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A TAXONOMIC STUDY OF
THE GENUS LOTONONIS (DC.) ECKL. & ZEYH.
(FABACEAE, CROTALARIEAE)

BY
BEN-ERIK VAN WYK

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ABSTRACT

The approach and methods used in a taxonomic study of the genus Lotononis (DC.) Eckl. & Zeyh. and related genera of the tribe Crotalarieae (Benth.) Hutch. are briefly introduced in Part 1. Morphological, cytological and chemical data was analyzed by cladistic methods to provide a sound basis for the generic delimitation of Lotononis and to formulate a natural infrageneric classification.

The generic limits of Lotononis and its relationships with 14 other genera of the Crotalarieae are discussed in Part 2. Detailed morphological studies by Polhill (1976) has shown the widespread occurrence of convergence and conflicting character information in the tribe. Only a few of the genera are monothetic taxa and very few characters are available for cladistic analyses. This is not so much due to a lack of data but rather to ambiguity as to how morphological characters should be interpreted. It was therefore decided to concentrate on a study of alkaloids to test the predictivity of the present generic delimitations in the Crotalarieae. With the exception of Crotalaria L., virtually nothing was known about the alkaloids of the tribe (Mears & Mabry 1971, Kinghorn & Smolenski 1981). In the tribe Genisteae, alkaloid patterns show a high degree of conformity with evolutionary patterns based on morphological evidence (Polhill 1976) and the value of alkaloids as a generic

character in the Leguminosae is well known (Kinghorn & Smolenski 1981). It seemed that more insight into generic relations in the Crotalarieae could be gained by concentrating on a hitherto much neglected field rather than to duplicate the detailed morphological studies of Polhill (1976). It was also clear that meaningful conclusions could be made about generic relationships, because the biogenetic pathways along which quinolizidine and pyrrolizidine alkaloids are formed are rather well known. The survey of major alkaloids (Appendices 1 to 11) indeed led to a much better understanding of the intricate relationships in the Crotalarieae, and made it possible to present a well supported and almost fully resolved cladogram for the tribe as a whole.

Infrageneric relationships in Lotononis is considered in Part 3. The genus is poorly known and detailed morphological studies were necessary. The existing sectional classification system was brilliantly conceived by Bentham (1843) when he reduced several genera described by Ecklon and Zeyher (1836) and Meyer (1836) to synonymy within a much enlarged Lotononis. Due to a large number of newly discovered species and a poor understanding of generic limits (particularly between Lotononis and Pearsonia Dümmer and also between Lotononis and Crotalaria) the system has progressively deteriorated in subsequent treatments by Harvey (1862) and Dümmer (1913). The present study has shown that a drastic rearrangement of the species has become necessary to make the system more natural. Evidence is presented to show that the genus Buchenroedera Eckl. & Zeyh. is better included in Lotononis.

as a section, as was tentatively suggested by Polhill (1981a). Morphological, cytological and chemical variation within Lotononis is discussed. The distribution of character states in the genus shows that it is a polythetic group and that there is not a single autapomorphy available which unambiguously supports monophyly. Nevertheless, a broad consideration of the taxonomy of the tribe as a whole and several unique character states indicate that the broad generic concept of Lotononis has considerable predictive value. This will be lost if smaller explicitly monophyletic genera are created. It is suggested that such smaller units should be treated as sections. Despite a large degree of homoplasy, cladistic analyses were successful. The cladogram which is considered to be the most likely reflection of phylogenetic relationships within the genus is used as a basis for the formal taxonomic treatment in Part 5. The recorded geographical distribution of the genus Lotononis and of each of the 15 sections is presented. Regional patterns in species richness and endemism are discussed. Attempts are made to explain the high species diversity and distinct geographical trends in southern Africa. It is suggested that past climatic and geomorphic changes have played an important part in the evolutionary history of Lotononis.

Part 4 gives a brief overview of the taxonomic history of Lotononis. Only a small number of species were known to Linnaeus (1759, 1771), Bergius (1767) and Thunberg (1800, 1823), most of which were included in the early broad concept of Ononis L.

Lotononis was first named and described by De Candolle (1825), who included all the species then known in a new section of the genus Ononis. Bentham (1843) undoubtedly made the most significant contribution and his generic concept has remained virtually unchanged. Much of the groundwork for Bentham's brilliant synthesis was done by Ecklon and Zeyher (1836), who used their own collections, and also by Meyer (1836), who based most of his generic descriptions on material collected by Drège. The revisions of Harvey (1862) and Dümmer (1913) followed Bentham's basic arrangement but collated new information into useful accounts. Due to an improved understanding of generic and infrageneric relationships, as well as many newly discovered species, Dümmer's treatment has become very outdated.

The formal taxonomic treatment of Lotononis is presented in the form of a synopsis in Part 5. The taxonomic structure is based on arguments presented in Part 3 and, except for the sequence, resembles that of Bentham (1843). Sectional limits had to be drastically modified however, and four new sections are described. The genera Buchenroedera, Euchlora and Listia are treated as sections of Lotononis. Subsections are used for the first time to accommodate closely related species within some of the large sections and to give a reflection of the most likely affinities. The synopsis gives the correct nomenclature, complete synonymy, typification, geographical distribution and diagnostic characters for all 151 known species, arranged in 15 sections (some with subsections). Keys to the sections and species are

provided. As an additional aid for identification, the diagnostic characters of all except one species are illustrated. The treatment includes 31 new species and some new subspecies, most of which are described in a series of short papers (Appendices 18 to 33). Distinct forms within the species, apart from subspecies, are illustrated and described but are not yet formally recognized. The rank of variety would be appropriate for most of these. Several specific names are reduced to synonymy and a number of name changes is made. An alphabetical index of all accepted names, all synonyms and some as yet unpublished names is given at the end of Part 5.

To avoid duplication, the reference list includes Appendices 1 to 33 but not all the references cited therein. For the same reason, references given in abbreviated form in Part 5 are also not included.

PART 1

GENERAL INTRODUCTION

The results of taxonomic studies in the genus Lotononis (DC.) Eckl. & Zeyh. and related genera of the tribe Crotalarieae (Benth.) Hutch. are presented in this thesis. A large part of the work has already been published or is currently in press and the papers are included as appendices. All information relevant to the generic and infrageneric relationships of Lotononis is considered here in an attempt to provide a sound empirical basis for the formal taxonomic revision of the genus, which forms the main objective of the study.

A survey of alkaloids as taxonomic characters in the Crotalarieae (a hitherto much neglected field) led to a better understanding of the intricate relationships in the tribe, and made it possible to present a well supported and almost fully resolved cladogram for the tribe as a whole. Chemical data from alkaloidal metabolites is largely congruent with morphological data, but allows refinement of the understanding of the phylogeny.

Cladistic methods present an appropriate tool for analyzing chemical data. Meaningful conclusions can be made about generic relationships in alkaloid-bearing Crotalarieae, because biogenetic pathways along which quinolizidine and pyrrolizidine

alkaloids are formed are rather well known. Generalizations are valid only when an appropriate sampling procedure is used and when compounds are identified by reliable spectroscopic methods. Data should be based on a rigorous quantitative assessment of the presence as well as the absence of compounds. With chemical or any other data, cladistic analyses are not only used to find phylogenies, but to explore patterns of character state distributions at various taxonomic levels.

A classification system should be predictive. By this I mean that an arrangement of taxa obtained from one set of characters should coincide with an arrangement obtained from another set of characters. In other words, it should be possible to predict that any new character information about the taxa will conform to the same hierarchical pattern as is specified in the particular classification system. Taxa should be monophyletic, i.e., they should be defined by at least one shared derived character. For practical reasons, my usage of the concept includes metataxa.

Results of cladistic analyses show that Crotalaria L. is the sister taxon of Lotononis. Similarities between Lotononis and Pearsonia Dümmer are interpreted as convergences and not as evidence of a close relationship between the two genera. The results also suggest that Lotononis and Crotalaria are the most likely outgroup for the four "typical" Cape genera: Rafnia Thunb., Aspalathus L., Wiborgia Thunb. and Lebeckia Thunb.

Within the genus Lotononis, the Benthamian classification is tested for its predictivity. The original sectional system was conceived by Bentham (1843) when he reduced several genera described by Ecklon and Zeyher (1836) and Meyer (1836) to synonymy within a much enlarged Lotononis. Due to a large number of newly discovered species and a poor understanding of generic limits, the system has progressively deteriorated in subsequent treatments by Harvey (1862) and Dümmer (1913). Morphological, cytological and chemical data is presented and analyzed to show the superiority of the original system. A new classification scheme, containing many elements of the original concept, is presented. The revised infrageneric classification makes provision for several newly described species, and reflects new insights into generic and infrageneric relationships.

Buchenroedera Eckl. & Zeyh., Euchlora Eckl. & Zeyh. and Listia E. Mey. are included in Lotononis as sections and four new sections are described. Newly discovered diagnostic characters showed the need to modify the circumscription of some of the sections.

The Crotalarieae are African, with the genus Lotononis diversifying in temperate southern Africa. Distribution patterns do not provide any clue to the origin of the genus, but suggest an early pan-African distribution, with subsequent speciation in localized areas. A few species are present in northern Mediterranean Africa and in eastern and central Africa, but the species richness increases dramatically from north to south. Major centres of species richness include the Cape Region,

Namaqualand, the eastern Cape and the Natal Drakensberg. Patterns of endemism agree with the concept of highland refugia which may have acted as survival centres during periods of unfavourable climatic conditions. Subsequent speciation in and around these centres would explain the localized distribution of the species and most of the sections.

The taxonomic treatment of the genus includes 151 species, arranged in 15 sections. Character variation and differences between the species are clearly illustrated. All illustrations included in this thesis are my own. Data were collected primarily from dried and preserved herbarium material, and from extensive field observations in southern Africa. Accurate information on the habit of many of the species was recorded for the first time. Some previously unknown species were found and several rare or poorly known taxa were rediscovered. Field work also provided material for cytological and chemical studies.

PART 2

GENERIC RELATIONSHIPS

The intricate relationships amongst the genera of the tribe Crotalarieae have been discussed by Dahlgren (1963a, 1967, 1970, 1975), Polhill (1976) and Van Wyk and Schutte (1989, Appendix 17). In the latest treatment at the tribal level, Polhill (1981a) includes 16 genera: Lebeckia Thunb. (ca. 35 spp.), Wiborgia Thunb. (10 spp.), Rafnia Thunb. (ca. 25 spp.), Aspalathus L. (275 spp.), Spartidium Pomel (1 sp.), Crotalaria L. (ca. 600 spp.), Bolusia Benth. (5 spp.), Lotononis (DC.) Eckl. & Zeyh. (151 spp. as presently circumscribed), Buchenroedera Eckl. & Zeyh. (11 spp., here treated as a section of Lotononis), Pearsonia Dümmer (12 spp.), Rothia Pers. (2 spp.), Robynsiophyton Wilczek (1 sp.), Melolobium Eckl. & Zeyh. (ca. 20 spp.), Dichilus DC. (5 spp.) and two other genera that were only tentatively included, namely Anarthrophyllum Benth. (15 spp.) and Sellocharis Taub. (1 sp.). It was recently suggested that Argyrolobium Eckl. & Zeyh. and the newly described Polhillia Stirton are very closely related and that both should be included in the Crotalarieae near Melolobium (Van Wyk & Schutte 1989, Appendix 17). The correct taxonomic position of the two highly modified South American genera Anarthrophyllum and Sellocharis is very doubtful (Polhill 1976, 1981a) and is not considered here. Cytological evidence (Goldblatt 1981) indeed suggests a position in the tribe

Genisteae near Lupinus L. The two small genera Bolusia and Robynsiophyton were also not included in this study, partly due to insufficient material, but also because they are assumed to be local derivatives of respectively Crotalaria and Pearsonia.

Detailed studies by Polhill (1976) have shown that single morphological characters rarely have diagnostic value at the generic level and that most of the genera can only be characterized by combinations of characters. Conclusions about generic relationships, as reflected in the sequence of genera in Polhill (1981a), were based on morphological similarities and considerable experience in legume taxonomy. It is possible to translate the sequence into the phylogenetic tree given in Figure 2.1. Polhill never gave explicit ideas about the sequence of branching and the figure is used here only to show what is probably a fairly accurate summary of presumed taxonomic relationships based on morphological evidence. Argyrolobium and Polhillia are included in the group of genera with bilabiate calyces, as suggested by Van Wyk and Schutte (1989, Appendix 17). Polhillia is not shown separately in Figure 2.1. The "Lotononis group" (Polhill 1981a) includes all the genera with zygomorphic calyces, i.e., those which have the upper and lateral lobes on either side fused higher up in pairs. This group is shown as the polychotomy B in Figure 2.1

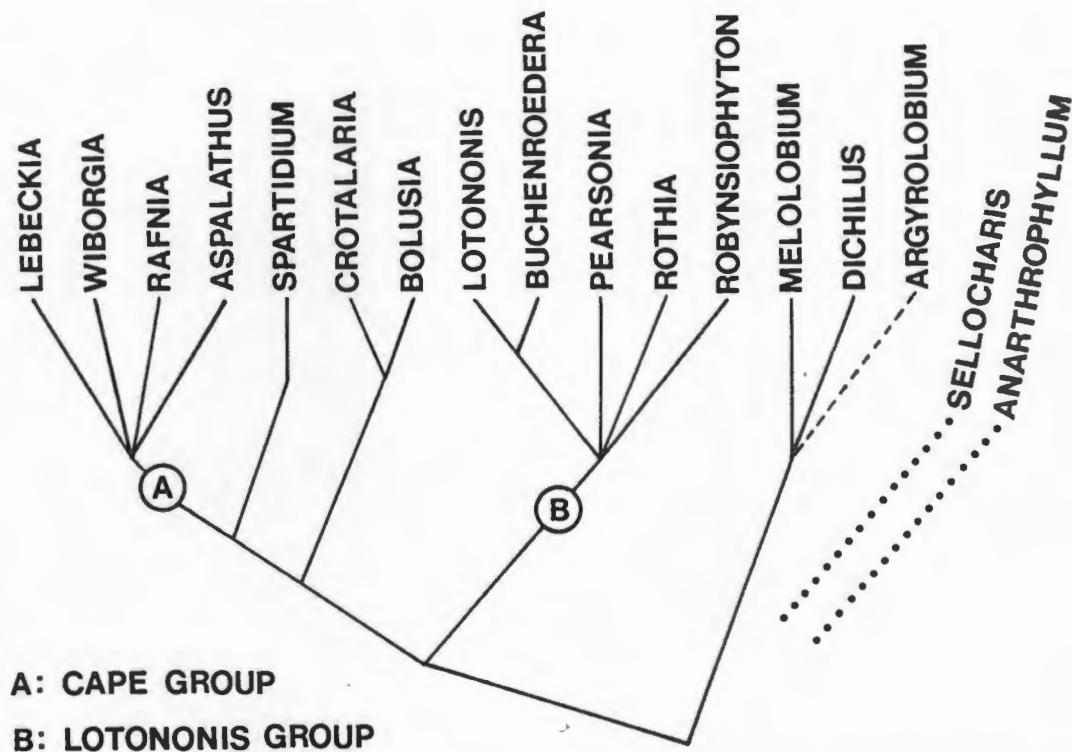


Figure 2.1. Phylogenetic tree showing relationships between genera of the tribe Crotalarieae (based on morphological evidence) as suggested by their sequence in Polhill (1976, 1981a).

A preliminary study of alkaloid patterns in some genera (Van Wyk *et al.* 1988c, Appendix 1) indicated that chemical evidence may have considerable value as a means of testing the predictivity of the presumed affinities as given in Figure 2.1. A systematic survey of alkaloids in all the major genera (Appendices 2 to 11) confirmed the presence of very definite qualitative and quantitative discontinuities. Several quinolizidine, piperidyl and pyrrolizidine alkaloids were identified in extracts from species of Argyrolobium (Van Wyk & Verdoorn 1989a, Appendix 6),

Aspalathus (Van Wyk & Verdoorn 1989d, Appendix 9), Dichilus (Van Wyk et al. 1988c, Appendix 5), Lebeckia (Van Wyk & Verdoorn 1989b, Appendix 7), Lotononis (Van Wyk & Verdoorn 1988, 1989c, Appendices 2 & 8), Melolobium (Van Wyk et al. 1988a, Appendix 3), Pearsonia (Van Wyk & Verdoorn 1989e, Appendix 10), Polhillia (Van Wyk et al. 1988b, Appendix 4), Rafnia (Van Wyk & Verdoorn 1989d, Appendix 9), Rothia (Hussain et al. 1988), Spartidium (Van Wyk et al. 1989, Appendix 11) and Wiborgia (Van Wyk & Verdoorn 1989d, Appendix 9). Of particular significance was the discovery of macrocyclic pyrrolizidine esters in Lotononis and Buchenroedera, which confirmed the idea of a very close relationship between the two genera and also indicated a possible relationship with the genus Crotalaria. The isolation of several lupanine-type esters from species of the genus Pearsonia was also of special interest, because these angelate and tiglate esters appear to be restricted to Rothia and Pearsonia. Some new compounds with unusual substitution patterns were found in Pearsonia and this discovery led to the structural elucidation of 3 β -hydroxy-lupanine, a compound previously known as 4 β -hydroxylupanine (nuttalline) (Verdoorn & Van Wyk 1989).

The biochemical pathways along which most of the alkaloids are formed have been studied by Nowacki and Waller (1977) and later workers and are now rather well known (for a review see Wink 1987 and references therein). A detailed summary of the pathways for quinolizidine alkaloids is given by Salatino and Gottlieb (1980, 1981) and Gomes et al. (1981). [See also Mattocks 1986 for a

recent review of the biosynthesis of pyrrolizidine alkaloids]. This information is very useful, because it allows meaningful comparisons of the biosynthetic routes in which the different genera seem to specialize. Figure 2.2 gives a diagrammatic summary of the most likely biosynthetic pathways of quinolizidine and pyrrolizidine alkaloids, the various steps of which are explained in the caption of Figure 2.2.

All available data on the distribution of alkaloids in the tribe (see Appendices 1 to 11 for details on the methods of extraction, isolation and identification of compounds) were summarized in the form of "alkaloid profiles" for each of the genera as shown in Figure 2.2. The alkaloid patterns suggest four major groups:

1. An unspecialized group without α -pyridone alkaloids and without esters of alkaloids (Aspalathus, Lebeckia, Rafnia, Wiborgia and Spartidium).
2. A group specializing in lupanine-type esters (Pearsonia and Rothia).
3. A group with macrocyclic pyrrolizidine alkaloids (Crotalaria and Lotononis sensu lato, i.e., Buchenroedera included).
4. A specialized group with α -pyridone alkaloids (Argyrolobium, Dichilus, Melolobium and Polhillia).

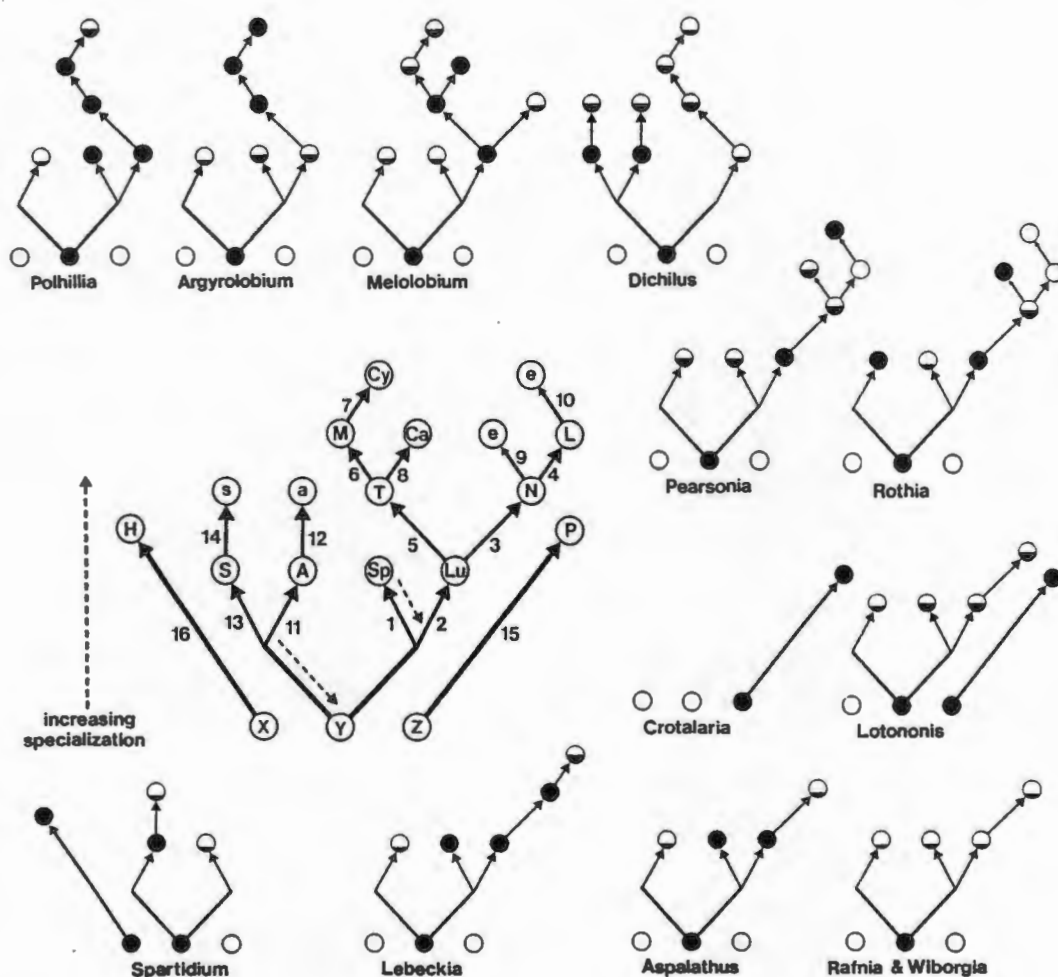


Figure 2.2. Diagrammatic summary of major biogenetic pathways of the alkaloids reported from the tribe Crotalarieae and a comparison of alkaloid profiles of 13 genera for which alkaloid data is available. Directions of arrows suggest increasing specialization. Major pathways: X, imidazole alkaloids; Y, quinolizidine alkaloids (lysine pathway); Z, pyrrolizidine alkaloids (ornithine pathway). Basic type(s) of major compounds (indicated by letters): H, histamine derivatives; S, smipine; s, N'-derivatives of smipine; A, ammodendrine; a, N'-derivatives and aromatic derivatives of ammodendrine; Sp, sparteine; Lu, lupanine and lupanine stereo-isomers; T, lupanine-type structures with α -pyridone ring (thermopsine and anagyrrine); M, N-methylcytisine; Cy, cytisine; Ca, camoesine and leontidine; N, monohydroxylated lupanines (nuttalline and 13-hydroxylupanine); L, polyhydroxylated lupanines (lebeckianine the only example reported from the Crotalarieae thus far); e, mono-esters of hydroxylated compounds. Steps in pathways (indicated by numbers): 1, cadaverine to sparteine (loss of ability to accumulate sparteine is taken to be a derived character state as indicated by broken arrow); 2, transformation of α -ring to carbonyl; 3, hydroxylation of lupanine; 4, increased hydroxylation; 5, olefination of α -ring; 6, fissure of δ -ring and removal of a propyl moiety; 7, demethylation of N-methylcytisine; 8, fissure of δ -ring, demethylenation of N-butyl moiety and ring fusion; 9, esterification with angelic-, tiglic- and Z & E cinnamic acids on C-13 position; 10, mono-esterification of C-4 or C-13 positions with angelic acid; 11, formation of piperidine ring; 12,

N'-derivatization of ammodendrine and aromatization of piperidine rings; 13, formation of pyrrole ring; 14, N'-derivatization; 15, formation of macrocyclic ester from pyrrolizidine base and necic acid; 16, amidation of histamine by Z & E cinnamic acids.

Furthermore, it was possible to polarize the character states for a cladistic analysis based on alkaloid data alone. These characters and the way in which they were polarized are shown in Table 2.1 below (the first 12 characters are from alkaloid data, characters 13 to 25 were added for later analyses).

Cladistic analyses were performed to evaluate the significance of the alkaloid data in determining the most likely phylogenetic relationships between the genera. The computer program "Hennig 86" (Farris 1988) was used in the following three analyses. The "mhennig*" and "bb*" commands were used to make sure that all possible topologies were found (see Part 3.2 for the various options available in the "Hennig 86" program).

The three analyses were:

- A. Alkaloid data only (characters 1 to 12, polarized as in Table 2.1)
- B. Morphological data and chromosome base number (characters 13 to 25, polarized as in Table 2.1).
- C. All characters combined (complete data set as in Table 2.1).

TABLE 2.1. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN 13 GENERA OF THE TRIBE CROTALARIEAE. (Autapomorphies in alkaloid characters were not removed because they show the way in which these characters were polarized)

TAXA	CHARACTERS & CHARACTER STATES																									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
hypothetical																										
ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<u>Argyrobolium</u>	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1
<u>Aspalathus</u>	0	0	0	1	0	0	0	0	0	1	0	0	1	0	2	0	1	0	1	0	1	0	0	0	0	2
<u>Crotalaria</u>	0	1	0	1	0	1	0	0	0	0	0	1	1	0	1	0	1	0	0	0	1	0	0	0	1	0
<u>Dichilus</u>	0	0	1	0	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
<u>Lebeckia</u>	0	0	0	1	0	0	0	0	0	2	0	0	1	0	1	0	1	0	1	0	1	0	1	0	1	2
<u>Lotononia</u>	0	0	0	1	0	0	0	0	0	1	0	1	1	0	1	0	1	1	1	0	1	0	0	0	1	0
<u>Melolobium</u>	0	0	0	0	0	0	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	2
<u>Pearsonia</u>	0	0	0	0	0	0	0	0	0	1	2	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0
<u>Polhillia</u>	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	1
<u>Rafnia</u>	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	1	0	1	0	1	0	0	0	0	1
<u>Rothia</u>	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1	0	1	0	1	0	0	0	0
<u>Spartidium</u>	1	0	1	0	0	0	0	0	0	0	0	0	1	0	2	0	1	0	1	0	0	0	0	0	0	?
<u>Wiborgia</u>	0	0	0	1	0	0	0	0	0	1	0	0	0	0	2	0	1	0	1	0	1	0	1	0	1	2

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

ALKALOIDAL EVIDENCE (Comments in brackets refer to Figure 2.2):

1. HISTAMINE DERIVATIVES (pathway X): absent = 0, present = 1.
2. QUINOLIZIDINE AND PIPERIDYL ALKALOIDS (lysine pathway, Y): present = 0, absent = 1.
3. SMIPINE AND DERIVATIVES (steps 13 & 14): absent = 0, present = 1.
4. AMMODENDRINE (step 11): present as a major compound in at least some species = 0, at best in trace quantities = 1.
5. AMMODENDRINE DERIVATIVES (step 12): absent = 0, present = 1.
6. SPARTEINE (step 1): present = 0, absent = 1.
7. α -PYRIDONE ALKALOIDS (step 5): absent = 0, present = 1.
8. THERMOPSINE, RATHER THAN ANAGYRINE (T): absent = 0, present = 1.
9. C₁₄- α -PYRIDONES (step 8): absent = 0, present = 1.
10. HYDROXYLATED LUPANINES (steps 3 & 4): \pm absent = 0, monohydroxy type (step 3) present = 1, polyhydroxy type (step 4) present = 2.
11. LUPANINE-TYPE ESTERS (steps 9 & 10): \pm absent = 0, monohydroxy type (step 9) present = 1, polyhydroxy type (step 10) present = 2.
12. PYRROLIZIDINE ALKALOIDS (pathway Z): absent = 0, present = 1.

MORPHOLOGICAL EVIDENCE:

13. LEAF TYPE: digitate = 0, often unifoliate or simple = 1.
14. PETIOLE ANATOMY: fibres usually not present on the adaxial side of the main vascular bundle = 0; fibres invariably present = 1. (This character state has been found in some species of Crotalaria and Lotononia, but so far not in any of the other genera -- see Van Wyk & Schutte 1989, Appendix 17).
15. STIPULES: invariably present = 0, often dimorphic and/or absent = 1, invariably absent = 2.
16. STIPULE ATTACHMENT: narrow = 0, clasping the stem = 1.
17. CALYX STRUCTURE (Genisteae or Podalyrieae/Liparieae as outgroup): with a trifid lower lip = 0, without a trifid lower lip = 1.
18. CALYX (LATERAL SINUSES): as deep or deeper than the upper and lower ones = 0, shallower = 1.
19. CARINAL ANTHER (Genisteae or Podalyrieae/Liparieae as outgroup): similar to basifixed ones (5 + 5 arrangement) = 0, intermediate in size (6 + 4 arrangement) = 1.
20. ANTHER DIMORPHISM (see Polhill 1974, who argued that lack of dimorphism is a derived condition in Pearsonia and Rothia): dimorphic = 0, all similar in size and shape = 1.
21. GYNOCIDIUM BASE: sessile or subsessile = 0, often stipitate = 1.
22. STYLE CURVATURE: curved upwards = 0, straight or downcurved = 1.
23. FRUIT APPENDAGES: pod not winged = 0, pod with at least the upper suture winged (in some species) = 1.
24. SEED SURFACE: smooth = 0, often rugose or tuberculate = 1.

CYTOLOGICAL EVIDENCE

25. CHROMOSOME BASE NUMBER (see Goldblatt 1981, p. 449; Van Wyk & Schutte 1988a, 1988b; and discussion in the text): 7 = 0, 8 = 1, 9 = 2.

Analysis A resulted in a single tree with a length of 12 character state changes and a consistency index of 75. This cladogram is shown in Figure 2.3a. As would be expected for such a small number of characters, the cladogram is only partly resolved and includes several polychotomies. Nevertheless, the very high consistency index shows that alkaloids are useful as cladistic characters and that the grouping based on similarities ("alkaloid profiles" in Figure 2.2) is valid.

The similarity between the alkaloid cladogram (Figure 2.3a) and the phylogenetic tree based on morphological similarities (Figure 2.1) is obvious. Both show an early divergence of the group of genera with bilabiate calyces, followed by the two genera with "gullet-type" flowers (Pearsonia and Rothia). The cladogram differs from the phylogenetic tree mainly in the relationships between Polhill's (1981a) "Cape genera" and the "Lotononis group". The "Cape genera" still forms a polychotomy but it now also includes Crotalaria and Lotononis, the latter shown to be misplaced in the "Lotononis group". The distribution of major alkaloids strongly suggests that Crotalaria and Lotononis are sister groups (defined by the presence of pyrrolizidine alkaloids) and that Pearsonia and Rothia represent a separate specialization (presence of lupanine-type esters). This conflict between morphological and alkaloidal evidence was explored in more detail, particularly because it has an important bearing on

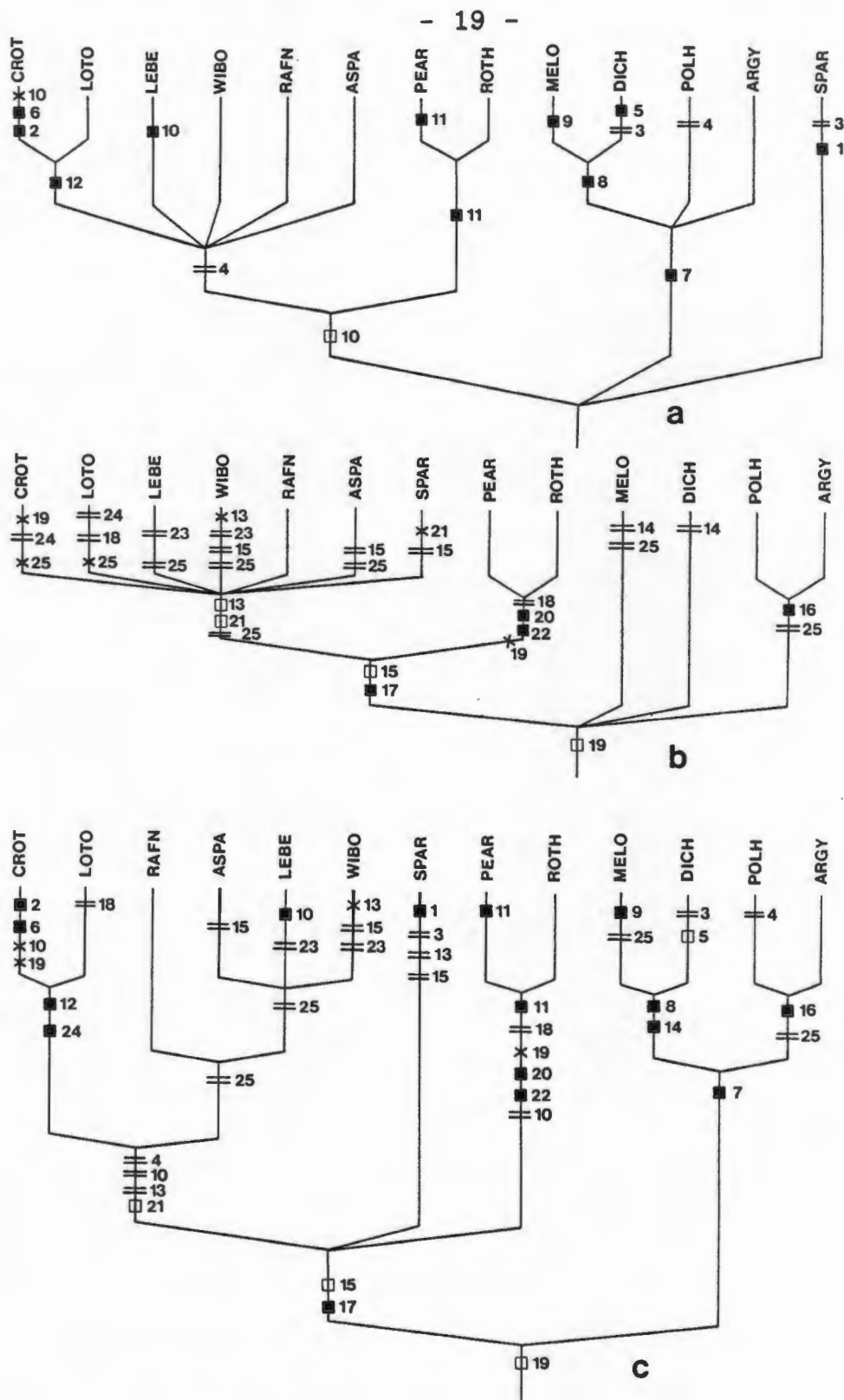


Figure 2.3. Phylogenetic relationships between 13 genera of the tribe Crotalarieae: a, cladogram based on alkaloid data only; b, Nelson Consensus Tree based on morphological data and chromosome base number only; c, Nelson Consensus Tree based on the complete data set as given in Table 2.1 (The four trees of minimum length which resulted from the combined data set are shown in Figure 2.4. Key to the symbols used: ■, apomorphies showing no reversal or convergence; □, apomorphies with reversal higher up in the cladogram; ×, reversals; =, convergences. Characters are numbered as in Table 2.1.

the phylogeny of Lotononis. It was therefore decided to do a second analysis, using only morphological data and chromosome base number (Analysis B).

The virtual absence of monothetic characters in the tribe Crotalarieae is well known, and makes it very difficult to find reliable characters for cladistic analyses. Many morphological characters are distributed in such a way that they can only be used if the present generic limits are ignored and totally artificial groups are created. Some of these characters would lead to an unsatisfactorily high incidence of homoplasy as a result of convergence. Pimentel and Riggins (1987) have argued that variable characters should be left out of analyses or should be coded as unknown, but this seems very restrictive and, except for some generic autapomorphies, would exclude virtually all of the few morphological characters that are available. Table 2.1 shows 13 characters (mainly morphological) that seemed potentially useful and which could be added to the alkaloid data. Polarity decisions (except for obvious ones) are motivated in the footnotes of Table 2.1. This data set of 13 characters produced 38 equally parsimonious trees (length 24, consistency index 62) with the bb* routine of Hennig 86. A Nelson Consensus Tree of the bb result is shown in Figure 2.3b. It shows the same terminal polychotomy ("Cape group") as the alkaloid cladogram (except that Spartidium is now included), the same position for Pearsonia and Rothia and also a basal position for the genera with bilabiate calyces. The latter however, is no longer shown as a clade. The

rather high consistency index of the 38 shortest trees indicates that the large number of trees is not entirely due to ambiguity in the data but rather to an imbalance between the number of characters and the number of genera. Interestingly, the morphological data also fail to resolve the "Cape genera" polychotomy, but it provides strong evidence that this group should in fact include Lotononis and Crotalaria, as was indicated by the alkaloid data.

Finally, the complete data set of 25 characters was analysed, using the "mhennig*", "bb*" and "ie*" commands of Hennig 86. The latter two options produced the same result, namely four shortest trees with a length of 37 character state changes and a consistency index of 64. The four cladograms are shown in Figure 2.4. This result is virtually the same as with the previous two analyses, except that the "Cape genera" polychotomy is now almost fully resolved. The only differences between the four cladograms in Figure 2.4 are the position of Spartidium and the sequence of branching in Lebeckia, Aspalathus and Wiborgia. This is obvious from the Nelson Consensus Tree, which is shown in Figure 2.3c (placed here to facilitate the comparison with previous results). The basic topology of all the cladograms shown in Figure 2.3 is quite similar. Clearly, there is a remarkable congruence between the alkaloid data and the morphological data. When combined, the two data sets produced an almost fully resolved cladogram.

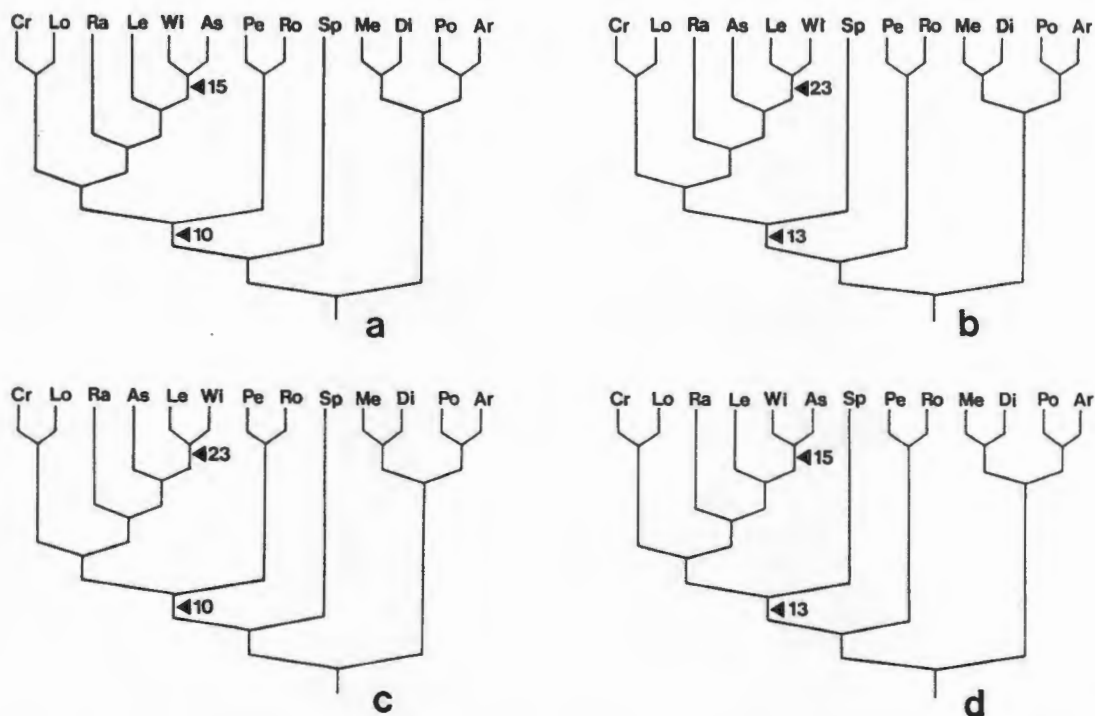


Figure 2.4. Phylogenetic relationships between 13 genera of the tribe Crotalarieae: a, b, c & d, four shortest cladograms produced by the complete data set in Table 2.1; The characters responsible for the lack of resolution are indicated.

A large number of modifications to the matrix shown in Table 2.1 was analyzed to study the effect of different polarizations on tree length and tree topology. When Crotalaria and Lebeckia are used as outgroups for the tribe as a whole, the consistency indices were generally much lower. The respective topologies produced with these two genera as outgroups were often equally parsimonious but very different from one another. Chromosome base number invariably showed the highest number of changes and seems critically important, particularly because even minor changes in the polarity decision have a dramatic effect on the topology of the "Cape group". When $x = 7$ was polarized as the base number for

the tribe as a whole (contrary to current belief that $x = 9$ is basic; see Goldblatt 1981) the tree lengths and consistency indices were generally much improved and never resulted in longer trees. When $x = 9$ is taken as basic, the character usually shows an early advance to $x = 7$, with subsequent reversals back to 8 and 9. Except for Crotalaria and Lotononis, base numbers for the genera were taken from Goldblatt (1981). The base number for Crotalaria is given here as $x = 8$, but Polhill has indicated (pers. comm.) that he considers $x = 7$ in some species to be the plesiomorphic condition. Several counts for Lotononis (Van Wyk & Schutte 1988a) have shown the common occurrence of $2n = 28$ and it is here suggested that $2n = 18$ may be a secondary development in Lotononis (all annual species have $2n = 18$, for example). Dichilus ($2n = 28$ in all five species) was recently shown to be tetraploid (Van Wyk & Schutte, unpublished) so that $x = 7$ can be accepted as the base number for this genus (the base number for Dichilus was not given in Goldblatt 1981). Dahlgren (1967, 1971) reported the presence of $x = 7$ in a few species of Aspalathus, but it was argued that the condition is secondary and that $x = 9$ is basic for Aspalathus. The chromosome number for Spartidium is not known and more counts, also for some of the other genera, are clearly needed. However, it seems that $x = 9$ as base number for the tribe as a whole may have to be reconsidered.

The Nelson Consensus Tree produced by the complete data set (Figure 2.3 c) shows a remarkable degree of conformity with the presumed evolutionary sequence suggested by morphological

evidence (Figure 2.1) and differs from the other two cladograms (Figure 2.3a & b) only in that it is much better resolved. It reflects the intricate relationships between Polhill's (1981a) "Cape genera" (Aspalathus, Lebeckia, Rafnia and Wiborgia) and suggests that Crotalaria and Lotononis should be included here as sister taxa. The position of Spartidium shows the lack of evidence (other than morphological similarity) to support a close relationship with Lebeckia. The Pearsonia/Rothia and Argyrolobium/Melolobium clades are quite robust and are defined by rather convincing and unambiguous apomorphies.

Of the four equally parsimonious trees in Figure 2.4, the cladogram shown as b appears to be superior for two reasons. Firstly, Spartidium is morphologically virtually indistinguishable from Lebeckia (Polhill 1976) and an affinity with the now broadened "Cape group" seems likely. The very long funicles in S. saharae (Coss.) Pomel indeed suggest an affinity with Lotononis, where such long funicles occur in several species. I am here arguing on "critical tendencies" (Wernham 1912) or "apomorphic tendencies" (Cantino 1982, 1985), well aware of the criticism of the term (Rasmussen 1983, but see Cronquist 1987). Cantino (1982, 1985) suggested that evolutionary parallelism in itself may give some indication of relationship. The ambiguous distribution of character states in the Crotalarieae, and particularly in the large genera, makes it difficult to summarily dismiss the possibility that homologous characters may be expressed in some taxa but suppressed in

others. Secondly, all available evidence points to a very close relationship between Lebeckia and Wiborgia. Dahlgren (1967, 1975) considered these two genera to be only marginally distinct at the generic level. Species of Lebeckia section Wiborgioides Benth. are morphologically almost identical to species of Wiborgia and the same is true for their alkaloids (Van Wyk & Verdoorn 1989b, 1989d, Appendices 7 & 9). Some of the phenetic similarities between Lebeckia and Wiborgia may indeed prove to be synapomorphies. The cladogram in Figure 2.4b is therefore presented here as the most likely estimate of evolutionary relationships in the tribe Crotalarieae.

As a final presentation of available evidence, and to illustrate the predictive value of the hierarchy in Figure 2.4b, the distribution of generic autapomorphies and some "apomorphic tendencies" was plotted on the chosen topology as shown in Figure 2.5.

The concept of predictivity is often discussed in the literature (for examples, see Kitts 1977, Nelson 1978, Cracraft 1978, Ruse 1979 & Cronquist 1987) and forms a central part of my thinking. According to Ruse (1979), William Whewell in 1840 was one of the first philosophers to formulate the concept. Cracraft (1979) expresses it in the following words: "There is an expectation -- a prediction -- that certain observational relationships will hold given the initial premises". Cronquist (1987) considers predictivity an attribute of natural classification: that new

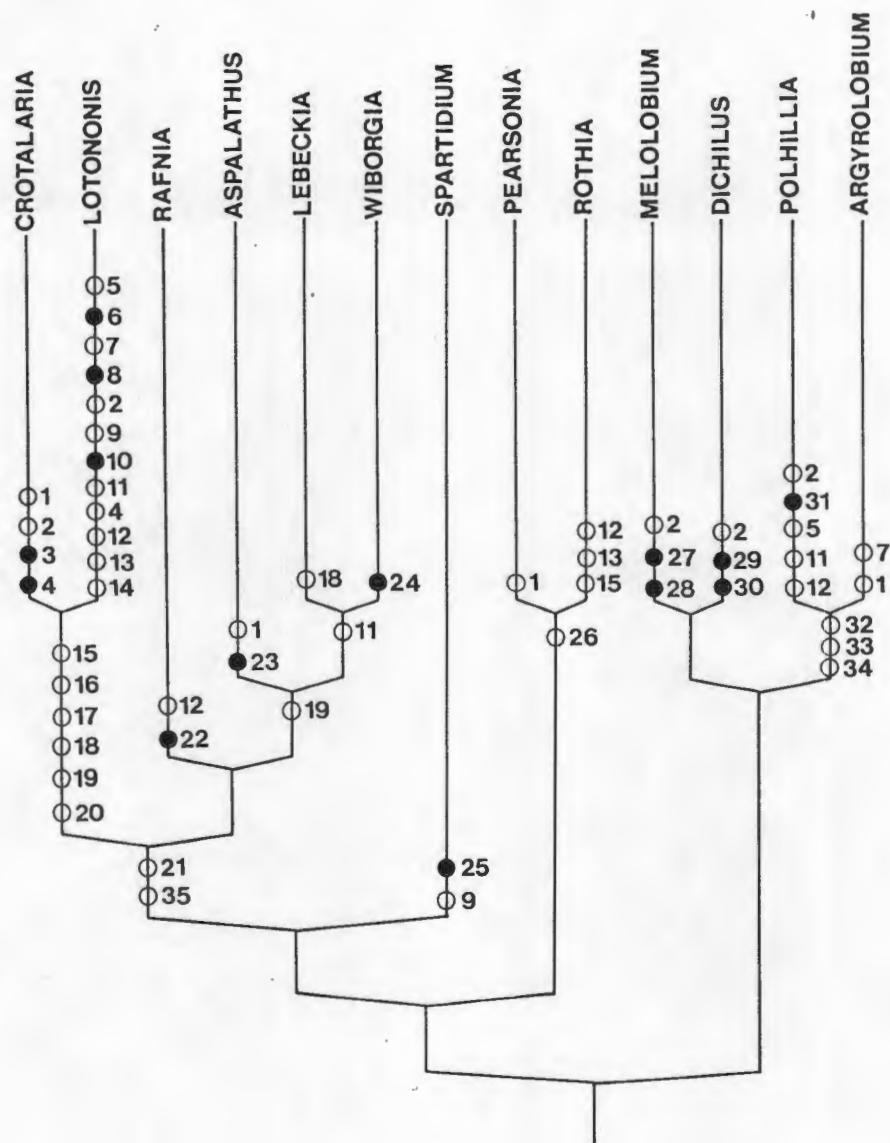


Figure 2.5. Chosen cladogram (from Figure 2.4b), showing taxonomically useful characters (●) and variable or convergent characters (○) that were not used in the cladistic analysis. The character states are: 1, aneuploidy; 2, chromosome number; 3, style geniculate; 4, keel strongly beaked; 5, flexuous-plicate pods; 6, cyanogenesis; 7, dimorphic flowers; 8, polyploidy; 9, long funicles; 10, fruit with the upper suture verrucose; 11, fruit indehiscent; 12, absence of bracteoles; 13, single stipules; 14, geoxylphytic habit; 15, annual habit; 16, style hairy; 17, lobes and callosities on standard petal; 18, turgid fruit; 19, stem thorns; 20, flowers at least partly blue (not to be confused with purple); 21, keel petals often acute; 22, leaves totally glabrous; 23, leaflets sessile (i.e. petiole absent); 24, fruit winged; 25, seed orientation (at right angle with the funicle); 26, resupinate flowers; 27, cordate (lobed) stipules; 28, epidermal glands; 29, spurred wing petals; 30, stipules minute; 31, internode below inflorescence elongated; 32, stipules often fused (with each other and/or with the petiole); 33, keel petals imbricate along lower side; 34, stamens fused into a closed sheath; 35, biramous epidermal hairs.

information will "tend to fall into line". To me, predictivity means that new information about the taxa of a particular classification will tend to agree with their hierarchical arrangement as previously obtained from other information. It also means that the hierarchical pattern in a classification does not depend merely on one or more defining characters.

The distribution of character states in Figure 2.5 clearly shows that the chosen topology has considerable predictive value. Examples are the presence of lupanine-type esters in the only two genera with resupinate flowers (Pearsonia & Rothia), the presence of pyrrolizidine esters in the only two genera which (at least occasionally) have rugose or tuberculate seeds, distinctly beaked keel petals and blue flowers, and the presence of α -pyridone alkaloids in all genera with bilabiate calyces. The position of Lotononis as a sister group of Crotalaria seems reasonable, and that both share a common ancestor with Rafnia, Aspalathus and Lebeckia is equally likely. Despite similarities between Lotononis and Pearsonia (notably the calyx structure), the data do not support a close relationship between these two genera but rather suggest a relatively early divergence of Pearsonia and Rothia from the rest of the Lebeckia clade. This agrees with the presence of Pearsonia on Madagascar (evidently separated from the African continent early in the geological history, as reviewed by Raven & Axelrod 1974) and also the presence of Rothia in Asia and Australia (the latter perhaps a result of early dispersal when land masses were somewhat less separated). It may be argued

that Crotalaria has an even wider distribution, but Polhill (1982) suggested an African origin for this genus with secondary diversification outside Africa. The divergence of the Argyrolobium clade seems even earlier and this basal dichotomy is clearly the most obvious place for a subtribal division.

The results presented here illustrate that the clues to solve phylogenetic problems may be found in rather unexpected characters. In the Crotalarieae it seems to have come, at least partly, from alkaloidal metabolites. The results also show that the cladistic methodology may significantly improve our understanding of character state distributions and the relationships between taxa.

Several generic apomorphies for Lotononis are shown in Figure 2.5. Various combinations of these characters are present in all the species and their distribution within the genus strongly supports a wide generic concept. Details are presented in Part 3.2, so that the most useful diagnostic characters are just briefly mentioned here: herbaceous (often annual) habit, single stipules, biramous hairs, absence of bracteoles, zygomorphic calyx (the lateral sinuses shallower than the upper and lower ones), fruit with a verrucose upper suture, densely tuberculate seeds and the presence of cyanogenic glucosides and pyrrolizidine alkaloids.

PART 3

INFRAGENERIC RELATIONSHIPS

INTRODUCTION

Polhill (1976) made a very significant contribution to generic delimitations in the Genisteae sensu lato. His study highlights the main patterns of character variation in the tribe Crotalarieae and provide the only broad review that is available. The notable gaps in comparative information for southern genera, and Lotononis in particular, was mentioned.

The sectional classification of Lotononis was conceived by Bentham (1843), who combined several smaller genera into a much enlarged generic concept. The arrangement of species in this system shows a remarkable insight into character variation, despite the relatively small number of species that was known at the time. Harvey (1862) and Dümmer (1913) followed Bentham's concepts, but their attempts to accommodate new species resulted in what appears to be an artificial system. Due to several new species and a much improved understanding of the distinction between Crotalaria and Lotononis (Polhill 1968b), Dümmer's synopsis has become very outdated. Improvements to generic delimitations have resulted in the transfer of Euchlora Eckl. &

Zeyh. and Listia E. Mey. to Lotononis by Dahlgren (1964) and Polhill (1976) respectively. Polhill (1976, 1981a) also suggested that the genus Buchenroedera Eckl. & Zeyh. may be no more than a natural section of Lotononis. It is therefore clear that a re-evaluation of relationships within Lotononis has become necessary.

This part of the thesis is an attempt at providing an empirical basis for a revised infrageneric classification of Lotononis. To find new criteria for defining more natural groups, a rather extensive analysis of all the species was necessary. The data and results are presented here. Morphological, cytological and some chemical characters were studied and data analyzed by cladistic methods. Distinct patterns in the geographical distribution of the sections and species were also examined, because these patterns suggested that some regional groups may have evolved independently.

3.1 CHARACTERS AND CHARACTER STATES

Detailed studies of the morphology, chromosome cytology and some chemical characters in Lotononis were necessary to determine relationships among the species. With the exception of Argyrolobium, Lotononis is the only large genus of the tribe that has not been studied in its entirety for more than half a century. It was therefore decided to concentrate on a rigorous

assessment of the more obvious and hitherto much neglected characters rather than to try and cover the whole spectrum of potentially useful characters. A number of reliable diagnostic characters were discovered, some of which clearly showed the need to modify the circumscription of existing sections or to describe new sections. A list of 63 characters and their character states is given in Table 3.1. This list also includes most of the characters that were used only at the specific level (In Table 3.1, these characters are the ones followed by a number). The characters listed in Table 3.1 are from the original inventory (not shown here) that served as a basic source of information for compiling the various smaller matrices that are given in Part 3.2. The initial polarizations of character states are shown, but several of these were subsequently reversed or modified.

Some of the characters listed in Table 3.1 are briefly discussed and illustrated below. Arguments for deciding the polarity of various character states and subsequent departures from the original polarizations are also mentioned. To avoid the need for disruptive qualifying statements about the circumscription of sections, I am using the modified infrageneric classification scheme and nomenclature as given in Part 5.

Details about the behaviour of characters in various cladistic analyses are dealt with in Part 3.2. The distribution of character states at the sectional level is shown there in Tables

TABLE 3.1. CHARACTERS AND CHARACTER STATES RECORDED IN THE GENUS LOTONONIS. (THE NUMBERS GIVEN HERE ARE USED IN THE TABLES AND FIGURES OF PART 3)

-
1. HABIT: woody shrub = 0; suffrutescent perennial = 1; annual = 2.
 2. BRANCHES: woody shrub with all branches \pm persistent = 0; suffrutescent perennial with at least the basal branches persistent = 1; annual flowering branches from a persistent woody caudex = 2; annual flowering branches from a large tuberous caudex = 3.
 - 2a. ADVENTITIOUS ROOTS: absent = 0; present on lateral branches = 1
 3. LEAF TYPE: digitate = 0; simple, sessile = 1.
 - 3a. LEAF COLOUR (WHEN DRIED): green = 0; black = 1.
 4. NUMBER OF LEAFLETS: invariably 3-digitate = 0; 3-digitate, rarely with some leaves 5-digitate = 1; predominantly 5-digitate = 2; 5- to 8-digitate = 3.
 5. UNIFOLIOLATE LEAFLETS: absent = 0; at least with some (often the juvenile) leaves unifoliolate = 1.
 6. NUMBER OF STIPULES: invariably paired, \pm equal in size = 0; paired but markedly dissimilar in size = 1; invariably single (or absent) = 2.
 7. STIPULE SIZE: similar to leaflets = 0; much smaller than leaflets = 1; inconspicuous = 2.
 8. PETIOLE LENGTH: similar to length of leaflets = 0; much longer than leaflets = 1.
 9. PETIOLE LENGTH: not much shorter than leaflets = 0; much shorter than leaflets = 1.
 10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy = 1; totally glabrous = 2.
 11. HAIR TYPE: simple, uniseriate = 0; biramous = 1.
 - 11a. HAIR SURFACE SCULPTURING: not polarized except that a smooth hair surface is considered to be an autapomorphy for Listia (see Figure 3.1.6).
 12. LEAF ARRANGEMENT ON FLOWERING NODES: alternate = 0; subopposite = 1; opposite = 2.
 13. INFLORESCENCE POSITION: invariably terminal = 0; terminal and leaf-opposed = 1; invariably leaf-opposed = 2.
 14. SECONDARY INFLORESCENCES: absent = 0; present = 1.
 15. PEDUNCLE LENGTH: much longer than the length of the flower(s) = 0; as long or shorter than the flower(s) = 1; \pm absent = 2.
 16. FLOWER NUMBER: 20 or more = 0; five to 20 = 1; one, two, three or four = 2; one, rarely two = 3.
 17. FLOWER ARRANGEMENT: evenly spaced on a rachis = 0; congested, at least towards the apex of the rachis = 1; densely umbellate or rachis \pm absent = 2.
 - 17a. FLOWER SIZE: large = 0; medium-sized = 1; small = 2. (Used at species level only).
 18. POSITION OF BRACT: at base of pedicel = 0; slightly above pedicel base = 1; inserted \pm halfway up the pedicel = 2.
 19. PEDICEL: long (more than 2 mm) = 0; very short (\pm 1 mm) = 1; absent = 2.
 20. BRACT SIZE: small, linear (not much wider than the pedicel) = 0; conspicuous, more than twice as wide as the pedicel = 1; very large, partly obscuring the flowers, longer than wide = 2; laterally expanded, wider than long = 3.
 21. FLOWER COLOUR: yellow = 0; not yellow (white, pink or more often blue) = 1.
 22. FLOWER DIMORPHISM (CLEISTOGAMY): absent = 0; present in most species = 1.
 23. BRACTEOLES: present = 0; absent or vestigial (less than 0,1 mm long) = 1.
 24. CALYX LOBES (LENGTH): as long or shorter than the fused part = 0; longer than the fused part = 1.
 - 24a. CALYX (RELATIVE LENGTH): much shorter than the corolla = 0; \pm half the length of the corolla = 1; \pm as long as the corolla = 2.
 25. CALYX (LATERAL SINUSES): \pm as deep as lower sinuses = 0; slightly shallower than lower sinuses = 1; much shallower than lower sinuses = 2.
 26. CALYX (SIZE OF CARINAL LOBE): \pm equal to upper lobes = 0; narrower than upper lobes = 1; much narrower and shorter than upper lobes = 2.

TABLE 3.1 CONTINUED

27. CALYX (SIZE OF UPPER LOBES): \pm equal to lateral lobes = 0; wider than lateral lobes = 1.
- 27a. CALYX (BASE OF LOBES): valvate = 0; lobed (and usually imbricate) = 1.
28. STANDARD PETAL (RELATIVE LENGTH): \pm as long or longer than keel = 0; much shorter than keel = 1.
29. STANDARD PETAL (SHAPE OF CLAW): not dilated = 0; dilated towards the base = 1; much dilated towards the base = 2.
- 29a. STANDARD PETAL (LENGTH OF CLAW): less than half as long as the lamina = 0; more than half as long as the lamina = 1.
30. STANDARD PETAL (SHAPE OF LAMINA): orbicular, ovate, oblong or lanceolate = 0; panduriform = 1.
31. STANDARD PETAL (VESTITURE): hairs on all or most of the abaxial surface = 0; hairs on at least a large part of the abaxial surface = 1; a line of several hairs along the midrib only = 2; a few hairs along midrib only = 3. (In most analyses at sectional level, hairiness was taken as apomorphic).
32. STANDARD PETAL (VEINATION): inconspicuous = 0; conspicuous (lamina distinctly striated, the abaxial surface often different in colour to the adaxial surface) = 1.
33. WING PETAL (VESTITURE): at least some hairs present = 0; totally glabrous = 1. (In most analyses at sectional level, hairiness was taken as apomorphic).
- 33a. WING PETAL (AURICLE): small = 0; large = 1. (Used at species level only).
34. KEEL (RELATIVE LENGTH): as long or longer than the standard and wing petals = 0; shorter than the standard and wing petals = 1.
35. KEEL (SHAPE OF APEX): rounded = 0; slightly pointed = 1; beaked = 2; very strongly beaked = 3. (Acute or beaked keel petals were considered plesiomorphic in most analyses at the sectional level).
36. KEEL (VESTITURE): densely hairy = 0; with some hairs towards the apex = 1; totally glabrous = 2. (In most analyses at sectional level, hairiness was taken as apomorphic).
37. KEEL (LENGTH OF CLAWS): shorter than the lamina = 0; as long or longer than the lamina = 1.
38. ANTHER DIMORPHISM: basifixed anthers up to twice as long as dorsifixed anthers = 0; basifixed anthers more than twice as long as dorsifixed anthers = 1.
- 38a. CARINAL ANTHER: similar to basifixed anthers = 0; intermediate = 1; similar to dorsifixed anthers = 2.
39. PISTIL SHAPE: linear (more than 3x longer than wide) = 0; oblong (2x to 3x longer than wide) = 1; ovate (less than 2x longer than wide) = 2.
- 39a. GYNOECIUM BASE: stipitate = 0; sessile or subsessile = 1. (Reversed in some analyses).
40. OVULE NUMBER: numerous (more than 9) = 0; few (3 to 8) = 1; one or two = 2.
41. FRUIT (SHAPE IN LATERAL VIEW): linear (more than 3x longer than wide) = 0; oblong (2x to 3x longer than wide) = 1; ovate (less than 2x longer than wide) = 2.
- 41a. FRUIT (SHAPE IN TOP VIEW): straight = 0; folded like a concertina = 1.
42. FRUIT (SHAPE IN TRANSVERSE SECTION): flat (not turgid) = 0; slightly turgid = 1; laterally much inflated = 2. (Reversed in some analyses).
43. FRUIT (UPPER SUTURE): smooth = 0; minutely or slightly verrucose = 1; conspicuously verrucose = 2. (Reversed in most analyses).
44. FRUIT (APEX IN LATERAL VIEW): acute = 0; obtuse = 1.
45. FRUIT (DEHISCENCE): dehiscent = 0; tardily dehiscent = 1; indehiscent = 2.
46. FUNICLE LENGTH: short (less than the seed length) = 0; long (more than the seed length) = 1; very long (more than 2x the seed length) = 2.
47. SEED SURFACE: smooth = 0; slightly and sparsely tuberculate = 1; conspicuously and densely tuberculate = 2.
48. CHROMOSOME NUMBER: base number 7 = 0; base number 9 = 1.
- 48a. PLOIDY LEVEL: diploid or tetraploid = 0; polyploid = 1.
49. CYANOGENESIS: totally acyanogenic = 0; most species/samples cyanogenic = 1; all species/samples cyanogenic = 2.
50. QUINOLIZIDINE ALKALOIDS: present = 0; \pm absent = 1.
51. PYRROLIZIDINE ALKALOIDS: \pm absent = 0; present = 1.

3.2.1 to 3.2.4 and the distributions at the species level (i.e., within each of 15 sections) are listed in Tables 3.2.5 to 3.2.20.

VEGETATIVE MORPHOLOGY

Habit

Habit is a variable and taxonomically important character in Lotononis. Previous infrageneric treatments by Harvey (1862) and Dümmer (1913) followed Bentham's (1843) progression, starting with the woody groups and ending with the presumably more derived herbaceous ones. This sequence is not congruent with other characters (see below). The assumption that "woody equals primitive" undoubtedly holds true as a general trend in the subfamily (Polhill 1981b) but allowance should be made for the possibility that highly derived species may have retained their woodiness. This appears to be true for the woody species of Lotononis and it seems likely that Bentham's sequence has been misunderstood by subsequent workers.

In situ studies have revealed the natural affinities of many species that were previously misplaced due to a lack of accurate information on habit. Field observations have indeed led to obvious improvements in the circumscription of most of the sections. Figure 3.1.1 gives a schematic summary of the range of

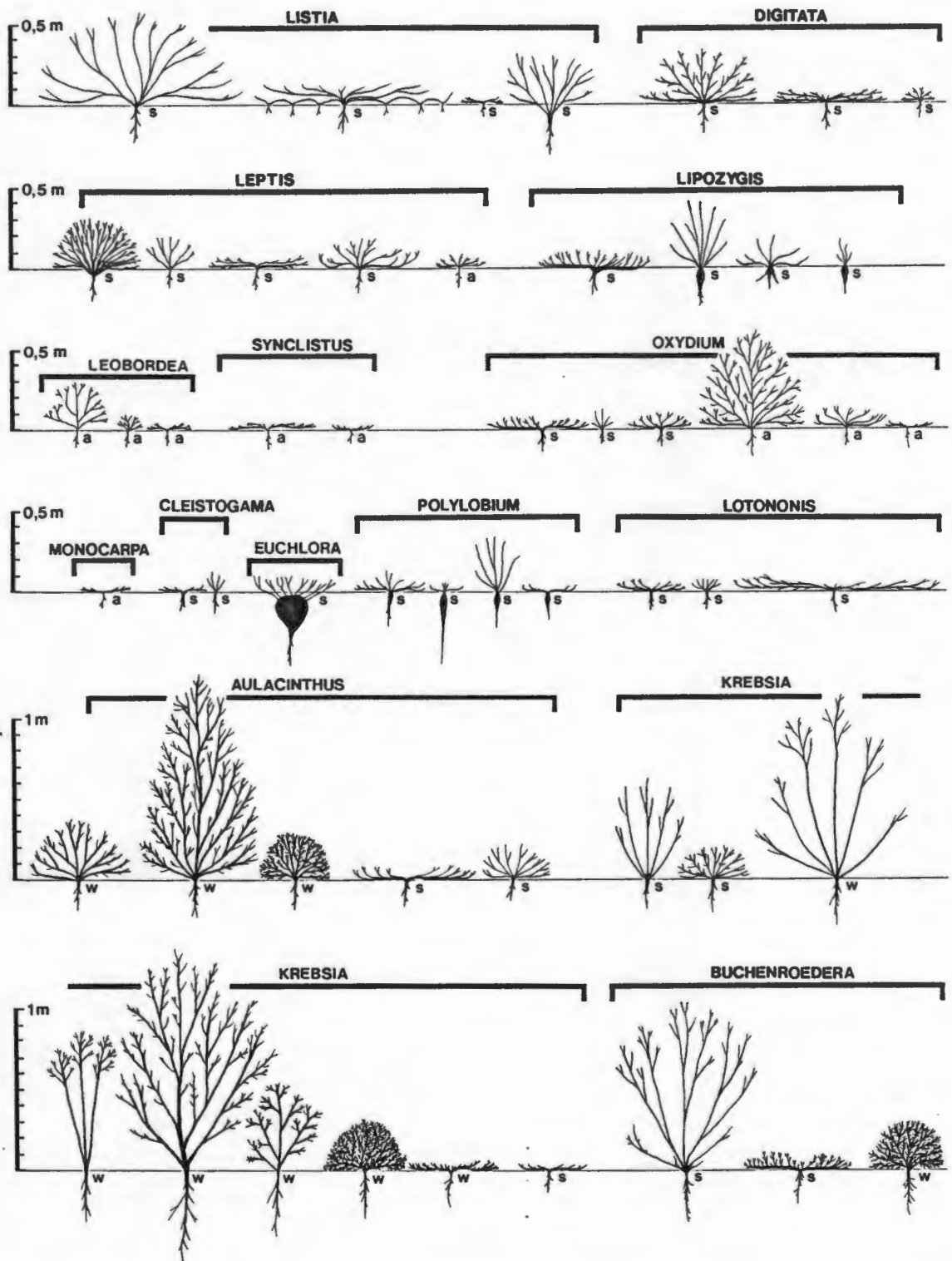


Figure 3.1.1. Schematic summary of variation in the habit of the sections of *Lotononis*. Note the almost stoloniferous habit in the section *Listia* and the thick woody caudex in the sections *Lipozygis*, *Polylobium* and *Euchlora*. a, annuals; s, suffrutescent perennials; w, woody shrubs.

variation in Lotononis. The majority of species are suffrutescent perennials with flowering shoots developing from a persistent woody base. Aulacanthus, Krebsia and Buchenroedera are the only sections which include erect shrubs with persistent woody branches. Prostrate shrubs (with all or most of the branches persistent) also occur in the section Leptis. An annual habit has diagnostic value for the sections Leobordea, Synclistus and Monocarpa, but three species of Leptis and several species of Oxydium are also annuals. The geographical distribution of annual species indicates that the annual habit is an adaptation to erratic or seasonal rainfall patterns (see Part 3.3). In Polylobium, Euchlora and in most species of Lipozygis, annual flowering shoots develop from a thick woody caudex. The caudex consists of a much thickened primary root together with the basal part of the primary stem. The enormous tuber in the monotypic Euchlora represents an extreme example of this development, which, in Polylobium and Euchlora, is probably an adaptation to summer drought. In the case of Lipozygis however, it is clearly a parallel development in response to frequent fires in a grassland habitat. This non-homologous similarity has led to obvious errors in past taxonomic treatments of the species here included in Polylobium, Lipozygis and even Synclistus (the annual habit of the latter was apparently not known before). Polylobium and Lipozygis are geographically completely isolated (see Part 3.3) and morphological similarities between the two groups are superficial only. Listia is the only section which shows an adaptation to wet or seasonally wet habitats. In most of the

species, vegetative reproduction may occur where adventitious roots are formed on side shoots. This almost stoloniferous habit may be an adaptation to unstable substrata resulting from periodic flooding. It is clearly exemplified by L. subulata, a species which forms large colonies on river banks after being covered by flood deposits.

Habit provided only one character for cladistic analyses at the infrageneric level, namely perennial vs annual (or woody vs suffrutescent vs annual). The annual habit has undoubtedly developed more than once in Lotononis, but it does support the presumed affinity between the sections Leobordea and Synclistus and also between Monocarpa and Oxydium. The tuberous habit in Lipozygis, Polylobium and Euchlora was not included in cladistic analyses due to the expectation of convergence. It does indicate a possible relationship between Euchlora and Polylobium (response to summer drought) but is unlikely to be homologous in Lipozygis (response to winter drought in grassland habitats, with its resultant high fire frequencies). Attempts were made to polarize the degree of woodiness in perennial species (woody vs suffrutescent) but there can be little doubt that a suffrutescent habit has developed independently in several different lines. It is however, very useful to determine relationships within the sections. Similarly, other characters such as an erect or prostrate habit and various branching patterns are only potentially useful at lower taxonomic levels. Autapomorphies for

terminal taxa (such as the "stoloniferous" habit in Listia) were excluded because it gives no information about relationships between the taxa.

Phyllotaxis

Leaves are alternately arranged in all but a few species of Lotononis. In the section Leobordea, the leaves on flowering shoots are invariably opposite and provides a very useful diagnostic character for this section. The subopposite leaf arrangement in some species of the section Leptis strongly suggests a relationship with Leobordea. Basal leaves which are formed during active vegetative growth (before flowering) are always alternate (also in Leobordea). L. lenticula (section Oxydium) is the only exception and the opposite arrangement of basal branches is an unique character in this annual species. The rare occurrence of opposite leaves in L. maximiliani (only at some nodes) agrees with the suggested affinity between Monocarpa and Oxydium.

Stipules

Most species of Lotononis have only one stipule at the base of each petiole. This is a very useful diagnostic character in the tribe as a whole and is shared only by the genus Rothia. The more

usual paired condition however, also occurs quite frequently in Lotononis. When paired, the two stipules are often markedly dissimilar in size and shape. Stipules are more rarely totally absent and only two species (L. carinata and L. lupinifolia) show the unique and interesting feature of having more than two stipules at some nodes. Examples of the different character states (stipule types) are shown schematically in Figure 3.1.2. The distribution of stipule types within the genus is summarized below the figure. The five basic types (Figure 3.1.2A to E) are:

Type A. Paired, symmetrical.

Stipules invariably paired at all the nodes and the two of each pair similar in size and shape.

Type B. Paired, asymmetrical. Stipules invariably paired at all the nodes but the two of each pair often conspicuously dissimilar in size and/or shape.

Type C. Variable:

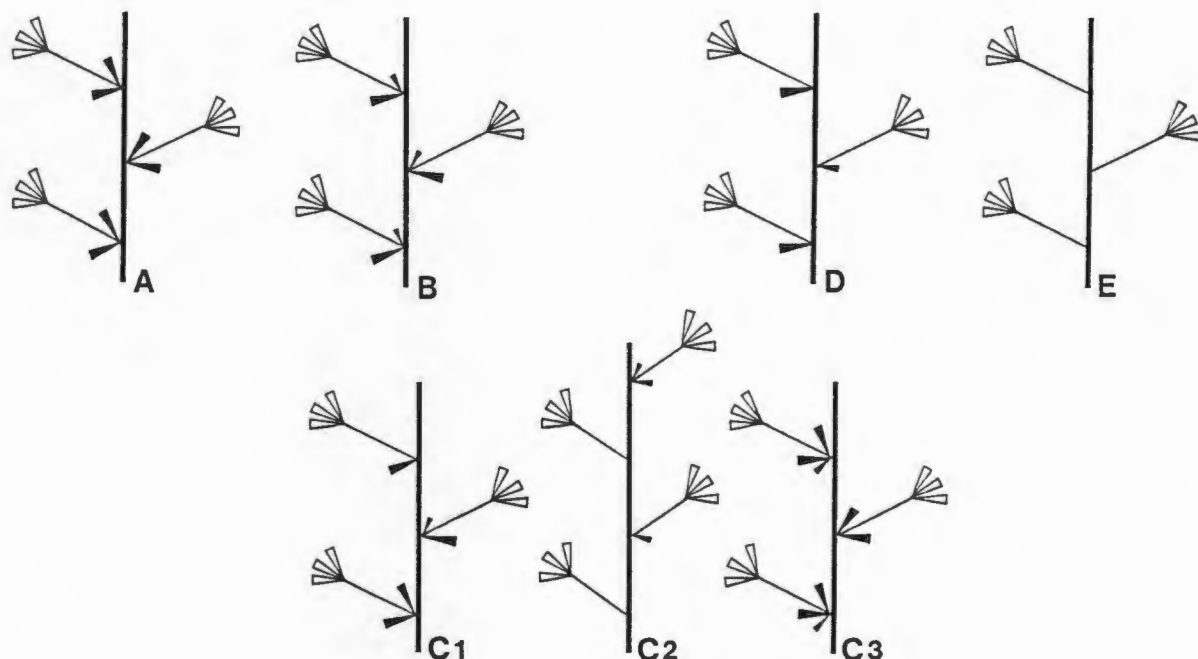
C1. Stipules paired at the basal nodes and single at the upper nodes.

C2. Stipules usually absent, but present (in pairs or single) at least at some nodes (or in some specimens).

C3. Stipule or stipules digitate (at least occasionally or rarely).

Type D. Single. Stipules invariably single at all the nodes.

Type E. Absent. Stipules invariably absent at all the nodes.



DISTRIBUTION OF STIPULE TYPES IN THE GENUS LOTONONIS:

SECTIONS	STIPULE TYPES AS ABOVE							EXCEPTIONS (RARE OCCURRENCES IN BRACKETS)
	A	B	C1	C2	C3	D	E	
NUMBER OF SPECIES:								
Listia	-	8	-	-	-	-	-	
Digitata	-	-	-	-	-	6	-	
Lipozygis	-	-	-	-	-	10	-	
Leptis	2	-	-	-	(2)	18	-	type A: <u>L. carinata</u> and <u>L. hirsuta</u> ; type C3: <u>L. carinata</u> and <u>L. lupinifolia</u>
Leobordea	1	-	-	-	-	5	-	type A: <u>L. newtonii</u>
Synclistus	-	-	-	-	-	9	-	
Euchlora	(1)	-	-	-	-	-	1	type A: a form of <u>L. serpens</u>
Oxydium	2	1	-	-	-	34	(1)	type A: <u>L. delicata</u> and <u>L. pseudodelicata</u> ; type B: <u>L. pallens</u> ; type E: <u>L. fruticoides</u>
Monocarpa	-	-	1	-	-	2	-	type C1: <u>L. venosa</u>
Cleistogama	-	-	-	-	-	2	-	
Polylobium	5	-	-	-	-	-	-	
Lotononis	-	4	-	-	-	7	-	type B: <u>L. varia</u> , <u>L. azurea</u> , <u>L. filiformis</u> and <u>L. elongata</u>
Aulacanthus	-	-	-	2	-	7	3	type C2: <u>L. dissitinodia</u> and <u>L. rigida</u> ; type E: <u>L. dahlgrenii</u> , <u>L. densa</u> and <u>L. exstipulata</u>
Krebsia	6	-	4	-	-	1	1	type C1: <u>L. sericophylla</u> , <u>L. divaricata</u> , <u>L. iacottetii</u> and <u>L. galpinii</u> ; type D: <u>L. minor</u> ; type E: <u>L. caerulescens</u>
Buchenroedera	8	-	-	-	-	-	3	type E: <u>L. amaiubica</u> , <u>L. glabrescens</u> and <u>L. viminea</u>

Figure 3.1.2. Variation in stipules in the genus Lotononis. A, paired, symmetrical; B, paired, asymmetrical; C, variable: C1, paired at the basal nodes and single at the upper nodes; C2, usually absent, but present (in pairs or single) at least at some nodes (or in some specimens); C3, digitate; D, single; E, absent. The distribution of stipule types in the 15 sections of Lotononis is shown below the figure.

For cladistic analyses, it seemed reasonable to polarize type A as the plesiomorphic condition, type B as intermediate, and type C through to E as the apomorphic state. A stepwise progression from type A through to type E may seem more logical, but this polarization resulted in much lower consistency indices. The variability of stipules in some undoubtedly monophyletic groups and indications that reversals are possible (as in L. serpens, where stipulate leaves may occur on the terminal parts of the branches but not towards the base) suggest that this character should not be excessively weighted. The results of the cladistic analyses indeed indicate that single stipules (type D) is not a uniquely derived character state. This is also true for the absence of stipules (type E), which occurs sporadically in unrelated species, even though this condition is restricted to the sections Aulacanthus, Krebsia and Buchenroedera (and one species of Oxydium).

Leaves

All the species of Lotononis have digitate leaves, mostly trifoliolate but occasionally also unifoliolate, 5-digitate and rarely, up to 8-digitate. Unifoliolate leaves have been observed in juvenile specimens of L. angolensis and L. bainesii (section Listia) but elsewhere only in the section Oxydium. A single leaflet appears to be of diagnostic value for two perennial groups (L. laxa and related species and L. monophylla and related

species). L. monophylla is the only species which has all the leaves unifoliolate -- in other species it occurs only in the juvenile stage or in coppice material. Unifoliolate juvenile leaves may be more widely distributed in Oxydium than is presently known and should be studied in more detail. It is curious that unifoliolate leaves occur in juvenile material, as one would expect these leaves to be ontogenetically younger. In the genus Lebeckia, juvenile leaves are 3-digitate when the mature leaves are unifoliolate (Polhill 1976). Digitata is the only section where the leaves are predominantly 5-foliolate in all the species. There are many other species from several of the sections which have at least some leaves 5-digitate. The co-occurrence of 3- and 5-digitate leaves is particularly common in the sections Synclistus and Listia. Only two species (L. brevicaulis and L. involucrata subsp. digitata) have more than 5 leaflets (up to 8-digitate) and both of these belong to the section Polylobium. An unique character for L. serpens is the occurrence of simple, sessile leaves. In one form of this species however, the leaves on the upper parts of the branches are trifoliolate and stipulate (see Figure 5.16 in Part 5).

Petioles

The relative length of the petiole seems to have taxonomic significance, at least in some groups. Two general trends, a shortening and a lengthening of the petiole, can be

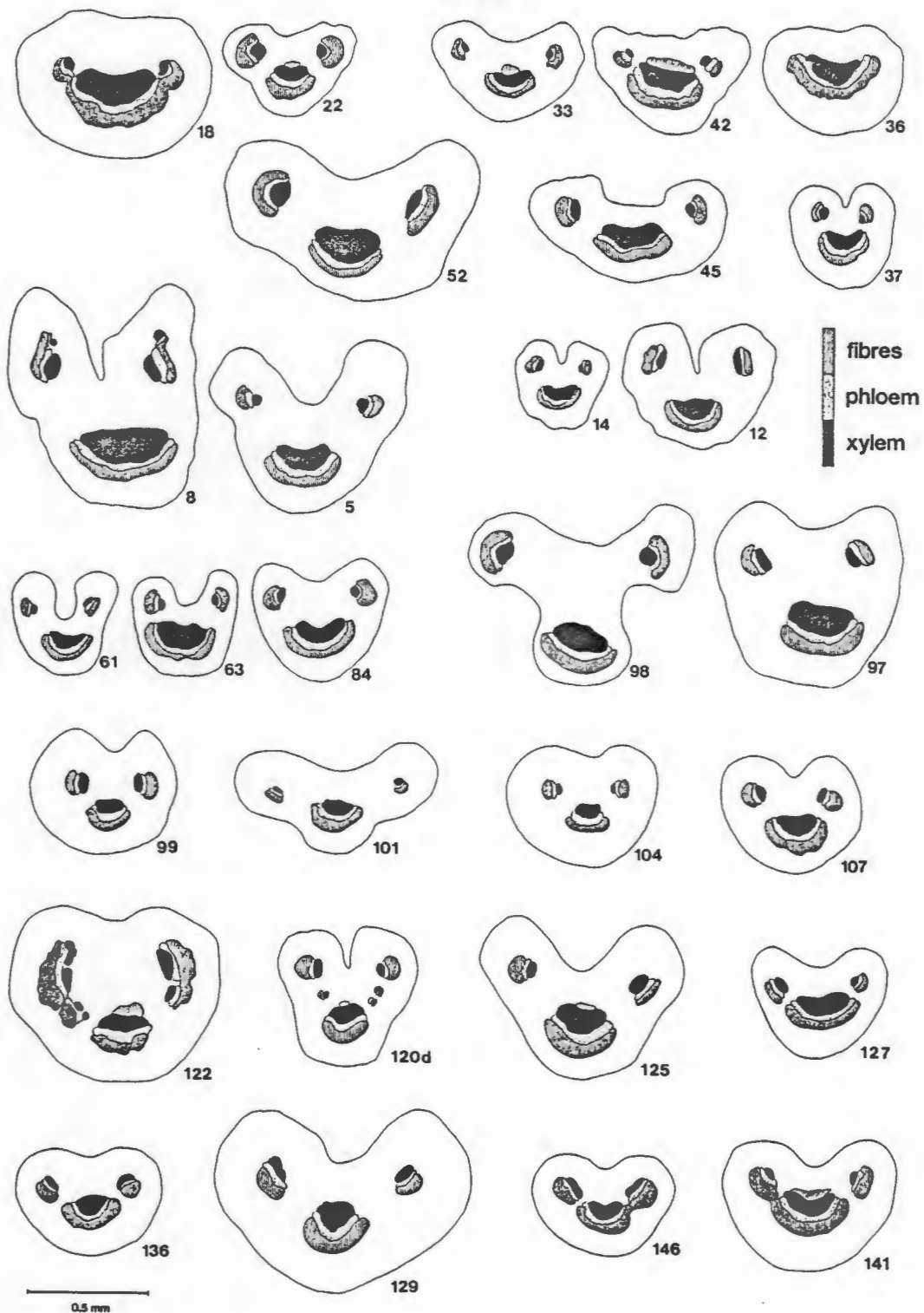


Figure 3.1.3. Diagrammatic illustration of petiole anatomy in the genus *Lotononis*, to show the range of variation found in a larger sample (virtually all the species were represented). Note the single vascular bundle in *L. hirsuta* (36) (small adaxial traces do occur in some specimens), the presence of additional traces in *L. densa* and *L. comptonii* (120d & 122) and the sporadic occurrence of adaxial fibres in some species. Species are numbered as in Part 5. Examples are from the sections *Listia* (5 & 8), *Digitata* (12 & 14), *Lipozygia* (18 & 22), *Leptis* (33, 36, 37 & 42), *Leobordea* (45), *Synclistus* (52), *Oxydium* (61, 63 & 84), *Monocarpa* (97 & 98), *Cleistogama* (99), *Euchlora* (101), *Polylobium* (104), *Lotononis* (107), *Aulacanthus* (120d, 122, 125, 127), *Krebsia* (129 & 136) and *Buchenroedera* (141 & 146).

distinguished. The former is characteristic of the section Lipozygis, while the latter seems to indicate a relationship between the section Digitata and two species of Leptis (L. mollis and L. mirabilis). The anatomy of the petiole was investigated for virtually all the species of Lotononis but it proved to be remarkably invariable and did not seem to have any value as a cladistic character, at least not at the sectional level. A diagrammatic representation of the petiole anatomy of selected examples from all the major groups in the genus is shown in Figure 3.1.3. All but one species [L. hirsuta (36), section Leptis] was found to have two adaxial leaf traces above the main vascular bundle (some leaves with three traces have also been found in L. hirsuta). More than three vascular bundles are occasionally present in L. densa and L. comptonii (120d and 122 in Figure 3.1.3), but no distinct or significant differences could be found in the distribution of fibres and various other characters.

Vestiture

Despite its variability, the vestiture of the adaxial surface of the leaflets (densely hairy, sparsely hairy or glabrous) may be used to distinguish between some of the species. This character is very useful within the sections Leptis and Krebsia, for example, but it has no apparent significance at higher taxonomic levels. Unlike the adaxial surface, the abaxial surface of the

leaflets are never totally glabrous. There are distinct differences in the structure and surface sculpturing of the epidermal hairs. The two basic hair types (uniseriate and biramous) are shown in Figures 3.1.4 and 3.1.5. Uniseriate (simple) hairs, with one or more basal cells and a long terminal cell, are found in all genera of the Crotalarieae (Metcalf & Chalk 1950, Polhill 1976). Biramous hairs, the most common hair type in the genus Lotononis, occur sporadically in species of Aspalathus, Crotalaria and Lebeckia (Polhill 1976) and have also been found in some species of Wiborgia (Dahlgren 1975). Uniseriate and biramous hairs do co-occur in some species of Lotononis (L. glabra, Figure 3.1.4c for example) but hair type is nevertheless quite a useful character at the species level and also at the sectional level. Biramous hairs are quite variable and may have the two arms equal in length (as in Figure 3.1.5a, b and c) or more often have the one arm much longer than the other (Figure 3.1.5d to h). It seems reasonable to consider biramous hairs as an apomorphic character even though the ontogeny of these hairs have not been investigated.

Figure 3.1.4. Uniseriate epidermal hairs in species of Lotononis and some other genera. a, L. benthamiana (Dowdle s.n. sub BOL 5622, BOL); b, L. exstipulata (Esterhuysen 3898, BOL); c, L. glabra (Penther 2765, BOL) [note biramous hair on upper right]; d, L. burchellii (Acocks 2431, PRE); e, L. schreiberi (Gies 8020, PRE); f, L. schoenfelderi (Dinter 7383, PRE); g, Lebeckia cytisoides (L.) Thunb. (Van Wyk 1408, JRAU); h, Bolusia capensis Benth. (Hansen 3191, PRE).

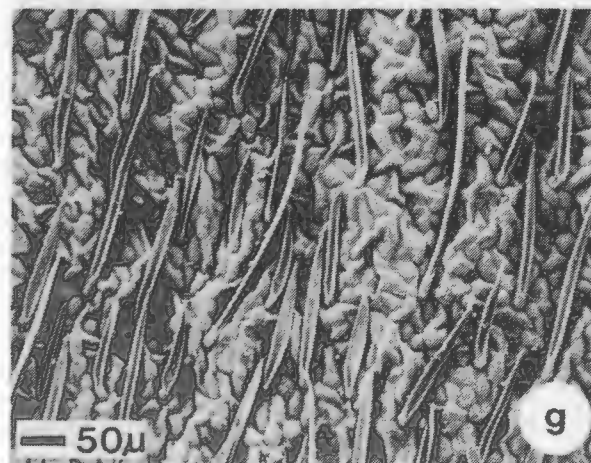
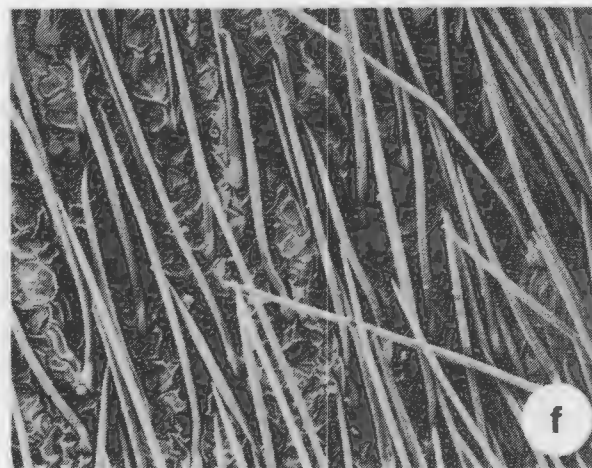
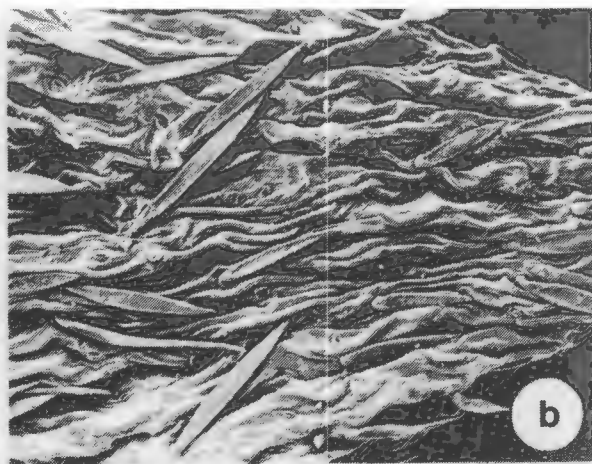
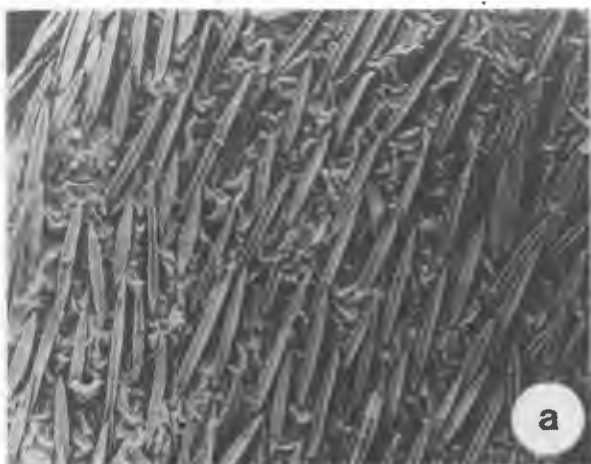


Figure 3.1.5. Biramous epidermal hairs in species of Lotononis.

a, L. glabra (Drège s.n. sub PRE 9392, PRE); b, L. pumila (Bolus 11768, BOL); c, L. laxa (Galpin 1078b, BOL); d, L. laxa (Ecklon & Zeyher 1276, SAM); e, L. curtii (Dinter 345, SAM); f, L. maculata (Leistner 2289, PRE); g, L. eriocarpa (Wood 799, BOL); h, L. brachyantha (Dinter 1682, SAM).

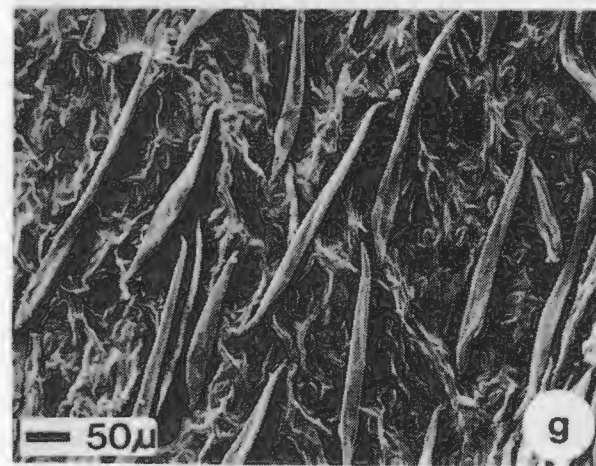
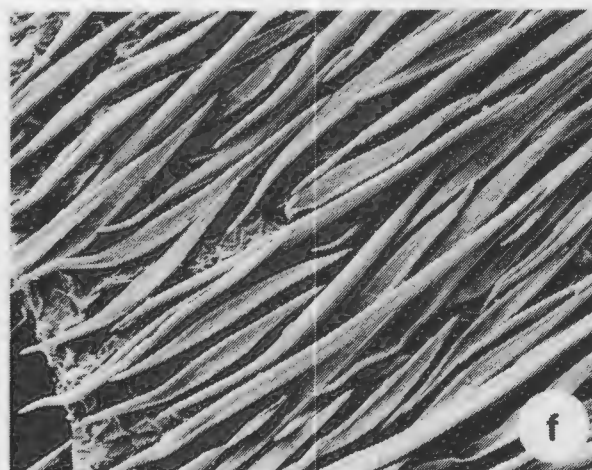
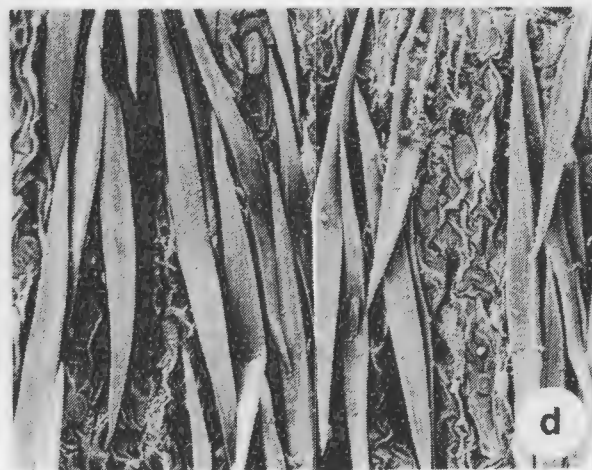
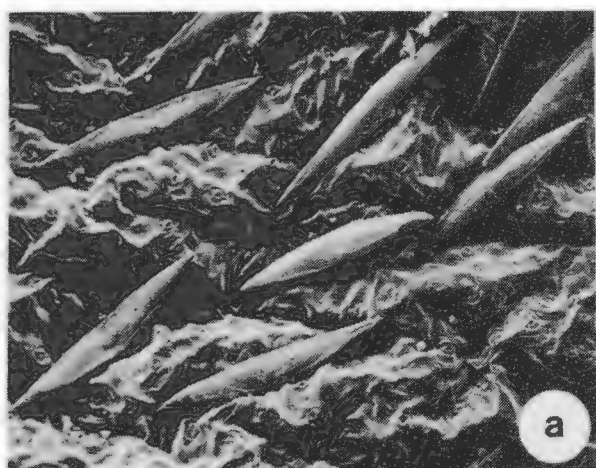
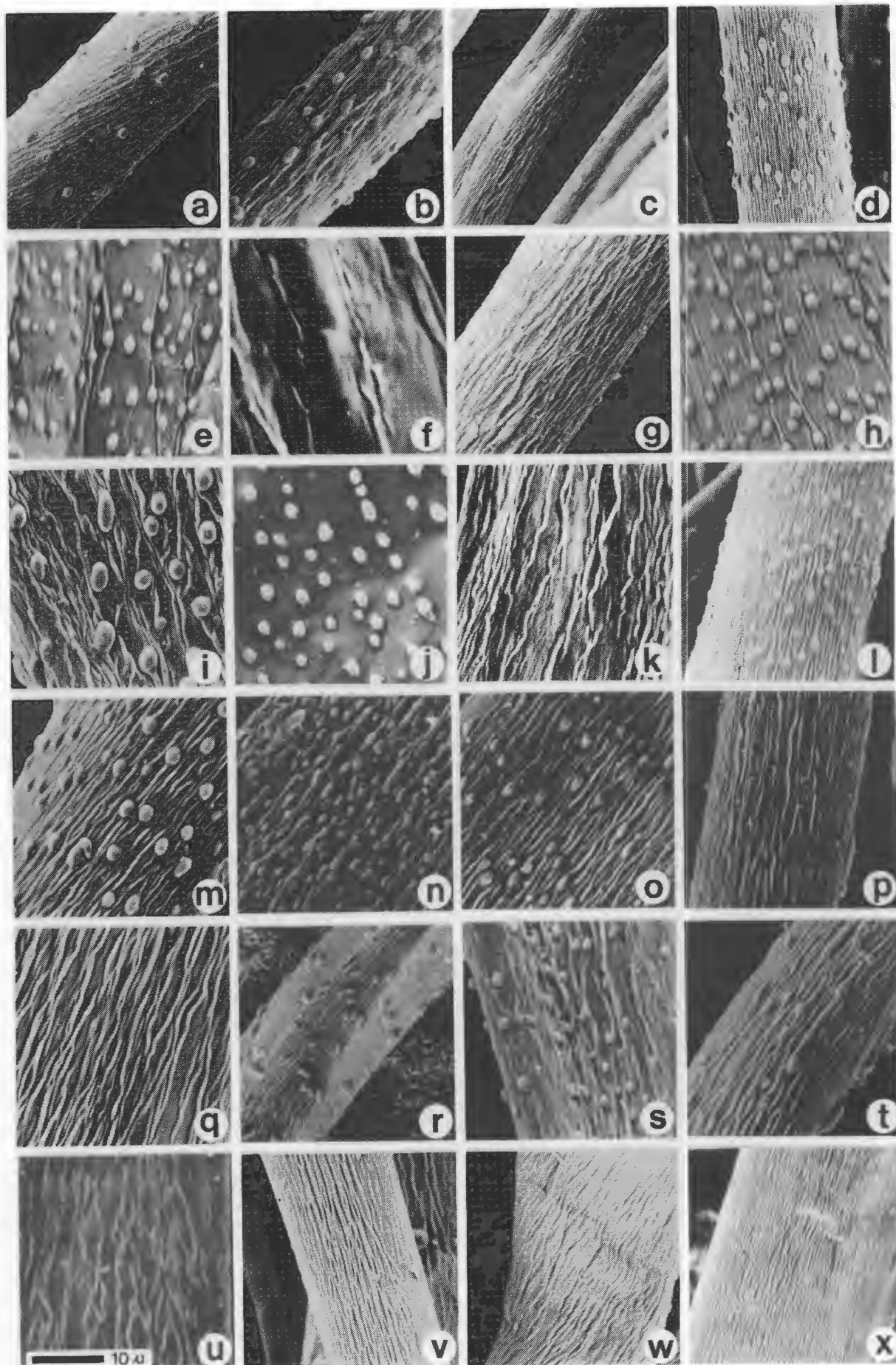


Figure 3.1.6. Hair surface sculpturing in Lotononis. Examples from different sections are shown to illustrate the range of variation observed in a much larger sample (see discussion in text). a, L. foliosa (Bolus 8140, BOL); b, L. carinata (Wood 9284, BOL); c, L. polycephala (Goldblatt 6684, PRE); d, L. platycarpa (Giess 3174, WIND); e, L. benthamiana (Dowdle s.n. sub BOL 5622, BOL); f, L. bainesii (Gerstner 5529, PRE); g, L. burchellii (Acocks 2431, PRE); h, L. curtii (Dinter 345, SAM); i, L. serpentinicola (Brummitt & Drummond 15836, C); j, L. pumila (Bolus 11768, BOL); k, L. rabenaviana (Giess 14479, PRE); l, L. maximiliani (Stokoe s.n. sub SAM 55951, SAM); m, L. umbellata (Penfold 7, NBG); n, L. viborgioides (Zeyher 2319, SAM); o, L. azurea (Long 273, PRE); p, L. argentea (Ecklon & Zeyher 1272, C); q, L. brevicaulis (Barker 3025, NBG); r, L. serpens (Van Wyk 1045, PRE); s, L. pottiae (Pott 5071, PRE); t, L. stricta (Ecklon & Zeyher 1284, TCD); u, L. divaricata (Drège s.n., PRE); v, L. caerulescens (Tyson 2260, SAM); w, L. lotononoides (Codd 2491, PRE); x, L. pulchella (Stirton 6256, PRE).



Examples of the surface sculpturing of hairs are shown in Figure 3.1.6. These examples were selected to show the full range of variation in Lotononis, as observed by scanning electron microscope studies of virtually all the species (at least one, but up to four leaf samples per species). Dahlgren (1972, 1975) studied hair surface sculpturing in the genera Hypocalyptus Thunb. and Wiborgia respectively, and found it to be of taxonomic value in the latter. Van Wyk and Schutte (1989, Appendix 17) have shown that a striated hair surface (without tubercles) is of diagnostic value for the genus Melolobium. In Lotononis, discontinuities and general trends agree rather well with other morphological patterns. Smooth hairs (without any furrows or tubercles, Figure 3.1.6f) are restricted to the section Listia and occur in all the species of this section (some hairs in L. macrocarpa and L. solitudinis may be sparsely tuberculate, however). A smooth or slightly striated surface with tubercles (Figure 3.1.6e and j) is characteristic of the section Digitata but also occurs sporadically in the section Oxydium (in L. strigillosa and L. serpentinicola, for example). A striated or furrowed surface without any tubercles is characteristic of the section Buchenroedera (Figure 3.1.6w and x), most species of Krebsia (Figure 3.1.6u and v) and some species of the sections Polylobium (L. brevicaulis for example, Figure 3.1.6q), Aulacanthus, Lotononis (Figure 3.1.6p), Oxydium (Figure 3.1.6g and k) and also Synclistus (Figure 3.1.6c). A striated and tuberculate surface (Figure 3.1.6a, b, d, h, i, m, n, o, r, s and t) is quite common in most genera of the Crotalarieae and is also

the most common state in Lotononis. Striate/verrucose hairs occur in all the species of the sections Lipozygis (Figure 3.1.6a), Leptis (Figure 3.1.6b) and Leobordea (Figure 3.1.6d) but also at least in some species of most other sections. General trends (such as the obvious similarity between Krebsia and Buchenroedera) do exist, but hair surface sculpturing is clearly too variable to be of much value as a cladistic character at the sectional level. Even if it could be used, the polarity decisions would be suspect. Soladoye (1982) for example, found the same large variation (smooth, striate/rugulate and verrucose hair surfaces) in species of Baphia Lodd. and in other genera of the Sophoreae. If the notion that "common equals primitive" is accepted, then the striate/rugulate or striate/verrucose condition should be taken as plesiomorphic. Striate hairs (without tubercles) may then be considered a synapomorphy for the sections Krebsia and Buchenroedera, but it should be noted that such hairs occur sporadically in several other sections.

REPRODUCTIVE MORPHOLOGY

Inflorescences

Variations in the structure of inflorescences are given schematically in Figure 3.1.7. This diagram summarizes the distribution of character numbers 12 to 20 and also characters 22

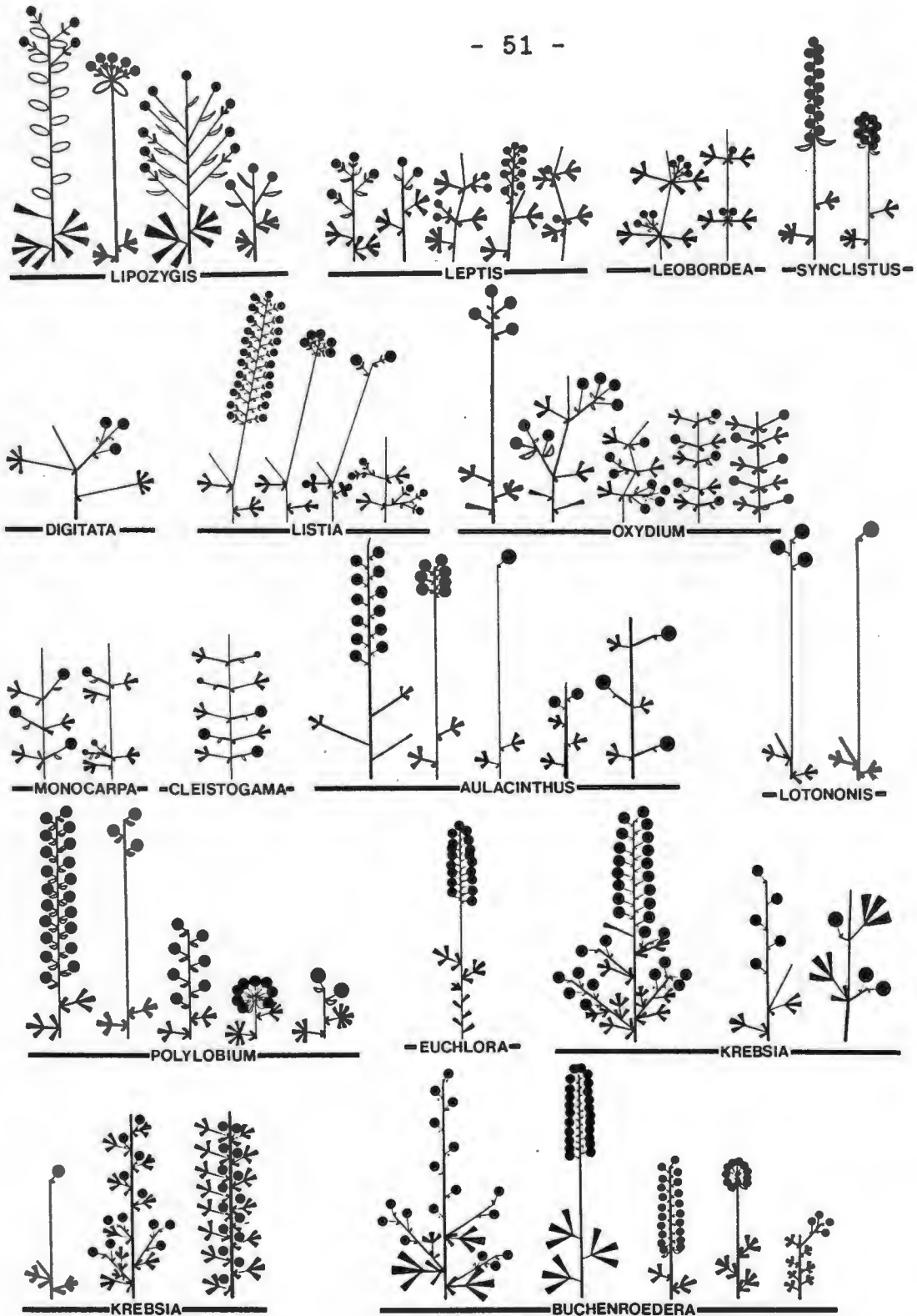


Figure 3.1.7. Schematic summary of variation in the structure of inflorescences in the genus *Lotononis*. Note the phyllotaxis of the flowering node, the terminal or leaf-opposed position of the inflorescence, the length of the peduncle and pedicel, the size of bracts, the absence or presence (only in sections *Listia*, *Lipozygis* and *Leptis*) of bracteoles, the relative size of flowers (dimorphism indicated in the sections *Monocarpa* and *Cleistogama*). Leaf type (simple, unifoliate or digitate) and the number of leaflets are also shown.

(cleistogamy) and 23 (presence of bracteoles), as given in Table 3.1. The absence of bracteoles in most species of Lotononis is taxonomically very significant and may be used as justification for the present circumscription of Lotononis. Bracteoles are invariably present in all the species of Listia, some species of Lipozygis (L. difformis, L. procumbens and sporadically in L. eriantha and L. corymbosa) and also in two species of Leptis (L. mollis and L. stolzii). Elsewhere in the genus, it is totally absent or vestigial (less than 0,1 mm long). The absence of bracteoles is a useful diagnostic character to distinguish various species of Lotononis from morphologically similar species of Argyrolobium, Crotalaria and Lebeckia. Some of the characters given in Figure 3.1.7 are useful at the sectional level, particularly when used in combination with other characters. Sessile flowers (total absence of a pedicel) is a useful sectional character for Synclistus and the slender single-flowered inflorescence is a useful character for the section Lotononis. There are however, clear indications of convergent trends in several of the sections. These trends include a reduction in the number of flowers per inflorescence, a shortening (or a lengthening) of the peduncle and/or the pedicels and an enlargement of bracts. Foliaceous bracts are found in several species but are most notable in the sections Synclistus and Polylobium. In all the species of Lipozygis and in some species of Leptis, the bracts are inserted above the base of the pedicel (usually halfway towards the calyx in Lipozygis). This apparent fusion of the bract to the pedicel was discussed by Van

Wyk (1989g, Appendix 27). I could find no indications that the position of the bract results from intercalary growth of the peduncle and suggest that the inflorescence in section Lipozygis is a simple terminal raceme and not a panicle. Longitudinal sections have shown that there are no discontinuities in the vascular tissue at the point of insertion of the bract. Figure 3.1.7 shows that the position of inflorescences (terminal or leaf-opposed) are linked to the habit of some of the species. A terminal inflorescence is more common in the woody species but also occurs in most species of the section Leptis. Species which flower only after a definite phase of vegetative growth (as in Polylobium and the suffrutescent species of Buchenroedera) usually have terminal inflorescences. The section Krebsia is particularly variable, with various modifications of both terminal and leaf-opposed inflorescences (note, for example, the long and slender "Lotononis-type" in L. minor). In L. stricta, the terminal inflorescences are all reduced to one or two flowers and are borne on very short axillary branches, thus resulting in a leafy, pseudo-racemose arrangement (see the last example given for the section Krebsia in Figure 3.1.7). Similar developments occur in Buchenroedera. Suffrutescent and herbaceous species generally have inflorescences in a leaf-opposed rather than terminal position as a result of continued growth from the terminal leaf axil immediately below the inflorescence. Such a subterminal and eventually leaf-opposed inflorescence is by far the most common type in the genus Lotononis.

Calyx

Variation in calyx structure of the genus is illustrated in Figure 3.1.8. Most species have the calyx zygomorphic due to a fusion (to various degrees) of the upper and lateral lobes on either side. The calyces of all the species of the sections Monocarpa and Cleistogama and virtually all the species of the section Oxydium are subequally lobed, but the carinal lobe is often much narrower than the upper ones. In most species of section Leobordea, the carinal lobe is not only narrower but also much shorter. This character was previously used as a diagnostic character for the section but it is clearly of limited value. Short carinal lobes also occur in the section Leptis (L. lupinifolia, L. genistoides and L. esterhuyseana, for example). The two upper lobes are occasionally much wider than the lower ones, but this character is diagnostically valuable at the specific rather than the sectional level. A widening of the upper lobes is particularly common in the section Oxydium (L. macrosepala, L. acutiflora and several other species), but it also occurs in Leptis (diagnostic character for L. pariflora) and in Synclistus (L. globulosa). The lobes of the calyx are usually valvate at the point of fusion, but are occasionally lobed and slightly imbricate in the section Oxydium. This is a useful diagnostic character to distinguish L. rabenaviana, L. burchellii and L. carnea from their close relatives but has no significance in terms of infrageneric relationships.

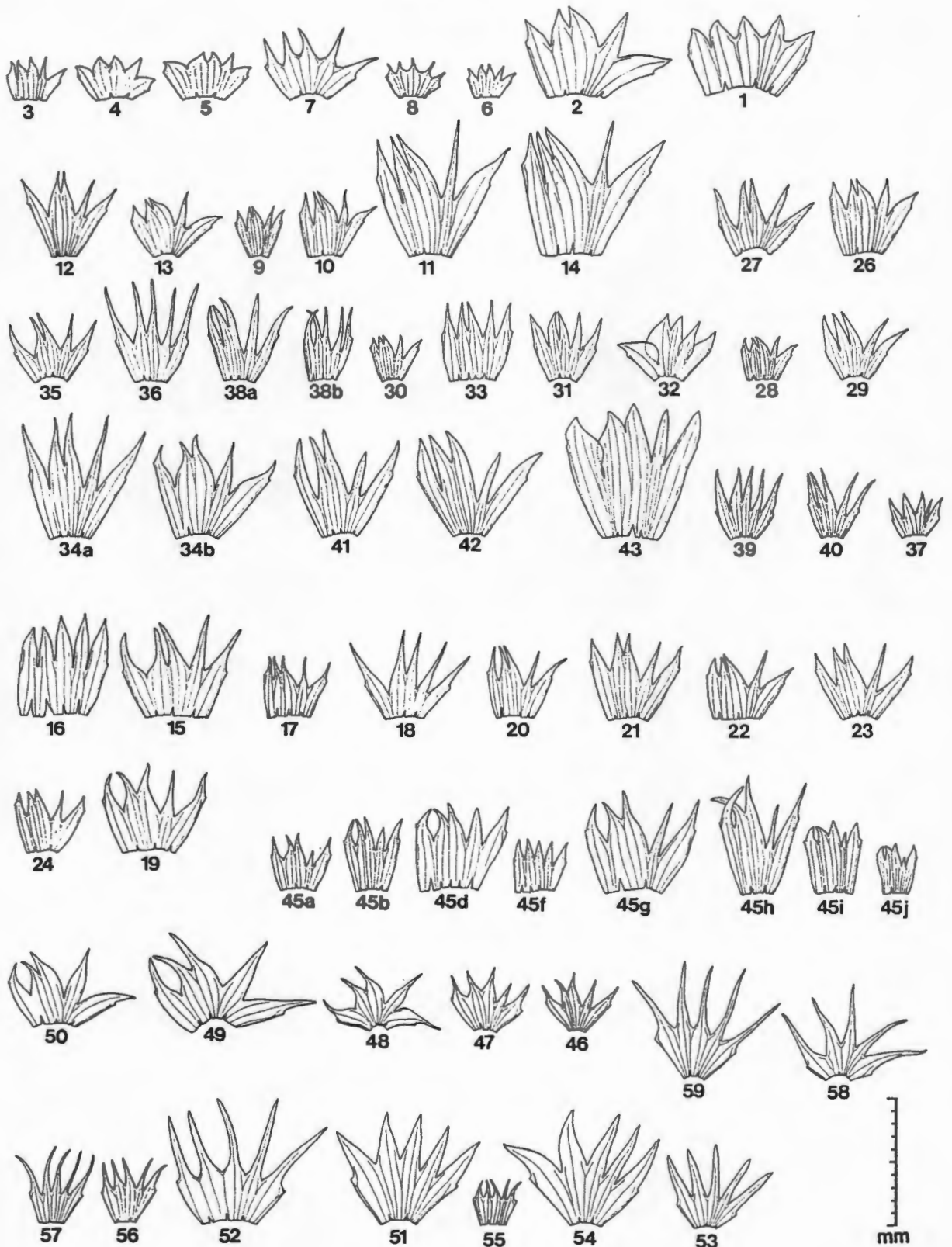


Figure 3.1.8. Variation in the size and structure of the calyx in the genus Lotononis. The calyces are opened out with the upper lobes to the left; vestiture is not shown. Species are numbered as in Part 5: sections Listia (1--8), Digitata (9--14), Lipozygis (15--24), Leptis (25--44), Leobordea (45--50) and Synclistus (51--59).

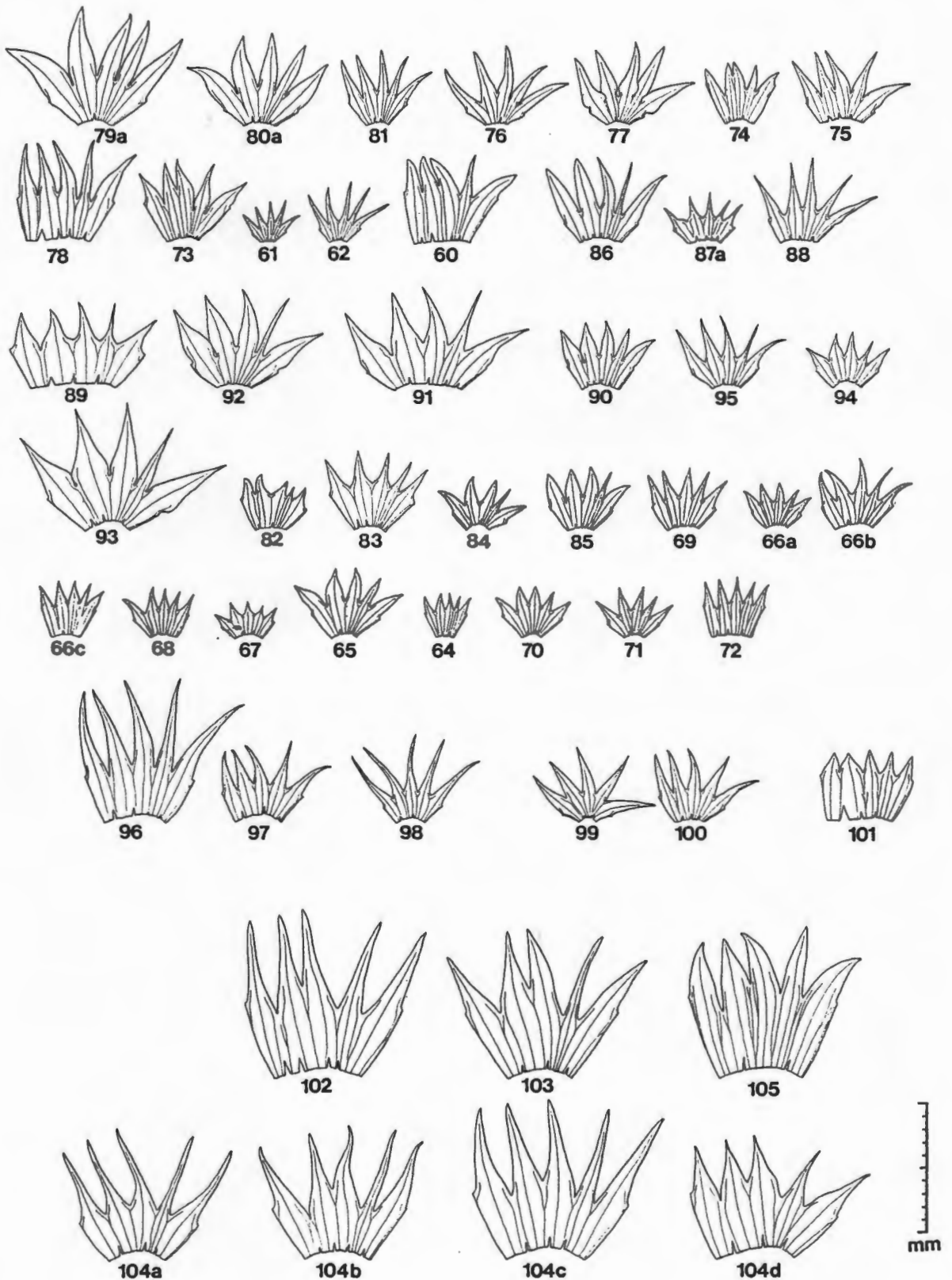


Figure 3.1.8 continued. Variation in the size and structure of the calyx in the genus *Lotononis*. Species are numbered as in Part 5: sections *Oxydium* (60--95), *Monocarpa* (96--98), *Cleistogama* (99 & 100), *Euchlora* (101) and *Polylobium* (102--105).

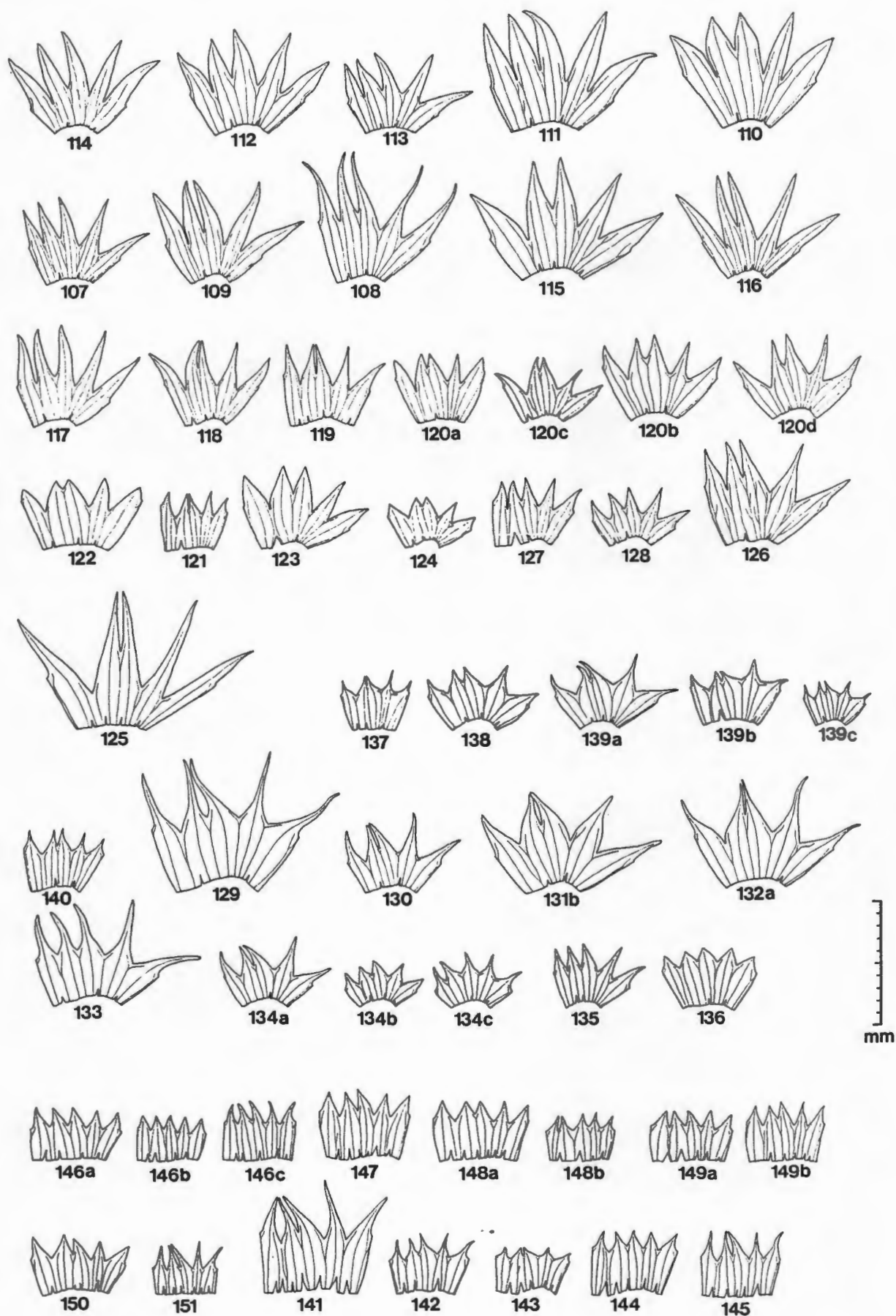


Figure 3.1.8 continued. Variation in the size and structure of the calyx in the genus *Lotononis*. Species are numbered as in Part 5: sections *Lotononis* (106--116), *Aulacinthus* (117--128), *Krebsia* (129--140) and *Buchenroedera* (141--151).

In Lotononis, the structure of the calyx is a useful diagnostic character at the generic, infrageneric and specific levels, but should be interpreted with caution. The shallow lateral sinus is a salient feature of Lotononis, but it breaks down as a diagnostic character in the sections Oxydium, Cleistogama, Monocarpa and Euchlora. Cladistic analyses suggest that the "Lotononis"-type calyx is not a uniquely derived character state, not even within the genus itself. The length of the lobes (exceptionally long in some sections and very short in others) indicates general trends towards increased specialization. Although useful to recognise some groups, the diagnostic value of this character is limited by the exceptions that occur in most of the sections.

The calyx structure in Buchenroedera (previously considered to be equally lobed) has been used as a generic character but it is in fact slightly zygomorphic as in most other species of Lotononis. The lobes are generally very short in this section, but a distinction between Buchenroedera and Krebsia is virtually impossible [note, for example, the very short lobes in L. caerulea (136) and the rather long lobes in L. lotononoides (141) and L. harveyi (151)].

Corolla

Variations in the size and structure of the corolla are shown in Figure 3.1.9. Except for conspicuous differences in size, the most obvious patterns are:

- The shape of the standard petal (suborbicular, oblong or panduriform). The standard petal is generally wider above the middle in some groups and wider below the middle in others.
- The length of the standard petal relative to that of the keel. It is much longer than the keel in all species of the sections Monocarpa, Lotononis, Polylobium and Buchenroedera, and also in L. serpens of the monotypic section Euchlora, L. dissitinodia of the section Aulacanthus and L. minor of the section Krebsia. The opposite is true for some species of the sections Synclistus and Leptis, and most species of Leobordea, where the standard is much shorter than the keel.
- The relative length and shape of the wing and keel petal. Note, for example, the small size and similarity in the shape of the keel petals in the sections Buchenroedera, Polylobium, Euchlora and Lotononis. In section Oxydium, most species have the keel distinctly rostrate or at least somewhat pointed (previously the cause of much confusion between Oxydium and the genus Crotalaria -- see Van Wyk 1989f, Appendix 26).

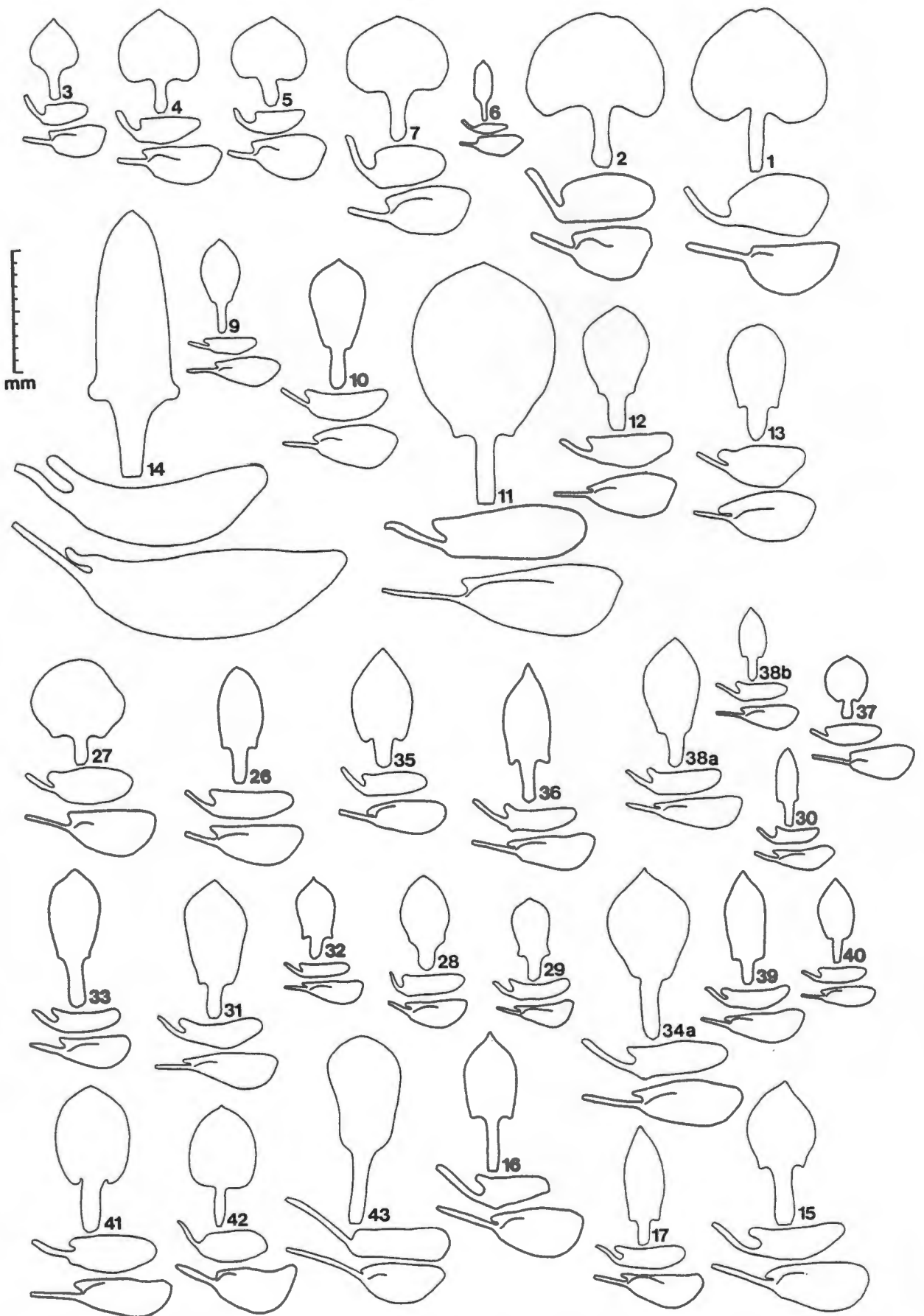


Figure 3.1.9. Variation in the size and structure of the corolla in the genus Lotononis (vestiture is not shown). Species are numbered as in Part 5: sections Listia (1--7), Digitata (9--14), Leptis (26--43) and Lipozygis (15, 16 & 17).

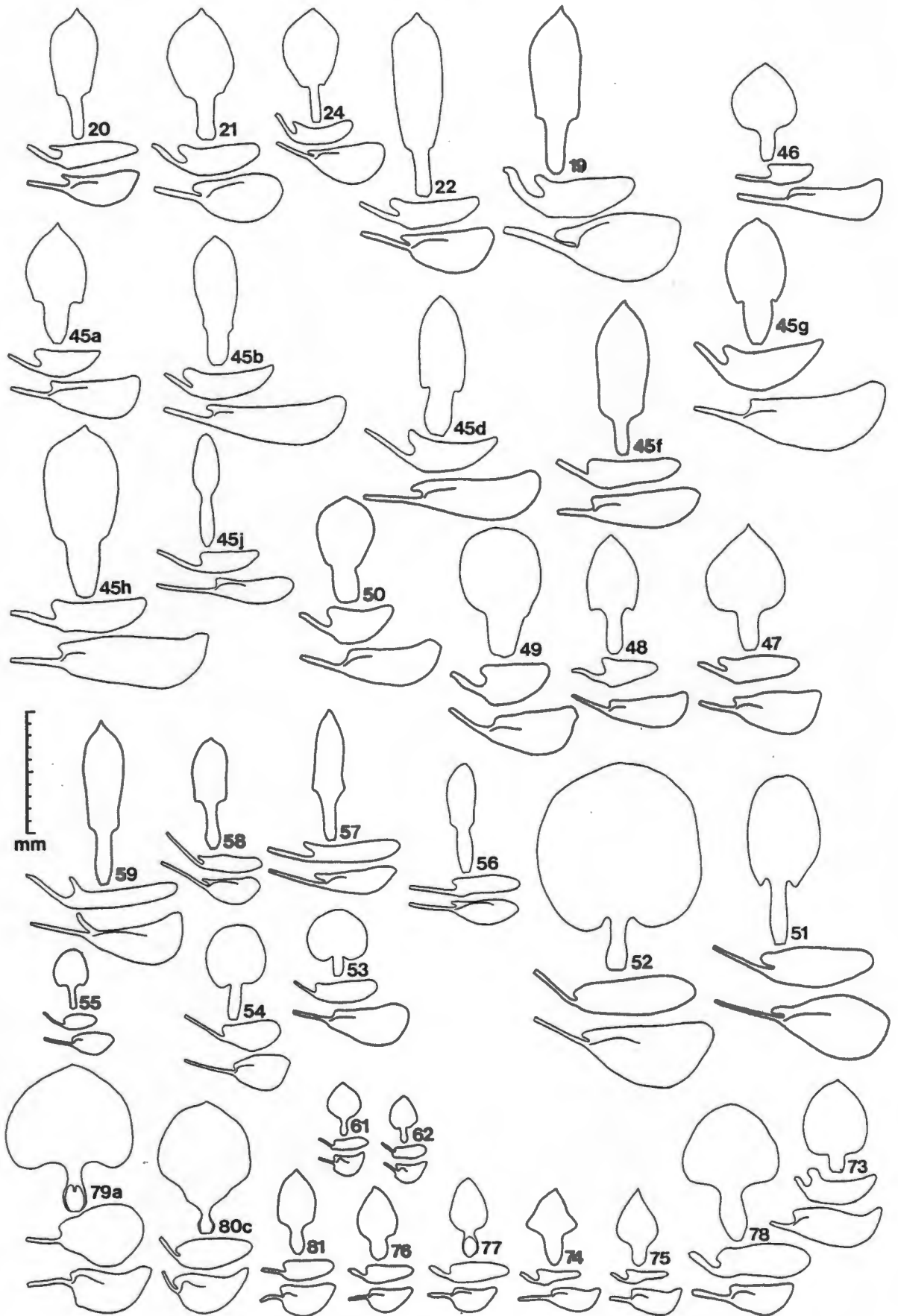


Figure 3.1.9 continued. Variation in the size and structure of the corolla in the genus *Lotononis*. Species are numbered as in Part 5: sections *Lipozygia* (20--24), *Leobordea* (45--50), *Synclistus* (51--59) and *Oxydium* (61--81).

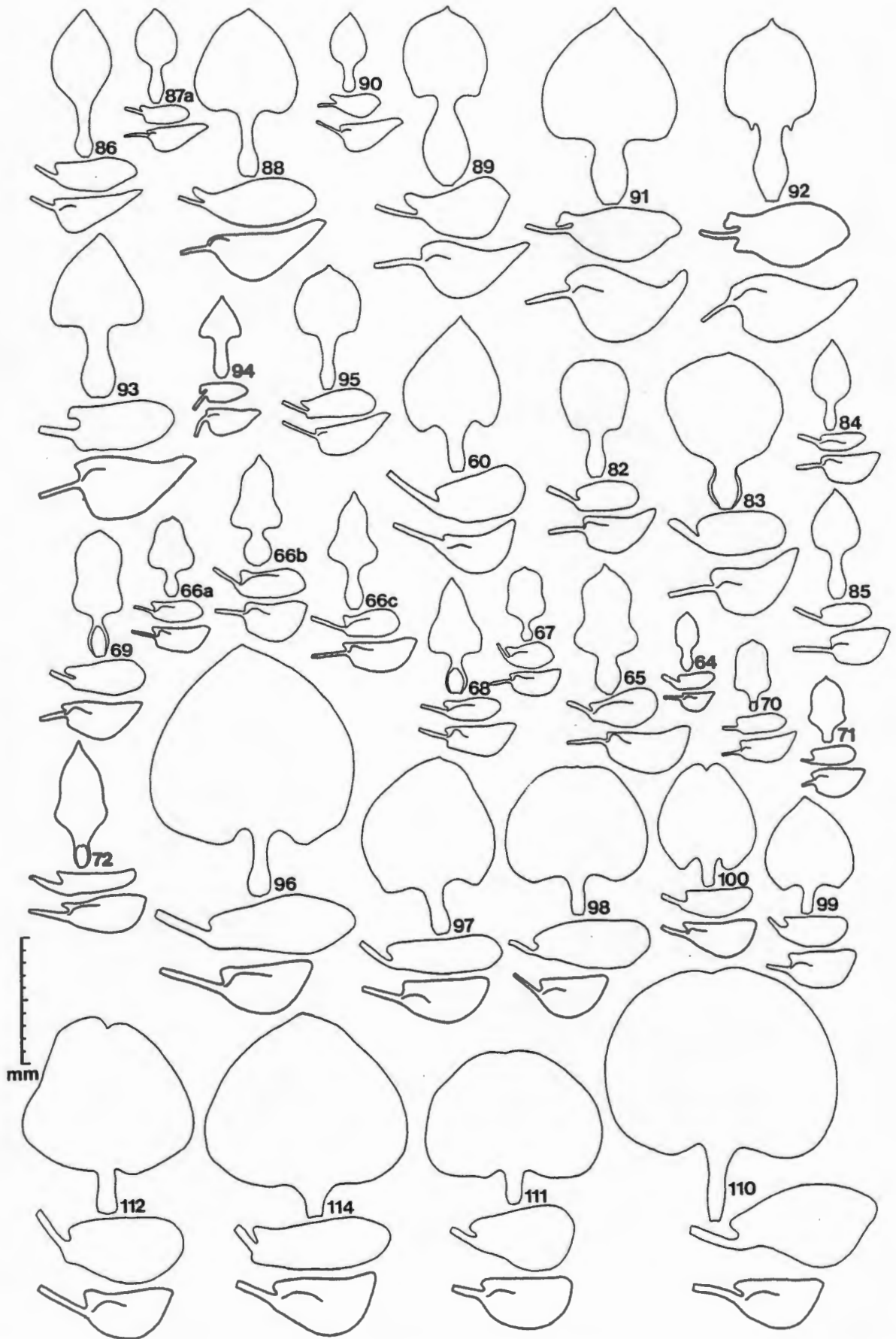


Figure 3.1.9 continued. Variation in the size and structure of the corolla in the genus Lotononis. Species are numbered as in Part 5: sections Oxydium (64--95), Monocarpa (96--98), Cleistogama (99 & 100) and Lotononis (110--114).

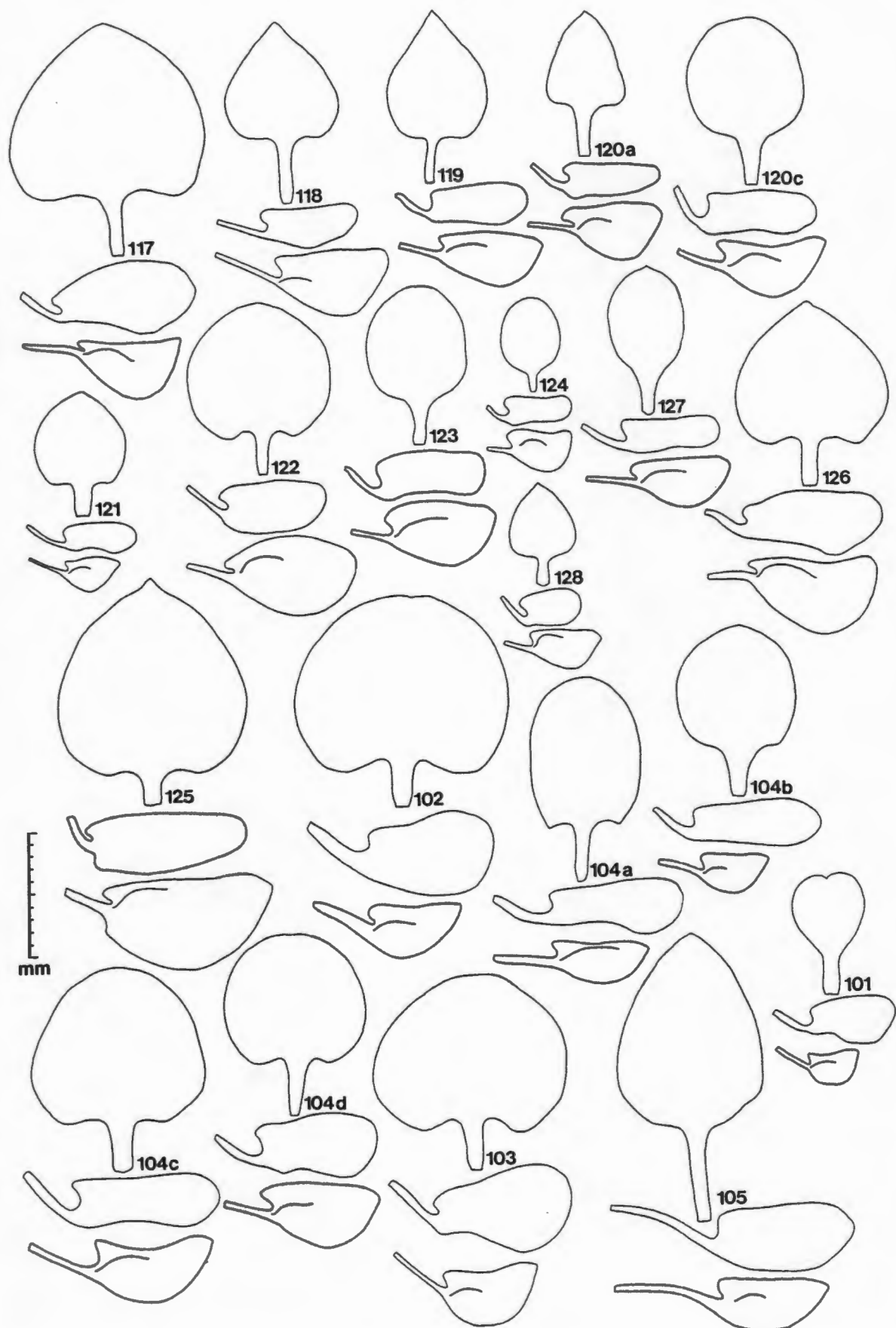


Figure 3.1.9 continued. Variation in the size and structure of the corolla in the genus Lotononis. Species are numbered as in Part 5: sections Aulacanthus (117--128), Euchlora (101) and Polylobium (102--105).

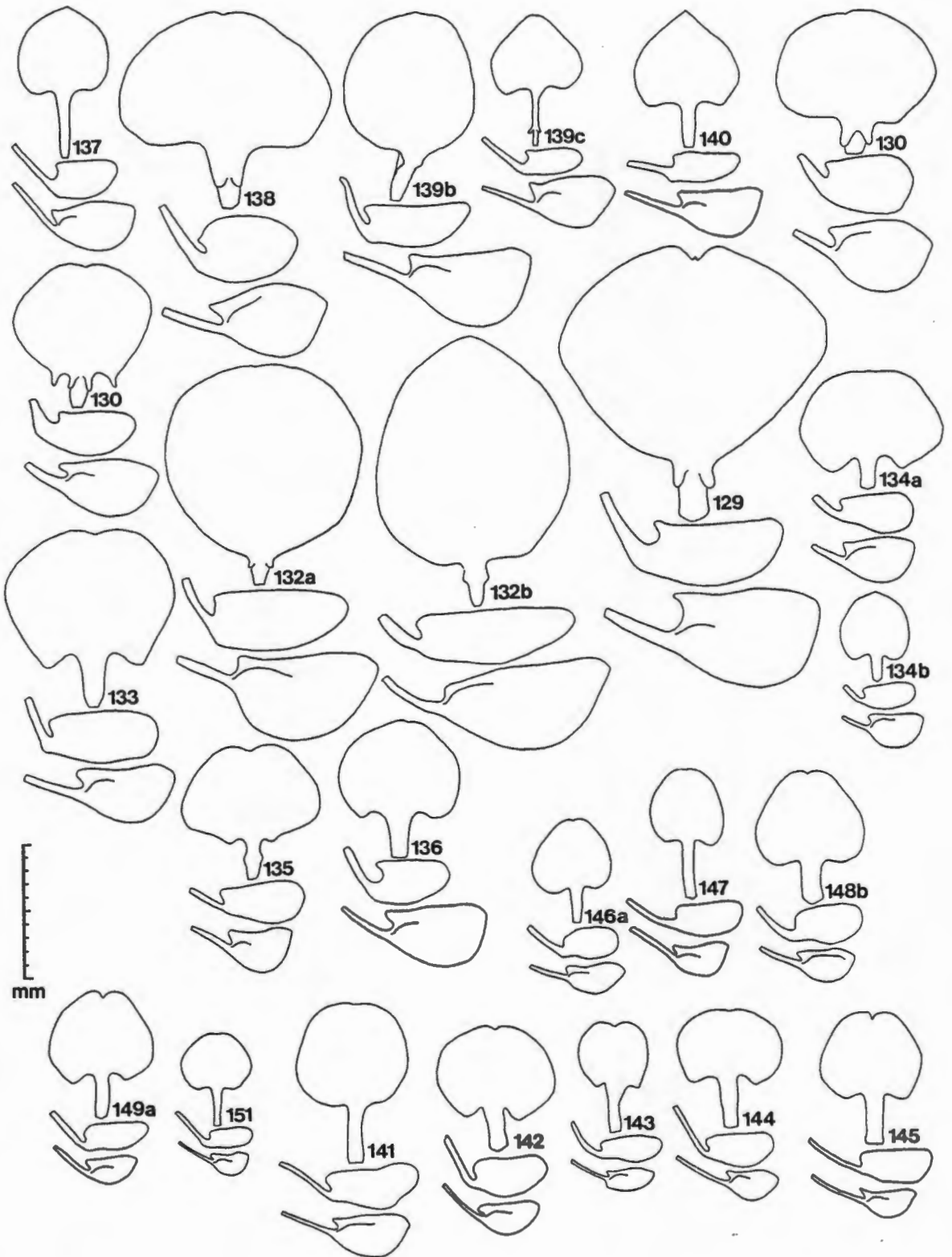


Figure 3.1.9 continued. Variation in the size and structure of the coralla in the genus *Lotononis*. Species are numbered as in Part 5: sections *Krebsia* (129--140) and *Buchenroedera* (141--151).

- The length and shape of claws. Note the distinctly dilated claw of the standard petal in section Oxydium (L. oxyptera and a form of L. falcata are good examples) and the very long claws in some sections and species, such as L. maroccana of the section Leptis and L. pentaphylla of the section Synclistus.

- The occurrence and size of lobes and callosities on the standard petal. Several species of the section Oxydium have a central callosity in an adaxial position near the apex of the claw. This callosity varies from a mere thickening (which is scarcely visible) to an elongated protuberance as in L. macrosepala. In the section Krebsia, most of the species have two callosities at variable positions on the claw, but they are often weakly developed and quite variable even within the species. Lobes near the base of lamina are a useful character to distinguish L. carnea from L. stenophylla but such lobes have been observed elsewhere only in the section Krebsia, where they are a rare phenomenon in L. stricta (Figure 3.1.9, 130 in the second row).

- The size and shape of auricles and pockets on the wing and keel petals. L. falcata and its relatives, for example, are the only species which have distinctly pocketed wing petals (this is incidentally also the only group where wing petal sculpturing is often totally absent).

The vestiture of the corolla is quite variable and provides several useful characters to distinguish between closely related species. It also contributes three characters that could be used

in cladistic analyses. The vestiture of the standard, wing petals and keel is not logically correlated in the genus Lotononis, and it was therefore interpreted as three different characters. Hairy wing and keel petals are apomorphies to separate the sections Lipozygis, Leptis, Leobordea and Synclistus from the rest of the genus. When hairiness is polarized as the plesiomorphic state, these four sections invariably form a basal grade. It seems reasonable to accept hairy petals as apomorphic because it is a rare condition in all the genera considered to be likely outgroups, and also rare in the Podalyrieae and Liparidae. The standard petal often has a distinctly striated appearance due to the contrasting colour of the veins (in species with striated standard petals, the abaxial surface of the standard is usually very different in colour from the adaxial surface, often reddish-brown, dark grey or greyish-green). A dramatic reduction in the size of the corolla as a result of cleistogamy (Van Wyk 1989, Appendix 32) provides evidence for an affinity between the sections Oxydium, Monocarpa and Cleistogama and occurs rarely elsewhere (only in the section Leptis). Yellow is by far the most common flower colour in Lotononis, but different shades of red, pink, purple, blue and white occur in some species. Blue flowers (not to be confused with purple) are characteristic of the section Krebsia and are very common in the sections Buchenroedera and Lotononis. One species of Aulacanthus (L. azureoides) and one species of Monocarpa (L. maximiliani) also have blue flowers. It seems reasonable to accept this state as apomorphic. The evolutionary significance of blue as a flower colour has been

discussed by Gottsberger and Gottlieb (1981), who showed that it is a rare character in the Angiosperms as a whole. Blue pigmentation is also rare in the Papilionoideae and does not occur in any other genera of the Crotalarieae except (rarely) in some species of Crotalaria (Polhill 1982).

Anthers

The shape and degree of dimorphism of anthers is of taxonomic value in Lotononis and some general trends may be distinguished (Figure 3.1.10). The large degree of dimorphism between the basifixed and dorsifixed anthers in the section Oxydium is the most obvious and useful character. In this section, the basifixed anthers are mostly several times longer than the dorsifixed ones. The carinal anther is usually similar to the dorsifixed anthers or slightly larger. L. macrocarpa of the section Listia (1 in Figure 3.1.10) is the only species where the usual condition in Crotalaria is approached, namely a 5 + 5 rather than a 6 + 4 arrangement as in Lotononis. The size and shape of the carinal anther in L. macrosepala and related species and also in L. delicata, L. pseudodelicata, L. pallens and L. schreiberi differ from other species of the section Oxydium in being much larger than the dorsifixed anthers. These species are all rather isolated in terms of their gross morphology but their position in section Oxydium seems reasonable. The species with beaked keels all have the carinal anther similar to the dorsifixed ones (6 + 4

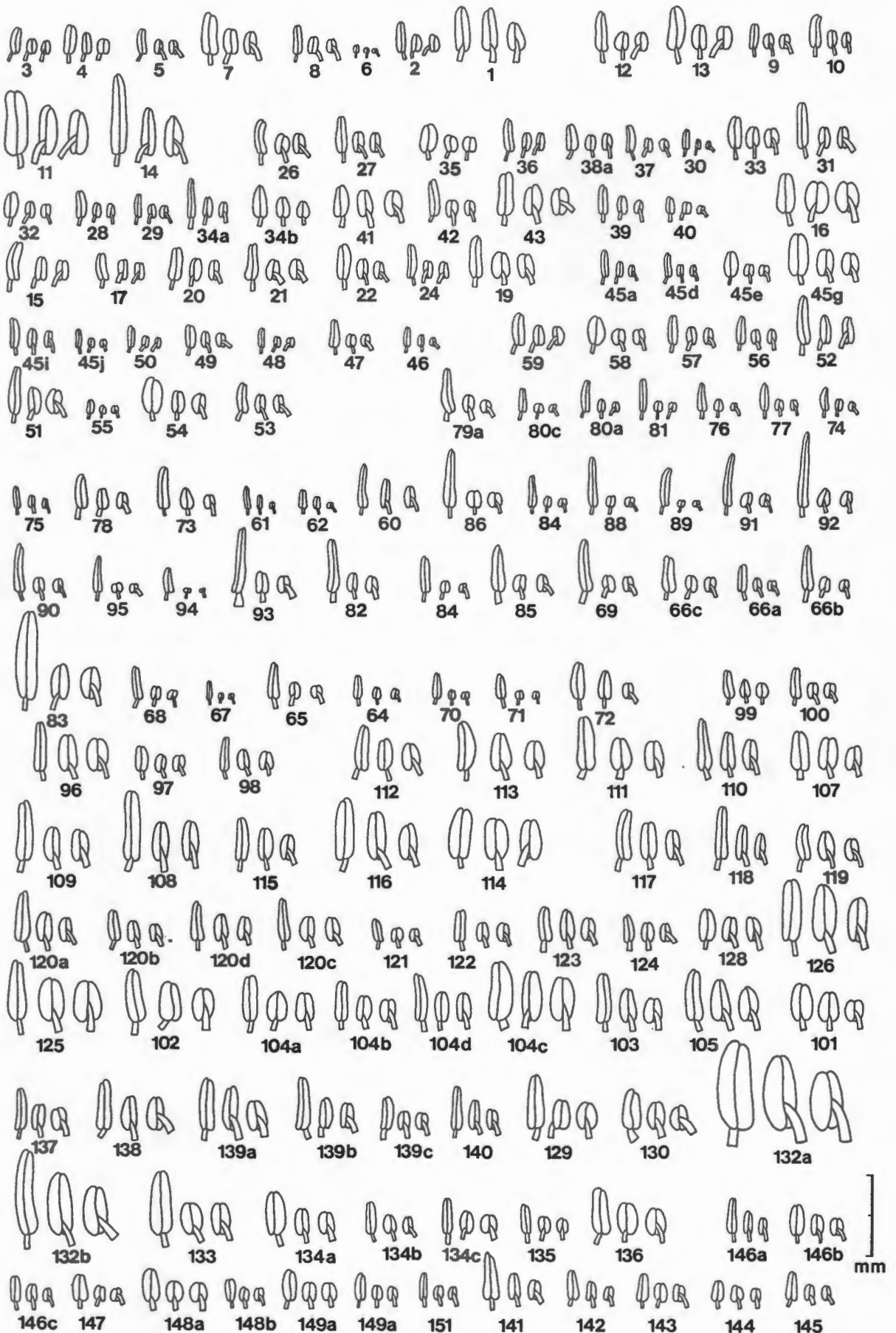


Figure 3.1.10. Variation in the shape and size of anthers in the genus *Lotononis*. Basifixed anther, carinal anther and dorsifixed anther from left to right. Species are numbered as in Part 5: sections *Listia* (1--8), *Digitata* (9--14), *Leptis* (25--44), *Lipozygia* (15--24), *Leobordea* (45--50), *Synclistus* (51--59), *Oxydium* (60--95), *Cleistogama* (99 & 100), *Monocarpa* (96--98), *Euchlora* (101), *Lotononis* (106--116), *Aulacanthus* (117--128), *Polylobium* (102--105), *Krebsia* (129--140) and *Buchenroedera* (141--151).

arrangement) and can therefore easily be distinguished from Crotalaria. The shape of the anthers in the sections Monocarpa and Cleistogama does not strongly an affinity with Oxydium and is similar to those of the sections Lotononis, Aulacanthus and Krebsia. It is interesting to note that the carinal anther is often distinctly larger than the dorsifixed anthers in those species that are considered to be the least specialized in their respective sections. Within the genus Lotononis, a long carinal anther is clearly the plesiomorphic condition and the 6 + 4 arrangement in all the species is a useful generic apomorphy. The 5 + 5 arrangement in Crotalaria (and in the tribe Genisteae, the obvious outgroup for the Crotalarieae) is almost certainly plesiomorphic.

Pistil

General trends were also found in the morphology of the pistil (Figure 3.1.11). The pistil is usually sessile or subsessile but distinctly stipitate in L. benthamiana and L. longiflora of the section Digitata. Some species of the section Oxydium (L. acutiflora and L. rabenaviana, for example) also have stipitate pistils. A linear or oblong ovary as in the sections Listia, Digitata, Lotononis and Krebsia is considered to be the unspecialized condition even though both linear and ovate pistils occur in Crotalaria (the most likely outgroup for Lotononis as shown in Part 2). From a wider consideration of the shape of the

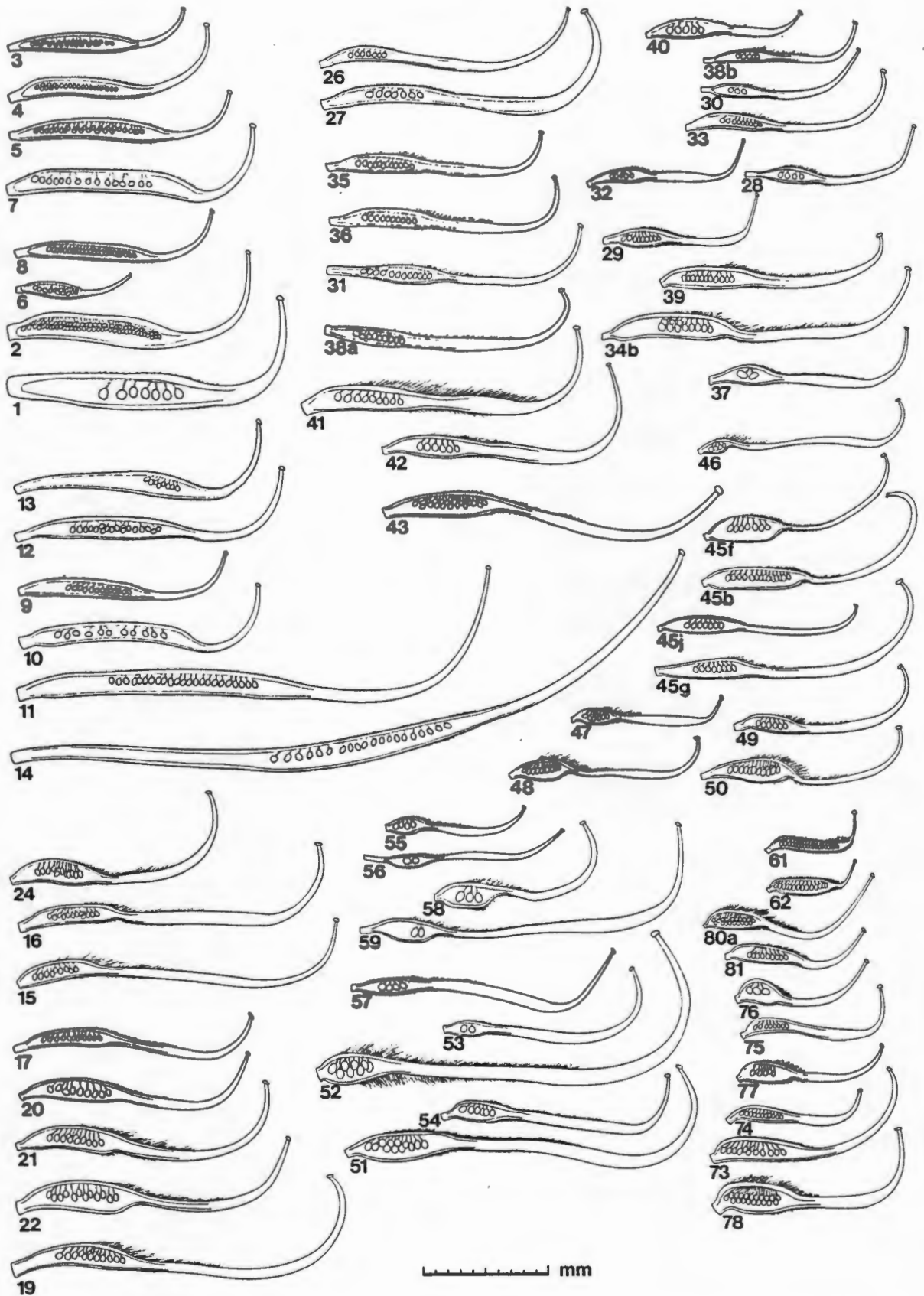


Figure 3.1.11. Variation in pistils in the genus *Lotononis*. Note the differences in attachment (a stipe is rarely present), size, shape, vestiture, style curvature and number of ovules. Species are numbered as in Part 5: sections *Listia* (1--8), *Digitata* (9--14), *Lipozygis* (15--24), *Leptis* (25--44), *Leobordea* (45--50), *Synclistus* (51--59), *Oxydium* (61--81).

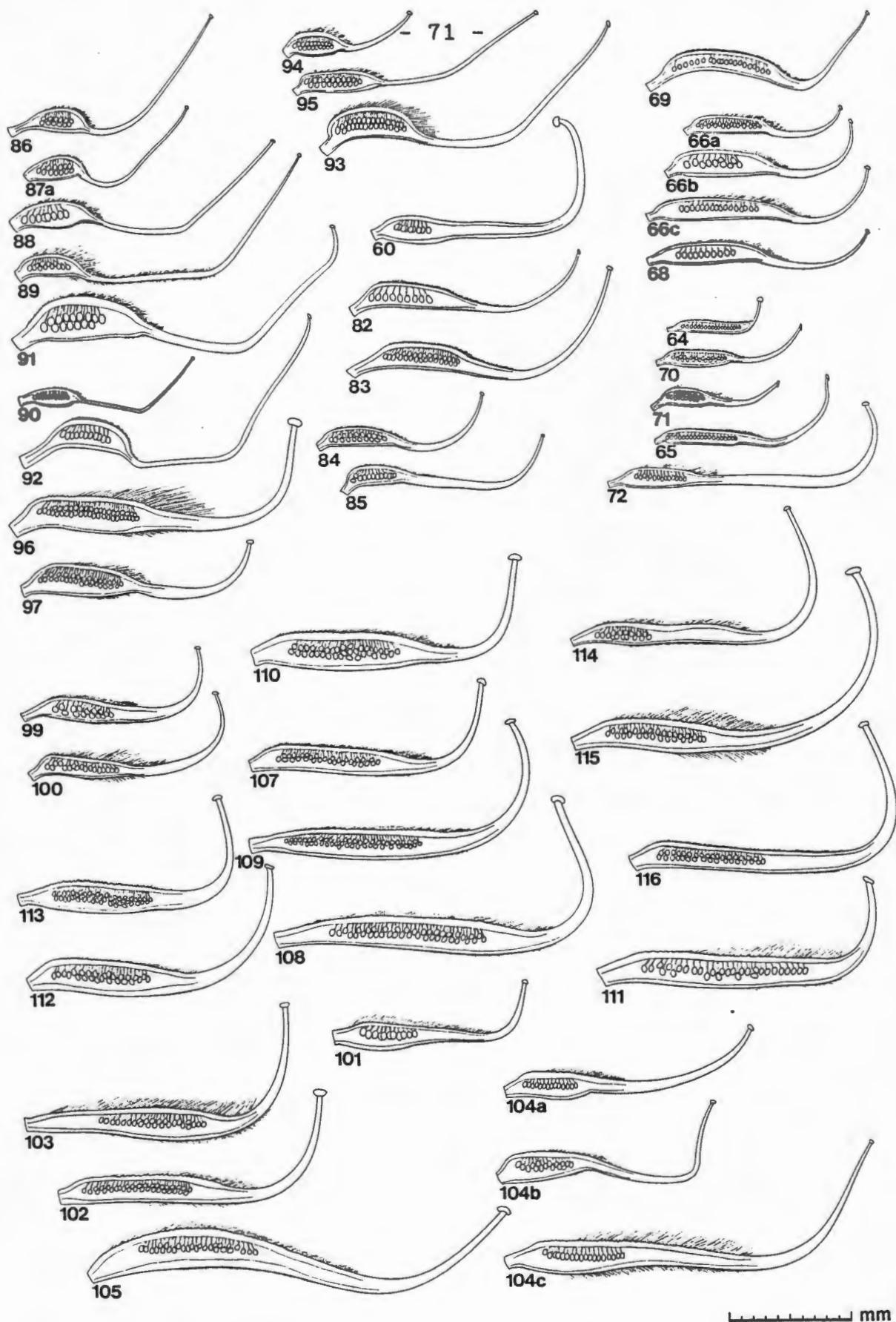


Figure 3.1.11 continued. Variation in pistils in the genus *Lotononis*. Species are numbered as in Part 5: sections *Oxydium* (64--95), *Monocarpa* (96--98), *Cleistogama* (99 & 100), *Lotononis* (106--116), *Euchlora* (101) and *Polylobium* (102--105).

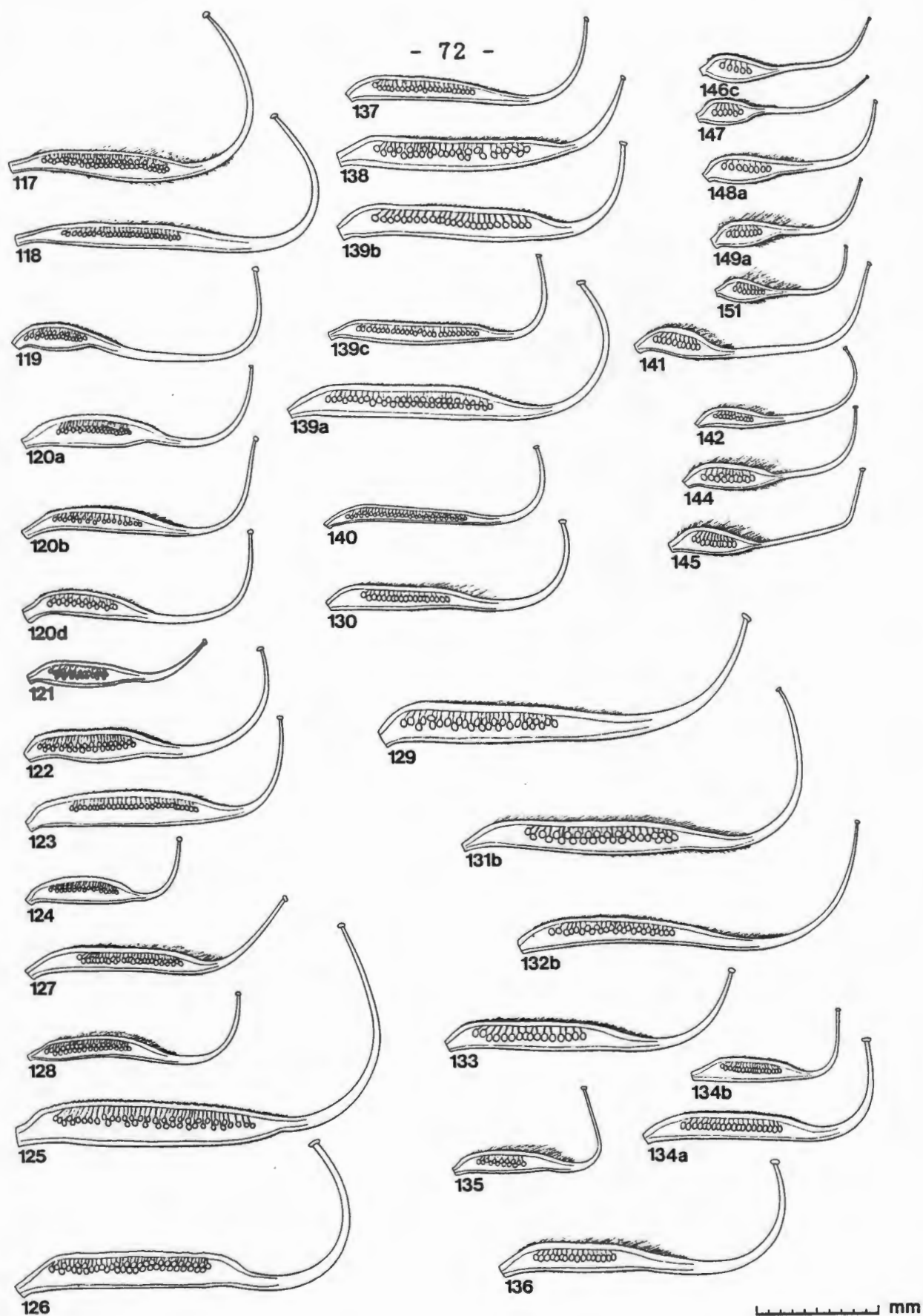


Figure 3.1.11 continued. Variation in pistils in the genus Lotononis. Species are numbered as in Part 5: sections Aulacanthus (117--128), Krebsia (129--140) and Buchenroedera (141--151).

pistil in the Genisteae sensu lato and related tribes (Polhill 1976), there appears to be a general trend towards a shortening of the ovary and a reduction in the number of ovules in several unrelated genera. It seems likely that the short and ovate shape as in most species of the sections Leptis, Lipozygis, Synclistus, Leobordea, Oxydium and in all the species of Buchenroedera has developed more than once, because in most of the sections with linear ovaries there are at least one species with an ovate ovary (L. minima in Listia, L. benthamiana in Digitata, L. elongata in Lotononis and L. minor in Krebsia, for example). There are also some significant differences in the number of ovules. A small number (one or two ovules only) is a diagnostic character for L. esterhuyseana, but some other species of the section Leptis, most species of section Synclistus and some species of section Leobordea also have a small number. This character may be taken as evidence of an affinity between these sections. A short and strongly upcurved style as in the sections Listia, Lotononis and Krebsia is considered to be the plesiomorphic condition. The very long and slender styles in most species of the sections Leptis, Lipozygis, Leobordea and Synclistus may be taken as supportive evidence that these sections together are indeed a monophyletic unit (as suggested in Part 3.2). Very long styles also occur in several annual species of the section Oxydium but I suggest that this is an independent development which resulted from the tendency towards a beaked keel. The shape of the ovary and the length and curvature of style generally agree well with the circumscription of the

sections and also tend to be quite uniform within the sections. A notable exception is the section Oxydium, where it is remarkably variable. This variability results in some very useful diagnostic characters for closely related species. L. delicata and L. pseudodelicata seem to differ from other species in the very short style, but it is interesting to note the similarity with L. tenuis. In L. schreiberi, the style is quite unlike any other species and rather similar to those of the section Leobordea. The diversity in Oxydium is perhaps an indication that the group is not monophyletic. It should be noted, however, that some species are virtually indistinguishable except for remarkable differences in the shape of the pistil or fruit. Some hairiness of the basal part of the style is quite common in the genus Lotononis, but it is probably not directly comparable with Crotalaria, where hairs generally occur on the upper part of the style, usually arranged in rows (Polhill 1976). The strongly curved styles in the section Oxydium are rather similar to the geniculate styles in Crotalaria, but in the latter the thicker basal part is usually clearly differentiated from the much thinner upper part. The size and shape of the stigma do not seem to have much potential as taxonomic characters. It is usually capitate or directed slightly to the front. L. strigillosa, L. linearifolia and L. pachycarpa are the only species where the stigmatic surface is clearly ventrally orientated and not terminal.

Fruit

Variation in the fruit morphology of Lotononis is shown in several of the figures in Part 5. The shape (and particularly the degree to which the pod is laterally inflated) is one of the most useful taxonomic characters and it is often virtually impossible to distinguish between closely related species when mature pods are not available. Predictably, the shape in lateral view closely agrees with the shape of the ovary. A notable exception occurs in the sections Listia and Digitata, where the pod is occasionally folded like a concertina at maturity (see Figures 5.1 & 5.2). In these species (L. plicata, L. listii, L. subulata and rarely L. bainesii) the ovules are often fewer in number and more widely spaced than in closely related species with linear pods. The shape of the pod in transverse section is a very useful character to distinguish between closely related species and also between some of the sections. When inflated, the pods are often short and ovate, but they can also be linear as in the sections Krebsia and Aulacanthus (Van Wyk 1988a, Appendix 16). The inflated (turgid) condition is here considered to be plesiomorphic and that flat pods developed independently in some of the different sections. Cladistic analyses in Part 3.2 showed that the similarity with Crotalaria is likely to be synapomorphic (or symplesiomorphic) rather than convergent. It should be noted that several species of Lebeckia also have inflated pods, and that both flat and turgid pods occur in the tribes Podalyrieae and Liparieae. It is therefore not clear from a comparison with

outgroups how this character should be polarized. The shape of fruit can be very variable and is often excessively weighted as a generic character (Polhill 1976). Indehiscent pods occur in several sections of Lotononis and is clearly a convergent character. An interesting development occurs in the section Synclistus, where the pods are totally indehiscent and enclosed within a much-inflated calyx (see figures in Appendix 28). This phenomenon is associated with wind-dispersal and was discussed by Van Wyk (1989h, Appendix 28).

A unique character for Lotononis is the presence of warty protuberances along the upper suture of the fruit (visible in several of the figures in Part 5). This character is not without ambiguity within Lotononis but has nonetheless been used to justify a wide generic concept. In Buchenroedera, the upper suture is invariably smooth, but this is also true for all except one species of Krebsia (L. caeruleascens). Another potentially useful character is the length of the funicles, but it is of value at the specific rather than sectional level. Long funicles occur sporadically in several of the sections, but are particularly evident in the sections Oxydium (L. rabenaviana and L. sparsiflora) and in Monocarpa (L. leptoloba and L. maximiliani). One species of the section Lotononis (L. complanata) also has exceptionally long funicles. Long funicles have been reported from the monotypic north African genus Spartidium (Polhill 1976) but there is no other evidence to suggest a direct affinity between this genus and Lotononis.

Seeds

(Polhill 1976) investigated the external and internal morphology of seeds in the genera of the Crotalarieae and related tribes. His study showed that there are general trends in some characters but very few distinct discontinuities between the genera of the Crotalarieae.

Examples of the range of variation found in the seeds of Lotononis are shown in Figure 3.1.12. Seeds vary in size from less than 1 mm in diameter in L. tenuis to over 6 mm in diameter in L. serpens and L. macrocarpa. The shape in side view is usually suborbicular or slightly oblong, but it may also be distinctly oblong (often in the sections Aulacanthus, Krebsia and Buchenroedera), round and compressed (as in L. brevicaulis) or angular (as in some forms of L. platycarpa). The radicular lobe is often very prominent and this leads to an almost triangular shape (as in L. maroccana). A rugose or tuberculate testa surface (visible in some of the seeds in Figure 3.1.12) occurs only in Lotononis and Crotalaria and this character state has been used to support the idea of a relationship between the two genera. Despite its variability in some sections, the surface sculpturing of seeds is a very useful diagnostic character for most species of the genus Lotononis and all but three of the sections. Euchlora, Buchenroedera and Krebsia are the only sections where the seed surfaces of all the species are invariably smooth (notice also the similarity in surface

Figure 3.1.12. Variation in the seeds of Lotononis. Examples from all the sections were chosen to illustrate the range of variation in size, shape, testa surface and colour patterns. Scales in mm. The species of each row are given from left to right:

- Row 1. Section Listia: L. angolensis, L. solitudinis, L. listii.
- Row 2. Section Digitata: L. digitata, L. quinata, L. magnifica.
- Row 3. Section Leptis: L. genistoides, L. maroccana,
L. lupinifolia, L. pusilla.
- Row 4. Section Leptis: L. prolifera, L. mucronata, L. calycina,
L. curvicarpa, L. arida, L. carinata.
- Row 5. Section Lipozygis: L. eriantha, L. foliosa, L. procumbens,
L. lanceolata, L. corymbosa.
- Row 6. Section Leobordea: L. platycarpa (all 6 seeds).
- Row 7. Section Leobordea: L. platycarpa (first 3 seeds),
L. schoenfelderi, L. furcata, L. stipulosa (2 seeds),
L. bracteosa.
- Row 8. Section Synclistus (except the first seed):
L. esterhuyseana (Leptis), L. polycephala, L. globulosa,
L. bolusii, L. longicephala.
- Row 9. Sections Polylobium and Aulacanthus: L. brevicaulis,
L. involucrata subsp. digitata, L. exstipulata,
L. umbellata, L. densa subsp. gracilis.
- Row 10. Section Lotononis (except the first seed): L. densa
subsp. leucoclada (Aulacanthus), L. complanata,
L. filiformis, L. elongata, L. acuminata.
- Row 11. Sections Euchlora and Krebsia: L. serpens (Euchlora),
L. caeruleascens (2 seeds), L. sericophylla (2 seeds).
- Row 12. Section Krebsia: L. divaricata (2 seeds), L. stricta
(2 seeds), L. eriocarpa (2 seeds).
- Row 13. Section Buchenroedera: L. lotononoides (2 seeds),
L. meyeri (2 seeds), L. pulchella (2 seeds).
- Row 14. Section Oxydium: L. delicata (2 seeds), L. tenuis,
L. pachycarpa, L. strigillosa, L. falcata, L. parviflora,
L. fruticoides, L. sabulosa.
- Row 15. Section Oxydium: L. schreiberi, L. pallidirosea,
L. macrosepala, L. laxa, L. curtii, L. brachyantha,
L. crumanina, L. maculata.
- Row 16. Section Oxydium: L. pumila, L. micrantha, L. acutiflora,
L. rostrata subsp. rostrata, L. rostrata subsp.
brachybotrys, L. oxyptera, L. perplexa.
- Row 17. Sections Oxydium (first 3 seeds), Monocarpa (next 2
seeds) and Cleistogama (last 2 seeds): L. rabenaviana,
L. sparsiflora, L. lenticula, L. leptoloba,
L. maximiliani, L. tenella, L. pungens.

colouration in these sections). The seeds of the sections Polylobium, Lotononis and Aulacanthus are all distinctly tuberculate and rather similar to those of the sections Oxydium, Monocarpa, Cleistogama, Digitata, Leptis and Leobordea. In the sections Listia, Lipozygis, Leptis, Leobordea and Synclistus, the seeds of some species are often not distinctly tuberculate but they are rarely quite smooth as in the sections Euchlora, Krebsia and Buchenroedera. The shape, size and surface colouration of the seeds have some taxonomic value at the specific level but limited use as a sectional character. Nevertheless, the general patterns agree rather well with the arrangement of the sections as proposed in Part 3.3. The range of variation in the sections Krebsia and Buchenroedera, for example, appears to be identical. As a general trend, the herbaceous and annual species tend to have smaller seeds with a more prominent radicular lobe (Polhill 1976). The enlarged radicular lobe suggests an affinity with Crotalaria, but the character appears to be too variable to more than a general indication of relationship.

In summary, it may be pointed out that there are several distinct "apomorphic tendencies" in Lotononis but that very few of these characters are without ambiguity in their expression. I could not find a single character that would unambiguously support the concept of Lotononis as a monophyletic unit. It may, however, be even more difficult to show that the wide generic concept (which includes Buchenroedera) is not monophyletic. The following character states support the present wide generic concept of

Lotononis: single stipules, biramous hairs, absence of bracteoles, a zygomorphic calyx, a verrucose upper suture of the fruit, tuberculate seeds and long funicles. To these may be added the presence of cyanogenic glucosides and pyrrolizidine alkaloids. The complete loss of bracteoles in most of the species appears to be a very reliable generic character. The few species that do have bracteoles can readily be identified by the solitary or at least distinctly dimorphic stipules and, except for L. macrocarpa, also by the shallow lateral sinuses of the calyx.

Convergences and reversals seem to have played an important role in the phylogeny of the genus and may have obscured the real evolutionary relationships between some of the sections and species. In terms of infrageneric relationships, morphological characters nevertheless have led to some significant new insights into relationships within the genus and those characters that have apparently become fixed in some groups provide useful diagnostic characters for the new and modified sections described in Part 5.

Chromosome cytology

Lotononis was very poorly known cytologically and only 5 counts were known previously. Chromosome numbers for 47 species were reported and discussed by Van Wyk and Schutte (1988a, Appendix 14) and provided the first evidence of a polyploid series in the

tribe Crotalarieae. The chromosome base numbers (9 or 7) closely agrees with the modified circumscription of the sections based on morphological evidence. It is now clear that a separation of the $2n = 18$ lineage from the one with $2n = 28$ would have little practical value. There are too many characters that would not support such a split. The results of cladistic analyses strongly suggest that $2n = 18$ is the most likely ancestral condition in Lotononis. An alternative explanation, namely that the base number of 9 developed repeatedly by early convergences should perhaps not be summarily dismissed. In the cladistic analyses, chromosome number behaved in much the same way as the habit, which also shows an early advance to herbaceous with a subsequent reversal to woody. I therefore favour the idea that the original base number of $x = 7$ was not lost in the woody species i.e., that this character state may in fact be a symplesiomorphy and not an apomorphy. Several counts are now available for the annual species of Lotononis and they all have $2n = 18$. Additional specific reports are needed to confirm the position of some of the species. The anomalous L. brevicaulis for example, was recently found to have $2n = 28$, so that its position in the section Polylobium seems reasonable. It may also be interesting to obtain more counts for species in the section Krebsia, where different ploidy levels were found in different populations of the same species.

Chemical characters

The occurrence and distribution of pyrrolizidine and quinolizidine alkaloids in several species of Lotononis were reported by Van Wyk & Verdoorn (1989c, Appendix 8). The alkaloidal evidence provided support for the idea that Crotalaria and Lotononis are closely related and that the latter and Buchenroedera are not distinct at the generic level (Van Wyk & Verdoorn 1988, Appendix 2). Despite very low yields in most of the species, it was possible to show that pyrrolizidine alkaloids occur in the sections Buchenroedera, Krebsia, Aulacanthus, Lotononis, Polylobium, Oxydium, Euchlora and Synclistus. Quinolizidine alkaloids rarely occur in more than trace quantities, but significant amounts have been found in species of the sections Listia, Leptis and Leobordea. The sample size does not allow a full evaluation of the significance of alkaloids as a sectional character, but the general trend (an apparent replacement of quinolizidine alkaloids by macrocyclic pyrrolizidine esters) is clear.

Despite the practical difficulty of low yields, it may be worthwhile to examine the large differences between some of the sections in more detail. Available evidence (Van Wyk & Verdoorn 1989c) suggests that the section Listia can be distinguished by relatively large quantities of 3 β -hydroxylupanine, the sections Lipozygis and Leptis by lupanine as the major alkaloid (a synapomorphy?), the section Leobordea by sparteine as the major

alkaloid, the section Oxydium by pyrrolizidine esters with a saturated necine moiety (autapomorphy?) and the group of sections with a chromosome base number of $x = 7$ (Polylobium, Lotononis, Aulacanthus, Krebsia and Buchenroedera) by pyrrolizidine esters with an unsaturated base. The data set is too small to allow the use of the data at this level, so that only the two major alkaloid types (quinolizidine and pyrrolizidine) could be confidently polarized for infrageneric analyses.

A survey of cyanogenesis in a large number of samples (Van Wyk 1989n, Appendix 12) has shown that Lotononis sensu lato is the only cyanogenic genus in the Crotalarieae. The chemical basis for cyanogenesis in Buchenroedera was found to be due to the glucoside prunasin (Van Wyk & Whitehead 1989, Appendix 13). Large quantities of prunasin and small quantities of a malonyl ester of prunasin have since been isolated from leaves of L. fruticoides (Seigler, pers. comm.), and consequently, cyanogenesis in Lotononis and Buchenroedera can be accepted as homologous. Cyanogenesis is a very useful infrageneric character because it seems to be closely correlated with morphological patterns. False positive results are perhaps less likely than false negative results and it is easier to show that a particular species is cyanogenic than to prove that it is not. Nevertheless, the major groups within Lotononis were found to be either cyanogenic or acyanogenic. Very few species did not fit this general pattern and there can be little doubt that cyanogenesis has considerable predictive value at the sectional level.

3.2 CLADISTIC ANALYSES

A review of the application of the cladistic methodology in botany was recently given by Linder (1988). Examples of its application in the Fabaceae are the studies of Lavin (1987), Crisp and Weston (1987), Zandee and Geesink (1987) and Schutte and Van Wyk (1989). The method was criticized by Cronquist (1987) and it is indeed true that the chosen cladogram may only partly depict the evolutionary events that actually happened. Given the limited spatiotemporal information on which all classifications are based, this is to be expected. There are however, no other methods for reconstructing phylogenies in an explicit way. I used cladistic analysis not only to find a phylogeny, but to explore the patterns of character distributions, both at sectional and specific levels, and to use these patterns to formulate a classification.

The program Hennig 86 Version 1.5 (Farris 1988) was used to analyse a large number of smaller data sets, using some of the characters given in Table 3.1 (and later also to determine relationships between the species of each major group - see below). As a general working procedure, the tree or trees obtained by the "mhennig*" command were used as input to find all possible alternatives by using the "bb*" command. The latter applies extended branch-swapping to the trees in the input file and will generate all the trees it can find (Farris 1988). When several different topologies resulted from the "bb" routine, a

Nelson Consensus Tree was generated using the "nelsen" command. This showed the presence (if any) of robust sections in the topologies of the various trees in the input file. To reduce the ambiguity in some data sets and to obtain groupings based on more reliable characters, successive weighting was applied in some of the analyses. This option, executed by the command "xsteps w", has the advantage that no prior assumptions on character weighting are necessary. Weighting is based on the consistency indices of individual characters. In the present study, it was based on the consistency indices of the "bb" results. Successive weighting often generated trees that are not empirically acceptable.

For cladistic analyses of infrageneric relationships in Lotononis, the four basic data sets given in Tables 3.2.1 to 3.2.4 were used. These matrices include the 15 major taxa (sections) and between 18 and 25 characters. The small size of the four data sets is due to the following:

- an elimination of subdivisions within larger taxa. In the original preliminary circumscription of groups within the genus, some of the larger sections were divided into several groups, each chosen to represent all the most likely monophyletic units. If there were no clear and unambiguous synapomorphies for a particular group of species with any other group, it was retained as a separate unit. This resulted in 15 basic groups.

- recoding of character states when smaller units within the large sections were combined. When a character shows variability within a group, it is usual to code for the plesiomorphic state. In this way, all those characters which defined only a part of a combined taxon were eliminated because they no longer showed any variability within the genus as a whole.

- removal of autapomorphies for terminal taxa because they serve no purpose as grouping characters.

- removal of very variable characters that do not define any particular group and which have doubtful value as cladistic characters at the sectional level.

Several modifications of the smaller data sets were analysed to study the effect of individual characters and to test the validity of certain assumptions about the polarization of character states. Even small modifications (such as eliminating a single character or reversing the polarity of a single character) often had a dramatic effect on the topology of the cladogram.

It is not practical to give details of all the cladistic analyses that were done at the sectional level. Six examples were therefore chosen to illustrate the basic pattern of character state distributions in Lotononis. A summary of the commands, data sets used, results and statistics of the six analyses is given below:

ANALYSIS NUMBER	DATA SET USED	NUMBER OF CHARACTERS	COMMANDS (OPTIONS)	RESULT	LENGTH OF TREE(S)	CONSISTENCY INDEX	ILLUSTRATION OF RESULT
No 1	Table 3.2.1	22	mhennig*	7 trees	68	41	-
			bb*	31 trees	68	41	-
			nelsen	1 tree			Figure 3.2.1b
			xsteps w	1 tree	194	51	Figure 3.2.1a
No 2	Table 3.2.2	22	mhennig*	1 tree	62	43	-
			bb*	1 tree	62	43	Figure 3.2.2a
No 3	Table 3.2.2, stipules deleted	21	mhennig*	4 trees	55	45	-
			bb*	6 trees	55	45	-
			nelsen	1 tree			Figure 3.2.2b
No 4	Table 3.2.3	18	mhennig*	1 tree	52	40	-
			bb*	6 trees	52	40	-
			nelsen	1 tree			Figure 3.2.3
No 5	Table 3.2.4, <u>Lebeckia</u> as outgroup	25	mhennig*	1 tree	80	42	-
			bb*	1 tree	80	42	Figure 3.2.4
No 6	Table 3.2.4, <u>Crotalaria</u> as outgroup	25	mhennig*	1 tree	80	42	-
			bb*	1 tree	80	42	Figure 3.2.4

The four data sets that were used for these six examples are given in Tables 3.2.1 to 3.2.4 and the polarizations of character states are explained in the footnotes of each table. In the first four analyses, polarizations were mostly based on a wider consideration of character states in the tribe as a whole (hypothetical ancestor), rather than to choose any specific genus as outgroup. In the final two analyses (which were more successful in terms of the stability of the topology), Lebeckia and Crotalaria were used as outgroups. The choice of either of these had little effect and the two analyses produced the same single topology (i.e., only one tree of minimal length). Surprisingly, the polarizations for pyrrolizidine alkaloids and chromosome base number did not have a dramatic effect in these last two analyses. It should be noted that Lebeckia, Crotalaria

and Lotononis are very similar and that several character states considered to be apomorphic in some groups of Lotononis are also present in some species of Lebeckia and Crotalaria. This is very evident from the fact that a basal polychotomy is produced in the final two analyses when the last-mentioned genera are both left in the matrix as outgroups.

Analysis 1

In this analysis, the branch-swapping routine resulted in 31 trees and a consistency index of 42. A Nelson Consensus Tree of the 31 trees was calculated, as shown in Figure 3.2.1b. A polychotomy of five main clades resulted, namely Listia, Digitata, Leptis/Synclistus (defined by hairy petals), Buchenroedera/Euchlora (rather well defined by flower colour, turgid pods and chromosome base number) and Oxydium/Monocarpa (defined by flower dimorphism and a reversal in calyx structure). It is interesting to note that these clades have recurred in several other analyses, also in some that are not reported here. These five clades can also be seen in the final result (Figure 3.2.4), where several polarizations were modified. I therefore suggest that this basal polychotomy accurately reflects the doubt that still exists about the correct positions of the five main clades. The positions of Listia and Digitata in particular,

TABLE 3.2.1. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE GENUS LOTONONIS AS USED IN ANALYSIS 1.

TAXA	CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)																								
	1	6	11	15	21	22	23	25	31	32	33	34	35	36	37	42	43	47	48	49	50	51			
hypothetical																									
ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0			
Listia	0	1	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	1	0	0	0	0			
Digitata	0	2	0	1	0	0	1	2	0	0	0	0	1	1	0	0	1	1	0	0	1	0			
Leptis	0	2	0	1	0	0	0	1	1	0	1	0	0	2	0	0	1	1	0	0	0	0			
Lipozygis	0	2	0	0	0	0	0	1	1	0	1	0	0	2	0	0	1	1	0	0	0	0			
Leobordea	1	2	0	2	0	0	1	1	1	0	1	0	0	2	0	0	1	1	0	0	0	0			
Synclictus	1	2	0	1	0	0	1	0	1	0	1	0	0	2	0	1	1	1	0	0	1	1			
Euchlora	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	2	1	0	0	0	1	1			
Oxydium	0	2	1	0	0	1	1	0	0	1	0	0	2	0	0	1	1	1	0	1	1	1			
Lotononis	0	1	0	0	1	0	1	1	1	1	0	1	1	0	0	2	1	1	1	1	1	1			
Aulacanthus	0	2	0	0	1	0	1	2	0	1	0	0	1	0	0	2	1	1	1	1	1	1			
Polylobium	0	0	0	0	0	0	1	1	1	1	0	1	1	0	1	2	1	1	1	1	1	1			
Cleistogama	0	2	0	2	0	1	1	0	0	1	0	0	1	0	0	2	1	1	1	0	1	1			
Monocarpa	1	2	0	2	1	1	1	0	0	1	0	1	1	0	1	1	1	1	0	1	1	1			
Krebsia	0	0	1	0	1	0	1	1	0	1	0	0	1	0	0	1	1	0	1	1	1	1			
Buchenroedera	0	0	1	0	1	0	1	1	1	1	1	1	1	2	1	1	0	0	1	1	1	1			
weights*:	2	4	2	2	1	10	3	1	2	10	3	3	10	3	3	3	0	3	2	2	3	4			

*These weights were used in successive weighting

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

1. HABIT: perennial = 0; annual = 1.
6. STIPULES: paired = 0; dimorphic = 1; single (or absent) = 2.
11. HAIR TYPE: uniseriate = 0; biramous = 1.
15. PEDUNCLE: long = 0; short = 1; \pm absent = 2.
21. FLOWER COLOUR: yellow = 0; not yellow = 1.
22. CLEISTOGAMY: chasmogamous = 0; cleistogamous = 1.
23. BRACTEOLAS: present = 0; absent = 1.
25. CALYX (LATERAL SINUSES): equal to others = 0; shallower = 1; much shallower = 2.
31. STANDARD VESTITURE: few hairs along midrib = 0; densely hairy = 1.
32. STANDARD VEINATION: inconspicuous = 0; distinct = 1.
33. WING PETAL VESTITURE: glabrous = 0; hairy = 1.
34. KEEL (RELATIVE LENGTH): \pm as long as standard = 0; much shorter = 1.
35. KEEL (SHAPE OF APEX): rounded = 0; acute = 1; beaked = 2.
36. KEEL VESTITURE: glabrous = 0; few hairs = 1; densely hairy = 2.
37. KEEL (LENGTH OF CLAWS): as long as lamina = 0; much longer = 1.
42. FRUIT TURGIDITY: flat = 0; slightly inflated = 1; much inflated = 2.
43. FRUIT (UPPER SUTURE): smooth = 0; verrucose = 1.
47. SEED SURFACE: smooth = 0; tuberculate = 1.
48. CHROMOSOME BASE NUMBER: 9 = 0; 7 = 1.
49. CYANOGENESIS: acyanogenic = 0; cyanogenic = 1.
50. QUINOLIZIDINE ALKALOIDS: present = 0; \pm absent = 1.
51. PYRROLIZIDINE ALKALOIDS: \pm absent = 0; present = 1.

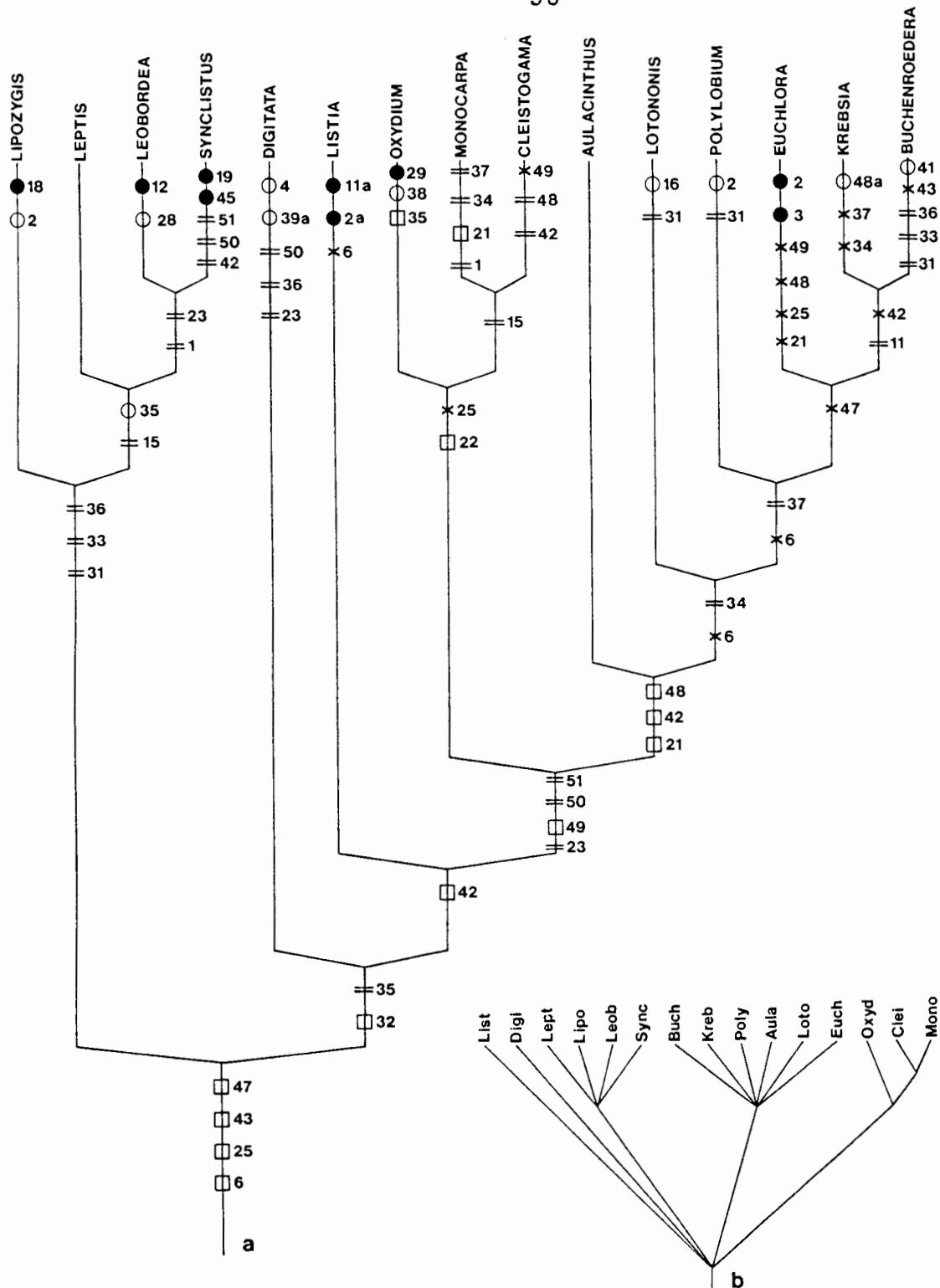


Figure 3.2.1. Estimate of phylogenetic relationships in the genus *Lotozonis* as obtained in analysis 1. a, Cladogram produced by successive weighting; b, Nelson Consensus Tree. For details see text. Symbols used: ■, synapomorphies showing no homoplasy; □, synapomorphies showing reversal higher up in the cladogram; ×, reversals; =, convergences; ●, autapomorphies not included in the analysis; ○, apomorphic tendencies not included in the analysis.

varied considerably in other analyses.

In an attempt to reduce ambiguity in the data set and to obtain a grouping based on more reliable characters, successive weighting was applied. This options has the advantage that no prior assumptions on character weighting are necessary. Weighting is based on the consistency indices of individual characters in the branch and bound result, the values are shown at the bottom of Table 3.2.1. Successive weighting resulted in a single fully resolved topology as shown in Figure 3.2.1a. This cladogram is very similar to the one obtained in analyses 5 and 6. It differs from the latter mainly in the position of Listia and Digitata, here associated with the cyanogenic groups that generally have a chromosome base number of $x = 7$. The apomorphies which resulted in this topology (striated petals and the shape of the keel), are quite variable and therefore not very convincing. Euchlora is somewhat uneasily placed as a sister group of Buchenroedera and Krebsia, with three reversals (calyx structure, chromosome number and cyanogenesis) suggesting that this position is suspect. The position of the Oxydium/Cleistogama clade is supported by amongst others, the presence of pyrrolizidine alkaloids and the loss of bracteoles (two characters which I consider to be taxonomically significant). The Lipozygis/Synclistus clade is also quite well-defined (by the hairy standard, wing and keel petals). Petal hairiness appears to be excessively weighted by having it as three different characters, but it should be pointed out that these three characters are not logically correlated in the genus

Lotononis. The four sections included in the Lipozygis/Synclistus clade share a number of other presumably apomorphic states that were considered too variable to use. The most conspicuous of these are the long and slender calyx-lobes that occur in most of the species. It is important to note that three of the four apomorphies defining the genus as a whole (characters 6, 25, and 47, i.e., stipules single, calyx zygomorphic and seed testa tuberculate) became convergent characters in later analyses where Lebeckia and Crotalaria were used as outgroups. These four apomorphies (in combination with some others) can be accepted as perhaps the most useful morphological information to separate Lotononis from other genera and their basal position is an appealing feature of this cladogram.

Analysis 2

This analysis illustrates the effect of considering hairy petals as a plesiomorphic condition (Table 3.2.2). There is however, no convincing justification for polarizing the three characters (31, 33 and 36) in this way. Hairy petals rarely occur in the most likely outgroups for Lotononis, and it seems more reasonable to accept a dense vestiture as a derived condition. Nevertheless, a single, fully resolved cladogram of minimal length resulted (Figure 3.2.2a).

TABLE 3.2.2. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE GENUS LOTONONIS AS USED IN ANALYSIS 2.

TAXA	CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)																							
	1	6	11	15	21	22	23	25	31	32	33	34	35	36	37	42	43	47	48	49	50	51		
hypothetical																								
ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0		
Listia	0	1	0	0	0	0	0	1	1	1	1	0	0	2	0	1	1	1	0	0	0	0		
Digitata	0	2	0	1	0	0	1	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0		
Leptis	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0		
Lipozygia	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0		
Leobordea	1	2	0	2	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0		
Synclistus	1	2	0	1	0	0	1	2	0	0	0	0	0	0	0	1	1	1	0	0	1	1		
Euchlora	0	0	0	0	0	0	1	2	1	1	1	1	0	1	1	2	1	0	0	0	1	1		
Oxydium	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	1	1	1	0	1	1	1		
Lotononis	0	1	0	0	0	0	1	1	0	1	1	1	0	1	0	2	1	1	1	0	1	1		
Aulacanthus	0	2	0	0	0	0	1	0	1	1	1	0	0	1	0	2	1	1	1	1	1	1		
Polylobium	0	0	0	0	0	0	1	1	0	1	1	1	0	1	1	2	1	1	1	1	1	1		
Cleistogama	0	2	0	2	0	1	1	2	1	1	1	0	0	1	0	2	1	1	1	0	1	1		
Monocarpa	1	2	0	2	0	1	1	2	1	1	1	1	0	1	1	1	1	1	0	0	1	1		
Krebsia	0	0	1	0	1	0	1	1	0	1	1	0	0	0	0	1	1	0	1	1	1	1		
Buchenroedera	0	0	1	0	1	0	1	1	0	1	0	1	0	0	1	1	0	0	1	1	1	1		

CHARACTERS AND POLARIZATIONS AS IN TABLE 3.2.1 EXCEPT FOR THE FOLLOWING:

25. CALYX (LATERAL SINUSES): much shallower than others = 0;
shallower = 1; subequal = 2.
31. STANDARD VESTITURE: densely hairy = 0; few hairs along midrib = 1.
33. WING PETAL VESTITURE: hairy = 0; glabrous = 1.
36. KEEL VESTITURE: densely hairy = 0; few hairs = 1; glabrous = 2.

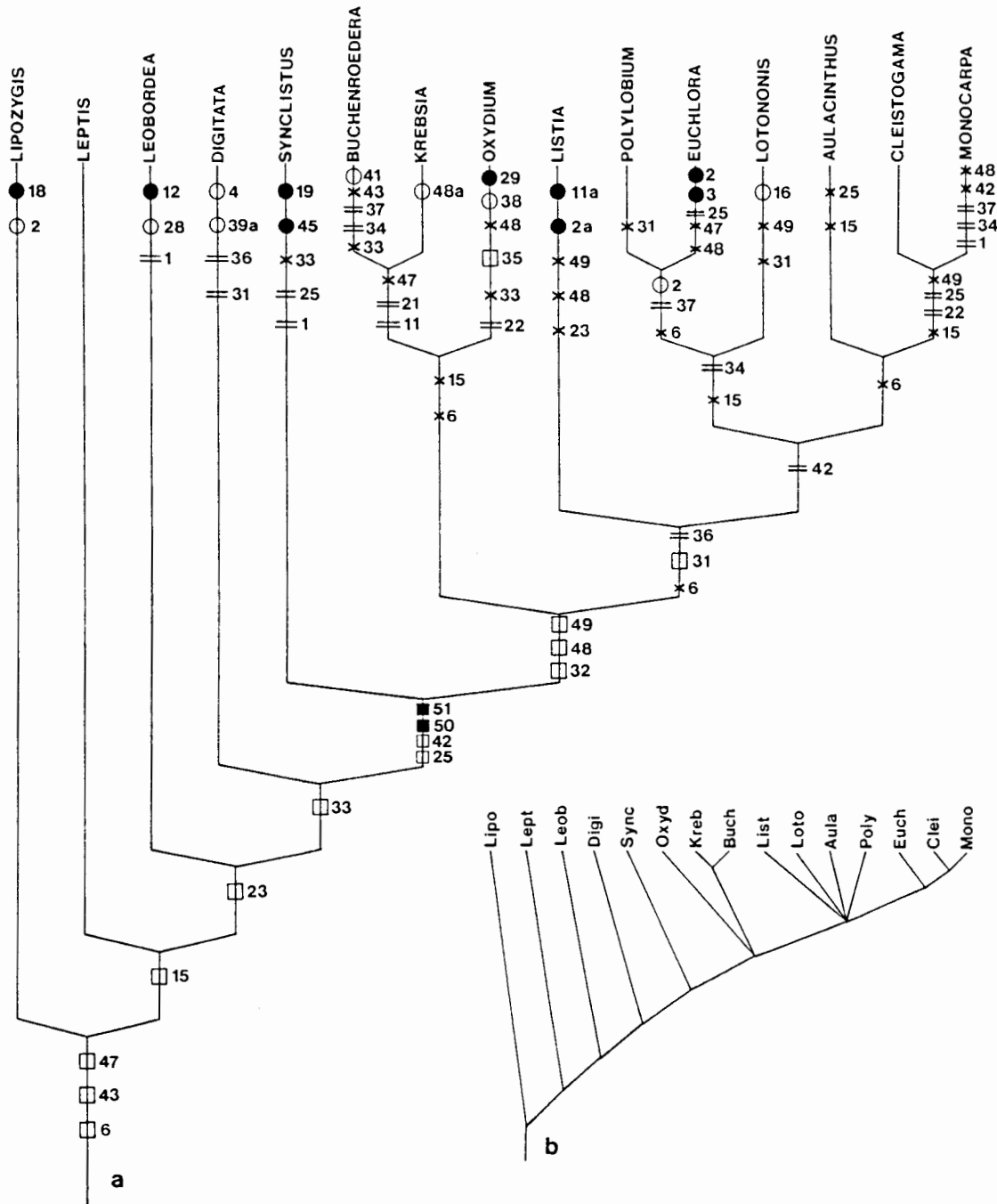


Figure 3.2.2. Estimate of phylogenetic relationships in the genus Lotononis as obtained in analyses 2 and 3. a, single cladogram of minimal length (analysis 2); b, Nelson Consensus Tree of the 6 trees produced by the data in Table 3.2.2 when character 6 was deleted (analysis 3). For details see text. Symbols as in Figure 3.2.1.

When a single topology such as this one is produced, one may be tempted to accept the result as the best estimate of the actual phylogeny of the group. I do not favour this particular result for two reasons. Firstly, the position of the section Listia is suspect, because it leads to doubtful reversals in some rather convincing apomorphies for the genus as a whole (loss of bracteoles, chromosome base number and cyanogenesis). There are several character states, although too variable for cladistic purposes, that strongly suggest a sister group relationship between the sections Listia and Digitata (for example, flexuous-plicate or linear pods; digitate and often glabrescent leaves with slender petioles; very small seeds). Furthermore, the flower structure of the two groups is remarkably similar. These two section are placed so far apart that I strongly doubt the accuracy of the cladogram. Secondly, the topology is not particularly stable, and minor changes in the data set (such as a single character state that is reversed in a single taxon) resulted in quite different topologies. In the next analysis (analysis 3) for example, it is shown that the elimination of a single character from the data set had a rather drastic effect on the terminal part of the topology.

Analysis 3

This analysis was done to test the effect of eliminating one character (stipules, character 6) from the data set in Table 3.2.2. All other characters and polarizations were the same as in Analysis 2. The result showed, as expected, a significant reduction in tree lengths but only a slight improvement in the consistency index. The data no longer resolved the terminal part of the cladogram, as is shown by the Consensus Tree in Figure 3.2.2b. Euchlora is now shown as a sister group for Cleistogama and Monocarpa rather than Aulacanthus.

Stipules performed very poorly as a cladistic character and the polarity decisions were shown to be rather critical, because it often had a dramatic effect on tree lengths. The main difficulty about this character is that the presumably plesiomorphic condition (paired stipules) is often present in only one or two species of a section, so that the group as a whole had to be polarized for the plesiomorphic state. The fact that reversals occur in L. serpens (see Figure 5.16 in Part 5) and in seedlings of L. sericophylla, suggests that stipules should not be excessively weighted as a cladistic character. It may indeed be argued that the instability of stipules in Lotononis should be considered apomorphic, and not their presence or number per se.

Analysis 4.

This analysis gives an example of the effect of deleting some variable characters from the data set and changing the assumptions about polarity in others (Table 3.2.3). Petal hairiness was still polarized as plesiomorphic, but the polarity of characters 35, 42, 48 and 51 was reversed (Crotalaria used as outgroup for these characters). Six equally parsimonious cladograms resulted from the branch and bound option. A Consensus Tree of this result is shown in Figure 3.2.3.

Even though the result was not particularly better than others (the consistency index was indeed lower), it shows some interesting features. The early advance in several characters, resulting in the large number of apomorphies at the base of the tree, is noteworthy, but so are the reversals in most of these higher up in the cladogram. Changing the polarities of the four characters (35,42,48 and 51) produced a result very similar to the one obtained in analysis 1 (where the hypothetical ancestor corresponds closely with Lebeckia). Lipozygis, Leptis, Leobordea and Synclistus are again shown as a clade (defined by reversals in petal vestiture) and Listia and Digitata are again placed towards the base of the cladogram. The way in which character 25 has been polarized, as well as the deletion of hair type and flower dimorphism, has a drastic effect on the positions of

TABLE 3.2.3. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE GENUS LOTONONIS AS USED IN ANALYSIS 4.

TAXA	CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)																		
	1	6	23	25	31	32	33	34	35	36	37	42	43	47	48	49	50	51	
hypothetical																			
ancestor	0	0	0	0	?	?	?	0	0	?	0	0	0	0	?	0	0	?	
<u>Listia</u>	0	1	0	1	1	1	1	0	1	2	0	1	1	1	1	0	0	1	
<u>Digitata</u>	0	2	1	0	1	0	1	0	1	1	0	1	1	1	1	0	1	1	
<u>Leptis</u>	0	2	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	
<u>Lipozygis</u>	0	2	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	
<u>Leobordea</u>	1	2	1	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	
<u>Synclistus</u>	1	2	1	2	0	0	0	0	1	0	0	1	1	1	1	0	1	0	
<u>Euchlora</u>	0	0	1	2	1	1	1	1	1	1	1	0	1	0	1	0	1	0	
<u>Oxydium</u>	0	0	1	1	0	1	0	0	0	0	0	0	1	1	1	1	1	0	
<u>Lotononis</u>	0	1	1	1	0	1	1	1	1	1	0	0	1	1	0	0	1	0	
<u>Aulacanthus</u>	0	2	1	0	1	1	1	0	1	1	0	0	1	1	0	1	1	0	
<u>Polylobium</u>	0	0	1	1	0	1	1	1	1	1	1	0	1	1	0	1	1	0	
<u>Cleistogama</u>	0	2	1	2	1	1	1	0	1	1	0	0	1	1	0	0	1	0	
<u>Monocarpa</u>	1	2	1	2	1	1	1	1	1	1	1	1	1	1	1	0	1	0	
<u>Krebsia</u>	0	0	1	1	0	1	1	0	1	0	0	1	1	0	0	1	1	0	
<u>Buchenroedera</u>	0	0	1	1	0	1	0	1	1	0	1	1	0	0	0	1	1	0	

CHARACTERS AND POLARIZATIONS AS IN TABLE 3.2.1 EXCEPT FOR THE FOLLOWING (NOTE THAT THE POLARITY OF CHARACTERS 31, 32, 33, 36, 48 AND 51 WAS NOT SPECIFIED IN THE OUTGROUP):

11. HAIR TYPE: deleted
15. PEDUNCLE: deleted
21. FLOWER COLOUR: deleted
22. CLEISTOGAMY: deleted
25. CALYX (LATERAL SINUSES): much shallower than others = 0; slightly shallower = 1; subequal = 2.
31. STANDARD VESTITURE: densely hairy = 0; few hairs along midrib = 1.
32. STANDARD VEINATION: inconspicuous = 0; distinct = 1.
33. WING PETAL VESTITURE: hairy = 0; glabrous = 1.
35. KEEL (SHAPE OF APEX): beaked = 0; rounded to acute = 1.
36. KEEL VESTITURE: densely hairy = 0; few hairs = 1; glabrous = 2.
42. FRUIT TURGIDITY: much inflated = 0; slightly inflated = 1.
48. CHROMOSOME BASE NUMBER: 7 = 0; 9 = 1.
51. PYRROLIZIDINE ALKALOIDS: present = 0; \pm absent = 1.

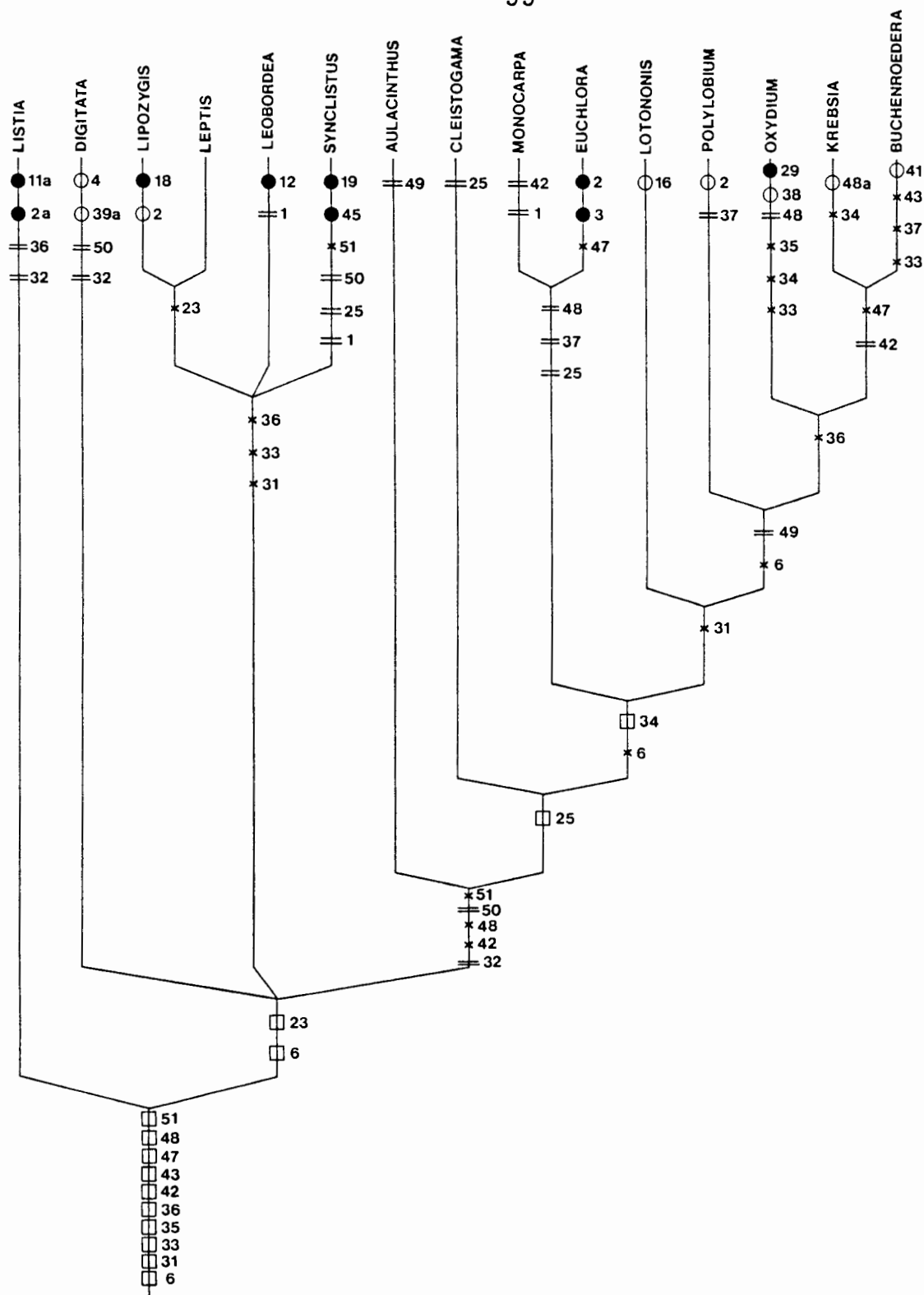


Figure 3.2.3. Estimate of phylogenetic relationships in the genus *Lotononis* as obtained in analysis 4. A Nelson Consensus Tree of 6 trees produced by the data in Table 3.2.3 is shown. For details see text. Symbols as in Figure 3.2.1.

Oxydium, Cleistogama and Monocarpa. The similarity between the topology produced in analysis 1 and the present one suggested that Lebeckia and Crotalaria should be used as outgroups rather than a hypothetical ancestor.

Analysis 5.

In this analysis, 25 characters were used with Crotalaria as outgroup (Table 3.2.4). A single tree of minimal length (80 character state changes, consistency index 42) resulted from both the "mhennig*" and "bb*" commands. The cladogram is shown in Figure 3.2.4. (The way in which characters 50 and 51 are plotted on the cladogram applies to the next analysis, see below).

This result is virtually identical to the result obtained in analysis 1. The cladogram is now fully resolved, but the same five major clades as shown in the Consensus Tree in Figure 3.2.1b are visible. Listia and Digitata are now part of the clade with hairy petals and Oxydium is grouped with the remaining sections, thus forming a basal dichotomy.

It is interesting to note the almost complete absence of convincing apomorphies to define the genus as a whole. The three characters (habit, upper suture of the fruit and chromosome base number) all reverse higher up in the cladogram. Except for the

TABLE 3.2.4. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE GENUS LOTONONIS AS USED IN ANALYSES 5 AND 6.

TAXA	CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)																								
	1	6	11	15	18	19	21	22	23	25	31	32	33	34	35	36	37	42	43	44	47	48	49	50	51
<u>LEBECKIA</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0
<u>CROTALARIA</u>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1
<u>Listia</u>	1	1	0	0	0	0	0	0	0	0	1	0	1	0	0	1	0	0	1	1	0	0	1	0	0
<u>Digitata</u>	1	2	0	1	0	0	0	0	1	2	0	0	0	0	1	1	0	1	1	0	0	1	0	1	0
<u>Leptis</u>	0	0	0	1	1	0	0	0	0	1	1	0	1	0	1	2	0	1	1	0	0	1	0	0	0
<u>Lipozygis</u>	1	2	0	0	2	0	0	0	0	1	1	0	1	0	1	2	0	2	1	0	0	1	0	0	0
<u>Leobordea</u>	2	2	0	2	0	1	0	0	1	1	1	0	1	0	1	2	0	2	1	0	0	1	0	0	0
<u>Synclistus</u>	2	2	0	1	0	2	0	0	1	0	1	0	1	0	1	2	0	1	1	0	0	1	0	1	1
<u>Euchlora</u>	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	2	1	1	1	0	1	1
<u>Oxydium</u>	1	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	2	0	0	1	1	1	1
<u>Lotononis</u>	1	1	0	0	0	0	1	0	1	1	1	1	0	1	0	0	0	0	2	1	0	0	1	1	1
<u>Aulacanthus</u>	0	1	0	0	0	0	1	0	1	2	0	1	0	0	0	0	0	0	2	1	0	0	1	1	1
<u>Polylobium</u>	1	0	0	0	0	0	0	0	1	1	1	1	0	1	0	0	1	0	2	1	0	0	1	1	1
<u>Cleistogama</u>	1	2	0	2	0	0	0	1	1	0	0	1	0	0	0	0	0	0	2	1	0	0	0	1	1
<u>Monocarpa</u>	2	1	0	2	0	0	1	1	1	0	0	1	0	1	0	0	1	1	2	0	0	1	1	1	1
<u>Krebsia</u>	0	1	1	0	0	0	1	0	1	1	1	1	0	0	0	0	0	1	0	1	1	0	1	1	1
<u>Euchenroedera</u>	0	0	1	0	0	0	1	0	1	1	1	1	1	1	0	2	1	1	0	0	1	0	1	1	1

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

1. HABIT: woody shrubs = 0; suffrutices = 1; annuals = 2.
6. STIPULES: paired, \pm equal in size = 0; paired but markedly dissimilar in size = 1; single (or absent) = 2.
11. HAIR TYPE: simple, uniseriate = 0; biramous = 1.
15. PEDUNCLE LENGTH: much longer than the length of the flower(s) = 0; as long or shorter than the length of the flower(s) = 1; \pm absent = 2.
18. POSITION OF BRACT: at base of pedicel = 0; slightly above pedicel base = 1; inserted \pm halfway up the pedicel = 2.
19. PEDICEL: long (more than 2 mm) = 0; very short (\pm 1 mm) = 1; absent = 2.
21. FLOWER COLOUR: yellow = 0; not yellow (white, pink or more often blue) = 1.
22. FLOWER DIMORPHISM (CLEISTOGAMY): absent = 0; present in most species = 1.
23. BRACTEOLAS: present = 0; absent or vestigial (less than 0,1 mm long) = 1.
25. CALYX (LATERAL SINUSES): \pm as deep as lower sinuses = 0; slightly shallower than lower sinuses = 1; much shallower than lower sinuses = 2.
31. STANDARD PETAL VESTITURE: glabrous or with a line of hairs along the midrib only = 0; hairs on at least part of the abaxial surface = 1.
32. STANDARD PETAL VEINATION: inconspicuous = 0; conspicuous (lamina distinctly striated, the abaxial surface often different in colour to the adaxial surface) = 1.
33. WING PETAL VESTITURE: totally glabrous = 0; at least some hairs present = 1.
34. KEEL (RELATIVE LENGTH): as long or longer than the standard and wing petals = 0; shorter than the standard and wing petals = 1.
35. KEEL (SHAPE OF APEX): slightly pointed or beaked = 0; rounded = 1.
36. KEEL VESTITURE: totally glabrous = 0; with some hairs towards the apex = 1; densely hairy = 2.
37. KEEL (LENGTH OF CLAWS): shorter than the lamina = 0; as long or longer than the lamina = 1.
42. FRUIT (SHAPE IN TRANSVERSE SECTION): laterally much inflated = 0; slightly turgid = 1; flat = 2.
43. FRUIT (UPPER SUTURE): smooth = 0; minutely or slightly verrucose = 1; conspicuously verrucose = 2.
44. FRUIT (LOWER SUTURE): not sunken = 0; sunken = 1.
47. SEED SURFACE: rugose or tuberculate = 0; smooth = 1.
48. CHROMOSOME BASE NUMBER: 7 = 0; 9 = 1.
49. CYANOGENESIS: totally acyanogenic = 0; most species/samples cyanogenic = 1.
50. QUINOLIZIDINE ALKALOIDS: present = 0; \pm absent = 1.
51. PYRROLIZIDINE ALKALOIDS: \pm absent = 0; present = 1.

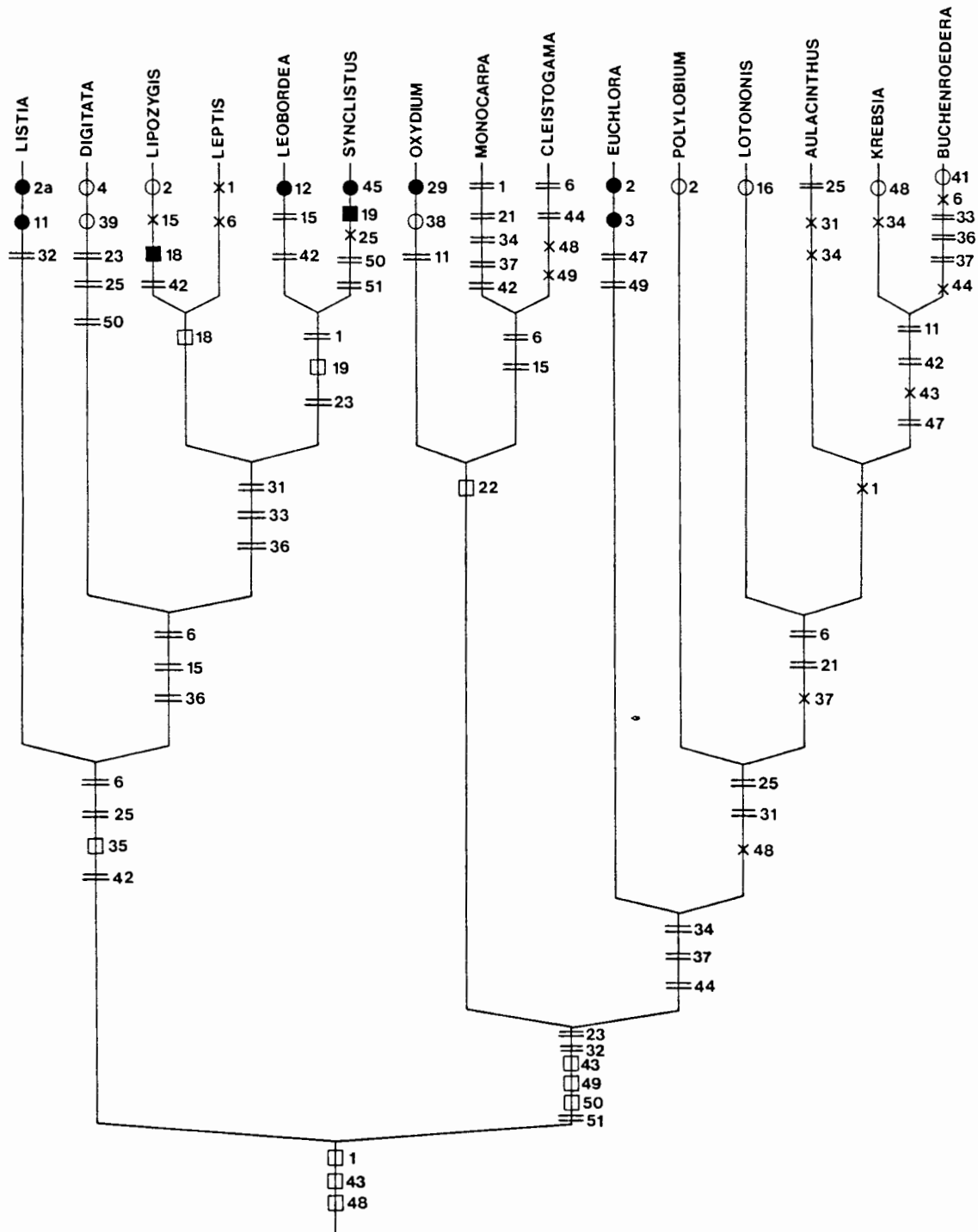


Figure 3.2.4. Estimate of phylogenetic relationships in the genus Lotononis as obtained in analyses 5 and 6. The single cladogram produced by the data in Table 3.2.4 is shown. For details see text. Symbols as in Figure 3.2.1.

upper suture of the fruit, the diagnostic characters of the genus no longer feature as generic apomorphies but are shown to be convergent within the genus. The zygomorphic structure of the calyx is shown to have evolved twice and dimorphic stipules at least three times. Similarly, the loss of bracteoles seems to have occurred several times, but only in the first of the two main clades (Listia/Synclistus). In the second clade (Oxydium/Buchenroedera), this character shows no homoplasy.

Analysis 6.

This analysis was done to study the effect of using Lebeckia rather than Crotalaria as outgroup for the same data as given in Table 3.2.4. As shown in the table, only a small number of polarizations had to be reversed. The same single topology of minimal length was produced and the length of the shortest tree (80 steps) and the consistency index (42) did not change. Except for the transformation of characters 47, 48, 50 and 51, this result was identical to the one shown in Figure 3.2.4.

Characters 47, 48, 50 and 51 are the only ones where the choice of outgroup (Lebeckia or Crotalaria) made a difference to the polarities. With Crotalaria as outgroup, a rugose or tuberculate seed surface (character 47) becomes a plesiomorphy in Lotononis, and the smooth seed surfaces of Euchlora, Krebsia and Buchenroedera become convergent apomorphies. When Lebeckia is

used as outgroup, these apparent apomorphies change to reversals (and the rugose/tuberculate seed surface becomes an additional generic apomorphy). Similarly, chromosome base number (character 48) reverses to $x = 7$ in the Polylobium/Buchenroedera clade with Crotalaria as outgroup, but becomes an apomorphy with Lebeckia as outgroup. The same applies to the absence of quinolizidine alkaloids (character 50) and the presence of pyrrolizidine alkaloids (character 51). In Figure 3.2.4, these last two characters are plotted in the way they behave when Lebeckia is used as outgroup. With Crotalaria as outgroup, the presence of quinolizidine alkaloids and the absence of pyrrolizidine alkaloids become apomorphies for the Listia/Synclistus clade, with subsequent reversals in Digitata and Synclistus.

I would suggest that the final result is an accurate reflection of the close relationships between Lotononis, Crotalaria and Lebeckia. Polarities in Table 3.2.4 would be virtually the same even if Rafnia, Aspalathus or Wiborgia (the rest of the now broadened "Cape group" of genera, see Part 2) were used as outgroups instead of Lebeckia.

Within the limits of available data, the cladogram in Figure 3.2.4 is presented here as the best estimate of the actual phylogeny of the genus Lotononis. This topology was also used as a basis for the classification scheme given in Part 5. There is such a large degree of ambiguity in the data however, that a

direct translation of the topology in Figure 3.2.4 into a classification scheme seems impractical at this stage. It was therefore decided not to introduce any ranks between that of genus and section and to treat all the terminal taxa as sections. No formal rank is therefore given to the two main clades. Since all the characters defining these clades are homoplasious, this approach seems justified because it limits the possibility of accepting paraphyletic units as taxa. Furthermore, it will allow future rearrangements of the sections without seriously affecting the infrageneric nomenclature.

All the sections except Leptis and Aulacanthus are likely to represent true clades, i.e. monophyletic units. Most of these terminal taxa are now defined by distinct apomorphies, indicating that the infrageneric classification of Lotononis has reached a reasonable degree of stability. Further investigations may reveal the presence of autapomorphies for some groups within Leptis (and perhaps also Aulacanthus) so that these may become established as new clades. The position of the sections Cleistogama and Monocarpa as subgroups of Oxydium is questionable despite some synapomorphies. I chose to treat them as distinct sections (and not subsections of Oxydium) because of the possibility that the synapomorphies may in fact be convergences. The chromosome number of $2n = 28$ and the sunken ventral suture of the fruit in Cleistogama suggest an affinity with the sections Aulacanthus or Lotononis. Likewise, the morphology and pigmentation of the corolla in Monocarpa indicate a possible relationship with

Euchlora or Polylobium. This is the only reservation I have about the chosen topology, but it affects the position of only five species and is therefore perhaps not too important.

As a final summary of available evidence, the distribution and rare occurrences of some variable characters ("apomorphic tendencies") were plotted onto the chosen cladogram as shown in Figure 3.2.5. The figure also shows the conflict between chromosome base number and other characters. Apomorphic states of some of the variable characters (that were not used in the analyses) are present in both of the two main clades, and others are restricted to adjoining members of some of the grades. Note for example, the sporadic occurrence of 5-digitate leaves and foliaceous bracts. The overall pattern of character state distributions and uncertainty about the exact sequence of the basal nodes (particularly of the sections Listia, Digitata and Oxydium) indicate that a subdivision of the genus into two subgenera is not justified. Detailed investigations of poorly known species (when this becomes possible) may reveal weaknesses in the proposed hypothesis and future discoveries of new species may lead to new insights. Nevertheless, some of the clades appear to be quite robust and it is unlikely that drastic modifications will have to be made in future.

It is interesting to note the similarity of the topology in Figure 3.2.4. with Bentham's (1843) original infrageneric classification. The most significant difference is the sequence

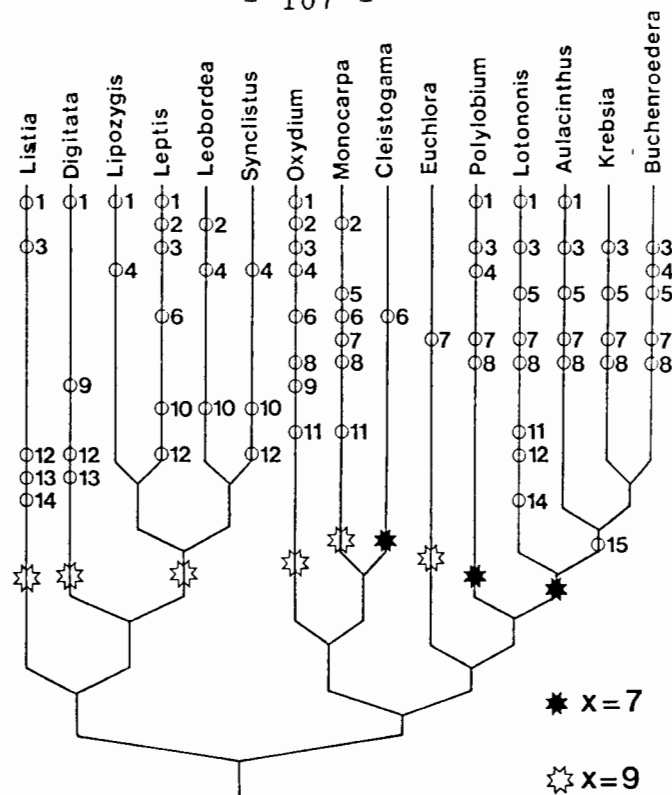


Figure 3.2.5. Chosen cladogram for the genus *Lotononis* (from the result in Figure 3.2.4), showing the distribution and/or rare occurrences of variable and convergent characters, most of which were not used in cladistic analyses. The character states are: 1, 5- to 8-digitate leaves; 2, subopposite or opposite leaves; 3, biramous hairs; 4, foliaceous bracts; 5, blue flowers; 6, cleistogamy; 7, "*Lotononis*-type" flower structure, i.e. with the keel acute and very much shorter than the standard and wing petals; 8, cyanogenesis (at least some species or samples); 9, gynoeceium stipitate; 10, a small number of ovules (one, two or three); 11, exceptionally long funicles; 12, indehiscent pods; 13, flexuous-plicate pods; 14, large number of seeds per pod (more than 40); 15, complete absence of stipules; ★, chromosome base number 7; ☆, chromosome base number 9.

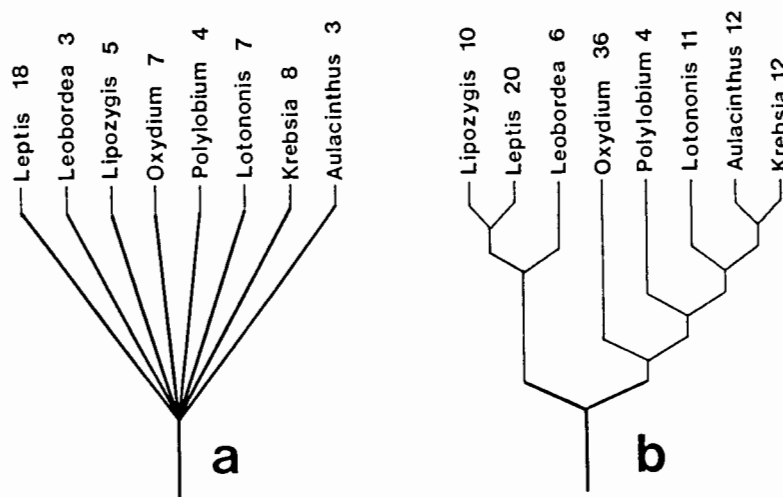


Figure 3.2.6. Comparison of the original infrageneric classification of Bentham (1843) and the topology in Figure 3.2.4: a, Bentham's sequence of sections (given in reverse order); b, sequence of sections in the chosen cladogram (modified to facilitate the comparison). The numbers of species included in each of the sections are given behind the names.

of the sections. Following Harvey (1862) and Dümmer (1913), I originally assumed that Bentham's sequence was intended to reflect increasing specialization from woody to herbaceous. The subsequent realization that Bentham usually treated groups in order of decreasing specialization, opened a new perspective. If Bentham's presentation was indeed from top to bottom (and not from bottom to top as is now customary) the two schemes are remarkably similar. Figure 3.2.6 gives a schematic comparison of Bentham's (1843) infrageneric classification (shown in reverse order) and my own (shown without recent modifications). The striking similarity (despite drastic changes in the circumscription of most of the sections) seems to indicate not only Bentham's brilliant understanding of character state distributions (he worked with a very skeletal sample), but also that the cladogram presented here is probably a reasonably objective estimate of the actual phylogeny of Lotononis.

Similar procedures were followed to determine the most likely phylogenetic relationships within each of the sections. The data sets that were used and the cladograms derived from them are given in Tables 3.2.5 to 3.2.20. A summary of the commands, data sets, results and statistics of sixteen different analyses is given below:

SECTION OR GROUP	DATA SET USED	NUMBER OF CHARACTERS	COMMANDS (OPTIONS)	RESULT	LENGTH OF TREE(S)	CONSISTENCY INDEX
<u>Listia</u>	Table 3.2.5	22	mhennig* bb*	1 tree 1 tree	38 38	71 71
<u>Digitata</u>	Table 3.2.6	11	mhennig* bb*	1 tree 1 tree	13 13	84 84
<u>Lipozygia</u>	Table 3.2.7	17	mhennig* bb*	1 tree 1 tree	28 28	78 78
<u>Leptis</u>	Table 3.2.8	24	mhennig* bb* xsteps w nelsen	5 trees 333 trees 293 trees 1 tree	68 68 209	48 48 63
<u>Leobordea</u>	Table 3.2.9	10	mhennig* bb*	1 tree 1 tree	16 16	87 87
<u>Synclistus</u>	Table 3.2.10	14	mhennig* bb*	1 tree 1 tree	26 26	61 61
<u>Oxydium</u> (major clades)	Table 3.2.11	29	mhennig* bb*	1 tree 1 tree	84 84	48 48
<u>Oxydium</u> (clade D)	Table 3.2.12	13	mhennig* bb*	1 tree 1 tree	19 19	78 78
<u>Oxydium</u> (clades G and H)	Table 3.2.13	16	mhennig* bb*	1 tree 1 tree	31 31	70 70
<u>Oxydium</u> (clade L)	Table 3.2.14	17	mhennig* bb*	1 tree 1 tree	29 29	72 72
<u>Monocarpa and</u> <u>Cleistogama</u>	Table 3.2.15	10	mhennig* bb*	2 trees 1 tree	13 13	76 76
<u>Polylobium</u>	Table 3.2.16	11	mhennig* bb*	1 tree 1 tree	17 17	82 82
<u>Lotononis</u>	Table 3.2.17	12	mhennig* bb*	1 tree 1 tree	32 32	56 56
<u>Aulacanthus</u>	Table 3.2.18	12	mhennig* bb* nelsen	10 trees 259 trees 1 tree	26 26	53 53
<u>Krebsia</u>	Table 3.2.19	17	mhennig* bb nelsen	11 trees >100 trees 1 tree	51 51	45 45
<u>Buchenroedera</u>	Table 3.2.20	15	mhennig* bb* nelsen	3 trees 8 trees 1 tree	27 27	59 59

Several additional characters (those which could not be used for infrageneric analyses), were introduced into these individual data sets. All characters not included in Table 3.1 are listed as X1, X2, etc. The polarization of character states was now slightly different because it was based on sections as outgroups. These modifications are shown in the footnotes to the tables.

The results for the different sections are preliminary estimates but nevertheless give useful information about the state of knowledge of relationships at the species level. It also provided a means to arrange species in a natural sequence. All the species of Lotononis are shown on the cladograms, numbered as in the synopsis in Part 5. Rigorous clades within some of the cladograms correspond with the newly described subsections in Part 5. This rank is not introduced for convenience only, but also to give an indication of basic affinities and major discontinuities within some of the sections. Satisfactory results were obtained for most of the sections, but I was unable resolve relationships within the sections Aulacanthus, Krebsia and to a lesser extent, Leptis and Buchenroedera.

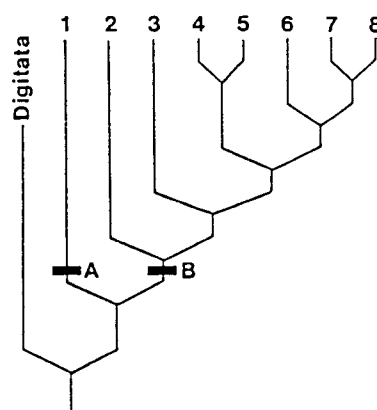
For each of the sections, a brief discussion of the results and its taxonomic implications is given below.

Section 1. Listia (Table 3.2.5)

This section has never been recognised as a group before, but the paired and dimorphic stipules, consistent presence of bracteoles, almost glabrous leaves and smooth hair surface sculpturing in all the species are quite distinct. L. macrocarpa (here recognised as a monotypic subsection, shown as clade A in the cladogram) is an unusual species of Lotononis and has some rather atypical characters, notably the long carinal anther, the equally lobed calyx and the exceptionally large seeds (more than 4 mm long, comparable in size only to those of the equally anomalous L. serpens of the monotypic section Euchlora). The pods are amongst the largest in the genus (again comparable only to those of L. serpens), with very large protuberances along the upper suture. Geographically, it is completely isolated from the remainder of the section, being endemic to the south-western Cape. (Interesting aspects of the biogeography of the section is discussed in Part 3.3). If this poorly known species can be rediscovered, chromosome counts and an alkaloid analysis may help to clarify uncertainty about the exact position of the section (I also suspect that sectional status for L. macrocarpa may prove to be more appropriate). The remainder of the section (which forms the typical subsection, shown as clade B) is a group of closely related species with very small seeds (ca. 1 mm long), uniseriate

TABLE 3.2.5. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTION LISTIA. INSET: SINGLE, FULLY RESOLVED CLADOGRAM (LENGTH 38, CONSISTENCY INDEX 71).

LISTIA



TAXA	CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)																				
	2	2a	3a	4	10	11	11a	15	16	17	17a	23	25	27	X1	38a	40	41a	43	45	
hypothetical																					
ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
<u>Digitata</u>	0	0	0	2	0	0	0	1	0	0	0	1	2	0	0	0	1	0	0	1	0
<u>L. macrocarpa</u> (1)	1	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	
<u>L. solitudinis</u> (2)	1	1	1	0	1	0	1	0	1	0	0	0	2	0	0	1	2	0	1	1	
<u>L. angolensis</u> (3)	1	1	0	0	1	0	2	0	0	0	1	0	1	0	0	1	1	0	1	1	
<u>L. bainesii</u> (4)	1	1	0	1	1	0	2	0	0	2	1	0	1	1	0	1	1	1	1	1	
<u>L. listii</u> (5)	1	1	0	1	1	0	2	0	0	1	1	0	1	1	0	1	1	1	1	2	
<u>L. minima</u> (6)	1	1	0	0	1	0	2	1	0	1	2	0	1	0	0	1	0	0	1	1	
<u>L. subulata</u> (7)	1	1	0	0	1	0	2	1	0	1	1	0	1	0	1	1	1	1	1	2	
<u>L. marlothii</u> (8)	1	1	0	0	1	0	2	1	0	1	1	0	1	0	1	1	1	0	1	1	

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

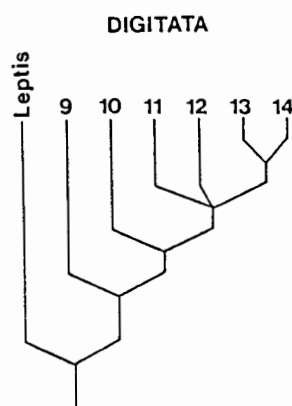
2. BRANCHES: woody branches, at least at the base = 0; suffrutescent = 1.
- 2a. ADVENTITIOUS ROOTS: absent = 0; present on lateral branches = 1.
- 3a. LEAF COLOUR (WHEN DRIED): green = 0; black = 1.
4. NUMBER OF LEAFLETS: invariably 3-digitate = 0; some leaves 5-digitate = 1; predominantly 5-digitate = 2.
10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely or sparsely hairy = 0; glabrous = 1.
11. HAIR TYPE: uniseriate = 0; biramous = 1.
- 11a. HAIR SURFACE SCULPTURING: densely tuberculate = 0; smooth, but with some tubercles = 1; invariably smooth = 2.
15. PEDUNCLE: long and slender = 0; very short = 1.
16. FLOWER NUMBER: more than two = 0; one, rarely two = 1.
17. FLOWER ARRANGEMENT: evenly spaced = 0; congested = 1; umbellate = 2.
- 17a. FLOWER SIZE: large = 0; small = 1; very small = 2.
23. BRACTEOLES: present = 0; absent = 1.
25. CALYX (LATERAL SINUSES): \pm equal to others = 0; slightly shallower = 1; much shallower = 2.
27. CALYX (SIZE OF UPPER LOBES): \pm equal to lateral lobes = 0; wider than lateral lobes = 1.
- X1. CALYX LOBES (SHAPE): triangular = 0; narrow, subulate = 1.
- 38a. CARINAL ANTHOR: similar to basifixed ones = 0; similar to dorsifixed ones = 1.
40. OVULE NUMBER: few (5 to 15) = 0; often more than 20 = 1; often more than 50 = 2.
- 41a. FRUIT SHAPE (TOP VIEW): straight = 0; folded like a concertina = 1.
43. FRUIT (UPPER SUTURE): slightly verrucose = 0; distinctly verrucose = 1.
45. FRUIT (DEHISCENCE): dehiscent = 0; tardily dehiscent = 1; indehiscent = 2.

hairs (biramous in *L. macrocarpa*) and the ability to produce adventitious roots on lateral branches. Despite reservations about the exact sequence of the last three species (6, 7 and 8), the result of this analysis seems very acceptable.

Section 2. Digitata (Table 3.2.6)

The data set in Table 3.2.6 shows the small number of characters that are available for this group of closely related species. There are striking similarities between the poorly known *L. mollis* (section Leptis) and species of this section. *L. mollis* is known only from the Drège type collection (fruit and seeds unknown) and it seems likely that evidence of a direct relationship may eventually be found. *L. benthamiana* and *L. longiflora* are the only two species of the genus Lotononis with distinctly stipitate pods. This character may be a symplesiomorphy and not a synapomorphy as the result seems to suggest. The shape of the pod in lateral view is a useful diagnostic character (Van Wyk 1989e, Appendix 25) but it is not clear how this character should be polarized. The high consistency index resulted from the small number of characters and the result is probably not as significant as the consistency value would seem to suggest.

TABLE 3.2.6. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTION DIGITATA. INSET: SINGLE, PARTIALLY RESOLVED CLADOGRAM (LENGTH 13, CONSISTENCY INDEX 84).



TAXA		CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)										
		1	4	10	16	31	33a	36	39a	40	41	41a
<u>Leptis</u>		0	0	0	0	0	0	0	1	0	0	0
<u>L. quinata</u>	(9)	1	1	1	1	0	0	0	1	0	0	0
<u>L. plicata</u>	(10)	0	1	1	1	0	0	1	1	0	0	1
<u>L. magnifica</u>	(11)	1	1	1	1	1	0	1	1	0	0	0
<u>L. digitata</u>	(12)	0	1	1	1	1	0	1	1	0	0	0
<u>L. benthamiana</u>	(13)	0	1	1	1	1	1	1	0	1	1	0
<u>L. longiflora</u>	(14)	0	1	0	1	1	1	1	0	0	0	0

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

- 1. HABIT: perennial = 0; short-lived perennial = 1.
- 4. NUMBER OF LEAFLETS: 3-digitate = 0; predominantly 5-digitate = 1.
- 10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy = 1.
- 16. FLOWER NUMBER: more than four = 0; one, two, three or four = 1.
- 31. STANDARD PETAL (VESTITURE): hairy = 0; glabrous = 1.
- 33a. WING PETAL (AURICLE): small = 0; large = 1.
- 36. KEEL (VESTITURE): hairy = 0; glabrous = 1.
- 39a. GYNOECIUM BASE: stipitate = 0; subsessile = 1.
- 40. OVULE NUMBER: often more than 15 = 0; few (± 8) = 1.
- 41. FRUIT (SHAPE IN LATERAL VIEW): linear to oblong = 0; ovate = 1.
- 41a. FRUIT SHAPE (TOP VIEW): straight = 0; folded like a concertina = 1.

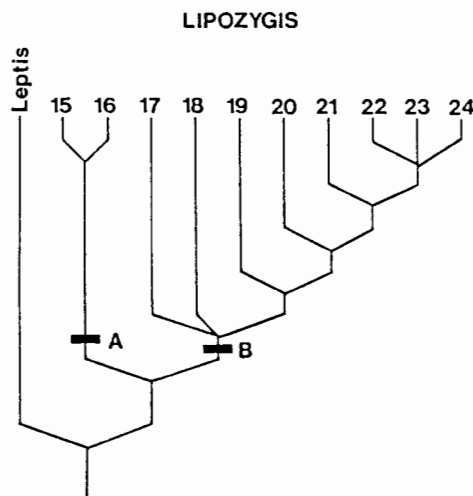
Section 3. Lipozygis (Table 3.2.7)

This section comprises two distinct subsections as suggested by the basal dichotomy in the cladogram shown with Table 3.2.7. Clade A is defined by foliaceous bracts and details of the calyx structure, and clade B by the short peduncles and long pedicels (the small size and virtual absence of bracteoles in clade B may be mentioned as another possible apomorphy) The typical subsection (clade B) is a variable complex of closely related species which would require a detailed study to produce a reliable phylogeny.

Section 4. Leptis (Table 3.2.8)

No autapomorphies are known for this section and the analysis indicated a very large number of equally parsimonious cladograms. Successive weighting (Table 3.2.8) showed that the habit, inflorescence structure and vestiture of the petals are important characters. The seven robust sections of the topology in the final result (indicated as A to G) are provisionally treated as informal groups rather than subsections. This is done to avoid biasing future work. The geographical distribution of the section appears to be relictual and may provide clues to the phylogeny.

TABLE 3.2.7. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTION LIPOZYGIS. INSET: SINGLE, PARTIALLY RESOLVED CLADOGRAM (LENGTH 28, CONSISTENCY INDEX 78).

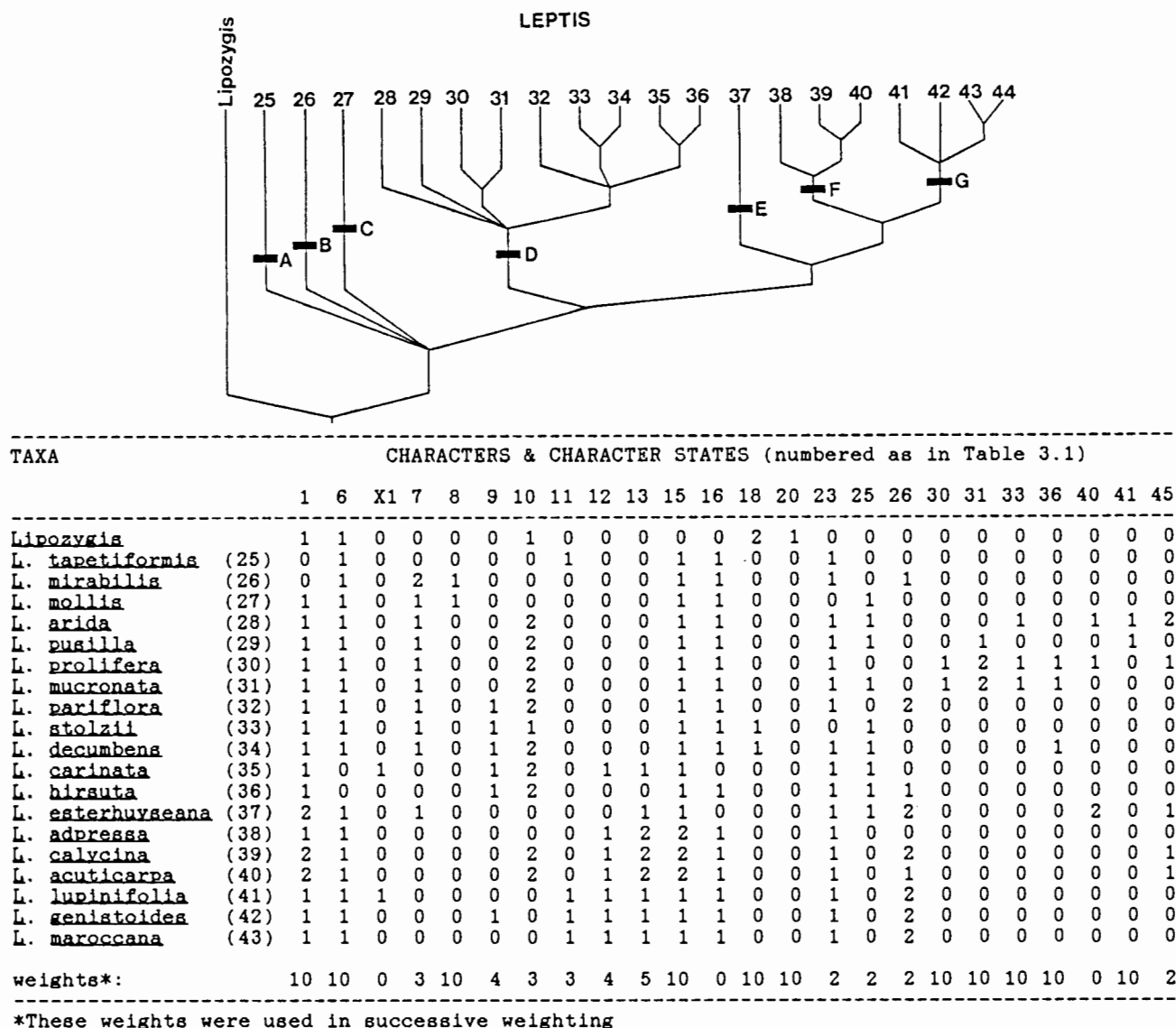


TAXA	CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)																
	2	3a	7	10	15	16	18	19	20	23	25	X1	27	30	31	33	36
LEPTIS	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
L. <u>procumbens</u> (15)	1	0	0	2	0	1	1	0	1	0	0	1	1	0	0	0	0
L. <u>difformis</u> (16)	2	0	1	1	0	1	1	0	1	0	0	1	1	0	0	0	0
L. <u>sutherlandii</u> (17)	2	0	1	1	1	2	1	1	0	0	0	0	0	0	0	1	0
L. <u>eriantha</u> (18)	2	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0
L. <u>grandis</u> (19)	2	1	1	1	1	0	1	1	0	1	0	0	0	0	0	0	0
L. <u>corymbosa</u> (20)	2	0	1	1	1	0	1	1	0	1	0	0	0	1	1	0	0
L. <u>pulchra</u> (21)	2	0	1	1	1	0	1	1	0	1	0	0	0	0	1	1	2
L. <u>lanceolata</u> (22)	2	1	1	1	1	0	1	1	0	1	1	0	0	1	2	1	1
L. <u>foliosa</u> (23)	2	1	1	1	1	1	1	1	0	1	1	0	0	0	2	1	1
L. <u>spicata</u> (24)	2	1	1	1	1	1	1	1	0	1	1	0	0	0	2	1	1

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

2. BRANCHES: woody = 0; suffrutescent, but with the basal branches woody = 1; annual flowering branches from a persistent woody caudex = 2.
- 3a. LEAF COLOUR (WHEN DRIED): green = 0; black = 1.
7. STIPULE SIZE: smaller than leaflets = 0; foliaceous = 1.
10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy = 1; glabrous = 2.
15. PEDUNCLE LENGTH: long = 0; short or absent = 1.
16. FLOWER NUMBER: 20 or more = 0; five to 20 = 1; one to four = 2.
18. POSITION OF BRACT: at or near the pedicel base = 0; inserted \pm halfway up the pedicel = 1.
19. PEDICEL: \pm as long as the calyx = 0; much longer than the calyx = 1.
20. BRACT SIZE: small = 0; large, foliaceous = 1.
23. BRACTEOLES: often present = 0; absent = 1.
25. CALYX (LATERAL SINUSES): shallower than lower sinuses = 0; much shallower = 1.
- X1. CALYX (WIDTH OF LOBES): narrow = 0; broad = 1.
27. CALYX (UPPER LOBES): as long as the lower lobes = 0; shorter than the lower lobes = 1.
30. STANDARD PETAL (SHAPE OF LAMINA): ovate or oblong = 0; narrow, linear = 1.
31. STANDARD PETAL (VESTITURE): all or most of the adaxial surface = 0; line of hairs along midrib = 1; few hairs along midrib = 2.
33. WING PETAL (VESTITURE): hairy = 0; glabrous = 1.
36. KEEL (VESTITURE): densely hairy = 0; some hairs towards the apex = 1; glabrous = 2.

TABLE 3.2.8. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTION LEPTIS. INSET: NELSON CONSENSUS TREE OF 293 TREES GENERATED BY SUCCESSIVE WEIGHTING.



CHARACTERS AND POLARIZATION OF CHARACTER STATES:

1. HABIT: branches woody = 0; woody at base only = 1; annuals = 2.
6. NUMBER OF STIPULES: paired = 0; single = 1.
- X1. DIGITATE STIPULES: absent = 0; rarely present = 1.
7. STIPULE SIZE: similar to leaflets = 0; much smaller than leaflets = 1; minute = 2.
8. PETIOLE LENGTH: \pm as long as terminal leaflet = 0; much longer than terminal leaflet = 1.
9. PETIOLE LENGTH: \pm as long as terminal leaflet = 0; much shorter than terminal leaflet = 1.
10. VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy = 1; glabrous = 2.
11. HAIR TYPE: uniseriate = 0; biramous = 1.
12. LEAF ARRANGEMENT ON FLOWERING NODES: alternate = 0; subopposite = 1.
13. INFLORESCENCE POSITION: terminal = 0; terminal and leaf-opposed = 1; invariably leaf-opposed = 2.
15. PEDUNCLE LENGTH: long = 0; short = 1; \pm absent = 2.
16. FLOWER NUMBER: 5 to 20 = 0; one, two, three or four = 1.
18. POSITION OF BRACT: at base of pedicel = 0; slightly above base = 1; \pm halfway up the pedicel = 2.
20. BRACT SIZE: small, linear = 0; more than twice as wide as the pedicel, or foliaceous = 1.
23. BRACTEOLES: present = 0; absent = 1.
25. CALYX (LATERAL SINUSES): much shallower than lower sinuses = 0; slightly shallower = 1.
26. CALYX (SIZE OF CARINAL LOBE): similar to upper lobes = 0; smaller than upper lobes = 1; much smaller than upper lobes = 2.
30. STANDARD PETAL (SHAPE OF LAMINA): ovate or oblong = 0; linear = 1.
31. STANDARD PETAL (VESTITURE): hairs on \pm whole abaxial surface = 0; hairs on central area = 1; line of hairs along the midrib only = 2.
33. WING PETAL (VESTITURE): hairy = 0; glabrous = 1.
36. KEEL (VESTITURE): densely hairy = 0; few hairs = 1.
40. OVULE NUMBER: numerous (6 to 20) = 0; few (3 to 5) = 1; one or two = 2.
41. FRUIT (SHAPE IN LATERAL VIEW): linear or oblong = 0; ovate = 1.
45. FRUIT (DEHISCENCE): dehiscent = 0; tardily dehiscent = 1; indehiscent = 2.

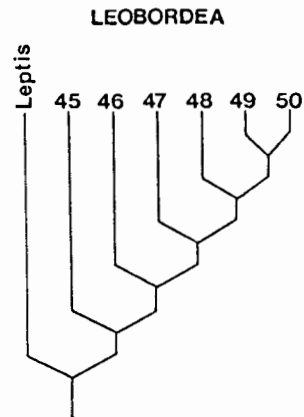
Section 5. Leobordea (Table 3.2.9)

The small number of characters used in this analysis produced a very satisfactory result (Table 3.2.9). L. platycarpa has the widest geographical range of all the species of Lotononis and its basal position in the cladogram suggests that the remarkable diversity in south-western Africa may be a secondary development. The characters of the calyx (characters 25 and 26) show an interesting pattern, suggesting that the ancestral form had a highly dimorphic calyx with a short carinal lobe. This would agree with a northern origin from an ancestor similar to extant species of the section Leptis, such as L. lupinifolia and L. genistoides (both these species have subopposite leaves).

Section 6. Synclistus (Table 3.2.10)

This distinct group of closely related annuals seems to have evolved from an ancestor with foliaceous bracts. The structure of the bracts, flowers and pods and the leaflet vestiture provided sufficient character information to resolve the phylogeny of the section. Note that the number of leaflets (a useful diagnostic character for some of the species) proved to be of little cladistic significance. The cladogram shows a very logical sequence of species, terminating in the group with linear petals.

TABLE 3.2.9. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTION LEOBORDEA. INSET: SINGLE, FULLY RESOLVED CLADOGRAM (LENGTH 16, CONSISTENCY INDEX 87).

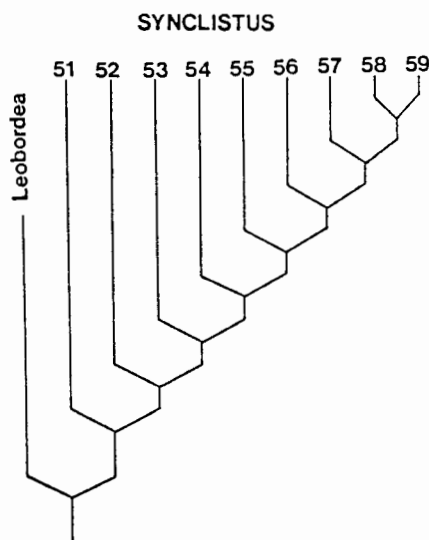


TAXA		CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)								
		6	7	12	15	16	20	25	26	28
<hr/>										
<u>Leptis</u>		?	?	0	0	0	0	?	?	0
<u>L. platycarpa</u>	(45)	1	0	1	0	0	0	1	2	1
<u>L. newtonii</u>	(46)	0	0	1	0	0	2	1	1	1
<u>L. bracteosa</u>	(47)	1	0	1	1	1	2	0	0	1
<u>L. stipulosa</u>	(48)	1	0	1	1	1	1	0	0	1
<u>L. schoenfelderi</u>	(49)	1	1	1	1	2	0	0	0	1
<u>L. furcata</u>	(50)	1	1	1	1	2	0	0	0	1

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

- 6. NUMBER OF STIPULES: paired = 0; single = 1.
- 7. STIPULE SIZE: similar to leaflets = 0; much smaller than leaflets = 1.
- 12. LEAF ARRANGEMENT ON FLOWERING NODES: alternate = 0; opposite = 1.
- 15. PEDUNCLE LENGTH: peduncle present = 0; peduncle absent = 1.
- 16. FLOWER NUMBER: 5 to 20 = 0; one, two, three or four = 1; one, rarely two = 2.
- 20. BRACT SIZE: small, linear = 0; more than twice as wide as the pedicel = 1; large and foliaceous = 2.
- 25. CALYX (LATERAL SINUSES): slightly shallower than lower sinuses = 0; much shallower = 1.
- 26. CALYX (SIZE OF CARINAL LOBE): similar to upper lobes = 0; smaller than upper lobes = 1; much smaller than upper lobes = 2.
- 28. STANDARD PETAL (RELATIVE LENGTH): as long as the keel = 0; much shorter than the keel = 1.

TABLE 3.2.10. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTION SYNCLISTUS. INSET: SINGLE, FULLY RESOLVED CLADOGRAM (LENGTH 26, CONSISTENCY INDEX 61).



TAXA	CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)													
	4	10	16	20	X1	24	26	30	X2	33	33a	36	37	40
<i>Leobordea</i>	0	0	1	0	0	0	1	0	0	0	0	0	0	0
<i>L. oligocephala</i> (51)	1	0	1	0	0	0	1	0	0	1	0	1	0	0
<i>L. polycephala</i> (52)	0	0	1	0	1	0	0	0	0	1	0	0	0	0
<i>L. laticeps</i> (53)	0	1	1	0	1	1	1	0	0	1	0	0	0	1
<i>L. globulosa</i> (54)	0	1	1	0	1	0	1	0	0	1	0	0	1	1
<i>L. longicephala</i> (55)	0	1	0	2	1	0	1	0	0	0	0	0	1	1
<i>L. pentaphylla</i> (56)	1	1	1	0	1	0	1	1	1	0	1	0	1	1
<i>L. rosea</i> (57)	1	1	1	0	1	1	1	1	1	0	1	0	1	1
<i>L. bolusii</i> (58)	1	2	1	1	1	1	1	0	1	1	1	1	1	1
<i>L. anthyllopsis</i> (59)	0	2	1	0	1	1	0	1	1	0	1	0	1	0

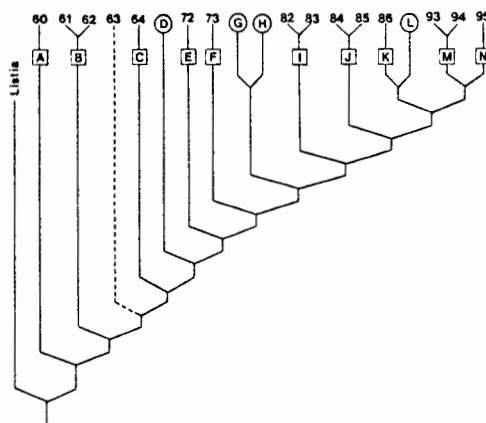
CHARACTERS AND POLARIZATION OF CHARACTER STATES:

4. NUMBER OF LEAFLETS: invariably 3-digitate = 0; 3- and/or 5-digitate = 1.
10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy = 1; totally glabrous = 2.
16. FLOWER NUMBER: more than 20 = 0; 5 to 20 = 1.
20. BRACT SIZE: large and foliaceous = 0; more than twice as wide as the pedicel = 1; small, linear = 2.
- X1. CALYX LOBES (SHAPE): broadly triangular = 0; narrow, slender = 1.
24. CALYX LOBES (LENGTH): as long or shorter than the fused part = 0; longer than the fused part = 1.
26. CALYX (SIZE OF CARINAL LOBE): similar to upper lobes = 0; narrower than upper lobes = 1.
30. STANDARD PETAL (SHAPE OF LAMINA): ovate or oblong = 0; linear = 1.
- X2. WING PETAL (SHAPE OF LAMINA): ovate or oblong = 0; linear = 1.
33. WING PETAL (VESTITURE): hairy = 0; glabrous = 1.
- 33a. WING PETAL (AURICLE): small = 0; very long = 1.
36. KEEL (VESTITURE): hairy = 0; glabrous = 1.
37. KEEL (LENGTH OF CLAWS): shorter than the lamina = 0; as long or longer than the lamina = 1.
40. OVULE NUMBER: numerous (5 to 15) = 0; few (3 to 4) = 1.

Section 7. Oxydium (Tables 3.2.11 to 3.2.14)

When species are used as experimental units, the analyses give poor results (many trees, low consistency indices). The *mhennig** option, for example, produce more than 100 trees with a length of 125 and a consistency index of 36. The problem associated with the phylogeny of this group appears to be that character evolution in some of the terminal clades differs from that of the section as a whole. This leads to extensive homoplasy when the species are all included in a single analysis. When monophyletic clades are used as experimental units, a good result is obtained. Monophyletic clades were formed by carefully combining only those species that share distinct apomorphies. If any doubt existed about a species, it was kept as a separate clade. The final result of an analysis using 14 monophyletic clades is shown in Table 3.2.11. (The most likely position for L. *erisemoides*, a poorly known species from Angola which could not be included in the analysis, is shown by the broken line). Very similar, but poorly resolved topologies resulted from earlier analyses when all the species were included. The result suggests that Oxydium can be accepted as monophyletic, although I still have doubt about the position of clades A and B. The next step was to analyse each of the larger clades, i.e., those with more than two species. The ease with which the phylogenies of the four larger clades could be worked out, was quite unexpected. I assume that the success was due to the choice of outgroups, which was

TABLE 3.2.11.
CHARACTERS AND POLARIZATION
OF CHARACTER STATES IN 14
MAJOR CLADES OF THE SECTION
OXYDIUM. INSET: SINGLE, FULLY
RESOLVED CLADOGRAM (LENGTH
84, CONSISTENCY INDEX 48).



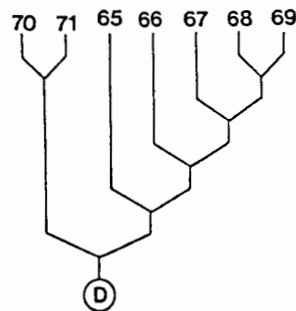
CLADES	CHARACTERS & CHARACTER STATES (numbered as in Table 3.2)																													
	1	X1	4	5	6	7	10	11	13	16	19	24	25	26	27	29	29a	30	31	33	35	X2	38	38a	39	42	43	46	49	
<i>Listia</i> *	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
clade A	1	0	1	1	1	1	2	0	1	1	0	1	1	1	0	1	0	0	0	0	1	0	1	0	2	2	1	0	0	
clade B	1	0	1	1	0	0	1	0	1	2	0	2	0	0	0	1	0	0	1	0	1	0	1	0	0	0	1	0	0	
clade C	1	0	1	1	2	1	1	0	2	2	0	0	0	1	0	1	0	1	0	0	1	0	1	1	0	0	1	0	1	
clade D	1	0	1	1	2	1	0	0	2	1	0	0	0	1	0	2	0	1	0	0	0	1	1	1	0	0	0	0	1	
clade E	1	0	1	1	2	2	0	0	2	2	0	0	0	0	0	1	0	1	1	1	0	0	1	0	1	1	0	0	1	
clade F	0	0	1	0	2	1	0	1	2	2	0	1	2	0	0	1	0	0	0	0	1	1	1	1	1	1	0	0	1	
clade G	0	0	1	0	2	1	0	1	2	1	0	2	1	0	0	1	0	0	0	0	1	1	1	1	1	1	1	0	0	
clade H	0	0	1	0	2	1	0	1	2	1	0	2	0	0	1	1	0	0	0	0	1	1	1	1	1	1	0	0	1	
clade I	0	0	1	0	2	1	0	1	0	1	0	0	0	1	0	1	0	0	0	0	1	1	2	1	1	1	1	0	0	
clade J	1	0	1	0	2	1	0	1	1	1	1	1	0	1	0	2	1	0	0	0	1	1	2	1	1	1	1	0	0	
clade K	0	0	0	1	2	1	2	1	2	1	1	2	0	1	1	2	1	0	0	0	2	1	2	1	2	2	0	0	1	
clade L	1	0	1	1	2	1	0	1	2	1	0	1	0	1	0	2	1	0	0	0	2	1	2	1	2	2	0	0	1	
clade M	1	1	1	0	2	1	0	1	2	2	0	1	0	1	0	2	1	0	1	0	2	1	2	1	2	2	0	1	1	
clade N	1	1	1	0	2	1	1	1	2	2	0	0	0	1	0	2	1	0	0	0	2	1	2	1	1	1	0	1	1	

* In a large number of analyses, the section *Liatia* invariably proved to be the most suitable outgroup for the section *Oxydium*.

1. HABIT: suffrutescent perennial = 0; annual = 1.
- X1. BRANCHES: not brittle = 0; brittle = 1.
4. NUMBER OF LEAFLETS: 3- or 5-digitate = 0; 3-digitate = 1.
5. UNIFOLIOLATE LEAFLETS: absent = 0; at least with some (often the juvenile) leaves unifoliate = 1.
6. NUMBER OF STIPULES: invariably paired, \pm equal in size = 0; paired but markedly dissimilar in size = 1; invariably single = 2.
7. STIPULE SIZE: similar to leaflets = 0; much smaller than leaflets = 1; inconspicuous = 2.
10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy = 1; glabrous = 2.
11. HAIR TYPE: simple, uniseriate = 0; biramous = 1.
13. INFLORESCENCE POSITION: terminal = 0; terminal and leaf-opposed = 1; invariably leaf-opposed = 2.
16. FLOWER NUMBER: 5 to 20 = 0; one, two, three or four = 1; one, rarely two = 2.
19. PEDICEL: \pm as long as the calyx = 0; much longer than the calyx = 1.
24. CALYX: much shorter than the corolla = 0; \pm half as long as corolla = 1; as long or nearly as long as the corolla = 2.
25. CALYX (LATERAL SINUSES): as deep as lower sinuses = 0; shallower than lower sinuses = 1; much shallower = 2.
26. CALYX (SIZE OF CARINAL LOBE): \pm equal to upper lobes = 0; much narrower than upper lobes = 1.
27. CALYX (SIZE OF UPPER LOBES): \pm equal to lateral lobes = 0; wider than lateral lobes = 1.
29. STANDARD PETAL (SHAPE OF CLAW): not dilated = 0; dilated towards the base = 1; much dilated = 2.
- 29a. STANDARD PETAL (LENGTH OF CLAW): \pm half the lamina length = 0; more than half the lamina length = 1.
30. STANDARD PETAL (SHAPE OF LAMINA): not panduriform = 0; panduriform = 1.
31. STANDARD PETAL (VESTITURE): glabrous or with a line of hairs along the middle = 0; hairy on at least part of dorsal surface = 1.
33. WING PETAL (VESTITURE): glabrous = 0; hairy = 1.
35. KEEL (SHAPE OF APEX): obtuse or slightly pointed = 0; beaked = 1; strongly beaked = 2.
- X2. STAMINAL TUBE: even width = 0; much widened towards the base = 1.
38. ANTHER DIMORPHISM: basifixed anthers up to twice as long as dorsifixed anthers = 0; basifixed anthers more than twice as long as the dorsifixed ones = 1; basifixed anthers more than 3x as long as dorsifixed ones = 2.
- 38a. CARINAL ANTHER: intermediate (longer than dorsifixed anthers) = 0; similar to basifixed anthers = 1.
39. PISTIL SHAPE: linear = 0; oblong = 1; ovate = 2.
42. FRUIT (SHAPE IN TRANSVERSE SECTION): flat = 0; slightly turgid = 1; much inflated = 2.
43. FRUIT (UPPER SUTURE): conspicuously verrucose = 0; minutely verrucose = 1.
46. FUNICLE LENGTH: short or long (up to 3x the seed length) = 0; very long (several times the seed length) = 1.
49. CYANOGENESIS: acyanogenic = 0; most species /samples cyanogenic = 1.

clade A, *L. pallens*; clade B, *L. delicata* & *L. pseudodelicata*; clade C, *L. tenuis*; clade D, *L. falcata* group (see Table 3.2.12); clade E, *L. schreiberi*; clade F, *L. pallidirosea*; clade G, *L. burchellii* group (see Table 3.2.13); clade H, *L. laxa* group (see Table 3.2.13); clade I, *L. glabra* & *L. monophylla*; clade J, *L. pumila* & *L. micrantha*; clade K, *L. acutiflora*; clade L, *L. rostrata* group (see Table 3.2.14); clade M, *L. rabenaviana* & *L. sparsiflora*; clade N, *L. lenticula*.

TABLE 3.2.12. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN CLADE D OF THE SECTION OXYDIUM (SEE TABLE 3.2.11). INSET: SINGLE, FULLY RESOLVED CLADOGRAM (LENGTH 19, CONSISTENCY INDEX 78).

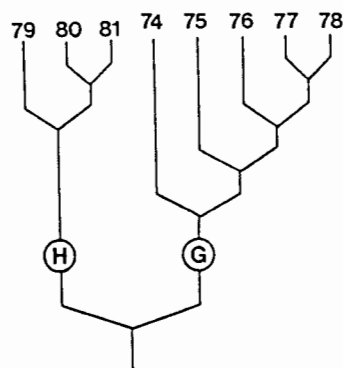


SPECIES		CHARACTERS & CHARACTER STATES (numbered as in Table 3.2)													
		15	16	17a	19	25	29	X1	35	X2	38	39	43	X3	
L. <u>TENUIS</u>	(64)	2	1	0	0	0	0	0	1	0	0	0	0	1	
L. <u>strigillosa</u>	(65)	2	1	1	0	0	1	1	1	1	0	0	1	1	
L. <u>falcata</u>	(66)	2	1	1	0	0	1	1	0	1	1	0	1	1	
L. <u>parviflora</u>	(67)	2	1	1	0	0	1	1	0	1	1	0	1	0	
L. <u>fruticoides</u>	(68)	1	0	1	0	0	1	1	0	1	1	0	1	0	
L. <u>sabulosa</u>	(69)	0	0	1	0	0	1	0	1	1	1	0	1	0	
L. <u>linearifolia</u>	(70)	2	1	1	1	1	0	0	1	1	0	1	1	0	
L. <u>pachycarpa</u>	(71)	2	1	1	1	1	0	0	1	1	1	2	1	0	

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

15. PEDUNCLE LENGTH: long = 0; short = 1; \pm absent = 2.
 16. FLOWER NUMBER: one, two, three or four = 0; one, rarely two = 1.
 17a. FLOWER SIZE: small = 0; large = 1.
 19. PEDICEL: short = 0; as long or longer than the calyx = 1.
 25. CALYX (LATERAL SINUSES): as deep as lower ones = 0; shallower than lower ones = 1.
 29. STANDARD PETAL (SHAPE OF CLAW): dilated towards the base = 0; much dilated = 1.
 X1. WING PETAL (SCULPTURING): present = 0; absent = 1.
 35. KEEL (SHAPE OF APEX): slightly pointed = 0; beaked = 1.
 X2. STAMINAL TUBE: even width = 0; widened towards the base = 1.
 38. ANTHOR DIMORPHISM: basifixed anthers more than twice as long as dorsifixed anthers = 0; basifixed anthers more than 3x as long as dorsifixed ones = 1.
 39. PISTIL SHAPE: linear = 0; oblong = 1; ovate = 2.
 43. FRUIT (UPPER SUTURE): smooth = 0; distinctly verrucose = 1.
 X3. FRUIT IN LATERAL VIEW: straight = 0; falcate = 1.

TABLE 3.2.13. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN CLADES G AND H OF THE SECTION OXYDIUM. INSET: SINGLE, FULLY RESOLVED CLADOGRAM (LENGTH 31, CONSISTENCY INDEX 70).

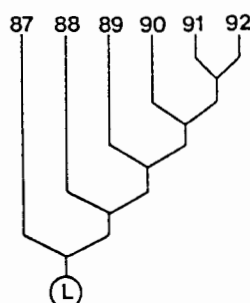


SPECIES		CHARACTERS & CHARACTER STATES (numbered as in Table 3.2)															
		1	6	7	15	16	19	24	25	27	27a	29	35	38	39	42	49
L.	<u>PALLIDIROSEA</u> (73)	0	1	1	2	2	0	0	2	0	0	0	1	0	0	0	1
L.	<u>curtii</u> (74)	1	1	1	2	0	0	0	1	0	0	0	1	0	1	1	0
L.	<u>brachyantha</u> (75)	1	1	1	2	0	1	1	1	0	0	0	1	0	1	1	0
L.	<u>crumanina</u> (76)	1	1	1	2	0	1	1	1	0	0	0	1	0	2	2	0
L.	<u>burchellii</u> (77)	1	1	0	1	0	1	1	0	0	1	1	1	0	2	2	1
L.	<u>maculata</u> (78)	1	1	2	2	2	1	1	0	0	0	0	0	0	2	2	1
L.	<u>macrosepala</u> (79)	0	1	1	1	0	0	1	0	1	0	0	1	0	0	0	0
L.	<u>laxa</u> (80)	0	1	1	1	0	0	1	0	1	0	0	1	1	0	0	0
L.	<u>serpentinicola</u> (81)	0	0	0	0	2	0	1	0	1	0	0	1	1	0	0	0

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

1. HABIT: perennials (base woody) = 0; short-lived perennials = 1.
6. NUMBER OF STIPULES: at least rarely paired = 0; invariably single = 1.
7. STIPULE SIZE: similar to leaflets = 0; much smaller than leaflets = 1; inconspicuous = 2.
15. PEDUNCLE LENGTH: long = 0; short = 1; \pm absent = 2.
16. FLOWER NUMBER: 5 to 20 = 0; one, two, three or four = 1; one, rarely two = 2.
19. PEDICEL: long (more than 2 mm) = 0; very short (\pm 1 mm) = 1.
24. CALYX: \pm half as long as corolla = 0; as long or nearly as long as the corolla = 1.
25. CALYX (LATERAL SINUSES): as deep as lower sinuses = 0; shallower than lower sinuses = 1; much shallower = 2.
27. CALYX (SIZE OF UPPER LOBES): \pm equal to lateral lobes = 0; wider than lateral lobes = 1.
- 27a. CALYX: lobes valvate = 0; lobes imbricate = 1.
29. STANDARD PETAL (SHAPE OF CLAW): dilated towards the base = 0; much dilated = 1.
35. KEEL (SHAPE OF APEX): obtuse or slightly pointed = 0; beaked = 1.
38. ANTHER DIMORPHISM: basifixed anthers more than twice as long as the dorsifixed ones = 0; basifixed anthers more than 3x as long as dorsifixed ones = 1.
39. PISTIL SHAPE: linear = 0; oblong = 1; ovate = 2.
42. FRUIT (SHAPE IN TRANSVERSE SECTION): flat = 0; slightly inflated = 1; much inflated = 2.
49. CYANOGENESIS: cyanogenic = 0; acyanogenic = 1.

TABLE 3.2.14. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN CLADE L OF THE SECTION OXYDIUM. INSET: SINGLE, FULLY RESOLVED CLADOGRAM (LENGTH 29, CONSISTENCY INDEX 72).



SPECIES		CHARACTERS & CHARACTER STATES (numbered as in Table 3.2)																
		1	X1	4	10	15	16	17a	19	20	27a	29	29a	31	33	33a	39a	49
L.	<u>ACUTIFLORA</u> (86)	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	0
L.	<u>rostrata</u> (87)	1	1	2	1	0	0	0	1	0	0	0	1	0	0	0	1	0
L.	<u>arenicola</u> (88)	1	1	2	0	2	2	0	1	0	0	0	1	1	1	0	1	1
L.	<u>oxyptera</u> (89)	1	1	1	0	0	0	0	1	1	0	1	1	1	0	1	1	0
L.	<u>perplexa</u> (90)	1	1	2	0	0	1	0	1	1	1	1	0	1	0	1	0	0
L.	<u>stenophylla</u> (91)	1	1	2	0	0	0	1	1	1	0	1	0	0	0	1	0	0
L.	<u>carnea</u> (92)	1	1	2	0	1	0	1	1	1	1	1	1	0	0	1	0	1

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

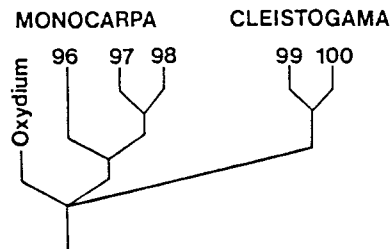
1. HABIT: perennial = 0; annual = 1.
- X1. ROOTS: not bright yellow = 0; bright yellow = 1.
4. NUMBER OF LEAFLETS: predominantly 5-digitate = 0; 3-digitate, rarely 5-digitate = 1; invariably 3-digitate = 2.
10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy = 1; glabrous = 2.
15. PEDUNCLE LENGTH: long = 0; short = 1; \pm absent = 2.
16. FLOWER NUMBER: 5 to 20 = 0; one, two, three or four = 1; one, rarely two = 2.
- 17a. FLOWER SIZE: small = 0; very large = 1.
19. PEDICEL: long (more than 4 mm) = 0; short (less than 3 mm) = 1.
20. BRACT SIZE: small, inconspicuous = 0; conspicuous, wider than the pedicel = 1.
- 27a. CALYX: lobes valvate = 0; lobes imbricate = 1.
29. STANDARD PETAL (SHAPE OF CLAW): dilated towards the base = 0; much dilated = 1.
- 29a. STANDARD PETAL (LENGTH OF CLAW): \pm half the lamina length = 0; more than half the lamina length = 1.
31. STANDARD PETAL (VESTITURE): glabrous or with a line of hairs along the middle = 0; hairy over part of surface = 1.
33. WING PETAL (VESTITURE): glabrous = 0; hairy = 1.
- 33a. WING PETAL (AURICLE): not lobed = 0; often lobed = 1.
- 39a. GYNOCIDIUM BASE: stipitate = 0; sessile or subsessile = 1.
49. CYANOGENESIS: cyanogenic = 0; acyanogenic = 1.

strictly according to the sequence in the main analysis. The results for clade D (L. falcata group), clades G and H (L. burchellii and L. laxa groups) and clade L (L. rostrata group) are presented in Tables 3.2.12 to 3.2.14 respectively. The 14 major clades (A to M in Table 3.2.11) are treated as subsections in Part 5.

Sections 8 and 9. Monocarpa and Cleistogama (Table 3.2.15)

The correct phylogenetic position of these two anomalous sections is very uncertain. I am taking the equally lobed calyces and the high frequency of flower dimorphism resulting from cleistogamy at face value to place them near the section Oxydium. It should be noted that the claw of the standard is not distinctly dilated as in Oxydium, and that the anthers are also not strongly dimorphic. Relationships within the two sections can easily be visualized without the need for detailed analyses. The result in Table 3.2.15 is nevertheless useful because it highlights the problems associated with the correct position of the two sections. The chromosome number in Cleistogama is in conflict with other characters but a reinvestigation has confirmed the counts reported by Van Wyk and Schutte (1988a, Appendix 14). The structure of the corolla in Monocarpa is typical of the sections Euchlora, Polylobium and Lotononis rather than Oxydium.

TABLE 3.2.15. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTIONS MONOCARPA AND CLEISTOGAMA. INSET: SINGLE, PARTIALLY RESOLVED CLADOGRAM (LENGTH 13, CONSISTENCY INDEX 76).



TAXA		CHARACTERS & CHARACTER STATES (numbered as in Table 3.2)									
		1	6	21	22	34	X1	42	X2	48	49
<u>Oxydium</u>		0	0	0	0	0	0	0	0	0	0
<u>Monocarpa</u>											
	<u>L. venosa</u> (96)	1	0	0	0	1	0	1	0	0	1
	<u>L. leptoloba</u> (97)	1	1	0	1	1	0	1	0	0	0
	<u>L. maximiliani</u> (98)	1	1	1	1	1	0	1	0	0	0
<u>Cleistogama</u>											
	<u>L. pungens</u> (99)	0	1	0	1	0	0	0	1	1	1
	<u>L. tenella</u> (100)	0	1	0	1	0	1	0	1	1	1

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

1. HABIT: perennial = 0; annual = 1.
6. NUMBER OF STIPULES: paired, at least in some species /specimens = 0; invariably single = 1.
21. FLOWER COLOUR: yellow = 0; blue = 1.
22. FLOWER DIMORPHISM (CLEISTOGAMY): absent = 0; present = 1.
34. KEEL (RELATIVE LENGTH): as long or longer than the standard and wing petals = 0; much shorter than the standard and wing petals = 1.
- X1. KEEL (COLOUR OF APEX): not dark purple ("pollen guide" absent) = 0; dark purple ("pollen guide" present) = 1.
42. FRUIT (SHAPE IN TRANSVERSE SECTION): laterally much inflated = 0; slightly inflated = 1.
- X2. FRUIT (LOWER SUTURE): not sunken = 0; sunken = 1.
48. CHROMOSOME NUMBER: base number 9 = 0; base number 7 = 1.
49. CYANOGENESIS: cyanogenic = 0; acyanogenic = 1.

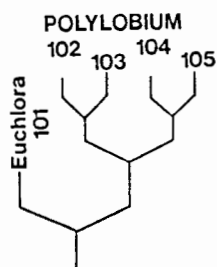
Sections 10 and 11. Euchlora and Polylobium (Table 3.2.16)

The result of this analysis, shown in Table 3.2.16, is preliminary only. A sister group relationship between L. involucrata and L. brevicaulis is doubtful and probably resulted from the small number of characters that were used. I suspect most of the apparent synapomorphies to be convergences. The discovery of relatively large quantities of pyrrolizidine alkaloids in L. involucrata (and the presence of an unstable N-oxide which has not yet been positively identified) suggest that alkaloidal evidence may provide valuable clues to the phylogeny of the section.

Section 12. Lotononis (Table 3.2.17)

The uniform structure of the inflorescence and flower in this section makes it an easily recognizable group, but the character distributions within the section show a relatively high level of homoplasy. The result of the analysis (Table 3.2.17) suggests six main clades, but a formal recognition of these would have little practical value.

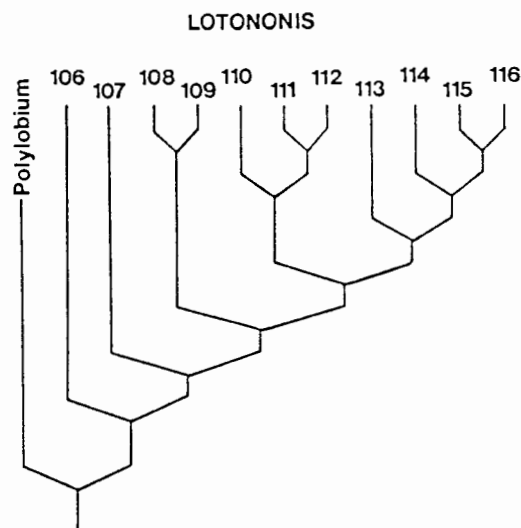
TABLE 3.2.16. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTION POLYLOBIUM. INSET: SINGLE, FULLY RESOLVED CLADOGRAM (LENGTH 17, CONSISTENCY INDEX 82).



TAXA		CHARACTERS & CHARACTER STATES (numbered as in Table 3.2)											
		4	7	10	11	15	16	17	20	25	26	49	
<u>EUCHLORA</u>	(101)	0	0	1	0	0	0	1	0	0	0	1	
<u>L. racemiflora</u>	(102)	0	0	1	0	0	0	0	1	2	0	0	
<u>L. fastigiata</u>	(103)	0	0	1	0	0	1	1	1	2	1	0	
<u>L. involucreata</u>	(104)	1	1	1	0	1	0	2	2	1	1	0	
<u>L. brevicaulis</u>	(105)	1	1	0	1	1	1	2	2	1	0	1	

4. NUMBER OF LEAFLETS: 3-digitate = 0; 5- to 8-digitate = 1.
7. STIPULE SIZE: similar to leaflets = 0; much smaller than leaflets = 1.
10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy = 1.
11. HAIR TYPE: uniseriate = 0; biramous = 1.
15. PEDUNCLE LENGTH: long = 0; short = 1.
16. FLOWER NUMBER: 5 to 20 = 0; one, two, three or four = 1.
17. FLOWER ARRANGEMENT: evenly spaced = 0; congested = 1; umbellate = 2.
20. BRACT SIZE: very narrow = 0; wider than the pedicel = 1; foliaceous = 2.
25. CALYX (LATERAL SINUSES): as deep as lower ones = 0; shallower than lower ones = 1; much shallower than the lower ones = 2.
26. CALYX (SIZE OF CARINAL LOBE): similar to upper ones = 0; narrower = 1.
49. CYANOGENESIS: cyanogenic = 0; acyanogenic = 1.

TABLE 3.2.17. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTION LOTONONIS. INSET: SINGLE, FULLY RESOLVED CLADOGRAM (LENGTH 32, CONSISTENCY INDEX 56).



TAXA	CHARACTERS & CHARACTER STATES (numbered as in Table 3.2)											
	2	6	7	10	11	16	21	25	31	39	42	49
hypothetical												
ancestor	0	0	0	0	0	0	0	0	0	0	0	0
<u>POLYLOBIUM</u>	1	0	0	0	0	0	0	0	0	1	0	0
<u>L. lamprifolia</u> (106)	0	2	0	0	0	2	0	0	0	0	0	1
<u>L. acuminata</u> (107)	0	2	1	0	0	2	1	1	0	0	0	0
<u>L. gracilifolia</u> (108)	1	2	2	0	1	2	0	0	0	0	0	1
<u>L. argentea</u> (109)	1	2	1	0	1	2	2	0	0	0	0	1
<u>L. prostrata</u> (110)	1	2	1	2	1	2	0	0	1	0	0	0
<u>L. villosa</u> (111)	1	2	1	2	0	2	2	0	1	0	0	0
<u>L. varia</u> (112)	1	1	1	2	0	1	2	0	0	0	0	0
<u>L. complanata</u> (113)	1	2	1	2	0	2	2	0	0	0	1	0
<u>L. elongata</u> (114)	2	1	1	1	1	2	1	0	1	1	0	1
<u>L. azurea</u> (115)	2	1	1	1	1	2	2	0	1	0	0	0
<u>L. filiformis</u> (116)	2	1	1	1	0	2	2	0	1	0	0	0

2. BRANCHES: branched, erect = 0; short, unbranched, prostrate = 1; long and slender, unbranched, prostrate = 2.

6. NUMBER OF STIPULES: paired, similar to leaflets = 0; paired, dissimilar in size and shape = 1; invariably single = 2.

7. STIPULE SIZE: similar to leaflets = 0; much smaller than leaflets = 1; minute = 2.

10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy = 1; glabrous = 2.

11. HAIR TYPE: uniseriate = 0; biramous = 1.

16. FLOWER NUMBER: 5 to 20 = 0; one, two, three or four = 1; invariably single = 2.

21. FLOWER COLOUR: yellow = 0; at least partly blue = 1; blue = 2.

25. CALYX (LATERAL SINUSES): shallower than lower ones = 0; much shallower than the lower ones = 1.

31. STANDARD PETAL (VESTITURE): glabrous or with a line of hairs along the middle = 0; hairs on part of dorsal surface = 1.

39. PISTIL SHAPE: linear = 0; ovate = 1.

42. FRUIT (SHAPE IN TRANSVERSE SECTION): much inflated = 0; flat = 1.

49. CYANOGENESIS: cyanogenic = 0; acyanogenic = 1.

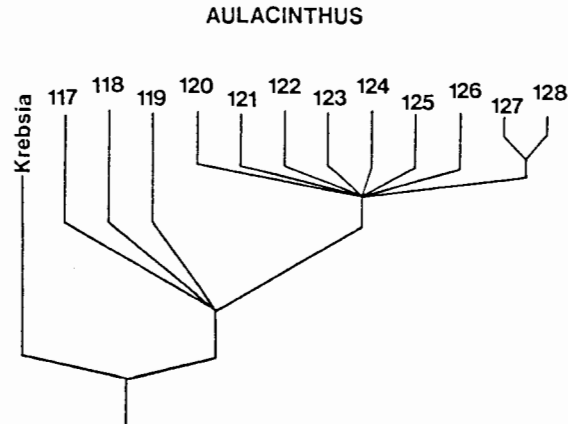
Section 13. Aulacanthus (Table 3.2.18)

The character information available for this essentially woody section failed to resolve the phylogeny. One particular combination of characters produced a single fully resolved cladogram, showing a linear sequence of all the species. This result is not reported here because closely related species were widely separated as a result of reversals in rather trivial characters. The species are all very similar and many of them are difficult to distinguish from one another when the habit is not recorded. There are however, no convincing apomorphies to support the section as a monophyletic group. Persistent petioles (the leaflets are usually shed in summer) provide some evidence of monophyly. The species are all very strongly cyanogenic. The sequence presented in Table 3.2.18 is based on morphological similarities. Morphological evidence indicates seven basic groups within the section and cladistic evidence to support these may eventually be found. The groups are described in Part 5.

Section 14. Krebsia

Despite a relatively large number of characters, a likely estimate of the phylogeny of this section could not be found. Several different analyses have shown the presence of a robust clade within the section (indicated by B in the cladogram above Table 3.2.19). This group is treated as a subsection in Part 5,

TABLE 3.2.18. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTION AULACINTHUS. INSET: NELSON CONSENSUS TREE OF 259 TREES GENERATED BY BRANCH-SWAPPING.

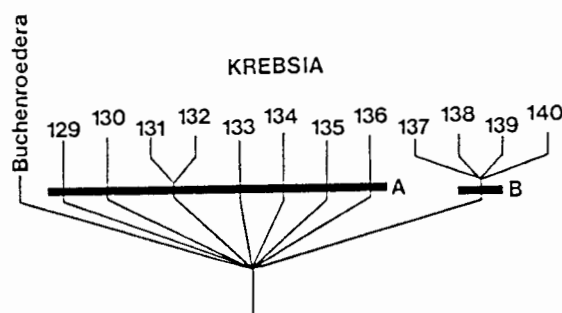


TAXA	CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)											
	2	6	10	X1	X2	15	16	21	26	35	41	42
KREBSIA	0	0	0	0	0	0	0	0	0	0	0	1
L. <u>dissitinodia</u> (117)	0	0	0	1	0	1	2	0	0	1	0	1
L. <u>dahlgrenii</u> (118)	0	1	0	1	0	1	2	0	0	0	0	0
L. <u>rigida</u> (119)	0	0	0	1	0	1	1	0	0	0	0	0
L. <u>densa</u> (120)	0	1	1	1	1	0	0	0	1	0	1	0
L. <u>viborgioides</u> (121)	0	1	1	1	0	0	0	0	0	1	1	0
L. <u>comptonii</u> (122)	1	1	1	1	1	0	0	0	0	0	1	0
L. <u>acocksii</u> (123)	1	1	1	1	0	0	1	0	0	0	1	0
L. <u>nutans</u> (124)	1	1	1	1	0	0	0	0	0	0	1	0
L. <u>exstipulata</u> (125)	1	1	1	1	0	0	0	0	0	1	0	1
L. <u>azureoides</u> (126)	0	1	1	1	0	0	2	1	0	0	1	0
L. <u>umbellata</u> (127)	2	1	1	1	0	0	0	0	1	0	0	1
L. <u>purpurescens</u> (128)	2	1	1	1	0	0	1	1	1	0	0	1

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

2. BRANCHES: woody shrub with all branches \pm persistent = 0; woody branches at the base only = 1; suffrutescent = 2.
6. NUMBER OF STIPULES: paired = 0; single (or absent) = 1.
10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy or glabrous = 1.
- X1. PETIOLES: not persistent = 0; persistent after the leaflets are shed = 1.
- X2. PETIOLE ANATOMY: three leaf traces = 0; often five traces = 1.
15. PEDUNCLE: long = 0; very short = 1.
16. FLOWER NUMBER: 5 to 20 = 0; one, two, three or four = 1; one, rarely two = 2.
21. FLOWER COLOUR: yellow = 0; blue or purple = 1.
26. CALYX (SIZE OF CARINAL LOBE): \pm equal to upper lobes = 0; narrower than upper lobes = 1.
35. KEEL (SHAPE OF APEX): obtuse = 0; acute = 1.
41. FRUIT (SHAPE IN LATERAL VIEW): oblong = 0; ovate = 1.
42. FRUIT (SHAPE IN TRANSVERSE SECTION): slightly inflated = 0; much inflated = 1.

TABLE 3.2.19. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTION KREBSIA. INSET: NELSON CONSENSUS TREE OF >100 TREES GENERATED BY BRANCH-SWAPPING.



TAXA	CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)																
	2	6	7	10	13	15	16	21	25	31	34	36	39	41	42	43	49
BUCHENROEDERA	0	0	0	0	0	0	0	0	0	0	0	0	2	2	0	0	0
L. <u>eriocarpa</u> (129)	0	0	0	0	0	1	1	1	0	0	0	1	0	0	0	0	0
L. <u>stricta</u> (130)	0	0	0	0	0	1	1	1	0	2	0	1	0	0	0	0	0
L. <u>sericophylla</u> (131)	0	1	1	0	1	2	2	1	0	0	0	1	0	0	0	0	0
L. <u>divaricata</u> (132)	0	1	1	1	1	2	2	1	0	0	0	1	0	0	0	0	0
L. <u>iacottetii</u> (133)	0	2	1	0	1	1	2	1	1	0	0	0	0	0	0	0	0
L. <u>galpinii</u> (134)	0	2	0	0	1	1	2	1	1	0	0	1	1	1	0	0	0
L. <u>minor</u> (135)	2	2	0	0	1	0	2	1	1	0	1	1	0	1	0	1	1
L. <u>caerulea</u> (136)	0	2	?	0	1	1	2	1	1	2	0	1	1	1	1	1	0
L. <u>dichiloides</u> (137)	1	0	0	2	0	1	1	0	1	1	0	1	0	0	0	0	0
L. <u>bachmanniana</u> (138)	1	0	0	2	1	0	0	1	1	1	0	1	0	0	0	0	0
L. <u>carnosa</u> (139)	1	0	0	2	1	1	1	1	1	1	0	1	0	0	0	0	0
L. <u>pottiae</u> (140)	1	0	0	2	0	1	1	1	1	1	0	1	0	0	0	0	0

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

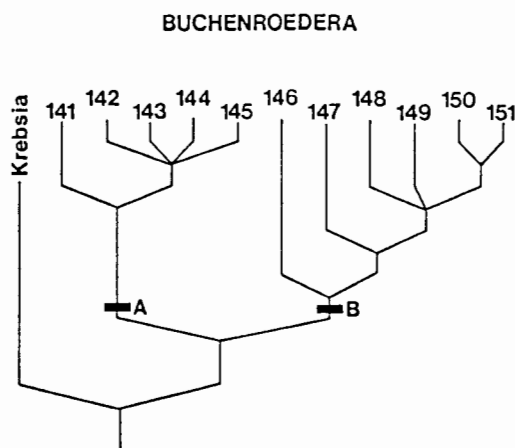
2. BRANCHES: woody shrub with all branches ± persistent = 0; suffrutescent perennial with at least the basal branches persistent = 1; prostrate suffrutescent herb = 2.
6. NUMBER OF STIPULES: invariably paired = 0; paired or single = 1; single (or absent) = 2.
7. STIPULE SIZE: similar to leaflets = 0; much smaller than leaflets = 1.
10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy = 1; glabrous = 2.
13. INFLORESCENCE POSITION: invariably terminal = 0; terminal and leaf-opposed = 1.
15. PEDUNCLE LENGTH: much longer than the length of the flowers = 0; as long or shorter than the flowers = 1; ± absent = 2.
16. FLOWER NUMBER: 5 to 20 = 0; one, two, three or four = 1; one, rarely two = 2.
21. FLOWER COLOUR: yellow = 0; at least partly blue = 1.
25. CALYX (LATERAL SINUSES): much shallower than lower sinuses = 0; slightly shallower than lower sinuses = 1.
31. STANDARD PETAL (VESTITURE): hairs on at least part of the abaxial surface = 0; line of hairs along the midrib only = 1; totally glabrous = 2.
34. KEEL (RELATIVE LENGTH): as long or longer than the standard and wing petals = 0; shorter than the standard and wing petals = 1.
36. KEEL (VESTITURE): hairy = 0; glabrous = 1.
39. PISTIL SHAPE: linear = 0; oblong = 1; ovate = 2.
41. FRUIT (SHAPE IN LATERAL VIEW): linear = 0; oblong = 1; ovate = 2.
42. FRUIT (SHAPE IN TRANSVERSE SECTION): slightly turgid = 0; much inflated = 1.
43. FRUIT (UPPER SUTURE): smooth = 0; verrucose = 1.
49. CYANOGENESIS: cyanogenic = 0; acyanogenic = 1.

which leaves no choice but to provisionally accept the basal grade as a second subsection. The intricate relationships amongst the species of this second group (all have blue flowers and are rather similar) should be investigated in more detail. Chromosome numbers of $2n = 28, 42, 56$ and 84 have been found in the section Krebsia (Van Wyk and Schutte 1988a, Appendix 14) so that a detailed cytological investigation may provide useful clues.

Section 15. Buchenroedera

Unlike the other two essentially woody sections (Aulacanthus and Krebsia), relationships within this section are more easily visualized. A reasonably well supported cladogram could be produced (Table 3.2.20). The two major clades agree exactly with the subdivision of Buchenroedera as proposed by Edwards and Getliffe Norris (1989). The two groups are treated as subsections in Part 5. The vestiture of the wing and keel petals is a very reliable character to distinguish between the two subsections. The terminal polychotomies in the cladogram give an accurate reflection of the intricate relationships between the species of these terminal clades.

TABLE 3.2.20. CHARACTERS AND POLARIZATION OF CHARACTER STATES IN THE SECTION BUCHENROEDERA. INSET: NELSON CONSENSUS TREE OF 8 TREES GENERATED BY BRANCH-SWAPPING.



TAXA	CHARACTERS & CHARACTER STATES (numbered as in Table 3.1)														
	2	6	7	10	14	17	20	21	21	25	33	36	40	41	49
KREBSIA	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
<i>L. lotononoides</i> (141)	1	0	1	0	1	0	0	0	1	0	1	1	1	1	0
<i>L. amaiubica</i> (142)	1	1	1	0	0	0	0	0	1	0	1	1	1	1	1
<i>L. glabrescens</i> (133)	1	1	1	1	1	0	0	0	1	0	1	1	1	1	1
<i>L. virgata</i> (144)	1	0	1	0	0	0	0	1	0	0	1	1	1	1	1
<i>L. viminea</i> (145)	1	1	1	0	1	0	0	1	0	0	1	1	1	1	1
<i>L. pulchella</i> (146)	0	0	1	0	0	1	0	0	1	1	0	0	1	1	0
<i>L. trichodes</i> (147)	1	0	1	0	0	1	1	0	1	1	0	0	1	1	1
<i>L. alpina</i> (148)	0	0	0	0	0	1	1	0	0	1	0	0	1	1	0
<i>L. meyeri</i> (149)	0	0	1	0	0	1	1	1	0	1	0	0	1	1	0
<i>L. holosericea</i> (150)	0	0	0	0	0	1	2	1	0	1	0	0	1	1	1
<i>L. harvevi</i> (151)	1	0	0	0	0	1	1	1	0	1	0	0	1	1	1

CHARACTERS AND POLARIZATION OF CHARACTER STATES:

2. BRANCHES: woody shrub with all branches \pm persistent = 0; suffrutescent perennial with at least the basal branches persistent = 1.
6. STIPULES: present, paired = 0; absent = 1.
7. STIPULE SIZE: similar to leaflets = 0; much smaller than leaflets (or absent) = 1.
10. LEAFLET VESTITURE (ADAXIAL SURFACE): densely hairy = 0; sparsely hairy = 1.
14. SECONDARY INFLORESCENCES: absent = 0; present = 1.
17. FLOWER ARRANGEMENT: evenly spaced on a rachis = 0; congested = 1.
20. BRACT SIZE: small linear (not wider than the pedicel) = 0; conspicuous, wider than the pedicel = 1; foliaceous = 2.
21. FLOWER COLOUR: yellow = 0; not yellow (pink or white) = 1.
21. FLOWER COLOUR: not blue = 0; blue = 1.
25. CALYX (LATERAL SINUSES): much shallower than lower sinuses = 0; slightly shallower than lower sinuses or subequal = 1.
33. WING PETAL (VESTITURE): hairy = 0; glabrous = 1.
36. KEEL (VESTITURE): hairy = 0; glabrous = 1.
40. OVULE NUMBER: numerous = 0; few = 1.
41. FRUIT (SHAPE IN LATERAL VIEW): linear or oblong = 0; ovate = 1.
49. CYANOGENESIS: cyanogenic = 0; acyanogenic = 1.

3.3 GEOGRAPHICAL DISTRIBUTION AND EVOLUTIONARY HISTORY

Raven and Polhill (1981) provide an overview of the biogeography of the Leguminosae. There is no direct evidence for the age of the southern temperate elements, but the evolutionary history of the major groups can be estimated from geological evidence and extant distribution patterns. Raven and Polhill (1981) suggest that the unusual combinations of characters in the Podalyrieae-Liparieae and the more derived Crotalarieae of southern Africa resulted from extensive radiation into habitats not previously available and which were very different from those occupied by ancestral forms. The diversity in Crotalarieae appears to be closely linked to the development of new habitats in Africa as a result of major climatic and geomorphological changes since the Oligocene (Raven & Axelrod 1974).

The geographical distribution of the tribe Crotalarieae is summarized in Table 3.3.1. All the genera except Crotalaria and Rothia are restricted to Africa and adjoining areas (Madagascar and the southern Mediterranean Region to India). Polhill (1968b, 1981a) suggested an African origin for Crotalaria with early extensions across the Atlantic and secondary diversification elsewhere. It seems reasonable to accept that the distribution of one of the two annual species of Rothia outside Africa has resulted from dispersal. In general terms, the Crotalarieae may

TABLE 3.3.1. GEOGRAPHICAL DISTRIBUTION OF THE GENERA OF THE TRIBE CROTALARIEAE. [Data from Polhill (1981a) and Van Wyk & Schutte (1989)]

GENERA	GEOGRAPHICAL AREAS							
	CAPE REGION	SOUTHERN AFRICA	CENTRAL AFRICA	NORTH AFRICA	SOUTHERN EUROPE TO INDIA	MADAGASCAR	SOUTH AMERICA	ASIA TO AUSTRALIA
<u>Argyrolobium</u>	+	+	+	+	+	+		
<u>Polhillia</u>	+							
<u>Melolobium</u>	+	+						
<u>Dichilus</u>		+						
<u>Pearsonia</u>		+	+			+		
<u>Rothia</u>		+	+	+	+			+
<u>Robynsiophyton</u>			+					
<u>Spartidium</u>				+				
<u>Crotalaria</u>	+	+	+	+	+	+	+	+
<u>Bolusia</u>		+	+					
<u>Lotononis</u>	+	+	+	+	+			
<u>Rafnia</u>	+	+						
<u>Aspalathus</u>	+	+						
<u>Lebeckia</u>	+	+						
<u>Wiborgia</u>	+							

be subdivided into a tropical element (Crotalaria and perhaps Robynsiophyton) and a temperate element (the rest of the tribe). Spartidium is the only genus endemic to the northern temperate region of Africa, while all the other genera except Lotononis, Argyrolobium and Rothia are restricted to the central and southern parts of Africa (including Madagascar). Northern Mediterranean Africa (as defined by Quézel 1978) therefore has only one endemic genus (Spartidium), while southern Mediterranean Africa (the Cape Floristic Region as defined by Goldblatt 1978)

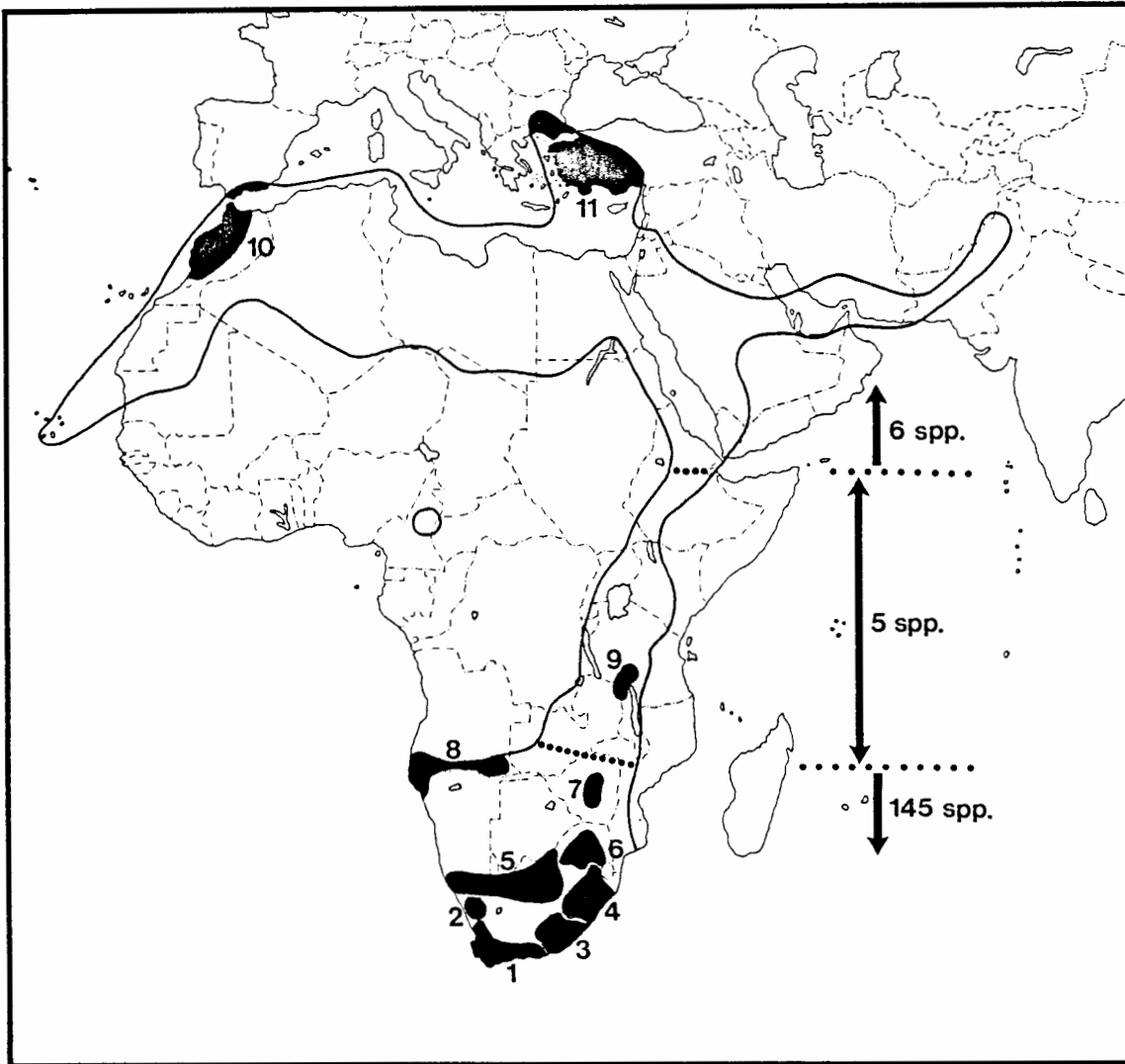


Figure 3.3.1. The approximate geographical distribution of the genus *Lotononis*. Endemic centres (see text and Table 3.3.2) are numbered 1 to 11: 1, Cape Region; 2, Namaqualand; 3, eastern Cape; 4, Natal-Drakensberg area; 5, southern Namibia and Griqualand-West; 6, Transvaal; 7, central Zimbabwe; 8, north-western Namibia and southern Angola; 9, Nyika Plateau; 10, Morocco and southern Spain; 11, Turkey and south-eastern Bulgaria.

has two endemic genera (Wiborgia and Polhillia) and two which are subendemic (Aspalathus and Rafnia). At the species level, this pattern of endemism is repeated in Argyrolobium (Polhill 1968a) and in Lotononis.

The approximate geographical distribution of the genus Lotononis is given in Figure 3.3.1. This distribution includes the whole of the African continent and the adjoining extreme southern parts of the Mediterranean region. Only six species occur in the northern part of the distribution range, with five species restricted to the Mediterranean area and one widespread annual (L. platycarpa) occurring right across the saharo-asiatic region (and also southwards to southern Africa). The central part of Africa (Ethiopia to Zambia, as indicated in Figure 3.3.1) has a total of five species, with only one (L. stolzii) restricted to this area (the distributions of L. laxa, L. angolensis, L. listii and L. platycarpa extend southwards into southern Africa). The southern part has a total of 145 species and only five of these do not occur in the Flora of Southern Africa region (L. angolensis, L. newtonii, L. erisemoides, L. delicata and L. pseudodelicata). L. platycarpa is the only species that occurs across all three areas.

The remarkable species density of Lotononis in southern Africa is illustrated in Figure 3.3.2. This map shows the total number of species recorded from each degree square. The figures suggest "centres of richness" or "diversity": the south-western Cape,

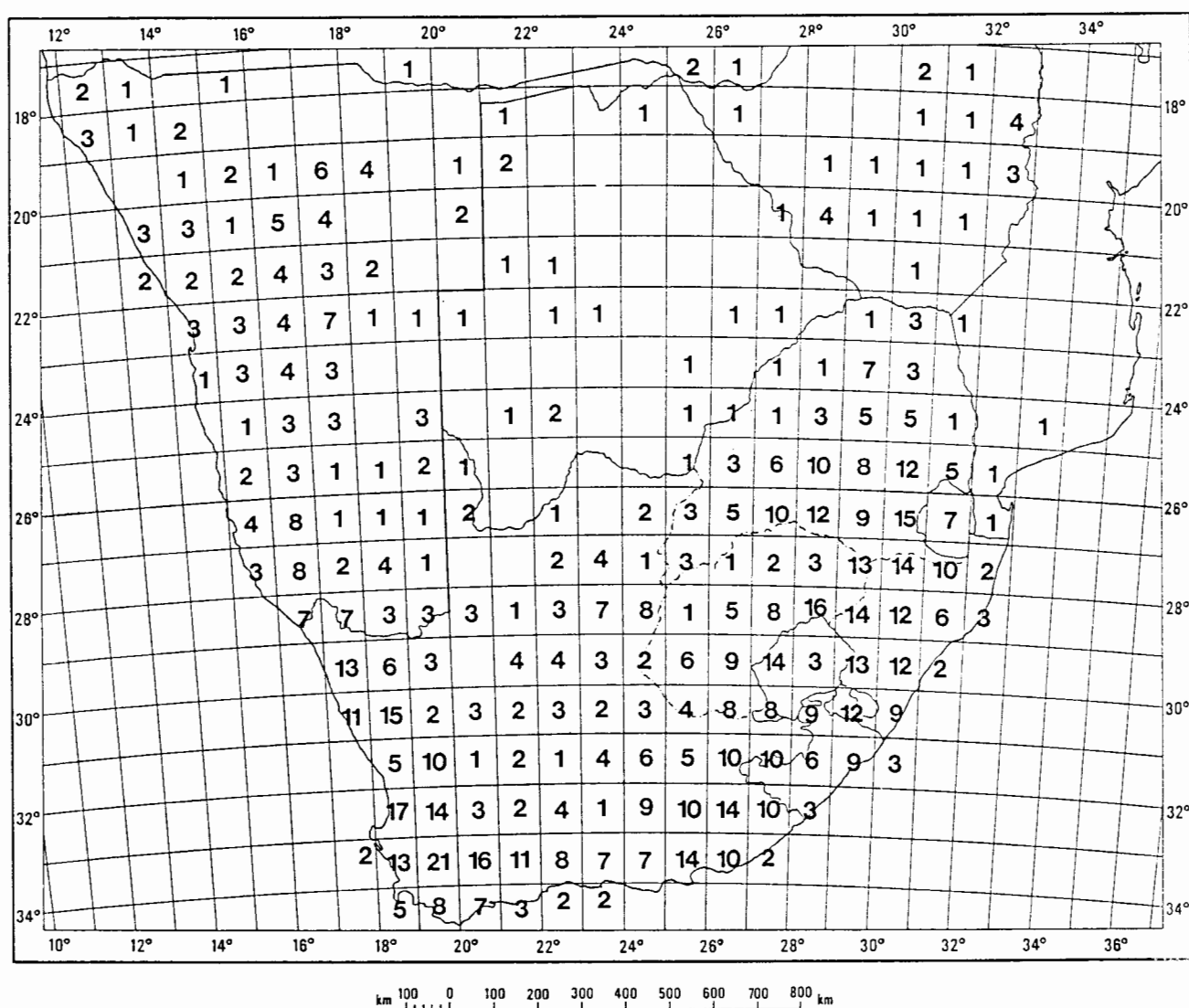


Figure 3.3.2. Species density of *Lotononis* in southern Africa. The number of species recorded from each degree square is shown.

the north-western Cape, the eastern Cape and the Drakensberg. The south-western Cape is, however, substantially richer. There is no doubt some distortion as a result of uneven collecting, but the sudden decrease in numbers towards the dry central interior (and also the Mozambique coast) is unlikely to be significantly changed by more thorough botanical explorations in future.

It is clear that the diversity of Lotononis in southern Africa is not restricted to the Cape Region as in "typical" Cape genera such as Aspalathus (Dahlgren 1963b) and Muraltia DC. subgenus Muraltia (Levyns 1954), but that the eastern afromontane areas and the north-western Cape make a significant contribution. The pattern in Lotononis is similar to the patterns in Euryops Cass. (Nordenstam 1969) and in Muraltia subgenus Psiloclada (Levyns 1954). It should be noted that very few species of Lotononis occur in fynbos and that the diversity in the Cape Region is due to a high concentration of species in the ecotones to other vegetation types. In contrast to Aspalathus, for example, the species that occur on sandy soils are usually suffrutescent or more often annuals. The diversity pattern supports the well-established concept of southern Africa as a survival centre for mesic and temperate floristic elements that have subsequently evolved in relative isolation (Goldblatt 1978).

An examination of the geographical distributions of the various sections of Lotononis (here accepted as monophyletic units), revealed definite patterns. Figures 3.3.3 to 3.3.5 show the total distribution area of each of the sections. Only four of the sections are not endemic to southern Africa (Figure 3.3.3). These are the sections Leptis (Figure 3.3.3a), Leobordea (Figure 3.3.3b), Listia (Figure 3.3.3c) and Oxydium (Figure 3.3.3d). The remaining sections have a very localized distribution in southern Africa, as shown in Figures 3.3.4 and 3.3.5. Three sections are restricted to the eastern part of southern Africa: Lipozygis

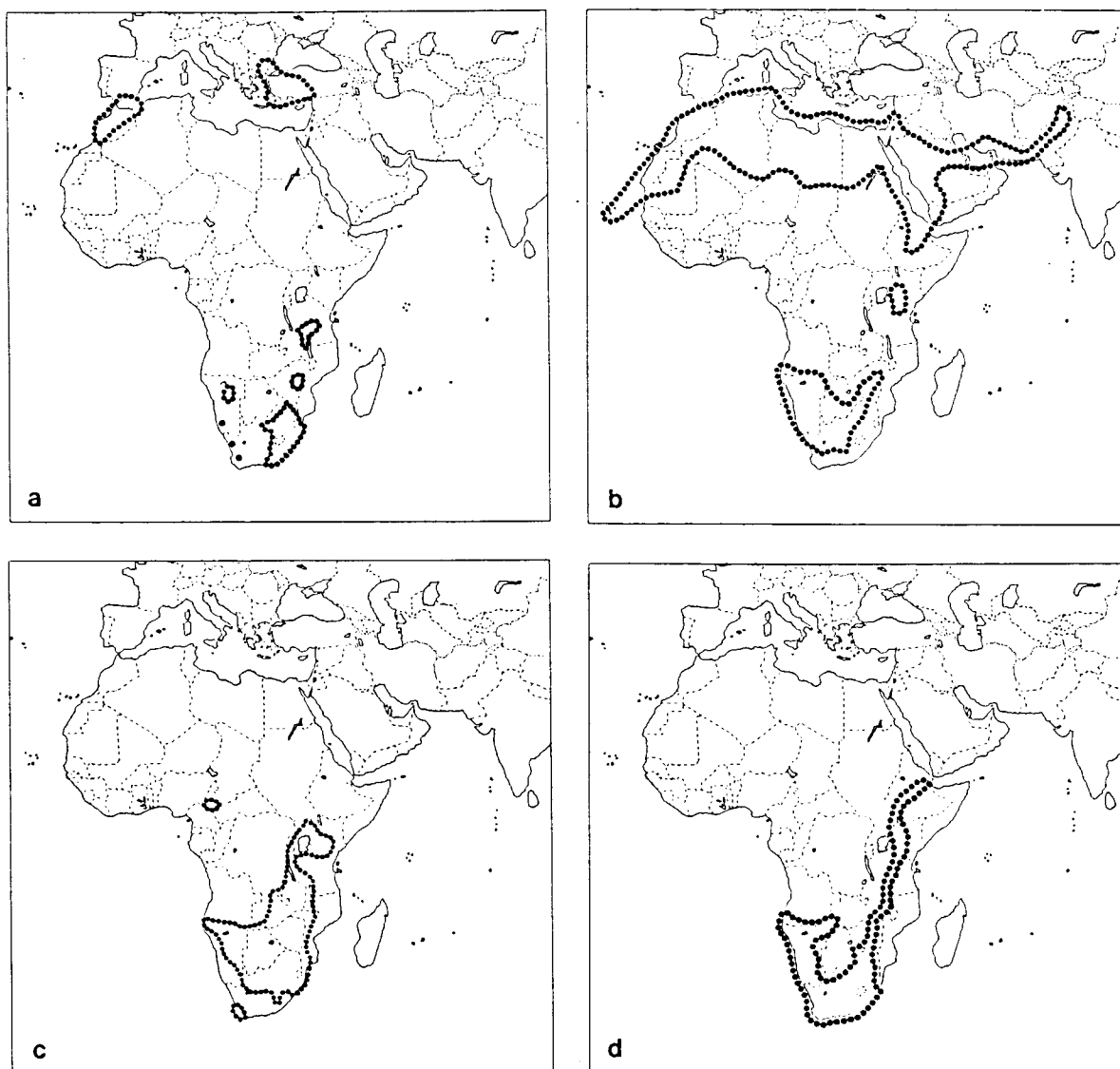


Figure 3.3.3. Approximate geographical distribution of four sections of the genus *Lotoononis*: a, section *Leptis*; b, section *Leobordea*; c, section *Listia*; d, section *Oxydium*.

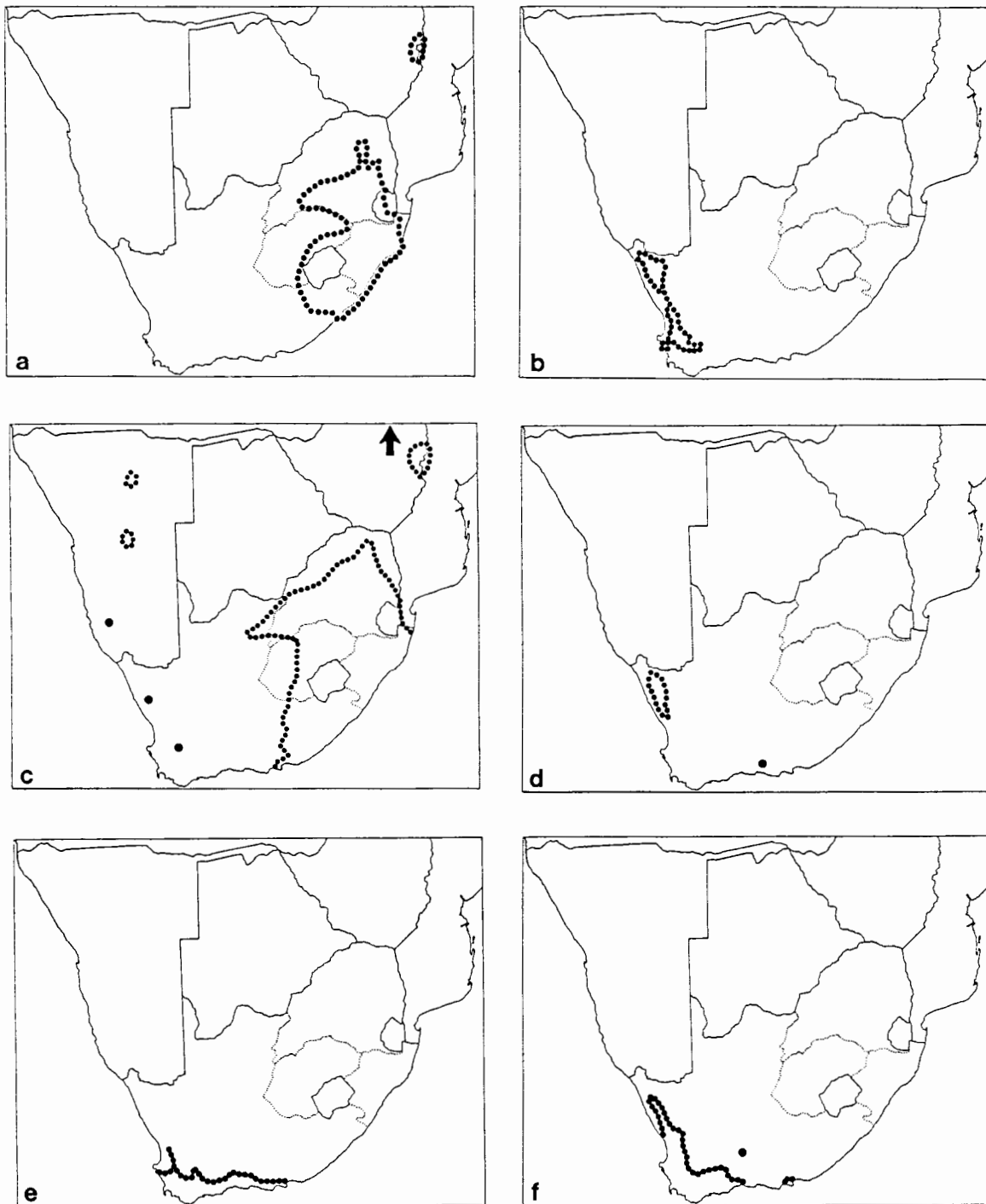


Figure 3.3.4. Approximate geographical distribution of six sections of the genus *Lotoononis* (all except c are restricted to southern Africa): a, section *Lipozygis*; b, section *Synclistus*; c, section *Leptis*; d, section *Digitata*; e, section *Lotoononis*; f, section *Aulacanthus*.

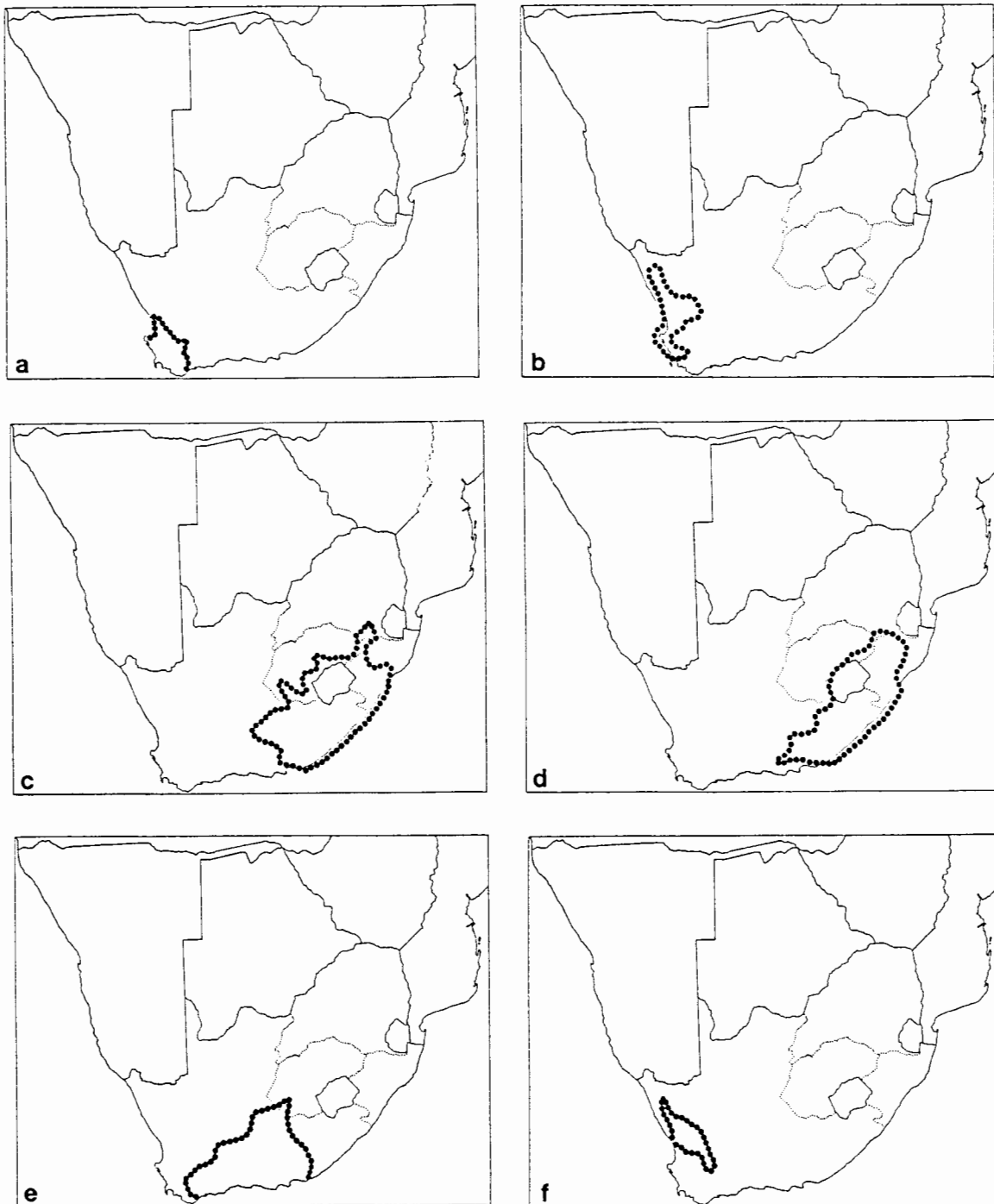


Figure 3.3.5. Approximate geographical distribution of six sections of the genus *Lotoonopsis* (all restricted to southern Africa): a, section *Polylobium*; b, section *Euchlora*; c, section *Krebsia*; d, section *Buchenroedera*; e, section *Cleistogama*; f, section *Monocarpa*.

(Figure 3.3.4a), Krebsia (Figure 3.3.5c) and Buchenroedera (Figure 3.3.5d). The section Leptis shows a similar distribution pattern in southern Africa (Figure 3.3.4c), with only four species present in the western part of the subcontinent. The remaining sections are all more or less restricted to the Cape Region and Namaqualand. The sections Synclistus (Figure 3.3.4b), Digitata (Figure 3.3.4d), Euchlora (Figure 3.3.5b) and Monocarpa (Figure 3.3.5f) have a north-western distribution in the Cape Province, while the sections Lotononis (Figure 3.3.4e), Aulacanthus (Figure 3.3.4f) and Polylobium (Figure 3.3.5a) are more or less confined to the Cape Region. The distribution of the section Cleistogama extends slightly into the north-eastern and eastern Cape (Figure 3.3.5 e).

For the genus as a whole, 11 centres of endemism could be identified, as shown in Figure 3.3.1. The distribution of endemic species within each of the endemic centres is summarized in Table 3.3.2.

The geographical distribution of the sections in Figures 3.3.3 to 3.3.5 and the patterns of endemism summarized in Table 3.3.2 show that most of the species are very restricted in their distribution and that only a few (mostly annuals) are widely distributed. At the supraspecific level, three areas of endemism are suggested by the maps in Figures 3.3.3 to 3.3.5:

TABLE 3.3.2. REGIONAL ENDEMISM IN THE SECTIONS OF THE GENUS LOTONONIS. THE NUMBER OF ENDEMIC SPECIES IN EACH OF THE ENDEMIC CENTRES IN FIGURE 3.3.1 IS SHOWN. (Distributions which extend slightly outside the endemic centres are indicated by brackets; the monotypic section Euchlora is endemic to the combined area of centres 1 and 2).

SECTION	NUMBER OF ENDEMIC SPECIES										
	ENDEMIC CENTRES (numbered as in Figure 3.3.1)										
	1	2	3	4	5	6	7	8	9	10	11
<u>Listia</u>	1	-	-	(1)	2	-	-	-	-	-	-
<u>Digitata</u>	-	5	-	-	-	-	-	-	-	-	-
<u>Lipozygis</u>	-	-	-	4	-	(1)	-	-	-	-	-
<u>Leptis</u>	1	1	1	-	1	2	-	-	1	4	1
<u>Leobordea</u>	-	-	-	-	-	-	(1)	1	-	-	-
<u>Synclistus</u>	4	3	-	-	-	-	-	-	-	-	-
<u>Oxydium</u>	5	2	1	-	5	-	1	3	-	-	-
<u>Monocarpa</u>	(1)	-	-	-	-	-	-	-	-	-	-
<u>Cleistogama</u>	(1)	-	-	-	-	-	-	-	-	-	-
<u>Euchlora</u>	--1--	-	-	-	-	-	-	-	-	-	-
<u>Polylobium</u>	4	-	-	-	-	-	-	-	-	-	-
<u>Lotononis</u>	11	-	-	-	-	-	-	-	-	-	-
<u>Aulacanthus</u>	10	-	-	-	-	-	-	-	-	-	-
<u>Krebsia</u>	-	-	3	7	-	-	-	-	-	-	-
<u>Buchenroedera</u>	-	-	4	4	-	-	-	-	-	-	-

1. The Cape Region.

Endemic: sections Lotononis and Polylobium.

Subendemic: sections Aulacanthus and Cleistogama.

2. Namaqualand.

Endemic: none of the sections.

Subendemic: section Digitata (only a single locality is known from the south-eastern Cape).

3. The Drakensberg area (including the eastern Cape, Natal and Transvaal).

Endemic: sections Krebsia and Buchenroedera.

Subendemic: sections Leptis and Lipozygis.

A more detailed analysis of endemism is given in Figure 3.3.6. This figure shows the total number of perennial and annual species present in each centre (indicated by "t"), as well as the number of perennials and annuals endemic to each centre (indicated by "e"). For the Cape Region, the phytogeographical centres of Weimarck (1941) and Oliver et al. (1983) were used to determine regional endemism. The approximate boundaries of the endemic centres in southern Africa are shown in Figure 3.3.7. The way in which the endemic centres were established and delimited, is explained below. Some comments are made on the extent to which my endemic centres agree with the phytogeographical centres

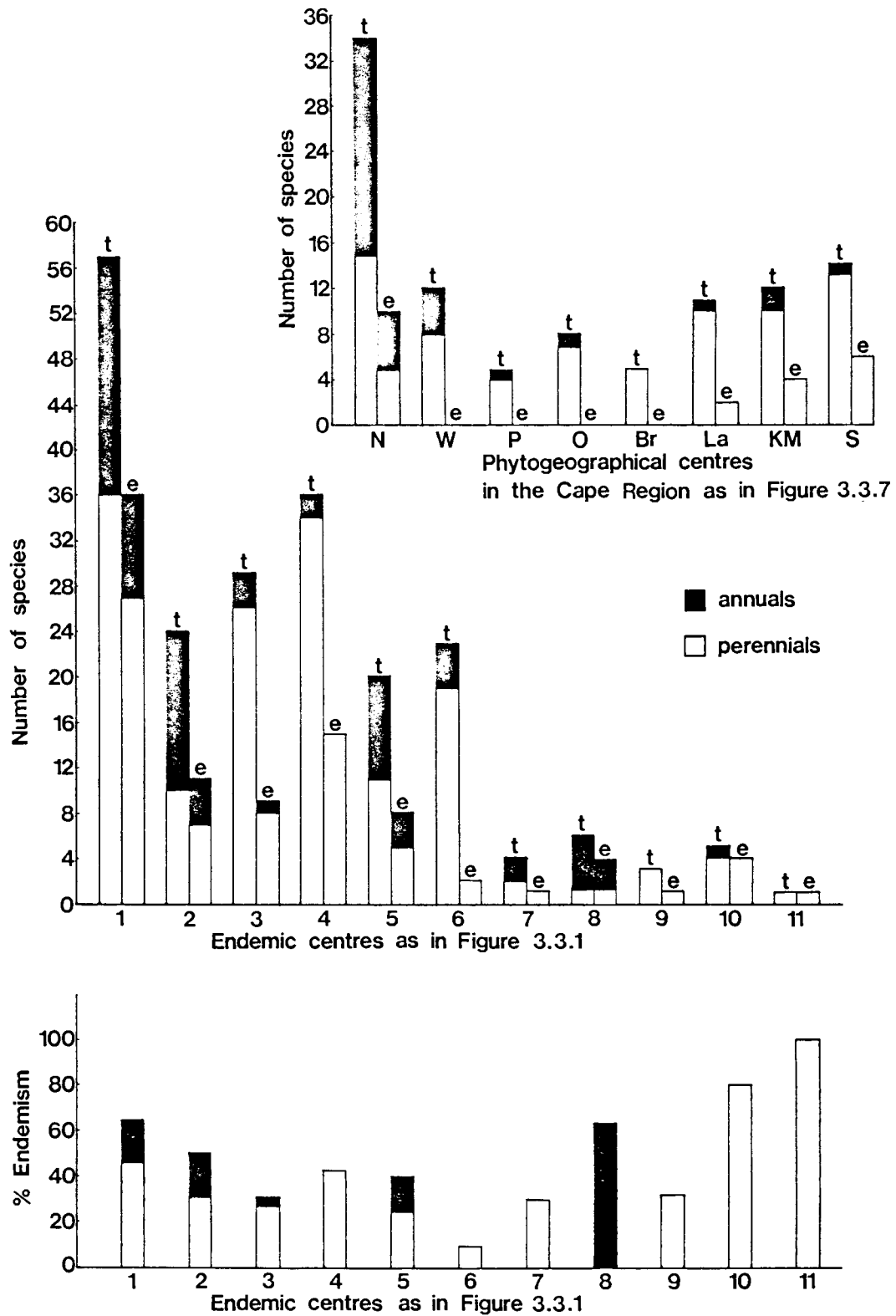


Figure 3.3.6. Endemism in the genus *Lotononis*. Endemic centres are numbered as in Figures 3.3.1 and 3.3.7. The total number of perennial and annual species present in each centre (t) and the number of endemic perennials and annuals (e), are shown.

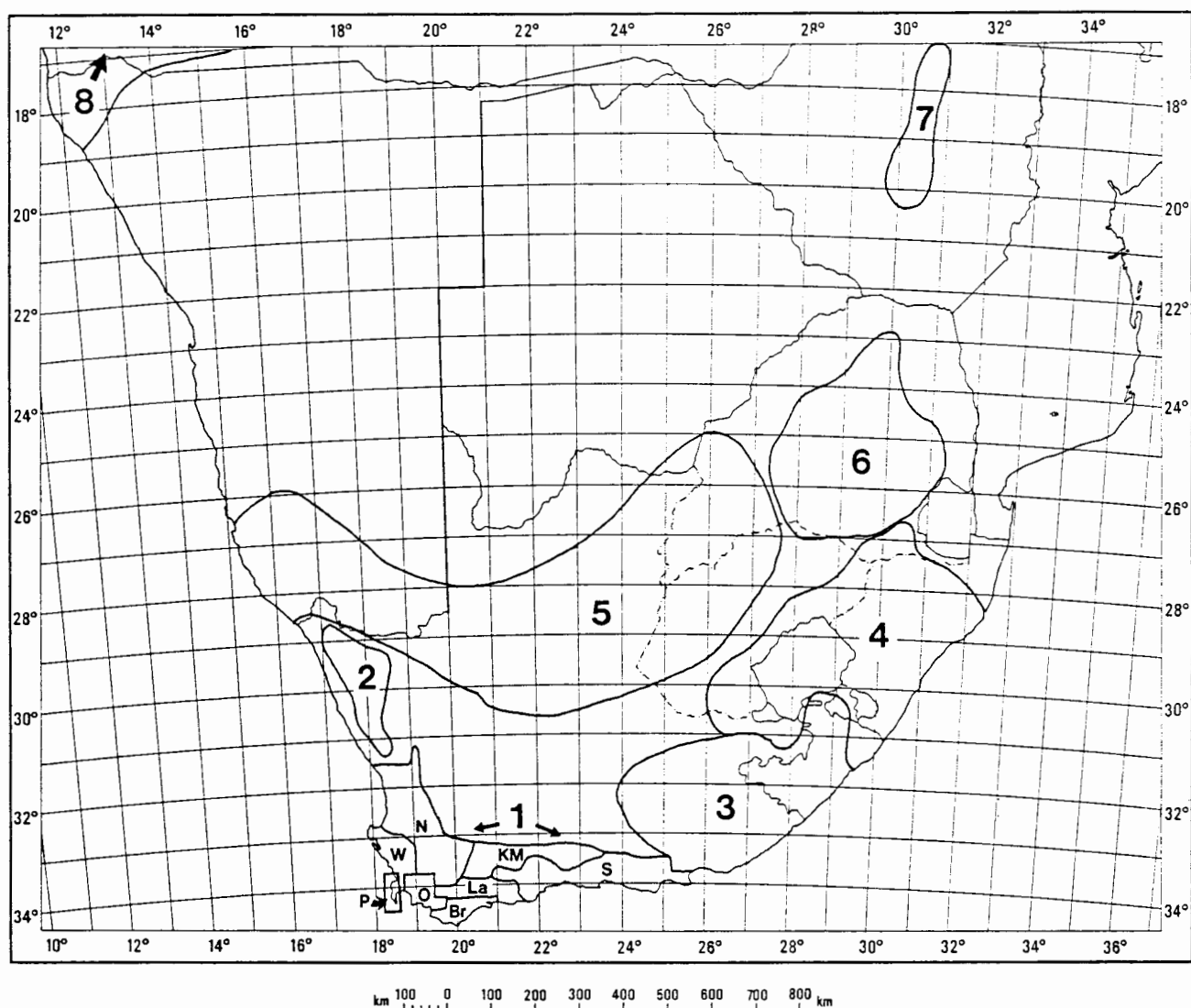


Figure 3.3.7. The approximate boundaries of endemic centres in southern Africa (see discussion in text). 1, Cape Region, the centres of Oliver *et al.* (1983) and Weimarck (1941) are shown: N, Northern; W, West coastal; P, Peninsula; O, South-Western; Br, Bredasdorp; La, Langeberg; KM, Karoo Mountain; S, Southern centre of Oliver *et al.*, but with Weimarck's Langeberg and Karoo Mountain centres excluded. 2, Namaqualand. 3, eastern Cape. 4, Natal-Drakensberg. 5, southern Namibia and Griqualand-West. 6, Transvaal. 7, central Zimbabwe. 8, north-western Namibia and southern Angola (partly).

recognised by Weimarck (1941), Nordenstam (1969) and Oliver et al. (1983). In other words, to what extent they reflect a pattern common to the southern African flora.

Endemic Centre 1. Cape Region.

Endemic taxa:

section Listia - L. macrocarpa

section Leptis - L. esterhuyseana

section Synclistus - L. laticeps

- L. globulosa

- L. longicephala

- L. bolusii

section Oxydium - L. pallens

- L. sabulosa

- L. monophylla

- L. oxyptera

- L. perplexa

section Polylobium - all four species

section Lotononis - all 11 species

section Aulacanthus - 10 species

(all except L. densa and L. azureoides)

The limits of this centre agree exactly with the limits of the Cape Floristic Region as defined by Goldblatt (1978) and the study area used by Oliver *et al.* (1983). Weimarck (1941) included a part of the eastern Cape in his South-eastern Subregion. The western limits of the Cape Region are defined by the distribution of the section Polylobium, and the eastern limits by the distribution of the sections Aulacanthus and Lotononis.

Figure 3.3.6 shows that the Cape Region has the highest endemism. A total of 57 species occur in this centre and 36 of these are endemic. A similar proportion of Cape endemic species is found in the genus Euryops (Nordenstam 1969). Weimarck (1941) and Oliver *et al.* (1983) distinguished several subregions or subcentres within the Cape Region, based on the distributions of "typical" Cape genera. I used the centres of Oliver *et al.* (1983) to determine patterns of endemism within the Cape Region. I did not use their Southern Centre, however, but prefer to use the subdivisions of Weimarck (1941), namely the Langeberg, Karoo-Mountain and Southern-Eastern Centres. It is clear from the histogram in Figure 3.3.6 that Lotononis is not a typical Cape genus. The pattern seems exactly opposite to the one found in Muraltia (Levyns 1954), where endemism decreases from the South-Western Centre towards the north and east. The six centres recognised by Oliver *et al.* (1983) agree with the major edaphic and climatic systems in the south-western and southern Cape (see their Table 1). In Lotononis, edaphic and climatic factors only partly explain endemism in the Cape Region. The highest endemism

is found in the Northern Centre. It is clear from Figure 3.3.6 that high proportions of endemic annuals are found in arid areas, so that seasonal drought may have been an important factor in speciation.

Endemic Centre 2. Namaqualand.

Endemic taxa:

section Digitata - all except L. digitata

section Leptis - L. mollis

section Synclistus - L. oligocephala

- L. polycephala

- L. anthyllopsis

section Oxydium - L. acutiflora

- L. arenicola

This centre agrees with Weimarck's (1941) Kamiesberg Subcentre. The limits are defined here as the distribution area of the section Digitata and the northern part of the distribution area of the section Synclistus. Namaqualand is an important centre for Lotononis. Of the 22 species present in this centre, 11 are endemic. Nordenstam (1969) reported the total absence of endemic species of Euryops in this centre.

The distributions of the sections Synclistus, Aulacanthus and Oxydium agree with the North-Western Interval of Weimarck (1941). This interval, here called the Namaqualand track, is shown in Figure 3.3.9.

Endemic Centre 3. Eastern Cape.

Endemic taxa:

section Leptis - L. prolifera

section Oxydium - L. micrantha

section Krebsia - L. stricta

- L. caerulescens

- L. carnosa

section Buchenroedera - L. trichodes

- L. alpina

- L. holosericea

- L. harveyi

This centre is defined by the distribution areas of the subsection Buchenroedera and three species of the section Krebsia (L. stricta, L. carnosa and L. caerulescens). It is also an important centre in Euryops (Nordenstam 1969).

Several species are shared with the Drakensberg Centre, but remarkably few with the Cape Region. The disjunction agrees with the Kaffrarian Interval of Weimarck (1941) and is shown as part of a southern afromontane track in Figure 3.3.9.

Endemic Centre 4. Natal-Drakensberg.

Endemic taxa:

section Lipozygis - L. procumbens

- L. difformis
- L. sutherlandii
- L. grandis

section Krebsia - L. eriocarpa

- L. sericophylla
- L. jacottetii
- L. galpinii
- L. minor
- L. dichiloides
- L. bachmanniana

section Buchenroedera - L. amajubica

- L. glabrescens
- L. virgata
- L. viminea

The limits of this centre agrees with the distribution areas of seven species of the section Krebsia and four species of the subsection Racemosa of section Buchenroedera. It is an important centre in montane species of Euryops (Nordenstam 1969). Several species of Lotononis have a continuous distribution from the Eastern Cape Centre to the Transvaal Centre, shown as a southern afromontane track in Figure 3.3.9. This larger area agrees exactly with the Drakensbergen Centre of Weimarck (1941). The coastal areas of Natal should perhaps be considered part of a Madagascan Region (Brenan 1978). In Lotononis, however, there is no distinct discontinuity in endemism between high and low altitudes in Natal.

Endemic Centre 5. Southern Namibia and Griqualand-West.

Endemic taxa:

section Listia - L. minima

- L. subulata

section Leptis - L. mirabilis

section Oxydium - L. linearifolia

- L. pachycarpa

- L. burchellii

- L. maculata

- L. rabenaviana

This centre agrees closely with the Gariep centre of Nordenstam (1969). It is defined here as the distribution area of three species of the section Oxydium, namely L. pachycarpa, L. linearifolia and L. maculata. The distributions of the sections Listia, Leptis and Oxydium provide evidence of a Griqualand-West track, as shown in Figure 3.3.9. Discontinuities in the distributions of the sections Listia and Oxydium (clades G and H) are interpreted as evidence of a northern Cape-Drakensberg interval, shown as a Kalahari-Drakensberg track in Figure 3.3.9.

Endemic Centre 6. Transvaal.

Endemic taxa:

section Leptis - L. pariflora
 - L. hirsuta

Weimarck (1941) suggested that high altitude areas of the Transvaal should be included in the Drakensberg Centre. It is indeed true that many species have a continuous distribution in both centres. The Transvaal centre is defined by the distribution areas of L. hirsuta and L. pariflora. This centre agrees with the distribution area of the five species of Euryops included by Nordenstam (1969) in a Highveld Group. It is a transitional centre between the Drakensberg and northern centres, such as Weimarck's (1941) Inyangani Subcentre. The Transvaal Centre is completely isolated from the Inyangani Subcentre by the Limpopo

Interval (Weimarck 1941). The Limpopo Interval (shown as part of an eastern afromontane track in Figure 3.3.9) can be observed in four species of Lotononis, namely L. calycina, L. decumbens, L. eriantha and L. mucronata.

Endemic Centre 7. Central Zimbabwe.

This centre is relatively unimportant in Lotononis and has a single endemic species, L. serpentinicola (section Oxydium). The centre is defined to include the northern and southern parts of the distribution area of L. serpentinicola, i.e., both the northern and southern serpentines in Zimbabwe (Wild 1964).

Endemic Centre 8. North-western Namibia and southern Angola.

Endemic taxa:

section Leobordea - L. newtonii

section Oxydium - L. delicata

- L. pseudodelicata

- L. tenuis

Distribution records for the four species endemic to this centre are incomplete, so that the exact limits are not clear. The isolated position of the centre is obvious from the histograms in Figure 3.3.6. Four of the six species present in this centre are

endemic, and all of them are annuals. Furthermore, the endemic species are morphologically rather isolated within their respective sections.

The Angolan Subcentre of Weimarck (1941) includes the highlands of Angola, of which only one (Huila) forms part of my Endemic Centre 8. Huila is also an important centre in Crotalaria (Polhill 1982). Weimarck (1941) suggested affinities to the east (Inyangani and Drakensberg Centres) and also to the south (the highlands of Namibia) and gave examples of taxa to support these connections. The distribution of the sections Oxydium, Leobordea and Listia (see Figure 3.3.3 and the more accurate maps in Part 5) agrees with the postulated eastern and southern intervals, indicated in Figure 3.3.9 as a southern Angolan track and a Namibian track.

Endemic Centre 9. Nyika Plateau.

The single endemic species of this centre, L. stolzii, is one of only two species of the section Leptis with distinct bracteoles. The sister species, L. decumbens (undoubtedly more derived because it completely lacks bracteoles), occurs in the Inyangani, Transvaal, Drakensberg and eastern Cape Centres. This interesting

afromontane distribution is similar to the distributions of *L. laxa* (section *Oxydium*) and *L. platycarpa* (section *Leobordea*) and is shown in Figure 3.3.9 as an eastern afromontane track.

Weimarck (1941) included the Nyika Plateau in his Rungwe Subcentre and suggested strong connections to the south. This view is supported by the examples given above. Nyika is a centre of major importance in *Crotalaria* (Polhill 1982).

Endemic Centre 10. Morocco and southern Spain

Endemic taxa:

section *Leptis* - *L. tapetiformis*
 - *L. lupinifolia*
 - *L. maroccana*
 - *L. bullonii*

Four species of the section *Leptis* are present in this Centre, and all four are endemic. The discontinuous distribution of the section *Leptis* is interpreted here as evidence of a former more wide-spread pan-African distribution. It is difficult to explain the isolated distributions of the closely related *L. tapetiformis* and *L. mirabilis* (both prostrate woody shrubs) in terms of dispersal and it seems more reasonable to accept that these two species are relicts of a former more wide-spread temperate element. The interval between Centres 10 and 11 and the

distribution of L. platycarpa along the Mediterranean coast (Figure 3.3.3b) suggest a Mediterranean track (shown as "a" in Figure 3.3.9).

Endemic Centre 11. Turkey and south-eastern Bulgaria.

The single species present in this centre, L. genistoides (section Leptis), is the only species absent from the African continent and has its closest relatives in Centre 10. Species of Argyrolobium also occur in both these Mediterranean centres and a detailed analysis of the biogeography of Argyrolobium may lead to a better understanding of the relationship between the two centres.

Regional endemism in Lotononis agrees rather well with the generalized patterns distinguished by Weimarck (1941). Although many species are endemic to the Cape Region, endemism within this region does not show a "typical" Cape pattern as in Aspalathus (Dahlgren 1963b), Muraltia subgenus Muraltia (Levyms 1954) or the taxa analyzed by Oliver *et al.* (1983). There are distinct similarities with the patterns in Muraltia subgenus Psiloclada (Levyms 1954) and particularly those in the genus Euryops (Nordenstam 1969). The latter is also not regarded as a "typical" Cape genus (Nordenstam 1969).

Dispersal clearly does not obscure the distinct geographical patterns that exist for most of the sections. Differences in the approach of dispersalist and cladistic biogeographers were discussed by Humphries and Parenti (1986) who also gave a useful review of the principles and methods of cladistic biogeography. The geographical patterns in Lotononis may be interpreted as evidence of a series of vicariance events, but the exact nature or sequence of these could not be determined.

Area cladograms are shown in Figure 3.3.8. The cladogram for the sections of Lotononis in Figure 3.3.8a is very complex and shows no distinct or logical progression of events. The complex patterns in the widely distributed sections Listia, Leptis and Oxydium (and the absence of a single endemic centre for each) suggested the possibility of convergence in the sense that the area cladograms for these sections may show similarities with that of the genus as a whole. This indeed proved to be the case, as is shown in Figure 3.3.8b to d. There is no evidence of a progression to reduced area cladograms, but there is some pattern in the sections Listia and Leptis.

Figure 3.3.8d shows two components in the area cladogram for the section Listia, namely a Southern Africa Component and a Summer Rainfall Component. The corresponding events may have been: 1, the south-western Cape becomes isolated from the rest of southern Africa, and 2, the north-western Cape (Endemic Centre 5) becomes isolated from Natal. Figure 3.3.8c also has two components,

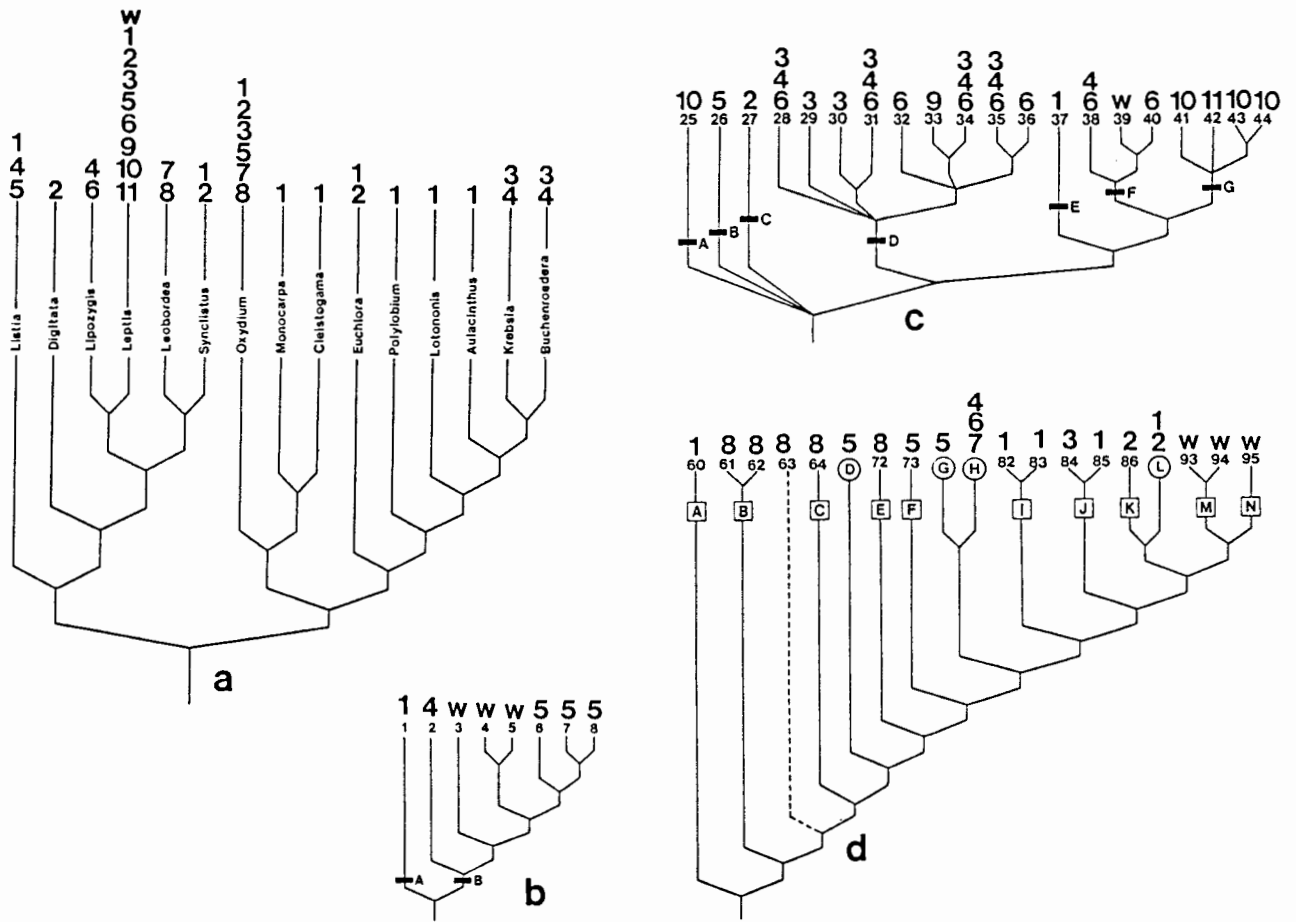


Figure 3.3.8. Area cladograms (topologies from Part 3.2; endemic centres are numbered as in Figure 3.3.1; w indicates widely distributed species): a, sectional cladogram of the genus Lotononis; b, section Listia; c, section Leptis; d, section Oxydium.

namely a Widespread Component and a Southern Afromontane/Northern Component. I suggest the following events: 1, the isolation of the south-western Cape from the southern afromontane area, and 2, the isolation of the southern afromontane area from central Africa (Centre 9) and northern Africa (Centre 10).

The area cladograms, and the relationships between Endemic Centres as highlighted above, indicate a generalized track for the genus Lotononis. The tracks within some of the sections are clearly similar to those of the genus as a whole. Such a generalized track for the genus is shown in Figure 3.3.9. Recurrent parts of the track within the sections are indicated below the figure. Most of these tracks agree with Weimarck's (1941) intervals, as mentioned above. The significance of this pattern is that the same vicariance events seem to account for speciation within some of the sections and the evolution of the sections per se. It is particularly interesting to note that the two large sections (Leptis and Oxydium) occupy virtually all of the suggested generalized track for Lotononis and that some of the tracks are even present in the small section Listia.

The interrelationships between the endemic areas given in Figure 3.3.1 are not explored in detail here, but possible explanations for some of the patterns in the distribution of Lotononis are briefly given below. Other genera of the Papilionoideae may show similar patterns. There are, for example, slight but interesting similarities with the genus Crotalaria (shown to be the sister

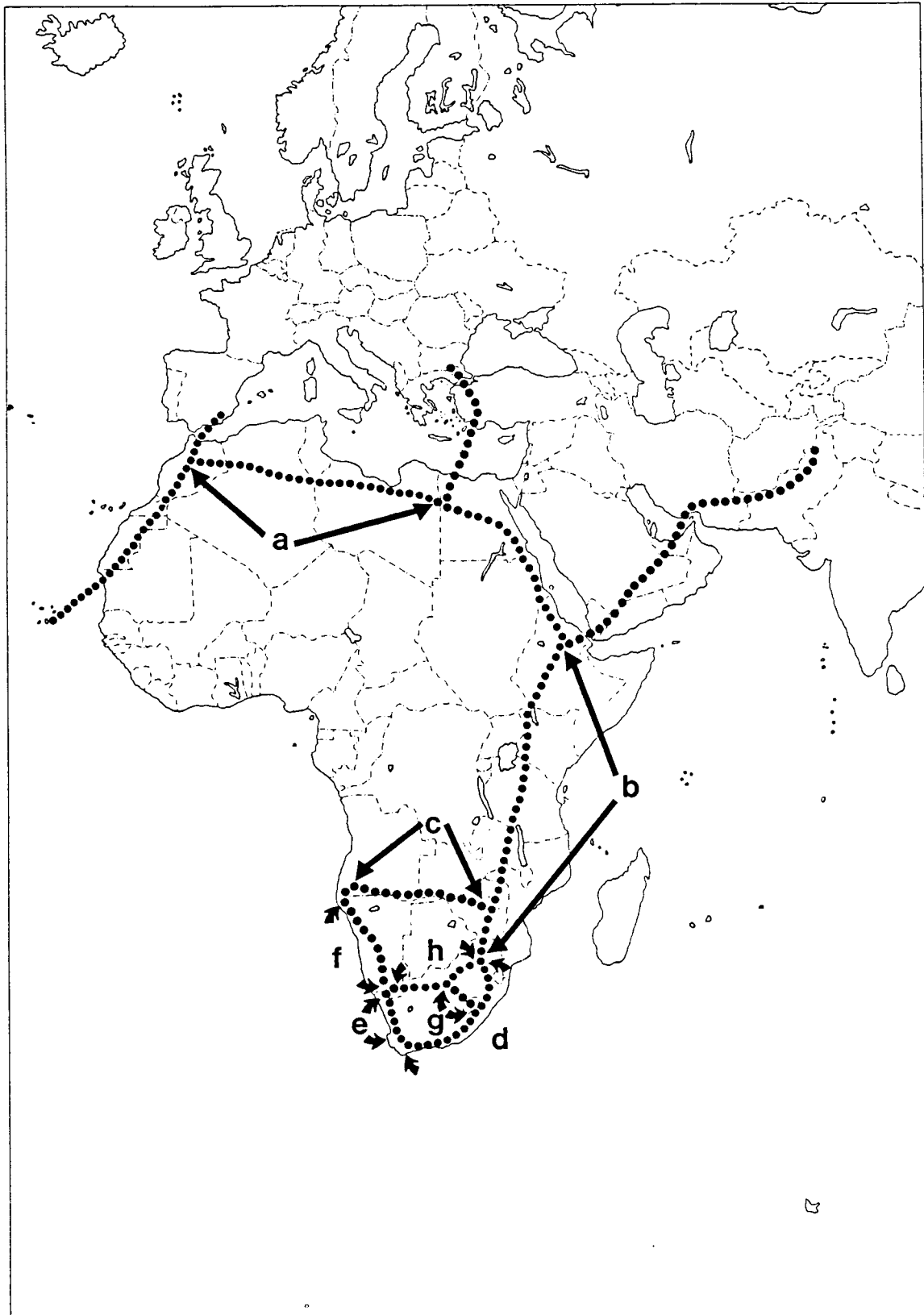


Figure 3.3.9. Distribution track of the genus *Lotononis*. Recurrent parts, suggesting a generalized track, are indicated by arrows: a, Mediterranean track (sections *Leptis* and *Leobordea*); b, eastern afromontane track (sections *Leptis*, *Leobordea*, *Listia* and *Oxydium*); c, southern Angolan track (sections *Listia* and *Oxydium*); d, southern afromontane track (most of the sections); e, Namaqualand track (most of the sections); f, Namibian track (sections *Oxydium* and *Leobordea*); g, Kalahari-Drakensberg track (sections *Listia* and *Oxydium*); h, Griqualand-West track (sections *Oxydium*, *Leptis* and *Leobordea*).

group of Lotononis in Part 2) that suggest the idea of generalized tracks. Two of the endemic centres identified by Polhill (1982) are also minor centres of endemism in Lotononis, namely the Huila and Nyika centres (see his Map 2). According to Polhill (1982), the overall pattern for Crotalaria agrees with the concept of highland refuges and this is clearly also the case in Lotononis. Crotalaria is virtually absent from the Cape Region however, and most of the endemic areas of this genus are situated in central Africa. From a cladistic biogeography point of view, tropical Africa and temperate Africa would form the two clades of an area cladogram for Crotalaria and Lotononis.

Direct migration between Africa, Madagascar and India was last possible about 100 million years ago or perhaps more recently (Raven & Axelrod 1974). It seems reasonable to assume that Lotononis originated well after the separation of Africa from Western Gondwanaland since it is, unlike Crotalaria, not present on Madagascar or in South America. In their review of angiosperm biogeography, Raven and Axelrod (1974) gave a convincing account of the evidence for large-scale extinctions of the African flora during the Neogene and later times (probably mainly during the Miocene and Pliocene). Brennan (1978) concluded, from many years' work on the flora of tropical Africa, that drastic climatic changes in the past are the only means of explaining

discontinuous and unpredictable distribution patterns. He summarized the most likely factors responsible for the biotic poverty in tropical Africa:

1. Elimination of taxa by drought.
2. Increases in altitude, leading to a cooler and drier climate.
3. The development of the Benguela Current, resulting in a dry climate along the west coast of Africa.
4. Major climatic fluctuations in the Quaternary.

Large-scale extinctions would explain the disjunct distribution of the genus Lotononis and its diversity in southern Africa, which is regarded as one of the "survival areas" of the African flora. The geoxylphytic, herbaceous or annual habit of most of the species and their present-day distribution strongly suggest that drought-resistance must have been an important factor in the evolution of the genus. The ability to survive extreme temperatures is another important consideration. The essentially tropical distribution of Crotalaria and the temperate distribution of Lotononis may at least partly be explained by the apparent inability of the former to adapt to low temperatures (Polhill 1982).

If southern Africa or parts thereof were indeed survival centres during cold and dry periods, then one would expect both terminal and basal taxa (sections) in this region. The repeated patterns in the distribution may be ascribed to recurrent disturbances leading to repeated survivals in certain areas. Furthermore,

subsequent speciation would have led to higher concentrations of species in and around these survival centres. This is clearly the case. The remarkable degree of taxic isolation between the Drakensberg area and the south-western Cape is particularly noteworthy. Linder (1983) showed a similar Drakensberg/Cape disjunction in the Disinae (Orchidaceae). Very few species and only four of the sections (Oxydium, Cleistogama, Leptis and Listia) occur in both these areas. The dichotomies in the two main clades of the cladogram for the genus seem to indicate a repeated isolation between a widespread eastern afro-montane group (perhaps representing part of an original pan-African temperate element) and a south-western Cape group, the latter perhaps originally part of a south-western tropical element (see discussion on the section Listia below). Within Oxydium, this pattern is repeated, with an eastern group of perennials (L. laxa and related species) and a south-western Cape group of annuals (L. oxyptera and related species). The only evidence of a colonization of the south-western Cape by the Leptis clade is the presence of L. esterhuyseana (an annual and undoubtedly derived). It is difficult to explain the isolated distributions of L. mollis, L. mirabilis and L. tapetiformis in terms of dispersal and it seems more reasonable to assume that these woody species are the only surviving members of an early temperate element. Leobordea may have attained its very wide distribution by early dispersal along the eastern afro-montane track and a northern origin (from an ancestor similar to L. lupinifolia and L. genistoides) seems likely. Wild (1968) postulated that dispersal

along the east African ridge could have happened before the Limpopo and Zambezi rivers dissected it. *L. platycarpa* probably reached Arabia and Pakistan by an eastward migration. A direct connection between Africa and Eurasia was re-established some 17 million years BP (Raven & Axelrod 1974).

In southern Africa, the sections and the endemic areas are arranged in a wide circle, more or less following the marginal areas of the Great Escarpment. The geomorphic evolution of southern Africa has been reviewed by Partridge and Maud (1987), who give an excellent account of erosion cycles, successive uplifts and changes in drainage patterns. These events must have had significant effects on the biogeography of *Lotononis* and may provide feasible explanations for extant distribution patterns. The distribution of the section *Listia* for example, may be ascribed to a second major uplift at the end of the Pliocene, which raised the eastern parts of the sub-continent by as much as 900 m (Partridge & Maud 1987). The resultant dry southeastern interior probably resulted in the isolation of the terminal part of the *Listia* clade (*L. minima*, *L. subulata* and *L. marlothii*) along the northern parts of the Griqualand-Transvaal axis. A similar pattern is found in the section *Oxydium* (clades F, G and H in Figure 3.3.8d). An element of the section *Listia* in the south-western Cape (perhaps similar to *L. macrocarpa* or *L. serpens*) may have given origin to the south-western Cape- and Drakensberg-endemic sections *Aulacanthus*, *Lotononis*, *Polylobium*, *Euchlora*, *Krebsia* and *Buchenroedera*. *L. macrocarpa*

comes very close to what I would imagine as a likely ancestor for the Polylobium/Buchenroedera clade. This species has not been collected in recent years so that some important taxonomic information (such as the chromosome number) is not yet available. Listia is an interesting section, because it shows a higher diversity in the Kalahari region than in the Cape or Drakensberg regions (only a single species endemic to each of the latter areas). This section is undoubtedly one of the basal groups of the genus and the only one with an essentially tropical distribution (see Figure 3.3.4c). All the species except L. macrocarpa are invariably associated with wet or seasonally wet habitats, even in the dry northern Cape. Listia may be the only surviving taxon of a tropical element -- the erosion pattern of the central interior of southern Africa is an ancient one even though the Orange River had migrated northwards from its Cretaceous position on at least two occasions (Partridge & Maud 1987). It may be interesting to see if other evidence supports the idea of the Kalahari region as a survival centre for tropical elements. It does, for example, represent a minor endemic centre for an element of the section Geniculatae of Crotalaria (Polhill 1982).

A large number of species is present in the Cape and Drakensberg endemic centres and all the sections of the Euchlora/Buchenroedera clade are endemic to these regions. The large degree of diversification may be due to ecological and climatic gradients. A discontinuity between the Cape and Drakensberg areas

of endemism appears to be a very significant factor in the evolutionary history of the sections which have a chromosome base number of $x = 7$. A possible explanation, as mentioned above, lies in the dramatic Pliocene uplift of the eastern parts of the subcontinent along the Ciskei-Swaziland axis, which varied from 600 to 900 m (Partridge & Maud 1987). Uplift in the southern Cape was only 100 m or less. These late Tertiary disturbances coincided with an equally dramatic phase of very strong cooling which resulted in mass extinctions of fauna and flora around 2,5 million years ago (Preston-Whyte & Tyson 1988). The uplift in the eastern region may have provided a survival centre which was (and still is) climatically different from the Cape Region, leading to an isolation of the eastern groups (Krebsia and Buchenroedera) from the southern groups (Aulacanthus, Lotononis, Polylobium and Euchlora). A similar but minor discontinuity seems to occur between the north-western limits of the Cape Region and Namaqualand, but many annuals and even perennials (species of Aulacanthus, for example) have a continuous distribution along the western coastal parts of the Cape Province.

Lotononis is an interesting example of a genus where Cape (fynbos) elements only partly account for the high species diversity in southern Africa as a whole. It is suggested that the evolutionary history of the genus reflects the dramatic climatic changes in the African continent during the Neogene and more particularly, the increased aridity during the Pliocene. It is not clear where the centre of origin of the genus is located. The

presence of a few species of the section Leptis in the Mediterranean region and in central Africa is considered to be relictual rather than a result of dispersal or migration. It is also suggested that a southern origin, with secondary diversification towards the north, may be true for some groups but that this is unacceptable as a general pattern. The diversity in habit clearly indicates adaptations to regional climatic changes, so that the distinct biogeographic patterns in southern Africa are probably closely linked to the geomorphic evolution of the subcontinent.

PART 4

TAXONOMIC HISTORY

The early taxonomic history of the species presently included in Lotononis reflects the uncertainty that existed about generic concepts. Species have been described under various generic names, involving several genera of the tribe Crotalarieae and even genera from other tribes. The classification and nomenclature reached stability only when Bentham (1843) combined a number of smaller genera into a much enlarged generic concept.

All the species of Lotononis described or listed up to 1825 and their correct names or current status are given in Table 4.1. Only a few species were known in the eighteenth century, so that the nomenclature and typification of the early names do not present much difficulty. The first species of Lotononis was named by Linnaeus (1759) in the Systema naturae ed. 10 as Lotus prostratus. A detailed description was given in the second edition of Species Plantarum (Linnaeus 1763) and this work usually provides the information relevant for the typification of names that appear in the Systema but not in Species Plantarum of 1753 (Baum 1968). Bergius (1767) described two new species from the Grubb collection (see Gunn & Codd, 1981) under the generic name Ononis L. Linnaeus's Mantissa plantarum altera of 1771 included two new species and two new combinations under three

TABLE 4.1. LIST OF LOTONONIS SPECIES DESCRIBED BY VARIOUS AUTHORS DURING THE PERIOD 1759 TO 1825.

AUTHOR	PUBLICATION AND DATE	SPECIES DESCRIBED OR LISTED	CURRENT STATUS (see footnotes)
Linnaeus	<u>Systema naturae</u> ed. 10 (1759)	<u>Lotus prostratus</u> L.	1
Linnaeus	<u>Species Plantarum</u> ed. 2 (1763)	<u>Lotus prostratus</u> L.	1
Bergius	<u>Descriptiones plantarum ex Capite Bonae Spei</u> (1767)	<u>Ononis involucrata</u> Berg. <u>Q. parviflora</u> Berg.	2 3
Linnaeus	<u>Mantissa plantarum altera</u> (1771)	<u>Aspalathus laxata</u> L. <u>Anthyllis involucrata</u> (Berg.) L. <u>Ononis prostrata</u> (L.) L. <u>Q. umbellata</u> L.	2 2 1 4
Linnaeus fil.	<u>Supplementum plantarum</u> (1782)	<u>Ononis involucrata</u> (Berg.) L.f.	5
Thunberg	<u>Prodromus plantarum capensium</u> (1800); <u>Flora capensis</u> (1823)	<u>Ononis hirsuta</u> Thunb. <u>Q. parviflora</u> Berg. <u>Q. villosa</u> Thunb. <u>Q. heterophylla</u> Thunb. <u>Q. prostrata</u> (L.) L. <u>Q. decumbens</u> Thunb. <u>Q. elongata</u> Thunb. <u>Q. micranthus</u> Thunb. <u>Q. involucrata</u> Berg. <u>Q. umbellata</u> L. <u>Q. secunda</u> Thunb. <u>Q. strigosa</u> Thunb. <u>Q. glabra</u> Thunb. <u>Q. quinata</u> Thunb. <u>Crotalaria villosa</u> Thunb. <u>Lebeckia densa</u> Thunb.	6 3 7 1 1 8 9 10 5 5 5 4 11 12 6 13
De Candolle	<u>Prodromus systematis regni vegetabilis</u> 2 (1825)	All <u>Ononis</u> spp. of Thunberg <u>Ononis anthyllodes</u> DC.	4

1, Lotononis prostrata (L.) Benth.; 2, L. involucrata (Berg.) Benth. subsp. involucrata; 3, L. parviflora (Berg.) D. Dietr.; 4, L. umbellata (L.) Benth.; 5, L. involucrata (Berg.) Benth. subsp. peduncularis (E. Mey.) B-E. van Wyk; 6, L. serpens (E. Mey.) Dahlg.; 7, L. azurea (Eckl. & Zeyh.) Benth.; 8, L. decumbens (Thunb.) B-E. van Wyk; 9, L. elongata (Thunb.) D. Dietr.; 10, L. rostrata Benth.; 11, L. glabra (Thunb.) D. Dietr.; 12, L. quinata (Thunb.) Benth.; 13, L. densa (Thunb.) Harv.

different genera. Thunberg (1800, 1823), who used his own rich collection of Cape legumes, added several new species. De Candolle (1825, 1826) made the first significant contribution towards the establishment of a generic concept. He included all the species then known in a newly described section, Ononis section Lotononis DC., and expressed the view that his section should be recognised as a distinct genus when more information becomes available.

Many new species were included in extensive collections by Ecklon and Zeyher and Drège and several new genera were described to accommodate them. The present infrageneric classification [and subsequent revisions by Harvey (1862) and Dümmer (1913)] was based largely on these rich herbarium collections. In the following discussions on the locality of type specimens, I am referring only to the legume literature. It should be noted that type specimens of other families are located in different herbaria. Comprehensive taxonomic accounts were published by Ecklon and Zeyher (1836) and Meyer (1832, 1836). The latter used early collections of Ecklon for the 1832 publication of Plantae Ecklonianae and the rich collections of Drège for the 1836 treatment. The second part of Ecklon and Zeyher's Enumeratio plantarum (Jan. 1836) has priority over the Commentariorum of Meyer (Feb. or later, 1836) (see Stafleu & Cowan 1976, 1981). A detailed summary of all the relevant genera and species described by Ecklon and Zeyher (1836) and Meyer (1832, 1836) is given in Table 4.2.

TABLE 4.2. LIST OF GENERA, SECTIONS AND SPECIES DESCRIBED BY MEYER (1832), ECKLON & ZEYHER (1836) AND MEYER (1836) THAT WERE LATER INCLUDED IN A BROADENED CONCEPT OF LOTONONIS.

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GENERA/SECTIONS DESCRIBED OR LISTED	SPECIES OF <u>LOTONONIS</u> <u>SENSU LATO</u> INCLUDED	PRESENT STATUS OR POSITION
-----	-----	-----
Meyer (1832):		
<u>Crotalaria</u> L.	9	various sections
Ecklon & Zeyher (Jan. 1836):		
<u>Euchlora</u> Eckl. & Zeyh. (new genus)	1	section <u>Euchlora</u>
<u>Crotalaria</u> L.	2	sections <u>Oxydium</u> and <u>Lotononis</u>
<u>Leptis</u> E. Mey. ex Eckl. & Zeyh. (new genus*)	5	section <u>Leptis</u>
<u>Lotononis</u> (DC.) Eckl. & Zeyh. (new genus**)	14	various sections, mostly <u>Lotononis</u>
<u>Krebsia</u> Eckl. & Zeyh. (new genus)	4	section <u>Krebsia</u>
<u>Polylobium</u> Eckl. & Zeyh. (new genus)	12	various sections
<u>Buchenroedera</u> Eckl. & Zeyh. (new genus)	5	section <u>Buchenroedera</u>
Meyer (Feb. or later, 1836):		
<u>Crotalaria</u> L.	7	section <u>Oxydium</u>
<u>Aspalathus</u> L.	7	various sections
<u>Microtropis</u> E. Mey. (new genus)	1	section <u>Euchlora</u>
<u>Telina</u> E. Mey. (new genus)		
section 1. <u>Cytisoidae</u> E. Mey. (new section)	3	section <u>Krebsia</u>
section 2. <u>Brachypodae</u> E. Mey. (new section)	2	section <u>Krebsia</u>
section 3. <u>Chasmoneae</u> E. Mey. (new section)	6	section <u>Lotononis</u>
<u>Aulacanthus</u> E. Mey. (new genus)	2	section <u>Aulacanthus</u>
<u>Lipozygia</u> E. Mey. (new genus)		
section 1. (not named)	1	section <u>Aulacanthus</u>
section 2. (not named)	2	sections <u>Oxydium</u> and <u>Digitata</u>
section 3. (not named)	6	sections <u>Leptis</u> , <u>Oxydium</u> and <u>Cleistogama</u>
section 4. (not named)	4	sections <u>Leptis</u> , <u>Lipozygia</u> and <u>Synclistus</u>
section 5. (not named)	3	sections <u>Polylobium</u> and <u>Leptis</u>
<u>Listia</u> E. Mey. (new genus)	1	section <u>Listia</u>
<u>Capnitis</u> E. Mey. (new genus)	2	section <u>Leobordea</u>

*Based on the genus Leptis E. Mey. ined.

**Based on Ononis section Lotononis DC.

The typification of names in Meyer's Plantae Ecklonianae is relatively easy even though no duplicates seem to exist. The collection is conserved in the Stockholm Museum of Natural History (S) and is remarkably complete. The specimens often have a characteristic label (Figure 4.1a) and specimens with these labels can be accepted as part of Ecklon's early collection. The handwriting has been ascribed to Ecklon or Steudel (Gunn & Codd 1981), but according to Nordenstam (pers. comm.), the writer is unknown. All the names in Plantae Ecklonianae are therefore lectotypified by material in the Stockholm herbarium. Annotations by Meyer himself on many of the sheets ("mihi", see Figure 4.1b) testifies to the authenticity of the material.

Nordenstam (1980) gave useful historic information on the Ecklon and Zeyher collection in the Stockholm. This collection is by far the most complete set of specimens and should therefore be consulted when typifying names in Ecklon and Zeyher's (1836) Enumeratio plantarum. Some specimens which may be part of the top set are also conserved in the South African Museum herbarium (presently housed in the Compton herbarium at Kirstenbosch). The handwriting of Ecklon and Zeyher appears on a number of these sheets (for examples see Nordenstam 1980 and Gunn & Codd 1981). Ecklon and Zeyher names should be lectotypified with caution, because their numbers often include mixed collections. Another important consideration is that some of the original printed labels [cut from copies of the original publication that was specially printed on one side of the page (Gunn & Codd 1981)]

Crotalaria truncata E.M.
Oenonis umbellata L?

Frage y rubra Thellus an ...
 Laysa von ... August:

E. Meyer 1829 / 1858.

a

Crotalaria prolifera mibi
Oenonis decumbens Th.

var. a. foliis floribusque pubescentibus
 'b. " " " pubescentibus

9/2 *Oenonis umbellata*. Benth.

In locis humidis ad ped. mont.
 Tabulari. Dec.

100. *Oenonis gracilis*. Benth.

In Hamabuge (Clanwillim).
 Nov.

d

b

c

1295. *KREBSIA divaricata* — foliis trifoliolatis subternis, foliolis cuneato-oblongis mucronatis subcomplicatis incanis patentibus vix puberulis, pedunculis oppositifoliis 1 floris subterminalibus flores aequantibus, stipulis foliiformibus subsolitariis petiolo brevioribus, leguminibus 7 spermis erectis calycibusque adpresse-puberulis. — In lapidosis (altit. IV) laterum montium prope „Silo" ad flumen „Klipplaatrivier" (Tambukiland). Nov. — Frutex 2-3 pedalis ramosissimus parce florens. Rami rigidi glabri. Ramuli tenues adpresse puberuli. Folia 2-4 lin. longa. Petioli folium adaequant v. breviores.

Aulacanthus gracilis E.H.G.

e

Telina eriocarpa E.H.G.

Lotononis maculata Dümmer

RD. IV. 12. Type

L. Bolusii, Dümmer.

Type

g

Crotalaria Ecklonii H.

(non *C. stenophylla*, Vog.)

f

HARVEY ET SONDER; FLORA CAPENSIS.

Lotononis pungens.
 var.

f

W. H. H. determinavit.

Figure 4.1. Examples of labels and handwritings on specimens of *Lotononis*: a, label of early Ecklon collection in S (handwriting unknown); b, handwriting of Meyer; c, an example of the printed labels on Ecklon & Zeyher type specimens (these were cut from the *Enumeratio*); d, examples of the labels (blue paper) with which Pappe replaced original Ecklon & Zeyher labels in SAM; e, labels of the Drège collection (the handwriting is his); f, examples of the handwriting of Harvey; g, examples of the handwriting of Dümmer.

were removed from the sheets in the SAM collection. Many of Zeyher's original specimens were acquired by Pappe (and later formed the nucleus of the SAM collection) and he unfortunately replaced the original labels with his own. An example of the original Enumeratio plantarum label and two examples of Pappe's labels (usually on blue paper, the handwriting is that of Pappe) is shown in Figure 4.1c and d.

Meyer's personal herbarium was largely destroyed during World War II but fortunately, many duplicates of the Drège collection had been distributed to other herbaria. The most complete set of original sheets is in the Paris herbarium (Gunn & Codd 1981, Schrire 1989). Good duplicates can be found in K, MO, S and TCD, so that most of the species in Meyer's (1836) Commentariorum could be lectotypified without any difficulty. For a few of the names (mostly synonyms), no authentic material could be found and I am not typifying these names until the Paris collection can be studied. Examples of the characteristic labels under which the Drège duplicates were distributed, are shown in Figure 4.1e.

Apart from the important revision of Bentham (1843), a number of relatively minor contributions were made by several workers during the period 1826 to 1847. These publications mostly involved name changes and new combinations rather than original descriptions (Walpers 1839, 1842, 1845, 1852; Steudel 1840, 1841; Presl 1845; Dietrich 1847). Dietrich's treatment of several species presently included in Lotononis has apparently been

overlooked by Harvey (1862) and Dümmer (1913), so that some name changes have to be made. Bentham (1843) did not study the Thunberg collection and most of the name changes are necessitated by Dietrich's rather hesitant but effective transfer of most of Thunberg's Ononis species to the genus Lotononis.

The fact that Bentham's basic classification system of the Papilionoideae has persisted (with relatively minor changes) to this day, testifies to his remarkable knowledge of the subfamily. As pointed out by Polhill (1981b), the merits of Bentham's taxonomic categories (in terms of predictivity) usually transcend the inadequacy of his diagnoses. Bentham started his rearrangement of the genera presently included in Lotononis by a short paper in 1837 (published separately under the title "De leguminosarum generibus commentationes" in 1839). It is interesting to note several discrepancies between these early ideas and his final infrageneric treatment of Lotononis in 1843. The original concept of Lotononis (De Candolle 1825, 1826; subsequently raised to generic status by Ecklon & Zeyher 1836) was considerably broadened to include several genera. The genera were treated as sections according to their priority, but the sectional delimitations did not necessarily coincide with the original concepts. Only two of the eight sections did not originate from Ecklon and Zeyher or Meyer, namely Leobordea (a genus described by Delile) and Oxydium (the only new name and totally new concept). Table 4.3 shows the structure of Bentham's infrageneric classification, and also gives a comparison with the

one proposed in Part 5. Bentham retained the monotypic Euchlora Eckl. & Zeyh. (Bentham 1843) and Listia E. Mey. (Bentham 1844) as distinct genera, but noted the similarities with Lotononis. In the case of the genus Listia, he suggested that it should perhaps be included as a section within Lotononis. Buchenroedera was considered to be related to Aspalathus (Bentham 1848) but the similarity with Lotononis was also mentioned. Despite some rearrangements, the sectional classification proposed in Part 5 is rather similar to Bentham's original system.

The latest available comprehensive treatments of Lotononis are the revisions of Harvey (1862) and Dümmer (1913). Harvey's account for the Flora Capensis included a number of new species, described from a large collection of specimens in Dublin. Examples of his handwriting are shown in Figure 4.1f. Species were arranged as in Bentham's system but sectional limits were modified to accommodate newly described species. In Dümmer's (1913) synopsis, several new species were described, virtually all from material in Kew herbarium. Annotations on the type specimens (Figure 4.1g) provide useful guidelines for lectotypification. Many of the new species are no longer considered to be specifically distinct, however. The circumscriptions of some of the sections were further modified and the system became unsatisfactorily artificial. Most of the species with beaked keels for example, were excluded from Lotononis and referred to the genus Crotalaria. New species described by various authors in subsequent years (details are not

TABLE 4.3. THE ORIGINAL INFRAGENERIC CLASSIFICATION SYSTEM OF LOTONONIS AS PROPOSED BY BENTHAM (1843), COMPARED TO THE REVISED SYSTEM IN PART 5.

SYSTEM OF BENTHAM (1843)		REVISED SYSTEM AS PROPOSED IN PART 5	
SECTIONS	NUMBER OF SPECIES	SECTIONS	NUMBER OF SPECIES
(genus <u>Buchenroedera</u>)	7	15. <u>Buchenroedera</u>	11
1. <u>Aulacanthus</u>	3	13. <u>Aulacanthus</u> *	12
2. <u>Krebsia</u>	5	14. <u>Krebsia</u>	12
3. <u>Telina</u>	8	12. <u>Lotononis</u> **	11
4. <u>Polylobium</u>	4	11. <u>Polylobium</u> *	5
(genus <u>Euchlora</u>)	1	10. <u>Euchlora</u>	1
(spp. of <u>Leptis</u>)	2	9. <u>Cleistogama</u> ***	2
(not known)	-	8. <u>Monocarpa</u> ***	3
5. <u>Oxydium</u>	7	7. <u>Oxydium</u> *	36
(spp. of <u>Lipozygis</u>)	2	6. <u>Synclistus</u> ***	9
6. <u>Lipozygis</u>	5	3. <u>Lipozygis</u> *	10
7. <u>Leobordea</u>	3	5. <u>Leobordea</u>	6
8. <u>Leptis</u>	18	4. <u>Leptis</u> *	20
(spp. of <u>Leptis</u>)	1	2. <u>Digitata</u> ***	6
(genus <u>Listia</u>)	1	1. <u>Listia</u> ****	8

*Modified circumscriptions.

**Name change - this section includes the type of the genus.

***Newly described sections.

****Much broadened concept.

given here) have led to a much improved knowledge about relationships within the genus. As a result, Dümmer's synopsis has become very outdated. More recently, the generic limits of Lotononis were slightly broadened to include Euchlora (Dahlgren 1964) and Listia (Polhill 1976). Valuable contributions to the taxonomy of Lotononis also appeared in regional floras, such as the treatments for Namibia (Schreiber 1970), tropical East Africa (Milne-Redhead 1971) and North Africa (Maire 1987).

Recent species lists for southern Africa (Gibbs Russell *et al.* 1987) and for Africa (Lock 1989) show how outdated the nomenclature has become. Of the 104 Lotononis names listed for southern Africa, 29 are placed in synonymy, nine are changed, three are excluded and 56 have to be added. The list for Africa (144 names) includes 39 synonyms and seven illegitimate names. Despite the conservative treatment in Part 5, the number of known species in southern Africa (with Buchenroedera included) now increases to 140, and the number in Africa to 150.

The generic name Lotononis (DC.) Eckl. & Zeyh. (1836) was conserved against the earlier names Amphinomia De Candolle (1825) and Leobordea Delile in Laborde (1830, reprint 1833). A motivated proposal for the long overdue conservation of Lotononis was given by Gillett and Bullock (1957), who also proposed that Lotononis vexillata (E. Mey.) Eckl. & Zeyh. [now Lotononis prostrata (L.)

Benth.] be conserved as the type species. The proposal was accepted unanimously (Rickett 1960) and was adopted by the 10th International Botanical Congress (Lanjouw et al. 1966).

The problem around Amphinomia was first highlighted by Rothmaler (1940) and Janchen (1943). De Candolle (1825) described the genus Amphinomia and included it under his Leguminosae non satis notae. The new genus was based on the description and plate of Connarus decumbens Thunb. [Roem. Arch. Bot. 1,1 (1796)]. Bentham (1865) suspected (from the description and plate) that C. decumbens may be the same species as Lotononis polycephala. Gillett and Bullock (1957) showed that this is not the case and thereby removed the only basis for retaining Amphinomia as a synonym of Lotononis. Amphinomia has been used for a few binomials, often only because the authors believed they were compelled by the rules to do so. The real identity of A. decumbens is still uncertain.

The name Leobordea Delile, based on Lotononis platycarpa, has been used only for a distinct genus and not as a substitute for Lotononis. The concept of Leobordea never included more than a few of the northern species of Lotononis. Bentham (1843) therefore preferred to use the name Lotononis rather than Leobordea for the broad generic concept. For the same reason, Lotononis was conserved against Leobordea (Gillett & Bullock 1957, Rickett 1960).

PART 5

TAXONOMIC TREATMENT OF THE GENUS LOTONONIS

Lotononis (DC.) Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 176 (Jan. 1836); Benth. in Hook., Lond. J. Bot. 2: 594 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 47 (1862); Benth. & Hook. f., Gen. Pl. 1: 476 (1865); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 275 (1913); Burt Davy, Man. pl. Transvaal: 384 (1932); Phill., Gen. S. Afr. Fl. Pl.: 405 (1951); Hutch., Gen. Fl. Pl. 1: 360 (1964); Schreiber in FSWA 60: 76 (1970); Dyer, Gen. S. Afr. Fl. Pl. 1: 249 (1975); Polhill in Bot. Syst. 1: 324 (1976); Polhill in Polhill & Raven, Adv. Leg. Syst. 2(1): 401 (1981), nom. cons. Type species: Lotononis vexillata (E. Mey) Eckl. & Zeyh. (typ. cons.). [now L. prostrata (L.) Benth.].

Ononis section Lotononis DC., Prodr. 2: 166 (1825) & Mém. Lèg. 6: 223 (1826).

Telina E. Mey., Comm. Pl. Afr. Austr. 1(1): 67 (Feb. or later 1836). Lectotype species (designated here): Telina heterophylla (Thunb.) E. Mey. [now Lotononis prostrata (L.) Benth.].

Amphinomia DC., Prodr. 2: 522 (1825); Font Quer & Rothm. in Broteria 9: 149 (1940); Maire in Bull. Soc. Hist. Nat. Afr. Nord 32: 209 (1941); Schreiber in Mitt. Bot. Staatssamm. München 16: 286 (1957); Maire, Fl. Afr. Nord 16: 78 (1987), nom. rej. Type species: Amphinomia decumbens (Thunb.) DC.

Leobordea Del. in Laborde, Voy. Arab. Pêtr.: 86 (1830); Jaub. & Spach in Ann. Sci. Nat. 19: 232 (1843), nom. rej. Type species: Leobordea lotoidea Del. [now Lotononis platycarpa (Viv.) Pic.-Serm.].

Capnitis E. Mey., Comm. Pl. Afr. Austr. 1(1): 81 (Feb. or later 1836). Lectotype species (designated here): Capnitis porrecta (Thunb.) E. Mey. [now Lotononis platycarpa (Viv.) Pic.-Serm.].

Euchlora Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 171 (Jan. 1836); Benth. in Hook., Lond. J. Bot. 2: 470 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 38 (1862); Benth. & Hook. f., Gen. Pl. 1: 475 (1865); Phill., Gen. S. Afr. Fl. Pl.: 404 (1951); Hutch., Gen. Fl. Pl. 1: 346 (1964); Dahlgr. in Bot. Not. 117: 371 (1964). Type species: Euchlora serpens (E. Mey.) Eckl. & Zeyh. [now Lotononis serpens (E. Mey.) Dahlgr.].

Microtropis E. Mey., Comm. Pl. Afr. Austr. 1(1): 65 (Feb. or later 1836). Type species: Microtropis hirsuta (Thunb.) E. Mey. [now Lotononis serpens (E. Mey.) Dahlgr.].

Leptis E. Mey. ex Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 174 (Jan. 1836); Benth. in Ann. Wien. Mus. 2: 142 (1839); Steud., Nom. Bot. 2(2): 29 (1841); Walp., Rep. Bot. Syst. 1: 619 (1842); D. Dietr., Syn. pl. 4: 959 (1847). Lectotype species (designated here): Leptis debilis Eckl. & Zeyh. [now Lotononis prolifera (E. Mey.) B-E. van Wyk].

Krebsia Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 179 (Jan. 1836); Benth. in Ann. Wien. Mus. 2: 142 (1839); Steud., Nom. Bot. 2(1): 850 (1840); D. Dietr., Syn. pl. 4: 963 (1847). Lectotype species (designated here): Krebsia stricta Eckl. & Zeyh. [now Lotononis stricta (Eckl. & Zeyh.) B-E. van Wyk].

Polylobium Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 180 (Jan. 1836); Benth. in Ann. Wien. Mus. 2: 142 (1839); Steud., Nom. Bot. 2(2): 377 (1841); D. Dietr., Syn. pl. 4: 961 (1847). Lectotype species (designated here): Polylobium tenuifolium Eckl. & Zeyh. [now Lotononis involucrata (Berg.) Benth.].

Buchenroedera Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 194 (Jan. 1836); Benth. in Lond. J. Bot. 7(4): 580 (1848); Harv. in Harv. & Sond., Fl. Cap. 2: 92 (1862); Benth. & Hook. f., Gen. Pl. 1: 478 (1865); Phill., Gen. S. Afr. Fl. Pl.: 407 (1951); Hutch., Gen. Fl. Pl. 1: 361 (1964); Dyer, Gen. S. Afr. Fl. Pl. 1: 251 (1975); Polhill in Bot. Syst. 1: 324 (1976); Polhill in Polhill & Raven, Adv. Leg. Syst. 2(1): 401 (1981); Edwards & Getliffe Norris in S. Afr. J. Bot. 55 (1989), synon. nov. Lectotype species (designated by Hutchinson 1964): Buchenroedera alpina Eckl. & Zeyh. [now Lotononis alpina (Eckl. & Zeyh.) B-E. van Wyk].

Aulacanthus E. Mey., Comm. Pl. Afr. Austr. 1(1): 156 (Feb. or later 1836). Lectotype species (designated here): Aulacanthus gracilis E. Mey. [now Lotononis densa (Thunb.) Harv.].

Lipozygis E. Mey., Comm. Pl. Afr. Austr. 1(1): 76 (Feb. or later 1836). Lectotype species (designated here): Lipozygis corymbosa E. Mey. [now Lotononis corymbosa (E. Mey.) Benth.].

Listia E. Mey., Comm. Pl. Afr. Austr. 1(1): 80 (Feb. or later 1836); Benth. in Hook., Lond. J. Bot. 3: 338 (1844); Harv. in Harv. & Sond., Fl. Cap. 2: 66 (1862); Benth. & Hook. f., Gen. Pl. 1: 476 (1865); Phill., Gen. S. Afr. Fl. Pl.: 405 (1951); Hutch., Gen. Fl. Pl. 1: 362 (1964); Schreiber in FSWA 60: 73 (1970). Dyer, Gen. S. Afr. Fl. Pl. 1: 250 (1975); Polhill in Bot. Syst. 1: 324 (1976). Type species: Listia heterophylla E. Mey. [now Lotononis listii Polhill].

Annuals, perennial suffrutescent herbs or small shrubs. Leaves alternate or rarely opposite, digitately 3(--8)-foliolate, rarely simple or 1-foliolate, petiolate. Stipules small or foliaceous, usually single at each node, less commonly paired or absent, rarely digitate. Inflorescences terminal, leaf-opposed or rarely terminal on short axillary branches. Flowers occasionally cleistogamous, usually yellow (often partly orange, pink or white) or blue, rarely pink, pale purple or white, in racemes or heads, often fascicled or solitary; peduncle variable in length; pedicel usually short, sometimes very long or totally absent; bract invariably present, inserted at the base of the pedicel or sometimes halfway towards the calyx, usually very small or occasionally large and foliaceous; paired bracteoles almost

invariably absent, usually small when present. Calyx usually with the lateral and upper lobes joined in pairs on either side, sometimes with 5 subequal lobes, the upper 2 lobes occasionally wider than the lateral lobes, the carinal lobe sometimes narrower or shorter than the lateral and upper lobes. Standard hairy or glabrous outside, the lamina usually ovate to oblong, occasionally panduriform, rarely linear, very rarely with lobes near the attachment of the claw; the claw usually narrow, sometimes much dilated at the base to form a cupular structure, rarely with protuberant callosities. Wing petals hairy or glabrous, shorter or longer than the keel, sculpturing rarely absent. Keel hairy or glabrous, with apex rounded, obtuse, acute or less often beaked. Stamens fused into a sheath invariably open along on the upper (vexillary) side; anthers markedly dimorphic, 4 oblong to linear and basifixed, 5 ovate and dorsifixed, the basifixed ones usually very much larger than the dorsifixed ones, carinal anther usually intermediate in size and shape, sometimes similar to the dorsifixed ones, rarely similar to the basifixed ones. Pistil subsessile or rarely long-stipitate, linear, oblong or ovate; style curved up and tapering, occasionally hairy towards the base; stigma small and capitate, rarely directed slightly to the front; ovules usually numerous, rarely 1 or 2. Pods subsessile or rarely long-stipitate, flat or turgid, linear to oblong or ovate, sometimes falcate in lateral view, rarely folded and twisted, dehiscent or tardily dehiscent, sometimes indehiscent, usually with wart-like protuberances along the upper suture, usually many-seeded; funicles often exceptionally long.

Seeds without an aril, variable in size, less than 1 mm to more than 4 mm long, suborbicular to obliquely cordiform, rarely somewhat angular, radicular lobe often prominent, hilar area sunken, testa surface smooth or more often sparsely to densely tuberculate.

About 151 species, with 145 in southern Africa and a few extending to east tropical Africa, the Mediterranean and Pakistan.

The generic concept of Lotononis is broadened here to include Buchenroedera, as was tentatively suggested by Polhill (1976, 1981a). The ovate shape of the pods is the only reliable diagnostic character that could be found for Buchenroedera. Polhill (1976) correctly pointed out that excessive weighting of fruit characters at the generic level often leads to artificial groups. Morphological studies (reported in Part 3) have shown similarities in macroscopic and cryptic characters between Buchenroedera and the section Krebsia. Evidence from alkaloids and cyanogenic glucosides (Van Wyk & Verdoorn 1988, 1989c; Van Wyk 1989n; Van Wyk & Whitehead 1989) and chromosome numbers (Van Wyk & Schutte 1988a) have shown that the two groups are more than just superficially similar. It is clear that Buchenroedera is more closely related to Krebsia, than Krebsia is to some other sections of Lotononis. Therefore the exclusion of Buchenroedera

from Lotononis would make the latter paraphyletic. This then would lower the predictive and heuristic value of the classification.

Lotononis is distinguished from Crotalaria by the glabrous upper part of the style, which is not differentiated from the lower part, the intermediate size of the carinal anther, the general absence of bracteoles, the verrucose upper suture of the fruit and also the chromosome number ($2n = 18, 28, 36, 42, 56$ or 84 in Lotononis; $2n = 14, 16$ or 32 in Crotalaria). Lotononis can be distinguished from Lebeckia by the zygomorphic calyx, the general absence of bracteoles, the presence of stipules, the verrucose upper suture of the fruit and the tuberculate seed surface. The chromosome numbers are not diagnostic (Lebeckia has $2n = 18$) but it should be noted that those species previously misplaced in Lebeckia all have $2n = 28, 56$ or 84 . The salient characteristics of Lotononis, including the absence of bracteoles, the structure of the calyx and the single stipules, can be found sporadically in other genera of the tribe, but not in Lebeckia. Fruit with a verrucose upper suture and cyanogenic glucosides have not been found in any other genera of the tribe.

Changes at the sectional level are clearly long overdue. Diagnostic descriptions given by Harvey (1862) and Dümmer (1913) as keys to the sections, relied heavily on rather subtle differences in habit. Without prior knowledge of the sections, it is often virtually impossible to determine the correct

infrageneric position of a species from herbarium material. To accommodate newly described species and new information on generic relationships, the number of sections are here increased from eight (Bentham 1843, Harvey 1862) to 15. Some sectional circumscriptions are considerably narrowed to form groups that are more likely to represent monophyletic units. Other concepts (such as Oxydium and the previously monotypic Listia) are much widened.

The following key to the sections of Lotononis is comprehensive. Mature fruit and information on the precise habit of a plant are often not available, so that these characters have largely been excluded from the key. For more than just casual identification, dissecting a fully developed flower may be necessary. The presence or absence of bracteoles and the presence of hairs on the wing and keel petals are important key characters, so that considerable difficulties may be experienced without some form of magnification. In all the keys in Part 5, measurements given are for dried herbarium specimens. Flower length is measured from the base of the calyx in a straight line to the tip of the keel. Illustrations of all the important key characters are provided with each of the sectional treatments below, and further details (such as the structure of inflorescences and flower parts) are illustrated in Part 3.1.

- 14A Erect woody shrub; leaves very densely silky; stipules absent except at the flowering nodes; flowers yellow section 13. Aulacanthus
- 14B Prostrate annuals; leaves sparsely pubescent; stipules present at all the nodes; flowers yellow or blue section 8. Monocarpa
- 11B Inflorescences with 2 or more flowers:
- 15A Stipules inconspicuous or absent section 15. Buchenroedera
- 15B Stipules conspicuous:
- 16A Woody shrubs or shrublets; flowers blue, or white with purple veination (if rarely yellow then the wing and keel petals densely pubescent section 15. Buchenroedera
- 16B Perennial herbs with annual flowering branches from a persistent woody caudex; flowers yellow (never blue or white):
- 17A Leaves at the base of the stems simple, sessile, exstipulate; bracts narrowly linear, inconspicuous section 10. Euchlora
- 17B Leaves all digitate (also the basal ones); bracts lanceolate to ovate, conspicuous section 11. Polylobium
- 10B Standard and wing petals as long or shorter than the keel:
- 18A Keel petals pubescent, at least with a few hairs along the lower margin:
- 19A Veination of the keel petals conspicuous, striated in appearance; standard petal panduriform; annual from the north-western parts of Namibia section 7. Oxydium
- 19B Veination of the keel petals inconspicuous; standard petal not panduriform; distribution not as above:
- 20A Keel petals strongly beaked; north-western Cape Province section 7. Oxydium
- 20B Keel petals obtuse or rarely acute but not beaked; mostly from the eastern parts of southern Africa and Zimbabwe (if rarely from the north-western Cape then the standard petal much shorter than the keel):
- 21A Flowers blue; stipules usually absent on the upper parts of the branches; woody shrublets from the Drakensberg section 14. Krebsia
- 21B Flowers yellow (sometimes partly orange or pinkish), never blue; stipules present on the upper parts of the branches; prostrate or procumbent shrublets or herbaceous perennials, rarely annuals; widely distributed section 4. Leptis
- 18B Keel petals totally glabrous:
- 22A Keel acute or beaked, or if somewhat obtuse, then the lamina of the standard petal panduriform; claw of the standard petal dilated at the base, often forming a cupular structure; anthers usually strongly dimorphic, the basifixed anthers more than 2x as long as the dorsifixed ones; prostrate annuals or herbaceous perennials, if erect then annual; stipules single at each node or inconspicuous, paired only in three species (60, 61, 62) section 7. Oxydium
- 22B Keel obtuse or rounded (other characters not combined as above):

- 23A Stipules totally absent:
- 24A Calyx with the lateral sinuses only slightly shallower than the upper and lower ones; flowers blue; seed surface smooth; eastern parts of the Cape Province section 14. Krebsia
- 24B Calyx with the lateral sinuses distinctly shallower than the upper and lower ones; flowers yellow (or partly orange); seed surface tuberculate; western and south-western parts and southern parts of the Cape Province section 13. Aulacanthus
- 23B Stipules present, single or in pairs:
- 25A Inflorescence with 1 flower on a long, slender peduncle; flowers large, blue; known only from the Nuweveld Mountains at Beaufort West in the Cape Province section 13. Aulacanthus
- 25B Characters not combined as above:
- 26A Stipules invariably paired and the two of each pair similar in size and shape section 14. Krebsia
- 26B Stipules single at all or most leaf bases (if rarely paired then dissimilar in size and shape and then with the flowers blue, not yellow):
- 27A Flowers at least partly blue; rigid shrubs or shrublets section 14. Krebsia
- 27B Flowers yellow, orange or pinkish, never blue; shrubs or herbaceous perennials:
- 28A Calyx with the lateral sinuses as deep as the upper and lower ones (the calyx thus subequally lobed); flowers often cleistogamous (i.e., with the petals included within the calyx and the stylar remains on the fruit very short); herbaceous perennials (often mistaken for annuals), rarely slightly woody towards the base; inflorescences invariably 1-flowered and inserted in a leaf-opposed position (in stunted specimens, some inflorescences may be terminal) section 9. Cleistogama
- 28B Calyx with the lateral sinuses shallower than the upper and lower ones (the upper and lateral lobes on either side thus united in pairs); flowers large or small but never cleistogamous; shrubs or prostrate shrublets with woody branches, at least towards the base; inflorescences with 2 or more flowers or, if predominantly 1-flowered, then invariably inserted in a terminal position on short lateral branches and not in a leaf-opposed position:
- 29A Inflorescences with more than 2 flowers; peduncle usually much longer than the length of the flowers; leaves (including the petiole) usually much longer than 10mm; western, south-western and southern Cape Province section 13. Aulacanthus
- 29B Inflorescences usually 1-flowered, rarely with up to 3 flowers; peduncle short or \pm absent; leaves (including the petiole) usually much shorter than 10 mm; eastern Cape Province, eastern parts of southern Africa and Zimbabwe section 4. Leptis

Section 1. Listia (E. Mey.) B-E. van Wyk stat. nov., emend B-E. Van Wyk, emend. nov.

Listia E. Mey., Comm. Pl. Afr. Austr. 1(1): 80 (1836); Benth. in Hook., Lond. J. Bot. 3: 338 (1844); Harv. in Harv. & Sond., Fl. Cap. 2: 66 (1862); Bak. f., Leg. Trop. Afr. 1: 20 (1926); Schreiber in FSWA 60: 73 (1970). Type species: Listia heterophylla E. Mey. (now Lotononis listii Polhill).

Prostrate or procumbent herbaceous perennials, often mat-forming. All mature parts usually glabrous or glabrescent. Branches slender, prostrate, spreading from a woody caudex, often rooting at the lower nodes. Leaves digitately trifoliolate (occasionally with some leaves 1-, 4-, or 5-foliolate), very variable in size and shape, usually almost totally glabrous at maturity, somewhat fleshy; petiole usually slender, often narrowly winged; leaflets very variable in size, the terminal one much larger. Stipules invariably paired at each node, dimorphic (the one large and foliaceous, the other similar or more often much smaller). Inflorescences racemose, leaf-opposed or subterminal on lateral branches, subumbellately many-flowered, slender and few-flowered or with a single flower; bracts oblanceolate to linear; bracteoles consistently present, narrowly oblanceolate to linear. Flowers variable in size, yellow. Calyx with the upper and lateral lobes on either side fused higher up in pairs, the lower narrower, rarely subequally lobed, usually \pm glabrous. Standard orbicular, rarely oblong, longitudinally striated.

Keel half oblong-elliptic; apex obtuse or more often rounded. Anthers dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the carinal anther usually intermediate in size and shape, rarely similar to the basifixed ones. Pods sessile, oblong to linear, rarely ovoid, slightly inflated, straight or curved, occasionally folded like a concertina, thin-walled, upper suture \pm smooth or verrucose (with small wart-like protuberances), often indehiscent or tardily dehiscent, many-seeded; funicles usually very long. Seeds very small and numerous (except in *L. macrocarpa*), testa \pm smooth or sparsely and irregularly tuberculate. Chromosome base number 9 ($2n = 18, 36$). (Figure 5.1).

The concept of the monotypic genus *Listia* E. Mey. is broadened here to include eight species, six of which are centred in the interior of southern Africa (Map 5.1 & 5.2). *L. macrocarpa* occurs in the south-western Cape and *L. angolensis* occurs in the uplands encircling the Zaire basin, from the Adamoua Mountains in Cameroon to the Angolan highlands. *L. listii* also extends into South Central Africa, but the other six species are endemic to southern Africa. *L. bainesii* is cultivated as a fodder plant in many parts of the world.

The presence of bracteoles is a useful diagnostic character. Bracteoles are rarely present in other species of *Lotononis* and in these the stipules are single to each node, never paired. Unlike most species of *Lotononis*, the leaves, flowers and pods

are usually virtually glabrous at maturity. This is also the only group of species where the surface sculpturing of the hairs is smooth and not striate or verrucose. All the species except L. macrocarpa have the ability to produce adventitious roots on the lower parts of the branches. This almost stoloniferous habit has not been observed in any other sections of Lotononis and is clearly associated with wet or seasonally wet habitats, such as river banks and pans (Van Wyk 1988c, 1989m).

The section Listia is here subdivided into two subsections: subsection Listia (7 species) and subsection Macrocarpa (one species, see Part 3.2).

Key to subsections of section Listia:

1A. Calyx subequally lobed (the lateral sinuses not shallower than the upper and lower ones); carinal anther similar to the dorsifixed anthers; pods very large, > 20 mm long; seeds very large, \pm 4 mm long; lower parts of the branches without adventitious roots; south-western Cape subsection Macrocarpa

1B. Calyx zygomorphic (the lateral sinuses shallower than the upper and lower ones, the lateral and upper lobes on either side thus united in pairs); carinal anther much smaller than the dorsifixed anthers; pods relatively small, < 20 mm long; seeds very small, \pm 1 mm long; lower parts of the branches often with adventitious roots; interior parts of southern Africa to tropical Africa, not in the south-western Cape subsection Listia

1A. Subsectio Macrocarpa B-E. van Wyk, subsect. nov. subsectioni Listiae similis, sed calyce sub-pariter lobato, anthera carinali magna (antheris basifixis simili), leguminibus seminibusque valde maioribus, atque habitu alio (absentia radicum adventitiarum ramis lateralibus insidentium) differt.

Subsection Macrocarpa is similar to the subsection Listia but differs in the subequally lobed calyx, the large carinal anther (similar to the basifixed anthers), the much larger pods and seeds and in the different habit (absence of adventitious roots on the lateral branches).

Macrocarpa is a monotypic subsection and can easily be recognised by the characters given in the key (see also Figure 5.1).

1. L. macrocarpa Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 176 (1836); Benth. in Hook., Lond. J. Bot. 2: 601 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 55 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 298 (1913). Type: South Africa, Cape Province, Brackfontein, Clanwilliam, Ecklon & Zeyher 1271 (S!, lecto., designated here; C!, S!, SAM!).

Apparently a rare species, known only from a few localities in the south-western Cape Province (Map 5.1).

Vouchers: Hardy 253; Leighton 1743; Salter 8437; Schlechter 4925, 7969; Zeyher 403.

1B. Subsection Listia

- 1A. Flowers 10--14 mm long 2. *L. solitudinis*
- 1B. Flowers up to 10 mm long (if close to 10 mm, then with the upper calyx lobes narrow and subulate, not triangular):
- 2A. Lateral calyx lobes long and narrow, subulate:
- 3A. Flowers 8--10 mm long; calyx 4--6 mm long; leaves and calyx pubescent; pod folded like a concertina, pubescent all over 7. *L. subulata*
- 3B. Flowers up to 8 mm long; calyx up to 3,5 mm long; leaves and calyx \pm glabrous; pod not folded like a concertina, \pm glabrous 8. *L. marlothii*
- 2B. Lateral calyx lobes broadly or narrowly triangular, obtuse or acute but not subulate:
- 4A. Flowers up to 7 mm long; lateral calyx lobes narrowly triangular, acute:
- 5A. Inflorescence many-flowered; flowers 6--7 mm long; tropical Africa, not in southern Africa ... 3. *L. angolensis*
- 5B. Inflorescence few-flowered (1--4 flowers); flowers 4--5 mm long; northern Cape 6. *L. minima*
- 4B. Flowers 7--10 mm long; lateral calyx lobes broadly triangular, short, obtuse:
- 6A. Calyx \pm glabrous; inflorescence racemose, rarely subumbellate; pistil and pod glabrous or pubescent only along the upper suture; pod folded like a concertina, rarely not folded 5. *L. listii*
- 6B. Calyx pubescent; inflorescence densely subumbellate, rarely racemose; pistil and at least the young pod pubescent all over; pod rarely folded 4. *L. bainesii*

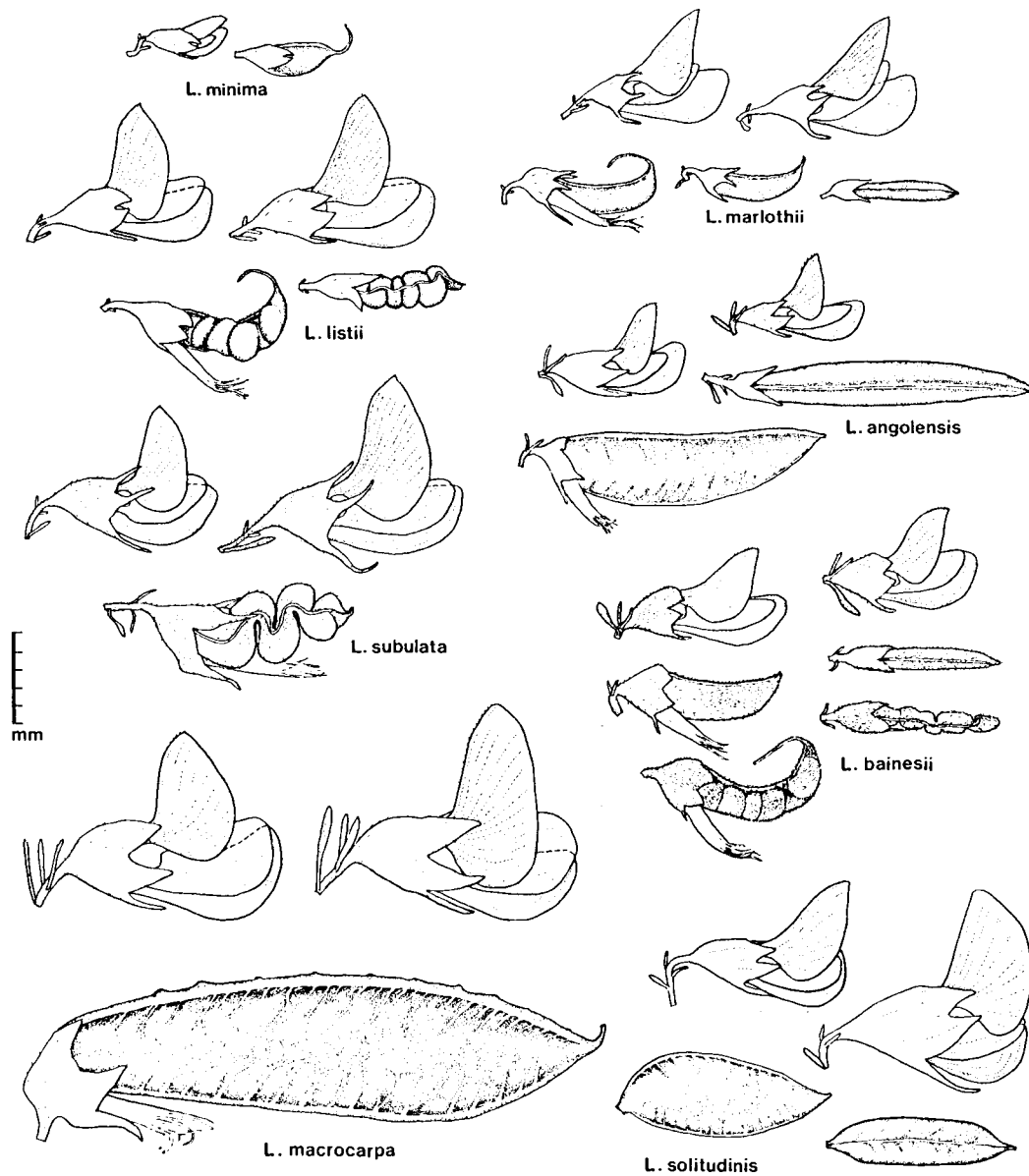


Figure 5.1. Flowers and pods of the species of section *Listia*.

2. *L. solitudinis* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 297 (1913); Burt Davy, Man. pl. Transvaal: 387 (1932). Type: South Africa, Vaal River [probably North Eastern Natal], Wilms 400 (BM!, holo.).

L. solitudinis is a very distinct species, easily recognised by the inflorescence (a long slender peduncle with one or rarely two flowers). The relatively large flowers, the very broad leaflets, the shape of the pods (Figure 5.1) and the large number of seeds (± 60) are also useful diagnostic characters. *L. solitudinis* appears to be a rare species and is known only from isolated localities in Natal, south-eastern Transvaal and north-eastern Orange Free State (Map 5.1).

Vouchers: Acocks 11773; Edwards 1040; Johnstone 443; Repton 449; Strey 3877.

3. *L. angolensis* Welw. ex Bak. in Oliv., Fl. Trop. Afr. 2: 6 (1871); Hiern, Cat. Afr. Pl. Welw. 1: 195 (1896); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 301 (1913); Bak. f., Leg. Trop. Afr. 1: 16 (1926); Wilczek in Fl. Cong. Belg. 4: 274, t. 18 (1953); Torre in Consp. Fl. Angolensis 3(2): 3 (1962); Milne-Redhead in Fl. Trop. E. Afr., Pap.: 814 (1971). Types: Angola, Huilla District, Welwitsch 1896 (BM!, with latin description by Welwitsch, lecto., designated here; BM!, C!, K!); Angola, Pungo Andongo District, Welwitsch 1895 (BM!).

Argyrolobium deflexiflorum Bak. in Kew Bull. 1897: 253 (1897).

Type: Malawi, N. Nyasa District, Fort Hill, Whyte s.n. (K!,
holo.).

Easily distinguished from L. bainesii (with which it is often confused) by the narrowly triangular shape of the lateral calyx lobes (broadly triangular in L. bainesii, Figure 5.1). The flowers of L. angolensis are generally much smaller than those of L. bainesii and not subumbellately arranged as in the latter. L. angolensis is widely distributed in tropical Africa (Map 5.2), recorded from Cameroon (Adamoua), Uganda, Kenya, Tanzania, Burundi, Zaire, Angola, Zambia and Malawi. The distribution records for Mozambique (Baker f. 1926, Milne-Redhead 1971, p. 816) were based on specimens of L. bainesii (q.v.).

Vouchers: Greenway & Kanuri 13798; Liebenberg 344; Richards 11155; Rogers 10946; Verdcourt 508.

4. L. bainesii Bak. in Oliv., Fl. Trop. Afr. 2: 6 (1871); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 301 (1913); Bak. f., Leg. Trop. Afr. 1: 16 (1926); Burt Davy, Man. pl. Transvaal: 387 (1932); Schreiber in FSWA 60: 81 (1970). Type: In the interior near the Tropic of Capricorn [probably in the Waterberg District, Transvaal], Chapman & Baines s.n. (K!, holo.).

L. bainesii Bak. var. *pottiae* Burttt Davy, Man. pl. Transvaal: 387 (1932). Types: South Africa, Transvaal, Pretoria, Leendertz 441 (K!, lecto., designated here); Transvaal, Warmbaths, Leendertz 1363 (K!, isosyn.).

L. bainesii may be confused with *L. listii*, but the flowers are usually subumbellately arranged and the calyx and pods are distinctly pubescent (Figure 5.1). The known distribution area includes Namibia, Botswana, Transvaal and Mozambique (Map 5.1). Specimens from Mozambique were previously confused with *L. angolensis*, a species which does not seem to occur in southern Africa. These specimens have the calyx and fruit less hairy than in typical *L. bainesii*, but the general morphology (particularly the shape of the lateral calyx lobes and the size of the flowers and pods) agrees with the latter.

Vouchers: Balsinhas 3589; Burttt Davy 2134; Codd 8383; De Winter 715; Mogg 24600.

5. *L. listii* Polhill in Bot. Syst. 1: 324 (1976), nom. nov. pro Listia heterophylla E. Mey., Comm. Pl. Afr. Austr. 1(1): 81 (1836) non Lotononis heterophylla Eckl. & Zeyh.; Benth. in Hook., Lond. J. Bot. 3: 338 (1844); Harv. in Harv. & Sond., Fl. Cap. 2: 66 (1862); Bak. f., Leg. Trop. Afr. 1: 20 (1926); Burttt Davy, Man. pl. Transvaal: 389 (1932); Schreiber in FSWA 60: 74 (1970). Types: South Africa, Cape Province, Gaatje [3026 CC Aliwal

North], Drège s.n. a (K!, Herb. Benth. specimen, lecto., designated here; BM!, K!, Herb. Hook. specimen, S!); Cape Province, "prope Wildschutshoek" [Queenstown district], Drège s.n. b (BM!, K!, S!).

In a few specimens (particularly from the eastern Transvaal and northern Natal), most of the pods are straight or only slightly folded. Folded pods have previously been used as a generic character for the genus Listia, but it now appears to be of limited diagnostic value even at the specific level. Diagnostic characters for L. listii are shown in Figure 5.1. Folded pods are also found in L. subulata (but note the very narrow lateral lobes of the calyx in the latter) and occasionally also in L. bainesii. L. plicata (section Digitata) is the only other species of Lotononis where this character can be found. L. listii has a wide geographical distribution and occurs in Zambia, Zimbabwe, Namibia, Botswana, Swaziland, Transvaal, Orange Free State, Lesotho and the northern and eastern parts of the Cape Province (Map 5.2).

Vouchers: Acocks 23559; Codd 993; Dieterlen 1043a; Dinter 7701; Drummond 5772.

6. L. 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 (PRE!, holo.; K!, iso.).

A poorly known species that may be confused with *L. listii* and *L. marlothii*, but the very small flowers (Figure 5.1) are quite distinct (See Van Wyk 1988c, Appendix 22, for more details). *L. minima* is known only from the type collection, which is from a single locality in the northern Cape Province (Map 5.1).

Voucher: Acocks 12664.

7. *L. subulata* B-E. van Wyk sp. nov. ined. [Bothalia (in press); Appendix 33]. Type: South Africa, Transvaal, Parys, near bridge over Vaal River on Potchefstroom Road, B-E. van Wyk 2884 (PRE!, holo.; JRAU!, K!, MO!, S!, iso.).

L. subulata is very closely related to *L. listii* and *L. marlothii*. It differs from *L. listii* in the long and subulate lateral calyx lobes (short and broadly triangular in *L. listii*), the pubescent calyx, leaves and pods (very sparsely pubescent or glabrous in *L. listii*) and in the fewer (up to 4) flowers per inflorescence (rarely fewer than 6 in *L. listii*). It differs from *L. marlothii* in the larger flowers and the folded (flexuous-plicate) pods (see Van Wyk 1989m, Appendix 33). *L. subulata* is apparently restricted to the banks of the Vaal River, in the south-western Transvaal, eastern Orange Free State and the northern Cape Province (Map 5.1).

Vouchers: Acocks & Hafström 1279; Giess 103; Krynauw 61; Louw 1691; Volk 228.

8. L. marlothii Engl. in Engl., Bot. Jahrb. 10: 26 (1888); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 298 (1913); Burt Davy, Man. pl. Transvaal: 387 (1932). Type: South Africa, Cape Province, Griqualand West, Kimberley, Marloth 765 (K!, Herb. Engler specimen, lecto., designated here; BOL!, K!, PRE!).

L. listioides Dinter & Harms in Fedde, Repert. 16: 358 (1920); Bak. f., Leg. Trop. Afr. 1: 16 (1926); Schreiber in FSWA 60: 83 (1970), synon. nov. Type: Namibia, Rehoboth, Dinter 2159 (B+; SAM!, lecto., designated here).

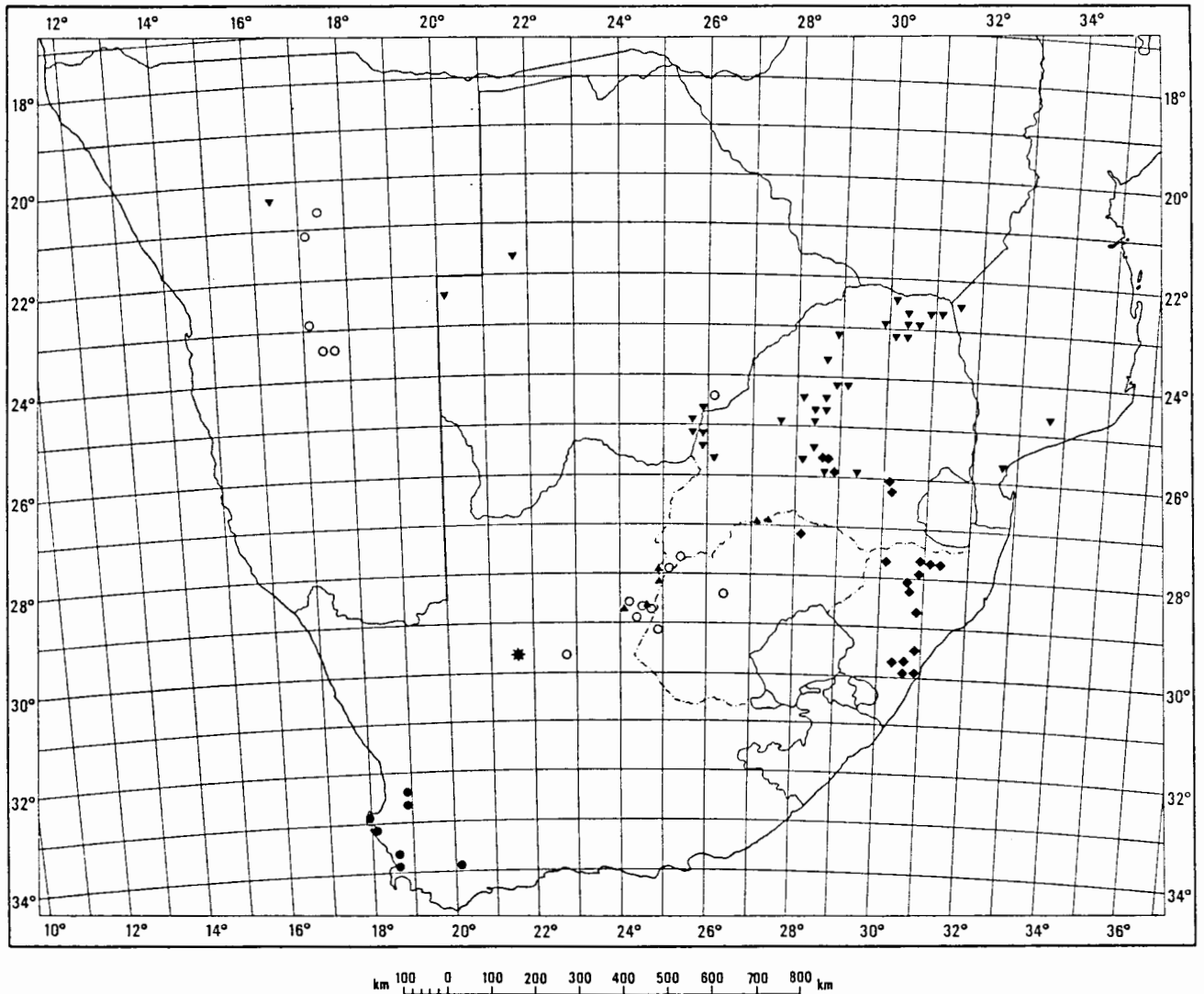
Amphinomia listioides (Dinter & Harms) Schreiber in Mitt. Bot. Staatssamm. München 16: 287 (1957). Type as above.

L. barberae Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 298 (1913), synon. nov. Type: South Africa, Cape Province, Kalahari Region, without precise locality, Barber s.n. (K!, holo.).

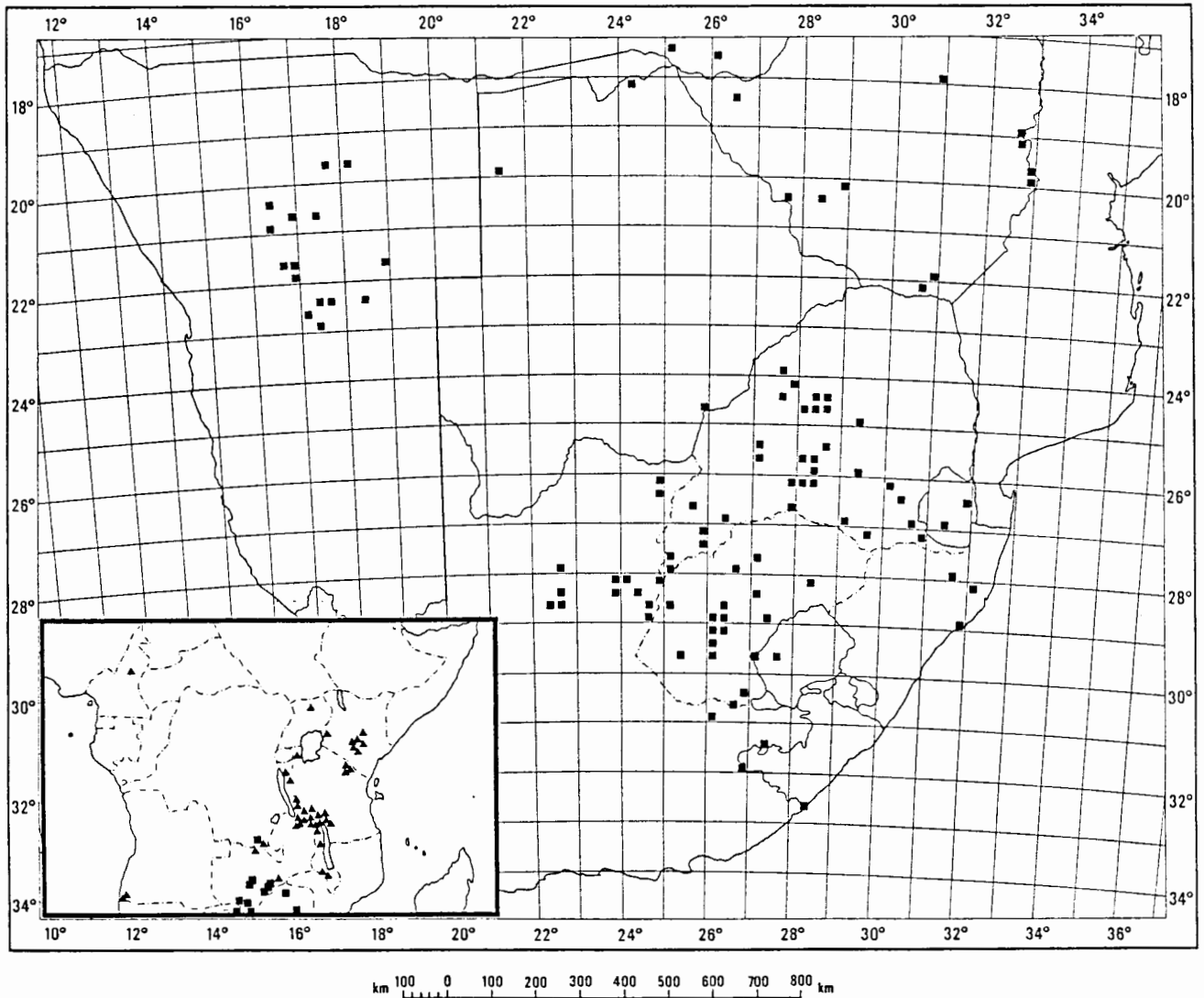
Recent herbarium collections have shown that the types of L. listioides and L. barberae are no more than vigorous specimens of L. marlothii. The number of flowers per inflorescence was used by Dümmer as a diagnostic character to distinguish between L. barberae and L. marlothii. The latter is said to be single-flowered, but the type is a very stunted specimen, hence the small number of flowers. Diagnostic characters are shown in Figure 5.1. L. marlothii has been recorded from seasonally wet

habitats in the dry central interior of southern Africa and occurs in Namibia, Botswana, the northern Cape Province and south-western Orange Free State (Map 5.1).

Vouchers: Acocks 714, 2528, 23340; Bryant 1164; Harbor s.n. sub KMG 949; Leippert 4638; Strickland 792.



Map 5.1. The known geographical distribution of six species of the section *Listia* endemic to southern Africa. *Lotononis macrocarpa* (●), *L. marlothii* (○), *L. subulata* (▲), *L. minima* (*), *L. solitudinis* (◆) and *L. bainesii* (▼).



Map 5.2. The known geographical distribution of *Lotononis listii* in southern Africa. Inset: distribution of *L. angolensis* (▲) and *L. listii* (■) in tropical Africa.

Sectio 2. Digitata B-E. van Wyk sect. nov. Species huius sectionis describerentur basibus lignosis perennibus, sed a speciebus lignosis perennibus sectionum aliarum habitu prostrato, foliis plerumque 5-foliolatis, petiolis longis gracilibus, corolla fere omnino glabra atque leguminibus stipitatis differt.

The species of this section are characterized by having woody, perennial bases, but differ from woody perennial species of other sections in the prostrate habit, the predominantly 5-foliolate leaves, the long and slender petioles, the almost totally glabrous corolla and the stipitate pods.

Type species: *L. digitata* Harv.

Prostrate shrubs or shrublets with the basal parts of the branches thick and woody. Mature parts \pm glabrous or minutely pubescent to sericeous. Leaves alternate, digitate, always predominantly 5-foliolate (some leaves may be 3- or 4-foliolate), \pm glabrous or densely sericeous on both surfaces; petiole long, slender. Stipules single at each node, small, lanceolate. Inflorescences shortly pedunculate to subsessile, short congested racemes, 1- to 4-flowered, invariably leaf-opposed; bracts small, linear; bracteoles absent. Flowers on a short pedicel, very variable in size, yellow. Calyx narrowly campanulate, with the upper and lateral lobes on either side fused much higher up in pairs, lobes long, narrowly acuminate,

lower lobe similar to upper ones or slightly narrower, minutely pubescent to densely sericeous. Standard obovate, rarely very large and oblong-hastate (L. longiflora), as long or slightly shorter than the keel, glabrous or with a few minute hairs dorsally along the middle of the lamina. Wing petals broadly oblong, rarely oblong-falcate (L. longiflora), slightly shorter or much shorter than the keel, glabrous. Keel petals broadly oblong, rarely very large and narrowly half oblong-elliptic and conspicuously auriculate (L. longiflora); apex obtuse, rarely somewhat pointed (L. longiflora), glabrous. Anthers dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the carinal anther similar to the dorsifixed ones or slightly longer. Pods shortly stipitate, long-stipitate in two species, flat or only slightly turgid, linear to oblong, rarely ovoid-oblong, occasionally falcate or folded like a concertina, much longer than the calyx, thin-walled, upper suture \pm smooth or more often minutely verrucose, dehiscent, tardily dehiscent or indehiscent, \pm 10- or more-seeded; funicles long or short. Seeds small, \pm 1 mm in diameter, suborbicular, testa minutely tuberculate. Chromosome base number 9 ($2n = 18$). (Figure 5.2).

Six species with a very localized distribution in the dry mountainous region between Vanrhynsdorp and Springbok in the north-western Cape Province, and a single isolated locality in the southern-eastern Cape (Maps 5.3 and 5.4). The plants are

usually found growing in cracks in the large granite rocks that form such a characteristic feature of the landscape in Namaqualand.

The following combination of characters is of diagnostic value to distinguish the section Digitata from other sections, particularly the closely related Listia and Leptis: prostrate shrubs or shrublets, with the basal parts of the branches thick and woody; calyx narrowly campanulate with long narrow lobes, the lateral sinuses much shallower than the upper and lower ones; leaves always predominantly 5-foliolate; petioles long and slender; stipules single at each node; bracts very small; bracteoles totally absent; keel petals obtuse (if rarely somewhat pointed then the flowers more than 20 mm long), \pm glabrous; standard petals glabrous or with a few minute hairs; keel petals \pm glabrous; pods with a short or long stipe, flat, linear, falcate or folded like a concertina (if rarely ovoid-oblong and slightly turgid then distinctly stipitate).

Harvey (1862) separated L. digitata from L. quinata by placing it in the section Krebsia, presumably because of the woody habit and the eastern distribution (see type citation below). L. quinata however, was retained in Leptis, following Bentham (1843). Dümmer (1913) included a new species, L. benthamiana, with L. digitata in Krebsia. These three species are very closely related and often difficult to identify when no pods are available. The

chromosome number of $2n = 18$ supports the idea of only a superficial similarity with Krebsia, where $2n = 28, 42, 56$ or 84 (Van Wyk & Schutte 1988a, Appendix 14).

The diagnostic characters in the following key to the species are illustrated in Figure 5.2. The flowers of some species are rather similar and vary considerably in size, depending on the vigour of the plant. The shape of mature pods is by far the most reliable diagnostic character (Van Wyk 1989e, Appendix 25).

Key to the species of section Digitata:

- 1A. Pods folded like a concertina 10. L. plicata
- 1B. Pods straight or falcate, never folded like a concertina:
 - 2A. Leaflets narrowly linear:
 - 3A. Leaves \pm glabrous; pods linear, distinctly
falcate, flowers usually > 12 mm long
..... 12. L. digitata
 - 3B. Leaves densely sericeous at least when young;
pods oblong, never falcate, flowers usually
< 12 mm long 9. L. quinata
 - 2B. Leaflets oblanceolate to obovate:
 - 4A. Flowers very large, > 20 mm long 14. L. longiflora
 - 4B. Flowers relatively small, < 20 mm long:
 - 5A. Leaflets minutely and inconspicuously pubescent;
pods slightly turgid, oblong-obovate, stipitate
..... 13. L. benthamiana
 - 5B. Leaflets densely sericeous at least when young;
pods flat, linear to broadly oblong, subsessile:
 - 6A. Flowers > 12 mm long; leaflets densely
sericeous, not glabrescent 11. L. magnifica
 - 6B. Flowers < 12 mm long; leaflets densely
sericeous when young but glabrescent
with age 9. L. quinata

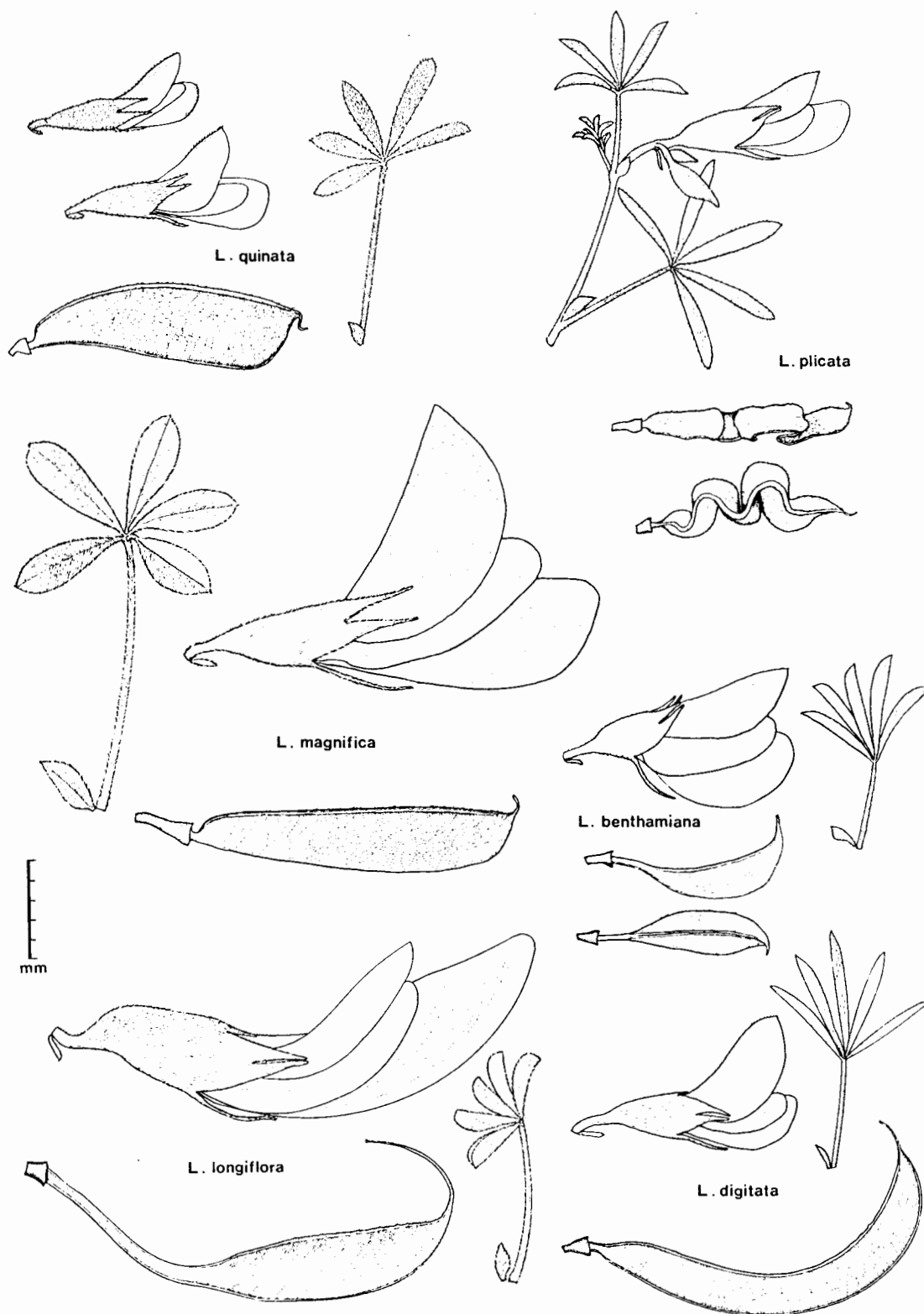


Figure 5.2. Leaves, flowers and pods of the species of section *Digitata*.

9. L. quinata (Thunb.) Benth. in Hook., Lond. J. Bot. 2: 608 (1843); Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845); Harv. in Harv. & Sond., Fl. Cap. 2: 63 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 312 (1913). Type: "e Cap. b. Spei", Thunberg s.n. sub Thunb. Herb. 16636 (UPS!, lecto., designated here).

Ononis quinata Thunb., Prodr. pl. Cap.: 130 (1800), Fl. Cap.: 589 (1823); DC., Prodr. 2: 167 (1825). Type as above.

Lipozygis quinata (Thunb.) E. Mey., Comm. Pl. Afr. Austr. 1(1): 77 (1836). Type as above.

Lotononis quinata (Thunb.) Benth. var. minor Harv. in Harv. & Sond., Fl. Cap. 2: 63 (1862). Type: South Africa, Cape Province, "Kamiesbergen ... prope Modderfontein", Drège s.n. (K!, Herb. Benth. specimen, holo.; MO!, iso.).

Lotononis delicatula H. Bol. ex De Wildeman, Pl. Nov. Hort. Then. 1(6): 187 & t.41 (1904); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 313 (1913), synon. nov. Type: South Africa, Brackdam, Schlechter 11106 (BOL!, holo., K!, MO!, iso.).

Although the leaves and flowers are usually very small, vigorous forms of L. quinata may easily be confused with L. digitata when no pods are available. The type specimens of Thunberg and Schlechter (on which L. quinata and L. delicatula were respectively based) represent two extremes of the variation in size. The species is restricted to Namaqualand, where it appears to be quite common (Map 5.3).

Vouchers: Esterhuysen 5444, 23616; Goldblatt 5771; Hutchinson 884; Salter 4592; Van Wyk 2416, 2419, 2420.

10. *L. plicata* B-E. van Wyk sp. nov. ined. [S. Afr. J. Bot. (in press), Appendix 25]. Type: South Africa, Cape Province, near Bitterfontein, between Vanrhynsdorp and Bitterfontein, Salter 1601 (K!, holo.; BOL!, iso.).

Listia salteri Bak. f. in sched.

This poorly known species is very similar to *L. digitata* and difficult to identify when pods are not available. The standard petal is more hairy than in *L. digitata*, however, and the leaflets are often narrowly oblanceolate rather than narrowly linear as in the latter (Figure 5.2). *L. plicata* appears to have a very localized distribution in southern Namaqualand (Map 5.3).

Vouchers: Acocks 14782; Salter 1601.

11. *L. magnifica* B-E. van Wyk sp. nov. ined. [S. Afr. J. Bot. (in press), Appendix 25]. Type: South Africa, Cape Province, summit of Kamiesberg, 3 km south of radio tower, B-E. van Wyk 2421 (PRE!, holo.; K!, NBG!, MO!, iso.).

L. magnifica is similar to L. quinata but differs in the larger and more woody habit, the slightly larger and more densely sericeous leaflets (not glabrescent), the much larger flowers and the slightly longer pods (Figure 5.2). It is also similar to L. mollis (E. Mey.) Benth. and L. mirabilis Dinter (section Leptis) but in these species the leaves are trifoliate and the standard, wing and keel petals are densely pubescent. Both L. mollis and L. magnifica are known only from the Kamiesberg (Map 5.3).

Vouchers: Van Wyk 2421--2422, 2549--2556.

12. L. digitata Harv. in Harv. & Sond., Fl. Cap. 2: 52 (1862); Dummer in Trans. Roy. Soc. S. Afr. 3(2): 293 (1913). Type: South Africa, in some part of the eastern provinces, Capt. Carmichael s.n. (TCD!, holo.).

L. digitata is very closely related to L. quinata and L. benthamiana but the long, falcate pods are quite distinct (Figure 5.2). It is the only species of the section that is not entirely restricted to Namaqualand (Map 5.4). The type locality ("somewhere in the eastern provinces") may well be in or near the Kouga mountains where a recent collection (Bayliss 5864) was made.

Vouchers: Bayliss 5864; Esterhuysen 5700; Hutchinson 842; Martin 520; Van Wyk 2344--2347.

13. *L. benthamiana* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 294 (1913). Types: South Africa, Western Region, Little Namaqualand: Near Ookiep, Scully s.n. sub Herb. Norm. Austr. Afr. 1127 (K!, lecto., designated here; BOL!, SAM!, islecto.), Scully 150 (BM!, isosyn.), Morris s.n. sub BOL 5622 (BOL!, K!, isosyn.); Steinkopf, Schlechter 39 (BM!, BOL!, GRA!, MO!, isosyn.).

L. pseudoquinata Schltr. in sched.

The short, distinctly stipitate pods and very broad keel petals are useful diagnostic characters for *L. benthamiana* (Figure 5.2). It is known only from a restricted area around the town of Springbok (Map 5.4), where it seems to be restricted to cracks in granite rocks. The corolla is highly persistent, so that the small and tardily dehiscent pods are effectively dispersed by wind.

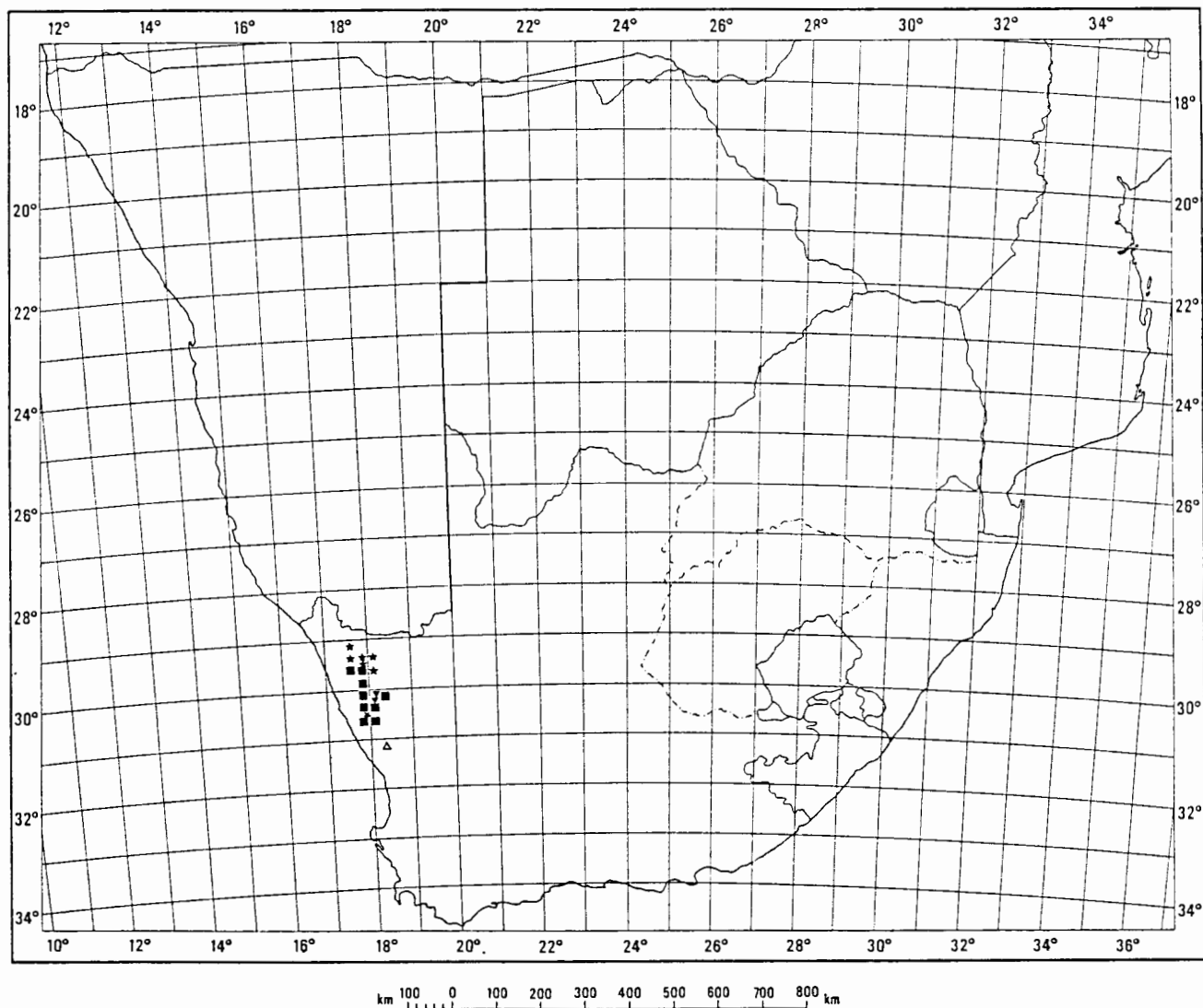
Vouchers: Acocks 19555; Leach & Forrester 17446; Van Wyk 2537--2539.

14. *L. longiflora* H. Bol. in J. Linn. Soc. 25: 159 (1889); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 313 (1913). Type: South Africa, Cape Province, Namaqualand, Dowdle s.n. sub BOL 6568 (BOL!, holo.; K!, iso.).

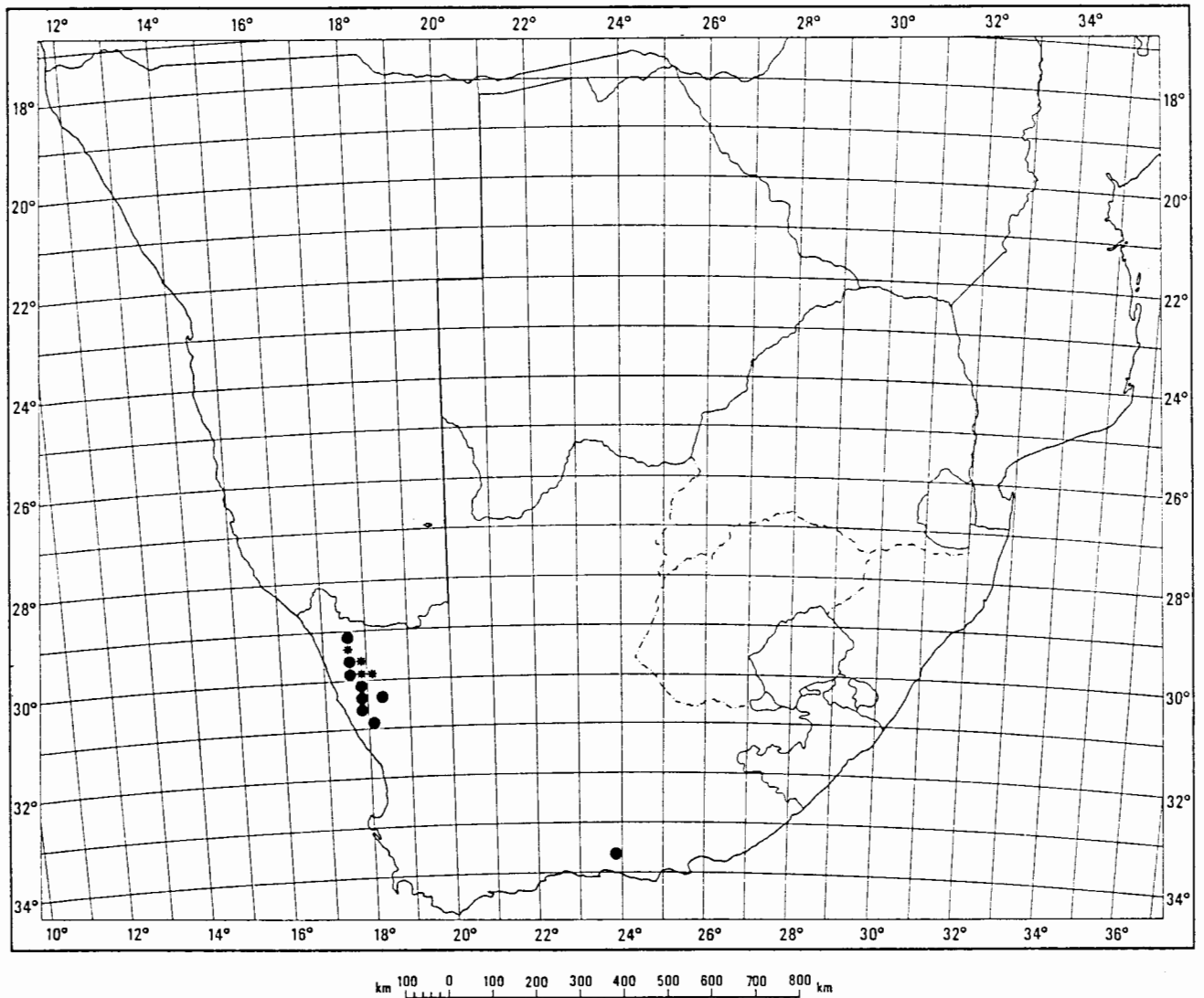
L. speciosa Hutch., A Botanist in Southern Africa: 170
(1946), synon. nov. Type: South Africa, Cape Province,
Namaqualand: Steinkopf, near Klipfontein, Hutchinson 912 (K!,
holo.; BM!, BOL!, iso.).

L. longiflora is a very distinct species, known from only a few
localities in the north-western Cape (Map 5.3). The flowers are
quite unlike any other species of Lotononis and are, in terms of
length, the largest in the genus. Mature pods and seeds are
unfortunately unknown, but the very long stipe of the pistil
shows that the pods must also be quite unusual (Figure 5.2).

Vouchers: Barker 6635; Scully 1128; Strauss 135; Van der
Westhuizen 189; Wisura 2274.



Map 5.3. The known geographical distribution of *Lotononis quinata* (■), *L. magnifica* (▼), *L. longiflora* (★) and *L. plicata* (△).



Map 5.4. The known geographical distribution of *Lotononis digitata* (●) and *L. benthamiana* (*).

Section 3. Lipozygis (E. Mey.) Benth. emend. B-E. van Wyk, emend.
nov.

Lotononis section Lipozygis (E. Mey.) Benth. in Hook., Lond. J.
Bot. 2: 605 (1843), pro parte; Harv. in Harv. & Sond., Fl. Cap.
2: 49 (1862), pro parte; Dümmer in Trans. Roy. Soc. S. Afr. 3(2):
279 (1913), pro parte; Burt Davy, Man. pl. Transvaal: 385
(1932). Lectotype species: Lipozygis corymbosa E. Mey. [now
Lotononis corymbosa (E. Mey.) Benth.].

Lipozygis (section 4) E. Mey., Comm. Pl. Afr. Austr. 1(1): 79
(1836), pro parte.

Note: The sectional limits of Lipozygis are here modified to
include only perennial pyrophytes from the eastern parts of
southern Africa. The bracts (not to be confused with bracteoles)
in this group of species are invariably inserted well above the
base of the pedicel (Figures 5.3 and 5.4). This very reliable
diagnostic character has apparently escaped the notice of
previous authors. The circumscription of section Lipozygis by
Bentham (1843), Harvey (1862) and Dümmer (1913) is undoubtedly
artificial (Van Wyk 1989g, Appendix 27). All annual species from
the western Cape Province are therefore excluded and referred to
the new section Synclistus (q.v.).

Suffrutescent pyrophytic herbs with procumbent or erect annual
flowering branches from a woody subterranean rootstock or caudex.
Caudex branched or unbranched, often thick and carrot-like.

Mature parts usually sparsely pubescent with long spreading hairs, often turning black when dried. Branches slender, densely leafy, rarely woody towards the base. Leaves alternate, digitately trifoliolate, very rarely with some leaves 5-foliolate; leaflets often very large, usually broadly oblanceolate to elliptic, adaxially glabrous or very sparsely pubescent, abaxially densely to sparsely pubescent or hirsute; petiole short, usually much shorter than the leaflets. Stipules invariably single at each node (rarely absent), usually large and foliaceous, resembling the leaflets in size and shape, occasionally slightly smaller than the leaflets. Inflorescences invariably terminal, subsessile or shortly pedunculate, occasionally also with secondary inflorescences towards the terminal parts of the branches, umbellately many-flowered (rarely fewer than 6-flowered, usually 10- to 30-flowered); bract small but conspicuous, very large and foliaceous in two species, invariably fused with the pedicel and inserted \pm halfway towards the calyx; bracteoles rarely present, usually minute and inconspicuous (relatively large in two species). Flowers small, very uniform in size and shape, usually densely pubescent, yellow (often black when dried); pedicel often exceptionally long, rarely short. Calyx campanulate, with the upper and lateral lobes on either side fused much higher up in pairs, lower lobe usually as long as the upper ones but much narrower. Standard oblong to oblong-ovate, \pm as long as the keel, usually densely pubescent or at least with a line of hairs dorsally along the middle of the lamina. Wing petals narrowly oblong, slightly shorter than the

keel, pubescent or \pm glabrous; apex obtuse; base auriculate. Keel petals half oblong-elliptic, usually densely pubescent, rarely \pm glabrous; apex obtuse or rounded. Anthers dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the carinal anther similar to the dorsifixed ones. Pods sessile, small, scarcely longer than the calyx, very uniform in size and shape, ovoid, flat, thin-walled, upper suture \pm smooth, dehiscent, \pm 8-seeded; funicles long. Seeds small, 1.5--2 mm in diameter, suborbicular to broadly oblong, the radicular lobe usually prominent, testa smooth or irregularly and sparsely tuberculate. Chromosome base number 9 ($2n = 18$). (Figures 5.3 & 5.4).

The section now comprises ten closely related species restricted to the summer rainfall grassland areas of the eastern parts of southern Africa (Maps 5.5, 5.6 and 5.7).

Diagnostic characters: suffrutescent pyrophytic herbs with short-lived procumbent or erect branches from a woody perennial base; leaves 3-foliolate (only rarely 5-foliolate in one species); stipules single at each node and usually similar to the leaflets in size and shape (rarely absent in one species); inflorescences terminal, more than 4-flowered, congested racemes or umbels; pedicel often exceptionally long; bracts conspicuous, often very large, invariably fused to the pedicel and situated well above the base of the pedicel; bracteoles present or absent,

relatively large in two species; flowers very uniform in size and shape; standard and keel usually densely pubescent; pods sessile, flat, very short (scarcely longer than the calyx).

Within the section Lipozygis, two distinct groups can be distinguished (see Part 3.2) and are here recognised as subsections: subsection Bracteolata (two species) and subsection Lipozygis (eight species). The latter is an extremely variable complex of species and should be investigated in more detail.

Key to the subsections and species of section Lipozygis:

- 1A. Bracts broadly obovate, > 4 mm wide; paired
bracteoles invariably present, relatively
large and conspicuous, > 2 mm long
..... subsection Bracteolata:
- 2A. Bracts congested at the apex of the
peduncle; stipules much smaller than
the leaflets; upper surface of mature
leaflets glabrous 15. L. procumbens
- 2B. Bracts widely spaced along the peduncle;
stipules foliaceous, not much smaller than
the leaflets; upper surface of mature
leaflets sparsely hairy 16. L. difformis
- 1B. Bracts linear to narrowly lanceolate, < 1 mm
wide; paired bracteoles usually absent, small and
inconspicuous when present, < 1 mm long
..... subsection Lipozygis:
- 3A. Stipules absent 19. L. grandis
- 3B. Stipules present:

4A. Leaves (and flowers) not turning black when dried:

5A. Standard petal \pm glabrous or with a line of
hairs along the middle of the lamina 21. *L. pulchra*

5B. Standard petal densely pubescent (at least
the upper half of the lamina):

6A. Leaflets oblanceolate to elliptic; standard
petal \pm 4 mm wide; inflorescences mostly
with < 8 flowers:

7A. Flowering twigs woody, divaricately
branched; stipules much smaller
than the leaflets 17. *L. sutherlandii*

7A. Flowering twigs herbaceous, unbranched;
stipules usually similar to the
leaflets in size 18 *L. eriantha*

6B. Leaflets obovate; standard petal
 \pm 2--3 mm wide; inflorescences
usually with > 8 flowers 20. *L. corymbosa*

4B. Leaves (and usually also the flowers) turning
black when dried:

- 8A. Inflorescences > 40 mm in diameter; standard
and keel petals usually densely pubescent;
leaflets > 8 mm wide L. grandis
- 8B. Inflorescences < 40 mm in diameter; standard and keel
petals usually ± glabrous; leaflets < 8 mm wide:
- 9A. Inflorescences terminal and on short
lateral branches (pseudo-spicate arrangement),
leaflets usually < 5 mm wide, known only
from Swáziland 24. L. spicata
- 9B. Inflorescences invariably terminal; leaflets
usually > 5 mm wide, widely distributed:
- 10A. Standard petal < 3 mm wide; flowering
branches > 300 mm long 22. L. lanceolata
- 10B. Standard petal > 3 mm wide; flowering
branches < 200 mm long 23. L. foliosa

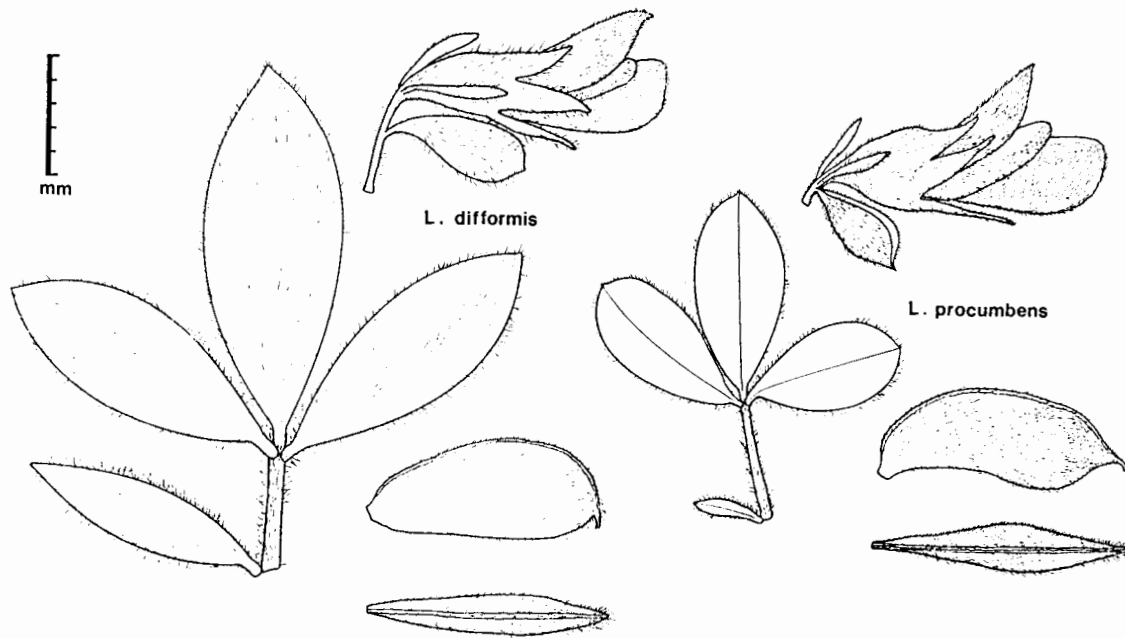


Figure 5.3. Leaves, flowers and pods of the species of section *Lipozygis*, subsection *Bracteolata*.

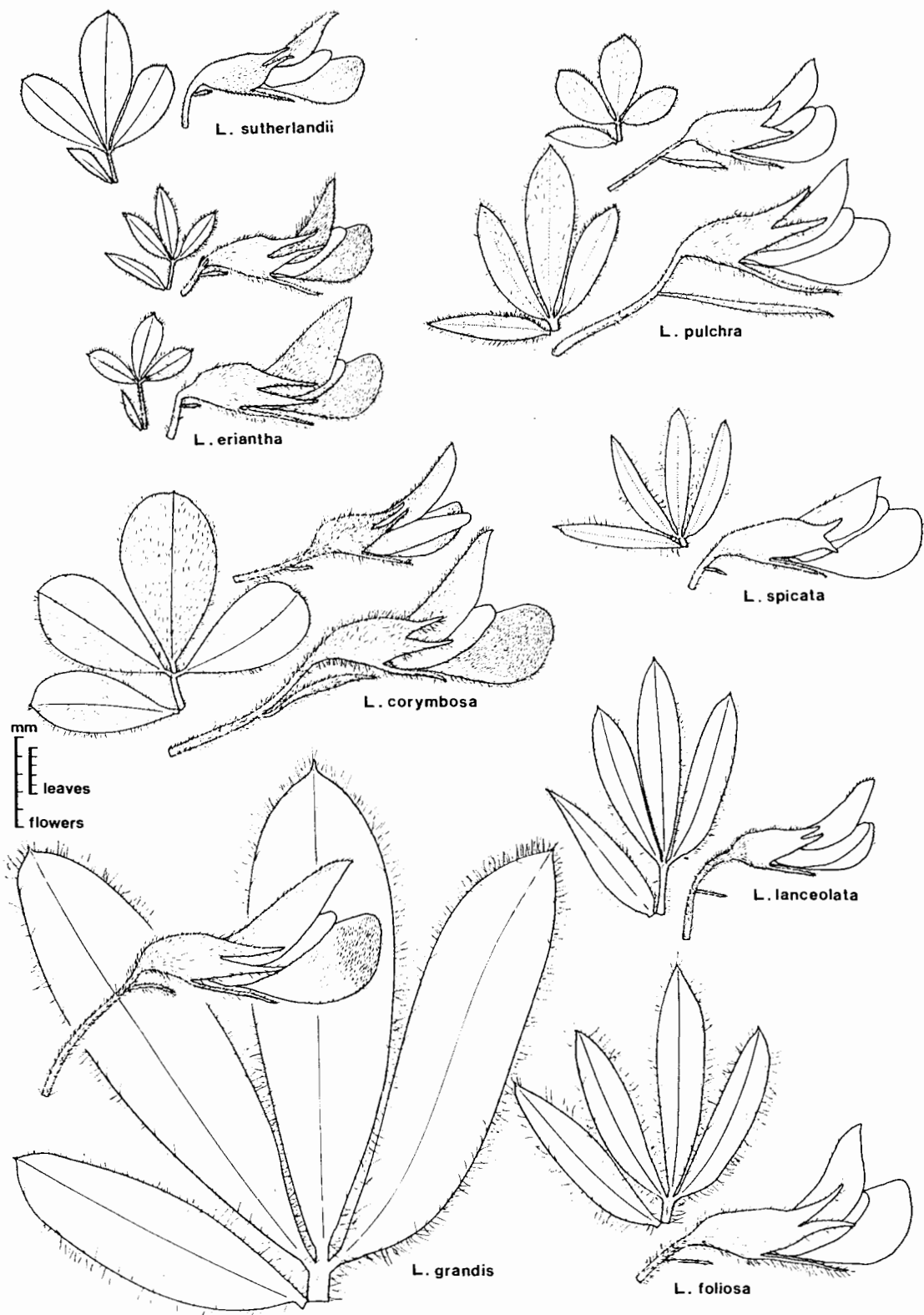


Figure 5.4. Leaves and flowers of the species of section Lipozygis, subsection Lipozygis.

3A. Subsectio Bracteolata B-E. van Wyk, subsect. nov. Subsectio haec a subsectio typica bracteis latis foliaceis et bracteolis magnis differt.

This subsection differs from the typical subsection in the broad, foliaceous bracts and in the large bracteoles.

Type species: *L. difformis* B-E. van Wyk.

The two species of subsection Bracteolata (*L. procumbens* and *L. difformis*) can easily be identified by the size and shape of the bracts and bracteoles. Figure 5.3.

15. *L. procumbens* H. Bol. in J. Bot. 1896: 18 (1896); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 300 (1913). Type: South Africa, Orange Free State, Harrismith district, plateau and mountains at Bester's Vlei, Bolus 8139 (BOL!, holo.; NBG!, iso.).

This species is superficially similar to some forms of *L. eriantha* and *L. pulchra* but the habit and bracts (Figure 5.3) are quite distinct. The subumbellate inflorescences of *L. procumbens* was previously taken as evidence for an affinity with the section Polylobium but it was clearly misplaced in the latter. The recorded geographical distribution is given in Map 5.5.

Vouchers: Acocks 23822; Dieterlen 65; Galpin 10223; Jacobsz 3034; Van Wyk 2506.

16. *L. difformis* B-E. van Wyk sp. nov. ined. [S. Afr. J. Bot. (in press), Appendix 27]. Type: South Africa, Transvaal, Piet Retief District, Iswepe, Sidey 1609 (PRE!, holo.; S!, iso.).

This poorly known species is easily distinguished by the foliaceous, widely spaced bracts and the broad calyx lobes (Figure 5.3). The upper lobes of the calyx are distinctly shorter than the lower three lobes. *L. difformis* is known only from a single locality in south-eastern Transvaal (Map 5.5).

Vouchers: Sidey 1579, 1609.

3B. Subsection Lipozygis

17. *L. sutherlandii* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 307 (1913). Type: South Africa, Natal, without precise locality, Sutherland s.n. (K!, holo.).

Very similar to *L. eriantha* and perhaps not distinct from it at the specific level. The habit and general appearance of this poorly known species seem rather different, however. I consider it advisable to retain *L. sutherlandii* as a distinct species until more complete material (fruit and seeds in particular) becomes available for study. The distribution appears to be limited to the vicinity of Pietermaritzburg in Natal (Map 5.5).

Voucher: McKenzie 11.

18. *L. eriantha* Benth. in Hook., Lond. J. Bot. 2: 605 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 59 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 308 (1913); Burt Davy, Man. pl. Transvaal: 387 (1932). Type: South Africa, "Macalisberg" [Magaliesberg], Burke 383 (K!, Herb. Benth. specimen, holo.; K!, Herb. Hook. specimen, PRE!, iso.).

The distinction between *L. eriantha* and *L. corymbosa* is not very clear. Forms of the species from the Transvaal Highveld agree well with the type and are easy to distinguish from *L. corymbosa* by the size and shape of the leaflets (rather small and narrowly oblanceolate to narrowly elliptic, see Figure 5.4). Forms along the Drakensberg and in Natal seem to merge gradually with typical *L. corymbosa*. A final decision about the status of *L. eriantha* should be based on a more detailed study of the habit and geographical variation within the subsection as a whole (see

notes under L. corymbosa). The geographical distribution of the typical Highveld form of the species and what appears to be intermediate forms is shown separately in Map 5.6.

Vouchers: Acocks 18726; Buthelezi 394; Compton 26701; Jacobsz 2283; Young A199.

19. L. grandis Dümmer & 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 (K!, holo.).

The dense vestiture of the corolla is a useful character to distinguish this species from L. foliosa. The habit is very robust and the leaves are by far the largest in the section (Figure 5.4). This striking plant appears to be endemic to Natal (Map. 5.7).

Vouchers: Burt Davy 11448; Codd 1790; Germishuizen 2099; Schrire 1052, 1092.

20. L. corymbosa (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 605 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 59 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 308 (1913); Burt Davy, Man. pl.

Transvaal: 387 (1932). Type: South Africa, Transkei, "prope Omtata" [Umtata], Drège s.n. (S!, lecto., designated here; BM!, K!, 2 sheets, M!, S!, isosyn.).

Lipozygis corymbosa E. Mey., Comm. Pl. Afr. Austr. 1(1): 79 (1836). Type as above.

Polylobium corymbosa (E. Mey.) Benth. in Ann. Wien. Mus. 2: 142 (1839). Type as above.

Polylobium corymbosa (E. Mey.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845). Type as above.

L. eriantha Benth. var. obovata Scott Elliot in J. Bot. 1891: 69 (1891). Type: South Africa, Natal, near Maritzburg [Pietermaritzburg], Wood 3163 (K!).

The type of the variety listed above agrees with the Drège type of L. corymbosa. Specimens cited by Bentham (1843) differ from the latter in the more robust habit, the very large number of flowers per inflorescence, the smaller flowers and the very narrow standard petal. Flowers of both these extremes of the spectrum of variation are shown in Figure 5.4. The known geographical distribution of L. corymbosa (both forms) is shown in Map 5.6.

Vouchers. Typical form: Barker 7960; Coleman 735; Schrire 1535; Taylor 5492; Tyson 141. Form with small flowers: Lawson 1105; Nicholas 1590a; Rycroft 2034; Schrire 1381, 1588; Venter 4567.

21. *L. pulchra* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 308 (1913). Types: South Africa, Transvaal, Lydenburg, Wilms 280 (K!, lecto., designated here; BM!), Wilms 279a p.p. (BM!), Atherstone s.n. (not seen).

L. tenuipes Burt Davy, Man. pl. Transvaal: 387 (1932), synon. nov. Type: South Africa, Transvaal, Lydenburg division, Machadodorp, Rogers 18174 (PRE!, lecto., designated here; K!, PRE!, iso.).

This species is extremely variable but can be distinguished from *L. eriantha* and *L. corymbosa* by the totally glabrous wing and keel petals (Figure 5.4). The standard petal has a line of hairs dorsally along the middle, while it is covered in hairs for most of the surface in *L. eriantha* and *L. corymbosa*. The known distribution is shown in Map 5.5.

Vouchers: Coleman 305; Germishuizen 1079; Mogg 2193; Moll 633; Schrire 2233.

22. *L. lanceolata* (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 606 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 60 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 310 (1913); Burt Davy, Man. pl. Transvaal: 387 (1932). Type: South Africa, Cape Province, "Witbergen ... prope Leeuwenspruit" [3027DC Lady Grey], Drège s.n. (K!, lecto., designated here; BM!, K!, PRE!, MO!, S!, SAM!, isosyn.).

Aspalathus lanceolatus E. Mey., Comm. Pl. Afr. Austr. 1(1): 37 (1836). Type as above.

Buchenroedera lanceolata (E. Mey.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 477 (1845). Type as above.

L. lanceolata may be confused with L. foliosa, but the flowering branches are much longer (usually more than 300 mm) and the flowers are much smaller (Figure 5.4). Of the four species of which the leaves turn black when dried, L. lanceolata has the widest geographical distribution (Map 5.7).

Vouchers: Dieterlen 437; Germishuizen 182; Liebenberg 7548; Van Wyk 1884, 1887.

23. L. foliosa H. Bol. in J. Linn. Soc. (Bot.) 24: 173 (1887); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 310 (1913); Burt Davy, Man. pl. Transvaal: 387 (1932). Type: South Africa, Transvaal, "prope Pretoria", Maclea s.n. sub BOL 5620 (BOL!, holo.; K!, iso.).

L. foliosa is generally easy to identify by the very small habit (the flowering branches are rarely more than 200 mm long). In the north-western parts of Natal however, the habit and leaves are very similar to that of L. grandis. The most reliable distinction between the two species appears to be the pubescence of the petals -- densely hairy in L. grandis, nearly glabrous in L.

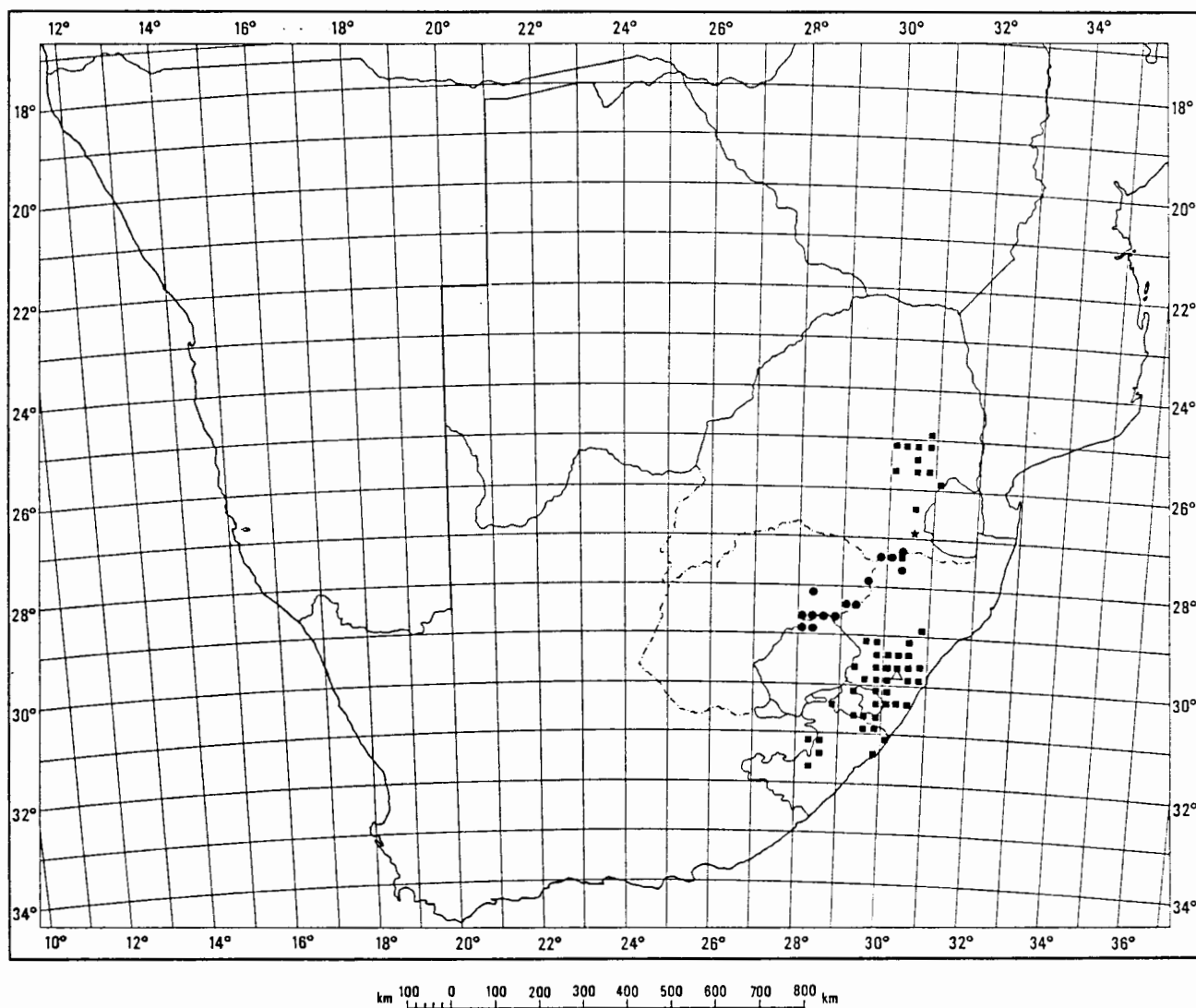
foliosa (Figure 5.4). L. foliosa is geographically more or less separated from L. grandis and occurs only at high altitudes (Map 5.7).

Vouchers: Devenish 1045; Germishuizen 2261; Liebenberg 8464; Story 678; Van Wyk 1799.

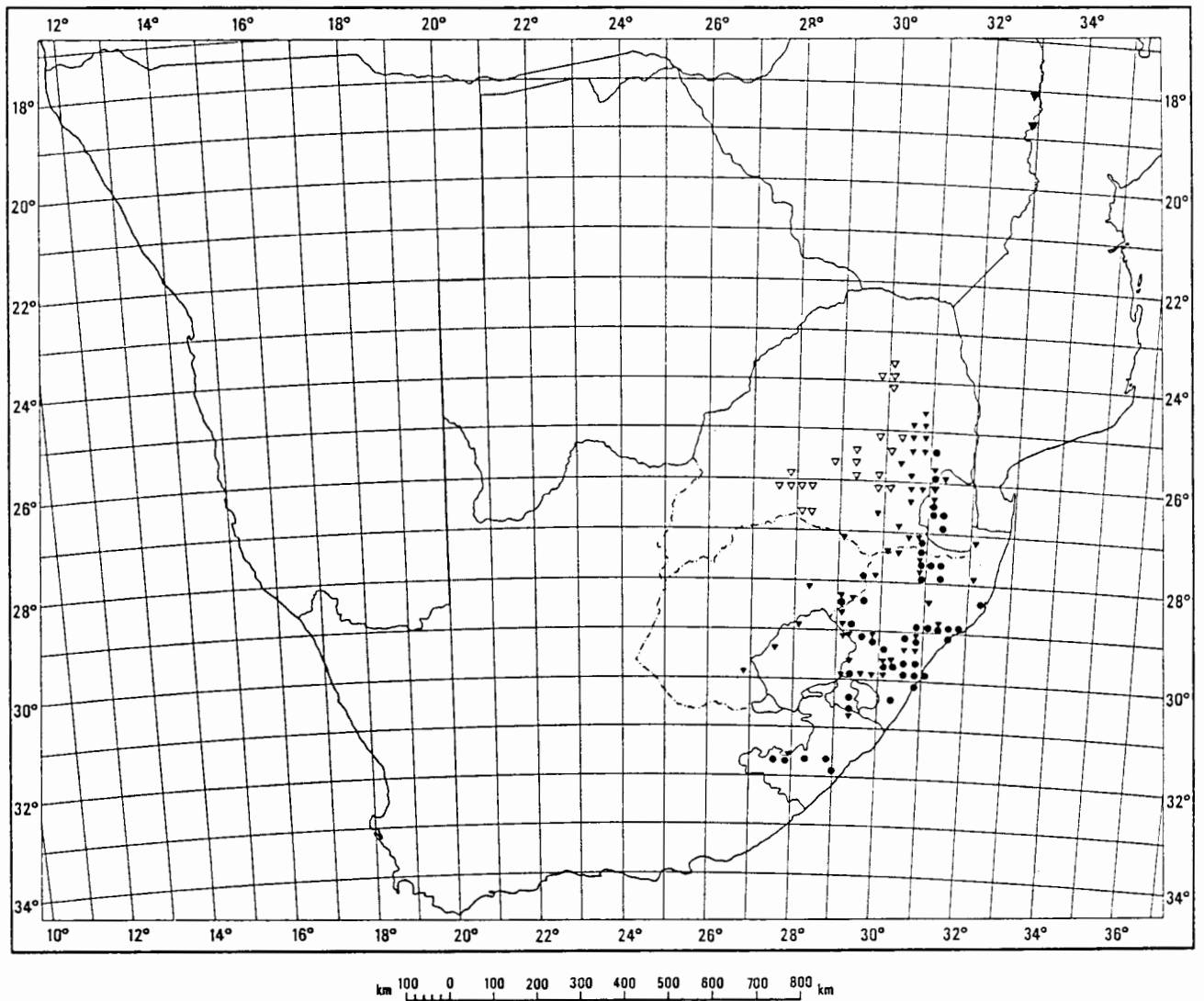
24. L. spicata Compton in J. S. Afr. Bot. 41(1): 48 (1975). Type: Swaziland, Mpaleni, Compton 32111 (NBG!, holo.; K!, 2 sheets, PRE!, iso.).

This species is very similar to L. foliosa but can be distinguished by the much smaller leaves (Figure 5.4) and the presence of axillary inflorescences along the flowering branches (strictly terminal in L. foliosa). L. spicata is known only from a few specimens collected in Swaziland (Map 5.7).

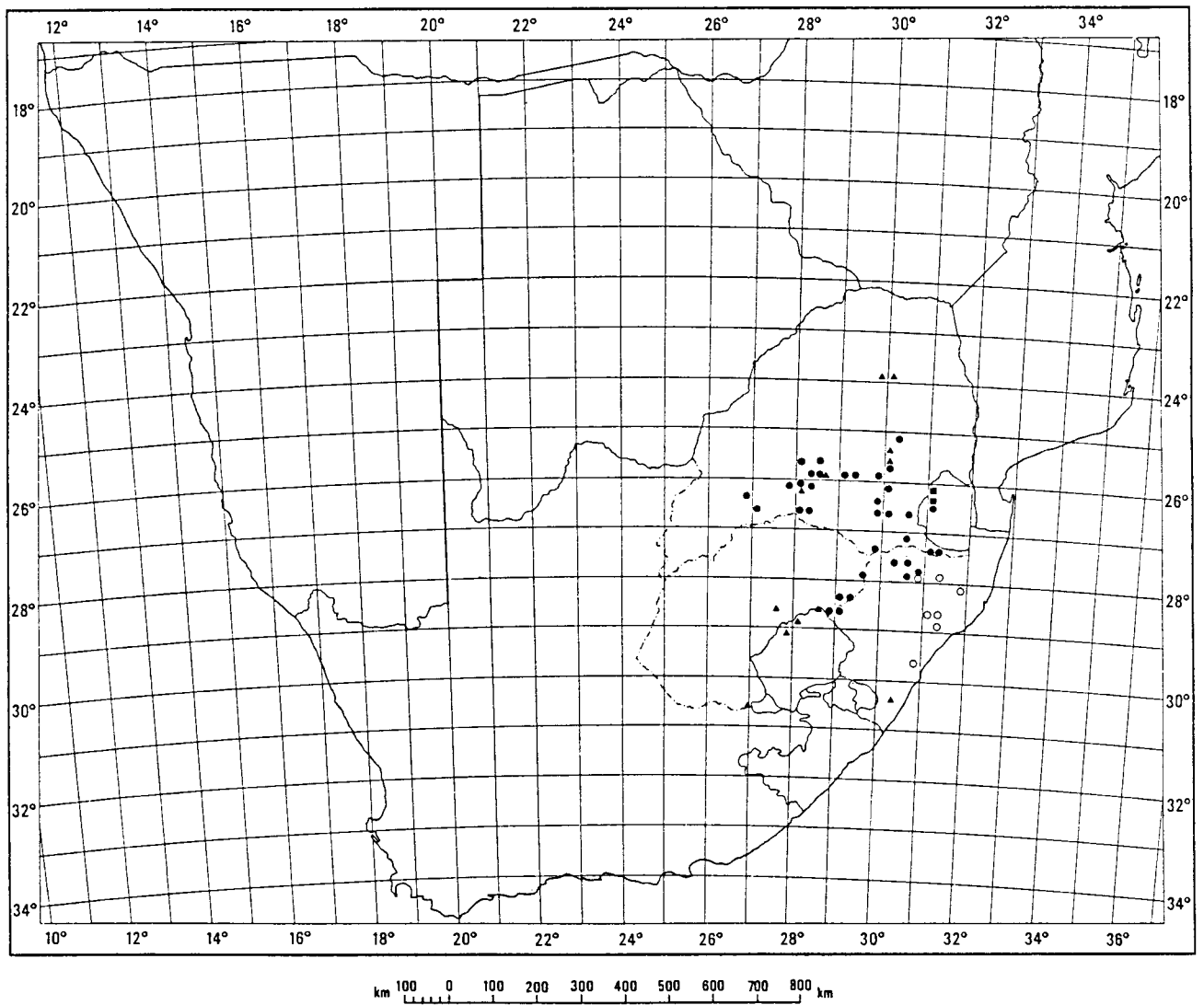
Vouchers: Compton 26737, 28666, 32111.



Map 5.5. The known geographical distribution of
L. procumbens (●), *L. difformis* (★), *L. sutherlandii* (△)
and *L. pulchra* (■).



Map 5.6. The known geographical distribution of *L. eriantha* [typical form (▼), intermediate forms (▽)] and *L. corymbosa* (●).



Map 5.7. The known geographical distribution of *L. grandis* (○), *L. lanceolata* (▲), *L. foliosa* (●) and *L. spicata* (■).

Section 4. Leptis (E. Mey. ex Eckl. & Zeyh.) Benth. emend. B-E. van Wyk, emend. nov.

Lotononis section Leptis (E. Mey. ex Eckl. & Zeyh.) Benth. in Hook., Lond. J. Bot. 2: 607 (1843), pro parte; Harv. in Harv. & Sond., Fl. Cap. 2: 49 (1862), pro parte; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 280 (1913), pro parte. Lectotype species: Leptis debilis Eckl. & Zeyh. [now Lotononis prolifera (E. Mey.) B-E. van Wyk].

Leptis E. Mey. ex Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 174 (1836); Benth. in Ann. Wien. Mus. 2: 142 (1839); Steud., Nom. Bot. 2(2): 29 (1841); Walp., Rep. Bot. Syst. 1: 619 (1842); D. Dietr., Syn. pl. 4: 959 (1847).

Lipozygis (section 3) E. Mey., Comm. Pl. Afr. Austr. 1(1): 77 (1836), pro parte mai.

Leptidium Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845), pro parte.

Note: The sectional limits are here modified to exclude all those species with subequally lobed calyces, acute keel petals, markedly dimorphic anthers and which have the claw of the standard petal dilated towards the base. These species are mostly cyanogenic and have pyrrolizidine alkaloids (rather than quinolizidine alkaloids as the rest of Leptis) and are therefore referred to the section Oxydium. All the species retained in Leptis are acyanogenic, have hairy petals and have the lateral

and upper lobes of the calyx fused in pairs on either side. The narrowed circumscription is an obvious improvement and agrees closely with the original concept of Ecklon and Zeyher (1836).

Prostrate or procumbent perennial suffrutescent herbs, rarely prostrate shrublets with thick woody branches, or annuals. All mature parts usually densely pubescent or sericeous, rarely glabrescent. Leaves alternate, digitately trifoliolate, rarely 5-foliolate (*L. lupinifolia*), leaflets small, variable in shape, usually densely pubescent or sericeous at least on the abaxial surface, rarely glabrescent. Stipules usually single at each leaf base, occasionally paired, rarely digitate, similar to the leaflets or usually much smaller. Inflorescences subsessile, short congested racemes, subumbellately 1- to 4-flowered, rarely with up to 20 flowers, leaf-opposed or terminal on short lateral branches; bracts small, linear; bracteoles absent except in two species, minute and inconspicuous when present. Flowers on short pedicels, usually small, yellow. Calyx campanulate, not inflated, with the upper and lateral lobe on either side fused higher up in pairs, the carinal lobe narrower and often much shorter than the upper lobes. Standard as long or slightly longer than the keel, rarely much shorter than the keel, never totally glabrous, often densely pubescent or hirsute. Wing petals usually shorter than the keel, often pubescent at least along the lower edge of the lamina. Keel petals half oblong-elliptic to narrowly oblong; apex rounded or obtuse, pubescent, rarely glabrescent. Anthers dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the

carinal anther similar to the dorsifixed anthers. Pods sessile, small, usually scarcely longer than the calyx or up to twice as long as the calyx, ovoid, obovoid to broadly oblong, flat or slightly inflated, thin-walled, upper suture \pm smooth, dehiscent, rarely tardily dehiscent, usually \pm 10-seeded, occasionally 2--4-seeded, rarely 1- or 2-seeded. Seeds small, usually \pm 2 mm in diameter, rarely up to 3 mm, variable in shape, testa usually tuberculate, rarely rugose or smooth. Chromosome base number 9 ($2n = 18$). (Figures 5.5 & 5.6).

The section has a disjunct distribution in central and southern Africa and in the Mediterranean region (Map 5.8). Sixteen of the 20 species are concentrated in the summer rainfall area of southern Africa, extending northwards to eastern tropical Africa. Only four species occur in the dry western part of southern Africa (Maps 5.8 & 5.9) and five others occur in Spain, Morocco, Algeria, south-eastern Bulgaria, north-eastern Greece and Turkey (Map 5.8).

There are no obvious apomorphies for the section Leptis, so that it is a rather poorly defined group. The species are all very similar in their general morphology however, and it is difficult to imagine that they are not closely related. Diagnostic characters of various other sections are absent or occur in different combinations. For example, the stipules are never paired as in Listia and Euchlora (except in L. carinata, L. hirsuta and L. bullonii); flowering leaves are never opposite as

in Leobordea (but often subopposite in L. lupinifolia and related species); the inflorescences are few-flowered and never grouped in a many-flowered subumbellate arrangement as in Lipozygis (except in L. esterhuyseana); the flowers are never sessile as in Synclistus; bracteoles are never present as in Listia (except in L. stolzii and L. mollis); the keel petals are never acute and the standard petal never basally dilated as in Oxydium (the pods also never conspicuously turgid); the pods are never stipitate as in Digitata, and the leaves also never predominantly 5-foliolate (except in L. lupinifolia).

Some of the species that were included in Leptis by Benthams (1843), Harvey (1862) and Dümmer (1913) are here retained in the section, but several are referred to other sections, so that the group is now much smaller. Of the 46 species of Leptis in Dümmer's (1913) synopsis, only 11 are retained here. The fate of the remaining 35 is as follows: two referred to other genera, 16 placed in synonymy, 12 referred to the section Oxydium and five referred to the sections Digitata, Monocarpa and Cleistogama.

Key to the groups and species of section Leptis:

- 1A. Inflorescence with more than 8 flowers; standard petal half as long as the keel; ovules 1 or 2; pods 1- or 2-seeded; rare annual from the south-western Cape Province
..... Group E (37. L. esterhuyseana)
- 1B. Inflorescence with up to 5 flowers (if rarely more than 5 then the stipules paired); standard petal as long or slightly shorter than the keel; ovules 3 or more; pods usually more than 2-seeded; not from the south-western Cape:
 - 2A. Stipules invariably paired (rarely more than two stipules per node), similar to the leaflets in size
..... Group D, partly:
 - 3A. Vestiture of long spreading hairs; stipules similar to the leaflets or often larger, often cordate at the base; plant often drying black; flowers often turning pink with age ...
..... 36. L. hirsuta
 - 3B. Vestiture of short appressed hairs; stipules usually smaller than the leaflets; not distinctly cordate at the base; plant not drying black; flowers rarely turning pink with age 35. L. carinata
 - 2B. Stipules single at each node (paired at some nodes in one species, then with the two of each pair dissimilar in size and shape, occasionally digitate but then all inserted on one side of the petiole):

4A. Bracteoles present:

5A. Petioles much longer than the leaflets; leaflets
conduplicate, densely hairy on both surfaces; known only
from the Kamiesberg in the north-western Cape Province ...
..... Group C (27. *L. mollis*)

5B. Petioles shorter than the leaflets (usually much shorter);
leaflets not conduplicate, sparsely hairy; known only from
the Nyika Plateau and surrounding areas in central Africa
..... Group D, partly (33. *L. stolzii*)

4B. Bracteoles absent:

6A. Upper surface of the leaflets densely hairy:

7A. Leaflets strongly conduplicate; prostrate shrubs with thick
woody branches:

8A. Leaflets linear-oblong; stipules similar to the leaflets
in size and shape; known only from Morocco
..... Group A (25. *L. tapetiformis*)

8B. Leaflets obovate; stipules inconspicuous; known only from
southern Namibia Group B (26. *L. mirabilis*)

7B. Leaflets not conduplicate; prostrate or procumbent
suffrutescent herbs with thin non-woody branches:

- 9A. Lower (carinal) lobe of the calyx shorter than the upper
4 lobes; epidermal hairs biramous (two-armed);
Mediterranean region (Morocco, Algeria, southern Spain,
Turkey and south-eastern Bulgaria)
..... Group G:
- 10A. Leaves mostly 5-digitate 41. *L. lupinifolia*
- 10B. Leaves 3-digitate:
- 11A. Petiole much shorter than the
terminal leaflet; corolla scarcely
longer than the calyx 42. *L. genistoides*
- 11B. Petiole \pm as long as the terminal leaflet:
- 12A. Leaves and calyx silky; flowers
1 or 2 per inflorescence; stipules
single 43. *L. maroccana*
- 12B. Leaves and calyx hirsute; flowers
up to 4 per inflorescence; stipules
often paired, at least at some
nodes 44. *L. bullonii*
- 9B. Lower (carinal) lobe of the calyx similar to
the upper 4; epidermal hairs uniseriate
(one-armed); eastern parts of southern
Africa Group F, partly (38. *L. adpressa*)

6B. Upper surface of the leaflets glabrous:

13A. Inflorescences invariably leaf-opposed; corolla as long or
scarcely longer than the calyx; annuals

..... Group F, partly:

14A. Calyx slightly inflated; pods not longer
than the calyx, with the apex obtuse and
curved downwards 39. *L. calycina*

14B. Calyx not inflated; pods \pm 2x as long as
the calyx, with the apex acute and curved
upwards 40. *L. acuticarpa*

13B. Inflorescences terminal on short lateral branches; corolla
longer than the calyx; perennial herbs

..... Group D, partly:

15A. Calyx with the upper 4 lobes very much expanded, several
times wider than the lower lobe; the fused part of the
calyx usually bright red 32. *L. pariflora*

15B. Calyx not as above:

- 16A. Flowers relatively large, more than
9 mm long..... 34. *L. decumbens*
- 16B. Flowers relatively small, up to 8 mm long:
 - 17A. Standard petal with a line of hairs along
the middle only, keel nearly glabrous; pods
much longer than the calyx:
 - 18A. Flowers very narrow in shape, with the corolla
curved upwards; pods broadly obovate, densely
covered with short hairs 30. *L. prolifera*
 - 18B. Flowers not very narrow and the
corolla not curved upwards; pods
oblong, virtually glabrous 31. *L. mucronata*
 - 17B. Standard petal hairy for at least a large
part of the surface; keel densely hairy;
pods as long or only slightly longer than
the calyx:
 - 19A. Leaflets narrowly oblanceolate; leaves of vigorous
shoots with the petioles much longer than the
leaflets; twigs densely silky-sericeous,
at least when young 28. *L. arida*
 - 19B. Leaflets obovate; leaves of vigorous
shoots with the petioles as long or shorter
than the leaflets; twigs minutely and
inconspicuously pubescent 29. *L. pusilla*

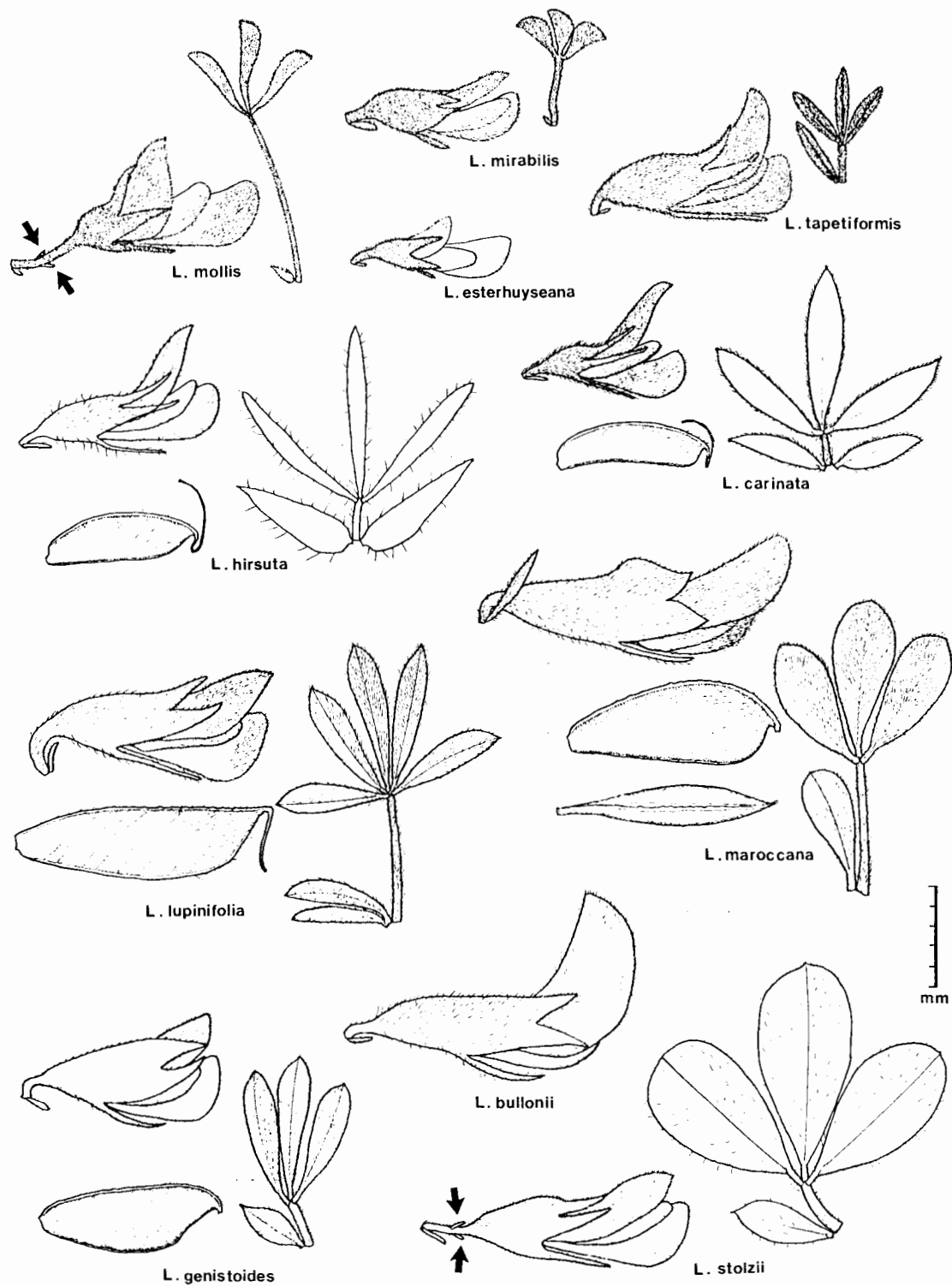


Figure 5.5. Leaves, flowers and pods of the species of the section *Leptis*.

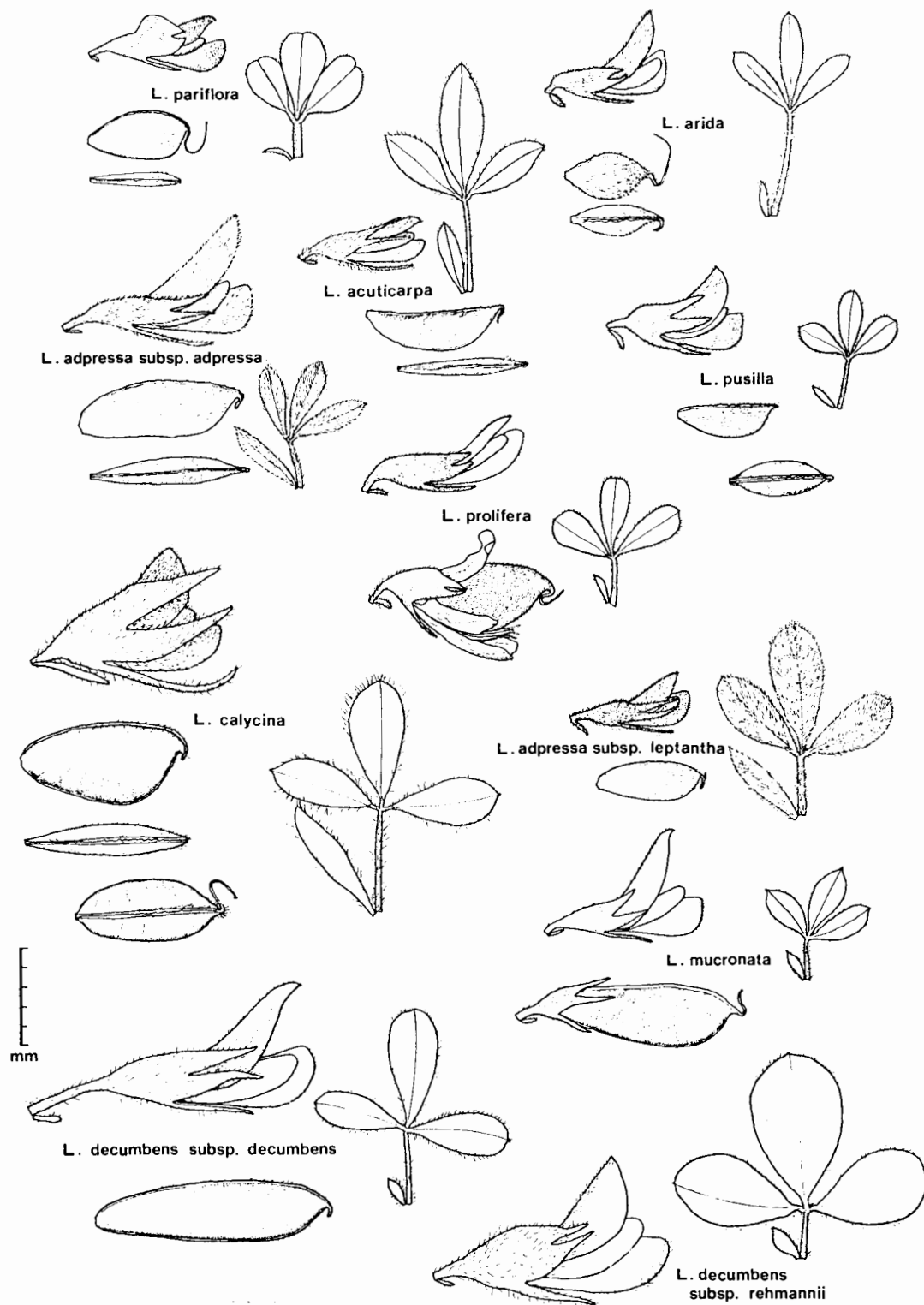


Figure 5.6. Leaves, flowers and pods of the species of the section *Leptis*.

Group A (one species)

Prostrate shrub with thick woody branches; leaflets narrowly oblong, conduplicate, densely sericeous on both surfaces, the hairs biramous; stipules single at each node, similar to the leaflets in size and shape; bracteoles absent; petals densely hairy. One species, endemic to Morocco (Map 5.8).

25. *L. tapetiformis* Emberger & Maire in Bull. Soc. Hist. nat. Afrique Nord 28(6): 349 (1937); Emberger & Maire, Cat. Pl. Maroc. 4: 1025 (1941). Type: Morocco, ... "Atlantis Majoris orientalis ad radices australes montis Masker, inter Tagoudimt et Anemzi, ad alt. 2200--2400 m", Emberger & Maire s.n. 1936 (not seen).

Amphinomia tapetiformis (Emberger & Maire) Maire, Contr. 3328 in Bull. Soc. Hist. nat. Afrique Nord (1941); Maire, Fl. Afrique Nord 16: 86 (1987). Type as above.

L. tapetiformis is remarkably similar to *L. mirabilis*, but differs in the shape of the leaflets and the much larger stipules and flowers (Figure 5.5).

Voucher: Maire & Weiller 697.

Group B (one species)

Prostrate shrub with thick woody branches; leaflets broadly obovate, conduplicate, densely sericeous on both surfaces, the hairs uniseriate; stipules single at each node, inconspicuous; bracteoles absent; petals densely hairy. One species, known only from southern Namibia (Map 5.9).

26. *L. mirabilis* Dinter in Fedde, Repert. 30: 200 (1932); Schreiber in FSWA 60: 83 (1970). Types: Namibia, "Granitflachberge von Aus und Gubub", Dinter 3597 (SAM!, lecto., designated here; BOL!, K!, PRE!); "Granitberge von Zwartaus (6 km nordl. Aus)", Dinter 6098 (BM!, BOL!, K!, M!, PRE!, S!, SAM!).

Amphinomia mirabilis (Dinter) Schreiber in Mitt. Bot. Staatssamm. München 2: 288 (1957). Type as above.

L. mirabilis is very similar to *L. tapetiformis*. The habit of the two species appears to be identical. It can be distinguished from the latter by the obovate leaflets, the very small stipules and the smaller flowers. (Figure 5.5).

Vouchers: Dinter 3597, 6098; Pillans 5970.

Group C. (one species)

Prostrate shrublet (?), with the branches somewhat woody towards the base; leaflets broadly oblanceolate, conduplicate, on long slender petioles, densely sericeous on both surfaces, the hairs uniseriate; stipules single at each node; bracteoles present; petals densely hairy. One species, known only from the type collection in the north-western Cape Province (Map 5.9).

27. L. mollis (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 609 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 64 (1862); Dümmer in Trans. R. Soc. S. Afr. 3(2): 317 (1913). Type: South Africa, Cape Province, Leliefontein [Kamiesberg, Namaqualand], Drège s.n. (K!, lecto., designated here; MO!, S!).

Lipozygis mollis E. Mey., Comm. Pl. Afr. Austr. 1(1): 79 (1836); Walp., Rep. Bot. Syst. 1: 622 (1842). Type as above.

Lipozygis villosa E. Mey. sensu Benth., Harv. (sphalm, = L. mollis).

Leptis mollis (E. Mey.) Benth. in Ann. Wien. Mus. 2: 142 (1839); Steud., Nom. Bot. 2(2): 29 (1841). Type as above.

Leptidium molle (E. Mey.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845). Type as above.

Polylobium molle (E. Mey.) D. Dietr., Syn. pl. 4: 962 (1847). Type as above.

This poorly known species has apparently not been rediscovered since the time of the type collection. It is quite distinct, and can easily be identified by the presence of bracteoles, the slender petioles, the conduplicate leaflets and the densely hairy petals (Figure 5.5).

Group D. (nine species)

Suffrutescent perennial herbs with erect or usually prostrate branches from a woody base, the branches often somewhat woody towards the base; leaves 3-foliolate; leaflets not conduplicate, totally glabrous on the adaxial surface (if rarely sparsely hairy then with distinct bracteoles); the hairs uniseriate; stipules single at each node, less often paired (2 species); inflorescences invariably terminal on short lateral branches, 1- to 4-flowered fascicles (if rarely more than 4-flowered then the stipules paired at each node); corolla pubescent, the wing and keel petals rarely glabrescent; pods flat or only slightly inflated, very short or up to 2x as long as the calyx.

28. *L. arida* Dummer in Trans. R. Soc. S. Afr. 3(2): 324 (1913).
Type: South Africa, Cape Province, mountain tops, Eland's Hoek [3026 DC] near Aliwal North, E. Bolus 31 sub BOL 10559 (K!, lecto., designated here; BOL!).

L. myriantha Bak. f. ex Gibbs Russell et al. in Mem. Bot. Surv. S. Afr. 56: 76 (1987), nom. nud. [Note: this name is associated with several collections from Forest Hill, Johannesburg, Mogg 5236 (BM!, PRE!) but has apparently never been published].

This rather poorly known species is superficially similar to *L. prolifera* and *L. pusilla*. It can be distinguished from these species by the long petioles (often persistent for some time after the leaflets are shed), the densely silky-sericeous vestiture of the young twigs and by the shape of the pods, which are almost orbicular in lateral view. *L. arida* is known from a few isolated localities along the eastern parts of southern Africa (Map 5.10).

Vouchers: Acocks 11722, 20970; Germishuizen 197; Moss 5236; Murray 19; Van Wyk 1825.

29. *L. pusilla* Dümmer in Trans. R. Soc. S. Afr. 3(2): 324 (1913). Type: South Africa, Cape Province, slopes of mountains, Eland's Hoek [3026 DC] near Aliwal North, F. Bolus s.n. sub BOL 10535 (K!, lecto., designated here), F. Bolus 122 sub BOL 8141 (BOL!, isolecto.), F. Bolus 122 (PRE, isolecto.). [Note: this collection was wrongly labelled in BOL. The specimen in the type cover (BOL 8141) is not *L. pusilla*, but rather *L. laxa*. F. Bolus 122 sub BOL 8141 (upper right hand side of the sheet) is identical to Dümmer's type specimen in K].

L. dregeana Dümmer in Trans. R. Soc. S. Afr. 3(2): 329 (1913),
synon. nov. Type: South Africa, Cape Province, Queenstown Div.,
Shiloh, Drège s.n. b (K!, holo.; S!).

Lipozygis calycina, var. b. E. Mey., Comm. Pl. Afr. Austr.
1(1): 78 (1836). Type as for *L. dregeana*.

L. ambigua Dümmer in Trans. R. Soc. S. Afr. 3(2): 327 (1913),
synon. nov. Types: South Africa, Cape Province, near Somerset
East, MacOwan 1739 (K!, lecto., designated here); Natal,
Boschberg, MacOwan 2022 pro parte (isosyn., not seen).

This poorly known species is often confused with *L. mucronata*,
but the flowers and pods are quite different (Figure 5.6). In
comparison with other perennial species, the habit is often
exceptionally small. *L. pusilla* is quite common in the eastern
Cape and the south-eastern Orange Free State (Map 5.11).

Vouchers: MacOwan 1870; Muller 1782; Reid 198; Thode A1803,
A1845; Van Wyk 1583.

30. *L. prolifera* (E. Mey.) B-E. van Wyk, comb. nov.

Crotalaria prolifera E. Mey. in Linnaea 7: 152 (1832). Type:
South Africa, Cape Province, "Nieuwe feld", Distr. Beaufort,
Drège s.n. (S!, annotated by Meyer, lecto., designated here).

Leptis prolifera (E. Mey.) Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 175 (1836); Walp., Rep. Bot. Syst. 1: 619 (1842). Type as above.

Leptis debilis Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 175 (1836); Walp., Rep. Bot. Syst. 1: 619 (1842); D. Dietr., Syn. pl. 4: 959 (1847). Type: South Africa, Cape Province, "Zwartkopsrivier (Uitenhage)", Ecklon & Zeyher 1264 (S!, lecto., designated here; C!, S!, SAM!).

Leptidium falcatum Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845), as nom. nov. for Leptis debilis Eckl. & Zeyh. non Leptidium debile (Eckl. & Zeyh.) Presl.

Lotononis porrecta (E. Mey.) Benth. sensu Harv. in Harv. & Sond., Fl. Cap. 2: 60 (1862), excl. syn. Capnitis porrecta (E. Mey.) Benth. [Note: following Bentham's (1843) guess that Leptis debilis and Leptis prolifera may be the same as Capnitis porrecta E. Mey., Harvey used Ecklon & Zeyher 1264 and 1265 for his description].

Lotononis microphylla Harv. in Harv. & Sond., Fl. Cap. 2: 65 (1862); Dümmer in Trans. R. Soc. S. Afr. 3(2): 327 (1913), synon. nov. Type: South Africa, without precise locality, Zeyher s.n. (TCD, holo.; S!, iso.). [Note: Harvey (1862) remarked in the original diagnosis that L. microphylla is "Apparently a distinct species"]].

Lotononis neglecta Dümmer in Trans. R. Soc. S. Afr. 3(2): 322 (1913), synon. nov. Type: South Africa, Cape Province, Uitenhage, Pappe s.n. (K!, holo.). [Note: the holotype is probably a small piece of the Ecklon & Zeyher 1265 collection that was relabelled by Pappe].

L. prolifera is superficially similar to other species and has been confused with L. porrecta (E. Mey.) Benth. and even L. decumbens. The narrow corolla is usually curved upwards (Figure 5.6) and the short but very broad pods are also quite distinct. The species is endemic to the eastern Cape Province (Map 5.11).

Vouchers: Ecklon & Zeyher 1265; Galpin 2334; Paterson 680; Van Wyk 1700, 1701.

31. L. mucronata Conrath in Kew Bull. 1908: 222 (1908); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 325 (1913); Burt Davy, Man. pl. Transvaal: 288 (1932). Type: Transvaal, Modderfontein, Conrath 124 (K!, holo.).

L. gerrardii Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 325 (1913); Burt Davy, Man. pl. Transvaal: 388 (1932), as synonym of L. mucronata. Type: Natal, without precise locality, Gerrard 1075 (K!, holo.; BM).

L. gerrardii Dümmer var. *transvaalensis* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 326 (1913); Burt Davy, Man. pl. Transvaal: 388 (1932), as synonym of *L. mucronata*. Type: Transvaal, near the Klein Olifants River, Schlechter 3809 (K!, holo.; Z).

L. ornata Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 327 (1913), synon. nov. Type: Lesotho, without precise locality, Cooper 745 (K!, holo.).

L. affinis Burt Davy, Man. pl. Transvaal: 389 (1932) non Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 178 (1836), synon. nov. Type: Transvaal, Lydenburg District, Belfast, Burt Davy 1399 (PRE!, holo.; PRE!).

L. mucronata is geographically widespread (Map 5.9) and quite variable. I could find no distinct morphological discontinuities and suggest that it is impractical to retain floriferous forms ("*L. ornata*") and stunted forms ("*L. affinis*") as distinct species. A form of the species from Zimbabwe however, has exceptionally long pedicels and may be distinct at the infraspecific level. *L. mucronata* can easily be distinguished from other species by the broadly oblong, glabrescent pods (Figure 5.6).

Vouchers: Bayliss "Lesotho 026"; Compton 25587; Galpin 1497; Hilliard & Burt 9850; Van Wyk 1794, 1806, 1807. Form with long pedicels (Zimbabwe): Pope, Muller & Polhill 2031.

32. *L. pariflora* N. E. Br. in Burt Davy, Man. pl. Transvaal: 388 (1932). Types: Transvaal, Pietersburg District, The Downs, Rogers 21994 (K!, lecto., designated here; PRE!); Rogers 22017 (PRE!).

[Note: incorrectly listed by Lock (1989, p. 222) as "*L. parviflora*" Burt Davy].

The unusual calyx (see Figure 3.1.8, 32) and densely hairy corolla (Figure 5.6) are useful characters to distinguish this species from the superficially similar *L. mucronata*. *L. pariflora* is known only from the immediate vicinity of "The Downs" near Pietersburg (Map 5.10).

Vouchers: Junod 4374; Stalmans 884, 1843.

33. *L. stolzii* Harms in Engl., Bot. Jahrb. 54: 379 (1917); Bak. f., Leg. Trop. Afr. 1: 16 (1926); Milne-Redhead in Fl. Trop. E. Afr., Pap.: 816 (1971). Type: Tanzania, (North of Lake Nyasa, Kyimbila District), Western Njombe District, Madehani, Stolz 2602 (B+; K!, lecto., designated here; BM!, BOL!, C!, K!, MO!, PRE!).

This species is closely related to *L. decumbens* (superficially almost identical to *L. decumbens* subsp. *rehmannii*) but can be recognised by the presence of bracteoles and the isolated geographical distribution. Unlike all other species of the group,

the adaxial surface of the leaflets is sparsely hairy and not glabrous (Figure 5.5). L. stolzii is the only species of Lotononis endemic to central Africa and is known only from Tanzania and Malawi (Map 5.8).

Vouchers: Brummitt 10697; Pawek 9271; Phillips 1417; Polhill & Paulo 1680; White 2594.

34. L. decumbens (Thunb.) B-E. van Wyk comb. nov.

Two geographically isolated subspecies are recognised here (see Map 5.10):

34a. subsp. decumbens

Ononis decumbens Thunb., Prodr. pl. Cap.: 129 (1800), Fl. Cap.: 586 (1823); DC., Prodr. 2: 166 (1825); E. Mey., Comm. Pl. Afr. Austr. 1(1): 77 (1836), as doubtful synonym of Lipozygis humifusa. Type: "Roggeveld", Thunberg s.n. sub Thunb. Herb. 16604 (UPS!, lecto., designated here).

Crotalaria versicolor E. Mey. in Linnaea 7: 152 (1832). Type: South Africa, Cape Province, Distr. Uitenhage, Ecklon s.n. (S!, original Plantae Ecklonianae label, lecto., designated here; SAM!, two fragments).

Leptis versicolor (E. Mey.) Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 175 (1836); Walp., Rep. Bot. Syst. 1: 619 (1842); D. Dietr., Syn. pl. 4: 959 (1847). Type as above.

Lotononis versicolor (E. Mey.) Benth. in Hook., Lond. J. Bot.: 610 (1843), pro parte; Harv. in Harv. & Sond., Fl. Cap. 2: 66 (1862) pro parte, excl. syn. Leptis divaricata Eckl. & Zeyh. Type as above.

[Note: Benthams (1843) confused Crotalaria versicolor E. Mey. with C. tenella E. Mey. The cited specimen Zeyher 465 (K!) is not L. decumbens, but L. tenella (E. Mey.) Eckl. & Zeyh. Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 322 (1913) also confused L. versicolor with L. tenella q.v.; Harvey (1862) confused L. versicolor with L. calycina, and the latter with L. tenella].

Leptidium versicolor (E. Mey.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845). Type as above.

Leptis filicaulis Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 175 (1836); Walp., Rep. Bot. Syst. 1: 619 (1842); D. Dietr., Syn. pl. 4: 959 (1847). Type: South Africa, Cape Province, between Grahamstown and "Vischrivier", Ecklon & Zeyher 1268 (S!, specimen with fruit, lecto., designated here; C!, SAM!, S!).

Leptidium filicaulis (Eckl. & Zeyh.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845). Type as above.

Lipozygis humifusa E. Mey., Comm. Pl. Afr. Austr. 1(1): 77 (1836); Walp., Rep. Bot. Syst. 1: 621 (1842). Types: Cape Province, 'prope Schiloh', Drège s.n. a (not seen); Witbergen, Drège s.n. b (not seen).

Lotononis humifusa Burch. ex Benth. in Hook., Lond. J. Bot.: 609 (1843), synon. nov.; Harv. in Harv. & Sond., Fl. Cap. 2: 64 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 326 (1913). Type: Cape Province, Riet Fontein and vicinity, between Kasouga River and Port Alfred [3326 DA/DB Grahamstown], Burchell 3927 (K!, lecto., designated here).

Polylobium humifusum (E. Mey.) D. Dietr., Syn. pl. 4: 962 (1847). Type as for Lipozygis humifusa.

Lipozygis radula E. Mey., Comm. Pl. Afr. Austr. 1(1): 77 (1836); Walp., Rep. Bot. Syst. 1: 622 (1842). Type: Cape Province, "Nieuwe Hantom" [3026 CC Aliwal North], Drège s.n. (not seen).

Polylobium radulum (E. Mey.) D. Dietr., Syn. pl. 4: 962 (1847). Type as above.

Lotononis humifusa Burch. ex Benth. var. radula (E. Mey.) Harv. in Harv. & Sond., Fl. Cap. 2: 64 (1862). Type as above.

It is fortunate that an original specimen of Meyer's Crotalaria versicolor is still available in S, because it clears up the confusion caused by wrongly labelled specimens in SAM. Meyer cited Ononis decumbens Thunb. as a possible synonym, but he and later authors (Bentham, Dümmer) did not study the Thunberg type specimen.

Differences between the two subspecies of L. decumbens are given under subsp. rehmannii below. The typical subspecies is very often confused with L. calycina and L. tenella. The

co-occurrence (in the eastern Cape) of *L. decumbens* subsp. *decumbens* and a form of *L. calycina* with rather long pods (which is identical to Ecklon & Zeyher's *Leptis divaricata*, see below) has caused much confusion in the past. *L. decumbens* may be distinguished from *L. calycina* by the glabrescent keel petals (the lamina of the keel petals in the latter is completely covered with hairs). *L. decumbens* subsp. *decumbens* appears to be endemic to the eastern Cape Province (Map 5.10).

Vouchers: Bayliss 5001; Britten 698; Dyer 2125; MacOwan 2869; Story 2284.

34b. subsp. *rehmannii* (Dümmer) B-E. van Wyk stat. nov.

L. rehmnnii Dümmer in Trans. R. Soc. S. Afr. 3(2): 326 (1913).
Type: South Africa, Transvaal, "Hogge Veld, Perekopberg"
[Highveld, Perdekopberg, near Standerton], Rehmann 6831 (K!, lecto., designated here, BM!, Z).

This subspecies is geographically separated from subsp. decumbens, and occurs at high altitudes in Lesotho, Transvaal and Zimbabwe (Map 5.10). As shown in Figure 5.6, it can easily be distinguished by the shorter and wider flowers, the very shallow lateral sinuses of the calyx and the broadly obovate leaflets. The apex of the keel is marked with dark purple in all the

specimens I have seen (uniformly yellow in the typical subspecies). The differences between L. decumbens and L. stolzii is noted under the latter.

Vouchers: Corby 1258; Dieterlen 519b; Fawkes 176; Scheepers 1799; Venter 9722.

35. L. carinata (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 609 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 64 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 323 (1913). Type: South Africa: North-eastern Transkei, between "Omsamculo" [3030 CB Port Shepstone] and "Umcomas" [3030 BB Port Shepstone], Drège s.n. (K!, lecto., designated here; MO!, S!).

Lipozygis carinata E. Mey., Comm. Pl. Afr. Austr. 1(1): 80 (1836); Walp., Rep. Bot. Syst. 1: 622 (1842). Type as above.

Polylobium carinatum (E. Mey.) Benth. in Ann. Wien. Mus. 2: 142 (1839); D. Dietr., Syn. pl. 4: 963 (1847). Type as above.

Lotononis transvaalensis Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 292 (1913), synon. nov.; Burt Davy, Man. pl. Transvaal: 387 (1932). Types: South Africa, Transvaal, at Lydenburg, Wilms 266 (K!, holo.; BM!, PRE!); Krugerspost at Lydenburg, Wilms 266a (BM!).

L. florifera Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 323 (1913), synon. nov.; Burt Davy, Man. pl. Transvaal: 388 (1932). Type: South Africa, Natal, Zululand, N'Tondweni, Wood 9284 (K!, holo.; BOL!, NH, SAM!).

L. florifera Dümmer var. *major* Burt Davy: 388 (1932). Type: South Africa, Transvaal, Machadodorp, Burt Davy 5396 (K!, holo.).

L. pauciflora Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 293 (1913), *synon. nov.* Type: South Africa, Natal, Drakensberg Range, Coldstream, Rehmann 6904 (K!, holo.).

This species and the following are easily distinguished from others of the section by the paired stipules (Figure 5.5). The number of flowers and the size of leaflets have been used to describe several taxa as shown above, but I doubt the value of keeping them separate, even at varietal level. The known distribution area includes the Transvaal, Natal and north-eastern Transkei (Map 5.11).

Vouchers: Jenkins 6745, 9970; Schlechter 3830; Theron 3443; Thode 3142; Van Wyk 1872.

36. *L. hirsuta* Schinz in Bull. Herb. Boiss. 7: 33 (1899); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 292 (1913). Type: Transvaal, Houtbosch [2329 DD Pietersburg], Rehmann 6265 (Z, holo.; K!, iso.).

L. wilmsii Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 307 (1913), *synon. nov.*; Burt Davy, Man. pl. Transvaal: 387 (1932). Type: Transvaal, between Middelburg and Crocodile River, Wilms 277 (K!, holo.).

The habit of *L. hirsuta* is quite different from that of *L. carinata* and the two species are geographically separated (Map 5.11). As shown in Figure 5.5, the shape and vestiture of the leaflets and stipules are also useful diagnostic characters. The type specimen of *L. wilmsii* is a stunted plant of *L. hirsuta*.

Vouchers: Acocks 19162; Germishuizen 72; Louw 1264; Smith 1371; Van Wyk 2734.

Group E. (one species)

Prostrate annual; leaves 3-foliolate; leaflets minutely pubescent on the adaxial surface, the hairs uniseriate; stipules single at each node; inflorescences terminal and leaf-opposed, many-flowered congested racemes; calyx with the carinal lobe much smaller than the upper lobes; corolla pubescent; standard petal very short, only half as long as the keel; pods small, flat or only slightly inflated, 1 or 2-seeded.

37. *L. esterhuyseana* B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 29]. Type: South Africa, Cape Province, Ceres District, Stompiesvlei, Swartruggens, Esterhuysen 29341 (BOL!, holo.; C!, K!, MO!).

The unusual combination of characters in this poorly known species is discussed by Van Wyk (1989i, Appendix 29). It fits somewhat uneasily in the section Leptis and can readily be distinguished by the short standard petal (Figure 5.5), the many-flowered inflorescences and the 1- or 2-seeded pods. L. esterhuyseana is the only species of the section Leptis that occurs in the Cape Region (Map 5.9) and is known only from the type collection.

Group F (three species).

Prostrate perennial or annuals; branches often somewhat woody towards the base; leaves 3-foliolate, the leaves on flowering nodes usually subopposite; leaflets densely pubescent on the adaxial surface (L. adpressa) or totally glabrous (L. calycina & L. acuticarpa), the hairs uniseriate; stipules single at each node; inflorescences leaf-opposed, in 1- to 5-flowered fascicles; calyx nearly as long or longer than the corolla; corolla densely pubescent, the wing petals and keel not glabrescent; pods flat or slightly inflated, very short or up to 2x as long as the calyx. Three species from the eastern parts of southern Africa, with one extending into the northern Cape and Namibia.

38. *L. adpressa* N. E. Br.

Two subspecies are recognised here:

38a. subsp. *adpressa*

L. adpressa N. E. Br. in Kew Bull. 1906: 18 (1906); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 317 (1913). Type: Natal, Stony hill near Charlestown, Wood 5712 (K!, holo.).

L. sericoflora Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 317 (1913), synon. nov.; Burt Davy, Man. pl. Transvaal: 388 (1932). Type: Transvaal, "Hogge Veld", Standerton, Rehmann 6802 (K!, holo. Z, iso.).

Differences between the two subspecies are given under subsp. *leptantha* below (see Figure 5.6). *L. sericophylla* can no longer be considered distinct from *L. adpressa*. The number of flowers and the vestiture of the leaves were used by Dümmer (1913) to distinguish between the two species, but these characters are variable. The flowers of *L. adpressa* are similar to those of *L. calycina*, but this perennial species is readily distinguished from the latter (an annual) by the densely silky-sericeous leaflets (the adaxial surface of the leaflets is never glabrous as in *L. calycina*). The typical subspecies has a relatively wide geographical distribution in the eastern parts of southern Africa (Map 5.11).

Vouchers: Germishuizen 717; Muller 772; Pott 2973; Van Wyk 1557,
1567, 1568, 1899, 1916.

38b. subsp. leptantha B-E. van Wyk subsp. nov. A typo habitu
valde minore procumbenti non prostrato, foliolis parum maioribus
atque floribus leguminibusque minoribus.

Subspecies leptantha differs from the type in the much smaller
and procumbent rather than prostrate habit, the slightly larger
leaflets and the smaller flowers and pods.

Type: South Africa, Transvaal, Farm Waterval, 2 miles [3,2 km]
WNW of Krugersdorp, Mogg 22844 (PRE! holo.; PRE!, 2 sheets,
iso.).

The habit of this subspecies is different from that of the type
and the flowers and pods are less than 7 mm long, while they are
9 to 10 mm long in the typical subspecies (Figure 5.6). These
differences seem insignificant but it gives the plant a very
distinctive appearance. Subspecies leptantha is known only from
the Transvaal Highveld (Map 5.11).

39. L. calycina (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 611
(1843); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 323 (1913);
Burt Davy, Man. pl. Transvaal: 388 (1932); Schreiber in FSWA 60:

81 (1970). Types: South Africa: Cape Province, Katberg, Drège s.n. a (K!, Herb. Benth., lecto., designated here; BM!, K!, Herb. Hook.); Klipplaatrivier, Drège s.n. c (S!); Bothasberg, Drège s.n. d (not seen).

Lipozygis calycina E. Mey., Comm. Pl. Afr. Austr. 1(1): 78 (1836, Feb. or later), pro parte maj. (excl. var. b). Type as above.

Polylobium calycinum (E. Mey.) Benth. in Ann. Wien. Mus. 2: 142 (1839); D. Dietr., Syn. pl. 4: 962 (1847). Type as above.

Leptis calycina (E. Mey.) Steud., Nom. Bot. 2(2): 29 (1841). Type as above.

Leptidium calycinum (E. Mey.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845). Type as above.

Lotononis tenella (E. Mey.) Eckl. & Zeyh. var. calycina (E. Mey.) Harv. in Harv. & Sond., Fl. Cap. 2: 65 (1862). Type as above.

L. calycina (E. Mey.) Benth. var. hirsutissima (Harv.) Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 328 (1913). Type: South Africa, Transvaal, Magaliesberg, Burke s.n. (K!, determined by Harvey, lecto., designated here).

L. tenella (E. Mey.) Eckl. & Zeyh. var. hirsutissima Harv. in Harv. & Sond., Fl. Cap. 2: 65 (1862). Type as above.

L. calycina (E. Mey.) Benth. var. acuta Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 328 (1913). Type: South Africa, Transvaal, Lydenburg, Wilms 272 (K!, annotated by Dümmer, lecto., designated here), Wilms 273 (BM!, K!, isosyn.); Orange River Colony, Cooper

863 (K!, isosyn.); Natal, Valley of the Buffalo River near Charlestown, Wood 4796 (K!, isosyn.); Natal, between Pietermaritzburg and Newcastle, Wilms 1924 (K!, isosyn.).

Leptis divaricata Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 175 (1836, Jan.) non Lotononis divaricata (Eckl. & Zeyh.) Benth. Type: South Africa, Cape Province, side of Bothasberg, not far from "Vischrivier" [near Grahamstown], Ecklon & Zeyher 1266 (S!, lecto. designated here; C!; M!; SAM!, S!).

Leptidium divaricatum (Eckl. & Zeyh.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845). Type as above.

Lotononis orthorrhiza Conrath in Kew Bull. 1908: 222 (1908); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 322 (1913), synon. nov. Type: South Africa, Transvaal, Modderfontein, Conrath 121 (K!, notes by Conrath, lecto., designated here).

L. calycina is one of the most common species of Lotononis in southern Africa and is widely distributed in the eastern and central interior, extending into Namibia (Map 5.9). The shape and vestiture of the leaflets, and the size and shape of the pods are very variable but I could find no justification for retaining any infraspecific taxa. The calyx is usually as long or longer than the corolla and the pod broadly obovate, with the apex sharply downcurved (Figure 5.6).

Vouchers: Acocks 11319; Germishuizen 781; Potts 1328; Repton 1959; Van Wyk 1542, 1632, 1679.

40. *L. acuticarpa* B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 32]. Type: South Africa, Transvaal, Springs district, 5 km from Devon radar station to Leandra, Van Wyk 1815 (PRE!, holo.; JRAU!, K!, MO!, NBG!, iso.).

This annual species can easily be distinguished from *L. calycina* by the smaller habit and the distinctive shape of the pods (Figure 5.6). *L. acuticarpa* is known only from three localities in the southern Transvaal (Map 5.10).

Vouchers: Turner 1468, 1624; Van Wyk 1815, 2625.

Group G. (four species)

Prostrate or procumbent perennial herbs; leaves 3-foliolate or 5-foliolate, the leaves on flowering nodes usually subopposite; leaflets densely pubescent on the adaxial surface, the hairs biramous; stipules single at each node or occasionally paired; inflorescences leaf-opposed, in 1- to 4-flowered fascicles; calyx often nearly as long as the corolla, the carinal lobe much shorter than the upper lobes; corolla densely pubescent, the wing petals and keel not glabrescent; pods flat or slightly inflated, very short or up to 2x as long as the calyx. Four closely related species endemic to the Mediterranean (Map 5.8).

I have not seen type specimens of all the names, but the species are all well known and a large number of authentic specimens are available for most of them. The varieties distinguished by some authors may be useful at a regional level, but in terms of the variation within the genus as a whole, the differences are rather trivial.

41. Lotononis lupinifolia (Boiss.) Benth. in Hook., Lond. J. Bot.: 607 (1843); Dümmer in Trans. R. Soc. S. Afr. 3(2): 313 (1913); Jahandiez & Maire, Cat. Pl. Maroc. 2: 348 (1932), as Lotononis lupinifolia (Boiss.) Willk.; Smythies in Englera 3(2): 349 (1984). Type: Spain, Malaga Province, "in arenis torrentium Malaga, Motril", Boissier El. 61 (G; K! 2 sheets, M! 2 sheets, iso.).

Leobordea lupinifolia Boiss. in Bibl. univ. Genève (Feb. 1838), Elench. pl. nov.: 36 (Jan. 1838 according to Maire 1987, June 1838 on title page), Voy. bot. Espagne: 148, t. 52 (1840); Walp., Rep. Bot. Syst. 1: 623 (1842). Type as above.

Leobordea lupinifolia Boiss. ex Jaub. & Spach in Ann. Sci. Nat. 19: 237 (1843). Type as above.

Amphinomia lupinifolia (Boiss.) Pau. in Mem. Mus. Cienc. Barcelona, ser. Bot. 1,1: 35 (1922); Maire, Fl. Afr. Nord 16: 81 (1987).

Lotononis lupinifolia (Boiss.) Willk. var. eu-lupinifolia Maire in Jahandiez & Maire, Cat. Pl. Maroc. 2: 348 (1932), as new name for Cytisus pentaphyllus Salzman ined; Emberger & Maire, Cat. Pl. Maroc. 4: 1025 (1941); Maire, Fl. Afr. Nord 16: 83 (1987).

Leobordea villosa Pomel, Fl. Atl. 1: 162 (1874), as Leobardia villosa. Type from Algeria (not seen).

Leobordea villosa Pomel var. intermedia Pomel, Fl. Atl. 1: 162 (1874). Type not seen.

Lotononis lupinifolia (Boiss.) Willk. var. villosa (Pomel) Batt., Fl. Alg. 1: 209 (1889); Jahandiez & Maire, Cat. Pl. Maroc. 2: 348 (1932); Emberger & Maire, Cat. Pl. Maroc. 4: 1025 (1941); Maire, Fl. Afr. Nord 16: 83 (1987).

Lotononis lupinifolia Willk. var. intermedia (Pomel) Batt., Fl. Alg. 1: 209 (1889).

The only species known from southern Europe (Spain), also present in Marocco and Algeria (Map 5.8). Easily identified by the 5-digitate leaves (Figure 5.5).

Vouchers: Boissier & Reuter s.n.; Faure s.n.; Lange s.n.; Reverchon 191; Samuelsson 6238; Wall 197.

42. L. genistoides (Fenzl) Benth. in Hook., Lond. J. Bot.: 607 (1843); Boiss., Fl. Orient. 2: 31 (1872); Dümmer in Trans. R. Soc. S. Afr. 3(2): 318 (1913); Ball, Fl. Eur. 2: 104 (1968);

Jordanov, Fl. Reipubl. Bulgar. 6: 28 (1976); Chamberlain in Davis, Fl. Turkey 3: 36 (1970). Type: Turkey, "in monte Tauro prope Gulek", Kotschy 159 (K!, 2 sheets, iso.).

Leobordea genistoides Fenzl, Pug. pl. nov. Syr.: 6 (1842), as Leobordea lotoides sphalm., non. Leobordea lotoidea Del.; Fenzl, Ill. Pl. Syr. Tauri: 901 (1843); Walp., Rep. Bot. Syst. 1: 623 (1842); Jaub. & Spach in Ann. Sci. Nat. 19: 236 (1843). Type as above.

Amphinomia genistoides (Fenzl) Hayek, Prodr. Fl. Penins. Balc. 1: 891 (1926). Type as above.

Leobordea sericea Ledeb., Fl. ross. 1(3): 512 (1843). Type: "in provinciis transcausicis occidentalibus versus fines turcicas", Nordmann s.n. (not seen).

Leobordea argyrolobioides Jaub. & Spach in Ann. Sci. Nat. 19: 237 (1843). Type: "In Asia Minore, prope Karadjasan", Jaubert s.n. (not seen).

This is the only species of Lotononis absent from the African continent and one of only two species in the Flora Europaea area (Map 5.8). L. genistoides can easily be distinguished by the sparsely leafy twigs and the very short petioles (Figure 5.5).

Vouchers: Balansa s.n.; Bourgeau 95; Coode & Jones 2551; Davis & Coode 36967; McNeill 397.

43. *L. maroccana* Ball in J. Bot. 11: 302 (1873), Ball in J. Linn. Soc. (Bot.) 16: 394 & t. 15 (1878); Dümmer in Trans. R. Soc. S. Afr. 3(2): 318 (1913); Jahandiez & Maire, Cat. Pl. Maroc. 2: 348 (1932); Emberger & Maire, Cat. Pl. Maroc. 4: 1025 (1941); Maire, Fl. Afr. Nord 16: 83 (1987). Types: Morocco, "in regione inferiori Atlantis Majoris: prope Tasseremout", Ball s.n. (K!, isosyn.); "Ourika", Ball s.n. (K!, upper specimen on sheet with illustration, lecto., designated here; BM!; K!, bottom of second sheet, isolecto.), Hooker s.n. (K!, isosyn.); "Ait Mesan", Ball s.n. (K!, 2 sheets, isosyn.); "Amsmiz", Ball s.n. (K!, 2 sheets, isosyn.), Hooker s.n. (K!, isosyn.).

Amphinomia maroccana (Ball) Font Quer & Rothm. in Broteria 36: 149 (1940); Maire, Fl. Afr. Nord 16: 83 (1987). Type as above.

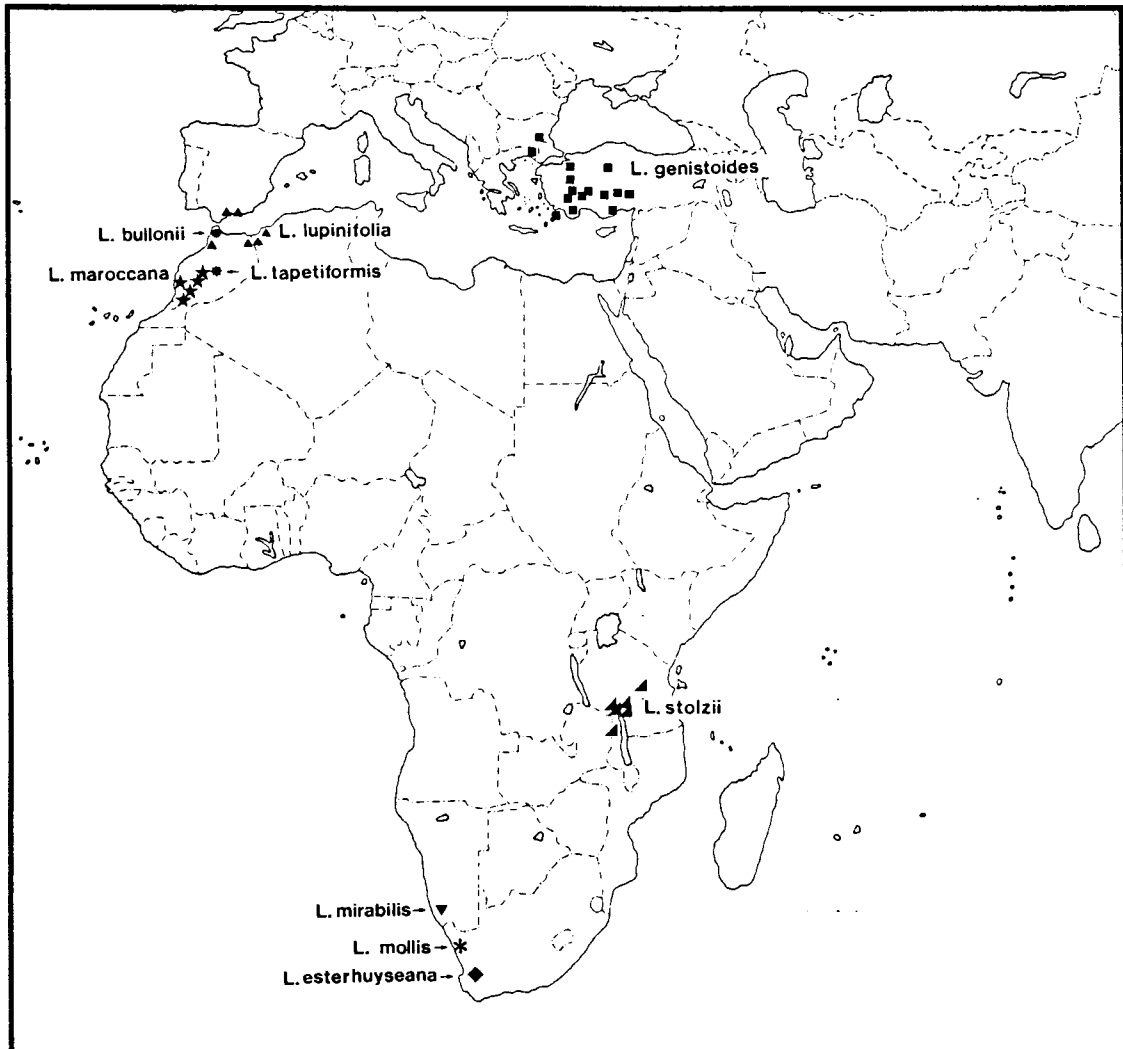
A species restricted to the Atlas Mountains in Morocco, where it seems to be fairly common (Map 5.8). *L. maroccana* can be distinguished from the closely related *L. bullonii* by the invariably single stipules and the short appressed vestiture (Figure 5.5).

Vouchers: Jahandiez 55; Lindberg 3511; Maw s.n.; Romieux 1260; Whiting & Richmond 241, 249.

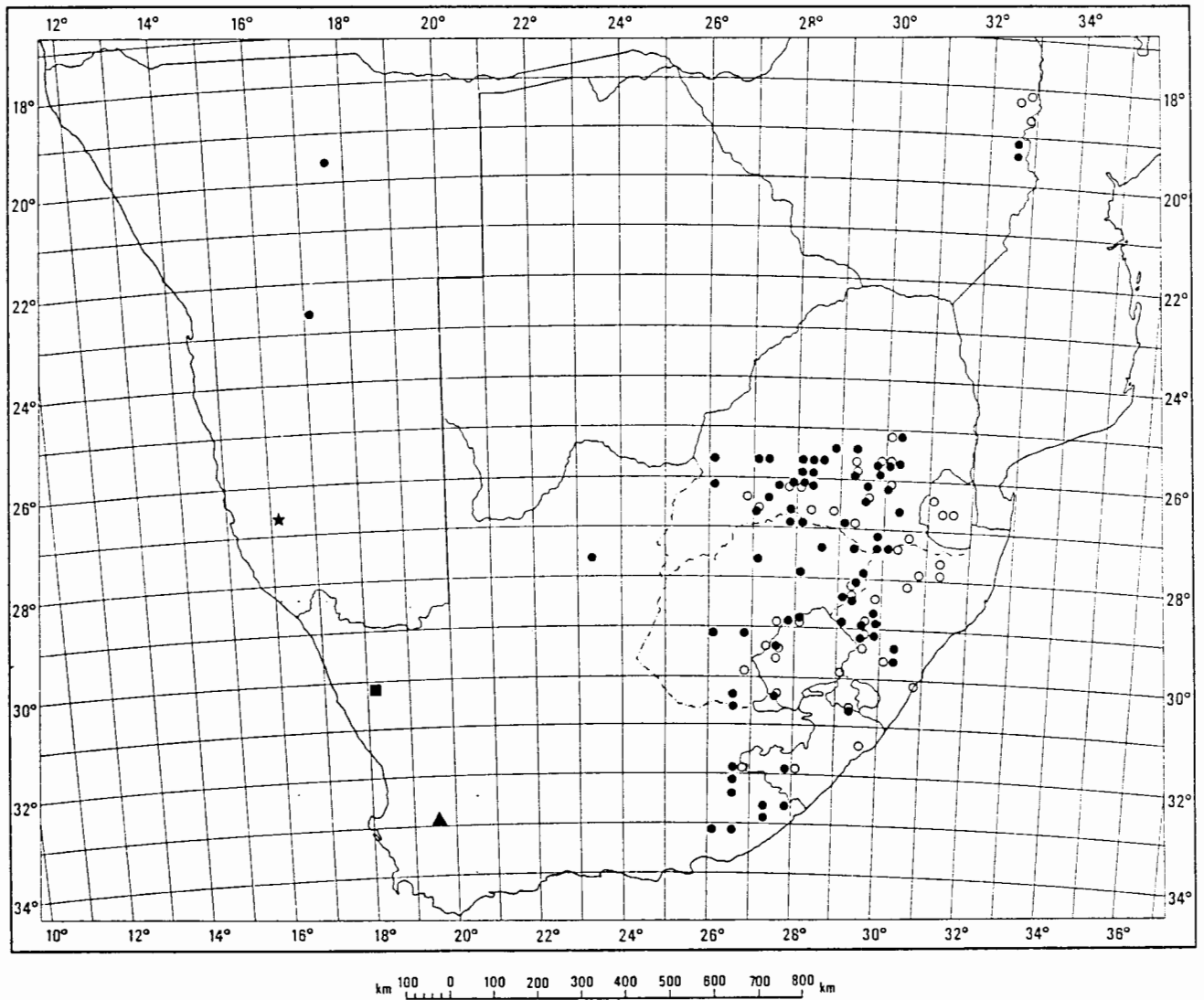
44. *L. bullonii* Emberger & Maire, Pl. Marocc. Nov. (Arch. Sc. Maroc.) Fasc. 1: 1 (1929); Emberger & Maire, Mat. Fl. Maroc. 27 (1930); Jahandiez & Maire, Cat. Pl. Maroc. 2: 348 (1932); Maire, Fl. Afr. Nord 16: 84 (1987). Type not seen.

L. bullonii is known only from northern Morocco (Map 5.8) and is very closely related to *L. maroccana*. It can easily be distinguished by the longer, more spreading hairs on the leaflets and calyx and the shape of the calyx lobes (Figure 5.5). The stipules are often paired and are not invariably single as in *L. maroccana*.

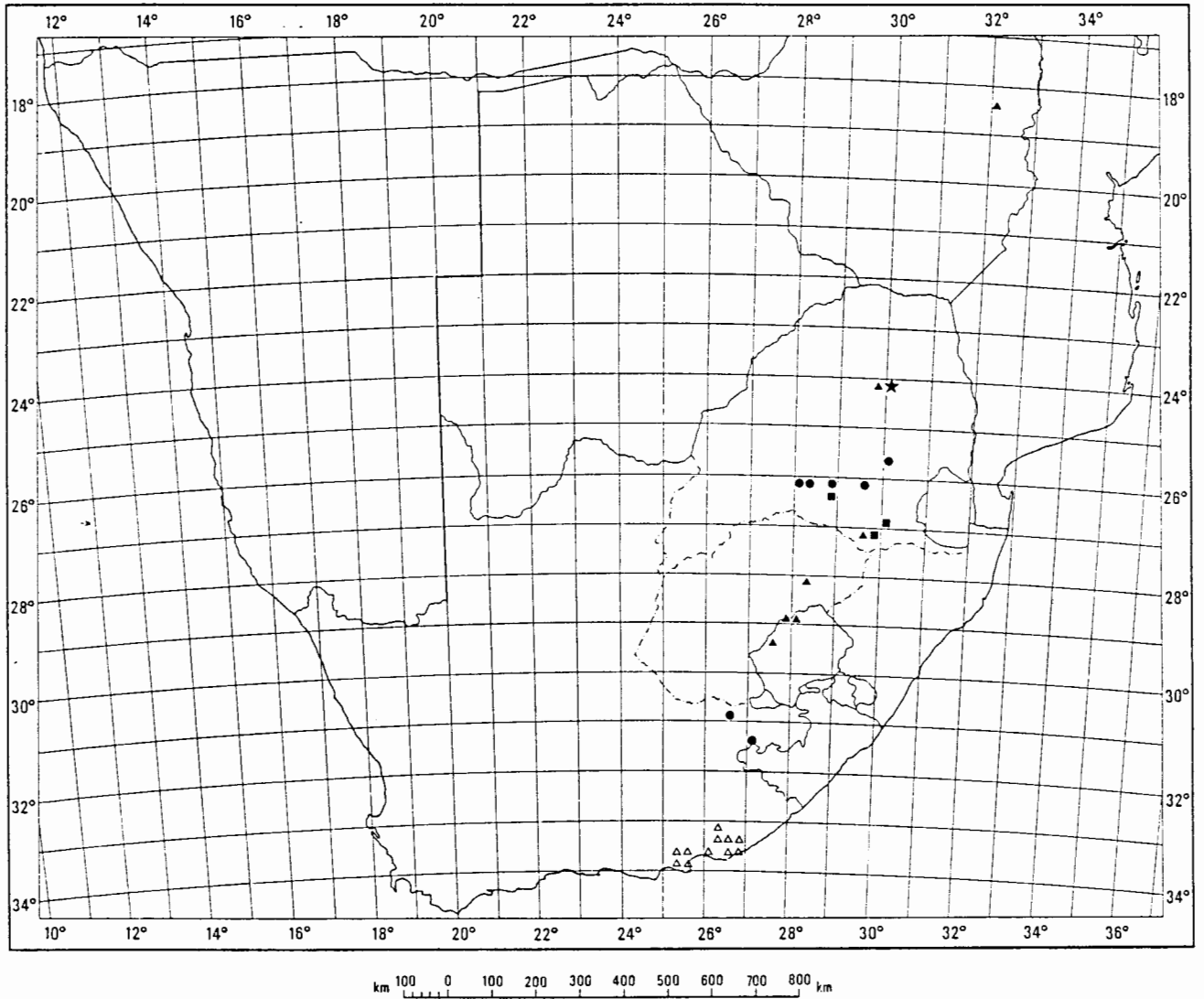
Vouchers: Font Quer s.n. ("Iter Maroccanum" 288); Merxmüller & Oberwinkler 220.



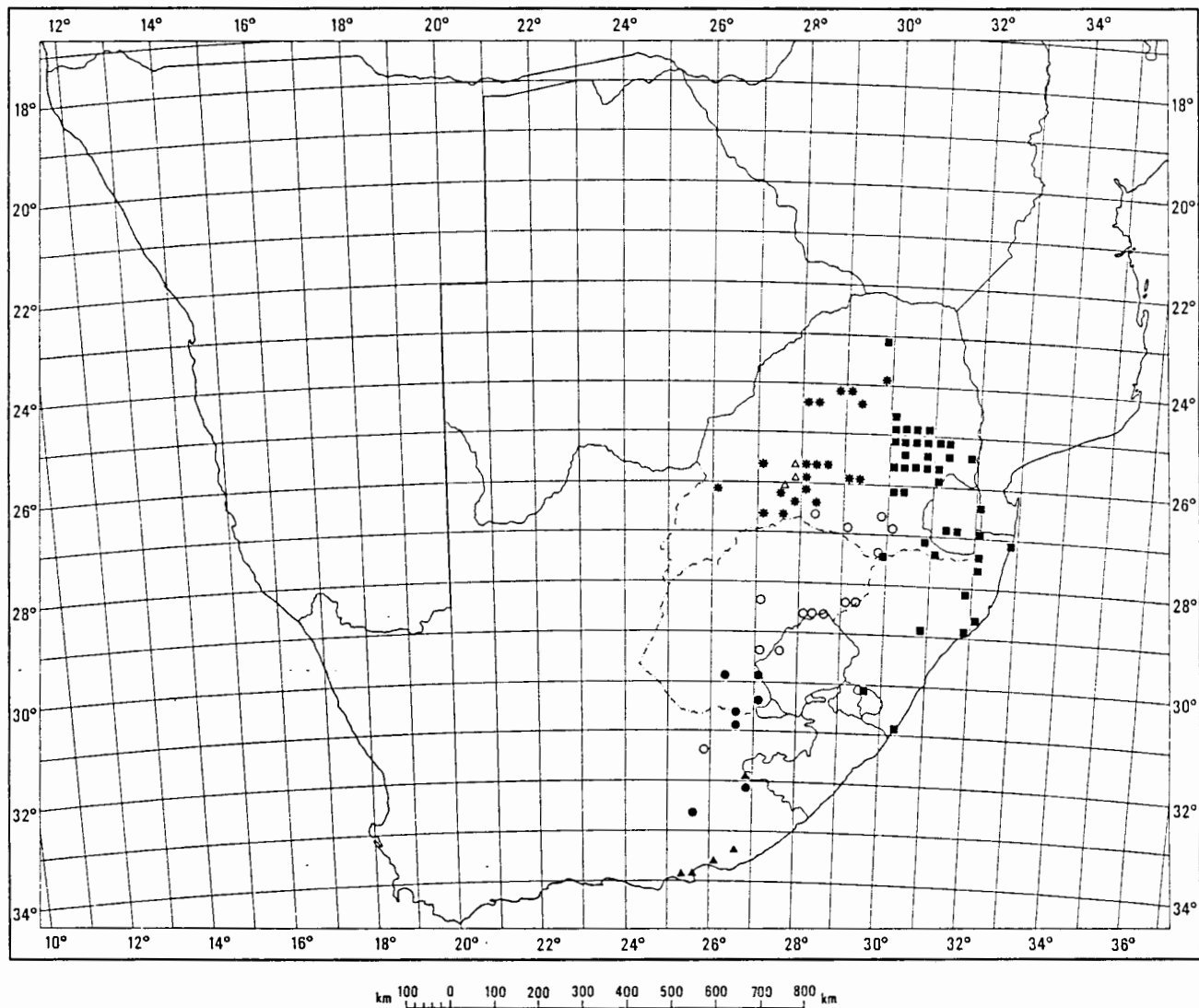
Map 5.8. The known geographical distribution of all the species of section *Leptis* that are not endemic to the eastern parts of southern Africa.



Map 5.9. The known geographical distribution of *L. mirabilis* (★), *L. mollis* (■), *L. mucronata* (○), *L. esterhuyseana* (▲) and *L. calycina* (●).



Map 5.10. The known geographical distribution of *L. arida* (●), *L. pariflora* (★), *L. decumbens* subsp. *decumbens* (△), *L. decumbens* subsp. *rehmannii* (▲) and *L. curvicarpa* (■).



Map 5.11. The known geographical distribution of *L. pusilla* (●), *L. prolifera* (▲), *L. carinata* (■), *L. hirsuta* (*), *L. addressa* subsp. *addressa* (○) and *L. addressa* subsp. *leptantha* (△).

Section 5. Leobordea (Del.) Benth.

Lotononis section Leobordea (Del.) Benth. in Hook., Lond. J. Bot. 2: 607 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 49 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 279 (1913).
Lectotype species: Leobordea lotoidea Del. [now Lotononis platycarpa (Viv.) Pic.-Serm.].

Leobordea Del. in Laborde, Fragm. fl. Arabie Pétrée (1833); Jaub. & Spach in Ann. Sci. Nat. 19: 232 (1843), pro parte.
[Note: the name Leobordea should perhaps be dated from 1830 and not 1833 -- see note in the synonymy of L. platycarpa].

Capnitis E. Mey., Comm. Pl. Afr. Austr. 1(1): 81 (1836).

The concept of the section Leobordea is broadened here to include three species from the section Leptis (L. stipulosa, L. furcata and L. schoenfelderi) and one species from the section Polylobium (L. newtonii). Three of the four species in Dümmer's (1913) revision are placed in synonymy. The leaves of flower-bearing nodes are opposite and not alternate or subopposite as in all other species of Lotononis. This is a more useful diagnostic character for the section Leobordea than the sessile or subsessile flowers and the short lower lobe of the calyx, characters which are also found in other sections. The species of Leobordea (all annuals) are very similar to some perennial species of the section Leptis and also to species of the

section Synclistus. In the latter, the flowers are invariably sessile, the leaves are never opposite and the pods are totally indehiscent.

Prostrate or procumbent annuals. All mature parts usually densely pubescent or villous. Leaves alternate on vegetative nodes, opposite on flowering nodes, digitately trifoliolate (occasionally with some leaves 4- or 5-foliolate), variable in size and shape, usually densely pubescent on both surfaces. Stipules single at each leaf base, rarely paired (L. newtonii), usually small and linear, rarely large and foliaceous. Inflorescences sessile or subsessile, short congested racemes, umbellately 1- to many-flowered, invariably inserted at opposite leaves; bracts small, linear or large and foliaceous; bracteoles absent. Flowers sessile or subsessile, small, yellow. Calyx inflated or usually not inflated, with the upper and lateral lobe on either side fused higher up in pairs, the lower lobe narrower and often much smaller, rarely subequally lobed, pubescent to densely hirsute. Standard ovate to oblong, usually shorter than the keel, pubescent to densely hirsute. Wing petals oblong to broadly triangular, often much shorter than the keel, pubescent at least along the lower edge of the lamina. Keel petals half oblong-elliptic to narrowly oblong; apex obtuse, rarely somewhat pointed, pubescent. Anthers dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the carinal anther similar to the dorsifixed anthers. Pods sessile, included in the calyx or slightly longer than the calyx, obovoid to broadly oblong,

slightly or distinctly inflated, thin-walled, upper suture \pm smooth or more often distinctly verrucose, dehiscent, usually \pm 10-seeded; funicles long. Seeds small, 1--2 mm in diameter, variable in shape, testa distinctly tuberculate, rarely smooth. Chromosome base number 9 ($2n = 18$). (Figure 5.7).

The six species now included in this section all occur in the dry parts of southern Africa (Maps 5.13 & 5.14), with one (L. platycarpa) extending through eastern tropical Africa to the saharo-asiatic desert region (West Pakistan to Mauritania) and also the Cape Verde Islands (Map 5.12). L. platycarpa is geographically the most widespread species of the genus and is, in terms of its morphology, also the most variable one.

Key to the species of section Leobordea:

- 1A. Stipules 2 at the base of each petiole (4 per
flowering node); known only from Angola46. L. newtonii
- 1B. Stipules 1 at the base of each petiole (2 per
flowering node); not restricted to Angola:
 - 2A. Calyx markedly inflated, \pm as long as wide at the
fruiting stage; flowers 1 or 2 per inflorescence:
 - 3A. Terminal leaflets 3--5 mm long; calyx lobes
relatively narrow; flowers usually 2 per
inflorescence; habit procumbent49. L. schoenfelderi
 - 3B. Terminal leaflets 7 mm or usually much longer;
calyx lobes relative broad; flowers usually
1 per inflorescence; habit prostrate50. L. furcata
 - 2B. Calyx not inflated, longer than wide at the fruiting
stage; flowers usually more than 2 per inflorescence:
 - 4A. Stipules large and foliaceous, $> 5 \times 3$ mm; bracts
lanceolate, much smaller than the stipules; Zambia,
Zimbabwe and Transvaal48 L. stipulosa
 - 4B. Stipules not large and foliaceous,
 $< 5 \times 3$ mm; bracts lanceolate or broadly
obovate, smaller or larger than the stipules;
not restricted to Zambia, Zimbabwe and Transvaal:
 - 5A. Bracts inconspicuous, linear to lanceolate,
 < 1 mm wide; widespread45. L. platycarpa
 - 5B. Bracts conspicuous, broadly obovate,
 > 2 mm wide; north-western Namibia47. L. bracteosa

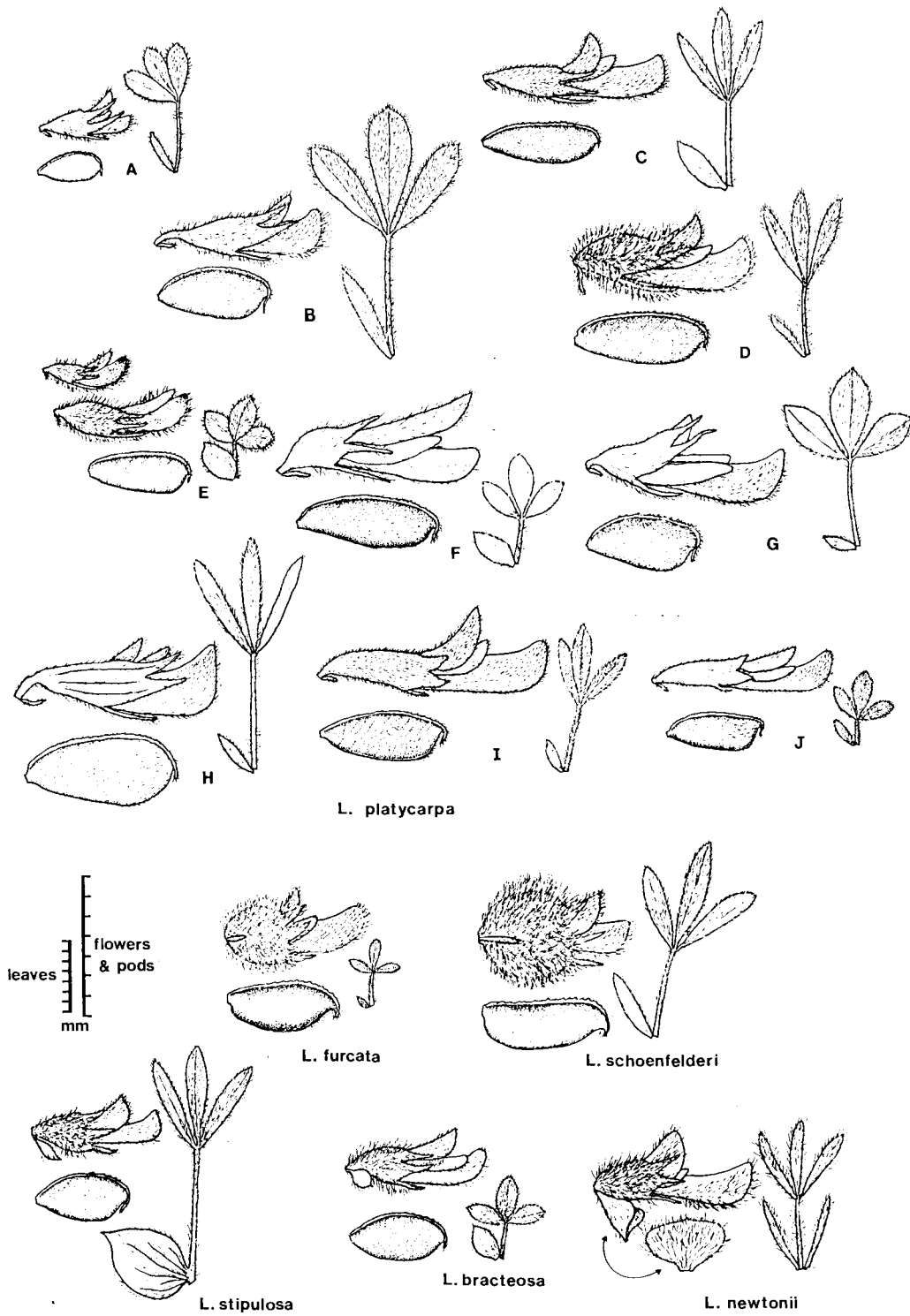


Figure 5.7. Leaves, flowers and pods of the species of section *Leobordea*.

45. L. platycarpa (Viv.) Pic.-Serm. in Webbia 7: 331 (1950); Torre, Consp. Fl. Angolensis 3(2): 4 (1962); Schreiber in FSWA 60: 83 (1970); Milne-Redhead in Fl. Trop. E. Afr., Pap.: 813 (1971); Zohary in Fl. Palaestina 1(2): 38 & fig. 49 (1972); Ali in Nasir & Ali, Fl. W. Pakist. 100: 33 & fig. 2 (1977); Rechinger in Fl. Iran. 2: 29 & t. 15 (1984). Type: "in desertis prope Kahirum" [Egypt, near Cairo], Figari s.n. (G, holo.).

Lotus platycarpus Viv., Pl. Aegypt., Dec. IV: 14, t. 2, fig. 9 (1830). Type as above.

Amphinomia platycarpa (Viv.) Cuf. in Bull. Jard. Bot. Brux. 25, Suppl.: 227 (1955) & Zweit. Nachtr.: 23 (1969). Type as above.

Lotononis lotoidea (Del.) Batt., Fl. Alg. 1: 209 (1889). Type: Arabia, De Laborde s.n. (G, holo.).

Leobordea lotoidea Del., Fragm. Fl. Arabie Pétrée: 23 (1830 or 1833). Type as above.

Lotononis lotoidea (Del.) Batt. var. micrantha Batt., B. Soc. Bot. France 54: 26 (1907). Type not seen.

Lotononis lotoidea (Del.) Druce in Rep. Bot. Exch. Cl. Brit. Isles, 1916: 634 (1917). Type as above.

Amphinomia lotoidea (Del.) Maire, Fl. Afr. Nord: 80 (1987). Type as above.

[Note: most modern authors prefer to date the name Leobordea Del. (and Leobordea lotoidea Del.) from 1833 and not 1830. According to Stafleu & Cowan (1976), the 1833 publication is a reprint from the original text entitled "Flore de l'Arabie pétrée" published

in 1830. Jaubert & Spach (1843) and Maire (1987) give the citation as Leobordea Del. in Laborde, Voyage de l'Arabie Pétrée, p. 86 (1830) (the botanical part is perhaps more correctly cited as Fl. Arabie pétrée). I have not seen the original publication and was unable to determine the exact date and month of publication. Maire (1987) may be correct in using the epithet "lotoidea" rather than "platycarpa" but this is uncertain, because both seem to date from 1830 (Maire did not cite L. platycarpa as a synonym). Until the exact dates of the two publications can be established, I provisionally follow most other authors by accepting Lotononis platycarpa (Viv.) Pic.-Serm. as the correct name rather than Lotononis lotoidea (Del.) Batt.].

Lotononis persica (Jaub. & Spach) Boiss., Fl. Orient. 2: 30 (1872). Type: "In Persia australi" [southern Iran], Aucher Eloy 1312 (P?), s.n. sub Herb. Hook (K!, iso.).

Leobordea persica Jaub. & Spach in Ann. Sc. Nat. Paris, Ser. 2, 19: 235 (1843). Type as above.

Lotononis platycarpa (Viv.) Pic.-Serm. var. persica (Jaub. & Spach) Tackh., Stud. Fl. Egypt ed. 2: 225 (1974). Type as above.

Lotononis dichotoma (Del.) Boiss. var. persica (Jaub. & Spach) Post, Fl. Syria, Palest. & Sinai: 211 (1896); Blatter, Fl. Arab. 8(2): 124 (1921). Type as above.

Lotononis sphaerocarpa Boiss., Fl. Orient. 2: 30 (1872). Types: "In peninsula Sinaica", Botta s.n. (P?); "prope Djedda" [Saudi Arabia, near Jiddah], Schimper s.n. (P?), 768 sub Herb. Hook. (K!, isosyn.?).

Leobordea sphaerosperma Jaub. & Spach in Ann. Sc. Nat. Paris, Ser. 2, 19: 235 (1843). Type as above.

Lotononis clandestina (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 607 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 61 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 311 (1913); Schreiber in FSWA 60: 81 (1970), synon. nov. Type: Between "Verleptpram and Natvoet" [between 2817 AA Violsdrif and 2816 DB Oranjemund], Drège s.n. (S!, lecto., designated here; K!, MO!).

Capnitis clandestina E. Mey., Comm. Pl. Afr. Austr. 1(1): 81 (1836). Type as above.

Leobordea clandestina (E. Mey.) Steud., Nom. Bot. 2(2): 23 (1841). Type as above.

Lotononis porrecta (E. Mey.) Benth. in Hook. Lond. J. Bot. 2: 606 (1843), excl. syns. Crotalaria prolifera, Leptis prolifera and Leptis debilis; Harv. in Harv. & Sond., Fl. Cap. 2: 60 (1862). Type: Near "Zwartbulletje" [untraced, in the vicinity of the Gamka river], Drège s.n. (S!, lecto., here designated; K!, MO!).

Capnitis porrecta E. Mey., Comm. Pl. Afr. Austr. 1(1): 81 (1836). Type as above.

Leobordea porrecta (E. Mey.) Steud., Nom. Bot. 2(2): 23 (1841).
Type as above.

Lotononis leobordea Benth. in Hook., Lond. J. Bot. 2: 607
(1843); Harv. in Harv. & Sond., Fl. Cap. 2: 61 (1862); Bak. in
Oliv., Fl. Trop. Afr. 2: 5 (1871); Dümmer in Trans. Roy. Soc. S.
Afr. 3(2): 311 (1913); Bak. f., Leg. Trop. Afr. 1: 17 (1926),
nom. illeg. Type: as for Leobordea lotoidea ("lotoides"),
Leobordea persica and Leobordea sphaerosperma.

Lotononis dichotoma (Del.) Boiss., Fl. Orient. 2: 30 (1872);
Post, Fl. Syria, Palest. & Sinai: 211 (1896); Blatter, Fl. Arab.
8(2): 123 (1921); Ozenda, Fl. Sahara, ed. 2: 291 (1977), nom.
illeg.

Lotus dichotomus Del. ex Walp., Repert. Bot. Syst. 2: 838
(1843). [based on Lotus dichotomus Del., Fl. Eg. t. 717 (1813),
nom. nud.]

Amphinomia dichotoma (Del.) Font Quer & Rothm. in Broteria 36:
149 (1940).

Lotononis abyssinica (Hochst. ex A. Rich.) Kotschy in Sitzb.
Acad. Wien, Math. Nat. 51 Abth. 2: 263 (1865); Blatter, Fl. Arab.
8(2): 123 (1921). Type: "... prope Arna" [Ethiopia], Schimper
2293 sub Un. itin. 1493 (P?, holo.; K! Herb. Benth., K! Herb.
Hook., M!, S!, iso.).

Leobordea abyssinica Hochst. ex A. Rich., Tent. Fl. Abyss. 1:
161 (1847). Type as above.

Lotononis leobordea Benth. var. abyssinica (Hochst. & Schweinf.) Bak. in Oliv., Fl. Trop. Afr. 2: 17 (1871). Type as above.

Lotononis platycarpa (Viv.) Pic.-Serm. var. abyssinica (Hochst. ex A. Rich.) Pic.-Serm. in Webbia 7: 332 (1950). Type as above.

Lotononis carinalis Harv. in Harv. & Sond., Fl. Cap. 2: 60 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 311 (1913). Type: Without precise locality, Namaqualand, A. Wyley s.n. (TCD, holo.).

Lotononis dinteri Schinz in Vierteljahrsschr. Nat. Ges. Zürich 52 (3 & 4): 423 (1907); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 317 (1913); Bak. f., Leg. Trop. Afr. 1: 18 (1926); Torre, Consp. Fl. Angolensis 3(2): 4 (1962). Type: Otavi, Dinter 664 (Z, holo., photo in M!; BOL!, K!, M!, PRE!, iso.).

Amphinomia dinteri (Schinz) Schreiber in Mitt. Bot. Staatssamm. München 2: 287 (1957). Type as above.

Lotononis dinteri Schinz var. amboensis Schinz in Vierteljahrsschr. Nat. Ges. Zürich 52 (3 & 4): 423 (1907). Type: Namibia, Amboland, "Uukuanyama" [?], Rautanen 549 (Z, holo.).

Lotononis clandestina (E. Mey.) Benth. sensu Bak., Bak. in Oliv., Fl. Trop. Afr. 2: 6 (1871).

Lotononis steingroeveriana (Schinz) Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 311 (1913). Type: Lower Orange River [northern Cape region], Steingroever 109 (Z, holo., K!, iso.).

Amphinomia steingroeveriana (Schinz) Schreiber in Mitt. Bot. Staatssamm. München 2: 289 (1957). Type as above.

Lotononis clandestina var. steingroeveriana Schinz in Verh. Bot. Ver. Brdbg. 30: 157 (1888). Type as above.

A very widely distributed species, found in desert regions from southern, eastern and northern Africa to Mauritania and the Cape Verde Islands and eastwards to Arabia and West Pakistan (Map 5.12).

The morphological variability of the species reaches a climax in the western parts of southern Africa. In this region, every conceivable diagnostic character that was previously used in attempts at infraspecific and specific delimitations occur in different combinations. Discontinuities in the size and shape of flowers, leaves, stipules and pods are not very distinct but show some geographical patterns. The most conspicuous of these geographical forms are described below, but the subdivisions are preliminary only. It is possible that the apparent instability in character variation is partly due to hybridization and introgression. A formal infraspecific treatment may be feasible when the relationships between various regional forms have been studied in more detail. The leaves, flowers and pods of each of the 10 major forms are shown in Figure 5.7 and the geographical distributions are shown in Map 5.13.

Form A ("typical" form)

Leaves and stipules small; flowers small; calyx narrowly tubular, lower lobe usually shorter than the upper ones; seeds smooth or tuberculate (sometimes in a single pod), often irregularly so; pubescence variable, but usually appressedly pubescent.

Widespread throughout the geographical range of the species.

Vouchers: Collenette 2981; De Winter & Hardy 7871; Giess 14572; Giess, Volk & Bleissner 5475; Rechinger 30373; Wilcox 162.

Form B ("L. abyssinica" form)

Similar to the previous but larger in all parts. The pubescence tend to be villous, with longer and more spreading hairs.

Southern distribution, extending to Ethiopia. Some specimens from Saudi Arabia however, also agree well with this form.

Vouchers: Giess 10364; Leitner sub Seydel 3509; Liebenberg 4914; Rutherford 335; Story 5091.

Form C ("Torra Bay" form)

Similar to B but more sparsely pubescent and the inflorescences usually densely and subumbellately many-flowered. This form occurs in the same geographical region as L. bracteosa and may be mistaken for it, but the bracts are small. Restricted to the coastal region of northern Namibia.

Vouchers: Craven 180; De Winter & Hardy 8151; De Winter & Leistner 5688; Giess, Volk & Bleissner 6142; Oliver, Muller & Steenkamp 7579.

Form D ("L. dinteri" form)

Merging with B but the flowers are very large, often sessile; calyx somewhat inflated, densely hirsute with reddish-brown hairs; seeds densely but minutely tuberculate. Known only from a few collections in Angola and the northern parts of Namibia.

Vouchers: De Winter & Marais 4951; Dinter 7649; Merxmüller & Giess 30267; Range 690.

Form E ("Windhoek" form)

Similar to B but the flowers variable in size, usually sessile as in D; stipules broadly oblong to ovate (not linear); pubescence always densely hirsute with golden hairs; keel with a distinct pollen guide. Robust specimens were previously been confused with L. bracteosa (and the latter with L. stipulosa q.v.). Apparently restricted to the central part of Namibia.

Vouchers: Giess 7630, 10468, 13460; Hanekom 15; Merxmüller & Giess 3573; Van Vuuren 690.

Form F ("Luderitz" form)

Similar to B but the calyx subequally lobed; standard petal very long (as long as the keel), broadly oblong. Only known from around Luderitz on the southern coast of Namibia. This may prove to be a distinct species.

Vouchers: Giess & Müller 14318; Kraeusel 2095b; Merxmüller & Giess 3161, 28842; Vendt sub Giess 14711.

Form G ("L. clandestina" form)

Similar to B but usually more sparsely pubescent; leaves usually broadly ovate to broadly elliptic; flowers often very large; keel broadly oblong, somewhat pointed; pods very large, broadly obovate. Northern parts of Namaqualand and northwards to the central parts of Namibia.

Vouchers: Giess 8747; Giess, Volk & Bleissner 5073; Jensen 249, Kers 61; Schulze sub PRE 53331.

Form H ("L. steingroeveriana" form)

Almost identical to the previous and merging with it but the leaves usually narrowly lanceolate and the calyx at the fruiting stage with distinct purple lines. Distribution as for G.

Vouchers: De Winter 3422; Giess & Müller 11923; Leistner 2343;
Mostert 1407; Oliver & Steenkamp 6250.

Form I ("L. carinalis" form)

Similar to B but the flowers very long, narrow and tubular; calyx narrow, tubular, the lobes very short; standard petal with a very long claw; pubescence sericeous. Only known from one locality in the north-western Cape near the Namibian border.

Vouchers: Acocks 17597; Krahpöhl sub Marloth 11140.

Form J ("L. porrecta" form)

Similar to A but the flowers narrow and tubular as in I; calyx long and narrow, membranous and transparent at the fruiting stage, the lobes very short, lower lobe often much smaller; pubescence of short silky hairs. Central and eastern Karoo, extending into the southern parts of Namibia. This is the original Capnitis porrecta of Meyer (1836), previously often confused with the superficially similar Leptis prolifera of Ecklon & Zeyher (1836).

Vouchers: Acocks 12603, 15581; Hugo 353; Moffett 847; Oliver & Steenkamp 6310; Thompson 3142.

46. L. newtonii Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 303 (1913) [as L. newtoni]; Bak. f., Leg. Trop. Afr. 1: 17 (1926); Torre, Consp. Fl. Angolensis 3(2): 4 (1962). Type: Angola, Mossamedes, Mouolino, Newton 95 (K!, lecto., designated here; Z, iso.).

Apparently a rare species, known only from the type collection near Mossamedes in Angola (Map 5.14, inset). It is superficially similar to L. bracteosa, but the paired stipules, the narrowly lanceolate leaflets, the very large bracts, the long keel petals and the hirsute vestiture are quite distinct (Figure 5.7).

47. L. bracteosa B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 30].

L. stipulosa Bak. f. sensu Schreiber in FSWA 60: 85 (1970). Type: Namibia, Outjo district, mountains 14 miles [22,4 km] east of Torra Bay, Giess, Volk & Bleissner 6198 (PRE!, holo.; M!, PRE!, WIND!, iso.).

L. bracteosa is closely related to L. stipulosa Bak. f. and was previously confused with it. Van Wyk (1989j, Appendix 30) has shown that the similarity between the two species is not homologous. The involucrate appearance of the inflorescences in L. stipulosa results from the very large stipules (the bracts are small), while in L. bracteosa it is a result of large bracteoles (hence the name). Another useful diagnostic character for L.

bracteosa is that the basal leaves are invariably opposite and not alternate as in L. stipulosa. The differences in the bracts and stipules are shown in Figure 5.7. L. bracteosa is geographically isolated from L. stipulosa and is endemic to Namibia (Map 5.14).

Vouchers: Craven 989; Giess & Leippert 7524; Giess, Volk & Bleissner 5772, 61981; Kers 1513.

48. L. stipulosa Bak. f., Leg. Trop. Afr. 1: 18 (1926); Schreiber in FSWA 60: 85 (1970), excluding the cited specimens. Type: Rhodesia [Zimbabwe], Macheke, Eyles 2020 (K!, holo.; K!, SAM!, iso.).

This species is known only from the Transvaal, Zimbabwe and the southern border of Zambia (Map 5.14). Specimens from Namibia were previously considered to be this species (Schreiber 1970) but these are now accommodated in a new species, L. bracteosa. Some of the most obvious differences between L. stipulosa and the latter are shown in Figure 5.7.

Vouchers: Breyer 21596; Corby 1443; Flanagan 3087; Gertenbach 5462; Miller 3436.

49. *L. schoenfelderi* (Dinter ex Merxmüller & Schreiber) Schreiber in Mitt. Bot. Staatssamm. München 3: 613 (1960); Schreiber in FSWA 60: 84 (1970). Type: Namibia, Grootfontein district, "Gross Huis", Dinter 7383 (M!, holo.; BM!, BOL!, K!, M!, PRE!, S!, WIND!, iso.).

Amphinomia schoenfelderi Dinter ex Merxmüller & Schreiber in Bull. Jard. Bot. Brux. 27: 273 (1957). Type as above.

A species with a more north-eastern distribution than the closely related *L. furcata* (Map 5.14). The size of the leaves (Figure 5.7) is a useful diagnostic character to separate it from the latter.

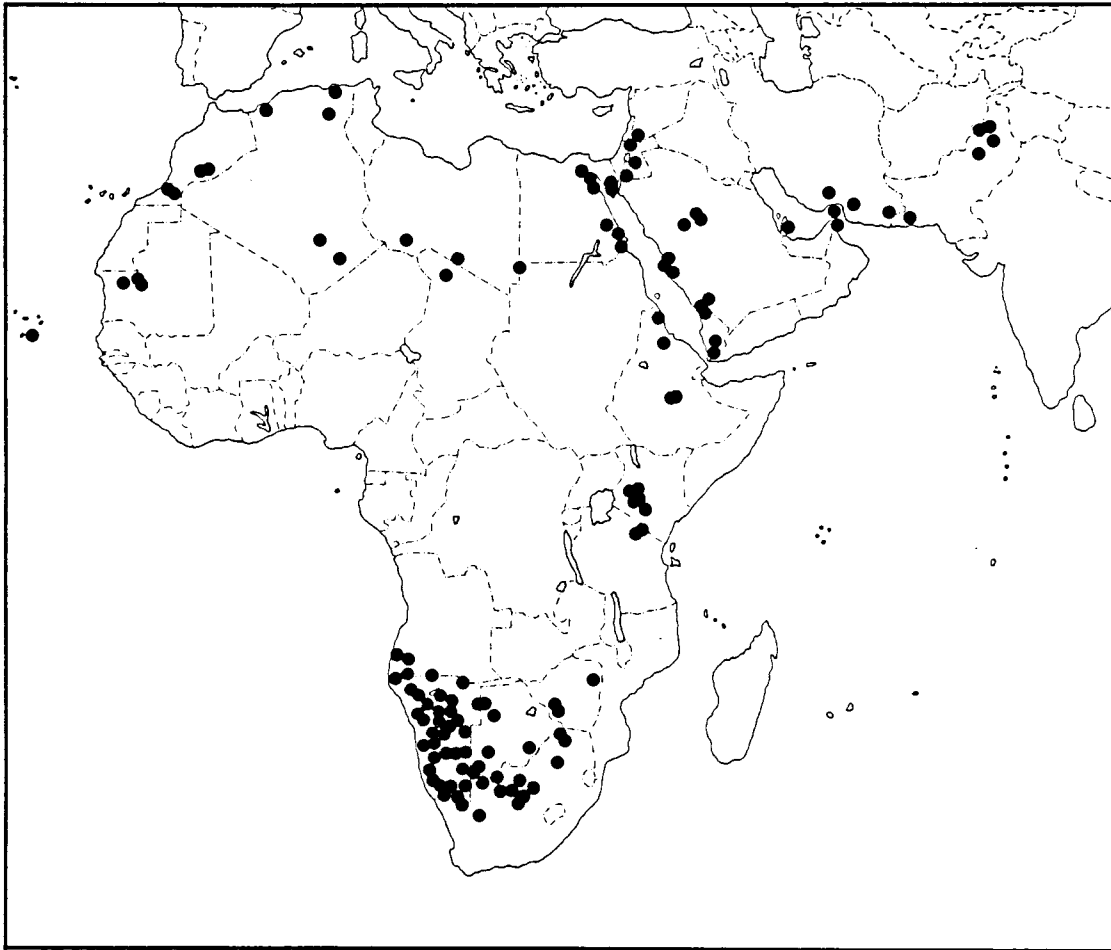
Vouchers: Dinter 7383; Giess 8551; Story 4924, 5119; Tolken & Hardy 914.

50. *L. furcata* (Merxmüller & Schreiber) Schreiber in Mitt. Bot. Staatssamm. München 3: 613 (1960); Schreiber in FSWA 60: 82 (1970). Type: Namibia, Rehoboth district, Buellspport, Strey 2614 (M!, holo.; K!, M!, PRE!, SAM!, iso.).

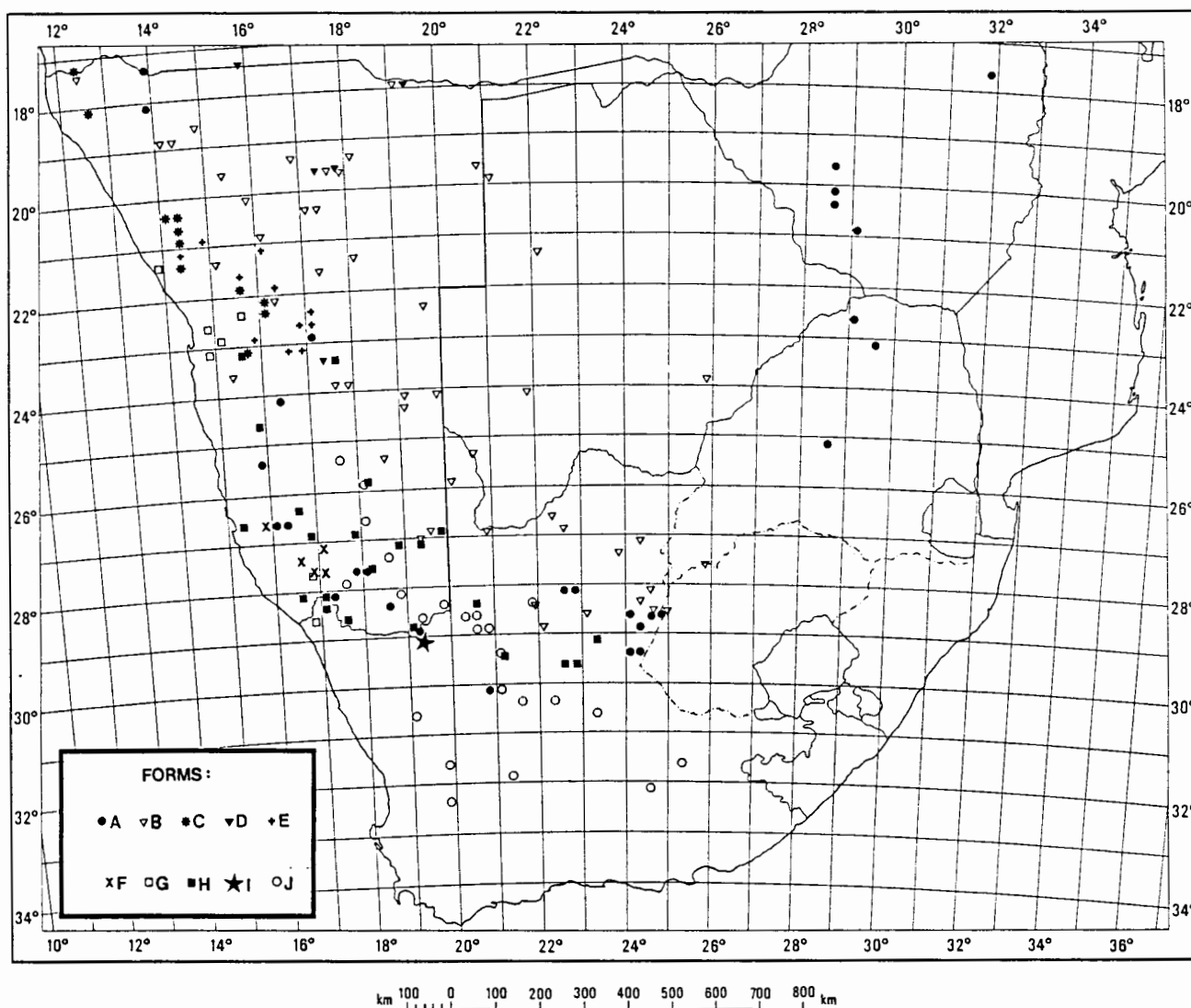
Amphinomia furcata Merxmüller & Schreiber in Bull. Jard. Bot. Brux. 27: 272 (1957). Type as above.

Very closely related to L. schoenfelderi and geographically isolated from it (Map 5.14), but some intermediate specimens (Vahrmeijer 3021, for example) indicate that these two species may eventually prove to be regional extremes of one variable species.

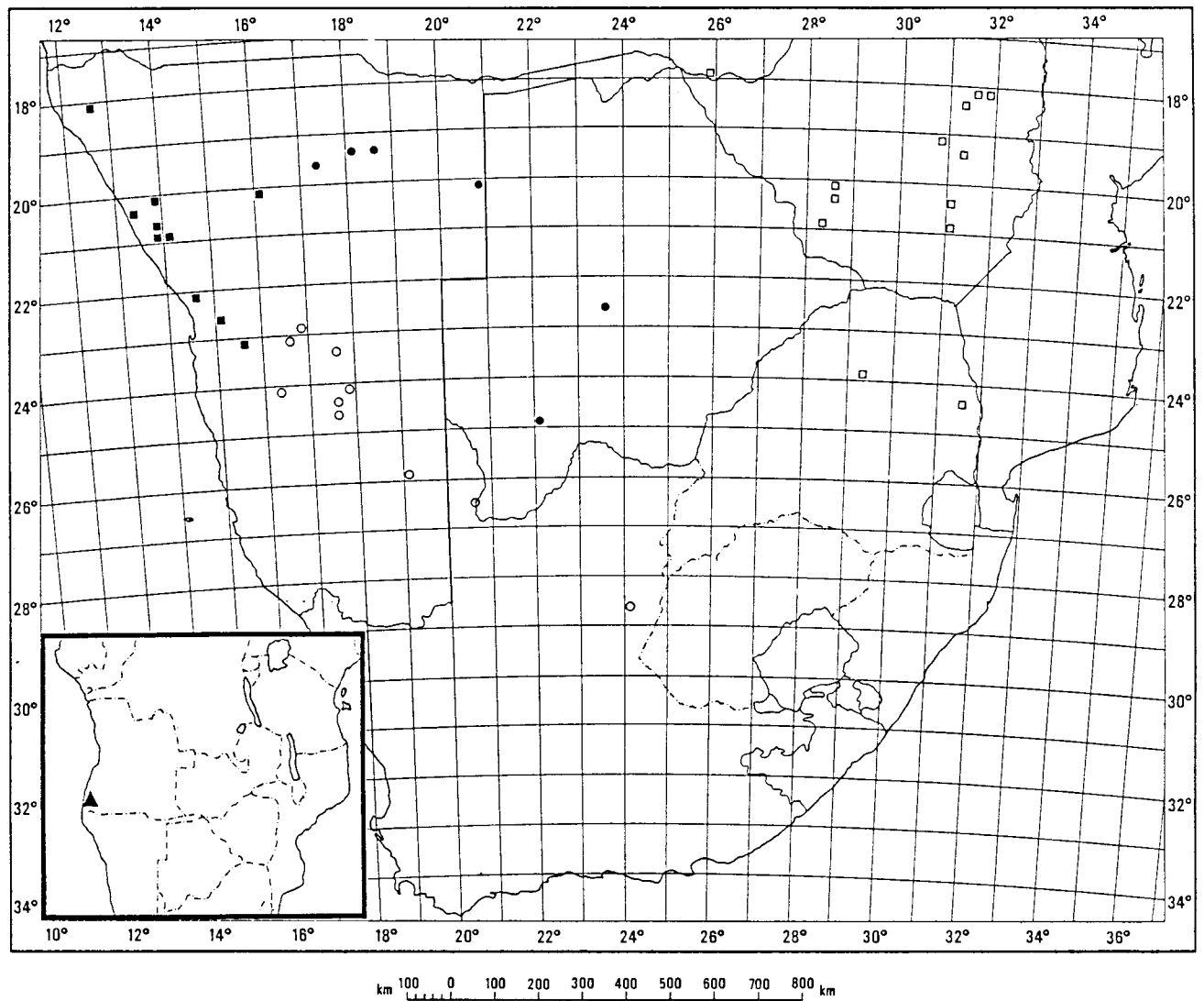
Vouchers: Acocks 15603; Giess, Volk & Bleissner 5604; Leippert 4654, 4723; Merxmüller & Giess 28075.



Map 5.12. The approximate geographical distribution of Lotononis platycarpa.



Map 5.13. The geographical distribution of the various forms of *Lotononis platycarpa* in southern Africa: A, "typical" form; B, "abyssinica" form; C, "Torra bay" form; D, "dinteri" form; E, "Windhoek" form; F, "Luderitz" form; G, "clandestina" form; H, "steingroeveriana" form; I, "carinalis" form; J, "porrecta" form.



Map 5.14. The known geographical distribution of the five species of *Lotononis* section *Leobordea* endemic to southern Africa: *L. newtonii* (inset, ▲), *L. bracteosa* (■), *L. stipulosa* (□), *L. schoenfelderi* (●) and *L. furcata* (○).

Sectio 6. Synclistus B-E. van Wyk, sect. nov. Grex distinctissima specierum. A sectionibus omnibus capitulis confertis florum sessilium et leguminibus minutis pauciseminatis omnino indehiscentibus intra calycem valde inflatum, dense pubescens inclusis, differt.

Lotononis section Lipozygis (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 605 (1843), pro parte; Harv. in Harv. & Sond., Fl. Cap. 2: 49 (1862), pro parte; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 279 (1913), pro parte.

Lipozygis (section 4) E. Mey., Comm. Pl. Afr. Austr. 1(1): 79 (1836), pro parte.

A very distinct group of species. It differs from all other sections in the dense heads of sessile flowers and in the minute, few-seeded, totally indehiscent pods that are enclosed within a much-inflated, densely hairy persistent calyx. It is similar to the section Leobordea, but the inflorescences are leaf-opposed or subterminal (not inserted at opposite leaves), the flowers are invariably sessile (not shortly pedicelled), the calyx very much inflated and the pods totally indehiscent and less than half as long as the calyx (dehiscent and as long or slightly longer than the calyx in Leobordea). It differs from the section Lipozygis in the annual habit, the sessile flowers and small, wind-dispersed pods.

Type species: L. longicephala B-E. van Wyk.

Prostrate short-lived annuals. All mature parts densely pubescent or sericeous. Leaves alternate, digitate, 3- or 5-foliolate, densely pubescent, hirsute or sericeous on both surfaces; petiole short; leaflets oblanceolate to broadly obovate. Stipules single at each node, small and lanceolate or rarely large and broadly ovate. Inflorescences on a short peduncle, in dense hemispherical, spherical or elongated many-flowered heads, leaf-opposed or subterminal; bracts small, linear and inconspicuous or often very large, lanceolate to broadly ovate; bracteoles absent. Flowers sessile, relatively small, yellow or rarely pink (*L. rosea*). Calyx much inflated, the lobes subequal, densely hirsute. Standard suborbicular to narrowly oblong, usually hairy on the adaxial surface. Wing petals oblong to linear, usually hairy, at least along the lower edge of the lamina, rarely glabrous. Keel petals oblong to narrowly oblong, usually hairy, often with a long, linear auricle. Anthers dimorphic, the carinal anther intermediate. Pods minute, up to 5 mm long, sessile, enclosed within the persistent calyx, laterally inflated, very thin-walled, membranous in texture; upper suture minutely but distinctly verrucose, totally indehiscent, few-seeded; funicles long. Seeds up to 5 per pod, small, up to 1,8 mm in diameter, suborbicular, testa smooth or minutely and sparsely tuberculate. Chromosome base number 9 ($2n = 18$). (Figure 5.8).

A very distinct group of annuals restricted to the western coastal regions of the Cape Province (Maps 5.15 and 5.16). The species of this section are very easily distinguished from all other species of Lotononis by the dense heads of sessile flowers and the minute, indehiscent wind-dispersed pods. The structure of the inflorescence leaves little doubt that the wide sectional concept of Lipozygis is artificial (Van Wyk 1989g, Appendix 27). The unusual structural adaptations associated with wind-dispersal were discussed by Van Wyk (1989h, Appendix 28).

The section includes nine species, most of which are very poorly represented in southern African herbaria. The diagnostic differences in the following key to the species are shown in Figure 5.8.

Key to the species of section Synclistus:

- 1A. Adaxial surface of the leaflets very densely
silky, almost totally obscuring the surface
of the lamina; bracts large, foliaceous:
 - 2A. Leaves 5-foliolate; standard and keel
petals glabrous 51. L. oligocephala
 - 2B. Leaves 3-foliolate; standard and keel
petals densely pubescent 52. L. polycephala
- 1B. Adaxial surface of the leaflets sparsely hairy
or glabrous, the surface of the lamina clearly
visible; bracts small and inconspicuous or if
large, then the leaflets adaxially glabrous or
very sparsely pubescent:
 - 3A. Flowers pink 57. L. rosea
 - 3B. Flowers yellow or cream-coloured:
 - 4A. Inflorescences more than 22 mm in
diameter; flowers \geq 10 mm long 59. L. anthyllopsis
 - 4B. Inflorescences less than 22 mm in
diameter; flowers $<$ 10 mm long:

- 5A. Bracts large, conspicuous, ovate to broadly
ovate, > 3 mm wide:
- 6A. Standard petal much shorter than the keel;
bracts \leq 4 mm wide; inflorescences discoid
(wider than long) 53. L. laticeps
- 6B. Standard petal \pm as long as the keel; bracts
> 5 mm wide; inflorescences globose (not
wider than long) 54. L. globulosa
- 5B. Bracts small, inconspicuous, linear to
lanceolate, < 2 mm wide:
- 7A. Leaves 3-foliolate, never 5-foliolate;
inflorescences spicate (longer than wide)
when fully developed, \pm 10 mm wide 55. L. longicephala
- 7B. Leaves predominantly 5-foliolate (or with at
least some of the leaves 5-foliolate); inflorescences
globose (if slightly elongated then > 10 mm wide):
- 8A. Wing and keel petals pubescent, at least
towards the apex; calyx lobes very narrow,
 \pm 0,5 mm wide at the point of fusion;
Namaqualand 56. L. pentaphylla
- 8B. Wing and keel petals totally glabrous; calyx
lobes \pm 1 mm wide at the point of fusion;
Malmesbury and Piquetberg districts 58. L. bolusii

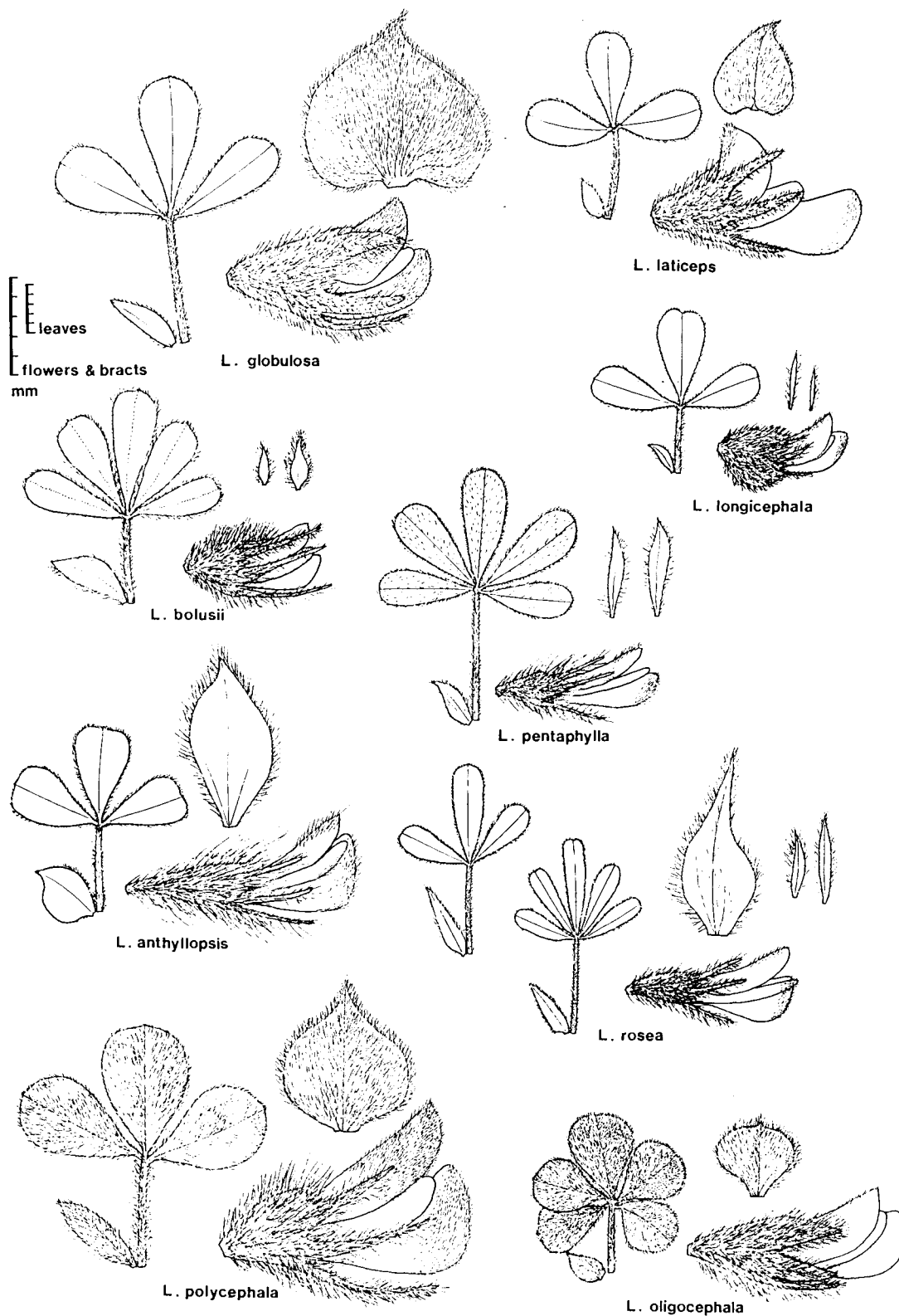


Figure 5.8. Leaves, bracts and flowers of the species of section Synclistus.

51. L. oligocephala B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 28]. Type: South Africa, Cape Province, Areb, ± 27 miles [43,2 km] NE of Springbok, Van der Westhuizen 276 (PRE!, holo.; K!, MO!, iso.).

This species is known only from the type collection. It is closely related to L. polycephala but the leaves, inflorescences, bracts and flowers are much smaller. It also differs from L. polycephala in the number of leaflets and the glabrous standard and keel petals (Figure 5.8). The single known locality is given in Map 5.15.

52. L. polycephala (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 605 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 59 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 305 (1913). Type: South Africa, Cape Province, "Kamiesbergen", Drège s.n. (K!, lecto., designated here; BM!, MO!, S!).

Lipozygis polycephala E. Mey., Comm. Pl. Afr. Austr. 1(1): 79 (1836). Type as above.

Polylobium polycephalum (E. Mey.) D. Dietr., Syn. Pl. 4: 962 (1847). Type as above.

A distinct species with densely silky leaves and a robust habit. With the exception of L. anthyllopsis, the inflorescences and flowers (Figure 5.8) are much larger than those of all other species of the section. L. polycephala is known from only a few localities in Namaqualand (Map 5.16).

Vouchers: Esterhuysen 1404; Goldblatt 6684; Leistner 747; Schlechter 11325; Van Wyk 2382--2388, 2408--2410.

53. L. laticeps B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 28]. Type: South Africa, Cape Province, Ceres District, Stompiesvlei, Swartruggens, Esterhuysen 29334 (BOL!, holo.; C!, K!, M!, MO!, S!, iso.).

L. laticeps is a poorly known species represented by a single collection from the vicinity of Ceres (Map 5.16). It is closely related to L. globulosa but differs in the smaller and discoid rather than globose heads, the smaller bracts, the narrower calyx-lobes, the longer keel petals and the very short standard petal (Figure 5.8).

54. L. globulosa B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 28]. Type: South Africa, Cape Province, 29,5 km from Touws River to Laingsburg, near Tweedside, B-E. van Wyk 2210 (PRE!, holo.).

This species has the general appearance of L. bolusii, but differs in the consistently trifoliolate leaves and in the very large and broad bracts, resembling those of L. polycephala (Figure 5.8). The rather slight differences between L. globulosa and L. laticeps are given under the latter. L. globulosa is a poorly known species, recorded only from a limited area between Ceres and Matjiesfontein in the south-western Cape Province (Map 5.16).

Vouchers: Compton 12074; Leipoldt 3123; Levyms 1053; Van Wyk 2210, 2211.

55. L. longicephala B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 28]. Type: South Africa, Cape Province, Flats east of Prince Alfred's Hamlet, Oliver 5063 (PRE!, holo.; K!, MO!, STE!, iso.).

L. longicephala can easily be distinguished from the other species of the section by the minute flowers (Figure 5.8) and the elongated (not globose) inflorescences. It is known only from a limited area in the south-western Cape Province (Map 5.15).

Vouchers: Esterhuysen 20631, 29299, Oliver 5063, Van Wyk 2200--2209, 2241.

56. *L. pentaphylla* (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 605 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 59 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 305 (1913). Type: South Africa, Cape Province, "Karakuis" [not located], Drège s.n. (K!, lecto., designated here; MO!, S!).

Lipozygis pentaphylla E. Mey., Comm. Pl. Afr. Austr. 1(1): 79 (1836). Type as above.

L. pentaphylla is the most common and well known species of the section and has been recorded from several different localities in Namaqualand (Map 5.15). It is easily recognised by the small, densely globose heads, the predominantly 5-foliolate leaves and the very small bracts (Figure 5.8).

Vouchers: Grobbelaar 1966, 1986; Meyer sub Marloth 13352; Rösch & Le Roux 837; Schlechter 11067; Van Wyk 2379.

57. *L. rosea* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 305 (1913). Type: South Africa, Cape Province, Clanwilliam, Mader 207 (K!, lecto., designated here; GRA!).

This species is closely related to *L. pentaphylla* but can easily be distinguished by the very long and slender calyx lobes (Figure 5.8), the larger and more sparsely flowered heads and the pink

flowers (yellow in L. pentaphylla). L. rosea appears to be fairly common along the Olifants River, from Citrusdal northwards to Vanrhynsdorp (Map 5.16).

Vouchers: Acocks 14732; Adamson 1483; Esterhuysen 17885; Stephens 7015; Van Wyk 2326, 2327.

58. L. bolusii Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 306 (1913). Type: South Africa, Cape Province, near Piquetberg, Bolus 8431 (K!, lecto., designated here; BOL! 2 sheets, NBG!, PRE!).

L. bolusii var. minor Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 306 (1913). Type: South Africa, Cape Province, near Hopefield, Bachmann 2228 (K!, lecto., designated here; Z).

L. bolusii Dümmer var. sessilis Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 306 (1913). Type: South Africa, Cape Province, between Tulbagh Kloof and Piqueniers Kloof, Bolus 8969 (K!, lecto., designated here; BOL!).

L. bolusii is very similar to L. pentaphylla and may easily be confused with this species. The leaves, flowers and inflorescences are generally much larger however, and the shape of the petals is different. The wing and keel petals are narrowly oblong and hairy in L. pentaphylla, oblong and glabrous in L. bolusii. L. bolusii also has a more southern distribution and

appears to be restricted to the vicinity of Malmesbury and Piquetberg (Map 5.15). The two varieties described by Dummer are very doubtfully distinct from the type.

Vouchers: Bolus 8431, 8969; Thompson 785; Van Wyk 2443, 2444.

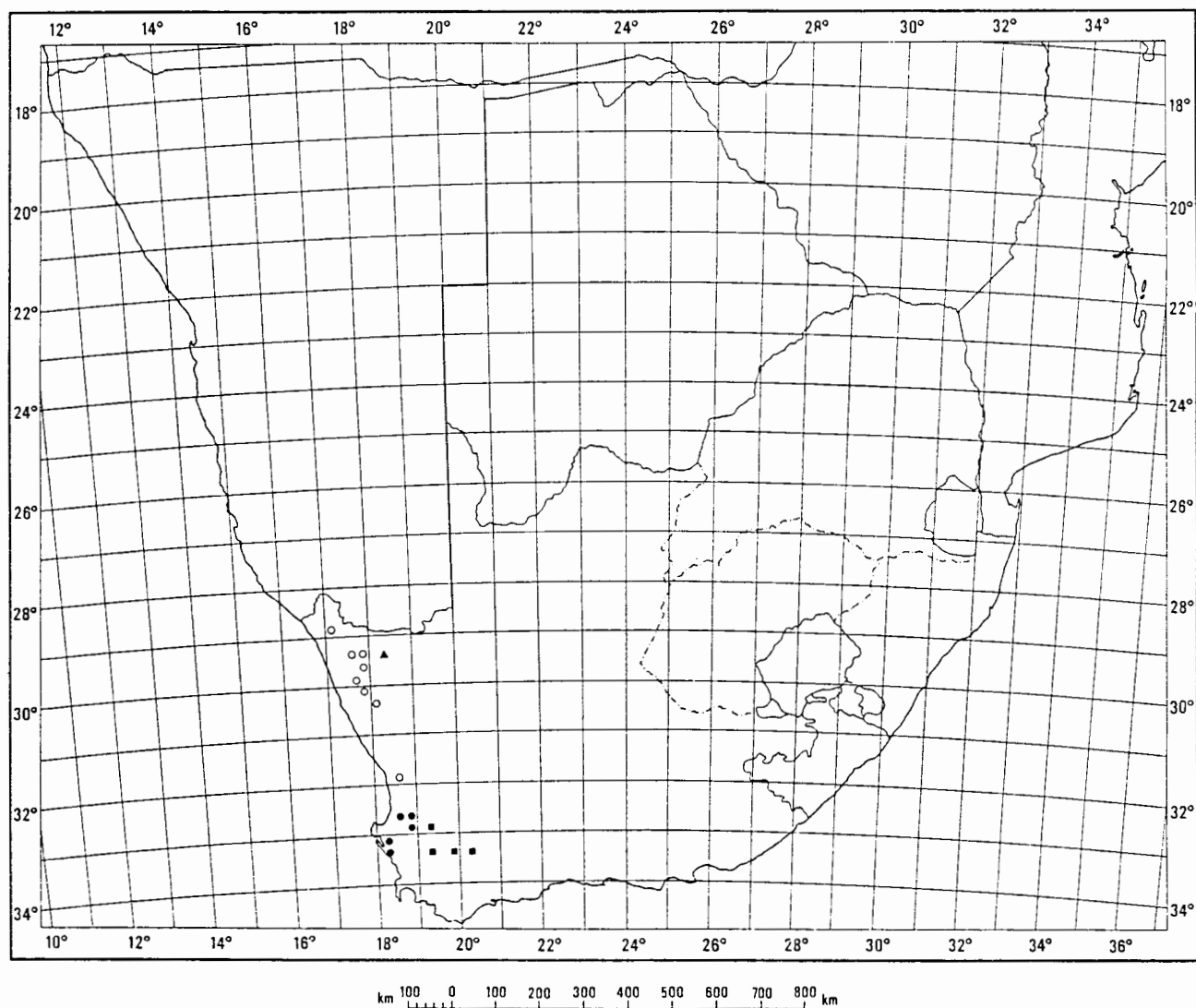
59. L. anthyllopsis B-E. van Wyk nom. nov.

L. anthylloides Harv. in Harv. & Sond., Fl. Cap. 2: 59 (1862), Dummer in Trans. Roy. Soc. S. Afr. 3(2): 306 (1913), non L. anthylloides (DC.) D. Dietr., Syn. pl. 4: 961 (1847). Type: South Africa, Cape Province, Namaqualand, Wyley s.n. (TCD, holo.; K!, S!, iso.).

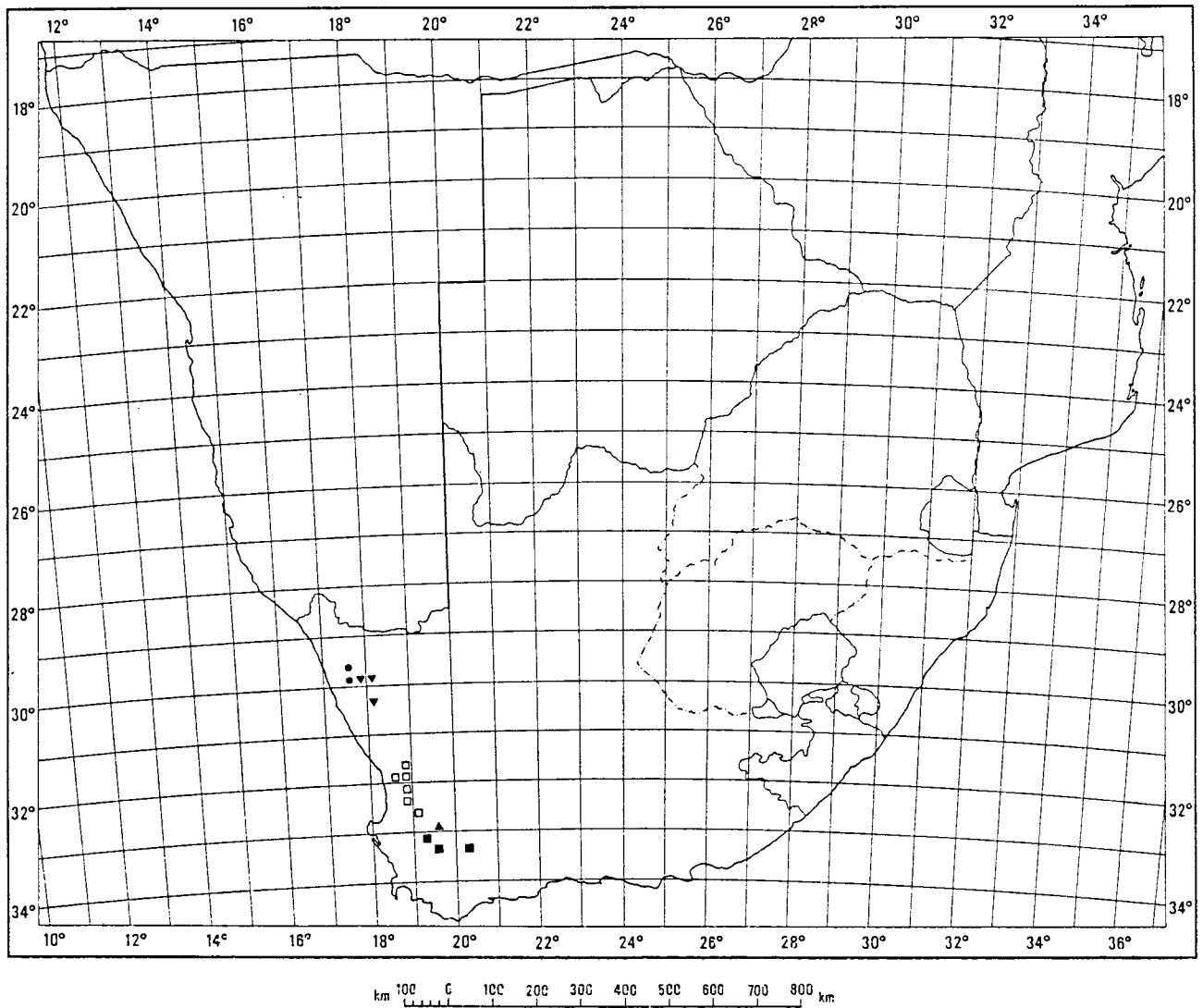
[Note: Lotononis anthylloides (DC.) D. Dietr., based on Ononis anthylloides DC., Prodr. 2: 168 (1825), is identical to L. umbellata (L.) Benth. (q.v.). Since the specific epithet had been used before, a name change is unavoidable].

L. anthyllopsis is similar to L. pentaphylla and L. bolusii but may be distinguished by the much larger flowers, inflorescences and bracts (Figure 5.8). It differs from L. rosea also in the colour of the flowers (yellow, not pink). This poorly known species has only been recorded from the vicinity of Steinkopf in Namaqualand (Map 5.16).

Vouchers: Herre sub STE 11888; Schlieben 11452; Taylor 1084.



Map. 5.15. The known geographical distribution of *L. oligocephala* (▲), *L. longicephala* (■), *L. pentaphylla* (○) and *L. bolusii* (●).



Map. 5.16. The known geographical distribution of *L. polycephala* (▼), *L. laticeps* (△), *L. globulosa* (■), *L. rosea* (□) and *L. anthyllopsis* (●).

Section 7. Oxydium Benth. emend. B-E. van Wyk emend. nov.

Lotononis section Oxydium Benth. in Hook., Lond. J. Bot. 2: 603 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 48 (1862).

Lotononis section Polylobium (Eckl. & Zeyh.) Benth. sensu Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 279 (1913), pro parte.

Crotalaria spp., Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 330 (1913) [species excluded from Lotononis].

Lotononis section Leptis (E. Mey. ex Eckl. & Zeyh.) Benth. in Hook., Lond. J. Bot. 2: 607 (1843), pro parte min.; Harv. in Harv. & Sond., Fl. Cap. 2: 49 (1862), pro parte min.; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 280 (1913), pro parte min.

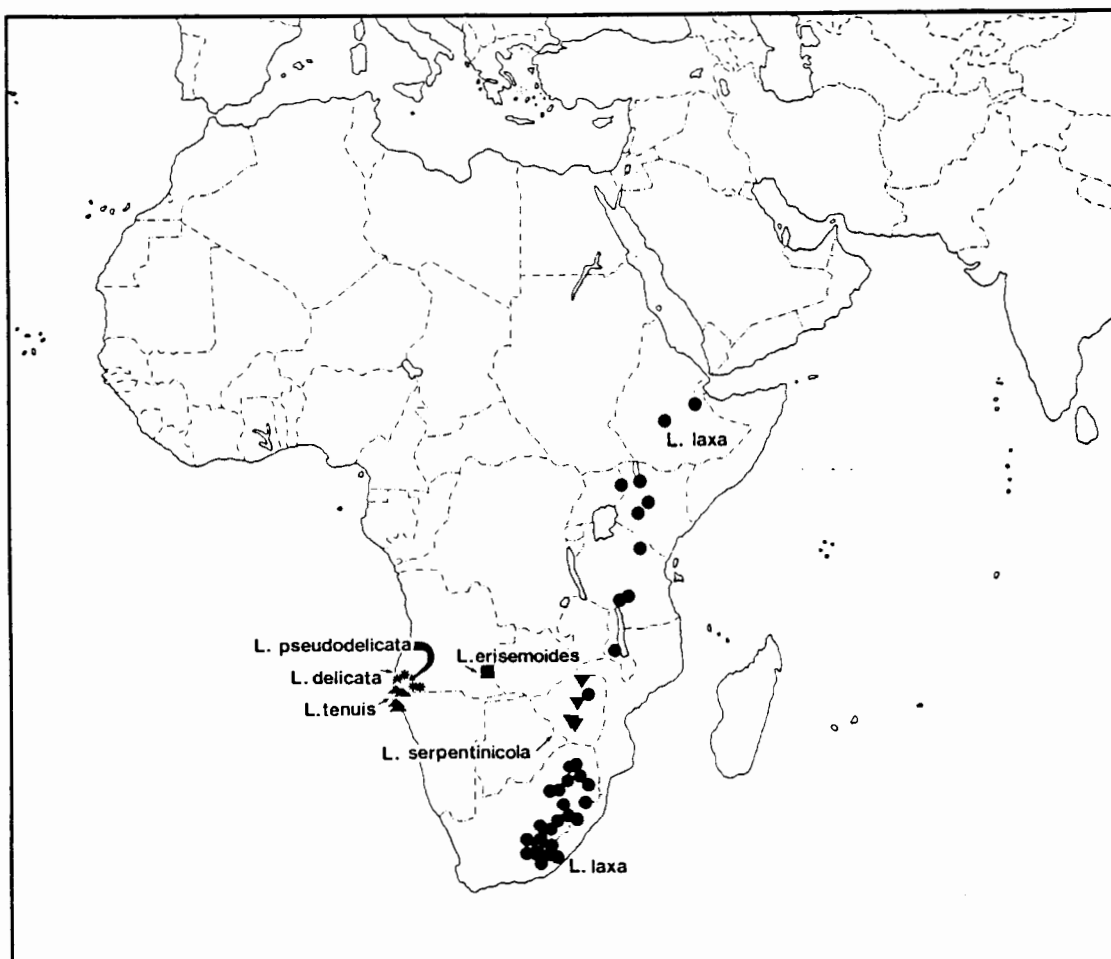
Type species (designated here): Lotononis trichopoda (E. Mey.) Benth. [now L. glabra (Thunb.) D. Dietr.].

Prostrate or procumbent (rarely erect) herbaceous annuals or less often prostrate suffrutescent perennials. All mature parts usually densely strigillose. Leaves alternate (basal leaves opposite in one species), digitately trifoliolate (occasionally with some basal leaves unifoliolate, rarely 3- to 5-foliolate, consistently unifoliolate in one species), variable in size and shape, usually densely pubescent on both surfaces, adaxial surface rarely glabrous. Stipules single at each leaf base (rarely paired), usually small and linear to lanceolate, less often ovate to broadly ovate. Inflorescences usually sessile or subsessile, short congested racemes; mostly single-flowered, less

often pedunculate and umbellately 1- to many-flowered; almost invariably leaf-opposed; bracts small, linear (large and foliaceous in one species); bracteoles absent. Flowers small to medium-sized, yellow (rarely pink or whitish), often seasonally cleistogamous. Calyx subequally lobed (rarely with the upper and lateral lobes on either side fused a little higher up in pairs), the lower lobe usually narrower, pubescent or more often strigillose. Standard broadly ovate or panduriform, \pm as long as the keel, mostly glabrous but with a line of hairs dorsally along the middle; claw conspicuously dilated towards the base, often forming a cupular structure, occasionally with a single callosity near the attachment of the blade; apex usually acute, less often obtuse to emarginate. Wing petals oblong to broadly obovate, shorter than the keel, glabrous. Keel petals half oblong-elliptic, often curved; apex at least somewhat pointed, usually distinctly beaked, glabrous (rarely pubescent). Anthers usually strongly dimorphic, 5 ovoid and dorsifixed, 4 oblong to linear and basifixed, the carinal anther usually similar to the dorsifixed ones. Pods sessile or shortly stipitate, obovoid to ovoid and much inflated, or broadly oblong, linear to linear-falcate and then only slightly inflated, thin-walled, upper suture \pm smooth or more often distinctly verrucose, dehiscent, usually many-seeded; funicles often very long. Seeds small, (0,8--1,5 (2) mm in diameter, variable in shape, the radicular lobe conspicuous, testa distinctly tuberculate. Chromosome base number 9 ($2n = 18$). (Figures 5.9 to 5.13).

Bentham's (1843) limits of the section Oxydium are here broadened to accommodate several species previously included in the section Leptis. The section now includes a total of 36 species centred in southern Africa, with one (L. laxa) extending into eastern Africa. The geographical distributions of the six species that are not endemic to the Flora of Southern Africa region are shown in Map 5.17: L. delicata, L. pseudodelicata and L. erisemoides are endemic to Angola; L. serpentinicola is endemic to Zimbabwe; L. laxa is widely distributed along the eastern parts of the African continent. The remaining 30 species of the section are all restricted to southern Africa (Maps 5.18 to 5.25).

The following combination of characters is of diagnostic value to distinguish species of the section Oxydium from species of other sections: stipules single at each leaf base (if rarely paired then the keel shortly beaked); lateral sinuses of the calyx as deep as the upper and lower ones (rarely slightly shallower); wing and keel petals totally glabrous (rarely pubescent in two species but then the standard petal panduriform or the keel beaked); claw of the standard petal dilated towards the base, often forming a cupular structure; keel petals acute or beaked (if rarely obtuse then the standard petal distinctly panduriform or the claw much dilated); anthers strongly dimorphic, the basifixed anthers more than 2x as long as the dorsifixed anthers (often several times longer); seed surface usually distinctly tuberculate.



Map 5.17. The known geographical distribution of six species of the section *Oxydium* that are not restricted to the Flora of Southern Africa region.

The beaked keel in section Oxydium has in the past led to artificial generic treatments, notably those of Meyer (1836) and Ecklon & Zeyher (1836). Bentham (1843), Harvey (1862) and Dümmer (1913) improved the generic limits but still included species of Lotononis under Crotalaria. The morphological distinction between the two genera (Baker 1914, Verdoorn 1928 and Polhill 1968b & 1982) is rather slight, but correlates well with the difference in chromosome numbers (Van Wyk & Schutte 1988a, Appendix 14). Similarities and differences between the two genera have been discussed by Van Wyk (1989f & 1989k, Appendices 26 & 31). The section Oxydium can easily be distinguished from Crotalaria by the single stipules and the absence of bracteoles. Except for L. pallens (which is clearly a Lotononis), L. delicata and L. pseudodelicata are the only species of Oxydium with paired stipules and therefore the only ones still likely to be confused with Crotalaria. Polhill (1982) transferred these two tiny Angolan ephemerals to Lotononis and they are here retained as an isolated group in Oxydium (see below). The total absence of bracteoles agrees with their position in Lotononis rather than Crotalaria.

Fourteen groups within the section Oxydium are here treated as subsections. These groups are shown as the 14 main clades in the cladogram for the section Oxydium (see Part 3.2). The subsections are recognised for practical purposes but they also reflect major discontinuities and show the most likely basic affinities within

the section. The following key makes provision for all the species of the section Oxydium except L. erisemoides, a poorly known species from Angola.

Key to the subsections of section Oxydium:

- 1A. Stipules paired, never inconspicuous or absent:
 - 2A. Flowers 3 or more per inflorescence;
south-western Cape 7A. subsection Distans
 - 2B. Flowers 1 (rarely 2) per inflorescence;
known only from Angola 7B. subsection Delicata
- 1A. Stipules single, often inconspicuous or absent:
 - 3A. Leaves predominantly 5-foliolate ... 7K. subsection Quinata
 - 3B. Leaves predominantly 3-foliolate (or 1-foliolate):
 - 4A. Wing and keel petals pubescent:
 - 5A. Keel not distinctly beaked;
standard and keel conspicuously
striated; Namibia 7E. subsection Striata
 - 5B. Keel distinctly beaked; standard
and keel not striated; Namaqualand
..... 7L. subsection Rostrata

4B. Wing and keel petals glabrous:

6A. Basal leaves opposite (the basal
branches opposite) 7N. subsection Oppositifolia

6B. Basal leaves alternate (the basal
branches alternate:

7A. Flowers < 5 mm long (never cleistogamous);
pods < 2 mm wide; north-western Namibia
and Angola 7C. subsection Tenuis

7B. Flowers > 5 mm long (unless obviously
cleistogamous); pods \geq 2 mm wide; not in
north-western Namibia or Angola:

8A. Calyx with the lateral sinuses shallower
than the upper and lower sinuses (the
upper and lateral lobes on either side
thus united in pairs:

9A. Flowers > 8 mm long; corolla
pink 7F. subsection Rosea

9B. Flowers < 7 mm long, corolla
yellow (only the tip of the
keel pink or purple 7G. subsection Brachyantha

8A. Calyx with the lateral sinuses \pm as deep
as the upper and lower sinuses (the
upper and lateral lobes on either side
not united in pairs:

10A. Calyx relatively long, more than half

as long as the corolla:

11B. Pods oblong, much longer

than the calyx 7H. subsection Laxa

11A. Pods short and ovate, scarcely

longer than the calyx:

12A. Pods circular in transverse section

(i.e., the width similar to the height

as seen in transverse section); hairs

on the pods neatly orientated; seeds

> 15 per pod, on exceptionally long

funicles; stems brittle 7M. subsection Fragilis

12B. Pods oval in transverse section (i.e.,

the width less than the height as seen in

transverse section), hairs on the pods not

neatly orientated; seeds < 15 per pod,

on relatively short funicles;

stems not brittle 7G. subsection Brachyantha

10B. Calyx relatively short, up to half as

long as the corolla:

- 13A. Perennials, with prostrate or procumbent
flowering branches from a woody base:
 - 14A. Inflorescences 3- or more-flowered;
peduncles several times longer than
the pedicels 7I. subsection Oxydium
 - 14B. Inflorescences 1-flowered, rarely
2-flowered, or if more than 2-flowered
then with the peduncles not much longer
than the pedicels 7H. subsection Laxa
- 13B. Annuals, prostrate (or rarely erect):
 - 15A. Pods ovoid, up to 2x longer than wide,
turgid (inflated):
 - 16A. Peduncles totally absent; pedicels as
long or longer than the length of
the calyx 7D. subsection Falcata
 - 16B. Peduncles present; pedicels much shorter
than the length of the calyx ... 7L. subsection Rostrata
 - 15B. Pods oblong to linear, more than 2x
longer than wide, flat (not inflated):

- 17A. Inflorescences 1-flowered, rarely 2-flowered,
peduncles absent 7D. subsection Falcata
- 17B. Inflorescences 2- or more-flowered,
distinctly pedunculate:
- 18A. Lamina of keel petal obovate; plants
prostrate; juvenile leaves 1-foliolate;
calyx \pm half as long as the corolla,
the lower lobe much narrower than
the upper 4 lobes 7J. subsection Pumila
- 18B. Lamina of keel petal panduriform;
plants erect or procumbent; juvenile
leaves 3-foliolate; calyx much less
than half as long as the corolla,
the lower lobe not much narrower
than the upper 4 lobes 7D. subsection Falcata

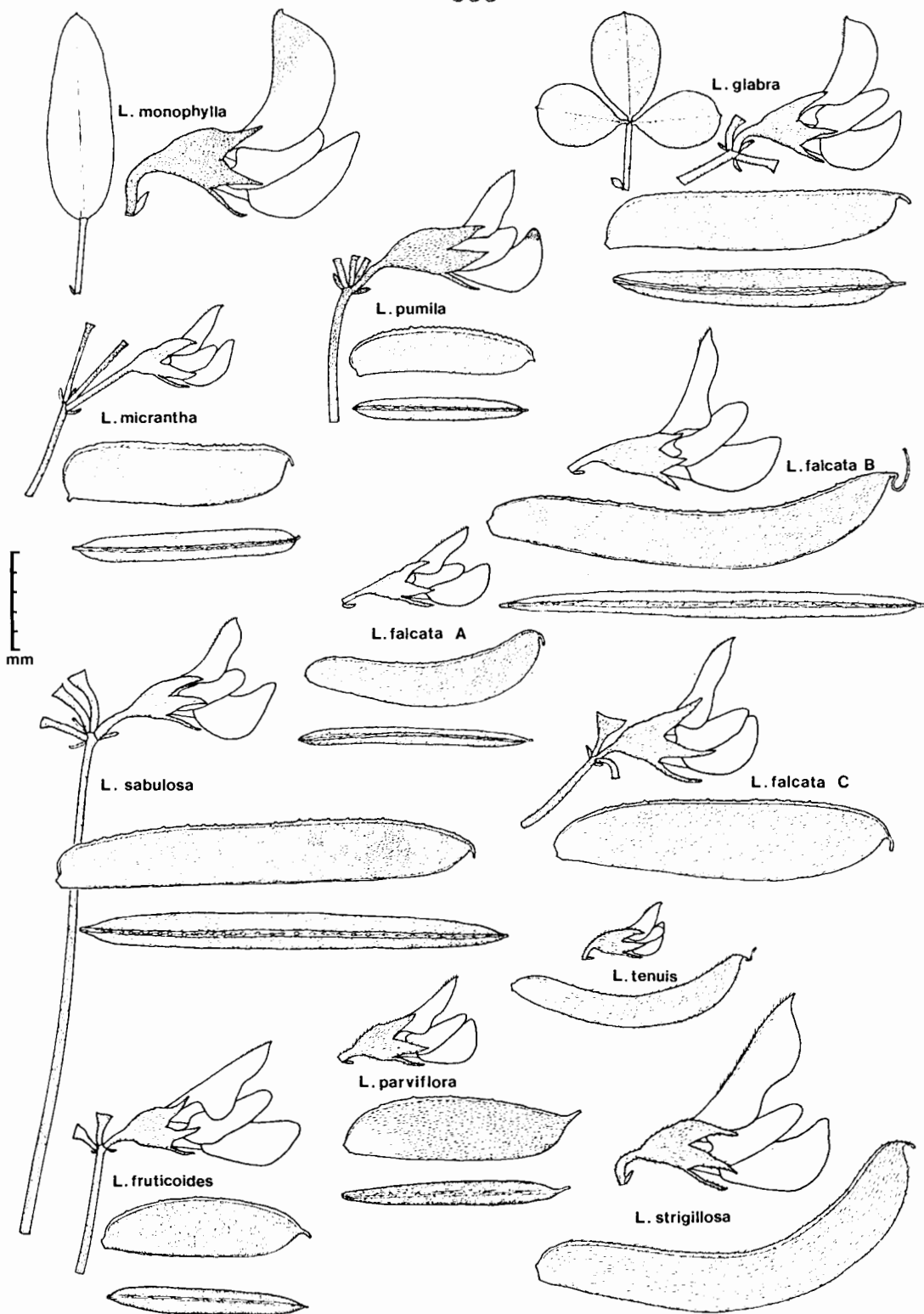


Figure 5.9. Leaves, flowers and pods of the section *Oxydium*: subsections *Tenuis*, *Falcata* (partly), *Oxydium* and *Pumila*.

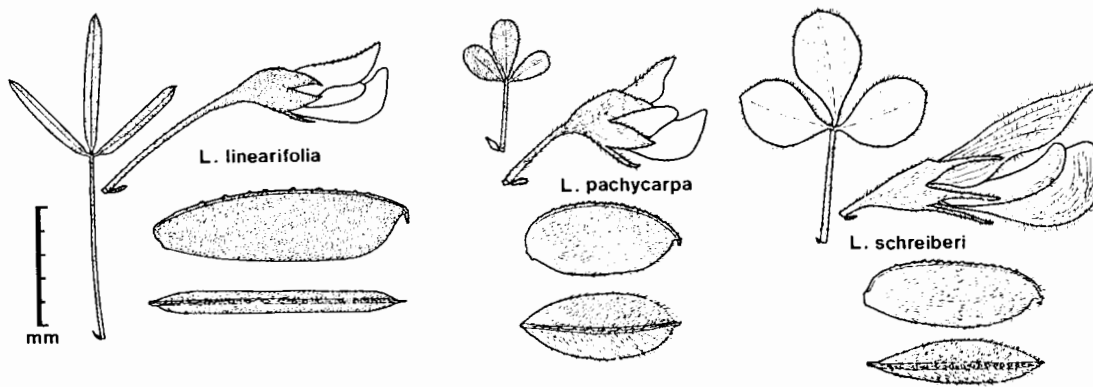


Figure 5.10. Leaves, flowers and pods of the section Oxydium: subsections Falcata (partly) and Striata.

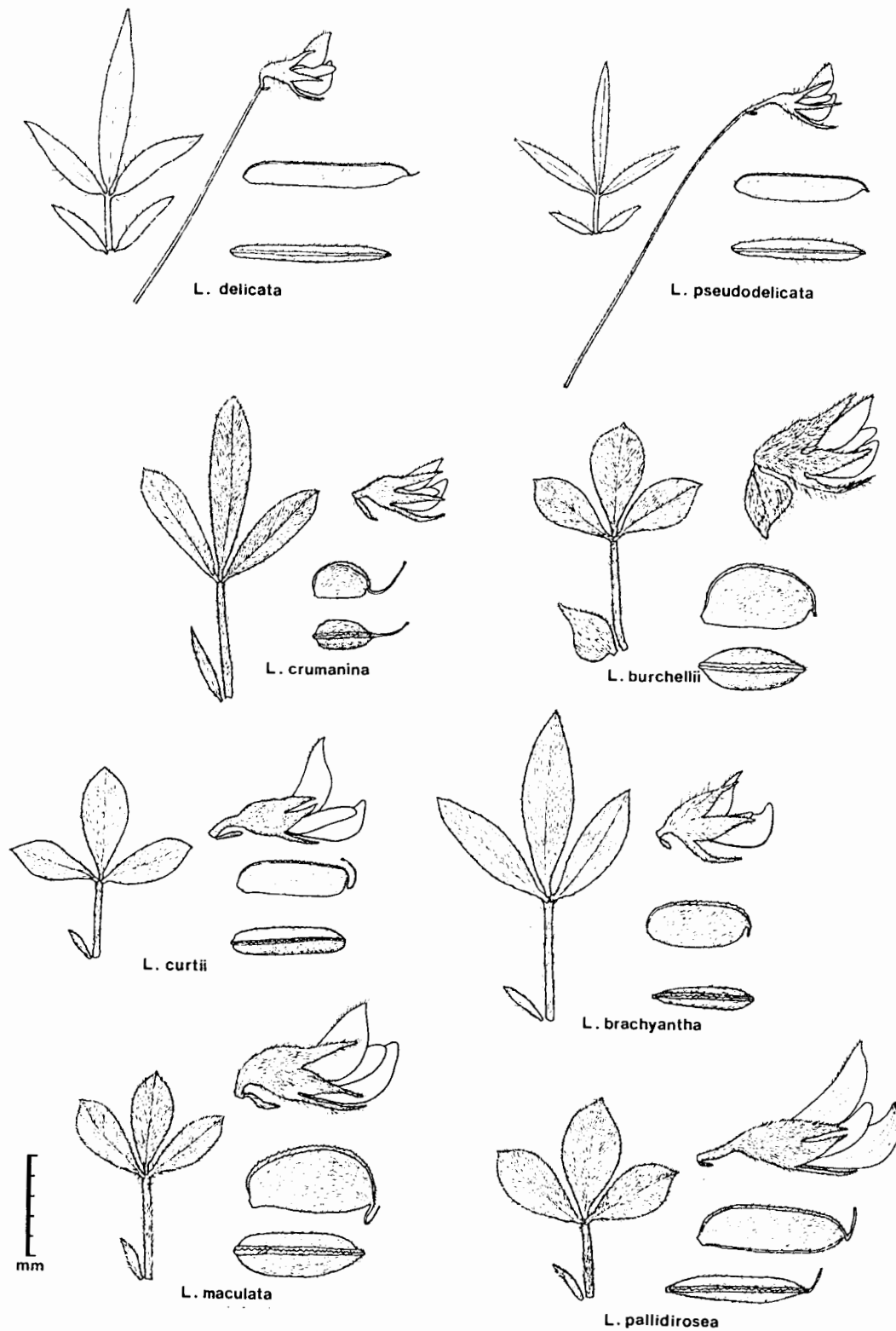


Figure 5.11. Leaves, flowers and pods of the section *Oxydium*: subsections *Delicata*, *Rosea* and *Brachyantha*.

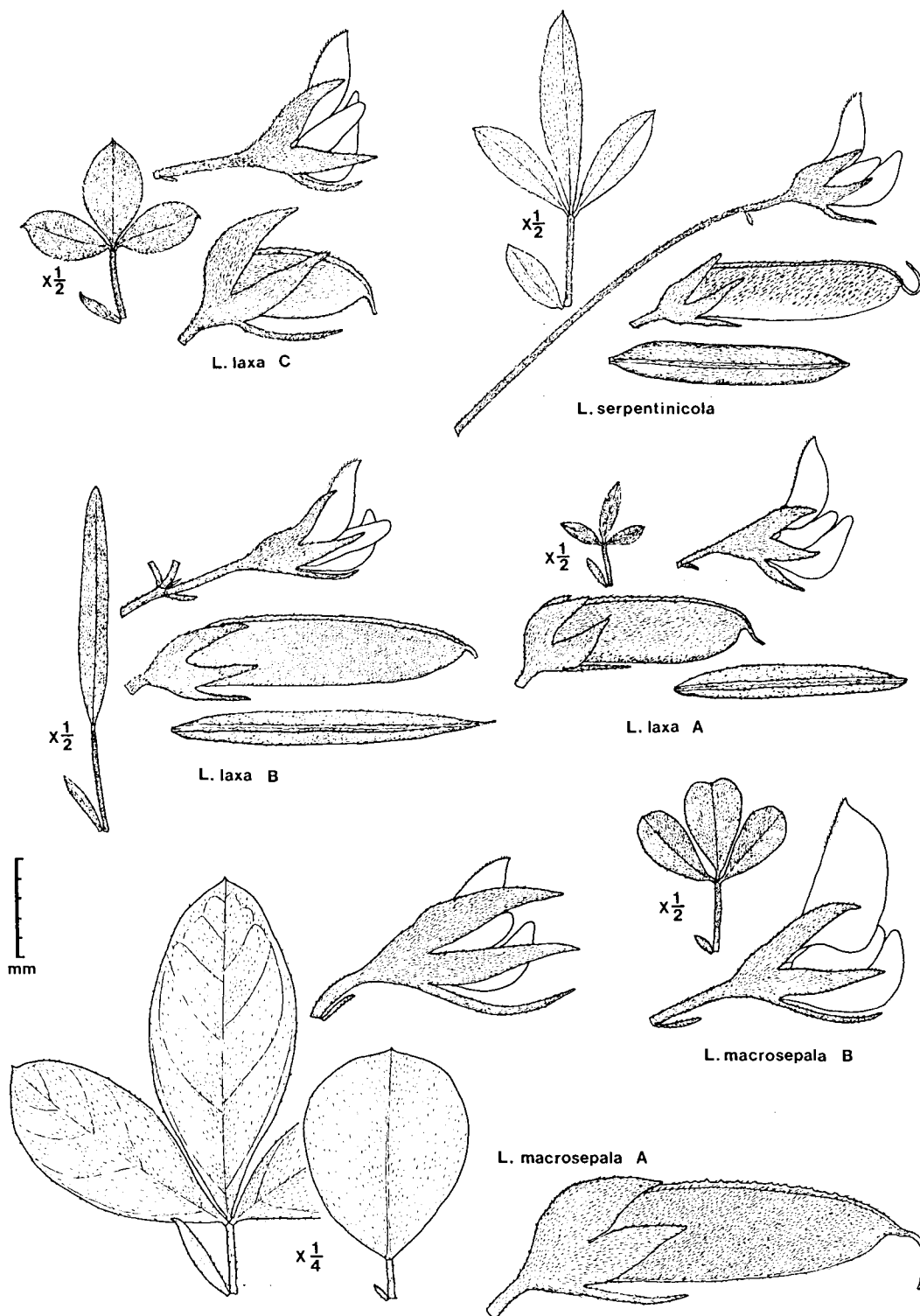


Figure 5.12. Leaves, flowers and pods of the section Oxydium: subsection Laxa.

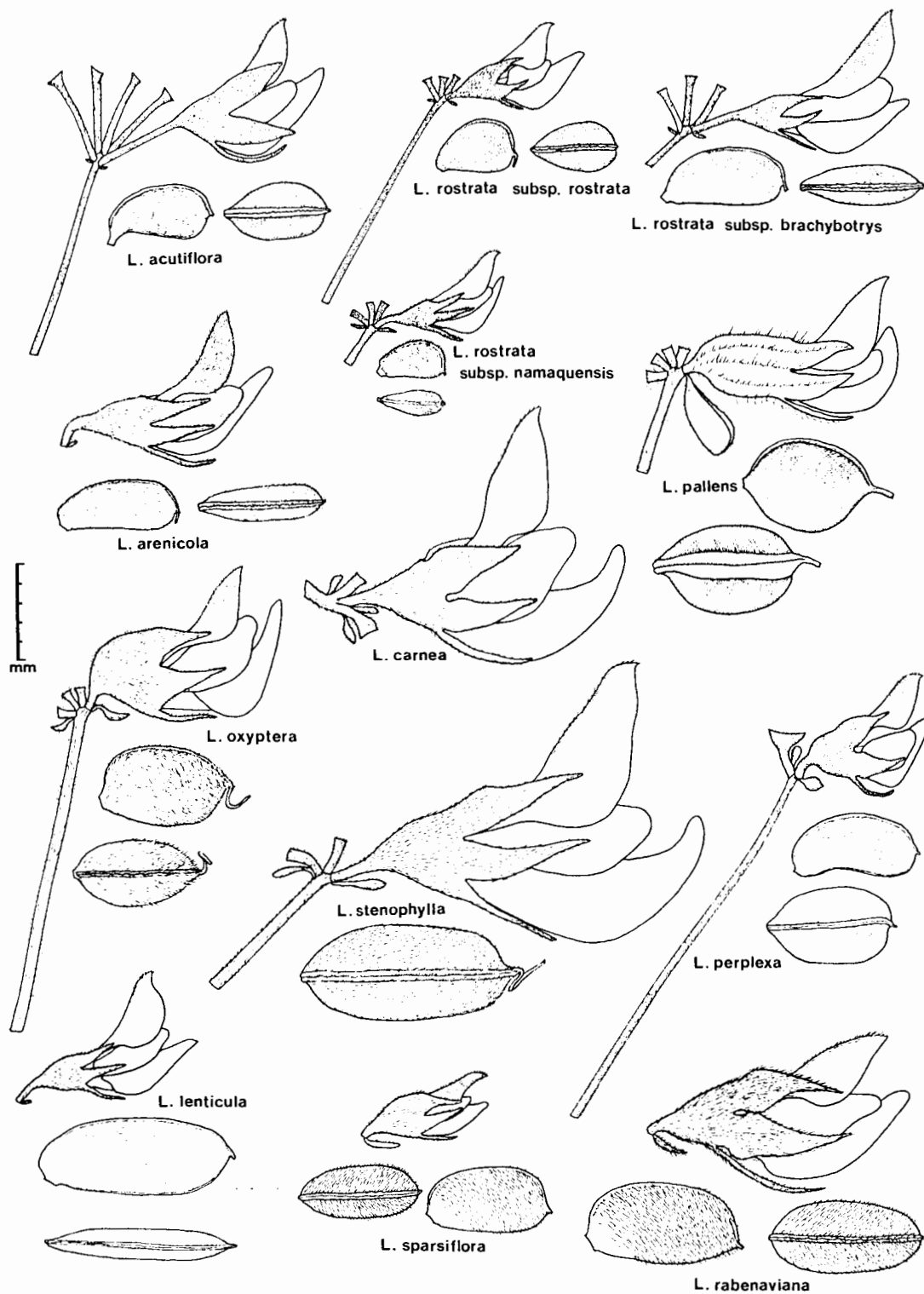


Figure 5.13. Leaves, flowers and pods of the section *Oxydium*: subsections *Distans*, *Quinata*, *Rostrata*, *Fragilis* and *Oppositifolia*.

7A. Subsectio Distans B-E. van Wyk, subsect. nov. Haec subsectio ab aliis stipulis geminatis dimorphis, bracteis magnis late obovatis, calycis vestitura (pili solum secus venas reperiuntur) atque sutura superiore leguminum percrassa, differt.

This subsection differs from other subsections in the paired dimorphic stipules, the large broadly obovate bracts, the vestiture of the calyx (hairs occur only along the veins) and the very thick upper suture of the pods.

Diagnostic characters: Prostrate annual; stipules paired, the two of each pair dissimilar in size and shape; inflorescences pedunculate, umbellately many-flowered; bracts large, obovate; calyx with the upper and lateral lobes on either side fused higher up in pairs, the lobes much shorter than the fused part; keel acute; pods short, suborbicular in side view, much inflated, the upper suture very thick (Figure 5.13). Only one poorly known species from the south-western Cape.

60. L. pallens (Eckl. & Zeyh.) Benth. in Hook., Lond. J. Bot. 2: 605 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 56 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 301 (1913). Type: South Africa, Cape Province, mountain sides near Brakfontein (Clanwilliam), Ecklon & Zeyher 1291 (S!, sheet with single specimen, lecto., designated here; S!, islecto.; C!, sub Herb. Sieber, C!, M!, SAM, partly -- larger piece, isosyn.).

Polylobium pallens Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 182 (1836); D. Dietr., Syn. pl. 4: 961 (1847). Type as above.

An unusual and distinct species, known only from the type collection (Map 5.18). It is superficially similar to L. oxyptera, but differs in the paired stipules, the broadly obovate bracts and the unusual vestiture of the calyx (Figure 5.13).

7B. Subsectio Delicata B-E. van Wyk, subsect. nov. Haec subsectio ab aliis habitu gracili, stipulis geminatis foliaceis, inflorescentiis gracilibus 1-floratis atque vestitura pilosa sparsa differt.

This subsection differs from other subsections in the slender habit, the paired foliaceous stipules, the slender 1-flowered inflorescences and the sparse, pilose vestiture.

Type species: L. delicata (Torre) Polhill.

Diagnostic characters: Small, erect, slender annuals; leaves trifoliolate, the leaflets narrowly linear-lanceolate and sparsely pilose; stipules paired, similar to the leaflets in size and shape, not dimorphic; flowers small, single (rarely paired), on a long slender peduncle, yellow; keel acute; style very short;

Pods linear or oblong, slightly inflated; seeds sparsely tuberculate (Figure 5.11). Two closely related species, known only from Angola (Map 5.17).

The taxonomic position of L. delicata and L. pseudodelicata was discussed by Polhill (1968b), who later (Polhill 1982) transferred both from Crotalaria to Lotononis. The minutely but distinctly tuberculate seed surfaces and especially the total absence of bracteoles are clear indications that they are indeed best accommodated in Lotononis. From a morphological and also a geographical point of view, some connection with L. tenuis or L. serpentinicola seems possible. The latter has the same inflorescence structure and paired stipules are occasionally present at the insertion of the peduncles. The chromosome base number of L. delicata and L. pseudodelicata, when it becomes known, would indicate more clearly if they are correctly placed in Lotononis. The two species nevertheless represent an isolated group not only in section Oxydium but in the genus as a whole.

Key to the species of subsection Delicata (see Figure 5.11):

- 1A. Pods linear, only slightly inflated 61. L. delicata
- 1B. Pods oblong, turgid 62. L. pseudodelicata

61. L. delicata (Bak. f.) Polhill, Crotalaria in Africa and Madagascar: 375 (1982). Type: Southern Angola, near the Monino River in the path to Capangombe, Pearson 2815 (K!, holo.).

Crotalaria delicata Bak. f., Leg. Trop. Afr. 1: 56 (1926); Polhill in Kew Bull. 22: 174 (1968). Type as above.

Vouchers: Da Silva 3091; Pearson 2815, 2491; Teixeira et al. 2311.

62. L. pseudodelicata (Torre) Polhill, Crotalaria in Africa and Madagascar: 376 (1982). Type: Angola, Huila, Chibia, rio Chacato, Gossweiler 10982 (COI, holo., K, photo!; K!, iso.).

Crotalaria pseudodelicata Torre in Mem. Junta Invest. Ultra., sér. 2, 19: 47 (1960); Polhill in Kew Bull. 22: 174 (1968). Type as above.

Voucher: Gossweiler 10983.

The exact position of the following poorly known species has not yet been determined.

63. L. erisemoides (Ficalho & Hiern) Torre in Mem. Junta Invest. Ultra., sér. 2, 19: 23 (1960), in Consp. Fl. Angolensis 3(2): 5 (1962). Type: Angola, Moxico, Ninda river, tributary of the Zambezi river, Serpa Pinto 3 (LISU).

Crotalaria erisemoides Ficalho & Hiern in Trans. Linn. Soc., Bot. Ser. 2(2): 17 (1881); Bak. f. in J. Linn. Soc. Bot. 42: 414 (1914), Leg. Trop. Afr. 1: 59 (1926). Type as above.

L. erisemoides occurs in Angola (Map 5.17) and is known only from the type collection. I have not yet had the opportunity to visit LISU and study this material.

7C. Subsectio Tenuis B-E. van Wyk, subsect. nov. Haec subsectio est similis subsectioni Delicatae sed stipulis inconspicuis, floribus subsessilibus et leguminibus falcatis differt.

This subsection is similar to the subsection Delicata but differs in the inconspicuous stipules, the subsessile flowers and the falcate pods.

Diagnostic characters: Small, slender annuals; leaves trifoliolate, the leaflets narrowly linear and almost glabrous; stipules single, inconspicuous; flowers small, single (rarely paired), subsessile, yellow; keel acute; pods falcate; seeds very small ($\pm 0,8$ mm long), smooth (Figure 5.9). Only one species.

64. *L. tenuis* Bak. in Oliv., Fl. Trop. Afr. 2: 5 (1871); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 320 (1913); Bak. f., Leg. Trop. Afr. 1: 19 (1926); Torre in Consp. Fl. Angolensis 3(2): 5 (1962). Type: Angola, Mossamedes, by the river Beco, Welwitsch 1900 (LISU, holo.; BM!, K!, iso.).

A small and slender plant known only from southern Angola and north-western Namibia (Maps 5.17 and 5.18). It is similar to *L. falcata* but can easily be distinguished by the slender habit and much smaller flowers and pods (Figure 5.9). The shape of the pistil suggests an affinity with the subsection Delicata, but *L. tenuis* is strongly cyanogenic and therefore perhaps more closely related to the following subsection.

Vouchers: Braine 79; Giess 9403.

7D. Subsectio Falcata B-E. van Wyk, subsect. nov. Species huius gregis ab aliis huius sectionis lobis calycis brevibus, ala carinaque glabris, atque imprimis vexilla panduriformi differt.

The species of this group differ from others of the section in the short calyx lobes, the glabrous wing and keel petals and particularly in the panduriform shape of the standard petal.

Type species: *L. strigillosa* (Merxmüller & Schreiber) Schreiber.

Diagnostic characters: Erect or prostrate annuals, all strongly cyanogenic; leaves trifoliolate, very rarely with some 5-foliolate; vestiture usually inconspicuous, minutely strigillose; calyx usually less than half as long as the corolla; flowers yellow, pink or white, never cleistogamous; standard acute, the lamina panduriform; keel \pm acute but not always distinctly beaked; pods usually oblong to oblong-linear or linear-falcate, flat, not turgid, rarely ovate and turgid (*L. pachycarpa*) (Figures 5.9 & 5.10). Seven species from the central and western parts of southern Africa.

Key to the species of subsection Falcata:

- 1A. Pedicel as long or longer than the calyx, peduncle absent:
 - 2A. Leaflets linear, pods oblong, not
inflated 70. L. linearifolia
 - 2B. Leaflets oblanceolate to obovate, pods
ovate, inflated 71. L. pachycarpa
- 1B. Pedicel shorter than the calyx, peduncle present or absent:
 - 3A. Inflorescence umbellately 3- or more-flowered,
the peduncle longer than the pedicels:
 - 4A. Plant robust, erect, 300 -- 500 mm high;
Leaflets narrowly linear, acute 68. L. fruticoides
 - 4B. Plant slender, prostrate or procumbent,
up to 300 mm high, leaflets oblong to broadly
obovate, obtuse to emarginate:
 - 5A. Peduncles short, not much longer than
the flowers; keel petals \pm obtuse;
pods oblong 66. L. falcata
 - 5B. Peduncles long and slender, much longer
than the flowers; keel petals acute;
pods linear 69. L. sabulosa
 - 3B. Inflorescence single-flowered, rarely 2- or 3-flowered
but then the peduncle shorter than the pedicels or \pm absent:

- 6A. Leaflets oblanceolate to broadly obovate;
pods falcate; flowers 8--10 mm long 65. L. strigillosa
- 6B. Leaflets linear to oblanceolate; pods
straight or falcate; flowers up to 7 mm long
(rarely 8--10 mm but then the leaflets linear
and the pods not falcate):
- 7A. Flowers white and pink; vestiture of
spreading hairs; pods oblong, straight,
apex conspicuously cuspidate 67. L. parviflora
- 7B. Flowers yellow; vestiture of short appressed
hairs; pod oblong to linear, often falcate,
not conspicuously cuspidate 66. L. falcata

65. L. strigillosa (Merxmüller & Schreiber) Schreiber in Mitt.
Bot. Staatssamm. München 3: 613 (1960); Schreiber in FSWA 60: 85
(1970). Type: Namibia, Luderitz area, plain east of the
Buchuberge, Dinter 6508 (M!, holo.; BOL!, GRA!, PRE!, SAM!,
iso.).

Amphinomia strigillosa Merxmüller & Schreiber in Bull. Jard.
Bot. Brux. 27: 273 (1957). Type as above.

Amphinomia leptoloba (H. Bol.) Schreiber sensu Schreiber in
Mitt. Bot. Staatssamm. München 2: 287 (1957).

Lotononis psammophila Dinter in sched.

Closely related to L. falcata, but readily distinguished by the shape of the leaflets, the vestiture and the size of the flowers and pods (Figure 5.9). The species occurs in southern Namibia and the north-western Cape (Map 5.18).

Vouchers: Dinter 3919, 4071, 6508; Giess & Müller 14391; Leistner 3440; Merxmüller & Giess 3294; Müller 762.

66. L. falcata (E. Mey.) Benth. in Hook. Lond. J. Bot. 2: 608 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 62 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 319 (1913); Bak. f., Leg. Trop. Afr. 1: 18 (1926); Schreiber in FSWA 60: 82 (1970). Type: South Africa, Cape Province, on the Gariep near "Verleptpram" [2817 AA Violsdrif], Drège s.n. a (B+; K!, lecto., designated here; BM!, PRE 24304!, S!, islecto.); "Ebenezer" [3118 CA Vanrhynsdorp?], Drège s.n. b (B+; no isotypes seen).

Lipozygis falcata E. Mey., Comm. Pl. Afr. Austr. 1(1): 78 (1836). Type as above.

Leptis falcata (E. Mey.) Benth. in Ann. Wien. Mus. 2: 142 (1839); Steud., Nom. Bot. 2(2): 29 (1841). Type as above.

Leptidium falcatum (E. Mey.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845). Type as above.

Polylobium falcatum (E. Mey.) D. Dietr., Syn. pl. 4: 962 (1847). Type as above.

Amphinomia falcata (E. Mey.) Schreiber in Mitt. Bot. Staatssamm. München 2: 287 (1957). Type as above.

Lotononis decipiens Schlechter in De Wildeman, Pl. Nov. Hort. Then. 1: 183, t. 40 (1906). Type: South Africa, Cape Province, south-western region, "Brackdam" [3017 BD Hondeklipbaai?], Schlechter 11113 (B+; BOL!, lecto., designated here; BM!, MO!, PRE!, S!, iso.).

A common and geographically widespread species (Map 5.18), showing considerable variation, particularly in the habit, the size of the flowers and in the size and shape of the leaves and pods. A formal infraspecific subdivision is not attempted here, but three major forms can be distinguished, as shown in Figure 5.9. These are briefly described below and the distributions have been plotted separately in Map 5.18.

Form A. ("typical" form)

Small, prostrate, rarely more than 100 mm high; branches slender; flowers not on a peduncle, invariably single, relatively small; pods small, falcate. This form is widely distributed along the west coast of the Cape Province, spreading into the southern part of Namibia (Map 5.18).

Vouchers: Acocks 23316; Compton 17221; Goldblatt 5733; Stirton 5998; Van Wyk 2227, 2228, 2360, 2366.

67. L. parviflora (Berg.) D. Dietr., Syn. pl. 4: 960 (1847).

Type: South Africa, Cape Province, "e Cap. b. Sp.", Grubb s.n.
sub Bergius 236.45 (SBT!, holo.).

Ononis parviflora Berg., Descr. pl.: 214 (1767); Thunb., Prod.
pl. Cap.: 129 (1800), Fl. Cap.: 585 (1823); DC., Prodr. 2: 166
(1825) non Lam. Type as above.

Lipozygis brachyloba E. Mey., Comm. Pl. Afr. Austr. 1(1): 78
(1836), synon. nov. Type: South Africa, Cape Province, "Karakuis"
[?], Drège s.n. (B+; K!, lecto., designated here; MO!, S!,
isolecto.).

Leptis brachyloba (E. Mey.) Benth. in Ann. Wien. Mus. 2: 142
(1839); Steud., Nom. Bot. 2(2): 29 (1841). Type as above.

Lotononis brachyloba (E. Mey.) Benth. in Hook., Lond. J. Bot.
2: 608 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 63 (1862);
Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 318 (1913). Type as
above.

Leptidium brachylobum (E. Mey.) Presl in Abh. k. Böhm. Ges.
Wiss. 5(3): 479 (1845). Type as above.

Polylobium brachylobum (E. Mey.) D. Dietr., Syn. pl. 4: 962
(1847). Type as above.

This species has often been confused with L. falcata, but it is readily distinguished by the pink flowers (yellow in all other related species), the more spreading vestiture and the conspicuously cuspidate pods (Figure 5.9). Restricted to the south-western and north-western Cape (Map 5.18), where it is very common, particularly in disturbed areas.

Form B. ("robust" form)

Robust, erect, up to 300 mm high; branches rigid, divaricate, the main stem thick and dark purple in colour; flowers not on a peduncle, single or rarely in pairs; pods large, falcate.

Compared to form A, the distribution is generally more inland (Map 5.18).

Vouchers: Dinter 1119; Giess & Müller 11843; Merxmüller & Giess 28249, 32546; Volk 12592; Zeyher 390.

Form C. ("pedunculate" form)

Procumbent, up to 200 mm high; branches slender; flowers usually on a short peduncle, up to 3 per inflorescence; pods short and broad, straight. This form is often confused with L. parviflora, but the flowers are yellow and not pink as in the latter. The distribution is restricted to the Calvinia and Sutherland districts (Map 5.18).

Vouchers: Hanekom 1544; Johnson 596; Oliver 4380; Schutte 298; Stokoe s.n. sub SAM 55933.

Vouchers: Barker 2533; Bond 1103; Compton 15045; Vlok 1572; Van Wyk 2238--2246.

68. *L. fruticoides* B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 31]. Type: South Africa, Cape Province, Naudesberg Pass, 39 km from Graaff Reinet, B-E. van Wyk 2020 (PRE!, holo.; K!, MO!, NBG!, SAAS!, iso.).

Closely related to *L. falcata*, but differs in the much more robust habit (a shrub-like annual of 300--600 mm high), the pedunculate and umbellate inflorescences, the linear and acute leaflets, the much shorter pods (Figure 5.9) and in the more eastern distribution (Map 5.18).

Vouchers: Bengis 474; Bolus 14075; Schutte 219, 220; Tyson s.n. sub PRE 54319; Van Wyk 2137, 2020--2026.

69. *L. sabulosa* Salter in J. S. Afr. Bot. 6: 2 (1940). Type: South Africa, Cape Province, Cape Peninsula, near Rugby, Levyng 7047 (BOL!, holo.).

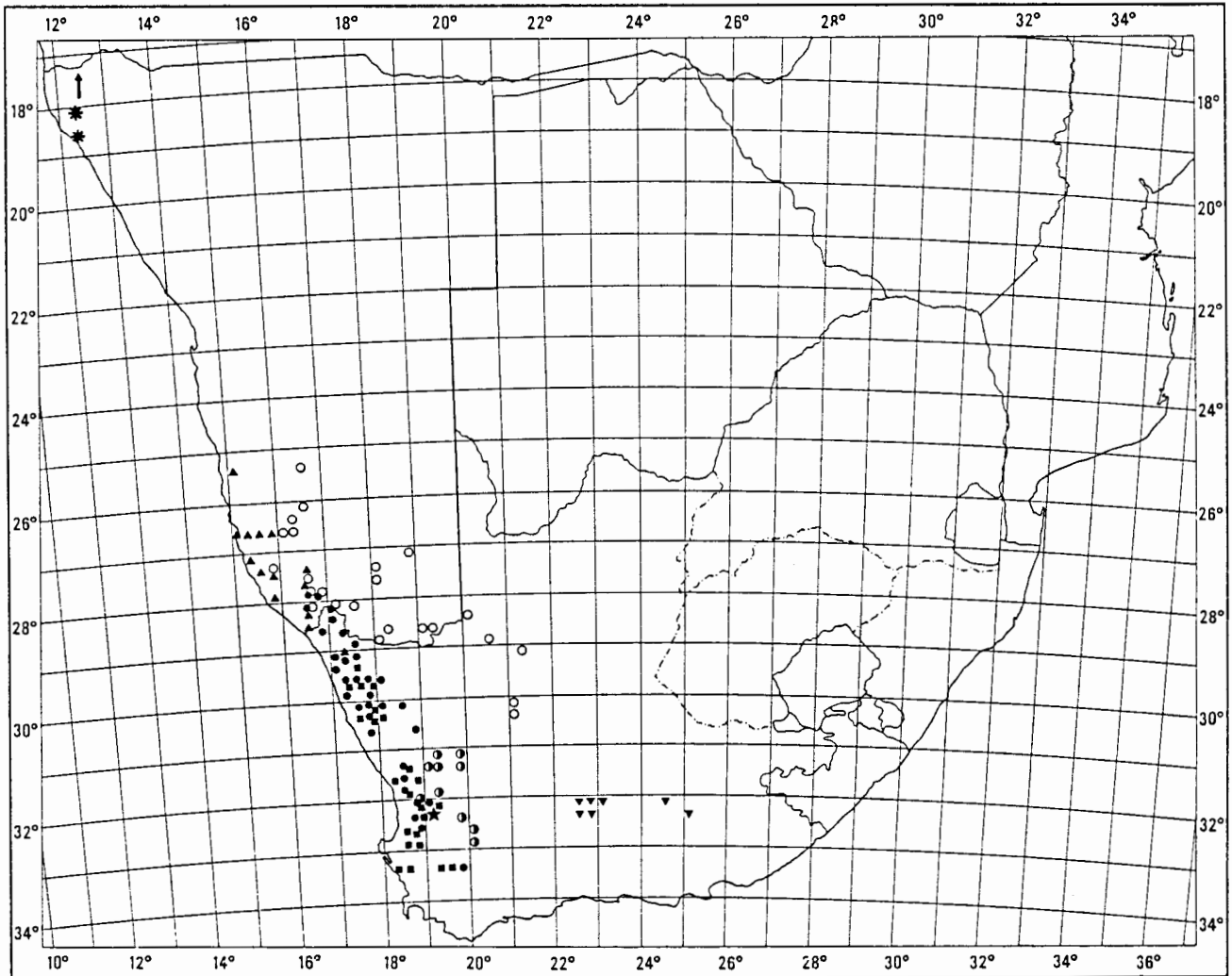
The slender umbellate inflorescences, acute keel petals and linear pods (Figure 5.9) are useful diagnostic characters for this appropriately named species from the south-western and north-western Cape Province (Map 5.19).

Vouchers: Acocks 24461; Boucher 2572; Grobbelaar 1224; Salter 8503; Van Wyk 2325; Walgate 742.

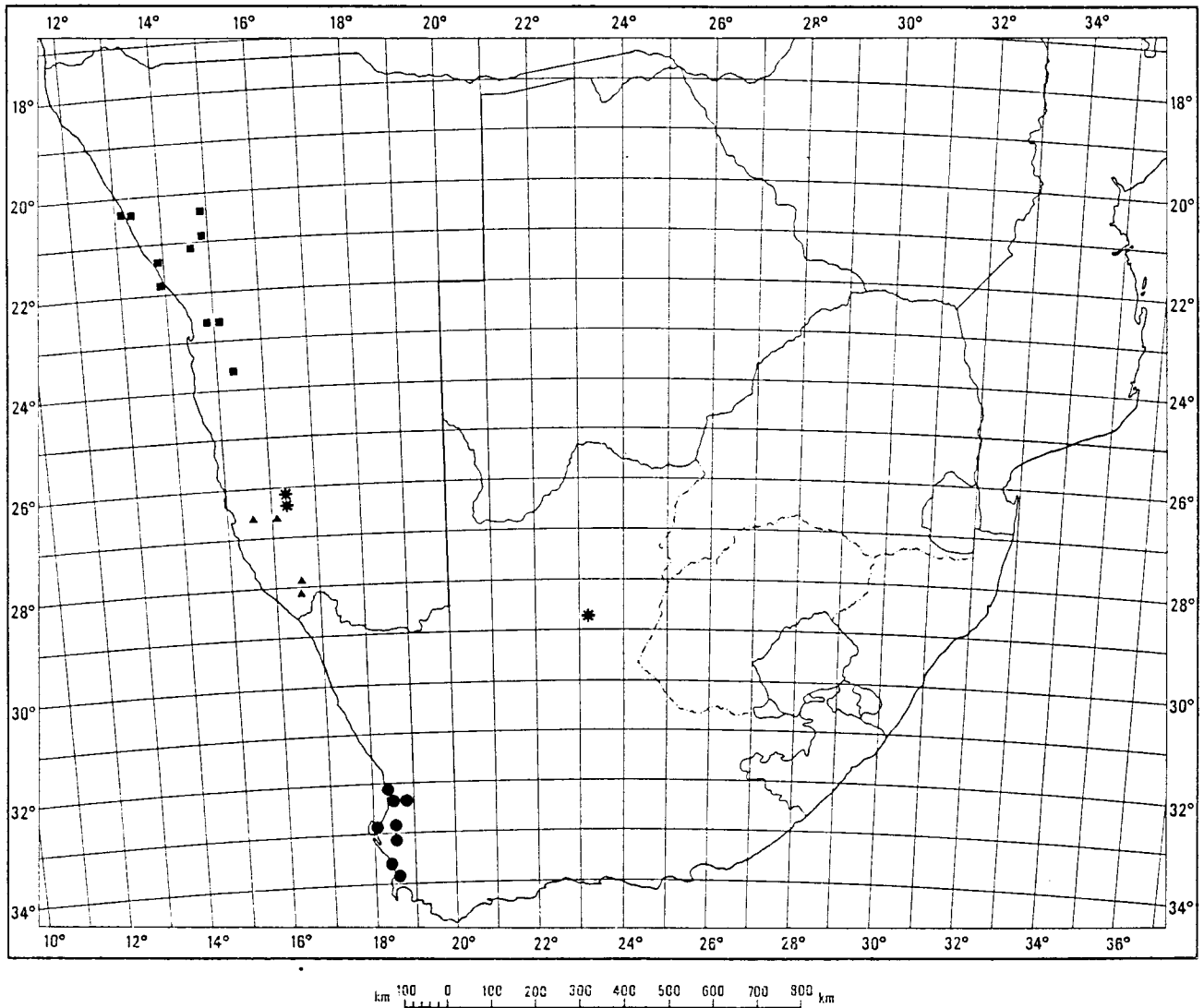
70. L. linearifolia B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 31]. Type: South Africa, Cape Province, "Hay 0.303" [2822 CD], Acocks 506 (PRE!, holo.; BOL!, KMG!, PRE!, iso.).

L. linearifolia is similar to L. pachycarpa but differs in the narrow, linear leaflets, the very small stipules, the minute and appressed vestiture and the oblong-linear and only slightly inflated pods (Figure 5.10). The long slender pedicel (often much longer than the calyx) is a useful character to distinguish L. linearifolia and L. pachycarpa from other species of the subsection. This distinct species is probably not as rare as the scanty herbarium record would suggest, but rather overlooked. The few known localities are shown in Map 5.19.

Vouchers: Kinges 2433; Merxmüller & Giess 2876.



Map 5.18. The known geographical distribution of *L. pallens* (★), *L. tenuis* (*), *L. strigillosa* (▲); *L. falcata* "form A" (●), *L. falcata* "form B" (○), *L. falcata* "form C" (◐), *L. parviflora* (■) and *L. fruticoides* (▼).



Map 5.19. The known geographical distribution of *L. sabulosa* (●), *L. linearifolia* (*), *L. pachycarpa* (▲) and *L. schreiberi* (■).

71. *L. pachycarpa* Dinter ex B-E. van Wyk sp. nov. ined. [*Bothalia* (in press), Appendix 31]. Type: Namibia, Halenberg, Dinter 6648 (PRE!, holo.; BOL!, K!, M!, SAM!, STE!, iso.).

L. pachycarpa Dinter in sched.

Amphinomia curtii (Harms) Schreiber sensu Schreiber in Mitt. Bot. Staatssamm. München 2: 286 (1957).

L. leptoloba H. Bol. sensu Schreiber in FSWA 60: 82 (1970).

L. pachycarpa is closely related to *L. linearifolia*, but differs in the shape of the leaflets, the much larger stipules, the more spreading hairs and the ovoid, turgid pods (Figure 5.10). It is superficially similar to *L. curtii* and *L. leptoloba*, but can easily be distinguished from these species by the long pedicel, the panduriform standard petal and particularly in the shape of the pods. *L. pachycarpa* has a limited geographical distribution and occurs only in southern Namibia (Map 5.19).

Vouchers: Dinter 4070; Giess, Volk & Bleissner 5462; Merxmüller & Giess 28505, 32363.

7E. Subsectio Striata B-E. van Wyk, subsect. nov. Subsectionis Falcatae similis, sed lobis calycis longis (lobi \pm tubam aequantes), petalis striatis pubescentibus atque carina obtusa vel parum acuta, differt.

Similar to the subsection Falcata, but differs in the long calyx lobes (lobes \pm as long as the fused part), the striated and pubescent petals and the obtuse or only slightly pointed keel.

Diagnostic characters: Prostrate annual; leaves trifoliolate; flowers yellow, never cleistogamous; calyx equally lobed, the lobes nearly as long as the fused part; petals long and narrow, pubescent, conspicuously striated; standard petal acute, panduriform; keel more or less obtuse; anthers strongly dimorphic, the carinal anther intermediate; pods oblong, slightly turgid (Figure 5.10). One species.

72. L. schreiberi B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 31]. Type: Namibia, Cape Cross, about 0,5 km from the coast, Giess 8070 (PRE!, holo.; K!, M!, WIND!, iso.).

L. schreiberi is a distinct species and its affinities is somewhat uncertain. It can easily be distinguished from all other species of the section Oxydium by the pubescent wing and keel petals and the conspicuously striated petals (Figure 5.10). The species is cyanogenic, and the highly dimorphic anthers and panduriform standard suggest that it is correctly placed in Oxydium. L. schreiberi appears to be a common species in the western parts of central Namibia, where several collections have been made (Map 5.19).

Vouchers: Galpin & Pearson sub Galpin 7547, 7579; Giess 8020, 3576; Giess, Volk & Bleissner 6277; Kers 4, 1311, 1532, 1580, 1586; Oliver & Muller 6660 (partly).

7F. Subsectio Rosea B-E. van Wyk, subsect. nov. Subsectionis Striatae similis, sed calyce zygomorphi (lobis superioribus lateralibusque altioribus utrinque binatim fuis), floribus roseis, alis carinaque glabris atque carina acuta differt.

Similar to the subsection Striata, but differs in the zygomorphic calyx (the upper and lateral lobes on either side fused higher up in pairs), the pink colour of the flowers, the glabrous wing and keel petals and the acute keel.

Diagnostic characters: Prostrate short-lived perennial; leaves densely silky, trifoliolate, the basal ones often unifoliolate; flowers pink, never cleistogamous; calyx zygomorphic; petals glabrous (a line of hairs on the standard only), conspicuously striated; standard ovate, not panduriform; keel acute and beaked; pods oblong, not turgid (Figure 5.11). One species.

73. L. pallidirosea Dinter & Harms in Fedde, Repert. 16: 359 (1920); Schreiber in FSWA 60: 83 (1970). Type: Namibia, Farm Hoffnung, Dinter 974 (B+; SAM!, label in Dinter's hand, lecto., designated here).

Amphinomia pallidirosea (Dinter & Harms) Schreiber in Mitt.

Bot. Staatssamm. München 2: 288 (1957). Type as above.

A somewhat poorly known short-lived perennial, easily recognised by the small but robust habit, the shallow lateral sinuses of the calyx, the densely silky vestiture and relatively large pink flowers. (Figure 5.11). L. pallidirosea has been recorded from a few isolated localities in the central and northern parts of Namibia (Map 5.20).

Vouchers: Dinter 3516, 7878; Giess 9435; Volk 585, 6542.

7G. Subsectio Brachyantha B-E. van Wyk subsect. nov. Subsectionis Roseae similis sed numero florum (saepe plus quam 1 per inflorescentiam), calyce sub-pariter lobato (in specie unica zygomorpho), floribus luteis, calyce perlongo (saepe corollam fere aequans) atque leguminibus brevibus ovatis plerumque turgidis differt.

Similar to the subsection Rosea, but differs in the number of flowers (often more than 1 per inflorescence), the subequally lobed calyx (zygomorphic in L. curtii), the yellow colour of the flowers, the very long calyx (often nearly as long as the corolla) and in the short, ovate and usually turgid pods.

Type species: L. crumanina Burch. ex Benth.

Diagnostic characters: Prostrate or procumbent short-lived perennials; leaves densely silky-strigillose, trifoliolate, the basal ones unifoliolate; flowers often more than one per inflorescence, yellow, occasionally cleistogamous; calyx subequally lobed, rarely zygomorphic; petals glabrous (a line of hairs on the standard only), not striated; standard ovate, not panduriform; keel acute but not distinctly beaked; pods ovate, rarely oblong, usually turgid (Figure 5.11). Five species with a wide distribution in the central and western parts of southern Africa (Map 5.20).

Key to the species of subsection Brachyantha:

- 1A. Lateral sinuses of the calyx much shallower than
the upper and lower sinuses; pods oblong, much
inflated (\pm circular in transverse section) ... 74. L. curtii
- 1B. Lateral sinuses of the calyx \pm as deep as the
upper and lower sinuses; pods ovate (if shortly oblong
then only slightly inflated):
 - 2A. Bracts large and foliaceous,
broadly ovate 77. L. burchellii
 - 2B. Bracts small, inconspicuous, linear
to lanceolate:
 - 3A. Flowers 3 or 4 per flowering node 76. L. crumanina
 - 3B. Flowers usually 1 per flowering node,
rarely up to 3:
 - 4A. Plant < 150 mm wide, densely leafy, the nodes
close together; calyx with the lobes \pm as long
as the fused part; petioles often much longer
than the terminal leaflet 78. L. maculata
 - 4B. Plant > 150 mm wide, sparsely leafy, the
nodes widely spaced; calyx with the lobes
much longer than the fused part; petioles
as long or shorter than the terminal
leaflet 75. L. brachyantha

74. *L. curtii* Harms in Fedde, Repert. 16: 359 (1920); Bak. f. in Leg. Trop. Afr. 1: 20 (1926); Schreiber in FSWA 60: 82 (1970). Type: Namibia, Okahandja, Kl. Windhoek, Dinter 345 (B+; SAM 73559!, label in Dinter's hand, lecto., designated here; SAM 73559!, SAM 73570!, islecto.).

Amphinomia curtii (Harms) Schreiber in Mitt. Bot. Staatssamm. München 2: 286 (1957). Type as above.

L. laxa Eckl. & Zeyh. sensu Burt Davy, Man. pl. Transvaal: 387 (1932), pro parte. [Some of the cited specimens, e.g. Rogers 20796 from Messina (K!, NH!, PRE!) belong to this species].

An annual or short-lived perennial with a relatively wide distribution in the central and western parts of southern Africa (Map 5.20). It is very often confused with other species, notably *L. laxa*, *L. brachyantha* and *L. pumila*. The relatively short calyx, the shallower lateral sinuses and particularly the size and shape of the flowers and pods (Figure 5.11) are useful diagnostic characters.

Vouchers: Giess 10412, 13571; Giess, Volk & Bleissner 6673; Hanekom 117; Kers 1288; Leistner 613, 922.

75. *L. brachyantha* Harms in Fedde, Repert. 16: 360 (1920); Bak. f., Leg. Trop. Afr. 1: 17 (1926); Schreiber in FSWA 60: 81 (1970). Type: Namibia, Tsumeb, Dinter 1682 (B+; SAM!, label in Dinter's hand, lecto., designated here).

Amphinomia brachyantha (Harms) Schreiber in Mitt. Bot.

Staatssamm. München 2: 286 (1957). Type as above.

Closely related to L. curtii and with a similar distribution (Map 5.20) but easily identified by the larger and more sericeous-pilose calyx and the much shorter, broader and only slightly turgid pods (Figure 5.11). L. brachyantha is usually considered to be an annual but it is more accurately described as a short-lived perennial.

Vouchers: Dinter 7327; Giess & Leippert 7360; Giess, Volk & Bleissner 6026; Van Vuuren & Giess 1077 (partly); Wild & Drummond 7061.

76. L. crumanina Burch. ex Benth. in Hook., Lond. J. Bot. 2: 612 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 62 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 313 (1913); Phill. in Ann. S. Afr. Mus. 16: 69 (1917); Burt Davy, Man. pl. Transvaal: 388 (1932). Type: South Africa, Cape Province, near sources of the Kuruman River at Little Klibbolikhonni [2723 CD Kuruman], Burchell 2445 (K!, lecto., designated here); on the Caledon river (branch of the Nu Gariep), Burke s.n. (K!, sub Herb. Benth.; K!, sub Herb. Hook., isosyn.)

L. crumanina Burch., nom. nud. (Cat. Geogr. 2445).

This perennial species occurs mostly on limestone or lime-rich soils in the central parts of southern Africa, but has also been recorded from Namibia (Map 5.20). It is very similar to *L. serpentinicola* and *L. laxa*, but differs in the 3- to 4-flowered subsessile fascicles and the small, ovoid, 1- or 2-seeded pods that scarcely protrude from the calyx (Figure 5.11).

Vouchers: Acocks 1566, 18786; Forsyth 4178, 5895; Grobbelaar 1939; Leistner 1283; Schutte 343, 344.

77. *L. burchellii* Benth. in Hook. Lond. J. Bot. 2: 612 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 61 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 313 (1913). Type: South Africa, without precise locality [northern Cape], Burchell 2539 (K!, specimen with handwritten note, lecto., designated here; K!, sub Herb. Hook., islecto.).

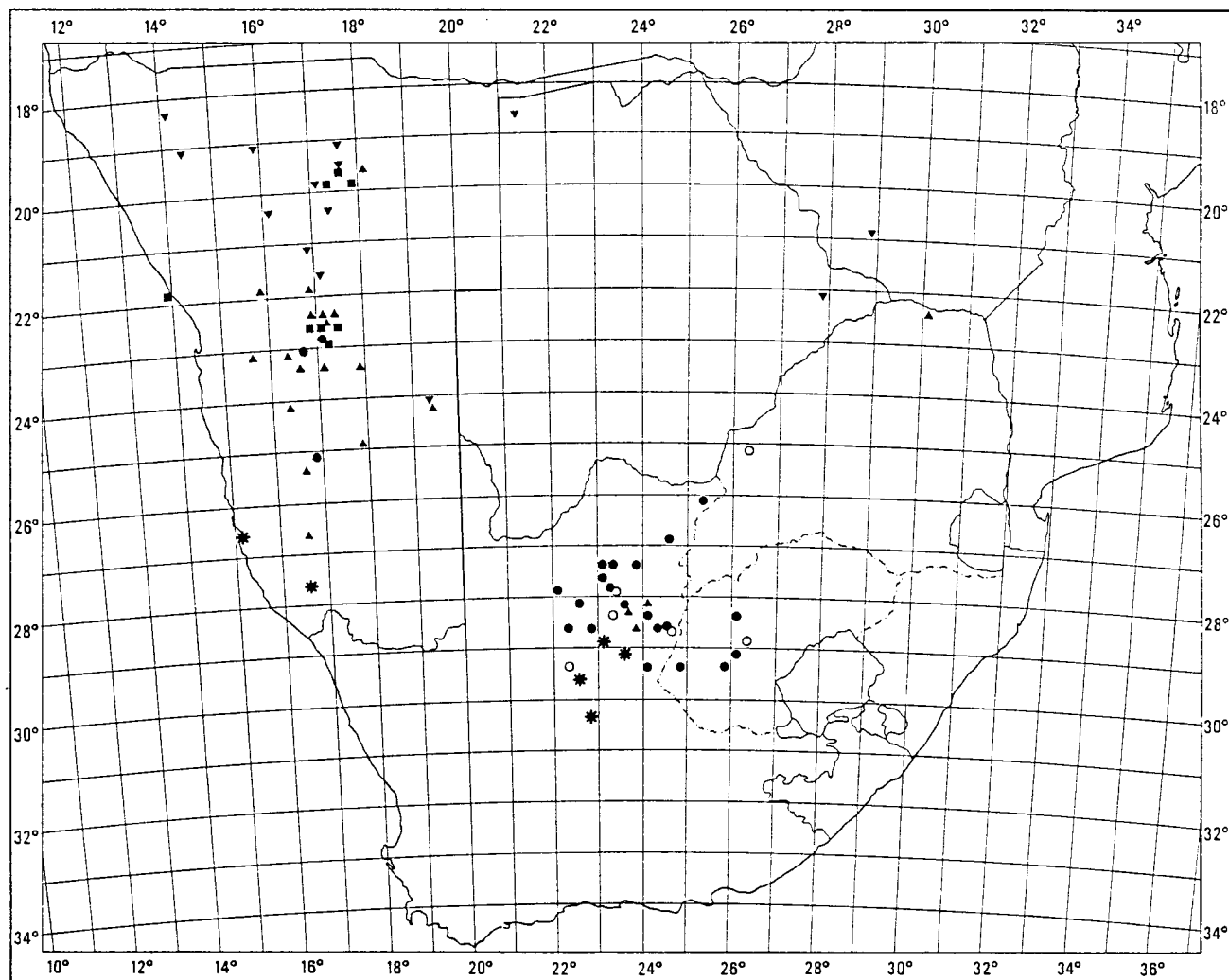
Closely related to *L. crumanina* (also perennial), but easily recognised by the very large, broadly ovate to subcordate bracts and the subsessile or pedunculate heads of flowers. The pods are as long as the calyx, ovoid, slightly turgid and \pm 4-seeded (Figure 5.11). The geographical distribution of *L. burchellii* is a little more restricted than that of *L. crumanina* and it occurs in the northern Cape, western Orange Free State and south-western Transvaal (Map 5.20).

Vouchers: Acocks 568, 1484, 2431; Brueckner 1044; Carter 900;
Moran s.n. sub. BOL 15839; Potts 2911.

78. L. maculata Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 314
(1913). Type: South Africa, northern Cape Province, "Griqualand,
Griqua Town", Burchell 1957 (K!, holo.).

A poorly known species with a relatively wide distribution in the
northern Cape and southern Namibia (Map 5.20). It is very similar
to L. crumanina but differs in the much smaller, more densely
leafy and prostrate habit, the single-flowered inflorescences and
the slightly longer, 6- to 8-seeded pods (Figure 5.11).

Vouchers: Acocks 2216, 14363; Giess 13761, 14670; Lavranos &
Pehlemann 21637; Leistner 2289; Page s.n. sub BOL 14394.



Map 5.20. The known geographical distribution of *L. pallidirosea* (■), *L. curtii* (▲), *L. brachyantha* (▼), *L. crumanina* (●), *L. burchellii* (○) and *L. maculata* (*).

7H. Subsectio Laxa B-E. van Wyk, subsect. nov. Grex a praecedente habitu plerumque valde lignosiore (herbae prostratae perennes), vestitura minus sericea plus strigillosa, inflorescentiis unifloris (raro plus quam 1 per nodum florentem), carinis brevirostratis atque leguminibus valde longioribus oblongis, differt.

This group differs from the previous one in the generally much more woody habit (prostrate perennial herbs), the less silky and more strigillose vestiture; the single-flowered inflorescences (rarely more than 1 per flowering node), the shortly beaked keel petals and the much longer, oblong pods.

Type species: L. laxa Eckl. & Zeyh.

Diagnostic characters: Prostrate or procumbent perennials; leaves densely strigillose, trifoliolate, the basal ones unifoliolate; flowers usually one per inflorescence, yellow or partly white, often cleistogamous; calyx subequally lobed, with the upper two lobes usually much wider than the lateral lobes; petals glabrous (a line of hairs on the standard only), not striated; standard ovate, not panduriform; keel acute and usually distinctly beaked; pods oblong, only slightly inflated (Figure 5.12). Three species from the eastern parts of southern Africa (Map 5.21), with one extending to Ethiopia (see Map 5.17).

Key to the species of subsection Laxa:

- 1A. Peduncle long, slender 81. L. serpentinicola
- 1B. Peduncle very short or more often absent:
 - 2A. Leaves large, the leaflets usually
> 10 mm wide; flowers > 9 mm long,
at least partly white 79. L. macrosepala
 - 2B. Leaves small, the leaflets < 6 mm wide;
flowers < 8 mm long, yellow 80. L. laxa

Although no formal recognition is here given to the various forms within L. laxa and L. macrosepala, some infraspecific rank may prove to be feasible and useful.

79. L. macrosepala Conrath in Kew Bull. 1908: 223 (1908); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 316 (1913); Burt Davy, Man. pl. Transvaal: 388 (1932). Type: South Africa, Transvaal, Modderfontein, Conrath 133 (K!, holo.).

L. humilior Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 315 (1913), synon. nov.; Burt Davy, Man. pl. Transvaal: 388 (1932). Types: South Africa, Transvaal, Lydenburg, Wilms 274 (K!, lecto., designated here; BM!, p.p. maj., isosyn.); Natal, without precise locality, Gerrard 1065 (K!, isosyn.).

L. basutica Phill. in Ann. S. Afr. Mus. 16: 71 (1917), synon. nov. Types: Lesotho, Leribe, Phillips 683 (SAM!, lecto., designated here), Dieterlen 268 (BM!, PRE!, SAM!, isosyn.).

A robust perennial pyrophyte from the eastern parts of southern Africa (Map 5.21), with flowering branches developing from a thick woody base. It may be confused with *L. laxa*, but the leaves and flowers are at least double the size of those of the latter. As shown below and in Figure 5.12, two forms can be distinguished. Field studies have suggested that the atypical morphology of form B (previously considered to be a distinct species) is at least partly a result of active regrowth after fire. The same phenomenon can be observed in *L. laxa*. I suggest that the floriferous forms of the two species are no more than varieties or ecotypes.

Form A. ("typical" form)

Leaves very large, the terminal leaflet up to 20 mm wide, sparsely strigillose, the venation conspicuous; basal leaves often unifoliate; flowers very large, often cleistogamous, invariably single, with the calyx as long or longer than the corolla (Figure 5.12). Distribution: Transvaal, northern Orange Free State and Lesotho (Map 5.21).

Vouchers: Bredenkamp 211, 846; Dieterlen 268, 1154; Grobbelaar 1411; Van Wyk 1820, 1826, 1891.

Form B. ("humilior" form).

Leaves and habit much smaller than in Form A; leaflets often very small, sometimes < 6 mm wide, densely silky, the venation invisible; flowers very large, not cleistogamous, often in fascicles of 2 or 3, occasionally with a distinct peduncle, partly or completely white, the corolla usually longer than the calyx (Figure 5.12). Distribution: recorded from a few isolated localities in Natal, eastern Orange Free State and eastern Transvaal (Map 5.21).

Vouchers: Buthlezi 155; Germishuizen 2203; Schlechter 3383; Thode 3409, 5559.

80. *L. laxa* Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 177 (1836, Jan.); Benth. in Hook., Lond. J. Bot. 2: 612 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 63 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 314 (1913); Phill. in Ann. S. Afr. Mus. 16: 69 (1917); Burt Davy, Man. pl. Transvaal: 387 (1932); Milne-Redhead in Fl. Trop. E. Afr., Pap.: 816 (1971). Type: South Africa, Cape Province, "prope Silo ad flumen Klipplaatrivier" [3226 BB], Ecklon & Zeyher 1276 (S!, lecto., designated here; C!, M!, S!, SAM!, islecto.).

L. laxa Eckl. & Zeyh. var. multiflora Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 315 (1913); Burt Davy, Man. pl. Transvaal: 388 (1932); Milne-Redhead in Fl. Trop. E. Afr., Pap.: 817 (1971), as synonym of *L. laxa*. Types: South Africa, Transvaal, Plains

near Barberton, Galpin 1078b (K!, lecto., specimen on far right, designated here; BOL!, GRA!, islecto.), Galpin 1078a (BOL!, K!, isosyn.).

Crotalaria diversifolia E. Mey., Comm. Pl. Afr. Austr. 1(1): 27 (1836, Feb. or later). Types: South Africa, Cape Province, Basche River [3128 CD], Drège s.n. a (S!, larger piece, lectotype, designated here; K!, islecto.); Cape Province, Queenstown Division, near Shiloh, Drège s.n. c (K!, isosyn.).

Crotalaria diversifolia E. Mey. var. unifoliata E. Mey., Comm. Pl. Afr. Austr. 1(1): 27 (1836). Type: South Africa, Cape Province, Shiloh near the Klipplaatrivier, Drège s.n. b (S!, lecto., designated here; K!, islecto.).

L. diversifolia (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 611 (1843). Type as above.

L. woodii H. Bol. in J. Bot. 1896: 19 (1896), synon. nov.; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 315 (1913); Phill. in Ann. S. Afr. Mus. 16: 70 (1917); Burt Davy, Man. pl. Transvaal: 388 (1932). Type: South Africa, Natal, Amawahqua Mountain, Wood 4603 (K!, lecto., designated here; BOL!, islecto.).

L. montana Schinz in Bull. Herb. Boiss. 6: 30 (1899). Types: Wood 4603 (same as above, isosyn.); Orange Free State, near Harrismith, Wood 4788 (K!, isosyn.).

L. schlechteri Schinz in Bull. Herb. Boiss. 6: 32 (1899). Type: South Africa, Natal, Near the Zuurbergen [3029 BC Kokstad], Schlechter 6589 (Z, holo.; K!, fragment).

L. laxa is by far the most common and widely distributed perennial species of Lotononis (see Map 5.17). Three more or less distinct forms can be distinguished:

Form A. ("typical" form)

Prostrate or procumbent short-lived perennial with very small, narrowly oblanceolate to elliptic leaves; flowers invariably single at each node, often cleistogamous, peduncle absent (Figure 5.12). This form appears to be associated with dry habitats and has a more western distribution than form C. The combined distribution of forms A and B is shown in Map 5.21.

Vouchers: Grobbelaar 1426; Herman 474; Jooste 162; Retief 990; Van Wyk 1565, 1586, 1816, 2019, 2059.

Form B. ("multiflora" form)

In grassland areas, the basal leaves are often unifoliolate and the inflorescences pedunculate and 2- to 5-flowered. This form (previously regarded as a distinct variety) seems superficially quite different, but in situ studies have indicated that unifoliolate leaves and multi-flowered inflorescences are produced during active regrowth after fire. Most of the East African material I have seen agrees with this form, but the distinction is not always clear.

Vouchers: Codd 1761; McDonald 126; Murray s.n. sub PRE 53525;
Rudatis 19; Van Wyk 2478.

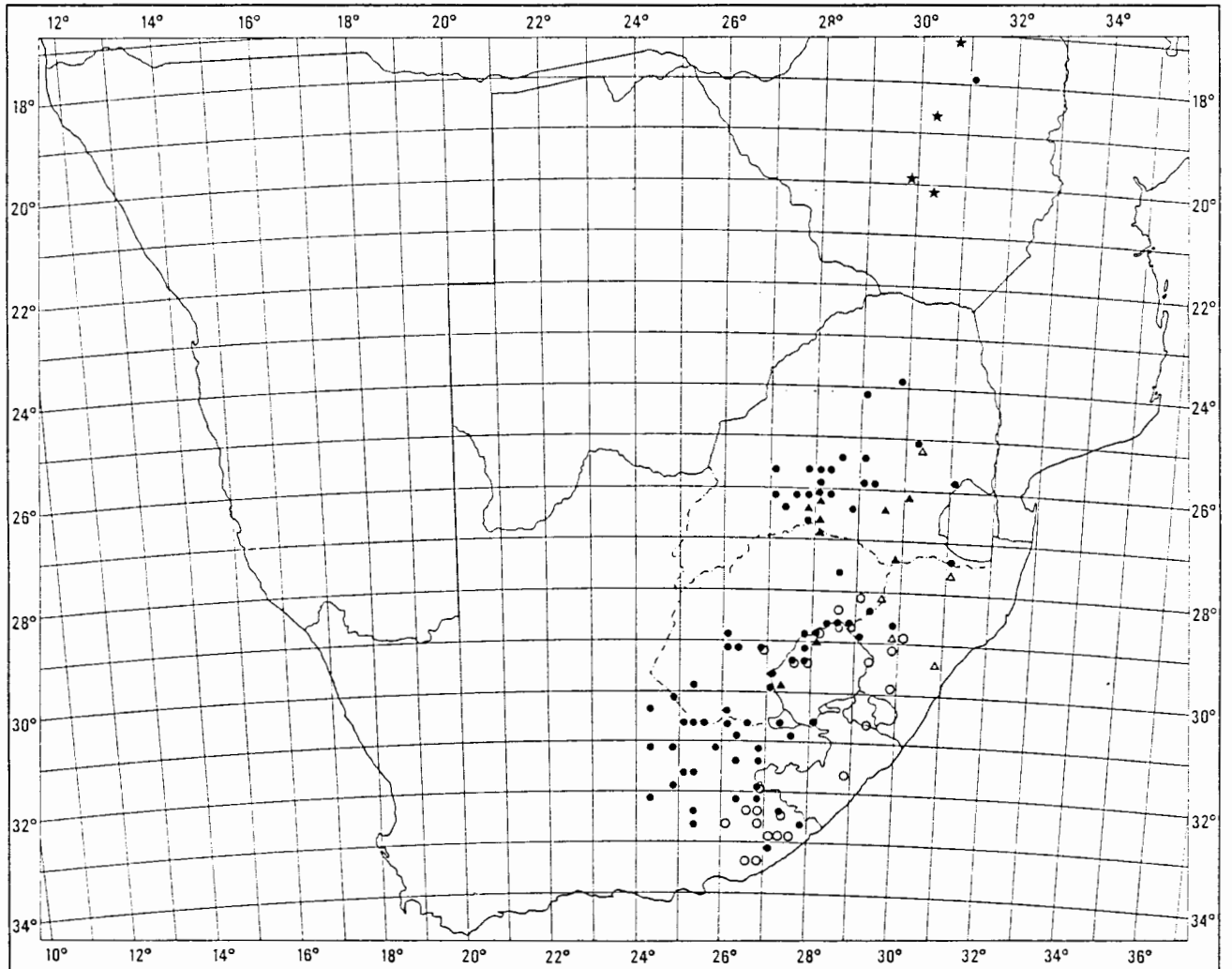
Form C. ("woodii" form)

A form of the species from higher altitudes in the eastern Cape and Drakensberg areas (Map 5.21). It has a prostrate habit, broad leaves, recurved leaflet apices and slightly broader calyx lobes (Figure 5.12). Previously known as distinct species (L. woodii), but a separation (at least at the specific level) seems no longer feasible. It should be noted that Drège s.n. a in K and S (type of Crotalaria diversifolia E. Mey. var. diversifolia) is identical to the type of L. woodii and that the latter is therefore a superfluous name.

Vouchers: Acocks 10114; Coleman 823; Marais 1465; Rennie 1205d;
Van Wyk 1686-1688.

81. L. serpentinicola Wild in Kirkia 5: 75 (1965). Type:
Zimbabwe, Sipolilo District, "Nyaruswiswe", Great Dyke soils,
Wild 5743 (SRGH, holo.; K!, M!, MO!, PRE!, iso.).

L. serpentinicola is similar to L. laxa but is easily recognised by the slender peduncles (Figure 5.12). The species appears to be endemic to serpentine soils and is known only from Zimbabwe (Map 5.21).



Map 5.21. The known geographical distribution of *L. macrosepala* "form A" (▲), *L. macrosepala* "form B" (△), *L. laxa* "forms A & B" (●), *L. laxa* "form C" (○) and *L. serpentinicola* (★).

Vouchers: Brummitt & Drummond 15836; Rutherford-Smith 574; Wild 5601, 5743, 6364, 7887.

7I. Subsection Oxydium

This subsection differs from the subsection Laxa in the minutely strigillose vestiture, the racemose and pedunculate inflorescences, the much shorter calyx and the distinctly beaked keel.

Diagnostic characters: Prostrate suffrutescent herbs with flowering branches from a perennial woody base; leaves consistently unifoliolate (L. monophylla) or trifoliolate but then with the basal leaves unifoliolate (L. glabra); flowers yellow or white, sometimes fading partly to pale pink, never cleistogamous; keel distinctly beaked; pods oblong-linear, flat (Figure 5.9). Distribution: known from isolated localities in the eastern Cape and along the southern Cape coast (Map 5.22).

Key to the species of subsection Oxydium:

- 1A. Leaves trifoliolate, only the basal ones
unifoliolate, leaflets broadly obovate 82. L. glabra

1B. Leaves consistently unifoliolate, leaflets

ovate to oblong 83. L. monophylla

82. L. glabra (Thunb.) D. Dietr., Syn. pl. 4: 961 (1847). Type: South Africa, Cape Province, "in colles urbis in Cap. b. Spei", Thunberg s.n. sub THUNB-UPS 16611 (UPS!, lecto., designated here; SBT!, isolecto.).

Ononis glabra Thunb., Prodr. pl. Cap.: 130 (1800), Fl. Cap.: 588 (1823); DC., Prodr. 2: 167 (1825). Type as above.

L. glabra (Thunb.) Druce in Rep. Bot. Exch. Cl. Brit. Isles 4: 634 (1917), nom. superfl. Type as above.

Polylobium typicum Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 180 (1836); D. Dietr., Syn. pl. 4: 961 (1847). Type: South Africa, Cape Province, "Adow" [Addo] (Uitenhage), Ecklon & Zeyher 1288 (S!, lecto., designated here; BOL!, M!, isolecto.).

Polylobium intermedium Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 181 (1836); D. Dietr., Syn. pl. 4: 961 (1847). Type: South Africa, Cape Province, between the rivers "Coega- and Zondagsrivier" (Uitenhage), Ecklon & Zeyher 1289 (S!, lecto., designated here; BOL!, C!, sub Herb. Sieber, C!, K!, M!, MO!, STE!, isolecto.).

Crotalaria trichopoda E. Mey., Comm. Pl. Afr. Austr. 1(1): 154 (1836). Type: South Africa, Cape Province, between Zondagsrivier and "Kuga" [Koega], Drège s.n. a (S!, lecto., designated here; BM!, BOL!, K!, isolecto.); Addo, Drège s.n. (SAM!, isosyn.).

Crotalaria trichopoda E. Mey. var. brachypoda E. Mey., Comm. Pl. Afr. Austr. 1(1): 154 (1836). Type: South Africa, Cape Province, "Van Staadesrivier" [Van Staadens River]. Drège s.n. h (S!, lecto., designated here; BM!, K!, MO!, PRE 24335!, PRE!, Herb. Benth. specimen, isolecto.).

Lotononis trichopoda (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 603 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 57 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 304 (1913), synon. nov. Type as above.

Polylobium trichopodum (E. Mey.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 123 (1845). Type as above.

Lotononis trifolioides Schlechter ex A. Zahlbr., Pl. Penth.: 16 (1905). Type: South Africa, Cape Province, between Port Elizabeth and Grahamstown, Penther 2465 (W?, BOL!, M!).

L. glabra appears to be restricted to calcareous areas along the southern and south-eastern Cape coast (Map 5.22) and is easily recognised by the perennial habit, acute keel petals and minutely stigillose leaves (Figure 5.9). The flower colour varies from yellow to white and it occasionally turns pinkish with age.

Vouchers: Acocks 23248; Barker 6922; Dahlstrand 2502; Liebenberg 7741; Vlok 1854.

83. *L. monophylla* Harv., Thes. Cap. 1: 39, t.63. (1859); Harv. in Harv. & Sond., Fl. Cap. 2: 58 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 304 (1913). Type: South Africa, Cape Province, stony places on the Vanstaadensberg Mountains, Zeyher 2313 (TCD, holo.; K!, S!, SAM!, iso.).

This rare and unusual species was previously known only from the type collection, but it was recently rediscovered by Mr J. H. J. Vlok (Saasveld Forestry Research Centre, George), probably at the same locality where it was first collected more than 150 years ago (Map 5.22). The leaves are invariably unifoliolate and the leaflets are sessile, ovate to oblong and totally glabrous above (Figure 5.9).

Voucher: Vlok 1703.

7J. Subsectio Pumila B-E. van Wyk, subsect. nov. Haec grex a subsectione Oxydio habitu annuale, et a subsectione Falcata vexillo ovato vel oblongo non panduriforme, differt.

This group differs from subsection Oxydium by the annual habit and from subsection Falcata by the ovate or oblong rather than panduriform standard petal.

Type species: *L. pumila* Eckl. & Zeyh.

Diagnostic characters: Small prostrate annuals; leaves trifoliolate, the basal ones often unifoliolate, sparsely but conspicuously stigillose; flowers up to four, umbellately arranged on a short peduncle; calyx with the lower lobe much narrower than the upper four; flowers yellow or pink and white, occasionally cleistogamous; keel acute; pods oblong to oblong-linear, only slightly turgid (Figure 5.9). Distribution: restricted to the south-eastern parts of the Cape Province (Map 5.22).

Key to the species of subsection Pumila:

- 1A. Pedicel longer than the length of the calyx; flowers 6--7 mm long when chasmogamous, yellow (tip of keel yellow); leaflets oblanceolate to elliptic; stipules lanceolate to ovate or elliptic ... 84. L. micrantha
- 1B. Pedicel shorter than the length of the calyx; Flowers 8--9 mm long when chasmogamous, at least partly pink (tip of keel dark purple); leaflets broadly obovate; stipules broadly ovate 85. L. pumila

84. L. micrantha Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 178 (1836); Benth. in Hook., Lond. J. Bot. 2: 612 (1843), non Ononis micrantha Thunb. Type: South Africa, Cape Province, at

"Grasrugg" [Grass Ridge?] not far from the river "Zondagsrivier" (Uitenhage), Ecklon & Zeyher 1280 (S!, specimen annotated by Harvey, lecto., designated here; C!, C! sub Herb. Sieber, M!, S!, SAM!, wrongly labelled, isolecto.).

L. pumila Eckl. & Zeyh. var. micrantha (Eckl. & Zeyh.) Harv. in Harv. & Sond., Fl. Cap. 2: 65 (1862). Type as above.

L. pumila Eckl. & Zeyh. sensu Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 320 (1913), pro parte.

A poorly known species apparently restricted to the eastern Cape (Map 5.22). Previously, the species was known only from the type collection, but it was recently rediscovered and is perhaps overlooked rather than rare. It is closely related to L. pumila, but quite distinct -- the diagnostic characters given in the key and in Figure 5.9 have apparently been overlooked by both Harvey (1862) and Dümmer (1913).

Voucher: Van Wyk 2481.

85. L. pumila Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 178 (1836, Jan.); Steud., Nom. Bot. 2(2): 73 (1841); Benth. in Hook., Lond. J. Bot.: 609 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 65 (1862), excl. var. micrantha; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 320 (1913), pro parte. Type: South Africa, near

"Gauritzrivier" [Gouritz River] (Swellendam), Ecklon & Zeyher 1283 (S!, separate sheet, lecto., designated here; C!, M!, S!, SAM!, islecto.).

Lipozygis erubescens E. Mey., Comm. Pl. Afr. Austr. 1(1): 76 (1836, Feb. or later). Type: South Africa, Cape Province, "Klein Vischrivier", Drège s.n. (S!, lecto., designated here; K!, islecto.).

Lipozygis erubescens E. Mey. var. macrophylla E. Mey., Comm. Pl. Afr. Austr. 1(1): 77 (1836, Feb. or later). Type as for Lipozygis erubescens.

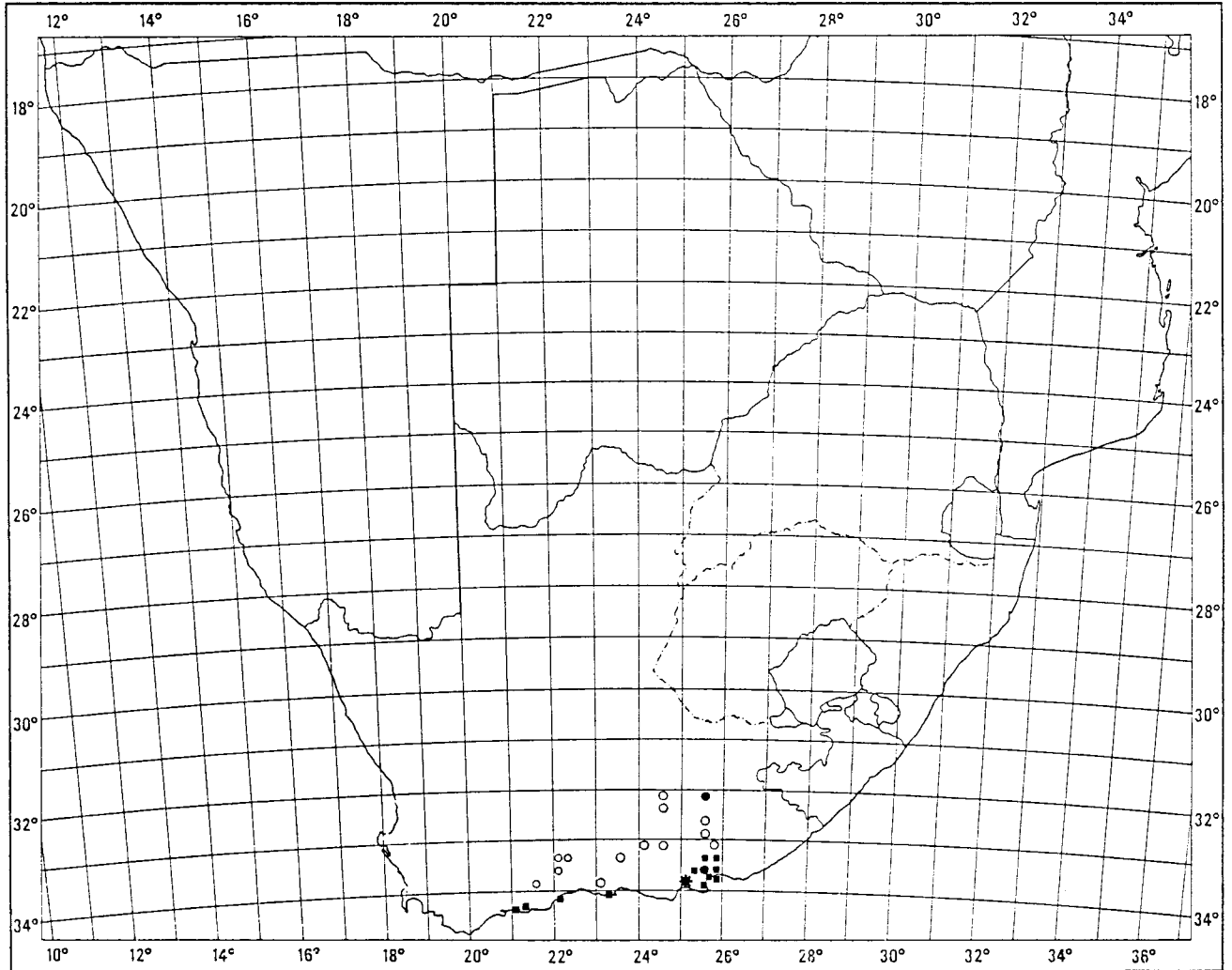
Lipozygis erubescens E. Mey. var. microphylla E. Mey., Comm. Pl. Afr. Austr. 1(1): 77 (1836, Feb. or later). Type: South Africa, Cape Province, Zwanepoelspoort, Drège s.n. (S!, lecto., designated here; BM!, K!, sub Herb. Benth., K!, sub Herb. Hook., MO!, islecto.).

Leptis erubescens (E. Mey.) Benth. in Ann. Wien. Mus. 2: 142 (1839). Type as for Lipozygis erubescens.

Leptidium erubescens (E. Mey.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845). Type as above.

Polylobium erubescens (E. Mey.) D. Dietr., Syn. pl. 4: 962 (1847). Type as above.

Lotononis erubescens (E. Mey.) Druce in Rep. Bot. Exch. Cl. Brit. Isles 4: 633 (1917). Type as above.



Map 5.22. The known geographical distribution of *L. glabra* (■), *L. monophylla* (*); *L. micrantha* (●), and *L. pumila* (○).

A common annual from dry areas in the south-eastern Cape (Map 5.22), easily recognised by the broadly obovate to almost orbicular leaflets and the conspicuous dark purple pollen guide on the tip of the keel (Figure 5.9).

Vouchers: Acocks 17536; Gillett 1681; Sniijman 457; Van Breda 4446; Van Wyk 1626.

7K. Subsectio Quinata B-E. van Wyk subsect. nov. Subsectio monotypica a subsectionibus aliis omnibus foliis plerumque 5-foliolatis et leguminibus breve stipitatis facile distinguitur.

A monotypic subsection, easily distinguished from all other subsections by the predominantly 5-foliolate leaves and the shortly stipitate pods.

Diagnostic characters: Prostrate suffrutescent perennial herb with flowering branches from a thick woody base; leaves predominantly 5-foliolate; calyx with the lower lobe very much narrower than the upper four; flowers yellow, never cleistogamous, umbellate; keel distinctly beaked; pods obovate, shortly stipitate, much inflated (Figure 5.13). Distribution: known only from a small area in the north-western Cape Province (Map 5.23).

86. *L. acutiflora* Benth. in Hook., Lond. J. Bot. 2: 604 (1843),
nom. nov. pro *Crotalaria quinata* (Thunb.) E. Mey.; Harv. in Harv.
& Sond., Fl. Cap. 2: 58 (1862). Type: South Africa, Cape
Province, near "Krakkeelskraal", Clanwilliam district, Drège s.n.
(B+; K!, sub Herb. Benth., lecto., designated here; K!, sub Herb.
Hook., MO!, S!, islecto.).

Crotalaria quinata (Thunb.) E. Mey., Comm. Pl. Afr. Austr.
1(1): 27 (1836) non *Lotononis quinata* (Thunb.) Benth. in Hook.,
Lond. J. Bot. 2: 608 (1843); Dümmer in Trans. Roy. Soc. S. Afr.
3(2): 330 (1913). Type as above.

L. acutiflora appears to be endemic to the Kamiesberg area in
Namaqualand (Map 5.23), where it was recently rediscovered after
more than 150 years. The structure of the flowers is very similar
to that of *L. rostrata* and related species (Figure 5.13).

Vouchers: Van Wyk 2361--2365, 2375--2377, 2417, 2418.

7L. Subsectio Rostrata B-E. van Wyk, subsect. nov. Species huius
subsectionis a subsectione Quinata habitu annuali, radicibus
laete flavis atque foliis trifoliolatis distingui possunt. A
subsectionibus aliis carinis valde rostratis, antheris valde
sigillatim dimorphis, stylo longo gracile atque leguminibus
ovatis, plerumque valde inflatis differt.

The species of this subsection can be distinguished from the subsection Quinata by the annual habit, the bright yellow roots and the trifoliolate leaves. It differs from other subsections in the strongly beaked keel petals, the very markedly dimorphic anthers, the long, slender style and the ovate, usually much inflated pods.

Type species: Lotononis rostrata Benth.

Diagnostic characters: Prostrate or procumbent annuals; roots bright yellow; leaves trifoliolate, rarely with some 5-foliolate; flowers yellow (rarely orange or fading to pinkish), never cleistogamous, usually umbellately many-flowered, rarely single-flowered; standard broadly ovate or broadly elliptic, claw much dilated towards the base; keel distinctly beaked; anthers strongly dimorphic, the basifixed anthers several times longer than the small dorsifixed anthers, carinal anther similar to the dorsifixed anthers; style long and slender, curved, glabrous; pods obovate-orbicular and much inflated to shortly oblong and then only slightly inflated (Figure 5.13). Distribution: restricted to the south-western and western parts of the Cape Province (Maps 5.23 and 5.24). The six species of this subsection are remarkably similar to species of Crotalaria, but the single stipules, small carinal anther and total absence of bracteoles are typical of Lotononis.

Key to the species of subsection Rostrata:

- 1A. Wing petals with at least some hairs along
the lower edge of the lamina; inflorescence
without a peduncle, invariably
1-flowered 88. L. arenicola
- 1B. Wing petal totally glabrous; inflorescence
with a distinct peduncle, 2- or more-flowered:
 - 2A. Flowers relatively small, ≤ 7 mm long:
 - 3A. Peduncle short or absent, < 20 mm long ... 87. L. rostrata
 - 3B. Peduncle long and slender, > 30 mm long:
 - 4A. Inflorescence 1- or 2-flowered 90. L. perplexa
 - 4B. Inflorescence more than 5-flowered 87. L. rostrata
 - 2B. Flowers relatively large, > 8 mm long:
 - 5A. Peduncle very short or absent (shorter
than the length of the flowers); calyx
lobes slightly imbricate 92. L. carnea
 - 5B. Peduncle long (at least as long as the flowers,
but often much longer); calyx lobes valvate:
 - 6A. Leaflets oblong, narrowly oblong or linear;
pods with sparse appressed strigillose
hairs 91. L. stenophylla
 - 6B. Leaflets oblanceolate to obovate;
pods with dense spreading hairs 89. L. oxyptera

87. L. rostrata Benth.

Three subspecies are recognised by Van Wyk (1989f, Appendix 26). The length of the peduncle, the size of the flowers, the pubescence of the standard and particularly the shape of the pods are useful diagnostic characters to distinguish between the subspecies (Figure 5.13).

87a. subsp. rostrata

L. rostrata Benth. in Hook., Lond. J. Bot. 2: 604 (1843), nom. nov. pro Ononis micranthus Thunb. non Lotononis micrantha Eckl. & Zeyh. Type: South Africa, "e Cap. b. Spei.", Thunberg s.n. sub THUNB-UPS 16620 (UPS!, lecto., designated by Van Wyk 1989f).

Ononis micranthus Thunb., Prodr. pl. Cap. 130 (1800), Fl. Cap.: 587 (1823); DC., Prodr. 2: 167 (1825), as Q. micrantha. Type as above.

Crotalaria micrantha (Thunb.) E. Mey., Comm. Pl. Afr. Austr. 1(1): 27 (1836); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 330 (1913). Type as above.

Lotononis micrantha (Thunb.) Harv. in Harv. & Sond., Fl. Cap. 2: 58 (1962) non Lotononis micrantha Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 178 (1836). Type as above.

Crotalaria tenuiflora Steud., Nom. Bot. 2(1): 445 (1840), as nom. nov. Type as above.

This subspecies is well known by the illegitimate name Lotononis micrantha (Thunb.) Harv. It can easily be distinguished by the small and narrow flowers, the slender peduncles and the very short, obovate pods (Figure 5.13). It is geographically isolated from the subspecies namaquensis and occurs only in the southwestern Cape (Map 5.23).

Vouchers: Barker 9623; Bolus 11922; Esterhuysen 12040; Grobbelaar 2849; Van Wyk 2321--2324.

87b. subsp. brachybotrys B-E. van Wyk subsp. nov. ined. [S. Afr. J. Bot. (in press), Appendix 26]. Type: South Africa, Cape Province, 800 m from Klawer turn-off on Vanrhynsdorp to Clanwilliam road, B-E. van Wyk 2429 (PRE!, holo., K!, NBG!, MO!, iso.).

Subsp. brachybotrys is similar to the type but differs in the more prostrate habit, the larger and broadly obovate leaves, the shorter peduncles, the larger flowers, the much more pubescent standard petal and the larger, obovate-oblong (not obovoid), less turgid pods (Figure 5.13). It can be distinguished from subsp. namaquensis by the larger and more sparsely pubescent leaves, and the much larger pods. The subspecies is superficially similar to L. arenicola Schlechter but differs from this species in the much larger habit, the multi-flowered and pedunculate inflorescences (not sessile and single-flowered) and the

sparsely strigillose leaflets (not densely silky). The distribution of the new subspecies partly overlaps with that of the subsp. rostrata but is geographically isolated from the subsp. namaquensis and L. arenicola (Map 5.23).

Vouchers: Acocks 19497; Bolus 8970; Lavis 20231; Pearson 6735; Schlechter 3368, 5188, 8346.

87c. subsp. namaquensis (H. Bol.) B-E. van Wyk comb. nov. et stat. nov. ined. [S. Afr. J. Bot. (in press), Appendix 26]. Type: South Africa, Cape Province, Little Namaqualand, near Klipfontein, H. Bolus 6569 (BOL!, lecto., designated by Van Wyk 1989f; K!, isolecto.).

L. namaquensis H. Bol. in J. Linn. Soc. 25: 159 (1889). Type as above.

Crotalaria namaquensis (H. Bol.) Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 330 (1913). Type as above.

Lotononis chrysophylla Schlechter in sched. (Schlechter 11185, BM!).

This subspecies can be distinguished from subsp. rostrata by the smaller and densely silky leaves and the short peduncles (Figure 5.13). It appears to be geographically isolated from the other two subspecies and occurs only in Namaqualand (Map 5.23).

Vouchers: Acocks 19588; Rösch & Le Roux 844; Schlechter 11306;
Van Breda 4206; Van der Westhuizen 310.

88. L. arenicola Schlechter in De Wildeman, P. Nov. Hort. Then.
1: 184, t. 40 (1906). Type: South Africa, Cape Province, "I`Aus"
[3017 BB Hondeklipbaai], Schlechter 11206 (B+; K!, lecto.,
designated here; BM!, BOL!, GRA!, MO!, S!, isosyn.).

Crotalaria arenicola (Schlechter) Dümmer in Trans. Roy. Soc. S.
Afr. 3(2): 330 (1913). Type as above.

This species is easily distinguished from all others of the
subsection by the densely silky-sericeous vestiture, the hairy
petals, the single-flowered inflorescences and the oblong,
scarcely inflated pods (Figure 5.13). It may be confused with L.
sparsiflora, but the vestiture of the fruit in the latter is
quite distinct. A poorly known species apparently restricted to
Namaqualand (Map 5.23).

Vouchers: Herre s.n. sub STE 11874; Meyer s.n. sub STE 9132;
Rösch & Le Roux 1461; Schlechter 11206; Van Wyk 2356, 2369--2372.

89. Lotononis oxyptera (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 605 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 58 (1862). Type: South Africa, Cape Province, "Klein Draakensteen" [Klein Drakenstein Mountain], Drège s.n. (B+; S!, lecto., designated here; K!, islecto., PRE!, fragment).

Crotalaria oxyptera E. Mey., Comm. Pl. Afr. Austr. 1(1): 28 (1836, Feb. or later); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 330 (1913). Type as above.

Lotononis oxyptera (E. Mey.) Benth. var. longipes Harv. in Harv. & Sond., Fl. Cap. 2: 58 (1862). Type as for Polylobium sparsiflorum.

Lotononis oxyptera (E. Mey.) Benth. var. brevipes Harv. in Harv. & Sond., Fl. Cap. 2: 58 (1862). Type as for Crotalaria oxyptera.

Polylobium sparsiflorum Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 181 (1836, Jan.); D. Dietr., Syn. pl. 4: 961 (1847), non Lotononis sparsiflora (E. Mey.) B-E. van Wyk. Type: South Africa, Cape Province, near Tulbagh (Worcester), Ecklon & Zeyher 1293 (S!, specimen annotated by Harvey, larger piece, lecto., designated here; C!, S!, islecto.).

This species is superficially similar to some species of Crotalaria, particularly in the structure of the flowers and pods. It may be confused with L. stenophylla but, apart from the obvious difference in the shape of the leaflets, the vestiture of

the pods and the shape of the flowers are also distinct (Figure 5.13). L. oxyptera is relatively widely distributed in the south-western Cape (Map 5.24).

Vouchers: Bolus 7582; Esterhuysen 6034; Salter 7686; Van Wyk 2317, 2318; Walters 344.

90. L. perplexa (E. Mey.) Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 177 (1836); Steud., Nom. Bot. 2(2): 73 (1841); Benth. in Hook., Lond. J. Bot. 2: 604 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 57 (1862). Type: South Africa, Cape Province, Table Mountain and Devil's Peak, Ecklon s.n. (S!, Plantae Ecklonianae label, lecto., designated here; MO!, Herb. Un. itin. 226, isolecto.).

Crotalaria perplexa E. Mey. in Linnaea 7: 151 (1832); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 330 (1913). Type as above.

This species is similar to L. stenophylla but is smaller in all parts and the inflorescences are sparsely 1- to 3-flowered on a long slender peduncle (Figure 5.13). L. perplexa has a restricted distribution in the south-western Cape Province (Map 5.24) and has not been collected in recent years.

Vouchers: Compton 12565; Penfold 205; Salter 8457, 8528; Schlechter 9195; Zeyher s.n. sub SAM 15356.

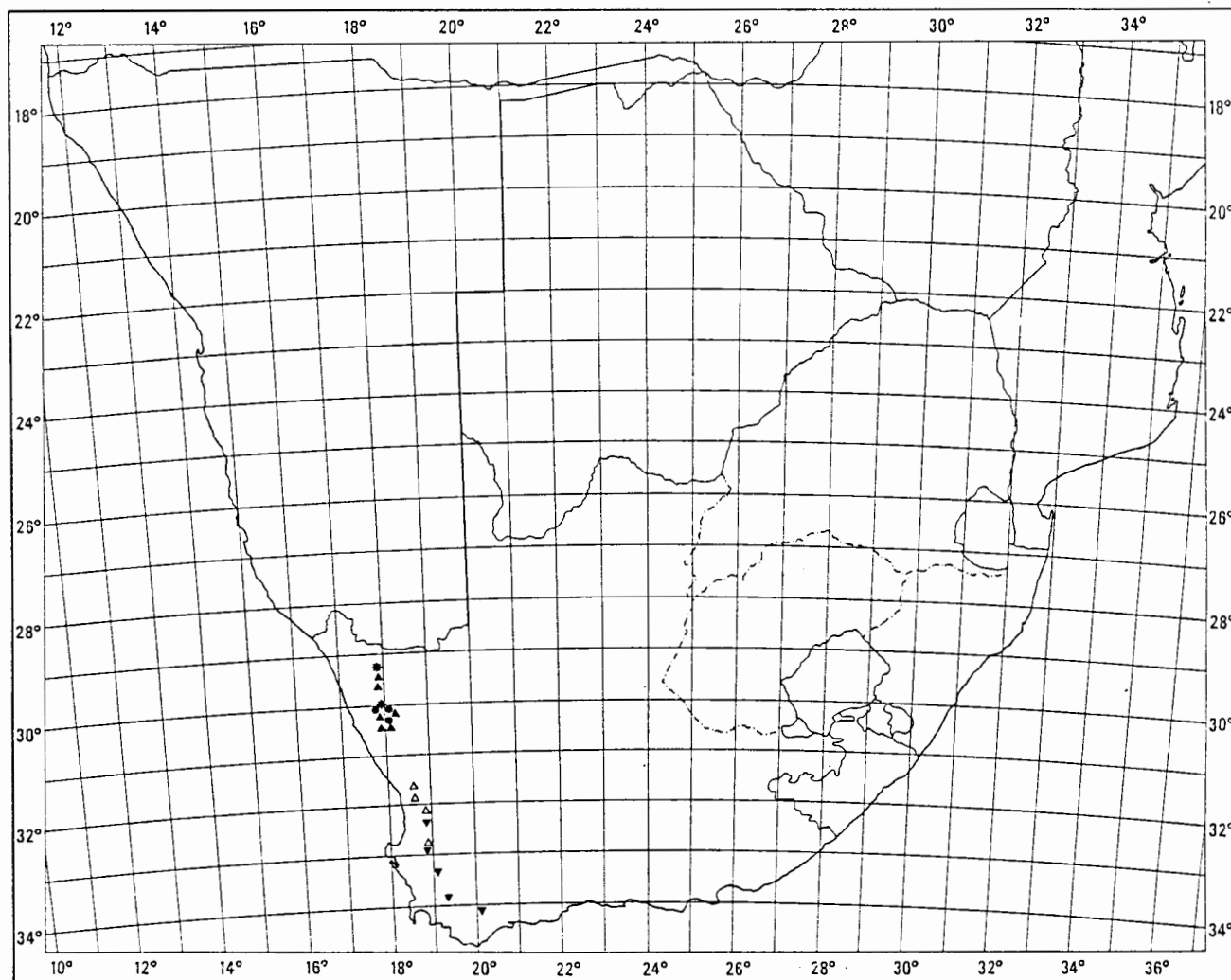
91. L. stenophylla (Eckl. & Zeyh.) B-E. van Wyk comb. nov. ined.
[S. Afr. J. Bot. (in press), Appendix 26]. Type: South Africa,
Cape Province, Olifants River (Clanwilliam), Ecklon & Zeyher 1261
(S!, specimen annotated by Harvey, lecto., designated by Van Wyk
1989f; S!, fragment, SAM!, isolecto.).

Crotalaria stenophylla Eckl. & Zeyh., Enum. Pl. Afr. Austr.:
174 (1836); Benth. in Hook., Lond. J. Bot. 2: 574 (1843), as
doubtful synonym of C. humilis Eckl. & Zeyh. Type as above.

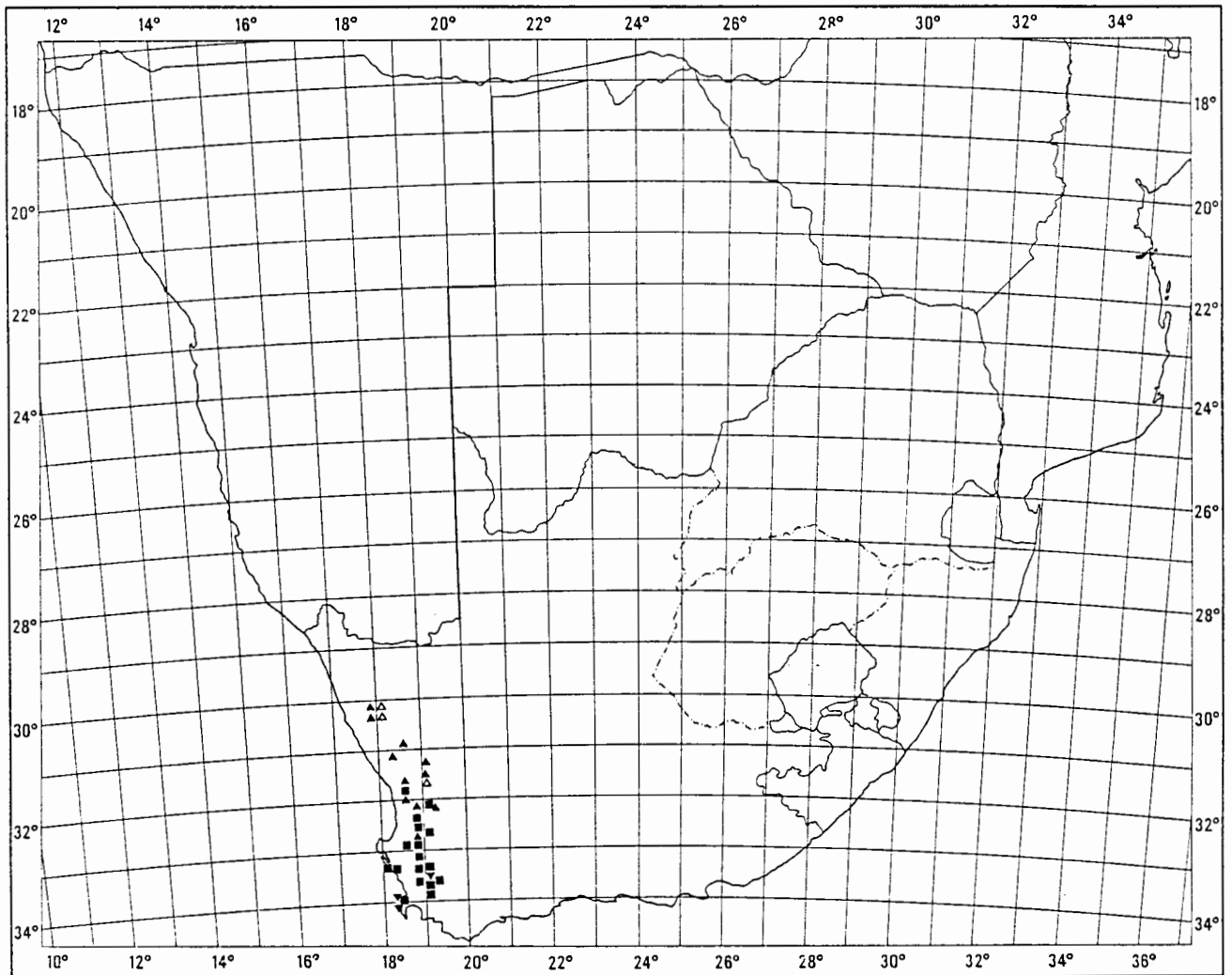
Crotalaria ecklonis Harv. in Harv. & Sond., Fl. Cap. 2: 42
(1862), as a nom. nov. for C. stenophylla Eckl. & Zeyh. non Vog.;
Bak. f. in J. Linn. Soc. Bot. 42: 395 (1914). Type as above.

Verdoorn (1928) and Polhill (1968b, 1982) correctly excluded this
species from Crotalaria and referred it to Lotononis, but the new
combination still remained to be made. It is similar to L.
oxyptera but can be distinguished by the strongly beaked keel,
the relatively narrow leaflets and the ovate-oblong, markedly
inflated pods (Figure 5.13). This poorly known species is closely
related to L. carnea and is also restricted to the south-western
and north-western Cape Province (Map 5.24).

Vouchers: Goldblatt 4251; Lavis 20231; Leipoldt 729; Salter 1495;
Van Wyk 2426--2428.



Map 5.23. The known geographical distribution of *L. acutiflora* (●), *L. rostrata* subsp. *rostrata* (▼), *L. rostrata* subsp. *brachybotrys* (△), *L. rostrata* subsp. *namaquensis* (▲) and *L. arenicola* (*).



Map 5.24. The known geographical distribution of *L. oxyptera* (■), *L. perplexa* (▼), *L. stenophylla* (▲) and *L. carnea* (△).

92. *L. carnea* B-E. van Wyk sp. nov. ined. [S. Afr. J. Bot. (in press), Appendix 26)]. Type: South Africa, Cape Province, Kamiesberg near Leliefontein, B-E. van Wyk 2405 (PRE!, holo.).

Closely related to *L. stenophylla*, but differs in the smaller habit, the more densely silky-strigillose vestiture, the broader, obcordate leaflets, the very short peduncles and in the broad and imbricate calyx lobes (narrow and valvate in *L. stenophylla*). Some of the diagnostic characters are shown in Figure 5.13. *L. carnea* is known only from a few localities in the north-western Cape (Map 5.24).

Vouchers: Leipoldt 3126, 3157; Snijman 894; Van Wyk 2400--2405, 2411--2414.

7M. Subsectio Fragilis B-E. van Wyk, subsect. nov. Haec subsectio habitu annuali, ramis fragillimis, inflorescentiis semper unifloris, pubescentia propria leguminum atque funiculis longissimis distingui potest.

This subsection can be distinguished by the annual habit, the very brittle branches, the invariably single-flowered inflorescences, and the distinctive pubescence of the pods and the very long funicles.

Type species: *L. sparsiflora* (E. Mey.) B-E. van Wyk.

Diagnostic characters: Prostrate annuals; branches distinctly brittle; leaves trifoliolate; flowers invariably single, yellow and white, not cleistogamous; keel distinctly beaked; anthers markedly dimorphic; style long and slender; pods ovate-oblong, much inflated, with neatly orientated strigillose hairs; seeds on exceptionally long funicles (Figure 5.13). Two closely related species from the dry central parts of southern Africa (Map 5.25), easily recognised by the distinctive pubescence of the pods.

93. *L. rabenaviana* Dinter & Harms in Fedde, Repert. 16: 344 (1920); Schreiber in FSWA 60: 84 (1970). Type: Namibia, "Kl.-Karas", Dinter 4748 (BOL!, neotype, designated here; M!, fragment). [Original Type: Schäfer 101 (B+), no isotypes found].

Amphinomia rabenaviana (Dinter & Harms) Schreiber in Mitt. Bot. Staatssamm. München 2: 288 (1957).

L. rabenaviana is very closely related to *L. sparsiflora* and may prove to be no more than a subspecies of the latter. It is, however, easily distinguished by the much larger flowers and pods and also the cordate, imbricate calyx lobes (Figure 5.13). The slightly more localized distribution of *L. rabenaviana* is shown in Map 5.25).

Vouchers: Giess 14479; Giess & Müller 12176; Giess, Volk & Bleissner 7040; Merxmüller & Giess 2948; Muller & Leach 331.

94. L. sparsiflora (E. Mey.) B-E. van Wyk comb. nov. ined. [S. Afr. J. Bot. (in press), Appendix 26]. Type: South Africa, Cape Province, "at the Garip near Verleptpram" [2817 AA Vioolsdrif], Drège s.n. (K!, lecto., designated by Van Wyk 1989f; MO!, S!, isolecto.).

Crotalaria sparsiflora E. Mey., Comm. Pl. Afr. Austr. 1(1): 27 (1836); Benth. in Hook., Lond. J. Bot. 2: 573 (1843).; Harv. in Harv. & Sond., Fl. Cap. 2: 41 (1862); Bak. f. in J. Linn. Soc., Bot. 42: 400 (1914), non Polylobium sparsiflorum Eckl. & Zeyh. Type as above.

Lotononis lenticula (E. Mey.) Benth. var. brachycarpa Harv. in Harv. & Sond., Fl. Cap. 2: 62 (1862). Type: South Africa, Cape Province, "Springbokkeel" [3019 CA Loeriesfontein], Zeyher 411 (K!, Herb. Benth. specimen, lecto., designated by Van Wyk 1989f; K!, Herb. Hook. partly, specimen on right, SAM!, minor part, isolecto.).

L. oocarpa Dinter ex Wilman, Checklist Fl. Pl. Griqualand-West: 52 (1945); Schreiber in FSWA 60: 84 (1970), nom nud.

The flowers and pods of L. sparsiflora are much smaller than those of the closely related L. rabenaviana and the calyx lobes are valvate rather than somewhat cordate and imbricate as in the latter (Figure 5.13). L. sparsiflora is widely distributed in the Cape Province and southern Namibia (Map 5.25).

Vouchers: Acocks 505; Dinter 4851; Giess 14497; Giess & Müller 12308; Van Wyk 2139, 2140, 2056, 2057.

7N. Subsectio Oppositifolia B-E. van Wyk, subsect. nov.

Subsectioni praecedenti valde affinis sed folia basales sunt opposita, non alterna ut in subsectionibus aliis omnibus.

Closely related to the previous subsection, but the basal leaves are opposite and not alternate as in all other subsections.

Diagnostic characters: Prostrate annual; branches brittle; leaves trifoliolate; flowers invariably single, yellow, not cleistogamous; keel distinctly beaked; anthers markedly dimorphic; style very long and slender; pods shortly oblong, only very slightly inflated, minutely pubescent; seeds on exceptionally long funicles (Figure 5.13). Monotypic.

95. L. lenticula (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 611 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 62 (1862), excl. var. brachycarpa (see L. sparsiflora). Type: South Africa, Cape Province, "in the Sneeuwbergen" [3124 DC Hanover], "on the flat between Rivertje and Nieuwkerkshoogte", Drège s.n. (K!, Herb. Benth. specimen, larger piece, lecto., designated by Van Wyk 1989f; BM!, K!, Herb. Hook. specimen, PRE 24334!, S!, isoleccto.).

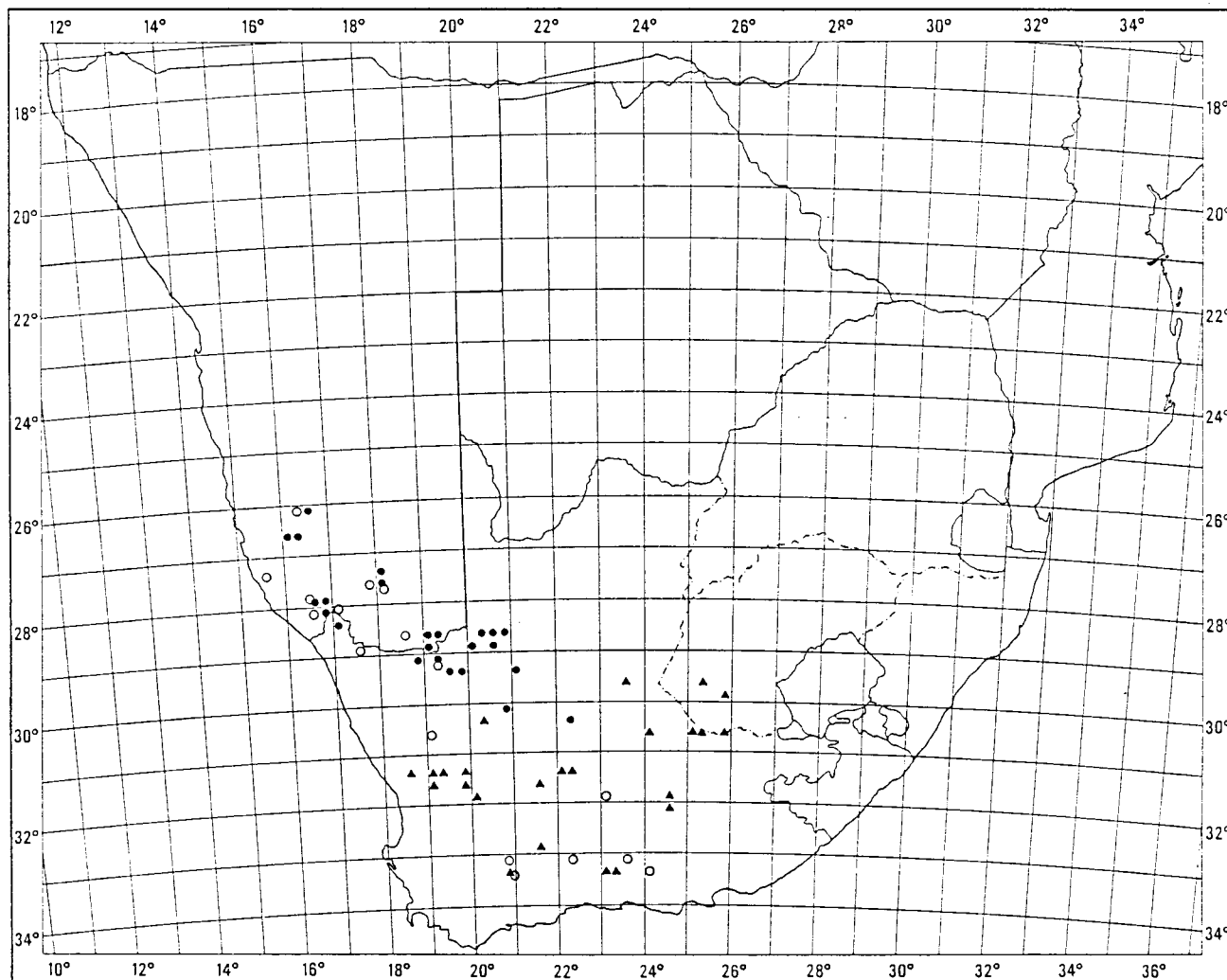
Crotalaria lenticula E. Mey., Comm. Pl. Afr. Austr. 1(1): 26 (1836); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 330 (1913). Type as above.

Lotononis lenticula (E. Mey.) Benth. var. biflora Kensit in Trans. Roy. Soc. S. Afr. 1: 148 (1909). Type: South Africa, Orange Free State, near Bethulie, Flanagan 1496 (BOL!, holo.; PRE!, with Flanagan label, PRE!, without original label, partly, iso.).

L. decrepita Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 322 (1913), nom. nud., synon. nov. [Based on part of the type collection of Lipozygis tenella, Drège s.n. (K!, holo.)].

This is the only species of Lotononis where the basal leaves are consistently opposite and not alternate, resulting in a distinctive branching pattern by which the species is easily recognised. The keel is rostrate and the pods are scarcely inflated (Figure 5.13). L. lenticula has a very wide distribution in the dry interior of southern Africa (Map 5.25).

Vouchers: Acocks 14346, 17729; Henrici 4352; Hugo 327; Smith 4412; Van Wyk 2017, 2018.



Map 5.25. The known geographical distribution of *L. rabenaviana* (●), *L. sparsiflora* (○) and *L. lenticula* (▲).

Sectio 8. Monocarpa B-E. van Wyk, sect. nov. Haec sectio est sectioni Oxydiae similis sed forma florum omnino dissimile, antheris solum parum dimorphis atque floribus caeruleis differt. Unguis vexillae non est basin versus dilatus, atque vexilla alaeque valde longiores carina sunt. Petala carinae sunt parva laete acuta sed non distincte rostrata ut in Oxydio; antheri basifixi non sunt compluries longiores antheris dorsifixis ut in Oxydio.

This section is similar to the section Oxydium but differs from it in the totally different structure of the flowers, the only slightly dimorphic anthers and the occurrence of blue flowers. The claw of the standard petal is not dilated towards the base and the standard and wing petals are much longer than the keel. The keel petals are small and somewhat pointed but not distinctly beaked as in Oxydium and the basifixed anthers are not several times longer than the dorsifixed anthers as in Oxydium. The section is also similar to the sections Polylobium and Lotononis but differs from these and other sections in the equally lobed calyx (zygomorphic in the latter), the annual habit, the only slightly inflated pods, the very long funicles, the occurrence of flower dimorphism (cleistogamy) and the chromosome number ($2n = 18$).

Type species: L. leptoloba H. Bol.

Small prostrate annuals. Mature parts sparsely to densely pubescent. Leaves alternate (very rarely opposite at some nodes), digitately trifoliolate, variable in size and shape, usually densely pubescent at least on the lower surface. Stipules paired or single at each leaf base (when paired, often dissimilar in size and shape), usually small, linear to lanceolate, occasionally similar to the leaflets in size and shape. Inflorescences almost invariably single-flowered (very rarely 2-flowered only at some nodes), on relatively long leaf-opposed peduncles; bracts small, usually inconspicuous, occasionally linear to narrowly lanceolate and almost as long as the calyx; bracteoles absent. Flowers large, yellow or blue, often cleistogamous. Calyx equally lobed (the upper and lateral lobes on either side not fused higher up in pairs), the lobes very long, usually as long or longer than the fused part of the calyx, lower lobe similar to the upper lobes; pubescent. Standard large, much longer than the keel, broadly ovate to orbicular; mostly glabrous but with at least a line of hairs dorsally along the middle; lamina very large, usually conspicuously striated; claw short, not dilated towards the base, without callosities; apex obtuse to emarginate. Wing petals oblong, usually much longer than the keel, glabrous. Keel petals very small, half oblong-elliptic, curved; apex shortly but distinctly beaked, glabrous. Anthers only slightly dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the carinal anther similar to the dorsifixed anthers. Pods sessile, broadly oblong, slightly inflated laterally, upper suture distinctly verrucose, dehiscent,

many-seeded; funicles often exceptionally long, several times longer than the length of the seeds. Seeds 1,5--2,5 mm in diameter, variable in shape, usually suborbicular, often with the radicular lobe conspicuous, testa distinctly tuberculate. Chromosome base number 9 ($2n = 18$). (Figure 5.14).

Three species from the south-western and western Cape Province (Map 5.26) are included in this new section. The species may be confused with species of the section Oxydium, but the following combination of characters can be used to distinguish them: Small prostrate annuals with brittle stems; leaves trifoliolate; flowers leaf-opposed, single or rarely paired, usually on a distinct peduncle, yellow or blue, very often cleistogamous; standard petal very large, much longer than the keel, distinctly striated (i.e., the venation conspicuous); wing petals much longer than the keel; keel very small, acute, glabrous; pods oblong to oblong-linear, only slightly turgid, many-seeded, the seeds on exceptionally long funicles.

Key to the species of section Monocarpa:

- 1A. Flowers blue 98. L. maximiliani
- 1B. Flowers yellow:
 - 2A. Leaflets obovate to oblanceolate 97. L. leptoloba
 - 2B. Leaflets narrowly lanceolate to linear 96. L. venosa

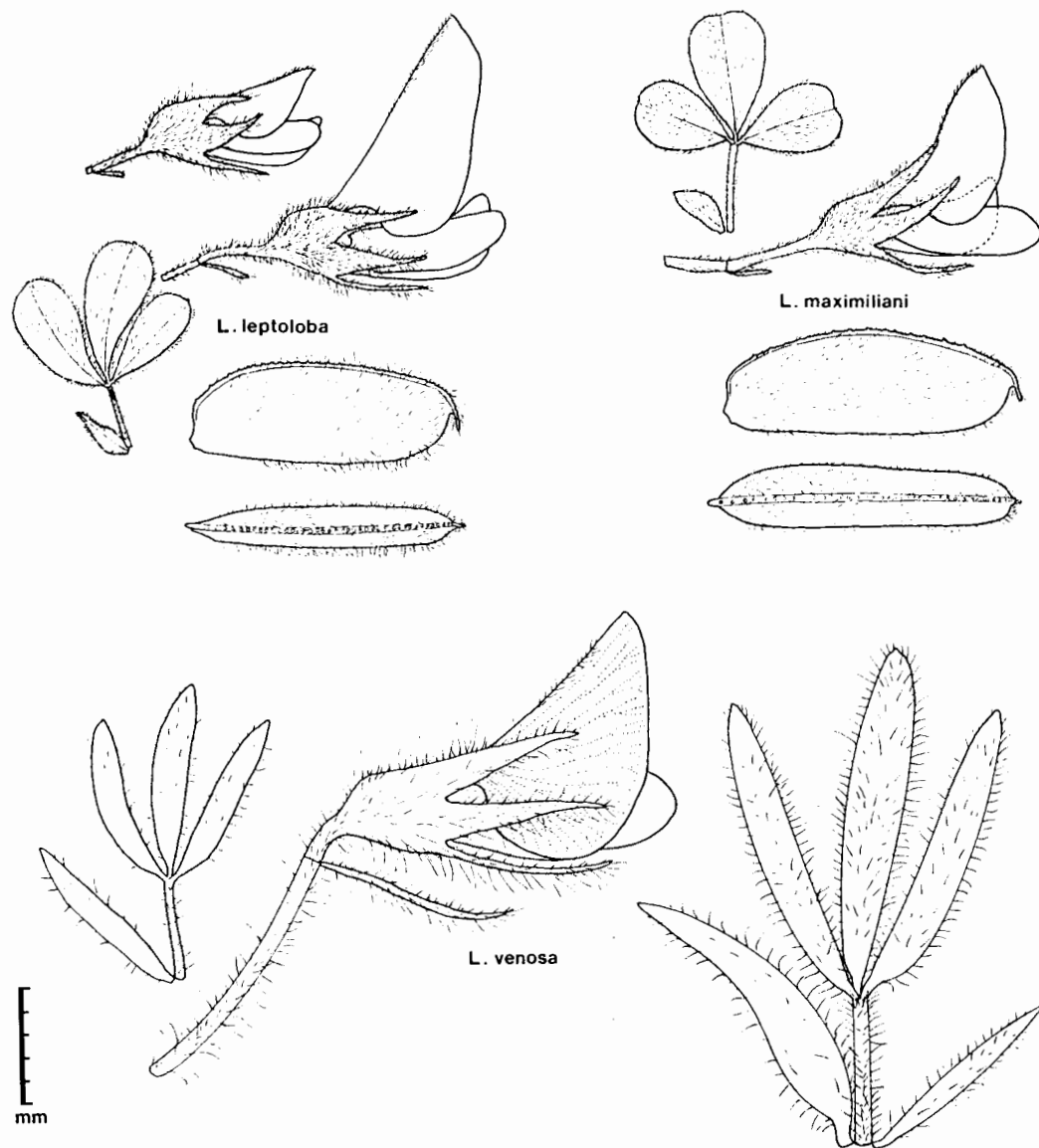


Figure 5.14. Leaves, flowers and pods of the species of section Monocarpa.

96. *L. venosa* B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 32]. Type: South Africa, Cape Province, De Hoop in Klein Roggeveld, Oliver 8965 (PRE!, holo; STE!, iso.).

A distinct species known only from two recent collections in the Roggeveld area (Map 5.26). The flowers turn blue when dried and the species may therefore be mistaken for *L. maximiliani*, but the shape of the leaflets and the very large flowers (Figure 5.14) are quite distinct. *L. venosa* is poorly known but the annual habit, general morphology, inflorescence structure and flower morphology are very similar to that of *L. leptoloba* (Van Wyk 19891, Appendix 32).

Vouchers: Oliver 8965; Schutte 259.

97. *L. leptoloba* H. Bol. in Engl., Bot. Jahrb. 24: 457 (1897); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 319 (1913). Type: South Africa, Cape Province, Zout Rivier, in the district of Van Rhyndorp, Schlechter 8143 (BOL!, lecto., designated here; BM!, partly, upper piece only, GRA!, K!, MO!, PRE, 3 sheets); Schlechter 8131 pro parte min. (BOL!).

Note: Schlechter 8131 and 8143 are mixed collections of two different species, *L. leptoloba* and *L. lenticula*. It is quite clear that Bolus used the two isosyntype specimens in BOL (Schlechter 8131 and 8143) for his description of *L. leptoloba*,

both of which agree with the diagnosis. Since most of the collections distributed as Schlechter 8131 are in fact L. lenticula and not L. leptoloba, Schlechter 8131 in BOL is not chosen as lectotype as this may cause further confusion. The following duplicates that I have examined are all L. lenticula (easily recognised by the opposite rather than alternate basal leaves and the acute keel petals) and must therefore be excluded: Schlechter 8131 in BM, K, MO, PRE and also in Z (photo in M!); Schlechter 8143 in BM (lower piece only).

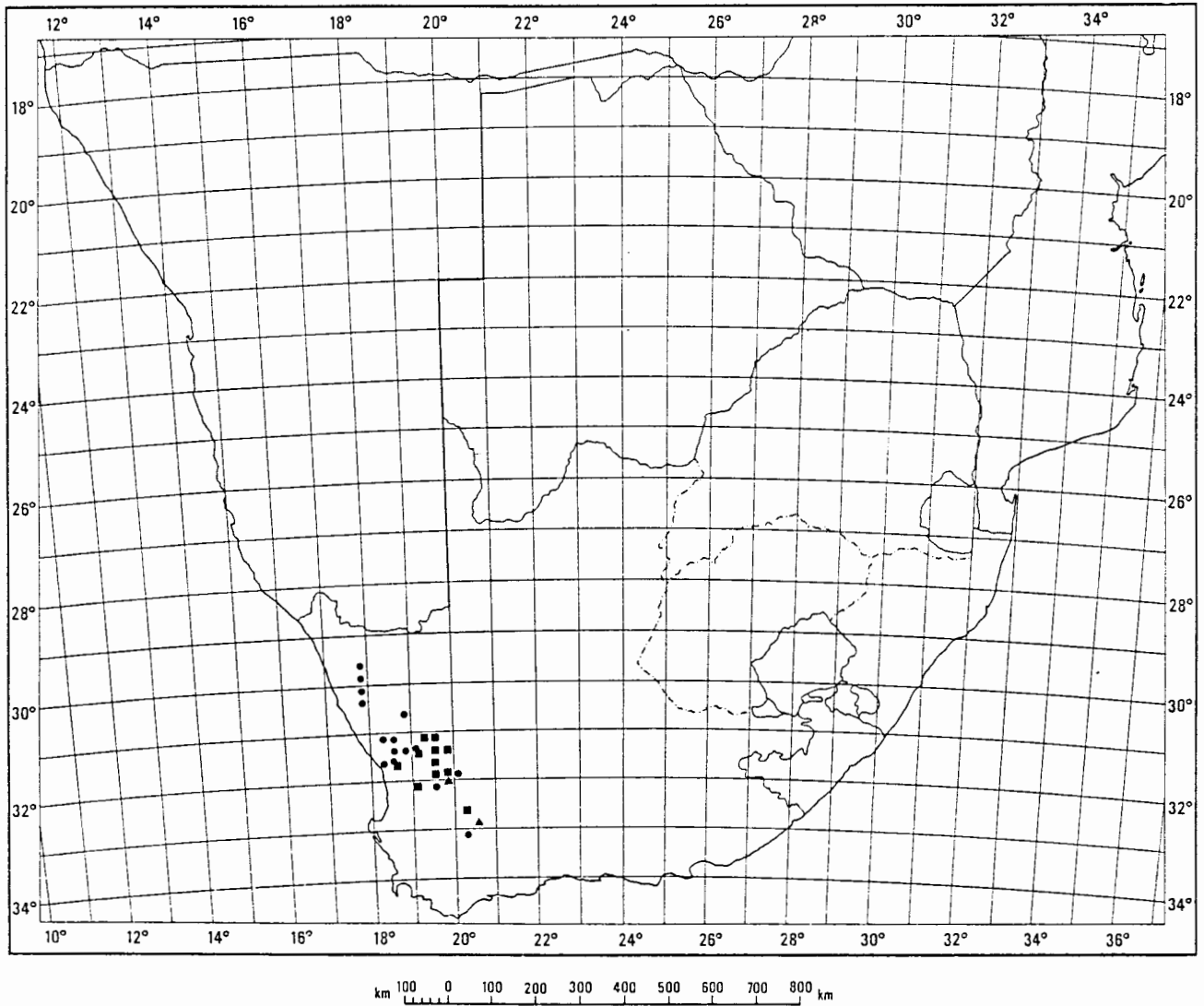
Specimens of this species are often misidentified as L. maximiliani (and vice versa) when the colour of the flowers has not been noted or is no longer obvious. These two species (and particularly the cleistogamous forms) are superficially very similar to some species of the section Oxydium. The shape of the standard, wing and keel petals however, is quite distinct (Figure 5.14).

Vouchers: Acocks 18949; Barker 2532; Compton 11155; Esterhuysen 5364; Hugo 465, 502.

98. L. maximiliani Schlechter ex De Wildeman, Pl. Nov. Hort. Then. 1: 188, t. 41 (1906); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 319 (1913). Type: South Africa, Cape Province, Achtertuin [Clanwilliam district] Schlechter 10851 (B+; K!, lecto., designated here; BM!, BOL!, GRA!, MO!, S!).

L. maximiliani is the only annual species of Lotononis with blue flowers and therefore relatively easy to identify. The structure of the flowers (Figure 5.14) is the only reliable character to distinguish L. maximiliani and the closely related L. leptoloba from species of the section Oxydium. L. maximiliani has a more western distribution than L. leptoloba and is very common in the Vanrhynsdorp and Calvinia districts (Map 5.26).

Vouchers: Bond 1158; Compton 11507; Goldblatt 3901; Schutte 271, 272, 280--282, Van Wyk 2425.



Map 5.26. The known geographical distribution of *L. venosa* (▲), *L. leptoloba* (●) and *L. maximiliani* (■).

Sectio 9. Cleistogama B-E. van Wyk, sect. nov. Haec sectio a sectionibus Polylobio, Lotonone et Aulacintho calyce aequilobato (in sectionibus tribus aliis zygomorpho), habitu (plantae perennes brevaevae) atque floribus saepe dimorphis propter cleistogamiam tempestivam differt. A sectione Oxydio forma floris (carina obtusa, vexilla basin non dilatata, antheris non valde dimorphis) et chromosomatum numero ($2n \pm 28$, non 18) differt.

This section differs from the sections Polylobium, Lotononis and Aulacanthus in the equally lobed calyx (zygomorphic in the latter), the habit (short-lived herbaceous perennials) and the frequent occurrence of flower dimorphism as a result of seasonal cleistogamy. It differs from the section Oxydium in the flower structure (keel petals \pm obtuse, base of standard petal not dilated, anthers not strongly dimorphic) and the chromosome number ($2n = 28$, not 18).

Type species: L. tenella (E. Mey.) Eckl. & Zeyh.

Small prostrate or procumbent perennial herbs. Mature parts sparsely to densely pubescent, sometimes sericeous. Leaves alternate, digitately trifoliolate, very variable in size and shape, usually densely pubescent at least on the lower surface. Stipules invariably single at each leaf base, small, linear to lanceolate. Inflorescences invariably single-flowered, on short leaf-opposed or rarely subterminal peduncles; bracts very small, inconspicuous; bracteoles absent. Flowers relatively large,

yellow, occasionally marked with dark purple, very often cleistogamous. Calyx equally lobed (the upper and lateral lobes on either side not fused higher up in pairs), the lower lobe rarely narrower than the upper ones (and then only slightly so), pubescent. Standard large, as long as the keel or slightly shorter, broadly obovate to orbicular; mostly glabrous but with at least a line of hairs dorsally along the middle; claw short, not dilated towards the base, without callosities; lamina large, often conspicuously striated, apex obtuse to emarginate. Wing petals oblong, shorter than the keel, glabrous. Keel petals oblong; apex obtuse, glabrous. Anthers only slightly dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the vexillary one intermediate. Pods sessile, ovoid to broadly oblong, strongly inflated laterally, thick-walled (except in one species), upper suture distinctly verrucose, dehiscent, many-seeded; funicles long to very long, often several times longer than the length of the seeds. Seeds \pm 1,5 mm in diameter, variable in shape, the radicular lobe conspicuous, testa distinctly tuberculate. Chromosome base number 7 ($2n = 28$). (Figure 5.15).

The section Cleistogama comprises two closely related herbaceous perennials with a wide geographical distribution in the southern parts of the Cape Province, extending into the Orange Free State (Map 5.27). The two species are exceptionally common and can be found in almost any habitat. In arid areas, L. pungens and L. tenella may adopt an annual habit and are therefore often confused with species of the section Oxydium. The affinities of

the section Cleistogama are very uncertain because it has diagnostic characters of different sections in a unusual combination. The perennial habit and the chromosome number of $2n = 28$ suggest that the similarity with the section Oxydium (where $2n = 18$) may be a result of convergence.

The two species are very variable and are often confused with other species, partly as a result of the common occurrence of flower dimorphism. The rather complicated synonymies for L. pungens and L. tenella show the difficulties that previous authors encountered in their interpretation of these species. Harvey (1862) for example, confused L. tenella with L. calycina (section Leptis) because the relative length of the calyx in cleistogamous flowers of L. tenella results in a superficial similarity with the flowers of L. calycina, where the calyx is as long as the corolla (in chasmogamous flowers). The following combination of characters may be useful to distinguish L. tenella and L. pungens from superficially similar species of various other sections: Prostrate or procumbent short-lived herbaceous perennials; leaves trifoliolate; stipules small, invariably single at each node; calyx equally lobed (the lateral and upper lobes on either side not fused higher up in pairs); flowers yellow, very often cleistogamous (cleistogamous flowers are small and often overlooked, but pods formed from such flowers can easily be distinguished by the very short styler remains); standard petal as long or slightly shorter than the keel; wing and keel petals totally glabrous, the latter obtuse and not

beaked; pods oblong or more rarely ovate, turgid, upper suture verrucose, lower suture often somewhat sunken, many-seeded, the seeds often on very long funicles.

Key to the species of section Cleistogama:

- 1A. Apex of keel petals yellow; veination of the
standard petal not conspicuous 99. L. pungens
1B. Apex of keel petals dark purple; veination
of the standard conspicuous, dark purple 100. L. tenella

99. L. pungens Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 177 (1836); Steud. Nom. Bot. 2(2): 73 (1841); Benth. in Hook., Lond. J. Bot. 2: 613 (1843); Harv. in Harv. & Sond., Fl Cap. 2: 62 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 321 (1913). Type: South Africa, Cape Province, "Konabshoogde" [Koonap Heights, 3226 DC Fort Beaufort], Ecklon & Zeyher 1277 (S!, lecto., designated here; S!, SAM!, islecto.).

L. depressa Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 178 (1836); Steud. Nom. Bot. 2(2): 73 (1841); Benth. in Hook., Lond. J. Bot. 2: 612 (1843); Harv. in Harv. & Sond., Fl Cap. 2: 62 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 321 (1913), synon. nov. Type: South Africa, Cape Province, between "Gauritzrivier et Langekloof" [3321 DC/3323 CA], Ecklon & Zeyher 1278 (S!, lecto., designated here; S!, islecto.).

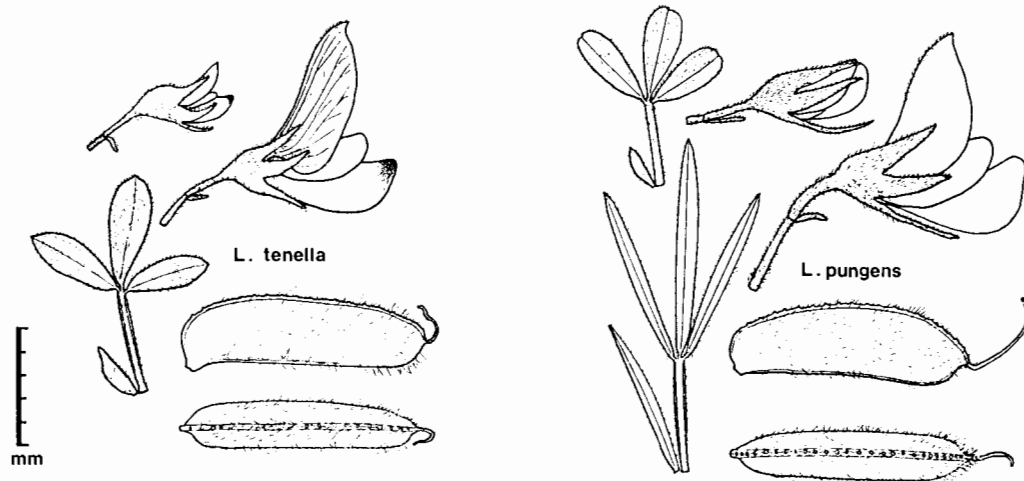


Figure 5.15. Leaves, flowers and pods of the species of section Cleistogama. Fully developed cleistogamous flowers are also shown.

L. affinis Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 178 (1836), nom. nud., non L. affinis Burt Davy, Man. pl. Transvaal: 389 (1932); Steud. Nom. Bot. 2(2): 73 (1841); Benth. in Hook., Lond. J. Bot. 2: 612 (1843); Harv. in Harv. & Sond., Fl Cap. 2: 62 (1862), as synonym of L. pungens; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 321 (1913), as synonym of L. pungens. Type: South Africa, Cape Province, near "Gauritzrivier" [3321 DC/DD], Ecklon & Zeyher 1279 (S!, lecto., designated here; S!, SAM!, isolecto.).

L. decidua Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 178 (1836); Steud. Nom. Bot. 2(2): 73 (1841); Benth. in Hook., Lond. J. Bot. 2: 612 (1843); Harv. in Harv. & Sond., Fl Cap. 2: 62 (1862), as synonym of L. pungens; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 321 (1913), as synonym of L. pungens. Type: South Africa, Cape Province, between "Bosjesmansrivier et Karregarivier" [3326 DA], Ecklon & Zeyher 1279 (S!, lecto., designated here; C!, M!, MO!, S!, SAM!).

Lipozygis tenella E. Mey. var. sericea E. Mey., Comm. Pl. Afr. Austr. 1(1): 65 (1836), non Crotalaria tenella E. Mey. in Linnaea 7: 152 (1832), nec Lipozygis tenella E. Mey. var. tenella. Types: South Africa, Cape Province, "Sneeubergen", Drège s.n. a (S!, lecto., designated here; K!, partly, isolecto.); near "Schiloh" [3226 BB Fort Beaufort], Drège s.n. b (not seen); near "Klein-Vischrivier" [probably 3225 DC], Drège s.n. c (not seen). [Note: Drège s.n. a in K is a mixture of this species and L. lenticula q.v.].

Lipozygis tenella E. Mey. var. piloso-villosa E. Mey., Comm. Pl. Afr. Austr. 1(1): 65 (1836), non Crotalaria tenella E. Mey. in Linnaea 7: 152 (1832), nec Lipozygis tenella E. Mey. var. tenella. Types: South Africa, Cape Province, "Klaarstrom" [Klaarstroom, near the Swartberg], Drège s.n. a (K!, lecto., designated here); "Ado" [Addo], Drège s.n. b (not seen).

Lipozygis kraussiana Meisner in Hook. Lond. J. Bot. 2: 79 (1843). Type: South Africa, Cape Province, "Winterhoeksberge", distr. Uitenhage, Krauss 875 (M!, MO!).

Lipozygis argentea Meisner in Hook. Lond. J. Bot. 2: 80 (1843), synon. nov. Type: South Africa, Cape Province, "Winterhoeksberge", distr. Uitenhage, Krauss 874 (not seen). (From the description of Krauss 874 (said to be from the same locality as Krauss 875) it is quite clear that L. argentea Meisner is merely a more sericeous form of L. kraussiana].

L. flava Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 321 (1913), synon. nov. Type: South Africa, Cape Province, Mossel Bay Div., Dry hills on the eastern side of the Gauritz River, Burchell 6420 (K!, holo.).

The pubescence and shape of the leaves are extremely variable but there are no distinct discontinuities that would seem to justify infraspecific taxa. I have seen most of the forms in situ and have no hesitation to include them all under L. pungens. Some specimens (particularly from around Knysna in the southern Cape) have very broad calyx lobes but these are unlikely to represent more than a variety or form of L. pungens. The distinction

between L. pungens and L. tenella is virtually impossible when no chasmogamous flowers are available and the two species may eventually prove to be only subspecifically distinct. With adequate material, L. pungens can readily be distinguished from L. tenella by the absence of a pollen guide (Figure 5.15). L. pungens has a more southern distribution than L. tenella (Map 5.27).

Vouchers: Bayliss 4905; Brink 236; Schutte 214--217; Van Niekerk 512; Van Wyk 2058, 2108, 2471. Form with wide calyx lobes: Acocks 21495; Archibald 5794; Ecklon & Zeyher 1283; Fourcade 1568; Theron 2089.

100. L. tenella (E. Mey.) Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 178 (1836); Steud. Nom. Bot. 2(2): 73 (1841); Benth. in Hook., Lond. J. Bot. 2: 613 (1843), pro parte, excl. syn. Crotalaria tenella E. Mey. in Linnaea 7: 152 (1832). Type: South Africa, Cape Province, "Zwartbulletje" [not traced], Drège s.n. (S!, lecto., designated here; K!, isolecto.).

L. tenella (E. Mey.) Eckl. & Zeyh. var. angustifolia Harv. in Harv. & Sond., Fl Cap. 2: 62 (1862), pro parte. Type as above. [Note: Zeyher 408 (K!) was cited by Harvey under this variety].

Leptidium tenellum (E. Mey.) Presl in Abh. Böhm 479 (1845). Type as above.

Polylobium tenellum (E. Mey.) D. Dietr., Syn. Pl. 4: 962 (1847). Type as above.

Lipozygis tenella E. Mey., Comm. Pl. Afr. Austr. 1(1): 65 (1836), non Crotalaria tenella E. Mey. in Linnaea 7: 152 (1832).
Type as above.

Lotononis versicolor (E. Mey.) Benth. sensu Harv. in Harv. & Sond., Fl Cap. 2: 66 (1862), pro parte; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 322 (1913), pro parte.

L. rara Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 322 (1913), synon. nov. Type: South Africa, Cape Province, near Graaff Reinet, Bolus 770 (K!, holo.; BOL!, iso.).

This species is morphologically very similar to some forms of L. pungens, but can be distinguished by the striated standard petal and the dark purple pollen guide of the keel (Figure 5.15). These characters are not lost in dried material and can usually be observed even in old herbarium specimens. L. tenella is common in the Karoo and generally has a more northern distribution than the closely related L. pungens (Map 5.27).

Vouchers: Acocks 17123; Bolus 11466; Compton 4663; Esterhuysen 4487; Van Wyk 1383--1385, 2136, 2144.

Map 5.27. The known geographical distribution of L. pungens (Δ), and L. tenella (\bullet).

Section 10. Euchlora (Eckl. & Zeyh.) B-E. van Wyk stat. nov.

Euchlora Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 171 (Jan. 1836); Benth. in Hook., Lond. J. Bot. 2: 470 (1843); Harv. in Harv. & Sond., Fl Cap. 2: 38 (1862); Dahlgr. in Bot. Not. 117: 371 (1964).

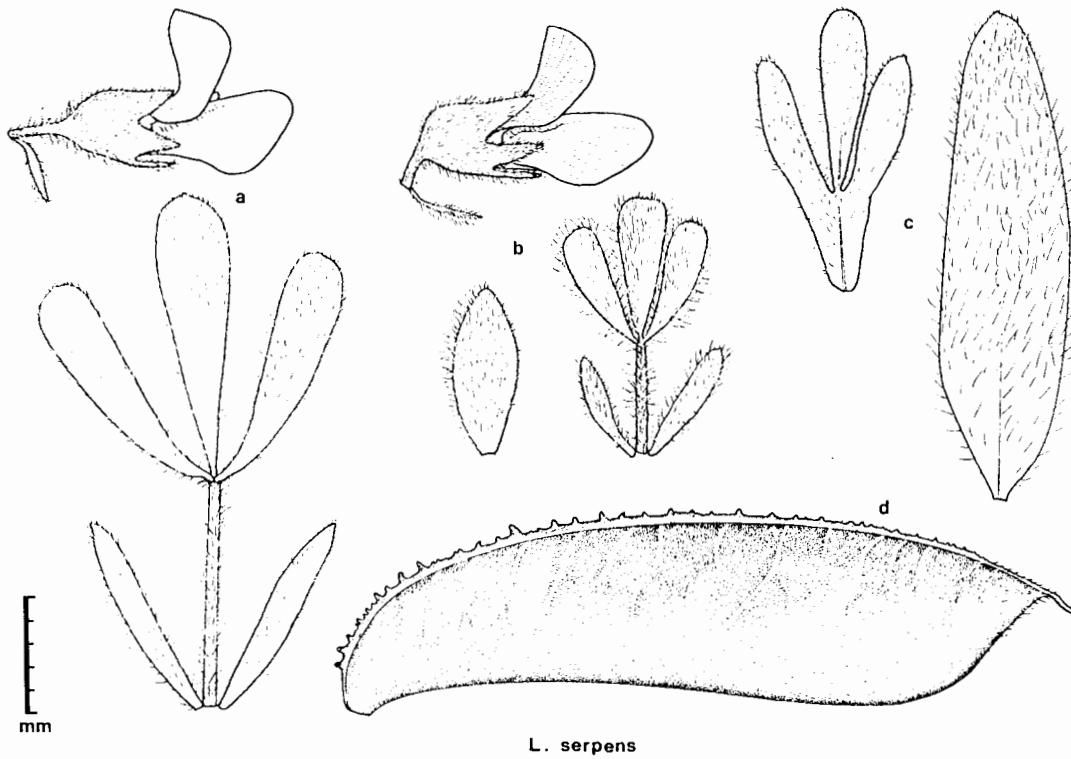
Microtropis E. Mey., Comm. Pl. Afr. Austr. 1(1): 65 (Feb. or later 1836).

Type species: Euchlora serpens (E. Mey.) Eckl. & Zeyh. [now Lotononis serpens (E. Mey.) Dahlgr.]

Geophytic herb with slender, herbaceous annual branches from a large woody caudex. Mature parts sparsely pubescent, with long thin spreading hairs. Leaves alternate, usually simple and sessile, occasionally digitately trifoliolate, at least on the upper parts of the branches. Stipules usually absent, paired and similar to the leaflets when present. Inflorescences many-flowered, on long slender terminal or subterminal peduncles; bracts small, filiform; bracteoles absent. Flowers relatively small, yellow and partly brown or dark purple, never cleistogamous. Calyx subequally lobed, with the upper (vexillary) sinus slightly deeper than the lateral and lower ones, the lateral and upper lobes never fused; sparsely to densely pubescent. Standard relatively small, but much longer than the keel, broadly obovate to orbicular; almost totally glabrous, with only a few hairs dorsally along the middle; claw short, without

callosities; lamina usually conspicuously striated, apex obtuse to emarginate. Wing petals broadly oblong, widening towards the apex, usually much longer than the keel, glabrous. Keel petals very small, half oblong-elliptic, curved; apex acute but not beaked, glabrous. Anthers dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the carinal anther similar to the dorsifixed ones. Pods sessile, exceptionally large, oblong, strongly inflated laterally, very thick-walled, upper suture distinctly verrucose, with large warty protuberances; lower suture sunken; few-seeded; funicles relatively short. Seeds exceptionally large, up to 6,5 mm long and 5 mm wide, suborbicular, radicular lobe not conspicuous; testa invariably smooth, usually mottled with dark purple. Chromosome base number 9 ($2n = 18$). (Figure 5.16).

The genus Euchlora is here treated as a section of Lotononis. The presence of simple sessile leaves, at least on the basal parts of the flowering branches, is an unique character for this monotypic section. Dahlgren (1964) discussed the unusual morphology of the species and transferred it to Lotononis. A form of the species with trifoliolate and stipulate leaves (see below) is very similar to species of the section Polylobium and it may be argued that L. serpens should be included in this section. There are, however, some important differences that do not support the idea of a close affinity. The chromosome number ($2n = 18$ in Euchlora,



L. serpens

Figure 5.16. Leaves, stipules, flowers and a pod of Lotononis serpens (section Euchlora). a, leaf and flower from a robust trifoliolate form of the species; b, leaves and flower from a form with simple and trifoliolate leaves; c, simple and partly trifoliolate leaf from the typical form of the species; d, pod in side view, showing the large warty protuberances along the upper suture.

2n = 28 in Polylobium) and the seed surface (smooth in Euchlora, invariably rugose or tuberculate in Polylobium) for example, indicate that the similarities may be due to convergence.

101. L. serpens (E. Mey.) Dahlgr. in Bot. Not. 117: 373 (1964). Type: South Africa, Cape Province, "Sandige Stellen unweit Salzrivier" [Salt River], Ecklon s.n. (S!, lecto., designated by Dahlgren 1964).

Crotalaria serpens E. Mey. in Linnaea 7: 153 (1832). Type as above.

Euchlora serpens Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 171 (1836); Walp. in Linnaea 13: 505 (1839), Rep. Bot. Syst. 1: 618 (1842); Benth. in Hook., Lond. J. Bot. 2: 470 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 38 (1862). Type as above.

Ononis hirsuta Thunb., Prodr. pl. Cap.: 129 (1800), Fl. Cap. 585 (1823); DC., Prodr. 2: 166 (1825). Type: South Africa, Cape Province, "prope Cap juxta Leuwestaart", Thunberg s.n. sub Thunb. Herb. 16614 (UPS!, lecto., designated by Dahlgren 1964).

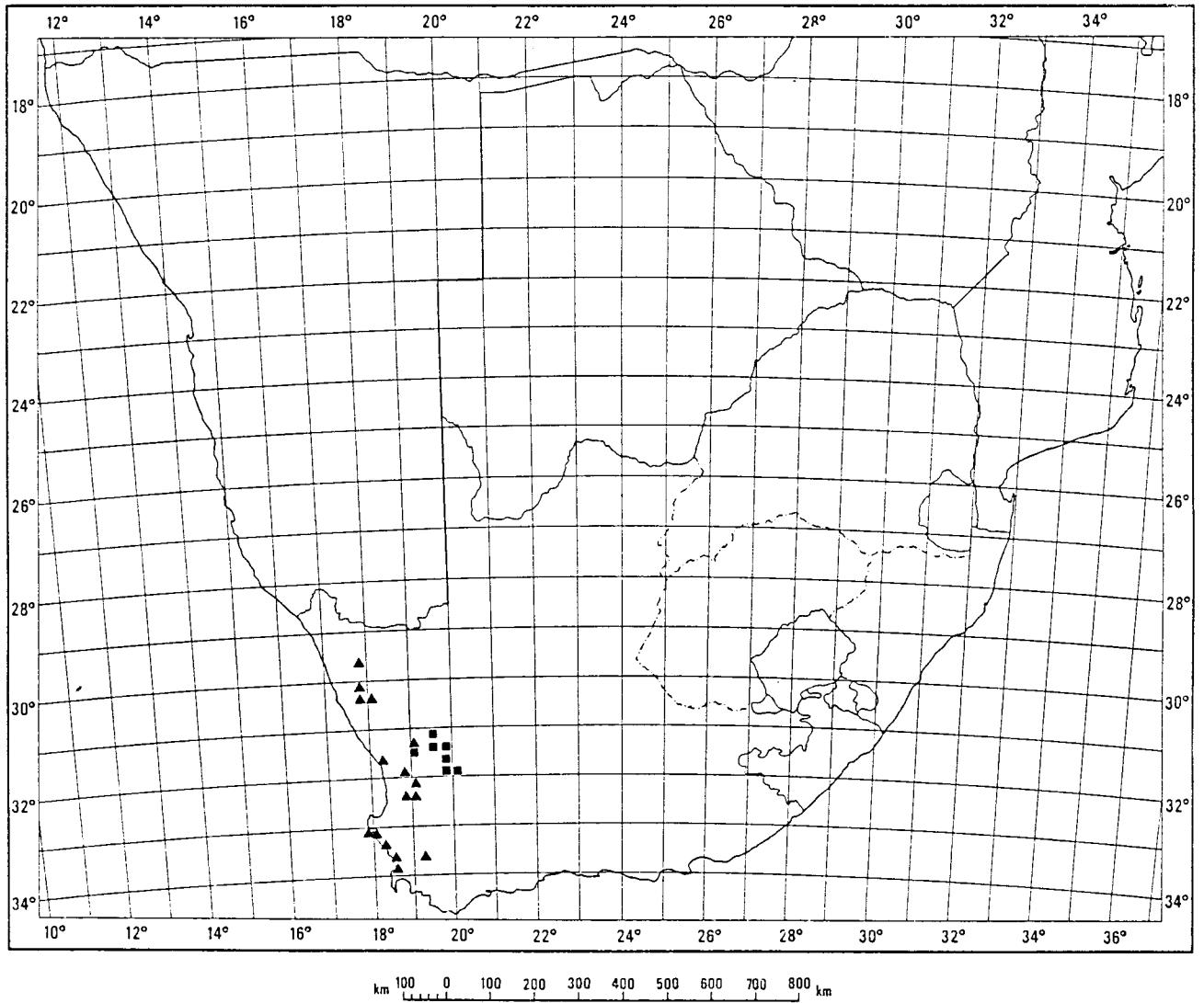
Microtropis hirsuta (Thunb.) E. Mey., Comm. Pl. Afr. Austr. 1(1): 65 (1836). Type as above.

Euchlora hirsuta (Thunb.) Druce in Rep. Bot. Exch. Cl. Brit. Isles, 1916: 622 (1917). Type as above.

The single species, L. serpens, can easily be recognised by the large tuberous caudex, the simple, sessile leaves and the large pods (Figure 5.16). A form of the species from the western parts

of the distribution range (Calvinia area) has most of the leaves trifoliolate and stipulate as in Figure 5.16a. Even when the leaves are predominantly digitate and stipulate, some simple leaves can usually be found along the basal parts of the branches (Figure 5.16b). It may be useful to recognise the trifoliolate form as a distinct infraspecific taxon even though intermediates (with leaves as in Figure 5.16c) are occasionally found. The known geographical distributions of the typical form and the predominantly trifoliolate form of the species are shown separately in Map 5.28.

Vouchers. Form with simple leaves: Acocks 24367; Johnson 195; Lavranos 10968; Perry & Snijman 2174; Van Wyk 1405. Form with digitate leaves: Coetzer 812; Leistner 356; Lewis 5805; Schutte 255--258, 290; Thompson 2502.



Map 5.28. The known geographical distribution of *L. serpens*: typical form with simple sessile leaves (▲); form with the leaves predominantly trifoliolate (■).

Section 11. Polylobium (Eckl. & Zeyh.) Benth. emend. B-E. van Wyk, emend. nov.

Lotononis section Polylobium (Eckl. & Zeyh.) Benth. in Hook., Lond. J. Bot. 2: 601 (1843), pro parte mai.; Harv. in Harv. & Sond., Fl. Cap. 2: 48 (1862), pro parte mai; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 279 (1913), pro parte min.

Polylobium Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 180 (1836); Benth. in Ann. Wien. Mus. 2: 142 (1839); Steud., Nom. Bot. 2(2): 377 (1841); D. Dietr., Syn. pl. 4: 961 (1847), pro parte.

Lipozygis (section 5) E. Mey., Comm. Pl. Afr. Austr. 1(1): 79 (1836).

Type species: L. involucrata (Berg.) Benth.

Note: The present circumscription agrees closely with the original concept of Ecklon & Zeyher (1836) except for the exclusion of L. umbellata and other species with single stipules. Bentham (1843) transferred Polylobium typicum Eckl. & Zeyh. (the implied type of the genus Polylobium, now Lotononis glabra) to the section Oxydium. The infrageneric nomenclature is therefore not affected by the present change. Dümmer (1913) added several species to the section Polylobium and in doing so created a totally artificial group.

Perennial shrublets with procumbent or erect annual flowering branches from a thick woody caudex. Mature parts sparsely to densely pilose or villous, rarely sericeous or \pm strigillose. Leaves alternate, usually digitately trifoliolate, 5- to 8-foliolate in two species, usually pubescent on both surfaces, more densely so on the lower surface. Stipules invariably paired at each leaf base (never single and never markedly dissimilar in size and shape), linear to lanceolate, usually similar to the leaflets. Inflorescences racemose to densely umbellate, 2- to several-flowered; peduncle \pm absent or more often very long and slender, terminal and leaf-opposed; bracts usually conspicuous, very variable in size and shape, linear or elliptic to broadly ovate; bracteoles absent. Flowers relatively large, yellow, never cleistogamous. Calyx subequally lobed, with the upper and lateral lobes on either side fused a little higher up in pairs, the lower lobe rarely narrower than the upper ones. Standard large, as long as the keel or usually much longer, broadly ovate, broadly oblong or suborbicular; dorsally hairy, at least along middle; claw long, without callosities; lamina large, usually conspicuously striated; apex obtuse to emarginate. Wing petals oblong to broadly obovate, longer than the keel, glabrous. Keel petals very small, half oblong-elliptic, curved; apex shortly but distinctly beaked; glabrous. Anthers dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the carinal anther intermediate. Pods sessile, ovoid to broadly oblong, strongly inflated laterally, thick-walled; upper suture distinctly verrucose; dehiscent; many-seeded; lower suture somewhat sunken; funicles relatively

short. Seeds 1,5--3 mm in diameter, variable in shape, often with the radicular lobe conspicuous, testa distinctly tuberculate. Chromosome base number 7 ($2n = 28$). (Figure 5.17).

Four species (one divided into four subspecies) with a restricted distribution in the extreme western and south-western parts of the Cape Province (Maps 5.29, 5.30 and 5.31).

Diagnostic characters: The species included in this section differ from species of related sections in their distinctive habit and paired stipules (stipules are never absent, single or dimorphic). All of them are decumbent suffrutescent perennials, with annual flowering branches developing from a thick and woody caudex. A similar habit occurs in the section Euchlora, but this section differs in the simple sessile leaves (at least towards the base of the branches) and in the inconspicuous bracts. The sections Polylobium and Euchlora are nevertheless considered to be closely related. The flower structure in both sections is very similar to that of the the section Lotononis. The standard and wing petals are much longer than the small, acute keel.

Key to the species and subspecies of section Polylobium:

1A. Peduncle short (< 20 mm) or \pm absent:

2A. Leaves 5- to 8-digitate:

3A. Leaflets densely sericeous on upper (and lower)
surface; inflorescence sparsely 1--2 (--4)
-flowered; flowering branches up to 100 mm
long 105. L. brevicaulis

3B. Leaflets sparsely villous, upper surface
 \pm glabrous; inflorescence densely umbellate,
> 4-flowered; flowering branches > 200 mm
long 104c. L. involucrata subsp. digitata

2B. Leaves 3-digitate:

4A. Stipules similar to the leaflets in
size and shape; bracts lanceolate to
narrowly ovate, cuneate at the
base 104a. L. involucrata subsp. involucrata

4B. Stipules much smaller than the leaflets;
bracts very broadly ovate, cordate at
the base 104b. L. involucrata subsp. bracteata

1B. Peduncle long (> 20 mm), slender:

5A. Flowers evenly spaced in a long
many-flowered raceme 102. L. racemiflora

5B. Flowers umbellate or subumbellate:

- 6A. Flowering branches erect; leaflets and
stipules firm in texture, pungent 103. *L. fastigiata*
- 6B. Flowering branches procumbent; leaflets and
stipules not firm in texture, obtuse to rounded:
 - 7A. Leaflets narrowly linear; stipules
similar to the leaflets in size and
shape 104a. *L. involucrata* subsp. *involucrata*
 - 7B. Leaflets oblanceolate to narrowly
oblanceolate; stipules distinctly
narrower and/or shorter than the
leaflets 104d. *L. involucrata* subsp. *peduncularis*

102. *L. racemiflora* B-E. van Wyk in Bothalia 19: 7 (1989d)
[Appendix 24]. Type: South Africa: Cape Province, Clanwilliam
District, Bokwater, W of Clanwilliam, Acocks 15171 (PRE!, holo.;
K!, iso.).

This species is easily distinguished from all others of the
section by the long, many-flowered racemose inflorescence (Figure
5.17). It is known only from the type collection, which is from
near Clanwilliam in the western Cape (Map 5.29).

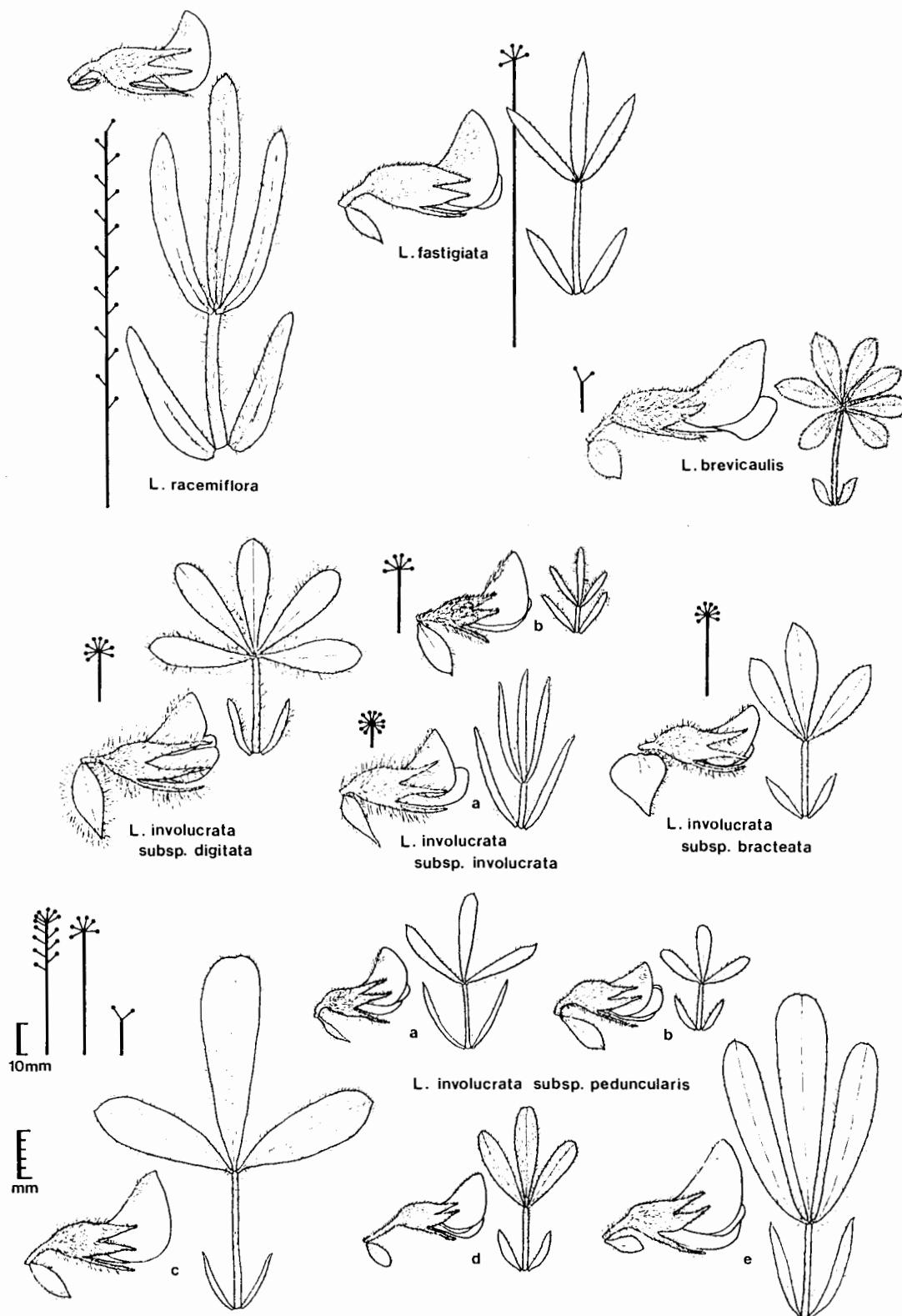


Figure 5.17. Leaves, inflorescence structure and flowers of the species of section Polylobium. (infraspecific variations in two subspecies of *L. involucrata* are indicated by numbers).

103. L. fastigiata (E. Mey.) B-E. van Wyk comb. nov. Type: South Africa, Cape Province, "Auf der Kapschen Fläche [Cape Flats] bay Zeekoevallai [Zeekoeivlei]", Ecklon s.n. (S!, original Plantae Ecklonae label, lecto., here designated).

[Note: the specimen in S with an Enumeratio label (Ecklon & Zeyher 1298) has been annotated by Meyer as "Crotalaria fastigiata mihi" and probably represents a duplicate of the original collection by Ecklon].

Crotalaria fastigiata E. Mey. in Linnaea 7: 152 (1832). Type as above.

Polylobium fastigiatum (E. Mey.) Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 183 (1836); D. Dietr., Syn. pl. 4: 962 (1841). Type as above.

Polylobium mundianum Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 183 (1836); D. Dietr., Syn. pl. 4: 962 (1841), as "P. mundtianum". Type: South Africa, Cape Province, Swellendam, Mund s.n. sub Ecklon & Zeyher 1299 (S!, lecto., designated here).

? Telina angustifolia E. Mey., Comm. Pl. Afr. Austr. 1(1): 70 (1836). Type: South Africa, Cape Province, Albany, Drège s.n. (B+). (No isotypes found).

Lotononis angustifolia (E. Mey.) Steud., Nom. Bot. 2(2): 73 (1841); Harv. in Harv. & Sond., Fl. Cap. 2: 54 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 297 (1913). Type as above.

[Note: it is strange that this name has been adopted by both Harvey and Dümmer despite the fact that it is not the oldest. Furthermore, neither Bentham nor Harvey saw the type of Telina angustifolia and both listed the latter as a doubtful synonym].

Lotononis secunda (Thunb.) Benth. sensu Benth. in Hook., Lond. J. Bot. 2: 603 (1843), non Ononis secunda Thunb. Type as for Ononis secunda Thunb.

[Note: the type of O. secunda Thunb. is a form of Lotononis involucrata subsp. peduncularis, q.v. Bentham did not study the Thunberg collection and apparently assumed Ononis secunda to be the same species as Crotalaria fastigiata E. Mey.].

L. fastigiata may be confused with L. involucrata subsp. peduncularis, particularly forms of the latter with long peduncles (such as Polylobium angustifolium Eckl. & Zeyh., see below). It may be distinguished by the erect flowering branches, the much longer peduncles, the larger flowers and the shape and texture of the leaflets and stipules (Figure 5.17). There are few recent collections of this species but it has been recorded from several localities around the Cape Peninsula and the distribution seems to extend towards Swellendam (Map 5.29).

Vouchers: Bolus 4867; Compton 4851; Hugo 2610; Salter 2955, 4938, 7930; Taylor 4292.

104. L. involucrata (Berg.) Benth.

L. involucrata represents a very variable complex and deserves more detailed study. The major forms may be considered specifically distinct but are here treated as subspecies until clear evidence for a less conservative approach becomes available. Some of the variation in the species is illustrated in Figure 5.17.

104a. subsp. involucrata

L. involucrata (Berg.) Benth. in Hook., Lond. J. Bot. 2: 602 (1843), pro parte, excl. syns. Ononis involucrata L.f., Ononis aspaltoides DC. and Polylobium angustifolium Eckl. & Zeyh.; Harv. in Harv. & Sond., Fl. Cap. 2: 56 (1862), pro parte, excl. syns.; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 301 (1913). Type: South Africa, "e Cap. b. sp.", Grubb s.n. sub Herb. Bergius 236.51 (SBT!, holo.).

Ononis involucrata Berg., Descr. pl.: 213 (1767), non L.f., Suppl. pl.: 324 (1781), neq Murray, Syst. veg. ed. 13: 652 (1784), neq Gmelin, Syst. nat. 2(2): 1098 (1792), neq Thunb., Prodr. pl. Cap.: 130 (1800), Fl. Cap.: 587 (1823), neq DC., Prodr. 2: 167 (1825). Type as above.

Anthyllis involucrata (Berg.) L., Mant. pl. alt.: 265 (1771). Type as above.

Crotalaria involucrata (Berg.) E. Mey. in Linnaea 7: 152 (1832). Type as above.

Polylobium involucratum (Berg.) Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 182 (1836), pro parte; D. Dietr., Syn. pl. 4: 962 (1841). Type as above.

Lipozygis involucrata (Berg.) E. Mey., Comm. Pl. Afr. Austr. 1(1): 78 (1836); Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845). Type as above.

Aspalathus laxata L., Mant. pl. alt.: 263 (1771), synon. nov. Type: South Africa, "Cap. b. Spei rupibus", Tulbagh collection (T. no. 35) sub LINN 893.45 (LINN!, lecto., designated here).

Polylobium tenuifolium Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 182 (1836), non Lotononis tenuifolia (Eckl. & Zeyh.) Dümmer. Type: South Africa, Cape Province, "Klynriviersberge" [Caledon district], "Hottentottshollandsberge" and "Winterhoeksberge" near "Tulbagh", Ecklon & Zeyher 1295 (S!, smaller specimen on sheet with two specimens, lecto., here designated; BOL!, partly, K!, Herb. Benth. specimen, M!, S!, SAM!).

The distinction between L. involucrata and L. peduncularis is a problem of long standing and the exact limit between the two has been differently interpreted by all previous authors. Both have been included under L. involucrata by all except Dümmer (1913), mainly because no-one seems to have studied the original type specimen of Ononis involucrata in the Bergius collection.

This subspecies usually occurs at higher altitudes and has a fairly wide distribution in the south-western Cape (Map 5.30). The most useful and reliable diagnostic characters are the shape

of the leaflets and the relative size of the stipules (Figure 5.17). The leaflets are narrowly oblong to linear, and the stipules are similar to the leaflets in size and shape. In all three the other subspecies, the stipules are shorter or narrower than the leaflets.

Vouchers: Acocks 24408; Boucher 4487; Mauve & Hugo 95; Oliver 4354; Walters 314.

104b. subsp. bracteata B-E. van Wyk, subsp. nov. Haec subspecies a typo differt bracteis late ovatis, et forma magnitudineque foliolorum stipularumque. Foliola sunt anguste oblanceolata (non lineares) et stipuli valde minori foliolis.

This subspecies differs from the type in the broadly ovate bracts and the size and shape of the leaflets and stipules. The leaflets are narrowly oblanceolate (not linear) and the stipules are much smaller than the leaflets.

Type: South Africa, Cape Province, Bredasdorp Division, Potteberg, Esterhuysen 23321 (BOL!, holo.).

Subsp. bracteata can easily be distinguished by the broadly ovate, often cordate bracts (Figure 5.17). The size and shape of the leaflets and stipules are similar to that of subsp. peduncularis. The few collections that are known are from the Bredasdorp district in the south-western Cape (Map 5.30).

Voucher: Bean & Viviers 2032.

104c. subsp. digitata B-E van Wyk, subsp. nov. Haec subspecies a typo differt foliolis 5- ad 8-foliolatis (non semper 3-foliolatis), vestitura foliolum clare alba atque calyce et pedunculis longioribus. Etiam forma magnitudineque foliolorum (late oblanceolatis valde maioribus typo) differt. Stipulae valde minores sunt foliolis (non eis similes ut in typo).

This subspecies differs from the type in the 5- to 8-foliolate leaflets (not consistently 3-foliolate), the distinctly white vestiture of the leaflets and calyx and the longer peduncles. It also differs in the shape and size of the leaflets (broadly oblanceolate and much larger than in the type). The stipules are much smaller than the leaflets (not similar to the leaflets as in the type).

Type: South Africa, Cape Province, between Worcester and Robertson, c. 1 km along turn-off to Eilandia, B-E. van Wyk 2873 (PRE!, holo.; BOL!, GRA!, JRAU!, K!, M!, MO!, NEB!, SAAS!, STE!, iso.).

Subsp. digitata is a very distinct taxon and may prove to be specifically distinct when the full range of variation in the morphology of the fruit of other subspecies becomes known. In subsp. digitata, the pods are very small, tardily dehiscent and scarcely longer than the calyx. The predominantly 5- to 8-foliolate leaves (Figure 5.17) and the long white hairs on the leaflets and calyx are the most obvious and reliable diagnostic characters. The subspecies is known from only one locality near Robertson in the south-western Cape (Map 5.30).

Vouchers: Granby 186; Van Wyk 2704, 2705.

104d. subsp. peduncularis (E. Mey.) B-E. van Wyk comb. nov. et stat. nov. Type: South Africa: Cape Province, near Paarl, Drège s.n. a (S!, lecto., designated here; K!, MO!); Groenekloof [3318 CB], Drège s.n. b (BM!, K!).

Lotononis peduncularis (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 602 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 56 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 303 (1913), excl. syn. Ononis umbellata L. Type as above.

Lipozygis peduncularis E. Mey., Comm. Pl. Afr. Austr. 1(1): 79 (1836). Type as above.

Polylobium pedunculare (E. Mey.) Benth. in Ann. Wien. Mus. 2: 142 (1839); D. Dietr., Syn. pl. 4: 963 (1941). Type as above.

L. peduncularis (E. Mey.) Benth. var. meyeri Harv. in Harv. & Sond., Fl. Cap. 2: 56 (1862). Type as above.

Ononis involucrata auct. non. Berg.: L.f., Syn. pl.: 324 (1782); Murray, Syst. veg. ed. 13: 652 (1784); Gmelin, Syst. nat. 2(2): 1098 (1792); Thunb., Prodr. pl. Cap.: 130 (1800), Fl. Cap.: 587 (1823); DC., Prodr. 2: 167 (1825).

Ononis umbellata L. sensu Thunb., Prodr. pl. Cap.: 130 (1800), Fl. Cap.: 587 (1823).

[Note: the specimen named O. umbellata in the Thunberg herbarium (THUNB-UPS 16654) belongs here and is not O. umbellata L. (the latter species is found under the name O. strigosa in the Thunberg herbarium)].

Ononis secunda Thunb., Prodr. pl. Cap.: 130 (1800), Fl. Cap.: 587 (1823); DC., Prodr. 2: 167 (1825), non Lotononis secunda sensu Benth. Type: South Africa, "e Cap. b. Spei", Thunberg s.n. sub THUNB-UPS 16641 (UPS!, lecto., designated here).

Lotononis peduncularis (E. Mey.) Benth. var. secunda (Thunb.) Harv. in Harv. & Sond., Fl. Cap. 2: 56 (1862). Type as for Ononis secunda Thunb.

? Ononis asphaltoides DC., Prodr. 2: 167 (1825). Based on Anthyllis asphaltoides Burm. Type not seen.

Polylobium angustifolium Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 182 (1836); D. Dietr., Syn. pl. 4: 962 (1841), non Lotononis angustifolia (E. Mey.) Steud. Type: South Africa, Cape Province, Groenekloof [Mamre, near Cape Town], Ecklon & Zeyher 1297 (S!, specimen with handwritten label and Enumeratio label, lecto., designated here; S!, TCD!).

Lotononis tenuifolia (Eckl. & Zeyh.) Dümmer sensu Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 302 (1913), non Polylobium tenuifolium Eckl. & Zeyh. Type as for Polylobium tenuifolium Eckl. & Zeyh.

[Note: Dümmer described subsp. peduncularis and cited numerous specimens that belong to this subspecies, but for some reason he also cited P. tenuifolia Eckl. & Zeyh. (the isotype in K is annotated by him)].

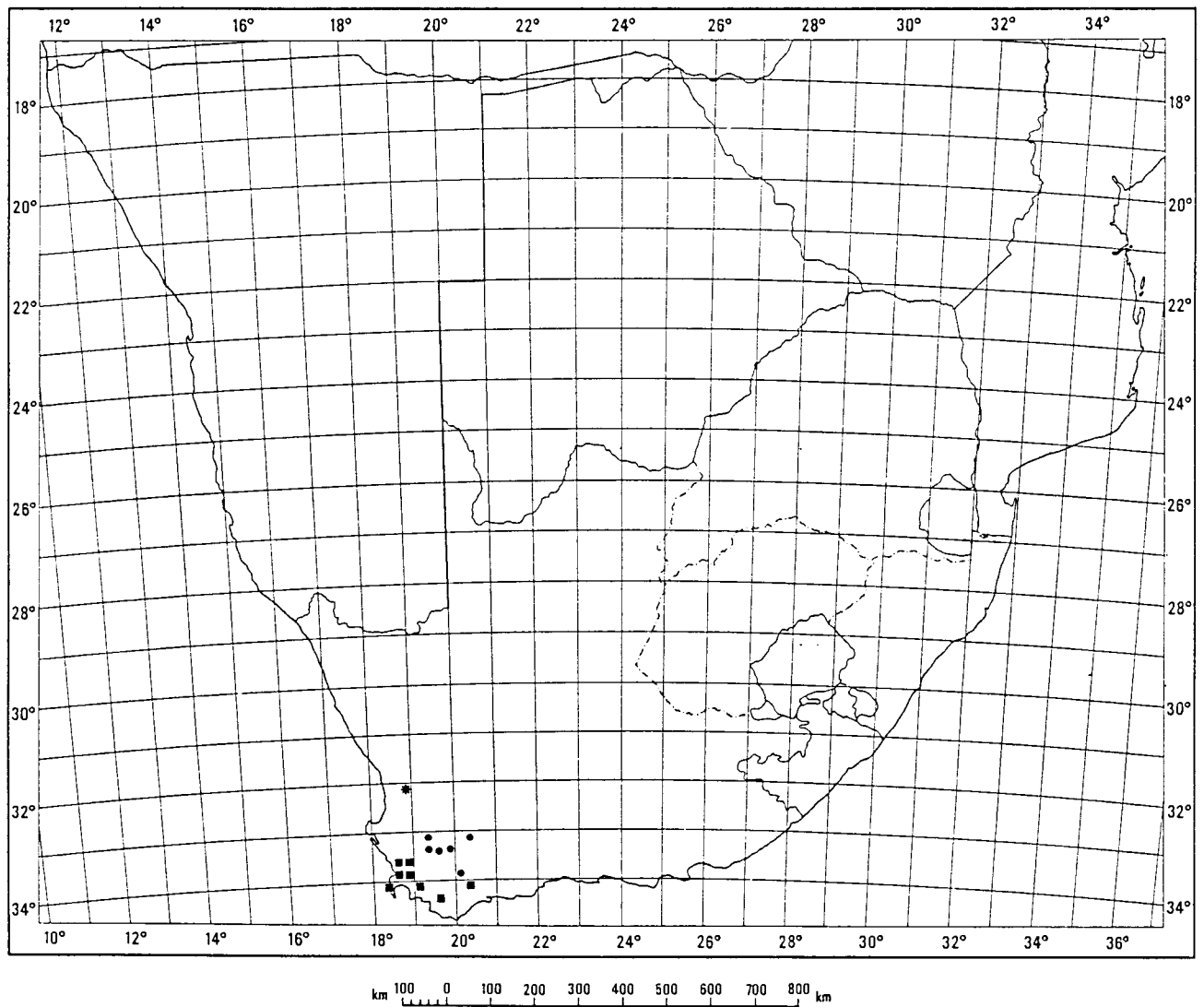
This subspecies shows considerable regional variation and some of the extreme forms are illustrated in Figure 5.17 (as a, b, c, d & e). It may be distinguished from subsp. involucrata by the shape and size of the leaflets and stipules and the distinctly pedunculate inflorescences. The known geographical distribution of the subspecies is shown in Map 5.31.

Vouchers: Barker 1686; Boucher 448; Compton 13801; Grobbelaar 2748; Taylor 7342.

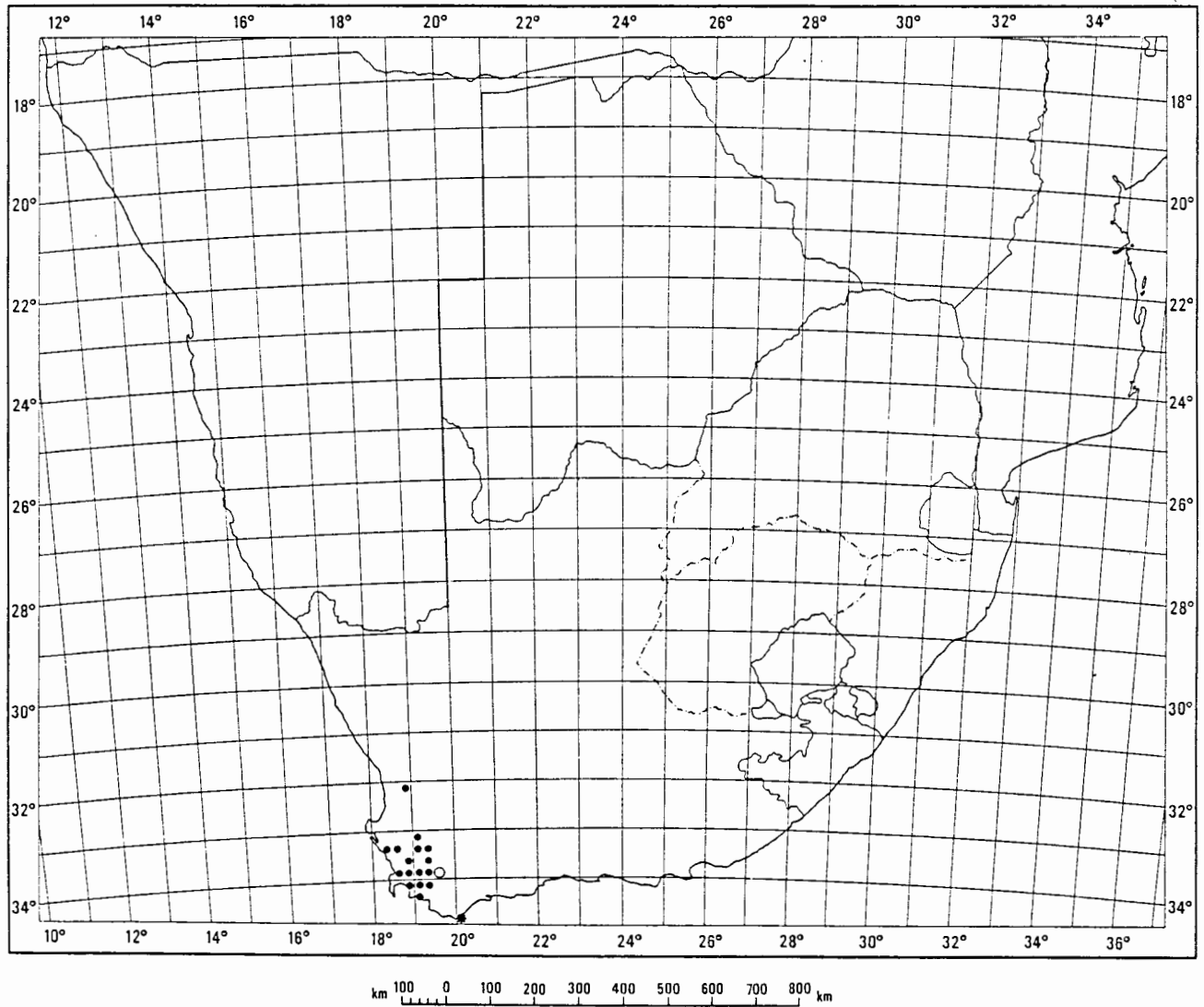
105. *L. brevicaulis* B-E. van Wyk in S. Afr. J. Bot. 53: 161 (1987). Type: South Africa, Cape Province, Laingsburg district, Tweedside, Compton 22867 (NBG!, holo.; NBG!, iso.).

A distinct and somewhat anomalous species with an unusual habit and dimorphic, 5- to 8-digitate and densely sericeous leaves (Figure 5.17). Van Wyk (1987b, Appendix 18) discussed the uncertain affinities of the species but the underground parts and the chromosome number were not known at the time. The woody caudex, flower structure, paired stipules and chromosome number of $2n = 28$ suggest that it is correctly placed here. The known geographical distribution is shown in Map 5.29.

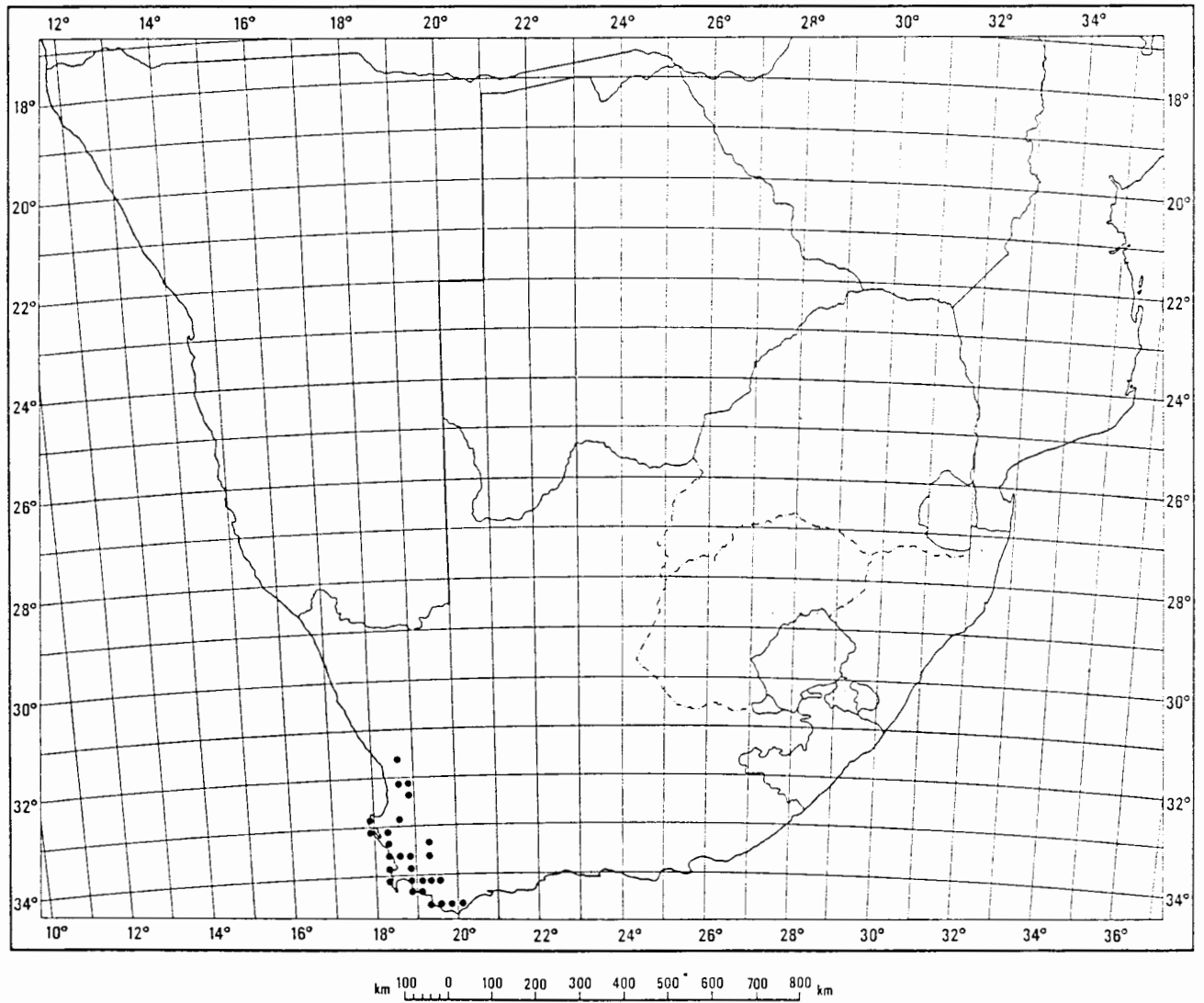
Vouchers: Barker 3025; Levyns 1502, 4610; Oliver 3496; Van Wyk 2212--2226.



Map 5.29. The known geographical distribution of *L. racemiflora* (*), *L. fastigiata* (■) and *L. brevicaulis* (●).



Map 5.30. The known geographical distribution of *L. involucrata* subsp. *involucrata* (●), *L. involucrata* subsp. *bracteata* (*) and *L. involucrata* subsp. *digitata* (○).



Map 5.31. The known geographical distribution of *L. involucrata* subsp. *peduncularis* (●).

Section 12. Lotononis

Lotononis Eckl. & Zeyh., Enum. Pl. Afr. Austr. 176 (1836); Steud., Nom. Bot. 2(2): 850 (1840).

Lotononis section Telina (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 599 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 48 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 279 (1913), synon. nov.

Telina E. Mey. section 3. Chasmoneae E. Mey., Comm. Pl. Afr. Austr. 1(1): 69 (1836).

Note: This group closely agrees with Ecklon & Zeyher's (1836) original concept of Lotononis. Since L. prostrata is also the type species of the broadened generic concept (Bentham 1843), the name Telina is here reduced to synonymy.

Prostrate or procumbent perennial shrublets. Mature parts sparsely to densely pubescent, sometimes sericeous. Leaves alternate, digitately trifoliolate, variable in size and shape, usually densely pubescent at least on the lower surface. Stipules paired or single at each leaf base (when paired, then the two of each pair dissimilar in size and shape), small and linear to lanceolate, or large and ovate to broadly ovate, rarely inconspicuous or absent. Inflorescences almost invariably single-flowered (1- to several-flowered only in one species), on long slender leaf-opposed peduncles; bracts very small, linear to oblanceolate; bracteoles absent. Flowers large, yellow or blue,

never cleistogamous. Calyx subequally lobed, with the upper and lateral lobes on either side fused a little higher up in pairs, the lower lobe rarely narrower than the upper ones (and then only slightly so), pubescent. Standard very large, much longer than the keel, broadly ovate to orbicular; mostly glabrous but with at least a line of hairs dorsally along the middle; claw short, without callosities; lamina very large, usually conspicuously striated; apex obtuse to emarginate. Wing petals oblong to broadly obovate, longer than the keel, glabrous. Keel petals very small, half oblong-elliptic, curved; apex shortly but distinctly beaked; glabrous. Anthers dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the carinal anther intermediate or similar to the dorsifixed anthers. Pods sessile, ovoid to broadly oblong, much inflated (except in one species), thick-walled (except in one species), upper suture distinctly verrucose, dehiscent (except in two species), many-seeded; funicles variable, exceptionally long in one species. Seeds 1,5--2 mm in diameter, variable in shape, often with the radicular lobe conspicuous, testa distinctly tuberculate. Chromosome base number 7 ($2n = 28$). (Figure 5.18).

A total of about 11 species, with a restricted distribution in the south-western, southern and south-eastern Cape Province (Maps 5.32 and 5.33). Some of the species are poorly known and appear to be rare or at least overlooked.

Diagnostic characters: large flowers that are borne singly at the ends of long slender peduncles is a useful and distinctive character for the section. The standard petal is always much larger than the small, acute keel. A similar flower structure is found in the section Polylobium, but in section Lotononis, however, there is a much larger size difference between the standard and keel. It seems reasonable to assume that the slender, single-flowered condition is derived from a many-flowered raceme, as is found in some robust specimens of L. varia. Some species from other sections have the same inflorescence structure, presumably as a result of convergence. Examples are L. minor (section Krebsia), L. dissitinodis (section Aulacanthus), L. azureoides (section Aulacanthus) and L. solitudinis (section Listia). These species can be distinguished by other characters: L. minor by the smooth seeds and uninflated pods; L. dissitinodis by the short peduncle and woody habit; L. azureoides by the terminal rather than leaf-opposed inflorescences and the relatively large keel; L. solitudinis by the presence of bracteoles, the relatively large keel and the "stoloniferous" habit.

Key to the species of section Lotononis:

1A. Flowers yellow:

2A. Pods ovoid, not more than twice as long as
the calyx, apex gradually tapering to the
style 114. L. elongata

2B. Pods oblong, much longer than the calyx,
apex rounded when mature:

3A. Leaves densely silky on both surfaces, the
surface of the lamina not visible:

4A. Leaflets acicular 108. L. gracilifolia

4B. Leaflets lanceolate to obovate 106. L. lamprifolia

3B. Leaves sparsely silky or pubescent, the surface
of the lamina visible:

5A. Leaves conspicuously netted-veined;
south-eastern Cape (Map 5.32) 107. L. acuminata

5B. Leaves not netted-veined;
south-western Cape (Map 5.32) 110. L. prostrata

1B. Flowers blue:

6A. Leaflets densely silky on the upper surface,
the surface of the lamina not visible 109. L. argentea

6B. Leaflets glabrous or minutely pubescent on
the upper surface, the surface of the lamina
clearly visible:

- 7A. Inflorescences (at least some of them) 2- or more-flowered; leaflets \pm glabrous, except for a few minute hairs on the lower surface 112. *L. varia*
- 7B. Inflorescences invariably 1-flowered; leaflets pubescent, at least on the lower surface:
 - 8A. Leaflets and calyx with long spreading hairs 111. *L. villosa*
 - 8B. Leaflets and calyx with short appressed hairs:
 - 9A. Stipules invariably single at the base of each petiole; leaflets with recurved apices; pods flat (not laterally inflated) 113. *L. complanata*
 - 9B. Stipules paired, at least on some of the lower leaves; leaflet apices straight; pods laterally inflated:
 - 10A. Leaflets linear, <2 mm wide; calyx lobes narrowly oblong; pods densely and minutely strigillose 116. *L. filiformis*
 - 10B. Leaflets oblanceolate or narrowly elliptic, > 2 mm wide, calyx lobes triangular; pods \pm glabrous or with sparse spreading hairs 115. *L. azurea*

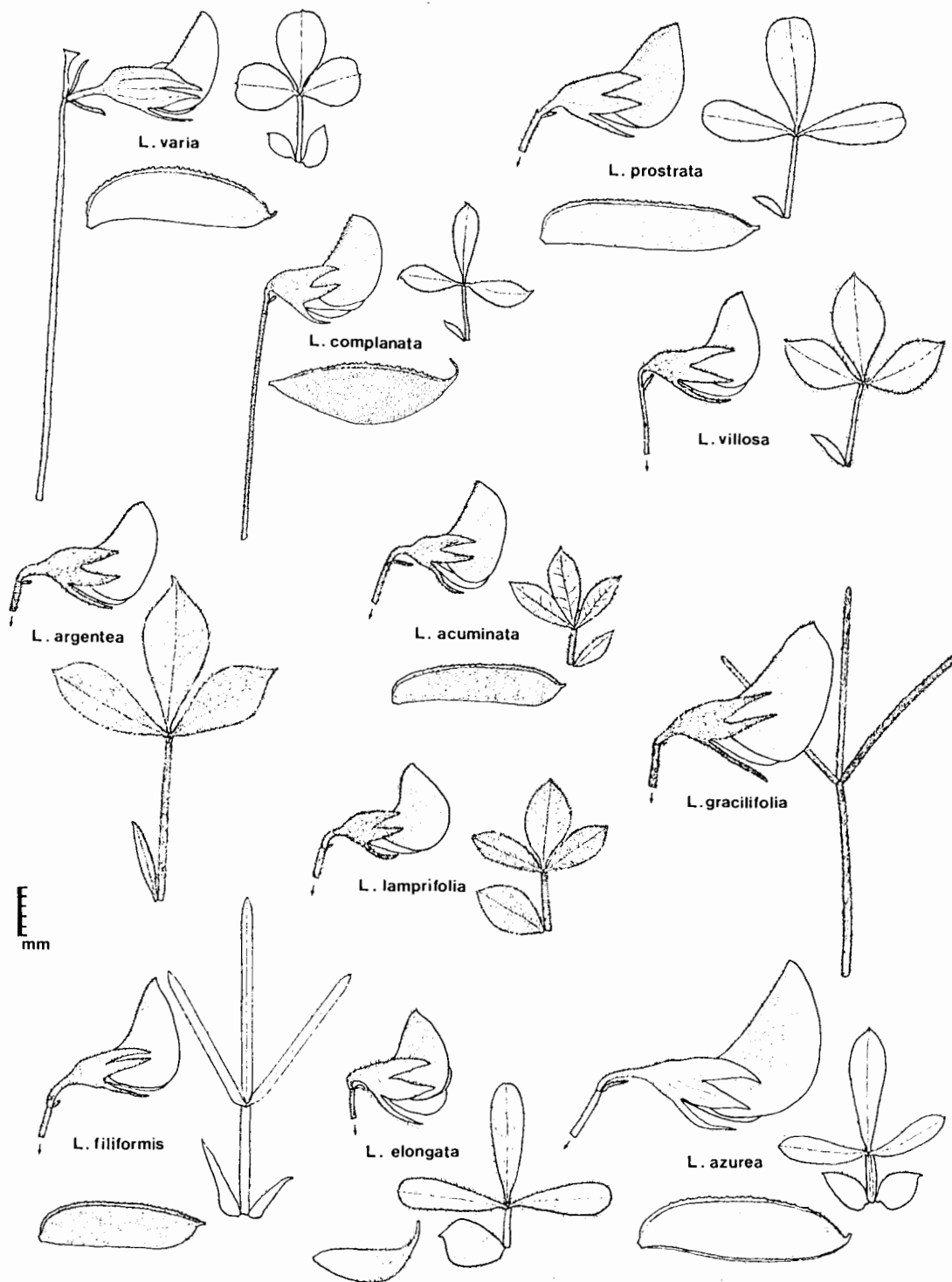


Figure 5.18. Leaves, flowers and pods of the species of section Lotononis.

106. *L. lamprifolia* B-E. van Wyk in Bothalia 19: 4 (1989)
[Appendix 20]. Type: South Africa, Cape Province, Riversdale and Swellendam Districts, between Muiskraal and Lemoenshoek, Barker 7374 (NBG!, holo.).

This poorly known species is closely related to *L. argentea* but can be distinguished by the yellow flowers, the shape of the stipules (Figure 5.18) and standard petal, as well as the more diffuse habit. It is known only from the type collection (Map 5.32).

107. *L. acuminata* Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 176 (1836); Benth. in Hook., Lond. J. Bot. 2: 601 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 54 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 297 (1913). Type: South Africa, Cape Province, "Zwartkopsrivier" [near Port Elizabeth], Ecklon & Zeyher 1276 (S!, with handwritten label by Ecklon, lecto., designated here; C!, M!, S!, SAM!, TCD!, islecto.).

A distinct species, easily recognised by the conspicuous venation of the leaflets (clearly visible on the lower surface) and the acute leaflet apices (Figure 5.18). The very localized distribution area in the south-eastern Cape is given in Map 5.32.

Vouchers: Cowling 912; Gillett 2433; Van Wyk 2580--2583; Vlok 1701; Zeyher 868.

108. *L. gracilifolia* B-E. van Wyk in Bothalia 19: 3 (1989)
[Appendix 20]. Type: South Africa, Cape Province, Laingsburg
District, Tweedside, Barker 7482 (NBG!, holo., NBG!, iso.).

A distinct species with large yellow flowers and slender acicular leaves. (Figure 5.18). Apparently very rare and known only from a single collection near Laingsburg in the Cape Province (Map 5.32).

109. *L. argentea* Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 176
(1836); Benth. in Hook., Lond. J. Bot. 2: 601 (1843); Harv. in
Harv. & Sond., Fl. Cap. 2: 54 (1862); Dümmer in Trans. Roy. Soc.
S. Afr. 3(2): 297 (1913). Type: South Africa, Cape Province,
"Zwartkopsrivier" [near Port Elizabeth], Ecklon & Zeyher 1276
(S!, with handwritten label by Ecklon, lecto., designated here;
C!, M!, S!, SAM!, TCD!, islecto.).

L. argentea is known only from a few collections along the northern parts of the Outeniqua Mountain range (Map 5.32) and appears to be rare or at least overlooked. The densely silky and shining vestiture of the leaves (Figure 5.18) is similar to that of the following species but the blue colour of the flowers is a useful character to separate *L. argentea* from the yellow-flowered *L. lamprifolia*.

Vouchers: Levyns 549; Middlemost 2043.

110. L. prostrata (L.) Benth. in Hook., Lond. J. Bot. 2: 600 (1843), excl. var. glabrior; Harv. in Harv. & Sond., Fl. Cap. 2: 53 (1862), excl. syn. Q. elongata Thunb.; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 296 (1913). Type: South Africa: "Cap. b. Spei", (LINN 931.35, lecto., microfiche!, designated here).

Lotus prostratus L., Syst. nat. ed. 10: 1179 (1759), Sp. pl. ed. 2: 1090 (1763). Type as above.

Ononis prostrata (L.) L., Mant. pl. alt.: 266 (1771); Gmelin, Syst. nat. 2(2): 1097 (1792); Thunb., Prodr. pl. Cap.: 129 (1800), Fl. Cap.: 586 (1823); DC., Prodr. 2: 166 (1825). Type as above.

Ononis heterophylla Thunb., Prodr. pl. Cap.: 129 (1800), Fl. Cap.: 586 (1823); DC., Prodr. 2: 166 (1825). Type: South Africa, "e Cap. b. Spei", Thunberg s.n. sub THUNB-UPS. 16612 (UPS!, lecto., designated here; SBT!, iso.).

Lotononis heterophylla (Thunb.) Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 177 (1836); Steud., Nom. Bot. 2(2): 73 (1841), excl. syn. Telina heterophylla E. Mey. Type as above.

L. prostrata (L.) Benth. var. heterophylla Harv. in Harv. & Sond., Fl. Cap. 2: 53 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 296 (1913). Type: South Africa, Cape Province, Tulbagh, Ecklon & Zeyher 1273 (TCD, BOL!, S!, SAM!).

Crotalaria vexillata E. Mey. in Linnaea 7: 153 (1832). Type: South Africa, Cape Province, Table Mountain and Lion's Head, Ecklon s.n. (S!, lecto., designated here).

Lotononis vexillata (E. Mey.) Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 176 (1836); Steud., Nom. Bot. 2(2): 73 (1841). Type as above.

L. prostrata is the only yellow-flowered species of the section that occurs in the south-western parts of the Cape Province (Map 5.32) and it is rarely confused with other species. It is superficially similar to L. elongata but can be distinguished from the latter by the much larger, oblong pods (Figure 5.18) and the much smaller habit.

Vouchers: Acocks 22749; Boucher 4470; Compton 14680; Goldblatt 5786; Salter 4753.

111. L. villosa (E. Mey.) Steud., Nom. Bot. 2(2): 73 (1841); Benth. in Hook., Lond. J. Bot. 2: 601 (1843), excl. syn. Ononis villosa Thunb.; Harv. in Harv. & Sond., Fl. Cap. 2: 54 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 297 (1913). Type: South Africa: Cape Province, "Riebekskasteel" [Riebeeck Kasteel Mountain], Drège s.n. (K!, sub Herb. Benth., lecto., designated here; K!, sub Herb. Hook., BM!, MO!, S!).

Telina villosa E. Mey., Comm. Pl. Afr. Austr. 1(1): 70 (1836). Type as above.

This species is very closely related to L. prostrata, but can readily be distinguished by the blue (not yellow) flowers and the hirsute golden hairs on the calyx, peduncle and leaves (Figure 5.18). It was previously considered to be limited to the type locality, but a few recent collections showed that it is more widely distributed (Map 5.33). Ononis villosa Thunb., cited by Benth. (1843) as a doubtful synonym of L. villosa, is a hairy form of L. azurea (q.v.).

Vouchers: Acocks 24425; Esterhuysen 16192; Johnson 298; Stephens 7029, 7030.

112. L. varia (E. Mey.) Steud., Nom. Bot. 2(2): 73 (1841); Benth. in Hook., Lond. J. Bot. 2: 601 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 54 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 297 (1913). Type: South Africa: Cape Province, "Klein Draakensteen" [Klein Drakenstein], Drège s.n. a (S!, lecto., designated here; BM!, K!, sub Herb. Benth., K!, sub Herb. Hook., MO!); "Draakensteensbergen" [Drakenstein Mountains], Drège s.n. b (K!, sub Herb. Benth., S!).

Telina varia E. Mey., Comm. Pl. Afr. Austr. 1(1): 70 (1836).
Type as above.

T. excisa (Thunb.) E. Mey. sensu E. Mey., Comm. Pl. Afr. Austr. 1(1): 70 (1836), excl. syn. Ononis excisa Thunb.

Lotononis excisa (E. Mey.) Steud., Nom. Bot. 2(2): 73 (1841), excl. syn. Thunb.

L. excisa Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845),
excl. syn. Thunb.

L. prostrata (L.) Benth. var. *glabrior* Benth. in Hook., Lond.
J. Bot. 2: 600 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 53
(1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 296 (1913).
Based on *Telina excisa sensu* E. Mey.

Lotononis stipularis Schlechter in Engl., Bot. Jahrb. 27: 147
(1900). Type: Cape Province, French Hoek Mountains, Schlechter
9237 (B+; K!, lecto., designated here; BM!, BOL!).

L. varia can be distinguished from other species of the section
by the almost glabrous leaves. It is the only species where some
of the inflorescences are usually 2-flowered (Figure 5.18).

L. varia has a restricted distribution and all the known
localities are at high altitudes in the south-western Cape (Map
5.33).

Vouchers: Barker 7164; Horrocks 21; Merriman s.n. sub BOL 6495;
Pillans 8432; Stokoe s.n. sub STE 31589.

113. *L. complanata* B-E. van Wyk sp. nov. ined. [Bothalia (in
press), Appendix 33]. Type: South Africa, Cape Province, near
Riebeeck-Wes, on Elandsberg nature reserve, Vlok 1941 (PRE!,
holo.; K!, NBG!, iso.).

This species is similar to *L. varia* but differs in the smaller habit, leaves, flowers and pods, the invariably single-flowered inflorescences (never 2- or more-flowered), the single stipules and particularly in the shape of the pods, which are quite flat and not laterally inflated as in all other species of the section (Figure 5.18). Other unique characters are the large number of seeds (pod up to 30-seeded) and the exceptionally long funicles (up to 4 mm long). *L. complanata* appears to be very rare and is known only from the type locality (Map 5.33).

Vouchers: Bowie s.n.; Van Wyk 2879.

114. *L. elongata* (Thunb.) D. Dietr., Syn. pl. 4: 960 (1847); Van Wyk in *Bothalia* 19: 32 (1989). Type: South Africa, Cape Province, "in Cap. b. Spei", Thunberg s.n. sub THUNB-UPS 16607 (UPS!, lecto., designated by Van Wyk 1989b, Appendix 21).

Ononis elongata Thunb., Prodr. pl. Cap.: 129 (1800), Fl. Cap.: 587 (1823); DC., Prodr. 2: 167 (1825); Harv. in Harv. & Sond., Fl. Cap. 2: 53 (1862), as synonym of *L. prostrata*; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 296 (1913), as synonym of *L. prostrata*. Type as above.

The diagnostic characters of this largely unknown species were given in detail by Van Wyk (1989b, Appendix 21). The habit and vestiture are similar to that of *L. azurea* and it may be confused

with the latter, but the yellow flowers and short, pointed pods (Figure 5.18) are quite distinct. The species is known from a few isolated localities in the southern Cape (Map 5.32).

Vouchers: Barker 8195; Grobbelaar 1401; Lewis 3734; Van Wyk 2573; Vlok 1718, 1762.

115. L. azurea (Eckl. & Zeyh.) Benth. in Hook., Lond. J. Bot. 2: 600 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 53 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 295 (1913). Type: South Africa, Cape Province, near Krakakamma and Port Elizabeth, Ecklon & Zeyher 1262 (S!, specimen with Plantae capenses label, lecto., designated here; C!, K!, M!, S!, SAM!, TCD!).

Crotalaria azurea Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 174 (1836, Jan.). Type as above.

Ononis villosa Thunb., Prodr. pl. Cap.: 129 (1800), Fl. Cap.: 585 (1823); DC., Prodr. 2: 166 (1825), non Lotononis villosa (E. Mey.) Benth. Type: South Africa, "e Cap. b. Spei", Thunberg s.n. sub THUNB-UPS 16652 (UPS!, lecto., designated here).

Telina heterophylla E. Mey., Comm. Pl. Afr. Austr. 1(1): 69 (1836), non Ononis heterophylla Thunb., nec Lotononis heterophylla Eckl. & Zeyh. Type: South Africa, Cape Province, between Eschenbosch and Gamtoos River, Drège s.n. (S!, lecto., designated here; BM!, isolecto!).

L. azurea (Eckl. & Zeyh.) Benth. var. *lanceolata* Harv. in Harv. & Sond., Fl. Cap. 2: 53 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 295 (1913). Type as for *Ononis villosa* Thunb.

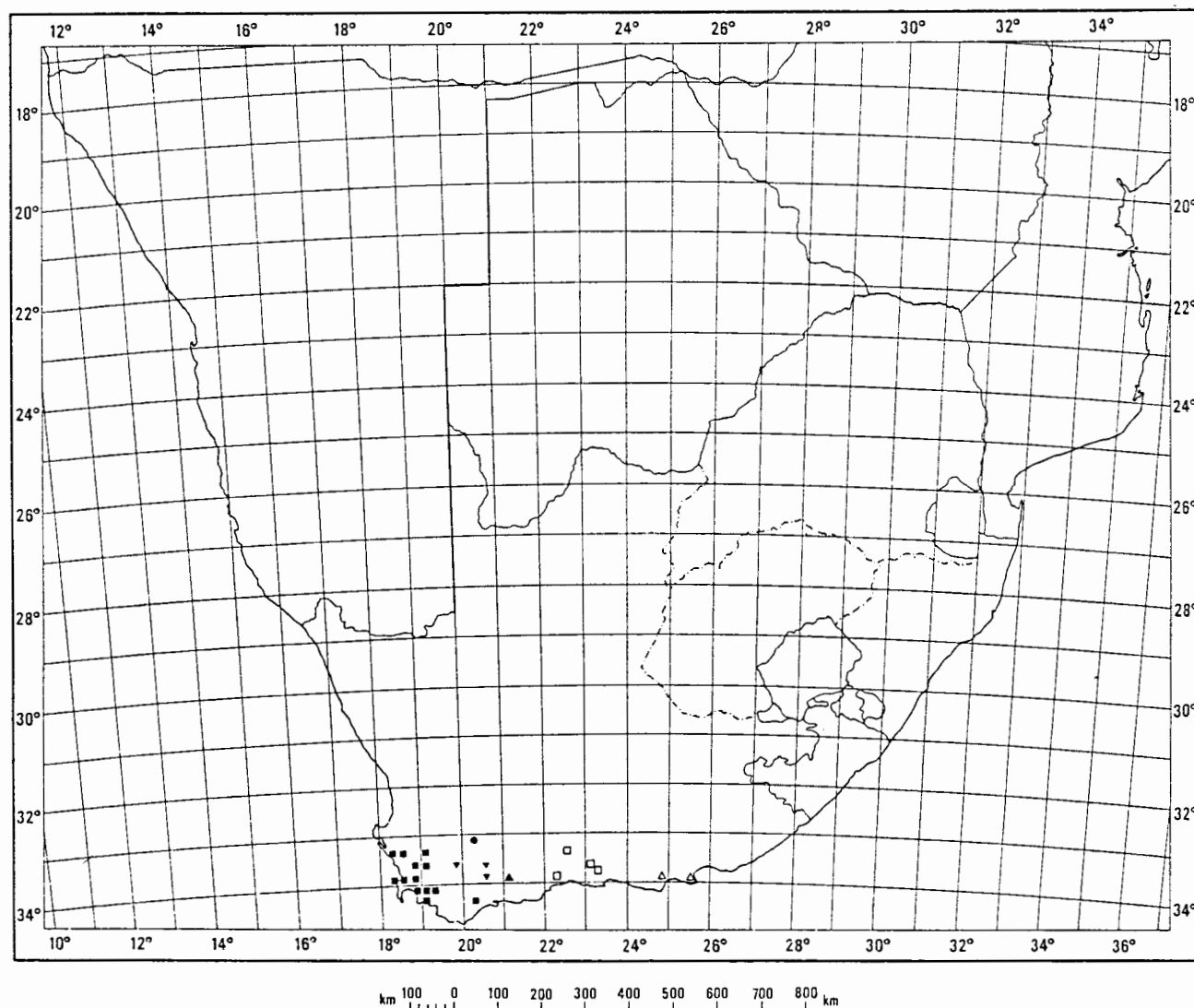
L. azurea is a well known species from the eastern parts of the Cape Province (Map 5.33). A form from the western limits of the distribution area (mostly around Humansdorp) have narrow, hairy leaflets and narrow calyx lobes and is identical to the type of *Ononis villosa* Thunb. (and Harvey's variety *lanceolata*).

Vouchers. typical form: Batten 6 (Pl.110); Hugo 1374; Olivier 1099; Rodin 1013; Sim 2671. "var. *lanceolata*": Acocks 13713, 21280; Bayliss 6779; Fourcade 721; Galpin 3920; Patterson 179.

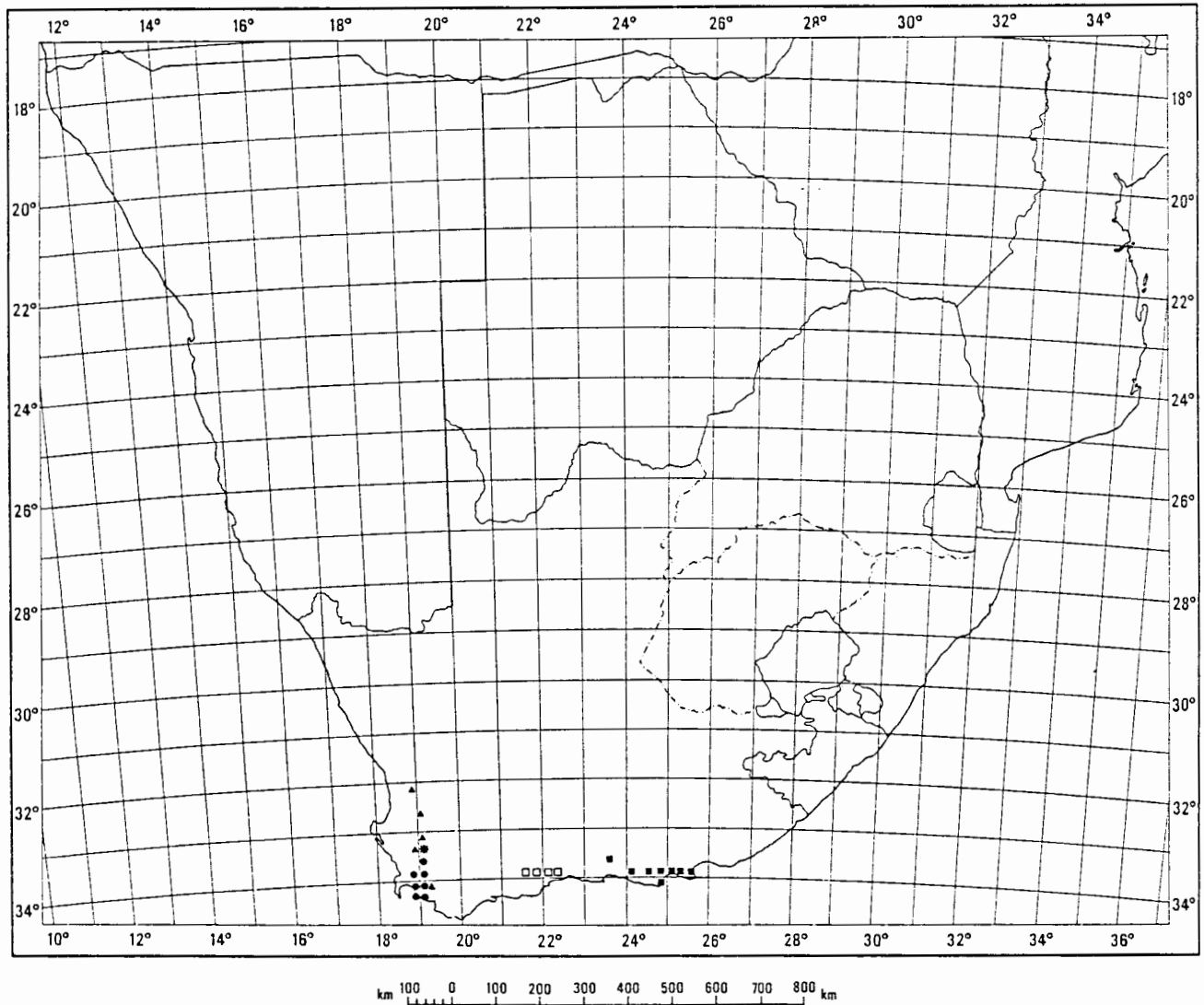
116. *L. filiformis* B-E. van Wyk sp. nov. ined. [Bothalia (in press), Appendix 33]. Type: South Africa, Cape Province, between farms Bonniedale and Woeska, Vlok 2030 (PRE!, holo.; JRAU!, K!, MO!, NBG!, SAAS, STE!, iso.).

This species is closely related to *L. azurea* but can be distinguished by the narrowly linear leaflets and the smaller, densely strigillose pods (not glabrous to sparsely hirsute as in *L. azurea*) (Figure 5.18). *L. filiformis* is known only from a few localities along the northern slopes of the Langeberg (Map 5.33).

Vouchers: Acocks 23250; Bolus 11767; Muir 2042; Van Wyk 2857.



Map 5.32. The known geographical distribution of *L. lamprifolia* (▲), *L. acuminata* (△), *L. gracilifolia* (●), *L. argentea* (▼), *L. prostrata* (■) and *L. elongata* (□).



Map 5.33. The known geographical distribution of *L. villosa* (▲), *L. varia* (●), *L. complanata* (*), *L. azurea* (■) and *L. filiformis* (□).

Section 13. Aulacanthus (E. Mey.) Benth. emend. B-E. van Wyk,
emend. nov.

Lotononis section Aulacanthus (E. Mey.) Benth. in Hook., Lond.
J. Bot. 2: 597 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 48
(1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 279 (1913).

Aulacanthus E. Mey., Comm. Pl. Afr. Austr. 1(1): 156 (1836).

Type species: L. gracilis (E. Mey.) Benth. [now L. densa (Thunb.)
Harv. subsp. gracilis (E. Mey.) B-E. van Wyk]

Note: The distinction between L. umbellata (previously included
in the section Polylobium) and species of the section Aulacanthus
is no longer clear. The subumbellate inflorescence and prostrate
habit of L. umbellata are present in several newly described
species.

Perennial shrubs or shrublets with procumbent or erect (rarely
prostrate) woody branches. Mature parts sparsely to densely
sericeous or \pm strigillose. Leaves alternate, digitately
trifoliolate, pubescent on the lower or both surfaces, more
densely so on the lower surface. Stipules single at each leaf
base or absent (rarely paired, and then only at some nodes),
linear to lanceolate, much smaller than the leaflets.
Inflorescences racemose to umbellate, (1--) 2- to

several-flowered; peduncle short and thick or long and slender, usually terminal, rarely leaf-opposed, occasionally ending in a thorn; bracts very small, inconspicuous, linear to oblanceolate; bracteoles absent. Flowers yellow, rarely pale purple or blue, never cleistogamous. Calyx with the upper and lateral lobes on either side usually fused much higher up in pairs, the lobes broadly to narrowly triangular, the lower lobe \pm equal to the upper ones. Standard \pm as long as the keel, rarely much longer (*L. dissitinodis*), broadly ovate to suborbicular; dorsally glabrous except for a line of hairs along the middle; claw short, without callosities; lamina relatively large, usually conspicuously striated, apex obtuse to emarginate. Wing petals oblong to broadly obovate, as long or shorter than the keel, rarely longer (*L. dissitinodis*); glabrous. Keel petals relatively large, rarely small (*L. dissitinodis*), half oblong-elliptic, apex obtuse, rarely \pm acute (*L. dissitinodis* & *L. viborgioides*); glabrous. Anthers dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the carinal anther intermediate, often similar to the dorsifixed anthers. Pods sessile, ovoid to broadly oblong, usually much inflated, (less so in three species), thick-walled, upper suture distinctly verrucose, lower suture usually slightly sunken, dehiscent, many-seeded; funicles relatively short. Seeds 1,5--3,5 mm in diameter, variable in shape, often with the radicular lobe conspicuous, testa invariably tuberculate. Chromosome base number 7 ($2n = 28$). (Figures 5.19 & 5.20).

A total of 11 species (one divided into four subspecies) with a restricted distribution in the western, south-western and southern parts of the Cape Province (Maps 5.34 and 5.35).

The species of Aulacanthus are all shrubs with woody perennial branches, at least at the base. The habit, leaves, vestiture and inflorescences are remarkably similar to species of Lebeckia, Wiborgia and Aspalathus. The calyx lobes are fused in pairs on either side of the calyx however, and the pods are laterally inflated and have a verrucose upper suture. The total absence of bracteoles is another useful character to distinguish species of Aulacanthus from Lebeckia, Wiborgia and Aspalathus. Stipules, if present, are single at each node (rarely paired in L. dissitinodis, and then only at flowering nodes). This group of species is closely related to the section Polylobium and differs from it mainly in the asymmetry of the stipules and in the habit. Aulacanthus is also closely related to the section Lotononis, but differs from it in the more woody habit and in the structure of the inflorescence and flower.

Key to the species of section Aulacanthus:

- 1A. Stipules totally absent, also at the insertion
of the peduncles:
 - 2A. Flowers very large, > 13 mm long 125. L. exstipulata
 - 2B. Flowers small, up to 12 mm long:
 - 3A. Upper surface of the leaflets totally
glabrous 120. L. densa
 - 3A. Upper surface of the leaflets at
least sparsely pubescent:
 - 4A. Flowers more than 4 per inflorescence ... 120. L. densa
 - 4B. Flowers 1, 2 or 3 per inflorescence:
 - 5A. Flowers 1, very rarely 2 per inflorescence;
calyx minutely and appressedly pubescent;
petioles shorter than the leaflets;
plant \pm 1 m tall 118. L. dahlgrenii
 - 5B. Flowers 1, 2 or 3 per inflorescence;
calyx with spreading hairs; petioles
as long or longer than the leaflets;
plant < 0,5 m tall 119. L. rigida
- 1B. Stipules present, at least at the insertion
of the peduncles:

6A. Flowers single on each peduncle:

7A. Standard much longer than the keel; leaflets

densely silky; flowers yellow 117. L. dissitinodis

7B. Standard as long as the keel; leaflets

minutely strigillose; flowers blue 126. L. azureoides

6B. Flowers (2--) 3 to several on each peduncle:

8A. Flowers pale purple 128. L. purpurescens

8B. Flowers yellow:

9A. Inflorescence umbellate:

10A. Flowers < 7 mm long; pods ovate 124. L. nutans

10B. Flowers > 8 mm long; pods oblong ... 127. L. umbellata

9B. Inflorescence racemose:

11B. Flowers 3 on each peduncle (rarely up
to 5); base of standard petal cuneate;

flowering branches > 0,5 m long 123. L. acocksii

11A. Flowers 6 or more on each peduncle (rarely

fewer than 5); base of standard petal cordate;

flowering branches < 0,5 m long:

12A. Flowers < 8 mm long; petiole

shorter than the leaflets 121. L. viborgioides

12B. Flowers > 9 mm long; petiole much

longer than the leaflets 122. L. comptonii

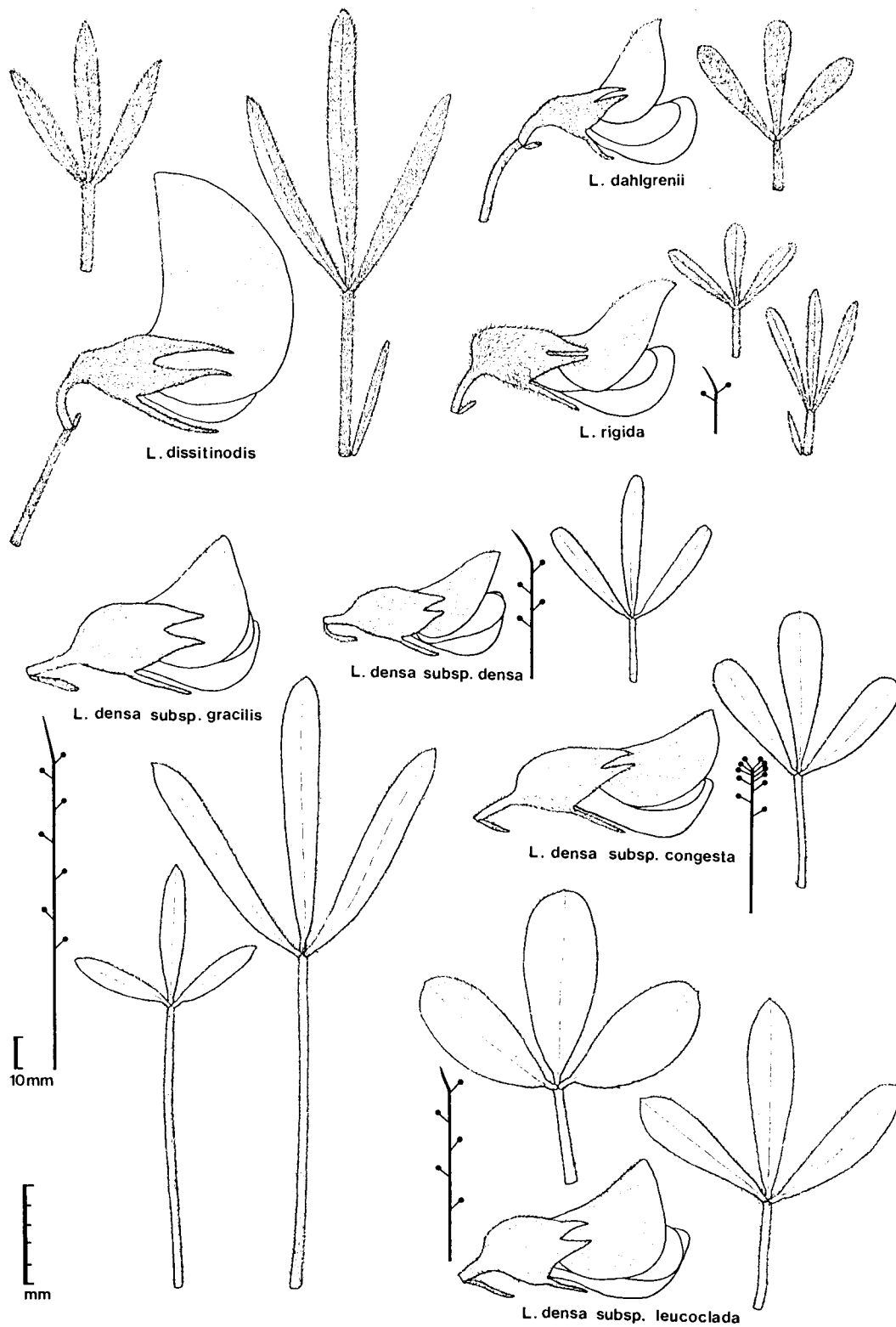


Figure 5.19. The leaves, inflorescence structure and flowers of some species of the section Aulacanthus.

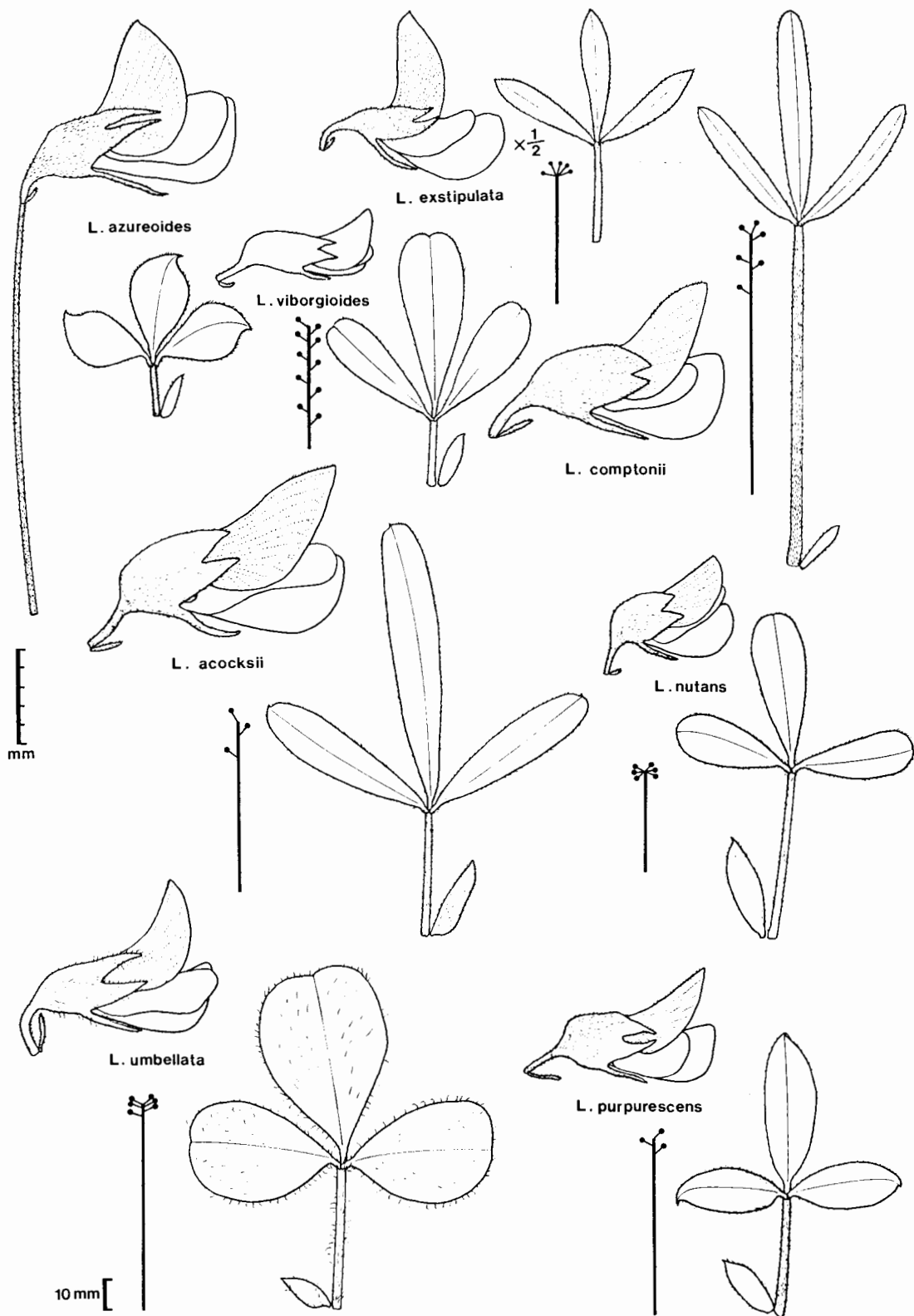


Figure 5.20. The leaves, inflorescence structure and flowers of some species of the section *Aulacanthus*.

As shown in Part 3.2, the relationships between the species are not clear and the arrangement presented here is based only on morphological similarities. The seven basic groups described below nevertheless give some idea of the patterns of variation in the section.

Group A

Structure of the corolla as in the section Lotononis; stipules absent except at flowering nodes; pods apparently not much inflated. One species, L. dissitinodis.

Group B

Closely related to the following, but differs in the rigid, woody habit, the densely silky vestiture of the leaflets and the small number of flowers per inflorescence. Two species, L. dahlgrenii and L. rigida.

Group C

Racemose and usually many-flowered inflorescences; adaxial surface of the leaflets sparsely hairy or usually glabrous; petioles relatively long (often exceptionally long); lower suture of the pods deeply sunken; stipules single at each node (totally absent in L. densa). Five species, L. densa, L. viborgioides, L. comptonii, L. acocksii and L. nutans.

Group D

Thickened primary root as in the section Polylobium but with persistent woody branches; stipules absent; flowers very large. One species, L. exstipulata.

Group E

Previously misplaced in the section Lotononis due to the single-flowered inflorescences, but these are terminal and not leaf-opposed as in section Lotononis; structure of the flowers similar to those of L. exstipulata but blue, not yellow; leaflet apices recurved; habit poorly known but apparently a prostrate woody shrub. One species, L. azureoides.

Group F

Differs from group C only in the prostrate, suffrutescent habit (persistent woody branches are present in old specimens, however) and in the flat oblong pods. One species, L. umbellata.

Group G

No obvious affinities; the habit is suffrutescent but some persistent woody branches are present in old specimens; corolla structure different from all other species; flowers pale purple (not pink or blue); leaflet apices recurved. One species, L. purpurescens.

117. *L. dissitinodis* B-E. van Wyk in *Bothalia* 18: 33 (1988)
[Appendix 19]. Type: South Africa, Cape Province, 14 miles [22,4 km] SSE of Laingsburg, Acocks 20502 (PRE!, holo.; BOL!, M!, NBG!, iso.).

This species differs from all others of the section in the large standard petal, the small keel petals and the linear, densely silky leaflets (Figure 5.19). The distribution appears to be limited to the Swartberg Mountains (Map 5.34).

Vouchers: Bohnen 8793; Levyys 7414; Viviers & Vlok 70; Wurts 1520.

118. *L. dahlgrenii* B-E. van Wyk in *Bothalia* 18: 33 (1988)
[Appendix 19]. Type: South Africa, Cape Province, Ladismith Div., near top of Roodeberg Pass, Lewis 4709 (NBG!, holo.).

L. dahlgrenii is a rigid woody shrub of up to 1,2 m high and differs from the closely related *L. rigida* in the taller habit, the thorny lateral branches, the longer, more widely spaced and single-flowered inflorescences, the sparsely puberulous calyx and details of the flower and fruit (Figure 5.19). This species is known only from two localities in the Little Karoo (Map 5.34).

Vouchers: Bond 263; Lewis 1211, Van Wyk 2864.

119. *L. rigida* (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 597 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 50 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 288 (1913). Type: South Africa, Cape Province, "Zwartland", Drège s.n. a (B+, no isotypes found); at "Mordkuil" [Moordkuil, near Worcester], Drège s.n. b (K!, lecto., designated here; MO!, S!).

Aulacanthus rigidus E. Mey., Comm. Pl. Afr. Austr. 1(1): 157 (1836). Type as above.

A rigid, widely branched shrublet of up to 0,6 m high. It is similar to *L. dahlgrenii* but can be distinguished by the 2- or 3-flowered inflorescences and the spreading hairs on the calyx (Figure 5.19). The distribution appears to be limited to the vicinity of Worcester and Robertson, where it is relatively common (Map 5.34).

Vouchers: Leipoldt 3196; Van Breda 1691; Van der Merwe 2866; Van Wyk 2464--2467, 2700, 2876; Walters 813, 1816.

120. *L. densa* (Thunb.) Harv.

A variable complex here treated as four geographically isolated subspecies. *L. leucoclada* and *L. gracilis* were formerly recognised as distinct species, but the differences between them are slight and the subspecific rank gives a better reflection of relationships within the section *Aulacanthus*.

Key to the subspecies of *L. densa*:

1A. Upper surface of the leaflets

sparsely pubescent 120b. subsp. *leucoclada*

1B. Upper surface of the leaflets

totally glabrous:

2A. Leaflets narrowly lanceolate to linear, apex

obtuse or acute; petiole usually much

longer than the terminal leaflet 120d. subsp. *gracilis*

2B. Leaflets oblanceolate to narrowly

oblanceolate, apex obtuse or emarginate;

petiole as long or shorter than the

terminal leaflet:

3A. Flowers separated from each other on

the rachis of the inflorescence, apex

of the rachis ending in a sharp thorn;

Pods totally glabrous 120a. subsp. *densa*

3B. Flowers subumbelately arranged on the

rachis of the inflorescence, apex of

the rachis short or absent, not ending
in a sharp thorn; pods at least
sparsely pubescent 120c. subsp. congesta

120a. subsp. densa

L. densa (Thunb.) Harv. in Harv. & Sond., Fl. Cap. 2: 52
(1862), excl. syn. Acanthobotrya decumbens. Type: South Africa,
"e Cap. b. Spei", Thunberg s.n. sub THUNB-UPS 16415 (UPS!,
lecto., designated here).

Lebeckia densa Thunb., Prodr. pl. Cap.: 122 (1800), Fl. Cap.:
562 (1823); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 330 (1913).
Type as above.

Lotononis gracilis (E. Mey.) Benth. var. brevipetiolata Dümmer
& Jennings in Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 288
(1913). Type: South Africa, Cape Province, Malmesbury Div.,
Moorreesberg, Bolus 9959 (BOL!, specimen on lower right hand
side, lecto., designated here; PRE!).

Dümmer (1913) excluded this taxon from Lotononis, but L. densa
(Thunb.) Harv. is clearly the same as his variety of L. gracilis.
Subsp. densa is closely related to subsp. gracilis and differs
only in the very small leaflets, the short petioles, the sparse
pubescence and the totally glabrous pods (Figure 5.19). It
appears to be rare and is known only from a few collections in an
area now largely under cultivation (Map 5.34).

Vouchers: Acocks 24507; Bolus 9959; Marsh 1072; Salter 6446.

120b. subsp. leucoclada (Schlechter) B-E. van Wyk stat. nov.

Lebeckia leucoclada Schlechter in Engl., Jahrb. 27: 143 (1899).

Type: South Africa, Cape Province, "Olifant-Rivier", Schlechter 8477 (BOL!, lecto., here designated; BM!, GRA!).

Lotononis leucoclada (Schlechter) Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 288 (1913). Type as above.

Distinguished from subsp. gracilis by the more robust habit (a woody shrub of up to 1,2 m high), the larger and broader leaflets and the slightly larger flowers. The upper surface of the leaflets is sparsely pubescent, while it is totally glabrous in the other three subspecies (Figure 5.19). It also differs from subsp. congesta in the larger habit, larger leaflets and the racemose, not subumbellate inflorescences. This subspecies has a more western distribution than subsp. gracilis (Map 5.34).

Vouchers: Acocks 14841; Bolus 23146; Hall 2859; Lewis 2464; Van Wyk 2430--2436.

120c. subsp. congesta B-E. van Wyk, subsp. nov. subsp. leucocladae similis, sed habitu valde minore, foliis minoribus, pagina superiore foliolorum omnino glabra atque floribus subumbellatis differt.

Type: South Africa, Cape Province, De Hoek, Piquetberg,
Compton 19946 (NBG, holo., BOL, iso.).

Subsp. congesta is closely related to subsp. leucoclada but differs in the much smaller habit, the smaller leaves, the totally glabrous upper surface of the leaflets and in the subumbellate arrangement of the flowers (Figure 5.19). The taxon is known from only a few collections and appears to be endemic to the Piquetberg (Map 5.34).

Vouchers: Compton 15000; Guthrie 2580; Schlechter 5243; Wilman 859.

120d. subsp. gracilis (E. Mey.) B-E. van Wyk stat. nov.

Aulacanthus gracilis E. Mey., Comm. Pl. Afr. Austr. 1(1): 156 (1836). Type: South Africa, Cape Province, Roodeberg [part of Kamiesberg], Drège s.n. a (BM!, M!, MO!, S!, fruiting specimen, SAM!); "Ezelkop" [part of Kamiesberg], Drège s.n. b (S!, larger specimen, lecto., designated here; BM!, PRE!).

Lotononis gracilis (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 597 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 50 (1862), excl. var. anomala; Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 287 (1913), excl. var. brevipedunculata, excl. syn. Buchenroedera meyeri. Type as above.

This subspecies is closely related to subsp. leucoclada, but can be distinguished by the smaller habit (up to 0,6 m high), the narrower leaflets, the glabrous upper surface of the leaflets and slightly smaller flowers (Figure 5.19). In forms from high altitudes in the southern part of the distribution area (Map 5.34), the petioles are exceptionally long.

Vouchers: Bolus 8971; Esterhuysen 1344, 20529; Guthrie 4793; Van Wyk 2250--2267.

The vegetative morphology of Lotononis densa and some species of Lebeckia is remarkably similar, but the chromosome number, calyx structure, fruit, seeds and chemical evidence have shown that the two groups are not closely related. The convergence in vegetative morphology, such as the loss of leaflets (but not the petiole) during the summer), has led to taxonomic errors. L. gracilis var. anomala Harv. for example, was based on a mixed collection (Pappe 100 in TCD!) comprising flowering twigs of Lotononis densa subsp. gracilis and fruiting twigs of Lebeckia sericea Thunb.

121. L. viborgioides Benth. in Hook., Lond. J. Bot. 2: 597 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 50 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 288 (1913). Type: South Africa,

Cape Province, without precise locality, Bowie s.n. sub Herb. Hook. (K!, lecto., designated here); without precise locality, Thom 537 sub Herb. Hook. (K!, isosyn.).

This species is similar to L. densa but the leaves are stipulate and the flowers and pods are much smaller (Figure 5.19). A poorly known species with a restricted distribution area in the south-western districts of the Cape (Map 5.34), but it is perhaps overlooked rather than rare.

Vouchers: Bayer 3107; Compton 11857; Muir 4296; Nel s.n. sub STEU 11580; Van Wyk 2867.

122. L. comptonii B-E. van Wyk in Bothalia 18: 31 (1988) [Appendix 19]. Type: South Africa, Cape Province, Laingsburg to Seweweekspoort Road, 9,5 km after entrance to Rietvlei Farm, Van Wyk 2160 (PRE!, holo.; BOL!, C!, JRAU!, K!, M!, MO!, NBG!, SAAS!, STE!).

Very similar to L. densa subsp. gracilis but differs in the lax habit, the sparsely strigillose leaves and the presence of stipules (Figure 5.20). L. comptonii is known from only two localities (Map 5.34) and appears to be a rare species.

Vouchers: Compton 12166; Van Wyk 2160--2163, 2185--2191.

123. *L. acocksii* B-E. van Wyk in S. Afr. J. Bot. 55: 178 (1989) [Appendix 23]. Type: South Africa, Cape Province, Ladismith District, 2 miles [3,2 km] ENE of Vanwyksdorp, Acocks 20573 (PRE!, holo.; K!, PRE!).

L. acocksii is closely related to *L. umbellata* but differs in the much larger habit, the narrowly oblanceolate leaflets, the few-flowered racemes and the larger flowers. (Figure 5.20). The only material known is a collection from the southern parts of the Rooiberg near Ladismith (Map 5.35).

124. *L. nutans* B-E. van Wyk in S. Afr. J. Bot. 55: 180 (1989). Type: South Africa, Cape Province, 43,5 miles [69,6 km] WSW of Uniondale, Acocks 21585 (PRE!, holo.).

This species resembles *L. umbellata* but differs in the sparser habit, the longer petioles, the shape of the leaflets and the ovate (not linear) ovary and fruit (Figure 5.20). *L. nutans* is known only from the type collection (Map 5.35).

125. *L. exstipulata* L. Bol. in Ann. S. Afr. Mus. 9: 247 (1915). Type: South Africa, Cape Province, Hottentot's Kloof [3319 BC Worcester], Pearson 4902 (BOL!, holo.; K!, iso.).

A poorly known species with a restricted distribution near Ceres in the south-western Cape (Map 5.35). It is easily distinguished from other species of the section by the large flowers (Figure 5.20) and the thick woody caudex. It is superficially similar to *L. fastigiata* (section *Polylobium*) but differs from this species in the flower structure, total absence of stipules and the short, almost strigillose pubescence.

Vouchers: Bond 1462; Esterhuysen 3898; Stokoe s.n. sub SAM 52715; Van Wyk 2271--2280.

126. *L. azureoides* B-E. van Wyk in *Bothalia* 19: 1 (1989) [Appendix 20]. Type: South Africa, Cape Province, Beaufort West, Karoo National Park, at Blouput, Bengis 442 (PRE!, holo.; PRE!).

L. azureoides is a poorly known species from the Nuweveld Mountains at Beaufort West (Map 5.35) and the isolated distribution is also reflected in its morphology. The slender, single-flowered inflorescences and the shape of the wing petals were previously used to justify a position in the section *Lotononis*, but it is now considered to be better accommodated here. The inflorescences are terminal or subterminal (not leaf-opposed as in the section *Lotononis*) and the habit, flower structure (particularly the relative size of the standard petal)

is very similar to other species of Aulacanthus. (Figure 5.20).
It is readily distinguished by the blue flowers and slender
peduncles.

Voucher: Shearing 2.2.85.

127. L. umbellata (L.) Benth. in Hook., Lond. J. Bot. 2: 602
(1843); Harv. in Harv. & Sond., Fl. Cap. 2: 55 (1862); Dümmer in
Trans. Roy. Soc. S. Afr. 3(2): 299 (1913). Type: South Africa,
"ad Cap. b. Spei", LINN 896.12 (LINN!, lecto., designated here).

Ononis umbellata L., Mant. pl. alt.: 266 (1771); DC., Prodr. 2:
167 (1825); non Ononis umbellata L. sensu Thunb. Type as above.

Lipozygis umbellata (L.) E. Mey., Comm. Pl. Afr. Austr. 1(1):
76 (1836). Type as above.

Polylobium umbellatum (L.) Benth. in Ann. Wien Mus. 2: 142
(1839); Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845). Type
as above.

Ononis strigosa Thunb., Prodr. pl. Cap.: 130 (1800), Fl. Cap.:
588 (1823). Type: South Africa, "e Cap. b. Spei", Thunberg
s.n. sub THUNB-UPS 16649 (UPS!, lecto., designated here).

Ononis anthylloides DC., Prodr. 2: 168 (1825). Type: South
Africa, without precise locality, Sieber 52 (G, holo., Herb.
Delessert; M!, S!, iso.). [Note: distributed as Psoralea herbacea
Sieber nom. nud. under exs. Fl. Cap. 52].

Lotononis anthylloides (DC.) D. Dietr., Syn. pl. 4: 961 (1841),
non L. anthylloides Harv. Type as for Ononis anthylloides.

Crotalaria truncata E. Mey. in Linnaea 7: 151 (1832). Type: South Africa, Cape Province, "Teufelsberge" [Table Mountain], Ecklon s.n. sub Herb. Un. itin. 568 (S!, original label, lecto., designated here; K!, S!).

Polylobium truncatum (E. Mey.) Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 181 (1836); D. Dietr., Syn. pl. 4: 961 (1841). Type as above.

Polylobium filiforme Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 181 (1836); D. Dietr., Syn. pl. 4: 962 (1841). Type: South Africa, Cape Province, "Rivier zonder Einde", near the village Linde, Ecklon & Zeyher 1291 (S!, specimen with larger leaflets, lecto., designated here; C!, M!, S!, SAM!).

Polylobium debile Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 181 (1836); D. Dietr., Syn. pl. 4: 962 (1841). Type: South Africa, Cape Province, Swellendam district, Hassaquaskloof [Stormsvlei kloof], Ecklon & Zeyher 1290 (S!, larger specimen, lecto., designated here; C!, S!).

Leptidium debile (Eckl. & Zeyh.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845). Type as for Polylobium debile.

Lotononis debilis (Eckl. & Zeyh.) Benth. in Hook., Lond. J. Bot. 2: 604 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 55 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 300 (1913), syn. nov. Type as for Polylobium debile.

This is by far the most common species of the section and occurs from the Cape Peninsula along the southern Cape coastal regions to Port Elizabeth (Map 5.35). The plant is quite prostrate, with

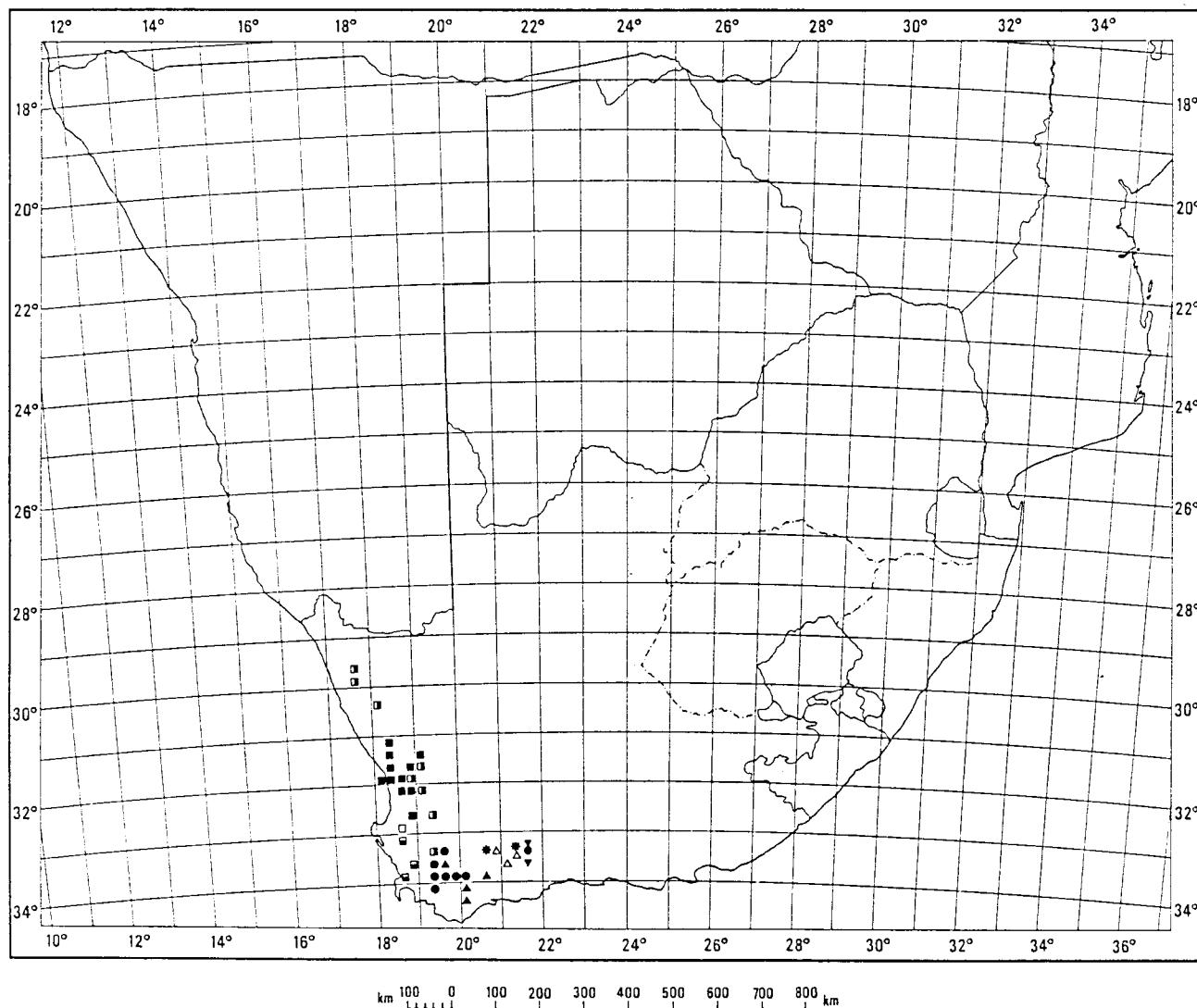
a herbaceous appearance when young, but older specimens develop thick woody branches at ground level. It can be distinguished from other species of the section by the prostrate habit, the umbellate inflorescences, the broadly obovate shape of the leaflets, the cuneate standard petal and the oblong uninflated pods (Figure 5.20). *L. debilis* is here reduced to synonymy because it is only slightly more hairy than the typical form and doubtfully distinct from it even at varietal level.

Vouchers: Acocks 16077, 22235; Bolus 2666; Hugo 2631, 2776; Van Niekerk 444; Van Wyk 2110--2117, 2684, 2707.

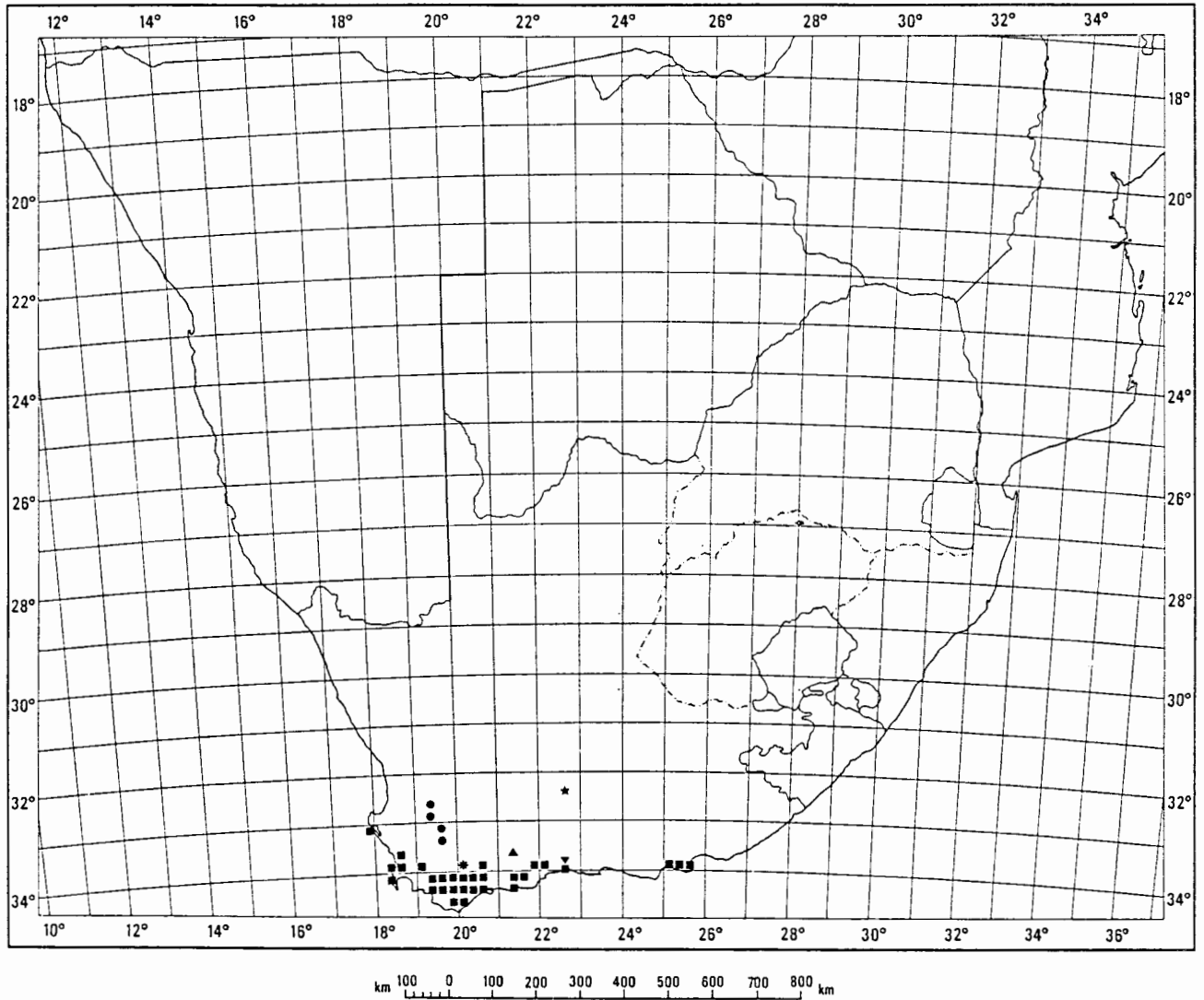
128. *L. purpurescens* B-E. van Wyk in S. Afr. J. Bot. 55: 180 (1989) [Appendix 23]. Type: South Africa, Cape Province, Montagu, c. 2,5 km along footpath to Donkerkloof, Van Wyk 2718 (PRE!, holo.; BOL!, JRAU!, K!, M!, MO!, NBG!, SAAS!, STE!).

A distinct species with no obvious affinities. The pods are similar to those of *L. umbellata*, but the habit, inflorescence and flower structure and flower colour are quite different (Figure 5.20). It is the only species of the section with pale purple flowers. *L. purpurescens* appears to be restricted to the mountains at Montagu (Map 5.35).

Vouchers: Compton 18472; Lewis 2087; Page s.n. sub BOL 15441, s.n. sub PRE 53522; Van Wyk 2654, 2655, 2718--2721.



Map 5.34. The known geographical distribution of *L. dissitinodis* (△), *L. dahlgrenii* (▼), *L. rigida* (●), *L. densa* subsp. *densa* (■), *L. densa* subsp. *leucoclada* (■), *L. densa* subsp. *congesta* (□), *L. densa* subsp. *gracilis* (■), *L. viborgioides* (▲) and *L. comptonii* (*).



Map 5.35. The known geographical distribution of *L. acocksii* (▲), *L. nutans* (▼), *L. exstipulata* (●), *L. azureoides* (★), *L. umbellata* (■) and *L. purpurescens* (*).

Section 14. Krebsia (Eckl. & Zeyh.) Benth.

Lotononis section Krebsia (Eckl. & Zeyh.) Benth. in Hook.,
Lond. J. Bot. 2: 598 (1843); Harv. in Harv. & Sond., Fl. Cap. 2:
48 (1862), pro parte; Dümmer in Trans. Roy. Soc. S. Afr. 3(2):
279 (1913), pro parte.

Krebsia Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 179 (1836);
Benth. in Ann. Wien. Mus. 2: 142 (1839); Steud., Nom. Bot. 2(1):
850 (1840); D. Dietr., Syn. pl. 4: 963 (1847).

Telina E. Mey. section 1. Cytisoideae E. Mey., Comm. Pl. Afr.
Austr. 1(1): 68 (1836).

Telina E. Mey. section 2. Brachypodae E. Mey., Comm. Pl. Afr.
Austr. 1(1): 69 (1836).

Type species: L. cytisoides (E. Mey.) Benth. [now L. stricta
(Eckl. & Zeyh.) B-E. van Wyk]

Note: Species added to this section by Harvey (1862) and Dümmer
(1913) are excluded, so that the circumscription now agrees
exactly with the original concept of Ecklon and Zeyher (1836) and
Bentham (1843).

Perennial shrubs or shrublets with procumbent or erect (rarely prostrate) woody branches. Mature parts sparsely to densely sericeous or \pm strigillose. Leaves alternate, digitately trifoliolate, pubescent on the lower or both surfaces, more densely so on the lower surface. Stipules paired or single at each leaf base or absent (often variable on the same plant), usually similar to the leaflets in size and shape. Inflorascences racemose to umbellate, (1--) 2- to several-flowered; peduncle short and thick or long and slender, terminal and/or leaf-opposed; bracts small, linear to oblanceolate; bracteoles absent or inconspicuous. Flowers relatively large, blue, rarely yellow, never cleistogamous. Calyx with the upper and lateral lobes on either side fused higher up in pairs, the lobes broadly to narrowly triangular, the lower lobe similar to the upper 4 lobes. Standard \pm as long as the keel, broadly ovate to suborbicular, dorsally densely pubescent or more rarely glabrous, claw short or rarely long, often with two callosities near the apex; lamina relatively large, usually conspicuously striated, apex obtuse to emarginate. Wing petals oblong, as long or shorter than the keel, glabrous. Keel petals relatively large, half oblong-elliptic; apex obtuse; glabrous, rarely pubescent (*L. jacottetii*). Anthers dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the carinal anther intermediate. Pods sessile, oblong, only slightly inflated, rarely somewhat turgid, thick-walled, upper suture smooth or rarely verrucose, dehiscent, many-seeded; funicles short. Seeds 2--3,5 mm in diameter, variable in shape, often with the radicular lobe conspicuous,

testa smooth, not tuberculate. Chromosome base number 7 ($2n = 28, 42, 56$ or 84). (Figures 5.21, 5.22 & 5.23).

A total of 12 variable species from the eastern parts of southern Africa (Maps 5.36, 5.37, 5.38 and 5.39).

The section Krebsia comprises woody shrubs or more rarely suffrutescent pyrophytes with branches from a perennial woody base. The species are similar to those of the section Aulacanthus but can readily be distinguished by the oblong and scarcely inflated pods, the predominantly blue flowers and the smooth (not tuberculate) seed surface. As a group, the section is distinct, but the species are often very difficult to identify because some of them show considerable regional variation. Relationships within some of the species complexes are not clear and should be investigated more thoroughly. Chromosome numbers are unusually variable and a detailed cytological study may lead to a better understanding of relationships. The morphological variability may also be partly a result of biogeographic factors because the distribution range of the section is an area with drastic topographic and climatic gradients.

The section Krebsia is here divided into two subsections (see Part 3.2): subsection Krebsia (8 species) and subsection Glabrifolia (4 species).

Key to the subsections of section Krebsia:

- 1A. Upper surface of the leaflets
with at least some hairs 14A. subsection Krebsia
- 1B. Upper surface of the leaflets
totally glabrous 14B. subsection Glabrifolia

14A. Subsection Krebsia

- 1A. Keel hairy towards the apex 133. L. jacottetii
- 1B. Keel totally glabrous:
 - 2A. Stipules absent, at least on all
mature leaves 136. L. caerulea
 - 2B. Stipules present on all or most mature
leaves, single or in pairs:
 - 3A. Stipules invariably paired at each leaf base, the
two of each pair similar in size and shape:
 - 4A. Standard petal totally glabrous 130. L. stricta
 - 4B. Standard petal pubescent 129. L. eriocarpa
 - 3B. Stipules mostly single at each leaf base, if
rarely paired (only at some nodes) then the
two of each pair markedly dissimilar in size:
 - 5A. Peduncle very long and slender, many
times longer than the flower 135. L. minor
 - 5B. Peduncle short, not more than 2x as
long as the flower:

- 6A. Upper surface of the leaflets densely
sericeous, the surface of the lamina not visible:
- 7A. Calyx with the lateral and upper
lobes on either side close together,
forming a pair on either side of the
calyx 131. *L. sericophylla*
- 7B. Calyx with the lateral and upper
lobes on either side well separated,
not forming a distinct pair on either
side of the calyx 134. *L. galpinii*
- 6B. Upper surface of the leaflets sparsely
hairy, the surface of the lamina visible:
- 8A. Calyx with the lateral and upper
lobes on either side close together,
forming a pair on either side of the
calyx 132. *L. divaricata*
- 8B. Calyx with the lateral and upper
lobes on either side well separated,
not forming a distinct pair on either
side of the calyx 134. *L. galpinii*

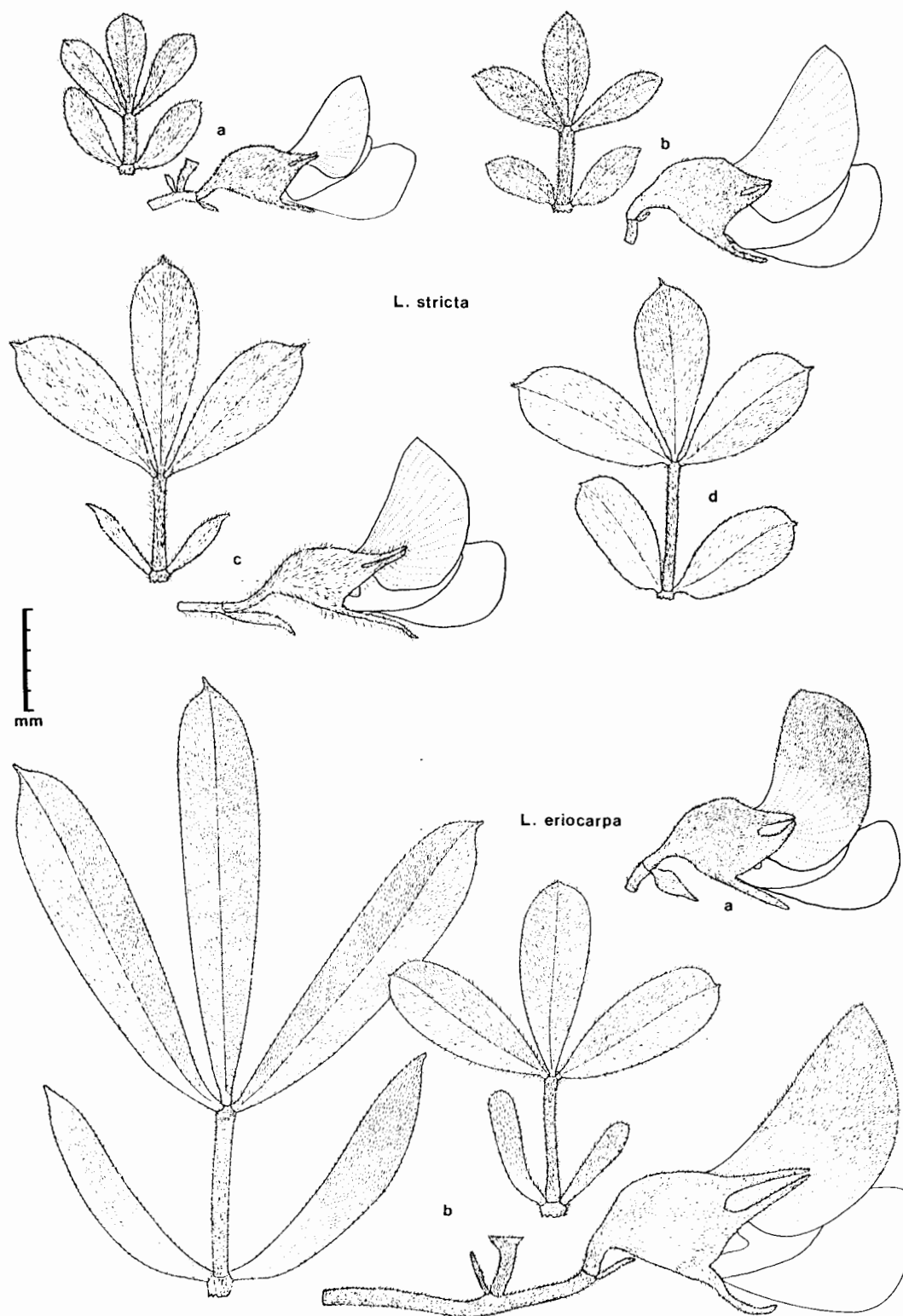


Figure 5.21. Leaves and flowers of the species of section *Krebsia*: subsection *Krebsia* (partly).

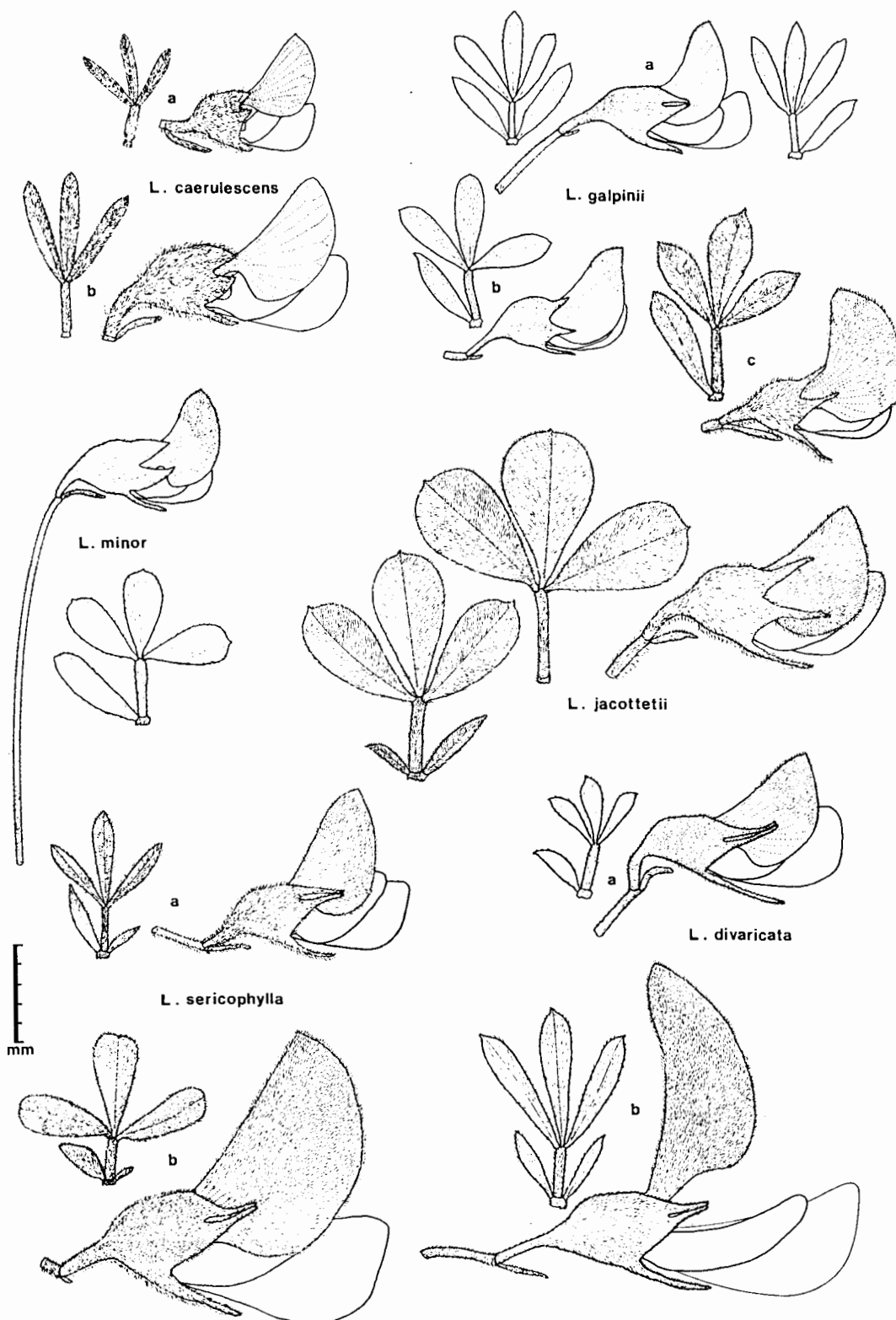


Figure 5.22. Leaves and flowers of the species of section *Krebsia*: subsection *Krebsia* (partly).

129. L. eriocarpa (E. Mey.) B-E. van Wyk comb. nov.

Type: South Africa, Cape Province, "near Omcomas" [3030 BB],
Drège s.n. a (S!, lecto., designated here; MO!); near Omsamcaba
[3129 BB], Drège s.n. b (no isotype found).

Telina eriocarpa E. Mey., Comm. Pl. Afr. Austr. 1(1): 68
(1836); Benth. in Hook., Lond. J. Bot. 2: 598 (1843); Harv. in
Harv. & Sond., Fl. Cap. 2: 50 (1862); Dümmer in Trans. Roy. Soc.
S. Afr. 3(2): 288 (1913). Type as above.

Krebsia eriocarpa (E. Mey.) Steud., Nom. Bot. 2(2): 850 (1841);
D. Dietr., Syn. pl. 4: 963 (1847). Type as above.

Buchenroedera biflora H. Bol. in J. Bot. 34: 18 (1896). Type:
South Africa, Natal, Zululand, Entumeni, Wood 3988 (BOL!, lecto.,
designated here; BM!, K!, NH).

Lotononis biflora (H. Bol.) Dümmer in Trans. Roy. Soc. S. Afr.
3(2): 289 (1913), synon. nov.; Hilliard & Burt in Notes of RBG
Edinb. 43(2): 210 (1986). Type as for Buchenroedera biflora.

L. wyliei Wood in Gard. Chron. 1904,2: 182 (1904); Wood, Natal
Pl. 4: t.350 (1906); Hilliard & Burt in Notes of RBG Edinb.
43(2): 210 (1986), as synonym of L. biflora. Type: South Africa,
Natal, Zululand, Entumeni, Wylie s.n. sub Wood 8962 (NH);
Wylie s.n. sub Wood 9442 (NH, to be selected as lecto.; BOL!, K!,
PRE!, SAM!).

L. cytisoides (E. Mey.) Benth. var. sericea Dümmer in Trans.
Roy. Soc. S. Afr. 3(2): 289 (1913), pro parte, excl. Flanagan
1543 [= L. divaricata]. Type: South Africa, Natal, Umhlongwe,
Wood 3011 (K!, lecto., designated here; BM!); Wood 488 (not
found).

L. eriocarpa is closely related to L. stricta ("L. cytisoides") but geographically more or less isolated from it (Map 5.36). Benthams (1843), Harvey (1862) and Dümmer (1913) all listed this species as a synonym of L. stricta. The more robust habit of L. eriocarpa was unknown to them, so that the pubescence of the standard (already used as a diagnostic character by Meyer in 1836) probably seemed unimportant. The upper half of the standard petal is densely pubescent in L. eriocarpa and totally glabrous in L. stricta (Figure 5.21). These two species may eventually prove to be only subspecifically distinct (see notes under L. stricta).

Vouchers: Abbott 970, 1198, 1470; Codd 1408; Hilliard & Burt 6765; Schrire 1735; Van Wyk 1950--1955.

130. L. stricta (Eckl. & Zeyh.) B-E. van Wyk comb. nov.

Type: South Africa, Cape Province, near Enon [3325 BC] and also "Chumiberg" [Tyumie Peak, 3226 DB], Ecklon & Zeyher 1284 (S!, Enum. label, lecto., designated here; C!, K!, M!, S!, TCD!).

Krebsia stricta Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 179 (1836, Jan.); Steud., Nom. Bot. 2(2): 850 (1841); D. Dietr., Syn. pl. 4: 963 (1847); Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 479 (1845); Harv. in Harv. & Sond., Fl. Cap. 2: 50 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 288 (1913). Type as above.

Krebsia striata Eckl. & Zeyh. sensu Benth. in Hook., Lond. J. Bot. 2: 598 (1843), sphalm. [= K. stricta].

Telina cytisoides E. Mey., Comm. Pl. Afr. Austr. 1(1): 68 (1836, Feb. or later); Drège in Linnaea 19: 639 (1847). Type: South Africa, Cape Province, near "Key" [Kei River, 3228 CA], Drège s.n. a (S!, lecto., designated here; BM!, BOL!, K!, PRE!); "Zuurebergen" [3325 AD], Drège s.n. b (BM!, BOL!, K!, MO!; S!, pro parte, excl. Zeyher 2308); Ado [Addo, 3325 DA], Drège s.n. c (K!).

Krebsia cytisoides (E. Mey.) Steud., Nom. Bot. 2(2): 850 (1841); Dietr: 963 (1847). Type as for Telina cytisoides.

Lotononis cytisoides (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 598 (1843), synon. nov.; Harv. in Harv. & Sond., Fl. Cap. 2: 50 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 288 (1913), excl. var. sericea. Type as for Telina cytisoides.

Telina brevifolia Eckl. & Zeyh. ex Drège in Linnaea 19: 639 (1847). Type: South Africa, Cape Province, "Adow" [Addo, 3325 DA] and above Salem [3326 AD?], Zeyher 2308 (S!, lecto., specimens with small leaflets on sheet with Drège s.n. b, designated here; K!, sub Herb. Hook., K!, PRE!, SAM!). [Based on Krebsia brevifolia Eckl. mss, part of Enumeratio ms attached to lectotype sheet in S].

Lotononis cytisoides (E. Mey.) Benth. var. brevifolia (Eckl. & Zeyh. ex Drège) Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 289 (1913). Type as for Telina brevifolia.

Closely related to *L. eriocarpa* but differs in the smaller habit, the generally smaller leaves and flowers and the totally glabrous standard petal (Figure 5.21). The distribution is centred in the eastern Cape (Map 5.36), where the typical form of the species (shown as a in Figure 5.21) is very commonly found in grassland habitats at higher altitudes. Some rather atypical forms occur in the north-western parts of Transkei, such as a form from Mt. Curry with a hirsute rather than sericeous pubescence (shown as b in Figure 5.21). Another atypical form with a robust habit and relatively large leaves and flowers (b in Figure 5.21) is found in the mountains north-west of Umtata. Specimens with large leaves and stipules (d in Figure 5.21) have been collected along the eastern Cape coast. Field studies and a detailed cytological study may lead to an improved understanding of the relationship between *L. stricta* and *L. eriocarpa*. Available chromosome counts (Van Wyk & Schutte 1988a, Appendix 14) indicate $2n = 28$ for the typical eastern Cape form of *L. stricta*, $2n = 56$ for a robust form from Mhlahlane in Transkei and $2n = 84$ for *L. eriocarpa* from the Natal Drakensberg.

The unfortunate name change results from a confusion between *Telina striata* E. Mey. [= *L. carnosa*] and *Krebsia stricta* Eckl. & Zeyh. As shown in the synonymy of *L. cytisoides* above, Bentham (1843) apparently confused the two names and later workers (Presl 1845, Harvey 1862 and Dümmer 1913) did not correct the error. Since the meanings are totally different (and rather appropriate

in both cases) the similarity in spelling should not lead to further confusion and is no justification for retaining Meyer's (1836) later epithet.

Vouchers: Compton 17010; Flanagan 1705; Story 3369; Taylor 3653; Van Wyk 1708--1721, 1752, 1761, 1775.

131. L. sericophylla Benth. in Hook., Lond. J. Bot. 2: 599 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 51 (18620); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 291 (1913). Type: South Africa, Orange Free State, "Wolve Kloof" near the Caledon River, Burke s.n. (K!, Herb. Benth. specimen, lecto., designated here; K!, Herb. Hook. specimen).

L. trisegmentata Phill. in Ann. S. Afr. Mus. 16: 73 (1917), synon. nov. Type: Lesotho, slopes near the Caledon River, Dieterlen 353 (PRE!, annotated by Phill., lecto., designated here; NBG!, PRE!, SAM!, STE!).

L. wyliei Wood sensu Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 290 (1913).

A variable complex showing considerable regional variation. Field studies have indicated three reasonably distinct forms but no formal infraspecific classification is attempted here.

Infraspecific taxa recognised by Phillips (1917) are listed under

each of the three forms. Two of the three forms are shown in Figure 5.22, but the geographical distributions are not given separately in Map 5.37.

Form A. ("typical" form)

L. sericophylla Benth.

L. trisegmentata Phill. var. trisegmentata forma sericea Phill. in Ann. S. Afr. Mus. 16: 74 (1917). Type: Lesotho, slopes of Litsoeneng Mountain, Botsabelo, near Maseru, Dieterlen 1020 (SAM!, lecto., designated here; BOL!).

Very similar to some forms of L. divaricata but differs from this species in the silky vestiture of the twigs, leaves and standard petal (a in Figure 5.22). It differs from the other two forms of L. sericophylla in the slender branches, the smaller leaves and the minutely silky vestiture. Distribution: western and south-western parts of the Drakensberg, spreading slightly into the interior.

Vouchers: Dieterlen 1020, 1212; Page s.n. sub BOL 17901; Millard 5; Rogers 5164.

Form B. ("trisegmentata" form)

L. trisegmentata Phill. var. trisegmentata forma trisegmentata. Type as for L. trisegmentata.

L. trisegmentata Phill. var. robusta Phill. forma robusta
Phill. in Ann. S. Afr. Mus. 16: 74 (1917). Type: South Africa,
Orange Free State, slopes of the Mont-aux-Sources, Elanagan 2095
(SAM!, lecto., designated here; BOL!, NBG!, PRE!, SAM!).

The two varieties described by Phillips (1917) are doubtfully
distinct from each other. Field studies have indicated that the
typical variety was based on slightly stunted coppice material of
the var. robusta. Some collections are very distinct due to dense
and slightly spreading white hairs on the twigs, leaves and calyx
and the relatively large flowers (b in Figure 5.22). This form is
commonly found in the north-eastern parts of the Drakensberg,
where it occurs as large populations in disturbed areas such as
roadsides and eroded river banks.

Vouchers: Esterhuysen 18665; Fawkes 77; Potts 3050, 3885; Roux
943; Van Wyk 1559, 1644, 1647.

Form C ("sericea" form)

L. trisegmentata Phill. var. robusta Phill. forma sericea
Phill. in Ann. S. Afr. Mus. 16: 74 (1917). Type: South Africa,
Natal, Polela, Evans 634 (BOL!, lecto., designated here).

In this form the leaves are appressedly silky rather than densely sericeous as in form B. Specimens agreeing with this form mostly originate from riverine vegetation (often from the boulder beds of rivers) along the eastern, northern and western slopes of the Drakensberg.

Vouchers: Compton 21352; Guillarmod 671; Killick 3846; Schrire 803; Van Wyk 1957, 1958.

132. L. divaricata (Eckl. & Zeyh.) Benth. in Hook., Lond. J. Bot. 2: 599 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 51 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 291 (1913). Type: South Africa, Cape Province, mountain side near "Silo" at the "Klipplaatrivier" [3226 BB], Ecklon & Zeyher 1285 (S!, lecto., designated here; C!, M!, MO!, S!, SAM!, TCD!).

Krebsia divaricata Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 179 (1836, Jan.); Steud., Nom. Bot. 2(2): 850 (1841); D. Dietr., Syn. pl. 4: 963 (1847). Type as above.

Telina genuflexa E. Mey., Comm. Pl. Afr. Austr. 1(1): 69 (1836, Feb. or later). Type: South Africa, Cape Province, between "Klipplaatrivier" [3226 BB] and "Zwartkey" [3226 BA], Drège s.n. a (S!, lecto., designated here; BM!; K!, sub Herb. Benth.; K!, sub Herb. Hook.; MO!, PRE!, PRE!, sub PRE 26824; TCD!); near "Gaatsje" [3026 CC], Drège s.n. b (not found).

Krebsia genuflexa (E. Mey.) Steud., Nom. Bot. 2(2): 850 (1841); D. Dietr., Syn. pl. 4: 963 (1847). Type as above.

Lotononis genuflexa (E. Mey.) Benth. in Hook., Lond. J. Bot. 2: 598 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 51 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 290 (1913), as synonym of L. divaricata. Type as above.

L. brierleyae Bak. f. in J. Bot. 17: 255 (1932), synon. nov.
Type: South Africa, Orange Free State, "Likatlong" (untraced, not likely to be Likatlong in Botswana, 2525 CA), Brierley 34 (BM!, holo.).

L. divaricata is closely related to L. sericophylla and it is not always easy to distinguish between them. The sparse pubescence of the leaves (Figure 5.22) is generally a useful diagnostic character. The type specimen of L. brierleyae agrees exactly with a form of the species previously known as L. genuflexa (shown as b in Figure 5.22). The geographical distribution of L. divaricata is similar to that of L. sericophylla but extends further south and further west (Map 5.37).

Vouchers: Du Toit 160; Hanekom 1944; Hutchinson 3090; Muller 624; Van Wyk 1668--1670.

133. L. jacottetii (Schinz) B-E. van Wyk comb. nov.

Buchenroedera jacottetii Schinz in Vierteljahrsschr. Nat. Ges. Zürich 66: 224 (1921). Type: Lesotho, White Hill [3028 AB], Jacottet 144 (Z, holo.; photocopy in NU!).

L. jacottetii differs from other species of the section *Krebsia* in the pubescent (not totally glabrous) keel petals, the broadly oblanceolate to obovate leaflets and the strongly caducous stipules. It is similar to *L. galpinii* but differs from this species also in the erect and robust habit, the much larger leaves and flowers and the longer calyx lobes (Figure 5.22). It is known from a few localities in the Drakensberg (Map 5.38).

Vouchers: Killick 1191, 1439, 1609, 1688.

134. *L. galpinii* Dümmer in Trans. Roy. Soc. S. Afr. 3: 291 (1913). Type: South Africa, Natal, source of the Tina River, summit of the Drakensberg, Galpin 6600 (K!, lecto., designated here; BOL!, GRA!, PRE!, SAM!).

L. galpinii Dümmer var. *prostrata* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 291 (1913). Type: South Africa, Natal, Eastern slopes of the Drakensberg, "Tsitsa Footpath" [c. 3028 CA], Galpin 6601 (K!, lecto., designated here; BOL!, GRA!, PRE!, SAM!).

A variable species (Figure 5.22) from high altitudes in the Drakensberg (Map 5.38). The pubescence of the leaves varies considerably and it may be possible to devise a formal infraspecific classification after a detailed study. A form of the species with an upright habit and sparsely pubescent leaves (a in Figure 5.22) can be confused with *L. divaricata* but the standard petal is almost glabrous in this form. A prostrate form

with sparsely pubescent leaves (b in Figure 5.22) is sometimes misidentified as L. divaricata and the typical form of the species (c in Figure 5.22) may be confused with L. jacottetii.

Vouchers. Typical form: Coetzee 594; Hilliard & Burt 12493, 15034; Killick 4172; Roux 1158; Trauseld 902. Form with glabrous standard (a in Figure 5.22): Killick 4260, 4261, 4266, 4305; Pole Evans 59, 97. Prostrate glabrescent form (b in Figure 5.22): Compton 21282; Guillarmod 3685; Staples 295; Van Rensburg 5298.

135. L. minor Dümmer & Jennings in Trans. Roy. Soc. S. Afr. 3 (2): 295 (1913). Type: South Africa, Cape Province, Mount Fletcher Div., "Doodman's Krans Mountain" [c. 3028 CA], Galpin 6602 (K!, holo.; BOL!, GRA!, PRE!, SAM!).

This poorly known species is similar to some forms of L. galpinii but it is easily distinguished by the long and slender peduncles (Figure 5.22). The morphology of the pods and the smooth seed surface suggest that it is only superficially similar to species of the section Lotononis (formerly Telina) and that it was previously misplaced in the latter section. L. minor has been recorded from only two localities in the southern Drakensberg (Map 5.38).

Voucher: Hilliard & Burt 6615.

136. L. caerulescens (E. Mey.) B-E. van Wyk in S. Afr. J. Bot. 54: 178 (1988) [Appendix 16]. Type: South Africa, Cape Province, between "Klipplaatrivier" [3226 BB] and "Zwart-Key" [3226 BA], Drège s.n. (K, sub Herb. Benth., photo!; K, sub Herb. Hook., photo!; W, photos!, 3 specimens).

Aspalathus caerulescens E. Mey., Comm. Pl. Afr. Austr. 1(1): 54 (1836, Feb. or later); Benth. in Hook., Lond. J. Bot. 3: 361 (1844), as synonym of Lebeckia microphylla E. Mey. Type as above.

Buchenroedera caerulescens (E. Mey.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 477 (1845). Type as above.

Krebsia argentea Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 179 (1836, Jan.), non Lotononis argentea Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 176 (1836); Benth. in Hook., Lond. J. Bot. 3: 361 (1844), as synonym of Lebeckia microphylla E. Mey.; Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 477 (1845). Type: South Africa, Cape Province, near "Silo" at the "Klipplaatrivier" [3226 BB], Ecklon & Zeyher 1286 (S!, lecto., designated here; M, photo!; W, photo!; SAM, photo!).

Lebeckia microphylla E. Mey., Comm. Pl. Afr. Austr. 1(1): 155 (1836, Feb. or later), non Lotononis microphylla Harv. in Harv. & Sond., Fl. Cap. 2: 65 (1862); Benth. in Hook., Lond. J. Bot. 3: 361 (1844); Harv. in Harv. & Sond., Fl. Cap. 2: 88 (1862). Type: South Africa, Cape Province, "Camdeboosberg" [3224 AC], Drège s.n. a (K, photo!; W, photo!); "Klein Bruintjeshoogte" [3225 CB], Drège s.n. b (BOL, photo!; K, photo!; PRE, photo!; W, photo!).

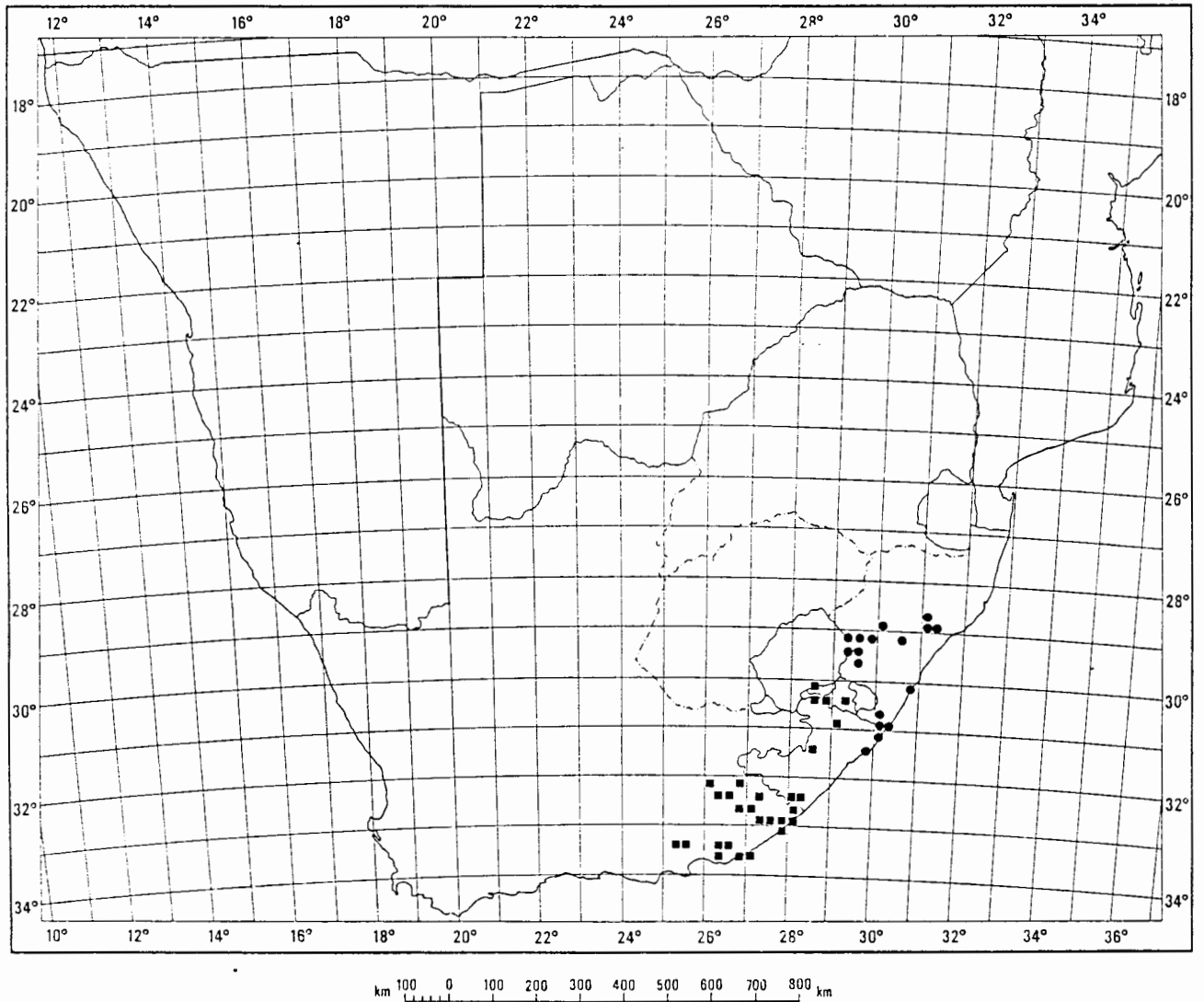
Lebeckia microphylla E. Mey. var. leptophylla E. Mey., Comm. Pl. Afr. Austr. 1(1): 155 (1836); Benth. in Hook., Lond. J. Bot. 3: 361 (1844). Type: near "Graafreynet" [3224 BC], Drège s.n. a (not found); "Los Tafelberg" [3226 BA], Drège s.n. b (not found).

Buchenroedera glabriflora N. E. Br. in Kew Bull. 1901: 120 (1901); Polhill in Bot. Syst. 1: 325 (1976). Type: South Africa, Cape Province, mountain sides near Queenstown, Galpin 1596 (K, holo., photo!; BOL!).

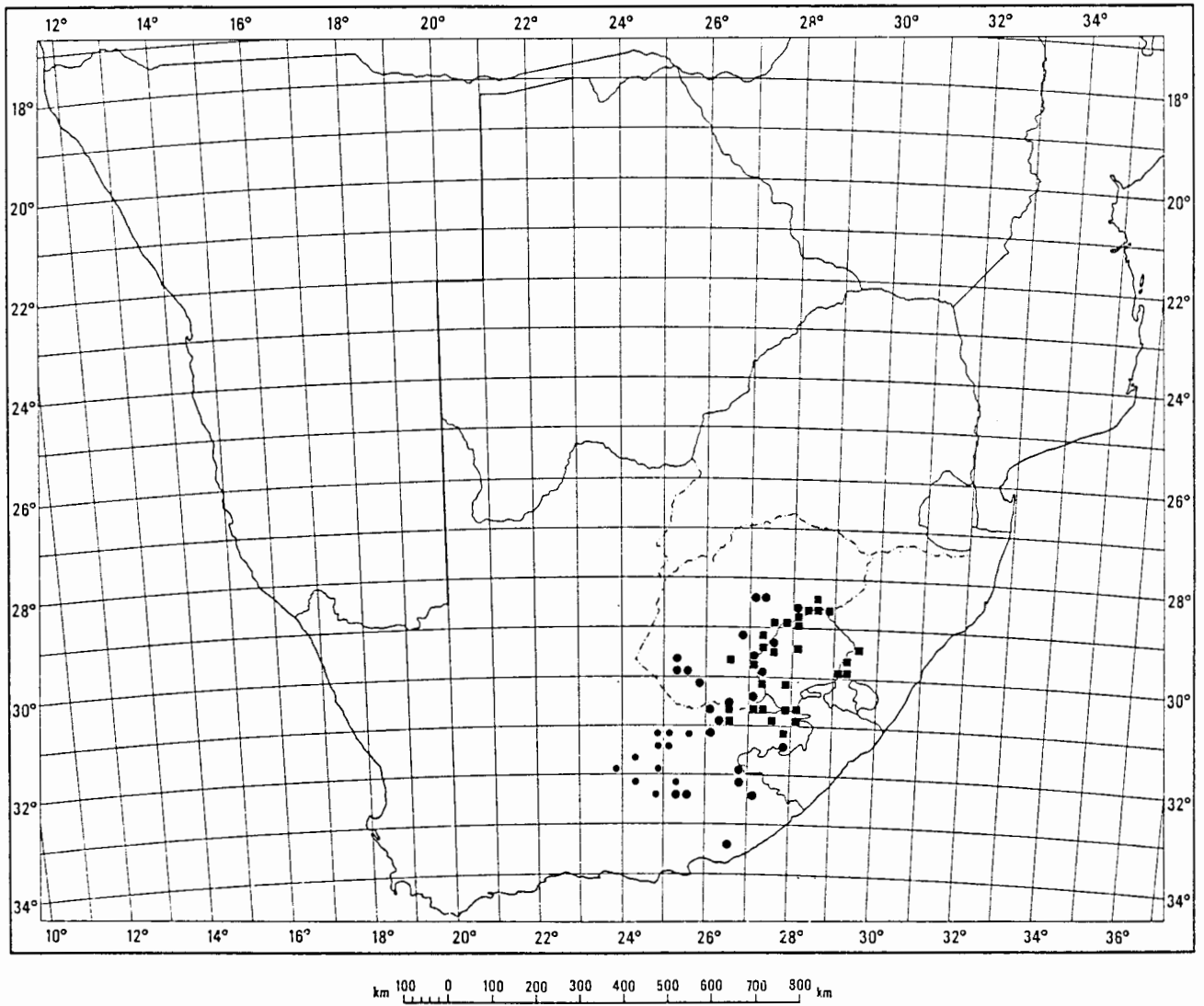
Buchenroedera uniflora Dümmer in Kew Bull. 1912: 226 (1912). Type: South Africa, Cape Province, Graaff Reinet Div.; on the summit of "Mount Koudveld", Sneeuwberg Range, Bolus 2580 (K, holo!; BOL!).

A variable species described in detail by Van Wyk (1988a, Appendix 16), where the long overdue transfer to Lotononis is motivated. A subsequent chromosome count ($2n = 56$, Van Wyk & Schutte 1988a, Appendix 14) confirmed the position in Krebsia. The total absence of stipules (Figure 5.38) is an unique character within the section. L. caerulescens is fairly common in the south-eastern and eastern Cape (Map 5.38). The locality record for Natal is based on a single specimen which probably represents a distinct species (see Van Wyk 1988a, Appendix 16).

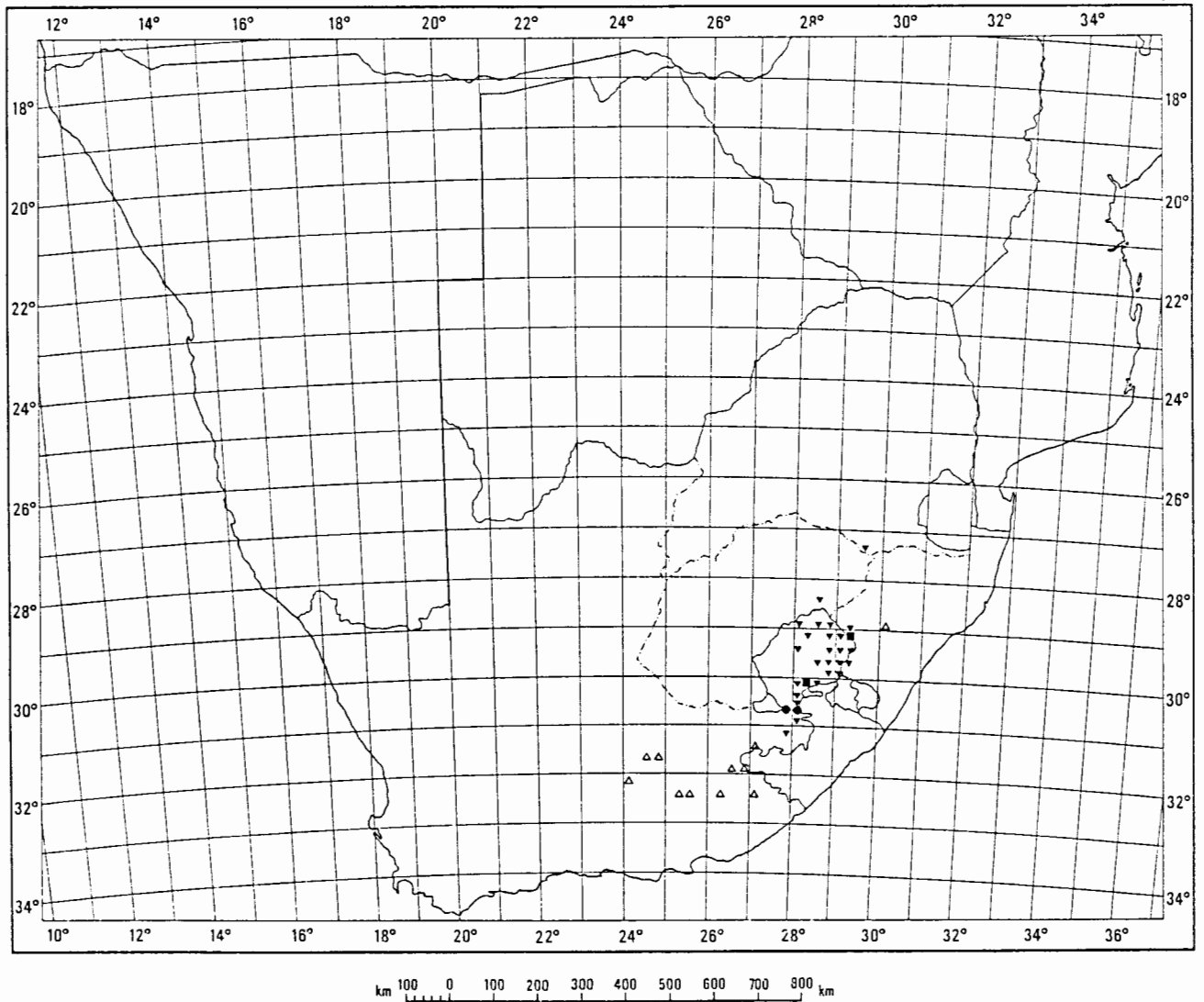
Vouchers: Acocks 15699, 16574; Bayliss 7949; Bolus 2580; Oliver 5272; Van Wyk 1614, 1724.



Map 5.36. The known geographical distribution of *L. eriocarpa* (●) and *L. stricta* (■).



Map 5.37. The known geographical distribution of *L. sericophylla* (■) and *L. divaricata* (●).



Map 5.38. The known geographical distribution of *L. jacottetii* (■), *L. galpinii* (▼), *L. minor* (●) and *L. caerulea* (△).

14B. Subsectio Glabrifolia B-E. van Wyk, subsect. nov. A subsectione Krebsia pagina adaxiali foliolorum omnino glabra, et lobis calycis brevibus angustibus, differt.

Type species: L. carnosa (Eckl. & Zeyh.) Benth.

The new subsection can easily be identified by the totally glabrous adaxial surface of the leaflets and the short, narrowly triangular calyx lobes. The stipules are invariably paired and the standard petal is always glabrous except for a few hairs along the midrib. (Figure 5.23).

1A. Flowers up to 4 per inflorescence, on short lateral branches:

2A. Leaves distinctly pubescent; flowers yellow or rarely white and fading to pink 137. L. dichiloides

2B. Leaves sparsely and minutely hairy, nearly glabrous; flowers at least partly blue:

3A. Leaflets linear, straight; claw of standard petal more than half the length of the lamina, without callosities; virgate shrub; north-eastern Natal and south-eastern Transvaal 140. L. pottiae

3B. Leaflets oblanceolate or if linear, then with the apices strongly recurved; claw of the standard petal less than half the length of the

- lamina, with two distinct callosities near the attachment of the blade; divaricately branched shrub; eastern Cape to the southern border of Natal 139. L. carnosa
- 1B. Flowers more than 4 per inflorescence, umbellate or subumbellate on a terminal or subterminal peduncle:
- 4A. Leaflets linear, < 9 mm long; stipules longer than the petiole 139. L. carnosa
- 4B. Leaflets oblanceolate, if rather narrow then > 10 mm long; stipules shorter than the petiole 138. L. bachmanniana

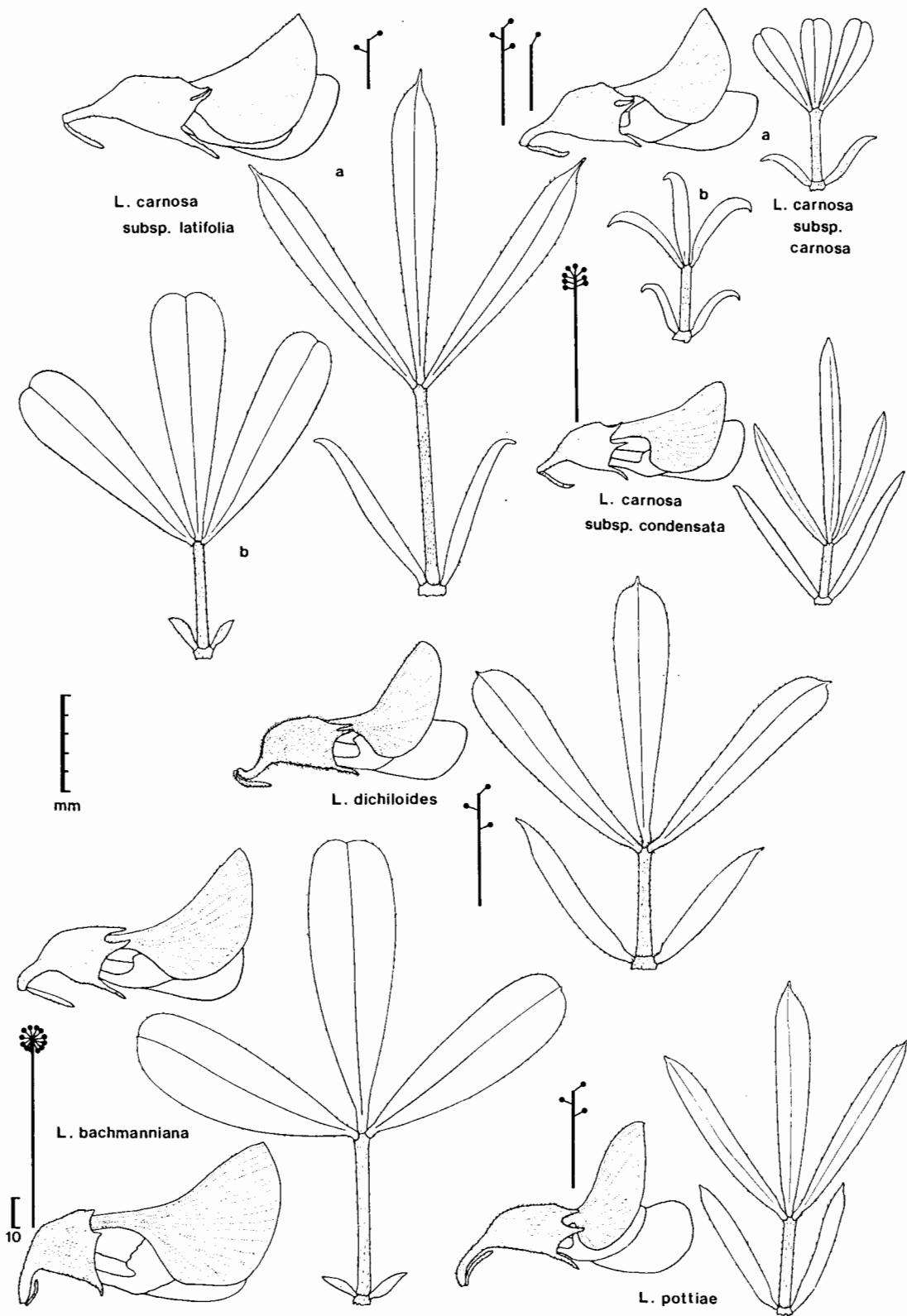


Figure 5.23. Leaves and flowers of the species of section *Krebsia*: subsection *Glabrifolia*.

137. L. dichiloides Sond. in Linnaea 23: 28 (1850); Harv. in Harv. & Sond., Fl. Cap. 2: 52 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 292 (1913). Type: South Africa, Natal, Port Natal [Durban], Gueinzus 25 (G!, lecto., designated here; C!, s.n. sub Herb. Sond., SAM!, s.n. sub SAM 15215; TCD!).

[Note: The specimen in G was marked by Sonder as "Dichilus floribundus", a name referred to in the original publication. It is therefore the best choice for lectotypification. I did not find any types in S, where most of the South African material of the Sonder herbarium is now located (Nordenstam 1980)].

A distinct but poorly known species recorded only from a limited area around Durban (Map 5.39). The habit of the plant is superficially similar to that of the genus Dichilus DC. but the structure of the flowers and pods are typical of the section Krebsia (Figure 5.23). The flowers are yellow although label information on some specimens suggests that it is sometimes white, and fades to pink.

Vouchers: Anon. s.n. in STEU 13561, 13562; Haygarth 12128; Thode 3134; Wood 958, 11444, 13137.

138. *L. bachmanniana* Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 300 (1913). Type: South Africa, Cape Province, Pondoland, Bachmann 578 (K!, lecto., designated here; Z).

This species is closely related to *L. carnosa* but differs in the suffrutescent habit, the umbellate inflorescences and slightly larger flowers (Figure 5.23). It appears to be limited to the north-eastern parts of the Transkei and the south-eastern parts of Natal (Map 5.39).

Vouchers: Abbott 250; Germishuizen 1183; Nicholson 1339; Venter & Vorster 28; Ward 5626.

139. *L. carnosa* (Eckl. & Zeyh.) Benth. in Hook., Lond. J. Bot. 2: 597 (1843); Harv. in Harv. & Sond., Fl. Cap. 2: 51 (1862); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 290 (1913). Type: South Africa, Cape Province, near "Silo" at the "Klipplaatrivier" [3226 BB], Ecklon & Zeyher 1287 (S!, Plantae capenses label, lecto., designated here; C!, M!, S!, SAM!, TCD!).

The three subspecies recognised below seem very different in their habit and field studies are necessary to determine if some of them are specifically distinct:

- 1A. Inflorescence subumbellate, with 5
or more flowers 139c. subsp. condensata
- 1B. Inflorescence sparsely racemose, with
up to 4 flowers:
- 2A. Leaflets small, usually linear, the
terminal leaflet up to 8 mm long 139a. subsp. carnosa
- 2B. Leaflets large, oblanceolate, the
terminal leaflet > 10 mm long 139b. subsp. latifolia

139a. subsp. carnosa

Krebsia carnosa Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 180
(1836, Jan.); Steud., Nom. Bot. 2(2): 850 (1841); D. Dietr., Syn.
pl. 4: 963 (1847). Type as above.

Telina striata E. Mey., Comm. Pl. Afr. Austr. 1(1): 68 (1836,
Feb. or later). Type: South Africa, Cape Province, between
"Omtata" and "Omsamwubo", Drège s.n. (B+; S!, lecto., designated
here; K!).

Krebsia striata (E. Mey.) Steud., Nom. Bot. 2(2): 850 (1841);
D. Dietr., Syn. pl. 4: 963 (1847). Type as above.

Lotononis buchenroederoides Schlechter in J. Bot. 35: 279
(1897); Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 290 (1913), as
synonym of L. carnosa. Type: South Africa, Cape Province,
"Lesseyton Neck" near Queenstown, Galpin 1951 (K!, lecto.,
designated here; BOL!).

Buchenroedera pauciflora Schlechter in J. Bot. 34: 391 (1896).

Type: South Africa, Cape Province, Hangklip mountain near Queenstown, Galpin 1608 (BOL!, lecto., designated here; PRE!).

A divaricately branched shrublet of up to 0,5 m high, widely distributed in the eastern Cape (Map 5.39). It is similar to subsp. latifolia but the latter is a more robust, erect shrub of up to 1 m high with larger leaves and slightly larger flowers (Figure 5.23).

Vouchers: Acocks 17652; Bigalke 92; Esterhuysen 29295; Tyson 1623; Van Wyk 1597, 1671--1673.

139b. subsp. latifolia B-E. van Wyk, subsp. nov. A typo habitu robustiore, foliis valde maioribus, late oblanceolatis et floribus parum maioribus differt.

Type: South Africa, Cape Province, Emgwali River near Engcobo [3227 DA], Flanagan 2805 (BOL, holo.).

This subspecies differs from the type in the more robust habit, the much larger, broadly oblanceolate leaves and larger flowers (Figure 5.23). It appears to be restricted to a small area in the eastern Cape (Map 5.39). More information is needed.

Vouchers: Acocks 9434, 9756; Bolus 8851; Galpin 8345.

139c. subsp. condensata (Harv.) B-E. van Wyk stat nov.

Lotononis carnosa (Eckl. & Zeyh.) Benth. var. condensata Harv.
in Harv. & Sond., Fl. Cap. 2: 594 (1862). Type: South Africa,
"Trans-Kei country", Bowker 107 (TCD!, holo.).

Subsp. condensata is similar to the type but differs in the following: much smaller habit (a suffrutescent pyrophyte); smaller, linear-lanceolate leaves and stipules; stipules longer than the petiole; inflorescences densely subumbellate and many-flowered; claw of the standard petal longer (\pm as long as the blade) with two callosities low down near the base (Figure 5.23). This taxon is known only from a few collections and appears to be restricted to the southern and north-western parts of the Transkei (Map 5.39).

Vouchers: Bandert 6; Barber 794; Pegler 1363, 4098; Tyson 1104.

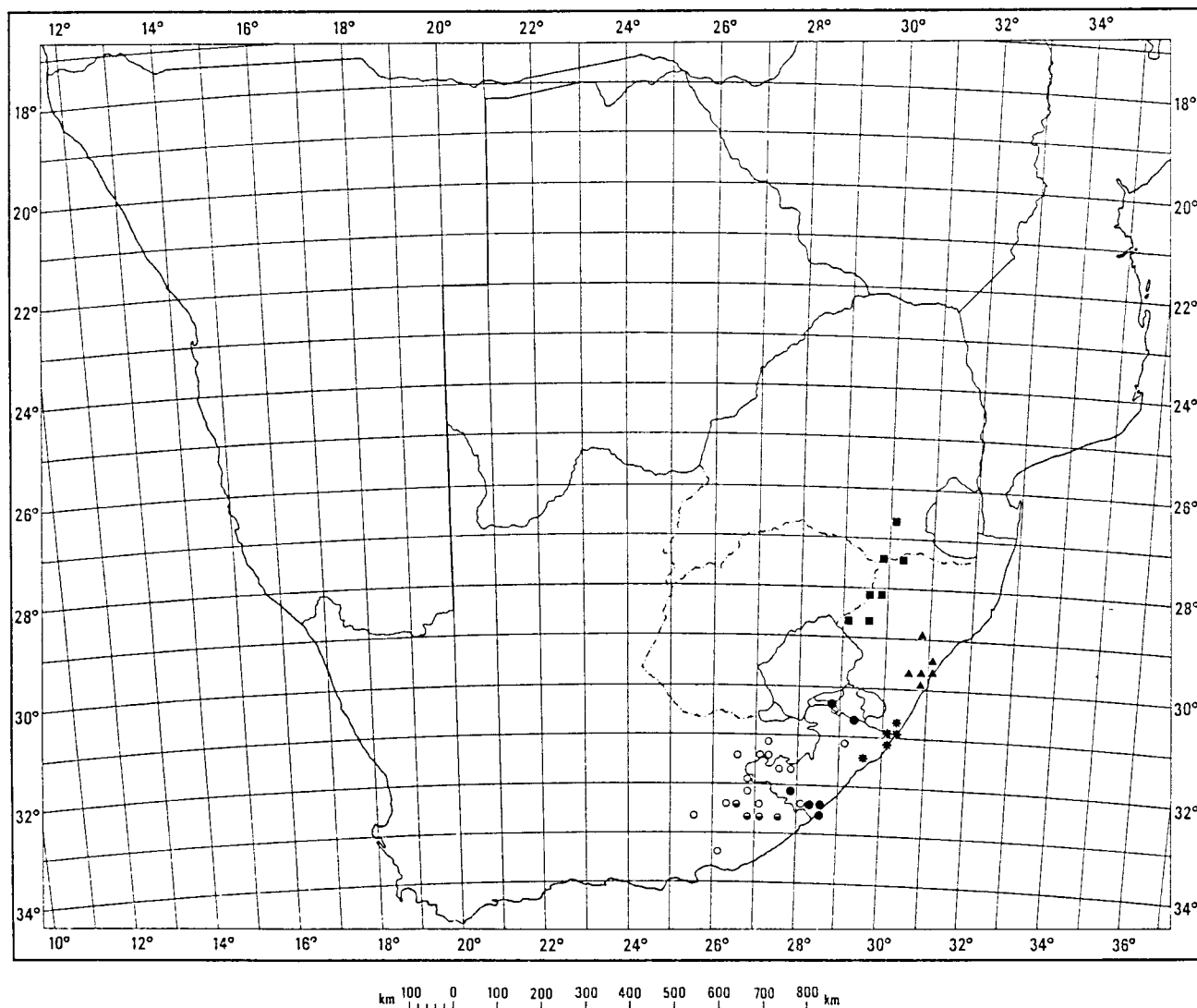
140. L. pottiae Burt Davy, Man. pl. Transvaal: 386 (1932).

Types: Transvaal, Mavrieriestad, Pott 5071 (K!, lecto., designated here; BOL!, PRE!).

Very closely related to L. carnosa but differs in the virgate habit, the narrow and straight (not recurved) leaflets and the apparent absence of callosities on the standard petal (Figure

5.23). It is geographically isolated from L. carnosa and occurs at high altitudes in the south-eastern Transvaal and north-western Natal (Map 5.39).

Vouchers: Gray H4529; Nicholson 1799; Shirley s.n. sub MO 2424781; Thode 3138, 5602.



Map 5.39. The known geographical distribution of *L. dichiloides* (▲), *L. bachmanniana* (*), *L. carnososa* subsp. *carnososa* (○), *L. carnososa* subsp. *latifolia* (◐), *L. carnososa* subsp. *condensata* (●) and *L. pottiae* (■).

Section 15. Buchenroedera (Eckl. & Zeyh.) B-E. van Wyk stat. nov.

Buchenroedera Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 194 (1836); Benth. in Lond. J. Bot. 7(4): 580 (1848); Harv. in Harv. & Sond., Fl. Cap. 2: 92 (1862); Benth. & Hook. f., Gen. Pl. 1: 478 (1865); Phill., Gen. S. Afr. Fl. Pl.: 407 (1951); Hutch., Gen. Fl. Pl. 1: 361 (1964); Dyer, Gen. S. Afr. Fl. Pl. 1: 251 (1975); Polhill in Bot. Syst. 1: 324 (1976); Polhill in Polhill & Raven, Adv. Leg. Syst. 2(1): 401 (1981); Edwards & Getliffe Norris in S. Afr. J. Bot. 55 (1989, in press).

Aspalathus spp., E. Mey., Comm. Pl. Afr. Austr. 1(1): 37 & 38 (1836); Walp. in Linnaea 13: 484 (1839); Steud., Nom. Bot. 2(1): 147 (1840).

Lectotype species (Hutchinson 1964): Buchenroedera alpina Eckl. & Zeyh. [now Lotononis alpina (Eckl. & Zeyh.) B-E. van Wyk]

Perennial shrubs or shrublets with erect or procumbent woody branches or suffrutescent shrubs with virgate erect branches from a woody base. Mature parts sparsely to densely sericeous or \pm strigillose. Leaves alternate, digitately trifoliolate, pubescent on both surfaces, more densely so on the lower surface. Stipules paired at each leaf base, occasionally absent, similar to the leaflets in size and shape or usually smaller and narrower. Inflorescences racemose to umbellate, 2- to several-flowered;

peduncles usually short and thick, rarely long and slender, terminal on the primary branches and/or on short axillary branches; bracts small, linear to lanceolate, rarely large and ovate; bracteoles absent. Flowers relatively small, blue, occasionally white with purple veins, rarely yellow, never cleistogamous. Calyx subequally lobed or with the upper and lateral lobes on either side fused higher up in pairs, the lobes usually very short, broadly to narrowly triangular, the lower lobe \pm equal to the upper ones. Standard usually much longer than the keel, broadly ovate to suborbicular, dorsally densely pubescent; claw long, without callosities; apex obtuse to emarginate. Wing petals oblong, as long as the keel, usually pubescent. Keel petals very small, half oblong-elliptic; apex somewhat pointed; pubescent or glabrous. Anthers dimorphic, 5 ovoid and dorsifixed, 4 oblong and basifixed, the carinal anther similar to the dorsifixed anthers. Pods sessile, ovoid, slightly inflated laterally, thick-walled, upper suture smooth, dehiscent, few-seeded; funicles short. Seeds 2--3,5 mm in diameter, broadly oblong to suborbicular, testa smooth, not tuberculate. Chromosome base number 7 ($2n = 28$). (Figures 5.24 & 5.25).

A group of about 11 species from the eastern parts of southern Africa (Maps 5.40, 5.41 5.42 & 5.43).

Buchenroedera is treated here as a section of Lotononis (see Part 3.2 and notes under the generic synonymy). There are several characters states to support the suggestion by Polhill (1976,

1981a) that Buchenroedera should be combined with Lotononis: absence of bracteoles, biramous hairs, blue flowers, chromosome base number of 7, integerrimine and senecionine as major alkaloids and cyanogenesis. All these character states are also found in the section Krebsia. The ovate shape of the pods is a useful and reliable diagnostic character for the section Buchenroedera and some of the species can be distinguished from Krebsia also by the pubescent wing and keel petals. The structure of the flowers (the long standard and the short, acute keel) may seem distinct but similar flowers are found in various other sections (Euchlora, Polylobium and Lotononis) and sporadically also in the sections Aulacanthus (L. dissitinodis) and Krebsia (L. minor).

Two subsections are recognised here (see Part 3.2): subsection Racemosa (5 species) and subsection Buchenroedera (6 species).

Key to subsections of section Buchenroedera:

- | | |
|--|--------------------------------------|
| 1A. Wing and keel petals glabrous | 15A. Subsection <u>Racemosa</u> |
| 1B. Wing and keel petals pubescent | |
| | 15B. Subsection <u>Buchenroedera</u> |

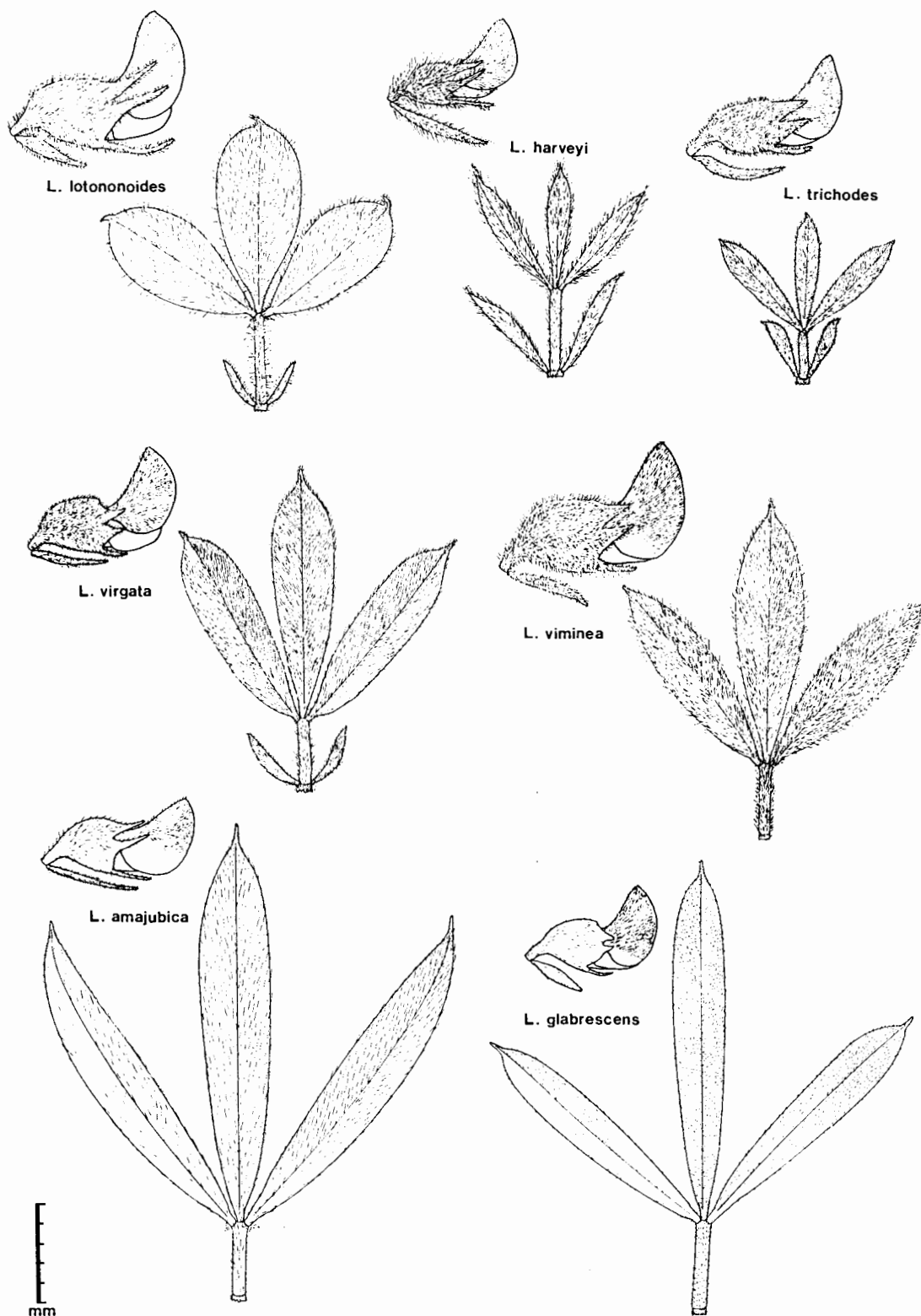


Figure 5.24. Leaves and flowers of species of the section Buchenroedera.

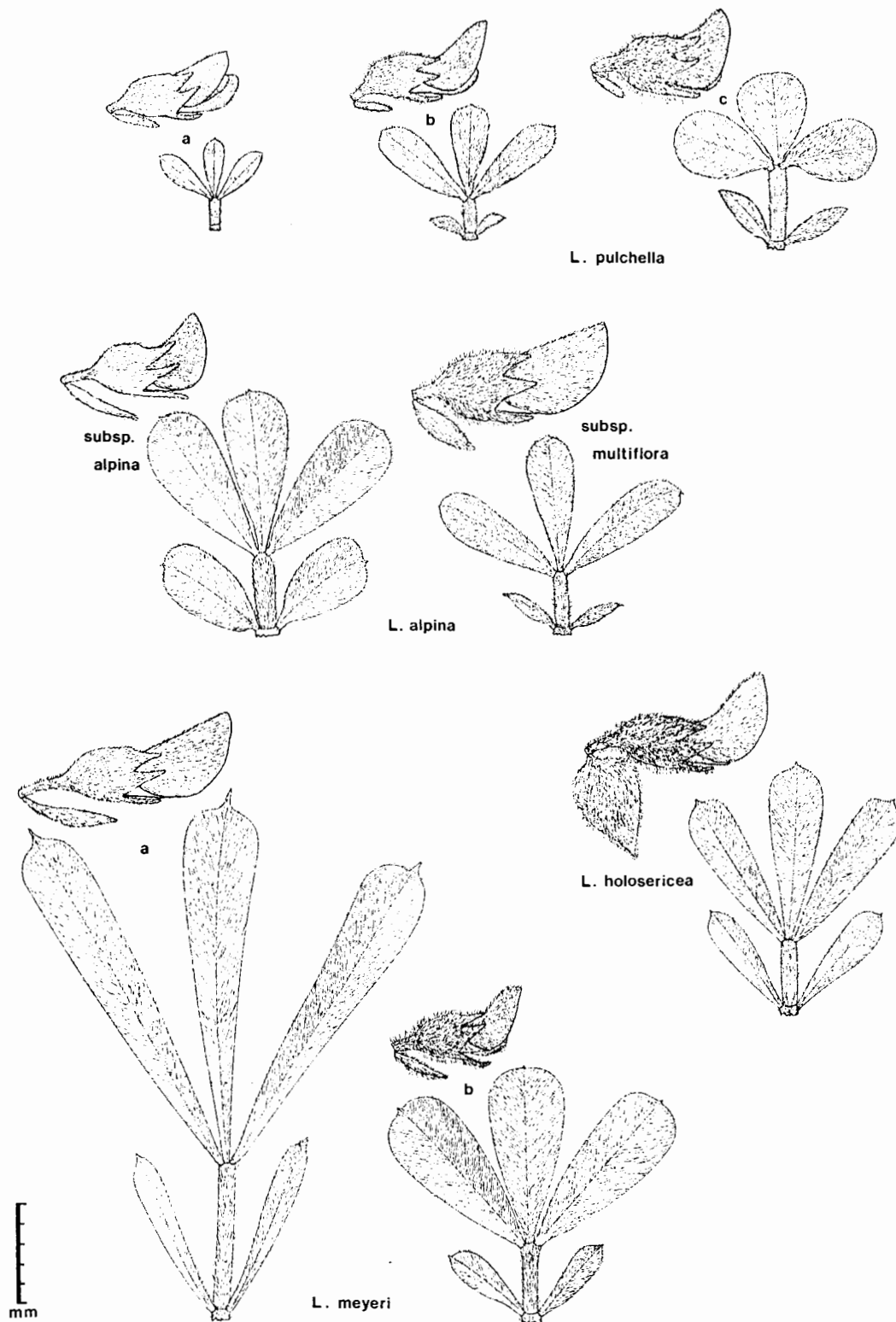


Figure 5.25. Leaves and flowers of species of the section Buchenroedera.

15A. Subsection Racemosa (Edwards & Getliffe Norris) B-E. van Wyk
stat. nov.

Buchenroedera Eckl. & Zeyh. section Racemosa Edwards & Getliffe
Norris in S. Afr. J. Bot. 55 (1989, in press).

Type species: Buchenroedera lotononoides Scott Elliot [now
Lotononis lotononoides (Scott Elliot) B-E. van Wyk.]

Suffrutescent perennials with erect flowering branches from a
woody base; inflorescences racemose; wing and keel petals totally
glabrous.

1A. Stipules present:

- 2A. Calyx with the lateral sinuses > 2 mm deep,
the lobes narrowly triangular; leaflets
usually obovate 141. L. lotononoides
- 2B. Calyx with the lateral sinuses < 2 mm deep,
the lobes broadly triangular; leaflets
oblanceolate to elliptic 144. L. virgata

1B. Stipules absent:

- 3A. Leaves and twigs densely sericeous to
tomentose, the hairs long and spreading ... 145. L. viminea
- 3B. Leaves and twigs sparsely sericeous to glabrescent,
the hairs short and appressed (if somewhat densely
sericeous then the flowers blue, not white):
- 4A. Calyx with the lateral sinuses < 1,5 mm
deep; bracts ovate or if narrowly

- lanceolate, then shorter than the calyx;
leaves sparsely and minutely sericeous
or glabrescent 143. L. glabrescens
- 4B. Calyx with the lateral sinuses > 1,5 mm
deep; bracts narrowly lanceolate, as
long or longer than the calyx; leaves
densely to sparsely sericeous but not
glabrescent 142. L. amajubica

141. L. lotononoides (Scott Elliot) B-E. van Wyk comb. nov.

Buchenroedera lotononoides Scott Elliot in J. Bot. 29: 69
(1891). Type: South Africa, Cape Province, Side Mt. Currie, near
Kokstad, East Griqualand, Tyson 1352 (K, lecto., designated here;
MO!, PRE!); Orange Free State, Nelson's Kop, Cooper 870, 1074 &
2191 (BM! 1074; BOL! 870 & 1074).

[Note: The Tyson specimen in K is the best choice for
lectotypification: this specimen was sent to Kew by Scott Elliot
in 1890; it has dissected flower parts probably used in the
description; it also has some notes (by Scott Elliot?) with
reference to B. viminea (see original diagnosis)].

Lotononis dieterlenii Phill. in Ann. S. Afr. Mus. 26: 72
(1917), synon. nov. Type: Lesotho, "Malavangeng", Leribe District
[probably Mochlanapeng, from Maboloka Mountain, 2927 CD, according
to a later note of Dieterlin], Dieterlin 871 (PRE! with notes by
Phillips, lecto., designated here; SAM!).

L. lotononoides is a common species of grassland areas in and around the Drakensberg (Map 5.40). It can be distinguished from other species by the sparsely pubescent, obovate leaflets and the recurved leaflet apices (Figure 5.24).

Vouchers: Arnold 875; Bolus 1942, 8142; Jacobsz 3555; Matthews 970; Van Wyk 1966.

142. *L. amajubica* (Burt Davy) B-E. van Wyk comb. nov.

Buchenroedera amajubica Burt Davy in Man pl. Transvaal: 389 (1932). Type: South Africa, Natal, Amajuba, Wood 4805 (NH, holo.; BOL!, K!, PRE!, SAM!).

L. amajubica is closely related to *L. glabrescens* but can be distinguished from the latter by details of the bracts and calyx lobes as given in the key. It is also similar to *L. viminea* but differs in the sparse and appressed vestiture, the narrower calyx lobes (Figure 5.24) and the blue colour of the flowers (white with purple veination in *L. viminea*). *L. amajubica* occurs at high altitudes in north-eastern Natal, eastern Orange Free State and south-eastern Transvaal (Map 5.41).

Vouchers: Beeton s.n. sub PRE 58194; Devenisch 1728; Wood 16448.

143. *L. glabrescens* (Dümmer) B-E. van Wyk comb. nov.

Buchenroedera glabrescens Dümmer in Kew Bull. 1912: 225 (1912).

Type: South Africa, Natal, without precise locality, Gerrard 1090 (K!, annotated by Dümmer, lecto., designated here; BM!, K!).

L. glabrescens can be distinguished from *L. amajubica* by the shorter calyx lobes and glabrescent leaves (Figure 5.24). Future studies may show that *L. glabrescens* and *L. amajubica* are only subspecifically distinct. The species appears to be limited to central and northern Natal (Map 5.41).

Vouchers: Edwards 132; Hilliard 1420; Johnstone 605.

144. *L. virgata* B-E. van Wyk, sp. nov. *L. lotononoidi* similis sed habitu plus virgato, vestitura densiori plus appresso, foliolis angustioribus oblanceolatis (non obovatis), inflorescentiis semper terminalibus, lobis calycis valde brevioribus atque floribus albis non caeruleis. Etiam similis est *L. vimineae*, sed ab haec specie habitu minore, praesentia stipularum atque vestitura brevior plus appressa differt.

Buchenroedera sparsiflora sensu auct. non Wood & Evans: Edwards & Getliffe Norris in S. Afr. J. Bot. 55 (1989, in press).

Type: South Africa, Natal, Estcourt District, Giant's Castle Game Reserve, Ncibitwane Valley [2929 BC], Trauseld 720 (PRE, holo.; NU, iso).

L. virgata is similar to L. lotononoides but differs in the more virgate habit, the denser and more appressed vestiture, the narrower, oblanceolate (not obovate) leaflets, the invariably terminal inflorescences, the much shorter calyx lobes (Figure 5.24) and the \pm white, not blue flowers. It is also similar to L. viminea, but differs from this species in the smaller habit, the presence of stipules, the shorter and more appressed vestiture.

A re-evaluation of the description of Buchenroedera sparsiflora Wood & Evans indicated that it is not the same taxon as L. virgata as was supposed by Edwards and Getliffe Norris (1989). I could also not find any type material of B. sparsiflora but the plant is said to be no more than 6 poll. (15 cm) tall, while L. virgata grows to a height of at least 40 cm. It is also described as divaricately much-branched, while L. virgata is virtually unbranched except at the very base (definitely not divaricately branched). Furthermore, the flowers are borne single (spicate in L. virgata) and are dark purple (dirty white with greyish mauve venation in L. virgata). This description clearly does not refer to L. virgata, but rather fits L. galpinii Dümmer in every detail. The type locality of B. sparsiflora is given as "Summit of Bushmans River Pass, 8--900 ped. alt." According to the

altitude, this locality refers to Bushman's Nek Pass (2929 CC) and not to the area of the Bushman's River (2929 BA). *L. galpinii* grows only at such high altitudes and is known to occur in Bushman's Nek Pass. *L. virgata* has been recorded from lower altitudes and is known only from a limited area in south-eastern Natal (Map 5.41).

Vouchers: Hilliard & Burt 19092; Wright 2343.

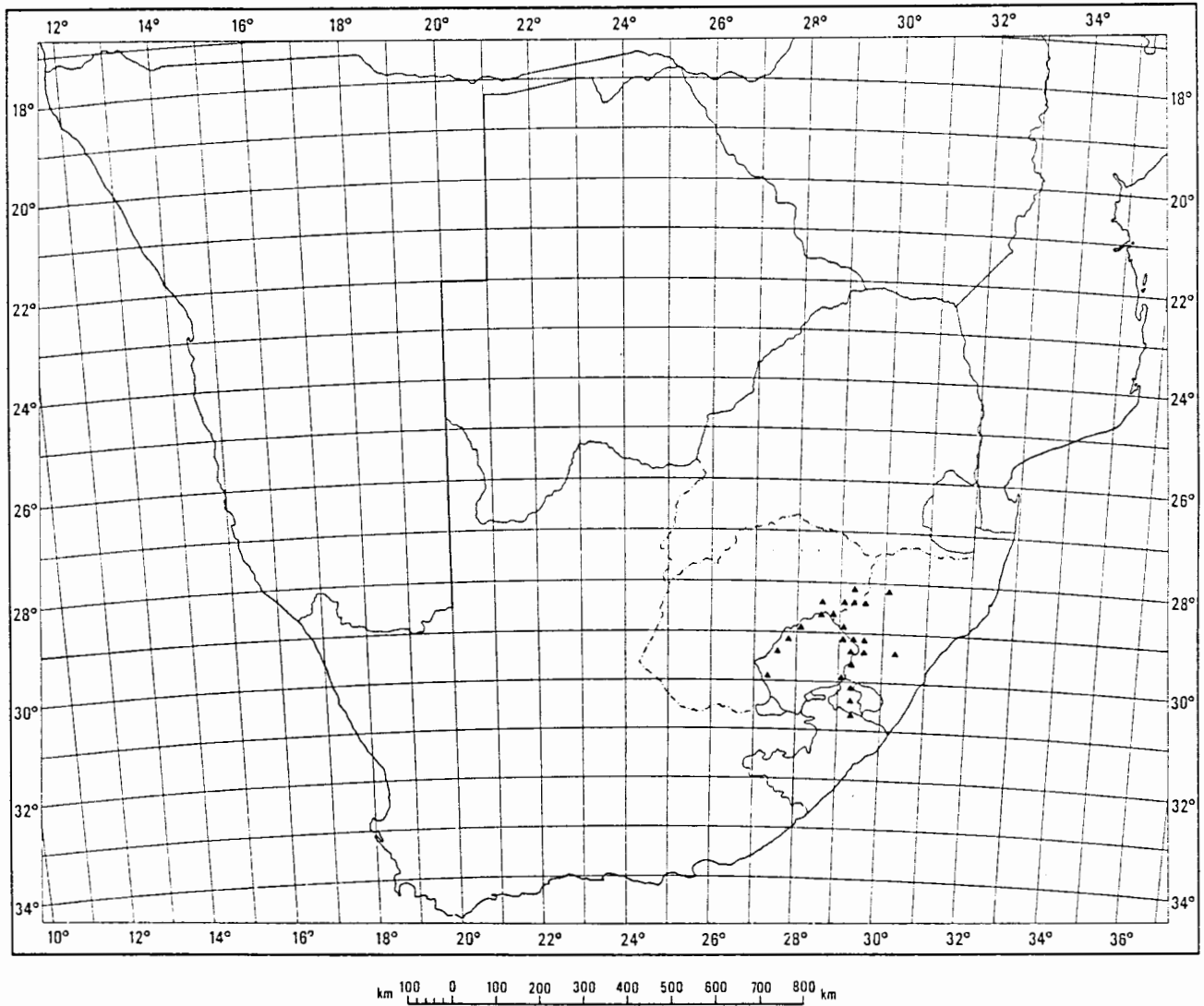
145. *L. viminea* (E. Mey.) B-E. van Wyk comb. nov.

Aspalathus viminea E. Mey., *Comm. Pl. Afr. Austr.* 1(1): 38 (1836). Type: South Africa, Transkei, between "Omsamcabo" [3129 BB] and Omtendo [also 3129 BB], Drège s.n. (S!, larger specimen, lecto., designated here; BM!, BOL, K!, 2 specimens, PRE!, S!).

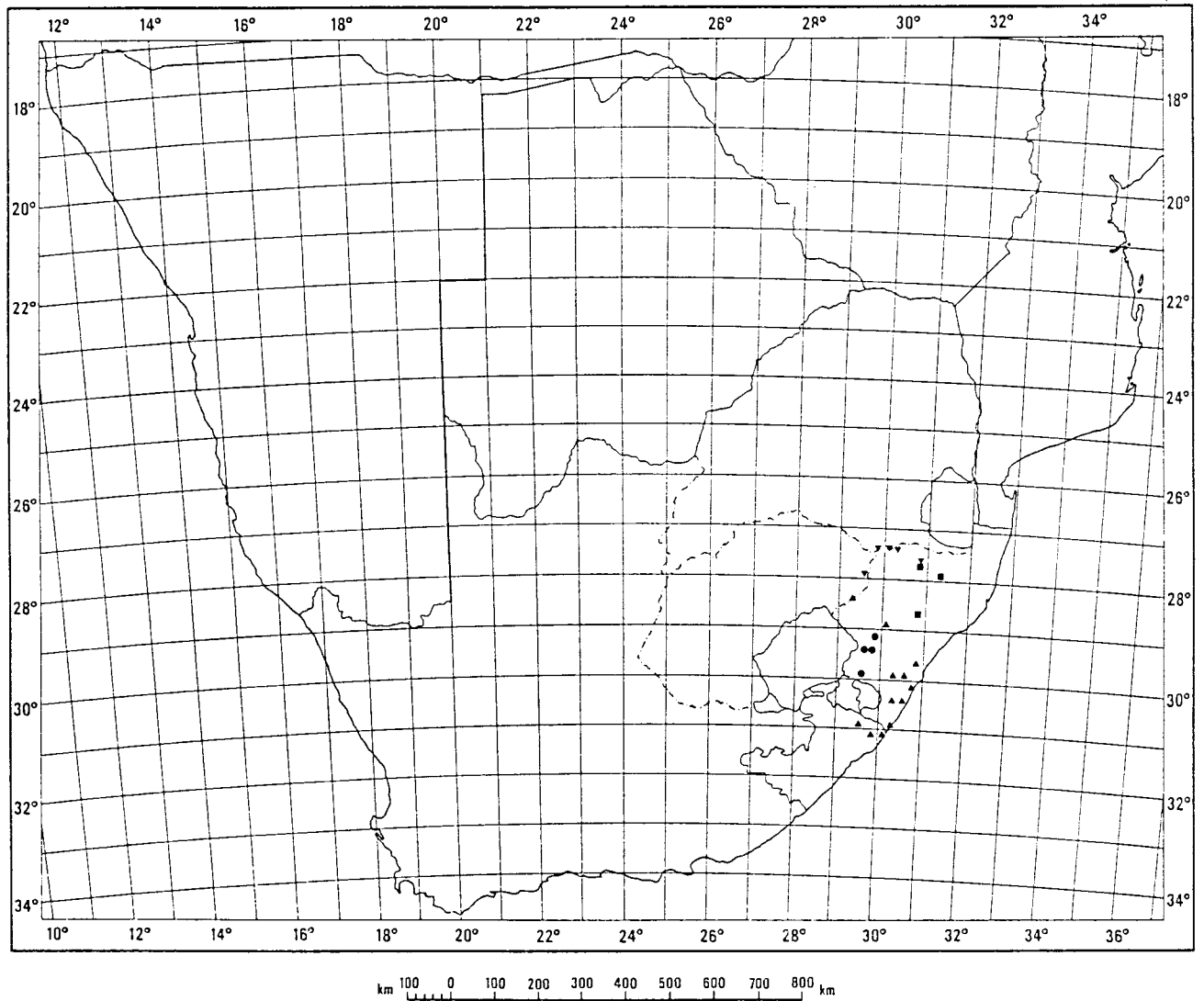
Buchenroedera viminea (E. Mey.) Presl in *Abh. k. Böhm. Ges. Wiss.* 5(3): 477 (1845); Benth. in *Lond. J. Bot.* 7(4): 583 (1848); Harv. in *Harv. & Sond., Fl. Cap.* 2: 94 (1862); Wood & Evans, *Natal Pl.* 1: 30 & t. 35 (1898). Type as above.

L. viminea may be confused with *L. amajubica*, but the vestiture is more dense and spreading (Figure 5.24), the flowers are white with purplish veins (blue in *L. amajubica*), the flowers are usually borne amongst the leaves and the distribution extends further south (Map 5.41).

Vouchers: Nicholson 2119; Tyson 2709; Wood 8552, 11135.



Map 5.40. The known geographical distribution of *L. lotononoides* (▲).



Map 5.41. The known geographical distribution of *L. amajubica* (▼), *L. glabrescens* (■), *L. virgata* (●) and *L. viminea* (▲).

15B. Subsection Buchenroedera

Woody shrubs or rarely suffrutescent perennials with short flowering branches from a prostrate woody base; inflorescences umbellate, rarely racemose; wing and keel petals pubescent.

- 1A. Inflorescence a spicate raceme; calyx with the lateral sinuses > 2 mm deep, the lobes narrowly triangular 151. L. harveyi
- 1B. Inflorescence umbellate or subumbellate; calyx with the lateral sinuses < 2 mm deep, the lobes broadly triangular:
 - 2A. Bracts > 3 mm wide 150. L. holosericea
 - 2B. Bracts up to 2 mm wide:
 - 3A. Flowers blue:
 - 4A. Erect shrub with robust woody branches; bracts shorter than the calyx 146. L. pulchella
 - 4B. Prostrate suffrutex with thin slender branches from a horizontal woody base; bracts as long or longer than the calyx 147. L. trichodes
 - 3B. Flowers white or yellow:
 - 5A. Petals white with the veins purple; tip of keel dark purple inside 149. L. meyeri
 - 5B. Petals yellow; tip of keel not purple inside 148. L. alpina

146. L. pulchella (E. Mey.) B-E. van Wyk comb. nov.

Aspalathus pulchella E. Mey., Comm. Pl. Afr. Austr. 1(1): 38 (1836, Feb. or later); Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 477 (1845), as synonym of Buchenroedera tenuifolia Eckl. & Zeyh.; Benth. in Lond. J. Bot. 7(4): 582 (1848), as synonym of B. tenuifolia. Type: South Africa, Cape Province, Katberg [3226 DA], Drège s.n. a (S!, lecto., designated here; K!); "Stromberg" [Stormberg, 3126 BC], Drège s.n. b (BM!, K!).

Buchenroedera tenuifolia Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 196 (1836, Jan.); Benth. in Lond. J. Bot. 7(4): 582 (1848); Harv. in Harv. & Sond., Fl. Cap. 2: 93 (1862); non Lotononis tenuifolia (Eckl. & Zeyh.) Dümmer in Trans. Roy. Soc. S. Afr. 3(2): 302 (1913), nec Polylobium tenuifolium Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 182 (1836). Type: South Africa, Cape Province, near "Silo" at the "Klipplaatrivier" [3226 BB], Ecklon & Zeyher 1355 (S!, lecto., designated here; C!, K!).

Buchenroedera tenuifolia Eckl. & Zeyh. var. pulchella (E. Mey.) Harv. in Harv. & Sond., Fl. Cap. 2: 93 (1862). Type as for A. pulchella.

B. macowanii Dümmer in Kew Bull. 1912: 225 (1912), synon. nov. Type: South Africa, Cape Province, Somerset Div., on "Bruintjes Hoogte" [3225 CB], MacOwan 1738 (K!, lecto., designated here; SAM!).

Distinguished from other species by the robust, woody branches, umbellate or subumbellate inflorescences and blue flowers. (Figure 5.25). The geographical distribution is shown in Map

5.42. Eastern Cape forms (b in Figure 5.25) tend to have narrower leaflets than those from high altitudes in the Drakensberg (c in Figure 5.25), the latter previously recognised as a distinct variety. Dümmer's (1912) B. macowanii (a in Figure 5.25) represents a geographically isolated form from the western limits of the distribution range with few-flowered inflorescences, small leaflets, caducous stipules and slightly smaller flowers.

Vouchers. Typical form with broad leaflets: Bayliss 1360; Beverley & Hoener 685; Dieterlen 1252; Hilliard & Burtt 9261, 7450, 13533; Symons 23233. Form with narrow leaflets: Barker 3496; Baur s.n. sub Marloth 6602; Grobbelaar 684; Stretton 198; Van Wyk 1592, 1593, 1675, 1676. Western form ("B. macowanii"):
Brynard 166; Liebenberg 7345; Van Wyk 1331--1334.

147. L. trichodes (E. Mey.) B-E. van Wyk comb. nov.

Aspalathus trichodes E. Mey., Comm. Pl. Afr. Austr. 1(1): 38 (1836). Type: South Africa, Cape Province, summit of the Katberg [3226 DA], Drège s.n. (S!, lecto., designated here; BM!, K! sub Herb. Benth., K!, sub Herb. Hook.).

Buchenroedera trichodes (E. Mey.) Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 477 (1845); Benth. in Lond. J. Bot. 7(4): 582 (1848); Harv. in Harv. & Sond., Fl. Cap. 2: 94 (1862). Type as above.

L. trichodes is the only species of the subsection with a prostrate habit (the habit in *L. harveyi* is unknown, however). It is similar to *L. pulchella* but can easily be distinguished by the prostrate and suffrutescent habit, the thin and slender twigs and the larger bracts (Figure 5.24). It appears to be restricted to high altitudes on the Winterberg (Map 5.42).

Vouchers: Baur s.n. sub SAM 15337; Ford s.n. sub Marloth 11391; Galpin 1729; Van Wyk 1682, 1685, 1693.

148. *L. alpina* (Eckl. & Zeyh.) B-E. van Wyk comb. nov.

Buchenroedera alpina Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 195 (1836); Benth. in Lond. J. Bot. 7(4): 581 (1848); Harv. in Harv. & Sond., Fl. Cap. 2: 93 (1862), as synonym of *B. multiflora*. Type: South Africa, Cape Province, "Winterberg" [3226 AD] near the "Klipplaatrivier" [3226 BB], Ecklon & Zeyher 1352 (S!, lecto., designated here; C!, S!).

L. alpina is the only species of the section *Buchenroedera* with yellow flowers. Two distinct subspecies are recognised here:

- 1A. Stipules oblanceolate to obovate, similar to the
leaflets in size and shape; flowers < 7 mm long;
branches thick and robust; tall erect shrub of
up to 1,5 m high 148a. subsp. alpina
- 1B. Stipules lanceolate or narrowly elliptical, much
smaller and narrower than the leaflets; flowers
> 8 mm long; branches slender; small much-branched
shrublet of up to 0,6 m high 148b. subsp. multiflora

148a. subsp. alpina

This subspecies has a limited distribution in the eastern Cape (Map 5.43) and can easily be distinguished from subsp. multiflora by the thick and robust branches, the larger and broader leaves and stipules and the smaller flowers (Figure 5.25). This taxon may prove to be specifically distinct from subsp. multiflora once the full range of morphological variation becomes known.

Vouchers: Bayliss 5779; Edwards, Cadman & Norris 3247; Gibbs Russell 3538; Hilliard & Burt 12397; Phillipson 793.

148b. subsp. multiflora (Eckl. & Zeyh.) B-E. van Wyk comb. nov.
et stat. nov.

Buchenroedera multiflora Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 195 (1836, Jan.); Benth. in Lond. J. Bot. 7(4): 582 (1848); Harv. in Harv. & Sond., Fl. Cap. 2: 93 (1862); non Lotononis multiflora Schinz. Type: South Africa, Cape Province, "Zuurebergskette" at a place called "Zwartehoogdens" near Grahamstown and at "Vischrivier" near "Hermanuskraal", Ecklon & Zeyher 1354 (S!, lecto., designated here; C!, K!).

B. gracilis Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 195 (1836, Jan.); Benth. in Lond. J. Bot. 7(4): 582 (1848), as synonym of B. multiflora; Harv. in Harv. & Sond., Fl. Cap. 2: 93 (1862), as synonym of B. multiflora; non Lotononis gracilis (E. Mey.) Benth. Type: South Africa, Cape Province, Bothasberg near "Vischrivier" [3326 BA], Ecklon & Zeyher 1353 (S!, with label in Ecklon's hand, lecto., designated here; C!, S!).

Aspalathus cuneata E. Mey. var. hamulosa E. Mey., Comm. Pl. Afr. Austr. 1(1): 37 (1836, Feb. or later); Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 477 (1845), as synonym of B. multiflora; Benth. in Lond. J. Bot. 7(4): 582 (1848), as synonym of B. multiflora; Harv. in Harv. & Sond., Fl. Cap. 2: 93 (1862), as synonym of B. multiflora. Type: South Africa, Cape Province, "Assagaybosch" [3326 AD], Drège s.n. a (K!); near "Gekau" [3228 AC], Drège s.n. b (BM!, K!, S!); "Zuurebergen" [3325 AD], Drège s.n. c (S!, lecto., designated here; BM!, K!).

Aspalathus polyantha Walp. in Linnaea 13: 485 (1839); Benth. in Lond. J. Bot. 7(4): 582 (1848), as synonym of B. multiflora; Harv. in Harv. & Sond., Fl. Cap. 2: 93 (1862), as synonym of B. multiflora. Type as for Buchenroedera multiflora.

This subspecies is similar to *L. meyeri* but the flowers are yellow and not white with purplish veins as in the latter. It is widely distributed in the eastern Cape (Map 5.43).

Vouchers: Acocks 9064; Bayliss 7442a; Esterhuysen 13261; Galpin 185; Schonland 1673.

149. *L. meyeri* (Presl) B-E. van Wyk comb. nov.

Buchenroedera meyeri Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 477 (1845); Benth. in Lond. J. Bot. 7(4): 581 (1848); Harv. in Harv. & Sond., Fl. Cap. 2: 93 (1862). Type: South Africa, Cape Province, between "Buffelrivier" [3327 BB] and "Key" [3228 CA], Drège s.n. a (S!, Plantae capenses label, lecto., designated here; BM!, K!, S!); near "Komga" [3227 DB], Drège s.n. b (BM!, K! sub Herb. Benth., K!, sub. Herb. Hook., S!).

Aspalathus cuneata E. Mey. var. retusa E. Mey., Comm. Pl. Afr. Austr. 1(1): 37 (1836); Presl in Abh. k. Böhm. Ges. Wiss. 5(3): 477 (1845), as synonym of *B. meyeri*; Benth. in Lond. J. Bot. 7(4): 582 (1848), as synonym of *B. meyeri*; Harv. in Harv. & Sond., Fl. Cap. 2: 93 (1862), as synonym of *B. meyeri*. Type as above.

B. umbellata Harv. in Harv. & Sond., Fl. Cap. 2: 93 (1862), synon. nov. Type: South Africa, Transkei Country, "on the Plains", Barber 35 (TCD, holo.; BOL!, K!, S!). [Note: the specimens in K and S have been annotated by Harvey].

L. meyeri is very similar to *L. alpina* subsp. *multiflora* and difficult to distinguish from it when not in flower. The petals are white with purple veins, the tip of the keel petals are dark purple inside and the leaflets are somewhat less recurved than those of *L. alpina* (Figure 5.25). It has a more northern distribution than *L. alpina* and occurs mainly in the Transkei (Map 5.42). Forms of the species with many-flowered umbels and large leaves, previously known as *L. umbellata* (a in Figure 5.25), is considered here to be best included under *L. meyeri*.

Vouchers. Typical form: Esterhuysen 29254; Hilliard & Burt 7290, 13110, 16325; Nicholson 1195; A.E. van Wyk 5150; Van Wyk 1764--1768. "*L. umbellata*" form: Barber 35; Pegler 1268; Tyson 2640.

150. *L. holosericea* (E. Mey.) B-E. van Wyk comb. nov.

Aspalathus holosericea E. Mey., *Comm. Pl. Afr. Austr.* 1(1): 37 (1836). Type: South Africa, Transkei, near "Omgaziana" [probably Umgazana, 3129 CB], Drège s.n. a (S!, lecto., designated here; K!); "Morley" [?], Drège s.n. b (not found).

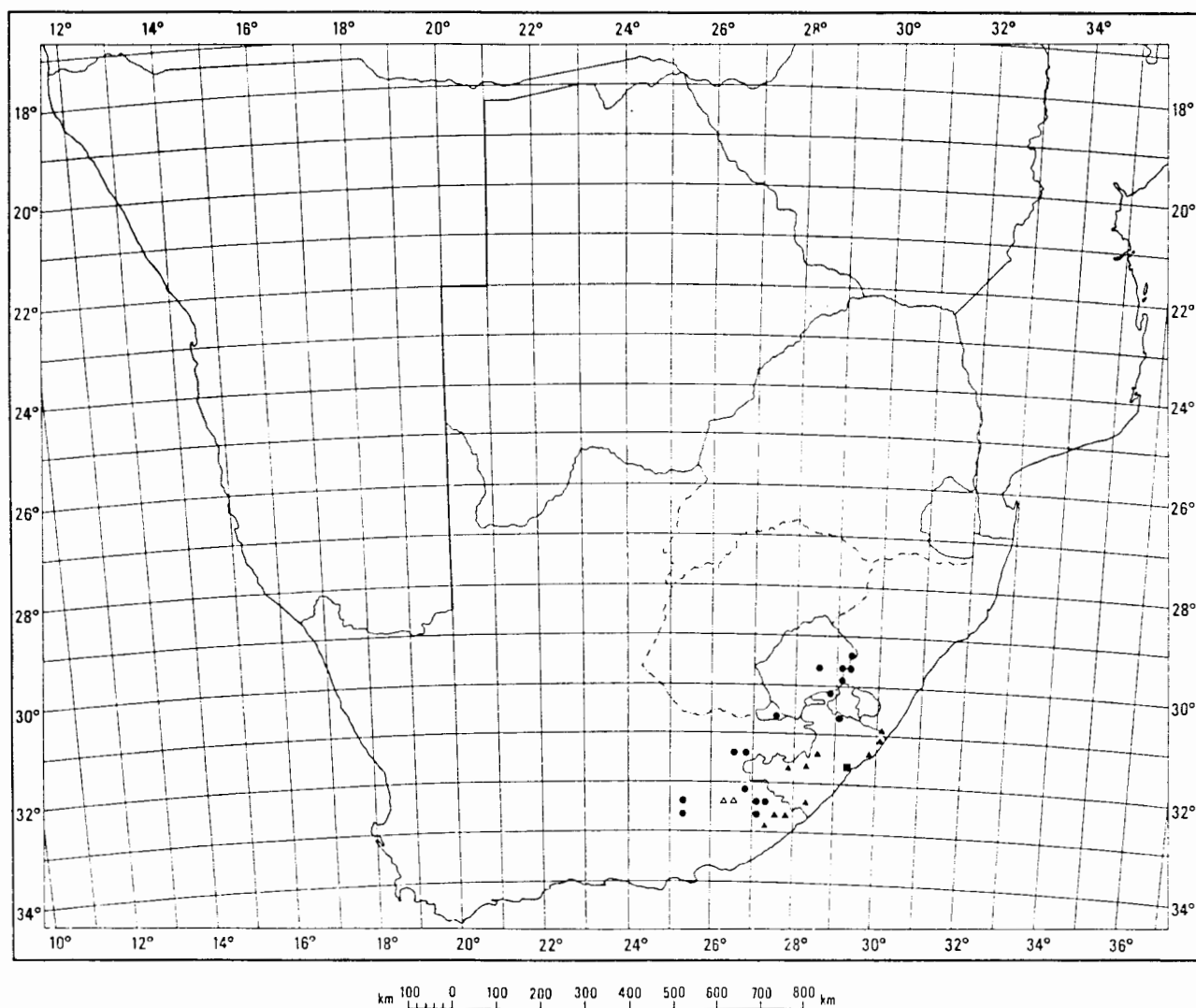
Buchenroedera holosericea (E. Mey.) Benth. in *Lond. J. Bot.* 7(4): 581 (1848); Harv. in *Harv. & Sond., Fl. Cap.* 2: 92 (1862). Type as above.

This poorly known species is perhaps not distinct from L. meyeri but the bracts (Figure 5.25) are unusually large and the vestiture is very densely silky. L. holosericea is known only from the type collection (Map 5.42).

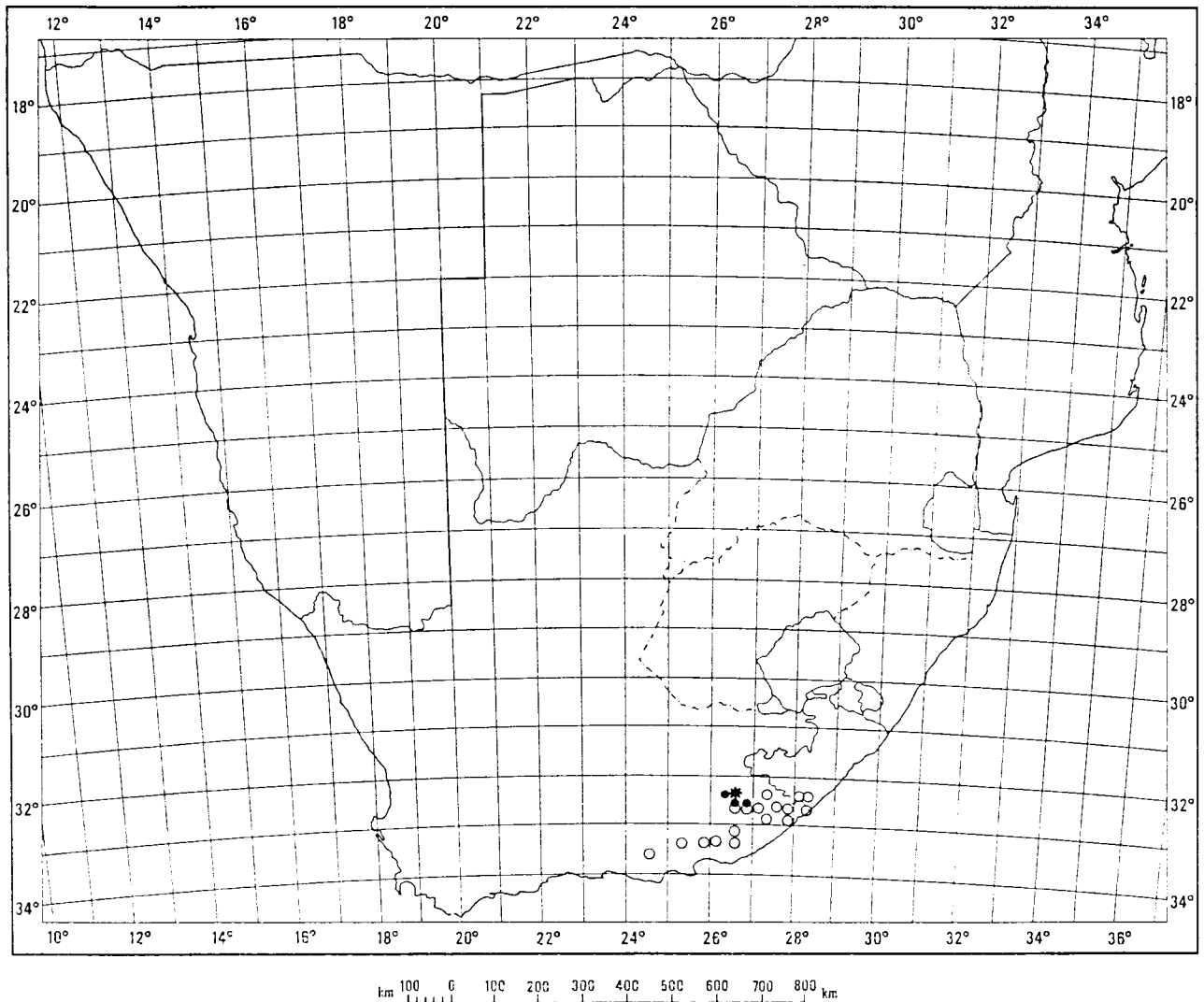
151. L. harveyi B-E. van Wyk nom. nov.

Buchenroedera spicata Harv. in Harv. & Sond., Fl. Cap. 2: 93 (1862) non Lotononis spicata Compton. Type: South Africa, Cape Province, sides of the Winterberg, Barber 43 (TCD, holo.; BOL!, K!).

This species is known only from the type collection (Map 5.43). It is similar to L. trichodes but can be distinguished by the elongate racemes, the white flowers, the densely hairy petals, the long calyx lobes and the hirsute leaflets (Figure 5.24).



Map 5.42. The known geographical distribution of *L. pulchella* (●), *L. trichodes* (△), *L. meyeri* (▲) and *L. holosericea* (■).



Map 5.43. The known geographical distribution of *L. alpina* subsp. *alpina* (●), *L. alpina* subsp. *multiflora* (○) and *L. harveyi* (*).

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<i>C. versicolor</i> E. Mey.	34a
<i>C. vexillata</i> E. Mey.	110
<i>Euchlora</i> Eckl. & Zeyh.	Sect. 10
<i>E. hirsuta</i> (Thunb.) Druce	101
<i>E. serpens</i> Eckl. & Zeyh.	101
<i>Krebsia</i> Eckl. & Zeyh.	Sect. 14
<i>K. argentea</i> Eckl. & Zeyh.	136
<i>K. carnosae</i> Eckl. & Zeyh.	139a
<i>K. cytisoides</i> (E. Mey.) Steud.	130
<i>K. divaricata</i> Eckl. & Zeyh.	132
<i>K. eriocarpa</i> (E. Mey.) Steud.	129
<i>K. genuflexa</i> (E. Mey.) Steud.	132

<i>K. striata</i> (E. Mey.) Steud.	139a
<i>K. striata</i> Eckl. & Zeyh. <u>sensu</u> Benth.	130
<i>K. stricta</i> Eckl. & Zeyh.	130
<i>Lebeckia densa</i> Thunb.	120a
<i>L. leucoclada</i> Schlechter	120b
<i>L. microphylla</i> E. Mey.	136
var. <i>leptophylla</i> E. Mey.	136
<i>Leobordea</i> Del.	Sect. 5
<i>L. abyssinica</i> Hochst. ex A. Rich.	45
<i>L. argyrolobioides</i> Jaub. & Spach	42
<i>L. clandestina</i> (E. Mey.) Steud.	45
<i>L. genistoides</i> Fenzl	42
<i>L. lotoidea</i> Del.	45
<i>L. lupinifolia</i> Boiss.	41
<i>L. lupinifolia</i> Boiss. ex Jaub. & Spach	41
<i>L. persica</i> Jaub. & Spach	45
<i>L. porrecta</i> (E. Mey.) Steud.	45
<i>L. sericea</i> Ledeb.	42
<i>L. sphaerosperma</i> Jaub. & Spach	45
<i>L. villosa</i> Pomel	41
var. <i>intermedia</i> Pomel	41
<i>Leptidium</i> Presl	Sect. 4
<i>L. brachylobum</i> (E. Mey.) Presl	67
<i>L. calycinum</i> (E. Mey.) Presl	39
<i>L. debile</i> (Eckl. & Zeyh.) Presl	127
<i>L. divaricatum</i> (Eckl. & Zeyh.) Presl	39
<i>L. erubescens</i> (E. Mey.) Presl	85
<i>L. falcatum</i> Presl	30
<i>L. falcatum</i> (E. Mey.) Presl	66
<i>L. filicaulis</i> (Eckl. & Zeyh.) Presl	34a
<i>L. molle</i> (E. Mey.) Presl	27
<i>L. tenellum</i> (E. Mey.) Presl	100
<i>L. versicolor</i> (E. Mey.) Presl	34a
<i>Leptis</i> E. Mey. ex Eckl. & Zeyh.	Sect. 4
<i>L. brachyloba</i> (E. Mey.) Benth.	67
<i>L. calycina</i> (E. Mey.) Steud.	39
<i>L. debilis</i> Eckl. & Zeyh.	30
<i>L. divaricata</i> Eckl. & Zeyh.	39
<i>L. erubescens</i> (E. Mey.) Benth.	85
<i>L. falcata</i> (E. Mey.) Benth.	66
<i>L. filicaulis</i> Eckl. & Zeyh.	34a
<i>L. mollis</i> (E. Mey.) Benth.	27
<i>L. prolifera</i> (E. Mey.) Eckl. & Zeyh.	30
<i>L. versicolor</i> (E. Mey.) Eckl. & Zeyh.	34a
<i>Lipozygis</i> (sect. 3) E. Mey.	Sect. 4
<i>Lipozygis</i> (sect. 4) E. Mey. partly	Sect. 3
<i>Lipozygis</i> (sect. 4) E. Mey. partly	Sect. 6
<i>Lipozygis</i> (sect. 5) E. Mey.	Sect. 11
<i>Lipozygis</i> (E. Mey.) Benth.	Sect. 3
<i>L. argentea</i> Meisner	99
<i>L. brachyloba</i> E. Mey.	67
<i>L. calycina</i> E. Mey.	39
var. <i>b.</i> E. Mey.	29

<i>L. carinata</i> E. Mey.	35
<i>L. corymbosa</i> E. Mey.	20
<i>L. erubescens</i> E. Mey.	85
var. <i>macrophylla</i> E. Mey.	85
var. <i>microphylla</i> E. Mey.	85
<i>L. falcata</i> E. Mey.	66
<i>L. humifusa</i> E. Mey.	34a
<i>L. involucrata</i> (Berg.) E. Mey.	104d
<i>L. kraussiana</i> Meisner	99
<i>L. mollis</i> E. Mey.	27
<i>L. peduncularis</i> E. Mey.	104d
<i>L. pentaphylla</i> E. Mey.	56
<i>L. polycephala</i> E. Mey.	52
<i>L. quinata</i> (Thunb.) E. Mey.	9
<i>L. radula</i> E. Mey.	34a
<i>L. tenella</i> E. Mey.	99
var. <i>piloso-villosa</i> E. Mey.	99
var. <i>sericea</i> E. Mey.	99
var. <i>tenella</i>	100
<i>L. umbellata</i> (L.) E. Mey.	127
<i>L. villosa</i> E. Mey. sensu Benth.	27
<i>Listia</i> E. Mey.	Sect. 1
<i>L. heterophylla</i> E. Mey.	5
<i>L. salteri</i> Bak.f.	10
<i>Lotononis</i> (DC.) Eckl. & Zeyh.	
sect. <i>Aulacanthus</i> (E. Mey.) Benth.	Sect. 13
sect. <i>Buchenroedera</i> (Eckl. & Zeyh.)	
B-E. van Wyk	Sect. 15
sect. <i>Cleistogama</i> B-E. van Wyk	Sect. 9
sect. <i>Digitata</i> B-E. van Wyk	Sect. 2
sect. <i>Euchlora</i> (Eckl. & Zeyh.) B-E. van Wyk ...	Sect. 10
sect. <i>Krebsia</i> (Eckl. & Zeyh.) Benth.	Sect. 14
sect. <i>Leobordea</i> (Del.) Benth.	Sect. 5
sect. <i>Leptis</i> (E. Mey. ex Eckl. & Zeyh.)	
Benth.	Sect. 4
sect. <i>Lipozygis</i> (E. Mey.) Benth.	Sect. 3
sect. <i>Listia</i> (E. Mey.) B-E. van Wyk	Sect. 1
sect. <i>Lotononis</i>	Sect. 12
sect. <i>Monocarpa</i> B-E. van Wyk	Sect. 8
sect. <i>Oxydium</i> Benth.	Sect. 7
sect. <i>Polylobium</i> (Eckl. & Zeyh.) Benth.	Sect. 11
sect. <i>Synclistus</i> B-E. van Wyk	Sect. 6
sect. <i>Telina</i> (E. Mey.) Benth.	Sect. 12
subsect. <i>Brachyantha</i> B-E. van Wyk	Subsect. 7G
subsect. <i>Bracteolata</i> B-E. van Wyk	Subsect. 3A
subsect. <i>Buchenroedera</i>	Subsect. 15B
subsect. <i>Delicata</i> B-E. van Wyk	Subsect. 7B
subsect. <i>Distans</i> B-E. van Wyk	Subsect. 7A
subsect. <i>Falcata</i> B-E. van Wyk	Subsect. 7D
subsect. <i>Fragilis</i> B-E. van Wyk	Subsect. 7M
subsect. <i>Glabrifolia</i> B-E. van Wyk	Subsect. 14B
subsect. <i>Krebsia</i>	Subsect. 14A
subsect. <i>Laxa</i> B-E. van Wyk	Subsect. 7H
subsect. <i>Lipozygis</i>	Subsect. 3B

<i>L. bullonii</i> Emberger & Maire	44
<i>L. burchellii</i> Benth.	77
<i>L. caerulea</i> (E. Mey.) B-E. van Wyk	136
<i>L. calycina</i> (E. Mey.) Benth.	39
var. <i>acuta</i> Dümmer	39
var. <i>hirsutissima</i> (Harv.) Dümmer	39
<i>L. carinalis</i> Harv.	45
<i>L. carinata</i> (E. Mey.) Benth.	35
<i>L. carnea</i> B-E. van Wyk	92
<i>L. carnosa</i> (Eckl. & Zeyh.) Benth.	139
subsp. <i>carnosa</i>	139a
subsp. <i>condensata</i> (Harv.) B-E. van Wyk	139c
subsp. <i>latifolia</i> B-E. van Wyk	139b
var. <i>condensata</i> Harv.	139c
<i>L. chrysophylla</i> Schlechter in sched.	87c
<i>L. clandestina</i> (E. Mey.) Benth.	45
var. <i>steingroeveriana</i> Schinz	45
<i>L. clandestina</i> (E. Mey.) Benth. <i>sensu</i> Bak.	45
<i>L. complanata</i> B-E. van Wyk	113
<i>L. comptonii</i> B-E. van Wyk	122
<i>L. corymbosa</i> (E. Mey.) Benth.	20
<i>L. crumanina</i> Burch. ex Benth.	76
<i>L. curtii</i> Harms	74
<i>L. cytisoides</i> (E. Mey.) Benth.	
var. <i>brevifolia</i> (Eckl. & Zeyh. ex Drège) Dümmer	130
var. <i>sericea</i> Dümmer	129
<i>L. dahlgrenii</i> B-E. van Wyk	118
<i>L. debilis</i> (Eckl. & Zeyh.) Benth.	127
<i>L. decidua</i> Eckl. & Zeyh.	99
<i>L. decipiens</i> Schlechter ex De Wildeman	66
<i>L. decrepita</i> Dümmer	95
<i>L. decumbens</i> (Thunb.) B-E. van Wyk	34
subsp. <i>decumbens</i>	34a
subsp. <i>rehmannii</i> (Dümmer) B-E. van Wyk	34b
<i>L. delicata</i> (Bak.f.) Polhill	61
<i>L. delicatula</i> H. Bol. ex De Wildeman	9
<i>L. densa</i> (Thunb.) Harv.	120
subsp. <i>congesta</i> B-E. van Wyk	120c
subsp. <i>densa</i>	120a
subsp. <i>gracilis</i> (E. Mey.) B-E. van Wyk	120d
subsp. <i>leucoclada</i> (Schlechter) B-E. van Wyk	120b
<i>L. depressa</i> Eckl. & Zeyh.	99
<i>L. dichiloides</i> Sond.	137
<i>L. dichotoma</i> (Del.) Boiss.	45
var. <i>persica</i> (Jaub. & Spach) Post	45
<i>L. dieterlenii</i> Phill.	141
<i>L. difformis</i> B-E. van Wyk	16
<i>L. digitata</i> Harv.	12
<i>L. dinteri</i> Schinz	45
var. <i>amboensis</i> Schinz	45
<i>L. dissitinodis</i> B-E. van Wyk	117
<i>L. divaricata</i> (Eckl. & Zeyh.) Benth.	132
<i>L. diversifolia</i> (E. Mey.) Benth.	80
<i>L. dregeana</i> Dümmer	29

<i>L. elongata</i> (Thunb.) D. Dietr.	114
<i>L. eriantha</i> Benth.	18
var. <i>obovata</i> Scott Elliot	20
<i>L. eriocarpa</i> (E. Mey.) B-E. van Wyk	129
<i>L. erisemoides</i> (Ficalho & Hiern) Torre	63
<i>L. erubescens</i> (E. Mey.) Druce	85
<i>L. esterhuyseana</i> B-E. van Wyk	37
<i>L. excisa</i> (E. Mey.) Presl	112
<i>L. excisa</i> (E. Mey.) Steud.	112
<i>L. exstipulata</i> L. Bol.	125
<i>L. falcata</i> (E. Mey.) Benth.	66
<i>L. fastigiata</i> (E. Mey.) B-E. van Wyk	103
<i>L. filiformis</i> B-E. van Wyk	116
<i>L. flava</i> Dümmer	99
<i>L. florifera</i> Dümmer	35
var. <i>major</i> Burt Davy	35
<i>L. foliosa</i> H. Bol.	23
<i>L. fruticoides</i> B-E. van Wyk	68
<i>L. furcata</i> (Merxmüller & Schreiber) Schreiber	50
<i>L. galpinii</i> Dümmer	134
var. <i>prostrata</i> Dümmer	134
<i>L. genistoides</i> (Fenzl) Benth.	42
<i>L. genuflexa</i> (E. Mey.) Benth.	132
<i>L. gerrardii</i> Dümmer	31
var. <i>transvaalensis</i> Dümmer	31
<i>L. glabra</i> (Thunb.) D. Dietr.	82
<i>L. glabra</i> (Thunb.) Druce	82
<i>L. glabrescens</i> (Dümmer) B-E. van Wyk	143
<i>L. globulosa</i> B-E. van Wyk	54
<i>L. gracilifolia</i> B-E. van Wyk	108
<i>L. gracilis</i> (E. Mey.) Benth.	120d
var. <i>brevipetiolata</i> Dümmer & Jennings	120a
<i>L. grandis</i> Dümmer & Jennings	19
<i>L. harveyi</i> B-E. van Wyk	151
<i>L. heterophylla</i> (Thunb.) Eckl. & Zeyh.	110
<i>L. hirsuta</i> Schinz	36
<i>L. holosericea</i> (E. Mey.) B-E. van Wyk	150
<i>L. humifusa</i> Burch. ex Benth.	34a
var. <i>radula</i> (E. Mey.) Harv.	34a
<i>L. humilior</i> Dümmer	79
<i>L. involuocrata</i> (Berg.) Benth.	104
subsp. <i>bracteata</i> B-E. van Wyk	104b
subsp. <i>digitata</i> B-E. van Wyk	104c
subsp. <i>involuocrata</i>	104a
subsp. <i>peduncularis</i> (E. Mey.) B-E. van Wyk	104d
<i>L. jacottetii</i> (Schinz) B-E. van Wyk	133
<i>L. lamprifolia</i> B-E. van Wyk	106
<i>L. lanceolata</i> (E. Mey.) Benth.	22
<i>L. laticeps</i> B-E. van Wyk	53
<i>L. laxa</i> Eckl. & Zeyh.	80
var. <i>multiflora</i> Dümmer	80
<i>L. laxa</i> Eckl. & Zeyh. <i>sensu</i> Burt Davy	74
<i>L. lenticula</i> (E. Mey.) Benth.	95
var. <i>biflora</i> Kensit	95

var. <u>brachycarpa</u> Harv.	94
L. <u>leobordea</u> Benth.	45
var. <u>abyssinica</u> (Hochst. & Schweinf.) Bak.	45
L. <u>leptoloba</u> H. Bol.	97
L. <u>leptoloba</u> H. Bol. <u>sensu</u> Schreiber	71
L. <u>leucoclada</u> (Schlechter) Dümmer	120b
L. <u>linearifolia</u> B-E. van Wyk	70
L. <u>listii</u> Polhill	5
L. <u>listioides</u> Dinter & Harms	8
L. <u>longicephala</u> B-E. van Wyk	55
L. <u>longiflora</u> H. Bol.	14
L. <u>lotoidea</u> (Del.) Batt.	45
L. <u>lotoidea</u> (Del.) Druce	45
var. <u>micrantha</u> Batt.	45
L. <u>lotononoides</u> (Scott Elliot) B-E. van Wyk	141
L. <u>lupinifolia</u> (Boiss.) Benth.	41
L. <u>lupinifolia</u> (Boiss.) Willk.	41
var. <u>eu-lupinifolia</u> Maire	41
var. <u>intermedia</u> (Pomel) Batt.	41
var. <u>villosa</u> (Pomel) Batt.	41
L. <u>macrocarpa</u> Eckl. & Zeyh.	1
L. <u>macrosepala</u> Conrath	79
L. <u>maculata</u> Dümmer	78
L. <u>magnifica</u> B-E. van Wyk	11
L. <u>marlothii</u> Engl.	8
L. <u>maroccana</u> Ball	43
L. <u>maximiliani</u> Schlechter ex De Wildeman	98
L. <u>meyeri</u> (Presl) B-E. van Wyk	149
L. <u>micrantha</u> Eckl. & Zeyh.	84
L. <u>micrantha</u> (Thunb.) Harv.	87a
L. <u>microphylla</u> Harv.	30
L. <u>minima</u> B-E. van Wyk	6
L. <u>minor</u> Dümmer & Jennings	135
L. <u>mirabilis</u> Dinter	26
L. <u>mollis</u> (E. Mey.) Benth.	27
L. <u>monophylla</u> Harv.	83
L. <u>montana</u> Schinz	80
L. <u>mucronata</u> Conrath	31
L. <u>myriantha</u> Bak.f. ex Gibbs Russell <u>et al.</u>	28
L. <u>namaquensis</u> H. Bol.	87c
L. <u>neglecta</u> Dümmer	30
L. <u>newtonii</u> Dümmer	46
L. <u>nutans</u> B-E. van Wyk	124
L. <u>oocarpa</u> Dinter ex Wilman	94
L. <u>oligocephala</u> B-E. van Wyk	51
L. <u>ornata</u> Dümmer	31
L. <u>orthorrhiza</u> Conrath	39
L. <u>oxyptera</u> (E. Mey.) Benth.	89
var. <u>brevipes</u> Harv.	89
var. <u>longipes</u> Harv.	89
L. <u>pachycarpa</u> Dinter ex B-E. van Wyk	71
L. <u>pachycarpa</u> Dinter in <u>sched.</u>	71
L. <u>pallens</u> (Eckl. & Zeyh.) Benth.	60
L. <u>pallidirosea</u> Dinter & Harms	73

<i>L. serpentinicola</i> Wild	81
<i>L. solitudinis</i> Dümmer	2
<i>L. sparsiflora</i> (E. Mey.) B-E. van Wyk	94
<i>L. speciosa</i> Hutch.	14
<i>L. sphaerocarpa</i> Boiss.	45
<i>L. spicata</i> Compton	24
<i>L. steingroeveriana</i> (Schinz) Dümmer	45
<i>L. stenophylla</i> (Eckl. & Zeyh.) B-E. van Wyk	91
<i>L. stipulosa</i> Bak.f.	48
<i>L. stipulosa</i> Bak.f. <i>sensu</i> Schreiber	47
<i>L. stolzii</i> Harms	33
<i>L. stricta</i> (Eckl. & Zeyh.) B-E. van Wyk	130
<i>L. strigillosa</i> (Merxmüller & Schreiber) Schreiber	65
<i>L. stipularis</i> Schlechter	112
<i>L. subulata</i> B-E. van Wyk	7
<i>L. sutherlandii</i> Dümmer	17
<i>L. tapetiformis</i> Emberger & Maire	25
<i>L. tenella</i> (E. Mey.) Eckl. & Zeyh.	100
var. <i>angustifolia</i> Harv.	100
var. <i>calycina</i> (E. Mey.) Harv.	39
var. <i>hirsutissima</i> Harv.	39
<i>L. tenuifolia</i> (Eckl. & Zeyh.) Dümmer <i>sensu</i> Dümmer	104d
<i>L. tenuipes</i> Burt Davy	21
<i>L. tenuis</i> Bak.	64
<i>L. transvaalensis</i> Dümmer	35
<i>L. trichodes</i> (E. Mey.) B-E. van Wyk	147
<i>L. trichopoda</i> (E. Mey.) Benth.	82
<i>L. trifolioides</i> Schlechter ex A. Zahlbr.	82
<i>L. trisegmentata</i> Phill.	131
var. <i>robusta</i> Phill. forma <i>robusta</i> Phill.	131
var. <i>robusta</i> Phill. forma <i>sericea</i> Phill.	131
var. <i>trisegmentata</i> forma <i>sericea</i> Phill.	131
var. <i>trisegmentata</i> forma <i>trisegmentata</i>	131
<i>L. umbellata</i> (L.) Benth.	127
<i>L. varia</i> (E. Mey.) Steud.	112
<i>L. venosa</i> B-E. van Wyk	96
<i>L. versicolor</i> (E. Mey.) Benth.	34a
<i>L. versicolor</i> (E. Mey.) Benth. <i>sensu</i> Harv.	100
<i>L. vexillata</i> (E. Mey.) Eckl. & Zeyh.	110
<i>L. viborgioides</i> Benth.	121
<i>L. viminea</i> (E. Mey.) B-E. van Wyk	145
<i>L. virgata</i> B-E. van Wyk	144
<i>L. villosa</i> (E. Mey.) Steud.	111
<i>L. wilmsii</i> Dümmer	36
<i>L. woodii</i> H. Bol.	80
<i>L. wyliei</i> Wood	129
<i>L. wyliei</i> Wood <i>sensu</i> Dümmer	131
<i>Lotus dichotomus</i> Del. ex Walp.	45
<i>L. platycarpus</i> Viv.	45
<i>L. prostratus</i> L.	110
<i>Microtropis</i> E. Mey.	Sect. 10
<i>M. hirsuta</i> (Thunb.) E. Mey.	101

<u>Ononis anthylloides</u> DC.	127
<u>Q. asphaltoides</u> DC.	104d
<u>Q. decumbens</u> Thunb.	34a
<u>Q. elongata</u> Thunb.	114
<u>Q. glabra</u> Thunb.	82
<u>Q. heterophylla</u> Thunb.	110
<u>C. hirsuta</u> Thunb.	101
<u>Q. involucrata</u> Berg.	104a
<u>Q. involucrata</u> auct. non Berg.	104d
<u>Q. micranthus</u> Thunb.	87a
<u>Q. parviflora</u> Berg.	67
<u>Q. prostrata</u> (L.) L.	110
<u>Q. quinata</u> Thunb.	9
<u>Q. secunda</u> Thunb.	104d
<u>Q. strigosa</u> Thunb.	127
<u>Q. umbellata</u> L.	127
<u>Q. umbellata</u> L. <u>sensu</u> Thunb.	104d
<u>Q. villosa</u> Thunb.	115
 <u>Polylobium</u> Eckl. & Zeyh.	Sect. 11
<u>P. angustifolium</u> Eckl. & Zeyh.	104d
<u>P. brachylobum</u> (E. Mey.) D. Dietr.	67
<u>P. calycinum</u> (E. Mey.) Benth.	39
<u>P. carinatum</u> (E. Mey.) Benth.	35
<u>P. corymbosa</u> (E. Mey.) Benth.	20
<u>P. corymbosa</u> (E. Mey.) Presl	20
<u>P. debile</u> Eckl. & Zeyh.	127
<u>P. erubescens</u> (E. Mey.) D. Dietr.	85
<u>P. falcatum</u> (E. Mey.) D. Dietr.	66
<u>P. fastigiatum</u> (E. Mey.) Eckl. & Zeyh.	103
<u>P. filiforme</u> Eckl. & Zeyh.	127
<u>P. humifusum</u> (E. Mey.) D. Dietr.	34a
<u>P. intermedium</u> Eckl. & Zeyh.	82
<u>P. involucratum</u> (Berg.) Eckl. & Zeyh.	104a
<u>P. molle</u> (E. Mey.) D. Dietr.	27
<u>P. mundianum</u> Eckl. & Zeyh.	103
<u>P. pallens</u> Eckl. & Zeyh.	60
<u>P. peduncularis</u> (E. Mey.) Benth.	104d
<u>P. polycephalum</u> (E. Mey.) D. Dietr.	52
<u>P. radulum</u> (E. Mey.) D. Dietr.	34a
<u>P. sparsiflorum</u> Eckl. & Zeyh.	89
<u>P. tenellum</u> (E. Mey.) D. Dietr.	100
<u>P. tenuifolium</u> Eckl. & Zeyh.	104a
<u>P. trichopodium</u> (E. Mey.) Presl	82
<u>P. truncatum</u> (E. Mey.) Eckl. & Zeyh.	127
<u>P. typicum</u> Eckl. & Zeyh.	82
<u>P. umbellatum</u> (L.) Benth.	127
 <u>Telina</u> E. Mey. sect. <u>Cytisoideae</u> E. Mey.	Sect. 14
sect. <u>Brachypodae</u> E. Mey.	Sect. 14
sect. <u>Chasmoneae</u> E. Mey.	Sect. 12
<u>T. angustifolia</u> E. Mey.	103
<u>T. brevifolia</u> Eckl. & Zeyh. ex Drège	130
<u>T. cytisoides</u> E. Mey.	130

T. <u>eriocarpa</u> E. Mey.	129
T. <u>excisa</u> (Thunb.) E. Mey. <u>sensu</u> E. Mey.	112
T. <u>genuflexa</u> E. Mey.	132
T. <u>heterophylla</u> E. Mey.	115
T. <u>striata</u> E. Mey.	139a
T. <u>varia</u> E. Mey.	112
T. <u>villosa</u> E. Mey.	111

MATERIALS AND METHODS

Morphological studies have been based on the collections of the following herbaria (abbreviated as in Holmgren et al. 1981; the complete collections were studied except for those herbaria marked by an asterisk): BM, BLFU, BOL, C, G*, GRA, JRAU, K, KMG, LINN, M, MO, NBG, NH, PEU, PRE, S, SAAS, SAM, SBT, STE, TCD*, UPS, WIND. Dried material of all except one species (L. erisemoides), and fresh or preserved material of approximately 80 species were used. Comprehensive lists of vouchers specimens for the material used in morphological studies have been deposited in the Rand Afrikaans University Herbarium.

Flowers were boiled in water for ca. 30 seconds, dissected and mounted in a 1:1 mixture of glycerine and water. To account for infraspecific variation, between three and 30 individuals of each species were included where possible. Anatomical sections were hand-cut with a razor blade and stained in aqueous Toluidine blue (O'Brien et al. 1964, Feder & O'Brien 1968). Morphological drawings (all by the author) were done with a drawing tube (camera lucida) mounted to a binocular microscope (Wild M5 or Wild M3Z).

Micromorphological characters were studied with an ISI-SS60 scanning electron microscope at 7 kV, after the material was coated with gold (Edwards sputter coater, 4,5 minutes). Ilford HP5 (400 ASA) film was used for SEM work, and Agfa XRG 100 for colour photographs.

The methods employed for cytological studies and chemical analyses are described in detail in the relevant appendices, where lists of voucher specimens are also given.

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