# Systematic studies of the genus *Lebeckia* and related genera of the tribe Crotalarieae (Fabaceae)

*by*

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“Success is not the key to happiness. Happiness is the key to success. If you love what you are doing, you will be successful.”

Albert Schweitzer

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# SUMMARY

The tribe Crotalarieae (Fabaceae) is a large and diverse group of papilionoid legumes that largely occur in Africa. A systematic study of generic relationships within the tribe was undertaken using nucleotide sequences from the internal transcribed spacer (ITS) of nuclear ribosomal DNA, the plastid gene *rbcL* and morphological data. The Crotalarieae are strongly supported to be monophyletic and sister to the tribe Genisteae. *Lebeckia*, *Lotononis* and *Wiborgia* are all polyphyletic in the molecular analyses and morphological data support the division of *Lebeckia* into three more natural genera (one of which includes the monotypic North African *Spartidium*). Four major lineages were identified within the tribe based on sequence data: the "Cape group", comprising *Aspalathus*, *Lebeckia*, *Rafnia*, *Spartidium* and *Wiborgia*; the *Lotononis* group, comprising *Lotononis* pro parte, *Pearsonia*, *Robynsiophyton* and *Rothia*; a group comprising *Lotononis* section *Leobordea*, *L.* section *Listia,* and allies; and the *Crotalaria* group, comprising *Bolusia*, *Crotalaria* and *Lotononis hirsuta* (*Lotononis* section *Euchlora*). Morphological analysis yielded a similar topology, except that *Lotononis* is monophyletic if *L. hirsuta* is excluded. When the molecular and morphological data sets are combined, the same major clades are retrieved as in the molecular analysis, with the notable exception that *Lotononis* and *Lebeckia* senso stricto are supported as monophyletic.

The study showed the need to reinstate the genus *Calobota* and to describe a new genus (*Wiborgiella*). Evidence from ITS and *rbcL* data clearly showed that the genus *Lebeckia* is not monophyletic. These analyses, along with morphological and anatomical data, showed that the genus should be divided into three genera: (1) *Lebeckia* senso stricto (*L.* section *Lebeckia*); (2) *Calobota* [*L.* section *Calobota* and *L.* section *Stiza*] including the monotypic, North African genus *Spartidium*; (3) a new genus, *Wiborgiella* [*L.* section *Viborgioides*, together with *L. inflata*, *L. mucronata* and *Wiborgia humilis*]. Taxonomic revisions of the genera *Calobota* and *Wiborgiella* are presented. Sixteen species are recognized in *Calobota*, one of which is described as new, and nine species in *Wiborgiella*, two of which are described as new. The anatomy of the leaves, stems and fruit walls of the two genera revealed important characters to distinguish these genera from each other and from other genera of the tribe Crotalarieae. Detailed taxonomic studies of these genera are presented, including keys to the species, descriptions, known geographical distributions, phylogenetic relationships and illustrations.

*Lotononis* is a large and taxonomically complex genus of the Crotalarieae, with the majority of its species occurring within South Africa. In this part of the study, sequence and morphological data of the rare *Lotononis macrocarpa* was added to existing data matrices and these were re-analyzed. Molecular systematic data (nrITS and *rbcL*) indicated that *Lotononis* is polyphyletic, with *Lotononis* section *Euchlora* as sister to *Bolusia* and *Crotalaria* and with *L. macrocarpa* close to the “Cape group” of the Crotalarieae. As a result, the genus *Euchlora* is here reinstated and the new genus *Ezoloba* is described herein to accommodate the anomalous *L. macrocarpa*. *Ezoloba* is distinct in its 5+5 anther configuration, exceptionally large fruit, paired stipules and presence of bracteoles. Within the remaining species of *Lotononis,* both combined and separate analyses of the morphological and sequence data sets revealed three strongly supported clades corresponding largely to clades recovered in previous cladistic analyses based on morphological, chemical and cytological data. These are here recognised at the generic level as *Lotononis* s.s., *Leobordea* and *Listia*. Characters supporting these generic re-alignments are discussed and a key to the 16 genera now recognized in the tribe Crotalarieae is presented.

The monotypic genus *Robynsiophyton* is revised. *Robynsiophyton vanderystii* occurs in central and southern tropical Africa and is unique in the reduction of the androecium to nine stamens and five fertile anthers. It is morphologically similar to *Pearsonia* and *Rothia* and sister to the latter based on morphological and DNA sequence data. A revision of the genus is presented, including illustrations of vegetative and reproductive features and distributional information.

*Rothia* is a genus of papilionoid legumes that consists of two species, *R. indica* and *R. hirsuta*. The genus is a member of the tribe Crotalarieae and is widely distributed in Africa, Asia and Australia. Molecular systematic studies have shown the genus to be closely related to *Robynsiophyton* and *Pearsonia*, but it is easily distinguished from these by its 10 small, rounded anthers and sub-equally lobed calyx (as opposed to the large, elongate anthers of *Pearsonia* or the nine stamens of *Robynsiophyton*). These three genera share characters such as uniform anthers, straight styles and the presence of angelate esters of lupanine-type alkaloids. The leaf and fruit anatomy of *Rothia* and *Robynsiophyton* were also studied but revealed no informative differences. Both genera have dorsiventral leaves (i.e. clearly differentiated into palisade parenchyma adaxially and spongy parenchyma abaxially) with mucilage cells in the epidermis and thin-walled fruit. A taxonomic revision of *Rothia* is presented, including a key to the species, correct nomenclature, descriptions, illustrations and distribution maps.

The patterns of evolution of 18 morphological, chemical and cytological characters within the Crotalarieae were investigated by reconstructing these onto the minimal length trees from the combined molecular and combined molecular/morphological analyses. This highlighted the taxonomic complexity of the crotalarioid genera, the extreme overlap of characters between genera, convergent patterns in some characters and the value of informative combinations of characters to circumscribe genera in the tribe in the absence of diagnostically useful generic apomorphies.

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# CHAPTER 1: GENERAL INTRODUCTION AND OBJECTIVES OF THE STUDY

## 1.1 GENERAL INTRODUCTION

Fabaceae or Leguminosae, the third largest flowering plant family, comprises ca. 727 genera and 19,235 species (Lewis et al. 2005). Its members have a cosmopolitan distribution and form an important component of various vegetation types across the world (Lewis et al. 2005). Lewis et al. (2005) presents a useful synthesis of the literature on the family and also the currently recognized genera. Molecular systematic studies over many years have added to our understanding of relationships within the family and especially within the Papilionoideae (e.g. Käss and Wink 1995, 1996, 1997; Crisp et al. 2000; Doyle et al. 2000; Wojciechowski et al. 2000; Kajita et al. 2001; Pennington et al. 2001; Wink 2003; Wink and Mohamed 2003; Wojciechowski et al. 2004).

In Africa the Fabaceae are represented by several tribes. The Papilionoideae are especially well-represented, in particular the genistoid legumes (*sensu* Polhill 1981; redefined by Crisp et al. 2000), the majority of which are contained in the tribes Crotalarieae (Benth.) Hutch., Genisteae (Bronn) Dumort. and Podalyrieae Benth. The Genisteae are widespread with species in Africa, Europe, the Americas, the Mediterranean and Macaronesia (Polhill and Van Wyk 2005). The Podalyrieae (with the exception of most species of *Calpurnia* and *Podalyria velutina* Burch. ex Benth.) are endemic to the Cape Floristic Region of South Africa (CFR; Schutte and Van Wyk

1998) and the Crotalarieae are sub-endemic to Africa, with species of *Crotalaria*, *Lotononis*, and *Rothia* extending to other continents (Van Wyk 1991a).

The tribe Crotalarieae is a large and diverse group of 11 genera and ca. 1,204 species (Van Wyk 2005). Polhill (1976, 1981) in his treatment of the tribe included 16 genera. However, in the latest treatment of the group by Van Wyk and Schutte (1995) the genera of the *Argyrolobium* group (*Dichilus*, *Melolobium* and *Polhillia*) were transferred to Genisteae and only 11 genera included in the Crotalarieae. To date a comprehensive molecular systematic study of the Crotalarieae has not been completed. Previous molecular studies confirmed the sister relationship of the tribe to the Genisteae, but no complete generic-level molecular phylogeny for the tribe exists. Such a phylogeny would provide insight into the monophyly of the genera in the tribe as well as their relationships to each other. Most of the genera have been revised in recent years (*Aspalathus*, Dahlgren 1988; *Bolusia*, Van Wyk 2003a, Van Wyk et al. submitted; *Crotalaria*, Polhill 1982; *Lotononis*, Van Wyk 1991b; *Pearsonia*, Polhill 1974; *Rafnia*, Campbell and Van Wyk 2001; *Wiborgia*, Dahlgren 1975), but some uncertainties still remain regarding the monophyly of some of the genera, especially *Lebeckia* and *Lotononis*. *Lebeckia*, *Robynsiophyton*, *Rothia* and *Spartidium* are the only genera that lack formal revisions. *Spartidium* has been included in the tribe Crotalarieae, but its tribal affinity and relationships have been uncertain for some time (Polhill 1976; Van Wyk 1991a).

*Lebeckia* was last revised in 1862 by Harvey in the Flora Capensis. It is a diverse group of species with high levels of morphological variation and the generic concept (broadened by Bentham in 1844 to include several crotalarioid genera) needs to be re-evaluated. Taxonomic and systematic studies of the type section of *Lebeckia* have recently been completed (Le Roux, 2006; Le Roux and Van Wyk 2007; Le Roux and Van Wyk 2008; Le Roux and Van Wyk 2009), but the other sections of the genus and their relationship to other genera in the tribe have yet to be ascertained. When this has been completed, a treatment of all the genera in the tribe Crotalarieae will have been completed and formally implemented taxonomically.

## 1.2 OBJECTIVES OF THE STUDY

This project was aimed at a multi-disciplinary study of the genus *Lebeckia* and related genera of the tribe Crotalarieae. Relationships within the Crotalarieae are explored using DNA sequences (ITS and *rbcL*) and morphological data and the monophyly of the various genera is assessed. A literature review of chemical characters (mainly alkaloids) was needed in order to evaluate the congruence between molecular, morphological and chemical data and how these patterns should be interpreted within the context of new generic and suprageneric concepts. The DNA study was also aimed at confirming the suspected polyphyly of *Lebeckia* and *Lotononis* (as currently circumscribed) and at improving generic circumscriptions. The aim was to propose and formalize new generic concepts for *Lebeckia* s.l. and *Lotononis* s.l. in order to ensure that all of the resultant genera are monophyletic. Part of the objectives was also to explore infrageneric relationships within the newly circumscribed lebeckioid genera through cladistic analyses based on morphological and anatomical data in addition to the DNA sequence data. The project aims included formal taxonomic revisions of the new genera derived from *Lebeckia* s.l., as well as the largely unstudied *Spartidium, Robynsiophyton* and *Rothia.* The overall objective was therefore to not only propose a new generic classification system for the tribe but to actually formalize all the proposed changes in order to eliminate uncertainty and to ensure long term nomenclatural stability.

# CHAPTER 2: MATERIALS AND METHODS

Authorities for scientific plant names (according to Brummit and Powell 1992) are given in Appendix A3 or in the taxonomic revisions (Chapters 6, 7, 9, 10) and are not repeated elsewhere.

## 2.1 MORPHOLOGY

Morphological data were obtained from herbarium specimens as well as fresh material of various taxa of the Crotalarieae collected during field excursions. During these collecting trips taxa were studied in their natural environment and fresh material collected. These were preserved in FAA (Sass 1958; formaldehyde: acetic acid: 96% alcohol: water; 10:5:50:35) and silica (Chase and Hill 1991). Observations made in the field provided invaluable insight into species and generic concepts. Photographs of habit and flowers or fruit were taken and all specimens collected are housed in the University of Johannesburg Herbarium (JRAU). Specimens of *Calobota* and *Wiborgiella* from the following herbaria were studied either on site or on loan: BM, BOL, GRA, J, JRAU, K, NBG (including SAM and STE), P, PRE, S, SBT, UPS and WIND (abbreviations according to Holmgren et al., 1990). Online photographs of the collections of B, M and Z were also studied. Specimens from BM, K and PRE along with digital images of critical specimens obtained from BR and LISC were studied for the revision of *Robynsiophyton*. Morphological characters of *Rothia* were assessed using specimens from BM, BOL, K, MEL, NBG (including SAM), PRE, S and UPS. The material studied for the revisions of *Calobota*, *Robynsiophyton*, *Rothia* and *Wiborgiella* were arranged according to geographical distribution so that the relevant measurements and observations could be done within several geographical populations. At least three measurements per specimen were done where possible.

Data on the distribution of the various species were gathered from the herbarium material, field notes and from Leistner and Morris (1976; for southern African taxa). These data are presented as maps. The specimen citation system used in the "specimens examined" sections of the revisions is that of Edwards and Leistner (1971), i.e. the quarter degree reference system. Additional information on flowering and fruiting phenology, habitat and habit were also noted.

Mature flowers from material fixed in FAA or flowers re-hydrated from rich herbarium specimens were dissected and mounted in glycerol. Specimens from which dissections were made are listed in Appendix A1. Floral characters recorded were: pedicel length, length of the bracts and bracteoles, flower length, length of the calyx, length of the calyx tube, depth of the upper, lateral and lower sinuses of the calyx, width of the upper, lower and lateral calyx lobes, length and width of the standard-, wing- and keel petals and the length of the claws of each petal. The measurements done on the vegetative and reproductive parts are illustrated in Fig. 2.1. Drawings of vegetative and reproductive structures were done using a stereoscope (WILD M3Z) with a camera *lucida* attachment. All the drawings were done by myself.

## 2.2 ANATOMY

For anatomical studies, material was fixed in FAA or dried material was re-hydrated by briefly boiling in distilled water and then fixed in FAA for 24 hours. The method of Feder and O'Brien (1968) for embedding in glycol methacrylate (GMA) was used, except that the final infiltration in GMA was done for a minimum of five days. Sections were stained according to the periodic acid Schiff/toluidine blue (PAS/TB) staining method (Feder and O'Brien 1968) and mounted. Voucher information for the material used in the anatomical studies are listed in Appendix A2. Photographs were taken with a JVC KY-F1030 digital camera.

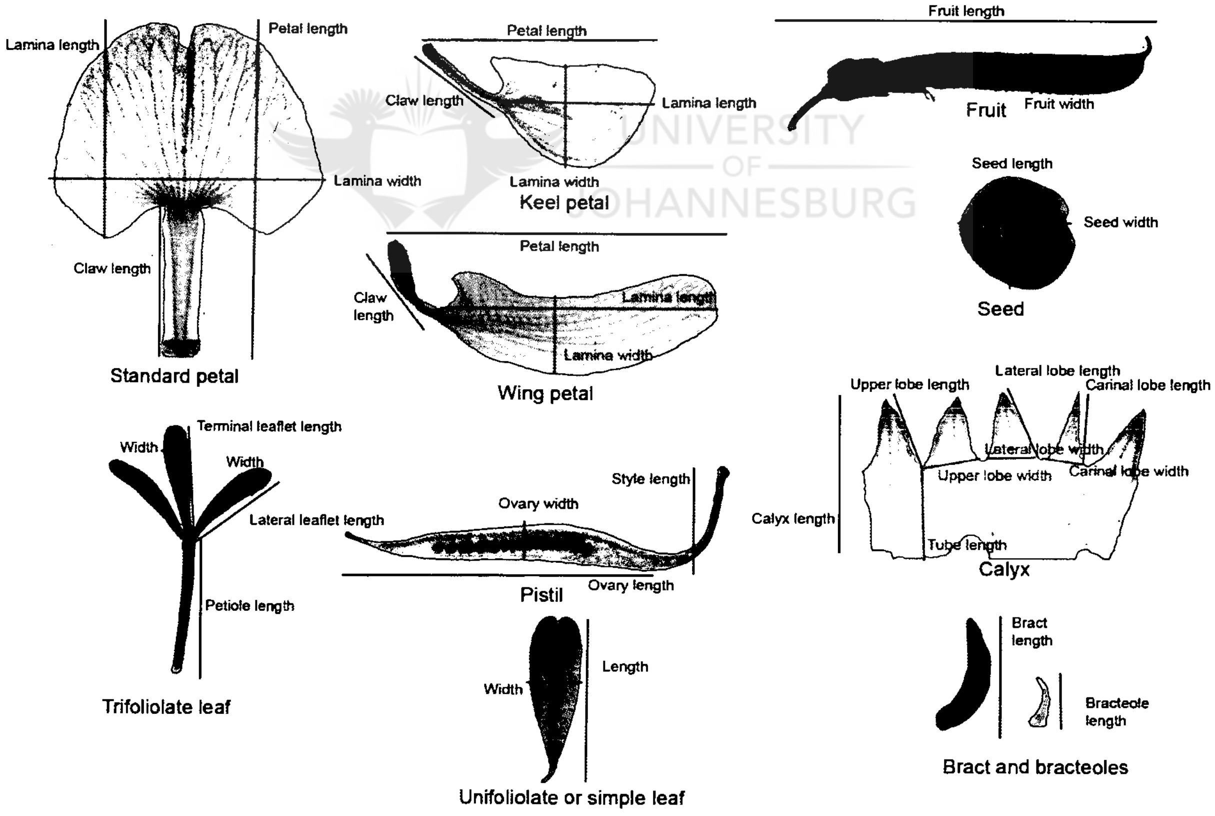

FIG. 2.1 Measurements of leaves and floral parts used for morphological descriptions.

## 2.3 DNA SEQUENCING AND PHYLOGENETIC ANALYSES

A phylogenetic study of the Crotalarieae was undertaken in collaboration with my supervisors and other co-workers (Chapter 3; Boatwright et al. 2008a; see Appendix B3). The methods followed in this study are discussed below.

***2.3.1 Plant accessions and choice of outgroups***—A total of 175 sequences of ITS (88% of the total ITS matrix) and 207 sequences for *rbcL* (91% of the total *rbcL* matrix) were produced from taxa of the Crotalarieae, representing a total of 135 out of ca. 1,204 species, and combined with previously published sequences of taxa from the tribes Genisteae and Podalyrieae as outgroups (Van Wyk and Schutte 1995; Crisp et al. 2000; Boatwright et al. 2008b). The gene regions ITS and *rbcL* were selected based on previous studies where they provided sufficient informative characters for analyses at the generic level. Sequences of both the ITS and *rbcL* regions were available for 161 taxa of the Crotalarieae and these were used for the combined molecular analysis. A morphological matrix was compiled for those species included in the combined molecular analysis, based on 31 characters (including a few chemical and cytological characters) that were scored from examining specimens from BM, BOL, GRA, JRAU, K, NBG (including SAM and STE), P, PRE, S, UPS and WIND for *Lebeckia*, *Robynsiophyton*, *Rothia* and *Spartidium* and from literature for the other genera (Polhill 1974, 1976, 1982; Dahlgren 1975, 1988; Schutte and Van Wyk 1988; Van Wyk 1991b; Van Wyk and Schutte 1995; Campbell and Van Wyk 2001; Van Wyk 2003a; Van Wyk et al. submitted). These data, along with sequences of the same species, were used to perform a combined molecular/morphological analysis. Subsequent to the study presented in Chapter 3 (Boatwright et al. 2008a), material of the rare and unusual *Lotononis macrocarpa*, a species which is pivotal in studying relationships within the genus *Lotononis*, was obtained from the Compton Herbarium (Chapter 8). The combined *rbcL*/ITS/morphology data set of Boatwright et al. (2008a) was used to evaluate relationships within *Lotononis* and assess the position of *L. macrocarpa*. DNA of this anomalous species was extracted using a DNeasy Plant Minikit (Qiagen Inc., Hilden, Germany) and sequenced following the procedures outlined below. These sequences of ITS and *rbcL* were added to the matrix of Boatwright et al. (2008a), which required minimal adjustments to the original alignment, and the matrix was re-analyzed with and without the morphological data. Parsimony (MP) analyses were conducted as described below (see Chapter 8).

***2.3.2 DNA extraction, amplification and sequencing***—Sequencing of the gene regions was carried out in two independent laboratories at the University of Johannesburg and University of Heidelberg. Therefore the strategies employed differed slightly. The gene sequencing methods of Käss and Wink (1997) were followed at University of Heidelberg, whereas sequences generated at the University of Johannesburg were gathered according to the methods described below. Sequences that were generated at the University of Johannesburg (by J.S. Boatwright) are marked with an asterix in Appendix A3.

DNA was extracted from silica-dried or herbarium leaf material using the 2x hexadecyltrimethylammonium bromide (CTAB) method of Doyle and Doyle (1987) and purified through QIAquick silica columns (Qiagen Inc., Hilden, Germany). Sources of material used in the study are listed in Appendix A3 (for species of *Lebeckia*, *Spartidium* and *Wiborgia* synonymous names in *Calobota* and *Wiborgiella* are provided in brackets). The internal transcribed spacers (ITS) of nuclear rDNA were amplified using the primers of White et al. (1990) and Sun et al. (1994), while for *rbcL* those of Fay et al. (1997) were used. Amplification reactions were carried out using polymerase chain reactions (PCR), in 25 µl reactions containing: 22.5 µl ABgene 1.1x PCR Mastermix (ABgene House, Blenheim Road, Epsom, Surrey, KT19 9AP, UK) consisting of 1.25 units Thermoprime Plus DNA Polymerase, 75 mM Tris-HCl (pH 8.8), 20 mM $(NH_4)_2SO_4$, 1.5 mM $MgCl_2$, 0.01% (v/v) Tween® 20, 0.2 mM each of deoxyribonucleotide triphosphates (dNTPs); 0.3 µl of both forward and reverse primers (0.1 ng/µl); 0.8 µl 0.004% bovine serum albumin (BSA); 1.2% dimethyl sulfoxide (DMSO; for ITS only); 20–50 ng DNA template; and sterile distilled water to make up a final volume of 25 µl. The DMSO was added to the amplification reactions as this may improve sequencing of ITS due to relaxation of the template secondary structure during amplification (Álvarez and Wendel 2003). The PCR cycles used for ITS consisted of 26 cycles of 1 min denaturation at 94°C, 1 min annealing at 48°C, 3 min extension at 72°C and 7 min final extension at 72°C; and for *rbcL*, there were 28 cycles of 1 min denaturation at 94°C, 1 min annealing at 48°C, 1:30 min extension at 72°C and 7 min final extension at 72°C. Sequencing reactions were performed using the Big Dye Terminator version 3.1 Cycle Sequencing Kit (Applied Biosystems Inc., Foster City, California, USA) and sequenced on a 3130 *xl* Genetic Analyzer (Applied Biosystems Inc.), with the addition of 5% DMSO for the ITS reactions. The cycle sequencing thermal profile consisted of 26 cycles of 10 sec denaturation at 96°C, 5 sec annealing at 50°C and 4 min at 60°C in a thermal cycler (PCR and cycle sequencing reactions were performed in a GeneAmp PCR system 9700 or 9800).

***2.3.3 Sequence alignment and phylogenetic analyses***— Complementary strands of the sequenced genes were edited in Sequencher version 3.1.2 (Gene Codes Corporation), and aligned manually in PAUP* version 4.0b10 (Swofford 2002). Alignments used in this study are available from TreeBASE (study accession number S2070). Insertions and deletions (indels) of nucleotides were scored as missing data and thus did not contribute to the combined analysis, but an additional search with gaps from the ITS data set coded as binary characters was performed (no gaps were present in the *rbcL* dataset). Gaps were coded in SeqState version 1.32 (Müller 2005) using simple indel coding as described by Simmons and Ochoterena (2000). Maximum parsimony analyses (MP; Fitch 1971) and Bayesian MCMC analysis (BI; Yang and Rannala 1997; Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; MRBAYES version 3.1.2) were performed as described in Boatwright et al. (2008b). Only the combined ITS/*rbcL* data set was analysed using BI. Internal support for MP was estimated with 1,000 bootstrap replicates (Felsenstein 1985) using tree bisection-reconnection (TBR) and holding 10 trees per replicate. The following scale for bootstrap support percentages (BP) was used: 50–74%, low; 75–84%, moderate; 85–100%, strong. Congruence of the separate datasets was assessed by examining the individual bootstrap consensus trees in order to compile a combined ITS and *rbcL* matrix for the 161 taxa where both sequenced regions were available. The bootstrap trees were considered incongruent only if they displayed ‘hard’ (i.e. strong bootstrap support) rather than ‘soft’ (i.e. low bootstrap support) incongruence (Seelanan et al. 1997; Wiens

1998). In addition, incongruence length difference tests (ILD, Farris et al. 1995) were performed using the partition-homogeneity test of PAUP*. The test was implemented with 1,000 replicate analyses, using the heuristic search option with simple addition of taxa, TBR and the MULTREES option in effect.

The GTR+I+G model [selected by MODELTEST v. 3.06 (Posada and Crandall 1998) using the corrected Akaike information criterion (AICc)] was implemented for the BI analysis and a total of three million generations were performed with a sampling frequency of 10. A majority rule consensus tree was produced to determine the posterior probabilities (PP) of all observed bi-partitions (only PPs above 0.5 are reported on the tree). The following scale was used to evaluate the PPs: 0.50–0.94, low; 0.95–1.0, strong.

Despite repeated attempts, it was only possible to amplify ITS1 for some samples of *Lotononis marlothii, L. pentaphylla, L. platycarpa* and *L. rostrata*. Only the first half of *rbcL* for some samples of *Aspalathus laricifolia* subsp. *laricifolia, A. shawii* subsp. *shawii, Lotononis falcata, L. platycarpa, Robynsiophyton vanderystii, Rothia hirsuta, Spartidium saharae* and *Wiborgia humilis* could be amplified. Missing data represented 4.3% of the entire combined molecular matrix due to the fact that both ITS and *rbcL* sequences were not available for some of the Genisteae included as outgroups.

***2.3.4 Morphological analyses***— Much debate currently surrounds the inclusion of morphological characters in phylogenetic analyses (e.g., Scotland et al. 2003). However, Wiens (2004) discusses the importance of morphological characters in phylogenetics, suggesting that their implementation in separate and combined analyses may provide more rigorous phylogenies, while improved resolution has been shown by Wortley and Scotland (2006) when morphology is combined with molecular data. Characters and character states used for the cladistic analysis are given in Appendix A4. The character states were polarised using the method of outgroup comparison. Phylogenetic analyses were performed in PAUP* (Swofford 2002) with the characters treated as unordered and equally weighted (Fitch 1971). A heuristic search with 1,000 random addition sequences, TBR and the MULTREES option off was performed with a limit of 10 trees held per replicate. Internal support was assessed using 1,000 bootstrap replicates (Felsenstein 1985) as described above. *Dichilus gracilis*, a suffrutex, was selected as the outgroup for the analysis. A second analysis was performed where *Genista tinctoria* L., a shrub, was used as outgroup to test whether polarising the shrubby habit as ancestral had an effect on the topology, but no difference was found in this analysis (tree not shown).

Morphological analyses were performed to study infrageneric relationships in *Calobota* (Chapter 6) and *Wiborgiella* (Chapter 7). All the species within each of these genera were included and thus the sampling was different to that of the combined molecular/morphological analyses. Character states were scored for 17 morphological and anatomical characters for *Calobota* (see Table 6.1) and 13 characters for *Wiborgiella* (see Table 7.1). Where two states were found to co-occur in a single taxon they were scored as polymorphic and autapomorphies were omitted from the analyses. The morphological data sets were analysed using parsimony (Fitch 1971) in PAUP*. All characters were treated as unordered and equally weighted. Tree searches were performed using the branch-and-bound algorithm for *Wiborgiella* (random sequence addition and MULTREES on) and a heuristic search for *Calobota* (1,000 random addition sequences, TBR and MULTREES on). Internal support was assessed using 1,000 bootstrap replicates (Felsenstein 1985) with TBR swapping and MULTREES off.

***2.3.5 Evolution of morphological characters.***—The patterns of evolution of 12 characters (Table 8.1) traditionally regarded as apomorphies for *Lotononis* s.l. or groups therein were examined by reconstructing these onto the minimal length trees of both the analysis with and without the morphological data included (presented in Chapter 8). An additional 6 characters within the Crotalarieae were also included in addition to the 12 mentioned before to examine their patterns of evolution within the tribe (see Appendix A5 and Chapter 11). The character reconstructions were done using parsimony in Mesquite version 2.58 (Maddison and Maddison 2008).

# CHAPTER 3: PHYLOGENETIC RELATIONSHIPS WITHIN THE TRIBE CROTALARIEAE (FABACEAE) INFERRED FROM DNA SEQUENCES AND MORPHOLOGY

## 3.1 INTRODUCTION

Crotalarieae is a tribe of legumes that currently comprises 11 genera and ca. 1,204 species (Van Wyk 2005). It represents the largest tribe of papilionoid legumes in Africa and also within the genistoid alliance, comprising about 51% of genistoid legumes (species totals in Lewis et al. 2005 used for calculation). The size of the tribe is mainly due to the fact that the genus *Crotalaria* contains ca. 690 species (Polhill 1982). Some of the species are important commercially such as *Aspalathus linearis*, which is used for the production of rooibos tea (Van Wyk et al. 1997), and *Lotononis bainesii* Bak., an important fodder plant (Bryan 1961). Some *Crotalaria* and *Lotononis* species have been reported to have medicinal properties (Van Wyk 2005) and a few are used as what is called *'Musa-pelo* in Lesotho traditional medicine to cure or ease a broken heart (Moteetee and Van Wyk 2007), while others from the same genera are poisonous (Van Wyk et al. 2002).

The Crotalarieae are subendemic to Africa, with species of *Crotalaria*, *Lotononis* and *Rothia* occurring on other continents. *Aspalathus*, *Rafnia* and *Wiborgia* are endemic to the Cape Floristic Region, while *Lebeckia* (as currently circumscribed) is distributed throughout the Cape and extends into the south-western and central parts of Namibia. Generic circumscriptions and relationships within the tribe are known to be complicated, with evidence of reticulation and convergence (Dahlgren 1970a; Polhill

1976, 1981; Van Wyk 1991a). The most recent evaluations of generic relationships in the tribe are those of Polhill (1976, 1981), Van Wyk (1991a) and Van Wyk and Schutte (1989, 1995). According to Van Wyk (1991a), two main groups can be identified within the tribe, namely the "Cape group" comprising *Aspalathus*, *Lebeckia*, *Rafnia* and *Wiborgia*, and the *Lotononis* group comprising *Lotononis*, *Pearsonia*, *Robynsiophyton* and *Rothia*. The placement of *Bolusia*, *Crotalaria* and *Spartidium* within these two groups is not clear, but a close relationship between the former two genera has been suggested. Recent revisionary studies of *Lebeckia* (the first since Harvey's treatment of 1862) have shown that the genus is unlikely to be monophyletic (Le Roux 2006; Le Roux and Van Wyk 2007; Boatwright, in prep.; Chapters 6 and 7).

Several molecular systematic studies of Fabaceae and specifically the genistoid legumes (sensu Polhill 1976, 1981) have been conducted in recent years (Käss and Wink 1995, 1996, 1997; Crisp et al. 2000; Doyle et al. 2000; Kajita et al. 2001; Wink and Mohamed 2003; Wojciechowski et al. 2004; Boatwright et al., 2008b). These studies indicate the placement of Crotalarieae within the "core" genistoid clade together with, among others, the South African tribes Podalyrieae and Genisteae, and confirm the exclusion of the *Argyrolobium* group (*Argyrolobium*, *Dichilus*, *Melolobium*, *Polhillia*) and the rest of the Genisteae from Crotalarieae (Van Wyk and Schutte 1995). A sister relationship between Crotalarieae and Genisteae, with Podalyrieae successively sister to these, is shown by the molecular studies cited above, but sampling limitations did not allow detailed evaluations at the generic level.

This chapter is aimed at exploring generic circumscriptions and relationships within Crotalarieae, using nrDNA ITS sequences, plastid *rbcL* sequences and morphological data, based on a sample of 135 species representing all of the 11 genera currently recognized, as well as major infrageneric groups within some of the genera. The aim was to assess the monophyly and relationships of the individual genera.

## 3.2 RESULTS

***3.2.1 rbcL data set***—The *rbcL* matrix comprised 1,296 aligned positions with 222 variable and 167 parsimony informative characters. Tree searches produced 2,650 equally parsimonious trees of 527 steps, a consistency index (CI) of 0.50 and a retention index (RI) of 0.92. Overall the strict consensus tree (Fig. 3.1) is poorly resolved with a few supported clades. A clade consisting of *Lebeckia* section *Calobota* (Eckl. & Zeyh.) Benth., *L.* section *Stiza* (E.Mey) Benth. and *Spartidium saharae* is weakly supported (60 BP). *Lotononis* s.s. (*L.* section *Lotononis* and allies) is moderately supported (74 BP), while the rest of the genus is unresolved except for *L.* section *Listia* (E.Mey.) B.-E.van Wyk, which has high support (89 BP). The *Crotalaria* clade is strongly supported (88 BP) and the sister relationship between *Bolusia* and *Crotalaria* is also strongly supported with a BP of 90. Both these genera are well-supported to be monophyletic (*Bolusia* 98 BP; *Crotalaria* 90 BP) and they are successively sister to *Lotononis hirsuta* [*L.* section *Euchlora* (Eckl. & Zeyh.) B.-E.van Wyk].

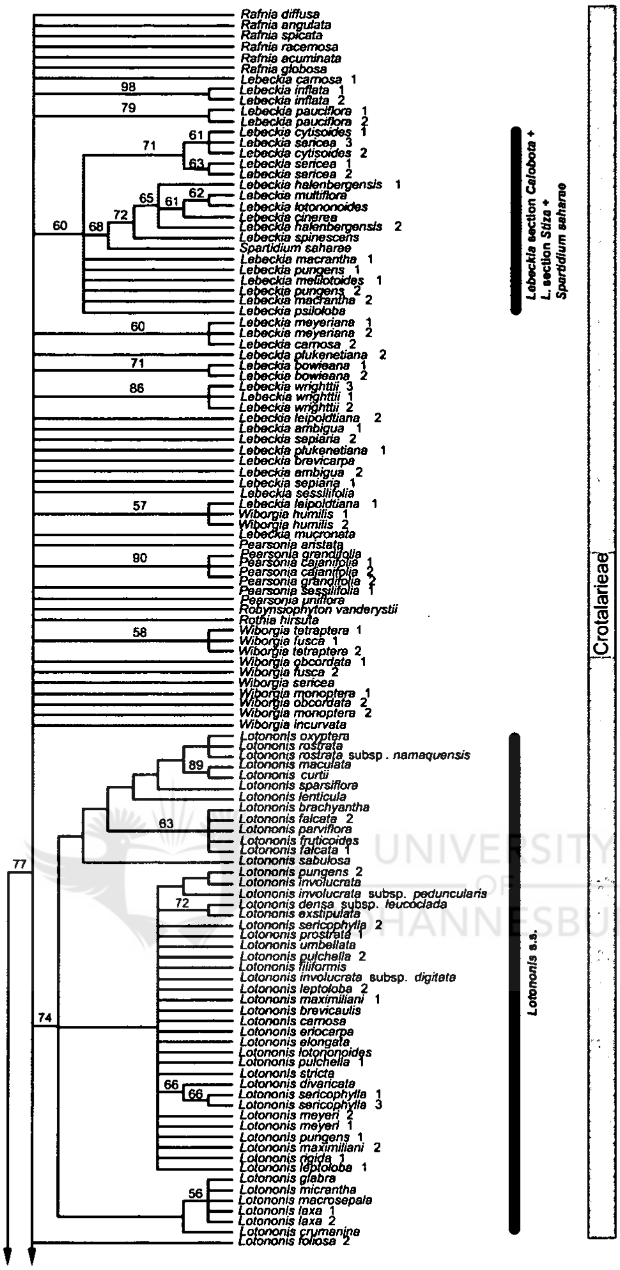

FIG. 3.1 Strict consensus tree of 2,650 equally parsimonious trees from the analysis of the *rbcL* data set (TL = 527; CI = 0.50; RI = 0.92). Numbers above the branches are bootstrap percentages above 50% from the parsimony analysis.

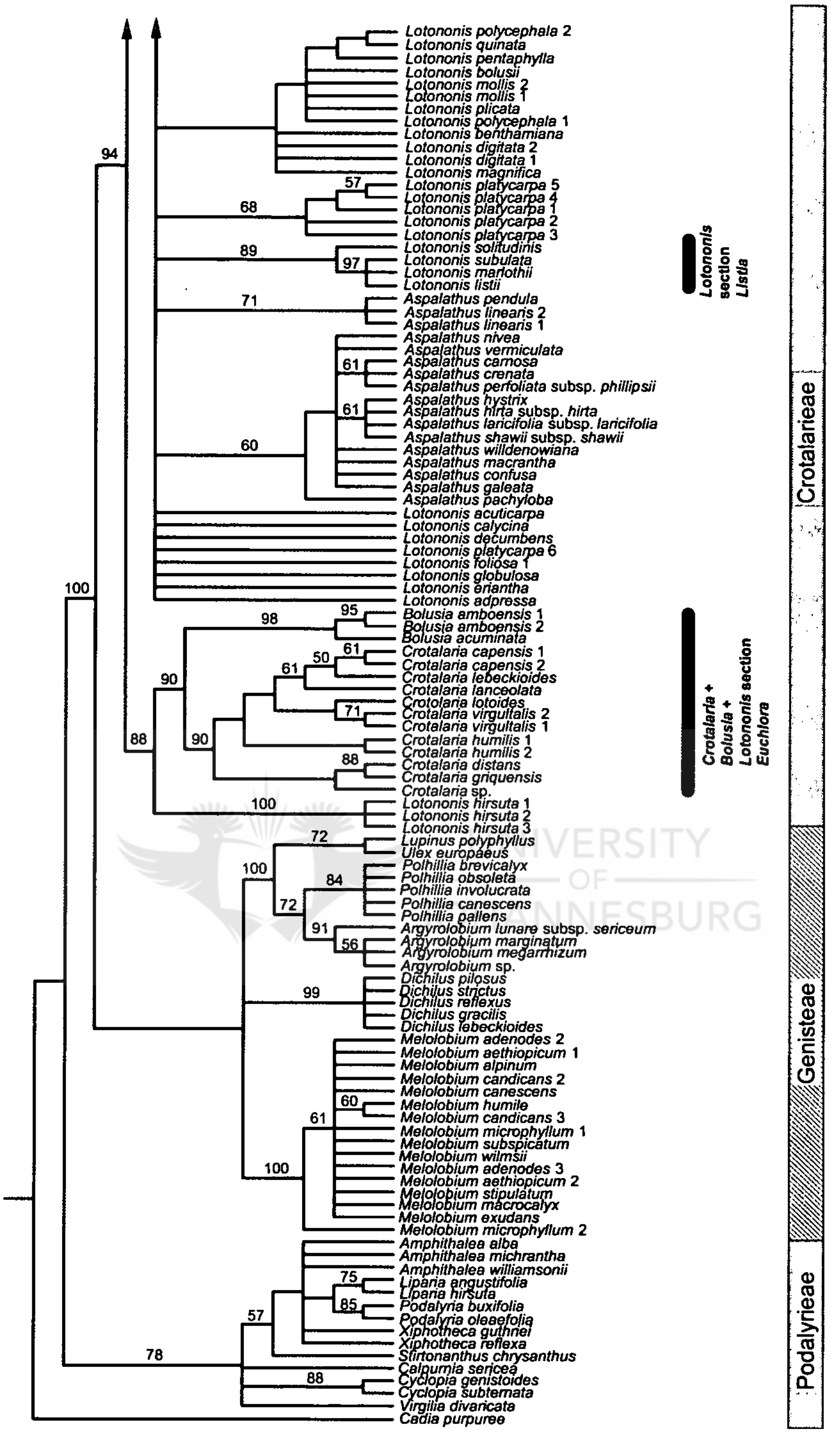

FIG. 3.1 Continued.

Tribe Crotalarieae as a whole is strongly supported as monophyletic (94 BP) and sister to the Genisteae (100 BP). Genisteae and Podalyrieae are both supported as monophyletic (89 BP and 78 BP, respectively).

***3.2.2 ITS data set***—The analysis of the ITS data set included 560 characters, of which 353 were variable and 256 parsimony informative. Analysis resulted in 5,970 equally parsimonious trees with a tree length (TL) of 1,031 steps, a CI of 0.51 and a RI of 0.85. The analysis in which gaps were coded resulted in identical clade resolution as the analysis without coded gaps, although some clades had stronger or weaker support (not shown). The analysis with coded gaps resulted in 2,540 trees (TL = 1,340; CI = 0.51; RI = 0.84). The strict consensus tree based on ITS data (Fig. 3.2) is better resolved than that of *rbcL*, with several well-supported clades. *Aspalathus* was weakly supported as monophyletic (64 BP), although this support percentage is higher when the gap characters are included (78 BP). *Lebeckia* and *Wiborgia* are both polyphyletic. *Lebeckia* section *Viborgioides* Benth. including *Wiborgia humilis* is moderately supported (80 BP), while the positions of *L. inflata* and *L. mucronata* are unresolved. The remaining species of *Wiborgia* form a weakly supported clade (61 BP; 79 BP with gap coding). *Rafnia* is weakly supported as monophyletic (75 BP) and *Lebeckia* section *Calobota* along with *L.* section *Stiza* and *Spartidium saharae* also has weak support (59 BP). *Lebeckia* section *Lebeckia* is unresolved. *Lotononis* is left unresolved and *L. hirsuta* is well separated from the rest of the genus. Three main clades can be distinguished.

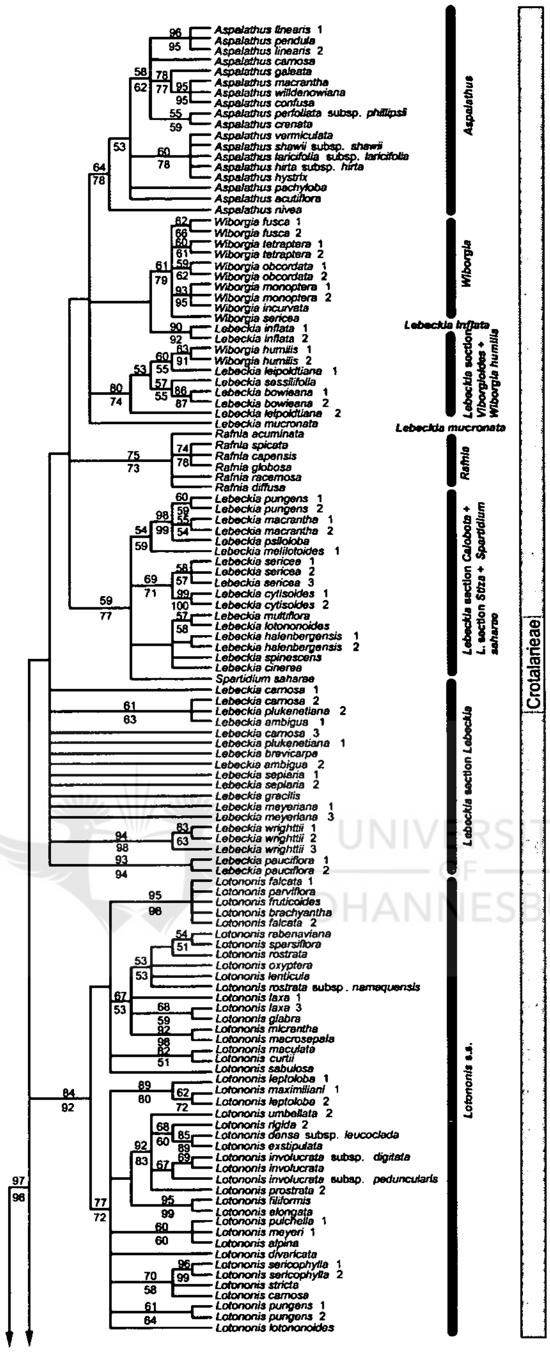

FIG. 3.2 Strict consensus tree of 5,970 equally parsimonious trees from the analysis of the ITS data set (TL = 1,031; CI = 0.51; RI = 0.85). Numbers above the branches are bootstrap percentages above 50% from the parsimony analysis.

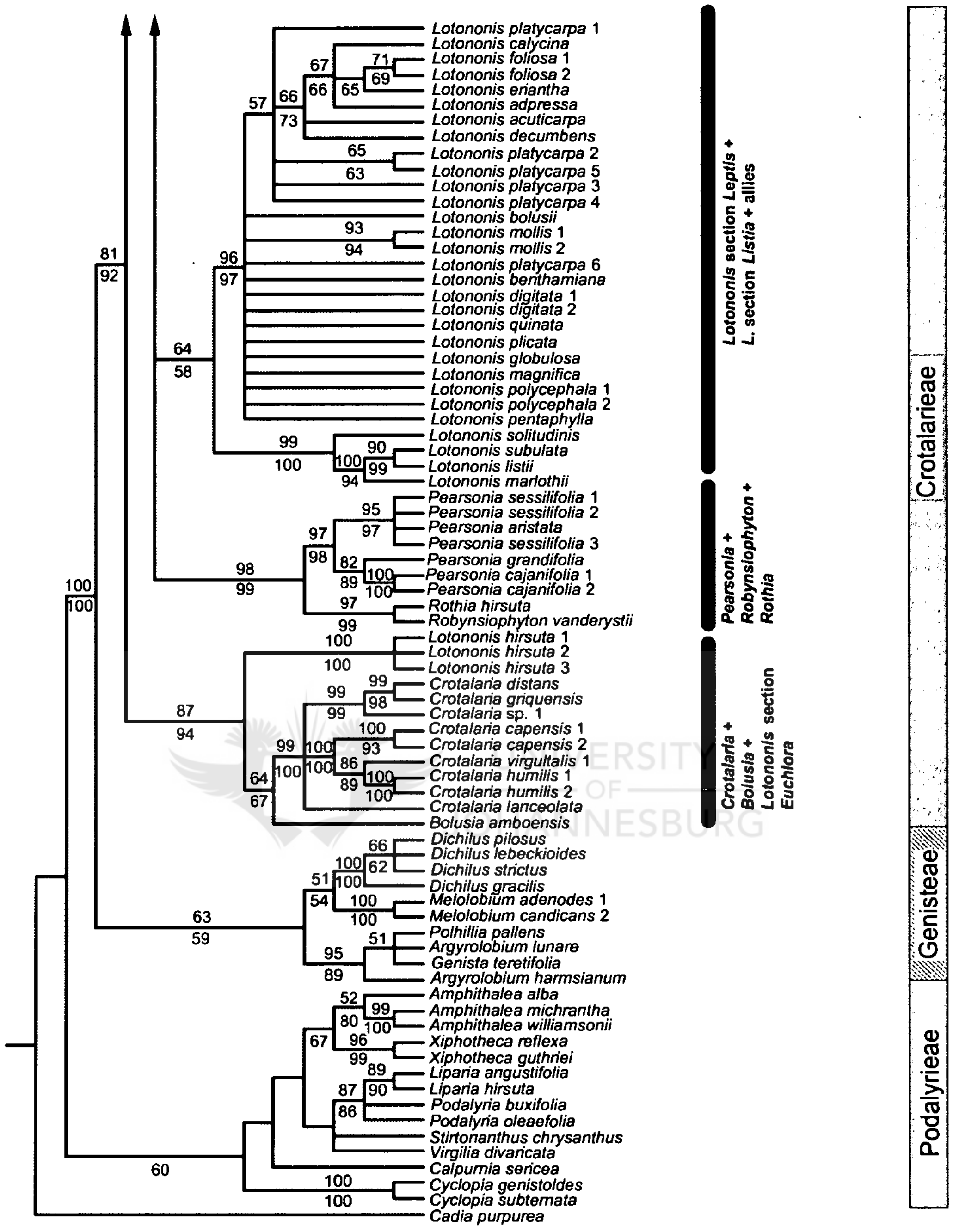

FIG. 3.2 Continued.

The first consists of *Lotononis* s.s. (also supported in the *rbcL* tree) with moderate support (84 BP). The second clade, comprising taxa from *Lotononis* section *Leptis* (E.Mey. ex Eckl. & Zeyh.) Benth., *L.* section *Listia* and their allies also has low support (64 BP). The third clade of *Lotononis* groups with *Bolusia* and *Crotalaria* with strong support (87 BP) and comprises one anomalous species, *L. hirsuta*, which makes up the monotypic section *Euchlora*. *Crotalaria* and *Bolusia* are weakly supported as sister taxa (64 BP) and *Crotalaria* is strongly supported to be monophyletic (99 BP). *Pearsonia*, *Robynsiophyton* and *Rothia* form a strongly supported clade (98 BP) and the latter two are strongly supported to be sister genera (97 BP). The taxa of this clade all possess a 17 base-pair deletion at positions 179–196 in the aligned ITS matrix. The Crotalarieae are strongly supported to be monophyletic (81 BP) and sister to Genisteae (100 BP).

***3.2.3 Combined ITS/rbcL data set***—Visual inspection of the bootstrap consensus trees resulting from separate analyses of ITS and *rbcL* sequences presented no strongly supported incongruent patterns. The ILD test indicated significant difference between the two datasets (p=0.001). Following the suggestions of Seelanan et al. (1997) and Wiens (1998), together with suggestions that the ILD test may be unreliable (Reeves et al. 2001; Yoder et al. 2001) these datasets were combined directly. The combined ITS and *rbcL* matrix consisted of 1,854 included positions, of which 540 were variable and 404 parsimony informative. The MP analysis produced 560 equally parsimonious trees (Fig. 3.3; TL = 1,473; CI = 0.50; RI = 0.86).

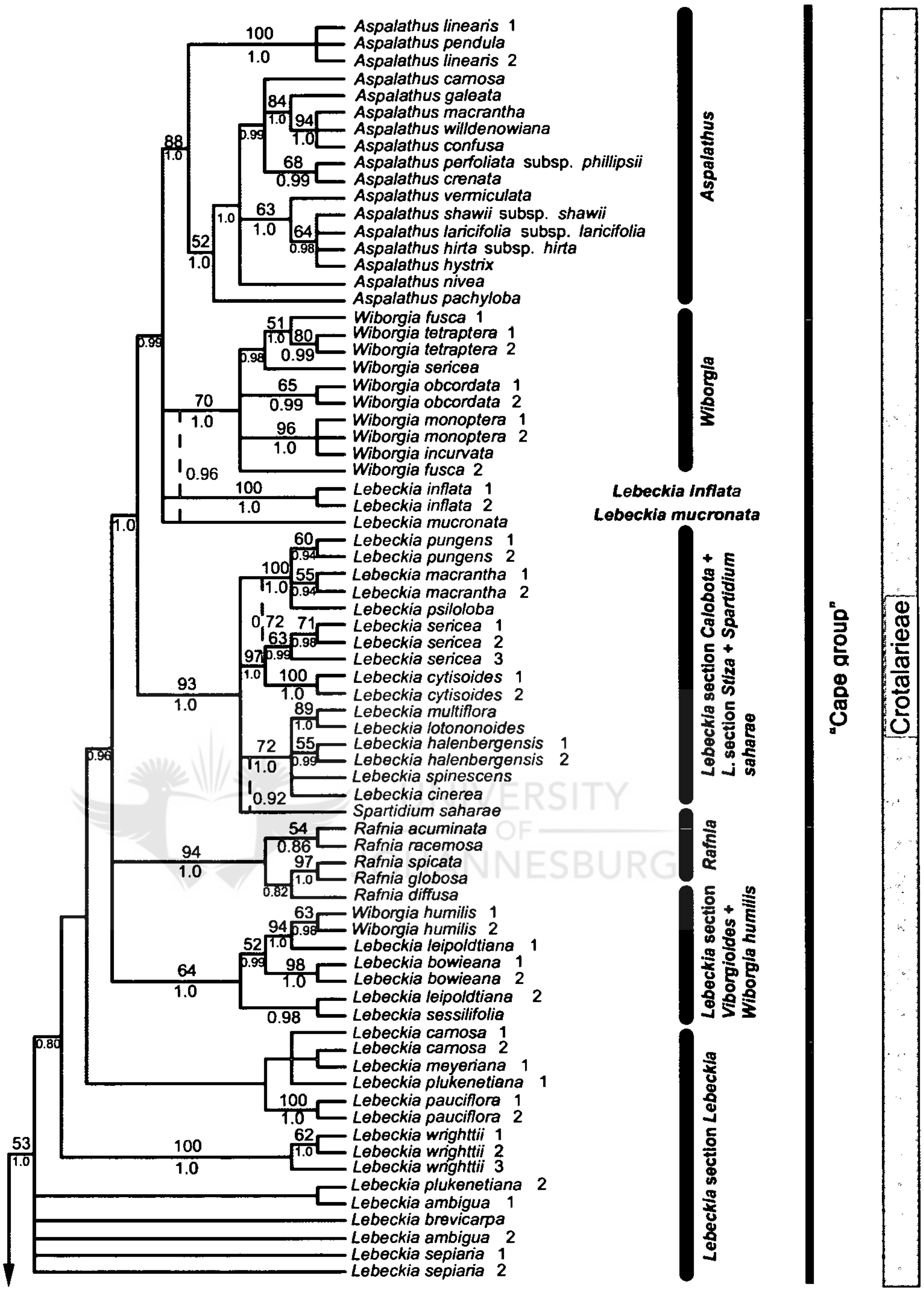

FIG. 3.3 Strict consensus tree of 560 shortest length trees from the combined analysis of the ITS and *rbcL* data sets (TL = 1,473; CI = 0.50; RI = 0.86). Numbers above the branches are bootstrap percentages above 50% from the maximum parsimony analysis and numbers below the branches are posterior probabilities above 0.5 from the Bayesian analysis.

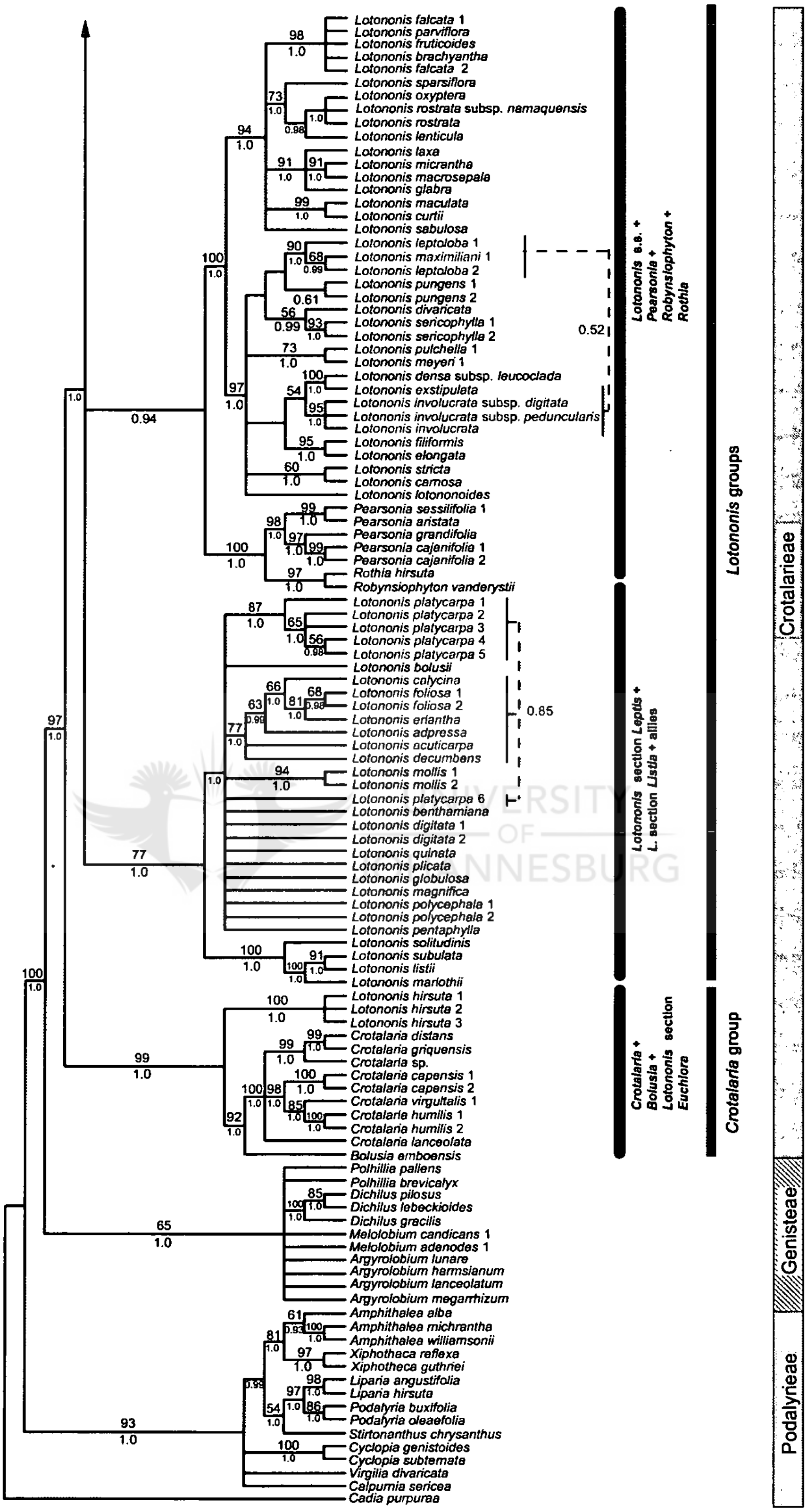

FIG. 3.3 (Continued).

In both the MP and BI analyses, the same major clades could be observed: the "Cape group" consisting of *Aspalathus*, *Lebeckia*, *Rafnia*, *Spartidium* and *Wiborgia* (53 BP; PP 1.0); the *Lotononis* group consisting of *Lotononis* s.s., *Pearsonia*, *Robynsiophyton* and *Rothia* (PP 0.94); a second *Lotononis* clade consisting of *Lotononis* section *Leptis*, *L.* section *Listia* and allies (77 BP; PP 1.0); and the *Crotalaria* group consisting of *Bolusia*, *Crotalaria* and *Lotononis hirsuta/L.* section *Euchlora* (99 BP; PP 1.0). *Lebeckia*, *Lotononis* and *Wiborgia* are all polyphyletic and *Lebeckia* section *Lebeckia* is unresolved in both the analyses.

Generic relationships are unresolved within the "Cape group" and represented as a polytomy at the base of this clade in the bootstrap consensus tree of the parsimony analysis (not shown). In the BI tree, *Aspalathus* (88 BP; PP 1.0) and *Wiborgia* (70 BP; PP 1.0) are sister to each other, with *L. mucronata* (PP 0.96) and *Lebeckia inflata* included in this clade. These positions are unresolved in the MP analysis. *Lebeckia* section *Calobota* (including *L.* section *Stiza* and *Spartidium saharae*; 93 BP; PP 1.0) is sister to *Aspalathus* and *Wiborgia*, followed by *L.* section *Viborgioides* (including *Wiborgia humilis*; 64 BP; PP 1.0) and *Rafnia* (94 BP; PP 1.0). *Lebeckia* section *Lebeckia* is unresolved in both the MP and BI trees.

*Lotononis* is polyphyletic in both the MP and BI trees. The *Lotononis* group is moderately supported in the BI tree (PP 0.94) and consists of those species of *Lotononis* from the sections *Aulacinthus* (E.Mey.) Benth., *Buchenroedera* (Eckl. & Zeyh.) B.-E.van Wyk, *Cleistogama* B.-E.van Wyk, *Krebsia* (Eckl. & Zeyh.) Benth., *Lotononis*, *Monocarpa* B.-E.van Wyk, *Oxydium* Benth. and *Polylobium* (Eckl. & Zeyh.) Benth. (100 BP; PP 1.0). These are sister to a strongly supported clade (BP 100; PP

1.0) consisting of *Pearsonia* (98 BP; PP 1.0), *Robynsiophyton* and *Rothia*. The sister relationship of the latter two genera has high bootstrap support (97%) and PP (1.0).

The next clade consists of species of *Lotononis* section *Listia* (100 BP; PP 1.0) and sections *Digitata* B.-E.van Wyk, *Leobordea* (Del.) Benth., *Leptis*, *Lipozygis* (E.Mey.) Benth. and *Synclistus* B.-E.van Wyk (99 BP; PP 1.0) and these are moderately to strongly supported as sister (77 BP; 1.0 PP).

The *Crotalaria* group consists of *Bolusia* and *Crotalaria* (100 BP; PP 1.0), strongly supported as sister groups (92 BP; PP 1.0), and *Lotononis hirsuta* (corresponding to *Lotononis* section *Euchlora*). This clade receives high support in both the MP and BI analyses (99 BP; PP 1.0).

The Crotalarieae are strongly supported as being monophyletic (97 BP; PP 1.0) and sister to Genisteae (100 BP; PP 1.0). The monophyly of the latter tribe receives low to strong support (65 BP; PP 1.0). The Podalyrieae s.s. are strongly supported as monophyletic (93 BP; PP 1.0) and the relationships within the tribe conform to those of previous studies (Boatwright et al., 2008b).

***3.2.4 Morphological analysis***—The morphological matrix included 31 polarised characters, 29 of which were parsimony informative. Parsimony analysis yielded 261 trees (not shown) of 101 steps (CI = 0.36, RI = 0.93). In the strict consensus tree (not shown), *Aspalathus* and *Rafnia* group together, albeit without support. *Aspalathus* (excluding *A. crenata* and *A. perfoliata*) and *Rafnia* are weakly supported as monophyletic (55 BP and 71 BP, respectively). *Lebeckia* section *Viborgioides*, *L. mucronata* and *Wiborgia* s.s. group together, while *L. inflata* groups with *Lebeckia* section *Lebeckia*, but without support. Only *Wiborgia* is weakly supported as monophyletic (78 BP). *Lebeckia* section *Lebeckia* is moderately supported as monophyletic (84 BP), but there is no resolution within this group. *Lotononis hirsuta* is not included in *Lotononis*, but groups with *Crotalaria* (63 BP) and *Bolusia* as in the molecular analysis. The rest of *Lotononis* is monophyletic (56 BP) in the morphological analysis as opposed to polyphyletic in the combined molecular analysis, but relationships within the genus are largely unresolved. *Pearsonia*, *Rothia* and *Robynsiophyton* form a strongly supported clade (87 BP) and a sister relationship between *Robynsiophyton* and *Rothia* is strongly supported (88 BP).

***3.2.5 Combined ITS/rbcL/morphological data set***—The bootstrap consensus trees from the combined ITS/*rbcL* analysis and the morphological analysis showed no strongly supported incongruent patterns, although an ILD test indicated significant difference between the data sets (p=0.002). The suggestions of Seelanan et al. (1997) and Wiens (1998) were followed and the data sets combined directly. The combined matrix consisted of 1,885 characters, 1,405 of which were constant, 480 variable and 303 parsimony informative. The MP analysis resulted in 370 trees (TL = 1,166, CI = 0.53, RI = 0.84; Fig. 3.4).

The trees resulting from this analysis are similar to those from the combined molecular analysis, except that *Lotononis* and *Lebeckia* section *Lebeckia* are monophyletic. The “Cape group” (73 BP), *Lotononis* group (including *Pearsonia*, *Robynsionphyton* and *Rothia*), and *Crotalaria* group (100 BP) found in the molecular analysis were also retrieved in the combined data set of molecular plus morphological characters. Within the “Cape group”, *Aspalathus*, *Lebeckia* section *Calobota* (including *L.* section *Stiza* and *Spartidium saharae*), *L.* section *Lebeckia*, *L.* section *Viborgioides* (including *Wiborgia humilis*), *Rafnia* and *Wiborgia* (excluding *Wiborgia humilis*) received moderate to strong support to be monophyletic (99 BP; 95 BP; 77 BP; 87 BP; 98 BP; 94 BP, respectively). *Lotononis* is monophyletic (75 BP; excluding *L. hirsuta*) and the groups retrieved within the genus are identical to the separate clades found in the molecular analysis, namely *Lotononis* s.s. (100 BP), *Lotononis* section *Leptis* and allies (100 BP) and *Lotononis* section *Listia* (100 BP). The sister relationship between the latter two is strongly supported with a BP of 88. *Pearsonia* is strongly supported as monophyletic (99 BP) and sister to *Robynsiophyton* and *Rothia* (100 BP). The sister relationship between *Robynsiophyton* and *Rothia* is strongly supported (99 BP). The *Crotalaria* group is strongly supported (100 BP) and consists of *Bolusia*, *Crotalaria* and *Lotononis hirsuta*. *Crotalaria* is strongly supported to be monophyletic (100 BP) and is sister to *Bolusia* (94 BP).

## 3.3 DISCUSSION

***3.3.1 Phylogenetic relationships***—The phylogenetic hypotheses presented in this study are based on a complete sample of Crotalarieae at the generic level and a representative sample of most of the taxonomic and morphological variation within these genera. The data were based not only on DNA sequences but also on salient morphological characters that were carefully polarised and proved to be informative at the generic level.

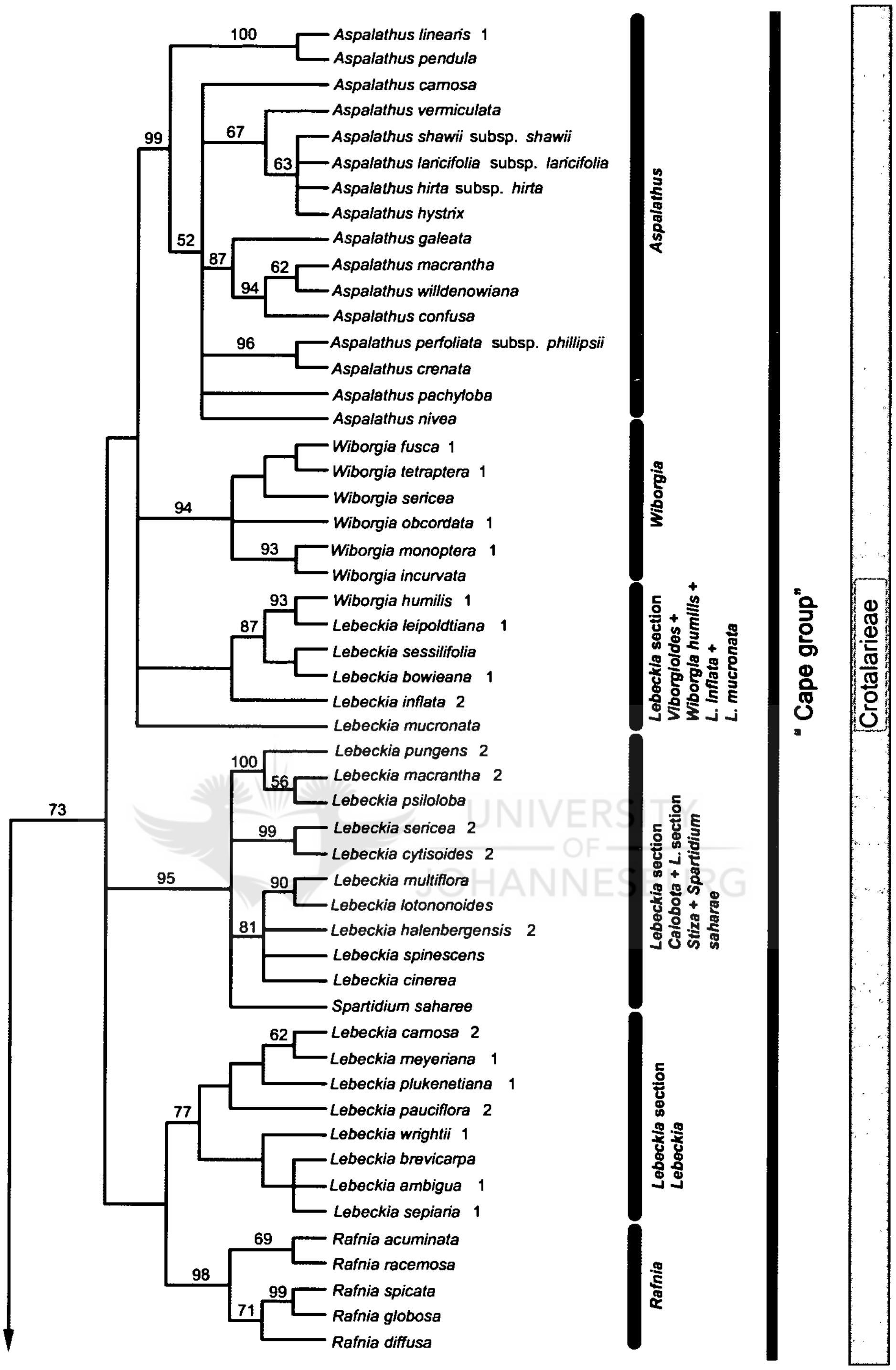

FIG.3.4 Strict consensus tree from the combined molecular (ITS and *rbcL*) and morphological analysis. Numbers above the branches are bootstrap percentages above 50% (no. of trees = 370; TL = 1,166; CI = 0.53; RI = 0.84).

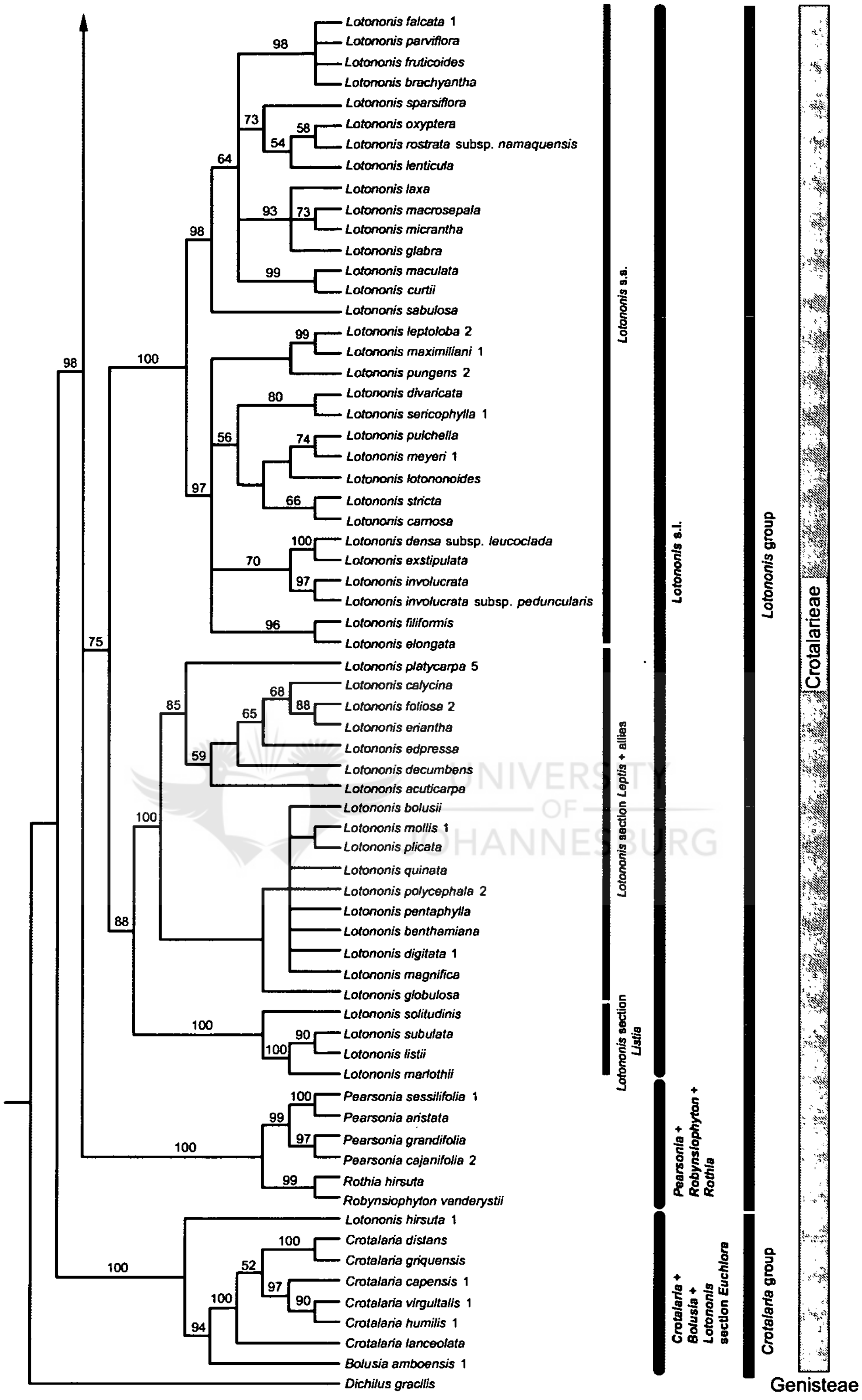

FIG. 3.4 (Continued).

The low resolution within the Crotalarieae based on morphology and some chemical and cytological characters reflects the somewhat reticulate relationships within the tribe (also mentioned by Van Wyk 1991a; Van Wyk 2005) with remarkable examples of parallelism, convergence and analogy with regard to vegetative and reproductive morphology as outlined by Dahlgren (1970a). The presence of seemingly identical apomorphic states in unrelated genera (e.g. hairy petals in *Lebeckia* section *Calobota* and *Lotononis* section *Leptis*) complicates the cladistic analysis. In the absence of single apomorphies with diagnostic value, natural groups can only be delimited using combinations of characters. The results presented here (both molecular and morphological) support some of the current generic concepts within the tribe, but provide novel insights into as yet phylogenetically unstudied groups such as *Lebeckia* and the smaller genera of the Crotalarieae, namely *Robynsiophyton*, *Rothia* and *Spartidium*.

Previous studies on relationships within the Crotalarieae have all suggested a close relationship between the "Cape" genera (viz., *Aspalathus*, *Lebeckia*, *Rafnia* and *Wiborgia*), as well as the genera that have a zygomorphic calyx (viz., *Lotononis*, *Pearsonia*, *Robynsiophyton* and *Rothia*; Dahlgren 1963, 1967a, 1970a; Polhill 1981; Van Wyk 1991a). The placement of *Bolusia*, *Crotalaria* and *Spartidium* has been uncertain. A sister relationship between the former two genera was suggested by Polhill (1976) and Van Wyk (1991a), while *Spartidium* was thought to either be closely allied to Genisteae or to *Lebeckia*, but the affinities remained unclear (Polhill 1976). The results of the current study indicate four major lineages within the Crotalarieae, namely the "Cape group" (*Aspalathus*, *Lebeckia*, *Rafnia*, *Wiborgia*, including *Spartidium saharae*), two lineages comprising genera with zygomorphic calyces (*Lotononis*, *Pearsonia*, *Robynsiophyton* and *Rothia*), plus *Bolusia*, *Crotalaria* and *Lotononis* section *Euchlora*.

***3.3.2 The "Cape group"***—The lack of resolution between genera in this group is caused by the low sequence divergence among these taxa. *Aspalathus* and *Rafnia* are both strongly supported as monophyletic and indicated as sister taxa by the analysis of morphological data alone because they share sessile leaves and an asymmetrical upper suture of the pod (Campbell and Van Wyk 2001). *Aspalathus* is placed closer to *Wiborgia* by both the MP analyses (combined ITS/*rbcL* and combined ITS/*rbcL*/morphology) and BI analysis (combined ITS/*rbcL*). Although the sample of *Aspalathus* is not at all comprehensive, some clades of interest can be noted. *Aspalathus linearis* and *A. pendula* both have simple, terete leaves and this clade corresponds to the Lebeckiiformes group (Dahlgren 1988), named for its similarity to *Lebeckia* section *Lebeckia*. *Aspalathus laricifolia*, *A. hirta*, *A. hystrix* and *A. shawii* all have spine-tipped leaves (corresponding to the Laterales group of Dahlgren 1988) and form a clade, which is well-supported in the BI tree (combined ITS/*rbcL*). The Borboniae group (Dahlgren 1988) represented by *A. perfoliata* and *A. crenata* form a weak to strongly supported clade. Within *Rafnia,* two clades can be identified that correspond to the two section of the genus described by Campbell and Van Wyk (2001): the *R. acuminata* clade representing *R.* section *Rafnia*, and the *R. spicata* clade representing *R.* section *Colobotropis* E.Mey. These two sections differ mainly in the rostrate keel petals and unequal calyx lobes of *R.* section *Colobotropis*.

It is clear from both the MP (combined ITS/*rbcL* and combined ITS/*rbcL*/morphology) and BI analysis (combined ITS/*rbcL*) that *Lebeckia* and *Wiborgia* are not monophyletic. *Lebeckia* is represented by several smaller clades within the "Cape group", while *Wiborgia humilis* is nested within the *Lebeckia leipoldtiana* clade and well-separated from the main *Wiborgia* clade.

The species of *Lebeckia* section *Calobota* form a well-supported clade with those of *L.* section *Stiza* and the monotypic genus *Spartidium*. These species are all shrubs with trifoliolate or unifoliolate leaves and green mature stems. The petals are usually pubescent and they possess a 4+1+5 anther configuration (five short dorsifixed anthers, four long basifixed anthers and an intermediate carinal anther). Some of these character states also occur in *Lotononis* species and are thus not informative in the morphological analysis. The species of *L.* section *Stiza* and *L.* section *Calobota* occur in the Cape and those of the latter also extend northwards into Namibia. *Spartidium saharae* is a North African plant that has had uncertain affinities within the tribe. The close relationship of this species to *L.* section *Calobota* has also been demonstrated independently by Edwards and Hawkins (2007) based on ITS data.

*Wiborgia* and species of *Lebeckia* section *Viborgioides* are superficially very similar in their rigid, woody habit, glabrous petals and highly reflexed standard petals in most species. However, they differ markedly in the winged, few-seeded samaras that are typical of *Wiborgia* species (Dahlgren 1975). However, *Wiborgia humilis* has thin-walled, inflated pods that lack the dorsal wing characteristic of *Wiborgia* (Dahlgren 1970b). The fruits of *Lebeckia* section *Viborgioides* are typically turgid, thin-walled, many-seeded and wingless. *Wiborgia humilis* is the only species of *Wiborgia* with a 4+6 anther arrangement (6 short, dorsifixed and 4 long basifixed anthers) instead of the

4+1+5 arrangement found in all other species. These characters therefore support the placement of *W. humilis* in the *L.* section *Viborgioides* clade.

*Lebeckia* section *Lebeckia* is unresolved in the BI and MP analyses (combined ITS/*rbcL*). This section is morphologically very distinct from the other sections in the genus and its monophyly is supported by four apomorphies, namely the suffrutescent habit, acicular (terete) leaves, a 5+5 anther arrangement and rugose seeds (Le Roux 2006; Le Roux and Van Wyk 2007). This is clear from the moderate support this group received in the morphological analysis as well as the combined morphological/molecular analysis. *Lebeckia lotononoides* and *L. inflata* are the only other species of *Lebeckia* with rugose seeds, but these species share characters with *L.* section *Calobota* and *L.* section *Viborgioides*, respectively (Boatwright and Van Wyk 2007; Boatwright, pers. obs.).

The positions of both *L. inflata* and *L. mucronata* are unresolved in the combined ITS/*rbcL* analysis. *Lebeckia mucronata* is currently placed within *L.* section *Calobota*. *Lebeckia inflata* was described by Bolus (1887) without any reference to its position in the infrageneric systems of Bentham (1844) and Harvey (1862). Both of these species, however, share several anatomical and morphological characters with species of *L.* section *Viborgioides*, such as a 4+6 anther arrangement, glabrous petals and the dorsiventral leaves with mucilage cells. When morphological characters were combined with the molecular ITS and *rbcL* data, *L. inflata* was included in a clade along with *L.* section *Viborgioides* and *Wiborgia humilis*, while the position of *L. mucronata* remained unresolved.

***3.3.3 The Lotononis clades***—Based on the molecular data, *Lotononis* is polyphyletic and consists of three clades. *Lotononis* s.s. groups with the *Pearsonia* clade (albeit without support in the combined ITS/*rbcL* MP analysis) and is strongly supported as monophyletic. Two groups were noted within this clade. The first consists of representatives of *L.* section *Oxydium* and the second of representatives of *L.* sections *Aulacinthus*, *Buchenroedera*, *Cleistogama*, *Krebsia*, *Lotononis*, *Monocarpa* and *Polylobium*. *Lotononis* section *Oxydium* is strongly supported to be monophyletic in the molecular analyses and currently consists of 35 species (accommodated in 14 subsections as described by Van Wyk 1991b) distinguished from other sections by several characters, including single stipules at each leaf base and glabrous wing and keel petals. In the second group, *L.* section *Cleistogama* is sister to *L.* section *Monocarpa*, while *L.* sections *Aulacinthus*, *Lotononis* and *Polylobium* form a clade without support. The resolution in the rest of the group is low and relationships not clear. In the molecular analysis, *Lotononis* s.s. and the *Pearsonia* clade clearly share similarities in their sequences but morphologically *Lotononis* s.s. allies with the rest of the genus to form a monophyletic assemblage. When the molecular data were combined with the morphology, *Lotononis* remained monophyletic, although with moderate support. It is interesting to note the close agreement between the sectional classification proposed by Van Wyk (1991b) and the results of this study.

*Pearsonia*, *Robynsiophyton* and *Rothia* share several morphological characters that are unique among the genera of Crotalarieae, such as the uniform anthers, straight styles and presence of angelate esters of hydroxylupanine. The generic concepts of *Robynsiophyton* and *Rothia*, based mainly on anther characters, have been doubtful and *Robynsiophyton* was thought to be a local derivative of *Pearsonia* (Van Wyk 1991a). Taxonomic studies of the former two genera and a thorough examination of their morphology and anatomy revealed that these generic concepts are indeed sound and emphasizes the value of androecial characters in the Crotalarieae (Chapter 10; Boatwright et al. 2008c; Chapter 9; Boatwright and Van Wyk 2009; see Appendices B4 and B5).

The second clade comprises those species from *Lotononis* section *Leptis*, *Lotononis* section *Listia* and allies. This clade is moderately to strongly supported in the molecular analyses but lacks resolution in the morphological analysis. The concept of a monotypic *Listia* was broadened by Van Wyk (1991b) and treated as a section of *Lotononis* with several distinct characters. This broadened concept is supported in the analyses presented in this study. The absence of suitable material of the rare *Lotononis macrocarpa* Eckl. & Zeyh. (an anomalous species within this group) prevented its inclusion in this study. See Chapter 8, where *L. macrocarpa* has indeed been included in a reassessment of *Lotononis* s.l. Van Wyk (1991b) mentions that no apomorphies exist for *L.* section *Leptis*, which is clear from the morphological analysis where this section is left unresolved. The molecular results, however, indicate a close relationship between this section and *L.* sections *Digitata*, *Leobordea*, *Lipozygis* and *Synclistus*, all of which are successively sister to *L.* section *Listia*. The third clade comprises *L. hirsuta*, which groups with the *Crotalaria* clade.

***3.3.4 The Crotalaria clade***—The close relationship between *Crotalaria* and *Bolusia* has been mentioned by both Polhill (1982) and Van Wyk (1991a) and these authors suggested that *Bolusia* could merely be a local derivative of *Crotalaria*. Data from the present study indicates that *Bolusia* is sister to and not embedded within *Crotalaria* (*rbcL* analysis with multiple representatives), so that its generic status seems justified. *Bolusia* differs from *Crotalaria* mainly in its glabrous style and strongly coiled keel petals. Also included in this clade is *Lotononis hirsuta*, representing the monotypic section *Euchlora*. This species differs from all other *Lotononis* species in its peculiar tuberous habit and from most others in the very large, inflated pods, equally lobed calyx and very large seeds with smooth surfaces. It shares with *Crotalaria* and *Bolusia* the strongly inflated pods.

***3.3.5 Implications for generic classification***—The results generated in this study have very important implications for the generic classification system of the Crotalarieae. Detailed studies of character variation in the tribe over a period of more than 23 years are now nearing completion, allowing an informed evaluation of the congruence between morphological and molecular patterns. The results clearly show that the genera *Calobota* Eckl. & Zeyh. and *Euchlora* Eckl. & Zeyh. should be reinstated. A new genus should be described that will include *Lebeckia* sect. *Viborgioides,* as well as *L. inflata* and *L. mucronata*. *Spartidium* will be transferred to *Calobota* and *Wiborgia humilis* to the new genus (Chapters 5, 6 and 7; Boatwright et al. submitted). A new generic classification should be devised for *Lotononis* given the polyphyly of the genus based on molecular evidence and also the lack of generic apomorphies for *Lotononis* s.l. if *L.* section *Euchlora* is excluded (many of these co-occur in the latter). These changes are discussed in Chapter 5 and Chapter 8 and will clearly result in a more practical and predictable generic classification system for the tribe Crotalarieae.

# CHAPTER 4: ALKALOIDS AND FLAVONOIDS OF THE TRIBE CROTALARIEAE

## 4.1 INTRODUCTION

The distribution patterns of secondary metabolites in plants, although sometimes erratic, have the potential to provide valuable insight into phylogenetic relationships. This is especially true for the Fabaceae and more specifically the Papilionoideae, where chemical patterns are often in agreement with other evidence (Gomes et al. 1981; Van Wyk 2003b; Wink 2003). Some classes of compounds have been found to be more useful markers than others, such as alkaloids and flavonoids in legumes. Several syntheses of the available data and literature on alkaloids and flavonoids of papilionoid legumes are available (e.g. Harborne 1969, 1971; Mears and Mabry 1971; Salatino and Gottlieb 1980; Gomes et al. 1981; Kinghorn and Smolenski 1981; Kinghorn et al. 1982; Hegnauer and Grayer-Barkmeijer 1993; Southon 1994; Hegnauer and Hegnauer 1992–2001). This chapter aims to briefly review the chemotaxonomic value of alkaloids, flavonoids and other taxonomically useful compounds (cyanogenic glucosides and non-protein amino acids) in the Crotalarieae.

## 4.2 ALKALOIDS OF THE TRIBE CROTALARIEAE

Detailed studies of alkaloids in the Crotalarieae have made it possible to thoroughly evaluate their distribution patterns (e.g. *Aspalathus* – Van Wyk and Verdoorn 1989a; *Lebeckia* – Van Wyk and Verdoorn 1989b; *Lotononis* – Van Wyk and Verdoorn 1988, Van Wyk and Verdoorn 1989c, Verdoorn and Van Wyk 1992;

*Pearsonia* – Van Wyk and Verdoorn 1989d, Verdoorn and Van Wyk, 1990; Van Wyk and Verdoorn 1991a; *Rafnia* – Van Wyk and Verdoorn 1989a; *Robynsiophyton* – Van Wyk and Verdoorn 1991b; *Rothia* – Hussain et al. 1988; *Spartidium* – Van Wyk et al. 1989; *Wiborgia* – Van Wyk and Verdoorn 1989a) and their taxonomic value was discussed by Van Wyk et al. (1988) and Van Wyk and Verdoorn (1990). The chemical structures of all the various alkaloids are presented in Van Wyk and Verdoorn (1990). The Podalyrieae and Crotalarieae differ from all other genistoids in the absence of α-pyridone alkaloids and from most other tribes in the accumulation of hydroxylated lupanines and their esters, especially in their seeds (Van Wyk 2003b). Within the Crotalarieae, three groups can be distinguished based on alkaloid data (Van Wyk and Verdoorn 1990; Van Wyk 1991a):

1. An unspecialised group without α-pyridone alkaloids and without esters of alkaloids (*Aspalathus*, *Lebeckia*, *Rafnia*, *Wiborgia* and *Spartidium*, the so-called "Cape group").
2. A group specializing in lupanine-type esters of alkaloids (*Pearsonia*, *Robynsiophyton* and *Rothia*, i.e. the *Pearsonia* clade)
3. A group with macrocyclic pyrrolizidine alkaloids (*Crotalaria* and *Lotononis*).

These groups are largely consistent with those retrieved by phylogenetic studies on the Crotalarieae based on molecular (nrITS and *rbcL*) and morphological data. The genera of the "Cape group" form a monophyletic, although moderately supported clade while the *Pearsonia* clade receives strong support (Chapter 3; Boatwright et al. 2008a), as is also indicated by the chemical data.

The presence of macrocyclic pyrrolizidine alkaloids in *Crotalaria* and *Lotononis* is unique within the Crotalarieae and was thought to support a sister relationship between these genera (Van Wyk and Verdoorn 1990; Van Wyk 2003b).

It is now clear, however, that the occurrence of these alkaloids are rather the result of convergence as these genera do not share a sister relationship (see Chapters 3 and 8; Boatwright et al. 2008a). Quinolizidine alkaloids, which are present in most of the other genera of the Crotalarieae, are absent from *Crotalaria*, but present in some species of *Lotononis*, although they do not co-occur with pyrrolizidine alkaloids in the same species (Van Wyk and Verdoorn 1990). The pattern of alkaloids generally supports the new generic classification system for *Lotononis* as discussed in Chapter 8. *Lotononis* s.s. appears to accumulate only pyrrolizidine alkaloids, while the sections *Listia*, *Leptis* and related groups have quinolizidine alkaloids, albeit often only in trace amounts. The presence of pyrrolizidine alkaloids also supports the sister relationship between the Crotalarieae and Genisteae as these are the only tribes that have genera bearing pyrrolizidine alkaloids (Van Wyk 2003b).

Van Wyk and Verdoorn (unpublished) studied alkaloids in the leaves of some Crotalarieae genera and compared them to alkaloids extracted from the seed of the same species. They observed large quantitative differences in the alkaloid profiles of the leaves and seeds and found that seeds usually contain only a single or a few major alkaloids and are therefore conservative taxonomic characters. The African Genisteae genera *Argyrolobium*, *Dichilus*, *Melolobium* and *Polhillia* differ from the Crotalarieae in accumulating ammodendrine, lusitanine, cytisine, *N*-methylcytisine and camoensine in their seeds, as opposed to lebeckianine, 3β-hydroxylupanine and 13α-hydroxylupanine accumulated by *Aspalathus*, *Lebeckia*, *Lotononis* and *Pearsonia*. Species of *Crotalaria* and *Lotononis* s.s. were again unique in accumulating macrocyclic pyrrolizidine alkaloids. A detailed and rigorous study of seed alkaloids of all genera of the Crotalarieae will clearly yield interesting information and will contribute towards a better understanding of how alkaloids evolved within the tribe. It is clear that the extreme alkaloidal diversity found in *Lotononis* s.l. by Van Wyk and Verdoorn (1988, 1989c) and Verdoorn and Van Wyk (1992) can now be newly interpreted in relation to the phylogeny as revealed by molecular evidence (see Chapter 8).

## 4.3 FLAVONOIDS OF THE TRIBE CROTALARIEAE

Flavonoids in legumes and within the Crotalarieae, have not been as well studied as alkaloids, possibly due to the somewhat erratic patterns found in flavonoid data which limits their utility (Harborne 1971; Van Wyk 2003b). The occurrence of isoflavonoids in the Papilionoideae and the absence of a hydroxyl group in position five in all legumes are useful characters from flavonoid data (Hegnauer and Grayer-Barkmeijer 1993; Van Wyk 2003b). Again seed flavonoids appear to be more conservative than those of the leaves (Hegnauer and Grayer-Barkmeijer, 1993; De Nysschen et al. 1998).

De Nysschen et al. (1998) showed that the Crotalarieae and the Podalyrieae have the same four major seed flavonoids (butin, 3'-hydroxydaidzein, orobol and vicenin-2; chemical structures presented in De Nysschen et al. 1998), but none of these compounds are present in African Genisteae. No other study has explored flavonoid patterns within the Crotalarieae, which represents an obvious topic for future investigation.

Information on anthocyanins in legumes is rather poor (Harborne 1971). Van Wyk et al. (1995) showed in the Podalyrieae that anthocyanins were taxonomically informative, with each of the pink- or purple-flowered genera of the tribe having a diagnostic combination of floral anthocyanins (cyanidin and/or peonidin and esters of these pigments). The Cape genus *Hypocalyptus* Thunb. was shown to be unrelated, as it accumulates methylated anthocyanins in its flowers (Van Wyk et al. 1995). However, no information is available for the Crotalarieae. Notable variation in flower colour, with the sporadic occurrence of pink, blue, white or purple flowers, is seen only in *Aspalathus*, *Crotalaria*, *Pearsonia* and *Lotononis*. However, pink and blue flowers are rather rare in these genera, so that anthocyanins have a limited potential from a chemosystematic point of view. It may nevertheless be interesting to investigate the homology of blue/white/purple/pink flowers in *Aspalathus*, *Pearsonia*, *Lotononis* and *Crotalaria*, as these four genera are now known to represent four different lineages within the tribe (see Chapter 3).

## 4.4 OTHER USEFUL COMPOUNDS

In addition to alkaloids and flavonoids other classes of compounds also provide useful systematic information. Two of these are cyanogenic glucosides and non-protein amino acids. The occurrence of cyanogenic glucosides in legumes was summarized by Seigler et al. (1989). These compounds occur widely in various tribes of legumes, but in the tribe Crotalarieae they are restricted to the genus *Lotononis* (Van Wyk 1989; Van Wyk and Whitehead 1990). In *Lotononis* the cyanogenesis is due to the glucoside prunasin (Van Wyk 1989) and esters thereof (Seigler et al. 1989). Variation in this character within *Lotononis* is apparent as some infrageneric groups are acyanogenic (Van Wyk 1991b). This is, however, generally a useful character to distinguish *Lotononis* from morphologically similar genera, such as *Pearsonia* and *Rothia*. It is noteworthy that cyanogenesis is restricted to the one major clade in *Lotononis* (sections *Oxydium*, *Monocarpa*, *Cleistogama*, *Polylobium*, *Lotononis*, *Aulacinthus* and *Buchenroedera*) and that it is absent from the sections *Listia*, *Leptis* and related sections. This was an important character to support the infrageneric classification system proposed by Van Wyk (1991b) and now becomes highly relevant in the context of new generic delimitations in *Lotononis*. Cyanogenesis is a useful diagnostic character for a narrowed generic circumscription of *Lotononis* (see Chapter 8).

Non-protein amino acids are present in *Crotalaria* (Pilbeam and Bell 1979). This character appears to be unique to *Crotalaria* within the Crotalarieae but the compounds are widely distributed in other papilionoid tribes as well as in the Mimosoideae and Caesalpinioideae. Wink (2003) and Wink and Mohamed (2003) mapped the distribution of these and other chemical compounds onto phylogenetic trees derived from DNA sequence data to demonstrate their systematic significance. The high congruence between molecular systematic data and chemical data is noteworthy. The authors speculate that the presence of these compounds as chemical defence or signal compounds are important for plant survival, but are subject to evolution and selection, thereby complicating their interpretation in a phylogenetic context.

## 4.5 THE USE OF CAPE LEGUMES AS SOURCES OF TEA

The presence of several beneficial compounds in the leaves of legume species has made them popular as traditional sources of tea. These teas have historically been well-documented by several authors under numerous common names, usually describing a property of the tea or the distribution of the source plant. Some of the earliest accounts are those of Thunberg during his travels from

1772–1775 (Forbes 1986), Pappe (1847, 1857) and Marloth (1925). The species utilized are mainly from three genera of the Crotalarieae and Podalyrieae, namely *Aspalathus*, *Cyclopia* and *Rafnia*. Some of these herbal teas are already produced commercially such as rooibos- and honeybush tea (Van Wyk et al. 1997; Van Wyk and Gericke 2000; Van Wyk and Wink 2004). These teas are popular mainly because they do not contain caffeine or harmful stimulants and the phenolic constituents are thought to have beneficial properties (Van Wyk et al. 1997; Joubert et al. 2008). The major phenolic compounds of rooibos- and honeybush tea have already been the focus of several studies (e.g. De Nysschen et al. 1996; Van Heerden et al. 2003). A detailed review of rooibos tea (*Aspalathus linearis*) and honeybush tea (*Cyclopia* spp.) was done by Joubert et al. (2008). Teas obtained from *Rafnia* are tannin-rich and black in colour due to the high concentration of unknown phenolic compounds (Van Wyk and Gericke, 2000). Unlike the related *Aspalathus*, there is very little known about its flavonoid chemistry. These legumes are important not only as beverages, but also for various medicinal applications. A short review of the species traditionally used and their common names, medicinal uses and correct taxonomic identities is presented here.

The common- and scientific names of the sources of tea are listed in Table 1, along with the various authors who documented their uses. Thunberg during his travels of the Cape in 1770-1775 mentioned the use of the leaves of *Borbonia cordata* as a source of tea. This plant is an old Cape remedy and was used for respiratory ailments such as respiratory catarrh, whooping cough and bronchitis (Pappe 1847; Kling 1923; Watt and Brandwijk 1962). A decoction of the leaves of *Rafnia acuminata* (recorded as *Crotalaria perfoliata, Vascoa perfoliata* or *Rafnia perfoliata*) was claimed to be a powerful diuretic and was considered a cure for dropsy (Pappe 1847, 1857; Watt and Breyer-Brandwijk 1962; Forbes 1986). Kling (1923) recommended various teas for an array of respiratory ailments (including bronchitis and coughs), among these 'heuningtee' and 'hottentotstee' (both teas from species of *Cyclopia*), 'Stekeltee' (made from *Aspalathus* species) and 'boesmanstee' (a tea brewed from *Rafnia amplexicaulis*; Anonymous 2001). 'Stekelthee' was also said to have diuretic properties, but was primarily used to treat asthma and hydrothorax, whereas 'honigthee/heuningtee' was considered to be a restorative and was used in the treatment of chronic catarrh or consumption (Pappe 1847, 1857; Speight 1931).

Marloth (1925) in his 'The Flora of South Africa' applied the term 'bush tea' to the tea yielded by *Cyclopia* species. There is a difference in the teas produced in various districts as different species of *Cyclopia* are used (Hofmeyr and Phillips 1922; Marloth 1925; Kies 1951). Other tea sources mentioned by Marloth (1925) is the 'stekeltee' (*Borbonia cordata*) and 'rooibostee' (naaldtee) which are produced from *Aspalathus corymbosa* (now *Aspalathus linearis*) that below a certain altitude turns black when fermented, thus yielding 'black tea'.

The leaves of some *Psoralea* species, another largely Cape legume genus, are aromatic due to pellucid glands on the leaves and yielded what has been called 'schaapbos tee'. Marloth (1925) and Smith (1966) mentioned *P. bracteata* as the species utilized, but other authors attributed it to *P. decumbens* (Watt and Breyer-Brandwijk 1962; Rood 1994). No apparent medicinal properties were mentioned for this tea.

Marloth (1925) gave an account of the process by which 'bush teas' are prepared: "The young twigs are gathered when in flower and submitted to a process of fermentation or sweating by piling them up in a heap. They are then dried in the sun, and if this is done with care and expedition, the tea possesses a sweet aroma". This process is similar to the commercial process applied to rooibos and honeybush tea. Hofmeyr and Phillips (1922) described a second method used in the preparation of 'bush teas': "...for local consumption is to heat the leaves in an oven for about an hour to produce 'sweating,' after which they are dried in the sun. When thoroughly dry the leaves and smaller twigs are removed from the stem and larger branches, packed, and sold under various names." They also gave a summary of the commercial varieties of the *Cyclopia* species, which was slightly modified by Kies (1951) and is summarised in Table 1. Kies (1951) in her revision of *Cyclopia* mentioned *Aspalathus contaminatus* and *A. tenuifolia* as alternative sources of 'bush tea'. Both these species are synonyms of *Aspalathus linearis*, which is today used to produce rooibos tea (Dahlgren 1988). Dahlgren (1968) described the processing of cultivated rooibostee as follows: "The leafy branch ends are harvested by cutting and when brought to the fermentation yard cut again finely to a length of ca. 0.5 cm, moistened, bruised (e.g. with wooden hammers), and placed in heaps to ferment. Then the material is spread open in the sun and stirred intermittently until dry. After drying it is sifted, classified, and packed." The preparation of honeybush tea is much the same and *Cyclopia genistoides* and *C. intermedia* are the main species used (Van Wyk et al. 1997; Van Wyk and Gericke 2000; Van Wyk and Wink 2004; Joubert et al. 2008).

The chemical compounds in rooibos tea and other herbal teas were reviewed by Joubert et al. (2008). The presence of *aspalathin* (a chalcone *C*-glycoside) as the dominant phenolic compound in commercial rooibos tea is well known (Koeppen and Roux 1965). However, Van Heerden et al. (2003) showed that the species is chemically complex, with several other phenolic compounds present as major compounds in various wild populations of the species. The closely related *A. pendula* R.Dahlgren had rutin as major constituent. Preliminary work by Campbell (1998) showed that *Rafnia* species accumulate *C*-glycosides, apparently similar to those of *Aspalathus linearis*. It may be of considerable chemotaxonomic interest to explore the main patterns of flavonoids (especially in the "Cape group" of genera) since, apart from *Aspalathus linearis*, almost nothing appears to be known for any of the genera and species in the tribe Crotalarieae.

Table 4.1. Common names of herbal teas derived from legumes, with their correct scientific names and literature reference recording their use ([a] Pappe 1847, [b] Pappe 1857, [c] Hofmeyr and Phillips 1922, [d] Kling 1923, [e] Marloth 1925, [f] Spreight 1931, [g] Kies 1951, [h] Watt and Breyer-Brandwijk 1962, [i] Smith 1966, [j] Forbes 1986, [k] Rood 1994, [l] Van Wyk et al. 1997, [m] Van Wyk and Gericke 2000, [n] Anonymous 2001, [o] Van Wyk and Wink 2004, *Dahlgren 1988, **Schutte 1997, ***Campbell and Van Wyk 2001, ****Stirton 1989, *****Stirton 1986).

| Common name | Scientific name |
|---|---|
| Bergtee | *Borbonia parviflora* Lam[i] (now *Aspalathus crenata* (L.) R.Dahlgren*), *Cyclopia genistoides* (L.) R.Br. and *Cyclopia* spp.[k] |
| Blouteebossie | *Psoralea glaucina* Harv.[i] |
| Boertee/-tea | *Cyclopia buxifolia* (Burm.f.) P.Kies[h], *C. genistoides* (L.) R.Br.[h], *C. longifolia* Vog.[h], *C. subternata* Vog.[h], *C. subternata* Vog. and *Cyclopia* spp.[i] |
| Boesmanstee | *Rafnia* (*Vascoa*) *amplexicaulis* ("vascobossie") but no scientific name recorded[d], *Rafnia amplexicaulis* (L.) Thunb.[n] |
| Bossie(s)tee | *Aspalathus linearis* (Burm.f.) R.Dahlgren[m], *Borbonia lanceolata* L.[i] (now *Aspalathus angustifolia* (Lam.) R.Dahlgren*), *B. trinervia* Thunb. *non* L.[i] (*Aspalathus alpestris* (Benth.) R.Dahlgren*), *Cyclopia aurescens* P.Kies[h], *C. buxifolia* (Burm.f.) P.Kies[h], *C. genistoides* (L.) R.Br.[h], *C. longifolia* Vog.[h], *C. subteretifolia* P.Kies[g], *C. subternata* Vog.[h] |
| Bostee/Bush tea | *Cyclopia buxifolia* (Burm.f.) P.Kies[h], *C. genistoides* (L.) R.Br.[h], *C. longifolia* Vog.[h], *C. maculata* (Andrews) P.Kies[h], *Cyclopia* spp.[e], *C. subternata* Vog.[h] |
| Cape tea | *Cyclopia genistoides* (L.) R.Br.[h], *C. subternata* Vog.[h] |
| Gewone bos(sies) tee/Common bush tea | *Cyclopia sessiliflora* Eckl. and Zeyh.[g, h], *Cyclopia* spp.[i], *C. subternata* Vog.[g, h] |
| Heidelbergtee/-tea | *Cyclopia brachypoda* Hofmeyr and E.Phillips[c] (now *C. sessiliflora* Eckl. and Zeyh.**), *C. falcata* (Harv.) P.Kies[i], *C. sessiliflora* Eckl. and Zeyh.[h] |
| Heuningtee/Honey tea | *Cyclopia burtonii* Hofmeyr and E.Phillips[c, h], *C. genistoides* (L.) R.Br.[g, h, l, k], *Cyclopia* spp.[k, n], no scientific name.[d] |
| Heuningbostee/Honeybush tea | *Cyclopia intermedia* E.Mey.[l, m, o] |

| | |
|---|---|
| Honigt(h)ee | *Cyclopia genistoides* Vent.[a, b, f] (same as *C. genistoides* (L.) R.Br.). |
| Hotnotstee | *Cyclopia sessiliflora* Eckl. and Zeyh.[h] |
| Hottentotstee/-tea | *Cyclopia sessiliflora* Eckl. and Zeyh.[g], *C. subternata* Vog.[c], no scientific name.[d] |
| Hunger tea | *Cyclopia subternata* Vog.[h] |
| Hunger tea of the Hottentots | *Cyclopia sessiliflora* Eckl. and Zeyh.[h] |
| Koopmanstee | *Aspalathus contaminatus* Druce[h], *A. contaminatus* (Thunb.) Druce[g] (both the former and the latter are now *Aspalathus linearis* (Burm.f.) R.Dahlgren*), *A. linearis* (Burm.f.) R.Dahlgren[k] |
| Kouga bush tea | *Cyclopia intermedia* E.Mey.[g] |
| Naald(e)tee | *Aspalathus contaminata* Druce (*Borbonia pinifolia* Marl.)[i], *A. contaminatus* Druce[h], *A. contaminatus* (Thunb.) Druce[g], *A. corymbosa* E.Mey.[e] (all these species are now *Aspalathus linearis* (Burm.f.) R.Dahlgren*), *A. linearis* (Burm.f.) R.Dahlgren[k], *A. tenuifolia* DC.[g, h] (now *Aspalathus linearis* (Burm.f.) R.Dahlgren but the name sometimes also applied to *A. pendula* R.Dahlgren*). |
| Rooitee | *Aspalathus contaminata* (Thunb.) Druce[i] (now *Aspalathus linearis* (Burm.f.) R.Dahlgren*), *Cyclopia maculata* (Andrews) P.Kies.[i] |
| Rooibostee/-tea | *Aspalathus contaminata* Druce (*Borbonia pinifolia* Marl.)[i], *A. contaminatus* Druce[h], *A. contaminatus* (Thunb.) Druce[g], *A. corymbosa* E.Mey.[e] (all these species are now *Aspalathus linearis* (Burm.f.) R.Dahlgren*), *A. linearis* (Burm.f.) R.Dahlgren.[k, l, o] |
| Schaapbostee/Skaapbostee | *Psoralea decumbens* Ait.[k] (*Otholobium virgatum* (Burm.f) C.H.Stirton****), *Psoralea bracteata* L.[e, l] (*Otholobium bracteolatum* (Eckl. And Zeyh.) C.H.Stirton*****). |
| Skagaltee | *Borbonia parviflora* Lam.[h, l] (now *Aspalathus crenata* (L.) R.Dahlgren*). |
| Speldetee | *Aspalathus contaminata* Druce[i] (now *Aspalathus linearis* (Burm.f.) R.Dahlgren), *Aspalathus linearis* (Burm.f.) R.Dahlgren.[k] |
| Speltentee | *Cyclopia maculata* (Andrews) P.Kies.[h] |
| Sprinkaantee | *Aspalathus linearis* (Burm.f.) R.Dahlgren.[k] |
| Stekelt(h)ee | *Borbonia cordata* L.[a, e, h, i] (now *Aspalathus cordata* (L.) R.Dahlgren*), *B. parviflora* Lam.[b] (now *Aspalathus crenata* (L.) R.Dahlgren*), no scientific name.[d] |
| Suikertee(bos)/Sugar tea | *Cyclopia burtonii* Hofmeyr and E.Phillips.[c, g, h] |
| Swarttee/Black tea | *Aspalathus contaminatus* Druce[h], *A. contaminatus* (Thunb.) Druce (*Borbonia pinifolia* Marl.)[e, g,], *A. tenuifolia* DC.[l] (all species now *A. linearis* (Burm.f.) R.Dahlgren and *A. tenuifolia* sometimes also applied to *A. pendula* R.Dahlgren*). |

| | |
|---|---|
| Swartbergtee | *Cyclopia aurescens* P.Kies[h], *C. burtonii* Hofmeyr and E.Phillips[g, h], *C. subteretifolia* P.Kies.[g] |
| Veldtee | *Rafnia amplexicaulis* (L.) Thunb.[i, m, n], *R. perfoliata* E.Mey.[i] (now *R. acuminata* (E.Mey.) G.J.Campbell and B.-E.van Wyk***). |
| Vleitee/-tea | *Cyclopia ashtonii* Hofmeyr and E.Phillips[c] (now *C. bowieana* Harv.*), *C. bowieana* Harv.[g, h, i], *C. maculata* (Andrews) P.Kies[g, h, i], *C. tenuifolia* Lehm.[c] |
| No name | *Vascoa perfoliata* (Thunb.) DC.[a, b] (now *Rafnia acuminata* (E.Mey.) G.J.Campbell and B.-E.van Wyk***). |
| No name | *Borbonia cordata* L.[j] (now *Aspalathus cordata* (L.) R.Dahlgren*). |
| No name | *Crotalaria perfoliata*[j] (now *Rafnia acuminata* (E.Mey.) G.J.Campbell and B.-E.van Wyk***). |
| No name | *Psoralea decumbens* Ait.[h] (*Otholobium virgatum* (Burm.f.) C.H.Stirton****). |
| No name | *Borbonia undulata* Thunb.[h] (now *Aspalathus commutata* (Vog.) R.Dahlgren*). |
| No name | *Rafnia perfoliata* E. Mey.[h] (now *Rafnia acuminata* (E.Mey.) G.J. Campbell and B.-E.van Wyk***). |
| No name | *Rafnia angulata* Thunb.[m] |

# CHAPTER 5: EVIDENCE FOR THE POLYPHYLY OF *LEBECKIA*

## 5.1 INTRODUCTION

The current broad generic concept of *Lebeckia* Thunb. dates back to Bentham (1844) and Harvey (1862) and refers to a group of ca. 36 species of papilionoid legumes that occur mainly in the southern and western parts of South Africa, with some extending into Namibia. The group is particularly common in the Cape Floristic Region (CFR). Bentham (1844) reduced several genera described by Meyer (1836) and Ecklon and Zeyher (1836) to the synonymy of an expanded *Lebeckia*. This broadened concept included Meyer's *Stiza* and *Sarcophyllum*, together with Ecklon and Zeyher's *Acanthobotrya* and *Calobota.* A new sectional classification was proposed, based mainly on the shape of the keel and the morphology of the fruit. This comprised five sections, viz. section *Calobota*, section *Eulebeckia* Benth., section *Phyllodiastrum* Benth., section *Stiza* and section *Viborgioides*. Harvey (1862) followed this sectional classification of *Lebeckia* for his treatment in the Flora Capensis. For nearly 150 years, the generic concept and relationships between the morphologically rather diverse species were never studied in depth. A revision of *Lebeckia* s.s. (sections *Eulebeckia* and *Phyllodiastrum*) was recently completed by Le Roux and Van Wyk (2007, 2008, 2009). Their results show that the 14 species of *Lebeckia* s.s. can easily be distinguished by their acicular leaves and 5+5 anther arrangement, not only from all other species of the so-called "Cape group" of the tribe Crotalarieae (i.e. *Aspalathus*, *Rafnia* and *Wiborgia*) but also from all other species hitherto included in *Lebeckia*.

*Spartidium* is a monotypic genus that occurs in North Africa. The affinities of the genus within the genistoid legumes have been unclear for some time as a possible relationship with both *Retama* Raf. and *Lebeckia* has been suggested (Polhill, 1976). The genus is currently placed within the Crotalarieae based on the open androecial sheath, but an evaluation of its systematic position is clearly desirable. Polhill (1981) considered *Spartidium* to be "virtually indistinguishable from *Lebeckia*". He used the orientation of the seeds in the fruit and the North African distribution as the only key characters to distinguish *Spartidium* from other genera.

In a broad study of molecular (ITS, *rbcL*) and morphological data of 117 species representing all the genera of the Crotalarieae, Boatwright et al. (2008a; Chapter 3) discovered that *Lebeckia* is polyphyletic (Fig. 5.1a and 5.1b). This study revealed important new relationships within the Crotalarieae as well as *Lebeckia* and showed the need for new generic circumscriptions. The species can be readily accommodated in three easily recognizable morphological groups (genera) as was proposed by Boatwright et al. (submitted; see Chapters 6 and 7): (1) *Lebeckia* s.s. (*L.* section *Lebeckia,* including sections *Phyllodiastrum* and *Eulebeckia*); (2) *Calobota* [*L.* section *Calobota* and *L.* section *Stiza*, together with the monotypic North African *Spartidium*] and (3) *Wiborgiella* [*L.* section *Viborgioides*, together with *L. inflata*, *L. mucronata* and *Wiborgia humilis*]. Although the position of *Lebeckia mucronata* is unresolved it shares many morphological and anatomical characters with the other species placed within *Wiborgiella* and is thus included in this group.

In this chapter, new morphological, anatomical and molecular systematic evidence is presented to show that Bentham's (1844) broad concept of *Lebeckia* is polyphyletic.

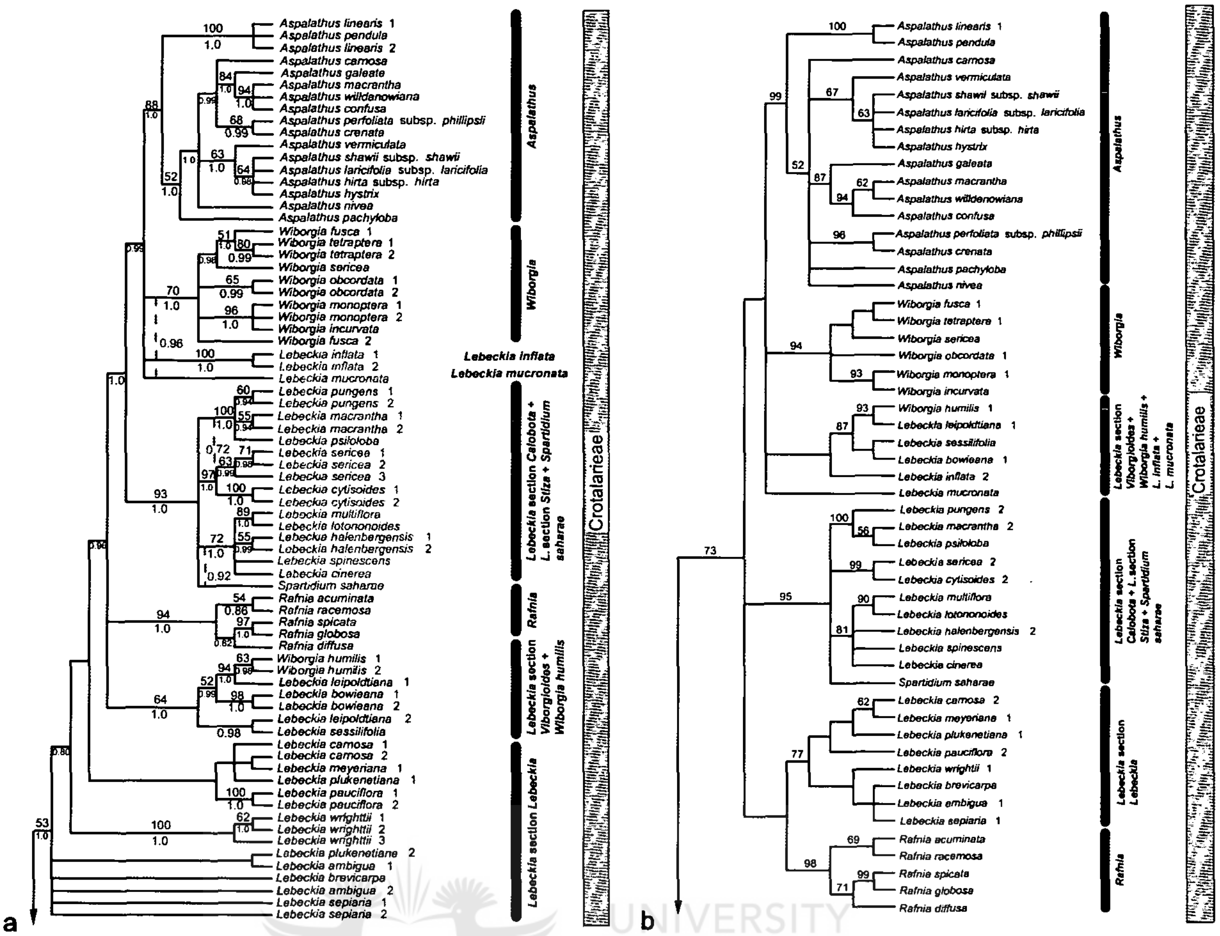

FIG. 5.1 The "Cape group" taken from (a) a strict consensus tree of the combined analysis of ITS and *rbcL* data (no. trees = 560; tree length = 1473 steps; consistency index = 0.50; retention index = 0.86); and (b) a strict consensus tree of the combined analysis of molecular (ITS and *rbcL*) and morphological data for the tribe Crotalarieae from Chapter 3 (Boatwright et al. 2008a; no. trees = 370; tree length = 1166 steps; consistency index = 0.53; retention index = 0.84). Bootstrap percentages are given above the branches and Bayesian posterior probabilities below the branches. Grey dotted lines indicate alternative topologies in the Bayesian analysis.

## 5.2 MORPHOLOGICAL AND ANATOMICAL EVIDENCE FOR THE PARAPHYLY OF *LEBECKIA*

***5.2.1 Habit and branches***—Most genera of the Crotalarieae have a shrubby habit (Polhill 1976), but variation in habit is quite pronounced within *Lebeckia*. Species of *Lebeckia* section *Lebeckia* are predominantly suffrutescent plants that branch mainly at ground level, whereas the species of the remaining sections are almost invariably woody shrubs. A strongly spinescent habit is characteristic of *Lebeckia* section *Stiza* but also of two species of section *Calobota*, viz. *L. acanthoclada* and *L. spinescens.* Both sections *Calobota* and *Stiza* have green young branches (except *L. acanthoclada*), as opposed to the woody, rigid, ramified brown to greyish branches of section *Viborgioides* (similar to the genus *Wiborgia*). In species with green stems [sections *Calobota*, *Lebeckia* and *Stiza*, and *Spartidium saharae*] a large part of the cortex is composed of chlorenchyma which serves a photosynthetic function (Metcalfe and Chalk 1950). This layer is absent in species of section *Viborgioides* and also *L. mucronata*.

***5.2.2 Leaves***—Leaves are extremely variable, ranging from trifoliolate and petiolate (sections *Calobota* and *Viborgioides*), to unifoliolate (section *Stiza*) or simple (section *Calobota* and *Spartidium*) to completely phyllodinous (and acicular) in section *Lebeckia*. Cultivated plants of the section *Stiza* showed that the juvenile leaves are petiolate and trifoliolate, but a loss of the lateral leaflets and shortening of the petioles result in unifoliolate leaves on the older branches, as was mentioned by Polhill (1976) and Dahlgren (1970a). This transition is also seen in *L. obovata* Schinz. Stipules are absent in all but two species of *Lebeckia* s.l.: *L. wrightii* and *L. uniflora* M.M.le Roux and B.-E.van Wyk (Le Roux and Van Wyk 2009).

Transverse sections through the leaves of *Lebeckia* species (Fig. 5.2) revealed a remarkable difference between the species of *Calobota*/*Stiza*/*Spartidium* on the one hand (hereafter called the *Calobota* group) and *Viborgioides*/*L. inflata*/*L. mucronata*/*Wiborgia humilis* on the other hand (hereafter called the *Viborgioides* group), namely that the former group has isobilateral leaves, while the latter has dorsiventral leaves. This difference was unexpected, as anatomical characters are generally regarded as conservative. Even more remarkable was the exact congruence between the anther arrangements of the two groups (respectively 4+1+5 and 4+6 – see later). Leaves of *Lebeckia* s.s. are completely different from the species mentioned above, as they are phyllodinous, acicular and terete in transverse section.

Another interesting difference between the *Calobota* group and the *Viborgioides* group is the presence of mucilage cells in the latter but not the former (Fig. 5.2). In this character, the *Viborgioides* group agrees with other Cape genera (*Aspalathus*, *Rafnia* and *Wiborgia*, as well as the predominantly Cape *Lebeckia* s.s.). In contrast, the *Calobota* group, which extends into arid regions (Northern Cape and Namibia), does not have mucilage cells in mature leaves.

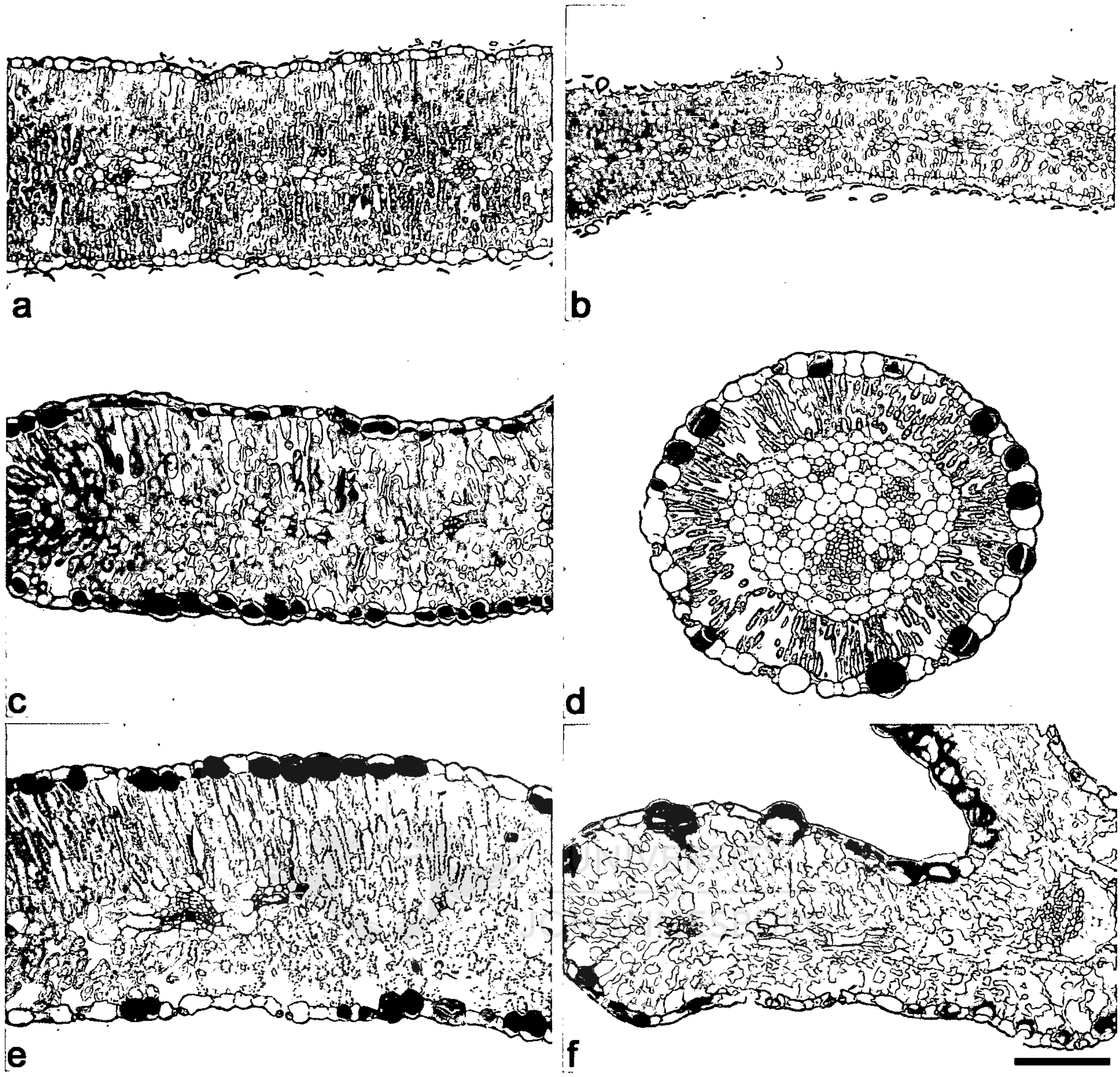

FIG. 5.2 Transverse sections through the leaves of *Lebeckia* species, showing isobilateral (a, b, *Calobota* group) and dorsiventral (c, e, f, *Viborgioides* group) leaflet laminas and an acicular, terete, phyllode with a circular arrangement of palisade cells (d, *Lebeckia* s.s.). Note the presence of mucilage cells in the epidermis. (a) *L. cytisoides;* (b) *L. pungens*; (c) *L. sessilifolia;* (d) *L. sepiaria*; (e) *L. inflata*; (f) *L. mucronata*.

Voucher specimens: (a) *Boatwright et al. 114* (JRAU); (b) *Boatwright et al. 106* (JRAU); (c) *Van Wyk 2120* (JRAU); (d) *Le Roux et al. 10* (JRAU); (e) *Johns 162* (JRAU); (f) *Vlok 1726* (JRAU). Scale bar = 0.2 mm.

The North African *Spartidium*, however, has mucilage cells in the epidermis, as do immature leaves of *L. pungens*, suggesting that there is a loss of these cells as the leaves mature (Boatwright, pers. obs.). Mucilage cells are widely distributed throughout the various plant families and several authors have speculated about their function (Gregory and Baas, 1989). Although experimental evidence is lacking, mucilage cells are thought to aid in water storage and reduction of transpiration, protection against intensive radiation and also against herbivory (Gregory and Baas, 1989). Mucilage cells are often associated with plants that occur in Mediterranean climates (Van der Merwe et al. 1994). Bredenkamp and Van Wyk (1999) speculated that in *Passerina* L. (Thymelaeaceae) the mucilage serves as a regulator of hydration in the leaves, protecting them against water loss, but also helping to accumulate reserve water in the leaves. *Lebeckia* s.s. and the *Viborgioides* group are restricted to the CFR and therefore diversifying in a Mediterranean climate could explain the presence of the mucilage cells in these taxa. It is interesting to note the presence of mucilage cells in *Spartidium saharae*, which also occurs in a Mediterranean climate. The *Calobota* group (excluding *Spartidium*) extend out of the CFR into summer rainfall, more arid regions and show a different adaptation to drought, viz. isobilateral leaves (Fig. 5.2 a, b; also in *Spartidium*). Van der Merwe et al. (1994) mention that the presence of more layers of palisade parenchyma improves the transport of water through the leaves and also offers increased protection to the chloroplasts. In contrast, the leaves of species within the *Viborgioides* group are dorsiventral (Fig. 5.2 c, e, f). In *Lebeckia* s.s., the acicular leaves have a complete circular zone of palisade cells, with no spongy parenchyma (Fig. 5.2 d).

The petioles are always shorter than the leaflets in the *Viborgioides* group. In this group the persistent petioles become hard and woody when the leaflets are shed, contributing to the rigid and somewhat thorny appearance of the branches. These characters are also found in some species of *Wiborgia* s.s. (Dahlgren 1975). In the *Calobota* group, the petioles are either longer or shorter than the leaflets and sometimes persistent, but never rigid and spinescent. The acicular leaves of most species of *Lebeckia* s.s. are articulated or "jointed" near the middle or reduced to petioles in species with unarticulated leaves, i.e. the leaves are phyllodinous (Dahlgren 1970a). This distinctive character serves as a convincing synapomorphy for this genus in its narrow circumscription.

***5.2.3 Inflorescences***—As in most Crotalarieae, the inflorescences in *Lebeckia* are all terminal, multi-flowered racemes, varying in length and number of flowers. In *Lebeckia* s.s., the inflorescences may be relatively long and are often densely flowered with up to 93 flowers per raceme, for example in *L. brevicarpa* (Le Roux and Van Wyk 2007). Species of section *Calobota* generally have fewer flowers per inflorescence, except in *L. melilotoides* Dahlgr., where more than 100 flowers are found on the elongated spikes (Dahlgren 1967b). The racemes of the three species of section *Stiza* are characteristically spine-tipped. Very short and few-flowered inflorescences are found in *L.* section *Viborgioides*, with the flowers often solitary in *L. bowieana* Benth.

***5.2.4 Flowers***—The calyx structure is often an important generic character in the Crotalarieae. *Lebeckia* species normally have equally lobed or "lebeckioid" calyces (Polhill 1976), as opposed to the zygomorphic calyx ("lotononoid") in *Lotononis* (DC.) Eckl. and Zeyh. and *Pearsonia* Dümmer or the bilabiate calyx typical of all members of the tribe Genisteae (Van Wyk 1991b; Van Wyk and Schutte

1995). In the *Calobota* and *Viborgioides* groups, the carinal lobe is slightly narrower than the upper and lateral lobes, whereas in *Lebeckia* s.s. it is equal to the other lobes (Fig. 5.3). In the former two groups, the calyces are pubescent or at least glabrescent as opposed to the usually glabrous calyces found in section *Lebeckia* (*L. wrightii* and *L. uniflora* are exceptions in having a sparsely pubescent calyx).

The pubescence of the petals, the shape of the keel petal and the arrangement of the anthers closely follow the three major groups within *Lebeckia* s.l. Glabrous petals are found in *Lebeckia* s.s. and the *Viborgioides* group, whereas species of the *Calobota* group generally have pubescent petals (or at least pilose along the dorsal midrib of the standard petal). *Lebeckia macrantha* and *L. psiloloba* are the only exceptions and have totally glabrous petals. The keel petals in *Lebeckia* s.s. are characteristically rostrate as opposed to the obtuse keel petals found in the other groups (Fig. 5.3).

***5.2.5 Anthers***—Surprisingly, it was found that the size and shape of the carinal anther are diagnostic for each of the three groups in *Lebeckia* s.l. In *Lebeckia* s.s., the carinal anther resembles the long, basifixed anthers (Fig. 5.3 h3) resulting in a 5+5 arrangement. In the *Calobota* group (including *Spartidium saharae*), the carinal anther is intermediate between the dorsifixed and basifixed anthers (Fig. 5.3 e3, f3, g3), resulting in a 4+1+5 anther configuration (i.e., four long basifixed anthers, an intermediate carinal anther and five short dorsifixed anthers). The carinal anther is usually attached a little higher up. In the *Viborgioides* group, the carinal anther resembles the short, dorsifixed anthers (Fig. 5.3 a3, b3, c3, d3), resulting in a 4+6 anther arrangement (i.e., four long anthers and six short anthers). The anther arrangement is therefore in perfect agreement with the leaf anatomy of the three groups.

***5.2.6 Fruit and seeds***—Pods in the Crotalarieae are an important source of systematic information, as specialisations for seed protection and dispersal may result in structural differences. *Lebeckia* s.l. displays a great diversity of fruit structure, including dehiscent and indehiscent fruits that are either inflated or laterally compressed, and with or without wings (Polhill 1976). Fruits of *Lebeckia* s.s. are terete to semi-terete and thick- or thin-walled, with wings on the upper suture in some species, e.g. *L. meyeriana.* Species of the *Calobota* group generally have terete or semi-terete pods that are thick-walled and spongy or the fruits are thin-walled (membranous), laterally compressed and pubescent or glabrous, as is also found in *Spartidium saharae*. In contrast, the fruits of section *Viborgioides* (and *L. inflata*) are inflated and always glabrous, with highly sclerified, thin walls. The placement of *Wiborgia humilis* within the *Viborgioides* group is supported by fruit structure. *Wiborgia humilis* has inflated pods that lack wings on the upper suture and do not have highly sclerified fruit walls. In contrast, the winged samaras of the rest of *Wiborgia* are laterally compressed and have highly sclerified fruit walls in most species (Dahlgren 1975).

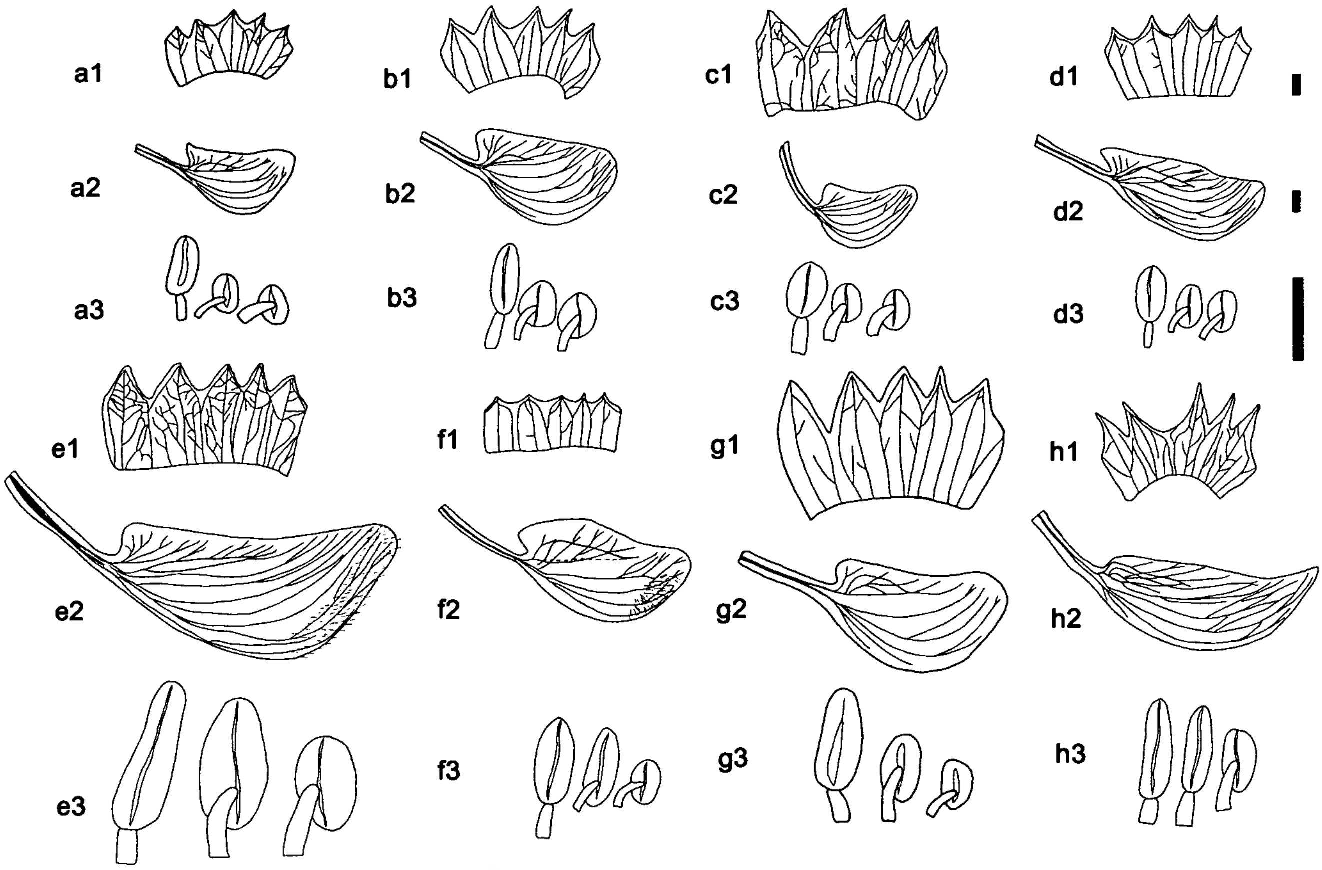

FIG. 5.3. Drawings of the calyces (vestiture not shown), keel petals and anthers of selected species of *Lebeckia* s.l., *Spartidium saharae* and *Wiborgia humilis*. Note the relative size of the carinal lobe of the calyx, the apex and vestiture of the keel petal and the relative size of the carinal anther. (a1–a3) *W. humilis*; (b1–b3) *L. mucronata*; (c1–c3) *L. inflata*; (d1–d3) *L. leipoldtiana*; (e1–e3) *L. cytisoides*; (f1–f3) *L. pungens*; (g1–g3) *S. saharae*; (h1–h3) *L. sepiaria*.

Voucher specimens: (a1, a3) *Van Wyk 3530* (JRAU); (a2) *Boatwright et al., 216* (JRAU); (b1–b3) *Stirton 10880* (JRAU); (c1–c3) *Vlok et al. 2* (JRAU); (d1–d3) *Boatwright et al. 123* (JRAU); (e1–e3) *Boatwright et al. 114* (JRAU); (f1) *Taylor 9386* (NBG); (f2) *Boatwright et al. 106* (JRAU); (f3) *Van Wyk 3252* (JRAU); (g1–g3) *Hill 1910* (K); (h1, h3) *Barker 6515* (NBG); (h2) *Le Roux et al. 24* (JRAU). Scale bars (for all calyces, all keel petals and all anthers, respectively) = 1.0 mm.

Polhill (1976, 1981) used the orientation of the seed in *Spartidium* as the only diagnostic character to separate this genus from *Lebeckia* s.l. A study of most of the species showed that at least three species of the *Calobota* group (*L. macrantha*, *L. psiloloba* and *L. pungens*) have the seed oriented at right angles to the placenta, exactly as in *Spartidum saharae*.

The seed surface of species in *Lebeckia* s.s. is invariably rugose, while the seeds of only one species in the *Calobota* group (*L. lotononoides*) and one species in the *Viborgioides* group (*L. inflata*) have rugose seeds (Le Roux and Van Wyk 2007, 2008, 2009; Boatwright and Van Wyk 2007).

## 5.3 MOLECULAR EVIDENCE FOR THE PARAPHYLY OF LEBECKIA

***5.3.1 Combined molecular analyses***—In the combined molecular analyses (Parsimony and Bayesian analyses; Fig. 5.1a) presented in Chapter 3 (Boatwright et al. 2008a), the *Calobota* group is clearly monophyletic with very strong support. In the Bayesian analysis, *Spartidium* groups with the *Lebeckia multiflora* group with strong support (Fig. 5.1a). *Lebeckia* section *Viborgioides* (including *Wiborgia humilis*) is monophyletic with weak to strong support, but the positions of *L. inflata* and *L. mucronata* are unresolved. It is interesting to note that molecular evidence strongly supports the exclusion of *Wiborgia humilis* from *Wiborgia* and the transfer of this species to the *Viborgioides* group. Surprisingly, *Lebeckia* s.s. is unresolved in the molecular analyses. Morphologically this group is very distinct from the other groups of *Lebeckia* s.l. and all other Cape Crotalarieae.

***5.3.2 Combined molecular and morphological analysis***—When the molecular data were combined with morphological data (Fig. 5.1b), the resolution within the “Cape group” and among the three groups of *Lebeckia* s.l. was much improved. The *Calobota* group is again strongly supported as monophyletic. Within the *Viborgioides* group, *L.* section *Viborgioides* including *Wiborgia humilis* is monophyletic with strong support and *L. inflata* is sister to this group, albeit without support. The position of *L. mucronata*, however, remains unresolved in this analysis, although abundant morphological and anatomical evidence suggests its placement within this group. The inclusion of *W. humilis* in the *Viborgioides* group again receives strong support. With the addition of morphological data *Lebeckia* s.s. is moderately supported as monophyletic as opposed to being unresolved in the molecular analyses (Chapter 3; Boatwright et al. 2008a).

## 5.4 TAXONOMIC IMPLICATIONS

Major continuities and discontinuities in morphological characters among the three groups discussed above closely agree with the three main clades revealed by genetic analysis (Fig. 5.1a and 5.1b). The new system proposed by Boatwright et al. (submitted) is based on a wider consideration of the intricate relationships amongst all genera of the tribe Crotalarieae, all of which have been revised in recent years (*Pearsonia* – Polhill 1974; *Wiborgia* – Dahlgren 1975; *Crotalaria* – Polhill 1982; *Aspalathus* – Dahlgren 1988; *Lotononis* – Van Wyk 1991b; *Rafnia* – Campbell and Van Wyk 2001; *Bolusia* – Van Wyk 2003a, Van Wyk et al. submitted; *Lebeckia* s.s. – Le Roux and Van Wyk 2007, 2008, 2009; *Robynsiophyton* – Chapter 9; Boatwright and Van Wyk 2009; *Rothia* – Chapter 10; Boatwright et al. 2008c). Dahlgren (1970a) and Polhill (1976) both discussed the high incidence of convergence in the tribe Crotalarieae and the intricate relationships between the genera. The difficulty in determining generic limits within the Crotalarieae is discussed by Polhill (1976), who emphasized that it would be unwise to propose modifications to the system without a clear understanding of the patterns of character state distributions. Furthermore, alterations to the system should result in a more predictive and useful system without running the risk of instability of circumscriptions and nomenclature. In existing keys to the genera of the Crotalarieae (Polhill 1981; Van Wyk and Schutte 1995), the lack of uniformity and clear-cut diagnostic characters for *Lebeckia* s.l. is clearly reflected in the fact that the genus keys out no less than three times (in both keys). Unique combinations of morphological characters have now been identified for the three main groups that clearly should be given generic status. The improvement in generic delimitations is also reflected in the following key.

### *5.4.1. Key to the genera of the Crotalarieae*

1. Leaves acicular, terete:
    2. Ovary 2 to 4 ovulate, pods few-seeded (±1 to 2-seeded)..........***Aspalathus***
    2. Ovary with more than 6 ovules, pods many-seeded (if rarely few-seeded, then the pods strongly inflated with spongy walls)....................***Lebeckia* s.s.**
1. Leaves digitate, unifoliolate or simple (flat, never terete)................................3
    3. Stipules present..........................................................................4
        4. Style curved upwards; anthers dimorphic..................................5
            5. Stipules asymmetrical or single; style glabrous and not helically coiled; keel obtuse or rostrate; anther arrangement 4+6, 4+1+5 or very rarely 5+5.................................***Lotononis***

5. Stipules symmetrical when present; style with 1 or 2 lines of hairs or glabrous and helically coiled; keel strongly rostrate (often at right angles) or helically coiled; anther arrangement 5+5........................................................................6

6. Stipules dentate; beak of keel and style helically coiled, style glabrous.........................................***Bolusia***

6. Stipules entire; beak of keel and style not helically coiled, style with 1 or 2 lines of hairs..............***Crotalaria***

4. Style straight or rarely down-curved; anthers similar in size and shape........................................................................7

7. Stamens nine (five fertile and four lacking anthers)..................................................***Robynsiophyton***

7. Stamens 10 (all fertile)..................................................8

8. Anthers all rounded; prostrate annuals.............***Rothia***

8. Four anthers basifixed, six attached slightly higher up, all elongate; perennial herbs or shrubs..........***Pearsonia***

3. Stipules absent:

9. Calyx with upper and lateral lobes fused on either side.....***Lotononis***

9. Calyx sub-equal (upper and lateral lobes not fused)...................10

10. Leaves sessile; upper suture of pod asymmetrically convex..................................................................11

11. Plants glabrous except occasionally on bracts and bracteoles; usually turning black when dried.........***Rafnia***

11. Plants usually pubescent on all parts, if leaves glabrous then standard petal hairy and inner surface of

calyx glabrous; not turning black when dried..................................................***Aspalathus***

10. Leaves usually petiolate, if leaves sessile then plants with many-seeded pods and at least some hairs on leaves or stems; upper suture of pod symmetrically convex..........................12

12. Petals pubescent; at least on the dorsal midrib of the standard petal (if glabrous then plants strongly spinescent, woody, practically leafless shrubs); twigs green (bark formation late, chlorenchyma present); leaves isobilateral.........................................***Calobota***

12. Petals glabrous; twigs brown (bark formation early, chlorenchyma absent; if twigs rarely green then plant a short-lived fireweed); leaves dorsiventral...................13

13. Fruits winged, indehiscent; carinal anther intermediate (anthers 4+1+5)...............***Wiborgia***

13. Fruits without wings, dehiscent (if rarely indehiscent then ovary and fruit distinctly stalked); carinal anther resembles short anthers (anthers 4+6).............................................***Wiborgiella***

# CHAPTER 6: TAXONOMY OF THE GENUS *CALOBOTA*

## 6.1 INTRODUCTION

The genus *Calobota* should clearly be reinstated to accommodate the 16 species of the *Calobota* group (Chapter 5; Boatwright et al. submitted). *Calobota* was originally described by Ecklon and Zeyher (1836) and consisted of two species, *C. cytisoides* and *C. pulchella*, which are actually the same species (now *C. cytisoides*). The genus was later reduced to a section of an expanded concept of *Lebeckia* by Bentham (1844). Several species which he included in the section were previously placed in other genera by Ecklon and Zeyher (1836). Harvey (1862) followed the sectional classification of Bentham in the last revision of the genus *Lebeckia*. In Chapter 5 and Boatwright et al. (submitted) the reinstatement of *Calobota* is proposed which now also includes *Lebeckia* section *Stiza* and the monotypic genus *Spartidium*, based on the results of a phylogenetic study of the tribe Crotalarieae (Chapters 3 and 5; Boatwright et al. 2008a). These studies, based on molecular (nrITS and *rbcL*) and morphological data, revealed that the genus *Lebeckia* is not monophyletic and a division into three genera is therefore proposed by Boatwright et al. (submitted), viz. *Lebeckia* s.s., *Calobota* and *Wiborgiella*. The species of *Calobota* occur throughout the Cape and extend into Namibia. Some of the species are important components of the Sperrgebiet, a species-rich area of south-western Namibia (Burke and Mannheimer 2004), while two other species, *C. namibiensis* and *C. obovata* are endemic to Namibia (Craven and Vorster 2006). *Calobota saharae*, however, is endemic to North Africa and occurs in Algeria, Morocco and Libya (Polhill 1976).

*Calobota* can be distinguished from *Lebeckia* and *Wiborgiella* by a combination of the following characters: green young twigs, uni- or trifoliolate to simple, laminar leaves, hairy petals (*C. cuspidosa* and *C. psiloloba* are exceptions), anther configuration of 4+5+1 and the laterally compressed or semi-terete, usually pubescent pods. The species within *Calobota* are often difficult to distinguish from one another due to the close similarity between related species. This motivated the need for a taxonomic revision that would provide clarity on the number of species within *Calobota* and a key to these species.

In this chapter, a detailed treatment of the genus *Calobota* is presented including a key to the species, complete nomenclature, typification, formal descriptions, the known geographical distribution and illustrations of all the species.

## 6.2 DISCUSSION OF CHARACTERS

***6.2.1 Vegetative morphology and anatomy***—HABIT AND BRANCHES—All the species of *Calobota* are perennial, multi-stemmed shrubs (Fig. 6.1) usually about 1.0–1.5 m in height, but *C. cuspidosa* can reach heights of up to 4 m. *Calobota lotononoides* is a decumbent shrublet that reaches heights of up to 0.5 m and has extensive underground branches. This species appears to be adapted to sandy habitats as the underground branches allow the stems and leaves to emerge above ground when they become buried (Boatwright and Van Wyk, 2007). *Calobota acanthoclada*, *C. cuspidosa*, *C. psiloloba*, *C. pungens* and *C. spinescens* are all spinescent shrubs, with the branch ends and inflorescences terminating in spines. The typical form of *C. sericea* sometimes also has spinescent branches, but they are more often unarmed.

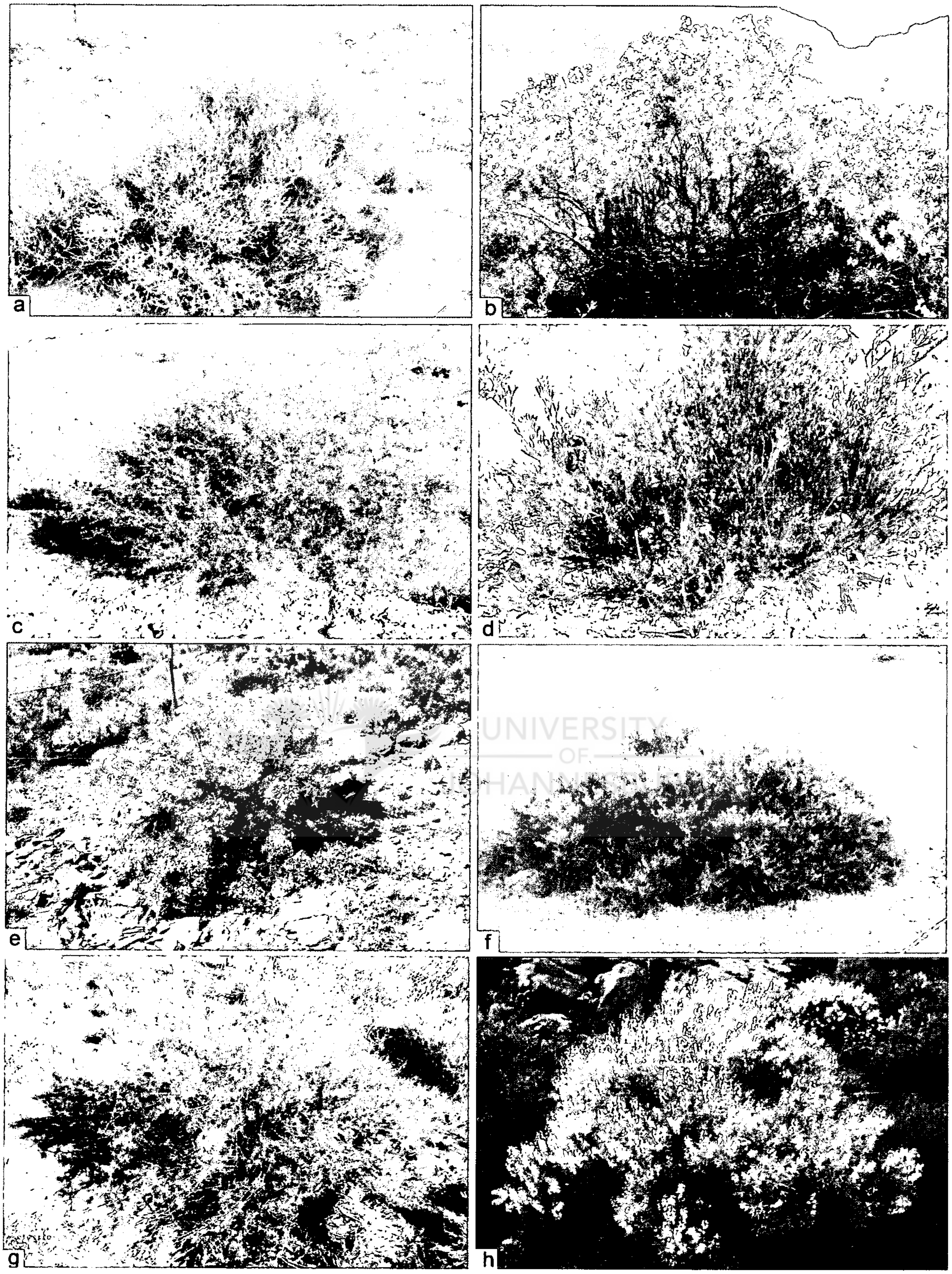

Fig. 6.1 Habit of *Calobota* species. (a) *C. cinerea*; (b) *C. cytisoides*; (c) *C. halenbergensis*; (d) *C. lotononoides*; (e) *C. pungens*; (f) *C. sericea*; (g) *C. spinescens*; (h) *C. thunbergii*.

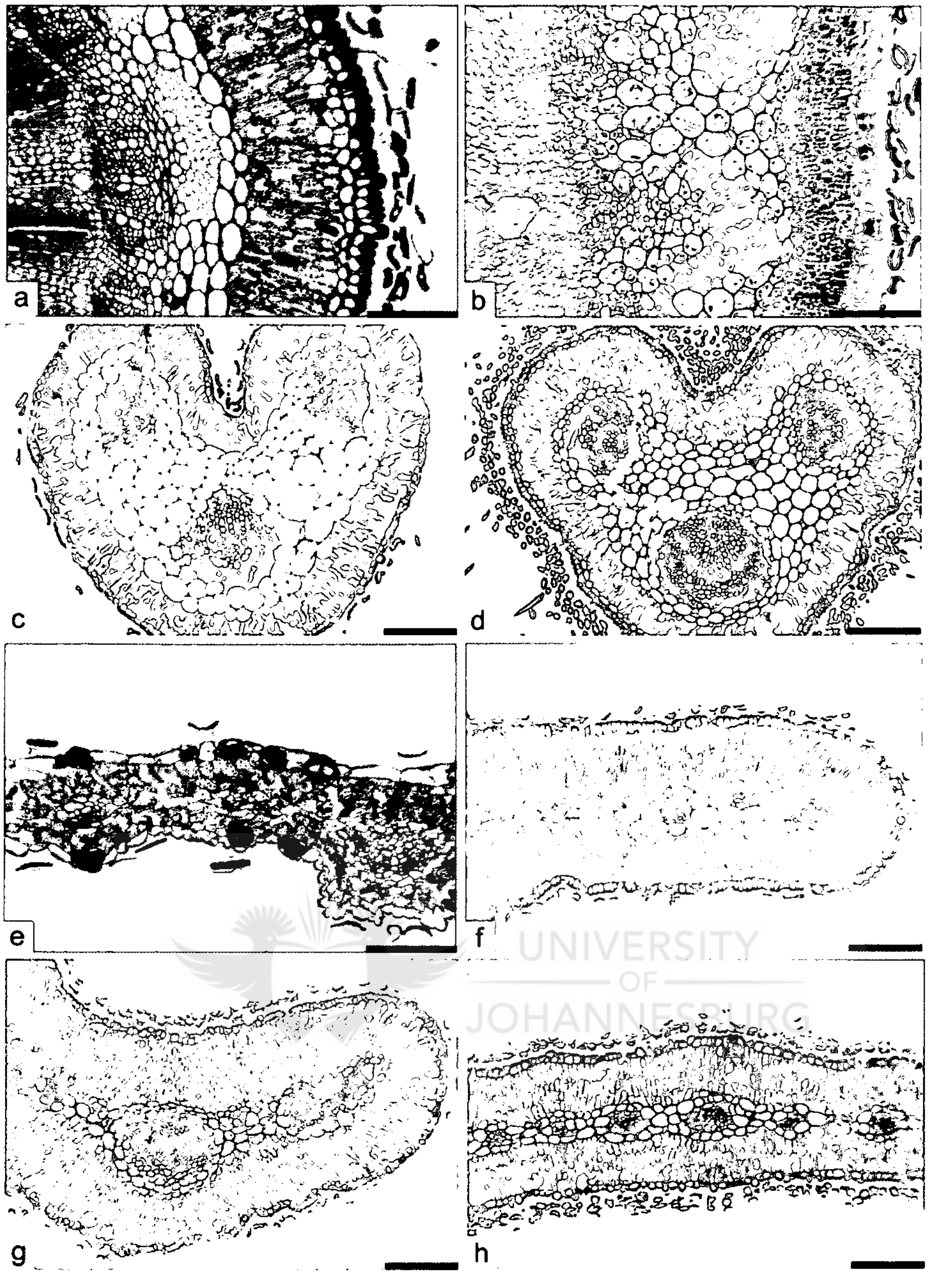

Fig. 6.2 Transverse sections through the stems and leaves of *Calobota* species. (a) Portion of the stem of *C. spinescens*; (b) Portion of stem the of *C. sericea*; (c) Petiole of *C. lotononoides;* (d) Petiole of *C. elongata*; (e) Portion of the juvenile leaf of *C. pungens*; (f) Portion of the leaf of *C. thunbergii*; (g) Potion of the leaf of *C. linearifolia*; (h) Portion of the leaf of *C. obovata*. Voucher specimens: (a) *Boatwright et al. 158* (JRAU); (b) *Boatwright et al. 138* (JRAU); (c) *Boatwright et al. 142* (JRAU); (d) *Van Wyk 2562b* (JRAU); (e) *Boatwright et al. 106* (JRAU); (f) *Boatwright et al. 151* (JRAU); (g) *Dean 673* (JRAU); (h) *Kers 152* (WIND). Scale bars: (a, b, e) 0.1 mm; (c, d, f, g, h) 0.2 mm.

The young branches in species of *Calobota*, with the exception of *C. acanthoclada*, are green as opposed to the brown branches found in most species of *Wiborgiella*. This is due to the presence of several chlorenchyma layers below the epidermis (Fig. 6.2), a feature usually found in papilionoid legumes where the leaves are reduced or absent (Metcalfe and Chalk 1950). Although green stems are also found in other genera of the Crotalarieae, notably *Crotalaria, Lebeckia*, *Lotononis* and *Rafnia*, it is a useful character to distinguish *Calobota* from *Wiborgiella* and *Wiborgia*. Some species of *Calobota* lack leaves on their mature branches and in these it is likely that the stem performs the main photosynthetic function. The epidermis in most species is covered by a thick cuticle and the epidermal cells are bottle-shaped.

LEAVES—Leaves in *Calobota* vary from trifoliolate or rarely 5-foliolate to unifoliolate or simple. In three species with unifoliolate leaves, *C. cuspidosa*, *C. psiloloba* and *C. pungens*, the juvenile leaves are trifoliolate and become unifoliolate on the mature branches due to a loss of the lateral leaflets and shortening of the petioles (Dahlgren 1970; Polhill 1976; Boatwright et al. submitted). A similar reduction has been observed in *C. obovata*, which also has unifoliolate leaves on the mature branches. The leaves of *Calobota* species are invariably laminar as opposed to the acicular, phyllodinous leaves of *Lebeckia* s.s. and usually have long, slender petioles. The leaf margins are entire and stipules are lacking. The leaves are always pubescent or at least pilose.

The leaf arrangement in *Calobota* is alternate and widely spaced, but in *C. acanthoclada* and *C. spinescens* the leaves are fasciculate. This is a useful character to distinguish especially *C. spinescens* from *C. sericea* with which it is often confused.

Leaflet shape varies from oblanceolate to elliptic or obovate to suborbicular and less often spathulate. The apices may be acute, obtuse, retuse, truncate, mucronulate or recurved-mucronate and the base of the leaves angustate, attenuate or cuneate. *Calobota sericea* is a highly variable species and four regional forms can be distinguished based mainly on leaf size, shape and especially the width of the leaflets.

The anatomy of the leaves of *Calobota* species (Fig. 6.2) provided some interesting characters to distinguish it from *Lebeckia* and *Wiborgiella*. In *Calobota*, the leaves are isobilateral and lack mucilage cells in the epidermis. Transverse sections through juvenile leaves of *C. pungens* do show mucilage cells in the epidermis, suggesting that there is a loss of these cells in *Calobota*. *Calobota saharae* is an exception in that mucilage cells are present in mature leaves. Gregory and Baas (1989) speculate that these cells are usually associated with plants that occur in Mediterranean climates. *Calobota saharae* is endemic to Mediterranean North Africa and this could explain the retention of these cells. In *Lebeckia* the leaves are acicular with palisade parenchyma adjacent to the epidermis and mucilage cells present. *Wiborgiella* species have dorsiventral leaves (cleary differentiated into palisade and spongy parenchyma) with mucilage cells present in the epidermis.

***6.2.2 Reproductive morphology and anatomy***—INFLORESCENCE—The structure of the inflorescence in *Calobota* is fairly uniform and all species have terminal racemes which only vary in length and in the number of flowers per raceme. This type of inflorescence is rather common in Papilionoideae and also in the Crotalarieae (Polhill 1976). In one species, *C. elongata*, the inflorescence is a spike rather than a raceme and very densely flowered, with more than 100 sessile flowers (Dahlgren 1967b).

FLOWERS—Flower size is somewhat diagnostic at species level. The largest flowers are found in *C. cytisoides* and *C. thunbergii* (up to 35 mm and 24 mm long, respectively) and *C. cuspidosa* has flowers of up to 20 mm. The rest of the species range from up to 17 mm in *C. linearifolia* and *C. saharae*, to below 12 mm in *C. elongata*, *C. halenbergensis*, *C. namibiensis*, *C. psiloloba* and *C. sericea*. The petals are usually pubescent in *Calobota* (at least pilose along the dorsal midrib) with the exception of *C. cuspidosa* and *C. psiloloba* that have glabrous petals. The petals of all the species are yellow. The pedicel is short in most species, but may be long in *C. cytisoides* (up to 11 mm) and *C. psiloloba* (up to 6 mm) or absent in *C. elongata*.

Bracts and bracteoles vary little between species. A single bract is located at the base of the pedicel, with two bracteoles further up near the middle of the pedicel. In *Calobota* the bracts and bracteoles are small, linear and pubescent on the upper surface, except in *C. cytisoides* and *C. obovata* where they are often ovate.

The calyces of *Calobota* species are typically of the "lebeckioid" type (Polhill 1976). They are sub-equally lobed, with the upper sinus often deeper than the lateral or lower sinuses and the carinal lobe consistently narrower than the others. The outer surface of the calyx is usually pubescent, pilose or at least glabrescent. The tips of the calyx lobes are minutely pubescent on the inner surface which is found in most of the genera of the "Cape group" of the Crotalarieae, with the notable exception of *Aspalathus*.

The standard petal is mostly widely ovate in the species of *Calobota*, but is elliptic in *C. elongata*, orbicular in *C. halenbergensis* and transversely oblong in *C. lotononoides*. The apices are either acute or obtuse, except in *C. psiloloba* and *C.*

*lotononoides* which have emarginated apices. The claws are relatively short and less than 6 mm, except in *C. cuspidosa*, *C. cytisoides* and *C. lotononoides* where the claws are longer than 6 mm long. The standard petal is usually pubescent in *Calobota* species or at least has pilose hairs along the dorsal midrib, except in *C. cuspidosa* and *C. psiloloba* which have totally glabrous standard petals.

The shape of the wing petals is fairly uniform in the genus and mostly oblong with obtuse apices. They are either shorter than the keel petals (*C. cinerea*, *C. cuspidosa*, *C. linearifolia*, *C. namibiensis*, *C. obovata*, *C. psiloloba*, *C. pungens*), as long as or shorter than the keel petals (*C. acanthoclada*, *C. cytisoides*, *C. spinescens*, *C. thunbergii*), as long as or longer than the keel petals (*C. elongata*, *C. saharae*, *C. sericea*) or markedly longer than the keel petals (*C. halenbergensis*, *C. lotononoides*). *C. lotononoides* is unique within the genus in having a wing- to keel lamina ratio of 2:1; the wing petal laminas of the other species are never more than 1.3 times longer than those of the keel petals (Boatwright and Van Wyk 2007). The wing petals are glabrous in most species, but pilose in *C. acanthoclada*, *C. cinerea*, *C. linearifolia*, *C. obovata* and *C. pungens*. Sculpturing is present in all species on the upper basal and upper central parts of the wing petals. In some species, e.g. *C. cytisoides*, *C. elongata* and *C. thunbergii*, the sculpturing extends to the lower basal, lower central and upper/lower distal parts of the wing petals (see Stirton 1981 for terminology).

The keel petals of all species are boat-shaped with obtuse apices and pockets are invariably present in all species. The petals are either pubescent (*C. acanthoclada*, *C. cinerea*, *C. linearifolia*, *C. cytisoides*, *C. namibiensis*, *C. obovata*, *C. pungens* and *C. thunbergii*) or glabrous (*C. psiloloba*, *C. cuspidosa*, *C. elongata*, *C. halenbergensis*, *C. lotononoides*, *C. saharae*, *C. sericea*). In *C. spinescens* the keel petals may be either pilose or glabrous.

The value of staminal characters in the genistoid legumes is well known (Polhill 1976; Schutte and Van Wyk 1995; Boatwright et al. submitted) and provided very reliable characters to segregate *Calobota* and *Wiborgiella* from *Lebeckia* s.s (see Chapter 5). The species of *Calobota* have a 4+5+1 anther arrangement (four long basifixed anthers, five short dorsifixed anthers and an intermediate carinal anther), while those of *Lebeckia* have a 5+5 arrangement (the carinal anther resembles the long basifixed anthers) and species of *Wiborgiella* have a 4+6 arrangement (the carinal anther resembles the short dorsifixed anthers). The anther arrangement was found to be in agreement with other evidence (morphological, anatomical and molecular) that support these generic concepts.

The pistil is subsessile or shortly stipitate, usually with a linear ovary and upcurved style. The ovary may be either pubescent or glabrous, while the style is always glabrous. The ovary may contain as few as 3 to 6 ovules (*C. elongata*, *C. namibiensis*) or as many as 34 ovules (*C. cytisoides*). The style is longer than the ovary in *C. namibiensis*.

The nectar of *Calobota* species is generally sucrose-rich (Van Wyk 1993), which is typical of most bee-pollinated legumes. The potential pollinators of some of the Cape genera of the Crotalarieae were studied by Gess and Gess (1994). They found that the flowers of *C. spinescens* and *C. thunbergii* were visited by solitary aculeate Hymenoptera, specifically Masarinae and Megachilinae of the tribes Megachilini and Anthidiini. Some species of Xylocopinae also occasionally visited *C. thunbergii* and *Apis mellifera* was also often abundant. The megachiline and masarine visitors were able to trip (displacement of the keel petals to come into contact with the pollen) the flowers of *C. spinescens*, but not those of *C. thunbergii* suggesting that they are potential pollinators of only the former. *Apis mellifera*, however, was the only species that was able to trip the flowers of *Calobota thunbergii* making it a potential pollinator of this species (Gess and Gess 1994, 2004, 2006). The diversity of flower visits to other species of *Calobota* and the Crotalarieae has been recorded by Gess and Gess (2003).

FRUIT—The pods of *Calobota* species vary from laterally compressed and membraneous to semi-terete and glabrous or pubescent. The pods are generally many-seeded, with the exception of *C. elongata*. In this species, the pods are small, light and usually single-seeded. The petals dry out but are persistent and serve as wings for the disperal of the tiny pod by wind, through a rolling action in the open sandy places where these plants typically grow. A similar adaptation to wind dispersal is found in *Lotononis* section *Synclistus* (Van Wyk 1991b).

The anatomy of the fruit revealed two types of fruit walls in species of *Calobota*, viz. thick- and thin-walled. Those with thick-walled pods usually have a thick mesocarp that may have several layers of sclerenchyma just below the endocarp. The endocarp in most species is composed of a loosely arranged mass of cells which have the appearance of white sponge to the naked eye and seem to envelope the seed, perhaps to serve some protective function. In the species with thin-walled pods, the mesocarp is thinner and has only one or two rows of sclereids adjacent to the endocarp. One or rarely two layers of cells make up the endocarp and the spongy, loosely arranged tissue is absent. In most other genera of the Crotalarieae, the endocarp is also composed of one or two layers of periclinally elongated or round cells (Fig 6.3). In *Lebeckia*, however, the pods may be either thin-walled as in *L. contaminata*, or extremely thick-walled as in *L. brevicarpa*. The spongy tissue present in some *Calobota* species is also found in *Lebeckia*, e.g. *L sepiaria*. Most of the other genera investigated had thin-walled pods. In *Wiborgia* the pods may be either highly sclerified as in *W. sericea* or thin-walled with only a few layers of sclerenchyma as in *W. incurvata*. *Crotalaria* and *Rafnia* lack sclerenchyma entirely, while *Wiborgiella* species have several layers of sclerenchyma adjacent to the endocarp. *Melolobium* was included to represent a member of the Genisteae with thin-walled pods. The structure of the fruit wall is practically identical to that of *Wiborgiella* (Fig. 6.3).

SEEDS—In *Calobota* the seeds are reniform or oblong-reniform and vary from light brown to pink, sometimes with brown mottling, and generally have a brown hilum. The surface is smooth in all but one species, namely *C. lotononoides* that has rugose seeds (Boatwright and Van Wyk 2007).

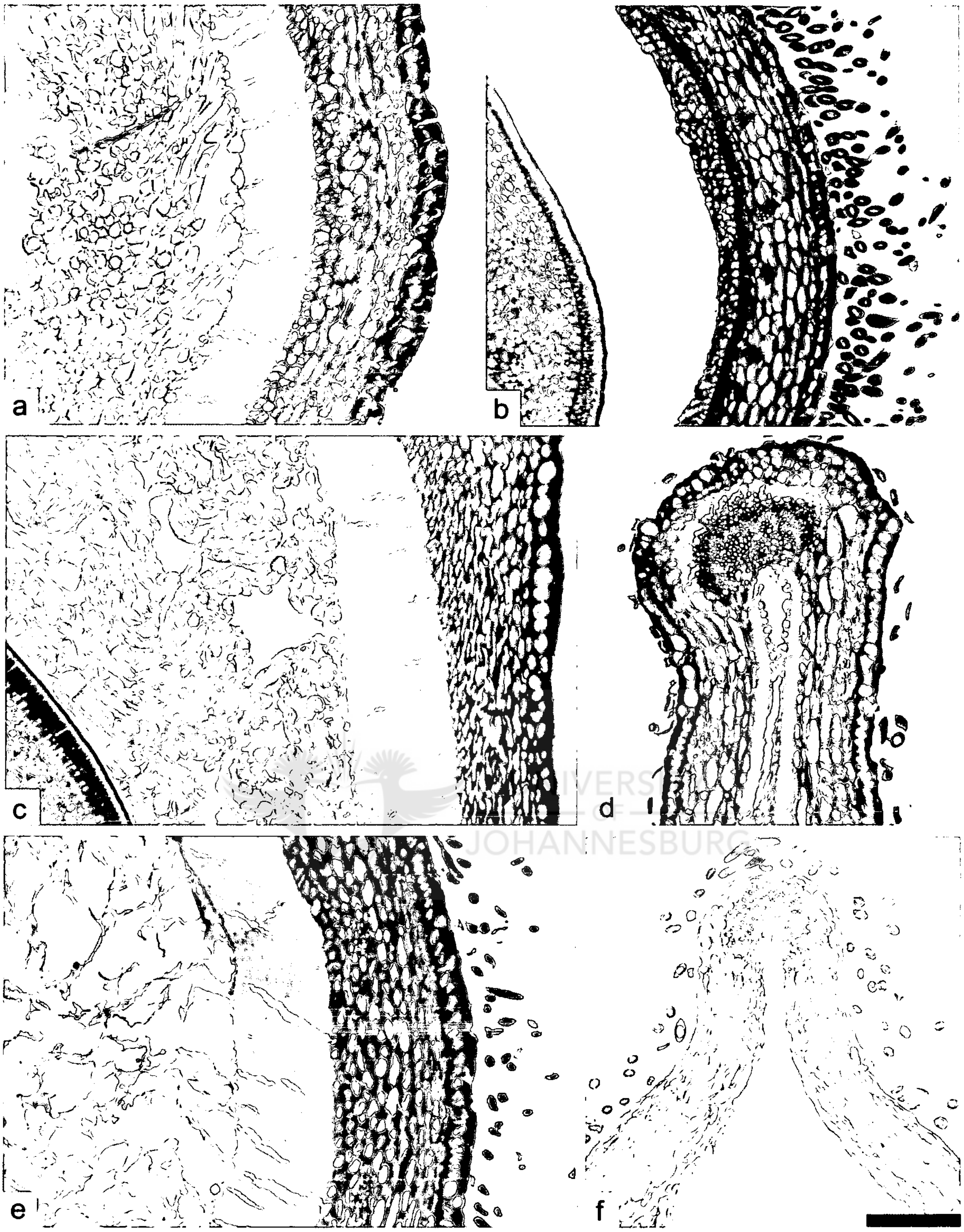

Fig. 6.3 Transverse sections through the fruit walls of *Calobota* species. (a) *C. sericea*; (b) *C. namibiensis*; (c) *C. thunbergii*; (d) *C. spinescens*; (e) *C. cinerea*; (f) *C. elongata*. Voucher specimens: (a) *Boatwright et al. 138* (JRAU); (b) *De Winter and Hardy 7919* (WIND); (c) *Boatwright et al. 151* (JRAU); (d) *Boatwright et al. 158* (JRAU); (e) *Boatwright et al. 150* (JRAU); (f) *Van Wyk 2562b* (JRAU). Scale bar represents 0.2 mm.

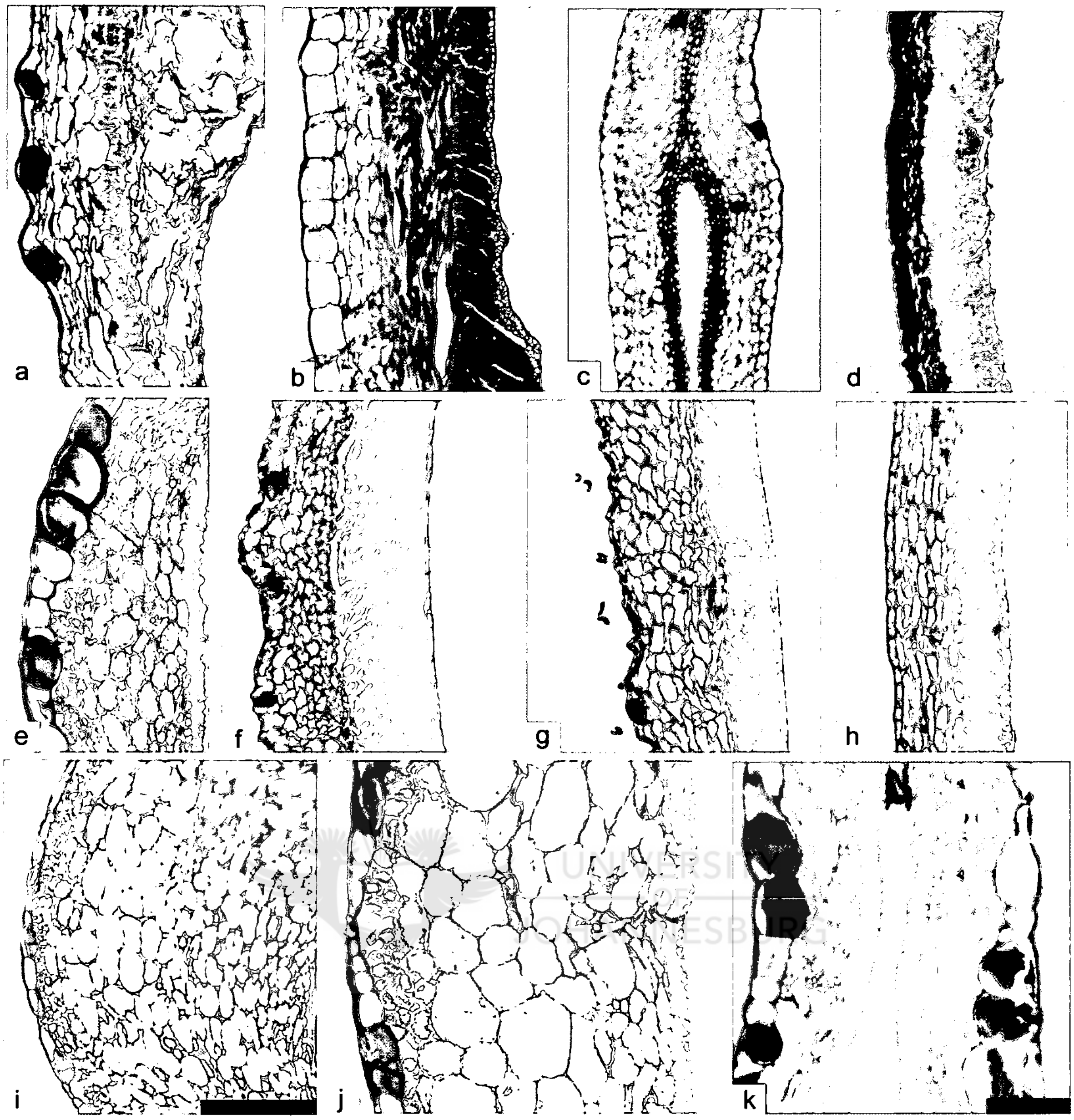

Fig. 6.4 Transverse sections through the fruit walls of representative genera of the Crotalarieae. (a) *Lebeckia wrightii*; (b) *Wiborgia sericea*; (c) *W. monoptera*; (d) *Melolobium alpinum*; (e) *Lebeckia ambigua*; (f) *Wiborgiella sessilifolia*; (g) *Crotalaria* sp.; (h) *Rafnia amplexicaulis*; (i) *Lebeckia brevicarpa*; (j) *L. pauciflora*; (k) *L. contaminata*. Voucher specimens: (a) *Johns 163* (JRAU); (b) *Boatwright et al. 124* (JRAU); (c) *Boatwright et al. 152* (JRAU); (d) *Schutte 160* (JRAU); (e) *Boatwright et al. 132* (JRAU); (f) *Taylor 4329* (PRE); (g) *De Villiers 106* (JRAU); (h) *Campbell and Van Wyk 40* (JRAU); (i) *Le Roux et al. 4* (JRAU); (j) *Le Roux et al. 12* (JRAU); (k) *Le Roux et al. 16* (JRAU). Scale bars: all 0.2 mm as in (k); (i) 0.8 mm.

***6.2.3 Phylogenetic Relationships***—MORPHOLOGICAL DATA—To assess infrageneric relationships within *Calobota*, 17 morphological and anatomical characters were scored for a total of 21 taxa (Table 6.1). *Wiborgiella* was used as outgroup and *Lebeckia* and *Rafnia* included as ingroups based on the results in Chapter 3 (Boatwright et al. 2008a). All 17 characters are parsimony informative and the analysis resulted in six equally parsimonious trees with a length of 36 steps, CI of 0.64 and RI of 0.81 (Fig. 6.5). The Crotalarieae are known for high incidences of convergence and parallelisms (Dahlgren 1970a, Boatwright et al. 2008a) and the co-occurrence of seemingly identical apomorphic states in distantly related genera complicate morphological analysis. Unique combinations of characters are important to circumscribe genera in the tribe (Boatwright et al. submitted), but these are not reflected in the analysis.

*Calobota* is weakly supported as monophyletic (63 BP). This is supported by the isobilateral leaves, pubescent petals (although this is reversed in *C. cuspidosa* and *C. psiloloba*), the 4+5+1 anther arrangement which is shared with *Rafnia* and pubescent pods (reversed in *C. cuspidosa*, *C. cytisoides*, *C. halenbergensis*, *C. psiloloba* and *C. saharae*). Two clades are present within *Calobota*, albeit without support, the *C. spinescens* clade and the *C. cytisoides* clade. *Calobota saharae* is sister to both these clades. The *C. spinescens* clade is supported by the spinescent habit and the laterally compressed fruit. The latter is also present in *C. saharae*, which differs from the rest of *Calobota* in having mucilage cells present in the epidermis (these have been lost in the mature leaves of the other species). The close relationship between *C. cuspidosa*, *C. psiloloba* and *C. pungens* receives weak bootstrap support (56 BP), but is supported by the virtual absence of leaves on mature plants (shared with *C. namibiensis* and *C. saharae*) and unifoliolate leaves (shared with *C. obovata*). The sister relationship between *C. cuspidosa* and *C. psiloloba* (74 BP) is furthermore supported by the presence of glabrous petals and pods. *Calobota acanthoclada* and *C. spinescens* share the fasciculate trifoliolate or simple leaves and are weakly supported as sister (51 BP).

The *C. cytisoides* group is supported by trifoliolate leaves (also present in *C. spinescens*), semi-terete and thick-walled fruit (reversed in *C. elongata*). *Calobota cytisoides* and *C. thunbergii* are sister taxa (73 BP) based on the large flowers (more than 20 mm long) and the wing petal sculpturing present on the upper basal, upper central, lower basal, lower central and upper/lower distal parts. The *C. sericea* clade all have wing petals that are longer than the keel petals, which they share with *C. saharae* and both *Rafnia* species.

*Lebeckia* and *Rafnia* are supported as sister by the glabrous vegetative parts (55 BP). *Lebeckia* is strongly supported by the suffrutescent habit, acicular, phyllodinous leaves and the 5+5 anther arrangement (100 BP), while *Rafnia* received weak support (50 BP).

MOLECULAR DATA—In Chapter 3 (see also Boatwright et al. 2008a), 11 species of *Calobota* were included in the phylogenetic study of the tribe Crotalarieae (see Figure 3.4). *Calobota* was weakly supported as monophyletic by separate analyses of *rbcL* and ITS, but strongly supported by combined *rbcL*/ITS and combined *rbcL*/ITS/morphological data. Although the sampling was not comprehensive, some strongly supported groups were noted. *Calobota cuspidosa*, *C. psiloloba* and *C. pungens* are strongly supported as being closely related. *Calobota cytisoides* and *C. thunbergii* are strongly supported as sister taxa, as are *C. sericea* and *C. lotononoides*. The expansion of *Calobota* to include *C. saharae* (previously the monotypic genus *Spartidium*) is also supported by molecular and morphological data.

TABLE 6.1 Characters and character state polarisations in *Calobota*, *Lebeckia*, *Rafnia* and *Wiborgiella*. Characters and character states are explained at the end of the table.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Calobota acanthoclada* | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 0 |
| *C. cinerea* | 0 | 0 | 0 | 0 | 0,1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 1 |
| *C. cuspidosa* | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *C. cytisoides* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 0 | 1 |
| *C. elongata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 0 |
| *C. halenbergensis* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 0 | 1 |
| *C. linearifolia* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 1 |
| *C. lotononoides* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 1 |
| *C. namibiensis* | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 1 |
| *C. obovata* | 0 | 0 | 0 | 0 | 0 | 0 | 0,1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 1 |
| *C. psiloloba* | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 |
| *C. pungens* | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 1 | 0 |
| *C. saharae* | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 2 | 0 | 0 |
| *C. sericea* | 0 | 0 | 0 | 0,1 | 0,1 | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 0 | 2 | 1 | 1 |
| *C. spinescens* | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 1 | 1 | 0 | 1 | 0 | 0 | 2 | 0,1 | 0 |
| *C. thunbergii* | 0 | 0 | 0 | 0 | 0,1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 0 | 1 | 2 | 1 | 1 |
| *Lebeckia pauciflora* | 1 | 1 | 0 | 0 | 2 | 1 | 3 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *L. sepiaria* | 1 | 1 | 0 | 0 | 2 | 1 | 3 | 1 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Rafnia amplexicaulis* | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 |
| *R. globosa* | 0 | 1 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 2 | 0 | 0 |
| *Wiborgiella leipoldtiana* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

**(1) Habit:** shrubs = 0, suffrutices = 1. **(2) Vestiture:** plants pubescent on vegetative parts = 0, plants glabrous on vegetative parts = 1. **(3) Leaf distribution:** dense = 0, sparse or virtually absent = 1. **(4) Branches:** not spinescent = 0, spinescent = 1. **(5) Petiole:** absent or shorter than leaflets = 0, longer than leaflets = 1, phyllodinous = 2. **(6) Leaf lamina:** flat =0, terete = 1. **(7) Leaf type:** trifoliolate = 0, unifoliolate = 1, simple = 2, phyllodinous = 3. **(8) Leaf spacing:** widely spaced = 0, dense =1, fasciculate = 2. **(9) Mesophyll:** dorsiventral = 0, isobilateral = 1, acicular = 2. **(10) Leaf epidermis:** with mucilage cells = 0, without mucilage cells = 1. **(11) Flower length:** less than 20 mm = 0, more than 20 mm = 1. **(12) Standard petal vestiture:** glabrous = 0, pubescent = 1. **(13) Wing petal length:** shorter than keel petals = 0, longer than keel petals = 1. **(14) Wing petal sculpturing:** restricted to upper basal and upper central parts = 0, on upper basal, upper central, lower basal, lower central and upper/lower distal parts = 1. **(15) Anther arrangement:** 4+6 = 0, 5+5 = 1, 4+1+5 = 2. **(16) Fruit vestiture:** glabrous = 0, pubescent = 1. **(17) Fruit wall:** thin = 0, thick = 1.

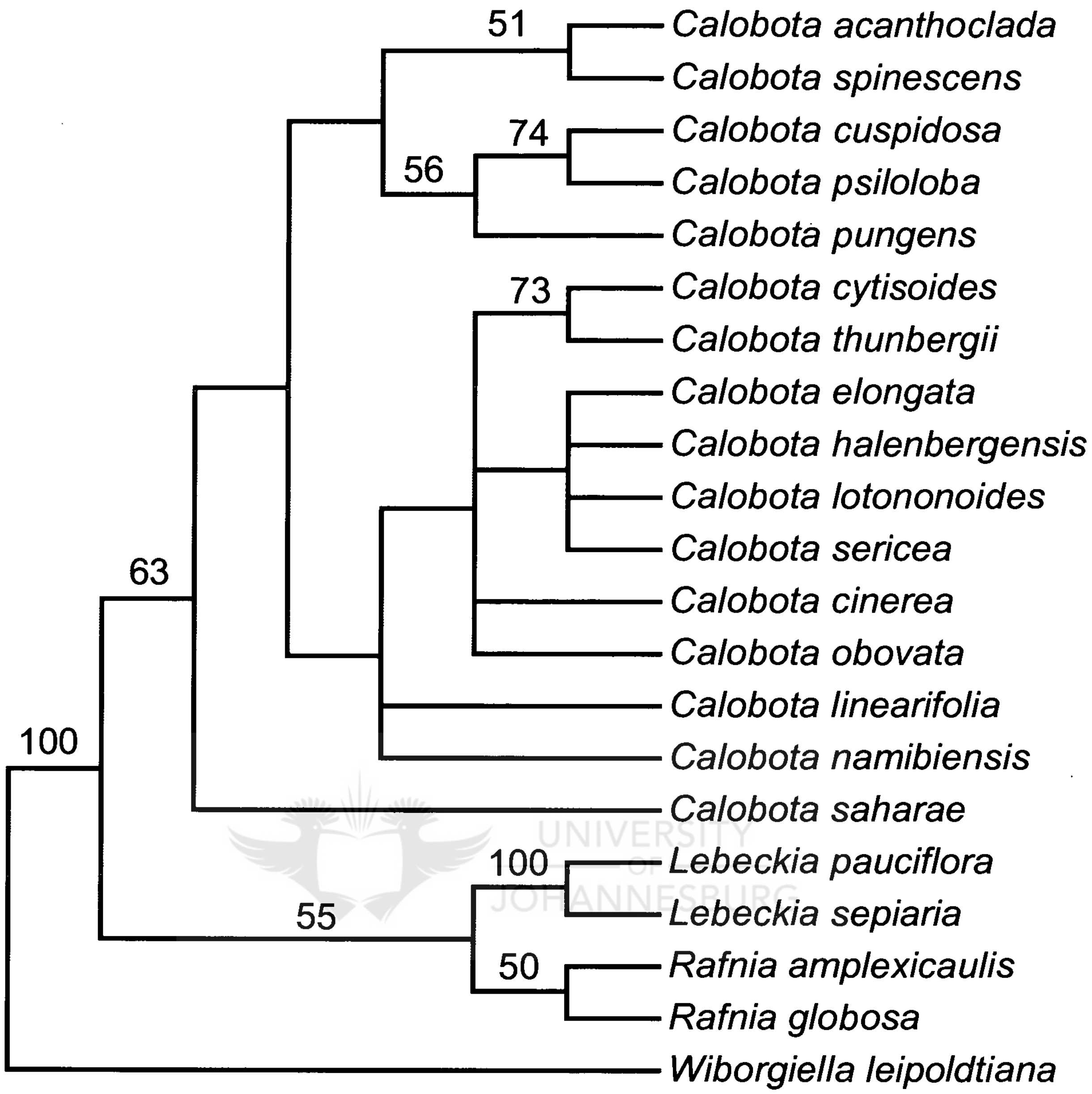

FIG. 6.5. Strict consensus of six trees produced by parsimony analysis of 17 morphological characters for the genera *Calobota*, *Lebeckia*, *Rafnia* and *Wiborgiella*. Values above the branches are bootstrap percentages above 50%.

## 6.3 TAXONOMIC TREATMENT

CALOBOTA Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 192. Jan. 1836, emend. Boatwr. and B.-E.van Wyk, emend. nov. *Lebeckia* section *Calobota* (Eckl. and Zeyh.) Benth. in Hook. Lond. J. Bot. 3: 358–361. 1844. *pro parte majore*.—LECTOTYPE species (here designated): *Calobota cytisoides* (Berg.) Boatwr. and B.-E.van Wyk. [Note: This species is chosen as lectotype as it is the only species included in Ecklon and Zeyher's original concept of *Calobota*.]

*Acanthobotrya* Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 192. Jan 1836, *pro parte*. Lectotype species (here designated): *A. pungens sensu* Eckl. and Zeyh. [now *Calobota psiloloba* (E.Mey.) Boatwr. and B.-E.van Wyk]. [Note: As mentioned by Bentham (1844), *Acanthobotrya* is a mixed concept representing at least four different genera. However, the diagnosis agrees with the concept of *Stiza* E.Mey. (e.g. linear-oblong, compressed fruits); furthermore, *C. psiloloba* (at the time still part of the concept of *A. pungens*), which has all the diagnostic characters mentioned in the diagnosis, is listed first.]

*Stiza* E.Mey., Comm. Pl. Afr. Austr. 1: 31. Feb. 1836, synon. nov. *Lebeckia* section *Stiza* (E.Mey.) Benth. in Hook. Lond. J. Bot 3: 355–356, 1844; Harv. in Harv. in Harv. and Sond., Fl. Cap. 2: 83. 1862.; Bentham and Hooker, Gen. Pl.: 447. 1865.—LECTOTYPE species (designated here): *Stiza erioloba* E.Mey. (now *Calobota pungens*) [Note: Meyer (1836) included only *Stiza erioloba* and *S. psiloloba* E.Mey. (now *Calobota psiloloba*) in *Stiza*. The original description of *Stiza* is too general to allow for a considered choice of lectotype, so we here choose *C. pungens* simply as it is the first-mentioned species.]

*Spartidium* Pomel, Nouv. Mat. Fl. Atl.: 173. 1874, synon. nov. Type species: *Spartidium saharae* (Coss. and Durr.) Pomel. [Note: *Spartidium* is monotypic.]

Woody, sometimes spinescent shrubs or shrublets. Branches thick and woody; young branches green, with chlorenchyma and lacking bark (except in *C. acanthoclada*), pubescent, often sericeous. Stipules absent. *Leaves* unifoliolate or digitately trifoliolate (rarely 5-foliolate); petioles shorter or longer than leaflets, pubescent; leaflets oblanceolate to elliptic or obovate to suborbicular, less often spathulate, pubescent. Inflorescence terminal, few to multi-flowered racemes or rarely a spike. Pedicel pubescent. Bracts linear to obovate, pubescent, caducous. Bracteoles linear, pubescent, caducous. Corolla yellow, usually pubescent or at least pilose along the median section of the standard petal (except in *C. cuspidosa* and *C. psiloloba*). Calyx subequally lobed, upper sinus often deeper than the lateral or lower sinuses, carinal lobe narrower than the others, pubescent or at least glabrescent, tips of lobes minutely pubescent on inner surface. Standard linear to widely ovate, with basal callosities in *C. cytisoides*. Wing petals narrowly oblong to oblong or slightly ovate, longer or shorter than the keel, terminal parts sometimes pubescent; apex obtuse. Keel petals oblong, pockets invariably present, terminal parts sometimes pubescent; apex obtuse. Anthers dimorphic, four long, basifixed anthers alternating with five ovate, dorsifixed anthers, carinal anther intermediate in size and shape between the basifixed and dorsifixed anthers. Pistil sub-sessile to very shortly stipitate, ovary linear to slightly elliptic, with 4 to many ovules, pubescent or glabrous; style longer or shorter than the ovary, curved upwards, glabrous. Pods laterally compressed or semi-terete, linear to oblong, few- to many-seeded, glabrous or pubescent, dehiscent or indehiscent. Seeds reniform to oblong-reniform, or less often suborbicular; colour variable, light pink to pink, sometimes mottled with brown; hilum round, brown or black; surface smooth (rugose only in *C. lotononoides*; seeds of *C. namibiensis*, *C. obovata* and *C. saharae* not seen).

***Diagnostic characters***— Bark formation is late, so that the twigs remain green and photosynthesizing, while bark formation is early in most species of *Wiborgiella*, so that even the young twigs are not green but covered in brown bark (this is also true of *Wiborgia* species). The green twigs are a useful diagnostic character, visible even in sterile herbarium specimens. *Calobota* also differs from *Wiborgiella* in the hairy petals (*C. cupidosa* and *C. psiloloba* are exceptions) seeing that the petals are glabrous in *Wiborgiella*. The most reliable diagnostic character to distinguish *Calobota* from *Wiborgiella* is the anther configuration of 4+1+5 (4+6 in the latter). The pods are semi-terete or laterally compressed in *Calobota* and usually pubescent (pods terete or rarely laterally compressed in species of *Wiborgiella* and always glabrous).

***Notes on distribution***— The species of *Calobota* occur in the Eastern, Northern and Western Cape Provinces, with some restricted to Namibia. One species, *Calobota saharae*, is endemic to North Africa where it occurs on sand dunes from Libya to Algeria and Morocco (Polhill 1976).

## KEY TO THE SPECIES OF CALOBOTA

1. Plants strongly spinescent shrubs, pods laterally compressed, often falcate........2

    2. Plants leafless shrubs, if leaves present then alternate and widely seperated..........................................................................................3

3. Petals pilose, ovary pubescent and pods densely tomentose……………………………………………… ***C. pungens***

3. Petals glabrous, pods glabrous……………………………………4

4. Flowers usually (15–) 16–18 (–20) mm long; pods (21–) 28–49 (–53) mm long; plants restricted to the Northern Cape…………………………………………………… ***C. cuspidosa***

4. Flowers usually 8–11 mm long; pods 14–17 (–33) mm long; plants restricted to the Eastern Cape……………… ***C. psiloloba***

2. Plants densely leafy, leaves alternate and fasciculate………………………5

5. Leaves trifoliolate, young stems green, pods constricted between the seeds……………………………………………… ***C. spinescens***

5. Leaves unifoliolate, young stems brown, pods not constricted between the seeds……………………………………… ***C. acanthoclada***

1. Plants not spinescent, pods semi-terete, if laterally compressed then plants unarmed, erect or virgate, leafless shrubs restricted to North Africa…………………6

6. Leaves widely obovate or orbicular (8–25 mm wide), short-sericeous……7

7. Leaves trifoliolate, inflorescences long, spicate and densely flowered (more than 100 flowers), pods ovate to elliptic, 1 to 2-seeded…………………………………………………… ***C. elongata***

7. Leaves unifoliolate (rarely trifoliolate), inflorescences short, racemose and 7- to 16-flowered, pods linear, 5 to 7-seeded…………………………………………………… ***C. obovata***

6. Leaves elliptic to oblanceolate, linear, spathulate, or rarely ovate or obovate and generally less than 10 mm wide, pubescent or sericeous……8

8. Wing petals longer than keel, leaflets narrow and much shorter than the petioles..........................................................................9

9. Plants pilose and not sericeous, pods and pistil glabrous............................................. ***C. halenbergensis***

9. Plants sericeous, pods and pistil pubescent or sericeous...10

10. Leaves not folded inward and directed to the same side, flowers 7–11 mm long, wing petals not extremely long (wing to keel lamina ratio of less than 1:1.3).....................................................***C. sericea***

10. Leaves conduplicate and secund, flowers 12–15 mm long, wing petals extremely long (wing to keel lamina ratio of 2:1).......................................***C. lotononoides***

8. Wing petals shorter than the keel, leaflets broad and as long as or slightly shorter than the petioles or petioles absent........................11

11. Plants densely leafy and sericeous at least on the young branches................12

12. Flowers generally large (between 13 and 35 mm long) large, wing petals with sculpturing extending to the lower basal, lower central and upper or lower distal parts..........................................................................13

13. Leaf apices mucronulate; calyx, ovary and pods glabrous..........................................................***C. cytisoides***

13. Leaf apices acute, calyx, ovary and pods sericeous.........................................................***C. thunbergii***

12. Flowers medium-sized (between 11 and 17 mm long), wing petals with sculpturing restricted to the upper basal and upper central parts..............14

14. Leaves trifoliolate with a distinct petiole, pods tomentose and not constricted between the seeds.....................................***C. cinerea***

14. Leaves simple and sessile, pods short-sericeous and somewhat constricted between the seeds.................................***C. linearifolia***

11. Plants practically leafless and not sericeous............................................15

15. Leaves if present elliptic to ovate, keel petals, pistil and pods glabrous, restricted to North Africa...........................................................***C. saharae***

15. Leaves if present linear, keel petals, pistil and pods densely pubescent, restricted to Namibia.....................................................***C. namibiensis***

1. CALOBOTA ACANTHOCLADA (Dinter) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia acanthoclada* Dinter, Feddes Repert. 30: 196. 1932; Merxm. and Schreiber, FSWA 60: 66. 1970.—TYPE: SOUTH AFRICA, Namibia, Granietberge [2715 AD], *Dinter 6694* (lectotype: B, photo!, here designated). [Note: The Berlin specimen cited by Dinter is still extant and is here chosen as lectotype.]

*Lebeckia spathulifolia* Dinter, Feddes Repert. 30: 197. 1932.—TYPE: SOUTH AFRICA, Namibia, Kleinfonteiner Fläche [2516 BB], *Dinter 3735* (lectotype: B, photo!, here designated; isolectotypes: BM!, PRE!, SAM!, Z, photo! 2 sheets). [Note: This collection is the only one cited by Dinter in the original description of this species. The specimen in B is still extant and is designated as lectotype.]

*Lebeckia candicans* Dinter, Feddes Repert. 30: 198. 1932.—TYPE: SOUTH AFRICA, Namibia, Kleinfonteiner Fläche [2516 BB], *Dinter 3737* (lectotype: B, photo!, designated here; isolectotypes: BM!, BOL!, NBG!, PRE!, S!, Z, photo!). [Note: This single specimen cited by Dinter is still extant in B and is chosen as lectotype.]

Small, erect or decumbent, multi-stemmed, spinescent shrub up to 1 m in height. Branches brown; young branches slightly sericeous to pilose; older branches covered with brown bark, pilose. Leaves simple; petiole absent; fasciculate, sericeous on both surfaces, spathulate, sessile, 6–20 mm long, 1–2 mm wide, apex recurved-mucronate, base angustate. Inflorescence 12–25 mm long, racemose, with 3 to 5 flowers; pedicel 2–3 mm long; bract 1.5–2.5 mm long, linear, sericeous; bracteoles 0.5–1.0 mm long, linear, sericeous. Flowers 9–12 mm long, bright yellow. Calyx 5–7 mm long, densely sericeous; tube 2.5–4.0 mm long; lobes 2–4 mm long, subulate. Standard 9.5–14.0 mm long; claw linear, 2–5 mm long; lamina ovate, 6.5–8.5 mm long, 7–8 mm wide; apex acute; dorsal surface densely sericeous. Wings 9.5–11.0 mm long; claw 2.5–3.5 mm long; lamina oblong, as long as or shorter than keel, 6.0–7.5 mm long, 2.5–3.0 mm wide, pilose, with 5–7 rows of sculpturing. Keel 10.0–12.5 mm long; claw 3–4 mm long; lamina boat-shaped, 6.5–8.5 mm long, 3.5–4.5 mm wide, pilose to sericeous on terminal parts. Pistil subsessile to shortly stipitate, pubescent; ovary linear, 7.0–9.5 mm long, 0.7–1.0 mm wide with 9 to 15 ovules; style longer than ovary, 3.5–5.5 mm long. Pods linear, laterally compressed, subsessile to shortly stipitate, 12–19 mm long, 1.5–3.0 mm wide, ±4 to 5-seeded, dehiscent. Seeds oblong-reniform to sub-orbicular, 1.5–2.5 mm long, 1.0–2.5 mm wide, mature seeds light brown to orange, surface smooth (Fig. 6.6). Flowering time: Flowering specimens have been collected from February through to October.

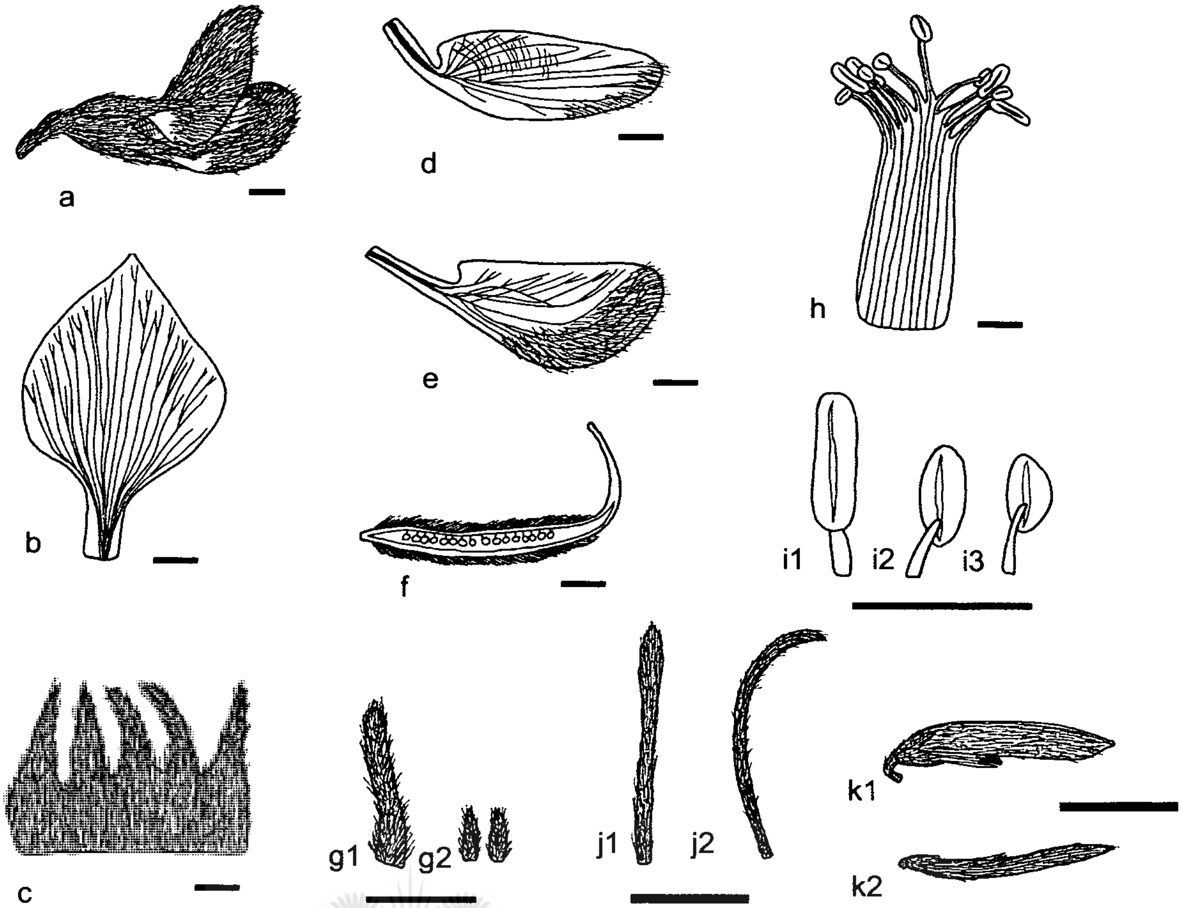

FIG. 6.6 Morphology of *Calobota acanthoclada*: (a) flower in lateral view; (b) standard petal; (c) outer surface of the calyx (upper lobes to the left); (d) wing petal; (e) keel petal; (f) pistil; (g1) bract; (g2) bracteoles; (h) androecium; (i1) long, basifixed anther; (i2) intermediate carinal anther; (i3) short, dorsifixed anther; (j1–j2) leaves in abaxial view; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a–g) *Mannheimer CM2012a* (WIND); (h–i) *Williamson 3376* (BOL); (j1–j2) *Mannheimer et al. CM 899* (WIND); (k1–k2) *Pillans 5149* (BOL). Scale bars: (a–i) 1 mm; (j–k) 1 cm.

***Diagnostic characters***—The species is similar to *Calobota spinescens* in the fasciculate leaves, ovate and sericeous standard petal and spinescent habit but the branches are brown and not green as in *C. spinescens*. It also differs in the simple leaves (trifoliolate leaves in *C. spinescens*), smaller flowers and shorter calyx lobes. The pods are not constricted between the seeds as is the case in *C. spinescens*.

***Distribution and habitat***—*Calobota acanthoclada* is largely restricted to Namibia but extends into the Richtersveld of South Africa in the south (Fig. 6.7). It grows on sandy loam, rocky soil, limestone or dolomitic limestone at altitudes of between 170 m and 1300 m.

***Additional specimens examined***

**–2516** (Helmeringhausen): Kleinfonteiner Flache (–BB), *Dinter 6269* (B, BOL).

**–2518** (Tses): Kovisberge (–BB), *Dinter 6293* (B, BM), *Merxmüller and Giess 28445* (PRE, WIND).

**–2615** (Lüderitz): Klinghardt Mountains (–CA), *Clark and Müller 345* (WIND); 1.0 ml. [1.61 km] south of Lagoon, Lüderitz Bay (–CA), *Giess and Van Vuuren 669* (K, PRE, WIND); between Elizabeth Bay and Kolmanskop, towards coast along old mine road (–CA), *Mannheimer CM2012a* (WIND); Lüderitz (–CA), *Merxmüller and Giess 3076* (PRE, WIND); Lüderitz, on road to Diazpunt (–CA), *Müller and Jankowitz 270* (WIND); proposed wind farm site, east of Grosse Bucht (–CC), *Mannheimer and Burke CM 1700* (WIND); Grillenthal, blue dolomite hills on the road south to Oranjemund from Lüderitz in the Diamond Area no. 1 (–CD), *Bean and Oliver 2425* (BOL, NBG); Sperrgebiet South, 1.5 km north of Grillenthal (–CD), *Jürgens 28103* (PRE).

**–2616** (Aus): 56 mls [90.1 km] west of Aus, Schotterhang (–CB), *Leippert 4080* (WIND).

**–2715** (Bogenfels): ca. 5 km north of Pomona (–AB), *Burgoyne 8270* (PRE); Pomona (–AB), *Dinter 6366* (BM, BOL, NBG 2 sheets, K, PRE, S, WIND); along road to Pomona (–AB), *Mannheimer et al. CM899* (WIND); Rote Kuppe, Chamais road (–BC), *Bartsch SB 1043*

(WIND); 13 km west of Bogenfels houses, at ridge running south of road (–BC), *Mannheimer CM961* (WIND); Klinghardt Mountains (–BD), *Dinter 3980* (BOL, PRE); Boegoeberg (–DD), *Dinter 6574* (B, photo!, BM!), *Mannheimer CM1015* (WIND); summit of the Boegoeberg (–DD), *Williamson 2594a* (BOL 2 sheets).

**–2816** (Oranjemund): Brandkaros (–BC), *Venter 8863* (PRE); 0.5 km east of Brandkaros on road to Anniesfontein (–DA), *Botha 3201* (PRE); Richtersveld, Kortdoorn (–DA), *Jürgens 22585* (PRE); Witbank (–DC), *Pillans 5149* (BOL, K).

**Precise locality unknown:** Nautilus, *Kinges 2580* (PRE); Summit of Kortderm, *Williamson 3376* (BOL).

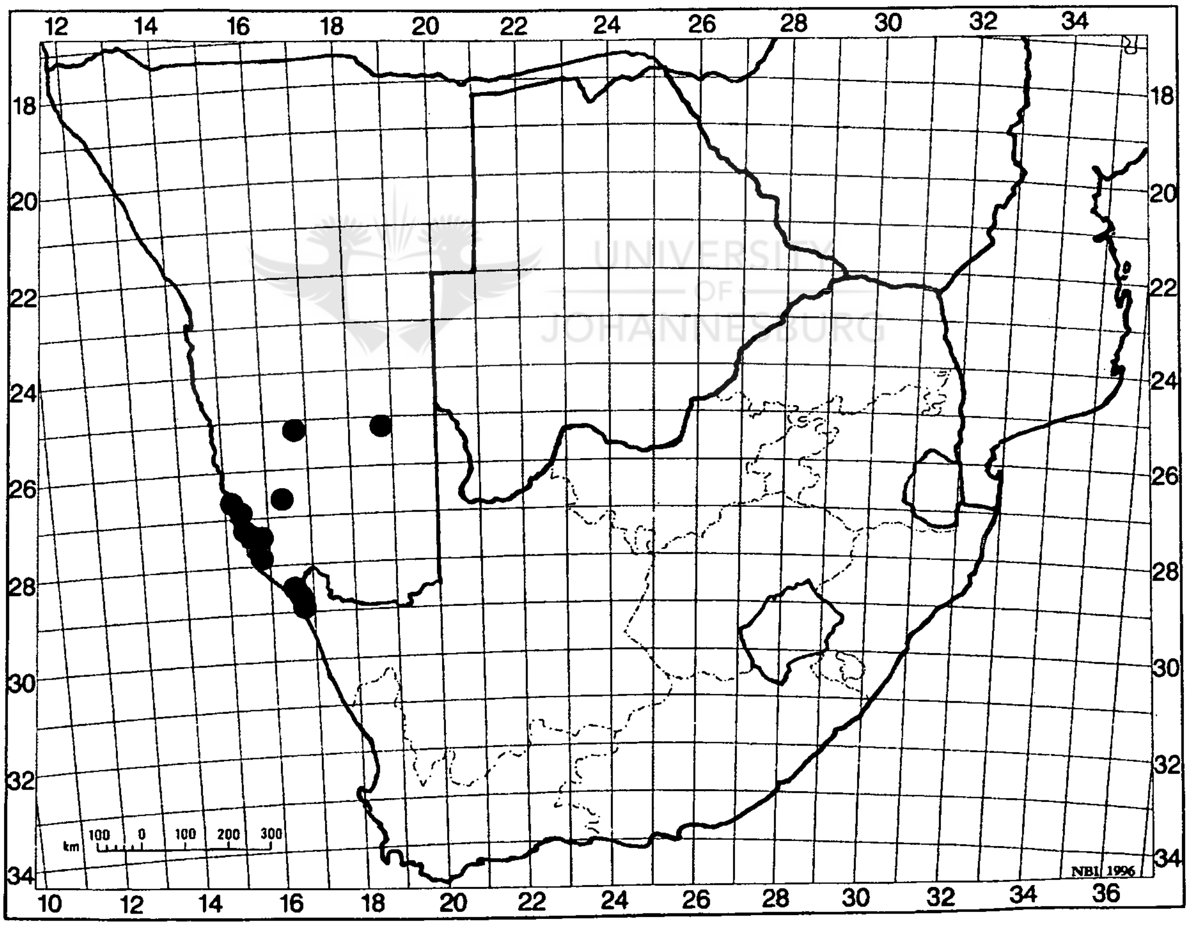

FIG. 6.7. Known geographical distribution of *Calobota acanthoclada*.

2. CALOBOTA CINEREA (E.Mey.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia cinerea* E.Mey., Comm. Pl. Afr. Austr. 1: 35. Feb. 1836; Benth. in Hook. Lond. J. Bot. 3: 359. 1844.; Walp., Rep. Bot. Syst.: 453. 1845.; Harv. in Harv. and Sond., Fl. Cap. 2: 87. 1862.; Merxm. and Schreiber, FSWA 60: 67. 1970.; Goldblatt and Manning, Cape Pl.: 493. 2000.—TYPE: SOUTH AFRICA, hills near Noagas [grid unknown], *Drège s.n "III, B"* (lectotype: P!, flowering specimen on the left, here designated; isolectotype: BM!, K!, P!). [Note: This specimen was annotated by Meyer himself and is chosen as lectotype.]

*Lebeckia cinerea* var. *schäferi* Dinter, Plantae novae Schäferianae: 342. 1920.—TYPE: SOUTH AFRICA, "Granitberg zwischen Bogenfels und Prinzenbucht" [2715 AD], *Schäfer 598* (B†?, specimen not located).

Erect, multi-stemmed, unarmed shrub up to 1.5 m in height. Branches green; young branches sericeous or silky to tomentose; older branches sericeous or silky with light brown bark. Leaves digitately trifoliolate; petiole 3–14 mm long, longer or shorter than leaflets; leaflets widely obovate to elliptic or oblanceolate, alternate, sericeous on both surfaces, subsessile, terminal leaflet 5–21 mm long, 1.5–6.0 mm wide, lateral leaflets 3–17 mm long, 1.5–5.0 mm wide; apex recurved-mucronulate to acute; base cuneate. Inflorescence 30–200 mm long, racemose, with 5 to 30 flowers; pedicel 2–3 mm long; bract 1–4 mm long, linear, sericeous; bracteoles 1–4 mm long, linear, sericeous. Flowers 11–16 mm long, pale to bright yellow. Calyx 5–8 mm long, sericeous; tube 3.5–5.0 mm long; lobes 1.5–3.5 mm long, deltoid. Standard 11.0–13.5 mm long; claw linear, 3.5–4.5 mm long; lamina ovate, 8–10 mm long, 7–11 mm wide; apex obtuse; dorsal surface densely pubescent. Wings 9–13 mm long; claw 2.5–3.5 mm long; lamina oblong, shorter than keel, 5.5–8.5 mm long, 3–4 mm wide, glabrous or rarely pilose, with 5–8 rows of sculpturing. Keel 11–14 mm long; claw 3.5–4.5 mm long; lamina boat-shaped, 7.5–10.0 mm long, 4.5–5.5 mm wide, pilose. Pistil subsessile to shortly stipitate, pubescent; ovary linear, 6–8 mm long, 0.8–1.2 mm wide with 10 to 16 ovules; style longer than ovary, 5.0–8.5 mm long. Pods linear, semi-terete, subsessile to shortly stipitate, 15–40 mm long, 2–4 mm wide, ±5 to 6-seeded, tomentose, dehiscent. Seeds oblong-reniform to reniform, 2–3 mm long, 1.5–2.0 mm wide, mature seeds light brown to orange, often mottled with brown, surface smooth (Fig. 6.8). Flowering time: Mainly flowering in spring (August to November) and fruiting within the same period. Some specimens collected in Namibia were flowing and fruiting in April and May.

***Diagnostic characters***—*Calobota cinerea* is similar to *Calobota linearifolia*, but differs in the low, spreading habit as opposed to the virgate or erect habit of *C. linearifolia*. The leaves are trifoliolate and obovate to elliptic or oblanceolate as opposed to the simple linear to oblanceolate or spathulate leaves of *C. linearifolia*. In *C. cinerea* the inflorescences are more densely flowered with up to 30 flowers (up to nine flowers in *C. linearifolia*), the pods are tomentose and not constricted between the seeds, and the seeds light brown to orange or mottled with brown (pods sericeous, constricted between the seeds and the seeds light brown or grey in *C. linearifolia*).

***Distribution and habitat***—*Calobota cinerea* occurs from south-western Namibia southwards to South Africa as far as Clanwilliam (Fig. 6.9). It occurs on well-drained, sandy, loamy soil or red sand often next to rivers, at altitudes of between ca. 100 m and 500 m. It is recorded to be grazed by livestock or gemsbok. According to Mucina et al. (2006), *C. cinerea* is an important component of

Richtersveld (SKr 6 Stinkfontein Eastern Apron Shrubland) and Namaqualand Sandveld (SKs 2 Northern Richtersveld Yellow Duneveld, SKs 5 Richtersveld Red Duneveld, Sks 6 Oograbies Plains Sandy Grassland, SKs 8 Namaqualand Coastal Duneveld).

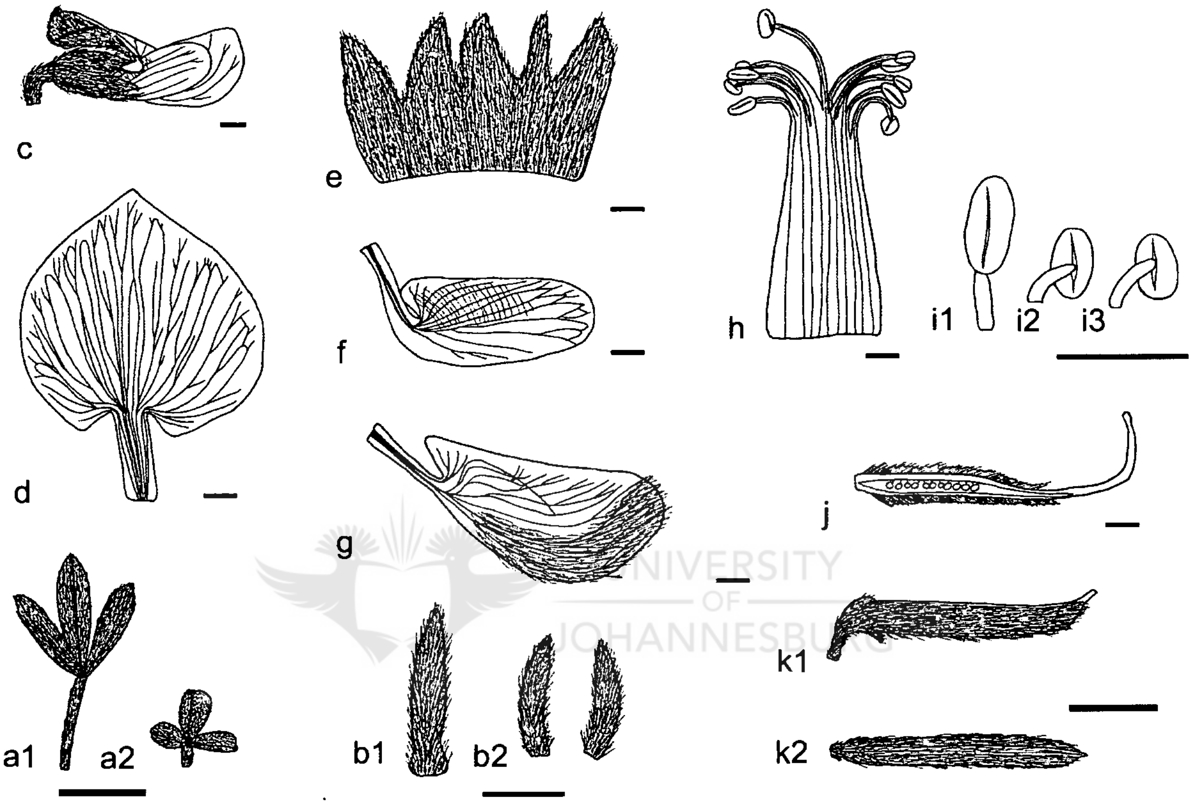

FIG. 6.8 Morphology of *Calobota cinerea*: (a1–a2) leaves in abaxial view; (b1) bract; (b2) bracteoles; (c) flower in lateral view; (d) standard petal; (e) outer surface of the calyx (upper lobes to the left); (f) wing petal; (g) keel petal; (h) androecium; (i1) long, basifixed anther; (i2) intermediate carinal anther; (i3) short, dorsifixed anther; (j) pistil; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a1) *Boatwright et al. 136* (JRAU); (a2–k2) *Boatwright et al. 150* (JRAU). Scale bars: (a1, a2, k1, k2) 1 cm; (b1–j) 1 mm.

### *Additional Specimens Examined*

**–2518** (Tses): Kovisberge (–BB), *Wall 2* (S).

**–2615** (Lüderitz): Angra Pequena (–BA), *Marloth 4809* (PRE), *Marloth 14109* (K); Kovisberge (–CB), *Dinter 6292* (BM, BOL, K, NBG); Halenberg (–CB), *Merxmüller and Giess 3089* (WIND).

**–2616** (Aus): near Aris on the Gariep (–BD), *Drège s.n. "III, B"* (BM, P); Farm Klein-Aus (–CA), *Merxmüller and Giess 2998* (PRE, WIND); 15 mls [24.14 km] west of Aus (–CB), *Giess and Van Vuuren 833* (K, WIND).

**–2715** (Bogenfels): Pomona (–AB), *Dinter 6346* (BM 2 sheets, BOL, K, NBG 2 sheets, PRE), *Wall s.n.* (S); Pomona area, west facing slope ±15 km from houses going east (–AB), *Mannheimer et al. CM889* (WIND); Prince of Wales Bay (–AB), *Marloth 5248* (PRE); Granite Mountain (Granietberg) near Bogenfels (–AD), *Schäfer 13* (NBG).

**–2716** (Witputz): Diamond Area 1, Inselberg, at beacon 992, end of Uguchab River (–CA), *Germishuizen 10170* (PRE).

**–2815** (Diamond Area): Klinghardt Mountains (–BB), *Dinter 3918* (BM, BOL, NBG, PRE, S).

**–2816** (Oranjemund): ±40 km from Brandkaros (red dune area) near farm fence (–BC), *Petersen s.n.* (NBG); Oranjemund (–CB), *Clark 8* (WIND); sandy depressions north of Witbank (–DA), *Pillans 5221* (BOL, K); 38 mls [61.14 km] north of Port Nolloth on way to Alexander Bay (–DA), *Werger 517* (K, PRE); Goariepvlakte (–DB), *Jürgens 22334* (PRE); 35 km from Port Nolloth on road to Alexander Bay at Holgat River (–DD), *Germishuizen 4772* (PRE, WIND); Holgat (–DD), *Jürgens 22734, 28804* (PRE).

**–2820** (Kakamas): Between Augrabies and Anenous (–CB), *Bolus 428* (BM, BOL, K, NBG, PRE), *Bolus 6548* (BOL, K).

**–2917** (Springbok): Anenous flats, ca. 8 km west of Farm Grasvlakte (–AB), *Goldblatt and Manning 9461* (K, NBG); on road to Port Nolloth from Steinkopf (–AC), *Boatwright et al. 150* (JRAU); sandy slope 40 km east of Port Nolloth (–AC), *Goldblatt and Manning 9289* (NBG); 15 mls [24.14 km] north of Port Nolloth (–AC), *Herre s.n.* (NBG); between Kaus, Natvoet and Doornpoort (–AD), *Drège s.n.* (S); Farm Nuwefontein 147 north-west of windmill at 28th mile (–DB), *Le Roux 4038* (NBG).

**–3017** (Hondeklipbaai): Taaibosvlei in dunes (–BC), *Marloth 12418* (NBG, PRE).

**–3118** (Vanrhynsdorp): Hardeveld south-west of Nuwerus (–AB), *Marloth 8233* (NBG, PRE); sanddunes near Doorn River (–BB), *Marloth 2637* (NBG, PRE); Farm Quaggaskop, 16 km on Douse the Glim turn-off, 24 km north of Vanrhynsdorp (–BC), *Le Roux 2066* (NBG); towards "Douse the Glim", Knersvlakte (–BD), *Stirton 9373* (PRE); Lutzville (–CB), *Stirton 6062* (PRE); Vredendal road (–DA), *Barker 5692* (BOL, NBG 2 sheets); Farm Liebendal (–DA), *Hall 3700* (NBG 2 sheets); between Vredendal and Lutzville (–DA), *Lückhoff s.n.* (NBG); 53 km from Clanwilliam to Vanrhynsdorp (–DA), *Stirton 5944* (K, PRE); Farm Spes Bona, Inedendahl (–DC), *Department of Agriculture 29* (PRE); Klawer (–DC), *Henrici 3344* (PRE); western aspect of koppie, Vanrhynsdorp road near Klawer (–DC), *Lavis 20235* (BOL).

**–3218** (Clanwilliam): 8 km from Clanwilliam on road to Vanrhynsdorp (–BB), *Boatwright et al. 136*, *210* (JRAU); 5 km north of Clanwilliam (–BB), *Grobbelaar 2004* (PRE); 10 km before Clanwilliam from Vanrhynsdorp (–BB), *Van Wyk 2598* (JRAU 2 sheets, PRE).

**Precise locality unknown:** without locality, *Drège s.n.* (K); Sandveld, Richtersveld, *Herre s.n. sub STE 11879* (NBG); Andaus Poort, *Marloth 12250* (NBG, PRE).

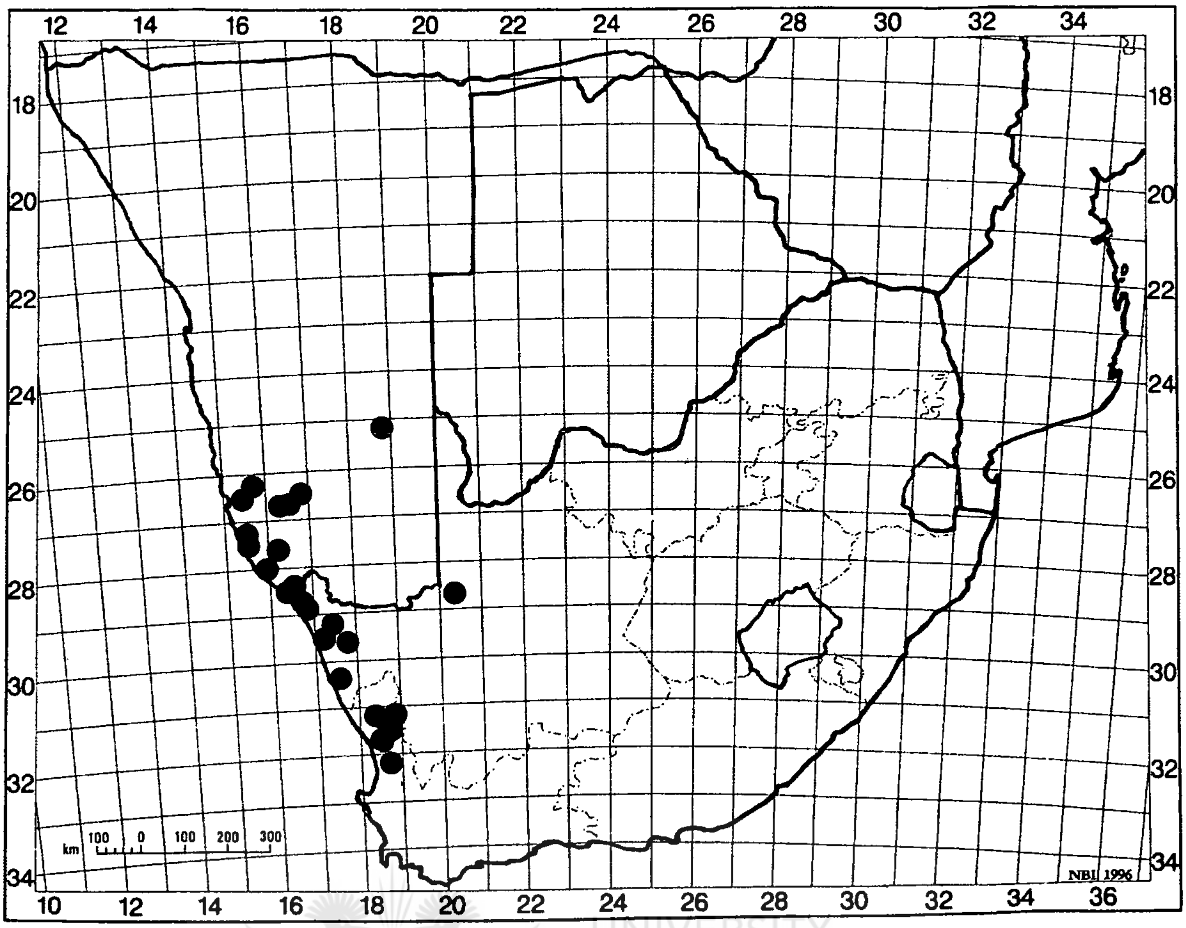

FIG. 6.9. Known geographical distribution of *Calobota cinerea*.

3. CALOBOTA CUSPIDOSA (Burch.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Spartium cuspidosum* Burch., Trav. S. Africa 1: 348. 1822. *Genista cuspidosa* (Burch.) DC., Prodr. 2: 147. 1825. *Lebeckia cuspidosa* (Burch.) Skeels, U.S. Dept. Agric. Bur. Pl. Industry, Bull. 233: 38 (1911).—TYPE: SOUTH AFRICA, Between 'Gatikamma' and 'Klaarwater' [now Griquatown; 2823 CC], *Burchell 1697* (holotype: K!).

*Lebeckia cuspidosa* (Burch.) Druce, Rep. Bot. Exch. Cl. Brit. Isles 1916: 631 (1917) *nom illeg.*

*Lebeckia macrantha* Harv. in Harv. and Sond., Fl. Cap. 2: 83–84. 1862; Wilman, Preliminary checklist of the flowering plants and ferns of Griqualand West (southern Africa): 53. 1946.—TYPE: SOUTH AFRICA, 'Zooloo country' [grid unknown], *Miss Owen s.n.* (lectotype: TCD, photo!, designated here). [Note: This is the only specimen cited by Harvey in the original description of this species and was also seen by him. It is therefore designated as lectotype.]

Erect, multi-stemmed spinescent shrub up to 4.0 m tall. Branches green; young branches sparsely pubescent; older branches pubescent to glabrous with light brown bark. Leaves unifoliolate or rarely trifoliolate; petiole short, 1–2 mm long (up to 5 mm long when trifoliolate); alternate, upper and lower surfaces pilose, linear to slightly obovate, 6–9 (–15) mm long, 2–3 (–6) mm wide; apex obtuse to shallowly retuse; base attenuate. Inflorescences (25–) 40–60 (–90) mm long, racemose, with (4–) 6 to 12 (–24) flowers; pedicel 2–4 (–5) mm long; bract 0.9–1.2 mm long, triangular to slightly linear; bracteoles 0.5–0.8 (–1.0) mm long, slightly ovate. Flowers (15–) 16–18 (–20) mm long, bright yellow. Calyx (3.8–) 4.4–5.4 mm long, pubescent on the outer surface; tube (2.5–) 3–4 mm long; lobes narrowly triangular, (1.2–) 1.8–2.4 (–2.9) mm long, deltoid. Standard 11.0–18.5 mm long; claw linear, 3–6 mm long; lamina ovate, 8.5–12.5 mm long, (7.5–) 8.0–10.0 mm wide, glabrous; apex obtuse. Wings 10–16 mm long; claw (3–) 5–6 mm long; lamina oblong, shorter than the keel, (7.5–) 9.0–10.5 mm long, (3.0–) 4.0–5.5 mm wide, glabrous, with 5 rows sculpturing. Keel 13.5–19.0 mm long; claw (3.5–) 5.0–7.0 mm long; lamina oblong, 10.0–12.5 mm long, 5–6 mm wide, glabrous. Pistil shortly stipitate, glabrous; ovary linear, 7–14 mm long, 1.0–1.6 mm wide with 9 to 11 ovules; style longer than ovary, 5.5–9.0 mm long. Pods oblong to slightly falcate, laterally compressed, shortly stipitate, (21–) 28–49 (–53) mm long, (5–) 6–10 mm wide, ±4 to 6-seeded, glabrous, indehiscent. Seeds reniform, 3–4 mm long, 2.5–3.0 mm wide, mature seeds light brown, surface smooth (Fig. 6.10). Flowering time: This species is mainly spring and summer flowering (October to January), but flowering also sometimes occurs in winter (April to May).

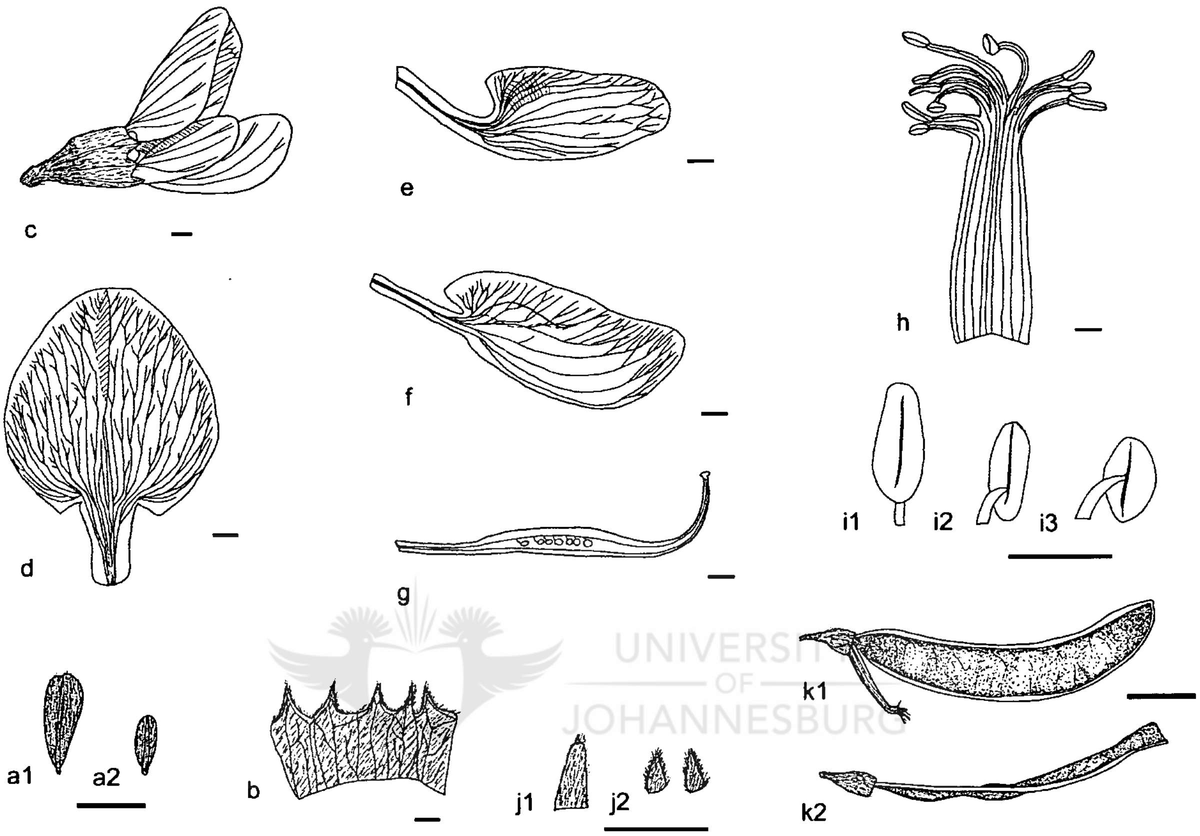

FIG. 6.10 Morphology of *Calobota cuspidosa*: (a1–a2) leaves in abaxial view; (b) outer surface of the calyx (upper lobes to the left); (c) flower in lateral view; (d) standard petal; (e) wing petal; (f) keel petal; (g) pistil; (h) androecium; (i1) long, basifixed anther; (i2) intermediate carinal anther; (i3) short, dorsifixed anther; (j1) bract; (j2) bracteoles; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a1) *MacDonald 76/3* (NBG); (a2) *Ethel Anderson 591* (BOL); (b, i) *Gubb 12584* (PRE); (c–h) *Van Wyk 3055* (JRAU); (k1–k2) *Boatwright et al. 92* (JRAU). Scale bars: (a1, a2, k1, k2) 1 cm; (b–j2) 1 mm.

***Diagnostic characters***—*Calobota cuspidosa* is similar to *C. psiloloba*, but the large flowers, pods and seeds are very distinctive for the former (in *C. psiloloba* the flowers, pods and seeds are much smaller). *Calobota cuspidosa* reaches heights of up to 4 m, while *C. psiloloba* only reaches heights of 1.2 m. The young stems in this species are normally densely tomentose and the older ones remain at least slightly pubescent (in *C. psiloloba* the branches are glarbous or only slightly pubescent).

***Distibution and habitat***—*Calobota cuspidosa* occurs in the Northern Cape Province and is centred around the towns of Kuruman and Griquatown at altitudes of between 975 m and 1700 m. It is mainly found in rocky, loamy or sandy soils (Fig. 6.11). According to Rutherford et al. (2006) this species is an important, prominent component of Kuruman Mountain Bushveld (SVk 10 Eastern Kalahari Bushveld) where it is common in low, open bushveld.

***Additional specimens examined***

**–2723** (Kuruman): Batlaros, Bosjesmans doorn (–AC), *Silke 16785* (BOL); ca. 10 km west of Kuruman on the road to Olifantshoek (–AD), *Dlamini, Nkuna and Van Wyk EvW577* (K); Kuruman (–AD); *Pole-Evans 2108, 2480* (K, PRE), *Van Son s.n. sub TRV 31766* (PRE); On road to Olifantshoek (–AD), *Germishuizen 5614* (BOL, PRE); 3 mls [4.8 km] east of Kuruman (–AD), *Grobbelaar 1112* (PRE); Kuruman Municipal Reserve (–AD), *MacDonald 76/3* (J, NBG, PRE); Buta Asbestos Mine (–AD), *Peeters, Gericke and Burelli 264* (J, PRE); ca. 12 km from Kuruman to Vryburg (–AD), *Van Wyk 3053* (JRAU); 11 km from Kuruman to Vryburg (–AD), *Van Wyk 3055* (JRAU); Kuruman Hills (–AD), *Verdoorn and Dyer 1763* (PRE, K); Vredebron, Blikfontein (–CA), *Gubb KMG 10989* (PRE); 10 km west of Kuruman on road to Upington (–CA), *Van Wyk BSA1241* (PRE, WIND); 30 km from Kuruman to Billingshurst (–CD), *Arnold and Musil 500* (PRE); Hillsides from Griquatown to Khosis (–

CD), *Bryant J379* (PRE); 30 km south-east of Kuruman (–DA), *Jordaan CBK 26* (PRE); Road from Reivilo to Kuruman, farm Mattana (–DB), *Joffe 650* (PRE).

**–2724** (Taung): Blesmanspost (–CA), *Burtt-Davy 9665* (K).

**–2820** (Kakamas): Cape Plateau, Baviaans "Kloof" [= Baviaans Krantz], (–DA), *Hutchinson 3001* (BOL, K, PRE).

**–2822** (Glen Lyon): Hills at Vaalwater (–DA), *Acocks 2455* (BOL 2 sheets, K 2 sheets); between Griquatown and Volop, Bakenkop, north of tarred road (–DB), *Gubb KMG 10988* (PRE).

**–2823** (Griquatown): Postmasburg (–AC), *Wilman s.n.* (K); 19.5 km from Griquatown to Campbell (–AD), *Boatwright et al. 92* (JRAU); between Postmasburg and Griquatown (–CA), *Hutchinson 3039* (BM, BOL, K, PRE); Jasper veld (–CB), *Wilman 4685* (K); Griquatown commonage, the Asbestos Hills (–CC), *Acocks H1049* (PRE); Griquatown (–CC), *Barret-Hamilton s.n.* (BM), *Botha 2996* (PRE), *Burchell 1697, Pole-Evans 22* (K, PRE); 1 ml [1.6 km] east of Griquatown (–CC), *Leistner 890* (K, PRE); ca. 5 km from Griquatown on R64 on the road to Upington (–CC), *Van Wyk 2534* (JRAU 3 sheets); Broken Hill, north of Campbell (–DA), *Germishuizen 8523* (PRE).

**–2824** (Kimberly): Koopmansfontein, Farm Geluk (–AA), *Hanekom 2214* (K, PRE); Schmidtsdrift, Ruigtefontein (–CA), *Gubb KMG 12584* (PRE); 9 mls [14.5 km] west of Schmidtsdrift (–CA), *Leistner and Joynt 2690* (K, PRE); Schmidtsdrif (–CA), *Wall s.n.* (S); Barkly West, Tierfontein (–DA), *Acocks 719* (K 2 sheets); 14 mls [22.5 km] from Vryburg on Schweizer Reneke road (–DD), *Carr 5* (PRE).

**–2922** (Prieska): 6 mls [9.6 km] west of Abrahmsdam (–BA), *Codd 1263* (K, PRE).

**–2923** (Douglas): Mazelsfontein Griqualand West (–BA), *Anderson 591* (BOL, PRE); near Douglas (–BB), *Kotze 783* (PRE).

**Precise locality unknown:** Namaland, *Marloth 1042* (PRE, 2 sheets).

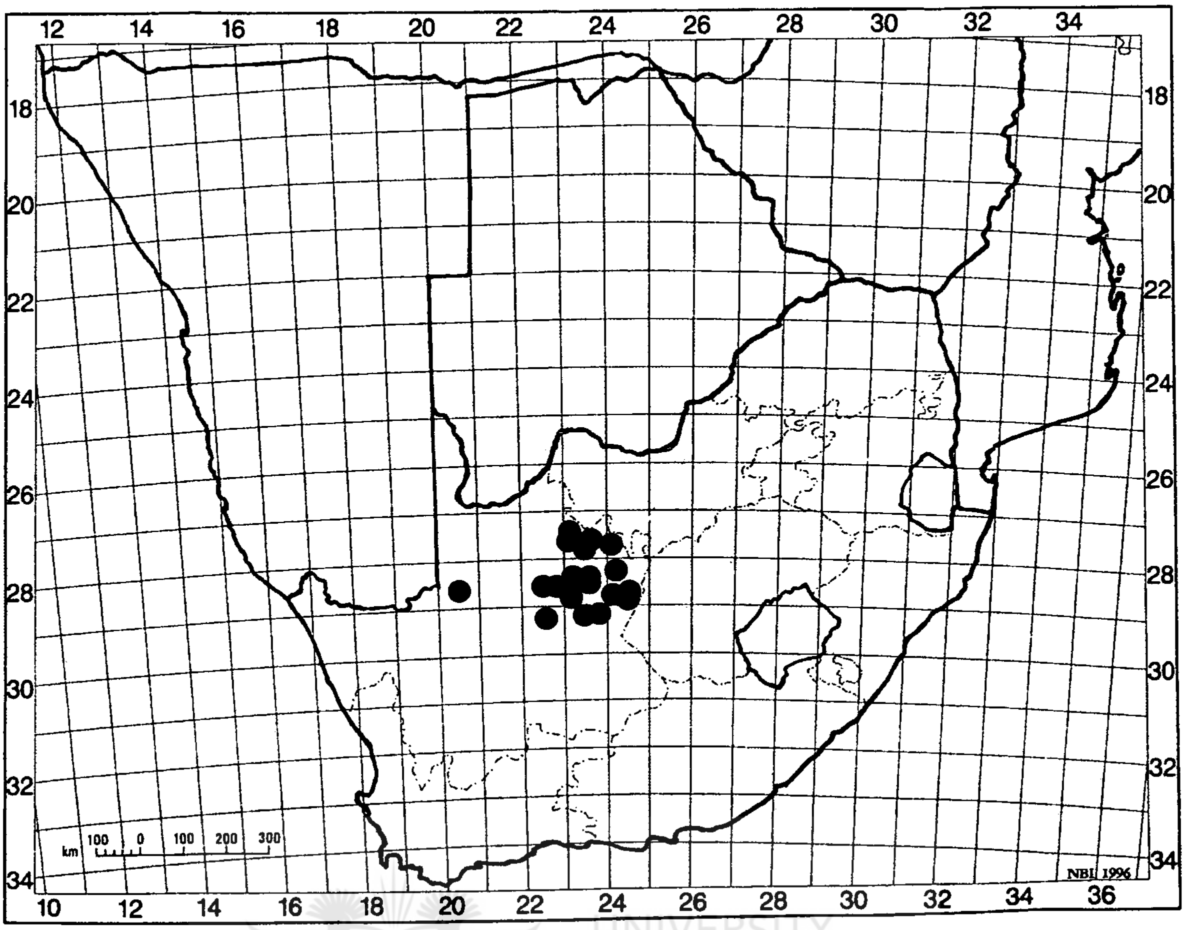

FIG. 6.11. Known geographical distribution of *Calobota cuspidosa*.

4. CALOBOTA CYTISOIDES (Berg.) Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 191 Jan. 1836. *Spartium cytisoides* Berg., Descr. Pl.: 199. 1767; L.f., Suppl. Pl. 320 1781. *Lebeckia cytisoides* (L.f.) Thunb., Nov. Gen.: 143. 1800; Prodr. Pl. Cap.: 122. 1800; Willd. Sp. Pl.: 948. 1800; Thunb., Fl. Cap.: 562. 1823; DC., Prodr. 2: 137. 1825; E.Mey., Comm. Pl. Afr. Austr. 1: 36. Feb. 1836; Benth. in Hook. Lond. J. Bot. 3: 359. 1844; Harv. in Harv. and Sond., Fl. Cap. 2: 87. 1862; Bond and Goldblatt, J. S. Afr. Bot. 13: 289. 1984; Goldblatt and Manning, Cape Pl.: 493. 2000.—TYPE: SOUTH AFRICA, e Cap. B. Spei [grid unknown], *Grubb s.n. sub Bergius 236.57* (holotype: SBT!).

*Ebenus capensis* L., Mant II: 264. 1771. *Cytisus capensis* Lam., Encycl. Meth. 2: 249 (1786); *Lebeckia capensis* (L.) Druce Rep. Bot. Exch. Cl. Brit. Isles 1916: 631. 1917, *nom. illeg.*

*Crotalaria pulchella* Andr., Bot. Repos. 6: plate 417 (Jan–Mar 1805); Sims, Bot. Mag. t. 1699 (1824); DC., Prodr. 2: 134 (1825). *Lebeckia pulchella* (Andr.) Walp. in Linnaea 13: 477 (1839). *Calobota pulchella* (Andr.) Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 191 (Jan. 1836).—TYPE: Andr. Bot. Repos. 6: plate 417. 1805. (iconotype). [Note: According to Stafleu and Cowan (1976) Henry Andrews was a botanical painter and engraver. His artworks were based on living specimens, but no herbarium specimens are known to exist. Due to the fact that the painting leaves no doubt as to its identity we here choose it as iconotype.]

?*Lebeckia marginata* E.Mey., Comm. Pl. Afr. Austr. 1: 35. Feb.1836; Walp. in Linnaea 13: 478. 1839; Benth. in Hook. Lond. J. Bot. 3: 359 1844; Harv. in Harv. and Sond., Fl. Cap. 2: 89 1862.—TYPE: without locality, *Drège s.n.* (S!). [Note: This species was described by Meyer (1836) without listing locality information. The only specimen located is in S and is sterile, but the mucronulate apices of the leaves look similar to those of *Calobota cytisoides*. This taxon might merely represent a synonym of the latter as suggested by Ecklon and Zeyher (1836), but its identity remains unclear.]

Erect, diffuse, multi-stemmed, unarmed shrub up to 2 m in height. Branches green; young branches sericeous; older branches sericeous to pilose with brown bark. Leaves digitately trifoliolate to rarely 5-foliolate; petiole (8–) 10–40 mm long, as long as or shorter than leaflets; leaflets elliptic to oblanceolate, alternate, sericeous, subsessile, terminal leaflet (12–) 14–55 mm long, 3–10 (–17) mm wide, lateral leaflets (11–) 13–45 mm long, 3–9 (–15) mm wide, apex mucronulate to somewhat truncate, base angustate. Stipules absent. Inflorescence 70–255 (–300) mm long, racemose, with 7 to 25 flowers; pedicel relatively long, 3–11 mm long; bract 3–6 mm long, elliptic to ovate, pubescent on outer surface; bracteoles 1–4 (–5) mm long, narrowly ovate to linear, pubescent on outer surface. Flowers 18–35 mm long, bright yellow. Calyx 9–13 mm long, glabrous or very rarely pilose; tube 6.5–10.5 mm long; lobes 1.5–4.0 mm long, deltoid. Standard 18.5–27.0 mm long; claw linear, 4–9 mm long; lamina widely ovate, 13–19 mm long, 14.5–26.5 mm wide; sericeous along dorsal midrib and apex; apex obtuse. Wings 18–28 mm long; claw 5.5–9.0 mm long; lamina oblong to ovate, shorter or ± as long as keel, 12.5–17.5 mm long, 7–12 mm wide, glabrous, with 9–16 rows of sculpturing; apex obtuse. Keel 19.0–29.5 mm long; claw 6.0–12.5 mm long; lamina boat-shaped, 13–20 mm long, 6–10 mm wide, sericeous on terminal parts; apex obtuse. Pistil subsessile to shortly stipitate, glabrous; ovary linear, 14–22 mm long, 1.2–2.0 mm wide with 20 to 34 ovules; style longer than ovary, 7.5–13.5 mm long, glabrous. Pods linear, sometimes somewhat clavate, semi-terete, subsessile to shortly stipitate, 45–70 mm long, 3–5 mm wide, ±5 to 18-seeded, glabrous, dehiscent. Seeds oblong-reniform, 2.8–3.5 mm long, 2.0–2.6 mm wide, mature seeds light brown, surface smooth (Fig. 6.12). Flowering time: Mainly flowering and fruiting in spring and late winter (June to November). One flowering specimen was collected in April.

***Diagnostic characters***—*Calobota cytisoides* is similar to *C. thunbergii*, but differs in the mucronulate leaf apices, long pedicels, larger flowers, sometimes ovate bracts and bracteoles, glabrous or pilose calyx, larger and glabrous pistil and pods (in *C. thunbergii* the leaf apices are acute, the pedicels shorter, the flowers smaller, the bracts and bracteoles always linear, the calyx sericeous and the pistil and pods shorter and pubescent).

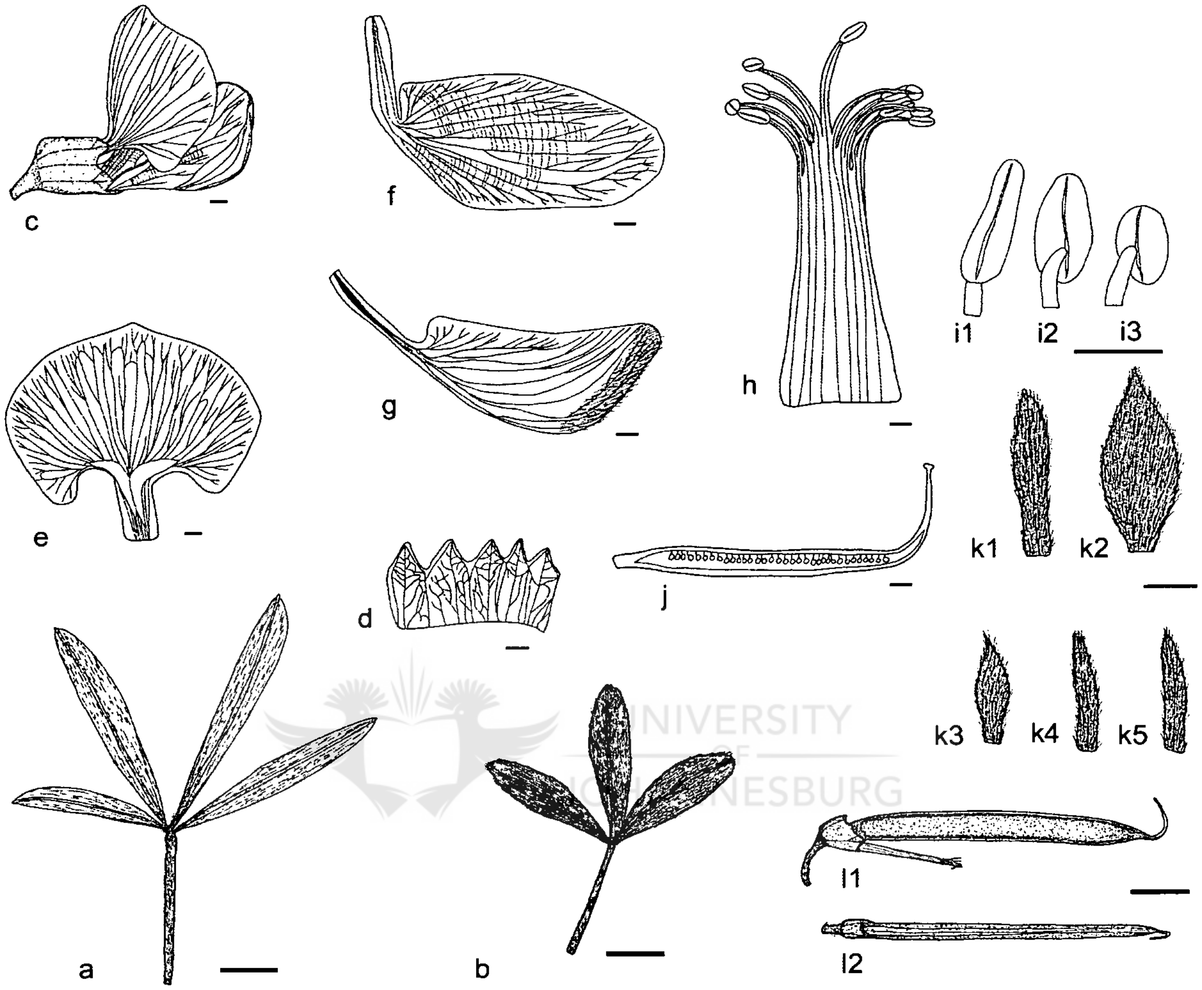

FIG. 6.12 Morphology of *Calobota cytisoides*: (a, b) leaves in abaxial view; (c) flower in lateral view; (d) outer surface of the calyx (upper lobes to the left); (e) standard petal; (f) wing petal; (g) keel petal; (h) androecium; (i1) long, basifixed anther; (i2) intermediate carinal anther; (i3) short, dorsifixed anther; (j) pistil; (k1, k2) bracts; (k3–k5) bracteoles; (l1) pod in lateral view; (l2) pod in dorsal view.

Voucher specimens: (a) *Van Wyk 3117* (JRAU); (b) *Le Roux 2* (JRAU); (c–k1, k4, k5) *Boatwright et al. 114* (JRAU); (k2, k3) Barker 9694 (NBG); (l1–l2) *Van Wyk 2439* (JRAU). Scale bars: (a, b, l1, l2) 1 cm; (c–k5) 1 mm.

***Distribution and habitat***—*Calobota cytisoides* can be found from Oudtshoorn in the Eastern Cape through to the Western Cape around Montagu and Worcester and south through Wupperthal and Clanwilliam as far as Vanrhynsdorp (Fig. 6.13). It has a more southern distribution than the closely related *C. thunbergii* and has been collected at altitudes of between 20 m and 1000 m in renosterveld vegetation on sandstone, shale, well-drained sand and clay. *Calobota cytisoides* is often found on western, southern or south-western slopes, along rivers or in riverbeds and also along disturbed roadsides. Rebelo et al. (2006) and Mucina et al. (2006) list this species as an important component of Shale Fynbos (FFh 8 Montagu Shale Fynbos), Shale Renosterveld (FRs 9 Swartland Shale Renosterveld, listed as *C. cinerea*), and Rainshadow Valley Karoo (SKv 7 Robertson Karoo).

***Additional specimens examined***

**–3118** (Vanrhynsdorp): "Pillar se punt", northern point of Bokkeveld Mountains, plateau on farm Paardekraal (–BB), *Van Wyk 1248* (NBG, PRE, UPS); Vleikraal, east of Klawer (–DA), *Walters 178* (K, NBG); 17.2 km from caravan park, Clanwilliam on old road to Citrusdal (–DC), *Gess 91/92/1* (GRA); 23.9 km from Clanwilliam (–DC), *Gess 91/92/10* (GRA); Klawer (–DC), *Lavis 29233* (BOL); 29 km from Clanwilliam to Vanrhynsdorp (–DC), *Stirton 5943* (K, PRE).

**–3119** (Calvinia): Vanrhyns Pass (–AC), *Acocks 14717* (K, PRE 2 sheets), *Bond 1147* (NBG), *Esterhuysen 5312* (BOL), *Schutte 286* (JRAU 2 sheets), *Van Wyk 3117* (JRAU); Skuinshoogte Pass (–AC), *Niemand 1* (JRAU); Niewoudtville, Oorlogskloof Nature Reserve (–AC), *Pretorius 105* (NBG, PRE, WIND); Nieuwoudtville (–AC), *Schmidt 636* (K); Meulsteenvlei near Nieuwoudtville (–AC), *Taylor 3942* (NBG); Lokenberg, Stinkfontein Hills (–CA), *Leistner 451* (NBG, PRE).

**–3217** (Vredenburg): Vredenburg (–DB), *Grobbelaar 2549* (PRE); above Stompneus (–DB), *Booysen 141* (NBG); 1 ml [1.61 km] east of Paternoster (–DD), *Barker 9694* (NBG 2 sheets); Kasteelberg (–DD), *Strid and Strid 38078* (NBG).

**–3218** (Clanwilliam): Graafwater (–BA), *Compton 24209* (NBG); Bulshoek Barrage, Olifants River Valley (–BB), *Barker 6426* (NBG 2 sheets); Clanwilliam (–BB), *Bayliss BRI593* (GRA, K, PRE, S), *Davidson s.n.* (J), *Ecklon and Zeyher 17* (NBG), *Eliovson 161* (J), *Henrici 2105* (PRE), *Levyns 1282* (BOL); along road from Clanwilliam to Algeria (–BB), *Boatwright et al. 207* (JRAU); Olifants Dam (–BB), *Compton 20015* (BOL, NBG 2 sheets); Clanwilliam south of town next to Olifants River (–BB), *De Vos 1717* (NBG, PRE); near Clanwilliam on road to Biedouw Valley (–BB), *Joffe 959* (PRE); Ramskop Wild Flower Garden (–BB), *Le Roux 2476* (BOL, NBG); rocky hills near Clanwilliam (–BB), *Parker 3589* (BOL, K, NBG); Pakhuis Pass (–BB), *Schutte 262, 264* (JRAU); Bakhoogte near Clanwilliam (–BB), *Stirton 9195* (PRE); Nardouwskloof Farm (–BB), *Stirton 9364* (PRE); Boschkloof (–BB), *Thorne s.n.* (NBG); between Koperfontein and Malmesbury (–BC), *Barker 4067* (BOL, NBG); on Citrusdal road 8 mls [12.87 km] from Clanwilliam (–BD), *Gillett 4082* (BOL, PRE); Olifants River Valley, 23 km north of Citrusdal (–BD), *Hugo 426* (K, NBG, PRE); Rondegat River, 10 km from Algeria to Clanwilliam (–BD), *Stirton 5926a* (K, PRE); roadside between Citrusdal and Clanwilliam (–BD), *Taylor 10630* (NBG, PRE), *Van Wyk 2313* (JRAU 2 sheets); halfway between Clanwilliam and Citrusdal (–BD), *Van Wyk 2439* (JRAU 2 sheets), *Van Wyk 2441* (JRAU); Olifants River Valley between Klawer and Citrusdal (–BD), *Wilman 828* (BOL); St Helena Bay, Steenberg Cove (–CA), *Wisaru 1710* (NBG); on road between Misverstand Dam and Velddrif (–CC), *Le Roux 2* (JRAU 2 sheets); 9 mls [14.48 km] from Velddrif to St. Helena Bay (–CC), *Marsch 1272* (K, NBG); 2 mls [3.22 km] north-west of Sauer Post Office (–CD), *Acocks 14534* (K, PRE 3 sheets); Moutonsvlei, west of Piquetberg Mountain complex (–DA), *Goldblatt 7197* (NBG, PRE, S); base of north slopes below nek at head of Kapteinskloof, Piquetberg (–DA), *Pillans 7701* (BOL); Het Kruis (–DA), *Stephens and Glover 8686* (BM, NBG 2 sheets, K, PRE); Kapteinskloof (–DA), *Stirton 6133a* (K, PRE); near Warmbad (–DB), *Hutchinson 1132* (BM, BOL, K, PRE); Olifants River Valley (–DB), *Marloth*

*7121* (PRE); Piekenierskloof Pass (–DB), *Van Wyk 3219* (JRAU); 3 km south of Piquetberg (–DC), *Ihlenfeldt 1023* (PRE); 3 mls [4.83 km] from Piquetberg up Versfeld Pass (–DC), *Thompson 762* (K, NBG, PRE); outside Piquetberg (–DC), *Thorne s.n.* (NBG); Piquetberg (–DD), *Bolus 13536* (BOL, PRE 2 sheets), *Grant 4714* (PRE), *Guthrie 2584* (NBG), *Schlechter 5233* (BM, BOL, K), *Schlechter s.n. sub TRV 3377* (PRE); roadside near Piquetberg (–DD), *Hafström and Acocks 2312* (PRE 2 sheets, S); 3 km south of Piquetberg (–DD), *Ihlenfeldt 1023* (PRE); 2 mls [3.22 km] along Piquetberg to Velddrif road (–DD), *Marsh 795* (NBG, PRE).

**–3219** (Wuppertal): pass into Biedouw Valley, 6.2 mls [9.98 km] from turnoff from Clanwilliam-Calvinia road (–AA), *Marsh 388* (K, NBG, PRE); Bottom of Biedouw Pass (–AA), *Mauve and Oliver 89* (NBG, PRE); Pakhuis (–AA), *Salter 1660* (BM, BOL, K); Pakhuisberg (–AA), *Schlechter 139* (PRE), *Schlechter 8657* (PRE), *Schlechter 8659* (BM, K, S); Pakhuis Pass (–AA), *Stokoe s.n. sub SAM 52520* (NBG); Pakhuis Pass, east side near Big Bends and gravel pit (–AA), *Taylor 11560* (NBG, PRE); Uitkyk Pass, into Biedouw valley (–AA), *Thompson 2926* (K, NBG); Cederberg State Forest, Grootkloof (–AC), *Andrag 272* (NBG, PRE); Nieuwoudt Pass (–AC), *Barnes s.n.* (BOL); Olifants River near Algeria (–AC), *Boatwright et al. 119* (JRAU) Cedarberg Reserve (–AC), *Hubbard 34* (NBG); Wupperthal, just outside town on road to Clanwilliam (–AC), *Grobbelaar 2975* (PRE); Wupperthal (–AC), *Stirton 6399* (K, PRE); Garskloof, near Algeria (–AC), *Stirton 9192* (PRE); near turn-off to Algeria on old National road (–AC), *Van der Walt s.n.* (NBG, PRE); ca. 8 km from Algeria on road to Clanwilliam (–AC), *Van Wyk 2568* (JRAU 2 sheets, PRE); Cedarberg, Forest Reserve, Langrug (–AC), *Viviers 510* (NBG, PRE); Brakfontein (–AD), *Ecklon and Zeyher 1332* (K, PRE, S); south of Trekkloof Pass (–AD), *Low 2942* (NBG); Wuppertal (–AD), *Thode A1987* (K, PRE), *Thorne s.n.* (NBG), *Van Rooyen et al. 696* (NBG); Warm Baths, Clanwilliam division (–CA), *Edwards 252* (PRE); near Citrusdal (–CA), *Steyn 391* (NBG 2 sheets); just north-east of Citrusdal (–CA), *Strid and Strid 37340* (NBG).

**–3318** (Cape Town): Riebeek Wes (–BD), *Coffer s.n.* (NBG); Riebeeck Castle (–BD), *Drège s.n. "III, D, a"* (BM, K, S), *Pillans 9788* (BOL), *Stark and Co. s.n.* (BOL).

**–3319** (Worcester): Farm Welbedacht, Biedouw Vally (–AA), *Johannesburg Botanical Garden 3876* (PRE); Hex River (–BC), *Bolus 5152* (K), *Marloth 1605* (PRE), *MacOwen 1605* (BM, K, NBG, UPS); main road passing De Doorns, east of town (–BC), *Mauve and Oliver 136* (NBG, PRE); Hex River Pass (–BD), *Eliovson 318* (J), *Gray s.n. sub BOL 26052* (BOL, K); 5 mls [8.05 km] from Worcester on Bains Kloof road (–CA), *Story 2902* (PRE); Fairy Glen Hiking trail, Worcester (–CB), *Cupido 146* (NBG); 3.5 mls [5.63 km] from Worcester on road to Rawsonville (–CB), *Grobbelaar 1183* (PRE); 6 km from Worcester on road to Ceres (–CB), *Grobbelaar 2796* (K, PRE); Worcester Veld Reserve (–CB), *Henrici 3807* (BOL, NBG), *Midgley and Bosenberg 7* (NBG 2 sheets, PRE), *Olivier 101* (NBG), *Van Breda and Joubert 2177* (K); Farm Vrolikheid, McGregor (–CB), *Jooste 192* (NBG); Blinkberg Pass, Tuinkloof (–CB), *Stirton 5907* (K); National road bridge at Breede River (–CB), *Taylor 3729* (BOL, K, NBG); Karoo Botanical Garden, Worcester (–CB), *Barker 5944* (BOL, NBG 3 sheets), *Dobay 52* (NBG), *Niemand 14* (JRAU), *Van Wyk 1408a* (JRAU); Fairy Glen, lower slopes of Brandwag Mountains (–CB), *Stirton 9143* (PRE); Brandwagt, in Fairy Glen Kloof (–CB), *Van Breda SKF574* (K, PRE); Robertson veld (–CB) *Walters 380* (NBG); roadside Worcester west en route Brandwacht (–CB), *Walters 588* (NBG); Brandwacht (–CB), *Walters 1237* (NBG); hillside Voordenberg, near De Wet station (–CB), *Walters 2481* (NBG); between Worcester and Stettyns (–CD), *Rycraft 1732* (NBG); De Doorns (–CD), *Moss 6798* (BM, J), *Schmidt s.n.* (NBG); Stettyns (–CD), *Van Rensburg 386* (K, NBG 2 sheets, PRE); Farm Doringkloof, southern foothills of Voetpadsberg (–DA), *Morley 506* (NBG); Hex River Kloof (–DA), *Sidey 1878* (PRE, S 2 sheets); Farm Doringkloof, foothills of Voetpadsberg (–DA), *Van Wyk 66* (NBG, PRE, UPS); Jonaskop (–DC), *Bayliss BRI1228* (K, PRE); on plains between Assegaaikloof and Breede River (–DC), *Bowie s.n.* (BM); Robertson (–DD), *Levyns 2812* (BOL); Vrolykheid Nature Reserve (–DD), *Van der Merwe 2969a* (K, PRE).

**–3320** (Montagu): Kogmanskloof (–CC), *Court 399* (GRA), *Gillett 4521* (BOL), *Mundt s.n.* (K); Bonnievale (–CC), *Du Preez 321* (NBG); *Rothman NBG221/34* (NBG), *Van Breda and Joubert 1948* (K); near Hassaquaskloof and Kogmanskloof (–CC), *Ecklon and Zeyher 1333* (K, S); 15 mls [24.14 km] beyond Montagu on Barrydale road (–CC), *Marais NBG525/62*

(NBG 2 sheets); Bonnievale, hills of Bokkeveld beds (–CC), *Marloth 11811* (NBG 2 sheets, PRE); 5 km before Montagu (–CC), *Van Wyk 544* (NBG, PRE); Goudmyn, between Bonnievale and Robertson (–CC), *Van Wyk 2705* (JRAU); Olifantsberg (–CC), *Viviers 422* (NBG 2 sheets, PRE); Scheepersrus (–CD), *Johnson 147* (NBG 2 sheets); Barrydale (–DC), *Galpin 3922* (GRA, PRE), *Morris 161* (BOL, NBG 2 sheets), *Wall 3* (S 2 sheets); 15 mls [24.14 km] west of Barrydale (–DC), *Gillett 1897* (BOL, K); 20 km from Barrydale on road to Montagu (–DC), *Grobbelaar 2246* (PRE); 47 km from Montagu on road to Barrydale (–DC), *Grobbelaar 2782* (K, PRE); shaly hills at Barrydale (–DC), *Hafström and Acocks 2314* (PRE); 19 mls [30.57 km] south of Barrydale (–DC), *Martin 403* (NBG 2 sheets); alongside road up to Wildehondskloof Pass between Montagu and Barrydale (–DC), *McDonald 1568* (NBG, PRE); crossroad at Barrydale (–DC), *Nel s.n. sub STE 18105* (NBG); between Barrydale and Montagu (–DC), *Rycraft 2627* (NBG 3 sheets), *Van Niekerk 582* (K); top of Wildehondskloof Pass (–DC), *Van Wyk 2651b* (JRAU).

**–3321** (Ladismith): Gamka Mountain Reserve, alongside road to Paardebond (–CB), *Cattell and Cattell 169* (K, NBG, PRE).

**–3322** (Oudtshoorn): 7 mls [11.26 km] south-west of De Rust (–BC), *Theron 2071* (BOL, K, PRE, UPS); Oudtshoorn (–CA), *Besselaar s.n.* (NBG); along roadside from Oudtshoorn to De Rust (–CA), *Boatwright et al. 114* (JRAU); Farm Die Krans (–CB), *Dahlstrand 2004* (NBG, PRE), *Dahlstrand 2312* (NBG, PRE); Oudtshoorn, near Farm Oude Muragie (–CB), *Vlok 2150* (PRE); Farm Doornkraal, 3 mls [4.83 km] east of De Rust (–DA), *Dahlstrand 1469* (J, PRE).

**–3418** (Simonstown): near Steenberg's Cove, Vredenburg (–BB), *Taylor 1535* (NBG 2 sheets).

**–3419** (Caledon): Brakfontein (–BB), *Schlechter 5279* (BM, BOL, S 2 sheets, PRE); Krommerivier (–BB), *Shaw 5624* (BOL, K).

**–3420** (Bredasdorp): Breede River (–AA), *Mundt 37* (K); 8 km from Stormsvlei to Swellendam (–AA), *Stirton 6147* (K, PRE); Stormsvlei (–AA), *Taylor 4048* (NBG 2 sheets);

Swellendam (–AB), *Burchell 7475* (K); barren mountain ridges on the Riviersonderend at Storm Valley, Hassaquaskloof and Breede River (–AB), *Zeyher 2320* (PRE 3 sheets). **–3421** (Riversdale): near Platte Kloof (–AA), *Muir 671* (PRE); Roadside near Riversdale (–AB), *Bayliss BRIB422* (PRE), *Martin 9649* (GRA).

**Precise locality unknown:** Cape, *Bowie s.n.* (K); without locality, *Drège s.n.* (K, PRE); e Cap. b. Spei, *Sparrman s.n.* (S), *Thunberg s.n.* (S), *Thunberg s.n. sub UPS 16413, 16414* (UPS); without locality, *Zeyher 2320* (K, PRE 2 sheets).

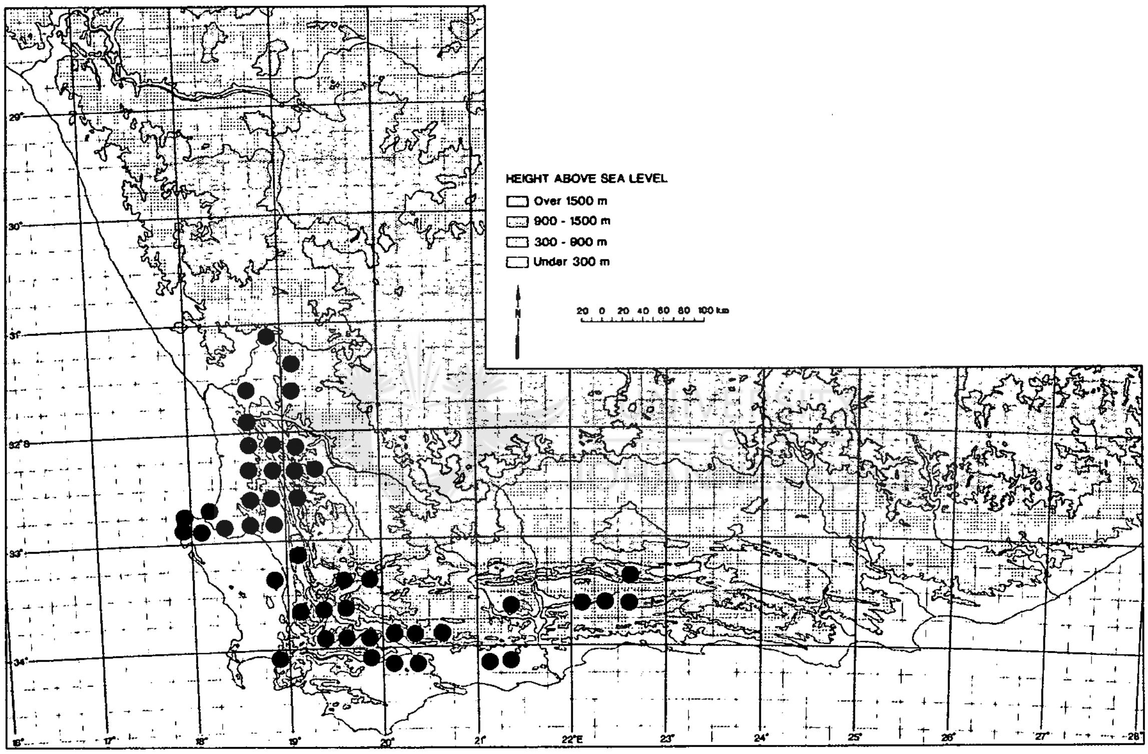

FIG. 6.13. Known geographical distribution of *Calobota cytisoides*.

5. CALOBOTA ELONGATA (Thunb.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Crotalaria elongata* Thunb., Fl. Cap.: 571. 1823.—TYPE: SOUTH AFRICA, 'Carro prope Bockeveld' [grid unknown], *Thunberg s.n. sub THUNB-UPS 16544* (lectotype: UPS!, designated here). [Note: This

is the only specimen in Thunberg's herbarium; it is annotated on the reverse side of the specimen by him and so is here designated as lectotype.]

*Lebeckia melilotoides* R.Dahlgren, Bot. Notiser 120: 268–271. 1967; Bond and Goldblatt, J. S. Afr. Bot. 13: 290. 1984; Goldblatt and Manning, Cape Pl.: 493 2000.—TYPE: SOUTH AFRICA, Platfontein, east of Hottentots Holland Kloof [3319 BB], *H. Hall 177* (holotype: NBG!; isotypes: NBG!, PRE!, S!).

Erect to procumbent, multi-stemmed, unarmed shrub up to 1 m in height. Branches green or light brown, young and older branches densely sericeous. Leaves digitately trifoliolate; petiole longer or shorter than leaflets, 8–29 mm long; leaflets widely obovate, alternate, sericeous, subsessile, terminal leaflet 13–32 mm long, 8–20 mm wide, lateral leaflets 10–32 mm long, 6–16 mm wide, apex obtuse or retuse, base cuneate. Inflorescence 80–432 mm long, spicate, with more than 100 flowers; flowers sessile, bract 5–7 mm long, linear, densely tomentose; bracteoles 2–5 mm long, linear, densely tomentose. Flowers 8–11 mm long, pale yellow. Calyx 4.5–6.0 mm long, tomentose; tube 3.5–5.0 mm long; lobes 1.1–1.7 mm long, deltoid. Standard 10–12 mm long; claw linear, 2.5–3.5 mm long; lamina narrowly ovate to elliptic, 7.5–9.0 mm long, 5–6 mm wide, pilose along dorsal midrib; apex obtuse. Wings 10.5–12.0 mm long, claw 3.5–4.0 mm long, lamina oblong, as long as or longer than keel, 6–8 mm long, 2.5–3.5 mm wide, glabrous, with 5–6 rows of sculpturing. Keel 9.5–12.0 mm long, claw 3.0–4.5 mm long, lamina boat-shaped, 6.5–8.0 mm long, 3.5–4.5 mm wide, glabrous. Pistil subsessile to shortly stipitate, densely pubescent, ovary linear to elliptic, 5.5–6.5 mm long, 0.6–1.0 mm wide with 3 to 6 ovules; style longer than ovary 6–7 mm long. Pods ovate to elliptic, semi-terete, subsessile, 5–8 mm long, 1.5–4.0 mm wide, 1 to 2-seeded, indehiscent. Seeds reniform, 2.4–3.0 mm long, 1.3–2.0 mm wide, mature seeds light brown to light pink, often mottled with brown or grey, surface smooth (Fig. 6.14). Flowering time: Late spring to summer (October to November).

***Diagnostic Characters***—This species is similar to *Calobota obovata*, but differs in the trifoliolate leaves, dense, spicate inflorescences with smaller, sessile flowers, long, narrow bracts and bracteoles, very short calyx lobes, ovate to elliptic standard petal with a pilose midrib, wing petals that are longer than keel, fewer ovules in the ovary and shorter, tomentose pods with less seeds (in *C. obovata* the leaves are unifoliolate, the inflorescences racemose with fewer, the flowers pedicellate, the bracts and bracteoles ovate, the calyx lobes longer, the standard petal densely pubescent and widely ovate and the wing petals shorter than the keel. Furthermore numerous ovules are present in the ovary and the pods are short-sericeous and many-seeded).

***Distribution and Habitat***—This species occurs between the Touws River and Ceres on sandy soil or dunes at ca. 600 m and has been recorded to be both avoided and grazed by livestock (Fig. 6.15).

***Note***—The conservation status of this species was assessed as vulnerable (VU D1+2) by Raimondo et al. (in press). *Calobota elongata* is largely restricted to the Tanqua Karoo and it is estimated that less than 1,000 individuals are left. It is threatened by overgrazing and building activies.

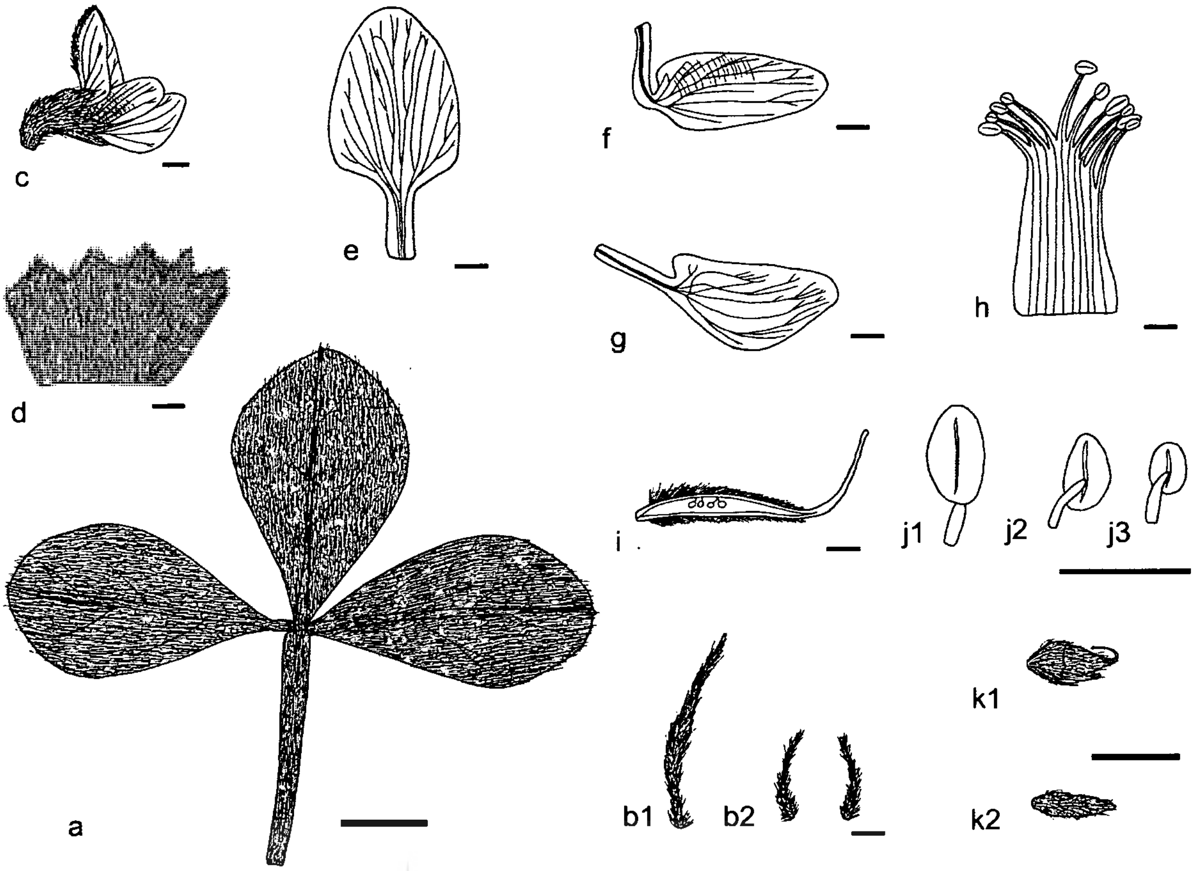

FIG. 6.14 Morphology of *Calobota elongata*: (a) leaf in abaxial view; (b1) bracts; (b2) bracteoles (c) flower in lateral view; (d) outer surface of the calyx (upper lobes to the left); (e) standard petal; (f) wing petal; (g) keel petal; (h) androecium; (i) pistil; (j1) long, basifixed anther; (j2) intermediate carinal anther; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a–b, d–j) *Van Wyk 2229* (JRAU); (c) *Hall 177* (NBG); (k1–k2) *Van Breda 4486* (PRE). Scale bars: (a, k1, k2) 1 cm; (b–j3) 1 mm.

### *Additional specimen examined*

**–3219** (Wuppertal): Ceres Karoo, near Beukes Fountain (–DC), *Schlieben and Van Breda 9811* (K, NBG, PRE).

**–3319** (Worcester): Verkeerdevlei (–BD), *Van Wyk 2229* (2 sheets), *2230*, *2562b* (2 sheets), *2710* (JRAU); Farm Littouw (–CB), *Van Breda 4461* (PRE).

**–3320** (Montagu): near Railway line ca. 5 km south of Touws River (–AC), *Van Breda 4486* (PRE).

**Precise locality unknown:** south end of Tanqua Karroo, *Story 3606* (K, PRE).

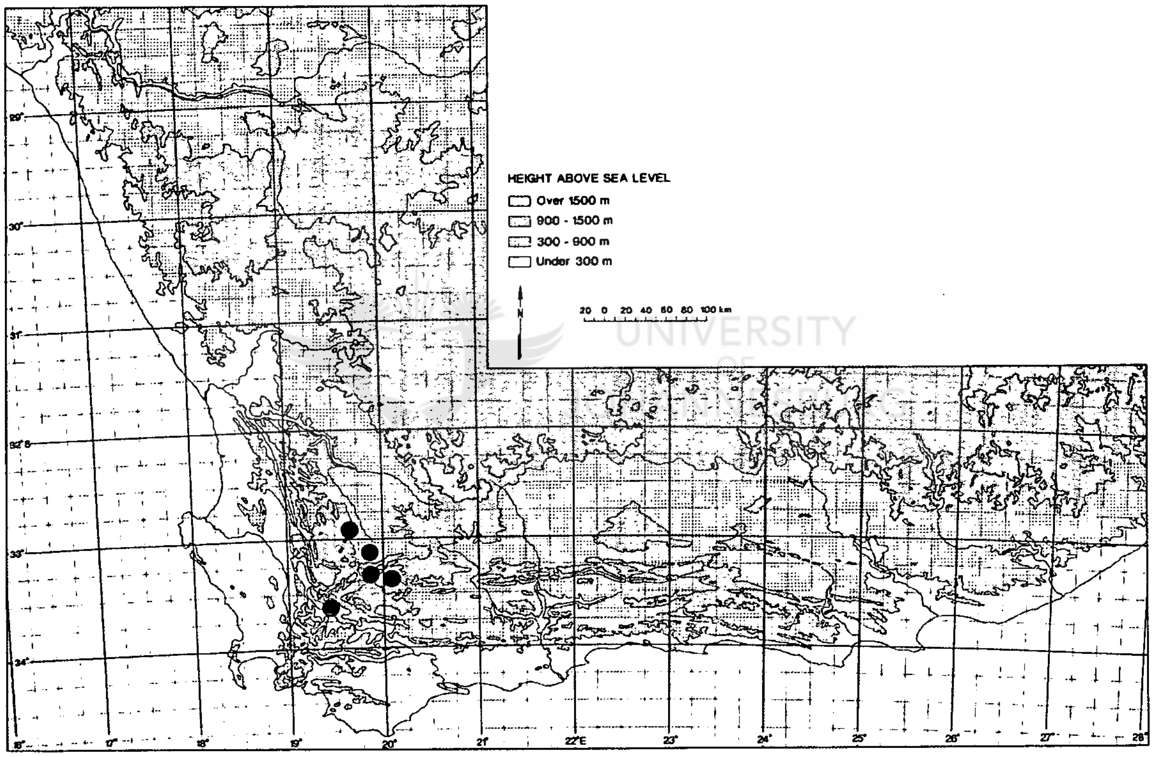

FIG. 6.15 Known geographical distribution of *Calobota elongata*.

6. CALOBOTA HALENBERGENSIS (Merxm. and Schreib.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia halenbergensis* Merxm. and Schreib., Bull. Jard. Bot. Bruxelles 27: 276. 1957; Merxm. and Schreib., FSWA 60: 67. 1970.—TYPE: SOUTH AFRICA, Namibia, Lüderitz

South, Halenberg [2615 CB], *Dinter 6632* (holotype: M, photo!; isotypes: BM! 2 sheets, K!, NBG!, PRE!, S!, Z, photo!).

*Lebeckia decutiens* var *β glabrata* E.Mey., Comm. Pl. Afr. Austr. 1: 31. Feb.1836, synon. nov.—TYPE: "Karroo inter Goedemanskraal et Kaus" [2917 AD], altit. 2000 ped., *Drège s.n. "III, B"* (lectotype: P!, designated here). [Note: The specimen in paris displays the type locality and the characteristic glabrous pods of *Calobota halenbergensis*.]

Multi-stemmed shrub up to 1.5 m in height. Branches green; young branches pilose; older branches pilose or glabrous with light brown bark. Leaves digitately trifoliolate; petiole 18–40 mm long, longer than leaflets; leaflets narrowly oblanceolate to linear, alternate, pilose on both surfaces, subsessile, terminal leaflet 5–30 mm long, 0.5–1.5 (–2.0) mm wide, lateral leaflets 4–16 mm long, 0.5–1.0 mm wide, apex acute, base cuneate. Inflorescence 47–155 mm long, with 10 to 20 flowers; pedicel 1–2 mm long; bract 1–3 mm long, linear, pubescent on outer surface; bracteoles 0.5–1.5 mm long, linear, pubescent on outer surface. Flowers 7–11 mm long, yellow. Calyx (3.5–) 4–6 mm long, pilose to glabrescent on outer surface; tube 2.5–4.0 mm long; lobes 1–2 mm long, subulate. Standard 7.0–11.5 mm long, claw linear, 2–4 mm long, lamina widely ovate to orbicular, 4–7 mm long, 4.5–8.0 mm wide, pilose along dorsal midrib; apex obtuse. Wings 8–11 mm long, claw 2.5–4.0 mm long, lamina oblong, longer than keel, (4.5–) 5.5–7.0 mm long, (2.2–) 2.5–3.5 mm wide, glabrous, with 6–9 rows of sculpturing. Keel 7.0–9.5 mm long, claw 2.5–4.0 mm long, lamina boat-shaped, 4.0–5.5 mm long, 2.5–4.0 mm wide, glabrous or sometimes pilose on terminal parts. Pistil subsessile to shortly stipitate, glabrous; ovary linear, 4.5–7.5 mm long, 0.8–1.1 mm wide with (8–) 13 to

18 (–22) ovules; style longer than ovary, 2–4 mm long. Pods linear, semi-terete, glabrous, subsessile to shortly stipitate, 16–32 mm long, 2–4 mm wide, ±3 to 7-seeded, dehiscent. Seeds oblong reniform to reniform, sometimes somewhat angular, 2.0–3.2 mm long, 1.3–2.0 mm wide, mature seeds light brown to light orange, often mottled with brown, surface smooth (Fig. 6.16). Flowering time: Specimens in flower and fruit have been collected from March to October. The main flowering period appears to be late winter to spring (June to October).

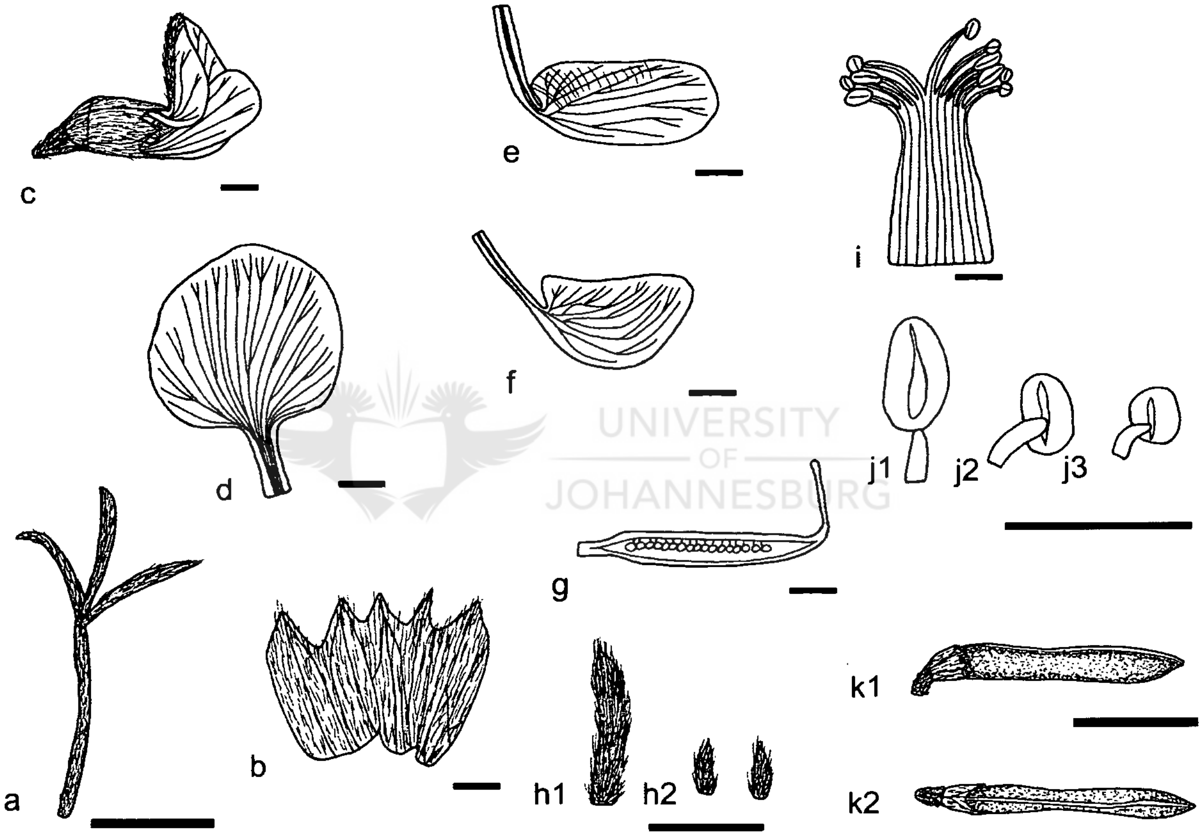

FIG. 6.16 Morphology of *Calobota halenbergensis*: (a) leaf in abaxial view; (b) outer surface of the calyx (upper lobes to the left); (c) flower in lateral view; (d) standard petal; (e) wing petal; (f) keel petal; (g) pistil; (h1) bract; (h2–h3) bracteoles; (i) androecium; (j1) long, basifixed anther; (j2) intermediate carinal anther; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a, c–f, h–k2) *Boatwright et al. 146* (JRAU); (b) *Middlemost 2129* (NBG); (g) *Salter 5549* (PRE). Scale bars: (a, k1, k2) 1 cm; (b–j3) 1 mm.

***Diagnostic characters***—*Calobota halenbergensis* is similar to *Calobota sericea*, but differs in the pilose leaves, glabrous keel petals and glabrous, fewer seeded pods (and pistil). In *C. sericea* the leaves are sericeous, the keel petals pilose and the pods (and pistil) sericeous with more seeds.

***Distribution and habitat***—*Calobota halenbergensis* occurs from the Lüderitz area in south-western Namibia southwards into South Africa as far as Garies south of Springbok (Fig. 6.17). It can be found on well-drained sandy loam, rocky sandstone, gravelly sand or loose red sand often in dry riverbeds or along disturbed roadsides at altitudes of between ca. 50 m and 1000 m above sea level. According to Mucina et al. (2006) it is an important component of Namaqualand Hardeveld (SKn 4 Namaqualand Heuweltjieveld) and Namaqualand Sandveld (SKs 7 Namaqualand Strandveld, SKs 8 Namaqualand Coastal Duneveld, SKs 11 Namaqualand Arid Grassland, SKs 12 Namaqualand Spinescent Grassland). Label information indicates that it is grazed by livestock.

***Note***—The conservation status of *Calobota halenbergensis* in Namibia has been assessed as lower risk (LR-nt) by Golding (2002).

***Additional specimens examined***

**–2615** (Lüderitz): Halenberg (–CB), *Dinter 3805* (BM, BOL 2 sheets, K, NBG); 23 km from Rotkop Station on power line track (–DC), *Kolberg and Maggs 184* (WIND).

**–2616** (Aus): plains around Garub (–CA), *Strohbach 577* (WIND).

**–2618** (Keetmanshoop): river at Spitzkop (–AD), *Wiss 2059* (WIND).

**–2715** (Bogenfels): 9.8 km south of Grillental on main north-south road between Lüderitz and Alexander Bay (–AB), *Powrie LWP1163* (WIND); Klinghardt Mountains, dark rock mountain east of a patch of shifting dunes in the valley ca. 5 km north-east of Sargdeckel, on the road south to Oranjemund from Lüderitz in the Diamond Area 1 (–BC), *Bean and Oliver 2445* (BOL, NBG, PRE); Klinghardt Mountains (–BC), *Dinter 3987* (BOL), *Müller 830*

(PRE, WIND); Namitsas, south of Klinghardt basin (–BD), *Mannheimer CM2107* (WIND); 20 km east of Kakaoberg-Escarpment (–DB), *Jürgens 28153* (PRE); Boegoeberg (–DD), *Dinter 6552* (BM).

**–2716** (Witputz): Klinghardt Mountains, koppie south-west face (–AC), *Mannheimer CM1455* (WIND); Diamond area 1, Polly Mountain (–AD), *Wendt 20/2* (WIND); Udabib Mountain (–BB), *Müller 810* (K, PRE, WIND); sandy flats at the base of Rooiberg sandstone mountain (–CB), *Bean and Oliver 2386* (NBG, PRE); Diamond Area 1, Aurusberg (–CB), *Burke 96225* (WIND), *Oliver 10112* (WIND); Sperrgebiet, central Aurus Valley (–CB), *Jürgens 28205* (PRE); Aurus at new camp (–CB), *Mannheimer CM2418* (WIND); Farm Spitzkop (–DC), *Giess 14639* (WIND), *Wiss 2059* (WIND 3 sheets); Zebrafontein (–DD), *Merxmüller and Giess 3310, 28861* (K, PRE, WIND), *Müller and Horn 1615* (WIND); Rosh Pinah, west of airfield (–DD), *Zietsman 1831* (WIND).

**–2816** (Oranjemund) 15 km west of Rosh Pinah on road to Obib (–BA), *Giess 13820* (K, WIND); Diamond Area 1, Valley between Obib Mountain Peak and Obib dunes (–BA), *Van Wyk 9034* (PRE, WIND); 40 km from Brandkaros (–BC), *Petersen s.n.* (NBG); between Brandkaros and Grootderm (–BC), *Venter 8199* (PRE); Numees (–BD), *Jürgens 22149* (PRE), *McDonald 739* (NBG, PRE); Annisvlakte (–BD), *Jürgens 22322* (PRE); Oranjemund (–CB), *Merxmüller and Giess 2266* (BM, K, PRE, WIND); 70 km north of Oranjemund (–CB), *Williamson 4900* (WIND); 38 mls [61.14 km] north of Port Nolloth, on way to Alexander Bay (–DA), *Werger 519* (K); Goariep-Passage (–DB), *Jürgens 22485* (PRE); Goariepvlakte (–DB), *Jürgens 23119* (PRE); near Doringbank, between Lekkersing and Kuboes (–DB), *Van Wyk 2836* (JRAU, 4 sheets); Holgat River (–DB), *Wisura 2499* (NBG); Sukkel (–DD), *Jürgens 22739* (PRE); between Port Nolloth and Holgat (–DD), *Pillans 5191* (K).

**–2817** (Vioolsdrif): bed of Kubus River (–AC), *Hardy and Venter 4757* (PRE, WIND); north-west slope of Noemiesberg down to Grasvlakte (–AD), *Smook 7937* (PRE); in flats between Blackhills and Wildepaardenrant (–CA), *Thompson and Le Roux 288* (K, NBG); Eksteensfontein (–CA), *Venter 8053* (PRE); 5 mls [8.05 km] west of Stinkfontein (–CC), *Leistner 3400* (K, WIND); Lekkersing (–CC), *Thorne s.n.* (NBG); 7 mls [11.26 km] beyond

Stinkfontein on way to Kuboos, near Skouerfontein (–CC), *Werger 431* (K, PRE, WIND); Blomhoek, 5 km from Eksteensfontein on road to Kubus (–DD), *Germishuizen 4723* (PRE).

**–2916** (Port Nolloth): 16 km north of Port Nolloth on road to Alexander Bay (–BB), *Germishuizen 5315* (BOL, PRE); 38 mls [61.14 km] east by south of Port Nolloth (–BD), *Acocks 14236* (K, PRE 2 sheets); Port Nolloth (–BD), *Bolus 427* (BM, BOL, K, NBG, PRE, UPS); 2 mls [3.22 km] east of Port Nolloth (–BD), *Marloth 12661* (NBG, PRE); between Port Nolloth road and Stinkfontein (–BD), *Middelmost 2129* (NBG 2 sheets, S); 25 mls [40.23 km] after Anenous Pass (–BD), *Schlechter sub STE 10890* (NBG 2 sheets, K, PRE).

**–2917** (Springbok): 37.5 km from Port Nolloth on road to Steinkopf (–AA), *Clarke 640* (K, PRE); Anenous Flats along road to Eksteenfontein (–AB), *Goldblatt and Manning 9284* (NBG); on road to Port Nolloth from Steinkopf (–AC), *Boatwright et al. 149, 190* (JRAU); Anenous Pass (–BA), *Germishuizen 4838* (PRE), *Goldblatt 6002* (K, PRE, S), *Van Wyk 3086* (JRAU 5 sheets), *Van Wyk 6189* (PRE); 10 mls [16.09 km] north-west of Steinkopf (–BC), *Salter 5549* (BM, BOL, K, PRE); 5 mls [8.05 km] south of Komaggas (–CA), *Compton 22794* (NBG); Sandkop gate at Kleinsee (–CA), *Le Roux 5183* (NBG); Komaggas (–CA), *Maguire 400* (NBG 4 sheets); Grootmis, at Springbok turnoff on Port Nolloth-Kleinsee road (–CA), *Rösch and Le Roux 560* (PRE); just north-east of Grootmis (–CA), *Strid and Strid 37734* (NBG); between Spektakel and Kleinsee (–CB), *Grobbelaar 1962* (PRE); Farm Langhoogte on Port Nolloth turn-off from Springbok-Kleinsee road just north of waterpipe (–CB), *Le Roux 3959* (NBG); Spektakel (–DA), *Compton 11508* (NBG, PRE), *Esterhuysen s.n. sub PRE 53706* (PRE); bottom of Wildepaardehoek Pass (–DC), *Van Jaarsveld 1392* (PRE).

**–2918** (Gamoep): Karuchabpoort, Lekkersing (–BB), *Oliver, Tölken and Venter 145* (PRE).

**–3017** (Hondeklipbaai): Farm Koingnaas 475 on road from Hondeklipbaai to Koingnaas (–AB), *Le Roux and Lloyd 353* (NBG); ca. 6 km north of Koingnaas on Springbok road (–AB), *Van Wyk 2848* (JRAU, 2 sheets); 3 km south-west of Soebatsfontein on road to Wallekraal (–BA), *Le Roux 2899* (NBG); Farm Doornfontein 464, Portion 1, Steenkamp Kraal (–BA), *Le Roux 4557, 4630* (NBG); on road from Garies to Hondeklipbaai (–BC), *Boatwright et al. 146*

(JRAU); Wallekraal, between Garies and Hondeklipbaai (–BC), *Compton 5485* (BOL, NBG); Wallekraal (–BC), *Pillans 17970* (BOL); 5 km from Wallekraal to Garies (–BC), *Stirton 6053* (K); Farm Sandkraal, 40 km west of Garies (–DA), *Hilton-Taylor 1371* (NBG, PRE); 12.9 km from Garies-Hondeklipbaai road on road to Soutfontein, Farm Sandkraal (–DA), *Steiner 2172* (NBG, PRE); in red sand near Garies (–DB), *Esterhuysen s.n.* (K, NBG 2 sheets, PRE).

**Precise locality unknown:** Arragaal, Richtersveld, *Here s.n. sub STE 11887* (NBG); between Port Nolloth and Augrabies Poort, *Bolus 6457* (K); Doornpoort, *Compton 20633* (NBG 3 sheets); Kalkfontein, near river, *Marloth 12273* (NBG 4 sheets, PRE); kloof by Doornpoort, Richtersveld, *Herre s.n. sub STE 11865, 11866* (NBG); Noagas, *Drège s.n. "III, B"* (BM, K, P); sandveld, Richtersveld, *Here s.n. sub STE 11868* (NBG 2 sheets, PRE); without locality, *Drège s.n. sub PRE 9367* (PRE).

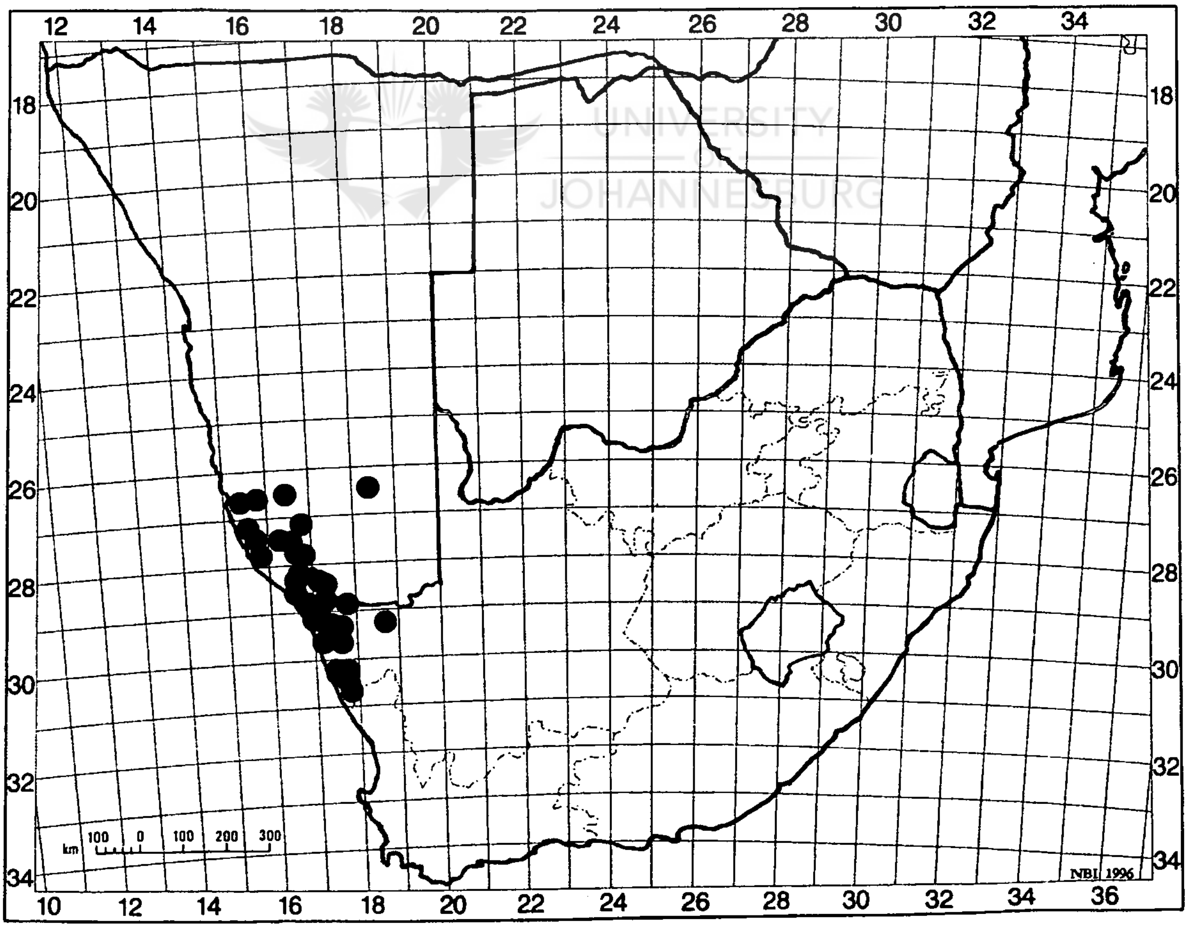

FIG. 6.17. Known geographical distribution of *Calobota halenbergensis*.

7. CALOBOTA LINEARIFOLIA (E.Mey.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia linearifolia* E.Mey., Comm. Pl. Afr. Austr. 1: 33. Feb. 1836; Benth. in Hook. Lond. J. Bot. 3: 358. 1844; Harv. in Harv. and Sond., Fl. Cap. 2: 86. 1862; Merxm. and Schreiber, FSWA 60: 67. 1970; Polhill, Fl. Zambesiaca: 246. 2003—TYPE: SOUTH AFRICA, Northern Cape Province, on the Gariep, near Verleptpraam [2817 AA], 300 ped., *Drège s.n. "III, B"* (lectotype: P!, designated here; isolectotypes: K!, P!, S!, Z photo!). [Note: The Paris specimen bears the type locality and was annotated by Meyer himself.]

*Lebeckia dinteri* Harms, Feddes. Repert. 16: 360. 1920; Merxm. and Schreib., FSWA 60: 67. 1970, synon. nov.—TYPE: SOUTH AFRICA, Namibia, Garub [2616 CA], *Dinter 1057* (lectotype: NBG!, designated here). [Note: No other specimens of the collection *Dinter 1057* could be traced in either B or Z. Both *Dinter 1056* and *Dinter 1058* were found in Z, but it is likely that all specimens of *Dinter 1057*, except the NBG specimen chosen as lectotype, have been destroyed.]

Erect or virgate, multi-stemmed, unarmed shrub up to 3 m in height. Branches green; young branches sericeous or silky; older branches sericeous or silky with light brown bark. Leaves simple; petiole absent; leaflets linear to oblanceolate or spathulate, sericeous, sessile, leaflets 11–45 mm long, 1.0–2.5 mm wide; apex acute; base cuneate. Inflorescence 38–170 mm long, with 5 to 9 flowers; pedicel 1–2 (–8) mm long; bract 1.5–2.5 mm long, linear to narrowly ovate, pubescent; bracteoles 1.0–1.5 mm long, linear to narrowly ovate, pubescent. Flowers 13–17 mm long, bright yellow. Calyx 5.5–7.5 mm long, sericeous; tube 4–6 mm long; lobes 1.0–2.5 mm long, deltoid. Standard 11.5–15.0 mm long; claw linear, 2.5–3.5 mm long; lamina ovate, 8.5–12.0 mm long, 8.5–10.5 mm wide, dorsal surface pubescent; apex acute. Wings 8.0–11.5 mm long, claw 3.0–4.5 mm long, lamina oblong, longer than keel, 5–7 mm long, 2.5–4.0 mm wide, pilose, with 4–8 rows of sculpturing. Keel 12–15 mm long, claw 3.5–6.0 mm long, lamina boat-shaped, 7.5–10.0 mm long, 4.0–5.5 mm wide, pubescent. Pistil subsessile to shortly stipitate, pubescent; ovary linear, 9–11 mm long, 0.8–1.5 mm wide with 12 to 18 ovules; style longer than ovary, 4.8–7.8 mm long. Pods linear, sometimes somewhat clavate, semi-terete, sericeous, subsessile to shortly stipitate, 25–40 mm long, 2–3 mm wide, ±4 to 8-seeded, dehiscent. Seeds oblong-reniform, 2.5–3.5 mm long, 1.5–2.5 mm wide, mature seeds light brown or grey, surface smooth (Fig. 6.18). Flowering time: Mainly between September and November, but flowering and fruiting specimens have been collected in January, April, May and August.

***Diagnostic characters***—*Calobota linearifolia* is similar to *C. cinerea* but differs in its virgate to erect habit, simple, linear leaves, fewer flowered inflorescences, sericeous pods that are constricted between the seeds and the light brown to grey seeds. *Calobota cinerea* has a low, spreading habit, obovate, elliptic or oblanceolate and trifoliolate leaves and the inflorescences more densely flowered. The latter species also has tomentose pods that are not constricted between the seeds and the seeds are light brown to orange and often mottled.

***Distribution and habitat***—*Calobota linearifolia* is widely distributed in the Northern Cape Province of South Africa and southern Namibia, with outlier populations around the Unjab River, Sima Hill and the Sanitatas area in north-western Namibia (Fig. 6.19). Polhill (2003a) mentioned that this species also occurs in Botswana in the Kgalagadi district, but no specimens from this region were available for study. *Calobota linearifolia* occurs in dune sand, red sand or brackish soil often along rivers or in dry watercourses, washes and gulleys. It occurs at altitudes of between ca. 300 m and 1350 m. It is suspected of poisoning livestock (according to label information).

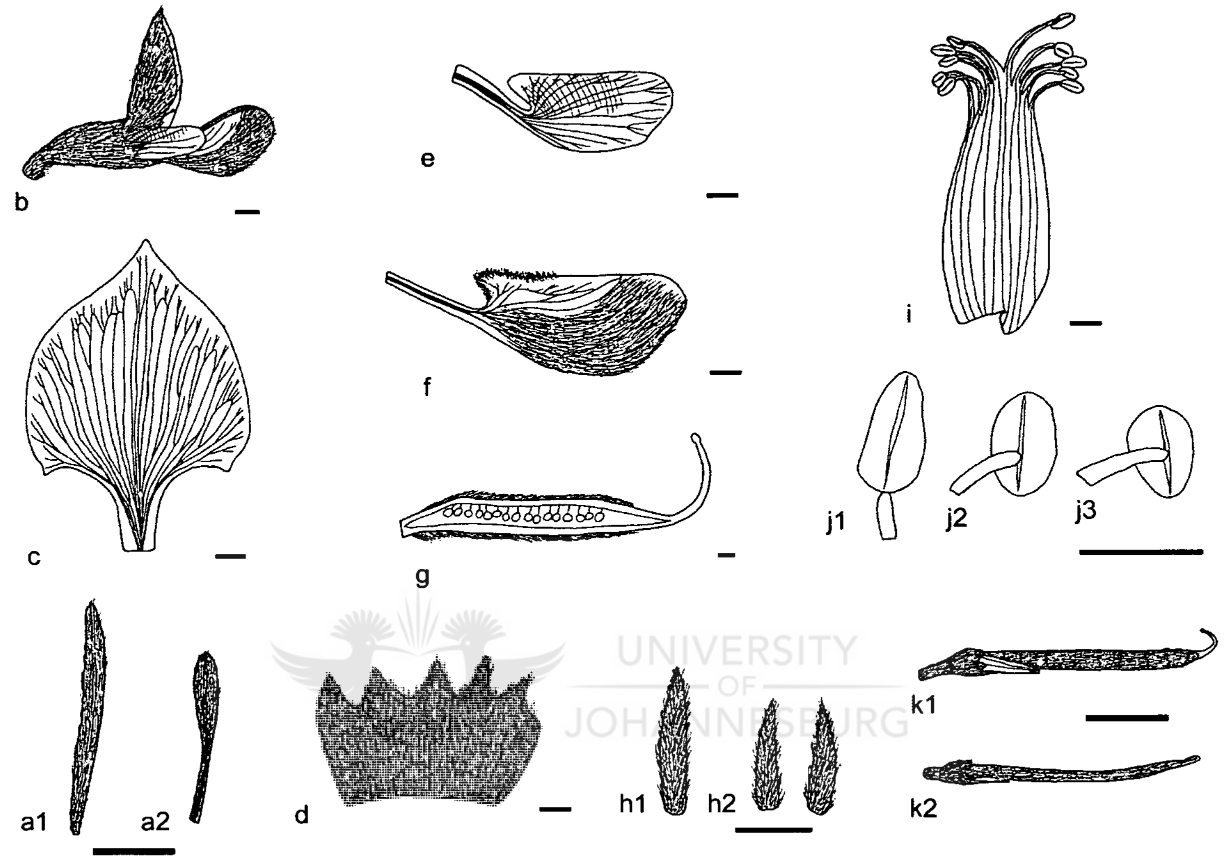

FIG. 6.18 Morphology of *Calobota linearifolia*: (a1–a2) leaves in abaxial view; (b) flower in lateral view; (c) standard petal; (d) outer surface of the calyx (upper lobes to the left); (e) wing petal; (f) keel petal; (g) pistil; (h1) bract; (h2) bracteoles; (i) androecium; (j1) long, basifixed anther; (j2) intermediate carinal anther; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a1, b) *Acocks 13195* (PRE); (a2) *Giess and Van Vuuren 821* (BOL); (c) *Giess 13803* (WIND); (d–g, j1–j3) *Dean 673* (JRAU); (h1–i) *Evrard 9285* (PRE); (k1–k2) *Keet 1668* (WIND). Scale bars: (a1–a2, k1–k2) 1 cm; (b–j3) 1 mm.

### *Additional specimens examined*

**–1812** (Sanitatas): 20 mls [32.18 km] south of Orupembe (–CD), *Giess and Leippert 7435* (WIND).

**–1913** (Sesfontein): 2 km north of Sima Hill, Koakoland (–AA), *Braine 68* (WIND); near Sima Hill, north-east of Möwe Bay (–AA), *Moss and Jacobsen K316* (PRE, WIND); between Hoamib and Unjab Rivers (–AC), *Tinley 1625* (WIND).

**–2013** (Unjab Mouth): 8 mls [12.87 km] east of Torrabay (–AA), *Giess et al. 6180* (PRE, WIND); Unjab River (–AB), *Kers 1875* (S).

**–2517** (Gibeon): Orion, Varsfontein (–AC), *Giess et al. 7190* (K); between Achterfontein and Gelwater (–BC), *Pearson 9233* (K).

**–2520** (Mata Mata): Kalahari Gemsbok National Park (–CA), *Schlieben 10433* (PRE).

**–2615** (Luderitz): Farm Gawachab KEE 114 (–BB), *De Winter and Giess 6424* (BOL, K, WIND).

**–2616** (Aus): between Neisip and Eureka (–BC), *Merxmüller and Giess 2986* (WIND); 13 mls [20.92 km] west of Aus (–CA), *Giess and Van Vuuren 821* (BOL, K, WIND); Kuibis (–DA), *Bayliss BRI.B.365* (K, PRE 2 sheets).

**–2617** (Bethanie): Felshang, near Seeheim (–DD), *Merxmüller and Giess 3615* (PRE, WIND); Seeheim (–DD), *Dinter 1205* (NBG).

**–2618** (Keetmanshoop): 7 mls [11.26 km] south by east of Naute Station (–DB), *Acocks 15659* (K, PRE); Sandmodder 73 (–DD), *Lensing A87/75* (WIND).

**–2619** (Aroab): east of Groot Karas Mountains (–CA), *Mannheimer et al. CM771* (WIND).

**–2620** (Twee Rivieren): Ashkam (–DD), *Evrard 9285* (PRE).

**–2715** (Bogenfels): Sperrgebiet South, 38 km east of Kakaoberg escarpment (–DB), *Jürgens 28176* (PRE); Chameis Valley (–DC), *Williamson 2647* (BOL).

**–2717** (Chamaites): Mara, Letterklip area in Konkiep River bed (–CD), *Craven 2634* (WIND); bed of Vis River, near Seeheim (–DA), *Keet 1663* (WIND, 2 sheets).

**–2719** (Tränental): Warmfontein 280 (–AB), *Lensing J14/76* (WIND), *Müller 87* (WIND); Farm Blaufontein WAR 276 (–AC), *Giess et al. 7131* (WIND).

**–2720** (Noenieput): 20 mls [32.18 km] north of Noenieput on way to Kalahari Gemsbok Park (–AD), *Werger 1489* (NBG, PRE); Askam area, 120 km from Van Zylsrus (–BB), *Dlamini et al. EvW568* (K).

**–2723** (Kuruman): 10 mls [16.09 km] south-west of confluence of the Kuruman and Molopo Rivers (–AA), *Leistner 2255* (K).

**–2817** (Vioolsdrif): 5 km west of Nuob River (–AA), *Giess 13803* (K, PRE, WIND); Garip (–AA), *Wyley s.n.* (S); Richtersveld (–BA), *Venter 8069* (PRE).

**–2818** (Warmbad): a little south of Dabegabis (–BC); *Pearson 4390* (BM 2 sheets, K); near Dabegabis (–BC), *Pearson 4896* (K); mountains between Wolftoon and Henkriesfontein (–CC), *Pearson 3105* (BM 2 sheets, BOL, K 2 sheets); Farm Aluriesfontein 308 (–DA), *Owen-Smith 1252* (WIND).

**–2819** (Ariamsvlei): Nababis, Guigatsis (–BA), *Evrard 9220* (PRE).

**–2820** (Kakamas): below Riemvastmaak, Upington (–AD), *Barnard s.n.* (NBG)

**–2821** (Upington): Swartpan, north-west of Upington (–AA), *Snijman 214* (NBG); 24 mls [38.62 km] south-east of Groblershoop (–DD), *Leistner and Joynt 2861* (K, PRE).

**–2822** (Glen Lyon): 9 mls [14.48 km] west south-west of Volop (–CD), *Leistner 1742* (K).

**–2824** (Kimberly): Gordonia (–BA), *Webb 16* (K, PRE).

**–2918** (Gamoep): Karasberg (–CB), *Van Schauroff s.n.* (K).

**–2921** (Kenhardt): 40 mls [64.36 km] north north-east of Kenhardt (–AC), *Acocks 18803* (K).

**–3020** (Brandvlei): sand dunes along Sak River near Brandvlei (–AD), *Acocks 13195* (BOL, K, PRE).

**–3022** (Carnarvon): Van Wyksvlei, Beesdam (–AD), *Dean 673* (JRAU 2 sheets).

**Precise locality unknown:** without locality, *Bolus 1935* (BOL), *Flanagan s.n. sub PRE 53667* (PRE), *Range 1935* (BOL, NBG).

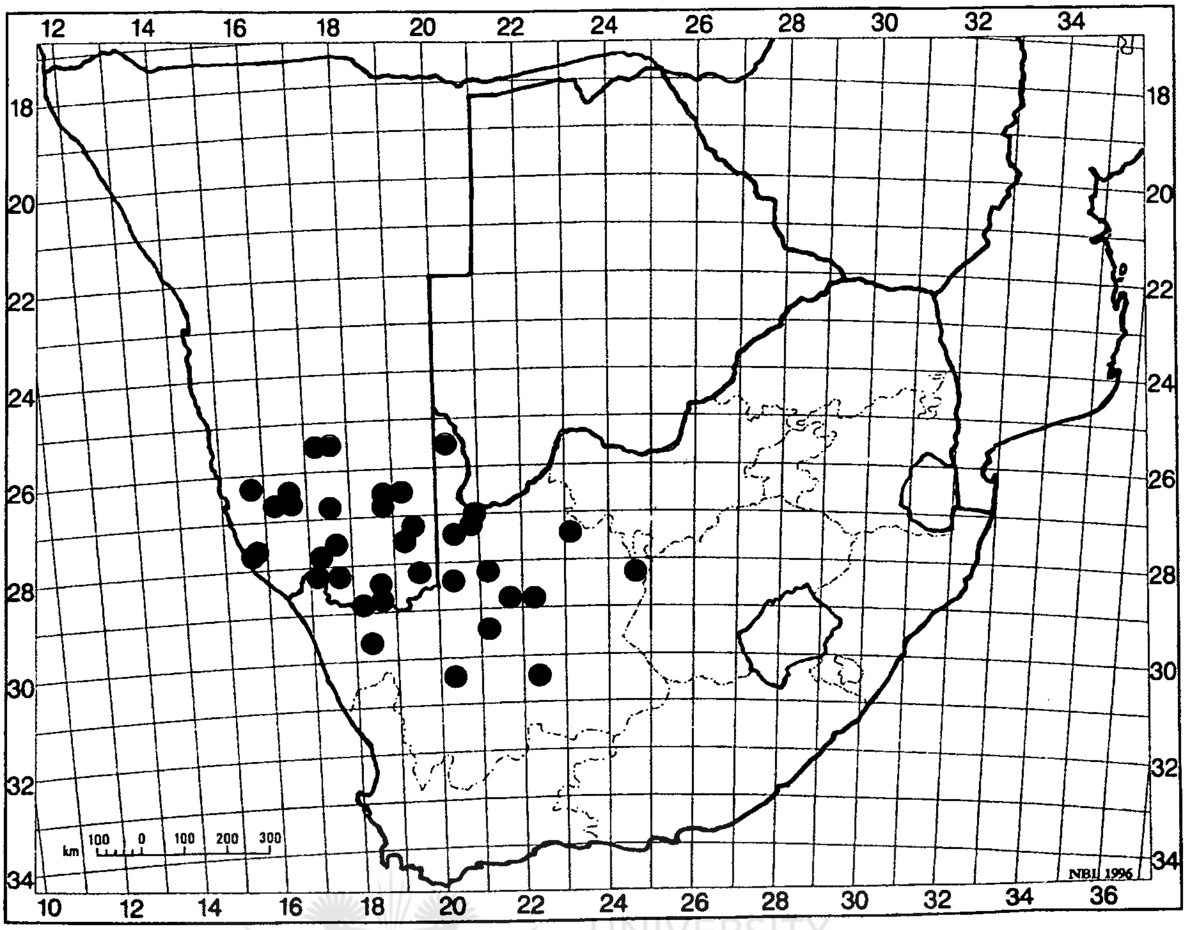

Fig. 6.19 Known geographical distribution of *Calobota linearifolia*.

8. CALOBOTA LOTONONOIDES (Schltr.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia lotononoides* Schltr. in Engler Bot. Jahr. 27: 143. 1900, as "*L. lotonoides*"; Germishuizen and Meyer, Plants of Southern Africa: an annotated checklist, Strelitzia 14: 523. 2003, *pro parte*, Boatwr. and Van Wyk, in S. Afr. J. Bot. 73 (4): 664–666. 2007, as "*L. lotononoides*", *non* Goldblatt and Manning. 2000.—TYPE: SOUTH AFRICA, 'In regione namaquensi: In sabulosis montium Karree-Bergen, alt. C. 4500 ped.' [3118 AB], *Schlechter 8214* (lectotype: K!, designated here; isolectotypes: BM!, BOL!, PRE!, S!, Z, photo!). [Note: A large number of

Schlechter's African collections are housed at Kew (Stafleu and Cowan 1985) and we therefore select the K specimen as lectotype.]

Small, decumbent, multi-stemmed, unarmed shrublet up to 0.5 m in height. Branches green; young branches sericeous, older branches pilose to glabrous with light brown bark, often buried. Leaves digitately trifoliolate or rarely 5-digitate with two additional leaflets; petiole 10–23 mm long, longer than leaflets; leaflets elliptic to narrowly oblanceolate, secund, alternate, sericeous, conduplicate, subsessile, terminal leaflet 10–17 mm long, 1.5–3.0 mm wide, lateral leaflets 8–14 mm long, 1.5–3.0 mm wide, mucronate, base narrowly cuneate. Inflorescence (15–) 24–54 mm long, with (3–) 4 to 14 flowers; pedicel 1–3 mm long; bract 0.7–1.5 mm long, linear, pubescent; bracteoles 0.3–0.6 mm long, linear, pubescent. Flowers 12–15 mm long, yellow. Calyx 5.0–6.5 mm long, pubescent; tube 3.0–3.5 mm long; lobes 2–3 mm long, subulate. Standard 13–16 mm long; claw linear, 4–7 mm long; lamina widely ovate to transversely oblong, 8–9 mm long, 9.0–12.5 mm wide, pilose along dorsal midrib; emarginate. Wings 14–15 mm long; claw 3.0–4.5 mm long; lamina narrowly oblong, subfalcate, longer than keel, 11.5–15.0 mm long, 2–4 mm wide, glabrous, with 7–8 rows of sculpturing. Keel 9–11 mm long; claw 3–4 mm long; lamina boat-shaped, 5.5–7.0 mm long, 3.0–4.5 mm wide, glabrous. Pistil subsessile to shortly stipitate, pubescent, ovary linear, 6.5–7.5 mm long, 0.7–0.9 mm wide with 15 to 19 ovules; style longer than ovary, 3.0–3.5 mm long. Pods narrowly oblong, sometimes somewhat clavate, sericeous, semi-terete, subsessile to shortly stipitate, 18–37 (–40) mm long, 3–4 mm wide, 7 to 12-seeded, dehiscent. Seeds suborbicular, 2.0–2.5 mm long, 1.5–2.0 mm wide, mature seeds brown with beige spots, hilum brown, surface rugose (Fig. 6.20). Flowering time: late winter to late spring.

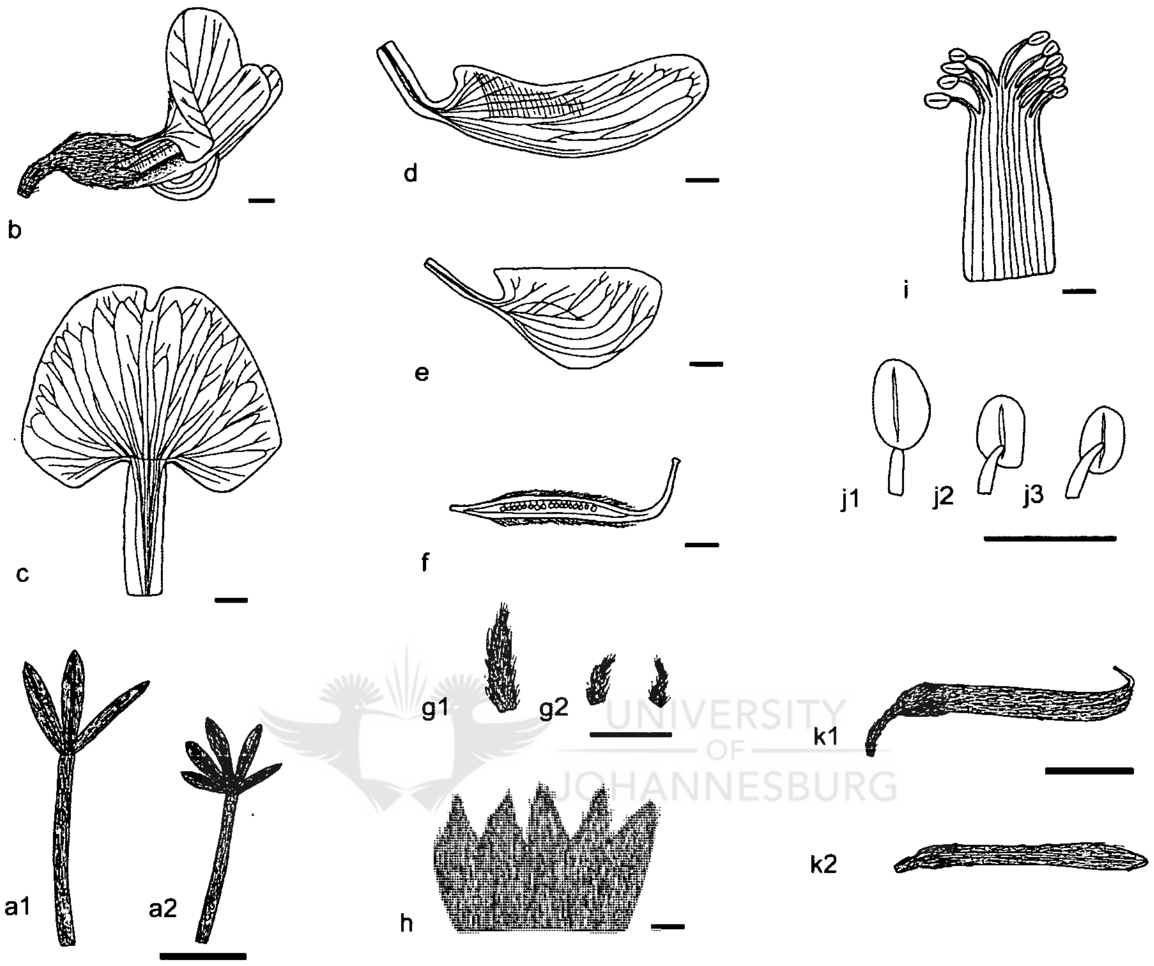

FIG. 6.20 Morphology of *Calobota lotononoides*: (a1–a2) leaves in abaxial view; (b) flower in lateral view; (c) standard petal; (d) wing petal; (e) keel petal; (f) pistil; (g1) bract; (g2) bracteoles; (h) outer surface of the calyx (upper lobes to the left); (i) androecium; (j1) long, basifixed anther; (j2) intermediate carinal anther; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a1–k2) *Boatwright et al. 142* (JRAU). Scale bars: (a1–a2, k1–k2) 1 cm; (b–j3) 1 mm.

***Diagnostic characters***—*Calobota lotononoides* superficially resembles *C. sericea*, notably the broad-leaved form on the West Coast and around Clanwilliam. In this form the leaflets are broad and sericeous much like those of *C. lotononoides*. However, *C. lotononoides* differs in its smaller, decumbent habit with buried stems and especially in the exceptionally long lamina of the wing petals, which is ± twice as long as those of the glabrous keel petals. The inflorescences are unarmed, and the sericeous pods contain spotted, rugose seeds. *Calobota sericea* can reach heights of up to 2 m and the wing petals are only slightly longer than the pilose keel petals.

***Distribution and habitat***—*Calobota lotononoides* occurs on the west coast of South Africa around Hondeklipbaai and Brandsebaai (Fig. 6.21). The type collection was made by Schlechter at "Karree-Bergen", close to Nuwerus in the Vanrhynsdorp district according to Leistner and Morris (1976). The species has been recorded on well-drained, sandy soils with the main stems becoming covered with sand. The multi-stemmed, decumbent habit appears to be an adaptation to moving sand dunes, as extensive underground branches enable the plant to emerge above the sand after being covered.

***Note***—According to Raimondo et al. (in press) the status of this species is declining. Although only a 5% habitat loss has been observed due to heavy mineral sand mining, the loss is still ongoing and could later become problematic.

***Additional specimens examined***

**–3017** (Hondeklipbaai): from Sandkraal, north of Bitter River, 25 km west of Garies (–CB), *Helme et al. 4720* (NBG); Farm Roodeheuwel, 9 km west of Nariep (–DC), *Boatwright et al. 142* (JRAU), *Perold 1646* (PRE).

**–3117** (Lepelfontein): Vredendal, south-east of Brandsebaai, on Farm Hartebeestekom (–BD), *Helme 2931* (NBG); Van Rhynsdorp/Vredendal, Brandsebaai (–BD), *Van Rooyen 2235* (PRE).

**–3118** (Vanrhynsdorp): Karree-Bergen (–AB), *Schlechter s.n. sub TRV 1059* (PRE); from Skaapvlei, some 10 km north-east of Olifants River mouth (–AC), *Helme 4684* (NBG).

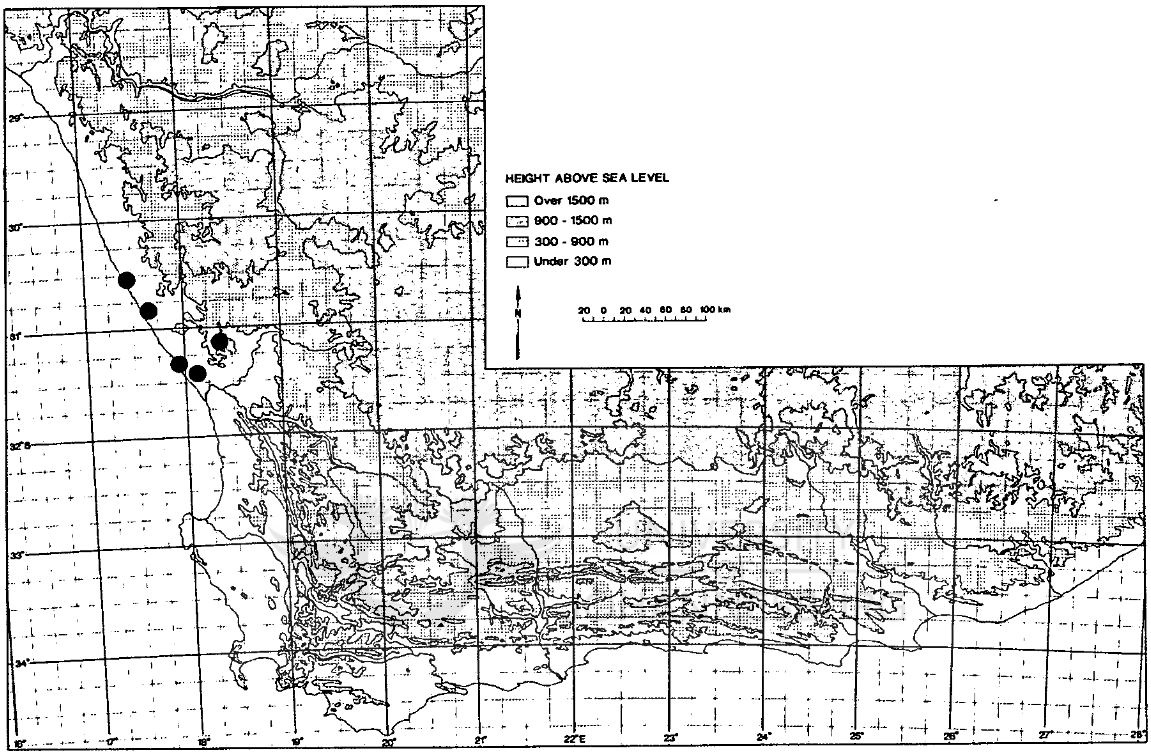

FIG. 6.21. Known geographical distribution of *Calobota lotononoides*.

9. **Calobota namibiensis** Boatwr. and B.-E.van Wyk, sp. nov., similar to *Calobota linearifolia* (E.Mey.) Boatwr. and B.-E.van Wyk, but differs in the short, elliptic to ovate leaves and short, tomentose pods. It is also similar to *Calobota saharae* (Coss. and Dur.) Boatwr. and B.-E.van Wyk but differs in the elliptic to ovate leaves, densely pubescent petals and the short, tomentose pods (to be translated into Latin).—TYPE: 25 mls [40.23 km] east of Lüderitz on road

to Aus [2615 CA], *De Winter and Hardy 7919* (holotype: WIND!, specimen on the right, here designated; isotypes: K!, PRE!).

*Lebeckia dinteri auct. non* Harms: Merxm. and Schreib., FSWA 60: 67. 1970. [Note: Harms described *Lebeckia dinteri* from a specimen that is actually *Calobota linearifolia*. Subsequent authors, however, referred to the species here described as new as "*Lebeckia dinteri*" which is distinct from *Calobota linearifolia*, but this taxon has not been formally described.]

Virgate, multi-stemmed shrubs up to 1.2 m tall. Branches green; young branches sericeous; older branches sericeous or glabrous with light brown bark. Leaves simple; petiole absent; elliptic to ovate, upper and lower surfaces sericeous, alternate, sessile, 6–12 mm long, 1–2 mm wide; apex acute; base cuneate. Inflorescences 70–110 mm long, with 3 to 8 flowers; pedicel 1–2 mm long; bract 2.5–3.5 mm long, linear, sericeous; bracteoles 1.5–3.0 mm long, linear, sericeous. Flowers 10–11 mm long, bright yellow. Calyx 6–8 mm long, densely pubescent on the outer surface; tube 3–4 mm long; lobes 3.0–4.5 mm long, subulate. Standard 9.5–12.0 mm long; claw linear, 2–3 mm long; lamina ovate, 7.5–9.0 mm long, 5–6 mm wide, densely pubescent on dorsal surface; apex acute. Wings 8.0–8.5 mm long; claw 2–3 mm long; lamina oblong, shorter than the keel, 5.5–6.5 mm long, 2.5–3.0 mm wide, with 6–8 rows sculpturing, glabrous. Keel 8.0–11.5 mm long; claw 2.5–3.5 mm long; lamina boat-shaped, 5.5–8.0 mm long, 3.5–4.5 mm wide, pubescent. Pistil shortly stipitate, pubescent; ovary linear, 4–5 mm long, 0.9–1.0 mm wide with about 5 ovules; style longer than the ovary, 5.0–9.5 mm long. Pods linear, semi-terete, 15–17 mm long, 2 mm wide, 3 to 4-seeded, tomentose, ?dehiscent.

Seeds not seen (Fig. 6.22). Flowering time: Flowering specimens have been collected in March, August and October.

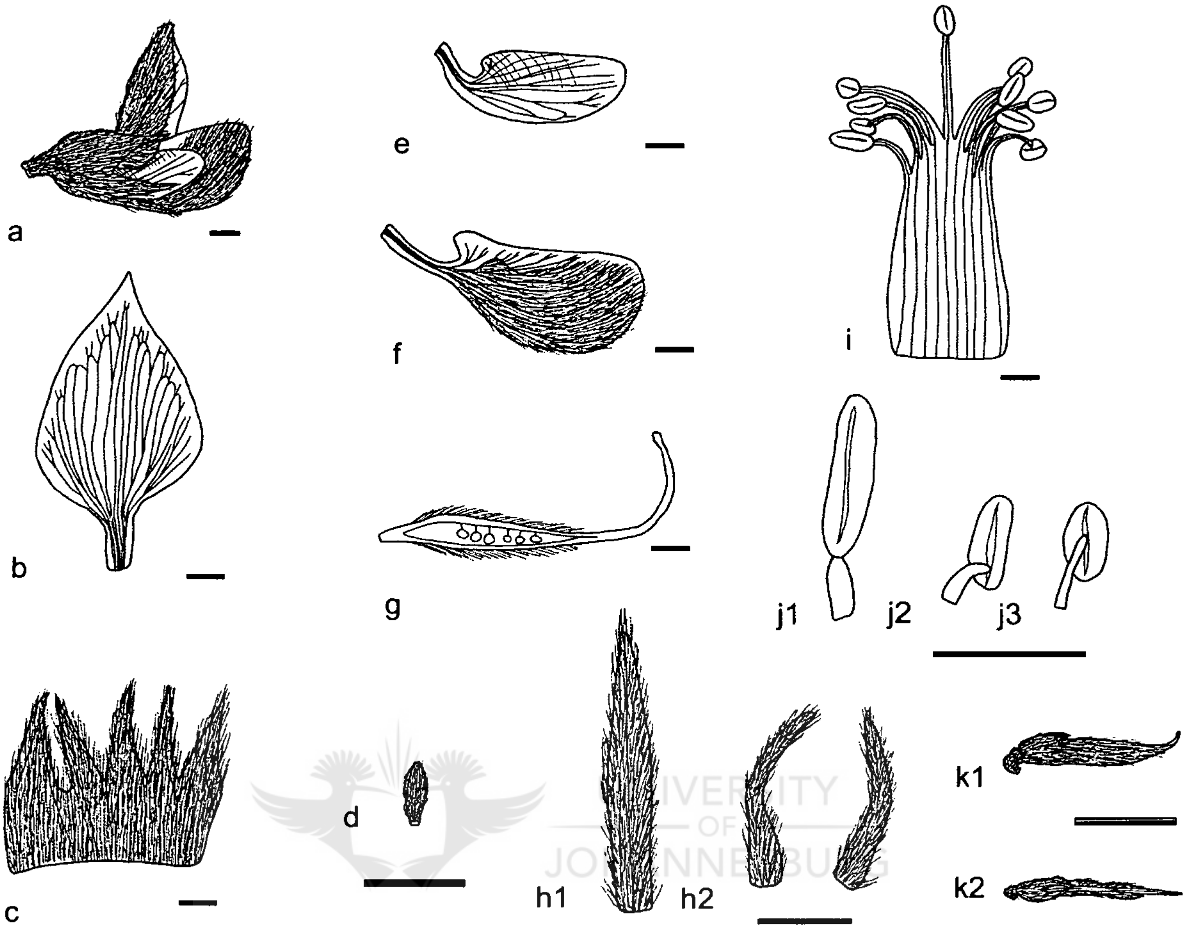

FIG. 6.22 Morphology of *Calobota namibiensis*: (a) flower in lateral view; (b) standard petal; (c) outer surface of the calyx (upper lobes to the left); (d) leaf in abaxial view (e) wing petal; (f) keel petal; (g) pistil; (h1) bract; (h2) bracteoles; (i) androecium; (j1) long, basifixed anther; (j2) intermediate carinal anther; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a–c, e–f, h1–h2, j1–j2) *Owen-Smith 1268* (WIND); (d) *Kolberg and Maggs 212* (WIND); (g, i) *Owen-Smith 117* (WIND); (k1–k2) *De Winter and Hardy 7919* (WIND). Scale bars: (d, k1–k2) 1 cm; (a–c, e–j3) 1 mm.

***Diagnostic characters***—A very poorly known and collected species. The lack of sufficient material makes it difficult to study the variation within this species. It is similar to *Calobota linearifolia* and *C. saharae*, but differs in the elliptic to ovate leaves, densely pubescent petals and the short, tomentose pods. In both *C. linearifolia* and *C. saharae* the leaves are linear. The petals are also pubescent in *C. linearifolia* while in *C. saharae* only the standard petal is pilose. The pods of *C. linearifolia* are sericeous, while those of *C. saharae* are glabrous and in both species they are longer than those of *C. namibiensis*.

***Distribution and habitat***—*Calobota namibiensis* is endemic to Namibia and occurs in the Lüderitz and Aus areas (Fig. 6.23). It grows on dunes in red sand or gravelly sandy soil along roadside up to 1800m above sea-level.

***Note***—The status of this species has been assessed as vulnerable (VU D2) by Golding (2002; included as *Lebeckia dinteri*) and as least concern (LC) recently by Loots (2005; included as *Lebeckia dinteri*).

***Additional specimens examined***

**–2615** (Lüderitz): dunes south of Koichab pump station (–AD), *Seely 2005* (WIND); Koichab State Land (–BC), *Owen-Smith 117*, *1268* (WIND); Halenberg (–CB), *Merxmüller and Giess 3088* (WIND); Rotkop, Lüderitz (–CB), *Dinter 1032* (NBG), *Merxmüller and Giess 3141* (WIND).

**–2616** (Aus): 13 mls [20.92 km] west of Aus (–CB), *Giess and Van Vuuren 821* (PRE, WIND); koppie south-west of Rotkop Station, next to power-line track (–CB), *Kolberg and Maggs 212* (PRE, WIND).

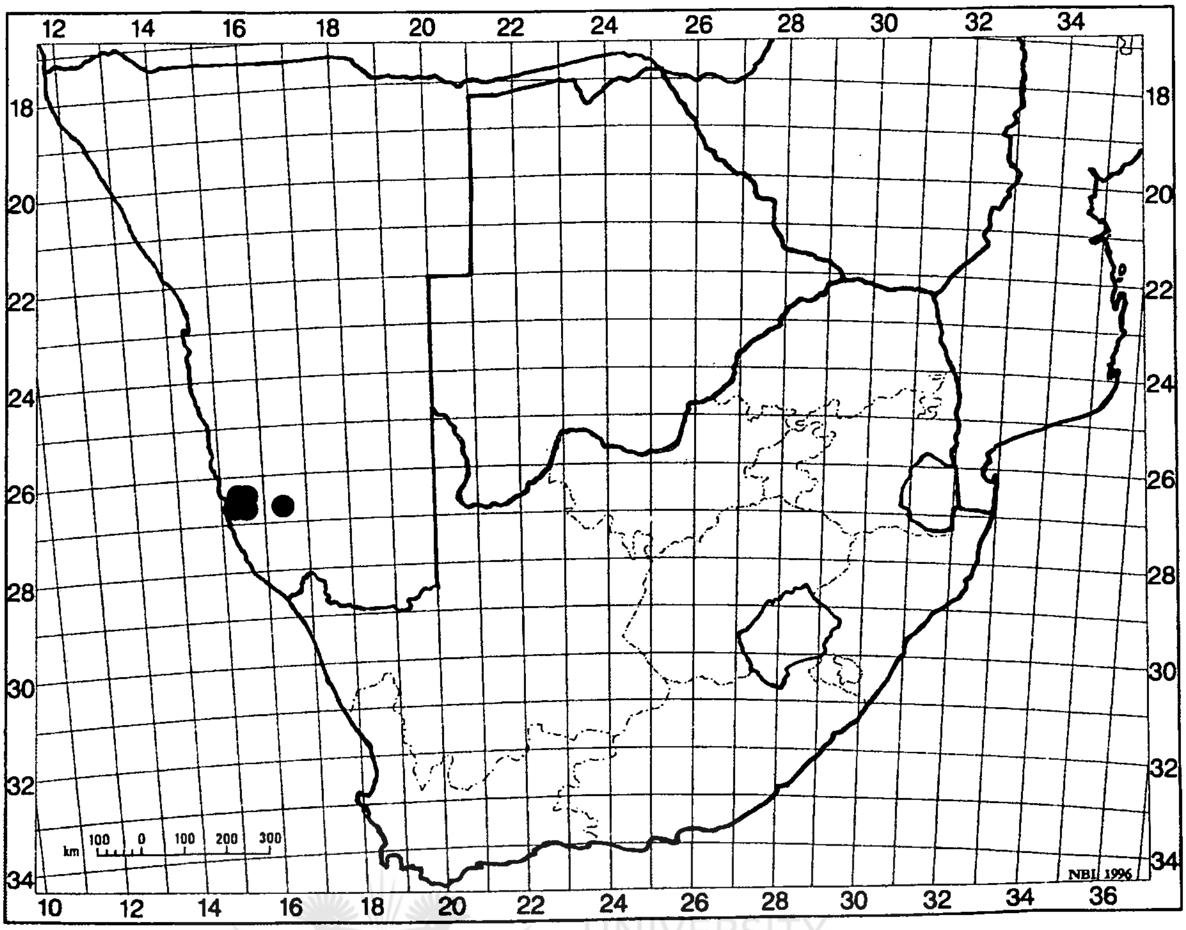

FIG. 6.23 Known geographical distribution of *Calobota namibiensis*.

10. CALOBOTA OBOVATA (Schinz) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia obovata* Schinz, Mem. Herb. Boiss. 1: 126. 1900; Merxm. and Schreiber, FSWA 60: 68. 1970.—TYPE: SOUTH AFRICA, Namibia, Gansberg [grid unknown], *Fleck 75* (lectotype: Z-000022914, photo!, specimen on the left, designated here; isolectotype: Z-000022915, photo!). [Note: According to Stafleu and Cowan (1985) Hans Schinz's main collection is in Z and we therefore designate one of the Z specimens as lectotype.]

Sericeous, multi-stemmed shrub up to 1 m in height. Branches green; young branches short-sericeous, older branches short-sericeous or glabrous with light brown bark. Leaves unifoliolate or rarely trifoliolate; petiole shorter than leaflets, 5–24 mm long; leaflets widely obovate to orbicular, rarely ovate, alternate, short-sericeous, subsessile, 12–36 mm long, 10–25 mm wide, apex obtuse or rarely acute, base cuneate. Inflorescence 24–85 mm long, with 7 to 16 flowers; pedicel 4–5 mm long; bract 3–5 mm long, ovate, pubescent; bracteoles 3–5 mm long, ovate to linear, pubescent. Flowers 13–16 mm long, bright yellow. Calyx 8.0–8.5 mm long, densely pubescent; tube 4.5–5.5 mm long; lobes 3–4 mm long, subulate. Standard 14.5–15.5 mm long, claw linear, 3.5–4.5 mm long, lamina widely ovate, 10.0–11.5 mm long, 12.5–14.5 mm wide, dorsal surface pubescent; apex obtuse. Wings 14.5–15.5 mm long, claw 3.0–3.5 mm long, lamina oblong, shorter than keel, 11–12 mm long, 5.5–6.0 mm wide, pilose, with 4–5 rows of sculpturing. Keel 14.5–16.5 mm long, claw 4–5 mm long, lamina boat-shaped, 10.0–11.5 mm long, 5.5–6.5 mm wide, pubescent. Pistil subsessile to shortly stipitate, pubescent, ovary linear, 11.5–12.5 mm long, 1.5–2.0 mm wide with ±15 ovules; style shorter than ovary, 6–7 mm long. Pods linear, semi-terete, subsessile to shortly stipitate, 30–40 mm long, 4–5 mm wide, 5 to 7-seeded, short-sericeous, dehiscent. Seeds not seen (Fig. 6.24). Flowering time: Flowering specimens have been collected in May, June, July, November and December suggesting that flowering occurs in spring and summer.

***Diagnostic characters***—Similar to *Calobota elongata* but differs in the unifoliolate leaves, racemose, few-flowered racemose inflorescences, pedicellate flowers, obovate bracts and bracteoles, widely ovate standard petal, pubescent wing petals that are shorter than the keel petals and the linear, sericeous pods (*C. elongata* differs in the trifoliolate leaves, dense, spicate inflorescences with smaller, sessile flowers, long, narrow bracts and bracteoles, ovate to elliptic standard petal with a pilose midrib, wing petals that are longer than keel and shorter, tomentose pods with less seeds).

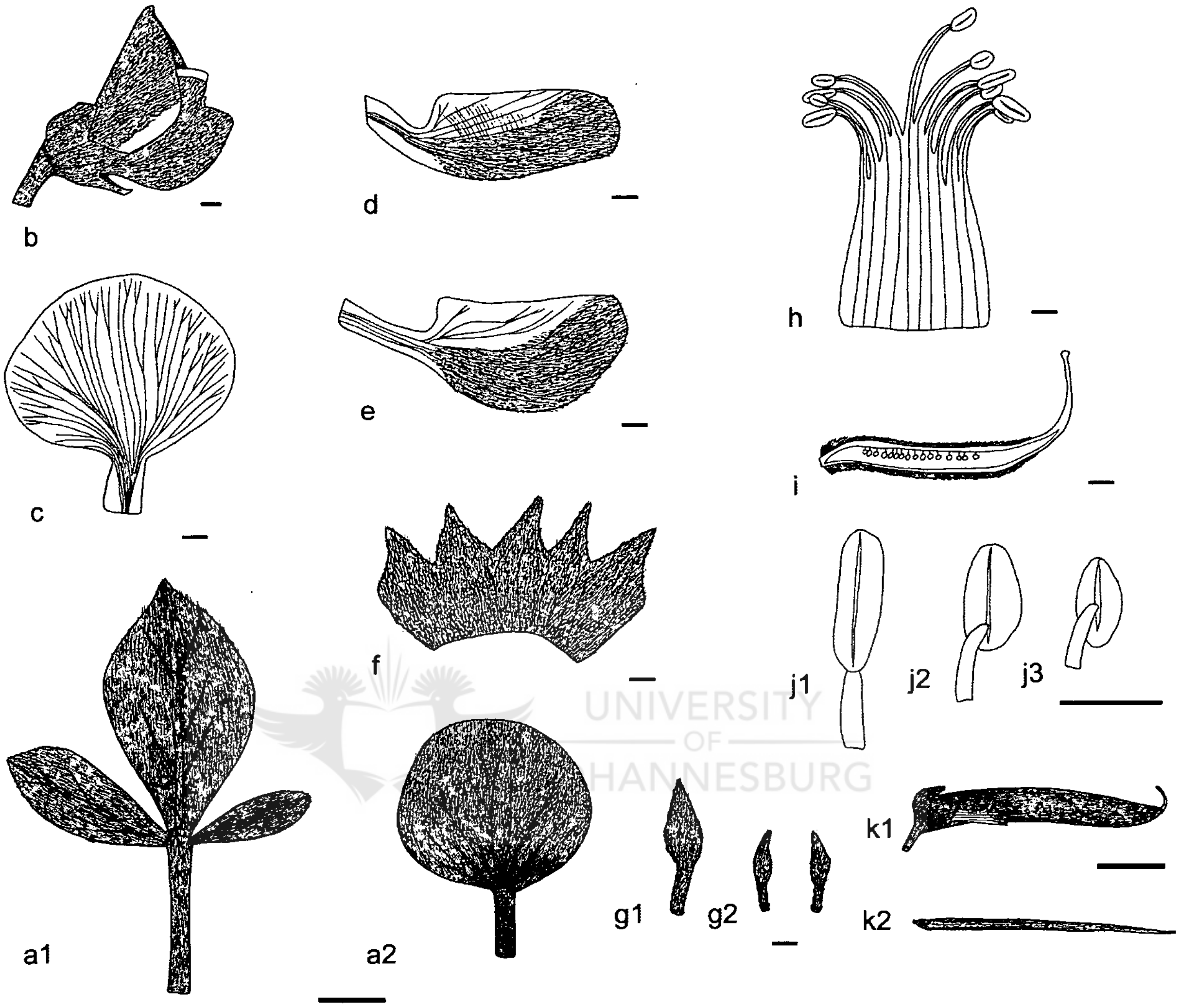

FIG. 6.24 Morphology of *Calobota obovata*: (a1–a2) leaves in abaxial view; (b) flower in lateral view; (c) standard petal; (d) wing petal; (e) keel petal; (f) outer surface of the calyx (upper lobes to the left); (g1) bract; (g2) bracteoles; (h) androecium; (i) pistil; (j1) long, basifixed anther; (j2) intermediate carinal anther; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a1) *Schweidfezer 4315* (WIND); (a2, k1–k2) *Dinter 1094* (NBG); (b, f, i) *Pearson 8036* (BOL); (c–e, h, j1–j3) *Kers 152* (WIND). Scale bars: (a1–a2, k1–k2) 1 cm; (b–j3) 1 mm.

***Distribution and habitat*****—***Calobota obovata* is endemic to Namibia and occurs from Windhoek southwards as far as Aus (Fig. 6.25). It grows on rocky outcrops or granite at altitudes of ca. 1600 m to 2230 m.

***Note*****—**The status of this species has been assessed as data deficient (DD) by Golding (2002) and Loots (2005).

***Additional specimens examined***

**–2217** (Windhoek): Farm Regenstein (–CA), *Giess and Giess 11765* (NBG, PRE, S, WIND), *Merxmüller and Giess 28010* (WIND).

**–2316** (Nauchas): Gamsberg (–AD), *Kers 152* (WIND), *Kers 154* (S), *Merxmüller and Giess 957* (BM, K, PRE, WIND), *Kolberg and Tholkes NAM2960-HK1418* (K), *Meyer 1016* (WIND), *Schweidfezer 4315* (WIND); Farm Hopefield (–AD), *Merxmüller and Giess 893* (WIND); Farm Weipenfels (–AD), *Walter and Walter 1686* (WIND).

**–2318** (Leonardville): Farm Rietfontein (–CA), *Leippert 4537* (WIND).

**–2516** (Helmeringhausen): Farm Aruab 23 on top edge of Great Escarpment (–DA), *Miller Mil1/036* (WIND).

**–2615** (Lüderitz): Lüderitz (–CA), *Rogers 2959* (K).

**–2616** (Aus): Urus Plateau, Lüderitz (–BA), *Logan and Seely 301* (WIND); Aus (–CB), *Dinter 1094* (NBG); Aus, rocks east of railway station (–CB), *Pearson 8036* (BM, BOL 2 sheets, K, NBG, PRE).

**Precise locality unknown:** Ruschberg, *Rusch 4379* (S).

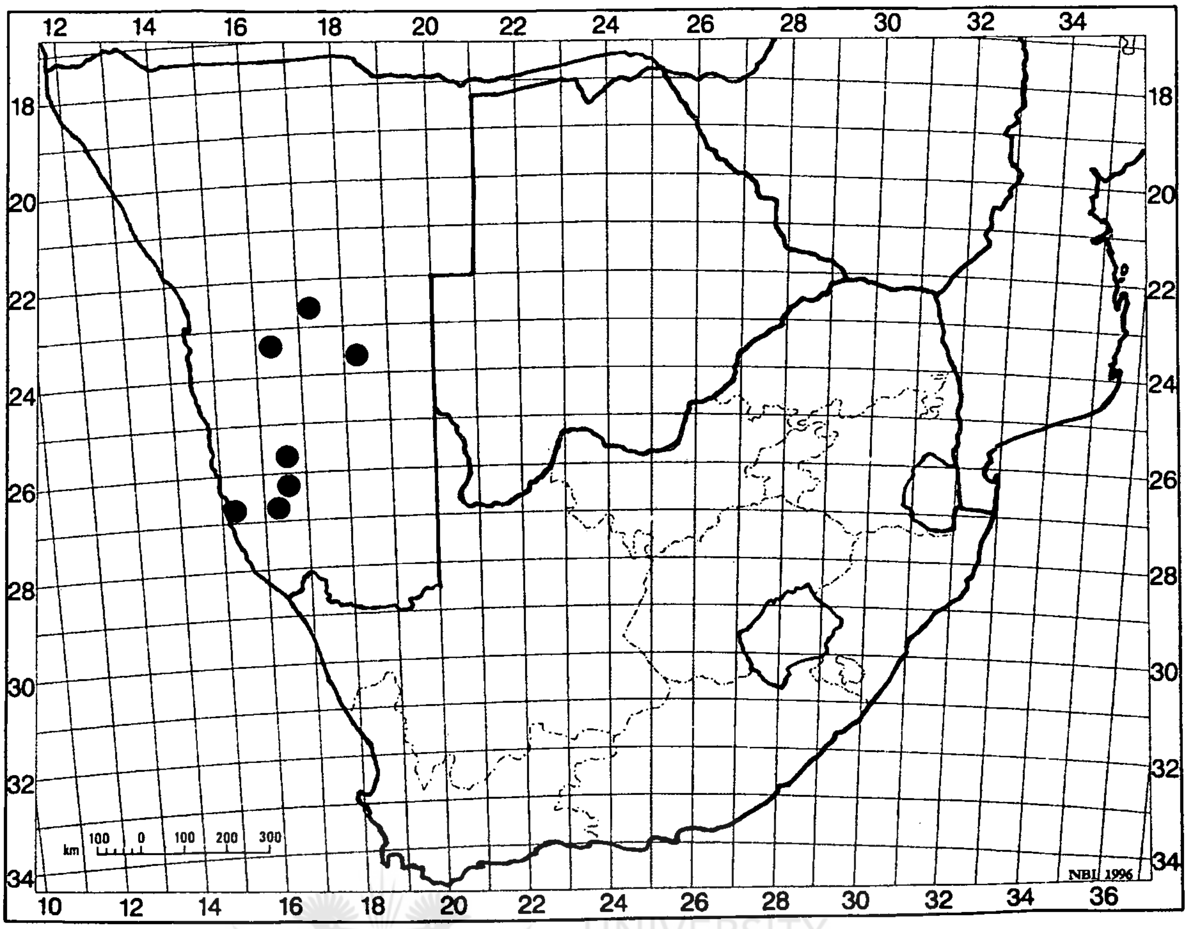

FIG. 6.25. Known geographical distribution of *Calobota obovata*.

11. CALOBOTA PSILOLOBA (E.Mey.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Stiza psiloloba* E.Mey. Comm. Pl. Afr. Austr. 1: 31. Feb. 1836; Meisner in Hook. Lond J. Bot. 2: 68. 1843. *Lebeckia psiloloba* (E.Mey.) Walp., Linnaea 13: 478. 1839; Benth. in Hook. Lond. J. Bot. 3: 356. 1844; Harv. in Harv. and Sond., Fl. Cap. 2: 84. 1862; Bond and Goldblatt, J. S. Afr. Bot. 13: 290. 1984; Goldblatt and Manning, Cape Pl.: 493. 2000.—TYPE: SOUTH AFRICA, without locality, *Drège 6470* (lectotype: P!, designated here; isolectotype: K!, S!). [Note: The Paris specimen bears a label with the words "*Stiza psiloloba mihi*" in Meyer's handwriting, and is therefore chosen as lectotype. The relatively thin, glabrous twigs and small,

leathery pods (in an envelope on the specimen) are characteristic of this species.]

*Acanthobotrya pungens* sensu Eckl. and Zeyh., Enum. 2: 193. Jan 1836, non *Lebeckia pungens* Thunb. Type: South Africa, "Zwartkops– et Zondagsrivier", *Ecklon and Zeyher 1340* (lectotype: NBG!, designated here; isolectotypes: P!, K!, S!). [Note: The specimen in NBG dislays the type locality and the Enumeratio label.]

Erect, multi-stemmed, spinescent shrub up to 1.2 m tall. Branches green; young branches glabrous to very sparsely pubescent, older branches glabrous with brown bark. Leaves unifoliolate or rarely trifoliolate; petiole short, 0.5–1.0 mm long (up to 5 mm long when trifoliate); leaflets slightly obovate to spathulate, alternate, upper and lower surfaces thinly pilose, 5–7 (–11) mm long, 1.5–3.0 (–4.0) mm wide; base attenuate; apex obtuse. Inflorescences 40–50 (–65) mm long, with 8 to 10 (–12) flowers; pedicel relatively long, (3–) 4–5 (–6) mm long; bract 0.3–0.4 (–0.6) mm long, triangular; bracteoles 0.1–0.3 mm long, linear to slightly ovate. Flowers 8–11 mm long; bright yellow. Calyx 2.2–2.6 mm long, slightly pubescent on the outer surface; tube 1.5–2.0 mm long; lobes widely triangular, 0.5–0.8 mm long; apices broadly acute. Standard 7–9 mm long; claw 2.5–3.0 (–4.0) mm long; lamina oblong to slightly ovate, 4–5 (–6) mm long, 3.0–4.5 mm wide, glabrous; apex emarginate. Wings 7.0–8.5 mm long; claw 2.5–3.0 (–3.5) mm long; lamina oblong, shorter than the keel, 4.0–4.5 (–5.0) mm long, 2–3 mm wide, with 4–5 rows sculpturing, glabrous. Keel 8.5–11.0 mm long; claw 3.5–4.0 (–4.5) mm long; lamina boat-shaped, 5–6 (–7) mm long, 3–4 mm wide, glabrous. Pistil stipitate, glabrous; ovary linear to elliptic, 5.5–7.5 mm long, 0.8–1.1 mm wide; ovules 6 to 8; style shorter than ovary, 3.5–5.0

mm long. Pods oblong, laterally compressed, membraneous, 14–17 (–33) mm long, 4–5 mm wide, glabrous; stipe up to 4 mm long, 2 to 6-seeded, indehiscent. Seeds reniform, 2.5–3.0 mm long, 2.0–2.5 mm wide, light brown, surface smooth (Fig. 6.26). Flowering time: The main flowering time of C. psiloloba is between March and June, but flowering also sometimes occurs in spring and summer (October to January).

***Diagnostic characters***—*Calobota psiloloba* is similar to *Calobota cuspidosa*, but differs in that this species only reaches heights of up to 1.2 m and has small flowers that are borne on long, thin pedicels (*C. cuspidosa* reaches heights of up to 4 m and has much larger flowers on relatively short pedicels). The older stems are almost completely glabrous and the standard petal notched, while in *C. cuspidosa* the older stems are pubescent and the standard petal is obtuse. The pods and seeds are also smaller than those of *C. cuspidosa*.

***Distribution and habitat***—*Calobota psiloloba* is restricted to the Eastern Cape Province and occurs mainly around Port Elizabeth, Grahamstown and Addo, but has outlier populations around Cradock at altitudes between 30 and 520 m (Fig. 6.27). It is normally found in open grasslands on sandy soils and is eaten by elephants (according to label information).

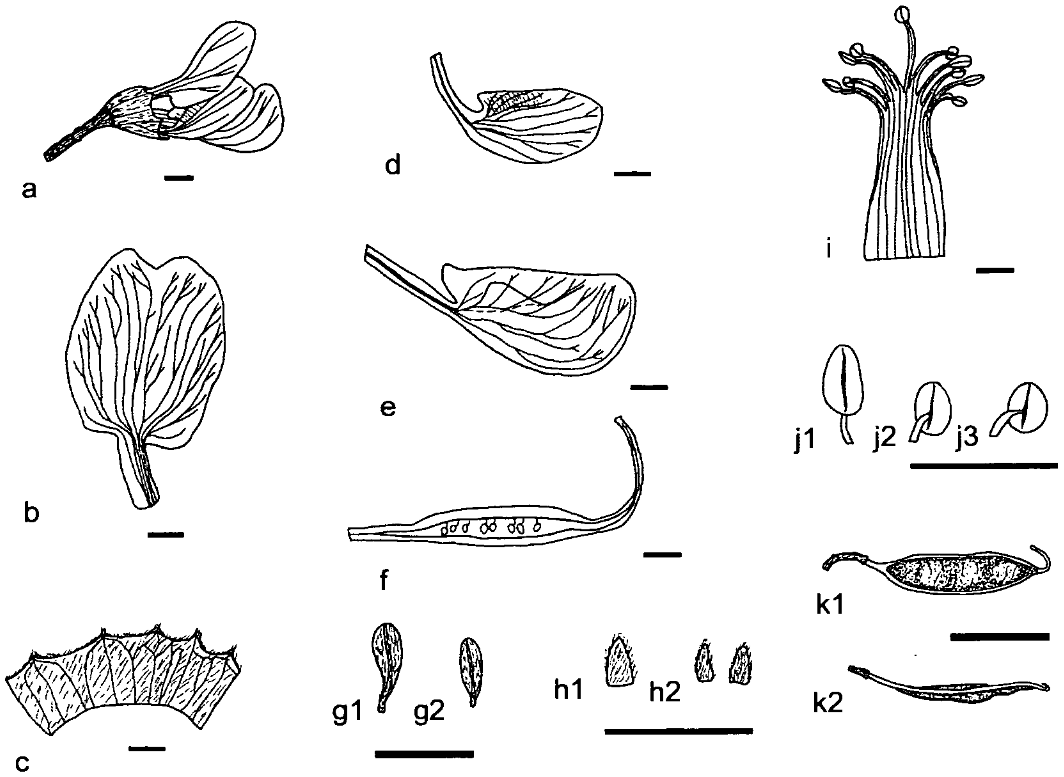

FIG. 6.26 Morphology of *Calobota psiloloba*: (a) flower in lateral view; (b) standard petal; (c) outer surface of the calyx (upper lobes to the left); (d) wing petal; (e) keel petal; (f) pistil; (g1–g2) leaves in abaxial view; (h1) bract; (h2) bracteoles; (i) androecium; (j1) long, basifixed anther; (j2) intermediate carinal anther; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a) *Story 3353* (PRE); (b–f, g1, h1–j3) *Van Wyk s.n.* (JRAU); (g2) *Zeyher 2317* (NBG); (k1–k2) *Le Roux et al. 20* (JRAU). Scale bars: (g1–g2, k1–k2) 1 cm; (a–f, h1–j3) 1 mm.

### *Additional specimens examined*

**–3125** (Steynsburg): Grootfontein, Middelburg district (–AC), *Burtt-Davy 9665* (PRE).

**–3225** (Somerset East): Cradock (–BA), *Botany Honours Students 320* (PRE, PRU); Somerset East, farm Kaboega (–DA), *Bayliss 6897* (K, S).

**–3324** (Steytlerville): on plains near Zondags River (–DB), *Bowie s.n.* (BM).

**–3325** (Port Elizabeth): in the valleys of the Zuurberg Mountains at Paarde Poort (–AC), *Bolus 2667* (BOL, K), *Wilson 422* (BM); Perdepoort (–AC), *Theron 685* (PRE); Bassons Kloof, Annes Villa (–BB), *Bayliss 3923* (NBG); Addo Elephant Park (–BD), *Archibald 3848* (GRA, K, PRE), *Brynard 445* (K, PRE), *Repton 5715* (PRE); 15th mile [24.1 km] on the road from Port Elizabeth to Addo (–BD), *Long 612* (GRA, K); along road from Grahamstown to Paterson (–BD), *Van Wyk s.n.* (JRAU); Uitenhage (–CD), *Alexander-Prior s.n.* (BM, K 3 sheets); Cradock Place, Port Elizabeth (–DC), *Galpin 6430* (GRA, PRE); district Uitenhage, Zwartkops River (–DC), *Ecklon and Zeyher 737* (BM, BOL 2 sheets, K 2 sheets, NBG, PRE 4 sheets), *Ecklon and Zeyher 1340* (K, NBG, P 3 sheets, PRE, S); New Brighton near Port Elizabeth (–DC), *Ethel West 395* (BOL); Coega (–DC), *Long 945* (GRA, K); Redhouse, near cemetary (–DC), *Troughton 425* (PRE 2 sheets); Redhouse (–DC), *Boatwright et al. 107* (JRAU), *Le Roux et al. 20* (JRAU), *Wells 3697* (PRE); Zwartkops River (–DC), *Zeyher 2317* (PRE 2 sheets, NBG, S).

**–3326** (Grahamstown): Table farm near Grahamstown (–BC), *Atherstone 24, 50* (K); Grahamstown (–BC), *MacOwen 1102* (K); Bushman's River bridge, main road from Grahamstown to Port Elizabeth (–CA), *Archibald 3958* (PRE), *Story 3353* (K, PRE).

**Precise locality unknown:** without locality, *Barber s.n.* (K), *Bowie s.n.* (K), *Zeyher 3317* (PRE).

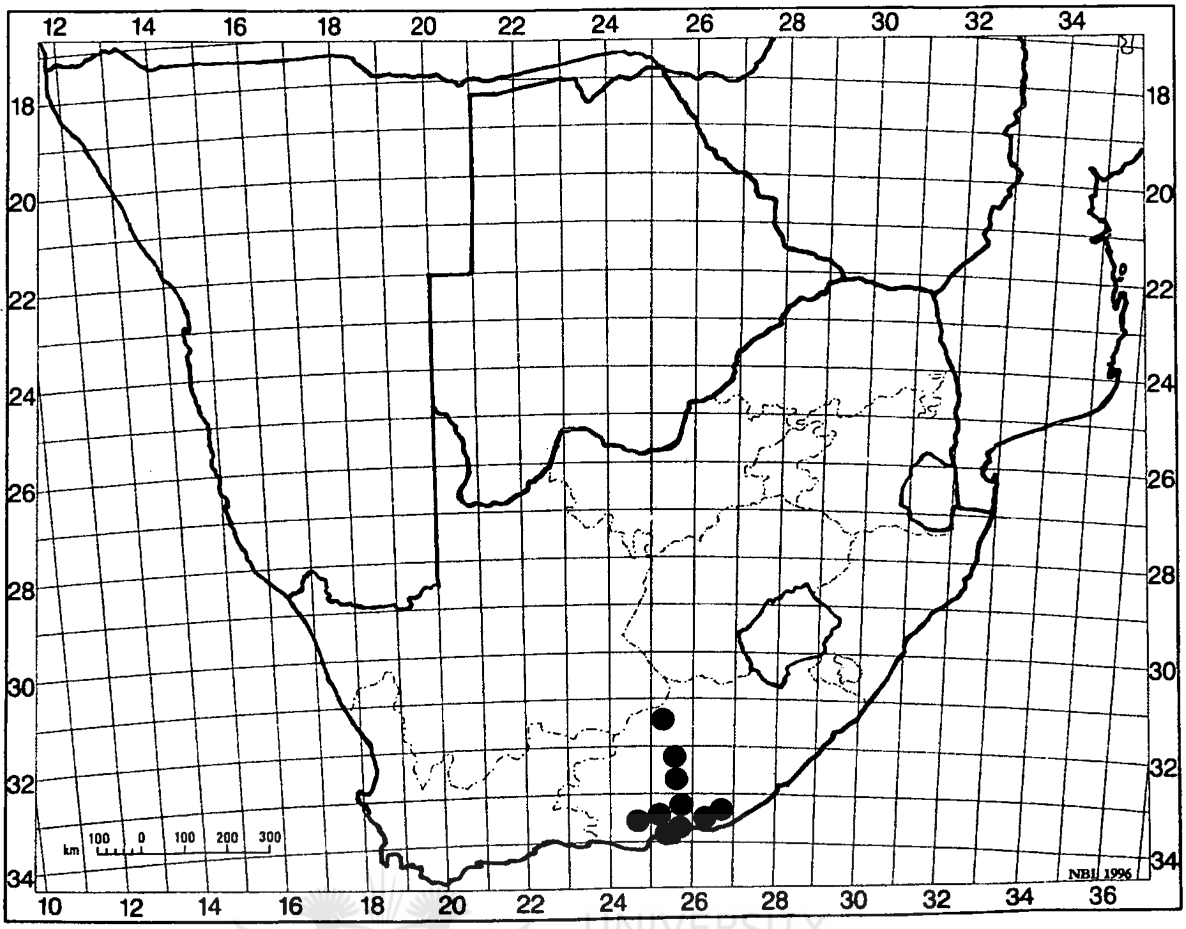

FIG. 6.27 Known geographical distribution of *Calobota psiloloba*.

12. CALOBOTA PUNGENS (Thunb.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia pungens* Thunb., Nov. Gen.: 141. 1800; Prodr. Pl. Cap.: 122. 1800; Willd., Sp. Pl.: 947. 1800; Thunb., Fl. Cap.: 562. 1823; DC., Prodr. 2: 137. 1825; Benth. in Hook. Lond. J. Bot. 3: 356. 1844; Harv. in Harv. and Sond., Fl. Cap. 2: 83. 1862; Compton, Trans. Roy. Soc. of S. A. 19: 294. 1931; Bond and Goldblatt, J. S. Afr. Bot. 13: 290. 1984; Goldblatt and Manning, Cape Pl.: 494. 2000.—TYPE: SOUTH AFRICA, Eastern Cape Province, near Olifant's River [close to Oudtshoorn] at Cannaland [now Little Karoo], *Thunberg s.n. sub THUNB-UPS 16417* (lectotype: UPS!, designated here). [Note: This is the only specimen in

Thunberg's herbarium and the type locality is written on the back of the sheets in Thunberg's handwriting. This specimen is therefore chosen as lectotype.]

*Stiza erioloba* E.Mey. Comm. Pl. Afr. Austr. 1: 31. Feb. 1836.—TYPE: SOUTH AFRICA, Eastern Cape Province, near Klaarstroom [close to Prince Albert, 3322BC], near the foot of the "Groote Zwartebergen" [Great Swartberg], *Drège s.n.* (lectotype: P!, specimen on the right, designated here; isolectotypes: K!, P!, S!). [Note: The Drège specimen in P is chosen as lectotype because it displays the type locality as well as the characteristic tomentose pods from which Meyer clearly derived the name for this species].

Erect, multi-stemmed woody spinescent shrub up to 2.5 m tall. Branches green; young branches densely sericeous; older branches sericeous with brown bark. Leaves unifoliolate or rarely trifolioilate; petiole short, 0.5–2.0 mm long (up to 5 mm long when leaves are trifoliate); leaflets obovate to broadly obovate, upper and lower surfaces sericeous, alternate, 3–13 (–18) mm long, 2–5 (–8) mm wide; base attenuate; apex retuse. Inflorescences (22–) 25–40 (–55) mm long, with (4–) 6–10 flowers; pedicel 2–4 mm long; bract 0.6–1.1 mm long, triangular; bracteoles 0.4–0.6 mm long, narrowly ovate. Flowers 10–13 (–14) mm long, bright yellow. Calyx 2.5–3.7 mm long, pubescent on the outer surface; lobes triangular, 0.4–1.0 mm long; tube 2–3 mm long, apices acute. Standard 9.5–12.0 mm long; claw 3–4 mm long; lamina widely ovate, 6–7 (–8) mm long, 4–6 (–9) mm wide, pilose along the dorsal midrib; apex broadly acute. Wings 7–12 mm long; claw (2.0–) 3.5–5.0 mm long; lamina oblong, shorter than the keel, 4–6 (–7) mm long, 2–3 (–4) mm wide with 4–5 rows of sculpturing, pilose. Keel 10–14 mm long; claw 4.0–5.5 mm long; lamina oblong, 6.0–8.5 mm long, (3.0–) 4.0–5.5 mm wide, pilose. Pistil subsessile to shortly stipitate, pubescent; ovary linear, 6.0–8.5 mm long, 0.8–1.0 mm wide; ovules 6 to 9; style shorter than ovary, 4.0–5.5 mm long. Pods oblong to slightly falcate, laterally compressed, membraneous, 11–21 (–28) mm long, (2.5–) 3.0–4.0 (–6.0) mm wide, densely tomentose; stipe very short (less than 1 mm long), ±4 to 6-seeded, indehiscent. Seeds reniform, 2.0–2.5 mm long, 1.5–2.0 mm wide, colour, surface smooth (Fig. 6.28). Flowering time: Flowering occurs from spring to summer (September to December).

***Diagnostic characters***—*Calobota pungens* is similar to *Calobota cuspidosa* and *C. psiloloba*, but differs from both in the sericeous stems, sericeous obovate leaves, pilose petals, pubescent ovary and tomentose pods (in *C. cuspidosa* the stems are pubescent and the leaves linear to slightly obovate, while in *C. psiloloba* the stems are glabrous or slightly pilose and the leaves slightly obovate to spathulate. In both these species the ovary and pods are glabrous).

***Distribution and habitat***—*Calobota pungens* occurs from Laingsburg through Ladysmith and Oudtshoorn to Baviaanskloof and Willowmore in the east at altitudes of between 790 m and 1100 m (Fig. 6.29). It is typically a fynbos species and occurs on rocky, loamy or quartzitic, soils.

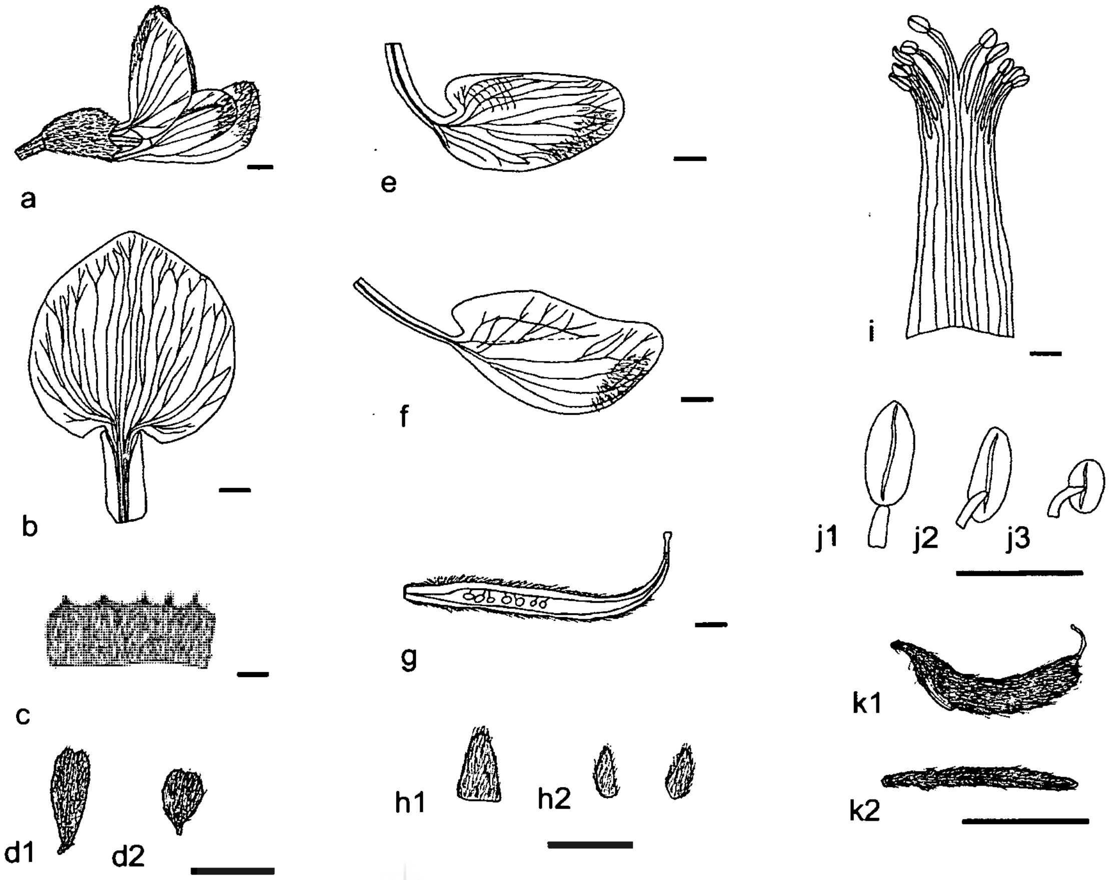

FIG. 6.28 Morphology of *Calobota pungens*: (a) flower in lateral view; (b) standard petal; (c) outer surface of the calyx (upper lobes to the left); (d1–d2) leaves in abaxial view; (e) wing petal; (f) keel petal; (g) pistil; (h1) bract; (h2) bracteoles; (i) androecium; (j1) long, basifixed anther; (j2) intermediate carinal anther; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a, b, d1, e–g, h2, i, k1–k2) *Boatwright et al. 106* (JRAU); (c) *Taylor 9386* (NBG); (d2) *Barker 9948* (NBG); (h1) *Acocks 15547* (PRE); (j1–j3) *Van Wyk 3252* (JRAU). Scale bars: (d1–d2, k1–k2) 1 cm; (a–c, e–j3) 1 mm.

### *Additional Specimens Examined*

**–3320** (Montagu): Cadibu (–AB), *Bond 12112* (BOL, NBG); Matjiesfontein (–BA), *Compton 2714, 3315* (BOL, K), *Compton 22233* (NBG 2 sheets), *Foley 58* (PRE), *Marloth 10764*

(NBG 2 sheets, PRE); top of Koppie near Matjiesfontein (–BA), *Thoday and Delf* (NBG); Rooikloof (–BD), *Van Wyk 2147* (JRAU).

**–3321** (Ladysmith): Farm Withoek (–AC), *Van Wyk 2154* (JRAU); road from Seweweeks Poort (–AD), *Levyns 2334* (BOL); Touwsberg, farm Rietfontein (–CA), *Germishuizen 6956* (PRE); Touwsberg, farm Wolwefontein (–CA), *Van Wyk et al. 3447* (JRAU, PRE).

**–3322** (Oudtshoorn): 14 mls [22.5 km] east of Prince Albert (–AA), *Sidey 1906* (PRE, S); Swartberg Pass (–AC), *Bond 1537* (NBG, PRE), *Markotter 9951* (NBG); Congo Valley close to Oudtshoorn (–AC), *Dreyer 18618* (NBG); northern foothills of Swartberg above farm Rietfontein (–AC), *Vlok 1152* (K, PRE); Venterskloof near Klaarstroom (–AD), *Taylor 9386* (K, NBG); 20 mls [32.2 km] west of Klaarstroom (–AD), *Acocks 15547* (K, PRE); on road between Prins Albert and Klaarstroom (–AD), *Van Wyk EvW0151* (K); Meiringspoort (–BC), *Boatwright et al. 106* (JRAU), *Levyns 6619* (BOL), *Stokoe 61389* (NBG); outside Meiringspoort, past Klaarstroom turn-off along roadsides (–BC), *Boatwright et al. 111* (JRAU); foot of Swartberg Mountains, near Klaarstroom (–BC), *Drège s.n.* (S, K); Klaarstroom, Prince Albert (–BC), *Barker 9948* (NBG 2 sheets).

**–3323** (Willowmore): Hot Springs (–AC), *Fourcade 5841* (NBG), *Fourcade 6086* (BOL, NBG); flats between Hot Springs and Toorwater (–AC), *Thompson 1398* (PRE); lower slopes of Zuurberg at Georgida (–AD), *Fourcade 4410* (BOL, K); 7 mls [11.26 km] south-west of Willowmore (–AD), *Horn s.n.* (PRE); 6–8 mls [9.6–12.8 km] south-east of Willowmore on Baviaanskloof road (–AD), *Wells 2606* (PRE); 7 mls [11.2 km] on Baviaanspoort road from Willowmore (–AD), *Wells 2838* (GRA, PRE); 18 ml [28.8 km] from Uniondale on Willowmore road (–AD), *Wells 3699* A and B (GRA, PRE); along road from Willowmore to Baviaanskloof near Uniondale turnoff (–BC), *Snijman 353* (NBG, PRE); Kammanassie hill sides 7 mls [11.3 km] from Uniondale (–CA), *Fourcade 3594* (BOL 2 sheets, K); Vet Vlei, 8 mls [12.8 km] from Uniondale (–CA), *Fourcade 6255* (BOL); Pietselaagte on road to Uniondale (–CA), *Van Wyk 3180* (JRAU); dirt road between De Rust and Uniondale (–CA), *Van Wyk 3252* (JRAU).

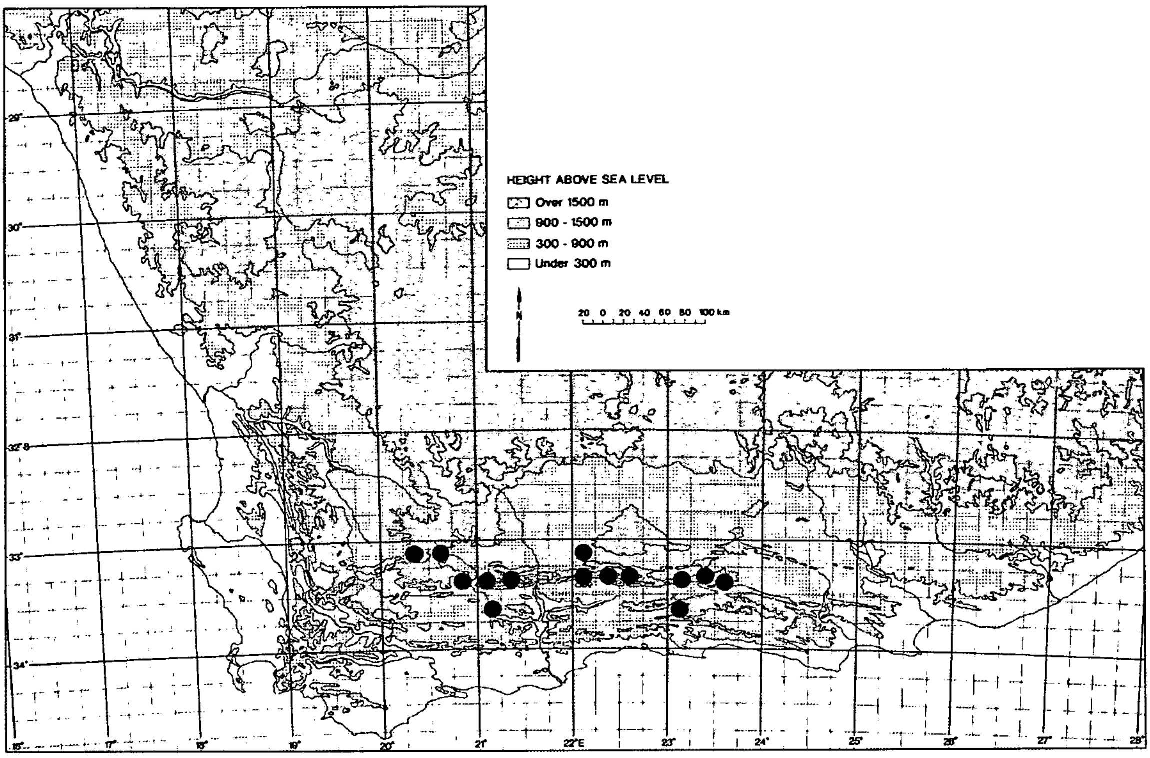

FIG. 6.29 Known geographical distribution of *Calobota pungens*.

13. CALOBOTA SAHARAE (Coss. and Dur.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Genista saharae* Coss. and Dur., B. Soc. Bot. France 2: 247. 1855. *Spartidium saharae* (Coss. and Dur.) Pomel, Nouv. Mat. Fl. Atl.: 173. 1874.—TYPE: ALGERIA, D'Oran Province, *Cosson s.n.* (P-COS?, type not seen).

Erect or virgate, multi-stemmed, unarmed shrub up to 2 m in height. Branches green; young branches densely pilose or glabrous; older branches pilose or glabrous with light brown bark. Leaves simple; petiole absent; linear, alternate, pilose on both surfaces, sessile, 6–10 x 1–2 mm, apex acute, base cuneate. Inflorescence 75–150 mm long, with 5 to 12 flowers; pedicel 1–2 mm long; bract 1.5–2.0 mm long, linear, pubescent; bracteoles 0.5–1.0 mm long, linear, pubescent. Flowers 13–17 mm long, yellow. Calyx 4.5–7.0 mm long, pilose; tube 3–4 mm long;

lobes 1.5–3.0 mm long, subulate. Standard 13–15 mm long, claw linear, 3.5–4.0 mm long, lamina ovate, 9.5–11.0 mm long, 7.5–8.0 mm wide, dorsal surface pubescent; apex obtuse. Wings 11.5–14.0 mm long, claw 4.0–4.5 mm long, lamina oblong, longer than keel, 7–9 mm long, 3–4 mm wide, glabrous, with 4 rows of sculpturing. Keel 12.5–13.0 mm long, claw 4–5 mm long, lamina boat-shaped, 8.0–8.5 mm long, 4.5–5.0 mm wide, glabrous. Pistil subsessile to shortly stipitate, glabrous; ovary linear, 9.0–11.5 mm long, 1.0–1.3 mm wide with 7 to 8 ovules; style shorter than ovary, 4.5–5.5 mm long. Pods oblong-linear, laterally compressed, membraneous, subsessile to shortly stipitate, 30–40 mm long, 6–10 mm wide, 4 to 6-seeded, indehiscent. Seeds reniform to oblong-reniform, 2.5–3.0 mm long, 1.5–2.0 mm wide, mature seeds light brown, surface smooth (Fig. 6.30). Flowering time: Flowering occurs between from March to May.

***Diagnostic characters***—*Calobota saharae* is similar to *Calobota cuspidosa* and *C. psiloloba* in the laterally compressed, membraneous pods, but differs in the unarmed habit, linear leaves and pubescent standard petal (in *C. cuspidosa* and *C. psiloloba* the branches are strongly spinescent, the leaves slightly obovate to elliptic or spathulate and the petals pubescent). *Calobota saharae* is also similar to *C. namibiensis*, but differs in the linear leaves, glabrous, the glabrous keel petals and the membraneous pods (in *C. namibiensis* the leaves are elliptic to ovate, the keel petals densely pubescent and the pods thick-walled and tomentose).

***Distribution and habitat***—*Calobota saharae* is endemic to North Africa and occurs in Morocco, Algeria, Libya and Tunisia. It is found on desert hills or dunes at altitudes of ca. 200m. (Fig. 6.31)

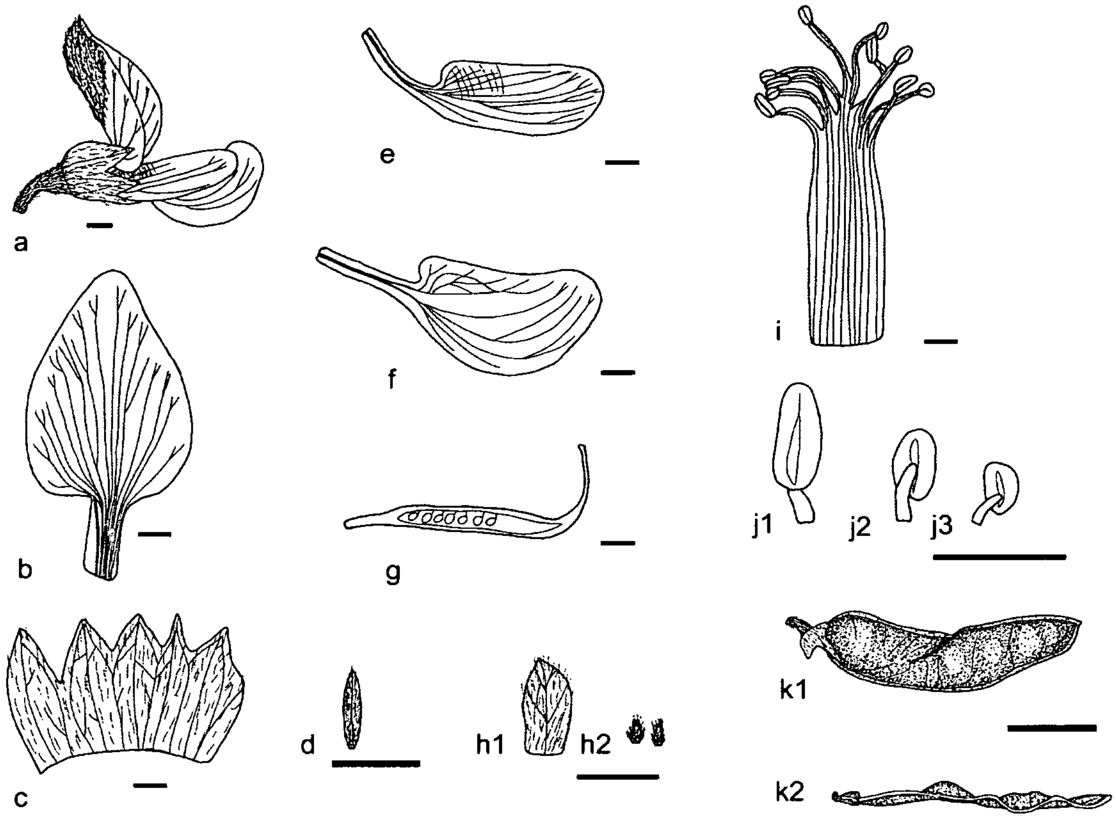

Fig. 6.30 Morphology of *Calobota saharae*: (a) flower in lateral view; (b) standard petal; (c) outer surface of the calyx (upper lobes to the left); (d) leaf in abaxial view; (e) wing petal; (f) keel petal; (g) pistil; (h1) bract; (h2) bracteoles; (i) androecium; (j1) long, basifixed anther; (j2) intermediate carinal anther; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a, e, g) *Keith 181* (K); (b, c, f, h1–j3) *Hill s.n.* (K); (d) *Pitard 3276* (K); (k1–k2) *Alleizette s.n. sub K 2007/014804* (K). Scale bars: (d, k1–k2) 1 cm; (a–c, e–j3) 1 mm.

### *Additional specimens examined*

**Algeria:** Aïn Sefra, *Alleizette s.n. sub K 2007/014804* (K), *Cosson s.n. sub K 000227004* (K), *Hill s.n.* (K), *Bourgeau 210* (K 2 sheets), *Le Cesve 5429* (BM), *Rothschild and Hartert s.n.* (BM), *Samuelsson 6994* (K); Constantine Province, Oued Souf, *Cosson s.n. sub K 000227008* (BM, K); Djebel Milogh, *Cosson s.n. sub K 000227003* (K); Oran Province, Aïn Sefifsifa, *Cosson s.n. sub K 000227005* (K); Oran Province, Abiod-Sisi-Cheihk, *Cosson s.n.*

*sub K 000227006* (K); Wadi Rummel, above Sidi Benour, *Guichard KG/Lib/289* (K); El Ardja, *Pitard 3275* (K); Oued el Khezoua/El Oued, *Pitard 3276* (K).

**Tunisia:** Nefta, *Cosson s.n. sub K 000227007* (K).

**Libya:** Aïn Zara, near Pripoli, *Brown s.n.* (K); Jebel Nefoussa, Azizia-Rhnem, *Davis 49544* (K); Jebel, north of Jefren, *Keith 181* (K).

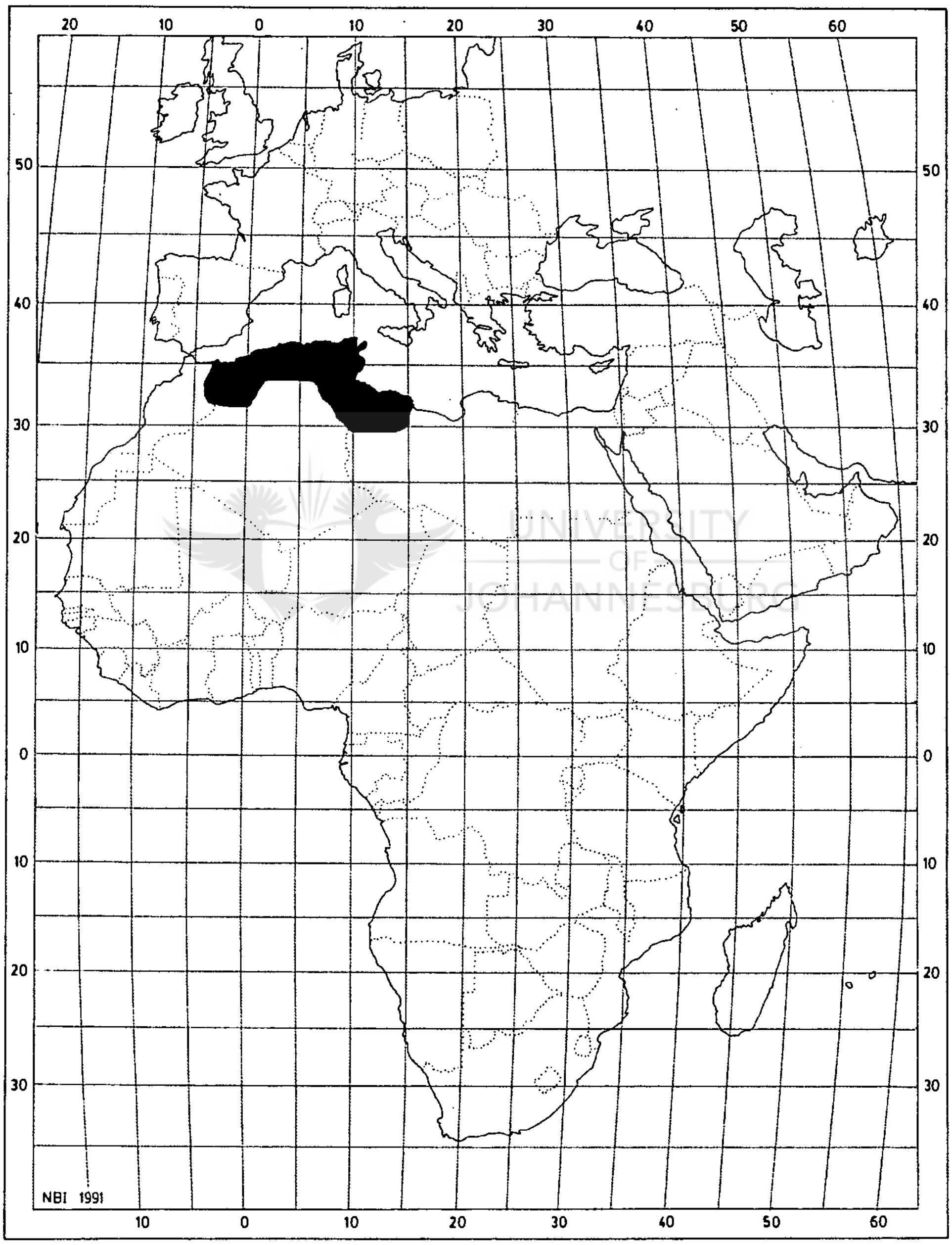

FIG. 6.31 Approximate geographical distribution of *Calobota saharae*.

14. CALOBOTA SERICEA (Ait.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Spartium sericeum* Ait. in Hort. Kew. 3: 12. 1789.—TYPE: SOUTH AFRICA, Cape of Good Hope, *Masson s.n. sub BM000794145* (lectotype: BM, photo!, specimen on the left, designated here). [The two specimens on the left were collected by Masson and are marked with '1' on the tape on the stems. The specimen on the right was grown in the gardens at Kew and has the note 'Hort. Kew 1781' associated with it. According to Stafleu and Cowan (1976), most of the Aiton types are in the Banks collection in BM).]

*Lebeckia angustifolia* E.Mey. in Linnaea 7: 155. 1832. *Acanthobotrya angustifolia* (E.Mey.) Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 194. Jan. 1836.—TYPE: SOUTH AFRICA, without locality, *Ecklon s.n.* (lectotype: S!, designated here). [Note: the type is represented by the two branches mounted at the bottom right hand side of the sheet – one with several flowers, the other with a single bud. Meyer (1932) incorrectly cites the type locality as "Uitenhage?" but expresses doubt by placing a question mark after the locality. The specimen in S comprises mixed elements but the two branches referred to above are accompanied by a label in Meyer's handwriting stating "*Lebeckia angustifolia mihi*".]

*Lebeckia multiflora* E.Mey., Comm. Pl. Afr. Austr. 1: 34. Feb. 1836; Benth. in Hook. Lond. J. Bot. 3: 360. 1844; Walp., Rep. Bot. Syst.: 453. 1845; Harv. in Harv. and Sond., Fl. Cap. 2: 88. 1862; Merxm. and Schreiber, FSWA 60: 68. 1970; Bond and Goldblatt, J. S. Afr. 13: 290. 1984; Goldblatt and Manning, Cape Pl.: 493. 2000.—TYPE: SOUTH AFRICA, between Holrivier and Mierenkasteel [3118 CB], *Drège 6474 "III, C"* (lectotype: P!, designated here;

isolectotypes: BM!, K!, PRE!, S!). [Note: This specimen bears the type locality, shows the features of the plant described by Meyer and bears the characteristic Drège field labels]

*Lebeckia decutiens* var. $\alpha$ *canescens* E.Mey., Comm. Pl. Afr. Austr. 1: 34. Feb. 1836.—TYPE: SOUTH AFRICA, near Heerenlogement [3118 DC], *Drège s.n. "III, E, a"* (lectotype: P!, designated here; isolectotype: BM!, K!). [Note: The specimen displays the diagnostic characters described by Meyer and bears the type locality.]

*Lebeckia parvifolia* (Schinz) Harms in Engl. Pflanzenw. Afr. 3(1) (Engl. and Drude, Veg. der Erde 9): 545 (1915). *Lebeckia multiflora* var *parviflora* Schinz in Abhandl. Bot. Ver. Prov. Brandenb. 30: 157. 1888.—TYPE: not seen.

Erect, multi-stemmed, unarmed or rarely spinescent shrub up to 2 m in height. Branches green; young branches sericeous, older branches sericeous or glabrous with brown bark. Leaves digitately trifoliolate; petiole longer or shorter than leaflets, 8–45 mm long; leaflets linear to oblanceolate, alternate, sericeous, subsessile, terminal leaflet 5–30 mm long, 0.5–5.0 mm wide, lateral leaflets 4–25 mm long, 0.5–4.0 mm wide, apex acute, base cuneate. Inflorescence 20–200 mm long, with 7 to 40 flowers; pedicel 1–2 mm long; bract 1–3 mm long, linear, pubescent; bracteoles 0.5–2.0 mm long, linear, pubescent. Flowers 7–11 mm long, bright yellow. Calyx 4.0–6.5 mm long, pubescent; tube 2.5–4.5 mm long; lobes 1.0–3.5 mm long, deltoid. Standard 6.5–13.0 mm long; claw linear, 2.0–4.5 mm long; lamina widely ovate, 4–9 mm long, (3.8–) 4.5–10.0 mm wide, pilose along dorsal midrib; apex obtuse. Wings 7–13 (–14) mm long; claw 2.5–4.5 (–5.5) mm long; lamina oblong, as long as but more often longer than keel, 4.5–8.5 mm long, 2.0–4.5

mm wide, glabrous, with 4–12 rows of sculpturing. Keel 6.5–12.5 mm long; claw 2.5–4.5 (–5.5) mm long; lamina boat-shaped, 4–8 mm long, 2.5–5.0 mm wide, glabrous. Pistil subsessile to shortly stipitate, pubescent; ovary linear, 5.0–9.5 mm long, 0.5–1.1 mm wide with 11 to 20 ovules; style shorter than ovary, 2.5–5.0 mm long. Pods linear, semi-terete, sericeous, subsessile to shortly stipitate, 18–35 mm long, 2–4 mm wide, 5 to 12-seeded, dehiscent. Seeds oblong-reniform, 2.5–3.5 mm long, 1.5–2.0 mm wide, mature seeds light brown or light orange, sometimes mottled with brown, surface smooth (Fig. 6.32). Flowering time: Flowers for most of the year January to November.

***Diagnostic characters***— *Calobota sericea* is similar to *C. lotononoides* but differs in that it is an erect, divaricately branched shrub usually more than 1 m in height with inflorescences that often terminate in a spine; the wing petals are almost as long as or slightly longer than the pilose keel petals and the seeds are pale pink with a smooth surface (*C. lotononoides* is a small, decumbent shrublet with unarmed inflorescences, extremely long wing petals, glabrous keel petals and the seeds are brown with beige spots and a rugose surface).

It is also similar to *C. halenbergensis* but differs in the sericeous leaves, pilose keel petals, hairy ovary and sericeous pods with more seeds (in *C. halenbergensis* the leaves are pilose, the keel petals glabrous and the ovary and pods glabrous with fewer seeds in the latter).

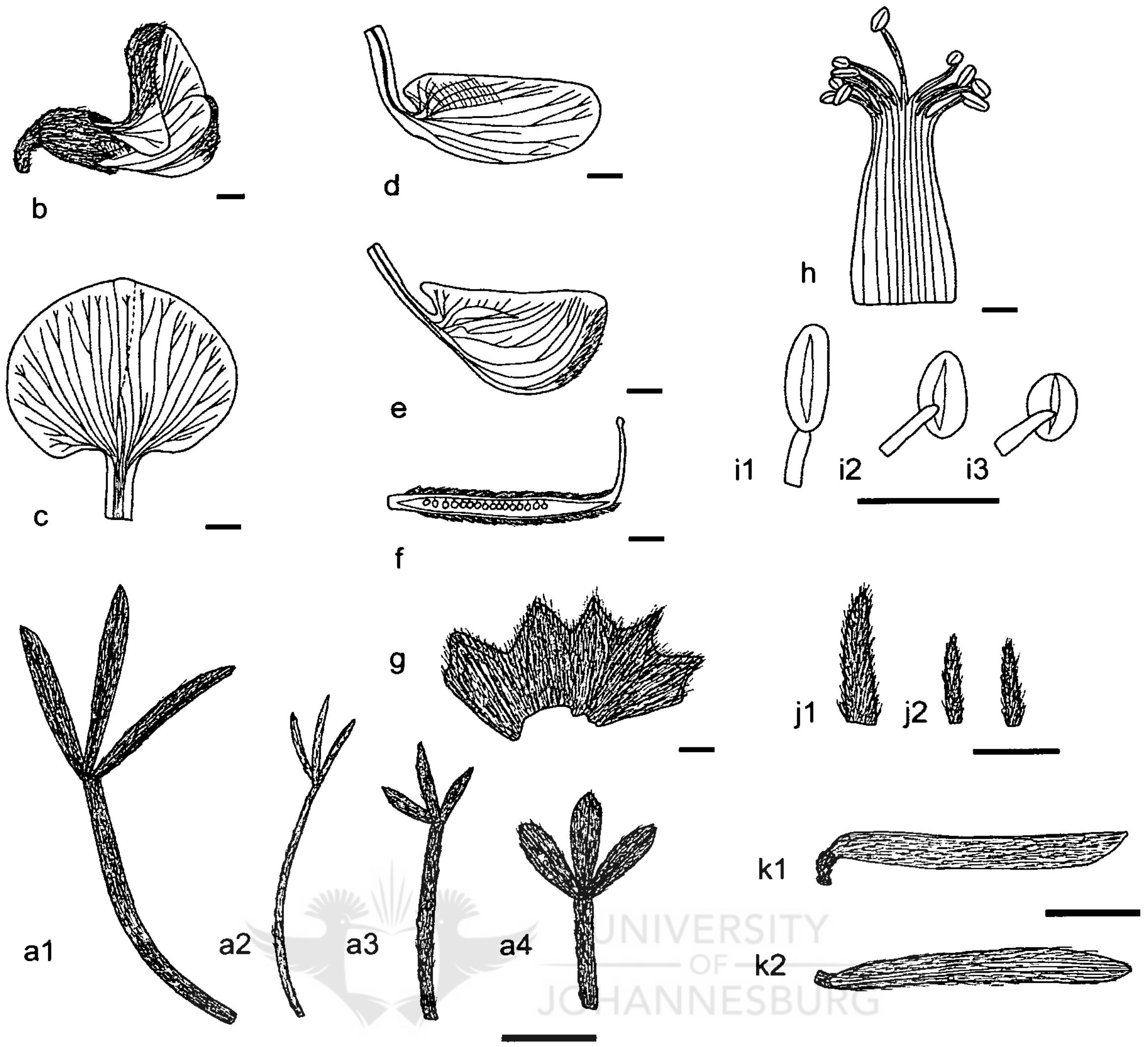

FIG. 6.32 Morphology of *Calobota sericea*: (a1) leaf in abaxial view (typical form); (a2) leaf in abaxial view (Oranjemund form); (a3) leaf in abaxial view (short-leaved form); (a4) leaf in abaxial view (broad-leaved form); (b) flower in lateral view; (c) standard petal; (d) wing petal; (e) keel petal; (f) pistil; (g) outer surface of the calyx (upper lobes to the left); (h) androecium; (i1) long, basifixed anther; (i2) intermediate carinal anther; (i3) short, dorsifixed anther; (j1) bract; (j2) bracteoles; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a1, k1–k2) *Boatwright et al. 138* (JRAU); (a2) *Ward 12435* (WIND); (a3) *Giess and Robinson 13177* (WIND); (a4) *Stirton and Zantovska 11426* (NBG); (b, d–f, h–i) *Boatwright et al. 139* (JRAU); (c) *Van Wyk 2847* (JRAU); (g) *Lewis 4705* (NBG); (j1–j2) *Whitehead 80.9.8* (WIND). Scale bars: (a1–a4, k1–k2) 1 cm; (a–c, ej3) 1 mm.

***Distribution and habitat***—*Calobota sericea* is widely distributed along the west coast of South Africa and Namibia (Fig. 6.33). It forms an important component of Western Strandveld (FS 1 Lambert's Bay Strandveld, FS 5 Langebaan Dune Strandveld; Rebelo et al. 2006), Richtersveld (SKr 3 Goariep Mountain Succulent Shrubland and disturbed areas of SKr 13 Southern Richtersveld Scorpionstailveld; Mucina et al. 2006) and Namaqualand Sandveld (SKs 2 Northern Richtersveld Yellow Duneveld, SKs 4 Richtersveld Sandy Coastal Scorpionstailveld, SKs 5 Richtersveld Red Duneveld, SKs 6 Oograbies Plains Sandy Grassland and SKs 13 Klawer Sandy Shrubland, the latter recorded as *C. halenbergensis* instead of *C. sericea*; Mucina et al. 2006). Rebelo et al. (2006) recorded *C. thunbergii* as an important component of FS 4 Saldanha Limestone Strandveld, but it is *C. sericea* that occurs in that area.

***Regional variation***—Four regional forms can be recognized based on leaf morphology and geographical distribution:

FORM A (Typical form)

Erect shrubs up to 1.8 m in height, often spinescent. Leaves linear to narrowly oblanceolate, sericeous, terminal 10–30 mm long, 0.5–2.0 (–2.5) mm wide, lateral 8–23 mm long, 0.5–2.0 (–2.5) mm wide; petiole 11–35 mm. Inflorescence 27–90 mm; with 10 to 27 flowers; pedicel 1–2 mm; bract 1.5–2.0 mm, bracteole 0.5–1.5 mm. Flowers 9–11 mm. Calyx 4.5–6.0 mm long; tube 3.5–4.5 mm long; lobes 1–3 mm long. Standard 9–13 mm long; claw 2.5–4.5 mm long; lamina 5.5–9.0 mm long, (–3.5) 4.5–10.0 mm wide. Wings 8.5–13.0 (–14.0) mm long; claw 3.0–4.5 (–5.5) mm long; lamina 5.5–8.5 mm long, 2.0–3.5 mm wide, glabrous, with 5–8 rows of sculpturing. Keel 8.0–12.5 (–13.0) mm long; claw 3.5–4.5 (–5.5) mm long; lamina

4.5–7.5 mm long, 2.5–4.5 mm wide, glabrous. Pistil ovary 5.5–9.5 mm long, 0.5–1.1 mm wide with 11 to 20 ovules; style 3–5 mm long. Pods sericeous, 18–35 x 2–3 mm.

***Diagnostic characters***—Populations of this form around Klawer and Van Rhynsdorp have very long wing petals and small flowers. It differs from the other forms in the long, narrow leaflets and relatively short pods. The inflorescences are often spine-tipped.

***Distribution and habitat***—This form occurs around Berg River, Piquetberg, Clanwilliam, Velddrif, Lambert's Bay, Vredenburg, Hopefield, Langebaan, Saldanha, Vanrhynsdorp, Heerenlogement, Wallekraal, Hondeklipbaai, Garies and Kleinsee on the West Coast of South Africa and does not extend into Namibia. It grows in well-drained sand, sandy loam red sand or sand dunes between sea level and 500 m above.

FORM B (Broad-leaved form)

Erect or spreading shrubs up to 2 m in height, sometimes spinescent. Leaves with petiole 8–30 mm long; leaflets obovate to widely oblanceolate, sericeous, terminal 5–25 mm long, 2–5 mm wide, lateral 5–25 mm long, 2–4 mm wide. Inflorescence 20–65 mm; with 7 to 18 flowers; pedicel 1–2 mm; bract 2 mm long, bracteole 1.0–1.5 mm long. Flowers 9–11 mm long. Calyx 5.0–6.5 mm long; tube 3.5–4.0 mm long; lobes 1.0–2.5 mm long. Standard 10–11 mm long; claw 3.0–3.5 mm long; lamina 6.5–8.0 mm long, 7.5–10.0 mm wide. Wings 10.5–11.5 mm long; claw 3–4 mm long; lamina 6.5–8.0 mm long, 2.5–4.5 mm wide, glabrous, with 4–7 rows of sculpturing. Keel 10–11 mm long; claw 3.5–4.0 mm long; lamina 6.5–8.0 mm long, 3.5–5.0 mm wide, glabrous. Pistil with ovary 7.0–8.5 mm long, 0.7–1.1 mm wide with 11 to 15 ovules; style 4.5–5.0 mm long. Pods sericeous, 25–35 mm long, 3 mm wide.

***Diagnostic characters***—This form differs from the others in the broad leaflets (always more than 2 mm wide) and relatively short inflorescences.

***Distribution and habitat***—Occurs from the Saldanha area, Elands Bay, Clanwilliam, Lambert's Bay, Doring Bay, mouth of Olifants River, Brandsebaai, Garies, Wallekraal, Port Nolloth and Walvis Bay along the West Coast of South Africa and Namibia. It grows in deep limestone or calcrete sand or dunes at altitudes of between 4 m and 50 m and is grazed by livestock.

FORM C (Short-leaved form)

Erect or virgate shrubs up to 2 m in height. Leaves with petiole relatively long, 9–45 mm long; leaflets linear to oblanceolate, very densely sericeous, terminal 2–13 mm long, 1–2 mm wide, lateral 2–7 mm long, 0.5–1.0 mm wide. Inflorescence 30–200 mm; with 8 to 40 flowers; pedicel 1 mm; bract 2–3 mm long, bracteole 1.5–2.0 mm long. Flowers 7–10 mm long. Calyx 4–6 mm long; tube 2.5–4.0 mm long; lobes 1.5–3.5 mm long. Standard 7.5–9.0 mm long; claw 2–3 mm long; lamina 5.5–6.5 mm long, 5.5–7.0 mm wide. Wings 8.5–10.0 mm long; claw 2.5–4.0 mm long; lamina 6–7 mm long, 3–4 mm wide, glabrous, with 4–10 rows of sculpturing. Keel 7.5–8.5 mm long; claw 2.5–3.5 mm long; semi-circular, 4–5 mm long, 3.0–3.5 mm wide, glabrous. Pistil with ovary 5.5–6.5 mm long, 0.7–1.0 mm wide with 13 to 18 ovules; style 3.0–3.5 mm long. Pods densely sericeous, 20–40 mm long, 3–4 mm wide.

***Diagnostic characters***—In this form the leaflets are very short with relatively long petioles.

***Distribution and habitat***—This form of *C. sericea* is restricted to Namibia and occurs in the Lüderitz Bay area, Boegoeberg, Bogenfels, Pomona, Chamais, Alexander Bay and Angra Pequena. It grows in well-drained sand or coarse sand, sometimes on rocky soil or dolomite outcrops at altitudes of between 20 m and 120 m. It is heavily grazed by livestock.

FORM D (Oranjemund form)

Erect shrubs up to 1.5 m (–1.8 m) in height. Leaves with petiole 12–35 mm; leaflets narrowly oblanceolate, sericeous, terminal 5–14 mm long, 0.5–1.0 mm wide, lateral 5–9 mm long, 0.5–1.0 mm wide. Inflorescence 30–100 mm; with 13 to 15 flowers; pedicel 1–2 mm long; bract 1–3 mm long, bracteole 1.0–1.5 mm long. Flowers 7–10 mm long. Calyx 4.5–5.0 mm long; tube 3.0–3.5 mm long; lobes 1–2 mm long. Standard 6.5–8.0 mm long; claw 2–3 mm long; lamina 4.0–5.5 mm long, 5.5–6.5 mm wide. Wings 7.0–8.5 mm long; claw 2.5–3.5 mm long; lamina 4.5–5.5 mm long, 3.0–3.5 mm wide, glabrous, with 8–12 rows of sculpturing. Keel 6.5–8.0 mm long; claw 2.5–3.5 mm long; lamina 4.0–4.5 mm long, 3.0–3.5 mm wide, glabrous. Pistil with ovary 5–6 mm long, 0.8–1.0 mm wide with 12 to 19 ovules; style 2.5–3.5 mm long. Pods sericeous, 20–32 mm long, 2–3 mm wide.

***Diagnostic characters***—Leaflets of the Oranjemund form are short and very narrow and the pods also relatively short.

***Distribution and habitat***—This form is centered in the Oranjemund district. It occurs in sandy areas, alluvial sand and dunes near the mouth of the Orange River and in the Oranjemund mining area at altitudes of between 10 m and 100m.

***Additional specimens examined***

**–2214** (Swakopmund): Walvis Bay (–DC), *Heywood s.n.* (NBG).

**–2514** (Spencer Bay): ca. 2 km east of coast near East Hill between Oyster Cliffs and Easter point (–BD), *Seely and Ward 54* (WIND); Spencer Bay (–DB), *Giess and Robinson 13177* (K, S, PRE, WIND), *Sydow 10179* (WIND).

**–2516** (Helmeringhausen): Halbinsel (–CA), *Walter 56* (WIND).

**–2615** (Lüderitz): Schurmhaudeberg (–AA), *Hardy and Venter 4437* (K, PRE, WIND); Angra Pequena, *Marloth 4663* (NBG, PRE), *Schenck 9* (PRE), *Schinz 811* (BOL, K); 14 mls [22.53 km] east of Lüderitz Bay (–CA), *Acocks 15654* (K, PRE 2 sheets); Lüderitz peninsula (–CA), *Clark and Müller 337* (WIND), *De Winter and Hardy 7894* (K, WIND), *Mannheimer CM2020* (WIND); Lüderitz Bay (–CA), *De Winter and Giess 6233* (BOL, K, PRE, WIND), *Dinter 3838* (BM, BOL, K, NBG, PRE, S), *Dinter 5996* (BM, BOL, K, NBG 2 sheets, PRE), *Giess and Van Vuuren 678* (PRE, WIND), *Lavranos and Pehleman 19641* (WIND 2 sheets), *Leuenberger et al. 3306* (PRE, WIND), *Merxmüller and Giess 28275* (K, PRE, WIND), *Metz s.n.* (WIND 2 sheets), *Peter 47177* (K), *Range 363* (BOL), *Meyer 56* (WIND), *Volk 12825* (WIND), *Wall s.n.* (S); 13 mls [20.92 km] east of Lüderitz, road to Aus, Grasplatz (–CA), *Giess and Van Vuuren 738* (PRE, WIND); Lüderitz (–CA), *Hobart-Hampden 11* (BM), *Lavranos and Barod 15409* (WIND), *Moss 11462* (BM), *Rogers 29588* (K 2 sheets); just outside Lüderitz along main road (–CA), *Mannheimer CM2015* (WIND); Lüderitz lagoon (–CA), *Merxmüller and Giess 3133* (WIND); Lüderitz, just outside township (–CA), *Müller and Jankowitz 275* (WIND); Essy Bay (–CA), *Strohbach 151* (WIND); Lüderitz Bay, Halbinsel (–CA), *Walter 56* (WIND), *Wendt s.n.* (WIND 2 sheets); Aus (–CB), *Regius 23c* (WIND); Grasplatz (–CB), *Merxmüller and Giess 3052* (PRE, WIND), *Venter 9160* (PRE).

**–2715** (Bogenfels): Pomona (–AB), *Dinter 6336* (BM, BOL, K, NBG 2 sheets, PRE), *Kolle 13560b* (NBG, PRE), *Wall s.n.* (S), *Whitehead 80.9.8* (WIND); along road to Pomona (–AB), *Mannheimer et al. CM898* (WIND); blue rocky ridge on way to Pomona town (–AB), *Mannheimer CM 924* (WIND); Bogenfels (–AD), *De Winter and Giess 6220* (K, PRE, WIND), *Merxmüller and Giess 28326* (WIND); area and surrounds north-east of Bogenfels Arch (–AD), *Powrie LWP1170* (WIND); Diamond Area 1 (–AD), *Watmough 867* (PRE); Chamais (–DC), *Merxmüller and Giess 28319* (K, PRE, WIND); Chamais valley in rock (–

DC), *Williamson 2647* (BOL); 3 km east of Chamais Bay (–DC), *Williamson 4980* (WIND); Boegoeberg (–DD), *Merxmüller and Giess 28304* (PRE, WIND), *Williamson 2575* (BOL).

**–2816** (Oranjemund): between Oranjemund and check point (–BC), *Gess and Gess 97/98/68* (J, WIND); Oranjemund (–CB), *Merxmüller and Giess 2267* (BM, K, WIND); sandy area near mouth of Orange at Oranjemund (–CB), *Metelerkamp 290* (BOL), *Schenck 238* (PRE); north of Orange River (–CB), *O'Callaghan et al. 5* (NBG, PRE); hills north-east of Alexander Bay (–CB), *O'Callaghan et al. 67* (NBG, PRE); south bank of lagoon at mouth of Orange River (–CB), *Pillans 5636* (BOL); near airport turnoff from main entrance road (–CB), *Ward 11136* (K, PRE, WIND); Orange River, upper estuary (–CB), *Ward 12435* (PRE); mining area 1 (–CB), *Williamson 4844, 4851* (WIND); k122 mining area Ev5 control plot (–CB), *Williamson 4884* (WIND); Witbank (–DC), *Pillans 5207* (BOL, K), 40 km from Port Nolloth on road to Alexander Bay (–DD), *Germishuizen 4770* (PRE, WIND), *Germishuizen 4771* (PRE); 32 km from Port Nolloth on road to Alexander Bay (–DD), *Germishuizen 4813* (PRE).

**–2817** (Vioolsdrif): "ad ostia fluvii Garip" (–AA), *Drège s.n. "III, B"* (P, K); sides of dry river bed at Kuboos (–AC), *Pillans 5429* (BOL).

**–2820** (Kakamas): Farm Harperspot, east of Riemvasmaak (–AD), *Gubb KMG13032* (WIND).

**–2916** (Port Nolloth): Port Nolloth (–BD), *Bolus 9503* (K), *Galpin and Pearson 7605* (BOL, K, NBG, PRE), *Marloth 4747* (NBG, PRE); 1 km south of McDougalls Bay (–BD), *Raitt 302* (NBG); between Port Nolloth and Holgat (–BD), *Schlechter s.n. sub STE 10850* (NBG 2 sheets); Port Nolloth, at turn-off to McDougall Bay (–BD), *Van Wyk 2847* (JRAU 2 sheets); 9 km east of Port Nolloth (–BD), *Zietsman and Zietsman 823* (PRE).

**–2917** (Springbok): sand by roadside between Anenous and Chubiessis outspan (–BA), *Pearson 5978* (BOL, K); Oubeep Bay (–BD), *Le Roux and Ramsey 144* (NBG); 2 km south of Kleinsee (–CA), *Hugo 2849* (PRE 2 sheets); Buffels River mouth (–CA), *Le Roux and Parsons 23* (PRE); Kleinsee (–CA), *Theron 3858* (PRE); between Brakwater and Komaggas (–DC), *Compton 22071* (BOL, NBG).

**–3017** (Hondeklipbaai): 6 mls [9.65 km] south-east of Hondeklipbaai (–AD), *Hall 899* (BOL, NBG); Farm Oubees 339, 1.2 km east of Oubees/Wildepaardehoek boundary fence and 4.7 km east of Springbok, Soebatsfontein road (–BA), *Le Roux and Lloyd 670* (NBG); between Brakwater and Komaggas (–BB), *Compton 22071* (BOL, NBG); 3 mls [4.83 km] north-west of Wallekraal Post Office (–BC), *Acocks 14933* (K, PRE 2 sheets); 5 mls [8.05 km] north-west of Wallekraal (–BC), *Hall 895* (NBG 2 sheets); Wallekraal, near Hondeklipbaai (–BC), *Stirton 6036b* (K, PRE); 15 mls [24.14 km] east of Wallekraal on road to Garies (–BC), *Thompson 1090* (K, NBG); Groen River Mouth (–DC), *Le Roux and Ramsey 276* (K, NBG, PRE), *Le Roux and Ramsey* 280 (NBG).

**–3018** (Kamiesberg): Ezelkop, Garies (–AC), *Scheffler 266* (NBG).

**–3117** (Lepelfontein): Brandsebaai (–BD), *De Villiers 34* (PRE, WIND), *De Villiers 48, 49* (PRE), *Van Rooyen 2200* (PRE).

**–3118** (Vanrhynsdorp): mouth of Olifants River, Papendorp (–CA), *Arnold 916* (PRE); Vredendal, Olifants River Mouth (–CA), *Le Roux and Ramsey 62* (NBG); Olifants River Mouth (–CA), *O'Callaghan 657* (NBG, PRE); Vredendal road (–CB), *Steyn 464* (NBG); Doringbaai (–CC), *Boucher 4054* (NBG, PRE), *Hugo 2924* (PRE); Holrivier (–CB), *Drège s.n.* (S); between Vredendal and Lambert's Bay (–CD), *Lewis 4705* (NBG), *Schutte 269* (JRAU); 10.7 km from Doringbaai to Donkinbaai (–CD), *Stirton 6077* (K, PRE); Zandkraal (–DA), *Acocks 14840* (PRE); 11.7 km south of Redelinghuys (–DA), *Acocks 24284* (K, PRE); Kys, south-east of Vredendal (–DA), *Bayer 6396* (PRE); Farm Liebendal, Vredendal (–DA), *Hall 3701* (NBG 2 sheets); Klawer (–DC), *Andreae 474* (NBG, PRE); Heerenlogement (–DC), *Drège s.n. "III, E, a"* (BM, K, P), *Esterhuysen 5547* (BOL); Vanrhynsdorp, foot of Nardousberge below Witbakenkop on old Clanwilliam, Vanrhynsdorp road (–DC), *Hilton-Taylor 1613* (NBG); western aspect of koppie on Vanrhynsdorp road, Klawer (–DC), *Lavis 20236* (BOL, K 2 sheets); 6 mls [9.65 km] north of Klawer (–DC), *Maguire* 142 (NBG 2 sheets); 6 mls. [9.65 km] south of Klawer (–DC), *Salter 5612* (BM, BOL, K, PRE).

**–3217** (Vredenberg): Stompneus Point (–DB), *Taylor 1515* (NBG); Brittania Bay (–DB), *Taylor 5189* (NBG, K, PRE); Farm Trekossenkraal (–DD), *Boucher 7065* (NBG); Cape

Columbine Lighthouse (–DD), *Horrocks 182* (NBG 2 sheets); slopes south of Vredenburg (–DD), *Hutchinson 247* (BM, BOL, K, PRE); granite hills near Vredenburg (–DD), *Marloth 7945* (PRE).

**–3218** (Clanwilliam): Farm Brakke Kuil 9, on road from Laaiplek to Elands Bay (–AB), *Bösenberg and Rutherford 394* (NBG); Lamberts Bay (–AB), *Acocks 14182* (K, PRE), *Clarke 633* (K, PRE), *Henrici 3309* (PRE), *Muir s.n.* (NBG), *Pole-Evans 26* (PRE), *Walsh s.n.* (PRE); Groendam (–AB), *Stirton 9349* (PRE); 5 km from Lamberts Bay to Elands Bay (–AB), *Stirton and Zantovska 11426* (JRAU, NBG, PRE); Wadrifsoutpan (–AB), *Stirton 9340* (PRE); Farm Middelpos (–AB), *Stirton 9387* (PRE); Nortier Experimental Station, Lambert's Bay (–AB), *Van Breda 614* (NBG), *Van Breda 4435* (PRE); 2 mls [3.22 km] from Redelinghuys on Aurora road (–AD), *Barker 9722* (NBG); Elands Bay (–AD), *Barker 2627* (NBG), *Britton 22* (NBG, PRE), *Pillans 7962* (BOL), *Taylor 3912* (NBG), *Taylor 3915* (PRE), *Walsh s.n.* (PRE); Vredendal road from Graafwater (–BA), *Barker 8545* (NBG 3 sheets); between Leipoldtville and Graafwater (–BA), *Esterhuysen 3765* (NBG), *Leipoldt 3765* (BOL, NBG); Nieuwoudtville turn-off after Graafwater on road to Lamberts Bay (–BA), *Stirton 9197* (PRE); Farm Rietfontein, Graafwater (–BA), *Van Blerk 38* (PRE); 5 mls [8.05 km] from Clanwilliam on Lamberts Bay road (–BB), *Gillett 4045* (PRE); Rocher Pan Nature Reserve (–CB), *Heyl 44* (NBG, PRE), *Le Roux and Van Rooyen 1* (NBG); on road to Hopefield from Velddrif (–CC), *Boatwright et al. 138* (JRAU); road from Velddrif to Saldanha Bay (–CC), *Boatwright et al. 139* (JRAU); Velddrif (–CC), *Compton 15940* (NBG), *Goldblatt 6016* (PRE), *Lewis 899* (NBG), *Mauve 5356* (K, PRE); 1 km from road between Velddrif and Vredenburg on road to Stompneusbaai (–CC), *Grobbelaar 2546* (PRE); Velddrif, next to road before the bridge going over the Berg River (–CC), *Le Roux 3* (JRAU 4 sheets); between Hopefield and Paternoster (–CC), *Leipoldt 3764* (BOL); 1 ml [1.61 km] from Velddrif, on banks of Berg River (–CC), *Marsch 1265* (K, NBG, PRE); ca. 6 km east of Velddrif, near Ouwerf (–CC), *O'Callaghan 1237* (NBG); Berg River Station (–CD), *Barker 4050* (NBG); railway enclosure along road 0.5 mls [0.8 km] from Berg River Station (–CD), *Boucher 83* (NBG, PRE); South side of Berg River (–CD), *Leighton 614* (BOL); Piquetberg (–DA), *Van Aarde s.n.* (NBG); Kapteinskloof (–DC), *Stirton 6132b* (K, PRE).

**–3219** (Wuppertal): Doorn River Mouth (–DA), *Compton 11036* (NBG), Doorn River (–DA), *Schlechter 8059* (BM, BOL, K, PRE 2 sheets).

**–3317** (Saldanha): 20 m off road in shooting range camp parallel to dunes (–BB), *Blake 91* (NBG); Hoedjies Bay (–BB), *Bolus 12652* (PRE); Saldanha Bay (–BB), *Grey s.n.* (K), *Marloth 10188* (PRE); koppie north of Saldanha Bay (–BB), *Van Wyk 2696* (JRAU 5 sheets).

**–3318** (Cape Town): Lagoonside, Langebaan (–AA), *Axelson 445* (NBG); roadside south of Langebaan village (–AA), *Boucher 2811a* (NBG); near Langebaan (–AA), *Chaplin s.n.* (NBG), *Marloth 13176* (PRE); Geelbek (–AA), *Compton 19906* (NBG); Langebaan peninsula above Preekstoel (–AA), *O'Callaghan and Steensma 1650* (NBG); Hopefield (–AB), *Bachmann 1889* (BM, K); 10.7 mls [17.22 km] from Hopefield to Vredenberg (–AB), *Marsch 182* (NBG, PRE); 14 km from Hopefield to Langebaanweg (–AB), *Stirton 10709* (K); Schrywers Hoek (–AD), *Macnac 1020* (PRE); near Bergrivier and Zwartland (–BD), *Ecklon and Zeyher 1346* (S); sandy hill slopes behind the village Langebaan (–DC), *Leighton s.n. sub BOL 32422* (BOL).

**–3322** (Oudtshoorn): Waenskloof, Cango Valley (–AC), *Moffett 494* (PRE).

**Precise locality unknown:** Olifantsrivier, *Drège s.n.* (P); without locality, *Galpin and Pearson 7579* (PRE), *Leipoldt s.n.* (NBG), *Range 1941* (NBG); Bokkeveld Mountains, *Leipoldt 730* (PRE); Little Namaqualand, *Krapohl 11142* (PRE); Lus district, *Merxmüller and Giess 2349* (WIND); sandy ravine below Doornpoort, *Pearson 6017* (BOL, K); Waterkloof at Doornpoort, *Pillans 5377* (BOL); Namaqualand, *Scully s.n.* (NBG).

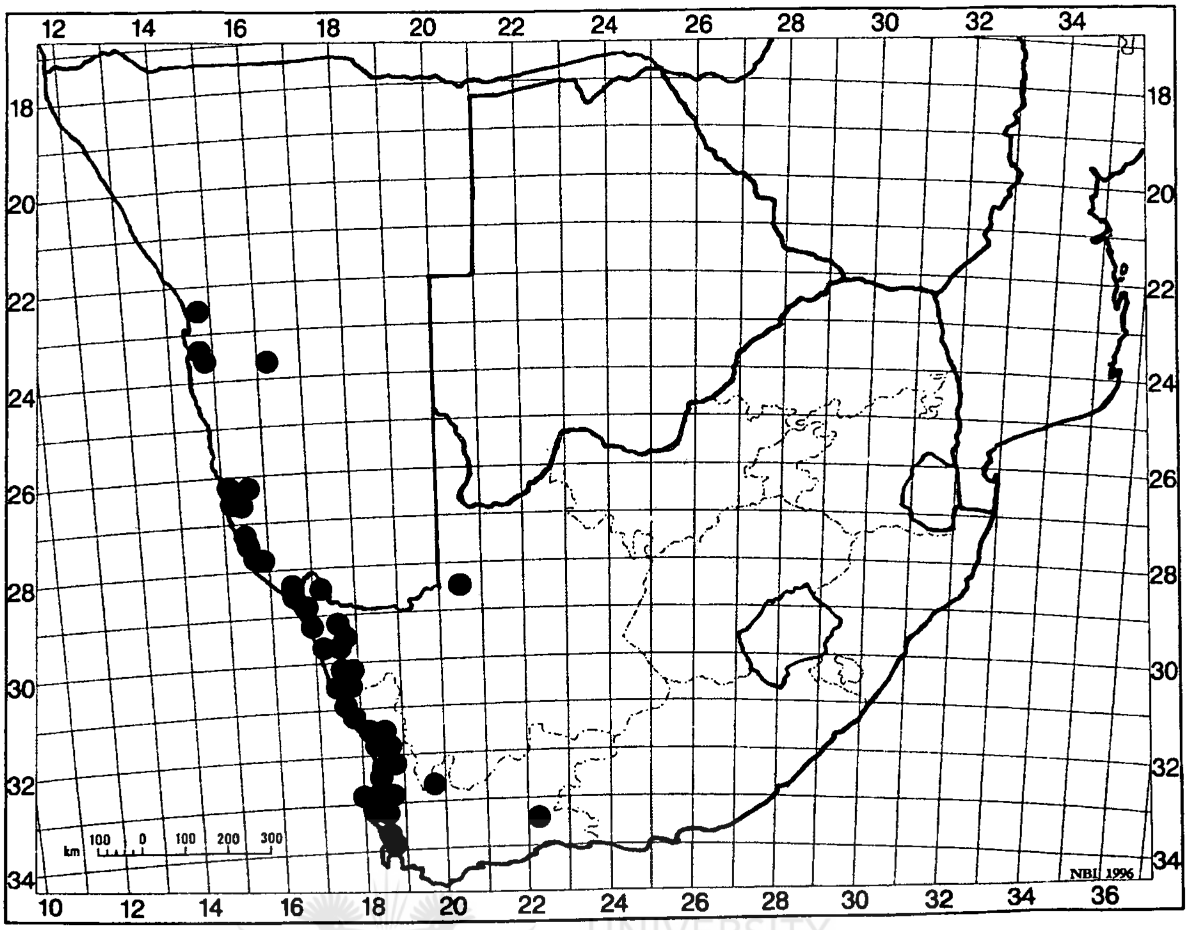

FIG. 6.33. Known geographical distribution of *Calobota sericea*.

15. CALOBOTA SPINESCENS (Harv.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia spinescens* Harv. in Harv. and Sond., Fl. Cap. 2: 88. 1862; Wilman, Preliminary checklist of flowering plants and ferns of Griqualand West (South Africa): 53. 1946; Merxm. and Schreib., FSWA 60: 68. 1970; Goldblatt and Manning, Cape Pl.: 494. 2000.—TYPE: SOUTH AFRICA, Dwaka River, *Burke s.n.* (lectotype: K!, designated here; isolectotypes: BM! 2 sheets). [Note: The Burke specimen in Kew was determined by Harvey himself as "*Lebeckia spinescens* Harv." and is here chosen as lectotype.]

*Lebeckia armata auct. non* Thunb.: E.Mey., Comm. Pl. Afr. Austr. 1: 35. Feb. 1836.

*Lebeckia elongata* Hutch. in Ann. Bol. Herb. 3: 2. 1923.—TYPE: NAMIBIA, without locality, *Pearson 9899* (holotype: BOL!, isotype: K!).

Erect to spreading, multi-stemmed, spinescent shrub up to 1.0 m in height. Branches green; young branches sericeous; older branches sericeous or glabrous with light brown bark. Leaves digitately trifoliolate; petiole longer than leaflets, 6–25 mm long; leaflets linear to oblanceolate or spathulate, alternate, sericeous, subsessile, terminal leaflet 3–12 mm long, 0.5–2.0 mm wide, lateral leaflets 2–11 mm long, 0.5–2.0 mm wide; apex acute; base cuneate. Inflorescence 25–105 mm long, with 3 to 10 flowers; pedicel 1–3 mm long; bract 1–2 mm long, linear, pubescent, caducous; bracteoles 0.5–1.5 mm long, linear, pubescent, caducous. Flowers 10–16 mm long, bright yellow. Calyx 4.5–7.0 mm long, pubescent; tube 3–5 mm long; lobes 1.0–2.5 mm long, subulate. Standard 10.0–15.5 mm long; claw linear, 2–4 mm long; lamina ovate, 8.5–12.0 mm long, 7.5–11.0 mm wide, dorsal surface sericeous; apex acute. Wings 10.5–14.0 mm long; claw 2.5–4.0 mm long; lamina oblong, as long as or shorter than keel, 7.5–10.0 mm long, 2–4 mm wide, glabrous or rarely pilose, with 4–6 rows of sculpturing. Keel 11–15 mm long; claw 3.5–5.0 mm long; lamina boat-shaped, 7–10 mm long, 3.5–6.0 mm wide, glabrous or rarely pilose. Pistil subsessile to shortly stipitate, pubescent or glabrous with pilose hairs on margins; ovary linear, 7.5–11.5 mm long, 1.0–1.5 mm wide with 10 to 16 ovules; style longer than ovary, 3.5–6.0 mm long. Pods linear, somewhat falcate, laterally compressed, subsessile to shortly stipitate, 20–40 mm long, 3–4 mm wide, ±4 to 6-seeded, either sericeous or glabrous and pilose along upper suture, dehiscent. Seeds suborbicular to reniform, 2.4–2.5 mm long, 2.1–2.2 mm wide (only one specimen available for measurement), mature seeds light brown, surface smooth (Fig. 6.34). Flowering time: Flowering occurs from February to May and September to October. One specimen collected in December (summer and spring flowering).

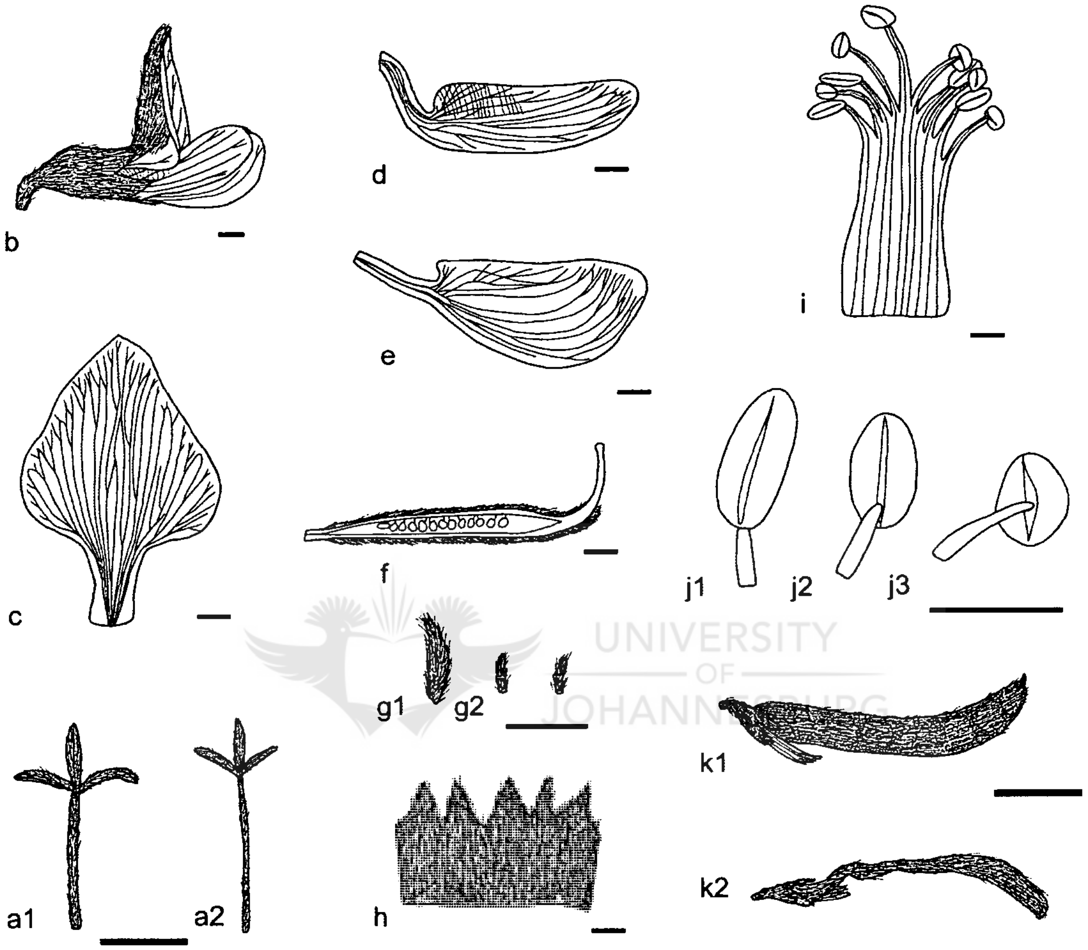

FIG. 6.34 Morphology of *Calobota spinescens*: (a1–a2) leaves in abaxial view; (b) flower in lateral view; (c) standard petal; (d) wing petal; (e) keel petal; (f) pistil; (g1) bract; (g2) bracteoles; (h) outer surface of the calyx (upper lobes to the left); (i) androecium; (j1) long, basifixed anther; (j2) intermediate carinal anther; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a1, b–e, g1–k2) *Boatwright et al. 158* (JRAU); (a2) *Koekemoer 248* (JRAU); (f) *Zietsman 3489* (PRE). Scale bars: (a1–a2, k1–k2) 1 cm; (b–j3) 1 mm.

***Diagnostic characters***—This species is similar to *Calobota acanthoclada* but differs in the green young branches, trifoliolate leaves, larger flowers, short calyx lobes and pods that are constricted between the seeds (in *C. acanthoclada* the young branches are brown, the leaves simple, the flowers smaller and the calyx lobes longer than in *C. spinescens*, and the pods not constricted between the seeds).

***Distribution and habitat***—*Calobota spinescens* is widely spread throughout the Cape and southern Namibia (Fig. 6.35). According to Mucina et al. (2006) it is an important component of Namaqualand sandveld (SKs 7 Namaqualand Strandveld) and Trans-Escarpment Succlent Karoo (SKt 1 Western Bushmanland Klipveld).

***Regional Variation***—Two forms can be distinguished based on the pubescens of the ovary and fruit:

FORM A (Typical form)

Leaves with petiole 6–25 mm long; leaflets with terminal 3–12 mm long, 0.5–2.0 mm wide, lateral 2–11 mm long, 0.5–2.0 mm wide. Inflorescence 25–105 mm; with 3 to 10 flowers. Flowers 11–15 mm. Calyx 5.5–6.5 mm long, pubescent or sericeous; tube 3.5–5.0 mm long; lobes 1.5–2.5 mm long. Standard 12.5–15.5 mm long; claw 3–4 mm long; lamina 9.5–12.0 mm long, 7.5–9.5 mm long. Wings 10.5–14.0 mm long; claw 2.5–4.0 mm long; lamina 7.5–10.0 mm long, 2.5–3.5 mm wide, with 4–5 rows of sculpturing, glabrous or rarely pilose. Keel 11–15 mm long; claw 4–5 mm long; lamina 7–10 mm long, 3.5–5.0 mm wide, glabrous or rarely pilose. Pistil pubescent; ovary 7.5–11.5 mm long, 1.0–1.5 mm wide with 10 to 16 ovules; style 3.5–5.5 mm long. Pods sericeous, 20–40 mm long, 3–4 mm wide.

***Diagnostic characters***—The ovary and pods of this form are densely sericeous.

***Distribution and habitat***—The typical form of *Calobota spinescens* is widely distributed in southern Namibia and the Northern Cape Province of South Africa, with some populations in the Western and Eastern Cape. It occurs on sandy soils along roadsides, in riverbeds or on sand dunes. It also grows on sand overlying limestone or granite koppies or calcareous sand at altitudes of between 600 m and 1100 m and is heavily grazed livestock.

FORM B (Prieska form)

Leaves with petiole 6–14 mm long; leaflets with terminal 3–10 mm long, 0.5–1.5 mm wide, lateral 2–10 mm long, 0.5–1.0 mm wide;. Inflorescence 30–70 mm; with 5 to 7 flowers. Flowers 10–16 mm. Calyx 4.5–7.0 mm long, glabrescent or pilose; tube 3–5 mm long; lobes 1.0–2.5 mm long. Standard 10–15 mm long; claw 2–4 mm long; lamina 8.5–11.5 mm long, 7.5–11.0 mm wide. Wings 10.5–13.0 mm long; claw 2.5–4.0 mm long; lamina 7.5–10.0 mm long, 2–4 mm wide, with 4–6 rows of sculpturing, glabrous. Keel 11–14 mm long; claw 3.5–5.0 mm long; lamina 7.5–10.0 mm long, 3.5–6.0 mm wide, glabrous. Pistil glabrous with pilose hairs along margins; ovary 9.5–11.0 mm long, 1.0–1.5 mm wide with 12–16 ovules; style 4.5–6.0 mm long. Pods glabrous and pilose along upper suture, 25–35 mm long, 3–4 mm wide.

***Diagnostic characters***—In the Prieska form the ovary and pods are largely glabrous with only some hairs along the upper suture.

***Distribution and habitat***—The Prieska form occurs in the central parts of South Africa (Prieska, Brandvlei, Britstown, Aberdeen and Willowmore) with an outlier population around Klinghardt. It grows on red-brown, well-drained, sandy soil, limestone, deep aeolitic sand banks, on calcretic flats or sand on dolerite rock at altitudes of between 250 m and 1100 m. It is heavily grazed by livestock.

### *Additional specimens examined*

**–2416** (Maltahöhe): Farm Grootplaas MAL 95 (–DD), *Giess et al. 5204* (PRE, WIND).

**–2418** (Stampriet): between Hofmeyr and Stamprietfontein, 1 ml [1.61 km] from the latter (–AD), *Wilman 383* (BOL, NBG, PRE).

**–2516** (Helmeringhausen): Grootfontein MAL 91 (–BB), *Volk 12875b* (WIND).

**–2618** (Keetmanshoop): west of Gellap-Ost 15 km north-west of Keetmanshoop (–CA), *Maggs 111* (WIND).

**–2619** (Aroab): 20.5 mls. [32.98 km] south-east of Aroab on Klipdam road (–DC), *De Winter 3440* (K, PRE, WIND); 3.6 mls [5.79 km] from Aroab on road to Koes (–DC), *De Winter 3458* (K, PRE, WIND).

**–2620** (Twee Rivieren): Twee Rivieren in bed of Nossob River (–BC), *Leistner 1497* (BOL, K, PRE); Kalahari-Gemsbok National Park (–BC), *Van Rooyen and Bredenkamp 76* (PRE); 40 mls [64.36 km] from Aroab (–CC), *Grobbelaar 1862* (K); 50 km south of the Kalahari Gemsbok National Park (–DA), *Koekemoer 248* (JRAU 6 sheets).

**–2715** (Bogenfels): Klinghardt Mountain, Diamond Area no. 1 (–BB), *Ward and Seely 10223* (WIND).

**–2717** (Chamaites): south of Lowen River, at Gawachab (–BB), *Pearson 4098* (BM, K); Wegdraai, Hottentots Plateau (–CB), *Helary and Batault 202* (WIND).

**–2719** (Tränental): Farm Blinkoog (–CA), *Waltu and Waltu 2403* (WIND); Farm Nuwerus (–CB), *Giess et al. 7125* (WIND); Farm Goedemoed (–DD), *Strobach et al. 3000* (WIND).

**–2722** (Olifantshoek): 4 mls [6.44 km] north of Gamotep Pan (–CC), *Leistner 1706* (K).

**–2816** (Oranjemund): Sendelingsdrif (–BB), *Metelerkamp 59* (BOL).

**–2818** (Warmbad): Ramansdrift (–CD), *Pearson 4046* (BM).

**–2819** (Ariamsvlei): Farm Udabis (–AD), *Giess et al. 7107* (WIND); Farm Skroef, near hot spring on bank of Orange River (–DA), *Van Hoepen 1942* (BOL, PRE).

**–2820** (Kakamas): approximately 70 km from Ariamisvlei on road to Upington (–AB), *Grobbelaar 1926* (K, PRE); Augrabies Waterfall National Park (–CB), *Werger 345* (K, WIND), *Zietsman 3489, 3920* (PRE); 31 km west of Kakamas along road to Pofadder and Onseepkans (–DC), *Davidse 6161* (K); 6 mls [9.65 km] south of kakamas (–DC), *Leistner and Joynt 2828* (K, PRE); north bank of Orange River near Kakamas (–DC), *Lewis 198* (NBG); 20 mls [32.18 km] south-east of Kakamas (–DC), *Theron 1943* (BOL, K); between Kakamas and Kenhardt (–DC), *Thorne s.n.* (NBG).

**–2821** (Upington): Karakul Research Station near Upington (–AC), *Labuschange s.n.* (NBG).

**–2822** (Glen Lyon): 8 mls [12.87 km] west-north-west of west entrance of Padkloof (–DA), *Leistner 1750* (K, PRE).

**–2824** (Kimberley): 60 mls [96.54 km] from Upington (–AC), *Pole-Evans 2160* (PRE); 21.5 mls [34.59 km] north of Witkop (–BA), *Pole-Evans 2132* (PRE).

**–2919** (Pofadder): Pofadder (–AB), *Conradie 25* (NBG); on N14 highway 25 km from Pofadder from Springbok (–BB), *Boatwright et al. 158* (JRAU).

**–2921** (Kenhardt): Kenhardt (–AC), *Wabberfall 1114* (K).

**–2922** (Prieska): Kwakwas (–AB), *Acocks 1759* (PRE); on sandy waste behind Draghoender hotel (–AC), *Acocks and Hafström H1343* (K, PRE 2 sheets); Boesmanland, Farm Mames-Pan 107, 0.5 km north of Kielder farmhouse (–CC), *Le Roux and Lloyd 173* (K, PRE); Boesmanland, Farm Doonies-Pan 106, 13.3 km north north-west of Copperton (–CD), *Le Roux and Lloyd 138* (PRE); Prieska (–DA), *Bryant J263* (K); North bank of Orange River (–DA), *Bryant 5404* (BOL).

**–2923** (Douglas): Lanyon-Vale (–AC), *Acocks 1982* (BOL, K).

**–3020** (Brandvlei): Boesmanland, Farm Bastiaans Kolk 331, on stabilized sand dunes in Groot Vloer (–BA), *Le Roux and Lloyd 111* (PRE).

**–3023** (Britstown): at Vissershoek turn-off 39 km north of Britstown (–BC), *Van Wyk 2849* (JRAU 2 sheets); 36.3 km from Britstown to Vissershoek turn-off, at Farm Fonteintjies 8 km from house (–BC), *Van Wyk 3081* (JRAU); 10 km south on Deelfontein road, Farm Witfontein (–DA), *Le Roux 236* (PRE).

**–3120** (Williston): Great Fish River and Zout River, Beaufort (–AD), *Zeyher 397* (BM, K, NBG); Williston Station (–BD), *Smith 2443* (K); Rietpoort (–DB), *Shearing 81* (K).

**–3122** (Loxton): Pampoenpoort (–BA), *Henrici 4750* (PRE).

**–3219** (Wuppertal): Grasberg South, Tanqua National Park (–BC), *Bayer 6244* (PRE); Sandkop (–BC), *Henrici 3333* (PRE).

**–3221** (Merweville): rocks at Driekoppe (–DC), *Drège s.n. "II, f"* (P).

**–3224** (Graaff-Reinet): 40 mls [64.36 km] from Aberdeen (–AC), *Hutchinson 3135* (BM, K 2 sheets); south-west of Aberdeen (–AC), *Maguire 742* (NBG).

**–3321** (Ladismith): near Grootfontein, 30 mls [48.27 km] north east of Laingsburg (–AB), *Wilman 1048* (BOL).

**–3322** (Oudtshoorn): Prince Albert (–AA), *Bolus 11774* (K, PRE), *Thoday and Dolf 66* (NBG).

**–3323** (Willowmore): Willowmore, near station Vondeling on banks of Olifantsriver (–AC), *Vlok 1932* (JRAU, PRE).

**Precise locality unknown:** without locality, *Acocks 1701* (PRE); Griqualand West, *Burchell 1965* (K); between Dweka River and Zwartbulletjie, *Drège s.n.* (S); Bushmanland, *Pearson 3633* (K).

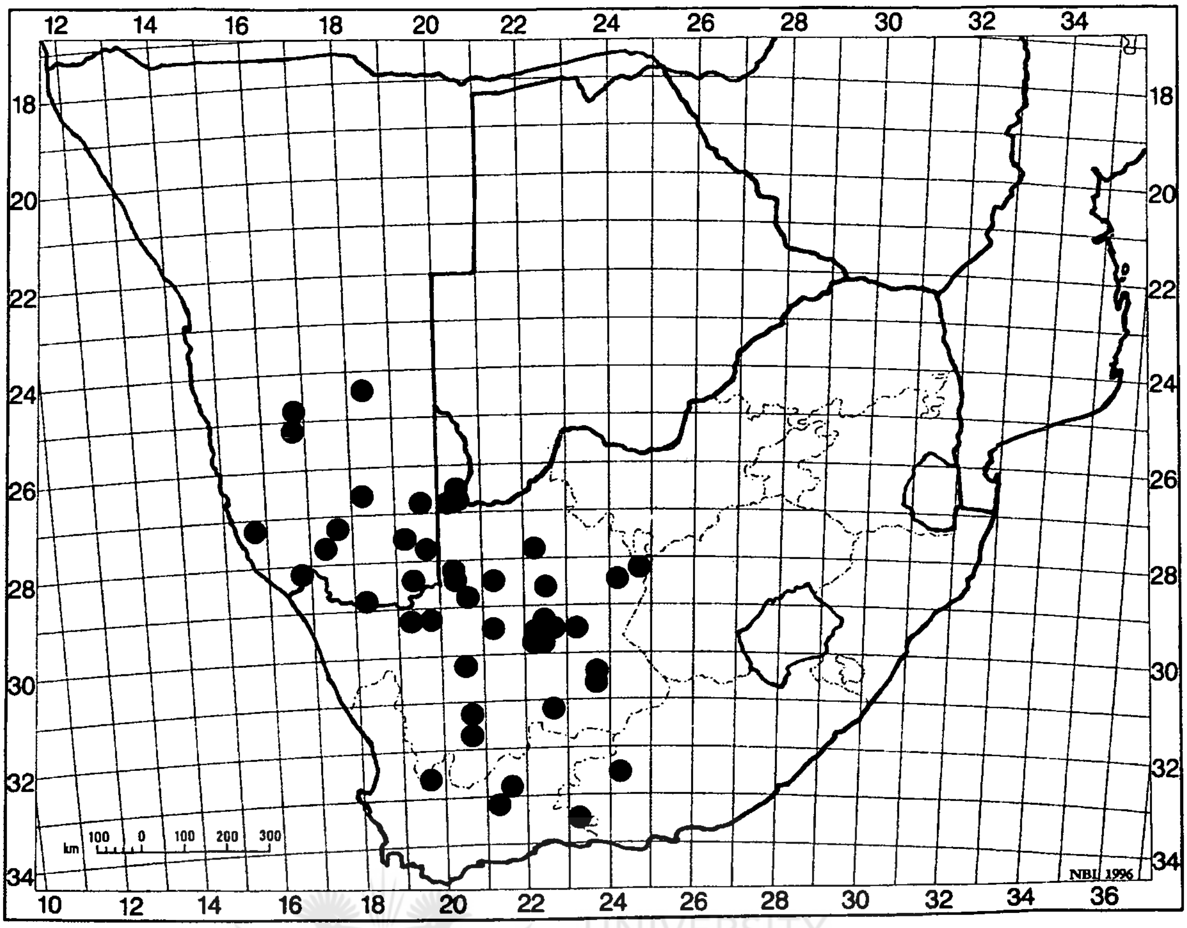

FIG. 6.35 Known geographical distribution of *Calobota spinescens*.

16. CALOBOTA THUNBERGII Boatwr. and B.-E.van Wyk, nom. nov. pro *Lebeckia sericea* Thunb. non *Calobota sericea* (Ait.) Boatwr. and B.-E.van Wyk. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia sericea* Thunb., Nov. Gen.: 143. 1800; Prodr. Pl. Cap.: 122. 1800; Willd., Sp. Pl.: 948. 1800; Thunb., Fl. Cap.: 562. 1823; DC., Prodr. 2: 137. 1825; Benth. in Hook. Lond. J. Bot. 3: 360. 1844; Harv. in Harv. and Sond., Fl. Cap. 2: 88. 1862; Bond and Goldblatt, J. S. Afr. Bot. 13: 290. 1984; Goldblatt and Manning, Cape Pl.: 494. 2000.—TYPE: SOUTH AFRICA, 'e Cap. b. Spei' [grid unknown], *Thunberg s.n. sub THUNB-UPS 16423* (lectotype: UPS!, designated here). [Note: The epithet '*sericea*' was applied to *Lebeckia multiflora* E.Mey. (now *Calobota sericea*) by Aiton

(1789), the basionym of which is *Spartium sericeum* Ait., and is thus not available for the current taxon. We therefore propose a new name in memory of Thunberg who first described this species]. [Note: The specimen listed is the only specimen in Thunberg's herbarium and is here chosen as lectotype].

*Lebeckia flexuosa* E.Mey., Comm. Pl. Afr. Austr. 1: 34. Feb. 1836; Walp in Linnaea 13: 478. 1839.—TYPE: SOUTH AFRICA, "In rupestribus prope Kwekrivier" [grid unknown], altit. 700 ped., *Drège s.n. "III, C"* (lectotype: P!, designated here; isolectotype: K!, P!). [Note:The specimen bears the diagnostic features described by Meyer and also the type locality.]

*Lebeckia decipiens* E.Mey., Comm. Pl. Afr. Austr. 1: 35. Feb. 1836.—TYPE: SOUTH AFRICA, Karroo prope Mierenkasteel [grid unknown], *Drège s.n. "III, C"* (lectotype: P!, designated here; isolectotype: BM!, K!, NBG!, P!, PRE!, S!). [Note: The P specimen bears the type locality and was annotated by Meyer himself.]

Sericeous, multi-stemmed unarmed shrub up to 2 m in height. Branches green; young branches sericeous; older branches sericeous or glabrous with brown bark. Leaves digitately trifoliolate; petiole longer or shorter than leaflets, 13–55 mm long; leaflets elliptic to narrowly oblanceolate, alternate, sericeous, subsessile, terminal leaflet (15–) 17–50 mm long, (1–) 2–8 mm wide, lateral leaflets 10–45 mm long, (1–) 2–5 mm wide, apex acute, base angustate. Inflorescence 70–220 mm long, with 10 to 28 flowers; pedicel 2–4 mm long; bract 2–7 mm long, linear, pubescent; bracteoles 1–5 mm long, linear, pubescent. Flowers 13–24 mm long, pale or bright yellow. Calyx 6.0–9.5 mm long, sericeous; tube 4.0–6.5 mm long; lobes 1–4 mm long, subulate. Standard (11.5–) 13.0–19.0 mm long; claw linear, 3–5 mm long; lamina widely ovate, 8.0–14.5 mm long, 9.5–17.0 mm wide, pilose along dorsal midrib; apex obtuse. Wings 12.0–17.5 mm long; claw 3.0–5.5 mm long; lamina oblong, as long as or shorter than keel, 8–12 mm long, 4.0–6.5 mm wide, glabrous, with (5–) 8–14 rows of sculpturing. Keel 12.5–19.5 mm long, claw 3.5–7.0 mm long, lamina boat-shaped, 8.5–13.0 mm long, 4.5–6.5 mm wide, pilose on terminal parts. Pistil subsessile to shortly stipitate, pubescent; ovary linear, 8.5–15.0 mm long, 0.8–1.5 mm wide with 19 to 28 ovules; style longer than ovary, 3.5–8.5 mm long. Pods linear, semi-terete, subsessile to shortly stipitate, 30–50 mm long, 3–4 mm wide, 7 to 14-seeded, pubescent, dehiscent. Seeds oblong-reniform, 2.3–3.5 mm long, 1.7–2.5 mm wide, mature seeds light brown to light pink, surface smooth (Fig. 6.36). Flowering time: *C. thunbergii* flowers mainly from May to October. One specimen collected in March was in flower.

***Diagnostic characters***—Similar to *Calobota cytisoides* but differs in the acute apices of the leaflets, short pedicels and smaller flowers, linear bracts and bracteoles, sericeous calyx and sericeous pistil and pods (in *C. cytisoides* the apices of the leaflets are mucronulate, the pedicels longer and the flowers larger. The bracts and bracteoles are often ovate, the calyx glabrous and the pistil and pods glabrous).

***Distribution and habitat***—*Calobota thunbergii* is widely distributed from Wupperthal south as far as the Oranjemund area (Fig. 6.37). It grows in well-drained sandy loamy soil, granite, rocky sand, sandy dunes, in riverbeds or along disturbed roadsides between 300 m and 1200 m above sea-level. This species, according to Mucina et al. (2006) and Jürgens (2006), is an important component of Richtersveld (SKr 14 Southern Richtersveld Inselberg Shrubland), Namaqualand Hardeveld (SKn 1 Namaqualand Klipkoppe Shrubland, SKn 2 Namaqualand Shale Shrubland, SKn 6

Kamiesberg Mountains Shrubland), Namaqualand Sandveld (SKs 9 Namaqualand Inland Duneveld) and Southern Namib Desert (Dn 1 Alexander Bay Coastal Duneveld).

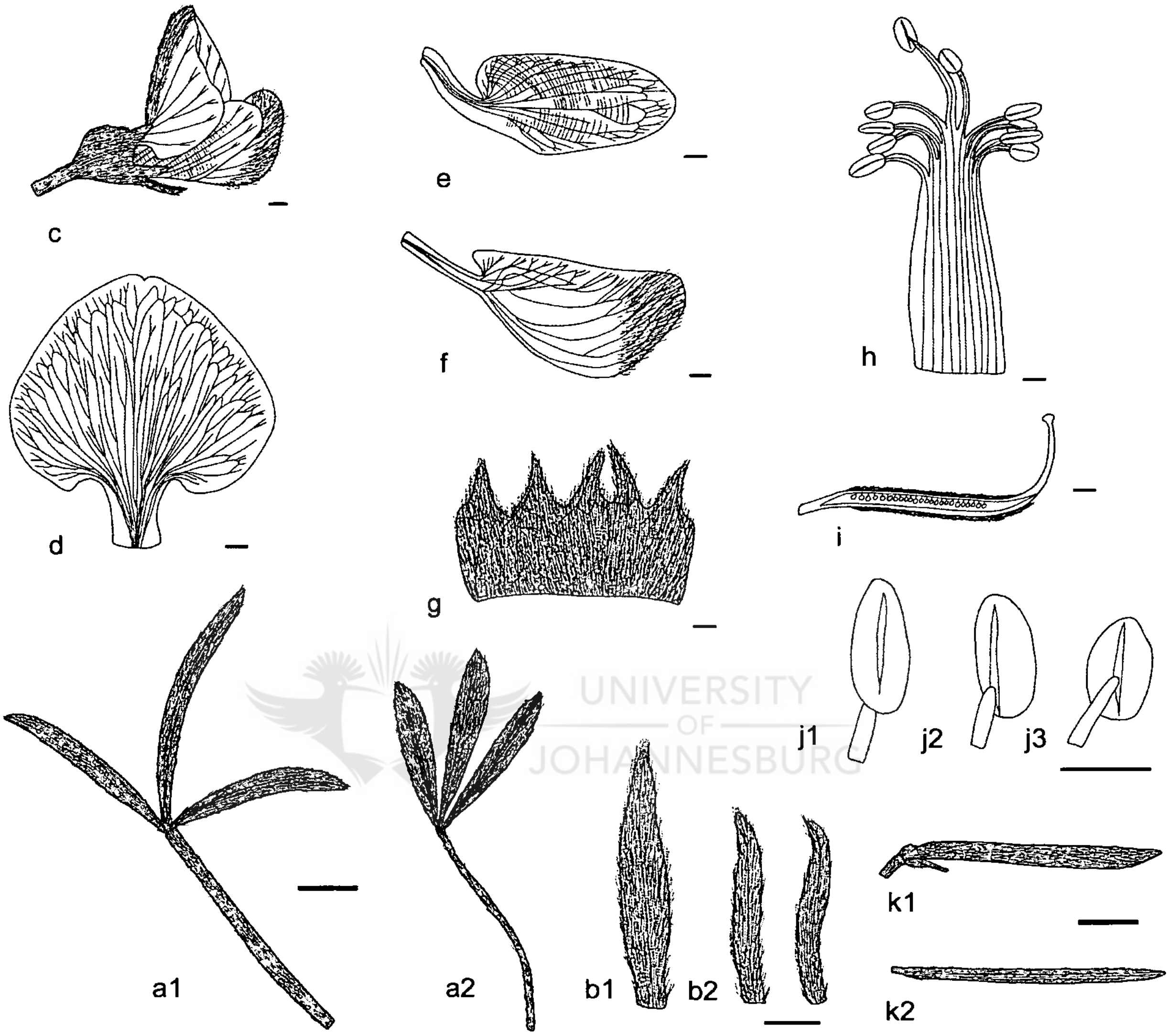

FIG. 6.36 Morphology of *Calobota thunbergii*: (a1–a2) leaves in abaxial view; (b1) bract; (b2) bracteoles; (c) flower in lateral view; (d) standard petal; (e) wing petal; (f) keel petal; (g) outer surface of the calyx (upper lobes to the left); (h) androecium; (i) pistil; (j1) long, basifixed anther; (j2) intermediate carinal anther; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a1, b1–j3) *Boatwright et al. 151* (JRAU); (a2, k1–k2) *Van Wyk 3119* (JRAU). Scale bars: (a1–a2, k1–k2) 1 cm; (b–j3) 1 mm.

### *Additional specimens examined*

**–2816** (Oranjemund): sand drifts on Witbank (–DC), *Pillans 5542* (BOL); sandy coast belt between Port Nolloth and Holgat River (–DD), *Pillans 5627* (BOL, K).

**–2817** (Vioolsdrif): Kodaspiek (–AA), *Oliver et al. 451* (K, NBG); Vandersterrberg north-east of Khubus north end south-east of the top of Helskloof and south-east of Paradysberg western slopes to summit (–AC), *Oliver et al. 151* (NBG, K, PRE); Vioolsdrif, Ridge above Koeskop, summit of Vandersterberg, Richterveld National Park (–AC), *Williamson and Williamson 5764* (NBG); Cornellsberg (–CA), *Bean 1258* (BOL), *Bean 1328* (S), *Van Jaarsveld 11977* (PRE), *Viviers 2046* (NBG); Jenkins Hill, 20 km from Eksteenfontein on road to Mount Stewart (–CB), *Germishuizen 4679a* (PRE 2 sheets); Spektakel Hill (–DA), *Johnson 216* (NBG).

**–2916** (Port Nolloth): sandy plain 2 mls [3.22 km] east of Port Nolloth (–BD), *Marloth 12660* (NBG, PRE).

**–2917** (Springbok): along roadside on road from Port Nolloth to Steinkopf (–AC), *Boatwright et al. 151* (JRAU); Klipfontein (–BA), *Bolus 429* (BM, BOL, K, NBG, PRE), *Bolus 6549* (K), *Hutchinson 904* (BM, BOL, K, PRE); Steinkopf (–BA), *Herre s.n. sub STE 11889* (NBG), *Meyer s.n. sub STE9068* (NBG); Anenous Pass (–BA), *Germishuizen 4839* (PRE, WIND), *Schutte 591* (JRAU 2 sheets), *Van Wyk 6266* (PRE); Spitskop, 6 mls [9.65 km] south of Steinkopf (–BD), *Lewis 5487* (NBG 2 sheets); Klipfontein Koppie (–CA), *Compton 5486* (BOL, NBG); Stinkfontein Mountains south-west of Van Zylsrus (–CA), *Oliver et al. 625* (NBG, PRE); Spektakel (–DA), *Compton 11524* (NBG); Spektakel Pass (–DA), *Eliovson 37* (NBG); 25 km from Springbok towards Spektakelberg Pass (–DA), *Glen 1463* (BOL, PRE); Spektakel Pass, 26 km west of Springbok (–DA), *Goldblatt 3651* (PRE); top of Spektakelberg Pass (–DA), *Grobbelaar 2584* (PRE); Farm Ezelfontein 214, 2 km north of Naries farmstead (–DA), *Le Roux 3233* (NBG); 21.7 km fro Springbok to Spektakel (–DA), *Stirton 6019* (K); 24 km from Springbok to Kleinsee (–DA), *Stirton 10149* (NBG); 9 mls [14.81 km] south-east by east of Springbok (–DB), *Acocks 19237* (K, PRE); 8.5 mls [13.68

km] west by south of Springbok (–DB), *Acocks 19550* (BOL, K, PRE); near O'kiep (–DB), *Barker 6244* (NBG 3 sheets); 1ml [1.61 km] south of Springbok (–DB), *Barker 8389* (NBG 2 sheets); 2 km east of Springbok (–DB), *Bellamy 12* (PRE); Springbok (–DB), *Bester and Pretorius 8* (JRAU), *Crosby 20* (PRE), *Salter 895* (BM, K), *Small et al. 82* (PRE), *Van Blerk 7* (PRE), *Van Hille 8* (BOL), *Venter 8820* (PRE); Nababeep, road to O'kiep (–DB), *Burrows 2950* (GRA); ±8 km north-east of Nababeep on gravel road to junction with tar road (–DB), *Botha 3170* (PRE); 2 mls [3.22 km] north-east of Springbok (–DB), *Compton 22012* (NBG); Concordia, near Springbok (–DB), *Clarke 687* (PRE), *Thorns s.n.* (NBG); just outside nababeep on road to O'kiep (–DB), *Germishuizen 4515* (PRE); Nababeep (–DB), *Gess and Gess 89/90/67* (GRA); Hester Malan Wild Flower Reserve north of Oxaliskoppie (–DB), *Le Roux 918*, *1231* (PRE); Nababeep, near golf course (–DB), *Le Roux 2674* (BOL); 2 mls [3.22 km] north of Springbok (–DB), *Lewis 3392* (NBG), *Schelpe 240* (BM, BOL); 4 mls [6.44 km] west of Springbok (–DB), *Macguire 369* (BOL, NBG 2 sheets); Springbok, weather station hill on west of town (–DB), *Manning 2774* (NBG); Okiep (–DB), *Dümmel s.n.* (K), *Marloth 6712* (NBG 3 sheets, PRE), *Morris 5623* (BM, BOL, NBG); 15 mls [24.14 km] north of Springbok (–DB), *Schlieben 9059* (BM, K, PRE); Springbok T'Karoep, on road between Nababeep and Okiep (–DB), *Scholtz 20* (NBG, PRE); Hester Malan Nature Reserve (–DB), *Stirton 6004* (PRE), *Struck 113* (NBG), *Van Wyk 5728* (PRE); 5 mls [8.05 km] north of O'kiep (–DB), *Van der Schijff and Schweickerd 5744* (K, PRE); 2 mls [3.22 km] north of Springbok (–DB), *Van Niekerk 240* (PRE, 2 sheets); 11 km from Springbok to Pofadder (–DB), *Van Wyk 3078* (JRAU 2 sheets); Modderfontein (–DB), *Whitehead s.n.* (S); 3 km east of Springbok (–DB), *Zietsman and Zietsman 667* (PRE); Messelpad between Springbok and Wallekraal (–DC) *Compton 20664* (NBG 2 sheets); near Komaggas (–DC), *Eliovson 69* (J); north slopes of Rooiberg above Buffels River on eastern approach to the Meselpad (–DC), *Hilton-Taylor 2140* (NBG, PRE); ca. 11 km from Springbok on sand road to Hondeklipbaai (–DC), *Joffe 96* (NBG, PRE); on road to Hondeklipbaai, 18 mls [28.96 km] from turn-off from national road to Springbok (–DC), *Van der Merwe 215* (NBG); 29 mls [46.66 km] from Springbok on road to Garies (–DD), *Grobbelaar 1119* (PRE); near Mesklip (–DD), *Leighton*

*1156* (BOL); on roadside of N7 highway 13 km south of Springbok, opposite 33.4 marker (–DD), *Powrie 652* (NBG 2 sheets, PRE); 30 mls [48.27 km] south of Springbok (–DD), *Rynolds 5440* (K); 20 mls [32.18 km] south-west of Springbok (–DD), *Verdoorn and Dyer 1791* (BOL, K 2 sheets).

**–2918** (Gamoep): Zilverfontein (–CC), *Drège s.n.* (BM, K, P, S).

**–3017** (Hondeklipbaai): Diknek (–AD), *Van Breda 4073* (PRE); Farm Doornfontein 464, Portion 1, Steenkamp Kraal (–BA), *Le Roux 4555* (NBG); on road to Leliefontein from Kamieskroon (–BB), *Boatwright et al. 219* (JRAU); Grootvlei, hillsides, Kamieskroon (–BB), *Compton 6839* (NBG); Skilpad Wild Flower Reserve, 100m from house (–BB), *Cruz 85* (NBG); Studer Pass (–BB), *Evrard 8960* (PRE); Kamieskroon (–BB), *Hutchinson 841* (BM, K 2 sheets, PRE), *Salter 863* (BM), *Salter 865* (K), *Thorne s.n.* (NBG), *Van Rooyen 2416* (PRE); portion of Wolwepoort 459, Skilpad Farm, north-west of Kamieskroon (–BB), *Johannesburg Botanical Garden 3877* (PRE); between Kamieskroon and Soebatfontein (–BB), *Meyer 7331* (PRE); ±4 km from Kamieskroon (–BB), *Meyer 7349* (PRE); Kamiesberg Pass (–BB), *Schutte 593* (JRAU), *Stirton 5993* (PRE), *Strid and Strid 37780* (NBG), *Van Wyk 2540, 3094* (JRAU); Farm Olienfontein (–BB), *Zietsman and Zietsman 1017* (PRE); 2.3 km from start of Kamiesberg Pass (–BB), *Van Wyk 2352* (JRAU 2 sheets); 5 km from Wallekraal to Garies (–BC), *Stirton 6054d* (K); Garies (–BD), *Compton 17180* (NBG), *Kruger K5* (K, NBG, PRE), *Lynes 1944* (BM); Brakdam (–BD), *Johnson 200* (NBG 2 sheets); 5 mls [8.05 km] north of Garies, top of pass (–BD), *Lewis 1308* (NBG); between Nuwerus and Karkams (–BD), *Pearson 6500* (K); Brakdam (–BD), *Schlechter 11150* (BM, BOL, K, PRE); 20 km from Kamieskroon to Garies (–BD), *Stirton 5982* (K); 16 km north of Garies (–BD), *Wisura 2924* (NBG); between Garies and Kamieskroon (–DB), *Jordaan 1225* (NBG), *Van der Schijff 6994* (PRE); 4 km north of Garies on road to Springbok (–DB), *Le Roux 2630* (BOL); 6 mls [9.65 km] north of Garies (–DB), *Leighton 1127* (BOL); near Garies (–DB), *Levyns 6984* (BOL), *Markotter s.n.* (NBG), *Stirton 5978* (K, PRE); 2.1 km from Garies to Bitterfontein (–DB), *Marsch 343* (NBG, PRE); 3 km north of Garies on the main road to Springbok, Garieshoogte (–DB), *McDonald 1329* (NBG, PRE, UPS); 5 km from Kotzerus turn-off from Wallekraal to Garies (–DB) *Stirton 6055* (K); 6mls [9.65 km] from Garies to Kamiesberg (–DB), *Thompson 415* (NBG, PRE); 23 km north of Garies beside N7 (–DB), *Van Wyk 2339* (JRAU); 24 km from Garies on main road to Springbok (–DB), *Van Wyk 2424* (JRAU); between Garies and Springbok (–DB), *Werdermann and Oberdieck 598* (K); Kotzerus (–DD), *Stirton 6058* (K); road between Kotzerus and Bitterfontein (–DD), *Van Wyk 3115* (JRAU).

**–3018** (Kamiesberg): Farm Pedroskloof, 18 km east of Kamieskroon (–AA), *Hilton-Taylor 2122* (NBG); north of Leliefontein (–AB), *Liede and Here s.n.* (JRAU); near Eselsfontein (–AC), *Van der Schijff and Schweikerd 5780* (PRE); on farm near Garies (–AC), *Van Der Walt 159* (NBG); slopes of hills near Garies (–CA), *Thorne s.n.* (NBG); on N7 towards Garies 30 km from town (–CC), *Boatwright et al. 140* (JRAU); 10 km from Garies on N7 (–CC), *Boatwright et al. 141* (JRAU); along N7 to Springbok 20 km from Garies (–CC), *Boatwright et al. 183* (JRAU); 35 mls [56.32 km] south of Garies (–CC), *Thompson 1014* (NBG, PRE); along main road 5 mls [8.05 km] from Garies to Springbok (–CC), *Van Breda 1283* (K, PRE); Kliprand (–DA), *Hall 891* (BOL, NBG), *Van Breda 1607* (K); 5.6 mls [9.01 km] from Bitterfontein to Pofadder (–DB), *Marsch 444* (NBG).

**–3117** (Lepelfontein): Lepelfontein (–BB), *Kolbe s.n. sub BOL 14269* (BOL).

**–3118** (Vanrhynsdorp): Nuwerus, Elandsfontein (–AB), *Barnard 307* (NBG); Bitterfontein (–AB), *Bond 1093* (NBG); Farm Quaggas Kop 125. 6 km west of Nuwerus (–AB), *Le Roux 2278* (NBG); slopes of Spitsberg south-east of Nuwerus (–AB), *Oliver 5930* (NBG, PRE); Karree-Bergen (–AB), *Schlechter s.n. sub TRV 1057* (PRE), *Schlechter 8182* (BM, BOL, K, PRE); 3 mls [4.83 km] north of Bitterfontein (–AB), *Schelpe 131* (BM, BOL, K); Nuwerus (–AB), *Steyn 472* (NBG); Vanrhynsdorp (–DA), *Van der Byl s.n. sub STE 17419* (NBG); top of Klein Kobee Pass (–DB), *Manning s.n.* (K, NBG 2 sheets); Klapmuts (–DD), *Schlechter 375* (BOL).

**–3119** (Calvinia): Bottom of Vanrhyns Pass (–AC), *Marsch et al. 312* (NBG, PRE); Nieuwoudtville (–AC), *Pearson 3468* (K); Vanrhyns Pass before Nieuwoudtville (–AC), *Schutte 285* (JRAU), *Van Wyk 3119* (JRAU); Vanrhyns Pass between Nieuwoudtville and

Vanrhynsdorp (–AC), *Van der Schijff 7183* (PRE), *Van Wyk 2584* (JRAU 2 sheets, NBG, PRE).

**–3218** (Clanwilliam): Nortier Experimental Station near Lamberts Bay (–AB), *Van Breda 4435* (PRE); near Nuwerus (–DC), *Acocks 14188* (K, PRE); few miles north of Nuwerus (–DC), *Wilman 702* (BOL).

**–3219** (Wuppetal): Citrusdal (–CA), *Thorns s.n.* (NBG); Doorn River (–DA), *Herre s.n. sub STE 11890* (NBG); Doorn River bridge (–DA), *Pillans 6305* (BOL, K).

**Precise locality unknown:** Platberg, *Drège s.n. "III, A, b"* (P); without locality, *Leipoldt 739* (NBG), *Marloth 11143* (NBG), *Zeyher 400* (K 2 sheets, S); north of Darters Grave, *Maguire 296* (NBG); Namaqualand, *Scully 7* (BM).

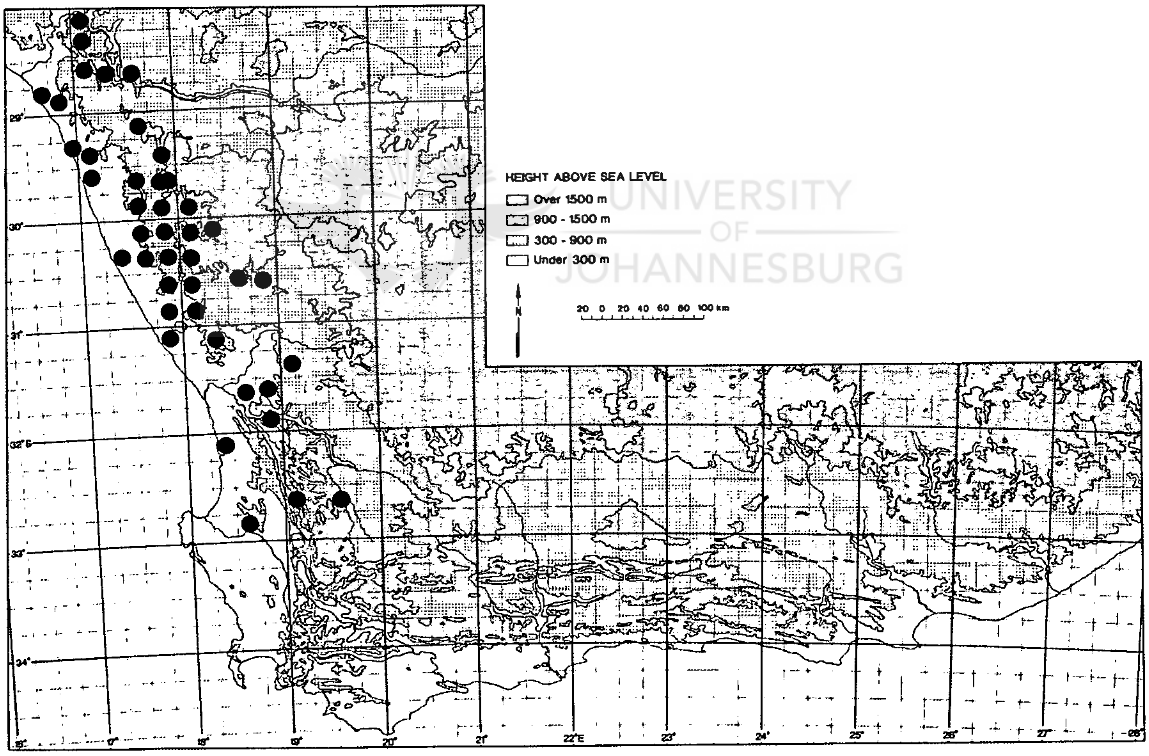

FIG. 6.37 Known geographical distribution of *Calobota thunbergii.*

# CHAPTER 7: TAXONOMY OF THE GENUS *WIBORGIELLA*

## 7.1 INTRODUCTION

*Wiborgiella* is here proposed as a new generic concept to accommodate nine species that are endemic to the Cape region of South Africa. The description of the genus followed a phylogenetic study of the tribe Crotalarieae (Chapter 2) which showed that the genus *Lebeckia*, of which these species formed a part, is polyphyletic (Boatwright et al. 2008a). These results together with morphological and anatomical data indicated that *Lebeckia* s.l. should be divided into three genera: *Lebeckia* s.s., *Calobota* and *Wiborgiella*. *Wiborgiella* comprises all the species that were previously included in *Lebeckia* section *Viborgioides*, along with the anomalous *Lebeckia inflata*, *L. mucronata* and *Wiborgia humilis*. Although the monophyly of *Wiborgiella* did not receive support in the phylogenetic analyses, a combination of salient morphological and anatomical characters support the recognition of this group at the generic level.

*Lebeckia* section *Viborgioides* was studied by Dahlgren (1975) in his revision of *Wiborgia* due to the superficial similarity between the former and *Wiborgia* species. He suggested that the taxa might be con-generic, but from the data in Chapter 2 (Boatwright et al. 2008a) it is clear that *Wiborgia* is strongly supported as a separate genus. *Wiborgiella* can be distinguished from *Calobota*, *Lebeckia* s.s. and *Wiborgia* by a unique combination of characters: brown or grey bark on young branches (the short-lived *W. inflata* and '*W. vlokii'* have green stems), laminar trifoliolate leaves, glabrous petals, 4+6 anther arrangement and oblong, wingless, much inflated fruit.

This chapter is aimed at describing the genus *Wiborgiella* and presenting a taxonomic revision of its species which includes a key, complete nomenclature, typification, formal descriptions, the known geographical distributions and illustrations of all the species.

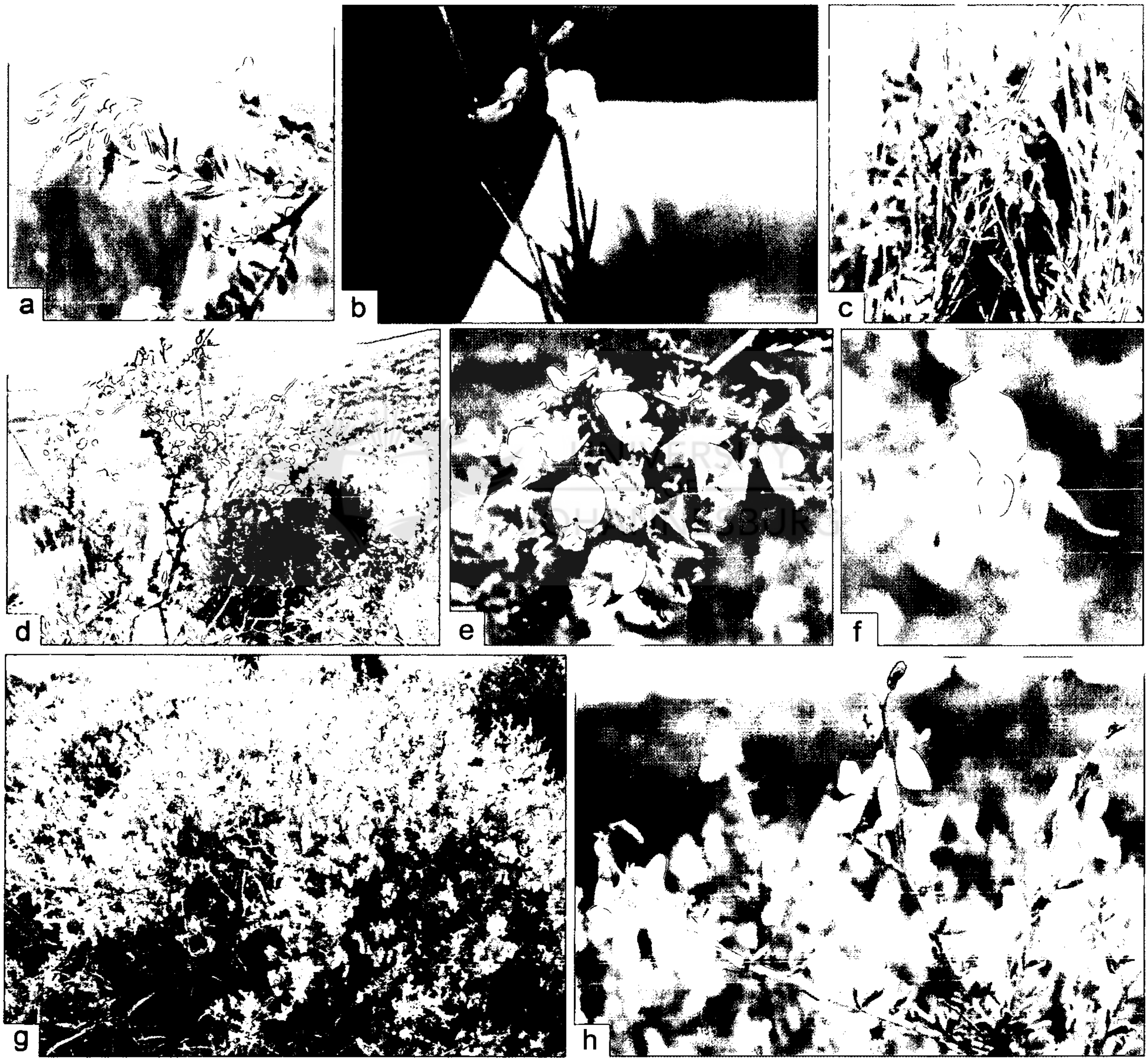

FIG. 7.1. Habit of *Wiborgiella* species. (a, d, e) *W. sessilifolia*. (b) *W. inflata*. (c) *W. humilis*. (f, g, h) *W. leipoldtiana*.

## 7.2 DISCUSSION OF CHARACTERS

***7.2.1 Vegetative morphology and anatomy***—HABIT AND BRANCHES—The species of *Wiborgiella* are either long-lived perennials or short-lived fire-weeds. In the former the branches are brown or grey and covered with longitudinally splitting bark whereas in the short-lived species the branches are green and the plants do not reach heights of more than 0.3 m. The perennial species are rigid shrubs or shrublets that are between 0.5 m and 1.5 m in height (Fig. 7.1).

The stem anatomy of *Wiborgiella* species revealed the presence of several chlorenchyma layers in the species with green stems that are absent in those species with brown, bark-covered stems. The genera *Calobota* and *Lebeckia* differ from most species of *Wiborgiella* in that they also have green stems, i.e. with chlorenchyma, but *Wiborgia* species have a similar habit and stem structure to that of *Wiborgiella* (Fig. 7.2).

Leaves of *Wiborgiella* species are invariably laminar, trifoliolate and petiolate (sessile on older branches of *W. sessilifolia*). The petioles of the shrubby species have a swollen base or tubercle and are persistent even after the leaflets have been shed. The branches in most perennial species become hard and pungent after flowering and have a thorn-like appearance similar to most *Wiborgia* species (Dahlgren 1975). The persistent petioles along with the somewhat spinescent branches give these plants a very rigid appearance. Transverse sections through the leaves of all *Wiborgiella* species revealed that the leaves are dorsiventral (clearly differentiated into palisade parenchyma adaxially and spongy parenchyma abaxially) and that they have mucilage cells in the epidermis (Fig. 7.2). This is a very reliable distinguishing character to separate *Wiborgiella* from *Lebeckia* and *Calobota*. *Lebeckia* has acicular leaves with only palisade parenchyma and *Calobota* has laminar, but isobilateral leaflets with no differentiation into palisade or spongy parenchyma.

***7.2.2 Reproductive morphology and anatomy***—INFLORESCENCE—Polhill (1976) mentions that the inflorescence tends to be an unreliable character in papilionoid legumes. In *Wiborgiella*, as in most Crotalarieae, the inflorescences are terminal racemes, except sometimes in *W. bowieana* where the flowers may be solitary. The inflorescences are either short as in *W. dahlgrenii* and *W. leipoldtiana* or long as in *W. inflata* and *W. mucronata*. The number of flowers per raceme also differs between species.

FLOWERS—The flowers are relatively large (more than 10 mm long) in *W. bowieana*, *W. leipoldtiana*, *W. mucronata* and *W. sessilifolia* and 10 mm or less in *W. dahlgrenii*, *W. fasciculata*, *W. humilis*, *W. inflata* and *W. vlokii*. The pedicel is short and less than 1.5 mm in *W. dahlgrenii*, *W. bowieana* and *W. fasciculata* but may be longer in the other species. The flowers in the genus are yellow, although the label information from the only available flowering specimen of *W. dahlgrenii* suggests that its flowers may be pale pink. The older petals in *W. inflata* turn purple and in *W. sessilifolia* and *W. vlokii* they turn orange. Gess and Gess (1994) suggest that this change in colour follows pollination and is a very effective pollination strategy as it discourages non-productive flower visits thereby increasing pollination efficiency. The petals are generally glabrous in *Wiborgiella* (although a few hairs may very rarely be present on the back of the standard petal).

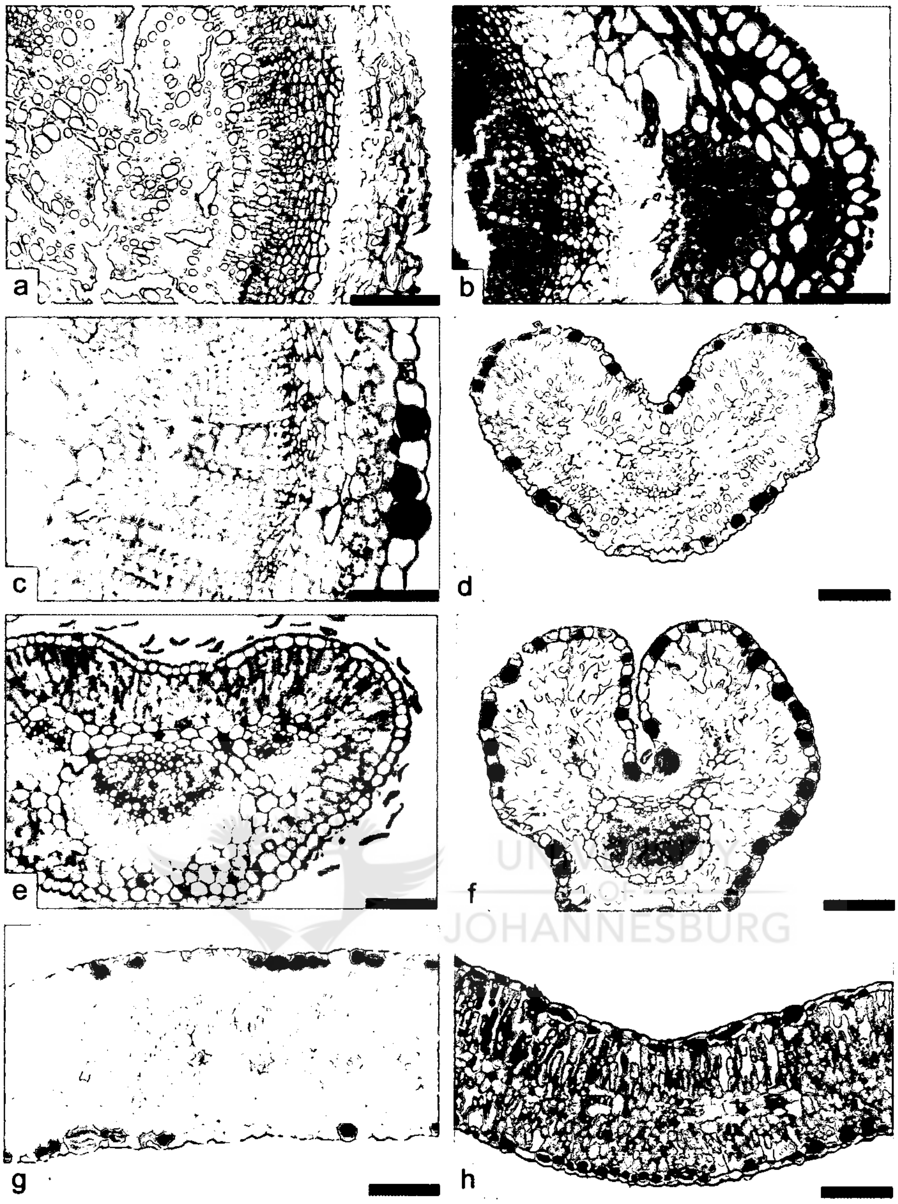

FIG. 7.2 Transverse sections through the stems and leaves of *Wiborgiella* species. (a) Portion of the stem of *W. humilis*; (b) Portion of the stem of *W. sessilifolia*; (c) Portion of the stem of *W. inflata*; (d) Petiole of *W. inflata*; (e) Petiole of *W. leipoldtiana*. (f) Petiole of *W. mucronata*; (g) Portion of the leaf of *W. inflata*; (h) Portion of the leaf of *W. sessilifolia*; Voucher specimens: (a) *Boatwright et al. 129* (JRAU); (b, h) *Van Wyk 2120* (JRAU); (c, d, g) *Johns 162* (JRAU); (e) *Boatwright et al. 123* (JRAU); (f) *Vlok 1726* (JRAU). Scale bars: (a–c) 0.1 mm; (d–h) 0.2 mm.

The bracts and bracteoles are linear to slightly lanceolate or ovate. Those of *Wiborgiella bowieana*, *W. mucronata* and *W. sessilifolia* are relatively long (generally more than 3 mm). The bracts and bracteoles may be either pilose or sericeous on the adaxial surface and are caducous.

The calyces of *Wiborgiella* species are subequally lobed with the upper sinus often deeper than the lateral or lower sinuses and the carinal lobe invariably narrower than the others. The outer surface may be either pubescent or glabrous, while the inner surface of the lobe tips is always minutely pubescent. This feature is present in many of the genera of the Crotalarieae but known to be absent in *Aspalathus*. The calyces are relatively large in *Wiborgiella bowieana* and *W. sessilifolia* (9.0–10.5 mm long) with very long lobes that are between 3.0 and 5.5 mm long and the calyx tubes that are longer than in the other species (always exceeding 4.5 mm).

The standard petal is ovate to widely ovate in most species, except in *Wiborgiella dahlgrenii* where it is obovate to cordate. The apex is shallowly emarginate in the former species, acute in *W. humilis* and obtuse in all the other species. The standard petal is erect in *W. dahlgrenii*, *W. bowieana*, *W. inflata*, *W. mucronata*, *W. sessilifolia* and *W. vlokii*, while it is reflexed in *W. fasciculata*, *W. humilis* and *W. leipoldtiana*. Reflexed standard petals are also present in *Wiborgia* (Dahlgren 1975). The claws are relatively long in *W. bowieana*, *W. fasciculata*, *W. inflata*, *W. leipoldtiana* and *W. vlokii*.

The wing petals of *Wiborgiella* species are oblong in *W. dahlgrenii* and *W. bowieana*, slightly down-curved in the former and longer than the keel petals in both species. In *W. fasciculata*, *W. humilis*, *W. leipoldtiana* and *W. mucronata* they are oblong to slightly elliptic and generally shorter than the keel petals. *Wiborgiella inflata* and *W. vlokii* have wing petals that are oblong and longer than the keel petals, while in *W. sessilifolia* they are obovate, longer than the keel petals and broaden towards the apex. All species have sculpturing on the upper basal parts of their wing petals. In *W. fasciculata*, *W. humilis* and *W. leipoldtiana* the wing petals are broadest near the middle, while in the other species they are broadest near the apex or base. The claws are relatively long in *W. bowieana*, *W. fasciculata*, *W. inflata*, *W. leipoldtiana* and *W. vlokii*.

The keel petals are boat-shaped in some species with the apex slightly upcurved, while they are lunate in the others generally with acute apices. Pockets are present in all species, except *W. inflata* and *W. vlokii*. The apices are acute in *W. dahlgrenii*, *W. bowieana*, *W. inflata*, and *W. vlokii,* sub-acute in *W. fasciculata* and *W. leipoltiana* and obtuse in *W. humilis*, *W. mucronata* and *W. sessilifolia*. The claws are relatively long in *W. bowieana*, *W. fasciculata*, *W. inflata*, *W. leipoldtiana* and *W. vlokii*.

Anther arrangement is an important character that distinguishes *Wiborgiella* from *Lebeckia*, *Calobota* and *Wiborgia* (Chapter 5; Boatwright et al. submitted). The anthers are dimorphic with alternatingly basifixed and dorsifixed anthers as in practically all other genera. However, the size and shape of the carinal anther is critical. Species of *Wiborgiella* have a 4+6 arrangement where the carinal anther resembles the short dorsifixed anthers, as opposed to the 4+1+5 arrangement found in *Calobota* and *Wiborgia* (the carinal anther is intermediate in size and shape between the long basifixed and short dorsifixed anthers) and the 5+5 arrangement of *Lebeckia* (carinal anther resembles the long basifixed anthers).

The pistil is subsessile to stipitate (long-stipitate in *W. humilis*). The ovary may be either linear (*W. fasciculata*, *W. leipoldtiana*, *W. mucronata* and *W. sessilifolia*), ovate (*W. dahlgrenii* and *W. bowieana*) or elliptic (*W. humilis*, *W. inflata* and *W. vlokii*) with from four up to 21 ovules. The style is always glabrous and shorter than the ovary, except in *W. dahlgrenii* and *W. bowieana* where the style exceeds the ovary in length.

The pods of species of *Wiborgiella* are generally inflated or turgid, except in *W. mucronata* and *W. vlokii*. In these two species the pods are linear and laterally compressed. The anatomy of the fruit wall showed that the pods of all species have a thin mesocarp with several layers of schlerenchyma adjacent to the endocarp. Mucilage cells are present in the exocarp of some species. The endocarp is composed of one or rarely two rows of periclinally elongated or round cells (Fig. 7.3). In some species of *Calobota* and *Lebeckia* the endocarp may be composed of several layers of loosely arranged cells that have a spongy macroscopic appearance. This feature is never present in *Wiborgiella*. The pods are few-seeded (one- or two-seeded) in *W. dahlgrenii* and *W. humilis* and many-seeded in the other species.

Seeds of most of the species were not available for study. The seeds of the two short-lived fire-weeds *W. inflata* and *W. vlokii* are black mottled with white and have a rugose surface. These are similar to those of two *Lebeckia* species that are also short-lived fire-weeds, namely *L. uniflora* and *L. wrightii*. In these two species the seeds are also black mottled with white and have rugose surfaces (Le Roux and Van Wyk 2009). As these short-lived species occur in recently burnt vegetation, the black colour could serve to camouflage the seeds as there would be no undergrowth to cover them. The seeds of *W. leipoldtiana* are light pink with a smooth surface, while those of *W. humilis* are light brown or light orange and mottled with brown with a rugose surface. It would be interesting to obtain seeds of all species to ascertain whether a smooth surface is more common than a rugose surface and to assess the colour variation in the genus.

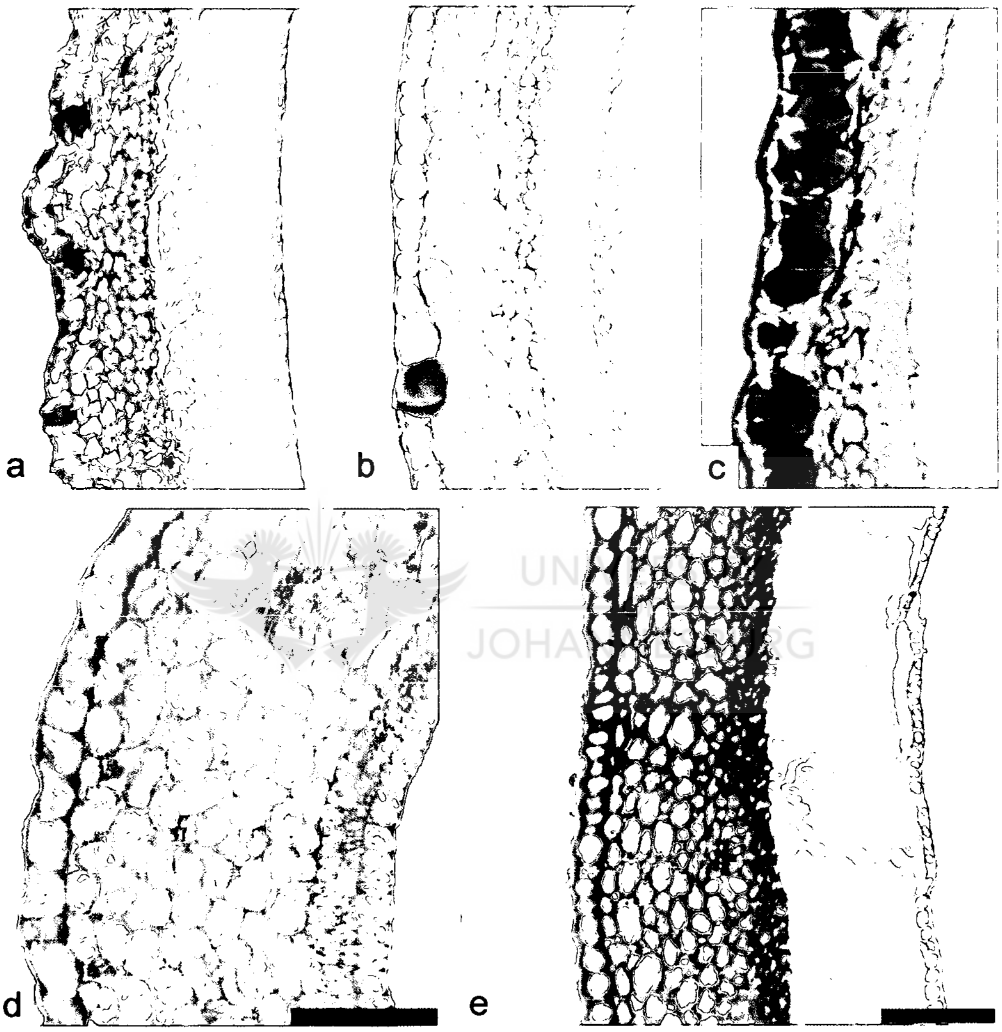

FIG 7.3 Transverse sections through the fruit walls of *Wiborgiella* species. (a) *W. sessilifolia*; (b) *W. inflata*; (c) *W. vlokii*; (d) *W. humilis* (young fruit); (e) *W. bowieana*. Voucher specimens: (a) *Taylor 4329* (PRE); (b) *Johns 162* (JRAU); (c) *Vlok 2045* (PRE); (d) *Boatwright et al. 212* (JRAU); (e) *Streicher s.n. sub Schutte 831* (JRAU). Scale bars: (a–c, e) 0.2 mm; (d) 0.1 mm.

***9.2.3 Phylogenetic relationships***—MORPHOLOGICAL DATA—Infrageneric relationships within *Wiborgiella* were assessed using 13 morphological characters scored for 14 taxa of the "Cape group" of the Crotalarieae (Table 7.1). *Calobota* was used as outgroup and *Wiborgia* and *Aspalathus* included as ingroups in the analyses based on the close relationship between these genera and *Wiborgiella* indicated by the molecular study in Chapter 3 (see also Boatwright et al. 2008a). All 13 included characters were parsimony informative and the analysis resulted in three equally parsimonious trees with a length of 20 steps, a CI of 0.65 and a RI of 0.82 (Fig. 7.4). Dahlgren (1975) discussed the close similarity of the shrubby species of *Wiborgiella* to species of *Wiborgia*. This and the high levels of convergence within the crotalarioid genera (Dahlgren 1970a) complicated the morphological analysis due to the lack of apomorphic states for genera and the extreme overlap of morphological characters. As a result a combination of characters is needed to define genera.

The monophyly of *Wiborgiella* is supported by the anther arrangement of 4+6, but the group lacks bootstrap support. *Wiborgiella bowieana* and *W. sessilifolia* are supported as sister taxa (61 BP) by the long calyx tube and long wing petals (shared with *W. dahlgrenii*) found in both species. The shrubby species of *Wiborgiella* form a clade which is supported by the presence of rigid branches and tuberculate petioles in these species. These characters are shared by *Wiborgia tetraptera* and other species of *Wiborgia*. The short-lived species of the genus, *Wiborgiella inflata* and *W. vlokii*, are sister based on their life history and long wing petals (70 BP). The position of *Wiborgiella mucronata* is unresolved due to the fact that it shares some characters with the shrubby species of the genus (e.g. brown stems), and others with the short-lived species (e.g. petioles that are neither tuberculate nor persistent). The close relationship between *Wiborgiella fasciculata*, *W. humilis* and *W. leipoldtiana* is supported (65 BP) by the wing petals that are broadest near the middle and the reflexed standard petals that are, however, also found in *Wiborgia*. *Aspalathus* and *Wiborgia* are sister genera based on the few ovules in the ovary (also in *Wiborgiella humilis*). The monophyly of *Aspalathus* is supported by the sessile leaves and glabrous inner surface of the calyx lobes (84 BP) and that of *Wiborgia* is supported by the few-seeded samaras and wings on the fruit (70 BP).

MOLECULAR DATA—*Wiborgiella* is closely related to *Wiborgia* and *Aspalathus* based on combined *rbcL*/ITS/morphological data presented in Chapter 3 (Boatwright et al. 2008a). Although the monophyly of the genus lacks support in these analyses due to the unresolved position of *Wiborgiella mucronata* and low sequence divergence within the "Cape group" (see Fig. 3.4), it is supported by a combination of morphological and anatomical characters that is unique to this group and not found in the other genera of the Crotalarieae. The close relationship between the shrubby species of *Wiborgiella* is strongly supported by these data.

TABLE 7.1 Characters and character polarisations in *Aspalathus*, *Calobota*, *Wiborgia* and *Wiborgiella.* Characters and character states are explained at the end of the table.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Wiborgiella bowieana* | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *W. dahlgrenii* | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *W. fasciculata* | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *W. humilis* | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 0 |
| *W. inflata* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *W. leipoldtiana* | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 0 | 0 |
| *W. mucronata* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| *W. sessilifolia* | 0 | 1 | 1 | 1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *W. vlokii* | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 |
| *Wiborgia fusca* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 0 |
| *W. tetraptera* | 0 | 1 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 |
| *Aspalathus cordata* | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| *A. nivea* | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| *Calobota cytisoides* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

**(1) Persistence:** perennial = 0, short-lived fireweeds = 1. **(2) Branches:** not rigid = 0, rigid = 1. **(3) Petiole:** not tuberculate = 0, tuberculate = 1. **(4) Petiole:** present = 0, absent = 1. **(5) Calyx tube:** short = 0, long = 1. **(6) Inner surface of calyx lobes:** pubescent = 0, glabrous = 1. **(7) Standard petal:** upright = 0, reflexed = 1. **(8) Wing petals:** shorter than keel = 0, longer than keel = 1. **(9) Wing petals:** broadest near base or apex = 0, broadest near middle = 1. **(10) Anther arrangement:** 4+5+1 = 0, 4+6 = 1. **(11) Ovules:** many = 0, few = 1. **(12) Fruit type:** legume = 0, samara = 1. **(13) Fruit:** without wings = 0, winged = 1.

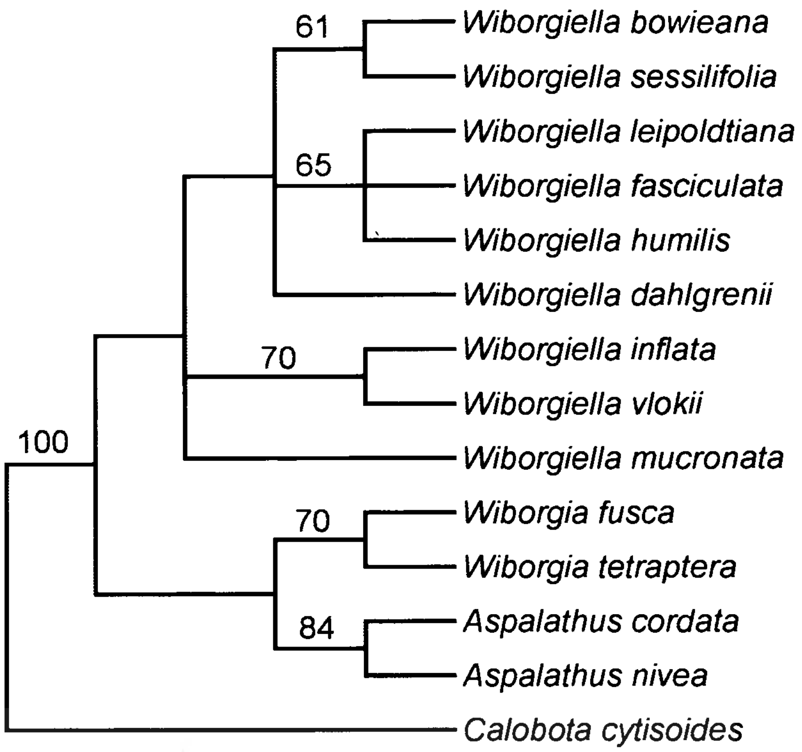

FIG. 7.4. Strict consensus of three trees produced by the analysis of 13 morphological characters for *Aspalathus*, *Wiborgia* and *Wiborgiella*. Values above the branches are bootstrap percentages above 50%.

## 7.3 TAXONOMIC TREATMENT

WIBORGIELLA Boatwr. and B.-E.van Wyk, gen. nov. (S. Afr. J. Bot.: submitted. 2008),

*Wiborgiae Thunb. similis sed fructibus oblongis non alatis valde inflatis, anthera carinali breve (aliis in eodem flore brevibus dorsifixis simile) differt; Calobotae Eckl. and Zeyh. similis sed petalis ubique glabris, antheris ut supra et foliis dorsiventralibus differt; Lebeckiae Thunb. sensu stricto similis sed foliolis planis* *non acicularibus valde differt.*—TYPE species: *Wiborgiella leipoldtiana* (R.Dahlgren ex Schltr.) Boatwr. and B.-E.van Wyk.

*Lebeckia* section *Viborgioides* Benth. in Hook. Lond. J. Bot. 3: 361. 1844. — LECTOTYPE species (designated here): *Wiborgiella fasciculata* (Benth.) Boatwr. and B.-E.van Wyk. [Note: As there is no indication as to which species would be a better choice of lectotype, we here choose the first listed species.]

[Note: the new genus proposed here conforms to Bentham's (1844) concept of *Lebeckia* section *Viborgioides*, a taxon for which no name is available at generic level. The name *Wiborgiella* reflects the vegetative similarity and close relation to the genus *Wiborgia.*]

Rigid, resprouting, woody shrubs (rarely a lignotuberous shrublet or short-lived fireweed). Branches thick and woody (except in two short-lived species); young branches brown, covered with bark (rarely green in two species), pubescent. Stipules absent. Leaves digitately trifoliolate; petioles shorter than leaflets, pubescent, usually persistent and becoming woody after leaflets are shed; leaflets linear to widely oblanceolate or obovate, pubescent. Inflorescence terminal, multi-flowered racemes or rarely single-flowered. Pedicel pubescent. Bracts linear to lanceolate or elliptic, at least slightly pubescent, caducous. Bracteoles linear to lanceolate, at least slightly pubescent, caducous. Corolla yellow, older petals fading purple or orange, glabrous. Calyx subequally lobed, upper sinus often deeper than the lateral or lower sinuses, carinal lobe narrower than the others, pubescent or glabrous. Standard ovate to widely ovate, obovate or cordate. Wing petals oblong, ovate or rarely obovate, shorter, as long as or longer than the keel petals, glabrous; apex obtuse. Keel petals boat-shaped or lunate, pockets present or absent, glabrous; apex obtuse, acute or sub-acute. Anthers dimorphic, four long, basifixed anthers alternating with five ovate, dorsifixed anthers, carinal anther resembling the ovate, dorsifixed anthers (4+6 configuration). Pistil subsessile to long-stipitate, ovary linear to slightly elliptic, with 4 to many ovules, glabrous, very rarely slightly pubescent on the upper basal parts; style shorter or longer than the ovary, curved upwards, glabrous. Pods inflated or turgid, rarely laterally compressed in *W. mucronata* and *W. vlokii*, linear to oblong to oblanceolate or lanceolate or elliptic, few- to many-seeded, glabrous, dehiscent (rarely indehiscent). Seeds reniform or suborbicular, light pink (*W. leipoldtiana*), light brown or orange mottled with brown (*W. humilis*), or black with white or light brown spots (*W. inflata* and *W. vlokii*), surface smooth or rugose (seeds of *W. bowieana*, *W. fasciculata*, *W. mucronata* and *W. sessilifolia* not seen).

***Diagnostic characters*****—**Bark formation is early and the young twigs are brown and covered with bark as opposed to the green twigs of *Calobota* (the short-lived *Wiborgiella inflata* and *W. vlokii* have green stems due to their herbaceous habit). The genus is similar to *Wiborgia*, but differs in the oblong, wingless, much inflated fruit (ovate to orbicular, markedly winged and laterally compressed in *Wiborgia*). It also differs in the carinal anther that resembles the short, dorsifixed anthers (carinal anther intermediate in both *Wiborgia* and *Calobota*). It further differs from *Calobota* in the totally glabrous petals (in *Calobota*, at least the standard petal has a few apical hairs) and in the dorsiventral leaves (isobilateral in *Calobota*). It differs markedly from *Lebeckia* sensu stricto in the flat leaflets (invariably acicular in *Lebeckia*).

***Notes on distribution***—The genus is endemic to the Cape region of South Africa.

## KEY TO THE SPECIES OF WIBORGIELLA

1. Branches green, short-lived fireweeds..........................................................2

    2. Pods inflated, leaves lanceolate.......................................... ***W. inflata***

    2. Pods laterally compressed, leaves oblanceolate........................ ***W. vlokii***

1. Branches brown, long-lived shrubs or resprouting shrublets..............................3

    3. Calyx 9.0–10.5 mm long, calyx lobes 3.0–5.5 mm long...........................4

        4. Inflorescences with 8 to 15 flowers, calyx lobes 4.0–5.5 mm long, claws of all petals relatively short, ovary linear, style shorter than ovary............................................................... ***W sessilifolia***

        4. Inflorescences with(1–) 2 to 5 flowers, calyx lobes 3.0–3.5 mm long, claws of all petals relatively long, ovary elliptic, style longer than ovary.............................................................. ***W. bowieana***

    3. Calyx <9 mm long, calyx lobes ≤3 mm long............................................5

5. Wings longer than the keel and down-curved, pods narrowly ovate, flowers pink, plants restricted to Saldanha Bay and Hopefield................................ ***W. dahlgrenii***

5. Wings shorter than the keel and straight, pods oblanceolate to elliptic, linear or obovate, flowers yellow, plants occurring in the Eastern Cape, Niewoudtville, Gifberg, Albertinia or from Sutherland north to Vioolsdrif..................................................6

6. Pods laterally compressed, petioles not tuberculate or persistent...... ..........................................................................***W. mucronata***

6. Pods inflated, petioles tuberculate and persistent...........................7

7. Leaves linear to spathulate, pods long-stipitate, pods 4–6 mm long...........................................................................***W. humilis***

7. Leaves linear-oblanceolate to ovate, pods short stipitate, pods more than 14 mm long.....................................................................8

8. Pods linear, flowers 9–10 mm long, Albertinia............... ........................................................***W. fasciculata***

8. Pods oblanceolate to elliptic, flowers 10–13 mm long, from Sutherland area northwards to Vioolsdrif (Nababeepberg)..................................***W. leipoldtiana***

1. WIBORGIELLA BOWIEANA (Benth.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia bowieana* Benth. in Hook. Lond J. Bot. 3: 362–363. 1844; Walp., Rep. Bot. Syst.: 454. 1845; Harv. in Harv. and Sond., Fl. Cap. 2: 89. 1862; R.Dahlgren, Op. Bot. 38: 79. 1975; Bond and Goldblatt, J. S. Afr. Bot. 13: 289. 1984; Goldblatt and Manning, Cape Pl.: 493. 2000.—TYPE: SOUTH AFRICA, 'Cape' [grid unknown], *Bowie s.n.* (lectotype: K!, designated by Dahlgren [1975]; isolectotype: BM!).

Erect, rigid, woody, single-stemmed shrub up to 1.5 m in height. Branches greyish-brown; young branches sericeous; older branches covered in longitudinally splitting brown-grey bark. Leaves digitately trifoliolate; petiole 1–2 mm long, tuberculate, becoming hard and persistent on older branches after leaflets have been shed; leaflets oblanceolate to spathulate, sericeous on both surfaces, subsessile, terminal leaflet 4–6 mm long, 1–2 mm wide, lateral leaflets 3–5 mm long, 1–2 mm wide; apex acute to apiculate or rarely retuse; base cuneate. Inflorescence 18–35 mm long, with flowers solitary or 2 to 5 per raceme; pedicel 1.0–1.5 mm long; bract 4–5 mm long, linear to lanceolate, relatively long, sericeous on adaxial surface; bracteoles 3–5 mm long, linear to lanceolate, relatively long, sericeous on adaxial surface. Flowers 10–15 mm long, yellow with brown markings on abaxial surface of standard (according to label information). Calyx 9.0–10.5 mm long, glabrous or rarely sparsely pilose; tube relatively long, 5.5–7.0 mm long; lobes 3.0–3.5 mm long, deltoid. Standard 16.0–16.5 mm long, glabrous, very rarely sparsely pilose along the dorsal midrib; claw linear, relatively long, 6.0–6.5 mm long; lamina ovate, 10.0–10.5 mm long, 7.5–8.0 mm wide; apex obtuse. Wings 15–16 mm long, glabrous; claw relatively long, 6–7 mm long; lamina oblong, 9–10 mm long, 4.0–4.5 mm wide, longer than keel, with 8–11 rows of sculpturing. Keel 14–15 mm long, glabrous; claw relatively long, 6–7 mm long, lamina lunate, 6.5–8.0 mm long, 4.0–4.5 mm wide; apex acute; pocket present. Pistil subsessile, glabrous; ovary elliptic, 5.5–6.5 mm long, 1.3–1.5 mm wide with ±8 ovules; style longer than ovary, 9–10 mm long. Pods ovate to lanceolate, dark brown, rugulose, strongly inflated, subsessile, 15–20 mm long, 5–7 mm wide, up to ?5 seeded, dehiscent. Seeds not seen (Fig. 7.5). Flowering time: May to July.

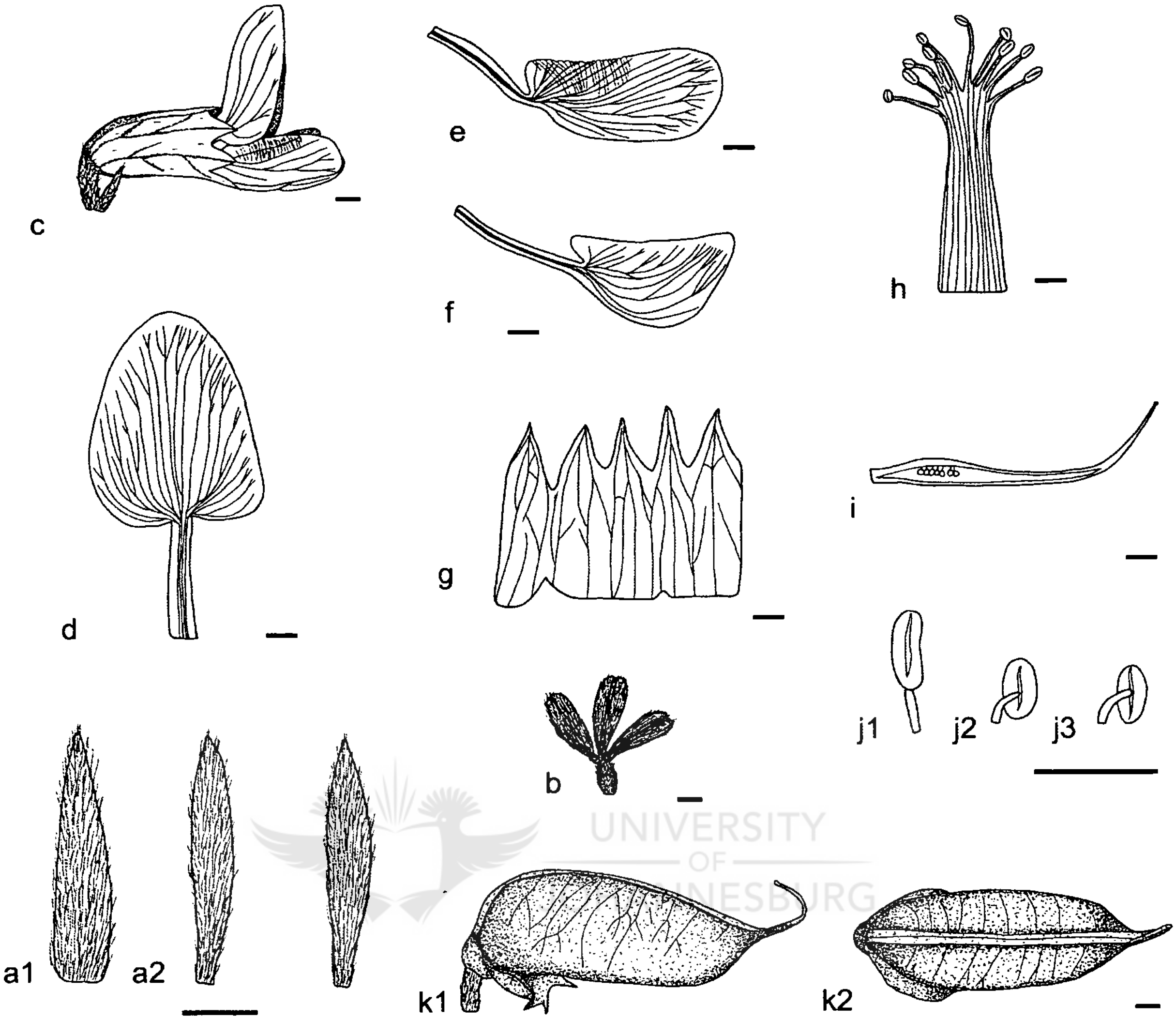

FIG. 7.5 Morphology of *Wiborgiella bowieana*: (a1) bract; (a2) bracteoles; (b) leaf in abaxial view; (c) flower in lateral view; (d) standard petal; (e) wing petal; (f) keel petal; (g) outer surface of the calyx (upper lobes to the left); (h) androecium; (i) pistil; (j1) long, basifixed anther; (j2) carinal anther resembling the short, dorsifixed anthers; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a1–j3) *Streicher s.n.* (JRAU); (k1–k2) *Van Wyk 2106* (JRAU). Scale bars: 1 mm.

***Diagnostic characters***—*Wiborgiella bowieana* is similar to *W. sessilifolia*, but differs in the petiolate leaves on older branches, narrower leaflets, few-flowered inflorescences, largely glabrous calyx, shorter calyx lobes, long petal claws and the elliptic ovary with the style longer than the ovary (in *W. sessilifolia* the leaves on the older branches are sessile, the leaflets broader, the inflorescences more densely flowered, the calyx pilose with longer lobes, the petals claws relatively short and the linear ovary is longer than the style). It is also similar to *W. dahlgrenii*, but differs from this species in the larger leaflets, long calyx tube and calyx lobes, larger flowers, long petal claws and larger pods (in *W. dahlgrenii* the leaflets are smaller, the calyx tube and lobes shorter, the petal claws shorter and the flowers and pods smaller than in *W. bowieana*).

***Distribution and habitat***—*Wiborgiella bowieana* is a rare and highly restricted species that occurs on rocky soils from Worcester in the west to around Bredasdorp in the east (Fig. 7.6).

***Note***—Raimondo et al. (in press) assessed the conservation status of this species as critically endangered (CR A2bc; C2a(i); D). They speculate that the habitat of this species has been transformed for wheat farming over the last few decades and as few as 50 individuals may be in existence today. Overgrazing leads to ongoing degradation of its habitat.

***Additional specimens examined***

**–3319** (Worcester): Robertson (–DD), *Schmidt 30* (PRE).

**–3321** (Ladismith): Attaquaskloof (–DD), *Zeyher 2345* (K, NBG, S).

**–3420** (Bredasdorp): Uitvlug Farm, north of Bredasdorp (–AB), *Streicher s.n.* (JRAU 2 sheets), *Streicher s.n. sub Schutte 831* (JRAU), *Van Wyk 2106* (JRAU).

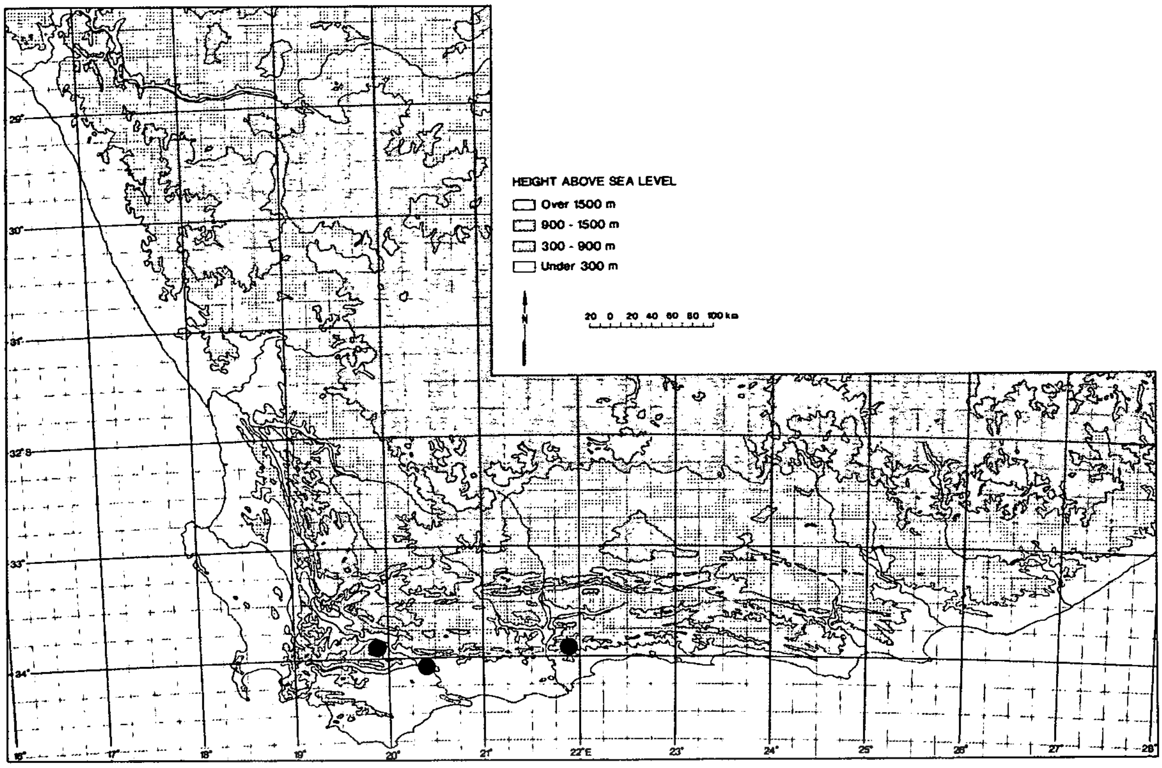

FIG. 7.6 Known geographical distribution of *Wiborgiella bowieana*.

2. **Wiborgiella dahlgrenii** Boatwr. and B.-E.van Wyk, sp. nov., similar to *W. bowieana* (Benth.) Boatwr. and B.-E.van Wyk but differs in the smaller leaves, shorter bracts and bracteoles, smaller flowers, relatively short claws, obovate to cordate standard petal lamina, down-curved wing petals, pilose calyx and shorter, few-seeded pods. It is also similar to *W. leipoldtiana* (Schltr. ex R.Dahlgren) Boatwr. and B.-E.van Wyk, but differs in the smaller flowers, obovate to cordate standard petal lamina, long, down-curved wing petals, style that is longer than the ovary and narrowly ovate, few-seeded pods (to be translated into Latin).—TYPE: SOUTH AFRICA, Langebaan, Abbus Farm [3318 AA], *Baker 10407* (holotype: NBG!).

Rigid, woody, multi-stemmed shrub of unknown height. Branches brown; young branches sericeous; older branches covered in longitudinally splitting light brown bark. Leaves digitately trifoliolate; petiole 2–8 mm long, somewhat tuberculate, not persistent although base or tubercle persistent on older branches after leaflets have been shed; leaflets obovate to oblanceolate or rarely elliptic, sericeous to sparsely sericeous on both surfaces, subsessile, terminal leaflet 3.5–7.0 mm long, 1.5–4.0 mm wide, lateral leaflets 3.0–5.5 mm long, 1.5–3.0 mm wide; apex retuse to obcordate or rarely acute; base cuneate. Inflorescence 22–40 mm long, with 4 to 8 flowers; pedicel 1 mm long; bract 1.5–2.0 mm long, linear to lanceolate, sericeous on adaxial surface; bracteoles 1.0–1.5 mm long, linear to lanceolate, sericeous on adaxial surface. Flowers 7–9 mm long, light pink (according to label information) or possibly yellow with older petals fading pink. Calyx 4.5–5.0 mm long, pilose; tube 3.0–3.5 mm long; lobes 1.5–2.0 mm long, deltoid. Standard 8.0–9.5 mm long, rarely sparsely pilose along dorsal midrib; claw linear, 3–4 mm long; lamina obovate to cordate, 5.0–5.5 mm long, 4.5–5.0 mm wide; apex shallowly emarginate. Wings 8.5–9.0 mm long, glabrous; claw 2.5–3.0 mm long; lamina oblong and somewhat down-curved, 5.5–6.5 mm long, 2.0–2.5 mm wide, longer than keel, with 4 rows of sculpturing. Keel 6–7 mm long, glabrous; claw 2.0–2.5 mm long; lamina lunate, 3.5–4.0 mm long, 2.0–2.5 mm wide; slight pocket present; apex acute. Pistil subsessile to shortly stipitate; ovary ovate, 3.0–3.5 mm long, 1.0–1.2 mm wide with 4 to 5 ovules; style as long as or longer than ovary, 3.5–4.0 mm long. Pods narrowly ovate, rugulose, inflated, subsessile to shortly stipitate, dark brown, 10–12 mm long, 3–5 mm wide, ±2-seeded, dehiscent. Seeds not seen (Fig. 7.7). Flowering time: There were two specimens of this species available for study. The single flowering specimen was collected in August, suggesting that the species flowers in early spring. The fruiting specimen was collected in September.

***Diagnostic characters***—This species is similar to *Wiborgiella bowieana* but differs in the smaller leaves, shorter bracts and bracteoles, smaller flowers, the pink flower colour, relatively short claws, obovate to cordate standard petal lamina, down-curved wing petals, pilose calyx and shorter, few-seeded pods. It is also similar to *W. leipoldtiana*, but differs in the smaller, pink flowers, obovate to cordate standard petal lamina, long, down-curved wing petals, style that is longer than the ovary and narrowly ovate, few-seeded pods. In both *W. bowieana* and *W. leipoldtiana* the flowers are yellow and larger than in *W. dahlgrenii*, the wing petals not down-curved and the standard petals ovate. In *W. bowieana* the calyx is large and pilose and the pods larger than in *W. dahlgrenii*. The pods are many seeded in *W. leipoldtiana* and the style shorter than the ovary.

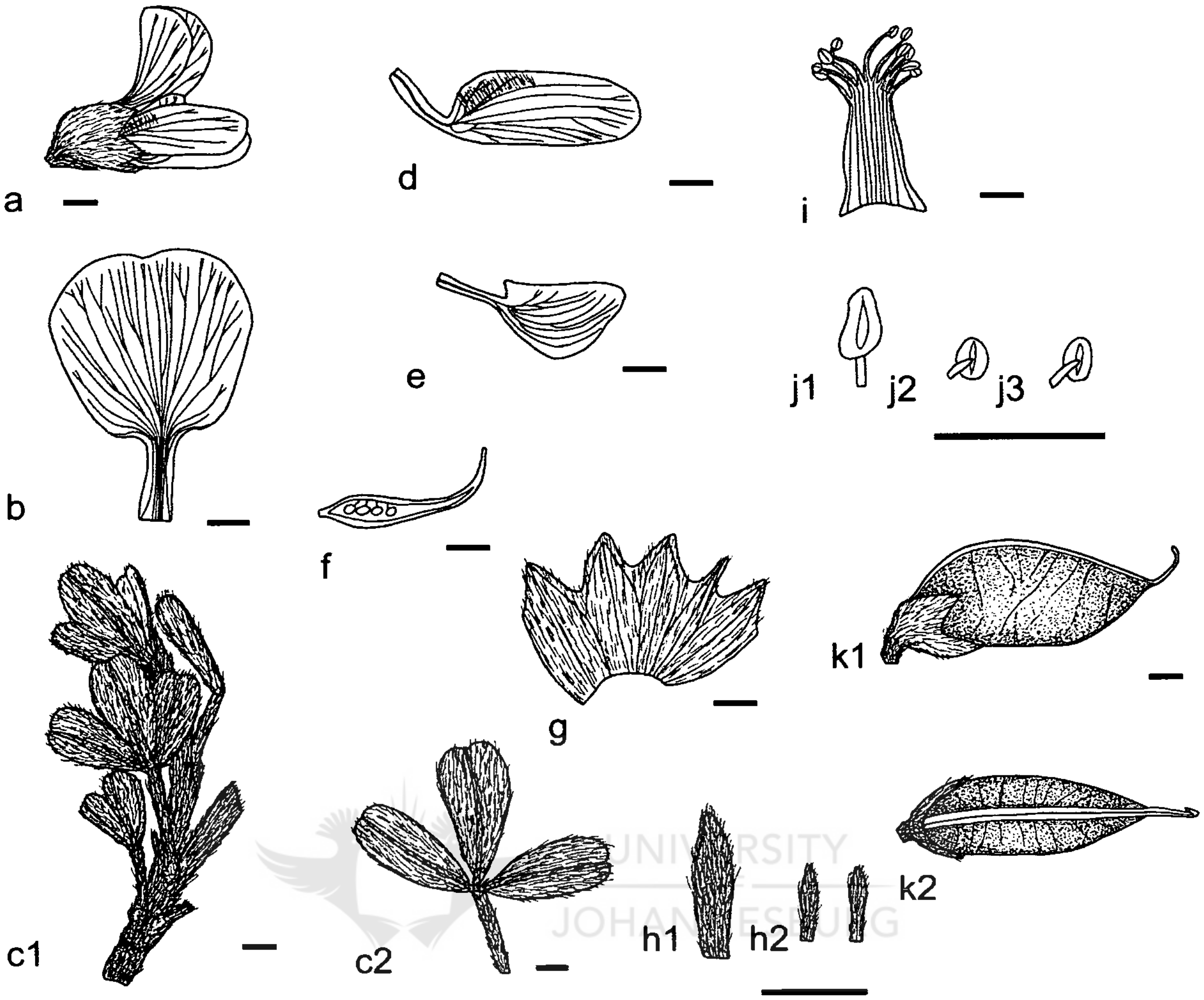

FIG. 7.7 Morphology of *Wiborgiella dahlgrenii*: (a) flower in lateral view; (b) standard petal; (c1, c2) leaves in abaxial view; (d) wing petal; (e) keel petal; (f) pistil; (g) outer surface of the calyx (upper lobes to the left); (h1) bract; (h2) bracteoles; (i) androecium; (j1) long, basifixed anther; (j2) carinal anther resembling the short, dorsifixed anthers; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a–c1, d–j3) *Barker 10407* (NBG); (c1, k1–k2) *Bolus 12915* (BOL). Scale bars: 1 mm.

***Distribution and habitat***—This is a very rare species which is poorly collected and known from only two collections (Fig. 7.8). It occurs in Strandveld vegetation around Saldanha Bay and Hopefield and has been recorded on sandy soil at an altitude of 15 m.

***Note***—This species is in desperate need of conservation attention. Collection attempts have been unsuccessful and it is possible that the plant is either very highly localised or extinct due to severe habitat disturbance. It is known only from the Saldanha Bay and Langebaan areas where the natural vegetation is severely fragmented.

***Additional specimens examined***

**–3317** (Saldanha): near Hoetje's Bay, Saldanha Bay (–BB), *Bolus 12915* (BOL) (fruiting material).

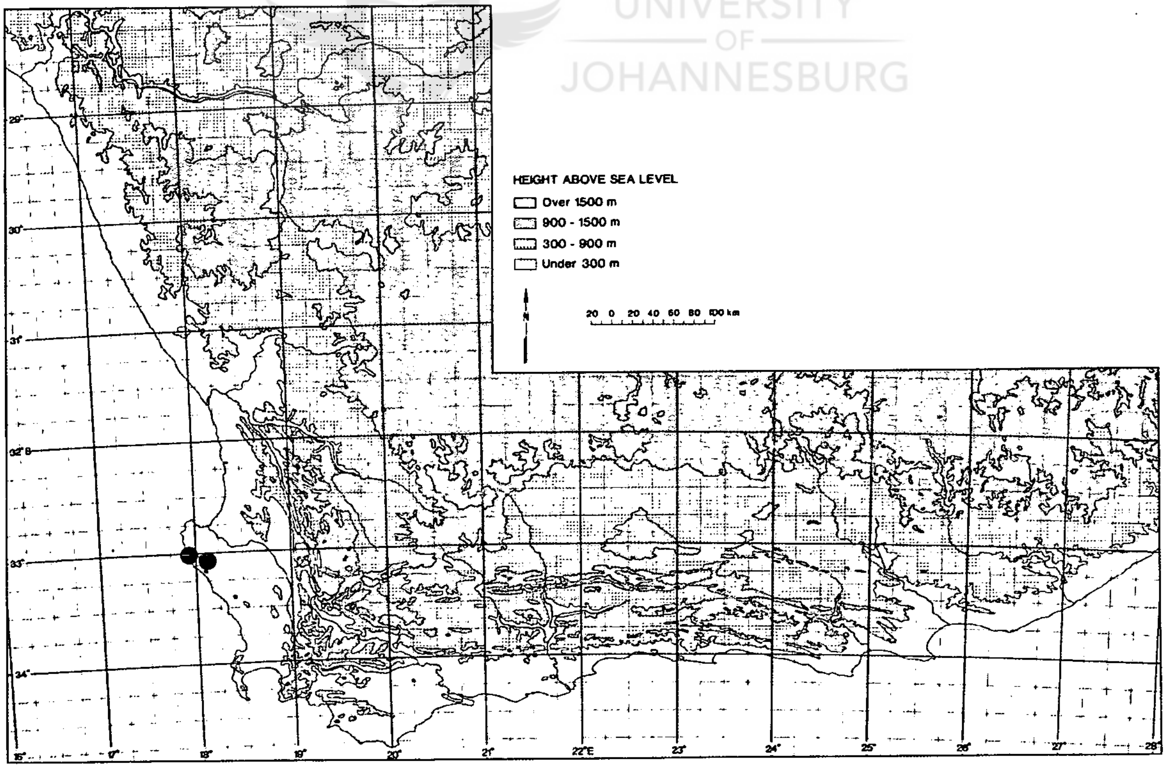

FIG. 7.8. Known geographical distribution of *Wiborgiella dahlgrenii.*

3. WIBORGIELLA FASCICULATA (Benth.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia fasciculata* Benth. in Hook. Lond. J. Bot. 3: 361. 1844; Walp., Rep. Bot. Syst.: 453. 1845; R.Dahlgren, Op. Bot. 38: 74. 1975; Bond and Goldblatt, J. S. Bot. 13: 289. 1984; Goldblatt and Manning, Cape Pl.: 493. 2000.—TYPE: SOUTH AFRICA, 'Cape' [grid unknown], *Bowie s.n.* (lectotype: K!, designated by Dahlgren [1975]; isolectotype: BM!).

Small, erect, rigid, multi-stemmed shrublet up to ?0.5 m in height. Branches greyish-brown; young branches densely pilose; older branches covered in longitudinally splitting brown-grey bark. Leaves digitately trifoliolate; petiole 0.5–1.0 mm long, tuberculate, becoming hard and persistent on older branches after leaflets have been shed; leaflets linear-oblanceolate to oblanceolate, pilose on both surfaces, subsessile, terminal leaflet 3–5 mm long, 1.0–1.5 mm wide, lateral leaflets 2–3 mm long, 1.0–1.5 mm wide; apex truncate or acute; base cuneate. Inflorescence 28–30 mm long, with 5 to 15 flowers; pedicel 1.0–1.5 mm long; bract 1.0–1.4 mm long, lanceolate to ovate, pilose along margins and adaxial surface; bracteoles 1.0–1.4 mm long, elliptic to lanceolate, pilose along margins and adaxial surface. Flowers 9–10 mm long, yellow. Calyx 4.0–4.5 mm long, glabrous; tube 2.5–3.0 mm long; lobes 1.0–1.5 mm long, deltoid. Standard 8.5–10.0 mm long, glabrous; claw linear, 3.0–3.5 mm long; lamina ovate, 5.5–6.5 mm long, 4.0–4.5 mm wide; apex obtuse. Wings 8.0–8.5 mm long, glabrous; claw 3.0–3.5 mm long; lamina oblong, 4.5–5.0 mm long, 2.0–2.5 mm, shorter than keel, wide with 6–7 rows of sculpturing. Keel 10.5–11.0 mm long, glabrous; claw 3.5–4.0 mm long; lamina boat-shaped, 6.5–7.5 mm long, 3.0–3.5 mm wide; apex sub-acute, pocket present. Pistil subsessile, glabrous; ovary linear, 6.0–6.2 mm long, 0.7 mm wide with 7 to 9 ovules; style shorter than ovary, ±4.3 mm long. Pods linear, rugulose, inflated, subsessile, 14–17 mm long, 3–4 mm wide, number of seeds unknown, dark brown to black, dehiscent. Seeds not seen (Fig. 7.9). Flowering time: September (spring).

***Diagnostic characters***—*Wiborgiella fasciculata* is similar to *Wiborgiella leipoldtiana*, but differs in the smaller, pilose leaves, smaller flowers and shorter, linear pods. In *W. leipoldtiana* the leaves and flowers are much larger and the pods oblanceolate to elliptic.

***Distribution and habitat***—*Wiborgiella fasciculata* is a very rare and localised species that occurs in the Riversdale area around Albertinia (Fig. 7.10).

***Note***—Raimondo et al. (in press) assessed the status of *Wiborgiella fasciculata* as critically endangered (CR B1ab(iii)+2ab(iii); D). The populations of this species are severely fragmented and declining due to the exclusion of fire. A total of about 13 plants are still in existence.

***Additional specimens examined***

**–3421** (Riversdale): Onverwacht, Albertinia, Riversdale division (–BA), *Muir 859* (BOL, PRE), *Muir 4775* (NBG).

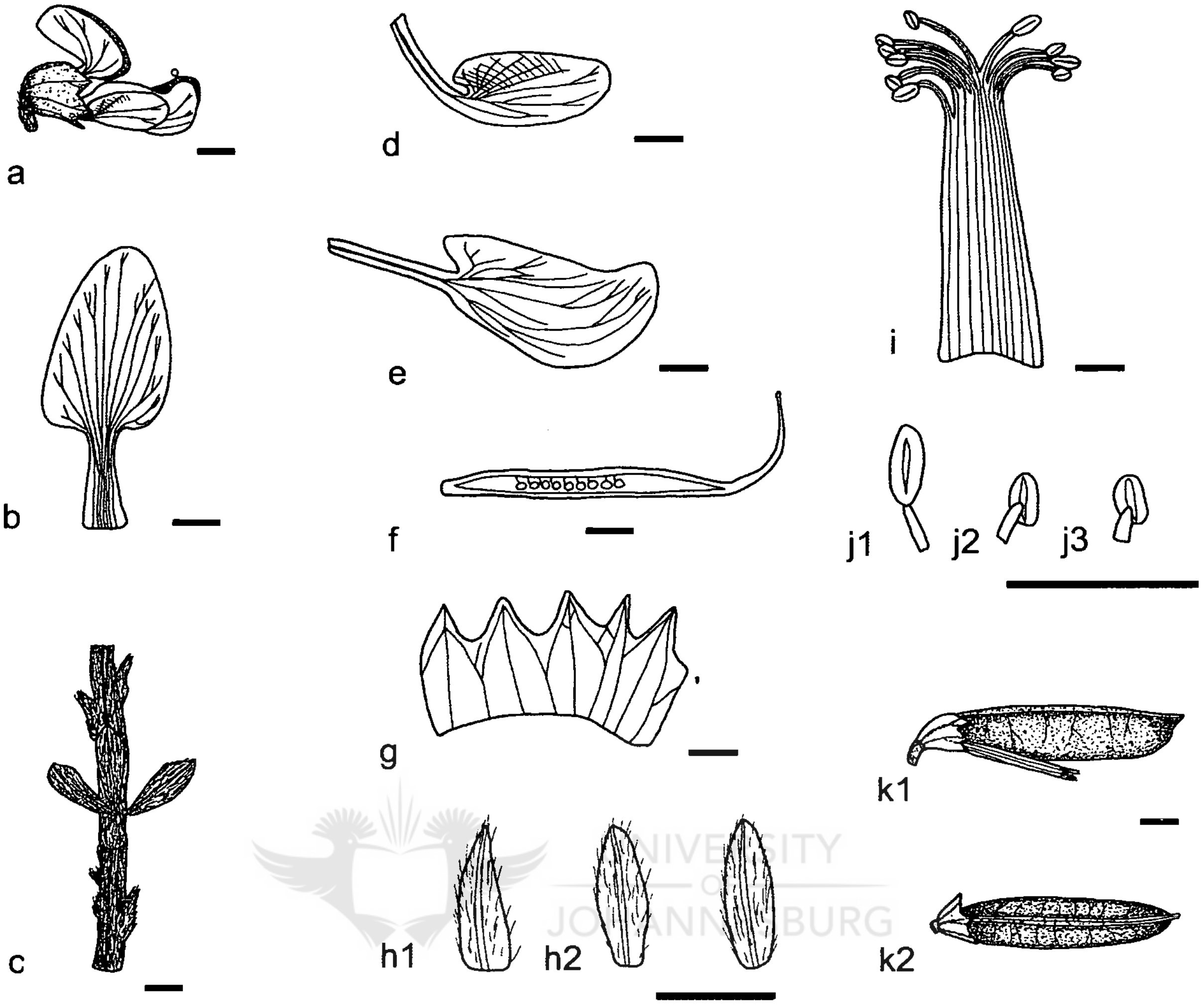

FIG. 7.9 Morphology of *Wiborgiella fasciculata*: (a) flower in lateral view; (b) standard petal; (c) leaf in abaxial view; (d) wing petal; (e) keel petal; (f) pistil; (g) outer surface of the calyx (upper lobes to the left); (h1) bract; (h2) bracteoles; (i) androecium; (j1) long, basifixed anther; (j2) carinal anther resembling the short, dorsifixed anthers; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a–j3) *Muir 859* (NBG); (k1–k2) *Bowie s.n.* (BM). Scale bars: 1 mm.

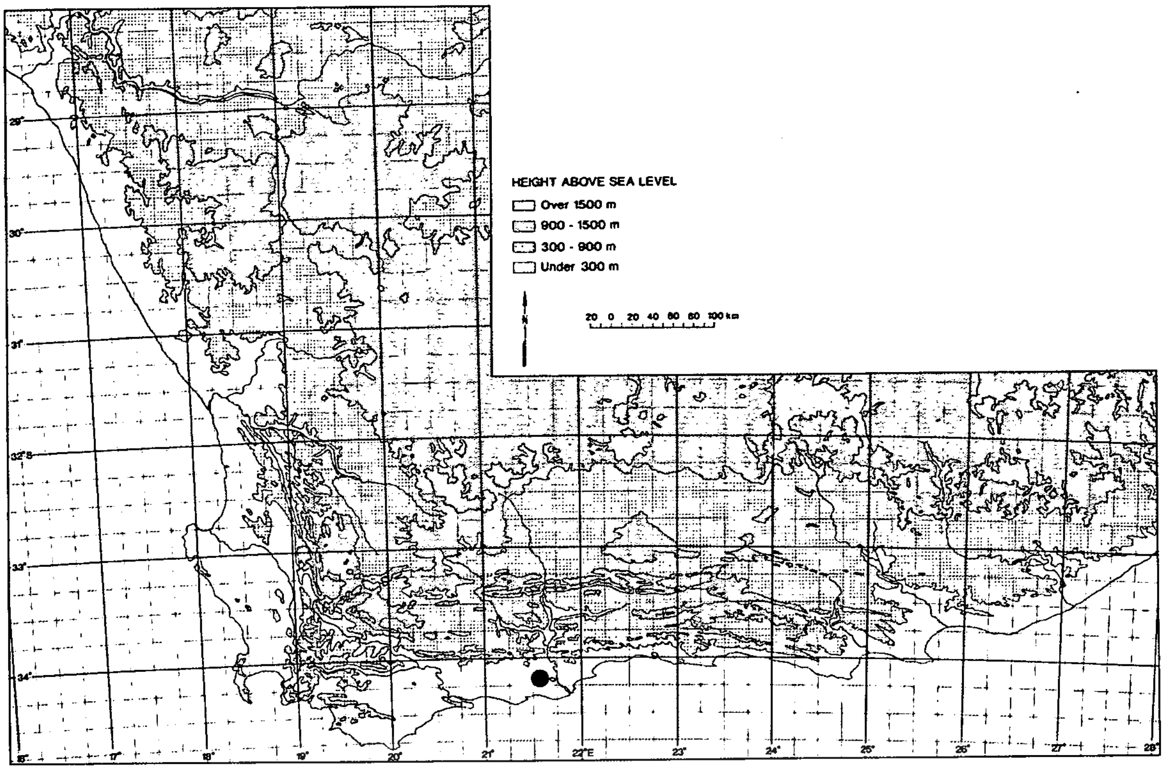

FIG. 7.10 Known geographical distribution of *Wiborgiella fasciculata*.

4. WIBORGIELLA HUMILIS (Thunb.) Boatwr. and B.-E.van Wyk in S. Afr. J. Bot.: submitted. 2008. *Lebeckia humilis* Thunb., Nov. Gen.: 142. 1800., Fl. Cap.: 562. 1823; Harv. in Harv. and Sond., Fl. Cap. 2: 89. 1862. *Wiborgia humilis* (Thunb.) R.Dahlgren, Op. Bot. 38: 31. 1975.—TYPE: SOUTH AFRICA, e Cap. B. Spei [grid unknown], *Thunberg s.n. sub THUNB-UPS 16416* (lectotype: UPS!, designated by Dahlgren [1975]).

*Wiborgia apterophora* R.Dahlgren, Bot. Notiser 123: 112. 1970.—TYPE: SOUTH AFRICA, Gifberg [3118 DC], sand at edge of lands, *Esterhuysen 22042* (holotype: BOL; isotype: K!).

Small, erect or decumbent, multi-stemmed shrublet up to 0.5 m in height. Branches brown; young branches densely pilose; older branches covered in longitudinally splitting brown bark. Leaves digitately trifoliolate; petiole 0.5 or less–1.5 mm long, tuberculate, becoming hard and persistent on older branches after leaflets have been shed; leaflets linear-spathulate, pilose on abaxial surface, adaxial surface glabrous, subsessile, terminal leaflet 5–12 mm long, 0.8–1.2 mm wide, lateral leaflets 5–10 mm long, 0.8–1.0 mm wide; apex truncate to retuse or acute, base cuneate. Inflorescence (32–) 35–70 mm long, with (5–) 8 to ±13 flowers; pedicel 1.0–2.5 mm long; bract 1.0–1.5 mm long, lanceolate to linear, pilose on adaxial surface; bracteoles 0.7–1.0 mm long, lanceolate to linear, pilose on adaxial surface. Flowers 6.5–10.0 mm long, yellow. Calyx 2.5–4.0 mm long, glabrescent; tube 2.0–3.0 mm long; lobes 0.8–1.1 mm long, deltoid. Standard 8.0–8.5 mm long, glabrous; claw linear, 2.0–2.5 mm long; lamina ovate, 5.0–6.0 mm long, 3.5–4.0 mm wide, apex acute. Wings 7.5–8.5 mm long, glabrous; claw 2.5–3.0 mm long; lamina oblong, 4.5–6.0 mm long, 2.5–3.5 mm wide, shorter than or as long as keel, with 6–7 rows of sculpturing. Keel 8.0–9.0 mm long, glabrous; claw 2.5–3.0 mm long; lamina boat-shaped, 6.0–6.5 mm long, 3.0–4.0 mm wide, apex obtuse; pocket present. Pistil long-stipitate (stipe 2.5–3.0 mm long), glabrous, sometimes pilose on upper basal parts; ovary elliptic, 5–6 mm long, 0.8–0.9 mm wide with ±5 ovules; style shorter than ovary, 3–4 mm long. Pods elliptic to obovate, rugulose, inflated, long-stipitate, 4–6 mm long, 1.0–1.5 mm wide, ±2-seeded, dehiscent. Seeds reniform, 2.0–2.7 mm long, 1.5–2.3 mm wide, mature seeds light brown or light orange mottled with brown, surface rugose (Fig. 7.11). Flowering time: Spring to summer (September to November).

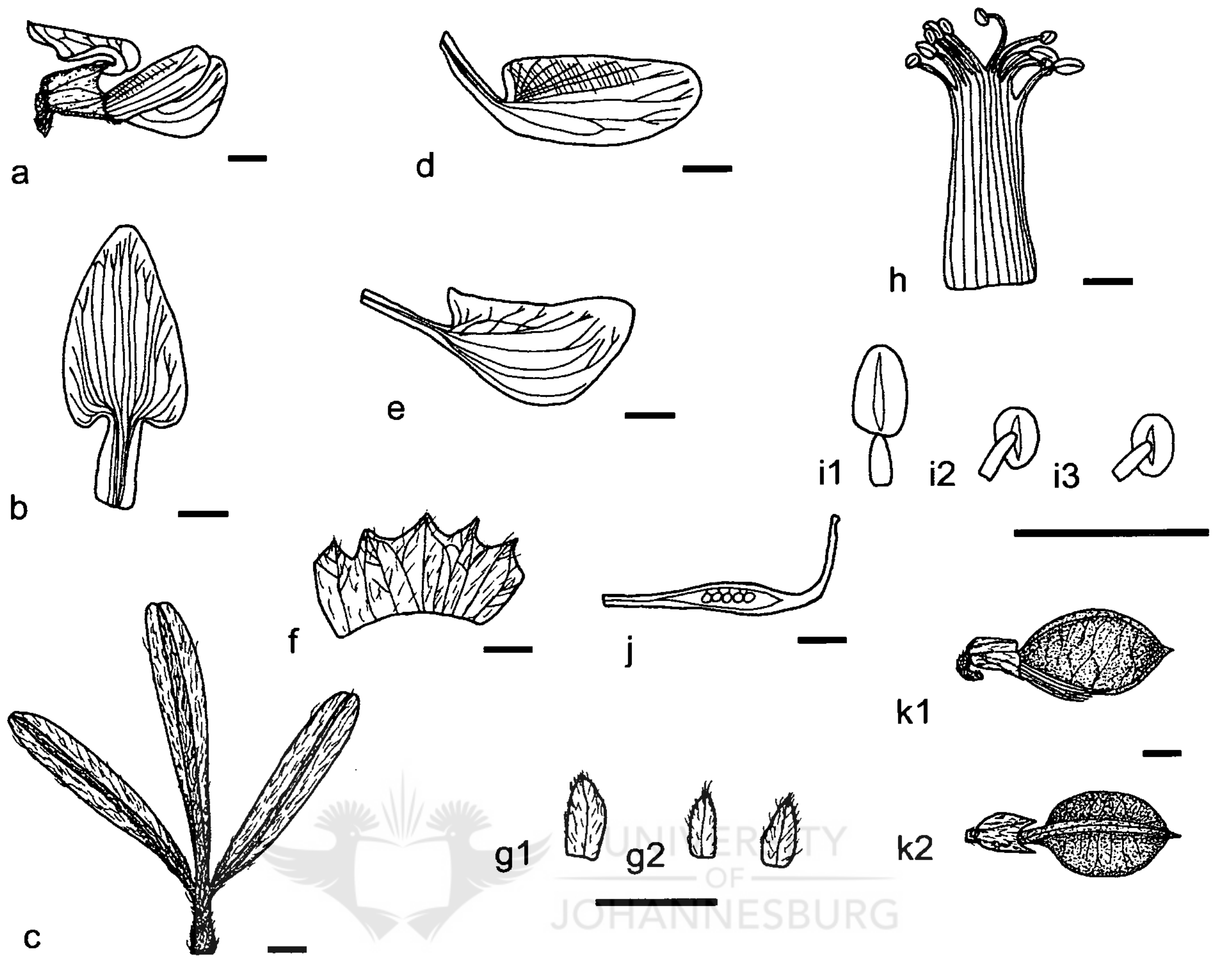

FIG. 7.11 Morphology of *Wiborgiella humilis*: (a) flower in lateral view; (b) standard petal; (c) leaf in abaxial view; (d) wing petal; (e) keel petal; (f) outer surface of the calyx (upper lobes to the left); (g1) bract; (g2) bracteoles; (h) androecium; (i1) long, basifixed anther; (i2) carinal anther resembling the short, dorsifixed anthers; (i3) short, dorsifixed anther; (j) pistil; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a–e, k1–k2) *Boatwright et al. 216* (JRAU); (f–i3) *Van Wyk 3530* (JRAU).

Scale bars: 1 mm.

***Diagnostic characters*****—**This species is similar to *W. leipoldtiana*, but differs in the linear-spathulate leaves, smaller flowers, shorter calyx tube and calyx lobes, long-stipitate fruit and pistil, small, few-seeded pods and rugose seeds (*W. leipoldtiana* has oblanceolate to obovate leaves, larger flowers, a longer calyx tube and calyx lobes, short-stipitate fruit and pistil, many-seeded pods with smooth seeds).

***Distribution and habitat*****—***Wiborgiella humilis* is a highly restricted species that occurs around Gifberg and Nieuwoudtville (Fig. 7.12). It has been recorded in sandy or rocky soils, often along streams, at altitudes of between 480 m and 800 m in fynbos.

***Additional specimens examined***

**–3118** (Vanrhynsdorp): Gifberg Plateau (–DC), *Acocks 14892* (PRE), *Acocks 14898* (K, PRE).

**–3119** (Calvinia): Keyzerfontein, Sanddraai on Farm Oorlogskloof (–AC), *Boatwright et al. 129* (JRAU); Farm Oorlogskloof (–AC), *Boatwright et al. 216* (JRAU); on road to Keyzerfontein, south of the Calvinia road, close to Nieuwoudtville (–AC), *Goldblatt 7068* (PRE); Farm Kleinarendskraal, close to edge of Nieuwoudtville plato (–AC), *Niemand 8* (JRAU); Oorlogskloof Nature Reserve, 15 km south-west of Nieuwoudtville, Farm Gipherkop 804, 300 m south of waterfall on burnt area (–AC), *Pretorius 392* (NBG); Kranskloof 792 (–AC), *Pretorius 646* (K, NBG, PRE); Nieuwoudtville, Arendskraal, Rooi pad (–AC), *Van Wyk 3530* (JRAU).

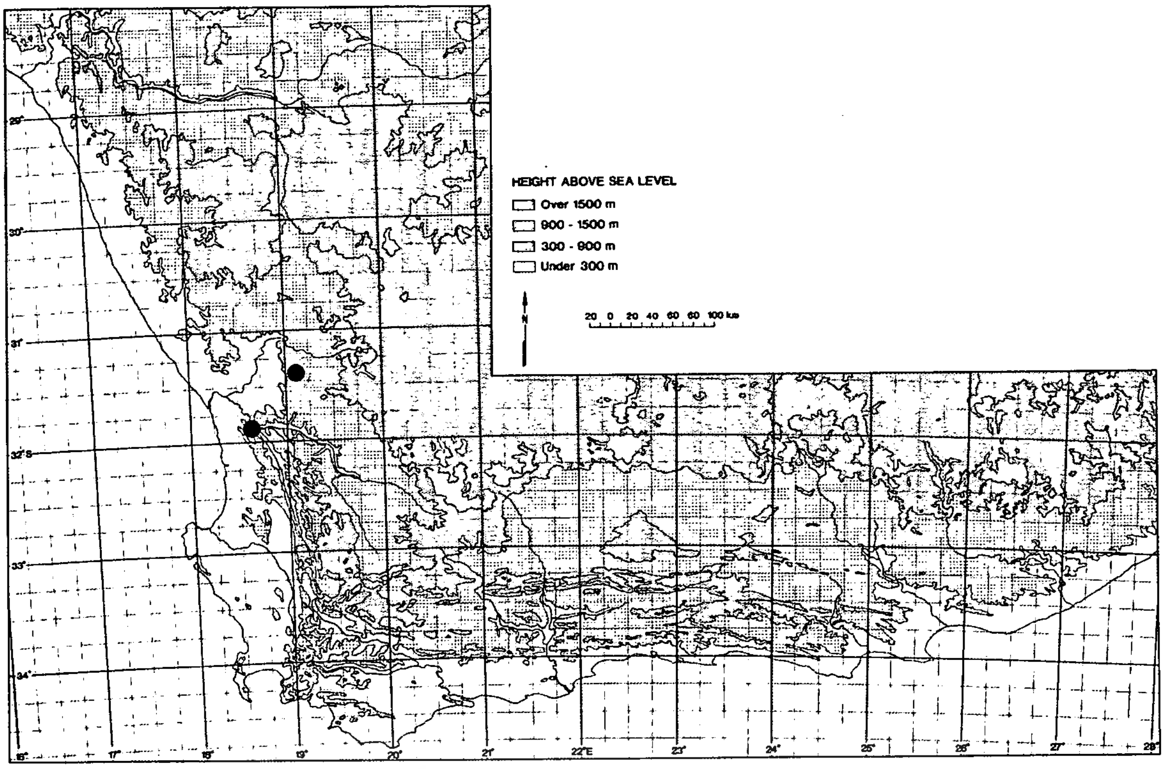

FIG. 7.12 Known geographical distribution of *Wiborgiella humilis*.

5. WIBORGIELLA INFLATA (H.Bolus) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia inflata* H.Bolus in Hook. Icones Pl. 16: pl. 1576. 1887; Salter in Adamson and Salter, Fl. Cape Peninsula: 471. 1950; Bond and Goldblatt, J. S. Afr. Bot. 13: 289. 1984; Goldblatt and Manning, Cape Pl.: 493. 2000.—TYPE: SOUTH AFRICA, Western Cape Province, eastern slopes of Devil's Peak [3318 CD], *Bolus 4826* (holotype: BOL!; isotypes: K!, NBG!).

Small, erect or decumbent, short-lived herb up to 0.3 m in height. Branches green, angular, densely to sparsely pilose. Leaves digitately trifoliolate; petiole 7–20 mm long, not tuberculate or persistent; leaflets lanceolate, subsessile, densely to sparsely pilose on both surfaces, terminal leaflet 14–36 mm long, 1.5–3.5 mm wide; lateral leaflets 10–23 mm long, 1–2 mm wide; apex acute; base cuneate. Inflorescence (27–) 50–135 (–255) mm long, with 4 to 13 flowers; pedicel 2–5 mm long; bract 1–2 mm long, elliptic to lanceolate, pilose on adaxial surface; bracteoles 1.5–2.5 mm long, linear, pilose on adaxial surface. Flowers 8–10 mm long, yellow, older petals fading purple. Calyx 3.5–5.0 mm long, glabrous or very sparsely pilose; tube 2.5–3.0 mm long; lobes 1–3 mm long, deltoid; acute. Standard 7–12 mm long, glabrous; claw linear, 3.0–5.5 mm long; lamina ovate, 4.0–7.5 mm long, 4.5–8.0 mm wide; apex obtuse. Wing petals 8–10 mm long, glabrous; claw 3.5–4.5 mm long; lamina oblong, 4.5–6.5 mm long, 2.0–3.0 mm, as long as or longer than the keel, wide with 6 to 8 rows of sculpturing. Keel petals 7.5–8.5 mm long, glabrous; claw 3.0–4.0 mm long; lamina lunate, 4.0–5.0 mm long, 2.0–2.5 mm wide, apex acute; pocket absent. Pistil sub-sessile, glabrous; ovary elliptic, 5.0–6.5 mm long, 0.8–1.5 mm wide with up to ±21 ovules; style 2–3 mm long, shorter than the ovary. Pods sessile, oblong, smooth, inflated, 28–35 mm long, 5.5–10.0 mm wide, glabrous. Seed suborbicular, 1.5–2.1 mm long, 1.7–2.0 mm wide, rugose, black mottled with white (Fig. 7.13). Flowering time: Spring to early summer (October to November).

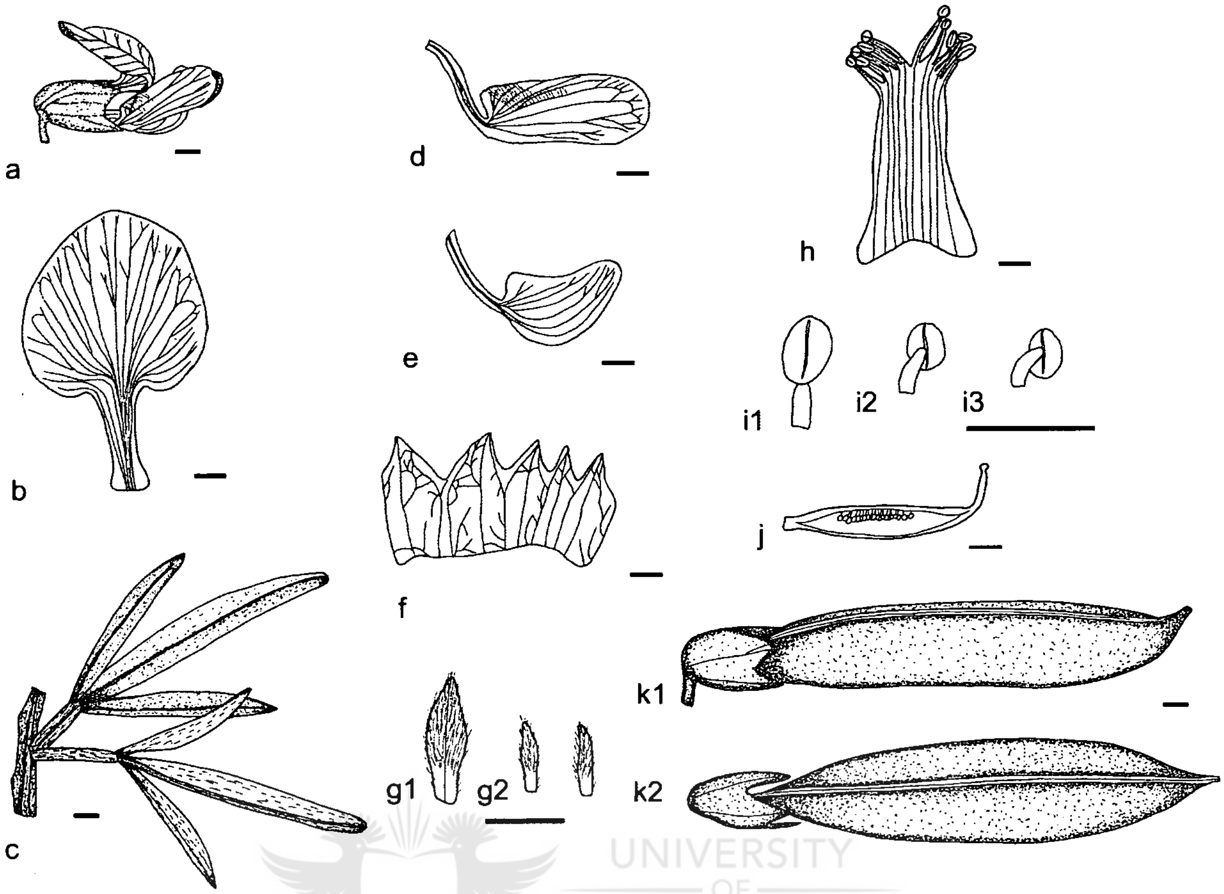

FIG. 7.13 Morphology of *Wiborgiella inflata*: (a) flower in lateral view; (b) standard petal; (c) leaf in adaxial and abaxial view; (d) wing petal; (e) keel petal; (f) outer surface of the calyx (upper lobes to the left); (g1) bract; (g2) bracteoles; (h) androecium; (i1) long, basifixed anther; (i2) carinal anther resembling the short, dorsifixed anthers; (i3) short, dorsifixed anther; (j) pistil; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a, b, d–f) *Vlok et al. 2* (JRAU); (c, k1–k2) *Johns 162* (JRAU); (g1–j) *Haynes H420* (PRE). Scale bars: 1 mm

***Diagnostic characters***—*Wiborgiella inflata* is closely related to *W. vlokii*, but differs in the inflated, oblong pods and lanceolate leaves. The latter species has oblanceolate leaves and laterally compressed, linear pods.

***Distribution and habitat***—*Wiborgiella inflata* occurs from the Cape Peninsula eastwards to the Kogelberg, the Hottentots Holland Mountains and also the Kleinrivier Mountains at Hermanus. It typically grows in recently burnt vegetation, one to two years after fire (Fig. 7.14). It can be found on Table Mountain Sandstones (TMS), in damp stream banks on clay soils or on rocky soils and east to south-west facing slopes between 40 m to 750 m. It is grazed by livestock.

***Additional specimens examined***

**–3318** (Cape Town): Kirstenbosch, Nursery Gorge (–CD), *Esterhuysen 6143* (BOL, K, NBG, PRE 2 sheets); Table Mountain, slopes above south end of Kirstenbosch (–CD), *Esterhuysen 22402* (BOL).

**–3418** (Simonstown): Cape Peninsula, between Constantia Corner and Castle Rock (–AB), *Lewis 1816* (NBG); locally common on upper south slopes of Gerbera Hill, west of the Muizenberg (–AB), *Pillans 3465* (BOL); Nuweberg south facing slopes of Dwarsrivier Mountains, above jeep track, Kogelberg Nature Reserve (–BD), *Le Maitre 578* (NBG, PRE).

**–3419** (Caledon): Lebanon Forest Reserve, Jakkalsrivier Catchment (–AA), *Haynes H420* (NBG, PRE), *Haynes 474* (PRE); Glenfrum Onrus Mountain, Hermanus (–AD), *Barker 204* (JRAU); Vogelgat Nature Reserve (–AD), *Stirton 11170* (K); Vogelgat above Dragon Fly Pool (–AD), *Williams 3693* (NBG 2 sheets, PRE); Kogelberg Nature Reserve (–BD), *Johns 162* (JRAU), *Vlok et al. 2* (JRAU).

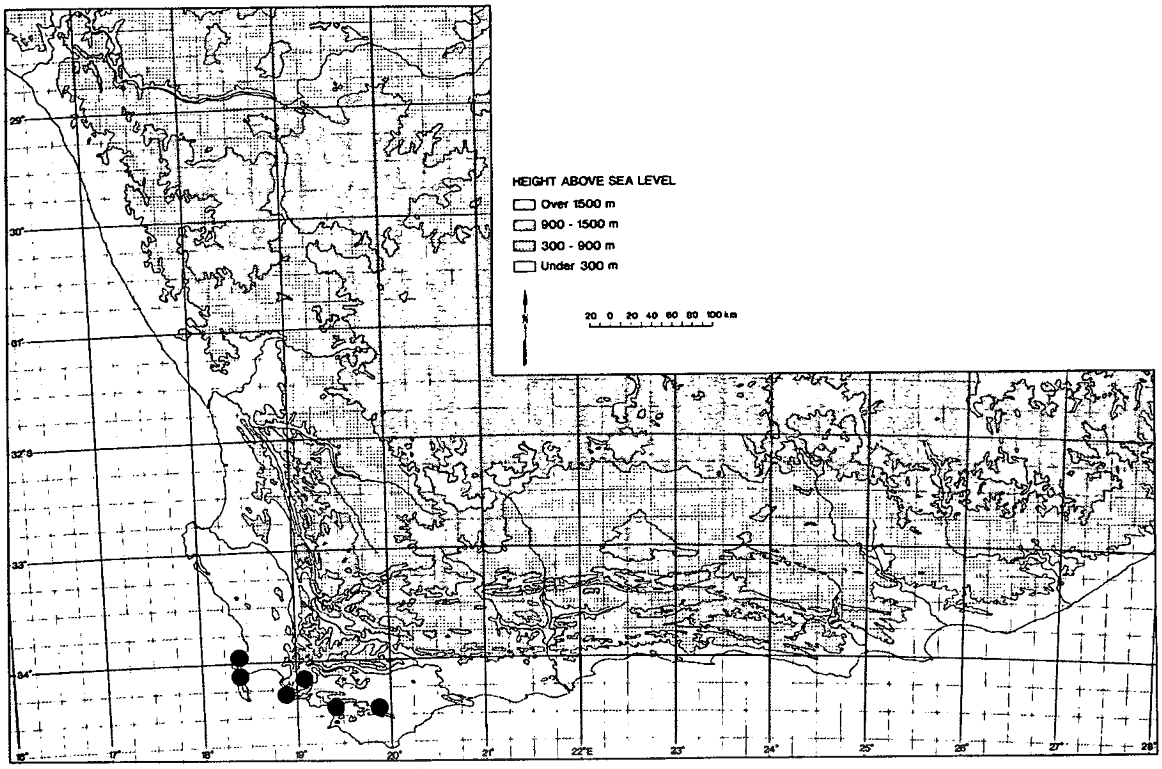

FIG. 7.14 Known geographical distribution of *Wiborgiella inflata*.

6. WIBORGIELLA LEIPOLDTIANA (Schltr. ex R.Dahlgren) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia leipoldtiana* Schltr. ex R.Dahlgren, Op. Bot. 38: 72. 1975; Bond and Goldblatt, J. S. Afr. Bot. 13: 289. 1984; Goldblatt and Manning, Cape Pl.: 493. 2000.—TYPE: SOUTH AFRICA, Western Cape Province, Calvinia Div.: 'Inter Grasberg et Nieuwoudtville' [3119 AC], *Lewis 5839* (holotype: NBG!; isotype: NBG!).

*Crotalaria aspalathoides auct. non* Lamarck: E.Mey., Comm. Pl. Afr. Austr. 1: 25. Feb. 1836; Benth. in Hook. Lond. J. Bot. 2: 591. 1843; Harv. in Harv. and Sond., Fl. Cap. 2: 46. 1862.

Erect, rigid, woody, multi-stemmed shrub up to 1.2 m in height. Branches brown; young branches sericeous; older branches covered in longitudinally splitting brown bark. Leaves digitately trifoliolate; petiole 1–3 mm long, tuberculate, becoming hard and persistent on older branches after leaflets have been shed; leaflets oblanceolate to obovate, sericeous to sparsely sericeous on both surfaces, subsessile, terminal leaflet 4–11 mm long, 1.5–4.0 mm wide, lateral leaflets 4–10 (–11) mm long, 1.5–3.0 mm wide; apex retuse to obcordate, base cuneate. Inflorescence (16–) 20–40 mm long, with 4 to 9 flowers; pedicel 1–3 mm long; bract 1.5–2.2 mm long, linear to lanceolate, sericeous on adaxial surface; bracteoles 1.0–1.5 mm long, linear to lanceolate, sericeous on adaxial surface. Flowers 10–13 mm long, yellow. Calyx 4.5–6.5 mm long, pilose; tube 3.0–4.5 mm long; lobes 1–2 mm long, deltoid. Standard 12.5–16.0 mm long, glabrous or very rarely sparsely pilose along dorsal midrib; claw linear, 4.0–6.5 mm long; lamina ovate, 8.5–9.5 mm long, 5.5–6.0 mm wide; apex obtuse or sub-acute. Wings 10.0–12.5 mm long, glabrous; claw 4.0–5.0 mm long; lamina oblong, 6.0–7.5 mm long, 3–4 mm wide, shorter than keel, with 4–6 rows of sculpturing. Keel 11.5–14.0 mm long, glabrous; claw 4.0–5.5 mm long; lamina boat-shaped, 8.0–9.5 mm long, 4–5 mm wide, apex acute; pocket present. Pistil subsessile to shortly stipitate, rarely pubescent on the upper basal parts; ovary linear, 8.5–10.0 mm long, 1.0–1.3 mm wide with 10 to 12 ovules; style shorter than ovary, 5–6 mm long. Pods oblanceolate to elliptic, inflated, smooth, subsessile to shortly stipitate, dark brown, 16–26 mm long, 3–6 mm wide, ±7-seeded, dehiscent. Seeds reniform, 2.5–3.0 mm long, 2.0–2.6 mm wide, mature seeds light pink, surface smooth (Fig. 7.15). Flowering time: Spring, August to October.

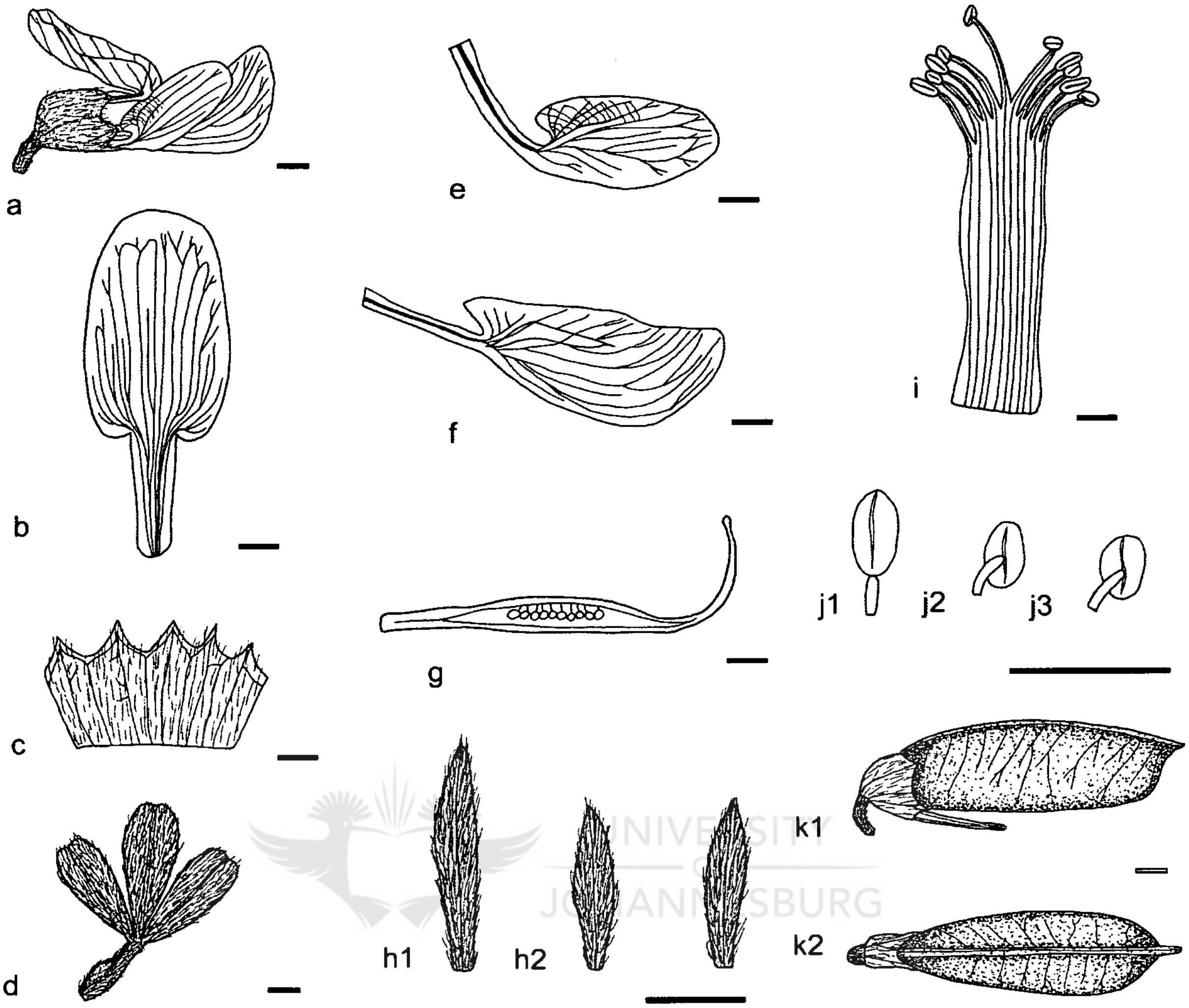

FIG. 7.15 Morphology of *Wiborgiella leipoldtiana*: (a) flower in lateral view; (b) standard petal; (c) outer surface of the calyx (upper lobes to the left); (d) leaf in abaxial view; (e) wing petal; (f) keel petal; (g) pistil; (h1) bract; (h2) bracteoles; (i) androecium; (j1) long, basifixed anther; (j2) carinal anther resembling the short, dorsifixed anthers; (j3) short, dorsifixed anther; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a, c–f, j1–j3) *Boatwright et al. 123* (JRAU); (b, h1–i) *Schutte 295* (JRAU); (g) *Hanekom 2125* (PRE); (k1–k2) *Van Wyk 3278* (JRAU). Scale bars: 1 mm

***Diagnostic characters***—This species is similar to *Wiborgiella fasciculata*, but differs in the longer leaflets, larger flowers and oblanceolate to elliptic, larger pods (the leaflets are short, the flowers small and the pods linear and shorter in *W. fasciculata*). It differs from *W. dahlgrenii* in the larger yellow flowers, ovate standard petal, short wing petals, many-seeded oblanceolate to elliptic pods and style that is shorter than the ovary (*W. dahlgrenii* has smaller pink flowers, an obovate to cordate standard petal lamina, long, down-curved wing petals, the style that is longer than the ovary and narrowly ovate, few-seeded pods). It is also similar to *W. humilis*, but differs in the oblanceolate to obovate leaves, larger flowers, longer calyx tube and calyx lobes, many-seeded, much larger pods and smooth seeds (in *W. humilis* the leaves are linear-spathulate, the flowers smaller, the calyx tube and calyx lobes shorter, the pods small and few-seeded and the seeds rugose). Furthermore, it differs from *W. mucronata* in the sericeous oblanceolate to obovate leaflets, shorter bracts and bracteoles, sub-acute keel petals and inflated, oblong to elliptic pods (*W. mucronata* has sparsely pilose, linear to oblanceolate leaflets, long bracts and bracteoles, obtuse keel petals and laterally compressed, linear pods).

***Distribution and habitat***—*Wiborgiella leipoldtiana* is widely distributed from the Sutherland area northwards as far as Nababeepberg in the Vioolsdrif area (Fig. 7.16). It occurs in Renosterveld on well-drained sandy loam, red clay or rocky slopes or disturbed roadsides between 600m and 850 m and is grazed by livestock.

***Additional specimens examined***

**–2917** (Springbok): Steinkopf (–BC), *Horrocks 14* (NBG); Anenous Mountain (–BC), *Taylor 1161* (BOL); Spektakel (–DA), *Bolus 9494* (PRE), *Bolus 9495* (BOL); Spektakel Hill (–DA), *Maguire 1013* (NBG); Nababeepberg, near top of mountain (–DC), *Van Wyk 3278* (JRAU).

**–3118** (Vanrhynsdorp): Kromme River (–BB), *Esterhuysen 20532* (BOL).

**–3119** (Calvinia): Grasberg road, 300 m along turn-off from tar near Nieuwoudtville (–AA), *Taylor 11787* (PRE); on Farm Oorlogskloof at Gletservloer (–AC), *Boatwright et al. 123* (JRAU); Redclay, Klip Koppies, trails northeast of Nieuwoudtville (–AC), *Bolus 19558* (BOL 2 sheets, K); Vanrhyns Pass (–AC), *Esterhuysen 5311* (BOL), *Bond 1148* (NBG); north-west of Nieuwoudtville in sandy soil near Grasberg (–AC), *Goldblatt 5842* (PRE); Namaqualand, Remhoogte 416, western slopes of northern end of Grasberg (–AC), *Le Roux 4346* (NBG); Oorlogskloof Nature Reserve, Nieuwoudtville (–AC), *Pretorius 104* (NBG, PRE, WIND), *Pretorius 133* (NBG, PRE); between Nieuwoudtville and Grasberg (–AC), *Schutte 295* (JRAU 2 sheets), *Taylor 11331* (JRAU, NBG, PRE 2 sheets).

**–3120** (Williston): Roggeveld Escarpment near Middelpos (–CC), *Levyns 9476* (BOL).

**–3219** (Wuppertal): Citadel Kop (–AA), *Compton 24254* (NBG); Biedouw Valley, Mertenhof (–AA), *Hanekom 3179* (NBG), *Van Breda 4311* (K); Pakhuis, along the road to Wuppertal (–AA), *Leipoldt 444* (BOL, K); Diamond Drift, Biedouw River between Pakhuis and Wuppertal (–AA), *Leipoldt 3131* (BOL); Brandewynrivier (–AA), *Schlechter 10823* (BM, BOL, K); Pakhuis Pass (–AA), *Stokoe s.n.* (NBG); Koudeberg Mountains, near Wuppertal (–AC), *Bolus 8974* (BOL, K, NBG); ca. 5 km northwest of Wuppertal (–AC), *Strid and Strid 37902* (NBG); Citrusdal (–CA), *Taylor 1219* (BOL).

**–3220** (Sutherland): Kleinfontein (Agterkop), peak Middelpos (–AA), *Hanekom 2125* (PRE); 13.5 mls [21.72 km] south south-west of Komsberg Pass (–DB), *Acocks 18449* (K).

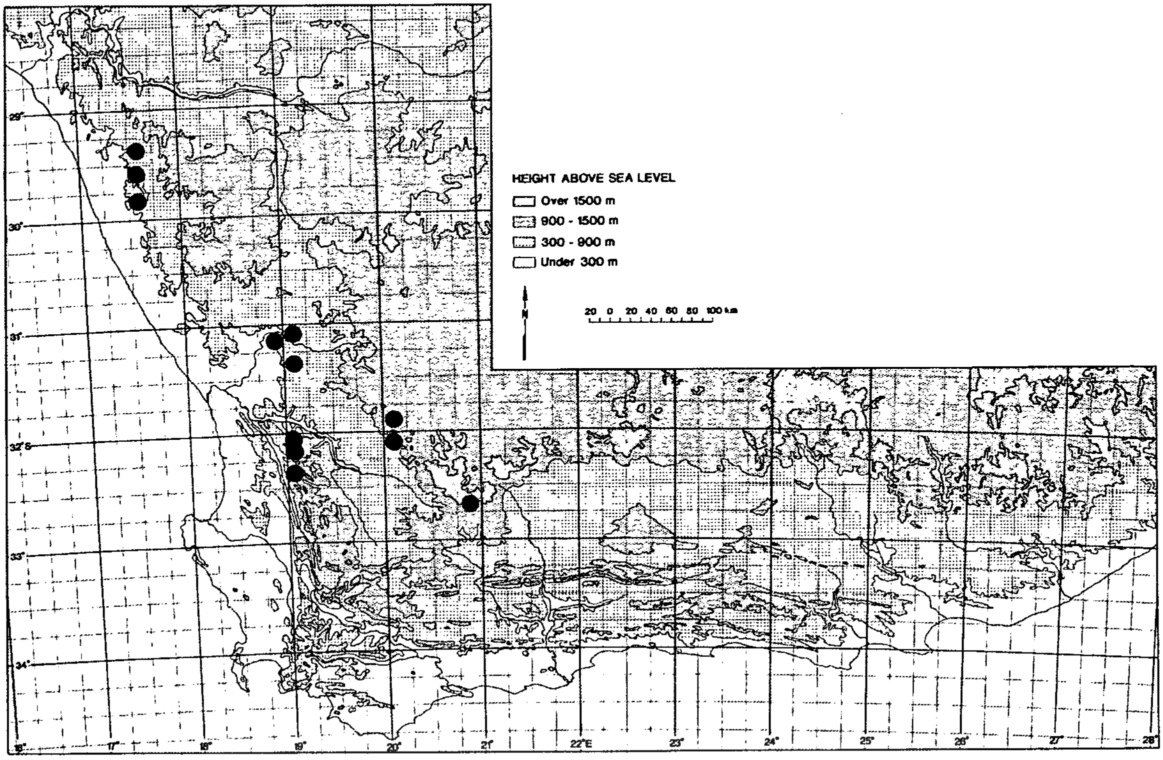

FIG. 7.16 Known geographical distribution of *Wiborgiella leipoldtiana*.

7. WIBORGIELLA MUCRONATA (Benth.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Lebeckia mucronata* Benth. in Hook. Lond. J. Bot. 3: 359. 1844; Walp., Rep. Bot. Syst.: 453. 1845; Harv. in Harv. and Sond., Fl. Cap. 2: 87. 1862; Bond and Goldblatt, J. S. Afr. Bot. 13: 290. 1984; Goldblatt and Manning, Cape Pl.: 493. 2000.—TYPE: SOUTH AFRICA, Uitenhage [3325 CD], *Zeyher 344* (lectotype: K!, designated here; isolectotypes: BM!, TCD, photo!). [Note: The K specimen is chosen as lectotype as most of Bentham's type material is housed in this herbarium (Stafleu and Cowan 1976).]

*Lebeckia leptophylla* Benth. in Hook. Lond J. Bot. 3: 359. 1844; Walp., Rep. Bot. Syst.: 453. 1845; Harv. in Harv. and Sond., Fl. Cap. 2: 87. 1862; Bond and Goldblatt, J.

S. Afr. Bot. 13: 289. 1984; Goldblatt and Manning, Cape Pl.: 493. 2000, synon. nov.—TYPE: SOUTH AFRICA, 'Grassy subalpine situations near Swellendam' [3420 AB], *Mundt 87* (lectotype: K!, designated here; isolectotype: S!). [Note: The K specimen is very rich with flowers and fruit and is a better choice of lectotype than the fairly poor specimen in S.]

Small, erect, multi-stemmed shrublet up to 0.3 m in height. Branches brown; young branches densely pilose; older branches covered in longitudinally splitting brown bark. Leaves digitately trifoliolate, petiole 2–10 (–15) mm long, not tuberculate or persistent; leaflets linear to oblanceolate, sparsely pilose, subsessile, terminal leaflet (4–) 7–23 mm long, 1–4 mm wide, lateral leaflets 4–12 mm long, 1.0–3.5 mm wide; apex mucronate; base angustate. Inflorescence (–23) 35–75 (–115) mm long, with (5–) 8 to 15 (–21) flowers; pedicel 1–2 mm long; bract 4.0–5.5 mm long, linear, pilose on adaxial surface; bracteoles 1.5–3.5 mm long, linear, pilose on adaxial surface. Flowers 8–13 mm long, yellow with back of standard reddish brown (according to label information). Calyx 5–7 mm long, pubescent; tube 3.0–4.5 mm long; lobes 1.5–3.0 mm long, deltoid. Standard 11.5–13.5 mm long, glabrous; claw linear, 2.5–4.5 mm long; lamina ovate, 7–9 mm long, 7.5–9.0 mm wide; apex obtuse. Wings 11.0–12.5 mm long, glabrous; claw 3.5–4.5 mm long; lamina oblong, 6.5–8.0 mm long, 3.5–5.0 mm wide, shorter than or as long as keel, with 5–7 rows of sculpturing. Keel 11.5–13.0 mm long, glabrous; claw 3.5–5.0 mm long; lamina boat-shaped, 7.5–8.5 mm long, 5–6 mm wide, apex obtuse; pocket present. Pistil subsessile to shortly stipitate, glabrous; ovary linear, 7.5–9.5 mm long, 1.3–1.5 mm wide with 16 to 22 ovules; style shorter than ovary, 4.5–

5.5 mm long. Pods linear to somewhat clavate, smooth, laterally compressed, subsessile to shortly stipitate, 20–25 mm long, 4–5 mm wide, ±10-seeded, dehiscent. Seeds not seen (Fig. 7.17). Flowering time: Most of the flowering specimens were collected in spring (September to October) and summer (November) and one in May. *Wiborgiella mucronata* appears to flower in response to fire.

***Diagnostic characters***—*Wiborgiella mucronata* is similar to *Wiborgiella leipoldtiana*, but differs in the sparsely pilose, linear to oblanceolate leaflets, long bracts and bracteoles, obtuse keel petals and laterally compressed, linear pods. In *W. leipoldtiana* the leaflets are sericeous and oblanceolate to obovate, the bracts and bracteoles shorter, the keel petals sub-acute and the pods inflated and oblong to elliptic.

***Distribution and habitat***—*Wiborgiella mucronata* occurs mainly in the Eastern Cape Province around Grahamstown, Port Elizabeth and Oudtshoorn, with some outlier populations around Bredasdorp (Fig. 7.18). It occurs in recently burnt vegetation up to the second or third year after fire. This species is found on south facing slopes on sandy soil or in moist fynbos at altitudes of between 300 m and 750 m.

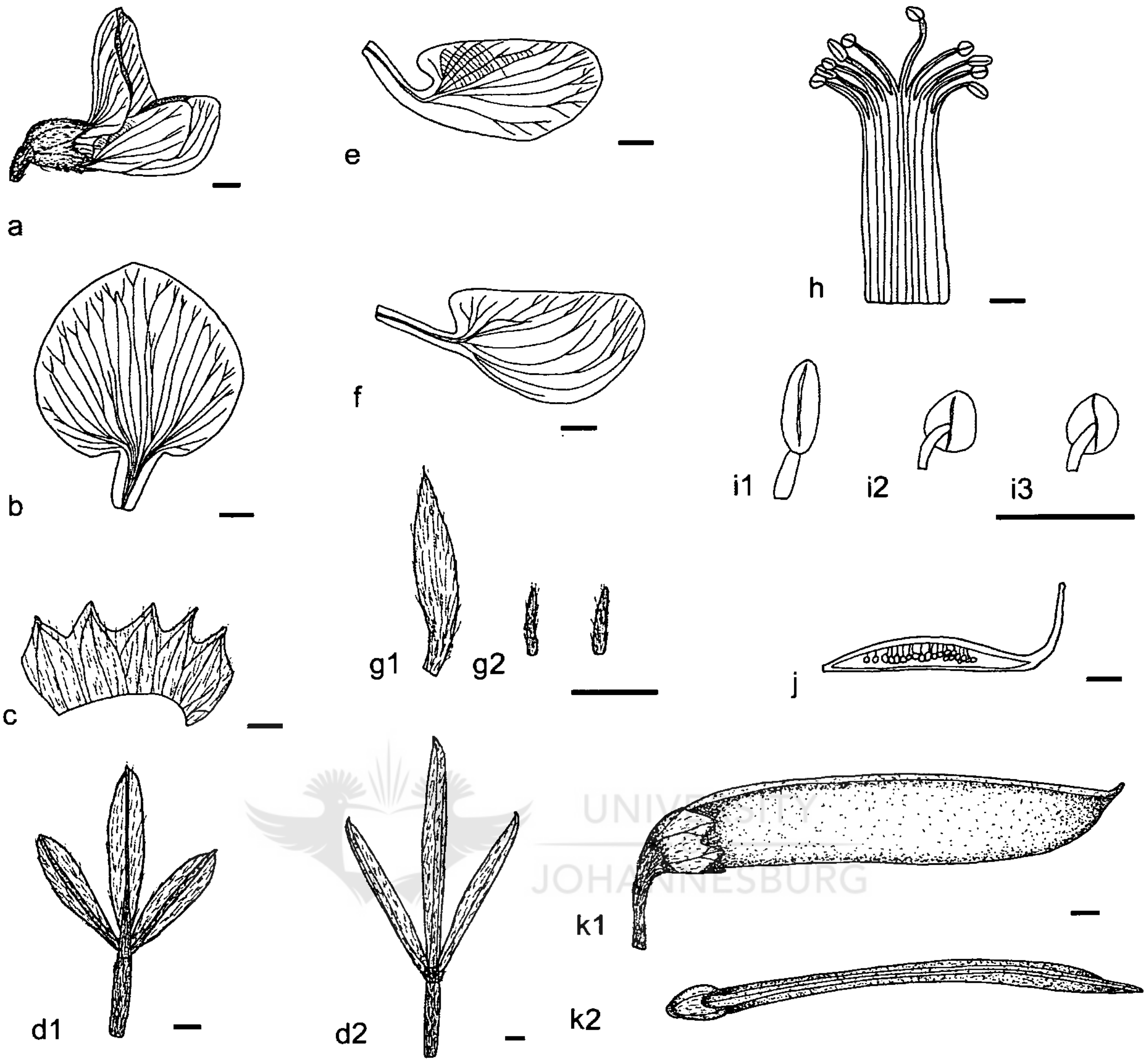

FIG. 7.17 Morphology of *Wiborgiella mucronata*: (a) flower in lateral view; (b) standard petal; (c) outer surface of the calyx (upper lobes to the left); (d1, d2) leaves in abaxial view; (e) wing petal; (f) keel petal; (g1) bract; (g2) bracteoles; (h) androecium; (i1) long, basifixed anther; (i2) carinal anther resembling the short, dorsifixed anthers; (i3) short, dorsifixed anther; (j) pistil; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a–c, e, f, h, i1–i3, j) *Stirton 10880* (JRAU); (d1) *Esterhuysen 27306* (BOL); (d2) *Vlok 1726* (JRAU), (g1–g2) *Stirton and Zantovska 11608* (PRE); (k1–k2) *Esterhuysen 6880* (BOL). Scale bars: 1 mm

### *Additional specimens examined*

**–3322** (Oudtshoorn): northern foothills of Outeniqua Mountains, about 3 km south-west of Herold at Camferskloof (–CD), *Vlok 1726* (JRAU, PRE).

**–3323** (Willowmore): Wagenbooms River (–CD), *Fourcade 2340* (BOL, K); Kouga Mountains, near Smutsburg (–DB), *Esterhuysen 10749* (BOL); De Hoek, northern base of Zitzikamma Mountains near Joubertina (–DC), *Esterhuysen 27306* (BOL, K); Joubertina (–DD), *Esterhuysen 6880* (BOL), *Esterhuysen 6904* (BOL, PRE).

**–3324** (Steytlerville): top of Elandsberg on road to Patensie above Erasmuskraal farm (–BD), *Schrire 2011* (GRA); Kareedouw Pass (–CD), *Gillett 2280* (BOL, NBG); poort between Patensie and Cambria (–DA), *Thompson 1889* (NBG); Elandsberg Mountains, north of Patensie (–DB), *Stirton 10880* (JRAU 2 sheets).

**–3325** (Port Elizabeth): Ten Stop Hill, Groendal, Uitenhage (–CA), *Olivier 3196* (PRE); Van Stadens River Mountains (–CC), *Bolus 1605* (BOL), *Zeyher 2318* (NBG, S); Van Stadensberg Mountains, Longmore Forest Station far eastern end (–CC), *Stirton and Zantovska 11608* (NBG, PRE).

**–3326** (Grahamstown): Howieson's Poort (–AD), *Britten 5157* (GRA); Faraway, portion 3 of Coldsprings (–AD), *Jacot Guillarmod 8387*, *9234* (GRA); Grahamstown (–BC), *Britten 5064* (GRA), *MacOwen 692* (K); Featherstone's Kloof (–BC), *Galpin 253* (GRA, PRE), *MacOwen 692* (NBG).

**–3420** (Bredasdorp): Marloth Nature Reserve (–AB), *Taylor 7688* (NBG); hill beyond Lemmetjiesdorp (–AB), *Wurts 470* (NBG).

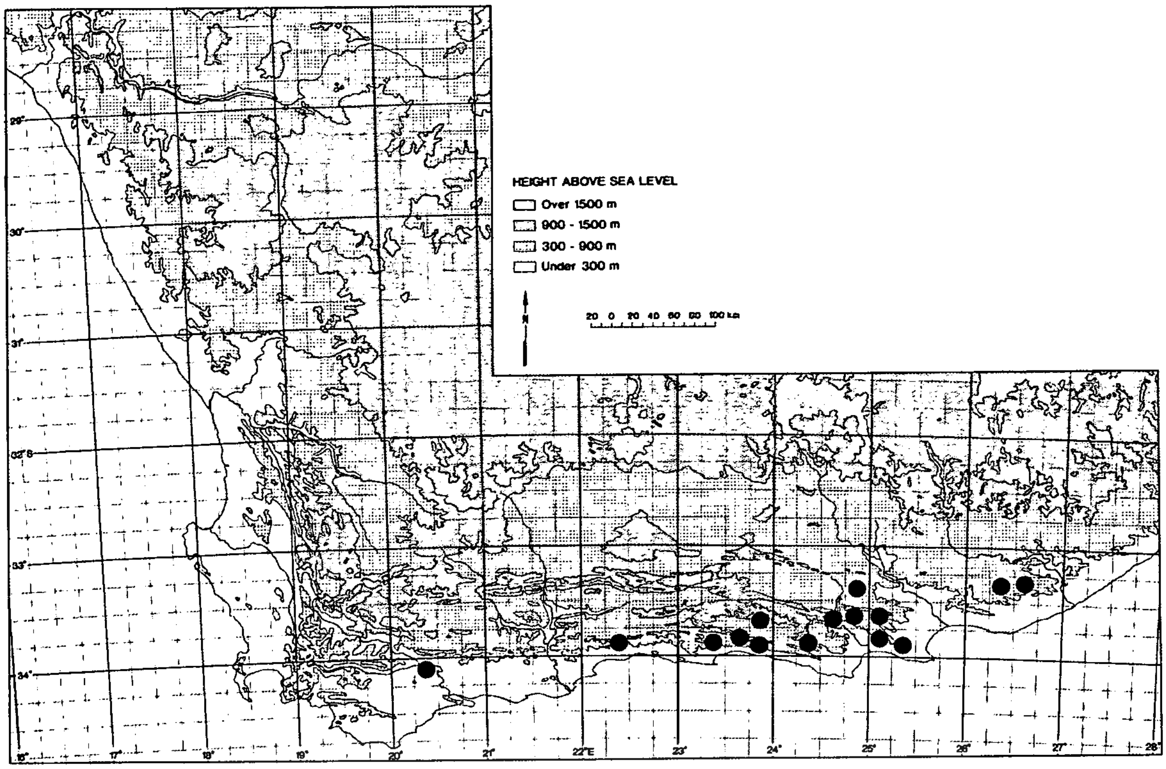

FIG. 7.18 Known geographical distribution of *Wiborgiella mucronata*.

8. WIBORGIELLA SESSILIFOLIA (Eckl. and Zeyh.) Boatwr. and B.-E.van Wyk, comb. nov. (S. Afr. J. Bot.: submitted. 2008). *Acanthobotrya sessilifolia* Eckl. and Zeyh., Enum. Pl. Afric. Austral. 2: 193. Jan. 1836. *Wiborgia (Viborgia) grandiflora* E.Mey., Comm. Pl. Afr. Austr. 1: 31. Feb. 1836. *Lebeckia sessilifolia* (Eckl. and Zeyh.) Benth. in Hook. Lond. J. Bot. 3: 362. 1844; Walp., Rep. Bot. Syst.: 453. 1845; Harv. in Harv. and Sond., Fl. Cap. 2: 89. 1862; R.Dahlgren, Op. Bot. 9: 261–262. 1963; R.Dahlgren, Op. Bot. 38: 76. 1975; Bond and Goldblatt, J. S. Bot. 13: 290. 1984; Goldblatt and Manning, Cape Pl.: 494. 2000.—TYPE: SOUTH AFRICA, 'between Breede River and Duyvelshoek', *Ecklon and Zeyher 1344* (lectotype: S!, designated by Dahlgren [1975]; isolectotypes: K!, SAM!).

Erect, rigid, woody, multi-stemmed shrub up to 1.5 m in height. Branches brown-grey; young branches densely sericeous; older branches covered in longitudinally splitting brown-grey bark. Leaves digitately trifoliolate; petiole tuberculate, becoming hard and persistent on older branches after leaflets have been shed, 1.5–3.0 mm long; leaflets widely oblanceolate, sericeous to sparsely pilose on both surfaces, those that appear first are subsessile and subsequently followed by leaves arising from the axil of the petiole that are sessile, terminal leaflet 4–13 mm long, 1.5–4.0 mm wide, lateral leaflets 4–12 mm long, 1–3 mm wide; apex retuse or truncate; base cuneate. Inflorescence 25–60 (–70) mm long, with 8 to 15 flowers; pedicel 1–3 mm long; bract 3–5 mm long, linear to lanceolate, pilose on adaxial surface; bracteoles 3–5 mm long, linear to lanceolate, pilose on adaxial surface. Flowers (–8) 10–12 mm long, yellow, older petals turning orange. Calyx 8.0–10.5 mm long, densely pilose; tube 4.5–6.0 mm long; lobes 4.0–5.5 mm long, subulate. Standard 11–13 mm long, glabrous; claw linear, 3.5–4.5 mm long; lamina widely ovate, 7.5–8.5 mm long, 9.5–11.0 mm wide; apex obtuse. Wings 12.0–14.5 mm long, glabrous; claw 4–5 mm long; lamina obovate, 8–10 mm long, 4–6 mm wide, longer than keel, with 7–8 rows of sculpturing. Keel 10.5–12.0 mm long, glabrous; claw 4.0–4.5 mm long; lamina boat-shaped, 6.0–7.5 mm long, 4–5 mm wide, apex obtuse; pocket present. Pistil subsessile to shortly stipitate, glabrous; ovary linear broadening towards the base, 7.5–9.0 mm long, 1.5–2.0 mm wide with 8 to 13 ovules; style shorter than ovary, 4.5–5.0 mm long. Pods linear-oblong to lanceolate, smooth, inflated, subsessile to shortly stipitate, 19–21 mm long, 4–5 mm wide, ±5-seeded, dehiscent. Seeds not seen (Fig. 7.19). Flowering time: Spring, mainly in September and October.

***Diagnostic characters***—*Wiborgiella sessilifolia* is similar to *W. bowieana*, but differs in the sessile leaves on older branches, many-flowered inflorescences, pilose calyx with longer calyx lobes, relatively short petal claws, linear ovary with the style shorter than the ovary and the linear oblong to lanceolate pods (*W. bowieana* has petiolate leaves on the older branches, few-flowered inflorescences, a largely glabrous calyx, shorter calyx lobes, long petal claws and an elliptic ovary with the style longer than the ovary).

***Distribution and habitat***—*Wiborgiella sessilifolia* occurs along the Cape coast from Bredasdorp to Still Bay. It appears to be restricted to limestone hills and grows on south or south-west facing slopes at altitudes of 100 m to 200 m (Fig. 7.20).

***Additional specimens examined***

**–3420** (Bredasdorp): 2.5 mls [4.02 km] south-west of Wydgelegen Post Office (–AD), *Acocks 23002* (K, PRE); Potberg Nature Reserve, Windhoek, Fonteinkloof on west side of De Hoopvlei, De Hoop Nature Reserve (–AD), *Burgers 1252* (NBG, PRE); De Hoop Hills, 3.10 mls [4.99 km] from Wydgelegen towards De Hoop (–AD), *Taylor 4329* (PRE); Wydgeleë, on road to De Hoop (–AD), *Thompson 3262* (K, NBG); on limestone hills after entrance to De Hoop Nature Reserve (–BC), *Boatwright et al. 170, 198* (JRAU); Hamerkop (–BC), *Van Wyk 1907* (NBG); along entrance road to De Hoop just after the main gate (–BC), *Van Wyk 2120* (JRAU 5 sheets); Zoetendals Valley, south Bredasdorp neat the old cemetery (–CA), *Albertyn 498a* (NBG); Grasrug downs on south side of Karsrivier near Drie Mond (–CA), *Albertyn 498b* (NBG, PRE); Die Mond (–CA), *Martin 591* (NBG); Agulhas, De Mond Nature Reserve on limestone outcrop on the west side of the river (–CC), *Euston-Brown 201* (NBG); Struisbaai, ridge west of Hotagterklip on Paapekuilfontein 281 (–CC), *Helme 3696* (NBG).

**–3421** (Riversdale): 17 mls (27.4 km) south of Riversdale (–AC), *Acocks 24111* (K, NBG, PRE); Stillbay, ridge east of bridge (–AD), *Bohnen 4203* (NBG, PRE); Stillbay rifle range kloof (–AD), *Bohnen 4832* (NBG); Hills at Melkhoutfontein, near Stillbay (–BD), *Muir 2444* (PRE).

**Precise locality unknown:** Caledon, *Mundt 22* (K).

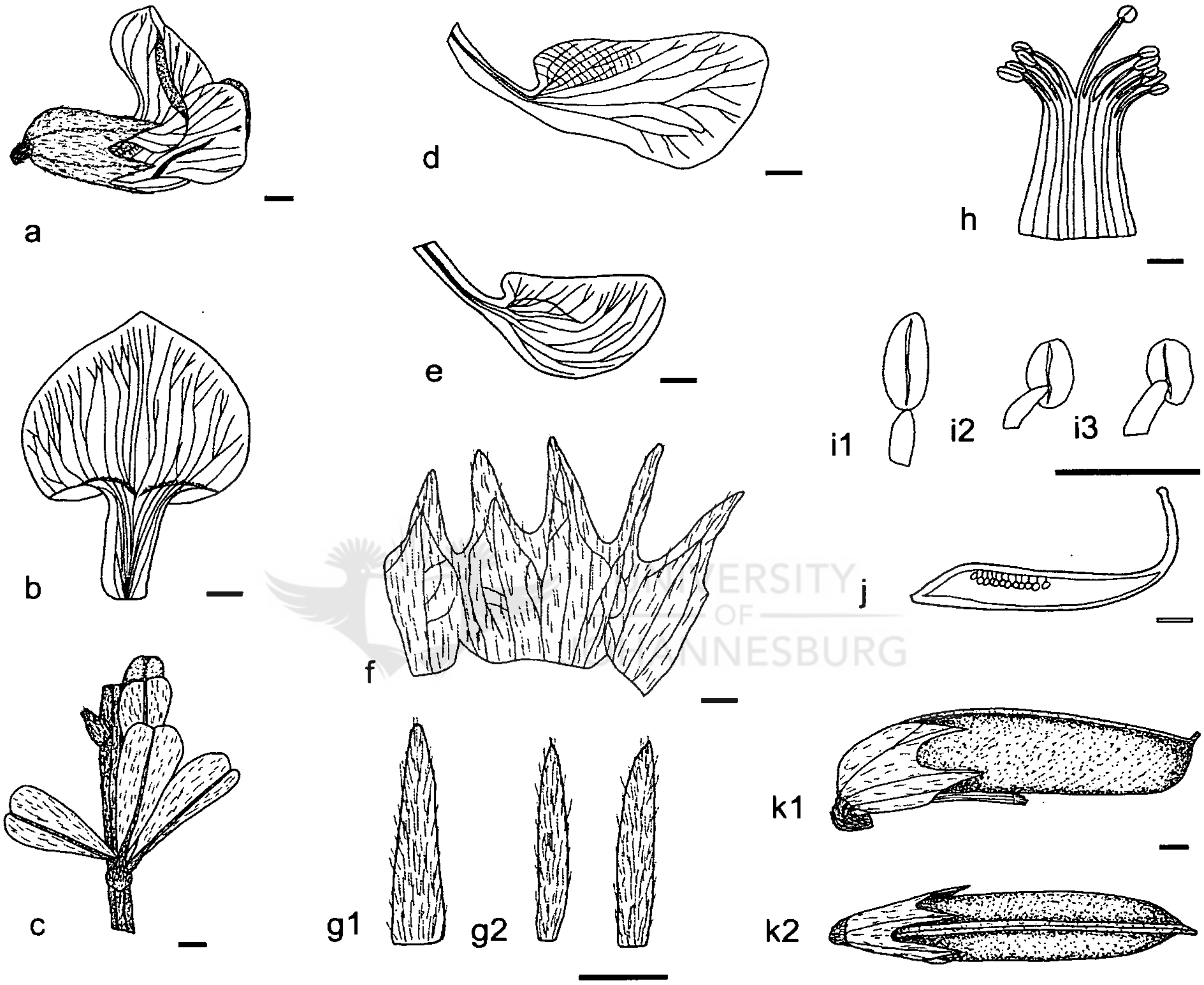

FIG. 7.19 Morphology of *Wiborgiella sessilifolia*: (a) flower in lateral view; (b) standard petal; (c) leaves in abaxial view; (d) wing petal; (e) keel petal; (f) outer surface of the calyx (upper lobes to the left); (g1) bract; (g2) bracteoles; (h) androecium; (i1) long, basifixed anther; (i2) carinal anther resembling the short, dorsifixed anthers; (i3) short, dorsifixed anther; (j) pistil; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a–i3) *Van Wyk 2120* (JRAU); (j) *Albertyn 498b* (NBG); (k1–k2) *Taylor 4329* (PRE). Scale bars: 1 mm

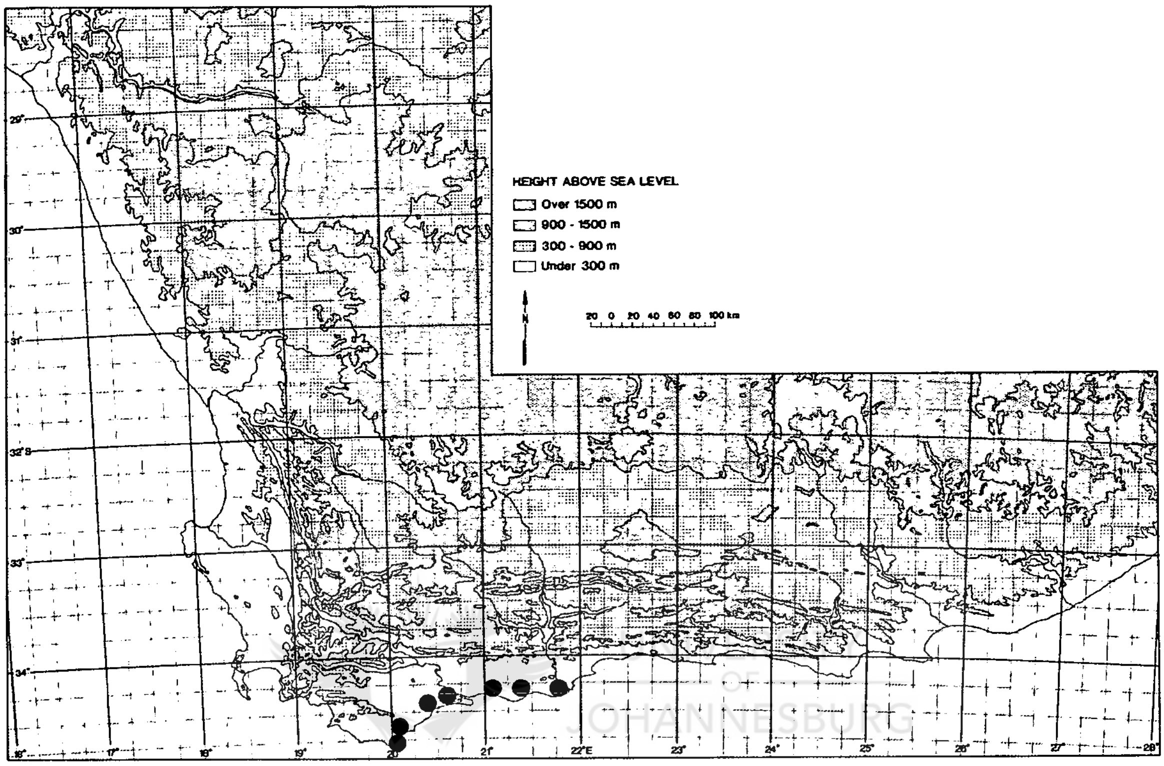

FIG. 7.20 Known geographical distribution of *Wiborgiella sessilifolia*.

9. **Wiborgiella vlokii** Boatwr. and B.-E.van Wyk, sp. nov., similar to *Wiborgiella inflata* (H. Bolus) Boatwr. and B.-E.van Wyk but differs in the laterally compressed pods and shorter, oblanceolate leaflets of up to 13 mm (in W. inflata the pods are strongly inflated, the leaflets are lanceolate and up to 36 mm long) (To be translated into Latin).—TYPE: SOUTH AFRICA, Western Cape Province, Langeberg Mountains, next to forestry track to Helderfontein [3320 DD], *Vlok 2045* (holotype: PRE!, designated here; isotype: PRE!).

Small, erect or decumbent, short-lived herb up to 0.15 m in height. Branches green, angular, densely to sparsely pilose. Leaves digitately trifoliolate; petiole 4–9 mm long, not tuberculate or persistent; leaflets oblanceolate, densely to sparsely pilose on both surfaces, subsessile, terminal leaflet 8–13 mm long, 2.5–3.5 mm wide; lateral leaflets 6–10 mm long, 2–3 mm wide; oblanceolate; apex apiculate or retuse; base cuneate. Inflorescence 43–90 mm long, with 3 to 5 flowers; pedicel 2–3 mm long; bract ±1.5 mm long, ovate to linear, pilose on adaxial surface; bracteoles ±1.1 mm long, ovate to linear, pilose on adaxial surface. Flowers 9–10 mm long, yellow, older petals turning orange (according to label information). Calyx 4.5–5.0 mm long, glabrous on the outer surface; tube 2.5–3.0 mm long; lobes 1.0–1.5 mm long, deltoid. Standard 9.5–10.0 mm long, glabrous; claw 3.5–4.0 mm long; lamina ovate, 5.5–6.0 mm long, 4.0–4.5 mm wide; apex obtuse. Wing petals 9.0–10.5 mm long, glabrous; claw 3.5–4.5 mm long; lamina oblong, 4.5–5.5 mm long, 2.0 mm wide, ± as long as the keel or longer, with 6 to 8 rows of sculpturing. Keel petals 8.5–10.0 mm long, glabrous; claw 3.5–4.5 mm long; lamina boat-shaped, 4.5–5.5 mm long, 2.5–3.0 mm wide; apex acute; pocket absent. Pistil sub-sessile, glabrous; ovary elliptic, 7.0–7.5 mm long, 1.0–1.2 mm wide, with 13 to 18 ovules; style shorter than the ovary, 2.5–3.0 mm long. Pods sessile, oblong, smooth, laterally compressed, 23–31 mm long, 4.0–5.5 mm wide, ±10-seeded, glabrous. Seed suborbicular, 2.3–2.4 mm long, 2.2–2.7 mm wide, rugose, black mottled with white (Fig. 7.21). Flowering time: Spring and summer. The only two available specimens with flowers and fruit and were collected in November.

***Diagnostic characters***—*Wiborgiella vlokii* is only known from the type collection. It is very similar to *W. inflata*, but differs in the shorter, oblanceolate leaves and linear, laterally compressed pods. *Wiborgiella inflata* has lanceolate leaves and inflated, oblong pods.

***Distribution and habitat***—*Wiborgiella vlokii* is a very rare species and is only known from the Langeberg Mountains where it occurs in deep, peaty soil on southern slopes in recently burnt mountain fynbos at an altitude of ca. 808 m (Fig. 7.22).

***Note***—This species is in need of conservation attention as it is known from a single collection in the Langeberg Mountains and has not subsequently been recollected.

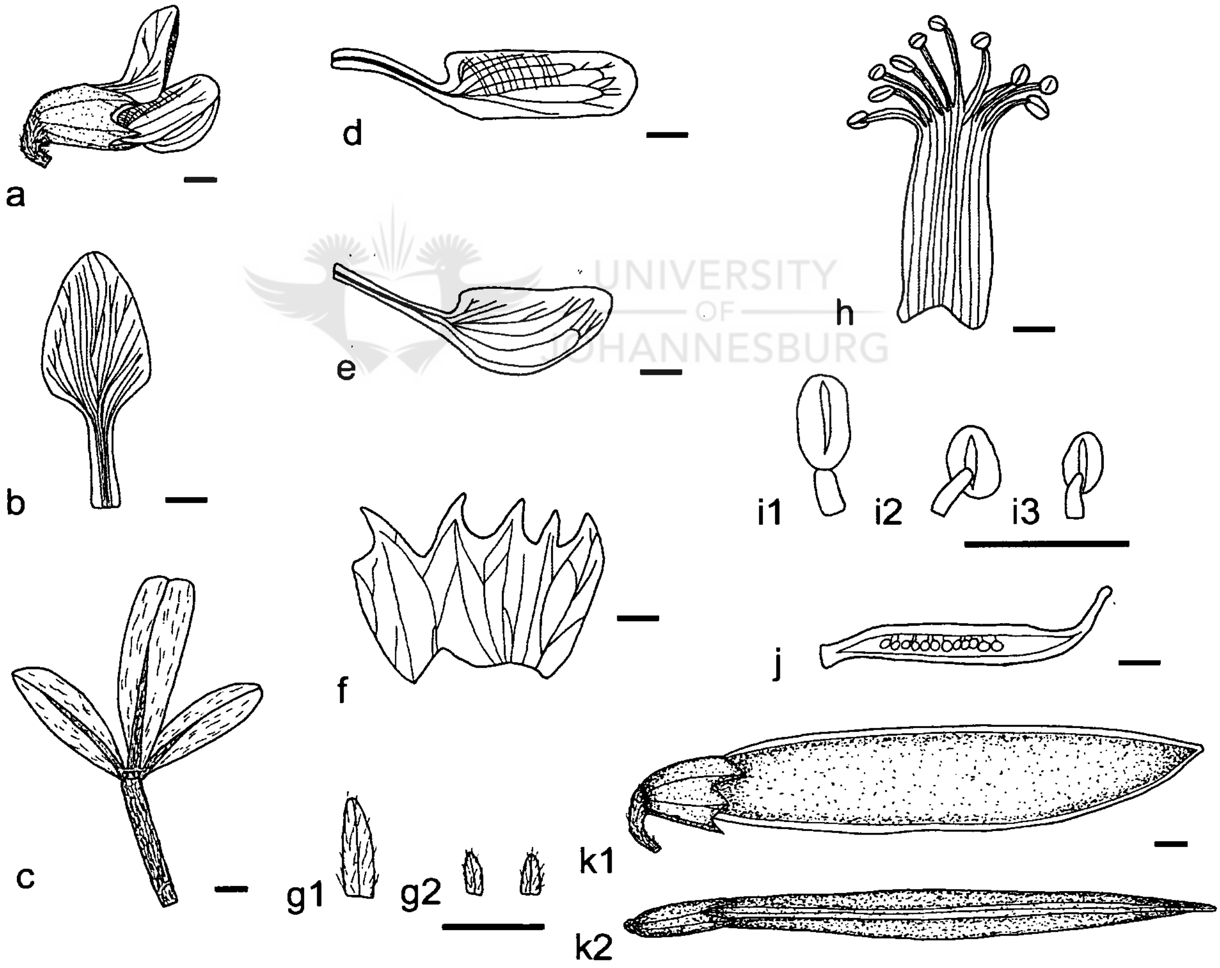

FIG. 7.21 Morphology of *Wiborgiella vlokii*: (a) flower in lateral view; (b) standard petal; (c) leaf in abaxial view; (d) wing petal; (e) keel petal; (f) outer surface of the calyx (upper lobes to the left); (g1) bract; (g2) bracteoles; (h) androecium; (i1) long, basifixed anther; (i2) carinal anther resembling the short, dorsifixed anthers; (i3) short, dorsifixed anther; (j) pistil; (k1) pod in lateral view; (k2) pod in dorsal view.

Voucher specimens: (a–k2) *Vlok 2045* (PRE). Scale bars: 1 mm

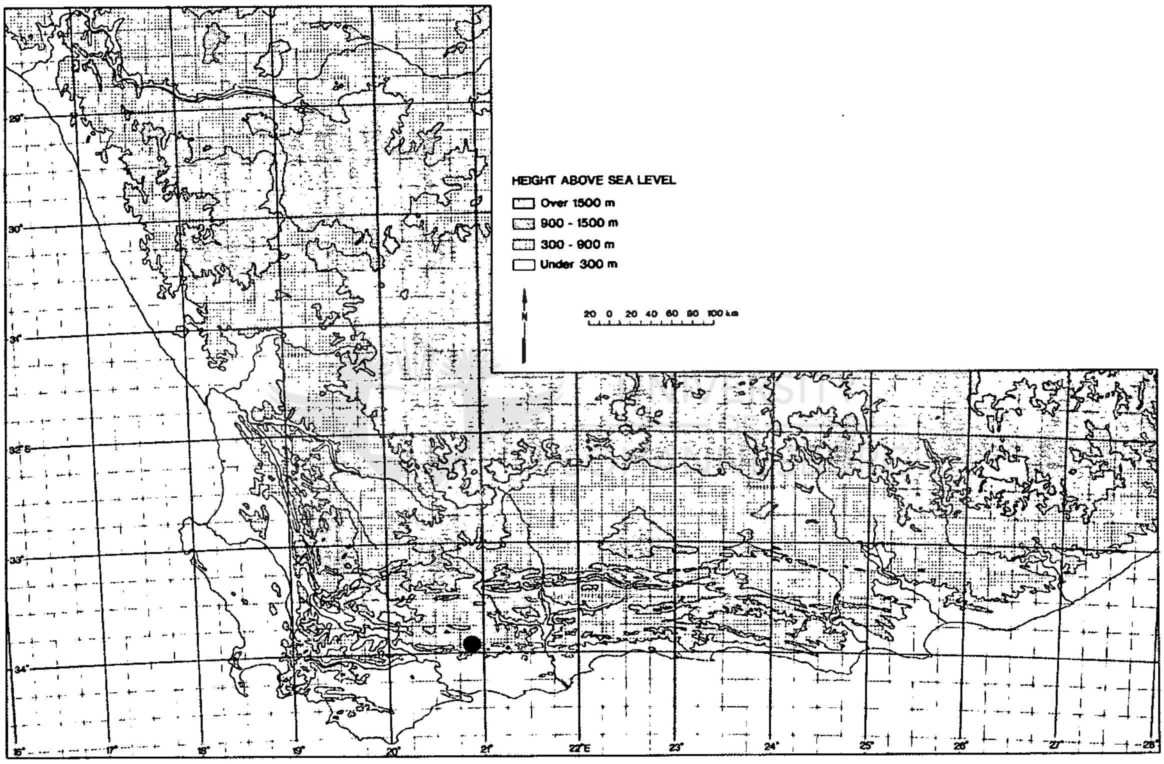

FIG. 7.22 Known geographical distribution of *Wiborgiella vlokii*.

# CHAPTER 8: THE GENERIC CONCEPT OF *LOTONONIS*, REINSTATEMENT OF *EUCHLORA*, *LEOBORDEA* AND *LISTIA* AND A NEW GENUS OF THE TRIBE CROTALARIEAE (FABACEAE)

## 8.1 INTRODUCTION

*Lotononis* is a large and complex genus of the tribe Crotalarieae with approximately 151 species [one recently described from Namibia by Van Wyk and Kolberg (2008)], 145 of which occur in South Africa. The classification system of the genus has been somewhat volatile since the original concept was established by De Candolle in 1925, published as *Ononis* section *Lotononis*. This section was thereafter raised to generic level by Ecklon and Zeyher (1836) who, along with Meyer (1836), proposed numerous other genera to accommodate the species of what is today *Lotononis*. The genus *Euchlora* was described by Ecklon and Zeyher (1836) to accommodate an anomalous plant that was placed in the genus *Ononis* by Thunberg (1800) and in *Crotalaria* and later *Microtropis* by Meyer (1832, 1836). Bentham (1843) expanded the concept of *Lotononis* to include the genera described by Ecklon and Zeyher (1836) and Meyer (1836), with the exception of *Euchlora*, and a sectional classification was proposed which Harvey (1862) also followed in the treatment of the genus in the Flora Capensis. Dahlgren (1964) discussed the taxonomic history and synonymy of *Euchlora* and mentioned the similarities between it and *Lotononis*, such as trifoliolate, stipulate leaves (in some forms of *Lotononis hirsuta*), a similar hair type and the warty upper suture of the pod. *Euchlora serpens* was subsequently transferred to *Lotononis* (as *L. hirsuta*) by Dahlgren (1964). The most recent revision of *Lotononis* by Van Wyk (1991b), follows Bentham (1843) to some extent but extended the generic concept to include

*Buchenroedera* Eckl. and Zeyh. Based on cladistic analyses of morphlogical, cytological and chemical data, a detailed infrageneric classification system was proposed, comprising 15 sections (Van Wyk 1991b). This detailed study, published as a series of papers and as a synopsis in 1991, represents the most rigorous treatment of the genus to date, and provided a framework for future studies on *Lotononis*.

*Lotononis* shares similarities with many of the genera in the tribe (viz. *Crotalaria*, *Lebeckia*, *Pearsonia*, *Rothia*) and a sister relationship with *Crotalaria* was suggested by Van Wyk (1991a) based on the presence of macrocyclic pyrrolizidine alkaloids and rugose seeds.

The data presented in Chapter 3 (Boatwright et al. 2008a) showed that *Lotononis* is polyphyletic, through the analysis of nrITS and plastid *rbcL* sequence data which included 52 species of *Lotononis* representing all the currently recognized sections of the genus. However, the analysis of morphological characters in combination with the sequence data indicated that *Lotononis* was in fact weakly supported to be monophyletic if *L. hirsuta* (*L.* section *Euchlora*) was excluded. However, the anomalous *Lotononis macrocarpa* could not be included in this study seeing that it is an extremely rare species and several attempts to collect this plant have failed. *Lotononis macrocarpa* possesses a unique combination of characters: paired stipules that are equal in size, a 5+5 anther arrangement, presence of bracteoles and large fruit. Subsequent to the study of Boatwright et al. (2008a) material of this species was obtained from a herbarium specimen of a recent collection of this plant. This in combination with available data from Boatwright et al. (2008a) has allowed for a re-evaluation of the generic circumscription of *Lotononis*.

This chapter is aimed at presenting a new generic classification system for *Lotononis* s.l. based on molecular and morphological evidence. A discussion of critical characters is also presented along with systematic data on the placement of the anomalous *Lotononis macrocarpa*. A key to the genera of the Crotalarieae is also presented in which the changes at generic level formalised in this chapter are incorporated.

## 8.2 RESULTS

***8.2.1 Combined ITS/rbcL data set***—The combined molecular data set consisted of 1,854 included characters, 1,401 of which were constant, 453 variable and 276 parsimony informative. A total of 560 trees were retrieved using MP with a tree length (TL) of 1,056, consistency index (CI) of 0.55 and a retention index (RI) of 0.82 (Fig. 8.1a). *Lotononis* was polyphyletic with *Lotononis* s.s. (*L.* section *Lotononis* and allies) sister to *Pearsonia*, *Robynsiophyton* and *Rothia*, i.e. the *Pearsonia* clade (51 bootstrap percentage [BP]). *Lotononis* s.s. was strongly supported to be monophyletic (100 BP). The *Leobordea* clade (*Lotononis* section *Leobordea* and allies) was sister to the *Listia* clade (*Lotononis* section *Listia* excluding *L. macrocarpa*) with a bootstrap percentage of 75 and both these groups were strongly supported as monophyletic (99 BP and 100 BP, respectively). *Lotononis hirsuta* (section *Euchlora*) was strongly supported as sister to *Bolusia* and *Crotalaria* (100 BP), while *L. macrocarpa* was placed within the "Cape group", albeit without support.

***8.2.2 Combined ITS/rbcL/morphological data set***—The analysis of the combined molecular and morphological matrix included 1,885 characters, 1,401 of which were constant, 484 variable and 404 parsimony informative. The resulting 370 trees from the MP analysis had a TL of 1,185 steps, CI of 0.52 and a RI of 0.84 (Fig. 8.1b). The topology differed slightly from that obtained by Boatwright et al. (2008a; Chapter 3), largely within the "Cape group". *Aspalathus* and *Wiborgia* were sister to each other and both monophyletic (98 BP and 94 BP, respectively). Successively sister was the genus *Wiborgiella*, which was also monophyletic, albeit without support. The following clade comprised *Lebeckia* and *Rafnia* that were sister taxa (without support) and moderately to strongly supported as monophyletic (82 BP and 99 BP, respectively). *Calobota* formed the next clade and was strongly supported as monophyletic (94 BP). The "Cape group" was weakly supported (69 BP) and *Lotononis macrocarpa* placed in a position sister to this group, but without bootstrap support. With the exclusion of *Lotononis hirsuta* and *L. macrocarpa*, the rest of *Lotononis* s.l. was weakly supported as monophyletic, as opposed to being polyphyletic in the combined molecular analysis. *Lotononis* s.s, the *Leobordea* clade and the *Listia* clade were strongly supported (100 BP; 100 BP; 100 BP, respectively) with the *Leobordea* and *Listia* clades strongly supported to be sister (86 BP). *Lotononis hirsuta* (section *Euchlora*) was strongly supported as sister to *Bolusia* and *Crotalaria* (100 BP).

***8.2.3 Evolution of morphological characters***—The reconstructions of the 12 morphological characters onto the minimal length trees are indicated in Fig. 8.2–8.13. These reconstructions are represented on one of the 560 or 370 equally most parsimonious trees from the combined molecular or combined molecular/ morphological analyses, respectively, but if more than one reconstruction was possible these are also shown. The large tuber (character 1) was reconstructed as an apomorphy for *Lotononis hirsuta* (Fig. 8.2). Digitate leaves are predominant in the basal taxa of the tribe, but in the "Cape group" some variation was found, notably in the reduction to simple or unifoliolate leaves (character 2; Fig. 8.3). *Lotononis hirsuta* has predominantly simple leaves, but digitate leaves are found in some forms. Asymmetrical stipules (character 3; Fig. 8.4) are found mostly in *Lotononis* s.l. Only one species of *Rothia*, *R. hirsuta* has single stipules. In the combined molecular analysis this character is convergent between *Lotononis* s.s. and the *Leobordea* and *Listia* clades, while in the combined molecular and morphological analysis it is reconstructed as an apomorphy for *Lotononis* s.l. with a reversal in *L.* sections *Aulacinthus* and *Polylobium.* Loss of bracteoles (character 4; Fig. 8.5) is convergent between *Lotononis hirsuta* and the other *Lotononis* clades, while the *Listia* clade is unique in having bracteoles. A zygomorphic calyx (character 5; Fig. 8.6) is reconstructed as a synapomorphy for *Lotononis* s.s., the *Leobordea* and *Listia* clades and *Pearsonia* with a reversal to an equal or subequal calyx in *Robynsiophyton* and *Rothia*. Rostrate or coiled keel petals (character 6; Fig. 8.7) evolved multiple times in Crotalarieae and are found in *Crotalaria*, *Bolusia*, *Lotononis* section *Oxydium*, *Lebeckia* and in some species of *Rafnia* and *Aspalathus.* An anther arrangement (character 7; Fig. 8.8) of 4+1+5 is most frequent in the "Cape group" with *Lebeckia* and *Wiborgiella* distinctly unique with a 5+5 and 4+6 arrangement, respectively. This character is variable within *Lotononis* s.l. with only the *Listia* clade having an exclusively 4+1+5 arrangement. A verrusoce upper suture of the pod (character 8; Fig. 8.9) is extremely convergent within the tribe and present in species of all the *Lotononis* clades, except the *Listia* clade. The presence of long funicles (character 9; Fig. 8.10) was reconstructed as an apomorphy for *Lotononis* s.l. in the combined molecular and morphological analysis, but is also present in *Lotononis macrocarpa.* A chromosome number (character 10; Fig. 8.11) of x=9 appears to be the base number in the Crotalarieae with a reduction to x=8 in *Crotalaria*, *Rafnia* and some *Aspalathus*, while x=7 is found in *Lotononis* s.s. and *Pearsonia*. Cyanogenesis (character 11; Fig. 8.12) is unique to *Lotononis* s.s. with a reversal in *L.* section *Cleistogama*, while macrocyclic pyrrolizidine alkaloids (character 12; Fig. 8.13) are present in *Crotalaria*, *Lotononis* s.s. and some species of the *Leobordea* clade (*Lotononis* section *Synclistus*).

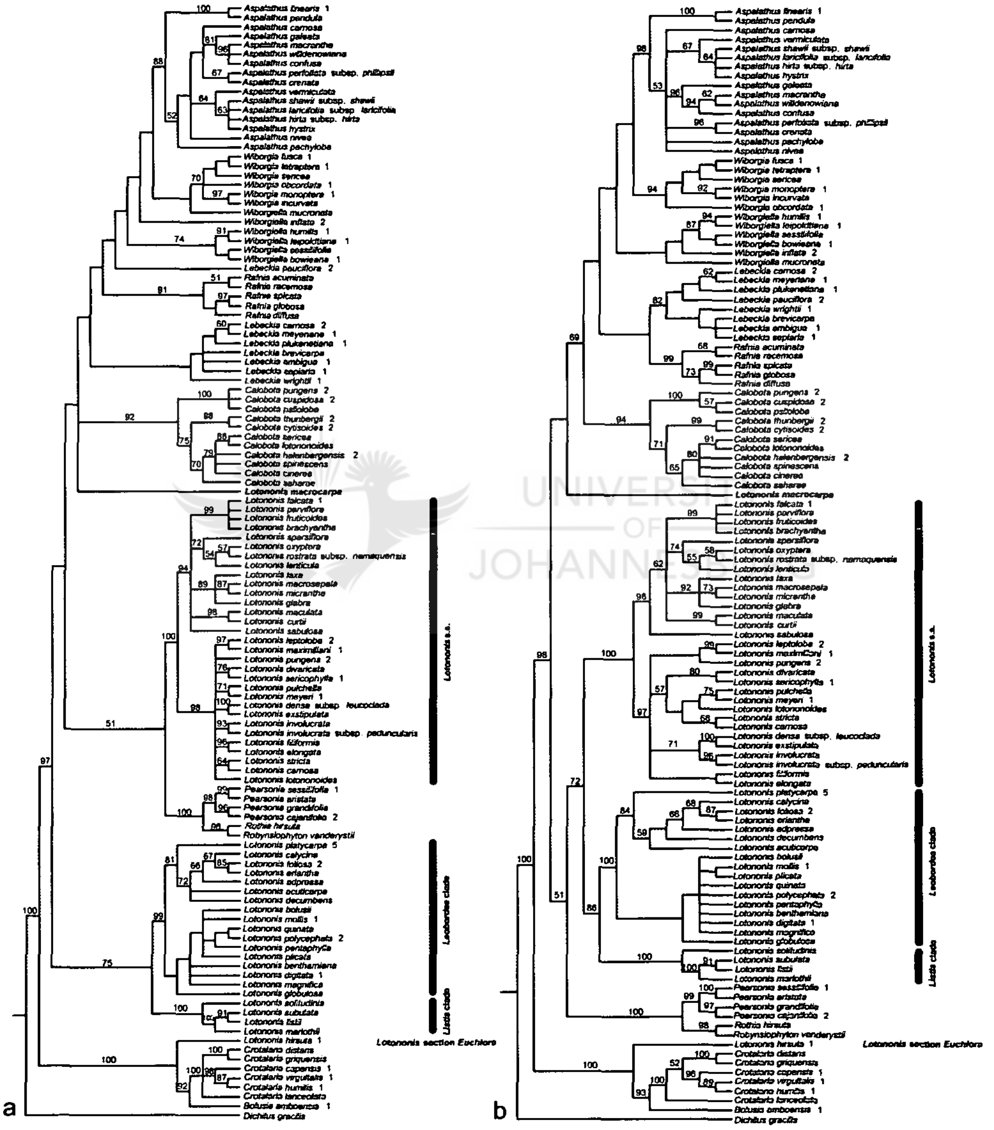

FIG. 8.1 (a) Strict consensus of the 560 most parsimonious trees from the combined molecular analysis; (b) Strict consensus of the 370 equally parsimonious trees from the

combined molecular/morphological analysis. Numbers above the branches are bootstrap percentages above 50%.

## 8.3 DISCUSSION

***8.3.1 Evolution of characters in the tribe Crotalarieae***—UNDERGROUND PARTS — The enormous underground tuber found in *Lotononis hirsuta* is reconstructed as an apomorphy for this taxon (Fig. 8.2). *Lotononis* sections *Polylobium* and *Lipozygis* are also somewhat tuberous with annual shoots produced from the underground tuber, but the extensive underground system of *Lotononis hirsuta* is not found in any of these sections. In *Lipozygis* the tuberous habit could be an adaptation to recurrent fires in the grassland habitat where these plants occur (Van Wyk 1991b).

LEAF TYPE—A diverse array of leaf-types are found within the Crotalarieae ranging from digitate with five, three or single leaflets, and simple or phyllodinous leaves. *Lebeckia* is the only example in the tribe where the acicular leaves of some species are articulated or “jointed” near the middle or completely reduced to petioles (without an articulation) and the leaves are phyllodinous (Dahlgren, 1970a). The genera of the “Cape group” of the Crotalarieae show an extreme diversity in leaf-types when compared to those genera outside the Cape region where the leaves are generally petiolate, trifoliolate and stipulate (Dahlgren, 1970a, Polhill, 1976). *Lotononis* section *Euchlora* has both simple, sessile leaves and digitately trifoliolate leaves with paired stipules in the latter (Dahlgren 1964; Van Wyk 1991b). Leaf type, however, does not provide any informative characters to circumscribe groups within *Lotononis* s.l. (Fig. 8.3).

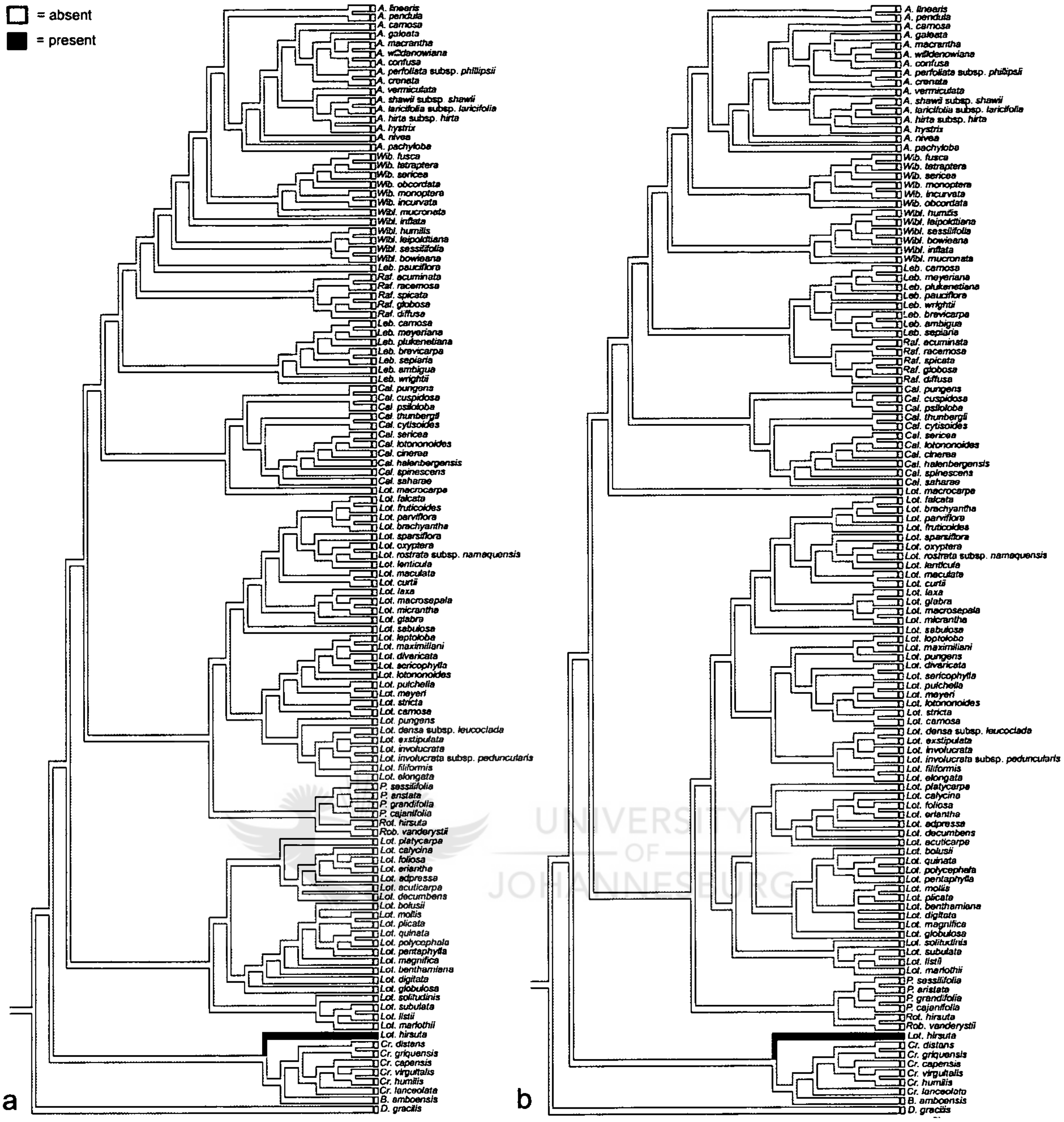

FIG. 8.2 Parsimony-based reconstructions of the presence or absence of a large underground tuber (character 1) on the 560 and 370 minimal length trees from (a) the combined molecular and (b) the combined molecular/morphological analyses, respectively.

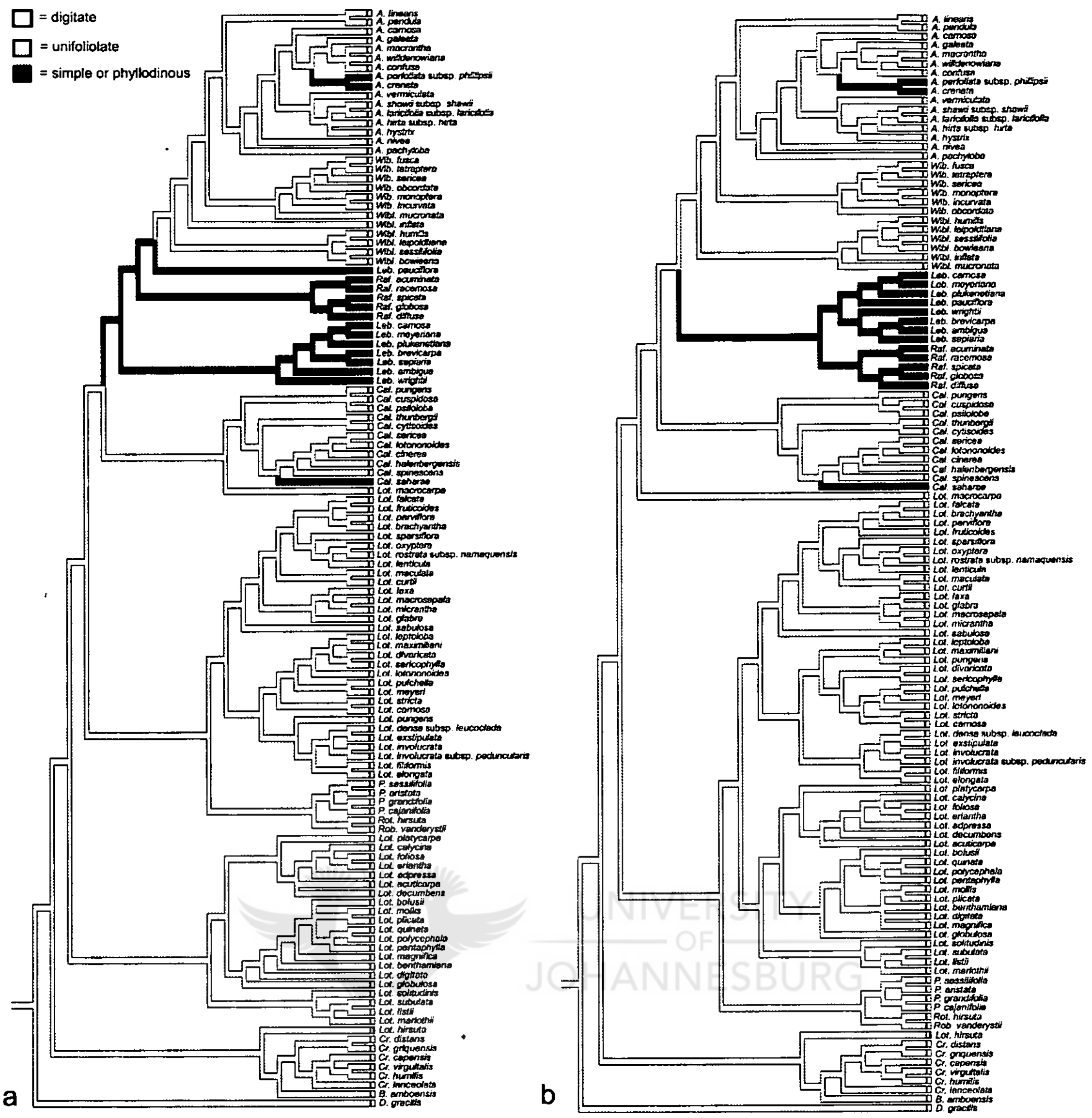

FIG. 8.3 Parsimony-based reconstructions of leaf type (character 2) on the 560 and 370 minimal length trees from (a) the combined molecular and (b) the combined molecular/morphological analyses, respectively.

STIPULE SYMMETRY—The stipules are often dimorhic in *Lotononis* s.s., the *Leobordea* clade and the *Listia* clade, a character which was regarded as an apomorphy for *Lotononis* s.l. In the trees from the combined molecular analysis the presence of asymmetrical or single stipules was reconstructed as a convergence between *Lotononis* s.s. and the *Leobordea* and *Listia* clades (Fig. 8.4). *Lotononis macrocarpa* and *L. hirsuta* are conspicuously different in having symmetrical stipules (when present in the latter). In *Rothia hirsuta*, the stipules are single as opposed to being paired in *R. indica* (Chapter 10; Boatwright et al. 2008c).Asymmetrical stipules were reconstructed as an apomorphy for *Lotononis* s.l. in the combined molecular/morphological analysis, with a reversal in species from sections *Aulacinthus* and *Polylobium*.

BRACTEOLE PRESENCE—The loss of bracteoles appears to be a largely convergent character within the tribe and not unique to *Lotononis* s.l. Bracteoles are absent in *Lotononis* section *Euchlora*, *Leptis* and *Lotononis*, as well as *Rothia* and *Robynsiophyton* (Van Wyk 1991b; Chapter 10; Boatwright et al. 2008c; Chapter 9; Boatwright and Van Wyk 2009). This character was reconstructed as convergences between the groups mentioned before in both the combined molecular and combined molecular/morphological analyses (Fig. 8.5).

CALYX TYPE—The tribe Crotalarieae can be distinguished from Genisteae by the trifid lower lip of the calyx found in the latter. However, two calyx types are found within the Crotalarieae; the lebeckioid calyx type (equally or sub-equally lobed) and the lotononoid calyx type (upper and/or lateral lobes fused higher up than the lower lobes to varying degrees). *Lotononis* s.s., the *Leobordea* clade, the *Listia* clade and *Pearsonia* all have calyces of the lotononoid type, while the remaining genera have the lebeckioid calyx type. The distinction of *Lotononis hirsuta* and *L. macrocarpa* from *Lotononis* s.l. based on this character is notable (Fig. 8.6).

KEEL SHAPE— The shape of the keel is very important to distinguish *Crotalaria* and *Bolusia* from the other genera in Crotalarieae. An extremely rostrate or beaked keel is characteristic of *Crotalaria*, while in *Bolusia* the keel (and style) is twisted through several turns and helically coiled as a result. *Lotononis* section *Oxydium* has often been confused with *Crotalaria* due to the presence of rostrate keels, but can be distinguished from the latter genus by the single stipules and loss of bracteoles (Van Wyk 1991b). The *Listia* and *Leobordea* clades also differ from *Lotononis* s.s. in their obtuse keel petals. Rostrate keel petals are shown to have evolved several times in different lineages of the Crotalarieae by the reconstructions on both the combined molecular and molecular/morphological trees (Fig. 8.7) and this character is convergent between *Crotalaria* and *Lotononis* section *Oxydium*.

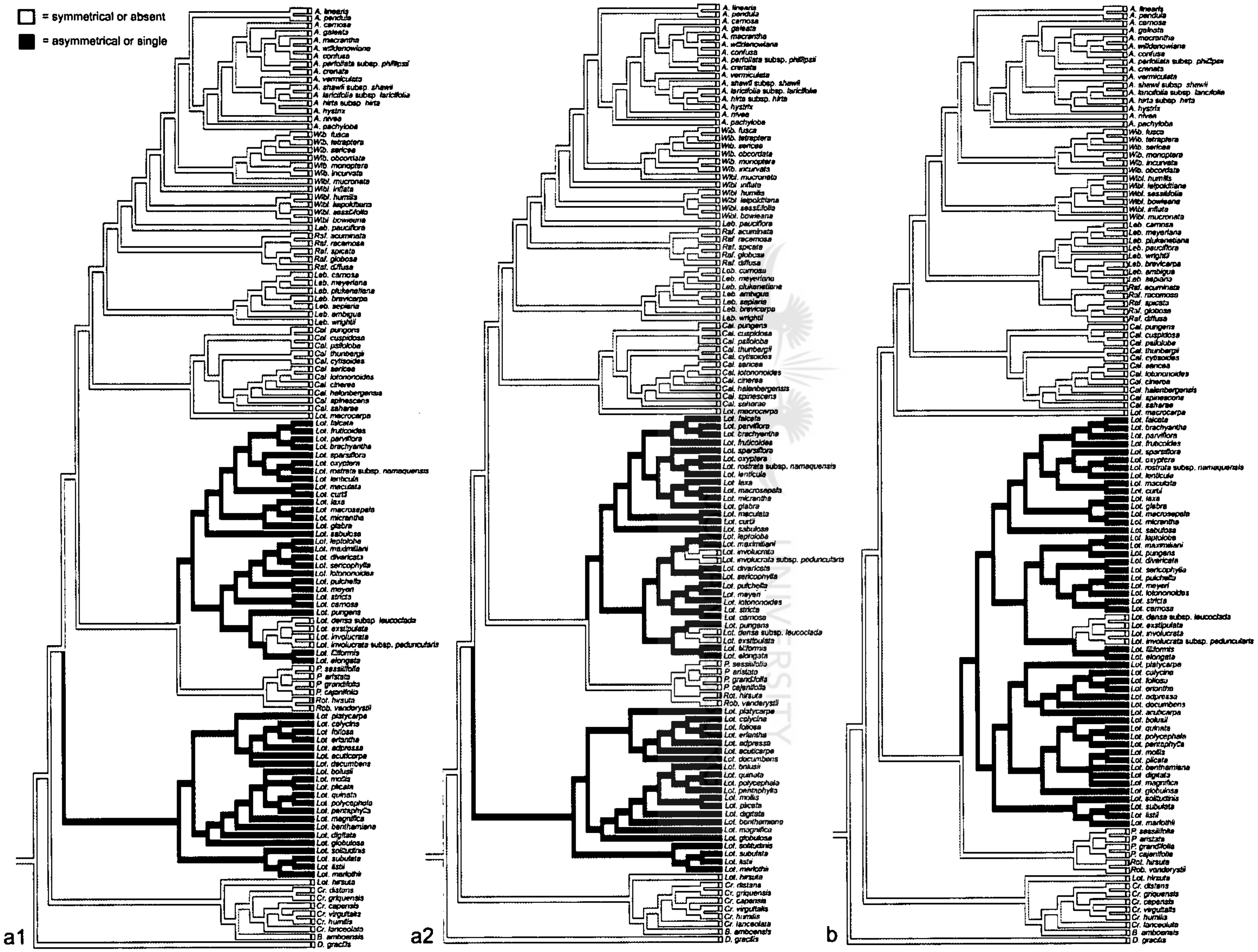

FIG. 8.4 Parsimony-based reconstructions of stipule symmetry (character 3) on the 560 and 370 minimal length trees from the (a1–a2) combined molecular and (b) the combined molecular/morphological analyses, respectively.

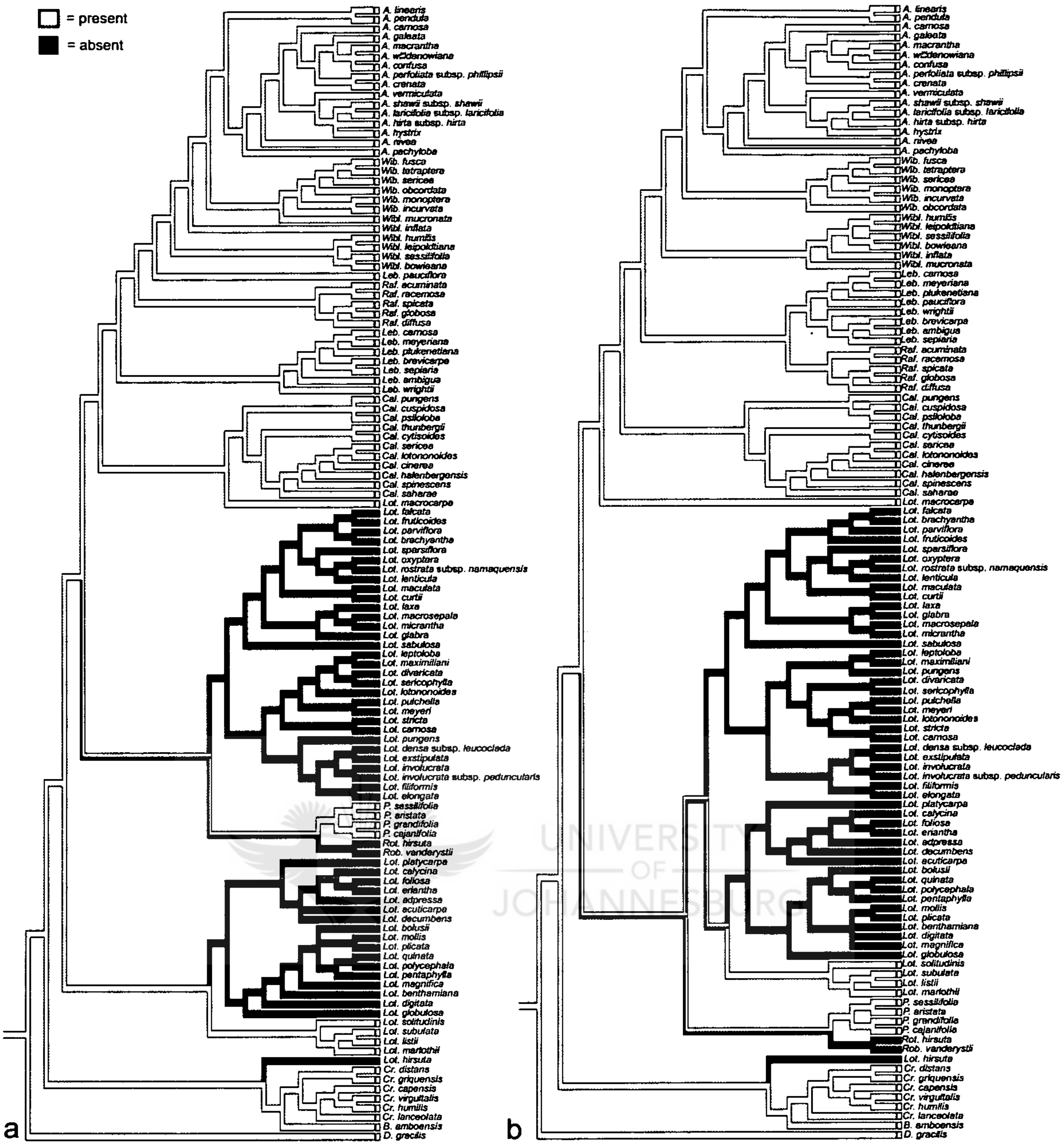

FIG. 8.5 Parsimony-based reconstructions of the presence or absence of bracteoles (character 4) on the 560 and 370 minimal length trees from (a) the combined molecular and (b) the combined molecular/morphological analyses, respectively.

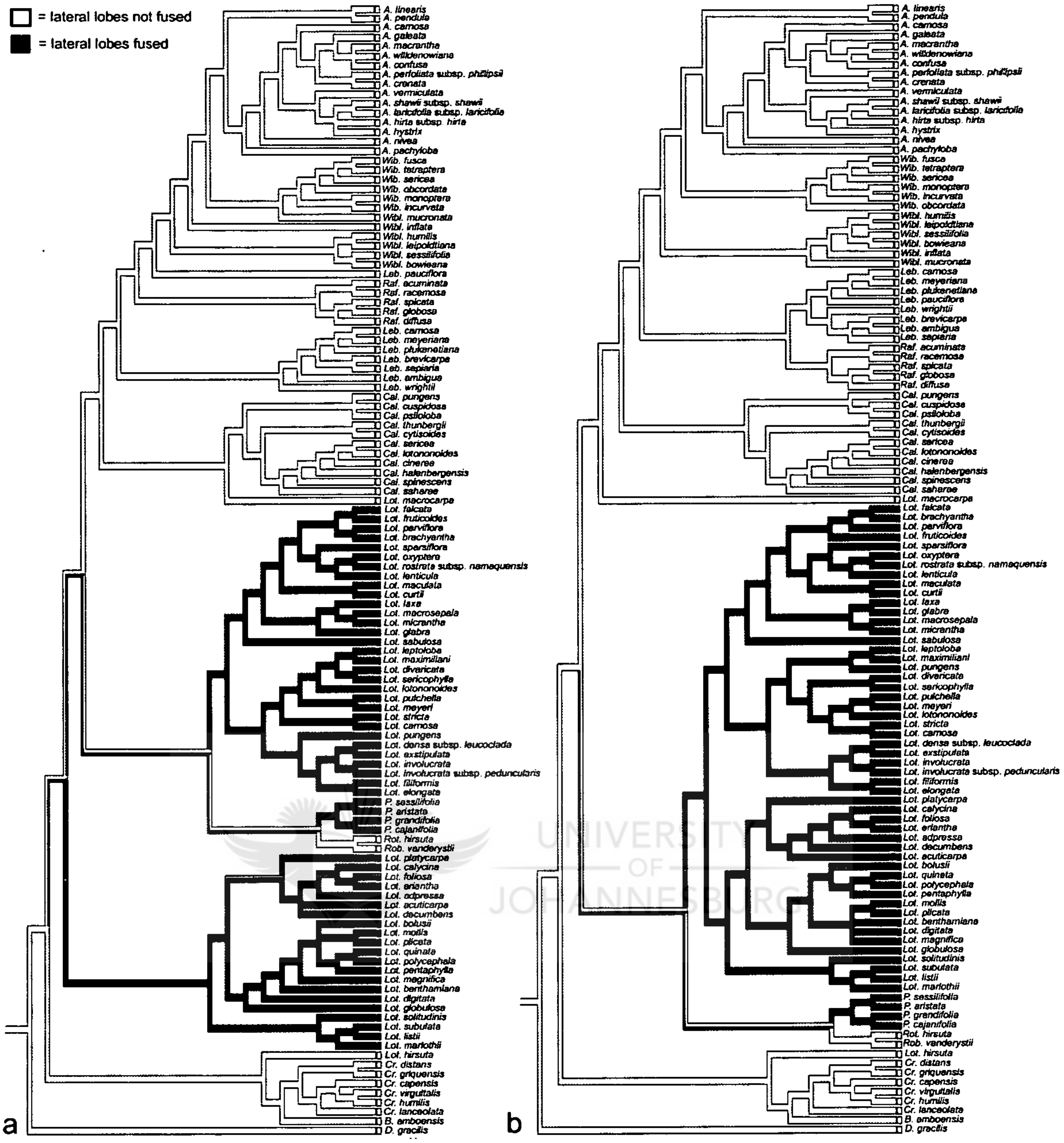

FIG. 8.6 Parsimony-based reconstructions of the calyx type (character 5) on the 560 and 370 minimal length trees from (a) the combined molecular and (b) the combined molecular/morphological analyses, respectively.

ANTHER ARRANGEMENT—Anther dimorphism and arrangement are important within Crotalarieae and informative at the generic level (Chapter 3; Boatwright et al., 2008a; Chapter 5; Boatwright et al., submitted). *Pearsonia*, *Rothia* and *Robynsiophyton* are unique within the tribe in having uniform anthers that are similar in shape and size. The rest of the tribe have dimorphic anthers with alternating dorsifixed and basifixed stamens. The size, shape and attachment of the carinal anther is important and three arrangements are found: 5+5 (carinal anther resembles the basifixed anthers) present in *Bolusia*, *Crotalaria*, *Lebeckia* and *Lotononis macrocarpa*; 4+1+5 (the carinal anther intermediate in between the dorsifixed and basifixed ones) present in *Aspalathus*, *Calobota*, *Lotononis* s.s., the *Listia* clade, *Rafnia* and *Wiborgia*; 6+4 (carinal anther resembling the dorsifixed anthers) present in *Lotononis hirsuta*, the *Leobordea* clade, *Lotononis* s.s. and *Wiborgiella*. Anther arrangement is fairly diagnostic for the genera within the "Cape group", but the distinction within *Lotononis* s.l. is not as clear (Fig. 8.8).

VERRUCOSE UPPER SUTURE OF POD—A verrucose upper suture of the pod was thought to represent a generic apomorphy for *Lotononis* s.l., but this character was reconstructed as a convergence between the *Leobordea* clade, *Lotononis* s.s., *L. hirsuta* and *L. macrocarpa* (Fig. 8.9).

FUNICLE LENGTH—Exceptionally long funicles are only found in species of *Lotononis* s.l. On the trees from the combined molecular analysis this character was reconstructed as a convergence between several lineages (Fig. 8.10). In the combined molecular/morphological analysis it is reconstructed as an apomorphy for *Lotononis* s.l., but it is also present in *L. macrocarpa* (Fig. 8.10).

CHROMOSOME BASE NUMBER—Goldblatt (1981) suggested a base number of x=9 for the tribe Crotalarieae, which seems to be likely from the reconstructions presented here with a reduced number in some genera (Fig. 8.11). *Crotalaria*, *Rafnia* and some *Aspalathus* species have a number of x=8, while some species of *Lotononis* s.s., *Pearsonia* and *Rothia* have a base number of x=7.

CYANOGENESIS—Chemical data are of important systematic value in the Crotalarieae (Van Wyk 2003b). Cyanogenesis was reconstructed as an apomorphy for *Lotononis* s.s. and is absent from the *Leobordea* and *Listia* clades, *Lotononis hirsuta* and *L. macrocarpa* (Fig. 8.12). The superficially similar genera *Pearsonia*, *Rothia* and *Robynsiophyton* are acyanogenic and accumulate esters of hydroxylupanine, a unique character in the Crotalarieae.

MACROCYCLIC PYRROLIZIDINE ALKALOIDS—The presence of pyrrolizidine alkaloids in some sections of *Lotononis* was thought to suggest a sister relationship with *Crotalaria* that also produces such alkaloids (Van Wyk, 1991b). The presence of these alkaloids was reconstructed as a convergence between *Lotononis* s.s. and *Crotalaria* in both the combined molecular and molecular/morphological analyses (Fig. 8.13).

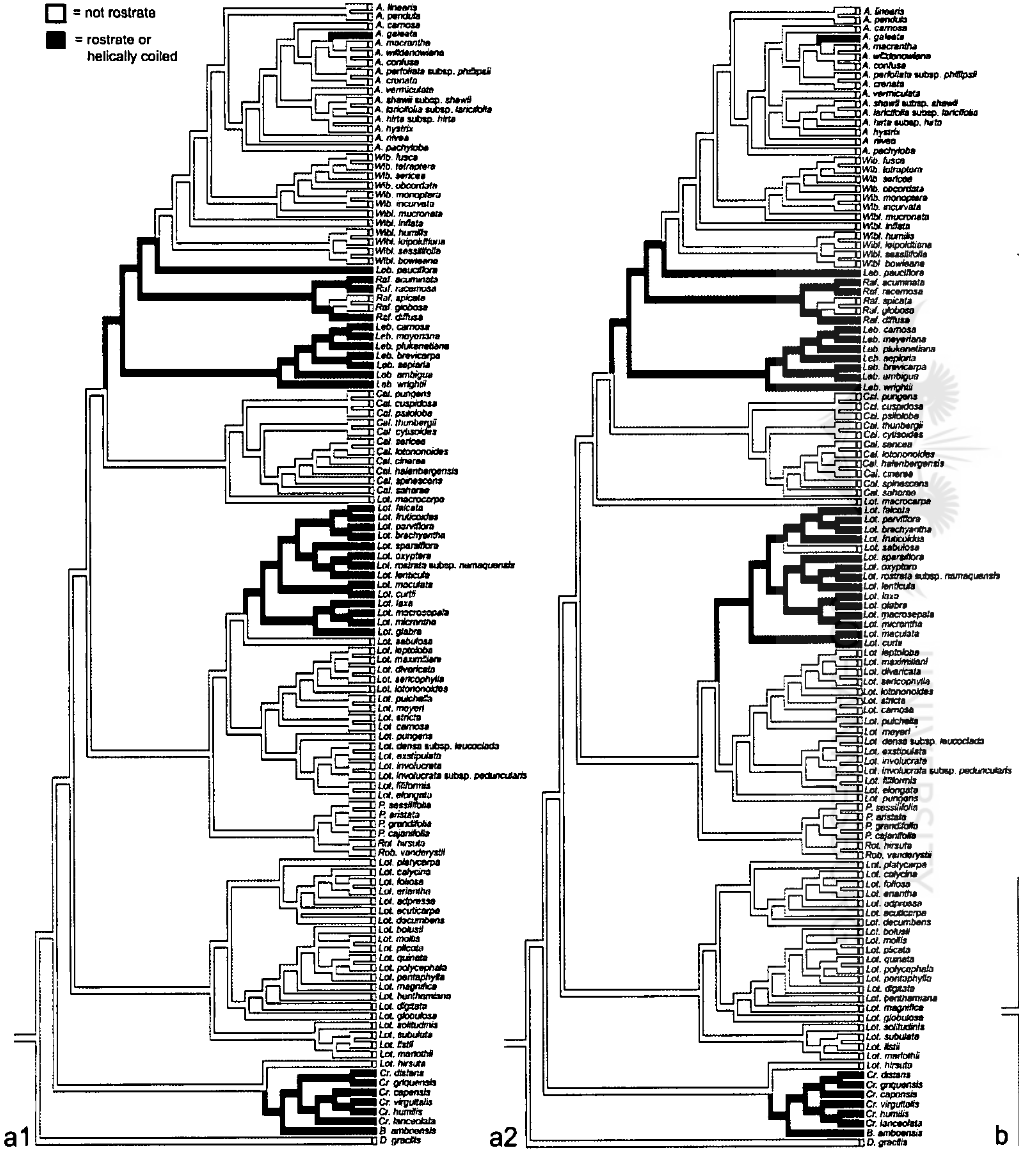

FIG. 8.7 Parsimony-based reconstructions of the presence of rostrate keel petals (character 6) on the 560 and 370 minimal length trees from (a1–a2) the combined molecular and (b) the combined molecular/morphological analyses, respectively.

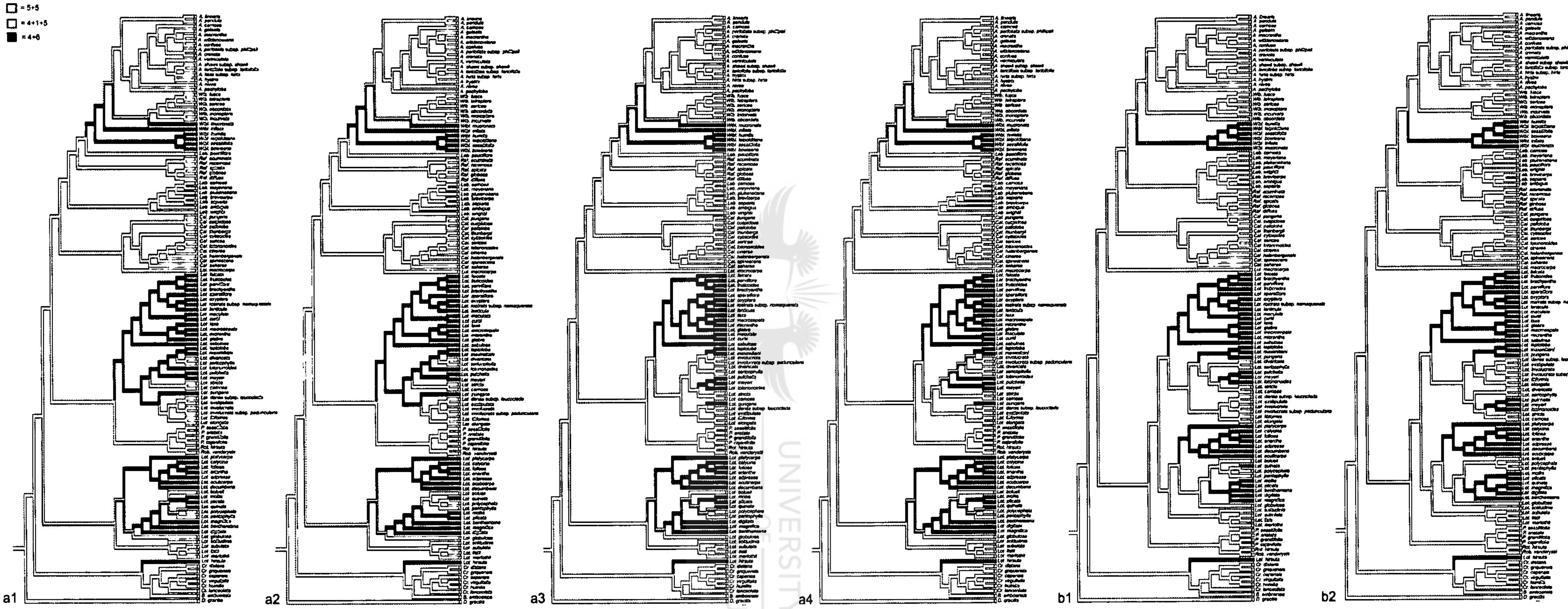

FIG. 8.8 Parsimony-based reconstructions of anther arrangement (character 7) on the 560 and 370 minimal length trees from (a1–a4) the combined molecular and (b1–b2) the combined molecular/morphological analyses, respectively.

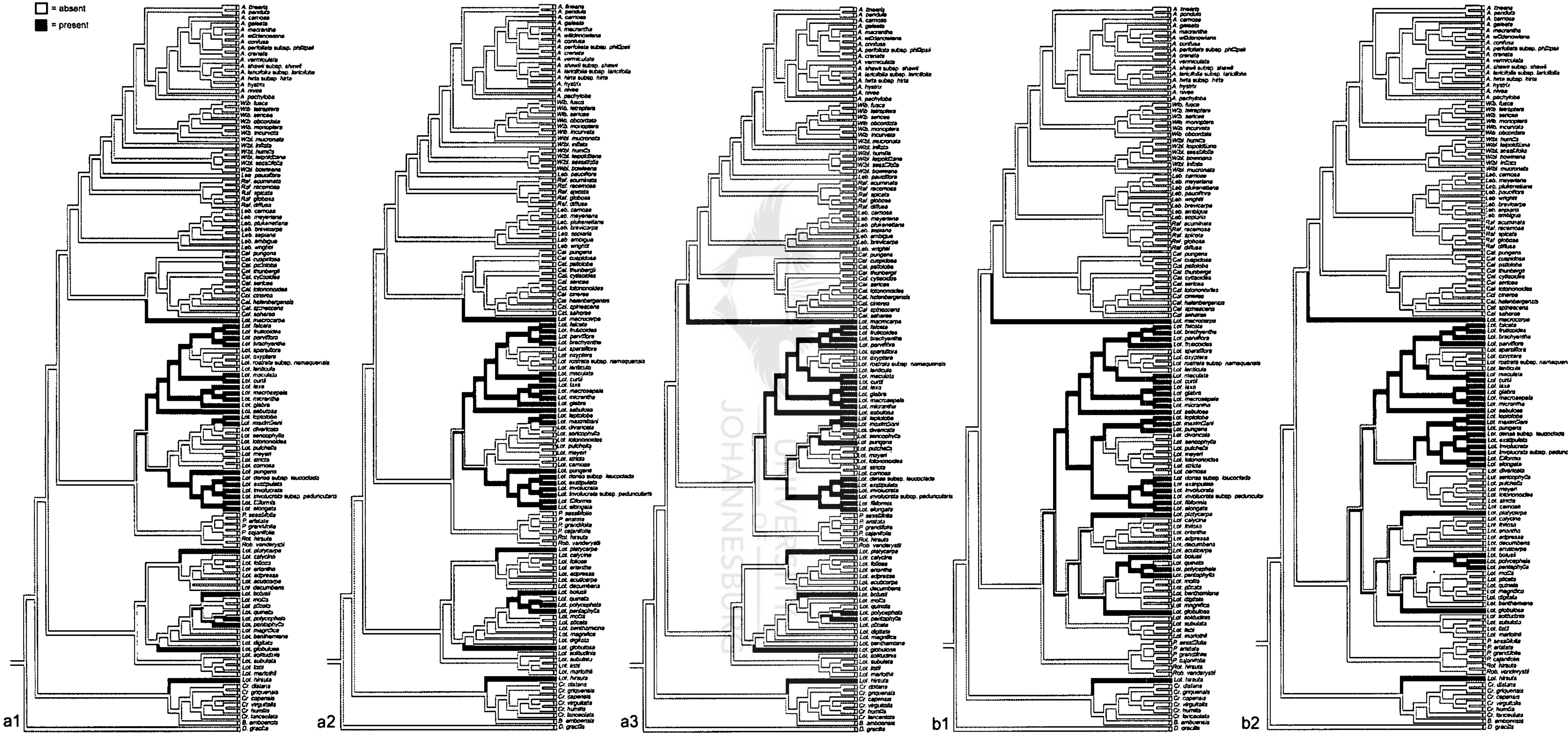

FIG. 8.9 Parsimony-based reconstructions of the presence or absence of a verrucose upper suture of the pod (character 8) on the 560 and 370 minimal length trees from (a1–a3) the combined molecular and (b1–b2) combined molecular/morphological analyses, respectively.

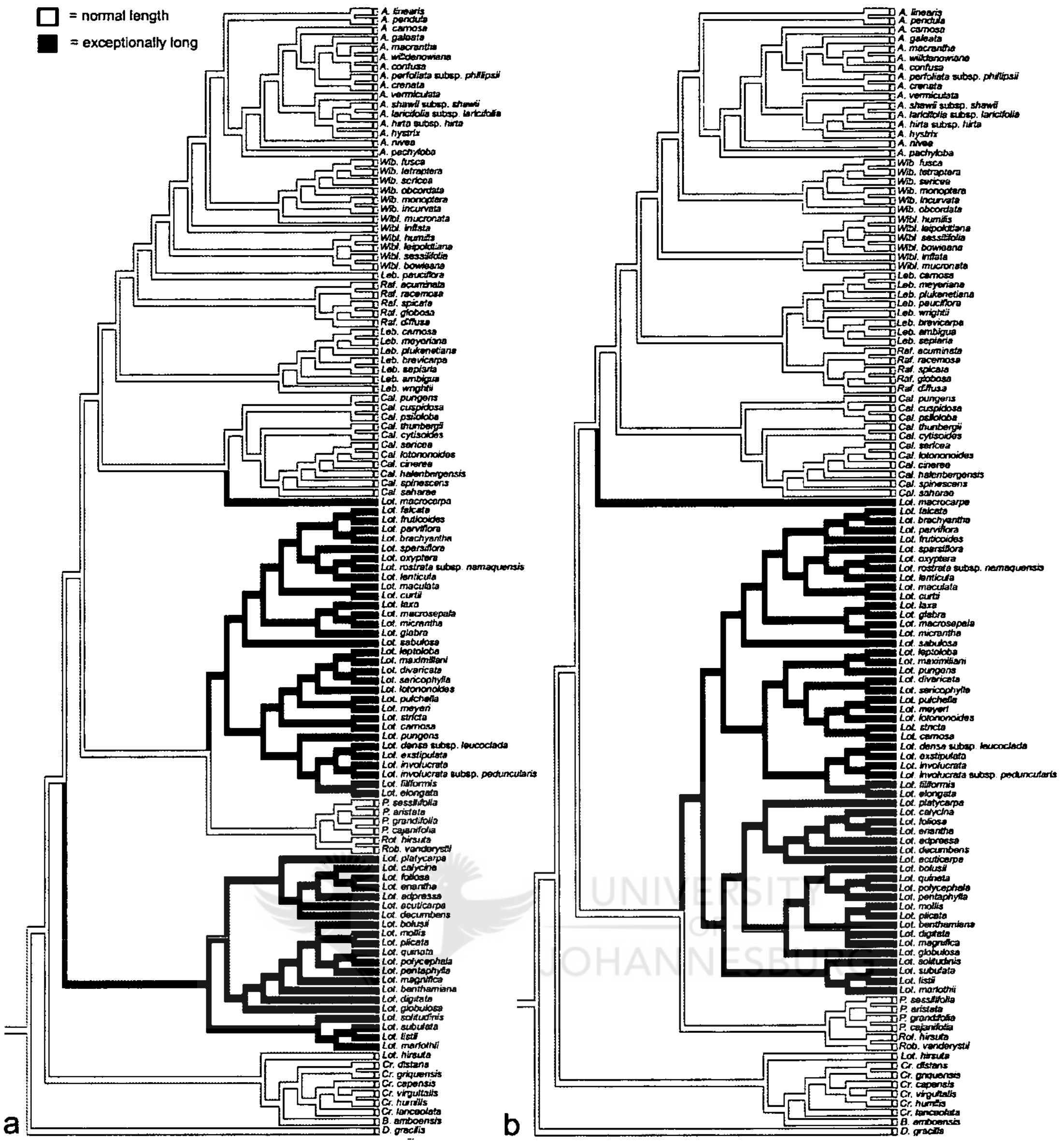

FIG. 8.10 Parsimony-based reconstructions of the funicle length (character 9) on the 560 and 370 minimal length trees from (a) the combined molecular and (b) the combined molecular/morphological analyses, respectively.

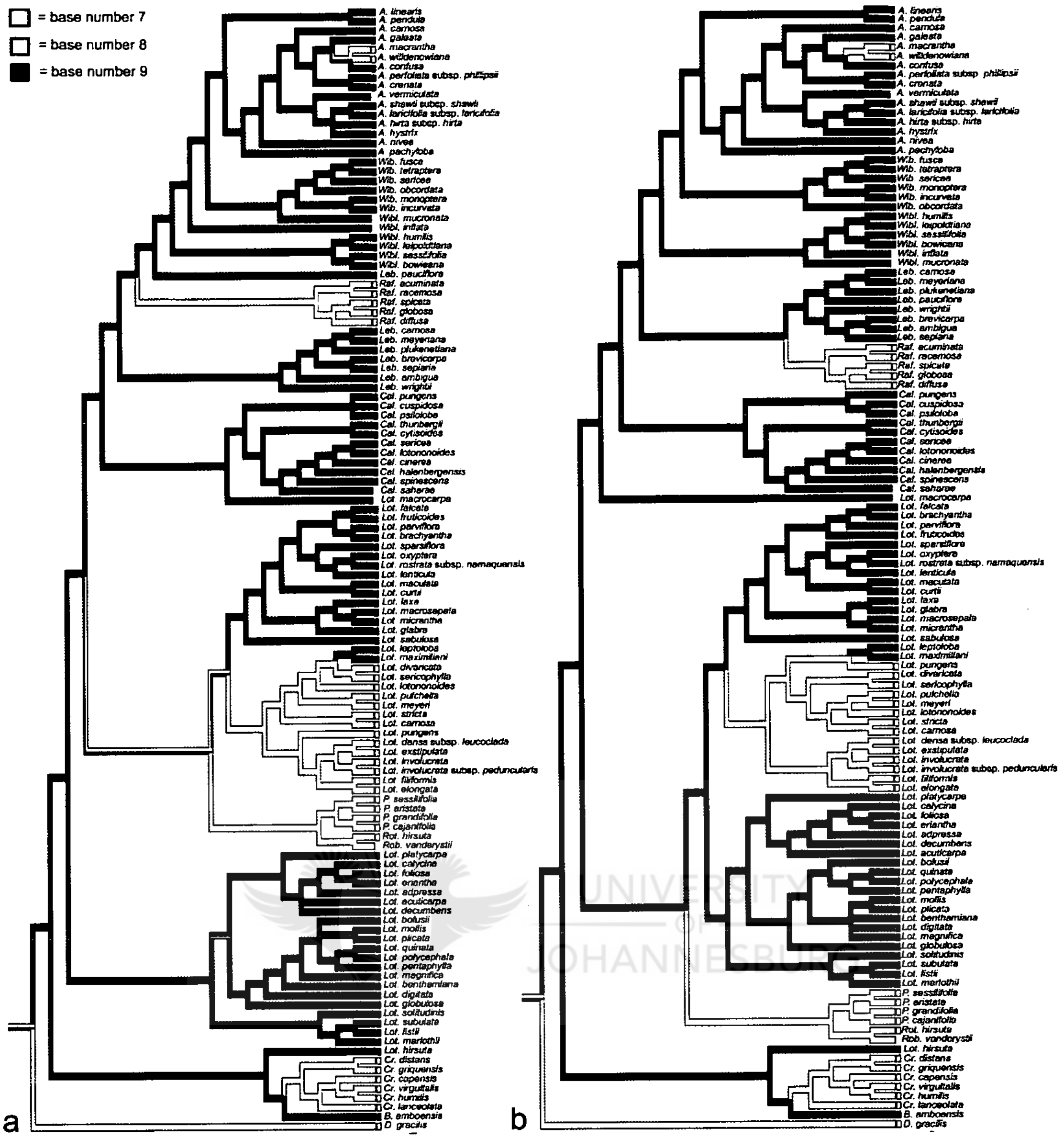

FIG. 8.11 Parsimony-based reconstructions of the chromosome base number (character 10) on the 560 and 370 minimal length trees from (a) the combined molecular and (b) the combined molecular/morphological analyses, respectively.

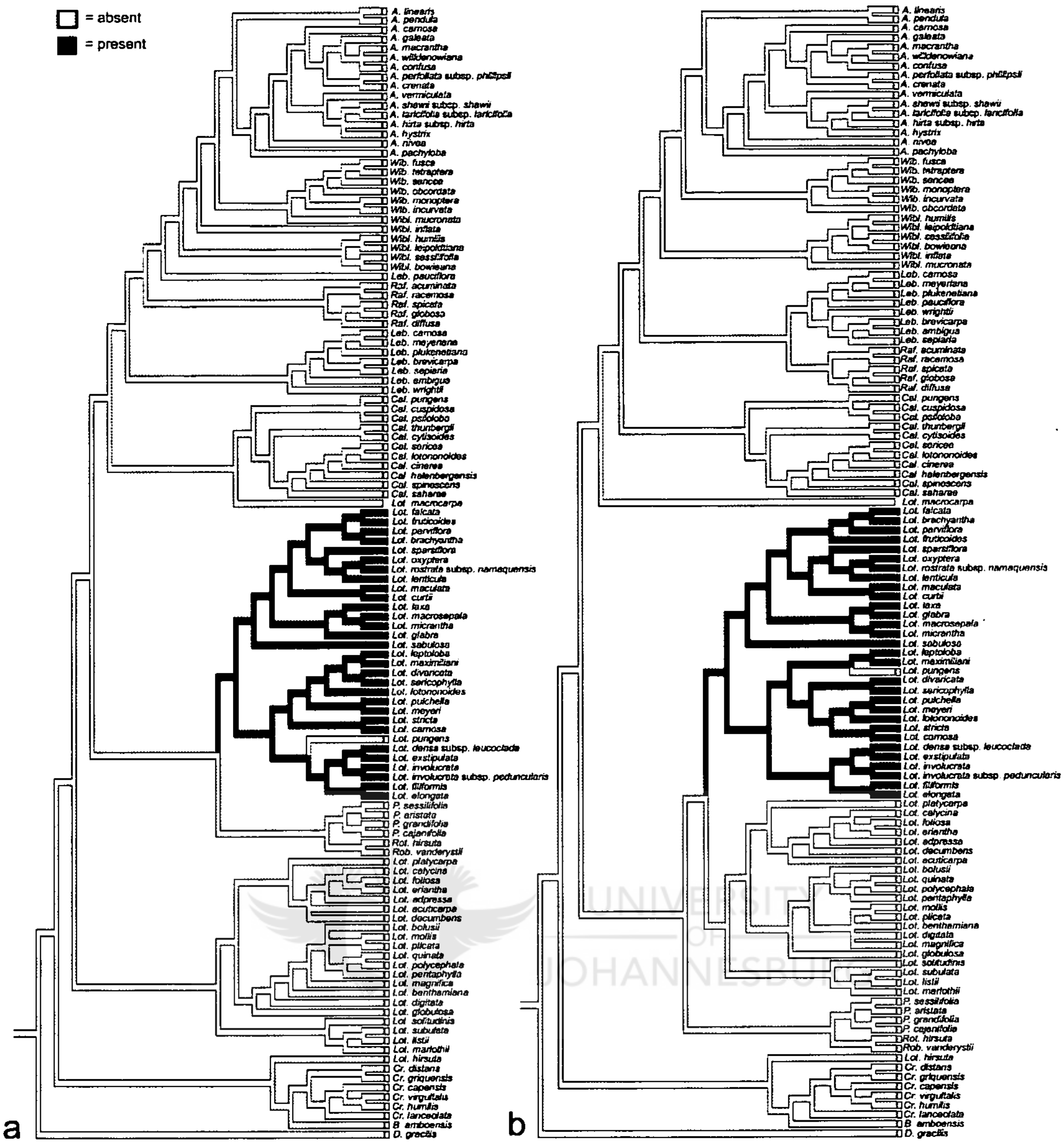

FIG. 8.12 Parsimony-based reconstructions of the presence or absence of cyanogenic glucosides (character 11) on the 560 and 370 minimal length trees from (a) the combined molecular and (b) the combined molecular/morphological analyses, respectively.

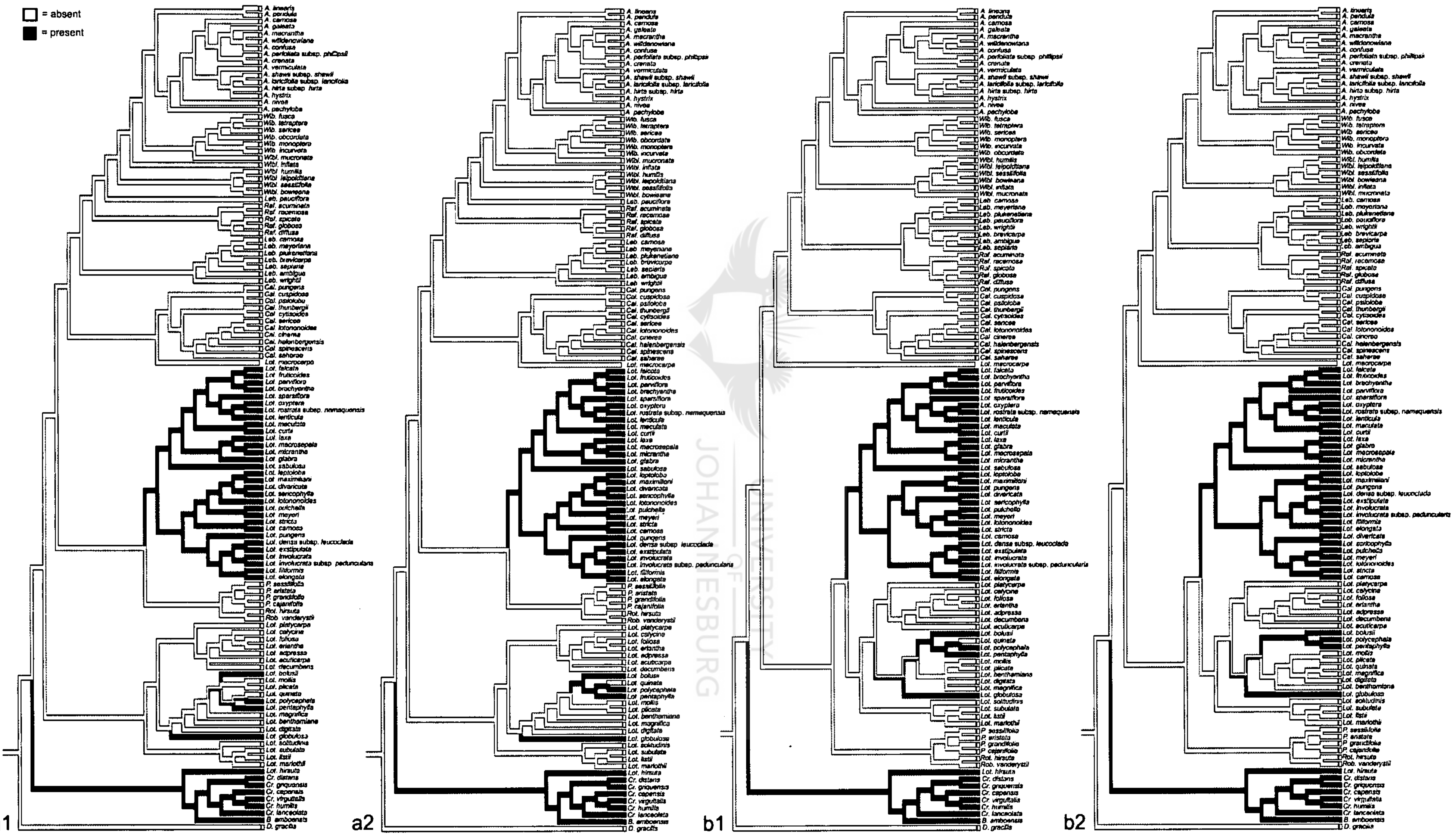

FIG. 8.13 Parsimony-based reconstructions of the presence or absence of macrocyclic pyrrolizidine alkaloids (character 12) on the 560 and 370 minimal length trees from (a1–a2) the combined molecular and (b1–b2) the combined molecular/morphological analyses, respectively.

***8.3.2 Lotononis hirsuta*—** *Lotononis* section *Euchlora* is only distantly related to the rest of *Lotononis*. It is placed within a clade comprising *Crotalaria* and *Bolusia* (100 BP) and this clade represents the earliest diverging lineage within the tribe. The placement of *Lotononis hirsuta* in this clade is supported by the strongly inflated pods and trifoliolate leaves (if present) with paired stipules that are equal in size found in these genera. Dahlgren (1964) transferred this species to *Lotononis* where it was treated as a section by Van Wyk (1991b). This anomalous plant differs markedly from species of *Lotononis* s.s., the *Leobordea* clade and the *Listia* clade by the large underground tuber (geophytic habit), simple, sessile leaves (in some forms), large pods and the subequally lobed calyx. The position of *Lotononis hirsuta* renders two important generic apomorphies for *Lotononis* s.l., to be the result of convergence, namely the loss of bracteoles and the verrucose upper suture of the pod (Van Wyk, 1991b).

***8.3.3 Lotononis s.s.*—**Although the resolution is low in *Lotononis* s.s., some sectional relationships were observed. *Lotononis* section *Oxydium* (BP 98) is sister to a clade with representatives of *L.* sections *Aulacinthus*, *Buchenroedera*, *Cleistogama*, *Krebsia*, *Lotononis*, *Monocarpa* and *Polylobium. Lotononis* section *Oxydium* is a large group comprising 35 species, and is shown to be monophyletic. This section is unique within the *Lotononis* s.s. in the chromosome base number of x=9 (the rest have x=7), the presence of long funicles and also its distribution throughout tropical Africa. The sections *Monocarpa* and *Cleistogama* are sister to each other as was also shown in the chosen cladogram of Van Wyk (1991b) in Fig. 8.14 where this combined clade was also shown to be sister to the section

*Oxydium*. However, Van Wyk (1991b) concluded that the sections *Monocarpa* and *Cleistogama* have their real affinities within the larger group of sections around sections *Polylobium* and *Aulacinthus* and not *Oxydium*. The shared presence of long funicles and a chromosome base number of x=9 in *L.* section *Monocarpa* is reconstructed as the result of convergence rather than common ancestry in Figs. 8.10 and 8.11. *Lotononis* section *Buchenroedera* is embedded within *L.* section *Krebsia*, albeit with low support. These two sections have paired stipules, a character shared only by *L.* sections *Polylobium* and the *Listia* clade. *Lotononis* sections *Aulacinthus* and *Polylobium* are weakly supported to be sister groups, the latter differing from section *Polylobium* in its single stipules and shrubby habit (Van Wyk 1991b). With the exception of section *Oxydium*, *Lotononis* s.s. is endemic to southern Africa. Two sections are mainly found in the eastern parts of southern Africa, namely sections *Krebsia* and *Buchenroedera*, while all the remaining sections are restricted to the Cape and Namaqualand. *Lotononis* section *Monocarpa* occurs in the north-western Cape, while sections *Lotononis*, *Aulacinthus* and *Polylobium* are more or less restricted to the Western Cape Province. *Lotononis* section *Cleistogama* has a more eastern distribution in the Cape region (Van Wyk 1991ba). *Lotononis* s.s. is chemically distinct from the *Leobordea* and *Listia* clades in that its members are cyanogenic (except for *L.* section *Cleistogama*) and accumulate macrocyclic pyrrolizidine alkaloids, the first of which is a synapomorphy for this group.

***8.3.4 The Leobordea clade***—The *Leobordea* clade comprises *L.* section *Leobordea* and its apparent relatives from *L.* sections *Digitata*, *Leptis*, *Lipozygis*, and *Synclistus*. This clade is well-supported as sister to the *Listia* clade as was also shown by Van Wyk (1991b) in his chosen cladogram (Fig. 8.14). The *Leobordea* clade shares with the *Listia* clade (and differs from *Lotononis* s.s.) the rounded keel petals, acyanogenesis and a chromosome base number of x=9, all pleisiomorphic states. The two groups differ in the non-stoloniferous habit, single stipules that are sometimes similar to the leaflets, pubescent vegetative and reproductive parts, absence of bracteoles (except in two species) and 4+6 anther arrangement (very rarely 4+1+5) found in the *Leobordea* clade. The latter group is also characterised by its wide distribution range throughout southern and tropical Africa. Sections *Leptis* and *Leobordea* extend into the Mediterranean region of Africa, with *L. genistoides* (section *Leptis*) extending into Europe and *L. platycarpa* (section *Leobordea*) extending into Pakistan and the Cape Verde Islands. Sections *Synclistus* and *Digitata* both occur in the north-western Cape, while section *Lipozygis* occurs in the eastern parts of southern Africa (Van Wyk 1991b).

***8.3.5 The Listia clade***—The *Listia* clade is a very distinct group with a unique combination of characters: stoloniferous habit, paired stipules, presence of bracteoles and a 4+1+5 anther arrangement (Van Wyk 1991b). The concept of Meyer's (1836) monotypic genus *Listia* was broadened by Van Wyk (1991b) and included as a section of *Lotononis*. It is interesting to note that the species of *Listia* have lupinoid (sleeve-like) root nodules (as are also found in the genus *Lupinus*) and not the conventional types that are present in all other species of *Lotononis* (and indeed all Crotalarieae) hitherto investigated (Yates et al. 2007). The species of this group are distributed throughout southern and tropical Africa.

***8.3.6 Lotononis macrocarpa*—** *Lotononis macrocarpa* was included in *Lotononis* section *Listia* as a distinct subsection (subsection *Macrocarpa*) by Van Wyk (1991b) based mainly on the presence of bracteoles and superficial similarities with the other species in *Listia* that were taken at face value. However, this anomalous species is unique in the 5+5 anther arrangement, equally lobed calyx, large fruit and systematic placement close to the "Cape group" of the Crotalarieae demonstrated in this study. It is endemic to the south-western Cape and geographically isolated from the rest of the *Listia* group. Based on the unique combination of characters found in this plant and the fact that it allies with the "Cape group" in the molecular study, it is here recognized as a monotypic genus.

***8.3.7 Generic circumscription*—**The close agreement of the relationships within *Lotononis* s.s. found in Chapter 3 (Boatwright et al. 2008a) and this study with those proposed by Van Wyk (1991a) is notable (Fig. 8.14). The only difference is the inclusion of *L.* section *Euchlora* in *Lotononis* and the sister relationship proposed between section *Oxydium* and sections *Cleistogama* and *Monocarpa*. The cladogram from Van Wyk (1991b), based on vegetative and reproductive morphological, cytological and chemical characters (Fig. 8.14), also shows *Lotononis* section *Listia* (the *Listia* clade) as sister to *L.* sections *Digitata*, *Leobordea*, *Leptis*, *Lipozygis*, and *Synclistus*, the *Leobordea* clade. This clade is sister to *L.* sections *Aulacinthus*, *Buchenroedera*, *Cleistogama*, *Euchlora*, *Krebsia*, *Lotononis*, *Monocarpa*, *Oxydium* and *Polylobium,* i.e. *Lotononis* s.s. (excluding section *Euchlora*).

Dahlgren (1970a) discussed some examples of convergence and parallelisms in the tribe, but the results presented in this study have uncovered that the relationships within the Crotalarieae are even more complex (Chapter 3; Boatwright et al. 2008a; Chapter 5; Boatwright et al. submitted) and revealed more examples of convergent evolution of morphological and chemical characters. Characters thought to be unique to certain groups, especially *Lotononis* s.l., have proven to be shared by distantly related groups. Due to the extreme overlap of character states in the genera of the Crotalarieae, unique generic apomorphies are frequently not available and a combination of characters is necessary for generic circumscription. The original generic concept of *Lotononis* s.l. is here shown to be polyphyletic, largely due to the positions of *L. macrocarpa* and *L. hirsuta* and also the paraphyly of *Lotononis* s.l. shown by combined molecular evidence. Despite weak support for the monophyly of *Lotononis* s.l. in the combined molecular/morphological analysis a narrower concept of *Lotononis* can be better circumscribed in light of the lack of generic apomorphies for *Lotononis* s.l. The recognition of smaller, monophyletic groups is now more practical and therefore the reinstatement of *Euchlora*, *Leobordea* and *Listia* is proposed and *Ezoloba* described as a new genus to accommodate *Lotononis macrocarpa*. Unique combinations of characters are available to circumscribe these genera that are strongly supported as monophyletic in the phylogenetic analyses presented in this Chapter and Chapter 3 (Boatwright et al. 2008a).

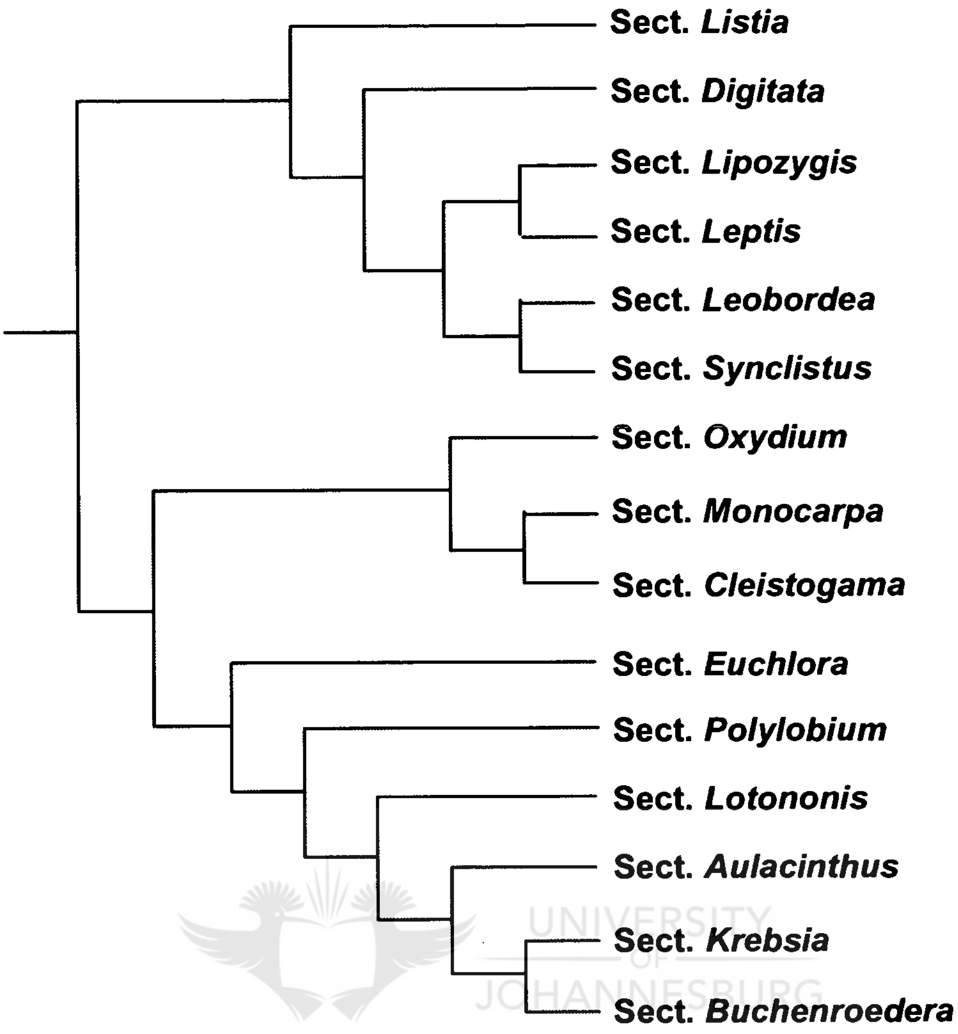

FIG. 8.14 Chosen cladogram (Fig. 17) from Van Wyk (1991b) based on morphological, cytological and chemical data.

## 8.4 TAXONOMIC TREATMENT

### *8.4.1 Key to the genera of the Crotalarieae*

1. Stipules absent (if stipules rarely present then leaves acicular and keel spirally twisted)........................................................................2

2. Calyx zygomorphic (upper and lateral lobes on either side fused higher up in pairs)............................................***Lotononis*** (partly)

2. Calyx subequally lobed........................................................................3

3. Style with 1-2 lines of hairs................................***Crotalaria***

3. Style glabrous..........................................................................4

4. Bracteoles absent, leaves (at least the basal ones) simple, flat and sessile; geophyte with large underground tuber........................................................***Euchlora***

4. Bracteoles present, leaves (is simple and flat) not sessile; annuals, suffrutices or shrubs........................5

5. Leaves acicular, terete........................................................................6

6. Ovary 2 to 4 ovulate, pods 1 to ±2-seeded..........***Aspalathus***

6. Ovary with more than 6 ovules, pods many-seeded..***Lebeckia***

5. Leaves digitate, unifoliolate or simple (flat, never terete)...................7

7. Upper suture of pod asymmetrically convex........................8

8. Plants glabrous except occasionally on bracts and bracteoles, usually turning black when dried..........***Rafnia***

8. Plants usually pubescent on all parts, if leaves glabrous then standard petal hairy and inner surface of calyx glabrous........................................***Aspalathus***

7. Upper suture of pod symmetrically convex........................9

9. Petals pubescent, if glabrous then plants strongly spinescent shrubs; twigs green (bark formation late); leaves isobilateral............................................***Calobota***

9. Petals glabrous; twigs brown (bark formation early), if twigs rarely green then plant an annual fireweed; leaves dorsiventral............................................................10

10. Fruits winged, indehiscent; carinal anther intermediate (anthers 4+1+5)................***Wiborgia***

10. Fruits without wings, dehiscent (if rarely indehiscent then ovary and fruit distinctly stalked); carinal anther resembles short anthers (anthers 4+6)..........................................***Wiborgiella***

1. Stipules present .................................................................11

11. Style straight or rarely down-curved, anthers similar in size and shape..................................................................................12

12. Stamens nine (five fertile and four lacking anthers)................................................***Robynsiophyton***

12. Stamens 10 (all fertile)..............................................13

13. Anthers monomorphic, prostrate annuals.......***Rothia***

13. Anthers slightly dimorphic, four basifixed, six attached slightly higher up, all elongate, perennial herbs or shrubs.................................................. ***Pearsonia***

11. Style curved upwards, anthers dimorphic.................................14

14. Bracteoles absent.....................................................15

15. Geophyte with woody tuber, leaves (at least the basal ones) flat, simple and sessile.......................... ***Euchlora***

15. Annuals, suffrutices, shrubs, leaves is flat and simple then not sessile..................................................16

16. Stipules paired or absent .........................17

17. Keel obtuse, hairy................ ***Leobordea***

17. Keel beaked, glabrous.......... ***Lotononis***

16. Stipules dimorphic or single.......................18

18. Keel obtuse, hairy................ ***Leobordea***

18. Keel beaked, glabrous.......... ***Lotononis***

14. Bracteoles present.....................................................19

19. Keel obtuse..................................................20

20. Calyx subequally lobed; fruit more than 20 mm long; stems without adventitious roots; seeds ± 4 mm long; anthers 5+5.............................. ***Ezoloba***

20. Calyx zygomorphic (upper and lateral lobes on either side fused higher up in pairs); fruit less than 20 mm long; stems often with adventitious roots; seeds ± 1 mm long; anthers 4+1+5.............. ***Listia***

19. Keel beaked or helically coiled............................21

21. Keel and style helically coiled through several turns......................................................***Bolusia***

21. Keel and style not helically coiled.....***Crotalaria***

### *8.4.2 Taxonomy*

1. EZOLOBA B.-E.van Wyk and Boatwr., gen. nov., similar to *Listia* E.Mey. but differs in the equally sized stipules, sub-equally lobed calyx, 5+5 anther arrangement, large pods (more than 20 mm long) and seeds (more than 4 mm long) and the non-stoloniferous habit (to be translated into Latin).—TYPE species: *Ezoloba macrocarpa* (Eckl. and Zeyh.) B.-E.van Wyk and Boatwr.

The generic concept proposed here is based on a unique combination of characters, namely the stipules that are equal in size, the sub-equally lobed calyx, presence of bracteoles, 5+5 anther arrangement, the very large fruit with a warty upper suture and the large seeds. The molecular and morphological evidence presented here indicates that this species is more closely related to the "Cape group" of the Crotalarieae than to *Lotononis* s.l. The single species is known from only a few localities in the Western Cape Province of South Africa. The generic name commemorates Ecklon and Zeyher who first described this species.

EZOLOBA MACROCARPA (Eckl. and Zeyh.) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis macrocarpa* Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 176.

1836.—TYPE: SOUTH AFRICA, Cape Province, Brackfontein, Clanwilliam, *Ecklon and Zeyher 1271* (lectotype: S!, designated by Van Wyk [1991b]; isolectotypes: C!, S!, SAM!, isolecto.).

2. EUCHLORA Eckl. and Zeyh., Enum Pl. Afr. Austr. 2: 171. 1836. *Microtropis* E.Mey., Comm. Pl. Afr. Austr. 1(1): 65. 1836. *Lotononis* section *Euchlora* (Eckl. and Zeyh.) B.-E.van Wyk, Contr. Bol. Herb. 14: 213. 1991b.—TYPE species: *Euchlora serpens* (E.Mey.) Eckl. and Zeyh.

The genus is easily recognisable by the large underground tuber, simple, sessile leaves (in some forms) and the large, inflated pods. The results presented here indicate that this genus forms part of the early diverging elements of the Crotalarieae and is closely related to *Bolusia* and *Crotalaria*. The single species occurs in the Northern and Western Cape Provinces of South Africa.

EUCHLORA HIRSUTA (Thunb.) Druce in Rep. Bot. Exch. Cl. Brit. Isles 1916: 622. 1917. ≡ *Ononis hirsuta* Thunb., Prodr. Pl. Cap.: 129. 1800. *Microtropis hirsuta* (Thunb.) E.Mey., Comm. Pl. Afr. Austr. 1(1): 65. 1836. *Lotononis hirsuta* (Thunb.) D. Dietr., Syn. Pl. 4: 960. 1847.—TYPE: SOUTH AFRICA, Cape Province, 'prope Cap juxta Leuwestaart', *Thunberg s.n. sub THUNB-UPS 16614* (lectotype: UPS!, designated by Dahlgren [1964]).

*Crotalaria serpens* E.Mey. in Linnaea 7: 153. 1832. *Euchlora serpens* (E.Mey.) Eckl. and Zeyh., Enum Pl. Afr. Austr. 2: 171 .1836. *Lotononis serpens* (E.Mey.) Dahlgr. in Bot. Not. 117: 373. 1964. *nom superfl.*—TYPE:

SOUTH AFRICA, Cape Province, ‘Sandige Stellen unweit Salzrivier’, *Ecklon s.n.* (lectotype: S!, designated by Dahlgren [1964]).

3. LISTIA E.Mey., Comm. Pl. Afr. Austr. 1(1): 80. 1836. *Lotononis* section *Listia* (E.Mey.) B.-E.van Wyk, Contr. Bol. Herb. 14: 99. 1991b.—TYPE species: *Listia heterophylla* E. Mey.

The concept of *Listia* proposed here conforms to that of *Lotononis* section *Listia* subsection *Listia* as described by Van Wyk (1991b), which includes seven species. The genus can be distinguished from especially *Ezoloba*, *Lotononis* s.s. and *Leobordea* by a unique combination of characters: stoloniferous habit, paired, dimorphic stipules, presence of bracteoles, 4+5+1 anther arrangement, largely glabrous petals and pods, the latter often folded like a concertina. The root nodules differ from all other members of the Crotalarieae in being lupinoid (sleeve-like). The species mainly occur in the interior of southern Africa, but *L. angolensis* and *L. heterophylla* extend into central Africa.

LISTIA ANGOLENSIS (Welw. ex Bak.) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis angolensis* Welw. ex. Bak. in Oliv. Fl. Trop. Afr. 2: 6. 1871.—TYPE: ANGOLA, Huilla District, *Welwitsch 1896* (lectotype: BM!, designated by Van Wyk [1991b]; isolectotypes: BM!, C!, K!); Angola, Pungo Andongo District, *Welwitsch 1895* (BM!).

LISTIA BAINESII (Bak.) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis bainesii* Bak. in Oliv., Fl. Trop. Afr. 2: 6. 1871.—TYPE: In the interior near the Tropic of Capricorn, *Chapman and Baines s.n.* (holotype: K!).

LISTIA HETEROPHYLLA E.Mey., Comm. Pl. Afr. Austr. 1(1): 81. 1836. *Lotononis listii* Polhill in Bot. Syst. 1: 324. 1976.—TYPE: SOUTH AFRICA, Cape Province, Gaatje, *Drège s.n. a* (lectotype: K!, Herb. Benth. specimen, designated by Van Wyk [1991b]; isolectotypes: BM!, K!, Herb. Hook. specimen, S!); Cape Province, 'prope Wild. schutshoek', *Drège s.n. b* (BM!, K!, S!).

LISTIA MARLOTHII (Engl.) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis marlothii* Engl. in Engl., Bot. Jahrb. 10: 26. 1888.—TYPE: SOUTH AFRICA, Cape Province, Griqualand West, Kimberley, *Marloth 765* (lectotype: K!, Herb. Engl. specimen, designated by Van Wyk [1991b]; isolectotypes: BOL!, K!, PRE!).

LISTIA MINIMA (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis minima* B.-E.van Wyk in S. Afr. J. Bot. 54(6): 628. 1988.—TYPE: SOUTH AFRICA, Cape Province, Kenhardt Div., Jagbult, floor of Uilpan, *Acocks 12664* (holotype: PRE!; isotype: K!).

LISTIA SOLITUDINIS (Dümmer) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis solitudinis* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 297. 1913.—TYPE: SOUTH AFRICA, Vaal River, *Wilms 400* (holotype: BM!).

LISTIA SUBULATA (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis subulata* B.-E.van Wyk in Bothalia 20(1): 79. 1990. —TYPE: SOUTH AFRICA, Transvaal, Parys, near bridge over Vaal River on Potchefstroom Road, *B.-E. van Wyk 2884* (holotype: PRE!; isotypes: JRAU!, K!, MO!, S!).

4. LEOBORDEA Del. in Laborde, Fragm. fl. Arabie Pétrée (1830) emend. B.-E.van Wyk and Boatwr., emend nov. *Lotononis* section *Leobordea* (Del.) Benth. in Hook., Lond. J. Bot. 2: 607 (1843).—LECTOTYPE species: *Leobordea lotoidea* Del. [*Lotononis platycarpa* (Viv.) Pic.–Serm.].

*Leptis* E.Mey. ex Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 174 (Jan. 1836). *Lotononis* section *Leptis* (E.Mey. ex Eckl. and Zeyh.) Benth. *emend.* B.-E van Wyk in Contr. Bol. Herb. 14: 124. 1991b.—LECTOTYPE species: *Leptis debilis* Eckl. and Zeyh. [*Lotononis prolifera* (E.Mey.) B.-E.van Wyk].

*Lotononis* section *Digitata* B.-E.van Wyk, Contr. Bol. Herb. 14: 107. 1991b.—TYPE species: *Lotononis digitata* Harv.

*Lipozygis* E.Mey., Comm. Pl. Afr. Austr. 1(1): 80 (1836, Feb. or later) *Lotononis* section *Lipozygis* (E.Mey.) Benth. *emend.* B.-E.van Wyk, Contr. Bol. Herb. 14: 114. 1991b.—LECTOTYPE species: *Lipozygis corymbosa* E.Mey. [now *Leobordea corymbosa* (E.Mey.) B.-E.van Wyk and Boatwr.].

*Lotononis* section *Synclistis* B.-E.van Wyk, Contr. Bol. Herb. 14: 157. 1991b.—TYPE species: *Lotononis longicephala* B.-E.van Wyk [*Leobordea longicephala* (B.-E.van Wyk) B.-E.van Wyk and Boatwr.].

[Note: *Leobordea* is here reinstated and its concept broadened to include *Lotononis* sections *Digitata*, *Lipozygis*, *Leptis*, *Leobordea* and *Synclistus*. Of the names available for the generic concept proposed here, *Amphinomia* is the oldest. This genus was described by De Candolle (1925) based on a plate of *Connarus decumbens* Thunb. in Roem. Arch. Bot. 1, 1: 1796. The identity of this species is, however, has until now been unclear. Gillet and Bullock (1957) mentioned that *Connarus decumbens* might not even be a legume and that *Amphinomia* is possibly not a synonym of *Lotononis*. A reinvestigation of the type specimen of *Connarus decumbens* in UPS has provided clarity regarding the identity of this plant. The unusual vestiture of the calyx (hairs in rows along the veins) and the short, few-seeded pods of the specimen are diagnostic characters of *Lotononis pallens* (Eckl. and Zeyh.) Benth. In light of this discovery, *Amphinomia* in actual fact represents a synonym of *Lotononis* s.s. Since *Amphinomia* has already been rejected in favour of *Lotononis* and *Leobordea* (Rickett 1960; Lanjouw et al. 1966), *Leobordea* is thus the oldest available name that can here be considered for reinstatement.]

The genus *Leobordea* now includes 51 species that occur mostly in the eastern parts of South Africa and extend into tropical Africa and the Meditteranean region. They can be distinguished from especially *Listia* by the habit that is never stoloniferous, the single stipules that are sometimes similar to the leaflets, pubescent vegetative and reproductive parts, abscence of bracteoles (except in two species) and 4+6 anther arrangement (very rarely 4+5+1). After *Lotononis* s.s. which now comprises 90 species, this is the largest of the genera proposed here. The species have been classified into distinct sections by Van Wyk (1991b). The number of species sampled for the molecular studies does not allow for a proper evaluation of the infrageneric classification system. Pending further studies, the species are simply listed alphabetically below. See Van Wyk (1991b) for complete synonymies as well as keys to the sections and species. Fortunately, the nomenclature of the 90 species remaining in *Lotononis* s.s. are not affected (see Van Wyk 1991b).

LEOBORDEA ACUTICARPA (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis acuticarpa* B.-E.van Wyk in Bothalia 20: 21. 1990. TYPE: SOUTH AFRICA, Gauteng, Springs district, 5 km from Devon radar station to Leandra, *Van Wyk 1815* (holotype: PRE!; isotypes: JRAU!, K!, MO!, NBG!).

LEOBORDEA ADPRESSA (N. E. Br.) B.-E.van Wyk and Boatwr., comb. nov. Two subspecies are recognised:

a. LEOBORDEA ADPRESSA (N. E. Br.) B.-E.van Wyk and Boatwr. subsp. ADPRESSA. *Lotononis adpressa* N. E. Br. subsp. *adpressa. Lotononis adpressa* N. E. Br. in Kew. Bull. 1906: 18. 1906.—TYPE: SOUTH AFRICA, Natal, Stony hill near Charlestown, *Wood 5712* (holotype: K!).

b. LEOBORDEA ADPRESSA (N. E. Br) B.-E.van Wyk and Boatwr. subsp. LEPTANTHA B.-E.van Wyk. *Lotononis adpressa* N. E. Br. subsp. *leptantha* B.-

E.van Wyk in Contr. Bol. Herb. 14: 141. 1991b.—TYPE: SOUTH AFRICA, Gauteng, Farm Waterval, 2 miles [3.2 km] WNW of Krugersdorp, *Mogg 22844* (holotype: PRE!; isotypes: PRE!, 2 sheets).

LEOBORDEA ANTHYLLOIDES (Harv.) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis anthylloides* Harv. in Harv. and Sond., Fl. Cap. 2: 59. 1862. *Lotononis anthyllopsis* B.-E.van Wyk in Contr. Bol. Herb. 14: 164. 1991b.—TYPE: SOUTH AFRICA, Cape Province, Namaqualand, *Wyley s.n.* (holotype: TCD; isotypes K!, S!).

LEOBORDEA ARIDA (Dümmer) B.-E. van Wyk and Boatwr., comb. nov. *Lotononis arida* Dümmer in Trans R. Soc. S. Afr. 3(2): 324. 1913.—TYPE: SOUTH AFRICA, Cape Province, mountain tops, Eland's Hoek near Aliwal North, *F. Bolus 31 sub BOL 10559* (lectotype: K!, designated by Van Wyk [1991b]; isolectotype: BOL!).

LEOBORDEA BENTHAMIANA (Dümmer) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis benthamiana* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 294. 1913.—TYPE: SOUTH AFRICA, Western Region, Little Namaqualand: Near Ookiep, *Scully s.n. sub Herb. Norm. Austr. Afr. 1127* (lectotype: K!, designated by Van Wyk [1991b]; isolectotypes: BOL!, K!), *Scully 150* (isosyntype: BM!), *Morris s.n. sub BOL 5622* (isosyntypes: BOL!, K!); Steinkopf, *Schlecther 39* (isosyntypes: BM!, BOL!, GRA!, MO!).

LEOBORDEA BOLUSII (Dümmer) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis bolusii* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 306. 1913.—TYPE: SOUTH AFRICA, Cape Province, near Piquetberg, *Bolus 8431* (lectotype: K!, designated by Van Wyk [1991b]; isolectotype: Z).

LEOBORDEA BRACTEOSA (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis bracteosa* B.-E.van Wyk in Bothalia 20: 73. 1990.—TYPE: NAMIBIA, Outjo district, mountains 14 miles [22.4 km] east of Torra Bay, *Giess, Vlok and Bleissner 6198* (holotype: PRE!; isotypes: M!, PRE!, WIND!).

LEOBORDEA BULLONII (Emberger and Maire) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis bullonii* Emberger and Maire, Pl. Marocc. Nov. (Arch. Sc. Maroc.) Fasc. 1: 1. 1929.—TYPE: not seen.

LEOBORDEA CARINATA (E.Mey.) B.-E.van Wyk and Boatwr., comb. nov. *Lipozygis carinata* E.Mey., Comm. Pl. Afr. Austr. 1(1): 80. 1836. *Lotononis carinata* (E.Mey.) Benth. in Hook. Lond. J. Bot. 2: 609. 1843.—TYPE: SOUTH AFRICA: North-eastern Transkei, between 'Omsamculo' and 'Umcomas', *Drège s.n.* (lectotype: K!, designated by Van Wyk [1991b]; isolectotypes: MO!, S!).

LEOBORDEA CORYMBOSA (E.Mey.) B.-E.van Wyk and Boatwr., comb. nov. *Lipozygis corymbosa* E.Mey., Comm. Pl. Afr. Austr. 1(1): 80. 1836. *Lotononis corymbosa* (E.Mey.) Benth. in Hook. Lond. J. Bot. 2: 605. 1843 – Lectotype:

South Africa, Transkei, 'prope Omtata', *Drège s.n.* (lectotype: S!, designated by Van Wyk [1991b]; isolectotypes: BM!, K!, 2 sheets, M!, S!).

LEOBORDEA DECUMBENS (Thunb.) B.-E.van Wyk and Boatwr., comb. nov. Two subspecies are recognised:

a. LEOBORDEA DECUMBENS (Thunb.) B.-E.van Wyk and Boatwr. subsp. DECUMBENS. *Ononis decumbens* Thunb., Prodr. Pl. Cap.: 129. 1800. *Lotononis decumbens* (Thunb.) B.-E.van Wyk subsp. *decumbens.* —TYPE: SOUTH AFRICA, 'Roggeveld', *Thunberg s.n. sub THUNB-UPS 16604* (lectotype: UPS!, designated by Van Wyk [1991b]).

b. LEOBORDEA DECUMBENS (Thunb.) B.-E.van Wyk and Boatwr. subsp. REHMANNII (Dümmer) B.-E.van Wyk, Contr. Bol. Herb. 14: 139. 1991b. *Lotononis rehmannii* Dümmer in Trans. R. Soc. S. Afr. 3(2): 326. 1913. *Lotononis decumbens* (Thunb.) B.-E.van Wyk subsp. *rehmannii* (Dümmer) B.-E.van Wyk, Contr. Bol. Herb. 14: 139. 1991b.—TYPE: SOUTH AFRICA, Gauteng, 'Hogge Veld, Perekopberg', *Rehmann 6831* (lectotype: K!, designated by Van Wyk [1991b]; isolectotypes: BM!, Z).

LEOBORDEA DIFFORMIS (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis difformis* B.-E.van Wyk in S. Afr. J. Bot. 55(5): 529. 1989.—TYPE: SOUTH AFRICA, Gauteng, Piet Retief District, Iswepe, *Sidey 1609* (holotype: PRE!; isotype: S).

LEOBORDEA DIGITATA (Harv.) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis digitata* Harv. in Harv. and Sond., Fl. Cap. 2: 52. 1862.—TYPE: SOUTH AFRICA, in some part of the eastern provinces, *Capt. Carmichael s.n.* (holotype: TCD!).

LEOBORDEA DIVARICATA Eckl. and Zeyh., Enum. Pl. Afr. Austr.: 175. 1836.—TYPE: SOUTH AFRICA, Cape Province, side of Bothasberg, not far from 'Vischrivier', *Ecklon and Zeyher 1266* (lectotype: S!, designated by Van Wyk [1991b]; isolectotype: C!; M!; S!, SAM!).

*Lipozygis calycina* E.Mey., Comm. Pl. Afr. Austr. 1(1): 78. 1836. *Lotononis calycina* (E.Mey.) Benth. in Hook. Lond. J. Bot. 2: 611. 1843.—TYPE: SOUTH AFRICA: Cape Province, Katberg, *Drège s.n. a* (lectotype: K!, Herb. Benth., designated by Van Wyk [1991b]; isolectotype: BM!, K!, Herb. Hook.); Klipplaatrivier, *Drège s.n. c* (S!); Bothasberg, *Drège s.n. d* (not seen).

LEOBORDEA ERIANTHA (Benth.) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis eriantha* Benth. in Hook. Lond. J. Bot. 2: 605. 1843.—TYPE: SOUTH AFRICA, 'Macalisberg', *Burke 383* (holotype: K!, Herb. Benth. specimen; isotypes: K!, Herb. Hook. specimen, PRE!).

LEOBORDEA ESTERHUYSEANA (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis esterhuyseana* B.-E.van Wyk in Bothalia 20: 70 (1990).—TYPE: SOUTH AFRICA, Cape Province, Ceres District, Stompiesvlei, Swartruggens, *Esterhuysen 29341* (holotype: BOL!; isotypes: C!, K!, MO!).

LEOBORDEA FOLIOSA (H. Bolus) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis foliosa* H. Bolus in J. Linn. Soc. (Bot.) 24: 173. 1887.—TYPE: SOUTH AFRICA, Gauteng, '*prope* Pretoria', *Maclea s.n. sub BOL 5620* (holotype: BOL!; isotype: K!).

LEOBORDEA FURCATA (Merxmüller and Schreiber) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis furcata* (Merxmüller and Schreiber) Schreiber in Mitt. Bot. Staatssamm. Muenchen 3: 613. 1960.—TYPE: NAMIBIA, Rehoboth district, Buellsport, *Strey 2614* (holotype: M!; isotype: K!, M!, PRE!, SAM!)

LEOBORDEA GENISTOIDES Fenzl, Pug. Pl. Nov. Syr.: 6. 1842. *Lotononis genistoides* (Fenzl) Benth. in Hook. Lond. J. Bot. 2: 607. 1843.—TYPE: TURKEY, 'in monte Tauro prope Gulek', *Kotschy 159* (K!, 2 sheets).

LEOBORDEA GLOBULOSA (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis globulosa* B.-E.van Wyk in Bothalia 20: 2. 1990.—TYPE: SOUTH AFRICA, Cape Province, 29.5 km from Touws River to Laingsburg, near Tweedside, *B.-E. van Wyk 2210* (holotype: PRE!).

LEOBORDEA GRANDIS (Dümmer and Jennings) B.-E. van Wyk and Boatwr., comb. nov. *Lotononis grandis* Dümmer and Jennings in Trans. Roy. Soc. S. Afr. 3(2): 310. 1913.—TYPE: SOUTH AFRICA, Natal, at the Umzinyati River, *Wylie s.n. sub Wood 11525* (holotype: K!).

LEOBORDEA LANCEOLATA (E.Mey.) B.-E.van Wyk and Boatwr., comb. nov. *Aspalathus lanceolatus* E.Mey., Comm. Pl. Afr. Austr. 1(1): 37. 1836. *Lotononis lanceolata* (E.Mey.) Benth. in Hook. Lond. J. Bot. 2: 606. 1843.—TYPE: SOUTH AFRICA, Cape Province, 'Witbergen ... *prope* Leeuwenspruit', *Drège s.n.* (lectotype: K!, designated by Van Wyk [1991b]; isolectotype: BM!, K!, PRE!, MO!, S!, SAM!).

LEOBORDEA LATICEPS (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis laticeps* B.-E.van Wyk in Bothalia 20: 3. 1990.—TYPE: SOUTH AFRICA, Cape Province, Ceres District, Stompiesvlei, Swartruggens, *Esterhuysen 29334* (holotype: BOL!; isotypes: C!, K!, M!, MO!, S!).

LEOBORDEA LONGICEPHALA (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis longicephala* B.-E.van Wyk in Bothalia 20: 5. 1990.—TYPE: SOUTH AFRICA, Flats east of Prince Alfred's Hamlet, *Oliver 5063* (holotype: PRE!; isotypes: K!, MO!, STE!).

LEOBORDEA LONGIFLORA (H. Bolus) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis longiflora* H. Bolus in J. Linn. Soc. 25: 159. 1889.—TYPE: SOUTH AFRICA, Cape Province, Namaqualand, *Dowdle s.n. sub BOL 6568* (holotype: BOL!; isotype: K!).

LEOBORDEA LUPINIFOLIA Boiss. in Bibl. Univ. Genève, Elench. Pl. Nov.: 36. 1838. *Lotononis lupinifolia* (Boiss.) Benth. in Hook. Lond. J. Bot. 2: 607.

1843.—TYPE: SPAIN, Malaga Province, 'in arenis torrentium Malaga, Motril', *Boissier El. 61* (G; K! 2 sheets, M! 2 sheets).

LEOBORDEA MAGNIFICA (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis magnifica* B.-E.van Wyk in S. Afr. J. Bot. 55(6): 647. 1989.—TYPE: SOUTH AFRICA, Cape Province, Summit of Khamiesberg, 3 km south of radio tower, *B.-E. van Wyk 2421* (holotype: PRE!; isotypes: K!, MO!, NBG!).

LEOBORDEA MAROCCANA (Ball) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis maroccana* Ball in J. Bot. 11: 302. 1873.—TYPE: 'Ourika', *Ball s.n.* (lectotype: K!, upper specimen on sheet with illustration, designated by Van Wyk [1991b]; isolectotypes: BM!, K!, bottom of second sheet), *Hooker s.n.* (isosyntype: K!); Marocco, 'in regione inferiori Atlantis Majoris: prope Tasseremout' *Ball s.n.* (isosyntype: K!); 'Ait Mesan', *Ball s.n.* (isosyntypes: K! 2 sheets); 'Amsmiz', *Ball s.n.* (isosyntypes: K!, 2 sheets), *Hooker s.n.* (isosyntype: K!).

LEOBORDEA MIRABILIS (Dinter) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis mirabilis* Dinter in Feddes, Repert. 30: 200. 1932.—TYPE: NAMIBIA, 'Granitflachberge von Aus und Gubub', *Dinter 3597* (lectotype: SAM, designated by Van Wyk [1991b]; isolectotypes: BOL!, K!, PRE!); 'Granitberge von Zwartaus (6 km nordl. Aus)', *Dinter 6098* (BM!, BOL!, K!, M!, PRE!, S!, SAM!).

LEOBORDEA MOLLIS (E.Mey.) B.-E.van Wyk and Boatwr., comb. nov. *Lipozygis mollis* E.Mey., Comm. Pl. Afr. Austr. 1(1): 79. 1836. *Lotononis mollis* (E.Mey) Benth. in Hook. Lond. J. Bot. 2: 609. 1843.—TYPE: SOUTH AFRICA, Cape Province, Leliefontein, *Drège s.n.* (lectotype: K!, designated by Van Wyk [1991b]; isolectotypes: MO!, S!).

LEOBORDEA MUCRONATA (Conrath) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis mucronata* Conrath in Kew Bull. 1908: 222. 1908.—TYPE: SOUTH AFRICA, Gauteng, Modderfontein, *Conrath 124* (holotype: K!).

LEOBORDEA NEWTONII (Dümmer) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis newtonii* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 303. 1913.—TYPE: ANGOLA, Mossamedes, Moulino, *Newton 95* (lectotype: K!, designated by Van Wyk [1991b]; isolectotype: Z).

LEOBORDEA OLIGOCEPHALA (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis oligocephala* B.-E.van Wyk in Bothalia 20: 1. 1990.—TYPE: SOUTH AFRICA, Cape Province, Areb, ± 27 miles [43.2 km] NE of Springbok, *Van der Westhuizen 276* (holotype: PRE!; isotypes: K!, MO!).

LEOBORDEA PARIFLORA (N. E. Br.) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis pariflora* N. E. Br. in Burtt Davy, Man. Pl. Transvaal: 388. 1932.—TYPE: SOUTH AFRICA, Gauteng, Pietersburg District, The Downs, *Rogers 21994* (lectotype: K!, designated by Van Wyk [1991b]; isolectotype: PRE!); *Rogers 22017* (PRE!).

LEOBORDEA PENTAPHYLLA (E.Mey.) B.-E.van Wyk and Boatwr., comb. nov. *Lipozygis pentaphylla* E.Mey., Comm. Pl. Afr. Austr. 1(1): 79. 1836. *Lotononis pentaphylla* (E.Mey.) Benth. in Hook. Lond. J. Bot. 2: 605. 1843.—TYPE: SOUTH AFRICA, Cape Province, 'Karakuis', *Drège s.n.* (lectotype: K!, designated by Van Wyk [1991b]; isolectotype: MO!, S!).

LEOBORDEA PLATYCARPA (Viv.) B.-E.van Wyk and Boatwr., comb. nov. *Lotus platycarpos* Viv., Pl. Aegypt., Dec IV: 14, t. 2, fig. 9. 1830. *Lotononis platycarpa* (Viv.) Pic-Serm. in Webbia 7: 331. 1950.—TYPE: 'in desertis prope Kahirum', *Figari s.n.* (holotype: G).

LEOBORDEA PLICATA (B.-E.van Wyk) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis plicata* B.-E.van Wyk in S. Afr. J. Bot. 55(6): 649. 1989.—TYPE: SOUTH AFRICA, Cape Province, near Bitterfontein, between Vanrhynsdorp and Bitterfontein, *Salter 1601* (holotype: K!; isotype: BOL!).

LEOBORDEA POLYCEPHALA (E.Mey.) B.-E.van Wyk and Boatwr., comb. nov. *Lipozygis polycephala* E.Mey., Comm. Pl. Afr. Austr. 1(1): 79. 1836. *Lotononis polycephala* (E.Mey.) Benth. in Hook. Lond. J. Bot. 2: 605. 1843.—TYPE: SOUTH AFRICA, Cape Province, 'Khamiesbergen', *Drège s.n.* (lectotype: K!, designated by Van Wyk [1991b]; isolectotype: BM!, MO!, S!).

LEOBORDEA PROCUMBENS (H. Bolus) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis procumbens* H. Bolus in J. Bot. 1896: 18. 1896.—TYPE: SOUTH

AFRICA, Free State, Harrismith district, plateau and mountains at Bester's Vlei, *Bolus 8139* (holotype: BOL!; isotype: NBG!).

LEOBORDEA PROLIFERA (E.Mey.) Eckl. and Zeyh., Enum. Pl. Afr. Austr.: 175. 1836. *Crotalaria prolifera* E.Mey. in Linnaea 7: 152. 1832. *Lotononis prolifera* (E. Mey.) B.-E.van Wyk in Contr. Bol. Herb. 14: 135. 1991b.—TYPE: SOUTH AFRICA, Cape Province, 'Nieuwe feld', Distr. Beaufort, *Drège s.n.* (lectotype: S!, designated by Van Wyk [1991b]).

LEOBORDEA PULCHRA (Dümmer) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis pulchra* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 308. 1913.— TYPE: SOUTH AFRICA, Gauteng, Lydenburg, *Wilms 280* (lectotype: K!, designated by Van Wyk [1991b]; isolectotype: BM!), *Wilms 279a p.p.* (BM!), *Atherstone s.n.* (not seen).

LEOBORDEA PUSILLA (Dümmer) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis pusilla* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 324. 1913.— TYPE: SOUTH AFRICA, Cape Province, slopes of mountains, Eland's hoek near Aliwal North, *F. Bolus 122 sub BOL 10535* (lectotype: K!, designated by Van Wyk [1991b]); *F. Bolus 122 sub BOL 8141* (isolectotype: BOL!), *F. Bolus 122* (isolectotype: PRE!).

LEOBORDEA QUINATA (Thunb.) B.-E.van Wyk and Boatwr., comb. nov. *Ononis quinata* Thunb., Prodr. Pl. Cap.: 130. 1800. *Lotononis quinata* (Thunb.) Benth.

in Hook., Lond. J. Bot. 2: 608. 1843.—TYPE: 'e Cap. B. Spei', *Thunberg s.n. sub THUNB-UPS 16636* (lectotype: UPS!, designated by Van Wyk [1991b]).

LEOBORDEA ROSEA (Dümmer) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis rosea* Dümmer in Trans. Roy. Soc. S.Afr. 3(2): 305. 1913.—TYPE: SOUTH AFRICA, Cape Province, Clanwilliam, *Mader 207* (lectotype: K!, designated by Van Wyk [1991b]; isolectotype: GRA!).

LEOBORDEA SCHOENFELDERI (Dinter ex Merxmüller and Schreiber) B.-E.van Wyk and Boatwr., comb. nov. *Amphinomia schoenfelderi* Dinter ex Merxmüller and Schreiber in Bull. Jard. Bot. Brux. 27: 273. 1957. *Lotononis schoenfelderi* (Dinter ex Merxmüller and Schreiber) Schreiber in Mitt. Bot. Staatssamm. Muenchen 3: 613. 1960.—TYPE: NAMIBIA, Grootfontein district, 'Gross Huis', *Dinter 7383* (holotype: M!; isotypes: BM!, BOL!, K!, M!, PRE!, S!, WIND!).

LEOBORDEA SPICATA (Compton) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis spicata* Compton in J. S. Afr. Bot. 41(1): 48. 1975.—TYPE: SWAZILAND, Mpaleni, *Compton 32111* (holotype: NBG!; isotypes: K!, 2 sheets, PRE!).

LEOBORDEA STIPULOSA (Bak. f.) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis stipulosa* Bak. f., Leg. Trop. Afr. 1: 18. 1926.—TYPE: RHODESIA [ZIMBABWE], Macheke, *Eyles 2020* (holotype: K!; isotypes: K!, SAM!)

LEOBORDEA STOLZII (Harms) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis stolzii* Harms in Engl., Bot. Jahrb. 54: 379. 1917.—TYPE: TANZANIA, (North of Lake Nyasa, Kyimbila District), Western Njombe District, Madehani, *Stolz 2602* (B†; lectotype: K!, designated by Van Wyk [1991b]; isolectotypes: BM!, BOL!, C!, K!, MO!, PRE!).

LEOBORDEA SUTHERLANDII (Dümmer) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis sutherlandii* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 307. 1913.—TYPE: SOUTH AFRICA, Natal, without precise locality, *Sutherland s.n.* (holotype: K!).

LEOBORDEA TAPETIFORMIS (Emberger and Maire) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis tapetiformis* Emberger and Maire in Bull. Soc. Hist. Nat. Afrique Nord 28(6): 349. 1937.—TYPE: MOROCCO, ... 'Atlantis Majoris orientalis ad radices australes montis Masker, inter Tagoudimt et Anemzi, ad alt. 2200-2400 m', *Emberger and Maire s.n. 1936* (not seen).

LEOBORDEA WILMSII (Dümmer) B.-E.van Wyk and Boatwr., comb. nov. *Lotononis wilmsii* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 307. 1913.—TYPE: SOUTH AFRICA, Gauteng, between Middelburg and Crocodile River, *Wilms 277* (holotype: K!).

TABLE 8.1 Characters states for 12 morphological, chemical and cytological characters scored for the accessions included in the combined molecular and morphological analyses. Characters and character states are explained at the end of the table.

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Aspalathus carnosa* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus confusa* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus crenata* | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus galeata* | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus hirta subsp. hirta* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus hystrix* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus laricifolia subsp. laricifolia* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus linearis* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus macrantha* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Aspalathus nivea* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus pachyloba* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus pendula* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus perfoliata subsp. perfoliata* | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus shawii subsp. shawii* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Aspalathus vermiculata* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | ? | 0 | 0 |
| *Aspalathus willdenowiana* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Bolusia amboensis* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 1 |
| *Crotalaria capensis* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Crotalaria distans* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Crotalaria griquensis* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Crotalaria humilis* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Crotalaria lanceolata* | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Crotalaria virgultalis* | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 |
| *Calobota cinerea* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Calobota cuspidosa* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Calobota cytisoides* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Calobota halenbergensis* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Calobota lotononoides* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Calobota pungens* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Calobota psiloloba* | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Calobota saharae* | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | ? | 0 | 0 |
| *Calobota sericea* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Calobota spinescens* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Calobota thunbergii* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Lebeckia ambigua* | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Lebeckia brevicarpa* | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Lebeckia carnosa* | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Lebeckia meyeriana* | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Lebeckia pauciflora* | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Lebeckia plukenetiana* | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Lebeckia sepiaria* | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Lebeckia wrightii* | 0 | 2 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 2 | 0 | 0 |
| *Lotononis adpressa* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis acuticarpa* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis benthamiana* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis bolusii* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *Lotononis brachyantha* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis calycina* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Lotononis carnosa* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 |
| *Lotononis curtii* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis decumbens* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis densa subsp. leucoclada* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Lotononis digitata* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis divaricata* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 |
| *Lotononis elongata* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Lotononis eriantha* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis exstipitata* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Lotononis falcata* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis filiformis* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Lotononis foliosa* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis fruticoides* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis glabra* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis globulosa* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *Lotononis hirsuta* | 1 | 0/2 | 0 | 1 | 0 | 0 | 2 | 1 | 0 | 2 | 0 | 1 |
| *Lotononis involucrata* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Lotononis involucrata subsp. peduncularis* | 0 | 0 | 0 | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 1 | 1 |
| *Lotononis laxa woodii* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis lenticula* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 2 | 1 | 1 |
| *Lotononis leptoloba* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis listii* | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis lotononoides* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 1 |
| *Lotononis macrocarpa* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | ? | ? | ? |
| *Lotononis macrosephala* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis maculata* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Lotononis magnifica* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis marlothii* | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis maximilianii* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis meyeri* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 1 |
| *Lotononis micrantha* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis mollis* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis oxyptera* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 2 | 1 | 1 |
| *Lotononis parviflora* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis platycarpa* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 2 | 0 | 0 |
| *Lotononis plicata* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis pentaphylla* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *Lotononis polycephala* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 1 | 2 | 0 | 1 |
| *Lotononis pulchella* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 0 | 1 | 1 |
| *Lotononis pungens* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 1 |
| *Lotononis quinata* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis rostrata subsp. namaquensis* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 2 | 1 | 1 |
| *Lotononis sabulosa* | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 2 | 1 | 1 |
| *Lotononis sericophylla* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 |
| *Lotononis solitudinis* | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 |
| *Lotononis sparsiflora* | 0 | 0 | 1 | 1 | 1 | 1 | 2 | 0 | 1 | 2 | 1 | 1 |
| *Lotononis stricta* | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 1 |
| *Lotononis subulata* | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 2 | 0 | 0 |
| *Pearsonia aristata* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pearsonia cajanifolia* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pearsonia grandifolia* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pearsonia sessilifolia* | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Rafnia diffusa* | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Rafnia globosa* | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Rafnia perfoliata* | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Rafnia racemosa* | 0 | 2 | 0 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Rafnia spicata* | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| *Robynsiophyton vanderystii* | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | ? | 0 | 0 |
| *Rothia hirsuta* | 0 | 0 | 0/1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Wiborgia fusca* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Wiborgia incurvata* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Wiborgia monaptera* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Wiborgia obcordata* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Wiborgia sericea* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Wiborgia tetraptera* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Wiborgiella bowieana* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 |
| *Wiborgiella inflata* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | ? | 0 | 0 |
| *Wiborgiella humilis* | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 |
| *Wiborgiella leipoldtiana* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 |
| *Wiborgiella mucronata* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | ? | 0 | 0 |
| *Wiborgiella sessililfolia* | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 2 | 0 | 0 |
| *Dichilus gracilis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

**(1) Large underground tuber:** present = 0, absent = 1. **(2) Leaf type:** digitate = 0, unifoliolate = 1, simple or phyllodinous = 2. **(3) Stipules:** symmetrical or absent = 0, asymmetrical or single = 1. **(4) Bracteoles:** present = 0, absent = 1. **(5) Calyx:** lateral lobes not fused higher up = 0, lateral lobes fused higher up = 1. **(6) Keel:** not rostrate =0, rostrate or helically coiled = 1. **(7) Anther arrangement:** 5+5 = 0, 4+1+5 = 1, 4+6 = 2. **(8) Verrucose upper suture:** absent = 0, present=1. **(9) Funicle length:** normal = 0, exceptionally long = 1. **(10) Chromosome base number:** x=7 = 0, x=8 = 1, x=9 = 2. **(11) Cyanogenic glucosides:** absent = 0, present = 1. **(12) Macrocyclic pyrrolizidine alkaloids:** absent = 0, present = 1.

# CHAPTER 9: TAXONOMY OF THE GENUS *ROBYNSIOPHYTON*

## 9.1. INTRODUCTION

*Robynsiophyton* is a poorly known, monotypic genus that occurs in south-central tropical Africa. It is morphologically similar to *Pearsonia* and *Rothia*, suggesting a close relationship with these genera (Polhill 1976, 1981; Van Wyk 1991a). *Pearsonia* occurs in central and southern tropical Africa, while *Rothia* is widely distributed throughout tropical Africa, Asia and Australia (Polhill 1974; Chapter 10; Boatwright et al. 2008c). These three genera differ from the rest of the tribe in their monomorphic anthers and straight styles (Polhill 1976; Van Wyk 1991a; Van Wyk and Schutte 1995; Chapter 10; Boatwright et al. 2008c). Chemically they are also unique within Crotalarieae in accumulating angelate esters of hydroxylupanine-type alkaloids (Van Wyk and Verdoorn 1991b). In Chapter 3 (Boatwright et al. 2008a) the study of molecular (ITS and *rbcL*) and morphological data, demonstrated that *Pearsonia*, *Robynsiophyton* and *Rothia* form a strongly supported clade and that the latter two are strongly supported as sister genera (Fig. 9.1). Doubt regarding the generic status of *Robynsiophyton* has been expressed by previous authors (Polhill 1976; Van Wyk 1991a), who suggested that it could merely be a local derivative of *Pearsonia*. However, as shown in Chapter 3 (Boatwright et al. 2008a) the genus is not embedded within *Pearsonia*, but sister to *Rothia* with both of these subsequently sister to *Pearsonia*. These data in combination with the annual life history and the unusual androecium (nine stamens with only five fertile anthers) support the generic concept of *Robynsiophyton*.

The aim of this chapter is to present a revision of *Robynsiophyton* with illustrations, a discussion on diagnostic characters and a distribution map.

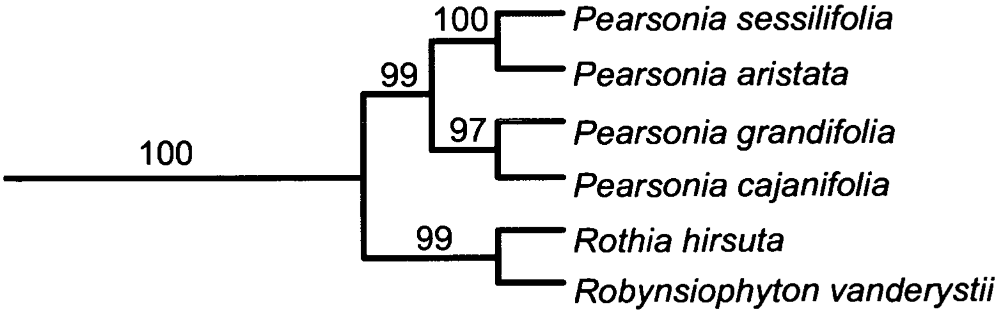

FIG. 9.1 Phylogenetic position of *Robynsiophyton vanderystii* based on gene sequences (ITS and *rbcL*) and morphological data (strict consensus of 370 trees Chapter 2 – see Boatwright et al. 2008a; tree length = 1166; consistency index = 0.53; retention index = 0.84). Numbers above the branches are bootstrap percentages above 50%.

## 9.2 DISCUSSION OF CHARACTERS

A summary of the diagnostic characters for *Robynsiophyton*, *Rothia* and *Pearsonia* is presented in Table 9.1. *Robynsiophyton vanderystii* Wilczek is a small annual (or rarely a short-lived perennial) with hairy, reddish-brown branches. It shares with *Rothia* the annual life history, a trait which is not found in *Pearsonia,* a genus comprising perennial herbs or small shrubs. The leaves are digitately trifoliolate and sparsely pubescent adaxially but densely pubescent on the abaxial surface. The narrow stipules are paired at the base of the petiole. *Rothia hirsuta* has single stipules at each leaf; *Rothia indica* has paired stipules; and *Pearsonia* has the stipules paired or less often absent (Polhill 1974; Chapter 10; Boatwright et al. 2008c).

The flowers of *Pearsonia*, *Robynsiophyton* and *Rothia* are all relatively unspecialised, with straight or even down-curved styles and monomorphic anthers (Polhill 1976). In *Rothia* the anthers are all small and rounded as opposed to the large, elongate anthers of *Pearsonia*, six of which are attached slightly higher up to the filament (Polhill 1974, 1976). *Robynsiophyton* has a reduced number of stamens (from 10 to nine) and only five fertile stamens (the other four stamens lack anthers and are sterile). This is the most notable feature of the genus. In the Crotalarieae, Genisteae and Podalyrieae there is great variation in staminal arrangement from completely free stamens (Podalyrieae) to those joined in either an open sheath (Crotalarieae) or closed tube (most Genisteae). The anthers may be either dimorphic with alternating basifixed and dorsifixed anthers, or monomorphic as found in *Pearsonia*, *Robynsiophyton* and *Rothia* (a feature that is unique to this clade within the Crotalarieae). Anther characters are very reliable in legumes and usually consistent with other characters, thus providing important insight especially at generic and tribal levels (Bentham 1843; Polhill 1976; Chapter 3; Chapter 10; Boatwright et al. 2008a, 2008c).

The calyx of *Robynsiophyton* is equally lobed, while in *Pearsonia* and *Rothia* the upper lobes are larger than the three lower lobes. In *Pearsonia*, the upper and lateral lobes on either side are often fused higher up (the so-called "lotononoid" calyx type). Bracts are present in all three genera, but bracteoles are generally lacking in *Pearsonia* (if present very small) and completely absent in *Robynsiophyton* and *Rothia* (Polhill 1974, 1976).

The pods of *Robynsiophyton* are relatively short and few-seeded when compared to those of *Rothia*. The mature seeds are brown, smooth and similar in size to those of *Rothia indica*. *Robynsiophyton vanderystii* has larger seeds than *Rothia hirsuta* that are even coloured with a smooth surface, whereas those of *Rothia hirsuta* are mottled with a somewhat rugose surface (Chapter 10; Boatwright et al. 2008c).

TABLE 9.1 Summary of diagnostic characters for *Robynsiophyton*, *Rothia* and *Pearsonia*

| Character | *Robynsiophyton* | *Rothia* | *Pearsonia* |
|---|---|---|---|
| Life history | annual or short-lived perennial | annual | perennial |
| Stipules | paired | paired or single | paired or absent |
| Bracteoles | absent | absent | small or absent |
| Calyx | equally lobed | sub-equally lobed | zygomorphic |
| Androecium | 9 stamens, 5 rounded anthers, 4 staminodes | 10 stamens, 10 rounded anthers, 0 staminodes | 10 stamens, 10 elongated anthers, 0 staminodes |
| Fruit | oblong to ovate | linear to ovate or falcate | ellipsoid to linear-oblong |
| Seeds | brown, smooth | brown or mottled, smooth or rugose | light or dark brown, sometimes mottled, smooth |

## 9.3 TAXONOMIC TREATMENT

ROBYNSIOPHYTON Wilczek in Bull. Jard. Bot. État. 23: 128. 1953.; in F. C. B. 4: 286. 1953; Hutchinson, Genera of Flowering Plants: 362. 1964; Polhill in Bot. Syst. 1: 326. 1976; Van Wyk and Schutte, Advances in Legume Systematics 7: 306. 1995; Polhill, Fl. Zam. 3 (7): 66. 2003; Leistner, Seed Plants of southern Tropical Africa: Families and Genera: 202. 2005; Van Wyk in Legumes of the World, Lewis et al. (Eds): 281. 2005.—TYPE species: *Robynsiophyton vanderystii* Wilczek.

The genus is monotypic and distinguished by the reduced number of stamens (nine instead of 10) and presence of four staminodes (Table 9.1). It occurs in central tropical Africa extending from Angola to Zambia in the east.

1. ROBYNSIOPHYTON VANDERYSTII Wilczek in Bull. Jard. Bot. État. 23: 128. 1953; in F. C. B. 4: 286, t. 17. 1953; White, F. F. N. R.: 164. 1962; Torre in C. F. A. 3: 6. 1962; Lock, Leg. Afr. Check-list: 232. 1989; Polhill, Fl. Zam. 3 (7): 66. 2003.—TYPE: Democratic Republic of Congo, Lazaret du Sacré-Coeur [1025 BA], *Vanderyst s.n.* (holotype: BR, photo!).

Small, prostrate or ascending annual or short-lived perennial up to ±0.3 m in height. *Branches* reddish-brown, pubescent. *Stipules* 5–8 mm long, linear to lanceolate, invariably paired, pubescent. *Leaves* digitately trifoliolate; petiole shorter than leaflets, 4–7 mm long; leaflets elliptic to oblanceolate, subsessile, sparsely pubescent adaxially and densely so abaxially, terminal leaflet 14–22 mm long, 4–9 mm wide, lateral leaflets 7–16 mm long, 2.5–6.0 mm wide, obtuse, base cuneate. *Inflorescence* axillary or rarely terminal congested racemes, with (2–) 5 to 9 (–10) flowers; pedicel less than 1 mm long; bract linear, 1.5–3.0 mm long, pubescent, caducous; bracteoles absent. *Flowers* pale yellow, 3–6 mm long. *Calyx* equally lobed, pubescent, 4–5 mm long; tube 1.5–2.0 mm long; lobes subulate, 1.5–3.0 mm long, tips minutely pubescent on inner surface. *Standard* 3–5 mm long; claw 1.0–1.5 mm long; lamina elliptic to ovate, 2–4 mm long, 1.0–1.5 mm wide, obtuse to very slightly emarginate, pilose along dorsal midrib. *Wings* 2.5–4.5 mm long; claw 1.5–1.8 mm long; lamina oblong to obovate, as long as or slightly longer than keel, 1.0–2.5 mm long, 0.5–1.0 mm wide, obtuse, glabrous, with 1–2 rows of sculpturing. *Keel* 3–4 mm long; claw 1–2 mm long; lamina boat-shaped, 1.5–3.0 mm long, 0.5–0.8 mm wide, obtuse, glabrous, sometimes with a very slight pocket. *Stamens* 9, anthers monomorphic with 5, sub-basifixed anthers alternating with 4 staminodes. *Pistil* subsessile, pubescent, ovary elliptic, 1.5–2.0 mm long, 0.5–0.8 mm wide with ±5 to 8 ovules; style straight, 1.5–1.8 mm long, glabrous. *Pods* oblong to ovate, laterally compressed, subsessile, 7–10 mm long, 3–4 mm wide, ±2 to 8 seeded, dehiscent. *Seeds* oblique-cordiform, 1.0–1.5 mm long, 1.0–1.2 mm wide, brown, smooth (Fig. 9.2). Flowering time: April. Plants appear to be inconspicuous and are poorly collected so that the flowering time needs confirmation.

***Distribution and habitat***—*Robynsiophyton vanderystii* occurs in moist, sandy soils and is especially common along roadsides. Very few specimens are available for study and these include collections from Angola, the Democratic Republic of Congo and Zambia, but it is likely that the distribution range is more extensive (Fig. 9.3).

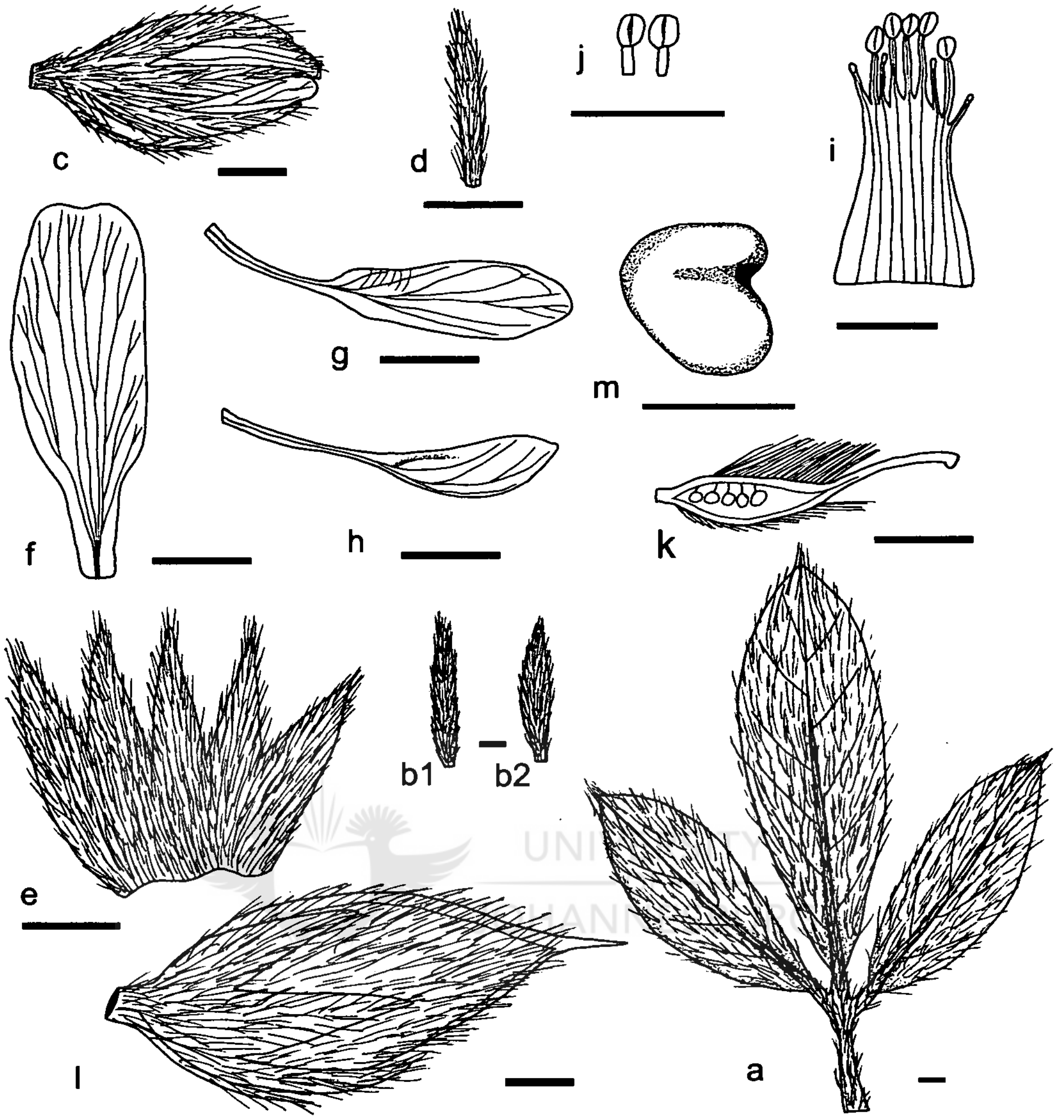

FIG. 9.2. Morphology of *Robynsiophyton vanderystii*: (a) leaf in abaxial view; (b1–b2) stipules; (c) flower in lateral view; (d) bract; (e) outer surface of the calyx (upper lobes to the left); (f) standard petal; (g) wing petal; (h) keel petal; (i) androecium showing the five uniform anthers and four staminodes; (j) anthers (carinal anther on the left); (k) pistil; (l) pod in lateral view; (m) seed in lateral view.

Voucher specimens: (c, d, f, g, h, i, j, k) *McCallum Weston 717* (K); (e) *Lisowski 20326* (K); (l) *Richards 9321* (K); (a, b1–b2) *Richards 18144* (K); (m) *Exell and Mendonça 657* (K). Scale bars: (a–m) 1 mm.

### *Additional specimens examined*

**Angola:**

**–0614:** Kimbambu, Madimba (–AA), *Pauwels 6470* (PRE).

**–0720:** Lunda, Chicapa (–BC), *Exell and Mendonça 657* (BM, K, LISC 3 sheets).

**Democratic Republic of Congo:**

**–0416:** Bakama (–AB), *Flamigni s.n.* (K).

**–0515:** Bas-Congo, Kisantu (–AA), *Vanderyst s.n.* (BM, K); Bas-Congo, Kimpako (–AB), *Vanderyst 42290* (K).

**–1025:** Haut-Shaba, Kolwezi (–DA), *Lisowski 20326, 20333* (K).

**Zambia:**

**–0831:** Chilongowelo, Abercorn (–CA), *McCallum Weston 717* (K); Mpulungu Abercorn road, close to Chilongowelo turning (–CA), *Richards 5309, 5317, 18144* (K), *Richards 11097* (K, PRE).

**–0929:** Kawambwa, Timnatushi Falls (–CC), *Richards 9319a, 9321* (K).

**–1124:** Mwinilunga (–CD), *Mutimushi 3416* (K).

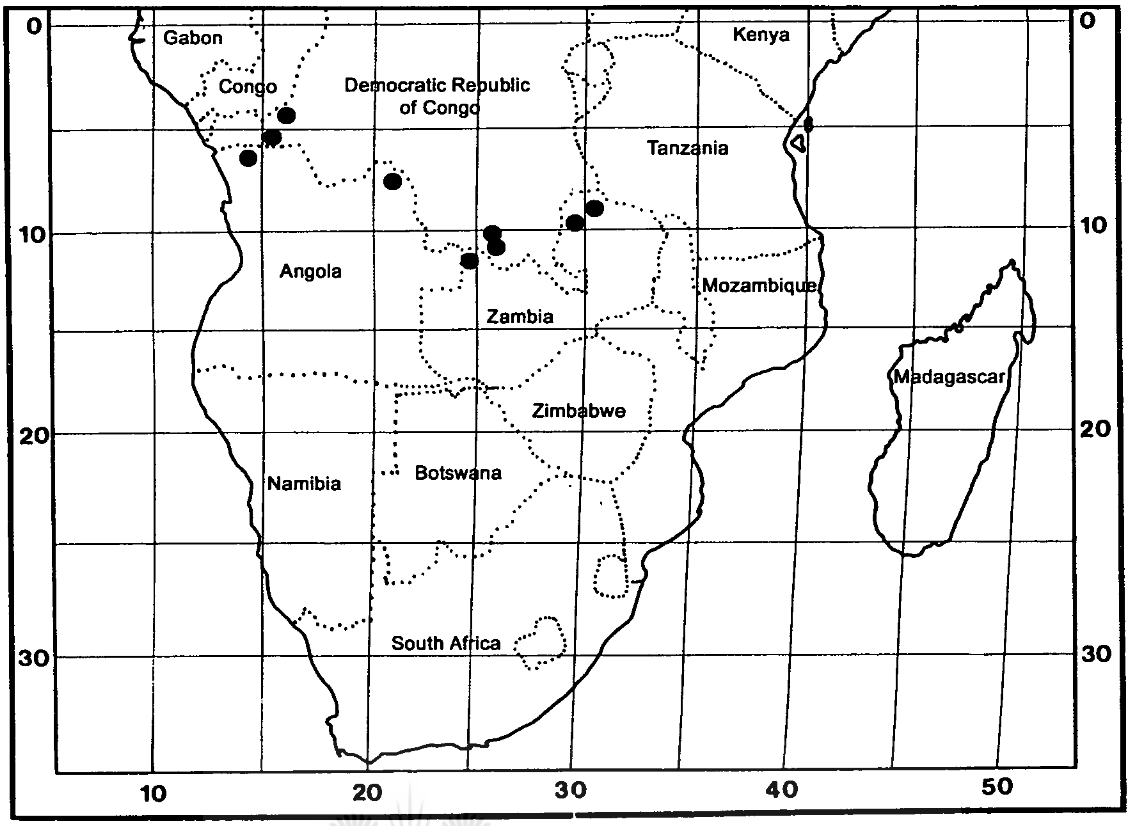

FIG. 9.3. Known geographical distribution of *Robynsiophyton vanderystii*.

# CHAPTER 10: TAXONOMY OF THE GENUS *ROTHIA*

## 10.1 INTRODUCTION

The genus *Rothia* was described in 1806 and comprises two species, *R. hirsuta* and *R. indica*. The species have been treated in several floristic studies [e.g. The Flora of Tropical Africa (Baker 1926), Flora of West Tropical Africa (Hepper 1958), Flora of Tropical East Africa (Milne-Redhead 1971), Flora Zambesiaca (Polhill 2003b), A revised Handbook of the Flora of Ceylon (Rudd 1991)] but no comprehensive revision of the genus exists. An Australian-endemic subspecies of *R. indica* namely *R. indica* subsp. *australis* was described by Holland (1997). It is morphologically distinct from the typical Asian subspecies.

The genus is a member of the Papilionoideae and is placed within the tribe Crotalarieae. The Crotalarieae form part of a monophyletic assemblage of tribes, the "core" genistoid legumes (Crisp et al. 2000; Boatwright et al. 2008b), which comprises the Crotalarieae, Euchresteae, Genisteae, Podalyrieae, Sophoreae (in part) and Thermopsideae. The Crotalarieae are sub-endemic to Africa with a few species of *Crotalaria*, *Lotononis* and *Rothia* extending to other continents. The study of the tribe based on gene sequences (ITS and *rbcL*) and morphological data (Chapter 3; Boatwright et al. 2008ab), showed *Rothia* to be in a well-supported clade along with *Pearsonia* and *Robynsiophyton*, i.e. the *Pearsonia* clade. A sister relationship between *Robynsiophyton* and *Rothia* was strongly supported (Fig. 10.1). This confirmed hypotheses by Polhill (1976), Van Wyk (1991a) and Van Wyk and Schutte (1995) who suggested an affinity between these genera. The close relationship between *Pearsonia*, *Robynsiophyton* and *Rothia* is supported by three synapomorphies, i.e. uniform anthers, straight or down-curved styles and the presence of angelate esters of lupanine-type alkaloids. *Rothia* can be distinguished from *Pearsonia* and *Robynsiophyton* by its 10 small, rounded anthers and sub-equally lobed calyx.

In this chapter a taxonomic account of *Rothia* is presented with illustrations, descriptions and distribution maps of the species. The results of anatomical studies of the leaves and fruits of *Rothia* and *Robynsiophyton* are also presented.

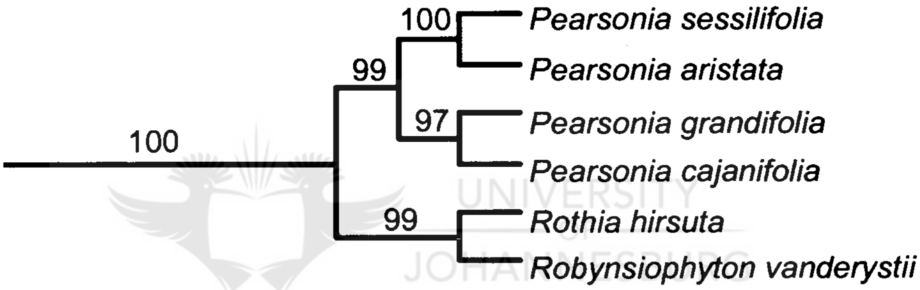

FIG. 10.1 The *Pearsonia* clade taken from a strict consensus of 370 trees showing the relationship between *Pearsonia*, *Robynsiophyton* and *Rothia* based on the combined analysis of molecular (ITS and *rbcL*) and morphological data (Chapter 3; see also Boatwright et al. 2008a; tree length = 1166; consistency index = 0.53; retention index = 0.84). Numbers above the branches are bootstrap percentages above 50%.

## 10.2 DISCUSSION OF CHARACTERS

***10.2.1 Generic relationships***—In Chapter 3 (Boatwright et al. 2008a), the *Pearsonia* clade is well-separated from the "Cape group" of the Crotalarieae (*Aspalathus*, *Lebeckia*, *Rafnia*, *Spartidium* and *Wiborgia*) and placed closer to *Lotononis*, a genus with which they share the lotononoid or zygomorphic calyx. However, the three genera of the *Pearsonia* clade possess a 17 base-pair deletion at positions 179–196 in the aligned ITS matrix and unique floral characters such as straight styles and uniform anthers. The *Crotalaria* clade [*Bolusia*, *Crotalaria* and *Lotononis* section *Euchlora*] is early diverging within the Crotalarieae and all have strongly inflated pods (Chapter 3; Boatwright et al. 2008a).

Van Wyk (2003b) discussed the importance of chemical characters in genistoid legumes and mentions that their distribution is not random, but in fact provides reliable information supporting phylogenetic relationships retrieved by studies of DNA sequence data. The *Pearsonia* clade is chemically distinct within the tribe Crotalarieae in having unique alkaloids (Van Wyk and Verdoorn 1990; Van Wyk 1991a; Van Wyk and Schutte 1995; Van Wyk 2005). *Pearsonia*, *Robynsiophyton* and *Rothia* produce tetracyclic quinolizidine alkaloids such as lupanine together with angelate esters such as lupanine-13$\alpha$-angelate, cajanifoline, sessilifoline and pearsonine (Hussain et al. 1988; Van Wyk and Verdoorn 1989d, 1991a). These chemical characters are especially useful in distinguishing this clade from the morphologically similar genus *Lotononis* where pyrrolizidine and quinolizidine alkaloids are present but no esters of lupanine-type alkaloids (Van Wyk 1991b). Also, some sections of *Lotononis* are cyanogenic, a trait which is unique within Crotalarieae (Van Wyk 1991b).

***10.2.2 Vegetative morphology and anatomy***—The species of *Rothia* are prostrate to procumbent or erect annuals. They share this life history with the monotypic African genus *Robynsiophyton*. This character lends support to the sister relationship found between these genera in Chapter 3 (Boatwright et al. 2008b) and distinguishes them from the closely related genus *Pearsonia* which consists of perennial herbs or shrubs.

The leaves of *Rothia* are digitately trifoliolate as in many of the Crotalarieae, and pubescent both adaxially and abaxially. *Rothia indica* subsp. *australis* has densely pubescent leaves with long whitish hairs that are more or less spreading. In contrast, the leaves of *R. indica* subsp. *indica* are moderately hairy with shorter, more or less appressed hairs. The stipules of *Rothia hirsuta* are linear to slightly falcate and single at each node, whereas those of *Rothia indica* are elliptic to lanceolate or ovate and invariably paired.

Anatomical studies of the lamina (Fig. 10.2 a, b) and petiole (Fig. 10.2 c, d) revealed no informative differences between *Rothia hirsuta* and *R. indica*, or even between these and *Robynsiophyton vanderystii*. The leaves are dorsiventral with mucilage cells present in the epidermis in both *Rothia* and *Robynsiophyton* (Fig. 10.2 a, b). These cells are thought to contribute to the retention of water and reduction of transpiration but their function has not been accurately ascertained (Gregory and Baas 1989).

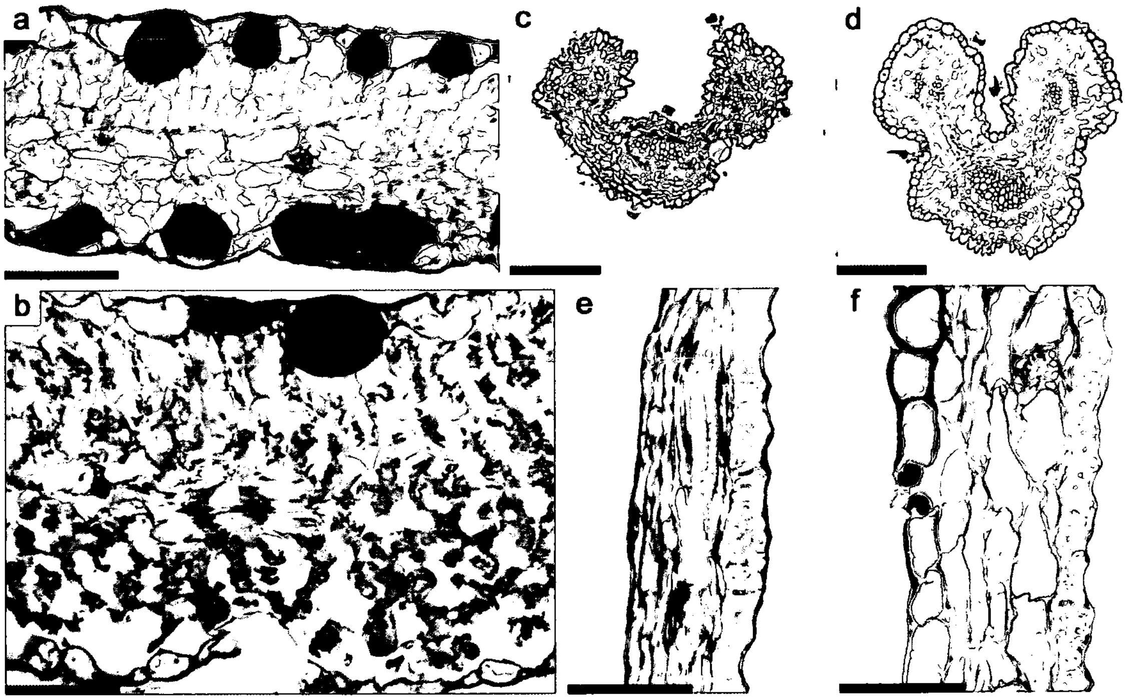

FIG. 2 Transverse sections through the leaves and fruit of *Rothia* and *Robynsiophyton*. (a) Portion of leaf of *Robynsiophyton vanderystii* (scale bar = 0.1 mm). (b) Portion of leaf of *Rothia indica* (scale bar = 0.1 mm). (c) Petiole of *Robynsiophyton vanderystii* (scale bar = 0.2 mm). (d) Petiole of *Rothia indica* (scale bar = 0.2 mm). (e) Portion of fruit wall of *Robynsiophyton vanderystii* (scale bar = 0.07 mm). (f) Portion of fruit wall of *Rothia indica* (scale bar = 0.07 mm). Voucher specimens. (a, e) *Lisowski 20326* (K). (b, d, f) *Latz 16126* (MEL). (c) *Exell and Mendonça 657* (K).

***10.2.3 Reproductive morphology and anatomy***—Both species of *Rothia* have axillary racemes. *Rothia hirsuta* has up to seven flowers per raceme as opposed to *R. indica* where up to four flowers per raceme are found, although the flowers are often solitary or in pairs. Terminal racemes are found in most genera of the Crotalarieae (Polhill 1976), but are either terminal or axillary in *Pearsonia* and strictly axillary in *Rothia* and *Robynsiophyton*. Bracts are present in *Rothia*, but bracteoles are lacking.

Bracteoles are also absent in *Robynsiophyton* and most species of the genus *Lotononis*, but present in almost all *Pearsonia* species.

The flowers of *Rothia* and its relatives are relatively unspecialised compared to the rest of the Crotalarieae. *Rothia*, *Robynsiophyton* and *Pearsonia* have a "gullet" type flower where the style is straight or down-curved and the anthers uniform and/or further reduced, as opposed to the more specialised and reflexed floral parts found in the other crotalarioid genera (Polhill 1976). In *Rothia* the two upper calyx lobes are larger than the other three lobes and distinctly falcate. The calyces of *Pearsonia* species have the upper sinus often shallower than the others or in some species the lateral sinus is the shallowest with the carinal lobe always narrower than the other lobes (Polhill 1974). *Robynsiophyton* differs from both these genera in having an equally lobed calyx (Chapter 9; Boatwright and Van Wyk 2009).

The most useful generic character to distinguish between *Pearsonia*, *Robynsiophyton* and *Rothia* is the androecium. These genera are unique within the Crotalarieae in having uniform anthers as opposed to the dimorphic anthers found in other genera of the tribe with alternating basifixed and dorsifixed anthers (Polhill 1976). The anthers of *Pearsonia* are elongate and large, whereas in *Rothia* and *Robynsiophyton* they are small and rounded (Fig. 10.3). *Robynsiophyton* has a reduced number of stamens (nine rather than 10) and four anthers are infertile (Fig. 10.3). Although the generic concepts of *Rothia* and *Robynsiophyton* have been questioned by previous authors, the informative value of androecial characters (the main distinction between these three genera) at both tribal and generic level is usually closely correlated with relationships suggested by both molecular and morphological data

(Polhill 1976; Chapter 3; Boatwright et al. 2008b) and should be taken at face value as strong, sound generic apomorphies.

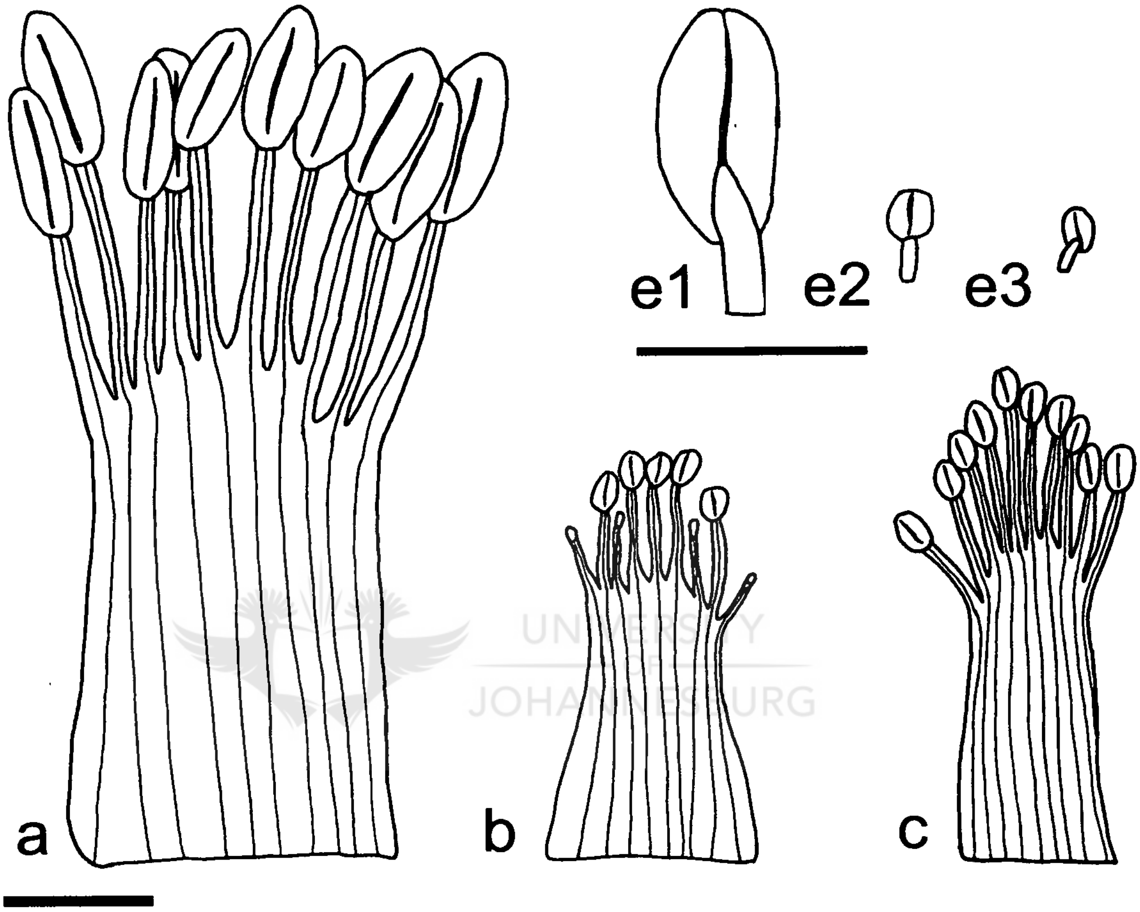

FIG. 10.3 Androecia and anthers of *Pearsonia* (a, e1), *Robynsiophyton* (b, e2) and *Rothia* (c, e3). Voucher specimens: (a, e1) *Swanepoel 1* (JRAU). (b, e2) *McCallum Weston 717* (K). (c, e3) *Greenway and Kanuri 14269* (K). All scale bars represent 1 mm.

The pods of *Rothia hirsuta* are ovate to falcate and much shorter and fewer seeded (up to 18 mm long with ±25 seeds) than the linear pods of *R. indica* that are up to 55 mm long with ±35 seeds. The pods of *Rothia* and *Robynsiophyton* are thin-walled and sclerified on the inner surface with no apparent anatomical differences (Fig. 10.2 e, f).

*Rothia indica* and *Robynsiophyton* have similar sized seeds that are larger than those of *Rothia hirsuta* (Chapter 9; Boatwright and Van Wyk 2009). The seeds of the latter are light brown with dark mottling and have a rugose surface in contrast to the brown, smooth seeds of *R. indica* and *Robynsiophyton vanderystii.*

## 10.3 TAXONOMIC TREATMENT

***Key to the genus Rothia***

1. Anthers dimorphic, styles upcurved..........................................other Crotalarieae

1. Anthers uniform, styles straight or down-curved.............................................2

    2. Perennial herbs or small shrubs, anthers large and elongate............*Pearsonia*

    2. Annual herbs, anthers small and rounded...........................................3

        3. Upper two calyx lobes larger than others (calyx sub-equally lobed), stamens 10, all fertile.........................................................*Rothia*

        3. Upper two calyx lobes similar to others (calyx equally lobed), stamens nine, five fertile, four reduced and infertile......................*Robynsiophyton*

ROTHIA Pers., Syn. Pl. 2: 302, 638. 1807. *nom. conserv.*; Benth. in Hook., Lond. J. Bot. 3: 338. 1844; Benth. and Müller, Fl. Austral. 2: 185. 1864; Baker, Fl. Trop. Africa: 7. 1871; Trimen, Handb. Fl. Ceylon: 7. 1894; Thonner, Flowering Plants of Africa: 274. 1915; Baker, Leg. Trop. Africa: 21. 1926; Hutchinson and Dalziel, Fl.

West Trop. Africa: 543. 1954; Hutchinson, The Genera of Flowering Plants: 361. 1964; D'Orey and Liberato, Fl. Guine Portuguesa: 71. 1971; Polhill in Bot. Syst. 1: 326. 1976; Thulin in Op. Bot. 68: 153. 1983; Hedberg and Edwards, Fl. Ethiopia: 195. 1989; Rudd, A revised handbook to the flora of Ceylon: 184. 1991; Van Wyk and Schutte, Advances in Legume Systematics 7, M. D. Crisp and J. J. Doyle (Eds.): 306. 1995; Leistner, Seed Plants of southern Africa: Families and Genera: 295. 2000; Du Puy et al., The Leguminosae of Madagascar: 671. 2002; Polhill, Fl. Zambesiaca: 64. 2003; Leistner, Seed Plants of southern Tropical Africa: Families and Genera: 202. 2005; Van Wyk in Legumes of the World, Lewis et al. (Eds.), 281. 2005.—TYPE species: *R. trifoliata* (Roth) Pers. (=*Dillwynia trifoliata* Roth)

*Dillwynia* Roth, Catal. Bot. 3: 71. 1806 non *Dillwynia* Sm. in Koenig and Sims, Ann. Bot. 1: 510 (1805).—TYPE species*: D. trifoliata* Roth

*Westonia* Spreng., Syst. Veg. 3: 152, 230. 1826 *nom. illeg.*—TYPE species*: W. humifusa* (Willd.) Spreng.

*Goetzea* Reichb., Consp. Regn. Veg.: 150. 1828 *nom. rej.*

*Xerocarpus* Guill. and Perr., Fl. Seneg. Tent.: 169. 1832.—TYPE species: *X. hirsutus* Guill. and Perr.

*Harpelema* J.Jacq., Ecl. Pl. Rar. 2: t. 129 (1844).—TYPE species: *H. dillwynia* J.Jacq.

Prostrate, annual herbs. Branches up to 40 cm long, densely to sparsely pubescent. Leaves digitately trifoliolate, elliptic to oblanceolate or obovate, pubescent; leaflets sub-sessile, apex apiculate, obtuse or slightly acute, base cuneate; petioles shorter than leaflets, pubescent. Stipules linear to slightly falcate or elliptic to lanceolate or ovate, single in *R. hirsuta*, paired in *R. indica*, pubescent. Inflorescence axillary, racemose, flowers solitary or up to 7 per raceme; pedicel up to 2 mm long; bract linear, pubescent, caducous; bracteoles absent. Flowers pale yellow to white. Calyx pubescent, sub-equally lobed; lobes triangular to lanceolate, upper lobes wider than others, falcate, carinal lobe slightly narrower than others, tips minutely pubescent inside. Standard elliptic to ovate, pilose along dorsal midrib; claw linear; apex obtuse. Wing petals oblong to obovate, glabrous, with 2 to 3 rows of sculpturing, as long as keel; apex obtuse. Keel boat-shaped, glabrous, pocket sometimes present; apex obtuse. Stamens 10, anthers uniform, sub-basifixed. Pistil sub-sessile, pubescent; ovary linear to narrowly ovate; style straight, glabrous. Pods linear to ovate or falcate, laterally compressed, sub-sessile, many-seeded, pubescent, dehiscent. Seeds oblique-cordiform, brown or brown mottled with dark brown, surface smooth or rugose.

***Etymology***—The genus is named in honour of the German physician and botanist Albrecht Wilhelm Roth (1757–1834).

***Diagnostic characters***—*Rothia* can be distinguished from *Robynsiophyton* in that the latter has an equally lobed calyx (in *Rothia* the upper two lobes are larger than the others) and the 10 stamens with 10 fertile anthers found in *Rothia* (in *Robynsiophyton* the stamens are reduced to nine and only five anthers are fertile). Furthermore it differs from *Pearsonia* by its sub-equally lobed calyx and small, rounded anthers in contrast to the 'lotononoid' calyx (zygomorphic due to the fusion of the upper and lateral lobes on either side) and large, elongate anthers of *Pearsonia*.

***Chromosome number***—A count of n = 7 has been reported for *Rothia indica* (Goldblatt 1981; Bairiganjan and Patnaik 1989).

***Distribution***—The genus occurs in tropical Africa, Asia and Australia (Fig. 10.5 and Fig. 10.7). It appears to have been well-collected in areas for which regional floras have been compiled, e.g. the Flora of Tropical East Africa and Flora of West Tropical Africa.

***Key to the species of Rothia***

1. Stipules linear and single at each node, up to seven flowers per inflorescence, pods ovate to falcate and up to 18 mm long, seeds light brown with dark mottling and a rugose surface, Africa and Madagascar.................................**1. *R. hirsuta***

1. Stipules elliptic to lanceolate or ovate and paired at each node, up to four flowers per inflorescence, pods linear or slightly falcate and up to 55 mm long, seeds brown with a smooth surface, Asia and Australia...............................................**2. *R. indica***

1. ROTHIA HIRSUTA (Guill. and Perr.) Baker in Fl. Trop. Africa 2: 7. 1871; Eyles in Trans. Roy. Soc. South Africa 5: 369. 1916; E.G.Baker, Leg. Trop. Africa: 21. 1926; Broun and Massey, Fl. Sudan: 176. 1929; Andrews, The Flowering Plants of the Anglo-Egyptian Sudan: 230. 1952; Hepper in Fl. West Trop. Africa, ed. 2, 1: 543. 1958; Torre, Consp. Fl. Angolensis 3: 5. 1962; White, Forest Fl. Northern Rhodesia: 164. 1962; Schreiber in Merxmüller, Prodr. Fl. SW. Africa, fam. 60: 107. 1970; Milne-Redhead, Fl. Trop. East Africa, Leguminosae, Pap.: 811. 1971; Drummond in Kirkia 8: 226. 1972; Thulin in Op. Bot. 68: 153. 1983; Hedberg and

Edwards, Fl. Ethiopia: 195. 1989; Du Puy et al., The Leguminosae of Madagascar: 671. 2002. *Xerocarpus hirsutus* Guill. and Perr. in Guillemin, Perrottet and Richard, Fl. Seneg. Tent.: 44 (1832).—TYPE: SENEGAL, *Leprieur s.n.* (lectotype: P photo!, designated here). [Note: According to Stafleu and Cowan (1983) the type material of Perrottet is housed in P or G. No specimens were traced in G and the Paris specimen is therefore designated as lectotype.]

*Amphinomia desertorum* (Dümmer) Schreiber in Mitt. Bot. München 2: 286. 1957; *Lotononis desertorum* Dümmer in Trans. Roy. Soc. S. Africa 3: 316. 1913.—TYPE: Great Barmen, Buschsteppe, 23.iv.1907, *Dinter 518* (lectotype: Z photo!, designated here; isolectotypes: BM!, BOL!, NBG!, K!). [Note: Dümmer was based at K during his revision of *Lotononis*. However, the K isotype is a small piece taken from the specimen in Z (as annotated by Dümmer himself). The Z specimen is therefore chosen as lectotype.]

Small, pubescent, prostrate or semi-erect to procumbent herb. Branches ±10–40 cm long, brown, sparsely hairy (pilose). Leaves with leaflets elliptic to oblanceolate, terminal leaflet 10–30 mm long, 3.5–12.0 mm wide, lateral leaflets 6–20 mm long, 2–7 mm wide; apex apiculate; base cuneate; petiole 3–13 mm long. Stipules linear to slightly falcate, 2–8 mm long, single. Inflorescence with 2 to 7 flowers; pedicel up to 1 mm long; bract 1.0–2.5 mm long. Flowers 4–8 mm long. Calyx 5–7 mm long; tube 1.5–2.0 mm long; lobes 3–4 mm long. Standard 4.0–5.5 mm long; claw 1.0–1.5 mm long; lamina 3.0–4.5 mm long, 1–2 mm wide. Wings 4–5 mm long; claw 1.5–2.0 mm long; lamina 2.5–4.0 mm long, 0.5–0.7 mm wide. Keel 2.5–4.0 mm long; claw 1.5–2.0 mm long; lamina 1–3 mm long, 0.5–1.0 mm wide. Pistil ovary narrowly ovate, 2–3 mm long, 0.5–0.7 mm wide with ±7 to 13 ovules; style 1.3–1.6 mm long. Pods ovate, falcate, tapering towards apex, 10–18 mm long, 2–3 mm wide with up to ±25 seeds per pod. Seeds 1.1–1.5 mm long, 0.8–1.1 mm wide, mature seeds light brown with dark mottling, surface rugose (Fig. 10.4). Flowering time: *Rothia hirsuta* flowers mainly from February to November, but flowering and fruiting specimens have been recorded throughout the year.

***Distribution and ecology***—*Rothia hirsuta* is widespread in the dry parts of tropical Africa from South Africa northwards to Eritrea and westwards up to Guinea (Fig. 10.5). Plants occur on sandy loam or clay soils, often in grassland or forest openings. It is common on sandy soils along watercourses or disturbed roadsides.

***Diagnostic characters***—The linear stipules are invariably single at each node in *Rothia hirsuta*, whereas they are paired and elliptic to ovate in *Rothia indica*. The inflorescences are more densely flowered (up to 7 flowers) in *R. hirsuta* as opposed to *R. indica* where the flowers are often solitary or up to 4 per inflorescence. The linear pods of *R. indica* are three times longer (up to 55 mm) than the ovate pods of *R. hirsuta* that are only up to 18 mm long. In *R. hirsuta* the seeds are brown with dark mottling and have a rugose surface, while those of *R. indica* are brown (unmottled) with a smooth surface.

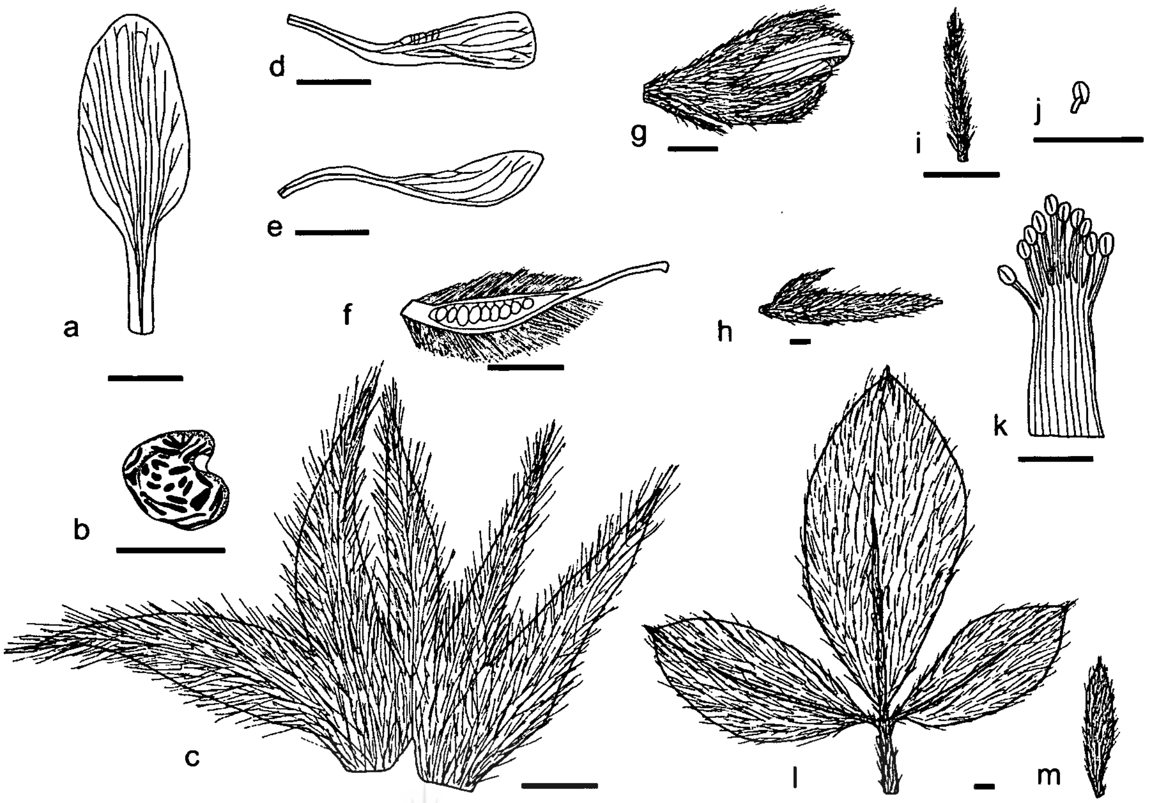

FIG. 10.4 Morphology of *Rothia hirsuta*. *(a)* Standard petal. *(b)* Seed in lateral view. *(c)* Outer surface of the calyx (upper lobes to the left). *(d)* Wing petal. *(e)* Keel petal. *(f)* Pistil. *(g)* Flower in lateral view. *(h)* Pod in lateral view. *(i)* Bract. *(j)* Anther. *(k)* Androecium. *(l)* Leaf in abaxial view. *(m)* Stipule. Voucher specimens. *(a, c) Davey 173* (K). *(b) Milne-Redhead and Taylor 11245* (K). *(d, g, h, j, k) Greenway and Kanuri 14269* (K). *(e) Jackson and Apejoye 413973* (K). *(f) Hepper 1021* (K). *(i) Polhill and Paulo 2089* (K). *(l, m) Siame 162* (K). All scale bars represent 1 mm.

### ***Selected specimens***

ERITREA: Bocos, Cheren, *Pappi 2527*, 10.xi.1902 (BM 2 sheets, K). SUDAN: Kordofan, *Kotsch 420*, without date (K). CHAD: Dioura, Macina, *Davey 173*, Oct. 1954 (K). NIGER: Niamey, *Olufsen 476*, 8.x.1947 (BM, S). GUINEA: Guine-Bissau, Pussuli, *Santos 1438*, 17.xii.1942 (K). BURKINA FASO: Haute Volta, Lergo, *Ake Assi 13587*, 13.xi.1976 (K). GHANA: Tefle, on Volta River, *Akpabla 1982*, 13.8.1959 (K). NIGERIA: Naraguta, Jos Plateau, rough ground near Forestry Department, amongst grass, *Hepper 1021*, 14.x.1957 (K). CAMEROON: Ganglani village, 6 mls [9.65 km] from confluence of Kam and Kimiri Rivers, Vogel Peak area, *Hepper 1441*, 23.xi.1957 (K). DEMOCRATIC REPUBLIC OF CONGO: 50 km north-east of Mokolo, on route to Mora, *Bounougou 173*, 18.ix.1964 (K, S). UGANDA: Matuga, *Robertson 3312*, 29.vii.1982 (K). KENYA: Thika-Garissa road, 2.6 km towards Garissa after junction with Kitui road, near Kongonde, *Faden and Faden 74/737*, 7.vi.1974 (K, PRE). TANZANIA: Imagi Hill, 1 ml. [1.61 km] south of Dodoma, *Polhill and Paulo 2089*, 20.iv.1962 (K, PRE). ZAMBIA: Livingstone, Chief Mukuni area, 2.1 km along road to Chief Mukuni Palace from junction with Victoria Falls road in Baikiae forest, *Zimba et al. 913*, 19.ii.1997 (K). MALAWI: Lilongwe, *Banda 250*, 14.ix.1956 (BM). MOZAMBIQUE: Niassa, Mossuril para Lumbo, 4.5 km na estrada de Nampula, *Pedro and Pedrogao 3131*, 5.v.1948 (K, PRE). ANGOLA: Huilla, *Welwitsch 1904,* Apr. 1860 (K, BM). NAMIBIA: Grey sandy flats below Musese Camp west of Lupala Mission Station; *De Winter and Marais 4978*, 4.iii.1969 (K). ZIMBABWE: Gwanda, Sezane Reservoirs, *Davies 1296*, May 1955 (K, PRE). SOUTH AFRICA: Kruger National Park, Punda Milia, *Van Rooyen 494*, 19.iii.1976 (PRE). MADAGASCAR: Ankazoabo, *Bosser 17241*, Feb. 1963 (K). (150 specimens examined.)

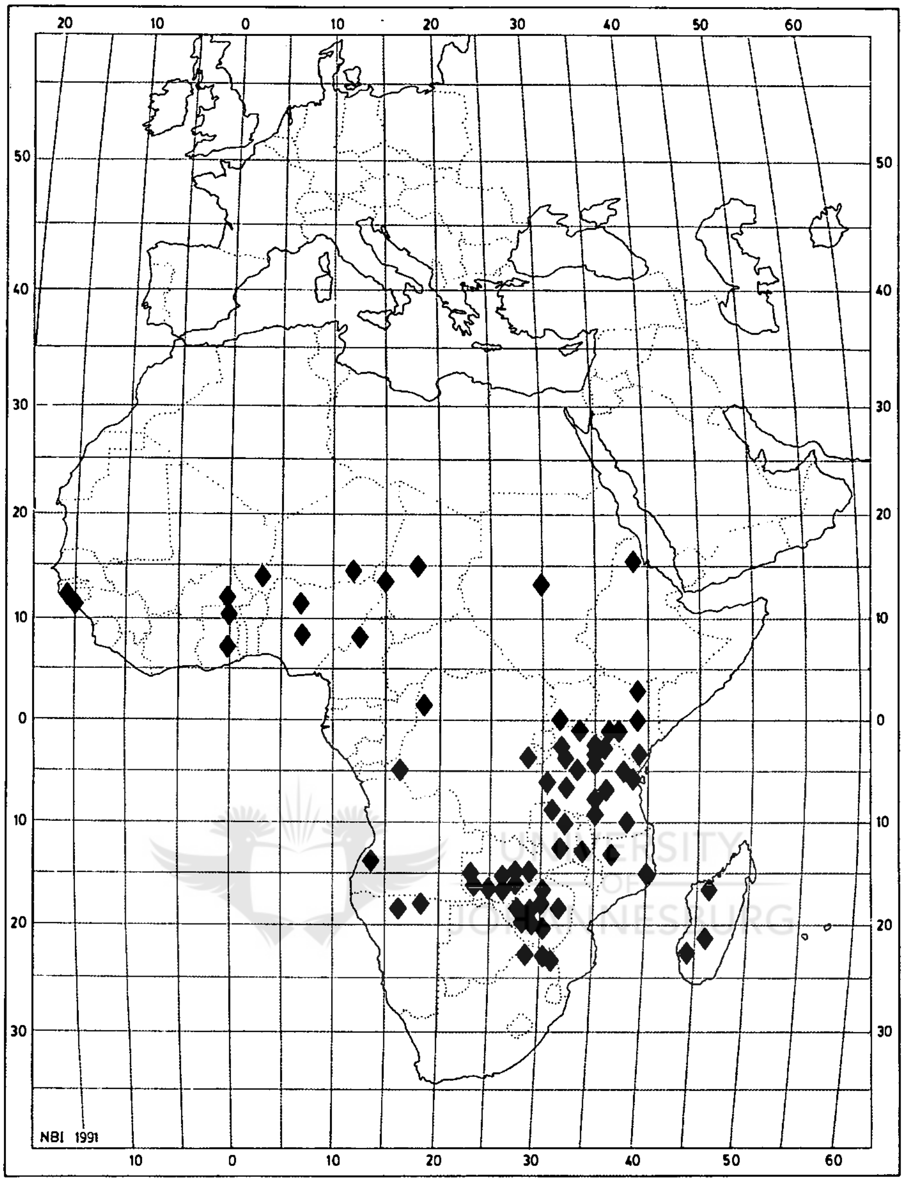

FIG. 10.5 Known geographical distribution of *Rothia hirsuta*.

2. ROTHIA INDICA (L.) Druce in Bot. Exch. Club Soc. Brit. Isles 3: 423. 1914; Rudd, A revised handbook to the flora of Ceylon: 184. 1991; Holland, Austrobaileya 5: 93 (1997); *Trigonella indica* L., Sp. Pl. 2: 778. 1753.—TYPE: Herb. Hermann 3: 24 no. 285 BM-000621888 (lectotype: BM photo!, designated by Rudd [1991])

*Lotus indicus* Desr. in Lam., Encyc. 3: 606. 1759.—TYPE: as for *T. indica*

*Hosackia indica* Graham in Wallich, Numer. List n. 5940. 1831–1832. *nom. nud.*

*Glycine leptocarpa* Graham in Wallich, Numer. List n. 5515. 1831–1832. *nom. nud.*

*Rothia trifoliata* (Roth) Pers., Syn. Pl. 2: 638 and 659. 1807; Benth. in Hook., Lond. J. Bot. 3: 339. 1844; Bentham and Müller, Fl. Austr. 2: 185. 1864; Trimen, Handb. Fl. Ceylon: 7. 1894; *Dillwynia trifoliata* Roth, Catal. Bot. 3: 71. 1806.—TYPE: 'horto medico Amsteledamensi' (B†?)

Small, pubescent, prostrate, herb. Branches up to 40 cm long, brown, either covered with dense, woolly hairs or sparsely hairy (pilose). Leaves with leaflets elliptic to obovate, terminal leaflet (7–) 9–26 mm long, (2–) 3–5 mm wide, lateral leaflets (5–) 8–20 mm long, (1.5–) 2.5–6.0 mm wide; apex obtuse or slightly acute; base cuneate; petiole 4–13 mm long. Stipules elliptic to lanceolate or ovate, 2–8 (–10) mm long, paired. Inflorescence with flowers solitary or up to 4 per raceme; pedicel up to 2 mm long; bract 1–3 mm long. Flowers 5–8 mm long. Calyx 4–7 mm long; tube 1.5–4.0 mm long; lobes 1–4 mm long. Standard 4.0–6.5 mm long; claw 1.5–2.5 mm long; lamina 2.5–4.0 mm long, 2.0–2.5 mm wide. Wings 4.0–6.5 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.5 mm long, 1.0–1.5 mm wide. Keel 4.0–6.5 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.5 mm long, 1.0–1.5 mm wide. Pistil ovary linear, 3.0–4.5 mm long, 0.5–1.0 mm wide with ±13 to 18 ovules; style 1.4–1.7 mm long. Pods linear or slightly falcate, (30–) 35–55 mm long, 1.5–3.0 mm wide with up to ±35 seeds per pod. Seeds 1.3–1.8 mm long, 1.0–1.3 mm wide, mature seeds brown, surface smooth (Fig. 10.6). Flowering time: Flowering and fruiting all year round from January to December.

***Distribution and ecology***—The species occurs in India, Sri Lanka, China, Vietnam, Malaysia and Australia (Fig. 7).

***Diagnostic characters***—The paired, ovate stipules, sparse inflorescences, long, linear pods and smooth, brown seeds distinguish *Rothia indica* from *R. hirsuta*.

***Notes***—Two subspecies can be recognised based predominantly on their geographical distribution, size and pubescence of vegetative and reproductive parts.

1. Vegetative parts sparsely hairy, terminal leaflets (7–) 10–26 x (2–) 4–8 mm, lateral leaflets (5–) 8–20 x (1.5–) 3.0–6.0 mm, petiole 5–13 mm long, stipules elliptic to lanceolate 2–8 (–10) mm long, pods (–33) 35–55 x (1.5–) 2.0–3.0 mm, seeds 1.3–1.6 x 1.0–1.3 mm, India, Sri Lanka, China, Vietnam and Malaysia.......................................................................2a. subsp. *indica*
1. Vegetative parts covered with dense, woolly hairs, terminal leaflets 9–15 x 3–5 mm, lateral leaflets 9–12 x 2.5–4.0 mm, petiole 4–8 mm long, stipules elliptic to ovate 2–5 mm long, pods (30–) 35–45 x 1.5–2.0 mm, seeds 1.5–1.8 x 1.2–1.3 mm, restricted to Australia..............................................................2b. subsp. *australis*

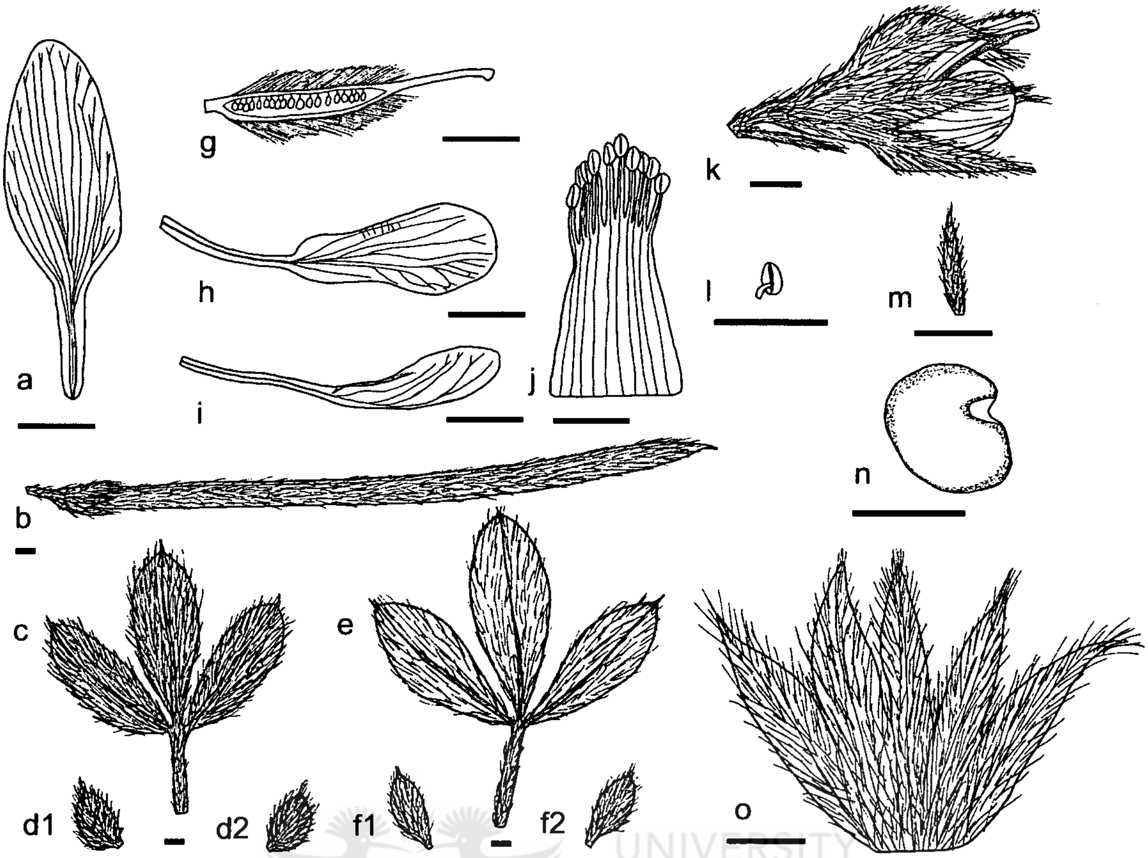

FIG. 10.6 Morphology of *Rothia indica*. *(a)* Standard petal. *(b)* Pod in lateral view. *(c)* Leaf of *R. indica* subsp. *australis* in abaxial view. *(d1, d2)* Stipules of *R. indica* subsp. *australis*. *(e)* Leaf of *R. indica* subsp. *indica* in abaxial view. *(f1, f2)* Stipules of *R. indica* subsp. *indica*. *(g)* Pistil. *(h)* Wing petal. *(i)* Keel petal. *(j)* Androecium. *(k)* Flower in lateral view. *(l)* Anther. *(m)* Bract. *(n)* Seed in lateral view. *(o)* Outer surface of the calyx (upper lobes to the left). Voucher specimens. *(a, g, h, i, k) Cooray 70020117R* (K). *(b, n) Gamble 13771* (K). *(c, d1, d2) Latz 16126* (MEL). *(e, f1, f2) Barber 55* (K). *(j, l, o) Wight 828.* (K). *(m) Wight 571* (K). All scale bars represent 1 mm.

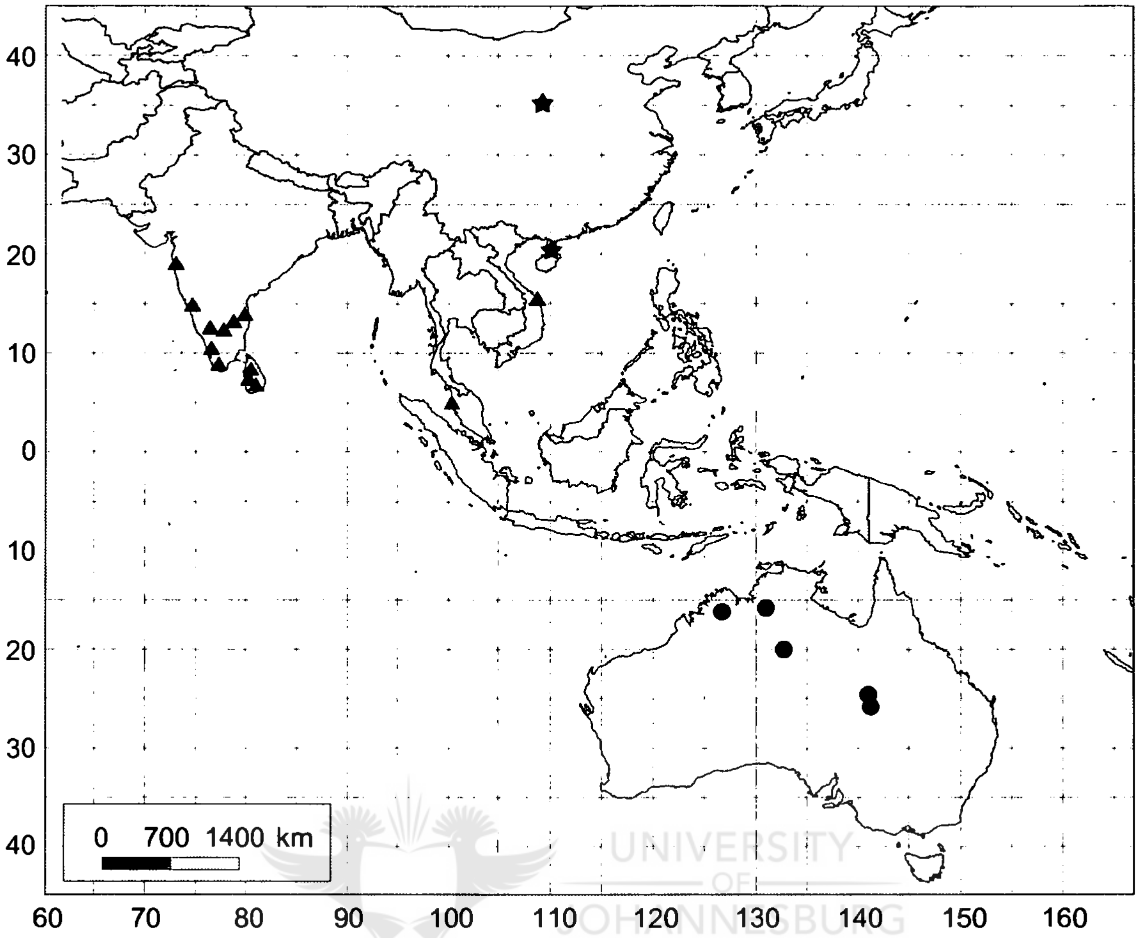

FIG. 10.7. Known geographical distribution of *Rothia indica* subsp. *indica* (triangles) and *R. indica* subsp. *australis* (dots). Specimens cited in Chen and Li (1997) from China are represented by stars.

**2a. *Rothia indica* (L.) Druce** subsp. ***indica***

Leaves with terminal leaflet (7–) 10–26 long, (2–) 4–8 mm wide, lateral leaflets (5–) 8–20 mm long, (1.5–) 3.0–6.0 mm wide; petiole 5–13 mm long. Stipules elliptic to lanceolate, 2–8 (–10) mm long. Inflorescence with flowers solitary or 2 to 4 per raceme. Calyx 5.0–6.5 mm long; tube 2–4 mm long; lobes 1–3 mm long. Standard 4.0–6.5 mm long; claw 1.5–2.0 mm long; lamina 2.5–4.0 mm long, 2.0–2.5 mm wide. Wings 4–6 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.0 mm long, 1.0–1.5 mm wide. Keel 4–6 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.0 mm long, 1.0–1.5 mm wide. Pistil with ovary 3–4 mm long, 0.5–0.7 mm wide with ±14 to 18 ovules; style 1.4–1.6 mm long. Pods (–33) 35–55 mm long, (1.5–) 2.0–3.0 mm wide with up to ±35 seeds per pod. Seeds 1.3–1.6 mm long, 1.0–1.3 mm wide.

***Distribution and ecology***—Collections from India, Sri Lanka, Vietnam and Malaysia were studied (Fig. 10.7), but this subspecies has also been recorded from China (Chen and Li 1997) and the specimens cited by these authors were included on the map. The subspecies favours sandy soils, grassy slopes or moist open fields. It is common in disturbed areas such as roadsides.

***Selected specimens***

INDIA: Chinglepul, *Barber 55*, 10.i.1899 (K); Bombay (Mumbai), *Dalzell s.n.*, Apr. 1878 (K); Ganjam district, Chennai, *Gamble 13771*, Feb. 1884 (K); Bengaluru, *Gough 162*, Dec 1937 (K); Tirunelveli, Tamil Nadu, *Matthew 16388*, 26.i.1979 (BM); Denkanikotta, Dharmapuri, Denkanikotta Rest House, *Matthew RHT 24647*, 15.xi.1979 (K); Kodaikanal, Dindigul, Law's Ghat road, *Matthew RHT 51949*, 4.xii.1987 (K); Mysore, *Mimso 607*, Oct. 1837 (K); Hassan, Mysore, Belvathally, *Ramamoorthy 1956,* 13.xii.1971 (K); 70 km north of Munnar, Palani hills, Tamilnadu, *Van der Maesen 3453*, 20.i.1979 (K). VIETNAM: Tourane (now Da Nang), *Clemens and Clemens 4294*, May–Jul 1927 (BM). SRI LANKA: Ruhuna National Park, block 1 near Buttawa Bungalow, *Cooray and Balakrishnan 69010909R*, 9.vi.1969 (BM); Trincomalee, near China Bay Airport, *Rudd and Balakrishnan 3134*, 24.ii.1970 (K); Hambantota, Yala, *Fagerlind 1695*, Jan. 1974 (S). MALAYSIA: Pulau Pinang, *Haihtmu 2996*, 21.xii.1917 (K). (33 specimens examined.)

**2b. *Rothia indica*** subsp. ***australis*** A.E.Holland, *Austrobaileya* 5: 94 (1997)

*Type:* Queensland, Gregory South District, Site 195, Warlus 1, 7 Aug 1971, *Boyland 4016*; holo BRI (photo seen)

Leaves with terminal leaflet 9–15 mm long, 3–5 mm wide, lateral leaflets 9–12 mm long, 2.5–4.0 mm wide; petiole 4–8 mm long. Stipules elliptic to ovate 2–5 mm long. Inflorescence with flowers solitary or 2 per raceme. Calyx 4–7 mm long; tube 1.5–3.0 mm long; lobes 3.5–4.0 mm long. Standard 4.0–6.5 mm long; claw 1.5–2.0 mm long; lamina 2.5–4.0 mm long, 2.0–2.5 mm wide. Wings 4.0–6.5 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.5 mm long, 1.0–1.5 mm wide. Keel 4.0–6.5 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.5 mm long, 1.0–1.5 mm wide. Pistil with ovary 4.0–4.5 mm long, 0.6–1.0 mm wide with ±13 to 17 ovules; style 1.5–1.7 mm long. Pods (30–) 35–45 mm long, 1.5–2.0 mm wide with up to ±30 seeds per pod. Seeds 1.5–1.8 mm long, 1.2–1.3 mm wide.

***Distribution and ecology*****—**The subspecies is restricted to Australia where it occurs on sandy hills and flats (Fig. 10.7).

***Specimens examined***

AUSTRALIA: 100 mls [160.9 km] west of Windorah, *Everist 3898*, 9.vi.1949 (K); Boomerang Waterhole, Lander River, 20°38'00"S 132°11'00"E, *Latz 16126*, 10.v.2000 (MEL); Upper Victoria River, *von Müller s.n.*, without date (K, MEL 2 sheets); near the Ord River, *O'Donnell s.n.,* without date (MEL 2 sheets).

# CHAPTER 11: GENERAL CONCLUSIONS

The results presented in this study have provided clarity on relationships within the Crotalarieae and also generic circumscriptions within the tribe. The new insights gained have resulted in new generic classifications for both *Lebeckia* s.l. and *Lotononis* s.l. As a result the number of genera included in the tribe has increased from 11 to 16. The new hypothesis of phylogenetic relationships (Fig. 11.1) provides the opportunity to re-interpret the patterns of evolution of various characters within the tribe and to ascertain the apomorphic states for the various genera. Polhill (1976) and Van Wyk and Schutte (1995) discussed the distribution of characters within the Crotalarieae and related tribes, but given the high incidence of convergence, some doubt has remained about the circumscription of genera, particularly *Lebeckia* s.l. The new insights into generic delimitations and relationships allow for a re-evaluation of diagnostic characters and apomorphic states. The characters that are most informative for generic circumscription were therefore reconstructed onto the minimal length trees from the combined molecular/morphological analysis (some already presented in Chapter 8). The characters included are listed in Table 8.1 (Chapter 8) and Appendix A5. Where more than one reconstruction is possible two or more trees are shown. The reconstructions were done on one of the 370 most parsimonious trees from the combined molecular/morphological analysis presented in Chapter 8 in order to examine the evolution of the specific characters (Appendix A5) on that particular hypothesis of relationships.

HABIT AND PERSISTENCE—Most of the basally diverging lineages of the Crotalarieae have a herbaceous or suffrutescent habit and woodiness or a shrubby habit appears to have become pronounced in especially the "Cape group". Most of the species are, however, perennial and the development of a short-lived or annual life history appears to be a secondary and convergent character, possibly to survive recurrent fires, periods of aridity or unfavourable weather conditions (Figs. 11.2 and 11.3). Van Wyk and Schutte (1995) discussed the taxonomic value of the secondary xylem within the Podalyrieae and identified two types of arrangement, one where the vessels are arranged in small isolated radial or tangential groups and another where the vessels are arranged in large confluent or dendritic groups. The latter has been suggested to be associated with strongly seasonal habitats or Mediterranean climates. The great variety of habitats in which the Crotalarieae occur indicate that a comparative study of wood anatomy would be of considerable interest. It will allow a comparison of the patterns of vessel arrangement with those in the closely related Podalyrieae and Genisteae.

LEAVES—The evolution of leaf types within the Crotalarieae was explored in Chapter 8 (Fig. 8.3) and indicated that within the *Crotalaria* and *Lotononis* clades the leaves are mostly digitate with little variation. The diversity of leaf types increases in the "Cape group" where unifoliolate and simple leaves become pronounced in groups such as *Rafnia* and *Lebeckia*, with the latter having a further development to phyllodinous leaves. In the study of the lebeckioid genera *Calobota*, *Lebeckia* and *Wiborgiella*, lamina anatomy provided important characters that were informative at the generic level (Chapter 5; Boatwright et al. submitted) especially with regard to the arrangement of the mesophyll (isobilateral or dorsiventral) and presence or absence of mucilage cells. These characters may potentially be informative throughout the Crotalarieae and should in future be explored with a larger sampling of genera within the tribe to ascertain their taxonomic value.

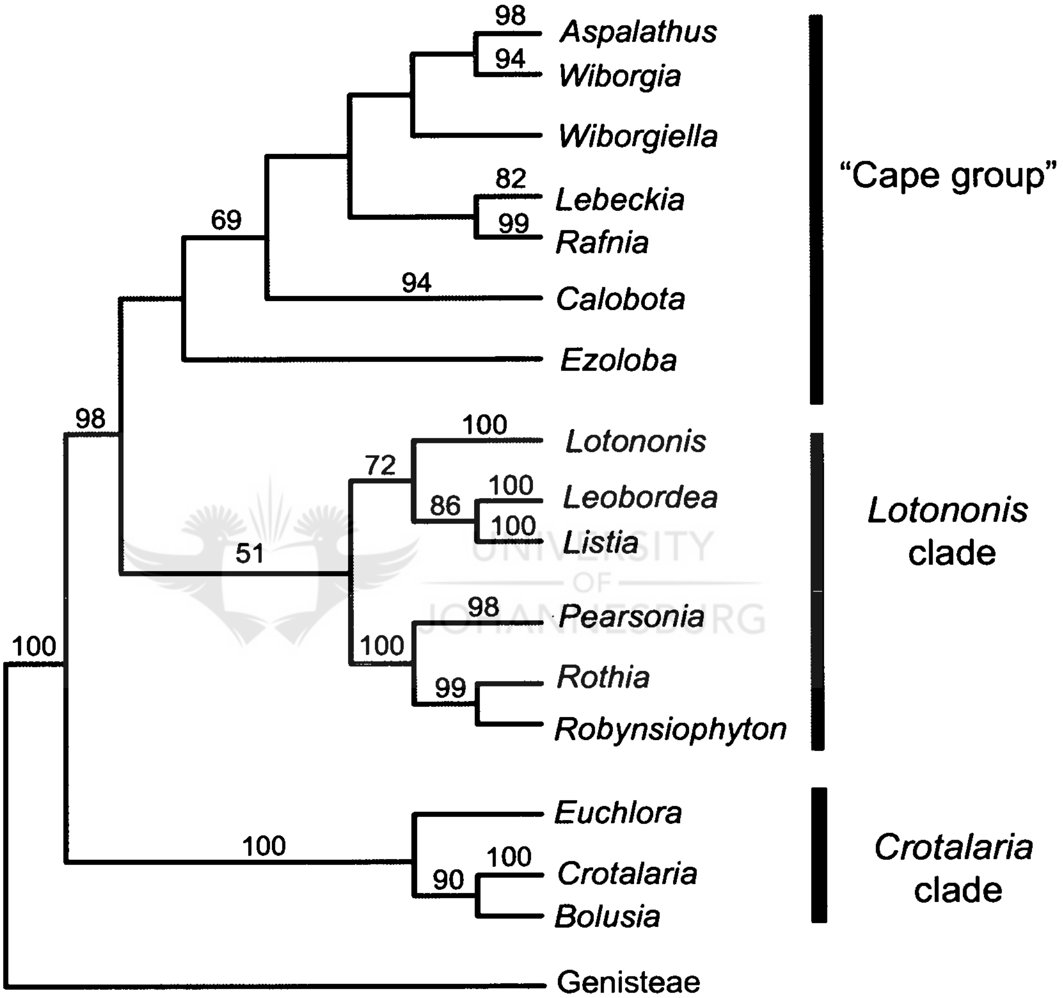

FIG. 11.1 Hypothesis of phylogenetic relationships in the tribe Crotalarieae. The cladogram is a simplified strict consensus tree of the 370 trees from the combined molecular and morphological analysis presented in Chapter 8.

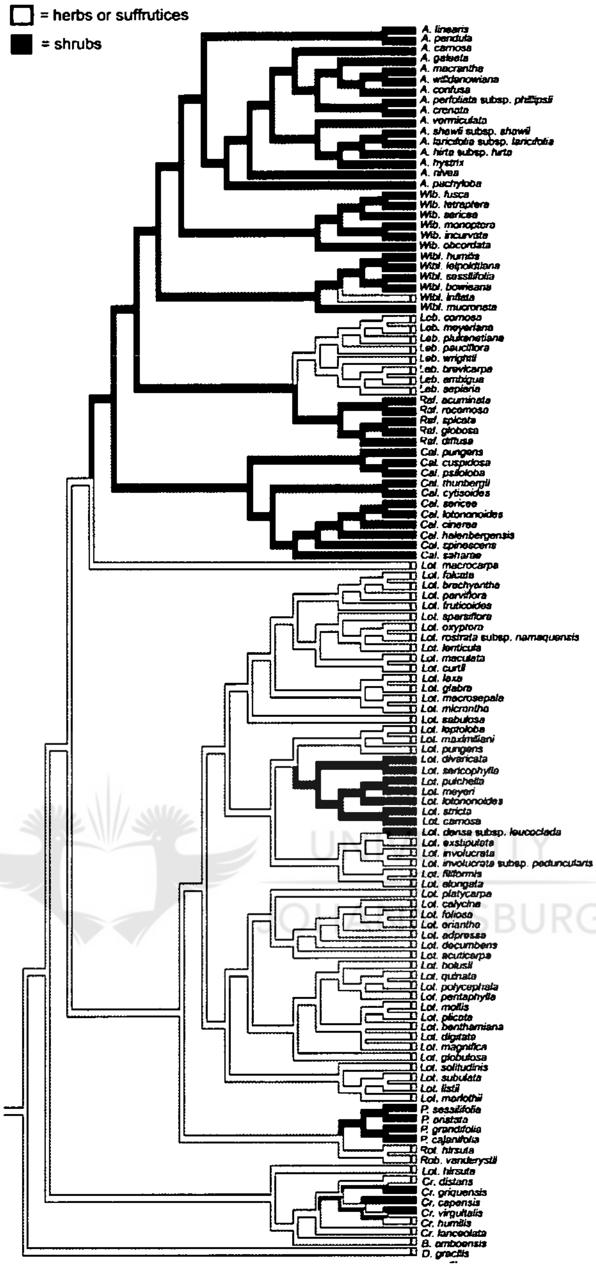

FIG. 11.2 Parsimony-based reconstruction of habit on the 370 minimal length trees from the combined molecular/morphological analysis presented in Chapter 8.

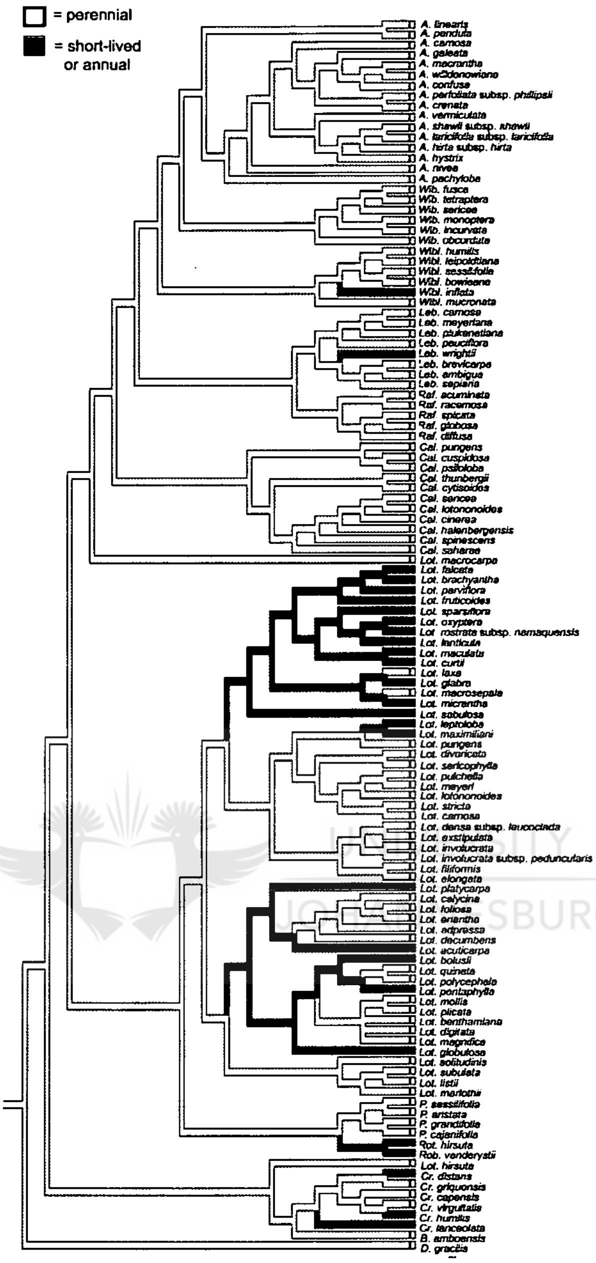

FIG. 11.3 Parsimony-based reconstruction of life history on the 370 minimal length trees from the combined molecular/morphological analysis presented in Chapter 8.

STIPULES—The loss of stipules is reconstructed as an apomorphy for the "Cape group" and stipules are only present in *Lebeckia wrightii* and *L. uniflora.* A loss of stipules is autapomorphic for some species of the *Leobordea* clade, *Pearsonia* and *Crotalaria* where stipules are largely present (Fig. 11.4). Asymmetrical stipules are unique to the lotononoid groups, i.e. *Lotononis* s.s., together with the *Leobordea* and *Listia* clades (Fig. 8.4) and *Rothia hirsuta*, while *Euchlora* and *Ezoloba* are conspicuously different in having symmetrical stipules (when present in the former).

BRACTEOLES—Bracteoles are present in all genera of the "Cape group", *Ezoloba*, *Listia*, *Pearsonia*, *Bolusia* and *Crotalaria.* A loss of bracteoles has been regarded as an apomorphy for *Lotononis* s.l., but this character is reconstructed as a convergence between *Lotononis* s.s., *Leobordea*, *Rothia*, *Robynsiophyton* and *Euchlora* (Fig. 8.5). Prenner (2004) mentions that "initiated but suppressed" bracteoles represents a new character state in Papilionoideae and is a refinement of the traditional presence or absence of bracteoles as presented here. However, ontogenetic studies (investigation of the floral primordium) are necessary to evaluate whether bracteoles are indeed initiated and later suppressed in *Lotononis* s.s., *Leobordea*, *Rothia*, *Robynsiophyton* and *Euchlora* or whether a total absence is found in Crotalarieae.

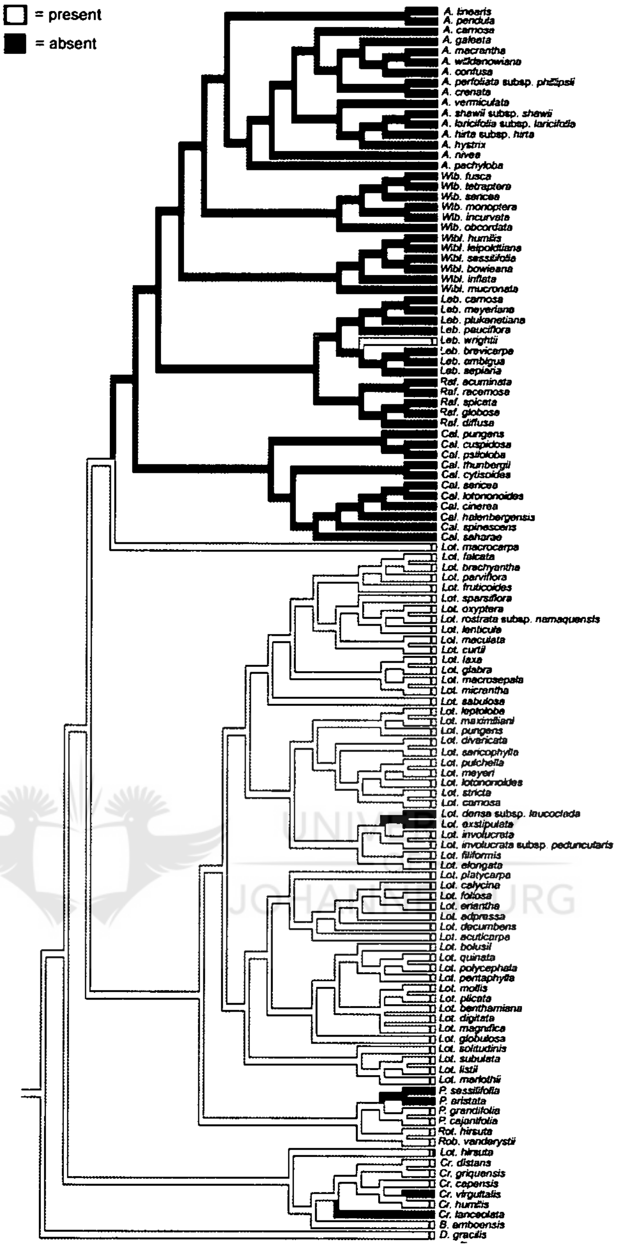

FIG. 11.4 Parsimony-based reconstruction of the presence or absence of stipules on the 370 minimal length trees from the combined molecular/morphological analysis presented in Chapter 8.

FLOWERS—Flowers often provide important characters in legumes (Polhill 1976). In the Crotalarieae two floral types are found. Most genera have specialised flowers with petals that are reflexed to various degrees. *Pearsonia*, *Robynsiophyton* and *Rothia* have gullet type flowers where the floral parts are rather unspecialised with a straight or down-curved style and uniform anthers. Overall the flowers are largely yellow, but some species of *Aspalathus*, *Lotononis* s.s., *Pearsonia* and *Crotalaria* have blue, purple, white or pink flowers. It may be interesting to investigate anthocyanins in these groups to identify the compounds responsible for colour variation and their homology.

CALYX—The Crotalarieae differ from Genisteae in the absence of a two-lipped calyx. The lotononoid calyx found in some Crotalarieae was reconstructed as an apomorphy for the *Lotononis* clades and *Pearsonia*, whereas a reversal to the more lebeckioid calyx type is found in *Rothia* and *Robynsiophyton* (Fig. 8.6). The carinal lobe of the calyx is narrower than the other lobes in most genera of the tribe and very pronounced in some *Rafnia* species where the carinal lobe is extremely thin and almost hair-like (Campbell and Van Wyk 2001). *Lebeckia*, however, has the carinal lobe equal to the other lobes, i.e. an equally lobe calyx (Le Roux 2006).

KEEL—Rostrate keel petals appear to have developed several times in the Crotalarieae (Fig. 8.7). A beaked keel is often associated with a more pronounced differentiation between the stamens (Polhill 1976) where species with beaked keel petals tend to have the carinal stamen either similar to the long, basifixed anthers or somewhat intermediate between the long and short stamens.

ANTHER ARRANGEMENT—Three basic arrangements were identified within the Crotalarieae (Fig. 8.8): 5+5 (carinal anther resembles the basifixed anthers) present in

*Bolusia*, *Crotalaria*, *Ezoloba* and *Lebeckia*; 4+1+5 (the carinal anther intermediate in between the dorsifixed and basifixed ones) present in *Aspalathus*, *Calobota*, *Lotononis*, *Listia*, *Rafnia* and *Wiborgia*; 4+6 (carinal anther resembling the dorsifixed anthers) present in *Euchlora*, *Leptis*, *Lotononis* and *Wiborgiella*. Anther characters in combination with other data are very useful at the generic level and were very important in segregating *Calobota* and *Wiborgiella* from *Lebeckia* s.s. Most genera of the "Cape group" as well as *Lotononis macrocarpa* have a 4+1+5 anther arrangement with the exception of *Lebeckia* (5+5 configuration) and *Wiborgiella* (4+6 configuration). In *Lotononis* s.s. and the *Leobordea* clade both a 4+1+5 and 4+6 is found, while the *Listia* group has an exclusively 4+1+5 arrangement. *Crotalaria* and *Bolusia* share a 5+5 anrrangement, while *Lotononis hirsuta* differs from these in its 4+6 arrangement.

GYNOECIUM—Straight styles are a unique feature found in *Pearsonia*, *Rothia* and *Robynsiophyton*. The other genera in the tribe Crotalarieae have upcurved styles. *Crotalaria* is unique within the tribe in having hairs on the style as opposed to the glabrous styles of the other genera. This style-brush facilitates the "pollen pump" mechanism which is found in flowers of *Crotalaria* where the pollen is shed into the keel before the flowers are fully open and then pushed out by the hairs of the style when the keel is depressed by a pollinator (Polhill 1982).

FRUIT—Fruit types within the Crotalarieae are variously modified, but some general trends can be observed. A verrucose upper suture of the pod was thought to be unique to *Lotononis* s.l., but in light of the new generic classification for the genus this character is convergent between the *Leobordea* clade, *Lotononis* s.s., *L. hirsuta* (section *Euchlora*) and *L. macrocarpa* (Fig. 8.9).

*Aspalathus* and *Wiborgia* both have few-seeded (1 to 2-seeded) fruit (Fig. 11.5) that are sporadically found in *Calobota* and some species of the *Leobordea* clade (*Lotononis* section *Synclistus*).

The shape of the pods in transverse section (inflated, terete or laterally compressed) is informative at especially the generic level, with *Bolusia*, *Crotalaria* and *Euchlora*, i.e. the *Crotalaria* clade, all having inflated pods, as well as most species of *Wiborgiella* (Fig. 11.6). The *Lotononis* clades have predominantly semi-terete pods and the *Pearsonia* clade differ in their laterally compressed pods. In most of the "Cape group" the pods are laterally compressed. The samaras found in *Wiborgia* represent a unique fruit-type in the tribe and also a generic apomorphy for the genus. *Lebeckia meyeriana*, *L. plukenetiana* and some *Rafnia* species are the only other examples of winged fruit in the Crotalarieae and their pods are oblong, in contrast to the ovoid pods of *Wiborgia* species.

The anatomy of the fruit wall is an interesting character that deserves further investigation within the Crotalarieae. Most of the genera have thin-walled pods, but the fruit wall structure is not necessarily similar. The presence or absence of sclerenchyma and the amount of sclerification when present differ between genera. Thick-walled pods with a spongy inner surface are found in *Lebeckia* and *Calobota* but may also be present in species of other genera such as *Lotononis* s.s. (e.g. *L. pallens*).

SEEDS—The seeds of members of Genisteae are usually transversely oblong in contrast to the oblong seeds found in Crotalarieae. Seed characters are not very informative between genera but may be valuable at the species level. A rugose seed surface, for example, is an important generic character for *Lebeckia*, but occurs sporadically in other genera such as *Calobota*, *Lotononis* s.l., *Rafnia*, *Rothia* and *Wiborgiella*.

CHROMOSOME BASE NUMBER—The reconstruction of chromosome base numbers is shown in Fig. 8.11. A base number of x=9 seems probably for the tribe with x=8 in *Crotalaria*, *Rafnia* and some species of *Aspalathus* and x=7 in *Pearsonia*, *Rothia* and *Lotononis* s.s. It is possible that this pattern may become more complex as more counts become available if for example material of *L. macrocarpa* (*Ezoloba*) can be found.

CHEMISTRY—The chemical data available for the Crotalarieae are very informative and provide additional insight into generic relationships. Quinolizidine alkaloids are present in most genera of the tribe, but absent from *Lotononis* s.s. and *Crotalaria* (Fig. 11.7). This is due to the presence of macrocyclic pyrrolizidine alkaloids in these genera (see Fig. 8.13). In *Lotononis* s.s. and *Crotalaria* the quinolizidine alkaloid biogenetic pathway appears to have been replaced by a macrocyclic pyrrolizidine pathway. Species of *Lotononis* s.s. furthermore produce cyanogenic glucosides (Fig. 8.12), a trait not found in any other genus of the tribe. The accumulation of esters of alkaloids in *Pearsonia*, *Robynsiophyton* and *Rothia* lends support to the close relationship shown between these genera. Seed alkaloids and seed flavonoids are worth while exploring in future due to the conservative nature of these compounds in the seeds versus the leaves. This may erradicate the problem of overly complex chemical patterns that are not chemotaxonomically useful. The flavonoids of the Crotalarieae are especially poorly studied and in light of the utilisation of some species as teas it would be interesting to ascertain their phenolic chemistry.

The diversity and taxonomic complexity of the Crotalarieae mentioned by Polhill (1976), Dahlgren (1970a) and Van Wyk (1991a) have been highlighted by the results of this study. Molecular characters in combination with the vast volume of morphological and chemical data for the Crotalarieae were extremely useful in unravelling the phylogenetic structure of the tribe and has led to a new generic classification that is both practical and highly predictable. In light of the overlap of morphological characters and lack of generic apomorphies informative combinations of characters are available to distinguish between the crotalarioid genera.

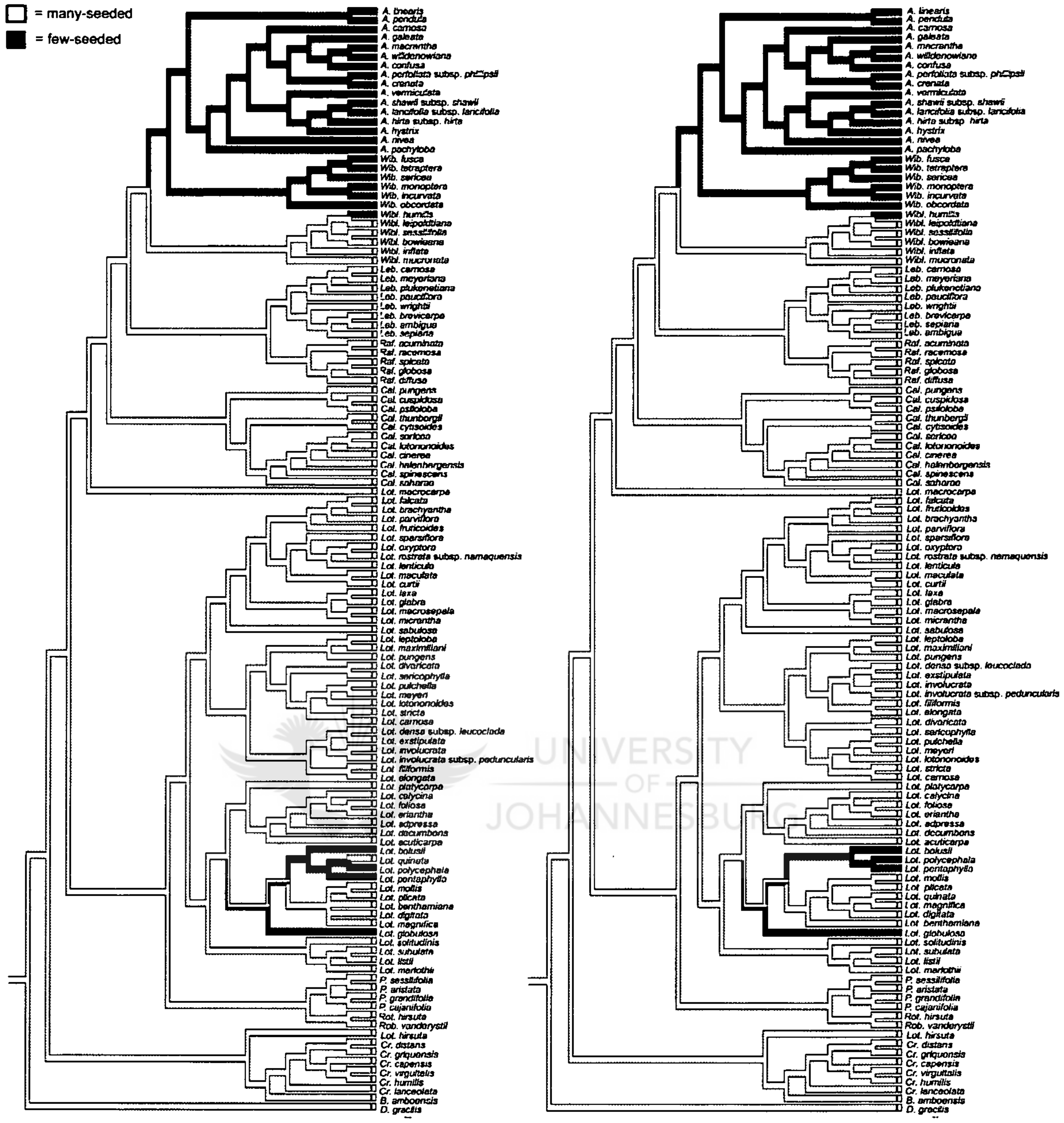

FIG. 11.5 Parsimony-based reconstruction of few- versus many seeded fruit on the 370 minimal length trees from the combined molecular/morphological analysis presented in chapter 8.

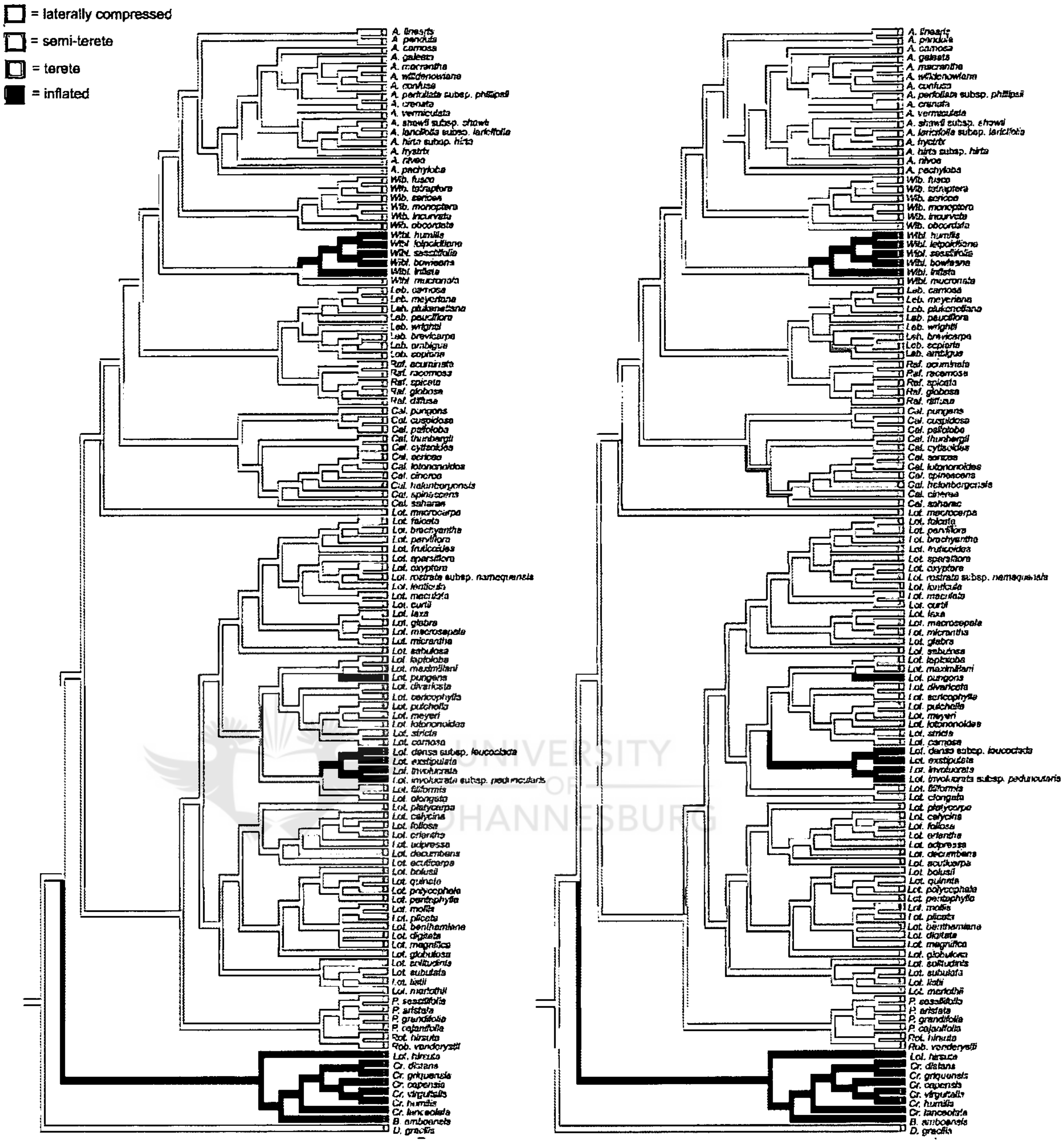

FIG. 11.6 Parsimony-based reconstruction of fruit shape in transverse section on the 370 minimal length trees from the combined molecular/morphological analysis presented in chapter 8.

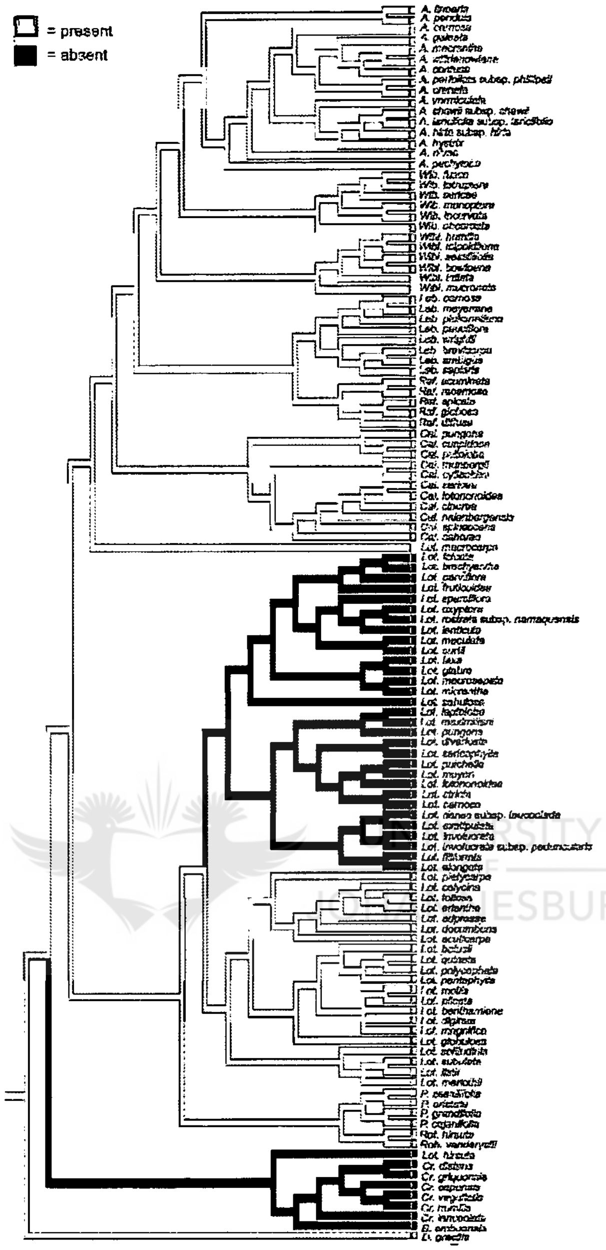

FIG. 11.7 Parsimony-based reconstruction of the presence or absence of quinolizidine alkaloids on the 370 minimal length trees from the combined molecular/morphological analysis presented in chapter 8.

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APPENDIX A1. Voucher specimens from which floral dissections were made in order to study and illustrate reproductive morphology.

**Calobota acanthoclada**: *Dinter 6269* (BOL); *Mannheimer CM2012a* (WIND); *Williams 2594a* (BOL); *Williams 3376* (BOL). **C. cinerea**: *Boatwright et al. 150* (JRAU); *Dinter 3998* (BOL); *Jürgens 2234* (PRE); *Le Roux 2066* (NBG); *Mannheimer et al. CM 899* (WIND); *Merxmüller and Giess 3089* (WIND). **C. cuspidosa**: *Acocks 2455* (BOL); *Ethel Anderson 591* (BOL); *Gubb 12584* (PRE); *Van Wyk BSA1241* (PRE); *Van Wyk 3055* (JRAU) 3 dissections. **C. cytisoides**: *Andrag 272* (PRE); *Barker 6426* (NBG); *Barker 9694* (NBG); *Boatwright et al. 114* (JRAU); *Mauve and Oliver 136* (PRE); *McDonald 1568* (PRE); *Pillans 7701* (BOL); *Pretorius 105* (NBG); *Schutte 262* (JRAU); *Schutte 286* (JRAU); *Stirton 6167* (PRE); *Van Breda SKF574* (PRE); *Van Wyk 2568* (JRAU). **C. elongata**: *Hall 177* (NBG); *Van Breda 4486* (PRE); *Van Wyk 2229* (JRAU). **C. halenbergensis**: *Bean and Oliver 2445* (BOL); *Boatwright et al. 146* (JRAU); *Esterhuysen s.n.* (NBG); *Giess 13820* (WIND); *Johnson 22071* (NBG); *Jürgens 22739* (PRE); *Mannheimer CM2418* (WIND); *McDonald 739* (NBG); *Middlemost 2129* (NBG); *Müller 810* (PRE) 2 dissections; *Müller 830* (WIND); *Van Wyk 3086* (JRAU); *Werger 431* (PRE); *Salter 5549* (PRE). **C. linearifolia**: *Acocks 13195* (PRE); *Braine 98* (WIND); *Dean 673* (JRAU); *Evrard 9285* (PRE); *Giess 13803* (WIND); *Keet 1663* (WIND); *Merxmüller and Giess 3615* (PRE); *Snijman 214* (NBG). **C. lotononoides**: *Boatwright et al. 142* (JRAU); *Perold 1646* (PRE); *Schlechter s.n. sub TRV 1059* (PRE); *Schlechter 8214* (PRE). **C. namibiensis**: *Kolberg and Maggs 12* (WIND); *Owen-Smith 117* (WIND); *Owen-Smith 1268* (WIND). **C. obovata**: *Kers 152* (WIND); *Pearson 8036* (BOL). **C. psiloloba**: *Archibald 3848* (GRA); *Story 3353* (PRE); *Troughton 425* (PRE); *Van*

*Wyk s.n.* (JRAU) 3 dissections; *Zeyher 31438* (NBG). ***C. pungens*: *Boatwright et al. 106*** (JRAU); *Bond 12112* (NBG); *Markotter 9951* (NBG); *Sidey 1906* (PRE); *Snijman 353* (NBG); *Taylor 19386* (NBG); *Thompson 9948* (NBG); *Van Wyk 2147* (JRAU); *Van Wyk 3252* (JRAU). ***C. saharae*:** *Hill 1910* (K); *Keith 181* (K) 2 dissections. ***C. sericea*:** TYPICAL FORM—*Boatwright et al. 139* (JRAU); *Compton 19906* (NBG); *Hall 899* (NBG); *Hall 3701* (NBG); *Hilton Taylor 1366* (NBG, PRE); *Leipoldt 3765* (NBG); *Lewis 4705* (NBG); *O'Callaghan and Steensma 1650* (NBG); *Salter 5612* (BOL). BROAD-LEAVED FORM—*Arnold 916* (PRE); *Clark 633* (PRE); *Heywood s.n.* (NBG); *Van Wyk 2847* (JRAU). SHORT-LEAVED FORM—*Clark and Müller 337* (WIND); *Giess and Van Vuuren 678* (WIND); *Giess and Robinson 13177* (WIND); *Mannheimer CM2020* (WIND); *Watmough 867* (WIND); *Whitehead 80.9.8* (WIND); *Williamson 2575* (BOL).ORANJEMUND FORM—*Gess and Gess 97/98/68* (WIND); *Ward 11136* (WIND); *Williamson 4884* (WIND). ***C. spinescens*:** TYPICAL FORM—*Boatwright et al. 158* (JRAU); *Koekemoer 248* (JRAU); *Leistner 1897* (BOL); *Wilman 838* (PRE); *Zietsman 3489* (PRE). PRIESKA FORM—*Bryant 5404* (BOL); *Maguire 742* (NBG); *Van Wyk 3081* (JRAU); *Vlok 1932* (JRAU); *Williams 2594a* (BOL). ***C. thunbergii*:** *Boatwright et al. 141* (JRAU); *Boatwright et al. 151* (JRAU); *Germishuizen 4839* (PRE); *Hall 891* (NBG); *Johnson 200* (NBG); *Manning s.n.* (NBG); *Schutte 591* (JRAU); *Schutte 593* (JRAU); *Thorns s.n.* (NBG); *Van Jaarsveld 11977* (PRE); *Van Wyk 2584* (JRAU). ***Pearsonia cajanifolia*** subsp. ***cryptantha*:** *Posthumus 1b* (JRAU). ***Pearsonia sessilifolia*:** *Swanepoel 1* (JRAU). ***Robynsiophyton vanderystii*:** *Lisowski 20326* (K); *McCallum Weston 717* (K); *Richards 5309* (K); *Richards 9321* (K). ***Rothia hirsuta*:** *Akpabla 1982* (K); *Bidgood et al. 1194* (K); *Davies 1296* (K); *Davey 173* (K); *Greenway & Kanuri 14269* (K); *Hepper 1021* (K); *Horndy 20206* (K); *Jackson and Apejoye 413973* (K); *Polhill and*

*Paulo 2089* (K); *Robinson 151* (K); *Saadou 1798* (K); *Saime 162* (K). ***R. indica***: *Cooray 70020117R* (K); *Latz 16126* (MEL); *Wight 571* (MEL); *Wight 828* (K); *Wight 5821* (K); *Von Müller s.n.* (MEL). ***Wiborgiella aspalathoides***: *Barker 10407* (NBG) 3 dissections. ***W. bowieana***: *Streicher s.n.* (JRAU) 2 dissections. ***W. fasciculata***: *Muir 4775* (NBG) 2 dissections. ***W. humilis***: *Boatwright et al. 216* (JRAU); *Niemand 8* (JRAU); *Van Wyk 3530* (JRAU). ***W. inflata***: *Belle Barker 204* (JRAU); *Haynes H420* (PRE) 2 dissections; *Lewis 1816* (NBG); *Vlok et al. 2* (JRAU). ***W. leipoldtiana***: *Boatwright et al. 123* (JRAU); *Bolus 8974* (BOL); *Hanekom 2125* (PRE); *Schutte 295* (JRAU). ***W. mucronata***: *Guillarmod 8387* (GRA); *Stirton 10880* (JRAU); *Stirton and Zantovska 11608* (PRE). ***W. sessilifolia***: *Albertyn 498b* (NBG); *Muir 2144* (PRE); *Van Wyk 2120* (JRAU). ***W. vlokii***: *Vlok 2045* (PRE) 2 dissections.

APPENDIX A2. Voucher information for species of *Calobota*, *Lebeckia*, *Robynsiophyton*, *Rothia*, *Wiborgia* and *Wiborgiella* used to study stem, petiole, leaf and fruit wall anatomy.

***Calobota cinerea***: Stem—*Boatwright et al. 150* (JRAU); Petiole—*Boatwright et al. 150* (JRAU); Leaf—*Boatwright et al. 150* (JRAU); Fruit wall—*Boatwright et al. 150* (JRAU). ***C. cuspidosa***: Stem—*Boatwright et al. 92* (JRAU); Petiole—*Boatwright et al. 92* (JRAU); Leaf—*Boatwright et al. 92* (JRAU); Fruit wall—*Boatwright et al. 92* (JRAU). ***C. cytisoides***: Stem—*Boatwright et al. 114* (JRAU); Petiole—*Boatwright et al. 114* (JRAU); Leaf—*Boatwright et al. 114* (JRAU); Fruit wall—*Boatwright et al. 114* (JRAU). ***C. elongata***: Petiole—*Van Wyk 2562b* (JRAU); Leaf—*Van Wyk 2562b* (JRAU); Fruit wall—*Van Wyk 2562b* (JRAU). ***C. halenbergensis***: Stem—*Boatwright et al. 149* (JRAU); Petiole—*Boatwright et al. 149* (JRAU); Leaf—*Boatwright et al. 149* (JRAU); Fruit wall—*Boatwright et al. 149* (JRAU). ***C. linearifolia***: Leaf—*Dean 673* (JRAU); Fruit wall—*Giess et al. 6180* (WIND). ***C. lotononoides***: Stem—*Boatwright et al. 142* (JRAU); Petiole—*Boatwright et al. 142* (JRAU); Leaf—*Boatwright et al. 142* (JRAU); Fruit wall—*Boatwright et al. 142* (JRAU). ***C. namibiensis***: Leaf—*De Winter and Hardy 7919* (WIND); Fruit wall—*De Winter and Hardy 7919* (WIND). ***C. obovata***: Petiole—*Kers 152* (WIND); Leaf—*Kers 152* (WIND). ***C. pungens***: Stem—*Boatwright et al. 106* (JRAU); Petiole—*Boatwright et al. 106* (JRAU); Leaf—*Boatwright et al. 106* (JRAU); Fruit wall—*Boatwright et al. 106* (JRAU). ***C. psiloloba***: Stem—*Le Roux et al. 20* (JRAU); Petiole—*Le Roux et al. 20* (JRAU); Leaf—*Van Wyk s.n.* (JRAU); Fruit wall—*Le Roux et al. 20* (JRAU). ***C. saharae***: Stem—*Keith 181* (K), *Alleizette s.n. sub K*

*2007/014804* (K); Leaf—*Pitard 3276* (K), *Alleizette s.n. sub K 2007/014804* (K), *Bourgeau 210* (K); Fruit wall— *Alleizette s.n. sub K 2007/014804* (K), *Davis 49544* (K). ***C. sericea***: Stem—*Boatwright et al. 138* (JRAU); Petiole—*Boatwright et al. 138* (JRAU); Leaf—*Boatwright et al. 138* (JRAU); Fruit wall—*Boatwright et al. 138* (JRAU). ***C. spinescens***: Stem—*Boatwright et al. 158* (JRAU); Petiole—*Boatwright et al. 158* (JRAU); Leaf—*Boatwright et al. 158* (JRAU); Fruit wall—*Boatwright et al. 158* (JRAU). ***C. thunbergii***: Stem—*Boatwright et al. 151* (JRAU); Petiole—*Boatwright et al. 141* (JRAU), *Boatwright et al. 151* (JRAU); Leaf—*Boatwright et al. 151* (JRAU); Fruit wall—*Boatwright et al. 151* (JRAU). ***Crotalaria* sp.**: Fruit wall—*De Villiers 106* (JRAU). ***Lebeckia ambigua:*** Stem—*Boatwright et al. 132* (JRAU); Fruit wall—*Boatwright et al. 131* (JRAU). ***L. brevicarpa***: Fruit wall—*Le Roux et al. 4* (JRAU). ***L. contaminata***: Fruit wall—*Le Roux et al. 16* (JRAU). ***L. pauciflora***: Fruit wall—*Le Roux et al. 12* (JRAU). ***L. wrightii***: Fruit wall—*Johns 163* (JRAU). ***Melolobium alpinum***: Fruit wall—*Schutte 160* (JRAU). ***Rafnia amplexicaulis***: Fruit wall—*Campbell and Van Wyk 40* (JRAU). ***Rothia hirsuta***: Stem—*Davies 1296* (K); Petiole—*Davies 1296* (K), *Greenway and Kanuri 14269* (K), *Bogdon 2205* (K); Leaf—*Davies 1296* (K), *Greenway and Kanuri 14269* (K), *Bogdon 2205* (K); Fruit wall—*Bogdon 2205* (K), *Davies 1296* (K), *Greenway and Kanuri 14269* (K). ***R. indica***: Stem— —; Petiole—*Ramamoorthy 1956* (K), *Gamble 13771* (K), *Latz 16126* (MEL); Leaf—*Ramamoorthy 1956* (K), *Gamble 13771* (K), *Latz 16126* (MEL); Fruit wall—*Ramamoorthy 1956* (K), *Gamble 13771* (K), *Latz 16126* (MEL). ***Robynsiophyton vanderystii***: Stem—*Lisowski 20326* (K); Petiole—*Exell and Mendonça 657* (K), *Richards 18144* (K), *Lisowski 20326* (K); Leaf—*Exell and Mendonça 657* (K), *Lisowski 20326* (K), *Richards 18144* (K); Fruit wall—*Exell and*

*Mendonça 657* (K), *Lisowski 20326* (K), *Richards 18144* (K). ***Wiborgia monoptera***: Fruit wall—*Boatwright et al. 152* (JRAU). ***W. sericea:*** Stem—*Boatwright et al. 124* (JRAU); Petiole—*Boatwright et al. 124* (JRAU); Leaf—*Boatwright et al. 124* (JRAU); Fruit wall—*Boatwright et al. 124* (JRAU). ***Wiborgiella bowieana***: Petiole—*Streicher s.n. sub Schutte 831* (JRAU); Leaf—*Streicher s.n. sub Schutte 831* (JRAU); Fruit wall—*Streicher s.n. sub Schutte 831* (JRAU). ***W. humilis***: Stem—*Boatwright et al. 129* (JRAU); Petiole—*Boatwright et al. 129* (JRAU); Leaf— *Boatwright et al. 129* (JRAU); Fruit wall—*Boatwright et al. 212* (JRAU). ***W. inflata***: Stem—*Johns 162* (JRAU); Petiole—*Johns 162* (JRAU); Leaf—*Johns 162* (JRAU); Fruit wall—*Johns 162* (JRAU). ***W. leipoldtiana***: Stem—*Boatwright et al. 123* (JRAU); Petiole—*Boatwright et al. 123* (JRAU); Leaf—*Boatwright et al. 123* (JRAU); Fruit wall—*Boatwright et al. 123* (JRAU). ***W. mucronata***: Petiole—*Vlok 1726* (JRAU); Leaf—*Vlok 1726* (JRAU); Fruit wall—*Esterhuysen 6880* (BOL). ***W. sessilifolia***: Stem—*Van Wyk 2120* (JRAU); Leaf—*Van Wyk 2120* (JRAU); Fruit wall—*Taylor 4329* (PRE). ***W. vlokii***: Petiole—*Vlok 2045* (PRE); Leaf—*Vlok 2045* (PRE); Fruit wall—*Vlok 2045* (PRE).

APPENDIX A3. Voucher information and GenBank accession numbers of the taxa sampled in this study. Voucher specimens are deposited in the following herbaria: Australian National Herbarium (CANB), University of Johannesburg Herbarium (JRAU), Kew Herbarium (K), National Herbarium, Pretoria (PRE), Southern Cape Herbarium (SCHG). The information is listed as follows: *taxon*—GenBank accessions: *rbcL*, ITS; Voucher specimen. Those regions not sampled for a taxon are represented by a dash [[1]Boatwright et al. (2008b); [2]Crisp et al. (2000); [3]Käss and Wink (1997); [4]Doyle et al. (1997); [5]Pardo et al. (2004); [6]Motsi (2004); [7]Van der Bank et al. (2002); [8]Le Roux (2006); *Sequenced by J.S. Boatwright; **Sequenced at University of Heidelberg].

***Amphithalea* Eckl. & Zeyh.:** *A. alba* Granby— AM180171[1], AM261217 [1]; *Van Wyk 2125* (SCHG). *A. micrantha* (E.Mey.) Walp.— AM180182 [1], AM261227 [1]; *Schutte 751* (SCHG). *A. williamsonii* Harv.— AM177372 [1], AM261436 [1]; *Euston-Brown s.n.* (SCHG). ***Argyrolobium* Eckl. & Zeyh.:** *A. harmsianum* Schltr. ex Harms— —, AF287685[2]; *Crisp 9042* (CANB). *A. lunare* (L.) Druce 1— —, AF287686[2]; *Crisp 9039* (CANB). *A. lunare* (L.) Druce subsp. *sericeum* (Thunb.) T.J.Edwards 2— EU348013**, —; *Van Wyk 2080* (JRAU). *A. marginatum* Bolus— EU348014**, —; *Van Wyk 3038* (JRAU). *A. marginatum* Bolus— Z95547[3], —; *Edwards 471*. *A. megarrhizum* Bolus— EU348015**, —; *Germishuizen s.n.* (JRAU). *Argyrolobium* sp.— EU348016**, —; *Van Wyk 2173* (JRAU). ***Aspalathus* L.:** *A. acutiflora* R.Dahlgren— —, EU347735*; *Boatwright & Magee 22* (JRAU). *A. carnosa* Berg. — EU348022*, EU347723*; *Boatwright & Magee 61* (JRAU). *A. confusa* R.Dahlgren— EU348031*, EU347736*; *Boatwright et al. 97* (JRAU). *A. crenata* (L.) R.Dahlgren— EU348028*, EU347729*; *Boatwright & Magee 70*

(JRAU). *A. galeata* E.Mey.— EU348032*, EU347726*; *Boatwright et al. 100* (JRAU). *A. hirta* E.Mey. subsp. *hirta*— EU348025*, EU347732*; *Boatwright & Magee 43* (JRAU). *A. hystrix* L.f.— EU348023*, EU347734*; *Boatwright & Magee 30* (JRAU). *A. laricifolia* Berg. subsp. *laricifolia*— EU348026*, EU347731*; *Boatwright & Magee 46* (JRAU). *A. linearis* (Burm.f.) R.Dahlgren 1— EU348020*, EU347722*; *Van Wyk et al. 4192* (JRAU). *A. linearis* (Burm.f.) R.Dahlgren 2— EU348019**, EU347739**; *Van Wyk s.n.* (JRAU). *A. macrantha* Harv.— EU348029*, EU347728*; *Boatwright & Magee 71* (JRAU). *A. nivea* Thunb.— EU348018**, EU347737**; *Van Wyk 2938* (JRAU). *A. pachyloba* Benth.— EU348024*, EU347733*; *Boatwright & Magee 42* (JRAU). *A. pendula* R.Dahlgren— EU348017**, EU347738**; *Van Wyk s.n.* (JRAU). *A. perfoliata* (Lam.) R.Dahlgren subsp. *phillipsii* R.Dahlgren— EU348030*, EU347727*; *Boatwright & Magee 82* (JRAU). *A. shawii* Bol. subsp. *shawii*— EU348033*, EU347725*; *Boatwright & Magee 27* (JRAU). *A. vermiculata* Lam.— EU348021*, EU34772*; *Boatwright & Magee 15* (JRAU). *A. willdenowiana* Benth.— EU348027*, EU347730*; *Boatwright & Magee 69* (JRAU). ***Bolusia* Benth.:** *B. acuminata* (DC.) Polhill— EU347944**, —; *Morris 1193* (PRE). *B. amboensis* (Schinz) Harms 1— EU347943**, EU347891**; *Robinson 1558* (K). *B. amboensis* (Schinz) Harms 2— EU347943**, —; *Giess 10091* (K). ***Cadia* Forssk.:** *C. purpurea* (Ait.) Forssk.— AM260751 [1], AM261740 [1]; *Beckett 1702* (K). ***Calpurnia* E.Mey.:** *C. sericea* Harv.— AM177374 [1], AM268374 [1] & AM268375 [1]; *Boatwright 86* (JRAU). ***Crotalaria* L.:** *C. capensis* Jacq. 1— EU348034**, EU347884**; *Van Wyk 2933a* (JRAU). *C. capensis* Jacq. 2— EU348045*, EU347888*; *Van der Bank 14* (JRAU). *C. distans* Benth.— EU348038**, EU347882**; *de Castro 137* (JRAU). *C. griquensis* Bolus— EU348043*, EU347887*; *Van Wyk et al. 4173*

(JRAU). *C. humilis* Eckl. & Zeyh. 1— EU348041*, EU347889*; *Boatwright et al. 143* (JRAU). *C. humilis* Eckl. & Zeyh. 2— EU348042*, EU347890*; *Boatwright et al. 156* (JRAU). *C. lanceolata* E.Mey.— EU348040**, EU347885**; *Van Wyk 1985* (JRAU). *C. lebeckioides* Bond— EU348036**, —; *Van Wyk 3315e* (JRAU). *C. lotoides* Benth.— EU348035**, —; *Van Wyk s.n.* (JRAU). *Crotalaria* sp.— EU348039**, EU347883**; *Van Wyk 3367* (JRAU). *C. virgultalis* Burch. ex DC. 1— EU348044*, EU347886*; *Van Wyk et al. 4175* (JRAU). *C. virgultalis* Burch. ex DC. 2— EU348037**, —; *Van Wyk 3060* (JRAU). ***Cyclopia* Vent.:** *C. genistoides* (L.) R.Br.— AM261716 [1], AM050819 [1]; *Boatwright & Magee 53* (JRAU). *C. subternata* Vogel— AM261725 [1], AM050821 [1]; *Boatwright & Magee 35* (JRAU). ***Dichilus* DC.:** *D. gracilis* Eckl. & Zeyh.— EU347962**, EU347893**; *Schutte 247* (JRAU). *D. lebeckioides* DC.— EU347963**, EU347894**; *Schutte 151* (JRAU). *D. pilosus* Conrath ex Shinz— EU347959**, EU347892**; *Schutte 363* (JRAU). *D. reflexus* (N.E.Br.) A.L.Schutte— EU347961**, —; *Schutte 177* (JRAU). *D. strictus* E.Mey.— —, AJ287684[2]; *Crisp 9073* (CANB). *D. strictus* E.Mey.— EU347960**, —; *Schutte 150* (JRAU). ***Genista* L.:** *G. teretifolia* Willk.— —, AY263668[5]; *MAF 162924*. ***Lebeckia* Thunb.:** *L. ambigua* E.Mey. 1— EU347917**, EU347852**; *Van Wyk 2900* (JRAU). *L. ambigua* E.Mey. 2— EU347934[8], EU347851[8]; *Le Roux et al. 6* (JRAU). *L. bowieana* Benth. [*Wiborgiella bowieana* (Benth.) Boatwr. & B.-E.van Wyk] 1— EU347909*, EU347868*; *Streicher s.n.* (JRAU). *L. bowieana* Benth. 2— EU347910**, EU347869**; *Van Wyk 2106* (JRAU). *L. brevicarpa* M.M.le Roux & B.-E.van Wyk— EU347933[8], EU347850[8]; *Le Roux et al. 4* (JRAU). *L. carnosa* (E.Mey.) Druce 1— EU347900**, EU347845**; *Vlok et al. s.n.* (JRAU). *L. carnosa* (E.Mey.) Druce 2— EU347937[8], EU347846[8]; *Le Roux et al. 15* (JRAU). *L. carnosa* (E.Mey.)

Druce 3— —, EU347847[8]; *Le Roux et al. 16* (JRAU). *L. cinerea* E.Mey. [*Calobota cinerea* (E.Mey.) Boatwr. & B.-E.van Wyk]— EU347930*, EU347840*; *Boatwright et al. 150* (JRAU). *L. cytisoides* Thunb. [*Calobota cytisoides* (Berg.) Eckl. & Zeyh.] 1— EU347903**, EU347837**; *Van Wyk 2313* (JRAU). *L. cytisoides* Thunb. 2— EU347925[8], EU347838[8]; *Le Roux et al. 2* (JRAU). *L. gracilis* Eckl. & Zeyh.— —, EU347855[8]; *Le Roux et al. 17* (JRAU). *L. halenbergensis* Merxm. & A.Schreib. [*Calobota halenbergensis* (Merxm. & A.Schreib.) Boatwr. & B.-E.van Wyk] 1— EU347908**, EU347836**; *Van Wyk 3086* (JRAU). *L. halenbergensis* Merxm. & A.Schreib. 2— EU347927*, EU347842*; *Boatwright et al. 146* (JRAU). *L. inflata* H. Bolus [*Wiborgiella inflata* (H. Bolus) Boatwr. & B.-E.van Wyk] 1— EU347901**, EU347863**; *Vlok et al. 2* (JRAU). *L. inflata* H. Bolus 2— EU347940*, EU347864*; *Johns 162* (JRAU). *L. leipoldtiana* Schltr. ex R.Dahlgren [*Wiborgiella leipoldtiana* (Schltr. ex R.Dahlgren) Boatwr. & B.-E.van Wyk] 1— EU347939*, EU347866*; *Boatwright et al. 123* (JRAU). *L. leipoldtiana* Schltr. ex R.Dahlgren 2— EU347914**, EU347865**; *Van Wyk 3278* (JRAU). *L. lotononoides* Schltr. [*Calobota lotononoides* (Schltr.) Boatwr. & B.-E.van Wyk]— EU347928*, EU347843*; *Boatwright et al. 142* (JRAU). *L. macrantha* Harv. [*Calobota cuspidosa* (Burch.) Boatwr. & B.-E.van Wyk] 1— EU347916, EU347828; *Van Wyk s.n.* (JRAU). *L. macrantha* Harv. 2— EU347922*, EU347831*; *Boatwright et al. 92* (JRAU). *L. melilotoides* R.Dahlgren [*Calobota elongata* (Thunb.) Boatwr. & B.-E.van Wyk] 1— EU347919**, —; *Van Wyk 2562b* (JRAU). *L. melilotoides* R.Dahlgren 2— —, EU347841*; *Van Wyk 2229* (JRAU). *L. meyeriana* Eckl. & Zeyh. ex Harv. 1— EU347904**, EU347856**; *Van Wyk 3351* (JRAU). *L. meyeriana* Eckl. & Zeyh. ex Harv. 2— EU347905**, —; *Van Wyk 3009* (JRAU). *L.*

*meyeriana* Eckl. & Zeyh. ex Harv. 3— —, EU347857[8]; *Van Wyk 4043* (JRAU). *L. mucronata* Benth. [*Wiborgiella mucronata* (Benth.) Boatwr. & B.-E.van Wyk]— EU347941*, EU347870*; *Vlok 1726* (JRAU). *L. multiflora* E.Mey. [*Calobota sericea* (Ait.) Boatwr. & B.-E.van Wyk]— EU347926*, EU347833*; *Boatwright et al. 138* (JRAU). *L. pauciflora* Eckl. & Zeyh. 1— EU347902**, EU347861**; *Van Wyk 3024* (JRAU). *L. pauciflora* Eckl. & Zeyh. 2— EU347935[8], EU347862[8]; *Le Roux et al. 7* (JRAU). *L. plukenetiana* E.Mey. 1— EU347932*, EU347849*; *Le Roux et al. 24* (JRAU). *L. plukenetiana* E.Mey. 2— EU347906**, EU347848**; *Van Wyk 4043* (JRAU). *L. psiloloba* (E.Mey.) Walp. [*Calobota psiloloba* (E.Mey.) Boatwr. & B.-E.van Wyk]— EU347923*, EU347830*; *Le Roux et al. 20* (JRAU). *L. pungens* Thunb. [*Calobota pungens* (Thunb.) Boatwr. & B.-E.van Wyk] 1— EU347918**, EU347827**; *Van Wyk s.n.* (JRAU). *L. pungens* Thunb. 2— EU347921*, EU347829*; *Boatwright et al. 106* (JRAU). *L. sepiaria* (L.) Thunb. 1— EU347936[8], EU347853[8]; *Le Roux et al. 10* (JRAU). *L. sepiaria* (L.) Thunb. 2— EU347920**, EU347854**; *Van Wyk 2979* (JRAU). *L. sericea* Thunb. [*Calobota thunbergii* Boatwr. & B.-E.van Wyk] 1— EU347907**, EU347832**; *Van Wyk 3115* (JRAU). *L. sericea* Thunb. 2— EU347924*, EU347834*; *Boatwright et al. 151* (JRAU). *L. sericea* Thunb. 3— EU347915**, EU347835**; *Van Wyk 3119* (JRAU). *L. sessililfolia* (Eckl. & Zeyh.) Benth. [*Wiborgiella sessilifolia* (Eckl. & Zeyh.) Boatwr. & B.-E.van Wyk]— EU347938*, EU347867*; *Boatwright et al. 170* (JRAU). *L. spinescens* Harv. [*Calobota spinescens* (Harv.) Boatwr. & B.-E.van Wyk]— EU347929*, EU347839*; *Boatwright et al. 158* (JRAU). *L. wrightii* (Harv.) Bolus 1— EU347912**, EU347858**; *Vlok et al. s.n.* (JRAU). *L. wrightii* (Harv.) Bolus 2— EU347913**, EU347860**; *Vlok et al. s.n.* (JRAU). *L. wrightii* (Harv.) Bolus 3—

EU347911[8], EU347859[8]; *Van Wyk 3354* (JRAU). ***Liparia* L.**: *L. angustifolia* (Eckl. & Zeyh.) A.L.Schutte— AM177376 [1], AM261478 [1]; *Boatwright & Magee 66* (JRAU). *L. hirsuta* Thunb.— AM259357 [1], AM261486 [1]; *Boatwright & Magee 33* (JRAU). ***Lotononis* (DC.) Eckl. & Zeyh.**: *L. acuticarpa* B.-E.van Wyk— EU348047**, EU347770**; *Van Wyk 2625* (JRAU). *L. adpressa* N.E.Br. subsp. *adpressa*— EU348100**, EU347780**; *Van Wyk 1899* (JRAU). *L. alpina* (Eckl. & Zeyh.) B.-E.van Wyk— —, AM262446 [6]; *Van Wyk & Van Wyk 1478* (JRAU). *L. benthamiana* Dümmer— EU348051**, EU347771**; *Van Wyk 2528* (JRAU). *L. bolusii* Dümmer— EU348046**, EU347761**; *Van Wyk 2443* (JRAU). *L. brachyantha* Harms— EU347998**, EU347816**; *Boatwright et al. 117* (JRAU). *L. brevicaulis* B.-E.van Wyk— EU348080**, —; *Schutte 447* (JRAU). *L. calycina* (E.Mey.) Benth.— EU348052**, EU347762**; *Van Wyk 1433* (JRAU). *L. carnosa* (Eckl. & Zeyh.) Benth.— EU348083**, EU347800**; *Van Wyk 1663* (JRAU). *L. curtii* Harms— EU348006**, EU347815**; *Van Wyk et al. 4172* (JRAU). *L. crumanina* Burch. ex Benth.— EU348062**, —; *Van Wyk 3057* (JRAU). *L. decumbens* (Thunb.) B.-E.van Wyk subsp. *decumbens*— EU348058**, EU347778**; *Van Wyk 1701* (JRAU). *L. densa* (Thunb.) Harv. subsp. *leucoclada* (Schltr.) B.-E.van Wyk— EU348048**, EU347792**; *Van Wyk 2430* (JRAU). *L. digitata* Harv. 1— EU348071**, EU347772**; *Van Wyk 2350* (JRAU). *L. digitata* Harv. 2— EU348057**, EU347773**; *Van Wyk 2342* (JRAU). *L. divaricata* (Eckl. & Zeyh.) Benth.— EU348092**, EU347788**; *Van Wyk 2484* (JRAU). *L. elongata* (Thunb.) D.Dietr.— EU348087**, EU347821**; *Van Wyk 2573* (JRAU). *L. eriantha* Benth.— EU348086**, EU347784**; *Schutte 383* (JRAU). *L. eriocarpa* (E.Mey.) B.-E.van Wyk— EU348084**, —; *Van Wyk 1952* (JRAU). *L. exstipulata* Bolus— EU348055**, EU347796**; *Van Wyk*

*2271* (JRAU). *L. falcata* (E.Mey.) Benth. 1— EU348103*, EU347756*; *Boatwright et al. 184* (JRAU). *L. falcata* (E.Mey.) Benth. 2— EU347999**, EU347817**; *Boatwright et al. 120* (JRAU). *L. filiformis* B.-E.van Wyk— EU348074**, EU347794**; *Vlok 2030* (JRAU). *L. foliosa* Bolus 1— EU348073**, EU347776**; *Van Wyk 2481* (JRAU). *L. foliosa* Bolus 2— EU347993**, EU347819**; *Boatwright & Magee 88* (JRAU). *L. fruticoides* B.-E.van Wyk— EU348085**, EU347801**; *Van Wyk 2021* (JRAU). *L. galpinii* Dümmer— Z95538[3], —; *T. Edwards 480. L. glabra* (Thunb.) D.Dietr.— EU348005**, EU347814**; *Van Wyk 2014* (JRAU). *L. globulosa* B.-E.van Wyk— EU348075**, EU347777**; *Van Wyk 2210* (JRAU). *L. hirsuta* (Thunb.) D.Dietr. 1— EU348069**, EU347879**; *Van Wyk 1338* (JRAU). *L. hirsuta* (Thunb.) D.Dietr. 2— EU348070**, EU347880**; *Van Wyk s.n.* (JRAU). *L. hirsuta* (Thunb.) D.Dietr. 3— EU348102**, EU347881**; *Schutte 290* (JRAU). *L. involucrata* (Berg.) Benth.— EU947997**, EU347809**; *Boatwright et al. 116* (JRAU). *L. involucrata* (Berg.) Benth. subsp. *digitata* B.-E.van Wyk — EU348076**, EU347805**; *Van Wyk 2873* (JRAU). *L. involucrata* (Berg.) Benth. subsp. *peduncularis* (E.Mey.) B.-E.van Wyk— EU348007**, EU347806**; *Van Wyk et al. 4195* (JRAU). *L. laxa* Eckl. & Zeyh. 1— EU348059**, EU347795**; *Van Wyk 2608* (JRAU). *L. laxa* Eckl. & Zeyh. 2— EU348060**, —; *Van Wyk 1726* (JRAU). *L. laxa* Eckl. & Zeyh. 3— —, AF287677[2]; *Crisp 9075* (CANB). *L. lenticula* (E.Mey.) Benth.— EU348088**, EU347802**; *Van Wyk 2017* (JRAU). *L. leptoloba* Bolus 1— EU348104*, EU347757*; *Boatwright et al. 185* (JRAU). *L. leptoloba* Bolus 2— EU348077**, EU347804**; *Schutte 276* (JRAU). *L. listii* Polhill— EU348012**, EU347826**; *Van Wyk et al. 4207* (JRAU). *L. lotononoides* (Scott Elliot) B.-E.van Wyk— EU348089**, EU347822**; *Van Wyk 1962* (JRAU). *L. macrocarpa* Eckl. & Zeyh.— FM875934*, FM875935* &

FM875936*; *Helme 2076* (NBG). *L. macrosepala* Conrath— EU348056**, EU347810**; *Van Wyk 2622* (JRAU). *L. maculata* Dümmer— EU348004**, EU347813**; *Van Wyk et al. 4169* (JRAU). *L. magnifica* B.-E.van Wyk— EU348079**, EU347779**; *Van Wyk 2421* (JRAU). *L. marlothii* Engl.— EU348010**, EU347825**; *Van Wyk et al. 4203* (JRAU). *L. maximiliani* Schltr. ex De Wildeman 1— EU348078**, EU347799**; *Schutte 282* (JRAU). *L. maximiliani* Schltr. ex De Wildeman 2— EU348098**, —; *Schutte 271* (JRAU). *L. meyeri* (Presl) B.-E.van Wyk 1— EU348095**, EU347811**; *Van Wyk 1766* (JRAU). *L. meyeri* (Presl) B.-E.van Wyk 2— EU348094**, —; *Van Wyk 1765* (JRAU). *L. micrantha* Eckl. & Zeyh.— EU348049**, EU347798**; *Van Wyk 2481* (JRAU). *L. mollis* (E.Mey.) Benth. 1— EU348068**, EU347763**; *Koekemoer 524* (PRE). *L. mollis* (E.Mey.) Benth. 2— EU348067**, EU347764**; *Van Wyk 3113* (JRAU). *L. oxyptera* (E.Mey.) Benth.— EU347992**, EU347787**; *Boatwright s.n.* (JRAU). *L. parviflora* (Berg.) D.Dietr.— EU348050**, EU347797**; *Van Wyk 2442* (JRAU). *L. pentaphylla* (E.Mey.) Benth.— EU348001**, EU347783**; *Boatwright et al. 148* (JRAU). *L. platycarpa* (Viv.) Pic.-Serm. 1— EU348105*, EU347759*; *Boatwright et al. 192* (JRAU). *L. platycarpa* (Viv.) Pic.-Serm. 2— EU348063**, EU347766**; *Van Wyk 3066* (JRAU). *L. platycarpa* (Viv.) Pic.-Serm. 3— EU348064**, EU347767**; *Koekemoer 942* (JRAU). *L. platycarpa* (Viv.) Pic.-Serm. 4— EU348011**, EU347768**; *Boatwright et al. 159* (JRAU). *L. platycarpa* (Viv.) Pic.-Serm. 5— EU348003**, EU347769**; *Van Wyk et al. 4204* (JRAU). *L. platy*carpa (Viv.) Pic.-Serm. 6— EU348065*, EU347765*; *Friis et al. 9080* (K). *L. plicata* B.-E.van Wyk— EU348072**, EU347775**; *Van Wyk 3382* (JRAU). *L. polycephala* (E.Mey.) Benth. 1— EU348082**, EU347781**; *Van Wyk 2408* (JRAU). *L. polycephala* (E.Mey.) Benth. 2— EU347994**, EU347782**; *Boatwright et al. 94*

(JRAU). *L. prostrata* (L.) Benth. 1— EU348054**, —; *Van Wyk 3229* (JRAU). *L. prostrata* (L.) Benth. 2— —, EU347808**; *Boatwright et al. 115* (JRAU). *L. pulchella* (E.Mey.) B.-E.van Wyk 1— EU348090**, EU347785**; *Van Wyk 1659* (JRAU). *L. pulchella* (E.Mey.) B.-E.van Wyk 2— EU348066**, —; *Van Wyk 1659* (JRAU). *L. pungens* Eckl. & Zeyh. 1— EU348096**, EU347790**; *Van Wyk 1725* (JRAU). *L. pungens* Eckl. & Zeyh. 2— EU347996**, EU347807**; *Boatwright et al. 105* (JRAU). *L. quinata* (Thunb.) Benth.— EU347995**, EU347774**; *Boatwright et al. 95* (JRAU). *L. rabenaviana* Dinter & Harms— —, EU347758*; *Boatwright et al. 191* (JRAU). *L. rigida* (E.Mey.) Benth. 1— EU348101**, —; *Van Wyk 2700* (JRAU). *L. rigida* (E.Mey.) Benth. 2— —, EU347791**; *Van Wyk s.n.* (JRAU). *L. rostrata* Benth. subsp. *namaquensis* (Bolus) B.-E.van Wyk — EU348002**, EU347812**; *Boatwright et al. 155* (JRAU). *L. rostrata* Benth.— EU348000**, EU347818**; *Boatwright et al. 147* (JRAU). *L. sabulosa* Salter— EU348081**, EU347820**; *Van Wyk 2325* (JRAU). *L. sericophylla* Benth. 1— EU348093**, EU347789**; *Van Wyk 1956* (JRAU). *L. sericophylla* Benth. 2— EU348053**, EU347803**; *Van Wyk 1917* (JRAU). *L. sericophylla* Benth. 3— EU348097**, —; *Van Wyk 1958* (JRAU). *L. solitudinis* Dümmer— EU348008**, EU347823**; *Van Wyk et al. 4198* (JRAU). *L. sparsiflora* (E.Mey.) B.-E.van Wyk— EU348099**, EU347786**; *Van Wyk 2057* (JRAU). *L. stricta* (Eckl.& Zeyh.) B.-E.van Wyk— EU348091**, EU347793**; *Van Wyk 1718* (JRAU). *L. subulata* B.-E.van Wyk— EU348009**, EU347824**; *Van Wyk et al. 4202* (JRAU). *L. umbellata* (L.) Benth. 1— EU348061**, —; *Van Wyk 3234* (JRAU). *L. umbellata* (L.) Benth. 2— —, EU347760*; *Boatwright s.n.* (JRAU). ***Lupinus* L.**: *L. polyphyllus* Lindley— Z70052[3], —; *Planchuelo 95*. ***Melolobium* Eckl. & Zeyh.**: *M. adenodes* Eckl. & Zeyh. 1— —, AM050832[6]; *Van*

*Wyk 4036* (JRAU). *M. adenodes* Eckl. & Zeyh. 2— EU347976**, —; *Van Wyk 2159* (JRAU). *M. adenodes* Eckl. & Zeyh. 3— EU347986**, —; *Van Wyk 4036* (JRAU). *M. aethiopicum* (L.) Druce 1— EU347977**, —; *Strydom 5* (PRE). *M. aethiopicum* (L.) Druce 2— EU347987**, —; *Van Wyk 4040* (JRAU). *M. alpinum* Eckl. & Zeyh.— EU347978**, —; *Schutte 158* (JRAU). *M. candicans* (E.Mey.) Eckl. & Zeyh. 1— —, AM050833[6], *Van Wyk 4016* (JRAU). *M. candicans* (E.Mey.) Eckl. & Zeyh. 2— EU347980**, —; *Van Wyk 3072* (JRAU). *M. candicans* (E.Mey.) Eckl. & Zeyh. 3— EU347991*, —; *Boatwright et al. 187* (JRAU). *M. canescens* (E.Mey.) Benth.— EU347981**, —; *Schutte 303* (JRAU). *M. exudans* Harv.— EU347990**, —; *Van Wyk 2234* (JRAU). *M. humile* Eckl. & Zeyh.— EU347982**, —; *Van Wyk 2543* (JRAU). *M. macrocalyx* Dümmer— EU347989**, —; *Van Wyk 3061b*. *M. microphyllum* (L.f.) Eckl. & Zeyh. 1— EU347983**, —; *Van Wyk 4006* (JRAU). *M. microphyllum* (L.f.) Eckl. & Zeyh. 2— EU347979**, —; *Moteetee & Van Wyk 3* (JRAU). *M. microphyllum* (L.f.) Eckl. & Zeyh. 3— Z95539[3], —; *Edwards 470*. *M. obcordatum* Harv.— Z95540[3], —; *Edwards 470*. *M. stipulatum* (Thunb.) Harv.— EU347988**, —; *Van Wyk 4037* (JRAU). *M. subspicatum* Conrath— EU347984**, —; *Van Wyk 1779* (JRAU). *M. wilmsii* Harms— EU347985**, —; *Van Wyk 2724* (JRAU). ***Pearsonia* Dümmer:** *P. aristata* (Shinz) Dümmer— EU347945**, EU347873**; *De Castro 346* (JRAU). *P. cajanifolia* (Harv.) Polhill 1— EU347948**, EU347875**; *Posthumus 7* (JRAU). *P. cajanifolia* (Harv.) Polhill 2— EU347950*, EU347876*; *Boatwright & Magee 90* (JRAU). *P. grandifolia* (Bolus) Polhill— EU347946**, EU347874**; *Van Wyk 3047* (JRAU). *P. sessilifolia* (Harv.) Dümmer 1— EU347947**, EU347871**; *Schutte 463* (JRAU). *P. sessilifolia* (Harv.) Dümmer 2— —, EU347872**; *Schutte 589b* (JRAU). *P. sessilifolia* (Harv.)

Dümmer 3— —, AJ287675[2]; *Crisp 9078* (CANB). *P. uniflora* (Kensil) Polhill— EU347949**, —; *Van Wyk 3033* (JRAU). ***Podalyria* Willd.:** *P. buxifolia* (Retz.) Lam.— AM261693 [1], AM261496 [1]; *Boatwright & Magee 34* (JRAU). *P. oleaefolia* Salisb.— AM261708 [1], AM261667 [1]; *Boatwright & Magee 79* (JRAU). ***Polhillia* C.H.Stirton:** *P. brevicalyx* (C.H.Stirton) B.-E.van Wyk & A.L.Schutte— EU347954**, —; *Van Wyk 2100* (JRAU). *P. canescens* C.H.Stirton— EU347957**, —; *Van Wyk 2092* (JRAU). *P. involucratum* (Thunb.) B.-E.van Wyk & A.L.Schutte— EU347956**, —; *Schutte 339* (JRAU). *P. obsoleta* (Thunb.) B.-E.van Wyk— EU347955**, —; *Van Wyk 2701* (JRAU). *P. pallens* C.H.Stirton— EU347958**, —; *Van Wyk 2095* (JRAU). ***Rafnia* Thunb.:** *R. acuminata* (E.Mey.) G.J.Campbell & B.-E.van Wyk— AM931036**, AM931034** & AM931035**; *Schutte 437* (JRAU). *R. angulata* Thunb.— EU347896*, —; *Boatwright et al. 103* (JRAU). *R. capensis* (L.) Schinz— —, EU347742*; *Boatwright & Magee 26* (JRAU). *R. diffusa* Thunb.— EU347895*, AJ744944 [6]; *Campbell & Van Wyk 44* (JRAU). *R. globosa* G.J.Campbell & B.-E.van Wyk — EU347899*, EU347743*; *Boatwright et al. 180* (JRAU). *R. racemosa* Eckl. & Zeyh.— EU347895*, EU347741*; *Boatwright & Magee 29* (JRAU). *R. spicata* Thunb.— EU347897*, EU347740*; *Boatwright et al. 102* (JRAU). ***Robynsiophyton* R. Wilczek:** *R. vanderystii* R. Wilczek— EU347952*, EU347878*; *Lisowski 20326* (K). ***Rothia* Pers.:** *R. hirsuta* (Guill. & Perr.) Baker— EU347953*, EU347877*; *Saadou 1798* (K). ***Spartidium* Pomel:** *S. saharae* (Coss. & Dur.) Pomel [*Calobota saharae* (Coss. & Dur.) Boatwr. & B.-E.van Wyk]— EU347931*, EU347844*; *Davis 49544* (K). ***Stirtonanthus* B.-E.van Wyk & A.L.Schutte:** *S. chrysanthus* (Adamson) B.-E.van Wyk & A.L.Schutte— AM259367 [1], AM268386 [1] & AM268387 [1]; *Van Wyk & Schutte 3297* (JRAU). ***Ulex* L.:** *U. europaeus* L.— Z70111 [3],

—; *Botanical Garden Heidelberg, Germany*. ***Virgilia*** **Poir.**: *V. divaricata* Adamson— AM260737 [1], AJ409910 [7]; *Van Wyk 879–888* (JRAU). ***Wiborgia*** **Thunb.**: *W. fusca* Thunb. 1— EU347966**, EU347744**; *Schutte 736* (JRAU). *W. fusca* Thunb. 2— EU347967*, EU347754*; *Van Wyk et al. 4186* (JRAU). *W. humilis* (Thunb.) R.Dahlgren [*Wiborgiella humilis* (Thunb.) Boatwr. & B.-E.van Wyk] 1— EU347969*, EU347752*; *Boatwright et al. 129* (JRAU). *W. humilis* (Thunb.) R.Dahlgren 2— EU347970*, EU347753*; *Van Wyk 3530* (JRAU). *W. incurvata* Thunb.— EU347975*, EU347751*; *Boatwright et al. 188* (JRAU). *W. monoptera* E.Mey. 1— EU347971*, EU347749*; *Boatwright et al. 152* (JRAU). *W. monoptera* E.Mey. 2— EU347974*, EU347750*; *Boatwright et al. 153* (JRAU). *W. obcordata* (Berg.) Thunb. 1— EU347965**, EU347746**; *Van Wyk 2686* (JRAU). *W. obcordata* (Berg.) Thunb. 2— EU347972*, EU347748*; *Boatwright et al. 98* (JRAU). *W. sericea* Thunb.— EU347968*, EU347755*; *Boatwright et al. 124* (JRAU). *W. tetraptera* E.Mey. 1— EU347964**, EU347745**; *Schutte 737* (JRAU). *W. tetraptera* E.Mey. 2— EU347973*, EU347747*; *Boatwright et al. 104* (JRAU). ***Xiphotheca*** **Eckl. & Zeyh.**: *X. guthriei* (Bolus) A.L.Schutte & B.-E.van Wyk— AM260744 [1], AM261741 [1]; *Vlok & Schutte 4* (SCHG). *X. reflexa* (Thunb.) A.L.Schutte & B.-E.van Wyk— AM260747 [1], AM261744 [1]; *Schutte 760* (JRAU).

APPENDIX A4. List of morphological characters and character states used in the morphological analysis of the Crotalarieae in Chapter 3.

1. **Habit:** herbs or suffrutices = 0; shrubs = 1. **2. Persistence:** perennial = 0; annual = 1. **3. Young twigs:** without bark formation (bark formation late or absent) = 0; with bark formation (bark formation early) = 1. **4. Leaves:** digitate = 0; unifoliolate = 1; simple or phyllodinous = 2. **5. Lamina:** flat = 0; terete (acicular) = 1. **6. Petiole presence:** present = 0; absent (leaves sessile) = 1. **7. Petiole base:** normal or leaves sessile = 0; tuberculate or with persistent spur = 1. **8. Stipules presence:** present = 0; vestigial or absent = 1. **9. Stipules symmetry:** symmetrical or absent = 0; asymmetrical (dissimilar in size or single) = 1. **10. Bracteole presence:** present = 0; vestigial or absent = 1. **11. Standard petal vestiture:** hairy at least along the dorsal midrib = 0; totally glabrous = 1. **12. Keel shape:** not rostrate = 0; markedly rostrate or helically coiled = 1. **13. Calyx lower lobes:** with trifid lower lip = 0; without trifid lower lip = 1. **14. Calyx lateral lobes:** not fused higher up = 0; fused higher up = 1. **15. Anthers:** dimorphic = 0; uniform = 1. **16. Carinal anther:** resembling basifixed anthers = 0; intermediate = 1; resembling dorsifixed anthers = 2. **17. Gynoecium base:** sessile or subsessile = 0; stipitate = 1. **18. Style:** upcurved = 0; straight = 1; helically coiled = 2. **19. Style vestiture:** glabrous = 0; hairy = 1. **20. Fruit type:** not a samara = 0; fruit an ovoid, winged samara = 1. **21 Fruit upper suture:** upper suture straight or symmetrically convex = 0; upper suture asymmetrically convex = 1. **22. Fruit:** many-seeded = 0; few-seeded (1–2) = 1. **23. Funicle length:** normal length = 0; exceptionally long = 1. **24. Seed shape:** transversely oblong = 0; oblong = 1. **25. Seed surface:** smooth = 0; rugose = 1. **26.**

**Chromosome base number:** 7 = 0; 8 = 1; 9 = 2. **27. Cyanogenesis:** absent = 0; present = 1. **28. Quinolizidine and piperidyl alkaloids (Lysine pathway):** present = 0; absent = 1. **29. Sparteine:** present = 0; absent = 1. **30. Lupanine type esters:** ±absent = 0; present as major alkaloid = 1. **31. Macrocyclic pyrrolizidine alkaloids:** absent = 0; present = 1.

APPENDIX A5. Character states for 6 morphological and chemical characters scored for the taxa included in the combined molecular and morphological analysis presented in Chapter 8. Characters and character states are explained at the end of the table.

| | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| *Aspalathus carnosa* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus confusa* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus crenata* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus galeata* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus hirta* subsp. *hirta* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus hystrix* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus laricifolia* subsp. *laricifolia* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus linearis* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus macrantha* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus nivea* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus pachyloba* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus pendula* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus perfoliata* subsp. *phillipsii* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus shawii* subsp. *shawii* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus vermiculata* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Aspalathus willdenowiana* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Bolusia amboensis* | 0 | 0 | 0 | 3 | 0 | 1 |
| *Crotalaria capensis* | 1 | 0 | 0 | 3 | 0 | 1 |
| *Crotalaria distans* | 0 | 1 | 0 | 3 | 0 | 1 |
| *Crotalaria griquensis* | 1 | 0 | 0 | 3 | 0 | 1 |
| *Crotalaria humilis* | 0 | 1 | 0 | 3 | 0 | 1 |
| *Crotalaria lanceolata* | 0 | 1 | 1 | 3 | 0 | 1 |
| *Crotalaria virgultalis* | 1 | 0 | 1 | 3 | 0 | 1 |
| *Calobota cinerea* | 1 | 0 | 1 | 1 | 0 | 0 |
| *Calobota cuspidosa* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Calobota cytisoides* | 1 | 0 | 1 | 1 | 0 | 0 |
| *Calobota halenbergensis* | 1 | 0 | 1 | 1 | 0 | 0 |
| *Calobota lotononoides* | 1 | 0 | 1 | 1 | 0 | 0 |
| *Calobota pungens* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Calobota psiloloba* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Calobota saharae* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Calobota sericea* | 1 | 0 | 1 | 1 | 0 | 0 |
| *Calobota spinescens* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Calobota thunbergii* | 1 | 0 | 1 | 1 | 0 | 0 |
| *Lebeckia ambigua* | 0 | 0 | 1 | 1 | 0 | 0 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Lebeckia brevicarpa* | 0 | 0 | 1 | 2 | 0 | 0 |
| *Lebeckia carnosa* | 0 | 0 | 1 | 0 | 0 | 0 |
| *Lebeckia meyeriana* | 0 | 0 | 1 | 0 | 0 | 0 |
| *Lebeckia pauciflora* | 0 | 0 | 1 | 1 | 0 | 0 |
| *Lebeckia plukenetiana* | 0 | 0 | 1 | 0 | 0 | 0 |
| *Lebeckia sepiaria* | 0 | 0 | 1 | 2 | 0 | 0 |
| *Lebeckia wrightii* | 0 | 1 | 0 | 0 | 0 | 0 |
| *Lotononis adpressa* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis acuticarpa* | 0 | 1 | 0 | 1 | 0 | 0 |
| *Lotononis benthamiana* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis bolusii* | 0 | 1 | 0 | 1 | 1 | 0 |
| *Lotononis brachyantha* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis calycina* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis carnosa* | 1 | 0 | 0 | 1 | 0 | 1 |
| *Lotononis curtii* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis decumbens* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis densa* subsp. *leucoclada* | 1 | 0 | 1 | 3 | 0 | 1 |
| *Lotononis digitata* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis divaricata* | 1 | 0 | 0 | 1 | 0 | 1 |
| *Lotononis elongata* | 0 | 0 | 0 | 1 | 0 | 1 |
| *Lotononis eriantha* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis exstipulata* | 0 | 0 | 1 | 3 | 0 | 1 |
| *Lotononis falcata* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis filiformis* | 0 | 0 | 0 | 1 | 0 | 1 |
| *Lotononis foliosa* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis fruticoides* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis glabra* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis globulosa* | 0 | 1 | 0 | 1 | 1 | 0 |
| *Lotononis hirsuta* | 0 | 0 | 0/1 | 3 | 0 | 1 |
| *Lotononis involucrata* | 0 | 0 | 0 | 3 | 0 | 1 |
| *Lotononis involucrata* subsp. *peduncularis* | 0 | 0 | 0 | 3 | 0 | 1 |
| *Lotononis laxa* | 0 | 0 | 0 | 1 | 0 | 1 |
| *Lotononis lenticula* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis leptoloba* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis listii* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis lotononoides* | 1 | 0 | 0 | 1 | 0 | 1 |
| *Lotononis macrocarpa* | 0 | 0 | 0 | 1 | 0 | ? |
| *Lotononis macrosepala* | 0 | 0 | 0 | 1 | 0 | 1 |
| *Lotononis maculata* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis magnifica* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis marlothii* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis maximiliani* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis meyeri* | 1 | 0 | 0 | 1 | 0 | 1 |
| *Lotononis micrantha* | 0 | 1 | 0 | 1 | 0 | 1 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Lotononis mollis* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis oxyptera* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis parviflora* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis platycarpa* | 0 | 1 | 0 | 1 | 0 | 0 |
| *Lotononis plicata* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis pentaphylla* | 0 | 1 | 0 | 1 | 1 | 0 |
| *Lotononis polycephala* | 0 | 0 | 0 | 1 | 1 | 0 |
| *Lotononis pulchella* | 1 | 0 | 0 | 1 | 0 | 1 |
| *Lotononis pungens* | 0 | 0 | 0 | 3 | 0 | 1 |
| *Lotononis quinata* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis rostrata* subsp. *namaquensis* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis sabulosa* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis sericophylla* | 1 | 0 | 0 | 1 | 0 | 1 |
| *Lotononis solitudinis* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Lotononis sparsiflora* | 0 | 1 | 0 | 1 | 0 | 1 |
| *Lotononis stricta* | 1 | 0 | 0 | 1 | 0 | 1 |
| *Lotononis subulata* | 0 | 0 | 0 | 1 | 0 | 0 |
| *Pearsonia aristata* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Pearsonia cajanifolia* | 1 | 0 | 0 | 0 | 0 | 0 |
| *Pearsonia grandifolia* | 1 | 0 | 0 | 0 | 0 | 0 |
| *Pearsonia sessilifolia* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Rafnia acuminata* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Rafnia diffusa* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Rafnia globosa* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Rafnia racemosa* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Rafnia spicata* | 1 | 0 | 1 | 0 | 0 | 0 |
| *Robynsiophyton vanderystii* | 0 | 1 | 0 | 0 | 0 | 0 |
| *Rothia hirsuta* | 0 | 1 | 0 | 0 | 0 | 0 |
| *Wiborgia fusca* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Wiborgia incurvata* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Wiborgia monoptera* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Wiborgia obcordata* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Wiborgia sericea* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Wiborgia tetraptera* | 1 | 0 | 1 | 0 | 1 | 0 |
| *Wiborgiella bowieana* | 1 | 0 | 1 | 3 | 0 | 0 |
| *Wiborgiella inflata* | 0 | 1 | 1 | 3 | 0 | ? |
| *Wiborgiella humilis* | 1 | 0 | 1 | 3 | 1 | 0 |
| *Wiborgiella leipoldtiana* | 1 | 0 | 1 | 3 | 0 | 0 |
| *Wiborgiella mucronata* | 1 | 0 | 1 | 0 | 0 | ? |
| *Wiborgiella sessililfolia* | 1 | 0 | 1 | 3 | 0 | 0 |
| *Dichilus gracilis* | 0 | 0 | 0 | 0 | 0 | 0 |

**(1) Habit:** herbs or suffrutices = 0, shrubs = 1. **(2) Persistence:** perennial = 0, short-lived or annual = 1. **(3) Stipules:** present = 0, absent = 1. **(4) Fruit:** laterally compressed = 0, semi-terete = 1, terete = 2, inflated = 3. **(5) Fruit:** many-seeded = 0, few-seeded = 1. **(6) Quinolizidine alkaloids:** present =0, absent = 1.

Appendix B. Publications to date resulting from this PhD study:

Appendix B1. Boatwright, J. S. and B.-E. van Wyk. 2007. A new species of *Rafnia* (Crotalarieae, Fabaceae). *South African Journal of Botany* 73 (3): 471–473.

Appendix B2. Boatwright, J. S. and B.-E. van Wyk. 2007. The identity of *Lebeckia lotononoides* (Crotalarieae, Fabaceae). *South African Journal of Botany* 73 (4): 664–666.

Appendix B3. Boatwright, J. S., M. M. le Roux, M. Wink, T. Morozova and B.-E. van Wyk. 2008. Phylogenetic relationships of the tribe Crotalarieae (Fabaceae) inferred from DNA sequences and morphology. *Systematic Botany* 33 (4): 752–761.

Appendix B4. Boatwright, J. S., P. M. Tilney and B.-E. van Wyk. 2008. A taxonomic revision of the genus *Rothia* (Crotalarieae, Fabaceae). *Australian Systematic Botany* 21 (6): 422–430.

Appendix B5. Boatwright, J. S. and B.-E. van Wyk. 2009. A revision of the African genus *Robynsiophyton* (Crotalarieae, Fabaceae). *South African Journal of Botany* 75 (2): 367–370.

Appendix B6. Boatwright, J. S., P. M. Tilney and B.-E. van Wyk. The generic concept of *Lebeckia*, reinstatement of the genus *Calobota* and a new genus of the tribe Crotalarieae (Fabaceae). *South African Journal of Botany*, submitted for publication.

# Appendix B1. Boatwright, J. S. and B.-E. van Wyk. 2007. A new species of *Rafnia* (Crotalarieae, Fabaceae). *South African Journal of Botany* 73 (3): 471–473.

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www.elsevier.com/locate/sajb

Short communication

# A new species of *Rafnia* (Crotalarieae, Fabaceae)

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**Abstract**

The new species *Rafnia lebeckioides* J.S. Boatwright and B.-E. Van Wyk is described. It is known only from a few collections in the mountains around Worcester in the Western Cape Province of South Africa. The species differs from all others in the genus in its linear fruits, which are similar to those found in species of *Lebeckia* Thunb.

*Keywords:* Crotalarieae; Fabaceae; *Rafnia*; new species

## 1. Introduction

The genus *Rafnia* Thunb. comprises 19 species endemic to the fynbos regions of the Western and Eastern Cape Provinces (Campbell and Van Wyk, 2001). *Rafnia* differs from all other Cape legumes of the tribe Crotalarieae in the simple, sessile leaves combined with an almost complete absence of hairs, except at the tips of the calyx lobes and sometimes on the bracts and bracteoles (Van Wyk and Schutte, 1995; Campbell and Van Wyk, 2001). All the species are resprouting shrubs that regenerate from an underground lignotuber after fire.

An unusual and rare new species that is superficially similar to species of *Lebeckia* is described here as *Rafnia lebeckioides*. The linear leaves of this taxon resemble the acicular leaves found in *L.* sect. *Lebeckia* but differ in being flat and not terete. The fruits are especially unusual for *Rafnia* in being linear and flat, almost exactly like the fruits of some *Lebeckia* species, including *L. mucronata* Benth. and *L. gracilis* Eckl. and Zeyh. However, the sessile, simple, flat and glabrous leaves are typical for *Rafnia* and are not found in any species of *Lebeckia*. *R. lebeckioides* is superficially similar to those species of *Lebeckia* with a 5+5 or 6+4 arrangement of the anthers, but differs in its 5+4+1 anther configuration, which is found in all other species of *Rafnia*.

It is unfortunate that the only known collections of this seemingly rare species were filed among the unidentified specimens of *Lebeckia* in both the Bolus herbarium and the herbarium of the Royal Botanic Gardens, Kew, and were thus overlooked in the recent revision of the genus *Rafnia* (Campbell and Van Wyk, 2001). During ongoing studies in the genus *Lebeckia* it became clear that the material was misplaced in *Lebeckia* and that it represented an undescribed species of *Rafnia*.

## 2. Species treatment

**Rafnia lebeckioides** J.S. Boatwright and B.-E. Van Wyk, *sp. nov.*, a speciebus omnibus aliis leguminis linearibus multiseminibus, et seminibus valde angularibus differt. Nonnihil R. spicatae Thunb., R. angulatae Thunb. et R. capensi (L.) Schinz similis habitu parvo et foliis parvis, sed inflorescentiis racemosis non pseudo racemosis ex inflorescentiis 1–6-floris factis differt.

TYPE — South Africa, Western Cape Province, slopes of Fonteintjiesberg, south aspect [3319 CB], *Esterhuysen 30582* (BOL!, holo.; K!, iso.).

Small, glabrous, multi-stemmed perennial up to ?0.3 m. *Branches* densely leafy. *Leaves* simple, markedly secund, linear to subspathulate, (15–) 17–23 (–27) × 1.5–3.0 mm, sessile, acute, base narrowly cuneate, glabrous. *Stipules* absent. *Inflorescence* terminal, racemose, on slender peduncle 40–70 mm long; racemes 20–40 mm long, with 9–13 flowers; pedicels 1.0–1.5 mm long; *bract* narrowly lanceolate, leaf-like, 3.0–

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3.5 mm long, glabrous; *bracteoles* 0.9–1.5 mm long, glabrous. *Flowers* 8–9 mm long, yellow, standard with brown streaking and wing petals turning red-brown (according to label information). *Calyx* 3.7–4.0 mm long, glabrous on outer surface, subequally lobed but upper sinus slightly deeper than lateral and lower sinuses, tube 1.4–1.6 mm long, lobes 1.6–2.3 mm long, subulate, with carinal lobe narrower than the others, tips minutely pubescent on inner surface. *Standard* suborbicular, 5.8–6.0 × 5.5–5.8 mm, slightly emarginate, glabrous, claw 1.0–1.2 mm long. *Wings* oblong, shorter than keel, 6.0–6.3 × 2.5–2.8 mm, obtuse, glabrous, with 7–8 rows of sculpturing, claw 1.8–2.2 mm long. *Keel* slightly rostrate, 6.7–6.9 × 2.8–3.1 mm, obtuse, glabrous, pocket absent, claw 2.0–2.2 mm long. *Anthers* dimorphic, four long, basifixed anthers alternating with five ovate, dorsifixed anthers, carinal anther intermediate in size and shape. *Pistil* subsessile, glabrous, ovary linear, 5.0–5.3 × 0.7–0.9 mm with 9–10 ovules; style 3.7–4.5 mm long, curved upwards, glabrous. *Pods* laterally compressed, subsessile, linear, 22–28 × 2.5–4.0 mm, 5–10 seeded, indehiscent. *Seeds* markedly angular, 2.5–2.6 × 2.2–2.3 mm, predominantly black with white spots, surface rugose (Fig. 1). Flowering occurs in summer, mainly in December.

## 3. Diagnostic characters and relationships

*R. lebeckioides* differs from all other species in the linear, many-seeded (five- to 10-seeded) pods and the markedly angular seeds. In all other *Rafnia* species the pods are obliquely lanceolate to oblanceolate or oblong and one- to five-seeded. Furthermore, the seeds are oblong-reniform to oblong-cordiform (Campbell and Van Wyk, 2001).

*R. lebeckioides* has the subequally lobed calyx, sessile and simple leaves, and glabrous vegetative and reproductive parts typical of all other *Rafnia* species. Within the genus, it shares some apomorphies with species of section *Rafnia*, notably the calyx without a trifid upper lip, sculpted wing petals and rostrate keel petals without pockets (Campbell and Van Wyk, 2001). It is one of only two species with a multi-flowered raceme — the other is *R. racemosa* Eckl. and Zeyh. (a large woody shrub). *R. lebeckioides* is small in stature and appears to only reach heights of up to 0.3 m (exact height unknown). As it is unlike

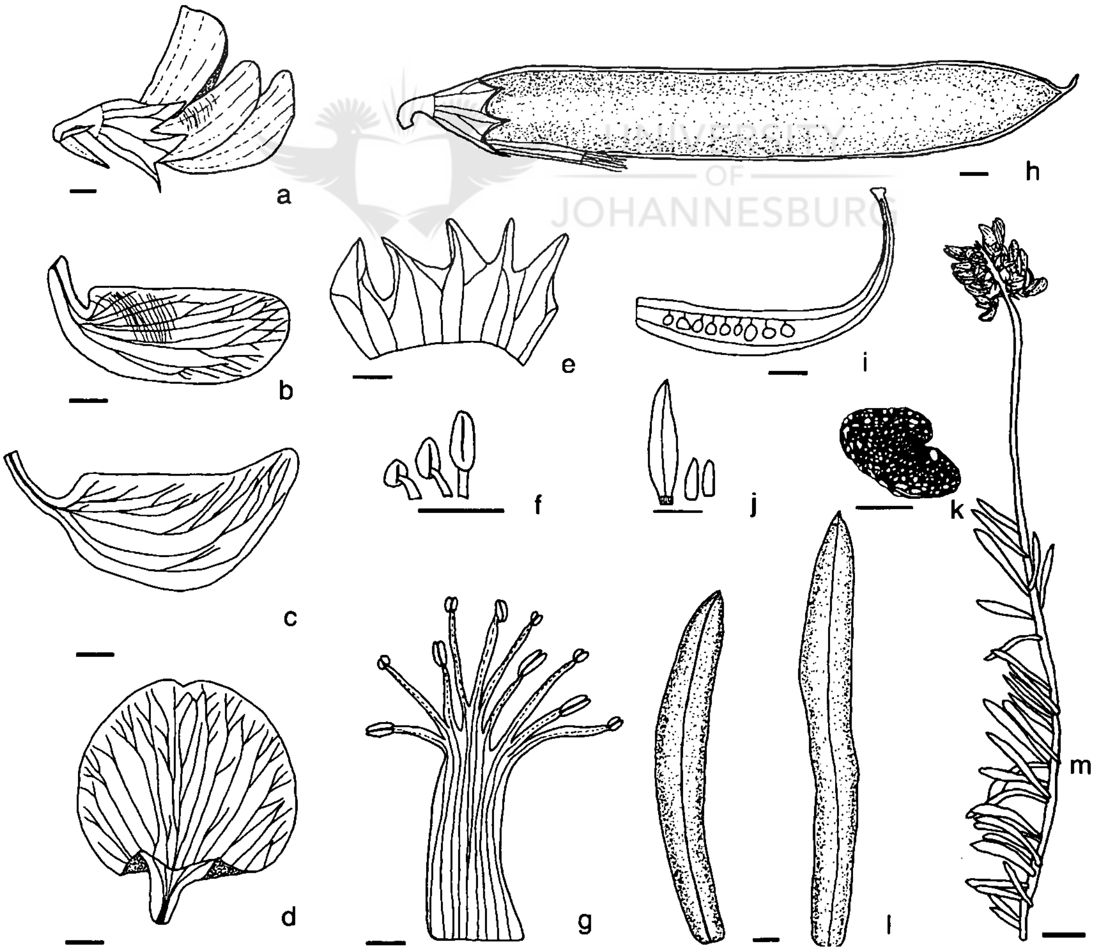

Fig. 1. Morphology of *Rafnia lebeckioides* (drawings by JSB): (a) lateral view of flower; (b) wing petal; (c) keel petal; (d) standard petal; (e) outer surface of the calyx (upper lobes to the left); (f) short, dorsifixed anther, intermediate carinal anther and long, basifixed anther; (g) androecium; (h) lateral view of pod; (i) pistil; (j) bract and bracteoles; (k) lateral view of seed; (l) abaxial surface of leaf; (m) flowering branch, showing the densely leafy branches and racemose inflorescence structure. Voucher specimens: (a, c, d, f, g, i, j bract only, l, m) *Esterhuysen 8297* (BOL); (b, e, j bracteoles only) *Esterhuysen 30582* (BOL); (h, k) *Esterhuysen 28900* (BOL). Scale bars: (a–l) 1 mm; (m) 10 mm.

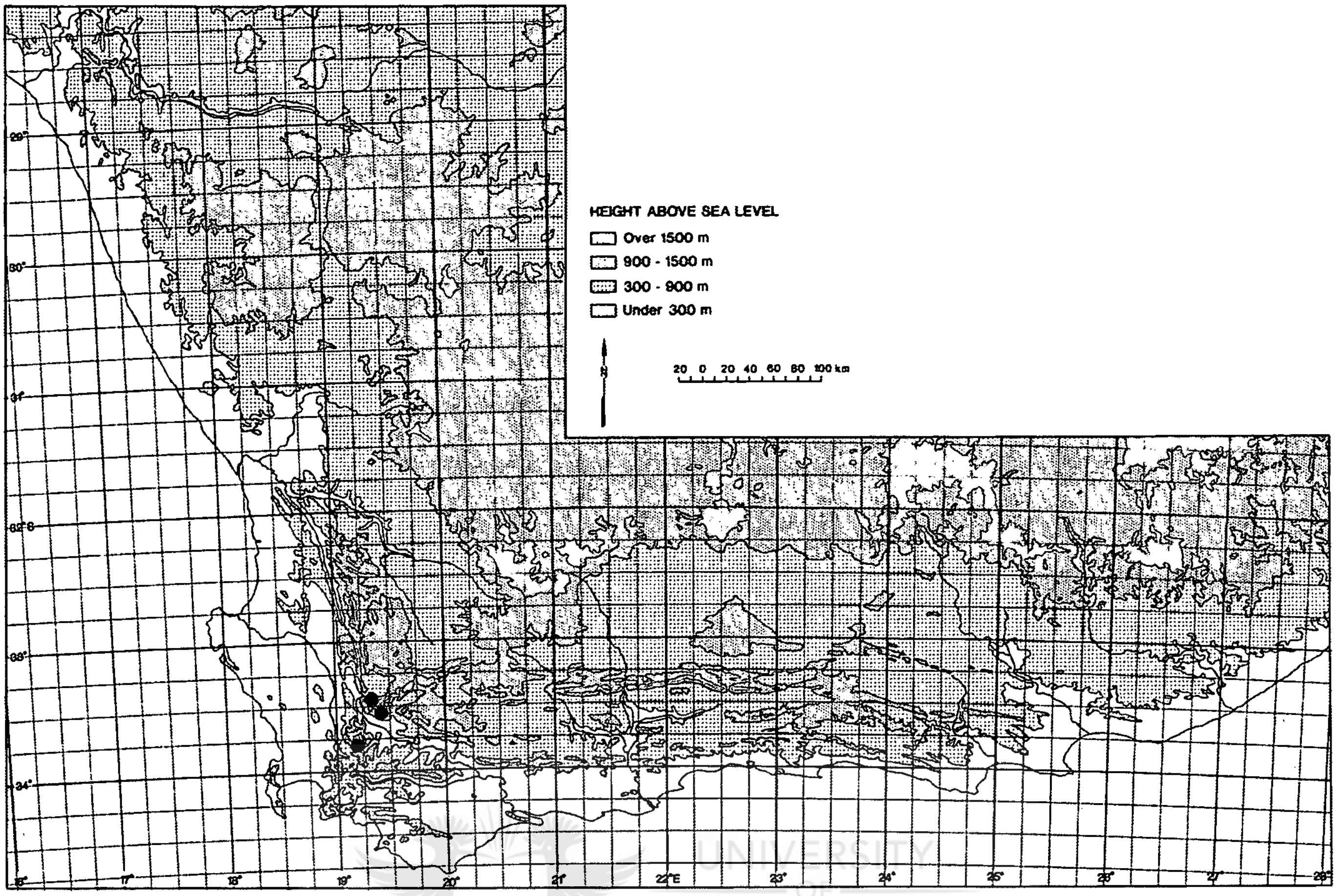

Fig. 2. The known geographical distribution of *Rafnia lebeckioides*.

any of the species of *Rafnia* it is not clear to which members of the genus it is related. Obtaining fresh material for molecular systematic studies is imperative to assess the phylogenetic position of this species.

## 4. Distribution and habitat

*R. lebeckioides* occurs on the Hex River and Du Toit's Mountains around Worcester in the South Western Cape Province at altitudes between 1500 and 1800 m (Fig. 2). It has mainly been collected on southern to south-eastern slopes in recently burnt vegetation, where it has been recorded on stony, slightly marshy soil.

### *Additional specimens examined*

−**3319** (Worcester): Waaihoek Mountain (−AD), *Esterhuysen 8297* (BOL); Waaihoek Peak, south-eastern slopes (−AD), *Esterhuysen 28900* (BOL); Du Toit's Peak, summit ridge (−CC), *Esterhuysen 29038* (BOL).

## Acknowledgements

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Edited by JC Manning

**Appendix B2. Boatwright, J. S. and B.-E. van Wyk. 2007. The identity of *Lebeckia lotononoides* (Crotalarieae, Fabaceae). *South African Journal of Botany* 73 (4): 664–666.**

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Research note

# The identity of *Lebeckia lotononoides* (Crotalarieae, Fabaceae)

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**Abstract**

*Lebeckia lotononoides* Schltr. is a rare species of the Western Cape Province of South Africa. It is anomalous in the genus in its decumbent habit with buried stems and unique wing- to keel lamina ratio. Poorly collected, the species has been confused with *Lebeckia multiflora* E. Mey. Recent collections have increased our understanding of the taxon and provided insight into its sectional placement. The trifoliolate leaves with long petioles, pubescent standard petal, 5+4+1 anther arrangement, and semi-terete, thick-walled pods place *L. lotononoides* in section *Calobota* (Eckl. & Zeyh.) Benth. *L. lotononoides* differs from *L. multiflora* in its decumbent habit, wing- to keel lamina ratio of ±2:1, and rugose, spotted seeds.

*Keywords:* Crotalarieae; Fabaceae; *Lebeckia lotononoides*; *Lebeckia multiflora*

## 1. Introduction

*Lebeckia* Thunb. is a genus of legumes, comprised of ±36 species, that occurs in the southern and western parts of South Africa and Namibia. The last comprehensive revision of the genus was that of Harvey (1862), who followed the sectional classification proposed by Bentham (1844). Since then several new species have been described with some doubt as to their correct systematic placement within the genus. One such species is *Lebeckia lotononoides*, described by Schlechter (1900). Until recently this very rare species was known only from the type material. Recent collections as well as studies of plants in the wild have increased our understanding of the species, which has been confused with other species of *Lebeckia* such as *Lebeckia multiflora*. In this paper we give a complete description of the species, correct the spelling of its name, and provide notes on its distribution, habit and diagnostic characters.

## 2. Taxonomy

*Lebeckia lotononoides* Schltr. in Engl. Bot. Jahrb. 27: 143 (1900), as "*L. lotonoides*"; Germishuizen and Meyer, Plants of Southern Africa: an annotated checklist, Strelitzia 14: 523 (2003), *pro parte*, *non* Goldblatt and Manning (2000). *Type:* South Africa, [Western Cape Province], "In regione namaquensi: In sabulosis montium Karree-Bergen, alt. c. 4500 ped.", *Schlechter 8214* (BM!, BOL!, K!, PRE!, S!, syn.).

[Note: In accordance with Art. 60 and Art. 61 of the Vienna Code (www.ibot.sav.sk), it is here formally proposed that the name *Lebeckia lotonoides* be regarded as a correctable, orthographic error and that *L. lotononoides* be accepted as the correct form of the name. Schlechter clearly intended to name the species after the genus *Lotononis* (DC.) Eckl. & Zeyh., with which it has a superficial similarity, as is evidenced by his handwritten labels on all the type specimens cited above. The inadvertent elision of a few letters has reduced Schlecther's meaningful epithet to a jumble of nonsense syllables. It is easy to see that this tongue-twisting epithet could have been misspelt by a non-specialist copy-editor or typesetter. The Code recommends that "The liberty of correcting a name is to be used with reserve, especially if the change affects the first syllable and, above all, the first letter of the name" (Art. 60.3). In this case the change is deep within the word and has a minimal effect on indexing.]

Small, sericeous, multi-stemmed, decumbent perennial up to 0.5 m in height. *Branches* woody at base, often buried. *Leaves* digitately trifoliolate (rarely 5-digitate with two additional leaflets), secund, sericeous; leaflets elliptic to narrowly

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oblanceolate, conduplicate, subsessile, terminal leaflet 10–17 × 1.5–3.0 mm, lateral leaflets 8–14 × 1.5–3.0 mm, mucronate, base narrowly cuneate; petiole longer than leaflets, 10–23 mm long. *Stipules* absent. *Inflorescence* terminal, racemose, (15–) 24–54 mm long, with (3–) 4–14 flowers; pedicel 1–3 mm long; bract linear, 0.7–1.5 mm long, pubescent, caducous; bracteoles linear, 0.3–0.6 mm long, pubescent, caducous. *Flowers* 12–15 mm long, yellow. *Calyx* 5.0–6.5 mm long, pubescent, subequally lobed but upper sinus slightly deeper than lateral and lower sinuses, tube 3.0–3.5 mm long, lobes 2–3 mm long, subulate, carinal lobe narrower than others, tips minutely pubescent on inner surface. *Standard* 13–16 mm long, claw linear, 4–7 mm long, lamina widely ovate to transversely oblong, 8–9 × 9.0–12.5 mm, emarginate, pilose along dorsal midrib. *Wings* 14–15 mm long, claw 3.0–4.5 mm long, lamina narrowly oblong, subfalcate, longer than keel, 11.5–15.0 × 2–4 mm, obtuse, glabrous, with 7–8 rows of sculpturing. *Keel* 9–11 mm long, claw 3–4 mm long, lamina semi-circular, 5.5–7.0 × 3.0–4.5 mm, obtuse, glabrous, pocket present, 1.5–3.0 mm long. *Anthers* dimorphic, four long, basifixed anthers alternating

Fig. 1. Morphology, habit and distribution of *Lebeckia lotononoides*: (a1–a3) leaves in abaxial view: (a1 and a2) trifoliolate leaves, (a3) 5-digitate leaf; (b1–b3) pods: (b1 and b2) lateral view (note the slightly clavate shape), (b3) dorsal view; (c1–c3) seeds in lateral view; (d1–d3) petals: (d1) standard petal (note the long, linear claw), (d2) wing petal (note the exceptionally long lamina length), (d3) keel petal; (e) flower in lateral view showing the long wing petals; (f) flowers of *L. lotononoides*; (g) decumbent habit of *L. lotononoides*; (h) known geographical distribution. Photographs taken by J.S. Boatwright at Roodeheuwel Farm. Voucher specimen: (a–d) *Boatwright et al. 142* (JRAU). Scale bars: (a, b) 10 mm; (c) 1 mm; (d) 4 mm.

with five ovate, dorsifixed anthers, carinal anther intermediate in size and shape. *Pistil* subsessile to shortly stipitate, pubescent, ovary linear, 6.5–7.5 × 0.7–0.9 mm with 15–19 ovules; style 3.0–3.5 mm long, curved upwards, glabrous. *Pods* narrowly oblong, sometimes somewhat clavate, semi-terete, subsessile to shortly stipitate, 18–37 (–40) × 3–4 mm, 7–12-seeded, dehiscent. *Seeds* suborbicular, 2.0–2.5 × 1.5–2.0 mm, mature seeds brown with beige spots, hilum brown, surface rugose (Fig. 1). *Flowering time:* late winter to late spring.

## 3. Diagnostic characters

*L. lotononoides* superficially resembles broad-leaved forms of *L. multiflora*, notably some northern populations on the West Coast and around Clanwilliam. In these forms the leaflets are broad and sericeous much like those of *L. lotononoides*. However, *L. lotononoides* differs in its smaller, decumbent habit with buried stems and especially in the exceptionally long lamina of the wing petals, which is ± twice as long as those of the glabrous keel petals. The inflorescences are unarmed, and the sericeous pods contain spotted, rugose seeds. *Lebeckia multiflora*, in contrast, is an erect, divaricately branched shrub usually more than 1 m in height with inflorescences that often terminate in a spine; the wing petals are almost as long as or slightly longer than the pilose keel petals; the pods are pubescent; and the seeds are pale pink with a smooth surface.

The trifoliolate leaves with long petioles, pubescent standard petal, 5 + 4 + 1 anther arrangement, and semi-terete, thick-walled pods place *L. lotononoides* in section *Calobota* (Eckl. & Zeyh.) Benth.

The shape and relative size of the petals are most unusual in this species (Fig. 1d). Not only that the lamina of the wing petals is exceptionally long but also that the standard petal is strongly differentiated into a long, linear claw and a transversely oblong lamina. In other species of *Lebeckia* section *Calobota*, the wing petal laminas are never more than 1.3 times as long as the lamina of the keel petals, whereas in *L. lotononoides* these are almost twice the length of the keel lamina.

## 4. Distribution and habitat

*L. lotononoides* occurs on the west coast of South Africa around Hondeklipbaai and Brand se baai. The type collection was made by Schlechter at "Karree-Bergen", close to Nuwerus in the Vanrhynsdorp district according to Leistner and Morris (1976) (Fig. 1h). The species has been recorded on well-drained, sandy soils with the main stems becoming covered with sand. The multi-stemmed, decumbent habit (Fig. 1g) appears to be an adaptation to moving sand dunes, as extensive underground branches enable the plant to emerge above the sand after being covered.

### 4.1. Additional specimens examined

**–3017** (Hondeklipbaai): Farm Roodeheuwel, 9 km west of Nariep (–DC), *Boatwright et al. 142* (JRAU), *Perold 1646* (PRE).

**–3117** (Lepelfontein): Vredendal, south-east of Brandsebaai, on Farm Hartebeestekom (–BD), *Helme 2931* (NBG); Van Rhynsdorp/Vredendal, Brandsebaai (–BD), *Van Rooyen 2235* (PRE).

**–3118** (Vanrhynsdorp): Karree-Bergen (–AB), *Schlechter s.n. sub TRV 1059* (PRE).

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**Appendix B3. Boatwright, J. S., M. M. le Roux, M. Wink, T. Morozova and B.-E. van Wyk. 2008. Phylogenetic relationships of the tribe Crotalarieae (Fabaceae) inferred from DNA sequences and morphology. *Systematic Botany* 33 (4): 752–761.**

*Systematic Botany* (2008), 33(4): pp. 752–761

# Phylogenetic Relationships of Tribe Crotalarieae (Fabaceae) Inferred from DNA Sequences and Morphology

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*Communicating Editor: Gregory M. Plunkett*

*Abstract*—Tribe Crotalarieae is a large and diverse group of papilionoid legumes that largely occur in Africa. A systematic study of generic relationships within the tribe was undertaken using nucleotide sequences from the internal transcribed spacer (ITS) of nuclear ribosomal DNA, the plastid gene *rbcL*, and morphological data. The Crotalarieae are supported strongly as monophyletic and sister to the tribe Genisteae. *Lebeckia*, *Lotononis*, and *Wiborgia* are all paraphyletic in the molecular analyses and morphological data support the division of *Lebeckia* into three more natural genera (one of which includes the monotypic North African *Spartidium*). Four major lineages were identified within the tribe based on sequence data: the "Cape" group, comprising *Aspalathus*, *Lebeckia*, *Rafnia*, *Spartidium*, and *Wiborgia*; the *Lotononis* group, comprising *Lotononis* pro parte, *Pearsonia*, *Robynsiophyton*, and *Rothia*; a group comprising *Lotononis* section *Leptis*, *L.* section *Listia*, and allies; and the *Crotalaria* group, comprising *Bolusia*, *Crotalaria*, and *Lotononis hirsuta* (*Lotononis* section *Euchlora*). Morphological analysis yields a similar topology, except that *Lotononis* is monophyletic if *L. hirsuta* were excluded. When the molecular and morphological data sets are combined, the same major clades are retrieved as in the molecular analysis, with the notable exception that *Lotononis* and *Lebeckia* senso stricto are supported as monophyletic. The results from this study have important implications for the classification of the tribe Crotalarieae and present an important step towards a natural and phylogenetic generic classification for the tribe.

*Keywords*—Crotalarieae, Fabaceae, genistoid legumes, ITS, morphology, phylogeny, *rbcL*.

Crotalarieae (Benth.) Hutch. is a tribe of legumes that currently comprises 11 genera and ca. 1204 species (van Wyk 2005). It represents the largest tribe of papilionoid legumes in Africa and also within the genistoid alliance, comprising about 51% of genistoid legumes (species totals in Lewis et al. 2005 used for calculation), largely due to the fact that the genus *Crotalaria* contains ca. 600 species (Polhill 1982). Some of the species in the tribe are important commercially such as *Aspalathus linearis*, which is used for the production of Rooibos tea (van Wyk et al. 1997), and *Lotononis bainesii* Bak., an important fodder plant (Bryan 1961). Some *Crotalaria* and *Lotononis* species have been reported to have medicinal properties (van Wyk 2005) and a few are used as what is called '*Musa-pelo* in Lesotho traditional medicine to cure or ease a broken heart (Moteetee and van Wyk 2007), while others from the same genera are poisonous (van Wyk et al. 2002).

The Crotalarieae are subendemic to Africa, with only a few species of *Crotalaria*, *Lotononis*, and *Rothia* occurring on other continents. *Aspalathus*, *Rafnia*, and *Wiborgia* are endemic to the Cape Floristic Region, while *Lebeckia* (as currently circumscribed) is distributed throughout the Cape and extends into the south-western and central parts of Namibia. Generic circumscriptions and relationships within the tribe are known to be complicated, with evidence of reticulation and convergence (Dahlgren 1970a; Polhill 1976, 1981; van Wyk 1991a). The most recent evaluations of generic relationships in the tribe are those of Polhill (1976, 1981), van Wyk (1991a), and van Wyk and Schutte (1989, 1995). According to van Wyk (1991a), two main groups can be identified within the tribe, namely the "Cape" group comprising *Aspalathus*, *Lebeckia*, *Rafnia*, and *Wiborgia*, and the *Lotononis* group comprising *Lotononis*, *Pearsonia*, *Robynsiophyton*, and *Rothia*. The placement of *Bolusia*, *Crotalaria*, and *Spartidium* within these two groups is not clear, but a close relationship between the former two genera has been suggested. Recent revisionary studies of *Lebeckia* (the first since Harvey's treatment of 1862) have shown that the genus is unlikely to be monophyletic (Le Roux 2006; Le Roux and van Wyk 2007; Boatwright, in prep.).

Several molecular systematic studies of Fabaceae and specifically the genistoid legumes (sensu Polhill 1976, 1981) have been conducted in recent years (Käss and Wink 1995, 1996, 1997; Crisp et al. 2000; Doyle et al. 2000; Kajita et al. 2001; Wink and Mohamed 2003; Wojciechowski et al. 2004; Boatwright et al. 2008). These studies place Crotalarieae within the "core" genistoid clade together with, among others, the South African tribes Podalyrieae Benth. and Genisteae (Bronn) Dumort., and confirm the exclusion of the *Argyrolobium* group (*Argyrolobium*, *Dichilus*, *Melolobium*, *Polhillia*) and the rest of the Genisteae from Crotalarieae (van Wyk and Schutte 1995). A sister relationship between Crotalarieae and Genisteae, with Podalyrieae successively sister to these, is shown by the molecular studies cited above, but sampling limitations did not allow detailed evaluations at the generic level.

The present study is aimed at exploring generic circumscriptions and relationships within Crotalarieae, using nrDNA ITS sequences, plastid *rbcL* sequences, and morphological data, based on a sample of 135 species representing all of the 11 genera currently recognized, as well as major infrageneric groups within some of the genera. The aim was to assess the monophyly and relationships of the individual genera.

## MATERIALS AND METHODS

***Plant Accessions and Choice of Outgroups***—A total of 175 sequences of ITS (88% of the total ITS matrix) and 207 sequences for *rbcL* (91% of the total *rbcL* matrix) were produced from taxa of the Crotalarieae and combined with previously published sequences from the tribes Genisteae and Podalyrieae as outgroups (van Wyk and Schutte 1995; Crisp et al. 2000; Boatwright et al. 2008). Sequences of both the ITS and *rbcL* regions were available for 161 taxa of the Crotalarieae and these were used for the combined molecular analysis. A morphological matrix was compiled for those species included in the combined molecular analysis, based on 31 characters (including a few chemical and cytological characters) that were scored from examining specimens from BM, BOL, GRA, JRAU, K, NBG (including SAM and STE), P, PRE, S, UPS, and WIND for *Lebeckia*, *Robynsiophyton*, *Rothia*, and *Spartidium* and from literature for the other genera (Polhill 1974, 1976, 1982; Dahlgren 1975, 1988; Schutte and van Wyk 1988; van Wyk 1991b; van Wyk and Schutte 1995; Campbell and van Wyk 2001; van Wyk 2003). These data, along with sequences of the same species, were used to perform a combined molecular/morphological analysis.

*DNA Extraction, Amplification, and Sequencing*—Sequencing of the gene regions was carried out in two independent laboratories, therefore the strategies differed slightly. The gene sequencing methods of Käss and Wink (1997) were followed at University of Heidelberg, whereas sequences generated at the University of Johannesburg were gathered according to the methods described below.

DNA was extracted from silica-dried or herbarium leaf material using the 2× hexadecyltrimethylammonium bromide (CTAB) method of Doyle and Doyle (1987) and purified through QIAquick silica columns (Qiagen Inc., Hilden, Germany). Sources of material used in the study are listed in Appendix 1. The internal transcribed spacers (ITS) of nuclear rDNA were amplified using the primers of White et al. (1990) and Sun et al. (1994), while for *rbcL* those of Fay et al. (1997) were used. Amplification reactions were carried out using polymerase chain reactions (PCR), in 25 µl reactions containing: 22.5 µl ABgene 1.1x PCR Mastermix (ABgene House, Blenheim Road, Epsom, Surrey, KT19 9AP, U.K.) consisting of 1.25 units Thermoprime Plus DNA Polymerase, 75 mM Tris-HCl (pH 8.8), 20 mM $(NH_4)_2SO_4$, 1.5 mM $MgCl_2$, 0.01% (v/v) Tween® 20, 0.2 mM each of deoxyribonucleotide triphosphates (dNTPs); 0.3 µl of both forward and reverse primers (0.1 ng/µl); 0.8 µl 0.004% bovine serum albumin (BSA); 1.2% dimethyl sulfoxide (DMSO; for ITS only); 20–50 ng DNA template; and sterile distilled water to make up a final volume of 25 µl. The DMSO was added to the amplification reactions as this may improve sequencing of ITS due to relaxation of the template secondary structure during amplification (Álvarez and Wendel 2003). The PCR cycles and cycle sequencing reactions followed Boatwright et al. (2008).

*Sequence Alignment and Phylogenetic Analyses*—Complementary strands of the sequenced genes were edited in Sequencher v. 3.1.2 (Gene Codes Corporation), and aligned manually in PAUP* version 4.0b10 (Swofford 2002). Alignments used in this study are available from TreeBASE (study number S2070). Insertions and deletions (indels) of nucleotides were scored as missing data and thus did not contribute to the combined analysis, but an additional search with gaps from the ITS data set coded as binary characters was performed (no gaps were present in the *rbcL* dataset). Gaps were coded in SeqState version 1.32 (Müller 2005) using simple indel coding as described by Simmons and Ochoterena (2000). Maximum parsimony analyses (MP; Fitch 1971) and Bayesian MCMC analysis (BI; Yang and Rannala 1997; Huelsenbeck and Ronquist 2001; Ronquist and Huelsenbeck 2003; MRBAYES version 3.1.2) were performed as described in Boatwright et al. (2008). Internal support for MP was estimated with 1,000 bootstrap replicates (Felsenstein 1985) using tree bisection-reconnection (TBR) and holding 10 trees per replicate. The following scale for bootstrap support percentages (BP) was used: 50–74%, low; 75–84%, moderate; 85–100%, strong. Congruence of the separate datasets was assessed by examining the individual bootstrap consensus trees in order to compile a combined ITS and *rbcL* matrix for the 161 taxa where both sequenced regions were available. The bootstrap trees were considered incongruent only if they displayed 'hard' (i.e. strong bootstrap support) rather than 'soft' (i.e. low bootstrap support) incongruence (Seelanan et al. 1997; Wiens 1998). In addition, incongruence length difference tests (ILD, Farris et al. 1995) were performed using the partition-homogeneity test of PAUP*. The test was implemented with 1,000 replicate analyses, using the heuristic search option with simple addition of taxa, TBR, and the MULTREES option in effect.

The GTR + I + G model [selected by MODELTEST v. 3.06 (Posada and Crandall 1998) using the corrected AKAIKE information criterion (AICc)] was implemented for the BI analysis and a total of three million generations were performed with a sampling frequency of 10. A majority rule consensus tree was produced to determine the posterior probabilities (PP) of all observed bipartitions (only PPs above 0.5 are reported on the tree). The following scale was used to evaluate the PPs: 0.50–0.84, low; 0.85–0.94, moderate; 0.95–1.0, strong.

Despite repeated attempts, we were only able to amplify ITS1 for some samples of *Lotononis marlothii*, *L. pentaphylla*, *L. platycarpa*, and *L. rostrata*. We could also amplify only the first half of *rbcL* for some samples of *Aspalathus laricifolia* subsp. *laricifolia*, *A. shawii* subsp. *shawii*, *Lotononis falcata*, *L. platycarpa*, *Robynsiophyton vanderystii*, *Rothia hirsuta*, *Spartidium saharae*, and *Wiborgia humilis*. Missing data represented 4.3% of the entire combined molecular matrix due to the fact that both ITS and *rbcL* sequences were not available for some of the Genisteae included as outgroups.

*Morphological Analysis*—Much debate currently surrounds the inclusion of morphological characters in phylogenetic analyses (e.g. Scotland et al. 2003). However, Wiens (2004) discusses the importance of morphological characters in phylogenetics, suggesting that their implementation in separate and combined analyses may provide more rigorous phylogenies, while improved resolution has been shown by Wortley and Scotland (2006) when morphology is combined with molecular data. Characters and character states used for the cladistic analysis are given in Appendix 2. The character states were polarised using the method of outgroup comparison. Phylogenetic analyses were performed in PAUP* (Swofford 2002) with the characters treated as unordered and equally weighted (Fitch 1971). A heuristic search with 1,000 random addition sequences, TBR, and the MULTREES option off was performed with a limit of 10 trees held per replicate. Internal support was assessed using 1,000 bootstrap replicates (Felsenstein 1985) as described above. *Dichilus gracilis*, a suffrutex, was selected as the outgroup for the analysis. A second analysis was performed where *Genista tinctoria* L., a shrub, was used as outgroup to test whether polarising the shrubby habit as ancestral had an effect on the topology, but no difference was found in this analysis (tree not shown).

## RESULTS

***rbcL* Data Set**—The *rbcL* matrix consisted of 1,296 aligned positions with 222 variable and 167 parsimony informative characters. Tree searches produced 2,650 equally parsimonious trees of 527 steps, a consistency index (CI) of 0.50, and a retention index (RI) of 0.92. Overall the strict consensus tree (not shown) is poorly resolved with a few supported clades. A clade consisting of *Lebeckia* section *Calobota* (Eckl. & Zeyh.) Benth., *L.* section *Stiza* (E.Mey) Benth., and *Spartidium saharae* is weakly supported (60 BP). *Lotononis* s.s. (*L.* section *Lotononis* and allies) is moderately supported (74 BP), while the rest of the genus is unresolved except for *L.* section *Listia* (E.Mey.) B.-E.van Wyk, which has high support (89 BP). The *Crotalaria* clade is strongly supported (88 BP) and the sister relationship between *Bolusia* and *Crotalaria* is also strongly supported with a BP of 90. Both these genera are well-supported to be monophyletic (*Bolusia* 98 BP; *Crotalaria* 90 BP) and they are successively sister to *Lotononis hirsuta* [*L.* section *Euchlora* (Eckl. & Zeyh.) B.-E.van Wyk]. Tribe Crotalarieae as a whole is strongly supported as monophyletic (94 BP) and sister to the Genisteae (100 BP). Genisteae and Podalyrieae are both supported as monophyletic (89 BP and 78 BP, respectively).

**ITS Data Set**—The analysis of the ITS data set included 560 characters, of which 353 were variable and 256 parsimony informative. Analysis resulted in 5,970 equally parsimonious trees with a tree length (TL) of 1,031 steps, a CI of 0.51, and a RI of 0.85. The analysis in which gaps were coded resulted in identical clade resolution as the analysis without coded gaps, although some clades had stronger or weaker support (not shown). The analysis with coded gaps resulted in 2,540 trees (TL = 1,340; CI = 0.51; RI = 0.84). The strict consensus tree based on ITS data (not shown) is better resolved than that of *rbcL*, with several well-supported clades. *Aspalathus* was weakly supported as monophyletic (64 BP), although this support percentage is higher when the gap characters are included (78 BP). *Lebeckia* and *Wiborgia* are both paraphyletic. *Lebeckia* section *Viborgioides* Benth. including *Wiborgia humilis* is moderately supported (80 BP), while the positions of *L. inflata* and *L. mucronata* are unresolved. The remaining species of *Wiborgia* form a weakly supported clade (61 BP; 79 BP with gap coding). *Rafnia* is weakly supported as monophyletic (75 BP) and *Lebeckia* section *Calobota* along with *L.* section *Stiza* and *Spartidium saharae* also has weak support (59 BP).

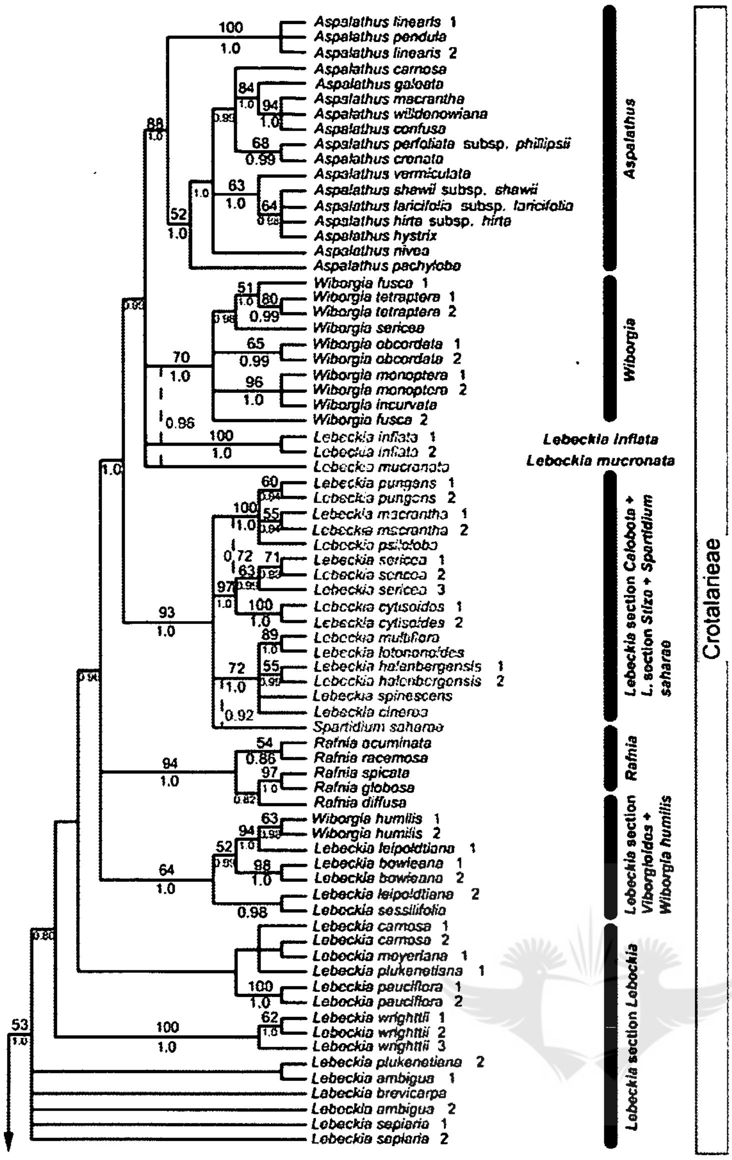

FIG. 1. Strict consensus tree of 560 shortest length trees from the combined analysis of the ITS and *rbcL* data sets (TL = 1,473; CI = 0.50; RI = 0.86). Numbers above the branches are bootstrap percentages above 50% from the maximum parsimony analysis and numbers below the branches are posterior probabilities above 0.5 from the Bayesian analysis. The grey names or lines indicate where the topology differed in the Bayesian analysis.

*Lebeckia* section *Lebeckia* is unresolved. *Lotononis* is left unresolved and *L. hirsuta* is well separated from the rest of the genus. Three main clades can be distinguished. The first consists of *Lotononis* s.s. (also supported in the *rbcL* tree) with moderate support (84 BP). The second clade, comprising taxa from *Lotononis* section *Leptis* (E.Mey. ex Eckl. & Zeyh.) Benth., *L.* section *Listia*, and their allies also has low support (64 BP). The third clade of *Lotononis* groups with *Bolusia* and *Crotalaria* with strong support (87 BP) and comprises one anomalous species, *L. hirsuta*, which makes up the monotypic section *Euchlora*. *Crotalaria* and *Bolusia* are weakly supported as sister taxa (64 BP) and *Crotalaria* is strongly supported to be monophyletic (99 BP). *Pearsonia*, *Robynsiophyton*, and *Rothia* form a strongly supported clade (98 BP) and the latter two are strongly supported to be sister genera (97 BP). The taxa of this clade all possess a 17 base-pair deletion at positions 179–196 in the aligned ITS matrix. The Crotalarieae are strongly supported to be monophyletic (81 BP) and sister to Genisteae (100 BP).

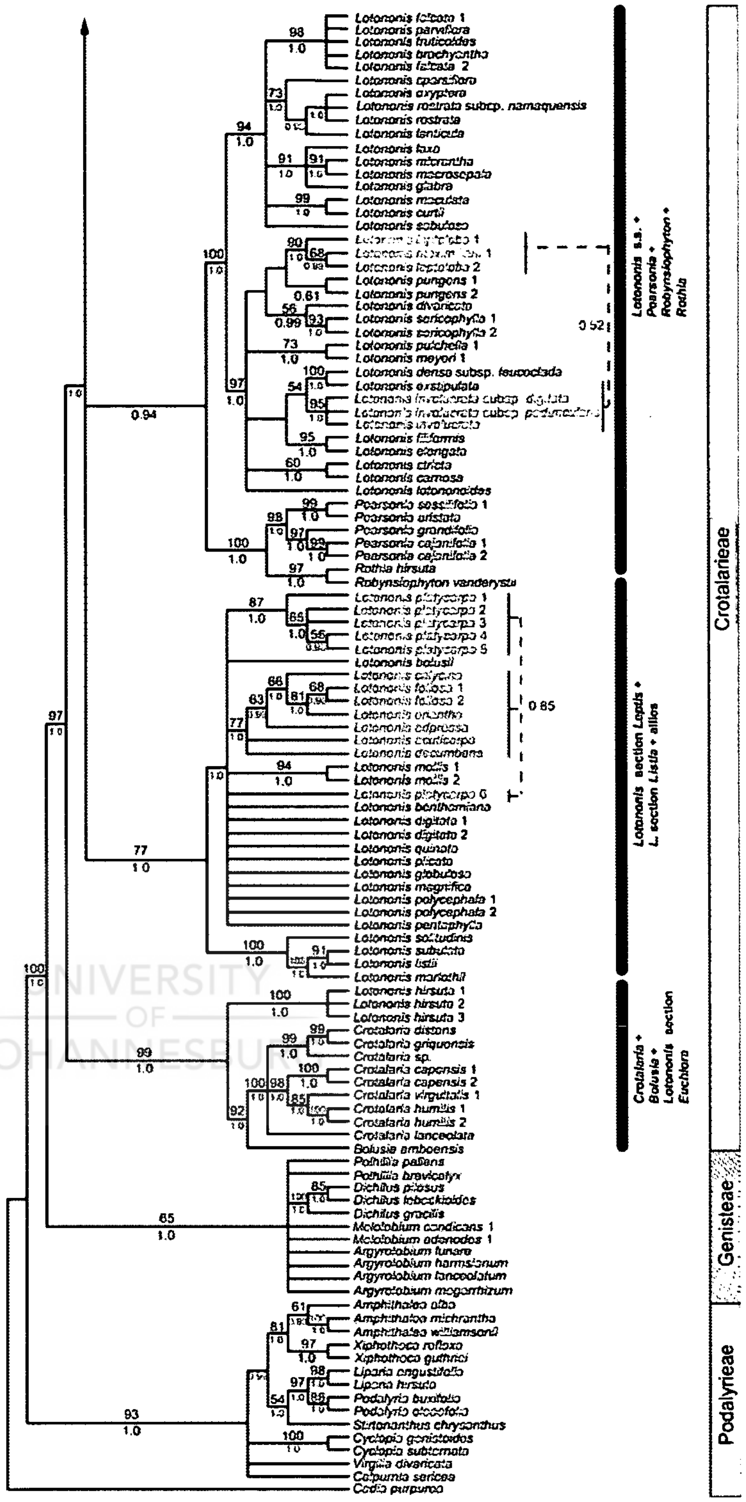

FIG. 1. (Continued)

***Combined ITS/rbcL Data Set***—Visual inspection of the bootstrap consensus trees resulting from separate analyses of ITS and *rbcL* sequences presented no strongly supported incongruent patterns. The ILD test indicated significant difference between the two datasets (p=0.001). Following the suggestions of Seelanan et al. (1997) and Wiens (1998), together with suggestions that the ILD test may be unreliable (Reeves et al. 2001; Yoder et al. 2001) these datasets were combined directly. The combined ITS and *rbcL* matrix consisted of 1,854 included positions, of which 540 were variable and 404 parsimony informative. The MP analysis produced 560 equally parsimonious trees (Fig. 1 ; TL = 1,473; CI = 0.50; RI = 0.86).

In both the MP and BI analyses, the same major clades could be observed: the "Cape" group consisting of *Aspalathus, Lebeckia, Rafnia, Spartidium,* and *Wiborgia* (53 BP; PP 1.0); the *Lotononis* group consisting of *Lotononis* s.s., *Pearsonia, Robynsiophyton,* and *Rothia* (PP 0.94); a second *Lotononis* clade consisting of *Lotononis* section *Leptis, L.* section *Listia,* and allies (77 BP; PP 1.0); and the *Crotalaria* group consisting of *Bolusia, Crotalaria,* and *Lotononis hirsuta/L.* section *Euchlora* (99 BP; PP 1.0). *Lebeckia, Lotononis,* and *Wiborgia* are all paraphyletic and *Lebeckia* section *Lebeckia* is unresolved in both the analyses.

Generic relationships are unresolved within the "Cape" group and represented as a polytomy at the base of this clade in the bootstrap consensus tree of the parsimony analysis (not shown). In the BI tree, *Aspalathus* (88 BP; PP 1.0) and *Wiborgia* (70 BP; PP 1.0) are sister to each other, with *L. mucronata* (PP 0.96) and *Lebeckia inflata* included in this clade. These positions are unresolved in the MP analysis. *Lebeckia* section *Calobota* (including *L.* section *Stiza* and *Spartidium saharae*; 93 BP; PP 1.0) is sister to *Aspalathus* and *Wiborgia*, followed by *L.* section *Viborgioides* (including *Wiborgia humilis*; 64 BP; PP 1.0) and *Rafnia* (94 BP; PP 1.0). *Lebeckia* section *Lebeckia* is unresolved in both the MP and BI trees.

*Lotononis* is paraphyletic in both the MP and BI trees. The *Lotononis* group is moderately supported in the BI tree (PP 0.94) and consists of those species of *Lotononis* from the sections *Aulacinthus* (E.Mey.) Benth., *Buchenroedera* (Eckl. & Zeyh.) B.-E.van Wyk, *Cleistogama* B.-E.van Wyk, *Krebsia* (Eckl. & Zeyh.) Benth., *Lotononis, Monocarpa* B.-E.van Wyk, *Oxydium* Benth., and *Polylobium* (Eckl. & Zeyh.) Benth. (100 BP; PP 1.0). These are sister to a strongly supported clade (BP 100; PP 1.0) consisting of *Pearsonia* (98 BP; PP 1.0), *Robynsiophyton,* and *Rothia*. The sister relationship of the latter two genera has high bootstrap support (97%) and PP (1.0).

The next clade consists of species of *Lotononis* section *Listia* (100 BP; PP 1.0) and sections *Digitata* B.-E.van Wyk, *Leobordea* (Del.) Benth., *Leptis, Lipozygis* (E.Mey.) Benth., and *Synclistus* B.-E.van Wyk (99 BP; PP 1.0), and these are moderately to strongly supported as sister (77 BP; 1.0 PP).

The *Crotalaria* clade consists of *Bolusia* and *Crotalaria* (100 BP; PP 1.0), strongly supported as sister groups (92 BP; PP 1.0), and *Lotononis hirsuta* (corresponding to *Lotononis* section *Euchlora*). This clade receives high support in both the MP and BI analyses (99 BP; PP 1.0).

The Crotalarieae are strongly supported as being monophyletic (97 BP; PP 1.0) and sister to Genisteae (100 BP; PP 1.0). The monophyly of the latter tribe receives low to strong support (65 BP; PP 1.0). The Podalyrieae s.s. are strongly supported as monophyletic (93 BP; PP 1.0) and the relationships within the tribe conform to those of previous studies (Boatwright et al. 2008).

***Morphological Analysis***—The morphological matrix included 31 polarised characters, 29 of which were parsimony informative. Parsimony analysis yielded 261 trees (not shown) of 101 steps (CI = 0.36, RI = 0.93). In the strict consensus tree (not shown), *Aspalathus* and *Rafnia* group together, albeit without support. *Aspalathus* (excluding *A. crenata* and *A. perfoliata*) and *Rafnia* are weakly supported as monophyletic (55 BP and 71 BP, respectively). *Lebeckia* section *Viborgioides, L. mucronata,* and *Wiborgia* s.s. group together, while *L. inflata* groups with *Lebeckia* section *Lebeckia*, but without support. Only *Wiborgia* is weakly supported as monophyletic (78 BP). *Lebeckia* section *Lebeckia* is moderately supported as monophyletic (84 BP), but there is no resolution within this group. *Lotononis hirsuta* is not included in *Lotononis*, but groups with *Crotalaria* (63 BP) and *Bolusia* as in the molecular analysis. The rest of *Lotononis* is monophyletic (56 BP) in the morphological analysis as opposed to paraphyletic in the combined molecular analysis, but relationships within the genus are largely unresolved. *Pearsonia, Rothia,* and *Robynsiophyton* form a strongly supported clade (87 BP) and a sister relationship between *Robynsiophyton* and *Rothia* is strongly supported (88 BP).

***Combined ITS/rbcL/Morphological Data Set***—The bootstrap consensus trees from the combined analysis of ITS and *rbcL* and the morphological analysis showed no strongly supported incongruent patterns, although an ILD test indicated significant difference between the data sets (p=0.002). The suggestions of Seelanan et al. (1997) and Wiens (1998) were followed and the data sets combined directly. The combined matrix consisted of 1,885 characters, 1,405 of which were constant, 480 variable, and 303 parsimony informative. The MP analysis resulted in 370 trees (TL = 1,166, CI = 0.53, RI = 0.84; Fig. 2 ).

The trees resulting from this analysis are similar to those from the combined molecular analysis, except that *Lotononis* and *Lebeckia* section *Lebeckia* are monophyletic. The "Cape" group (73 BP), *Lotononis* group (including *Pearsonia, Robynsionphyton,* and *Rothia*), and *Crotalaria* group (100 BP) found in the molecular analysis were also retrieved in the combined data set of molecular plus morphological characters. Within the "Cape" group, *Aspalathus, Lebeckia* section *Calobota* (including *L.* section *Stiza* and *Spartidium saharae*), *L.* section *Lebeckia, L.* section *Viborgioides* (including *Wiborgia humilis*), *Rafnia,* and *Wiborgia* (excluding *Wiborgia humilis*) received moderate to strong support as monophyletic (99 BP; 95 BP; 77 BP; 87 BP; 98 BP; 94 BP, respectively). *Lotononis* is monophyletic (75 BP; excluding *L. hirsuta*) and the groups retrieved within the genus are identical to the separate clades found in the molecular analysis, namely *Lotononis* s.s. (100 BP), *Lotononis* section *Leptis* and allies (100 BP), and *Lotononis* section *Listia* (100 BP). The sister relationship between the latter two is moderately supported with a BP of 88. *Pearsonia* is strongly supported as monophyletic (99 BP) and sister to *Robynsiophyton* and *Rothia* (100 BP). The sister relationship between *Robynsiophyton* and *Rothia* is strongly supported (99 BP). The *Crotalaria* group is strongly supported (100 BP) and consists of *Bolusia, Crotalaria* and *Lotononis hirsuta. Crotalaria* is strongly supported to be monophyletic (100 BP) and is sister to *Bolusia* (94 BP).

## DISCUSSION

***Phylogenetic Relationships***—The phylogenetic hypotheses presented in this study are based on a complete sample of Crotalarieae at the generic level and a representative sample of most of the taxonomic and morphological variation within these genera. The data were based not only on DNA sequences but also on salient morphological characters that were carefully polarised and proved to be informative at the generic level. The low resolution within the Crotalarieae based on morphology and some chemical and cytological characters reflects the somewhat reticulate relationships within the tribe (also mentioned by van Wyk 1991a; van Wyk 2005) with remarkable examples of parallelism, convergence, and analogy with regard to vegetative and reproductive morphology as outlined by Dahlgren (1970a). The presence of

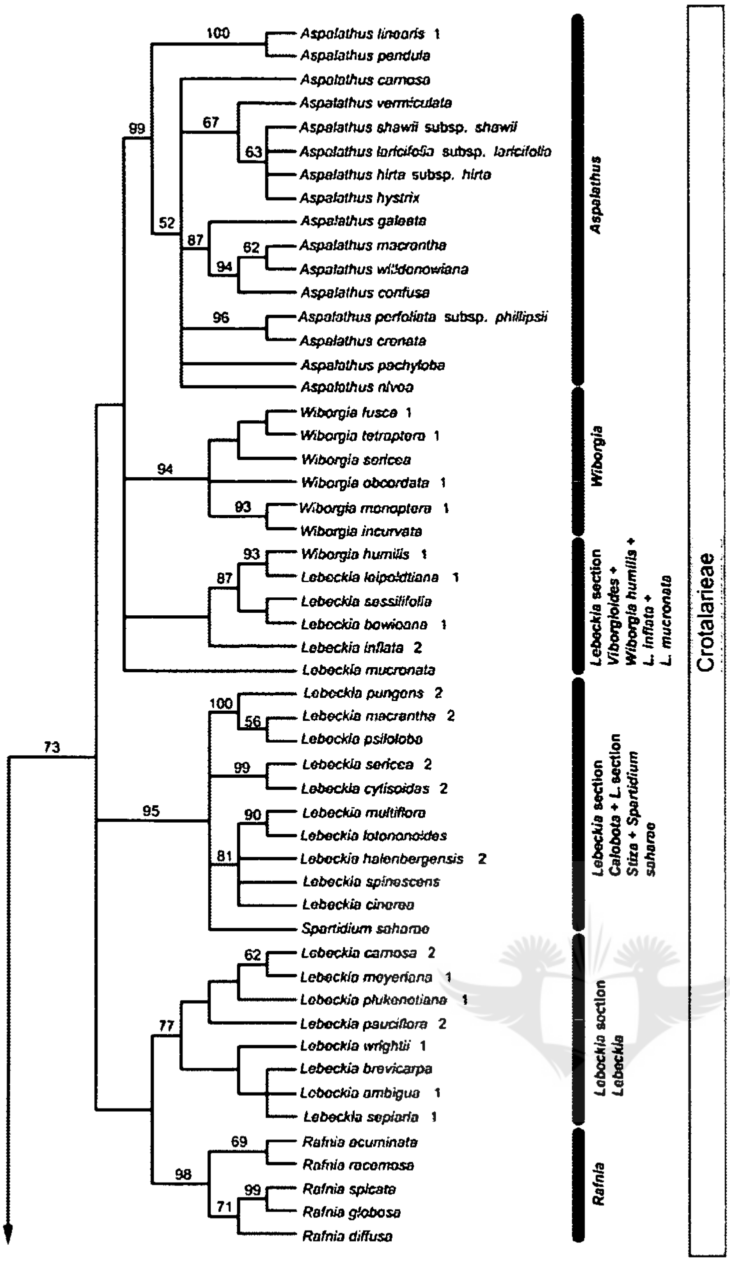

FIG. 2. Strict consensus tree from the combined molecular (ITS and *rbcL*) and morphological analysis. Numbers above the branches are bootstrap percentages above 50% (no. of trees = 370; TL = 1,166; CI = 0.53; RI = 0.84).

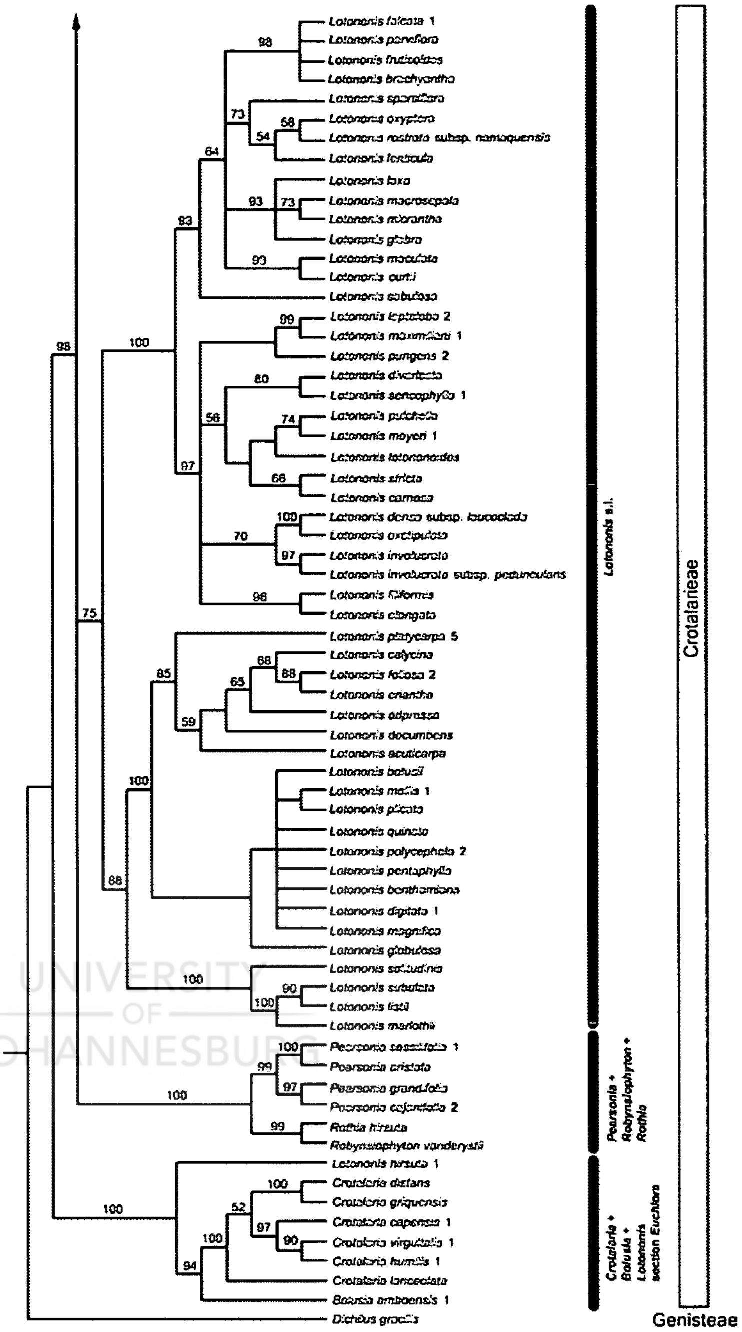

FIG. 2. (Continued)

seemingly identical apomorphic states in unrelated genera (e.g. hairy petals in *Lebeckia* section *Calobota* and *Lotononis* section *Leptis*) complicates the cladistic analysis. In the absence of single apomorphies with diagnostic value, natural groups can only be delimited using combinations of characters. Our results (both molecular and morphological) support some of the current generic concepts within the tribe, but provide novel insights into as yet phylogenetically unstudied groups such as *Lebeckia* and the smaller genera of the Crotalarieae, namely *Robynsiophyton*, *Rothia*, and *Spartidium*.

Previous studies on relationships within the Crotalarieae have all suggested a close relationship between the "Cape" genera (viz., *Aspalathus*, *Lebeckia*, *Rafnia*, and *Wiborgia*), as well as the genera that have a zygomorphic calyx (viz., *Lotononis*, *Pearsonia*, *Robynsiophyton*, and *Rothia*; Dahlgren 1963, 1967, 1970a; Polhill 1981; van Wyk 1991a). The placement of *Bolusia*, *Crotalaria*, and *Spartidium* has been uncertain. A sister relationship between the former two genera was suggested by Polhill (1976) and van Wyk (1991a), while *Spartidium* was thought to either be closely allied to Genisteae or to *Lebeckia*, but the affinities remained unclear (Polhill 1976). The results of the current study indicate four major lineages within the Crotalarieae comprising the "Cape" group (*Aspalathus*, *Lebeckia*, *Rafnia*, *Wiborgia*, including *Spartidium saharae*), two lineages comprising genera with zygomorphic calyces (*Lotononis*, *Pearsonia*, *Robynsiophyton* and *Rothia*), plus *Bolusia*, *Crotalaria*, and *Lotononis* section *Euchlora*.

***The "Cape" Group***—The lack of resolution between genera in this group is caused by the low sequence divergence among these taxa. *Aspalathus* and *Rafnia* are both strongly supported as monophyletic and indicated as sister taxa by the morphological data because they share sessile leaves and an asymmetrical upper suture of the pod (Campbell and van Wyk 2001). *Aspalathus* is placed closer to *Wiborgia* by both the MP and BI analyses. Although the sample of *Aspalathus* is not at all comprehensive, some clades of interest can be noted.

*Aspalathus linearis* and *A. pendula* both have simple, terete leaves and this clade corresponds to the Lebeckiiformes group (Dahlgren 1988), named for its similarity to *Lebeckia* section *Lebeckia*. *Aspalathus laricifolia*, *A. hirta*, *A. hystrix*, and *A. shawii* all have spine-tipped leaves (corresponding to the Laterales group of Dahlgren 1988) and form a clade, which is well-supported in the BI tree. The Borboniae group (Dahlgren 1988) represented by *A. perfoliata* and *A. crenata* form a weak to strongly supported clade. Within *Rafnia*, two clades can be identified that correspond to the two sections of the genus described by Campbell and van Wyk (2001): the *R. acuminata* clade representing *R.* section *Rafnia*, and the *R. spicata* clade representing *R.* section *Colobotropis* E.Mey. These two sections differ mainly in the rostrate keel petals and unequal calyx lobes of *R.* section *Colobotropis*.

It is clear from both the MP and BI analyses that *Lebeckia* and *Wiborgia* are not monophyletic. *Lebeckia* is represented by several smaller clades within the "Cape" group, while *Wiborgia humilis* is nested within the *Lebeckia leipoldtiana* clade and well-separated from the main *Wiborgia* clade.

The species of *Lebeckia* section *Calobota* form a well-supported clade with those of *L.* section *Stiza* and the monotypic genus *Spartidium*. These species are all shrubs with trifoliolate or unifoliolate leaves and green mature stems. The petals are usually pubescent and they possess a 5 + 4 + 1 anther configuration (five short dorsifixed anthers, four long basifixed anthers, and an intermediate carinal anther). Some of these character states also occur in *Lotononis* species and are thus not informative in the morphological analysis. The species of *L.* section *Stiza* and *L.* section *Calobota* occur in the Cape and those of the latter also extend northwards into Namibia. *Spartidium saharae* is a North African plant that has had uncertain affinities within the tribe. The close relationship of this species to *L.* section *Calobota* has also been demonstrated independently by Edwards and Hawkins (2007) based on ITS data.

*Wiborgia* and species of *Lebeckia* section *Viborgioides* are superficially very similar in their rigid, woody habit, glabrous petals and highly reflexed standard petals in most species. However, they differ markedly in the winged, few-seeded samaras that are typical of *Wiborgia* species (Dahlgren 1975). However, *Wiborgia humilis* has thin-walled, inflated pods that lack the dorsal wing characteristic of *Wiborgia* (Dahlgren 1970b). The fruits of *Lebeckia* section *Viborgioides* are typically turgid, thin-walled, many-seeded, and wingless. *Wiborgia humilis* is the only species of *Wiborgia* with a 6 + 4 anther arrangement (6 short dorsifixed and 4 long basifixed anthers) instead of the 5 + 4 + 1 arrangement found in all other species. These characters therefore support the placement of *W. humilis* in the *L.* section *Viborgioides* clade.

*Lebeckia* section *Lebeckia* is unresolved in the BI and MP analyses. This section is morphologically very distinct from the other sections in the genus and its monophyly is supported by four apomorphies, namely the suffrutescent habit, acicular leaves, a 5 + 5 anther arrangement, and rugose seeds (Le Roux 2006; Le Roux and van Wyk 2007). This is clear from the moderate support this group received in the morphological analysis as well as the combined morphological and molecular analysis. *Lebeckia lotononoides* and *L. inflata* are the only other species of *Lebeckia* with rugose seeds, but these species share characters with *L.* section *Calobota* and *L.* section *Viborgioides*, respectively (Boatwright and van Wyk 2007; Boatwright, pers. obs.).

The positions of both *L. inflata* and *L. mucronata* are unresolved in the combined ITS and *rbcL* analysis. *Lebeckia mucronata* is currently placed within *L.* section *Calobota*. *Lebeckia inflata* was described by Bolus (1887) without any reference to its position in the infrageneric systems of Bentham (1844) and Harvey (1862). Both of these species, however, share several anatomical and morphological characters with species of *L.* section *Viborgioides*, such as a 6 + 4 anther arrangement, glabrous petals, and the dorsiventral leaves with mucilage cells. When morphological characters were combined with the molecular ITS and *rbcL* data, *L. inflata* was included in a clade along with *L.* section *Viborgioides* and *Wiborgia humilis*, while the position of *L. mucronata* remained unresolved.

***The Lotononis Clades***—Based on the molecular data, *Lotononis* is paraphyletic and consists of three clades. *Lotononis* s.s. groups with the *Pearsonia* clade (albeit without support in the MP analysis) and is strongly supported as monophyletic. Two groups were noted within this clade. The first consists of representatives of *L.* section *Oxydium* and the second of representatives of *L.* sections *Aulacinthus*, *Buchenroedera*, *Cleistogama*, *Krebsia*, *Lotononis*, *Monocarpa*, and *Polylobium*. *Lotononis* section *Oxydium* is strongly supported to be monophyletic in the molecular analyses and currently consists of 35 species (accommodated in 14 subsections as described by van Wyk 1991b) distinguished from other sections by several characters, including single stipules at each leaf base and glabrous wing and keel petals. In the second group, *L.* section *Cleistogama* is sister to *L.* section *Monocarpa*, while *L.* sections *Aulacinthus*, *Lotononis*, and *Polylobium* form a clade without support. The resolution in the rest of the group is low and relationships not clear. In the molecular analysis, *Lotononis* s.s. and the *Pearsonia* clade clearly share similarities in their sequences but morphologically *Lotononis* s.s. allies with the rest of the genus to form a monophyletic assemblage. From these results it is clear that some generic apomorphies support the current concept of the genus. When the molecular data were combined with the morphology, *Lotononis* remained monophyletic, although with moderate support. It is interesting to note the close agreement between the sectional classification proposed by van Wyk (1991b) and the results of this study. *Pearsonia*, *Robynsiophyton*, and *Rothia* share several morphological characters that are unique among the genera of Crotalarieae, such as the uniform anthers, straight styles, and presence of angelate esters of hydroxylupanine. The generic concepts of *Robynsiophyton* and *Rothia*, based mainly on anther characters, have been doubtful and *Robynsiophyton* was thought to be a local derivative of *Pearsonia* (van Wyk 1991a). Taxonomic studies of the former two genera and a thorough examination of their morphology and anatomy revealed that these generic concepts are indeed sound and emphasizes the value of androecial characters in the Crotalarieae (Boatwright and van Wyk, unpubl.; Boatwright et al., unpubl.).

The second clade comprises those species from *Lotononis* section *Leptis*, *Lotononis* section *Listia*, and allies. This clade is moderately to strongly supported in the molecular analysis but lacks resolution in the morphological analysis. The concept of the hitherto monotypic *Listia* was broadened by van Wyk (1991b) and treated as a section of *Lotononis* with several distinct characters. This broadened concept is supported in the analyses presented in this study. The absence of suitable material of the rare *Lotononis macrocarpa* Eckl. & Zeyh. (an anomalous species within this group) prevented its inclusion in this study. Special efforts should be made to obtain DNA from this species in order to evaluate its placement within *L.* section *Listia*. van Wyk (1991b) mentions that no apomorphies exist for *L.* section *Leptis*, which is clear from the morphological analysis where this section is left unresolved. The molecular results, however, indicate a close relationship between this section and *L.* sections *Digitata*, *Leobordea*, *Lipozygis*, and *Synclistus*, all of which are successively sister to *L.* section *Listia*. The third clade comprises *L. hirsuta*, which groups with the *Crotalaria* clade.

***The Crotalaria Clade***—The close relationship between *Crotalaria* and *Bolusia* has been mentioned by both Polhill (1982) and van Wyk (1991a) and these authors suggested that *Bolusia* could merely be a local derivative of *Crotalaria*. Data from the present study indicates that *Bolusia* is sister to and not embedded within *Crotalaria* (*rbcL* analysis with multiple representatives), so that its generic status seems justified. *Bolusia* differs from *Crotalaria* mainly in its glabrous style and strongly coiled keel petals. Also included in this clade is *Lotononis hirsuta*, representing the monotypic section *Euchlora*. This species differs from all other *Lotononis* species in its peculiar tuberous habit and from most others in the very large, inflated pods, equally lobed calyx, and very large seeds with smooth surfaces. It shares with *Crotalaria* and *Bolusia* the strongly inflated pods.

***Implications for Generic Classification***—The results generated in this study have important implications for the generic classification system of the Crotalarieae. Detailed studies of character variation in the tribe over a period of more than 23 yr are now nearing completion, allowing us to make an informed evaluation of the congruence between morphological and molecular patterns. The results clearly show that the genera *Calobota* Eckl. & Zeyh. and *Euchlora* Eckl. & Zeyh. should be reinstated. A new genus should be described that will include *Lebeckia* sect. *Viborgioides*, as well as *L. inflata* and *L. mucronata*. *Spartidium* will be transferred to *Calobota* and *Wiborgia humilis* to the new genus (Boatwright et al., unpubl.). These changes, about to be formalized, will clearly result in a more practical and predictable generic classification system for the tribe Crotalarieae.

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APPENDIX 1. Voucher information and GenBank accession numbers of the taxa sampled in this study. Voucher specimens are deposited in the following herbaria: Australian National Herbarium (CANB), University of Johannesburg Herbarium (JRAU), Kew Herbarium (K), National Herbarium, Pretoria (PRE), Southern Cape Herbarium (SCHG). The information is listed as follows: *taxon*—GenBank accessions: *rbcL*, ITS; Voucher specimen. Those regions not sampled for a taxon are represented by a dash [[1]Boatwright et al. (2008); [2]Crisp et al. (2000); [3]Käss and Wink (1997); [4]Doyle et al. (1997); [5]Pardo et al. (2004); [6]Motsi (2004); [7]Van der Bank et al. (2002)].

***Amphithalea* Eckl. & Zeyh.:** *A. alba* Granby— AM180171[1], AM261217 [1]; *Van Wyk 2125* (SCHG). *A. micrantha* (E.Mey.) Walp.— AM180182 [1], AM261227 [1]; *Schutte 751* (SCHG). *A. williamsonii* Harv.— AM177372 [1], AM261436 [1]; *Euston-Brown s.n.* (SCHG). ***Argyrolobium* Eckl. & Zeyh.:** *A. harmsianum* Schltr. ex Harms— —, AF287685[2]; *Crisp 9042* (CANB). *A. lunare* (L.) Druce 1— —, AF287686[2]; *Crisp 9039* (CANB). *A. lunare* (L.) Druce subsp. *sericeum* (Thunb.) T.J.Edwards 2— EU348013, —; *Van Wyk 2080* (JRAU). *A. marginatum* Bolus— EU348014, —; *Van Wyk 3038* (JRAU). *A. marginatum* Bolus— Z95547[3], —; *Edwards 471*. *A. megarrhizum* Bolus— EU348015, —; *Germishuizen s.n.* (JRAU). *Argyrolobium* sp.— EU348016, —; *Van Wyk 2173* (JRAU). ***Aspalathus* L.:** *A. acutiflora* Dahlgren— —, EU347735; *Boatwright & Magee 22* (JRAU). *A. carnosa* Berg. — EU348022, EU347723; *Boatwright & Magee 61* (JRAU). *A. confusa* Dahlgren— EU348031, EU347736; *Boatwright et al. 97* (JRAU). *A. crenata* (L.) Dahlgren— EU348028, EU347729; *Boatwright & Magee 70* (JRAU). *A. galeata* E.Mey.— EU348032, EU347726; *Boatwright et al. 100* (JRAU). *A. hirta* E.Mey. subsp. *hirta*— EU348025, EU347732; *Boatwright & Magee 43* (JRAU). *A. hystrix* L.f.— EU348023, EU347734; *Boatwright & Magee 30* (JRAU). *A. laricifolia* Berg. subsp. *laricifolia*— EU348026, EU347731; *Boatwright & Magee 46* (JRAU). *A. linearis* (Burm.f.) Dahlgren 1— EU348020, EU347722; *Van Wyk et al. 4192* (JRAU). *A. linearis* (Burm.f.) Dahlgren 2— EU348019, EU347739; *Van Wyk s.n.* (JRAU). *A. macrantha* Harv.— EU348029, EU347728; *Boatwright & Magee 71* (JRAU). *A. nivea* Thunb.— EU348018, EU347737; *Van Wyk 2938* (JRAU). *A. pachyloba* Benth.— EU348024, EU347733; *Boatwright & Magee 42* (JRAU). *A. pendula* Dahlgren— EU348017, EU347738; *Van Wyk s.n.* (JRAU). *A. perfoliata* (Lam.) Dahlgren subsp. *phillipsii* Dahlgren— EU348030, EU347727; *Boatwright & Magee 82* (JRAU). *A. shawii* Bol. subsp. *shawii*— EU348033, EU347725; *Boatwright & Magee 27* (JRAU). *A. vermiculata* Lam.— EU348021, EU34772; *Boatwright & Magee 15* (JRAU). *A. willdenowiana* Benth.— EU348027, EU347730; *Boatwright & Magee 69* (JRAU). ***Bolusia* Benth.:** *B. acuminata* (DC.) Polhill— EU347944, —; *Morris 1193* (PRE). *B. amboensis* (Schinz) Harms 1— EU347943, EU347891; *Robinson 1558* (K). *B. amboensis* (Schinz) Harms 2— EU347943, —; *Giess 10091* (K). ***Cadia* Forssk.:** *C. purpurea* (Ait.) Forssk.— AM260751 [1], AM261740 [1]; *Beckett 1702* (K). ***Calpurnia* E.Mey.:** *C. sericea* Harv.— AM177374 [1], AM268374 [1] & AM268375 [1]; *Boatwright 86* (JRAU). ***Crotalaria* L.:** *C. capensis* Jacq. 1— EU348034, EU347884; *Van Wyk 2933a* (JRAU). C. *capensis* Jacq. 2— EU348045, EU347888; *Van der Bank 14* (JRAU). *C. distans* Benth.— EU348038, EU347882; *de Castro 137* (JRAU). *C. griquensis* Bolus— EU348043, EU347887; *Van Wyk et al. 4173* (JRAU). *C. humilis* Eckl. & Zeyh. 1— EU348041, EU347889; *Boatwright et al. 143* (JRAU). *C. humilis* Eckl. & Zeyh. 2— EU348042, EU347890; *Boatwright et al. 156* (JRAU). *C. lanceolata* E.Mey.— EU348040, EU347885; *Van Wyk 1985* (JRAU). *C. lebeckioides* Bond— EU348036, —; *Van Wyk 3315e* (JRAU). *C. lotoides* Benth.— EU348035, —; *Van Wyk s.n.* (JRAU). *Crotalaria* sp.— EU348039, EU347883; *Van Wyk 3367* (JRAU). *C. virgultalis* Burch. ex DC. 1— EU348044, EU347886; *Van Wyk et al. 4175* (JRAU). *C. virgultalis* Burch. ex DC. 2— EU348037, —; *Van Wyk 3060* (JRAU). ***Cyclopia* Vent.:** *C. genistoides* (L.) R.Br.— AM261716 [1], AM050819 [1]; *Boatwright & Magee 53* (JRAU). *C. subternata* Vogel— AM261725 [1], AM050821 [1]; *Boatwright & Magee 35* (JRAU). ***Dichilus* DC.:** *D. gracilis* Eckl. & Zeyh.— EU347962, EU347893; *Schutte 247* (JRAU). *D. lebeckioides* DC.— EU347963, EU347894; *Schutte 151* (JRAU). *D. pilosus* Conrath ex Shinz— EU347959, EU347892; *Schutte 363* (JRAU). *D. reflexus* (N.E.Br.) A.L.Schutte— EU347961, —; *Schutte 177* (JRAU). *D. strictus* E.Mey.— —, AJ287684[2]; *Crisp 9073* (CANB). *D. strictus* E.Mey.— EU347960, —; *Schutte 150* (JRAU). **Genista L.:** *G. teretifolia* Willk.— —, AY263668[5]; *MAF 162924*. **Lebeckia Thunb.:** *L. ambigua* E.Mey. 1— EU347917, EU347852; *Van Wyk 2900* (JRAU). *L. ambigua* E.Mey. 2— EU347934, EU347851; *Le Roux et al. 6* (JRAU). *L. bowieana* Benth. 1— EU347909, EU347868; *Streicher s.n.* (JRAU). *L. bowieana* Benth. 2— EU347910, EU347869; *Van Wyk 2106* (JRAU). *L. brevicarpa* M.M.Le Roux & B.-E.van Wyk— EU347933, EU347850; *Le Roux et al. 4* (JRAU). *L. contaminata* (L.) Thunb. 1— EU347900, EU347845; *Vlok et al. s.n.* (JRAU). *L. contaminata* (L.) Thunb. 2— EU347937, EU347846; *Le Roux et al. 15* (JRAU). *L. contaminata* (L.) Thunb. 3— —, EU347847; *Le Roux et al. 16* (JRAU). *L. cinerea* E.Mey.— EU347930, EU347840; *Boatwright et al. 150* (JRAU). *L. cytisoides* Thunb. 1— EU347903, EU347837; *Van Wyk 2313* (JRAU). *L. cytisoides* Thunb. 2— EU347925, EU347838; *Le Roux et al. 2* (JRAU). *L. gracilis* Eckl. & Zeyh.— —, EU347855; *Le Roux et al. 17* (JRAU). *L. halenbergensis* Merxm. & A.Schreib. 1— EU347908, EU347836; *Van Wyk 3086* (JRAU). *L. halenbergensis* Merxm. & A.Schreib. 2— EU347927, EU347842; *Boatwright et al. 146* (JRAU). *L. inflata* Bolus 1— EU347901, EU347863; *Vlok et al. 2* (JRAU). *L. inflata* Bolus 2— EU347940, EU347864; *Johns 162* (JRAU). *L. leipoldtiana* Schltr. ex Dahlgren 1— EU347939, EU347866; *Boatwright et al. 123* (JRAU). *L. leipoldtiana* Schltr. ex Dahlgren 2— EU347914, EU347865; *Van Wyk 3278* (JRAU). *L. lotononoides* Schltr.— EU347928, EU347843; *Boatwright et al. 142* (JRAU). *L. macrantha* Harv. 1— EU347916, EU347828; *Van Wyk s.n.* (JRAU). *L. macrantha* Harv. 2— EU347922, EU347831; *Boatwright et al. 92* (JRAU). *L. melilotoides* Dahlgren 1— EU347919, —; *Van Wyk 2562b* (JRAU). *L. melilotoides* Dahlgren 2— —, EU347841; *Van Wyk 2229* (JRAU). *L. meyeriana* Eckl. & Zeyh. ex Harv. 1— EU347904, EU347856; *Van Wyk 3351* (JRAU). *L. meyeriana* Eckl. & Zeyh. ex Harv. 2— EU347905, —; *Van Wyk 3009* (JRAU). *L. meyeriana* Eckl. & Zeyh. ex Harv. 3— —, EU347857; *Van Wyk 4043* (JRAU). *L. mucronata* Benth.— EU347941, EU347870; *Vlok 1726* (JRAU). *L. multiflora* E.Mey.— EU347926, EU347833; *Boatwright et al. 138* (JRAU). *L. pauciflora* Eckl. & Zeyh. 1— EU347902, EU347861; *Van Wyk 3024* (JRAU). *L. pauciflora* Eckl. & Zeyh. 2— EU347935, EU347862; *Le Roux et al. 7* (JRAU). *L. plukenetiana* E.Mey. 1— EU347932, EU347849; *Le Roux et al. 24* (JRAU). *L. plukenetiana* E.Mey. 2— EU347906, EU347848; *Van Wyk 4043* (JRAU). *L. psiloloba* Walp.— EU347923, EU347830; *Le Roux et al. 20* (JRAU). *L. pungens* Thunb. 1— EU347918, EU347827; *Van Wyk s.n.* (JRAU). *L. pungens* Thunb. 2— EU347921, EU347829; *Boatwright et al. 106* (JRAU). *L. sepiaria* (L.) Thunb. 1— EU347936, EU347853; *Le Roux et al. 10* (JRAU). *L. sepiaria* (L.) Thunb. 2— EU347920, EU347854; *Van Wyk 2979* (JRAU). *L. sericea* Thunb. 1— EU347907, EU347832; *Van Wyk 3115* (JRAU). *L. sericea* Thunb. 2— EU347924, EU347834; *Boatwright et al. 151* (JRAU). *L. sericea* Thunb. 3— EU347915, EU347835; *Van Wyk 3119* (JRAU). *L. sessilifolia* (Eckl. & Zeyh.) Benth.— EU347938, EU347867; *Boatwright et al. 170* (JRAU). *L. spinescens* Harv.— EU347929, EU347839; *Boatwright et al. 158* (JRAU). *L. wrightii* (Harv.) Bolus 1— EU347912, EU347858; *Vlok et al. s.n.* (JRAU). *L. wrightii* (Harv.) Bolus 2— EU347913, EU347860; *Vlok et al. s.n.* (JRAU). *L. wrightii* (Harv.) Bolus 3— EU347911, EU347859; *Van Wyk 3354* (JRAU). **Liparia L.:** *L. angustifolia* (Eckl. & Zeyh.) A.L.Schutte— AM177376 [1], AM261478 [1]; *Boatwright & Magee 66* (JRAU). *L. hirsuta* Thunb.— AM259357 [1], AM261486 [1]; *Boatwright & Magee 33* (JRAU). **Lotononis (DC.) Eckl. & Zeyh.:** *L. acuticarpa* B.-E.van Wyk— EU348047, EU347770; *Van Wyk 2625* (JRAU). *L. adpressa* N.E.Br. subsp. *adpressa*— EU348100, EU347780; *Van Wyk 1899* (JRAU). *L. alpina* (Eckl. & Zeyh.) B.-E.van Wyk— —, AM262446 [6]; *Van Wyk & Van Wyk 1478* (JRAU). *L. benthamiana* Dümmer— EU348051, EU347771; *Van Wyk 2528* (JRAU). *L. bolusii* Dümmer— EU348046, EU347761; *Van Wyk 2443* (JRAU). *L. brachyantha* Harms— EU347998, EU347816; *Boatwright et al. 117* (JRAU). *L. brevicaulis* B.-E.van Wyk— EU348080, —; *Schutte 447* (JRAU). *L. calycina* (E.Mey.) Benth.— EU348052, EU347762; *Van Wyk 1433* (JRAU). *L. carnosa* (Eckl. & Zeyh.) Benth.— EU348083, EU347800; *Van Wyk 1663* (JRAU). *L. curtii* Harms— EU348006, EU347815; *Van Wyk et al. 4172* (JRAU). *L. crumanina* Burch. ex Benth.— EU348062, —; *Van Wyk 3057* (JRAU). *L. decumbens* (Thunb.) B.-E.van Wyk subsp. *decumbens*— EU348058, EU347778; *Van Wyk 1701* (JRAU). *L. densa* (Thunb.) Harv. subsp. *leucoclada* (Schltr.) B.-E.van Wyk— EU348048, EU347792; *Van Wyk 2430* (JRAU). *L. digitata* Harv. 1— EU348071, EU347772; *Van Wyk 2350* (JRAU). *L. digitata* Harv. 2— EU348057, EU347773; *Van Wyk 2342* (JRAU). *L. divaricata* (Eckl. & Zeyh.) Benth.— EU348092, EU347788; *Van Wyk 2484* (JRAU). *L. elongata* (Thunb.) D.Dietr.— EU348087, EU347821; *Van Wyk 2573* (JRAU). *L. eriantha* Benth.— EU348086, EU347784; *Schutte 383* (JRAU). *L. eriocarpa* (E.Mey.) B.-E.van Wyk— EU348084, —; *Van Wyk 1952* (JRAU). *L. exstipulata* Bolus— EU348055, EU347796; *Van Wyk 2271* (JRAU). *L. falcata* (E.Mey.) Benth. 1— EU348103, EU347756; *Boatwright et al. 184* (JRAU). *L. falcata* (E.Mey.) Benth. 2— EU347999, EU347817; *Boatwright et al. 120* (JRAU). *L. filiformis* B.-E.van Wyk— EU348074, EU347794; *Vlok 2030* (JRAU). *L. foliosa* Bolus 1— EU348073, EU347776; *Van Wyk 2481* (JRAU). *L. foliosa* Bolus 2— EU347993, EU347819; *Boatwright & Magee 88* (JRAU). *L. fruticoides* B.-E.van Wyk— EU348085, EU347801; *Van Wyk 2021* (JRAU). *L. galpinii* Dümmer— Z95538 [3], —; *T. Edwards 480*. *L. glabra* (Thunb.) D.Dietr.— EU348005, EU347814; *Van Wyk 2014* (JRAU). *L. globulosa* B.-E.van Wyk— EU348075, EU347777; *Van Wyk 2210* (JRAU). *L. hirsuta* (Thunb.) D.Dietr. 1— EU348069, EU347879; *Van Wyk 1338* (JRAU). *L. hirsuta* (Thunb.) D.Dietr. 2— EU348070, EU347880; *Van Wyk s.n.* (JRAU). *L. hirsuta* (Thunb.) D.Dietr. 3— EU348102, EU347881; *Schutte 290* (JRAU). *L. involucrata* (Berg.) Benth.— EU947997, EU347809; *Boatwright et al. 116* (JRAU). *L. involucrata* (Berg.) Benth. subsp. *digitata* B.-E.van Wyk — EU348076, EU347805; *Van Wyk 2873* (JRAU). *L. involucrata* (Berg.) Benth. subsp. *peduncularis* (E.Mey.) B.-E.van Wyk— EU348007, EU347806; *Van Wyk et al. 4195* (JRAU). *L. laxa* Eckl. & Zeyh. 1— EU348059, EU347795; *Van Wyk 2608* (JRAU). *L. laxa* Eckl. & Zeyh. 2— EU348060, —; *Van Wyk 1726* (JRAU). *L. laxa* Eckl. & Zeyh. 3— —, AF287677 [2]; *Crisp 9075* (CANB). *L. lenticula* (E.Mey.) Benth.— EU348088, EU347802; *Van Wyk* 2017 (JRAU). *L. leptoloba* Bolus 1— EU348104, EU347757; *Boatwright et al. 185* (JRAU). *L. leptoloba* Bolus 2— EU348077, EU347804; *Schutte 276* (JRAU). *L. listii* Polhill— EU348012, EU347826; *Van Wyk et al. 4207* (JRAU). *L. lotononoides* (Scott Elliot) B.-E.van Wyk— EU348089, EU347822; *Van Wyk 1962* (JRAU). *L. macrosepala* Conrath— EU348056, EU347810; *Van Wyk 2622* (JRAU). *L. maculata* Dümmer— EU348004, EU347813; *Van Wyk et al. 4169* (JRAU). *L. magnifica* B.-E.van Wyk— EU348079, EU347779; *Van Wyk 2421* (JRAU). *L. marlothii* Engl.— EU348010, EU347825; *Van Wyk et al. 4203* (JRAU). *L. maximiliani* Schltr. ex De Wildeman 1— EU348078, EU347799; *Schutte 282* (JRAU). *L. maximiliani* Schltr. ex De Wildeman 2— EU348098, —; *Schutte 271* (JRAU). *L. meyeri* (Presl) B.-E.van Wyk 1— EU348095, EU347811; *Van Wyk 1766* (JRAU). *L. meyeri* (Presl) B.-E.van Wyk 2— EU348094, —; *Van Wyk 1765* (JRAU). *L. micrantha* Eckl. & Zeyh.— EU348049, EU347798; *Van Wyk 2481* (JRAU). *L. mollis* (E.Mey.) Benth. 1— EU348068, EU347763; *Koekemoer 524* (PRE). *L. mollis* (E.Mey.) Benth. 2— EU348067, EU347764; *Van Wyk 3113* (JRAU). *L. oxyptera* (E.Mey.) Benth.— EU347992, EU347787; *Boatwright s.n.* (JRAU). *L. parviflora* (Berg.) D.Dietr.— EU348050, EU347797; *Van Wyk 2442* (JRAU). *L. pentaphylla* (E.Mey.) Benth.— EU348001, EU347783; *Boatwright et al. 148* (JRAU). *L. platycarpa* (Viv.) Pic.-Serm. 1— EU348105, EU347759; *Boatwright et al. 192* (JRAU). *L. platycarpa* (Viv.) Pic.-Serm. 2— EU348063, EU347766; *Van Wyk 3066* (JRAU). *L. platycarpa* (Viv.) Pic.-Serm. 3— EU348064, EU347767; *Koekemoer 942* (JRAU). *L. platycarpa* (Viv.) Pic.-Serm. 4— EU348011, EU347768; *Boatwright et al. 159* (JRAU). *L. platycarpa* (Viv.) Pic.-Serm. 5— EU348003, EU347769; *Van Wyk et al. 4204* (JRAU). *L. platycarpa* (Viv.) Pic.-Serm. 6— EU348065, EU347765; *Friis et al. 9080* (K). *L. plicata* B.-E.van Wyk— EU348072, EU347775; *Van Wyk 3382* (JRAU). *L. polycephala* (E.Mey.) Benth. 1— EU348082, EU347781; *Van Wyk 2408* (JRAU). *L. polycephala* (E.Mey.) Benth. 2— EU347994, EU347782; *Boatwright et al. 94* (JRAU). *L. prostrata* (L.) Benth. 1— EU348054, —; *Van Wyk 3229* (JRAU). *L. prostrata* (L.) Benth. 2— —, EU347808; *Boatwright et al. 115* (JRAU). *L. pulchella* (E.Mey.) B.-E.van Wyk 1— EU348090, EU347785; *Van Wyk 1659* (JRAU). *L. pulchella* (E.Mey.) B.-E.van Wyk 2— EU348066, —; *Van Wyk 1659* (JRAU). *L. pungens* Eckl. & Zeyh. 1— EU348096, EU347790; *Van Wyk 1725* (JRAU). *L. pungens* Eckl. & Zeyh. 2— EU347996, EU347807; *Boatwright et al. 105* (JRAU). *L. quinata* (Thunb.) Benth.— EU347995, EU347774; *Boatwright et al. 95* (JRAU). *L. rabenaviana* Dinter & Harms— —, EU347758; *Boatwright et al. 191* (JRAU). *L. rigida* (E.Mey.) Benth. 1— EU348101, —; *Van Wyk 2700* (JRAU). *L. rigida* (E.Mey.) Benth. 2— —, EU347791; *Van Wyk s.n.* (JRAU). *L. rostrata* Benth. subsp. *namaquensis* (Bolus) B.-E.van Wyk — EU348002, EU347812; *Boatwright et al. 155* (JRAU). *L. rostrata* Benth.— EU348000, EU347818; *Boatwright et al. 147* (JRAU). *L. sabulosa* Salter— EU348081, EU347820; *Van Wyk 2325* (JRAU). *L. sericophylla* Benth. 1— EU348093, EU347789; *Van Wyk 1956* (JRAU). *L. sericophylla* Benth. 2— EU348053, EU347803; *Van Wyk 1917* (JRAU). *L. sericophylla* Benth. 3— EU348097, —; *Van Wyk 1958* (JRAU). *L. solitudinis* Dümmer— EU348008, EU347823; *Van Wyk et al. 4198* (JRAU). *L. sparsiflora* (E.Mey.) B.-E.van Wyk— EU348099, EU347786; *Van Wyk 2057* (JRAU). *L. stricta* (Eckl.& Zeyh.) B.-E.van Wyk— EU348091, EU347793; *Van Wyk 1718* (JRAU). *L. subulata* B.-E.van Wyk— EU348009, EU347824; *Van Wyk et al. 4202* (JRAU). *L. umbellata* (L.) Benth. 1— EU348061, —; *Van Wyk 3234* (JRAU). *L. umbellata* (L.) Benth. 2— —, EU347760; *Boatwright s.n.* (JRAU). **Lupinus L.:** *L. polyphyllus* Lindley— Z70052 [3], —; *Planchuelo 95*. **Melolobium Eckl. & Zeyh.:** *M. adenodes* Eckl. & Zeyh. 1— —, AM050832 [6]; *Van Wyk 4036* (JRAU). *M. adenodes* Eckl. & Zeyh. 2— EU347976, —; *Van Wyk 2159* (JRAU). *M. adenodes* Eckl. & Zeyh. 3— EU347986, —; *Van Wyk 4036*

(JRAU). *M. aethiopicum* (L.) Druce 1— EU347977, —; *Strydom 5* (PRE). *M. aethiopicum* (L.) Druce 2— EU347987, —; *Van Wyk 4040* (JRAU). *M. alpinum* Eckl. & Zeyh.— EU347978, —; *Schutte 158* (JRAU). *M. candicans* (E.Mey.) Eckl. & Zeyh. 1— —, AM050833 [6], *Van Wyk 4016* (JRAU). *M. candicans* (E.Mey.) Eckl. & Zeyh. 2— EU347980, —; *Van Wyk 3072* (JRAU). *M. candicans* (E.Mey.) Eckl. & Zeyh. 3— EU347991, —; *Boatwright et al. 187* (JRAU). *M. canescens* (E.Mey.) Benth.— EU347981, —; *Schutte 303* (JRAU). *M. exudans* Harv.— EU347990, —; *Van Wyk 2234* (JRAU). *M. humile* Eckl. & Zeyh.— EU347982, —; *Van Wyk 2543* (JRAU). *M. macrocalyx* Dümmer— EU347989, —; *Van Wyk 3061b. M. microphyllum* (L.f.) Eckl. & Zeyh. 1— EU347983, —; *Van Wyk 4006* (JRAU). *M. microphyllum* (L.f.) Eckl. & Zeyh. 2— EU347979, —; *Moteetee & Van Wyk 3* (JRAU). *M. microphyllum* (L.f.) Eckl. & Zeyh. 3— Z95539[3], —; *Edwards 470. M. obcordatum* Harv.— Z95540[3], —; *Edwards 470. M. stipulatum* (Thunb.) Harv.— EU347988, —; *Van Wyk 4037* (JRAU). *M. subspicatum* Conrath— EU347984, —; *Van Wyk 1779* (JRAU). *M. wilmsii* Harms— EU347985, —; *Van Wyk 2724* (JRAU). ***Pearsonia* Dümmer:** *P. aristata* (Shinz) Dümmer— EU347945, EU347873; *De Castro 346* (JRAU). *P. cajanifolia* (Harv.) Polhill 1— EU347948, EU347875; *Posthumus 7* (JRAU). *P. cajanifolia* (Harv.) Polhill 2— EU347950, EU347876; *Boatwright & Magee 90* (JRAU). *P. grandifolia* (Bolus) Polhill— EU347946, EU347874; *Van Wyk 3047* (JRAU). *P. sessilifolia* (Harv.) Dümmer 1— EU347947, EU347871; *Schutte 463* (JRAU). *P. sessilifolia* (Harv.) Dümmer 2— —, EU347872; *Schutte 589b. P. sessilifolia* (Harv.) Dümmer 3— —, AJ287675[2]; *Crisp 9078* (CANB). *P. uniflora* (Kensil) Polhill— EU347949, —; *Van Wyk 3033* (JRAU). ***Podalyria* Willd.:** *P. buxifolia* (Retz.) Lam.— AM261693 [1], AM261496 [1]; *Boatwright & Magee 34* (JRAU). *P. oleaefolia* Salisb.— AM261708 [1], AM261667 [1]; *Boatwright & Magee 79* (JRAU). ***Polhillia* C.H.Stirton:** *P. brevicalyx* (C.H.Stirton) B.-E.van Wyk & A.L.Schutte— EU347954, —; *Van Wyk 2100* (JRAU). *P. canescens* C.H.Stirton— EU347957, —; *Van Wyk 2092* (JRAU). *P. involucratum* (Thunb.) B.-E.van Wyk & A.L.Schutte— EU347956, —; *Schutte 339* (JRAU). *P. obsoleta* (Thunb.) B.-E.van Wyk— EU347955, —; *Van Wyk 2701* (JRAU). *P. pallens* C.H.Stirton— EU347958, —; *Van Wyk 2095* (JRAU). ***Rafnia* Thunb.:** *R. acuminata* (E.Mey.) G.J.Campbell & B.-E.van Wyk— AM931036, AM931034 & AM931035; *Schutte 437* (JRAU). *R. angulata* Thunb.— EU347896, —; *Boatwright et al. 103* (JRAU). *R. capensis* (L.) Schinz— —, EU347742; *Boatwright & Magee 26* (JRAU). *R. diffusa* Thunb.— EU347895, AJ744944 [6]; *Campbell & Van Wyk 44* (JRAU). *R. globosa* G.J.Campbell & B.-E.van Wyk — EU347899, EU347743; *Boatwright et al. 180* (JRAU). *R. racemosa* Eckl. & Zeyh.— EU347895, EU347741; *Boatwright & Magee 29* (JRAU). *R. spicata* Thunb.— EU347897, EU347740; *Boatwright et al. 102* (JRAU). ***Robynsiophyton* R. Wilczek:** *R. vanderystii* R. Wilczek— EU347952, EU347878; *Lisowski 20326* (K). ***Rothia* Pers.:** *R. hirsuta* (Guill. & Perr.) Baker— EU347953, EU347877; *Saadou 1798* (K). ***Spartidium* Pomel:** *S. saharae* (Coss. & Dur.) Pomel— EU347931, EU347844; *Davis 49544* (K). ***Stirtonanthus* B.-E.van Wyk & A.L.Schutte:** *S. chrysanthus* (Adamson) B.-E.van Wyk & A.L.Schutte— AM259367 [1], AM268386 [1] & AM268387 [1]; *Van Wyk & Schutte 3297* (JRAU). ***Ulex* L.:** *U. europaeus* L.— Z70111 [3], —; *Botanical Garden Heidelberg, Germany.* ***Virgilia* Poir.:** *V. divaricata* Adamson— AM260737 [1], AJ409910 [7]; *Van Wyk 879–888* (JRAU). ***Wiborgia* Thunb.:** *W. fusca* Thunb. 1— EU347966, EU347744; *Schutte 736* (JRAU). *W. fusca* Thunb. 2— EU347967, EU347754; *Van Wyk et al. 4186* (JRAU). *W. humilis* (Thunb.) Dahlgren 1— EU347969, EU347752; *Boatwright et al. 129* (JRAU). *W. humilis* (Thunb.) Dahlgren 2— EU347970, EU347753; *Van Wyk 3530* (JRAU). *W. incurvata* Thunb.— EU347975, EU347751; *Boatwright et al. 188* (JRAU). *W. monoptera* E.Mey. 1— EU347971, EU347749; *Boatwright et al. 152* (JRAU). *W. monoptera* E.Mey. 2— EU347974, EU347750; *Boatwright et al. 153* (JRAU). *W. obcordata* (Berg.) Thunb. 1— EU347965, EU347746; *Van Wyk 2686* (JRAU). *W. obcordata* (Berg.) Thunb. 2— EU347972, EU347748; *Boatwright et al. 98* (JRAU). *W. sericea* Thunb.— EU347968, EU347755; *Boatwright et al. 124* (JRAU). *W. tetraptera* E.Mey. 1— EU347964, EU347745; *Schutte 737* (JRAU). *W. tetraptera* E.Mey. 2— EU347973, EU347747; *Boatwright et al. 104* (JRAU). ***Xiphotheca* Eckl. & Zeyh.:** *X. guthriei* (Bolus) A.L.Schutte & B.-E.van Wyk— AM260744 [1], AM261741 [1]; *Vlok & Schutte 4* (SCHG). *X. reflexa* (Thunb.) A.L.Schutte & B.-E.van Wyk— AM260747 [1], AM261744 [1]; *Schutte 760* (JRAU).

APPENDIX 2. List of morphological characters and character states used in the morphological analysis.

**1. Habit**— herbs or suffrutices = 0; shrubs = 1. **2. Persistence**— perennial = 0; annual = 1. **3. Young twigs**— without bark formation (bark formation late or absent) = 0; with bark formation (bark formation early) = 1. **4. Leaves**— digitate = 0; unifoliolate = 1; simple or phyllodinous = 2. **5. Lamina**— flat = 0; terete (acicular) = 1. **6. Petiole presence**— present = 0; absent (leaves sessile) = 1. **7. Petiole base**— normal or leaves sessile = 0; tuberculate or with persistent spur = 1. **8. Stipules presence**— present = 0; vestigial or absent = 1. **9. Stipules symmetry**— symmetrical or absent = 0; asymmetrical (dissimilar in size or single) = 1. **10. Bracteole presence**— present = 0; vestigial or absent = 1. **11. Standard petal vestiture**— hairy at least along the dorsal midrib = 0; totally glabrous = 1. **12. Keel shape**— not rostrate = 0; markedly rostrate or helically coiled = 1. **13. Calyx lower lobes**— with trifid lower lip = 0; without trifid lower ip = 1. **14. Calyx lateral lobes**— not fused higher up = 0; fused higher up = 1. **15. Anthers**— dimorphic = 0; uniform = 1. **16. Carinal anther**— resembling basifixed anthers = 0; intermediate = 1; resembling dorsifixed anthers = 2. **17. Gynoecium base**— sessile or subsessile = 0; stipitate = 1. **18. Style**— upcurved = 0; straight = 1; helically coiled = 2. **19. Style vestiture**— glabrous = 0; hairy = 1. **20. Fruit type**— not a samara = 0; fruit an ovoid, winged samara = 1. **21 Fruit upper suture**— upper suture straight or symmetrically convex = 0; upper suture asymmetrically convex = 1. **22. Fruit**— many-seeded = 0; few-seeded (1–2) = 1. **23. Funicle length**— normal length = 0; exceptionally long = 1. **24. Seed shape**— transversely oblong = 0; oblong = 1. **25. Seed surface**— smooth = 0; rugose = 1. **26. Chromosome base number**—7 = 0; 8 = 1; 9 = 2. **27. Cyanogenesis**— absent = 0; present = 1. **28. Quinolizidine and piperidyl alkaloids (Lysine pathway)**— present = 0; absent = 1. **29. Sparteine**— present = 0; absent = 1. **30. Lupanine type esters**— ±absent = 0; present as major alkaloid = 1. **31. Macrocyclic pyrrolizidine alkaloids**— absent = 0; present = 1.

## Appendix B4. Boatwright, J. S., P. M. Tilney and B.-E. van Wyk. 2008. A taxonomic revision of the genus *Rothia* (Crotalarieae, Fabaceae). *Australian Systematic Botany* 21(6): 422–430.

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# A taxonomic revision of the genus *Rothia* (Crotalarieae, Fabaceae)

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**Abstract.** *Rothia* Pers. is a genus of papilionoid legumes that consists of two species, *R. indica* (L.) Druce and *R. hirsuta* (Guill. & Perr.) Baker. The genus is a member of the tribe Crotalarieae and is widely distributed in Africa, Asia and Australia. Recent molecular systematic studies have shown the genus to be closely related to *Robynsiophyton* Wilczek and *Pearsonia* Dümmer; however, it is easily distinguished from these by its 10 small, rounded anthers and subequally lobed calyx (as opposed to the large, elongate anthers of *Pearsonia* or the 9 stamens of *Robynsiophyton*). These three genera share characters such as uniform anthers, straight styles and the presence of angelate esters of lupanine-type alkaloids. Leaf and fruit anatomy of *Rothia* and *Robynsiophyton* were also studied but revealed no informative differences. Both genera have dorsiventral leaves with mucilage cells in the epidermis and thin-walled fruits. A taxonomic revision of *Rothia* is presented, including a key to the species, correct nomenclature, descriptions, illustrations and distribution maps.

## Introduction

The genus *Rothia* Pers. was described in 1806 and comprises two species, *R. hirsuta* (Guill. & Perr.) Baker and *R. indica* (L.) Druce. The species have been treated in several floristic studies (e.g. The Flora of Tropical Africa (Baker 1926), Flora of West Tropical Africa (Hepper 1958), Flora of Tropical East Africa (Milne-Redhead 1971), Flora Zambesiaca (Polhill 2003), A revised Handbook of the Flora of Ceylon (Rudd 1991)); however, no comprehensive revision of the genus exists. An Australian-endemic subspecies of *R. indica*, namely *R. indica* (L.) Druce subsp. *australis* A.E.Holland, was described by Holland (1997). It is morphologically distinct from the typical Asian subspecies.

The genus is a member of the Papilionoideae and is placed within the tribe Crotalarieae. The Crotalarieae form part of a monophyletic assemblage of tribes, the 'core' genistoid legumes (Crisp *et al.* 2000; Boatwright *et al.* 2008*a*), which comprises the Crotalarieae, Euchresteae, Genisteae, Podalyrieae, Sophoreae (in part) and Thermopsideae. The Crotalarieae are subendemic to Africa, with a few species of *Crotalaria* L., *Lotononis* (DC.) Eckl. & Zeyh. and *Rothia* extending to other continents. A recent study of the tribe by Boatwright *et al.* (2008*b*), based on gene sequences (ITS and *rbcL*) and morphological data, showed *Rothia* to be in a well supported clade along with *Pearsonia* Dümmer and *Robynsiophyton* Wilczek, i.e. the *Pearsonia* clade. A sister relationship between *Robynsiophyton* and *Rothia* was strongly supported (Fig. 1). This confirmed hypotheses by Polhill (1976), Van Wyk (1991*a*) and Van Wyk and Schutte (1995) who suggested an affinity between these genera. The close relationship between *Pearsonia*, *Robynsiophyton* and *Rothia* is supported by three synapomorphies, i.e. uniform anthers, straight or down-curved styles and the presence of angelate esters of lupanine-type alkaloids. *Rothia* can be distinguished from *Pearsonia* and *Robynsiophyton* by its 10 small, rounded anthers and subequally lobed calyx.

In this paper we present a taxonomic account of *Rothia*, with illustrations, descriptions and distribution maps of the species. The results of anatomical studies of the leaves and fruits of *Rothia* and *Robynsiophyton* are also presented.

## Materials and methods

### Morphology

Morphological characters were assessed through the study of material from the following herbaria: BM, BOL, K, MEL, NBG (including SAM), PRE, S, UPS (abbreviations according to Holmgren *et al.* 1990). Drawings of reproductive features (all by JSB) were done by using a stereoscope (WILD M3Z) with a camera *lucida* attachment.

### Anatomy

Two or three samples per species of the leaves and fruits of *Rothia* and *Robynsiophyton* were studied. Dried material was first rehydrated and then fixed in formaldehyde : acetic acid : 96% alcohol : water (10 : 5 : 50 : 35; FAA) for 24 h. The method of Feder and O'Brien (1968) for embedding in glycol methacrylate (GMA) was used except that the final infiltration in GMA was done for a minimum of 5 days. Sections were stained according to the periodic acid Schiff/toluidine blue (PAS/TB) staining method and mounted. Photographs were taken with a JVC KY-F1030 digital camera.

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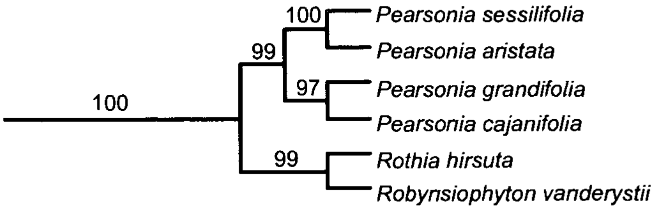

**Fig. 1.** The *Pearsonia* clade taken from a strict consensus of 370 trees, showing the relationship between *Pearsonia*, *Robynsiophyton* and *Rothia*, based on the combined analysis of molecular (ITS and *rbcL*) and morphological data (from Boatwright *et al.* 2008*b*; tree length = 1166; consistency index = 0.53; retention index = 0.84). Numbers above the branches are bootstrap percentages above 50%.

## Results and discussion

### Generic relationships

In the study of Boatwright *et al.* (2008*b*), the *Pearsonia* clade is well separated from the 'Cape' group of the Crotalarieae (*Aspalathus* L., *Lebeckia* Thunb., *Rafnia* Thunb., *Spartidium* Pomel and *Wiborgia* Thunb.) and placed closer to *Lotononis*, a genus with which they share the lotononoid or zygomorphic calyx. However, the three genera of the *Pearsonia* clade possess a 17 base-pair deletion at positions 179–196 in the aligned ITS matrix and unique floral characters such as straight styles and uniform anthers. The *Crotalaria* clade (*Bolusia* Benth., *Crotalaria* and *Lotononis* section *Euchlora* (Eckl. & Zeyh.) B.-E.van Wyk) is early diverging within the Crotalarieae and all members of this clade have strongly inflated pods (Boatwright *et al.* 2008*b*).

Van Wyk (2003) discussed the importance of chemical characters in genistoid legumes and mentioned that their distribution is not random, but in fact provides reliable information supporting phylogenetic relationships retrieved by studies of DNA sequence data. The *Pearsonia* clade is chemically distinct within the tribe Crotalarieae in having unique alkaloids (Van Wyk and Verdoorn 1990; Van Wyk 1991*a*, 2005; Van Wyk and Schutte 1995). *Pearsonia*, *Robynsiophyton* and *Rothia* produce tetracyclic quinolizidine alkaloids such as lupanine, together with angelate esters such as lupanine-13α-angelate, cajanifoline, sessilifoline and pearsonine (Hussain *et al.* 1988; Van Wyk and Verdoorn 1989, 1991). These chemical characters are especially useful in distinguishing this clade from the morphologically similar genus *Lotononis* where pyrrolizidine and quinolizidine alkaloids are present but where no esters of lupanine-type alkaloids are found (Van Wyk 1991*b*). Also, some sections of *Lotononis* are cyanogenic, a trait which is unique within Crotalarieae (Van Wyk 1991*b*).

### Vegetative morphology and anatomy

The species of *Rothia* are prostrate to procumbent or erect annuals. They share this life history with the monotypic African *Robynsiophyton*. This character lends support to the sister relationship found between these genera by Boatwright *et al.* (2008*b*) and distinguishes them from the closely related genus *Pearsonia* which consists of perennial herbs or shrubs.

The leaves of *Rothia* are digitately trifoliolate as in many of the Crotalarieae, and pubescent both adaxially and abaxially. *R. indica* subsp. *australis* has densely pubescent leaves with long whitish hairs that are more or less spreading. In contrast, the leaves of *R. indica* subsp. *indica* are moderately hairy with shorter, more or less appressed hairs. The stipules of *R. hirsuta* are linear to slightly falcate and single at each node, whereas those of *R. indica* are elliptic to lanceolate or ovate and invariably paired.

Anatomical studies of the lamina (Fig. 2*a*, *b*) and petiole (Fig. 2*c*, *d*) revealed no informative differences between *R. hirsuta* and *R. indica*, or even between these and *Robynsiophyton vanderystii* Wilczek. The leaves are dorsiventral with mucilage cells present in the epidermis in both *Rothia* and *Robynsiophyton* (Fig. 2*a*, *b*). These cells are thought to contribute to the retention of water and reduction of transpiration, although their function has not been accurately ascertained (Gregory and Baas 1989).

### Reproductive morphology and anatomy

Both species of *Rothia* have axillary racemes. *R. hirsuta* has up to seven flowers per raceme as opposed to *R. indica* where up to four flowers per raceme are found, although the flowers are often solitary or in pairs. Terminal racemes are found in most genera of the Crotalarieae (Polhill 1976) and they are either terminal or axillary in *Pearsonia* and strictly axillary in *Rothia* and *Robynsiophyton*. Bracts are present in *Rothia*, but bracteoles are lacking. Bracteoles are also absent in *Robynsiophyton* and most species of the genus *Lotononis*, but present in almost all *Pearsonia* species.

The flowers of *Rothia* and its relatives are relatively unspecialised compared with the rest of the Crotalarieae. *Rothia*, *Robynsiophyton* and *Pearsonia* have a 'gullet'-type flower where the style is straight or down-curved and the anthers uniform and/or further reduced, as opposed to the more specialised and reflexed floral parts found in the other crotalarioid genera (Polhill 1976). In *Rothia* the two upper calyx lobes are larger than the other three lobes and distinctly falcate. The calyces of *Pearsonia* species have the upper sinus often shallower than the others or in some species the lateral sinus is the shallowest with the carinal lobe always narrower than the other lobes (Polhill 1974). *Robynsiophyton* differs from both these genera in having an equally lobed calyx (J. S. Boatwright and B.-E. van Wyk, unpubl. data).

The most useful generic character to distinguish among *Pearsonia*, *Robynsiophyton* and *Rothia* is the androecium. These genera are unique within the Crotalarieae in having uniform anthers, as opposed to the dimorphic anthers found in other genera of the tribe with alternating basifixed and dorsifixed anthers (Polhill 1976). The anthers of *Pearsonia* are elongate and large, whereas in *Rothia* and *Robynsiophyton* they are small and rounded (Fig. 3). *Robynsiophyton* has a reduced number of stamens (9 rather than 10) and four anthers are infertile (Fig. 3). Although the generic concepts of *Rothia* and *Robynsiophyton* have been questioned by previous authors, the informative value of androecial characters (the main distinction among these three genera) at both tribal and generic level is usually closely correlated with relationships suggested by both molecular and morphological data (Polhill 1976; Boatwright *et al.* 2008*b*) and should be taken at face value as strong, sound generic apomorphies.

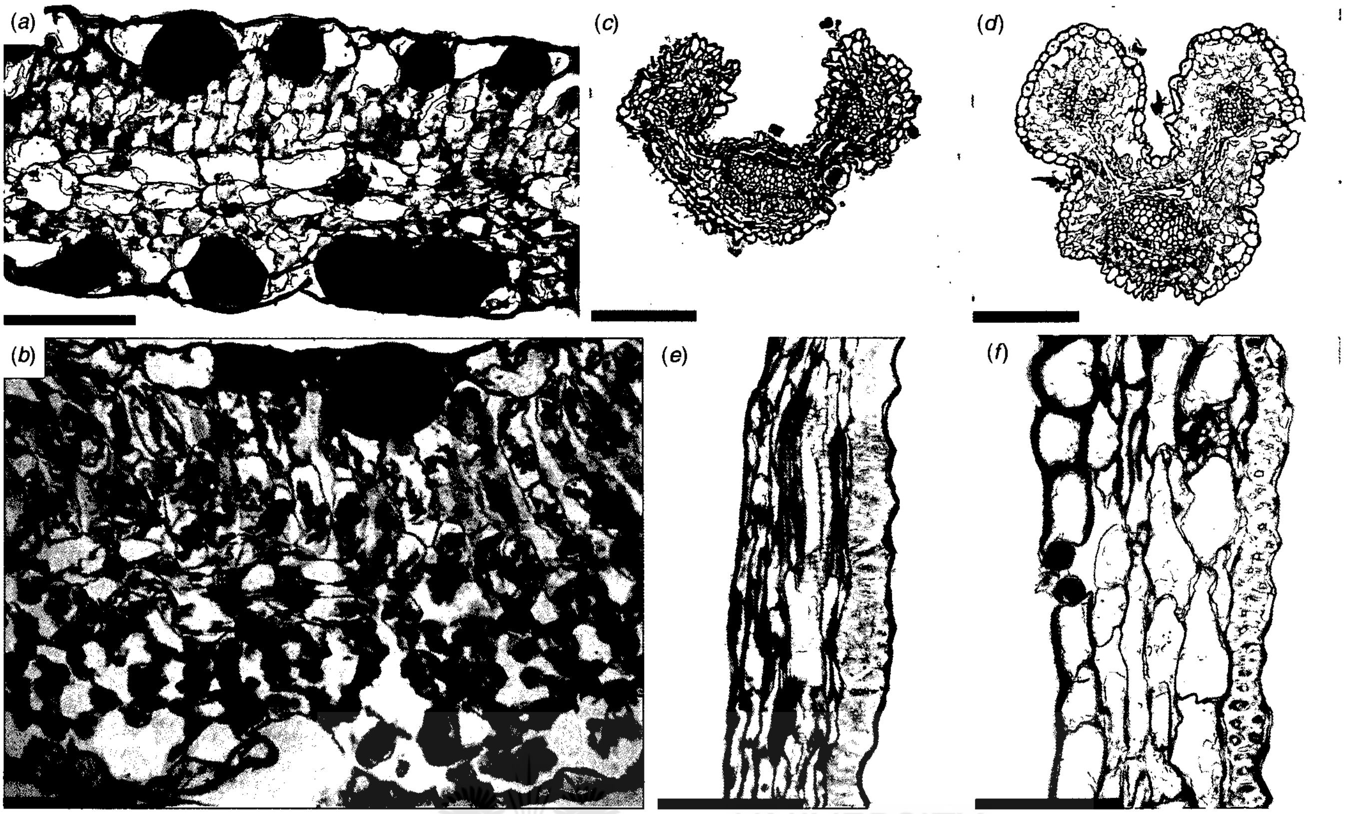

**Fig. 2.** Transverse sections through the leaves and fruit of *Rothia* and *Robynsiophyton*. (*a*) Portion of leaf of *Robynsiophyton vanderystii* (scale bar = 0.1 mm). (*b*) Portion of leaf of *Rothia indica* (scale bar = 0.1 mm). (*c*) Petiole of *Robynsiophyton vanderystii* (scale bar = 0.2 mm). (*d*) Petiole of *Rothia indica* (scale bar = 0.2 mm). (*e*) Portion of fruit wall of *Robynsiophyton vanderystii* (scale bar = 0.07 mm). (*f*) Portion of fruit wall of *Rothia indica* (scale bar = 0.07 mm). Voucher specimens. (*a, e*) *Lisowski 20326* (K). (*b, d, f*) *Latz 16126* (MEL). (*c*) *Exell & Mendonça 657* (K).

The pods of *Rothia hirsuta* are ovate to falcate and much shorter and fewer-seeded (up to 18 mm long with ±25 seeds) than the linear pods of *R. indica* that are up to 55 mm long with ±35 seeds. The pods of *Rothia* and *Robynsiophyton* are thin-walled and sclerified on the inner surface, with no apparent anatomical differences (Fig. 2*e*, *f*).

*Rothia indica* and *Robynsiophyton* have similar-sized seeds that are larger than those of *Rothia hirsuta* (J. S. Boatwright and B.-E. van Wyk, unpubl. data). The seeds of the latter are light brown with dark mottling and have a rugose surface, in contrast to the brown, smooth seeds of *Rothia indica* and *Robynsiophyton vanderystii*.

## Taxonomic treatment

### Key to the genus *Rothia*

1. Anthers dimorphic, styles upcurved ............................ other Crotalarieae
   Anthers uniform, styles straight or down-curved .................................. 2
2. Perennial herbs or small shrubs, anthers large and elongate ....*Pearsonia*
   Annual herbs, anthers small and rounded ............................................ 3
3. Upper two calyx lobes larger than others (calyx subequally lobed), stamens 10, all fertile ................................................................ *Rothia*
   Upper two calyx lobes similar to others (calyx equally lobed), stamens nine, five fertile, four reduced and infertile ................ *Robynsiophyton*

***Rothia*** Pers., *Syn. Pl. 2*: 302, 638 (1807). *nom. conserv.*; Benth. in Hook., *Lond. J. Bot. 3*: 338 (1844); Benth. & Müller, *Fl. Austral. 2*: 185 (1864); Baker, *Fl. Trop. Africa*: 7 (1871); Trimen, *Handb. Fl. Ceylon*: 7 (1894); Thonner, *Flowering Plants of Africa*: 274 (1915); Baker, *Leg. Trop. Africa*: 21 (1926); Hutchinson & Dalziel, *Fl. West Trop. Africa*: 543 (1954); Hutchinson, *The Genera of Flowering Plants*: 361 (1964); D'Orey & Liberato, *Fl. Guine Portuguesa*: 71 (1971); Polhill in *Bot. Syst. 1*: 326 (1976); Thulin in *Op. Bot.* 68: 153 (1983); Hedberg & Edwards, *Fl. Ethiopia*: 195 (1989); Rudd, *A Revised Handbook to the Flora of Ceylon*: 184 (1991); Van Wyk & Schutte, *Advances in Legume Systematics 7*, M. D. Crisp & J. J. Doyle (Eds): 306 (1995); Leistner, *Seed Plants of Southern Africa: Families and Genera*: 295 (2000); Du Puy *et al.*, *The Leguminosae of Madagascar*: 671 (2002); Polhill, *Fl. Zambesiaca*: 64 (2003); Leistner, *Seed Plants of Southern Tropical Africa: Families and Genera*: 202 (2005); Van Wyk in *Legumes of the World*, Lewis *et al.* (Eds), 281 (2005)

*Type species*: *R. trifoliata* (Roth) Pers. (= *Dillwynia trifoliata* Roth).

*Dillwynia* Roth, *Catal. Bot.* 3: 71 (1806) non *Dillwynia* Sm. in Koenig & Sims, Ann. Bot. 1: 510 (1805). *Type species: D. trifoliata* Roth.

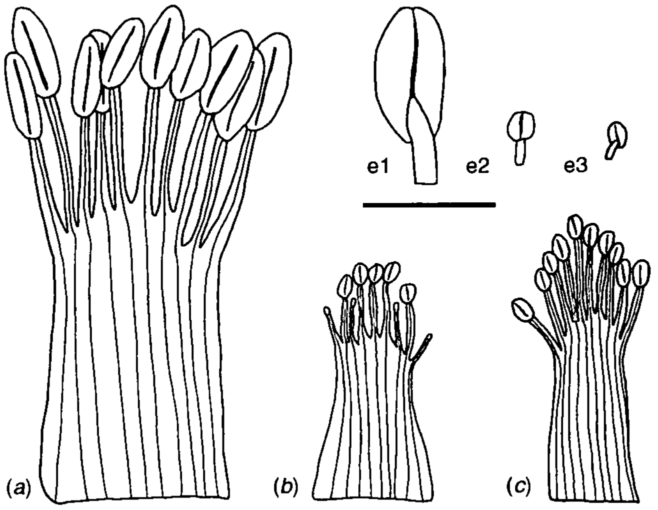

**Fig. 3.** (*a*, e1) Androecia and anthers of *Pearsonia*, (*b*, e2) *Robynsiophyton* and (*c*, e3) *Rothia*. Voucher specimens: (*a*, e1) *Swanepoel 1* (JRAU), (*b*, e2) *McCallum Weston 717* (K), (*c*, e3) *Greenway & Kanuri 14269* (K). All scale bars represent 1 mm.

*Westonia* Spreng., *Syst. Veg.* 3: 152, 230 (1826) *nom. illeg. Type species: W. humifusa* (Willd.) Spreng.

*Goetzea* Reichb., *Consp. Regn. Veg.*: 150 (1828) *nom. rej.*

*Xerocarpus* Guill. & Perr., *Fl. Seneg. Tent.*: 169 (1832). *Type species: X. hirsutus* Guill. & Perr.

*Harpelema* J.Jacq., *Ecl. Pl. Rar.* 2: t. 129 (1844). *Type species: H. dillwynia* J.Jacq.

Prostrate, annual herbs. Branches up to 40 cm long, densely to sparsely pubescent. Leaves digitately trifoliolate, elliptic to oblanceolate or obovate, pubescent; leaflets subsessile, apex apiculate, obtuse or slightly acute, base cuneate; petioles shorter than leaflets, pubescent. Stipules linear to slightly falcate or elliptic to lanceolate or ovate, single in *R. hirsuta*, paired in *R. indica*, pubescent. Inflorescence axillary, racemose, flowers solitary or up to 7 per raceme; pedicel up to 2 mm long; bract linear, pubescent, caducous; bracteoles absent. Flowers pale yellow to white. Calyx pubescent, subequally lobed; lobes triangular to lanceolate, upper lobes wider than others, falcate, carinal lobe slightly narrower than others, tips minutely pubescent inside. Standard elliptic to ovate, pilose along dorsal midrib; claw linear; apex obtuse. Wing petals oblong to obovate, glabrous, with 2 or 3 rows of sculpturing, as long as keel; apex obtuse. Keel boat-shaped, glabrous, pocket sometimes present; apex obtuse. Stamens 10, anthers uniform, sub-basifixed. Pistil subsessile, pubescent; ovary linear to narrowly ovate; style straight, glabrous. Pods linear to ovate or falcate, laterally compressed, subsessile, many-seeded, pubescent, dehiscent. Seeds oblique-cordiform, brown or brown mottled with dark brown, surface smooth or rugose.

*Etymology*: the genus is named in honour of the German physician and botanist Albrecht Wilhelm Roth (1757–1834).

*Diagnostic characters*: *Rothia* can be distinguished from *Robynsiophyton* in that the latter has an equally lobed calyx (in *Rothia* the upper two lobes are larger than the others) and in that there are 10 stamens with 10 fertile anthers in *Rothia* (in *Robynsiophyton* the stamens are reduced to nine and only five anthers are fertile). Furthermore, it differs from *Pearsonia* by its subequally lobed calyx and small, rounded anthers in contrast to the 'lotononoid' calyx (zygomorphic owing to the fusion of the upper and lateral lobes on either side) and large, elongate anthers of *Pearsonia*.

*Chromosome number*: a count of $n = 7$ has been reported for *Rothia indica* (Goldblatt 1981; Bairiganjan and Patnaik 1989).

*Distribution*: the genus occurs in tropical Africa, Asia and Australia (Figs 5 and 7). It appears to have been well collected in areas for which regional floras have been compiled, e.g. the Flora of Tropical East Africa and Flora of West Tropical Africa.

## Key to the species of *Rothia*

1. Stipules linear and single at each node, up to 7 flowers per inflorescence, pods ovate to falcate and up to 18 mm long, seeds light brown with dark mottling and a rugose surface, Africa and Madagascar.... 1. *R. hirsuta*

Stipules elliptic to lanceolate or ovate and paired at each node, up to 4 flowers per inflorescence, pods linear or slightly falcate and up to 55 mm long, seeds brown with a smooth surface, Asia and Australia .......................................................................... 2. *R. indica*

**1. *Rothia hirsuta*** (Guill. & Perr.) Baker in *Fl. Trop. Africa* 2: 7 (1871); Eyles in *Trans. Roy. Soc. South Africa* 5: 369 (1916); E.G.Baker, *Leg. Trop. Africa*: 21 (1926); Broun & Massey, *Fl. Sudan*: 176 (1929); Andrews, *The Flowering Plants of the Anglo-Egyptian Sudan*: 230 (1952); Hepper in *Fl. West Trop. Africa*, ed. 2, 1: 543 (1958); Torre, *Consp. Fl. Angolensis* 3: 5 (1962); White, *Forest Fl. Northern Rhodesia*: 164 (1962); Schreiber in Merxmüller, *Prodr. Fl. SW. Africa*, fam. 60: 107 (1970); Milne-Redhead, *Fl. Trop. East Africa*, Leguminosae, Pap.: 811 (1971); Drummond in *Kirkia* 8: 226 (1972); Thulin in *Op. Bot.* 68: 153 (1983); Hedberg & Edwards, *Fl. Ethiopia*: 195 (1989); Du Puy *et al.*, *The Leguminosae of Madagascar*: 671 (2002)

*Xerocarpus hirsutus* Guill. & Perr. in Guillemin, Perrottet & Richard, *Fl. Seneg. Tent.*: 44 (1832). *Type*: Senegal, *Leprieur s.n.* lecto (here designated) P (photo seen).

[Note: according to Stafleu and Cowan (1983) the type material of Perrottet is housed in P or G. No specimens were traced in G and we therefore designate the Paris specimen as lectotype.]

*Amphinomia desertorum* (Dümmer) Schreiber in *Mitt. Bot. München* 2: 286 (1957); *Lotononis desertorum* Dümmer in *Trans. Roy. Soc. S. Africa* 3: 316 (1913). *Type*: Great Barmen, Buschsteppe, 23. iv.1907, *Dinter 518*; lecto (here designated) Z (photo seen), isolecto BM!, BOL!, NBG!, K!

[Note: Dümmer was based at K during his revision of *Lotononis*. However, the K isotype is a small piece taken from the specimen in Z (as annotated by Dümmer himself). The Z specimen is therefore chosen as lectotype.]

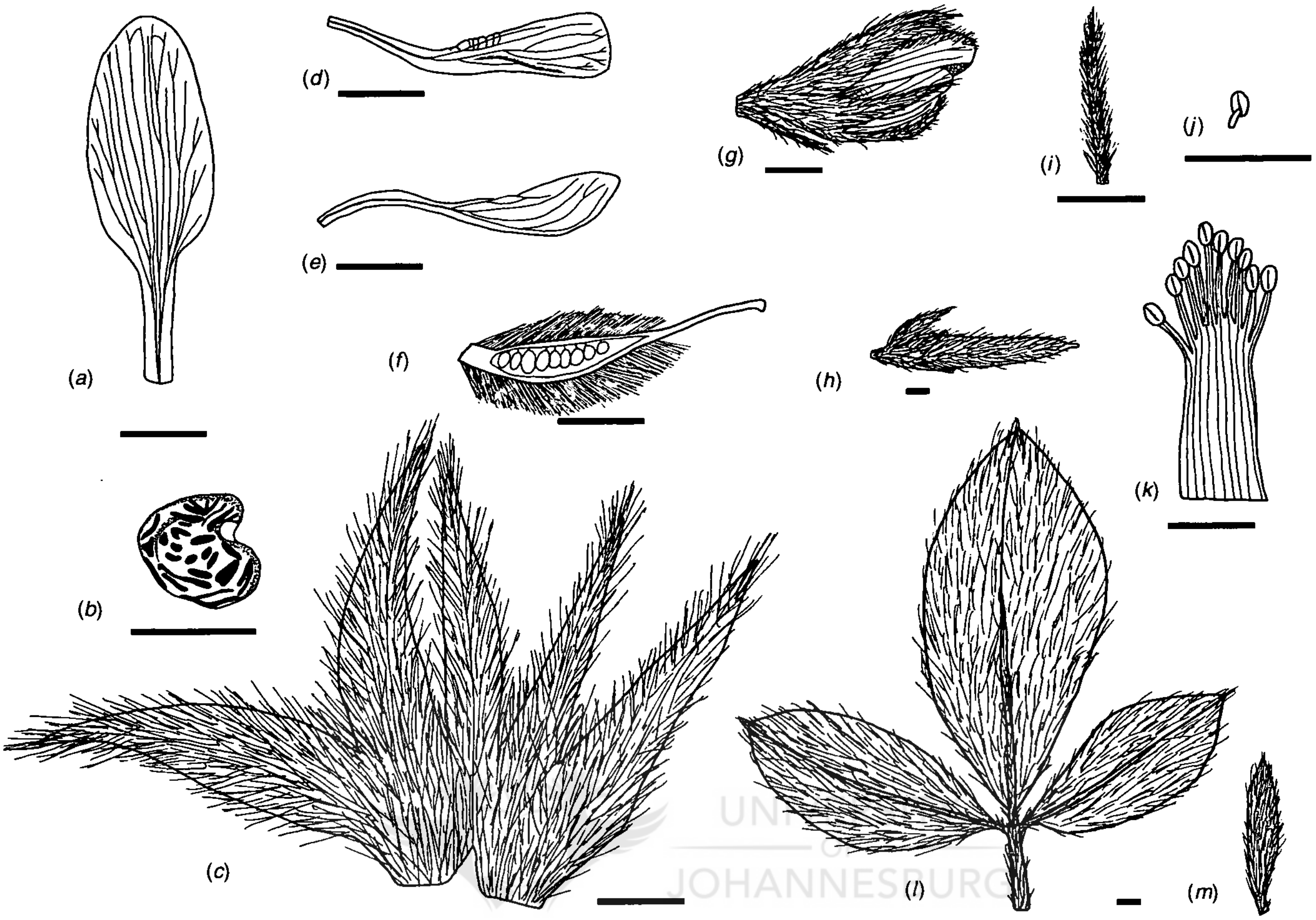

**Fig. 4.** Morphology of *Rothia hirsuta*. (*a*) Standard petal. (*b*) Seed in lateral view. (*c*) Outer surface of the calyx (upper lobes to the left). (*d*) Wing petal. (*e*) Keel petal. (*f*) Pistil. (*g*) Flower in lateral view. (*h*) Pod in lateral view. (*i*) Bract. (*j*) Anther. (*k*) Androecium. (*l*) Leaf in abaxial view. (*m*) Stipule. Voucher specimens. (*a, c*) *Davey 173* (K). (*b*) *Milne-Redhead & Taylor 11245* (K). (*d, g, h, j, k*) *Greenway & Kanuri 14269* (K). (*e*) *Jackson & Apejoye 413973* (K). (*f*) *Hepper 1021* (K). (*i*) *Polhill & Paulo 2089* (K). (*l, m*) *Siame 162* (K). All scale bars represent 1 mm.

Small, pubescent, prostrate or semi-erect to procumbent herb. Branches ±10–40 cm long, brown, sparsely hairy (pilose). Leaves with leaflets elliptic to oblanceolate, terminal leaflet 10–30 mm long, 3.5–12.0 mm wide, lateral leaflets 6–20 mm long, 2–7 mm wide; apex apiculate; base cuneate; petiole 3–13 mm long. Stipules linear to slightly falcate, 2–8 mm long, single. Inflorescence with 2–7 flowers; pedicel up to 1 mm long; bract 1.0–2.5 mm long. Flowers 4–8 mm long. Calyx 5–7 mm long; tube 1.5–2.0 mm long; lobes 3–4 mm long. Standard 4.0–5.5 mm long; claw 1.0–1.5 mm long; lamina 3.0–4.5 mm long, 1–2 mm wide. Wings 4–5 mm long; claw 1.5–2.0 mm long; lamina 2.5–4.0 mm long, 0.5–0.7 mm wide. Keel 2.5–4.0 mm long; claw 1.5–2.0 mm long; lamina 1–3 mm long, 0.5–1.0 mm wide. Pistil with ovary narrowly ovate, 2–3 mm long, 0.5–0.7 mm wide with ±7–13 ovules; style 1.3–1.6 mm long. Pods ovate, falcate, tapering towards apex, 10–18 mm long, 2–3 mm wide with up to ±25 seeds per pod. Seeds 1.1–1.5 mm long, 0.8–1.1 mm wide, mature seeds light brown with dark mottling, surface rugose (Fig. 4).

*Distribution and ecology*: widespread in the dry parts of tropical Africa from South Africa north to Eritrea and west up to Guinea (Fig. 5). Occurs on sandy loam or clay soils, often in grassland or forest openings. Common on sandy soils along watercourses or disturbed roadsides.

*Diagnostic characters*: the linear stipules are invariably single at each node in *Rothia hirsuta*, whereas they are paired and elliptic to ovate in *R. indica*. The inflorescences are more densely flowered (up to 7 flowers) in *R. hirsuta* than in *R. indica* where the flowers are often solitary or up to 4 per inflorescence. The linear pods of *R. indica* are three times longer (up to 55 mm) than the ovate pods of *R. hirsuta* that are only up to 18 mm long. In *R. hirsuta* the seeds are brown with dark mottling and have a rugose surface, whereas those of *R. indica* are brown (unmottled) with a smooth surface.

*Flowering period*: *R. hirsuta* flowers mainly from February to November, but flowering and fruiting specimens have been recorded throughout the year.

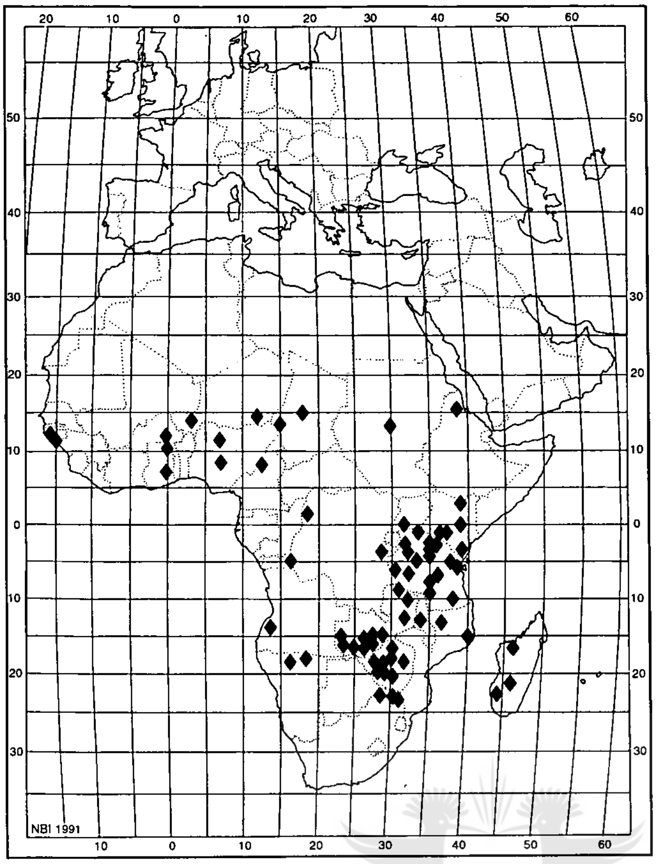

**Fig. 5.** Known geographical distribution of *Rothia hirsuta*.

*Selected specimens (150 specimens examined)*

ERITREA: Bocos, Cheren, *Pappi 2527*, 10.xi.1902 (BM 2 sheets, K). SUDAN: Kordofan, *Kotsch 420*, without date (K). CHAD: Dioura, Macina, *Davey 173*, Oct. 1954 (K). NIGER: Niamey, *Olufsen 476*, 8.x.1947 (BM, S). GUINEA: Guine-Bissau, Pussuli, *Santos 1438*, 17.xii.1942 (K). BURKINA FASO: Haute Volta, Lergo, *Ake Assi 13587*, 13.xi.1976 (K). GHANA: Tefle, on Volta River, *Akpabla 1982*, 13.8.1959 (K). NIGERIA: Naraguta, Jos Plateau, rough ground near Forestry Department, among grass, *Hepper 1021*, 14.x.1957 (K). CAMEROON: Ganglani village, 6 miles [9.65 km] from confluence of Kam and Kimiri Rivers, Vogel Peak area, *Hepper 1441*, 23.xi.1957 (K). DEMOCRATIC REPUBLIC OF CONGO: 50 km NE of Mokolo, on route to Mora, *Bounougou 173*, 18.ix.1964 (K, S). UGANDA: Matuga, *Robertson 3312*, 29.vii.1982 (K). KENYA: Thika–Garissa road, 2.6 km towards Garissa after junction with Kitui Rd, near Kongonde, *Faden & Faden 74/737*, 7.vi.1974 (K, PRE). TANZANIA: Imagi Hill, 1 mile [1.61 km] S of Dodoma, *Polhill & Paulo 2089*, 20.iv.1962 (K, PRE). ZAMBIA: Livingstone, Chief Mukuni area, 2.1 km along road to Chief Mukuni Palace from junction with Victoria Falls Rd in Baikiae forest, *Zimba et al. 913*, 19.ii.1997 (K). MALAWI: Lilongwe, *Banda 250*, 14.ix.1956 (BM). MOZAMBIQUE: Niassa, Mossuril para Lumbo, 4.5 km na estrada de Nampula, *Pedro & Pedrogao 3131*, 5.v.1948 (K, PRE). ANGOLA: Huilla, *Welwitsch 1904*, Apr. 1860 (K, BM). NAMIBIA: grey sandy flats below Musese Camp, W of Lupala Mission Station, *De Winter & Marais 4978*, 4.iii.1969 (K). ZIMBABWE: Gwanda, Sezane Reservoirs, *Davies 1296*, May 1955 (K, PRE). SOUTH AFRICA: Kruger NP, Punda Milia, *Van Rooyen 494*, 19.iii.1976 (PRE). MADAGASCAR: Ankazoabo, *Bosser 17241*, Feb. 1963 (K).

2. ***Rothia indica*** (L.) Druce in *Bot. Exch. Club Soc. Brit. Isles* 3: 423 (1914); Rudd, *A Revised Handbook to the Flora of Ceylon*: 184 (1991); Holland, *Austrobaileya* 5: 93 (1997); *Trigonella indica* L., Sp. *Pl. 2*: 778 (1753)

*Type*: Herb. Hermann 3: 24 no. 285 BM-000621888, lecto (designated by Rudd 1991) BM (photo seen).

*Lotus indicus* Desr. in Lam., *Encyc.* 3: 606 (1759). *Type:* as for *T. indica.*

*Hosackia indica* Graham in Wallich, *Numer. List* n. 5940 (1831–1832). *nom. nud.*

*Glycine leptocarpa* Graham in Wallich, *Numer. List* n. 5515 (1831–1832). *nom. nud.*

*Rothia trifoliata* (Roth) Pers., *Syn. Pl.* 2: 638 & 659 (1807); Benth. in Hook., *Lond. J. Bot. 3*: 339 (1844); Bentham & Müller, *Fl. Austr. 2*: 185 (1864); Trimen, *Handb. Fl. Ceylon*: 7 (1894); *Dillwynia trifoliata* Roth, *Catal. Bot.* 3: 71 (1806). *Type*: 'horto medico Amsteledamensi' (B†?).

Small, pubescent, prostrate, herb. Branches up to 40 cm long, brown, either covered with dense, woolly hairs or sparsely hairy (pilose). Leaves with leaflets elliptic to obovate, terminal leaflet (7–)9–26 mm long, (2–)3–5 mm wide, lateral leaflets (5–)8–20 mm long, (1.5–)2.5–6.0 mm wide; apex obtuse or slightly acute; base cuneate; petiole 4–13 mm long. Stipules elliptic to lanceolate or ovate, 2–8(–10) mm long, paired. Inflorescence with flowers solitary or up to 4 per raceme; pedicel up to 2 mm long; bract 1–3 mm long. Flowers 5–8 mm long. Calyx 4–7 mm long; tube 1.5–4.0 mm long; lobes 1–4 mm long. Standard 4.0–6.5 mm long; claw 1.5–2.5 mm long; lamina 2.5–4.0 mm long, 2.0–2.5 mm wide. Wings 4.0–6.5 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.5 mm long, 1.0–1.5 mm wide. Keel 4.0–6.5 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.5 mm long, 1.0–1.5 mm wide. Pistil with ovary linear, 3.0–4.5 mm long, 0.5–1.0 mm wide with ±13–18 ovules; style 1.4–1.7 mm long. Pods linear or slightly falcate, (30–)35–55 mm long, 1.5–3.0 mm wide with up to ±35 seeds per pod. Seeds 1.3–1.8 mm long, 1.0–1.3 mm wide, mature seeds brown, surface smooth (Fig. 6).

*Distribution and ecology*: occurs in India, Sri Lanka, China, Vietnam, Malaysia and Australia (Fig. 7).

*Diagnostic characters*: the paired, ovate stipules, sparse inflorescences, long, linear pods and smooth, brown seeds distinguish *Rothia indica* from *R. hirsuta*.

*Flowering period*: flowering and fruiting all year round from January to December.

*Notes*: two subspecies can be recognised based predominantly on their geographical distribution, size and pubescence of vegetative and reproductive parts.

1. Vegetative parts sparsely hairy, terminal leaflets (7–)10–26 × (2–) 4–8 mm, lateral leaflets (5–)8–20 × (1.5–)3.0–6.0 mm, petiole 5–13 mm long, stipules elliptic to lanceolate 2–8(–10) mm long, pods (–33)35–55 × (1.5–)2.0–3.0 mm, seeds 1.3–1.6 × 1.0–1.3 mm, India, Sri Lanka, China, Vietnam and Malaysia .................. 2a. subsp. *indica*

Vegetative parts covered with dense, woolly hairs, terminal leaflets 9–15 × 3–5 mm, lateral leaflets 9–12 × 2.5–4.0 mm, petiole 4–8 mm long, stipules elliptic to ovate 2–5 mm long, pods (30–)35–45 × 1.5–2.0 mm, seeds 1.5–1.8 × 1.2–1.3 mm, restricted to Australia .............................................................. 2b. subsp. *australis*

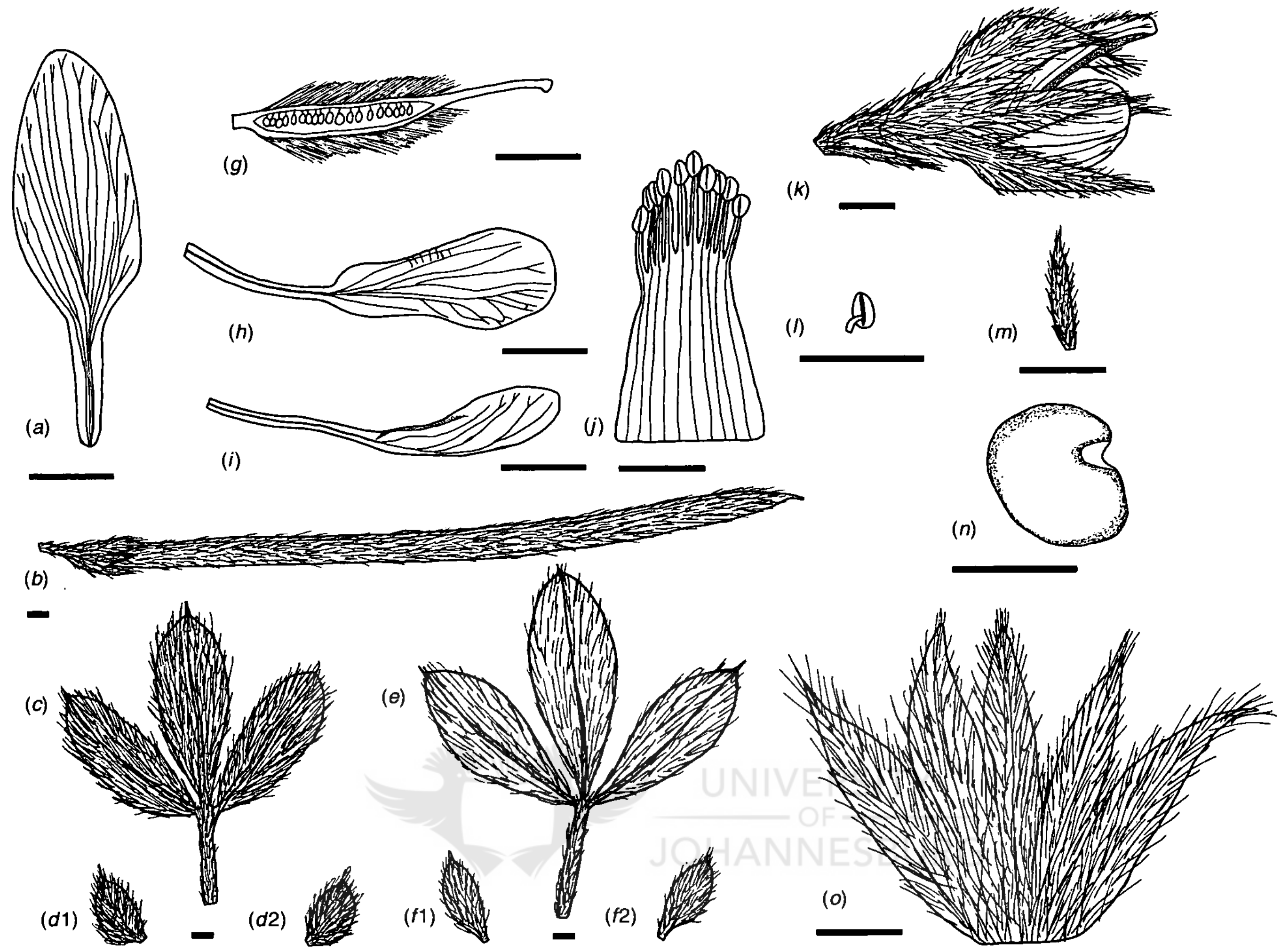

**Fig. 6.** Morphology of *Rothia indica*. (*a*) Standard petal. (*b*) Pod in lateral view. (*c*) Leaf of *R. indica* subsp. *australis* in abaxial view. (*d1, d2*) Stipules of *R. indica* subsp. *australis*. (*e*) Leaf of *R. indica* subsp. *indica* in abaxial view. (*f1, f2*) Stipules of *R. indica* subsp. *indica*. (*g*) Pistil. (*h*) Wing petal. (*i*) Keel petal. (*j*) Androecium. (*k*) Flower in lateral view. (*l*) Anther. (*m*) Bract. (*n*) Seed in lateral view. (*o*) Outer surface of the calyx (upper lobes to the left). Voucher specimens. (*a, g, h, i, k*) *Cooray 70020117R* (K). (*b, n*) *Gamble 13771* (K). (*c, d1, d2*) *Latz 16126* (MEL). (*e, f1, f2*) *Barber 55* (K). (*j, l, o*) *Wight 828*. (K). (*m*) *Wight 571* (K). All scale bars represent 1 mm.

## 2a. *Rothia indica* (L.) Druce subsp. *indica*

Leaves with terminal leaflet (7–)10–26 long, (2–)4–8 mm wide, lateral leaflets (5–)8–20 mm long, (1.5–)3.0–6.0 mm wide; petiole 5–13 mm long. Stipules elliptic to lanceolate, 2–8(–10) mm long. Inflorescence with flowers solitary or 2–4 per raceme. Calyx 5.0–6.5 mm long; tube 2–4 mm long; lobes 1–3 mm long. Standard 4.0–6.5 mm long; claw 1.5–2.0 mm long; lamina 2.5–4.0 mm long, 2.0–2.5 mm wide. Wings 4–6 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.0 mm long, 1.0–1.5 mm wide. Keel 4–6 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.0 mm long, 1.0–1.5 mm wide. Pistil with ovary 3–4 mm long, 0.5–0.7 mm wide with ±14–18 ovules; style 1.4–1.6 mm long. Pods (–33)35–55 mm long, (1.5–)2.0–3.0 mm wide with up to ±35 seeds per pod. Seeds 1.3–1.6 mm long, 1.0–1.3 mm wide.

*Distribution and ecology*: collections from India, Sri Lanka, Vietnam and Malaysia were studied (Fig. 7); this subspecies has also been recorded from China (Chen and Li 1997) and the specimens cited by these authors were included on the map. It favours sandy soils, grassy slopes or moist open fields. Common in disturbed areas such as roadsides.

### *Selected specimens (33 specimens examined)*

INDIA: Chinglepul, *Barber 55*, 10.i.1899 (K); Bombay (Mumbai), *Dalzell s.n.*, iv.1878 (K); Ganjam district, Chennai, *Gamble 13771*, ii.1884 (K); Bengaluru, *Gough 162*, Dec 1937 (K); Tirunelveli, Tamil Nadu, *Matthew 16388*, 26.i.1979 (BM); Denkanikotta, Dharmapuri, Denkanikotta Rest House, *Matthew RHT 24647*, 15.xi.1979 (K); Kodaikanal, Dindigul, Law's Ghat Rd, *Matthew RHT 51949*, 4.xii.1987 (K); Mysore, *Mimso 607*, x.1837 (K); Hassan, Mysore, Belvathally, *Ramamoorthy 1956*, 13.xii.1971 (K); 70 km N of Munnar, Palani hills, Tamilnadu, *Van der Maesen 3453*, 20.i.1979 (K). VIETNAM: Tourane (now Da Nang), *Clemens & Clemens 4294*, v–vii.1927 (BM). SRI LANKA: Ruhuna NP, Block 1 near Buttawa Bungalow, *Cooray & Balakrishnan 69010909R*, 9.vi.1969 (BM);

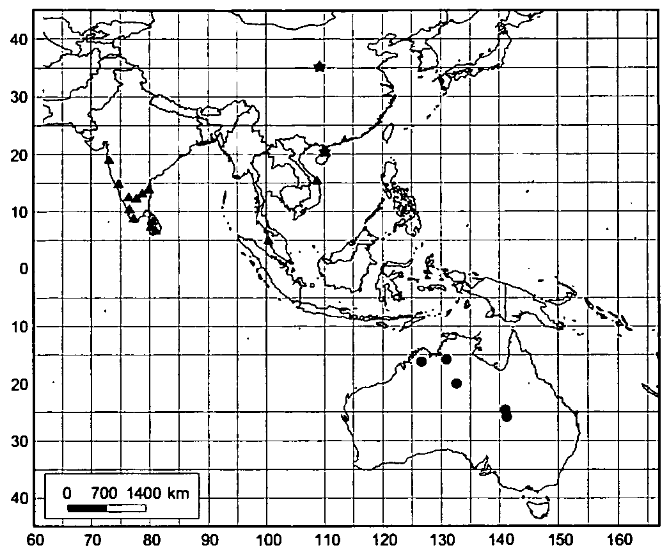

**Fig. 7.** Known geographical distribution of *Rothia indica* subsp. *indica* (triangles) and *R. indica* subsp. *australis* (dots). Specimens cited in Chen and Li (1997) from China are represented by stars.

Trincomalee, near China Bay Airport, *Rudd & Balakrishnan 3134*, 24.ii.1970 (K); Hambantota, Yala, *Fagerlind 1695*, i.1974 (S). MALAYSIA: Pulau Pinang, *Haihtmu 2996*, 21.xii.1917 (K).

### 2b. ***Rothia indica*** subsp. ***australis*** A.E.Holland, *Austrobaileya* 5: 94 (1997)

*Type*: Queensland, Gregory South District, Site 195, Warlus 1, 7 Aug. 1971, *Boyland 4016*; holo BRI (photo seen).

Leaves with terminal leaflet 9–15 mm long, 3–5 mm wide, lateral leaflets 9–12 mm long, 2.5–4.0 mm wide; petiole 4–8 mm long. Stipules elliptic to ovate, 2–5 mm long. Inflorescence with flowers solitary or 2 per raceme. Calyx 4–7 mm long; tube 1.5–3.0 mm long; lobes 3.5–4.0 mm long. Standard 4.0–6.5 mm long; claw 1.5–2.0 mm long; lamina 2.5–4.0 mm long, 2.0–2.5 mm wide. Wings 4.0–6.5 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.5 mm long, 1.0–1.5 mm wide. Keel 4.0–6.5 mm long; claw 2.0–2.5 mm long; lamina 2.5–4.5 mm long, 1.0–1.5 mm wide. Pistil with ovary 4.0–4.5 mm long, 0.6–1.0 mm wide with ±13–17 ovules; style 1.5–1.7 mm long. Pods (30–)35–45 mm long, 1.5–2.0 mm wide with up to ±30 seeds per pod. Seeds 1.5–1.8 mm long, 1.2–1.3 mm wide.

*Distribution and ecology*: restricted to Australia where it occurs on sandy hills and flats (Fig. 7).

### *Specimens examined*

AUSTRALIA: 100 miles [160.9 km] W of Windorah, *Everist 3898*, 9.vi.1949 (K); Boomerang Waterhole, Lander River, 20°38′00″S 132°11′00″E, *Latz 16126*, 10.v.2000 (MEL); Upper Victoria River, *von Müller s.n.*, without date (K, MEL 2 sheets); near the Ord River, *O'Donnell s.n.*, without date (MEL 2 sheets).

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**Appendix B5. Boatwright, J. S. and B.-E. van Wyk. 2009. A revision of the African genus *Robynsiophyton* (Crotalarieae, Fabaceae). *South African Journal of Botany* 75: 367–370.**

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Short communication

# A revision of the African genus *Robynsiophyton* (Crotalarieae, Fabaceae)

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**Abstract**

The monotypic genus *Robynsiophyton* is revised. *Robynsiophyton vanderystii* occurs in central and southern tropical Africa and is unique in the reduction of the androecium to nine stamens and five fertile anthers. It is morphologically similar to *Pearsonia* and *Rothia* and sister to the latter based on morphological and DNA sequence data. A revision of the genus is presented, including illustrations of vegetative and reproductive features and distributional information.

*Keywords:* Crotalarieae; Fabaceae; *Robynsiophyton vanderystii*; Taxonomic revision

## 1. Introduction

*Robynsiophyton* Wilczek is a poorly known, monotypic genus that occurs in south-central tropical Africa. It is morphologically similar to *Pearsonia* Dümmer and *Rothia* Pers., suggesting a close relationship with these genera (Polhill, 1976, 1981; Van Wyk, 1991). *Pearsonia* occurs in central and southern tropical Africa, while *Rothia* is widely distributed throughout tropical Africa, Asia and Australia (Polhill, 1974; Boatwright et al., in press). These three genera differ from the rest of the tribe in their monomorphic anthers and straight styles (Polhill, 1976; Van Wyk, 1991; Van Wyk and Schutte, 1995; Boatwright et al., in press). Chemically they are also unique within Crotalarieae in accumulating angelate esters of hydroxylupanine-type alkaloids (Van Wyk and Verdoorn, 1991). Recently, Boatwright et al. (2008), through the study of molecular (ITS and *rbcL*) and morphological data, demonstrated that *Pearsonia*, *Robynsiophyton* and *Rothia* form a strongly supported clade and that the latter two are strongly supported as sister genera (Fig. 1). Doubt regarding the generic status of *Robynsiophyton* has been expressed by previous authors (Polhill, 1976; Van Wyk, 1991), who suggested that it could merely be a local derivative of *Pearsonia*. However, according to Boatwright et al. (2008) the genus is not embedded within *Pearsonia*, but sister to *Rothia* with both of these subsequently sister to *Pearsonia*. These data in combination with the annual life history and the unusual androecium (nine stamens with only five fertile anthers) support the generic concept of *Robynsiophyton*.

The aim of this paper is to present a revision of *Robynsiophyton* with illustrations, a discussion on diagnostic characters and a distribution map.

## 2. Materials and methods

### 2.1. Morphology

Morphological data were obtained through the study of herbarium material from BM, K and PRE (abbreviations according to Holmgren et al., 1990). Digital images of critical specimens were obtained from BR and LISC. Illustrations were prepared using a stereoscope (WILD M3Z) with a camera *lucida* attachment.

## 3. Results and discussion

A summary of the diagnostic characters for *Robynsiophyton*, *Rothia* and *Pearsonia* is presented in Table 1. *Robynsiophyton vanderystii* Wilczek is a small annual (or rarely a short-lived perennial) with hairy, reddish-brown branches. It shares with *Rothia* the annual life history, a trait which is not found in

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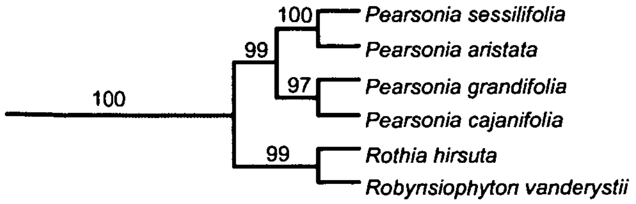

Fig. 1. Phylogenetic position of *Robynsiophyton vanderystii* based on gene sequences (ITS and *rbcL*) and morphological data (strict consensus of 370 trees from Boatwright et al., 2008; tree length = 1166; consistency index = 0.53; retention index = 0.84). Numbers above the branches are bootstrap percentages above 50%.

*Pearsonia*, a genus comprising perennial herbs or small shrubs. The leaves are digitately trifoliolate and sparsely pubescent adaxially but densely pubescent on the abaxial surface. The narrow stipules are paired at the base of the petiole. *Rothia hirsuta* (Guill. & Perr.) Bak. has single stipules at each leaf; *Rothia indica* (L.) Druce has paired stipules; and *Pearsonia* has the stipules paired or less often absent (Polhill, 1974; Boatwright et al., in press).

The flowers of *Pearsonia*, *Robynsiophyton* and *Rothia* are all relatively unspecialised, with straight or even down-curved styles and monomorphic anthers (Polhill, 1976). In *Rothia* the anthers are all small and rounded as opposed to the large, elongate anthers of *Pearsonia*, six of which are attached slightly higher up to the filament (Polhill, 1974, 1976). *Robynsiophyton* has a reduced number of stamens (from 10 to nine) and only five fertile stamens (the other four stamens lack anthers and are sterile). This is the most notable feature of the genus. In the Crotalarieae, Genisteae and Podalyrieae there is great variation in staminal arrangement from completely free stamens (Podalyrieae) to those joined in either an open sheath (Crotalarieae) or closed tube (most Genisteae). The anthers may be either dimorphic with alternating basifixed and dorsifixed anthers, or monomorphic as found in *Pearsonia*, *Robynsiophyton* and *Rothia* (a feature that is unique to this clade within the Crotalarieae). Anther characters are very reliable in legumes and usually consistent with other characters, thus providing important insight especially at generic and tribal levels (Bentham, 1843; Polhill, 1976; Boatwright et al., 2008, in press).

The calyx of *Robynsiophyton* is equally lobed, while in *Pearsonia* and *Rothia* the upper lobes are larger than the three lower lobes. In *Pearsonia*, the upper and lateral lobes on either side are often fused higher up (the so-called "lotononoid" calyx type). Bracts are present in all three genera, but bracteoles are generally lacking in *Pearsonia* (if present very small) and completely absent in *Robynsiophyton* and *Rothia* (Polhill, 1974, 1976).

The pods of *Robynsiophyton* are relatively short and few-seeded when compared to those of *Rothia*. The mature seeds are brown, smooth and similar in size to those of *R. indica*. *Robynsiophyton vanderystii* has larger seeds than *Rothia hirsuta* that are even coloured with a smooth surface, whereas those of *R. hirsuta* are mottled with a somewhat rugose surface (Boatwright et al., in press).

## 4. Taxonomy

### 4.1. *Robynsiophyton*

Wilczek in Bull. Jard. Bot. État. 23: 128 (1953); in F. C. B. 4: 286 (1953); Hutchinson, Genera of Flowering Plants: 362 (1964); Polhill in Bot. Syst. 1: 326 (1976); Van Wyk and Schutte, Advances in Legume Systematics 7: 306 (1995); Polhill, Fl. Zam. 3 (7): 66 (2003); Leistner, Seed Plants of southern Tropical Africa: Families and Genera: 202 (2005); Van Wyk in Legumes of the World, Lewis et al. (Eds): 281 (2005).

Type species: *R. vanderystii* Wilczek.

The genus is monotypic and distinguished by the reduced number of stamens (nine instead of 10) and presence of four staminodes (Table 1). It occurs in central tropical Africa extending from Angola to Zambia in the east.

### 4.2. *R. vanderystii*

Wilczek in Bull. Jard. Bot. État. 23: 128 (1953); in F. C. B. 4: 286, t. 17 (1953); White, F. F. N. R.: 164 (1962); Torre in C. F. A. 3: 6 (1962); Lock, Leg. Afr. Check-list: 232 (1989); Polhill, Fl. Zam. 3 (7): 66 (2003).

Type: Democratic Republic of Congo, Lazaret du Sacré-Coeur [1025 BA], *Vanderyst s.n.* (BR, holo., photo!).

Small, prostrate or ascending annual or short-lived perennial up to ±0.3 m in height. *Branches* reddish-brown, pubescent. *Stipules* 5–8 mm long, linear to lanceolate, invariably paired, pubescent. *Leaves* digitately trifoliolate; petiole shorter than leaflets, 4–7 mm long; leaflets elliptic to oblanceolate, subsessile, sparsely pubescent adaxially and densely so abaxially, terminal leaflet 14–22 × 4–9 mm, lateral leaflets 7–16 × 2.5–6.0 mm, obtuse, base cuneate. *Inflorescence* axillary or rarely terminal congested racemes, with (2–) 5 to 9 (–10) flowers; pedicel less than 1 mm long; bract linear, 1.5–3.0 mm long, pubescent, caducous; bracteoles absent. *Flowers* pale yellow, 3–6 mm long. *Calyx* equally lobed, pubescent, 4–5 mm long; tube 1.5–2.0 mm long; lobes subulate, 1.5–3.0 mm long, tips minutely pubescent on inner surface. *Standard* 3–5 mm long; claw 1.0–1.5 mm long; lamina elliptic to ovate, 2–4 × 1.0–1.5 mm, obtuse to very slightly emarginate, pilose along dorsal midrib. *Wings* 2.5–4.5 mm long; claw 1.5–1.8 mm long;

Table 1
Summary of diagnostic characters for *Robynsiophyton*, *Rothia* and *Pearsonia*.

| Character | *Robynsiophyton* | *Rothia* | *Pearsonia* |
|---|---|---|---|
| Life history | Annual or short-lived perennial | Annual | Perennial |
| Stipules | Paired | Paired or single | Paired or absent |
| Bracteoles | Absent | Absent | Small or absent |
| Calyx | Equally lobed | Sub-equally lobed | Zygomorphic |
| Androecium | 9 Stamens,<br>5 rounded anthers,<br>4 staminodes | 10 Stamens,<br>10 rounded anthers,<br>0 staminodes | 10 Stamens,<br>10 elongated anthers,<br>0 staminodes |
| Fruit | Oblong to ovate | Linear to ovate or falcate | Ellipsoid to linear-oblong |
| Seeds | Brown, smooth | Brown or mottled, smooth or rugose | Light or dark brown, sometimes mottled, smooth |

lamina oblong to obovate, as long as or slightly longer than keel, 1.0–2.5 × 0.5–1.0 mm, obtuse, glabrous, with 1–2 rows of sculpturing. *Keel* 3–4 mm long; claw 1–2 mm long; lamina boat-shaped, 1.5–3.0 × 0.5–0.8 mm, obtuse, glabrous, sometimes with a very slight pocket. *Stamens* 9, anthers monomorphic with 5, sub-basifixed anthers alternating with 4 staminodes. *Pistil* subsessile, pubescent, ovary elliptic, 1.5–2.0 × 0.5–0.8 mm with ±5 to 8 ovules; style straight, 1.5–1.8 mm long, glabrous. *Pods* oblong to ovate, laterally compressed, subsessile, 7–10 × 3–4 mm, ±2 to 8 seeded, dehiscent. *Seeds* oblique-cordiform, 1.0–1.5 × 1.0–1.2 mm, brown, smooth (Fig. 2). Flowering time: April. Plants appear to be inconspicuous and are poorly collected so that the flowering time needs confirmation.

## 5. Distribution and habitat

*R. vanderystii* occurs in moist, sandy soils and is especially common along roadsides. Very few specimens are available for study and these include collections from Angola, the Democratic Republic of Congo and Zambia, but it is likely that the distribution range is more extensive (Fig. 3).

### 5.1. Additional specimens examined

Angola:
– *0614:* Kimbambu, Madimba (–AA), Pauwels 6470 (PRE).
– *0720*: Lunda, Chicapa (–BC), Exell and Mendonça 657 (BM, K, LISC 3 sheets).

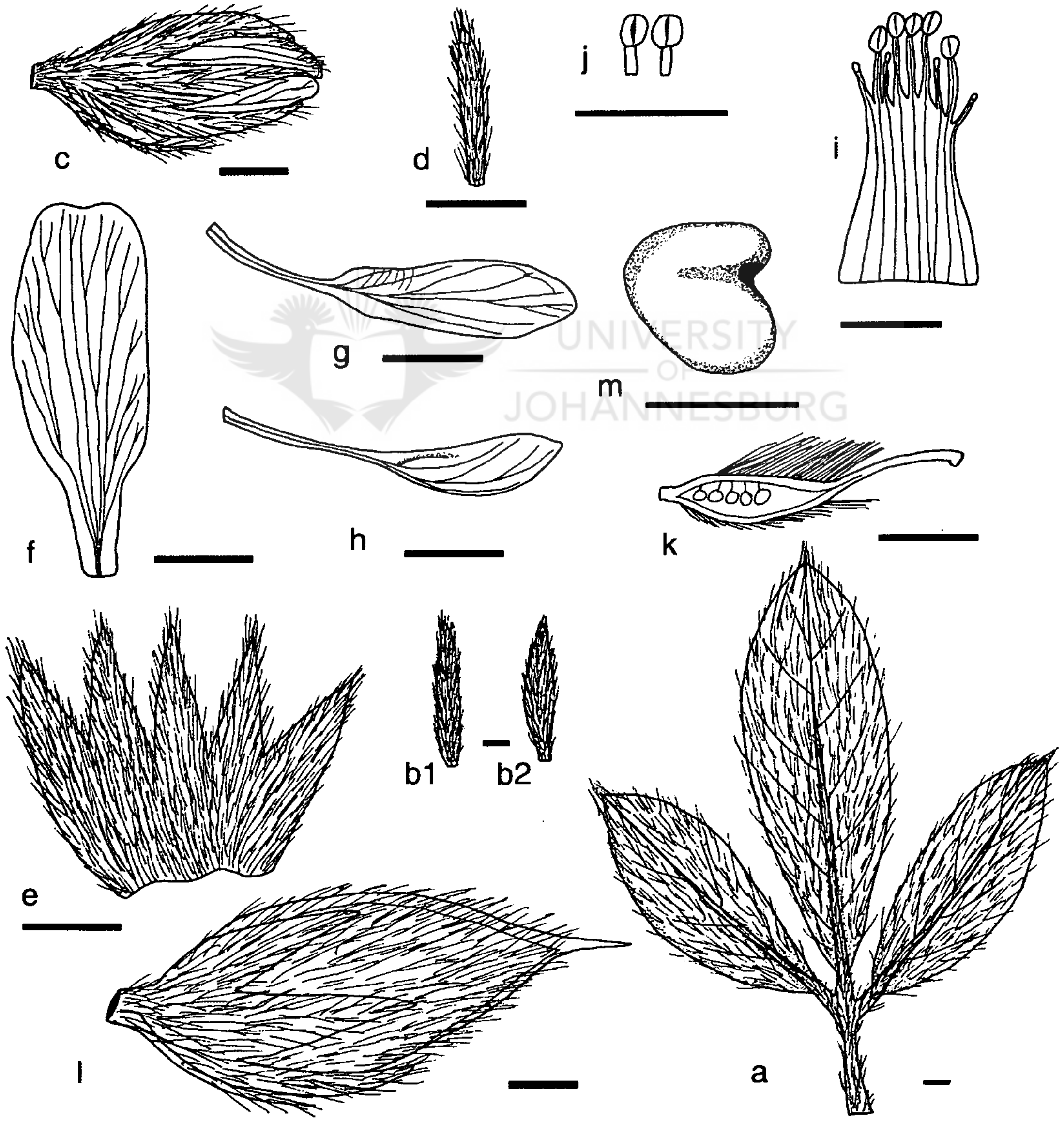

Fig. 2. Morphology of *Robynsiophyton vanderystii* (drawings by JSB): (a) leaf in abaxial view; (b1–b2) stipules; (c) flower in lateral view; (d) bract; (e) outer surface of the calyx (upper lobes to the left); (f) standard petal; (g) wing petal; (h) keel petal; (i) androecium showing the five uniform anthers and four staminodes; (j) anthers (carinal anther on the left); (k) pistil; (l) pod in lateral view; (m) seed in lateral view. Voucher specimens: (c, d, f, g, h, i, j, k) *McCallum Weston 717* (K); (e) *Lisowski 20326* (K); (l) *Richards 9321* (K); (a, b1–b2) *Richards 18144* (K); (m) *Exell and Mendonça 657* (K). Scale bars: (a–m) 1 mm.

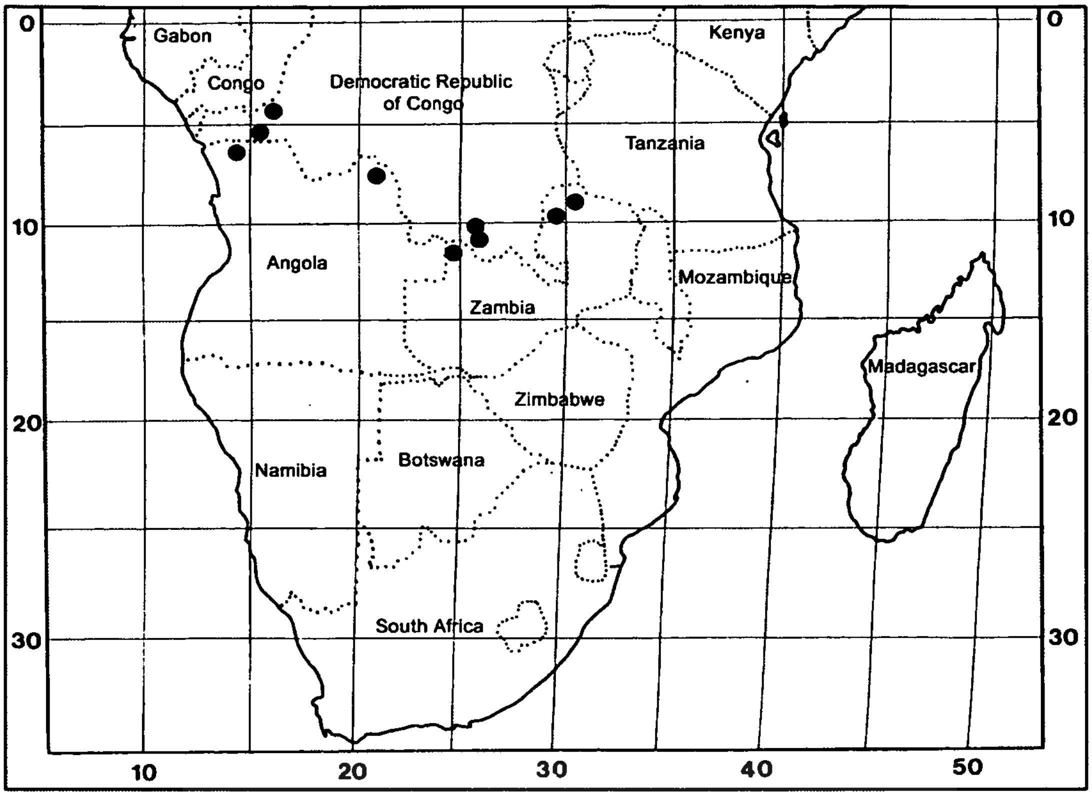

Fig. 3. Known geographical distribution of *Robynsiophyton vanderystii*.

Democratic Republic of Congo:

– *0416*: Bakama (–AB), Flamigni s.n. (K).

– *0515*: Bas-Congo, Kisantu (–AA), Vanderyst s.n. (BM, K); Bas-Congo, Kimpako (–AB), Vanderyst 42290 (K).

– *1025*: Haut-Shaba, Kolwezi (–DA), Lisowski 20326, 20333 (K).

Zambia:

– *0831*: Chilongowelo, Abercorn (–CA), McCallum Weston 717 (K); Mpulungu Abercorn road, close to Chilongowelo turning (–CA), Richards 5309, 5317, 18144 (K), Richards 11097 (K, PRE).

– *0929*: Kawambwa, Timnatushi Falls (–CC), Richards 9319a, 9321 (K).

– *1124*: Mwinilunga (–CD), Mutimushi 3416 (K).

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**Appendix B6. Boatwright, J. S., P. M. Tilney and B.-E. van Wyk. The generic concept of *Lebeckia*, reinstatement of the genus *Calobota* and a new genus of the tribe Crotalarieae (Fabaceae). *South African Journal of Botany*, submitted for publication.**

# The generic concept of *Lebeckia*, reinstatement of the genus *Calobota* and a new genus of the tribe Crotalarieae (Fabaceae)

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## Abstract

The reinstatement of the genus *Calobota* Eckl. and Zeyh. is proposed and *Wiborgiella* Boatwr. and B.-E.van Wyk described as new. Evidence from the internal transcribed spacer (ITS) of nuclear ribosomal DNA and plastid *rbcL* data revealed that the genus *Lebeckia* Thunb. is not monophyletic. These analyses, along with morphological and anatomical data, showed that the genus should be divided into three genera: (1) *Lebeckia* senso stricto (*L.* section *Lebeckia*); (2) *Calobota* [*L.* section *Calobota* (Eckl. and Zeyh.) Benth. and *L.* section *Stiza* (E.Mey.) Benth.] including the monotypic, North African genus *Spartidium* Pomel; (3) a new genus, *Wiborgiella* [*L.* section *Viborgioides* Benth., together with *L. inflata* Bolus, *L. mucronata* Benth. and *Wiborgia humilis* (Thunb.) Dahlgr.]. Brief synopses of the genera *Calobota* and *Wiborgiella*, including nomenclature, synonymy, descriptions and diagnostic characters are presented.

*Keywords: Calobota*, Crotalarieae, Fabaceae, *Lebeckia*, new genus, *Wiborgiella*

## 1. Introduction

The current broad generic concept of *Lebeckia* Thunb. dates back to Bentham (1844) and Harvey (1862) and refers to a group of ca. 36 species of papilionoid legumes that occur mainly in the southern and western parts of South Africa, with some extending into Namibia. The group is particularly common in the Cape Floristic Region (CFR). Bentham (1844) reduced several genera described by Meyer (1836) and Ecklon and Zeyher (1836) to the synonymy of an expanded *Lebeckia*. This broadened concept included Meyer's *Stiza* and *Sarcophyllum*, together with Ecklon and Zeyher's *Acanthobotrya* and *Calobota.* A new sectional classification was proposed, based mainly on the shape of the keel and the morphology of the fruit. This comprised five sections, viz. section *Calobota* (Eckl. and Zeyh.) Benth., section *Eulebeckia* Benth., section *Phyllodiastrum* Benth., section *Stiza* (E.Mey.) Benth., and section *Viborgioides* Benth. Harvey (1862) followed this sectional classification of *Lebeckia* for his treatment in the Flora Capensis. For nearly 150 years, the generic concept and relationships between the morphologically rather diverse species were never studied in depth. A revision of *Lebeckia* sensu stricto (sections *Eulebeckia* and *Phyllodiastrum*) was recently completed by Le Roux and Van Wyk (2007, 2008, in press). Their results show that the 14 species of *Lebeckia* s.s. can easily be distinguished by their acicular leaves and 5+5 anther arrangement, not only from all other species of the so-called "Cape" group of the tribe Crotalarieae (i.e. *Aspalathus* L., *Rafnia* Thunb. and *Wiborgia* Thunb.) but also from all other species hitherto included in *Lebeckia*.

*Spartidium* Pomel is a monotypic genus that occurs in North Africa. The affinities of the genus within the genistoid legumes have been unclear for some time as a possible relationship with both *Retama* Raf. and *Lebeckia* have been suggested (Polhill, 1976). The genus is currently placed within the Crotalarieae based on the open androecial sheath, but an evaluation of its systematic position is clearly desirable. Polhill (1981) considered *Spartidium* to be "virtually indistinguishable from *Lebeckia*". He used the orientation of the seeds in the fruit and the North African distribution as the only key characters to distinguish *Spartidium.*

In a broad study of molecular (ITS, *rbcL*) and morphological data of 117 species representing all the genera of the Crotalarieae, Boatwright et al. (in press) discovered that *Lebeckia* is paraphyletic (Fig. 1a and b). This study revealed important new relationships within the Crotalarieae as well as *Lebeckia* and showed the need for new generic circumscriptions. The species can be readily accommodated in three easily recognizable morphological groups (genera): (1) *Lebeckia* s.s. (*L.* section *Lebeckia,* including sections *Phyllodiastrum* and *Eulebeckia*); (2) *Calobota* Eckl. and Zeyh. [*L.* section *Calobota* (Eckl. and Zeyh.) Benth. and *L.* section *Stiza* (E.Mey.) Benth., together with the monotypic North African *Spartidium* Pomel] and (3) "*Wiborgiella*" [*L.* section *Viborgioides* Benth., together with *L. inflata* Bolus, *L. mucronata* Benth. and *Wiborgia humilis* (Thunb.) Dahlgr.].

In this paper, new evidence is presented to show that Bentham's (1844) broad concept of *Lebeckia* is paraphyletic. We propose a new generic classification system to reflect new insights into morphological discontinuities within the tribe which are also supported by molecular systematic evidence (Boatwright et al., in press).

## 2. Materials and methods

### *2.1. Morphology*

Morphological data were obtained from herbarium specimens as well as fresh material collected while studying various taxa of the Crotalarieae in the field. Specimens of *Lebeckia* from the following herbaria were studied: BM, BOL, GRA, J, JRAU, K, NBG (including SAM and STE), P, PRE, S, SBT, UPS and WIND (abbreviations according to Holmgren et al., 1990). Online photographs of the collections of B, M and Z were studied. Drawings of reproductive structures (all by JSB) were done using a stereoscope (WILD M3Z) with a camera *lucida* attachment.

### *2.2. Anatomy*

For anatomical studies, material was fixed in FAA (formaldehyde: acetic acid: 96% alcohol: water; 10:5:50:35 ) or dried material was rehydrated and then fixed in FAA for 24 hours. A modification of the method of Feder and O'Brien (1968) was used for embedding in glycol methacrylate (GMA). A minimum of five days was used for the third infiltration in GMA. Sections were stained according to the periodic acid Schiff/toluidine blue (PAS/TB) staining method.

## 3. Morphological and anatomical evidence for the paraphyly of *Lebeckia*

### *3.1. Habit and branches*

Most genera of the Crotalarieae have a shrubby habit (Polhill, 1976), but variation in habit is quite pronounced within *Lebeckia*. Species of *Lebeckia* section *Lebeckia* are predominantly suffrutescent plants that branch mainly at ground level, whereas the species of the remaining sections are almost invariably woody shrubs. A strongly spinescent habit is characteristic of *Lebeckia* section *Stiza* but also of two species of section *Calobota*, viz. *L. acanthoclada* Dinter and *L. spinescens* Harv. Both sections *Calobota* and *Stiza* have green young branches (except *L. acanthoclada*), as opposed to the woody, rigid, ramified brown to greyish branches of section *Viborgioides* (similar to the genus *Wiborgia* Thunb.). In species with green stems [sections *Calobota*, *Lebeckia* and *Stiza*, and *Spartidium saharae* (Coss. and Dur.) Pomel] a large part of the cortex is composed of chlorenchyma which serves a photosynthetic function (Metcalfe and Chalk, 1950). This layer is absent in species of section *Viborgioides* and also *L. mucronata*.

### *3.2. Leaves*

Leaves are extremely variable, ranging from trifoliolate and petiolate (sections *Calobota* and *Viborgioides*), to unifoliolate (section *Stiza*) or simple (section *Calobota* and *Spartidium*) and completely phyllodinous (and acicular) in section *Lebeckia*. Cultivated plants of the section *Stiza* showed that the juvenile leaves are petiolate and trifoliolate, but a loss of the lateral leaflets and shortening of the petioles result in unifoliolate leaves on the older branches, as was also mentioned by Polhill (1976) and Dahlgren (1970). This transition is also seen in *L. obovata* Schinz. Stipules are absent in all but two species of *Lebeckia* s.l.*:* *L. wrightii* (Harv.) Bolus and *L. uniflora* M.M.le Roux and B.-E.van Wyk (Le Roux and Van Wyk, in press).

Transverse sections through the leaves of *Lebeckia* species (Fig. 2) revealed a remarkable difference between the species of *Calobota/Stiza/Spartidium* on the one hand (hereafter called the *Calobota* group) and *Viborgioides/L. inflata/L. mucronata/Wiborgia humilis* on the other hand (hereafter called the *Viborgioides* group), namely that the former group has isobilateral leaves, while the latter has dorsiventral leaves. This difference was unexpected, as anatomical characters are generally regarded as conservative. Even more remarkable was the exact congruence between the anther arrangements of the two groups (respectively 4+1+5 and 4+6 – see later). Leaves of *Lebeckia* s.s. are completely different from the species mentioned above, as they are phyllodinous, acicular and terete in transverse section.

Another interesting difference between the *Calobota* group and the *Viborgioides* group is the presence of mucilage cells in the latter but not the former (Fig. 2). In this character, the *Viborgioides* group agrees with other Cape genera (*Aspalathus*, *Rafnia* and *Wiborgia*, as well as the predominantly Cape *Lebeckia* s.s.). In contrast, the *Calobota* group, which extends into arid regions (Northern Cape and Namibia), does not have mucilage cells in mature leaves. The North African *Spartidium*, however, has mucilage cells in the epidermis, as do immature leaves of *L. pungens*, suggesting that there is a loss of these cells as the leaves mature (Boatwright, pers. obs.). Mucilage cells are widely distributed throughout the various plant families and several authors have speculated about their function (Gregory and Baas, 1989). Although experimental evidence is lacking, mucilage cells are thought to aid in water storage and reduction of transpiration, protection against intensive radiation and also against herbivory (Gregory and Baas, 1989). Mucilage cells are often associated with plants that occur in Mediterranean climates (Van der Merwe et al., 1994). Bredenkamp and Van Wyk (1999) speculated that in *Passerina* L. (Thymelaeaceae) the mucilage serves as a regulator of hydration in the leaves, protecting them against water loss, but also helping to accumulate reserve water in the leaves. *Lebeckia* s.s. and the *Viborgioides* group are restricted to the CFR and therefore diversifying in a Mediterranean climate could explain the presence of the mucilage cells in these taxa. It is interesting to note the presence of mucilage cells in *Spartidium saharae* (Coss. and Dur.) Pomel, which also occurs in a Mediterranean climate. The *Calobota* group (excluding *Spartidium*) extend out of the CFR into summer rainfall, more arid regions and show a different adaptation to drought, viz. isobilateral leaves (Fig. 2 a, b; also in *Spartidium*). Van der Merwe et al. (1994) mention that the presence of more layers of palisade parenchyma improves the transport of water through the leaves and also offers increased protection to the chloroplasts. In contrast, the leaves of species within the *Viborgioides* group are dorsiventral (Fig. 2 c, e, f). In *Lebeckia* s.s., the acicular leaves have a complete circular zone of palisade cells, with no spongy parenchyma (Fig. 2 d).

The petioles are always shorter than the leaflets in the *Viborgioides* group. In the *Viborgioides* group the persistent petioles become hard and woody when the leaflets are shed, contributing to the rigid and somewhat thorny appearance of the branches. These characters are also found in some species of *Wiborgia* s.s. (Dahlgren, 1975). In the *Calobota* group, the petioles are either longer or shorter than the leaflets and sometimes persistent, but never rigid and spinescent. The acicular leaves of some species of *Lebeckia* s.s. are articulated or "jointed" near the middle or reduced to petioles in species with unarticulated leaves, i.e. the leaves are phyllodinous (Dahlgren, 1970), which serves as a distinct synapomorphy for this group.

### *3.3. Inflorescences*

As in most Crotalarieae, the inflorescences in *Lebeckia* are all terminal, multi-flowered racemes, varying in length and number of flowers. In *Lebeckia* s.s., the inflorescences may be relatively long and are often densely flowered with up to 93 flowers per raceme, for example in *L. brevicarpa* M.M.le Roux and B.-E.van Wyk (Le Roux and Van Wyk, 2007). Species of section *Calobota* generally have fewer flowers per inflorescence, except in *L. melilotoides* Dahlgr., where more than 100 flowers are found on the elongated racemes (Dahlgren, 1967). The racemes of the three species of section *Stiza* are characteristically spine-tipped. Very short and few-flowered inflorescences are found in *L.* section *Viborgioides*, with the flowers often solitary in *L. bowieana* Benth.

### *3.4. Flowers*

The calyx structure is often an important generic character in the Crotalarieae. *Lebeckia* species normally have equally lobed or "lebeckioid" calyces (Polhill, 1976), as opposed to the zygomorphic calyx ("lotononoid") in *Lotononis* (DC.) Eckl. and Zeyh. and *Pearsonia* Dümmer or the bilabiate calyx typical of all members of the tribe Genisteae (Van Wyk, 1991a; Van Wyk and Schutte, 1995). In the *Calobota* and *Viborgioides* groups, the carinal lobe is slightly narrower than the upper and lateral lobes, whereas in *Lebeckia* s.s. it is equal to the other lobes (Fig. 3). In the former two groups, the calyces are pubescent or at least glabrescent as opposed to the usually glabrous calyces found in section *Lebeckia* (*L. wrightii* is an exception in having a sparsely pubescent calyx).

The pubescence of the petals, the shape of the keel petal and the arrangement of the anthers closely follow the three major groups within *Lebeckia* s.l. Glabrous petals are found in *Lebeckia* s.s. and the *Viborgioides* group, whereas species of the *Calobota* group generally have pubescent petals (or at least pilose along the dorsal midrib of the standard petal). *Lebeckia macrantha* Harv. and *L. psiloloba* (E.Mey.) Walp. are the only exceptions and have totally glabrous petals. The keel petals in *Lebeckia* s.s. are characteristically rostrate as opposed to the obtuse keel petals found in the other groups (Fig. 3).

### *3.5. Anthers*

Surprisingly, it was found that the size and shape of the carinal anther are diagnostic for each of the three groups in *Lebeckia* s.l. In *Lebeckia* s.s., the carinal anther resembles the long, basifixed anthers (Fig. 3 h3) resulting in a 5+5 arrangement. In the *Calobota* group (including *Spartidium saharae*), the carinal anther is intermediate between the dorsifixed and basifixed anthers (Fig. 3 e3, f3, g3), resulting in a 4+1+5 anther configuration (i.e., four long basifixed anthers, an intermediate carinal anther and five short dorsifixed anthers). The carinal anther is usually attached a little higher up. In the *Viborgioides* group, the carinal anther resembles the short, dorsifixed anthers (Fig. 3 a3, b3, c3, d3), resulting in a 4+6 anther arrangement (i.e., four long anthers and six short anthers). The anther arrangement is therefore in perfect agreement with the leaf anatomy of the three groups.

### *3.6. Fruit and seeds*

Pods in the Crotalarieae are an important source of systematic information, as specialisations for seed protection and dispersal may result in structural differences. *Lebeckia* s.l. displays a great diversity of fruit structure, including dehiscent and indehiscent fruits that are either inflated or laterally compressed, and with or without wings (Polhill, 1976). Fruits of *Lebeckia* s.s. are terete to semi-terete and thick- or thin-walled, with wings on the upper suture in some species, e.g. *L. meyeriana* Eckl. and Zeyh. ex Harv. Species of the *Calobota* group generally have terete or semi-terete pods that are thick-walled and spongy or the fruits are thin-walled (membranous), laterally compressed and pubescent or glabrous, as is also found in *Spartidium saharae*. In contrast, the fruits of section *Viborgioides* (and *L. inflata*) are inflated and always glabrous, with highly sclerified, thin walls. The placement of *Wiborgia humilis* within the *Viborgioides* group is supported by fruit structure. *Wiborgia humilis* has inflated pods that lack wings on the upper suture and do not have highly sclerified fruit walls. In contrast, the winged samaras of the rest of *Wiborgia* are laterally compressed and have highly sclerified fruit walls in most species (Dahlgren, 1975).

Polhill (1976, 1981) used the orientation of the seed in *Spartidium* as the only diagnostic character to separate this genus from *Lebeckia* s.l. A study of most of the species showed that at least three species of the *Calobota* group (*L. macrantha*, *L. psiloloba* and *L. pungens* Thunb.) have the seed oriented at right angles to the placenta, exactly as in *Spartidum saharae*.

The seed surface of species in *Lebeckia* s.s. is invariably rugose, while the seeds of only one species in the *Calobota* group (*L. lotononoides* Schltr.) and one species in the *Viborgioides* group (*L. inflata*) have rugose seeds (Le Roux and Van Wyk, 2007, 2008, in press; Boatwright and Van Wyk, 2007).

## 4. Molecular evidence for the paraphyly of *Lebeckia*

### *4.1. Combined molecular analyses*

In the combined molecular analyses (Parsimony and Bayesian analyses; Fig. 1a) of Boatwright et al. (in press), the *Calobota* group is clearly monophyletic with very strong support. In the Bayesian analysis, *Spartidium* groups with the *Lebeckia multiflora* group with strong support (Fig. 1a). The *Viborgioides* group is partly monophyletic with weak to strong support, but the positions of *L. inflata* and *L. mucronata* are unresolved. It is interesting to note that molecular evidence strongly supports the exclusion of *Wiborgia humilis* from *Wiborgia* and the transfer of this species to the *Viborgioides* group. Surprisingly, *Lebeckia* s.s. is unresolved in the molecular analyses. Morphologically this group is very distinct from the other groups of *Lebeckia* s.l. and all other Cape Crotalarieae.

### *4.2. Combined molecular and morphological analysis*

When the molecular data were combined with morphological data (Fig. 1b), the resolution within the "Cape" group and among the three groups of *Lebeckia* s.l. was much improved. The *Calobota* group is again strongly supported as monophyletic. The *Viborgioides* group is partly monophyletic with strong support and *L. inflata* is sister to this group, albeit without support. The position of *L. mucronata*, however, remains unresolved in this analysis, although abundant morphological and anatomical evidence suggests its placement within this group. The inclusion of *W. humilis* in the *Viborgioides* group again receives strong support. With the addition of morphological data *Lebeckia* s.s. is moderately supported as monophyletic as opposed to being unresolved in the molecular analyses (Boatwright et al., 2008).

## **5. Taxonomic treatment**

Major continuities and discontinuities in morphological characters amongst the three groups discussed above closely agree with the three main clades revealed by genetic analysis (Fig. 1a and b). The new system proposed here is based on a wider consideration of the intricate relationships amongst all genera of the tribe Crotalarieae, all of which have been revised in recent years (*Pearsonia* – Polhill, 1974; *Wiborgia* – Dahlgren, 1975; *Crotalaria* – Polhill 1982; *Aspalathus* – Dahlgren 1988; *Lotononis* – Van Wyk, 1991b; *Rafnia* – Campbell and Van Wyk, 2001; *Bolusia* – Van Wyk, 2003, Van Wyk et al., submitted; *Lebeckia* s.s. – Le Roux and Van Wyk 2007, 2008, in press; *Robynsiophyton* – Boatwright and Van Wyk, submitted; *Rothia* – Boatwright et al., submitted). Dahlgren (1970) and Polhill (1976) both discussed the high incidence of convergence in the tribe Crotalarieae and the intricate relationships between the genera. The difficulty in determining generic limits within the Crotalarieae is discussed by Polhill (1976), who emphasized that it would be unwise to propose modifications to the system without a clear understanding of the patterns of character state distributions. Furthermore, alterations to the system should result in a more predictive and useful system without running the risk of instability of circumscriptions and nomenclature. In existing keys to the genera of the Crotalarieae (Polhill, 1981; Van Wyk and Schutte, 1995), the lack of uniformity and clearcut diagnostic characters for *Lebeckia* s.l. is clearly reflected in the fact that the genus keys out no less than three times (in both keys). Unique combinations of morphological characters have now been identified for the three main groups that we are convinced should be given generic status. The improvement in generic delimitations is also reflected in the following key.

### *5.1. Key to the genera of the Crotalarieae*

1a. Leaves acicular, terete:

2a. Ovary 2 to 4 ovulate, pods 1 to 8-seeded......................***Aspalathus***

2b. Ovary with more than 6 ovules, pods many-seeded........***Lebeckia* s.s.**

1b. Leaves digitate, unifoliolate or simple (flat, never terete):

3a. Stipules present:

4a. Style curved upwards; anthers dimorphic:

5a. Stipules asymmetrical or single; style glabrous and not helically coiled; keel obtuse or rostrate; anther arrangement 4+6, 4+1+5 or very rarely 5+5.............................................................................................***Lotononis***

5b. Stipules symmetrical when present; style with 1 or 2 lines of hairs or glabrous and helically coiled; keel strongly rostrate (often at right angles) or helically coiled; anther arrangement 5+5:

6a. Stipules dentate; beak of keel and style helically coiled, style glabrous.............................................................................................***Bolusia***

6b. Stipules entire; beak of keel and style not helically coiled, style with 1 or 2 lines of hairs...........................................................................***Crotalaria***

4b. Style straight or rarely down-curved; anthers similar in size and shape:

7a. Stamens 9 (5 fertile and 4 lacking anthers)..............***Robynsiophyton***

7b. Stamens 10 (all fertile):

8a. Anthers all rounded; prostrate annuals.................................***Rothia***

8b. 4 anthers basifixed, 6 attached slightly higher up, all elongate; perennial herbs or shrubs.............................................***Pearsonia***

3b. Stipules absent:

9a. Calyx with upper and lateral lobes fused on either side.........***Lotononis***

9b. Calyx sub-equal (upper and lateral lobes not fused):

10a. Leaves sessile; upper suture of pod asymmetrically convex:

11a. Plants glabrous except occasionally on bracts and bracteoles; usually turning black when dried.........................................................***Rafnia***

11b. Plants usually pubescent on all parts, if leaves glabrous then standard petal hairy and inner surface of calyx glabrous; not turning black when dried...................................................................................***Aspalathus***

10b. Leaves usually petiolate, if leaves sessile then plants with many-seeded pods and at least some hairs on leaves or stems; upper suture of pod symmetrically convex:

12a. Petals pubescent; at least on the dorsal midrib of the standard petal (if glabrous then plants strongly spinescent, woody, practically leafless shrubs); twigs green (bark formation late. chlorenchyma present); leaves isobilateral.........................................................***Calobota***

12b. Petals glabrous; twigs brown (bark formation early, chlorenchyma absent; if twigs rarely green then plant a short-lived fireweed); leaves dorsiventral:

13a. Fruits winged, indehiscent; carinal anther intermediate (anthers 4+1+5) ...........................................................................***Wiborgia***

13b. Fruits without wings, dehiscent (if rarely indehiscent then ovary and fruit distinctly stalked); carinal anther resembles short anthers (anthers 4+6) ..................................................................***Wiborgiella***

*5.2. Calobota*

*Calobota* Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 192 (Jan. 1836) *emend.* Boatwr. and B.-E.van Wyk, emend. nov., *Lebeckia* section *Calobota* (Eckl. and Zeyh.) Benth. in Hook. Lond. J. Bot. 3: 358–361 (1844) *pro parte majore*. Lectotype species (here designated): *Calobota cytisoides* (Berg.) Boatwr. and B.-E.van Wyk [Note: This species is chosen as lectotype as it is the only species included in Ecklon and Zeyher's original concept of *Calobota*].

*Acanthobotrya* Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 192 (Jan 1836) *pro parte*. Lectotype species (here designated): *A. pungens sensu* Eckl. and Zeyh. [now *Calobota psiloloba* (E.Mey.) Boatwr. and B.-E.van Wyk]. [Note: As mentioned by Bentham (1844), *Acanthobotrya* is a mixed concept representing at least four different genera. However, the diagnosis agrees with the concept of *Stiza* E.Mey. (e.g. linear-oblong, compressed fruits); furthermore, *C. psiloloba* (at the time still part of the concept of *A. pungens*), which has all the diagnostic characters mentioned in the diagnosis, is listed first].

*Stiza* E.Mey., Comm. Pl. Afr. Austr. 1: 31 (Feb. 1836), synon. nov. *Lebeckia* section *Stiza* (E.Mey.) Benth. in Hook. Lond. J. Bot. 3: 355–356 (1844). Lectotype species (here designated): *Stiza erioloba* E.Mey. [now *Calobota pungens* (Thunb.) Boatwr. and B.-E.van Wyk]. [Note: Meyer (1836) included only *Stiza erioloba* and *S. psiloloba* E.Mey. (now *Calobota psiloloba*) in *Stiza*. The original description of *Stiza* is too general to allow for a considered choice of lectotype, so we here choose *C. pungens* simply as it is the first-mentioned species.].

*Spartidium* Pomel, Nouv. Mat. Fl. Atl.: 173 (1874), synon. nov. Type species: *Spartidium saharae* (Coss. and Dur.) Pomel. [Note: *Spartidium* is monotypic].

[Note: The concept of *Calobota* is here expanded to include the genus *Stiza* and also the monotypic North African *Spartidium* (but excluding *Lebeckia mucronata*)].

Woody, sometimes spinescent shrubs or shrublets. *Branches* thick and woody; young branches green, lacking bark (except in *C. acanthoclada*), pubescent, often sericeous. *Leaves* unifoliolate, digitately trifoliolate (rarely 4- or 5-foliolate in some species) or simple; leaflets flat, oblanceolate to elliptic or obovate to suborbicular, less often spathulate, pubescent; petioles shorter or longer than leaflets. *Stipules* absent. *Inflorescence* terminal, few to multi-flowered racemes. *Bracts* linear to obovate, pubescent. *Bracteoles* linear, pubescent. *Corolla* yellow, usually pubescent or at least pilose along the median section of the standard petal (except in *C. cuspidosa* (Burch.) Boatwr. and B.-E.van Wyk and *C. psiloloba*). *Calyx* subequally lobed, upper sinus often deeper than the lateral or lower sinuses, carinal lobe narrower than the others, pubescent or at least glabrescent. *Standard* linear to widely ovate, with basal callosities in *C. cytisoides*. *Wing petals* narrowly oblong to oblong or slightly ovate, longer or shorter than the keel, terminal parts sometimes pubescent; apex obtuse. *Keel petals* oblong, pockets invariably present, terminal parts sometimes pubescent; apex obtuse. *Anthers* dimorphic, four long, basifixed anthers alternating with five ovate, dorsifixed anthers, carinal anther intermediate in size and shape between the basifixed and dorsifixed anthers (4+1+5 configuration). *Pistil* sub-sessile to very shortly stipitate; ovary linear to slightly elliptic, with four to many ovules, pubescent or glabrous; style shorter than the ovary, curved upwards, glabrous. *Pods* laterally compressed, semi-terete or terete, linear to oblong, few- to many-seeded, glabrous or pubescent, dehiscent or indehiscent. *Seeds* reniform to oblong-reniform, or less often suborbicular; colour variable, light pink to pink, sometimes mottled with brown; hilum round, brown or black; surface smooth [rugose only in *C. lotononoides* (Schltr.) Boatwr. and B.-E.van Wyk; seeds of *C. dinteri* (Harms) Boatwr. and B.-E.van Wyk, *C. obovata* (Schinz) Boatwr. and B.-E.van Wyk and *C. saharae* (Coss. and Durr.) Boatwr. and B.-E.van Wyk not seen].

### *5.2.1. Diagnostic characters*

Bark formation is late, so that the twigs remain green and photosynthesizing, whereas it is early in most species of *Wiborgiella*, so that even the young twigs are not green but covered in brown bark (as in *Wiborgia* species). The green twigs are a useful diagnostic character, visible even in sterile herbarium specimens. *Calobota* also differs from *Wiborgiella* in the hairy petals (*C. cupidosa* and *C. psiloloba* are exceptions); they are glabrous in *Wiborgiella*. The most reliable diagnostic character to distinguish *Calobota* from *Wiborgiella* is the anther configuration of 4+1+5 (4+6 in the latter). The pods are never inflated in *Calobota* and usually pubescent (pods inflated in most species of *Wiborgiella* and always glabrous).

### *5.2.2. Notes on distribution*

The species of *Calobota* occur in the Eastern and Western Cape Provinces, with some restricted to Namibia. One species, *Calobota saharae*, is endemic to North Africa where it occurs on sand dunes from Libya to Algeria and Morocco (Polhill, 1976).

### *5.3. The species of Calobota*

The following 16 species are recognised:

*5.3.1. Calobota acanthoclada* (Dinter) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia acanthoclada* Dinter, Feddes Repert. 30: 196 (1932). Type—South Africa, Namibia, Kleinfonteiner Fläche, *Dinter 6269* (B, photo!); Kovisberge, *Dinter 6293* (B, photo!, BM!); Buchuberge, *Dinter 6574* (B, photo!, BM!); Granietberge, *Dinter 6694* (B, photo!).

*Lebeckia spathulifolia* Dinter, Feddes Repert. 30: 197 (1932) . Type—South Africa, Namibia, Kleinfonteiner Fläche, *Dinter 3735* (B, photo!, SAM!, Z, photo! 2 sheets).

*Lebeckia candicans* Dinter, Feddes Repert. 30: 198 (1932), synon. nov.. Type—South Africa, Namibia, Kleinfonteiner Fläche, *Dinter 3737* (B, photo!, BOL!, NBG!, PRE!, S!, Z, photo!).

*5.3.2. Calobota cinerea* (E.Mey.) Boatwr. and B.-E.van Wyk, comb. nov.

*Lebeckia cinerea* E.Mey., Comm. Pl. Afr. Austr. 1: 35 (Feb. 1836). Type—South Africa, hills near Noagas and near Aris on the Gariep, *Drège s.n.* (P!).

*5.3.3. Calobota cuspidosa* (Burch.) Boatwr. and B.-E.van Wyk, comb. nov.

*Spartium cuspidosum* Burch., Trav. S. Africa 1: 348 (1822). Type—South Africa, Between 'Gatikamma' and 'Klaarwater' [now Griquatown], *Burchell 1697* (K!).

*Lebeckia macrantha* Harv. in Harv. and Sond., Fl. Cap. 2: 83–84 (1862), synon. nov. Type—South Africa, 'Zooloo country', *Miss Owen s.n.* (TCD, photo!).

*5.3.4. Calobota cytisoides* (Berg.) Boatwr. and B.-E.van Wyk, comb. nov.

*Spartium cytisoides* Berg., Descr. Pl.: 199. 1767; L.f., Suppl. Pl. 320 (1781). Type—South Africa, 'e Cap. b. Spei', *Grubb s.n. sub Bergius 236.57* (SBT!).

*Ebenus capensis* L., Mant II: 264 (1771) *nom. illegit.*

*Lebeckia cytisoides* Thunb., Nov. Gen.: 143 (1800). [Note: Thunberg incorrectly cited *Spartium cytisoides* L.f.]

*5.3.5. Calobota elongata* (Thunb.) Boatwr. and B.-E.van Wyk, comb. nov.

*Crotalaria elongata* Thunb., Fl. Cap.: 571 (1823). Type—South Africa, 'Carro prope Bockeveld', *Thunberg s.n. sub THUNB-UPS 16544* (UPS!).

*Lebeckia melilotoides* Dahlgr., Bot. Notiser 120: 268–271 (1967). Type—South Africa, Platfontein, E of Hottentots Holland Kloof, *H. Hall 177* (NBG! , 2 sheets, S!).

*5.3.6. Calobota halenbergensis* (Merxm. and Schreib.) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia halenbergensis* Merxm. and Schreib., Bull. Jard. Bot. Bruxelles 27: 276 (1957). Type—South Africa, Namibia, Lüderitz South, Halenberg, *Dinter 6632* (M, photo!; K!, NBG!, PRE!, S!, Z, photo!).

*5.3.7. Calobota linearifolia* (E.Mey.) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia linearifolia* E.Mey., Comm. Pl. Afr. Austr. 1: 33 (Feb. 1836). Type—South Africa, Northern Cape Province, on the Gariep, near Verleptpraam, *Drège s.n.* (P!, S!).

*Lebeckia dinteri* Harms, Feddes. Repert. 16: 360 (1920), synon. nov. Type—South Africa, Namibia, Garub, *Dinter 1057* (NBG!).

*5.3.8. Calobota lotononoides* (Schltr.) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia lotononoides* Schltr. in Engler Bot. Jahr. 27: 143 (1900). Type—South Africa, 'In regione namaquensi: In sabulosis montium Karree-Bergen, alt. C. 4500 ped.', *Schlechter 8214* (BM!, BOL!, K!, PRE!, S!, Z, photo!).

*5.3.9. Calobota obovata* (Schinz) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia obovata* Schinz, Mem. Herb. Boiss. 1: 126 (1900). Type—South Africa, Namibia, Gansberg, *Fleck 75* (Z, 2 sheets, photo!).

*5.3.10. Calobota psiloloba* (E.Mey.) Boatwr. and B.-E.van Wyk, comb. nov. *Stiza psiloloba* E.Mey. Comm. Pl. Afr. Austr. 1: 31 (Feb. 1836). *Lebeckia psiloloba* (E.Mey.) Walp., Linnaea 13: 478 (1839). Type—South Africa, without locality, *Drège 6470* (P!, K!, S!).

*5.3.11. Calobota pungens* (Thunb.) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia pungens* Thunb., Nov. Gen.: 141 (1800). Type—South Africa, Eastern Cape Province, near Olifant's River [close to Oudtshoorn] at Cannaland [now Little Karoo], *Thunberg s.n. sub THUNB-UPS 16417* (UPS!).

*5.3.12. Calobota saharae* (Coss. and Dur.) Boatwr. and B.-E.van Wyk, comb. nov. *Genista saharae* Coss. and Dur., B. Soc. Bot. France 2: 247 (1855). *Spartidium saharae* (Coss. and Dur.) Pomel, Nouv. Mat. Fl. Atl.: 173 (1874). Type—Algeria, D'Oran Province, *Cosson s.n.* (K!, P).

*5.3.13. Calobota sericea* (Ait.) Boatwr. and B.-E.van Wyk, comb. nov. *Spartium sericeum* Ait. in Hort. Kew. 3: 12 (1789). Type—South Africa, Cape of Good Hope, *Masson s.n. sub BM000794145* (BM, photo!). [The two specimens on the left were collected by Masson and are marked with '1' on the tape on the stems. The specimen on the right was grown in the gardens at Kew and has the note 'Hort. Kew 1781' associated with it. According to Stafleu and Cowan (1976), most of the Aiton types are in the Banks collection in BM)].

*Lebeckia angustifolia* E.Mey. in Linnaea 7: 155 (1832). Type—South Africa, without locality, *Ecklon s.n.* (S!) [Note: the type is represented by the two branches mounted at the bottom right hand side of the sheet – one with several flowers, the other with a single bud. Meyer (1932) incorrectly cites the type locality as "Uitenhage?" but expresses doubt by placing a question mark after the locality. The specimen in S comprises mixed elements but the two branches referred to above are accompanied by a label in Meyer's handwriting stating "*Lebeckia angustifolia mihi*"].

*Lebeckia multiflora* E.Mey., Comm. Pl. Afr. Austr. 1: 34 (Feb. 1836). Type—South Africa, near Heerenlogement, *Drège s.n.* (P!); Olifantsrivier, *Drège s.n.* (P!); between Holrivier and Mierenkasteel, *Drège 6474* (P!, S!).

*5.3.14. Calobota spinescens* (Harv.) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia spinescens* Harv. in Harv. and Sond., Fl. Cap. 2: 88 (1862). Type—South Africa, Rocks of Driekoppe, *Drège s.n.* (K, P!), Dwaka River, *Burke s.n.* (K!), Great Fish River and Zout River, Beaufort, *Zeyher 397* (K).

*5.3.15. Calobota thunbergii* Boatwr. and B.-E.van Wyk, nom. nov. pro *Lebeckia sericea* Thunb. non *Calobota sericea* (Ait.) Boatwr. and B.-E.van Wyk. *Lebeckia sericea* Thunb., Nov. Gen.: 143 (1800); Prodr. Pl. Cap.: 122 (1800). Type—South Africa, 'e Cap. b. Spei', *Thunberg s.n. sub THUNB-UPS 16423* (UPS!) [Note: The epiphet '*sericea*' was applied to *Lebeckia multiflora* E.Mey. (now *Calobota sericea*) by Aiton (1789), the basionym of which is *Spartium sericeum* Ait., and is thus not available for the current taxon. We therefore propose a new name in memory of Thunberg who first described this species].

*5.3.16. Calobota* sp. 1. *De Winter and Hardy 7919* (WIND!, K!, PRE!).

## *5.4. Wiborgiella*

*Wiborgiella* Boatwr. and B.-E.van Wyk, gen. nov., *Wiborgiae Thunb. similis sed fructibus oblongis non alatis valde inflatis, anthera carinali breve (aliis in eodem flore brevibus dorsifixis simile) differt; Calobotae Eckl. and Zeyh. similis sed petalis ubique glabris, antheris ut supra et foliis dorsiventralibus differt; Lebeckiae Thunb. sensu stricto similis sed foliolis planis non acicularibus valde differt.* Type species: *Wiborgiella leipoldtiana* (Dahlgr. ex Schltr.) Boatwr. and B.-E.van Wyk.

*Lebeckia* section *Viborgioides* Benth. in Hook. Lond. J. Bot. 3: 361 (1844). Lectotype species (here designated): *Wiborgiella fasciculata* (Benth.) Boatwr. and B.-E.van Wyk [Note: As there is no indication as to which species would be a better choice of lectotype, we here choose the first listed species]. [Note: the new genus proposed here conforms to Bentham's (1844) concept of *Lebeckia* section *Viborgioides*, a taxon for which no name is available at generic level. The name *Wiborgiella* reflects the vegetative similarity and close relation to the genus *Wiborgia*].

Rigid, resprouting, woody shrubs (rarely lignotuberous shrublets or short-lived fireweeds). *Branches* thick and woody (except in two short-lived species); young branches brown, covered with bark (green in only two species), pubescent. *Leaves* digitately trifoliolate; leaflets flat, linear to widely oblanceolate or obovate, pubescent; petioles shorter than leaflets, usually persistent and becoming woody after leaflets are shed, with prominent tubercles in some species. *Stipules* absent. *Inflorescence* terminal, multi-flowered racemes or rarely single-flowered. *Bracts* linear to lanceolate or elliptic, at least slightly pubescent. *Bracteoles* linear to lanceolate, at least slightly pubescent. *Corolla* yellow, glabrous, very rarely a few hairs along the dorsal midrib. *Calyx* subequally lobed, upper sinus often deeper than the lateral or lower sinuses, carinal lobe narrower than the others, pubescent or glabrous. *Standard* ovate to widely ovate to oblong. *Wing petals* oblong, ovate or rarely obovate, shorter, as long as or longer than the keel petals, glabrous; apex obtuse. *Keel petals* oblong or lunate, pockets present or absent, glabrous; apex obtuse. *Anthers* dimorphic, four long, basifixed anthers alternating with five ovate, dorsifixed anthers, carinal anther resembling the ovate, dorsifixed anthers (4+6 configuration). *Pistil* subsessile to stipitate; ovary linear to slightly elliptic, with 4 to many ovules, glabrous, very rarely slightly pubescent on the upper basal parts; style shorter or rarely longer than the ovary, curved upwards, glabrous. *Pods* terete or semi-terete, without wings, inflated or turgid (laterally compressed only in *W. mucronata* (Benth.) Boatwr. and B.-E.van Wyk and *Wiborgiella* sp. 1), oblong to oblanceolate or lanceolate or elliptic, few- to many-seeded, glabrous, dehiscent (rarely indehiscent). *Seeds* reniform, light pink (*W. leipoldtiana*) or black with white or light brown spots (*W. inflata* and *Wiborgiella* sp. 1), surface smooth or rugose [seeds of *W. bowieana*, *W. fasciculata*, *W. humilis* (Thunb.) Boatwr. and B.-E.van Wyk, *W. mucronata* and *W. sessilifolia* (Eckl. and Zeyh.) Boatwr. and B.-E.van Wyk not seen].

### *5.4.1 Diagnostic characters*

The genus is similar to *Wiborgia*, but differs in the oblong, wingless, much inflated fruits (ovate to orbicular, markedly winged, samara-like and laterally compressed in *Wiborgia*). It also differs in that the carinal anther resembles the short, dorsifixed anthers (carinal anther intermediate in both *Wiborgia* and *Calobota*). It further differs from *Calobota* in the glabrous petals (in *Calobota*, at least the standard petal has a few apical hairs) and in the dorsiventral leaves (isobilateral in *Calobota*). It differs markedly from *Lebeckia* s.s. in the flat leaflets (invariably acicular in *Lebeckia*). Bark formation is early and the young twigs are brown and covered with bark as opposed to the green twigs of *Calobota* (the short-lived *W. inflata* and *Wiborgiella* sp. 1 have green stems).

### *5.4.2. Notes on distribution*

The genus is endemic to the Greater Cape Floristic Region.

### *5.5. The species of Wiborgiella*

The following eight species are recognised:

*5.5.1. Wiborgiella bowieana* (Benth.) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia bowieana* Benth. in Hook. Lond. J. Bot. 3: 362–363 (1844). Type—South Africa, ‘Cape’, *Bowie s.n.* [K!, lectotype, designated by Dahlgren (1975)].

*5.5.2. Wiborgiella fasciculata* (Benth.) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia fasciculata* Benth. in Hook. Lond. J. Bot. 3: 361 (1844). Type—South Africa, 'Cape', *Bowie s.n.* [K!, lectotype, designated by Dahlgren (1975)].

*5.5.3. Wiborgiella humilis* (Thunb.) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia humilis* Thunb., Nov. Gen.: 143 (1800). *Wiborgia humilis* (Thunb.) Dahlgr., Op. Bot. 38: 31 (1975). Type—South Africa, 'e Cap. b. Spei', *Thunberg s.n. sub THUNB-UPS 16416* [UPS!, lectotype, designated by Dahlgren (1975)].

*Wiborgia apterophora* Dahlgr., Bot. Notiser 123: 112 (1970). Type—South Africa, Gifberg, sand at edge of lands, *Esterhuysen 22042* (BOL).

*5.5.4. Wiborgiella inflata* (Bolus) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia inflata* Bolus in Hook. Icones Pl. 16: pl. 1576 (1887). Type—South Africa, Western Cape Province, eastern slopes of Devil's Peak, *Bolus 4826* (BOL!, K!, NBG!).

*5.5.5. Wiborgiella leipoldtiana* (Schltr. ex Dahlgr.) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia leipoldtiana* Schltr. ex Dahlgr., Op. Bot. 38: 72 (1975). Type—South Africa, Western Cape Province, Calvinia Div.: 'Inter Grasberg et Nieuwoudtville', *Lewis 5839* (NBG!).

*5.5.6. Wiborgiella mucronata* (Benth.) Boatwr. and B.-E.van Wyk, comb. nov. *Lebeckia mucronata* Benth. in Hook. Lond. J. Bot. 3: 359 (1844). Type—South Africa, Uitenhage, *Zeyher 344* (K!, TCD, photo!); Van Stadensberg, *Zeyher 2318* (S!, SAM!).

*Lebeckia leptophylla* Benth. in Hook. Lond. J. Bot. 3: 359 (1844), synon. nov. Type—South Africa, 'Grassy subalpine situations near Swellendam', *Mundt 87* (K!, S!).

*5.5.7. Wiborgiella sessilifolia* (Eckl. and Zeyh.) Boatwr. and B.-E.van Wyk, comb. nov. *Acanthobotrya sessilifolia* Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 193 (Jan. 1836). *Lebeckia sessilifolia* (Eckl. and Zeyh.) Benth. in Hook. Lond. J. Bot. 3: 362 (1844). Type—South Africa, 'between Breede River and Duyvelshoek', *Ecklon and Zeyher 1344* [S!, lecto.; K!, SAM!, isolecto., designated by Dahlgren (1975)].

*5.5.8. Wiborgiella* sp. 1. *Vlok 2045* (PRE!, 2 sheets).

*5.5.9. Wiborgiella* sp. 2. *Baker 10407* (NBG!).

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Figure captions:

Fig. 1. The "Cape group" taken from (a) a strict consensus tree of the combined analysis of ITS and *rbcL* data(no. trees = 560; tree length = 1473 steps; consistency index = 0.50; retention index = 0.86); and (b) a strict consensus tree of the combined analysis of molecular (ITS and *rbcL*) and morphological data for the tribe Crotalarieae from Boatwright et al. (in press; no. trees = 370; tree length = 1166 steps; consistency index = 0.53; retention index = 0.84). Bootstrap percentages are given above the branches and Bayesian posterior probabilities below the branches. Grey dotted lines indicate alternative topologies in the Bayesian analysis.

Fig. 2. Transverse sections through the leaves of *Lebeckia* species, showing isobilateral (a, b, *Calobota* group) and dorsiventral (c, e, f, *Viborgioides* group) leaflet laminas and an acicular, terete, phyllode with a circular arrangement of palisade cells (d, *Lebeckia* s.s.). Note the presence of mucilage cells in the epidermis. (a) *L. cytisoides;* (b) *L. pungens*; (c) *L. sessilifolia;* (d) *L. sepiaria*; (e) *L. inflata*; (f) *L. mucronata*.

Voucher specimens: (a) *Boatwright et al. 107* (JRAU); (b) *Boatwright et al. 106* (JRAU); (c) *Van Wyk 2120* (JRAU); (d) *Le Roux et al. 10* (JRAU); (e) *Johns 162* (JRAU); (f) *Vlok 1726* (JRAU). Scale bar = 0.2 mm.

Fig. 3. Drawings of the calyces (vestiture not shown), keel petals and anthers of selected species of *Lebeckia* s.l., *Spartidium saharae* and *Wiborgia humilis*. Note the relative size of the carinal lobe of the calyx, the apex and vestiture of

the keel petal and the relative size of the carinal anther. (a1–a3) *W. humilis*; (b1–b3) *L. mucronata*; (c1–c3) *L. inflata*; (d1–d3) *L. leipoldtiana*; (e1–e3) *L. cytisoides*; (f1–f3) *L. pungens*; (g1–g3) *S. saharae*; (h1–h3) *L. sepiaria*.

Voucher specimens: (a1, a3) *Van Wyk 3530* (JRAU); (a2) *Boatwright et al., 216* (JRAU); (b1–b3) *Stirton 10880* (JRAU); (c1–c3) *Vlok et al. 2* (JRAU); (d1–d3) *Boatwright et al. 123* (JRAU); (e1–e3) *Boatwright et al. 107* (JRAU); (f1) *Taylor 9386* (NBG); (f2) *Boatwright et al. 106* (JRAU); (f3) *Van Wyk 3252* (JRAU); (g1–g3) *Hill 1910* (K); (h1, h3) *Barker 6515* (NBG); (h2) *Le Roux et al. 24* (JRAU). Scale bars (for all calyces, all keel petals and all anthers, respectively) = 1.0 mm.

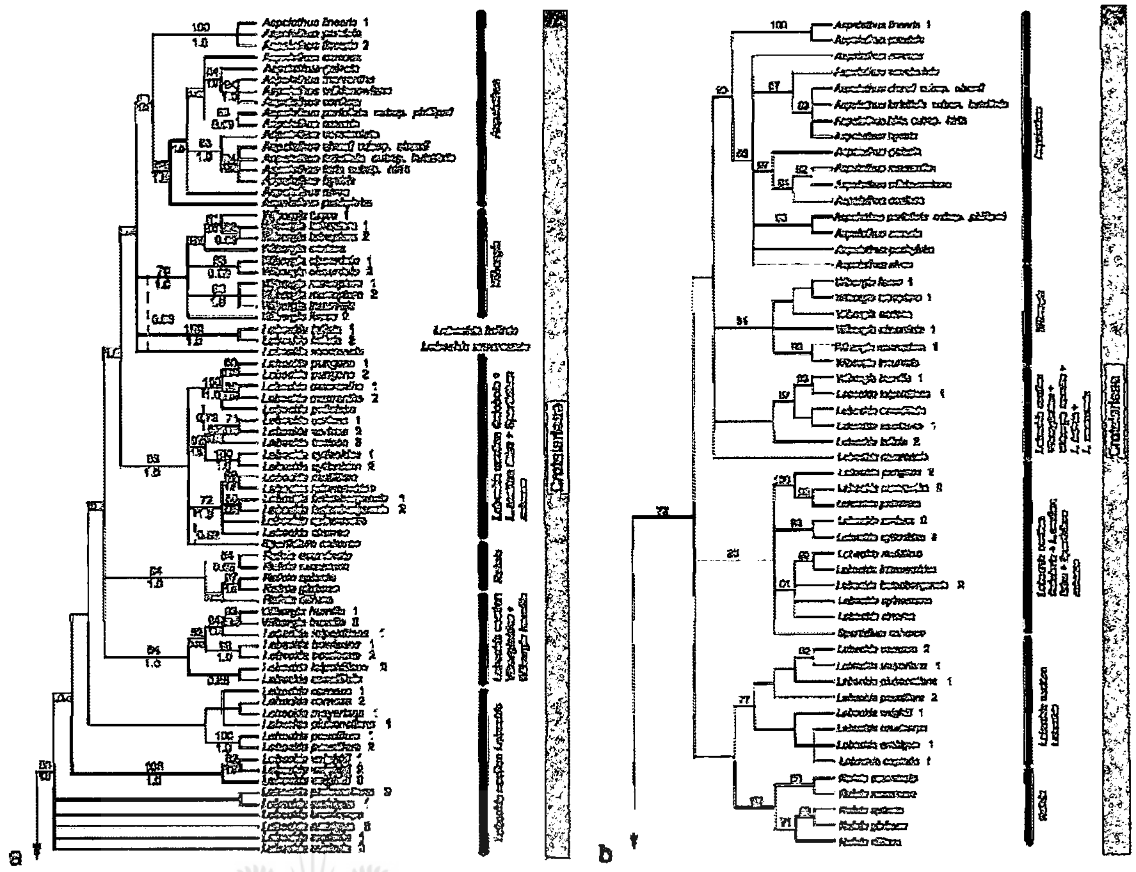

Fig. 1

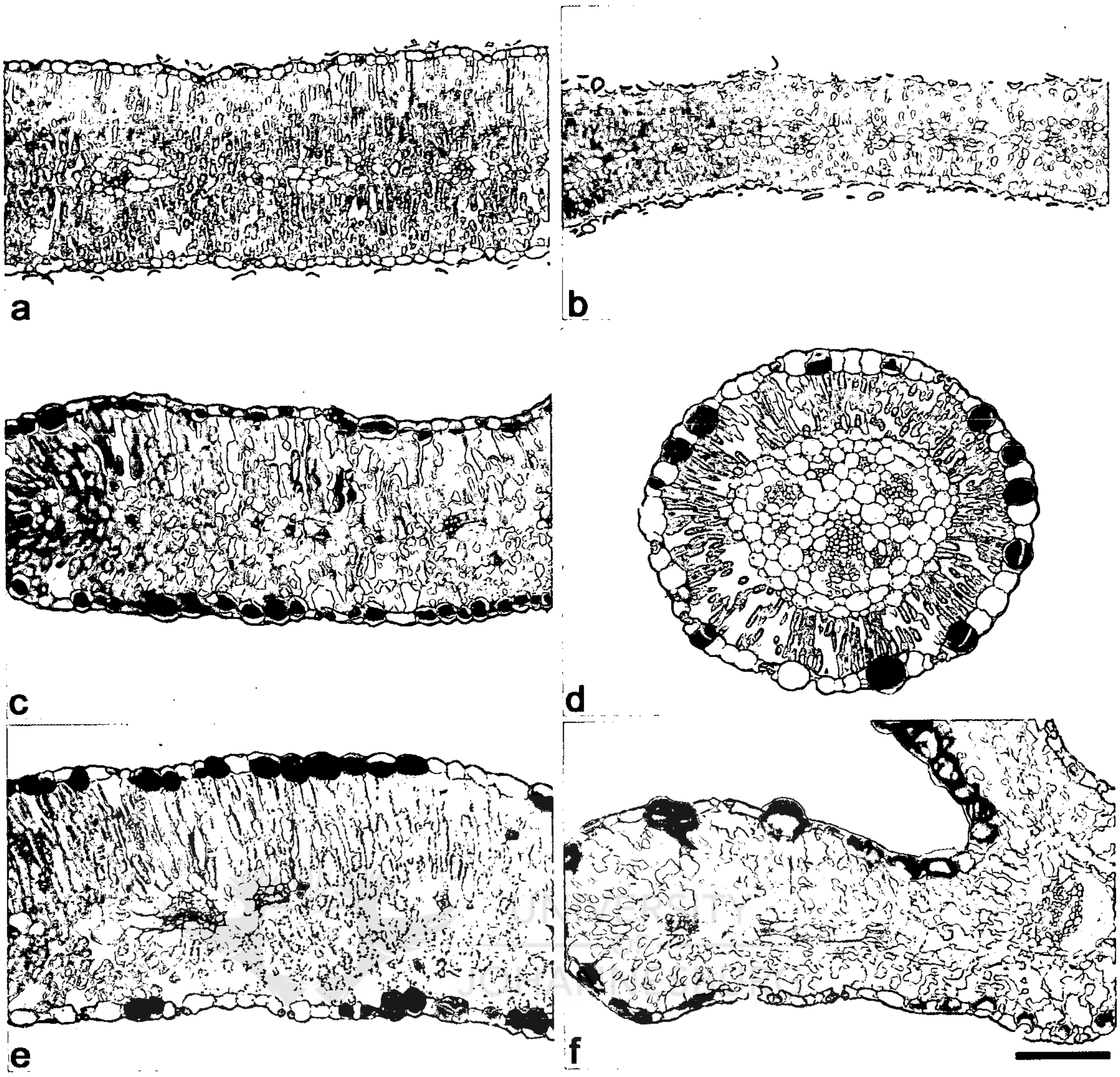

Fig. 2

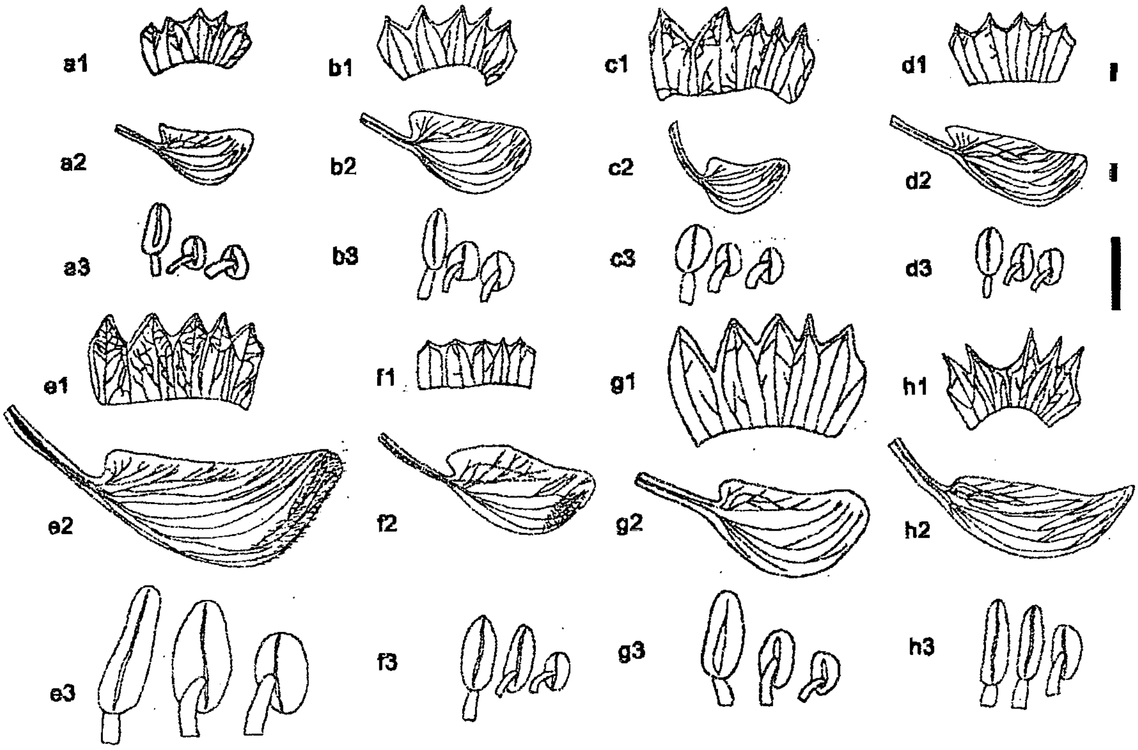

Fig. 3

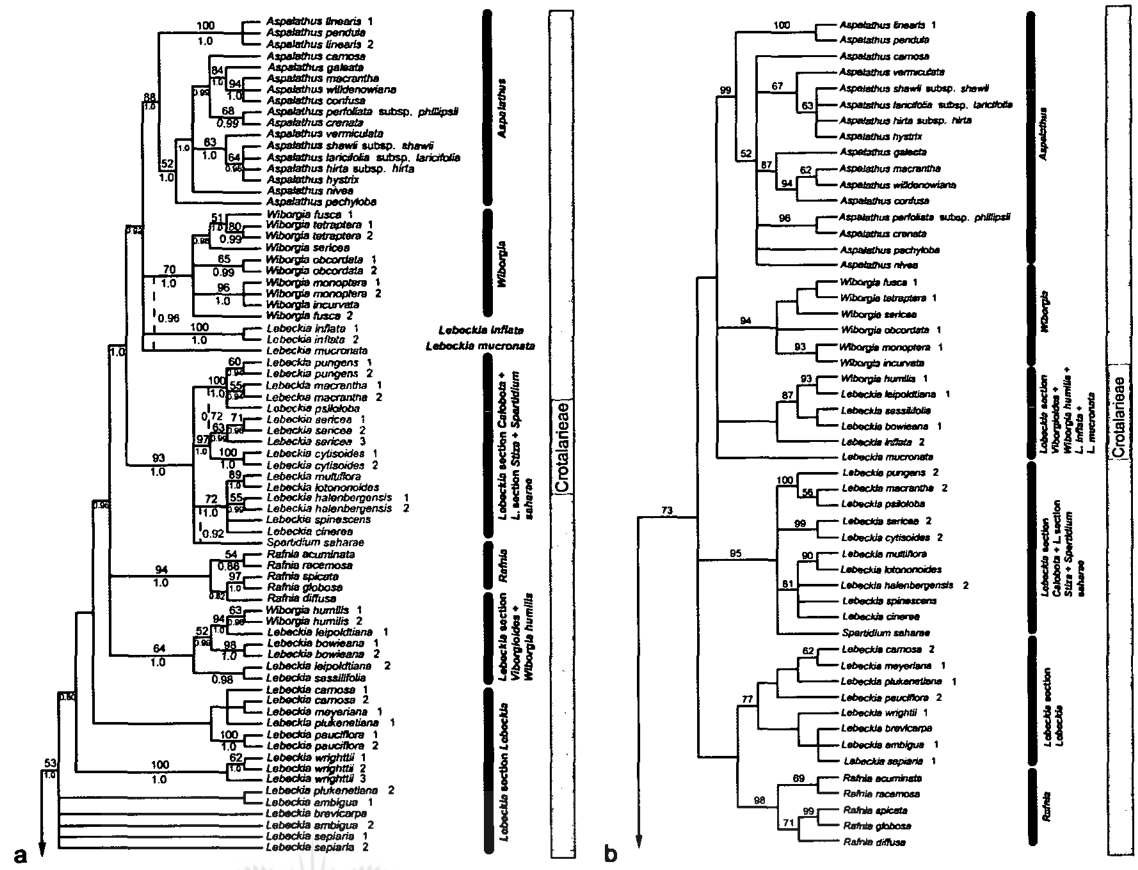
a
Aspalathus linearis 1
Aspalathus pendula
Aspalathus linearis 2
Aspalathus carnosa
Aspalathus galeata
Aspalathus macrantha
Aspalathus willdenowiana
Aspalathus confusa
Aspalathus perfoliata subsp. phillipsii
Aspalathus crenata
Aspalathus vermiculata
Aspalathus shawii subsp. shawii
Aspalathus laricifolia subsp. laricifolia
Aspalathus hirta subsp. hirta
Aspalathus hystrix
Aspalathus nivea
Aspalathus pachyloba
Wiborgia fusca 1
Wiborgia tetraptera 1
Wiborgia tetraptera 2
Wiborgia sericea
Wiborgia obcordata 1
Wiborgia obcordata 2
Wiborgia monoptera 1
Wiborgia monoptera 2
Wiborgia incurvata
Wiborgia fusca 2
Lebeckia inflata 1
Lebeckia inflata 2
Lebeckia mucronata
Lebeckia pungens 1
Lebeckia pungens 2
Lebeckia macrantha 1
Lebeckia macrantha 2
Lebeckia psiloloba
Lebeckia sericea 1
Lebeckia sericea 2
Lebeckia sericea 3
Lebeckia cytisoides 1
Lebeckia cytisoides 2
Lebeckia multiflora
Lebeckia lotononoides
Lebeckia halenbergensis 1
Lebeckia halenbergensis 2
Lebeckia spinescens
Lebeckia cinerea
Spartidium saharae
Rafnia acuminata
Rafnia racemosa
Rafnia spicata
Rafnia globosa
Rafnia diffusa
Wiborgia humilis 1
Wiborgia humilis 2
Lebeckia leipoldtiana 1
Lebeckia bowieana 1
Lebeckia bowieana 2
Lebeckia leipoldtiana 2
Lebeckia sessilifolia
Lebeckia carnosa 1
Lebeckia carnosa 2
Lebeckia meyeriana 1
Lebeckia plukenetiana 1
Lebeckia pauciflora 1
Lebeckia pauciflora 2
Lebeckia wrightii 1
Lebeckia wrightii 2
Lebeckia wrightii 3
Lebeckia plukenetiana 2
Lebeckia ambigua 1
Lebeckia brevicarpa
Lebeckia ambigua 2
Lebeckia sepiaria 1
Lebeckia sepiaria 2
Aspalathus
Wiborgia
Lebeckia inflata
Lebeckia mucronata
Lebeckia section Calobota + L. section Stiza + Spartidium saharae
Rafnia
Lebeckia section Viborgioides + Wiborgia humilis
Lebeckia section Lebeckia
Crotalarieae
b
Aspalathus linearis 1
Aspalathus pendula
Aspalathus carnosa
Aspalathus vermiculata
Aspalathus shawii subsp. shawii
Aspalathus laricifolia subsp. laricifolia
Aspalathus hirta subsp. hirta
Aspalathus hystrix
Aspalathus galeata
Aspalathus macrantha
Aspalathus willdenowiana
Aspalathus confusa
Aspalathus perfoliata subsp. phillipsii
Aspalathus crenata
Aspalathus pachyloba
Aspalathus nivea
Wiborgia fusca 1
Wiborgia tetraptera 1
Wiborgia sericea
Wiborgia obcordata 1
Wiborgia monoptera 1
Wiborgia incurvata
Wiborgia humilis 1
Lebeckia leipoldtiana 1
Lebeckia sessilifolia
Lebeckia bowieana 1
Lebeckia inflata 2
Lebeckia mucronata
Lebeckia pungens 2
Lebeckia macrantha 2
Lebeckia psiloloba
Lebeckia sericea 2
Lebeckia cytisoides 2
Lebeckia multiflora
Lebeckia lotononoides
Lebeckia halenbergensis 2
Lebeckia spinescens
Lebeckia cinerea
Spartidium saharae
Lebeckia carnosa 2
Lebeckia meyeriana 1
Lebeckia plukenetiana 1
Lebeckia pauciflora 2
Lebeckia wrightii 1
Lebeckia brevicarpa
Lebeckia ambigua 1
Lebeckia sepiaria 1
Rafnia acuminata
Rafnia racemosa
Rafnia spicata
Rafnia globosa
Rafnia diffusa
Aspalathus
Wiborgia
Lebeckia section Viborgioides + Wiborgia humilis + L. inflata + L. mucronata
Lebeckia section Calobota + L. section Stiza + Spartidium saharae
Lebeckia section Lebeckia
Rafnia
Crotalarieae

Fig. 1

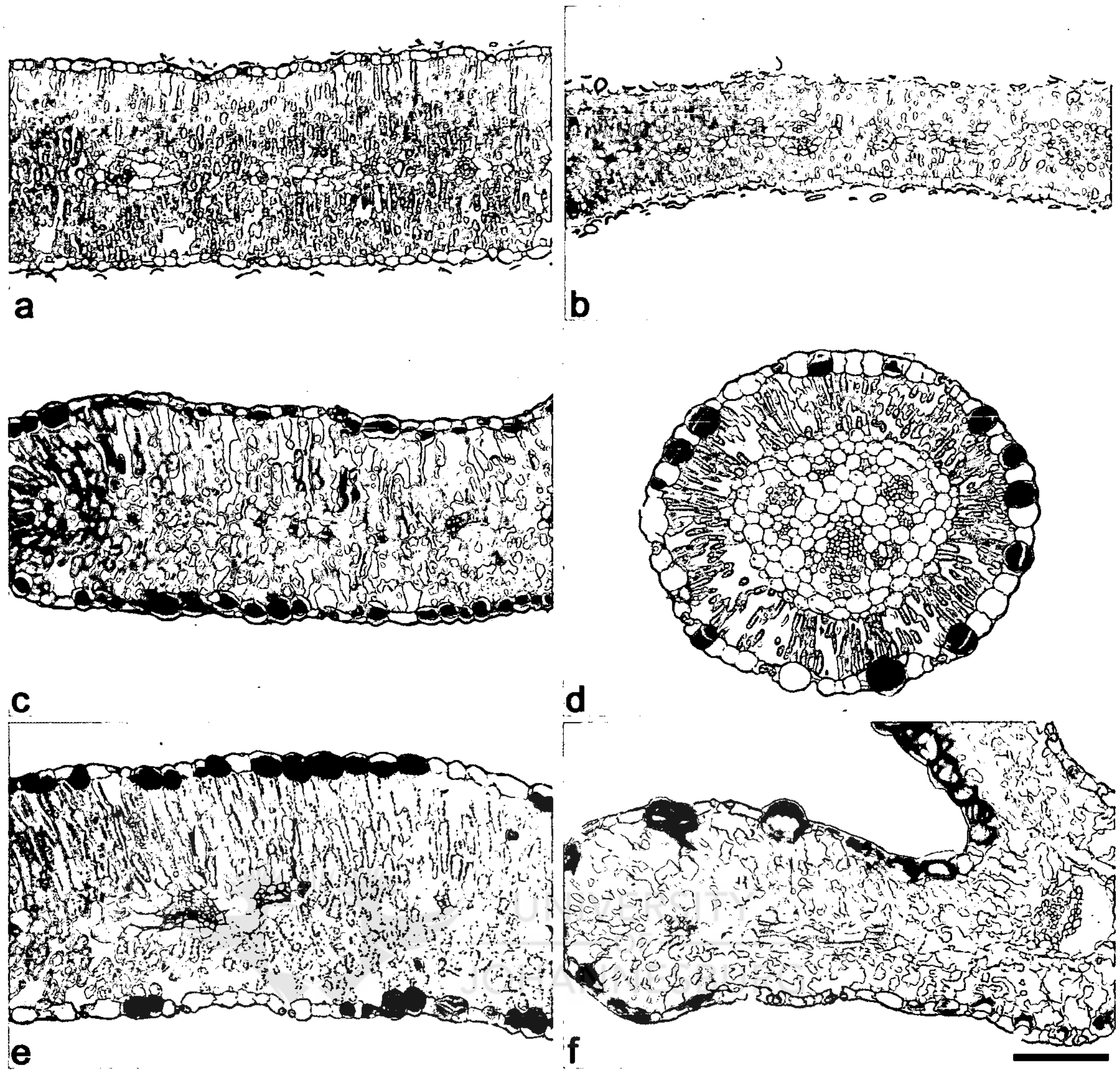

Fig. 2

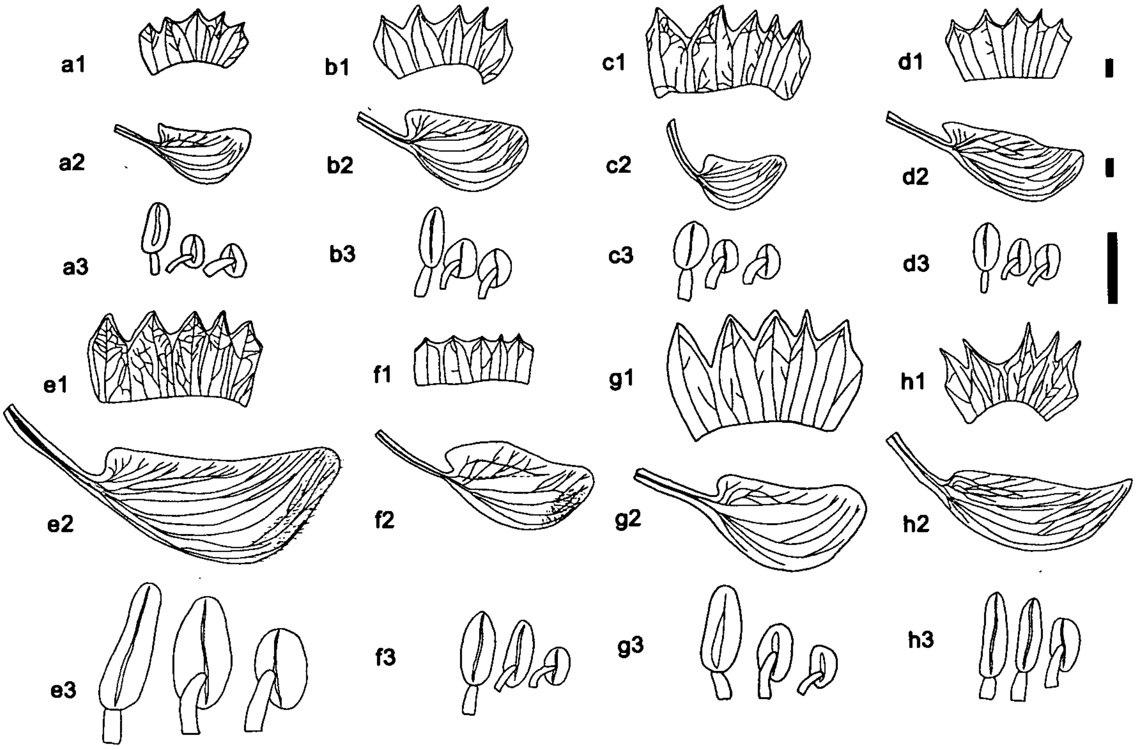

Fig. 3