Jussieu (1789) and Nees (1847)(see Table 2.2). Oersted (1854) had a far narrower generic concept and split *Barleria* into 10 segregate genera: *Barleria*, *Barleriacanthus*, *Barlerianthus*, *Barleriola*, *Barleriopsis*, *Barleriosiphon*, *Barlerites*, *Dicranacanthus*, *Pseudobarleria* and *Prionitis*. In 1864, Anderson resurrected the Linnaean concept of *Barleria*, but it was Bentham (1876) who laid the foundation for the genus as it is accepted today. All but one of the genera created by Oersted, *Barleriola*, and another genus, *Wahabia* Fenzl., were placed in synonymy with *Barleria* by Bentham (*l.c.*). Bentham expressed the view that the characters used by Oersted (*l.c.*) occurred in many species not seen by him (Oersted) and thus his genera, with the possible exception of *Prionitis*, were better retained within *Barleria* as sections. Four other genera, *Barreliera* Gmel., *Parabarleria* Baill., *Somalia* Oliv., and *Soubeyrania* Neck. were later placed into synonymy with *Barleria* by Lindau

(1895). Thus, the broad generic concept established by Bentham was accepted and added to by subsequent authors (Clarke, 1885; Lindau, 1895; Clarke 1899, 1901; Ridley, 1923; Obermeijer, 1933; Hutchinson and Dalziel, 1931; Benoist, 1963).

2.3. Characters used in the delimitation of *Barleria*

A survey of the kinds of features used in previous accounts of *Barleria* has important bearing on the characters used in this research. Twelve accounts of *Barleria* have been published to date (see Table 2.3). Three of these have considered the genus on a global scale (Nees, 1847; Bentham, 1876 and Lindau, 1895), but the number of species dealt with in these accounts is small relative to all the species of *Barleria* known today. All other accounts of the genus have been regional (see Table 2.3).

The feature most widely used to distinguish *Barleria* from other closely related genera, is the quadripartite calyx with the adaxial (posticous) and abaxial (anticous) lobes outermost and larger than the lateral inner lobes (Linnaeus, 1754; Nees, 1847; Bentham, 1876; Clarke, 1899, 1901; Hutchinson and Dalziel, 1931). Features frequently used in conjunction with this include an infundibuliform corolla with unequally five-lobed limb (Linnaeus, Nees, *l.c.*); two fertile stamens; honeycombed, globose pollen and the presence of hygroscopic hairs on the seeds (Clarke, 1899, 1901).

Table 2.2 presents a summary of all the features used in generic descriptions of *Barleria* since the genus was first described by Linnaeus (1754). The Linnaean description is interesting because it reveals so little of the variation in characters evidently seen by him. His description of *Barleria* (see Table 2.2) is not so much broad as it is lacking in details of features, such as axillary spines, definitely seen by him (1753) when he described the first five species of the genus. It is most likely, as discussed earlier, that he saw no need to make the generic description any more detailed and exclusive at the time. Strict application of the concept of *Barleria* embodied in the Linnaean generic description, would result in the exclusion of numerous currently included species. The description of Bentham (*l.c.*), (Table 2.2), reflects a far greater proportion of the variability present in features such as the androecium, corolla morphology and the form of the capsules.

Table 2.2: Summary of main characters used in previous generic descriptions of *Barleria*.

	Linnaeus 1764	de Jussieu 1789	Nees 1847	Oersted 1854	Bentham 1876	Clarke 1885	Lindau 1895	Clarke 1899	Obermeijer 1933
Spines	-	single or paired in some leaf axils	sometimes present	-	sometimes present	present or absent	often present (converted bracteoles)	sometimes present (modified bracts)	sometimes present
Bracts	-	2 sometimes spiniform	broad or narrow	awl-shaped or linear-muronate	-	large, small or absent	frequently dry, margins spinescent	2, variable, spinescent or foliaceous	spinous or not; leafy, spinoso-dentate, toothed or entire
Bracteoles		-	narrow ciliate or spinose	linear, mucronately awl-shaped	-	large, small or absent	present spinous	0	as for bracts
Calyx	4-partite persistent outer lobes largest	4-partite unequal 2 lateral lobes narrow	4-partite, in 2 opposite pairs; outers: large entire or slightly dentate	4 lobes, uppers and lowers broad, conspicuously reticulate-veined, dentate	4-fid posticous & anticous lobes large laterals interior	4 lobes in opposite pairs, outers larger anticous often bifid	4-partite, anteriors mostly 2-toothed, laterals long...ate	of 4 segments, 2 outer (anticous and posticous) 2 inner (lateral, smaller)	4 sepals fused almost to base, enlarged in fruit; anticous lobe 2-partite
Corolla	sympetalous funnel-shaped; lobes 5, sub-equal, 5th more deeply divided	funnel-shaped 5-fid; 5th lobe more deeply divided	funnel-shaped	funnel-shaped gaping; upper lip entire; lower lip 4-lobed	tube long to very long, variously enlarged above; limb imbricate, spreading, 5-lobed	tube elongate to very long; funnel-shaped above; 5 subequal lobes, imbricate	5-partite, very big or very small	tube cylindric below, funnel-iform above; of 5 unequal lobes or 2-lipped	large; tube rarely short; cylindrical or funnel shaped; limb 2-lipped or subequally 5-lobed
Flower Colour	-	-	blue, white or yellow	-	-	blue, white or yellow	white, violet or yellow	yellow or blue	various
Androecium	filaments 4; 2 very short	2 fertile stamens, others shorter	4 didynamous stamens	2 long fertile stamens; 3 staminodes	2 fertile stamens 3 staminodes (1 very reduced)	2 bithecous stamens; 2 rudimentary, 5th sometimes present	4 fertile or 2 fertile plus 2/3 staminodes	2 perfect stamens; 2 or 3 staminodes	4-5 stamens, 2 or 3 of them imperfect
Gynoecium	ovary ovate, stigma bifid	stigmas 2, rarely 1	stigma compressed-truncate, entire	stigma conical	style thick at apex; stigma obtuse, flat, simple	ovary 4-ovulate; style long, shortly bifid or subentire	-	stigma 2-lobed; lobes unequal, subconfluent	ovary glabrous or pilose; 2 perfect ovules per locule or 1 in each aborted
Inflorescence	-	flowers axillary or terminal	axillary spikes	solitary or paired in axils	-	solitary, sessile or in sub-lax spikes	axillary cymes or terminal bunches	scorpioid cymes condensed into heads or reduced to 1; sometimes terminal	dichasia or uni-lateral cymes; or solitary, axillary flowers, or running into terminal spikes
Fruit morphology	acute, compressed quadrangular; bilocular	quadrangular; bursting elastically	conic-acuminate; bilocular at base	oblong-acuminate, 4-sided, compressed	ovoid or oblong, with or without long apical nose	ovoid or oblong, 2 4 seeds below middle	elongate or ovate; with a long beak	ovoid (2 seeds) or oblong-ellipsoid (4 seeds)	2-seeded, rostrate, rounded at base; or 4 or 2-seeded, oblong or ovoid, narrowed at base and apex
Septum	longitudinally divided into 2	-	entire, adnate	-	-	-	-	-	-
Seeds	2, sub-rotund, compressed	1 - 2 per locule	4	4	seeds in middle of capsule	seeds compressed; ovate with wavy-silky hairs	4 or 2, mostly hairy	2 or 4 with hygroscopic hairs	2 or 4, with shaggy hygroscopic hairs
Other	Intermediate between Justicias and Ruellias	-	-	-	-	disc large, often a toothed cup half enclosing ovary	-	-	disc large, cup-shaped, sinuate, persistent; pollen globose

The generic concept employed by Oersted (1854) was exceptionally and impractically narrow. However, many of the features on which he based his genera are particularly interesting. These features will be discussed in some detail here, because

Table 2.3: Past accounts of *Barleria*.

AUTHOR	DATE	AREA COVERED	NUMBER OF SPECIES
Linnaeus, C.	1753	World-wide	5
Nees von Esenbeck, C.J.D.	1847	World-wide	66
Oersted, A.S.	1854	Asia, Americas	28
Bentham, G.	1876	World-wide	60
Clarke, C.B.	1885	India	26
Lindau, G.	1895	World-wide	approx. 100
Clarke, C.B.	1899	Tropical East Africa	79
Clarke, C.B.	1901	South Africa	28
Ridley	1923	Malay Peninsula	3
Hutchinson & Dalziel	1931	West Tropical Africa	6
Obermeijer, A.A.	1933	Southern Africa, some Zimbabwean species	62
Benoist	1967	Madagascar	27

they are used, although at different taxonomic levels, in the classification presented in

In his description of *Barleria* Oersted described the 4-partite calyx in much the same way as other authors, but he did not use this feature as a marker for the genus. Instead, he based his concepts of genera on variations in the form of the corolla; details of the texture, venation and dentition of the outer calyx lobes; composition of the androecium, differences in the position and structure of the inflorescences and morphology of the capsule. The variation in these features can become quite bewildering if one does not use the form of the calyx as a unifying feature, particularly if a large number of species is included in the study. All ten of the genera created by Oersted possess a 4-lobed calyx with two large, outer lobes and two narrow, inner lobes. *Barleria sensu* Oersted shares with *Barleriopsis*, *Barleriacanthus* and *Barleriosiphon* a membranous or scarious calyx with prominent reticulate venation, with or without dentition on the margins of the outer lobes. *Barleria sensu* Oersted was distinguished from the other genera on the basis of its awl-shaped bracteoles (not large like the outer calyx lobes or absent), and its funnel-shaped corolla with the lower part of the tube equal in length to the inflated upper portion (not short as in *Barleriopsis*, or very long and narrow as in *Barleriacanthus* and *Barleriosiphon*). It should be noted here that Oersted's further descriptions of corolla morphology reveal a fundamental misinterpretation on his part. Several of his genera, are described as having flowers with an undivided upper lip and a 4-partite lower lip. Clearly, Oersted must have examined flowers that were upside-down as the 4-lobed lip, when present, is always in the adaxial position in *Barleria*.

Oersted divided his ten genera into two groups (without any formal status) based on differences in the morphology of the fruits. All genera with oblong, tetragonous fruits were placed in one group. The remaining genera, *Barlerites* and *Prionitis* (possessing 2-seeded capsules with a long, solid apical beak) were placed in a second group. Not only did Oersted draw attention to the presence or absence of beaks on the fruits and differences in the number of seeds, but he noticed differences in the structure of the septum that divides the two valves of the capsule. In *Prionitis* (in which the capsules are two-seeded with a solid apical beak), the septum is described as entire, woody and robust. In contrast, the septum in *Barlerites* is described as entirely membranous. In *Barleriopsis*, Oersted noted that the septum was membranous from the centre to the tip of the capsule. It is particularly interesting to me that these differences in structure were

not noted by any authors prior to or since Oersted (1854). The only authors who specifically described any aspect of the septum before Oersted were Linnaeus (1754), who described it as longitudinally divided in two, and Nees (1847), who described it as entire and adnate. Structural differences in the septum were noted at an early stage of the current study, before Oersted's descriptions were available to me. It was thus extremely interesting to find that he had noticed the same differences and that the groups in which they occurred correspond fairly closely with two of the infra-generic groups proposed in this thesis. It is strange that authors who post-date Oersted have apparently ignored his use of characters relating to the nature of the septum. It seems that due to his untenably narrow generic concept, and perhaps due to his misinterpretations of other characters such as the corolla, later authors totally discounted his work. This is unfortunate, as some of the characters used by him are extremely useful, but at the infra-generic level rather than as generic markers.

The descriptions of more recent authors such as Clarke (1885, 1899 & 1901) and Obermeijer (1933), are considerably detailed (see Table 2.2), but, because they were prepared for the species in particular geographic regions, tend to omit certain variations in some characters, and in some cases are too specific to accommodate taxa from other areas. What is quite apparent from Table 2.2 is that the characters considered important in the delimitation of the genus, are strongly influenced by the sample of species seen by the author. This, in turn, affected the circumscription of the genus provided by different workers.

2.4. Conclusions

Previous authors working on *Barleria* have not specifically addressed the question of generic delimitation. It is not surprising, therefore, that there are few statements to be found on the generic concept employed by these workers. From the theoretical discussions found in the literature, it would seem that the major question that needs to be answered is whether or not a "broad" or "narrow" generic concept should be adopted. If the broad approach is followed, uniformity in one or a few characters would provide the basis for circumscribing a genus in which most other characters vary widely. If a narrow concept is adopted, then uniformity in one or a few characters has to be overlooked in favour of creating smaller genera in which most other characters show greater homogeneity. The concept adopted in this research is neither deliberately

"broad" nor "narrow", but a phylogenetic one in which monophyly is taken as the criterion for delimiting groups at all levels (Bremer & Wanntorp, 1978; Stevens, 1985). This has lead to the acceptance of a broad circumscription of *Barleria*, in which there are three unifying characters (apomorphies) for the genus (basic morphology of the calyx, pollen morphology and type of cystoliths) and most other characters vary considerably. Variation in these other characters has been used to produce an infra-generic classification of the genus (Chapter 7). Detailed discussion of the characters on which the generic circumscription and infra-generic classification are based is given in Chapter 5.

CHAPTER 3

The placement of *Barleria* in the Acanthaceae

3.1. Introduction

Barleria has been grouped with different genera in different classifications of the Acanthaceae (Nees, 1847; Anderson, 1864; Bentham, 1876; Clarke, 1885, 1899 & 1901; Lindau, 1895; Bremekamp, 1965; Balkwill & Getliffe Norris, 1988). It is not an aim of this thesis to reconsider the classification of the family or even to reconsider the position of *Barleria* within the family in any detail. However, it was necessary to review the existing classifications of the family and to combine the findings of this review with my own observations, in order to establish which genera are likely to be the closest relatives of *Barleria*. This information was crucial in the selection of the most probable outgroup (sister group) for the polarisation of character states. None of the existing classifications of the family has been produced from a cladistic standpoint, so it is not possible to state with absolute certainty which genus is the outgroup of *Barleria*. The classifications (*l.c.*) were surveyed both to establish which genera have been most frequently grouped with *Barleria* and to establish the distribution of the characters on which such groupings are based.

3.2. The placement of *Barleria* in the Acanthaceae

The Acanthaceae comprises about 2 500 species in 250 genera (Willis, 1980). Summaries of the classifications of the Acanthaceae proposed by various authors to date are presented in Figures 3.1 to 3.6. In these systems the taxa not possessing retinacula in the fruits are placed in separate families (Bremekamp, 1965), subfamilies (Nees, 1847; Anderson, 1864; Lindau, 1895) or tribes (Bentham, 1876; Clarke, 1885, 1899 & 1901). The remaining taxa (with retinacula), representing 95% of the species (Scotland, Endress & Lawrence, in press) are variously divided into 2 (Anderson, 1864; Lindau, 1895), 3 (Bentham, 1876; Clarke, 1899) or many (Nees, 1847) groups of equal rank. In each of these classifications *Barleria* has usually been placed in its own tribe, the Barlerieae (Nees, 1847; Anderson, 1864; Lindau, 1895) or subtribe, the "Barlerieae" (Bentham,

1876; Clarke, 1885, 1901; Burkill & Clarke, 1899) or Barleriinae (Bremekamp, 1965; Balkwill & Getliffe Norris, 1988). On the whole, the different subdivisions of the family have not resulted in the recognition of many conflicting groups (Scotland, 1992); however, a major difference between the classifications involves the position of the Barlerieae (or Barleriinae) within the family (pers. obs.; Scotland *et al*, in press).

In the classification of Nees (1847), the tribe Barlerieae comprised five genera (see Figure 3.1) and was distinguished from other tribes by possession of 4 didynamous stamens and a 4-partite calyx. *Barleria* could be distinguished from the other genera in the tribe by its infundibuliform (not distinctly bilabiate) corolla. It is interesting to note, however, that several of the genera included in this tribe have 5-partite calyces and 4 didynamous stamens, features not shared with *Barleria*. The only genera from this classification that have been included with *Barleria* in later classifications are *Lepidagathis* Willd., *Lophostachys* Pohl and *Neuracanthus* Nees. It should be noted that Nees placed *Crabbea* Harv. in an adjacent tribe to the Barlerieae (i.e. the Ruellieae), unlike Bentham, Anderson and Lindau (*l.c.*), who placed it in the same tribe as *Barleria*.

In Anderson's classification (1864), morphology of the calyx, aestivation of the corolla and the nature of the placental bases were used to divide the family into three suborders (equivalent to sub-families in later systems). The tribe Barlerieae was included under the suborder Acanthidae and comprised five genera placed in two sections (Figure 3.2). Differences in the number of stamens and the number of anther thecae were important in dividing the genera between the two sections of the tribe. The placement of *Crossandra* Salisb. in the same tribe as *Barleria* seems entirely anomalous as these genera share very few features. It is interesting to note that *Barleria* is placed in the same tribe as *Crabbea*.

Bentham (1876) divided the Acanthaceae into five tribes (see Figure 3.3) based on differences in aestivation of the corolla, various aspects of corolla morphology, the number of ovules and morphology of the seeds. Subtribes were recognised in the tribes Ruellieae and Justicieae on the basis of variation in the form of the calyx, inflorescences, further details of corolla morphology and the number of stamens. *Barleria* was placed in a subtribe of the Justicieae along with six other genera including *Crabbea* and *Neuracanthus* (Figure 3.3).

Figure 3.1: Summary of the classification of the Acanthaceae proposed by Nees (1847), showing the position of *Barleria* and allied genera.

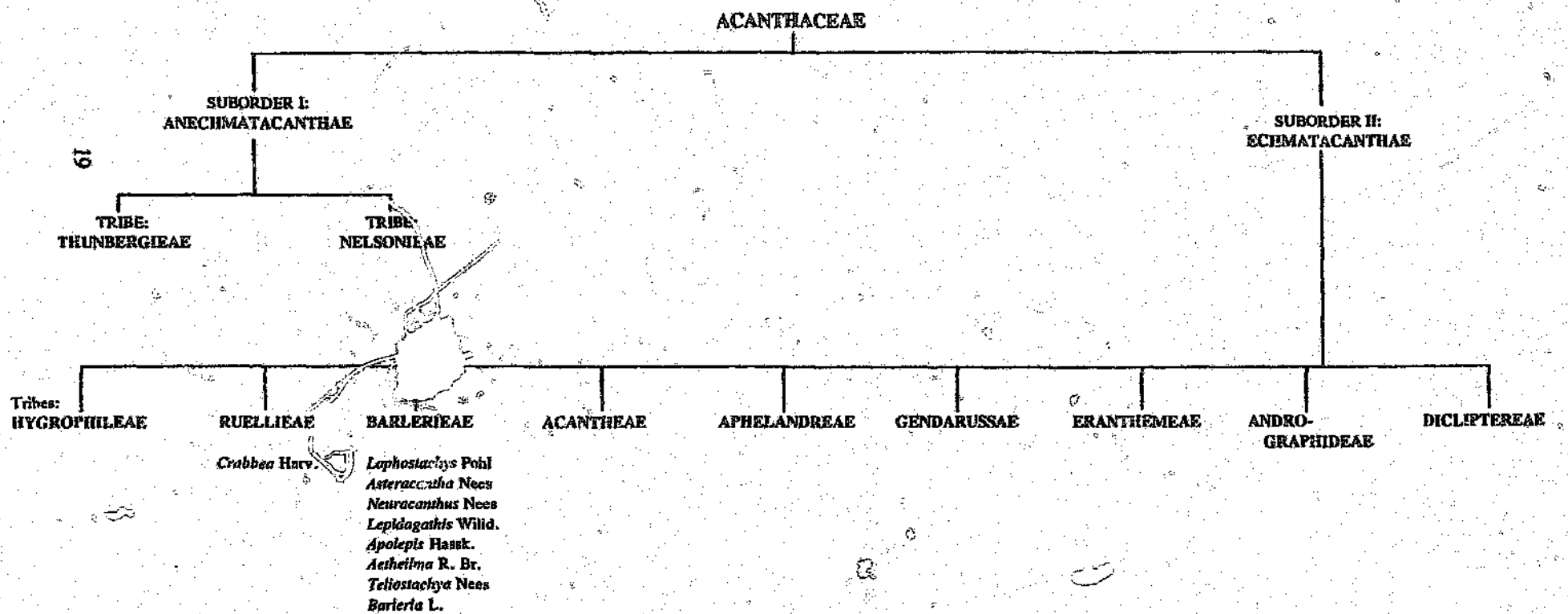


Figure 3.2: Summary of the classification of the Acanthaceae proposed by Anderson (1864), showing the position of *Barleria* and allied genera.

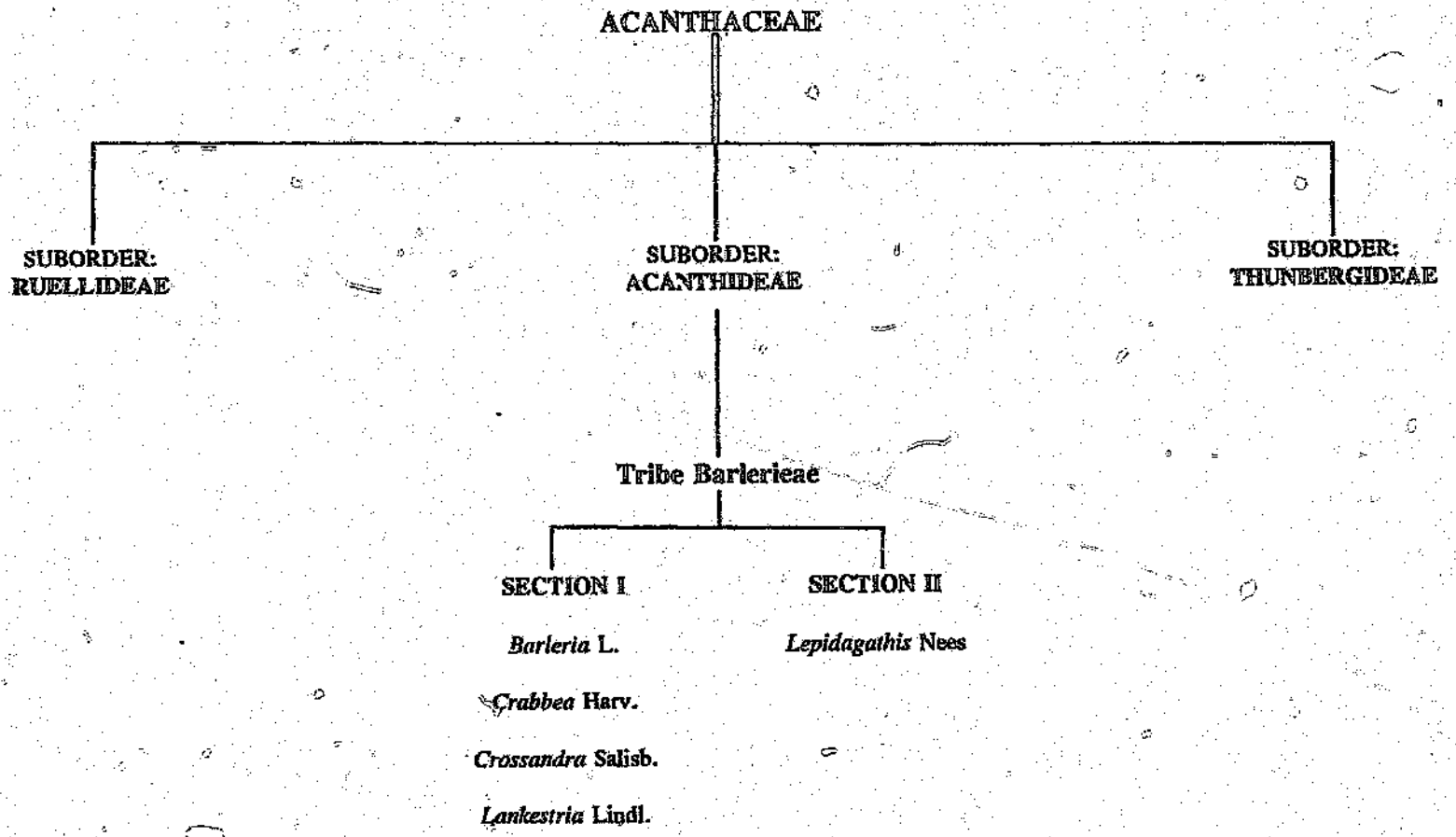
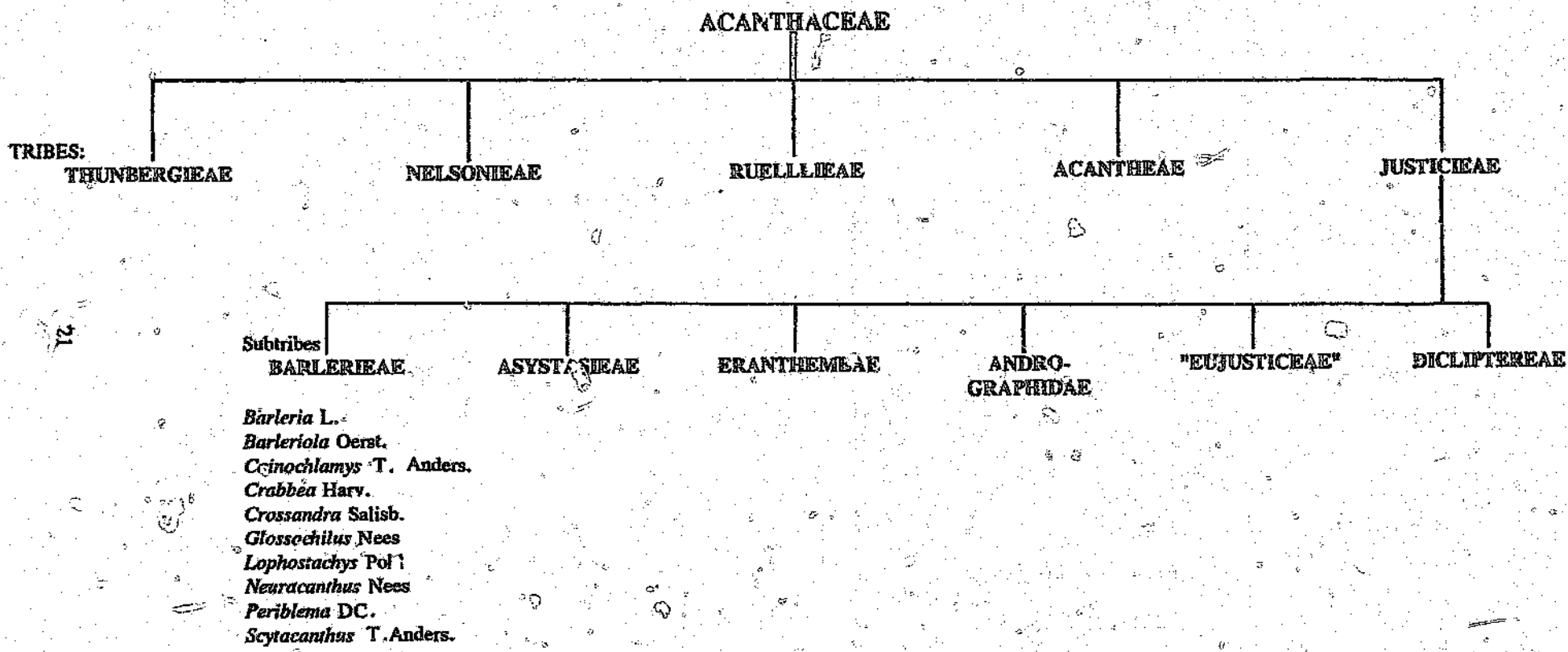


Figure 3.3: Summary of the classification of the Acanthaceae proposed by Bentham (1876), showing the position of *Barleria* and allied genera.



Lindau (1895) placed the retinacula-bearing genera of the Acanthaceae in a single subfamily, the Acanthoideae. This was subdivided into two groups of equal rank, the Contortae and Imbricatae, each of which was further divided into numerous tribes (Figure 3.4). The tribe Barlerieae, including *Barleria, Crabbea, Lepidagathis, Neuracanthus* and five other genera (Figure 3.4), was included under the Contortae. Clarke (1885) and Burkill & Clarke (1899), like Bentham (1876), divided the family into five tribes. The subtribe Barlerieae, comprising *Barleria* only, was placed in part of their tribe Justicieae (Figure 3.5). In these classifications the characters used at the tribal level included aestivation and lobing of the corolla, the number of stamens, pollen morphology, the number of ovules and the presence or absence of hygroscopic hairs on the seeds. Two of the characteristics of the Justicieae *sensu* Clarke and Burkill & Clarke (*l.c.*) are the absence of hygroscopic hairs on the seeds and imbricate aestivation of the corolla ("one lobe wholly within, one lobe wholly without"). It is difficult to understand why *Barleria* and *Crabbea*, both genera with hygroscopic hairs on the seeds and quincuncial rather than imbricate aestivation, were placed in this tribe at all. Interestingly, *Crabbea*, so frequently placed in the Barlerieae by earlier authors, was placed in a separate subtribe (the Tetrandrae) of the Justicieae.

Bremekamp (1965) divided his Acanthaceae into two subfamilies, the Acanthoideae (with no cystoliths) and the Ruellioideae (with cystoliths), each of which was divided into numerous tribes (Figure 3.6). *Barleria* was placed in a sub-tribe (the Barleriinae) of the Ruellieae. The Barleriinae was characterised by possession of a distinctly zygomorphic corolla with quincuncial or decussate aestivation, free stamens and globose, prolate or rarely trigonous pollen grains. The group included taxa such as *Crabbea* and *Glossochilus* Nees. The circumscription of the family proposed by Bremekamp was followed by Balkwill and Getliffe Norris (1988). These authors also placed *Barleria* in a subtribe of the Ruellieae, but removed all other genera from that sub-tribe. *Glossochilus* was thought to be more compatible with the Odontoneminae, where similar aestivation and corolla shape were thought to suggest a close affinity with *Asystasia* Blume (Balkwill, 1985; Balkwill & Getliffe Norris, 1988). It was also suggested that *Crabbea* would be more appropriately placed in the subtribe Ruellinae, as the two inner corolla lobes are opposed to one another, not adjacent as in *Barleria*. According to Scotland *et al.* (in press), however, these are both forms of quincuncial aestivation.

Figure 3.4: Summary of the classification proposed by Lindau (1895) showing the position of *Barleria* and allied genera.

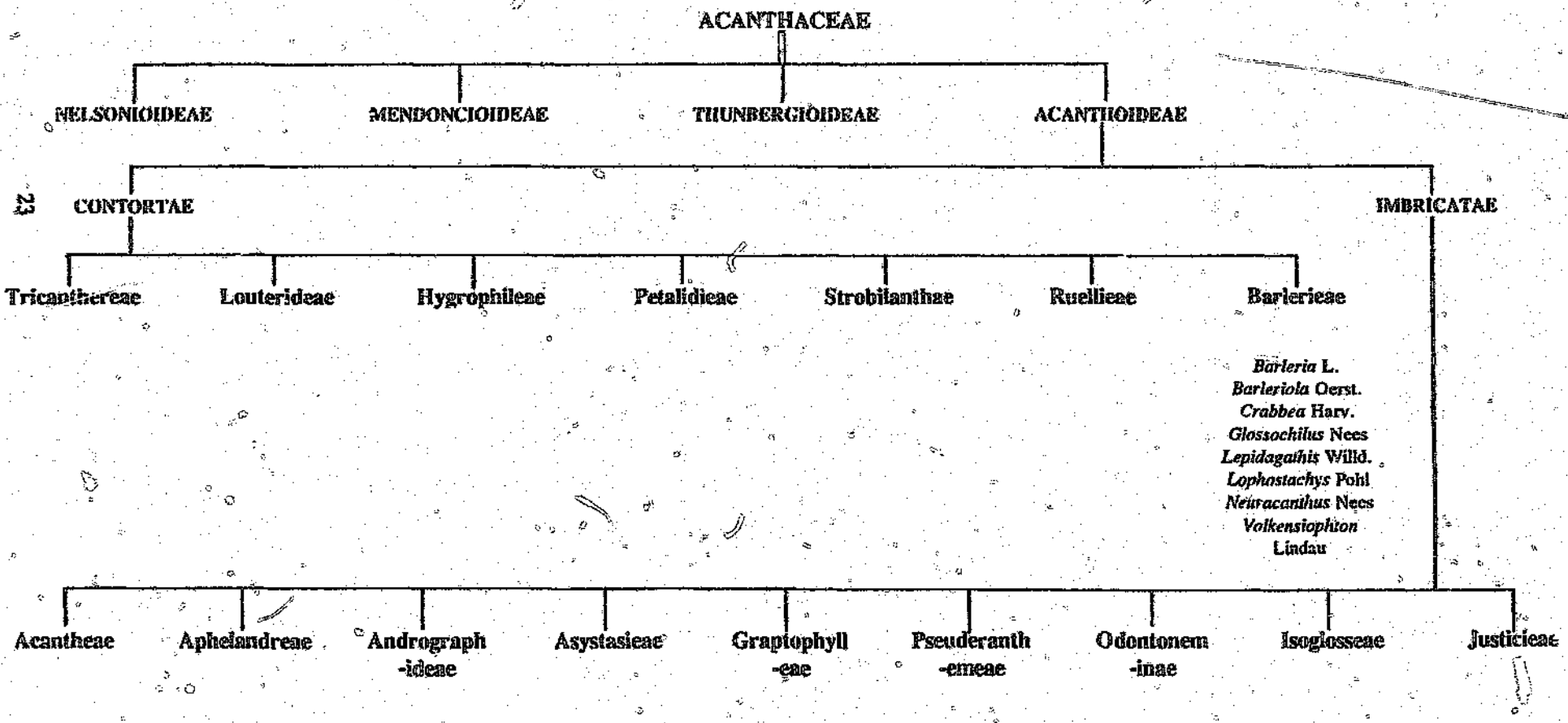


Figure 3.5: Summary of the classification proposed by Burkill & Clarke (1899), showing the position of *Barleria* and allied genera.

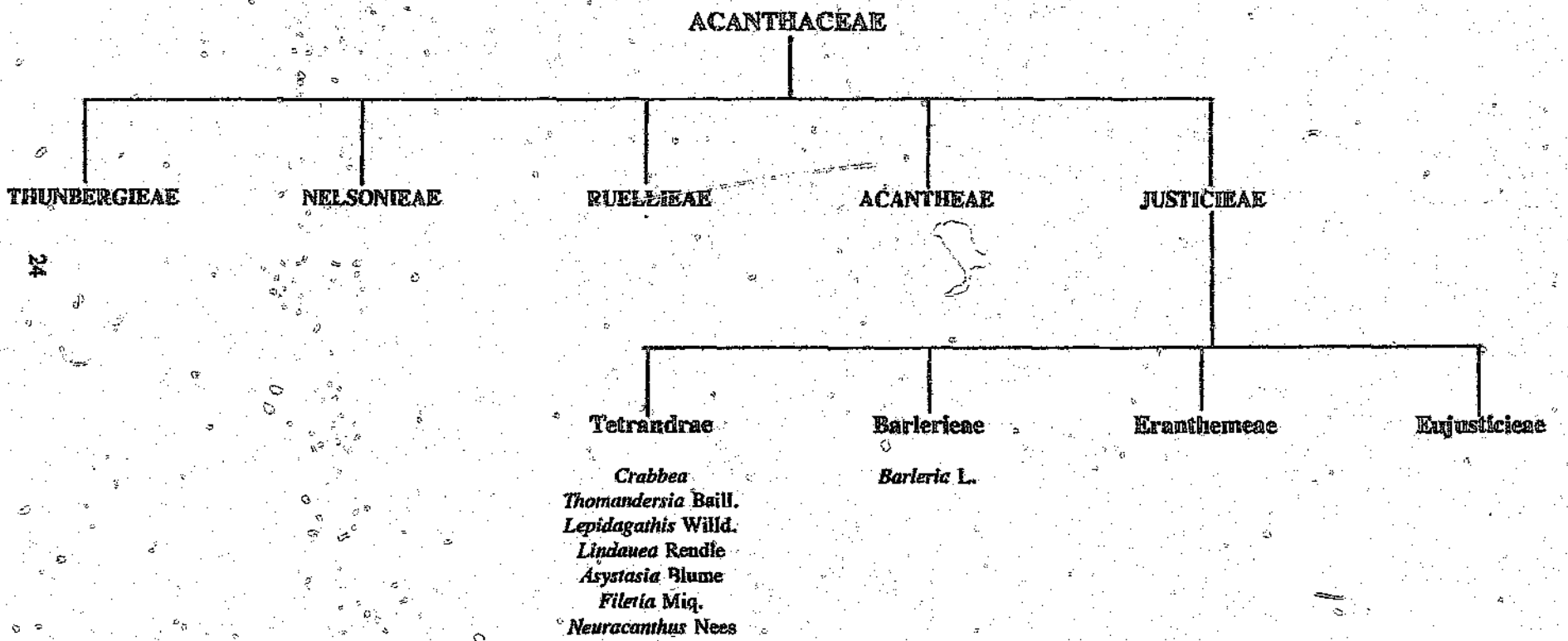
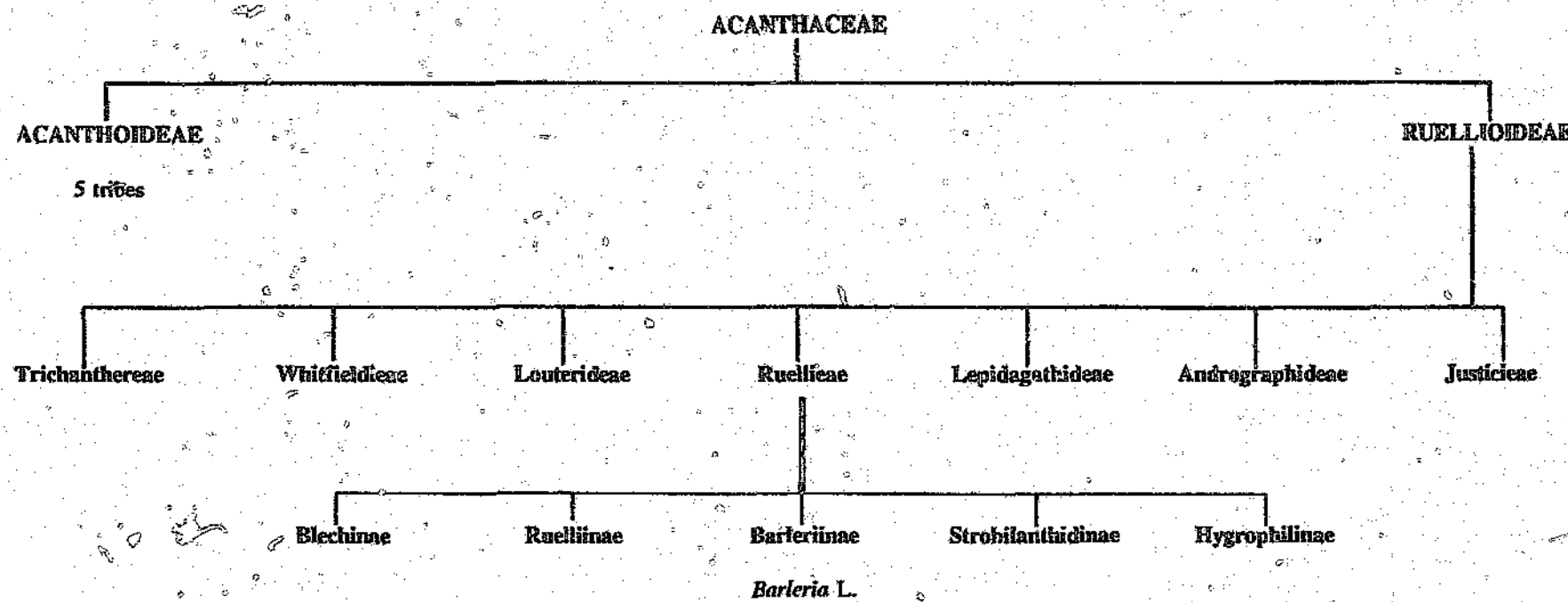


Figure 3.6: Classification of the Acanthaceae proposed by Bremekamp (1965), showing the position of *Barleria*.



One of the characters most frequently used in all the classifications is the aestivation pattern of the corolla. Corolla aestivation patterns seem to be constant within many taxa and thus are of potential use for delimitation of major groups (Scotland *et al.*, in press). Anderson (1864), Bentham (1876), Lindau (1895), Clarke (1885, 1901), Burkill & Clarke (1899), Bremekamp (1965) and Balkwill & Getliffe Norris (1988) all placed considerable emphasis on aestivation in their classifications, but their interpretations of corolla aestivation patterns do not always coincide (Scotland *et al*, in press), partly due to problems associated with terminology. Some authors have used the same terms to describe different aestivation patterns or have used different terms to describe the same pattern (Scotland *et al.*, in press). This is partly why the classifications have differed with respect to the placement of the Barlerieae even though it has seemed as if the authors were using very similar characters.

Scotland *et al.* (*l.c.*) investigated aestivation patterns through ontogenetic studies (as investigation of aestivation in dried specimens can be difficult). Their results indicate that developmental patterns do differ, but do not provide discrete data for systematic analysis (Scotland *et al.*, *l.c.*). The developmental differences that exist seem to be directly related to the mature aestivation patterns. These mature aestivation data do not support the placement of *Barleria* and allied genera in a group that have either left contort or cochlear aestivation. Scotland *et al.* (l.c.) accept as monophyletic a group roughly equivalent to the Barlerieae of Lindau. This group (including *Barleria*, *Crabbea*, *Lophostachys*, *Lindauea* Rendle, *Lepidagathis* and *Neuracanthus*), has quincuncial aestivation (Scotland, pers. comm.) and is the sister group of those genera with contorted aestivation (the Contortae of Lindau). These two groups share hygroscopic hairs on the seeds, with a few exceptions (Scotland, pers. comm.). In-group analysis of the Barlerieae *sensu* Scotland has not been undertaken, so the relationships of the taxa within the group are unclear. The inclusion of *Lepidagathis* in this group, however, seems slightly anomalous if the observations of Balkwill & Getliffe Norris (1988) are considered. At this point it is important to stress that direct comparisons cannot be made between the classifications of Balkwill & Getliffe Norris (1988) and Scotland (1992). These studies have included a different sample of genera, different sets of characters and have been produced using different methodologies. The apparent differences between the authors are important in the sense that they point to areas where

further clarification of relationships may be necessary. Scotland *et al.* (in press) took the aestivation pattern for *Lepidagathis* from a floral diagram in Lessert (1838, see Scotland, *l.c.*). Balkwill and Getliffe Norris (1988), however, found that the southern African representatives of this genus possesses imbricate aestivation; Scotland (pers. comm.) has subsequently suggested that *Lepidagathis* is polymorphic for aestivation. That the corolla in *Lepidagathis* has a distinct rugula (a feature present in many members of Justicieae, but not of Barlerieae), is suggested by both Scotland (pers. comm.) and Balkwill (pers. comm.) to represent a convergence. *Lepidagathis* has emerged as the sister group of *Barleria* in a recent study that sequences the plastid gene, *rbcL1*, across all angiosperms (Chase, Soltis & Olmstead *et al.*, unpublished manuscript); *Lepidagathis* is clearly closely related to *Barleria*, but the sample of genera from the Acanthaceae included in this study is rather small and excludes other likely candidates such as *Crabbea*. Furthermore, there seems to be less variation in other crucial apomorphies within *Crabbea* than is apparent in other closely related genera such as *Lepidagathis*.

The placement of *Neuracanthus* in the Barlerieae by Scotland and other earlier authors is particularly interesting; the African material of this genus has induplicate aestivation and differs markedly from other members of the Barlerieae in many features (Balkwill, 1985; Balkwill & Getliffe Norris, 1988). Vollesen and Bidgood (*fide* Balkwill, pers. comm.) have also expressed the view that *Neuracanthus* might be better placed in the Acantheae rather than in the Ruellioideae.

Lophostachys and *Lindauea* both seem superficially similar to *Barleria* on the grounds of possessing a 4-partite calyx (Clarke, 1899; Rendle, 1896). I was able to study material of both *Lophostachys* and *Lindauea* (see Appendix 2 for list of voucher specimens) at Kew. Both of these genera possess 4-lobed calyces, similar to the calyx of *Barleria*, and it seems that the 4-lobed condition (as with other characters in the family) has been attained independently a number of times. It is not sensible to suggest that these genera be included in *Barleria* as they do not possess the other apomorphies for the genus. It also seems unlikely that either *Lophostachys* or *Lindauea* is the outgroup for *Barleria*, although the genera are clearly reasonably closely related to *Barleria*. *Lophostachys* is a relatively small genus (less than 25 species) occurring only in South America where *Barleria* is represented by a single species. *Lindauea* is a monotypic genus occurring in Tropical Africa, but its distribution is extremely restricted.

It thus seems likely that these genera represent specialised offshoots from the same ancestral stock as *Barleria*. A further factor mitigating against the selection of either *Lindauea* or *Lophostachys* as the outgroup, is that no fruits were present on the specimens seen. As many of the characters used in the cladistic analyses relate to some aspect of fruit structure, it would have been impossible to make sensible statements regarding the polarity of these characters. *Barleria* and *Crabbea* share spheroidal pollen grains with honeycomb sculpturing of the exine. *Lepidagathis*, *Lindauea* and *Lophostachys* share prolate, tricolporate grains with very similar surface-sculpturing, with the pollen grains of *Lophostachys* and *Lepidagathis* being very similar indeed (pers. obs.; Scotland, pers. comm.).

3.3. Conclusions

Classifications of the Acanthaceae have differed quite considerably with respect to the placement of *Barleria*. Part of the difficulty associated with the satisfactory placement of this genus arises because some of the characters that are stable within other genera (and, therefore, that are useful in linking or separating genera) are variable within *Barleria* (e.g. composition of the androecium, overall morphology of the corolla and the type of inflorescence). Although different authors have often used the same characters in their classifications (e.g. aestivation), terminology has not always been consistent and interpretations of certain features have differed. There is thus a need for the classification of the family to be re-assessed, preferably from a phylogenetic standpoint so that statements can be made with more confidence regarding the closest relatives of particular genera. Scotland (*l.c.*) has made valuable progress in this direction for particular parts of the family, but so far has considered evidence from a limited number of characters (Scotland, 1991 & 1992; Scotland *et al.*, in press). It would be interesting to know how the cladograms obtained and groups formed would differ if other characters (e.g. presence of a rugula in the corolla) were added to the data, and if the analyses were expanded to include other groups within the family.

Despite the somewhat disparate conclusions of the existing classifications, it would seem that corolla aestivation and pollen morphology are relatively reliable characters at the supra-generic level. Many of the classifications have placed *Barleria* and *Crabbea* in the same tribe or in closely related tribes or subtribes. Both genera have quincuncial corolla

aestivation and spheroidal, honeycombed pollen. Scotland (pers. comm.), whilst not having any concrete ideas on a sister group of *Barleria*, supports my suggestion that *Barleria* and *Crabbea* are very closely related. He has recently sequenced a chloroplast gene, ndhF, for 16 taxa and finds that the sequences for *Barleria* and *Crabbea* are very similar. Although he has not had access to living material of any other members of the Barlerieae, he nevertheless feels that there is little doubt that the two genera are more closely related to each other than they are to any other members of the Contortae, Acanthae or Imbricatae (Scotland, pers. comm.). Based on the available evidence, *Crabbea* is apparently one of the likeliest candidates for the position of sister group to *Barleria*. It has thus been selected as the outgroup for polarisation of character states in this thesis. This choice has been supported by Ensermu (pers. comm.).

CHAPTER 4

Previous infra-generic classifications of *Barleria*

4.1. Introduction

Past infra-generic classifications of *Barleria* have contributed greatly to an understanding of the relationships of taxa within the genus, particularly in Africa. Only two of these classifications (Nees, 1847; Lindau, 1895) dealt with this pantropical genus on a world-wide scale. Neither of them is suitable for use today because it has become apparent that some of the discontinuities perceived by the authors do not exist. Furthermore, many more species are now known in the genus and they exhibit some combinations of character states that cannot be accommodated in the older classifications. The most recent regional classifications of *Barleria* (Clarke, 1885, 1899 & 1901; Obermeijer, 1933) have worked well in the regions for which they were written. None of them, however, is sufficiently representative of the genus as a whole. Many of the characters used in these previous classifications are of considerable taxonomic value and are used, although in somewhat different combinations, in the classification presented in Chapter 7. These infra-generic classifications, and the characters on which they were based, are reviewed below in order to provide an appropriate historical background against which the proposals made in this thesis can be viewed.

4.2. The classifications

Infra-generic classifications of *Barleria* were proposed in the accounts of Nees (1847), Lindau (1895), Clarke (1885, 1899 & 1901) and Obermeijer (1933). These classifications are summarised in Tables 4.1 to 4.6 (a and b). The six classifications have a number of points in common, although they were prepared for widely differing numbers of species (see Table 2.3). Firstly, all authors have placed the spiny, yellow - flowered species with beaked, two-seeded fruits (such as *B. prionitis* L.) into a separate section (Nees, 1847; Lindau, 1895; Clarke, 1899, 1901; Obermeijer, 1933) or subgenus (Clarke, 1885). The second common factor is the tendency of authors to divide the

genus into armed (or spiny) and unarmed (not spiny) groups.

Nees (1847) divided *Barleria* into three Sections: *Propriae*, *Prionitis* and *Fruticulosae* (Table 4.1). The first of these, Propriae, was further divided into two groups, referred to as A and B, on the basis of differences in the inflorescences and the number of stamens. No use was made of the capsules in this classification. Instead, the subdivisions were made primarily on differences in growth form, the presence or absence of spines, inflorescences and the number of stamens. These features are very variable and are not sufficiently discriminating when a larger number of species is considered.

Table 4.1: Infra-generic classification of *Barleria sensu* Nees (1847).

<table>
<tr><th colspan="2">SECTION PROPRIAE</th><th>SECTION PRIONITIS</th><th>SECTION FRUTICULOSAE</th></tr>
<tr><td colspan="2">plants tall, without spines

flowers spicate or subsessile in axils; corolla tubular for most part</td><td>plants shrubby; spines (modified bracts) present in axils

flowers axillary, subsessile, subverticillate or solitary

calyx apices often spiny

seeds 2</td><td>plants strongly branched, low -growing, unarmed

flowers axillary; peduncles often triflorate; corolla blue or white

bracts often spinoso-dentate

calyx apex spinescent

stamens 2 - 4</td></tr>
<tr><td>A
inflorescence spicate, axillary and terminal, often aggregated in sub-capitate heads

stamens 2 - 4</td><td>B
flowers axillary, in few-flowered spikes, glomerate or solitary

stamens 4 or 2</td><td></td><td></td></tr>
</table>

In *Flora of British India*, Clarke (1885) recognised two subgenera within *Barleria*; Subgenus *Prionitis*, essentially the same as Section *Prionitis* of Nees, was characterised by two-seeded, beaked capsules. In Subgenus *"Eubarleria"* the capsule was oblong or ellipsoid with 4 seeds or rarely two seeds by abortion of the lower two ovules (Table 4.2). Section *"Eubarleria"* contained the bulk of the species and was further subdivided into three groups (not assigned any formal rank) on the basis of differences in the size and shape of the bracteoles and the relative size of the calyx lobes. A further subdivision of one of these groups into spiny and unarmed forms was made (Table 4.2).

Table 4.2: Infra-generic classification of *Barleria sensu* Clarke (1885).

<table>
<tr><td rowspan="4">SUBGENUS PRIONITIS

capsule ovoid

solid beak on capsule

2 seeds</td><td colspan="3">SUBGENUS "EUBARLERIA"

capsule oblong or narrowly ellipsoid

no beak

4 seeds (rarely 2 seeds by abortion)</td></tr>
<tr><td colspan="2">Bracteoles divaricate, long-linear or spinous

outer sepals large</td><td rowspan="2">Bracteoles narrow much smaller than outer sepals</td><td rowspan="2">Bracteoles lanceolate or elliptic often nearly as long as the calyx</td></tr>
<tr><td>armed</td><td>unarmed</td></tr>
</table>

The classification proposed by Lindau (1895) was based partly on that of Clarke (1885). Lindau recognised three Sections: *"Eubarleria"* (*sensu* Clarke, 1885), *Prionitis* and *Somalia* (see Table 4.3). Like Clarke, Lindau also subdivided Section *"Eubarleria"*, but he divided it more simply into two broad subsections based on presence or absence of spines and the texture of the bracts (Table 4.3) [NOTE: "bracts" here must refer to bracteoles as not all species included in this group possess bracts]. Whereas Clarke had used the fruit form and number of seeds to define Section *Prionitis*, Lindau, like Nees,

did not; the main feature used to define the section in this classification is the presence of spines formed by modification of the bracts. The Section *Somalia*, not recognised before, was characterised by the absence of spines and the presence of biramous hairs (a feature that had not been used in previous classifications) and beaked, two-seeded fruits.

Table 4.3: Infra-generic classification of *Barleria* sensu Lindau (1895).

<table>
<tr><td colspan="2">SECTION EUBARLERIA
capsule oblong/narrowly ellipsoid
4 (rarely 2) seeds</td><td rowspan="2">SECTION PRIONITIS
bracts thorny
hairs simple</td><td rowspan="2">SECTION SOMALIA
bracts herbaceous
hairs biramous
capsule beaked
2 seeds
2 stamens and 2 or 3 staminodes</td></tr>
<tr><td>Subsection INERMES
bracts herbaceous
no spines</td><td>Subsection ARMATAE
bracts chartaceous
spiny</td></tr>
</table>

The classifications proposed by Clarke (1899 & 1901) are very similar to each other (see Tables 4.4 and 4.5). In both cases the genus is divided into two series, A and B, based on the presence or absence of spines and a spinous tip to the posticous sepal. In *Flora of Tropical Africa*, Clarke divided each of the series into two sections (Table 4.4), but in *Flora Capensis* he only subdivided Series A into sections (Table 4.5). In both cases, Series A (with spines) was divided into Sections *Prionitis* and *Acanthoidea* based on the number of seeds and the form of the capsules (in *Flora Capensis* differences in dentition of the calyx and colour of the flowers were added (see Tables 4.4 and 4.5). In *Flora of Tropical East Africa*, Series B (spineless) was broken into Section *Somalia* (capsules beaked, 2 seeds present) and Section *"Eubarleria"* (capsules not beaked, 4 seeds present). Again, Section *"Eubarleria"* was a large and variable assemblage of species and thus was further divided into three subsections based on differences in pubescence and the structure of the inflorescence (Table 4.4). A notable feature of Clarke's classifications is that Section *Prionitis* is not separated from the other sections

immediately - it is first grouped with Section *Acanthoidea* based on their common possession of spiny structures. This is significant, as it goes against the general tendency of other authors to separate it immediately because superficially it seems so different from the rest of the genus.

Table 4.4: Infra-generic classification of *Barleria sensu* Clarke (1899).

<table>
<tr><td colspan="4">SERIES A
spines present, posticous sepal spine-tipped</td></tr>
<tr><td colspan="2">Section PRIONITIS
2 seeds
capsule beaked</td><td colspan="2">Section ACANTHOIDEA
4 seeds
capsule not beaked</td></tr>
<tr><td colspan="4">SERIES B
spines absent, posticous sepal not spine-tipped</td></tr>
<tr><td>Section SOMALIA
2 seeds
capsule beaked
ovary and fruit hairy
hairs simple</td><td colspan="3">Section "EUBARLERIA"
4 seeds
capsule not beaked
ovary and fruit hairy or not
hairs simple or stellate</td></tr>
<tr><td></td><td>Subsection VILLOSAE
leaves hairy
flowers in short cymes in upper axils</td><td>Subsection GLABRATAE
leaves glabrate
flowers in clusters at tips</td><td>Subsection STELLATO-HIRTAE
hairs stellate
flowers in dense ovoid heads</td></tr>
</table>

Table 4.5: Infra-generic classification of *Barleria sensu* Clarke (1901).

SERIES A spines present	
SECTION PRIONITIS seeds 2 capsule beaked posticous sepal spine-tipped, no teeth on margins corolla yellow	SECTION ACANTHOIDEA seeds 4 capsule not beaked posticous sepal often with teeth on margins corolla bluish/white
SERIES B spineless	

Obermeijer's classification (1933), based on a study of southern African material, divides *Barleria* into three Sections: *Prionitis*, *Somalia* and *"Eubarleria"* (Table 4.6a). Sections *Prionitis* and *Somalia* are very clearly defined. Both sections have beaked fruits with two-seeded capsules, and Section *Prionitis* is characterised by the presence of spines and yellow flowers (Section *Somalia* lacks both of these features). In contrast, Section *"Eubarleria"* is a diffuse and variable assemblage of species that can only be separated from the other two sections by the absence of beaks on the fruits and the predominance of four rather then two seeds in the capsules. Obermeijer subdivided Section *"Eubarleria"* into seven subsections using variations in spinescence, particularly of the bracteoles and calyx, the nature of the pubescence, habit and the presence or absence of distinctive hair types at the base of the style (Table 4.6b).

Some of the features on which these classifications are based work reasonably well for small groups of species. However, when the whole genus is considered they become unreliable as markers for infra-generic groups. For example, "flowers yellow" or "flowers blue" is sufficiently discriminating to separate members of the Sections *Prionitis* and *Somalia (sensu* Clarke or Obermeijer) in southern Africa, but is not useful if tropical African species such as *B. waggana* Rendle (a blue-flowered member of Section

Table 4.6a: Infra-generic classification of *Barleria sensu* Obermeijer (1933).

	Section PRIONITIS	Section SOMALIA	Section EUBARLERIA
spines	present	absent	present or absent
capsules	beaked	beaked	not beaked
number of seeds	2	2	2 or 4
flower colour	yellow	never yellow	white, blue or yellow
bracts, bracteoles and sepals	entire, tip cuspidate	entire, tip never cuspidate	entire, dentate or serrate; tip cuspidate or not

Table 4.6b: Characters used to sub-divide Section *Barleria sensu* Obermeijer (1933).

SUB-SECTION	DEFINING CHARACTERS
PUNGENTES	plants spinous; sepals usually toothed, ring of curly white hairs at base of style
ACULEATAE	bracts and bracteoles solid and spinous; scattered bristles at base of style
CRYPTOPHYTAE	plants with subterranean, woody crown
INNOCUAE	much-branched shrubs; spineless; large flowers
DISPERMAE	ovary with 2 ovules fertile and 2 abortive
HETEROTRICHAE	4-seeded; hairs multicellular and dendroid
THAMNOTRICHAE	2-seeded, hairs dendroid

Prionitis) and *B. calophylla* Lindau (a yellow-flowered member of Section *Somalia*) are included. Likewise, there are several southern African species that would be most appropriately placed in *Somalia sensu* Clarke (1899), except that they have glabrous rather than pubescent ovaries and capsules, one of the defining characters of this section.

The presence or absence of spines has often been used to delimit major infra-generic groups within *Barleria*. Clarke (1900) considered the spines to be modified vegetative shoots. Nees (1847) and Lindau (1895) thought the spines (in Section *Prionitis* at least) represented modified bracts, whilst Obermeijer (1933) and Vollesen (1990) have suggested that the axillary spine systems are sterile, aborted inflorescences. To use this character safely, it would be important to establish the homology of the spinous structures.

A further question that arises is whether or not the infra-generic groups in existing classifications are natural in a phylogenetic sense (i.e. are monophyletic). Considering the classification of Obermeijer (1933), Section *"Eubarleria"* seems to be something of a dumping ground for all the taxa which did not fit into the other more clearly defined sections. The numerous subsections into which the section has been split are too exclusive with the result that taxa from out of the area (and even some from within) cannot be accommodated.

4.3. General Conclusions

The characters most frequently used in infra-generic classifications of *Barleria* to date include presence or absence of spines, nature of the posticous sepal, form of the capsule, number of seeds and the colour of the flowers. In some classifications the nature of the pubescence and inflorescence has also been useful. In addition to these characters, Obermeijer (1933) has used variation in growth form and the presence or absence of particular hair types at the base of the style at the subsectional level. Clearly, many of these characters are taxonomically useful as markers for infra-generic taxa. It is important, however, that their homology be determined first, otherwise hypotheses of mistaken or false similarity (Scotland, 1992) could be inferred. It would also be desirable, from a theoretical point of view, if the groups, and the scheme in which they

are placed, represented the most parsimonious distribution of character states. None of the existing classifications can accommodate all species of *Barleria*. Establishing the homology of previously used characters and the inclusion of new characters, could provide the framework for a revised, phylogenetic classification of *Barleria* on a global scale.

CHAPTER 5

Variation in Characters and Character States

5.1. General Introduction

A character is any attribute of an organism and character states are the various manifestations of each character (Stevens, 1980). The selection of characters and the assignment of evolutionary polarity to the states of those characters is a crucial step in any taxonomic study, but particularly in a cladistic or phylogenetic one (Stevens, 1980). The latter approaches to classification are said to be beneficial because of their explicit assumptions and procedures (Bremer & Wanntorp, 1978; Humphries & Funk, 1984; Linder, 1988). However, all too often in the recent literature, little explanation is given for the initial polarisation of character states and the procedures of the authors thus become unclear (Stevens, 1980). Solbrig (1970) demonstrated that estimates of evolutionary relationship depend on the decision about which character states are derived ; different phylogenies could be produced if three different criteria for the decision were used. For this reason, careful explanation of the criteria used to assign evolutionary polarity to character-states in this study is given below.

An extensive analysis of characters across the entire genus was necessary in order to provide an empirical basis for a revised infra-generic classification of *Barleria*, and to find suitable criteria for delimiting more natural groups. Considerable attention was given to the definition and description of characters and character-states and to the distribution of these character-states within the genus (and in other genera, where appropriate). Evolutionary polarity was assigned to the character states using the outgroup comparison method of character analysis (Watrous & Wheeler, 1981; Stevens, 1980; Humphries & Funk, 1984; Linder, 1988). In particular, the "operational rules" outlined in Watrous & Wheeler (1981) and Stevens (1980) were followed. *Crabbea* Harv. was used as the outgroup. In some cases polarity had to be determined by congruence with other characters used and by parsimony. The terms primitive (basal or plesiomorphous) and advanced (derived or apomorphous) are used

here only in a relative sense, within the context of the distribution of character-states in *Barleria, Crabbea* and the rest of the family, particularly the Ruelliinae (a likely outgroup for the Barlerilinae). The hypotheses of polarity made in this thesis are clearly defined, testable and potentially falsifiable. Results of the cladistic analyses of the data are presented in Chapter 6.

A relatively small number of the total number of characters investigated was selected for use in the cladistic analyses, for reasons given below. However, the variation in most of the characters studied is also presented below. Only the general trends in variation are discussed here, but more detailed discussion of the variation within particular groups or species is included in Chapter 7. *Barleria* has not been studied on a global scale since the time of Lindau (1895); it was thus considered more useful and practical to concentrate on re-assessing characters that have been used before and on those that have been neglected in previous works, rather than to attempt covering the full spectrum of potentially useful characters.

The modified classification and nomenclature in *Barleria* that is presented in Chapter 7 will be used throughout the discussion below (except where comparison is made to older classifications). The classification of Bremekamp (1965) will be used for higher order ranks, unless stated otherwise.

5.2. Materials and Methods

This study combined extensive work in the herbarium with laboratory and field work wherever possible. Herbarium material was borrowed from the following herbaria (abbreviations follow Holmgren, Holmgren & Barnett, 1990): BLFU, BOL, E, EA, FT, GAB, GRA, K, MO, NBG, NH, NU, PRE, SAM, SRGH, STE & WIND. In addition, the complete collections of *Barleria* housed at BM, K and E were studied. In this study considerable emphasis was placed on morphological characters. Aspects of anatomy, karyology and phytochemistry were investigated, but these studies were restricted to southern African species as fresh material of other species was not readily obtainable. The data sets for the latter characters are, therefore, incomplete, but some potentially interesting trends are discernible and are discussed in this chapter.

5.2.1. Morphological Studies

Morphological studies were based on dried herbarium material and were augmented by extensive field work in southern Africa during the period 1988 to 1992. Field work allowed for the examination of living plants, and for the collection of material for cultivation, anatomical and phytochemical studies. Studies of morphological characters were made with the aid of various microscopes: a Wild-Heerbrugg M8 Stereo dissecting microscope (6 — 50X magnification); a Nikon Multiphot System; a Wild Makroskop M420 (6.2 — 32X magnification) with a Wild MPS45 Photoautomat System and a Zeiss MC63 Compound Microscope with photographic attachment. Where fresh material was not available for study, dried material was removed from herbarium specimens, gently heated in water to soften it and then dissected and examined. After it had been studied, such material was placed in paper capsules, re-dried and returned to the specimen from which it had been removed. A full list of species studied and selected voucher specimens is included in Appendix 2. Where illustrations have been prepared from particular specimens, vouchers are cited in the captions of these figures. To account for infra-specific variation, at least 5 individuals of each taxon were studied in detail; specimens were selected for detailed investigation in such a way that taxa were sampled over their full geographic range. All line drawings in this thesis are the original work of the author. The geographic subdivisions used in later discussions of distribution patterns follow a system similar to the one employed in the Herbarium, Royal Botanic Gardens, Kew.

a. Micromorphological Studies

Light microscope studies of epidermal features were made using cleared leaf material (O'Brien & von Teichman, 1974). Transverse sections of leaves were cut by hand with a razor blade, or using a freezing microtome. The sections were viewed unstained and were photographed using a Zeiss MC63 Compound microscope with a photographic attachment.

b. Anatomical studies of fruits

Fruits at different stages of development were collected from plants growing in the Lowveld Botanic Gardens, Nelspruit, and placed in Kew Cocktail. Serial sections were cut by hand using a Feathercut razor blade after the fruits had been soaked in lactic acid

for 24 hours. Sections were viewed and photographed using a Wild Makroskop M420 microscope linked to a Wild MPS45 Photoautomat system. Attempts were made to section the fruits using a freezing microtome and using conventional wax-embedding techniques (Sass, 1958; O'Brien & McCully, 1981). Neither of these methods was successful as the hygroscopic hairs on the seeds either interfered with the uniform freezing of the material or with the penetration of the inner tissues by wax. This resulted in considerable disruption of the softer tissues during sectioning. An additional problem with wax-embedding is that the woody parts of the fruit become exceptionally hard during dehydration and infiltration, causing the material to break out of the embedding material during cutting. For the preparation of hand-cut sections lactic acid was used, to soften the material so that intact sections could be obtained. Although the resolution thus obtained was fairly coarse, it was adequate for the purposes of this study.

5.2.2. Phytochemical Studies

Fresh corollas (calyces removed) were placed directly into each of two extraction solvents: 1% methanolic HCl (for extraction of anthocyanins) and ethanol : water : acetic acid in the proportions 8:1:1 (for extraction of esters of anthocyanins). A list of the taxa sampled, source of the material and voucher specimens is given in Table 5.1. The extracts were filtered through celite and concentrated by passing through a solid phase extraction column packed with C18 reversed phase silica. These extracts were then analysed using High Performance Liquid Chromatography by Professor B-E. van Wyk and Mr P. Winter of the Rand Afrikaans University, Johannesburg.

Table 5.1: Taxa sampled for analysis of flavonoids, source of material and voucher specimens.

Taxon	Voucher	Source
B. rotundifolia	Balkwill & Balkwill *et al.* 5809	Nelspruit
B. ovata (yellow)	Balkwill & Balkwill 6280	Kaapsehoop
B. ovata (pink)	Balkwill & Cadman 2565	Barberton

5.3. Characters and character states in *Barleria*

5.3.1. Vegetative Morphology

Vegetative features are often overlooked due to their variability (Baden, 1981; Balkwill, 1985) and because they can be difficult to assess in the dried herbarium specimens on which many taxonomic studies are based. Balkwill (1985) has provided a useful review of the use of vegetative morphology as a source of taxonomic characters in the Acanthaceae. Previous infra-generic classifications of *Barleria* have paid little attention to vegetative features. Nees (1847) used habit as one of several characters to distinguish between sections of the genus. Hair types were used at the sectional level by Lindau (1895) and at the subsectional level by Clarke (1899) and Obermeijer (1933). Lindau made a fairly extensive study of trichomes in the Acanthaceae but few of the observations made by him with respect to hair types in *Barleria* seem to have been noticed by subsequent workers. The presence or absence of spines is a feature that has been frequently used in prior classifications. Detailed discussion of this feature is given in part 5.3.2 of this chapter, as spines in *Barleria* may or may not be regarded as vegetative features.

Studies of leaf architecture (Ahmad, 1975), foliar trichomes (Ahmad, 1978), foliar morphology and anatomy (Kumar & Paliwal, 1978) and cuticular and epidermal features (Chaudahari & Imadar, 1984) have been conducted on various members of the Acanthaceae (mostly from India), including a number of species of *Barleria*. Wood anatomy was investigated in one species of *Barleria* by Carlquist and Zona (1988) as part of a larger study of wood characters in the Acanthaceae.

During the current study, accurate information on vegetative features was collected for the southern African species, many of which were seen in the field. However, for the other species in the genus only herbarium material was available, making the assessment of certain vegetative features, particularly habit, rather difficult. Nonetheless, a number of vegetative characters have diagnostic value and others show considerable potential as taxonomic characters.

a. Habit

Variation in habit in selected species of *Barleria* is depicted in Plates 5.1 to 5.3. Most species are perennial, weakly to densely branching herbs, shrublets or suffrutices reaching heights of approximately 1 m (Plate 5.1). In species such as *B. oxyphylla* C.B. Cl. and *B. argillicola* Oberm., the plants are erect, few-stemmed herbs (Plate 5.1b.), but more often than not, they form somewhat sprawling, densely branched bushes, with slender, semi-prostrate to decumbent stems (e.g. *B. cristata* L., *B. elegans* S. Moore and *B. virgula* C.B. Cl.; see Plate 5.3c.). Many of the species in Section *Barlerites* grow at the edges of forests (or thickets) or on forest floors. In this group the plants are herbaceous and soft-leaved, with several stems from the base (Plate 5.2). *B. lukwangulensis* Mildbr., which is also the only species in Section *Barlerites* with red flowers, grows as a creeper or vine in tropical forests of Tanzania. In southern Africa, two species, *B. gueinzii* and *B. obtusa* (both Section *Barleria*), show a tendency towards a creeping habit and can climb to considerable heights in the surrounding, arborescent vegetation (see Plate 5.1c.). In these species, as well as a number of others with herbaceous, semi-prostrate or prostrate stems, rooting at the nodes can take place giving rise to a limited amount of vegetative reproduction.

Large shrubs with persistent woody branches are uncommon in *Barleria*. This growth form is well-developed in *Barleria greenii* M-J. & K. Balkwill (Section *Barleria*), which forms densely branched, woody shrubs attaining heights of about 1.8 m and girths of about 1.2 m (Plate 5.3a) if protected from fire. Certain members of Section *Stellatohirtae* (e.g. *B. rogersii* S. Moore) and Section *Prionitis* (e.g. *B. rotundifolia* Oberm.) also form large, densely branched shrubs (Plate 5.3b), but the branches in these are less woody than in *B. greenii*. Shrubby forms also occur in certain species within Section *Barleria*, such as *B. bremekampii* Oberm. (Plate 5.1d).

No annual forms are known in *Barleria*, although a number of species produce annual stems that die back in winter and re-sprout from a woody rootstock the next spring. This condition is well-developed in *B. ovata* Nees and *B. monticola* Oberm. (Section *Barleriopsis*), two species restricted to high altitude grasslands in the eastern parts of Southern Africa (Plate 5.1a). These species possess a large, sometimes branched, underground woody caudex (or tuber) that has perennating buds from which the new shoots are produced. These buds are protected by scales that are eventually deciduous.

Obermeijer (1933) placed *B. ovata* and *B. monticola* in a subsection of their own, the *Cryptophytae*, based on the presence of this underground, woody caudex. Associated with this kind of habit (in these two species at least) is the presence of a terminal synflorescence. Production of flowering shoots is stimulated by fire and it seems likely that the caudex with perennating buds is an adaptation to fire.

The exact form of plants in *Barleria*, regardless of the species, is often strongly correlated with the type of habitat in which they grow. In species such as *B. obtusa* Nees and *B. gueinzii*, which have a broad geographic distribution, a wide range of habitats from forest edge through open savanna to coastal scrub, may be occupied. At forest edges the plants form soft-leaved, soft-stemmed, straggly herbs or shrublets that show a tendency to creep into the canopy. In more open, exposed situations, the plants tend to be more compact and low-growing, with more leathery leaves and ligneous, extensively branched stems from a slightly woody base. When members of these species occur at the coast, a very dense, low-growing form with small, thickly-textured leaves is assumed.

Many species of *Barleria* tend to form dense "thickets" comprising a few profusely branched shrublets (Plate 5.3a & b). A number of these thickets is usually found in close proximity to one another, with the effect that, where they occur, these species of *Barleria* are dominant in the vegetation. The distribution of these groups of thickets, however, tends to be fairly patchy within a larger area. This is an interesting pattern, with implications for gene flow within and between populations of a species and therefore for patterns of diversification within species.

In Southern Africa a clear trend is discernible in which the species in the drier, western parts of the region tend to form small, strongly spinous dwarf shrublets with small, often coriaceous leaves and fairly ligneous stems. Conversely, the species in the damper eastern parts of the region are usually softer- and larger-leaved, branched herbs or shrublets in which spinescence is less well-developed or entirely absent. This trend was noticed by Obermeijer (1933) and has been confirmed by the current study. The tendency to form spinescent dwarf shrubs with small leaves is prevalent in Section *Barleria* and parts of Sections *Prionitis* and *Somalia*. The geographic distribution of the species with this growth form indicates a strong correlation with arid habitats.

In parts of the genus a prevalent growth form is that in which a few, straggly, weakly-branched prostrate stems are produced from a woody rootstock. This habit occurs in all members of Group 4 in Section *Barleria* (e.g. *B. macrostegia*). Many of these species, such as *B. lichtensteiniana* C.B. Cl., grow in extremely arid situations. All members of this group also possess very densely crowded, many-flowered cymose inflorescences that are held erect in the axils of the leaves.

Habit did not provide any characters that were useful for cladistic analysis, due partly to the incompleteness of the data set; extensive field studies outside of southern Africa are required to collect accurate information on habit and thus to verify the observations made on herbarium material. Several types of habit are strongly associated with certain infra-generic groups but also show sporadic occurrence in other groups. These characters have probably arisen independently in a number of lineages within the genus. This seems especially likely as, in certain species at least, habit is strongly influenced by environmental conditions.

Evolutionary advancement with respect to habit has probably proceeded in a number of directions from a basal condition ("typical" shrublet). Woodiness is uncommon in *Barleria*, as it is in the Acanthaceae as a whole (Carlquist & Zona, 1988). It has sporadic occurrence in a number of genera in different parts of the family, e.g. *Mackaya* Harv., *Duvernoia* E. Mey. ex Nees (Balkwill, pers. comm.), *Sclerochiton* Harv. and *Blepharis* Juss. (Vollesen, 1990a), *Graptophyllum* Nees and *Sanchezia* Ruiz et Pavon (Carlquist & Zona, 1988) and is unlikely to be homologous in all cases. Usually woodiness is regarded as basal in the angiosperms (Cronquist, 1988) and is, likewise, often regarded as primitive in the Acanthaceae (Vollesen, 1990a). The Acanthaceae is generally a derived group, and a plausible explanation of the occurrence of woodiness could be that only a few members have retained the primitive condition or show reversal to the plesiomorphous state. However, this hypothesis is not congruent with some of the other characters in the woody species of *Barleria*. It may be that woodiness in these taxa is secondarily derived. Investigation of wood anatomy in *Barleria* and other members of the family may cast further light on interpretations of evolutionary polarity in wood characters.

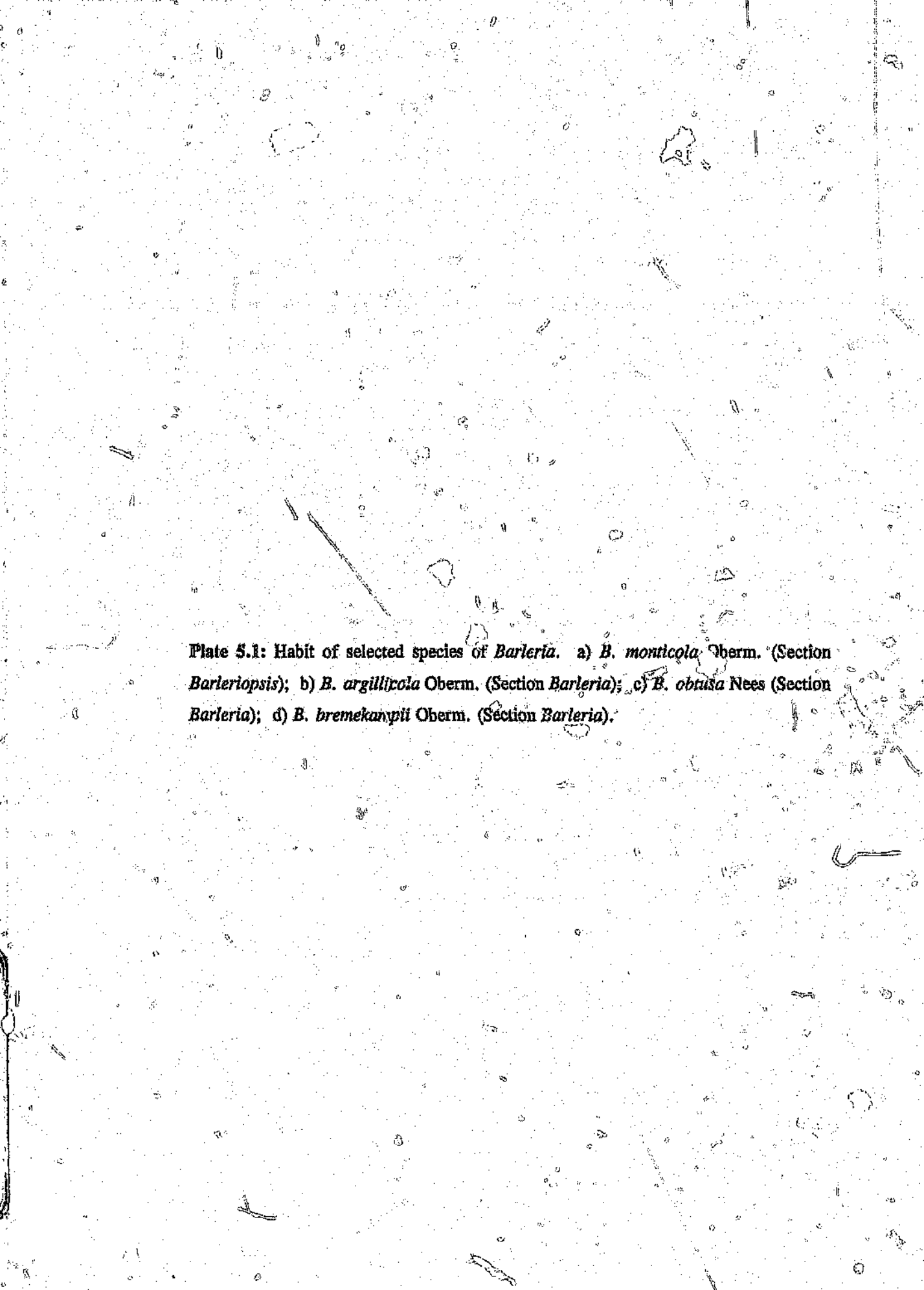


Plate 5.1: Habit of selected species of *Barleria*. a) *B. monticola* Oberm. (Section *Barleriopsis*); b) *B. argillicola* Oberm. (Section *Barleria*); c) *B. obtusa* Nees (Section *Barleria*); d) *B. bremekampii* Oberm. (Section *Barleria*).

a
b
c
d

Plate 5.2: Habit of *B. scindens* Oberm. (Section *Barlerites*), photographed in the Lowveld Botanic Gardens, Nelspruit, Eastern Transvaal (South Africa).

Plate 5.3: Habit in selected species of *Barleria*: a) *B. greenii* M-J. & K. Balkwill (Section *Barleria*); b) *B. rogersii* S. Moore (Section *Stellatohirtae)*; c) *B. virgula* C.B. Cl. (Section *Barleria*).

a
b
c

Because it is expected that evolutionary change with respect to habit has not proceeded in a linear fashion, and because the same habit has arisen in parallel in different groups, it was very difficult to polarise characters with any certainty. The only habit that can clearly be regarded as diagnostic (and apomorphic) for a group is the woody caudex with annual stems in *B. ovata* and *B. monticola*. Further field work may reveal that other species in this section, (most of which also have terminal synflorescences) show the same kind of habit. Habit characters could be useful in the elucidation of affinities within groups, especially if more data can be gathered through field observations.

b. Morphology of leaves

Several aspects of leaf morphology are extremely useful in distinguishing between closely related species or groups of species within *Barleria*. Some characters of the leaves are rather variable. Features such as shape, size and texture of the leaves are sensitive to environmental conditions and tend to be strongly correlated with certain habitats. In contrast, pubescence is a particularly rich source of taxonomically useful characters, providing a number of autapomorphies for various groups. Some of the variation in the morphology of the leaves is depicted in Figure 5.1.

One of the features that distinguishes *Barleria* from all other genera in the Acanthaceae is the predominance of double cystoliths in the epidermal cells of the leaves (Obermeijer, 1933; Ahmad, 1975). Cystoliths are calcium oxalate deposits present in the epidermal cells of all members of the subfamily Ruellioideae (Bremekamp, 1965). In *Barleria*, cystoliths occur in both the costal and intercostal regions of the epidermis and may either be very conspicuous (e.g. in *B. aculeata*) or inconspicuous (e.g. *B. ovata*). They are usually double (i.e. lie in two adjacent epidermal cells), but may be solitary (pers. obs.; Ahmad, 1975) or may form groups or chains of three or more (Ahmad, 1975). Whilst double cystoliths do occur in other genera of the family, they are not as conspicuous or as common as they are in *Barleria* (Metcalfe & Chalk, 1950; Amhad, 1975). Within Section *Barleria*, species that grow in characteristically dry habitats have leaves that are particularly dense with cystoliths. A more detailed study of the cystoliths within the genus may reveal taxonomically useful characters.

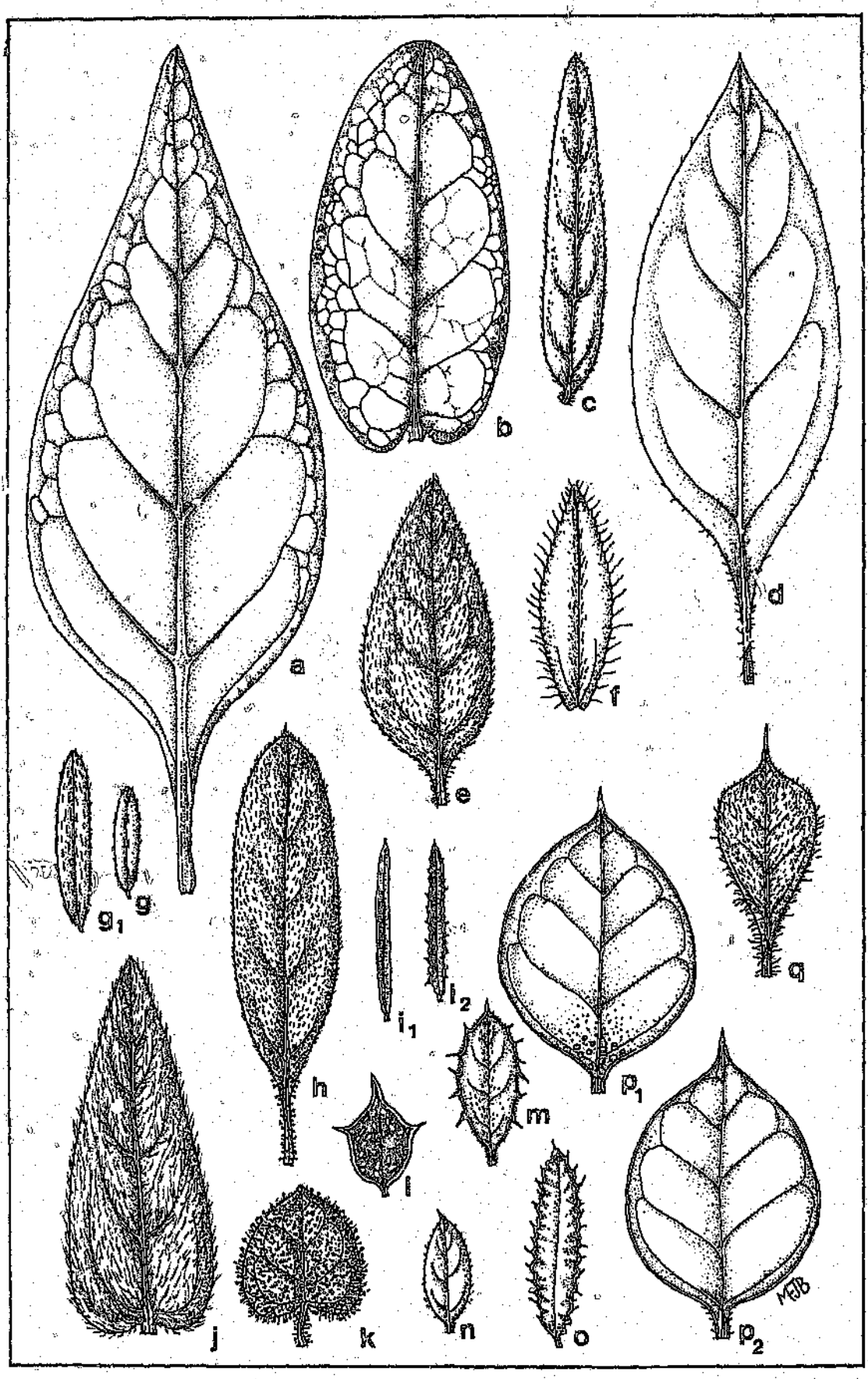
The leaves in all species of *Barleria* are opposite and decussate. Leaf morphology can be variable, especially in species with a broad geographic distribution (e.g. *B. prionitis*

sensu Wood, Hillcoat & Brummitt, 1983; *B. eranthemoides* R.Br. and *B. lancifolia* T. Anders.). Plants growing in dry, harsh environments tend to have smaller, thickly-textured or coriaceous leaves and those plants in damper, more mesic habitats have larger, more softly- and thinly-textured leaves. As in *Anisotes* (Baden, 1981), a useful distinction can be made between those species in which the leaves are predominantly sessile (parts of Section *Somalia*) and those which have distinctly petiolate leaves (all other sections). Sessile leaves are considered to be apomorphic in *Barleria*.

The colour of the leaves is another source of useful characters. All members of Section *Stellatohirtae* have discolourous leaves. The discolouration in these species is caused to a large extent by the extremely dense pubescence on the undersurfaces of the leaves. Within Section *Somalia*, the leaves of almost all species are glaucous at least on one surface. In the "typical" species of this section (e.g. *B. argentea*) the leaves are not glaucous but they are characteristically blue-green when dried. Some specimens of *B. gibsonii* and *B. montana* (Section *Barlerianthus*) appear either to be glaucous or dry grey-blue, but this is difficult to assess because of the age (e.g. 70 - 100 years) of most of the specimens.

In the majority of species the leaves are innocuous, entire and have unthickened margins (Figure 5.1a - c, g, j, k). In Section *Prionitis*, all species possess a stiff, sharp point at the leaf apex, although this may be more well developed in some species than in others (Figure 5.1d, p, & q). In several of the species within this group the leaf margins are slightly thicker than the rest of the leaf blade, and may be semi-translucent or hyaline. In *B. randii* (Section *Prionitis*), the margins are conspicuously thickened, with a white, cartilaginous rim (Figure 5.1p). The leaf margins are decurrent on the stem, forming two prominent ridges on each side. Within Section *Barleria* all the "typical" species, such as *B. elegans* S. Moore (see Chapter 7), possess a sharp apiculus at the leaf apex (Figure 5.1h, i, l - o). This apiculus is more prominent in some species than in others, but is usually not as robust as in Section *Prionitis*. Several species within this sub-group have leaves with a conspicuously thickened, white-cartilaginous rim along the margins; these leaves may or may not develop some degree of dentition along the margins (Figure 5.1i, m & o). Dentition may also be present on the leaf margins of species that lack cartilaginous rims. In some cases, e.g. *B. mysorensis* Roth, *B. bornuensis* S. Moore, *B. stocksii* T. Anders. and *B. rehmannii*, the leaf margins are only minutely denticulate,

Figure 5.1: Variation in leaf morphology in *Barleria*: a) *B. montana* x 1, Wight 2214 (K), Section *Barlerianthus*; b) *B. calophylloides* x 1, Bally & Carter 16 481 (MO), Section *Somalia*; c) *B. hirta* x 1, Teaugue 8 (BOL), Section *Somalia*; d) *B. crossandriformis* x 1, Balkwill 1489 (NU), Section *Prionitis*; e) *B. scindens* x 1, Rogers 13592 (PRE), Section *Barlerites*; f) *B. rehmannii* x 1,5, Codd 3492 (PRE), Section *Somalia*; g) & g1) *B. argentea* x 2, Thulin & Warfa 4063 (K), Section *Somalia*; h) *B. acanthoides* x 2, Carr 171 (EA), Section *Barleria*; i) *B. bechuanensis* x 2, Esterhuysen 1007 (PRE), Section *Barleria*; j) *B. ovata* x 1, Thorncroft 19 175 (PRE), Section *Barleriopsis*; k) *B. heterotricha* x 2, Smuts 2039 (PRE), Section *Barleria*; l) *B. aculeata* x 2, Miller, Guarino, Obadi Hassan Mohammed M8643 (K), Section *Barleria*; m) *B. papillosa* x 2, Kruger K16 (STE), Section *Barleria*; n) *B. eylesii* x 1, Plowes 3455 (K), Section *Barleria*; o) *B. rigida* x 2, Herman 561 (PRE), Section *Barleria*; p) *B. randii* x 1, Kolbe 4015 (BOL), Section *Prionitis*: 1 - abaxial surface, 2 - adaxial surface; q) *B. holubii* x 2, Miller 43 764 (SRGH), Section *Prionitis*.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an effect created by the presence of bulbous-based trichomes along the margins (Figure 5.1f). In contrast, the leaves of species such as *B. aculeata* Balf. *f.* are equipped with stout, stiff spines along the margins (see Figure 5.1l). In those species with cartilaginous leaf margins, the development of dentition is variable and the leaf margins may also become markedly sinuous (see Figure 5.1 i, l, m & o). Thickened leaf margins of the kind seen in *Barleria* are not known in *Crabbea* and are considered to be an apomorphic feature. This character, however, has a somewhat patchy distribution in the genus and, like so many other apomorphic states, has probably arisen in parallel in different groups.

Several of the vegetative characters that have been discussed have not been used in cladistic analyses at the sectional level, but they could provide useful information regarding the relationships of taxa if in-group analysis of sections is undertaken.

c. Pubescence

Epidermal hairs of the Acanthaceae have been investigated by a number of authors, but particularly by Ahmad (1974, 1974a, 1975 & 1978) and by Singh & Jain (see Ahmad, 1978). Balkwill (1985) has provided a review of the use of pubescence and types of trichomes as taxonomic characters in the Acanthaceae. Kelbessa (1990) found indumentum characters to be enormously unstable in Section *Anisostachya* of *Justicia*. In contrast, I have found pubescence characters in *Barleria* to be reliable; they have provided a rich source of taxonomically useful data, including a number of apomorphies for infra-generic groups. Although the trichomes in any given species, or group of species, may display some variation, it is always within clearly definable limits. Variation in the density of hairs or the overall presence or absence of hairs may occur, caused by mutation or small environmental changes. The production of particular types of hairs, however, requires the action of a number of genes and so is considered to have taxonomic usefulness (Theobold, *et al.*, in Metcalfe & Chalk, 1950).

Lindau (1895) noted the presence of so-called "biramous" hairs in *Barleria*, using this feature to characterise his Section *Somalia*. Clarke (1899) made the distinction between plants with a pubescence of simple hairs only (Section *Prionitis*) and those in which the hairs could be simple and complex (Section *"Eubarleria"*). Clarke did not mention the presence of biramous hairs in the genus. Obermeijer (1933) used the presence of multicellular dendroid and stellate hairs as a diagnostic character for one of the

subsections she recognised within her Section *"Eubarleria"*. None of the earlier authors, however, recorded the great diversity in trichome types that is reported in this thesis. *Barleria* possesses a wide range of glandular and eglandular trichomes (see Figure 5.2). A useful distinction can be made between those species in which the plants are almost entirely glabrous (subgroup 4 of Section *Somalia*, e.g. *B. lactiflora* Brummitt & Seyani) and those in which hairs of some kind are present, at least on some parts of the plant. In those species that are characteristically glabrous or glabrescent, the young axillary shoots are always extremely densely and conspicuously hairy. Within those groups that are pubescent, a distinction can be made between species in which only simple trichomes are present and those in which both simple and complex hairs occur.

Types of Foliar Trichomes in *Barleria*

i) Glandular trichomes:

Ahmad (1975 & 1978) recorded the presence of "sub-sessile, short-stalked glands" in several genera of the Acanthaceae, including seven Indian species of *Barleria*. The term "sunken glands" is preferred for these structures in this thesis as they are deeply sunken in the epidermis of fresh leaves and are not simply sessile or sub-sessile. Use of the term "sunken glands" means that these trichomes can be distinguished from other short-stalked glands (that are not sunken) found in members of the genus.

All members of Section *Prionitis* have sunken glands present at least on the abaxial surfaces of the leaves. In dried specimens (viewed at magnifications of 10 - 30 X), these glands have the appearance of small, discrete black or reddish-black spots scattered fairly uniformly over the surface of the leaf. In fresh leaves at these magnifications they appear as small crystalline structures embedded in a distinct depression (see Plate 5.4). A view of a sunken gland in transverse section is shown in Plate 5.4. Each sunken gland comprises a single-celled stalk that is deeply embedded in the epidermis, and a globular head of four cells. This type of gland is distinguishable from short-stalked, saucer-shaped glands that are largely restricted to the bases of the leaves, particularly on the abaxial surface in the region of the petiole (see Plate 5.4). These glands are milky-white in fresh material (orange or brown in dried specimens) and clearly project above the surface of the leaf or petiole. They comprise a single- or two-celled stalk and a large, saucer-shaped head of four to eight cells. Studies conducted on leaves of different

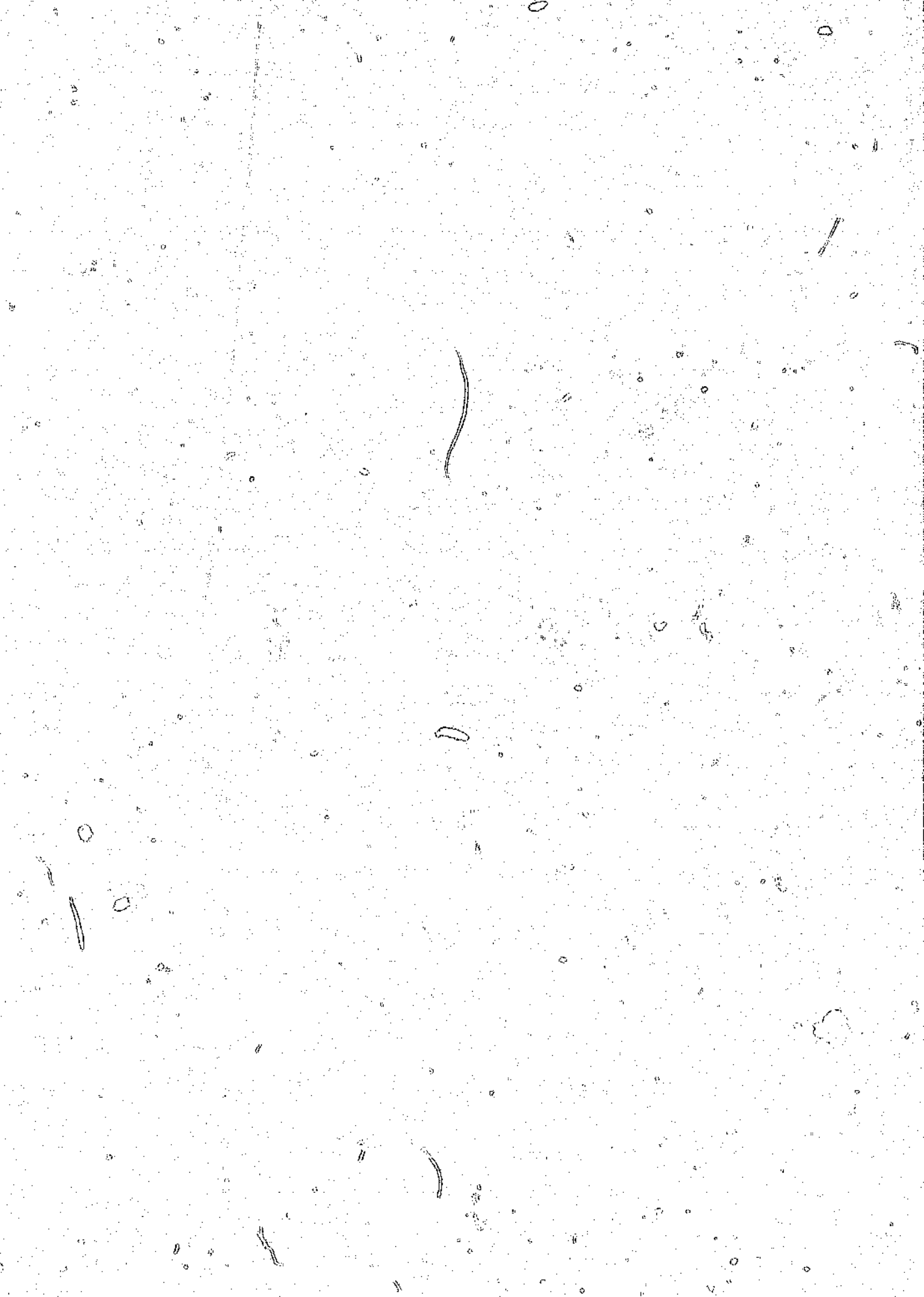
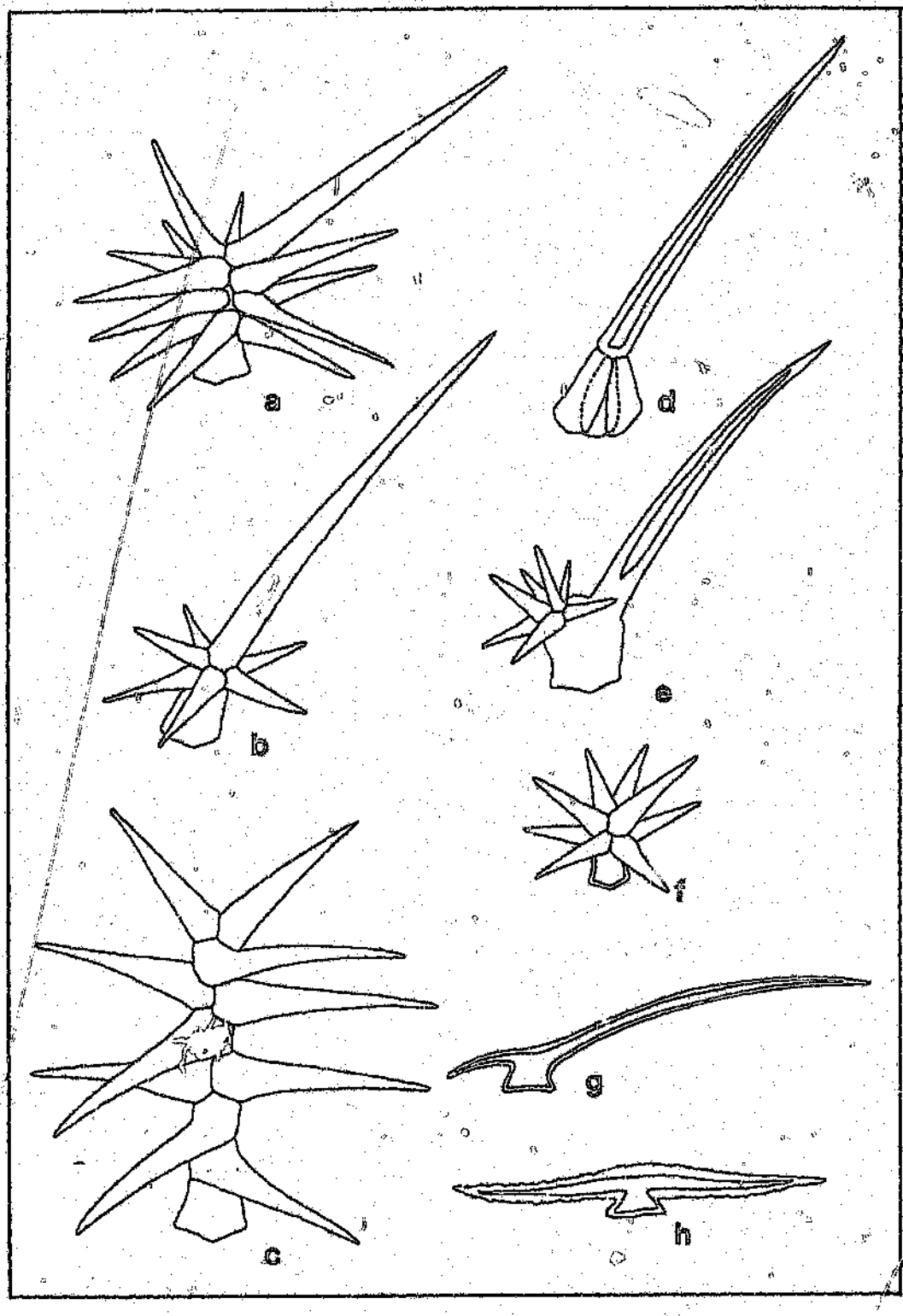


Figure 5.2: Selected examples of eglandular trichomes in the genus *Barleria*. a) long-armed stellate hair of *B. rogersii* (Section *Stellatohirtae*), x 100: Balkwill & Balkwill 6353 (J); b) long-armed stellate hair of *B. heterotricha* (Section *Barleria*), x 100: Smuts 2039 (PRE); c) dendroid hair of *B. albostellata* (Section *Stellatohirtae*), x 100: Balkwill & Balkwill *et al.* 5811 (J); d) eglandular trichome of *B. micans* (Section *Barleriopsis*) with multiseriate, bulbous base, x 100: Steyermark & Dunsterville 105796 (MO); e) long-armed stellate hair of *B. hildebrandtii* (Section *Stellatohirtae*) with swollen, bony base, x 100: Gilbert, E. Amu & Vollesen 7723 (K); f) stellate hair of *B. rogersii* (Section *Stellatohirtae*), x 100: Balkwill & Balkwill 6353 (J); g) anvil hair of *B. meyeriana* (Section *Somalia*), x 100: Balkwill & Balkwill *et al.* 5873 (J); h) medifixed hair of *B. argentea* (Section *Somalia*), x 100: Thulin & Warfa 4013 (K).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h

ages provide no evidence that the saucer-shaped glands are a later developmental stage of the sunken glands. The short-stalked, saucer-shaped glands are present in all members of Section *Prionitis* and have a scattered distribution elsewhere in the genus. Within Section *Prionitis*, the saucer glands are particularly numerous and conspicuous in species such as *B. randii* and *B. quadrispina* Lindau, whilst in other species, e.g. *B. norbertii* Benoist and *B. her* Benoist, they are not very abundant. Although saucer-shaped glands have been found to be widespread in Section *Prionitis* in this study, Wood, Hillcoat & Brummitt (1983) considered the presence of these glands on the bracteoles to be a characteristic feature of *B. trispinosa* (Forssk.) Vahl. They used their presence on the bracteoles in other closely related species to place them in synonymy with *B. trispinosa*.

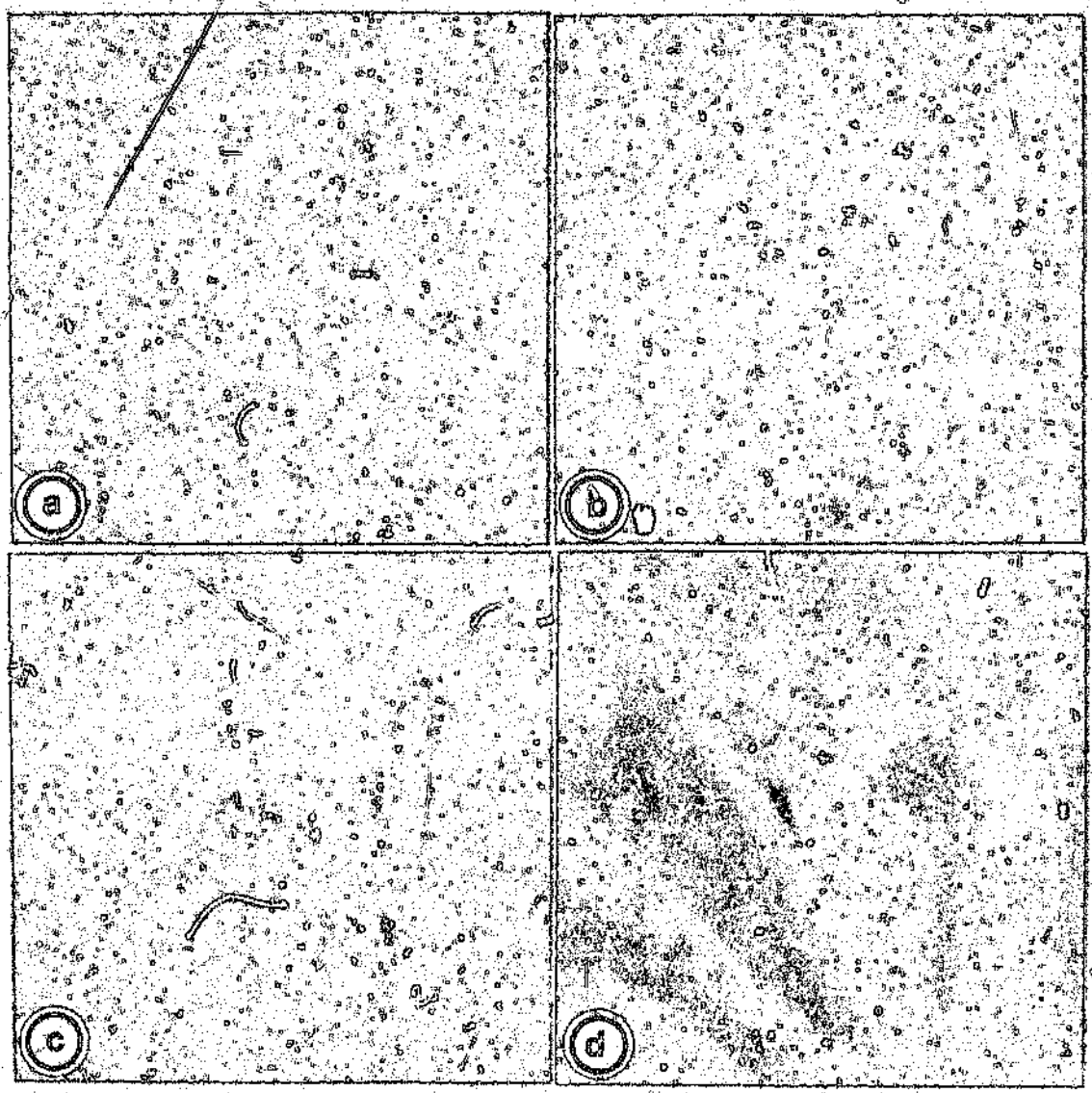
Short-stalked or sessile glands of some description occur in a number of species that do not belong to Section *Prionitis* . The structure of these glands has not been thoroughly investigated in these taxa, due to a lack of suitable material for sectioning, so it is not known whether they are homologous with the glands in Section *Prionitis*. Ahmad (1978) recorded the presence of "subsessile" glands in 111 species belonging to 39 genera in the Acanthaceae. As part of the current research, a survey of glands in a number of southern African Acanthaceous genera was made. Glands similar in appearance (in dried material) to the sunken glands were found in a number of genera, but nothing equivalent to the saucer-shaped glands was found. All species of *Crabbea* possess glands on the abaxial leaf surfaces, but their detailed structure is not known and their presence in this genus has not been reported before. The members of the Ruelliineae that were investigated lack glands of the type present in *Barleria*. The evolutionary polarity of a character that occurs in both the study group and its sister group is unclear (Stevens, 1980). The presence of these glands in *Barleria* is regarded as apomorphic in this thesis, based on congruence with other derived character states.

(ii) Long-stalked glandular trichomes:

Glandular trichomes with stalks of several cells and glandular heads are widespread in *Barleria*. The presence or absence of such trichomes, and their location on the plant, provides useful characters at the species level.

Plate 5.4: Sunken glands on the leaves of *B. rotundifolia* (Section *Prionitis)*, as viewed with a light microscope.

a) adaxial view of freshly-picked leaf; b) abaxial view of freshly-picked leaf; c) Transverse section through a freshly-picked leaf, showing a longitudinal section of a sunken gland; d) petiole of *B. rotundifolia* leaf showing saucer-glands.


a
b
c
d

(iii) Eglandular trichomes:

The range of eglandular trichomes in *Barleria* is illustrated in Figure 5.2. A number of highly characteristic trichome types is present in the genus. These hairs may be broadly categorised as complex or simple.

(iv) Complex hairs:

In Section *Stellatohirtae* multicellular dendroid and stellate hairs are present in all species (see Figure 5.2). The presence of these hairs is considered to be apomorphic. Dendroid hairs have a restricted distribution within the genus, occurring only in *B. albostellata* C.B. Cl. and *B. salicifolia* S.Moore. There are very few records of dendroid hairs in the literature on Acanthaceae. Munday (1980) noted the presence of dendroid hairs in *Monechma incanum* (Nees) C.B. Cl., but describes them as T-shaped, a much simpler structure than that found in species such as *B. albostellata* (see Figure 5.2). Stellate hairs (Figure 5.2) are more common in *Barleria* than dendroid hairs, and are present in all members of Section *Stellatohirtae*. Another type of complex trichome occurs in all members of the subgroup 3 of Section *Barleria*, e.g. *B. heterotricha* (see Figure 5.2). These hairs have been termed long-armed stellate hairs in this study. Their presence is regarded as apomorphic.

(v) Simple trichomes:

Simple eglandular trichomes in *Barleria* are uniseriate, uni-or multi-cellular and of variable length and shape (see Figure 5.2). These hairs may bear cuticular ornamentation of a tuberculate type, or they may have smooth surfaces. In species such as *B. micans* Nees and *B. strigosa* Willd., the pubescence is characteristically composed of harsh, yellow adpressed hairs. These hairs are usually unicellular with swollen bases and heavily thickened, ornamented walls. Hairs with conspicuously bulbous, multiseriate bases (but not yellow) are present in all members of Section *Barlerites*, but also occur in a number of other groups.

In the "typical" part of Section *Somalia* (e.g. *B. argentea*), all species possess an extremely characteristic hair type (Figure 5.2). The hairs are attached to the epidermal cells at a central point along their length such that approximately equal length "arms" project on either side of the point of attachment (Figure 5.2). Lindau (1985) referred to these hairs as biramous, but the term "medifixed" is preferred here as a more accurate

descriptor. Correlated with the presence of medifixed hairs in this group is the presence of extremely small fruits and corollas with contrasting spots of colour.

In other subgroups of Section *Somalia* (e.g. *B. meyeriana* and *B. lancifolia*) anvil-shaped hairs occur (Figure 5.2). These hairs superficially resemble the medifixed hairs of species such as *B. argentea*, but are attached to the epidermal cells near the end of the hair rather than in the middle. These hairs are similar to the "anvil hairs" described by Munday (1980) in *Monechma robustum*. Although some of the species in this group are only sparsely pubescent when mature, at least some of the eglandular hairs that are present are of the anvil type.

5.3.2 Spine systems

The presence or absence of spines has been extensively used in past classifications of *Barleria*. In Section *Prionitis* the spines are highly modified two, four, or six-rayed structures borne in the leaf axils. These structures have been thought to represent modified lateral (vegetative) branches (Clarke, 1899) or the modified bracts and bracteoles of reduced or sterile inflorescences (Nees, 1847; Lindau, 1895 & Obermeijer, 1933). In Section *Barleria* the spinous nature of many of the species seems to derive from the spinous nature of the bracteoles. Little attention has, however, been paid by previous authors to establishing the homology of the different kinds of spinous structures in this genus. Obermeijer (1933) suggested that the spines in Section *Prionitis* represent reduced inflorescences in which the rays of the spines represent a pair of bracts and one or two pairs of bracteoles. Vollesen (1990) has recorded the development of axillary spine systems from sterile inflorescences in *Crossandra praecox* Vollesen and *C. horrida* Vollesen. He states that the spine systems in *Crossandra* are strikingly like those in *Neuracanthus* and *Barleria* and that there can be little doubt that they developed in the same way (Vollesen, 1990). The findings presented below do not support this hypothesis.

A common feature in *Barleria* is the development of two serial buds in the axil of each leaf. Both buds may give rise to ordinary, vegetative lateral branches or, at the onset of flowering, the upper bud may give rise to an inflorescence unit instead (see Plate 5.5a). In Section *Prionitis*, the formation of a spine-system and an inflorescence unit in

Plate 5.5: Axillary spine systems in Section *Prionitis* (a) and Section *Barleria* (b). a) *B. rotundifolia*, ex hort., University of the Witwatersrand; b) *B. elegans*, ex hort, University of the Witwatersrand.

a
b

the same axil has been observed in numerous species, particularly *B. cuspidata, B. randii, B. her, B. proxima, B. setigera* and *B. trispinosa*. When this occurs, the inflorescence always develops from the upper serial bud and the spine system from the lower serial bud. Lower down on the stem, vegetative laterals and spine systems may share the same axil, but again the spine system always develops from the lower serial bud (Plate 5.5b). The only species in which some apparent divergence from this pattern has been observed is *B. waggana* (a blue-flowered member of Section *Prionitis*). The spine systems at the lower nodes of the stem develop normally (as described above). At the lowermost node of the synfloresecence, however, a spine system sometimes develops in what appears to be the place of the first flower within the dichasium. Close examination of the material reveals that this spine system also develops from the lower of two buds in this axil, and that a flower can be produced later from the upper bud. Furthermore, no transitional stages, (such as those observed by Vollesen in *Crossandra*) showing reduction and modification of an inflorescence unit to form a spine system, have been observed in Section *Prionitis*. The spines in this part of the genus are, therefore, considered to represent highly modified shoot systems.

In Section *Barleria* the spine systems present in the axils of the leaves represent aborted, sterile or old (persistent) inflorescences (Plate 5.5). The spinous nature of the bracteoles in the fertile inflorescences may also add to the overall spinescence of the plants. The spines in the lower leaf axils seldom occur simultaneously with a vegetative lateral and have never been observed in the same axil as a fertile inflorescence unit. In this section, the spine system always develops from the upper of the two buds in the leaf axil. The lower bud (which in Section *Prionitis* gives rise to spines) seldom undergoes further development, but if it does it gives rise to a vegetative shoot. In some species (e.g. *B. buxifolia* Nees) the spine systems present in the lower leaf axils appear to be "three-rayed" and bear a strong resemblance to the three-rayed axillary spines sometimes seen in Section *Prionitis*. However, in the former the third "ray" represents the aborted floral bud between a pair of spinous bracteoles. Thus, any resemblance between the spine systems in Section *Prionitis* and Section *Barleria* is superficial as these structures develop from different axillary buds and are not homologous. The precence of the two different kinds of spines has been regarded as two separate characters and has, thus been coded separately. The presence of either kind of spine represents an apomorphic condition in *Barleria*.

Spine systems are not equally well developed in all species of Section *Prionitis*. In *B. crossandriformis*, *B. norbertii*, *B. setigera*, and *B. marginata* the plants may sometimes be almost entirely spineless, and those spines that are present are extremely small. This is in strong contrast with the situation in species such as *B. tetracantha* Balf. f, *B. tetraglochin* Milne-R. and *B. trispinosa*, in which spines are present in most leaf axils and may attain lengths of 50 mm. In many species the spines are sessile in the leaf axils, but in others such as *B. proxima*, *B. quadrispina*, *B. tetracantha* and *B. trispinosa*, the spines are raised on a long stalk. The only species within the section in which spines seem to be entirely lacking is *B. sacleuxii* Benoist from Tanzania.

Within Section *Barleria* spine systems are present in almost all members of the "typical" group (e.g. *B. elegans)* and in group 2 (e.g. *B. bremekampii*). The form of the spinous bracteoles is usually very similar to the form of the bracteoles in fertile inflorescences. Important characters for distinguishing between groups of species include the presence of dentition on the margins of the spinous bracteoles (Figure 5.3) and their curvature. Variation in these characters is illustrated in Figure 5.3).

5.3.3. Inflorescences

The structure of the inflorescence is an important source of taxonomic characters which have been used to delimit taxa at various levels within the Acanthaceae (see Balkwill, 1985 for a brief review; also: Baden, 1981; Cadman, 1987; Graham, 1988). Within *Barleria* differences in the structure and position of the inflorescences were used by Nees (1847) to delimit sections and by Clarke (1899) to distinguish the three subsections of his Section *"Eubarleria."*

Inflorescence structure in *Barleria*, as in many other groups (Cronquist, 1988), exhibits a considerable degree of variation that is sometimes difficult to interpret. This situation has not been improved by the inconsistent application of terminology by previous authors. In his generic description, Clarke (*l. c.*) described the inflorescences of *Barleria* as axillary, scorpioid cymes, but throughout his account of the species refers to the inflorescences as racemes. Obermeijer (1933) regarded the fully developed inflorescence in *Barleria* as a dichasium, often showing reduction to unilateral cymes or solitary flowers.

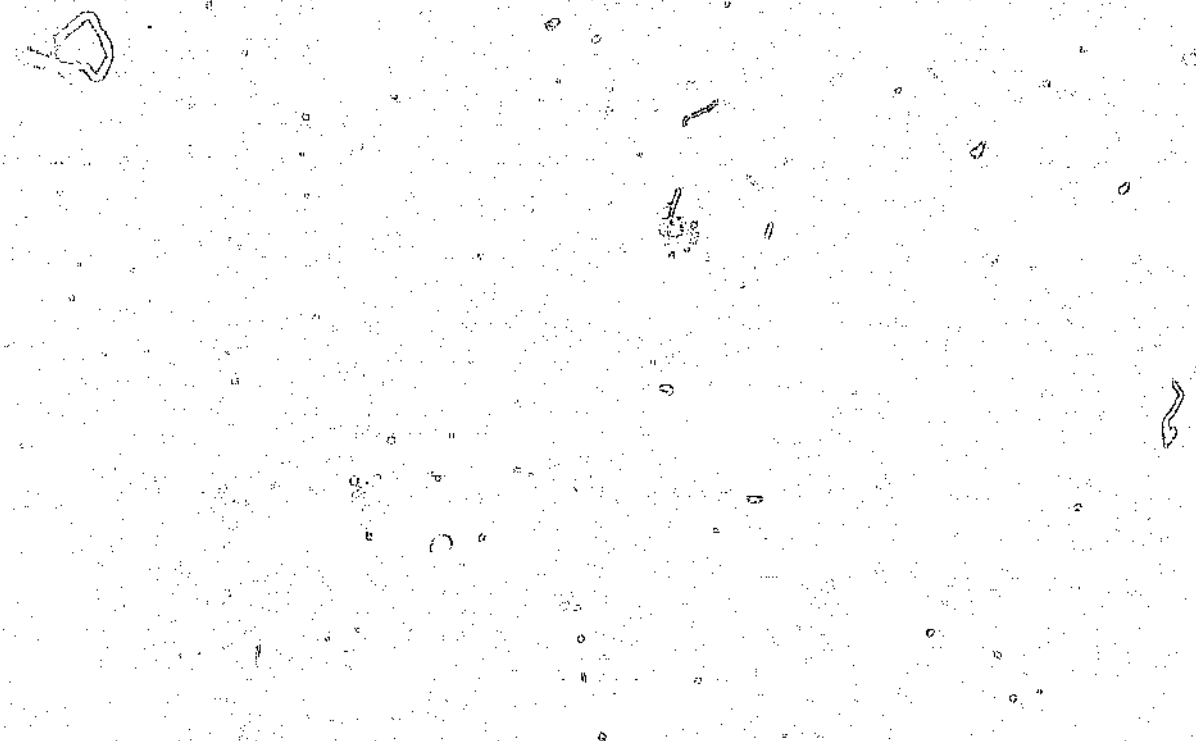
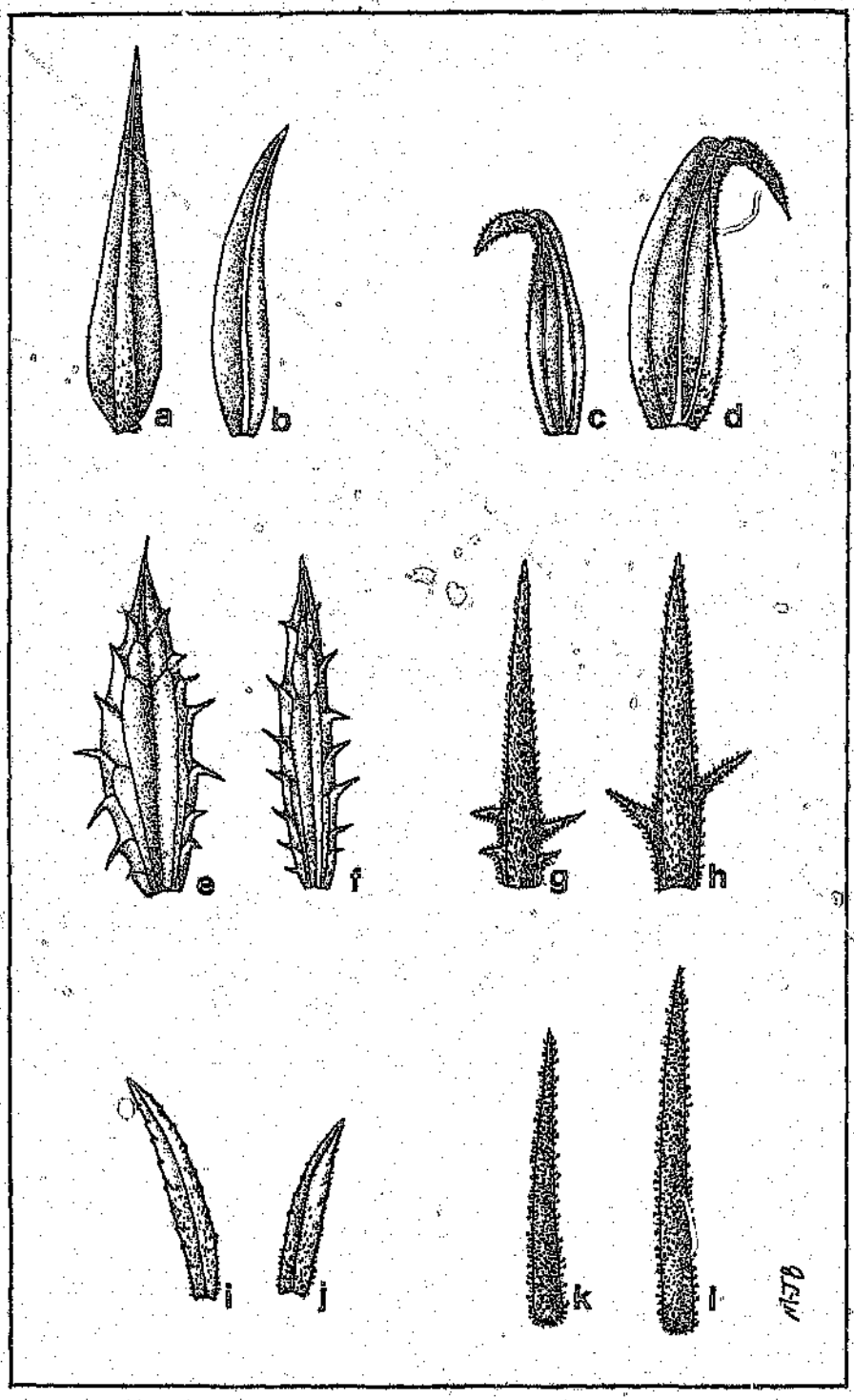


Figure 5.3: Variation in the morphology of spinous bracteoles in selected species of Section *Barleria*.

In each case the two bracteoles of a pair are shown.
a) & b) *B. greenii*: Balkwill, Balkwill & Green 5404 (J); c) & d) *B. argillicola*: Edwards 2458 (NU); e) & f) *B. elegans*: Davies 1247 (SRGH); g) & h) *B. hillcoatiae*: Wood 2751 (K); i) & j) *B. grandicalyx*: Friis, Zerihun & Vollesen 2506 (K); k) & l) *B. bremekampii*: Codd 5449 (PRE).


a
b
c
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k
l

In certain species the inflorescences are clearly either terminal or axillary. In the case of solitary flowers, this distinction is particularly difficult to make as the difference may only be a matter of degree, depending on the lengths of the upper internodes. Wood, Hillcoat & Brummitt (1983) have drawn attention to this problem in the *Barleria prionitis* complex. In *B. prionitis* subsp. *appressa* (Forssk.) Vahl the internodes between the uppermost leaves are long and the flowers are easily classed as solitary and axillary. In *B. prionitis* subsp. *prionitis*, the internodes are very short giving the appearance that the flowers (which are borne in all the upper leaf axils) are arranged in a dense terminal head. Many intermediate forms between these two extremes may exist. In these situations it is also difficult to decide whether or not the flowers are truly bracteate or not. The leaves subtending the flowers may be indistinguishable from the sterile vegetative leaves, or may show varying degrees of modification in size, shape, colour, texture and vestiture from the ordinary leaves of the plant. Clearly, earlier authors experienced some difficulty in trying to interpret this variation through conventional application of terminology. Clarke (*l. c.*) considered bracteoles to be absent in *Barleria*. The pair of modified leaves subtending each flower was seen by him to represent a pair of bracts, one sterile and one fertile in each pair. He added, though, that in species such as *B. prionitis*, in which the inflorescence closely approximates a spike, the bracts have often been regarded as bracteoles and that he has referred to them as bracts merely "by analogy" (Clarke, *l. c.*). In his descriptions of certain species, in addition to describing "bracts" he has also described "foliar leaves". In contrast, Obermeijer (*l. c.*) considered bracts and bracteoles to be present in all members of the genus seen by her. In the species in which the solitary flowers "run into heads", she has also described the presence of "bract-like" leaves. Clearly, in this kind of system it is difficult to decide on the homology of certain structures.

a. Classification of inflorescence structure in *Barleria*.

The categorisation of inflorescence types presented below represents an attempt to adopt a simple and consistent system that facilitates the comparison of homologous structures. In this system, the structure of inflorescence units and their arrangement (or position) are regarded as separate characters. An inflorescence unit is defined as the smallest identifiable unit showing determinate growth. Such units may be of 4 basic types. In the classification that follows, dichasia and monochasia have been recognised as basic

organisational units and, based on modification of these, a number of structural patterns have been identified. No attempt has been made to further sub-divide these broad categories on the basis of differences in finer details such as the degree of contraction of the inflorescence axes. Whilst the interpretation of inflorescence structure in *Barleria* is open to other explanations, the one presented below provides at least a reasonable conceptual framework for the organisation of the data.

All inflorescence units in *Barleria* are basically cymose. Within each unit, every flower is subtended first by a pair of bracteoles and in addition may be subtended by a highly modified floral bract. The flowers are usually sessile or only very shortly pedicellate or pedunculate. Simple inflorescences are those comprising only one inflorescence unit; these can occur in any leaf axil of the plant. Complex inflorescences, or synflorescences, are those in which a number of inflorescence units are present. Synflorescences include all those forms in which flowers (often solitary) are present in all the upper leaf axils of a stem. Variation in the structure of inflorescence units in *Barleria* is illustrated diagrammatically in Figures 5.4 - 5.6. Some particularly unusual modifications of the basic structures are shown in Figure 5.7.

Inflorescence units may be of one of the four following types: dichasial cymes, cymes combining dichasial and monochasial elements, monochasial cymes or solitary flowers. In some groups the structure of the inflorescence units is very uniform, but in others the unit structure can be variable at both the inter- and infra-specific levels.

i) Dichasial cymes:

Dichasial units are usually simple, comprising only three flowers, each subtended by a pair of bracteoles (Figure 5.4a). Dichasial inflorescence units are widespread throughout the genus; the only section in which they are entirely absent is Section *Stellatohirtae*. Simple dichasia occur in most groups but are particularly prevalent in Section *Barlerites* and species such as *B. argentea* within Section *Somalia*. Compound dichasia (Figure 5.4b) have a more restricted distribution within the genus and are found mainly in parts of Section *Somalia* and Section *Barleriopsis*.

The inflorescence axes within dichasial units are usually very short, and the flowers often appear to be borne in tight clusters. In species such as *B. hochstetteri* Nees (Section

Somalia), each dichasial unit is raised on a long peduncle and the individual flowers are conspicuously pedicellate. In *B. lukwangulensis* (Section *Barlerites*), the flowers are borne on long, slender, flexuous pedicels and are pendulous. This is an unusual feature correlated with a climbing habit.

Within Section *Somalia* some interesting modifications of the basic dichasial pattern are found. In *B. sp. aff. glandulifera* Nees two separate dichasial units may be present in each axil (Figure 5.4c) or the more usual structure is complicated by the activity of additional accessory buds. In the blue-flowered species within Section *Prionitis* (e.g. *B. waggana* Rendle and *B. quadrispina*), the inflorescence units are simple dichasia in which the pedicels of the second and third flowers and the bracteoles of the first-formed flower are partially fused.

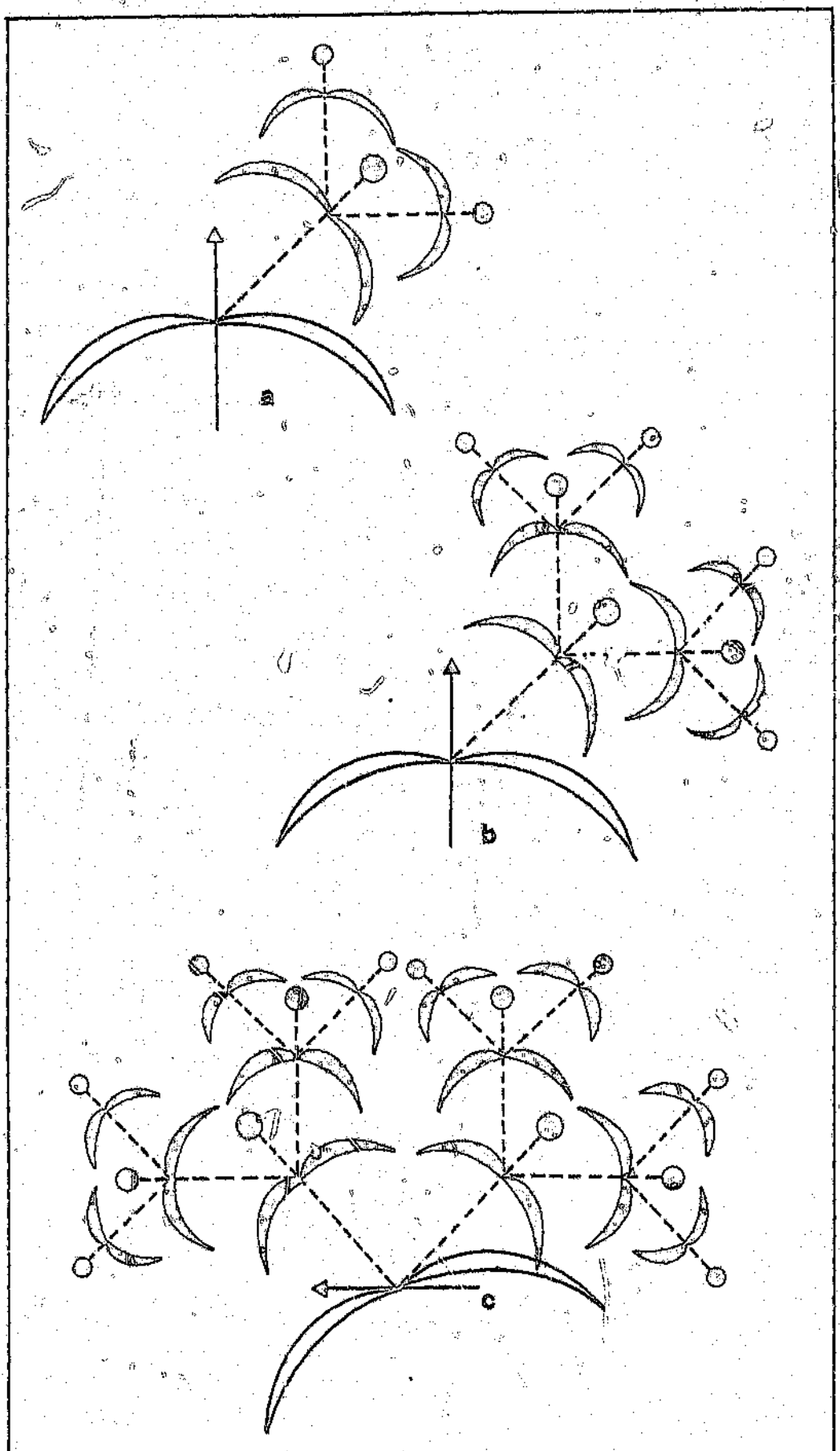
ii) Units comprising dichasial and monochasial elements:

A number of different permutations exist for the structure of inflorescence units showing combinations of dichasial and monochasial branching (Figure 5.5). In these forms, the initial dichasial cluster can be compound, comprising seven flowers. Further development involves the activity of only one bud at each node, so that monochasial growth occurs (see Figure 5.5). Alternatively the dichasial cluster can be simple; only one bud in the axils of both the second and third flowers develops (Figure 5.5). In both cases, the monochasial part of the cyme is scorpioid. Inflorescence units with either of these types of structure have a limited distribution within the genus, occurring in parts of Section *Barleriopsis* and in occasional species in Section *Barlerites* (e.g. *B. opaca* Nees).

iii) Monochasial cymes:

Monochasial scorpioid cymes (see Figure 5.6a) predominate in Section *Barleria*. Each flower in units of this kind is subtended by a pair of bracteoles, the sterile one of which is often slightly larger than the other. These cymes may become secund, a tendency that is particularly well-developed in species such as *B. macrostegia* (Section *Barleria)* and *B. strigosa* (Section *Barleriopsis).* In these two groups, a further modification of the basic pattern is found. The bracteoles in each pair are strongly dimorphic and the larger one in each pair is displaced to the other side of the inflorescence axis where it is subtended by the smaller bracteole (see Figure 5.6b and Figure 5.7a).

Figure 5.4: Diagrammatic representation of the structure of inflorescence units showing dichasial branching only. Black circles denote the position of flowers; black arcs denote bracteoles; open arcs denote leaves; arrow indicates direction of growth of main stem axis; dashed lines indicate axes of the inflorescence unit that may be contracted. a) simple dichasial unit; b) compound dichasial unit; c) combination of two separate dichasial units in the same leaf axil (drawing turned through 90 degrees).


a
b
c

Another very unusual form of inflorescence unit was noted in *B. biloba* Imlay. The unit structure is based on a scorpioid cyme, but each flower within the unit is subtended by a pair of highly modified bracts in addition to a pair of bracteoles. Furthermore, the axis bearing the second-formed flower in the cyme is contracted such that the second and first flowers appear to be borne side by side (see Figure 5.7b). Only one inflorescence of this type was dissected (as very few were available) and this was immature, so the observations made here would need to be compared with those made on more mature inflorescences of this species.

iv) Solitary Flowers:

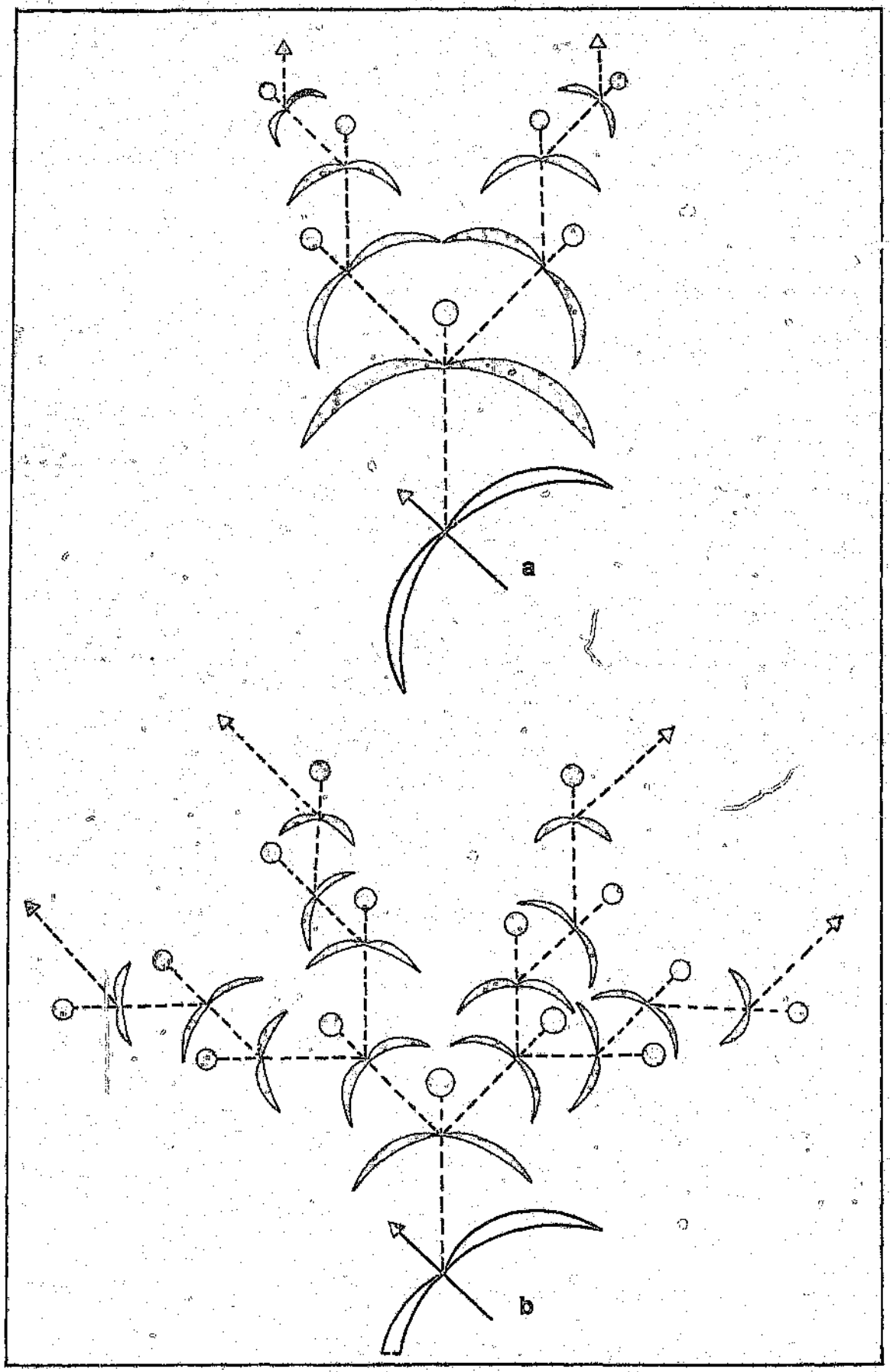
Inflorescence units comprising solitary flowers have a scattered occurrence throughout *Barleria* but are particularly dominant in the Section *Stellatohirtae*, parts of Section *Somalia* and Section *Prionitis*. Solitary flowers could be derived in numerous ways (see Figure 5.8). In most cases, axillary buds can be found in one or both axils of the flower, but these buds seldom undergo development. The arrangement of these buds can provide clues to the derivation of the structure of these units in different cases. Occasionally, the axillary buds may develop into mature flowers, but usually only long after the first-formed flower has dropped from the plant.

b. Evolutionary Trends in Inflorescence Structure

Some of the putative evolutionary trends in the structure of inflorescence units are shown in Figure 5.8. The primitive inflorescence type in the Acanthaceae is generally accepted as a dichasium (Baden, 1981; Balkwill, 1985; Balkwill & Getliffe Norris, 1988; Ensermu, 1990 & Graham, 1988). This hypothesis is supported in a more general context by Cronquist (1983), Rickett (1944) and Stebbins (1973).

In *Crabbea*, the outgroup of *Barleria*, the inflorescence is always axillary and has an almost capitulum-like appearance; tight clusters of almost sessile flowers are arranged on a flattened "receptacle" surrounded by a large number of bract-like structures. The exact structure of this type of inflorescence is obscured by the extreme reduction of the inflorescence axes, but the arrangement of mature flowers and buds indicates derivation from a compound dichasium by direct reduction of the axes (Figure 5.8). Within

Figure 5.5: Diagrammatic representation of the structure of inflorescence units showing dichasial and monochasial branching. Notation as for Figure 5.4.
a) unit based on a simple dichasium; b) unit based on a compound dichasium.


a
b

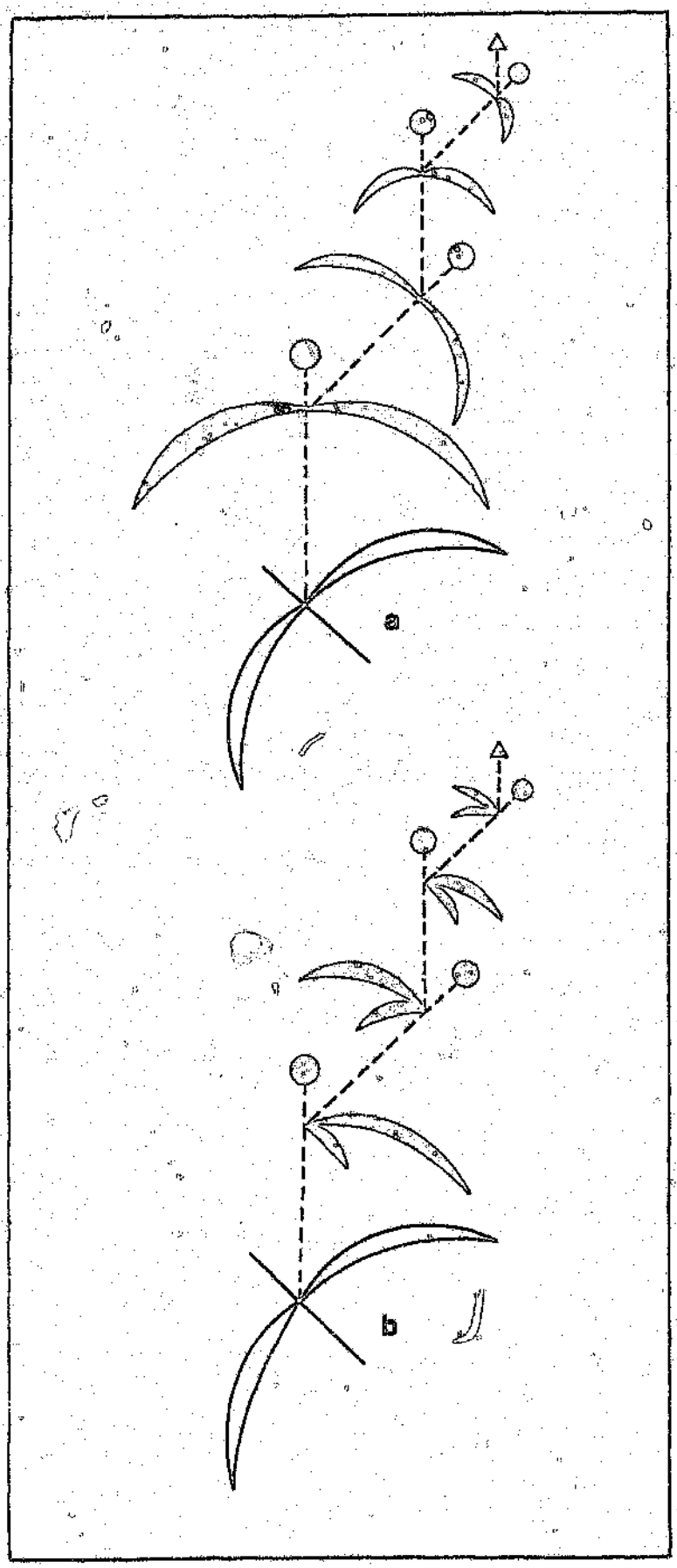
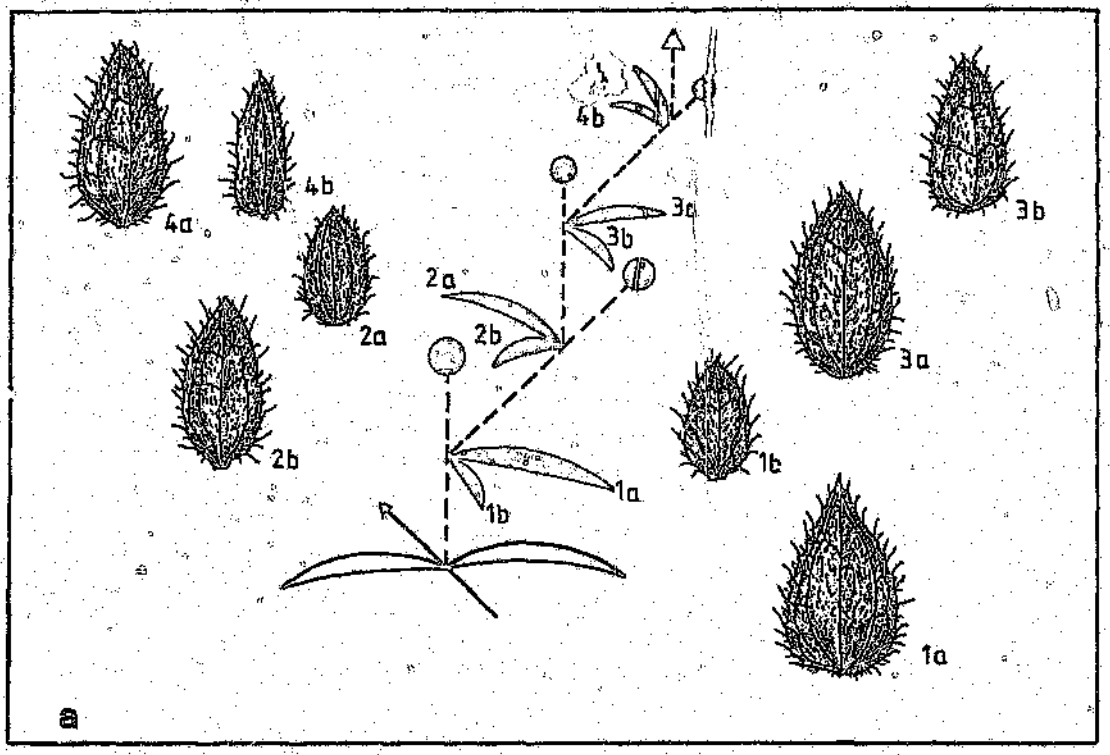
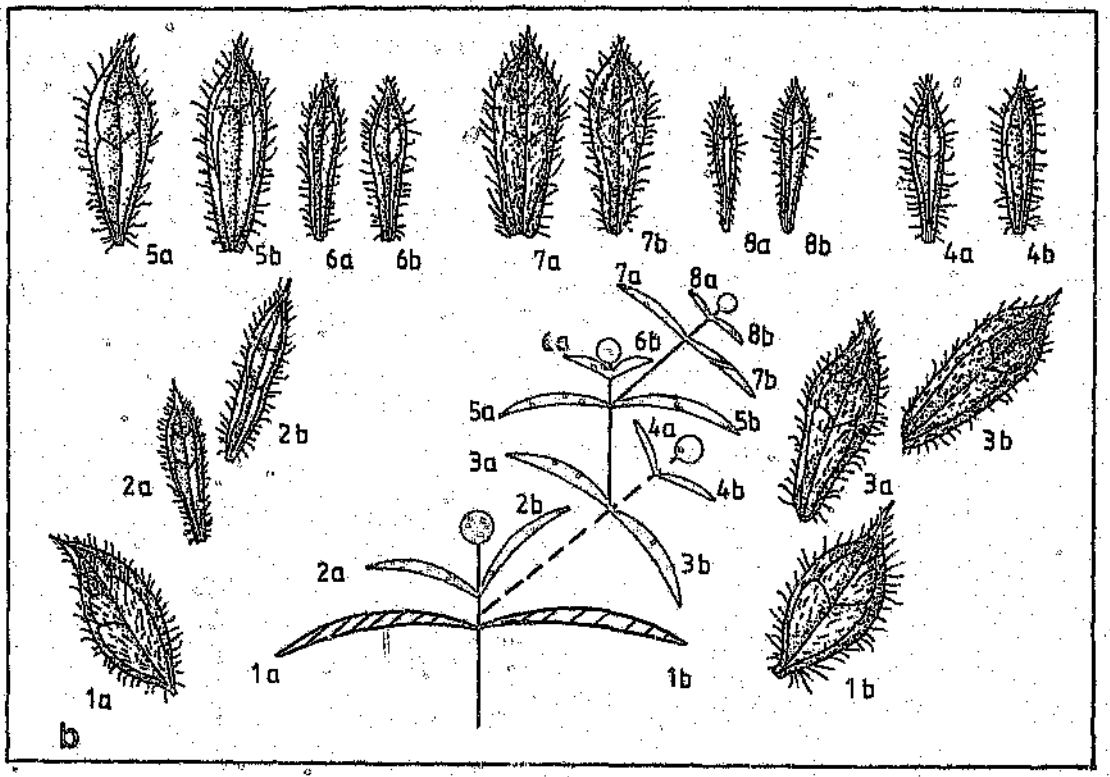

a
b

Figure 5.7: Inflorescence units exhibiting unusual structure.
Notation as for Figure 5.4, unless stated otherwise below.
a) Structure of inflorescence units in taxa such as *B. macrostegia* (Section *Barleria)* and *B. nitida* (Section *Barleriopsis)*. Each flower is subtended by two bracteoles (e.g. 1a and 1b), one of which is considerably smaller than the other. Voucher: *B. nitida*, van Steenis 10 408 (K).

b) Structure of inflorescence units in *B. biloba* (tentatively placed in Section *Barleria*). The inflorescence is subtended by a pair of modified bracts (hatched arcs). Each flower is subtended by two bracteoles (2a & b, 4a & b, 6a & b, 8a & b) and a bract (3a & b, 5a & b, 7a & b). Voucher: Sangkhachand 1060 (K).


4a
4b
2a
2b
3a
3b
1a
1b
a


5a
5b
6a
6b
7a
7b
8a
8b
4a
4b
2a
2b
1a
1b
3a
3b
b

Barleria, it seems likely that evolutionary advancement in the structure of inflorescence units has proceeded in a number of directions from the basal form (i.e. a compound dichasium). In one possible line of development, the first step in the transformation series involves successive suppression of one bud at each node after the initial formation of a compound dichasium. If the activity of buds lower down in the inflorescence is suppressed, the formation of monochasial cymes is eventually achieved (see Figure 5.8). Simple dichasial clusters could be derived by direct reduction from the compound dichasium or by condensation in units combining dichasial and monochasial elements. Likewise, scorpioid cymes could be derived by reduction from either of the types that combine dichasial and monochasial patterns (see Figure 5.8). Solitary flowers could be derived by extreme reduction of any of the other types of inflorescence unit (Figure 5.8). Thus, to avoid inferring hypotheses of mistaken similarity on the basis of common possession of solitary flowers, it is important to first establish the derivation of the solitary condition.

It seems reasonable to assume that evolution in the structure of the inflorescence units has followed a route of increasing reduction and simplification. In contrast, evolution in the arrangement of these units seems to have followed a line of increasing elaboration and aggregation into complex synflorescences. Terminal inflorescences have been regarded as primitive in the Acanthaceae (Baden, 1981; Balkwill & Getliffe Norris, 1988). However, as all inflorescences in the outgroup *Crabbea* are axillary, axillary arrangement of inflorescence units is considered basal in *Barleria*. In its least advanced state, the terminal synflorescence is a lax, open structure in which the internodes are only very slightly reduced if at all, and the leaves subtending the flowers are indistinguishable from the ordinary vegetative leaves (Figure 5.9). Contraction of the internodes gives rise to a more congested, "head-like" structure, such as that found in some forms of *B. prionitis*; in these cases the leaves subtending the flowers may show some morphological differentiation from the other vegetative leaves (Figure 5.9b). In other cases, the leaves supporting the flowers are highly modified and are quite unlike the vegetative leaves of the plant (see Figure 5.9c & d). The most highly evolved condition in this transformation series is that in which the last pair of leaves before the lowermost flowering nodes becomes morphologically modified so that they are clearly different from the ordinary leaves (Figure 5.9d). This condition characterises all members of Section *Stellatohirtae* and Section *Barleriopsis* and has sporadic occurrence

Figure 5.8: Putative evolutionary trends in the structure of inflorescence units in *Barleria*. Arrows between drawings indicate the possible routes along which structural change has proceeded. All notation as for Figure 5.4.

a) compound dichasium, primitive form; b) unit derived from a compound dichasium, but also showing monochasial growth; c) further reduction by suppression of one bud in the axils of the second and third flowers of the dichasium; d) simple dichasium; e) scorpioid cyme; f) scorpioid cyme with dimorphic, unilaterally arranged bracteoles; g) solitary flower.

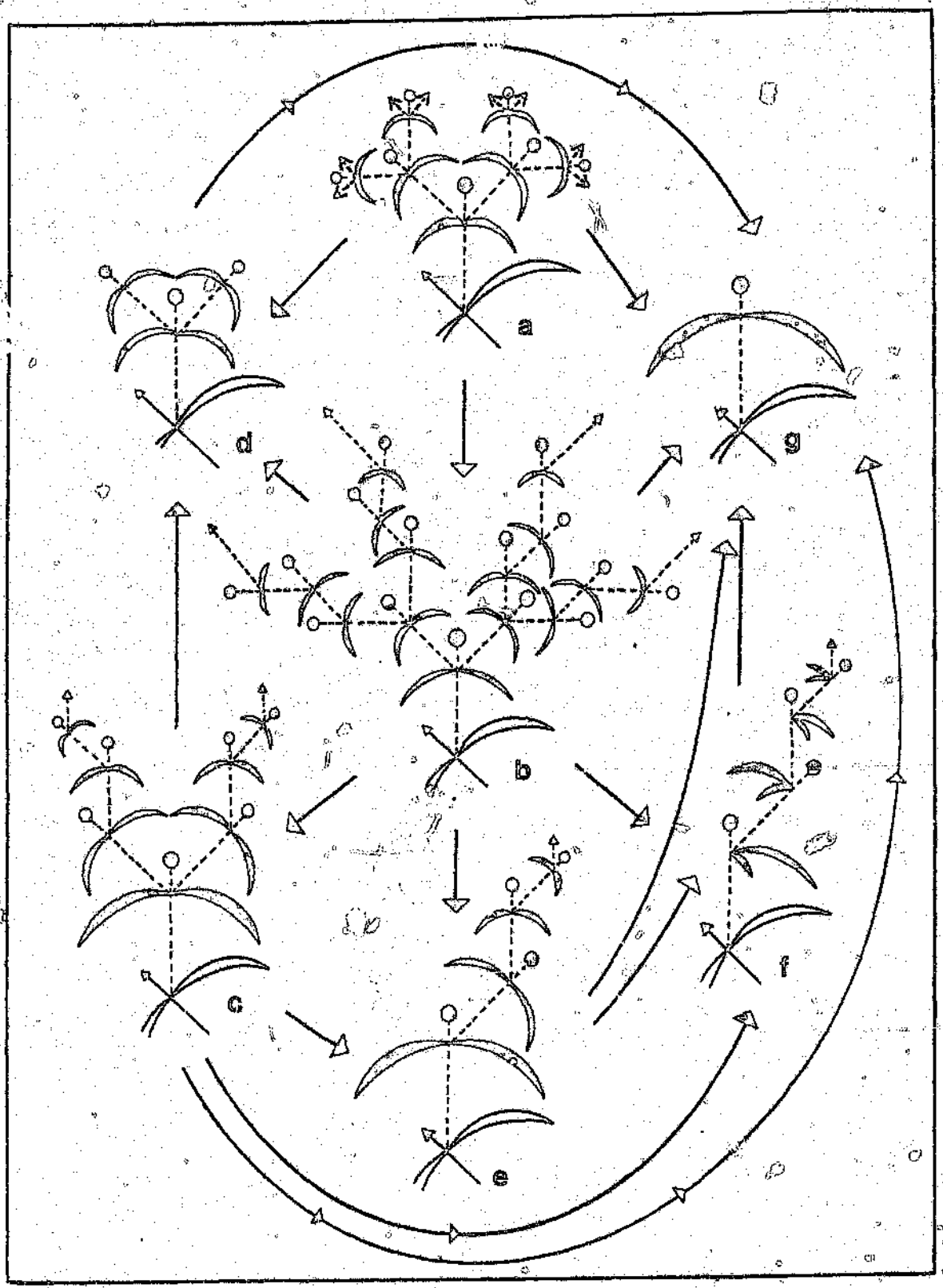

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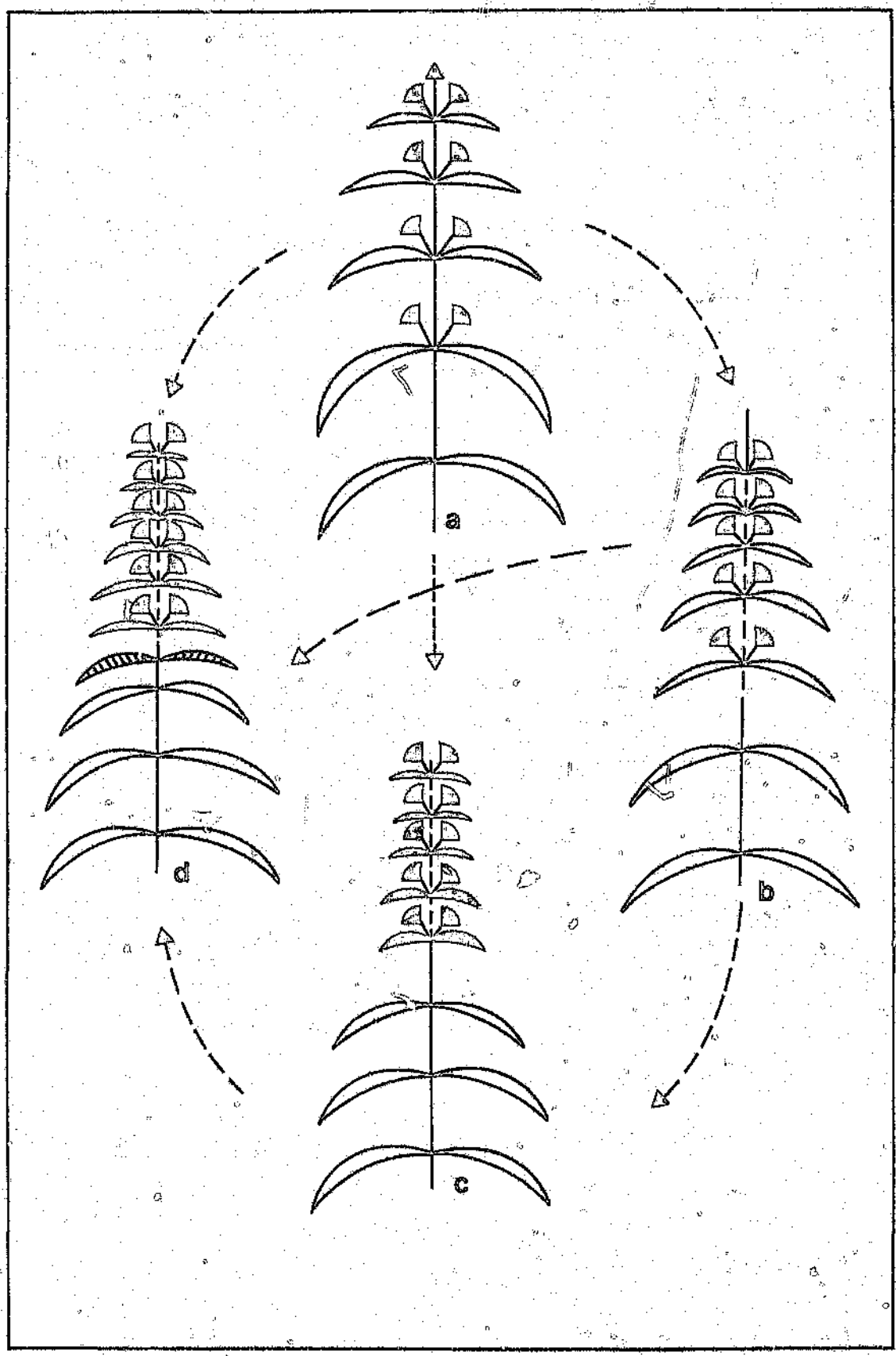
Figure 5.9: Possible routes along which formation of terminal synflorescences may proceed. ⚲ denote the position of single inflorescence units; black arcs denote modified inflorescence bracts; hatched arcs denote synflorescence bracts; open arcs denote vegetative leaves.

a) Lax terminal synflorescence in which the flowers are borne in all the upper leaf axils; b) Contraction of internodes at tip of stem leads to condensation of synflorescence and subtending leaves become slightly modified; c) subtending leaves become highly modified, forming specialised bracts; d) Last pair of leaves before the first flowering node becomes modified forming a pair of synflorescence bracts.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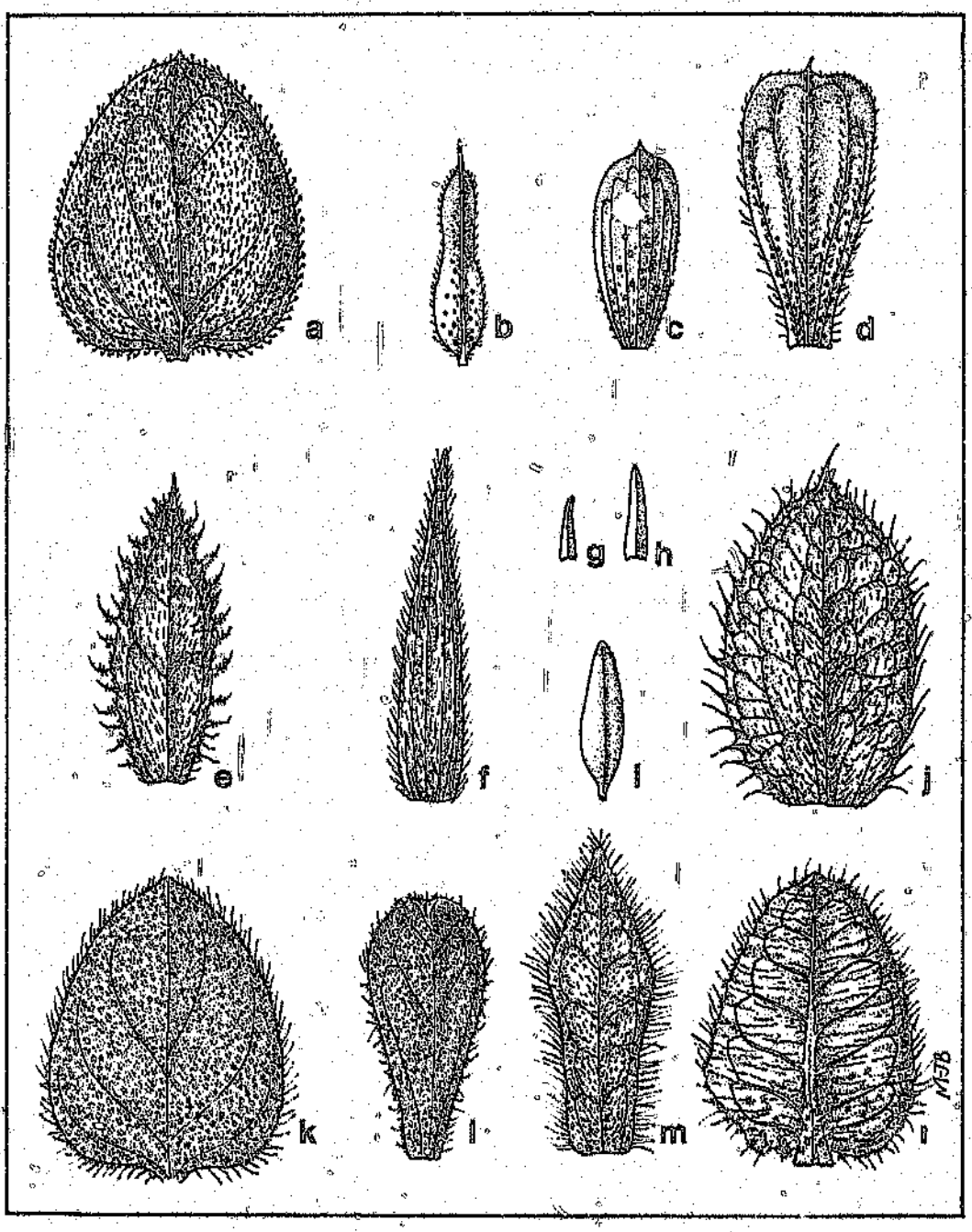
in other groups.

5.3.4 Bracts and Bracteoles

A prominent feature of the Acanthaceae is their bracteate inflorescences. Bracts and bracteoles have been extensively used as taxonomic characters in the family, but as earlier discussion should have indicated, the terms have been inconsistently applied by many authors. I have followed the definitions in Heywood (1981) for these terms and, in so doing, have used them in much the same way as Graham (1988) and Ensermu (1990). In *Barleria* a bract is a leaf or leaf-like structure that subtends an inflorescence unit. Bracteoles are paired leaf-like structures borne on the pedicel or peduncle of each flower, between the bract (or leaf) and the calyx of the flower.

Variation in the morphology of bracts in *Barleria* is illustrated in Figure 5.10. In the greater part of the genus (Sections *Barlerites*, *Somalia*, *Barlerianthus* and *Barleria*), the bracts are simply ordinary leaves in the axils of which an inflorescence unit is borne. In Sections *Stellatohirtae*, *Barleriopsis* and some members of Sections *Prionitis*, the bracts show varying degrees of modification from the ordinary vegetative leaves of the plant. In Section *Prionitis* a full range is found, from those species in which the bracts are hardly different from leaves to those in which the bracts are highly modified (see Figure 5.10 a - d). In those species in which the bracts differ greatly from the ordinary leaves, the calyx of each flower is usually obscured by the subtending bract. In Sections *Stellatohirtae* and *Barleriopsis*, the pair of leaves at the node immediately below the first node of the inflorescence becomes highly modified and constitutes a "synflorescence bract". In most species the bracts are herbaceous and entire. They are seldom spinous, although the apex may be sharply mucronate, particularly in Section *Prionitis* (see Figure 5.10b, c & d). In Section *Stellatohirtae* and parts of Section *Barleriopsis* the margins of the bracts may be shallowly and irregularly toothed (Figure 5.10 e & j). In most members of Section *Stellatohirtae* (Figure 5.10 k - n), the bracts are broadly ovate, sessile (or subsessile) and scarious with a very prominent pattern of reticulate venation. In addition, the bracts in this group are usually flushed dark purplish and are provided with stellate hairs. Large saucer-shaped glands of the type found on the leaves in Section *Prionitis* are found on the bracts in *B. rotundifolia*, *B. trispinosa*, *B.*

Figure 5.10: Variation in the morphology of modified floral bracts in *Barleria*. a) *B. crossandriformis* x 3 (Section *Prionitis*): Strey 6593 (PRE); b) *B. eranthemoides* x 4 (Section *Prionitis*): Ash 880 (MO); c) *B. norbertii* x 4 (Section *Prionitis*): Gentry 11 507 (MO); d) *B. senensis* x 4 (Section *Prionitis*): van Jaarsveld 1232 (PRE); e) *B. natalensis* x 1.5 (Section *Barleriopsis*): Galpin s.n. (NH); *B. monticola* x 1.5 (Section *Barleriopsis*): Pole Evans s.n. (PRE); g) *B. nutans* x 3 (Section *Barleriopsis*): Wight 777 (K); h) *B. courtallica* x 3 (Section *Barleriopsis*): Fischer s.n. (K); i) *B. conspicua* x 2.5 (Section *Prionitis*): Wallich s.n. (K); j) *B. micans* x 2 (Section *Barleriopsis*): Steyermark and Dunsterville 105796 (MO); k) *B. splendens* x 3 (Section *Stellatohirtae*): Burtt 2475 (K); l) *B. rogersii* x 2 (Section *Stellatohirtae*): Leistner 5579 (PRE); m) *B. albostellata* x 2 (Section *Stellatohirtae*): Gerstner 6066 (PRE); n) *B. albostellata* x 1 (Section *Stellatohirtae*): Gerstner 6066 (PRE).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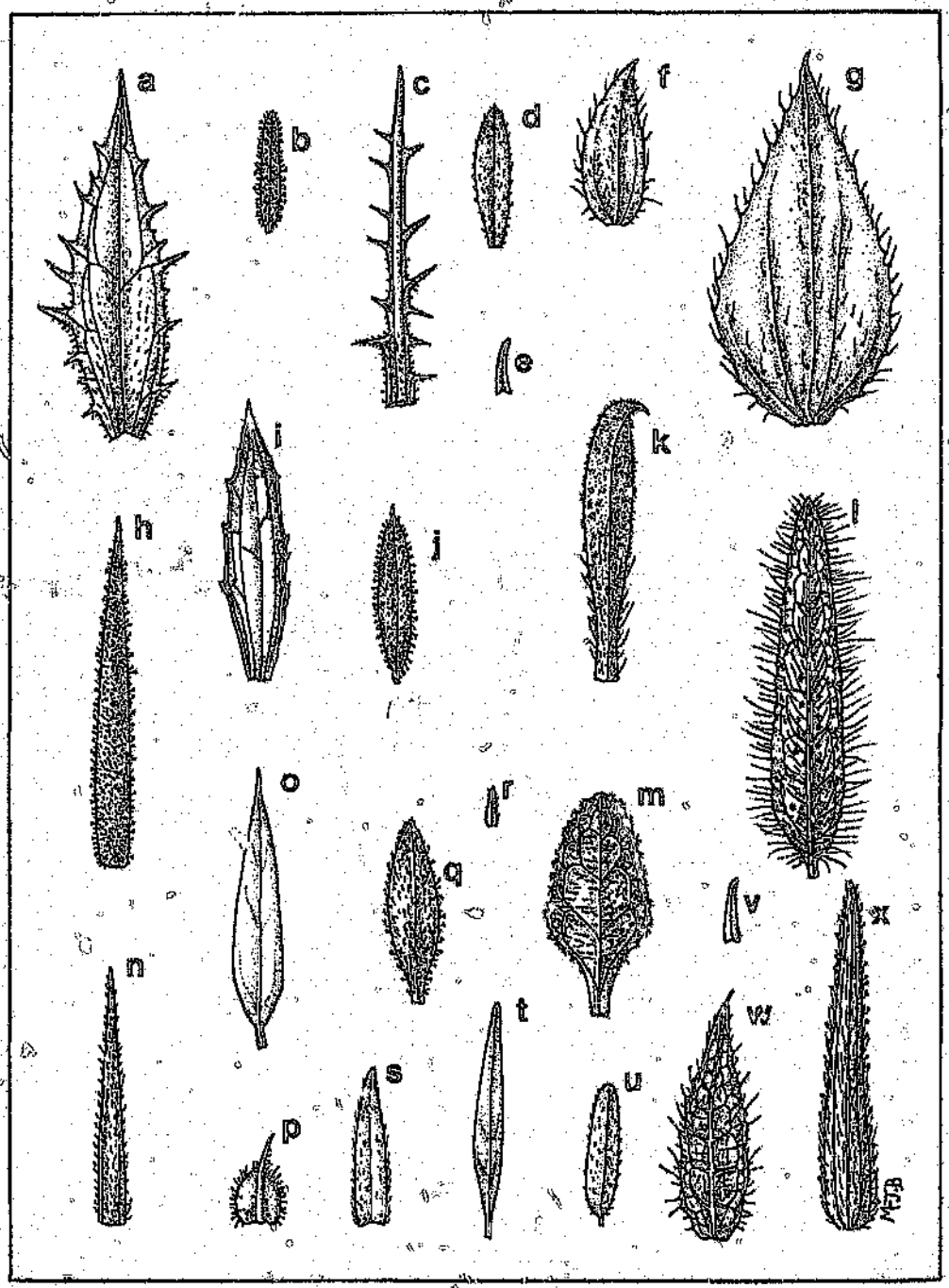
eranthemoides, B. senensis, B. randii, B. norbertii and B. setigera (Figure 5.10 b - d).

Each flower in an inflorescence unit is subtended by a pair of opposite bracteoles. The bracteoles may be predominantly herbaceous, entire and innocuous (Sections *Barlerites, Somalia, Barleriopsis, Stellatohirtae*| *Barlerianthus* and some members of Section *Barleria,* see Figure 5.11 b, d, e, j, q, r - v, x), scarious (some members of Section *Stellatohirtae*, e.g. Figure 5.11 l & m), or variously reduced and spinous (Section *Barleria*, Figure 5.11 c & h, and Section *Prionitis*, see Figure 5.11 n & p). The smallest bracteoles of the herbaceous variety are found in Section *Barlerites* (2 — 6 x 2 — 4 mm, see Figure 5.11 r). In this section, the bracteoles are triangular or linear-lanceolate structures, the largest forms occurring in *B. opaca* and *B. submollis* Lindau. Highly reduced bracteoles of the kind seen in Section *Barlerites*, also occur in some members of Section *Barleriopsis* such as *B. courtallica* (Figure 5.11 v). In species such as *B. argentea* (Section *Semalia*) the bracteoles are small (8 — 20 x 3 — 6 mm) and have the appearance of miniature leaves Figure 5.11 q, s - u). The largest bracteoles in the genus generally occur in Sections *Barlerianthus, Barleriopsis* and *Stellatohirtae*. In the latter, and in parts of Section *Barleriopsis*, the bracteoles are ovate, oblong or obovate and tend to be scarious, particularly with age (Figure 5.11 l, m & w). In many of the species in these groups the margins of the bracteoles are shallowly toothed, but are seldom spinous. In Section *Prionitis*, the bracteoles are stiffly spinous. In the majority of these species, most of the bracteole has been reduced to form a spine (Figure 5.11 n), but in a few species a narrow, leaf-like blade may be present (Figure 5.11 o & p). In *B. allaudii* Benoist, *B. decaryi* Benoist, *B. randii*, *B. senensis* and *B. trispinosa*, saucer-shaped glands are present near the bases of the bracteoles. In Section *Barleria*, the bracteoles are predominantly spinous, often with teeth or stiff spines along the margins (see Figure 5.11a, c, f, g, h, i). Variation in the kind of dentition on the margins, the presence or absence of a leaf-like blade and the curvature of the bracteoles provides useful characters for distinguishing between the species in this group.

The bracts and bracteoles in *Crabbea* are difficult to tell apart because of the extreme condensation of the inflorescences. The bract-like structures in *Crabbea* are not greatly differentiated from the leaves in that they have a relatively broad herbaceous blade (rarely scarious) that may be equipped with spinous projections along its margins. In *Barleria*, those bracts and bracteoles that show the greatest degree of modification from

Figure 5.11: Variation in the morphology of bracteoles in selected species of *Barleria*. a) *B. elegans* x 4 (Section *Barleria*): Rushworth 4 (SRGH); b) *B. heterotricha* x 5 (Section *Barleria*): Meeuse 9645 (SRGH); c) *B. merxmuelleri* x 2.5 (Section *Barleria*): Schmidt 1016 (WIND); d) *B. solitaria* x 2 (Section *Barleria*): Giess 9713 (WIND); e) *B. vincaefolia* x 3 (Section *Barleria*): du Puy and Rafamanantsoa MB187 (K); f) *B. macrostegia*, small bracteole of a pair, x 3 (Section *Barleria*): Mogg 35 677 (J); *B. macrostegia*, large bracteole of a pair, x 3: Mogg 35 677 (J); h) *B. bremekampii* x 2 (Section *Barleria*): Codd 5449 (PRE); i) *B. argillicola* x 2 (Section *Barleria*): Balkwill, Balkwill & Green 5948 (J); j) *B. fulvostellata* x 3 (Section *Barleria*): Bidgood, M asumbi & Vollesen 717 (K); k) *B. rogersii* x 3 (Section *Stellatohirtae*): Balkwill & Balkwill 6353 (J); l) *B. albostellata* x 2 (Section *Stellatohirtae*): Gerstner 6066 (PRE); m) *B. stellato-tomentosa* x 2 (Section *Stellatohirtae*): Welwitsch 5165 (K); n) *B. holubii* x 2 (Section *Prionitis*): Miller 2138 (SRGH); o) *B. marginata* x 1 (Section *Prionitis*): Peter 31 728 (K); p) *B. allaudii* x 3 (Section *Prionitis*): Phillipson 2673 (K); q) *B. albi-pilosa* x 3.5 (Section *Somalia*): Walter 412 (PRE); r) *B. scindens* x 2 (Section *Barlerites*): Balkwill & Balkwill 4308 (J); s) *B. lugardii* x 6 (Section *Somalia*): Leach 10595 (PRE); t) *B. montana* x 1 (Section *Barlerianthus*): Wight 2214 (K); u) *B. cucherana* x 3 (Section *Somalia*): Wood s/72/38 (K); v) *B. courtallica* x 2 (Section *Barleriopsis*): Fischer s.n. (K); w) *B. micans* x 2 (Section *Barleriopsis*): Steyermark & Dunsterville 105796 (MO); x) *B. monticola* x 3 (Section *Barleriopsis*): Botha & Coetzee 1578 (PRE).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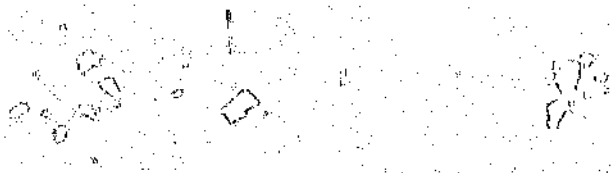
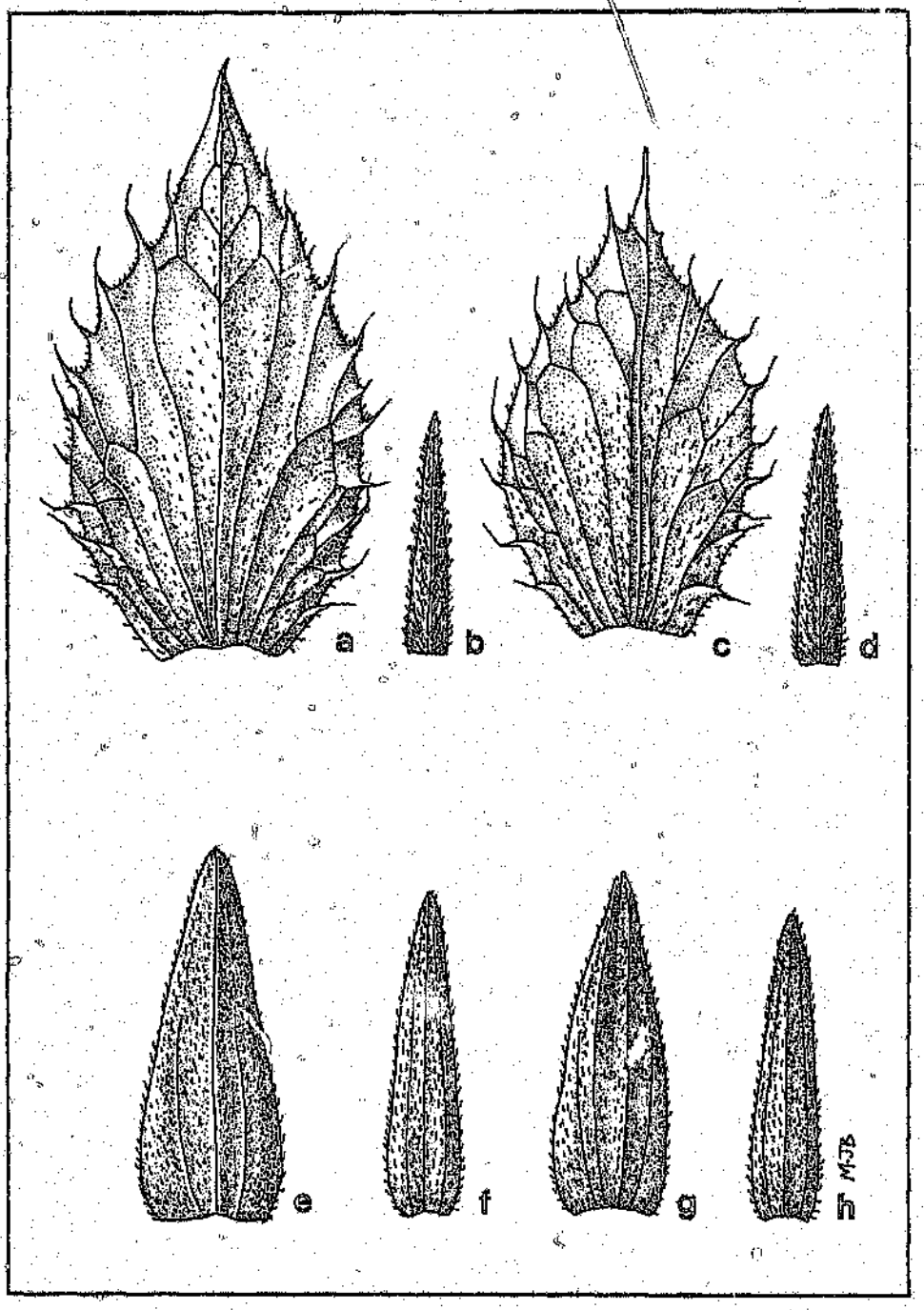


Figure 5.12: Calyx morphology in *Barleria*.

a) - d) calyx in which the outer lobes (a & c) differ markedly from the inner lobes (b & d), all x 9: a) posticous outer lobe; c) anticous outer lobe; Voucher: *B. elegans* (Section *Barleria*), Rushworth 4 (SRGH).

e) - f) calyx in which outer lobes (e & g) do not differ markedly from the inner lobes (f & h), all x 9: e) posticous outer lobe; g) anticous outer lobe; Voucher: *B. prionitis* (Section *Prionitis*), Giess 3671 (PRE).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the ordinary vegetative leaves, either by elaboration or reduction, are considered to represent the apomorphic condition. Those species in which the bracteoles are entirely reduced to spines are considered to be the most advanced in the genus and occur in parts of Sections *Barleria* and *Barleriopsis*.

5.3.5. Floral Morphology

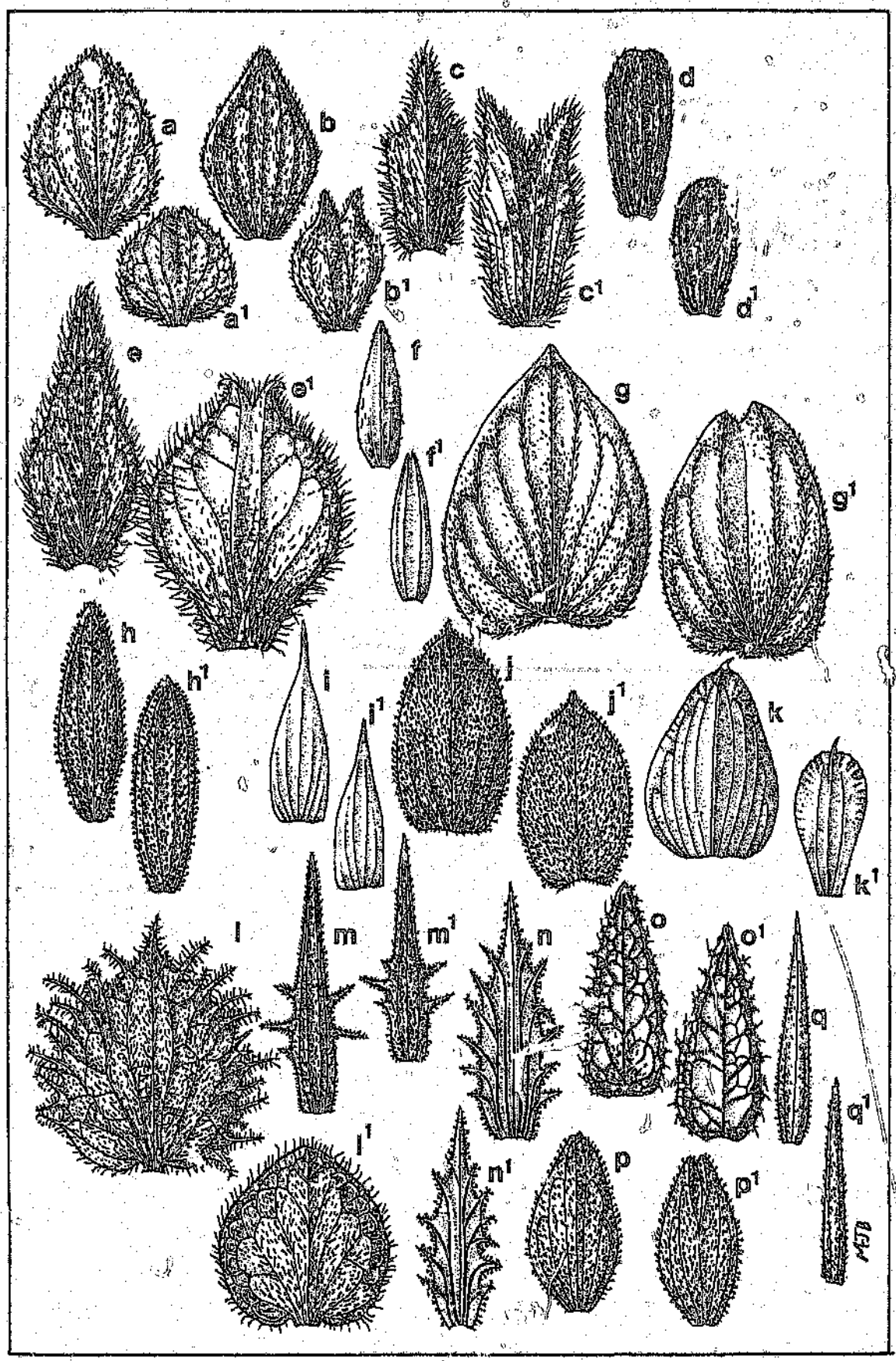
5.3.5.1 Calyx

The morphology of the calyx provides one of the important diagnostic characters for *Barleria*. It comprises four lobes arranged as two outer and two inner segments, fused shortly at the base to form a shallow tube. The four-lobed condition is derived from a five-lobed state. The anticous and posticous calyx lobes are outermost and are usually much larger than the inner, lateral lobes. The anticous lobe comprises two fused sepals. The anticous and posticous lobes usually differ markedly from the inner lobes in size and various aspects of morphology, although within Section *Prionitis* these differences are often less pronounced (see Figure 5.12). The form of the inner lobes is fairly consistent throughout the genus, although there are minor variations in some features, particularly size and pubescence. The outer lobes, however, show considerable variation in features such as size, shape, pubescence, colour, texture, venation, dentition of the margins and spinescence of the tip (see Figure 5.13). Thus, although the basic morphology of the calyx is consistent throughout the genus, variation in morphology of the outer lobes provides several characters that can be used to distinguish closely related species from each other and to characterise certain infra-generic groups.

In Sections *Barlerianthus*, and *Somalia*, the outer calyx lobes are entire, herbaceous and innocuous (i.e. lacking both dentition on the margins and a spinous tip, see Figure 5.13 f, g, h). In these taxa the derivation of the 4-lobed calyx from a 5-lobed condition is clearly detectable, as the anticous calyx lobe is always bifid, even if only shortly so (Figure 5.13 f - h). This feature also has sporadic occurrence in other parts of the genus (Figure 5.13 a - c, e). In Sections *Barlerianthus* and *Somalia* the outer lobes have three or more prominent veins from the base, but the tertiary venation does not form a prominent reticulate pattern (Figure 5.13 g, h). Within these groups the calyx can either

Figure 5.13: Variation in the morphology of anticous and posticous calyx lobes in selected species of *Barleria*. Notation used: a = posticous lobe, a' = anticous lobe etc...

a) *B. scindens* x 2 (Section *Barlerites*): Fanshawe 7196 (SRGH); b) *B. ventricosa* x 3 (Section *Barlerites*): Friis, Getachew Aweki, Rasmussen & Vollesen 1714 (K); c) *B. albostellata* x 2 (Section *Stellatohirtae*): Balkwill, Balkwill, Geseli & Melville 5811 (J); d) *B. descampsii* x 1 (Section *Stellatohirtae*): Fanshawe 11 993 (K); e) *B. rogersii* x 3 (Section *Stellatohirtae*): Balkwill & Balkwill 6353 (J); f) *B. aucherana* x 3 (Section *Somalia*): Wood s/72/38 (K); g) *B. mackenii* x 3 (Section *Somalia*): Mogg 17268 (PRE); h) *B. grandis* x 1 (Section *Barlerianthus*): Scott 223 (K); i) *B. cuspidata* x 2 (Section *Somalia*): Wight 2215 (K); j) *B. crossandriformis* x 3 (Section *Prionitis*): Balkwill & Balkwill 6340 (J); k) *B. rotundifolia* x 3.5 (Section *Prionitis*): Balkwill, Balkwill, Barlow-Kearsley, Geseli & Cron 6144 (J); l) *B. lichtensteiniana* x 2.5 (Section *Barleria*): Giess, Volk & Bleissner 7115 (WIND); m) *B. hillcoatiae* x 2 (Section *Barleria*): Wood 3083 (K); n) *B. meeuseana* x 3 (Section *Barleria*): le Roux & Jankowitz 1488 (J); o) *B. heterotricha* x 5 (Section *Barleria*): Meeuse 9654 (SRGH); p) *B. vincaefolia* x 2 (Section *Barleria*): du Puy & Rafamantantsoa MB187 (K); q) *B. holubii* x 4 (Section *Prionitis*): Miller 2138 (SRGH).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be very large (30 x 20 mm as in *B. mackenii* Hook.f, Section *Somalia*, Figure 5.13 g) or very small (10 x 3 mm, as in *B. argentea*, Section *Somalia*, Figure 5.13 f). In Section *Prionitis* the calyx lobes are herbaceous but tend to be rather thickly textured and may become coriaceous. The margins of the lobes are usually entire, but the apex of the anticous lobe at least (and often of the posticous lobe too) is stiffly spinous (Figure 5.13 i - k). In some species within this group, such as *B. holubii* C.B. Cl. and *B. her*, each calyx lobe is completely reduced to a stiff spine (Figure 5.13 q). In subgenus *Barleria* and Sections *Barlerites* and *Stellatohirtae* the margins of the outer lobes may be entire, but more commonly are dentate (Figure 5.13 a, c, e, o) or equipped with stiff spines (Figures 5.13 l, m, n). They may be herbaceous, but in some groups are characteristically scarious. In most of the species exhibiting the latter feature, the calyx is particularly distinctive due to the presence of conspicuous reticulate venation (Figure 5.13 l & o). Differences in the pubescence of the outer calyx lobes provide extremely useful characters at the species level.

The calyx in *Crabbea* is evenly five-lobed, a common condition in many Acanthaceae. The calyx lobes are herbaceous, linear-lanceolate structures without conspicuous venation and lacking dentition along the margins. Thus the plesiomorphous condition in *Barleria* is that in which the calyx lobes are herbaceous and entire, without conspicuous reticulate venation. There is no evidence to suggest that the various modifications of the calyx seen in *Barleria* can be placed in a single, linear transformation series. It seems much more probable that a number of different lines of modification have radiated from the plesiomorphous condition. The trends that can be traced are: increased fusion of the two sepals comprising the anticous lobe; development of serrate or spinous margins; a change in texture from herbaceous to scarious or coriaceous; development of a prominent pattern of reticulate venation and reduction of the calyx lobes to spines. Any particular form of the calyx may thus combine a number of plesiomorphic and apomorphic states for these characters.

5.3.5.2 Corolla

a. Morphology

The morphology of the corolla is highly variable in *Barleria*, possibly due to rapid co-evolution with a wide variety of pollinators. If the basic form of the corolla is examined

a number of trends are observed including: reduction in the number of corolla lobes from five to four; changes in the arrangement of the corolla lobes leading to increased zygomorphy, and changes in the relative width and length of the upper and lower portions of the corolla tubes. These changes in the relative lengths of the upper and lower tubes have important implications for the pollination biology of the plants.

The least advanced corolla form in the genus is found in species such as *B. morrisslana* R. Barnes & C.E.C. Fischer (Section *Barleria*) and *B. monticola* (Section *Barleriopsis*). In these species the corolla is only weakly zygomorphic; the five corolla lobes are similar to each other in shape and size, although the two adaxial lobes are slightly smaller than the lower three lobes. The adaxial lobes form the upper "lip" (Figure 5.14.a; Plate 5.6 a). The corolla tube is divided into a short lower, cylindrical portion and an inflated upper portion. From this relatively unspecialised form a number of lines of development can be traced (see Figure 5.14). The distinction between the upper and lower portions of the corolla tube is made at the point of insertion of the stamens on the corolla and can be identified by a sudden, even if slight, narrowing of the tube (see Figure 5.14). In most species, the lower tube remains narrowly cylindrical, although in species such as *B. monticola*, this tube may be fairly broad and shallow (Figure 5.14 a). The upper tube shows considerable variation in width; it may be narrowly tubular (e.g. *B. acanthoides* Vahl, *B. heterotricha* C.B. Cl., *B. pilosa*, see Figure 5.14 f; Plate 5.7 a & c), gradually inflated (e.g. *B. greenii* M-J.& K. Balkwill, Plate 5.6 c & d) or broadly sub-campanulate or campanulate (Figure 5.14 c & d; Plate 5.6 b). In addition, the relative lengths of the upper and lower corolla tubes may vary considerably. In many species the upper and lower tubes are of approximately equal length (Figure 5.14 c; Plate 5.6 b); in most members of Section *Barlerites* the lower tube is extremely short relative to the upper (Figure 5.14 l), and in species such as *B. heterotricha*, the upper tube is considerably shorter than the lower (Figure 5.14 f). These differences have important implications for the comparison of corolla forms in the genus, especially if hypotheses of similarity are inferred on the basis of corolla length. Superficially the corollas of *B. acanthoides* and *B. heterotricha* may appear to be similar, as both are extremely long and are more or less uniformly narrow throughout their length. However, in the latter it is the lower tube which has undergone extension and in *B. acanthoides* both the upper and lower tubes have increased in length.

Figure 5.14: Diagrammatic summary of variation in corolla morphology in *Barleria*. In all cases M denotes the median abaxial corolla lobe and s denotes the point of insertion of the stamens on the corolla tube.

a) *B. monticola* (Section *Barleriopsis*): Balkwill & Balkwill 5418 (J); b) *B. irritans* (Section *Barleria*): Mauve 5238 (J); c) *B. repens* (Section *Barleria*): Henrico s.n. (NBG); d) *B. obtusa* (Section *Barleria*): Balkwill 668 (NU); e) *B. elegans* (Section *Barleria*): Rushworth 4 (SRGH); f) *B. heterotricha* (Section *Barleria*): Balkwill & Balkwill 6321 (J); g) *B. bremekampii* (Section *Barleria*): Balkwill & Balkwill 5830 (J); h) *B. lancifolia* (Section *Somalia*): Balkwill & Balkwill 4302 (J); *B. lugardii* (Section *Somalia*): Leach 10595 (PRE); j) *B. popovii* (Section *Barleria*): Popov GP/SO/315 (BM); k) *B. pretoriensis* (Section *Somalia*): Obermeyer 943 (SAM); l) *B. lukwangulensis* (Section *Barlerites*): Congdon 209 (K); m) *B. eranthemoides* (Section *Prionitis*): Ash 880 (MO); n) *B. albostellata* (Section *Stellatohirtae*): Balkwill, Balkwill, Gesell & Melville 5811 (J); o) *B. randii* (Section *Prionitis*): Eyles 88 (SRGH); p) *B. argentea* (Section *Somalia*): Thulin & Warfa 4663 (K); q) *B. rotundifolia* (Section *Prionitis*): Buitendag 444 (PRE).

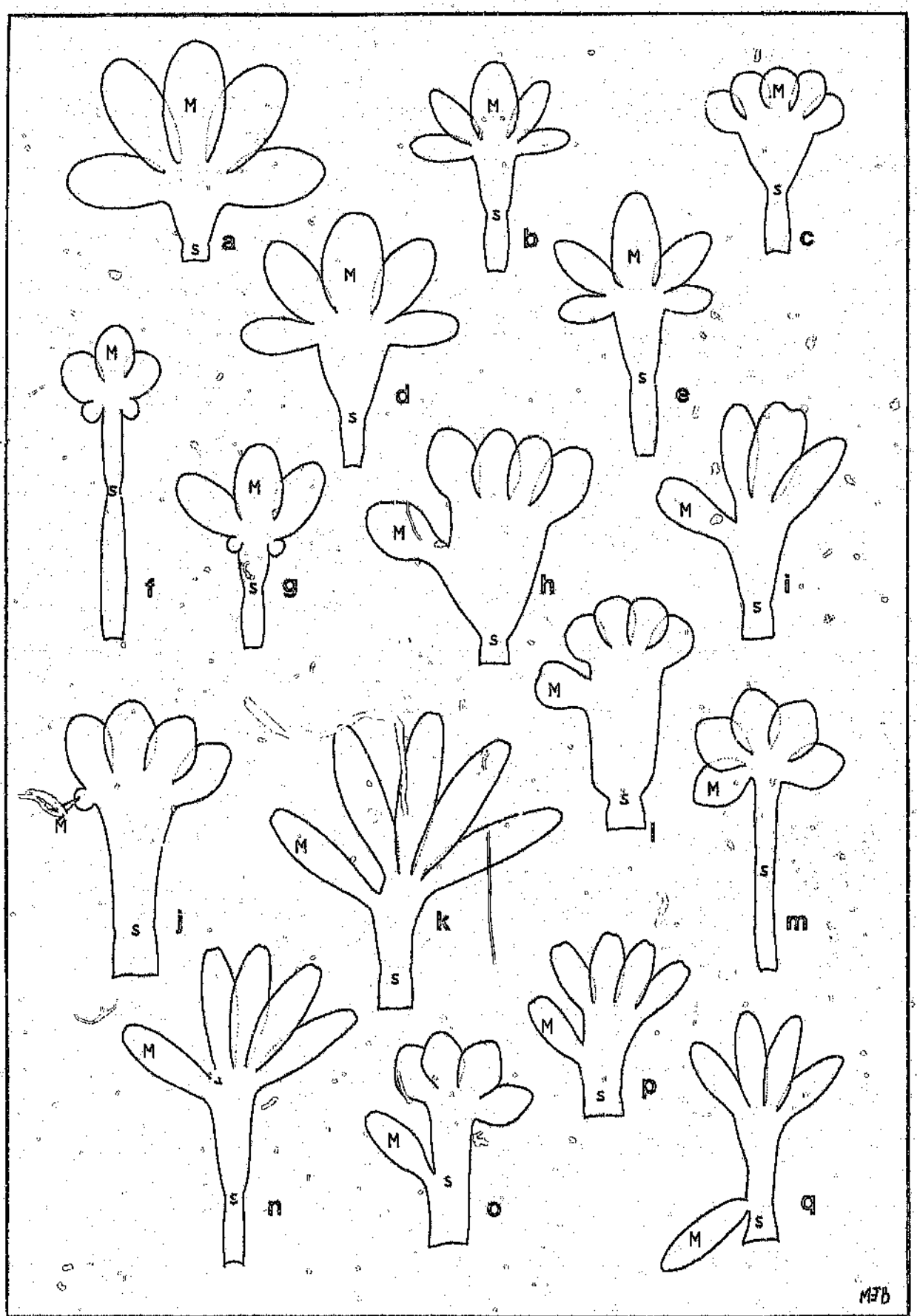
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Plate 5.6: Corolla morphology in selected species of Sections *Barleria* and *Barleriopsis*. a) *B. monticola* (Section *Barleriopsis*) showing "typical" 2+3 configuration of corolla lobes; b) *B. repens* (Section *Barleria*) with narrowly cylindrical lower tube and inflated upper tube, lower and upper tubes of approximately equal length; c) *B. greenii* (Section *Barleria*), lateral view showing median abaxial lobe split from corolla for slightly greater distance than other lobes; d) *B. greenii* (Section *Barleria*), frontal view to show the shift from 2+3 configuration to 4+1 configuration of corolla lobes.

a
b
c
d

Plate 5.7: Variation in corolla morphology in selected representatives of Section *Barleria*.

a) *B. heterotricha*, showing upper two lobes reduced relative to lower three, corolla tube uniformly narrow throughout and more than twice as long as longest lobe; b) *B. sp. nov.* nr. *heterotricha*, showing increased reduction of upper lobes relative to lower lobes; c) *B. argillicola*, showing upper two lobes only slightly smaller than lower lobes, corolla tube uniformly narrow throughout and only twice as long as longest lobe.

a
b
c

Plate 5.8: Corolla morphology in selected representatives of Section *Somalia*.
a) *B. meyerlana*, showing "typical" 4+1 corolla morphology of Section *Somalia*, upper lobes with streaks of contrasting coloration. b) *B. pretoriensis*, showing 4+1 configuration of lobes and narrow corolla tube.

a
b

There are a number of ways in which the arrangement and form of the corolla lobes can be modified. In *Crabbea* and the more primitive forms in *Barleria*, the five lobes of the corolla are subsimilar. Two slightly smaller lobes are in the upper position and three slightly broader lobes constitute the lower limb. This arrangement is referred to here as the "2 + 3" configuration (Plate 5.6 a). Corollas that conform to the basic "2 + 3" configuration predominate in Subgenus *Barleria*. One of the trends that can be traced in this line is that of increased differentiation between the upper and lower lobes (Plate 5.7). This trend is carried to an extreme in taxa such as *B. bremekampii* and *B. heterotricha* in which the two upper lobes are very greatly reduced relative to the lower ones (Figure 5.14 f & g; Plate 5.7). The second trend that can be traced is the shift from a "2 + 3" configuration to one in which four lobes comprise the upper lip, and only one (the median abaxial lobe) constitutes the lower lip or limb (Figure 5.14 h, i, k, l, n - q; Plates 5.6 d and 5.8 a & b). The latter arrangement is referred to as a "4 + 1" configuration and it predominates in Subgenus *Prionitis* (see Figure 5.14 o & q; Plate 5.9 d & e).

In taxa with a "4 + 1" configuration of lobes, the lower lip is usually split away from the corolla tube for some of its length (Figure 5.14; Plates 5.8 and 5.9). There is a trend towards increasing separation of the median abaxial lobe (i.e. the lower lip) from the remainder of the corolla such that the corollas become increasingly zygomorphic (Plate 5.9). A consequence of this trend is that the corolla tube is open on its abaxial side for part of its length. In many of the species the closed part of the corolla tube is uniformly narrow, or might be only very slightly inflated in the upper portion (Figure 5.14 i, k, n, p; Plate 5.8). In Section *Barleritcs* and parts of Sections *Barlerianthus* and *Somalia*, the upper part of the tube may be very broadly inflated (Figure 5.14 h & l; Plate 5.9 b). The overall length of the corolla in species showing this configuration is variable; those species showing the greatest separation of the lower lip often have the shortest corolla tubes and show the greatest degree of zygomorphy (e.g. *B. rotundifolia*, Figure 5.14 q; Plate 5.9 d & e). An exception to the general trends outlined above is found in a group of species within Section *Prionitis*. In these species, such as *B. eranthemoides*, the corolla tube is long and narrow and is closed throughout its length; the median abaxial lobe is not separated from the remainder of the corolla but is partially fused to the upper lip (Figure 5.14m). A very unusual corolla form occurs in *B. popovii* Verdcourt (tentatively placed in Section *Somalia*). The corolla tube is long and narrow

Plate 5.9: Corolla morphology in selected representatives of Sections *Somalia*, *Stellatohirtae* and *Prionitis*.

a) *B. sp. nov.* nr. *B. angustiloba* (Section *Somalia*), showing spots of contrasting coloration on four lobes of the upper lip; b) *B. lancifolia* (Section *Somalia*), showing lobes in 4+1 configuration, upper tube more than twice as long as lower tube, upper tube broadly inflated; c) *B. albostellata* (Section *Stellatohirtae*), with corolla tube more or less uniformly narrow throughout; d) *B. prionitis* (Section *Prionitis*), showing strongly zygomorphic corolla with yellow coloration, lobes in 4+1 configuration; e) *B. rotundifolia*, showing yellow coloration, strongly developed zygomorphy, median abaxial lobe split away from remainder of corolla for almost the entire length, tubular part very short.

a
b
c
d

(upper tube equal to the lower tube); the lobes are in the "4 + 1" configuration, but the median abaxial lobe is extremely reduced and is not noticeably separated from the corolla tube (Figure 5.14 j).

In most species of *Barleria* the corolla comprises five lobes. In *B. lugardii* C.B. Cl. and *B. rehmannii* C.B.Cl. (both Section *Somalia*), the two adaxial lobes are fused giving rise to a four lobed corolla (Figure 5.14 l). This character state has a very restricted distribution within the genus, but is constant for those species in which it occurs. It represents an apomorphic condition.

b. Pigmentation:

Previous classifications have used differences in corolla colour to characterise particular infra-generic groups; Section *Prionitis* of both Clarke and Obermeijer (*l. c.*) was characterised by yellow flowers, and all the other sections by the absence of yellow flowers. Within the latter group, flowers could be red, blue, lilac, purple or white (see Plate 5.6). This study, however, has revealed a high level of colour polymorphism within certain infra-generic groups of *Barleria*; "yellow" flowers occur in Sections *Barleriopsis*, *Somalia* and *Prionitis*. Furthermore, colour polymorphism occurs at the infra-specific level within at least two species of *Barleria*; *B. cristata* L. has white, pink and purple forms (Grant, 1955; Raman & Kesavan, 1964) and in *B. ovata* populations with yellow, white, pink and purple flowers are known. Furthermore, yellow and pink-flowered forms occur in the same populations of this species. A wide range of corolla colours has been reported within *Justicia* (Graham, 1988), *Ruellia* (Bloom, 1976; Cadman, 1987), *Dyschoriste* (Vollesen, pers. comm.) and *Sclerochiton* (Vollesen, 1990). Few attempts have been made to investigate the chemical basis of such polymorphism in these genera. Bloom (1976) investigated floral flavonoid patterns in red and blue-flowered, New World species of *Ruellia* and found that two different flavonoid sets were present, indicating a basic division within the genus. Interestingly, the two groups also possess disparate floral morphology. A broad-scale survey of floral flavonoids in *Barleria* was well beyond the scope of this study, however, an attempt was made to establish the chemical basis for yellow flowers in different parts of the genus. The results of a preliminary phytochemical investigation conducted in collaboration with Professor B-E. van Wyk (Rand Afrikaans University) have indicated that *Barleria* is chemically very diverse; the spectra of the species studied show massive diversification

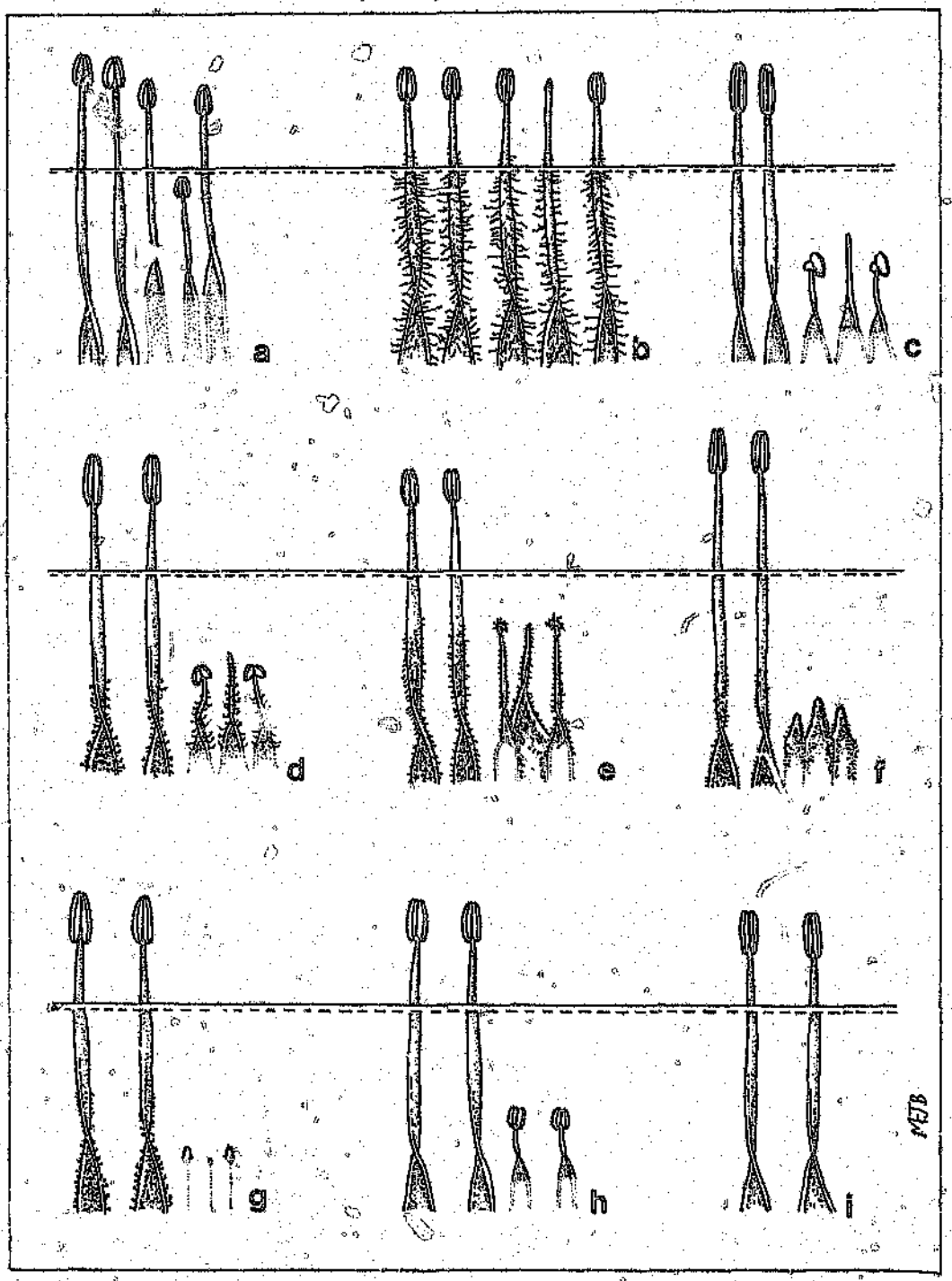
of flavonoids and a wide range of anthocyanin pigments including a number of chemically unusual and unstable compounds.

The flavonoid and anthocyanin composition of *B. ovata* (butter-yellow flowers), *B. ovata* (purple flowers) and *B. rotundifolia* (orange-yellow flowers) was investigated. The spectra obtained for these three taxa differed widely with respect to both the anthocyanins and other flavonoid pigments. In *B. ovata* (butter-yellow form) anthocyanins are totally absent; the yellow flower colour is due to the presence of a number of other flavonoid pigments (probably flavonols, but unidentified at this stage). In *B. rotundifolia* (with orange-yellow flowers) the pigmentation is due to the presence of high concentrations of a very large number of flavonoids (probably flavonols), which, although unidentified at present, seem to differ from those in *B. ovata* (yellow), as the spectra for these two taxa show very little correspondence. Furthermore, in *B. rotundifolia* the yellow pigmentation is due to the masking effect of the yellow flavonoids over the anthocyanins that are present. Yellow flower colour in *B. ovata* and *B. rotundifolia* is, thus, not homologous. The anthocyanin pigments in *B. ovata* (purple) and *B. rotundifolia* are not the same. In *B. rotundifolia*, cyanidin and delphinidin glycosides are present as major compounds with a number of esters of these present as minor pigments. Within *B. ovata* (purple), malvidin-3,5-diglucoside is present as a major pigment, with glycosides of peonidin, petunidin, cyanidin and an unknown ester (probably of petunidin - *fide* van Wyk, pers. comm.) as minor pigments. Thus, not only do the spectra of *B. ovata* and *B. rotundifolia* differ greatly, but even within *B. ovata* (i.e. in yellow and purple forms) the spectra are not entirely similar.

It is unusual to find such chemical heterogeneity within a single genus (van Wyk, pers. comm.); it would be interesting to investigate the possible relationship between chemical heterogeneity and diversification in floral morphology within *Barleria*. Clearly, a more detailed investigation of flavonoid pigments in *Barleria* will prove to be worthwhile and may cast interesting light on interpretations of phylogenetic relationships within the genus. The chemical data obtained thus far were not included in the cladistic analyses due to their preliminary nature (i.e. only a small number of species has been investigated and some of the compounds have not been identified).

Figure 5.15: Variation in the composition of the androecium in selected representatives of *Barleria*. In all cases the two stamens shown on the left hand side of the drawing are the two abaxial stamens. The second stamen or staminode from the right is the median adaxial stamen.

a) *B. morrisiana* (Section *Barleria*): Barnes 2122 (K); b) *B. ovata* (Section *Barleriopsis*): Balkwill, Balkwill & Green 6261 (J); c) *B. rigida* (Section *Barleria*): Herman 561 (PRE); d) *B. jubata* (Section *Barleria*): Pearson 9895 (BOL); e) *B. lukwangulensis* (Section *Barlerites*): Adelyser 163 (K); f) *B. dolomiticola* (Section *Somalia*): Moffett 1084 (PRE); g) *B. wilmsiana* (Section *Somalia*): Balkwill, Balkwill & Kidger 8086 (J); h) *B. crossandriformis* (Section *Prionitis*): Balkwill 1489 (NU); i) *B. hildebrandtii* (Section *Stellatohirtae*): Gilbert, Ensermu & Vollesen 7723 (K).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5.3.5.3. Androecium

In most genera of the Acanthaceae the androecium comprises either four or two stamens and may include a number of staminodes. It is unusual in this family for five parts to be present in the androecium, as occurs in *Barleria*. Variation in the composition of the androecium in *Barleria* is bewildering. In all species the stamens (including those modified to form staminodes) are epipetalous. The filaments are twisted through 180 degrees just above their point of fusion with the corolla. The filaments also cross over each other at this point. This presumably has functional significance for the pollination biology of these plants (Figure 5.15).

In *Barleria* the androecium may comprise five, four or two parts. Some of these parts are fertile and others are variously reduced to form staminodes (see Figure 5.15 for variations). In all species the two stamens attached on either side of the median abaxial corolla lobe (hereafter referred to as the abaxial stamens) are fertile and have bithecous, muticous anthers with parallel anther thecae. In *B. morrissiana* (Section *Barleria*) all five stamens are fertile and may be of approximately equal length, or the fifth stamen may be slightly shorter than the others (Figure 5.15 a). This represents the plesiomorphic state for composition of the androecium. Evolutionary advancement involves the progressive reduction and eventual loss of the fifth, adaxial stamen. This is usually coupled with reduction of the two lateral stamens to staminodes. Alternatively, the adaxial and lateral stamens may undergo more or less simultaneous reduction until only two stamens are present in the androecium (Figure 5.15 i). The presence of two stamens only is the most advanced condition for this character (composition of the androecium).

The androecium consists of five parts in all members of Subgenus *Barleria* and Section *Barlerites*. In *B. ovata* (Section *Barleriopsis*) four of the stamens are fertile and are more or less equally well-developed; the fifth stamen is about as long as the others but does not bear anthers (Figure 5.15 b). In most of the other species within these groups the lateral and adaxial stamens are greatly reduced, but the lateral staminodes still bear anthers or anther rudiments. The contribution these staminodes make to pollen production is unclear; in some species pollen is present in the reduced anthers of the staminodes, but the viability of this pollen has not been tested. The adaxial staminode

lacks anther rudiments and is often reduced to a fine, hair-like filament (Figure 5.15 c - e). In Sections *Barlerianthus* and *Somalia*, the lateral and adaxial stamens are equally reduced to staminodes bearing no anther rudiments (Figure 5.15 f). In occasional species within these groups (e.g. *B. wilmsiana* Lindau, Section *Somalia*), the adaxial staminode is lost entirely (Figure 5.15 g). In Sections *Prionitis* and *Stellatohirtae* the adaxial stamen is usually absent and the lateral stamens are reduced to short staminodes bearing bithecous anthers (Figure 5.15 h). Some species within Section *Stellatohirtae* (e.g. *B. stelligera)* show complete loss of all three staminodes, so that the androecium consists only of the two fertile, abaxial stamens (Figure 5.15 i).

Although the composition of the androecium initially appears to be a useful character for delimiting groups, it is labile within certain groups (e.g. Sections *Somalia* and *Prionitis*, as shown above), thus rendering it somewhat unreliable.

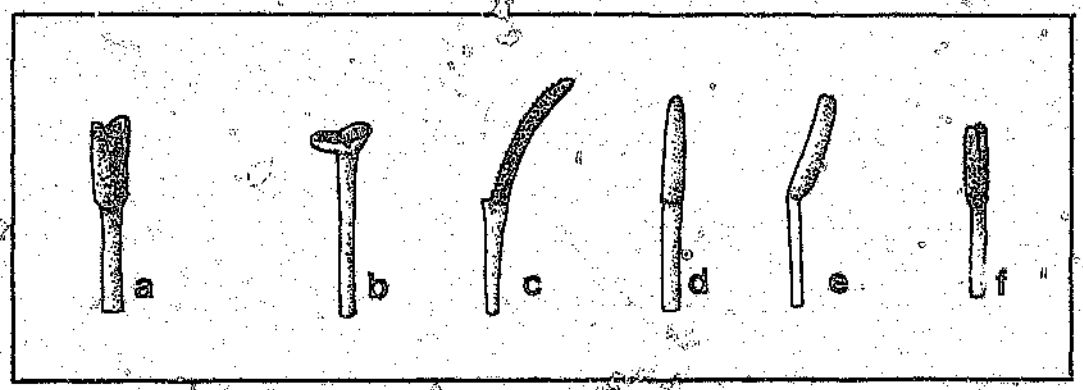
5.3.5.4. Gynoecium

Few characters of the gynoecium proved useful in the delimitation of sections or subsections within *Barleria*. Features such as pubescence of the ovary and the type of pubescence present at the base of the style are important in distinguishing between species within groups.

The morphology of the stigma proved useful in the delimitation of groups and was included in the cladistic analyses. The stigma in *Crabbea* is very weakly two-lobed with the abaxial lobe very reduced relative to the adaxial one (this may initially make it appear to be single-lobed). Two-lobed stigmas are very widespread in the Acanthaceae and are considered to be the plesiomorphic state for this character. In Subgenus *Barleria* the stigma is usually two-lobed, although both lobes are seldom equally well developed. In most members of Sections *Barleria* and *Barlerites* the two lobes are subconfluent and reduced so that the stigma is capitate in appearance (Figure 5.16 a & e). In some members of Section *Barlerlopsis* the two lobes of the stigma are flattened out to form a disc-shaped structure (Figure 5.16 b). In other species within this subgenus one of the lobes is very much longer than the other and, superficially, these stigmas may appear to consist of only one lobe (Figure 5.16 c). In Subgenus *Prionitis*, the stigma is characteristically reduced to a single, filiform lobe, although vestiges of the second,

Figure 5.16: Morphology of the stigma in *Barleria*.

a) 2-lobed, capitate stigma, *B. obtusa* (Section *Barleria*): Balkwill 668 (NU); b) 2-lobed, discoid stigma, *B. monticola* (Section *Barleriopsis*): Balkwill & Balkwill 5418 (J); c) 1-lobed, filiform, papillate stigma, *B. strigosa* (Section *Barleriopsis*): Grierson & Long 3382 (E); d) 1-lobed, filiform, smooth stigma, *B. albostellata* (Section *Stellatohirtae*): Balkwill, Balkwill, Gesell & Melville 5811 (J); e) 1-lobed, filiform, smooth stigma, *B. crossandriformis* (Section *Prionitis*): Balkwill 1148 (NU); f) *B. scindens* (Section *Barlerites*), Balkwill & Balkwill 4308 (J).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ventral lobe may be visible in some individuals (Figure 5.16 d).

Observations made on fresh stigmas of southern African species indicate that the two-lobed stigmas are conspicuously papillate, whilst the one-lobed stigmas (in Subgenus *Prionitis*) are smooth; these observations indicate that further investigation of this character in a wider range of species is warranted.

5.3.6. Capsules and Seeds

a. Morphology of the Fruit

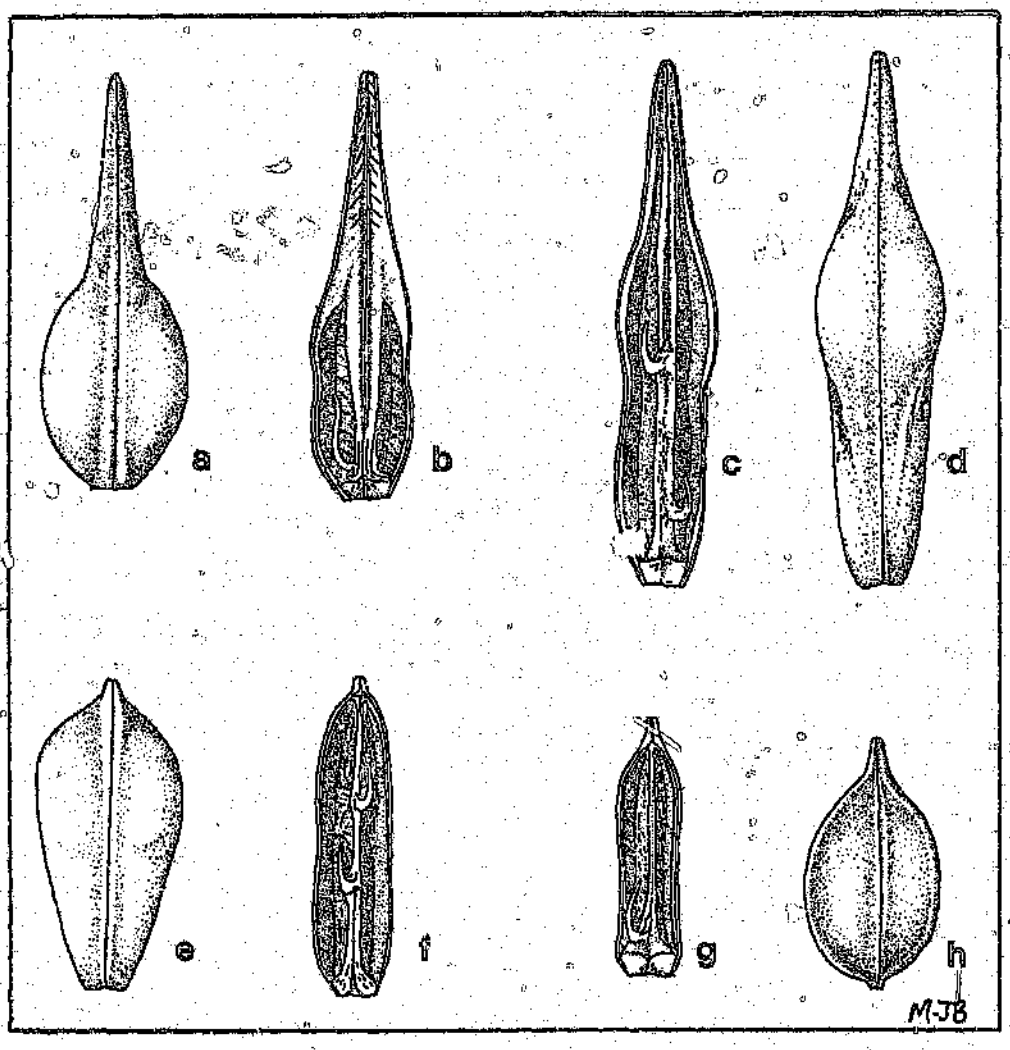
The fruit in *Barleria* is a dry, explosively dehiscent, 2-locular, estipitate capsule. Fruit morphology provides several reliable characters for subdivision of the genus and for use in cladistic analyses. These characters include the number of seeds present in the mature capsule, the presence or absence of a beak and the composition of the septum (discussed separately below). In *Barleria* each locule of the ovary initially contains 2 ovules, one above and one below. In several infra-generic groups the lower two ovules abort and the mature capsule contains only two seeds. The presence or absence of an apical beak on the fruit has been used to subdivide *Barleria* in various ways (see Clarke, 1899, 1901 & Obermeijer, 1933). However, in using this character it is important to distinguish between the different types of beaks that may be present.

Capsules in *Barleria* may have a solid apical beak, a hollow apical beak or no beak (Figure 5.17). In Sections *Prionitis* and *Somalia*, the capsule is turgid and rounded at the base and the apex is produced into a stout, solid, conical beak of the type seen in *Thunbergia* (Figure 5.17 a). In *Barleria* only two seeds are produced in capsules of this form, as the lower two ovules abort early during the development of the fruit. In Section *Barlerianthus*, the capsule possesses an apical beak, but this beak is not solid - the locules extend into it for some distance (Figure 5.17 b). The capsules in this group are basically spindle-shaped, but become markedly narrowed below the point of attachment of the upper seeds (Figure 5.17 b). These capsules contain four seeds at maturity.

In the whole of Subgenus *Barleria* and in Sections *Barlerites* and *Stellatohirtae* the capsules are not beaked (Figure 5.17 e - h). In Subgenus *Barleria*, they are laterally

Figure 5.17: Variation in the morphology of the capsule in *Barleria*.
a) & b) *B. senensis* (Section *Prionitis*) x 5: Balkwill & Balkwill 6331 (J);
c) & d) *B. montana* (Section *Barlerianthus*) x 5; Ritchie s.n. (E); e) & f) *B. elegans* (Section *Barleria*): Balkwill, Balkwill, Gesell & Melville 5811 (J); g) & h) *B. albostellata* x 5 (Section *Stellatokirtae*): Balkwill, Balkwill, Gesell & Melville 5811 (J).

a), d), e) and h) show an external view of closed capsules; b), c), f) and g) show an internal view of capsules opened along the longitudinal line of dehiscence of the capsule.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compressed, obtrulloid or spindle-shaped and the locules occupy the entire length of the capsule (Figure 5.17 f & g). Variations in the size, colour and pubescence of these fruits, as well as differences in the thickness of the fruit walls provide useful characters for distinguishing between closely related species within these groups. All capsules in Subgenus *Barleria* contain four seeds at maturity, the plesiomorphous condition.

In Sections *Barlerites* and *Stellatohirtae* the capsules are laterally compressed as in Subgenus *Barleria*, but they are rounded or ovoid rather than obtrulloid (Figure 5.17 g & h). The apex of these fruits is usually shortly acuminate, but in species such as *B. splendens* E.A. Bruce and *B. descampsii* de Willd it may become long-pointed. In Section *Barlerites* the broad-lateral walls of the capsule are extremely thin, but the narrow flanks of the capsule are sclerenchymatous and woody, forming a frame over which the walls are "stretched". When these capsules dehisce, the thin walls tear away from the woody flanks for about half their length, in much the same way as happens in fruits with elastic placental bases (see Figure 5.18). This is a diagnostic character for this section. Oersted (1854) had noticed this feature in his genus *Barlerites* (the members of which are included in Section *Barlerites* here), and Lindau (1895) mentioned it in his general discussion of fruits in Acanthaceae, but other authors do not seem to have noticed it. Obermeijer (1933) included a drawing of a capsule of this kind in her account of *Barleria*, but did not use the feature to characterise the group in which it occurred. It is possible that as she only saw one species from this group, she did not realise the importance of this feature as a diagnostic character.

The fruits of *Crabbea* are similar to those in Sections *Barleria* and *Barleriopsis*. They are unbeaked and contain four seeds. The presence of a solid beak and only two seeds in Sections *Prionitis* and *Somalia* are regarded as apomorphic states. I could find no evidence to suggest whether the hollow beaks in Section *Barlerianthus* represent an intermediate stage between "no beaks" and "solid beaks" or whether they represent an independent line of advancement from the basal state (beaks absent). These character states were thus coded non-additively, with the presence of a hollow beak on the fruit regarded as an apomorphic state.

Within Sections *Prionitis* and *Somalia*, the beaks on the capsules are usually only as long as or shorter than the lower, inflated part of the fruit. In the "typical" part of Section

Figure 5.18: Comparison of a dehisced acanthaceous capsule with elastic placental bases and a dehisced capsule of *B. scindens*.

a) *Dicliptera clinopodia* Nees x 17; Moura 47 (COI); b) *Barleria scindens* x 10 (Section *Barlerites*): Balkwill & Balkwill 5402 (J).

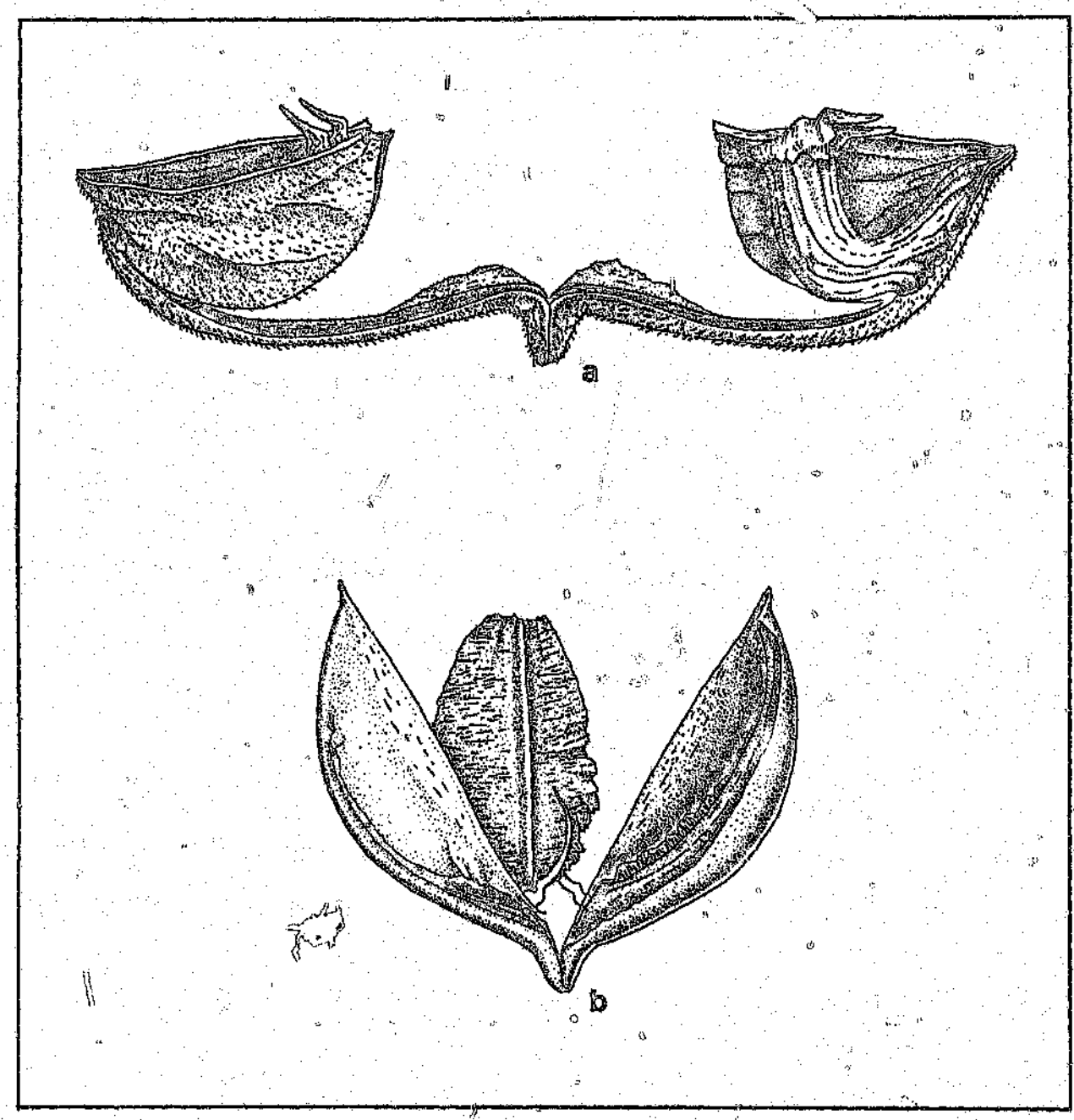
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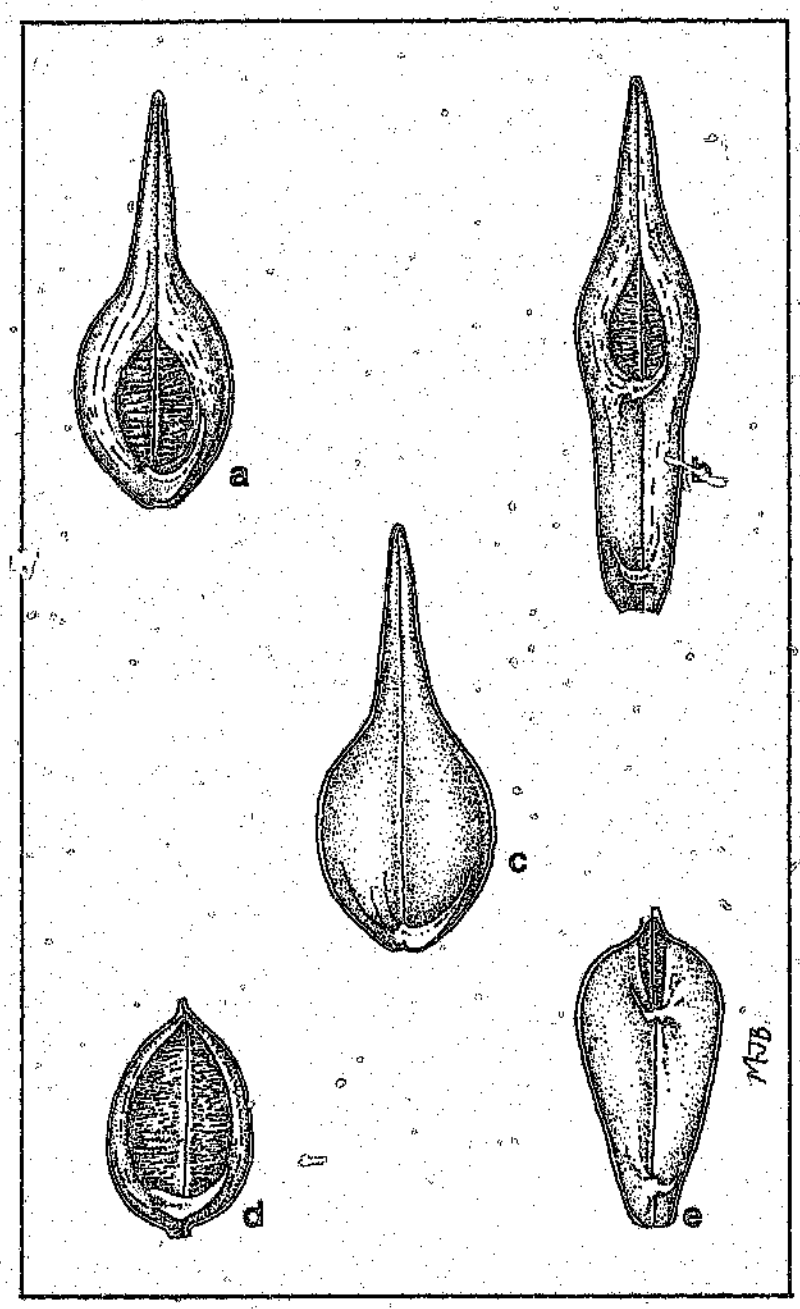
Figure 5.19: Variation in the composition of the septum in *Barleria* (all drawings approximately x 5).

a) *B. lancifolia* (Section *Somalia):* Balkwill & Balkwill 4302 (J); b) *B. montana* (Section *Barlerianthus*): Ritchie s.n. (E); c) *B. crossandriformis* (Section *Prionitis*): Balkwill & Balkwill 6340 (J); d) *B. scindens* (Section *Barlerites*): Balkwill & Balkwill 6402 (J); e) *B. elegans* (Section *Barleria*): Balkwill & Balkwill 6340 (J).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Somalia, however, the beaks are conspicuously and consistently longer than the inflated part of the fruit; the entire fruit is also very much smaller in this group than in the rest of Section *Somalia*. The smallest fruits in the genus (5 — 9 x 3 — 4 mm) are found in Section *Somalia* (within species such as *B. argentea*) and Section *Barlerites*, and the largest (25 — 40 x 10 — 13 mm) in Section *Barlerianthus* and some species of Section *Barleriopsis*.

Clarke used the presence of hairs on the fruits as a diagnostic character for his Section *Somalia* (Clarke, 1899), but this cannot be upheld here. The presence or absence of hairs, and the types of hairs present in pubescent fruits, provide very useful characters at the species level, but are generally unreliable as markers for larger infra-generic groupings.

b. Composition of the Septum

A feature of the capsule that has not been used in past infra-generic classifications of *Barleria* is the composition of the septum. Oersted (1854) had used such differences as diagnostic characters for some of his segregate genera, but other authors have paid scant attention to this character. The septum is variously divided into woody (or ligneous) and membranous portions. The woody parts are heavily sclerified and the membranous portions are mainly parenchymatous. Anatomical studies have shown that the different septum types are constant within species, are largely unaffected by changes in age of the fruits and show no intergradation. The functional significance of the different types of septum is unclear and was not investigated in this study.

In Sections *Prionitis* and *Somalia* (with a solid beak on the fruit), two different types of septum are present. In the former, the septum is entirely ligneous (Figure 5.19 c), but in Section *Somalia* the central portion of the septum is membranous (see Figure 5.19 a). In Section *Barlerianthus* (with hollow beaks on the fruits), the lower portion of the septum (i.e. below the upper retinacula) is ligneous, but most of the upper portion is membranous (Figure 5.19 b). In unbeaked fruits two types of septum present. In Subgenus *Barleria* (with 4-seeded fruits) the septum is almost entirely ligneous, with only a very small membranous portion at the apex (see Figure 5.19 e). In contrast, the septum in Sections *Barlerites* and *Stellatohirtae* is almost entirely membranous (Figure

5.19 d).

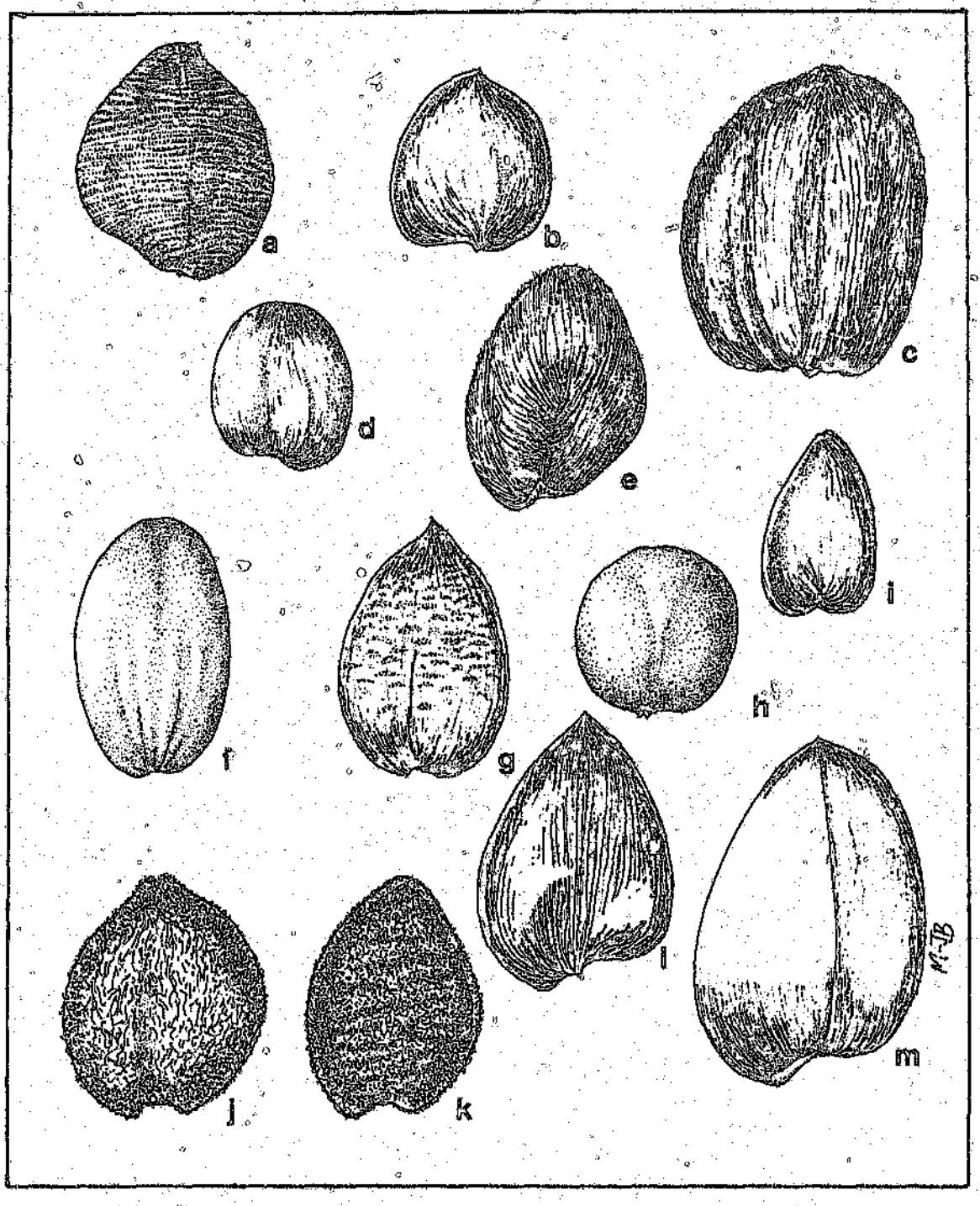
No information is available in the literature for this character in other members of the Acanthaceae. The fruits of *Crabbea* have a septum that is uniformly thick in texture, although this is not quite as woody as in *Barleria*. Entirely woody septa are regarded here as plesiomorphous, as they are the only type in which the texture of the septum is uniform, as in the outgroup.

c. Seeds

The mature capsules of *Barleria* contain either two or four seeds (see earlier discussion under point 5.3.6a above). The seeds in *Barleria* vary from orbicular to discoid to almost ovoid (see Figure 5.20) and always have an indentation at the base of the seed (at the site of the hilum). The base of the seed is usually somewhat asymmetrical about the hilum. The seeds are mostly laterally flattened and are often flatter on one side than on the other. The more convex side is usually marked with a longitudinal ridge indicating where the seed has been in contact with the walls of the fruit (i.e. along the line of dehiscence). Mature seeds are seldom present on herbarium sheets of *Barleria*, a problem also experienced with other acanthaceous genera (Graham, 1988). Explosive dehiscence of the capsule often occurs in response to drying so that the seeds are shed from the material during collection and pressing. The data set for seed characters is thus incomplete. Nevertheless, it was still possible to detect a number of interesting trends in seed morphology.

Some of the variation in seed morphology is illustrated in Figure 5.20. One of the most perplexing features is the occurrence of glabrous seeds in various parts of the genus. Glabrous seeds occur in all but one member (*B. montana*) of Section *Barlerianthus* and in *B. descampsii* de Willd (Section *Stellatohirtae*) (Figure 5.20 f & h). In most of the species of *Barleria* the seeds are covered in hygroscopic hairs (see Figure 5.20). Most members of the Ruellioideae (in which *Barleria* is currently placed) have hygroscopic hairs or scales of some description on the seeds and there are reports of hygroscopic hairs occurring in parts of the Justicieae (Graham, 1988) and Acanthoideae (Balkwill, 1985). By direct outgroup comparison the presence of hygroscopic hairs on the seeds of *Barleria* could be regarded as plesiomorphous. The occurrence in *Barleria* of only

Figure 5.20: Variation in seed morphology in selected representatives of *Barleria*. All drawings approxim[illegible] x 8.
a) *B. greenii* (Section *Barleria*): Green 625 (J); b) *B. lichtensteiniana* (Section *Barleria*): van Wyk 8689 (J); c) *B. monticola* (Section *Barleriopsis*): Balkwill, Balkwill & Green 6265 (J); d) *B. heterotricha* (Section *Barleria*): Balkwill & Balkwill 4299 (J); e) *B. strigosa* (Section *Barleriopsis*): Grierson & Long 3382 (E); f) *B. gibsonii* (Section *Barlerianthus*): Haines 2406 (K); g) *B. scindens* (Section *Barlerites*): Balkwill & Balkwill 6402 (J); h) *B. descampsii* (Section *Stellatohirtae*): Fanshawe 11 993 (K); i) *B. rogersii* (Section *Stellatohirtae*): Balkwill & Balkwill 6353 (J); j) *B. galpinii* (Section *Somalia*): van Heerden 143 (PRU); k) *B. rehmannii* (Section *Somalia*): Meeuse 9575 (PRE); l) *B. senensis* (Section *Prionitis*): Balkwill & Balkwill 4066 (J); m) *B. rotundifolia* (Section *Prionitis*): van der Schyff 2418 (PRE).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a few species with glabrous seeds would then be apomorphic. However, in the family as a whole the presence of hygroscopic hairs on the seeds is generally regarded as a derived feature (Scotland, pers. comm.) and this is the view that has been adopted here. The occurrence of glabrous seeds in *Barleria* is thus regarded as a reversal to the basal condition. It is interesting to note that the occurrence of glabrous seeds in these two groups within *Barleria* is coincidental with the reversion to four-seeded capsules (another plesiomorphous condition) in a part of the genus that is predominantly two-seeded. Reversion to four-seededness is not always correlated with the occurrence of glabrous seed surfaces, as in *B. montana* (Section *Barlerianthus*) four seeds with hygroscopic hairs on their surfaces are produced.

Variation in the colour and appearance of the hygroscopic hairs on fresh seeds provides characters that are useful in distinguishing between closely related groups of species. However, because only herbarium material was available of many species (and in some of this material seeds were not present), the full potential of these characters, particularly as a source of diagnostic characters for infra-generic groups, could not be investigated.

5.4. General Conclusions

Many characters in *Barleria* are highly variable, but the genus is clearly defined by the presence of a four-lobed calyx (with two outer and two inner lobes), spheroidal honeycombed pollen and a predominance of double cystoliths in the leaves. Although these characters occur elsewhere in the family, their consistent co-occurrence is restricted to *Barleria*. The consistent co-occurrence of these three characters was thus considered to support the concept of *Barleria* as a monophyletic assemblage and, thereby, to support the broad generic concept presented here (for further discussion see Conclusion of Chapter 2). Even though this circumscription of the genus requires some hypotheses of homoplasy to explain character distributions, I believe it would be extremely difficult to demonstrate as convincingly that *Barleria* is polyphyletic or paraphyletic. Based on a knowledge of the wider distribution of many of the characters throughout the family, I believe that the most parsimonious explanation is to accept *Barleria* as a single, monophyletic genus. Any attempt to subdivide the genus into smaller segregates would require the formulation of further hypotheses of homoplasy to explain the distribution of character states at the supra-generic level.

Some character states (e.g. medifixed hairs) have become fixed in particular groups and thus have an unambiguous distribution within the genus. However, many of these kinds of characters are autapomorphies for terminal taxa and thus are not useful in resolving relationships between the larger infra-generic groups. In other cases (e.g. the composition of the androecium) certain character states show a strong association with particular groups, but also show sporadic occurrence in other groups. In these cases, the predominance of the apomorphic state in a group was taken as an indicator of phylogenetic relationship. Other characters, such as the basic configuration of the corolla and the form of the stigma, either fit the description of "non-unique" apomorphies or show "apomorphic tendencies" (Linder, 1988). Apomorphic tendencies occur when a derived state evolves in parallel in two or more monophyletic units. The apomorphic state does not, however, occur in all the members of the terminal taxa (Linder, 1988). Apomorphic tendencies and non-unique apomorphies have widespread occurrence in a general context (Linder, 1988). Their usage in cladistic analyses has been criticised by various authors (see Linder, 1988), but as they indicate at least some degree of underlying genetic relationship, they have been used (with caution) in this study.

Although a fairly wide range of characters was studied in *Barleria*, the number of characters ultimately included in the cladistic analyses was rather small. Initial data sets (analyses of which are not presented here), included a greater number and wider range of characters, but many of these were eliminated for reasons given below:

i) All synapomorphies for the genus and autapomorphies for terminal taxa were excluded as they contributed no information about grouping relationships within the genus. This lead to the exclusion of many characters from the data sets; within *Barleria* it seems that the derived states of several characters provide clear autapomorphies for infra-generic groups, but there are few reliable characters that have the ability to resolve relationships between these groups.

ii) Very variable characters that did not define any particular group were eliminated from the data sets as they were of little value as cladistic characters at the sectional level. The number of characters that fell into this category was greatly increased when smaller groups were incorporated into larger ones (see Chapter

6 for full explanation). Many of the apomorphic character states in *Barleria* are autapomorphies for some of the smaller groups within the seven sections, so they were unhelpful in resolving the branching patterns at lower nodes of the cladograms.

iii) Characters for which information was not available for taxa across the whole range of variation were excluded from the data sets. This meant that several characters (such as the texture of the stigma lobes) could not be included, even though they show considerable potential as good cladistic characters.

Generally it is thought desirable to include as many characters as possible in a taxonomic study, so to better represent the range of variation within the group (Estabrook, 1978). In cladistics, however, only those characters with high cladistic information are needed or wanted (Ashlock, 1974). Some characters may be far better indicators of evolutionary relationship than others, as explained above. A relatively small number of distinct, true cladistic characters should be sufficient to reconstruct the cladistic history of a taxon (Estabrook, 1978). Scotland, Lawrence & Endress (in press) used only seven characters in a study of seven taxa, as they believed it was necessary to include only those characters which were present across the full range of variation. In the cladistic analyses of *Barleria* that follow (Chapter 6) it was considered preferable to include a smaller number of reliable characters, rather than to include a larger number of characters whose distribution was not fully known in the genus, or for which homology and polarity could not be determined with some degree of confidence.

CHAPTER 6

Phylogenetic Relationships

6.1. General Introduction

The phylogeny of an organism, or group of organisms, includes its total evolutionary history (Linder, 1988). One of the primary interpretive activities of a systematist is placing classificatory results in an evolutionary context (Hennig, 1965; Duncan, 1980). Investigation of the phylogenetic relationship between extant species, and the expression of the results of this research in an understandable and unambiguous way, is the task of phylogenetic systematics (Hennig, 1965 & 1966). A phylogenetic relationship of varying degree exists between all living species; the aim of phylogenetic systematics is to discover the degree of relationship within a given group of organisms (Hennig, 1965). In 1950, Hennig published *Grundzuge einer Theorie der Phylogenetischen Systematik* in which he outlined his ideas on the nature of phylogenetic relationship, how it could be established and how knowledge of it is best expressed (Wiley, 1981; Humphries & Funk, 1984). Revolutionary though they were, these ideas did not receive much attention, especially not in the English-speaking botanical community, until English versions of the work (Hennig, 1965 & 1966) were published (Wiley, 1981; Humphries & Funk, 1984; Linder, 1988).

Studies of phylogeny can include both the amount of evolutionary change within lineages (anagenesis) and the branching events within lineages (cladogenesis). Cladistics is a discipline that deals only with the sequence and pattern of branching events (i.e. cladogenesis) within phyletic lines (Estabrook, 1978; Humphries & Funk, 1984 and Linder, 1988). In this discipline, these patterns are expressed in the form of branching diagrams (cladograms) that summarise the sequence and direction of evolutionary change that could have occurred within a set of characters for a particular group of organisms (Duncan, 1980). Each cladogram is an hypothesis, the best explanation of the distribution of characters using all the available information. Depending on what data is available, some of these estimates or hypotheses will be more reliable than others

(Ashlock, 1974; Duncan, 1980). Cladistics covers a wide range of methods of phylogenetic inference (Humphries & Funk, 1984) that can be broadly divided into two classes: (i) parsimony analysis (i.e. "Hennigian cladistics"), and (ii) character compatibility analysis (Ashlock, 1974; Duncan, 1980; Humphries & Funk, 1984; Linder, 1988).

Parsimony analysis operates on the principle that evolutionary change occurs infrequently. The evolutionary estimate requiring the fewest character state changes and *ad hoc* hypotheses of homoplasy (similarity not due to common ancestry) is the most probable or preferable (Duncan, 1980; Humphries & Funk, 1984, Linder, 1988). In a cladistic study of this kind there are three basic steps: (i) selection of taxa and study of the characters; (ii) polarisation of characters: character states are placed in a sequence from most primitive, or plesiomorphous, to the most derived or apomorphous (thus forming a "transformation series"); this process leads to the identification of synapomorphies (shared derived characters) for particular taxa; (iii) search for the most robust cladogram requiring the fewest assumptions. In this search data sets can be analysed manually, but use of a computer expedites the analysis, especially when data sets are large and a number of alternative hypotheses is possible (Ashlock, 1974; Humphries & Funk, 1984; Linder, 1988). Parsimony is thus used to choose between alternative hypotheses of relationship to find the one with the greatest explanatory power (Humphries & Funk, 1984).

Character compatibility is concerned with an examination of the characters, but with little emphasis on the length of the various parts of the cladogram, as measured by the number of character state changes (Estabrook, 1978). The basic idea underlying this method is that characters are hypotheses of evolutionary relationships (Meacham & Estabrook, 1985). If two such hypotheses are logically consistent (congruent or compatible), then they may be combined into a single hypothesis. Groups of taxa are thus established on the basis of groups of compatible characters (or "cliques"). The phylogeny is found which has the largest number of compatible characters (Estabrook, 1978; Linder, 1988). A criticism of this method is that it uses only a very small portion of the data set, whereas parsimony analysis allows all characters to be used (Linder, 1988). Detailed discussions of character compatibility can be found in Estabrook (1978), Duncan (1980) and in Meacham & Estabrook (1985). Although parsimony analysis and

character compatibility analysis differ in a number of ways, they hold in common the principle that overall morphological resemblance or similarity is not a good measure of the degree of phylogenetic relationship between organisms. In cladistics, shared similarity plays a crucial role in the reconstruction of phylogenies, but distinction is made between various categories of similarity (Hennig, 1965; Scotland, 1992). Those characters whose shared states are thought to be uniquely derived (i.e. apomorphic) are thought to provide the most accurate reflection of the phylogeny of the organisms (Duncan, 1980; Scotland, 1992)

An analysis of Hennig's concepts and their influence on the philosophy and practice of taxonomy has been given by Dupuis (1984). Some of Hennig's ideas are still considered to be basic to the discipline (e.g. monophyly as the basis for recognising groups), but others (as listed by Linder, 1988) have been discarded. One of the most important developments in recent years has been the emergence of "transformed cladistics" (Humphries & Funk, 1984; Linder, 1988). Transformed cladistics involves the grouping of taxa into monophyletic units on the basis of shared, derived characters (synapomorphies or homologies). The monophyly is interpreted as being due to common ancestry, but does not depend on it practically or theoretically (Linder, 1988). Transformed cladistics attempts to find the pattern of character state distributions without any assumptions about the nature of the evolutionary processes involved (Humphries & Funk, 1984; Linder, 1988). The resulting cladograms can then be used to make hypotheses regarding the evolutionary processes and biogeography (Linder, 1988).

A detailed discussion of the terminology, principles and methods of cladistics has not been included here as these topics have been extensively described and debated in numerous publications, particularly in the pages of *Cladistics*, *Systematic Botany*, *Systematic Zoology* and *Taxon*. Excellent reviews of general methods and principles include Bremer & Wanntorp (1978), Funk & Stuessy (1978), Wiley (1981), Humphries & Funk (1984) and Linder (1988). Detailed discussion of the criteria used in the determination of homology (and the problems associated with this) can be found in Estabrook (1978), Stevens (1984b), Wagner (1989) and in the general review articles cited above. Comprehensive reviews of the methods used in the determination of evolutionary polarity have been provided by Estabrook (1977), Stevens (1980) and Linder (1988). Detailed attention is given to the use of outgroup comparison and

parsimony in Watrous & Wheeler (1981), Maddison, Donoghue & Maddison (1984) and Nelson (1985). Many authors, notably Ashlock (1974) and Cronquist (1987) have criticised various aspects of cladistic methodology and reasoning, but it still remains the only explicit method (with a sound theoretical foundation) for the reconstruction of phylogenies (van Wyk, 1991). One of Cronquist's (1987) strong objections to cladistics is that minor issues seem to be debated in great detail in the literature and that this does not benefit the non-cladist interested in producing general purpose classifications. However, I do not believe that this debate detracts from the usefulness of the methodology or from its theoretical foundation; besides, as so clearly put by Hennig (1965), differences of opinion are not a defect peculiar to cladistics but the "universal mark of every science."

Relatively few cladistic studies have been published for the Acanthaceae. The main ones known to me are those of McDade (1984), Ensermu (1990), Scotland (1990; 1990a & 1992), Hansen (1992) and Scotland, Lawrence & Endress (in press). I undertook a cladistic analysis of *Barleria* in order to assess the patterns of character distribution in the genus and to re-construct phylogenetic relationships within the group. The principles and methods of "transformed cladistics" (following Humphries & Funk, 1984) based on parsimony analysis were used. Analyses were carried out using the computer programme Hennig '86 (Hennig, 1988). The results of these analyses provided an empirical basis for the formulation of a classification of *Barleria* on a world-wide scale.

6.2. Selection of taxa

In the original circumscription of infrageneric groups made in the early stages of this study, *Barleria* was divided into numerous small taxa, chosen to represent all the most likely monophyletic units. Most of these were defined by clear synapomorphies. However, the units or taxa that did not share any obvious synapomorphies with other groups were retained as separate entities for inclusion in the cladistic analyses. This resulted in the recognition of seven major taxa (accorded the status of sections, as explained below). Smaller groups (described in Chapter 8) can be identified within four of these major taxa; in early cladistic analyses (not presented here), these smaller groups were retained as separate entities, but not all of them could be fully resolved. It was thus thought preferable for the smaller groups to be included in the larger ones, as they

represented a different level of organisation within the genus that could not be resolved fully with the information currently to hand. It is likely that with more information many of these small groups will be properly resolved and most will be found to represent true clades (i.e. true monophyletic units) that should be accorded formal status, but at a lower hierarchical level (e.g. subsections).

6.3. Selection and coding of characters

The data sets used in the cladistic analyses included a total of ten characters (the criteria used in the elimination of all other characters from the data sets are explained in the concluding section (5.4) of Chapter 5). These ten characters are those for which homology and polarities could be determined with a reasonable degree of confidence and include: basic configuration of the corolla lobes; structure of the stigma; the presence of a solid or hollow apical beak on the fruit; the number of seeds in the capsule; composition of the septum (three characters); composition of the androecium; nature of the hygroscopic hairs on the seeds and the structure of the fruit wall.

Polarisation of characters was achieved mainly by outgroup comparison, following the operational principles of Stevens (1980), Watrous & Wheeler (1981) and Maddison *et al.* (1985). *Crabbea* was used as the outgroup, for reasons discussed in Chapter 3. In some cases (e.g. composition of the septum), good information was not available for the outgroup, or the outgroup was also thought to possess an advanced state for a particular character (e.g. presence of hygroscopic hairs on the seeds); in these cases (discussed in detail in Chapter 5), polarity was determined by congruence with other characters used in the analysis. This was thought to be acceptable as congruence is the preferred test of homology (de Pinna, 1992). When smaller groups were included in larger ones, the characters were re-coded. The result of this was that characters highly characteristic of the smaller groups (e.g. medifixed hairs in the typical group within Section *Somalia*), became variable within the larger group. These characters were then coded for the plesiomorphic state, as is usual in this kind of situation (van Wyk, 1991). The effect of this was to eliminate from the analysis all those characters that only defined parts of the larger groups and thus were not helpful in resolving the relationships between these groups. The particular set of characters used in each analysis is provided in Tables 6.1

and 6.2. Appendix 3 contains the data matrices used in the cladistic analyses.

6.4. Cladistic analyses

Numerous cladistic analyses were conducted, but only the results of the more informative ones are presented below. The general procedure followed in all cases was to first analyse the data sets using the "mhennig*" option in Hennig '86. If a reasonably small number of trees was found (less than five), the trees thus obtained were used as input to find all possible trees using the "bb*" command - this routine applies extended branch-swapping to the data and finds all possible trees (Farris, 1986). If a number of different trees was generated, a Consensus Tree was produced using the "Nelsen" command. This gave an indication of which were the most robust portions of the cladograms and which parts still lacked resolution. The performance of the different characters in the analyses was also assessed; "noisy" characters could be determined and eliminated from the data set in order to use only the most reliable and informative characters. These "refined" data sets were then analysed using the "ie" (implicit enumeration) option. The implicit enumeration routine guarantees to find all of the shortest trees (Scotland *et al.*, in press). A summary of the different analyses conducted and the results obtained is presented in Table 6.1. The cladograms obtained using the different data sets are illustrated in Figures 6.1 to 6.3.

Analysis 1

This analysis shows the effect of the first interpretation of the composition of the septum. Initially, only two characters were recognised: one in which the septum has a narrow membranous portion above the upper seeds, and one in which this membranous area of the septum is broad. Six trees resulted from this analysis (see Table 6.1), all exhibiting a high degree of homoplasy in all characters except the number of seeds (3), the nature of the hygroscopic hairs on the seeds (7) and the composition of the androecium (6). In one of the topologies obtained all characters (except the three above) arise convergently, mainly in terminal taxa (Figure 6.1c). The other topologies obtained show reversal in at least one character (either the presence of a solid beak on the fruit or the number of lobes in the stigma) and convergence in one, two or three characters (involving characters 2 to 5; Figure 6.1a & b). The only two characters showing congruence in these cladograms are the nature of the hygroscopic hairs and the composition of the

Table 6.1: Summary of the cladistic analyses conducted to determine phylogenetic relationships within *Barleria*. "ci" = consistency index; "ri" = retention index

Analysis	data set	Hennig option	number of trees	length of tree/s	ci	ri	no. c* chars.
1	Table 6.2, chars. 0-7	mhennig*	6	13	61	63	8
2	Table 6.2, chars. 0-5,7,8	ie	2	11	72	78	8
3	Table 6.2, chars. 0-5,7-9	ie	1	12	75	79	9
4	Table 6.2, chars. 0-9	ie	2	14	71	73	10
5	Table 6.2, chars. 0-6,7-9	ie	1	12	75	78	9
6	Table 6.2, chars. 0-2,3a, 4-9	ie	3	11	72	75	9

androecium, with the result that the only resolved part of the cladogram (see Consensus Tree, Figure 6.1d) is the Stellatohirtae/Prionitis clade. Although the presence of silky, gold hygroscopic hairs on the seeds is a consistent feature for Sections *Stellatohirtae* and *Prionitis*, the full range of hair types present on the seeds of *Barleria* is not known and the polarity relationships are thus not fully understood at present. The composition of the androecium is one of those characters in *Barleria* that shows apomorphic tendencies,

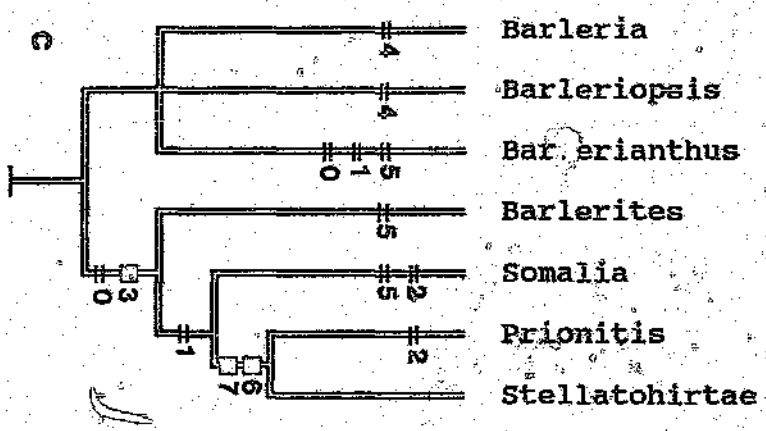
Table 6.2: Character set and polarisations used for cladistic analyses.

Character	plesiomorphic state (0)	apomorphic state (1)
0	corolla 2+3 or 4+1	corolla invariably 4+1
1	stigma of 1 or 2 lobes	stigma 1-lobed
2	capsules unbeaked	capsules with a solid terminal beak
3	seeds mostly 4	seeds mostly 2
3a	seeds always 4	seeds always 2
4	septum without narrow membranous portion at tip	septum with narrow membranous portion at tip
5	septum without broad membranous portion at centre	septum with broad membranous portion at centre
6	androecium mostly of 5 parts	androecium mostly of 4 or 2 parts
7	hygroscopic hairs variable	hygroscopic hairs gold, silky
8	septum not entirely membranous	septum almost entirely membranous
9	capsule without woody flanges	capsules with woody flanges

Table 6.3: Additional characters not used in cladistic analyses.

Character	plesiomorphic state (0)	apomorphic state (1)
10	cystoliths predominantly single	cystoliths predominantly double
11	pollen variable	pollen globose, honey-combed
12	calyx of 5 lobes, or if . 4 then not in 2 pairs	calyx of 4 lobes in 2 pairs
13	spine systems (from upper bud in leaf axil) absent	spine systems (from upper bud in leaf axils)invariably present
14	calyx herbaceous	calyx scarious
15	inflorescence units variable	inflorescence units invariably based on scorpioid cymes
16	inflorescence units invariably solitary, axillary	inflorescence units invariably aggregated into a terminal synflorescence
17	plants glabrous or pubescent, but pubescence not usually of conspicuous yellow hairs	plants usually with conspicuous pubescence of yellow hairs
18	capsules without prominent hollow beak	capsules with prominent hollow beak
19	plants with pubescence of simple hairs only	plants with pubescence of complex hairs (stellate and dendroid)
20	walls of capsule remaining intact upon dehiscence	walls of capsule tearing upon dehiscence
21	hygroscopic hairs on seeds variable	hygroscopic hairs on seeds white-woolly
22	leaves usually without sunken glands on lower surfaces	leaves always with sunken glands on lower surfaces
23	plants without axillary spine systems formed from lower bud in leaf axils	plants invariably with spines formed from lower bud in leaf axils
24	flowers usually blue, white or pink	flowers usually yellow or apricot yellow

Figure 6.1: Estimates of phylogenetic relationships in the genus *Barleria* as obtained in Analysis 1. Trees 0 (a), 3 (b), and 5 (c) of the six trees obtained are shown here. (d) shows the Consensus Tree obtained in this Analysis. For details see text. Notation used: ▣, synapomorphies showing no homoplasy; □, synapomorphies showing reversal higher up in the cladogram; X, reversals; =, convergences; ⊙, autapomorphies not used in the analysis; ○, variable and/or convergent apomorphies not included in the analysis.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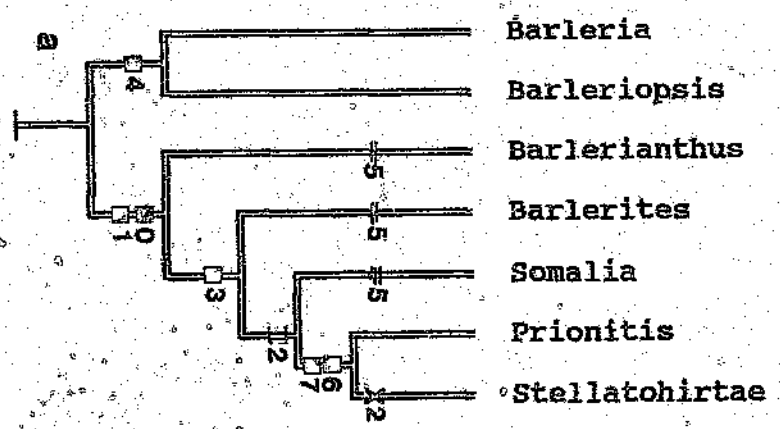
Somalia
Prionitis
Stellatohirtae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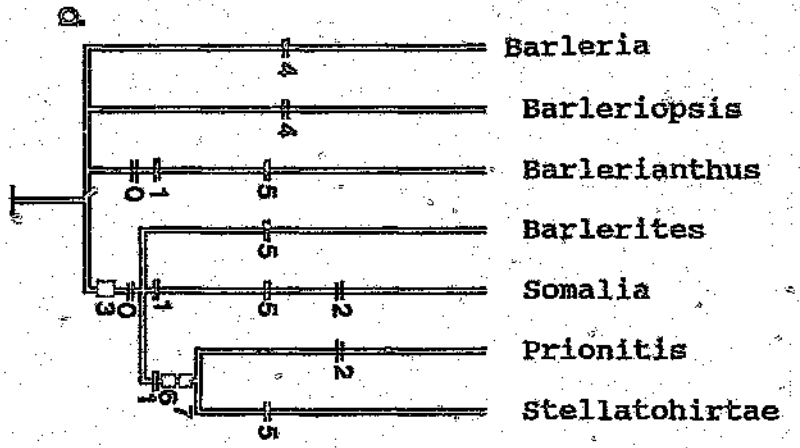
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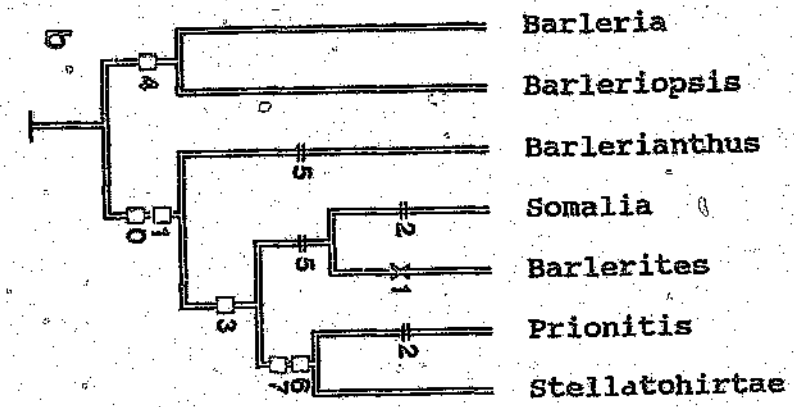
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but can be variable within groups (e.g. Section *Barleria)*. It thus seems unsatisfactory to accept a topology in which characters that are variable or of unknown polarity are used to determine the position of clades, whilst characters known to be more stable within groups arise convergently or show reversals. The most acceptable tree produced in this analysis is that illustrated in Figure 6.1a. This tree shows reversal in only one character (the presence of a solid beak on the fruit) and convergence in one character (the presence of a broad membranous portion in the septum). An attractive feature of this cladogram is that the apomorphies show no homoplasy at the lower nodes of the tree. This topology is similar to the ones obtained in analyses 3 and 5, particularly with respect to the positions of the **Barleria/Barleriopsis** and **Barlerianthus** clades and in the presence of reliable apomorphies (characters 0, 1, 3 and 4) in basal positions. The high degree of homoplasy and uncertainty regarding the positions of most clades using this data set was thought to indicate mistaken similarity in the definition of the characters relating to the composition of the septum.

Analysis 2.

This analysis shows the effect of changing the interpretation of the structure of the septum and of exclusion of character 6 (composition of the androecium) from the data set. A third septum character was introduced in this analysis (see Table 6.1) and was retained in all subsequent analyses: a distinction was made between those septa in which there is a broad membranous portion above the upper ovule, and those in which almost the entire septum is membranous. These two conditions were treated as the apomorphic states of two separate characters. Whilst this could be seen to weight composition of the septum too heavily, there is no evidence suggesting that the different septum conditions form a single sequence and they do not seem to show any direct correlation with each other within *Barleria*. Only two trees were obtained using the ie routine on this data set (Table 6.1). The trees obtained in this analysis are shorter than those obtained in analysis 1 (although the same number of characters was used). This interpretation of characters thus seems to produce a more parsimonious solution than that obtained in analysis 1. The consistency index obtained in analysis 2 is also considerably higher than that obtained in analysis 1 (see Table 6.1). These data clearly resolved the **Barleria/Barleriopsis** part of the cladogram, with this clade supported by the presence of a narrow membranous portion in the septum (which I consider to be a very stable

character). The positions of the remaining clades, however, could not be clearly resolved. Of the two trees generated in this analysis (see Figure 6.2a &b), the first one (which corresponds exactly with that obtained in analysis 5) is clearly preferable (see Figure 6.2a). It shows reversal in only one character (the number of stigmatic lobes, (1)) and convergences in characters 5 and 7 in the terminal taxa. Empirically, this is a more satisfying estimation of the relationships than the one shown in the second tree (Figure 6.2b): this tree also shows reversal in only one character (the number of seeds, (3)) and convergence in three characters (2,5 and 8) in terminal taxa. Convergence in two of these characters (presence of a solid beak on the fruit (2) and an almost entirely membranous septum (8)) is not convincing. The distribution of these characters is extremely consistent and unambiguous within the genus and it seems unreasonable to infer that they have arisen convergently.

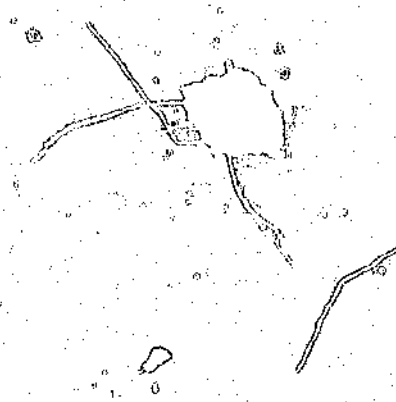
Analysis 3.

This analysis shows the effect of adding another character, presence of woody flanges in the fruit wall (9), to the data set (see Tables 6.1 & 6.2). A single fully resolved cladogram (Figure 6.2c) was produced using the ie routine. I consider the apomorphies resulting in this topology to be very reliable and thus find this to be a particularly convincing cladogram. The combination of Sections *Stellatohirtae* and *Barlerites* in the same clade is supported by common possession of the apomorphies for characters 8 and 9 (Table 6.2). Sections *Somalia* and *Prionitis* are included in the same clade, supported by common possession of a woody beak at the apex of the fruit (a very stable character within the genus). Characters 5 and 7 arise convergently in some of the terminal taxa. It seems more reasonable to assume that these characters (the full distribution of which is not known or the homology not fully understood) may have arisen independently, than to presume that woody beaks and woody flanges (both unusual and stable characters) would have arisen convergently.

Analysis 4.

In this analysis the effect of adding a single character, composition of the androecium (6), to the previous data set was tested. Two trees were obtained using the ie option (see Table 6.1). That these trees are the longest (14 character changes) of any of the trees

Figure 6.2: Estimates of phylogenetic relationships in the genus *Barleria* as obtained in Analyses 2, 3 and 4. Notation as for Figure 6.1. a) Tree 0, Analysis 2; b) Tree 1, Analysis 1; c) Single, fully resolved cladogram produced using the ie option in Analysis 3; d) Consensus Tree of the two trees produced using the ie option in Analysis 4. All notation as for Figure 6.1.



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Stellatohirtae
Prionitis

generated thus far, was not considered too important as an additional character had been included in the analysis. Furthermore, the consistency indices were only slightly lower than those obtained in other analyses (see Table 6.1). This combination of characters, however, results in uncertainty regarding the positions of all clades except **Barleria/Barleriopsis** (see Consensus Tree, Figure 6.2d). Both of the trees generated in this analysis show reversal in one character and convergence in three characters. The second tree that was obtained in this analysis (identical to the one obtained in Analysis 3) is considered to represent a more acceptable hypothesis of the phylogeny as the convergences occur in characters that are known to be variable. Convergences are far more likely to occur in these kinds of characters than in characters such as woody beaks that show a very definite distribution within the genus and the Acanthaceae as a whole. The two characters that seem to create the greatest uncertainty with respect to the position of the major clades are the composition of the androecium (6) and the presence of gold, silky hairs on the seeds (7). Inclusion of both characters in the analysis leads to convergences or reversal in other more convincing apomorphies such as the solid beak on the capsule, woody flanges in the fruit wall and the number of seeds in the capsule. I thus decided to omit one of these characters, character 6 (about which I had the greatest uncertainty regarding homology and polarity), from the next analysis.

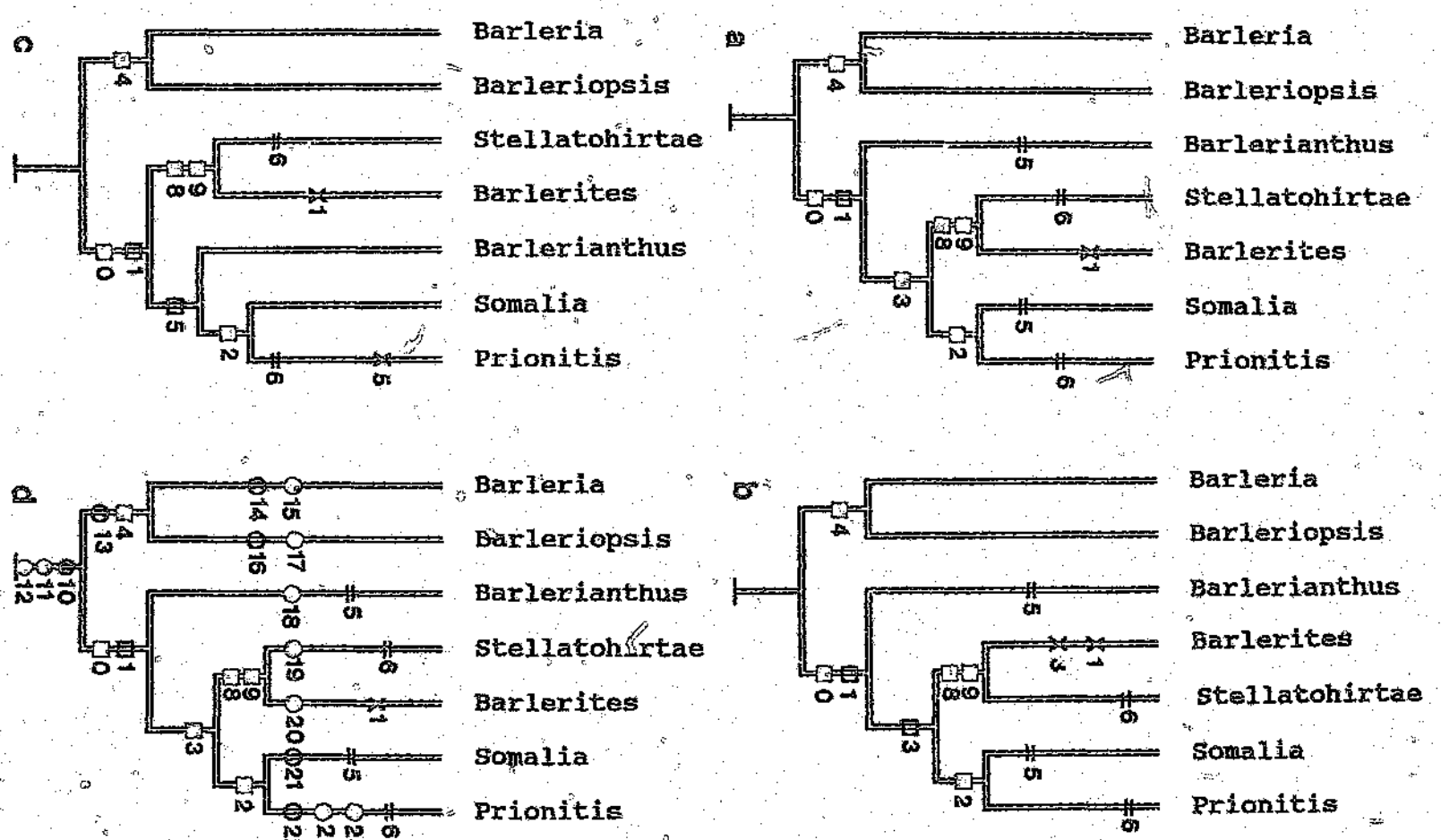
Analysis 5

In this analysis character 7 (gold, silky hairs on the seeds) was omitted, resulting in the production of a single, fully resolved cladogram with the same topology as that obtained in analysis 3 (Figure 6.3a). The only characters still showing homoplasy are the number of stigma lobes (1), which reverse in *Barlerites*, the composition of the androecium (6), (which arises convergently in *Stellatohirtae* and *Prionitis*) and the presence of a broad membranous portion in the septum (5) (arising convergently in **Barlerianthus** and **Somalia**).

Analysis 6

The number of seeds present in members of the seven major taxa is very consistent with one exception. In Section *Stellatohirtae*, which characteristically has two seeds, one species, *B. descampsii*, consistently has four seeds. This is regarded as reversion to the

Figure 6.3: Estimates of phylogenetic relationships in the genus *Barleria* as obtained in Analyses 5 (a) and 6 (b & c) and chosen cladogram (d) for the genus. All notation as for Figure 6.1; a key to the characters used is provided in Tables 6.2 and 6.3.
a) Single fully resolved cladogram obtained using the ie option in Analysis 5; b) Tree 0 of three equally parsimonious trees obtained using the ie option in Analysis 6; c) Tree 2 of three equally parsimonious trees obtained using the ie option in Analysis 6; d) final cladogram chosen to represent the most likely estimate of the phylogenetic relationships in *Barleria*. The distribution of apomorphies not used in the analyses has been plotted onto this cladogram.


c
Barleria
Barleriopsis
Stellatohirtae
Barlerites
Barlerianthus
Somalia
Prionitis
b
Barleria
Barleriopsis
Barlerianthus
Stellatohirtae
Barlerites
Somalia
Prionitis
d
Barleria
Barleriopsis
Barlerianthus
Stellatohirtae
Barlerites
Somalia
Prionitis
a
Barleria
Barleriopsis
Barlerianthus
Barlerites
Stellatohirtae
Somalia
Prionitis

plesiomorphic condition and, interestingly, co-occurs with the production of glabrous seeds (also regarded as reversion to a more plesiomorphic state). The character for seed number in all previous analyses was divided into two states: "seeds usually 4" and "seeds usually 2". This meant that it was not necessary to code Stellatohirtae for the plesiomorphic state, as it would have been if the two states had been "seeds always four" and "seeds always two". In this analysis, the character states were defined in the latter way and Stellatohirtae was coded as primitive for the number of seeds. The effect of this was that three trees could be found using the "ie" routine in Hennig. One of these was the same as that obtained in Analyses 3 and 5. In the other two trees the positions of the Stellatohirtae, Barlerites and Barlerianthus clades were affected, depending on whether character 3 (the number of seeds) or character 5 (broad membranous portion in the septum) was used to support the major clade in the terminal part of the topology (see Figures 6.3b & c). The basal dichotomy in the cladogram remained the same with the same apomorphies in basal positions as in analyses 3 & 5. The Consensus Tree of these three trees is identical to the single tree generated in Analyses 3 and 5.

6.5. General Discussion and Conclusions

Based on the data currently available, the cladogram presented in Figure 6.3d is chosen here as the most acceptable explanation of the distribution of character states within *Barleria* and, therefore, as the best estimate of the phylogeny of *Barleria*. The apomorphies for the terminal taxa (not included in the analyses) and the distribution of some other characters (not included in the analyses) are also plotted onto this cladogram. Whilst slightly shorter trees could be generated using different data sets (see Table 6.1), the apomorphies in the slightly longer topology are thought to represent the most reliable characters within *Barleria* for resolving relationships at this level of inclusiveness.

From cladogram to classification

For most cladists a cladogram is a classification (Humphries & Funk, 1984; Funk, 1985). The question that needs to be answered is how best to convert the cladogram into a hierarchy of ranks (Humphries & Funk, 1984; Funk, 1985; Linder, 1988). The use of cladistics for the circumscription of groups and assignment of rank has been extensively debated in the literature (Duncan, 1980; Linder, 1988). Cladistic

classifications strive to recognise monophyletic groups with as little change to the existing nomenclature as possible (Humphries & Funk, 1984; Funk, 1985). One of the strongest objections raised by opponents of cladistics is that the requirement for sister groups to be given equal rank (Hennig, 1966), leads to an over-proliferation of ranks, thus creating nomenclatural confusion. This argument is no longer valid as this concept is one of those that is no longer strictly applied (Linder, 1988). Furthermore, Funk (1985) has clearly demonstrated that application of cladistic principles need not automatically result in splitting of previously accepted groups. The findings presented in this thesis support this view.

Several criteria have been published for the translation of cladograms into classifications (Linder, 1991). The general principle that should be followed is that a good classification should be minimally novel, minimally redundant and maximally informative (Wiley, 1981; Humphries & Funk, 1984, Funk, 1985). Where possible, taxa can be retained at their traditional ranks as long as they remain consistent with the phylogeny (Farris, 1983; Linder, 1988). Generally only a few nodes of a cladogram are named formally. If one can establish which nodes have the highest confidence rating, then these nodes can be selected for formal naming with the result that the classification established from them will be maximally stable (Linder, 1991). There are different ways of assessing confidence in the nodes of a cladogram, including statistical testing such as "bootstrapping" (Linder, 1991). The most commonly used indication of confidence is the nature of the data supporting the nodes of the cladogram. Linder (1991) has recommended that some indication of the relative confidence levels of the different nodes in a cladogram should be given (preferably by doing a bootstrap analysis) so that it is known which parts of the resultant classification may undergo later change. A bootstrap analysis has not been undertaken here as the data set, particularly with respect to number of characters, is small, and the characters that have been used are considered to be very reliable and stable.

The basal dichotomy shown in Figure 6.3d (and in most other cladograms obtained) is supported by reasonably convincing apomorphies. As it seems unlikely that future analyses will lead to a drastic change in this basic topology, the two major clades have been assigned formal status as subgenera. The cladogram does, however, include characters that show homoplasy and some of the nodes are supported by non-unique

apomorphies or characters that show apomorphic tendencies, so I have elected to assign all terminal taxa in the cladogram equal status as sections. This approach was adopted by van Wyk (1991) in his classification of *Lotononis* (Fabaceae). This approach averts the possibility of accepting taxa that may be shown to be paraphyletic after further in-group analysis. This kind of system also ensures that future re-arrangements within the sections (e.g. recognition of smaller subdivisions as sub-sections) will be possible without necessitating serious changes to the infrageneric nomenclature.

Most of the terminal taxa are defined by convincing apomorphies and are thought to represent true monophyletic groups. The only exception to this is the **Barleriopsis** clade, which is supported by two characters, but both are non-unique apomorphies. It is thus possible that this clade may not represent a true monophyletic unit, but it will only be possible to establish this once full data sets are available for some of the taxa currently included in this group (for further discussion see Chapter 7). Further investigations will almost certainly reveal apomorphies for the smaller groups that were identified within some of the sections. Most of these groups are likely to represent true clades which should be accorded formal status, probably as subsections. These sub-groups are described informally in Chapter 7, under the formal descriptions of the Sections.

Future investigations of some of the more poorly known species, or species that were not included in this study, may reveal flaws in the hypotheses presented here. However, most of the clades (i.e. all except **Barleriopsis**) are fairly robust, with terminal taxa supported by clear apomorphies. I, therefore, consider that the proposed classification will be reasonably stable at the sectional level and do not expect that drastic modifications will need to be made in the future. This classification is also the first to use a phylogenetic approach for the whole genus. Whilst the system proposed may require some refinement, it provides a clear conceptual framework, in the context of which future research can be conducted.

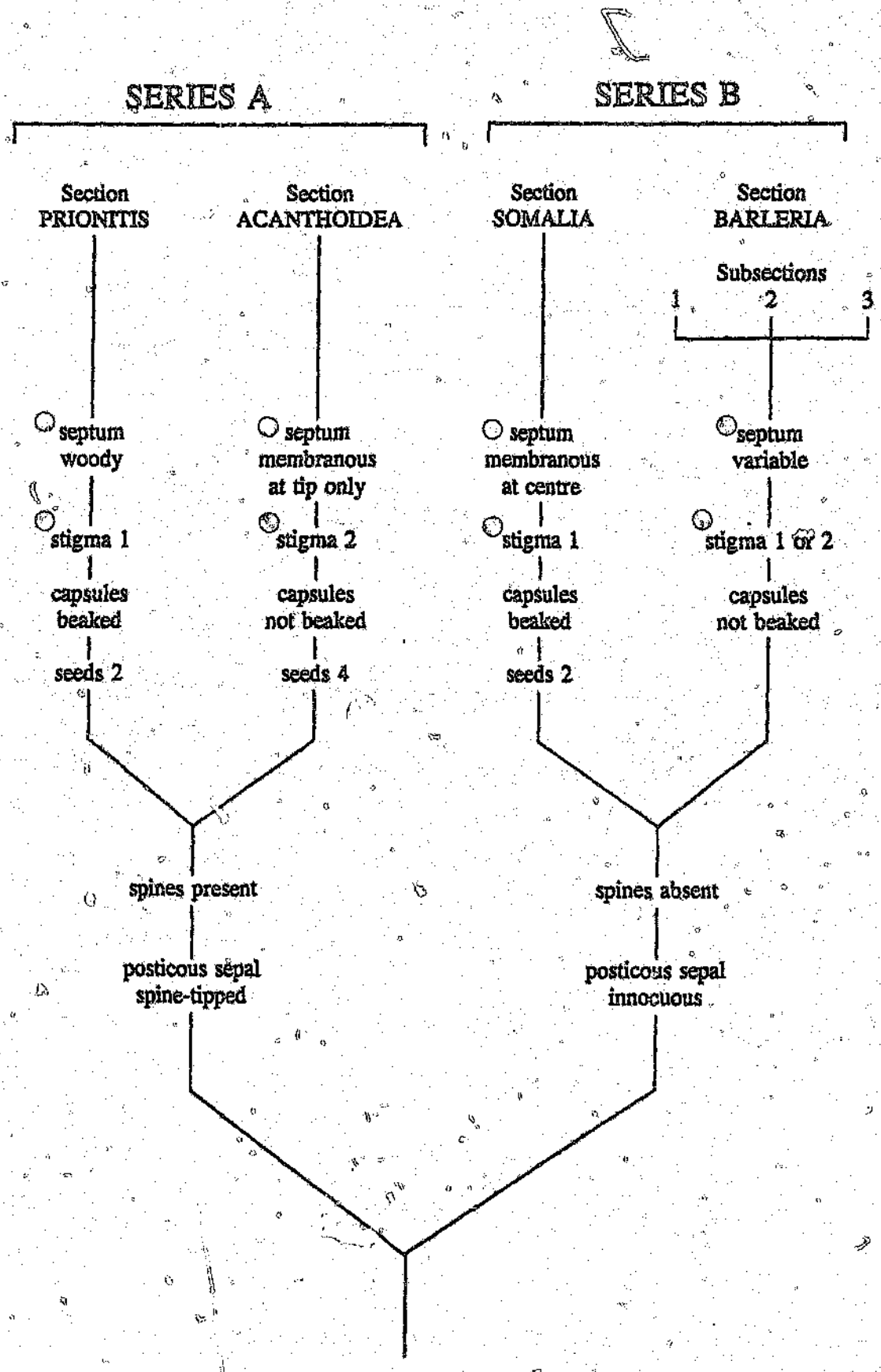
In an attempt to create the least possible disruption to the existing infra-generic nomenclature, I have used the same names for corresponding taxa as used by Clarke (1989) wherever this has been possible. Furthermore, some of the names used by Oersted (1854) for corresponding groups have been adopted to avoid creating a further

proliferation of names within the genus.

It is interesting to compare the classification proposed here with those of Clarke (1899) and Obermeijer (1933). At the outset it should be emphasised that direct comparisons between the older classifications and the one proposed in Chapter 7 of this thesis cannot be made; each has been produced for a different group of species, using a different character set and different methodologies. To facilitate at least a superficial comparison, I have converted the classifications of Clarke (1899) and Obermeijer (1933) into simple branching diagrams (see Figures 6.4 and 6.5), onto which the distribution of the main characters used by these authors has been plotted. In addition, the distribution of characters used in this study has been plotted onto these diagrams.

It is important to note that in the classifications of both Clarke (1899) and Obermeijer (1933), no distinction is made between primitive and derived character states. The consequence of this is that characters such as "4 seeds present" and "beaks absent on capsules" (considered primitive in the current study) have been used to delimit groups. A result of this is that several other important character states often representing apomorphies (e.g. presence of a solid beak on the capsule, 2 seeds) arise convergently or in parallel in the main taxa recognised in these classifications (see Figures 6.4 & 6.5). Clarke divided the species of *Barleria* seen by him into two main groups (represented by the basal dichotomy in Figure 6.4). Obermeijer (1933) recognised three sections within the genus; she did not make any comments regarding the degree of similarity or difference between these groups. In converting her classification into a "cladogram", however, it would seem that Sections *Prionitis* and *Somalia* are more closely allied to each other than to Section *Barleria*, through their common possession of beaked , 2-seeded capsules. Thus, as in the classification of Clarke (1899), a basal dichotomy exists but different groups fall into the two major clades in this system. One of the main characters used by these authors to form these basic groups is the presence or absence of spines. Herein lies one of the causes of the high degree of homoplasy evident in most other characters in these classifications - grouping all taxa with spinous structures together is a case of mistaken similarity (*sensu* Scotland, 1992). As has been demonstrated in this thesis, the derivation of spines is not homologous in all cases, with the result that a group based on possession of such a feature is artificial, polyphyletic and thus unacceptable. Likewise, grouping on the simple absence of spines (or absence of

Figure 6.4: Branching diagram representing the classification of *Barleria* proposed by Clarke (1[illegible]). The distribution of characters considered important by Clarke has been plotted onto the cladogram. Those characters marked with a black spot were not used by Clarke.


SERIES A
SERIES B
Section PRIONITIS
Section ACANTHOIDEA
Section SOMALIA
Section BARLERIA
Subsections
1
2
3
septum woody
septum membranous at tip only
septum membranous at centre
septum variable
stigma 1
stigma 2
stigma 1
stigma 1 or 2
capsules beaked
capsules not beaked
capsules beaked
capsules not beaked
seeds 2
seeds 4
seeds 2
spines present
spines absent
posticous sepal spine-tipped
posticous sepal innocuous

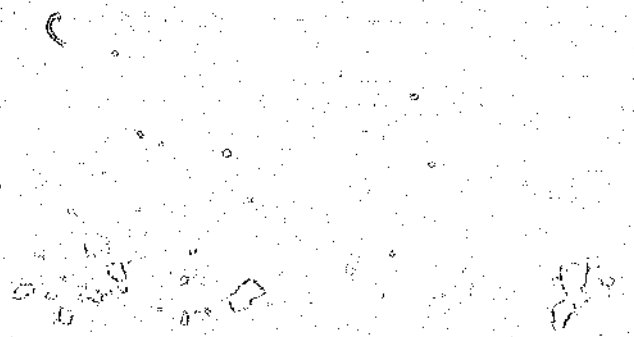
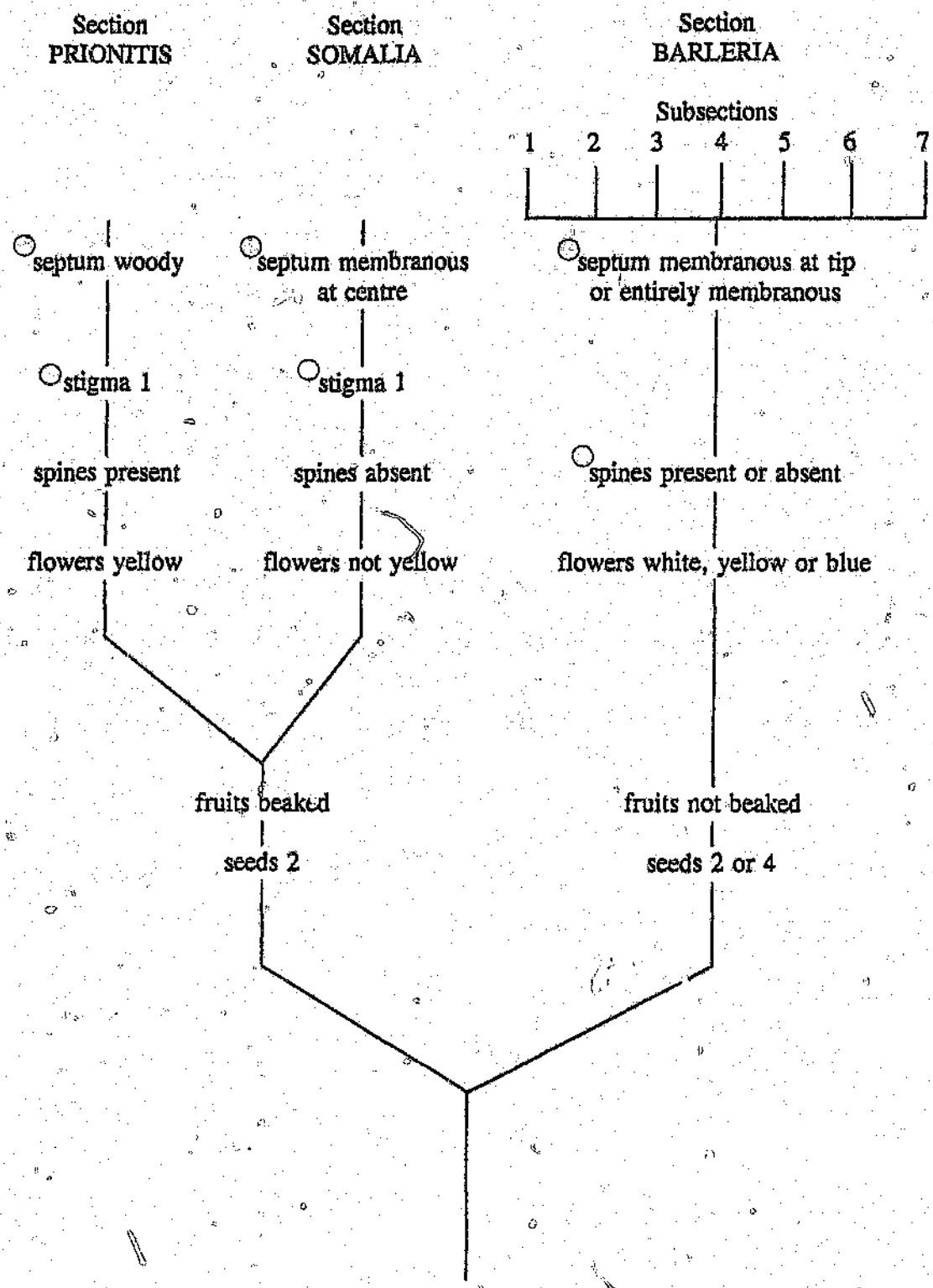


Figure 6.5: Branching diagram representing the classification of *Barleria* proposed by Obermeijer (1933). The distribution of characters considered important by Obermeijer has been plotted onto the diagram. Characters marked with a black spot are those that were not used by Obermeijer.


Section PRIONITIS
Section SOMALIA
Section BARLERIA
Subsections
1
2
3
4
5
6
7
septum woody
septum membranous at centre
septum membranous at tip or entirely membranous
stigma 1
stigma 1
spines present
spines absent
spines present or absent
flowers yellow
flowers not yellow
flowers white, yellow or blue
fruits beaked
fruits not beaked
seeds 2
seeds 2 or 4

any other character) results in the formation of paraphyletic groups. In both of the earlier classifications almost all characters are homoplasious and only Sections *Somalia* and *Prionitis* seem to represent monophyletic assemblages. Sections *Prionitis* and *Somalia* in these classifications correspond exactly with the sections of the same name in my classification, but the suggested affinities of these groups are rather different and different characters have been used to define these taxa. A major difference between the classifications lies in the circumscription of Section "*Eubarleria*". This section was found to be unnatural (i.e. not monophyletic) in both of the previous classifications and seemed to comprise all those species that would not fit properly into the more neatly defined sections. Obermeijer's Section "*Eubarleria*" included Section *Acanthoidea* of Clarke. Section *Barleria* as circumscribed in this thesis corresponds closely with Section *Acanthoidea* of Clarke, but also includes non-spinous forms (placed in various other subsections by both Clarke and Obermeijer before). Sections *Stellatohirtae* and *Barlerites* (subsection *Dispermae* sensu Obermeijer) proposed in this thesis were previously included as part of Section *"Eubarleria"*. My research has shown that these two groups should be accorded equal rank with the others and that their affinities, judged on common possession of two seeds, lie more closely with Sections *Somalia* and *Prionitis* than with the members of Section *Barleria*. Section *Barlerites* corresponds with the genus of the same name described by Oersted (1854) and Section *Stellatohirtae* corresponds with a subsection of the same name in the classification of Clarke (1899).

The circumscription of some groups (e.g. Section *Prionitis*) is the same in all three classifications, but the suggested affinities of the groups is different. Furthermore, two new Sections that have not been recognised in previous classifications are described in my classification. This may not be surprising considering that a far greater number of species has been included in the current study and a number of new characters has been used. The suggested distribution of character states is far more parsimonious in the newly proposed system than in the older classifications.

CHAPTER 7

FORMAL TAXONOMY

Barleria L., *Sp. Pl.*: 636 (1753); Linn., *Gen. Pl.*: no. 785 (1764); de Jussieu, *Gen. Pl.*: 103 (1789); Nees, in DC. *Prod.* xi: 222 (1847); Benth. & Hook. f. *Gen. Pl.* II: 1091 (1876); Clarke, in Hook., *Fl. Brit. Ind.* iv: 482 (1885); Lindau, in Engl. & Prantl., *Pflanzenfam.* iv (IIIB) (1895); Clarke, in Thiselton-Dyer, *Fl. Trop. Afr.* v: 141 (1899); Clarke, in Thiselton-Dyer, *Fl. Cap.* v (1): 41 (1901); Ridley, in *Fl. Malay. Pen.* II: 587 (1923); Obermeijer, in *Ann. Transvaal Museum* 16 (1): 123 (1933); Benoist in Humbert, *Flore de Madagascar et des Comores* I: 134 (1967).

Type: *B. cristata* L., designated by Brummitt & Vollesen (1992); Herb. Linn. No. 805. 12, (LINN), typ. cons. prop.

Barleriacanthus Oerst., in *Kjoeb. Vidensk. Meddel.*: 24 (1854); Type: *non designatus*

Barlerianthus Oerst., *l.c.*: 24; Type: *B. grandis* Hochst. (= *B. grandiflora* Dalz.)

Barleriopsis Oerst., *l.c.*: 21; Type: *non designatus*

Barleriosiphon Oerst, *l.c.*: 24; Type: *B. longiflora* L. *f.*

Barlerites Oerst., *l.c.*: 25; Type: *non designatus*

Barreliera J.F. Gmel., *Syst.*: 959 (1791); *fide* Lindau (1895)

Crabbea Harv., *Gen. Pl. Cap.* ed. 1: 276 (1838), *nom. rej.*; Type: *Crabbea pungens* Harv., *non Crabbea* Harv. (1842), *nom. cons.*; Type: *C. hirsuta* Harv.

Dicranacanthus Oerst., *l.c.*; Type: *non designatus*

Prionitis Oerst., *l.c.*: 24; Type: *P. hystrix* Miquel. (= *B. prionitis* L.)

Pseudobarleria Oerst., *l.c.*: 23; Type: *non designatus*

Soubeyrania Neck., *Elem.* i: 365 (1790), *fide* Lindau (1895)

Wahabia Fenzl., in *Flora* 27: 312 (1844); Type: *B. acanthoides* Vahl.

Herbs, shrubs, suffrutices or, rarely, climbers and vines; plants with or without axillary spine systems; 2 serial buds present in each axil. *Leaves* simple, opposite, decussate, usually entire or occasionally toothed; epidermal cells dense with cystoliths; cystoliths usually double (occurring in 2 adjacent cells). *Inflorescence* cymose, sometimes reduced

to a solitary flower; flowers arranged in inflorescence units showing monochasial, dichasial or combined mono- and dichasial branching; inflorescences of a single unit or compound (synflorescences of numerous units), axillary or terminal, flowers subtended by 2 bracteoles, with or without an additional modified bract. *Bracts* 1 per flower, variously shaped, often foliaceous (ordinary vegetative leaves) or highly modified and reduced, herbaceous, leathery or membranous, margins entire or toothed. *Bracteoles* 2 per flower, subsimilar or rarely strongly dimorphic; usually opposite or occasionally both bracteoles displaced to one side of inflorescence axis; leaf-like and innocuous or stiff with variously toothed or spinous margins, occasionally completely reduced to a solid, cylindrical spine. *Calyx* of 4 segments: anticous and posticous lobes outermost, sub-similar, large; anticous lobe of 2 fully or partially fused sepals; lateral lobes innermost and smaller than outer lobes; shape, colour and pubescence of lobes variable, outer lobes usually with 3 or more prominent veins from the base, sometimes with prominent pattern of reticulate venation; margins entire, toothed or spinous. *Flowers* usually showy, sub-actinomorphic, zygomorphic to strongly bilabiate; tubular (even if shortly so) below, spreading at tip where 5 or rarely 4-lobed; white, pink, lilac, blue, purple, red, butter-yellow or apricot-yellow, sometimes with patches or spots of contrasting colour; corolla tube divided into lower and upper portions at point of insertion of stamens; lower tube usually narrowly cylindrical; upper tube either narrow or variously inflated, relative lengths of lower and upper tubes variable; 5-lobed corollas either with 2 lobes in upper lip and 3 below; or with 4 lobes in upper lip and 1 below; in latter cases the median abaxial lobe usually split from corolla for greater distance than other lobes; 4-lobed corollas with the upper lip largest, usually notched at the apex. *Androecium* of 5, 4 or 2 epipetalous stamens; 2 median abaxial stamens always fertile, usually exserted from flower or at least conspicuously longer than other staminal elements; upper 3 stamens rarely fertile, usually variously reduced to staminodes or occasionally absent; filaments usually hairy at base, twisted through 180 degrees and crossing over near base; anthers of fertile stamens bithecous, thecae parallel, muticous, with longitudinal dehiscence; staminodes with or without anther thecae. *Pollen* spheroidal, deeply honeycombed. *Ovary* bicarpellary, 2-chambered, with 2 ovules or apparently 1 per locule (lower ovules sometimes very reduced); style terete, variously hairy or glabrous at base; stigma either 2-lobed, lobes sub-confluent, capitate or discoid, or stigma of 1 lobe, filiform. *Fruit* a dry, loculicidal, estipitate, 2-locular capsule; either compressed-quadrangular, obtrulloid without an apical beak or with a more or less

hollow apical beak; or compressed, spindle shaped without an apical beak (small apical point may be present); or turgid below with a prominent, solid, conical apical beak; septum either entirely ligneous or with membranous and ligneous portions, or almost entirely membranous. *Seeds* 2 or 4; usually discoid, flattened on one side, asymmetrical about the hilum, surfaces covered in hygroscopic hairs of various appearance, rarely entirely glabrous.

Approximate number of species: 300

Distribution: Africa, Madagascar, southern Asia, Indo-China, Phillipines, Japan, Mexico, Panama, the Caribbean.

Specimens seen: Listed in Appendix 2.

DISCUSSION:

Barleria is a large, polymorphic genus, the circumscription and sub-division of which has received attention from a number of authors (see Chapters 2, 3 and 4). The genus is readily distinguished from others in the Acanthaceae by a combination of three features: i) a 4-partite calyx with 2 large outer segments and 2 smaller inner ones; (ii) globose, honeycombed pollen, and (iii) the predominance of double cystoliths in the epidermal cells. In addition, many of the genera that are closely related to *Barleria* have didynamous stamens, a feature not present in this genus. Ideas on the affinities of *Barleria* are discussed in detail in Chapter 3 of this thesis. The views of modern authors (Balkwill & Getliffe Norris, 1988; Scotland, 1992) differ on certain details, but there is general agreement that genera such as *Lophostachys*, *Crabbea* and possibly *Lepidagathis* are probably the most closely related to *Barleria*. These genera all share quincuncial aestivation of the corolla. *Lepidagathis* is readily distinguishable from *Barleria* on the basis of differences in several characters, notably the pollen morphology and aspects of floral structure. The pollen of *Crabbea* is very similar to that of *Barleria*, but these genera are also easily separated as the calyx of *Crabbea* is equally 5-fid, not 4-partite with 2 inner and 2 outer lobes. Two other genera that on superficial appearances could be confused with *Barleria* are *Ruellia* (in Africa) and *Petalidium*. These genera differ markedly with respect to the form of the calyx, fruits, seeds and detailed structure of the flowers, thus reducing the possibility of misidentification.

B. cristata has been designated as the lectotype of *Barleria* by Brummitt and Vollesen

(1992; also see Jarvis, Barrie, Allan & Reveal, 1993). *B. prionitis* was the earlier choice of Britton & Wilson (1923 - 1926), but where sub-divisions of the genus have been made this species has usually been dealt with in Subgenus or Section *Prionitis*. *B. cristata* (designated by Green, 1929) has generally been treated as the generitype and, as Brummitt has observed, it would be unfortunate to have to rename Section *Prionitis* (which is a highly distinctive taxon), as Section *Barleria*. The choice of *B. cristata* as the type of *Barleria* is supported in this thesis.

i) Distributions and Numbers of Species.

Barleria is a widespread genus occurring from Japan in the Far East, through southern Asia, Africa, Madagascar and as far west as Mexico, Panama and Guatemala. It is however, predominantly an Old World genus with its greatest representation in Africa, followed by India, Madagascar and Asia (see Figure 7.1). The number of species in different regions tails off rapidly towards both the East and West, with 9 species recorded from the Far East and only two (which are probably conspecific) from the West. There are two major centres of diversity within Africa, the first comprising approximately 77 species in Tropical East Africa (an area including Tanzania, Kenya, Ethiopia and Somalia) and a second, comprising approximately 69 species, in Southern Africa (an area including South Africa, Namibia and Botswana). The figure for East Africa should probably be higher as there are a number of currently undescribed taxa in this region that were not included in the species counts made.

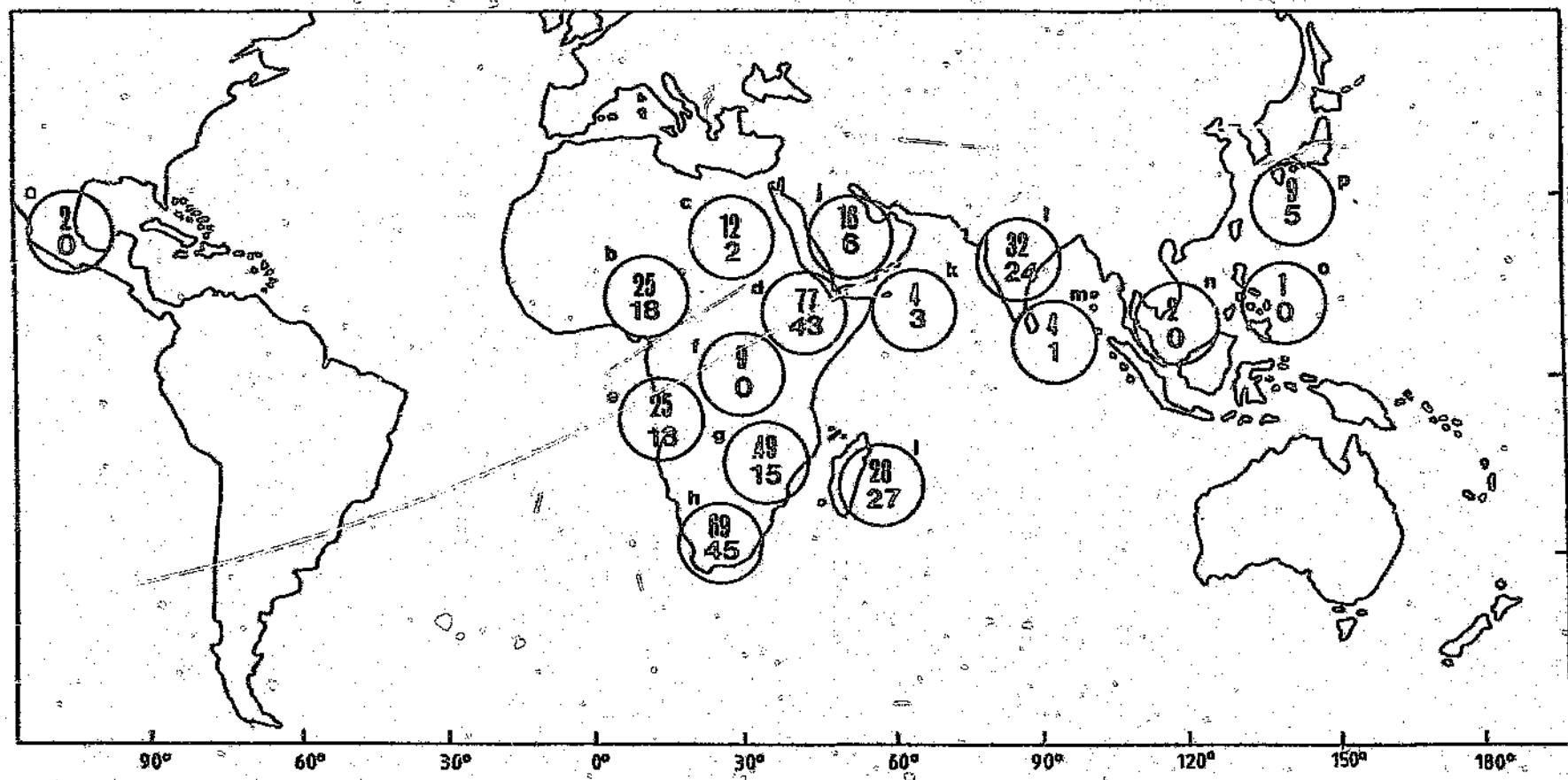
The distribution of numbers of species of *Barleria* in different regions of the world is shown in Figure 7.1 and Table 7.1. Reasonably accurate distribution records were obtained for all species of which herbarium material was seen (i.e. approximately 240 of the 300 species). For the remaining taxa it was necessary to rely on distribution records from the literature. As many of these records are possibly incomplete (often the only literature available being the original descriptions), the figures presented in the tables, maps and discussions below may be slightly inaccurate. However, a number of interesting trends can still be discerned using these figures as a general guide to make observations that could be tested in future investigations. Table 7.1 shows the number of species recorded in each of the major areas in which *Barleria* is represented; the regions represented in the maps and referred to in the following discussion were chosen

Table 7.1: Total numbers of species, number of endemics and number of representatives from each Section in each major area in which *Barleria* occurs. Abbreviations used: B-ia = Section *Barleria*; B-ops = Section *Barleriopsis*; B-anth = Section *Barlerianthus*; B-ites = Section *Barlerites*; Stel = Section *Stellatohirtae*; Som1 = Section *Somalia*, "typical" group, e.g. *B. aucherana*; Som2 = remainder of Section *Somalia*; Prio = Section *Prionitis*.

area	total no. of species	no. endemic	numbers of species from different Sections in each major area								
			B-ia	B-ops	B-anth	B-ites	Stel	Som1	Som2	Prio	not seen
Far East	9	6	2	1	-	-	-	-	-	1	5
India	32	24	10	8	5	-	-	1	1	3	4
Sri Lanka	4	1	1	3	-	-	-	-	-	-	1
Arabia	16	6	4	-	-	1	1	4	-	3	3
North Africa	12	2	4	-	-	2	-	2	1	2	1
East Africa	77	43	13	2	1	18	4	6	3	16	14
Uganda etc.	9	-	1	-	-	7	-	1	-	-	-
West Africa	28	18	4	2	1	8	3	-	2	1	4
Fl. Zam. area	49	15	24	-	-	1	5	-	10	7	5
Angola	25	13	5	-	-	2	5	-	10	0	3
Southern Africa	69	45	32	3	-	1	3	-	17	8	2
Central Americas	2(1)	-	-	2(1)	-	-	-	-	-	-	-
Madagascar	28	27	7	-	-	1	-	-	5	11	4
Socotra	4	3	1	-	-	-	-	1	1	1	-
Malaya and Phillipines	3	-	-	-	-	-	-	-	-	3	-

Figure 7.1: Map showing global distribution of *Barleria* and the numbers of species occurring in different regions of the world.

Lettered circles represent the major regions in which *Barleria* is represented; the region denoted by each letter, and the countries included in it, are given in Table 7.2. Within each circle the upper letter represents the approximate number of species recorded from the region and the lower letter represents the number of those species that is endemic to the region.


a
2
0
b
25
18
c
12
2
d
77
43
e
25
18
f
9
0
g
49
15
h
69
45
i
28
27
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0°
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60°
90°
120°
150°
180°
30°
0°
30°

Table 7.2: Symbols used to denote major areas of the world in which *Barleria* occurs.

Symbol used	Area denoted	Countries included in area
a	Central Americas	Mexico, Panama, Guatemala
b	West Africa	Senegal, Sierra Leone, Liberia, Togo Ivory Coast, Ghana, Nigeria, Cameroon, Congo
c	North Africa	Egypt, Sudan
d	East Africa	Ethiopia, Somalia, Djibouti, Tanzania, Kenya
e	Angola	Angola
f	Uganda	Uganda, Rwanda, Birundi, Zaire
g	Flora Zambeziaca regions	Malawi, Zimbabwe, Mocambique, Zambia
h	Southern Africa	Namibia, Botswana, South Africa
i	Madagascar	Madagascar and the Mascarene Islands
j	Arabia	Saudi Arabia, Yemen, Oman
k	Socotra	Socotra
l	India	India, Bhutan
m	Sri Lanka	Sri Lanka
n	Malaya	Malayan Peninsula, Malayan Islands
o	Phillipines	Phillipines and associated Islands
p	Far East	Japan, China, Thailand

to correspond with the major areas for which Floras have been or are being written. They also correspond reasonably closely with major phytogeographic zones recognised in Africa. The countries included in each of the regions referred to are listed in Table 7.2. The number of taxa restricted or endemic to each region is given and the numbers of representatives of each Section within each Section is provided in Table 7.1. The number of species shared by the major regions was determined and used to calculate a Sorenson's Index (Mueller-Dombois & Ellenberg, 1974) which was used as a simple measure of the degree of similarity between the regions on the basis of the occurrence

Table 7.3: Matrix of Sørenson's Indices showing similarity (as a percentage) between different areas in terms of species of *Barleria* present. Symbols used to denote regions are the same as those given in Table 7.2 and Figure 7.1

Area	a	b	c	d	e	f	g	h	i	j	k	l	m	p
a	-	0	0	0	0	0	0	0	0	0	0	0	0	0
b		-	16.2	.8	12	11.7	5.4	2.1	0	4.8	0	0	0	5.4
c			-	20.2	5.4	28.5	3.2	2.1	0	28.5	0	9.0	0	9.5
d				-	3.9	18.6	15.8	6.8	1.9	21.5	2.4	2.7	0	2.5
e					-	0	13.5	6.3	0	0	0	0	0	0
f						-	0	0	0	16	15	0	0	11.1
g							-	44	2.5	0	0	0	0	3.4
h								-	2.0	0	0	1.9	0	2.5
i									-	0	0	3.3	0	5.0
j										-	0	11.1	0	0
k											-	0	0	0
l												-	16.6	14.6
m													-	0
p														-

of species of *Barleria*. These indices are provided in Table 7.3.

A particularly interesting aspect of the distribution patterns within *Barleria* is the relatively high level of endemism in many of the major regions (Figure 7.1; Table 7.1). All but one of the species occurring in Madagascar is endemic to the island. In itself this may not seem remarkable as high levels of endemism are known in many other plant and animal groups on this island. It is, thus, particularly interesting to note how high the levels of endemism are in other regions such as India (75% endemism), West Africa (72 % endemism), Southern Africa (65% endemism) and East Africa (55,8% endemism). The figure for East Africa represents an underestimate as it was not possible to include a number of as yet undescribed taxa endemic to this area in the counts made.

These relatively high levels of endemism are paralleled by correspondingly low degrees of similarity between the regions. The highest degree of similarity shown between any two regions is that of 44% between Southern Africa and the countries of the Zambezian region. The Zambezian region in turn shares 15.8% of its species with East Africa, a higher degree of similarity than it shows to Angola, which spans a similar latitude. Approximately half of the species occurring in Angola are also endemic to it and the remaining species provide a link between southern Africa and the Guineo-Congolian region of West Africa. The index of similarity between Southern Africa and East Africa is low (6.8%). Balkwill (1985) found that a number of species of *Dicliptera* Juss. and *Peristrophe* Nees occur in Southern Africa (particularly the dry western parts) and East Africa with a distinct Arid Corridor link. This pattern is not reflected in the distribution of species of *Barleria*, as only a few species, notably *B. lugardii*, *B. rogersii* (= *B. taitensis*) and *B. mackenii*, from the Namibian region are shared with East Africa. The East African region shows a greater similarity to Arabia and North Africa than it does to any other region of Africa (Table 7.3). The number of species shared between North Africa and the central region including Uganda, Rwanda and Birundi is greater than the number shared by this region and neighbouring East Africa. The degree of similarity between the Ugandan region and North Africa is the same as that between North Africa and Arabia. The degree of similarity shown between India and all other regions is generally low (less than 17%), but the affinities it does show lie more strongly with the Far East, Sri Lanka and Arabia than they do with any African region. The only African regions sharing any species with India are North Africa (Sorenson's Index of 9%), East

Africa (2,7%) and Southern Africa (1.9%).

An interesting point that emerges from the data presented in Table 7.1 is that the members of the different sections of *Barleria* tend to be concentrated in certain geographic regions. Furthermore, many of the endemics in the different regions belong predominantly to only one or two of the sections. East and West Africa are the only regions of the world in which all sections of *Barleria* are represented. The *Barleria* flora of the East African region is, however, dominated by members of Sections *Barlerites* and *Prionitis*, followed by Section *Barleria* and small numbers of species from each of the other sections (Table 7.1). The neighbouring Ugandan region is also dominated by members of Section *Barlerites*, with all but two of the species belonging to this section. The only other sections represented in this region are *Barleria* and *Somalia*. The North African and Arabian regions are similar in that the Sections *Barleria, Prionitis* and *Barlerites* are more or less equally well represented. Neither of these regions has any members of the Sections *Barleriopsis* and *Barlerianthus*. A point of difference between these two regions is that Section *Somalia* (which has only one representative in North Africa) is represented by four species in Arabia, and Section *Stellatohirtae* (which is absent from North Africa) has one species in Arabia. All of the sections are represented in West Africa, but about one third of the species in this area belong to section *Barlerites*; the remaining two thirds of the species fall mainly into Section *Barleria*, with only one or two representatives from each of the other sections. Members of the "typical" group of Section *Somalia* are present in West Africa, but there are no representatives from the other parts of the Section in this region. The Zambezian and southern African regions are dominated by members of Section *Barleria*, which account for just about half of the total number of species in each case. Section *Somalia* is also well-represented in these two regions, especially in Southern Africa. The Angolan region is dominated by members of section *Somalia*, with about equal proportions of sections *Barleria* and *Stellatohirtae* accounting for the bulk of the remaining species. Section *Barlerianthus* is absent from the Zambezian, southern African and Angolan regions. Section *Barleriopsis* is represented in southern Africa but not in the Zambezian or Angolan regions. The *Barleria* floras of all other regions tend to have representatives from only a few of the sections. In Madagascar, for example, only Sections *Barleria, Prionitis, Somalia* and *Barlerites* are represented and in the Americas only Section *Barleriopsis* is present.

Placing an interpretation on these distribution patterns may seem premature at this stage; the numbers of species indicated for different regions are slightly inaccurate and are likely to change when the genus is revised fully. However, from the observations made using the available data it is at least possible to formulate an hypothesis which can be tested when more data become available. All of the sections are represented in East Africa and this region also has the highest number of species. It seems reasonable, using traditional criteria (Humphries & Parenti, 1986) to propose that this region represents the probable centre of origin of the genus. This, however, does not fit strictly with Hennig's Progression Rule (Humphries & Parenti, *l.c.*). Central to Hennig's method for locating the "centre of origin" of a monophyletic group, was the idea that phylogenetically primitive members would be found close to that centre. Within *Barleria* some of the phylogenetically more basal groups are found at the proposed centre of origin, but they also occur in geographically more peripheral areas and, in the case of Section *Barleria* have the centre of diversity far away from the centre of origin. Likewise, some of the more derived groups (e.g. *Section Prionitis*) have their greatest representation in the proposed centre of origin. I believe, however, that it is still possible to find a reasonably sensible explanation of these patterns that satisfies the theoretical criteria of biogeography and cladistics.

All sections, both phylogenetically basal and derived, are represented in the East African region. An initial wave of evolution occurred in this region giving rise to a wide variety of forms. This was followed by differential dispersal away from the centre of origin into the various regions now occupied by members of the genus. The taxa within each region then underwent a secondary flush of adaptive radiation leading to a great diversification within a particular part of the entire range of variation. This could account both for the high degree of endemism shown in many of the regions and the predominance of particular sections (representing monophyletic lineages) in certain geographic regions. The affinity shown between India and North Africa also points to a relatively recent invasion of species and so would fit with the hypothesis presented above. The hypothesis would also fit with the known pattern of seed dispersal in *Barleria* and with the fine scale distribution patterns displayed by many of the species. Seed dispersal occurs over relatively short distances (up to a few metres) and is effected by explosive, often hygrochastic dehiscence of the capsules. This results in the "clumping" of plants within areas (see Chapter 5); although many of the species have a fairly restricted

distribution on a broad scale, where they occur they tend to dominate the vegetation. This hypothesis should be well worth testing on a more rigorous basis. It would also be interesting to compare the apparent trends detected here with distribution patterns in other widely distributed acanthaceous genera.

ii) Infra-generic Taxa

Barleria is a highly variable genus; variation in characters and character states has been discussed in detail in Chapter 5 of this dissertation and will not be discussed here. Almost all characters in the genus show some degree of variability, but certain characters, especially those that might influence the type of pollination system (e.g. morphology of the androecium, morphology of the corolla), are more labile than others. Other characters, which initially may seem to provide useful criteria for the delimitation of groups have sporadic occurrence throughout the genus and so are somewhat unreliable. Any attempt to divide all the species of *Barleria* into groups based on co-occurrence of a wide range of characters or on details of corolla morphology, is bound to result in a plethora of very small, para- or polyphyletic taxa and despair on the part of the taxonomist. The classification presented below is based on fundamental differences in only a few characters, the homology and evolutionary polarity of which could be determined with some confidence (see earlier discussion, Chapter 5). Each taxon described below is clearly defined by the presence of at least one shared derived character state. Two sub-genera are recognised, one comprising two sections and the other comprising five. Variation in certain aspects of corolla morphology, pubescence and the morphology of the bracts and inflorescence is used to identify smaller groups within some of the sections, but these groups are only described informally here. Although some of these smaller groupings are defined by unambiguous synapomorphies, and are thought to represent likely monophyletic groups, synapomorphies could not be found for all of them with the available data. It is likely that with more complete data sets for some of the taxa, especially those from Madagascar and India, full resolution of these groups could be achieved; they should then be formally described and accorded sub-sectional status.

KEY TO THE INFRA-GENERIC TAXA OF *BARLERIA*

1. Seeds usually 2, only rarely 4 (if 4 seeds present then in a capsule with a hollow apical beak); septum of fruit either entirely woody or with a broad membranous portion above the upper ovules, or almost entirely membranous; corolla invariably with 4 lobes in upper lip, 1 lobe in lower lip, this split from corolla for some distance . . . . . (Sub-genus Prionitis) . . 2

   Seeds 4, always covered in hygroscopic hairs; capsule without a prominent apical beak; septum of fruit predominantly woody with a narrow membranous portion at tip above upper ovules; corolla variable . . . . . (Sub-genus Barleria) . . 6

2. Capsules with a prominent, solid, conical apical beak; seeds 2, housed in turgid base of capsule 3

   Capsules usually without an apical beak; seeds 2; if capsule beaked then beak more or less hollow and capsule with 4 seeds 4

3. Plants with sunken glands scattered on lower leaf surfaces (appear as small black or brown dots in dried material or as crystalline structures in fresh material); septum of capsule entirely woody; plants invariably armed with 2, 4 or 6-rayed axillary spine systems developed from the lower axillary bud; flowers usually apricot yellow, rarely burnt orange or blue . . . . . Section *Prionitis*

   Plants variously pubescent or glabrous, but lacking scattered sunken glands on lower leaf surfaces; septum of capsule with membranous section above ovules; plants innocuous; flowers usually blue, white, mauve or lilac, rarely butter-yellow . . . . . Section *Somalia*

4. Septum of capsule almost entirely membranous; capsules flattened, spindle-shaped with strong woody flanks, usually without a prominent beak; seeds usually 2, but if 4 then glabrous and in a capsule with a hollow apical beak 5

Septum of capsule woody in lower parts, and membranous above the upper ovule; capsules obtrulloid and markedly tapered below the upper seeds, somewhat flattened laterally but without woody flanks, with a prominent hollow beak; seeds 4, glabrous or with creamy-buff hygroscopic hairs . . . . . Section *Barlerianthus*

5. Plants with a pubescence of simple hairs; walls of capsule tearing away from woody flanks upon dehiscence; stigma 2-lobed, sub-confluent, capitate . . . . . Section *Barlerites*

Plants with a conspicuous pubescence of stellate or dendroid hairs (with or without additional simple trichomes); walls of capsules remaining intact upon dehiscence; stigma 1-lobed, filiform . . . . . Section *Stellatohirtae*

6. Inflorescences simple, axillary; inflorescence units based on scorpioid cymes sometimes reduced to solitary flowers; calyx scarious, often with toothed or spinous margins; leaves usually with a sharp apiculus; pubescence variable, of simple or complex hairs; flowers white, lilac, blue or red . . . . . Section *Barleria*

Inflorescences compound, units arranged in lax or congested terminal synflorescences; calyx variable, but if scarious then without prominent spines along margins; leaves generally herbaceous, softly-textured and without a sharp apiculus; pubescence of simple hairs only, usually conspicuously yellow; flowers butter-yellow, white or blue . . . . . Section *Barleriopsis*

Enumeration of the Taxa

In the following account, two sub-genera and seven sections are formally described and typified. Lists of the species included in each taxon are provided and where type material has been seen it is indicated in the list of voucher specimens in Appendix 2. A selection of the material seen is cited in Appendix 2. The lists of taxa included in each group do not include those names that are thought to be synonyms of others (see Appendix 1). Smaller groups are described informally within some of the sections. For each of these, a "typical"species is cited; this species typifies my concept of the group. Should any of these smaller groups be formally described at a later stage, the typical species given should be the type of the group, once the typification of this species has been checked. A list of all the species that could not be placed in a Section (either because material was not seen or descriptions did not provide adequate detail) is provided at the end of this Chapter. For each taxon the following illustrations are provided: photographic plates showing typical representatives of the group; line drawings showing range of variation in certain characters; distribution map.

Subgenus I: Barleria

Type: *B. cristata* L.

Herbs, shrubs or suffrutices; plants either innocuous or spinescent; spinescence due to presence of spinous tips or margins of leaves and calyces or due to presence of axillary spine systems in lower leaf axils (spine systems derived from upper bud in each leaf axil as a sterile or aborted inflorescence with spinous bracteoles). *Flowers* either sub-zygomorphic with 2 lobes in upper position and three in lower or strongly bilabiate with 4 lobes in upper lip, one in lower lip split from corolla for greater distance than other lobes; corolla red, blue, white or yellow. *Stigma* of 1 or usually 2 lobes. *Androecium* of 5 parts, rarely all 5 or 4 fertile; 2 abaxial stamens fertile; 3 adaxial stamens reduced to staminodes, 2 with anther rudiments, median adaxial one highly reduced to thread-like

filament. *Capsule* without a prominent apical beak, compressed-quadrangular, broadest in upper half or third; septum ligneous for most part with narrow membranous portion above upper ovule. *Seeds* 4, surfaces covered with hygroscopic hairs.

Included sections: *Barleria, Barleriopsis.*

Approximate number of taxa: 100

Section I: ***Barleria***

Type: *B. cristata* L.

Herbs, shrubs and suffrutices, perennial or rarely with annual stems from a perennial rootstock; plants often with aborted inflorescences (developed from upper axillary bud) present in leaf axils, these usually forming axillary spine systems due to spinous nature of bracteoles. *Leaves* of variable size and texture, usually dense with cystoliths; apex invariably sharply apiculate or mucronate; margins usually entire, sometimes serrate or spinous, sometimes white-cartilaginous with small undulations. *Inflorescence* simple, axillary; inflorescence units based on scorpioid cymes (sometimes reduced to solitary flowers) or with dichasial and monochasial branching but then the monochasial part scorpioid. *Bracteoles* often stiff, spinous with serrate or spinous margins, sometimes entirely reduced to solid, cylindrical spines; occasionally leaf-like and innocuous. *Calyx* scarious, outer and inner lobes very strongly differentiated in shape and size; apex of outer lobes often spine tipped, anticous lobe often shortly bifid; margins of outer lobes rarely entire, usually serrate or equipped with spines; venation conspicuous, often with prominent pattern of reticulation. *Flowers* weakly to strongly zygomorphic, lobes often in 2+3 configuration, more rarely in 4+1 configuration; median abaxial lobe not noticeably split from corolla tube; tube well-developed, usually considerably longer than corolla lobes, upper tube equal to or longer than the lower; corolla blue, red or white. *Androecium* of 5 parts, rarely all fertile; usually 2 abaxial stamens fertile and exserted; 3 adaxial elements greatly reduced to staminodes, 2 usually with anther rudiments, the third reduced to a thread-like filament. *Stigma* of 2 sub-confluent, capitate lobes. *Ovary* with 4 equally well-developed ovules.

Approximate number of taxa: 67

Figures: 7.2 and 7.3

Plates: 7.1 and 7.2.

Figure 7.2: Variation in the morphology of the leaves, corollas, bracteoles and calyces of selected representatives of Section *Barleria*.

a) - g) posticous calyx lobes, abaxial surfaces shown; h) - l) corollas, opened along median adaxial line, between upper two corolla lobes; m) - t) leaves, adaxial surfaces shown; u) - z) bracteoles, adaxial surfaces shown, excepting z1 and z2.

a) *B. meeuseana* x 4: le Roux & Jankowitz 1488 (WIND); b) *B. hillcoatiae* x 4: Wood 3038 (K); c) *B. lichtensteiniana* x 2: van Wyk 8689 (J); d) *B. heterotricha* x 5: Balkwill & Balkwill 6321 (J); e) *B. vincaefolia* x 2: du Puy & Rafamantantsoa MB187 (K); f) *B. obtusa* x 2.5: Balkwill 668 (K); g) *B. repens* x 2.5: Henrico s.n. (NBG); h) *B. bremekampii* x 2.5: Balkwill & Balkwill 5830 (J); i) *B. irritans* x 2.5: Mauve 5238 (PRE); j) *B. acantholdes* x 1.5: Gillett 13437 (K); k) *B. virgula* x 3: Reyneke 67 (PRE); l) *B. solitaria* x 1.5: Giess & Barnard 8034 (NBG); m) *B. eylesii* x 1: Plowes 3455 (K); n) *B. acantholdes* x 2: Carr 171 (EA); o) *B. stimulans* x 2: Bolus 11 616 (BOL); p) *B. heterotricha* x 2: Balkwill & Balkwill 6321 (J); q) *B. aculeata* x 2: Miller, Guarino, Obadi Hassan Mohammed M8643 (K); r) *B. papillosa* x 2: Kruger K16 (STE); s) *B. rigida* x 2: van Wyk 8587a (J); t1) *B. bechuanensis* x 2, without cartilaginous margins: Esterhuysen 1007 (PRE); t2) *B. bechuanensis* x 2, with cartilaginous, undulate margins: Esterhuysen 1007 (PRE); u) *B. irritans* x 2: Mauve 5238 (PRE); v) *B. bremekampii* x 2: Balkwill & Balkwill 5830 (J); w) *B. argillicola* x 2: Balkwill, Balkwill & Green 5948 (J); x) *B. fulvostellata* x 2: Bidgood, Mwasumbi & Vollesen 717 (K); y) *B. solitaria* x 4: Giess & Barnard 8034 (NBG); z1) *B. macrostegia*, small bracteole of a pair, x 2.5: Mogg 35 677 (J); z2) *B. macrostegia*, large bracteole of a pair, x 2.5: Mogg 35 677 (J).

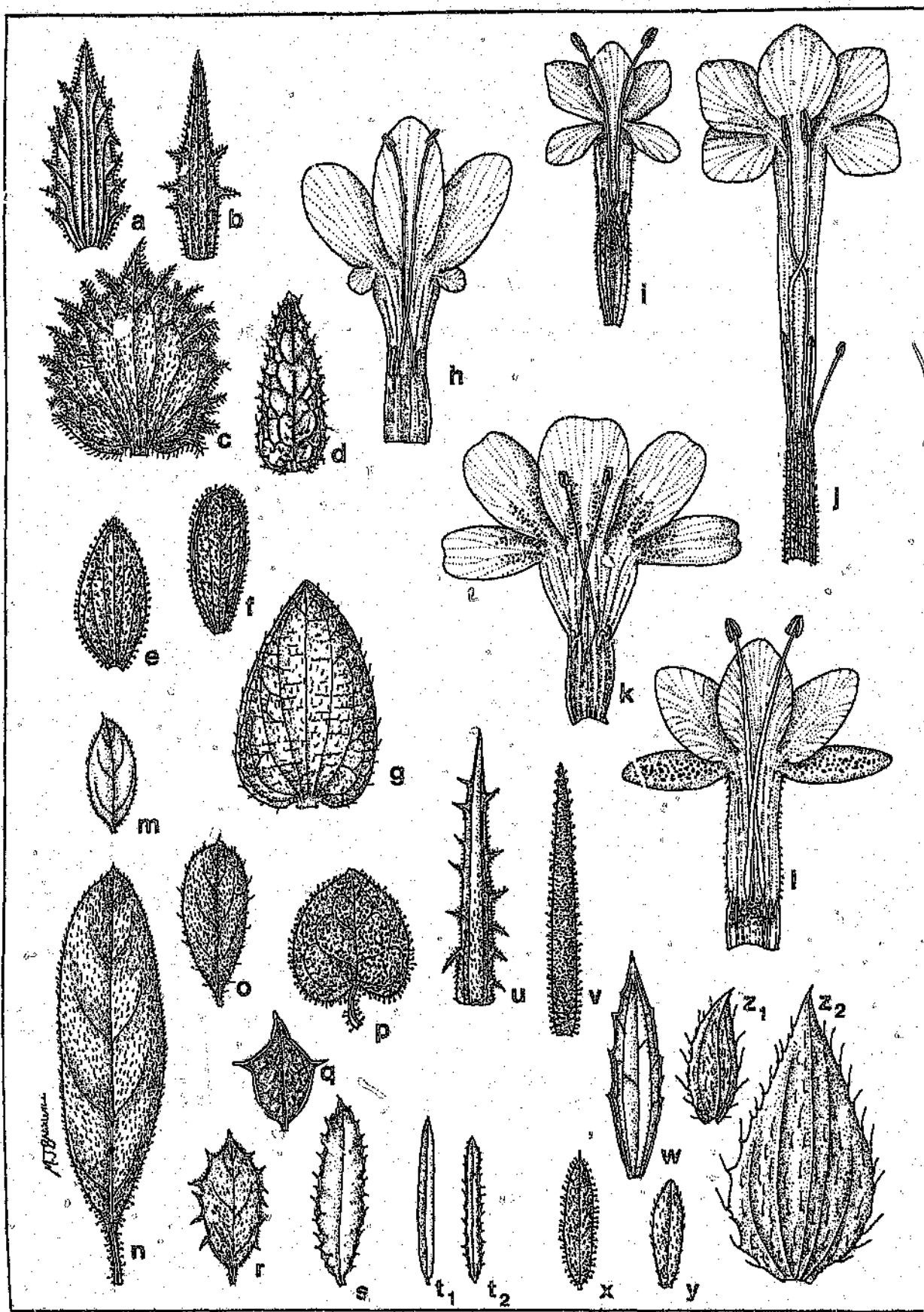
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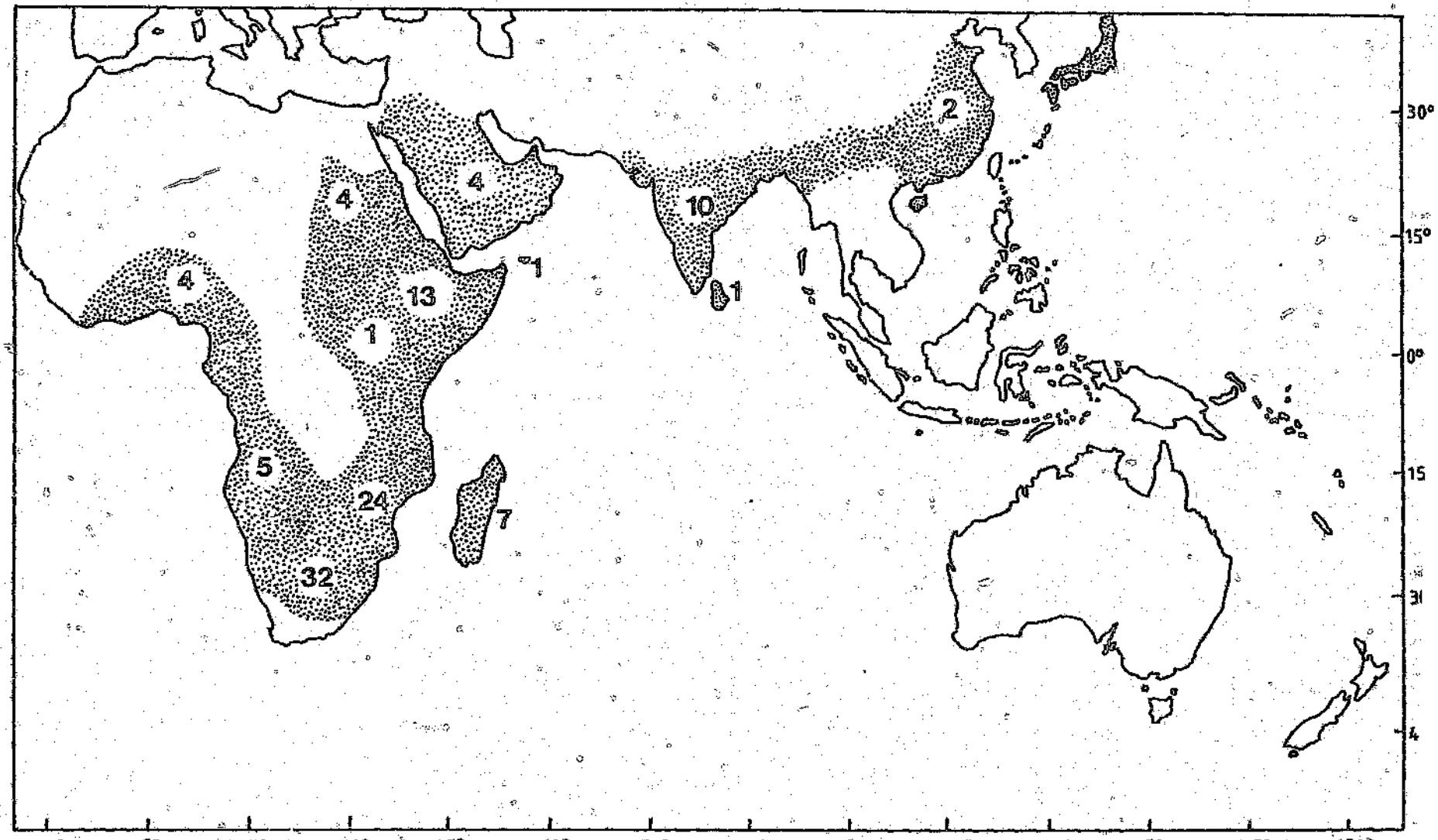
Figure 7.3: Global distribution of members of Section *Barleria* (stippled area). The number of species occurring in each of the major regions is indicated.



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7
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30°
15°
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30
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15°
0°
15°
30°
45°
60°
75°
90°
105°
120°
135°
150°
165°
180°

Section *Barleria* is very easily distinguished from the others in the genus by its conspicuously scarious calyx and axillary inflorescences based on scorpioid cymes. Many of the plants in this section are prickly or harshly spinous, whereas those in Section *Barleriopsis* generally are not.

Section *Barleria* is the most widespread section occurring almost throughout the entire range of the genus. It is absent only from the New World and is only weakly represented in the Far East. Its greatest representation is in Africa where it is present in all regions, particularly along the eastern part of the continent. Members of this section predominate in sub-tropical and temperate southern Africa and in the Zambezian region, where they account for approximately half of the total number of species of *Barleria* present. The next greatest number of species from this section is found in East Africa (see Table 7.1).

Included taxa: *B. acanthoides, B. aculeata, B. affinis, B. argillicola, B. aromatica, B. asterotricha, B. bechuanensis, B. biloba, B. bolusii, B. bornueinsis, B. bremekampii, B. buxifolia, B. candida, B. capitata B. carruthersiana, B. crassa, B. cristata, B. cyanea, B. damarensis, B. elegans, B. eylesii, B. fulvostellata, B. grandicalyx, B. greenii, B. gueinzii, B. heterotricha, B. hillcoatiae, B. homoiotricha , B. humbertii, B. irritans, B. jubata, B. kirkii, B. kitchingii, B. lanceata, B. lanceolata, B. lateralis, B. lichtensteiniana, B. longiflora, B. longissima, B. macrostegia, B. meeuseana, B. merxmeulleri, B. molensis, B. morrisiana, B. mucronata, B. mucronifolia, B. mysorensis, B. noctiflora, B. nyasensis ,B. obtusa, B. oxyphylla, B. papillosa ,B. paucidentata, B. pilosa, B. pungens, B. querimbensis, B. ramulosa, B. repens, B. rigida, B. rotundisepala, B. saxatilis, B. scabriuscula, B. sepalosa, B. siamensis, B. solitaria, B. spinifolia, B. spinisepala, B. spirulosa, B. steudneri, B. stimulans, B. sunzuana, B. tomentosa, B. transvaalensis, B. variabilis, B. vincaefolia, B. violascens, B. virgula.*

This Section can be subdivided into a number of more or less clearly defined groups based on variations in particular characters. A short description and discussion of each is provided below.

Group 1: "Typical".

Plates: 7.1a and 7.2a

Members of this group almost always have a sharp apiculus or stiff mucron present at the tip of the leaf. The bracteoles are usually spinous and are equipped with stiff or spinous teeth along the margins. Axillary spine systems are almost always present in the lower leaf axils. The presence of stiff spines or small teeth along the margins of the calyx often add to the general prickliness of the plants. The cystoliths are often extremely dense and are easily visible in dried specimens. This group accommodates the bulk of species included in the section, and repeats the general trend in distribution of the section.

Included taxa: *B. argillicola, B. acanthoides, B. bechuanensis, B. candida, B. cristata, B. cyanea, B. damarensis, B. elegans, B. eylesii, B. grandiculyx, B. greenii, B. hillcoatiae, B. homoiotricha, B. humbertii, B. irritans, B. jubata, B. lanceata, B. lanceolata, B. longissima, B. meeuseana, B. merxmeulleri, B. noctiflora, B. nyasensis, B. mucronata, B. mucronifolia, B. oxyphylla, B. papillosa, B. pungens, B. ramulosa, B. rigida, B. saxatilis, B. scabriuscula, B. spinisepala, B. spinifolia, B. stimulans, B. transvaalensis, B. virgula.*

Group 2

Typical species: *B. bremekampii.*

Plate: 7.1d

The most prominent characteristic of this group is the presence of a stout pair of solid, cylindrical spines (aborted inflorescences) in almost all the lower leaf axils. The fertile bracteoles are totally reduced to solid, cylindrical spines. The inflorescence units in this group are usually reduced to solitary flowers, but may be few-flowered scorpioid cymes. The corolla has five lobes in the "2+3" configuration and the upper two lobes are usually markedly reduced relative to the lower three, a feature also seen in Group 3. The corolla tube is usually equally narrow throughout its length with the upper tube equal in length to the lower. The calyx is typically scarious, but the margins are either entire or only shallowly denticulate, rather than stiffly spinous as seen in the "typical" group.

This assemblage of species is mainly African, but includes 2 species from India and one

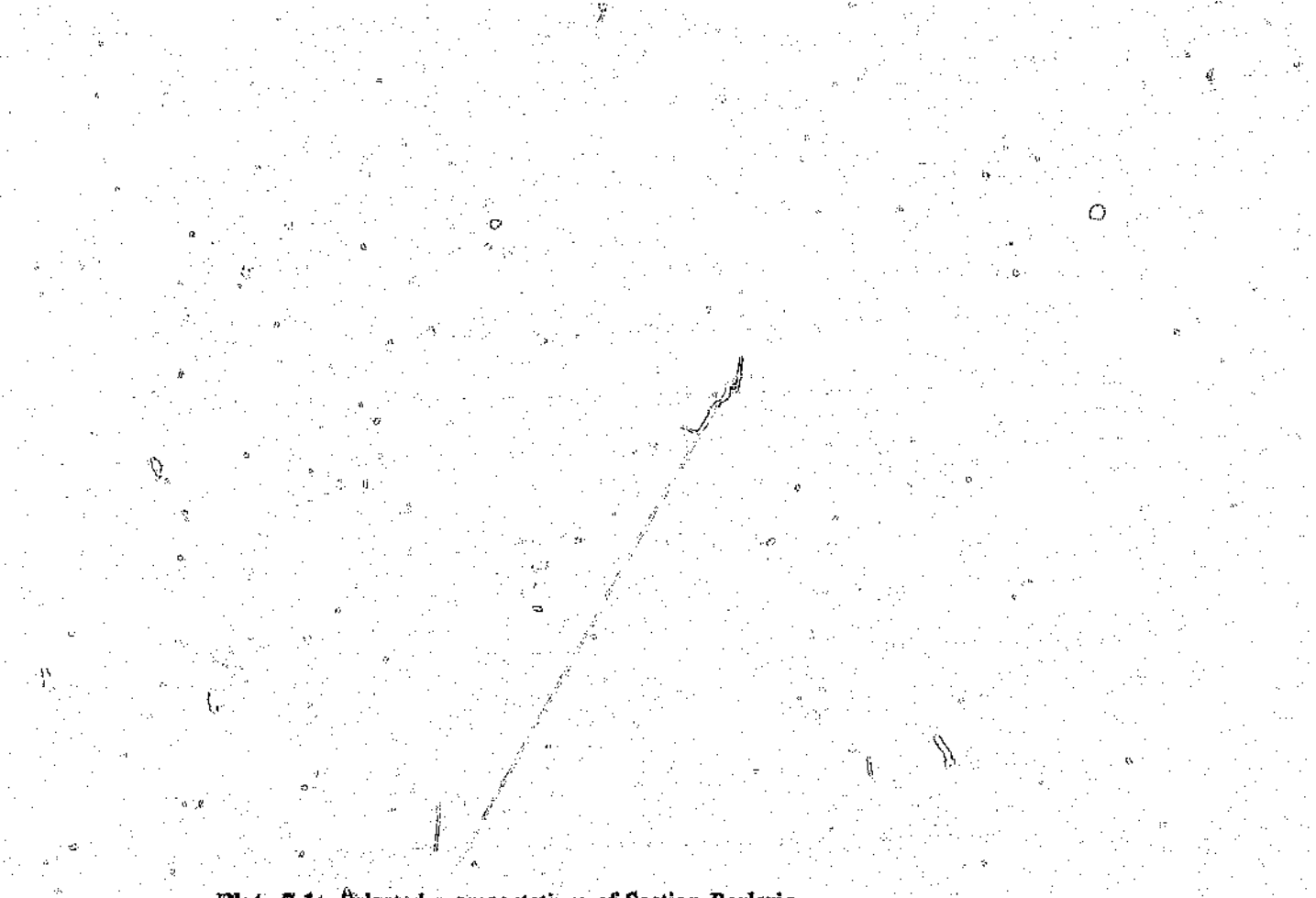
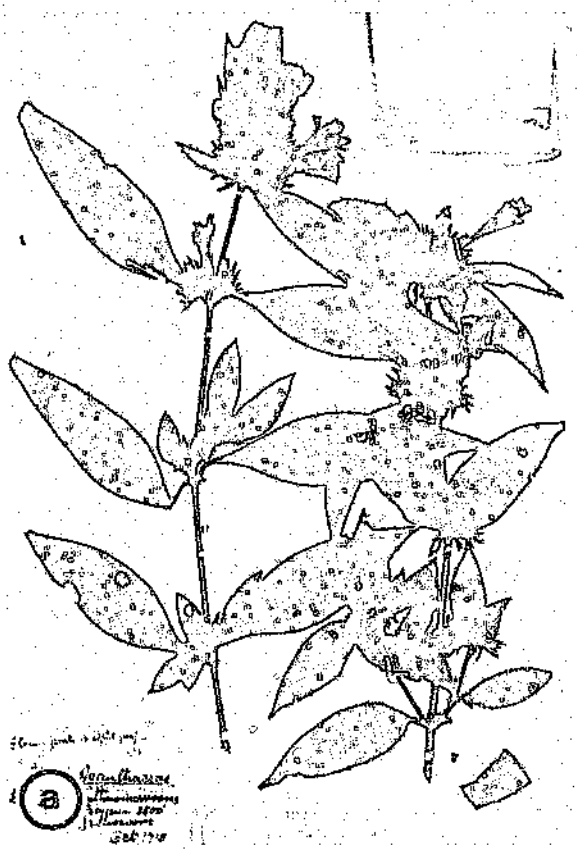


Plate 7.1: Selected representatives of Section *Barleria*.
a) *B. cristata*: Anderson 73 (E); b) *B. morissiana*: Barnes 2122 (K); c) *B. longiflora*: Bourne s.n. (K); d) *B. bremekampii*: Meeuse 9331 (K).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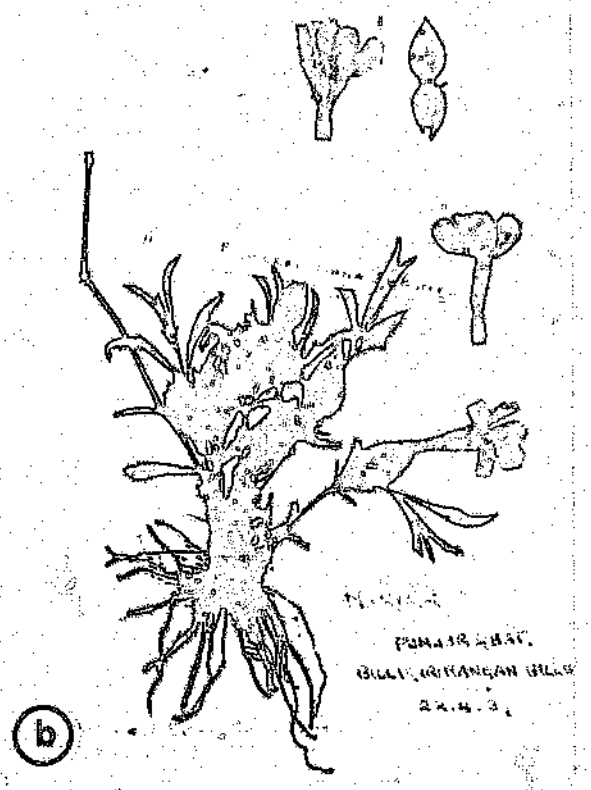
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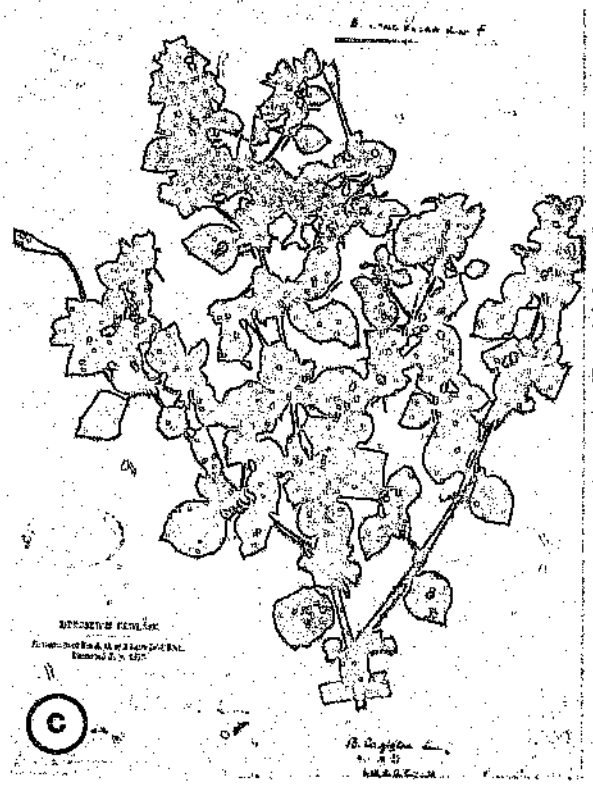
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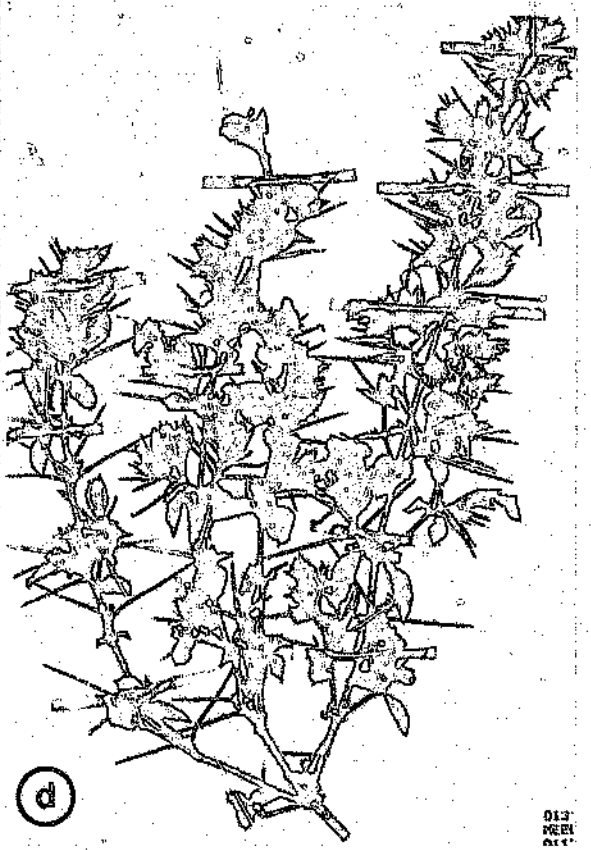
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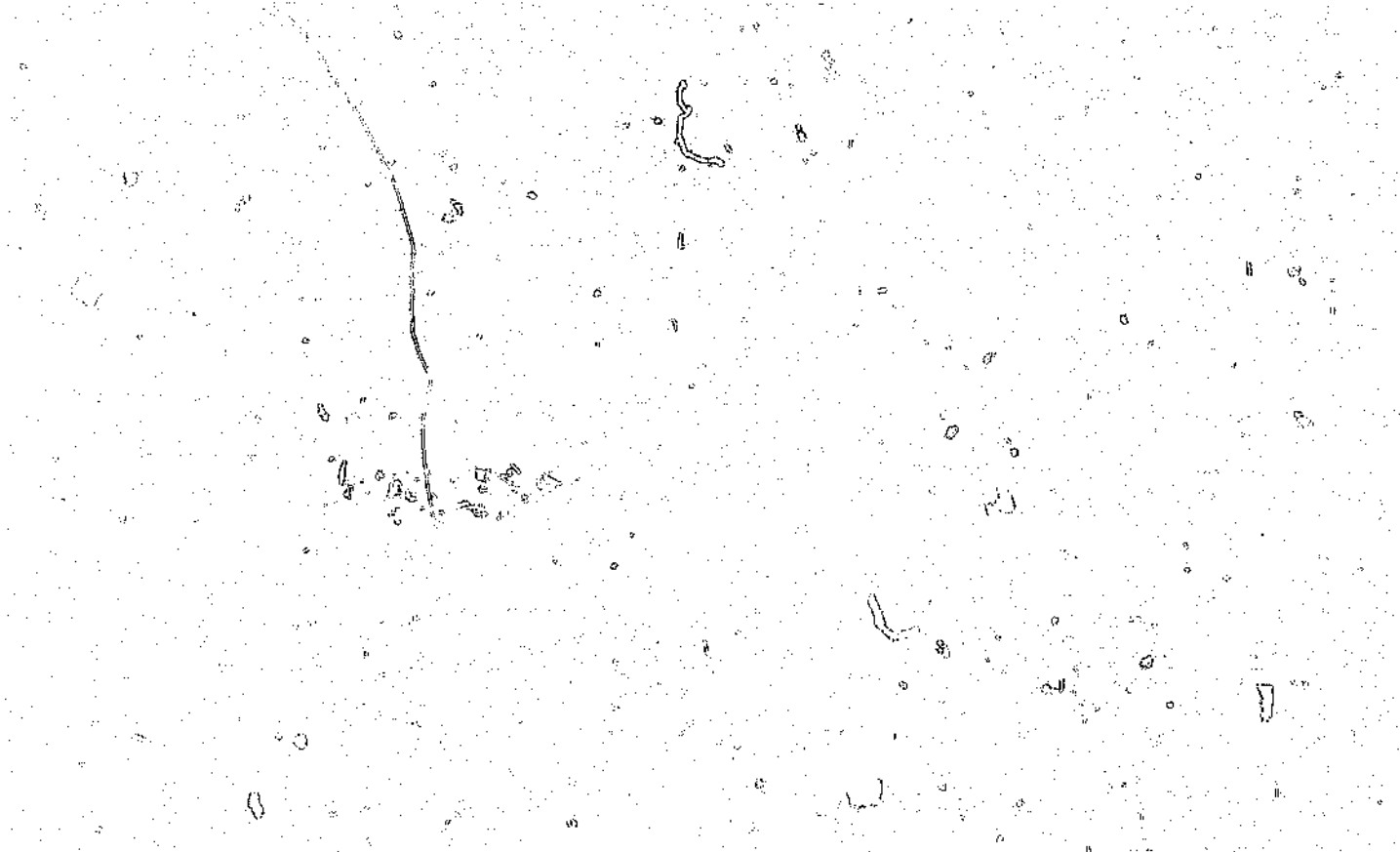
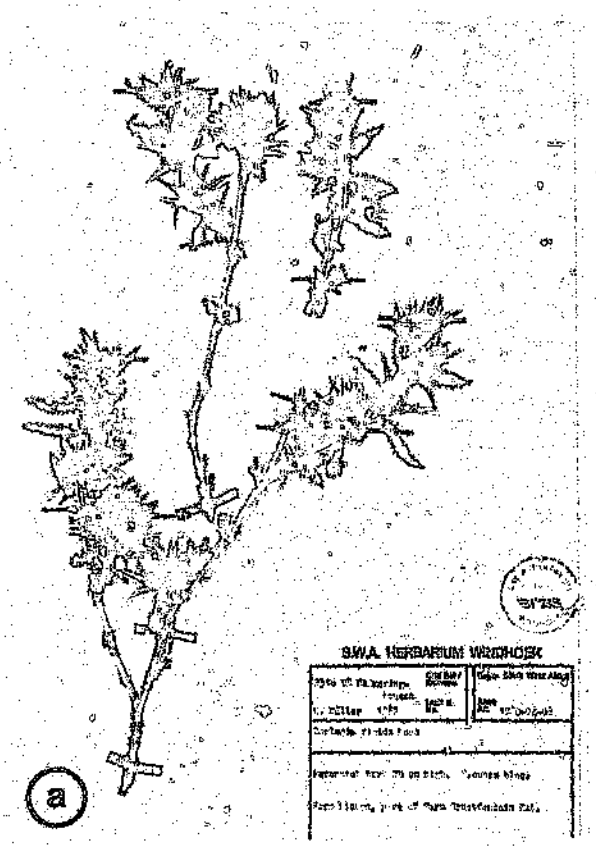
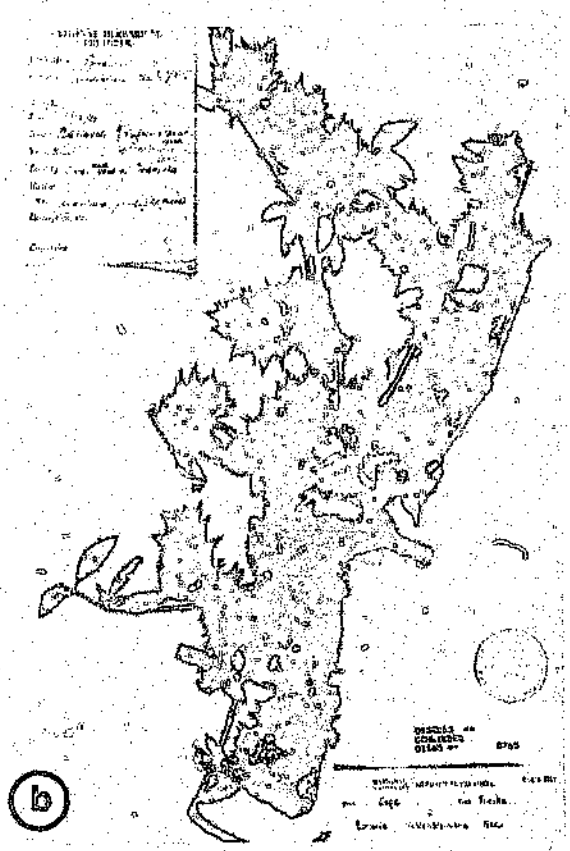


Plate 7.2: Selected representatives of Sections *Barleria* and *Barleriopsis*. a) *B. rigida* (Section *Barleria*): Muller 1282 (WIND); b) *B. lichtensteiniana* (Section *Barleria*): Schlieben 8765 (PRE); c) *B. macrostegia* (Section *Barleria*): Germishuizen 2671 (PRE); d) *B. strigosa* (Section *Barleriopsis*): Grierson & Long 3382 (E).


S.W.A. HERBARIUM WINDHOEK
a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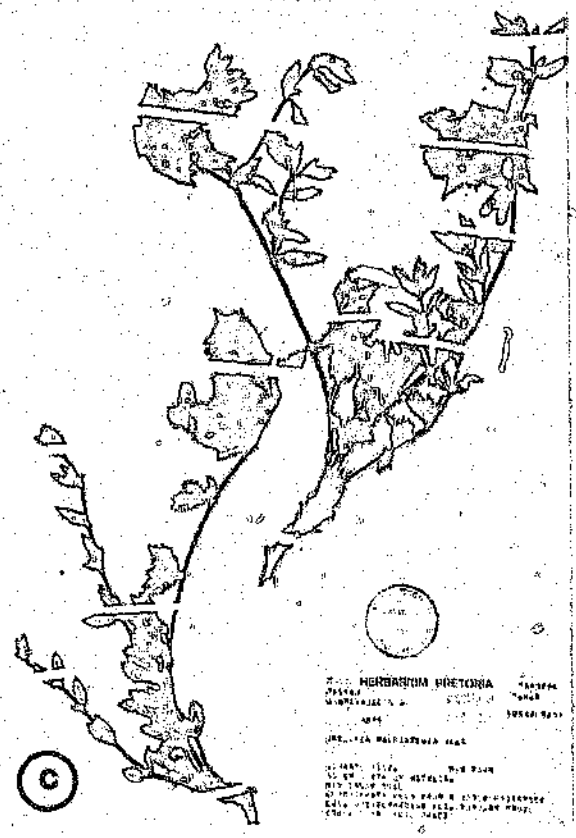

HERBARIUM PRETORIA
c

d

from the island of Socotra.

Included taxa: *B. aculeata, B. bornuensis, B. bremekampii, B. buxifolia, B. molensis, B. mysorensis.*

Group 3:

Typical species: *B. heterotricha.*

Plate: 7.1c

This is one of the most clearly defined groups within Section *Barleria*, characterised by unambiguous synapomorphies. It corresponds fairly closely with sub-section *Heterotrichae* of Section *Barleria sensu* Obermeijer (1933). The most obvious diagnostic character for this group is the presence of long-armed stellate hairs; the occurrence of a complex hair type in this section is particularly interesting as all the other complex hair types known in this genus occur in Subgenus Prionitis. The members of this group generally do not possess spinous bracteoles, although the bracteoles may become fairly stiff upon drying. Thus, the aborted inflorescences that may be produced in the lower leaf axils do not function as spine systems. The calyx is another highly characteristic feature of this group; it is typically scarious and usually has a very prominent pattern of reticulate venation, usually much darker than the background of the calyx segment. The corolla conforms to the same basic pattern as that seen in Group 2, although the overall length attained by the corolla may be far greater in Group 3. This group is generally fairly restricted geographically, most of the species occurring in the Zambezian and East African regions. It does, however, also include species from India and West Africa.

Included taxa: *B. affinis, B. asterotricha, B. crassa, B. fulvostellata, B. heterotricha, B. kirkii, B. lateralis, B. longiflora, B. spinulosa, B. tomentosa.*

Group 4:

Typical species: *B. macrostegia.*

Plate: 7.2c and d.

This is a very distinctive group of species, easily separated from all others in the section as the inflorescences have a highly characteristic structure and appearance. In most species of *Barleria* the 2 opposite bracteoles of each pair may differ slightly in size and

shape. In this group, the inflorescence is a secund scorpioid cy. ^ in which the bracteoles of each pair are strongly dimorphic and one of them is displaced to the same side of the inlorescence axis as the other; this results in the larger bracteole (i.e. that which directly subtends the flower) being subtended itself by the other very much smaller bracteole. This modification gives a very characteristic appearance to the inflorescence; the characteristic appearance is further exaggerated by the very large size of the outer calyx lobes. These inflorescences are axillary but may appear to be terminal if the inflorescence is borne in a subterminal axil of the stem. The stems in these species are prostrate or semi-prostrate, but the inflorescences, which may bear up to 15 flowers or more, are held erect. Another character shared by all members of this group, but not unique to it, is the presence of eglandular trichomes with bulbous, multiseriate bases on the leaves, bracts and calyces. These hairs impart a characteristic rough texture to the plants, especially to dried specimens. The corolla lobes are in the 2+3 configuration and the corolla tube is usually uniformly narrow throughout its length; this corolla tube can reach considerable lengths (e.g. 100mm in *B. capitata*), but the upper and lower tubes are usually of approximately equal length regardless of the overall length of the corolla.

Included taxa: ***B. bolusii, B. capitata, B. carruthersiana, B. lichtensteiniana, B. microstegia, B. steudneri, B. sunzuana.***

Remaining taxa:

There are a number of species that clearly possess the apomorphies for Section *Barleria*, but that are not clearly re[illegible]ble to any of the smaller groups identified within the section; these species do not possess any features not represented in the other groups, but lack the apparent apomorphies for these groups. Clearly such species cannot be considered to form a monophyletic group. In the case of some of these species, e.g. *B. kitchingii* from Madagascar, inability to place the plants satisfactorily within the section may be related more to lack of information on all features, rather than to the absence of appropriate synapomorphies, and it is possible that these taxa would be better placed in Section *Barleriopsis*. The data sets for a number of the species, from Madagascar in particular, are incomplete as very little herbarium material was available for study. Others of the species, such as *B. obtusa*, could be accommodated in the "typical" group, but only if the concept of this group is broadened to allow more variation in certain

features. For example, *B. obtusa* and *B. gueinzii* could be quite satisfactorily housed in Group 1 on the basis of most features, but do not possess stiffly spinous bracteoles and do not always produce aborted inflorescences in the lower leaf axils.

B. popovii is a particularly unusual species endemic to the island of Socotra. It clearly belongs in Subgenus *Barleria*, based on fruit morphology and the number of seeds. Its affinities within the subgenus, however, are not very clear. A particularly unusual feature of this species is the corolla morphology. The corolla lobes are arranged in the 4+1 configuration. The median abaxial lobe is extremely reduced relative to the upper lobes and is not split from the corolla for a greater distance than the other lobes.

It is hoped that future research will adequately resolve the current uncertainty regarding the placement of these taxa within the section.

Included taxa: *B. aromatica, B. gueinzii, B. morrissiana, B. obtusa, B. popovii, B. repens, B. solitaria, B. vincaefolia, B. violascens.*
Taxa that could be placed in Section *Barleriopsis*: *B. decaisneana, B. dulcis, B. kitchingii, B. paucidentata, B. siamensis.*

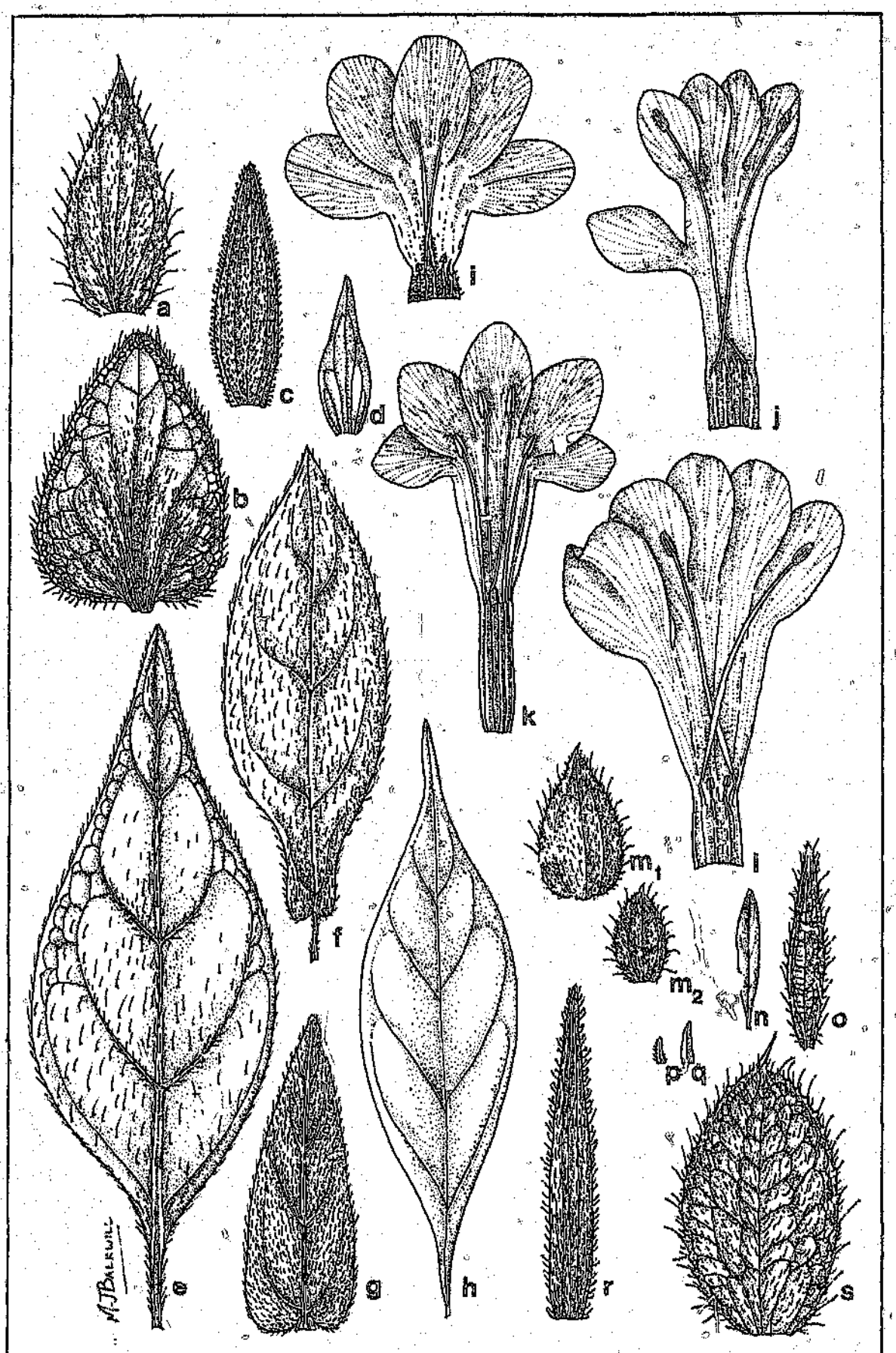
Section II: ***Barleriopsis*** (Oerst.) M. Balkwill, *stat. nov.*
Type: *B. micans* Nees.
Figures: 7.4 and 7.5
Plate: 7.2

Forest undershrubs with herbaceous stems or grassland species with annual herbaceous stems from a perennial, woody, underground caudex; plants usually completely innocuous, without aborted inflorescences produced in the lower leaf axils. *Leaves* herbaceous, either large (at least 100 x 30 mm), softly-textured, broadly ovate or elliptic, tapered at both ends, often attenuate at tip, strongly petiolate or, more rarely, ovate, approximately 30 - 45 x 20 - 30 mm, softly-textured, apex acute, base broadly cuneate, truncate to slightly cordate, very shortly petiolate or almost sessile; plants generally with pubescence of conspicuously yellow, simple eglandular trichomes, with or without multiseriate, bulbous bases; short-stalked or sessile glandular trichomes present on abaxial leaf surfaces in some species. *Inflorescences* compound, aggregated into lax or

Figure 7.4: Variation in the morphology of the leaves, corollas, bracteoles, bracts and calyces in selected representatives of Section *Barleriopsis*.

a) - d) posticous calyx lobes, abaxial surfaces shown; e) - h) leaves, adaxial surfaces shown; i) - l) corollas, i and k opened along median adaxial line, j and l opened along line between median abaxial lobe and lateral lobe; m) - r) bracteoles; s) bract.

a) *B. micans* x 2: Steyermark & Dunsterville 105769 (MO); b) *B. strigosa* x 3: Grierson & Long 3382 (E); c) *B. monticola* x 2: Balkwill & Balkwill 5418 (J); d) *B. courtallica* x 1: Fischer s.n. (K); e) *B. micans* x 1: Steyermark & Dunsterville 105796 (MO); f) *B. whytei* x 1: Drummond & Hemsley 3923 (K); g) *B. ovata* x 1: Stalmans 2672 (J); h) *B. courtallica* x 1: Fischer s.n. (K); i) *B. monticola* x 1: Balkwill & Balkwill 5418 (J); j) *B. micans* x 1: Steyermark & Dunsterville 105679 (MO); k) *B. ovata* x 1: Balkwill, Balkwill & Green 6261 (J); l) *B. courtallica* x 1: Fischer s.n. (K); m1) *B. nitida*, large bracteole of a pair, x 1: Hooper & Ramaswami 3926 (K); m2) *B. nitida*, small bracteole of a pair, x 1: Hooper & Ramaswami 3926 (K); n) *B. conspicua* x 1: Wallich s.n. (K); o) *B. micans* x 1.5: Steyermark & Dunsterville 105796 (MO); p) *B. nutans* x 1: Wight 777 (K); q) *B. courtallica* x 2: Fischer s.n. (K); r) *B. monticola* x 2.5: Balkwill & Balkwill 5418 (J); s) *B. micans* x 2: Steyermark & Dunsterville 105796 (MO).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M.J. Balkwill

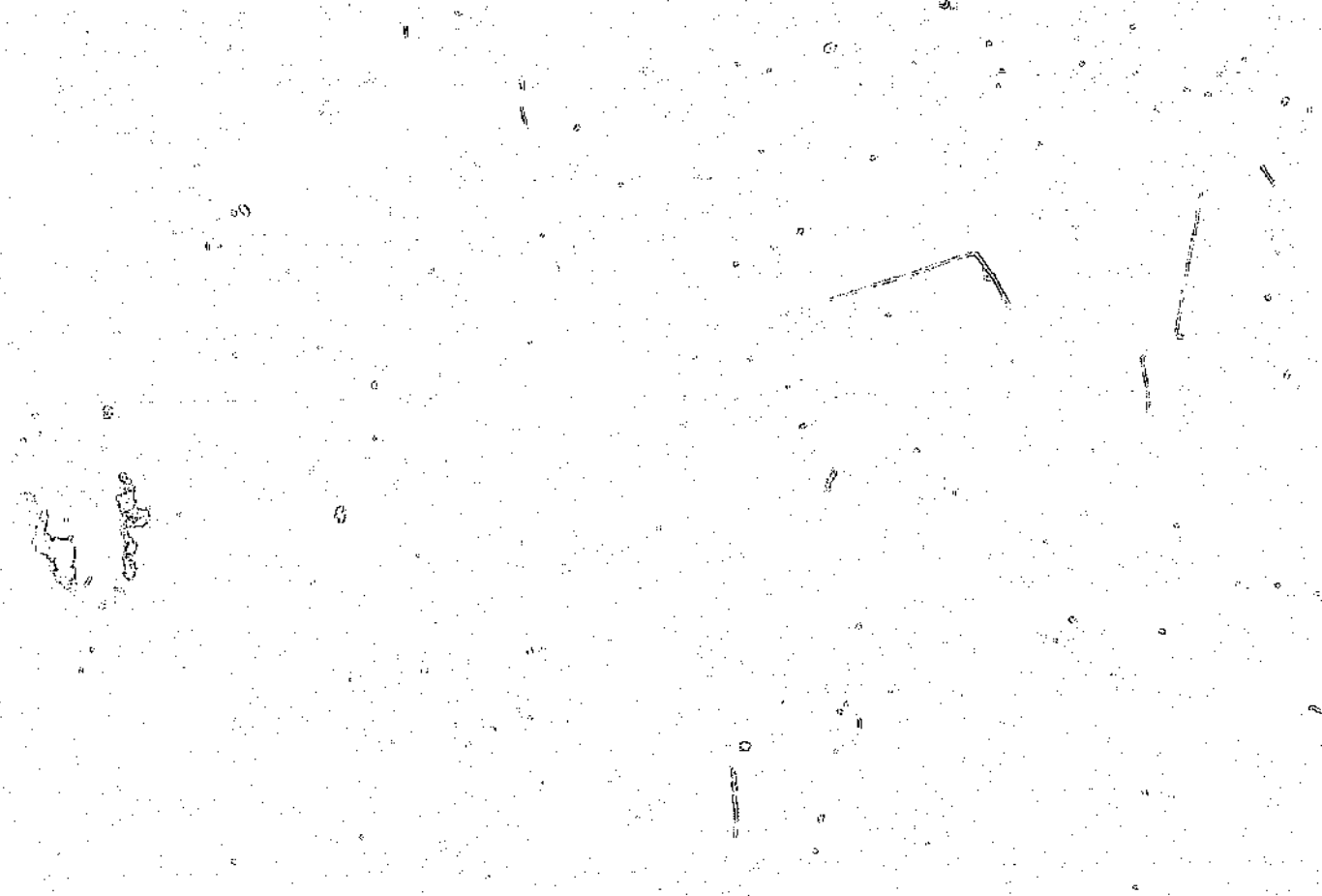
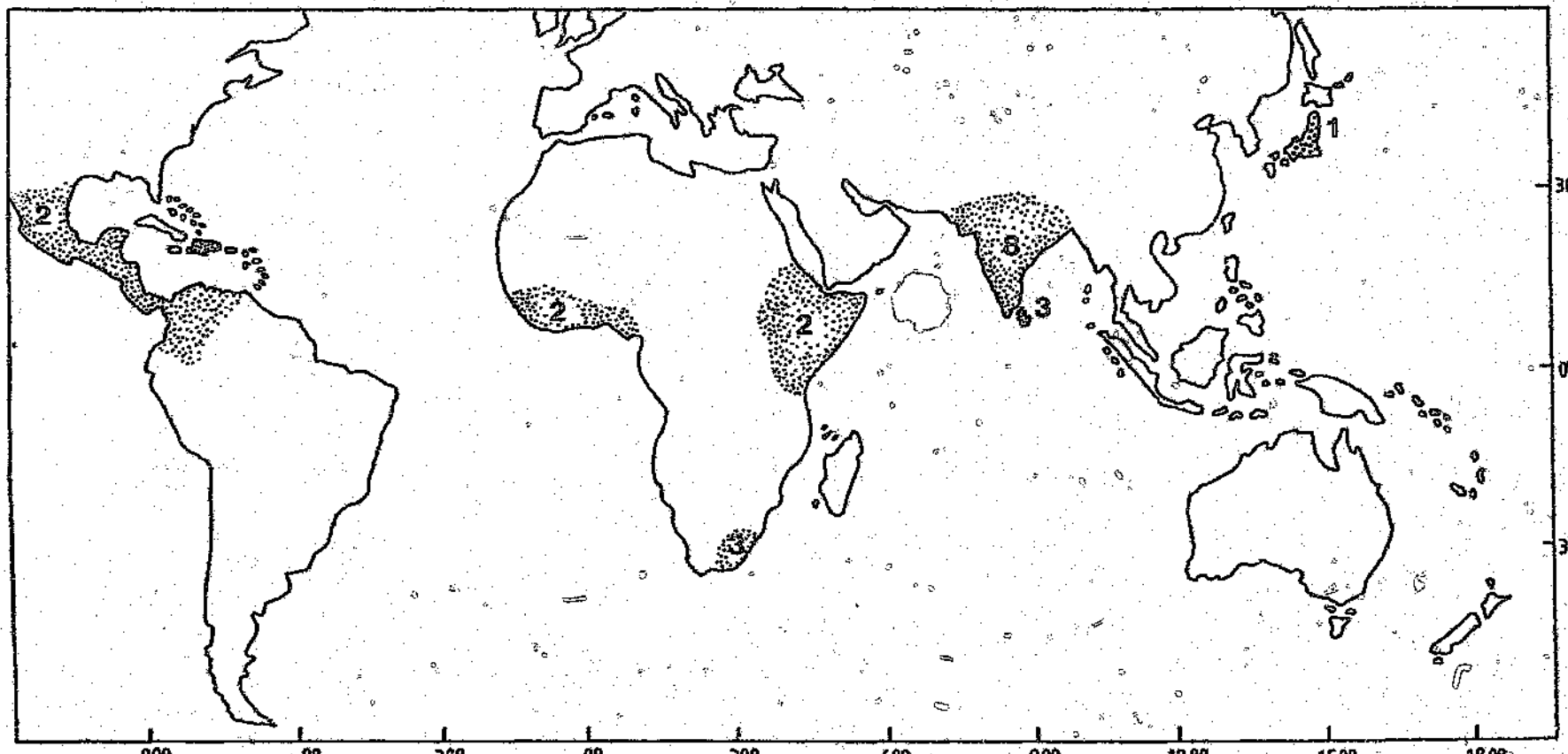


Figure 7.5: Global distribution of members of Section *Barleriopsis* (stippled area). The number of species recorded from each of the major regions is indicated.


1
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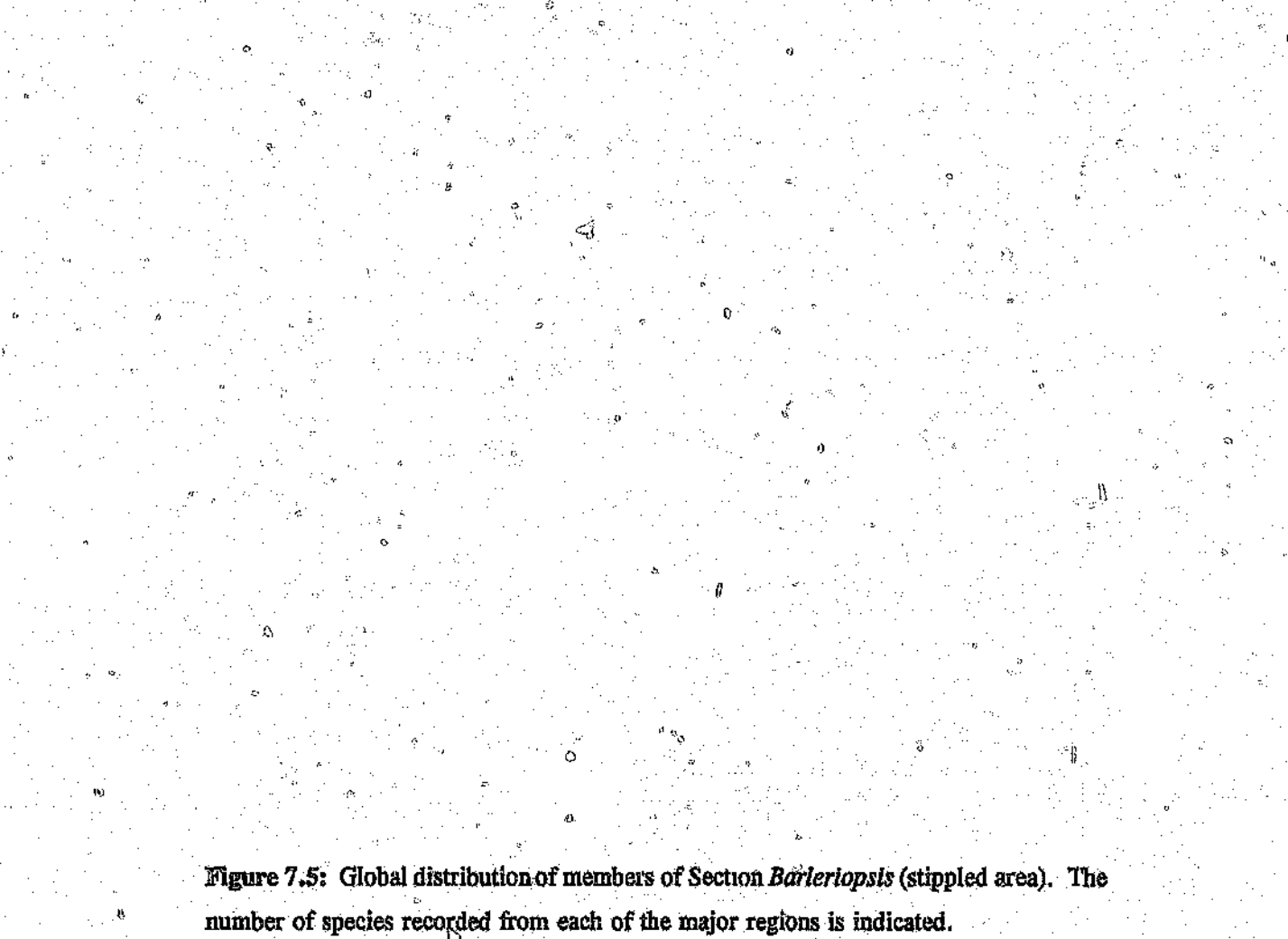
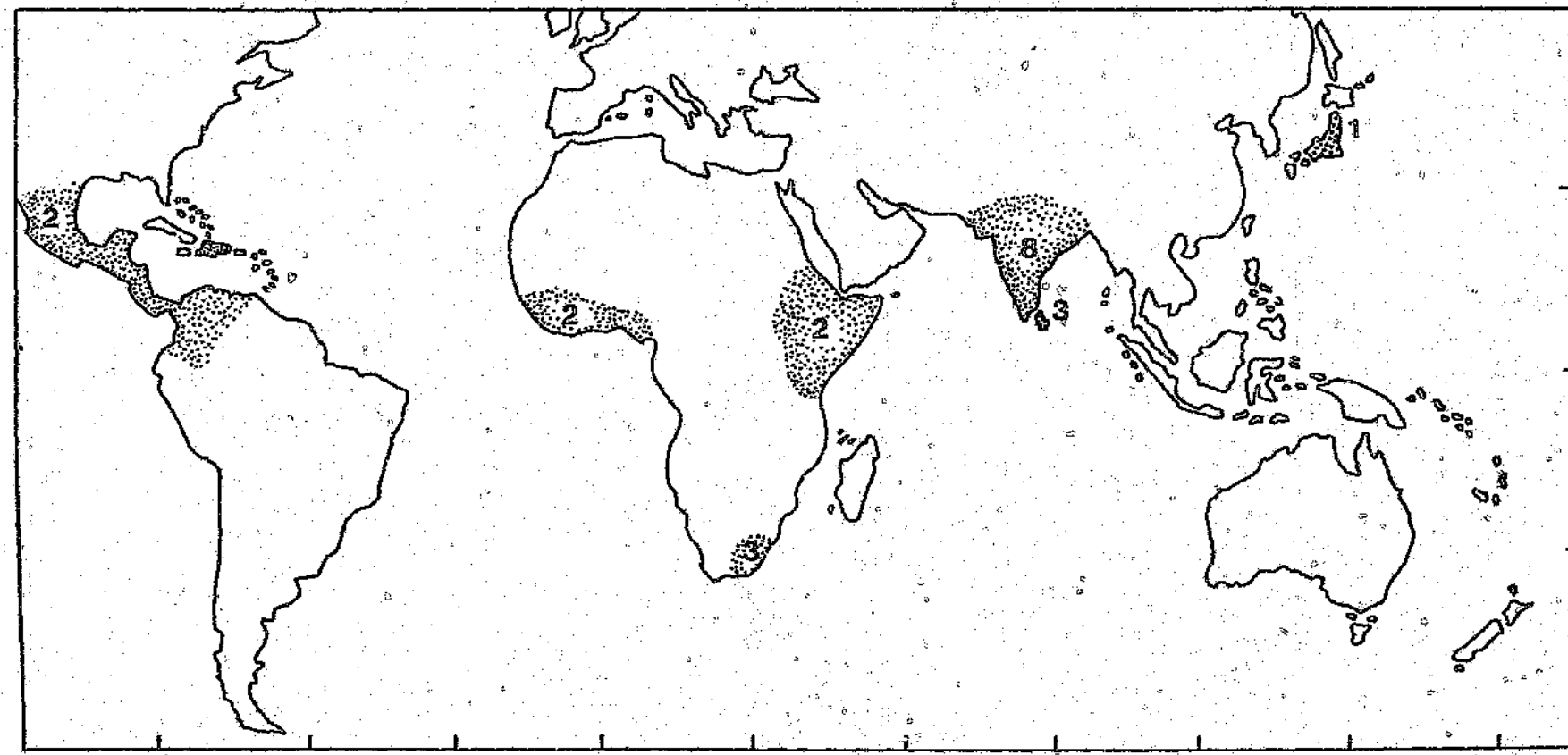


Figure 7.5: Global distribution of members of Section *Barleriopsis* (stippled area). The number of species recorded from each of the major regions is indicated.


1
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30°
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30°
60°
90°
120°
150°
180°

congested terminal synflorescences; unit structure of solitary flowers or dichasial clusters of 3 or more flowers, or of scorpioid cymes with displaced and dimorphic bracteoles or units combining monochasial and dichasial branching; corolla mostly with lobes in 4+1 configuration; median abaxial lobe split from corolla for greater distance than other lobes, or, more rarely corolla with lobes in 2+3 arrangement, upper tube broadly inflated, lower tube narrowly cylindrical and shorter than upper tube; corolla blue or yellow.

Included taxa: *B. arnottiana, B. conspicua, B. courtallica, B. flava, B. holstii, B. involucrata, B. lawii, B. maclaudii, B. micans, B. monticola, B. natalensis, B. nitida, B. nitida, B. nutans, B. ovata, B. strigosa, B. vestita, B. whytei.*

This section has a fairly restricted distribution, occurring mainly in India and Sri Lanka, with three representatives in southern Africa and one in West Africa and Central America (see Figure 7.5). (NOTE: although the plants occurring in West Africa and Central America are currently placed in two separate species, examination of the material has revealed that these are possibly conspecific).

The members of this Section are all clearly referable to Subgenus *Barleria* on the basis of fruit morphology. The satisfactory placement of the species within the subgenus, however, has been extremely difficult. In part, this is due to the data sets for a number of the species being incomplete. Many of the taxa occur only in India and the material that was available for study did not always include fruits, seeds or adequate flowering material; this imposed particular limitations on the investigation of floral morphology and the structure of the inflorescences. It was particularly difficult to make satisfactory decisions regarding the nature of the inflorescence. The most distinctive apomorphy for the group is the possession of a terminal synflorescence. This character does occur elsewhere in the genus, but not in combination with the distinctive yellow pubescence which is a characteristic of most members of this group. Furthermore, the other taxa in which a terminal synflorescence is present, are easily placed in other sections on the basis of other synapomorphies not present in members of Section *Barleriopsis*. The use of a terminal synflorescence as an apomorphy for a section may be problematical in another respect. Evolution of inflorescence types seems to have followed a number of routes (see Chapter 5). It is possible, therefore, that the synflorescences present in

members of Section *Barleriopsis* have been derived in different ways and may not be homologous. This would mean that Section *Barleriopsis*, as circumscribed here, would be polyphyletic and would have to be rejected. The species placed in this section could be absorbed into Section *Barleria*, but the circumscription of the smaller groups (possible sub-sections) within this group would have to be altered, resulting in the recognition of a greater number of groups each including smaller numbers of taxa. This would also necessitate the formulation of more hypotheses of homoplasy to explain the distribution of certain characters within the groups. With the information currently to hand, it seems more parsimonious to accept *Barleriopsis* a separate section within Subgenus *Barleria*. It does seem likely, though, that if any of the sections proposed in this thesis undergo a future change in circumscription, it will be this one. This will produce negligible instability with regard to nomenclature, as the members of the section would be incorporated into Section *Barleria* at the sub-sectional level, and taxa of this rank have not been formally described or named here.

Acceptance of Section *Barleriopsis* as currently circumscribed allows for the recognition of four or five sub-groups, one of which can only be provisionally included within this section at this stage.

Group 1:

Typical species: *B. micans* Nees.

Plate: 7.3a

This taxon is similar to those in Group 2 of this section in a number of respects. The inflorescence is a many-flowered, strobilate synflorescence in which the subtending bracts are considerably different from the ordinary vegetative leaves. *B. micans* and *B. flava* have a conspicuous yellow pubescence of bulbous-based eglandular hairs, a feature shared with many other species in this section. Various aspects of floral morphology set *B. micans* and *B. flava* apart from Group 2. The corolla, which is yellow, is strongly zygomorphic with 4 lobes in the upper lip and one lobe in the lower lip. The lower lobe is noticeably split from the corolla for a greater distance than the other corolla lobes. All other groups within this section (except Group 2) share this corolla form. The stigma is also 1-lobed and filiform in Group 1, not 2-lobed and discoid as in Group 2.

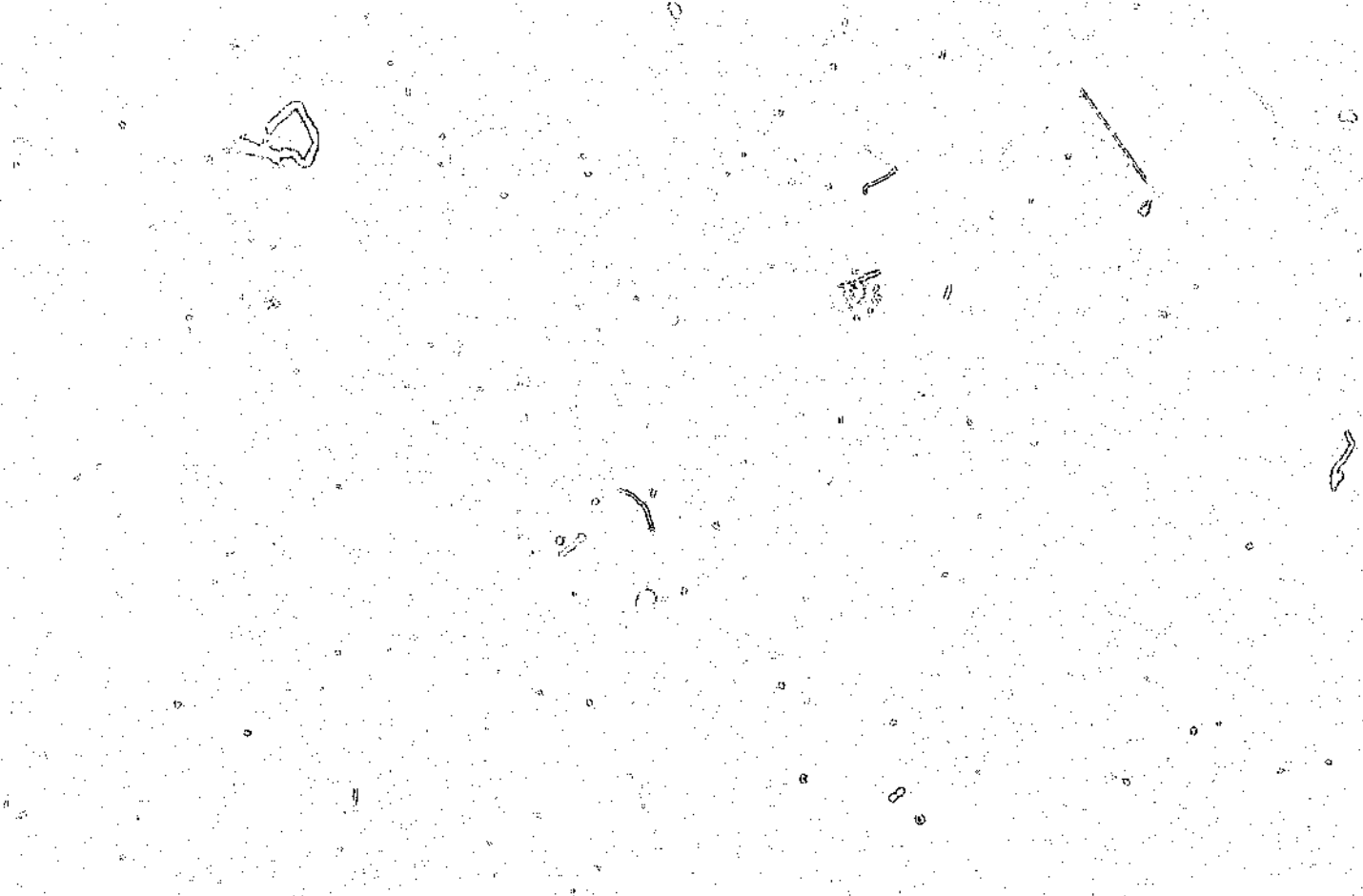
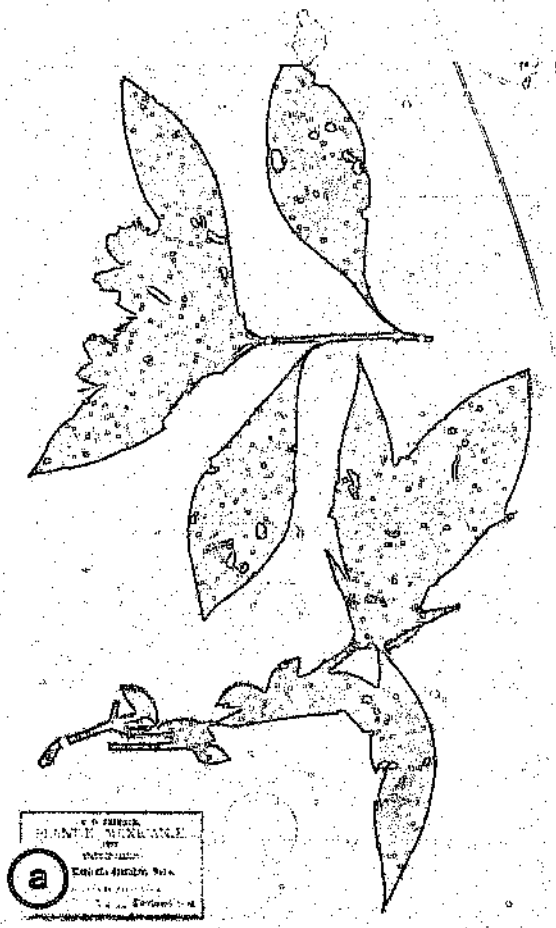


Plate 7.3: Selected representatives of Section *Barleriopsis*.
a) *B. micans*: Pringle 4587 (MO); b) *B. monticola*: Pole-Evans 40567 (PRE): c) *B. involucrata*: Watson s.n. (E); d) *B. courtallica*: McIvor 13 (K).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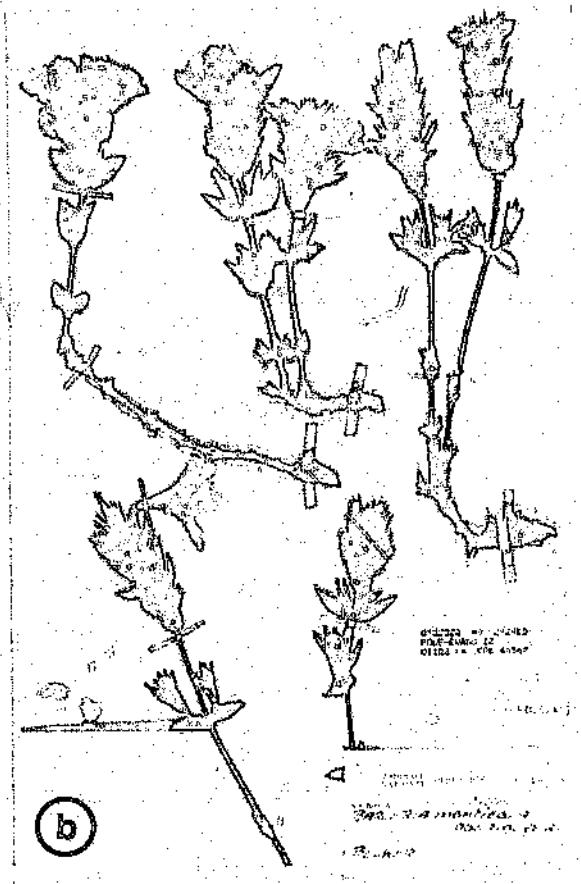
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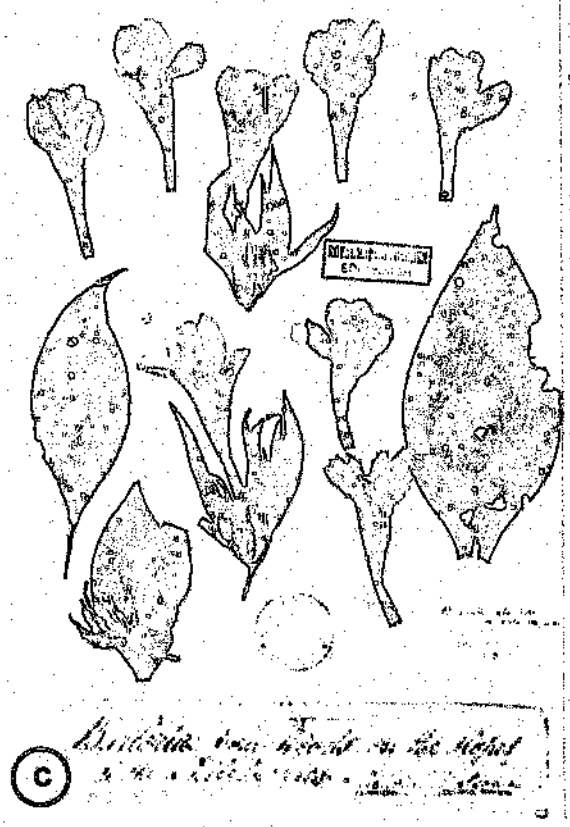
c

d

B. micans occurs in Central Mexico, Panama and Guatemala where it is the only representative of the genus (see Figure 7.5). Section *Barleriopsis* is also represented in West Africa; the species in this region is currently referred to as *B. flava* which is very similar to *B. micans* with which could be conspecific.

Included taxa: *B. flava, B. micans.*

Group 2:

Typical species: *B. monticola.*

Plate: 7.3b

These species are restricted to grasslands, mainly at high altitudes in the Eastern parts of southern Africa. They are characterised by the possession of a perennial, underground, woody caudex that gives rise to annual herbaceous stems. It is not known whether any of the other taxa in this section possess this growth form, although it is known that most of the other species are forest under-shrubs and not grassland species. Members have well-developed strobilate synflorescences, the units of which are usually solitary flowers or, more rarely, dichasial clusters of 3 flowers. The bracts, bracteoles and calyx segments are foliaceous and innocuous. Yellow pubescence is strongly developed in these taxa, but the hairs are silky rather than harsh in *B. monticola*. The hairs have prominent bulbous bases that make the margins of the bracts, bracteoles and calyx appear minutely denticulate. This group of taxa is unusual in the Section, as it is the only one in which the corolla is arranged in the 2+3 configuration and the stigma is discoid rather than filiform.

Included taxa: *B. monticola, B. [illegible]ata, B. natalensis, B. sp. (from Mocambique).*

Group 3:

Typical species: *B. involucrata*

Plate: 7.3c

Members of this group are linked to the previous two through common possession of yellow hairs with bulbous, multiseriate bases. The morphology of the stigma and corolla are similar to that found in *B. micans*. These taxa, however, differ from *B. micans* in

two important respects. The first is that the leaves have sessile glands on the lower surfaces (a feature not present in Group 1 or 2, but shared with the next group in this section). The second difference relates to the structure of the inflorescence and inflorescence units. Each inflorescence unit initially comprises a 3-flowered dichasium, whereafter a scorpioid cyme develops in one axil of both the second and third flowers of the dichasium. In some cases the internodes between the flowering nodes are elongate, giving rise to a lax terminal synflorescence. In other cases this is more difficult to judge as many of the specimens seen were plants in which the inflorescences were immature.

All members of this group are restricted to India and Sri Lanka (see Figure 7.5).

Included taxa: *B. arnottiana, B. lawii, B. involucrata, B. vestita.*

Group 4:

Typical species: *B. courtallica*

Plate: 7.3d

This group shares the same corolla morphology and androecium as *B. micans* and Group 3, but differs from them in that it lacks conspicuous yellow hairs. In addition the stigma is 2-lobed, not single-lobed and filiform. The species in this group share with Group 3 the presence of sessile glands on the abaxial leaf surfaces. The inflorescences are highly distinctive in these species comprising dichasial units that are arranged into large, terminal synflorescences that can become extensively branched.

The only member of this group that is not restricted to India is *B. maclaudii*, which occurs in West Africa. A similar pattern is seen in Section *Barlerianthus*, which is endemically restricted to India, but has one species that occurs in West Africa (and is not shared with India).

Included taxa: *B. conspicua, B. courtallica, B. maclaudii, B. nutans.*

Group 5:

Typical species: *B. strigosa*

Plates: 7.2d

This group of species has been the most difficult to place satisfactorily within a section. It clearly belongs in Subgenus Barleria on the basis of fruit morphology. It shares with Section *Barleria* a conspicuously scarious calyx with a prominent pattern of venation. The structure of the inflorescence units is the same as that in Group 4 of Section *Barleria* containing species such as *B. capitata* and *B. macrostegia*. The inflorescence units form secund, scorpioid cymes in which the bracteoles are dimorphic with the smaller one subtending the larger on the same side of the inflorescence axis. In species such as *B. macrostegia* (Group 4, Section *Barleria*), these inflorescence units are borne in only one of the leaf axils at each flowering node. In *B. strigosa* and its allies, the inflorescence units are borne in both of the axils at each flowering node, usually at all the upper nodes of the stem. It thus would seem that the units in these species are arranged in lax terminal synflorescences; this was sometimes difficult to judge as the inflorescences were immature in many specimens, or the specimens were incomplete.

This group shares a number of features with the remainder of Section *Barleriopsis*, including a distinctive pubescence of yellow hairs with multi-seriate bases (hairs with multiseriate bases occur in *B. macrostegia* and its allies, but these are usually not yellow); a corolla with lobes arranged in the "4+1" configuration; a single-lobed, filiform stigma. All members of Group 4 of Section *Barleria* have corollas with lobes in the 2+3 configuration and 2-lobed capitate stigmas. There are two possible solutions to the placement of this group within *Barleria*; it can placed in Group 4 of Section *Barleria*, but this necessitates inferring that terminal synflorescences and yellow pubescence have arisen convergently in this Group and the remainder of Section *Barleriopsis*. Alternatively, it can be retained within Section *Barleriopsis*, as I have done here, thus inferring that the very distinctive structure of the inflorescence units has arisen independently in this group and Group 4 of Section *Barleria*. The latter possibility seemed to be the most satisfactory solution to me based on the data currently available.

Included taxa: *B. holstii*, *B. nitida*, *B. polytricha*, *B. strigosa*, *B. whytei*.

Subgenus II: Prionitis

Type: *B. prionitis* L.

Herbs, shrubs, suffrutices or creepers; plants either innocuous or with 2-, 4- or 6-rayed axillary spine systems in lower leaf axils, spine systems forming from lower axillary bud. *Flowers* usually zygomorphic, 4 lobes in upper lip, 1 lobe (median abaxial lobe) in lower lip; median abaxial lobe split from corolla for greater distance than other corolla lobes; corollas blue, pink, red, white or yellow. *Stigma* predominantly 1-lobed, filiform; rarely 2-lobed. *Capsule* with or without a prominent apical beak, beaks either solid and conical or more or less hollow; septum either entirely ligneous or with broad membranous portion above ovules or almost entirely membranous. *Seeds* usually 2, covered with hygroscopic hairs; rarely 4, glabrous.

Included Sections: *Prionitis, Somalia, Stellatohirtae, Barlerites* and *Barleriunthus*.
Approximate number of taxa: 120

Section III: *Prionitis* Nees ex. M. Balkwill

Type: *B. prionitis* L.

Herbs, small shrublets or suffrutices; plants mostly spinescent due to presence of 2-, 4- or 6-rayed axillary spine systems (formed from lower axillary bud) in lower leaf axils. *Leaves* variable, usually with a pungent apex; margins entire, sometimes thickened and cartilaginous; abaxial surfaces with scattered sunken glands, often with saucer-glands near base; other pubescence, if present, of simple hairs only. *Inflorescence* either axillary or running into more or less discrete terminal synflorescences; unit structure of dichasial cymes or, more usually, reduced to solitary flowers. *Bracteoles* foliaceous or reduced to spines. *Calyx* inner and outer lobes not always strongly differentiated; tip of anticous and posticous lobes often spinous, margins entire. *Flowers* strongly zygomorphic, 4 lobes in upper lip; one lobe (median abaxial lobe) in lower lip, median abaxial lobe usually split from corolla for greater distance than other lobes; corolla usually apricot-yellow, more rarely orange, reddish or blue. *Stigma* of 1, filiform lobe. *Ovary* with upper 2 ovules developed, lower 2 ovules minute and abortive or absent. *Androecium* usually of 4 parts; 2 fertile abaxial stamens; adaxial staminodes 2, with

anther rudiments or staminodes entirely absent. *Capsule* turgid below, produced into solid apical beak; septum entirely woody. *Seeds* 2, ovoid with distinct notch at hilum, surfaces covered with adpressed gold hygroscopic hairs.

Approximate number of taxa: 38

Figures: 7.6 and 7.7

Plates: 7.4 and 7.5

Section *Prionitis* is usually very easily distinguished from others in the genus by means of its sharp, axillary spine systems and yellow flowers. Indeed, Section *Prionitis* is one of the most clearly defined in the genus and has been recognised by all authors since the time of Nees (1847). Use of axillary spines and flower colour as diagnostic characters, however, can be problematical. There is at least one species, *B. sacleu*[illegible] regularly spineless, and in other species (e.g. *B. marginata, B. crossa*[illegible] spine systems may be very weakly developed or entirely absent in certa[illegible]iduals. Species such as *B. waggana* have well-developed spine-systems, but the flowers are bright blue rather than yellow, thus rendering flower colour somewhat unreliable as a diagnostic character. Two features that are consistent throughout all members of this Section and, thus, represent the most reliable synapomorphies for it, are the entirely woody septum and the presence of sunken glands on the abaxial leaf surfaces. Although sunken glands of some sort seem to have sporadic occurrence throughout the genus, they do not occur in conjunction with woody septa anywhere else except in Section *Prionitis*. Use of these two apomorphies, with the usual presence of axillary spine systems and yellow flowers as confirmatory characters, allows for easy identification of members of this section.

Section *Prionitis* occurs almost throughout the entire geographic range of the genus, being absent only from Central America, Angola and the Ugandan region (Figure 7.7). It is only weakly represented in West Africa, southern Asia and the Far East. The section has its greatest number of species in East Africa, particularly in Somalia and Tanzania, with smaller centres of abundance in Madagascar, southern Africa and the Zambezian region. If one considers the number of species of Section *Prionitis* relative to the total number of species of *Barleria* in these regions, then the greatest centre of diversity for this Section would be in Madagascar, where Section Prionitis accounts for approximately 40% of the total number of species of *Barleria*. It should, however, be

Figure 7.6: Variation in the morphology of the leaves, corollas, bracteoles, bracts and calyces of selected representatives of Section *Prionitis*.

a) - e) posticous calyx lobes, abaxial surfaces shown; f) - k) leaves, adaxial surfaces shown; l) - m) bracteoles, abaxial surfaces shown; n) - q) corollas, opened along line between median abaxial corolla lobe and lateral lobe; r) - u) bracts, abaxial surfaces shown.

a) *B. rotundifolia* x 4.5: Balkwill, Balkwill, Barlow-Kearsley, Gesell & Cron 6144 (J); b) *B. cuspidata* x 2: Wight 2215 (K); c) *B. crossandriformis* x 3.5: Balkwill & Balkwill 6340 (J); d) *B. eranthemoides* x 3: Ash 880 (MO); e) *B. holubii* x 2.5: Miller 2138 (SRGH); f) *B. cuspidata* x 2: Wight 2215 (K); g) *B. crossandriformis* x 2: Balkwill & Balkwill 6340 (J); h) *B. rotundifolia* x 3: Balkwill, Balkwill, Barlow-Kearsley, Gesell & Cron 6144 (J); i) *B. randii* x 1: Eyles 88 (SRGH); j) *B. marginata* x 1: Peter 31728 (K); k & l) *B. holubii* x 2.5: Miller 2138 (SRGH); m) *B. allaudii* x 3: Phillipson 2673 (K); n) *B. rotundifolia* x 1.5: Balkwill *et al.* 6144 (J); o) *B. senensis* x 3: Balkwill & Balkwill 6331 (J); p) *B. randii* x 2.5: Eyles 88 (SRGH); q) *B. eranthemoides* x 4: Ash 880 (MO); r) *B. senensis* x 4: Balkwill & Balkwill 6331 (J); s) *B. eranthemoides* x 4: Ash 880 (MO); t) *B. norbertii* x 4: Gentry 11507 (MO); u) *B. crossandriformis* x 3: Balkwill & Balkwill 6340.

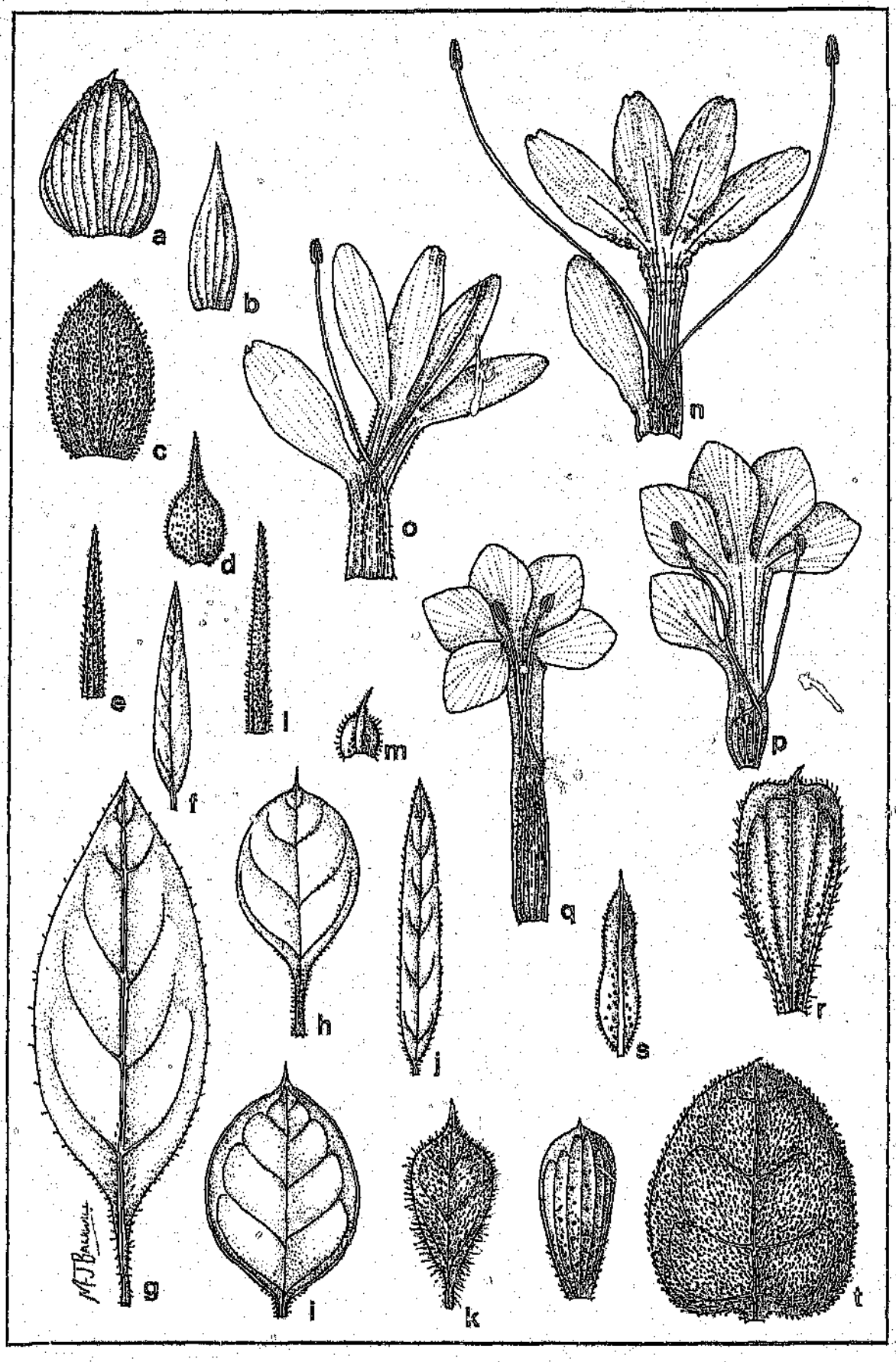
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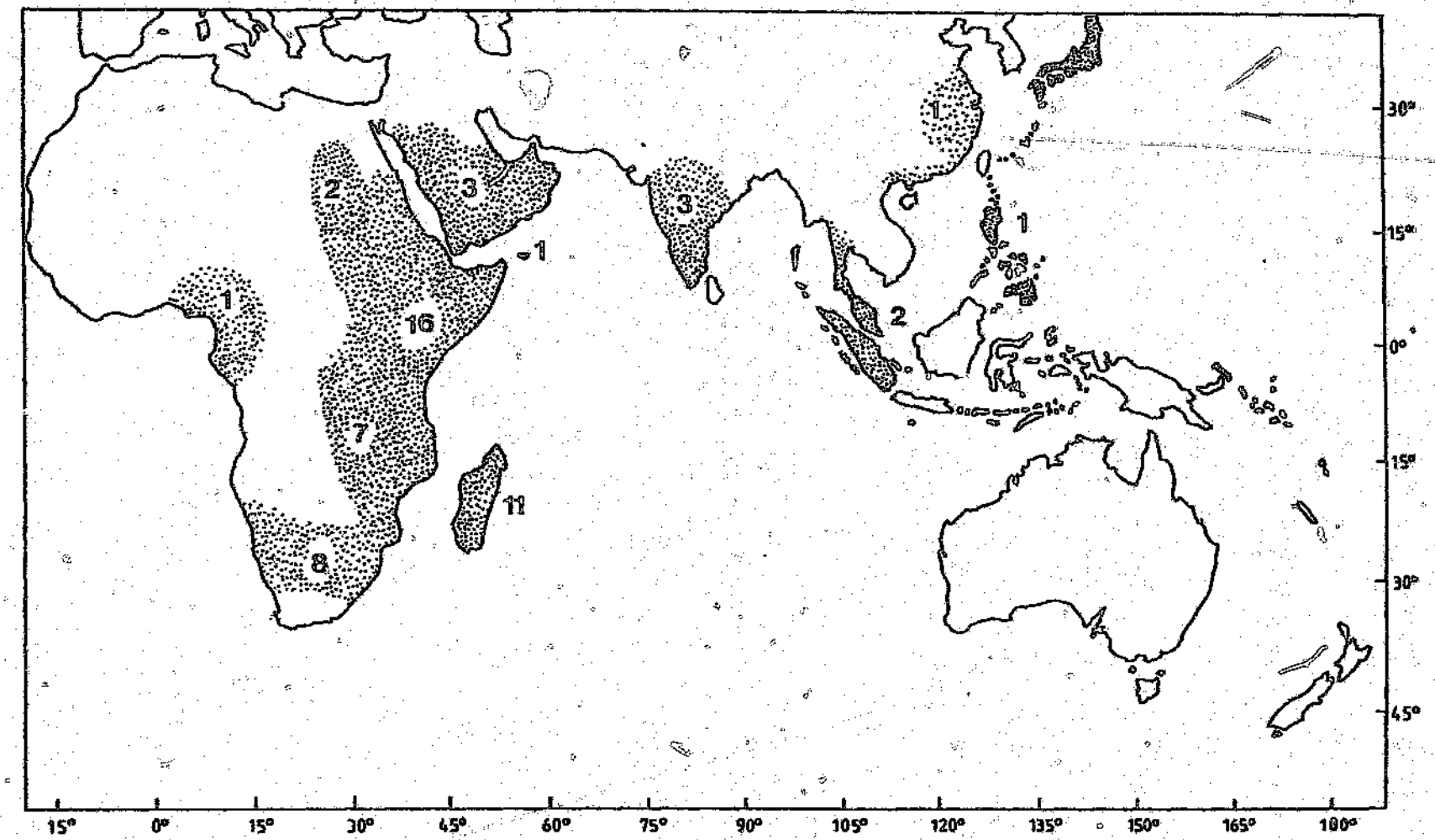
Figure 7.7: Global distribution of members of Section *Prionitis* (stippled area). The number of species occurring in each of the major regions is indicated.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2
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7
11
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15°
0°
15°
30°
45°
15°
0°
15°
30°
45°
60°
75°
90°
105°
120°
135°
150°
165°
180°

Plate 7.4: Selected representatives of Section *Prionitis*.

a) *B. her*: McPherson & Pigeon 14955 (MO); b) *B. sacleuxii*: Faulkner 2337 (K); c) *B. lupulina*: Meagher 268 (MO); d) *B. waggana*: Thulin, Hedren, Abdi M. Dahir 7589 (K).

noted that there are a number of undescribed species that belong in Section *Prionitis* in the East African region. When this genus is next revised, it will probably emerge that the number of species recognised within Section *Prionitis* is increased, and the Section would then account for a greater proportion of the total number of species than is reflected by the number of species given here. Some of the most widespread species within the genus, e.g. *B. prionitis*, are members of this section.

Included taxa: *B. allaudii, B. bispinosa, B. brevituba, B. casatiana, B. cephalophora, B. crossandriformis, B. cuspidata, B. decaryi, B. eranthemoides, B. her, B. holubii, B. horrida, B. kaloxytona, B. leandrii, B. lupulina, B. marghilomanae, B. marginata, B. migiurtinorum, B. norbertii, B. parvispina, B. perrieri, B. prionitis, B. proxima, B. pulchella, B. punctata, B. quadrispina, B. randii, B. rhodesiaca, B. rotundifolia, B. sacleuxii, B. senensis, B. setigera, B. smithii, B. tetracantha, B. tetraglochin, B. trispinosa, B. ukamensis, B. waggana.*

A number of fairly distinct sub-groups can be recognised within Section *Prionitis*.

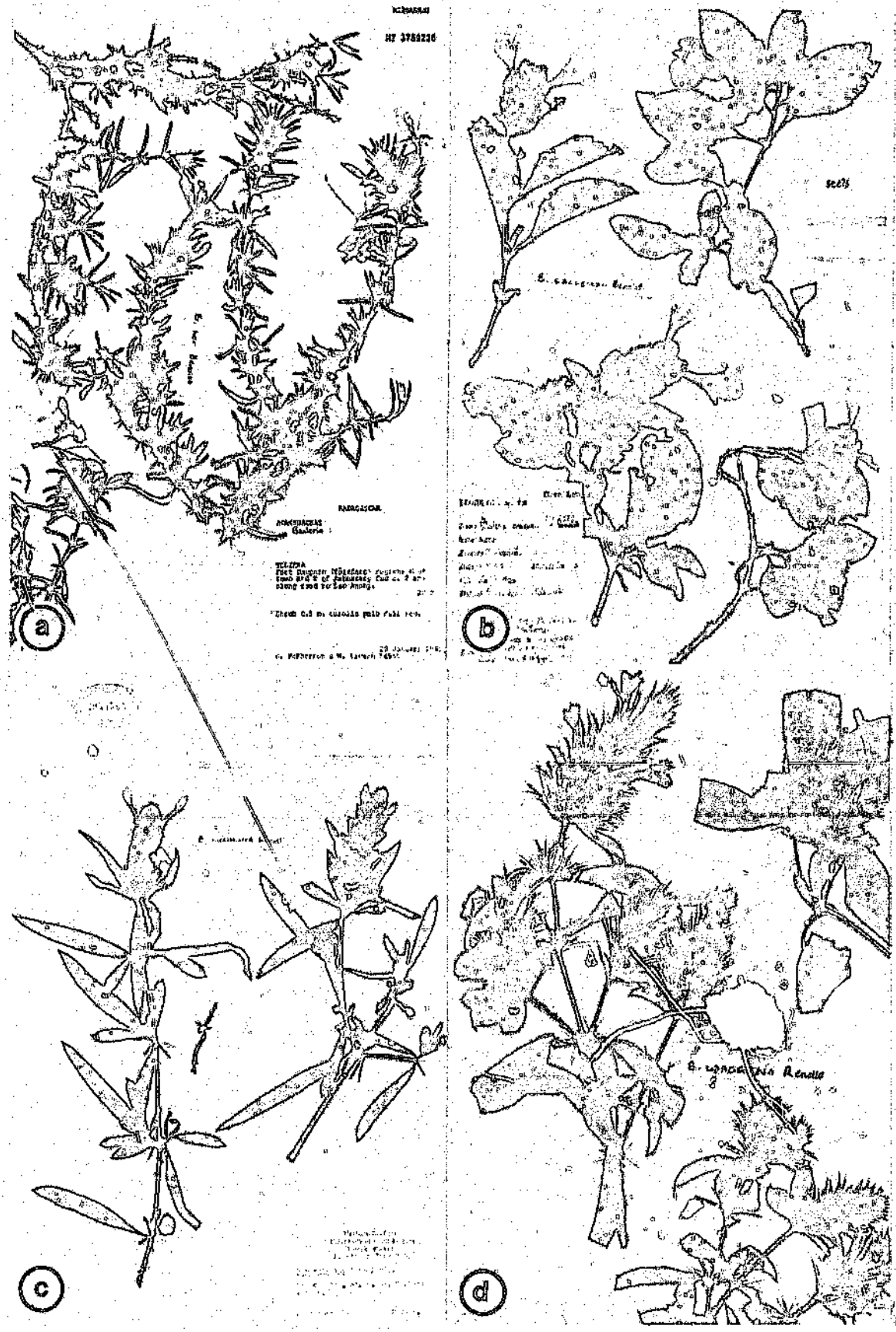
Group 1:

Type: *B. prionitis* L.

Plate: 7.4a and 7.5a & b

Those taxa in which the inflorescence units are not usually aggregated into terminal synflorescences or, if they are, then the leaves subtending the flowers are not greatly modified, form the "typical group"; about half of the total number of species included in the Section would fall into this category. The remaining taxa can be segregated into three groups on the basis of differences in the flowers and inflorescences.

Included taxa: *B. bispinosa, B. casatiana, cuspidata, B. her, B. horrida, B. kaloxytona, B. leandrii, B. marginata, B. migiurtinorum, B. prionitis, B. proxima, B. pulchella, B. punctata, B. rotundifolia, B. tetraglochin, B. trispinosa, B. ukamensis.*


a
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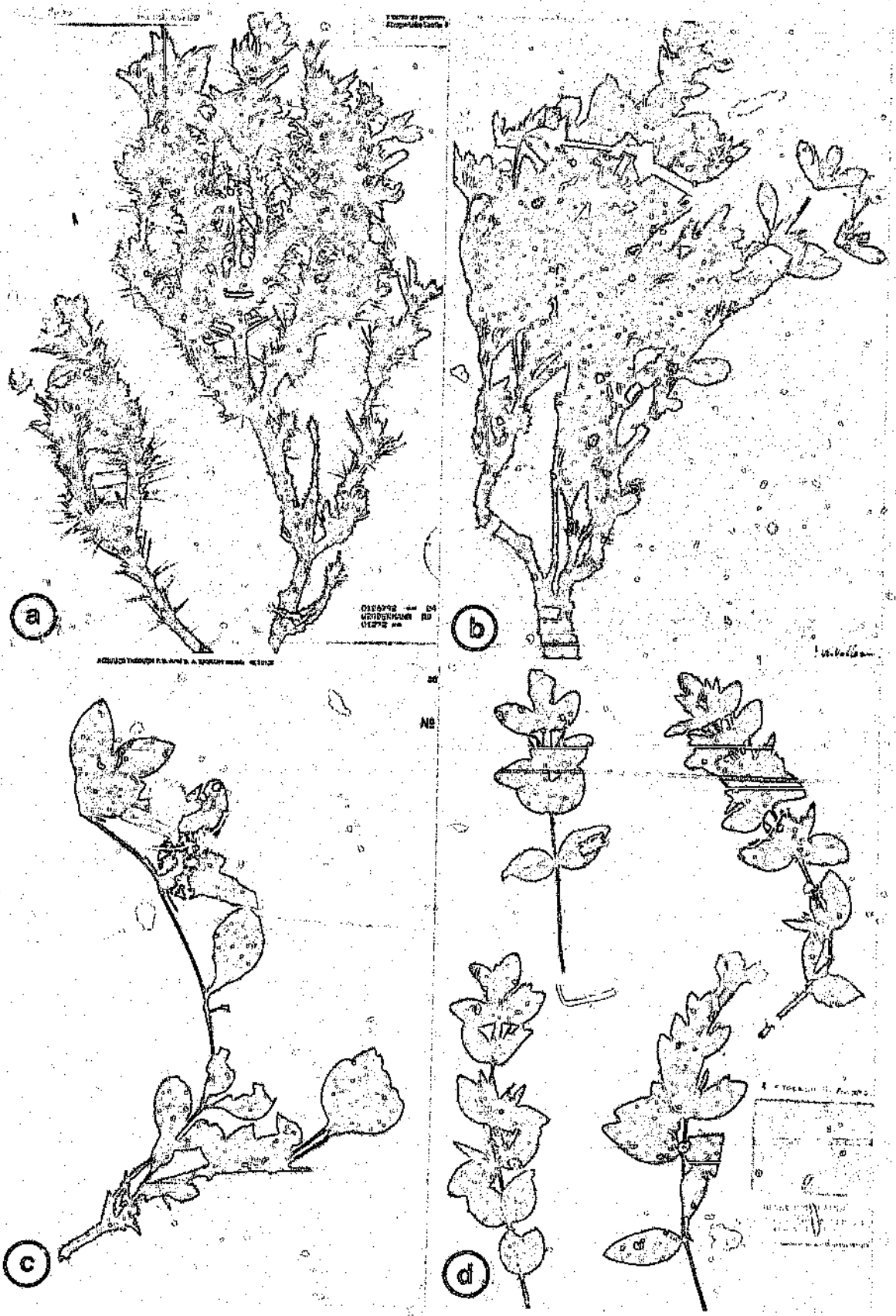
c
d

Plate 7.5: Selected representatives of Sections *Prionitis* and *Somalia*.
a) *B. prionitis*: Werdemann & Oberdieck 2427 (PRE); b) *B. kaloxytona*: Dinter 3354 (PRE); c) *B. calophylloides*: Pawek 10904 (MO); d) *B. stocksii*: Gamble 20438 (K).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Group 2:

Typical species: *B. crossandriformis*

Plate: 7.4b & c

The main character separating this group from other species within the section is the presence of a many-flowered, strobilate, terminal synflorescence in which each flower is subtended by two bracteoles and a highly modified floral bract. In the more typical members of section *Prionitis*, the leaves subtending the flowers near the tip of the stem sometimes undergo slight modification in size and form, but not to the extent seen in species such as *B. crossandriformis*. It is also interesting that the floral bracts in this group generally do not have scattered, sunken glands on the abaxial surfaces. This group includes species from Madagascar, the eastern parts of Africa and one species from Asia and the Far East.

Included taxa: *B. allaudii, B. crossandriformis, B. lupulina, B. norbertii, B. perrierii, B. rhodesiaca, B. sacleuxii, B. senensis.*

Group 3:

Typical species: *B. eranthemoides*

Members of this group are characterised on the basis of their unusual corolla morphology. The corolla tube in these species is usually much longer than the lobes and is extremely narrow throughout its length. Furthermore, the tube is not split along either side of the median abaxial lobe as is typical for most members of subgenus *Prionitis*. The 5 corolla lobes are subequal and the corolla is not bilabiate; instead the median abaxial lobe is partially fused to the upper four corolla lobes. Members of this group occur in Africa and Madagascar. It is interesting that although many of the Madagascan species are endemic to the island, most of them are clearly referable to the same sections and sub-groups represented in Africa (and elsewhere in some cases).

Included taxa: *B. brevituba, B. decaryi, B. eranthemoides, B. holubii, B. parvispina, B. tetracantha.*

Group 4:

Typical species: *B. waggana*

Plate: 7.4d

The species in this group are characterised by their blue flowers, not yellow as is more typical, and by certain details of the inflorescence structure. The inflorescences are usually highly congested, terminal synflorescences. A dichasial cluster of flowers is present at each node of the synflorescence. Within the dichasium the short pedicels of the second and third flowers are fused to the bases of the bracteoles of the first flower, giving these inflorescences a highly characteristic appearance. The oldest dichasial units are subtended by unmodified leaves, but the subtending leaves become increasingly modified in size and shape towards the apex of the stem. The species of this group are all restricted to East Africa, occurring mainly in Somalia.

Included taxa: *B. cephalophora, B. quadrispina, B. setigera, B. smithii, B. waggana.*

Section IV: *Somalia* Lindau

Type: *B. aucherana* Nees.

Herbs or shrubs, plants innocuous, often glabrescent or if pubescent then often with hairs of the anvil or medifixed type. *Leaves* of variable size and shape, usually glaucous or at least drying a distinctive bluish-grey. *Inflorescence* either simple with axillary units or compound with units in lax or condensed terminal synflorescences; unit structure either solitary flowers or dichasial clusters of 3 or more flowers. *Bracteoles* herbaceous, foliaceous, innocuous; margins entire or occasionally irregularly denticulate, but never spinous. *Calyx* herbaceous; apex of anticous lobe always bifid; margins entire. *Flowers* strongly zygomorphic, with 5 or 4 lobes; 5-lobed corollas with 4 lobes in upper lip, 1 in lower lip; median abaxial lobe split from corolla for greater distance than other lobes; 4-lobed corollas with one lobe in upper position, 2 lateral lobes and one lobe in abaxial position, upper lobe broadest, comprising 2 fused petals; corolla white, pink or blue, sometimes with contrasting spots on upper lobes, occasionally butter yellow. *Stigma* of 1 filiform lobe. *Androecium* of 5 parts; 2 abaxial stamens fertile; adaxial staminodes 3, greatly reduced without any anther rudiments, or only 2 staminodes present. *Capsule* turgid below with prominent solid, conical apical beak; septum woody with central membranous portion above ovules. *Seeds* 2, covered with conspicuous

white, woolly hygroscopic hairs.

Approximate number of taxa: 43

Figures: 7.8 and 7.9

Plates: 7.5c & d and 7.6

Section *Somalia* has been recognised by authors since the time of Lindau (1895). It is easily distinguished from others in the genus on the basis of fruit and seed morphology alone, although a number of floral features provide useful confirmatory characters. Lindau did not typify the section when he described it, but all the species seen by him are those with medifixed hairs and spotty corollas, such as *B. aucherana*. This has, therefore, been selected to represent the "typical" group from which a type species was selected. There are, however, far fewer species with this kind of morphology than there are in some of the other groups within the Section. The Section as a whole is largely limited to Africa although a few representatives are found in Arabia and India. Different groups within the Section tend to be concentrated in different geographic regions, with the "typical" part of the Section concentrated in East Africa.

Included taxa: *B. albi-pilosa, B. angustiloba, B. argentea, B. aucherana, B. benguellensis, B. calophylla, B. calophylloides, B. clinopodium, B. dolomiticola, B. galpinii, B. glandulifera, B. gossweilerl, B. grandipetala, B. hirta, B. hochstetterl, B. insericata, B. kacondensis, B. lactiflora, B. lancifolia, B. latiloba, B. limnogeton, B. longipes, B. lugardii, B. mackenii, B. matopensis, B. meyeriana, B. obtusisepala, B. orbicularis, B. pabularis, B. phaylopsis, B. phillyraefolia, B. polyneura, B. pretoriensis B. puberula, B. rehmannii, B. separata, B. seyrigii, B. stocksii, B. violacea, B. welwitschii, B. wilmsiana, B. yemense.*

<u>Group 1</u>: "Typical".

Typical species: *B. aucherana.*

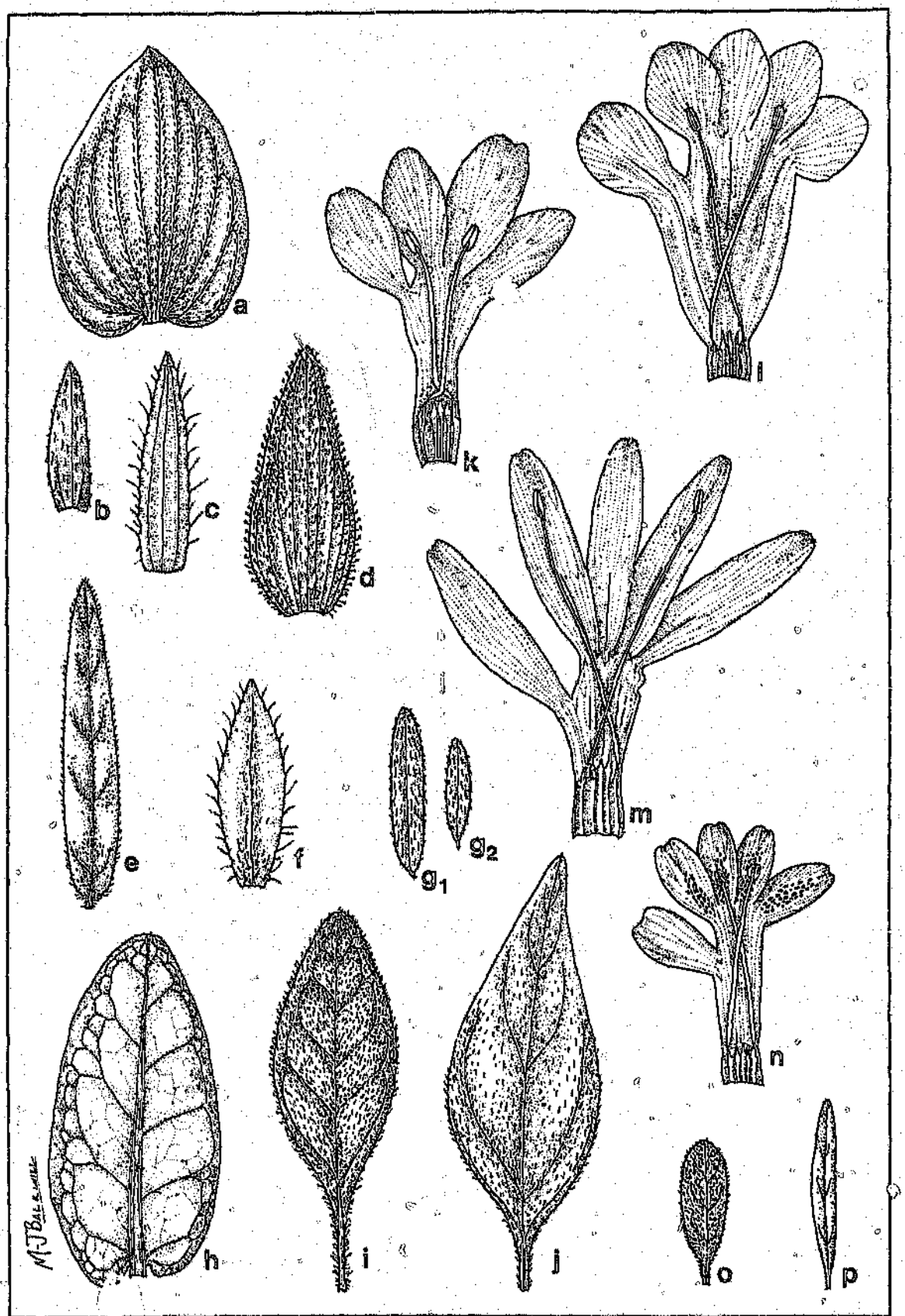
Plates: 7.6a & b

This is a highly distinctive group characterised by the presence of medifixed hairs (absent in only one species), leaves that dry a distinctive blue-green colour and white or pink corollas in which the 4 upper lobes have speckles of contrasting coloration. The corolla lobes are usually very much longer than the corolla tube and the two adaxial corolla

Figure 7.8: Variation in the morphology of the leaves, corollas, bracteoles and calyces of selected representatives of Section *Somalia*.

a) - d) posticous calyx lobes, abaxial surfaces shown; e) - j) leaves, adaxial surfaces shown; k) - n) corollas, opened along line between median abaxial corolla lobe and lateral lobe; o) - p) bracteoles.

a) *B. mackenii* x 3: Mogg 17268 (J); b) *B. aucherana* x 3: Wood s/72/38 (K); c) *B. stocksii* x 3: Gamble 21163 (K); d) *B. meyeriana* x 3: Balkwill, Balkwill, Gesell & Melville 5873 (J); e) *B. hirta* x 1: Teague 8 (BOL); f) *B. rehmannii* x 1.5: Codd 3492 (PRE); g1 and g2) *B. argentea* x 2: Thulin & Warfa 4663 (K); h) *B. calophylloides* x 1: Bally & Carter 16481 (MO); i) *B. albi-pilosa* x 1: Walter 412 (PRE); j) *B. mackenii* x 1: Mogg 17268 (J); k) *B. lugardii* x 2.5: Leach 10595 (FRE); l) *B. lancifolia* x 1.5: Balkwill & Balkwill 4302 (J); m) *B. pretoriensis* x 1.5: Balkwill & Balkwill 4373 (J); n) *B. argentea* x 3: Thulin & Warfa 4663 (K); o) *B. clinopodium* x 2: Thulin, Hedren & Adbi M. Dahir 7726 (K); p) *B. lancifolia* x 3: Balkwill & Balkwill 4302 (J).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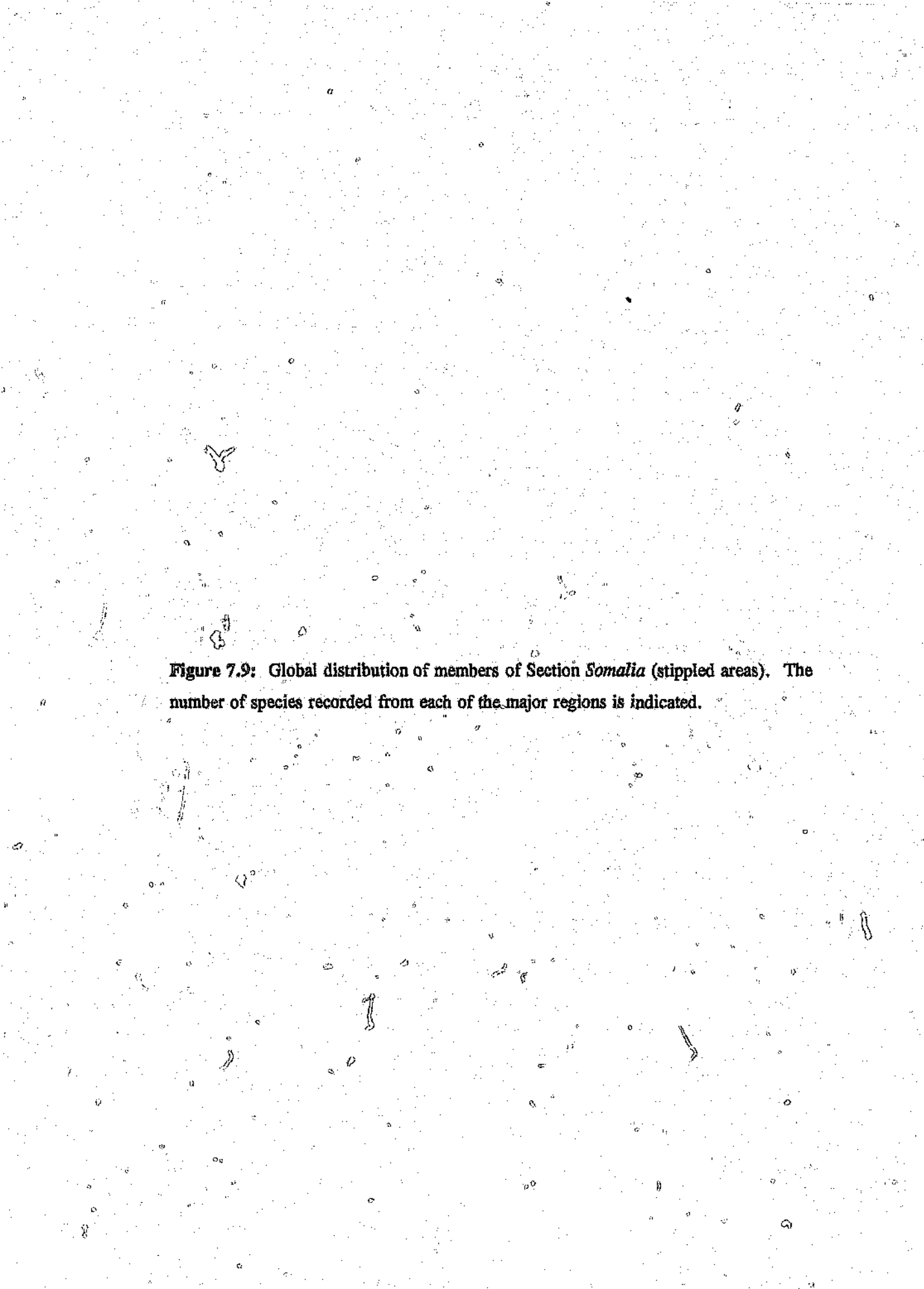
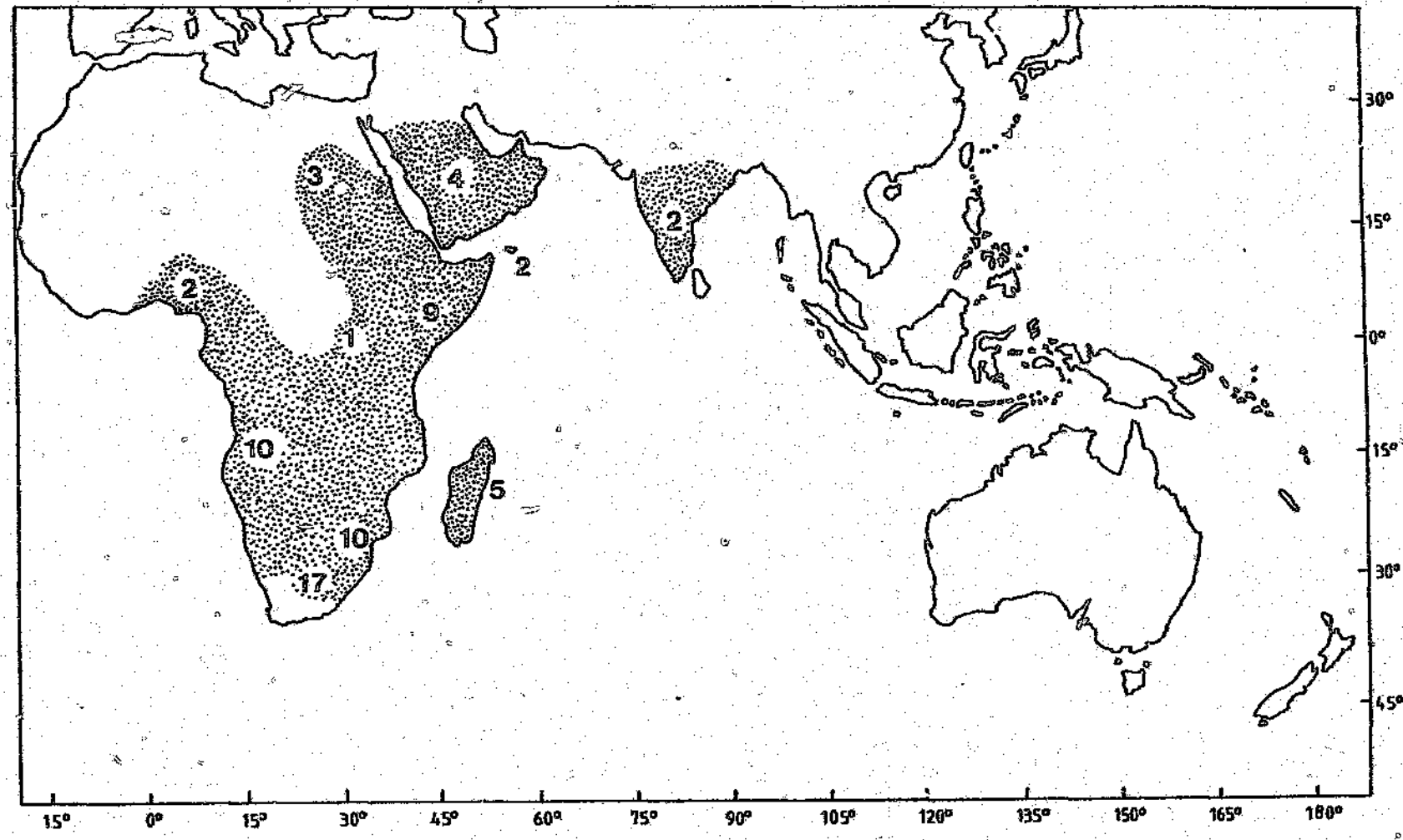


Figure 7.9: Global distribution of members of Section *Somalia* (stippled areas). The number of species recorded from each of the major regions is indicated.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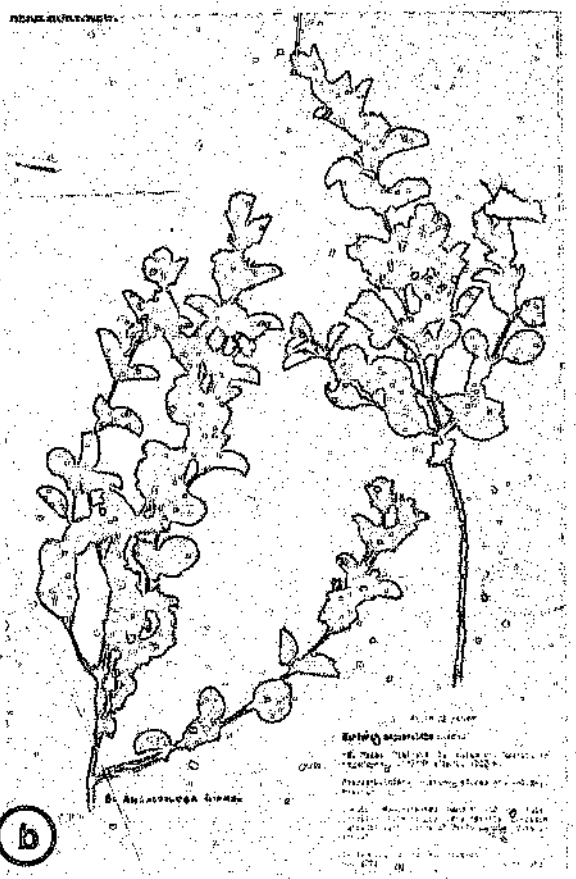
165°
180°

Plate 7.6: Selected representatives of Section *Somalia*.

a) *B. sp. aff glandulifera*: Greenway 13534 (PRE); b) *B. angustiloba:* Bidgood & Vollesen 1272 (K); c) *B. mackenii*: Merxmuller & Giess 1821 (PRE); d) *B. meyeriana*: Edwards 25 (NU).

a



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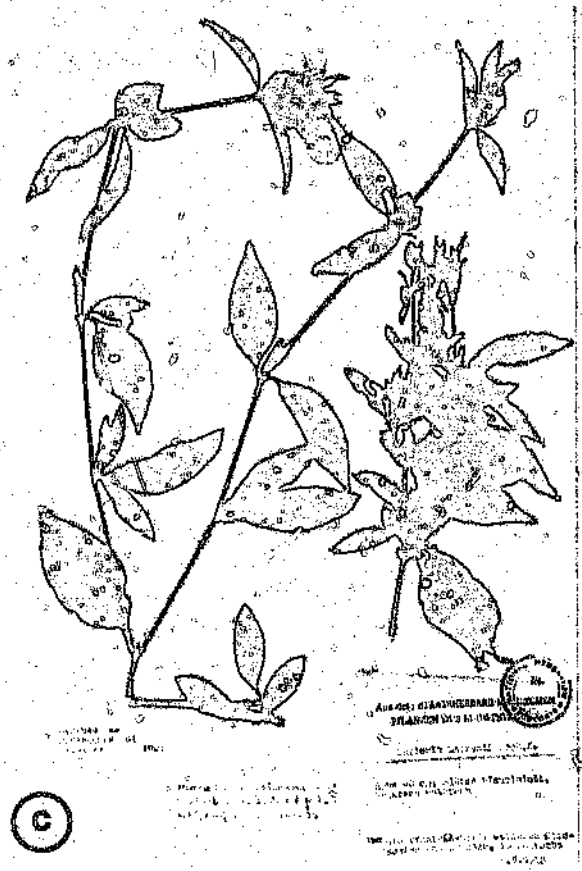

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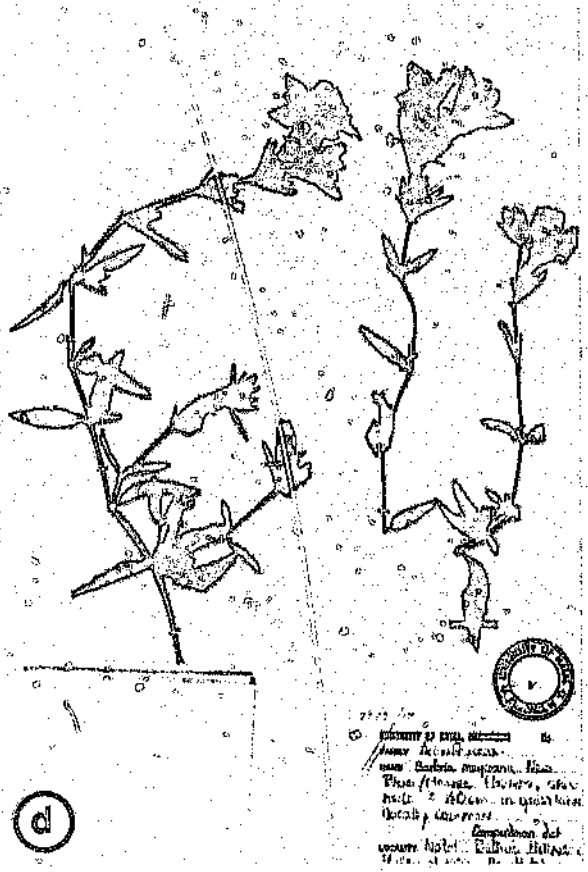


d

lobes are often partially fused. The inflorescence units in this group are usually dichasial and include some unusual forms. In most of the species single inflorescence units occur in the leaf axils, but occasionally in this group, two separate inflorescence units occur in the same axil. The capsules have the same basic morphology as that found in the rest of the section, but they are extremely small and the apical beak is usually much longer than the lower part of the fruit in which the seeds are borne. In most of the other members of this Section the beak on the capsule is usually only as long as or shorter than the lower part of the fruit.

The distribution of this group is particularly interesting. Most of the species occur in East Africa, with a few occurring in North Africa and Arabia (see Table 7.1) and only one (unnamed, very similar to *B. angustiloba* and not included in Table 7.1) known from Southern Africa. In contrast, the remaining species in the Section are only poorly represented in East Africa (only 6 species), the majority occurring in Southern Africa and the Zambezian region.

Included taxa: *B. angustiloba, B. argentea, B. aucherana, B. clinopodium, B. glandulifera, B. hochstetteri, B. insericata, B. orbicularis, B. yemense.*

Group 2:

Typical species: *B. mackenii.*

Plate: 7.6c

The plants in this group share a number of distinctive characters. The young leaves developing from the axillary buds are densely white-woolly; the mature leaves, however, are often glabrescent but may retain a thin pubescence of soft, weak, eglandular trichomes on the abaxial surfaces. Some of the hairs in this group, particularly on the stems, are of the anvil variety. The inflorescences are usually simple, with solitary flowers borne in any leaf axil or occasionally in most of the upper leaf axils. These flowers are usually only shortly pedunculate at best, but in *B. longipes*, from Madagascar, the flowers are borne on peduncles up to 40 mm long, or more.

Included taxa: *B. albi-pilosa, B. galpinii, B. grandipetala, B. kacondensis, B. lancifolia, B. longipes, B. mackenii, B. matopensis, B. obtusisepala, B. violacea, B. violacea.*

Group 3:

Typical species: *B. meyeriana.*

Plate: 7.6d

This group is very similar to the previous one, but the young leaves in the axils are not usually white-woolly as they are in Group 1. Furthermore, most of the eglandular trichomes in these species are of the anvil variety, whilst anvil hairs occur only infrequently in the previous group.

Included taxa: *B. dolomiticola, B. hirta, B. meyeriana, B. pretoriensis.*

Group 4:

Typical species: *B. lactiflora.*

Plate: 7.5c

A conspicuous feature of this group is the sessile (or almost sessile) leaves that are often glaucous. The plants are usually almost entirely glabrous, but if any trichomes are present they are simple and not of the anvil or medifixed variety. The inflorescence units comprise single flowers that are usually arranged into fairly condensed terminal synflorescences. The corollas of several species in this group are butter-yellow or white, rather than blue which is more typical for Section *Somalia* as a whole. Indeed, the only species of this group known to have purple corollas, rather than yellow or white, is *B. wilmsiana*, which is also the only species in the group not from East Africa or the Zambezian region.

Included taxa: *B. benguellensis, B. calophylla, B. calophylloides, B. gossweileri, B. lactiflora, B. limnogeton, B. pabularis, B. phaylopsis, B. polyneura, B. wilmsiana.*

Taxa of unknown affinity:

B. lugardii, B. phillyraefolia, B. puberula, B. rehmannii, B. separata, B. seyrigii, B. stocksii.

B. lugardii and *B. rehmannii* are the only two species in the genus in which only 4 lobes are present in the corolla. *B. lugardii* is fairly widespread in the eastern parts of Africa and *B. rehmannii* is restricted to southern Africa where it has an extremely limited distribution. Both of these species could be comfortably accommodated within Group

2 on the basis of most characters. *B. lugardii* is particularly easily placed in Group 2 as it possesses young axillary shoots that are extremely densely pubescent. *B. rehmannii* bears strong resemblance to *B. stocksii* from India (see Plate 7.5d), as both taxa have bulbous-based hairs along the margins of leaves, bracteoles and calyces. What is unclear is whether *B. lugardii* and *B. rehmannii* should be placed in a group of their own based on possession of only 4 corolla lobes (clearly a derived condition), or whether it should be assumed that reduction from 5 to 4 lobes in the corolla has occurred twice within Group 2.

B. phillyraefolia, B. puberula, B. separata and *B. seyrigii* are imperfectly known species from Madagascar.

Section V: ***Barlerianthus*** (Oerst.) M.Balkwill, *comb. et stat. nov.*
Type: *B. grandiflora* Dalz.

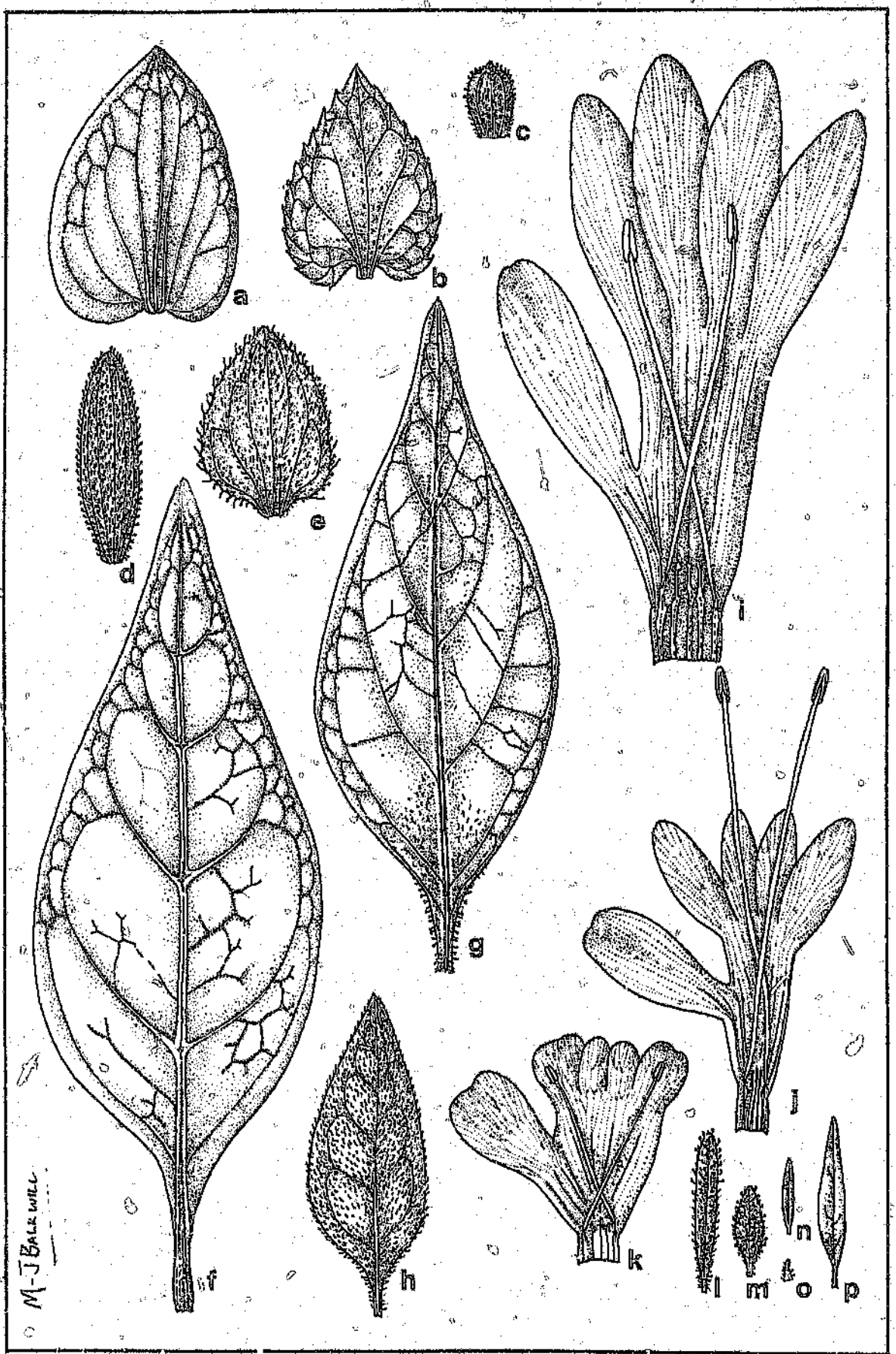
Large branched herbs or small shrubs; stems soft, herbaceous, with conspicuous swellings above each node; spines absent. *Leaves* large (approximately 140 x 45mm), broadly ovate or elliptic; apex gently tapered, acute to acuminate, often with a short drip tip; margins entire; base suddenly drawn in and then attenuate; surfaces usually glabrous or glabrescent (densely glandular pubescent in *B. grandis)*, often glaucous; petiole usually long (25 — 30 mm). *Inflorescence* lax terminal synflorescences, flowers solitary or in dichasial clusters of 3. *Bracteoles* foliaceous, entire, innocuous. *Calyx* herbaceous, margins entire, anticous lobe always bifid. *Flowers* strongly zygomorphic, 4 lobes in upper lip, 1 lobe (median abaxial) in lower lip, median abaxial lobe split from corolla for greater distance than other lobes; corolla blue, white or lilac. *Stigma* of 1 filiform lobe. *Androecium* as for Section *Barleria*. *Capsule* with a prominent, more or less hollow apical beak, broadest in region of upper ovules, tapering narrowly below; septum mostly ligneous with a membranous portion above upper ovules. *Seeds* 4, either flat and discoid, covered in hygroscopic hairs, or more or less rounded, black, glabrous.
Approximate number of taxa: 7
Figures: 7.10 and 7.11
Plates: 7.7 and 7.8

This is a very distinctive group of species, differing from the others in a number of

Figure 7.10: Variation in the morphology of the leaves, corollas, bracteoles and calyces of Sections *Barlerianthus* and *Barlerites*.

a) - e) posticous calyx lobes, abaxial surfaces shown; f) - h) leaves, adaxial surfaces shown; i) - k) corollas, opened along line between median abaxial lobe and lateral lobe; l) - p) bracteoles, adaxial surfaces shown.

a) *B. gibsonii* x 1.5 (Section *Barlerianthus*): Haines 2406 (K); b) *B. scasselati* x 1.5 (Section *Barlerites*): Friis, Vollesen & Abdisalam Sheikh Hassan 5009 (K); c) *B. brownii* x 1.5 (Section *Barlerites*): Eggeling 427 (K); d) *B. grandis* x 1 (Section *Barlerianthus*): Scott 223 (K); e) *B. scindens* x 3 (Section *Barlerites*): Balkwill & Balkwill 4308 (J); f) *B. gibsonii* x 1.5 (Section *Barlerianthus*): Haines 2406 (K); g) *B. grandis* x 1 (Section *Barlerianthus*): Ash 1330 (MO); h) *B. scindens* x 1.5 (Section *Barlerites*): Balkwill & Balkwill 4308 (J); i) *B. grandis* x 1 (Section *Barlerianthus*): Scott 223 (K); j) *B. brownii* x 1 (Section *Barlerites*): Eggeling 437 (K); k) *B. scindens* x 2.5 (Section *Barlerites*): Balkwill & Balkwill 4308 (J); l) *B. opaca* x 2 (Section *Barlerites*): Coombe 61 (K); m) *B. submollis* x 1 (Section *Barlerites*): Gilbert, Ensermu & Vollesen 7721 (K); n) *B. brownii* x 1.5 (Section *Barlerites*): Eggeling 427 (K); o) *B. scindens* x 1 (Section *Barlerites*): Balkwill & Balkwill 4308 (J); p) *B. grandis* x 2.5 (Section *Barlerianthus*): Ash 1330 (MO).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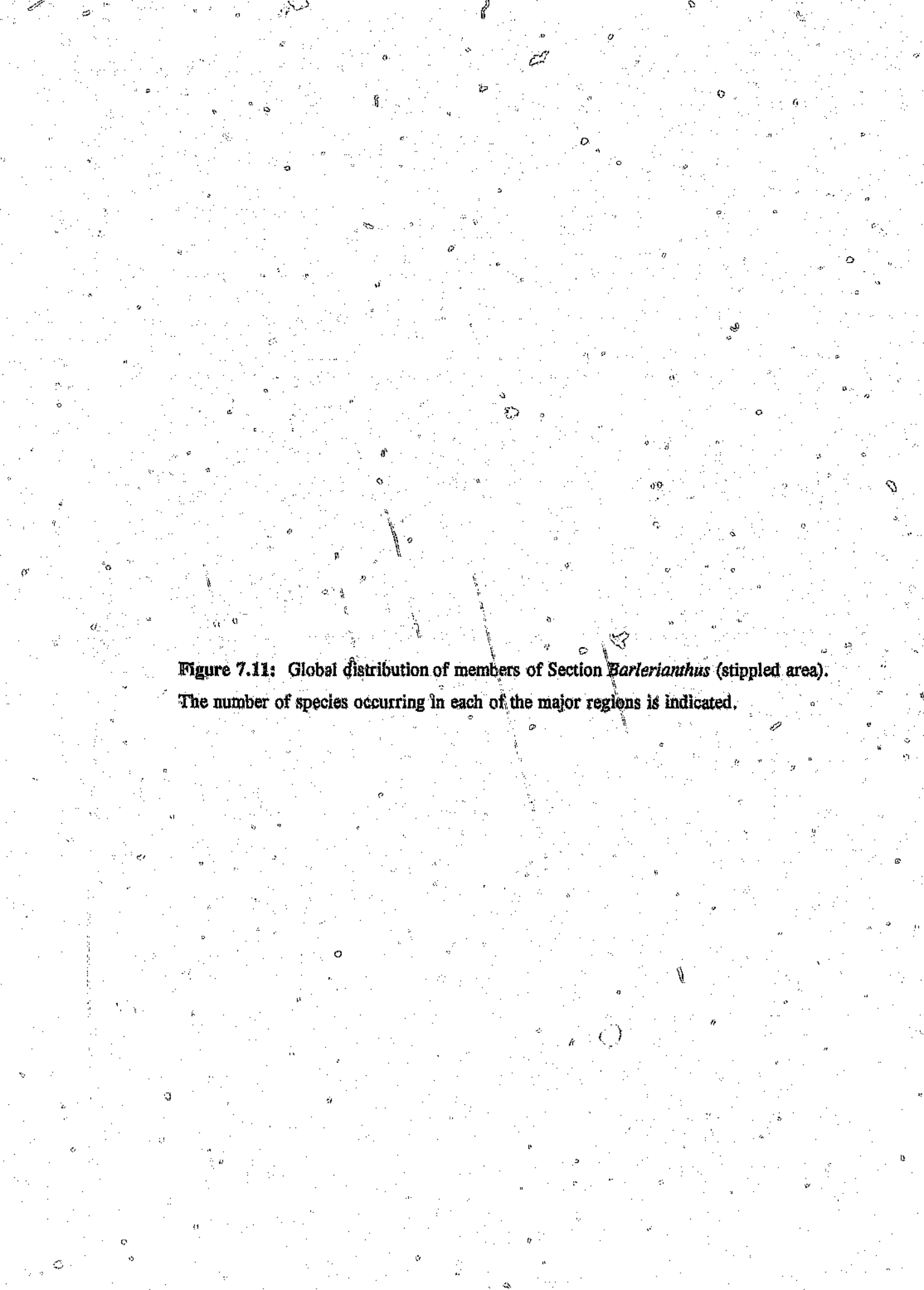
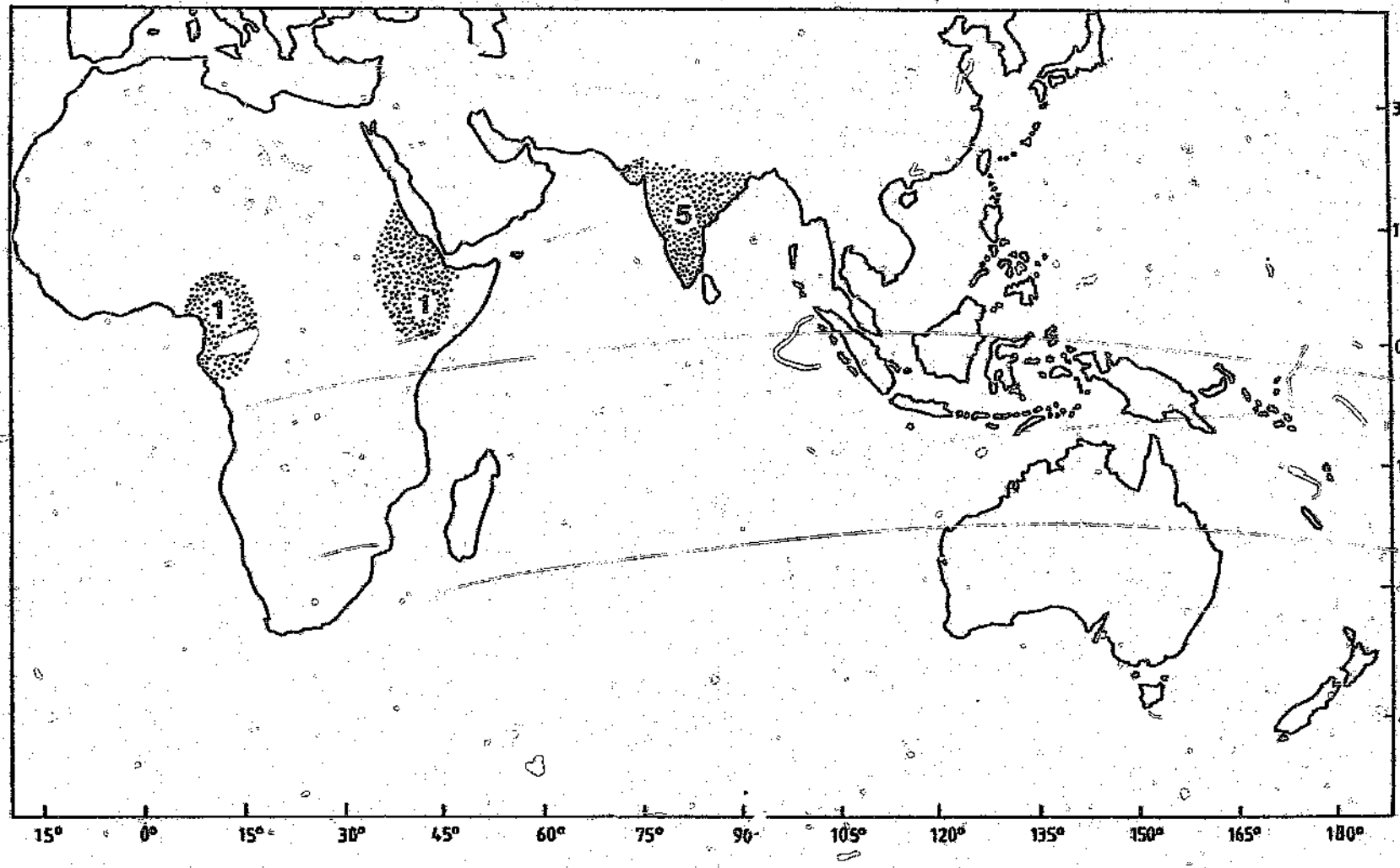


Figure 7.11: Global distribution of members of Section *Barlerianthus* (stippled area). The number of species occurring in each of the major regions is indicated.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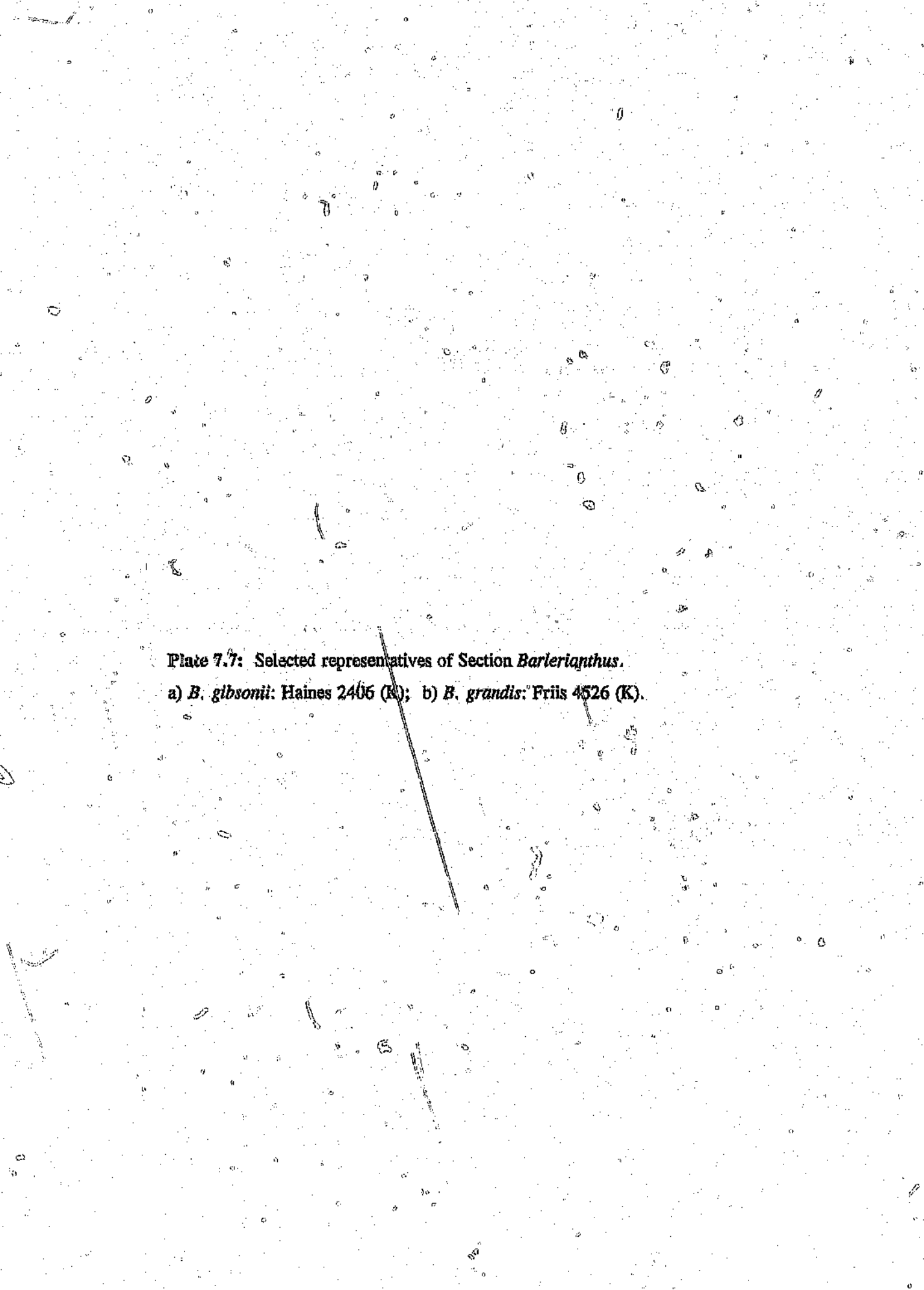
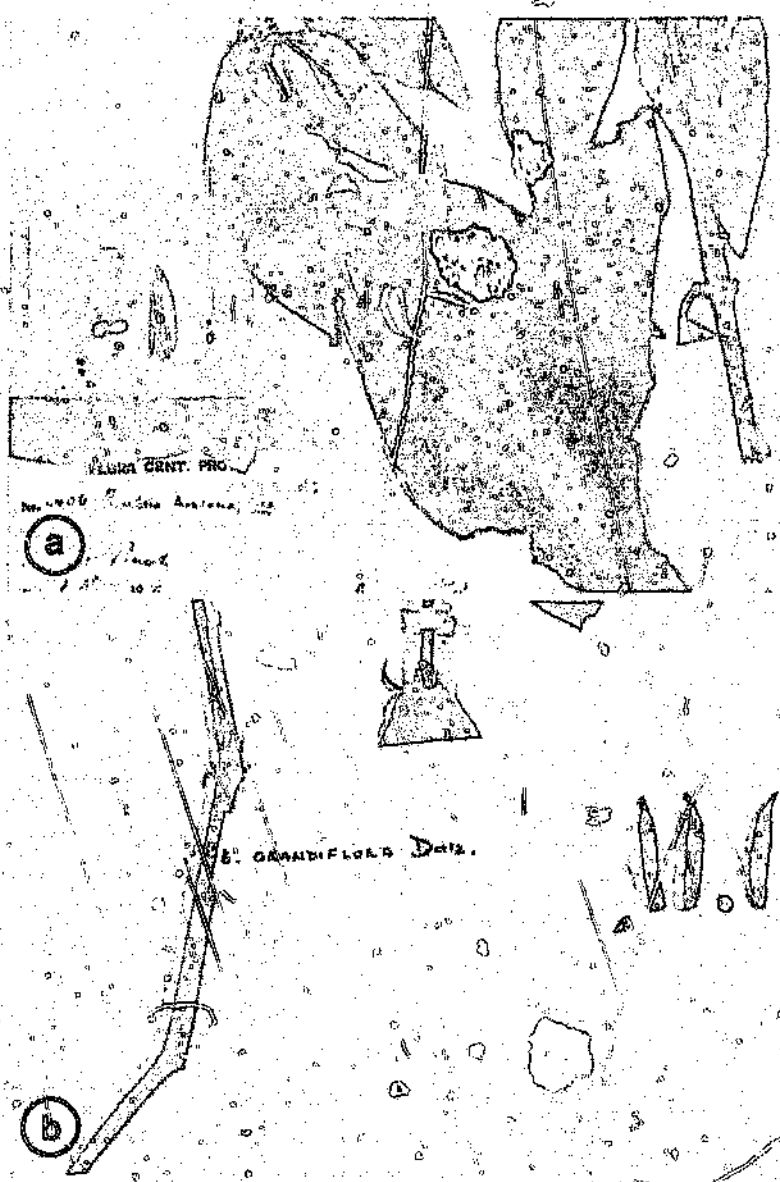


Plate 7.7: Selected representatives of Section *Barlerianthus*.
a) *B. gibsonii*: Haines 2406 (K); b) *B. grandis*: Friis 4526 (K).

a
b

Plate 7.8: Selected representatives of Section *Barlerianthus*, showing the morphology of the capsules and glabrous seeds.
a) *B. gibsonii*: Haines 2406 (K); b) *B. grandiflora*: Ritchie s.n. (E).


FLORA CENT. PRO.
a
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important and unusual characters. One of the most startling features of the group is the occurrence of glabrous seeds; this is unusual not only in *Barleria*, but in this part of the Acanthaceae. The occurrence of glabrous seeds is combined with the occurrence of 4-seededness (a reversal), in a predominantly 2-seeded part of the genus. This reversion to the plesiomorphic condition in both of these features also occurs in *B. descampsii*, which is placed in Section *Stellatohirtae* on the basis of fruit morphology and the possession of stellate hairs. The 4-seeded capsules with hollow apical beaks are also highly unusual and distinctive. The evolution of hollow beaks is considered here to represent a separate development form the evolution of solid, conical beaks, thus providing a clear apomorphy for this Section. In all other features Section *Barlerianthus* shows strong superficial resemblance to Section *Somalia*. All but two of the species within this section are restricted to India where they occur as forest undershrubs or at forest edges. Of the remaining two species, *B. grandis* occurs in East Africa only and is the only member of the group in which the plants are conspicuously pubescent rather than glabrous or glabrescent. The other species occurs in West Africa; the taxonomic status and identity of this taxon is not well understood at present. The plant is only known from one collection which has been misidentified as *B. alata* S. Moore. The capsule morphology, however, clearly places this specimen in Section *Barlerianthus* and not in Section *Somalia* into which *B. alata* (= *B. lancifolia)* falls.

Included taxa: *"B. alata"*, *B. gibsonii*, *B. gibsonioides*, *B. grandiflora*, *B. grandis*, *B. montana*, *B. prattensis*.

Section VI: ***Barlerites*** (Oerst.) M. Balkwill, *comb. et stat. nov.*
Type: *B. ventricosa* Hochst. ex Nees.

Herbs with many erect, semi-erect or sprawling herbaceous stems that may become woody near the base, rarely climbers or vines; plants innocuous. *Leaves* herbaceous, softly-textured, usually conspicuously hairy, pubescence of simple trichomes with multiseriate bulbous bases. *Inflorescence* variable, units either solitary in axils or arranged in loose to congested terminal synflorescences; unit structure of solitary flowers, lax scorpioid cymes or, more usually, units combining monochasial and dichasial branching. *Bracteoles* herbaceous, foliaceous, innocuous; margins usually entire or finely toothed, but not spinous. *Calyx* outer and inner lobes clearly

differentiated; apex of anticous lobe usually shortly bifid; margins of outer lobes shallowly serrate or entire, but never sharply spinous. *Flowers* zygomorphic, 4 lobes in upper lip, 1 in lower lip; median abaxial lobe split from corolla for greater distance than other lobes; upper corolla tube broadly inflated, usually considerably longer than narrowly cylindric lower tube; corolla white, blue or red. *Stigma* of 2, sub-confluent, capitate lobes. *Androecium* of 5 parts, as for Section *Barleria*. *Capsule* without a beak, although a small apical point may be present; laterally flattened, spindle-shaped with a woody flank on each side; side walls thin, tearing away from woody flanks upon dehiscence; septum almost entirely membranous. *Seeds* 4, flattened, with dense covering of brown or golden-brown hygroscopic hairs.

Approximate number of taxa: 20

Figures: 7.10 and 7.12

Plate: 7.9d

Section *Barlerites* is almos entirely African, with only one species from Madagascar and one uncertain record from the Fiji Islands. The centre of diversity is in East Africa, particularly in Kenya and Tanzania. Members of this section also dominate the Ugandan and West African regions. Very few species of this section are present in the Southern African and Zambezian regions (Figure 7.12).

The species in this group are characterised by thin fruit walls that tear upon dehiscence of the capsules. Other aspects of fruit morphology are shared with Section *Stellatohirtae* with which Section *Barlerites* is most closely related. Most members of this group occur as forest understorey components, at forest edges or at least in shaded conditions. Only one species, *B. lukwangulensis* from the Uluguru Mountains of Tanzania, grows as a true creeper or vine. This species is also unusual in the genus on account of its red, pendulous flowers that are most probably pollinated by birds. Although characters such as inflorescence structure show some variability, this section is relatively homogeneous with respect to most characters and it is not easily divisible into any smaller units.

Section *Barlerites* was recognised by both Clarke (1899) and Obermeijer (1933) as a subsection of their respective Sections *Barleria*. The current research has revealed that the phylogenetic affinity of the group lies more closely with Sections *Somalia* and *Stellatohirtae* than it does with Section *Barleria* (as circumscribed here). The species

Figure 7.12: Global distribution of members of Section *Barlerites* (stippled areas). The number of species occurring in each of the major areas is indicated.

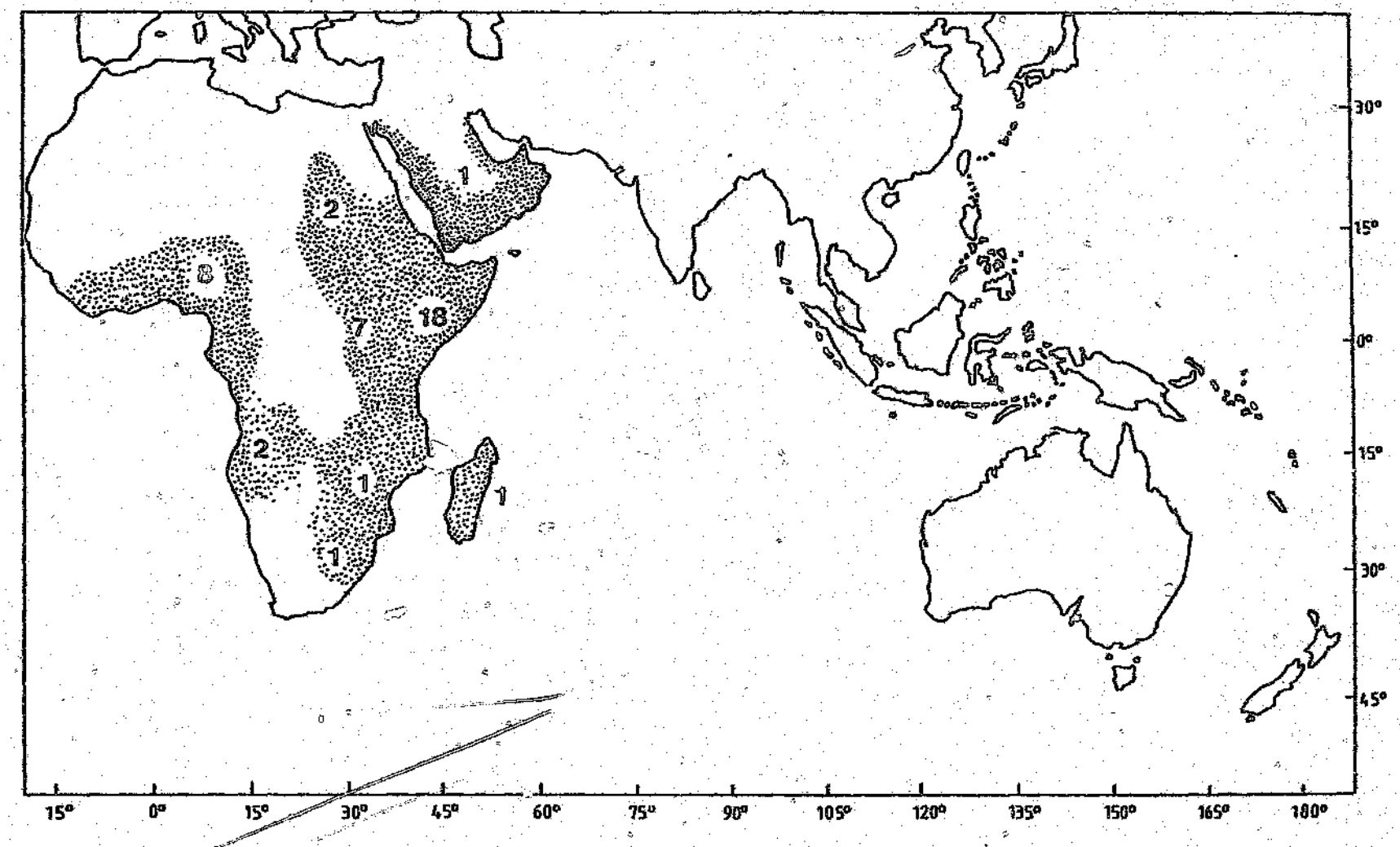
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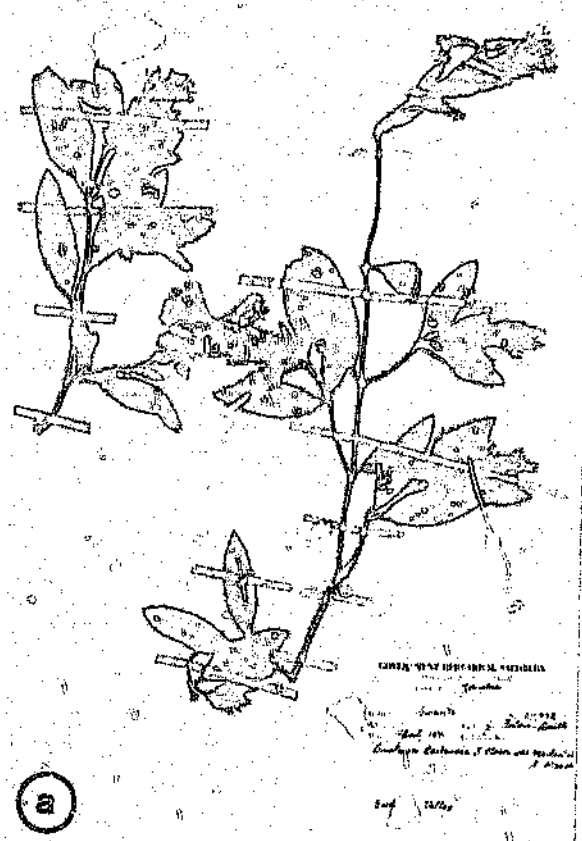
Plate 7.9: Selected representatives of Sections *Stellatohirtae* and *Barlerites*.
a).- c) Section *Stellatohirtae*; d) Section *Barlerites*.
a) *B. rogersii*: Anton-Smith s.n. (SRGH); b) *B. splendens*: Bidgood, Mwasumbi & Vollesen 1096 (K); c) *B. salicifolia*: Pocock 39 145 (SAM); d) *B. lukwangulensis*: Congdon 209 (K).



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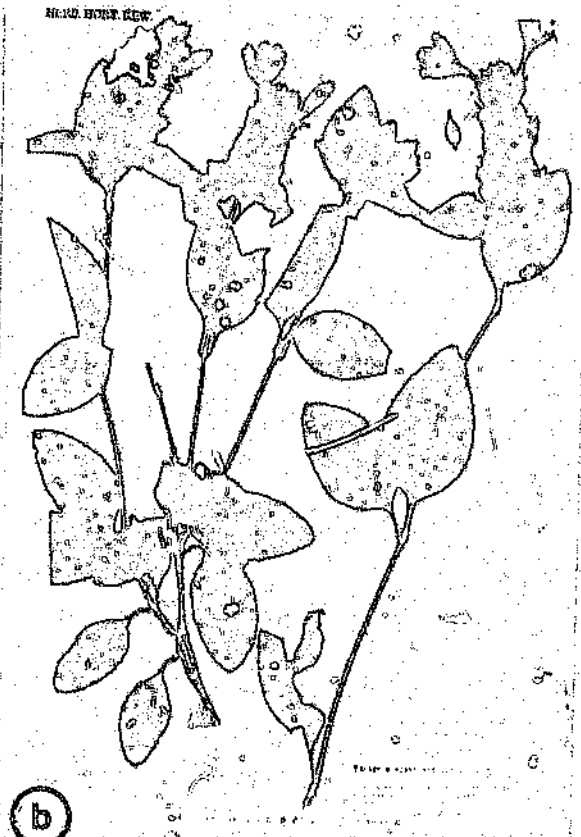

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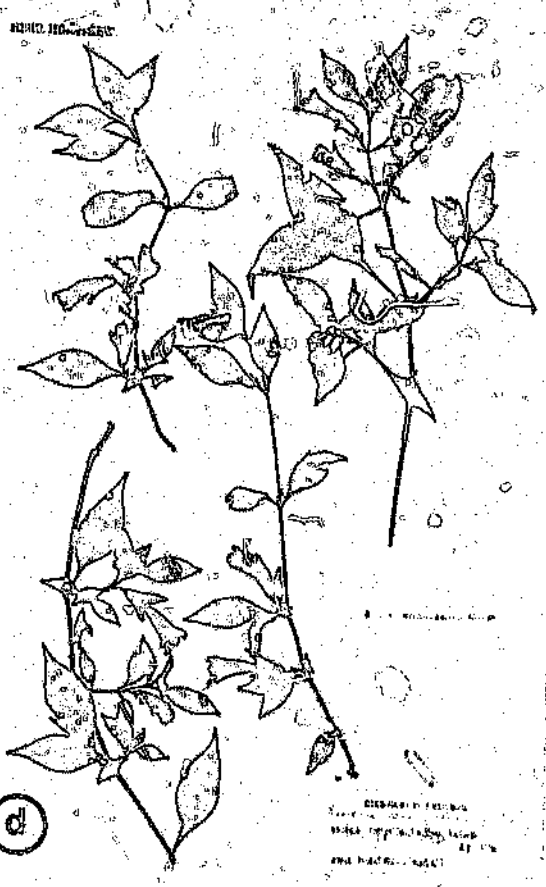

d

limits within this Section are poorly defined and future taxonomic revision should pay particular attention to this group.

Included taxa: *B. amanensis, B. boehmii, B. boranensis, B. brownii, B. grantii, B. keniensis, B. laeta, B. lukafuensis (possibly a synonym of B. lukwangulensis), B. lukwangulensis, B. micrantha, B. neurophylla, B. opaca, B. ruellioides, B. scindens, B. stuhlmanii, B. submollis, B. talbotii, B. usambarica, B. ventricosa, B. villosa, B. vix-dentata.*

Section VII: *Stellatohirtae* (Clarke) M. Balkwill, *stat. nov.*
Type: *B. albostellata* C.B.Cl.

Small shrubs or suffrutices; plants unarmed. *Leaves* usually discolorous, darker above than below, largely due to density of pubescence on lower leaf surfaces; all vegetative parts densely covered with stellate or dendroid hairs. *Inflorescence* a compound, terminal synflorescence, either strobilate or capitate; units of solitary flowers. *Bracts* highly modified, foliaceous or somewhat chartaceous, often with prominent pattern of reticulate venation; margins entire or irregularly dentate or serrate. *Bracteoles* similar to bracts but smaller. *Calyx* herbaceous, anticous lobe bifid for approximately one third of length, posticous lobe rarely with sharp, recurved apiculus; margins of lobes entire or irregularly toothed but not spinous. *Flowers* zygomorphic, lobes in 4+1 configuration, median abaxial lobe split from corolla for greater distance then other lobes. *Capsule* lateral walls remain intact upon dehiscence of fruit, otherwise as for Section *Barlerites* (excepting *B. descampsii* which has a short, hollow apical beak). *Seeds* 2, covered with golden hygroscopic hairs except in *B. descampsii* (seeds 4, glabrous).
Approximate number of taxa: 12
Figures: 7.13 and 7.14
Plate: 7.9a — c

The members of this section were previously placed in Sub-section *Stellatohirtae* of Section *Barleria* sensu Clarke (1899) and in Sub-section *Thamnotrichae* of Section *Barleria* sensu Obermeijer (1933). The current study has shown, however, that this Section is most closely related to Sections *Barlerites, Somalia* and *Prionitis* based on

Figure 7.13: Variation in the morphology of the leaves, corollas, bracteoles, bracts and calyces of selected representatives of Section *Stellatohirtae*.

a) - c) posticous calyx lobes, outer surfaces shown; d) - f) bracteoles, abaxial surfaces shown; g) - j) leaves, adaxial surfaces shown; k) - l) corollas, opened along line between median abaxial lobe and lateral lobe; m) - p) bracts, abaxial surfaces shown. a) *B. rogersii* x 3: Balkwill & Balkwill 6353 (K); b) *B. albostellata* x 2: Balkwill *et al.* 5811 (J); c) *B. descampsii* x 2.5: Richards 5364 (K); d) *B. albostellata* x 1: Balkwill *et al.* 5811 (J); e) *B. rogersii* x 3.5: Balkwill & Balkwill 6353 (J); f) *B. stellato-tomentosa* x 2: Welwitsch 5165 (K); g) *B. salicifolia* x 1: Pocock 604 (BOL); h) *B. descampsii* x 1: Fanshawe 8683 (SRGH); i) *B. albostellata* x 1: Balkwill *et al.* 5811 (J); j) *B. rogersii* x 1: Balkwill & Balkwill 6353(J); k) *B. albostellata* x 1.5: Balkwill *et al.* 5811 (J); l) *B. rogersii* x 3: Balkwill & Balkwill 6353 (J); m) *B. rogersii* x 3.5: Balkwill & Balkwill 6353 (J); n) *B. splendens* x 2.5: Bidgood, Mwasumbi & Vollesen 1096 (K); o) *B. albostellata* x 2: Balkwill *et al.* 5811 (J); p) *B. albostellata* x 1: Balkwill *et al.* 5811 (J).

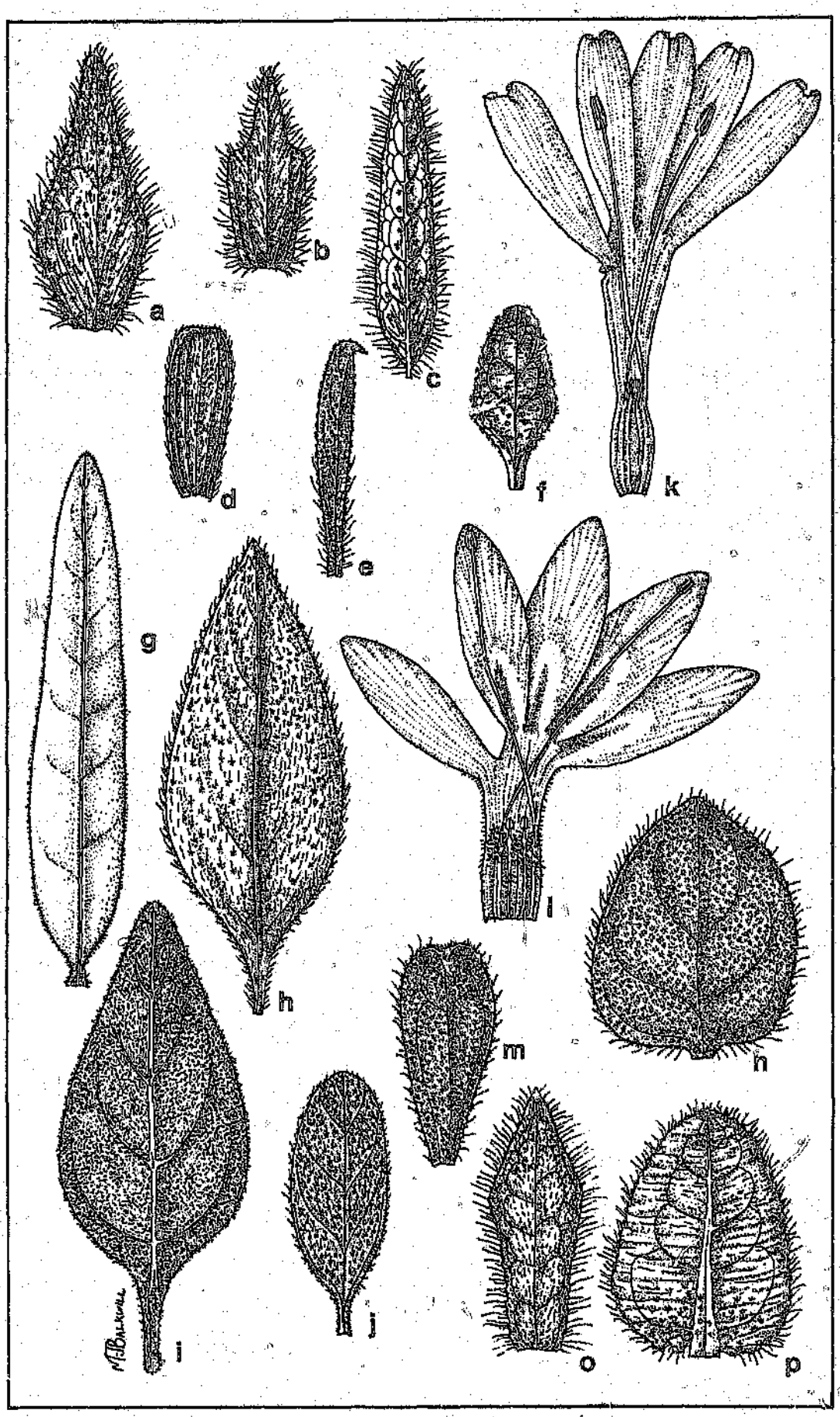
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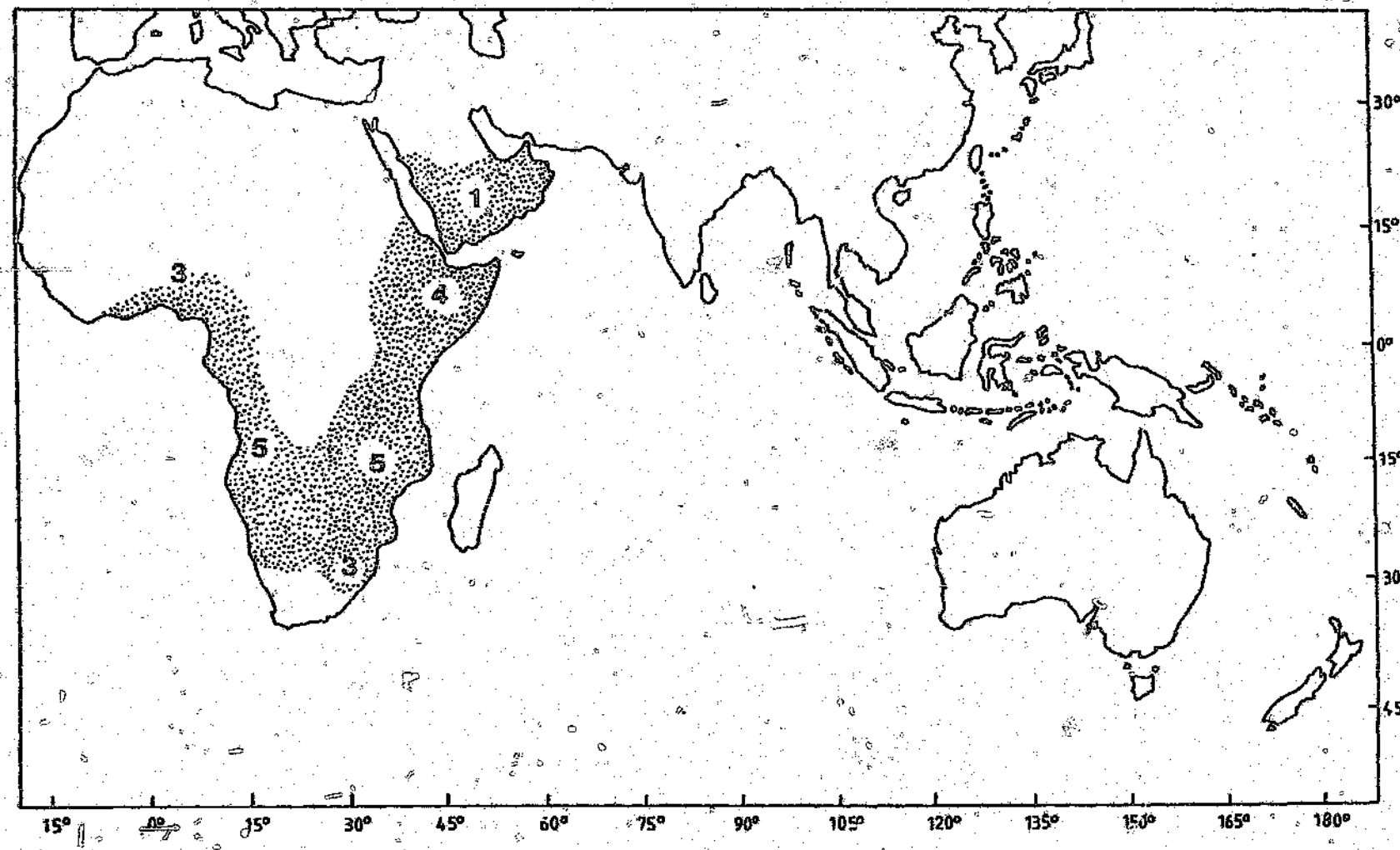
Figure 7.14: Global distribution of members of Section *Stellatohirtae* (stippled area). The number of species occurring in each of the major regions is indicated.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their common possession of 2 seeds and strongly zygomorphic corollas in which the lobes are arranged in the 4+1 configuration. Section *Stellatohirtae* is clearly recognisable by its dense pubescence of complex hairs and its conspicuous capitate or strobilate inflorescences. A wide range of complex hair types is found in Section *Stellatohirtae*. A particularly unusual hair type is found in *B. hildebrandtii*; the bracts of this species appear to be studded with small "knobs" due to the presence of long-armed stellate hairs, the bases of which are conspicuously swollen and bony.

This group is essentially restricted to Africa, with only one species, *B. hildebrandtii*, extending into Arabia. It is best represented in East Africa, Angola and the Zambezian regions, although the relative proportion that the group constitutes of the total number of species is much lower in East Africa than it is further south. The species limits in this group are particularly poorly defined and taxonomic revision is sorely needed, particularly in the Angolan region.

Included taxa: *B. albostellata, B. argenteo-calycina, B. briartii, B. buddleioides, B. descampsii, B. hildebrandtii, B. paludosa, B. rogersii, B. salicifolia, B. splendens, B. stellato-tomentosa, B. stelligera , B. subglobosa, B. taitensis.*

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Taxa of unknown Affinity

B. acanthophora, B. bagshawei, B. benadirensis, B. bituminosa, B. blepharoides, B. bonafacei, B. brasiliensis, B. cavalerei, B. comorensis, B. crotalaria, B. cunenensis, B. delamerei, B. elliptica, B. exellii, B. farinosa, B. glabra, B. humilis, B . insolita, B. iodocephala, B. jucunda, B. kaessneri, B. kilimandscharica, B. laceratiflora, B. linearifolia, B. longifolia, B. longipedunculata, B. longistyla, B. macraei, B. macrolemma, B. maculata, B. mairei, B. massae, B. methueni, B. mitis, B. multiflora, B. newtonii, B. observatrix, B. pannosa, B. paolii, B. procumbens, B. puccioni, B. reticulata, B. richardiana, B. rubra, B. satureiodes, B. schmittii, B. schweinfurthiana, B. somaliensis, B. stenophylla, B. subinermis, B. sudanica, B. tischeriana, B. umbrosa, B. verdickii.

CHAPTER 8

Concluding Remarks

Introduction

The aims of the research presented in this thesis were threefold:

i) To re-assess the delimitation of *Barleria*.

ii) To provide a modern infra-generic classification of the genus on a world-wide scale.

iii) To assess evolutionary relationships and lineages within the genus.

All three aims have been achieved. A multidisciplinary approach was adopted combining research in the laboratory, herbarium and field (where possible). Due to the monographic scale of the work, it was not possible to conduct fieldwork in many areas in which *Barleria* occurs and the study was, therefore, largely herbarium-based and emphasised characters that could be readily studied in dried herbarium material (e.g. various aspects of morphology and anatomy, and distribution patterns). The generic concept adopted in this account is a phylogenetic one based on monophyly, although some of the concepts of phylogenetic systematics have been applied in a looser manner than may always be preferable.

Conclusions, contributions and limitations

The overall conclusion of this research is that *Barleria* is a single genus, considered here to represent a monophyletic group clearly delimited by the co-occurrence of three characters: globose, honeycombed pollen; the predominance of double cystoliths in the epidermal cells and a 4-partite calyx with two large, outer lobes (adaxial and abaxial) and two, small, inner lobes (lateral). The members of the genus have been placed in seven sections: two of these (Sections *Prionitis* and *Somalia)* are retained as circumscribed in previous classifications although additional characters have been found to delimit them; one section (*Barleria*) is retained partially as previously circumscribed, but with two of the groups previously included removed and elevated to sectional status; two sections

(*Barlerites* and *Stellatohirtae*) are recognised for the first time at the sectional level and the remaining two sections (*Barleriopsis* and *Barlerianthus*) are described here for the first time. This infra-generic classification is the first produced since the time of Lindau (1895) that covers the genus on a global scale. Whilst the status of Section *Barleriopsis* may be slightly unclear, the other sections are very well defined. Thus, this classification will provide a relatively stable framework in the context of which further taxonomic research can be conducted. The analysis of distribution patterns undertaken as part of this research, has revealed that each of the Sections described here is concentrated in a particular geographic region. Furthermore, there is a relatively high degree of endemism in each of the major geographic regions in which *Barleria* is represented.

During the course of this research much attention was focussed on the search for reliable characters on which to base an infra-generic classification. In this search, a number of new characters (or characters that had been previously neglected) were found and used with good effect. Of particular interest are the differences in the structure of the septum. No information is available in the literature regarding the nature of the septum in other members of the Acanthaceae. A detailed investigation of this character across a wide sample of acanthaceous genera could provide useful information for assessing affinities and trends within the family. Use of data from similar new sources could provide new perspectives on the classification of the family, rather than limiting such studies to the traditionally used characters such as pollen and aestivation of the corolla. Attempts at ascertaining the distribution of certain characters or character-states within the family (in order to assess how "noisy" they were on a broader scale and, therefore how reliable they may be as generic markers), were frequently frustrated by lack of information. A thorough knowledge of the variation in particular characters across the family would greatly facilitate decisions regarding the reliability of characters to be used at the generic and supra-generic levels. This knowledge would also be invaluable for those conducting cladistic analyses within the family, as decisions regarding evolutionary trends and homology could be made with far greater confidence.

The monographic scale on which this work was conducted had a number of important implications and consequences. In a group such as the Acanthaceae in which there are numerous large, widespread and variable genera such as *Barleria*, it is absolutely

essential that workers obtain a thorough knowledge of the full range of variation before making decisions regarding the circumscription of genera or infra-generic sub-divisions. For example, many of the Indian taxa are not represented in other geographic regions or are represented by only one or a few species in other regions. Many of the unusual character states or combinations of character states occur in these Indian taxa. Had the Indian region not been included in this study, these taxa would not have been seen and the conclusions drawn regarding the distribution and polarity of character states would have been considerably different and the weaker for it. There are a number of difficulties associated with conducting this kind of research on a monographic scale, particularly if the period over which the research can be conducted is fairly limited. The first difficulty relates to the kinds of characters that can be investigated. For the current research it was only possible to conduct fieldwork in southern Africa, with the consequence that the investigations of the bulk of species had to be restricted to the study of herbarium material. This limited the kinds of characters that could be used. Attempts were made to obtain data from sources such as karyology and phytochemistry, but these had to be limited to southern African species of which fresh material was available. The data thus obtained were not particularly useful in devising an infra-generic classification as they were too fragmentary to be meaningful. Such investigations did, however, highlight sources of potentially useful characters that would be worthy of future investigation. It would be particularly interesting to test the robustness of the classification proposed in this thesis using data obtained from other sources such as phytochemistry. A further difficulty associated with conducting this research on a monographic scale was that it was not possible to obtain fully representative material of all described species. The herbarium material did not always include fruits, seeds or flowers which provide important characters and it was not possible to collect new material of these taxa. Nonetheless, a very broad range of taxa was sampled including approximately 240 of the 300 described species and I believe that this was sufficient to formulate a classification that will be relatively stable; furthermore, this classification can be further refined when information regarding the imperfectly known taxa becomes available. I also believe that whilst the classification proposed here may not be without flaws, it represents a considerable advancement over the previous, disparate regional classifications as it provides a consistent treatment for the entire genus.

The cladistic approach has been extremely useful in this thesis, even if problematic at

times. The main difficulty encountered with using this approach in *Barleria* was finding good cladistic characters. *Barleria* is a particularly frustrating genus: whilst there is immense variation in many characters, few of them behave well as cladistic characters. Many character states show strong associations with particular taxa but then also have sporadic occurrence elsewhere in the genus. This problem was also encountered by Ensermu (1990) in his analyses of *Justicia* sect. *Ansellia* (Ensermu, pers. comm.) and possibly relates to the apparently frequent incidence of hybridisation in this family. Successful use of cladistic methodology in such situations requires particularly careful analysis and definition of characters and character-states, and use of only a few, reliable characters rather than a larger number of mostly homoplasious, "noisy" characters. A further cautionary note is that if considerable care is not taken in the selection of characters, the shortest (most parsimonious) trees may not always be the best as they may be based on highly unreliable characters. Some of the difficulties associated with previous classifications of *Barleria* relate to the use of "absence characters" (eg. fruits without a beak) to delimit groups; use of cladistic methodology prevented the use of such characters and resulted in a tidier classification in terms of the distribution of character states. The rigorous requirement of cladistics for the use of homologous characters only, focussed attention on the nature of the spine systems in *Barleria*. Previous classifications have used the general presence or absence of "spines" to circumscribe groups; this research has demonstrated that the spine systems in different infra-generic groups within *Barleria* are not homologous, thus facilitating reliable use of these structures as separate characters.

The major contributions made by this research include: clarification of the generic limits of *Barleria* and provision of a revised infra-generic classification of the genus on a global scale; a detailed investigation of morphological features revealing previously neglected characters and new interpretations of more well-known characters and the formulation of preliminary hypotheses regarding the distribution patterns within the genus. *Barleria*, however, still provides enormous scope for future research.

Future Directions

Many interesting characters that have been used in this thesis are worthy of more detailed investigation, either within *Barleria* (to further refine the classification) or in the

Acanthaceae in a broader sense. In particular, developmental studies of the diverse array of hair types would provide useful information regarding the homology of these structures. Karyology and phytochemistry hold great potential as useful sources of data, although the preliminary investigations conducted as part of the current research indicate that both of these fields are highly complex in *Barleria* and would require full-scale investigations in their own right.

A number of interesting biogeographical trends have emerged during the course of this research. The conclusions drawn from these can only be regarded as preliminary working hypotheses, as the numbers of species calculated for each area may be slightly inaccurate due to confused taxonomy at the species level. These hypotheses, however, could be tested more rigorously when taxonomic confusion has been clarified and species numbers confirmed. They would also form a useful starting point for an in-depth investigation of biogeography and endemism. Biogeography has not been extensively investigated in the Acanthaceae and it would be particularly interesting to compare the biogeographical trends apparent in *Barleria* with those of other large, widespread genera in the family.

It has been a source of considerable frustration to this author to leave the numerous nomenclatural problems and hazy species circumscriptions that are evident in *Barleria* unresolved. Particular attention is required in Sections *Prionitis*, *Barlerites*, *Barleria* and *Stellatohirtae* where it is probable that many of the existing names will be reduced to synonymy. Furthermore, the activities of collectors in East Africa in particular have brought to light material of numerous undescribed taxa which await formal recognition and description. The current research has also revealed that a number of taxa (which probably represent sub-sections) can be identified within most of the Sections. The circumscription of these taxa needs to be clarified, whereafter they can be formally described.

In conclusion, my research on *Barleria* has pointed clearly to a number of avenues along which future research in this genus, and the Acanthaceae in general, could be profitably directed. Briefly summarised these are:

i) The most urgent need is for a full-scale taxonomic revision of *Barleria* to be undertaken.

Full revision of *Barleria* on a monographic scale would be a daunting task requiring considerable time if it is to be undertaken thoroughly. One more pragmatic approach would be for the species within certain regions to be revised as parts of regional Floras. Another equally pragmatic and theoretically more satisfying approach would be for the species to be revised section by section.

ii) Another important need is for in-group analysis of each of the Sections. This is necessary to facilitate the clear circumscription and description of sub-groups within each section. It should also clarify some of the problems that have emerged from the current research regarding the circumscription of Section *Barleriopsis*. It is essential, though, that the species limits within each Section are clarified before a meaningful attempt can be made at conducting investigations of relationships within each Section.

iii) A thorough investigation of the biogeography of *Barleria* is required to test the hypotheses formulated in this thesis. Meaningful biogeographical studies in this genus, or any other, require clarification of the taxonomic confusion that currently exists at the species level. It would also be important to clarify the phylogenetic relationships at the species level before embarking on a study of cladistic biogeography within the genus.

iv) In a more general context, a direction in which I would like to see research in the Acanthaceae moving is towards broad-scale investigations of particular characters across the whole family. Thorough knowledge of the variation in particular characters would be invaluable for those conducting studies at the generic and supra-generic levels; it would also be of great benefit to those using cladistic methodology as the reliability of characters as generic markers would be far easier to assess.

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APPENDIX 1

List of known species of *Barleria*. Names printed in bold type are those in current usage and are followed by a reference to the original description, broad areas of distribution and section to which each species has been assigned. Names printed in italics are published synonyms and are followed by the currently accepted name in capital letters. In cases where synonymy is suspected, but has not been published, it is indicated.

* indicates those species seen by the author.

NOTE: Although every attempt has been made to establish synonymy accurately, the confused state of the taxonomy at the species level in *Barleria* means that inaccuracies may occur in the following list.

***B. acanthoides** Vahl, *Symb. Bot.* i: 47; India, Arabia, Oman, Yemen, Egypt, Sudan, Djibouti, Ethiopia, Kenya; Section Barleria

B. acanthophora Nees, in DC., *Prod.* xi: 726; Tropical Africa; section unknown

***B. aculeata** Balf. f., in *Proc. Roy. Soc. Edinburgh* xii: 85; Socotra; Section Barleria

B. acuminata Wight, *Icones* t. 450 = B. TOMENTOSA

B. adelensis Delile, in Rochet, *Se. Voy. Choa.*: 341; Tropical Africa; section unknown

***B. affinis** C.B. Cl., in *Fl. Cap.* 5 (i): 50; South Africa, Zimbabwe; Section Barleria

B. affinis Wildem. in *Ann. Mus. Congo* iv: 140 = ?

B. afzelia Lindau in Engl. *Bot. Jahrb.* xxiv: 319 = B. FLAVA

B. alata S. Moore. in *Journ. Bot.* xviii: 266 = B. LANCIFOLIA

***"B. sp."** Gabon; Section Barlerianthus

B. alba Lodd. *Bot. Cab.* iv t 360 = B. CRISTATA

***B. albida** Lindau, in *Engl. Bot. Jahrb.* lvii: 22; Namibia; Section Prionitis (probably synonomous with *B. senensis*)

***B. albi-pilosa** Hainz in *Mitt. Bot. Staatss. Munch.* 12: 67; Namibia; Section

Somalia

*B. **albostellata** C.B.Cl., in *F. T. A.* 5: 162; South Africa, Zimbabwe; Section **Stellatohirtae**

*B. **allaudii** Benoist, in Lecomte *Not. Syst.* 1: 362; Madagascar; Section **Prionitis**

*B. **amanensis** Lindau in *Engl. Jahrb.* xliii: 352 (1909); Tanzania, Kenya; Section **Barlerites**

B. ameliae A. Meeuse in *Bothalia* vii: 443 = B. PRIONITIS subsp. AMELIAE

B. anomala Spreng., *Syst.* ii: 828 = BRAVAISIA FLORIBUNDA

*B. **angustiloba** Lindau, in *Engl. Jahrb.* xx: 20 (1894); Tanzania, Kenya; Section **Somalia**

B. **antenusii** Lindau, in Engl. Bot. Jahrb. xxii (1895): 116; Angola; section unknown

B. **arabica** Belang. ex Nees, in DC. *Prod.* xi: 725; Arabia; section unknown

*B. **argentea** Balf. f., in *Proc. Roy. Soc. Edinburgh* xii: 86; Socotra, Arabia, Yemen, Uganda, Ethiopia, Kenya, Tanzania, Somalia; Section **Somalia**

*B. **argenteo-calycina** De Willd., in *Bull. Jart. Bot. Brux.*: 10 ; Congo; Section **Stellatohirtae**

*B. **argillicola** Oberm., in *Bothalia* vii: 444; South Africa; Section **Barleria**

*B. **arnottiana** Nees, in Hooker, *Compt. Bot. Mag.* ii: 311; India; Section **Barleriopsis**

*B. **aromatica** Oberm., in *Ann. Transvaal Museum* 16 (II): 169; Zimbabwe; Section **Barleria**

*B. **asterotricha** Benoist, in Lecomte *Not. Syst.* ii: 1955; French Guinea; Section **Barleria**

*B. **aucherana** Nees in DC. *Prod.* xi: 234; Arabia, Sudan, Somalia, Ethiopia; Section **Somalia**

B. auriculata Schum., *Beskr. Guin. Pl.*: 285 = HYGROPHILA SPINOSA

B. axillaris Steud., *Nom.II* i: 187 = LEPIDAGATHIS TRINERVIS

B. **bagshawei** S. Moore, in *Journ. Bot.* xlviii: 252; Tropical Africa; section unknown

B. barbata E. Mey., *Zwei Pfl. Docum.*: 152 = B. GUEINZII

*B. bechuanensis C.B. Cl., in *Fl. Cap.* 5 (i): 48; South Africa, Botswana; Section Barleria

B. beddomei T. Anders. ex Bedd., *Ic. Ind. Or.* i: 62 = B. LAWII

B. benadirensis Chiov., *Fl. Somalia* :265; Somalia; section unknown

*B. benguellensis S. Moore, in *Journ. Bot.* xlix: 305; Angola; Section Somalia

B. bicolor Chiov., *Fl. Somalia* 1932: 352; Somalia

*B. biloba Imlay, in *Kew Bull.* 1939: 124; Thailand; Section Barleria

*B. bispinosa Vahl, in *Symb. Bot.* i: 46; Arabia, Yemen, Kenya, Ethiopia, Somalia; Section Prionitis

B. bispinosa Hochst. ex A. Rich., *Tent. Fl. Abyss.* ii: 1444 = B. PRIONITIS

B. bispinosa Nees in Wall., *Pl. As. Rar.* iii: 94 = B. MYSORENSIS

B. bituminosa Noronha, in *Verh. Batav. Gen.* v: 8; Malaya; section unknown

B. blepharoides Lindau, in *Engl. Bot. Jahrb.* xx (1894): 24; Tropical East Africa; section unknown

B. blinii Leveille in Fedde *Repert.* xii: 19 = STROBILANTHES BLINII

*B. boehmii Lindau, in *Engl. Bot. Jahrb.* xx: 19; Tanzania; Section Barlerites

B. boivinii T. Anders., in *Journ. Linn. Soc.* vii: 31; Madagascar; Section Somalia (likely synonym of *B. decaisneana*)

*B. bolusii Oberm., in *Ann. Transvaal Museum* 16(II): 159; South Africa; Section Barleria

B. bonafacei Benoist, in *Bull. Soc. Bot. France* xcix: 325; Madagascar; section unknown

*B. boranensis Fiori, in *Miss. Biol. Borana, Racc. Bot.* 1939: 217; Ethiopia, Somalia, Kenya; Section Barlerites

*B. bornueinsis S. Moore, in *Cat. Talbot's Nigerian Pl.* :85; Nigeria, Cameroun; Section Barleria

B. bracteata Heyne ex C.B.Cl., Hook. *Fl. Brit. Ind.* iv: 490 = B. NITIDA

B. brasiliensis Spreng., in *Neue Entdeck.* iii: 26; Brasil; section unknown

*B. bremekampii Oberm., in *Ann. Transvaal Museum* 16 (II): 162; South Africa, Zimbabwe; Section Barleria

B. brevispina R. Br., in *Salt. Abyss. App.*: 64 = B. PRIONITIS

*B. brevituba Benoist, in *Bull. Mus. Hist. Nat. Paris* vi: 81; Madagascar;

(descriptions seen) Section Prionitis

B. breyeri Oberm., in *Ann. Transvaal Mus.* 16: 159 = B. LUGARDII

*B. briartii Wildem. & Th. Dur. in *Compt. Rend. Soc. Bot. Belg.* xxxviii: 212; Congo; Section Stellatohirtae

*B. brownii S.Moore, in *Journ. Bot.* xlvi: 73 (1908); Gabon, Cameroun, Congo, Ethiopia, Uganda, Tanzania, Angola; Section Barlerites

*B. buddleioides S.Moore, in *Journ. Bot.* 1902: 307; Angola, Namibia; Section Stellatohirtae

B. burchelliana Nees in DC. *Prodr.* xi: 235 = B. MACROSTEGIA

B. burkeana Sond. in *Linnaea* xxiii: 92 = B. MACROSTEGIA

*B. buxifolia L., *Sp. Pl.*: 636; India; Section Barleria

B. buxifolia Roxb., in *Hort. Bengal.*: 4; *Fl. Ind.* iii: 37 = B. OBOVATA

B. caerulea Herb. Lamb. ex Nees in DC. *Prodr.* xi: 228 = B. CRISTATA

B. caerulea Wall., *Cat.* n. 2509 partim. = B. POLYTRICHA

*B. calophylla Lindau, in *Engl. Bot. Jahrb.* xx: 17; Central African Republic, Sudan, Angola; Section Somalia

*B. calophylloides Lindau, in Engl. Bot. Jahrb. xx: 17; Tanzania, Zambia; Section Somalia

*B. candida Nees, in . *Prod.* xi: 240; Arabia; Section Barleria

*B. capitata Klotzsch, in Peters, *Reis. Bot. Mossamb.*: 208; (=B. megalosiphon Mildbr.); Malawi, Zambia, Zimbabwe, Namibia; Section Barleria

B. cardiocalyx Solms ex Schweinf., *Beitr. Fl. Aethiop.* = B. ORBICULARIS

*B. carruthersiana S. Moore, *Journ. Bot.* xviii: 270; Angola; Section Barleria

*B. casatiana Buscalioni & Muschler, in *Engl. Bot. Jahrb.* xlix: 496; Ethiopia; Section Prionitis

B. caudata Boiv. ex Benoist, in *Cat. Pl. Madag. Acanthac.*: 18 = B. PHILLYRAEFOLIA

B. cavalerei Leveille, in Fedde *Repert.* xii: 21 (non-praec.); China; section unknown

*B. cephalophora Lindau, in *Engl. Jahrb.* xliii: 353; Tanzania; Section Prionitis

B. chegosa Herb. Madr. ex Wall., *Cat.* n. 2506 = B. CRISTATA

B. chlamydocalyx Lindau, in *Ann. Inst. Bot. Roma* vi: 73 = B. ORBICULARIS

B. ciliata E.Mey. ex Nees in DC., *Prod.* xi: 230 = B. MEYERIANA

B. ciliata Roxb., in *Hort. Bengal.*: 45; *Fl. India* iii: 38 = B. CRISTATA

*B. clinopodium Fiori, in *Bull. Soc. Bot. Ital.* 1915: 55; Somalia; Section Somalia

*B. clivorum C.B.Cl. in Thiselton-Dyer, *F.T.A.* v: 153; Mocambique; Section Barleria (probable synonym)

B. coccinea L., *Sp. Pl.*: 637 = RUELLIA COCCINEA

B. comorensis Lindau, *Engl. Jahrb.* xx :18; Comores Islands; section unknown

*B. consanguinea Klotzch, in Peters, *Reise Nacht Mossam.*: 206; Mocambique (probably syn. of *B. spinulosa*); Section Barleria

*B. conspicua Nees in Wallich, *Plantae As. Rar.* iii: 92; Penang Islands; Section Barleriopsis

B. cordifolia Hochst. ex T. Anders., in *Journ. Linn. Soc.* vii: 29 = B. PARVIFLORA

B. cornigera Very ex Nees in DC., *Prod.* xi: 248 = HYGROPHILA SPINOSA

*B. courtallica Nees in Wight, *Icones* iv: t. 1529; India; Section Barleriopsis

*B. crassa C.B.Cl., in *F.T.A.* 5: 151; Tropical Africa, Zambia, Zimbabwe, Mocambique; Section Barleria

*B. cristata L., *Sp. Pl.*: 636; India; Burma; Nepal, Bengal, Bhutan, Japan, China; Section Barleria

B. cristata Lam., *Encyc.* i: 380 = B. NOCTIFLORA

*B. crossandriformis C.B.Cl., in *Fl. Cap.* 5 (1): 51; South Africa, Mocambique, Zimbabwe; Section Prionitis

B. crotalaria Leveille, in Fedde *Repert.* xii: 285; China; section unknown

B. cunenensis Benoist, in *Bul. Soc. Brot.* Ser. II, xxiv: 19; ?Angola; section unknown

*B. cuspidata Heyne ex Nees in Wallich, *Pl. As. Rar.* iii: 93; India; Section Prionitis

*B. cyanea S. Moore, *Journ. Bot.* xviii: 265; Angola; Section Barleria

*B. damarensis T. Anders., in *Journ. Linn. Soc.* vii: 29; Namibia; Section Barleria

*B. decaisneana Nees in DC., *Prod.* xi: 230; Madagascar, Comores Islands,

Aldabra Island, Astove Island; Section Barleria

*B. decaryi Benoist, in *Bull. Soc. Bot. France* lxxvi: 1032; Madagascar; Section Prionitis

B. delagoensis Oberm., in *Ann. Transvaal Mus.* 16 = B. PRIONITIS subsp. DELAGOEINSIS

B. delamerei S. Moore, in *Journ. Bot.* 1900: 206; Tropical Africa; section unknown

*B. descampsii Lindau, in *Engl. Bot. Jahrb.* xxiiv: 318; Ziare, Zambia, Congo; Section Stellatohirtae

B. dewevrei Schum. in Just's *Jahresb.* xxvii (I): 514, sphalm. = BARTERIA DEWEVREI

B. diacantha Hochst. ex Nees in DC., *Prod.* xi: 238 = B. TRISPINOSA

B. diandra Heyne ex Nees in Wall., *Pl. As. Rar.* iii: 92 = ?B. POLYTRICHA

B. diandra Hochst. ex Nees in DC., *Prod.* xi: 231 = B. HOCHSTETTERI

B. diandra Schlecht. ex Nees in DC., *Prod.* xi: 231 = B. OBTUSA

B. dianthera Herb. Madr. ex Wall., *Cat.* n. 2391 = PERSTROPHE MONTANA

B. dichotoma Roxb., *Hort. Bengal.*: 45; *Fl. India* iii: 39 = B. CRISTATA

B. diffusa Wight ex C.B.Cl. in Hook , *Fl. Brit. Ind.* iv: 518 = LEPIDAGATHIS DIFFUSA

*B. dolomiticola M-J. & K. Balkwill, *S. Afr. J. Bot.* 58 (4): 287; South Africa; Section Somalia

*B. dulcis Benoist, in *Bull. Soc. Bot. France* l[illegible]: 1033; Madagascar; section uncertain, Barleria or Barleriopsis

B. echinata St. Lag., in *Ann. Soc. Bot. Lyon* vii: 120 = B. PRIONITIS

B. elata Dalz. in Hook. *Kew Journ.* iii: 227 = B. INVOLUCRATA

*B. el[illegible]s S. Moore, in *Journ. Bot.* 1830: 269; Angola, Mocambique, Zimbab[illegible]on[illegible]o, South Africa; Section Barleria

B. elliptica Benoist, in *Bol. Soc. Brot.* Ser. II, xxiv: 16; ? South Tropical Africa; section unknown

*B. eranthemoides R.Br. ex C.B.Cl., in *F.T.A.* v: 147; Zimbabwe, Mocambique, Tanzania, Kenya, Ethiopia, Somalia, Sudan, Cameroun, Congo, Nigeria; Section Prionitis

B. eranthemoides R.Br., in *Salt. Abyss. App.* : 64 = B. ACANTHOIDES

B. esquirolii Leveille & Bodinier, in Fedde *Repert.* xii: 18 = STROBILANTHES ESQUIROLII

B. exellii Benoist, in *Bol. Soc. Brot.* Ser., xxiv: 19; ? South Tropical Africa; section unknown

*B. eylesii S.Moore, in *Journ. Bot.* 1905: 50; Zimbabwe; Section Barleria

B. farinosa Deflers, in *Bull. Soc. Bot. France* xliii: 222; Arabia; section unknown

B. fasciculata Russ. ex Wall. *Cat.* n. 2509 = ?B. POLYTRICHA

B. fissiflora Roj. ex Nees, in DC. *Prod* xi: 238; Madagascar

*B. flava Jacq., *Ecl.* 67: t. 46; Sierra Leone, Senegal, French & Portuguese Guinea, Liberia, Ivory Coast, Gold Coast, Ghana; Section Barleriopsis

*B. fulvostellata C.B.Cl., in *F.T.A.* v:163; Malawi, Tanzania; Section Barleria

*B. galpinii C.B.Cl., in *Fl. Cap.* 5 (i): 54; South Africa, Namibia, Botswana; Section Somalia

B. gentainoides Desf. ex Nees, in DC. *Prod.* xi: 224 = B. FLAVA

*B. gibsonii Dalz. in Hooker, *Kew Journ.* ii: 339; India; Section Barlerianthus

*B. gibsonioides Blatter, in *Journ. Bombay Nat. Hist. Soc.* xxxii: 733; India; Section Barlerianthus

B. glabra Noronha, in *Verh. Batav. Gen.* v: 8; Malaya; section unknown

B. glabrata Vahl ex Nees in DC., *Prod.* xi: 248 = HYGROPHILA SPINOSA

*B. glandulifera Lindau, in *Engl. Bot. Jahrb.* xx: 22; Somalia; Section Somalia

B. glandulosa Hochst. ex Nees in DC., *Prod.* xi: 243 = LEPIDAGATHIS GLANDULOSA

B. glauca T. Anders., in *Journ. Linn. Soc.* ix: 493 = B. GIBSONII

*B. gossweileri S. Moore, in *Journ. Bot.* xlix: 305; Angola (probably synonymous with *B. lancifolia*); Section Somalia

*B. grandicalyx Lindau, in *Engl. Bot. Jahrb.* xx: 25; Sudan, Uganda, Tanzania, Kenya, Ethiopia, Angola; Section Barleria

B. grandiflora R.Br., in Salt., *Abyss. App.*: 64 = B. GRANDIS

*B. grandiflora Dalz. in Hooker, *Kew Journal* ii: 339; India; Section Barlerianthus

B. grandifolia R. Br. ex T. Anders, in *Journ. Linn. Soc.* vii: 30, sphalm. = B. GRANDIFLORA

*B. grandipetala De Wild., in *Bull. Jart. Bot. Brux.*: 10; Congo; Section Somalia

*B. grandis Nees in DC., *Prod.* xi: 233; Ethiopia; Section Barlerianthus

B. grandis Hochst. ex Nees in DC., *Prod.* xi: 233 = B. GRANDIFLORA

*B. grantii Oliv., in *Trans. Linn. Soc.* xxix: 127; Uganda, Kenya, Tanzania; Section Barlerites

*B. greenii M.J. & K. Balkwill, in *S. Afr. J. Bot.* 58 (4): 571; South Africa; Section Barleria

*B. gueinzii Sond., in *Linnaea* xxii: 91; South Africa; Section Barleria

B. halimodes Nees in DC., *Prod.* xi: 231 = PETALIDIUM HALIMODES

B. harnieri Solms in Schweinf., *Beitr. Fl. Aethiop.* = B. PARVIFLORA

*B. her Benoist, in *Bull. Soc. Bot. France* lxxvi: 1032; Madagascar; Section Prionitis

B. hereroensis Engl., in *Bot. Jahrb.* x: 261 = B. LANCIFOLIA

*B. heterotricha Lindau, in *Engl. Jahrb.* xxxviii: 69; Southern Africa, Zimbabwe; Section Barleria

B. hexacantha Bertol., in *Ann. Stor. Nat. Bolog. fasc.* ix: 445; Disq. *Pl. Nov.*: 3 = B. LONGIFOLIA

B. hexacantha Moris, in *Mem. Acc. Torin.* xxxvi: 200 t. 7 = HYGROPHILA SPINOSA

*B. hildebrandtii S. Moore, in *Journ. Bot.* xv: 69; Arabia, Somalia, Kenya, Ethiopia; Section Stellatohirtae

*B. hillcoatiae J.R.I.Wood, in *Kew Bull.* 41 (1): 222; Yemen, Arabia; Section Barleria

B. hirsuta Herb. Madr. ex Wall., *Cat.* n. 2503 = B. TOMENTOSA

B. hirsuta Jacq., *Obs. Bot.* ii: 7 = GONZALEA SPICATA

*B. hirta Oberm., in *Ann. Transvaal Museum* 16 (II): 148; Zimbabwe, Botswana, Zambia, Mocambique; Section Somalia

*B. hochstetteri Nees ex DC., *Prod.* xi: 231; Arabia, Yemen, India, Somalia, Ethiopia, Kenya, Sudan; Section Somalia

*B. holstii Lindau, in *Bot. Jahrb.* xx: 19; Tanzania; Section Barleriopsis

*B. holubii C.B.Cl., in *Fl. Cap.* 5 (i): 47; South Africa, Zimbabwe, Botswana; Section Prionitis

*B. homolotricha C.B. Cl., in *F.T.A.* v: 154; Somalia; Section Barleria

*B. horrida Buscalioni & Muschler, in *Engl. Bot. Jahrb.* xlix: 495; Ethiopia; Section Prionitis

*B. humbertii Benoist, in *Bull. Soc. Bot. France* lxxvi: 1031; Madagascar; Section Barleria

B. humilis Benoist, in *Bull. Soc. Bot. France* cxiii 532; Madagascar (description and illustration seen); section unknown

B. hypocrateriformis Hochst. ex T. Anders., in *Journ. Linn. Soc.* vii: 28 = B. PRIONITIS

B. hystrix L., *Mant.* i: 89 = B. ERANTHEMOIDES

B. inequalis Benth., in *Flora* xxxii: 557 = B. COURTALLICA

B. indica Linn. ex T. Anders., in *J. Linn. Soc.* vii: 115 = B. CRISTATA

*B. insericata Chiov., in *Fl. Somalia* 1929: 263; Somalia; Section Somalia

*B. insolita Benoist, in *Adansonia Ser. II* vi: 86; Madagascar; section unknown, possibly Somalia

*B. involucrata Nees in Wallich, *Pl. As. Rar.* iii: 92; India, Sri Lanka; Section Barleriopsis

B. iodocephala Chiov., in *Fl. Somalia* 1929: 261; Somalia; section unknown

*B. irritans Nees, in *Linnaeae* xv: 359; South Africa; Section Barleria

*B. jasminiiflora C.B. Cl., in *Fl. Cap.* 5 (i): 50; South Africa (probably synonymous with *B. pungens*); Section Barleria

*B. jubata S.Moore, in *Journ. Bot.* xlv: 229 (1907); Namibia; Section Barleria

B. jucunda Benoist, in *Bol. Soc. Brot.* Ser. II, xxiv: 18; ? locality; section unknown

B. jucunda Lindau in *Ann. Inst. Bot. Roma* vi: 75 = B. ARGENTEA

*B. kacondensis S. Moore, in *Journ. Bot.* xlix: 306; Angola; Section Somalia

B. kaessneri S.Moore, in *Journ. Bot.* xlvii: 295 (1909); Tropical Africa; section unknown

*B. kaloxytona Lindau in Engl., *Jahrb.* xliii: 354 (1909); Namibia; Section

Prionitis

*B. keniensis Mildbr., in *N.B.G.B.* ix: 500; Kenya; Section Barlerites

B. kilimandscharica Lindau, in *Engl. Bot. Jahrb.* xx: 26; East Tropical Africa; section unknown

*B. kirkii T. Anders., *J. Linn. Soc.* vii: 28; Tropical Africa, Zimbabwe, Zambia, Mocambique; Section Barleria

*B. kitchingii Baker, in *Journ Linn. Soc.*xxi: 510; Madagascar; Section uncertain, Barleria or Barleriopsis

B. laceratiflora Lindau, in *Engl. Jahrb.* xxxviii: 68; Tropical Africa; section unknown

B. lacinata Wall., *Pl. As. Rar.* iii: 91; *Cat.* n. 7144 = B. CRISTATA

B. lactea Desf. ex Steud., *Nom.* ed. II: 187 = B. CRISTATA

*B. lactiflora R.K. Brummitt & Seyani, in *Kew Bull.* 32 (4): 723; Malawi, Tanzania; Section Somalia

B. laeta Benoist, in *Bull. Mus. Hist. Nat. Paris* vi: 82; Madagascar (description and illustration seen); Section Barlerites

*B. lanceata (Forssk.) C.Chr., in *Dansk. Bot. Ark.* 4 (3): 10; Sudan, Somalia, Djibouti, Ethiopia; Section Barleria

*B. lanceolata (Schinz) Oberm., in *Ann. Transvaal Museum* 16 (ii): 155; Namibia; Section Barleria

*B. lancifolia T. Anders., in *Journ. Linn. Soc.* vii: 28; South Africa, Namibia, Angola, Botswana, Zimbabwe; Section Somalia

*B. lateralis Oberm., in *Ann. Transvaal Museum* 16 (ii): 176; Zimbabwe; Section Barleria

B. latiloba Engl., in *Bot. Jahrb.* x: 261; Namibia = B. LANCIFOLIA

*B. lawii T. Anders., in *Journ. Linn. Soc.* ix: 492; India; Section Barleriopsis

B. leandrii Benoist, in *Bull. Soc. Bot. France* lxxx: 789; Madagascar (descr. and illustration seen); Section Prionitis

*B. lichtensteiniana Nees in DC., *Prod.* xi: 235; South Africa; Section Barleria

*B. limnogeton S. Moore, in *Journ. Linn. Soc.* xv: 95; Celebes Islands, Tanzania, Zambia; Section Somalia

*B. linearifolia Rendle, in *Journ. Bot.* 1896: 397; Tropical Africa; Section

Prionitis

*B. longiflora Linn. f., *Suppl.*: 290; India; Section Barleria

B. longifolia Lindau, in *Engl. Bot. Jahrb.* xx: 32; Tropical East Africa (possibly synonymous with *B. lancifolia*)

B. longifolia Linn., *Cent. Pl.* ii: 22; *Ampoen. Acad.* iv: 320 = HYGROPHILA SPINOSA

(?)B. longipedunculata Britton, in *Bull. Torr. Bot. Club* 1900: 69; Bolivia; section unknown; no material traceable

*B. longipes Benoist, in *Adansonia Ser. II* vi: 85; Madagascar; Section Somalia

*B. longissima Lindau, in *Ann. Inst. Bot. Roma* vi: 93; Somalia; Section Barleria

B. longistyla Lindau, in *Wiss. Ergebn Deutsch Zentr-Afr. Exped.* ii: 298; Congo; section unknown

*B. lugardii C.B.Cl., in *F.T.A.* v: 161; South Africa, Tanzania, Namibia, Botswana; Section Somalia

B. lukafuensis Wildem., in *Ann. Mus. Congo* iv: 140 - Tropical Africa (? possibly a synonym of *B. lukwangulensis*); Section Barlerites (?)

*B. lukwangulensis Mildbr.; original description not known; Tanzania; Section Barlerites

*B. lupulina Lindl., in *Bot. Reg.* t. 1483; India, Mauritius, Indo-Chino, Java, Christmas Islands; Section Prionitis

*B. mackenii Hook. F., in *Bot. Mag.* t. 5866; South Africa, Namibia, Botswana, Zimbabwe, Angola, Zambia; Section Prionitis

*B. maclaudii Benoist in Lecomte, *Not. Syst.* ii: 156; Senegal, French Guinea; Section Barleriopsis

B. macracantha R. Br., in *Salt. Abyss. App.*: 64 = HYGROPHILA SPINOSA

B. macraei Arn. in Hooker, *Compt. Bot. Mag.* ii: 311; India; section unknown

B. macrolemma Peyr. in Sitzb., *Wien Math-Nat.* xxxviii: 574; Tropical Africa; section unknown

B. macrophylla Heyne ex C.B.Cl. in Hook., *Fl. Brit. Ind.* iv: 489 = B. STRIGOSA

B. macrostachya Boj., *Hort. Maurit.*: 260 = B. LUPULINA

*B. macrostegia Nees in DC., *Prod* xi: 235; South Africa, Namibia; Section Barleria

B. maculata S. Moore, in *Journ. Bot. liv:* 289; Kenya; section unknown

B. mairei Leveille in Fedde, *Repertorum* xii: 285 1913); China; section unknown

B. marghilomanae Volkens & Schweinfurth in Gl'ka, *Pays des Somalis*: 216; Somalia; Section Prionitis

*B. marginata Oliv., in *Trans. Linn. Soc.* xxix: 127; Tanzania; Section Prionitis

B. massae Chiov. in Atti, *R. Acad. Ital. Mem, Pl. Nov. Aethiop.* xi: 52; Ethiopia; section unknown

*B. matopensis S. Moore, in *Journ. Bot. xlv:* 91 (1907); Zambia, Zimbabwe, Namibia, South Africa; Section Somalia

*B. media C.B.Cl., in *Fl. Cap.* 5 (I): 51; South Africa (synonymous with *B. macrostegia* Nees); Section Barleria

*B. meyeriana Nees in DC., *Prod.* xi: 230; South Africa; Section Somalia

*B. meeuseana P.G.Meyer, *Mitt. Bot. Staatss. Munch.* 4: 59; Namibia; Section Barleria

*B. megalosiphon Mildbr., in *N.B.G.B.* xi: 62; Namibia, Zimbabwe, Zambia, Malawi (syn. with *B. capitata* but not published); Section Barleria

*B. merxmuelleri P.G.Meyer, in *Mitt. Bot. Staats. Munch.* ii: 382; Namibia; Section Barleria

B. methuenii Turrill, in *Kew Bull.* 1914: 81; Madagascar; section unknown

*B. micans Nees in Benth., *Bot. Voy. Sulph.*: 146; Panama, Guatemala, Mexico, Venezuela; Section Barleriopsis

*B. micrantha C.B.Cl., in *F.T.A.* v: 168; Birundi, Uganda, Somalia, Kenya, Tanzania; Section Barlerites

B. migiurtinorum Chiov., in *Fl. Somalia* 1929: 264; Somalia; Section Prionitis

B. mitis Ker-Gawl., in *Bot. Reg.*, t. 191; India; section unknown

*B. molensis Wild, in *Kirkia* 5: 80; Zimbabwe; Section Barleria

B. mollis R. Br. in Salt., *Abyss. App.*: 64 = B. VENTRICOSA

*B. monostachya Boj., in *Journ. Bot.* 1834: 356; Mauritius; Section Prionitis

(synonymous with *B. lupulina*)

*B. montana Herb. Madr. ex Nees in Wallich, *Pl. As. Rar.* iii: 92; India; Section Barleriantlus

B. montana Wight & Nees ex C.B.Cl. in Hook. f., *Fl. Brit. India* iii: 487, pro parte = B. GIBSONII

*B. monticola Oberm., in *Ann. Transvaal Museum* 16 (ii): 165; South Africa; Section Barleriopsis

*B. morrisiana E.Barnes & C.E.C.Fischer, in *Kew Bull.* 1939:659; India; Section Barleria

*B. mosdenensis Oberm., in *Ann. Transvaal Mus.* 19 (ii): 161; South Africa (synonymous with *B. bolusii*, not publ.); Section Barleria

*B. mucronata Lindau, in *Engl. Bot. Jahrb.* xx: 24; Tanzania, Kenya (?possibly synonymous with *B. grandicalyx*); Section Barleria

*B. mucronifolia Lindau, in *Ann. Inst. Bot. Roma* vi: 71; Ethiopia, Somalia; Section Barleria

B. multiflora Hassk., in *Cat. Fl. Bogor. Alt.*: 149; Bogor.; section unknown

*B. mysorensis Heyne in Roth, *Nov. Sp. Pl.*: 313; India; Section Barleria

B. napalensis Nees in Wall., *Pl. As. Rar.* iii: 91 = B. CRISTATA

*B. natalensis Lindau, in *Engl. Bot. Jahrb.* xx: 23; South Africa; Section Barleriopsis

*B. neurophylla C.B.Cl., in *F.T.A.* v: 166; Congo, Tanzania; Section Barlerites

B. newtonii Lindau, in *Engl. Bot. Jahrb.* xxii: 117; Angola; section unknown

*B. nitida Nees in Wallich, *Pl. As. Rar.* iii: 91; India

*B. noctiflora Linn. F., *Suppl.*: 290; India; Section Barleria

B. noctiflora Hochst. ex A. Rich., *Tent. Fl. Abyss.* ii: 145 = B. ACANTHOIDES

*B. norbertii Benoist, in *Bull. Soc. Bot. France* cix: 132; Madagascar; Section Prionitis

B. nuda Nees in Wall., *Pl. As. Rar.* iii: 92 = B. CRISTATA

*B. nutans Nees in DC., *Prod.* xi: 227; Sri Lanka, India; Section Barleriopsis

*B. nyasensis C.B.Cl., in *F.T.A.* v: 150; Malawi, Zambia, Mocambique;

Section Barleria

B. obovata Buch-Ham., in *Trans. Linn. Soc.* xiv: 239 = B. MYSORENSIS

*B. obtusa Nees, in *Linnaea* xv: 358; South Africa; Section Barleria

*B. obtusisepala C.B.Cl., in *F.T.A.* 5: 158; Angola; Section Somalia

B. observatrix J. Bosser & H. Heine, in *Adansonia* Ser.4, 10(2): 145; Mauritius; section unknown

B. oenotheroides Dum-Cours., in *Bot. Cult. Cat.* vii: 7 = B. FLAVA

*B. opaca Nees in DC., *Prod.* xi: 230; Ivory Coast, Togo, Nigeria, Ghana, Gold Coast, Cameroun; Section Barlerites

*B. orbicularis Hochst. ex T. Anders., in *Journ. Linn. Soc.* vii: 29; Somalia, Ethiopia, Kenya, Yemen; Section Somalia

B. otaviensis Dinter ex Oberm., in *Ann. Transvaal Mus.* 18: 162 = PETALIDIUM OTAVIENSE

*B. ovata E.Mey. ex Nees in DC., *Prod.* xi: 230; South Africa; Section Barleriopsis

*B. oxyphylla Lindau, in *Engl. Bot. Jahrb.* xxxviii: 69; South Africa, probably Mocambique; Section Barleria

*B. pabularis S.Moore, in *Journ. Bot.* (1911) xlix: 307; Angola; Section Somalia

*B. paludosa S. Moore, in *Journ. Bot.* xlviii: 251 (1910); Congo (?possibly synonymous with *B. descampsii*); Section Stellatohirtae

B. pannosa Chiov., in *Nuov. Giorn. Bot. Ital.* n.s. xxxvi: 367; Ethiopia; section unknown

B. paolii Fiori, in *Bull. Soc. Bot. Ital.* (1915): 54; Somalia; section unknown

*B. papillosa T. Anders., in *Journ. Linn. Soc.* vii: 31; South Africa, Namibia; Section Barleria

*B. parvispina Benoist, in *Adansonia Ser. II* vi: 80; Madagascar; Section Prionitis

*B. paucidentata Benoist, in *Adansonia Ser. II* vi: 83; Madagascar; Section Barleria

B. pentandra Am. ex Nees, in *DC. Prod.* xi: 232 = B. INVOLUCRATA

*B. perrierii Benoist, in *Adansonia Ser. II* vi: 78; Madagascar; Section Prionitis

B. petrophila Rendle, in *Journ. Bot.* 1897; 377 = B. SENENSIS

*B. phaylopsis Milne-Redh. in *Kew Bull.* 1940: 65; Zambia; Section Somalia

*B. phillyraefolia Baker, in *Journ. Linn. Soc.* xxii: 510; Madagascar; section unknown, possibly Somalia

*B. pilosa Heyne ex Nees in Wallich, *Pl. As. Rar.* iii: 93; India; Section Barleria

B. pirottaei Lindau, in *Ann. Inst. Bot. Roma* vi: 75 = B. HOCHSTETTERI

*B. polyneura S. Moore, in *Journ. Bot.* xviii: 266; Angola, Malawi; Section Somalia

B. polystachya Hook. ex Nees in DC., *Prod.* xi: 226 = B. STRIGOSA

*B. polytricha Wall., in *Pl. As. Rar.* i: 72, t. 82; India; Section Barleria

B. polytricha Boj. ex Nees in DC., *Prod.* xi: 226 = POLYTHRIX STENANDRIUM

*B. popovii Verdc., in *Kirkia* 5: 279; Socotra; Section Barleria

*B. prattensis Santapau, in *Kew Bull.* 1948: 487; India; Section Barleriopsis

*B. pretoriensis C.B.Cl., in *Fl. Cap.* 5 (i): 55; South Africa; Section Somalia

B. prinoides Hort. Monsp. ex Nees in DC., *Prod.* xi: 229 = B. CRISTATA

*B. prionitis L., in *Sp. Pl.* : 636 *sensu lato* ; India, Phillipines, Malay Peninsula, Malay Islands, Indo-China, Seychelles, Somalia, Ethiopia, Tanzania, Kenya, Malawi, Zambia, Angola, Zimbabwe, Botswana, South Africa, Mocambique, Madagascar; Section Prionitis

- subsp. ameliae (A. Meeuse) R.K. Brummitt & J.R.I. Wood, in *Kew Bull.* 38 (3): 441; South Africa
- subsp. delagoensis (Oberm.) R.K.Brummitt & J.R.I.Wood, in *Kew Bull.* 38 (3): 440; South Africa, Mocambique
- subsp. induta (C.B. Cl.) R.K.Brummitt & J.R.I. Wood, in *Kew Bull.* 38 (3): 438 (Tropical Africa)
- subsp. prionitoides (Engl.) R.K. Brummitt & J.R.I. Wood, in *Kew Bull.* 38 (3): 442; Namibia
- subsp. pubiflora (Benth. ex Hohen.) R.K. Brummitt & J.R.I. Wood, in *Kew Bull.* 38 (3): 436; Tropical Africa
- subsp. tanzaniana R.K. Brummitt & J.R.I. Wood, in *Kew Bull.* 38 (3):

439; Tanzania

*B. procumbens Lour, in *Fl. Cochinc.* : 377; China; probably *Hemigraphis procumbens* (Lour) Merrill

B. pseudoprionitis Hochst. ex Nees in DC., *Prod.* xi: 372 = JUSTICIA DIFFUSA

B. puberula Benoist, in *Adansonia Ser. II.* vi: 86; Madagascar (descr. and illustr. seen) (= var. of *B. longipes*); Section Somalia

*B. proxima Lindau, in *Ann. Inst. Bot. Roma* vi: 72; Arabia, Kenya; Section Prionitis

B. pu[illegible]flora Benth., in *Flora* xxxii: 558 = B. PRIONITIS

B. puccioni Chiov., in *Fl. Somalia* 1929: 260; Somalia; section unknown

B. pulchella Benoist, in *Adansonia Ser. II.* vi: 84; Madagascar (descr. and illustration seen); Section Prionitis

*B. pulchra Lindau, in *Engl. Bot. Jahrb.* xx: 18; Madagascar; Section uncertain, either Barleria or Barleriopsis

B. pumila Hochst. ex Nees, in *DC. Prod.* xi: 372 = JUSTICIA SIMPLEX

*B. punctata Milne-Redhead, in *Kew Bull.* 1941: 170; Somalia; Section Prionitis

*B. pungens Linn. F., *Suppl.*: 290; South Africa; Section Barleria

B. pungens Heyne ex Nees in Wallich, *Pl. As. Rar.* iii: 91 = ?B. POLYTRICHA

B. pungens Thunb., *Prod. Pl. Cap.*: 98 = B. IRRITANS

B. pungens Wall., *Cat.* n. 2498 = LEPIDAGATHIS PUNGENS

B. purpurea Lodd., *Bot. Cab.* iv: t. 344 = B. MONTANA

B. pyramidalis Lam. ex Nees in DC., *Prod.* xi: 243 = BLECHUM BROWNI

*B. pyramidata Lam., in *Encycl. Meth. Bot.* i: 380; Fiji Islands; Section Barlerites

*B. quadrispina Lindau, in *Ann. Inst. Bot. Roma* vi: 72; Somalia, Ethiopia; Section Prionitis

B. quadrispinosa Stokes, in *Bot. Mat. Med.* iii: 411 = B. PRIONITIS

B. querimbensis Klotzsch in Peters, *Reis. Nacht Mossam.* = B. REPENS

B. racemosa Herb. Madr. ex Wall., *Cat.* n. 295 = B. TOMENTOSA

B. ramosa Buch-Ham., in *Trans. Linn. Soc.* xiv: 295 = B. NOCTIFLORA

*B. ramulosa C.B.Cl., in *F.T.A.* v: 150; Zimbabwe, Kenya, Tanzania, Somalia, Ethiopia; Section Barleria

*B. randii S. Moore, in *Journ. Bot.* 1900: 203; Botswana, Zimbabwe, South Africa; Section Prionitis

B. rautanenii Schinz, in *Viertelljaarschn Nat. Ges. Zurich* lxi: 437: Namibia = B. LANCIFOLIA

*B. rehmannii C.B.Cl., in *Fl. Cap.* 5 (I): 53; South Africa; Section Somalia

*B. repens Nees in DC., *Prod.* xi: 230; South Africa, Mocambique, Tanzania, Kenya; Section Barleria

B. reticulata Haines, in *Indian Forester* xl: 394; India; section unknown

*B. rhodesiaca Oberm., in *Ann. Transvaal Museum* 16 (ii): 144; Zimbabwe, Botswana; Section Prionitis

B. rhynchocarpa Klotzsch in Peters, *Reise Nacht Mossam.*: 205 = CROSSANDRA NILOTICA

B. richardiana Nees in DC., *Prod.* xi: 225; Madagascar; section unknown

*B. rigida Willd. ex Nees in DC., *Prod.* xi: 242; South Africa, Namibia; Section Barleria

B. rigida Spreng. in Zeyh. ex Schlecht., in *Linnaea* xiv: 304 = PACHYPODIUM TOMENTOSUM

B. rivaei Lindau, in *Ann. Inst. Bot. Roma* vii: 74 = B. HOCHSTETTERI

*B. rogersii S.Moore, in *Journ. Bot.* 57: 38; South Africa, Zimbabwe (probably a synonym of *B. taitensis)*; Section Stellatohirtae

*B. rotundifolia Oberm., in *Ann. Transvaal Museum* 16 (ii): 145; South Africa; Section Prionitis

B. rotundisepala Rendle, in *Journ. Bot.* 1897: 376; East Africa; Section Barleria

B. rubra Buch-Ham, in *Trans. Linn. Soc.* xiv: 296; India (doubtful species); section unknown

*B. ruellioides T. Anders., in *Journ. Linn. Soc.* vii: 30; Ghana, Nigeria, Gold Coast, Central African Republic, Cameroun; Section Barlerites

B. ruellioides Rottl. ex Nees in DC., *Prod.* xi: 240 = B. NODIFLORA

*B. sacleuxii Benoist in Lecomte, *Not. Syst.* ii: 17 (1911); Tanzania; Section Prionitis

*B. salicifolia S. Moore, in *Journ. Bot.* xviii: 268; Angola; Section Stellatohirtae

B. satureiodes Griseb., in *Cat. Pl. Cuba* :195; Cuba; probably *Barleriola*

*B. scabriuscula Schwartz, in *Mitt. Inst. Bot. Hamb.* 10: 252; Arabia; section uncertain

*B. scasselatii Chiov., in *Bull. Soc. Bot. Ital.* 1915: 56; Somalia

B. schenckii Schinz, in *Verh. Bot. Ver. Brand.* xxxi: 199; Namibia (probably synonymous with *B. rigida*); Section Barleria

B. schmittii Benoist, in Lecomte *Not. Syst.* 3: 318; French West Africa; section unknown

B. schweinfurthiana Lindau, in *Engl. Bot. Jahrb.* xx: 26; Tropical East Africa; section unknown

*B. scindens Oberm., in *Ann. Transvaal Museum* 16 (ii): 171; South Africa; Zimbabwe; Section Barlerites

B. senegalensis Nees in DC., *Prod.* XI: 224 = B. NODIFLORA (??)

*B. senensis Klotzsch in Peters, *Reis. Mossamb.* : 209; South Africa, Mocambique, Zambia, Zimbabwe, Botswana; Section Prionitis

*B. sepalosa C.B.Cl. in Hook. f., *Fl. Brit. India* IV: 487; India; Section Barleria

*B. separata Benoist, in *Adansonia Ser. II.* vi: 87; Madagascar; Section Somalia

B. sericea T. Anders., in *Journ. Linn. Soc.* vii: 115 = B. LONGIFLORA

*B. setigera Rendle, in *Journ. Bot.* 1897: 395; Tanzania, Kenya; Section Prionitis

*B. seyrigii Benoist, in *Bull. Soc. Bot. France* cix: 132; Madagascar; Section Somalia (?)

*B. siamensis Craib., in *Kew Bull* 1911: 437; Thailand; section uncertain, Barleria or Barleriopsis

*B. smithii Rendle, in *Journ. Bot.* 1896: 396; Somalia; Section Prionitis

B. solanifolia L., *Sp. Pl.* 637 = BARLERIOLA SOLANIFOLIA

*B. solitaria P.G. Meyer, in *Mitt. Staatss. Munch.* 6: 513; Namibia; Section

B. somaliensis Franch. in Revoil, *Comali*: 51; Somalia; section unknown

B. spicata Roxb., in *Hort. Bengal.*: 45 = B. PRIONITIS

B. spina-ceylanica Nees in DC., *Prod.* xi: 242 = B. MYSORENSIS

*B. spinifolia J.R.I. Wood, in *Kew Bull.* 39 (1): 125 (1984); South Yemen; Section Barleria

*B. spinisepala E.A. Bruce, in *Kew Bull.* 1932: 98; Kenya, Ethiopia, Tanzania; Section Barleria

B. spinosa Wall., *Cat.* n. 2497 = LEPIDAGATHIS SPINOSA

*B. spinulosa Klotzsch in Peters, *Reis. Mossam. Bot.*: 208; Tanzania, Angola, Zambia, Botswana, Malawi, Mocambique, Zimbabwe; Section Barleria

*B. splendens E.A.Bruce, in *Kew Bull.* 1934: 305; Tanzania; Section Stellatohirtae

B. squarrosa Klotzsch in Peters, *Reise Nacht Mossam.*: 207 = B. SPINULOSA

*B. stellato-tomentosa S. Moore, in *Journ. Bot.* xviii: 268; Angola; Section Stellatohirtae

*B. stelligera Lindau, in *Ann. Inst. Bot. Roma* vi: 71; Ethiopia, Somalia; Section Stellatohirtae

B. stenophylla Kurz., in *Journ. As. Soc. Beng.* xlii (1873) II: 95; Burma; Section unknown

*B. steudneri C.B.Cl., in *F.T.A.* v:155; Ethiopia, Sudan; Section Barleria

*B. stimulans E.Mey. ex Nees in D.C., *Prodromus* xi: 241; South Africa; Section Barleria

*B. stocksii T. Anders., in *Journ. Linn. Soc.* ix 1876): 493; India; Section Somalia

*B. strigosa Willd., *Sp. Pl.* iii: 379; India, Sikkim, Bhutan, Thailand; Section Barleriopsis

*B. stuhlmanii Lindau, in *Engl. Bot. Jahrb.* xx: 20; Tanzania, Kenya, Rwanda; Section Barlerites

B. subinermis Chiov., *Nuov. Giorn. Bot. Ital. n.s.* xxxvi: 367; Ethiopia; section unknown

*B. subglobosa S. Moore, in *Journ. Bot.* 1911: xlix: 307; Angola, Zambia;

Section Stellatohirtae

*B. submollis Lindau, in *Engl. Bot. Jahrb.* xx:21; Uganda, Ethiopia, Tanzania, Kenya; Section Barlerites

*B. sunzuana R.K. Brummitt & Seyani, in *Kew Bull.* 32 (4): 721; Zambia, Malawi; Section Barleria

*B. swynnertonii S. Moore, in *Journ. Linn. Soc. Bot.* (1911) xl: 160; Mocambique (identical to *B. repens*); Section Barleria

B. sudanica Lindau in Engl., *Pflanzenw. Ost. Afr. C.*: 368; Sudan; section unknown

*B. taitensis S. Moore, in *Journ. Bot.* 1902: 343; Tanzania, Kenya, Zambia, Angola, Zimbabwe, South Africa; Section Stellatohirtae

*B. talbotii S. Moore, in *Cat. Talbot's Nigerian Pl.*: 86; Nigeria; Section Barlerites

B. terminalis Nees in DC., *Prod.* xi: 225 = B. STRIGOSA

*B. tetracantha Balf. f., *Proc. Roy. Soc. Edinburgh* xii (1884): 85; Socotra; Section Prionitis

*B. tetraglochin Milne-Redhead in Hooker, *Icones* xxxiii: t. 3291; Sudan; Section Prionitis

B. tischeriana Chiov., in *Nouv. Giorn. Bot. Ital. n.s.* xxxvi: 367; Ethiopia; section unknown

*B. tomentosa Roth, *Nov. Sp. Pl.*: 314; India, Sri Lanka; Section Barleria

B. tomentosa Herb. Madr. ex Wall., *Cat.* n. 2503 = B. ACUMINATA

*B. transvaalensis Oberm., in *Ann. Transvaal Museum* 16 (ii): 156; South Africa; Section Barleria

B. triacantha Hochst. ex Nees in DC., *Prod.* xi: 240 = B. LANCEATA

B. trinervis Herb. Ham. ex Nees in DC., *Prod.* xi: 243 = LEPIDAGATHIS TRINERVIS

*B. trispinosa Vahl, in *Symb. Bot.* i: 46; Arabia, Ethiopia, Tanzania; Section Prionitis

B. uitenagensis Hochst. ex Nees in DC., *Prod.* xi: 231 = B. OBTUSA

*B. ukamensis Lindau in Engler, *Pfl. Ost-Afr.*: 368; Tanzania; Section Prionitis

B. umbrosa Lindau, in *Engl. Jahrb.* xxxiii: 188 - Tropical Africa; Section

unknown

B. unilateralis Buch-Ham. ex Wall., *Cat.* n. 2509 = B. POLYTRICHA

*B. usambarica Lindau, in *Engl. Bot. Jahrb.* xx:21; Kenya, Tanzania; Section Barlerites

*B. variabilis Oberm., in *Ann. Transvaal Museum* 16 (ii); 174; Zimbabwe; Section Barleria

*B. variabilis Robyns, in *Nat. Tijdschr.* xiv: 104; Congo (?nomen nudum)

*B. ventricosa Hochst. ex Nees in D.C., *Prodromus* xi: 230; Birundi, Rwanda, Congo, Uganda, Sudan, Ethiopia, Somalia, Tanzania, Kenya, Yemen; Section Barlerites

B. venulosa Nees in DC., *Prod.* xi: 228 = B. CRISTATA

*B. verdickii Wildem., in *Ann. Mus. Congo* iv: 139 (1903); Congo; Section unknown

*B. vestita T. Anders., in Thw. *Enum. Pl. Zeyl.*: 230; Sri Lanka; Section Barleriopsis

*B. villosa T. Anders., in *Journ. Bot.* xviii, 1880): 267; Nigeria, Cameroun, Congo, Ghana, Angola; Section Barlerites

*B. vincaefolia Baker, in *Journ. Linn. Soc.* xxv: 339; Madagascar; Section Barleria

*B. violacea Hainz, in *Mitt. Bot. Staatss. Munch.* 12: 67; Namibia; Section Somalia

*B. violascens T. Anders., in *Journ. Bot.* xviii (1880): 265 - 7; Angola; Section Barleria

*B. virgula C.B. Cl., in *Fl. Cap.* 5 (i): 48; South Africa; Section Barleria

*B. vix-dentata C.B. Cl., in *F.T.A.* 5: 165; Sudan, Tanzania, Uganda; Section Barlerites

*B. volkensii Lindau, in *Engl. Bot. Jahrb.* xx: 22; Ethiopia, Tanzania, Kenya; Section Baarlerites

*B. waggana Rendle, in *Journ. Bot.* 1897: 377; Ethiopia, Somalia; Section Prionitis

*B. welwitschii S.Moore, in *Journ. Bot.* xviii: 267; Zambia, Angola; Section Somalia

*B. whytei S. Moore, in *Journ. Bot.* 1903: 138; Kenya; Section Barleriopsis

*B. wilmsiana Lindau, in *Engl. Jahrb.* xxxIII; South Africa; Section Somalia

B. wilmsii Lindau ex C.B. Cl., in *Fl. Cap.* 5: 54 = B. WILMSIANA

B. woodii C.B. Cl., in *Fl. Cap.* 5: 50 = B. OVATA

B. yemense Schweinf. ex Lindau, in Engl. & Prantl, *Nat. Plf.* iv (IIIb): 315; Yemen; Section Somalia

APPENDIX 2

List of voucher specimens seen by the author

In cases where large numbers of specimens were seen, not every one is cited; instead, a selection of specimens from all different localities at which the plant has been collected is given.

***B. acanthoides** Vahl

Arabia: *Grainger 538* (E), *Schimper 745* (BM), *Vesey-Fitzgerald 16338/3* (BM).

Djibouti: *Naegelé 135* (K).

Ethiopia: *Amshoff 10500* (SRGH), *Barbey 599* (K), *Burger 926* (K), *Ellis 24* (K), *Friis, Tadesse & Vollesen 2978* (K), *Gilbert 2354* (K), *Kotschy 48* (K) *&73* (BM), *Puff & Ensermu K. 8212/7-4/2* (K), *Schimper 1856* (BM, K), *Strecker 64* (K).

India: *Dalzell 28* (K), *Drummond 15230* (K), *Duthie 4802* (K), *Edgeworth 7047* (K), *Stocks s.n.* (K).

Kenya: *Ameshoff 10500* (SRGH), *Bally 9088* (K), *Carr 171* (EA), *Faden & Faden 74/758* (K), *Gilbert, Kanuri & Mungani 5649* (K), *Gillett 13437* (K, PRE), *Hepper & Jaeger 6999a* (K), *Kirrika 48* (PRE). *Leippert 5053* (SRGH), *Mathew 6516* (K), *Vincens 48* (EA).

Oman: *Greenway 2103* (BM), *Miller 2776* (E).

Somalia: *Gillett 4298* (K), *4360* (K) *& 4535* (K), *Gillet & Watson 23735* (K, PRE), *Wood 5/73/177* (K).

Sudan: *Bent s.n.* (K), *Carr 808* (K), *Kotschy 58* (BM, K), (K), *Myers 14010* (K), *Rosetti 128* (BM).

Tanzania: *Batty 594* (K), *Greenway 2103* (K), *Greenway & Kanuri 14823* (PRE), *Piemelsel & Kephart 199* (BM), *Richards 24221* (K), *25486* (K) *& 25553* (K).

Uganda: *Lye & Lester 449* (K), *Tweedie 2022* (K), *Wilson 411* (K) *& 412* (K).

W. Pakistan: *Lamond 769* (E), *Rechinger 28586* (K).

Yemen: *Forsskal s.n.* (BM, isotype), *Monod 17318* (BM), *Popov P8/41* (BM), *Wood 2136* (E), *2563* (E, BM) *& Y/75/418* (BM).

***B. aculeata** Balf. f.

Socotra: *Balfour 12/83* (K) *& 399* (K), *Bent s.n. (1897) (K), Miller, Guarino, Obadi, Hassan & Mohammed M8643* (E, K), *Radcliffe-Smith & Lavranos 324* (K) *& 599 (K), Schweinfurth 553* (K, type), *Smith & Lavranos 324* (K, PRE).

***B. affinis** C.B. Cl.

Belgian Congo: *Verdick ?501* (K).

Botswana: *Holub s.n.* (K, type), *Kerfoot & Falconer 45* (PRE).

Transvaal: *Holub s.n.* (K).

Zimbabwe: *Eyles 7116* (K), *Hopkins 7946* (K), *Mahlangu 309* (SRGH), *Philcox & Leppard 8814* (K), *Rogers 5264* (K), *West 2147* (K), *Wild 1065* (K).

***B. albi-pilosa** Hainz

Namibia: *Potgieter 161* (WIND), *Tinley 1567* (WIND), *Walter 412* (PRE, WIND, type).

***B. albostellata** C.B. Cl.

Transvaal: *Codd 5304* (BM, PRE), *Colesby s.n.* (PRU), *Fourie 1460* (TPA Lydenburg), *Gerstner 6066* (PRE, SRGH), *Netshungani 1163* (J), *Theron 2992* (BLFU, PRE), *van Tonder s.n.* (PRU), *van WYK 3598* (PRU).

Zimbabwe: *Biegel & Pope 3323* (K, SRGH), *Chase 645* (K, SRGH), *Corner s.n.* (E), *Crook 383* (K, PRE, SRGH), *Drewe 11* (SRGH), *Flower 1439* (PRE, SRGH), *Hall 17* (SRGH), *Holub 1397* (K, type), *Mavi 220* (SRGH), *Norlindh, Henning & Weimarck 5124* (K), *Orpen 43/53* (SRGH), *Phelps 230* (K, SRGH), *Phipps 2892* (SRGH), *Plowes 3456* (K), *Rogers 5637* (BOL, K, PRE, SAM, SRGH) *& 7900* (K), *Sherry 144/71* (SRGH), *West 2540* (SRGH), *White 6004* (K), *Wild 960* (K, SRGH).

***B. allaudii** Benoist

Madagascar: *Croat 31201* (MO), *31411* (MO) *& 31644* (MO).

***B. amanensis** Lindau

Tanzania: *Bidgood, Mwasumbi, Pocs & Vollesen 446* (K), *Braun 1871* (K, type), *Drummond & Hemsley 3203* (K), *Greenway 2798* (K), *Kanuri 186* (K), *Koritschoner 656* (K), *Peter 60375* (K), *60423* (K) *& 60578* (K), *Rogers H28/32* (K), *Toms H26/3115* (K).

*B. angustiloba Lindau

Kenya: *Bidgood & Vollesen 1272* (K), *Luke 2444 (K), Napper 1924* (K).

Tanzania: *Tanner 1316 (K), Burtt 2456 (K) & 3734 (K), Kreulen 45 (K).*

*B. argentea Balf. f.

Arabia: *Vesey-Fitzgerald 12318/5* (BM).

Ethiopia: *Gilbert 2103* (K, MO), *Gillett, Ensermu K. & Vollesen 7584* (K), *Friis, Mesfin T & Vollesen 2980* (K).

Kenya: *Faden & Beentjie 8514 (K), Faden & Faden 74/752* (K) & *741784* (K), *Gillett 2012* (K), *13419* (BM, K), *16510* (K), *19514* (K) & *21333* (K), *Greenway & Kanuri 13048* (PRE, SRGH) & *13016* (K), *Heinz Smith 8/63* (EA), *Linsen & Giesen 87* (EA), *Lye 9016* (K), *MacKinnon 11* (K), *Mathew 6815* (K), *Newbould 69596* (K), *Stannard & Gilbert 971* (K), *Steam 21600* (K), *Tweedie 1932* (K).

Oman: *Lawton 2460* (BM), *Mandaville 6848* (BM) & *6870* (BM), *Miller 2291* (E).

Socotra: *Balfour 544* (K, type).

Somalia: *Ahmed Munin Warfa 1017* (K), *Alstrup & Michelsen 66* (K), *Bally & Melville 15513* (K), *Donaldson-Smith s.n. 1895* (BM), *Ellis 390* (K), *Gilbert, Ensermu K. & Vollesen 7758* (K), *Gillett 4093* (K), *Gillett & Beckett 411* (K), *Gillett & Hemming 4662 (K), Gillett & Watson 23372* (K) & *23379* (K), *Hemming & Deshmuth 321* (K), *Kuchar 17037* (K), *17605* (K) & *17792* (K), *Thulin & Bashir Mohammed 798* (K), *Wilde 179 (K), Wieland 4022* (MO), *4183* (MO) & *4542* (MO).

Tanzania: *Bidgood & Vollesen 1266 (K), Drummond & Hemsley 2377 (K), Leippert 5539* (K), *Richards 25500* (K).

Uganda: *Dyson & Hudson 285* (K), *Eggeling 2948 (K), Kerfoot 913 (K), Symes 594* (K), *Wilson 879 (K).*

Yemen: *Mandaville 6938* (BM), *Wood 2477* (BM, E).

*B. argenteo-calycina De Willd.

Belgian Congo: *Descamps 1891* (K).

*B. argillicola Oberm.

Natal: *Acocks 9068* (PRE) & *10701* (PRE, holotype), *Balkwill, Balkwill & Green 5948* (J), *Edwards 2458* (BM, NU).

*B. arnottiana Nees

Ceylon: *Gardner 697* (K), *Walker s.n.* (E, K).

India: *Ferreira 288* (K). *Gardner 697* (K), *Maxwell s.n.*, *Thomson 310* (K) & *1845* (K), *Walter s.n.* (K).

*B. aromatica Oberm.

Zimbabwe: *Barker 1003* (NBG), *Chase 6936* (K), *Corner s.n.* (E), *Eyles 8610* (K), Fisher 1619 *(PRE)*, Leach & Brunton 9858 *(PRE)*, *Obermeyer s.n.* (PRE), *Plowes 2692* (PRE), *Whellan 915* (K, PRE), *Wild 6530* (K, PRE, SRGH), *6936* (K), *7559* (K, PRE) & *7756* (K), *Wright T314* (K).

*B. asterotricha Benoist

French Guinea: *Jacques-Felix 1484* (K).

*B. aucherana Nees

Arabia: *Bent 1895* (K), *Lawton 1934* (K) & *2394* (K), *Maconochie 3528* (K), *Miller 7651* (K), *Miller & Nyberg 9358* (K), *Radcliffe-Smith 5131* (K), *5165* (K), *5239* (K) & *5580* (K).

Ethiopia: *Burger 2322 (K) & 3293 (K), de Wilde 5010 (K) & 7211 (K), de Wilde & Gilbert 348* (MO), *Gilbert 2044* (K), *Gilbert & Gilbert 1865* (K), *Gilbert, Vollesen & Ensemu K. 7441* (K) & *7719* (K), Schimper 2291 (Type of *B. parviflora*, K).

Kenya: *Linsen & Giesen 41* (MO).

Oman: *Edmondson 3205* (E), *Lawton 2394* (BM), *Miller 7651* (E), *Miller & Nyberg M9358* (E).

Somalia: *Bally 9955* (K) & *22113* (EA), *Friis, Vollesen & Hassan 5012* (K), *Gillett 4365* (K), *Hemming & Wa[illegible]n 318* (K), *Kucher 17046 & 17325* (K), *Wood S/72/38* (K).

Sudan: *Schweinfurth 255* (K).

*B. bechuanensis C.B. Cl.

Botswana: *Holub s.n.* (K, type), *Nelson 151* (K, type).

Cape: *Acocks 2121* (PRE), *Brueckner 136* (PRE), *Esterhuysen 1007* (BOL) & *2046* (BOL), *Leistner 593* (PRE) & *1396* (NBG, PRE, SRGH), *Moran 15919* (BOL), *Rogers 10413* (BOL), *Wilman 16418* (BOL).

Orange Free State: *Burtt-Davy 12930* (BOL), *Pole-Evans 53* (PRE).

*B. benguellensis S. Moore

Angola: *Gossweiler 3621* (K).

*B. biloba Imlay
Thailand: *Kerr 2508* (BM, K, type) & *7997* (BM), *Put 2508* (K, type), *Sangkhachand 1060* (K).
*B. bispinosa Vahl
Arabia: *Ahmed Khattab 512* (BM), *Barbey 287 (K)* & *625* (K), *Collenette 335* (K), *591* (K), *1240* (K) & *1974/39* (K), *Hillcoat 93* (BM), *Popov 71/264* (BM), *Tothill 230* (BM), *Vesey-Fitzgerald 16282/2* (BM).
Kenya, Ethiopia, Somalia
Yemen: *Brunt 2360* (BM), *Coshim & Bazara 12* (K), *Leach 71/38* (BM), *Radcliffe-Smith & Henchie 4809 (K)*, *Wood 1371* (BM, K), *2942* (BM, K), *73/38* (BM), *Y/74/102* (BM) & *Y/75/446* (BM).
*B. boehmii Lindau
Tanzania: *Greenway & Kanuri 11828* (PRE), *Lloyd 10* (K), *Peter 60104* (K).
*B. bolusii Oberm.
Transvaal: *Bolus 11140* (BOL, syntype), *Bredenkamp & van Vuuren 202* (PRE) & *475* (PU), *Galpin M272a & b* (PRE, types of varieties of *B. mosdenensis*), *Gillett sub STE 31782* (STE), *Gomes-Pedro 1065* (PRE), *Meeuse 9467* (SRGH), *9505* (PRE) & *9546* (SRGH), *Mogg 37202* (PRE), *van der Meulen 1024* (PRE), *Wager 22965* (PRE, syntype).
*B. boranensis Fiori
Ethiopia: *Ash 197* (K) & *2264* (MO), *Gilbert, Thulin & Awete 517* (K), *Gillett 14753* (K).
Tanzania: *Carmichael 490* (EA), *Tanner R.T. 5748* (EA).
?Tanzania: *Gilbert, Ensermu K. & Vollesen 7789* (K), *Gilbert, Sebsebe & Vollesen 7817* (K), *Mesfin T. & Vollesen 4198* (K).
*B. bornueinsis S. Moore
East Cameroon: *Bonny 1* (K), *de Wilde 5006* (K), *Fotius 2362* (K), *Talbot 1911* (K).
Kenya: *Verdcourt 2219* (PRE).
Nigeria: *Dalziel 359* (K), *Hepburn 53* (K), *Linnavuori s.n.* (K), *McElderry 16352* (K), *Talbot 1911* (K, type).
*B. bremekampii Oberm.
Mozambique: *Moss 1928* (J).
Transvaal: *Balkwill & Balkwill 5830* (J), *Codd 1097* (PRE) & *5449* (PRE), *Fourie 153* (PRE), *Germishuizen 368* (PRE), *Hall 4* (NBG), *Hutchinson & Gillett 4437* (SRGH), *Meeuse 9331* (PRE) & *10219* (PRE), *Netshiungani 839* (J, PRE), *O. meyer, Schweickerdt & Verdoorn 124* (PRE), *Pole Evans H18279* (PRE), *Rogers 20707* (J), *Selaledi 50* (PRE), *Thorp sub NH 29673* (NH), *van Wyk 5543* (PRE, PRU), *Venter 8845* (TPA Lydenburg), *Westfall 1005* (PRE).
Zimbabwe: *Bremekamp 27520* (PRE, type).
*B. briartii Wildem. & Th. Dur.
?Belgian Congo: *Briart 51* (K, photo).
*B. brownii S. Moore
Angola: *Gossweiler 1948* (K).
Belgian Congo: *Furron 4257* (K), *Hart 346* (K), *Jean-Louis 7708* (K), *Pitnan 52* (K), *Robyns 1182* (K), *Talbot 1396* (K).
Cameroun: *Letouzey 9790* (K).
Central African Republic: *Fidao s.n.* (K), *le Testu 4327* (K).
Ethiopia: *Friis, Gilbert & Vollesen 3925* (K), *Friis & Vollesen 731* (K).
Gabon: *le Testu 8150* (K).
Tanzania: *Makwilo Semkiwa 52* (K), *Procter 963* (K).
Uganda: *Brown 313* (K, type), *Chandler 1264* (K), *Eggeling 2304* (K), *Loveridge 116* (K), *Loveridge 31* (K), *McMahan s.n.* (K), *Mummand & Tensley 4548* (K), *Rwaburindore 2830* (MO), *Synott 491* (K), *Synott 749* (K), *Thomas 1486* (K).
*B. buddleioides S. Moore
Namibia: *Baum s.n.* (K), *Kunene-Zambezi expedition* (K).
*B. buxifolia L.
India: *Bourne 5053* (K), *Fischer 1686* (K), *Gamble 10868 (K)*, *15049 (K)* & *17949* (K), *Gough 5* (K), *King s.n.* (K), *Lawson 155* (K), *Perianayagam & Xavier 26597* (K), *Ramamoorthy HFP1428* (K), *Saldanha 16305* (MO), *Stahl 1891* (K), *Wagh 6243* (MO), *Wight 130 (4061)* (K), 2218 (E, K) & *2637* (E).
*B. calophylla Lindau
Central African Republic: *Fay 5545* (K), *le Testu 4212* (K).

Sudan: *MacIntosh 42K* (K), *78K* (K) & *97K* (K), *Myers 7054* (K) & *9372* (K), *Schweinfurth 2182* (K, type) & *3922* (K), *Turner 254* (K).

*B. **calophylloides** Lindau

Malawi: *Pawek 10904* (MO).

Tanzania: *Bally & Carter 16481* (EA, K, MO), *Balyorugulu 4* (K), *Bidgood, Congdon & Vollesen 1299* (K), *Boater 456* (K), *Burtt 2142* (K) & *4619* (K), *Moors K22* (K), *Nutt s.n. 1896* (K), *Polhill & Paulo 1365* (K), *Verdcourt 2879A* (BA), *Welch 54* (K).

Zambia: *Bullock 2623* (K), *Nutt 1896* (K), *Richards 656* (K), *4302* (K), *10956* (K), *19636* (K) & *22126* (MO).

*B. **candida** Nees

Aden: *Maxwell-Darling 209* (K).

Arabia: *Aucher-Eloy-Herbier 223* (BM, K, type), *Gulchard KG/HAD/9* (BM), *Rauh & Lavranos 13208* (K), *Popov P44/2* (BM), *Popov, Tillin & Gilliland 4148* (BM, K) & *4215* (BM, K), *Wissman 2572* (BM), *2589* (BM) & *333* (BM).

Oman: *Mandaville 6261* (BM), *Miller 6601* (K), *Miller & Whitcombe 2810a* (K), *Radcliffe-Smith 3825* (K).

Southern Yemen: *Lunt 97* (K), *Thesiger s.n.* (BM).

*B. **capitata** Klotszch

Angola: *Menezes, Henr. & Brites 302b* (SRGH).

Botswana: *Henry 37* (SRGH), *Mutakele 197* (SRGH).

Malawi: *Brummitt & Osborne 15055* (K) & *15533* (K), *Phipps 2735* (K).

Namibia: *Killick & Leistner 3354* (K, PRE, SRGH, WIND).

Tanzania: *Burtt 3306* (BM), *Koritschoner 1926* (EA).

Uganda: *Katende K1378* (MO), *Synnott 1226* (EA).

Zambia: *Angus 1113* (BM, K, PRE), *Gilges 517* (SRGH).

Zimbabwe: *Eyles 7299* (K, SRGH), *Holub s.n.* (K), *Walter 6* (K, SRGH).

*B. **carruthersiana** S. Moore

Angola: *Bamps & Martins 4352* (K), *Grandroux & Barbosa 11730* (K), *Humbert 16064* (BM), *Johnston s.n.* (K), *Milne-Redhead 2513* (K), *Pearson 2125* (BOL, K), *Welwitsch 5040* (BM, type), *5044* (K, type) & *s.n.* (K, type).

*B. **casatiana** Buscalioni & Muschler

Ethiopia: *Troll 4222* (K).

*B. **cephalophora** Lindau

Tanzania: *Peter 60291* (K).

*B. **clinopodium** Fiori

Somalia: *Thulin, Hedren & Abdi Dahir 7726* (K), *Thulin & Bashir Mohammed 6873* (K), *Kazmi, Marian & Istambul 5339* (K), *Paoli 527* (K, syntype), Gillett & Heinming 24638 (K), *Kuchar 16910* (K), *17042* (K) & *17331* (K), *Paoli 527* (K, type).

*B. **clivorum** C.B. Cl.

Mozambique: *Kirk 10/83* (K, syntype), *Whyte (July 1896)* (K, syntype).

*B. **conspicua** Nees

Penang Islands: *Wallich 2460* (K, type).

*B. **courtallica** Nees

India: *Bouraillon 1591* (K), *Dalzell s.n.* (K), *Fischer s.n.* (K), *Gamble 534* (K) & *16025* (K), *Gough 521* (K), *Hocko s.n.* (K), *Hohentacker 534* (K), *Imlay 778* (K), *Lawson 1884* (K), *Lushington s.n.* (K), *Mathhew 27238* (K), *McIvor s.n.* (K), *Ramamoorthy HFP 1379* (MO) & *s.n.* (K), *Ritchie 1853* (K), *Saldanha 16274* (E), *Talbot s.n.* (K), *Wight 2821* (K).

*B. **crassa** C.B. Cl.

Zambia: Bullock 3000 *(EA), Edwards 595* (K), *Fanshawe 6589* (K), *Gilliland Q619* (K), *Loveridge 726* (K), *Robinson 6681* (K).

Zimbabwe: *Alice & Godman 184* (BM), *Baines s.n.* (K, type), *Carter & Coates Palgrave 2222* (K), *Eyles 766* (BM, K), *Fries, Norlindh & Weimarck 2381* (BM), *Gilliland 41* (BM), *Grosvenor 45* (K), *Hislop 106* (K), *Hutchinson & Gillet 3390* (K), *Leach & Bullock 128[illegible]*, *Loveridge 1483* (K), *Monro 1135* (BM) & *1811* (BM), *Miller 4431* (K), *Plowes 2860* (K), *Rodin 4408* (K), *van Son sub TM 28686* (PRE, type of *B. venosa*).

*B. **cristata** L.

Assam: *Bar 6512* (K), *Pary 336* (K).

Bengal: *Gamble 8693* (K) *& 10138* (K), *Mooney 4098* (K), *Panigrah 6320* (K).
Bhutan: *Bigger 2993* (E), *Grierson & Long 1335* (K), *Haines 582* (K), *Sinclair & Long 5597* (K).
Burma: *Gammie 18242* (K), *Duthie 24811* (K), *Lace 2709* (K) *& 4283* (E, K), *Parish 410* (K).
China: *Cavalerie 4521* (K), *Chow 78233* (E, K), *Forrest 9203* (K), *11385* (E), *& 22491* (K), *Hancock 26* (K), *Levine 545* (MO), *Playfair 95* (K), *Shiu Ying Hu 11901* (K), *Sorvig 31* (K), *Vachell for Heuten 170* (E).
Christmas Island: *Powell 505* (K).
Fiji Island: *Dominco 7422* (K).
India: *Aitchison 215* (K), *Anderson s.n.* (E), Bourne 2315 (K), *Drummond 14457* (K), *26426* (K) *& 26431* (E), *Falconer 729* (K), *Gamble 3548* (K) *& 18456* (K), *Haines 3451* (K) *& 4973* (K), *Hohenhadar 238* (K), *Mooney 150* (K), *1584* (K) *& 2540* (K), *Ritchie 581* (K), *Stocks 263* (K), *Wight 2213* (K) *& 2224* (K).
Indonesia: *Kostermans & Soegengi s.n.* (K).
Kashmir: *Mohammad 4185* (MO).
Nepal: *Schilling 1056* (K) *& 2116* (K), *Stainton 7191* (E), *Strachey & Winterbottom 1* (K) *& 4* (K), *Vautier 2147* (K), *Wallich 1821* (K).
North West Himalayas: *Dilwar & Naemshah s.n.* (K), *Gamble 24598* (K) *& 27440* (K), *van der Maesen 2867* (K).
Pakistan: *Burtt B1353* (E).
Phillipines: *Merrill 227* (BM, K) *& 3490* (K).
Samoan Islands: *Soala 924* (K), *1005* (K) *& 1061* (K).
Singapore: *Samsuri Ahmad SA2* (BM).
Thailand: *Collins 2383* (K), *Kerr 815* (BM), *2351* (K) *& 3994* (K), *Koyama, Tagawa & Wongprasert 31713* (K), *Merrill 3490* (BM), *Put 4425* (K), *Sørensen, Larsen & Hansen 4799* (E), *Zimmerman 19* (BM).

***B. crossandriformis** C.B. Cl.
Mozambique: *Marques 2799-A* (NBG).
Transvaal: *Balkwill 1489* (NU, PRE, PRF) *& 1636* (NU), *Balkwill & Balkwill 6340* (J), *Brown 16752* (PRF), *Bruce 36* (PRE, SRGH) *& 184* (PRE, SRGH), *Burger 389* (PRE), *Codd 3706* (PRE) *& 7780* (PRE, SRGH), *Coetzee 946* (PRE), *Compton 29804* (NBG, PRE), *Fourie 2* (PRU), *Galpin 887* (BOL, K, PRE, SAM, type), *Germishuizen 305* (PRE), *Haygarth 15914* (NH), *Herman 751* (PRE), *Jacobsen 2811* (PRE), *Kirk 96* (PRE), *Klopper 120/B/11* (PRU), *Maguire 2522* (NBG, STE), *McDonald 25* (PU), *Meeuse 9597* (PRE, SRGH), *Mogg sub PRE 40352* (PRE), *Oatley C14* (NU, PRE), *Obermeyer sub PRE 35542* (PRE, SRGH), *Pooley 48* (NU), *Raal 2* (PRE, TPA Lydenburg), *Repton 4569* (PRE) *& 6420* (PRE), *Stephen 685* (PRE, SRGH), *Strey 3996* (PRE), *6593* (NU, PRE) *& 47796* (NH), *Theron 1229* (PRE, PRU), *Thorncroft 857* (PRE), *van der Schyff 3524* (PRE), *van Heerden 128* (PRU), *van Rooyen 1448* (PRU), *van Wyk 3402* ((PRU), *Ward 2057* (NH, PRE) *& 4081* (PRE), *Zambatis 1023* (PRE).
Zimbabwe: *Drummond 670* (K), *Drummond & Rutherford-Smith 7552* (K, PRE, SRGH).

***B. cuspidata** Heyne ex Nees
India: *Bourre 4809* (K) *& 5079* (K), *Lawson 10309a* (K), *Rottler 27* (K), *Thomson 2499* (K, type), *van der Maesen 2609* (K), *Wight 2215* (K) *& 2633* (E).

***B. cyanea** S. Moore
Angola: *Gossweiler 10825* (K), *Pearson 2470* (K), *Stopp BO 176* (K), *Welwitsch 5000* (K, type).
Namibia: *de Winter & Leistner 5217* (WIND).

***B. damarensis** T. Anders.
Namibia: *Bass A97* (PRE), *Davies, Thompson, & Miller 23* (WIND), *de Winter 2650* (PRE, WIND), *de Winter & Leistner 5818* (PRE, WIND) *& 5910a* (PRE, WIND), *Dinter 2830* (SAM), *Giess 3180* (WIND), *3474* (WIND), 12743 (PRE) *& 15085* (PRE, WIND), *Giess & Ramard 8136* (WIND), *Jensen 83* (WIND), *sub WIND 31448* (WIND), *31450* (WIND) *& 31452* (WIND), *Joubert 176-165* (WIND), *Kers 1217* (WIND), *le Roux 1515* (WIND), *MacDonald 596* (BM), *Marloth 1315* (BOL, SAM, type of *B. marlothii*), *Rusch 8* (WIND), *Seydel 3100* (SRGH) *& 5501* (SRGH).

***B. decnisneana** Nees
Aldabra Group Islands: *Dupont 118* (K).
Astove Islands: *Fryer & Gardivet 3* (K), *Stoddart and Poore 1264 (K).*
Comoro Islands: *Humblot 113 (K).*
Madagascar: *Boivin 10* (K, type).

Mayotte: *Boivin 1850* (K) & *1854* (K).

*B. decaryi Benoist

Madagascar: *Croat 31625* (MO), *Decary 3211* (BM) & *3259* (K, type), *White s.n.* (BM).

*B. descampsii Lindau

Congo: *Robyns 1715* (SRGH).

Zaire: *Brooks, Baker, Schat & Malaisse 44* (K), *Descamps 3/1896* (K, photo), Fanshawe F 11993H (K), *Richards 5364* (K), *Hooper & Townsend 538* (K), *Kassner 2619* (K, type).

Zambia: *Anton-Smith s.n.* (SRGH), *Argus 2662* (K), *Bands 769* (K), *Burtt 6223* (K), *Fanshawe 8683 & F11993* (K), *Lawton 564* (K), *Marks 126* (K), *McCallum 612* (K), *Msanane 532* (K), *Mutimushi 3339* (K) & *JMM22* (K), *Richards 1122* (K), *5364 (EA) & 11085* (K).

*B. dulcis Benoist

Madagascar: *du Puy, du Puy, Carlson & Andrianatna MB7700* (K).

*B. elegans S. Moore

Angola: *Dawe 386* (K), *Exell & Mendonca 3083* (BM), *Johnston s.n.* (K), *Pearson 2463* (K) & *2472* (K), *Welwitsch 5068* (BM, type) & *5114* (BM).

Congo: *Soyaux 26* (K, type).

Mozambique: *Balsinhas 135* (K), *Barbosa & de Lemos 8613* (K), *Borle 1103* (EA), *Grandvaux & de Lemos 8613* (PRE), *Miller 7233* (K), *Moss 8/7/22* (BM), *Nuvunga, Dungo & Covane 1956* (J).

Swaziland: *Nel 125* (EA).

Transvaal: *Balkwill & Balkwill et al. 5627* (J) & *5639* (J), *Balkwill & Manning 650* (PRE), *Bredenkamp 1558* (PRE, PRU), *Codd 4219* (PRE) & *6079* (PRE), *Codd & de Winter 5532* (PRE), *Crawford 327* (PRE), *de Souza 473* (PRE), *du Toit 1* (PRE), *Gertenbach 5459* (PRE), *Killian 23* (PRE), *Meyer 7248* (PRE), *Obermeyer sub TM 36097* (PRE), *Raal 489* (PRE), *Retief 389* (PRE), *Rogers 12480/20705* (PRE), *Rushworth 4* (NU), *Schlieben & Strey 8397* (PRE), *van der Schyff 2885* (PU), *van Rooyen 918* (PRU), *van Wyk 340* (PU), *Wager sub PRE 58905* (PRE), *Zambatis 1141* (PRE).

Zimbabwe: Davies 1247 (K, PRE, SRGH) & *2033* (K, PRE), *Drummond 5688* (PRE) & *7701* (K, PRE), *Goodier 967* (K, SRGH), *Hall 72* (NBG), *Mavi 1272* (PRE, SRGH), *Muller 2338* (K, PRE), *West 7542* (SRGH).

*B. eranthemoides R. Br.

Cameroon: *Biholong 126* (K), *Letouzey 6863* (K), *McClintock 149* (K).

Ethiopia: *Amshoff 10666* (K), *Ash 880* (K), *Burger 657* (K), *1170* (K) & *3569* (K), *Carr 317* (K), *Gereau 1300* (K), *Gilbert & Gilbert 1545A* (K), *Gilbert, Ensermu K. & Vollesen 7837* (K), *Gillet 5070* (K), *Mesfin T. & Kagnew G7 157B* (K) & *1586* (K), *Robertson 1291* (K), *Schimper 111* (K) & *1179* (K), *Strecker 47* (K).

Kenya: *Miller & Miller 1086* (E), *Schultka 30* (EA), *Shikano 20* (EA).

Mozambique: *Peters 5* (K), *29* (K) & *s.n.* (K).

Nigeria: *Keay 28030* (K), *Latilo 63494* (K).

Somalia: *Appleton s.n.* (K), *Drake-Burkman 404* (K), *Elam 477* (K), *Gillett 4564* (K), *Gillett, Henning & Watson 22255* (K), *Godding 152* (K), *Lort-Phillips 6/95* (K), *Maunder 36* (K), *Pignatti s.n.* (K), *Thulin, Hedren & Dahir 7551* (K).

Sudan: *Wickens 837* (K).

Tanzania: Greenway 2113 (PRE).

*B. eylesii S. Moore

Zimbabwe: *Chase 776* (K, SRGH), *Davies 1811* (K, SRGH), *Eylesii 160* (SRGH, type), *Miller 42713* (SRGH) & *45955* (K), *Plowes 3455 (K), Rogers 5412* (BOL), *West 25780* (K, SRGH), *Wright T198* (SRGH).

*B. flava Jacq.

Ghana: *Morton 1961* (K) & *8394* (K), *Enti & Hall 37516 (K).*

Gold Coast: *Irvine 474* (K), *Darko 598* (K), *Andoh 5108* (K), *Morton 23329.*

Guinea: *Adam 25243* (MO), *Alves Pereira 1895* (K), *Farmar 260* (BM) & *260a* (K), *Lisowski 10610* (K) & *51257* (K), *Santo 2240* (K).

Guinea-Bissau: *Santo 2240* (MO).

Ivory Coast: *Amshoff 2609* (K), *Hepper & Maley 8043* (K) & *8257* (K).

Liberia: *Amshoff 273* (K), *2752 (K)* & *2865* (K).

Nigeria: *Jones & Onochie 14726* (K) & *16741* (K).

Senegal: *Chevalier 2794* (K), *Heldelot 1838* (K, type of *B. flava*).

Sierra Leone: *Adam 22426* (MO), *23076* (PRE) & *23651* (MO), *Deighton 2936* (K), *Glanville 391* (K), *Gledhill 266* (K), *Jaeger 8809* (K), *Jones 120* (K), *Morton & Gledhill SL292* (K), *Thomas 8254* (K), *Tindall 35* (K).

*B. **fulvostellata** C.B. Cl.

Malawi: *Bidgood & Vollesen 2162* (K), *Salubeni & Patel 3798* (K), *Iwarsson & Lyding 748* (K), *Brummitt & Patel 15466* (K), *Leach 9893* (K).

Tanzania: *Greenway & Kanuri* (EA), *Mwasumbi & Vollesen 717* (K), *Nevers & Cahmley 3401* (K), *Rees 218* (EA), *Schlieben 2358* (BM), *Vollesen 3888* (K) & *4617* (K).

Zambia: *Argus 1519* (K), *Astle 4652* (K), *Bidgood, Mwasumbi & Vollesen 717* (K), *Bush 1930* (K), *Fanshawe 2031* (K) & *4504* (K), *Jameson & Mutimushi 2164* (K), *Kornos 3351* (K), *Nevers & Chamley 3401* (K), *Robson 1028* (K), *Vollesen 1617* (K) & *MRC 3888* (K), *Whyte s.n. (July 1896)* (K, type), *Wright 70* (K).

*B. **galpinii** C.B. Cl.

Botswana: *Miller N/994* (PRE).

Namibia: *de Winter 3418* (NBG).

South Africa: *Galpin 1331a* (K, type).

Transvaal: *Ballowill 1653* (E, NU), *Codd 5316* (PRE, SRGH), *Meeuse 10593* (PRE, SRGH), *van Heerden 143* (PRU), *Visser 247* (PRE), *Young 37* (PRE).

*B. **gibsonii** Dalz.

India: *Stocks s.n.* (K), *Wight 2639* (E).

*B. **glandulifera** Lindau

Somalia: *Gillett & Becket 23317* (EA, K), *Hildebrandt 860e* (K, type), *Kuchar 16215* (K), *16573* (K), *17641* (K) & *17766* (K).

*B. sp. *aff.* B. **glandulifera** Lindau

Kenya: *Greenway 13534* (PRE).

*B. **gossweileri** S. Moore (probably synonymous with *B. lancifolia*)

Angola: *Gossweiler 4948* (K, type).

*B. **grandicalyx** Lindau

Angola: *Humbert 16253* (K).

Belgian Congo: *Germain 6181* (K, PRE).

Central African Republic: *le Testu 3390* (K).

Ethiopia: *Friis, Zerihn W. & Vollesen 2506* (K), *Mooney 6835* (K).

Kenya: *Bally 656* (K), *Glover, Gwynne & Samuel 298* (K), *Glover, Gwynne, Samuel & Tucker 2546* (PRE), *Gillett 19287* (EA), *Tweedie 1691* (K), *Verdcourt 519* (EA, PRE).

Rwanda & Burundi: *Lewalle 5900* (K), *Raynol 20776* (K), *Reekmans 4514 (MO) & 5623* (K, SRGH).

Saudi Arabia: *Scott & Britton 176* (BM), *Wissman 2938* (BM).

Sudan: *Andrews 952* (K), *Brown 56* (K), *Freeman & Lucas 88* (K), *Johnston 14K* (K), *Schweinfurth 2512* (K, type), *Smith 5* (K).

Tanzania: Burtt *5767 (BM)*, *Greenway & Kanuri 15301* (MO), *Hornby 680* (K), *Hoyle 381* (BM), *Lovette 3246* (K), *Richards & Arasululu 29154* (K), *Richards 23879* (K), *Schlieben 3305* (BM), *Taylor 3390* (BM).

Uganda: *Eggeling 1676* (K), *Langdale-Brown 2413* (K), *Lye & Lester 2153* (K), *Purseglove P1011* (K), *Scott-Elliot 8132* (BM).

Yemen: *Guichard KG/HAD/212* (BM), *Popov 6/5* (BM), *Wood 1683* (BM), *1875* (BM) & *7/75/720A* (BM).

Zambia: *Chisumpa 168* (K), *Mutimushi JMM 3222* (K) & *3298* (K).

*B. **grandiflora** Dalz.

India: *Rao 85* (K), *Ritchie s.n.* (E), *Talbot 282* (K).

*B. **grandipetala** De Wild.

Congo: *Descamps 61* (K).

*B. **grandis** Nees

Ethiopia: *Ash 1330* (K, MO), *Burger 3609* (K), *de Wilde & Gilbert 261* (K), *de Wilde & Gilbert 261* (EA), *Friis 4526* (K), *Gilbert 1* (K), *Mooney 6259* (FT, K), *Pappi 2999* (FT), *Parkyns 1861* (K), *Quarton-Dillon & Petit 283* (K), *Schimper 702* (K, type) & *1842* (K, type), *Scott 223 (K)*, *Steudner 1509* (K).

*B. **grantii** Oliv.

Kenya: *Dawson 282* (K) & *484* (K), *Harper 2474* (K), *Hemsted 573* (K), *Linton 129* (K), *Napier 268* (K) & *2474* (K), *MacDonald 764* (K), *Newbould 5794* (K) & *5861* (K), *Verdcourt 487* (K) & *684* (K).

Tanzania: *Newbold 5794* (K), *5861* (K).
Uganda: *Eggling 554* (K) & *929* (K), *Liebenberg 966* (K), *Lye 385* (K), *402* (K) & *3623* (K), *Lye & Hamilton 3623* (K), *Lye & Rwaburindore 3402* (K), *Maitland 992* (K), *Speke & Grant 665* (K, type).

***B. greenii** M. & K. Balkwill
Natal: *Balkwill & Balkwill 4391* (J), *Green* (J, holotype).

***B. gueinzii** Sond.
Cape: *Flanagan 1773* (BOL, SAM, PRE), *Pegler 1190* (BOL).
Mozambique: *Borle 451* (PRE), *Marques 2674* (NBG), *Mogg 29492* (J), *Moss sub J 28180* (J), *Nuvunga & Mafumo 97* (J).
Natal: *Bourquin 292* (NU), *Morriss 898* (NU, PRE), *Nicholson 560* (NH), *Pillans 16574* (BOL), *Strey 7462* (NU) & *8159* (NU, PRE, SRGH), *Ward 1475* (NH).
Swaziland: *Compton 26819* (PRE), *28599* (PRE), *28685* (NBG, PRE) & *31416* (NBG, PRE), *Maguire 7626/194* (J), *Murdock 172* (NBG).
Transkei: *Davidson 3879* (J).
Transvaal: *Balkwill 1568* (NU), *Balkwill & Balkwill et al. 5607* (J), *Balkwill & Manning 719* (E, NU), *Buitendag 439* (NBG, PRE, STE) & *810* (STE), *Burrows 3508* (J), *Galpin 842* (SAM), *Junod 2383* (PRE), *Schlechter 4603* (NBG), *Thorncroft 3120* (PRE).

***B. her** Benoist
Madagascar: *Bernardi 11413* (E, K), *Cloisel 33* (BM), *Croat 30816* (MO), Decary 8306 (K) & *16221* (K), *Dumetz et al. 815* (MO), *du Puy, du Puy & Ravonjiarison MB20* (K), *Keraudren 714* (K), *MacPherson & Pigeon 14955* (MO), *Miller & Randkianasolo 6107* (K) & *6268* (K), *Phillipson & Rabenantanaka 3125* (K), *Willing 10* (MO) & *13* (MO).

***B. heterotricha** Lindau
Mozambique: *Schlechter 11822* (PRE, isotype).
Transvaal: *Balkwill 1547* (NU, PRE) & *1637* (NU), *Balkwill & Balkwill 4299* (J) & *6321* (J), *Fruce 185* (PRE, SRGH), *Chase 4803* (SRGH) & *Chase 6098* (SRGH), *Codd 2972* (PRE) & *4225* (SRGH), *Codd & Dyer 7740* (PRE, SRGH), *Cole & Catt 262* (PRE), *Davies 1228* (SRGH), *Drummond 590* (PRE, SRGH) & *5709* (PRE), *Faurie 20* (PRU), *Galpin 9184* (J, PRE) & *Galpin 14924* (SRGH), *Goodier 780* (SRGH), *Hardy 435* (PRE, SRGH), *Hopkins s.n.* (SRGH), *Johnson 3080* (NBG), *Krynauw 12* (PRE, TPA Lydenburg), *Long s.n.* (PRE), *Maguire 1473* (NBG, PRE, STE) & *Maguire 8580* (J), *Meeuse 9203* (PRE), *9645* (PRE, SRGH) & *9645* (SRGH), *Miller 2178* (SRGH), *Noel 2002* (SRGH), *Pienaar 315* (PRE), *Pole-Evans 1692* (PRE), *Rogers 19409* (BOL, J), *Schlechter 11822* (K, type), *Smuts 2039* (PRE), *Theron 2812* (BLFU, PRU), *van Wyk* (PRE, PRU), *Venter 8832* (TPA Lydenburg), *von Teichman 206* (PRE), *Werdemann & Oberdieck 1983* (PRE), *Wild 5334* (SRGH), *Zambatis 972* (PRE).
Southern Africa: *Leistner 3514* (BM).
Zimbabwe: *Corner s.n.* (E), *Davies 1228* (K).

***B. hildebrandtii** S. Moore
Arabia: *Lunt 216* (K).
Ethiopia: *Friis, Mesfin T. & Vollesen 3134* (K), *Gilbert, Ensermu K. & Vollesen 7723* (K), *Gilbert & Gilbert 1866* (K).
Kenya: *Kirk 12/73* (K), *Linder 3652* (K).
Somalia: *Bally 9977* (K), *10831* (K) & *11243* (K), *Curle 45* (K), *Gillett 4005* (K) & *4593* (K), *Guichard EAH 10689* (K), *Hansen & Heemstra 6260* (K), *Hemming 1913* (K), *Hildebrandt 866* (K, type), Kuchar 17654 (K), *Newbould 874 (K)* & *1044* (K), *Popov P050, P186* (EA) & *1354* (EA, K), *Thulin & Mohammed 6871* (K), *White 126* (K), *Wood 572/11* (K).
Yemen: *Heemstra 3014* (EA), *Popov 53/46* (BM).

***B. hillcoatiae** J.R.I. Wood
Arabia: *Wissman 2517* (BM).
Yemen: *Aires 29N* (K), *Guichard KG/HAD/93* (BM), *Wood 2745* (BM), *2751* (BM) & *3083* (BM, K, type) (K), *Wood 2751* (E, K), *2745* (K) & *3150* (K), *Bisset 214* (K).

***B. hirta** Oberm.
Malawi: *Blackmore & Brummitt 614* (K), *Brummitt, Patel & Tawakali 18562* (K) & *18576* (K).
Mozambique: *de Lemos & Balsinhas 302* (K, SRGH).
Tanzania: *Faulkner 4375* (SRGH).

Zimbabwe: *Chase 308* (K, NU, SRGH) & *3659* (K, MO), *Dehn R27* (SRGH), *Eyles 7567* (K) & *8613* (K), *Fisher 1528* (NU, SRGH), *Hopkins B533* (SRGH), *Masterson 361* (SRGH), *Mavi 1506* (SRGH), *Plowes 2225* (K, SRGH), *Seward 13/51* (NU), *Teague 8* (BOL, isotype, K, holotype) & *438* (BOL, K).

***B. hochstetteri** Nees ex DC.

Arabia: *Collenette 1023* (K), *1481* (K), *1469* (K), *1474* (K), *4713* (E), *4750* (E), *6651* (K), *7309A* (K) & *7342* (K), *Fischer 114* (K), *Kercher AL.110* (BM), *Popov 69/99* (BM) & *69/102* (BM), *Schimper 919* (BM), *Trott 173* (K), *Vesey-Fitzgerald 16720/22* (BM), *Zeller B126* (BM).

Ethiopia: *Ellis 225* (K), *Gilbert 2114* (K, MO), *Gilbert, Sebsebe & Vollensen 8199* (K), *Schweinfurth & Riva 581* (K).

India: *Dalzell s.n.* (K) & *31* (K), *Singh 71* (K), *Stocks s.n.* (K) & *501* (K).

Kenya: *Kirrika 76 (K).*

Oman: *Mandaville 6414* (BM) & *6585* (BM), *Miller 2379 (E), 2489* (K), *2512* (K), *2689 (E), 6130* (K), *7555* (K) & *7651* (E).

Somalia: *Ashall 11929* (EA), *Bally 9569* (K), *Collenette 206* (K), *Edmondson 3205* (E), *Gillett 22924* (K), *Glover & Gilliland 439* (EA), *Hansen & Heemstra 6189* (K), *Kuchar 16881* (K) & *17614* (K), *Thulin & Warta 6203* (K), *Wieland 4548* (K, MO) & *4724* (MO).

Sudan: *Jackson 4357* (K), *Kotschy 119* (K) & *159* (K, type), *Schweinfurth 426* (K).

Yemen: *Wood 1633* (BM, K) & *2037* (BM).

***B. holstii** Lindau

Angola: *Monteiro & Murta 217* (PRE).

Tanzania: *Drummond & Hemsley 3204* (K), *Greenway & Kanuri 15141* (EA), *Holst 3516* (K, type), *Koritschoner 951* (EA), *Lovett & Congdon 2014* (K), *Nevers & Chamley 3443* (K), *Peter K 1020* (K), *K 1074* (K), *60017* (K) & *60325* (K), *Procter 3901* (K), *Schleiben 2411* (K) & *3790* (K), *Vollesen MRC3723* (K).

***B. holubii** C.B. Cl.

Botswana: *Setsogo, Sydes & Turton 5156* (K), *Woolland 924* (SRGH).

Namibia: *Giess, Volk & Bleissner 7115* (WIND).

South Africa: *Holub s.n.* (K, type).

Transvaal: *Brynard & Pienaar 4352* (PRE), *Galpin 9185* (PRE, SRGH), *Nel 5559* (PRE), *van der Schyff 2601* (PRE).

Zimbabwe: *Biegel 2105* (K, SRGH), *Miller 2138* (K, SRGH), *Philcox & Leppard 8817* (K).

***B. homoiotricha** C.B. Cl.

Ethiopia: *Burger 3013* (K), *de Wilde 9875* (K).

Somalia: *Cole 395* (K, type).

***B. horrida** Buscalioni & Muschler

Ethiopia: *Illegible 652* (K).

***B. humbertii** Benoist

Madagascar: *Croat 31273* (K, MO), *Dorr 4089* (K), *Humbert, Perrier de la Bathie 2807* (BM), *Humbert & Swingle 5311* (K, type), *Humbert 20299* (K).

***B. insericata** Chiov.

Somalia: *Gillett & Beckett 276* (K).

***B. involucrata** Nees

Ceylon: *Balakrishnan NBK 551* (K, MO), *Gardner 698* (K), *Macrae 114* (K), *C.V. 310* (K), *Waas 2084* (K), *Walker 698* (K).

India: *Anglade 891* (K), *Baines 216* (K) & *TV4a* (K), *Barber 3078* (K), *Bourne 193* (K) & *388* (K), *Dalzell s.n.* (K), *Fischer 3247* (K), *Gamble 11535* (K) & *11975* (K), *12325* (K) & *16882* (K), *Gardner 698* (K, type), *Gough s.n.* (K), *Jarrett, Saldanha & Ramamoorthy HFP 841* (MO), *Jarrett & Ramamoorthy HFP 964* (E), *Matthew, Britto & Rani 28826* (K), *Saldanha 15252* (K), *Stocks s.n.* (K), *Thomson s.n.* (K), *van der Maesen 3476* (K), *Watson s.n.* (E), *Whyte s.n.* (K), *Wight 2220* (K), *Wynaad & Lawson 1884* (K).

***B. irritans** Nees

South Africa: *Archibald 4234* (K), *Bolus 7/1868* (K), *Bowker s.n (?652)* (K), *Day s.n.* (BM), *Drège s.n.* (K), *Galpin 9972* (K), *Long 561* (K), *Marais 162* (K), *Mauve 5238* (K), *Zeyher 1421* (BM, K).

*B. jubata S. Moore
Namibia: *Boss sub TM 34948* (PRE), *Giess & Leippert 7588* (NBG, WIND), *Pearson 9895* (BOL, K, SAM, type), *Rutherford 352* (WIND), *Schelpe 201* (BM), *Wr..er 283* (WIND), *Wanntorp & Wanntorp 641* (K), *Wiess 12375* (PRE).
*B. kacondensis S. Moore
Angola: *Gossweiler 2909* (K) & *4147* (K).
*B. kaloxytona Lindau
Namibia: *Dinter 5288* (BLFU, BM).
*B. keniensis Mildbr.
Kenya: *Thomas III.30* (K, type).
*B. kirkii T. Anders.
Mozambique: *Biegel & Pope 3536* (K) & *3537* (K), *Chase 2646* (BM), *Hornby 2732* (K), *Kirk s.n.* (K, type), *Leach & Brunton s.n.* (K), *Wild 6541* (K).
Zambia: *Angus 1572* (K) & *2944* (K), *Fanshawe 4537* (K), *Greenway & Brenan 8506* (K), *Mwimushi 920* (K), *Sandwith 85* (K), *van Rensburg 2227* (K).
Zimbabwe: *Chase 8282* (K), *Davies 2444* (K), *Gonde 235* (K), *Muller 2157* (K), *Plowes 2690* (K), *Whellan 873* (K).
*B. kitchingii Baker
Madagascar: *Baron 4048* (K, type), *4348* (K), *6158* (K) & *6174* (K), *Deans Cowan s.n. 1881* (BM), *Decary 2560* (BM) & *Decary 2826* (K), *du Puy, du Puy & Rafamantanantsoa MB195* (K), *Gentry 11545* (MO), *Niccol & Maraham 681* (K), *Schatz 1284* (K), *White s.n.* (BM).
*B. lactiflora Brummitt & Seyani
Malawi: *Brummitt, Polhill & Banda 16325* (K, SRGH), *Pawek 8152* (K, SRGH), *8338* (K), 10899 (K, type), *11172* (K), *11381* (SRGH), *12700* (K), *13930* (K), *13700* (K) & *14018* (K), *Wiyte 229* (K).
Tanzania: *Bally & Carter 16490* (K), *Bidgood, Mwasumbi Vollesen 683* (K), *Bjvrnstad AB1617* (K), *Bullock 2694* (K), *Carter, Abdallah & Newton s.n* (K), *Gereou & Kayombo s.n.* (K), *Richards 11177* (K), *19850* (K) & *21253* (K), *Stolz 1941* (K, SAM), *Vollesen 3433* (K).
*B. lanceata (Forssk.) C. Chr.
Djibouti: K) *Naegele 124* (K).
Ethiopia: *Bally 7028* (EA, K), *Schimper 1004* (K, type).
Saudi Arabia: *Schimper 745* (K).
Somalia: *Kuchar 17160* (K), *Pery 10/78* (K).
Sudan: *Kassar 625* (K), *Jaason 2821* (K) & *3939* (K).
Yemen: *Boulos, Rawaished, Gifri, Saered, Hussein 16633* (BM), *Wood 2076* (BM, K).
*B. lanceolata (Schinz) Oberm.
Botswana: *Brown sub Manuno 4* (SRGH).
Namibia: *Craven & Craven 432* (WIND), *Dinter 43* (SAM), *1161* (SAM), *2094* (SAM) & *2218* (SAM), *Giess & Müller 12055* (FRE, WIND), *Kinges 2148* (PRE) & *2762* (PRE), *Orlendahl 546* (PRE), *Range 616* (SAM), *Seydel 1062* (PRE), *1507* (SRGH, WIND), *1963* (SRGH) & *37641* (WIND), *Volk 3023* (PRE), *Walter & Walter 1656* (FRE, WIND) & *2373* (WIND).
*B. lancifolia T. Anders.
Angola: *Welwitsch 5013* (BM) & *5024* (BM).
Botswana: *Allen 247* (J, PRE), *Baines & Parry 68* (J), *Biggs M136* (PRE), *Brown 8684* (SRGH), *Drummond & Seagrief 5236* (SRGH), *Long & Rae 124* (K), *156* (K) & *303* (K), *Smith 3346* (SRGH), *Thorne 54074* (NBG, SAM), *Tyers 23* (SRGH), *van Son s.n.* (NH, PRE, SRGH), *West 3874* (PRE, SRGH), *West 3874* (PRE, SRGH).
Cape: *Acocks 1760* (BOL, PRE), *Barnard 36165* (SAM), *Bryant 961* (STE), *Leistner 1351* (SRGH), *Marloth 2005* (PRE), *Pearson 7993* (BOL).
Namibia: *Acocks 18082* (NBG, PRE), *Barnard 634a* (SAM), *Bayliss 1738* (NBG), *Craven 797* (WIND) & *2209* (WIND), *de Winter 2346* (NBG, PRE, WIND) & *3418* (PRE, WIND), *de Winter & Leistner 5230* ((PRE, WIND) & *5502* (PRE), *Dinter 72* (PRE, SAM) & *7401* (PRE, WIND), *Een s.n. 1879* (BM), *Giess 1326* (NBG, PRE, WIND), *1766* (WIND), *Giess 8483* (PRE, WIND), *9272* (WIND) & *10371* (PRE, WIND), *Giess & Müller 12206* (PRE, WIND), *Hall 321* (NBG, PRE), *Hardy 19..4* (PRE, WIND), *Hines 287* (WIND), *Kinges 3271* (PRE), *Leippert 4882* (WIND), *Marloth 1316* (PRE, SAM, type of *B. latiloba*) & *1460* (PRE, isotype of *B. hereroensis*), *Merxmuller & Giess 1089*

(WIND), *Müller 183* (PRE, WIND), *Oliver, Müller & Steenkamp 6557* (PRE), *Pearson 4001* (BM, SAM), *4022* (BOL, SAM) & *9606* (BOL), *Range 1042* (SAM), *Rutherford 386* (WIND), *Schelpe 202* (BM), *Schmidt 298* (PRE, WIND), *Smook s.n.* (NU), *Stery 2026* (NH), *Steyn 7973* (WIND) & *22512* (PRE), *Thorne sub SAM 35758* (SAM).

Natal: *Edwards 2500* (NU, PRE), *Gerrard 1266* (BM, K, type) & *Medley Wood's Collector sub NH 8892* (NH).

Swaziland: *Acocks 18082* (NBG, PRE).

Transvaal: *Balkwill 674* (NU), *1484* (NU, PRE) & *1542* (NU), *Balkwill & Balkwill 4302* (J), *Breyer 19393* (PRE), *Bruce 177* (PRE, SRGH), *Burger 426* (PRE) & *599* (PRE), *Codd 4281* (PRE, SRGH), *Codd & Dyer 7705* (PRE, SRGH), *Fourie 2579* (PRE), *Goodier 1044* (SRGH), *Holland sub BOL 19564* (BOL), *Krantz 6422* (PRE), *McDonald 212* (PU, PRE), *Meeuse 9626* (PRE, SRGH), *9789* (PRE) & *10549* (PRE), *Obermeyer 961* (BOL), *Pole-Evans 1693* (PRE), *Rogers 24072* (PRE), *Smuts 2040* ((PRE), *van Jaarsveld 365* (NBG, PRE), *von Teichman 208* (NU, PRE, PRU), *Zambatis 1131* (PRE).

Zimbabwe: *Davies 2453* (K), *Drummond 5809* (K, SRGH) & *5899* (PRE, SRGH), *Goodier 1044* (K), *Goodier 1044* (PRE), *Mavi 223* (PRE, SRGH), *Whellan 1024* (K, PRE, SRGH).

***B. lateralis** Oberm.

. alawi: *Salubeni, Seyani & Nachamba 3859* (MO).

Mozambique: *Leach & Rutherford-Smith 10820* (K), *Pole Evans & Erens 501* (K, PRE).

Zimbabwe: *Allen 75* (K), *Borle 170* (K, PRE, type), *Hutchinson & Gillett 3410* (K), *Phipps 2894* (PRE), *West 3332* (K).

***B. lawii** T. Anders.

India: *Blatter 773A* (K), *Cooke 8/88* (K), *Dalzell s.n.* (K), *Santapau 11601* (MO), *Stocks 33* (K), *Talbot 5057* (K), *Woodrow 830* (K).

***B. lichtensteiniana** Nees

Cape: *Acocks 302* (PRE), *Dean 539* (J), *Leistner 1027* (SRGH, WIND) & *2919* (SRGH), *Merxmüller 690* (PRE, WIND), *Nicholas 1522* (CPF, PRE), *Pole-Evans 2163* (PRE), *Schlieben 8765* (PRE), *Theron 1931* (NBG, PRE), *van Wyk 6146* (PRE, PRU), *Wilman 1435* (PRE).

Namibia: *Auret 5636* (PRE), *de Winter 3295* (PRE, WIND), *Dinter 4750* (BOL, NH, SAM), *Giess & Müller 11919* (PRE, WIND), *Giess, Volk & Bleissner 7084* (PRE, WIND), *van Wyk 8689* (J).

South Africa

***B. limnogeton** S. Moore

Tanzania: *Cameron s.n.* (K, type).

***B. linearifolia** Rendle

Kenya: *Donaldson-Smith s.n. 1900* (BM).

***B. longiflora** Linn. f.

India: *Bourne 167b* (K) & *2200* (K), *2720* (K) & *5030* (K), *Coromandel s.n.* (K), *Diravian & Xavier 20687* (K), *Gamble 18576* (K) & *HF10738* (K), *Rottler s.n.* (K), *Talbot 4441* (K), *Thomas (Forster 379)* (K), *Wight (?15)* (K), *(1900)* (K), *2211* (K) & *2636* (E).

***B. longipes** Benoist

Madagascar: *Bosser 19237* (K) & *19331* (K), *Chauvet 43* (K), *Croat 30997* (K), *Humbert 20165* (K).

***B. longissima** Lindau

Kenya: *Bally 15101* (EA), *Jackson 36* (EA).

Somalia: *Gillett 22936* (K), *Gillett, Henning & Watson 22670* (K), *Henning & Watson 3199* (K), *Wieland 4646* (K, MO).

***B. lugardii** C.B. Cl.

Botswana: *Cudmore K6* (K), *Curson 394* (PRE), *de Winter 4334* (K), *Lambrecht 73* (K), *Lugard 106* (K) & *128* (K, type) *Mott 690* (SRGH, UCBG).

Namibia: *Breyer sub TM 20642* (PRE, type of *B. breyeri*), *Giess, Watt & Snyman 11068* (PRE, WIND), *Killick & Leistner 3355* (PRE, WIND), *Maguire 2273* (NBG, PRE), *Merxmüller & Giess 1371* (PRE, WIND), *Müller & Giess 515* (PRE, WIND).

Tanzania: *Bax 306* (K), *Bidgood, Congdon & Vollesen 2213* (K), *Bidgood, Mwasumbi & Vollesen 666* (K), *718* (K), *889* (K) & *948* (K), *Chamley 3432* (K), *Greenway & Kanuri 14167* (K), *Greenway & Polhill 11729* (K), *Hammond 278* (K), *Hornby 2065* (K), *Lovett & Congdon 2001* (K), *Lynes I.G. 232* (K), *Nevers & Chamley 3432* (K), *Pederson 1031* (EA), *Pesambili & Vollesen MRC 2362* (K), *Polhill & Paulo 2036* (K), *Richards 21285* (K), *Thulin & Mhoro 3164* (K).

Transvaal: *Mogg 30264* (J), *O'Connor sub J 66885* (J), *Rogers 22548* (PRE, holotype of *B. quadriloba*), *van Rooyen 3393* (PRE, PRU).

Zimbabwe: *Davidson 1770* (J), *Goldsmith 98/55* (K), *Levy 146* (PRE), *Lugard 128* (K, type), *Rushworth 219* (K, SRGH), *Wild 6016* (K, PRE, SRGH).

*B. lukwangulensis Mildbr.

Tanzania: *Adelyser 163* (K), *Bidgood, Lovett & Pocs 201* (K), *Congdon 209* (K, MO), *Drummond & Hemsley 1528* (K), *Schlieben 3471* (K) & *3478* (K).

*B. lupulina Lindl.

Barbados: *Meagher 268* (MO).

Christmas Islands: *Powell 405* (K).

Florida: *Brumbach 9762* (MO).

Guatemala: *Box 994* (MO).

Jamaica: *Proctor 16170* (MO).

Java: *Backer 18325* (K).

Madagascar: *Baillon 148* (K), *Baron 4759* (K), *4577* (K), *5337* (K) & *6427* (BM), *Blackburn 1911* (K), *du Puy, du Puy & Rafamanantsoa MB 224* (K), *Hildebrandt 2904* (BM), *Humbert & Capuron 29142* (K), *Phillipson 1944* (K).

Malay Peninsula: *Sinclair 6618* (E).

Thailand: *Kerr 315* (BM) & *s.n.* (BM), *Marcan 506* (BM, K).

West Indies: *Blackburn s.n.* (K).

*B. mackenii Hook. f.

Angola: *Martins & Matos 4454* (K) & *4490* (K, SRGH), *Pearson 2579* (K), *Rozeira, Wild & Barbosa 10880* (SRGH).

Botswana: *Gibson 178* (WIND), *Kerfoot 8008* (J), *Long & Rae 591* (K), *Ngoni 241* (K), *Smith 434* (K, SRGHZ), *817* (K) & *818* (K, PRE), *West 3881* (PRE, SRGH).

Malawi: *Pawek 13669* (K).

Namibia: *Barnard 46* (WIND) & *563* (SAM), *de Winter & Wiss 4467* (PRE, WIND), *Dinter 5686* (BOL, PRE, SAM), *Giess & Loutit 14168* (PRE, WIND), *Killick & Leistner 3128* (PRE, WIND), *Maguire 2311* (NBG, PRE), *Merxmüller & Giess 1821* (PRE), *Müller & Giess 413* (PRE, WIND), *Story 6394* (PRE, WIND).

Transvaal: *Codd 8437* (PRE, SRGH), *Galpin M270* (BOL, PRE), *Leendertz 1939* (BOL, PRE), *Meeuse & Strey 10440* (NBG, PRE, SRGH), *Mogg 33173* (J), *Theron 982* (PRE, PRU, PU).

Zambia: *Fanshawe F6417* (K), *Richards 15077A* (SRGH), *van Rensburg 1476* (K, SRGH), *White 1957* (K).

Zimbabwe: *Cross 313* (K, PRE, SRGH), *Elliot s.n.* (K), *Evans 5* (K, NU), *Goldsmith 97/55* (BOL), *Holub 917* (K) & *918* (K), *Philcox & Leppard 8804* (K), *Rogers 13585* (BOL, J, PRE), *Wild 5309* (K, SRGH).

*B. maclaudii Benoist

French Guinea: *Jacques-Felix 1430* (K).

Senegal: *Adam 20001* (K).

*B. macrostegia Nees

Botswana: *Baker 27* (K, PRE), *Brown 1194* (K, SRGH), *Burchell 2386* (K, type of *B. media*), *Galala 19* (K), *Long & Rae 51* (E), *Mott 799* (SRGH), *Lugard 295* (K), *Story 4880* (PRE), *Skarpe S-264* (K), *van Son 28682* (K), *Wild & Drummond 7268* (K, SRGH).

Cape: *Adams 13* (BOL), *Burke 451* (SAM), *Brueckner 397* (PRE), *Codd 1315* (PRE), *Esterhuysen 1014* (BOL), *MacDonald 77/46* (J, NBG, PRE), *Rodger 26973* (SAM), *Rogers 22704* (PRE), *Volk W83* (WIND).

Namibia: *Bradfield 38* (PRE), *de Winter* (PRE, WIND), *Dinter 2708* (K, M), *Dinter 2708a* (PRE, SAM), *Dinter 3363* (SAM), *Germishuizen 2671* (PRE), *Giess 2237* (WIND), *Giess & Smook 10615* (WIND), *Jankowitz Ja 1116* (WIND), *Kers 312* (WIND), *Merxmuller & Giess 1156* (PRE), *Seydel 1815* (WIND), *Skarpe 5264* (PRE, SRGH).

Orange Free State: *Burtt-Davy 10352* (PRE), *Channel 55* (NBG), *Herman 263* (PRE), *Lessing 6* (PU), *Muller 52* (NBG) & *1751* (PRE), *Odendaal 2628* (PRE), *Pont 412* (BLFU), *Zietsman 370* (PRU).

Transvaal: *Bolus 6429* (BOL), *Brain 10113* (SRGH), *Burger 551* (PRE), *Burke s.n.* (K, PRE, type), *Burtt Davy 7515* (PRE, SAM), *Codd 2878* (PRE), *de Winter 7498a* (PRE), *Ellery 407* (PRE), *Galpin M272* (BOL, PRE), *Jenkins 11684* (PRE), *Leendertz 9482* (PRE), *Louw 737* (PRE), *Mogg 35677* (J), *Moss*

14081 (J) & *16677* (J), *Nation 133* (BOL), *Repton 3212* (PRE), *Schilz 157* (PRE), *Seydel 2338* (SRGH), *Smith 691* (PRE), *Stainbank 3473* (NH), *van Wyk* (PRE, PU), *Watt 4985* (J).

Zimbabwe: *Bunzle 47674* (K, SRGH), *Davies 528* (K, SRGH).

*B. **marginata** Oliv.

Tanzania: *Peter 31725* (K) & *31728* (K), *Speke & Arant s.n.* (K, NH, type).

*B. **matopensis** S. Moore

Zambia: *Angus 1548* (K), *Brummitt 16916* (K), *Fanshawe 6128* (K), *Gilges 574* (K, SRGH), *Robinson 517* (K), *2775* (K) & *2825* (K, SRGH), *Rogers 5680* (BOL), *White 2242* (K).

Zimbabwe: *Biegel 2852* (K, SRGH), *Bingham 1125* (K), *Eyles 1165* (SRGH, type) & *4488* (K), *Garley 123* (K), *Kabisa 9* (K), *Kabisa 9* (SRGH), *Lovemore 237* (K), *Phipps 2893* (SRGH), *Rushworth 164* (SRGH), *Whellan 1586* (SRGH), *Wild 4749* (PRE), *Wild 5365* (SRGH).

*B. **meeuseana** P.G. Meyer

Namibia: *Compton 351* (NBG), *de Winter & Leistner 5489* (PRE, isotype), *Giess & Barnard 7907* (WIND), *le Roux & Jankowitz 1488* (WIND), *Merxmüller & Leistner 5489* (PRE), *Story 5874* (PRE), *Volk 2890* (NH).

*B. **merxmeulleri** P.G. Meyer

Namibia: *Giess 8482* (PRE, WIND), *MüLLER & Giess 372* (PRE), *Schmidt 1016* (WIND), *Seydel 1052* (NU), *Ward 168* (NU, WIND).

*B. **meyeriana** Nees

Natal: *Abbott 1700* (NH), *Edwards 25* (NU), *Gerrard 1268* (K, NH, type), *Medley Wood 792* (BOL, NH) & *9918* (NH, NU), *Moll 3082* (NU, PRE), *Nicholson 2164* (PRE), *Strey 9649* (NH, NU, PRE).

South Africa: *Drege 1829* (K, type).

Swaziland: *Barnett 316* (PRE), *Compton 29821* (NBG, PRE, SRGH) & *31418* (NBG, PRE), *Culverwell 725* (PRE).

Transkei: *van Wyk 8075* (NH).

Transvaal: *Balkwill & Balkwill et al. 5873* (J), *Bultendag 463* (NBG, PRE, STE), *Galpin 880* (BOL, PRE, SAM), *Mogg 30430* (J, PRE), *Onderstall 1214* (PRE).

*B. **micans** Nees

Costa Rica: *Smith 6684* (K).

Guatemala: *Heyde & Lux 3117* (K), *Contreras 746* (K), 3544 (K) & 7482 (K), *Lundell & Contreras 18900 (K).*

Mexico: *Andre 1092* (K), *Breedlove 37559* (K), *Bilimek 339* (K), *Feddema, Dieterle & Rzedowski 2488* (MO), *Gentry 5072* (MO), *Hinton 11008* (MO), *Mexia 8904* (MO), *Palmer 1144* (MO), *Pringle 4587* (K), *6162* (K) & *11075* (K), *Ramamoorthy 6161*, (K) *Daniel & Bartholomew 4875* (K), *Daniel & Buttenwick 3205* (K), *Hinton 2857* (K), *8738* (K) & *161666* (K), *Palmer 181* (K), *Pringle 4587* (E, MO), *8/10/1893* (E), *Langlasse 703* (K).

Panama: *Agrazal M. 7* (MO), *Cumming 1138* (E, K), *Durkee 1112* (MO) & *1319* (MO), *Dwyer 8395* (MO), *Hurter & Allen 451* (K), *Jaën 18* (MO), *Leemann s.n.* (K), *Sinclair s.n.* (K, type).

Venezuela: *Liesner, González, Stergios & Aymard 12483* (MO), *Steyermark, Dunsterville & Dunsterville 105796* (MO).

*B. **micrantha** C.B. Cl.

Burundi: *Reekmans 10481* (K).

Kenya: *Bridson 137* (K), *Cameron, Evans & Powys 314* (EA), *Glover, Gwynne, Samuel, & Tucker 1918* (K) & *2540* (K), *Linlingston 36* (EA), *Napper 1886* (K), *Napper & Faden 1925* (K).

Somalia:

Uganda: *Eye 6560* (K), *Purseglove P 3518* (K), *Scott-Elliot s.n.* (K, type).

*B. **molensis** Wild

Zimbabwe: *Biegel 4183* (SRGH), *5297* (K) & *5312* (K), *Carter & Coates Palgrave 2685* (K), *Cross 164* (K, SRGH), *Ingle 4* (K), *Mullin 7/51* (SRGH), *West 4774* (SRGH), *Wild 5604* (K, MO, type), *5618* (K, SRGH) & *7999* (K, SRGH).

*B. **montana** Herb. Madr. ex Nees

India: *Haines 2406* (K), *Wight 2214* (K).

*B. **monticola** Oberm.

Natal: *Balkwill & Balkwill 5418* (J), *Balkwill, Balkwill & Green 6256* (J), *Browning & Paton 14* (NU), *Pole-Evans sub PRE 40567* (PRE), *Rudatis 1579* (BM), *Schweickerdt sub TM 29926* (PRE, type).

*B. **morrisiana** E. Barnes & C.E.C. Fischer.
India: *Barnes 2121* (K), *2122* (K), *2148* (K), *2155* (K, holotype) & *2166* (K).
*B. **mucronata** Lindau (? = *B. kilimandscharica*)
Tanzania: *Richards & Arasululu 26810* (EA), *Schlieben 5110* (BM, PRE), *Volkens 2142* (BM).
*B. **mucronifolia** Lindau
Ethiopia / Somalia: *Appleton s.n.* (K), *Ash 1237* (K), *de Wilde 9875* (K), *Gillett 4436* (K), *Gillett & Watson 260* (K), *Hemming & Watson 3113* (K).
Yemen: *Kamal Mustafa Ibrahim 2430* (BM), *Wood Y/75/958* (BM).
Sine loc.: *Lort Phillips s.n.* (BM).
*B. **mysorensis** Heyne
Ceylon: *Cooray 690011708R* (MO), *Cramer 4329* (K), *Townsend 73185* (K), *Walker 1600* (K).
India: *Gamble 13015* (K) & *14797* (K), *Wight 1966* (K), *Boune 4808* (K) & *s.n.* (K), *Hepper & de Silva 4709* (K), *Hohenhader 356* (K) & *702* (K).
*B. **natalensis** Lindau
South Africa: *Wood 803* (K, NH, type).
*B. **neurophylla** C.B. Cl.
Belgian Congo: *Kidston 7/1890* (K).
Tanzania: *Kassner 3048* (K).
*B. **nitida** Nees
India: *Diraviam & Xavier 20690* (K), *Fischer s.n.* (K), *Foulkes s.n.* (K), *Hooper & Ramaswami 39216* (K), *Lace 2478* (E), *Masters s.n.* (K), *Thomson 79* (K), *Wight 778* (E), 2219. (K) & *s.n.* (K).
Indonesia: *van Steenis 10408* (K).
*B. **noctiflora** Linn. f.
India: *Barber 309* (K), *Fischer 2849* (K), *Gamble 11216* (K) & *15027* (K), *Heyne 2496c* (K), *Matthew & Perumal 20097* (K), *Wight* 1964 *(K)*, 2217 *(K)*, *2223* (K) & *s.n.* (K).
*B. **norbertii** Benoist
Madagascar: *Croat 31578* (MO), *Gentry 11932* (K) & *11507* (MO).
*B. **nutans** Nees
Ceylon: *Wight 777* (K), *Cp 2559* (K), *Walker s.n.* (K), *Champion s.n.* (K), *Gardner 696* (K).
*B. **nyasensis** C.B. Cl.
Malawi: *Brummitt & Seyani 14937* (K), *Hall-Martin 609* (BA), *Walter 4/1884* (K, type).
Mozambique: *Rev. Johnson Comm Weier 411884* (K, type).
Zambia: *Fanshawe 3512* (K) & *8076* (K), *Lawton 862* (K), *Robinson 3781* (K), *Bullock 3000* (K), *Richards 9316* (K), *Pole-Evans 3029* (K), *Hutchinson & Gillett 3962* (K).
*B. **obtusa** Nees
Cape: *Dyer 899* (PRE), *Ecklon & Zeyher 930* (BOL, K, SAM, type), *Flanagan 726* (PRE, SAM), *Fourcade 3229* (BOL), *Gordon-Gray 374* (NU), *Hutchings 1526* (KEI), *Lewis 2863* (PRE, SAM), *Strey 8653* (PRE, SRGH).
Mozambique: *Borle 1101* (K), *Marques 1991* (NBG), *Quintas 129* (SRGH).
Natal: *Baijnath 364* (NU,PRE), *du Toit 2734* (NH), *Edwards 733* (NU, SRGH), Galpin 14771 (BOL, PRE), *Hillary 169* (NU), *Kroon 10063* (PRE, *MacDevette 798* (CPF, NH), *Moll 1944* (NU, PRE) & *5000* (PRE, SRGH), *Rudatis 121* (STE), *Strey 9744* (NH, PRE), *Venter* (BLFU, PRE), *Wood 880* (BOL, SAM).
South Africa: *Drège s.n.* (K, type).
Swaziland: *Compton 31575* (NBG, PRE), *Karsten s.n.* (NBG, PRE), *Murdoch 63* (NBG, PRE).
Transvaal: *Balkwill 128* (E, NU), *1495* (E, K, NU, PRE) & *1565* (E, NU), *Bolus 10845* (BOL, PRE), *Botha* (PRE, PU), *Breyer* (SRGH), *Codd* (SRGH), *Galpin 1330* (SAM), *Leendertz 772* (PRE, SAM), *Meeuse 9312* (PRE), *Mogg 18387* (J), *Obermeyer 944* (BOL, SAM, SRGH), *Theron 1319* (PRE, PRU, PU), *van Jaarsveld 408* (NBG, PRE).
Zambia: *McCallum-Webber s.n.* (NU).
*B. **obtusisepala** C.B. Cl.
Tanzania: *Mdelwa 8* (K).
*B. **opaca** (Vahl) Nees
British Cameroons: *Baldwin Jn. 13851* (K), *Dunlop 142* (K) & *Dunlop 161* (K), *Hepper 1679* (K), *Keay 28419* (K) & *28424* K), *Maitland 139* (K) & *272* (K), Dodowah: *Harris K4* (K).

Akpabla 6133 (K), Enti 6829 (K), Morton A758 (K), 6133 (K) & 7902 (K).
Ghana: Onochie 7490 (K).
Ivory Coast: Breteler 6178 (K).
Nigeria: Gledhill 762 (K), Idahosa 23876 (K), Meikle 814 (K), Miller 56 (K) & 179 (K), Onochie 8135 (K) & 34948 (K), Rowland s.n. (K), Savory & Keay 25146 (K), Sharland 1502 (K).
Togo: Raats 119 (K) & 3022 (K), Gummin 30 (K).

***B. orbicularis** Hochst. ex T. Anders.
Ethiopia: *de Wilde 10613* (K), *Friis, Mesfin T. & Vollesen 2904* (K), *Gilbert & Sebsebe 8689* (K), *Gilbert, Sebsebe & Vollesen 8117* (K), *Puff, Ensermu K. & Dave 8209-13-2/12* (K).
Kenya: *Gilbert & Thulin 1461* (EA, K), *Gillett 13066* (EA, K) & *13329* (K).
Somalia: *Collett 4435* (K), *Friis, Vollesen & Abdisalam Hassan 5010* (K) & *4826* (K), *Hemming & Dechmuth 375* (K), *Schimper 2189* (K), *Thulin, Bashir Mohammed 6765* (K), *Thulin, Hedren, Adbi Dohir 7574* (K).
Yemen: Wood 1383 (BM, K), *2072* (BM, E, K), *3287* (BM, K), *Y/75/415* (BM) & *Y/75/720B* (BM).

***B. ovata** E.Mey. ex Nees
Natal: *Balkwill & Balkwill 6280* (J), *Balkwill & Cadman 2565* (J), *Balkwill, Balkwill & Green 6261* (J), *Codd 7651* (PRE), *Fisher 920* (NU), *Galpin 14721* (BOL, NH), *Gerstner 3862* (NH, PRE), *Medley Wood 6253* (NH) & *7931* (NH), *Mogg 6748* (PRE), *Strey 8041* (NH), *Taylor 5349* (NBG), *van Wyk 2475* (PRE), *Vassilatos & Mantell 132* (PRE), *Wood 470* (BOL).
South Africa: *Drège s.n.* (K, type).
Swaziland: *Bolus 12212* (BOL, PRE), *Burtt & Hilliard 3675* (NU), *Compton 25631* (NBG, PRE) & *31265* (NBG, PRE), *Hilliard 3548* (NU), *Rogers 11493B* (PRE).
Transkei: *Flanagan 2485* (PRE), *Pegler 1565* (PRE, STE).
Transvaal: *Balkwill 1451* (NU), *Balkwill, Balkwill & Kidger 8087* (J), *Balkwill & Manning 616* (NU), *Galpin 832* (PRE, SAM), *Meeuse 10094* (NH, PRE, SRGH), *Onderstal 1192* (PRE), *Rogers 11493* (PRE), *14290* (NBG) & *23599* (J, PRE), *Stalmans 2672* (J), *Story 5460* (PRE), *Thorncroft 15175* (J, PRE, SAM, STE), *Wilms 1222* (PRE).

***B. oxyphylla** Lindau
Transvaal: *Bremekamp 1588* (UNIN) & *1601* (UNIN), *Gertenbach 5469* (PRE), *Schlechter 11813* (BM, K, type).

***B. pabularis** S. Moore
Angola: *Gossweiler 3063* (BM, type), *3083* (K) & *3622* (BM).

***B. paludosa** S. Moore
Congo: *Kassner 2619* (BM, type).
Zambia: *Burtt 6223* (BM), *Gamwell 22* (BM).

***B. papillosa** T. Anders.
Cape: *Acocks 5768* (BOL), *Middlemast 2076* (NBG), *Thorne sub SAM 51598* (SAM), *van Jaarsveld, Forrester & Jacobs 8407* (NBG).
Namibia: *Kruger K16* (STE), *Verdoorn & Dyer 1787* (PRE).

?B. paniculata Wall. ?
Ceylon: Walker 143 (E).

***B. parviflora** R. Br.
Ethiopia: *de Wilde 4815* (MO) & *7211* (MO).

***B. parvispina** Benoist
Madagascar: *Bernardi 11405* (K), *du Puy, du Puy & Ravonjiarisoa MB27* (K), *MB70* (K) & *MB78* (K), *Miller & Keating 4505* (K), *Phillipson & Rabesihanaka 3168* (K), *Phillipson 2404* (K), *Schatz 1274* (K).
- var. **longifolia** ??
Madagascar: *Humbert & Swingle 5318* (K).

***B. paucidentata** Benoist
Madagascar: *Gentry 11745* (K).

***B. perrierii** Benoist
Madagascar: *Decary 7798* (K, type), *Gentry 11507* (K).

***B. phaylopsis** Milne-Redh.
Zambia: *Fanshawe 68* (K), *Holmes 1488* (K), *Lawton 732* (K), *Milne-Redhead 690* (K), *Mutimushi 3137* (K).

*B. phillyraefolia Baker
Madagascar: *Baron 4555* (BM, K, type), *du Puy, du Puy & Rafamantanfantsoa & Ranjamalala MB108* (K), *Soalala 6380* (K).
*B. pilosa Heyne ex Nees
India: *Beddome 315* (K, type), *Wight 2222* (K), *808/1830* (E, K) & *?654* (E), *E.T.C. 2502* (K).
*B. polyneura S. Moore
Angola: *Bamps & Martins 4413* (K), *Barbosa & Moreno 10002* (K, PRE), *Welwitsch 5029* (K, type).
Malawi: *Pawek 8375* (K, MO), *10904* (K, SRGH), *11395* (K) & *14003* (K), *Salubeni 1009* (K, SRGH).
*B. polytricha Wall.
India: *Comm 10/77* (K), *Helfer 6135* (K), *Kurz 820* (K), *MacLelland 154* (K), *Masters ?182* (K), *Meebold s.n.* (K), *Parish 1859* (K).
*B. popovii Verdc.
Socotra: *Bent s.n. (June 1897)* (K), *Popov GP/50/315* (BM), *Miller, Guarino, Obadi, Hassan & Motommed M8694* (K).
*B. prattensis Santapau
India: *Saldanha 15188* (E), *17881* (K).
*B. pretoriensis C.B. Cl.
Botswana: *Abel 45* (PRE), *Miller s.n.* (PRE), *Woollard 215* (SRGH) & *230* (SRGH).
Transvaal: *Acocks 18735* (PRE), *Balkwill & Balkwill 4373* (J), *Balkwill & Sebola 7996* (J), *Barker 103* (J), *Burtt-Davy 5274* (PRE), *Coetzee 889* (PRE, SRGH), *Fourie 2590* (PRE, Tr[illegible]denburg), *Galpin 9052* (PRE), *Letty 397* (PRE), *Meeuse 9650* (PRE, SRGH), *Obermeyer 94?:* [illegible], SAM) & *955* (BOL, SAM, SRGH), *Prasser 1596* (J, NBG, PRE), *Rehmann 4103* (K, type), *Schuechter 4372* (BOL, NBG, PRE), *Thode A1477* (NH, PRE), *Young 2444* (J, PRE).
*B. prionitis L. *sensu lato.*
Angola: *Abreu 71* (BM), *Cariso & Sousa 289* (BM), *Exell & Mendonca 2101* (BM) & *2383* (BM), *Gossweiler 10507* (BM), *Welwitsch 5067* (BM), *5138* (BM) & *5190* (BM).
Bombay: *Mooney 1996* (K), *Raizada 22797* (K), *Santapau 1160* (K), *Stocks s.n.* (K).
Borneo: *Elsener H140* (K), *eyer 6/1884* (K).
Buma: *Griffith s.n.* (K), *McKee 5963* (K).
Ceylon: *Cramer 4849* (K), *Gooray 70020310R* (K), *Thomson 249* (K), *Townsend 73/[illegible]*, *Walker 1409* (K), *Worthington 4565* (K).
Ethiopia: *Ryding, Teferi & Mengisteab 1151* (K).
India: *Crow 132* (K), *Drummond 15209 & 26437* (K), *Gamble 10717* (K) & *10756* (K), *Misra 112* (K), *Shuter s.n.* (K), *Sinclair 4526* (E), *Wight 2216* (K).
Indonesia: *Cunningham 316* (BM).
Malay Islands: *Eyma 333* (K), *Griffith s.n.* (BM), *Jaag 6* (BM) & *400* (BM), *Kostermans 22049* (K) & *22086* (K), *Merrill 273* (BM), *Nedi & Edjan 247* (K).
Malay Peninsula: *Griffith 1845* (K), *Ridley 2969* (K).
Maldive Island: *Adams & Shafeeg 15088* (K).
Mozambique: *Gomes Souza 4474* (K).
Namibia: *Busse 2941* (BM), *Dinter 1981* (PRE, isotype of *B. dinteri*), *Een s.n. 1879* (BM).
Pakistan: *Duthie 6692* (K), *Stocks 52* (K).
Phillipines: *Borden 2343* (E), *Loher 4290* (K) & *7291* (K), *Merril 273* (K).
Seychelles: *Gadiner s.n.* (K), *Jeffrey 771* (K), *Procter 4472* (K).
Siam: *Collins 48* (K), *Harmond 871* (K), *Kerr 495* (BM), *2041* (K), *2828* (BM) & *2841* (BM), *Marcan 495* (K), *Put 2067?* (BM), *Zimmerman 92* (K).
Sumbawa Island: *Kuswata 283* (K).
Tanzania: *Burtt 5163* (BM), *Scheffler 141* (EM), *Swynnerton 192* (BM).
Yemen: *Cope & Murtland 25* (K).
* - subsp. ameliae (A. Meeuse) R.K. Brummitt & J.R.I. Wood
Namibia: *Leistner 3391* (PRE, holotype).
Zimbabwe: *Kerfoot K7823* (J), *Levy 1113* (E), *Wild 4751* (PRE).
* - subsp. appressa R.K. Brummitt & J.R.I. Wood
Yemen: *Forsskal s.n.* (BM, type), *Hepper 5856* (K), *Radcliffe-Smith & Henchie 4438* (K), *Wood 2460* (BM, K), *2543* (K), *2630* (K), *72145* (BM) & *7/74/267* (BM).

¤ - subsp. **delagoensis** (Oberm.) R.K. Brummitt & J.R.I. Wood
Mozambique: *Breyer 20492* (PRE), *Miller 5821* (PRE), *Mogg 28481* (PRE) & *31994* (PRE), *van Dam sub TM 25321* (PRE).
Natal: *Pooley 426* (E) & *769* (E).

¤ - subsp. **induta** (C.B. Cl.) R.K. Brummitt & J.R.I. Wood
Ethiopia: *Ash 1827* (K), *Hemming 1118* (EA, K), *Ryding, Teferi & Mengisteab 1551* (K), *Scott 214* (K).

¤ - subsp. **prionitoides** (Engl.) R.K. Brummitt & J.R.I. Wood
Namibia: *Breyer sub TM 20646* (PRE, type of *B. namutonensis*), *Werderman & Oberdieck 2427* (PRE), *Marloth 1430* (PRE, type).

¤ - subsp. **pubiflora** (Benth. ex Hohen.) R.K. Brummitt & J.R.I. Wood
Pakistan: *Drummond 24116* (K) & *26350* (K).

¤ - subsp. **tanzaniana** R.K. Brummitt & J.R.I. Wood
Mozambique: *Gomes-Souza 4474* (K).
Tanzania: *Drummond & Hemsley 3076* (K), *Faulkner K641* (K) & *36091* (K), *Tanner 3012* (K).

¤**B. procumbens** Lour.
China: *Kerr 8511* (BM).

¤**B. proxima** Lindau
Arabia: *Bisset 276* (K), *Collenette 1451* (K), *Lanton 1858* (K), *Maxwell-Darling 1936* (K), *Radcliffe Smith 5130* (K), *Radcliffe-Smith & Hendire 4774* (K), *Raut & Lauranos 13310* (K), *Smith & Lauranos 848* (K), *Wood 1389* (K) & *2326* (K).
Ethiopia: *Gilbert 2113* (MO) & *2134* (MO).
Kenya: *Bally & Smith B14599* (K), *Faden & Faden 74/1208* (K), *Field 111* (K), *Gilbert, Kibui & Mungai 5715* (K), *Gillett 13403* (K), *19513* (K) & *21149* (K), *Gilbert, Kanuri & Mungai 5715* (EA), *Luke, Kabuye, Robertson, Mungai & Mathenge TPPR 392* (K), *Mooman 905* (EA).
Oman: *Miller 2291* (E).
Somalia: *Wieland 4680* (MO).

¤**B. pulchra** Lindau
Madagascar: *Hildebrandt 2969* (BM, K, type).

¤**B. punctata** Milne-Redhead
Somalia: *Gillett 4522* (K, type), *Wood S/73/143A* (K).

¤**B. pungens** Linn. f.
Cape: *?Anonymous s.n.* (BM, type), *Adamson D309* (PRE), *Archibald 4234* (PRE), *Balkwill & Balkwill 4050* (J), *Bayliss 3155* (NBG), *Bohnen 7829* (PRE, STE), *Botha 5721* (PRE), *Bryant 958* (STE), *Burchell 4759* (K, type of *B. jasminiflora*), *Compton 20295* (NBG), *Ecklon 18953* (SAM), *Forbes 1822* (BM), *Galpin 9972* (PRE), *Hoffman 512* (NBG), *Kies 487* (NBG), *Lewis 5912* (NBG, STE), *Levyns 2864* (BOL), *Long 561* (PRE), *Marais 162* (PRE), *Martin 703* (NBG), *Mauve 5238* (PRE), *Moss 15394* (J), *Niven 134* (BM), *Olivier 1487* (STE), *Sim 20021* (NU, PRE), *Story 2312* (PRE), *Zeyher 1421* (BOL, SAM).

¤**B. pyramidata** Lam.
Fiji Islands: *Parham 10204* (K).

¤**B. quadrispina** Lindau
Ethiopia: *Brichess 10* (K), *Burger 887* (K), *2200* (K), *2224* (K) & *2233* (K), *Friis, Mestin T. & Vollesen 3193* (K), *Gilbert 2061* (K), *Gilbert, Ensermu K. & Vollesen 7439* (K), *7590* (K), *7720* (K), *7722* (K), *7832* (K), *7856* (K) & *8017* (K), *Puff, Ensermu K. & Dawe 820913-2/11* (K), *Roth 487* (K).
Kenya: *Adamson 568* (EA), *Bally & Smith 14586* (K) & *14596* (K), *Gilbert & Thulin 1628* (K).
Somalia: *Bally 9954* (K), *10007* (K), *10231* (K) & *11804* (K), *Bally & Melville 154666* (K), *Gillett 3994* (K), *Godding 82* (K), *Guichard 16582* (K), *Hansen, Heemstra & Sheith 6467* (K), *Hemming & Deshmuth 270* (K) & *323* (K), *Hemming 2270* (K), *Thulin & Mohamed 6918* (K), *Wieland 1290* (MO), *4120* (MO), *4567* (MO) & *4657* (MO), *Wood 5/72/91* (K).
Sudan: *Padwe 243* (EA).

¤**B. ramulosa** C.B. Cl.
Ethiopia: *Burger 2066* (K), *de Wilde 4348* (K) & *9856* (K), *Gilbert 1474* (K).
Kenya: *Bally 16771* (K), *Brenan, Gillett & Kanuri 14794* (K), *Coatam 2240* (K), *Gillett 13379* (K), *Graham 2240* (BM), *Greenway & Rawlins 9458* (K), *Greenway & Kanuri 13046* (K), *Irvin 110* (K), *Kassner*

465 (BM) & *697* (BM), Napper 2176 (K), *Scheffler 184* (BM), *Tweedie 4040* (K).
Somalia: *Gillett, Hemming, Watson & Julin 5202* (K), *Hemming & Deshmuukh 23* (K) & *63* (K).
Tanzania: *Batty 884* (K), *Bidgood & Vollesen 1263* (K), *Buchanan s.n. 1916* (BM), *Drummond & Hemsley 2336* (K), *Foulkner 4560* (K), *Harris 777* (K), *Leippert 5371* (EA), *Nevers & Chamley 3254* (K), *Peter 600083* (K), *Peterson 586* (EA), *Procter 3681* (K), *Richards 25677* (K).

***B. randii** S. Moore
Botswana: *Leach & Noel 74* (K, PRE, SRGH), *Plowes 7038* (PRE), *Reyneke 436* (K).
Transvaal: *Leistner 3186* (PRE), *Louw 2553* (PU), *Pauw 183* (PRU).
Zimbabwe: *Cecil 99* (K), *Eyles 88* (SRGH) & *3755* (BOL, K), *Goldsmith 48/58* (K, SRGH), *Leach 9714* (K, SRGH).

***B. rehmannii** C.B. Cl.
Transvaal: *Codd 3492* (PRE), *Meeuse 9575* (PRE), *Rehmann 4968* (K, type), Smuts & Gillett 2532 (PRE).

***B. repens** Nees
Natal: *Balkwill 186* (NU), *Balsinhas 2350* (PRE), *de Winter & Vahrmeijer 8508* (PRE), *Pooley 249* (NU).
Mozambique: *de Koning 7344* (K), *de Lemos & Balsinhas 173* (PRE), *Forbes s.n.* (K), *Gomes & Souza 1670* (K), *Junod 144* (PRE), *Leach & Bayliss 11809* (K), *Mogg 28481* (K, PRE) & *32190* (K, PRE), *Munch 259* (K), *Pole Evans 5889* (K), *Schäfer 7247* (K), *Schlechter 2133* (K).
Tanzania: *Greenway 5159* (K), *Wallace 799* (K), *Wingfield 4191* (K) & *4206* (K).
Kenya: *Graham 2102* (K, PRE), *Luke & Robertson 2598* (K), *Robertson & Luke 5973* (K), *Forbes 1871* (K, type).
Zanzibar & Pemba: *Faulkner 2615* (K) & *3367* (EA, K), *Forbes s.n.* (K, type), *Toms 94M* (K).

***B. rhodesiaca** Oberm.
Botswana: *Brown 8731* (K).
Zimbabwe: *Bingham 1206* (K), *Davies 2001* (K, PRE, SRGH) & *2062* (K), *Grosvenor 112* (K, SRGH), *Jarman B2-46* (K, SRGH), *Leach 11623* (BM, K, PRE), *Noel 1919* (K), *Raymond* (K), *Rogers 13401* (BOL, K, PRE, type), *Wild 6046* (K, SRGH).

***B. rigida** Willd. ex Nees
Cape: *Acocks 323* (PRE), *Barnard 828* (PRE), *Bryant J68* (PRE), *Dean 552* (J), *Esterhuysen 1004* (BOL, NBG, PRE), *Leistner 1708* (NBG, PRE), *Martin 957* (NBG, STE), *Müller 1282* (WIND), *Oliver & Steenkamp 6234* (PRE), *Schlieben 8769* (NBG, PRE, SRGH), *Thompson 3115* (PRE, STE), *van Wyk 5719* (PRE, PRU).
Botswana: *Moss & Jacobsen K35* (PRE), *Mott 1117* (SRGH), *Pole-Evans 2502* (PRE), *Skarpe S-289* (K, PRE, SRGH).
Namibia: *Barnard 156* (PRE, WIND), *Dinter 4358* (SAM), *Giess & van Vuuren 848* (PRE, SRGH, WIND), *Maggs 108* (WIND), *Pearson 4525* (BOL), *Seydel 3944* (WIND) & 4206, (SRGH), *van Vuuren & Giess 1105* (PRE, WIND), *van Wyk 8587a* (J), *Wilman 319* (PRE).
Orange Free State: *Anderson H 15* (PRE), *Herman 294* (PRE), *Henrici 3032* (PRE), *Sidey 358* (PRE).

***B. rotundifolia** Oberm.
Transvaal: *Acocks 16703* (PRE), *Balkwill 707* (E, NU), *Balkwill & Balkwill et al. 6144* (J) & *5809* (J), *Buitendag 809* (NBG, PRE, STE), *Ellery 356* (PRE), *Gerstner 5939* (PRE), *Henm 1139* (J), *Meeuse 9791* (PRE, SRGH), *Mogg sub PRE 58915* (PRE), *Rogers 23907* (BOL, PRE, type), *Scholes s.n.* (J), *Strey 3304* (SRGH), *van der Schyff 2418* (PRE).

***B. ruellioides** T. Anders.
Angola: *Teixeira s.n.* (PRE).
Ibidan: *Hepper 1331* (K), *Latilo & Daramda 28949* (K), *Daley 32281 (K).*
Nigeria: *Keay 37306* (K) & *21691* (K), *?Barker 932* (K, type) (K), *Savory & Keay 25009* (K), *Tuley 2126* (K), *Lo 1582* (K), *Meikle 1028* (K) & *787* (K), *Olorunfemi 55654* (K), *Chapman 5125* (K), *Hall 2008* (K).
Gold Coast: *Morton GC25157* (K), *Jaeger 3* (K), *Akpabla 1831 (K).*
Ghana: *Morton A1173a.*
Central African Republic: *Hepper 4089* (K), *Fay 6277* (K).
French Cameroons: *Letouzey 3625* (K).

***B. sacleuxii** Benoist
Tanzania: *Batty 171* (K), *Faulkner 2268* (K), *2337* (K), *Leach & Brunton* 10143 (K), *Oxtoby 13* (K), *Sacleux 545* (K, type), *Schlieben 6551* (K), *Tanner 2916* (K), *Taylor 881* (K), *Toms 198* (K), *Turrill s.n.* (K), *Vaughan 1364* (K), *Vollesen M.R.C. 2404* (K) & *4000* (K).

Zanzibar: *Benoist 2337* (K).

*B. salicifolia S. Moore

Angola: *Faulkner A405* (SRGH), *Pocock 604* (SAM, PRE).

Zambia: *Mitchell 26/4* (SRGH).

*B. saxatilis Oberm.

Natal: *Gush 16* (PRE), *Pooley 630* (NH, NU), *Ward 5660* (NU, PRE).

Swaziland: *Compton 28636* (NBG) & *31452* (NBG).

Transvaal: *Balkwill & Balkwill 6309* (J), *Balkwill & Balkwill et al. 5633* (J), *Codd 4257* (PRE), *Ellery 404* (PRE), *Fourie 1386* (PRE) & *2666* (PRE), *Krynauw 638* (PRE), *Maguire 1-49-36* (J), *Meeuse 9790* (PRE, SRGH), *10023* (PRE) & *10203* (PRE, holo), *Schrire 84* (PRE), *Smith 1900* (PRE, SRGH), *Taylor 1943* (PRE), *Theron 2654* (PRU), *van der Schyff 2294* (PRE), *van Jaarsveld 1212* (NBG, PRE), *Venter 1957* (SRGH).

B. scabriuscula Schwartz. Arabia

*B. scasselatii Chiov.

Somalia: *Friis, Vollesen & Abdisalam Sheith Hassan 5009* (K), *Paoli 373* (K, syntype).

*B. scindens Oberm.

Malawi: *Agnew 529* (SRGH).

Tanzania: *Faulkner 4416* (SRGH).

Transvaal: *Balkwill & Balkwill 4308* (J) & *6402* (J), *van Jaarsveld 1242* (NBG).

Zambia: *Fanshawe 7196* (SRGH).

Zimbabwe: *Biegel 2037* (K, SRGH), *Chase 309* (BM, K), *3695* (BM) & *7664* (K), *Davies 1153* (SRGH) & *2907* (K), *Eyles 3329* (BOL, SAM, SRGH) & *8611* (K), *Fisher 1532* (NU, PRE, SRGH), *Gilliland* (J, PRE), *Mavi 217* (K, SRGH), *Myers 714* (K), *Norlindh & Weimarck 4456* (K), *Rogers 13592* (BOL, PRE, type), *Savory 360* (PRE), *Teague 105* (BOL, NH), *Wild 1870* (K) & *5485* (K, PRE).

*B. senensis Klotzsch.

Angola: *Codd 7532* (K, SRGH).

Botswana: *Allen 75* (PRE, SRGH), *Camerik 238* (K), *Codd 7090* (PRE), *Glanville 618* (K), *Guy 26/64* (SRGH), *Long & Rae 253* (K), *Lugard 5a* (K), *MacDonald 10* (PRE, SRGH), *Moss 18606* (J), *Smith 3043* (PRE, SRGH), *Wild & Drummond 6877* (PRE, SRGH).

Malawi: *Brummitt 10010* (K, PRE, SRGH), *Moriarty 25* (K).

Mozambique: *Chase 2678* (SRGH), *de Aular Macêdo 5177* (PRE, SRGH), *Hornby 2731* (K, PRE), *Leach 9878* (K, PRE, SRGH), *Leach & Rutherford-Smith 10817* (K), *Peters s.n.* (K and a scrap at PRE, type), *Wild 256* (PRE).

Namibia: *Craven 1970* (WIND), *de Winter 3119* (PRE, WIND), *de Winter & Leistner 5885* (PRE, WIND), *Dinter 2646* (PRE, SAM), *Een s.n. 1879* (BM), *Giess & Leippert 7323* (NBG, PRE, WIND), *le Roux 901* (PRE, WIND), *Maguire 1690* (NBG), *Story 5274* (PRE, SRGH).

Transvaal: *Balkwill 165* (B, K, J, NU, PRE), *Balkwill & Balkwill 6331* (J), *Bruce 181* (PRE, SRGH), *Galpin 12233* (BOL, PRE, SRGH), *Rogers 19363* (J, PRE), *van Jaarsveld 1232* (NBG, SRGH), *Zambatis 923* (PRE).

Zambia: *Angus 1543* (K) & *2963* (K, SRGH), *Fanshawe 4524* (K), *Gilges 625* (K), *Greenway & Brennan 7962* (EA, K), *Leach & Rutherford-Smith 11091* (PRE, SRGH).

Zimbabwe: *Drummond 5744* (K), *Grosvenor 139* (SRGH), *Goldsmith 71/60* (K, SRGH), *Levy 51* (PRE, SRGH), *Rogers 13401a* (SAM), *Wild 5451* (SRGH).

*B. sepalosa C.B. Cl.

India: *Gibson 35* (K, type).

*B. separata Benoist

Madagascar: *Humbert 11217* (K, type).

*B. setigera Rendle

Kenya: *Bally 1891* (K), *Graham 2055* (K), *Heinz-Smith* (EA), *Hildebrandt 20026* (K), *Jeffrey K129* (K), *Moggridge 197* (K), *Napier 230* (K), *Thomas 4* (K), *Tweedie 3107* (K), *Verdcourt 3907* (EA, K).

Tanzania: *Batty 63* (K), *Frazier 1164* (K), *Hilderbrandt 1223* (K), *Jaeger 117* (K) & *152* (K), *Whyte s.n.* (K).

Zanzibar: *Faulkner 2894* (K) & *2895* (K), *Krause s.n.* (K), *Stuhlmann 471* (K) & *542* (K), *Vaughan 1403* (K).

*B. setigera Rendle var. brevispinosa ??

????: *Grote 4077* (K), *Heinsen 114* (K), *Hildebrandt 1223* (K), *Holtz 2041* (K), *Neumann 95* (K), *Schlieben 2409* (K).

*B. siamensis Craib
Malay Peninsula: *Corner 37807* (BM).
Thailand: *Bunchai 1345* (K), *Chin 3422* (K), *Corner 37807* (K), *Dee 93* (K), *Henderson 29150* (K), *Kerr 1415* (K, type) (K) & *2754* (K), *Garrett 95* (K), *Rock 1870* (K), *Sangkhachand 1060* (K), *Sørensen, Larsen & Hansen 5428* (E).
*B. smithii Rendle
Somalia: *Hildebrandt 857* (K), *Riva 953* (K).
*B. solitaria P.G. Meyer
Namibia: *Craven 26* (WIND), *Giess 9713* (PRE, WIND), *Giess & Barnard 8034* (NBG), *Giess, Volk & Bleissner 6181* (WIND), *Müller & Loutit 1199* (PRE, WIND).
*B. spinisepala E. A. Bruce
Ethiopia: *Ash 2802* (K), *Bally 9157* (K), *Gilbert & Jefford 4517* (K), *Gillett 14210* (K) & *14471* (K), *Haugen 1852* (K), *Mooney 5542* (K), *Puff & Ensermu K. 82/1224-3/3* (K).
Kenya: *Bally & Smith B14814* (K), *Carter & Stannard 339* (K), *Dowson 542* (K), *Greenway 13903* (PRE), *Napier 755* (K, type), *Nesbit-Evans 37* (K), *Oteke 8* (K), *Polhill 106* (K), *Sangai 832* (SRGH), *Thairu 40* (PRE), *Verdcourt 3010* (K, PRE) & *3012* (K, PRE).
Somalia: *Thulin & Bashir A. Muhammed 7108* (E).
Tanzania: *Greenway 4273* (K, PRE), *Richards 23727* (K) & *25664* (K).
*B. spinulosa Klotzsch.
??: *Fries 1346* (K, type - photo.)
Angola: *Gossweiler 2686* (BM), *3013* (BM), *3800* (BM), *3860* (BM) & *3977* (BM).
Botswana: *Harbor 6546* (BM).
Kenya: *Graham 2102* (BM).
Malawi: *Bellingham s.n. 1887* (BM), *Bidgood & Vollesen 2178* (K), *Blackmore, Patel & Msiye 805* (K), *Brummitt 10280* (K), *109481* (K) & *18411* (K), *Buchanan 122* (BM) & *244* (BM), Chapman & Chapman 7437 (K), *Chase 3888* (BM), *Goyder, Pope & Radcliffe-Smith 3247* (K), *Medley Wood 7091* (E), *Pawek 11721* (K), *Peters sub TM 29993* (PRE), *Salubenio & Patel* (K), *Webb s.n.* (BM).
Mozambique: *Faulkner 235* (K), *Hornby 3738* (K), *Kirk s.n.* (K) & *s.n.* (K), *Lemos & Macuacua 130* (K), *Meller s.n.* (K), *Pereira & Correia 2346* (J).
Namibia: *Baum 795* (BM).
Transvaal: *Froneman WFM 152* (J).
Zambia: *Angus 1285* (K), *Astle 5361* (K), *Fanshawe 3802* (K), *Robinson 273b* (K), *van Rensburg 2362* (K) & *2922* (K).
Zimbabwe: *Chase 334* (BM), *917* (BM) & *1680* (BM), *Chipunga 113* (K), *Davis 1333* (K), *Nyoni 381* (K), *Wild 7705* (K).
*B. splendens F.A. Bruce
Tanzania: *Bidgood, Mwasumbi & Vollesen 994* (K) & *1096* (K), *Burtt 2409* (K, type), *2457* (K), *3577* (K), *5093* (BM), *5136* & *5137* (BM, K), *Hooper & Townsend 1965* (K), *Koritschoner 2[illegible]* (K), *MacInnes 485* (BM).
*B. stellato-tomentosa S. Moore
Angola: *Anonymous 9290* (K), *Humbert 16512* (K), *Welwitsch 5095* (K, type) & *5165* (K, type).
*B. stelligera Lindau
Somalia: *Allen & Elmi 310* (E).
*B. steudneri C.B. Cl.
Ethiopia: *Friis, Mesfin & Vollesen 3141* (K), *Puff & Ensemu 8212/6-3/3* (K).
Oman: *Miller 2776* (K).
Sudan: *Andrews 209* (K), *Braun 1334* (K).
*B. stimulans E. Mey. ex Nees
Cape: *Acocks 14557* (PRE), *Bolus 7894* (BOL) & *11616* (BOL), *Drège s.n.* (K, type), *Novellie 286* (PRE), *Pillans 16464* (BOL), *Thoday & Delf 67* (STE), *van Brede 4630* (STE).
*B. stocksii T. Anders.
India: *Gamble 20938* (K) & *21163* (K), *Stock s.n.* (K, type).
*B. strigosa Willd.
Bhutan: *Bernardi 2075A* (K), *Dickson 6587* (K), *Grierson & Long 3382* (E, K), *Haines 2754* (K), *Hara, Kurosawa, Murata & Togashi 6303645* (K), *Jenkins 329* (K), *Keenan, Tun Aung & Rule 1532* (K),

Lace 6295 (K), *Meebold 8024* (K), *Rastler 389* (K).

India: *Beddome s.n.* (K), *Bourne 2317* (K) & *3379* (K), *Gamble 13704* (K), *14036* (K), *16007* (K) & *15903* (K), *Lace 2478* (E), *Law 37* (K), *Ponigrah 5472* (K), *Ritchie 582* (K), *Rottler s.n.* (K), *Stocks s.n.* (K) & *146* (K), *Talbot 1625* (K).

Malay Islands: *Robinson s.n.* (BM).

Sikkim: *Cooper 4970* (K), *Mooney 601* (K) & *2487* (K), *Treutler 122* (K), *van der Maesen 3953* (K).

Thailand: *Collins 1465* (K), *Collins 813* (K), *Du 348* (K), *Kerr* 822 *(BM), 2050* (BM, K), *9091* (K), *19831* (K), & *19598* (K), *Lakshnakara 910* (K), *Marcan 2355* (BM), *Nimanang & Phusomsaeng 296* (K), *Put 2396* (K) & *4366* (K), *Put 4274* (K), *Shimuzu, Hutch & Chaiglam, Larsen, Santisuk & Warneke, Marcan 2355* (K).

***B. stuhlmanii** Lindau

Kenya: *Chandler 2069* (K), *Brown 368* (K), *Glover, Gwynne & Samuel 1589* (K), *Hepper & Jaeger 6670* (K), *Perclue & Kibuwa 9308* (K).

Tanzania: *Congdon 196* (K), *200* (K) & *285* (K), *Lovett & Congdon 3195* (K), *Holst 8736 (K).*

Uganda: *Harrington 338* (EA).

***B. subglobosa** S. Moore

Angola: *Foulkner A405* (K), *Gossweiler 3131* (K) & 3139 (BM).

Zambia: *Bands 752* (K), *Fanshawe 6211* (K), *Mitchell 26/04* (K), *Richards 22215* (K).

***B. submollis** Lindau

Ethiopia: *Fritis, Mesfin & Vollesen 3238* (K), *Gilbert 1600* (K), *Gilbert, Ensermu & Vollesen 7721* (K), *Kiman 44* (PRE), *Mesfin, Sebsebe & Vollesen 4080* (K), *Napper 1237* (PRE), *Robertson 2073* (PRE).

Kenya: *Bally & Smith 14739* (K), *Carter & Stannard 486* (K), *Gillett 14125* (K), *13418* (K) & *12646* (K), *Hepper & Jaeger 6617* (K), *Kerfoot 7559* (K), *Lye 9087* (K), Tweedie 2311 (K).

Tanzania: *Greenway & Polhill 11458* (K), *Kassner 283* (BM), *Mwasumbi 10215* (K), *Richards 24985* (K) & 24234 (K), *Ruffe 1377* (K), *Schlieben 2517* (BM), *Tanner 844* (K), *Volkens 314* (K, type), *Whyte s.n. 1902* (BM).

Uganda: *Verdcourt 811* (K), *Wilson 991* (K).

***B. sunzuana** Brummitt & Seyani

Zambia: *Burtt 6131* (K), *Lawton 213* (K), *Richards 15077* (K), *16369* (K, type) & *21380* (K).

***B. swynnertonii** S. Moore

Mozambique: *Dümmer 80* (BM), *Swynnerton 1958* (BM, type).

***B. taitensis** S. Moore

Angola: *Bamps & Martins 4351* (K), *Barbosa & Correia 9135* (K, PRE), *Levy 18* (PRE), *Pearson 2123* (K), *2469* (K), *2531* (K) & *2828* (K), *Teixeira 2378* (PRE), *Welwitsch 5119* (BM).

Kenya: *Bally 1761* (K), *Gilbert 6127* (K), *Gilbert & Thulin 1726* (K), *Gillett & Gachathi 20489* (K), *Greenway & Kanuri 13070* (K, PRE), *Hucks 371* (K), *Irwin 409* (K, PRE), *Jacobsen 3930* (549) (PRE), *Kassner 600* (BM, K, type, PRE photo), *Kimani 38* (K, PRE), *Linder 3662* (PRE), *Napper 1238* (K, PRE) & *1948* (K), *Polhill & Paulo 935* (PRE), *Raymond 259* (PRE), *Tweedie 2389* (K), *Verdcourt 5309* (K).

Namibia: *Merxmüller & Giess 30442* (PRE).

Tanzania: *Thulin & Mhoro 557* (K).

Zambia: *Anton-Smith sub SRGH 211772* (SRGH), *Lawton 1071* (K), *Leach 11624* (K), *West 2912* (K), *White 2361* (K), *Wild 5430* (K).

Zimbabwe: *Dawes 2003A* (K), *Jarman B2-49* (K), *Levy 18* (BM), *Plowes 1800* (K), *Raymond 259* (K), *Rogers 13239* (BM, BOL, type of *B. rogersii*), *Wild 3450* (PRE, SRGH).

***B. talbotii** S. Moore

Nigeria: *Gossweiler 6530* (BM), *Talbot 1396* (BM, K, type).

***B. tetracantha** Balf. f.

Socotra: *Bailey Balfour 605* (K), *Bent s.n. (1897)* (K), *Miller, Bazara'a, Guarino & Kassim M10252* (E), *Miller, Guarino, Obadi, Hassan & Mohammed M8546* (K), *Popov GP/50/94* (BM) & *GP/50/282* (BM), *Schweinfurth 334* (K, type), *Smith & Lavranos 77* (K), *Virgo S.40* (K).

Yemen: *Miller, Bazara'a, Guarino & Kassim M 10252* (E).

***B. tetraglochin** Milne-Redhead

Sudan: *Aylmar 53* (K), *Dandy 322* (K, type), *Jackson 412* (K).

***B. tomentosa** Roth.

Ceylon: *Jayasuriya 102* (K), *Jayasuriya & Sumithraarachchi 1615* (K, MO) & *1617* (K), *Jayasurtya,*

Dassanayake & Balasubramaniam 671 (K).

India: *Anonymous 9760* (K), *Browne 778* (K), *Dalzell s.n.* (K), *Foulkes s.n.* (K), *Gamble 10978* (K) & *11931* (K), *Gardner s.n.* (K), *Joppuapaoli 28* (K), *Wight s.n.* (E, K), *1900* (K), *1960* (E, K, [illegible]), *2212* (K) & *2639/1837* (K).

*B. transvaalensis Oberm.

Transvaal: *Balkwill 1628* (NU), *Balkwill & Balkwill 6452* (J), *Codd & Dyer 4684* (PRE), *Froneman WFM 148* (J), *Meeuse 9485* (PRE), *Rogers sub TM 20321* (PRE, type).

Zimbabwe: *Drummond 6128* (K, SRGH), *Myers 620* (K).

*B. trispinosa Vahl

Arabia: *Collenette 1146* (K), *154* (K), *365* (K), *586* (K) & *1146* (K), *Trott 1629* (K).

Ethiopia: *Bally 7101* (EA, K), *Deflers 1036* (K), *Mooney 8088* (K), *Petit s.n.* (K), *Quartin-Dillon et Petit 13* (K), *Schimper 14* (K), *1008* (K) & *1922* (K, type), *Schweinfurth & Riva 1407* (K) & *1666* (K), *Steudner 1504* (K).

Tanzania: *Braun 1206* (K), *Holst 3213* (K), *Stuhlmann 8530* (K).

Yemen: *Barbey 303* (K), *Trott 1065* (K), *Wood 2233* (K), *2621* (K), *2684* (K), *2868* (K) & *3039* (E, K).

*B. ukamensis Lindau

Tanzania: *Harris 3159* (EA, K), *Jaasund 2087* (EA).

*B. usambarica Lindau

Kenya: *Faden & Faden 74/1157* (K), *Jaasund 2089* (EA), ***& Robertson 6558* (K).

Tanzania: *Archbold 3404* (K), *Faulkner 4130* (K) & *4145* (K) & *4374* (K), *Greenway & Kanuri 15116* (K), *Holst 3165* (K, type), *Pócs 88057/G* (K) & *88058/C* (K), *Vollesen 3395* (K).

*B. variabilis Oberm.

Zambia: *Fanshawe 5722* (K).

Zimbabwe: *Allen 406* (PRE), *Rogers 13309* (BOL, type).

*B. variabilis Robyns (?nomen nudum)

Congo: *Robyns 1715* (K).

*B. ventricosa Hochst. ex Nees

Belgian Congo: *Germain 4426* (K), *Ghesquiere 3846* (K), *Hendelo 3251* (PRE), *Humbert 7888* (K), *Smuts 2204* (K), *Stauffer 86* (PRE).

Burundi: *Burtt 3230* (K), *Raynal 20633* (K), *Reekmans 6771* (K) & *9451* (K).

Ethiopia: *Alberts 61200* (K), *Amshoff 1970* (SRGH), *Ash 16* (K), *Boulos 11390* (K), *Burger 1272* (K) & *2340* (K), *Chojnack in Mooney 8158* (K), *Friis, Getachew Aweke, Rasmussen & Vollesen 1714* (K), *Friis, Gilbert, Rasmussen & Vollesen 1130* (K), *Meyer 8716* (K), *Mooney 5418* (K), *Pich-Sermolli 1518* (K), *Robertson 1205 (K)*, *Schimper 42* (K, type) & *1840* (K, type), *Schweinfurth & Riva 1346* (K), *Scott 195* (K), *Steudner 1511* (K), *Tekleh Hagos 196* (K).

Kenya: *Bally 5594* (K) & *8523* (K), *Gillett 18780* (K), *Graham 776* (PRE) & *2140* (K), *Granvik 81* (PRE), *Kerfoot 1997* (K), *Mayor 61* (K), *Newbould 3091* (K), *Oteke 67* (K), *Paulo 532* (PRE) & *1089* (K), *Tweedie 297* (K), *879* (K) & *3744* (SRGH), *Williams 35* (K).

Rwanda: *Michel 5480* (K), *Stauffer 86* (K).

Somalia: *Gillett 511A* (K), *Godding 4B* (K) & *124* (K).

Sudan: *Broun 1104* (K) & *1289* (K), *Friis & Vollesen 9f59* (K), *Kosper 182* (K), *Lankester s.n.* (K).

Tanzania: *Archibold 2548* (K), *Greenway & Kanuri 12396* (K), *Greenway, Myles Turner & Owen 10312* (EA), *Leippert 5879* (K) & *5972* (EA), *Nevers & Charnley 3416* (MO), *Procter 972* (K).

Uganda: *Brown 88* (K), *Eggeling 2389* (K), *Lye 1558* (K), *Snowden 63* (K), *156* (K) & *955* (K), *Thomas 2281* (K) & *3191* (K).

Yemen: *Hepper 5851* (K), *King 59* (E), *Miller 548* (K) & *188* (K), *Radcliffe-Smith & Henchie 4481* (K), *Wood 2259* (E, K), *1321* (K) & 2993 (K).

*B. verdickii Wildem.

?Tropical Africa: *Verdick 716* (K).

*B. vestita T. Anders.

Ceylon: *C.P. 2004* (K), *Walker s.n.* (K, type).

*B. villosa S. Moore

Angola: *Dawe 1921* (K), *Gossweiler 1078* (K), *Welwitsch 5071* (K, type).

Belgian Congo: *Devred 1208* (K).

British Cameroons: *Hepper 1578* (K).

Cameroon: *Bauer 141* (K), *de Wilde 4546* (K), *Letouzey 11184* (K) & *13130* (K), *Sanford 5596* (K).
Central African Republic: *le Testu 3509* (K), *Tisserant 297* (K).
Ghana: *Jenik & Hall 1176* (K), *Morton K992* (K).
Nigeria: *Barren-Poole 206* (K), *Coombe 61* (K), *Daramola 62455* (K), *Garland 391* (K), *McGregor 406* (K), *Peter & Tuley 43* (K).

***B. villosa** T. Anders.
Nigeria (+), Cameroon, Congo, Ghana, Angola:

***B. vin. jefolia** Baker
Madagascar: *Baron 3372* (K) & *5552* (K, type), *Dorr 3921* (K), *du Puy, du Puy & Rafamantanantsoa MB187* (K), *Kerandren 372* (K), *Perrier 16159* (K), *Phillipson 1980* (K).

***B. violacea** Hainz
Namibia: *Schwerdtfeger 2/71* (WIND).

***B. virgula** C.B. Cl.
Botswana: *Reyneke 67* (PRE).
South Africa: *Holub s.n.* (K, type).
Transvaal: *Codd 8871* (SRGH), *Galpin 514M* (NBG, PRE, SRGH), *Harbor 17014* (PRE).

***B. vix-dentata** C.B. Cl.
Sudan: *Dandy 534* (K), *Friis & Vollesen 644* (K).
Tanzania: *Wilson a?36* (K).
Uganda: *Langdale-Brown 1685* (K), *Lind 2112* (K), *Synott 1381* (K), *Wilson 37* (K, type).

***B. volkensii** Lindau
Ethiopia: *Friis, Gilbert & Vollesen 3971* (K), *Friis, Hounde & Jacobsen 237* (K), *Mesfin & Kagrew 2347* (K), *Meyer 8824* (K), *Mooney 6873* (K) & *5929* (K), *Palmer 63A* (K), *Puff & Ensermu 8208.18-7/3* (K), *Siegenthaler X-52* (K).
Kenya: *Bally & Smith B14815* (K), *Gilbert, Kibui & Mungai 5532-5615* (K), *Haeper & Jaeger 6641* (K), *Oteke 19* (K), *Richards 25527* (K), *Verdcourt 1823* (K), *Wapier 1080* (K).
Tanzania: *Davies 1061* (K), *Dingle 2544D* (K), *Greenway 7483* (K) & *11801* (EA), *Greenway & Kanuri 11801* (EA, K), *Haarer 516* (K), *Newbould & Jefford 1159* (K), *Richards 24240* (K), *Volkens 380* (K, type).

***B. waggana** Rendle
Ethiopia: *Friis, Mesfin T. & Vollesen 3002* (K).
Somalia: *Bally B9954* (EA) & *10231a* (K), *Bally & Melville 15292* (K), *Gillett, Hemming & Watson 22097* (K), *22257* (K) & *23592* (K), *Glover & Gilliland 410* (K), *Hemming & Watson 3309* (K), *Kuchar 17068* (K), *Lort-Phillips 6/95* (K), *Newbould 711* (K), *Thomas 79a* (K), *Thulin, Hedren & Abdi M. Dahir 7420* (K), *7471* (K), *7589* (K) & *7691* (K), *Virgo 34* (K), *Wieland 4671* (MO), *Wood 5/72/99* (K).

***B. welwitschii** S. Moore
Angola: *Gossweiler 11975* (BM), *Welwitsch 5091* (K).
Zambia: *Mutimushi 3036* (K).

***B. whytei** S. Moore
Kenya: *Drummond & Hemsley 3923* (K), *Luke 2907* (K), *Whyte s.n.* (K) & *s.n. 1902* (BM).
Tanzania: *Schlieben 2676* (K).

***B. wilmsiana** Lindau
Transvaal: *Balkwill, Balkwill & Kidger 8086* (J), *Brown & Shapiro 437* (SRGH), *Galpin 863* (BOL, PRE, SAM, syntype) & *12249* (BOL, PRE), *Kluge 2433* (NBG, PRE), *Wilms 1217* (E, K, PRE, syntype).

APPENDIX 3

Data matrices used for cladistic analyses at the sectional level in *Barleria*

Matrix 1: Character set and scores used in Analysis 1

Taxon	Scores for characters 0 1 2 3 4 5 6 7 8 9
Outgroup	0 0 0 0 0 0 0 0 - -
Barleria	0 0 0 0 1 0 1 0 - -
Barleriopsis	0 0 0 0 1 0 0 0 - -
Barlerites	1 0 0 1 0 1 0 0 - -
Barlerianthus	1 1 0 0 1 0 0 0 - -
Somalia	1 1 1 1 0 1 0 0 - -
Prionitis	1 1 1 1 0 0 1 1 - -
Stellatohirtae	1 1 0 1 0 1 1 1 - -

- denotes a character not used in the analysis

Matrix 2: Character set and scores used in Analysis 2

Taxon	Scores for characters 0 1 2 3 4 5 6 7 8 9
Outgroup	0 0 0 0 0 0 - 0 0 -
Barleria	0 0 0 0 1 0 - 0 0 -
Barleriopsis	0 0 0 0 1 0 - 0 0 -
Barlerites	1 0 0 1 0 0 - 0 1 -
Barlerianthus	1 1 0 0 0 1 - 0 0 -
Somalia	1 1 1 1 0 1 - 0 0 -
Prionitis	1 1 1 1 0 0 - 1 0 -
Stellatohirtae	1 1 0 1 0 1 - 1 1 -

- denotes a character not used in the analysis

Matrix 3: Character set and scores used in Analysis 3

Taxon	Scores for characters 0 1 2 3 4 5 6 7 8 9
Outgroup	0 0 0 0 0 0 - 0 0 0
Barleria	0 0 0 0 1 0 - 0 0 0
Barleriopsis	0 0 0 0 1 0 - 0 0 0
Barlerites	1 0 0 1 0 0 - 0 1 1
Barlerianthus	1 1 0 0 0 1 - 0 0 0
Somalia	1 1 1 1 0 0 - 0 0 0
Prionitis	1 1 1 1 0 0 - 1 0 0
Stellatohirtae	1 1 0 1 0 0 - 1 1 1

- denotes a character not used in the analysis

Matrix 4: Character set and scores used in Analysis 4

Taxon	Scores for characters 0 1 2 3 4 5 6 7 8 9
Outgroup	0 0 0 0 0 0 0 0 0 0
Barleria	0 0 0 0 1 0 0 0 0 0
Barleriopsis	0 0 0 0 1 0 0 0 0 0
Barlerites	1 0 0 1 0 0 1 0 1 1
Barlerianthus	1 1 0 0 0 1 0 0 0 0
Somalia	1 1 1 1 0 1 0 0 0 0
Prionitis	1 1 1 1 0 0 1 1 0 0
Stellatohirtae	1 1 0 1 0 0 1 1 1 1

Matrix 5: Character set and scores used in analysis 5

Taxon	Scores for characters 0 1 2 3 4 5 6 7 8 9
Outgroup	0 0 0 0 0 0 0 - 0 0
Barleria	0 0 0 0 1 0 0 - 0 0
Barleriopsis	0 0 0 0 1 0 0 - 0 0
Barlerites	1 1 1 1 0 0 0 - 1 1
Barlerianthus	1 1 0 0 0 1 0 - 0 0
Somalia	1 1 1 1 0 1 0 - 0 0
Prionitis	1 1 1 1 0 0 1 - 0 0
Stellatohirtae	1 1 0 0 0 0 1 - 1 1

- denotes a character not used in the analysis

Matrix 6: Character set and scores used in Analysis 6

Taxon	Scores for characters 0 1 2 3a 4 5 6 7 8 9
Outgroup	0 0 0 0 0 0 0 0 0 0
Barleria	0 0 0 0 1 0 0 0 0 0
Barleriopsis	0 0 0 0 1 0 0 0 0 0
Barlerites	1 1 0 1 0 0 0 0 1 1
Barlerianthus	1 1 0 0 0 1 0 0 0 0
Somalia	1 1 1 1 0 1 0 0 0 0
Prionitis	1 1 1 1 0 0 1 1 0 0
Stellatohirtae	1 1 0 0 0 0 1 1 1 1

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