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

BY

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APPENDICES

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APPENDIX 1

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Observations on the occurrence and distribution of alkaloids in some genera and species of the tribe Crotalarieae (Fabaceae)

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A general survey of alkaloids in the tribe Crotalarieae showed that useful chemotaxonomic data may be obtained. Although the pyrrolizidine alkaloids of *Crotalaria* L. have been studied in considerable detail, virtually nothing is known for the other, predominantly southern African genera. The genera *Dichilus* DC., *Lebeckia* Thunb., *Melolobium* Eckl. & Zeyh. and *Polhillia* Stirton were found to contain several alkaloids in sufficient quantities to warrant further investigation. The major alkaloids (presumably all of the quinolizidine type) seem to be characteristic for each of these genera. *Aspalathus* L., *Buchenroedera* Eckl. & Zeyh., *Lotononis* (DC.) Eckl. & Zeyh., *Pearsonia* Duemmer, *Rafnia* Thunb. and *Wiborgia* Thunb. appear to produce much smaller amounts. The possibility of obtaining useful information from these genera seems limited in view of the large quantities of plant material required to enable proper identification of the compounds. Methods of extraction and detection are described. The R_f values of the major alkaloids are given for the different thin-layer chromatographic systems used. Some preliminary identifications were confirmed by mass spectrometry.

'n Algemene opname van alkaloïede in die tribus Crotalarieae het aangetoon dat nuttige chemotaksonomiese data verkry kan word. Hoewel die pirrolisidien-alkaloïede van *Crotalaria* L. reeds deeglik bestudeer is, is feitlik niks bekend vir die ander, hoofsaaklik suidelike Afrikaanse genera nie. Daar is bevind dat die genera *Dichilus* DC., *Lebeckia* Thunb., *Melolobium* Eckl. & Zeyh. en *Polhillia* Stirton verskeie alkaloïede in genoegsame hoeveelhede bevat om verdere ondersoeke te regverdig. Die hoof alkaloïede (vermoedelik almal van die quinolisidien-tipe) blyk kenmerkend te wees van elkeen van hierdie genera. *Aspalathus* L., *Buchenroedera* Eckl. & Zeyh., *Lotononis* (DC.) Eckl. & Zeyh., *Pearsonia* Duemmer, *Rafnia* Thunb. en *Wiborgia* Thunb. produseer blykbaar veel kleiner hoeveelhede. Die moontlikheid om bruikbare inligting van hierdie genera te verkry is skynbaar beperk, aangesien groot hoeveelhede plantmateriaal nodig sal wees om die verbindings behoorlik te identifiseer. Metodes van ekstraksie en waarneming word beskryf. Die R_f-waardes van die hoof alkaloïede vir die verskillende dunlaagchromatografiese sisteme wat gebruik is, word aangegee. Sommige voorlopige identifikasies is deur massaspektrometrie bevestig.

Keywords: Alkaloids, Crotalarieae, Fabaceae, southern Africa

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Introduction

More than 350 different alkaloids have been identified from about 60 genera of the legume subfamily Papilionoideae (Mears & Mabry 1971; Kinghorn & Smoleski 1981). Quinolizidine (lupine) alkaloids are known to occur in the tribes Sophoreae, Loteae, Bossiaeeae, Podalyrieae, Liparieae, Crotalarieae, Euchresteae, Thermopsideae and Genisteae. The record for the Crotalarieae is based on a single study of *Lebeckia plukenetiana* E. Mey. (Nattrass 1973; Gerrans *et al.* 1976), which was found to contain tetracyclic alkaloids of the sparteine type. The pyrrolizidine alkaloids of the genus *Crotalaria* have been the subject of numerous studies, but surprisingly, there has not been a single report of the occurrence of quinolizidine alkaloids in this genus (Kinghorn & Smolenski *op. cit.*). If *Crotalaria* is excluded, it means that only one out of an estimated total of more than 500 species representing 16 genera has ever been studied analytically. This paper documents a survey of some genera and species to determine the occurrence of alkaloids and to find out where to concentrate future efforts.

Materials and Methods

A total of 38 samples, including 36 species and 11 genera of the Crotalarieae and two species of the tribe Genisteae were extracted in boiling methylene chloride for at least 2 days. Full details of the species and plant material used are given in Table 1. The alkaloids were extracted as salts with 2N hydrochloric acid and then re-extracted with methylene chloride after basifying the aqueous phase with ammonia. Evaporation of the solvent under reduced pressure yielded a brown viscid substance and varying quantities of a white crystalline matter. The latter was found to be very polar and immobile on silica gel thin-layer plates with the systems we used. The presence of this presumably non-alkaloid material and other impurities greatly influenced the yield. As a result, the figures in Table 1 give only an indication of relative yields and do not accurately reflect the actual quantity of alkaloids in each sample.

The crude extracts were diluted in methylene chloride (1:10 mass/vol) and chromatographed on Whatman K6F- and LK6DF silica gel plates (catalogue nos. 4861-820 and 4866-821) in the following systems:

a: cyclohexane – chloroform – diethylamine (50:40:10)
b: cyclohexane – diethylamine (90:10)
c: methanol – chloroform – ammonium (85:20:1)
d: ethyl acetate – methanol (80:20)
e: *n*-butanol – acetic acid – water (12:3:5)

The sheets were oven-dried at 100°C for 3 min, studied for fluorescence in ultraviolet light (254 and 365 nm) and then sprayed with iodoplatinate reagent. To allow for variations in adsorption, the dye Rhodamine B was co-chromatographed on all plates to standardize the R_f values (Waldi 1965).

Preliminary identifications were made by comparison with authentic samples of 6 different quinolizidine alkaloids. For mass spectrometry, pure samples of some of the major alkaloids were obtained by separation on preparative silica gel plates. No attempts were yet made to elucidate the structures of any alkaloids.

Table 1 List of material used for alkaloid extraction and yields of crude extract obtained. All samples consisted of air-dried leaves and branches. The voucher specimens are all in the Rand Afrikaans University Herbarium (JRAU)

Species	Provenances	Voucher specimens	Mass of sample (g)	Mass of extract (g)	Yield (%)
Argyrolobium crassifolium Eckl. & Zeyh.	Zuurberg, E. Cape	*B-E. & M. van Wyk 2115*	59	0,16	0,27
Argyrolobium variopile N.E.Br.	Volksrust, Transvaal	*A.L. Schutte 364*	148	0,76	0,51
Aspalathus hirta E. Mey. subsp. *hirta*	Villiersdorp, SW Cape	*B-E. van Wyk 2070*	44	0,17	0,39
Buchenroedera lotononoides Scott Elliot	Sani Pass, Natal	*B-E. van Wyk 2630*	83	0,07	0,09
Buchenroedera multiflora Eckl. & Zeyh.	Zuurberg, E. Cape	*B-E. & M. van Wyk 1523*	61	0,14	0,23
Crotalaria capensis Jacq.	Ivuna, Natal	*B-E. van Wyk 2525*	98	0,17	0,18
Dichilus gracilis Eckl. & Zeyh.	Fauresmith, Orange Free State	*A.L. Schutte 351*	125	0,22	0,18[a]
Dichilus lebeckioides DC.	Johannesburg, Transvaal	*A.L. Schutte 362*	50	0,16	0,32[b]
Dichilus pilosus Conrath ex Schinz	Roodepoort, Transvaal	*A.L. Schutte 359*	119	0,12	0,10[b]
Dichilus reflexus (N.E.Br.) A.L. Schutte *ined.*	Pongola, Transvaal	*A.L. Schutte 368*	82	0,22	0,27
Dichilus strictus E. Mey.	Harrismith, Orange Free State	*A.L. Schutte 372c*	122	0,13	0,11[b]
Lebeckia cytisoides Thunb.	Clanwilliam, NW Cape	*B-E. van Wyk 2441*	200	0,52	0,25[a]
Lebeckia multiflora E. Mey.	Kamieskroon, NW Cape	*B-E. van Wyk 2353*	295	0,78	0,26[a]
Lebeckia sessilifolia (Eckl. & Zeyh.) Benth.	De Hoop, SW Cape	*B-E. van Wyk 2120*	96	0,11	0,12[a]
Lotononis acuminata Eckl. & Zeyh.	Humansdorp, S. Cape	*B-E. van Wyk 2580*	95	0,06	0,06
Lotononis cf. *adpressa* N.E.Br.	Ermelo, Transvaal	*B-E. van Wyk 2618*	138	0,27	0,20
Lotononis brachyloba (E. Mey.) Benth.	Ceres, SW Cape	*B-E. van Wyk 2244*	65	0,04	0,06[a]
Lotononis caerulescens (E. Mey.) B-E. van Wyk *ined.*	Cradock, E. Cape	*B-E. van Wyk 1614*	61	0,15	0,24
Lotononis divaricata (Eckl. & Zeyh.) Benth.	Burgersdorp, NE Cape	*B-E. van Wyk 2597*	165	0,15	0,09
Lotononis foliosa H. Bol.	Johannesburg, Transvaal	*B-E. van Wyk 2607*	30	0,11	0,36[c]
Lotononis gracilis (E. Mey.) Benth.	Ceres, SW Cape	*B-E. van Wyk 2265*	228	0,21	0,09
Lotononis leucoclada (Schltr.) Duemmer	Clanwilliam, NW Cape	*B-E. van Wyk 2434*	116	0,10	0,08
Lotononis listii Polhill	Bloemfontein, Orange Free State	*B-E. van Wyk 2475*	114	0,06	0,05[b]
Lotononis myriantha Bak. f. *in sched.*	Bethal, Transvaal	*B-E. van Wyk 1825*	145	0,13	0,09[c]
Lotononis oxyptera (E. Mey.) Benth.	Citrusdal, NW Cape	*B-E. van Wyk 2319*	69	0,07	0,09
Lotononis polycephala (E. Mey.) Benth.	Kamieskroon, NW Cape	*B-E. van Wyk 2408*	93	0,07	0,07[a]
Lotononis transvaalensis Duemmer	Pongola, Transvaal	*B-E. van Wyk 2614*	86	0,14	0,16[a]
Lotononis umbellata (L.) Benth.	Swellendam, SW Cape	*B-E. van Wyk 2110*	52	0,22	0,43[a]
Lotononis woodii H. Bol.	Harrismith, Orange Free State	*A.L. Schutte 374*	75	0,14	0,18[b]
Melolobium alpinum Eckl. & Zeyh.	Sani Pass, Natal	*B-E. van Wyk 2631*	58	0,15	0,25
Melolobium microphyllum (L.f.) Eckl. & Zeyh.	Rouxville, Orange Free State	*B-E. van Wyk 2628*	107	0,14	0,13
Melolobium obcordatum Harv.	Harrismith, Orange Free State	*A.L. Schutte 373a*	126	0,05	0,04
Melolobium subspicatum Conrath	Irene, Transvaal	*De Beer 38*	160	0,46	0,29
Melolobium wilmsii Harms	Hendrina, Transvaal	*B-E. van Wyk 2624*	123	0,93	0,76
Pearsonia sessilifolia (Harv.) Duemmer	Roodepoort, Transvaal	*A.L. Schutte 382*	81	0,34	0,43[c]
Polhillia pallens C.H.Stirton	Bredasdorp, SW Cape	*B-E. van Wyk 2095*	100	0,21	0,21
Rafnia perfoliata E. Mey.	Villiersdorp, SW Cape	*B-E. van Wyk 2067*	159	0,18	0,12[b]
Wiborgia sericea Thunb.	Laingsburg, SW Cape	*B-E. van Wyk 2193*	43	0,09	0,21[a]

[a, b, c] — small, medium and large quantities respectively of crystalline material present

Results

Figure 1 shows the thin-layer chromatography results for systems a and b of all extracts in which at least some alkaloids were detected. The estimated number of major alkaloids in all the samples totals 34. Their respective R_f values and spot characteristics are given in Table 2. Identities not confirmed by mass spectrometry are tentative only (see Table 3), since thin-layer chromatography is known to lack precision. Closely related compounds may often not be distinguished by this method alone.

Discussion

The results seem to indicate that the genera represented differ considerably both in the quantity and the numbers of alkaloids produced. Within each genus there is much less variation and morphologically similar species also tend to have similar alkaloids (Table 3). What differences there are may be attributed to inadequate sampling. Cranmer & Mabry (1966) have shown that many factors affect the actual quantity of alkaloid within a sample. Alkaloids that are apparently absent may well be present in some individuals of a species, albeit in trace amounts. The only genus of which the species are all included (*Dichilus*), shows remarkably little variation and it seems that at least two of the alkaloids (nos 11 and 14) may turn out to be taxonomic markers for this genus. Our results differ markedly from those of Stirton (1986a), whose findings are difficult to interpret because he only extracted small quantities of seeds and did not include any standards in his chromatograph. He suggested similarities between *Dichilus strictus* and *Lebeckia*, but our data is in contrast to this view. It is tempting to equate alkaloid no. 11 with lupanine and alkaloid no. 14 with no. 10 (which would indeed make the two genera similar) but the UV-fluorescences are totally different.

It is obvious from Table 3 that the genera *Lebeckia, Melolobium, Polhillia* and *Dichilus* warrant further study. In view of the somewhat anomalous position of *Argyrolobium* (Polhill 1976, 1981) and uncertainty regarding its affinities with *Polhillia, Melolobium* (Stirton 1986b) and perhaps *Dichilus*, this genus should be included in comparative studies. The two

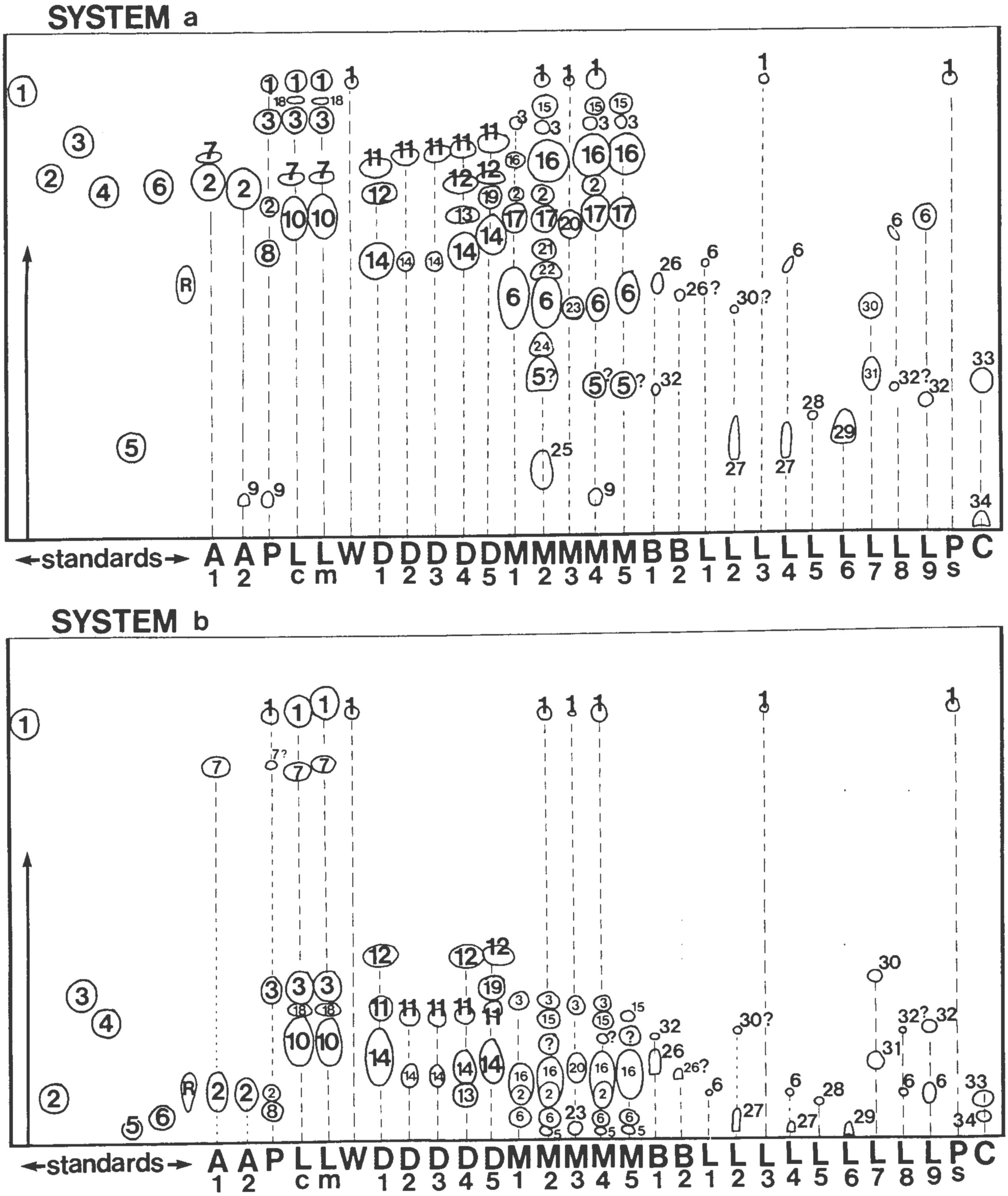

Figure 1 Thin-layer chromatography results (systems a and b) of all crude extracts in which at least some alkaloids were detected. Standards and unknown alkaloids are numbered as in Tables 2 and 3, (R: Rhodamine B). A1, *Argyrolobium variopile*; A2, *Argyrolobium crassifolium*; P, *Polhillia pallens*; Lc, *Lebeckia cytisoides*; Lm, *L. multiflora*; W, *Wiborgia sericea*; D1, *Dichilus gracilis*; D2, *D. lebeckioides*; D3, *D. pilosus*; D4, *D. reflexus*; D5, *D. strictus*; M1, *Melolobium alpinum*; M2, *M. microphyllum*; M3, *M. obcordatum*; M4, *M. subspicatum*; M5, *M. wilmsii*; B1, *Buchenroedera lotononoides*; B2, *B. multiflora*; L1, *Lotononis* cf. *adpressa*; L2, *L. brachyloba*; L3, *L. foliosa*; L4, *L. leucoclada*; L5, *L. listii*; L6, *L. myriantha*; L7, *L. oxyptera*; L8, *L. polycephala*; L9, *L. transvaalensis*; Ps, *Pearsonia sessilifolia*; C, *Crotalaria capensis*.

species represented in our sample contain significant quantities of anagyrine as the dominant alkaloid and this appears to be a new record for *Argyrolobium*. Only one species has been studied before. Tsuda & Marion (1963) isolated cytisine, aphyllidine and argyrolobine from *A. megarhizum* H. Bol.

In the lotononoid genera, the prospects of obtaining useful information seem limited. There is no clear pattern and the amount of plant material required for extraction would be prohibitive for many of the species. An interesting question needs to be answered, however. Is the remarkable similarity

Table 2 Spot characteristics of major alkaloids on silica gel plates (systems a, b, c, d and e) with iodoplatinate as detecting reagent. The dye Rhodamine B was used to allow standardization of the R_f values. Spot shapes: r = round, t = transversely oblong, o = oblong, e = extended, s = streaked. The standards and unknown alkaloids are numbered as in Figure 1

		R_f values and spot shapes					UV – visible			
		a	b	c	d	e	254 nm	365 nm	Colour UV 365 nm	Colour iodoplatinate
1	Sparteine	0,79 r	0,76 r	0,30 s	0,06 e	0,23 s	–	–	–	greyish-blue
2	Anagyrine	0,55 r	0,09 r	0,94 t	0,26 s	0,20 e	+	+	bluish	brown to purple
3	Lupanine	0,65 r	0,28 r	0,77 r	0,04 e	0,23 o	–	–	–	purple
4	Lupinine	0,50 r	0,24 r	0,91 r	0,06 e	0,31 e	–	–	–	blue
5	13-OH-Lupanine	0,17 r	0,02 r	0,44 o	0,04 e	0,20 o	–	–	–	blue
6	*N*-Me-cytisine	0,48 r	0,05 r	0,82 r	0,22 s	0,19 e	+	–	–	blue-grey
7		0,80 t	0,75 t	>0,9 t	? ?	? ?	–	+	pink	pale blue
8		0,61 r	0,06 r	>0,9 r	? ?	? ?	+	–	–	greenish-grey
9		0,08 o	0,08 ?	? ?	? ?	? ?	+	–	–	purplish-brown
10		0,60 r	0,20 o	0,75 r	? ?	? ?	+	+	violet-blue	violet-purple
11		0,73 t	0,25 r	0,94 ?	? ?	? ?	+	+	purple	pale purple
12		0,70 t	0,49 t	0,30 e	0,28 r	? ?	–	+	purple	pale blue
13		0,69 t	0,09 r	>0,9 ?	<0,1 ?	0,12 r	–	+	purple	pale purple
14		0,55 r	0,16 o	0,52 e	<0,1 ?	0,37 r	+	–	–	brown and blue
15		0,81 t	0,26 r	>0,8 ?	0,25 r	? ?	–	–	–	blue
16		0,65 r	0,14 o	0,94 t	0,41 o	0,32 o	+	+	pale blue	blue and green
17		0,50 r	0,11 o	0,87 ?	? ?	? ?	–	–	–	greenish-grey
18		0,81 t	0,27 t	? ?	? ?	? ?	–	+	bluish	pale blue
19		0,70 r	0,30 r	>0,9 ?	0,54 r	0,61 r	+	+	purplish	pale blue
20		0,50 r	0,13 o	0,85 t	0,07 e	0,37 r	+	+	purple	pale purple
21		0,46 r	0,33 r	0,84 ?	? ?	? ?	–	–	–	pale blue
22		0,42 t	0,06 ?	? ?	? ?	? ?	–	+	bluish	purple
23		0,40 r	0,02 r	0,82 ?	0,07 ?	0,28 r	+	–	–	purple
24		0,30 t	<0,1 ?	>0,9 ?	0,65 s	0,67 s	–	+	blue	reddish-violet
25		0,12 o	<0,1 ?	>0,9 ?	0,15 o	? ?	–	–	–	reddish-purple
26		0,45 o	0,10 e	0,78 o	0,15 e	0,24 r	–	+	purple	pink
27		0,22 o	0,02 e	0,04 o	0,03 e	? ?	+	–	–	orange-brown
28		0,25 r	0,05 r	0,26 r	0,04 e	0,62 t	+	–	–	purple
29		0,25 o	0,01 o	0,29 o	0,37 s	0,48 e	+	+	pale yellow	bluish-purple
30		0,43 r	0,23 r	0,23 s	0,07 s	0,41 r	–	–	–	purple
31		0,34 o	0,11 r	0,23 ?	0,07 s	0,31 r	+	–	–	brownish-purple
32		0,27 r	0,15 r	0,38 r	0,01 r	0,19 r	–	–	–	blue
33		0,30 r	0,05 r	0,30 o	0,04 e	0,40 r	+	–	–	brownish-purple
34		0,03 o	0,02 r	0,13 o	0,01 r	0,32 t	+	–	–	brownish-purple
Rhodamine B		0,45 o	0,10 o	0,74 o	0,12 e	0,65 o	+	+	bright red	bright red

between species of *Lotononis* and *Crotalaria* merely the result of convergence? The two genera do appear to be chemically different. Many species of *Lotononis* are cyanogenic, suggesting a nitrogen metabolism directed towards the production of glucosides rather than alkaloids. The occurrence of at least some quinolizidine alkaloids in *Lotononis* (here reported for the first time) does not preclude the possibility that pyrrolizidine alkaloids may also be present. *Lotononis* and *Buchenroedera* appear to be similar, but the alkaloids are in such low concentrations that more detailed studies to prove relationship seem unpractical unless more sophisticated extraction methods are used.

The systematic value of alkaloid data at the generic level is now well established (Cranmer & Turner 1967; Kinghorn & Smolenski *op. cit.*). In the Crotalarieae, it is precisely at this level where more information is needed. Our preliminary results indicate that a more thorough investigation of some genera holds great promise.

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Table 3 Distribution of the major alkaloids extracted from 38 species of the Crotalarieae and Genisteae (^{c}identity confirmed by mass spectrometry)

	Distribution of major alkaloids																																
	Identified						Unidentified																										
	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	26	27	28	29	30	31	32	33	34
Argyrolobium crassifolium		2							?																									
Argyrolobium variopile		2^c					7																											
Aspalathus hirta																																		
Buchenroedera lotononoides																										26						32		
Buchenroedera multiflora																										?								
Crotalaria capensis																																	33	34
Dichilus gracilis											11	12		14																				
Dichilus lebeckioides											11			14																				
Dichilus pilosus											11			14																				
Dichilus reflexus											11	12	13	14																				
Dichilus strictus											11	12		14					19															
Lebeckia cytisoides	1^c		3				7			10								18																
Lebeckia multiflora	1		3^c				7			10								18																
Lebeckia sessilifolia																																		
Lotononis acuminata																																		
Lotononis cf. *adpressa*						6																												
Lotononis brachyloba																											27			?				
Lotononis caerulescens																																		
Lotononis divaricata																																		
Lotononis foliosa	1																																	
Lotononis gracilis																																		
Lotononis leucoclada						6																					27							
Lotononis listii																												28						
Lotononis myriantha																													29					
Lotononis oxyptera																														30	31			
Lotononis polycephala						6																										?		
Lotononis transvaalensis						6																										32		
Lotononis umbellata																																		
Lotononis woodii																																		
*Melolobium alpinum**		2	3			6										?	17																	
Melolobium microphyllum	1	2	3		?	6									15	16	17				21	22		24	25									
Melolobium obcordatum	?		3																	20			23											
Melolobium subspicatum	1	2^c	3		?	6			9						15	16	17																	
Melolobium wilmsii					?	6									15	16	17																	
Pearsonia sessilifolia	1																																	
Polhillia pallens	1	2	3				?	8	9																									
Rafnia perfoliata																																		
Wiborgia sericea	1																																	

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APPENDIX 2

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The Chemotaxonomic Significance of Integerrimine in *Buchenroedera* and *Lotononis* Section *Krebsia*

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Key Word Index—*Buchenroedera*; *Lebeckia*; *Lotononis*; Leguminosae; Crotalarieae; pyrrolizidine alkaloid; integerrimine; chemotaxonomy; generic relationships.

Abstract—Integerrimine, a pyrrolizidine alkaloid previously known only from species of *Cacalia*, *Senecio* and *Crotalaria*, has been identified as the major alkaloid of several species of *Buchenroedera* and *Lotononis* section *Krebsia*. Chemotaxonomic implications are discussed. Our conclusions are that the genera *Buchenroedera* and *Lotononis* are more closely related to *Crotalaria* than to *Lebeckia*, despite morphological evidence to the contrary; that *Buchenroedera* and *Lotononis* may not be distinct at the generic level and that *Lebeckia microphylla* should be transferred to *Lotononis* section *Krebsia*.

Introduction

In a general survey of alkaloids in the tribe Crotalarieae (Van Wyk, B-E., Verdoorn, G. H. and Schutte, A. L., *S. Afr. J. Botany*, in press) we have shown that useful chemotaxonomic information may be obtained. The pyrrolizidine alkaloids of the genus *Crotalaria* have been the subject of numerous studies, but the only previous reported occurrence of alkaloids from the remaining 16 genera was that of tetracyclic quinolizidine alkaloids in *Lebeckia plukenetiana* E. Mey. [1]. In view of suggestions that the genus *Buchenroedera* Eckl. & Zeyh. may be no more than a section of *Lotononis* (DC.) Eckl. & Zeyh. [2, 3], we investigated the major alkaloid of this genus and that of the closely related section *Krebsia* (Eckl. & Zeyh.) Benth. of *Lotononis*.

Results

The major alkaloid of *Buchenroedera lotononoides* Scott Elliot, previously referred to as alkaloid no. 26 (Van Wyk *et al., op. cit.*), was isolated and identified as integerrimine, a pyrrolizidine alkaloid previously reported only from species of *Cacalia*, *Senecio* and *Crotalaria* [4, 5]. All the spectroscopic data we obtained was in correlation with that given for integerrimine in the literature [6–8]. A total yield of *ca* 140 μg/g dry wt (0.014%) was obtained. Integerrimine was subsequently also identified by TLC and MS as the major alkaloid of all the species of *Buchenroedera* and *Lotononis* section *Krebsia* examined (Table 1). At least four other minor alkaloids were present in all of these species, but not in sufficient quantities to allow their identification. This is the first report of the presence of pyrrolizidine alkaloids in *Buchenroedera* and *Lotononis*.

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Discussion

In the Leguminosae, pyrrolizidine alkaloids were at first thought to be limited to *Crotalaria*, but have subsequently also been found in the tribe Genisteae (*Adenocarpus, Cytisus* and *Laburnum*) [9, 10], where they may co-occur with quinolizidine alkaloids. The presence of a pyrrolizidine alkaloid in *Buchenroedera* and *Lotononis* would seem to erode the apparent isolation of *Crotalaria* within the tribe *Crotalarieae* and indicates new possibilities for testing current tribal and generic concepts. A more detailed survey of *Lotononis* (a diverse genus of some 130 species) and related genera would therefore be most worthwhile. This may well lead to a better understanding of evolutionary relationships within a group that shows a high incidence of convergence and conflicting character information.

TABLE 1. TAXA AND PLANT MATERIAL EXAMINED

Species	Locality	Date collected	Collector and No.
Buchenroedera lotononoides Scott Elliot	Sani Pass, Natal	April 1987	*B-E. van Wyk 2630*
B. meyeri Presl	Mhlahlane, Transkei	January 1986	*B-E. van Wyk 1765*
B. multiflora Eckl. & Zeyh.	Zuurberg, Eastern Cape	April 1986	*B. & M. van Wyk 1523*
B. tenuifolia Eckl. & Zeyh. var. *tenuifolia*	Penhoek Pass, Queenstown	December 1985	*B-E. van Wyk 1593*
var. *pulchella* (E. Mey.) Harv.	Cradock, Eastern Cape	July 1985	*B-E. van Wyk 1334*
B. trichodes Presl	Katberg Pass, Eastern Cape	January 1986	*B-E. van Wyk 1693*
Lotononis caerulescens (E. Mey.) B-E. van Wyk *ined.* (= *Lebeckia microphylla* E. Mey.)	Nonesi's Nek, Queenstown	April 1987	*B-E. van Wyk 1632*
L. divaricata (Eckl. & Zeyh.) Benth.	Burgersdorp, Eastern Cape	January 1987	*B-E. van Wyk 2597*
	Rouxville, Orange Free State	April 1987	*B-E. van Wyk 2629*
L. trisegmentata Phill. var. *robusta* Phill. forma *robusta*	Clarens, Orange Free State	May 1987	*B-E. van Wyk 1561*
forma *sericea* Phill.	Sani Pass, Natal	April 1987	*B-E. van Wyk 1968*

The presence of integerrimine as a major alkaloid in extracts of all these species was confirmed by mass spectrometry. Voucher specimens are deposited in the Rand Afrikaans University Herbarium.

Some species of *Lotononis* are morphologically very similar to species of *Lebeckia* Thunb. This similarity has led to considerable taxonomic and nomenclatural confusion over the last two centuries. The alkaloidal metabolites however, now appear to be quite different. We suggest that the two genera are not closely related and that similarities may be ascribed to convergent evolution in response to the same environmental pressures, such as increasing summer drought during recent geological times. The phenomenon that leaflets are individually shed leaving the petioles, is a clear example of such an adaptation that occurs in both genera. The presence of integerrimine as a major alkaloid of *Lebeckia microphylla* supports the morphological evidence that was found for the transfer of this species to *Lotononis* (Van Wyk, B-E., *S. Afr. J. Botany,* in press).

The *Lotononis* species listed in Table 1 all belong to the section *Krebsia*, which is so closely related to *Buchenroedera* that the status of the latter has been questioned [2, 3]. Only a single diagnostic character (fruit shape) was found to separate the two genera and sectional rank for the latter within *Lotononis* was therefore suggested. This view is strongly supported by the evidence at hand.

Experimental

Plant materials. Collection details of all the species examined are listed in Table 1.

Procedures. Ground air-dried leaves and twigs were extracted with cold CH_2Cl_2. Extracts were acidified with 2 N HCl and re-extracted with CH_2Cl_2 (50 ml × 3) after basifying the aqueous phase with conc. NH_3. *Buchenroedera lotononoides* (930 g) yielded 600 mg of crude alkaloidal material after 2 days of extraction and an additional 300 mg after 4 more days. The first 600 mg portion was chromatographed on silica gel 60 using cyclohexane–$CHCl_3$–Et_3N (20:25:6) as eluent. Fractions of 2 ml of each were collected. Fractions 28 to 64 with R_f, 0.18 were combined and upon evaporation of the solvent gave 88 mg of a white crystalline solid. Colourless prisms obtained from $CHCl_3$ were used to determine the mp and specific rotation, as well as IR, ^1H NMR, ^{13}C NMR and MS spectra. Mixtures of all the other species were studied by TLC (silica gel: eluent cyclohexane–$CHCl_3$–Et_2NH, 5:4:1, detecting reagent iodoplatinate) and the identity of integerrimine as the major alkaloid was confirmed by MS.

Acknowledgements—Prof. C. W. Holzapfel is thanked for his support of this project. Dr L. Burger and Ms A. L. Schutte assisted with the extraction process. Taxonomic research on *Buchenroedera* and *Lotononis* by B. V. W. is registered as a Ph.D. project at the University of Cape Town. Funding for research on legume alkaloids is from the Rand Afrikaans University, which is gratefully acknowledged.

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APPENDIX 3

S.-Afr. Tydskr. Plantk., 1988, 54(4): 386–388

The major alkaloids of the genus *Melolobium*

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The major alkaloids of 12 species of the genus *Melolobium* Eckl. & Zeyh. have been characterized. Variable quantities of anagyrine, camoensine, leontidine, lupanine, *N*-methylcytisine and thermopsine are present in nearly all of the extracts. Sparteine, cytisine and some unidentified alkaloids occur less frequently. If one species [*Melolobium involucratum* (Thunb.) Stirton] is excluded, the genus is morphologically very uniform and also appears to be uniform in its alkaloidal metabolites. Within the tribe Crotalarieae, the combination of thermopsine and the two C_{14} alkaloids leontidine and camoensine may prove to be a unique chemotaxonomic character for *Melolobium.*

Die hoof alkaloïede van 12 spesies van die genus *Melolobium* Eckl. & Zeyh. is gekarakteriseer. Variërende hoeveelhede anagirien, camoensien, leontidien, lupanien, *N*-metielcitisien en thermopsien was teenwoordig in feitlik al die ekstrakte. Sparteien, citisien en enkele ongeïdentifiseerde alkaloïede kom minder algemeen voor. As een spesie [*Melolobium involucratum* (Thunb.) Stirton] buite rekening gelaat word, is die genus morfologies baie eenvormig en skynbaar ook eenvormig in akaloïedmetaboliete. In die tribus Crotalarieae, mag dit blyk dat die kombinasie van thermopsien en die twee C_{14}-alkaloïede leontidien en camoensien, 'n unieke chemotaksonomiese kenmerk vir *Melolobium* is.

Keywords: Chemotaxonomy, Crotalarieae, Fabaceae, *Melolobium*, quinolizidine alkaloids

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Introduction

In recent review papers on the distribution of alkaloids in the Leguminosae (Mears & Mabry 1971; Salatino & Gottlieb 1980, 1981; Kinghorn & Smolenski 1981), conclusions for the tribe Crotalarieae are based on reports from only two genera (*Lebeckia* Thunb. and *Crotalaria* L.). A preliminary survey (van Wyk *et al.* 1988) has shown the presence of alkaloids in several other genera. The possibility to gain new insights into generic relationships within this predominantly southern African tribe was indicated.

As part of a continuing study of alkaloids in the Crotalarieae, we investigated the genus *Melolobium* Eckl. & Zeyh. (a genus of *ca.* 20 species endemic to southern Africa) and identified the major alkaloids of 12 different species.

Materials and Methods

Voucher specimens of the plant material used in this study are listed in the appendix. The samples consisted of air-dried leaves and twigs, some with flowers and fruit as indicated.

Melolobium subspicatum Conrath was chosen for the isolation and identification of its major alkaloids since extracts of this species contained nearly all of the alkaloids observed in other species. The major alkaloids were isolated, identified and then used as reference samples in the wider survey of several other species.

Extraction methods used are as previously described (van Wyk *et al.* op. cit.; van Wyk & Verdoorn 1988). All crude extracts were purified by elution through columns of Dowex 50 resin prior to gas chromatography. The major alkaloids of *M. subspicatum* were isolated by column chromatography as previously described and the alkaloids identified by m.p., specific rotation, as well as IR, ^{1}H NMR, ^{13}C NMR and MS spectrometry. The identity of camoensine was confirmed by characterization of the hydrogenated product (camoensidine). All the spectroscopical data obtained was in correlation with literature data (Leonard 1960; Santamaria & Khuong-Huu 1975). GC spectra were obtained with a DB-1 fused silica capillary column (length 15 m, internal diameter 0,25 mm) with PND/FID parallel detection. (Temperature programme: 150°C 2-min isotherm, 10°C min^{-1} to 250°C, 20°C min^{-1} to 300°C, isotherm 5 min; injector 250°C, PND-detector 310°C, split 1:30, flow 2,4 ml min^{-1}, helium as carrier gas at 80 kPa, H_2 as make-up gas for PND at 60 kPa). The GC results confirmed earlier identifications by analytical TLC.

Results and Discussion

Table 1 shows the yields of alkaloidal extract obtained after purification and the estimated total number of alkaloids present in each sample. Major alkaloids, minor alkaloids and traces were taken as those with concentrations of more than 10%, less than 10% and less than 1% of the total extract respectively. The distribution of major alkaloids in 12 species of *Melolobium* as determined by gas chromatography is shown in Table 2. Only those alkaloids that occur as a major component in at least one of the species were

Table 1 Total yields and estimated number of alkaloids extracted from 12 species of *Melolobium*

		Estimated number[b] of alkaloids:			
Species	Total yield[a] ($\mu g\ g^{-1}$ dry wt)	Major (>10%)	Minor (>1%)	Traces (<1%)	Total
M. aethiopicum	1253	2	5	3	10
M. alpinum	445	2	3	10	15
M. cf. *burchellii*	600	1	4	5	10
M. candicans	100	2	4	5	11
M. canescens	149	3	8	3	14
M. exudans	822	2	4	10	16
M. microphyllum	67	3	4	3	10
M. obcordatum	192	2	8	2	12
M. stipulatum	193	2	6	7	15
M. subspicatum	396	3	3	8	14
M. wilmsii	1380	3	2	7	12
M. involucratum[c]	387	4	2	13	19

[a]Yield figures are for purified alkaloidal extracts
[b]Estimated from GC results
[c]Sparteine is taken as a major alkaloid for reasons explained in the text

Table 2 Distribution of alkaloids in extracts of 12 species of *Melolobium* as determined by gas chromatography

	Distribution of major alkaloids (% of total alkaloid yield)												
Species	spar	lupa	anag	ther	leon	camo	cyt	m-cyt	X1	X2	X3	X4	X5
M. aethiopicum		10	7	tr	25	52		tr	3	2		2	
M. alpinum		1	7	tr	29	54	tr?	tr	tr	tr		1	
M. cf. *burchellii*		1	4	1	4	88		tr	tr	tr		2	
M. candicans		20	71	2	tr	1		1	1	1	1		
M. canescens		19	4	1	tr	tr		2	39	2	7	2	
M. exudans	tr?	3	22	tr	6	63	tr	tr		1	tr	2	
M. microphyllum		2	21	tr	tr	10	tr	5			56		
M. obcordatum		9	28	5	1	42		2	5		tr	4	
M. stipulatum		19	4	1	tr	69		tr	tr	2	2	1	
M. subspicatum		tr	11	26	6	8		41	tr	tr		5	
M. wilmsii		1	2	38	2	21		tr	tr	tr		36	
M. involucratum	tr	6	23	tr?	tr	tr	1	28	tr	1			33

Abbreviations: spar = sparteine, lupa = lupanine, anag = anagyrine, ther = *l*-thermopsine, leon = leontidine, camo = camoensine, cyt = cytisine, m-cyt = *n*-methylcytisine, X1 = 4-OH-lupanine?, X2 = 5,6-dehydrolupanine?, X3 = ammodendrine?, X4 = unidentified, X5 = unidentified

entered. These results closely corresponded with earlier identifications made by analytical thin-layer chromatography.

Lupanine, anagyrine, thermopsine, leontidine, camoensine and *N*-methylcytisine are clearly the most common alkaloids in *Melolobium*. Within the Crotalarieae this combination, and especially the common occurrence of thermopsine, camoensine and leontidine may prove to be a unique chemotaxonomic character for *Melolobium*. The two C_{14} alkaloids camoensine and leontidine were previously known only from *Camoensia maxima* Welw. ex Benth. of the tribe Sophoreae (Santamaria & Khuong-Huu op. cit.). Sparteine and cytisine are virtually absent, while other alkaloids provisionally identified as ammodendrine, 4-OH-lupanine (nuttalline) and 5,6-dehydrolupanine seem to occur only in some of the species. Small amounts of isolupanine and 17-oxo-lupanine (not shown in Table 2) appear to be present in *M. alpinum* and *M. canescens* respectively.

Melolobium involucratum, an anomalous species recently transferred from *Argyrolobium* (Stirton 1986) seems to differ from other species of *Melolobium*. Its major alkaloid (X5 in Table 2) does not occur in any of the other species; thermopsine, leontidine and camoensine are absent or virtually absent, while sparteine and cytisine are present. The apparently low concentration of sparteine in *M. involucratum* resulted from a loss of this alkaloid during purification of the extract. This is the only significant discrepancy between the GC results and our earlier TLC results — the latter clearly showed the presence of large quantities of sparteine in both the crude alkaloidal extract and in the methanolic eluent from the resin. The loss of sparteine may be explained by its low basicity compared to other alkaloids (K_1 value of $5{,}7 \times 10^{-3}$ compared to $7{,}7 \times 10^{-7}$ of cytisine, for example). Morphological and cytological evidence strongly suggest that *M. involucratum* is misplaced in *Melolobium* (van Wyk & Schutte, unpublished data). A comparison with the alkaloids of other genera may indicate a more natural position for this species. *Melolobium canescens, M. microphyllum* and *M. wilmsii* also differ from other species in the presence of respectively nuttalline, ammodendrine and an unidentified alkaloid (X4) as the major alkaloids. These alkaloids do however occur as minor compounds elsewhere.

Tetracyclic and tricyclic α-pyridone alkaloids are known to be formed along a biogenetic pathway which starts with lupanine and has methylcytisine as end product (Nowacki & Waller 1977; Salatino & Gottlieb 1980). Each step along the pathway involves a specific enzyme system and leads to an enhancement of alkaloid toxicity, so that cytisine-bearing genera are considered to be phylogenetically advanced (Salatino & Gottlieb op. cit.). The presence of several such specialized quinolizidine alkaloids of the cytisine type in the tribe Crotalarieae is here reported for the first time. Some modifications to previously proposed phylogenetic relationships in the Papilionoideae (Salatino & Gottlieb 1980, 1981) are therefore necessary. An additional route of adaptive radiation is suggested, namely a southern temperate 'cytisine' route. This new route presumably represents an extension of a southern temperate 'pre-cytisine' route proposed by Salatino & Gottlieb (1980).

It is not yet clear how *Melolobium* relates to other genera of the tribe Crotalarieae. The particular combination of alkaloids that occurs in this genus however, may prove to be a unique chemotaxonomic character. The absence of sparteine and the presence of camoensine and leontidine as major alkaloids seem particularly significant. Our results clearly indicate that alkaloids have considerable taxonomic value at the generic level and that it may eventually lead to a better understanding of relationships amongst genera of the Crotalarieae and Genisteae.

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Appendix 1 Plant material of *Melolobium* species used for alkaloid extraction. Voucher specimens are all in the Rand Afrikaans University Herbarium (JRAU)

M. aethiopicum (L.) Druce: Velddrif Rd., 24 km from Cape Town, *Van Wyk 2685*, flowering twigs. *M. alpinum* Eckl. & Zeyh.: Sani Pass, Natal, *Van Wyk 2631*, mostly vegetative twigs. *M.* cf. *burchellii* N.E. Br.: Noupoortnek, 2 km from Clarens, O.F.S., *Schutte 393*, flowering twigs. *M. candicans* (E. Mey.) Eckl. & Zeyh.: ± 20 km from Cathcart to Stutterheim, E. Cape, *Koekemoer s.n.*, flowering and fruiting twigs. *M. canescens* Benth.: Bloemfontein, O.F.S., *Van Wyk 2714*, flowering twigs. *M. exudans* Harv.: Velddrif Rd., ± 20 km from Cape Town, *Van Wyk 2683*, flowering twigs. *M. involucratum* (Thunb.) Stirton: Blomfontein Farm, Calvinia district, NW Cape, *Steenkamp sub Schutte 396*, fruiting twigs. *M. microphyllum* (L.f.) Eckl. & Zeyh.: Naudesberg Pass near Graaff Reinet, Cape, *Van Wyk 2634*, flowering twigs. *M. obcordatum* Harv.: Noupoortnek, 2 km from Clarens, O.F.S., *Schutte 394*, mostly vegetative twigs. *M. stipulatum* Harv.: Verkeerdevlei near Touw's River, Cape, *Van Wyk 2711*, vegetative twigs. *M. subspicatum* Conrath: Irene, Transvaal, *De Beer 38*, flowering twigs. *M. wilmsii* Harms: Hendrina, Transvaal, *Van Wyk 2624*, fruiting twigs.

APPENDIX 4

S. Afr. J. Bot., 1988, 54(4): 389–391

The major alkaloids of the genus *Polhillia*

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The major alkaloids of three species of *Polhillia* Stirton and three species of *Argyrolobium* Eckl. & Zeyh. have been identified. The presence of sparteine, lupanine, anagyrine and *N*-methylcytisine as major alkaloids in *Polhillia* and in the morphologically similar *Argyrolobium brevicalyx* Stirton indicates a direct phylogenetic link between *Polhillia* (Crotalarieae) and *Argyrolobium* (Genisteae). The data also supports the transfer of *Melolobium involucratum* (Thunb.) Stirton to *Polhillia*.

Die hoof alkaloïede van drie spesies van *Polhillia* Stirton en drie spesies van *Argyrolobium* Eckl. & Zeyh. is geïdentifiseer. Die voorkoms van sparteïen, lupanien, anagirien en *N*-metielcitisien as hoof alkaloïede van *Polhillia* en van die morfologies-eenderse *Argyrolobium brevicalyx* Stirton dui op 'n direkte filogenetiese verband tussen *Polhillia* (Crotalarieae) en *Argyrolobium* (Genisteae). Die data ondersteun ook die oorplasing van *Melolobium involucratum* (Thunb.) Stirton na *Polhillia*.

Keywords: *Argyrolobium*, chemotaxonomy, generic relationships, *Polhillia*, quinolizidine alkaloids

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Introduction

The genus *Polhillia* was recently described by Stirton (1986a) and comprises 5 rare species of woody shrubs endemic to the south-western Cape Province of South Africa. Based on presumed affinities with *Melolobium* Eckl. & Zeyh. and *Dichilus* DC., the new genus was placed in the tribe Crotalarieae.

In view of obvious morphological similarities with *Argyrolobium* Eckl. & Zeyh., and especially the anomalous *A. brevicalyx* Stirton (1984), we investigated the major alkaloids of three species of *Polhillia* and some species of *Argyrolobium*. *Melolobium involucratum* (Thunb.) Stirton was also included in the study because its major alkaloids were previously shown to be different from those of other *Melolobium* species (van Wyk *et al.* 1988a).

Material and Methods

The species studied and voucher specimens of the material used for alkaloid extraction are listed in the appendix. Authorities for names are not repeated elsewhere.

Methods of extraction and identification are as previously described (van Wyk *et al.* 1988a, b; van Wyk & Verdoorn 1988). All reference samples used in analytical TLC and GC were fully characterized by IR, ^{1}H NMR, ^{13}C NMR and MS spectrometry.

Results and Discussion

The estimated number of alkaloids present in each of the samples and the total yields obtained are shown in Table 1. *Polhillia canescens*, *P. pallens*, *P. waltersii*, *Melolobium involucratum* and *Argyrolobium brevicalyx* (all of which are morphologically similar) seem to differ from *A. crassifolium* and *A. variopile* in both the diversity and total number of alkaloids. The latter two species have only one major alkaloid each, while the others have at least three. The difference is even more distinct if the yields of major alkaloids are taken as percentages of the total (Table 2). The sample size does not allow generalizations (especially for *Argyrolobium*), but it is clear from Table 2 that the species are all rather similar. Anagyrine is by far the most common alkaloid. *N*-methylcytisine, sparteine and lupanine occur at least in trace quantities in all of the species, while cytisine, lusitanine and two unidentified alkaloids

Table 1 Total yields and estimated number of alkaloids extracted from species of *Argyrolobium*, *Polhilla* and *Melolobium*

Species	Total yield[a] (μg g^{-1} dry wt)	Estimated number[b] of alkaloids: Major (> 10%)	Minor (> 1%)	Traces (< 1%)	Total
Polhillia canescens	478	3	6	5	14
P. pallens	241	4	1	10	15
P. waltersii	987	4	8	5	17
M. involucratum	387	4	2	13	19
Argyrolobium brevicalyx	731	5	2	11	18
A. crassifolium	590	1	5	6	12
A. variopile	976	1	6	5	12

[a] Yield figures are for purified alkaloidal extracts
[b] Estimated from GC results

Table 2 Distribution of major alkaloids in extracts of *Polhillia* spp., *Argyrolobium* spp. and *Melolobium involucratum* as determined by gas chromatography

	Distribution of major alkaloids[a] (% of total alkaloid yield)							
Species	spar	lupa	anag	cyt	m-cyt	lusi	X1	X2
Polhillia waltersii	1	9	52	13	11	5		tr?
P. pallens	tr	27	25	4	42			tr
P. canescens	tr	4	57	7	24	tr		
Melolobium involucratum	tr	6	23	1	28		3	33
Argyrolobium brevicalyx	1	16	40	tr	18		19	tr
A. crassifolium	tr	tr	90		1			
A. variopile	tr	1	89		2		tr	

Abbreviations: spar = sparteine, lupa = lupanine, anag = anagyrine, cyt = cytisine, m-cyt = *N*-methylcytisine, lusi = lusitanine, X1 & X2 = unknown

[a] Yield figures for sparteine are totally underestimated except in *Argyrolobium crassifolium* and *A. variopile* (see Figure 1). Sparteine was lost from the crude extracts during resin purification — the poor adsorbsion of this alkaloid on cationic exchange resin may be explained by its low basicity compared to the other alkaloids

appear to be less common.

All available information on the major alkaloids of the genera *Lebeckia, Polhillia, Argyrolobium* and *Melolobium* is summarized in Table 3. The presence of minor alkaloids and unidentified major alkaloids is not shown. Sparteine is entered as a major alkaloid despite the low yield figures. The loss of this alkaloid from the crude alkaloidal extracts is explained in the footnotes of Table 2. It is clear that the present generic boundaries do not conform to the alkaloid data. The major alkaloids of *Polhillia canescens, P. pallens, P. waltersii, Melolobium involucratum* and *Argyrolobium brevicalyx* are almost identical. A reappraisal of the circumscription of *Polhillia* seems necessary, as morphological and cytological evidence (van Wyk & Schutte, unpublished data) strongly correlate with the distribution of alkaloids. Our results support the initial idea of Stirton (1986b) to include *Melolobium involucratum* in *Polhillia* rather than the transfer to *Melolobium*. Figure 1 shows the result of thin-layer chromatography of crude alkaloidal extracts of some of the species. It is clear that there are distinct differences between the genera but that the major alkaloids of *Argyrolobium brevicalyx, Polhillia pallens* and *Melolobium involucratum* are very similar.

The position of *Argyrolobium* in the tribe Genisteae is somewhat uncertain (Polhill 1976, 1981). Some of the species treated here are of particular interest in that they may help explain the origins and affinities of *Argyrolobium*. *Argyrolobium brevicalyx* for example, is presently a member of the tribe Genisteae but it is morphologically and cytologically almost identical to the species of *Polhillia* (tribe Crotalarieae). The alkaloids of this species indeed strongly indicate that it should also be transferred to *Polhillia*. Attempts by Salatino & Gottlieb (1980, 1981) to link *Argyrolobium* to *Lupinus* L. and *Sarothamnus* Wimm. have in our opinion rather shown the opposite, as is evidenced by the isolated position of *Argyrolobium* in their affinity diagram (Figure 2 in Salatino & Gottlieb 1981). A connection with *Lebeckia* seems much more likely. The data for *Lebeckia* is incomplete and a more detailed survey of this genus is necessary, especially since it is considered to be one of the basal groups of the tribe Crotalarieae (Polhill 1981). The absence of *N*-methylcytisine, anagyrine and cytisine needs to be confirmed. Biogenetic pathways leading to sparteine and cytisine are now well known and the ability to transform ring A into a pyridone is considered to be an advanced character (Nowacki & Waller 1977; Salatino & Gottlieb 1980). Shrubby and tree species of the Papilionoideae tend to contain sparteine, while derived ones contain more elaborate compounds such as methylcytisine (Nowacki & Waller op. cit.). The common occurrence of α-pyridone alkaloids in southern African genera of the Crotalarieae was not known before, and opens up the possibility of a southern origin for *Argyrolobium*. The species around *Polhillia* thus seem to form a connecting link between *Lebeckia* and *Argyrolobium*, since they contain both phylogenetically primitive sparteine- and lupanine-type alkaloids and advanced cytisine-type alkaloids. In *Melolobium* and the less woody species of *Argyrolobium* the trend appears to be one of increasing specialization in a cytisine-type chemistry. Large amounts of anagyrine and cytisine are characteristic of *Argyrolobium*, while *Melolobium* shows a predominance of thermopsine and the two C_{14} alkaloids leontidine and camoensine.

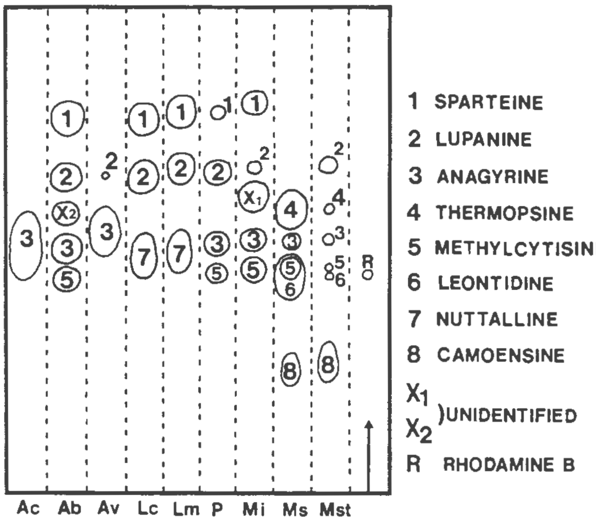

Figure 1 Major alkaloids of some species of *Argyrolobium, Lebeckia, Polhillia* and *Melolobium* as observed by thin-layer chromatography (silica gel: eluent cyclohexane–$CHCl_3$–Et_2 NH, 50:40:10, detecting reagent iodoplatinate). Ac, *Argyrolobium crassifolium*; Ab, *A. brevicalyx*; Av, *A. variopile*; Lc, *Lebeckia cytisoides* Thunb.; Lm, *L. multiflora* E. Mey.; P, *Polhillia pallens*; Mi, *Melolobium involucratum*; Ms, *M. subspicatum* Conrath; Mst, *M. stipulatum* Harv.

Table 3 Distribution of 11 major alkaloids known from the genera *Lebeckia, Polhillia, Argyrolobium* and *Melolobium*. [Data for *Lebeckia* and *Melolobium* from Gerrans *et al.* (1976) and van Wyk *et al.* (1988a, b). Cytisine occurs as a major alkaloid in seeds of *Argyrolobium saharae* Pomel and lusitanine in seeds of *A. zononii* (Turra) P.W. Ball (Greinwald, unpublished data); argyrolobine was reported as the major alkaloid of *A. megarhizum* H. Bol. (Tsuda & Marion 1964)]

	Lebeckia	*Polhillia*	*Melolobium involucratum*	*Argyrolobium brevicalyx*	*Argyrolobium* (other spp.)	*Melolobium* (other spp.)
Nuttalline	+++					+?
Sparteine	+++	+++	+++	+++		
N-methylcytisine		+++	+++	+++		+
Lupanine	+++	++	++	++		++
Anagyrine		+++	+++	+++	++	++
Cytisine		+			+	
Lusitanine					+	
Argyrolobine					+	
Thermopsine						+
Camoensine						++
Leontidine						+

Occurs as a major component in: +++ all species/samples, ++ most species/samples, + at least some species/samples

Acknowledgements

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Appendix 1 Plant material used for alkaloid extraction. Voucher specimens are all in the Rand Afrikaans University Herbarium (JRAU)

Argyrolobium brevicalyx Stirton: Uitvlug Farm, between Bredasdorp & Swellendam, *Van Wyk 2134*, flowering twigs. *A. crassifolium* Eckl. & Zeyh.: Zuurberg, E. Cape, *B & M Van Wyk 2115*, flowering twigs. *A. variopile* N. E. Br.: Volksrust, Transvaal, *Schutte 364*, flowering twigs. *Melolobium involucratum* (Thunb.) Stirton: Blomfontein Farm, Calvinia district, NW Cape, *Steenkamp sub Schutte 396*, fruiting twigs (fruit not included). *Polhillia canescens* Stirton: Adoonskop, between Bredasdorp & Swellendam, *Van Wyk 2709*, vegetative twigs. *P. pallens* Stirton: Remhoogte, between Bredasdorp & Swellendam, *Van Wyk 2708*, flowering twigs. *P. waltersii* (Stirton) Stirton: Worcester commonage, *Van Wyk 2701*, flowering twigs.

APPENDIX 5

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Chemotaxonomic Value of Alkaloids in the Genus *Dichilus*

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Key Word Index—*Dichilus*; Leguminosae; Crotalarieae; piperidyl alkaloids; quinolizidine alkaloids; chemotaxonomy; generic relationships.

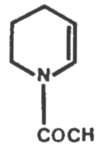
Abstract—Two bicyclic piperidyl alkaloids (ammodendrine and smipine) and a quinolizidine alkaloid (thermopsine) were identified as major alkaloids of the genus *Dichilus*. Other piperidyl alkaloids positively identified were bipyridyl, *N*-methylammodendrine, *N*-acetylhystrine, 1-acetyl-1,2,3,4-tetrahydropyridine and piperidinone. The latter two compounds have not been previously reported from the Leguminosae. In the tribe Crotalarieae, the dominance of piperidyl alkaloids appears to be a unique chemotaxonomic character for *Dichilus*. Our results strongly support the present circumscription and also the isolated position of the genus. An affinity with *Melolobium* rather than *Lebeckia* is suggested.

Introduction

In a general survey of alkaloids in the tribe Crotalarieae [1], we have shown that a distinctive combination of several unidentified alkaloids occur in the genus *Dichilus*. This genus is morphologically remarkably similar to other genera of the tribe and its circumscription on morphological evidence alone is somewhat problematic. Superficial similarities with the genus *Lebeckia* have led to suggestions of affinity with the latter [2], but the chromosome cytology (Van Wyk, B-E. and Schutte, A. L., submitted for publication in *Kew Bull.*) does not support this view. The apparent absence in *Dichilus* of the common quinolizidine alkaloids of other genera has indicated that a full characterization of at least the major compounds would be of considerable chemotaxonomic interest.

Results

The distribution of 18 different alkaloids in 15 extracts of the five species of *Dichilus* is shown in Table 1. Yields of alkaloids were very low and allowed comparative identification of only the major alkaloids, ammodendrine, smipine and thermopsine. Due to their unusual mass spectra [3, 4] however, positive identification of most of the compounds was possible. The presence of 1-acetyl-1,2,3,4-tetrahydropyridine (**1**) and piperidinone (**2**) appears to be a new record for the Leguminosae. We have also found trace amounts of anabasine, 3-(3,4-dihydro-2H-pyrrol-5-yl)-pyridine, 3-(1-pyridinyl)-1,2,3,4-tetrahydropyridine, *N*-acetyl-3-(1-piperidincarboxaldehyde-2-yl)-piperidine and 1-acetyl-5-(1-formyl-2-piperidinyl)-2,3-dihydro-1H-pyrrole. The identity of these minor compounds could not be confirmed however and we considered it best to list them under the unknown alkaloids in Table 1. Trace quantities of alkaloids that were present as single occurrences are also not shown.



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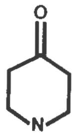

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(*Revised received* 23 *April* 1988)

Discussion

Table 1 shows that the species of *Dichilus* are very similar and that the unusual combination of alkaloids leaves little doubt that the group is monophyletic. What differences there are appear to be quantitative only. *Dichilus gracilis*, for example, contained almost exclusively piper-

TABLE 1. DISTRIBUTION OF ALKALOIDS IN 3 EXTRACTS OF EACH OF THE FIVE SPECIES OF *DICHILUS*

Species	*D. strictus*			*D. reflexus*			*D. lebeckioides*			*D. pilosus*			*D. gracilis*		
Sample number	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Piperidyl alkaloids															
Ammodendrine	39	10	25	31	45	16	36	41	59	27	25	45	53	57	38
Smipine	28	18	34	31	24	27	23	3	8	36	9	18	20	13	19
Piperidinone	11	5	14	5	9	4	6	tr	—	7	14	7	6	tr	tr
Bipyridyl	tr	6	11	4	4	3	4	tr	4	4	tr?	3	3	tr	2
1-acetyl-1,2,3,4-tetrahydropyridine	tr	tr	tr	6	—	11	tr	9	2	tr?	tr?	tr?	7	9	19
N'-Methylammodendrine	1	tr	—	5	—	2	—	—	2	tr	5	tr	tr	tr	2
N-Acetylhystrine	5	—	—	3	2	3	2	—	2	—	—	—	—	—	4
Quinolizidine alkaloids															
Thermopsine	2	28	19	tr	5	1	7	21	6	13	7	2	tr	tr	tr
Lupanine	tr	1	tr	1	tr	1	1	tr	tr	tr	1	tr	tr	tr	—
N-Methylcytisine	tr	9	2	2	tr	2	tr	—	1	2	3	2	—	—	—
Anagyrine	—	2	tr	tr	—	2	tr	—	tr	tr	tr	tr	tr	tr	tr
Unknown alkaloids															
A	2	tr	tr	2	2	4	4	tr	1	3	4	3	2	1	2
B	tr	tr	—	2	8	2	8	6	3	3	tr	3	3	3	3
C	1	tr?	1	2	1	2	1	tr	tr	2	2	1	1	4	1
D	2	5	1	tr	1	2	1	1	3	tr	3	tr	tr	2	3
E	—	—	—	—	—	2	1	—	2	—	tr	2	3	—	5
F	—	1	tr?	—	—	1	—	—	tr	tr	tr	—	tr?	—	tr
G	—	—	—	—	—	—	—	—	—	—	2	tr	—	—	1

Figures given are percentages of the total alkaloid yield as estimated from GC results. Authorities for names and voucher specimen details, as well as Rt values and MS data of the unknown alkaloids are given in the experimental section.

idyl alkaloids, but thermopsine and other quinolizidine alkaloids are also present albeit in trace quantities. Qualitative differences between the species do not appear to be very significant and are more likely a result of sample limitations. The diversity and predominance of piperidyl alkaloids are of some interest. It has been postulated [5] that dipiperidine (bipiperidyl) alkaloids are biosynthetic intermediates between a cyclization product of cadaverine and a bicyclic quinolizidine alkaloid. The alkaloidal metabolites in *Dichilus* seem to show connections in a precursor–product relationship on at least two biogenetic pathways — one leading to ammodendrine and related compounds, and a minor one leading to the more conventional α-pyridone alkaloids.

The generic status and isolated position of *Dichilus* in the tribe Crotalarieae is strongly supported by the unusual combination of alkaloids. Other genera investigated so far have as major alkaloids only the more common tetracyclic and tricyclic quinolizidine types, or less frequently, pyrrolizidine alkaloids. A comparison between the genera *Lebeckia, Dichilus, Melolobium, Polhillia* and *Argyrolobium* is given in Table 2. (The position of *Argyrolobium* in the tribe Genisteae is somewhat doubtful and a transfer to the Crotalarieae was recently suggested [Van Wyk and Schutte, *op. cit.*].) *Melolobium* is the only other genus where piperidyl alkaloids have been found (Van Wyk, B-E., Verdoorn, G. H., Burger, L. and Greinwald, R., *S. Afr. J. Botany,* in press). Ammodendrine occurs as a major alkaloid in *M. microphyllum* and at least in trace quantities in several other species. We suggest that *Lebeckia* and *Dichilus* are only superficially similar and that the latter is more closely related to *Melolobium.* Morphological evidence such as the calyx structure and petiole anatomy [Van Wyk and Schutte, *op. cit.*] agrees with this view.

Piperidyl alkaloids have previously been reported from seven genera of the tribes Genisteae, Liparieae, Sophoreae and Bossiaeeae [6]. The presence of piperidyl alkaloids in the Genisteae and Crotalarieae (formerly both part of the Genisteae *sensu lato*), is further evidence of the close relationship between the two tribes. These alkaloids are known to coexist with quinolizidine and pyrrolizidine alkaloids in the genera *Ammodendron*

TABLE 2. DISTRIBUTION OF MAJOR ALKALOIDS IN THE GENERA *LEBECKIA, DICHILUS, MELOLOBIUM, POLHILLIA* AND *ARGYROLOBIUM*

	Lebeckia	*Dichilus*	*Melolobium*	*Polhillia*	*Argyrolobium*
Sparteine	+++			+++	
Lupanine	+++		++	++	
Nuttalline	+++		+?		
Argyrolobine					+
Anagyrine			++	+++	++
Thermopsine		+	+		
Camoensine			++		
Leontidine			+		
N-Methylcytisine			+	+++	
Cytisine				+	+
Lusitanine					+
Ammodendrine		+++	+		
Smipine		++			
Piperidinone		+			
Bipyridyl		+			
1-Acetyl-1,2,3,4-tetrahydropyridine		+			

Data for genera other than *Dichilus* are published elsewhere [Van Wyk *et al., op. cit.*; Van Wyk, B-E., Verdoorn, G. H. and Greinwald, R., *S. Afr. J. Botany*, in press]. +++: occurs as a major component in all species or samples, ++: most species or samples, +: at least some species or samples.

and *Adenocarpus* [6, 7], and are therefore likely to have a wider distribution in the Crotalarieae than is presently known.

Experimental

Plant materials. Collection details and voucher specimens of the species examined are listed below. All samples comprised twigs and leaves in the post-flowering stage. Voucher specimen numbers all refer to our own collections, which are housed in the Rand Afrikaans University herbarium. Yield figures (dry wt) in parentheses.

Dichilus gracilis Eckl. & Zeyh. Sample 1: Fauresmith, Orange Free State, Schutte 352 (130 μg g^{-1}); Sample 2; Jagersfontein, Orange Free State, Schutte 345 (154 μg g^{-1}); Sample 3: Colesberg, Cape, Schutte 337 (112 μg g^{-1}). *Dichilus lebeckioides* DC. Sample 1: Johannesburg, Transvaal, Schutte 380a (45 μg g^{-1}); Sample 2: Pretoria, Transvaal, Schutte 362 (10 μg g^{-1}); Sample 3: Johannesburg, Transvaal, Schutte 380c (47 μg g^{-1}). *Dichilus pilosus* Conrath ex Schinz. Sample 1: Roodepoort, Transvaal, Schutte 370a (84 μg g^{-1}); Sample 2: Roodepoort, Transvaal, Schutte 370b (9 μg g^{-1}); Sample 3: Roodepoort, Transvaal, Schutte 358 (31 μg g^{-1}). *Dichilus reflexus* (N. E. Br.) A. L. Schutte. Sample 1: Sani Pass, Natal, Van Wyk 2630b (100 μg g^{-1}); Sample 2: Pongola, Transvaal, Schutte 369 (126 μg g^{-1}, small sample; 12 μg g^{-1}, 19 kg sample); Sample 3: Pongola, Transvaal, Schutte 365 (53 μg g^{-1}). *Dichilus strictus* E. Mey. Sample 1: Noupoortnek, Orange Free State, Schutte 392 (12 μg g^{-1}); Sample 2: Between Clarens and Golden Gate, Orange Free State, Schutte 146 (73 μg g^{-1}); Sample 3: Reitz, Orange Free State, Schutte 376a (20 μg g^{-1}).

Procedures. Ground air-dried material was extracted by refluxing with CH_2Cl_2 for several days. Alkaloidal material was isolated from the crude extracts by water phase separation [1] and purified by ion exchange resin (Dowex 50 W H^+ form). Alkaloids were identified by analytical TLC and GC by comparison with and coinjection of reference samples that were studied by GC–MS. Pure samples of ammodendrine (120 mg) and smipine (7 mg) were obtained from 19 kg of air-dried leaves and twigs of *D. reflexus* (total alkaloid yield of 230 mg). Isolation was effected by silica gel 60 column chromatography as described previously [8] and Sephadex LH-20 gel filtration in MeOH as eluent. The identity of the two major compounds was confirmed by their MS spectra and characteristic signals of their ^1H NMR and ^{13}C NMR spectra. Both the ^1H and ^{13}C NMR spectra of ammodendrine showed amide isomerism and only ^{13}C signals of the major isomer are given below. Due to impurities, limited sample and amide isomerism, the ^{13}C NMR spectrum of smipine could not be assigned unambiguously. GC spectra were obtained with an OV-17 fused silica capillary column (30 m × 0.3 mm; He as carrier gas at 0.5 kg cm^{-2}, column temperature 50°, 1 min isotherm, 20°/min to 320°, 15 min isotherm; injector 320°; injector mode 1 μl splitless 30:1; FID 350°). Authentic reference samples of anagyrine (Rt 18.40), *N*-methylcytisine (Rt 13.32), thermopsine (Rt 19.32) and lupanine (Rt 17.50) were the same as used in a previous study [Van Wyk *et al., op. cit.*]. MS data were recorded on two samples (*D. reflexus* no. 3 and *D. gracilis* no. 3) and allowed positive identification of seven piperidyl and four quinolizidine alkaloids. The MS data for piperidyl alkaloids were identical to results obtained in a detailed study of the mass spectra of piperidyl alkaloids [3, 4]. Ammodendrine: Rt 14.08, ^{13}C NMR δ20.5, 21.6, 22.6, 24.8, 25.7, 31.5, 40.1, 47.2, 61.3, 119.5, 120.9, 167.7, M^+ 208; smipine: Rt 11.20, M^+ 180; piperidinone: Rt 6.20, M^+ 99; bipyridyl: Rt 10.04, M^+ 156; 1-acetyl-1,2,3,4-tetrahydropyridine: Rt 5.28, M^+ 125; *N′*-methylammodendrine: Rt 13.44, M^+ 222; *N*-acetylhystrine: Rt 15.10, M^+ 206. Data for uncharacterized or partially characterized piperidyl alkaloids — A: Rt 10.48, *m/z* 213 (2), 185 (2), 171 (3), 159 (12), 143 (13), 141 (10), 125 (3), 113 (12), 101 (12), 97 (18), 71 (31), 57 (100). B: Rt 7.24, *m/z* 202 (2), 173 (2), 167 (4), 139 (22), 138 (20), 122 (5), 111 (23), 110 (18), 97 (26), 96 (34), 83 (100), 69 (8), 55 (40), 42 (23). C: Rt 14.66, (no MS data). D: Rt 17.36, *m/z* 236 (9), 218 (100), 207 (20), 193 (15), 175 (63), 165 (25), 150 (31), 136 (19), 122 (34), 108 (26), 82 (31), 57 (22), 43 (47) [*N*-acetyl-3-(1-piperidine carboxaldehyde-2-yl)piperidine?]. E: Rt 15.20, *m/z* 298 (5), 281 (10), 261 (5), 221 (9), 202 (6), 184 (3), 171 (4), 150 (20), 137 (10), 111 (70), 97 (73), 84 (100), 71 (22), 57 (51). F: Rt 18.44, *m/z* 222 (56), 221 (11), 204 (53), 194 (16), 179 (58), 166 (13), 152 (80), 151 (72), 122 (17), 109 (100), 57 (57), 43 (99) [1-acetyl-5-(1-formyl-2-piperidinyl)-2,3-dihydro-1H-pyrrole?]. G: Rt 13.04, *m/z* 253 (4), 225 (17), 209 (30), 166 (21), 152 (19), 150 (28), 149 (28), 138 (100), 136 (70), 110 (59), 98 (89), 83 (72), 55 (51), 43 (40).

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APPENDIX 6

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The major alkaloids of the genus *Argyrolobium*

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The major alkaloids of 12 morphologically dissimilar species of *Argyrolobium* Eckl. & Zeyh. have been identified. All extracts contain large quantities of anagyrine as the dominant alkaloid. Cytisine, *N*-methylcytisine, lupanine, sparteine, 5,6-dehydrolupanine and ammodendrine are present as minor compounds in most of the species and as major compounds only in a few of them. The data do not reflect morphological dissimilarities and the species are remarkably uniform in their major alkaloids. Our conclusions are that *Argyrolobium* is closely related to the genus *Polhillia* Stirton, that large quantities of anagyrine may be taken as a chemotaxonomic marker for *Argyrolobium* and that a more detailed study of alkaloids may provide valuable taxonomic evidence in a genus without any obvious morphological specializations.

Die alkaloïede van 12 morfologies-verskillende spesies van *Argyrolobium* Eckl. & Zeyh. is geïdentifiseer. Alle ekstrakte bevat anagirien as die dominante alkaloïed. Sitisien, *N*-metielsitisien, lupanien, sparteïen, 5,6-dehidrolupanien en ammodendrien is teenwoordig as ondergeskikte verbindings in meeste van die spesies en as hoof verbindings in slegs 'n paar van hulle. Die data weerspieel nie morfologiese verskille nie en die spesies is merkwaardig eenvormig in hul hoof alkaloïede. Ons gevolgtrekkings is dat *Argyrolobium* naverwant is aan die genus *Polhillia* Stirton, dat groot hoeveelhede anagirien as 'n chemotaksonomiese merker vir *Argyrolobium* beskou kan word en dat 'n meer volledige studie van alkaloïede waardevolle taksonomiese getuienis mag bied in 'n genus sonder enige ooglopende morfologiese spesialisasies.

Keywords: *Argyrolobium*, chemotaxonomy, Fabaceae, generic relationships, quinolizidine alkaloids

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Introduction

The genus *Argyrolobium* Eckl. & Zeyh. comprises an estimated 70 species of papilionoid legumes, 50 or more of which occur in southern Africa. There is no convincing evidence to support its traditional position in the tribe Genisteae and a transfer to the predominantly southern African tribe Crotalarieae has been suggested (Polhill 1976, 1981; van Wyk & Schutte 1989). It has also been shown that the alkaloids of some *Argyrolobium* species are similar to those of other genera of the Crotalarieae, notably *Polhillia* Stirton and *Melolobium* Eckl. & Zeyh. (van Wyk *et al.* 1988a, b). In this study we investigated 12 morphologically dissimilar species of *Argyrolobium* to evaluate the taxonomic significance of alkaloids at the generic and infrageneric level.

Materials and Methods

To obtain a reasonable representation of the variation in the genus, species from different sections (Harvey 1862) were chosen. It was assumed that if all these species turn out to be similar in their major alkaloids, then at least a preliminary characterization of the genus would be possible.

The taxonomy of *Argyrolobium* is in such a state of confusion that some of the material could not be positively identified to species. Care was taken to keep voucher specimens of all the samples for future reference and verification. The species, authorities for names, and voucher specimens of the material used are listed in the appendix.

Methods of extraction and identification were as previously described (van Wyk *et al.* 1988a, b; van Wyk & Verdoorn 1988). The extracts were all purified by ion exchange resin (Dowex 50W H^+ form). All reference samples used in analytical TLC and GC were fully authenticated by ^1H and ^{13}C NMR spectroscopy and mass spectrometry. Identifications by analytical TLC and GC were confirmed by GC-MS studies of three extracts (two samples of *A. tomentosum* and one of *A. frutescens*).

Results and Discussion

Table 1 shows the yields of purified alkaloidal material obtained and the distribution of major alkaloids in 15 different samples. All the major alkaloids (>10% of total yield) and most of the minor ones (<10%) could be positively identified. The presence of unidentified minor compounds is not shown.

The distribution of alkaloids is surprisingly uniform and the variation is much less than expected. Anagyrine is by far the most common alkaloid and rarely represents less than half of the total yield. When the concentration of anagyrine is relatively low, large quantities of cytisine or *N*-methylcytisine are usually present. Lupanine, sparteine, 5,6-dehydrolupanine, ammodendrine and an alkaloid tentatively identified as aphylline are very often present but rarely as major compounds.

Our results differ from those of Tsuda & Marion (1964), who reported argyrolobine and aphyllidine as major alkaloids of *Argyrolobium megarhizum* H. Bol. Argyrolobine has never been reported since and no

Table 1 Yield and distribution of major alkaloids in 15 extracts from 12 species of *Argyrolobium*

Species	Material extracted (V)egetative twigs (F)lowering twigs	Total yield (mg g^{-1} dry wt)[a]	Distribution of major alkaloids (% of total alkaloid yield)[b]							
			anag	cyt	m-cyt	lupa	spar	5,6-deh	ammo	aphy
A. crassifolium										
sample 1	F	1,05	98	1	tr	tr	tr	tr	tr	–
sample 2	F	0,20	84	3	1	tr	–	2	–	–
A. frutescens	V	0,01	50	5	1	8	6	6	3	3
A. lanceolatum										
sample 1	F	1,33	96	tr	tr	2	tr	1	tr	–
sample 2	V	1,46	97	tr	tr	tr	1	tr	–	tr
A. lunare	F	0,24	56	3	5	21	3	3	–	tr
A. molle	F	0,10	41	3	2	4	34	2	11	–
A. rupestre	V	0,05	58	6	2	2	3	2	1	1
A. sankeyi	F	0,01	61	2	tr	6	4	6	1	1
A. speciosum	V	0,03	75	tr	19	2	1	2	tr	tr
A. tomentosum										
sample 1	F	0,60	79	10	7	1	–	tr	tr	1
sample 2	F	0,27	25	36	6	1	7	tr	tr	2
A. sp. cf. *A. tysonii*	F	0,03	53	16	2	2	12	9	tr	–
A. variopile	F	0,38	92	tr	tr	1	2	tr	–	–
A. velutinum	V	0,06	18	35	34	3	2	tr	3	1

Abbreviations: anag = anagyrine, cyt = cytisine, m-cyt = *N*-methylcytisine, lupa = lupanine, spar = sparteine, 5,6-deh = 5,6-dehydrolupanine, ammo = ammodendrine, aphy = aphylline?

[a] Yield figures are for purified extracts

[b] Estimated from GC results

voucher specimens of the plant which yielded this alkaloid could be traced. The reported presence of cytisine and *N*-methylcytisine agrees with our results, but the conspicuous absence of anagyrine and the presence of argyrolobine and aphyllidine as major alkaloids in *A. megarhizum* should be verified.

The uniformity in major alkaloids (much less variable than in *Melolobium*, for example) supports Polhill's (1976) conclusion that *Argyrolobium* is a uniform and natural genus. The relatively high yield figures and at least some indications of specific differences suggest that a more detailed survey may provide useful information about infrageneric relationships. There are no obvious morphological specializations (Polhill 1976) and it may be difficult to devise a natural infrageneric classification on morphological evidence alone. The most conspicuous difference between the species appears to be the proportion of anagyrine relative to sparteine, lupanine, cytisine or *N*-methylcytisine. Some of the northern species of *Argyrolobium* contain cytisine and lusitanine in the seeds (van Wyk *et al.* 1988b) but our results from leaf and twig samples are not directly comparable. Different organs of a plant may produce quite different combinations of major alkaloids (Cranmer & Mabry 1966; Greinwald *et al.* 1989) so that an appropriate sampling procedure is required to show significant differences between species. Seasonal fluctuations in the biosynthesis of alkaloids should also be considered. Such variations in the production of cytisine (known to be highly toxic) have been recorded in European species of the tribe Genisteae (R. Greinwald, unpublished). The observed variation in *Argyrolobium* may therefore be partly a result of seasonal differences, but perhaps also a result of the relative proportions of stems, leaves and flowers in the samples. Due to these sample limitations, it is not yet possible to evaluate the taxonomic significance of alkaloids at the infrageneric level. Qualitative discontinuities seem unlikely, but it may be worthwhile to investigate the relatively large quantitative differences between some of the species in a more detailed study.

At the generic level, however, the results indicate that high concentrations of anagyrine (less frequently also in combination with cytisine and *N*-methylcytisine) may be taken as a chemotaxonomic marker for *Argyrolobium*. The major alkaloids are similar to those in *Melolobium* (van Wyk *et al.* 1988a) and especially very similar to those in *Polhillia* (van Wyk *et al.* 1988b). It differs from the latter in the much higher concentrations of anagyrine and the lower concentrations of sparteine, lupanine and *N*-methylcytisine. The differences between the two genera appear to be quantitative only, so that the combination of alkaloids in some species of *Argyrolobium* is rather similar to that in *Polhillia*. Thermopsine, camoensine and leontidine are highly characteristic of *Melolobium* but these alkaloids have not been found in *Argyrolobium*. Although it also has thermopsine as a major alkaloid, the genus *Dichilus* differs from both *Argyrolobium* and *Melolobium* in the predominance of piperidyl alkaloids (van Wyk *et al.* 1988c). The combination of alkaloids in *Argyrolobium* clearly suggests a direct relationship of this genus with *Polhillia* and also appears to be a useful generic character.

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Appendix 1 Plant material of *Argyrolobium* species used for alkaloid extraction. Voucher specimens are all in the Rand Afrikaans University Herbarium (JRAU).

A. crassifolium Eckl. & Zeyh.: Zuurberg, E. Cape, 16/4/87, *B. & M. van Wyk 2115* (sample 1); N. slope of Van Stadensberg, E. Cape, 24/1/87, *van Wyk 2584* (sample 2). *A. frutescens* Burtt Davy: 19 km from Nelspruit on Kaapsehoop road, E. Transvaal, 20/2/88, *van Wyk 2815*. *A. lanceolatum* Eckl. & Zeyh.: Top of Du Toit's Kloof Pass, SW Cape, 4/7/87, *van Wyk 2698* (sample 1); Top of Constantiaberg, Cape Peninsula, 16/1/88, *van Wyk 2758* (sample 2). *A. lunare* (L.) Druce: Rotary road, Hermanus, SW Cape, 7/10/86, *van Wyk 2087*. *A. molle* Eckl. & Zeyh.: Zuurberg, E. Cape, 15/7/87, *B. & M. van Wyk 2131*. *A. rupestre* (Eckl. & Zeyh.) Walp.: 19 km from Nelspruit on Kaapsehoop road, E. Transvaal, 20/2/88, *van Wyk 2819*. *A. sankeyi* Harms: 19 km from Nelspruit on Kaapsehoop road, E. Transvaal, 20/2/88, *van Wyk 2817*. *A. speciosum* Eckl. & Zeyh.: 19 km from Nelspruit on Kaapsehoop road, E. Transvaal, 20/2/88, *van Wyk 2818*. *A. tomentosum* (Andr.) Druce: Mhlahlane, Transkei, 25/1/86, *van Wyk 1756* (sample 1); Magoebaskloof, NE Transvaal, 30/6/88, *Koekemoer 107* (sample 2). Argyrolobium sp. cf. *A. tysonii* Harms: 3 km from Harrismith to Van Reenen's Pass, E. Orange Free State, 13/3/86, *van Wyk 1924*. *A. variopile* N.E. Br.: Volksrust, Transvaal, 21/2/87, *Schutte 364*. *A. velutinum* Eckl. & Zeyh.: Hills at Saldanha Bay, W. Cape, 3/7/87, *van Wyk 2697*.

APPENDIX 7

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Chemotaxonomic Significance of Alkaloids in the Genus *Lebeckia*

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Key Word Index—*Lebeckia*; Leguminosae; Crotalarieae; quinolizidine alkaloids; novel alkaloid; 3β,4α-dihydroxylupanine; chemotaxonomy; generic relationships.

Abstract—The alkaloids of fourteen species of *Lebeckia* have been identified. Sparteine, lupanine and nuttalline were found to be the major alkaloids of all the species studied. α-Isolupanine and a novel alkaloid 3β,4α-dihydroxylupanine (lebeckianine) ~~were iden~~tified as minor compounds. *Lebeckia* differs from other quinolizidine-bearing genera of the tribe Crotalarieae by the abundance of α-pyridone alkaloids and esters of alkaloids. The combination of major alkaloids seems to be a useful chemotaxonomic marker for the genus and agrees with suggestions that *Lebeckia* is one of the basal groups in the tribe. Despite morphological dissimilarities, species from different sections of the genus are remarkably similar in their alkaloidal constituents.

Introduction

Lebeckia Thunb. comprises an estimated 35 species of woody or suffrutescent papilionoid legumes endemic to the western and southern parts of southern Africa. The genus is considered to be one of the basal groups of the tribe Crotalarieae [1, 2, 3, 4]. A previous investigation of *L. plukenetiana* [5] resulted in the isolation of sparteine, lupanine and 4β-OH-lupanine (nuttalline) as major alkaloids. The same result was obtained for *L. cytisoides* and *L. multiflora* [6].

The aim of the present investigation was to characterize the alkaloidal metabolites of the genus as a whole, so that more definite comparisons could be made with other genera. We studied 14 different species from various sections of the genus in an attempt to show that the combination of sparteine, lupanine and nuttalline may be taken as a chemotaxonomic marker for *Lebeckia*. In terms of a better understanding of generic relationships, the apparent absence of α-pyridone alkaloids such as anagyrine, thermospine, *N*-methylcystisine and cytisine seemed particularly relevant and needed confirmation. The relationship with *Crotalaria* [3] suggested that pyrrolizidine alkaloids may also be present.

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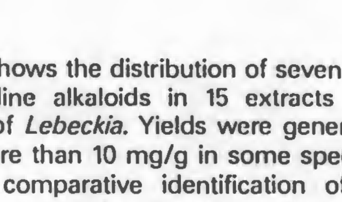
Results

Table 1 shows the distribution of seven different quinolizidine alkaloids in 15 extracts from 14 species of *Lebeckia*. Yields were generally very high (more than 10 mg/g in some species) and allowed comparative identification of all the major compounds. Sparteine, lupanine, α-isolupanine and 4β-OH-lupanine (nuttalline) were present in most of the samples. Small quantities of three unknown alkaloids occurred less frequently. One of the latter (isolated from *L. lotonoides* Schltr.) proved to be a new alkaloid. No evidence of α-pyridone alkaloids was found in any of the extracts.

The structure of the novel compound, 3β,4α-dihydroxylupanine (lebeckianine) (1), was established by ^1H and ^{13}C NMR spectroscopy and mass spectroscopy. The EI mass spectrum (Fig. 1) showed a fragmentation pattern very similar to that of lupanine type alkaloids in the lower



1

TABLE 1. YIELDS AND DISTRIBUTIONS OF ALKALOIDS IN 15 EXTRACTS FROM 14 SPECIES OF *LEBECKIA*

	Yields of major alkaloids (mg/g dry wt)							
Species	Sparteine	Lupanine	Isolupanine	Nuttalline	Lebeckianine	X1	X2	Total yield
Lebeckia section *Stiza*								
L. macrantha	4.0	0.1	tr	2.6	tr	tr	tr	6.664
L. pungens	2.6	0.2	tr	0.1	tr?	tr	tr?	2.910
Lebeckia section *Phyllodiastrum*								
L. plukenetiana	4.9	1.1	0.3	1.0	tr	0.1	tr	7.454
Lebeckia section *Eu-Lebeckia*								
L. simsiana	2.7	2.1	2.9	7.2	tr	tr	0.5	15.023
Lebeckia section *Calobata*								
L. cystisoides								
Sample 1	4.0	0.2	tr	0.1	—	tr	—	4.274
Sample 2	1.2	0.8	tr	0.3	—	tr	—	2.269
L. lotonoides	1.0	0.1	tr	tr	tr	0.1	—	1.170
L. melilotoides	8.3	0.1	tr	3.7	tr	tr	tr	12.283
L. mucronata	0.6	—	—	0.5	—	—	—	1.129
L. multiflora	3.8	0.2	tr	0.1	tr	tr	—	4.185
L. sericea	1.0	0.7	0.1	2.1	tr	tr	tr	3.832
L. spinescens	2.2	0.2	tr	0.6	0.1	tr	—	3.087
Lebeckia section *Wiborgioides*								
L. bowiena	tr	tr	tr	tr	tr	tr	tr	0.004
L. leipoldtiana	0.1	0.2	tr	0.1	—	tr	—	0.433
L. sessilifolia	tr	tr	tr?	tr	tr	—	tr?	0.002

Yield figures were esimated from GC results. X1 and X2 are unknown alkaloids with mass spectra almost identical to that of lupanine.

mass region. Typical peaks in this part of the mass spectrum are *m/z* 149, 136, 125, 110, 97, 84, 69 and 57. The molecular ion occurs at *m/z* 280, losing a hydroxyl group to produce a $[M^{+}-OH]$ peak of *m/z* 263 with a 72% intensity. This fragmentation indicated a dihydroxylupanine structure for the compound. The alcoholic character was also revealed in the IR spectrum showing a broad absorption band at 3400 cm^{-1}.

The ^1H NMR spectrum (Fig. 2) of this alkaloid showed a marked similarity with those of lupanine, nuttalline and also calpaurine, a compound extracted from *Calpurnea aurea* (Ait.) Benth. [7]. In spite of overcrowding in the upfield region, the medium and down field regions provided proof for the proposed structure of lebeckianine. Confirmation of the presence of two hydroxyl groups was found in a broad two

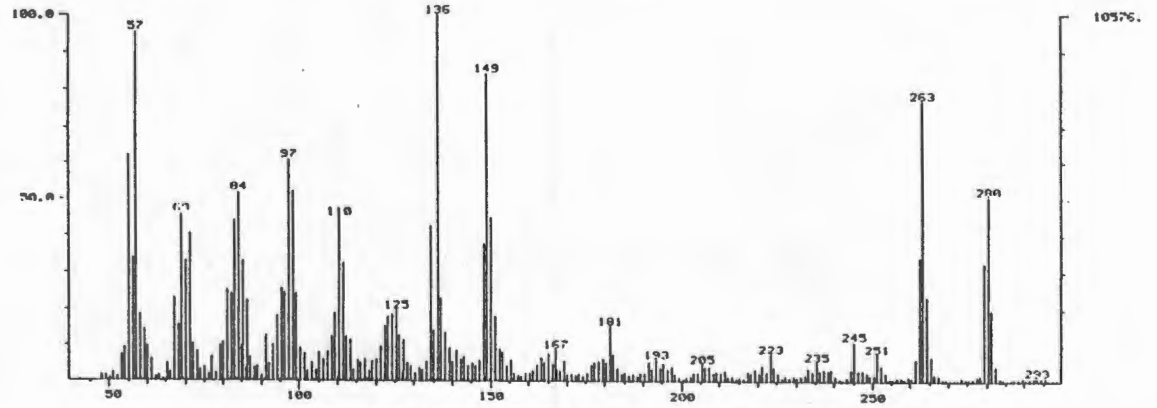


FIG. 1. THE MASS SPECTRUM OF LEBECKIANINE (Finnigan–Matt 8200 spectrometer, 70 eV electron impact).

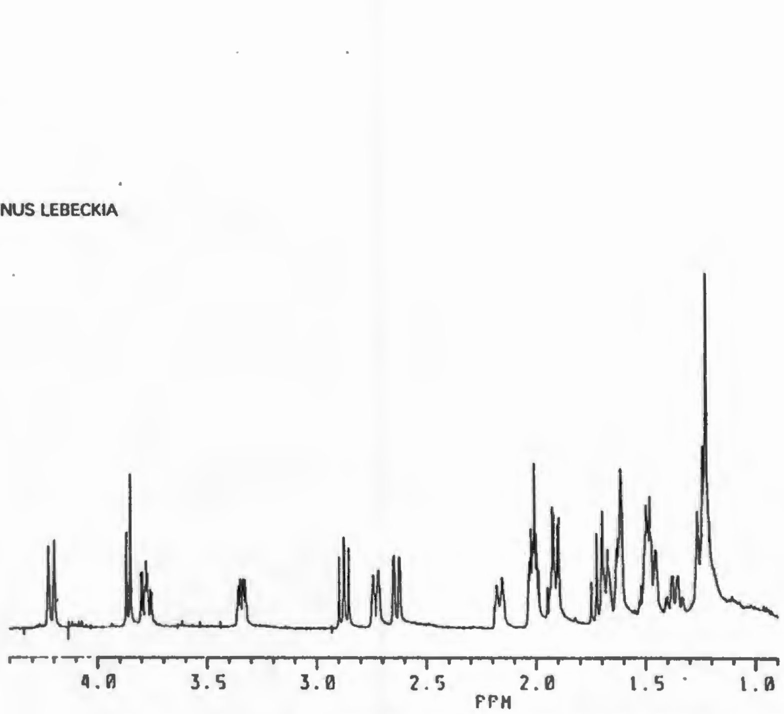


FIG. 2. THE ^1H NMR SPECTRUM OF LEBECKIANINE (200 MHz, $CDCl_3$, D_2O added).

proton signal at δ3.22 which was completely exchangeable with D_2O. The splitting pattern of the C-4 proton, which resonates at δ3.78, is practically identical to the C-4 proton of calpaurine. Furthermore, the H-3 is also identical to that of calpaurine. The $J_{3,4}=9.58$ Hz indicates a *trans*-diaxial relationship for these two protons, identical to calpaurine. Other protons in the medium field region such as H-6 (δ3.34), H-10a (δ4.20) and H-10b (δ2-62) compare favourably with the similar protons of nuttaline (δ3.29, 4.25 and 2.50, respectively). Because of overcrowding in the upfield region, the chemical shifts and coupling constants could not be assigned unambiguously for the high field protons. From the ^{13}C NMR spectrum (Fig. 3) the chemical shifts of the respective carbon atoms were assigned by comparison with the equivalent carbon atoms of lupanine and nuttalline, the published data for other structurally related compounds [7, 8] and 2D NMR experiments.

Discussion

It is clear from Table 1 that the various sections and species of *Lebeckia* are remarkably similar in their major alkaoids. Compared to other recently investigated genera of the Crotalarieae (*Melolobium* [9], *Polhillia* [10] and *Dichilus* [11]), the alkaloidal diversity is much less than expected. Qualitative differences between the species seem insignificant and do not reflect morphological dissimilarities. *Lebeckia melilotoides* for example, is superficially very different from other species, notably in having small indehiscent wind-dispersed pods. Its combination of alkaloids however, is almost identical to that present in the other species.

Unlike the qualitative uniformity, there are distinct quantitative differences. These differences do not appear to be random, but may well be linked to Harvey's [12] sectional classification of *Lebeckia.* Yield figures for the section *Wiborgioides,* for example (*L. bowieana, L. leipoldtiana* and *L. sessilifolia*), are extremely low when compared to most other sections. These species are morphologically similar to species of the genus *Wiborgia* Thunb., in which we have found alkaloids to be virtually absent. *Wiborgia* was previously thought not to be distinct from *Lebeckia* at the generic level [13] and the two genera are known to be very closely related [2]. The very low yield figure for *L. mucronata* is also noteworthy. Although traditionally placed in the section *Calobota,* it is morphologically intermediate between the sections *Calobota* and *Wiborgioides* [2].

Generic delimitations in the Crotalarieae have not yet reached stability [14], so that the results seem valuable as supporting evidence for the current genetic concept of *Lebeckia* and the close affinity with *Wiborgia.* We have found no evidence of ammodendrine or any other piperidyl alkaloids (characteristic of *Dichilus*) and also no pyrrolizidine alkaloids (common in

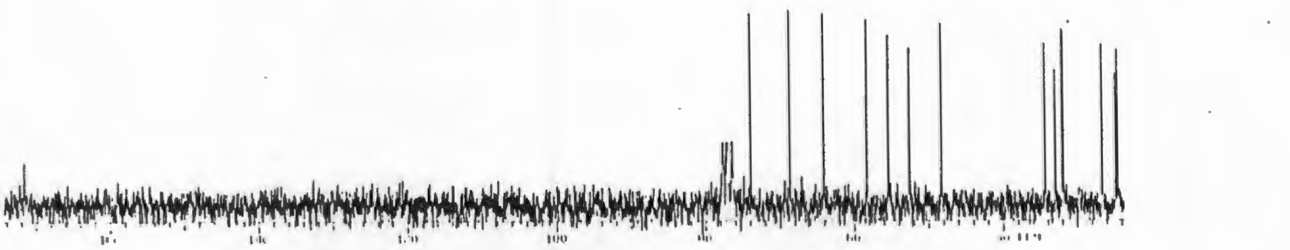


FIG. 3. THE ^{13}C NMR SPECTRUM OF LEBECKIANINE (50 MHz, CDCl$_3$, D$_2$O added).

Crotalaria and present in *Lotononis* and *Buchenroedera* [15]). Esters of tetracyclic quinolizidine alkaloids, recently found in the genus *Rothia* [16], also appear to be absent in *Lebeckia*. The combination of sparteine, lupanine and nuttalline and the absence of α-pyridone alkaloids and esters of alkaloids is clearly a useful diagnostic character and separates *Lebeckia* (and *Wiborgia*) from all other genera for which alkaloid data is available.

All of the alkaloids found in *Lebeckia* are structurally related to lupanine and the biosynthetic pathway does not seem to proceed beyond this basic type. It has been shown that the elaboration of ring A to α-pyridone requires specialized enzyme systems [17], so that the presence of cytisine-type alkaloids is considered to be a derived character state [18, 19, 20]. The apparant absence of C–C unsaturation in the alkaloids of *Lebeckia* therefore strongly agrees with suggestions [1, 2, 3, 4] that this genus represents part of the original lineage which gave rise to other genera of the tribe.

Experimental

Plant materials. The species studied and voucher specimen details of the material used are listed below. All voucher specimens are housed in the Rand Afrikaans University herbarium (JRAU), some of which have duplicates in various other herbaria.

Lebeckia bowieana Benth.: Uitvlug farm, N of Bredasdorp, *B-E. van Wyk 2106*; *L. cinerea* E. Mey.: 10 km from Clanwilliam to Van Rhynsdorp, *C. M. van Wyk 2598*; *L. cytisoides* Thunb., sample 1: Goudmyn, between Robertson and Bonnievale, *B-E. van Wyk 2705,* sample 2: Top of Wildehondkloof Pass, between Barrydale and Montagu, *B-E. van Wyk 2651b,* sample 3: between Citrusdal and Clanwilliam, *B-E. van Wyk 2439*; *L. leipoldtiana* Schltr. ex Dahlgr. Between Nieuwoudtville and Grasberg, *A. L. Schutte 295*; *L. lotonoides* Schltr.: hills at Saldanha Bay, *B-E. van Wyk 2696*; *L. macrantha* Harv.: 5 km from Griquatown to Upington, *B-E. van Wyk 2534*; *L. melilotoides* Dahlgr.: Verkeerdevlei near Touws River, *B-E. van Wyk 2562a*; *L. mucronata* Benth.: Elandsberg, N of Patensie, *Stirton 10880*; *L. multiflora* E. Mey.: between Lekkersing and Kuboes, Richtersveld, *B-E. van Wyk 2836*; *L. plukenetiana* E. Mey.: 40 km from Cape Town on West Coast Road, *B-E. van Wyk 2694*; *L. pungens* Thunb.: Rooikloof, 23 km SSE of Laingsburg, *B-E. van Wyk 2147*; *L. sericea* Thunb.: Kamiesberg Pass, *B-E. van Wyk 2353*; *L. sessilifolia* (Eckl. and Zeyh.) Benth.: De Hoop, Bredasdorp, *B-E. van Wyk 2120*; *L. simsiana* Eckl. and Zeyh.: Cedarberg, 3 km before Algeria, *C. M. van Wyk 2550*; *L. spinescens* E. Mey.: turn-off to Vlakfontein, 36 km N of Britstown, *C. M. van Wyk 3081.*

Isolation and identification of alkaloids. Ground air-dried leaves and twigs were extracted by refluxing with CH$_2$Cl$_2$ for several days. Alkaloidal extracts were obtained from the crude mixtures by water phase separation [6]. Previous experience [9, 10] has shown that differences in basicity may result in a partial loss of some alkaloids during resin purification. We therefore purified the alkaloidal extracts by repeating the water phase separation, followed by filtration through celite. Isolation was effected by silica gel 60 column chromatography with CHCl$_3$-Cyclohexane–Et$_2$NH (14:4:1) as eluent. Alkaloids were identified by analytical TLC as described previously [6] and GC using authentic reference samples. GC spectra were obtained with an SE-30 capillary glass column (25 m × 0.25 mm; N$_2$ as carrier gas at 0.5 kg/cm^2; column temperature 250°C isotherm; injector 300°C; FID 275°C). A large-scale extraction of *Lebeckia lotonoides* (2.5 kg) yielded reference samples of sparteine (2712 mg), lupanine (328 mg), 4β-OH-lupanine (107 mg) and 3β,4α-dihydroxylupanine (4.1 mg), all of which were fully authenticated by MS, ^{1}H and ^{13}C NMR. MS spectra of pure samples of sparteine, lupanine and 4-OH-lupanine extracted from *L. cytisoides* (sample 3) were identical to those from *L. lotonoides*. We obtained further confirmation of our TLC and GC identifications by GC–MS analyses of extracts from *L. plukenetiana* and *L. simsiana*. Sparteine: *Rt* 7.45, M$^+$ 234; X1 (unknown): *Rt* 10.05, M$^+$ 248; α-isolupanine: *Rt* 10.64, M$^+$ 248; lupanine: *Rt* 11.40, M$^+$ 248; X2 (unknown): *Rt* 12.17, M$^+$ 248; nuttalline: *Rt* 12.96, M$^+$ 264; lebeckianine (1): *Rt* 15.08, pale brown oil, $[\alpha]_D$ 61° (c −0.82 CHCl$_3$), ν_{max} 3400 br (OH) 1640 (lactam C = O) cm^{-1}; ^{1}H NMR δ4.21 (1H, dt, $J_{10ax,10eq}$ 13.27 and $J_{9,10eq}$ 2.09 Hz, H-10eq), 3.86 (1H, d, $J_{3,4}$ 9.58 Hz, H-3), 3.78 (1H, ddd, $J_{3,4}$ 9.58, $J_{4,5ax}$ 11.83, $J_{4,5eq}$ 4.14 Hz, H-4), 3.34 (1H, ddd, $J_{5ax,6}$ 11.87 $J_{5eq,6}$ 5.48 and $J_{6,7}$ 1.46 Hz, H-6), 3.20 (exchangeable with D$_2$O) (2H, bs, 2x OH), 2.89 (1H, dd, $J_{7,17a}$ 9.83 and $J_{17a,17b}$ 11.83 Hz, H-17a), 2.74 (1H, m, $J_{15a,15b}$ 12.54 Hz, H-15a), 2.64 (1H, dd, $J_{9,10ax}$ 13.27 and $J_{10ax,10eq}$ 1.96 Hz, H-10ax), 2.18 (1H, m, H-9), 2.04–2.00 (2H, m, H-5eq and H-7), 1.96–1.91 (1H, m, H-14a), 1.92 (1H, dd, $J_{7,17b}$ 3.98 and $J_{17a,17b}$ 11.83 Hz, H-17b), 1.72 (1H, dt, $J_{4,5ax}$ = $J_{5ax,5eq}$

11.83 Hz, $J_{5ax,6}$ 11.87 Hz, H-5ax), 1.70–1.20 (8H, m, 2x H-8, H-11, 2x H-12, 2x H-13 and H-14b); ^{13}C NMR δ171.47 (1C, s, C=O), 73.77 (1C, d, C-3), 68.42 (1C, d, C-4), 63.98 (1C, d, C-11), 58.24 (1C, d, C-6), 55.33 (1C, t, C-15), 52.56 (1C, t, C-17), 48.26 (1C, t, C-10), 34.30 (1C, d, C-7), 32.97 (1C, t, C-8), 31.95 (1C, d, C-9), 31.69 (1C, t, C-12), 26.58 (1C, t, C-5), 24.82 and 24.53 (2C, 2×s, C-13 and C-14); MS *m/z* 280 (51), 263 (72), 251 (7), 245 (11), 235 (5), 223 (7), 205 (4), 193 (6), 181 (15), 167 (9), 149 (84), 136 (100), 125 (20), 110 (45), 97 (61), 84 (52), 71 (40), 69 (46), 57 (96), 55 (62).

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APPENDIX 8

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A Chemotaxonomic Survey of Major Alkaloids in *Lotononis* and *Buchenroedera*

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Key Word Index—*Buchenroedera*; *Lotononis*; Leguminosae; Crotalaricae; macrocyclic pyrrolizidine alkaloids; quinolizidine alkaloids; co-occurrence; chemotaxonomy.

Abstract—A survey of alkaloids in five species of *Buchenroedera* and 27 species of *Lotononis* has shown the presence of several pyrrolizidine, quinolizidine and piperidyl alkaloids. Senecionine, integerrimine, platyphylline, neoplatyphylline, sparteine, lupanine, 11-epi-lupanine, nuttalline and ammodendrine have been positively identified. The co-occurrence of quinolizidine and macrocyclic pyrrolizidine alkaloids in the same genus is a new record for the Leguminosae and also appears to be a unique chemotaxonomic character for *Buchenroedera* and *Lotononis*. The distribution of alkaloids in *Lotononis* does not support the traditional infrageneric classification.

Introduction

A general survey of the tribe Crotalarieae [1] has shown the presence of alkaloids in several genera and indicated distinct differences between the genera. Small quantities of alkaloids were also found in *Buchenroedera* Eckl. & Zeyh. and *Lotononis* (DC.) Eckl. & Zeyh. but only the presence of integerrimine has so far been reported from these genera [2]. As part of a taxonomic study of *Buchenroedera* and *Lotononis*, we investigated the value of alkaloids as a chemotaxonomic character at the generic and infrageneric level.

Results

A total of 62 samples from 52 species were extracted but only those extracts in which alkaloids could be detected by TLC were considered for further analyses. Despite the low yields in most of the species, we did, however, positively identify nine different alkaloids that were present as major compounds in at least some of the extracts. The presence of four macrocyclic pyrrolizidine esters, four tetracyclic quinolizidine alkaloids and one piperidyl alkaloids in five species of *Buchenroedera* and 27 species of *Lotononis* is shown in Table 1.

Senecionine (1) and integerrimine (2) are the most common pyrrolizidine alkaloids, but relatively large quantities of platyphylline (3) and neoplatyphylline (4) were also isolated from some of the species. Sparteine (5), lupanine (6), 11-epi-lupanine (7), nuttalline (8) and ammodendrine (9) occur in several species but rarely in more than trace quantities.

Discussion

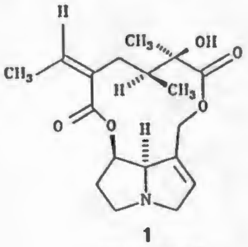
The morphological complexity of the genus *Lotononis* is also reflected in the alkaloid data and the variation is much greater than in other recently investigated genera of the tribe [3–9]. At the generic level, the co-occurrence of quinolizidine alkaloids, piperidyl alkaloids and macrocyclic pyrrolizidine esters is here reported for the first time. This appears to be a unique chemotaxonomic character for *Lotononis* and the closely related *Buchenroedera*. *Crotalaria* is the only other genus in the Leguminosae known to contain macrocyclic pyrrolizidine alkaloids. Despite several detailed studies, not a single quinolizidine alkaloid has ever been reported from this genus [10, 11]. *Adenocarpus*, *Cytisus* and *Laburnum* are also known to contain pyrrolizidine bases (which may co-occur with quinolizidine alkaloids) [10–13], but the macrocyclic "*Senecio*-type" is known only from *Crotalaria* and now also *Lotononis*. Recent studies on other

(*Received* 8 *February* 1989)

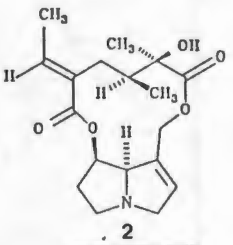
TABLE 1. DISTRIBUTION OF MAJOR ALKALOIDS IN 41 EXTRACTS FROM 32 SPECIES OF *LOTONONIS* AND *BUCHENROEDERA*

	Major alkaloids								
	Pyrrolizidine				Quinolizidine				Piperidyl
	int	sen	plat	neo	spar	lupa	iso	nutt	ammodendrine
Buchenroedera									
B. lotononoides 1, 2 & 3	+	tr							
B. meyeri	tr	tr							tr?
B. multiflora	tr	+							tr?
B. tenuifolia 1 & 2	tr	+							tr?
B. trichodes	tr	tr							
Lotononis section *Krebsia* (Eckl. & Zeyh.) Benth.									
L. caerulescens 1, 2 & 3	tr	tr							
L. divaricata 1, 2 & 3	+	tr							tr
L. trisegmentata 1 & 2	tr	+							
Lotononis section *Aulacinthus* (E. Mey.) Benth. and related species									
L. comptonii		+							tr
L. involucrata aff.		+							
L. purpurescens	+	tr							
L. rigida	tr								
Lotononis section *Telina* (E. Mey.) Benth.									
L. azurea aff.	+								
L. elongata	+	+							
Lotononis section *Lipozygis* (E. Mey.) Benth. and related species									
L. brevicaulis	+								
L. longicephala	tr?								tr
L. polycephala		+							
L. serpens	+								
Lotononis section *Oxydium* Benth. and related species									
L. brachyloba			+	+					
L. fruticoides			+	+					
L. lenticula			+	tr					
Lotononis angolensis group									
L. bainesii					tr	+	tr	+	tr
L. listii						tr	tr	+	tr
Lotononis section *Leptis* (Eckl. & Zeyh.) Benth. and related species									
L. carinata 1 & 2						+	tr		tr
L. adpressa						tr	tr		
L. calycina						+	tr		tr?
L. curvicarpa						+			
L. eriantha						+	tr	tr	tr
L. hirsuta						+			
L. lanceolata					tr	+	tr		
L. mucronata						+	tr		
Lotononis section *Leobordea* (Del.) Benth.									
L. platycarpa					+	tr	tr	tr	

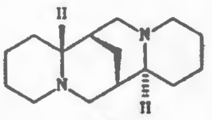
int—Integerrimine, sen—senecionine, plat—platyphylline, neo—neoplatyphylline, spar—sparteine, lupa—lupanine, iso—α-isolupanine (11-epi-lupanine), nutt—nuttalline. Authorities for names, voucher specimens and approximate yield figures are given in the Experimental section.



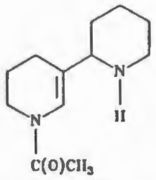
1
SENECIONINE



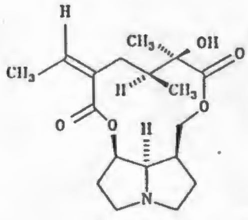
2
INTEGERRIMINE



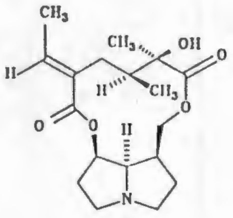
5
SPARTEINE



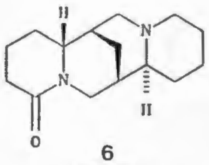
9
AMMODENDRINE



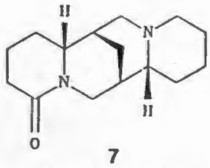
3
PLATYPHYLLINE



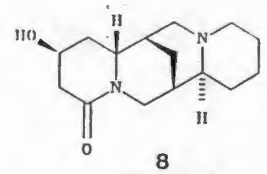
4
NEOPLATYPHYLLINE



6
LUPANINE



7
11-epi-LUPANINE



8
NUTTALLINE

genera of the Crotalarieae [3–9] have shown the presence of several quinolizidine and piperidyl alkaloids, but none of the pyrrolizidine type have so far been found. Esters of quinolizidine alkaloids are characteristic for *Rothia* [7] and *Pearsonia* [9], but no evidence of these compounds was found in *Lotononis*. In past taxonomic treatments, some species of *Rothia* and *Pearsonia* were included in *Lotononis*, but the alkaloidal evidence now points to a superficial similarity rather than a direct phylogenetic relationship.

The distribution of major alkaloids indicates anomalies in the existing sectional classification of Duemmer [14]. Species with the same major alkaloids are presently placed in different sections despite morphological and cytological similarities. Some of the patterns that emerged from the present study are therefore taxonomically significant and may provide supporting evidence for a more natural infrageneric classification. *Lotononis hirsuta* (presently in section *Krebsia*), *L. eriantha* and *L. lanceolata* (presently in section *Lipozygis*) and *L. adpressa* and *L. calycina* (presently in section *Leptis*), for example, are obviously closely related and have a very similar combination of quinolizidine alkaloids (pyrrolizidine alkaloids at best only in trace quantities) but are distributed amongst different sections. If these species and their allies are excluded from their respective sections and grouped together, a much more predictive classification would result. Another example is the *L. angolensis* group of section *Polylobium*, which is morphologically quite distinct and deserves formal recognition, at least at the sectional level. An isolated position also seems to be indicated by the absence of pyrrolizidine alkaloids and the presence of nuttalline as the major alkaloid of *L. bainesii* (a well-known pasture legume) and *L. listii*. Nuttalline is one of the major alkaloids of *Lebeckia* [8]) and an affinity with the latter is worth considering. *Lotononis angolensis* and related species represent the only group in *Lotononis* with well-developed bracteoles, a character which leaves little doubt about a basal position in the genus.

The available evidence in Table 1 also shows that the arrangement of the sections should be reconsidered. In view of the known distribution of pyrrolizidine esters in the plant kingdom [12, 13], it seems reasonable to interpret the accumulation of these compounds as a derived condition. The traditional sequence of species, originally conceived by Bentham [15], starts with the woody groups (superficially similar to *Lebeckia*) and ends with the presumably more derived herbaceous ones (Fig. 1A). A reversal of this sequence would more logically explain the alkaloid pattern and would also agree closely with morphological and cytological evidence. This somewhat paradoxical modification is shown diagramatically in Fig. 1B. *Lebeckia* is considered to be the least specialized genus of the Crotalarieae [16, 17] and it is therefore a logical outgroup for deciding the polarity of character states. Those species of *Lotononis* at the base of the sequence in Fig. 1B have the same chromosome number as *Lebeckia* and have a similar combination of alkaloids. The diagram suggests a gradual replacement of quinolizidine alkaloids by pyrrolizidine alkaloids, which is linked to other general trends such as a more localized geographical distribution, cyanogenesis [18], a change in chromosome base number from 9 to 7 [19], a loss of bracteoles and an increase in the incidence of other presumably apomorphic character states such as blue flowers, biramous hairs and inflated pods.

The alkaloids of *Lotononis*, although often present only in trace quantities, provide some insight into infrageneric relationships and may be useful as supportive evidence for the correct taxonomic position of some of the species. As previously suggested [2], the generic status of *Buchenroedera* is not supported by the alkaloid data. In the Crotalarieae, macrocyclic pyrrolizidine alkaloids appear to be restricted to *Lotononis* and *Crotalaria* and is a useful generic character to distinguish these two derived genera from other genera of the tribe.

Experimental

Plant materials. Voucher specimens of the species examined (all housed in the Rand Afrikaans University Herbarium),

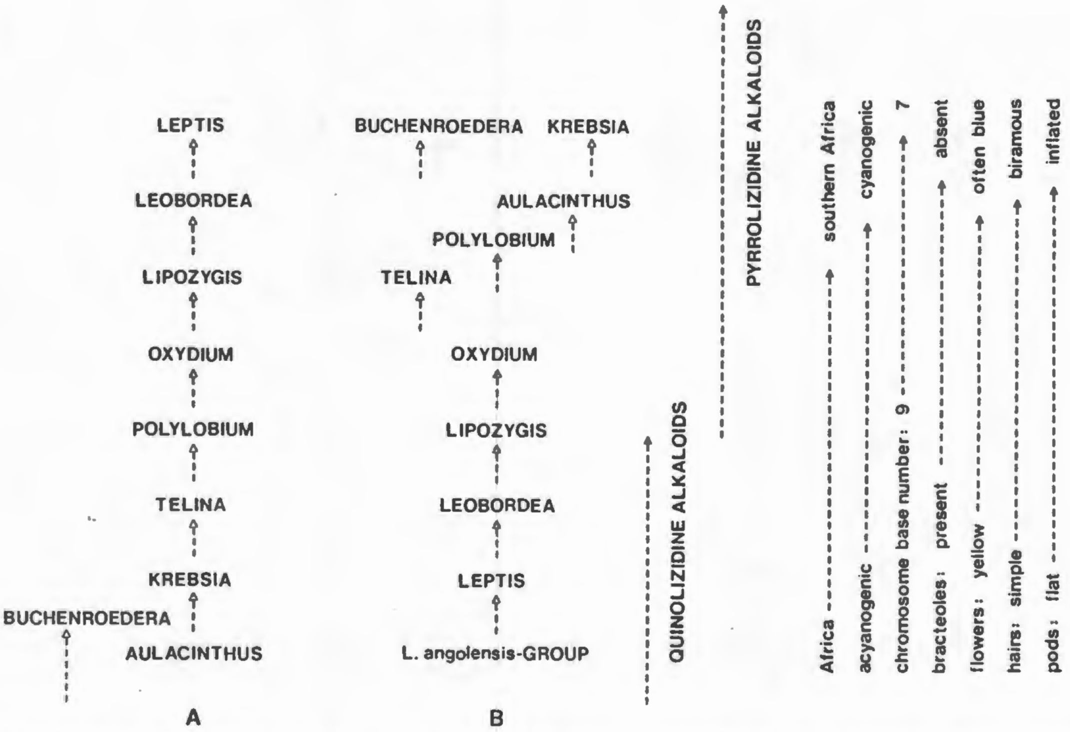


FIG. 1. THE SECTIONS OF THE GENUS *LOTONONIS*: (A), AS ORIGINALLY ARRANGED BY BENTHAM [15], AND (B) SUGGESTED REARRANGEMENT BASED ON THE DISTRIBUTION OF ALKALOIDS AND OTHER DATA.

correct authorities for names (not repeated elsewhere), and approximate yields of alkaloidal material (dry wt) are given below. (Collections of B.-E. van Wyk abbreviated as VW.)

Buchenroedera lotononoides Scott Elliot sample 1: VW 2630a (140 μg/g), sample 2: VW 2630b (25 μg/g), sample 3: VW 2630c (104 μg/g); *B. meyeri* Presl: VW 1765 (82 μg/g); *B. multiflora* Eckl. & Zeyh.: B & M van Wyk 1523 (88 μg/g); *B. tenuifolia* Eckl. & Zeyh. var *pulchella* (E. Mey.) Harv. (sample 1): VW 1334 (57 μg/g); *B. tenuifolia* Eckl. & Zeyh. var *tenuifolia* (sample 2): VW 1593 (35 μg/g); *B. trichodes* Presl. VW 1693 (40 μg/g); *Lotononis adpressa* N. E. Br.: VW 1567 (32 μg/g); *L. azurea* Eckl. & Zeyh. aff.: Vlok 2030 (187 μg/g); *L. bainesii* Bak.: Koekemoer 43 (121 μg/g); *L. brachyloba* (E. Mey.) Benth.: VW 2442 (78 μg/g); *L. brevicaulis* B.-E. van Wyk: VW 2212 (199 μg/g); *L. caerulescens* (E. Mey.) B.-E. van Wyk sample 1: VW 2034 (2 μg/g), sample 2: VW 1614 (13 μg/g), sample 3: VW 1632 (5 μg/g); *L. calycina* (E. Mey.) Benth.: VW 2735 (11 μg/g); *L. carinata* (E. Mey.) Benth. sample 1: VW 2614 (37 μg/g), sample 2: VW 2816 (31 μg/g); *L. comptonii* B.-E. van Wyk: VW 2186 (53 μg/g); *L. curvicarpa* B.-E. van Wyk ined.: VW 2725 (8 μg/g); *L. divaricata* (Eckl. & Zeyh.) Benth. sample 1: VW 2597 (5 μg/g), sample 2: VW 2729a (11 μg/g), sample 3: VW 2729b (15 μg/g); *L. elongata* (Thunb.) D. Dietr.: VW 2635 (76 μg/g); *L. eriantha* Benth.: Schutte 383 (11 μg/g); *L. fruticoides* B.-E. van Wyk ined.: VW 2137 (68 μg/g); *L. hirsuta* Schinz: VW 2734 (19 μg/g); *L. involucrata* (E. Mey.) Benth. aff.: VW 2704 (167 μg/g); *L. lanceolata* (E. Mey), Benth.: VW 1884 (91 μg/g); *L. lenticula* (E. Mey.) Benth.: VW 2018 (8 μg/g); *L. listii* Polhill: VW 2473 (4 μg/g); *L. longicephala* B.-E. van Wyk ined.: VW 2201 (91 μg/g); *L. mucronata* Conrath: VW 1804 (23 μg/g); *L. platycarpa* (Viv.) Pich.-Serm.: VW 2822 (203 μg/g); *L. polycephala* (E. Mey.) Benth.: VW 2408 (35 μg/g); *L. purpurescens* B.-E. van Wyk: VW 2720 (128 μg/g); *L. rigida* (E. Mey.) Benth.: VW 2876 (7 μg/g); *L. serpens* (E. Mey.) R. Dahlgr.: Schutte 257 (11 μg/g); *L. trisegmentata* Phillips forma *robusta* Phillips (sample 1): VW 1561 (2 μg/g); *L. trisegmentata* Phillips forma *sericea* Phillips (sample 2): VW 1968 (14 μg/g).

Procedures. Ground air-dried aerial parts were extracted by refluxing with $CH2Cl_2$ for several days. Alkaloidal material was isolated from the crude extracts by water phase separation [1] and purified by ion exchange resin (Dowex 50 H^+ form). The crude alkaloidal extract, dissolved in minimum MeOH, is slowly eluted through a small column of resin (activated with 4 N HCl and rinsed with distilled H_2O until pH 5.5). The resin is then washed with MeOH to remove non-basic impurities. Alkaloids are stripped from the column starting with H_2O–ammonia–MeOH (8:1:1) and the resin continuously rinsed with increasing proportions of ammonia until no more alkaloids are detected in the eluent. Alkaloids were identified by comparative TLC and GC using reference samples that were fully authenticated by m.p., specific rotation, MS-, IR-, ^1H NMR-, and ^{13}C NMR spectroscopy. GC conditions were the same as used in a previous study [8]. Reference samples were extracted from the following species: nuttalline from *Lebeckia lotonoides* Schltr. [8]; lupanine from *Lotononis hirsuta*; integerrimine from *Buchenroedera lotononoides*; senecionine from *Lotononis involucrata* and platyphylline and neoplatyphylline from *Lotononis fruticoides*. These pure alkaloid samples were obtained by column chromatography on silica gel and Sephadex LH-20 (cyclohexane–$CHCl_3$–Et_2NH, 5:4:1 and MeOH, respectively, as eluents). All spectroscopic data closely correlated with that given in the literature [12, 13, 20–23]. Extracts from *Buchenroedera lotononoides* (sample 1), *Lotononis bainesii*, *L. divaricata* (sample 3) and *L. longicephala* were studied by GC–MS and the results confirmed all earlier identifications by TLC and GC.

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APPENDIX 9

Alkaloids of the genera Aspalathus, Rafnia and Wiborgia (Fabaceae - Crotalarieae).

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The presence of alkaloids in three southern African genera of the tribe Crotalarieae is reported for the first time. Sparteine, lupanine and nuttalline were detected in several species of Aspalathus L., Rafnia Thunb. and Wiborgia Thunb., but rarely in more than trace quantities. Except for very large quantitative differences, the alkaloids are almost identical to those found in the genus Lebeckia Thunb. Available evidence suggests that the three genera are more closely related to Lebeckia than to any other genus of the tribe. The divergence of these genera seems to be linked to an almost total loss of the ability to produce alkaloids.

Die teenwoordigheid van alkaloïede in drie Suider-Afrikaanse genera van die tribus Crotalarieae word vir die eerste keer gerapporteer. Sparteïen, lupanien en nuttallien is waargeneem in verskeie spesies van Aspalathus L., Rafnia Thunb. en Wiborgia Thunb. maar slegs by uitsondering in meer as spoorhoeveelhede.

Afgesien van baie groot kwantitatiewe verskille, is die alkaloïede feitlik identies aan dié wat in die genus *Lebeckia* Thunb. aangetref word. Beskikbare getuienis dui daarop dat die drie genera nader verwant is aan *Lebeckia* as aan enige ander genus van die tribus. Die divergensie van hierdie genera hou skynbaar verband met ´n bykans totale verlies aan die vermoë om alkaloïede te produseer.

Keywords: *Aspalathus*, generic relationships, quinolizidine alkaloids, *Rafnia*, *Wiborgia*

Introduction

The high incidence of convergence and intricate relationships amongst the Cape Crotalarieae have been discussed by Dahlgren (1963) and Polhill (1976). *Lebeckia* Thunb. is considered to be the least specialized genus of the tribe and morphological similarities with other genera of the tribe are taken as evidence of a close relationship. The distinct pattern of alkaloids observed in the genus *Lebeckia* (Van Wyk & Verdoorn 1989a) indicated to us that alkaloids may provide valuable information about the generic affinities of three other genera of the tribe, namely *Aspalathus* L., *Rafnia* Thunb. and *Wiborgia* Thunb. These three genera are considered to be particularly closely related to *Lebeckia*, as is evidenced by their sequence in the latest generic and tribal revision (Polhill 1976, 1981).

An alkaloid tentatively identified as sparteine has been reported previously from one species of *Wiborgia* (Van Wyk *et al*. 1988a) but, except for *Lebeckia*, no other information is available for any of the genera. Our aim with the present study was, therefore, to provide alkaloid data for a comparison of above-mentioned genera.

Material and Methods

A total of 22 samples, representing 11 species of *Aspalathus*, 6 species of *Rafnia* and 3 species of *Wiborgia* were studied in this survey. The species, authorities for names and voucher specimens are listed in the appendix.

Methods of extraction and identification were as previously described (Van Wyk *et al*. 1988a & 1988b, Van Wyk & Verdoorn 1988). Gas chromatography conditions were the same as used by Van Wyk & Verdoorn (1989a). All reference samples used in analytical TLC and GC were fully authenticated by ^{1}H- and ^{13}C NMR spectroscopy and mass spectrometry. Identifications by analytical TLC and GC were confirmed by GC-MS studies of two extracts (*Aspalathus longifolia* and *Rafnia racemosa*).

Results and Discussion

The distribution of alkaloids in 20 species of *Aspalathus*, *Rafnia* and *Wiborgia* is shown in Table 1. Small amounts of sparteine, lupanine and nuttalline were present in several of the samples (α-isolupanine in a few of them), but rarely in more than trace quantities. We have also found some indications of the presence of ammodendrine (a piperidyl alkaloid) but this could not be confirmed. No evidence of α-pyridone alkaloids or pyrrolizidine alkaloids were found in any of the extracts.

Yield figures were extremely low, so that relative yields are not given except for one species of *Aspalathus* (*A. nivea*). The latter is a large shrub with flowers not unlike those of some species of *Lebeckia*. The almost total absence of alkaloids in *Aspalathus* (if taken to be a derived character state) indicates a more basal position for *A. nivea* than the sequence of species in Dahlgren's (1988) revision would suggest. However, Dahlgren explicitly stated that the affinities of this species are uncertain and it is interesting to note that it was placed in a monotypic infrageneric group.

-INSERT TABLE 1-

-INSERT TABLE 2-

Except for the large quantitative difference observed, the alkaloids of all three genera are virtually the same as those found in the genus *Lebeckia*, and the diversity is much less than expected. A comparison between various genera of the Crotalarieae is shown in Table 2. *Rothia* Pers., *Pearsonia* Dümmer, *Lotononis* (DC.) Eckl. & Zeyh. and *Crotalaria* L. have also been included but *Argyrolobium* Eckl. & Zeyh., *Dichilus* DC., *Melolobium* Eckl. & Zeyh. and *Polhillia* Stirton, all of which contain α-pyridone alkaloids such as cytisine, *N*-methylcytisine, anagyrine and thermopsine have been excluded from the comparison. The summary of available data in Table 2 leaves little doubt that *Aspalathus*, *Rafnia* and *Wiborgia* are more closely related to *Lebeckia* than to any of the other genera.

The alkaloid pattern shows a striking degree of conformity with presumed evolutionary trends based on morphological evidence. A relatively recent common ancestry with *Lebeckia* is suggested, and the subsequent divergence of *Apalathus*, *Rafnia* and *Wiborgia* seems to have been accompanied by the almost complete absence of alkaloids.

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TABLE 1. APPROXIMATE YIELDS AND DISTRIBUTION OF ALKALOIDS IN 20 SPECIES OF ASPALATHUS, RAFNIA AND WIBORGIA. (Authorities for names and voucher specimen details are given in appendix 1, *tr* indicates trace amounts)

	APPROXIMATE YIELD (μg/g dry wt)	DISTRIBUTION OF MAJOR ALKALOIDS (% of total yield)			
		sparteine	lupanine	isolupanine	nuttalline
Aspalathus					
A. capitata	4	tr	tr	-	-
A. carnosa	2	-	-	-	-
A. chortophila	2	tr	tr	-	-
A. cordata	20	tr	tr	-	-
A. hirta	14	tr	tr	-	-
A. juniperina	17	tr	tr	-	-
A. linearis	3	tr	-	-	-
A. longifolia	4	tr	tr	-	-
A. nivea	2587	47	45	2	1
A. perfoliata	2	tr	tr	tr	-
A. spinosa	<1	tr?	-	-	-
Rafnia					
R. angulata	3	tr	tr	-	tr
R. capensis	10	tr?	-	-	-
R. elliptica	14	tr	tr	-	tr
R. opposita	12	tr	tr	-	-
R. perfoliata	9	tr	tr	-	-
R. racemosa	4	tr	tr	-	-
Wiborgia					
W. fusca	21	tr	tr	-	tr
W. obcordata (1)	15	tr	tr	-	tr
W. obcordata (2)	31	tr	tr	-	tr
W. obcordata (3)	26	tr	tr	-	tr
W. sericea	11	tr	tr	tr?	tr

TABLE 2. DISTRIBUTION OF ALKALOIDS REPORTED FROM THE GENERA *LEBECKIA*, *WIBORGIA*, *ASPALATHUS*, *RAFNIA*, *PEARSONIA*, *ROTHIA*, *LOTONONIS* AND *CROTALARIA*. [Data for *Lebeckia* from Van Wyk & Verdoorn (1989a), *Pearsonia* from Van Wyk & Verdoorn (1989b), *Rothia* from Hussain *et al*. (1988) and *Lotononis* from Van Wyk & Verdoorn (1989c)]

	Lebeckia	*Wiborgia*	*Aspalathus*	*Rafnia*	*Pearsonia*	*Rothia*	*Lotononis*	*Crotalaria*
Tetracyclic quinolizidine alkaloids:								
nuttalline	+++	tr	tr	tr	tr	+	+	
sparteine	+++	tr	+	tr	+		+	
lupanine	+++	tr	+	tr	++	++	tr	
isolupanine	+	tr?	tr		+	tr	tr	
Piperidyl alkaloids:								
ammodendrine	tr?	tr?	tr?	tr?	+	++	tr	
Esters of quinolizidine alkaloids:					++	++		
Macrocyclic pyrrolizidine alkaloids:							++	++

occurs as a major component in: +++ all species/samples, ++ most species/samples, + at least some species/samples (*tr* = trace amount).

Appendix 1. Plant material of *Aspalathus*, *Rafnia* and *Wiborgia* used for alkaloid extraction. Voucher specimens are all in the Rand Afrikaans University Herbarium (JRAU).

Aspalathus capitata L. : Top of Constantiaberg, Cape Peninsula, *Van Wyk 2754*; *A. carnosa* Berg. : Top of Constantiaberg, Cape Peninsula, *Van Wyk 2752*; *A. chortophila* Eckl. & Zeyh. : Zuurberg National Park, E Cape, *B & M van Wyk 1436*; *A. cordata* (L.) Dahlg. : Between Constantiaberg and Vlakkenberg, Cape Peninsula, *Van Wyk 2759*; *A. hirta* E. Mey. subsp. *hirta* : N side of Garcia´s Pass, S Cape, *Van Wyk 2802*; *A. juniperina* Thunb. subsp. *juniperina* : Near top of Constantiaberg, Cape Peninsula, *Van Wyk 2756*; *A. linearis* (Burm. f.) Dahlg. : Eselbank, Cedarberg, *Van Wyk 2829*; *A. longifolia* Benth. : Garcia´s Pass, S Cape, *Van Wyk 2799*; *A. nivea* Thunb. : Kabeljous River near Humansdorp, E Cape, *Van Wyk 2813*; *A. perfoliata* (Lam.) Dahlg. subsp. *perfoliata* : Jonkershoek near Stellenbosch, *Van Wyk 2786*; *A. spinosa* L. subsp. *spinosa* : Top of Rooiberg Pass, Oudtshoorn district, *Van Wyk 2800*.

Rafnia angulata Thunb. : Somerset West, *Van Wyk 2788*; *R. capensis* (L.) Druce : Near top of Constantiaberg, Cape Peninsula, *Van Wyk 2757*; *R. elliptica* Thunb. : Zuurberg National Park, E Cape, *B & M van Wyk 615*; *R. opposita* Thunb. : Garcia´s Pass, S Cape, *Van Wyk 2798*; *R. perfoliata* E. Mey. : Jonaskop near Villiersdorp, *Van Wyk 2067*; *R. racemosa* Eckl. & Zeyh. : Between Seweweekspoort and Laingsburg, Cape, *Van Wyk 2171*.

Wiborgia fusca Thunb. subsp. *fusca* : 56 km from Cape Town on West Coast Road, *Van Wyk 2686*; *W*. *obcordata* Thunb. : near Rondeberg farm on West Coast Road, *Van Wyk 2691* (sample 1), Between Paarl and Wemmershoek, *Van Wyk 2678* (sample 2), At Eilandia, between Worcester and Robertson (sample 3); *W*. *sericea* Thunb. : Laingsburg, SW Cape, *Van Wyk 2193*.

APPENDIX 10

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Chemotaxonomic Significance of Alkaloids in the Genus *Pearsonia*

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Johannesburg, 2000, South Africa

Key Word Index—*Pearsonia*; Leguminosae; Crotalarieae; quinolizidine alkaloids; novel esters of alkaloids; chemotaxonomy; generic relationships.

Abstract—The alkaloids of six species and subspecies of *Pearsonia* have been studied to provide data for comparisons with other genera. Four different esters of tetracyclic quinolizidine alkaloids were found to be the major compounds in most of the extracts. These were lupanine-13α-angelate and three hitherto unknown esters, namely cajanifoline (lupanine-3β-hydroxy-13α-angelate), sessilifoline (lupanine-3β-hydroxy-4α-angelate) and pearsonine (lupanine-3β,8α-dihydroxy-13α-angelate). Other major alkaloids were sparteine, α-isolupanine, lupanine, nuttalline and ammodendrine. Our results strongly support the present generic concept of *Pearsonia* and provide evidence for a close taxonomic affinity with the genus *Rothia*. In *Pearsonia*, however, the major components are esters of higher oxidized quinolizidine alkaloids than those of *Rothia*. The presence of esters of alkaloids in *Pearsonia* and *Rothia* is a unique character to distinguish them from all other genera of the tribe Crotalarieae and once again confirms the chemotaxonomic value of alkaloids as a generic character.

Introduction

The concept of the genus *Pearsonia* Duemmer was broadened by Polhill [1] to include a total of eleven suffrutescent papilionoid legumes from southern tropical Africa, central Africa and Madagascar. It is distinguished from *Lotononis* (DC.) Eckl. & Zeyh. by the highly modified flowers, but otherwise the two genera are very similar. The floral features of *Pearsonia* are also present in the small genus *Rothia* Pers. and the two genera are therefore considered to be closely related.

As part of our survey of alkaloids as a generic character in the tribe Crotolarieae, we studied the alkaloids of six species and subspecies of *Pearsonia*. Data was needed to find out if the presumed affinities and generic distinctions between *Pearsonia* and other recently investigated genera (*Rothia* [2], *Lotononis* [3] and *Lebeckia* Thunb. [4]) are supported by the alkaloidal evidence.

Results

Table 1 shows the total yields and distribution of alkaloids in seven extracts from four species and two subspecies of *Pearsonia*. Four different angelate esters of quinolizidine alkaloids occurred as major constituents in most of the extracts. These were identified as lupanine-13α-angelate (13α-angeloyloxylupanine) (**1**) and three hitherto unknown esters, namely cajanifoline (lupanine-3β-hydroxy-13α-angelate) (**2**), sessilifoline (lupanine-3β-hydroxy-4α-angelate) (**3**) and pearsonine (lupanine-3β,8α-dihydroxy-13α-angelate) (**4**). The relatively high yields enabled us to isolate these compounds and fully characterize them by spectroscopic methods, details of which will be published elsewhere (Verdoorn and Van Wyk, in preparation for *Phytochemistry*. Sparteine (**5**), 11-epi-lupanine (α-isolupanine) (**6**), lupanine (**7**), 4α-OH-lupanine (nuttalline) (**8**) and ammodendrine (**9**) were also identified as major alkaloids of most of the species. No evidence of α-pyridone alkaloids or pyrrolizidine alkaloids was found in any of the extracts.

Discussion

The pattern of alkaloids in Table 1, particularly the presence of angelate esters in all the extracts, shows that the present generic concept of *Pearsonia* has predictive value and that the transfer of *Pleiospora* Harv. to *Pearsonia* [1] was justified. (*Pleiospora cajanifolia* Harv., now known as *Pearsonia cajanifolia*, was previously considered to be generically distinct from

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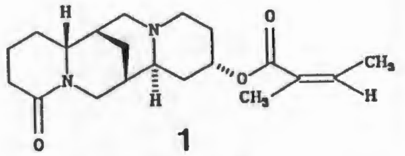

1

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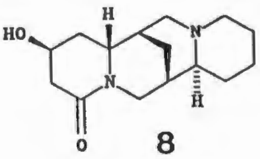
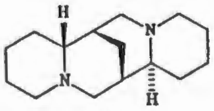


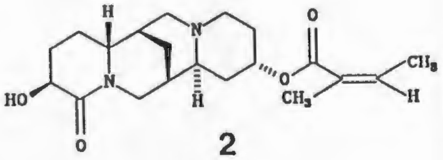
8

NUTTALLINE



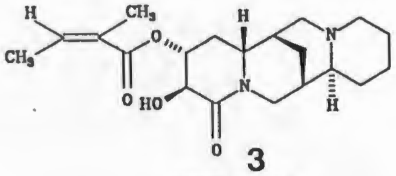
5

SPARTEINE



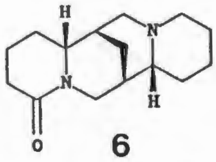
2

CAJANIFOLINE



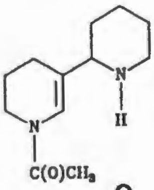
3

SESSILIFOLINE



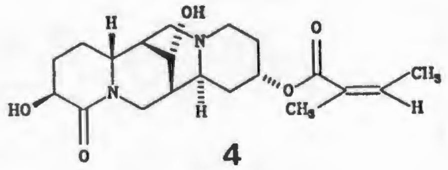
6

11–epi–LUPANINE



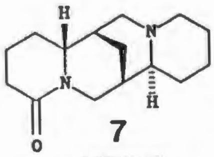
9

AMMODENDRINE



4

PEARSONINE



7

LUPANINE

Pearsonia). The relatively high yield figures indicate that a detailed study of alkaloids in the genus as a whole may provide interesting new taxonomic evidence about relationships between the species. It may also be worthwhile to study the variation in some of the species. The *Pearsonia sessilifolia* complex for example, is a variable aggregate which, until recently, comprised no less than eleven species. Large quantitative differences between the species and subspecies in Table 1 agrees with Polhill's [1] conclusion that *Pearsonia* is an exceptionally variable genus in some parts of its range.

At the generic level, the presence of esters of quinolizidine alkaloids is highly significant. These compounds, previously known only from a few genera of the tribes Sophoreae and Genisteae [5, 6], were recently also reported from the genus *Rothia* [2]. In the tribe Crotalarieae, *Rothia* and now also *Pearsonia* are therefore the only genera known to contain esters of tetracylic quinolizidine alkaloids. Esters of alkaloids were not found in *Lebeckia* [4] and those that occur in *Crotalaria* and *Lotononis* [3] are of the macrocyclic pyrrolizidine type. The idea that morphological similarities between *Pearsonia* and *Rothia* may be interpreted as indications of a common ancestry is therefore strongly supported by the alkaloidal metabolites. The major compounds of *Pearsonia* are esters of higher oxidized quinolizidine alkaloids than those of *Rothia*, suggesting that the divergence of the two genera may not have been very recent. A further difference is the apparent absence of tigliate- and other esters in *Pearsonia*.

Unfortunately, no information is available for the genus *Robynsiophyton* Wilczek. If the simi-

TABLE 1. DISTRIBUTION AND YIELDS OF MAJOR ALKALOIDS IN SIX SPECIES AND SUBSPECIES OF *PEARSONIA*

Species and subspecies	*P. aristata*	*P. cajanifolia* subsp. *cajanifolia*	*P. cajanifolia* subsp. *cryptantha*	*P. obovata*	*P. sessilifolia* subsp. *marginata* sample 1	*P. sessilifolia* subsp. *marginata* sample 2	*P. sessilifolia* subsp. *sessilifolia*
Total yield (mg/g dry wt)	0.728	1.691	0.908	0.547	0.488	0.472	0.850
Esters of quinolizidine alkaloids							
lupanine-13α-angelate	9	37	19	tr	12	tr	tr
cajanifoline*	—	55	40	43	tr	tr?	6
sessilifoline*	tr?	tr	11	tr?	62	tr	10
pearsonine*	—	4	28	tr?	tr	tr?	tr
Quinolizidine alkaloids							
sparteine	55	—	—	tr	tr	63	tr
α-isolupanine	3	1	tr	tr	15	tr	tr
lupanine	12	1	tr	2	tr	15	69
nutalline	2	tr	tr	tr	4	3	tr
Piperidyl alkaloids							
amodendrine	16	tr	tr	52	tr	2	tr

*New compounds (see experimental section).

Figures given are percentages of the total yields as estimated from GC results. Authorities for names and voucher specimen details are given in the experimental section.

larities with *Pearsonia* and *Rothia* [1, 7] are not merely a result of convergence, it is likely that this genus also contains lupanine-type esters. The distinct difference between the alkaloids of *Pearsonia* and those of *Lotononis* is particularly noteworthy. Although the two genera are morphologically very similar, the evidence presented here agrees with other distinctions based on floral morphology and chromosome cytology.

A summary of the differences between the above-mentioned genera of the Crotalarieae is shown in Table 2. From the distribution of major alkaloids, it may be concluded that most of the genera are related to *Lebeckia*, but that each of them has acquired a different biogenetic specialization. *Crotalaria* and *Lotononis* are distinct in the production of macrocyclic pyrrolizidine esters, while *Pearsonia* and *Rothia* share the unique ability to produce esters of quino-

TABLE 2. SUMMARY OF THE KNOWN DISTRIBUTION OF ALKALOIDS IN THE GENERA *CROTALARIA, LOTONONIS, LEBECKIA, ROTHIA* AND *PEARSONIA*

	Crotalaria	*Lotononis*	*Lebeckia*	*Rothia*	*Pearsonia*
Piperidyl alkaloids					
ammodendrine	—	tr	tr	**	*
Tetracyclic quinolizidine alkaloids					
sparteine	—	*	***	—	*
11-epi-lupanine	—	tr	*	tr	*
lupanine	—	tr	***	**	**
nuttaline	—	*	***	*	tr
Pyrrolizidine esters	**	**	—	—	—
Esters of quinolizidine alkaloids					
lupanine-13α-angelate	—	—	—	*	*
other angelate esters	—	—	—	—	**
tigliate- and various other esters	—	—	—	**	—

Occurs as a major component in: *** all species/samples, ** most species/samples, * at least some species/samples.

lizidine alkaloids. The results clearly demonstrate the chemotaxonomic value of alkaloids as a generic character in the tribe Crotalarieae.

Experimental

Plant materials. Voucher specimens representing the material used for extraction have been deposited in the Rand Afrikaans University Herbarium (JRAU). The taxa studied and voucher specimen details are given below.

Pearsonia aristata (Schinz) Duemmer: Roodepoort, near Botanical Garden, *Schutte 382*; *P. cajanifolia* (Harv.) Polhill subsp. *cajanifolia*: 26,4 km from Bronkhorstspruit on Rust De Winter Road, Van Wyk 2733; *P. cajanifolia* (Harv.) Polhill subsp. *cryptantha* (Bak.) Polhill: Magaliesberg, Scheerpoort area, *Verdoorn 3*; *P. obovata* (Schinz) Polhill: 18 km from Nelspruit on Kaapsehoop Road, Van Wyk 1864; *P. sessilifolia* (Harv.) Duemmer subsp. *marginata* (Schinz) Polhill, sample 1: Ngodwana River at intersection of N1 route, Van Wyk 2814, sample 2: 18 km from Nelspruit on Kaapsehoop Road, Van Wyk 1863; *P. sessilifolia* (Harv). Duemmer subsp. *sessilifolia*; Roadside between Bapsfontein and Bronkhorstspruit, Van Wyk 2728.

Procedures. Ground air-dried leaves and twigs were extracted by refluxing with CH_2Cl_2 for several days. Alkaloidal extracts were obtained by water phase separation [3, 4, 8] and purified by filtration through celite. Isolation of the four esters was effected by silica gel 60 column chromatography with $CHCl_3$–Cyclohexane–Et_2N (14:4:1) as eluent.

Alkaloids were identified by comparative TLC, as described elsewhere [8], combined with comparative GC using authentic reference samples obtained in previous studies [3, 4, 9]. GC spectra were obtained with an SE-30 capillary glass column (25 m × 0.25 mm; N_2 as carrier gas at 0.5 kg/cm_2; column temperature 250°C isotherm; injector 300°C; FID 275°C). The identity of the major alkaloids was confirmed by GC–MS analyses of two extracts (*P. cajanifolia* subsp. *cajanifolia* and *P. sessilifolia* subsp. *marginata*, sample 2). The mass spectra of the various alkaloids were identical to those obtained in several other studies. Large-scale extractions of the following species yielded pure samples of the ester compounds: *P. cajanifolia* subsp. *cajanifolia*; 47 mg of **1** and 54 mg of **2**; *P. cajanifolia* subsp. *cryptantha*: 380 mg of **1**, 800 mg of **2**, 220 mg of **3** and 560 mg of **4**; *P. sessilifolia* subsp. *marginata* (sample 1): 17 mg of **3**. These compounds were identified by MS, ^1H and ^{13}C NMR, including various 1D and 2D experiments. The results of the NMR studies will be published elsewhere as a detailed chemical report [Verdoorn and Van Wyk, *op cit.*].

Esters of quinolizidine alkaloids. lupanine-13α-angelate (13α-angeloyloxylupanine) (**1**): *Rt* 17.10 M^+ 346. Cajanifoline (lupanine-3β-hydroxy-13α-angelate) (**2**): *Rt* 19.50, pale yellow crystals, m.p. 87–91°C, $[\alpha]_D^{22} -11°$ (c = 1,4 in $CHCl_3$), ν_{max} 3400br (OH) 1640 (lactam C=O) cm^{-1}; MS *m/z* 362 (5), 277 (7), 262 (100), 246 (23), 234 (7), 205 (3), 186 (9), 165 (7), 148 (24), 134 (60), 122 (23), 108 (15), 91 (57), 69 (23), 55 (39). Sessilifoline (lupanine-3β-hydroxy-4α-angelate) (**3**): *Rt* 17.80, pale brown oil, $[\alpha]_D^{22} -72°$ (c = 1,6 in $CHCl_3$), ν_{max} 3400br (OH) 1640 (lactam C=O) cm^{-1}; MS *m/z* 362 (20), 279 (4), 263 (100), 245 (60), 233 (3), 221 (2), 205 (3), 191 (1), 177 (3), 163 (6), 148 (27), 136 (54), 122 (8), 110 (17), 98 (31), 84 (23), 67 (11), 55 (43). Pearsonine (lupanine-3β,8α-dihydroxy-13α-angelate) (**4**): *Rt* 20.65, pale yellow crystals, m.p. 93–96°C, $[\alpha]_D^{27} +7°C$ (C = 0,6 in $CHCl_3$), ν_{max} 3400br (OH) 1640 (lactam C=O) cm^{-1}; MS *m/z* 378 (25), 363 (9), 295 (6), 278 (100), 262 (29), 246 (12), 206 (6), 193 (5), 183 (19), 164 (15), 150 (28), 147 (28), 134 (24), 108 (18), 96 (20), 82 (31), 67 (21), 55 (42).

Quinolizidine alkaloids. Sparteine (**5**): *Rt* 7.45, M^+ 234; 11-epi-lupanine (α-isolupanine) (**6**): *Rt* 10,64, M^+ 248; lupanine (**7**): *Rt* 11.40, M^+ 248; nutalline (**8**) *Rt* 12.96, M^+ 264.

Piperidyl alkaloids. Ammodendrine (**9**): *Rt* 6.85, M^+ 208.

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APPENDIX 11

Chemotaxonomic significance of alkaloids in the genus *Spartidium* (Fabaceae - Crotalarieae)

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The presence of alkaloids in the monotypic North African genus *Spartidium* Pomel is reported for the first time. Comparative GC and MS analyses showed that *S. saharae* (Coss.) Pomel contains the bipiperidyl compounds ammodendrine and *N*′-formylammodendrine as major and minor alkaloids respectively. In addition, sparteine (a quinolizidine alkaloid) and two isomers of *N*-cinnamoylhistamine (an imidazole derivative) were present in small quantities. The morphological similarities between *Spartidium* and the genus *Lebeckia* Thunb. are not reflected in the alkaloid patterns. In *Spartidium* only a trace of one quinolizidine alkaloid was detected. Ammodendrine, the major *Spartidium* alkaloid, is absent or occurs only as a trace amount in *Lebeckia*. The results provide supporting evidence for Polhill´s (1976) decision to retain *Spartidium* as a distinct genus rather than to consider it a species of *Lebeckia*.

Die teenwoordigheid van alkaloïede in die monotipiese noord-Afrikaanse genus *Spartidium* word vir die eerste keer gerapporteer. Vergelykende GC en MS ontledings het aangetoon dat *S. saharae* (Coss.) Pomel die bipiperidielverbindings ammodendrien en *N*´-formielammodendrien as hoof en ondergeskikte alkaloïede onderskeidelik, bevat. Behalwe hiervoor, was sparteïen (´n kinolisidienalkaloïed) en twee isomere van *N*-sinnamoïelhistamien (´n imidasoolderivaat) teenwoordig in klein hoeveelhede. Die morfologiese ooreenkomste tussen *Spartidium* en die genus *Lebeckia* Thunb. word nie in die alkaloïedpatrone gereflekteer nie. In *Spartidium* is slegs spoorhoeveelhede van een kinolisidienalkaloïed waargeneem. Ammodendrien, die hoof alkaloïed van *Spartidium*, is afwesig of kom slegs as ´n spoorhoeveelheid in *Lebeckia* voor. Die resultate bied ondersteunende getuienis vir Polhill (1976) se besluit om *Spartidium* as ´n afsonderlike genus te behou eerder as om dit as ´n spesie van *Lebeckia* te beskou.

Keywords: alkaloids, chemotaxonomy, Fabaceae, generic relationships, *Spartidium*

Introduction

As part of a continuing evaluation of alkaloids as a generic character in the tribe Crotalarieae, we have investigated the North African genus *Spartidium* Pomel. Polhill (1976) was uncertain about the status and correct taxonomic position of this monotypic genus and expressed the hope that cryptic characters might eventually determine its real affinities. He decided to include it in the tribe Crotalarieae, near the genus *Lebeckia* Thunb. Morphologically, *Spartidium* and *Lebeckia* were found to be virtually indistinguishable, the orientation of the seeds and the rather long funicles in *Spartidium* being the only reliable characters to separate it from some species of *Lebeckia*. Polhill also suggested that both genera may be derivatives from a stock near the present-day *Retama* Raf. and *Gonocytisus* Spach of the Genisteae *sensu stricto*. Our aim with the present study was therefore to compare the major alkaloids of *Spartidium* with those of other genera. The distinct pattern observed in *Lebeckia* (Van Wyk & Verdoorn 1989) indicated to us that alkaloids may also provide valuable information about the generic status and affinities of *Spartidium*.

Material and Methods

Small samples of the aerial parts of *S. saharae* (Coss.) Pomel were obtained from the following herbarium specimens:

Sample 1 (leaves and twigs; 120 mg dry wt). Morocco: "Duel el Kherona", April 1913, *Pitard 3276* (K).

Sample 2 (flowers and young pods; 210 mg dry wt). Libya: "Gebel Nefoussa, Azizia -- Rhnem, 200 m", 15 March 1970, *Davis 49544* (K).

The dry plant material was homogenized in 0,05 M aqueous H_2SO and left at room temperature for 20 min. After filtration, the homogenate was made basic with conc. ammonium hydroxide and the precipitated alkaloids applied to a Chemelut column (0,6 g Chemelut/ml extract) (ICT, Frankfurt). The mixed alkaloids were eluted with 100 ml chloroform and the extract taken to dryness. The extract was then redissolved in 1 ml MeOH before GC injection. For preliminary identification by comparative gas chromatography, the following conditions were used: DB1 fused silica capillary column (15 m x 0.25 mm i.d.; He as carrier gas; column temperature 150°C 2 min isotherm, 10°C/min to 250°C, 20°C/min to 300°C, 10 min isotherm; split ratio 1:30; PND detection at 300°C). Authentic reference samples of several quinolizidine alkaloids and a number of extracts previously studied by GC-MS were available to us for comparison. Sample 2 was studied by GC-MS under the following conditions: DB1-30W fused silica capillary column (30 m x 0.32 mm i.d.; He as carrier gas; column temperature 150°C to 300°C, 6°C/min; split ratio 1:20.

The identity of the main alkaloid, ammodendrine (1) was confirmed by the mass spectrum (Figure 1a). The minor compounds were identified by their retention indices (RI) and mass spectra. Further proof was obtained by the mass spectra of the silylated ammodendrine and cinnamoylhistamines after treating the column-purified extract of Sample 2 with N-methyl-N-(trimethyl=silyl)-trifluoroacetamide. Due to the small quantity of material available to us and the very low yields of the minor compounds, the identity of the latter could not be confirmed by other spectroscopic methods. The mass spectra of N′-formylammodendrine (2) (Figure 1b) and sparteine (3) (Figure 1c) however, were identical to those obtained in several other studies. The mass spectrum of N′-formylammodendrine (Figure 1b) [with the characteristic loss of H_2O from the molecular ion (Fitch & Djerassi 1974; Fitch *et al*. 1974)] was identical to those obtained in GC-MS studies of extracts from the genus *Dichilus* (Van Wyk *et al*. 1988), where it was listed as "alkaloid D". The mass spectra of the compounds (4) and (5) (Figure 1d & e) strongly suggested the Z and E isomers of N-cinnamoylhistamine, an imidazole derivative reported from two species of *Acacia* by Fitzgerald (1964). In the subfamily Papilionoideae, imidazole is known to be widely distributed in the tribe Tephrosieae (Hayman & Gray 1987).

Results

Table 1 shows the distribution of alkaloids in the two samples studied. The combination of alkaloids in Sample 1 (leaves and twigs) and Sample 2 (flowers and young pods) were remarkably similar, despite the difference in age and origin of the material. Ammodendrine (1) was present as the major compound of both samples and represented 72% and 67% of the total yields respectively. Minor compounds were identified as N′-formylammodendrine (2), sparteine (3) and two isomers of *N*-cinnamoylhistamine (4) and (5). The mass spectra obtained for these compounds are shown in Figure 1.

-INSERT STRUCTURES-

-INSERT TABLE 1-

-INSERT FIGURE 1-

Discussion

A summary of the major alkaloids of some genera of the Crotalarieae is shown in Table 2. With the exception of *Dichilus* DC. (which also produce several piperidyl alkaloids), all genera which contain α-pyridone alkaloids and pyrrolizidine alkaloids were excluded from the comparison. *Retama* and *Gonocytisus* (Tribe Genisteae) were also excluded despite the suggestion by Polhill (1976) that it may be related to *Spartidium*. Both these genera contain α-pyridone alkaloids such as cytisine, thermopsine and anagyrine (summarized in Polhill, 1976) and there is no evidence (at least not from the available alkaloid data) of a direct affinity with *Spartidium*.

-INSERT TABLE 2-

Table 2 shows that the combination of alkaloids in *Spartidium* is quite different from those of other recently investigated genera of the tribe Crotalarieae. This is true even if the presence of histamine derivatives (not previously reported from any genus of the Genisteae or Crotalarieae) is ignored. Ammodendrine is present in most other genera (at least in trace quantities) but invariably co-occurs with several other major alkaloids. The virtual absence of quinolizidine alkaloids is quite unexpected and represents a significant difference between *Spartidium* and *Lebeckia*. Polhill (1976) found, on the basis of a total characterization, that *Spartidium* is virtually indistinguishable from *Lebeckia*. *Lebeckia* has a characteristic combination of quinolizidine alkaloids and contain large amounts of sparteine, lupanine and nuttalline (Van Wyk & Verdoorn 1989). The alkaloids of *Spartidium* therefore strongly support its present generic status.

The available alkaloid data provides no clear evidence of intergeneric relationships, but shows that the combination of alkaloids in each of the genera has diagnostic value at the generic level. The total absence of α-pyridone alkaloids and esters of alkaloids in Spartidium and Lebeckia agrees with the suggestion (Polhill 1976) of a basal position for these genera in the tribe Crotalarieae.

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TABLE 1. DISTRIBUTION OF ALKALOIDS IN TWO SAMPLES OF SPARTIDIUM SAHARAE. [Yield figures (given as percentages of the total yield) were estimated from GC results (data obtained from peak area)]

	RETENTION INDEX (RI)	SAMPLE 1 (leaves & twigs)	SAMPLE 2 (flowers & young pods)
TOTAL ALKALOID YIELD (mg/g dry wt):		5,16	7,29
DISTRIBUTION OF ALKALOIDS (% of total yield):			
ammodendrine	1865	72,4	67,2
N′-formylammodendrine	2210	1,7	1,3
sparteine	1785	0,2	0,6
N-cinnamoylhistamine (isomer 1)	2440	7,6	15,5
N-cinnamoylhistamine (isomer 2)	2700	5,7	5,5

TABLE 2. DISTRIBUTION OF ALKALOIDS KNOWN FROM THE GENERA *SPARTIDIUM*, *LEBECKIA*, *WIBORGIA*, *DICHILUS* AND *ROTHIA*. [Data for *Lebeckia* from Van Wyk & Verdoorn (1989), *Wiborgia* from Van Wyk (unpublished data), *Dichilus* from Van Wyk *et al*. (1988) and *Rothia* from Hussain *et al*. (1988)]

	Spartidium	*Lebeckia*	*Wiborgia*	*Dichilus*	*Rothia*
no. of species in genus:	1	c. 35	10	5	2
no. of species examined:	1	14	4	5	2
Tetracyclic quinolizidine alkaloids:					
nuttalline		+++	tr	tr	+
sparteine	tr	+++	tr		
lupanine		+++	tr	tr	+
isolupanine		+			tr
thermopsine				++	
Esters of tetracyclic quinolizidine alkaloids:					+++
Piperidyl alkaloids:					
ammodendrine	+++	tr		+++	++
N′-formylammodendrine	tr			tr	
smipine				++	
piperidinone				+	
bipiridyl				+	

- TABLE 2 CONTINUED -

	Spartidium	*Lebeckia*	*Wiborgia*	*Dichilus*	*Rothia*
1-acetyl-1,2,3,4-tetrahydropyridine				+	
Imidazole derivatives:					
N-cinnamoylhistamine	+++				

occurs as a major component in: +++ all species/samples, ++ most species/samples, + at least some species/samples. (*N*-cinnamoylhistamine is here entered as a major compound because the combined yield of the two isomers exceeded 10% of the total alkaloid yield in both samples).

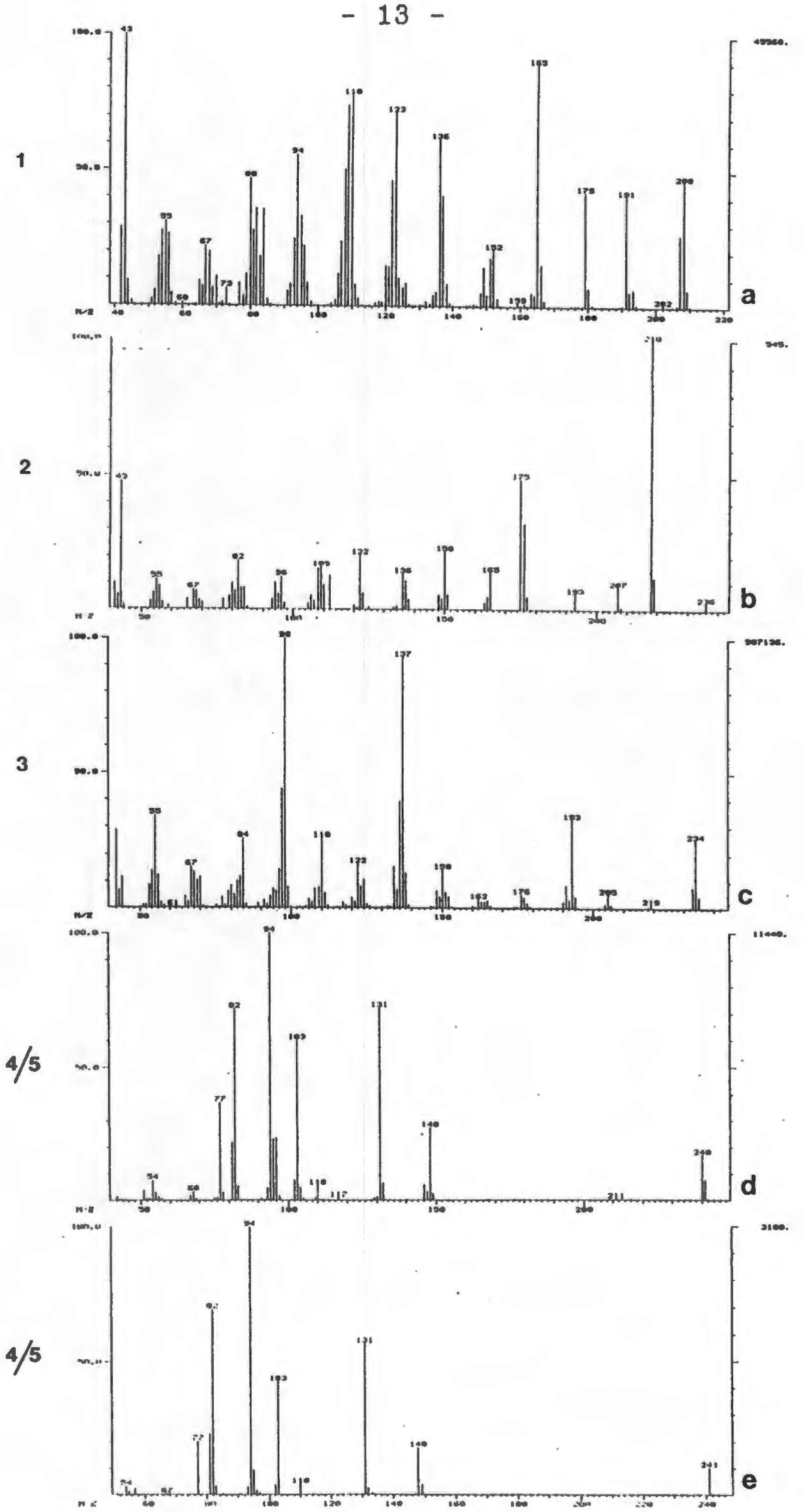
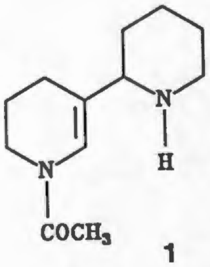


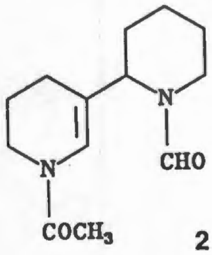
Figure 1. Mass spectra for 5 alkaloids identified from extracts of <u>Spartidium saharae</u> (Sample 2; Finnigan-Mat 4515 mass spectrometer; 45 eV electron impact).

--STRUCTURES OF ALKALOIDS- TO BE INSERTED IN THE TEXT UNDER RESULTS--



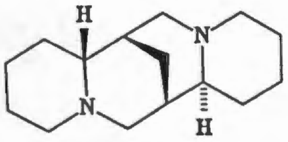
1

AMMODENDRINE



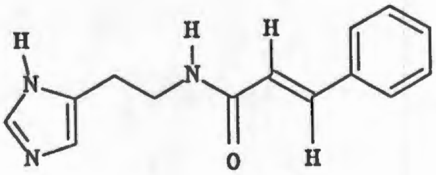
2

***N*'-FORMYLAMMODENDRINE**



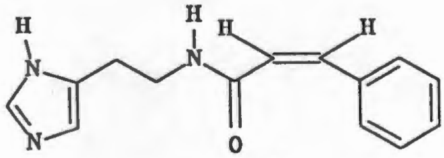
3

SPARTEINE



4

***E*-*N*-CINNAMOYLHISTAMINE**



5

***Z*-*N*-CINNAMOYLHISTAMINE**

APPENDIX 12

BSE 159

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The Taxonomic Significance of Cyanogenesis in *Lotononis* and Related Genera

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Key Word Index—*Buchenroedera*; *Lotononis*; Leguminosae; cyanogenesis; taxonomy; sectional classification.

Abstract—Reports on cyanogenesis in the genus *Lotononis* are limited to five species. In a survey using the Feigl–Anger spot test, a further 52 species of *Lotononis* and four species of the closely related *Buchenroedera* were found to by cyanogenic. Species of other genera in the tribe Crotalarieae all gave a negative result. Cyanogenesis appears to be a character of considerable chemotaxonomic value in *Lotononis*, with some groups of species cyanogenic and others acyanogenic. These groups usually follow the traditional sectional classification. Lack of morphological uniformity within a section is also reflected in the cyanogenesis data and this may provide useful additional evidence to improve the existing classification. The data support the view that the genera *Lotononis* and *Buchenroedera* are congeneric.

Introduction

Cyanogenesis is particularly common in the Leguminosae and is known to occur in at least 18 of the tribes (Seigler, personal communication). Among the Crotalarieae *sensu* Polhill [1], five species are reported to be cyanogenic [2, 3]: *Lotononis carnosa* (Eckl. & Zeyh.) Benth., *L. crumanina* Burch. ex Benth., *L. involucrata* (Berg.) Benth., *L. laxa* Eckl. & Zeyh. and *L. oxyptera* (E. Mey.) Benth. Some of these have proved to be responsible for hydrocyanic poisoning in stock [2]. Cyanogenesis in *Lotononis* is due to the presence of the glucoside prunasin (derived from L-phenylalanine) [3]. In the Leguminosae, this biochemical pathway to the production of cyanogenic compounds is less common than the more usual valine- and isoleucine pathways, which lead to linamarin and lotaustralin, respectively [4].

In the latest available taxonomic treatment of *Lotononis* [5], the original sectional limits of Bentham [6] were modified to accommodate newly described species. This resulted in what appears to be an unnatural classification. Not only were species of other genera included, but the section *Oxydium* was transferred to the genus *Crotalaria*. In view of new insights into generic limits [1] and numerous undescribed species, the sectional classification of *Lotononis* should be reconsidered as a first step towards a complete revision.

This survey was done to evaluate cyanogenesis as a chemotaxonomic character at generic and infrageneric levels in *Lotononis* and related genera.

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Results

The tests showed at least 57 species of *Lotononis* and four species of *Buchenroedera* are cyanogenic (Table 1). Not a single positive result was obtained for 98 samples from nine other genera of the tribe.

Within the genus *Lotononis*, a distinct pattern emerged amongst the various groups of related species (Table 2). Very few species showed indications of intra- and/or interpopulational variation. Such differences were observed only in a few species of section *Krebsia*, the *L. falcata*- and *L. laxa* groups of section *Leptis* and in *Buchenroedera*. The data for individual species and species groups of *Lotononis* and *Buchenroedera* are presented in Table 3 and discussed below.

Discussion

In Tables 2 and 3, the existing sectional classification of Bentham [6], Harvey [7] and Duemmer [5] is followed, except for some modifications:

TABLE 1. SUMMARY OF CYANOGENESIS TEST RESULTS FOR VARIOUS GENERA OF THE TRIBE, CROTALARIEAE

Genus	Total number of samples	Total number of species		
		In group	Tested	HCN^{+}
Lotononis (DC.) Eckl. & Zeyh.	351	*ca* 130	113	57
Buchenroedera Eckl. & Zeyh.	32	*ca* 14	9	4
Argyrolobium Eckl. & Zeyh.	7	*ca* 70	4	0
Aspalathus L.	9	278	8	0
Crotalaria L.	22	*ca* 600	17	0
Dichilus DC.	9	5	5	0
Lebeckia Thunb.	21	*ca* 35	11	0
Melolobium Eckl. & Zeyh.	11	*ca* 20	6	0
Pearsonia Duemmer	6	11	4	0
Polhillia Stirton	9	5	4	0
Wiborgia Thunb.	4	10	3	0

TABLE 2. SUMMARY OF CYANOGENESIS TEST RESULTS FOR THE DIFFERENT SECTIONS OF *LOTONONIS*. Some of the sections are divided into informal groups, as defined in the footnotes

Section/Group	Total number of species			
	In group	Tested	HCN^{+}	%HCN^{+}
Aulacinthus (E. Mey.) Benth.	*ca* 7	7	7	100
Krebsia (Eckl. & Zeyh.) Benth.				
L. carnosa group*	*ca* 10	10	9	90
L. carinata group†	2	2	0	0
L. digitata group‡	*ca* 2	2	0	0
Telina (E. Mey.) Benth.	*ca* 13	11	5	48
Polylobium (Eckl. & Zeyh.) Benth.				
L. umbellata group§	*ca* 9	8	7	88
L. angolensis group‖	*ca* 5	5	0	0
Oxydium Benth.	*ca* 9	8	6	75
Lipozygis (E. Mey.) Benth.				
L. anthylloides group¶	*ca* 8	7	0	0
L. eriantha group**	*ca* 8	7	0	0
Leobordea (Del.) Benth.	*ca* 6	3	0	0
Leptis (Eckl. & Zeyh.) Benth.				
L. laxa group††	*ca* 9	9	8	90
L. falcata group‡‡	*ca* 22	20	15	75
L. quinata group§§	*ca* 5	5	0	0
L. calycina group‖‖	*ca* 16	9	0	0
Total	*ca* 130	113	57	50

**Krebsia* (Eckl. & Zeyh.) Benth. *sensu stricto*; †species added to *Krebsia* by Duemmer [5]; ‡species added to *Krebsia* by Harvey [7] and Duemmer [5]; §*Polylobium* (Eckl. & Zeyh.) Benth. *sensu stricto*; ‖species later added to *Polylobium* and related species; ¶species with indehiscent fruit; **species with dehiscent fruit; ††perennials with the carina acute and glabrous; ‡‡annuals with the carina acute and glabrous; §§short-lived, prostrate perennials usually with 5-digitate leaves; ‖‖annuals or perennials with the carina obtuse and pubescent.

—Morphologically heterogenous sections are split into smaller groups of related species.

—Species that were obviously misplaced are transferred to more appropriate positions.

—Species of other genera wrongly assigned to *Lotononis* are excluded.

—Newly described or undescribed species are allocated to those groups that seem the most appropriate on morphological considerations.

The groups are used here in an informal sense for comparative purposes and no formal taxonomic hierarchy or rank is implied. Future studies however, may show some of these to be worthy of sectional status, while others (and even some

TABLE 3. RESULTS OF CYANOGENESIS TESTS FOR INDIVIDUAL SAMPLES AND SPECIES OF *LOTONONIS* AND *BUCHENROEDERA*

Groups and species	Number of samples tested			
	Total	HCN^+	HCN?	HCN^-
Lotononis (DC.) Eckl. & Zeyh.				
Section *Aulacinthus* (E. Mey.) Benth.				
L. leucoclada (Schltr.) Duemmer	6	6	—	—
L. gracilis (E. Mey.) Benth.	6	6	—	—
L. rigida (E. Mey.) Benth.	2	2	—	—
L. viborgioides Benth.	3	3	—	—
L. dahlgrenii B.-E. van Wyk	1	1	—	—
L. comptonii B.-E. van Wyk	7	7	—	—
L. dissitinodis B.-E. van Wyk	2	2	—	—
Section *Krebsia* (Eckl. & Zeyh.) Benth.				
Part 1: *L. carnosa* group				
L. carnosa (Eckl. & Zeyh.) Benth.	3	3	—	—
L. biflora (H. Bol.) Duemmer	4	3	1	—
L. cytisoides (E. Mey.) Benth.	7	4	1	2
L. trisegmentata Phillips	5	—	—	5
L. divaricata (Eckl. & Zeyh.) Benth.	12	8	—	4
L. galpinii Duemmer	2	2	—	—
L. pottiae Burtt Davy	1	1	—	—
L. dichiloides Sond. (yellow)	1	1	—	—
L. dichiloides Sond. (pink)	1	—	1	—
L. bachmanniana Duemmer	3	3	—	—
L. caerulescens (E. Mey.) B.-E. van Wyk	5	5	—	—
Part 2: *L. carinata* group				
L. carinata (E. Mey.) Benth.	5	—	—	5
L. hirsuta Schinz	3	—	—	3
Part 3: *L. digitata* group				
L. digitata Harv.	2	—	—	2
L. benthamiana Duemmer	3	—	—	3
Section *Telina* (E. Mey.) Benth.				
L. minor Duemmer	1	—	—	1
L. azurea (Eckl. & Zeyh.) Benth.	2	2	—	—
L. prostrata (L.) Benth.	2	2	—	—
L. acuminata Eckl. & Zeyh.	3	3	—	—
L. varia (E. Mey.) Steud.	2	2	—	—
L. argentea Eckl. & Zeyh.	2	—	—	2
L. azureoides B.-E. van Wyk	1	1	—	—
L. gracilifolia B.-E. van Wyk	2	—	—	2
L. elongata (Thunb.) D. Dietr.	2	—	—	2
L. macrocarpa Eckl. & Zeyh.	3	—	—	3
L. solitudinis Duemmer	2	—	—	2
Section *Polylobium* (Eckl. & Zeyh.) Benth.				
Part 1: *L. umbellata* group				
L. umbellata (L.) Benth.	6	6	—	—
L. acocksii B.-E. van Wyk	1	1	—	—
L. purpurescens B.-E. van Wyk	2	2	—	—
L. peduncularis (E. Mey.) Benth.	2	2	—	—
L. involucrata (Berg.) Benth.	3	3	—	—
L. angustifolia (E. Mey.) Steud.	3	2	—	1
L. exstipulata L. Bol.	3	3	—	—
L. serpens (E. Mey.) Dahlgr.	7	—	1	6
Part 2: *L. angolensis* group				
L. angolensis Welw. ex Bak.	4	—	—	4
L. bainesii Bak.	4	—	—	4
L. listii Polhill	4	—	—	4
L. listioides Dinter & Harms	2	—	—	2
L. marlothii Engl.	2	—	—	2

TABLE 3—*CONTINUED*

Groups and species	Number of samples tested			
	Total	HCN⁺	HCN?	HCN⁻
Section *Oxydium* Benth.				
L. monophylla Harv.	1	1	—	—
L. trichopoda (E. Mey.) Benth.	4	4	—	—
L. rostrata Benth.	3	3	—	—
L. acutiflora Benth.	3	3	—	—
L. oxyptera (E. Mey.) Benth.	3	3	—	—
L. stenophylla Eckl. & Zeyh.	5	4	1	—
L. carnea B.-E. van Wyk *ined.*	9	—	1	8
L. arenicola Schltr.	5	—	1	4
Section *Lipozygis* (E. Mey.) Benth.				
Part 1: *L. anthylloides* group				
L. anthylloides Harv.	2	—	—	2
L. bolusii Duemmer	3	—	1	2
L. rosea Duemmer	2	—	—	2
L. pentaphylla (E. Mey.) Benth.	2	—	—	2
L. polycephala (E. Mey.) Benth.	5	—	—	5
L. longicephala B.-E. van Wyk *ined.*	3	—	—	3
L. brevicaulis B.-E. van Wyk	4	—	—	4
Part 2: *L. eriantha* group				
L. eriantha Benth.	4	—	—	4
L. sutherlandii Duemmer	1	—	—	1
L. puchra Duemmer	1	—	—	1
L. corymbosa (E. Mey.) Benth.	1	—	—	1
L. foliosa H. Bol.	1	—	—	1
L. lanceolata (E. Mey.) Benth.	1	—	—	1
L. procumbens H. Bol.	3	—	—	3
Section *Leobordea* (Del.) Benth.				
L. platycarpa (Viv.) Pichi-Serm.	5	—	—	5
L. furcata (Merxm. & A. Schreib.) A. Schreib.	2	—	—	2
L. stipulosa Bak. f.	4	—	—	4
Section *Leptis* (Eckl. & Zeyh.) Benth.				
Part 1: *L. laxa* group				
L. laxa Eckl. & Zeyh.	6	5	—	1
L. woodii H. Bol.	5	4	—	1
L. humilior Duemmer	3	3	—	—
L. macrosepala Conrath	3	3	—	—
L. curtii Harms	3	3	—	—
L. brachyantha Harms	4	4	—	—
L. serpentinicola Wild	3	3	—	—
L. crumanina Burch. ex Benth.	3	3	—	—
L. burchellii Benth.	3	—	—	3
Part 2: *L. falcata* group				
L. falcata (E. Mey.) Benth.	4	4	—	—
L. fruticoides B.-E. van Wyk *ined.*	2	2	—	—
L. brachyloba (E. Mey.) Benth.	5	5	—	—
L. aurea B.-E. van Wyk *ined.*	5	5	—	—
L. strigillosa (Merxm. & A. Schreib.) A. Schreib.	1	1	—	—
L. schreiberi B.-E. van Wyk *ined.*	1	1	—	—
L. sabulosa Salter	2	2	—	—
L. pachycarpa Dinter *in sched.*	1	1	—	—
L. leptoloba H. Bol.	3	2	—	—
L. maximiliani Schltr.	7	4	—	—
L. pumila Eckl. & Zeyh.	1	1	—	—
L. tenuis Bak.	1	1	—	—
L. linearifolia B.-E. van Wyk *ined.*	1	1	—	—

TABLE 3—*CONTINUED*

		Number of samples tested		
Groups and species	Total	HCN$^-$	HCN?	HCN
L. sparsiflora (E. Mey.) B.-E. van Wyk *ined.*	4	—	1	3
L. rabenaviana Dinter & Harms	3	1	—	2
L. lenticula (E. Mey.) Benth.	1	1	—	—
L. maculata Duemmer	2	—	—	2
L. pallidirosea Dinter & Harms	2	—	—	2
L. delicata (Bak. f.) Polhill	2	—	—	2
L. pungens Eckl. & Zeyh.	3	—	—	3
L. flava Duemmer	3	—	—	3
Part 3: *L. quinata* group				
L. quinata (E. Mey.) Benth.	4	—	—	4
L. delicatula H. Bol.	3	—	—	3
L. longiflora H. Bol.	3	—	—	3
L. mirabilis Dinter	2	—	—	2
L. magnifica B.-E. van Wyk *ined.*	3	—	—	3
Part 4: *L. calycina* group				
L. calycina (E. Mey.) Benth.	4	—	—	4
L. adpressa N. E. Br.	3	—	—	3
L. lupinifolia (Boiss. ex Jaub. & Spach) Benth.	2	—	—	2
L. genistoides (Fenzl) Benth.	1	—	—	1
L. maroccana Ball	2	—	—	2
L. stolzii Harms	3	—	—	3
L. arida Duemmer	3	—	—	3
L. humifusa Burch. ex Benth.	1	—	—	1
L. mucronata Conrath	3	—	—	3
Buchenroedera Eckl. & Zeyh.				
B. amajubica Burtt Davy	3	—	—	3
B. glabrescens Duemmer	2	—	—	2
B. lotononoides Scott Elliot	3	2	—	1
B. meyeri Presl	5	3	—	2
B. multiflora Eckl. & Zeyh.	6	4	—	2
B. sparsiflora Wood & Evans	2	—	—	2
B. tenuifolia Eckl. & Zeyh.				
var. *tenuifolia*	3	3	—	—
var. *pulchella* (E. Mey.) Harv.	3	—	—	3
B. trichodes Presl	3	—	—	3
B. viminea (E. Mey.) Presl	2	—	—	2

of the existing sections) may have to be combined. Similarly, some of the species will probably be reduced to subspecific rank.

Lotononis, section *Aulacinthus*, consists of woody shrubs with a remarkable similarity to species of *Lebeckia*. This similarity is so marked that a mixed collection comprising flowering twigs of *Lotononis gracilis* and fruiting twigs of *Lebeckia sericea* have, in the past, been designated as a type specimen [7]. All the material of this section reacted strongly positive, while none of the *Lebeckia* species tested appear to be cyanogenic. The Feigl–Anger test allows the rapid identification of vegetative material of these two groups that would otherwise be very difficult.

The section, *Krebsia*, comprises the only other essentially woody group. Species added to it by Harvey [7] and Duemmer [5] are treated here as separate groups. *Lotononis digitata* and *L. benthamiana* are closely related to *L. quinata* and its allies, traditionally placed in the section *Leptis*. *L. carinata* and *L. hirsuta* are very different from the species of *Krebsia sensu stricto* and are more closely related to species of the *L. calycina* group of *Leptis*. Nearly all the species of *Krebsia sensu stricto* are cyanogenic, while the other two groups are not. The test results supported the transfer of *L. caerulescens* (previously considered to be a species of *Lebeckia*) to *Lotononis*, section *Krebsia* [8].

The section, *Telina*, is poorly presented in the herbarium record so that the data are not conclusive for some species. It is the only group that is not predominantly cyanogenic or acyanogenic. This may be significant in view of some anomalous species that are included here. *L. minor* should perhaps be transferred to *Krebsia* and the last two species listed show a distinct affinity to the *L. angolensis* group of *Polylobium*. *Telina*, as presently circumscribed, may indeed not be a natural group.

The section, *Polylobium*, is readily divisible into two distinct groups. The first of these, consisting of *L. umbellata* and its allies, is restricted to the winter and all year rainfall areas of the south-western and southern Cape. These species all have a woody, usually subterranean, caudex from which flowering shoots develop annually. Newly described species such as *L. acocksii* are intermediate between this group and the section *Aulacinthus* (both predominantly cyanogenic), indicating that the traditional limits are not longer valid. A suggestion [9] that the anomalous *L. serpens* (previously classified in the monotypic genus *Euchlora* Eckl. & Zeyh.) belongs here is not supported by the results. *L. angolensis* and related species form the second group, which has a summer rainfall distribution in the central and eastern parts of southern Africa and also extends into tropical Africa. All these species have a tendency to produce adventitious roots at the nodes, giving it a stoloniferous appearance. It is also the only group in *Lotononis* where small but well-developed bracteoles are consistently present. Epidermal hairs are virtually absent, but those that do occur are devoid of the striations and tubercles found on the hair surfaces of all other species, with the exception of *L. macrocarpa* and *L. solitudinis*. The latter two also have well-developed bracteoles and are much better placed here than in *Telina*. That this second group of *Polylobium* is acyanogenic is perhaps predictable, since it includes *L. bainesii*, a well-known pasture legume cultivated in many parts of the world. *L. bainesii* was indeed previously also found to be acyanogenic [3].

Lotononis, section *Oxydium*, includes species that are superficially very similar to species of *Crotalaria*. For this reason, most members of the group were excluded from *Lotononis* in the last revision [5] but it has since been shown [10, 11] that the presumed relationship with *Crotalaria* was based on a superficial characterization. With the exception of two species, this group is cyanogenic, while none of the 17 species of *Crotalaria* tested reacted positively.

Lotononis, section *Lipozygis*, is kept here in its traditional circumscription, except for the inclusion of *L. procumbens*. It is obviously better placed here than in section *Polylobium*, with which it was previously associated on account of the pseudo-umbellate inflorescences [12]. The section falls naturally into two distinct groups with a winter and summer rainfall distribution, respectively. The first has a distinctive appearance due to the dense rounded inflorescences and prostrate habit. *L. brevicaulis* fits uneasily into this group [13] and further evidence may indicate other affinities, perhaps closer to *L. serpens*. The data indicate that both groups are acyanogenic.

The geographically most widespread section *Leobordea* is easily recognized by the opposite leaves and axillary, subsessile flowers. The species seem similar to the *Lotononis calycina* group of section *Leptis* and these two groups may be more closely related than previously thought. All samples reacted negatively.

Leptis, the largest section, is a poorly defined group, traditionally accommodating annuals and herbaceous perennials that do not seem to fit comfortably elsewhere. Even a cursory examination reveals suits of correlated characters and the section is here divided into four basic groups. The first (all perennial herbs from the central and eastern parts of southern Africa, extending thinly into tropical Africa) is similar to section *Oxydium* in the presence of an acute carina. The second group also has the carina acute as in *Oxydium*, but the species are all annuals with a south-western and western distribution in southern Africa. In these species the claw of the standard is markedly dilated at its base, a character also present in most species of *Oxydium*. The *L. quinata* group comprises short-lived perennials with a prostrate habit and usually digitate leaves. These species are closely related to *L. digitata* and *L. benthamiana* that were previously associated with the section *Krebsia* on account of the somewhat more woody habit.

Finally, all annuals and herbaceous perennials with an obtuse, usually pubescent carina are gathered in a somewhat poorly defined group. Some species are similar to the *L. eriantha* group of *Lipozygis*, others to the *L. angolensis* group of *Polylobium* and some perhaps also to *Leobordea*. The first two groups, as defined here, are predominantly cyanogenic, while the latter two appear to be totally acyanogenic. The data are therefore in close accordance with presumed affinities as stated above.

The genus, *Buchenroedera*, shows considerable variation, but four of the nine species tested are cyanogenic. This is roughly the same proportion as in *Lotononis* and would seem to indicate a chemical similarity. Polhill [1] found no consistent diagnostic characters other than the short ovate fruit to separate *Buchenroedera* from *Lotononis* and suggested that the two may not be distinct at generic level. This view is also supported by the presence of the same macrocyclic pyrrolizidine alkaloids in both genera [14, 15].

Conclusions

The data indicate that cyanogenesis in the tribe Crotalarieae is characteristic of *Lotononis* and *Buchenroedera*. Other genera should be tested in more detail, however. The data also support the view that *Buchenroedera* may be no more than a section of *Lotononis*.

Cyanogenesis is a useful taxonomic character in *Lotononis*, since the ability to produce HCN is correlated with patterns of morphological variation. It is clear from the data that the basic groups of *Lotononis* are either cyanogenic or acyanogenic and, furthermore, that the cyanogenic and acyanogenic groups are mutually more closely related. Very few species do not fit this general pattern and some may well turn out to conform if more material from different localities can be tested. The striking pattern that emerged from this survey shows that cyanogenesis may provide supporting evidence for a more natural infrageneric classification of the genus, *Lotononis*.

Experimental

Plant materials. Since care was taken to use only very rich collections, some species with poor herbarium records could not be tested and others are inadequately represented. Results obtained for 351 samples of *Lotononis* (129 samples from 41 species tested fresh), 32 samples of *Buchenroedera* and 98 samples of other genera are reported here. Authorities for names are given in Table 3 and are not repeated elsewhere. Species from genera other than *Lotononis* and *Buchenroedera* are not listed individually but have been included in a comprehensive list of voucher specimens. This has been deposited in the Rand Afrikaans University Herbarium.

Procedures. Fresh and dried leaf samples were tested for the presence of HCN using the spot test of Feigl and Anger [16], as modified [17]. This test is highly specific [17] and very sensitive, allowing the detection of only 1 μg HCN [16]. A few leaves (*ca* 0.5 cm^3) were crushed in polytop vials, moistened with deionized water and test strips suspended above the material. A deep blue discolouration, indicating the presence of HCN, usually developed after a few minutes. If no colour change occurred within 12 h, the sample was taken to be acyanogenic. In a few rare cases, only a very slight reaction was observed, usually after several hours. These are indicated by a question mark in Table 3 and interpreted as negative results. The response of fresh samples never differed significantly from dried ones, even after the latter was subjected to freezing at −18°C for 48 h.

Acknowledgements—I thank Prof. Dave Seigler (University of Illinois-Urbana) for arousing my interest in cyanogenesis and for supplying information about the test procedure. Financial support from the Rand Afrikaans University is acknowledged. The taxonomic study of *Lotononis* and *Buchenroedera* is registered as a Ph.D. project at the University of Cape Town.

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APPENDIX 13

The chemotaxonomic significance of prunasin in *Buchenroedera* (Fabaceae - Crotalarieae)

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Lotononis and *Buchenroedera* are the only genera of the tribe Crotalarieae so far known to be cyanogenic. A recent survey (Van Wyk 1989) has shown that at least 57 species of the former and 4 of the latter react positively to the Feigl-Anger test. Together with obvious similarities to *Lotononis* in morphology, chromosome cytology and alkaloids this raises doubts about the generic status of *Buchenroedera*. The chemical basis for cyanogenesis in *Buchenroedera* is here reported for the first time. A glucoside from the leaves of *B. multiflora* Eckl. & Zeyh. was isolated and identified as prunasin, a compound previously detected in *L. crumanina* Burch. ex Benth. This result shows that cyanogenesis is homologous in *Buchenroedera* and *Lotononis* and provides further evidence that the two genera should be combined.

Lotononis en _Buchenroedera_ is sovêr bekend die enigste genera van die tribus Crotalarieae wat sianogenies is. ´n Onlangse opname (Van Wyk 1989) het getoon dat ten minste 57 spesies van eersgenoemde genus en 4 spesies van laasgenoemde positief reageer op die Feigl-Anger toets. Saam met ooglopende ooreenkomste met _Lotononis_ in morfologie, chromosoomsitologie en alkaloïede ontstaan twyfel oor die generiese status van _Buchenroedera_. Die chemiese basis van sianogenese in _Buchenroedera_ word hier vir die eerste keer gerapporteer. ´n Glukosied is uit die blare van _B. multiflora_ Eckl. & Zeyh. geïsoleer en geïdentifiseer as prunasien, ´n verbinding wat voorheen in _L. crumanina_ Burch. ex Benth. waargeneem is. Hierdie resultaat toon dat sianogenese in _Buchenroedera_ en _Lotononis_ homoloog is en bied verdere getuienis dat die twee genera gekombineer behoort te word.

Keywords: _Buchenroedera_, cyanogenesis, generic relationships, _Lotononis_, prunasin

Introduction

In a preliminary survey of cyanogenesis in several genera and species of the tribe Crotalarieae (Van Wyk 1989), only two genera were found to react positively to the spot test of Feigl and Anger (1966) as modified by Tantisewie *et al*. (1969), i.e. four species of *Buchenroedera* Eckl. & Zeyh. and 57 species of *Lotononis* (DC.) Eckl. & Zeyh. This similarity was interpreted as supporting evidence for the idea that *Buchenroedera* is indistinct from *Lotononis* at the generic level. Morphological evidence (Polhill 1976), chromosome numbers (Van Wyk & Schutte 1988) and alkaloids (Van Wyk & Verdoorn 1988, 1989) have shown that *Buchenroedera* is almost identical to the section *Krebsia* (Eckl. & Zeyh.) Benth. of *Lotononis* except for the shape of the fruit. Using chromatographic methods, Fikenscher and Hegnauer (1981) reported that prunasin was the cyanogenic glucoside of *Lotononis crumanina* Burch. ex Benth. This is the only evidence for the source of HCN in *Lotononis* -- none of the other 4 species previously reported to be cyanogenic (Watt & Breyer-Brandwijk 1962) have been studied by analytical methods.

In this paper we report on an investigation into the chemical basis for cyanogenesis in *Buchenroedera*. In the Fabaceae, prunasin is less common than linamarin and lotaustralin and we argue that the presence of prunasin would leave little doubt that cyanogenesis is homologous in *Buchenroedera* and *Lotononis*.

Material and Methods

Buchenroedera multiflora Eckl. & Zeyh. was chosen for this study because of its rapid positive reaction to the Feigl-Anger test. [Voucher specimen: Zuurberg National Park, E Cape, B. & M. Van Wyk 1523 (JRAU, PRE)].

An enzyme preparation consisting of 1 mg β-glucosidase (prepared from sweet almonds; Boehringer-Mannheim) in 1 cm^3 phosphate buffer (0,5 mol dm^{-3}, pH 6,8)) was used to test for the presence of the cyanogen throughout the following procedures. Release of HCN was detected with paper strips prepared by the method of Feigl and Anger (1966) as modified (Tantisewie et al. 1969).

Fresh leaves and twigs (100 g) were boiled in 95% ethanol for several hours. After filtration, the crude ethanolic extract was evaporated to dryness, dissolved in H_2O and extracted 4x with an equal volume of chloroform. The H_2O was removed from the aqueous phase under reduced pressure to yield 1,27 mg of a brown syrup. A small quantity of this material reacted positively to the Feigl-Anger test after hydrolysis with β-glucosidase, indicating the presence of cyanogen in the extract. Most of the material was used to isolate the glycosides and sugars by column chromatography (see below). For isolation by paper chromatography, we followed a similar procedure to that described by Spencer and Seigler (1980). A small quantity of the brown syrup was chromatographed on paper (Whatman 3MM) in Me_2CO--H_2O (5:1). Strips 1 cm wide (Spencer and Seigler 1980) were tested for the release of HCN. The cyanogenic fractions (R_f ca. 0,9) were combined, eluted with H_2O, and chromatographed a second time in MeCOEt-- Me_2CO--H_2O (15:5:3). The cyanogenic fractions (R_f ca. 0,8) were again combined and eluted with H_2O. The eluent was divided into two equal portions and hydrolysed with β-glucosidase (releasing HCN) or HCl (no release of HCN). After hydrolysis, the two fractions were extracted 2x with equal volumes of diethyl ether. The aqueous phases both reacted strongly positive to the glucose oxidase test (Kusai *et al*. 1960). The ether fractions were dried with $CaCl_2$ and studied by mass spectrometry.

The cyanogen was isolated from the extract using a 600 x 25 mm glass column packed with silica gel and eluted with EtOAc--MeOH (95:5). Fractions of 10 cm^3 were collected and tested for the presence of the cyanogen. Fractions 31 to 45 with R_f 0,95 on TLC (isopropanol--H_2O--acetic acid, 20:4:1; baked at 200°C after spraying with chromic acid) were combined to yield 6,8 mg of a pale yellow solid.

Results

The cyanogenic glucoside of *Buchenroedera* was identified by mass spectrometry as prunasin (**1** in Figure 1). The mass spectrum of the material obtained after enzymatic hydrolysis clearly showed the presence of benzaldehyde (**3**), with an M^+ of m/z 106 and strong peaks at m/z 105 and 77. The absence of a peak at m/z 133 indicated that no cyanohydrin (**2**) was formed. Further proof of the identity of prunasin was found in the mass spectrum of the material obtained after acid hydrolysis. It showed, as would be expected for the cyanohydrin (D-mandelonitrile), an M^+ of m/z 133 and major peaks at m/z 106, 105 and 77. An attempt to study the purified glucoside directly by electron impact resulted in two large peaks at m/z 117 and 116, indicating the presence of fragment **4** (an immediate loss of oxygen and glucose). In view of the specificity of β-glucosidase and the positive reaction to the glucose oxidase test (Kusai *et al*. 1960), there can be little doubt about glucose being the sugar moiety of the cyanogen.

Discussion

The presence of prunasin in *Buchenroedera* confirms that at least one specimen in this genus and one in *Lotononis* both follow the phenylalanine pathway for the production of cyanogenic glucosides (Fikenscher & Hegnauer 1981) rather than the more usual valine and isoleucine pathways, which lead to the production of linamarin and lotaustralin respectively. Since we have shown that cyanogenesis in the two genera is likely to be homologous, this character provides further evidence of a close affinity between *Lotononis* and *Buchenroedera*.

A summary of similarities and differences between *Buchenroedera*, some sections of *Lotononis*, and other genera of the tribe Crotalarieae is given in Table 1. The distribution of character states shows that the predictivity of the present generic and infrageneric classification can be improved by reclassifying *Buchenroedera* as a group within *Lotononis*. This was also suggested by Polhill (1976, 1981), who could find no diagnostic character for *Buchenroedera* other that the shape of the pods. Cyanogenesis can now be added to the growing body of evidence suggesting a reduction in the status of *Buchenroedera*.

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Table 1. Summary of similarities and differences between some sections* of *Lotononis*, *Buchenroedera*, and other genera of the tribe Crotalarieae.

Characters	*Lotononis* section *Aulacinthus*	*Lotononis* section *Polylobium*	*Lotononis* section *Krebsia*	*Buchenroedera*	other genera of the Crotalarieae
Habit	woody and/or suffrutescent	suffrutescent	woody and/or suffrutescent	woody and/or suffrutescent	woody and/or suffrutescent, some annual
Stipules	solitary or absent	paired, rarely absent	paired, rarely solitary or absent	paired or absent	paired or absent, rarely solitary
Bracteoles	absent or vestigial	absent	absent or vestigial	absent	present
Flower colour	yellow, rarely pink	yellow	usually blue, rarely yellow or pinkish	usually blue, rarely yellow, white or pink	never blue, usually yellow
Standard petal	± as long as the keel	longer than the keel	± as long as the keel	longer than the keel	various
Keel petals	glabrous	glabrous	glabrous or pubescent	glabrous or pubescent	glabrous or pubescent

(TABLE 1 CONTINUED)

Fruit shape	linear to ovate; turgid	linear to ovate; turgid	linear, rarely ovate; only slightly turgid	ovate; turgid	various shapes, often turgid
Upper suture of fruit	verrucose	verrucose	smooth	smooth	smooth
Seed surface	tuberculate	tuberculate	smooth	smooth	smooth, rugose in some species of *Crotalaria*
Chromosome number (2n)	28	28	28, 42, 56, 84	28	never 28 except in *Dichilus*
Major alkaloid type	pyrrolizidine	pyrrolizidine	pyrrolizidine	pyrrolizidine	quinolizidine; pyrrolizidine only in *Crotalaria*
Cyanogenesis	cyanogenic	cyanogenic	mostly cyanogenic	often cyanogenic	acyanogenic

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*The sections *Aulacinthus* (E. Mey.) Benth. and *Krebsia* Eckl. & Zeyh. are used here in the same sense as in Dümmer (1913), except for the exclusion of *L. hirsuta* Schinz and allies from *Krebsia*. *Polylobium* (Eckl. & Zeyh.) Benth. refers here only to *L. involucrata* (E. Mey.) Benth. and related species.

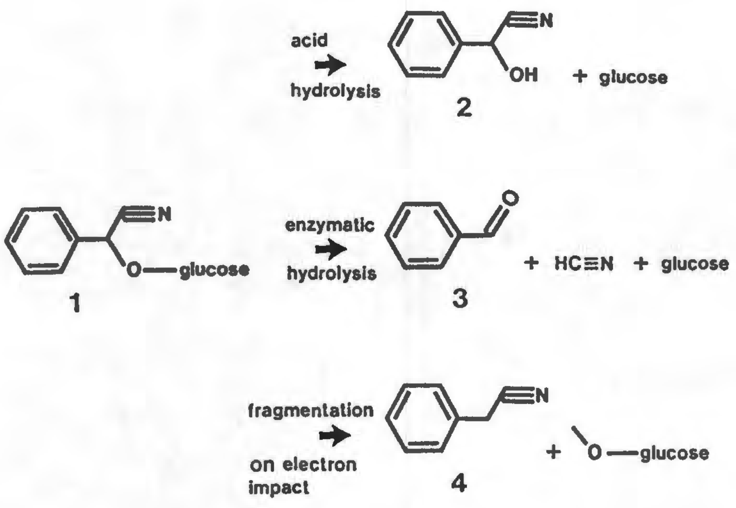

Figure 1. The degradation products of prunasin (1). The cyanohydrin (2), benzaldehyde (3) and the fragment (4) were identified by mass spectrometry in extracts from *Buchenroedera multiflora*.

APPENDIX 14

CHROMOSOME NUMBERS IN *LOTONONIS* AND *BUCHENROEDERA* (FABACEAE—CROTALARIEAE)[1]

Ben-Erik Van Wyk
and Anne Lise Schutte[2]

ABSTRACT

Original chromosome counts for Buchenroedera *(new generic report) and* Lotononis *(44 new specific reports) are presented. The most common somatic number in* Lotononis, *18, was found in 29 species. Three species of* Buchenroedera *and nine species of* Lotononis *have* $2n = 28$. *In* Lotononis *section* Krebsia $2n = 28, 42, 56,$ *and 84 were found in a closely related species group. This is the first report of a polyploid series in the Crotalarieae and includes the highest numbers recorded in the tribe. The chromosome numbers indicate anomalies in the existing sectional classification of* Lotononis *and may provide evidence for a more natural generic and infrageneric classification.*

The genera *Lotononis* (DC.) Eckl. & Zeyh. and *Buchenroedera* Eckl. & Zeyh. are poorly known cytologically, with only six species of the former and none of the latter having been investigated previously. As part of an ongoing taxonomic study of these genera, chromosome counts were made for 47 species, representing almost the full range of variation in *Lotononis* (ca. 120 species centered in southern Africa, with a few extending into Asia) and *Buchenroedera* (ca. 16 species restricted to the eastern parts of southern Africa). The results are presented here, and their systematic significance in terms of an improved generic and infrageneric classification is discussed.

MATERIALS AND METHODS

Mitotic counts were made from root tips of germinated seeds. Standard methods of pretreatment in hydroxyquinoline (0.02% mass/volume) and staining in lacto-propionic orcein were used. The duration of hydrolysis (1–8 minutes) and the concentration of HCl (0.2–0.5 N) proved to be important. The chromosomes are small (ca. 1–3 μm long). Voucher specimens (listed in Table 1) are housed at the Rand Afrikaans University Herbarium (JRAU). A list of the species studied and voucher specimen details are given in the Appendix. Our efforts to collect seeds have been rewarded by numerous rediscoveries of rare species and have provided a fairly representative sample of the two genera.

RESULTS AND DISCUSSION

The results listed in Table 1 are arranged according to Duemmer's (1913) sectional classification. Where morphologically heterogenous sections of *Lotononis* have been subdivided into two or more groups, or where species have been moved to more appropriate positions, the reasons for doing so are given in the footnotes. The arrangement of species in Table 1 is aimed at facilitating the discussion that follows and is not intended as a formal infrageneric classification, but it nevertheless reflects major discontinuities and shows basic affinities.

Several morphological characters provide links among the species of *Lotononis* with $2n = 28$ and among those with $2n = 18$. The latter are presently placed in various sections, indicating that Duemmer's infrageneric treatment is artificial; that the same chromosome number has evolved independently in several different groups seems unlikely. Section *Krebsia*, for example, presently comprises three distinct groups, two of which have obvious

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[1] *We thank Dr. Johan Spies (Botanical Research Institute, Pretoria) and Dr. Gerrit Davidse (Missouri Botanical Garden) for useful comments. Taxonomic research on* Lotononis *and* Buchenroedera *by the senior author is registered as a Ph.D. project at the University of Cape Town.*

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ANN. MISSOURI BOT. GARD. 75: 1603–1607. 1988.

TABLE 1. *Chromosome numbers in* Lotononis *and* Buchenroedera. *Species are arranged in sections following the treatment of Duemmer (1913), with some minor modifications that are explained in the footnotes. All known counts are included—those taken from the literature are preceded by an asterisk (*).*

Genera, Groups, and Species	Chromosome Number ($2n$)	Voucher or Reference
Buchenroedera Eckl. & Zeyh.		
B. lotononoides Scott Elliot	28	*BVW 1966*
B. meyeri Presl	28	*BVW 1765*
B. tenuifolia Eckl. & Zeyh. var. *tenuifolia*	28	*BVW 1675*
Lotononis (DC) Eckl. & Zeyh.		
Lotononis section *Aulacinthus* (E. Mey.) Benth.		
L. leucoclada (Schltr.) Duemmer	28	*BVW 2430*
L. gracilis (E. Mey.) Benth.	28	*BVW 2250*
Lotononis section *Krebsia* (Eckl. & Zeyh.) Benth.		
Part 1: *Krebsia* sensu stricto		
L. biflora (H. Bol.) Duemmer	± 84	*BVW 1952*
L. carnosa (Eckl. & Zeyh.) Benth.	84	*BVW 1663*
L. caerulescens (E. Mey.) B-E. van Wyk[1]	56	*BVW 2483*
L. cytisoides (E. Mey.) Benth.	28	*BVW 1721*
L. cytisoides (E. Mey.) Benth. aff.	56	*BVW 1761*
L. divaricata (Eckl. & Zeyh.) Benth.	56	*BVW 2484*
L. divaricata (Eckl. & Zeyh.) Benth. aff.	42	*BVW 1666*
L. trisegmentata Phill. var. *robusta* Phill. forma *robusta*	28	*BVW 1917*
L. trisegmentata Phill. var. *robusta* Phill. forma *sericea* Phill.	28	*BVW 1956, 1958*
Part 2: *L. digitata* group[2]		
L. digitata Harv.	18	*BVW 2341*
L. benthamiana Duemmer	18	*BVW 2538*
"L. magnifica" B-E. van Wyk ined.	18	*BVW 2549*
Part 3: *L. transvaalensis* group[3]		
L. transvaalensis Duemmer	18	*BVW 1860*
L. procumbens H. Bol.[4]	18	*BVW 2504*
Lotononis section *Polylobium* (Eckl. & Zeyh.) Benth.		
Part 1: *Polylobium* sensu stricto		
L. exstipulata L. Bol.	28	*BVW 2280*
**L. involucrata* (Berg.) Benth.	28	(Dahlgren, 1967)
**L. serpens* (E. Mey.) Dahlgr.[5]	18	(Goldblatt, 1981b)
Part 2: *L. angolensis* group[6]		
**L. angolensis* Bak.	18	(Byth, 1964)
**L. listii* Polhill	18	(Byth, 1964)
**L. bainesii* Bak.	36	(Byth, 1964)
Lotononis section *Telina* (E. Mey.) Benth.		
L. acuminata Eckl. & Zeyh.	28	*BVW 2581*
"L. repens" B-E. van Wyk ined.	28	*BVW 2573*
L. pungens Eckl. & Zeyh.[7]	28	*BVW 1725*
L. versicolor (E. Mey.) Benth.[7]	28	*BVW 1386*
Lotononis section *Oxydium* Benth.[8]		
L. rostrata Benth.[9]	18	*BVW 2324*
L. rostrata aff.	18	*BVW 2429*
L. acutiflora Benth.	18	*BVW 2544*
L. oxyptera (E. Mey.) Benth.	18	*BVW 2318*
L. lenticula (E. Mey.) Benth.	18	*BVW 2018*
L. rabenaviana Dinter & Harms	18	*BVW 2057*

TABLE 1. *Continued.*

Genera, Groups, and Species	Chromosome Number (2*n*)	Voucher or Reference
Lotononis section *Lipozygis* (E. Mey.) Benth.		
Part 1: *L. polycephala* group[10]		
L. polycephala (E. Mey.) Benth.	18	*BVW 2408*
L. bolusii Duemmer	18	*BVW 2443*
"L. longicephala" B-E. van Wyk ined.	18	*BVW 2241*
Part 2: *L. eriantha* group[11]		
L. eriantha Benth.	18	*ALS 383*
L. foliosa H. Bol.	18	*BVW 2607*
L. lanceolata (E. Mey.) Benth.	18	*BVW 1884*
Lotononis section *Leobordea* (Del.) Benth.		
**L. platycarpa* (Viv.) Pic.-Serm.	18	(Goldblatt, 1981b)
Lotononis section *Leptis* (Eckl. & Zeyh.) Benth.		
Part 1: *L. laxa* group[12]		
L. laxa Eckl. & Zeyh.	18	*BVW 2015*
L. woodii H. Bol.	18	*BVW 2608*
L. macrosepala Conrath	18	*BVW 2622*
Part 2: *L. brachyloba* group[13]		
L. brachyloba (E. Mey.) Benth.	18	*BVW 2244*
"L. fruticoides" B-E. van Wyk ined.	18	*BVW 2020*
L. leptoloba H. Bol.	18	*ALS 276*
L. maximilianii Schltr. (cleistogamous)	18	*ALS 271*
L. maximilianii (chasmogamous)	18	*ALS 282*
Part 3: *L. calycina* group[14]		
L. calycina (E. Mey.) Benth.	18	*BVW 2621*
L. sericoflora Duemmer	18	*BVW 1899*
L. humifusa Benth.	18	*BVW 1700*
L. mucronata Conrath aff.	18	*BVW 2619*
"L. curvicarpa" B-E. van Wyk ined.	18	*BVW 2725*

[1] Better known as *Lebeckia microphylla* E. Mey.
[2] Species added to section *Krebsia* by Harvey (1862) and Duemmer (1913).
[3] Species added to *Krebsia* by Duemmer (1913).
[4] Position in section *Polylobium* was based on a superficial characterization.
[5] An anomalous species. Dahlgren (1964) suggested similarities with *L. involucrata.*
[6] Species added to section *Polylobium* by Baker (1871) and related species.
[7] Superficially similar to *L. laxa* and previously associated with the section *Leptis.*
[8] This section was referred to the genus *Crotalaria* by Duemmer (1913).
[9] Better known as *L. micrantha* (E. Mey.) Benth.
[10] A distinct group of *Lipozygis* with indehiscent, wind-dispersed fruit.
[11] A distinct group of pyrophytes from grassland areas of the eastern parts of southern Africa.
[12] Perennial herbs with acute keel petals as in section *Oxydium.*
[13] Annuals with acute keel petals as in section *Oxydium.*
[14] Annuals and perennials with obtuse keel petals as in the *L. eriantha* group of section *Lipozygis.*

affinities elsewhere in the genus. The woody habit of *L. digitata* and *L. transvaalensis* was used to place them in *Krebsia*, but both are morphologically very similar to various species of section *Leptis*. Another example is section *Polylobium*; *Lotononis umbellata* and its allies are closely related to section *Aulacinthus* and perhaps not distinct from it at the sectional level. The *L. angolensis* group is quite different from other species of section *Polylobium* and its position in this section is unsatisfactorily artificial.

Two separate phylogenetic lines with base numbers of $x = 9$ and $x = 7$ are suggested, and further research will show if other evidence supports such a dichotomy in the genus. Not a single count of $2n = 16$ or 32 has been made, so that a base number of 8, which is common in some of the other genera, so far appears to be totally absent in *Lotononis*.

At the generic level, the data also give some indications of affinity. *Buchenroedera* is so closely related to *Lotononis* (especially to section *Krebsia*) that its generic status has been questioned (Polhill, 1976, 1981). The shared chromosome number of $2n = 28$ (and presumably a base number of 7) agrees with chemical evidence (Van Wyk & Verdoorn, 1988) that *Buchenroedera* is perhaps best considered a section of *Lotononis*.

The remarkable similarities between species of *Crotalaria* and *Lotononis* have caused confusion in past taxonomic treatments. For example, most species of *Lotononis* section *Oxydium* were transferred to *Crotalaria* by Duemmer (1913). The presence of macrocyclic pyrrolizidine alkaloids in both genera (Van Wyk & Verdoorn, in prep.) indeed indicates that *Lotononis* is more closely related to *Crotalaria* than to other genera of the tribe, all of which seem to contain only quinolizidine alkaloids. *Crotalaria*, however, have $2n = 16$, 32, or rarely 14 (Goldblatt, 1981a), while those species of *Lotononis* that closely resemble *Crotalaria* (section *Oxydium* and some groups of *Leptis*) all have $2n = 18$. The morphological distinction between *Lotononis* and *Crotalaria* (Polhill, 1968) is therefore strongly supported by the data at hand.

Some of the woody species of *Lotononis* (sections *Aulacinthus* and *Krebsia*) are very similar to species of *Lebeckia*. *Lotononis caerulescens* (E. Mey.) B-E. van Wyk, for example, has until recently been known as *Lebeckia microphylla* E. Mey., but morphological and chemical evidence (Van Wyk, 1988; Van Wyk & Verdoorn, 1988) clearly showed it to be misplaced in *Lebeckia*. The sections *Aulacinthus* and *Krebsia* sensu stricto have $2n = 28$, 42, 56, and 84, while four counts of $2n = 18$ are known for *Lebeckia* (Dahlgren, 1967). Here again, the cytological data agree with the morphological distinction between *Lotononis* and *Lebeckia*. *Lotononis angolensis* and related species (section *Polylobium*) are chemically similar to *Lebeckia* and also have the same chromosome number. Morphological characters such as the zygomorphic calyx and dimorphic stipules, however, are typical of *Lotononis*.

Not a single count of $2n = 14$ is known for *Lotononis*; so it seems to be cytologically different from the genus *Pearsonia*. The only available count for the latter genus was by Frahm-Leliveld (1969), who reported $2n = 14$ for *P. flava* (Bak. f.) Polhill. The species of *Pearsonia* are similar to *Lotononis* except for their highly modified flowers (Polhill, 1973), and the shared chromosome base number of $x = 7$ may indeed indicate a common ancestry.

From a phylogenetic point of view, the different base numbers in *Lotononis* suggest interesting questions about generic relationships in the Crotalarieae. The base number of the tribe is almost certainly $x = 9$ (Goldblatt, 1981a), and $2n = 18$ in some species of *Lotononis* is presumably the ancestral condition. The only way to achieve $2n = 28$ (if *Lotononis* is monophyletic) is to postulate descending aneuploidy from $n = 9$ to 8 and 7 and subsequent polyploidy. Since $2n = 16$ and 14 appear to be totally absent in *Lotononis*, it may be argued that *Crotalaria* and *Pearsonia* form part of the lineage that gave rise to the group of species with $2n = 28$, 42, 56, and 84. If *Lotononis* proves to be polyphyletic, this possibility can be seriously considered, but the generic characters of the current concept of *Lotononis* are present in at least some species of each major group. Although there are marked phenetic similarities linking all the major groups, *Lotononis* as a whole is not monothetic. It is defined by combinations of apomorphic tendencies, such as single stipules, suffrutescent or herbaceous habit, absence of bracteoles, fusion of the lateral calyx lobes, verrucose upper suture of the fruit, tuberculate testa, elongated funicles, flower dimorphism associated with cleistogamy, ability to produce HCN, and presence of macrocyclic pyrrolizidine alkaloids. There is not a single apomorphy known to us that would unambiguously support monophyly. A possible solution would be to separate the lineage with $2n = 28$ from the one with $2n = 18$ and to split the latter into several smaller groups. Despite conflicting character information, there are some indications from the morphology that the geographically widespread and generally herbaceous $2n = 18$ lineage is more primitive than the predominantly woody and essentially southern African $2n = 28$ lineage.

In a tribal context, the occurrence of polyploidy in *Lotononis* (section *Krebsia*) is of some interest. Polyploidy and high chromosome numbers are typical of the Genisteae but have never been reported from any genus of the Crotalarieae (Goldblatt, 1981a). It is also noteworthy that polyploidy should occur in an essentially woody group (previously considered to be one of the basal groups of *Lotononis*) and not in the supposedly more derived herbaceous groups. Unlike the situation in the other large genera of the Crotalarieae (*Aspalathus* and to some extent *Crotalaria*), there is no direct evidence of aneuploidy, although it must have played a significant role in the phylogeny of *Lotononis*.

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APPENDIX

List of species, collection data, and voucher specimen details of the material used for chromosome counts. Voucher specimen numbers refer to our own collections (abbreviated as *BVW* and *ALS*) and are all housed in the Rand Afrikaans University Herbarium (JRAU). Authorities for names are given in Table 1.

Buchenroedera lotononoides: Loteni, Natal, *BVW 1966*. ***B. meyeri***: Mhlahlane, Transkei, *BVW 1765*. ***B. tenuifolia*** var. ***tenuifolia***: Queenstown, E Cape, *BVW 1675*.

Lotononis acuminata: Humansdorp district, S Cape, *BVW 2581*. ***L. acutiflora***: Khamiesberg, Cape, *BVW 2544*. ***L. benthamiana***: Springbok district, Cape, *BVW 2538*. ***L. biflora***: Loteni, Natal, *BVW 1952*. ***L. bolusii***: Piquetberg, Cape, *BVW 2443*. ***L. brachyloba***: Ceres, Cape, *BVW 2244*. ***L. caerulescens***: Cradock, E Cape, *BVW 2483*. ***L. calycina***: Bethal, Transvaal, *BVW 2621*. ***L. carnosa***: Queenstown, E Cape, *BVW 1663*. "***L. curvicarpa***" (ined.): Devon, Transvaal, *BVW 2725*. ***L. cytisoides***: Winterberg, E Cape, *BVW 1721*. ***L. cytisoides*** aff.: Mhlahlane, Transkei, *BVW 1761*. ***L. digitata***: Garies, Cape, *BVW 2341*. ***L. divaricata***: Swagershoek Pass, E Cape, *BVW 2484*. ***L. divaricata*** aff.: Queenstown, E Cape, *BVW 1666*. ***L. eriantha***: Roodepoort, Transvaal, *ALS 383*. ***L. exstipulata***: Ceres district, Cape, *BVW 2280*. ***L. foliosa***: Johannesburg, Transvaal, *BVW 2607*. "***L. fruticoides***" (ined.): Graaff Reinet district, Cape, *BVW 2020*. ***L. gracilis***: Ceres, Cape, *BVW 2250*. ***L. humifusa***: Grahamstown district, E Cape, *BVW 1700*. ***L. lanceolata***: Dullstroom, Transvaal, *BVW 1884*. ***L. laxa***: Colesberg, Cape, *BVW 2015*. ***L. lenticula***: Colesberg, Cape, *BVW 2018*. ***L. leptoloba***: Nieuwoudtville, Cape, *ALS 276*. **L. leucoclada**: Clanwilliam, Cape, *BVW 2430*. "***L. longicephala***" (ined.): Touw's River, Cape, *BVW 2241*. ***L. macrosepala***: Bethal district, Transvaal, *BVW 2622*. "***L. magnifica***" (ined.): Khamiesberg, Cape, *BVW 2549*. ***L. maximiliani***: Nieuwoudtville, Cape, *ALS 271* (cleistogamous form), *ALS 282* (chasmogamous form). ***L. mucronata*** aff.: Ermelo district, Transvaal, *BVW 2619*. ***L. oxyptera***: Citrusdal, Cape, *BVW 2318*. ***L. polycephala***: Khamiesberg, Cape, *BVW 2408*. ***L. procumbens***: Volksrust district, Natal, *BVW 2504*. ***L. pungens***: Tarkastad district, E Cape, *BVW 1725*. ***L. rabenaviana***: Beaufort West district, Cape, *BVW 2057*. "***L. repens***" (ined.): Outeniqua Pass, S Cape, *BVW 2573*. ***L. rostrata***: Citrusdal, Cape, *BVW 2324*. ***L. rostrata*** aff.: Klawer, Cape, *BVW 2429*. ***L. sericoflora***: Harrismith, Orange Free State, *BVW 1899*. ***L. transvaalensis***: Nelspruit, E Transvaal, *BVW 1860*. ***L. trisegmentata*** var. ***robusta*** forma ***robusta***: Clarens, Orange Free State, *BVW 1917*. ***L. trisegmentata*** var. ***robusta*** forma ***sericea***: Loteni, Natal, *BVW 1956*; Sani Pass, Natal, *BVW 1958*. ***L. versicolor***: Beaufort West district, Cape, *BVW 1386*. ***L. woodii***: Wakkerstroom district, Natal, *BVW 2608*.

APPENDIX 15

S. Afr. J. Bot., 1987, 53(5): 395 – 397

Taxonomic notes on *Argyrolobium variopile* (Fabaceae), and the status of *Lotononis magnistipulata*

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The nomenclature and taxonomy of *Argyrolobium variopile* N.E. Br. has been studied. Morphologically the species resembles species of *Dichilus* DC. and *Lotononis* (DC.) Eckl. & Zeyh., but its taxonomic position in *Argyrolobium* is confirmed. It is also shown that *Lotononis magnistipulata* Duemmer is a synonym of this species.

Die nomenklatuur en taksonomie van *Argyrolobium variopile* N.E. Br. is bestudeer. Morfologies toon dit ooreenkoms met soorte van *Dichilus* DC. en *Lotononis* (DC.) Eckl. & Zeyh. maar die taksonomiese posisie in *Argyrolobium* word bevestig. Dit word ook bewys dat *Lotononis magnistipulata* Duemmer 'n sinoniem vir hierdie soort is.

Keywords: *Argyrolobium*, chromosome number, Fabaceae, *Lotononis*, taxonomy

Introduction

Argyrolobium variopile N.E. Br., a poorly defined perennial herb from the eastern parts of southern Africa, is often confused with species of *Dichilus* DC. and *Lotononis* (DC.) Eckl. & Zeyh. Duemmer (1913) apparently overlooked the characteristic trifid lower lip of the calyx and described it as a new species of *Lotononis*, viz. *L. magnistipulata*. The variability of the species no doubt added to the confusion. In this paper it is shown that *Argyrolobium variopile* is the correct name for *Lotononis magnistipulata* and some specimens found under various other names in South African herbaria.

Description

Argyrolobium variopile *N.E. Br.* in Kew Bulletin 1906: 18 (1906); Types: Natal, Charlestown, *Wood 5693* (BOL!, K, NH! PRE!), *Wood 6355* (K, NH!).

Lotononis magnistipulata Duemmer in Transactions of the Royal Society of South Africa 3(2): 299 (1913), synon. nov. Type: Natal, Faku's Territory [probably Pondoland, Transkei], *Sutherland s.n.* (K, holo.!).

Procumbent or erect perennial herb, up to 0,4 m tall. *Stems* often sparsely leafy, with conspicuous stipular scars on older parts; vestiture very variable, pubescent to sparsely pilose. *Leaves* (Figure 1H) densely to sparsely pubescent or pilose, rarely subglabrate. *Stipules* (Figure 1H) lanceolate-cordate, midrib excentric, variable in size, up to 12 mm long and 7 mm wide, free at the base, apex acute to acuminate, base very broad, cordate. *Petiole* slender, about as long as the terminal leaflet. *Leaflets* elliptic-obovate, (5 –)8 – 12(– 20) mm long, (3 –)4 – 6(– 12) mm wide; apex obtuse to rounded, minutely mucronate; base broadly cuneate; abaxially appressed-pubescent to pilose. *Inflorescence* a few-flowered subterminal raceme, often pseudo-umbellate; peduncle very variable in length, (5 –)15 – 30(– 65) mm long; bracts variable in size and shape, usually narrowly linear, but sometimes lanceolate, up to 7 mm long and 4 mm wide; bracteoles small, up to 2 mm long and 0,5 mm wide; pedicels short or almost absent, up to 2 mm long. *Flowers* (1 –)2 – 3(– 15) per inflorescence, bright yellow fading to orange-brown. *Calyx* (Figure 1J) deeply 2-lipped, 5 – 8 mm long, with narrow acuminate lobes; upper lip bifid with lobes almost free, lower lip trifid with lobes fused for about half their length. *Standard* (Figure 1A) broadly cordate-orbicular, 6 – 9 mm long; limb 5 – 8 mm long and wide, abaxially pubescent, slightly reflexed at anthesis; claw short, 1 – 2,5 mm long. *Wing petals* (Figure 1C) nearly as long as the keel, oblong; sculpturing present, upper basal and upper left central. *Keel* (Figure 1B) slightly shorter than the standard, semi-circular, only slightly pointed, pocketed. *Androecium* (Figure 1D) with staminal tube split above, vexillary stamen often nearly free; anthers dimorphic. *Pistil* (Figure 1E & F) oblong-linear, subsessile, densely hirsute; stigma oblique, with elongated papillae. *Fruit* variable in size and shape, oblong to linear, 6 – 25 mm long, 3 – 4 mm wide,

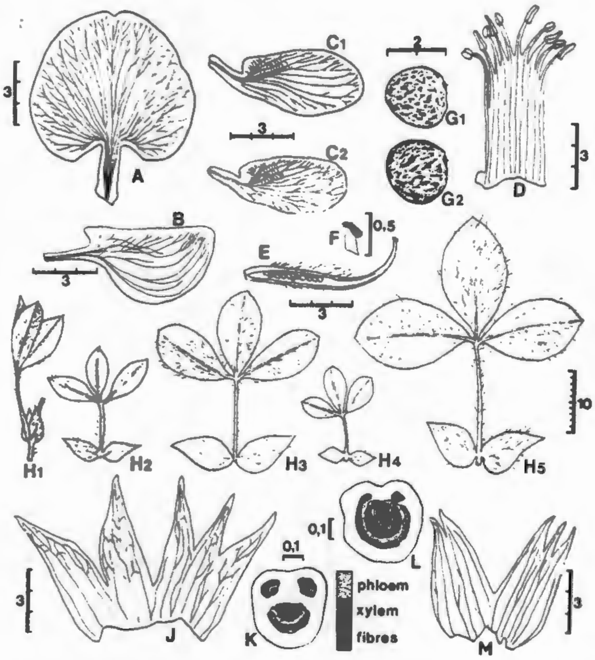

Figure 1 *Argyrolobium variopile*. A, standard; B, keel; C1, C2, wing petals; D, androecium; E, pistil; F, stigma; G1, G2, seeds; H1, leaf showing natural position of the stipules; H2 – H5, leaves and stipules opened out (abaxial surface) showing variation in size and vestiture; J, calyx opened out with upper lobes to the left, vestiture not shown; K, transverse section through middle of petiole showing vascular bundles. *Dichilus pilosus*. L, transverse section through middle of petiole showing group of fibres above abaxial vascular bundle; M, calyx opened out with upper lobes to the left, vestiture not shown. A, B, C1, D, E, F & J from *Jacot Guillarmod et al. 74*; C2, H1 & K from *Van Wyk 1781*; G1 & G2 from *Schutte 200*; H2 from *Devenish 587*; H3 from *Thode 3098*, H4 from *Van Wyk 1566*; H5 from *Van Wyk 1885*; L & M from *Schutte 94* (JRAU). Scale in mm.

pilose to glabrescent at maturity, not constricted between the seeds. *Seed* (Figure 1G) semi-orbicular in side view, laterally flattened, 1,4 – 2 mm long, 1,8 – 2,3 mm wide, pale brown mottled dark brown; hilar area conspicuously swollen, hilar valve hidden within; aril inconspicuous, with a small tongue-like remnant of the funicle to one side; surface reticulate. Chromosome number: 2n = 30! (Voucher specimen: *Schutte 201*, Rand Afrikaans University Herbarium). Flowering occurs from November to March.

The species is also referred to by Wood (1909), Phillips (1917), Bews (1921), Ross (1972) and Gibbs Russell *et al.* (1984). In the latter, it is listed under both *Argyrolobium* and *Lotononis*.

Distribution and Geographical variation

Argyrolobium variopile appears to be endemic to southern Africa where it has been recorded from summer-rainfall grassland areas. Although considered a perennial, observations of a population near Irene, Pretoria indicate that it does not have the ability to resprout after fire. The species often grows in rocky areas where it would be protected from fire. It is confined to high altitudes towards the northern parts of its range, but extends to coastal areas in the eastern Cape (Figure 2). This interesting distribution is shared by at least one other related legume, namely *Dichilus strictus* E. Mey. (Schutte pers. comm.)

Despite considerable variation in the size and vestiture of the leaflets, stipules and fruit, no significant discontinuities could be found to justify any infraspecific taxa. The habit is also very variable. At high altitudes (Sani Pass, for example) the plant has a prostrate habit and is no more than 0,1 m tall. In rocky areas along the eastern Transvaal escarpment, it grows to a rounded shrub of about 0,4 m tall. On the Witwatersrand it reaches the same height, but the habit is much sparser. When growing in shade, it is even more sparse and the leaf size increases dramatically. Some specimens (including the types cited above) dried to a dark brown or black colour, while others remained bright green. This character does not appear to be geographically correlated. I have studied most of the different forms *in situ* and consider it best to include them all under *A. variopile* until *Argyrolobium* as a whole is revised.

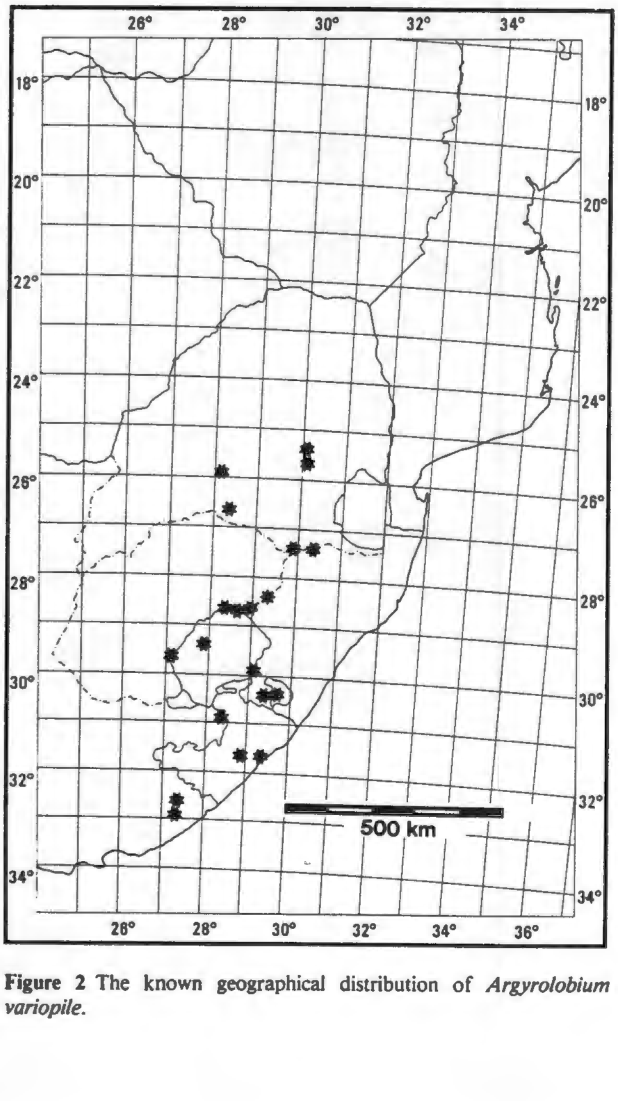

Figure 2 The known geographical distribution of *Argyrolobium variopile.*

Systematic position

Details of the calyx, corolla and stipules leave little doubt that *A. variopile* (*Lotononis magnistipulata*) is a species of *Argyrolobium*. The chromosome base number of 15 conforms to previous counts for this genus (Goldblatt 1981) and differs from *Dichilus*, where 2n = 28 (Goldblatt 1981; Schutte pers. comm.).

Argyrolobium variopile is remarkably similar to *Dichilus pilosus* Conr. ex Schinz, but differs in the much larger stipules, the pseudo-umbellate inflorescences and the lesser degree of fusion of the upper calyx lobes (Figure 1J & M). The anatomy of the petiole (Figure 1K & L) is also distinctly different. A group of fibres is present along the adaxial side of the main vascular bundle in all species of *Dichilus* (Schutte pers. comm.), but absent in *A. variopile*.

Argyrolobium variopile belongs to the section *Chasmone* (*Brevipedes* group) of Harvey (1862). It resembles *A. pilosum* Harv., but the latter is more robust and much larger in all parts. The recently described *A. summomontanum* Hilliard & Burtt is also similar, but differs in the dense reddish-brown vestiture and the much larger flowers and fruit. *A. variopile* contains significant quantities of anagyrine as the major alkaloid and is in this respect almost identical to the more distantly related *A. crassifolium* Eckl. & Zeyh. (Van Wyk *et al.* 1987). It does not match any of the species from tropical Africa enumerated by Polhill (1968). The taxonomy of *Argyrolobium* in southern Africa is in such a state of confusion (a fact also commented on by Polhill 1968) that speculation on relationships will serve no purpose at this stage. Suffice it to state that *Lotononis magnistipulata* is neither a *Lotononis* nor a *Dichilus*. It is clearly conspecific with *Argyrolobium variopile* N.E. Br. and should therefore be relegated to the synonymy of this species.

Specimens examined

(JRAU refers to the Rand Afrikaans University Herbarium. This acronym will be listed in the eighth edition of Index Herbariorum).

— **2528** (Pretoria): Koppie east of Irene (– CC), *Schutte 199, 200, 201* (JRAU); *Van Wyk 1781* (JRAU).

— **2530** (Lydenburg): 1 km from Dullstroom towards Lydenburg (– AC), *Van Wyk 1885* (JRAU); Belfast (– CA), *Leendertz 9179* (PRE) (the last not typical).

—**2628** (Johannesburg): Farm 'Houtpoort' 309, 53,6 km SE of Johannesburg, 9,6 km SE of Heidelberg (– CB), *Mogg 18541* (JRAU).

— **2729** (Volksrust): Hill-side near Charlestown (– BD), *Wood 5693* (BOL, NH, PRE); *Wood 6355* (NH).

— **2730** (Vryheid): Opposite the Zaaihoek Dam, between Volksrust and Groenvlei (– AC), *Van Wyk 2503* (JRAU); Wakkerstroom distr., Oshoek (–AD), *Devenish 587* (PRE); Altemooi (–AD), *Thode 3098 & 3124* (STE).

— **2828** (Bethlehem): Clarens commonage (–CB), *Ferreira 229* (PRE); Generaalskop, Golden Gate National Park (–DA), *Roberts 3100* (PRE); Witzie's Hoek (–DB), *Junod s.n. sub PRE 17364* (PRE).

— **2829** (Harrismith): 16 km SE of Harrismith (–AC), *Codd 10519* (PRE).

— **2927** (Maseru): 22 km from Wepener towards Hobhouse (–CA), *Van Wyk 1566* (JRAU); Bushman's Pass (–BD), *Schmitz 8483* (PRE).

— **2929** (Underberg): Sehlabathebe (–CC), *Jacot Guillarmod, Getliffe & Mzamane 74* (PRE).

— **3028** (Matatiele): Tsitsa footpath, E. slopes of the Drakensberg (–CD), *Galpin 6606* (BOL).

— **3029** (Kokstad): Kokstad, Franklin road (–AD), *Hilliard & Burtt 7222* (PRE); 25,6 km NE of Kokstad (–BC), *Acocks 22053* (PRE); Zuurbergen (–BC), *Schlechter 6571* (GRA).

— **3128** (Umtata): Near Umtata (–BD), *Flanagan 2857* (BOL, PRE).

— **3129** (Port St. Johns): Near Insinuka (–CB), *Bolus s.n. sub STEU 24864* (STE).

— **3227** (Stutterheim): Dohne Hill (–CB), *Sim 182* (PRE); King William's Town (–CD), *Sim 182* (GRA).

Without precise locality: Natal, Faku's Territory [perhaps Pondoland, Transkei], *Sutherland s.n.* (K).

Acknowledgements

I am grateful to the curators of BOL, GRA, K, NH, PRE and STE, who have kindly allowed me to study their material. Ms A.L. Schutte is thanked for technical assistance. Thanks are also due to anonymous referees for constructive comments. This study was partly financed by the Rand Afrikaans University.

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APPENDIX 16

S. Afr. J. Bot., 1988, 54(2): 175–181

Lotononis caerulescens (Fabaceae — Crotalarieae): A new combination for *Lebeckia microphylla*, with notes on the distinction between *Buchenroedera*, *Lebeckia* and *Lotononis*

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The generic position of *Lebeckia microphylla* E. Mey. has been subject to differing taxonomic interpretations. Previously the species has also been described as *Krebsia argentea* Eckl. & Zeyh. [*Krebsia* Eckl. & Zeyh. is now a section of *Lotononis* (DC.) Eckl. & Zeyh.] and later as *Buchenroedera glabriflora* N.E. Br. and *B. uniflora* Dümmer. Based on new evidence, this species is shown to be better placed in *Lotononis* section *Krebsia*. The new combination *Lotononis caerulescens* (E. Mey.) B-E. van Wyk is made.

Die generiese posisie van *Lebeckia microphylla* E. Mey. is onderhewig aan verskillende taksonomiese interpretasies. Voorheen is die spesie ook al beskryf as *Krebsia argentea* Eckl. & Zeyh. [*Krebsia* is tans 'n seksie van *Lotononis* (DC.) Eckl. & Zeyh.] en later as *Buchenroedera glabriflora* N.E. Br. en *B. uniflora* Dümmer. Aan die hand van nuwe getuienis word aangetoon dat die spesie meer tuis hoort in *Lotononis* seksie *Krebsia*. Die nuwe kombinasie *Lotononis caerulescens* (E. Mey.) B-E. van Wyk word gemaak.

Keywords: *Buchenroedera*, generic limits, *Lebeckia*, *Lotononis*, new combination

Introduction

Lebeckia microphylla E. Mey. is a common papilionoid legume of dry mountain slopes in the eastern Cape. It also seems to extend into Natal (see below).

Ecklon & Zeyher (1836) first validly named it *Krebsia argentea*, but Meyer (1836) described it as *Lebeckia microphylla* a few months later. In the same paper, the species is also described as *Aspalathus caerulescens* E. Mey. When Bentham (1843) relegated the genus *Krebsia* to sectional status within *Lotononis* (DC.) Eckl. & Zeyh., he excluded *Krebsia argentea* and later (Bentham 1844) listed it as a synonym of *Lebeckia microphylla*. Harvey (1862) followed this interpretation but remarked on the similarity with *Buchenroedera* Eckl. & Zeyh. Apparently unaware of the existing synonymy,

Table 1 Various characters of *Lebeckia microphylla* compared to those of other taxa

Characters	*Buchenroedera*	*Lotononis* section *Krebsia* s. str.	*Lebeckia microphylla*	*Lotononis* section *Aulacinthus*	*Lebeckia* (other spp.)
1. Stipules	present, in pairs; absent in some species	solitary or in pairs	absent	absent or present; usually solitary when present	usually absent
2. Bracteoles	absent	absent or vestigial	absent or vestigial	absent or vestigial	present
3. Calyx	lobes subequal or the lateral ones on either side fused a little higher	lobes subequal or the lateral ones on either side fused higher up in pairs	lobes subequal	lateral lobes on either side fused higher up in pairs; rarely subequally lobed	lobes equal
4. Flower colour	usually blue, rarely yellow, white or pink	usually blue, rarely yellow or pinkish	blue	yellow	yellow
5. Lobed callosities on claw of the standard	usually absent	usually present	usually present	usually absent (weakly developed in one species)	absent?
6. Fruit shape	short, ovate, few-seeded; laterally slightly inflated	linear, rarely ovate; laterally slightly inflated	linear; laterally inflated	linear to ovate; much inflated laterally	linear; laterally inflated in some species
7. Fruit — upper suture	smooth	smooth or inconspicuously verrucose	distinctly verrucose	distinctly verrucose	smooth
8. Fruit — lower suture	not sunken	not sunken	slightly sunken	distinctly sunken	not sunken
9. Seed surface	smooth	smooth	smooth	tuberculate	smooth
10. Ability to produce hydrocyanic acid (no. of spp. HCN^+ /no. of spp. tested)	often cyanogenic (4/7)	mostly cyanogenic (8/10)	cyanogenic (12/12 specimens)	cyanogenic (6/6)	acyanogenic? (0/11)
11. Major alkaloid type	pyrrolizidine	pyrrolizidine	pyrrolizidine	pyrrolizidine?	quinolizidine

Brown (1901) and Dümmer (1912) described it as new species of *Buchenroedera*, namely *B. glabriflora* and *B. uniflora* respectively.

The correct position of *Lebeckia microphylla* is therefore a problem of long standing. Although Meyer (1836) did not express any doubts, he went to some trouble to point out the differences between *Lebeckia microphylla* and other species that are presently included in *Lotononis*. Dahlgren (1975) remarked on the somewhat distant affinity of *Lebeckia microphylla* to other species of *Lebeckia* and the similarity with *Buchenroedera*. In his extensive re-evaluation of tribal and generic delimitations in the Genisteae *sensu lato*, Polhill (1976) also expressed uncertainty about *Lebeckia microphylla* and he considered it unwise to make any new combination until *Lotononis* had been studied in more detail.

A study of *Lotononis* sections *Aulacinthus* (E. Mey.) Benth. and *Krebsia* (Eckl. & Zeyh.) Benth. revealed new evidence to support the transfer of *Lebeckia microphylla* to *Lotononis*.

Discussion

Similarities and differences between *Lebeckia microphylla* and related groups are summarized in Table 1. All the taxa compared are essentially woody shrubs and are superficially very similar. *Krebsia* is used here in the original sense of Ecklon & Zeyher (1836) and Bentham (1843). The species added to it by Harvey (1862) and Dümmer (1913) are obviously quite different and are excluded from the section for the comparison here. *Buchenroedera* is so closely related to *Lotononis* (especially to section *Krebsia*) that the two genera will probably have to be united. These problems will be addressed elsewhere.

Absence of stipules is certainly not a character unique to *Lebeckia*. This condition is also present in two species of *Buchenroedera* and at least five species of *Lotononis*. It is perhaps significant that the exstipulate species of *Lotononis* are usually the ones that most closely resemble species of *Lebeckia*.

Bracteoles are extremely reduced or absent in *Lotononis* and *Buchenroedera*. Those that do occur are vestigial only and not visible without magnification (Figure 1: 15 – 18). In *Lebeckia*, bracteoles are well-developed and often relatively large. The total or virtual absence of bracteoles in *Lotononis* [the *Lotononis angolensis*-group of section *Polylobium* (Eckl. & Zeyh.) Benth. is an exception] is a useful character to

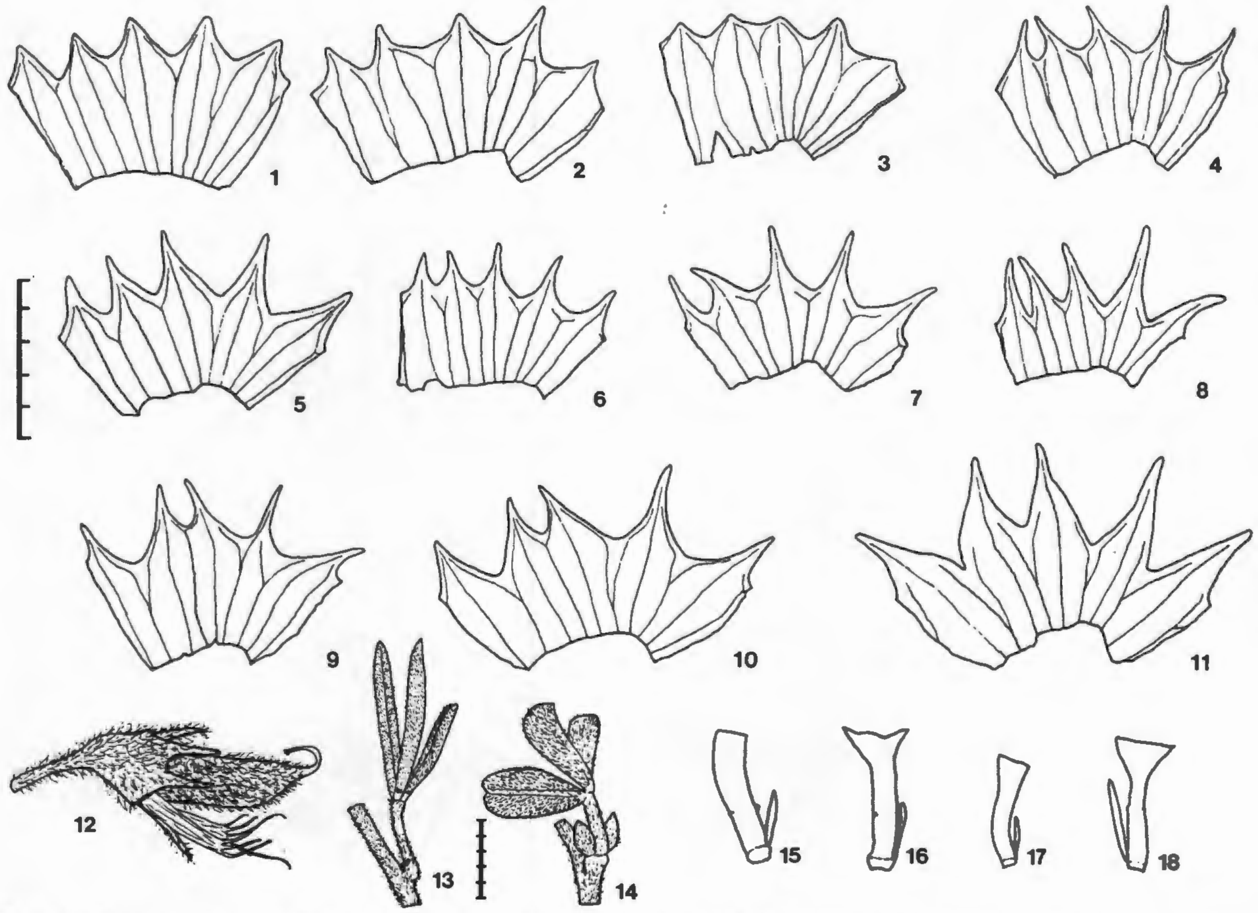

Figure 1 Calyx structure, leaves, bracts and bracteoles of *Lebeckia microphylla* and various species of *Lotononis* section *Krebsia*. 1 – 11, calyx opened out with the upper lobes to the left, vestiture not shown: 1, *L. microphylla*, subequal broadly triangular lobes (*Bayliss 7949*); 2, *L. microphylla*, lateral lobes fused slightly higher (*Tyson s.n. sub SAM 2260*); 3, *L. microphylla*, extremely short lobes, lateral ones fused slightly higher (*Thorns 42*); 4, *L. microphylla*, subequal elongated lobes (*Thode 3143*); 5, *Lotononis galpinii* Dümmer, lobes subequal (*Hilliard & Burtt 15034*); 6 & 7, *L. galpinii*, lobes subequal (*Compton 21482*); 8, *L. galpinii*, lateral lobes fused slightly higher (*Galpin s.n. sub BOL 37245*); 9, *Lotononis carnosa* (Eckl. & Zeyh.) Benth. var. *condensata* Harv., lateral lobes in pairs (*Bandert 6*); 10, *Lotononis bachmanniana* Dümmer, lateral lobes in pairs (*Abbott 250*); 11, *Lotononis cytisoides* (E. Mey.) Benth., lateral lobes in pairs (*Jacot-Guillarmod 8551*); 12, young fruit of *Lebeckia microphylla* — lateral lobes of the calyx fused much higher up (*Bolus 2580*); 13 & 14, leaves in side view: 13, *L. microphylla*, swollen exstipulate leaf base (*Oliver 5272*); 14, *Lotononis biflora* (H. Bol.) Dümmer, paired stipules and swollen leaf base (*Van Wyk 1953*). 15 – 18, pedicels, showing bracts and vestigial bracteoles: 15, *Lebeckia microphylla* (*Bayliss 7949*); 16, *L. microphylla* (*Oliver 5272*); 17, *Lotononis galpinii*, bracteoles absent (*Galpin s.n. sub BOL 37245*); 18, *Lotononis cytisoides*, bracteoles scarcely visible (*Jacot-Guillarmod 8551*). Scale in mm.

distinguish those species that closely resemble species of *Lebeckia* in various other characters.

The structure of the calyx is traditionally used as a key character in the Crotalarieae. *Lebeckia* is characterized by short, equal calyx-lobes with rounded sinuses. This character appears to be more variable than previously thought. In Figure 1, the calyx structure of some species of *Lotononis* section *Krebsia* is compared to that of *Lebeckia microphylla*. The lobes are often exceptionally short in *Lebeckia microphylla*, but the one collection from Natal (*Thode 3143*, Figure 1: 4) has the calyx-lobes similar to *Lotononis galpinii* Dümmer (Figure 1: 5 – 8). In two collections (*Tyson 122* and *Bolus 2580*), the lateral lobes are fused higher up in pairs, exactly as in most species of *Lotononis* (Figure 1: 12). In view of the variability of the calyx structure in *Lotononis* and *Buchenroedera*, this character seems to be of limited diagnostic value to separate *Lotononis* and *Lebeckia*.

The corolla of *Lebeckia microphylla* is typical of *Lotononis* section *Krebsia*, not only in colour (Table 1) but even in such detail as the presence of two callosities on the claw of the standard (Figure 2). These are as variable within different species of *Krebsia* as they are within *Lebeckia microphylla*. The full variation in *Lebeckia* is not known. Callosities were observed in *L. cytisoides* Thunb. for example, but these are merely thickenings of the claw and are not lobed as in *Lotononis*.

Perhaps the most significant morphological evidence is offered by the fruit (Figure 3). The presence of warty protuberances along the upper suture (Figure 3: 12, 13 & 14) clearly indicates an affinity with *Lotononis* rather than *Lebeckia*. Dahlgren (1964) first drew attention to this character, which occurs in many species of *Lotononis* but has never been observed in any other genus of the Crotalarieae. In terms of shape, the pods of *Lebeckia microphylla* are identical to some species of *Lotononis* section *Aulacinthus*, especially to *Lotononis rigida* (E. Mey.) Benth. Even the ventral suture tends to be slightly sunken, as is typical in the section *Aulacinthus* (Figure 3: 9 – 11).

The seeds of *Lebeckia microphylla* are, in terms of size, shape and surface colouration, entirely within the range of variation found in *Buchenroedera* and the two sections of *Lotononis* under discussion. An interesting difference between section *Aulacinthus* and the other groups is the presence of distinct warty tubercles on the seeds. These are quite large and visible under low (10×) magnification. It occurs in most species of *Lotononis*, but neither in the section *Krebsia sensu*

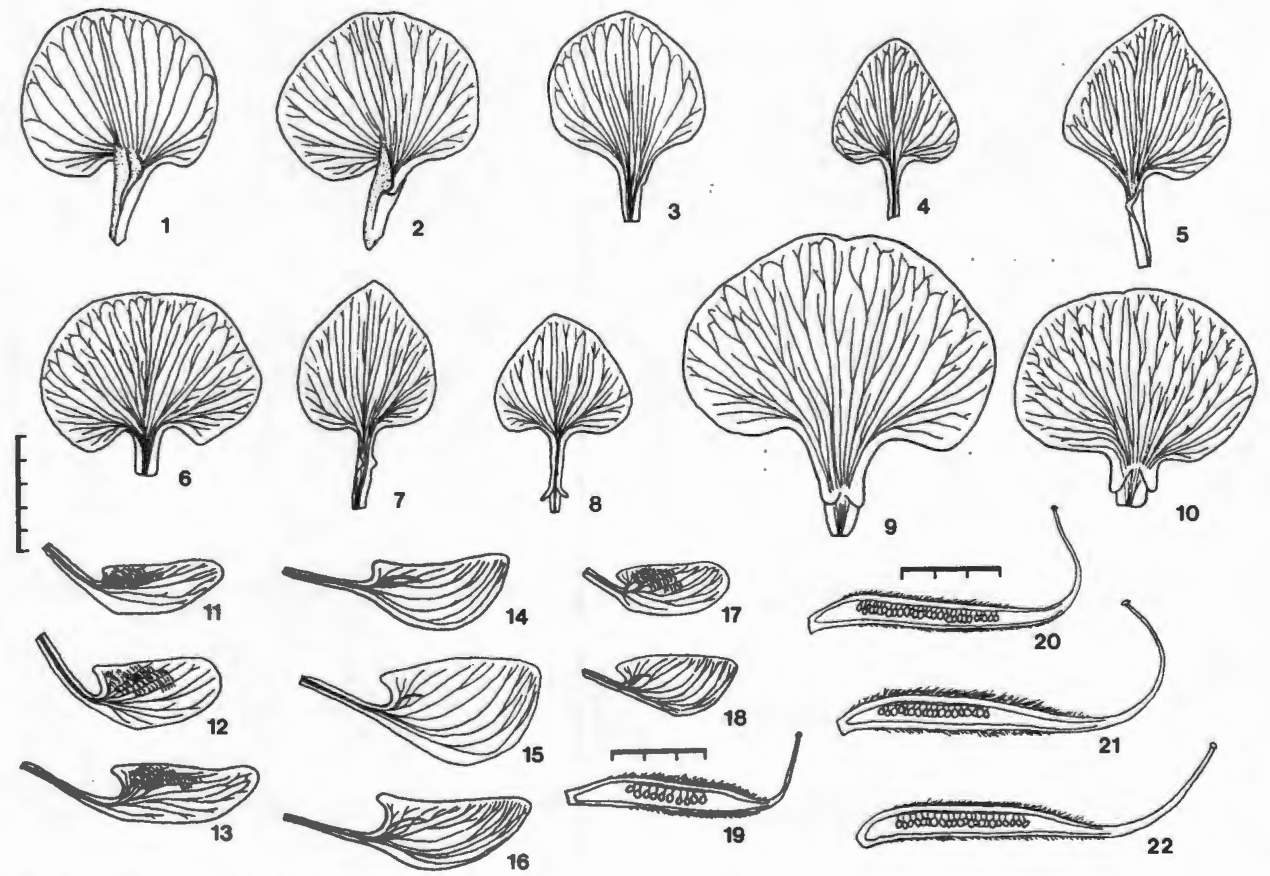

Figure 2 Corollas and pistils of *Lebeckia microphylla* and various species of *Lotononis* section *Krebsia*. 1 – 10, standard in adaxial view, showing presence of callosities on the claw: 1, *L. microphylla*, callosities well-developed (*Bayliss 7949*); 2, *L. microphylla*, only the one callosity well-developed (*Oliver 5272*); 3, *L. microphylla*, callosities nearly absent (*Thorns 42*); 4, *L. microphylla*, callosities absent (*Tyson s.n. sub SAM 2260*); 5, *L. microphylla*, only one callosity (*Thode 3143*); 6, *Lotononis galpinii* Dümmer, callosities absent (*Hilliard & Burtt 15034*); 7, *Lotononis carnosa* (Eckl. & Zeyh.) Benth. var. *condensata* Harv., short callosities near the middle of the claw (*Bandert 6*); 8, *Lotononis carnosa* var. *condensata*, elongated callosities near base of claw (*Pegler 1363*); 9, *Lotononis bachmanniana* Dümmer, well-developed callosities (*Abbott 250*); 10, *Lotononis cytisoides* (E. Mey.) Benth., well-developed callosities (*Jacot-Guillarmod 8551*); 11, 12 & 13, wing petals of *Lebeckia microphylla* showing variation in shape: 11, oblong, slightly pointed (*Oliver 5272*); 12, broad, obtuse (*Baylis 7949*); 13, oblong, pointed (*Thode 3143*); 14, 15 & 16, keel petals of *L. microphylla* showing variation in shape: 14, narrow, slightly pointed (*Oliver 5272*); 15, broad, obtuse (*Bayliss 7949*); 16, oblong, pointed (*Thode 3143*). 17, 18 & 19, wing petal, keel petal and pistil of *Lotononis galpinii* (*Compton 21482*). 20, 21 & 22, pistils of *Lebeckia microphylla* showing variation in the curvature of the style (*Oliver 5272, Baylis 7949 & Thode 3143* respectively). Scale in mm.

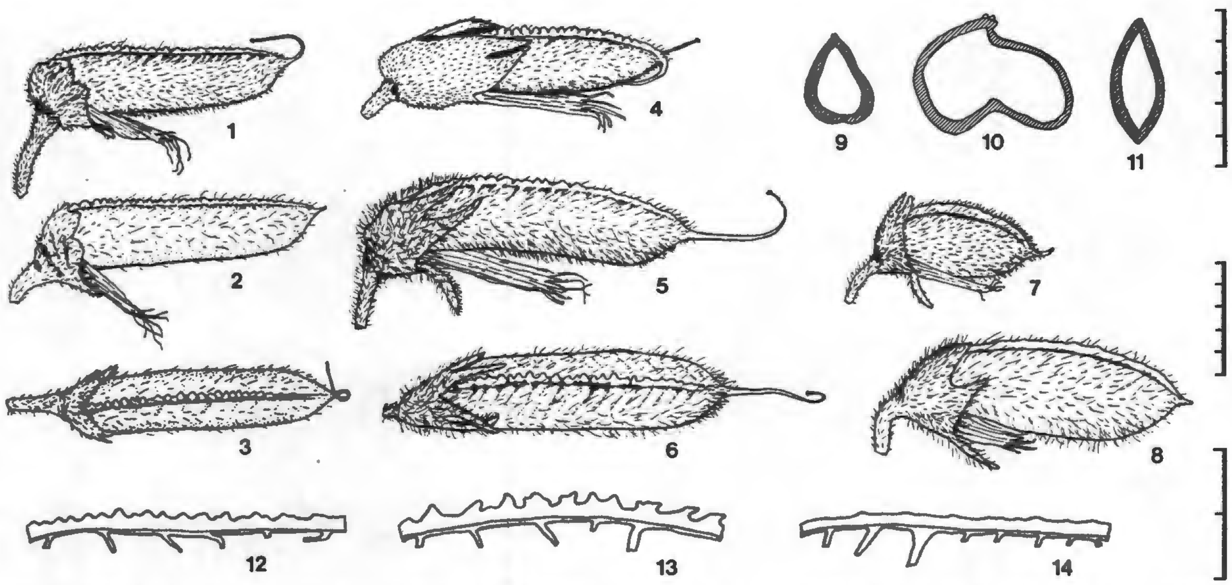

Figure 3 Detail of the fruit of *Lebeckia microphylla* and various species of *Lotononis*. 1 – 8, mature fruit in lateral or top view: 1, 2 & 3, *Lebeckia microphylla*, upper suture distinctly verrucose (*Van Wyk 2483*); 4, *Lotononis gracilis* (E. Mey.) Benth. (*Guthrie 2580*); 5 & 6, *Lotononis rigida* (E. Mey.) Benth. (*Van Breda & Joubert 1995*); 7 & 8, *Lotononis galpinii* Dümmer, upper suture only slightly verrucose (7, *Galpin s.n. sub BOL 37245*; 8, *Hilliard & Burtt 15034*). 9, 10 & 11, fruit in transverse section: 9, *Lebeckia microphylla*, pod laterally inflated at base, lower suture slightly sunken (*Van Wyk 2483*); 10, *Lotononis gracilis*, pod much inflated, lower suture sunken (*Van Wyk 2559*); 11, *Lotononis galpinii*, pod not much inflated, lower suture not sunken (*Roux 1158*). 12, 13 & 14, upper suture of the fruit after dehiscence, as viewed from inside: 12, *Lebeckia microphylla*, distinctly verrucose (*Van Wyk 2483*); 13, *Lotononis gracilis*, distinctly verrucose (*Van Wyk 2559*); 14, *Lotononis galpinii*, nearly smooth (*Roux 1158*). Scale in mm.

stricto nor in *Buchenroedera*.

Other characters, such as the inflorescence structure, prominent leaf-base (Figure 1: 13 & 14) and a tendency for side shoots to be abbreviated are present to various degrees in all the groups under consideration. The phenomenon that the leaflets of *Lebeckia microphylla* are individually shed leaving the petioles (Dahlgren 1963), is not unique to *Lebeckia* and *Wiborgia*, but is also characteristic of most species of *Lotononis* section *Aulacinthus*.

Cyanogenesis is a distinct feature of *Lotononis* (van Wyk, unpublished data) with nearly half of the species reacting strongly positive to the Feigl-Anger cyanogenesis test as described by Feigl & Anger (1966). I have tested numerous specimens of *Lebeckia microphylla* (both fresh and herbarium material from four different localities) and all reacted strongly positive. All of the 11 species of *Lebeckia* tested so far gave a negative result, while the other three taxa under discussion are predominantly cyanogenic (Table 1).

It is now known that *Lebeckia microphylla* contains integerrimine as one of its major alkaloids (van Wyk & Verdoorn 1988). In the Fabaceae, this pyrrolizidine alkaloid was previously known only from some species of *Crotalaria* L. Integerrimine was detected in all species of *Buchenroedera* and *Lotononis* section *Krebsia* examined so far. *Lebeckia* however, contains tetracyclic quinolizidine alkaloids (Gerrans *et al.* 1976; van Wyk *et al.* 1988) and it therefore seems that *Lebeckia microphylla* is chemically more closely related to *Lotononis* than *Lebeckia*.

Geographical distribution patterns are of considerable taxonomic importance in the Fabaceae. The splitting of larger tribes into smaller regional ones (Polhill 1976) is a case in point. Figure 4 shows the approximate geographical distribution of the taxa compared in Table 1. The distribution of *Lotononis* section *Aulacinthus* and *Lebeckia* shows a strong trend towards a winter rainfall distribution in the western part of southern Africa. In this sense, *Lebeckia microphylla* is perhaps better placed in *Lotononis* section *Krebsia* which, like *Buchenroedera*, is restricted to the eastern parts of southern Africa with a predominantly summer rainfall regime.

Conclusions

The subequally lobed calyx and absence of stipules were traditionally used when *Lebeckia microphylla* was placed in *Lebeckia* rather than *Lotononis* or *Buchenroedera*. Individually these characters break down as shown in Figure 1 and Table 1.

Lebeckia microphylla shares with *Lotononis* the virtual absence of bracteoles, a similar flower colour, the presence of lobed callosities on the claw of the vexillum, a verrucose upper suture of the fruit, the ability to produce HCN, integerrimine as a major alkaloid and a similar geographical distribution. It differs from *Buchenroedera* in the shape of the fruit, which is the only consistent diagnostic character known to separate this genus and *Lotononis*. The best position is therefore in the genus *Lotononis*, being most similar to species of the sections *Aulacinthus* and *Krebsia*. Considering the flower colour, corolla structure and smooth seed surface, it is more closely related to the latter.

The weight of evidence clearly shows that *Lebeckia microphylla* is a species of *Lotononis* and not *Lebeckia*. When placed in the section *Krebsia*, it may not even be considered anomalous. In terms of fruit characters, the existing morphological discontinuity between the sections *Aulacinthus* and *Krebsia* is in fact considerably reduced.

Lotononis caerulescens *(E. Mey.) B-E. van Wyk* comb. nov.

Type: In collibus saxosis inter Klipplaatrivier et Zwart-Key alt. 3500 – 4000 ped., *Drège s.n.* (K, *Herb. Benth.* specimen, photo!; K, *Herb. Hook.* specimen, photo!; W, photos!, 3 specimens).

Aspalathus caerulescens E. Mey., Commentariorum de plantis Africae australioris, Vol. 1(1): 54 (1836, February or later); Benth.: 361 (1844), as synonym of *Lebeckia microphylla* E. Mey.

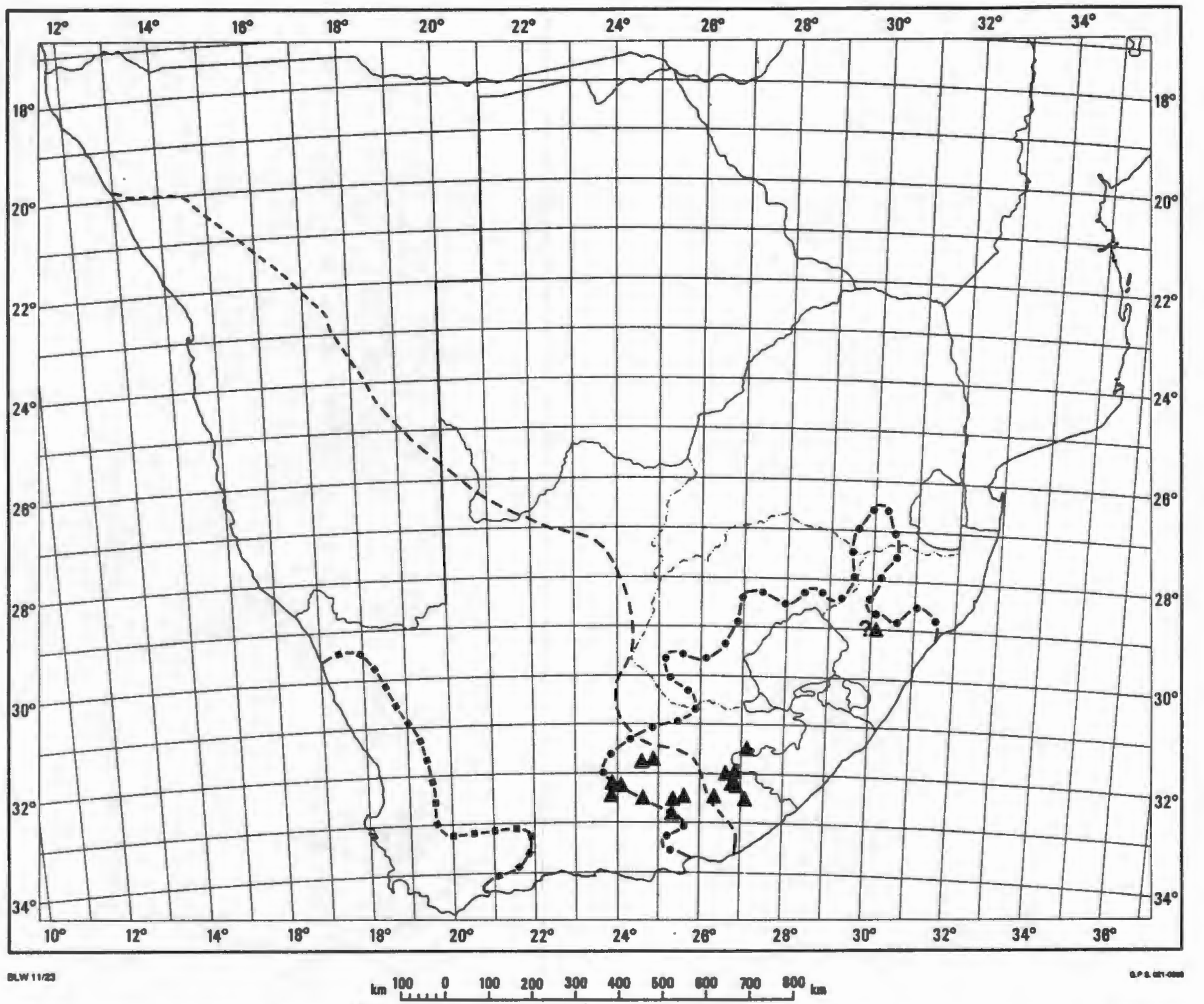

Figure 4 The known geographical distribution of *Lebeckia microphylla* (indicated by triangles), compared to the approximate distribution areas of *Lotononis* section *Krebsia sensu stricto* (–•–•–•–), *Lotononis* section *Aulacinthus* (–▪–▪–▪–) and *Lebeckia* (– – – –). (The distribution of the genus *Lebeckia* was contributed by Dr A Schreiber of München.)

Buchenroedera caerulescens (E. Mey.) Presl: 477 (1845).

Krebsia argentea Eckl. & Zeyh.: 179 (1836, January), non *Lotononis argentea* Eckl. & Zeyh.: 176 (1836); Benth.: 361 (1844), as synonym of *Lebeckia microphylla* E. Mey.; Presl: 477 (1845). Type: In lapidosis (altit. III, IV) laterum montium prope 'Silo' ad flumen 'Klipplaatrivier' (Tambukiland), *Ecklon & Zeyher 1286* (M, photo!; W, photo!; SAM, photo!).

Lebeckia microphylla E. Mey.: 155 (1836, February or later), non *Lotononis microphylla* Harv.: 65 (1862); Benth.: 361 (1844); Harv.: 88 (1862). Types: In montibus saxosis Camdeboosberg, alt. 4000 – 4500 ped., *Drège (a)* (K, photo!; W, photo!); In montibus saxosis Klein Bruintjeshoogte, alt. 2600 – 3000 ped., *Drège (b)* (BOL, photo!; K, photo!; PRE, photo!; W, photo!).

Lebeckia microphylla E. Mey. var. *leptophylla* E. Mey.: 155 (1836); Benth.: 361 (1844). Types: prope Graafreynet, alt. 3000 ped., *Drège (a)*; Los Tafelberg, alt. 5000 – 6000 ped., *Drège (b)* (not seen).

Buchenroedera glabriflora N.E. Br.: 120 (1901); Polhill: 325 (1976). Type: mountain sides near Queenstown, alt. 1220 m, *Galpin 1596* (K, holo., photo!; BOL!).

Buchenroedera uniflora Dümmer: 226 (1912). Type: Graaff Reinet Div.; on the summit of Mount Koudveld, Sneeuwberg Range, 1500 m, *Bolus 2580* (K, holo!; BOL!).

Ecklon & Zeyher 1287 in SAM is undoubtedly from the same collection as *Ecklon & Zeyher 1286* in M and W, and should be considered an isosyntype. When Pappe rewrote the label he made the mistake of writing '1287' instead of '1286'. The real *Ecklon & Zeyher 1287* is *Krebsia carnosa*, a totally different species and not likely to be confused with *Krebsia argentea*. This error is easily explained by the fact that both collections are from the same locality.

I have been unable to trace any type specimens of *Lebeckia microphylla* var. *leptophylla*. This name has been ignored by both Bentham (1844) and Harvey (1862), possibly due to a confusion between the Drège specimens 'a' and 'b' of the type and those of the variety. Judged by the description and the type localities however, it is obviously only a minor variation of the typical form and thus not of much importance.

Phillips (1917) erroneously cited *Thode 7* (the same collection as *Thode 6276* and *Thode 6282* in STE) as *Buchenroedera glabriflora* N.E. Br. *Thode 7* in BOL turns out to be *Lotononis galpinii* Dümmer, a species which, unlike '*B. glabriflora*', does occur in the Drakensberg.

Woody, much-branched shrub; procumbent, 0,2 – 0,5 m high and up to 1 m wide or erect, up to 1 m high. *Branches* densely leafy, canescent, glabrescent with age. *Leaves* exstipulate, digitately trifoliolate, densely canescent. *Petiole* (1 –)2 – 3(– 4) mm long, usually much shorter than the leaflets, on a prominent swollen leaf base. *Leaflets* (1 –)2 – 5(– 7) mm long, 0,5 – 1 mm wide, narrowly linear, conduplicate; apex acute, often slightly recurved. *Inflorescence* a terminal or leaf-opposed congested raceme, 1 – 3(– 6)-flowered; peduncle short or absent, rarely up to 5 mm long.

Flowers 7 – 10(– 12) mm long, bright blue; pedicel 1 – 4 mm long; bracteoles absent or vestigial, less than 0,1 mm long when present. *Calyx* 3 – 5 mm long, densely sericeous; lobes subequal, very short or up to 1,5 mm long, broadly to narrowly triangular, the upper and lateral lobes on either side occasionally fused slightly higher up in pairs. *Standard* up to 12 mm long; claw 2,5 – 4 mm long, with two callosities usually present near its apex; blade 5 – 7 mm long, 5 – 10 mm wide; broadly ovate, depressed ovate to rounded; glabrous, or with a line of hairs dorsally along the middle. *Wing petals* up to 10 mm long; claw shorter than the blade, 2,5 – 4 mm long; blade 4 – 6 mm long, up to 4 mm wide, broadly oblong, obtuse or somewhat pointed, auricled; sculpturing upper basal and upper central, lunate to lunate-lamellate, in 4 – 7 rows of 10 – 20 irregular reclined mostly intercostal lunae. *Keel petals* up to 11 mm long, as long or longer than the wing petals; claw up to 4 mm long; blade up to 7 mm long and 4 mm wide, broadly semicircular, obtuse, auricled and pocketed near the base. *Androecium* as long as the keel, in a sheath open on the upper side; anthers dimorphic. *Pistil* 7 – 12 mm long, subsessile; ovary 4 – 6 mm long, linear, nearly terete, densely sericeous; style merging gradually with ovary, curved gently to sharply upwards; stigma small, terminal; ovules *ca.* 15 – 25, funicles as long as or slightly longer than the ovules. *Fruit* 11 – 15 mm long, 3 – 4 mm wide, 4 – 6-seeded, linear, triangular-terete in transverse section, laterally inflated along the lower suture, densely pubescent, glabrescent with age, with distinct irregular warty protuberances along the upper suture; lower suture somewhat sunken before dehiscence. *Seed* up to 3,5 mm long and 2 mm wide, broadly obovate to oblong in lateral view, radicular lobe prominent; testa smooth, greenish-yellow with irregular dark purple-brown marks (Figures 1, 2 & 3).

There is considerable variation in habit, leaf size and flower size but no subspecific treatment is attempted here. I have studied most of the different forms *in situ*, and consider them all as geographical races of one variable species. The single specimen from Natal [*Thode 3143* (STE)] however, differs in a number of characters from the eastern Cape collections. The locality on the label ('Scottspoort') was traced by Killick (1977) to near Weenen in Natal (Figure 4). The plant seems much more erect and robust; the inflorescences are strictly terminal and up to 6-flowered; and the keel petals are narrower and more pointed. It is possible to separate it at subspecific level, but I am hesitant to do so before a wider range of material from Natal (especially fruiting material) becomes available for study.

Material examined

—**2830** (Dundee): Weenen district, Scottspoort (– CC), *Thode 3143* (STE) [not typical].

—**3124** (Hanover): Middelburg district, Gordonville (– DA), *Acocks 16574* (PRE); Lootsberg Pass, 63 km from Graaff-Reinet towards Middelburg (– DB), *Van Wyk 2033* (JRAU).

—**3126** (Queenstown): Queenstown district, Bowker's Kop (– DC), *Page s.n.* (BOL, photo in JRAU), *Tyson s.n. sub SAM 2260* (SAM), *s.n.* (K, 3 sheets, photos in JRAU); Queenstown district, Madeira Hill (– DD), *Everitt 4* (PRE); 'Madiera', Queenstown (– DD), *Thorns 42* (NBG); Mountain sides near Queenstown (– DD?), *Galpin 1596* (BOL, K, photo in JRAU); Queenstown district (– DD?), *Sidey 3732* (PRE).

—**3127** (Lady Frere): Clarke's Siding near Dordrecht (– AC), *Bayliss 7949* (GRA, M, NBG, photo in JRAU, PRE).

—**3223** (Rietbron): Murraysburg district, Grootberg slopes (– BB), *Acocks 21038* (K, photo in JRAU); Camdeboosberg (– BD), *Drège s.n.* (K, photo in JRAU, W, photo in JRAU).

—**3224** (Graaff-Reinet): Houd Constant Pass south of the farm to Moordenaarsrivier (– AA), *Oliver 5272* (STE); Sneeuberg in northern Koudeveld between Graaff-Reinet and Murraysburg (– AA), *Oliver 5192* (PRE); Summit of Koudveld mountain, Sneeuberge (– AA), *Bolus 2580* (BOL, K); Summit of Koudeberg (– AA), *Tyson 122* (BOL); Cave Mountain near Graaff-Reinet (– BC), *Bolus 153* (BOL, photo in JRAU); Foot of Spandouw Kop near Graaff-Reinet (– BC), *Sister Francis 4* (BOL, photo in JRAU); Graaff-Reinet (– BC), *Wall s.n.* (S, photo in JRAU).

—**3225** (Somerset East): Mountain Zebra National Park, Bankberg plateau (– AD), *Van Wyk 1329, 1330* (JRAU); Top of Swagershoek Pass (– BC), *Acocks 15699* (PRE); Near top of Swagershoek Pass on Pearston side (– BC), *Van Wyk 1612, 1613, 1614, 1615, 2483* (JRAU); Klein Bruintjeshoogte, between Zondagsrivier and Keiskamma (– CB), *Drège s.n.* (BOL, photo in JRAU, K, 2 sheets, photos in JRAU, PRE, photo in JRAU, W, photo in JRAU).

—**3226** (Fort Beaufort): Road between Adelaide and Tarkastad, 1 km south of turn-off to Bedford via Baviaansrivier (– AD), *Van Wyk 1724* (JRAU); Between Klipplaatrivier and Zwart-Key [Cathcart district] (– BA/ – BB), *Drège s.n.* (K, 2 specimens on 1 sheet, photo in JRAU, W, 3 sheets, photo in JRAU); Near Silo at the Klipplaatrivier (– BB), *Ecklon & Zeyher 1286* (M, photo in JRAU, W, photo in JRAU), *Ecklon & Zeyher '1287'* [= *1286*] (SAM, photo in JRAU).

—**3227** (Stutterheim): Vogelberg, Cathcart (– AC), *Pole Evans 1755* (K, photo in JRAU, PRE); Windvogelberg (– AC), *Baur 837?* (K, photo in JRAU).

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APPENDIX 17

Taxonomic relationships amongst some genera of _Leguminosae_ tribe _Crotalarieae_ and _Argyrolobium_ (_Genisteae_)

B-E. van Wyk* & Anne Lise Schutte*

Summary. Taxonomic relationships amongst the predominantly southern African genera _Dichilus_ DC., _Lebeckia_ Thunb., _Melolobium_ Eckl. & Zeyh., _Polhillia_ Stirton and _Wiborgia_ Thunb. of the tribe _Crotalarieae_ and _Argyrolobium_ Eckl. & Zeyh. of the tribe _Genisteae_ have been studied. The most obvious similarity between these genera is the fusion of the calyx lobes into a trifid lower lip, or at least a tendency towards such a fusion. The morphology, chromosome numbers and alkaloids of some species and the geographical distribution of the genera have been investigated in an attempt to reach a better understanding of relationships. A tentative phylogenetic tree is presented which indicates that _Argyrolobium_ is the sister group of _Polhillia_ and that it should be referred to the tribe _Crotalarieae_. The concept of the genus _Polhillia_ is broadened to include two anomalous species of _Argyrolobium_ and _Melolobium_. Diagnostic characters of the genera are illustrated and discussed.

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INTRODUCTION

Relationships amongst the genera *Dichilus* DC., *Lebeckia* Thunb., *Melolobium* Eckl. & Zeyh., *Polhillia* Stirton and *Wiborgia* Thunb. of the tribe Crotalarieae and *Argyrolobium* Eckl. & Zeyh. of the tribe *Genisteae* are not clear. When Polhill (1976, 1981) redefined the Genisteae *sensu lato*, he included some genera with bilabiate calyces in the Crotalarieae, but somewhat hesitantly referred *Argyrolobium* Eckl. & Zeyh. to the *Genisteae sensu stricto*. The fusion of the stamens into a closed tube is used as a diagnostic character for the *Genisteae*, but this character is unstable in *Argyrolobium*. Several attempts have been made to link *Argyrolobium* to genera of the Genisteae. Cristofolini & Chiapella (1977) for example, argued for the inclusion of *Argyrolobium* in the *Genisteae*, but their serological investigation did not include any of the above-mentioned genera and the evidence is therefore not conclusive. Polhill (1981) noted the similarities between *Dichilus*, *Lebeckia*, *Melolobium* and *Argyrolobium* and suggested that the latter may eventually also have to be referred to the *Crotalarieae*.

As part of a study of generic limits in the *Crotalarieae*, we investigated all genera which has at least a tendency for the calyx lobes to be fused into a trifid lower lip. Lack of material prevented us from including the South American *Anarthrophyllum*

Benth. and Sellocharis Taub. These genera are highly modified (Polhill 1976) and are probably not directly related to the remaining genera, which are all predominantly southern African. Goldblatt (1981) has indeed tentatively suggested a position of Anarthrophyllum and Sellocharis in the Genisteae near Lupinus L., since the chromosome number of n = 12 is discordant with the remainder of the Crotalarieae.

The genus Polhillia, recently described by Stirton (1986a) to accommodate some rare woody shrubs endemic to the south-western Cape Province of South Africa, is of particular relevance. It seems to have more in common with Argyrolobium than it has with any other genus of the Crotalarieae and the possibility that it provides a connecting link between the latter genus and Lebeckia is considered here. A study of alkaloids (Van Wyk et al. 1988c) has shown that Polhillia and Lebeckia contain sparteine and lupanine as major alkaloids. Species of Polhillia and two anomalous species of Argyrolobium and Melolobium [A. brevicalyx Stirton and M. involucratum (Thunb.) Stirton] were also shown to be very similar. The similarity in major alkaloids appeared to be correlated with morphological similarities and also agreed with cytological evidence. The present circumscription of Polhillia is therefore also examined, since it appears to be unsatisfactorily artificial.

All available evidence that may contribute to a better understanding of relationships is considered in this paper, including some new evidence that came to light during our study.

RESULTS AND DISCUSSION

Voucher specimens of the species of Argyrolobium, Dichilus, Lebeckia, Melolobium, Polhillia and Wiborgia that were examined in detail and used for the illustrations are listed in Table 1. The size and approximate geographical distribution of the genera, and the total number of species of each genus that was considered for the distribution of character states are shown in square brackets. Authorities for names are not repeated elsewhere.

Similarities and differences between the genera are summarized in Table 2 and depicted in Figures 1--11 & Maps 1--4. These are discussed in more detail below.

Nearly all the genera and species under consideration are woody shrubs. A suffrutescent habit occurs only in Argyrolobium, Dichilus and a few species of Lebeckia and Melolobium. The lesser degree of woodiness in most of these species is probably not an indication of affinity but more likely a convergent response to high fire frequencies in grassland habitats (see Maps 1--4).

Spinescence is limited to some species of Lebeckia, Wiborgia and Melolobium but is not characteristic of any particular genus.

Leaves and stipules are illustrated in Figure 1. There are some significant differences. The leaflets of some species of Lebeckia and Wiborgia are individually shed, leaving the petioles. The leaflets of Polhillia species, Argyrolobium brevicalyx and Melolobium involucratum are similar and differ from those of the other genera in that they are distinctly conduplicate.

Stipules are traditionally used as a diagnostic character at the generic level (Figure 1). Stipules are absent in all species of Wiborgia and Lebeckia except L. wrightii (Harv.) Bolus, where they are quite small. In other characters this species seems fairly similar to various other Lebeckia species, notably L. plukenetiana E. Mey., L. inflata Baker and L. longipes H. Bol. It is certainly not a species of Lotononis as Harvey (1862) suggested. Stipules are extremely reduced in Dichilus and are never more than 1 mm long (Figure 1: D2). Although caducous and often difficult to see, stipules are consistently present except in D. strictus and D. reflexus. In the genus Melolobium, stipule shape is a very useful diagnostic character. They have a small point of attachment and are always asymmetrical at their bases, often markedly lobed or ear-shaped (Figure 1: M1, M2, S1 & S2). The fusion of stipules (to various degrees) is a strong connecting link between Argyrolobium and Polhillia. In all the other genera, the stipules (when present) are free from each other and also free from the petiole. The sheathing stipules of Melolobium involucratum (Figure 1: M3 & S5) are exactly like those of the genus Polhillia (Figure 1: P1, P2, P3 & S6). We differ from Stirton (1986b) who suggested that the sheathing stipule originated from a fusion of the lobes as it occurs in Melolobium. The stipules in Melolobium and Polhillia seem exact opposites in that the point of attachment of the stipule in Melolobium is very narrow, while in Polhillia and indeed in many species of Argyrolobium, the stipule base (point of attachment) is so wide that it completely encircles the stem (Figure 1: S3 -- S6). A fusion of clasping stipules is much more conceivable than a fusion of narrow-based stipules, especially since there are many species of Argyrolobium (also A. brevicalyx, Figure 1: A1, S3 & S4) where various degrees of just such a fusion can be seen. The difference between Polhillia and Argyrolobium lies more in the fusion of the stipules to the petiole than the fusion of the two stipules with each other on the leaf-opposed side. There is however, considerable variation even within a single individual of a species. Juvenile and mature shoots of Melolobium involucratum for example, show a gradual progression from free to sheathing stipules (Figure 1: S5 & M3).

The petiole anatomy (Figure 2) also provides some evidence. A group of fibres is present along the adaxial side of the primary vascular bundle in all species of Dichilus and in all the Melolobium species (except M. involucratum) that were examined (Figure 2: D1, D2, M1 & M2). Several species from each of the other genera have been studied but none of them have such fibres. Adaxial leaf traces are weakly developed in some species of Argyrolobium (also in A. brevicalyx, Figure 2: A1) and in Dichilus (Figure 2: D1 & D2), where it is totally absent in three of the five species. We have not yet observed the absence of adaxial traces in any of the other genera.

The inflorescence structure of the various genera provides further evidence of affinities (Figure 3). In Lebeckia, Wiborgia and Melolobium, the inflorescence is strictly a terminal raceme. It is usually many-flowered, but may be shortened and then often with only two or three flowers. In suffrutescent species of Argyrolobium and in most species of Dichilus, vegetative growth proceeds from the terminal leaf axil which then results in a leaf-opposed inflorescence. Such leaf-opposed racemes are technically the same as terminal racemes - the only difference lies in the dormancy or non-dormancy of the uppermost axillary bud directly below the inflorescence. In Dichilus and Argyrolobium there is also a reduction in the number of flowers per inflorescence. Even when single-flowered, it is usually still possible to detect a peduncle, albeit very short. The apex of the inflorescence often forms a sharp thorn in species of Melolobium, Lebeckia and Wiborgia. Melolobium involucratum does not fit the very uniform pattern in all other species of Melolobium. The highly reduced peduncle in this species is typical of all the species of Polhillia and also of Argyrolobium brevicalyx. An interesting phenomenon in this group is the elongation of the last internode (the one directly below the inflorescence). This "pseudo-peduncle" is probably not homologous with the elongated peduncle that is so common in Argyrolobium. In the latter, the flowers are often grouped together in an umbellate arrangement, but then the flowers are subtended by bracts only and not leaves and bracts as in Polhillia, Argyrolobium brevicalyx and Melolobium involucratum. These species are also the only ones where bracts and bracteoles are strongly reduced and very often absent. In all other species of Argyrolobium, Melolobium, Dichilus, Lebeckia and Wiborgia bracts and bracteoles are consistently present.

Variations in the calyx structure of the various genera and species are shown in Figure 4. There is at least a tendency in species of Lebeckia and Wiborgia for the lower three lobes to be grouped together. The lobes are rarely as equal as standard texts suggest. Although the lateral sinuses are usually not deeper than the upper and lower ones, it is very often wider. The difference between Lebeckia species, Argyrolobium brevicalyx and Polhillia species is therefore rather slight. In other genera the calyx has a distinct trifid lower lip formed by deep lateral sinuses. Some species of Argyrolobium, Melolobium and all species of Dichilus have the upper lobes united as well, so that the calyces are truly bilabiate (Figure 4: D1, D2 & M2).

The flowers of all the genera are rather similar (Figure 5) but there are differences in the relative lengths of the flower parts and some other details. Lebeckia, Wiborgia and Dichilus usually have the wings markedly shorter than the keel, while the wings are longer or at least as long as the keel in other genera. The calyx is very short in Lebeckia, Wiborgia and in some species of Dichilus, Polhillia and Argyrolobium. This character appears to be of limited diagnostic value. Some species of Lebeckia (notably the section Calobota Benth.), Melolobium involucratum, Argyrolobium brevicalyx and all species of Polhillia are distinct in the presence of hairs on the wing petals and especially on the keel. Some degree of pubescence of the standard however, occurs in all the genera. The wing petals (Figure 6) vary in size, shape and sculpturing, but none of these characters appear to be of diagnostic value at the generic level. The wing petals of all the species of Dichilus are distinctly spurred (Figure 6: D1 & D2), while those of the other taxa are auriculate only. The structure of keel petals is shown in Figure 7. An interesting character that Polhillia species have in common with Melolobium involucratum and Argyrolobium brevicalyx is the distinctly imbricate arrangement of the keel petals. The area of overlap between the two keel petals is indicated by broken lines in Figure 7 (M3, P1, P2, P3 & A1). This development is particularly evident in Polhillia canescens, where the overlapping parts are elongated and lobed. Imbricate keel petals have also been observed Argyrolobium tuberosum Harv., but in all other taxa investigated, the keel is valvate along the lower side.

Argyrolobium differs from all genera of the Crotalarieae in the fusion of the stamens into a closed tube (Polhill 1976, 1981). This character is unstable however, and in most species that we have studied there are at least some flowers in which, as in all genera of the Crotalarieae, the staminal tube is split along the vexillary stamen. The closed staminal tube may have developed independently in Argyrolobium, just as the bilabiate calyx seems to have developed independently in the Crotalarieae. Polhill (1976), refering to Cytisus L. and Hypocalyptus Thunb., points out that allowance should be made for parallel developments. When one considers the obvious similarities between Argyrolobium and Polhillia, it would seem that the major discontinuity lies between Argyrolobium and other genera of the Genisteae and not between Argyrolobium and the Crotalarieae. The same applies to the size and shape of anthers (Figure 8). In the Genisteae, the anthers are differentiated into five long and five short ones (Polhill 1976), while Argyrolobium and Polhillia usually have the carinal anther a little shorter (Figure 8: P1, P2, P3, A1, A2 & A3). The carinal anther is shorter still in genera of the Crotalarieae and also attached a little higher up. The distinction is rather slight and certainly does not represent a significant discontinuity between Argyrolobium and genera of the Crotalarieae.

As pointed out by Polhill (1976), fruit characters are not very useful at the generic and tribal levels and often lead to a segregation of natural groups into smaller artificial ones. Wiborgia appears to be very different from Lebeckia in the distinctly winged fruit, but there is at least some indication of wing development in species of Lebeckia (Dahlgren 1975). Lebeckia is perhaps the most diverse in fruit morphology, with inflated fruit in some species (L. inflata Baker for example) and even indehiscent wind-dispersed fruit as in L. melilotoides R. Dahlgr., where persistent petals serve as wings. Dichilus, Melolobium and Argyrolobium have similar, unspecialized pods which hardly differ from those of some Lebeckia species. The indehiscence of the pods of Polhillia have in the past been excessively weighted as a generic character. The fruits of Argyrolobium brevicalyx are almost identical to those of Polhillia pallens and are also totally indehiscent. Melolobium involucratum has so many features in common with species of Polhillia, that the exclusion of this species on the basis of its dehiscent pods can no longer be accepted.

The structure and surface sculpturing of hairs appear to be of limited diagnostic value at the generic level. Only uniseriate hairs have been observed except in Melolobium, where glandular hairs (Figure 9 A) often co-occur with uniseriate hairs. Glands are quite common in Melolobium but not in all of the species. Dahlgren & Goldblatt (1981) reported the presence of glands on the fruit of M. involucratum and interpreted it as a

Melolobium-like feature. We have studied several fruits of M. involucratum but found no evidence of glands. It is possible that the basal parts of broken-off hairs (Figure 9 B & C) may have been mistaken for glands. Three types of hair surfaces have been found in the species studied, namely smooth, striated and verrucose (Figure 9 D, E & F respectively). Smooth hairs were observed only in some species of Lebeckia, Wiborgia and Melolobium. A striated surface without warty tubercles is typical of Melolobium and Polhillia. M. involucratum has most of its hairs striated, but the presence of at least some verrucose hairs on the fruit suggests a similarity to Argyrolobium rather than Melolobium. Most species of Lebeckia and Wiborgia, all species of Dichilus and all the species of Argyrolobium studied (including Argyrolobium brevicalyx) have verrucose hairs as in Figure 9 F.

Ovules and seeds provide no clear indication of relationships. Differences in size, shape and surface colouration are likely to be of value only at the specific level. The number of ovules however, appears to be of some significance. In Melolobium and Dichilus, the number of ovules per ovary is limited (c. 5--8) and all or nearly all develop into mature seeds. In other genera the ovary occasionally has up to 30 ovules and as many seeds, but often also lower numbers of seeds as a result of abortion. There is so much variation however, that this character is not diagnostic for Dichilus and Melolobium. The orientation of ovules in the ovary (oblique or vertical) have been used to indicate similarities, but differences are slight and not likely to be of value above the specific level.

Chromosome numbers do not provide strong indications of affinity except in Polhillia and Argyrolobium (Table 2). Available chromosome counts were taken from Goldblatt (1981), Stirton (1986a) and Van Wyk & Schutte (1988a). Lebeckia, Wiborgia and Melolobium have a base number of 9, with 2n = 18. All five species of Dichilus have 2n = 28 and therefore presumably a base number of 7. Polhillia and Argyrolobium have a base number of 8, although the latter appears to be cytologically diverse, with counts of n = 13, 15, 16 and 24 having been reported (Goldblatt 1981). The suggested affinity of Polhillia (2n = 32) with Argyrolobium is therefore supported by the chromosome number. Melolobium involucratum and Argyrolobium brevicalyx also have 2n = 32. The inclusion of these two species in Polhillia is consistent with existing cytological evidence. It is indeed a clear indication that the former is misplaced in Melolobium. The position of Argyrolobium in the Genisteae is not strongly supported by chromosomal evidence. The cytological complexity of the Genisteae makes it possible to show imaginary relationships with just about any genus of the Papilionoideae. Despite this, Goldblatt (1981) could not suggest any relation between Argyrolobium and genera of the Genisteae. Perhaps there is none. The only apparent link appears to be the common occurrence of polyploidy and aneuploidy in the Genisteae. A base number of 8 (if this is correct for *Argyrolobium*) is not uncommon in the *Crotalarieae*. Neither is aneuploidy and polyploidy. *Aspalathus* L. exhibits aneuploidy in several lines (Dahlgren 1971) and polyploidy has been found in the section *Krebsia* Eckl. & Zeyh. of *Lotononis* (DC.) Eckl. & Zeyh. (Van Wyk & Schutte 1988b), with counts of 28, 42, 56 and 84 amongst closely related species. A transfer of *Argyrolobium* to the *Crotalarieae* thus seems reasonable from a cytological point of view.

The occurrence of quinolizidine alkaloids have been used as a measure of phylogenetic relationships (Salatino & Gottlieb 1980 & 1981, Gomes *et al*. 1981). Efforts to show similarities between *Argyrolobium* and some genera of the Genisteae have, rather, indicated a dissimilarity. When the complexity of the ring structure and the oxidation of the rings are considered (as in Salatino & Gottlieb 1980 & 1981), the *Argyrolobium* species that we have examined scarcely differ from the genera of the *Crotalarieae*. These genera were previously not known to contain alkaloids, but some work has since been done which shows that α-pyridone alkaloids (Figure 10: 4--8) also occur in *Melolobium*, *Dichilus* and *Polhillia* (Van Wyk *et al*. 1988a, 1988b, 1988c, 1988d). The presence of sparteine (Figure 10: 1) as a major alkaloid in *Polhillia* and in the morphologically similar *Argyrolobium brevicalyx* and *Melolobium involucratum* (Van Wyk *et al*. 1988c) suggests an affinity with *Lebeckia* and also indicates a link between *Lebeckia* and *Argyrolobium*. The latter genus appears to specialize in more advanced cytisine-type alkaloids, while Lebeckia and Polhillia also have the phylogenetically more primitive sparteine and lupanine (Figure 10: 2) as major alkaloids. Melolobium is similar to Argyrolobium in the dominance of α-pyridone alkaloids but, unlike the latter, also specializes in the two C_{14} alkaloids camoensine and leontidine (Figure 10: 7 & 8) (Van Wyk et al. 1988b). Thermopsine (Figure 10: 4) is common in Melolobium but not in Argyrolobium, which has anagyrine (Figure 10: 5) as a dominant alkaloid (Van Wyk & Verdoorn 1989). Dichilus has a unique combination of major alkaloids (Van Wyk et al. 1988a & 1988d). It differs from the other genera in the presence of several piperidyl alkaloids of which ammodendrine and smipine (Figure 10: 9 & 10) are the dominant compounds. Thermopsine (one of the major alkaloids of Melolobium) is the only quinolizidine alkaloid that also occurs as a major alkaloid in Dichilus. The presence of sparteine as a major alkaloid in Lebeckia and Polhillia should perhaps be interpreted as a symplesiomorphy and is as such not of any cladistic significance. The dominance of α-pyridone alkaloids in all the genera except Lebeckia and Wiborgia however, is considered to be a useful synapomorphy. There is now also sufficient evidence to interpret the presence of the two C_{14} alkaloids and the dominance of piperidyl alkaloids as autapomorphies for Melolobium and Dichilus respectively.

The approximate geographical distributions of the genera Lebeckia, Wiborgia, Dichilus, Melolobium, Polhillia and Argyrolobium are shown in Maps 1--4. The distributions of

Melolobium involucratum and *Argyrolobium brevicalyx* are combined with that of *Polhillia* in Map 1. All except *Argyrolobium* are endemic to southern Africa. The latter is subendemic, with about 50 of the 70 species restricted to this region (Dyer 1976, Polhill 1968 & 1981). Biogeographical considerations (the assumption of local speciation and diversification) formed the basis of the latest tribal revision of the *Papilionoideae* (Polhill 1981). The *Crotalarieae* is predominantly but not strictly southern African. *Crotalaria* L. is the most widespread of the genera, with considerable diversification in tropical and subtropical regions outside Africa (Polhill 1981). The distributions of *Lotononis* and *Argyrolobium* are similar. Both these genera are concentrated in southern Africa with a few species distributed towards and around the Mediterranean and further east to India. The insert on Map 1 is not very accurate but gives at least an indication of the distribution of *Argyrolobium* outside southern Africa. The presence of *Argyrolobium* species on Madagascar (if relictual and not secondary) suggests that this genus is intermediate between *Lotononis* and *Crotalaria* in terms of age. Its predominantly southern distribution and obvious affinity with *Polhillia* makes its inclusion in the *Crotalarieae* at least convenient if not more consistent with Polhill's biogeographical subdivision of the *Genisteae sensu lato*. *Lebeckia* and *Wiborgia* are restricted to the western parts of southern Africa, with a predominantly winter rainfall regime (Map 2). *Melolobium* is more widespread and occurs in all climatic regions (Map 3), while *Dichilus* is restricted to summer rainfall areas in the central and eastern parts of southern Africa (Map 4).

Very few attempts at cladistic analyses of sizable groups of Papilionoideae have been made and the results are often inconclusive (Lavin 1987, Crisp & Weston 1987, Zandee & Geesink 1987. The widespread occurrence of convergence, the difficulty to establish homology and problems with character polarity may partly be the reason. The difficulties encountered in the reconstruction of legume phylogenies have been discussed and demonstrated by Zandee and Geesink (1987) in their attempt to analyze relations within the Milletieae and allied groups. A problem that seems particularly great in the Crotalarieae is that the genera are rather similar and that few distinct apomorphies are available for cladogram construction. The intricate relationships amongst the Cape Crotalarieae have been discussed by Dahlgren (1963 & 1970). The genera treated in the present study differ from all other Crotalarieae in the calyx, which has the three lower lobes different from the upper two. In Lebeckia and Wiborgia this character is weakly expressed. Further development leads to the distinct bilabiate calyx as in Dichilus and some species of Melolobium and Argyrolobium. There is only this one synapomorphy and our assumption of monophyly may be open to criticism. We regard this character as sufficient evidence to justify the choice of Lebeckia as outgroup for the other genera, and expect more such characters to be uncovered in future studies. Lebeckia is considered to be very closely related to other genera of the tribe (Dahlgren 1963, 1970 & 1975; Polhill 1976 & 1981) and there is currently no reason to doubt this assumption. Detailed studies of alkaloidal metabolites have revealed evidence of chemical similarities even with the more distantly related Pearsonia Duemmer, notably some hitherto unknown hydroxylation patterns of lupanine (Van Wyk & Verdoorn 1988b). The total absence of α-pyridone alkaloids in Lebeckia (Van Wyk & Verdoorn 1988a) also strongly agrees with Polhill's (1976) conclusion that Lebeckia is the least specialized genus of the tribe. The outgroup comparison method (with Lebeckia as outgroup) and the approach of Crisp and Weston (1987) were followed to derive the postulated transformation series shown in Table 3. Characters in which evolutionary direction could not be distinguished (such as hair surface sculpturing) were excluded from the analysis. The phylogenetic character states of the genera appear in Table 4. It seemed reasonable to us to code the states of character numbers 4 and 5 (absence of adaxial fibres in the main vascular bundle and a loss of stipules) as apomorphic in Lebeckia. Character numbers 15, 16 and 17 represent apomorphic tendencies in Lebeckia but the coding of these characters for the plesiomorphic state had no significant effect on the analysis. Character 14 (stamen fusion) is coded as apomorphic in Argyrolobium despite its variability in this genus. When terminal taxa exhibit variability in character states it is usual to code for the plesiomorphic state, but in this instance we suggest that the sporadic occurrence of a split tube in some species represents a reversal to the plesiomorphic condition. Chromosome base number is treated as of no more importance than the morphological features, some changes of which are likely to be effected by single genes. There appears to be as yet no generally accepted way of coping with this kind of problem in cladistic methodology. From Table 4 we constructed the postulated phylogenetic tree for the genera Lebeckia, Wiborgia, Dichilus, Melolobium, Polhillia and Argyrolobium shown in Figure 11. Even when some polarizations were reversed, the algorithmic method of Kluge & Farris (1969) did not indicate a more parsimonious or more acceptable alternative to the one shown, which has a consistency index of 0.900. The three convergences should perhaps not be taken too seriously. A suffrutescent habit, indehiscent fruit and a loss of fibres in the petiole (character numbers 1, 4 and 16) are known to have evolved independently in several unrelated genera of different tribes.

The first dichotomy results in a separation of Lebeckia and Wiborgia from the other genera. This grouping is defined by five apomorphies, two of which are convergent. The other group is defined by two apomorphies (the trifid lower lip of the calyx and the presence of advanced α-pyridone alkaloids). It is important to note that the sister group relationship suggested by the basal dichotomy is rather weakly supported by a single apomorphy. When other genera such as Aspalathus L. and Rafnia L. are eventually included in the analysis, the relationship at this level may have to be reconsidered. The Polhillia line then diverges into four monophyletic groups, each defined by at least two apomorphies.

The status of *Polhillia* as a genus distinct from *Argyrolobium* is supported by several derived character states. *Argyrolobium brevicalyx* and *Melolobium involucratum* have virtually the same character states as *Polhillia* and they have therefore been included in the concept of *Polhillia* in Table 4 . The cladogram suggests that the relationship between *Argyrolobium* and *Polhillia* is comparable to the relationship between *Wiborgia* and *Lebeckia*, i.e., it shows them to be sister taxa. *Wiborgia* has a single autapomorphy (the winged samara-like fruit). The suffrutescent habit in *Argyrolobium* is not a uniquely derived character state but is shared by *Dichilus* (and also a few species of *Lebeckia* and *Melolobium*). This leaves the closed staminal tube in most species as the only apomorphy for *Argyrolobium*. *Dichilus* and *Melolobium* are reasonably well defined since both have three distinct apomorphies.

CONCLUSIONS

Available information strongly suggests that the generic concepts of *Lebeckia*, *Wiborgia*, *Melolobium*, *Dichilus* and *Argyrolobium* are acceptable provided that *Argyrolobium brevicalyx* Stirton and *Melolobium involucratum* (Thunb.) Stirton are placed in an enlarged *Polhillia*. This broadened concept is supported by several unique character states not known from any other genus of the *Crotalarieae*. It is obvious from the summary in Table 2 that the transfer of *Argyrolobium brevicalyx* and *Melolobium* involucratum to Polhillia would result in a more natural and more predictive classification. The following new combinations are therefore made:

1. Polhillia brevicalyx (C. H. Stirton) Van Wyk & Schutte comb. nov.

Argyrolobium brevicalyx C. H. Stirton in J. S. Afr. Bot. 50 (4): 443 (1984). Type: South Africa, Cape Province, flats along watercourse 1 km SSE of Uitvlug farm, along road between Bredasdorp and Swellendam, 15 km SW of Swellendam, Burgers 3188 (holotype K; isotype STE!).

Polhillia brevicalyx differs from Argyrolobium in the following characters, which are all typical of other Polhillia species: Leaflets conduplicate; inflorescence pseudo-pedunculate (the internode directly below the inflorescence elongated and functioning as a peduncle -- a true peduncle being totally absent); bracts and bracteoles rarely present; calyx shorter than the keel; keel petals distinctly imbricate and pubescent; staminal sheath rarely closed; fruit indehiscent; sparteine, lupanine, anagyrine and N-methylcytisine as major alkaloids.

It differs from other species of Polhillia in the stipules, which are not fused to the petiole, although they are occasionally fused on the leaf-opposed side.

2. *Polhillia involucratum* (Thunb.) Van Wyk & Schutte *comb. nov*.

Psoralea involucrata Thunb., Prod. Pl. Cap. 2: 136 (1800) & Fl. Cap. 2: 607 (1823). Type: "e Cap. b. Spei. Thunberg *Psoralea involucrata*" *Thunberg s.n*. (UPS-THUNB 17575!, lectotype, chosen by Stirton 1986b).

Argyrolobium involucratum (Thunb.) Harv., Fl. Cap. 2 : 75 (1862).

Melolobium involucratum (Thunb.) C. H. Stirton in S. Afr. J. Bot. 52 (4): 355 (1986b). [as *M*. *involucratum* (Harv.) C. H. Stirton].

Polhillia involucratum is clearly misplaced in *Melolobium*. Unlike Dahlgren & Goldblatt (1981) and Stirton (1986b), we have found no evidence to suggest an affinity with the latter genus, but rather several characters in common with *Polhillia*. Convergence in all of these characters is highly unlikely:

Leaflets conduplicate; stipules fused to the petiole and fused on the leaf-opposed side (except in juvenile material); inflorescence pseudo-pedunculate (a true peduncle totally absent); bracts and bracteoles rarely present, calyx shorter than the keel; keel petals distinctly imbricate and pubescent; chromosome number $2n = 32$; sparteine, lupanine, anagyrine and *N*-methylcytisine as major alkaloids.

Polhillia involucratum differs from other species of Polhillia in the flower colour, which changes from yellow to purple or almost pure white with age; the elongation of the pedicels after fertilisation of the flowers; the almost glabrous leaflets and calyx; and the shorter carinal anther.

The slight modifications to generic limits that have resulted from the present study are reflected in the following key:

1\. Calyx with trifid lower lip (lateral sinuses deeper than the lower ones):

2\. Leaflets trifoliolate:

3\. Stipules semi-sagittate or semi-cordate at the base; glandular tubercles often present............. *Melolobium*

3\. Stipules, if present, not lobed; glandular tubercles absent:

4\. Stipules inconspicuous, less than 1 mm long, rarely absent; wing petals much shorter than the keel, distinctly spurred........................... *Dichilus*

4\. Stipules conspicuous; wing petals as long or longer than the keel, auriculate but not spurred:

5\. Peduncle absent, internode below inflorescence elongated, bracts and bracteoles rarely present, keel petals imbricate........................... *Polhillia*

5\. Peduncle present, internode below inflorescence not elongated, bracts and bracteoles consistently present, keel petals rarely imbricate.... *Argyrolobium*

2\. Leaflets unifoliolate............... *Lebeckia* (*L. wrightii*)

1\. Calyx without trifid lower lip (lateral sinuses may be wider than the lower ones, but not deeper):

6\. Pods not winged above (rarely narrowly winged but then several-seeded.................................... *Lebeckia*

6\. Pods winged above (if not, then single-seeded), up to 6-seeded.. *Wiborgia*

Available evidence seems to indicate that there are indeed close affinities between the genera Lebeckia, Wiborgia, Melolobium, Dichilus, Argyrolobium and Polhillia as was suggested by Polhill (1981) and Stirton (1986a). Our hypothesis on generic relationships (Figure 11) however, differs from earlier suggestions. The genus Dichilus is remarkably similar to Lebeckia, but we have found no evidence of a direct link. A connection with Argyrolobium and Melolobium seems more likely. We also have reason to believe that Polhillia is more closely related to Argyrolobium than to Melolobium. There is little doubt about the position of Polhillia in the tribe Crotalarieae, but the position of Argyrolobium in the Genisteae now appears to be artificial, since it is based on a single variable character.

Our studies have shown that Argyrolobium falls entirely within the range of variation present in the tribe Crotalarieae. It has too much in common with Polhillia and other genera of the Crotalarieae to be separated at the tribal level. No convincing evidence has yet been found to link Argyrolobium to any genus in the Genisteae. Even if tribal limits are only meant to show basic affinities and not necessarily to reflect major disjunctions in intergeneric variation, some degree of predictivity should still be aimed for. If the status quo is maintained purely for practical or historical reasons, attempts to prove relationships where none may exist, will continue. Polhill (1981) has clearly anticipated an eventual transfer of Argyrolobium to the Crotalarieae. We believe that sufficient evidence is now available for such a transfer.

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Table 1. Voucher specimens and other details of the material of Argyrolobium, Dichilus, Lebeckia, Melolobium, Polhillia and Wiborgia examined. The size and approximate geographical distribution of the genera, and the total number of species that was considered for the distribution of character states are shown in square brackets.

SPECIES	REF. NO. USED IN FIGURES	LOCALITY	VOUCHER
Argyrolobium Eckl. & Zeyh. [c. 70 spp.; Africa, southern Europe and Asia, with c. 50 spp. in the southern and eastern parts of southern Africa; 17 spp. examined]			
A. brevicalyx C. H. Stirton	V1	Uitvlug farm, Swellendam district	Burgers 3286 (STE)
	V2	Uitvlug farm, Swellendam district	Van Wyk 2100 (JRAU)
	V3	Uitvlug farm, Swellendam district	Van Wyk 2134 (JRAU)
A. molle Eckl. & Zeyh.	V4	Near Pearston	Van Wyk 1622 (JRAU)
A. variopile N. E. Br.	V5	Sehlabathebe, Underberg	Jacot Guillarmod et al. 74 (PRE)
	V6	Irene, Pretoria	Van Wyk 1781 (JRAU)
	V7	Golden Gate National Park	Van Wyk 1904 (JRAU)
Dichilus DC. [5 spp.; central and eastern parts of southern Africa; all 5 spp. examined]			
D. pilosus Conrath ex Schinz	V8	Krugersdorp Game Reserve	Schutte 94 (JRAU)
	V9	Helderkruin View, Roodepoort	Schutte 122 (JRAU)
D. strictus E. Mey.	V10	Butterworth	Pegler 1806 (PRE)
	V11	45,6 km N of Bethlehem	Schutte 155 (JRAU)

TABLE 1 CONTINUED

Lebeckia Thunb.

[c. 35 spp.; western and southern parts of southern Africa; 14 spp. examined]

L. cytisoides Thunb.	V12	Van Rhyns Pass, Nieuwoudtville	Schutte 286 (JRAU)
	V13	Halfway between Clanwilliam & Citrusdal	Van Wyk 2441 (JRAU)
	V14	Goldmine, Bonnievale district	Van Wyk 2705 (JRAU)
L. leipoldtiana R. Dahlgr.	V15	Nieuwoudtville	Schutte 295 (JRAU)
L. mucronata Benth.	V16	Elandsberg, N. of Patensie	Stirton 10880 (JRAU)

Melolobium Eckl. & Zeyh.

[c. 20 spp.; southern Africa; 13 spp. examined]

M. aethiopicum (L.) Druce	V17	Velddrif Rd, 24 km from Cape Town	Van Wyk 2685 (JRAU)
M. alpinum Eckl. & Zeyh.	V18	Giant's Castle Game Reserve	Schutte 160 (JRAU)
M. involucratum (Thunb.) C. H. Stirton	V19	Blomfontein farm, Calvinia district	Snyman 778b (NBG)
	V20	Blomfontein farm, Calvinia district	Schutte 377 (JRAU)
	V21	Blomfontein farm, Calvinia district	Cultivated from Schutte 396 (JRAU)
M. stipulatum Harv.	V22	Verkeerdevlei, Touw's River	Van Wyk 2238 (JRAU)
M. subspicatum Conrath	V23	Irene, Pretoria	Schutte 101 (JRAU)
	V24	Irene, Pretoria	Schutte 112 (JRAU)
	V25	Irene, Pretoria	Van Wyk 1779 (JRAU)
M. wilmsii Harms	V26	Komati Power Station, Witbank district	Du Toit 13 (PRE)
	V27	Nooitgedacht farms, Ermelo	Dyer 4158a (PRE)
	V28	Bethal to Hendrina Rd, Schurwekop turn-off	Van Wyk 2624 (JRAU)

TABLE 1 CONTINUED

Polhillia C. H. Stirton

[c. 5 spp.; south-western parts of the Cape Province; 4 spp. examined]

P. *canescens* C. H. Stirton	V29	Adoonskop, Bredasdorp district	*Van Wyk* *2092* (JRAU)
P. *pallens* C. H. Stirton	V30	Potberg Nature Reserve	*Burgers* *3129* (STE)
	V31	Near Remhoogte, Bredasdorp district	*Van Wyk* *2095* (JRAU)
	V32	Near Remhoogte, Bredasdorp district	*Van Wyk* *2096* (JRAU)
P. *waltersii* (C. H. Stirton) C. H. Stirton	V33	Worcester commonage	*Niemand* *17* (JRAU)
	V34	Worcester commonage	*Van Wyk* *2701* (JRAU)

Wiborgia

[11 spp.; south-western parts of the Cape Province; 5 spp. examined]

W. *fusca* Thunb. subsp. *fusca*	V35	Lambert's Bay Rd, 46 km from Clanwilliam	*Schutte* *268* (JRAU)
W. *obcordata* (Berg.) Thunb.	V36	Between Ceres and Swaarmoed Pass	*Van Wyk* *2242* (JRAU)

Table 2. Similarities and differences between the genera *Lebeckia*, *Wiborgia*, *Dichilus*, *Melolobium*, *Polhillia* and *Argyrolobium*.

	Lebeckia	*Wiborgia*	*Dichilus*	*Melolobium* (other spp.)	*Melolobium involucratum*	*Polhillia*	*Argyrolobium brevicalyx*	*Argyrolobium* (other spp.)
Habit	woody or suffrutescent	woody	suffrutescent	woody or suffrutescent	woody	woody	woody	suffrutescent rarely woody
Spines	some spp.	some spp.	absent	many spp.	absent	absent	absent	absent
Leaflets conduplicate	no	no	no	no	yes	yes	yes	no
Petiole anatomy	-	-	adax. fibres	adax. fibres	-	-	-	-
Stipules:								
presence	absent in all but 1 species	absent	rarely absent	present	present	present	present	present
fusion	free if present	-	free	free	fused on both sides	fused on both sides	often fused on one side	often fused on one side
Inflorescence:								
position	terminal	terminal	terminal or leaf-opposed	terminal	terminal	terminal	terminal	terminal or leaf-opposed
type	raceme	raceme	raceme	raceme	umbel	umbel	umbel	raceme or umbel
peduncle	present	present	present	present	absent	absent	absent	present
Bracts & bracteoles	present	present	present	present	± absent	± absent	± absent	present
Internode below inflorescence	normal	normal	normal	normal	elongated	elongated	elongated	normal

TABLE 2 CONTINUED	*Lebeckia*	*Wiborgia*	*Dichilus*	*Melolobium* (other spp.)	*Melolobium involucratum*	*Polhillia*	*Argyrolobium brevicalyx*	*Argyrolobium* (other spp.)
Vestiture:								
glands	absent	absent	absent	present	absent	absent	absent	absent
hair surface	verrucose	smooth or verrucose	verrucose	smooth	smooth or verrucose	smooth	verrucose	verrucose
Calyx:								
lower 3 lobes	± different from upper	grouped together	fused into a trifid lip	fused into a trifid lip	fused into a trifid lip	fused into a trifid lip	fused into a trifid lip	fused into a trifid lip
upper 2 lobes	free	free	fused	free or fused	free	free	free	free or fused
lateral sinus	wider than the lower	wider than the lower	deeper and wider than the lower	deeper and wider than the lower	deeper and wider than the lower	deeper and wider than the lower	deeper and wider than the lower	deeper and wider than the lower
Wing petals	auriculate	auriculate	spurred	auriculate	auriculate	auriculate	auriculate	auriculate
Keel petals	valvate	valvate	valvate	valvate	imbricate	imbricate	imbricate	rarely imbricate
	pubescent or glabrous	glabrous	glabrous	glabrous	pubescent	pubescent	pubescent	glabrous

TABLE 2 CONTINUED	*Lebeckia*	*Wiborgia*	*Dichilus*	*Melolobium* (other spp.)	*Melolobium involucratum*	*Polhillia*	*Argyrolobium brevicalyx*	*Argyrolobium* (other spp.)
Staminal tube	split	split	split	split	split	split	usually split	closed or split
Ovary	often stipitate	stipitate	sessile or subsessile	sessile or subsessile	sessile or subsessile	sessile or subsessile	sessile or subsessile	sessile or subsessile
Fruit								
dehiscence	often indehiscent	indehiscent	dehiscent	dehiscent	dehiscent	indehiscent	indehiscent	dehiscent
appendages	rarely winged	winged	not winged	not winged	not winged	not winged	not winged	not winged
Chromosome number (2n)	18	18	28	18	32	32	32	26,30,32,48
Major alkaloids	sparteine, lupanine, nuttalline	sparteine, lupanine, nuttalline	ammodendrine, smipine, thermopsine	lupanine, *N*-methyl-cytisine, anagyrine, thermopsine, camoensine, leontidine	sparteine, lupanine, *N*-methyl-cytisine, anagyrine	sparteine, lupanine, *N*-methyl-cytisine, anagyrine, cytisine	sparteine, lupanine, *N*-methyl-cytisine, anagyrine	*N*-methyl-cytisine, anagyrine, cytisine, lusitanine, argyrolobine
Distribution	SW parts of Southern Africa	SW Cape	central parts of Southern Africa	central parts of Southern Africa	SW Cape	SW Cape	SW Cape	widespread except central Southern Africa

Table 3. Postulated transformation series of 20 characters used in constructing the cladogram in Figure 11.

1. HABIT
    - 0 woody shrub
    - 1 often suffrutescent

2. GLANDS
    - 0 absent
    - 1 often present

3. LEAFLETS
    - 0 not conduplicate
    - 1 conduplicate

4. PETIOLE ANATOMY
    - 0 adaxial fibres in main vascular bundle
    - 1 without adaxial fibres

5. STIPULES
    - 0 mostly present
    - 1 mostly absent

6. STIPULE BASE
    - 0 not lobed
    - 1 lobed

7. STIPULE FUSION

0 free

1 clasping, often fused on the leaf-opposed side

2 mostly sheathing the stem

8. INFLORESCENCE

0 terminal raceme

1 mostly condensed raceme

2 fasciculate (umbellate, without a peduncle)

9. INTERNODE DIRECTLY BELOW INFLORESCENCE

0 not elongated

1 elongated (pseudo-peduncle)

10. BRACTS AND BRACTEOLES

0 consistently present

1 rarely present

11. CALYX

0 lobes equal

1 lower 3 lobes different from upper

2 trifid lower lip

12. WING PETALS

0 auriculate

1 spurred

13. KEEL PETALS

    0 valvate
    1 rarely imbricate
    2 imbricate

14. STAMEN FUSION

    0 tube split along vexillary stamen
    1 tube usually not split

15. OVARY

    0 sessile or subsessile
    1 often stipitate

16. FRUIT DEHISCENCE

    0 dehiscent
    1 often indehiscent

17. FRUIT APPENDAGES

    0 not winged
    1 rarely winged
    2 winged

18. CHROMOSOME BASE NUMBER

    0 base number 9
    1 base number 8
    2 base number 7

19. α-PYRIDONE ALKALOIDS

0 absent

1 present as major compounds

2 C_{14}-type as major compounds

20. PIPERIDYL ALKALOIDS

0 present as minor compounds or absent

1 present as major compounds

Table 4. Phylogenetic character states of the genera *Argyrolobium* (A), *Dichilus* (D), *Lebeckia* (L), *Melolobium* (M), *Polhillia* (P) and *Wiborgia* (W). Characters are numbered as in Table 3.

CHARACTER NUMBER:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
A	1	0	0	1	0	0	1	1	0	0	2	0	1	1	0	0	0	1	1	0
D	1	0	0	0	0	0	0	1	0	0	2	1	0	0	0	0	0	2	1	1
L	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	1	0	0	0
M	0	1	0	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	2	0
P	0	0	1	1	0	0	2	2	1	1	2	0	2	0	0	1	0	1	1	0
W	0	0	0	1	1	0	0	0	0	0	1	0	0	0	1	1	2	0	0	0
HYPANC	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

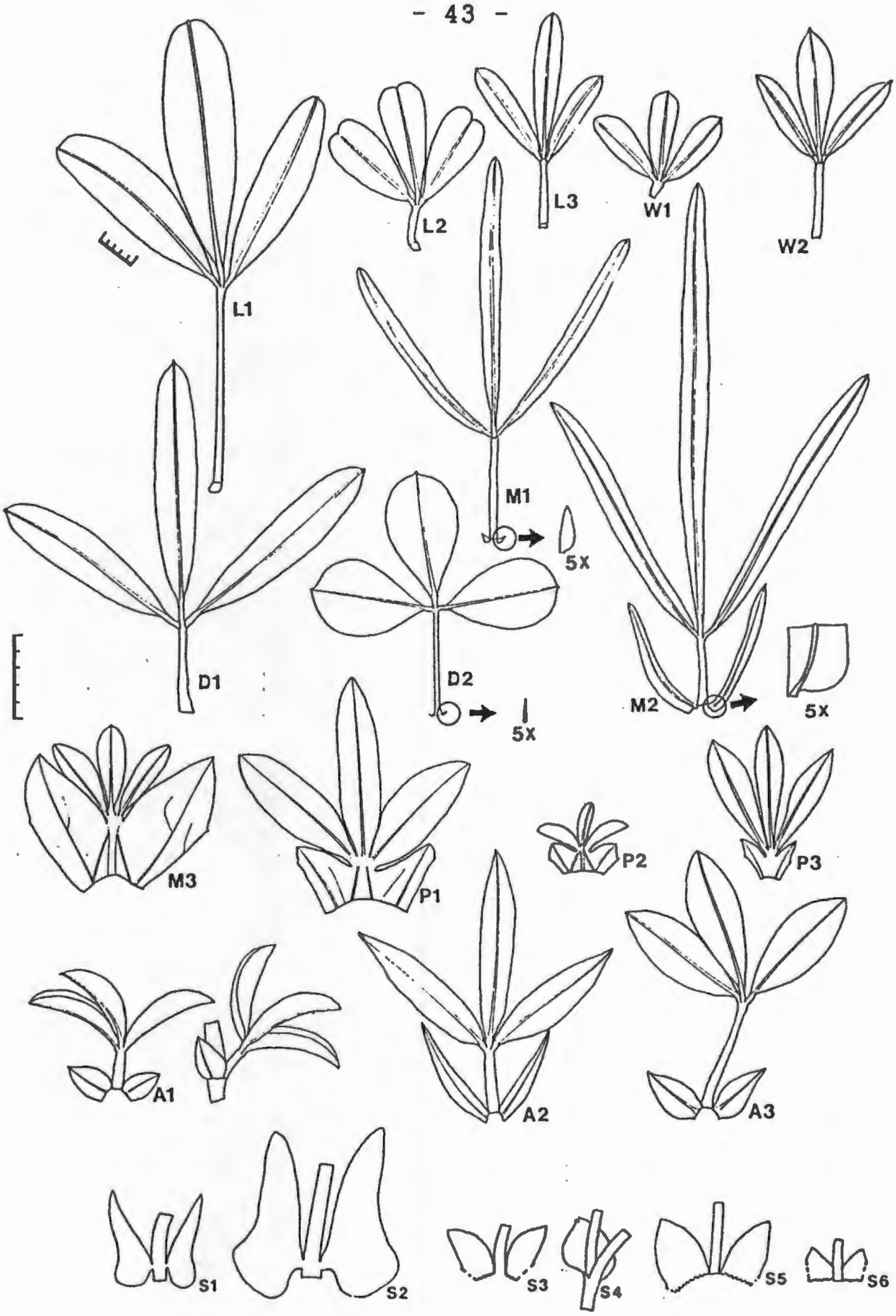


Figure 1. Leaflets and stipules in various species of *Lebeckia*, *Wiborgia*, *Dichilus*, *Melolobium*, *Polhillia* and *Argyrolobium*. The leaflets are opened out except in A1, vestiture not shown. L1, *Lebeckia cytisoides* (V13); L2, *L. leipoldtiana* (V15); L3, *L. mucronata* (V16); W1, *W. obcordata* (V36); W2, *Wiborgia fusca* subsp. *fusca* (V35); D1, *Dichilus strictus* (V11); D2, *D. pilosus* (V8); M1, *Melolobium subspicatum* (V24); M2, *M. wilmsii* (V28); M3, *M. involucratum* (V20); P1, *Polhillia canescens* (V29); P2, *P. pallens* (V31); P3, *Polhillia waltersii* (V34); A1, *Argyrolobium brevicalyx* (V2); A2, *A. molle* (V4); A3, *A. variopile* (V7); S1, *Melolobium alpinum*, auriculate stipules (V18); S2, *M. aethiopicum*, auriculate stipules (V17); S3, *Argyrolobium brevicalyx*, clasping stipules fused on leaf-opposed side, S4, clasping stipules totally fused on leaf-opposed side (V3); S5, *Melolobium involucratum* (V21); S6, *Polhillia pallens* (V32). Voucher numbers as in Table 1. Scale in mm.

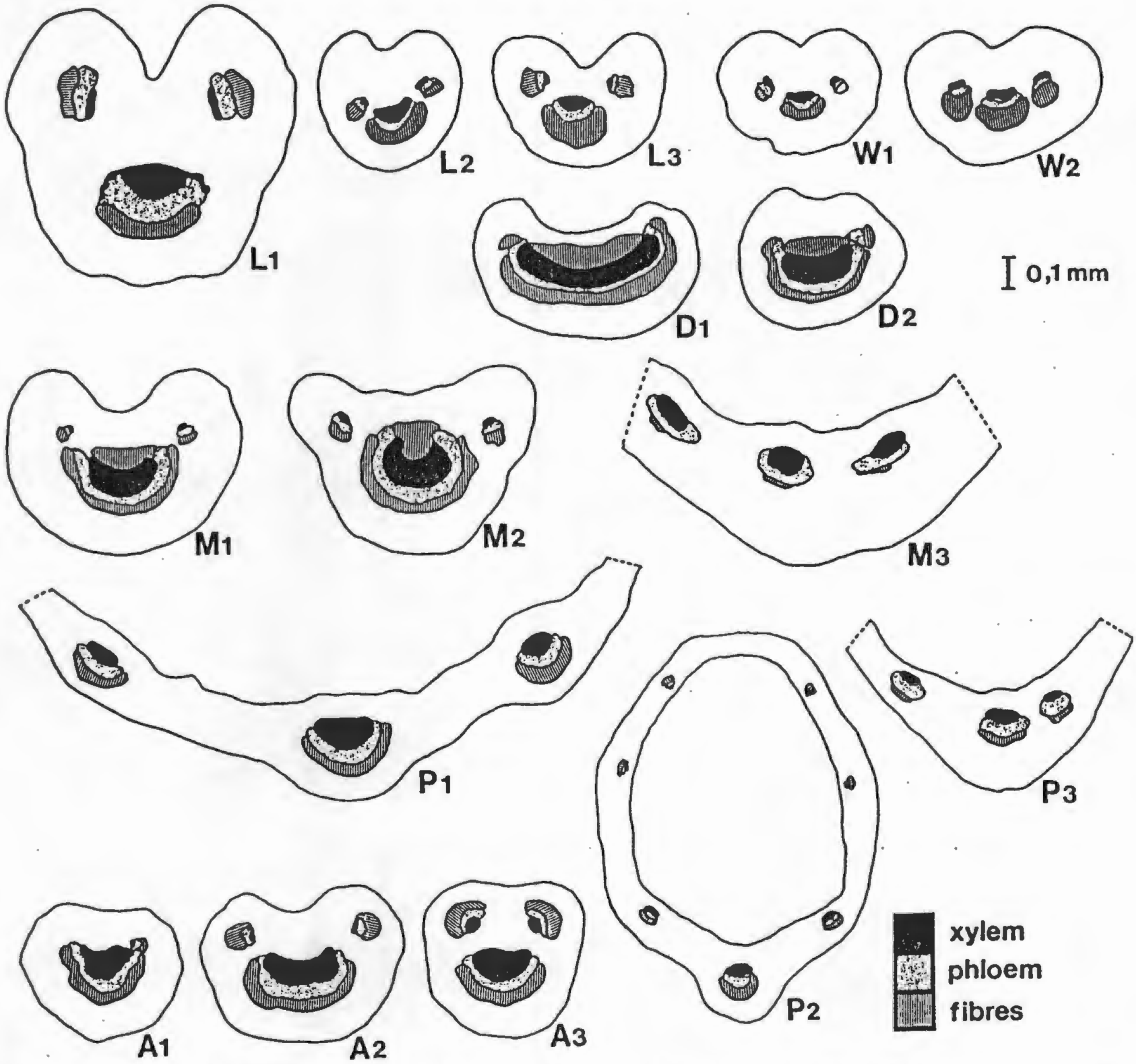


Figure 2. Petiole anatomy of various species of *Lebeckia*, *Wiborgia*, *Dichilus*, *Melolobium*, *Polhillia* and *Argyrolobium* as seen in transverse section (through middle of petiole). Fibres along the adaxial side of the main leaf trace are present only in *Dichilus* and *Melolobium*. Adaxial leaf traces are strongly reduced or absent in *Dichilus* and some species of *Argyrolobium*. L1, *Lebeckia cytisoides* (V12); L2, *L. leipoldtiana* (V15); L3, *L. mucronata* (V16); W1, *W. obcordata* (V36); W2, *Wiborgia fusca* subsp. *fusca* (V35); D1, *Dichilus strictus* (V10); D2, *D. pilosus* (V9); M1, *Melolobium subspicatum* (V23); M2, *M. wilmsii* (V26); M3, *M. involucratum* (V20); P1, *Polhillia canescens* (V29); P2, *P. pallens* (V30); P3, *Polhillia waltersii* (V33); A1, *Argyrolobium brevicalyx* (V1); A2, *A. molle* (V4); A3, *A. variopile* (V6). Voucher numbers as in Table 1.

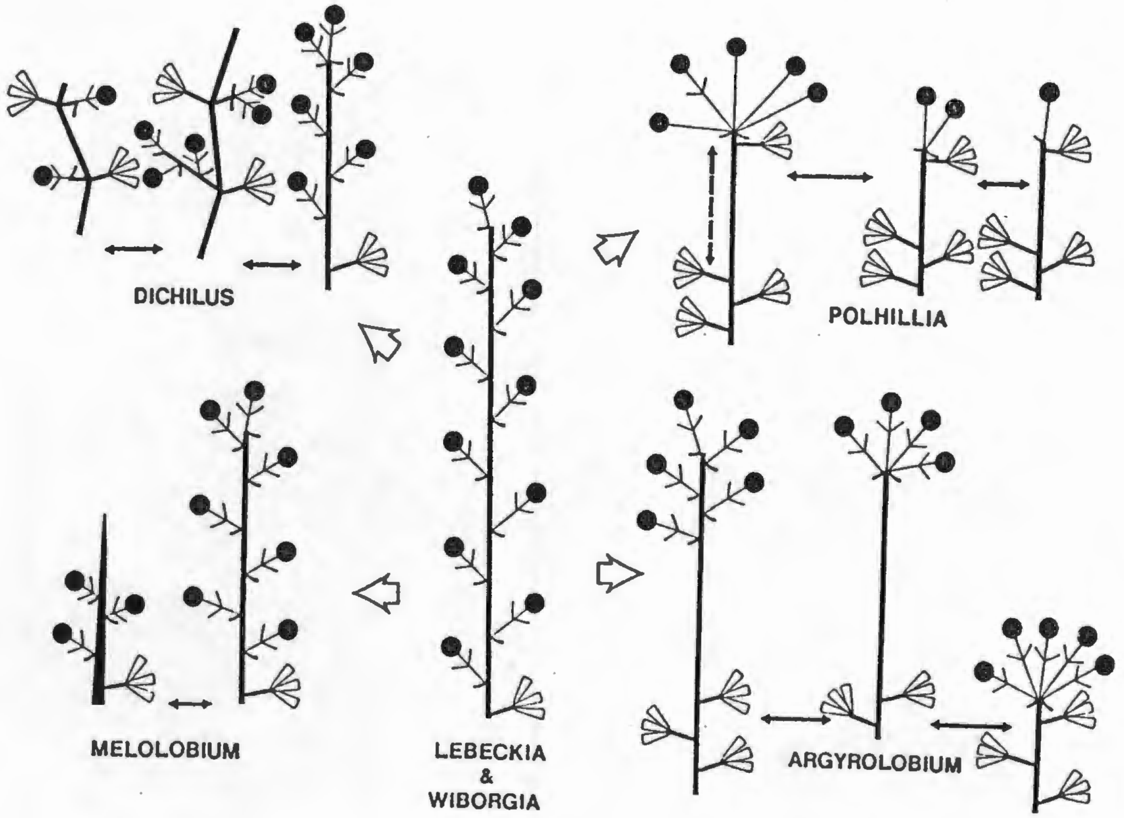


Figure 3. Inflorescence structure in the genera Lebeckia, Wiborgia, Dichilus, Melolobium, Polhillia and Argyrolobium. The inflorescences of Lebeckia, Wiborgia and Melolobium hardly differ in basic structure. Argyrolobium and Dichilus have sub-umbellate and condensed racemes respectively. These are usually leaf-opposed in Dichilus and occasionally also in Argyrolobium as a result of vegetative growth that may proceed from the upper leaf axil. The structure in Polhillia and Argyrolobium is superficially similar but differs in detail. In the former, the elongated uppermost internode functions as, and resembles the elongated peduncle as present in most species of Argyrolobium.

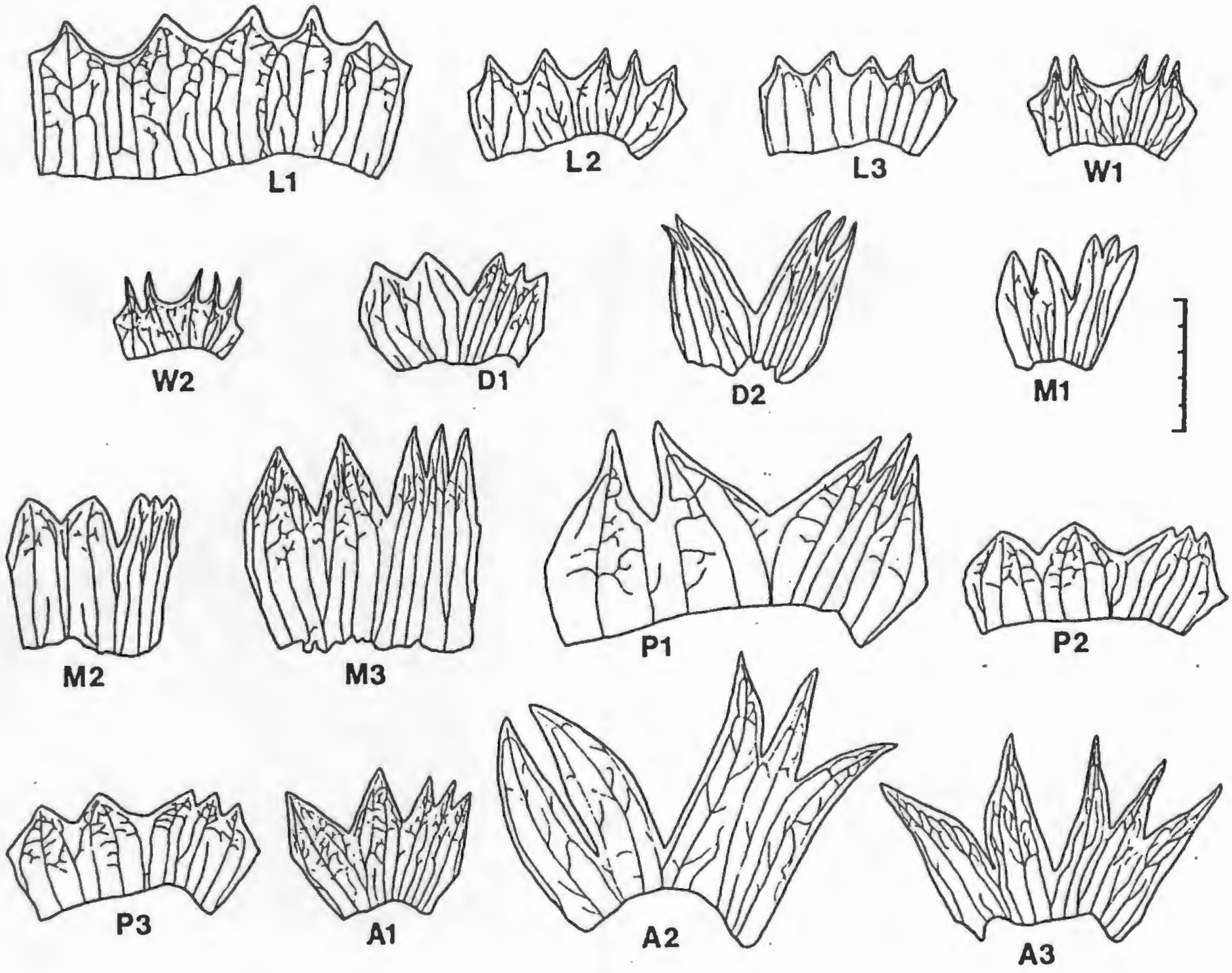


Figure 4. Calyx structure in various species of *Lebeckia*, *Wiborgia*, *Dichilus*, *Melolobium*, *Polhillia* and *Argyrolobium*. The calyces are opened out with the upper lobes to the left, vestiture not shown. In *Lebeckia*, the upper two lobes differ slightly from the lower ones, but all sinuses are of equal depth. *Wiborgia* species usually have the upper lobes separated by wider (but not deeper) sinuses from the lower. In the other genera, the three lower lobes form a distinct trifid lip. In *Dichilus* and in some species of *Melolobium* and *Argyrolobium*, the upper lobes are fused as well, resulting in a bilabiate calyx. L1, *Lebeckia cytisoides* (V14); L2, *L. leipoldtiana* (V15); L3, *L. mucronata* (V16); W1, *W. obcordata* (V36); W2, *Wiborgia fusca* subsp. *fusca* (V35); D1, *Dichilus strictus* (V11); D2, *D. pilosus* (V8); M1, *Melolobium subspicatum* (V24); M2, *M. wilmsii* (V26); M3, *M. involucratum* (V19); P1, *Polhillia canescens* (V29); P2, *P. pallens* (V31); P3, *Polhillia waltersii* (V34); A1, *Argyrolobium brevicalyx* (V2); A2, *A. molle* (V4); A3, *A. variopile* (V5). Voucher numbers as in Table 1.

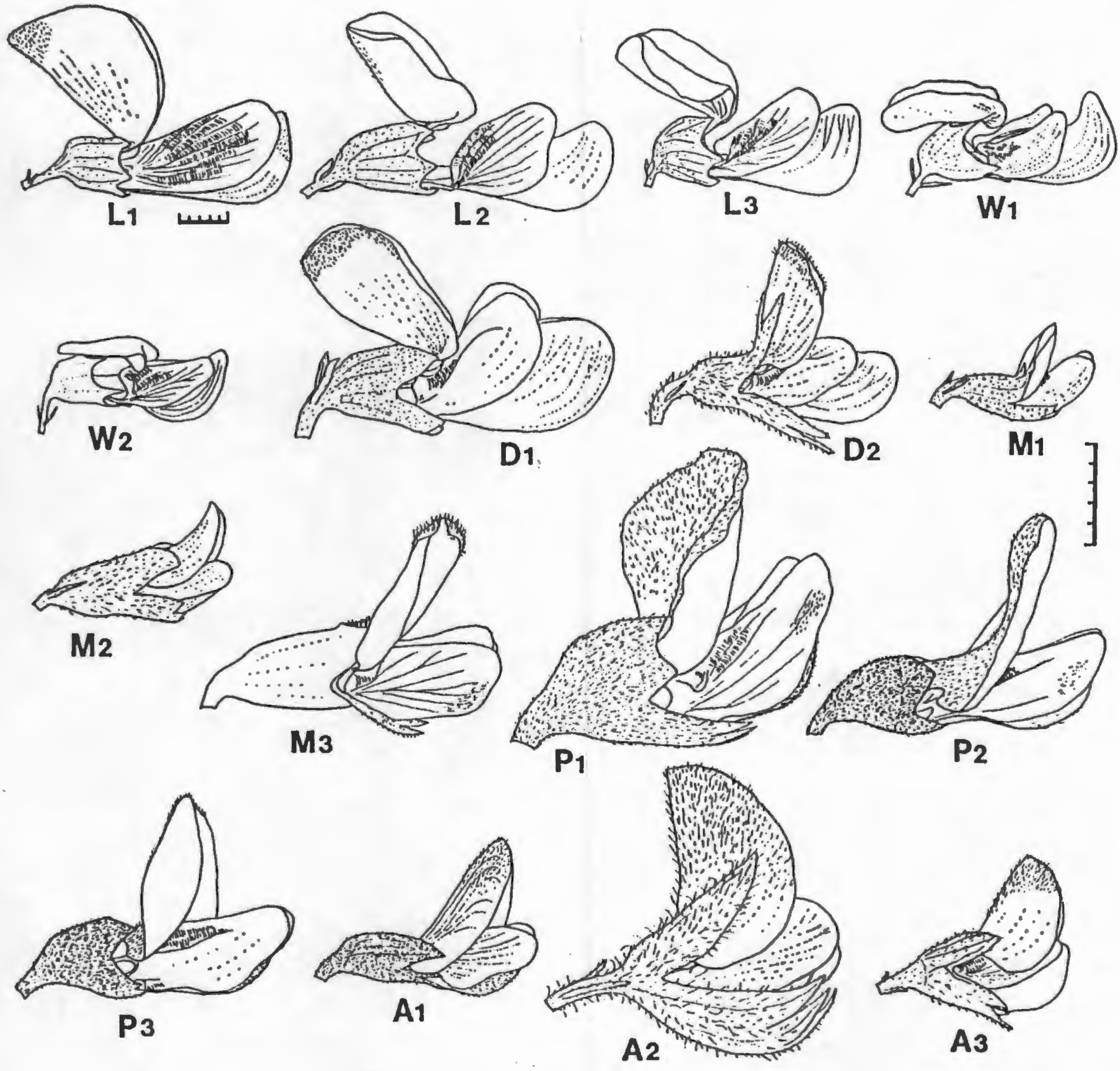


Figure 5. Flowers from various species of *Lebeckia*, *Wiborgia*, *Dichilus*, *Melolobium*, *Polhillia* and *Argyrolobium* as seen in lateral view. Note the presence or absence of bracteoles and the relative lengths, orientation and vestiture of flower parts. L1, *Lebeckia cytisoides* (V13); L2, *L*. *leipoldtiana* (V15); L3, *L*. *mucronata* (V16); W1, *W*. *obcordata* (V36); W2, *Wiborgia fusca* subsp. *fusca* (V35); D1, *Dichilus strictus* (V11); D2, *D*. *pilosus* (V8); M1, *Melolobium subspicatum* (V24); M2, *M*. *wilmsii* (V27); M3, *M*. *involucratum* (V20); P1, *Polhillia canescens* (V29); P2, *P*. *pallens* (V31); P3, *Polhillia waltersii* (V34); A1, *Argyrolobium brevicalyx* (V2); A2, *A*. *molle* (V4); A3, *A*. *variopile* (V7). Voucher numbers as in Table 1.

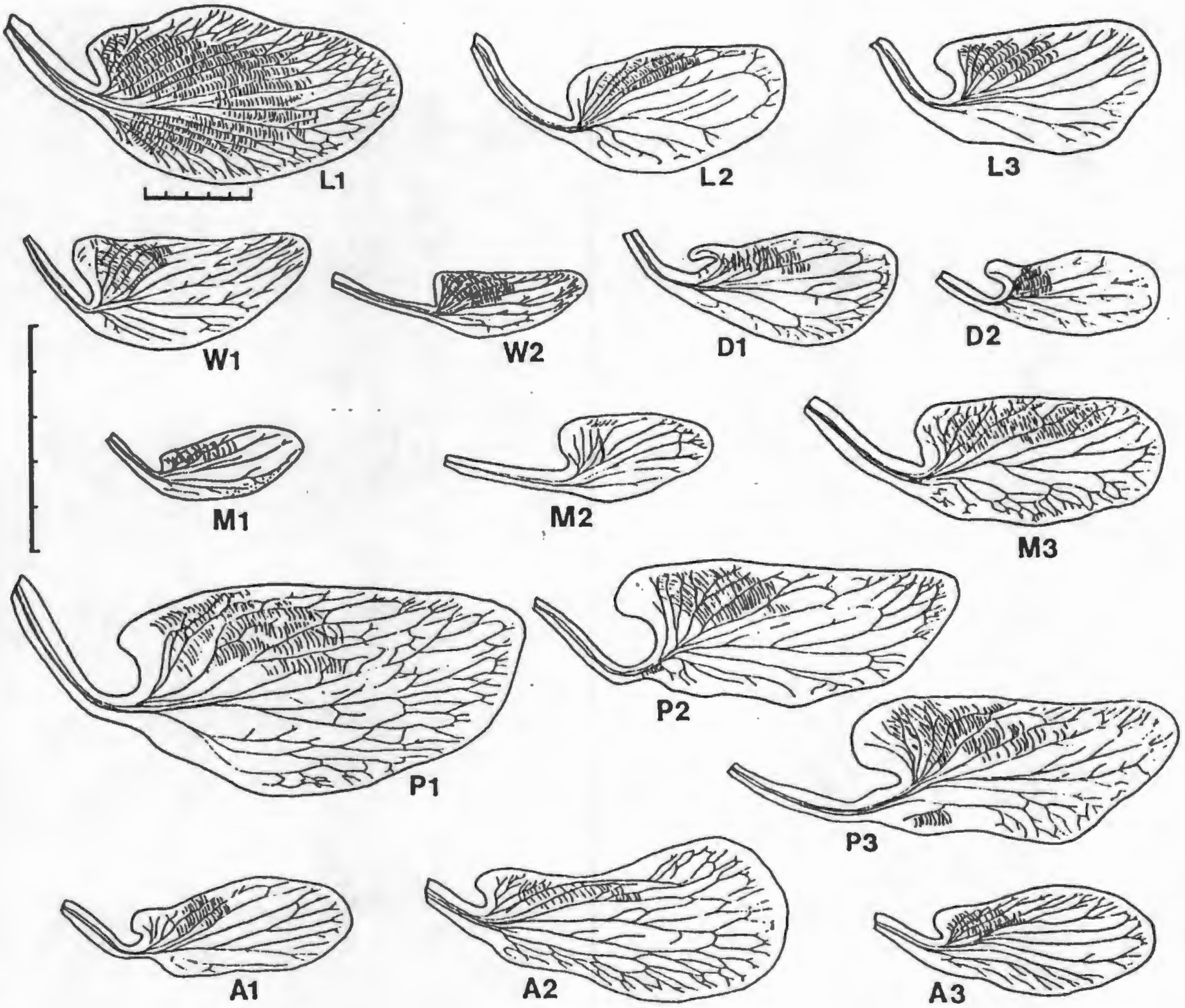


Figure 6. Wing petals of various species of *Lebeckia*, *Wiborgia*, *Dichilus*, *Melolobium*, *Polhillia* and *Argyrolobium*, vestiture not shown. There are considerable variation in size, shape and sculpturing, but none of these characters appear to be of taxonomic value at the generic level. The elongated auricles in *Dichilus* are distinct for this genus. L1, *Lebeckia cytisoides* (V14); L2, *L. leipoldtiana* (V15); L3, *L. mucronata* (V16); W1, *W. obcordata* (V36); W2, *Wiborgia fusca* subsp. *fusca* (V35); D1, *Dichilus strictus* (V11); D2, *D. pilosus* (V8); M1, *Melolobium subspicatum* (V25); M2, *M. wilmsii* (V26); M3, *M. involucratum* (V19); P1, *Polhillia canescens* (V29); P2, *P. pallens* (V31); P3, *Polhillia waltersii* (V34); A1, *Argyrolobium brevicalyx* (V1); A2, *A. molle* (V4); A3, *A. variopile* (V5). Voucher numbers as in Table 1.

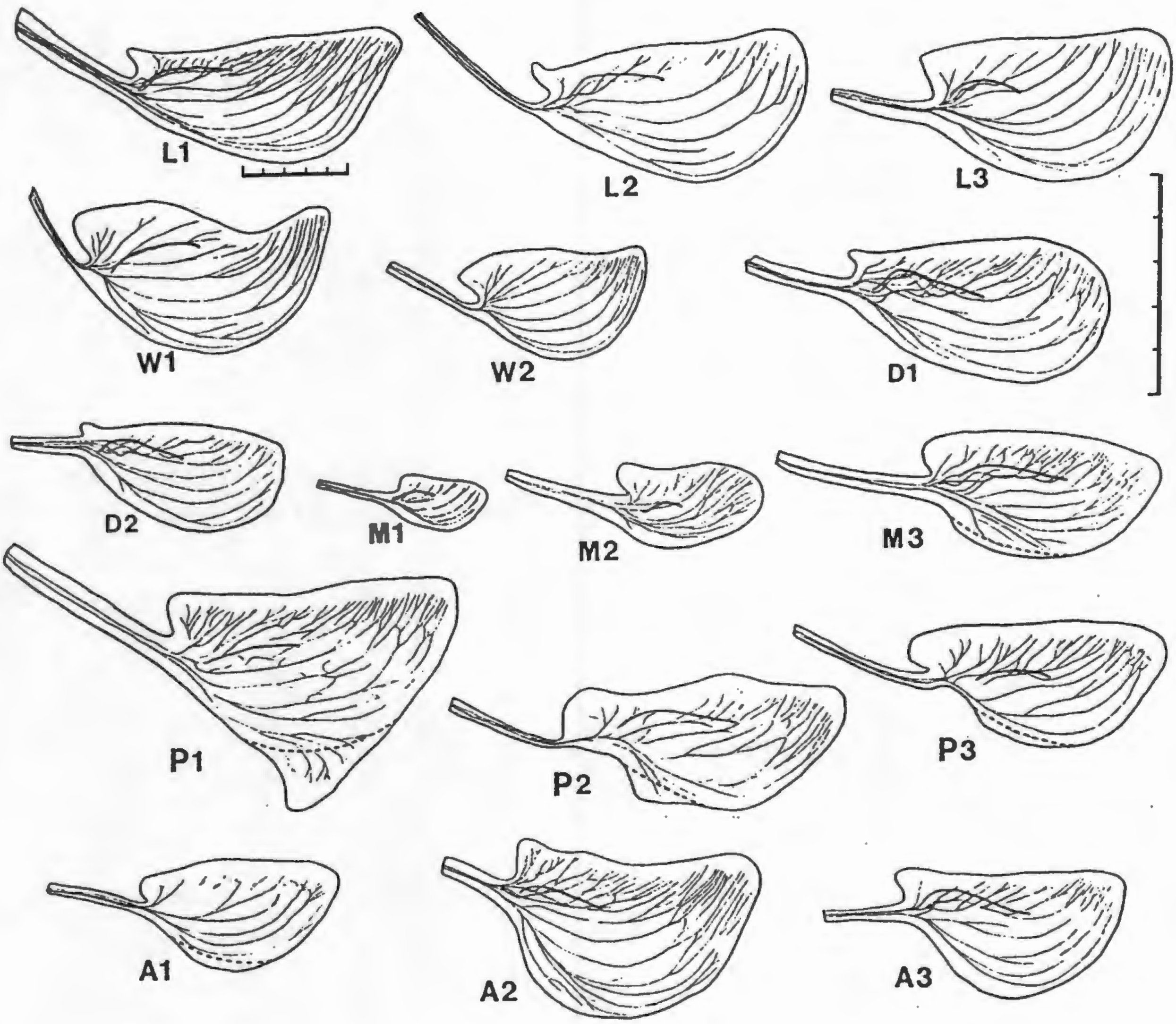


Figure 7. Keel petals of various species of *Lebeckia*, *Wiborgia*, *Dichilus*, *Melolobium*, *Polhillia* and *Argyrolobium*, vestiture not shown. The rather subtle differences in shape may be of some significance, especially in *Wiborgia* (rostrate) and *Dichilus* (obtuse). *Polhillia*, *Argyrolobium brevicalyx* and *Melolobium involucratum* are distinct in the imbricate arrangement of the keel petals. The area of overlap between the two petals are indicated by broken lines. L1, *Lebeckia cytisoides* (V14); L2, *L. leipoldtiana* (V15); L3, *L. mucronata* (V16); W1, *W. obcordata* (V36); W2, *Wiborgia fusca* subsp. *fusca* (V35); D1, *Dichilus strictus* (V11); D2, *D. pilosus* (V8); M1, *Melolobium subspicatum* (V25); M2, *M. wilmsii* (V26); M3, *M. involucratum* (V19); P1, *Polhillia canescens* (V29); P2, *P. pallens* (V31); P3, *Polhillia waltersii* (V34); A1, *Argyrolobium brevicalyx* (V1); A2, *A. molle* (V4); A3, *A. variopile* (V5). Voucher numbers as in Table 1.

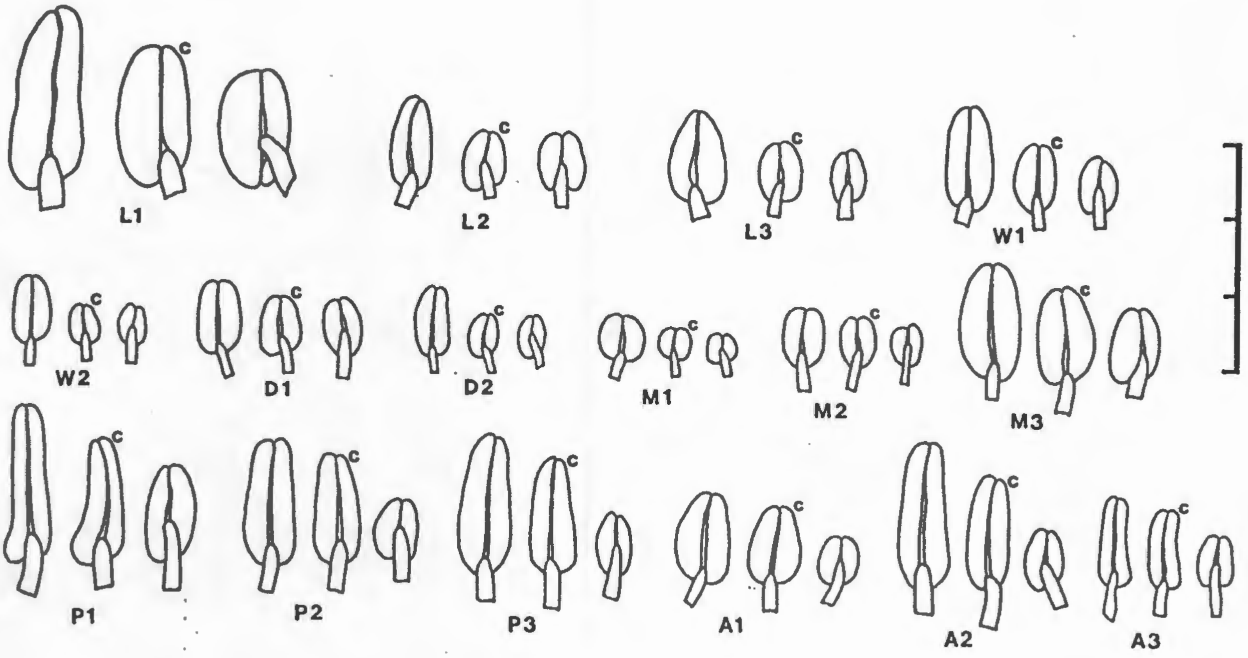


Figure 8. Size, shape and attachment of anthers in various species of Lebeckia, Wiborgia, Dichilus, Melolobium, Polhillia and Argyrolobium. Basifixed long anthers, carinal anthers (c) and short dorsifixed ones from left to right respectively. In Polhillia, Argyrolobium and Melolobium involucratum, the carinal anther is almost but not quite as long as the long anthers. The carinal anthers in all the other species are intermediate in size and attachment and usually more closely resemble the short ones. L1, Lebeckia cytisoides (V13); L2, L. leipoldtiana (V15); L3, L. mucronata (V16); W1, W. obcordata (V36); W2, Wiborgia fusca subsp. fusca (V35); D1, Dichilus strictus (V11); D2, D. pilosus (V8); M1, Melolobium subspicatum (V25); M2, M. wilmsii (V26); M3, M. involucratum (V20); P1, Polhillia canescens (V29); P2, P. pallens (V31); P3, Polhillia waltersii (V34); A1, Argyrolobium brevicalyx (V2); A2, A. molle (V4); A3, A. variopile (V5). Voucher numbers as in Table 1.

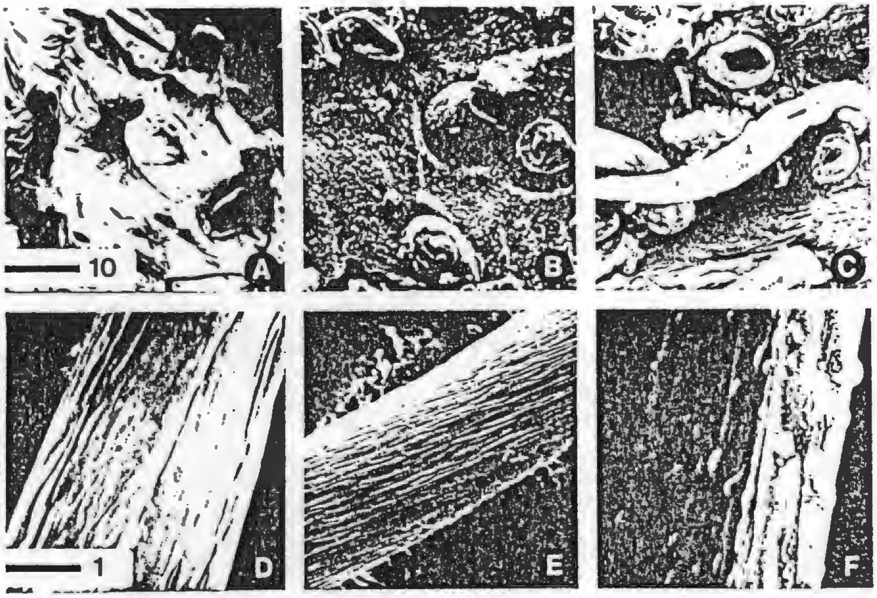


Figure 9. Trichome characteristics of some species of *Lebeckia*, *Wiborgia*, *Melolobium* and *Polhillia*. A, glandular hairs on the fruit of *Melolobium stipulatum* (V22); B, basal cells of broken-off hairs on the fruit of *Melolobium involucratum* (previously apparently mistaken for glands) (V20); C, hair and hair bases on the fruit of *Polhillia waltersii* (V34); D, smooth hair surface (*Wiborgia fusca* subsp. *fusca*, V35); E, striated hair surface (*Melolobium involucratum*, V20); verrucose hair surface (*Lebeckia mucronata*, V16). Voucher numbers as in Table 1. Scale in µm.

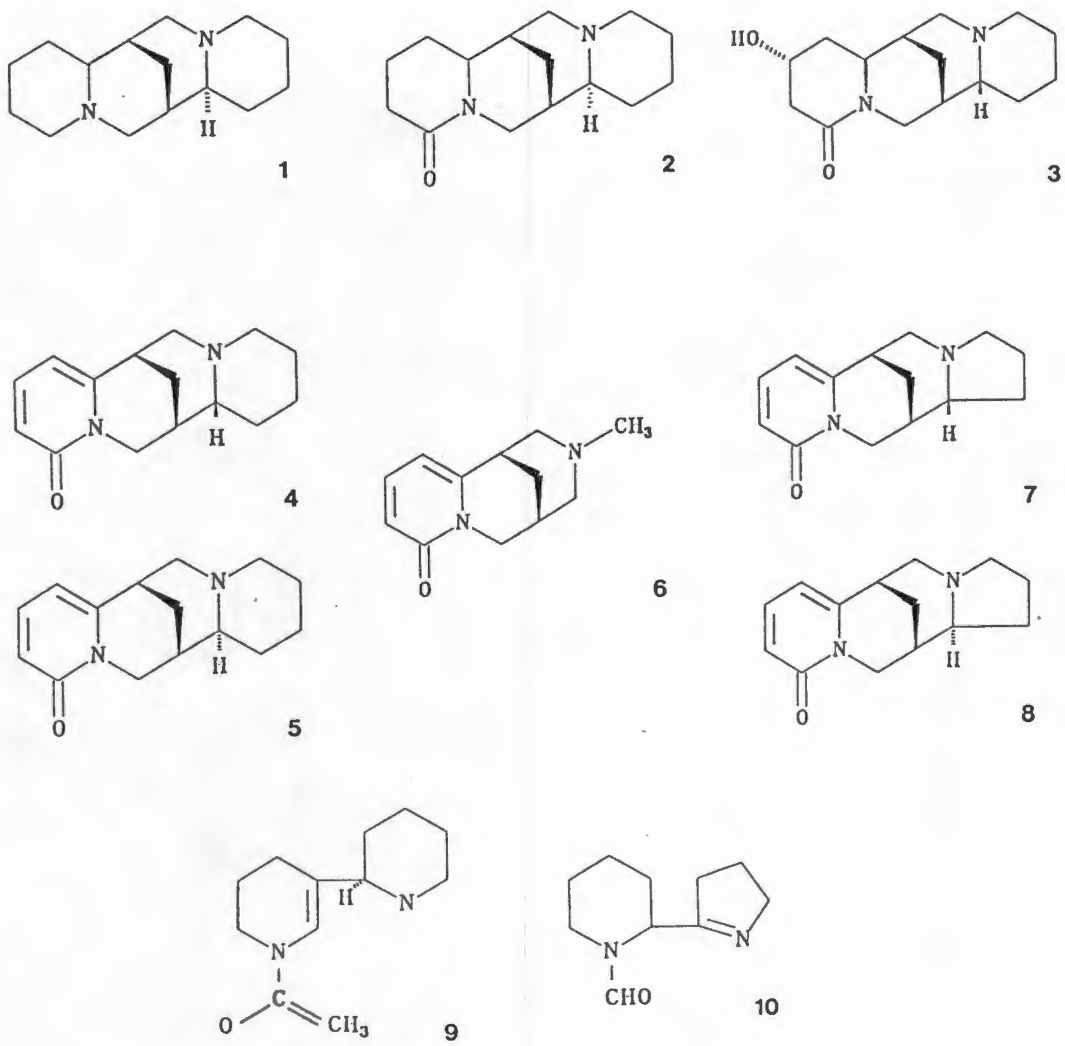


Figure 10. Major alkaloids of the genera *Lebeckia* (1,2,3), *Wiborgia* (1,2,3), *Dichilus* (4,9,10), *Melolobium* (2,4,5,6,7,8), *Polhillia* (1,2,5,6) and *Argyrolobium* (5,6). 1, sparteine; 2, lupanine; 3, nuttalline; 4, thermopsine; 5, anagyrine; 6, *N*-methylcytisine; 7, camoensine; 8, leontidine; 9, ammodendrine; 10, smipine.

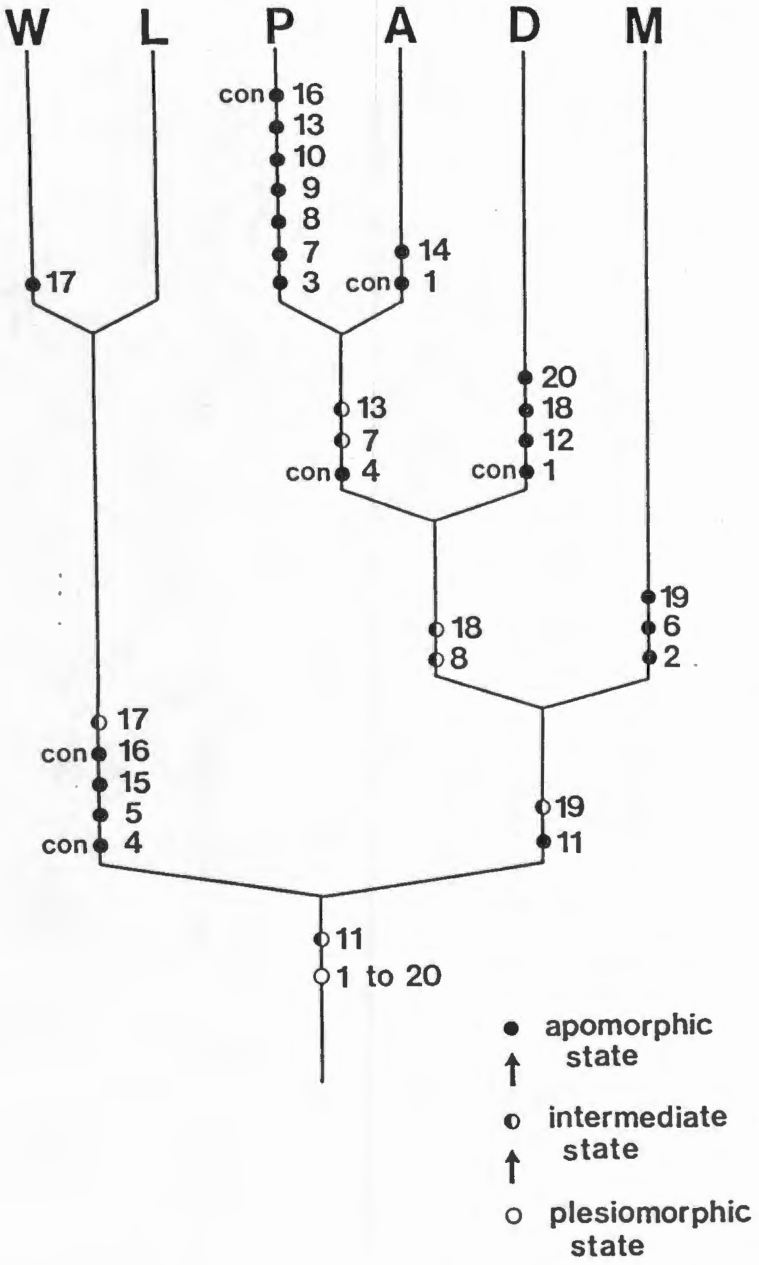
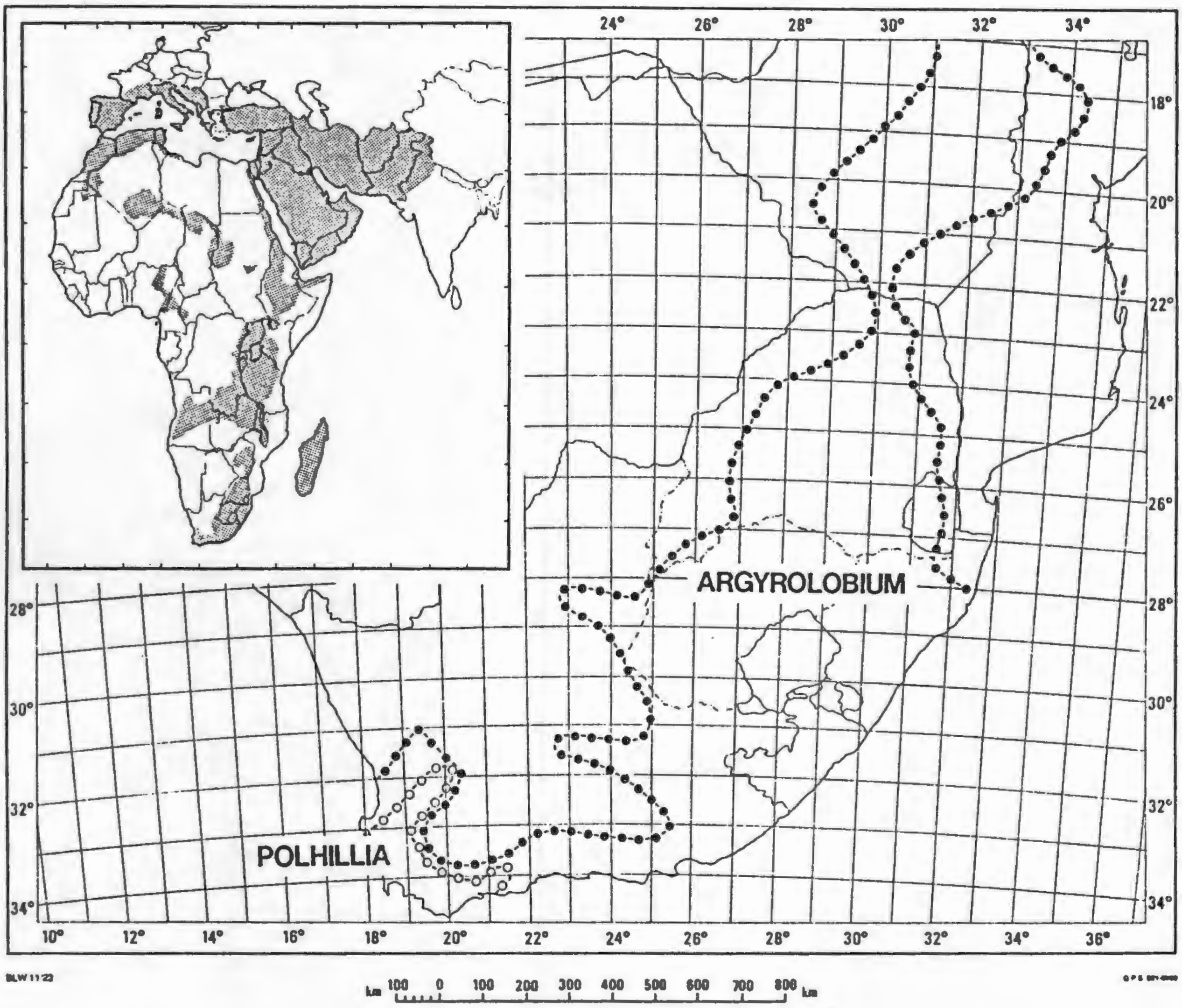
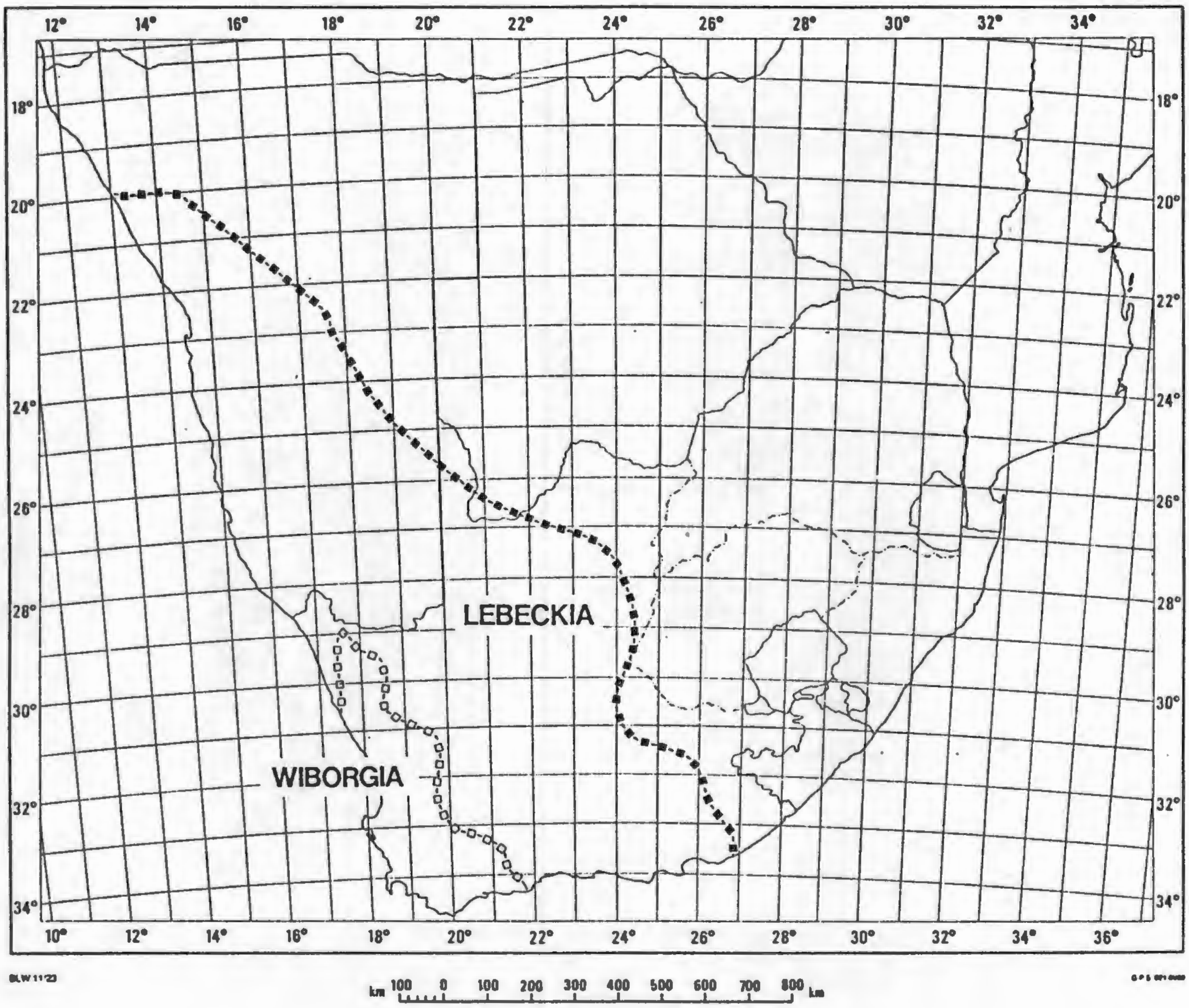


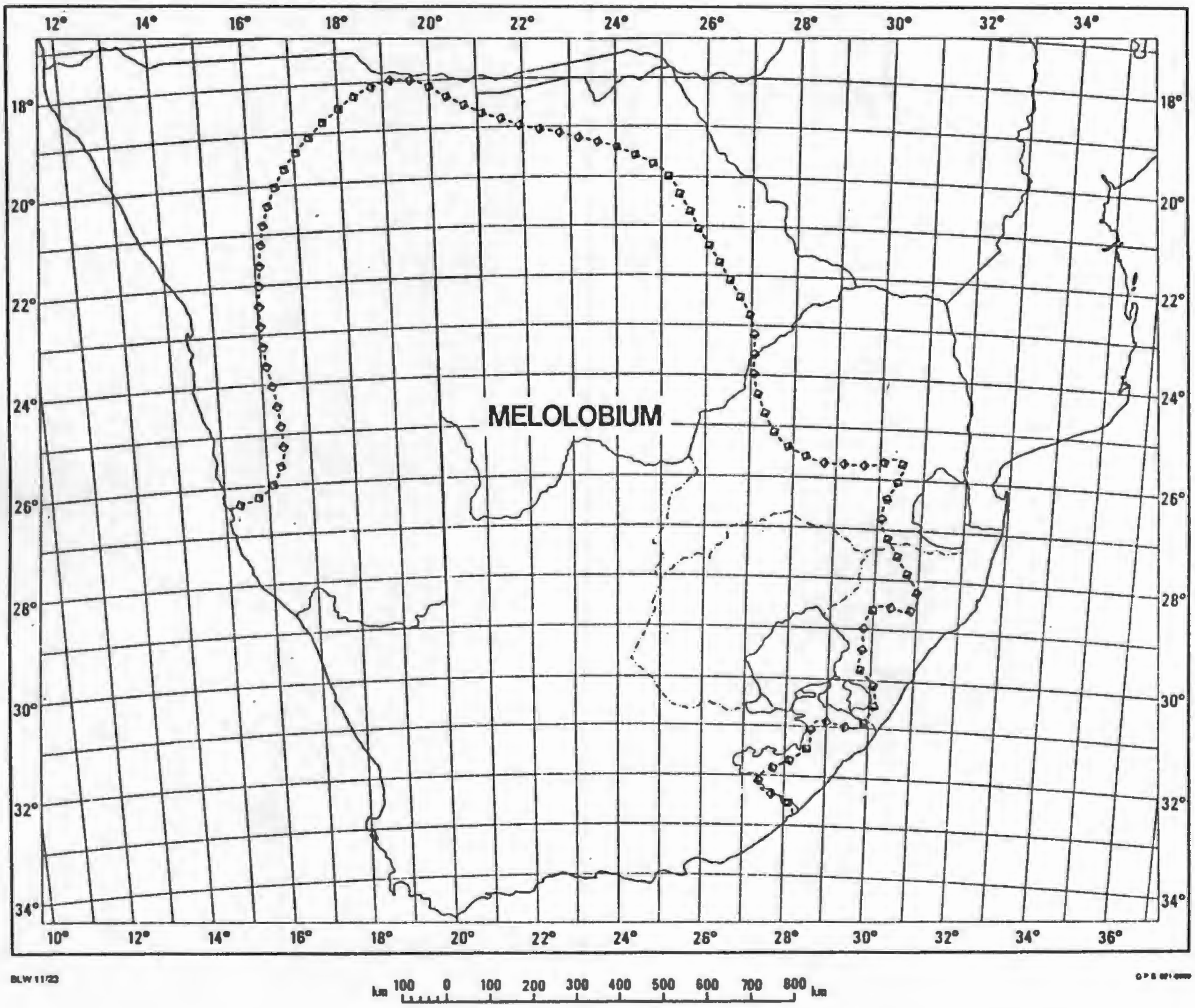
Figure 11. Cladogram of hypothetical phylogenetic relationships among the genera *Lebeckia*, *Wiborgia*, *Dichilus*, *Melolobium*, *Polhillia* and *Argyrolobium*. The most parsimonious result obtained by the algorithmic method of Kluge & Farris (1969) of the data in Table 4, is shown. Character states and character polarizations are also listed in Table 3.



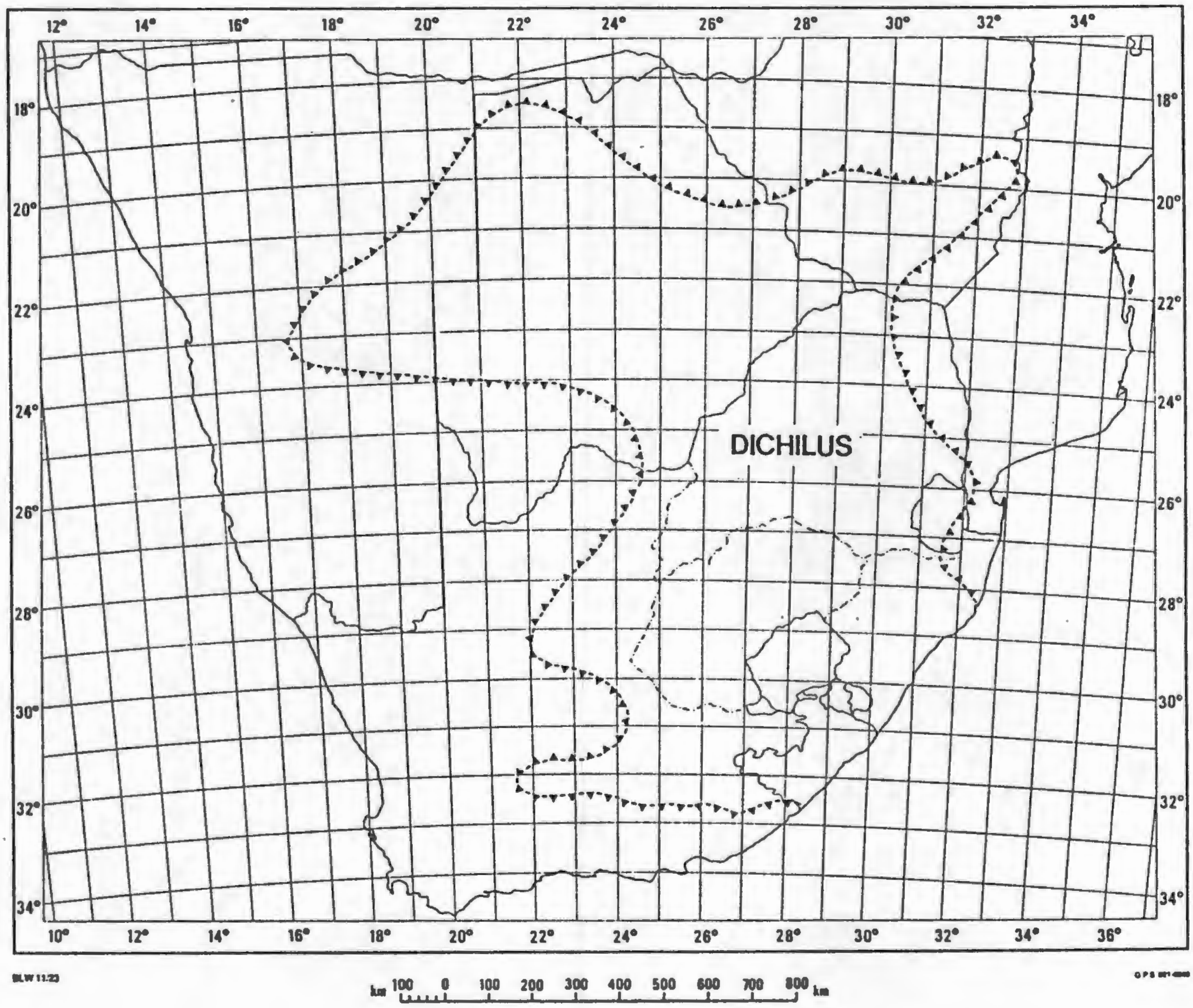
Map 1. Approximate geographical distribution of the genera *Argyrolobium* and *Polhillia*. The distributions of *Argyrolobium brevicalyx* and *Melolobium involucratum* are included under the latter. (Information taken from the PRE data base, Stirton 1986a and various other sources)



Map 2. Approximate geographical distribution of the genera Lebeckia and Wiborgia. (Information for Lebeckia from Van Wyk 1988 and for Wiborgia from Dahlgren 1975)



Map 3. Approximate geographical distribution of the genus Melolobium. (Information from the PRE data base and Schreiber 1970)



Map 4. Approximate geographical distribution of the genus Dichilus. (Information from Schutte & Van Wyk 1988)

APPENDIX 18

S. Afr. J. Bot., 1987, 53(2): 161 – 165

Lotononis brevicaulis (Fabaceae — Crotalarieae): A new species from the south-western Cape Province

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Lotononis brevicaulis B – E. van Wyk, an unusual new species, is described. It is not closely related to any known species and shows a unique combination of character states not previously recorded in *Lotononis*: a remarkable habit, with branch dimorphism and corresponding leaf dimorphism, a common occurrence of 6- and 7-foliolate leaves and large, tubular flowers. The known geographical distribution and morphological variation are described and illustrated. Based on available evidence, the new species is tentatively placed in *Lotononis* section *Lipozygis* (E. Mey.) Benth. near the *L. pentaphylla* (E. Mey.) Benth. group.

Lotononis brevicaulis B – E. van Wyk, 'n ongewone nuwe spesie, word beskryf. Dit is nie naverwant aan enige bekende spesie nie en toon 'n unieke kombinasie van kenmerke wat nog nie voorheen in *Lotononis* waargeneem is nie: 'n merkwaardige groeivorm, met stingeldimorfisme en ooreenstemmende blaardimorfisme, 'n algemene voorkoms van 6- en 7-gefolioleerde blare en groot, buisvormige blomme. Die bekende geografiese verspreiding en morfologiese variasie word beskryf en geïllustreer. Aan die hand van beskikbare inligting, word die nuwe spesie voorlopig in *Lotononis* seksie *Lipozygis* (E. Mey.) Benth. naby die *L. pentaphylla* (E. Mey.) Benth.-groep, geplaas.

Keywords: Crotalarieae, dimorphism, Fabaceae, *Lotononis*, taxonomy

Introduction

The genus *Lotononis* (DC.) Eckl. & Zeyh. is the third largest genus of the Fabaceae in southern Africa and comprises a variable assemblage of some 110 species.

Bentham (1843) had the greatest influence on the generic concept of *Lotononis* by reducing various genera of Ecklon & Zeyher (1836) and Meyer (1836) to sectional status within it. This treatment (with minor modifications) was followed by Harvey (1862) and Dümmer (1913). Many characters, the combinations of which are used as diagnostic features for related genera, are also present in *Lotononis*. Marked similarities exist between *Lebeckia* Thunb. and *Lotononis* section *Aulacinthus* (E. Mey.) Benth., *Buchenroedera* Eckl. & Zeyh. and *Lotononis* section *Krebsia* (Eckl. & Zeyh.) Benth., *Crotalaria* L. and *Lotononis* section *Oxydium* Benth. and also *Pearsonia* Dümmer and some species of *Lotononis*. The critical question is whether these similarities indicate evolutionary relationship or merely reflect similar adaptations in unrelated groups.

The significance of the new species described below is that it adds yet another unique combination of characters (branch dimorphism with corresponding leaf dimorphism and 6- and 7-foliolate leaves) to an already diverse and complex genus.

Lotononis brevicaulis *B – E. van Wyk*, sp. nov.

Caulis perennis erectus, simplex vel dichotome furcatus, (15 –)30 – 40 (– 60) mm longus, apicem versus valde incrassatus propter molem densam fundorum petiolorum persistentium atque residuorum surculorum annuorum superiorum. *Ramuli floriferi* procumbentes (20 –) 40 – 60(– 120) mm longi, post fructificationem emorientes. *Folia* digitate (5 –)6 – 7(– 8)-foliolata, valde dimorpha; folia caulina longipetiolata, petiolis (10 –)30 – 40(– 60) mm longis, parte tertia ima valde dilatata, dense lanata; parte superiore filiforme, terete, pilis sparsis brevibus; foliolis (5 –)10 – 15(– 18) mm longis, 2 – 5 mm latis, conduplicatis, ellipticis vel anguste oblanceolatis; folia surculis annuis insidentia breviora et minora, petiolis basin versus non dilatatis. *Stipulae* binatae. *Inflorescentiae* terminales, laxe (1 –)2 – 4(– 6) floratae. *Flores* magni flavi tubulares; bracteae magnae, foliiformes. *Calyx* 10 – 14 mm longus, lobo imo aegre angustiore. *Vexillum* 14 – 29 mm longum, late ovatum, longe unguiculatum. *Alae* longiores quam carina. *Androecium* monadelphum, antheris dimorphis. *Pistillum* 14 – 19 mm longum, stylo curvato. *Fructus* inflatus, suturam superiorem secus eminentiis.

Species omnino distinctus, haud arcte ullae speciei cognitae affinis. *L. anthylloidi* Harv., *L. pentaphyllae* (E. Mey.) Benth. et *L. polycephalae* (E. Mey.) Benth. habitu et forma foliolorum similis, sed foliis 6- vel 7-foliolatis et petiolis foliorum caulinum basin versus planatis, dilatatis, dense pilosis differt. Valde etiam racemo laxo pauciflorifero (non capitulis densis), stipulis binatis, floribus valde maioribus, calyce, corolla et vestitura a speciebus illis differt. Similis est speciebus sicut *L. involucratae* (E. Mey.) Benth. et *L. azureae* (Eckl. & Zeyh.) Benth. fructui margine superiore dentato.

TYPUS — Cape Province: Tweedside, Laingsburg. 27/12/1951, *Compton 22867 charta 1* (NBG, holotypus!)

Perennial dwarf shrublet with a distinctly dimorphic branch system consisting of a short, erect, persistent stem from which lax, horizontally divergent flowering shoots develop annually. *Perennial stem* (caudex) erect, single or dichotomously forked in older specimens, (15 –)30 – 40(– 60) mm long, much thickened apically due to a dense mass of persistent petiole bases and the remains of annual shoots of previous seasons. *Flowering branchlets* procumbent, (20 –)40 – 60(– 120) mm long, dying back after fruiting, the basal part remaining on the caudex for some years. *Leaves* digitately (5 –)6 – 7(– 8)-foliolate, markedly dimorphic; cauline leaves long-petiolate; petioles (10 –)30 – 40(– 60) mm long, the basal third much dilated, thin, chartaceous, distinctly 3-veined, densely covered with long reddish-brown woolly hairs, upper part filiform, terete, with sparse, short hairs; leaflets (5 –)10 – 15(– 18) mm long, 2 – 5 mm wide, equal in size and shape, conduplicate, elliptic to narrowly oblanceolate, base narrowly cuneate, apex rounded, obtuse, acute or acuminate, densely strigose-hirsute; leaves on annual shoots shorter and smaller; petioles (3 –) 5 – 12(– 22) mm long, not dilated basally; leaflets (2 –) 5 – 10(– 14) mm long, 1 – 4 mm wide, oblanceolate to obovate, base cuneate to narrowly cuneate, apex rounded or obtuse, less hairy than the cauline leaflets, often sparsely strigose and glabrescent abaxially. *Stipules* in pairs, (1 –) 2 – 4(– 10) mm long, up to 2 mm wide, narrowly lanceolate to narrowly elliptic, occasionally falcate. *Inflorescences* terminal on annual shoots, laxly (1 –)2 – 4(– 6)-flowered, the flowers mostly in pairs, opening ± simultaneously. *Flowers* very large, 15 – 30 mm long, yellow, tubular; pedicel 2 – 7 mm long; bracts large, 7 – 15 mm long, broadly lanceolate to ovate, leaf-like; bracteoles absent or very rarely present on the terminal pedicel only, 3 – 4 mm long, up to 0,5 mm wide. *Calyx* 10 – 14 mm long, tubular, slightly inflated, shorter than the corolla; lobes triangular, ± equal in length; lateral lobes fused a little higher in pairs; lower lobe not much narrower, densely hirsute or patently hirsute with reddish-brown hairs, glabrous inside. *Standard* large, 14 – 29 mm long, only the upper half of the blade slightly reflexed at anthesis; claw narrow, up to 10 mm long; blade up to 20 mm long, broadly ovate, dorsally densely hirsute on a well-defined triangular zone along the middle of the blade. *Wing petals* 15 – 22 mm long; claw 6 – 10 mm long, curved; blade 4 – 7 mm wide, only slightly auricled and pocketed; sculpturing exposed, upper basal and upper central, lamellate and lunate-lamellate, in 4 – 7 rows of 20 – 30 irregular reclined transcostal lunae, fading upper right central into a few intercostal lunae, a few transcostal lamellae occasionally present on the apex of the claw. *Keel petals* up to 20 mm long, shorter than wing petals; claw up to 10 mm long, curved; blade up to 10 mm long, 5 mm wide, semicircular, pointed, auriculate and pocketed near the base. *Androecium* as long as the keel, in a curved sheath open on the upper side; filaments flattened, ribbon-like; anthers dimorphic, alternately elongate, pointed, basifixed, 1,4 – 1,5 mm long and short, ovate, dorsifixed, 0,9 mm long, dorsifixed anthers on longer filaments at anthesis, carinal anther intermediate, on a yet longer filament. *Pistil* 14 – 19 mm long; ovary 6 – 9 mm long, lower side ± straight, upper side rounded, terete, sessile, densely hirsute; style merging gradually with ovary, basal half curving gently downwards, distal half curving gently upwards; stigma terminal, ovules *ca.* 25, funicles short, as long as the ovules. *Fruits* 17 mm long, 9 mm wide, longer than and partly covered by the persistent calyx, broadly elliptic, much inflated laterally, dark brown to black, densely hairy but glabrescent with age, with small peg-like projections and irregular narrow warty protuberances along the upper suture. Seed and chromosome number not known (Figures 1, 2, 3 & 4).

Geographical distribution and habitat

The species occurs in a relatively large area between the towns of Ceres, Worcester, Laingsburg and Swellendam in the south-western Cape Province (Figure 5). It is represented in South African herbaria by only 7 collections, made sporadically between 1926 and 1971. The known distribution corresponds closely to the Witteberg and Bokkeveld Group of the Cape Supergroup. Judged by information on herbarium labels, the species seems to favour sandy soils.

All known localities are situated in the dry transitional area

Figure 1 The peculiar habit of *Lotononis brevicaulis*, showing the short caudex densely covered with persistent leaf bases, the procumbent annual flowering shoots and the large tubular flowers (*Compton 22867*). Life size.

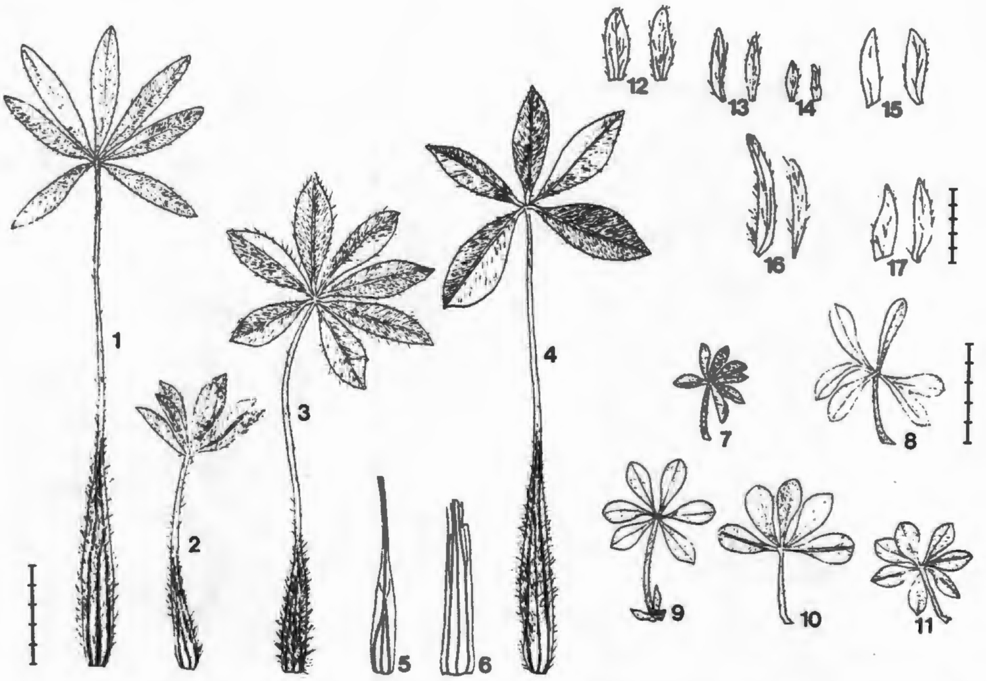

Figure 2 Variation in cauline leaves (1 – 6), leaves from annual shoots (7 – 11) and stipules (12 – 17) of *Lotononis brevicaulis*. 1, cauline leaf with leaflets opened out, showing the dilated petiole base (*Compton 22867*); 2, young cauline leaf showing the conduplicate leaflets (*Compton 22867*); 3, cauline leaf with leaflets opened out (*Barker 3025*); 4, cauline leaf with leaflets opened out (*Oliver 3496*); 5, petiole base of a young cauline leaf with the vestiture removed to show the venation (*Compton 22867*); 6, old petiole base, the vestiture removed (*Compton 22867*); 7, leaf from annual shoot showing the short petiole and conduplicate leaflets (*Compton 22867*); 8, unusual leaf with some leaflets only partially divided (*Compton 22867*); 9, leaf with stipules drawn in and leaflets opened out (*Compton 22867*); 10, quinquefoliolate leaf with leaflets opened out (*Barker 3025*); 11, 7-foliolate leaf with leaflets opened out (*Oliver 3496*); 12 & 13, stipule pairs (*Oliver 3496*); 14 & 15, stipule pairs (*Barker 3025*); 16 & 17, stipule pairs (*Compton 22867*). Scale in mm.

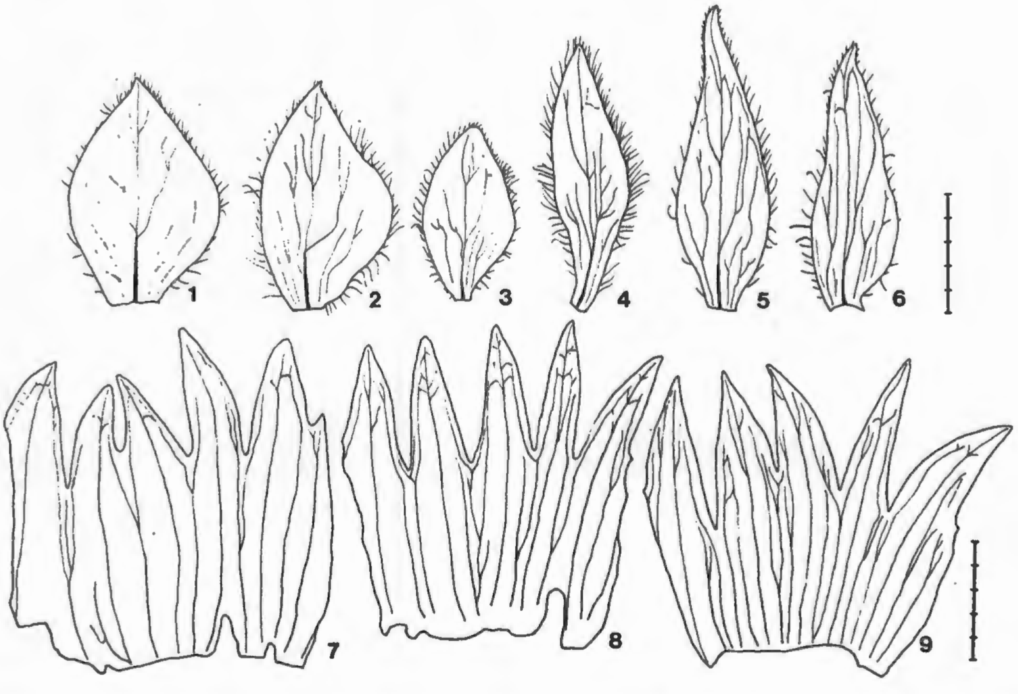

Figure 3 Variation in the bracts (1 – 6) and calyx structure (7 – 9) of *Lotononis brevicaulis*. 1 & 2, ovate bracts (*Barker 3025*); 3 & 4, ovate and elliptic bracts (*Compton 22867*); 5 & 6, lanceolate bracts (*Oliver 3496*); 7 – 9, calyx opened out with the upper lobes to the left, vestiture not shown: 7, upper lobes fused higher up in pairs, lower lobe slightly longer (*Barker 3025*); 8, lobes nearly equal in length and shape (*Compton 22867*); 9, upper lobes fused higher up in pairs, lower lobe narrowest (*Oliver 3496*). Scale in mm.

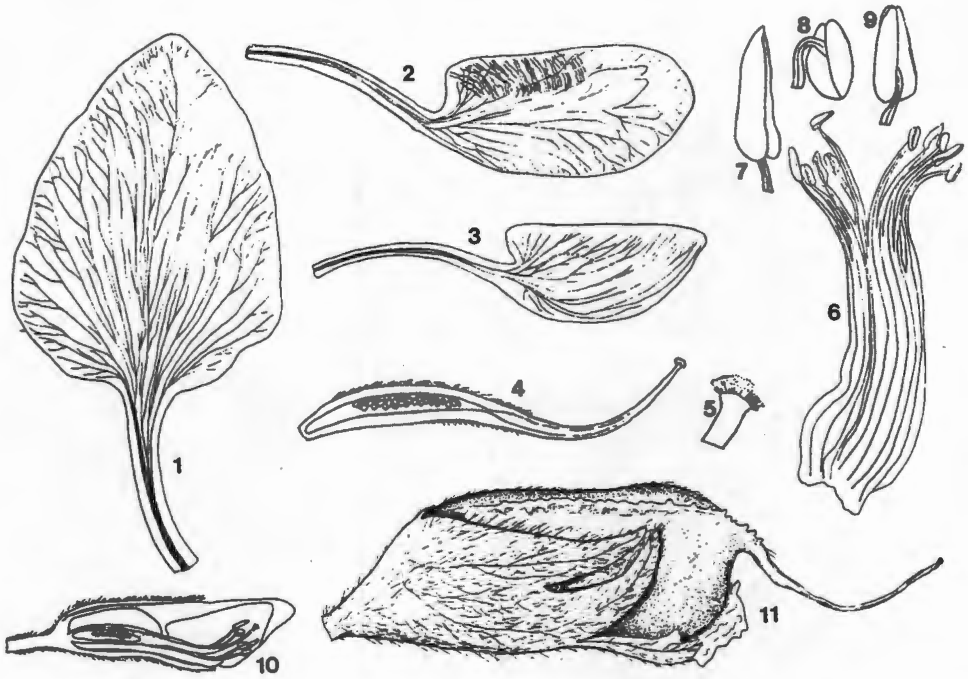

Figure 4 Detail of the flower and fruit of *Lotononis brevicaulis* (*Compton 22867*). 1, vexillum × 3; 2, wing petal, showing sculpturing × 3; 3, keel petal, showing auricle and pocket × 3; 4, longitudinal section of the pistil, showing the numerous ovules and the curvature of ovary and style × 3; 5, stigma × 12; 6, androecium at anthesis, showing the dimorphic anthers × 3; 7, basifixed anther, elongated and pointed × 12; 8, dorsifixed ovate anther × 12; 9, intermediate anther × 12; 10, longitudinal section of flower just before anthesis, showing the position and curvature of the pistil × 1,5; 11, fruit, showing the persistent calyx and protuberances along the upper suture × 3.

between fynbos and karroid vegetation with a recorded rainfall of 75 to 100 mm per annum. The peculiar habit of the plant (Figure 1) may be an adaptation to this low and highly seasonal rainfall.

Diagnostic features and systematic position

Lotononis brevicaulis is a very distinct species and its affinities are not obvious. *L. anthylloides* Harv., *L. pentaphylla* (E. Mey.) Benth. and *L. polycephala* (E. Mey.) Benth. are similar in habit and the shape of the leaflets. Apical dominance of the primary stem is not maintained as in *L. brevicaulis* however. A slight differentiation between stem and side shoots is only evident in young plants of these species. The stipules are paired in the new species (Figure 2), not solitary as in the abovementioned species.

L. brevicaulis appears to be unique in having a well-developed, erect, perennial caudex (covered with persistent petiole bases) which is clearly differentiated from the seasonal, short-lived flowering branches (Figure 1). This differentiation is extended to the leaves (Figure 2), where the long-petioled cauline leaves with dilated, clasping petiole bases differ markedly from the shorter and smaller leaves of the flowering shoots.

The quinquefoliolate condition is relatively common in *Lotononis*. It also occurs in the *L. pentaphylla* group and perhaps significantly, often unstably so, with 3, 4 and 5 leaflets on the same plant. In all the specimens of *L. brevicaulis* examined, 6- and 7-foliolate leaves predominate, although at least some 5-foliolate leaves are usually present (Figure 2). This is a new character state for *Lotononis*, not recorded in any other known species.

The inflorescences and flowers of the species referred to above differ markedly from those of *L. brevicaulis*, being arranged in dense, small-flowered heads rather than the lax, few- and large-flowered racemes of the latter. The flowers are amongst the largest in the genus and superficially resemble those of the genus *Pearsonia* Dümmer, where a 'gullet type' pollination mechanism occurs (Polhill 1973). Even the calyx (Figure 3) seems similar. As seen in Figure 4, however, the style is curved, the anthers are clearly dimorphic and the stamens remain within the keel. These characters would exclude the species from *Pearsonia* as presently circumscribed (Polhill 1973).

The large vexillum, pointed keel petals and turgid fruit (Figure 4) indicate an affinity with *Lotononis azurea* (Eckl. & Zeyh.) Benth. and its allies. Peg-like and warty projections are present along the upper suture of the fruit, such as are present in the section *Telina* (E. Mey.) Benth. and also elsewhere.

Even the vestiture does not provide a clear answer. The medifixed hairs of *L. brevicaulis*, with one arm short and the other similar or mostly very much longer, occur commonly in *Lotononis*. Medifixed hairs are found in *L. azurea* and its allies, but not in the *L. pentaphylla* group of species, which has ordinary uniseriate hairs. The longitudinally striated hair surface sculpturing, devoid of the round wart-like structures found on the hairs of most species of *Lotononis*, is present in both these groups.

A more definite decision on the systematic position of *L. brevicaulis* can only be taken once the full range of variation in the genus has been studied. Based on available evidence, the most appropriate position seems to be in the section *Lipozygis* (E. Mey.) Benth. near the *L. pentaphylla* group, where it is tentatively placed.

Specimens examined

—3319 (Worcester): Gydouw (–AB), 3/10/1942, *Leipoldt 4025* (BOL); Jakhalsnest, Ceres [probably Jakkalsnek] (–AD), 27/9/1944, *Barker*

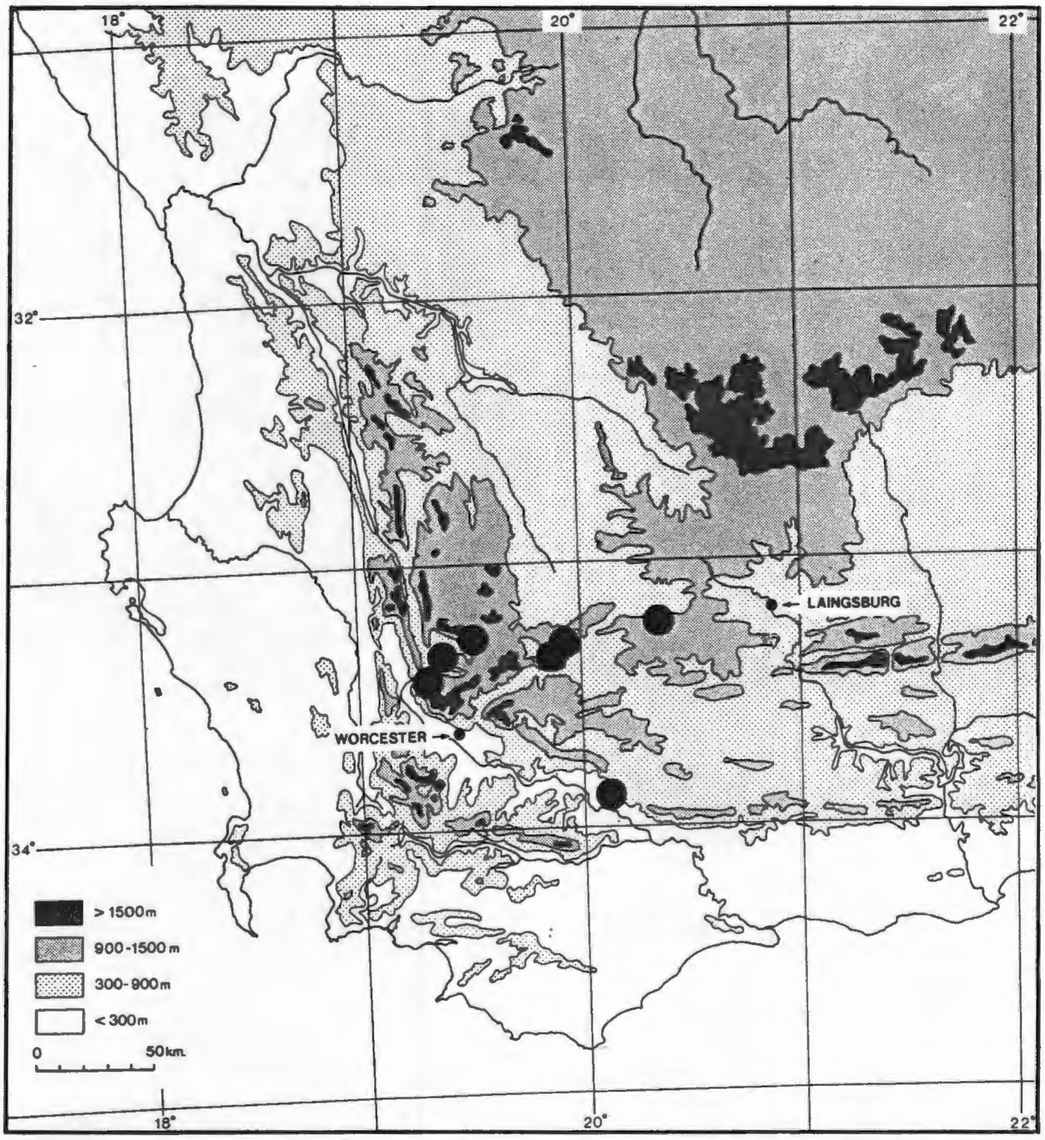

Figure 5 The known geographical distribution of *Lotononis brevicaulis*.

3025 (NBG, STE); Top of Theron's Berg Pass (– BC), 1/9/1926, *Levyns 1502* (BOL, K); Near Verkeerde Vlei (– BD), 9/1933, *Levyns 4610* (BOL); Bonteberg on farm Karrona, flats at base of mountain (– BD), 15/9/1971, *Oliver 3496* (PRE, STE).

—**3320** (Montagu): Tweedside, Laingsburg (– AB), 27/12/1951, *Compton 22867 sheet 1* (NBG), *22867 sheet 2* (NBG); Near Bonnievale (– CC), 9/1933, *Leighton 21160* (BOL).

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Studies in the genus *Lotononis* (Crotalarieae, Fabaceae). 1. Three new species of the section *Aulacinthus* from the Cape Province

B-E. VAN WYK*

Keywords: Cape Province, *Lotononis* section *Aulacinthus*, Fabaceae, new taxa

ABSTRACT

Three new species of the section *Aulacinthus* (E. Mey.) Benth. of *Lotononis* (DC.) Eckl. & Zeyh. are described: *L.* **comptonii** B-E. van Wyk, *L.* **dahlgrenii** B-E. van Wyk and *L.* **dissitinodis** B-E. van Wyk. These species are related to *L. gracilis* (E. Mey.) Benth. and *L. rigida* (E. Mey.) Benth. and are all endemic to marginal fynbos areas of the south-western Cape. The section now comprises seven species.

UITTREKSEL

Drie nuwe soorte van die seksie *Aulacinthus* (E. Mey.) Benth. van *Lotononis* (DC.) Eckl. & Zeyh. word beskryf: *L.* **comptonii** B-E. van Wyk, *L.* **dahlgrenii** B-E. van Wyk en *L.* **dissitinodis** B-E. van Wyk. Hierdie soorte is verwant aan *L. gracilis* (E. Mey.) Benth. en *L. rigida* (E. Mey.) Benth. en is almal endemies in marginale fynbosgebiede van die Suidwes-Kaap. Die seksie behels nou sewe soorte.

INTRODUCTION

The section *Aulacinthus* (E. Mey.) Benth. of *Lotononis* (DC.) Eckl. & Zeyh. comprises a small group of poorly known fynbos shrubs. Species of this section are remarkably similar in their leaves and habit to some species of *Lebeckia* Thunb., *Wiborgia* Thunb. and *Aspalathus* L.

When Bentham (1843) changed the status of *Aulacinthus* E. Mey. to a section of *Lotononis*, he remarked on its similarity to other genera of the Crotalarieae but also noted its distinguishing floral and fruit characters. The upper calyx lobes are usually fused in pairs on either side and the fruit is relatively short, laterally inflated and has the lower suture sunken to various degrees. In terms of fruit characters, the verrucose upper suture is perhaps the most significant and useful diagnostic feature. The seeds of all the species are distinctly tuberculate and not smooth as in other genera of the Crotalarieae. Bentham (1843) and Harvey (1862) listed for section *Aulacinthus*, three species [*L. gracilis* (E. Mey.) Benth., *L. rigida* (E. Mey.) Benth. and *L. viborgioides* Benth.] to which Dümmer (1913) added one [*L. leucoclada* (Schltr.) Dümmer, transferred from *Lebeckia*].

As part of a continuing taxonomic study of the genus *Lotononis*, I investigated the section *Aulacinthus* and found three undescribed species that clearly belong to this group. These are described below.

The circumscription of *Aulacinthus* and its status as a section need to be reconsidered. As a group it gradually merges (through yet another group of undescribed species) with the section *Polylobium* (Eckl. & Zeyh.) Benth. This problem, however, falls beyond the scope of the present paper.

Lotononis comptonii *B-E. van Wyk, sp. nov. L. gracili* (E. Mey.) Benth. valde affinis, sed habitu laxiore sparsiore, foliis ramunculisque sparse strigillosis (non dense albo-pubescentibus), stipulo unico in quoque nodo (in *L. gracili* stipulis omnino destitutis) et vexillo aurantiaco-rubro (in posteriore flavo) differt.

TYPE.—Cape, 3320 (Montagu): Laingsburg to Seweweekspoort Road, 9,5 km after entrance to Rietvlei Farm (–AD), 12.10.86, *B-E. van Wyk 2160* (PRE, holo.; BOL, C, JRAU, K, M, MO, NBG, SAAS, STE, iso.).

Lax, sparsely branched woody shrub, up to 0,4 m tall. *Branches* slightly corky, yellow-brown; young twigs sparsely strigillose. *Leaves* digitately trifoliolate (very rarely 4 or 5-foliolate); petiole (7–) 18–25 (–42) mm long, persistent for some time after the leaflets have been individually shed; leaflets obovate, narrowly oblong, or narrowly elliptical, (4–) 8–15 (–21) mm long, (1–) 2–3 (–5) mm wide, abaxially sparsely strigillose, adaxially glabrous. *Stipules* consistently present, single at each node, elliptic-oblong to narrowly lanceolate, (2–) 5–7 (–9) mm long. *Inflorescences* terminal, rarely subterminal, long-pedunculate, 60–150 mm long, sparsely (3–) 4–6 (–8) -flowered; bracts 2–3 (–5) mm long; bracteoles absent. *Flowers* 10–12 mm long, orange-red and yellow; pedicel 2–5 mm long. *Calyx* 6–8 mm long, with the lateral lobes on either side fused much higher up in pairs, minutely strigillose. *Standard* broadly ovate to orbicular, 8–12 mm long, longitudinally striate, orange to bright orange-red. *Wing petals* broadly oblong, slightly shorter than the keel; apex obtuse; sculpturing upper basal and upper central, in 4–5 rows of intercostal lunae. *Keel petals* broadly elliptical, auriculate and pocketed near the base. *Anthers* dimorphic. *Pistil* 10–12 mm long; ovary short, oblong-ovate, 4–6 mm long. *Fruit* 12–15 mm long, 4–5 mm wide, laterally much inflated, lower suture sunken, upper suture verrucose, glabrous. *Seed* suborbicular in side view, up to 2 mm long, distinctly tuberculate, reddish brown (Figure 1).

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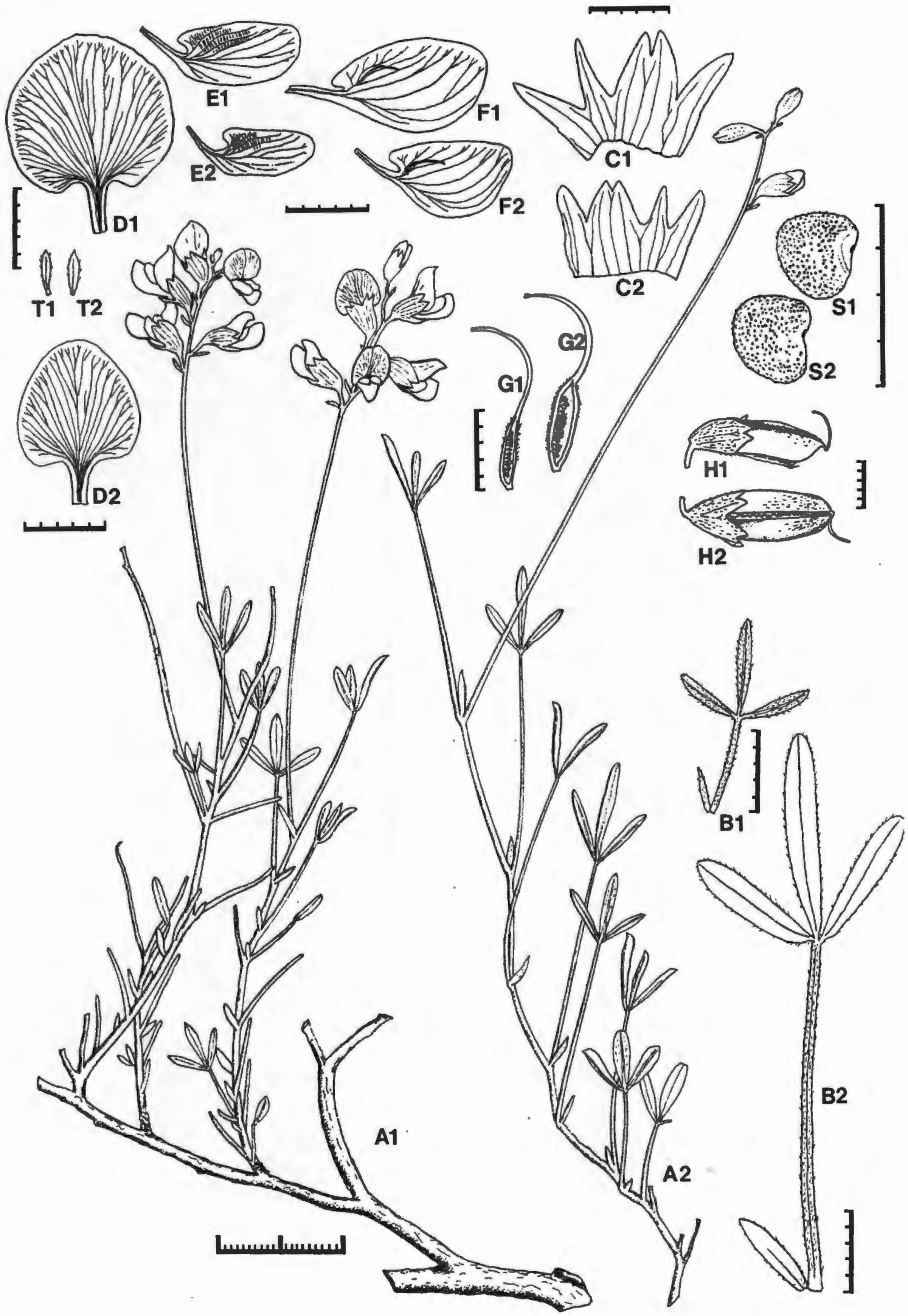

FIGURE 1.—*Lotononis comptonii*. A1, A2, flowering branches; B1, B2, leaves, showing the single stipule and vestiture; C1, C2, calyx opened out, with the upper lobes to the right (C1) and to the left (C2), vestiture not shown; D1, D2, standard petals; E1, E2, wing petals; F1, F2, keel petals; G1, G2, pistils; H1, H2, fruit, in side and top view; S1, S2, seeds, showing the tuberculate surface; T1, T2, bracts. (A1, B2, C1, C2, D2, E2, F2, G1 & T1 from *BVW 2160*; A2 & T2 from *BVW 2161*; D1, E1, F1 & G2 from *BVW 2185*; B1, H1 & H2 from *Compton 12166*; S1 & S2 from *BVW 2190*). Scale in mm.

This species is closely related to *L. gracilis* (E. Mey.) Benth., but differs in the more lax and sparse habit, the sparsely strigillose leaves and twigs (not densely white-pubescent), the presence of a single stipule to each node (stipules totally absent in *L. gracilis*) and in the orange-red vexillum (yellow in *L. gracilis*).

L. comptonii is known only from two small populations on the northern slopes of the Witteberg and the Klein Swartberg (Figure 2), where it was found in dry fynbos vegetation on shallow, rocky soil. The specific epithet commemorates Prof. R. H. Compton (1886–1979), director of Kirstenbosch Botanical Garden for 34 years. He was responsible for the only collection known prior to my rediscovery of the species in 1986.

CAPE.—3320 (Montagu): Bantamskop, Witteberg (–BC), 27.10.1941, *Compton 12166* (NBG, PRE); Bantamskop, 3 km from the top (–BC), 13.10.1986, *B-E. van Wyk 2185* (JRAU, PRE, NBG), *2186* (BOL, JRAU, PRE, MO, NBG), *2187* (JRAU, PRE), *2188*, *2189* (JRAU), *2190* (JRAU, PRE). 3321 (Ladismith): Laingsburg to Seweweekspoort Road, 9,5 km from entrance of Rietvlei Farm (–AD), 12.10.1986, *B-E. van Wyk 2160* (PRE, holo.; BOL, C, JRAU, K, M, MO, NBG, SAAS, STE, iso.), *2161* (BOL, JRAU, K, MO, NBG, STE), 2162 (BOL, GRA, JRAU, KMG, NH, PRE), *2163* (JRAU, PRE).

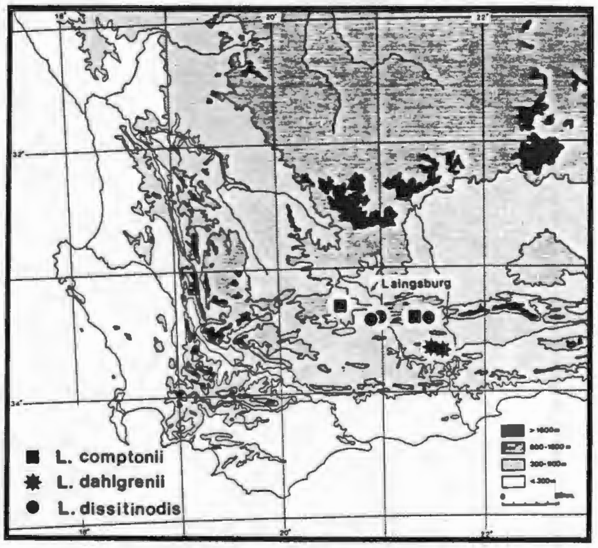

FIGURE 2.—The known geographical distribution of *Lotononis comptonii*, ■; *L. dahlgrenii*, ✱; and *L. dissitinodis*, ●.

Lotononis dahlgrenii *B-E. van Wyk, sp. nov. L. rigidae* (E. Mey.) Benth. similis, sed habitu etiam rigidiore lignosioreque, ramis lateralibus brevibus rigidis aliquantum spinescentibus, racemis longioribus latiore dispersis unifloratis (2 vel 3-floratis in *L. rigida*), calyce sparse puberulo (in *L. rigida* dense patente pubescens), vexillo carinaque maioribus, ovario fructuque longioribus, differt. Etiam *L. dissitinodi* mei similis, sed foliolis valde brevioribus, minus conduplicatis, stipulis omnino destitutis, lobis calycis lateralibus connatis et vexillo valde minore differt.

TYPE.—Cape, 3321 (Ladismith): Ladismith Div., near top of Roodeberg Pass (–DA), 19.7.1954, *Lewis 4709* (NBG, holo.).

Rigid woody shrub. *Branches* sparsely leafy; some of the lateral branches short, stiff and pungent; young twigs silky-sericeous. *Leaves* digitately trifoliolate, densely silky-sericeous; petiole very short, 1–3 mm long; leaflets small, narrowly oblanceolate to linear, 2–5 (–8) mm long, slightly conduplicate. *Stipules* absent. *Inflorescences* subterminal on short lateral branches, 1-flowered, rarely 2-flowered; peduncle long, (6–) 10–15 mm in length; bracts small, oblong, up to 1 mm long; bracteoles absent. *Flowers* 12–13 mm long, yellow; pedicel 2–4 mm long. *Calyx* 6–8 mm long, lobes long, acuminate, with the lateral ones on either side fused much higher up in pairs, sparsely puberulous. *Standard* ovate and pointed, 10–12 mm long, with a line of hairs dorsally along the middle. *Wing petals* shorter than the keel, oblong; sculpturing upper basal and upper central, in 7–8 rows of intercostal lunae. *Keel petals* semicircular, obtuse, auriculate and pocketed near base. *Anthers* dimorphic. *Pistil* long; ovary linear, 7–12 mm long. *Fruit* linear, 12–15 mm long, inflated laterally; lower suture distinctly sunken, upper suture verrucose. *Seed* (immature) densely tuberculate (Figure 3).

This species is similar to *L. rigida* (E. Mey.) Benth. but differs in the habit which is even more rigid and woody, the short stiff and somewhat thorny lateral branches, the longer, more widely spaced and single-flowered racemes (2 or 3-flowered in *L. rigida*), the sparsely puberulous calyx (densely and patently pubescent in *L. rigida*), the larger standard and keel and the longer ovary and fruit. It is also similar to *L. dissitinodis* B-E. van Wyk, but differs in the much shorter and less conduplicate leaflets, the total absence of stipules, the fused lateral calyx lobes and the much smaller standard.

L. dahlgrenii may easily be confused with species of *Wiborgia* and *Aspalathus* when not in flower. It appears to be a rare species and is only known from three specimens collected on the Rooiberg near Ladismith. The species is named after the late Prof. Rolf Dahlgren in recognition of his valuable contributions to the literature on Cape legumes.

CAPE.—3321 (Ladismith): Roodeberg summit (–CB), 24.3.1940, *Bond 263* (NBG); 3.1940, *Lewis 1211* (SAM); near top of Roodeberg Pass (–DA), 19.7.1954, *Lewis 4709* (SAM).

Lotononis dissitinodis *B-E. van Wyk, sp. nov.*, strictim *L. rigidae* (E. Mey.) Benth. et *L. dahlgrenii* mei similis, sed internodiis valde longioribus, foliolis longioribus anguste linearibus conduplicatis, stipulis ad pedunculorum insertionem semper praesentibus, inflorescentibus foliis oppositis (non subterminalibus), calycis lobis subaequalibus, vexillo maximo, carina minore acutioreque, fructu minus turgido differt.

TYPE.—Cape, 3320 (Montagu): 14 miles [22,4 km] SSE of Laingsburg (–BD), 25.7.1959, *Acocks 20502* (PRE, holo.; BOL, M, NBG, iso.).

Woody, sparsely branched shrub, up to 0,4 m tall. *Branches* with very long internodes, young twigs densely sericeous. *Leaves* widely spaced on the twigs, digitately trifoliolate (very rarely 4 or 5-foliolate), densely sericeous; petiole (2–) 5–8 (–10) mm long, adaxially grooved; leaflets narrowly linear, (5–) 7–12 (–15) mm long, conduplicate, apices recurved at maturity. *Stipules* rarely present, at the insertion of the peduncles only, single or paired, linear, variable in length, 1–8 mm long. *Inflorescences* leaf-opposed, 1-flowered (rarely 2-flowered); peduncles variable in length, 5–20 mm long; bracts small, up to 1 mm long; bracteoles absent. *Flowers* large, 15–20mm long, yellow; pedicel

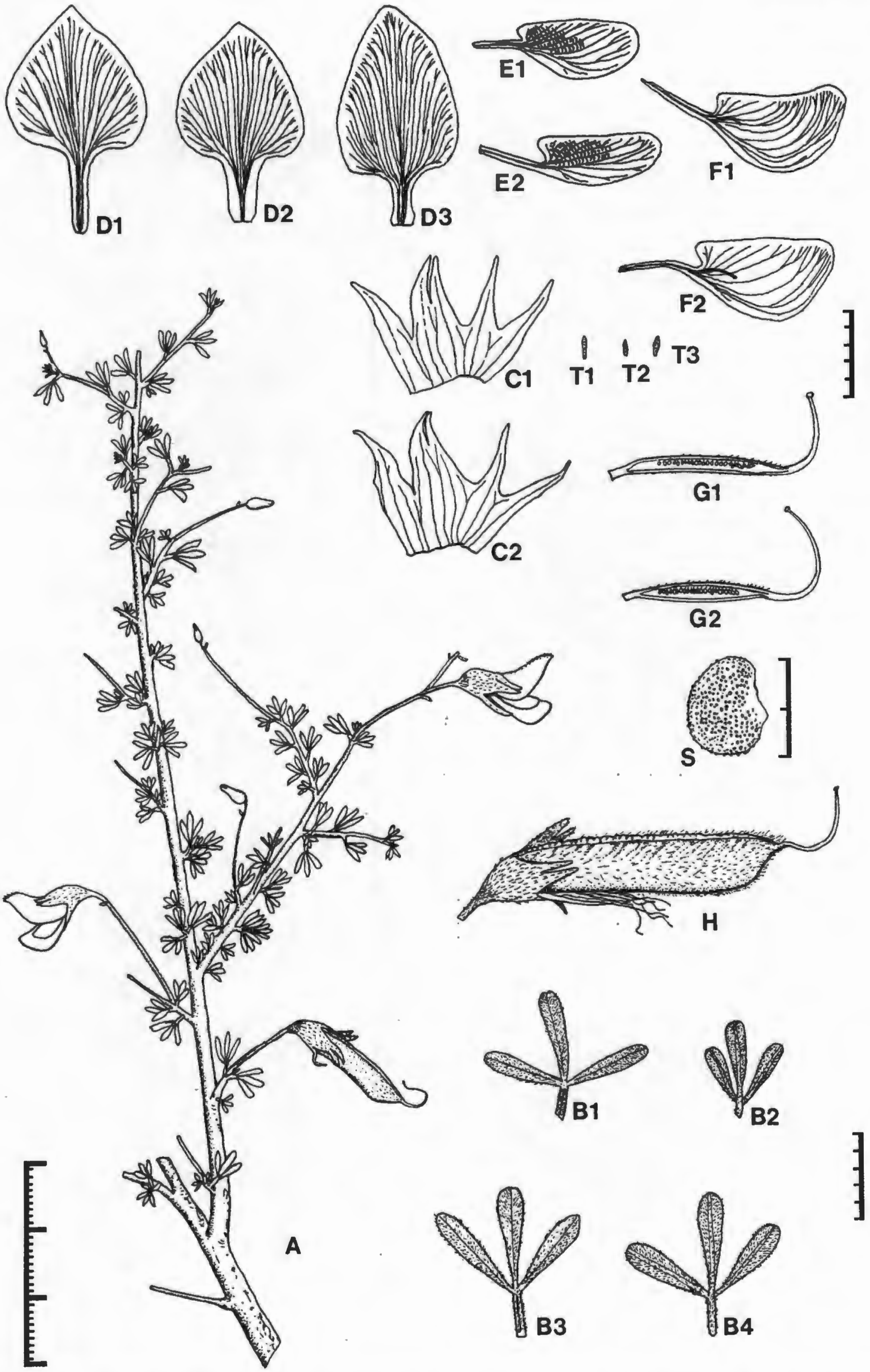

FIGURE 3.—*Lotononis dahlgrenii.* A, flowering branch; B1, B3, leaves in adaxial view; B2, B4, leaves in abaxial view; C1, C2, calyx opened out with upper lobes to the left, showing fusion of the lateral lobes; D1, D2, D3, standard petals, showing variation in shape; E1, E2, wing petals; F1, F2, keel petals; G1, G2, pistils; H, fruit; S, immature seed, showing tuberculate surface; T1, T2, T3, bracts. (A, B1, B2, C1, D1, E2, F2, G1 & T3 from *Lewis 4709*; B3, B4, D2, F1, G2, H & T2 from *Bond 263*; C2, D3, E1, S & T1 from *Lewis 1211*). Scale in mm.

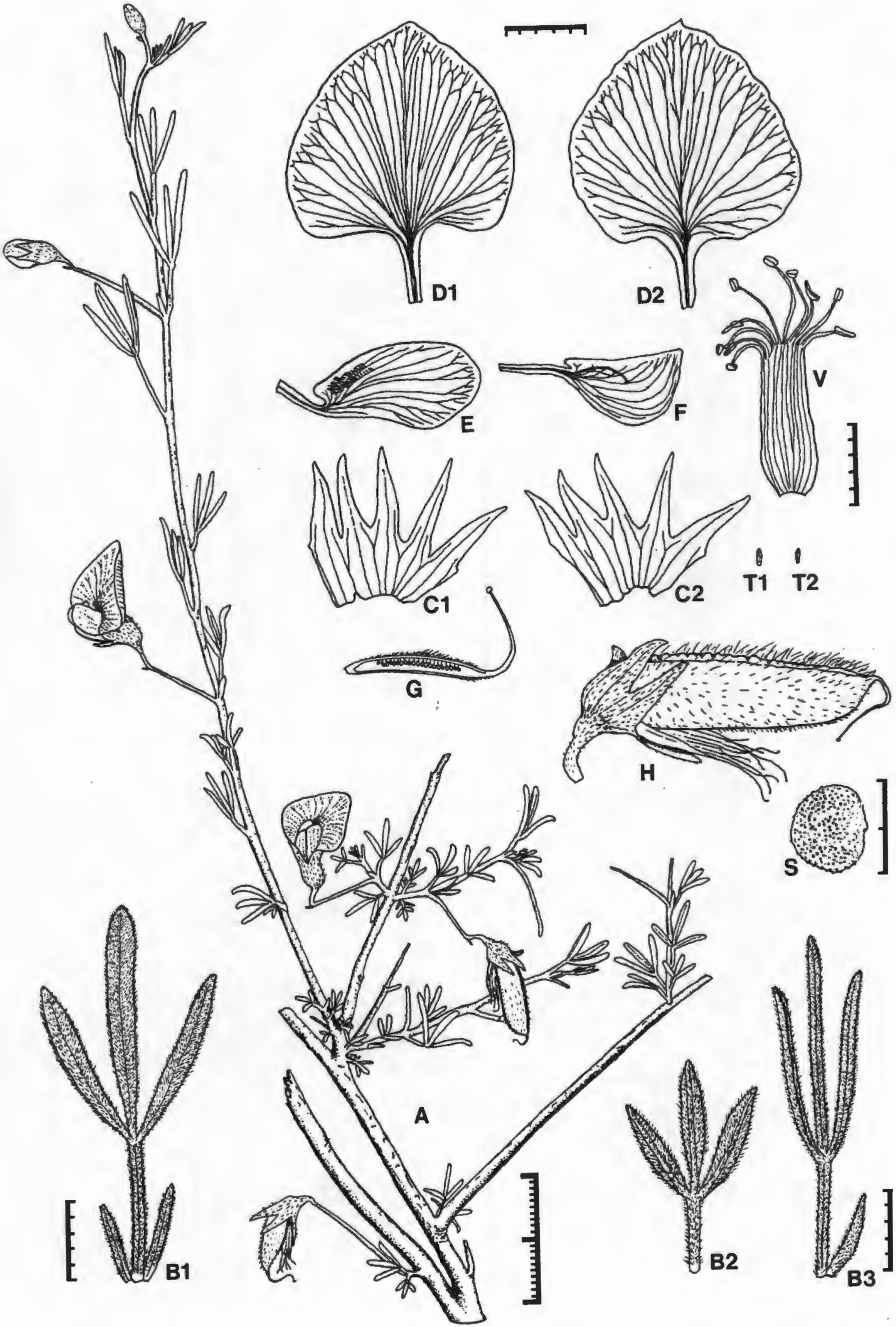

FIGURE 4.—*Lotononis dissitinodis*. A, flowering branch, showing the long internodes and leaf-opposed inflorescences; B1, B2, B3, leaves: B1, adaxial view, with leaflets opened out, showing paired stipules, B2, abaxial view, with leaflets opened out, stipules absent, B3, adaxial view, showing the normal conduplicate shape of the leaflets and a single stipule; C1, C2, calyx opened out, upper lobes to the left, showing the very slight fusion of the lateral lobes; D1, D2, standard petals (note the size); E, wing petal, showing the obovate shape; F, keel petal, showing the small size and pointed apex; V, androecium; G, pistil; H, fruit, showing verrucose upper suture; S, immature seed, showing tuberculate surface; T1, T2, bracts. (All from *Acocks 20502* except D2, V & T1 from *Wurts 1520* and T2 from *Levyns 7414*). Scale in mm.

1–3 mm long. *Calyx* 8–12 mm long; lobes long, subequal, minutely silky-puberulous. *Standard* large, broadly ovate, longer than the keel, 12–18 mm long, longitudinally striate. *Wing petals* obovate, longer than the keel; sculpturing upper basal, in ± 4 rows of intercostal lunae and irregular transcostal lamellae. *Keel petals* short, semicircular, 8–10 mm long, acute. *Anthers* dimorphic. *Pistil* 9–10 mm long; ovary linear, 6–8 mm long. *Fruit* oblong-linear, 16–20 mm long, 5 mm wide, not much inflated; lower suture not or only slightly sunken; upper suture verrucose. *Seed* (immature) densely tuberculate (Figure 4).

Superficially the species is similar to *L. rigida* and *L. dahlgrenii*, but it differs in the much longer internodes, the longer, narrowly linear, conduplicate leaflets, the consistent presence of stipules at the insertion of the peduncles, the leaf-opposed (not subterminal) inflorescences, the subequally lobed calyx, the very large standard, the smaller, more acute keel petals and the less turgid fruit.

L. dissitinodis appears to be restricted to the Klein Swartberg (Figure 2) and is only known from four collections. The very long internodes are a diagnostic character useful in distinguishing it from other woody species, hence the specific epithet. Although it is closely related to other species of the section *Aulacinthus*, the very large standard, obovate wing petals and relatively small, pointed keel approaches the flower structure typical of the section *Telina* (E. Mey.) Benth. [*L. prostrata* (L.) Benth. and its allies]. This similarity is of interest since it may help to explain the origin of the *Telina*-type flower and inflorescence.

CAPE.—3320 (Montagu): Buffels Poort Berg, lower slopes (–BD), 5.7.1941, *Levyns 7414* (BOL); Klein Swartberg, western end (–BD), 7.8.1957, *Wurts 1520* (NBG, 2 sheets); 14 miles SSE of Laingsburg (–BD), 25.7.1959, *Acocks 20502* (BOL, M, PRE); Seweweekspoort, N foothills of Klein Swartberg, Santo (–AD), 3.9.1982, *Viviers & Vlok 70* (STE).

ACKNOWLEDGEMENTS

I wish to thank Dr H. F. Glen (Botanical Research Institute, Pretoria) for the Latin translations and the Directors and staff of the cited herbaria for the loan of specimens. The taxonomic study of *Lotononis* is a registered Ph. D. project at the University of Cape Town.

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APPENDIX 20

Bothalia 19,1: 1–5 (1989)

Studies in the genus *Lotononis* (Crotalarieae, Fabaceae). 2. Three new species of the section *Telina* from the Cape Province

B-E. VAN WYK*

Keywords: Cape Province, Fabaceae, *Lotononis* section *Telina*, new taxa

ABSTRACT

Three new species of the section *Telina* (E. Mey.) Benth. of *Lotononis* (DC.) Eckl. & Zeyh. are described: *L.* **azureoides** B-E. van Wyk, *L.* **gracilifolia** B-E. van Wyk and *L.* **lamprifolia** B-E. van Wyk. These species appear to be very rare and are known from only a few localities in marginal fynbos areas of the south-western and southern Cape.

UITTREKSEL

Drie nuwe soorte van die seksie *Telina* (E. Mey.) Benth. van *Lotononis* (DC.) Eckl. & Zeyh. word beskryf: *L.* **azureoides** B-E. van Wyk, *L.* **gracilifolia** B-E. van Wyk en *L.* **lamprifolia** B-E. van Wyk. Hierdie soorte skyn baie skaars te wees en is bekend van slegs enkele lokaliteite in marginale fynbosgebiede van die Suidwes- en Suid-Kaap.

INTRODUCTION

The section *Telina* (E. Mey.) Benth. of *Lotononis* (DC.) Eckl. & Zeyh. comprises a group of prostrate or procumbent suffrutices easily recognized by their large, usually solitary flowers that are borne on long slender peduncles. The very large standard petal is a particularly useful diagnostic character.

Meyer (1836) included this group as one of three sections in his genus *Telina*, namely the section *Chasmoneae*. When Bentham (1843) changed the status of *Telina* to a section of *Lotononis*, he excluded the sections *Cytisoides* and *Brachypodae* and referred both of these to the section *Krebsia* (Eckl. & Zeyh.) Benth. *Chasmoneae* E. Mey. and *Telina* (E. Mey.) Benth. are therefore synonymous. Most of the species which Ecklon & Zeyher (1836) included in their concept of *Lotononis* belong to this section.

The section as circumscribed by Dümmer (1913) is not a natural group. Polhill (1973) and Van Wyk (1987) respectively, transferred *Lotononis bracteata* Benth. to *Pearsonia* Dümmer and *L. magnistipulata* Dümmer to *Argyrolobium* Eckl. & Zeyh. Some more changes are necessary, but these will be motivated elsewhere (Van Wyk in prep.). My own concept of the group does not include *L. minor* Dümmer & Jennings, *L. macrocarpa* Eckl. & Zeyh., *L. solitudinis* Dümmer and *L. marlothii* Engl. It does however include the three new species that are described below.

Lotononis azureoides *B-E. van Wyk*, sp. nov., *L. azureae* Eckl. & Zeyh. similis, sed habitu denso ramosissimo, foliolis conduplicatis valde recurvatis, stipulis anguste lanceolatis, inflorescentiis subterminalibus (in speciebus omnibus aliis *Telinae* foliis oppositis) atque vexillo pro ratione parvo carinam aequanti (vexillum quam carina valde longius in speciebus omnibus aliis *Telinae*) differt.

TYPE.—Cape, 3222 (Beaufort West): Beaufort West, Karoo National Park, at Blouput on steep rocky and bouldery sandstone slope (–BC), 2.11.1984, *Bengis 442* (PRE, charta 1, holo.; PRE, charta 2, iso.).

Procumbent, densely branched shrublet, ± 0,3 m wide. *Branches* smooth, glabrous; twigs densely strigillose, conspicuously white at the ends. *Leaves* digitately trifoliolate; petiole (2–) 3–4 (–7) mm long; leaflets conduplicate, strongly recurved, obovate, (2–) 4–6 (–8) × (1–) 2–3 (–5) mm, abaxially strigillose, adaxially glabrous. *Stipules* consistently present, single at each node, elliptic-oblong to narrowly lanceolate, 2–3 (–5) mm long. *Inflorescences* terminal or subterminal on lateral branches, slender, long-pedunculate, 25–40 mm long, invariably single-flowered; bracts small, up to 1 mm long; bracteoles absent. *Flowers* 12–14 mm long, deep blue; pedicel 2–3 mm long. *Calyx* 7–8 mm long, with the upper and lateral lobes on either side fused higher up in pairs, minutely strigillose. *Standard* broadly ovate to orbicular, 11–13 mm long, with a line of hairs dorsally along the middle, deep blue with yellow at the base. *Wing petals* oblanceolate, slightly longer than the keel; apex obliquely truncate; sculpturing upper basal and upper left central, in 4 rows of inter- and intracostal lunae. *Keel petals* semicircular, obtuse, auriculate and pocketed near the base. *Anthers* dimorphic. *Pistil* 12–14 mm long; ovary linear, 8–10 mm long. *Fruit* (slightly immature) 20 × 4–5 mm, laterally much inflated, lower suture sunken, upper suture verrucose, surface wrinkled, glabrous. *Seed* unknown. Figure 1.

This species is similar to *L. azurea* Eckl. & Zeyh. but differs in the dense and much branched habit, the conduplicate and strongly recurved leaflets, the narrowly lanceolate stipules, the subterminal inflorescences (leaf-opposed in all other species of *Telina*) and the relatively small standard petal, which is as long as the keel (standard petal much longer than the keel in all other species of *Telina*). The flower structure is reminiscent of some species in the section *Polylobium* (Eckl. & Zeyh.) Benth., but the slender single-flowered inflorescence and the shape of the calyx and wing petals are typical of other species in the section *Telina*.

L. azureoides is known only from two collections from the Nuweveld Mountains at Beaufort West (Figure 2). It was found on a rocky south-eastern slope in grassy dwarf shrubland at an altitude of 1 600 m. The specific

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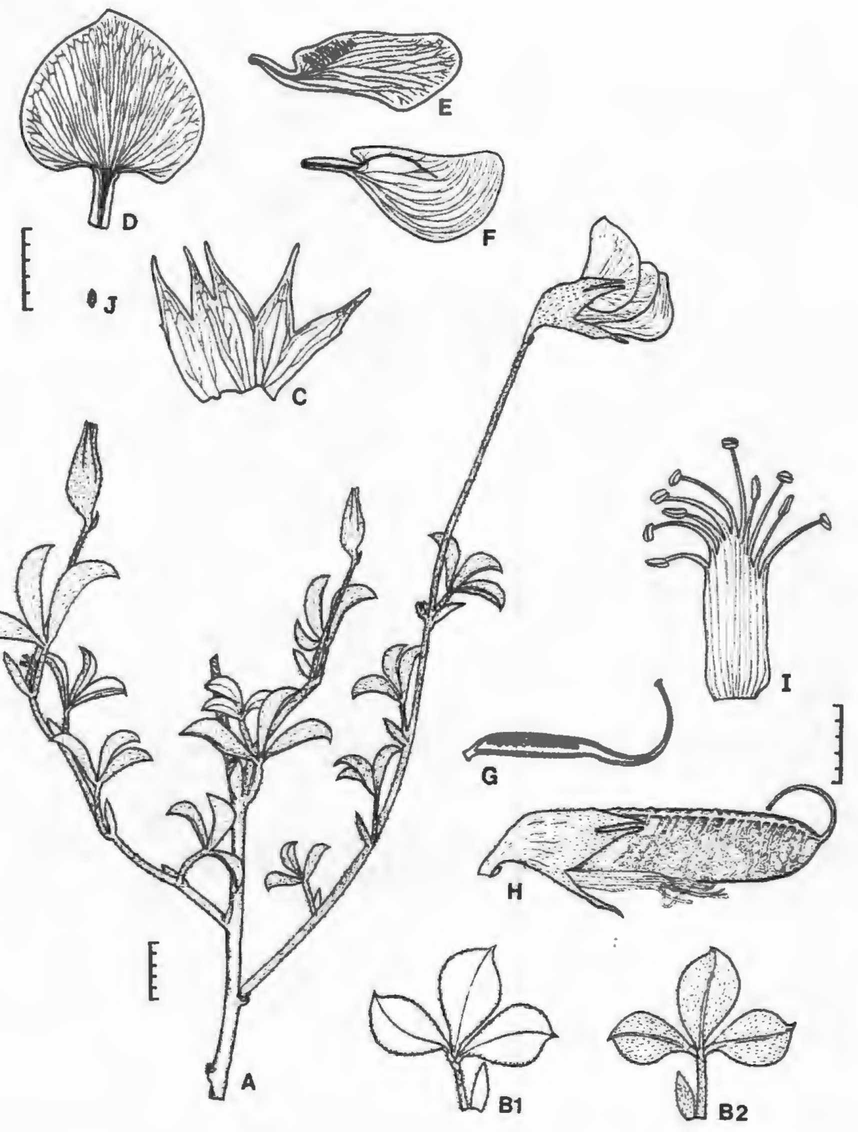

FIGURE 1.—*Lotononis azureoides*. A, flowering branch, showing the slender peduncles and conduplicate, recurved leaflets; B1, B2, leaves with leaflets opened out, showing the single stipule and sparsely strigillose vestiture: B1, adaxial view, B2, abaxial view; C, calyx opened out, with the upper lobes to the left, vestiture not shown; D, standard petal; E, wing petal; F, keel petal; G, pistil; H, fruit (slightly immature), showing the wrinkled surface and verrucose upper suture; I, androecium; J, bract (all from *Bengis 442*). Scales in mm.

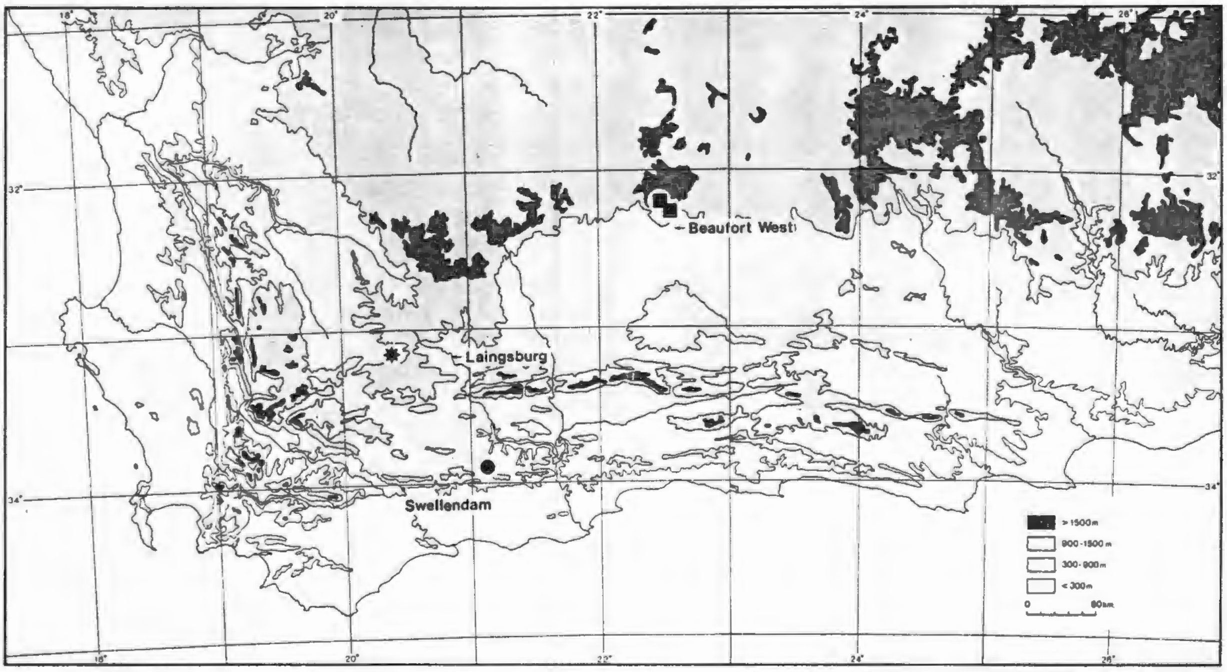

FIGURE 2.—The known geographical distribution of *Lotononis azureoides*, ■ ; *L. gracilifolia*, ★; and *L. lamprifolia*, ●.

epithet suggests a similarity with *L. azurea* Eckl. & Zeyh. which it superficially resembles, but the affinities of the species are not clear. More material is needed for a detailed study. Available evidence indicates that the *Telina*-type flower and inflorescence have evolved more than once from different lines in the sections *Aulacinthus* (E. Mey.) Benth. and *Polylobium*. The distinction between the latter two sections and indeed also the section *Telina* is becoming more and more obscured. Some newly discovered species such as *L. azureoides* have combinations of those characters previously used diagnostically for each of the three sections.

CAPE.—3222 (Beaufort West): Nuweveld Mountain, Mountain view, roadside near FM tower (−AB), *D. Shearing 2.2.85* (private herbarium on the farm Layton, Fraserburg District); Beaufort West, Karoo National Park, at Blouput on steep rocky and bouldery sandstone slope (−BC), 2.11.1984, *Bengis 442* (PRE, holo.; PRE, iso.).

Lotononis gracilifolia *B-E. van Wyk,* sp. nov., *L. argenteae* Eckl. & Zeyh. et speciebus aliis sectionis *Telinae* similis, sed distinctissima foliolis gracilibus acicularibus, stipulis inconspicuis, lobis calycis subulatis. *L. dissitinodi* B-E. van Wyk (sectionis *Aulacinthus*) valde similis sed habitu nano suffrutescente, foliolis valde angustioribus, stipulis inconspicuis, pedunculis longioribus et lobis calycis angustissimis differt.

TYPE.—Cape, 3320 (Montagu): Laingsburg District, Tweedside (−AB), 27.9.1951, *Barker 7482* (NBG, charta 2, holo.; NBG, charta 1, iso.).

Dwarf suffrutescent perennial up to 0,15 m tall. *Branches* procumbent from a central rootstock; sparsely branched and sparsely leafy; young twigs densely silky-sericeous. *Leaves* digitately trifoliolate, very slender, densely silky-sericeous; petiole up to 22 mm long; leaflets acicular, variable in length, (2−) 7−15 (−25) mm long, slightly conduplicate, almost terete. *Stipules* inconspicuous, caducous, rarely present, up to 0,5 mm long when present. *Inflorescences* subterminal or leaf-opposed on short lateral branches, 1-flowered, rarely 2-flowered; peduncle slender, variable in length, (3−) 20−50 (−60) mm long; bract small, oblong, up to 2 mm long; bracteoles absent. *Flowers* large, up to 18 mm long, yellow; pedicel 2−4 mm long. *Calyx* 10−13 mm long; lobes long, subulate, with the lateral ones on either side fused higher up in pairs, densely sericeous. *Standard* very large, broadly ovate to orbicular, 18−20 mm

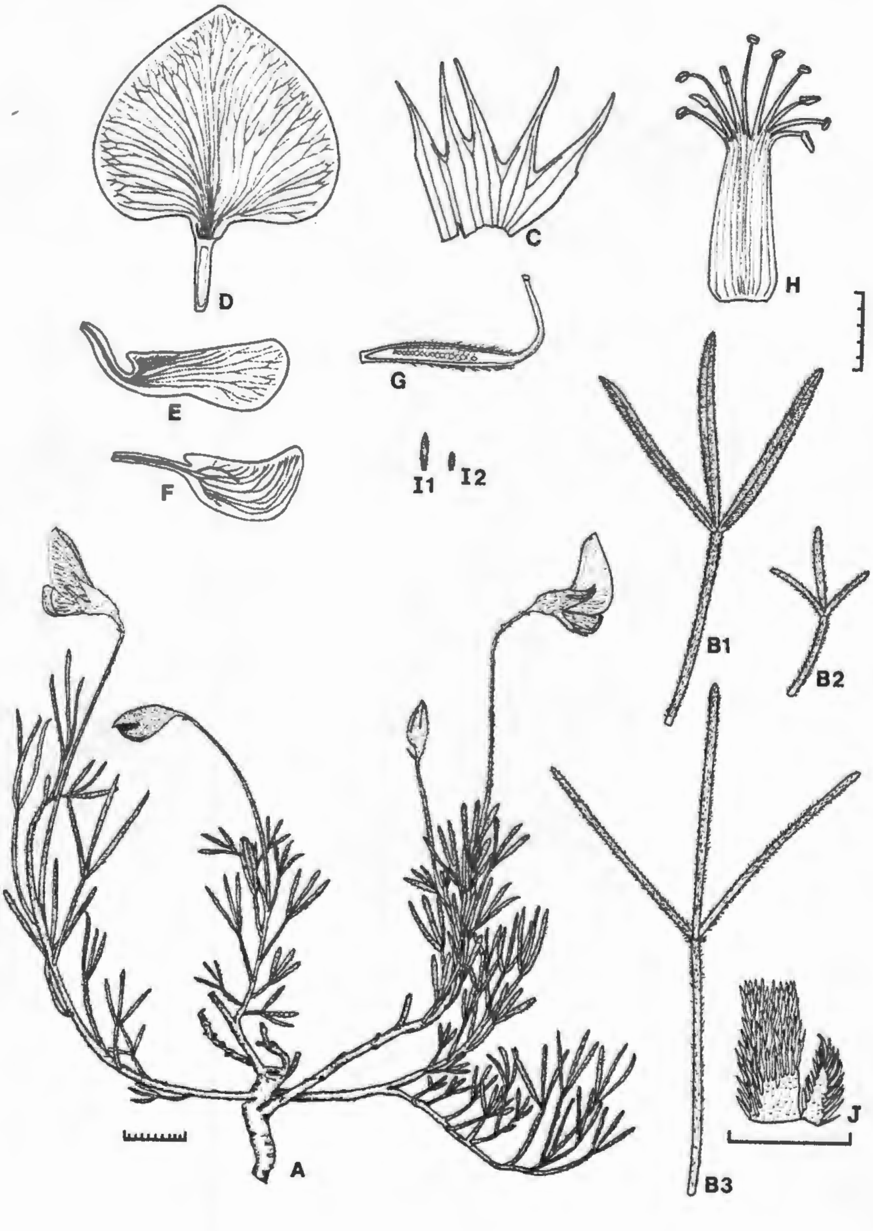

FIGURE 3.—*Lotononis gracilifolia*. A, habit, showing the procumbent flowering branches, acicular leaves and slender peduncles; B1, leaf in adaxial view, with leaflets opened out, B2, B3, leaves in abaxial view, showing variation in size, leaflets not opened out; C, calyx opened out with upper lobes to the left, showing fusion of the lateral lobes; D, standard petal; E, wing petal; F, keel petal; G, pistil; H, androecium; I1, I2, bracts; J, petiole base with vestiture partly removed to show the single, inconspicuous stipule (all from *Barker 7482*). Scales in mm.

long, with hairs dorsally along the middle. *Wing petals* as long or slightly longer than the keel, oblanceolate, ± 15 mm long; apex obliquely obtuse; sculpturing upper basal, in 3–4 rows of mostly intercostal lunae. *Keel petals* semicircular, obtuse, auriculate and pocketed near base. *Anthers* dimorphic. *Pistil* long; ovary linear, ± 10 mm long. *Fruit* and *seed* unknown. Figure 3.

This species is similar to *L. argentea* Eckl. & Zeyh. and other species of the section *Telina*, but it is very distinct in the acicular leaflets, the inconspicuous stipules and the subulate calyx lobes. It is remarkably similar to *L. dissitinodis* B-E. van Wyk (section *Aulacinthus*), but differs from this species in the dwarf and suffrutescent habit, the much narrower leaflets, the inconspicuous stipules, the longer peduncles and the very narrow calyx lobes.

L. gracilifolia appears to be a very rare species and is only known from the type collection (Figure 2). I have so far been unable to locate the plant. The slender, acicular leaves are a useful diagnostic character and the species is unlikely to be confused with any other. This very distinctive character has suggested the specific epithet.

CAPE.—3320 (Montagu): Tweedside, Laingsburg (–AB), 27.9.1951, *Barker 7482* (NBG, holo.; NBG, iso.).

Lotononis lamprifolia *B-E. van Wyk,* sp. nov., *L. argenteae* valde affinis, sed habitu diffusiore, stipulis obovatis foliolis valde similibus (in *L. argentea* linearibus vel lanceolatis), floribus flavis (in *L. argentea* caeruleis) et vexillo depresso ovato (in *L. argentea* late ovato vel orbiculato; etiam *L. acuminatae* Eckl. & Zeyh. similis, sed ab hac specie indumento dense sericeo et petiolis valde longioribus differt.

TYPE.—Cape, 3321 (Ladismith): Riversdale and Swellendam Districts, between Muiskraal and Lemoenshoek (–CC), 6.8.1951, *Barker 7374* (NBG, holo.).

Dwarf suffrutescent perennial ± 0,2 m tall. *Branches* sparse, woody at the base; young twigs densely sericeous. *Leaves* digitately trifoliolate, densely and silvery sericeous; petiole relatively thick, variable in length, 3–4 (–10) mm long, leaflets oblanceolate to obovate, (3–) 4–5 (–8) mm long, slightly conduplicate, thick in texture. *Stipules* present or absent; when present closely resembling the leaflets in shape, size and vestiture, usually single to each node, strongly persistent. *Inflorescences* leaf-opposed on short lateral branches, invariably single-flowered; peduncle slender, 18–35 mm

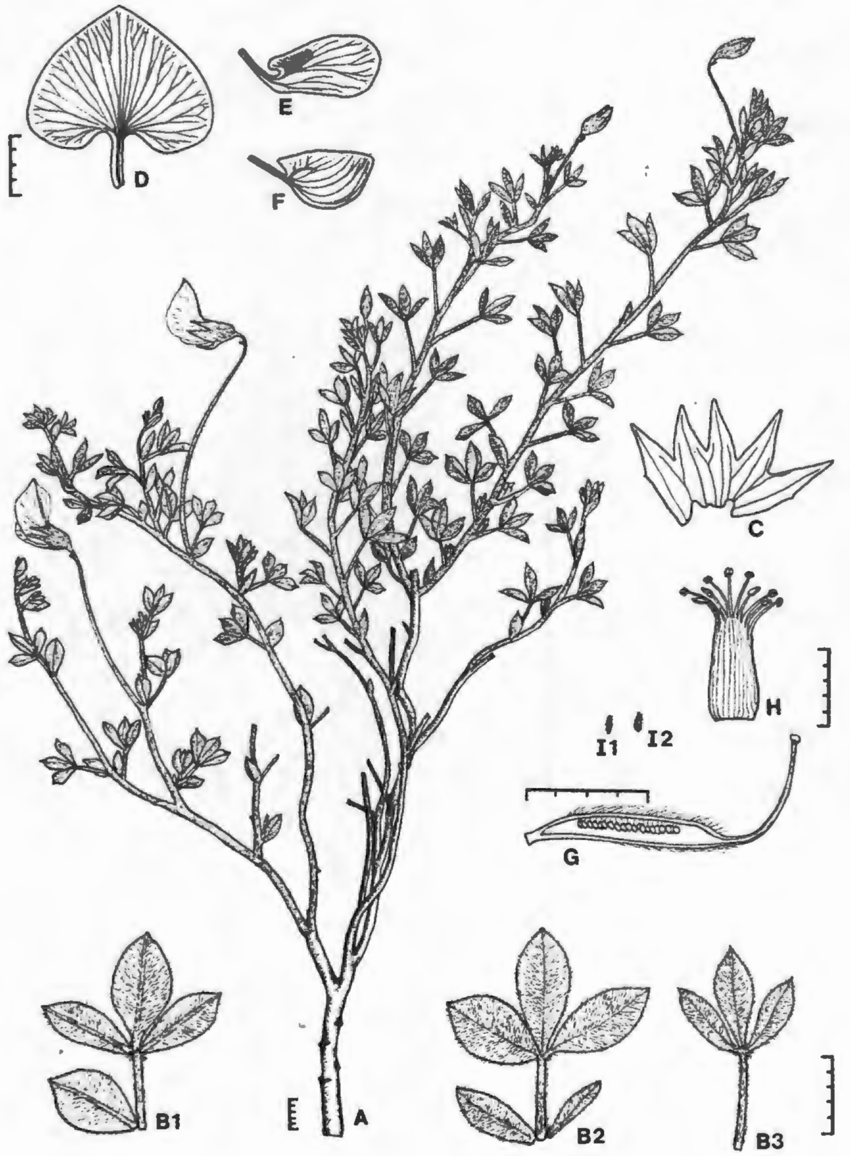

FIGURE 4.—*Lotononis lamprifolia.* A, habit; B1, B2, B3, leaves: B1, abaxial view, showing the single stipule and sericeous vestiture; B2, adaxial view, showing paired stipules; B3, adaxial view, stipules absent; C, calyx opened out, upper lobes to the left, showing the very slight fusion of the lateral lobes; D, standard petal (note the shape); E, wing petal; F, keel petal; G, pistil; H, androecium; I1, I2, bracts (all from *Barker 7374*). Scales in mm.

long; bracts small, oblong, ± 1 mm long; bracteoles absent. *Flowers* 10–12 mm long, yellow; pedicel 1–2 mm long. *Calyx* 6–7 mm long; lobes triangular, with the lateral ones on either side fused only slightly higher up in pairs, densely sericeous. *Standard* large, broadly depressed ovate, ± 12 mm long, with hairs dorsally along the middle. *Wing petals* longer than the keel, broadly oblanceolate, ± 10 mm long; apex obtuse, rounded; sculpturing upper basal and upper left central, in 4–5 rows of mostly intercostal lunae. *Keel petals* semicircular, obtuse, auriculate and pocketed near base. *Anthers* dimorphic. *Pistil* short; ovary linear, ± 7 mm long. *Fruit* and *seed* unknown. Figure 4.

This species is closely related to *L. argentea* Eckl. & Zeyh. but differs in the more diffuse habit, the obovate stipules which closely resemble the leaflets (linear to lanceolate in *L. argentea*), the yellow flowers (blue in *L. argentea*) and the depressed ovate standard (widely ovate to orbicular in *L. argentea*). It is also similar to *L. acuminata* Eckl. & Zeyh. but differs from this species in the densely sericeous vestiture and the much longer petioles.

L. lamprifolia is only known from a single specimen collected along the northern foothills of the Langeberg near Barrydale (Figure 2). The shining and silky appearance of the leaflets is very distinct (as in *L. argentea*), hence the specific epithet. The latter species is also very poorly represented in southern African herbaria and collectors are requested to look out for more complete material. Fruiting material in particular is required for a more detailed study of the full range of variation in these two closely related species and to verify the diagnostic features of the new species.

CAPE.—3321 (Ladismith): Riversdale and Swellendam Districts, between Muiskraal and Lemoenshoek (–CC), 6.8.1951, *Barker 7374* (NBG, holo.)

ACKNOWLEDGEMENTS

I wish to thank Dr H. F. Glen (Botanical Research Institute, Pretoria) for the Latin translations and the Directors and staff of the cited herbaria for the loan of specimens. The taxonomic study of *Lotononis* is a registered Ph. D. project at the University of Cape Town.

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APPENDIX 21

FABACEAE

THE IDENTITY OF *LOTONONIS ELONGATA* (CROTALARIEAE)

Several specimens of a species superficially similar to *Lotononis prostrata* (L.) Benth. and *L. azurea* (Eckl. & Zeyh.) Benth. have accumulated in southern African herbaria since 1953. The herbarium collections and an *in situ* study have shown that the species is quite distinct from all other species of the section *Telina* (E. Mey.) Benth. It was written up to be described as a new species under the name *L. repens* (Van Wyk unpublished manuscript).

A recent examination of the Thunberg Herbarium in Uppsala has revealed that '*L. repens*' is identical to *Ononis elongata* Thunb., a species treated by both Harvey (1862) and Dümmer (1913) as synonymous with *L. prostrata* (L.) Benth. Unlike Harvey, Dümmer apparently did not see the type specimen and presumably followed Harvey's interpretation of the species. Bentham (1843) did not study the Thunberg collection and did not cite *Ononis elongata* in his revision of *Lotononis*. Dietrich (1847) somewhat hesitantly transferred most of Thunberg's *Ononis* species to the genus *Lotononis*—amongst others also *O. elongata*. These and several other new combinations by Dietrich have apparently been overlooked by subsequent workers.

The type specimen of *Ononis elongata* is a small piece of flowering material only, so that the unusual pods, distinctive habit and other diagnostic characters were not known before.

Lotononis elongata *(Thunb.) D. Dietr.*, Synopsis plantarum 4: 960 (1847).

Ononis elongata Thunb., *Prodromus plantarum capensium* 2: 129 (1800); Thunb.: 587 (1823); DC.: 167 (1825); Harv. 2: 53 (1862), as synonym of *L. prostrata*; Dümmer: 296 (1913), as synonym of *L. prostrata*. Type: South Africa, Cape Province, 'in Cap. b. Spei', *Thunberg s.n. sub THUNB-UPS 16607* (UPS!, lecto., here designated).

Prostrate perennial herb up to 1,2 m wide and no more than 0,1 m high. *Branches* prostrate and creeping, spreading from a central rootstock; twigs densely pilose. *Leaves* digitately trifoliolate, very variable in size and shape; petiole (2–) 4–8 (–11) mm long, sparsely pubescent; leaflets oblanceolate, obovate or elliptic, (3–) 7–16 (–20) × (1,5–) 2–5 (–8) mm, abaxially sparsely pubescent, adaxially glabrous. *Stipules* consistently present, single at each node, lanceolate to broadly ovate, (1–) 2–8 (–11) mm long. *Inflorescences* leaf-opposed at each node, slender, long-pedunculate, 25–75 mm long, invariably single-flowered; bracts small, up to 2,5 mm long; bracteoles absent. *Flowers* 10–14 mm long, yellow; pedicel 1–3 mm long. *Calyx* 7–9 mm long, with the lateral lobes on either side fused higher up in pairs, sparsely pubescent. *Standard* large, broadly ovate to orbicular, 11–16 mm long, with a line of hairs dorsally along the middle, adaxially yellow, abaxially pale brown. *Wing petals* dimorphic, the one oblanceolate with an obliquely truncate apex, the other oblong-obovate with a rounded apex, the former positioned higher than the latter at anthesis; both longer than the keel; sculpturing similar in both, upper basal and upper left central, in 5–6 rows of inter- and intracostal lunae. *Keel petals* semicircular, obtuse, auriculate and pocketed near the base. *Anthers* dimorphic. *Pistil* 9–12 mm long; ovary linear, 6–8 mm long, the upper part without ovules and similar to the style, the lower fertile part very short, 2–3 mm long. *Fruit* ovate, terete, very short, 8–14 mm long (excluding the style), 3–6 mm in diameter; apex gradually tapering to the style; pubescent. *Seed* suborbicular in side view, up to 2 mm long, distinctly tuberculate, pale brown or with some irregular black marks; hilar area markedly swollen and black in colour, obscuring the hilar valve (Figure 8). *Chromosome number*: $2n = 28$!

Voucher specimen: *Van Wyk 2573* (BOL, C, GRA, JRAU, K, M, MO, NBG, NH, PRE, SAAS, STE).

Lotononis elongata is similar to *L. azurea* and *L. prostrata* but differs from these and related species in the shape of the flowers, the dimorphic wing petals, the sterile upper part of the ovary and in the short, ovate and distinctly pointed fruit. It differs from *L. azurea* also in the yellow colour of the flowers, the shape of the leaflets and the more hairy twigs and leaves. From *L. prostrata* it also differs in the more spreading habit, which can be up to 1,2 m wide (± 0,3 m in *L. prostrata*).

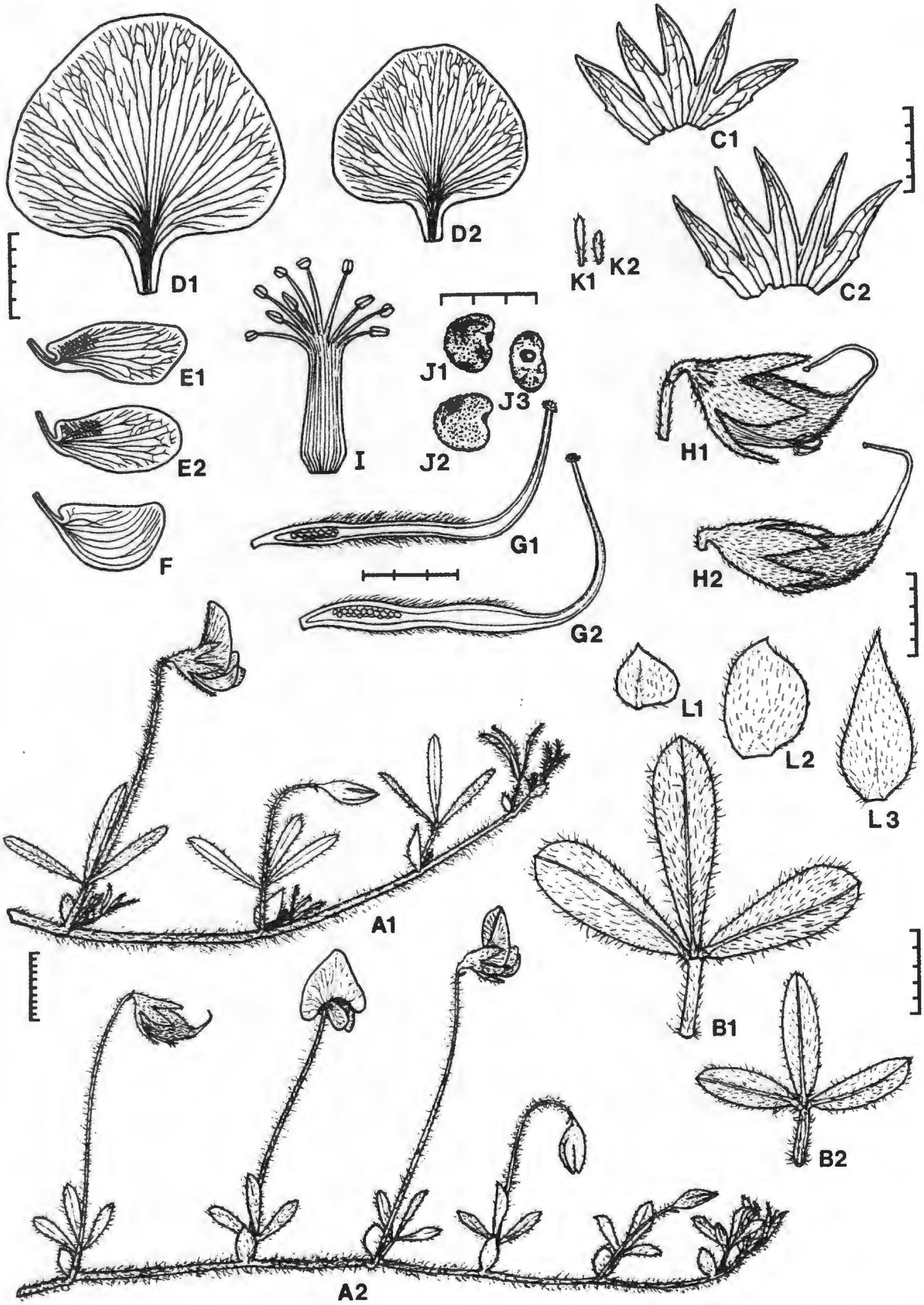

FIGURE 8.—*Lotononis elongata*. A1, A2, flowering branches, showing the prostrate habit and slender peduncles; B1, B2, leaves in abaxial view; C1, C2, calyx opened out, upper lobes to the left, showing the fusion of the lateral lobes; D1, D2, standard petals (note the difference in size); E1, E2, wing petals from the same flower, showing the dimorphic shape; F, keel petal; G1, G2, pistils, showing the sterile upper parts of the ovaries; H1, H2, mature fruit (note the size, shape and also the pointed, tapering apices, which are diagnostic for the species); I, androecium; J1, J2, seeds in side view, showing tuberculate surface; J3, seed in hilar view, showing the raised area around the hilar valve; K1, K2, bracts; L1, L2, L3, stipules, showing variation in size and shape. All from *Van Wyk 2573* except A1 & B2 from *Vlok 1762* and C2, D1, G2, I & L2 from *Vlok 1718*. Scales in mm.

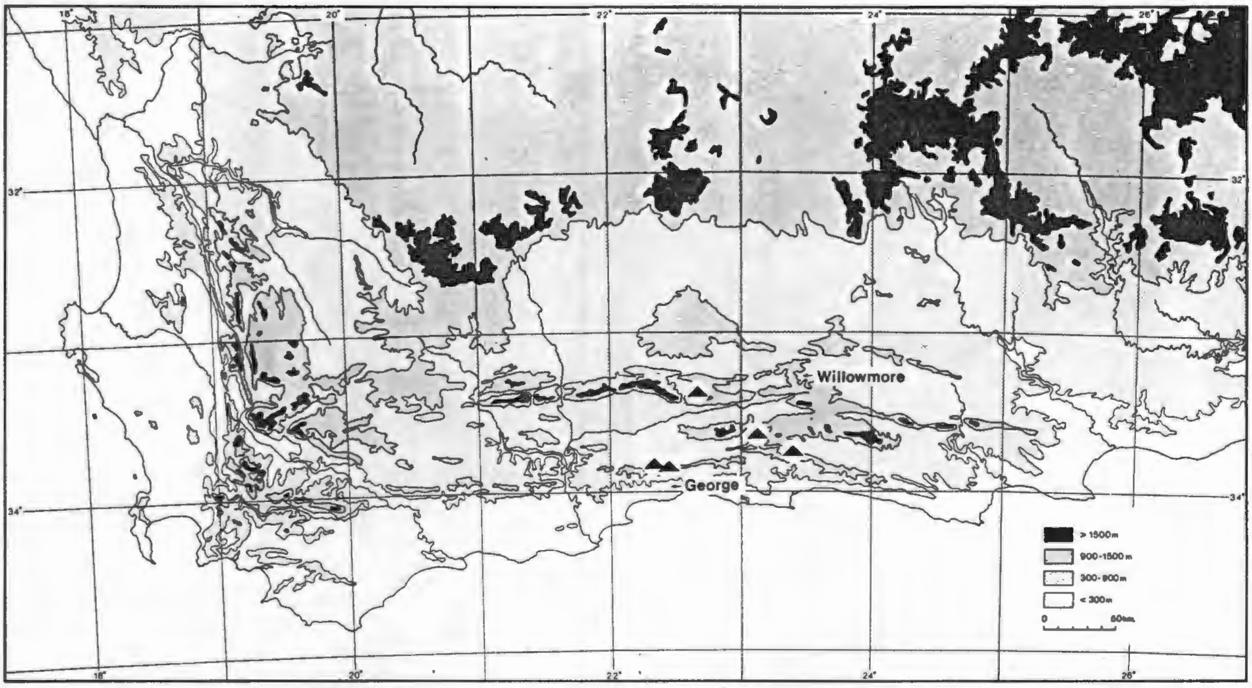

FIGURE 9.—The known geographical distribution of *Lotononis elongata*.

The species has a relatively wide distribution in the southern Cape (Figure 9). It seems to have escaped the notice of collectors for nearly 200 years—recent collections date back to 1953. Thunberg must have collected the type specimen on one of his two journeys to the eastern Cape between 1772 and 1774. It is known that he crossed the Outeniqua Mountains on several occasions during this period (Gunn & Codd 1981). Recent collections by Mr J. H. J. Vlok (Saasveld Forestry Research Centre, George) have considerably expanded the known distribution range.

The peculiar pistil, in which the upper sterile part of the ovary closely resembles the style, has not been observed in any other species of the section *Telina*. This development approaches the usual condition in the genus *Crotalaria* (where the style is geniculate and hairy), but in *L. elongata* the hairy part of the pistil is undoubtedly part of the ovary and not the style. The presence of macrocyclic pyrrolizidine alkaloids in *L. elongata* (Van Wyk & Verdoorn in prep.) also suggests an affinity with *Crotalaria*. The single stipules, calyx structure, tuberculate seed surface and chromosome number, however, leave little doubt about the correct generic position in *Lotononis*.

CAPE.—3322 (Oudtshoorn): Swartberg Mountains, mid-northern slopes of Blesberg, next to forestry track (–BC), 15.12.1986, *Vlok 1762* (JRAU, K, NBG, PRE); northern foothills of Outeniqua Mountains, about 3 km west of Herold at Camferskloof (–CD), 22.11.1986, *Vlok 1718* (BOL, C, GRA, JRAU, K, M, MO, NBG, NH, PRE, SAAS, STE); top of Outeniqua Pass (–CD), 23.1.1987, *B-E. van Wyk 2573* (PRE, BOL, C, GRA, JRAU, K, M, MO, NBG, NH, PRE, SAAS, STE); Zebra, top of Outeniqua Pass (–CD), 19.10.1953, *Lewis 3734* (SAM); Zebra, George District (–CD), 19.10.1953, *Barker 8195* (MO, NBG). 3323 (Willowmore): about 8 km from Uniondale on road to Avontuur (–CA), 20.12.1967, *Grobbelaar 1401* (PRE); 23,2 km east by south of Uniondale (–CB/–CD), 16.11.1958, *Acocks 19986* (K, M).

ACKNOWLEDGEMENTS

I am indebted to Mr J. H. J. Vlok (Saasveld Forestry Research Centre, George) for valuable collections of *L. elongata* and to Dr and Mrs Charles McDonald (Tarentaalbos, George) who kindly collected ripe fruits and seeds for chromosome counting. The taxonomic study of *Lotononis* is a registered Ph. D. project at the University of Cape Town. Financial support from the Rand Afrikaans University enabled me to study the Thunberg collection.

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APPENDIX 22

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Studies in the genus *Lotononis* (Crotalarieae, Fabaceae). III. A new species of the *L. angolensis* group from the northern Cape Province

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A new species of *Lotononis* (DC.) Eckl. & Zeyh. is described, namely *L. minima* B-E. van Wyk. It is closely related to *L. listii* Polhill and *L. marlothii* Engl. but the flowers are amongst the smallest of the chasmogamous type recorded in the genus. The species is known only from a single locality and was collected in a seasonal pan near Kenhardt in the northern Cape.

'n Nuwe spesie van *Lotononis* (DC.) Eckl. & Zeyh. word beskryf, naamlik *L. minima* B-E. van Wyk. Dit is naverwant aan *L. listii* Polhill en *L. marlothii* Engl. maar het die kleinste blomme van die chasmogame tipe wat nog in die genus aangeteken is. Die spesie is slegs bekend van 'n enkele lokaliteit en was versamel in 'n seisoenale pan naby Kenhardt in die Noord-Kaap.

Keywords: Cape Province, Fabaceae, *Lotononis* section Polylobium, new species

Introduction

The section Polylobium (Eckl. & Zeyh.) Benth. of *Lotononis* (DC.) Eckl. & Zeyh. is not only a poorly defined section, but is also undoubtedly an artificial one. As presently circumscribed (Dümmer 1913), the section comprises at least three very distinctive groups:

1. *L. umbellata* (L.) Benth. and related species. These species are very similar to species of the section Aulacinthus (E. Mey.) Benth. and are doubtfully distinct from them at the sectional level. All are shrubs or shrublets with persistent branches. Stipules are absent or single at each node, never paired.
2. *L. involucrata* (Berg.) Benth. and related species. All of these have a woody, subterranean caudex. Stipules, if present, are paired.
3. *L. angolensis* Welw. ex Bak. and related species. Within the genus *Lotononis*, this is perhaps the most distinct group. It has several unique features, such as well-developed bracteoles, glabrous mature leaves, very small seeds and the phenomenon that root formation may occur on side shoots.

This last group includes, amongst others, the closely related *L. bainesii* Bak., *L. barberae* Dümmer, *L. listii* Polhill, *L. listioides* Dinter & Harms and *L. marlothii* Engl. A study of these species has shown the presence of an allied undescribed species.

Description

Lotononis minima *B-E. van Wyk*, sp. nov.

L. listii Polhill et *L. marlothii* Engl. valde affinis, sed habitu valde minore (minus quam 0,2 m lato), floribus valde minoribus, vexillo anguste elliptico (late ovato vel cordate in speciebus aliis), petalis alis leniter evolutis et ovario breve oblongo (lineare in speciebus aliis) et glabro (in speciebus aliis certe pubescente).

TYPUS. — Cape Province: Kenhardt: Kenhardt Div., Jagbult, floor of Uilpan (–DA), 12/5/1946, *Acocks 12664* (PRE, holotypus).

Prostrate perennial herb, *ca.* 0,2 m in diameter. *Branches* smooth, glabrous; twigs glabrescent, sparsely pubescent when young. *Leaves* digitately trifoliolate; petiole (3–)4–7(–12) mm long; leaflets oblanceolate to obovate, (2–)4–7(–14) mm long, (1–)2–3(–4) mm wide, sparsely pubescent when young, almost totally glabrous when mature. *Stipules* consistently present, paired at each node, often very dissimilar in size and shape, broadly lanceolate to broadly ovate, usually asymmetrically lobed at the base, up to 2,5 mm long, or small and linear. *Inflorescences* leaf-opposed, short congested racemes, up to 10 mm long, 1–4-flowered; bracts up to 1,5 mm long; bracteoles consistently present, small but well-developed, up to 0,5 mm long. *Flowers* 4–5 mm long, yellow; pedicel 1–2 mm long. *Calyx* up to 3,5 mm long, with the lateral lobes on either side fused higher up in pairs, glabrous. *Standard* narrowly elliptic, 4–5 mm long, glabrous. *Wing petals* weakly developed, very narrowly elliptic, shorter than the keel; auricle and pocket absent; sculpturing absent. *Keel petals* oblong, obtuse, only slightly auriculate; pocket absent. *Anthers* dimorphic, spherical and ovoid. *Carpel* 4–4,5 mm long; ovary short, oblong, 2,5–3 mm long. Immature *fruit* 6 mm long, 2,5 mm wide, flat, not inflated or twisted, surface slightly wrinkled, glabrous. Mature fruit and seeds unknown (Figure 1).

L. minima is closely related to *L. listii* Polhill and *L. marlothii* Engl., but differs in the much smaller habit (less than 0,2 m in diameter) and flowers, the narrowly elliptic standard (broadly ovate to cordate in other species), the weakly developed wing petals, and the ovary which is short,

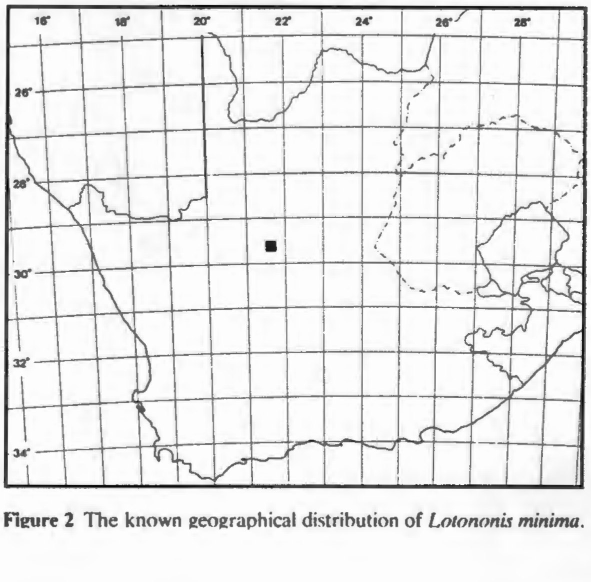

Figure 2 The known geographical distribution of *Lotononis minima*.

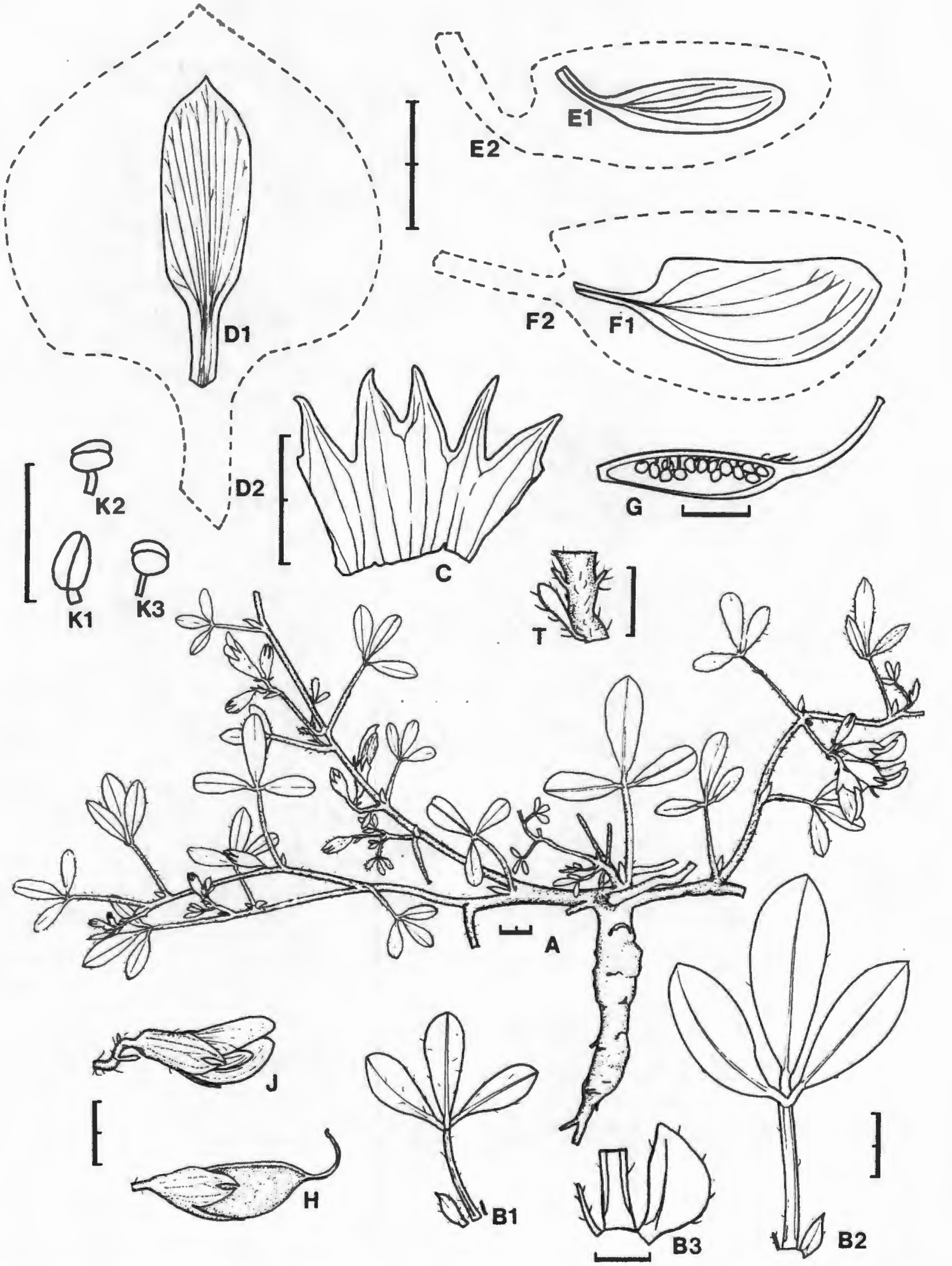

Figure 1 *Lotononis minima*. A, habit, showing the woody perennial caudex and prostrate flowering branches; B1, B2, mature leaves, showing the variation in size, the almost totally glabrous surface and the paired stipules: B1, adaxial view, B2, abaxial view; B3, petiole base with stipules; C, calyx opened out (outer face), with the upper lobes to the left; D1, standard petal; E1, wing petal (note the absence of an auricle and of sculpturing); F1, keel petal; G, carpel; H, immature fruit; J, flower in side view; K1, K2, K3, long anther, carinal anther and short anther respectively; T, pedicel, showing the bract and paired bracteoles. (all from *Acocks 12664*). *Lotononis marlothii*. D2, E2, F2, outlines of petals, showing the size and shape of the standard, wing and keel petal respectively. (all from *Acocks 23340*). Scale in mm.

oblong (linear in other species) and glabrous (distinctly hairy in other species). The young fruit is flat and not twisted between the seeds as in *L. listii*.

The flowers of the new species are extremely small, hence the specific epithet. It is comparable in size only to the cleistogamous flowers occasionally found in some species of the section Leptis. Byth (1964) has reported precocious bud pollination in the closely related species *L. bainesii* Bak. I have, however, found no evidence of the usual flower dimorphism that results from true cleistogamy in the *L. angolensis* group.

The only known locality (Figure 2) is situated in an arid area where seasonal pans are a conspicuous feature of the landscape. *L. marlothii* and *L. listii* occur in similar habitats. The distribution of most of the species in the group appears to be associated with moist or at least seasonally wet habitats.

Specimen examined

—**2921** (Kenhardt): Kenhardt Div., Jagbult, floor of Uilpan (–DA), 12/5/1946, *Acocks 12664* (PRE).

Acknowledgements

I wish to thank Dr H.F. Glen (Botanical Research Institute, Pretoria) for the Latin translation. The taxonomic study of *Lotononis* is a registered Ph.D. project at the University of Cape Town.

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S.-Afr.Tydskr. Plantk., 1989, 55(2): 178–183

Studies in *Lotononis* (Crotalarieae, Fabaceae). IV. Three new species of the *L. umbellata* group (section *Polylobium*) from the Cape Province

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Three new species of the section *Polylobium* (Eckl. & Zeyh.) Benth. of *Lotononis* (DC.) Eckl. & Zeyh. are described: *L. acocksii* B-E. van Wyk, *L. nutans* B-E. van Wyk and *L. purpurescens* B-E. van Wyk. Morphologically, these species are intermediate between *L. umbellata* (L.) Benth. and species of the section *Aulacinthus* (E. Mey.) Benth. The new species are all known only from the type localities in the south-western and southern Cape.

Drie nuwe soorte van die seksie *Polylobium (Eckl. & Zeyh.) Benth. van Lotononis* (DC.) Eckl. & Zeyh. word beskryf: *L. acocksii* B-E. van Wyk, *L. nutans* B-E. van Wyk en *L. purpurescens* B-E. van Wyk. Morfologies is hierdie soorte 'n oorgangvorm tussen *L. umbellata* (L.) Benth. en soorte van die seksie *Aulacinthus* (E. Mey.) Benth. Die nuwe soorte is almal slegs bekend van die tipe-lokaliteite in die Suidwes- en Suid-Kaap.

Keywords: Cape Province, Fabaceae, *Lotononis* section *Polylobium*, new taxa

Introduction

The section *Polylobium* (Eckl. & Zeyh.) Benth. of *Lotononis* (DC.) Eckl. & Zeyh. comprises three distinctive groups, namely the *L. umbellata, L. involucrata* and *L. angolensis* groups (van Wyk 1988). *L. umbellata* is the only species with single stipules originally included in *Polylobium* by Bentham (1843). Other species of the section are estipulate or have the stipules paired at each node. These other species also have a subterranean caudex from which flowering shoots develop annually, while *L. umbellata* is best described as a prostrate shrub. Woody, perennial branches are present, at least in old plants.

The three new species described below are morphologically intermediate between *L. umbellata* and some species of the section *Aulacinthus* (E. Mey.) Benth. It is indeed possible to accommodate them all in *Aulacinthus* without modifying the original diagnosis of the section. The section *Polylobium* as presently circumscribed is therefore unsatisfactorily artificial and the three new species are only tentatively placed in this section. A more natural sectional classification is in preparation.

Lotononis acocksii *B-E. van Wyk,* sp. nov.

L. umbellatae (L.) Benth. valde similis sed habitu multo maiore (frutex metralis), foliolis anguste oblanceolatis nec obovatis, inflorescentiliis racemosis pauciflorisque (nec subumbellatis nec multifloris), et floribus maioribus differt; *L. comptonii* B-E. van Wyk etiam similis, sed ab hac specie habitu maiore, petiolis brevioribus, lobis lateralibus calycis minus connatis, vexillo basi late cuneato (nec cordato), et forma alarum differt; a *L. nutante* B-E. van Wyk floribus multo maioribus, inflorescentia racemosa pauciflora (nec 4-vel pluriflora) et ovario lineari (nec ovato) differt.

TYPUS.— Cape Province: Ladismith district, 3,2 km [2 miles] ENE of Vanwyksdorp, 31/7/1959, *Acocks 20573* [PRE, charta 1, holotype; K, PRE (charta 2 & 3), isotypi].

Lax, sparsely branched woody shrub, up to 1 m tall. Branches slightly corky, yellow-brown; young twigs sparsely strigillose. *Leaves* digitately trifoliolate; petiole (4–)6–8(–10) mm long, persistent for some time after the leaflets are shed individually; leaflets narrowly oblanceolate, (4–)12–15(–18) mm long, (1,5–)2–3 (–4) mm wide, abaxially sparsely strigillose, adaxially glabrous. *Stipules* consistently present, single at each node, elliptic-oblong, midrib eccentric, (1–)3–5(–8) mm long. *Inflorescences* racemose, leaf-opposed, slender, long-pedunculate, 30–60(–80) mm long, sparsely (2–)3–4-flowered; bracts small, 1–2 mm long; bracteoles absent. *Flowers* 12–13 mm long, yellow; pedicel 2–5 mm long. *Calyx* 6–7 mm long, lobes triangular, with the lateral sinuses only slightly shallower than the upper or lower ones, minutely strigillose. *Standard* orbicular, 12 mm long, longitudinally striated, base broadly cuneate. *Wing petals* broadly oblong, as long as the keel; apex obtuse, subtruncate, sculpturing upper basal and upper central, in 6–7 rows of mostly intercostal lunae and lamellae. *Keel petals* broadly elliptical, 11 mm long, auriculate and pocketed near the base; apex obtuse. *Anthers* dimorphic. *Pistil* 10–12 mm long; ovary oblong-linear, 8 mm long, pubescent, verrucose along the upper suture. *Fruit* and *seed* unknown. (Figure 1).

Lotononis acocksii is closely related to *L. umbellata* (L.) Benth. but differs in the much larger habit (a sparse shrub of *ca.* 1 m tall), the narrowly oblanceolate leaflets (obovate in *L. umbellata*), the few-flowered racemes (many-flowered and sub-umbellate in *L. umbellata*) and the larger flowers. It is also similar to *L. comptonii* B-E. van Wyk, but differs from this species in the larger habit, the shorter petioles, the fusion, to a lesser degree, of the lateral and upper calyx lobes, the broadly cuneate base of the standard (cordate in *L. comptonii*) and the shape of the wing petals. From *L. nutans* B-E. van Wyk it differs in the habit, the much larger flowers, the racemose and few-flowered inflorescences (4- or more

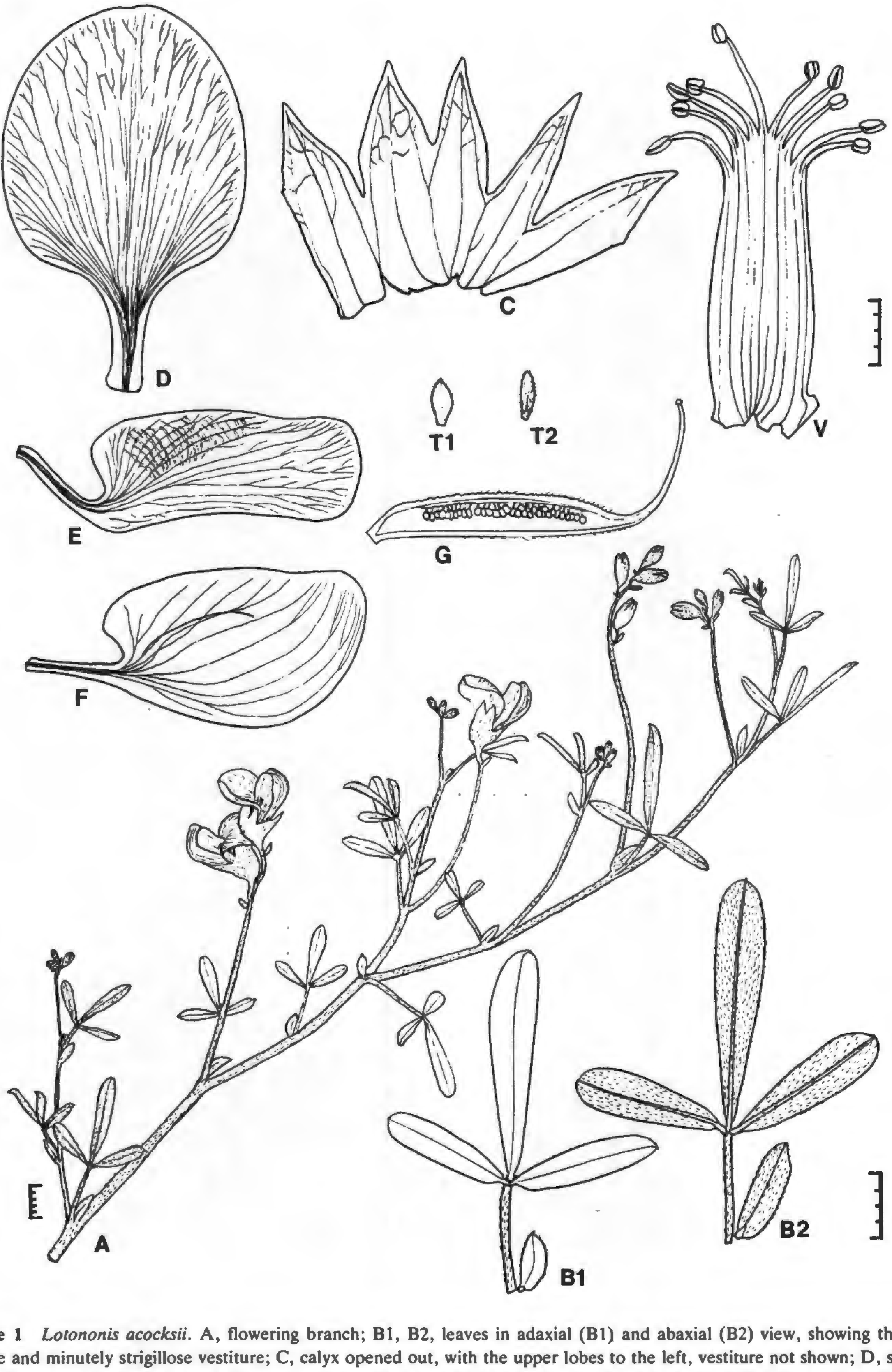

Figure 1 *Lotononis acocksii*. A, flowering branch; B1, B2, leaves in adaxial (B1) and abaxial (B2) view, showing the single stipule and minutely strigillose vestiture; C, calyx opened out, with the upper lobes to the left, vestiture not shown; D, standard petal; E, wing petal; F, keel petal; G, pistil (note the verrucose upper suture); T1, T2, bracts; V, androecium. (All from *Acocks 20573*). Scale in mm. (Note the scale difference between Figures 1 and 2. The flowers and flower parts of *L. acocksii* are almost double the size of those of *L. nutans*).

flowered and sub-umbellate in *L. nutans*) and the linear ovary (ovate in *L. nutans*).

The only known collection of *L. acocksii* is from the southern parts of the Rooiberg near Ladismith (Figure 4), where it was found in Spekboomveld (a veld type dominated by *Portulacaria afra* Jacq.) on a southern aspect. The specific epithet commemorates J.P.H. Acocks (1911–1979), one of the most prolific South African collectors. He has discovered several undescribed species of *Lotononis*, two of which are described here as new.

Material examined

—**3321** (Ladismith): Ladismith district, 3,2 km [2 miles] ENE of Vanwyksdorp (–CB), 31/7/1959, *Acocks 20573* [PRE, holo.; K, PRE (2 sheets), iso.].

Lotononis nutans *B-E. van Wyk*, sp. nov.

L. acocksii B-E. van Wyk valde similis, sed habitu prostrato, inflorescentiis subumbellatis multifloris, floribus multo minoribus nutantibus, ovario ovato differt. *L. umbellatae* (L.) Benth. etiam valde similis, sed ab hac habitu valde diffuso, petiolis longioribus aliquamdiu post exuendum foliolorum persistentibus, foliolis lanceolatis, ovario ovato (nec lineari), fructu multo breviore turgidiore differt.

TYPUS.— Cape Province: 69,6 km [43,5 miles] WSW of Uniondale, 20/9/1960, *Acocks 21585* (PRE, holotypus).

Prostrate, diffuse shrub. *Branches* sparsely leafy; young twigs minutely strigillose. *Leaves* digitately trifoliolate; petiole (5–)7–10(–12) mm long, persistent for some time after the leaflets are shed individually; leaflets oblanceolate, (3–)6–10(–12) mm long, (1,5–)3–4 mm wide, abaxially sparsely strigillose, adaxially glabrous. *Stipules* consistently present, single at each node, elliptic to elliptic-oblong, (2–)3–5(–6) mm long. *Inflorescences* subumbellate, leaf-opposed or terminal on short lateral branches, slender, long-pedunculate, 25–45 mm long, densely (4–)5–6(–7)-flowered; bracts small, up to 1,5 mm long; bracteoles absent. *Flowers* very small, 6–7 mm long, yellow; pedicel 1–2 mm long. *Calyx* 4 mm long, lobes triangular, with the lateral sinuses shallower than the upper and lower ones, minutely strigillose. *Standard* orbicular, 6–7 mm long, longitudinally striated, base broadly cuneate. *Wing petals* broadly oblong, as long as the keel; apex obtuse; sculpturing upper basal and upper central, in 6–7 rows of mostly intercostal lunae and lamellae. *Keel petals* broadly elliptical, 6 mm long, auriculate and pocketed near the base; apex obtuse. *Anthers* dimorphic. *Pistil* 5–6 mm long; ovary ovate, 4 mm long, pubescent. *Fruit* (immature) small, oblong-ovate, 8 mm long, 2,5 mm wide, laterally inflated, verrucose along the upper suture, glabrous. *Seed* unknown. (Figure 2).

L. nutans is closely related to *L. acocksii* but differs in the prostrate habit, the sub-umbellate and many-flowered inflorescences, the much smaller and nodding flowers and the ovate ovary. It is also very similar to *L. umbellata*, but differs from this species in the much sparser habit, the longer petioles that persist for some time after the leaflets are shed, the lanceolate shape of the leaflets, the ovate ovary (linear in *L. umbellata*) and in the much shorter and more turgid fruit.

The conspicuously nodding flowers and fruit have suggested the specific epithet. *L. nutans* is only known from a single specimen that was collected in stony Mountain Rhenosterveld between Uniondale and George in the southern Cape (Figure 4).

Material examined

3322 (Oudtshoorn): 68,6 km [43,5 miles] WSW of Uniondale (–DC), 20/9/1980, *Acocks 21585* (PRE, holo.).

Lotononis purpurescens *B-E. van Wyk*, sp. nov.

Distincta, haud manifeste speciei ullae cognitae similis; *L. umbellatae* (L.) Benth. distanter affinis sed habitu diffuso procumbenti (nec prostrato), foliolis ellipticis multo angustioribus, inflorescentia racemosa 2-vel 3-flora, raro usque 5-flora, floribus laete purpureis (nec flavis), petalis tenuibus cadentibus, vexillo acuto ala late oblongis vel sub-orbicularibis differt.

TYPUS.— Cape Province: Montagu, *ca.* 2,5 km along footpath to Donkerkloof, 4/10/1987, *B-E. van Wyk 2718* (PRE, holotype; BOL, JRAU, K, M, MO, NBG, SAAS, STE, isotypi).

Sparsely branched shrublet, up to 0,3 m tall and 0,5 m wide. *Branches* yellow and slightly corky, slender, sparsely leafy; young twigs minutely strigillose. *Leaves* digitately trifoliolate; petiole (3–)6–10(–17) mm long, persistent for some time after the leaflets are shed individually; leaflets elliptic to oblanceolate, (4–)8–15 (–22) mm long, (2–)3–4(–5) mm wide, very thin in texture, abaxially sparsely strigillose, adaxially glabrous. *Stipules* consistently present, single at each node, ovate, elliptic to elliptic-oblong or slightly falcate, (1,5–)3–6 (–8) mm long. *Inflorescences* racemose, leaf-opposed or sub-terminal, slender, long-pedunculate, (15–)40–70 (–90) mm long, sparsely (1–)2–3(–5)-flowered; bracts small, linear, up to 2 mm long; bracteoles absent. *Flowers* small, 8–10 mm long, pale purple; petals very thin in texture, caducous; pedicel 1,5–2,5 mm long. *Calyx* 5–6 mm long, lobes narrowly triangular, with the lateral sinuses only slightly shallower than the upper and lower ones, minutely strigillose. *Standard* ovate, pointed, 8–9,5 mm long, with two weakly developed callosities at the apex of the claw. *Wing petals* very broadly oblong to sub-orbicular, shorter than the keel; sculpturing upper basal and upper left central, in 6–7 rows of inter- and transcostal lunae and lamellae. *Keel petals* semicircular, 8–9 mm long, auriculate and pocketed near the base; apex obtuse. *Anthers* dimorphic. *Pistil* 8 mm long; ovary linear, 4–6 mm long, pubescent. *Fruit* (immature) oblong-ovate to oblong, 5–10 mm long, 3 mm wide, laterally only slightly inflated, verrucose along the upper suture, sparsely pubescent. *Seed* unknown. (Figure 3).

Lotononis purpurescens is a distinct species with no obvious affinities. It is similar to *L. umbellata*, but differs in the diffuse and procumbent habit (not prostrate as in

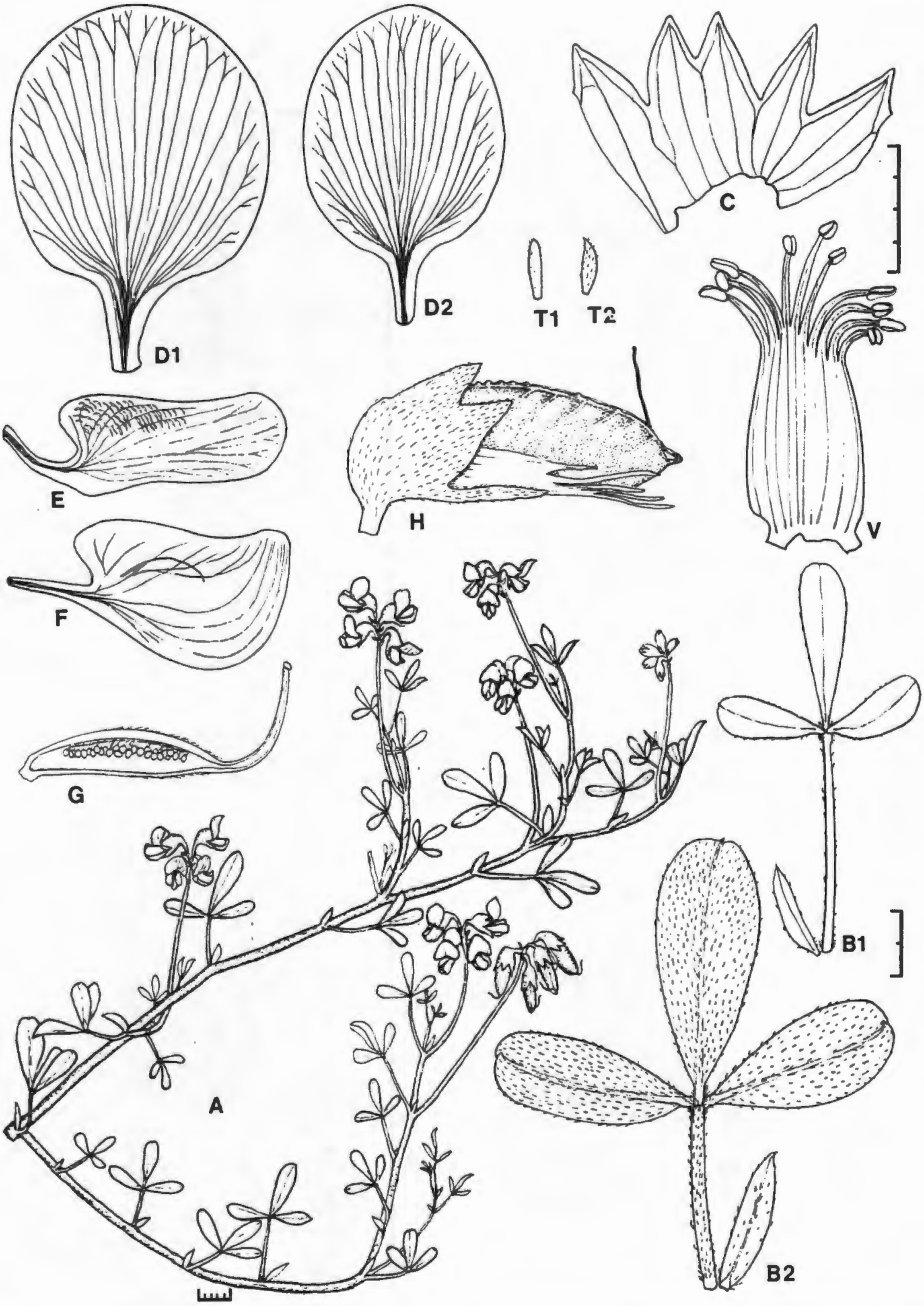

Figure 2 *Lotononis nutans*. A, flowering branch; B1, B2, leaves in adaxial (B1) and abaxial (B2) view; C, calyx opened out with upper lobes to the left, vestiture not shown; D1, D2, standard petals from an older (D1) and a younger (D2) flower; E, wing petal; F, keel petal; G, pistil; H, fruit, showing the verrucose upper suture; T1, T2, bracts; V, androecium. (All from *Acocks 21585*). Scale in mm.

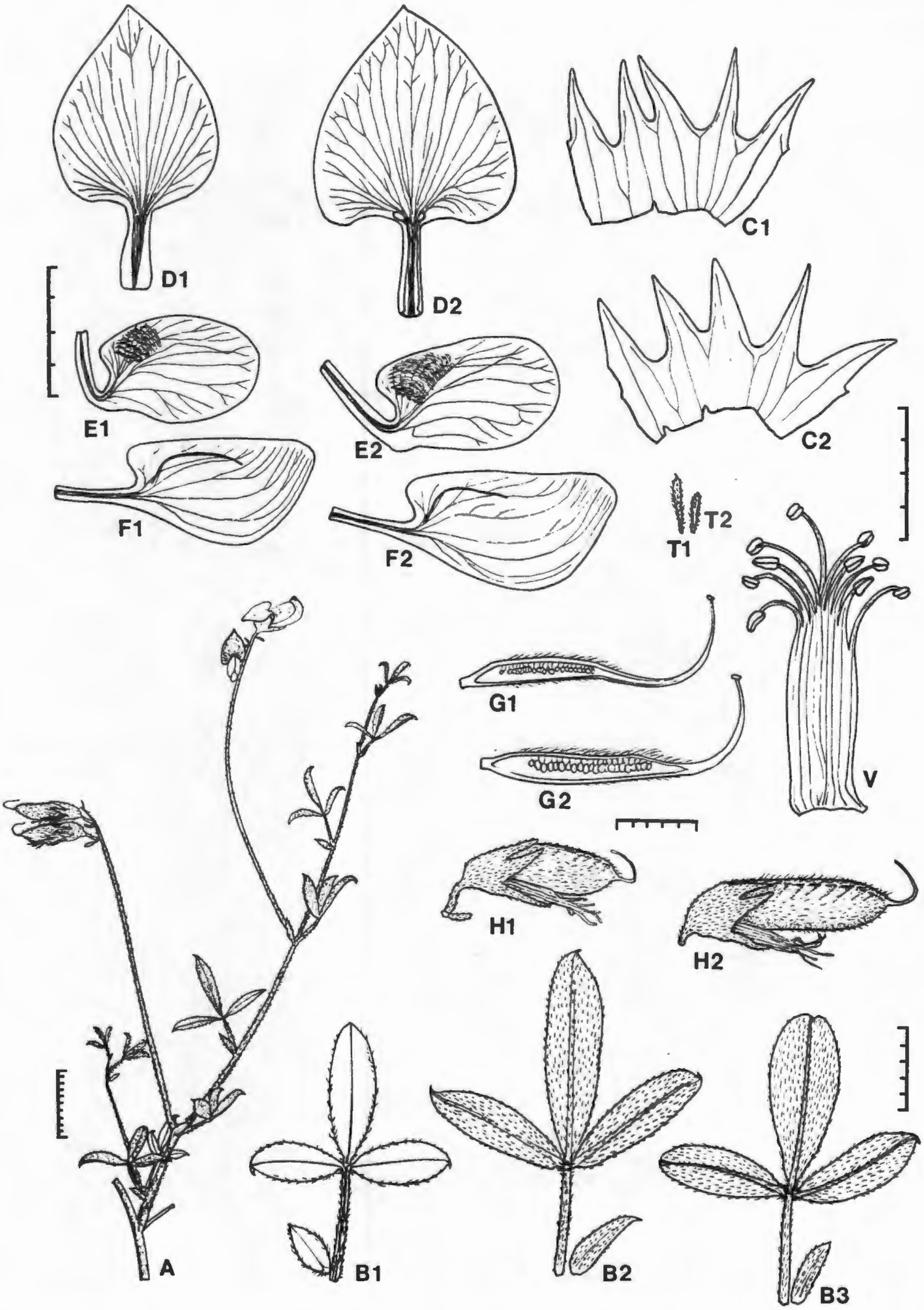

Figure 3 *Lotononis purpurescens*. A, flowering branch, showing the slender and sparsely flowered inflorescences; B1, B2, B3, leaves in adaxial (B1) and abaxial (B2, B3) view, showing the recurved leaflet apices and single stipules; C1, C2, calyx opened out, upper lobes to the left, showing the fusion of the lateral lobes; D1, D2, standard petals (note the shape); E1, E2, wing petals, showing the almost orbicular shape; F1, F2, keel petals; G1, G2, pistils; H1, H2, immature fruit, showing the slightly verrucose upper suture; T1, T2, bracts; V, androecium. (C1, D1, E1, F1 & G1 from a young flower, C2, D2, E2, F2 & G2 from an older flower; all from *B-E. van Wyk 2718*). Scale in mm.

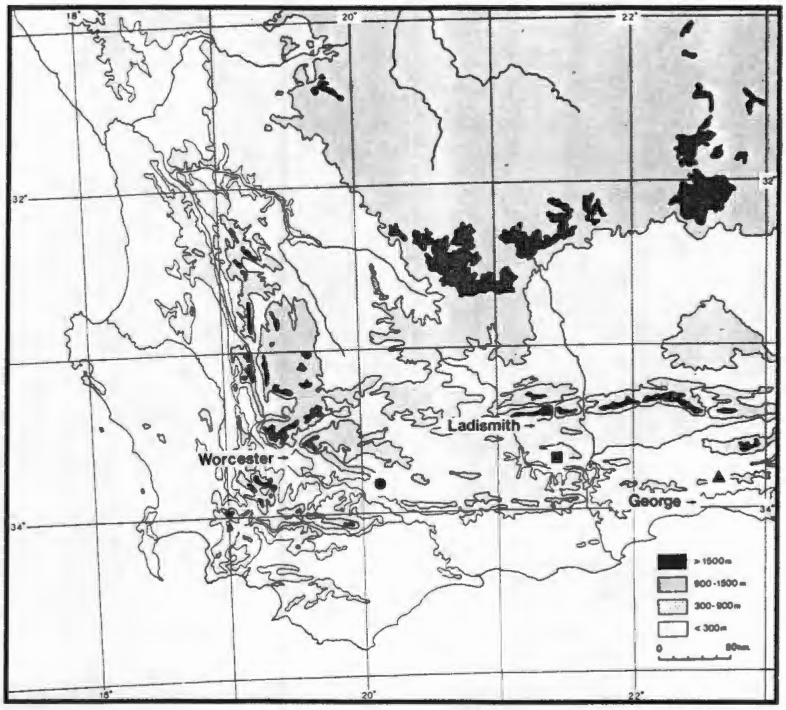

Figure 4 The known geographical distribution of *Lotononis acocksii* (■), *L. nutans* (▲) and *L. purpurescens* (●).

L. umbellata), the much narrower and elliptic leaflets, the racemose and few-flowered inflorescences (mostly 2- or 3-flowered, rarely up to 5-flowered), the pale purple flowers (yellow in *L. umbellata* and all other species of the sections *Polylobium* and *Aulacinthus*), the thinly textured and caducous petals, the pointed standard and the broadly oblong to almost orbicular wing petals.

The pale purple colour of the flowers is unusual. Pink flowers are known from a few annuals such as *L. brachyloba* (E. Mey.) Benth. and *L. rosea* Dümmer. Perennial species, and particularly the more woody ones, commonly have yellow or blue flowers but purple or pink have only been recorded in a form of *L. dichiloides* Sond. [section *Krebsia* (Eckl. & Zeyh.) Benth.] and also in *Buchenroedera meyeri* Presl. The general morphology is very similar to that of *L. umbellata* and some species of the section *Aulacinthus*, so that the species is readily accommodated in this group. A study of alkaloids (van Wyk & Verdoorn, in prep.) has indeed shown it to be very similar to *L. umbellata* and *L. rigida* (E. Mey.) Benth.

L. purpurescens is only known from the immediate vicinity of Donkerkloof at Montagu, where it was first collected in 1921. I found it in clayey soil on a dry western aspect. The rather unusual vegetation in which it grows is dominated by *Protea nitida* Mill., *Boophane disticha* (L. f.) Herb. and *Themeda triandra* Forssk.

Material examined

—**3320** (Montagu): Montagu district, Donkerkloof (–CC), 26/9/1946, *Compton 18472* (NBG), 9/1946, *Lewis 2087* (SAM); Montagu Baths (–CC), 10/1921, *Page s.n. sub BOL 15441* (BOL), *s.n. sub PRE 53522* (PRE); Montagu, *ca.* 2,6 km along footpath to Donkerkloof (–CC), 27/6/1987, *B-E. van Wyk 2654, 2655* (JRAU), 4/10/1987, *B-E. van Wyk 2718* (PRE, holo.; BOL, JRAU, K, M, MO, NBG, SAAS, STE, iso.), *2719* (GRA, K, PRE, NH), *2720* (K, PRE), *2721* (C, NBG).

Acknowledgements

I wish to thank Dr H.F. Glen (Botanical Research Institute, Pretoria) for the latin translations and the Directors and staff of the cited herbaria for the loan of specimens. The taxonomic study of *Lotononis* is a registered Ph.D. project at the University of Cape Town.

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Bothalia 19,1: 7–8 (1989)

Studies in the genus *Lotononis* (Crotalarieae, Fabaceae). 5. A new species of the *L. involucrata* group (section *Polylobium)* from the north-western Cape Province

B–E. VAN WYK*

Keywords: Cape Province, Fabaceae, *Lotononis* section *Polylobium*, new taxon

ABSTRACT

A new species of the section *Polylobium* (Eckl. & Zeyh.) Benth. of *Lotononis* (DC.) Eckl. & Zeyh. is described, namely *L.* **racemiflora** B–E. van Wyk. The species, known only from a single collection near Clanwilliam in the north-western Cape, is closely related to *L. involucrata* (Berg.) Benth. and *L. angustifolia* (E. Mey.) Steud.

UITTREKSEL

'n Nuwe soort van die seksie *Polylobium* (Eckl. & Zeyh.) Benth. van *Lotononis* (DC.) Eckl. & Zeyh. word beskryf, naamlik, *L.* **racemiflora** B–E. van Wyk. Die soort, wat slegs bekend is van 'n enkele versameling naby Clanwilliam in die Noord-wes Kaap, is naverwant aan *L. involucrata* (Berg.) Benth. en *L. angustifolia* (E. Mey.) Steud.

INTRODUCTION

Lotononis involucrata (Berg.) Benth. and related species differ from other species of the section *Polylobium* (Eckl. & Zeyh.) Benth. in the subterranean caudex from which flowering shoots develop annually. Stipules are paired or absent and never single or markedly dimorphic as in other species. The umbellate inflorescence in all the species which Dümmer (1913) included in *Polylobium* was used as a diagnostic character for the section.

The new species described below is morphologically intermediate between *L. involucrata* (Berg.) Benth. and *L. angustifolia* (E. Mey.) Steud. and is obviously very closely related to these species. However, the inflorescence is a true raceme. Inflorescence structure is therefore no longer a useful diagnostic character for distinguishing the section *Polylobium*. It may indeed be argued that *Polylobium sensu lato* is an artificial group which has resulted from the excessive weighting of inflorescence structure as a diagnostic character.

Lotononis racemiflora *B–E. van Wyk*, sp. nov., *L. angustifoliae* (E. Mey.) Steud. valde similis, sed inflorescentia multiflora racemosa (in *L. angustifolia* pauciflora umbellata vel subumbellata), basi stipulae semicordato, indumento densiore piloso differt; etiam *L. involucrata* (Berg.) Benth. similis, sed ab hac specie inflorescentia racemosa, foliolorum amplitudine texturaque (quam in *L. involucrata* maioribus coriaceoribus), stipularum amplitudine formaque, vexillo alisque multo maioribus differt.

TYPE.—Cape, 3218 (Clanwilliam): Clanwilliam District, Bokwater, W of Clanwilliam (–BB), 28.10.1948, *Acocks 15171* (PRE, holo.; K, iso.).

Suffrutescent herb, with annual flowering branches from a woody root. *Branches* procumbent, up to 0,3 m long, thick and rigid, densely leafy, more sparsely so towards the base, densely pilose. *Leaves* digitately trifoliolate, densely and softly pilose; petiole (3–) 8–12 (–14) mm long; leaflets linear to narrowly elliptical, (4–) 10–18 (–22) × 2–2,5 mm, with soft pilose hairs on both surfaces. *Stipules* similar to the leaflets, consistently present, paired at each node, ovate to lanceolate, (3–) 8–10 (–12) mm long; base distinctly semicordate; apex obtuse to acute. *Inflorescences* terminal on primary and secondary branches, racemose, lax, 90–140 mm long, up to 18-flowered; peduncle 28–50 mm long, densely and softly pilose; rachis up to 95 mm long, bracts conspicuous, thickly textured, ovate-cymbiform, up to 8 × 3 mm, pilose on both surfaces; bracteoles absent. *Flowers* large, 14–16 mm long, yellow; pedicel 3–5 mm long. *Calyx* 12–14 mm long, lobes narrowly acuminate, with the lateral ones on either side fused higher up in pairs, lanately pilose. *Standard* large, suborbicular, 15 mm long, longitudinally striated, base broadly cordate. *Wing petals* broadly obovate, much longer than the keel; apex obliquely rounded; sculpturing upper basal and upper central, in 7–8 rows of mostly intercostal lunae and lamellae. *Keel petals* small, semicircular, 11–12 mm long, auriculate and pocketed near the base; apex acute. *Anthers* dimorphic. *Pistil* 11–12 mm long; ovary oblong-linear, 6–7 mm long, pubescent. *Fruit* (immature) oblong-linear, twice as long as the calyx, much inflated laterally, sparsely pubescent, with evenly spaced warty protuberances along the upper suture. *Seed* unknown. Figure 1.

L. racemiflora is closely related to *L. angustifolia* but differs in the many-flowered racemose inflorescence (few-flowered and umbellate or subumbellate in *L. angustifolia*), the semicordate stipule base and the more densely pilose vestiture. It is also similar to *L. involucrata*, but differs from this species in the racemose inflorescence, the size and texture of the leaflets (larger and more coriaceous than in *L. involucrata*), the size and shape of the stipules and the much larger standard and wing petals.

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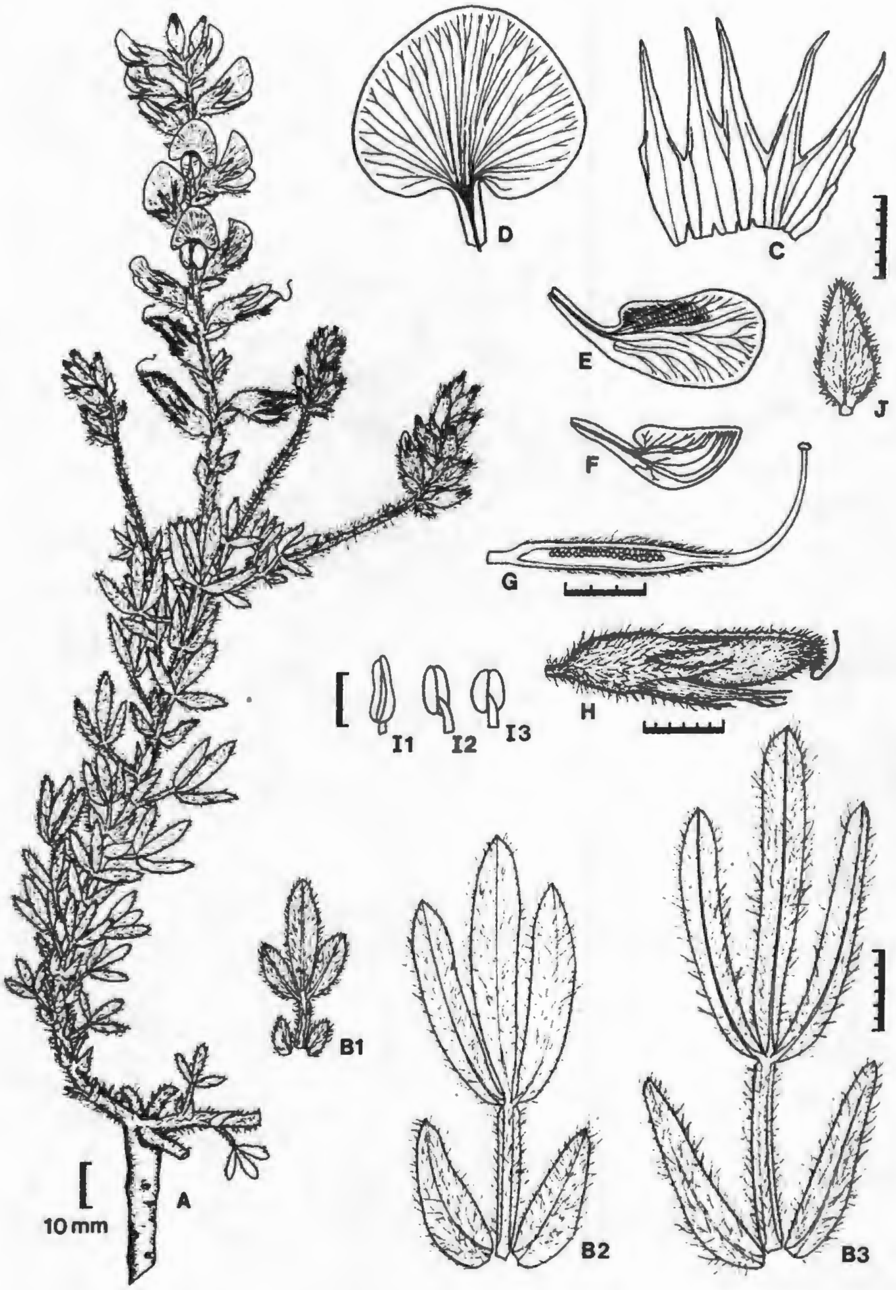

FIGURE 1.—*Lotononis racemiflora*. A, habit, showing a flowering branch, the persistant root and the long, racemose inflorescence. B1, B2, B3, leaves and stipules, showing the variation in size and shape and the pilose vestiture: B1, abaxial view of a mature leaf taken from a basal node, B2, adaxial view (note the vestiture), B3, abaxial view. C, calyx opened out, with the upper lobes to the left, vestiture not shown; D, standard petal; E, wing petal; F, keel petal, showing the small size and pointed apex; G, pistil; H, immature fruit in lateral view, showing the verrucose upper suture; I1, I2, I3, long anther, carinal anther and short anther respectively; J, bract. All from *Acocks 15171*. Scales in mm.

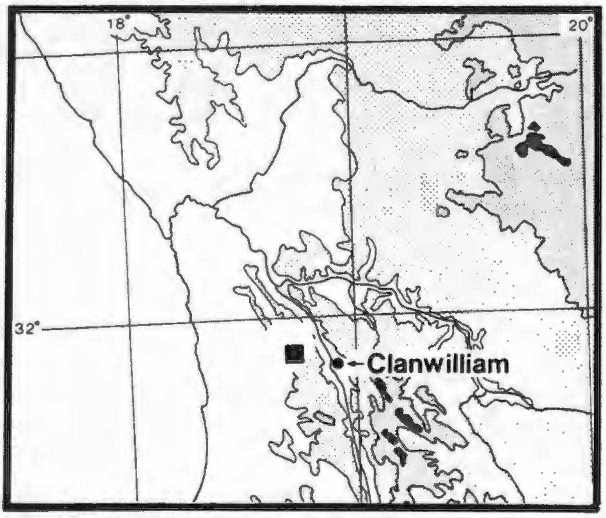

FIGURE 2.—The known geographical distribution of *Lotononis racemiflora*.

The new species may be confused with *L. angustifolia* and *L. involucrata* when not in flower, but the inflorescence structure is quite different. It is known from a single collection near Clanwilliam in the north-western Cape, where it was found on an old land in Fynbos-Strandveld vegetation. Figure 2.

CAPE.—3218 (Clanwilliam): Clanwilliam District, Bokwater, W of Clanwilliam (–BB), 28.10.1948, *Acocks 15171* (PRE, holo.; K. iso.).

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I wish to thank Dr H. F. Glen (Botanical Research Institute, Pretoria) for the Latin translation. The taxonomic study of *Lotononis* is a registered Ph. D. project at the University of Cape Town.

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APPENDIX 25

Studies in the genus Lotononis (Crotalarieae, Fabaceae). VI. Two new species of the L. digitata group from the north-western Cape Province

B-E. VAN WYK*

Keywords: Cape Province, Fabaceae, Lotononis, new taxa

ABSTRACT

Two new species of Lotononis (DC.) Eckl. & Zeyh. are described: L. magnifica B-E. van Wyk and L. plicata B-E. van Wyk. The new species are closely related to L. digitata Harv. and L. benthamiana Dümmer [section Krebsia (Eckl. & Zeyh.) Benth.], but also to L. quinata (Thunb.) Benth. and L. longiflora H. Bol. [section Leptis (Eckl. & Zeyh.) Benth.]. Within the genus Lotononis, these species together form an isolated group that should be recognised as a distinct section. The shape of the pods is a particularly useful character to distinguish between the species of the group.

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UITTREKSEL

Twee nuwe spesies van *Lotononis* (DC.) Eckl. & Zeyh. word beskryf: *L. magnifica* B-E. van Wyk en *L. plicata* B-E. van Wyk. Die nuwe spesies is naverwant aan *L. digitata* Harv. en *L. benthamiana* Dümmer [seksie *Krebsia* (Eckl. & Zeyh.) Benth.], maar ook aan *L. quinata* (Thunb.) Benth. en *L. longiflora* H. Bol. [seksie *Leptis* (Eckl. & Zeyh.) Benth.]. Hierdie spesies vorm gesamentlik 'n geisoleerde groep binne die genus *Lotononis* wat as 'n afsonderlike seksie erken behoort te word. Die vorm van die peule is 'n besonder handige kenmerk om tussen die spesies van die groep te onderskei.

Introduction

Lotononis digitata Harv. and related species form a distinct group of short-lived perennials that can easily be recognised by the 5-digitate leaves, slender petioles, uniform flower structure and stipitate pods. Except for *L. digitata*, which has also been recorded from the south-eastern Cape, the group is confined to the north-western Cape Province.

Dümmer (1913) placed *L. digitata* and *L. benthamiana* Dümmer in the section *Krebsia* (Eckl. & Zeyh.) Benth., but retained *L. quinata* (Thunb.) Benth. in the section *Leptis* (Eckl. & Zeyh.) Benth. *L. digitata* and *L. quinata* are very similar and indeed difficult to identify when pods are not available. It is suggested that *L. digitata* and related species should be formally recognised as a distinct section (Van Wyk, in prep.). The new section would include *L. digitata*, *L. benthamiana*, *L. quinata*, *L. longiflora* H. Bol. and the two new species described below.

Descriptions

1. *Lotononis magnifica* B-E. van Wyk sp. nov. *L. quinatae* (Thunb.) Benth. valde affinis, sed habitu maiore lignosiore, foliolis maioribus densius sericeis (in *L. quinata* glabrescentibus), floribus valde maioribus atque leguminibus parum longioribus differt. Similis est etiam *L. molli* (E. Mey.) Benth. et *L. mirabili* Dinter (sectionis *Lepti*), sed in his speciebus folia trifoliolata, vexillum, alae carinaque sunt dense pubescentes.

TYPE --- Cape Province, 3018 (Kamiesberg): top of Kamiesberg, 3 km south of radio tower (--AC), 16/10/1986, *B-E. van Wyk 2421* (PRE, holo.; K, NBG, MO, iso.).

Prostrate shrublet up to 0,3 m wide. Branches thick and woody below, upper parts sparsely leafy, densely and divaricately branched. All mature parts (except the corolla and pods) densely sericeous. *Leaves* slender, (10--) 15--20 (--25) mm long, digitate, invariably 5-foliolate, densely sericeous; petiole slender, (5--) 10--16 (--20) mm long; leaflets relatively large, oblanceolate, 5--8 mm long, 1--3 mm wide, abaxially densely silky-sericeous, adaxially glabrous. *Stipules* single at each node, small, lanceolate to ovate, up to 4 mm long. *Inflorescences* leaf-opposed, 1--4 (--6)-flowered; peduncle short, 2--6 mm long; bracts small, linear, up to 4 mm long; bracteoles absent. *Flowers* relatively large, (10--) 15--20 mm long, yellow; pedicel short, 2--4 mm long. *Calyx* narrowly campanulate, sericeous; lobes long, narrowly acuminate, the upper and lateral lobes on either side fused much higher up in pairs, the lower lobe similar to the upper ones. *Standard* obovate, as long as the keel; claw 3--5 mm long; lamina 8--14 mm long, glabrous or with a few minute hairs dorsally along the middle. *Wing petals* oblong, slightly shorter than the keel, distinctly auriculate, glabrous; apex obtuse; sculpturing in 4 rows of intercostal lunae, fading into transcostal lamellae towards the auricle. Keel petals broadly oblong, glabrous; apex obtuse. Pods shortly stipitate, (stipe ± 1 mm long), linear, 14--18 mm long, 3--4 mm wide, flat, upper suture minutely and inconspicuously verrucose, ± 10-seeded, the seeds on long funicles. Seeds suborbicular, testa minutely and densely tuberculate (Figure 1).

L. magnifica is closely related to L. quinata (Thunb.) Benth. but differs in the larger and more woody habit, the larger and densely sericeous leaflets (glabrescent in L. quinata), the much larger flowers and the slightly longer pods. It is also similar to L. mollis (E. Mey.) Benth. and L. mirabilis (section Leptis) and may be mistaken for it, but in these species the leaves are trifoliolate and the standard, wing petals and keel are densely pubescent. Both L. mollis and L. magnifica are known only from the Kamiesberg (Figure 4), where the new species was first collected in 1986. The specific epithet alludes to the striking appearance of the plant when in full flower (Figure 2).

---3018 (Kamiesberg): Kamieskroon to Kamiesberg road, ca. 1 km south from turn-off to Springbok (--AA), 16/10/1986, B-E. van Wyk 2389 (JRAU); top of Kamiesberg, 3 km south of radio tower (--AC), 16/10/1986, B-E. van Wyk 2421 (PRE, holotype; K, NBG, MO, isotypes), 2422 (BOL, JRAU, K, PRE), 2423 (STE), 20/01/1987, B-E. van Wyk 2549, 2550, 2551, 2552, 2553, 2554, 2555, 2556 (JRAU).

2. *L. plicata* B-E. van Wyk sp. nov. *L. quinatae* (Thunb.) Benth. et *L. digitatae* Harv. valde similis, sed leguminibus tortis plicatis differt. A *L. digitata* foliolis oblongis vel anguste oblanceolatis (in *L. digitata* anguste linearibus), floribus paulum minoribus atque vexillo pilosiori etiam differt. A *L. quinata* etiam habitu maiore diffusiore, foliis paulum maioribus atque pedunculis longioribus differt. Legumines similes sunt eis *L. listii* Polhill, sed bracteolae absunt et habitus, folia, stipulae fabricaque florum omnino differunt.

TYPE --- Cape Province, 3118 (Vanrhynsdorp): near Bitterfontein, between Vanrhynsdorp and Bitterfontein (--AB), 27/09/1931, *Salter 1601* (K, holo.; BOL, iso.).

Prostrate shrublet up to 0,4 m wide. Branches somewhat woody below, upper parts diffuse and slender, sparsely leafy. Mature parts inconspicuously and minutely pubescent. *Leaves* (8--) 10--20 (--28) mm long, digitate, invariably 5-foliolate, minutely pubescent; petiole slender, (4--) 6--12 (--24) mm long; leaflets narrowly oblanceolate to narrowly oblong, (4--) 6--8 (--13) mm long, 0,5--2 mm wide, abaxially sparsely and minutely pubescent, adaxially glabrous. *Stipules* single at each node, small, lanceolate to ovate, up to 3 mm long. *Inflorescences* leaf-opposed, 1--3 (--4)-flowered; peduncle (2--) 5--8 (--12) mm long; bracts small, linear, ± 1 mm long; bracteoles absent. *Flowers* 9--10 mm long, yellow; pedicel short, 1--2 mm long. *Calyx* narrowly campanulate, minutely pubescent; lobes long, narrowly acuminate, the upper and lateral lobes on either side fused much higher up in pairs, the lower lobe similar to the upper ones. *Standard* obovate, as long as the keel; claw 2,5--3 mm long; lamina 6--8 mm long, minutely pubescent on part of the dorsal surface. *Wing petals* oblong, slightly shorter than the keel, distinctly auriculate, glabrous; apex obtuse; sculpturing in 3--4 rows of intercostal lunae, fading into transcostal lamellae towards the auricle. *Keel petals* broadly oblong, glabrous; apex obtuse. *Pods* shortly stipitate, (stipe ± 1 mm long), folded like a concertina, 7--15 mm long, 2--3 mm wide, upper suture ± smooth, 5--8-seeded, the seeds on long funicles. *Immature seeds* suborbicular, testa minutely and sparsely tuberculate (Figure 3).

L. plicata is very closely related to *L. quinata* (Thunb.) Benth. and *L. digitata* Harv. but differs in the twisted and folded (plicate) pods. It also differs from *L. digitata* in the oblong to narrowly oblanceolate leaflets (narrowly linear in *L. digitata*), the slightly smaller flowers and the more hairy standard petal. From *L. quinata* it also differs in the larger and more diffuse habit, the slightly larger leaves and longer peduncles. The pods are similar to those of *L. listii* Polhill, but bracteoles are absent and the habit, leaves, stipules and flower structure are totally different. *L. plicata* is known only from two collections and appears to be restricted to southern Namaqualand (Figure 4).

The mature pods provide the only reliable character to distinguish *L. plicata* from its close relatives. Figure 3 shows that the shape of the pod and the length of the stipe are indeed useful diagnostic characters in the group as a whole.

---3118 (Vanrhynsdorp): near Bitterfontein, between Vanrhynsdorp and Bitterfontein (--AB), 27/09/1931, Salter 1601 (K, holotype; BOL, isotype); 8 miles [12,8 km] SE of Bitterfontein (--AB), 14/09/1948, Acocks 14782 (K).

Acknowledgements

Thanks are due to Dr H. F. Glen (Botanical Research Institute, Pretoria) for the Latin translations and the Directors and staff of the cited herbaria for the loan of specimens. The taxonomic study of Lotononis is a registered Ph. D. project at the University of Cape Town.

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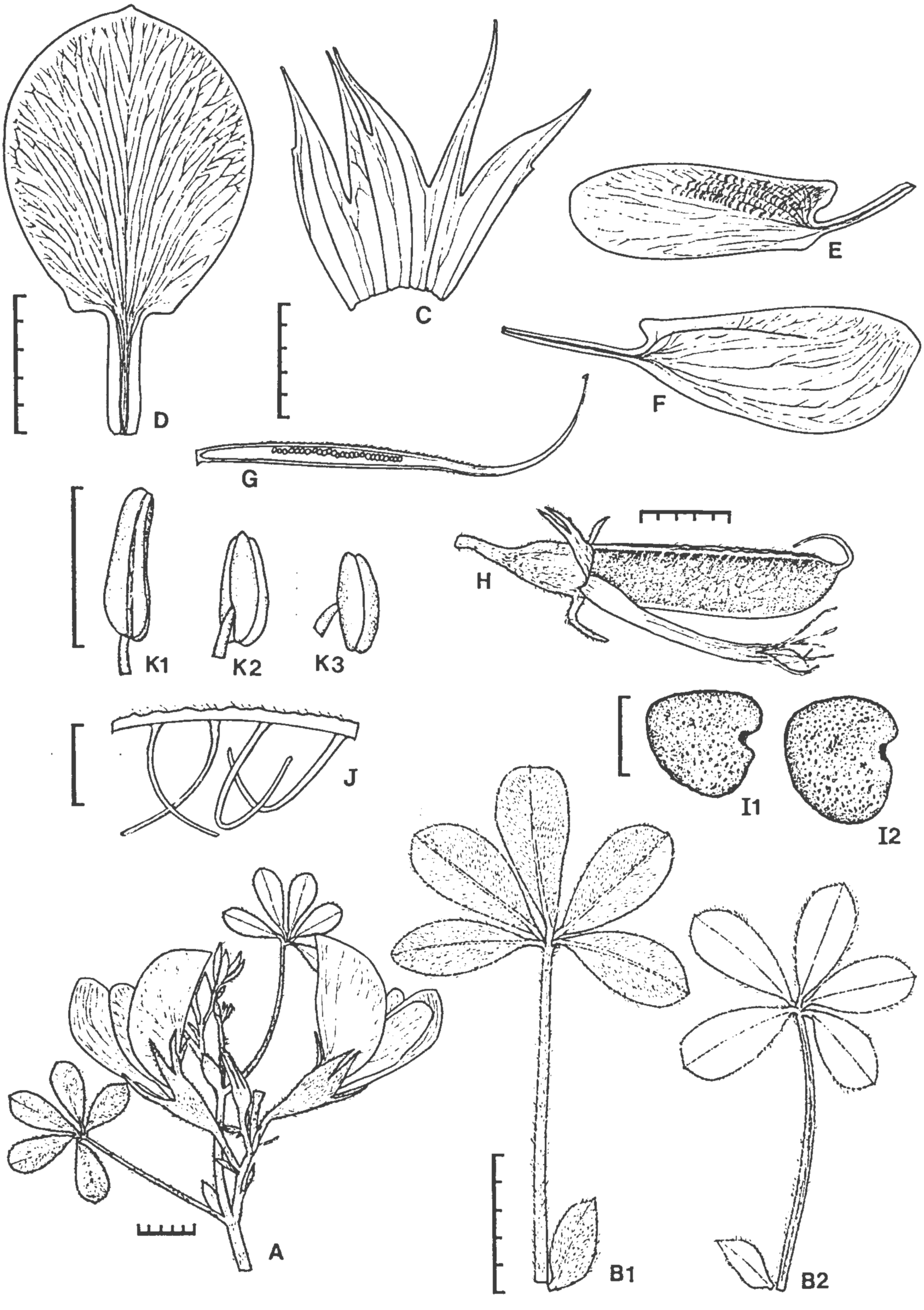

Figure 1. Lotononis magnifica. A, flowering twig, showing the short racemose inflorescence and the large flowers; B1 & B2, leaves and stipules: B1, abaxial view, B2, adaxial view; C, calyx opened out with the upper lobes to the left; D, standard petal; E, wing petal; F, keel petal; G, pistil, showing the short stipe; H, pod in lateral view; I1, I2, seeds, showing the tuberculate surface; J, part of pod after dehiscence as viewed from inside, showing the long funicles and slightly verrucose upper suture; K1, K2, K3, anthers: K1, long basifixed anther, K2, intermediate carinal anther, K3, short dorsifixed anther. All from B-E. van Wyk 2421 except the pod and seeds from B-E. van Wyk 2549. Scales in mm.

[PHOTOGRAPH]

Figure 2. *Lotononis magnifica* in full flower, showing the prostrate habit and large flowers (Type locality, 16/10/1986).

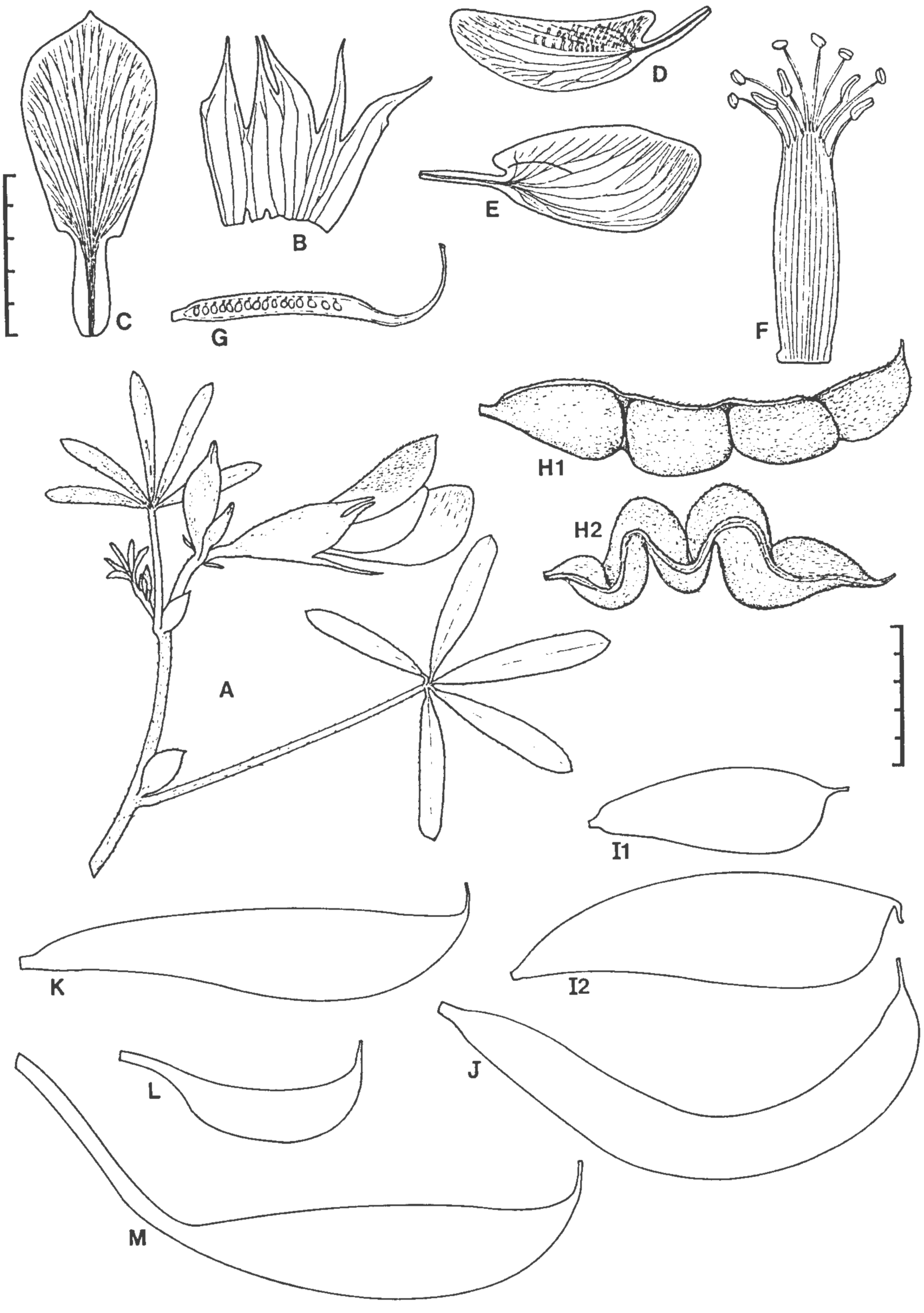

Figure 3. Lotononis plicata. A, flowering twig, showing the short racemose inflorescence, leaves and stipules (upper leaf in abaxial view, lower leaf in adaxial view); B, calyx opened out with the upper lobes to the left; C, standard petal; D, wing petal; E, keel petal; F, androecium; G, pistil, showing the short stipe; H1 & H2, mature pods: H1, lateral view, H2, top view. I to M, shape of the pod (lateral view) in L. quinata and related species: I1, I2, L. quinata; J, L. digitata; K, L. magnifica; L, L. benthamiana; M, L. longiflora. All except I to M from Salter 1601. Scales in mm.

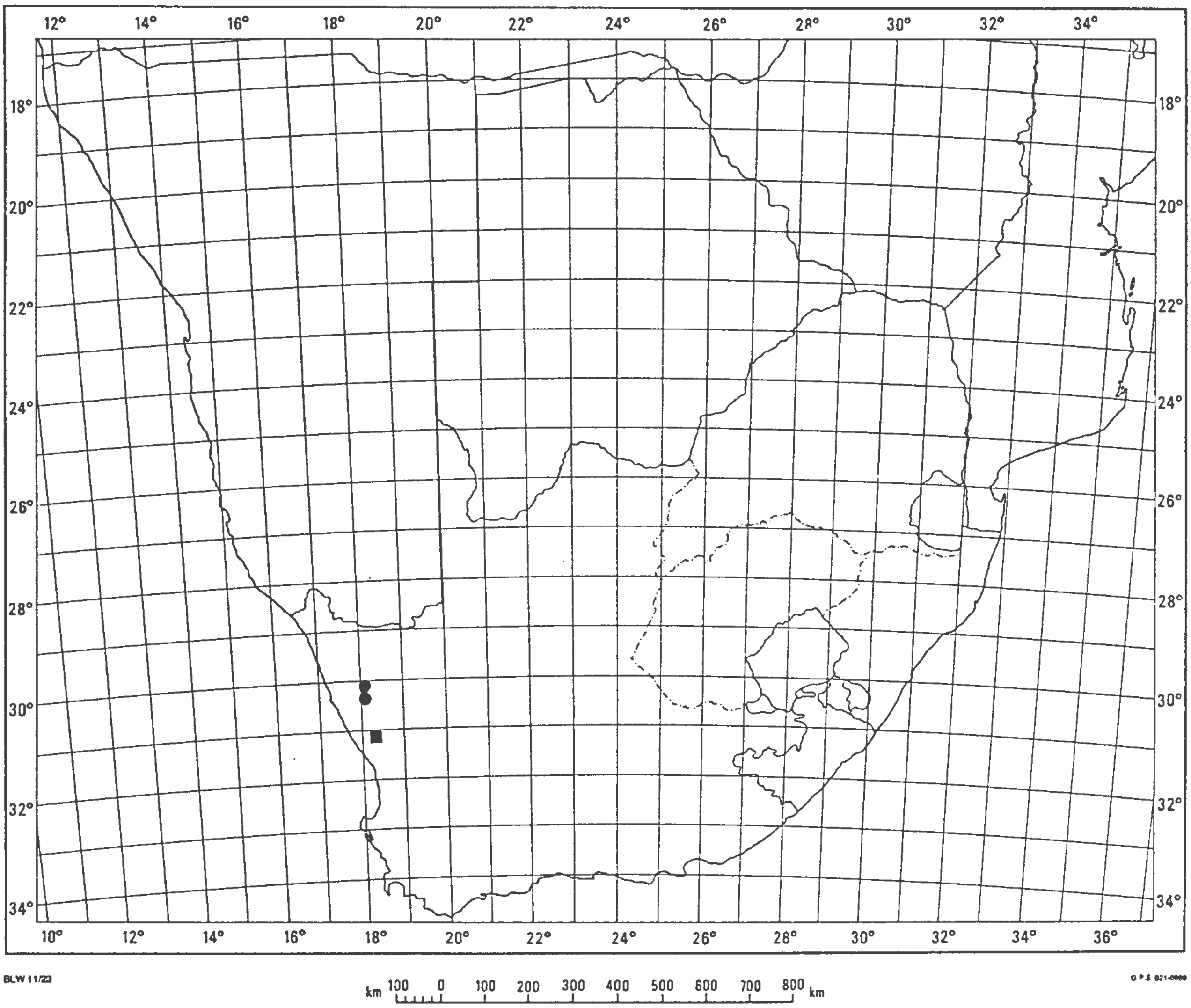

Figure 4. The known geographical distribution of Lotononis magnifica (●) and L. plicata (■).

APPENDIX 26

Studies in the genus Lotononis (Crotalarieae, Fabaceae). VII. New taxa and new combinations in the section Oxydium

B-E. VAN WYK*

Keywords: Crotalaria, Fabaceae, Lotononis section Oxydium, new combinations, new taxa

ABSTRACT

The taxonomy and nomenclature of some species of the section Oxydium Benth. of Lotononis (DC.) Eckl. & Zeyh. have been revised. Diagnostic characters to distinguish between this section and the genus Crotalaria L. are briefly discussed. Crotalaria stenophylla Eckl. & Zeyh. and C. sparsiflora E. Mey. are transferred to the genus Lotononis. A new species (L. carnea B-E. van Wyk) and a new subspecies (L. rostrata Benth. subsp. brachybotrys B-E. van Wyk) are described. L. namaquensis H. Bol. is treated as a subspecies of L. rostrata. The known geographical distribution of above-mentioned species is given.

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UITTREKSEL

Die taksonomie en nomenklatuur van enkele spesies van die seksie *Oxydium* Benth. van *Lotononis* (DC.) Eckl. & Zeyh. is hersien. Diagnostiese kenmerke om hierdie seksie van die genus *Crotalaria* L. te onderskei, word kortliks bespreek. *Crotalaria stenophylla* Eckl. & Zeyh. en *C. sparsiflora* E. Mey. word oorgeplaas na die genus *Lotononis*. 'n Nuwe spesie (*L. carnea* B-E. van Wyk) en 'n nuwe subspesie (*L. rostrata* Benth. subsp. *brachybotrys* B-E. van Wyk) word beskryf. *L. namaquensis* H. Bol. word beskou as 'n subspesie van *L. rostrata*. Die bekende geografiese verspreiding van bogenoemde spesies word aangegee.

Introduction

The section Oxydium Benth. of Lotononis (DC.) Eckl. & Zeyh. includes species that are remarkably similar to species of the genus Crotalaria L. For this reason, Dümmer (1913) referred a large part of the section to Crotalaria. Some of the nomenclatural difficulties that have resulted from this treatment are resolved in this paper.

The distinction between Lotononis section Oxydium and Crotalaria have been discussed by Baker (1914), Verdoorn (1928) and Polhill (1968, 1976). Most of the previously used diagnostic characters have resulted in different opinions about the placement of some species. Too much weight has been given to the shape of the keel, the presence of lobes and callosities on the standard petal and the shape of the pods for example, characters which are now known to be variable within both groups. Polhill (1968, 1976, 1982) has shown that the size of the carinal anther is a useful character. Crotalaria has 5 long and 5 short anthers (carinal anther similar to the basifixed ones) while Lotononis has 4 long and 6 short anthers (carinal anther similar to the dorsifixed ones).

I consider the total absence of bracteoles in Oxydium to be the most reliable diagnostic character, but the number of stipules is also very useful. Stipules are single at each node in Oxydium, while it is paired (or absent) in

Crotalaria. The only species of *Oxydium* with paired stipules are *L. delicata* (Bak. f.) Polhill and *L. pseudodelicata* (Torre) Polhill (both known only from Angola) and *L. pallens* Eckl. & Zeyh. (known only from the type collection made near Citrusdal in the south-western Cape). The standard petal provides another useful character. In *Oxydium*, the claw is usually very long and it is distinctly dilated (at least at the base) in all the species, while it is short and narrow in *Crotalaria*. A summary of similarities and differences between *Crotalaria* and *Lotononis* section *Oxydium* is given in Table 1.

The species treated in this paper are all rather poorly known, so that full descriptions are given also for the species that are here transferred from *Crotalaria*.

Descriptions and new combinations

1. *Lotononis stenophylla* (Eckl. & Zeyh.) B-E. van Wyk comb. nov.

Crotalaria stenophylla Ecklon & Zeyher, Enumeratio plantarum: 174 (1836); Benth.: 574 (1843), as a doubtful synonym of *C. humilis* Eckl. & Zeyh. Type: South Africa, Cape Province, Olifants River (Clanwilliam), *Ecklon & Zeyher 1261* (S!, specimen annotated by Harvey, lecto., designated here; S!, fragment, SAM!, isolecto.).

Crotalaria ecklonis Harv.: 42 (1862), as a new name for C. stenophylla Eckl. & Zeyh. non Vog.; Bak.f.: 395 (1914). Type as above.

Prostrate annual up to 0,7 m wide. Branches slender, sparsely leafy. All mature parts (except the corolla) sparsely and minutely strigillose. Leaves trifoliolate, (12--) 20--35 (--50) mm long; petiole ± as long as the terminal leaflet or slightly longer; leaflets relatively large, oblong to narrowly oblong, (5--) 10--25 (--32) mm long, (2--) 3--5 (--7) mm wide, minutely strigillose on both surfaces. Stipules single at each node, lanceolate to ovate, usually strongly falcate, 3--6 mm long, the midrib excentric. Inflorescences leaf-opposed, (1--) 3--6 (--8)-flowered; peduncle long and slender, (12--) 24--65 (--135) mm long, usually thick and rigid in the fruiting stage; bracts small, oblanceolate to obovate, up to 2,5 mm long; bracteoles absent. Flowers relatively large, (10--) 12--14 (--16) mm long, yellow; pedicel short, 1--3 mm long. Calyx subequally lobed but with the lower lobe much narrower than the upper four, the sinuses of equal depth; lobes narrowly triangular, acute. Standard broadly ovate, as long as the keel; claw much dilated, ± 5 mm long, 2--3 mm wide; lamina 9--12 mm long, 7--12 mm wide, without lobes or callosities, glabrous but with a few minute hairs dorsally along the middle. Wing petals oblong, ± as long as the keel, with a large and conspicuously lobed auricle, glabrous; apex obtuse; sculpturing in 4--5 rows of intercostal lunae, fading into transcostal lamellae towards the auricle. Keel petals broadly subtriangular, only slightly auriculate, glabrous; apex strongly beaked. Androecium conspicuously widened towards the base; anthers markedly dimorphic; basifixed anthers linear, several times longer than the small ovoid dorsifixed anthers; carinal anther similar to dorsifixed anthers. Gynoecium subsessile; pistil ovoid-oblong, pubescent; style long and slender. Pods subsessile, shortly oblong, 9--11 mm long, 4--5 mm wide, much inflated laterally, minutely strigillose, upper suture ± smooth, 8--14-seeded, the seeds on 1,5--2 mm long funicles. Seeds suborbicular, ± 1,5 mm in diameter, testa densely tuberculate (Figure 1).

Unlike Baker (1914), who hesitantly retained C. ecklonis in Crotalaria, Verdoorn (1928) and Polhill (1968, 1982) correctly excluded this species and referred it to Lotononis, but the new combination still remained to be made. It is similar to L. oxyptera (E. Mey.) Benth. but is readily distinguished from this species by the strongly beaked keel, the relatively narrow leaflets and the ovate-oblong, markedly inflated pods (Figure 1). This rather poorly known but relatively common species is very closely related to L. carnea (q.v.) and is also restricted to the north-western Cape Province (Figure 5).

---3017 (Hondeklipbaai): Grootvlei, W of Kamieskroon (--BB), Acocks 19589 (K, M, PRE), Macquire 973 (NBG); Between Grootvlei and Kamieskroon (--BB), Goldblatt 4251 (MO); Kamieskroon (--BB), Salter 1495 (K).

---3018 (Kamiesberg): Rietkloof (--DC), *Schlechter 11187* (GRA, K, PRE).

---3118 (Vanrhynsdorp): Bitterfontein (--AB), *Schlechter 11046* (MO, PRE, S); N of Vanrhynsdorp (--DA), *Leighton 1120* (BOL); Klawer (--DC), *Barker 3636* (NBG), *Lavis 20231* (BOL, K, NBG, PRE); Klawer turn-off on Vanrhynsdorp to Clanwilliam road (--DC), *B-E. van Wyk 2426*, *2427*, *2428* (JRAU).

---3119 (Calvinia): Nieuwoudtville (--AC), *Leipoldt 729* (BOL, K, PRE); Lokenburg (--CA), *Acocks 17389* (PRE).

---3218 (Clanwilliam): Between Citrusdal and Clanwilliam (--BB), *Barker 9624* (NBG); Nardouw Kloof (--BB), *Stokoe s.n. sub SAM 61434* (SAM); Olifants River (Clanwilliam) (--BB), *Ecklon & Zeyher 1261* (S, lectotype; S, SAM, isolectotypes); Pakhuisberg (--BB), *MacOwan s.n. sub Herb. Aust. Afr. 1833* (GRA, K, SAM, UPS).

---3219 (Wuppertal): Pakhuis Pass (--AA), *Stirton 6405* (PRE).

2. *L. carnea* B-E. van Wyk sp. nov. *L. stenophyllae* (Eckl. & Zeyh.) B-E. van Wyk valde affinis sed habitu minore, vestitura densiori sericeori, foliolis latioribus obcordatis (in *L. stenophylla* ellipticis vel oblongis), pedunculis brevissimis atque lobis calycis latis imbricatis (in *L. stenophylla* angustis valvatis) differt.

TYPE --- Cape Province, 3018 (Kamiesberg): Kamiesberg near Leliefontein, 16/10/1986, B-E. van Wyk 2400 (PRE, holo.; BOL, GRA, JRAU, K, MO, NBG, SAAS, STE, iso.).

Prostrate annual, 0,2--0,6 m wide. Branches slender, sparsely leafy. All mature parts (except the corolla) minutely but densely strigillose. Leaves trifoliolate, (5--) 8--15 (--30) mm long; petiole ± as long as the terminal leaflet or sometimes longer; leaflets relatively small, obovate, (3--) 5--10 (--14) mm long, (2--) 3--5 (--6) mm wide, minutely strigillose on both surfaces; apex rounded or more often emarginate. Stipules single at each node, lanceolate to ovate, often slightly falcate, up to 5 mm long, the midrib slightly excentric. Inflorescences leaf-opposed, (1--) 2--4 (--5)-flowered; peduncle very short, (1--) 2--4 (--7) mm long; bracts small, oblanceolate to obovate, 1,5--2 mm long; bracteoles absent. Flowers relatively large, (8--) 10--12 (--14) mm long, yellow, turning orange with age; pedicel short, 1,5--3 mm long. Calyx subequally lobed but with the lower lobe much narrower than the upper four, the sinuses of equal depth; lobes narrowly triangular, widened above the point of fusion, somewhat imbricate, acute. Standard broadly ovate, as long as the keel; claw much dilated, ± 6 mm long, 2--3 mm wide; lamina 8--10 mm long, 7--9 mm wide, distinctly lobed at the base, glabrous but with a few minute hairs dorsally along the middle. Wing petals oblong, ± as long as the keel, with a large and conspicuously lobed auricle, glabrous; apex obtuse; sculpturing in 4--5 rows of intercostal lunae, fading into transcostal lamellae towards the auricle. Keel petals broadly subtriangular, only slightly auriculate, glabrous; apex strongly beaked. Androecium conspicuously widened towards the base; anthers markedly dimorphic; basifixed anthers linear, several times longer than the small ovoid dorsifixed anthers; carinal anther similar to dorsifixed anthers. Gynoecium subsessile; pistil ovoid-oblong, pubescent; style long and slender. Pods and seeds unknown (Figure 2).

L. carnea is closely related to L. stenophylla, but differs in the smaller habit, the more dense and silky vestiture, the broader, obovate to obcordate leaflets, the very short peduncles and in the broad and imbricate calyx-lobes (narrow and valvate in L. stenophylla). Diagnostic characters of the new species are shown in Figure 2. The yellow flowers turn to an almost flesh-coloured orange with age, hence the specific epithet. L. carnea has been recorded from a few localities in the north-western Cape (Figure 5).

---3018 (Kamiesberg): Kamiesberg, near Leliefontein (--AA), B-E. van Wyk 2400 (PRE, holotype; BOL, GRA, JRAU, K, MO, NBG, SAAS, STE, isotypes); Kamiesberg, De Kom (now farm Karas), 3 miles [4,8 km] from Leliefontein (--AC), Leipoldt 3157 (BOL).

---3119 (Calvinia): Between Oorlogskloof and Papkuilsfontein (--CA), Leipoldt 3126 (BOL); Papkuilsfontein SE of Nieuwoudtville (--CA), Snijman 894 (MO, S).

3. L. rostrata Bentham in Hooker's London Journal of Botany 2: 604 (1843), as a new name for O. micrantha Thunb. non L. micrantha Eckl. & Zeyh. Type: South Africa, "e Cap. b. Spei", Thunberg s.n. sub THUNB-UPS 16620 (UPS!, lecto., designated here).

Ononis micranthus Thunb.: 130 (1800); Thunb. : 587 (1823); DC.: 167 (1825), as O. micrantha. Type as above.

Crotalaria micrantha (Thunb.) E. Mey.: 27 (1836); Dümmer: 330 (1913). Type as above.

Lotononis micrantha (Thunb.) Harv.: 58 (1862) non Lotononis micrantha Eckl. & Zeyh.: 178 (1836). Type as above.

Crotalaria tenuiflora Steud.: 445 (1841), as a new name. Type as above.

L. rostrata is relatively well known by the illegitimate name L. micrantha (Thunb.) Harv. but is still filed under Crotalaria in some southern African herbaria. The species is here subdivided into 3 subspecies:

3a. subsp. rostrata

Diffuse annual of up to 0,4 m high. Branches slender, sparsely leafy. All mature parts (except the corolla) sparsely and minutely strigillose. Leaves trifoliolate, (10--) 15--30 (--45) mm long; petiole ± as long as the terminal leaflet or slightly longer; leaflets oblong to narrowly oblong, rarely oblanceolate to obovate, (5--) 12--22 (--30) mm long, (1--) 2--5 (--8) mm wide, minutely strigillose on both surfaces; apex obtuse to emarginate. Stipules single at each node, lanceolate to ovate, usually strongly falcate, variable in size, up to 12 mm long, the midrib excentric. Inflorescences leaf-opposed, densely umbellate, (3--) 5--7 (--9)-flowered; peduncle long and slender, (10--) 25--50 (--70) mm long; bracts very small, oblanceolate to linear, up to 1 mm long; bracteoles absent. Flowers very small, 6--8 mm long, yellow; pedicel short, 1--2 mm long. Calyx subequally lobed but with the lower lobe much narrower than the upper four, the sinuses of equal depth; lobes narrowly triangular, acute. Standard ovate-oblong, as long as the keel; claw much dilated, 2--3 mm long, 1--1,5 mm wide; lamina 3--4 mm long, 3--4 mm wide, without lobes or callosities, glabrous but with a few minute hairs dorsally along the middle. Wing petals oblong, slightly shorter than the keel, auriculate, glabrous; apex obtuse; sculpturing in 4--5 rows of intercostal lunae, fading into transcostal lamellae towards the auricle. Keel petals narrowly subtriangular, only slightly auriculate, glabrous; apex acute, beaked. Androecium conspicuously widened towards the base; anthers very strongly dimorphic; basifixed anthers linear, several times longer than the small, ovoid dorsifixed anthers; carinal anther similar to dorsifixed anthers. Gynoecium subsessile; pistil ovoid-oblong, pubescent; style long and slender. Pods subsessile, obovoid, scarcely longer than the calyx, 3--5 mm long, 2--3 mm wide, much inflated laterally, minutely strigillose, upper suture ± smooth, 3--5-seeded, the seeds on ± 1,2 mm long funicles. Seeds suborbicular, ± 1,5 mm in diameter, testa densely tuberculate.

The typical subspecies is easily recognised by the small and narrow flowers, slender peduncles and obovoid, much inflated pods (Figure 3). It is widely distributed in the south-western parts of the Cape Province (Figure 6).

---3218 (Clanwilliam): Olifants River Valley, Hex River (--BD), *Esterhuysen 12040* (BOL, K); Between Citrusdal and Clanwilliam (BD), *Barker 9623* (NBG); 21,4 km from Citrusdal on old road to Clanwilliam (BD), *B-E. van Wyk 2321*, *2322*, *2323*, *2324* (JRAU); Piquetberg (--DD), *Bolus 7518* (BOL, PRE, SAM), *Bolus 11922* (PRE), *Guthrie 2581* (NBG); Near Pools Station (--DD), *Van Breda 4361* (PRE).
---3319 (Worcester): Gouda, Tulbagh Kloof (--AC), *Strey 367* (M); Rhoodesand (--AC), *Drège s.n.* (K, MO); Nieuwekloof (--CD), *Drège s.n.* (PRE, S); Between Rooihoogte and Worcester (--CD), *L. Bolus s.n. sub BOL 37210* (BOL); 22 km from Worcester on Villiersdorp road (--CD), *Grobbelaar 2849* (PRE).
--3420 (Bredasdorp): Swellendam district, Storms Vlei (--AA), *Fries*, *Norlindh* & *Weimarck 1514* (K, PRE, S).
Without precise locality: *Thunberg s.n. sub THUNB-UPS 16620* (UPS, lectotype).

3b. subsp. **brachybotrys** B-E. van Wyk subsp. nov., typo similis sed habitu prostratiori, foliolis maioribus obovatis, pedunculis brevioribus, floribus maioribus, vexillo valde maius pubescenti, leguminibus maioribus oblongis compressis (parvis obovoideis valde inflatis in typo) differt. A subsp. namaquensi (H. Bol.) B-E. van Wyk foliis maioribus sparsius pubescentibus leguminibusque valde maioribus differt.

TYPE --- Cape Province, 3118 (Vanrhynsdorp): 800 m from Klawer turn-off on Vanrhynsdorp to Clanwilliam road, 17/10/1986, B-E. van Wyk 2429 (PRE, holo.; K, NBG, MO, iso.).

Prostrate annual of up to 0,8 m wide. All mature parts (except the corolla) sparsely and minutely strigillose. Leaves trifoliolate, (10--) 15--35 (--52) mm long; petiole ± as long as the terminal leaflet or longer; leaflets relatively large, obovate to oblong, (6--) 10--18 (--27) mm long, (2--) 4--7 (--10) mm wide, minutely strigillose on both surfaces; apex rounded to emarginate. Stipules single at each node, lanceolate to ovate, usually strongly falcate, variable in size, up to 8 mm long, the midrib excentric. Inflorescences leaf-opposed, densely umbellate, (3--) 6--8 (--15)-flowered; peduncle very short, (1--) 3--5 (--24) mm long; bracts very small, oblanceolate to linear, up to 1 mm long; bracteoles absent. Flowers small, 6--9 mm long, yellow. Calyx, Corolla, Androecium and Gynoecium as in the type, but the petals larger and the standard petal dorsally pubescent. Pods subsessile, shortly oblong, more than twice as long as the calyx, 5--8 mm long, 2,5--4 mm wide, only slightly inflated laterally, upper suture ± smooth, 3--5-seeded, the seeds on ± 1,8 mm long funicles. Seeds suborbicular, ± 1,8 mm in diameter, testa unevenly tuberculate (Figure 3).

This subspecies is similar to the type but differs in the more prostrate habit, the larger and obovate leaves, the shorter peduncles, the larger flowers, the much more pubescent standard petal and the larger, oblong (not obovoid), less turgid pods (Figure 3). It is also similar to subsp. *namaquensis* (H. Bol.) B-E. van Wyk, but differs from the latter in the larger and more sparsely pubescent leaves, and in the much larger pods.

The new subspecies has a somewhat more northernly distribution than subsp. *rostrata* (Figure 6).

---3118 (Vanrhynsdorp): 7 miles [11,2 km] N of Vanrhynsdorp (--DA), *Acocks* *19497* (K, M); N of Vanrhynsdorp (--DA?), *Leighton* *1118* (BOL); Vanrhynsdorp (--DA), *Compton* *20860* (NBG); Between Driefontein and Heerelogement (--DC), *Pearson* *6735* (BOL, K); Clanwilliam District, Wind Hoek (--DC), *Schlechter* *8346* (BOL); 800 m from Klawer turn-off on Vanrhynsdorp to Clanwilliam road (--DC), *B-E*. *van* *Wyk* *2429* (PRE, holotype; K, NBG, MO, isotypes).
---3218 (Clanwilliam): near Clanwilliam (--BB), *Bolus* *8970* (BOL, K), *Galpin* *11215* (PRE), *Leipoldt* *268* (GRA, SAM); Piquetberg (--DD), *Schlechter* *3368* (PRE); Foot of Piquetberg mountain (--DD?), *Schlechter* *5188* (BOL, GRA, NH).

3c. subsp. *namaquensis* (H. Bol.) B-E. van Wyk stat. nov.

L. *namaquensis* H. Bolus in Journal of the Linnaean Society 25: 159 (1889). Type: South Africa, Cape Province, Little Namaqualand, near Klipfontein, *H*. *Bolus* *6569* (BOL!, lecto., designated here; K!, isolecto.).

Crotalaria *namaquensis* (H. Bol.) Dümmer: 330 (1913). Type as above.

Lotononis *chrysophylla* Schltr. in sched. (*Schlechter* *11185*, BM!).

Prostrate annual, 0,3--0,5 m wide. All mature parts (except the corolla) minutely but conspicuously silky-strigillose. *Leaves* small, trifoliolate, (6--) 10--15 (--24) mm long; petiole as long as the terminal leaflet or longer; leaflets usually very small, obovate to broadly obovate, (3--) 5--9 (--11) mm long, (1--) 2--4 (--6) mm wide, silky-strigillose on both surfaces; apex invariably emarginate. *Stipules* single at each node, lanceolate to broadly ovate, usually strongly falcate, up to 4 mm long, the midrib excentric. *Inflorescences* leaf-opposed, umbellate, (1--) 2--8 (--12)-flowered; peduncle very short, 1--3 (--7) mm long; bracts inconspicuous, < 1 mm long; bracteoles absent. *Flowers* small, variable in size, 5--10 mm long, yellow or white, fading to pink. *Calyx*, *Corolla*, *Androecium* and *Gynoecium* as in the type, but the petals usually larger and the standard petal dorsally pubescent. *Pods* subsessile, shortly oblong to obovoid, scarcely longer than the calyx, up to 4 mm long and 2 mm wide, only slightly inflated laterally, upper suture smooth or inconspicuously verrucose, 3--4-seeded. *Mature seeds* not seen.

Subsp. *namaquensis* differs from subsp. *rostrata* in the smaller and more densely pubescent leaves, the short peduncles and the smaller, less turgid pods (Figure 3). This subspecies may be mistaken for *L. arenicola* Schltr. but the latter has subsessile, invariably single-flowered inflorescences and a much more densely silky vestiture. The wing and keel petals are hairy in *L. arenicola*, totally glabrous in subsp. *namaquensis*.

This subspecies appears to be geographically isolated from the other two subspecies and is known only from northern Namaqualand (Figure 6).

---2917 (Springbok): 1 mile [1,6 km] SE of Steinkopf (--BD), *Merxmüller* & *Giess* *3723* (M); Near O'okiep (--DB), *L. Bolus s.n. sub BOL 37211*, *37212* (BOL); O'okiep Copper Co., "golflinks" at Nababeep (--DB), *Rösch* & *Le Roux 97* (STE); Springbok, Hester Malan Wild Flower Reserve (--DB), *Rösch* & *Le Roux 1351* (PRE); Vogelklip (--DB), *Schlechter 11306* (GRA, PRE).
---3017 (Hondeklipbaai): Dessiesfontein near Kamieskroon (--BB), *Van Breda 4206* (PRE); Grootvlei, W of Kamieskroon (--BB), *Acocks 19588* (K, M, PRE); near Klipfontein (--BD?), *Bolus 6569* (BOL, lectotype, K, isolectotype).

---3018 (Kamiesberg): Bovlei, c. 6 miles [9,6 km] NE of Kamieskroon (--AA), *Van der Westhuizen 310* (PRE); Leliefontein (--AC), *Esterhuysen 23651* (BOL).

4. *L. sparsiflora* (E. Mey.) B-E. van Wyk comb. nov.

Crotalaria sparsiflora E. Meyer, Commentariorum plantarum: 27 (1836); Benth. 573 (1843); Harv.: 41 (1862); Bak.f.: 400 (1914), non *Polylobium sparsiflorum* Eckl. & Zeyh. Type: South Africa, Cape Province, at the Garip near Verleptpram [2817 AA Vioolsdrif], *Drège s.n.* (K!, lecto., designated here; MO!, S!, isolecto.).

Lotononis lenticula (E. Mey.) Benth. var. *brachycarpa* Harv.: 62 (1862). Type: South Africa, Cape Province, Springbokkeel [3019 CA Loeriesfontein], *Zeyher 411* (K!, Herb. Benth. specimen, lecto., designated here; K!, Herb. Hook. partly, specimen on right, SAM!, minor part, isolecto.).

L. oocarpa Dinter in sched. (*Dinter 4851*, BOL!, K!, PRE!).

L. oocarpa Dinter ex Wilman: 52 (1946); Schreiber: 84 (1970), nom. nud.

Prostrate annual, up to 0,4 m wide. Branches rigid, divaricately much-branched, very brittle, sparsely leafy. All mature parts (except the corolla) densely silky-strigillose. *Leaves* trifoliolate, variable in size and shape, (5--) 8--18 (--25) mm long; petiole usually much longer than the terminal leaflet; leaflets small, elliptic, oblanceolate or obovate, (3--) 5--12 (--15) mm long, (1--) 2--4 (--8) mm wide, strigillose on both surfaces. Stipules single at each node, lanceolate to ovate, strongly caducous, inconspicuous, up to 1 mm long. Inflorescences leaf-opposed, single-flowered, rarely with some 2-flowered; peduncle ± absent; bracts small, lanceolate to linear, up to 3 mm long; bracteoles absent. Flowers small, variable in size, often cleistogamous, (4--) 5--8 (--9) mm long, yellow and white; pedicel short, ± 1 mm long. Calyx subequally lobed but with the lower lobe sometimes slightly narrower than the upper four, the sinuses of equal depth; lobes narrowly triangular, rarely somewhat lobed, acute. Standard broadly ovate, as long as the keel; claw much dilated, 2--4 mm long, 1,2--2 mm wide; lamina 4--6 mm long, 3--5 mm wide, without lobes or callosities, pubescent dorsally along the midrib; apex acuminate. Wing petals oblong, shorter than the keel, conspicuously auriculate, glabrous; apex obtuse; sculpturing in 3--4 rows of intercostal lunae, fading into a few transcostal lamellae towards the auricle. Keel petals broadly subtriangular, only slightly auriculate, glabrous; base more or less truncate; apex acute, beaked. Androecium exceptionally broad, conspicuously widened towards the base; anthers very strongly dimorphic; basifixed anthers linear, several times longer than the small, ovoid dorsifixed anthers; carinal anther similar to dorsifixed anthers. Gynoecium subsessile; pistil ovoid-oblong, pubescent; style long and slender. Pods subsessile, shortly oblong, 5--8 mm long, 2,5--3,5 mm wide, much inflated laterally, densely covered with long thick hairs, the hairs conspicuously parallel in orientation; upper suture ± smooth, 20--25-seeded, the seeds on very long funicles; funicles 2--3 mm long. Seeds suborbicular, ± 1,2 mm in diameter, testa minutely but densely tuberculate (Figure 4).

A distinct species easily recognised by the neatly orientated strigillose hairs on the pods, a character which it shares only with L. rabenaviana Dinter & Harms. The latter differs in the much larger flowers and pods and in the lobed, imbricate calyx-lobes but may eventually prove to be only subspecifically distinct. L. sparsiflora is widely distributed in southern Namibia and the dry interior of the Cape Province (Figure 5).

---2616 (Aus): Lüderitz district, Farm Weissenborn (--AB), Kinges 2432 (PRE).

---2715 (Bogenfels): Central Klinghardt Mts, on top of mountain (--BC), Müller 711 (PRE, WIND).

---2716 (Witputz): 8 km N of Rosh Pinah (--DC), Merxmüller & Giess 28514 (M).

---2717 (Chamaites): Farm Holoogberg (--DB), Giess & Müller 12308 (M, PRE, WIND).

---2718 (Grünau): Klein Karas (--CA), Dinter 4851 (BOL, K, KMG, NH, SAM).

---2816 (Oranjemund): Obibberge (--BA), Merxmüller & Giess 28605 (M).

---2817 (Vioolsdrif): At the Garip [Gariep, Orange River] near Verleptpram (--AA), Drège s.n. (K, lectotype; MO, S, isolectotypes); 9 miles [14,4 km] south of Vioolsdrif (--DC), Merxmüller & Giess 3689 (M).

---2818 (Warmbad): Farm Aluriesfontein (--DA), Giess 14497 (M, WIND).

---2822 (Glen Lyon): Hay 0.303 [see Acocks map in Wilman 1946] (--CD), Acocks 505 (KMG).

---2919 (Pofadder): Pofadder (--AB), Conradie 9 (STE).

---3019 (Loeriesfontein): Springbokkeel (--CA), Zeyher 411 (K, SAM).

---3123 (Victoria West): 66 km N of Beaufort West, near Drie Susters (--CC), B-E. van Wyk 2056, 2057 (JRAU).

---3320 (Montagu): Laingsburg (--BB), Bond 834 (NBG); 16,6 km SSE of Laingsburg (--BD), B-E. van Wyk 2139, 2140 (JRAU).

---3322 (Oudtshoorn): Near Boterkraal in the district of Prince Albert (--AB), Bolus s.n. sub BOL 12448 (BOL).

--3323 (Willowmore): Little Karroo, 19 miles [30,4 km] N of Willowmore (--BA), Acocks 18403 (PRE).

---3324 (Steytlerville): Hills at Gerts Kraal near Uitenhage Karroo (--AC), Prior s.n. (K).

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Table 1. Summary of similarities and differences between *Lotononis* section *Oxydium* and *Crotalaria*.

	Lotononis sect. *Oxydium*	*Crotalaria*
Bracteoles	absent	present
Anthers	4 long, 6 short	5 long, 5 short
Stipules	single at each node (paired in 3 spp.)	paired or absent, never single
Pod - upper suture	usually verrucose	smooth
- shape	usually inflated	usually inflated
Seed surface	tuberculate	smooth or rugose, rarely tuberculate
Standard petal		
- callosities	occasionally present	usually present
- claw	usually very long; dilated, at least at the base	short; not dilated

- TABLE 1 CONTINUED -

	<u>Lotononis</u> sect. <u>Oxydium</u>	<u>Crotalaria</u>
Keel	acute, often beaked but the beak never twisted	mostly beaked and the beak often twisted
Style	glabrous; not geniculate	hairy; mostly geniculate
Chromosome base number*	9	7, 8
Cyanogenesis**	mostly cyanogenic	acyanogenic
Alkaloids***	pyrrolizidine	pyrrolizidine

*See Van Wyk & Schutte 1988.

**See Van Wyk 1989.

***See Van Wyk & Verdoorn 1989.

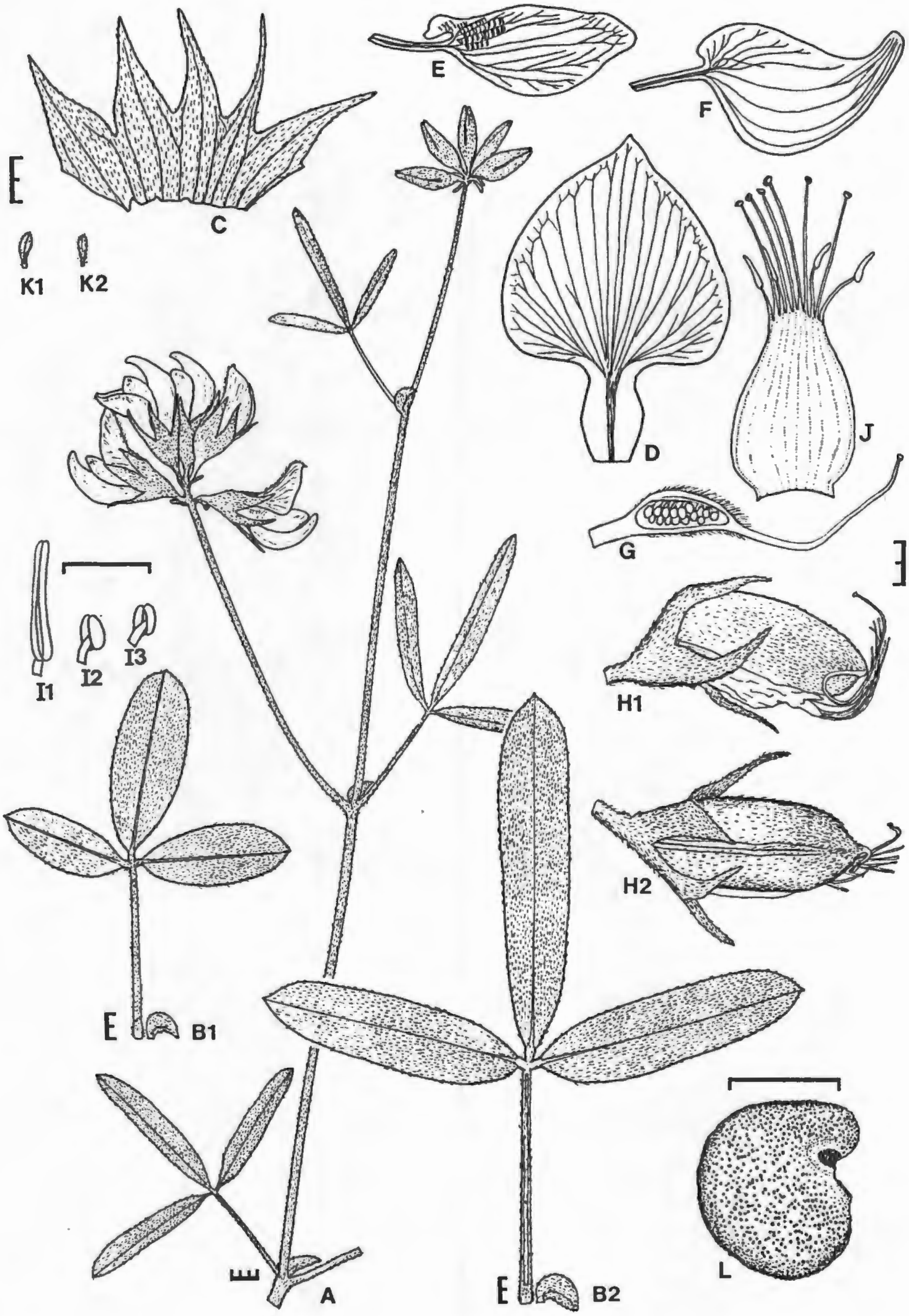

Figure 1. <u>Lotononis</u> <u>stenophylla</u>. A, flowering twig, showing the slender peduncle and narrowly oblong leaflets; B1 & B2, leaves and stipules: B1, abaxial view, B2, adaxial view (note the strongly falcate stipules); C, calyx opened out with the upper lobes to the left; D, standard petal, showing the dilated claw; E, wing petal; F, keel petal; G, pistil; H1 & H2, pods: H1, in lateral view, H2, in top view; I1, I2 & I3, anthers: I1, long basifixed anther, I2, carinal anther, I3, dorsifixed anther; J, androecium; K1 & K2, bracts; L, seed, showing the tuberculate surface. All from <u>Van</u> <u>Wyk</u> <u>2426</u>. Scales in mm.

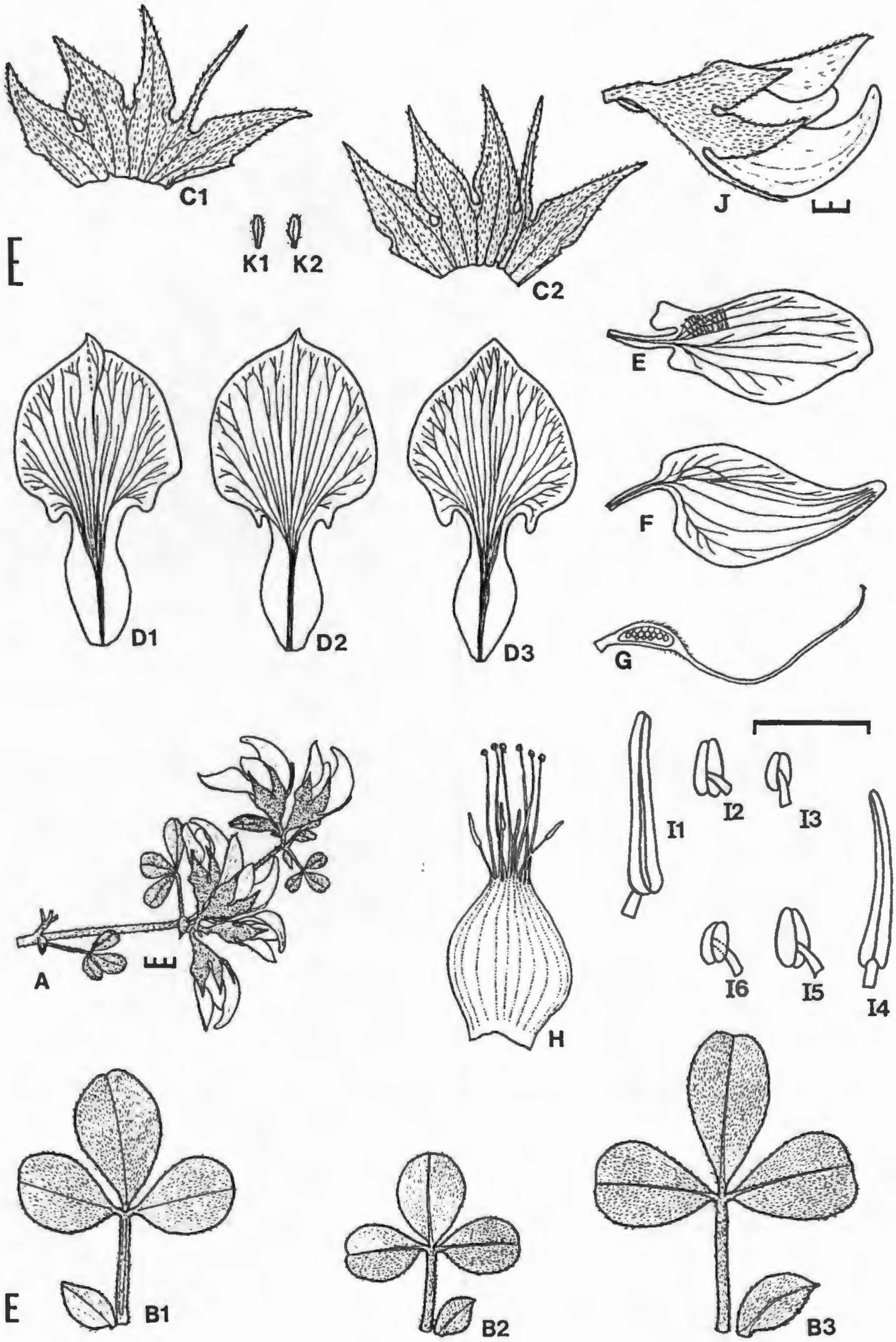

Figure 2. Lotononis carnea. A, flowering twig, showing the very short peduncles and obovate leaflets; B1, B2 & B3, leaves and stipules: B1, adaxial view, B2 & B3, abaxial; C1 & C2, calyx opened out with the upper lobes to the left, showing the slightly imbricate lobes; D1, D2 & D3, standard petals, showing the dilated claw and auriculate lamina; E, wing petal; F, keel petal; G, pistil; H, androecium; I1 to I6, anthers: I1 & I4, long basifixed anthers, I2 & I5, carinal anthers, I3 & I6, dorsifixed anthers; J, flower in lateral view; K1 & K2, bracts. A, C1, D1 & D2, E, F, C1, All from Van Wyk 2401 except B3, C2, D3, K4, K5 & K6 from Snijman 894; B1 from Van Wyk 2405; B2 from Van Wyk 2404. Scales in mm.

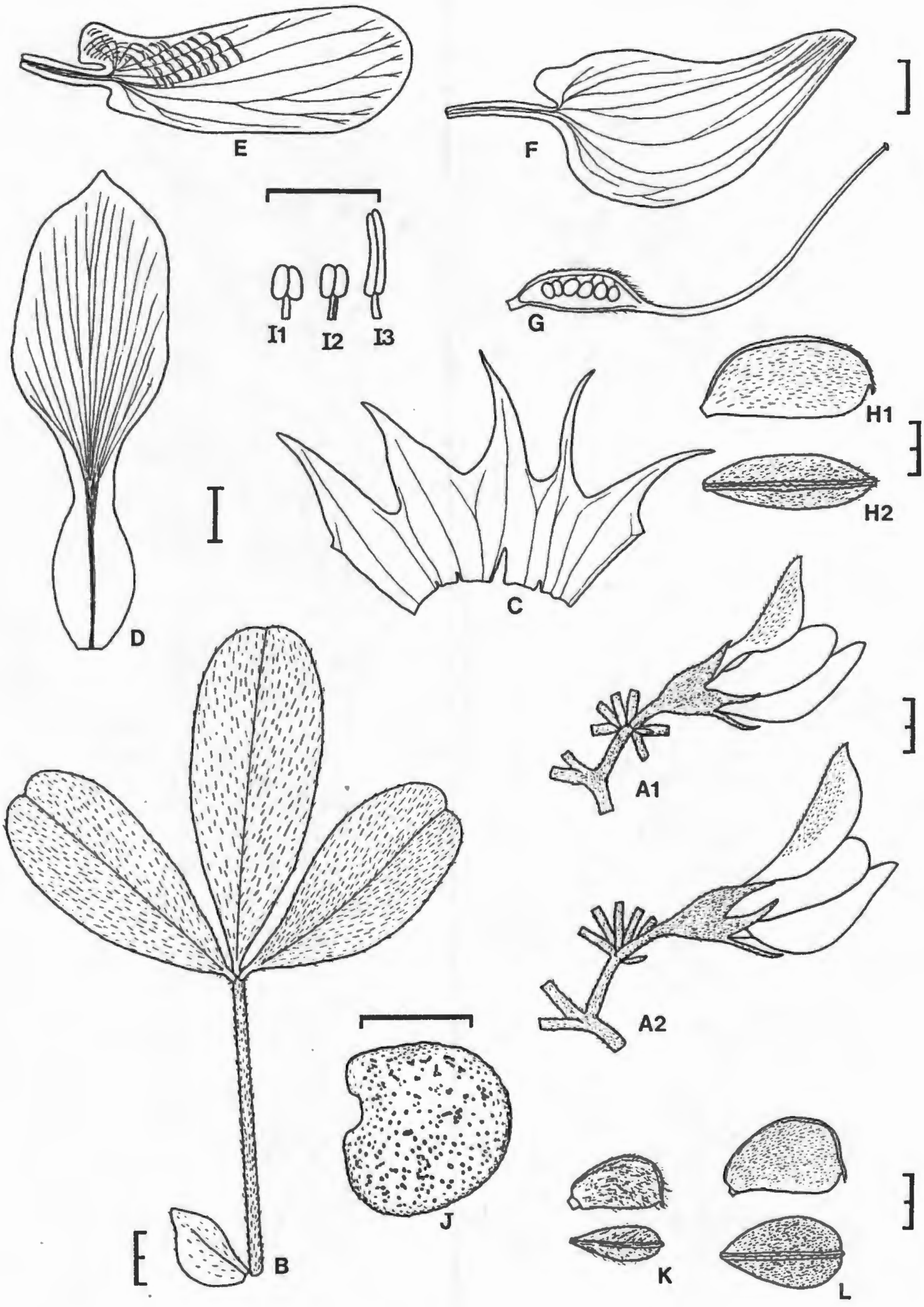

Figure 3. *Lotononis rostrata* subsp. *brachybotrys*. A1 & A2, flowers in lateral view showing the inflorescence structure; B, leaf in adaxial view; C, calyx opened out with the upper lobes to the left; D, standard petal; E, wing petal; F, keel petal; G, pistil; H1 & H2, pods: H1, lateral view, H2, top view; I1, I2 & I3, anthers: I1, dorsifixed anther, I2, carinal anther, I3, basifixed anther; J, seed, showing the sparsely tuberculate surface. K & L, pods of the other subspecies of *L. rostrata* (note the differences in size and shape: K, pods of subsp. *namaquensis* in lateral and top view; L, pods of subsp. *rostrata* in lateral and top view. All from *Van Wyk 2429* except A1 from *Compton 20860*, K from *Bolus 6569*, L from *Bolus s.n.* Scales in mm.

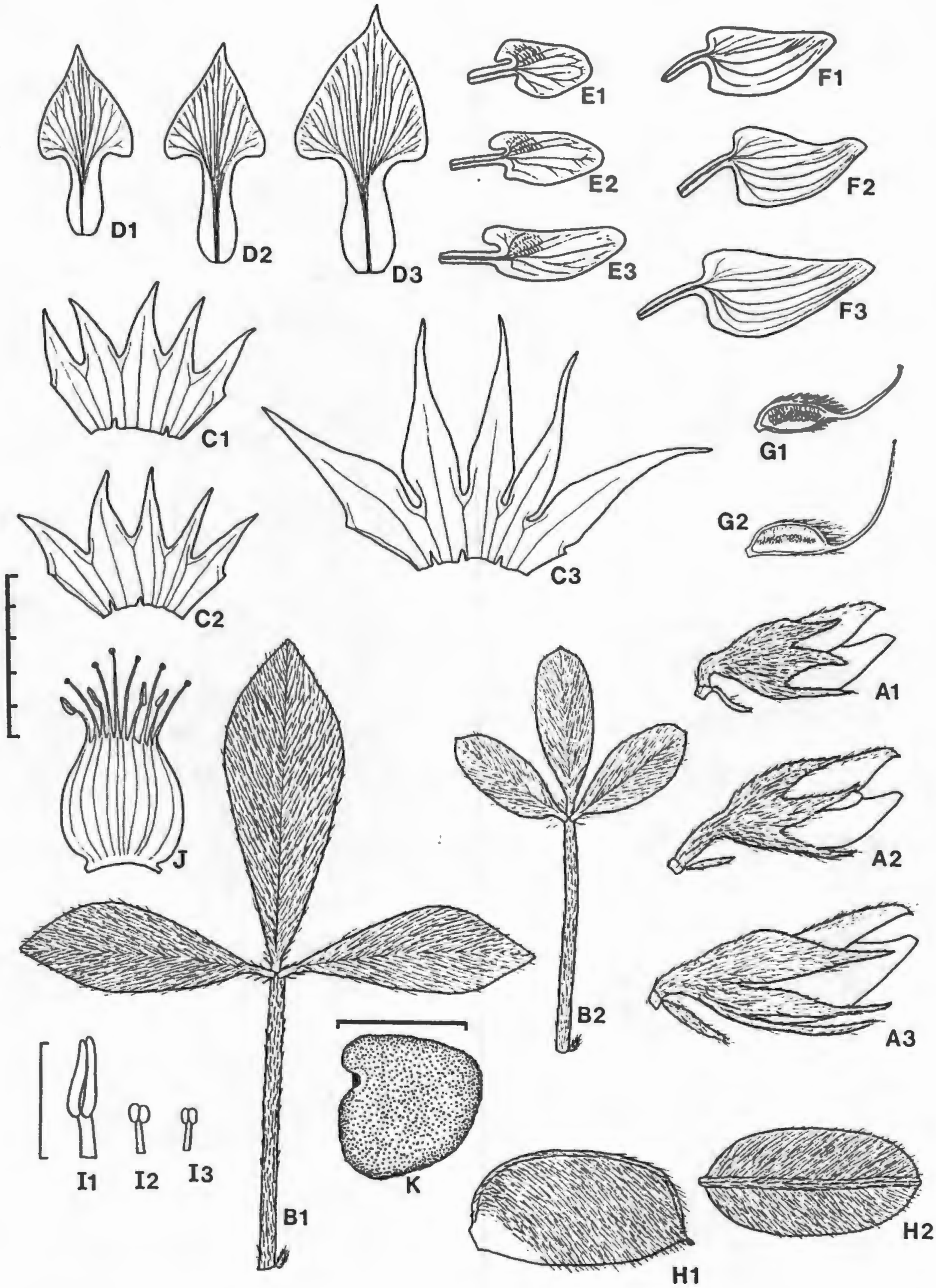

Figure 4. Lotononis sparsiflora. A1, A2 & A3, flowers in lateral view, showing the very short peduncles; B1 & B2, leaves in adaxial view, showing the small (caducous) stipules; C1, C2 & C3, calyces opened out with the upper lobes to the left; D1, D2 & D3, standard petals, showing the dilated claws; E1, E2 & E3, wing petals; F1, F2 & F3, keel petals; G1 & G2, pistils; H1 & H2, pods: H1, in lateral view, H2, in top view; I1, I2 & I3, anthers: I1, long basifixed anther, I2, carinal anther, I3, dorsifixed anther; J, androecium; K, seed, showing the tuberculate surface. A1, B2, C1, D1, E1, F1 & G1 from Giess 14497; A2, C2, D2, E2, F2, I1, I2, I3 & J from Giess & Müller 12308; A3, B1, C3, D3, E3, F3, G2, H1, H2 & K from Van Wyk 2056. Scales in mm.

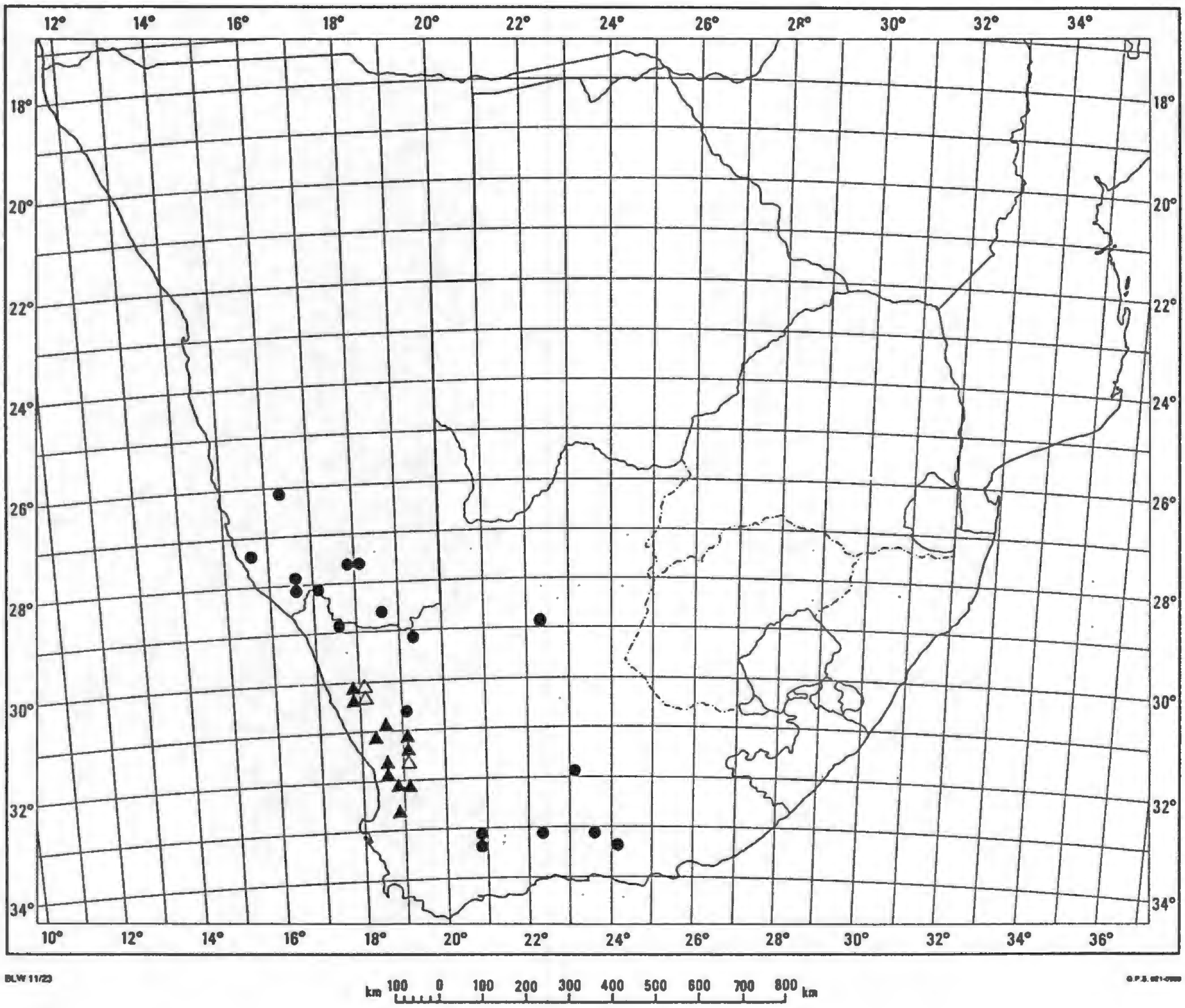

Figure 5. The known geographical distribution of Lotononis stenophylla (▲), L. carnea (△) and L. sparsiflora (●).

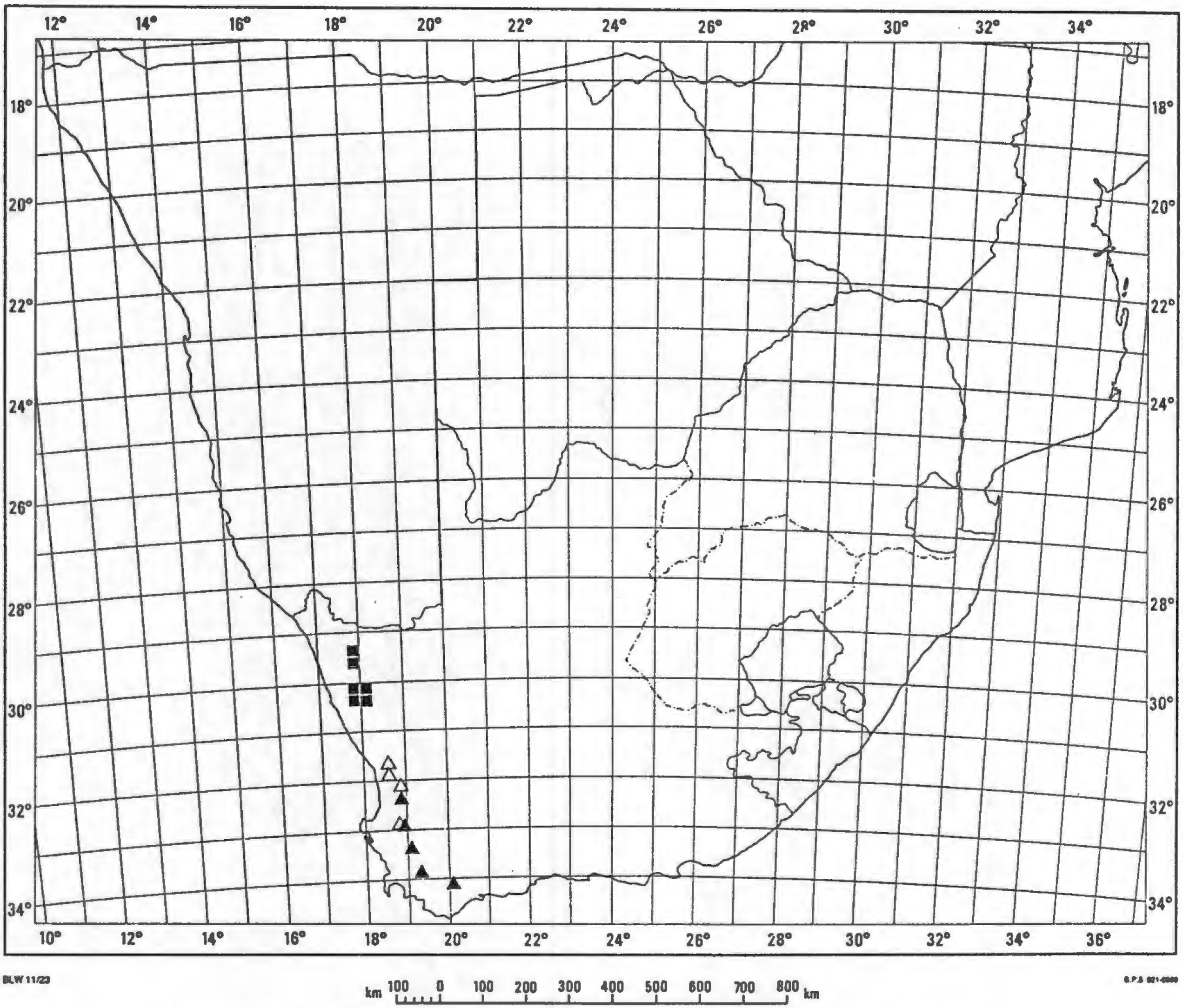

Figure 6. The known geographical distribution of the three subspecies of Lotononis rostrata: subsp. rostrata (▲), subsp. brachybotrys (△) and subsp. namaquensis (■).

APPENDIX 27

Studies in the genus Lotononis (Crotalarieae, Fabaceae). VIII. A new species of the L. corymbosa group and notes on the taxonomy of the section Lipozygis

B-E. VAN WYK*

Keywords: Fabaceae, Lotononis section Lipozygis, sectional limits, taxonomy

ABSTRACT

The section Lipozygis (E. Mey.) Benth. of Lotononis (DC.) Eckl. & Zeyh. is shown to be an artificial group that should be divided into two distinct and geographically isolated sections. L. pentaphylla (E. Mey.) Benth., L. polycephala (E. Mey.) Benth. and other annuals from the western Cape Province are to be excluded from the section. The remaining species [L. corymbosa (E. Mey.) Benth. and its allies] are all perennial pyrophytes from grassland areas along the eastern parts of southern Africa. A new species of this group, L. difformis B-E. van Wyk, is described. The unusual inflorescence of the new species provides a possible explanation for the evolutionary origin of the inflorescence structure in Lipozygis sensu stricto and related groups.

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UITTREKSEL

Daar word aangetoon dat die seksie *Lipozygis* (E. Mey.) Benth. van *Lotononis* (DC.) Eckl. & Zeyh. 'n kunsmatige groep is wat in twee duidelik onderskeibare en geografies geïsoleerde seksies verdeel behoort te word. *L. pentaphylla* (E. Mey.) Benth., *L. polycephala* (E. Mey.) Benth. en ander jaarplante van die westelike Kaapprovinsie sal uitgesluit word van die seksie. Die oorblywende spesies [*L. corymbosa* (E. Mey.) Benth. en verwante spesies] is almal meerjarige pirofiete van grasveldgebiede langs die oostelike dele van suider-Afrika. 'n Nuwe spesie van hierdie groep, *L. difformis* B-E. van Wyk, word beskryf. Die ongewone bloeiwyse van die nuwe spesie bied 'n moontlike verklaring vir die evolusionêre ontwikkeling van die bloeiwyse-struktuur in *Lipozygis sensu stricto* en verwante groepe.

Introduction

The section Lipozygis (E. Mey.) Benth. of Lotononis (DC.) Eckl. & Zeyh. was originally described to include species with terminal capitate inflorescences, oblong standard petals and obtuse keel petals. The habit and fruit of many of the species were not known before, so that the sectional characters of Bentham (1843) and Dümmer (1913) now appear to be superficial similarities rather than indications of a direct relationship. This study has shown that two distinct groups can be distinguished within the section.

A summary of differences between the two groups within Lipozygis is given in Table 1. It is clear that the infrageneric classification can be improved by excluding L. pentaphylla (E. Mey.) Benth. and related species from the section. As shown in Figure 1, these species are geographically isolated from the rest of the section and form a very natural group. It is the only group in Lotononis with truly capitate inflorescences, sessile flowers and indehiscent, wind-dispersed pods. The L. pentaphylla group will be discussed in more detail elsewhere.

The morphology of L. corymbosa (E. Mey.) Benth. and its close relatives appears to be related to a grassland habitat (see Figure 1) and also shows them to be a natural group. All of these species are suffrutescent herbs which produce annual flowering branches from a persistent, woody base. The morphology of the flowers and fruit are remarkably uniform, varying only in size and degree of pubescence. A very useful diagnostic character is the position of the bracts. Bracts are normally inserted at the base of the pedicel. In all species in the *L. corymbosa* group, the bracts are situated halfway up the pedicel, presumably as a result of fusion.

A study of the inflorescence structure in the *L. corymbosa* group has shown it to be quite different from the rest of the genus. This study has also shown the presence of an undescribed species with some unusual morphological features. The inflorescence structure of the new species indicates a direct relationship between *L. procumbens* H. Bol. [previously included in the section *Polylobium* (Eckl. & Zeyh.) Benth.] and the *L. corymbosa* group. *L. procumbens* is a prostrate suffrutescent shrub with umbellate inflorescences and a floral structure almost identical to that of the *L. corymbosa* group. *L. procumbens* and the new species both have very large, foliaceous bracts and well-developed bracteoles. A possible evolutionary sequence for the development of the inflorescence structure in the *L. corymbosa* group is given in Figure 2. This hypothesis suggests a progressive shortening of the rachis, a fusion of bracts to the pedicel and a gradual loss of bracteoles. It also provides a logical explanation for the origin of a group of the section *Leptis* (Eckl. & Zeyh.) Benth. [*L. mucronata* Conr. and related species]. This group differs from the *L. corymbosa* group mainly by the more herbaceous habit and the few-flowered inflorescences. *L. stolzii* Harms, a localized endemic from central Africa, has an inflorescence structure exactly intermediate between the many-flowered "corymbosa"-type and the sparse "leptis"-type as shown in Figure 2. Thus, I suggest that the *L. corymbosa* group (*Lipozygis sensu stricto*) and species of the *L. mucronata* group (*Leptis sensu stricto*) are sister groups in a phylogenetic sense and that the capitate inflorescence in the *L. pentaphylla* group is a separate development.

The similarities between *L. procumbens* and the new species described below clearly show the former to be misplaced in section *Polylobium* and that both should be included in section *Lipozygis sensu stricto*.

Lotononis difformis B-E. van Wyk sp. nov., *L. procumbenti* H. Bol. similis, sed haec specie habitu minus lignoso, axe inflorescentiae longo, bracteis late dispersis, conjunctione bractearum et pedicellorum atque lobis duobus summis calycis, quae valde breviores tribus inferis calycis sunt (lobi summi inferis similes in *L. procumbente* et speciebus aliis omnibus sectionis *Lipozygis*). Etiam *L. corymbosae* (E. Mey.) Benth. et speciebus affinibus, *L. difformis* similis est, sed ab illis fabrica inflorescentiae, bracteis maximis foliaceis atque fabrica calycis differt.

TYPUS --- Transvaal, 2630 (Carolina): Piet Retief District, Iswepe, 06/03/1949, Sidey 1609 (PRE, holotypus; S, isotypus).

Procumbent herbaceous perennial up to 0,18 m high and 0,5 m in diameter. Branches slender, densely leafy, woody at the base only. All mature parts sparsely pilose. Leaves trifoliolate, (10--) 14--26 mm long; petiole much shorter than the terminal leaflet, 2--7 mm long, the lateral leaflets slightly assymetrical; leaflets relatively large, thin in texture, broadly oblanceolate to elliptic, (6--) 8--18 (--20) mm long, (2--) 4--6 (--9) mm wide, sparsely pilose on both surfaces; midrib distinct on abaxial surface, invisible on adaxial surface. Stipules single at each node, foliaceous, similar to the leaflets but slightly smaller, 5--15 mm long, 1--3,5 mm wide. Inflorescences terminal, with large, foliaceous bracts along the lower part of the main axis, 4--12-flowered; peduncle (including the rachis) (15--) 24--40 (--60) mm long, usually thick and rigid in the fruiting stage; bracts large and foliaceous, broadly obovate, 6--14 mm long, 3--6 mm wide, the lower ones widely separated on the rachis and not subtending flowers, occasionally petiolate, the upper ones inserted ± halfway up the pedicel; bracteoles large, narrowly oblanceolate to linear, 4--6 mm long, 0,5--1 mm wide. Flowers subumbellately arranged at the apex of the inflorescence, relatively small, 10--12 mm long, yellow; pedicel 1--4 mm long. Calyx with the upper two lobes shorter than the lower three lobes, the lateral sinuses slightly shallower than the upper and lower sinuses; lobes relatively short and broad, ± as long as the tube, apices broadly triangular, acute. *Standard* broadly oblong, as long as the keel; claw ± 4 mm long; lamina 6--7 mm long, ± 4 mm wide, lobed at the base, apex acuminate, adaxially densely pubescent over the whole surface. *Wing petals* subtriangular, shorter than the keel, conspicuously auriculate, pubescent along the lower side; apex rounded to truncate; sculpturing in 5 rows of intercostal lunae, with a few large transcostal lamellae towards the auricle. *Keel petals* obovate-oblong, only slightly auriculate; claw slightly shorter than the lamina; lamina pubescent over most of the surface, apex rounded. *Androecium* with the stamens fused high up into a narrow sheath; anthers dimorphic, the basifixed ones oblong and slightly longer than the ovate dorsifixed ones, carinal anther similar to the dorsifixed anthers. *Gynoecium* subsessile; pistil oblong, pubescent; style with only the terminal part curved upwards; stigma small, directed to the front. *Pods* obovate-oblong, 6--7 mm long, ± 3 mm wide, compressed and not laterally inflated, upper suture ± smooth, 3--4-seeded, funicles 1--1,5 mm long. *Seeds* (immature) suborbicular, ± 1,5 mm in diameter, testa sparsely and minutely tuberculate. (Figure 3).

L. difformis is known only from two collections from the south-eastern Transvaal (Figure 1). It is similar to *L. procumbens* H. Bol. but differs from this species by the less woody habit, the long inflorescence axis, the widely spaced bracts, the fusion of the bracts to the pedicels and by the upper lobes of the calyx. The upper lobes of *L. difformis* are much shorter than the lower three (upper lobes are similar to the lower ones in L. procumbens and in all other species of Lipozygis). It is also similar to L. corymbosa (E. Mey.) Benth. and related species, but differs from these by the structure of the inflorescence (Figure 2), the very large foliaceous bracts, the large bracteoles and the structure of the calyx as mentioned above.

---2630 (Carolina): Piet Retief District, Iswepe (--DC), 06/03/1949, Sidey 1609 (PRE, holotype; S, isotype), 23/01/1949, Sidey 1579 (PRE).

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Table 1. Summary of differences between the *L. corymbosa* and *L. pentaphylla* groups of section *Lipozygis*.

	L. corymbosa group (10 species*)	*L. pentaphylla* group (9 species**)
Habit	perennial	annual
Inflorescence	racemose	capitate
Pedicel	present, often very long	absent
Bract position	on pedicel	on rachis
Bracteoles	often present	totally absent
Leaves	invariably 3-digitate	3- and/or 5-digitate
Petiole	much shorter than the leaflets	as long or longer than the leaflets
Stipules	foliaceous, similar to leaflets	much smaller than the leaflets

- TABLE 1 CONTINUED -

- TABLE 1 CONTINUED -

Pod - size	longer than the calyx	very small, included within the calyx
- shape	compressed	oval in cross-section
- dehiscence	dehiscent	indehiscent
Distribution	eastern parts of southern Africa	western coastal areas of the Cape Province

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**L*. *corymbosa* (E. Mey.) Benth., *L*. *eriantha* Benth., *L*. *lanceolata* (E. Mey.) Benth., *L*. *foliosa* H. Bol., *L*. *spicata* Compton, *L*. *sutherlandii* Dümmer, *L*. *grandis* Dümmer, *L*. *pulchra* Dümmer, *L*. *procumbens* H. Bol. and *L*. *difformis* B-E. van Wyk.

***L*. *pentaphylla* (E. Mey.) Benth., *L*. *polycephala* (E. Mey.) Benth., *L*. *anthylloides* Harv., *L*. *rosea* Dümmer, *L*. *bolusii* Dümmer and four as yet undescribed species.

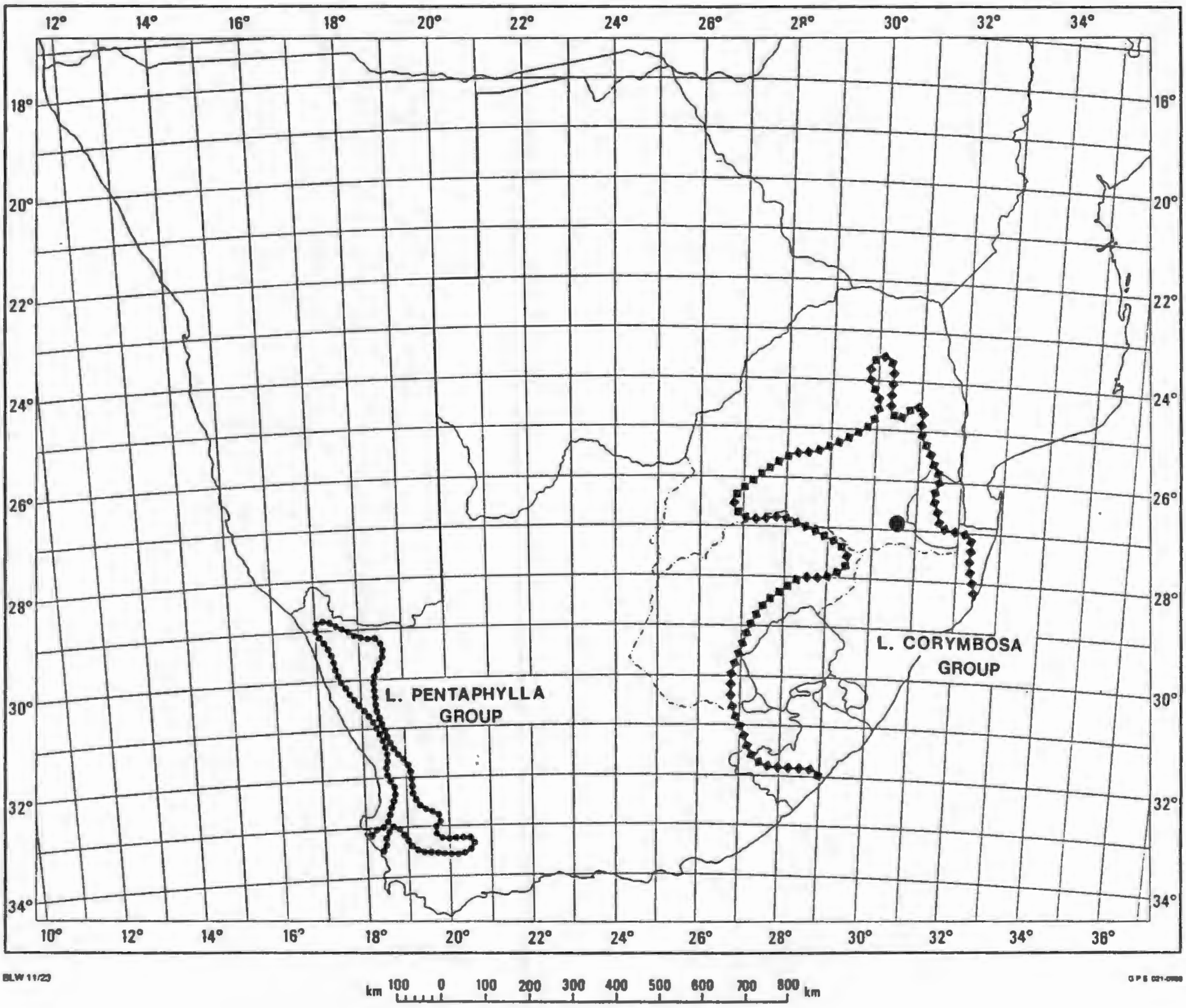

Figure 1. Approximate geographical distribution of the two groups of <u>Lotononis</u> section <u>Lipozygis</u> and the known distribution of <u>L. difformis</u> (●).

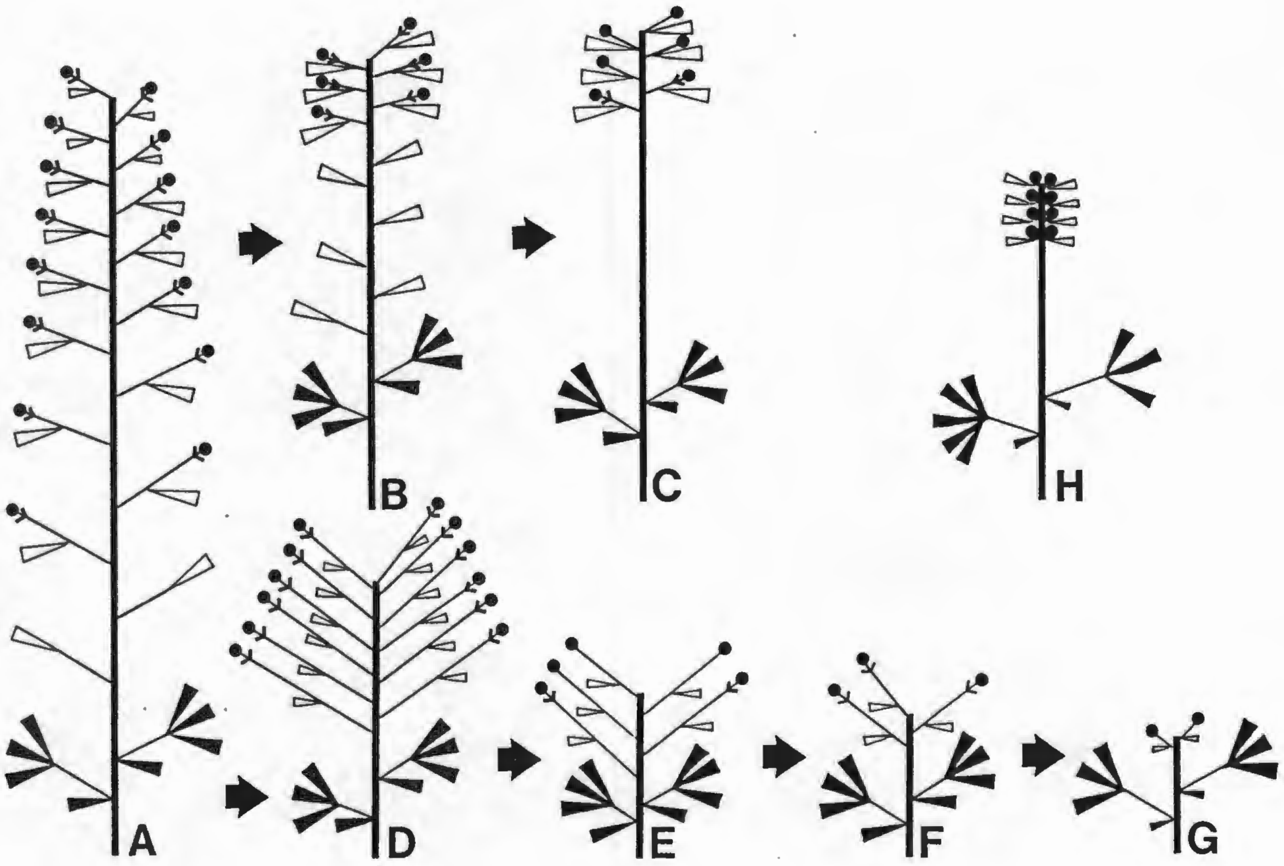

Figure 2. Inflorescence structure in Lotononis sections Lipozygis and Leptis. A hypothetical sequence of development is shown schematically (note the position of bracts and the presence or absence of bracteoles). Inflorescence structure in: A, hypothetical ancestor; B, L. difformis (Lipozygis sensu stricto); C, L. procumbens (Lipozygis sensu stricto); D & E, L. corymbosa and related species (Lipozygis sensu stricto); F, L. stolzii (Leptis, intermediate); G, L. mucronata and related species (Leptis sensu stricto); H, L. pentaphylla and related species (to be excluded from Lipozygis).

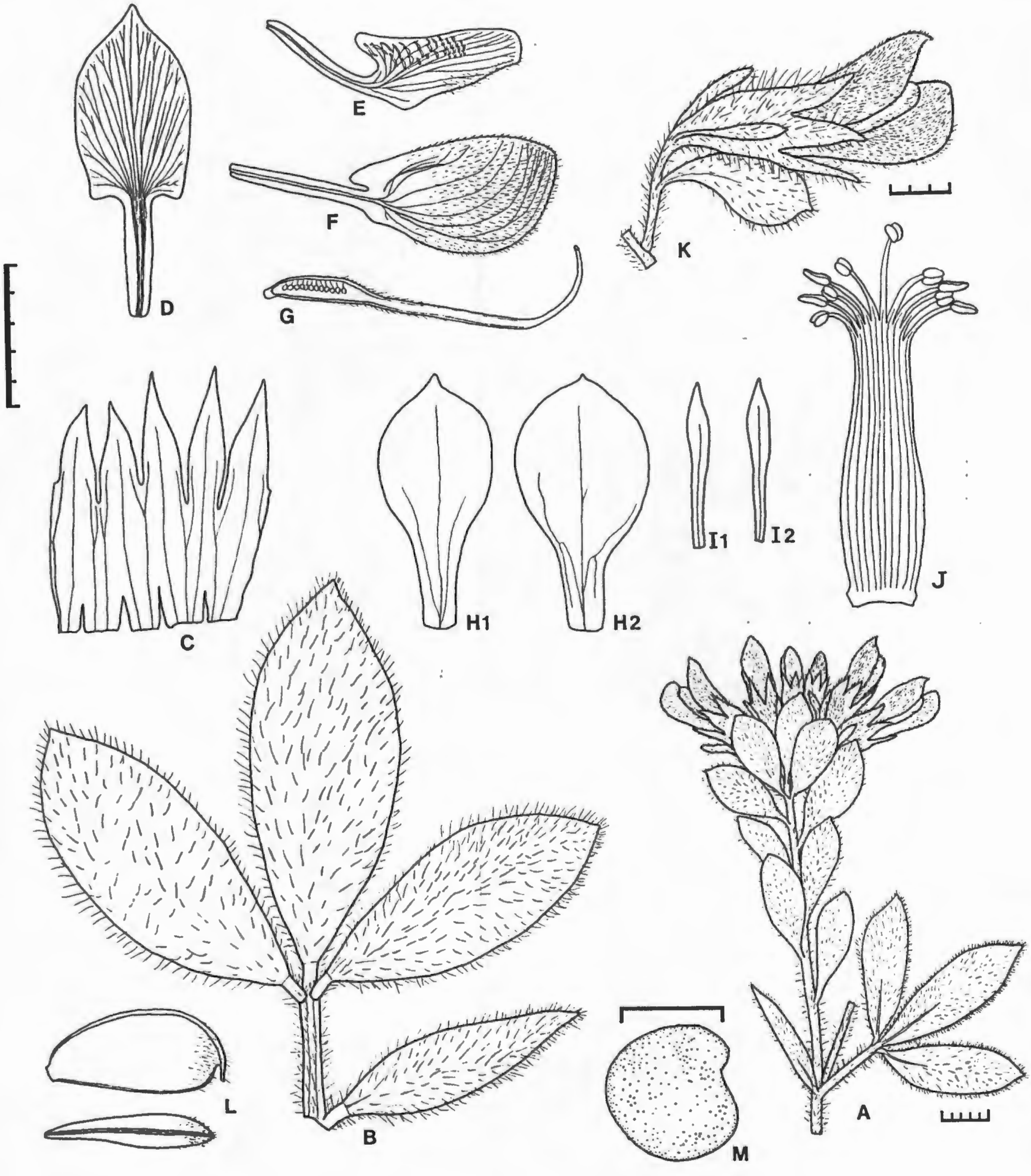

Figure 3. Lotononis difformis. A, inflorescence, showing the foliaceous bracts and a leaf in abaxial view; B, leaf and stipule in adaxial view; C, calyx opened out with the upper lobes to the left; D, standard petal; E, wing petal; F, keel petal; G, pistil; H1 & H2, bracts; I1 & I2, bracteoles; J, androecium; K, flower in lateral view, showing the position of the bract and bracteoles and the vestiture of the calyx and corolla; L, pods in lateral and top view; M, immature seed in lateral view. All from Sidey 1609. Scales in mm, the vertical one applies to all the drawings except a, k and m.

APPENDIX 28

Studies in the genus _Lotononis_ (Crotalarieae, Fabaceae). IX. Four new species of the _L. pentaphylla_ group (section _Lipozygis_)

B-E. VAN WYK*

Keywords: Fabaceae, _Lotononis_ section _Lipozygis_, sectional limits, new species

ABSTRACT

L. pentaphylla (E. Mey.) Benth. and related species were previously shown to be very different from the rest of the section _Lipozygis_ (E. Mey.) Benth. of _Lotononis_ (DC.) Eckl. & Zeyh. These species are all annuals and can easily be distinguished by their capitate inflorescences, sessile flowers and indehiscent, wind-dispersed pods. Four new species of this group are described, namely _L. oligocephala_ B-E. van Wyk, _L. globulosa_ B-E. van Wyk, _L. laticeps_ B-E. van Wyk and _L. longicephala_ B-E. van Wyk.

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UITTREKSEL

Daar is voorheen aangetoon dat *L. pentaphylla* (E. Mey.) Benth. en verwante spesies baie verskillend is van die res van die seksie *Lipozygis* (E. Mey.) Benth. van *Lotononis* (DC.) Eckl. & Zeyh. Hierdie spesies is almal jaarplante en kan maklik onderskei word aan hul hofievormige bloeiwyses, sittende blomme en nie-oopspringende, windverspreide peule. Vier nuwe spesies van hierdie groep word beskryf, naamlik *L. oligocephala* B-E. van Wyk, *L. globulosa* B-E. van Wyk, *L. laticeps* B-E. van Wyk en *L. longicephala* B-E. van Wyk.

Introduction

Lotononis pentaphylla (E. Mey.) Benth., L. polycephala (E. Mey.) Benth., L. anthylloides Harv., L. bolusii Dümmer and L. rosea Dümmer differ from all other annual species of Lotononis (DC.) Eckl. & Zeyh. in their densely capitate inflorescences, sessile flowers and indehiscent, wind-dispersed pods (Van Wyk 1989). These 5 species were previously included by Bentham (1843), Harvey (1862) and Dümmer (1913) in the section Lipozygis (E. Mey.) Benth., but their annual habit and unusual morphology have apparently been overlooked. Four new species that clearly belong to this group are described below.

Wind-dispersal is not uncommon in the tribe Crotalarieae but it is usually accomplished by winged pods, as in the genus Wiborgia Thunb. Personal observations have shown that wind-dispersal also occurs in Lotononis benthamiana Dümmer and in Lebeckia melilotoides Dahlgren. In these two species, the highly persistent corolla acts as a wing to fascilitate dispersal. L. pentaphylla and its allies however, show an unusual and interesting mode of seed dispersal. The tiny pods are few-seeded, totally indehiscent and are completely enclosed by a densely hirsute, much-inflated calyx. When the seeds have matured, the calyx with its enclosed pod is shed from the peduncle. At this stage, the petals are crumpled up and withered, but the total absence of a pedicel and the hairy, inflated calyx result in a very effective dispersal by wind. Only a slight wind is necessary to move the pod (diaspore) over long distances by a rolling rather than floating action. Morphological features associated with this dispersal mechanism are unique within the genus Lotononis and therefore valuable as diagnostic characters. The total absence of a pedicel is the most obvious one, and perhaps also the most useful.

1. Lotononis oligocephala B-E. van Wyk sp. nov. L. polycephalae (E. Mey.) Benth. valde affinis, sed foliis minoribus 5-foliolatis (in L. polycephala 3-foliolatis), inflorescentiis floribus bracteisque minoribus, lobis calycis brevioribus latioribusque, atque corolla omnino glabra (in L. polycephala dense pubescente) differt.

TYPE --- Cape Province, 2918 (Gamoep): Areb, ± 27 miles [43,2 km] NE of Springbok, 25/07/1972, Van der Westhuizen 276 (PRE, holo.; K, MO, iso.).

Prostrate annual up to 0,8 m wide. Branches sparsely leafy, densely silky. Leaves invariably 5-foliolate, (6--) 10--18 (--24) mm long; petiole ± as long as the terminal leaflet or longer; leaflets relatively small, broadly obovate, (3--) 5--8 (--10) mm long, (2--) 3--5 (--7) mm wide, base cuneate, apex truncate to emarginate, densely silky on both surfaces. Stipules single at each node, lanceolate to broadly ovate, 3--4 mm long, 2--3 mm wide, densely silky on both surfaces. Inflorescences in terminal heads, the heads somewhat flattened, 4--8-flowered; peduncle variable in length, 5--50 mm long; bracts large, broadly obovate, ± 4 mm long, ± 4 mm wide; bracteoles absent. Flowers relatively small, 12--14 mm long, yellow; pedicel absent. Calyx subequally lobed but with the lower lobe slightly narrower than the upper four lobes, the sinuses of equal depth; lobes broadly triangular, acute. Standard oblong, as long as the keel; claw 4--5 mm long; lamina ± 8 mm long, 5--6 mm wide, without lobes or callosities, glabrous but with a few hairs dorsally along the middle. Wing petals oblong, ± as long as the keel, glabrous; auricle small, ± 1 mm long; apex obtuse; sculpturing in 4--5 rows of intercostal lunae, fading into transcostal lamellae towards the auricle. Keel petals obovate-oblong, only slightly auriculate; claw 5 mm long; lamina 9 mm long, 5 mm wide, glabrous; apex rounded. Androecium long and narrow; anthers dimorphic; basifixed anthers oblong, slightly longer than the small ovoid dorsifixed anthers; carinal anther similar to dorsifixed anthers. Gynoecium sessile; pistil very small, ovoid-oblong, pubescent, with 5--12 ovules; style long and slender. Pods and seeds unknown. (Figure 1).

L. oligocephala is closely related to L. polycephala (E. Mey.) Benth. but can easily be distinguished by the much smaller and 5-foliolate leaves (3-foliolate in L. polycephala), the smaller inflorescences and flowers, the smaller bracts, the shorter and wider calyx-lobes, and the corolla, which is totally glabrous (densely pubescent in L. polycephala). This species is known only from the type collection, which is from northern Namaqualand (Figure 5).

---2918 (Gamoep): Areb, ± 27 miles [43,2 km] NE of Springbok (--AC), *Van der Westhuizen 276* (PRE, holotype; K, MO, isotypes).

2. *L. globulosa* B-E. van Wyk sp. nov. *L. pentaphyllae* (E. Mey.) Benth. et *L. bolusii* Dummer similis, sed bracteis maximis late ovatis, floribus paulo maioribus, vexillo suborbiculare (non oblongo) et foliis semper 3-foliolatis (folia quidem nonnulla 5-foliolata in *L. pentaphylla* et *L. bolusii*). Praesertim similis est *L. laticipi* B-E. van Wyk, sed ab illo specie inflorescentiis globosis (non discoideis), bracteis maioribus, vestitura densius hirsuta, vexillo longiore, lobis calycis latioribus, atque lobis calycis duobus superioribus latioribus quam inferioribus (superioribus inferioribus aequantibus in *L. laticeps*).

TYPE --- Cape Province, 3320 (Montagu): 29,5 km from Touws River to Laingsburg, near Tweedside, 13/10/1986, *B-E. van Wyk 2210* (PRE, holo.).

Prostrate annual up to 0,4 m wide. Branches sparsely leafy, densely to sparsely hirsute. *Leaves* invariably 3-foliolate, (5--) 8--16 (--32) mm long; petiole as long or usually longer than the terminal leaflet; leaflets relatively small, oblanceolate to obovate, (3--) 5--10 (--14) mm long, (1--) 3--4 (--6) mm wide, base cuneate, apex rounded or rarely emarginate, abaxial surface sparsely hirsute, adaxial surface glabrous. *Stipules* single at each node, lanceolate to oblong, 3--6 mm long, ± 1 mm wide. Inflorescences in terminal heads, the heads globose, 8--20-flowered; peduncle variable in length, usually short, 5--25 mm long; bracts large, very broadly ovate, (4--) 7--10 mm long, (4--) 7--10 mm wide; bracteoles absent. Flowers relatively small, 9--10 mm long, yellow; pedicel absent. Calyx subequally lobed but with the two upper lobes slightly wider than the lower lobes, the sinuses of ± equal depth; lobes narrowly triangular, acute. Standard suborbicular, as long as the keel or slightly shorter; claw ± 4 mm long; lamina 5--6 mm long, 5--8 mm wide, without lobes or callosities, pubescent over most of the abaxial surface. Wing petals oblong, ± as long as the keel, pubescent along the apex; auricle small, ± 0,5 mm long; apex obtuse; sculpturing in 4--5 rows of intercostal lunae, fading into transcostal lamellae towards the auricle. Keel petals obovate, only slightly auriculate; claw ± 4 mm long; lamina 4--6 mm long, 3--4 mm wide, pubescent over most of the surface; apex rounded. Androecium long and narrow; anthers dimorphic; basifixed anthers oblong, slightly longer than the small ovoid dorsifixed anthers; carinal anther similar to dorsifixed anthers. Gynoecium sessile; pistil very small, ovoid-oblong, pubescent, with 5--9 ovules; style long and slender. Pods very small, ovoid, ± 4 mm long, 2,5 mm wide, much inflated laterally, totally indehiscent, enclosed by the persistent and much-inflated calyx; upper suture minutely verrucose, 2--3-seeded. Seeds suborbicular, ± 1,5 mm in diameter, testa minutely but densely tuberculate (Figure 2).

L. globulosa is similar to L. pentaphylla (E. Mey.) Benth. and L. bolusii Dümmer but differs in the very large, broadly ovate bracts, the slightly larger flowers, the suborbicular (not oblong) standard petal and in the consistently 3-foliolate leaves (always at least some leaves 5-foliolate in L. pentaphylla and L. bolusii). It is particularly similar to L. laticeps B-E. van Wyk, but differs from this species in the globose (not discoid) inflorescences, the larger bracts, the more hirsute vestiture, the longer standard petal, the wider calyx-lobes and the two upper calyx-lobes, which are wider than the lower lobes (upper lobes as wide as the lower lobes in L. laticeps). These differences are clearly shown in Figures 2 and 3.

This species is known from a limited area in the south-western Cape (Figure 5), where it is perhaps more common than the very poor herbarium record would suggest.

---3319 (Worcester): Ceres Division, Gydouw (--AB), Leipoldt 3123 (BOL, K); Ceres District, Laken Vlei (--BC), Compton 12074 (NBG), Levyns 1053 (BOL, SAM).
---3320 (Montagu): 29,5 km from Touws River to Laingsburg, near Tweedside (--AD), B-E. van Wyk 2210 (PRE, holotype), 2211 (JRAU).

3. L. laticeps B-E. van Wyk sp. nov. valde affinis L. globulosae B-E. van Wyk, sed capitulis discoideis (non globosis), bracteis minoribus, vestitura sparsiori breviori, vexillo breve carina valde breviori (vexillum carinam in L. globulosa speciebusque affinibus aequans) differt. A L. globulosa calyce minori sub-pariter lobato (superioribus inferioribus haud latioribus), lobis angustioribus etiam differt. A L. pentaphylla, L. bolusii, L. roseaque etiam folios semper 3-foliolatis, bracteis valde maioribus late ovatis (non linearibus nec lanceolatis) atque vexillo suborbiculare (non oblongo) etiam differt.

TYPE --- Cape Province, 3219 (Wuppertal): Ceres District, Stompiesvlei, Swartruggens (sandy stony plateau, 3500 ft.), 19/11/1961, Esterhuysen 29334 (BOL, holo.; C, K, M, MO, S, iso.).

Prostrate annual up to 0,3 m wide. Branches sparsely leafy, minutely hirsute. Leaves invariably 3-foliolate, (6--) 12--15 (--17) mm long; petiole ± as long as the terminal leaflet or slightly longer; leaflets relatively small, oblanceolate to obovate, (3--) 5--8 (--10) mm long, (1,5--) 3--4 (--5) mm wide, base cuneate, apex rounded to truncate, sparsely hirsute on both surfaces. Stipules single at each node, lanceolate to oblong, 3--5 mm long, ± 1 mm wide. Inflorescences in terminal heads, the heads discoid (wider than long), 8--20-flowered; peduncle variable in length, 3--28 mm long; bracts large, broadly ovate, 4--5 mm long, 4--5 mm wide; bracteoles absent. Flowers relatively small, 9--10 mm long, yellow; pedicel absent. Calyx subequally lobed, the sinuses of ± equal depth; lobes narrowly linear, acute. Standard suborbicular, much shorter than the keel; claw 1--2 mm long; lamina ± 3 mm long, ± 4 mm wide, without lobes or callosities, pubescent over most of the abaxial surface. Wing petals oblong, shorter than the keel, pubescent along the apex; auricle small, ± 0,5 mm long; apex obtuse; sculpturing in 4--5 rows of intercostal lunae, fading into transcostal lamellae towards the auricle. Keel petals oblong, only slightly auriculate; claw ± 2,5 mm long; lamina ± 6 mm long, ± 3 mm wide, pubescent over most of the surface; apex rounded. Androecium long and narrow; anthers dimorphic; basifixed anthers oblong, slightly longer than the small ovoid dorsifixed anthers; carinal anther similar to dorsifixed anthers. Gynoecium sessile; pistil very small, ovoid-oblong, pubescent, with 2--4 ovules; style long and slender. Pods and seeds unknown. (Figure 3).

This poorly known species has so far been recorded only from a single locality in the Ceres district (Figure 5). It is very closely related to L. globulosa, but can easily be distinguished by the short standard petal. Other diagnostic characters (see Figures 2 and 3) are given under L. globulosa.

---3219 (Wuppertal): Ceres District, Stompiesvlei, Swartruggens (--DC), Esterhuysen 29334 (BOL, holotype; C, K, M, MO, S, isotypes).

4. L. longicephala B-E. van Wyk sp. nov. distincta sine affinitatibus manifestis. Similis est L. pentaphyllae (E. Mey.) Benth. et L. bolusii Dümmer, sed ab illis speciebusque omnibus affinibus foliis semper 3-foliolatis, capitulis valde minoribus oblongis (non globosis nec discoideis), floribus leguminibusque valde minoribus differt. A L. globulosa B-E. van Wyk et L. laticipe B-E. van Wyk etiam bracteis linearibus inconspicuis (non magnis ovatis) differt.

TYPE --- Cape Province, 3319 (Worcester): Flats east of Prince Alfred's Hamlet, 10/10/1974, Oliver 5063 (PRE, holo.; K, MO, STE, iso.).

Prostrate annual, 0,5--0,8 m wide. Branches sparsely leafy, sparsely pubescent. Leaves invariably 3-foliolate, (5--) 10--14 (--22) mm long; petiole ± as long as the terminal leaflet; leaflets relatively small, oblanceolate to obovate, (3--) 5--9 (--12) mm long, (1,5--) 3--4 (--6) mm wide, base cuneate, apex truncate to emarginate, abaxial surface sparsely pubescent, adaxial surface glabrous. Stipules single at each node, lanceolate, 2--6 mm long, ± 1 mm wide. Inflorescences in terminal or subterminal heads, the heads globose when young, oblong when fully developed, (4--) 12--52-flowered; peduncle variable in length, 5--24 mm long; bracts small, linear or narrowly lanceolate, 2--3 mm long, up to 0,5 mm wide; bracteoles absent. Flowers very small, ± 6 mm long, yellow; pedicel absent. Calyx subequally lobed, the sinuses of ± equal depth; lobes narrowly triangular, acute. Standard suborbicular, as long as the keel;

claw ± 1,5 mm long; lamina ± 2,5 mm long, ± 4 mm wide, without lobes or callosities, abaxially pubescent over most of the basal part. Wing petals oblong, almost as long as the keel, glabrous except for a few hairs on the auricle and near the attachment of the claw; auricle small; apex obtuse; sculpturing in 4--5 rows of intercostal lunae, fading into transcostal lamellae towards the auricle. Keel petals oblong, only slightly auriculate; claw ± 2 mm long; lamina ± 3 mm long, ± 1,5 mm wide, pubescent at least towards the apex; apex rounded. Androecium long and narrow; anthers dimorphic; basifixed anthers broadly oblong, much larger than the small ovoid dorsifixed anthers; carinal anther similar to dorsifixed anthers. Gynoecium sessile; pistil very small, ovoid-oblong, pubescent, with 3--4 ovules; style long and slender. Pods very small, ovoid, ± 2,5 mm long, ± 1,5 mm wide, much inflated laterally, totally indehiscent, enclosed by the persistent and much-inflated calyx; upper suture minutely verrucose, 2--3-seeded. Seeds suborbicular, ± 1,2 mm in diameter, testa sparsely tuberculate (Figure 4).

L. longicephala is a distinct species with no obvious affinities. It is similar to L. pentaphylla and L. bolusii, but differs from these and all related species in the consistently 3-foliolate leaves, the much smaller and oblong (not globose or discoid) heads, the much smaller flowers and the much smaller pods. It differs from L. globulosa and L. laticeps also in the inconspicuous, linear bracts (Figure 4). L. longicephala is known only from the vicinity of Touws River in the south-western Cape (Figure 5).

---3219 (Wuppertal): Ceres District, E foot of Schurweberg (next to Bokkeveld Tafelberg) (--CD), Esterhuysen 20631 (BOL); near the base of Schurweberg Peak (--CD), Esterhuysen 29299 (BOL, C, K, S).

---3319 (Worcester): Flats east of Prince Alfred's Hamlet (--AD), Oliver 5063 (PRE, holotype; K, MO, STE, isotypes); Verkeerdevlei, 64,5 km from Ceres to Touws River (--BD), B-E. van Wyk 2241 (BOL, C, GRA, JRAU, K, MO, NBG, PRE, SAAS, STE).

---3320 (Montagu): 29,5 km from Touws River to Laingsburg, near Tweedside (--AD), B-E. van Wyk 2200 (JRAU), 2202 (BOL), 2203 (GRA), 2204 (K), 2205 (MO), 2206 (NBG), 2207 (PRE), 2208 (S), 2209 (NH, SAAS, STE).

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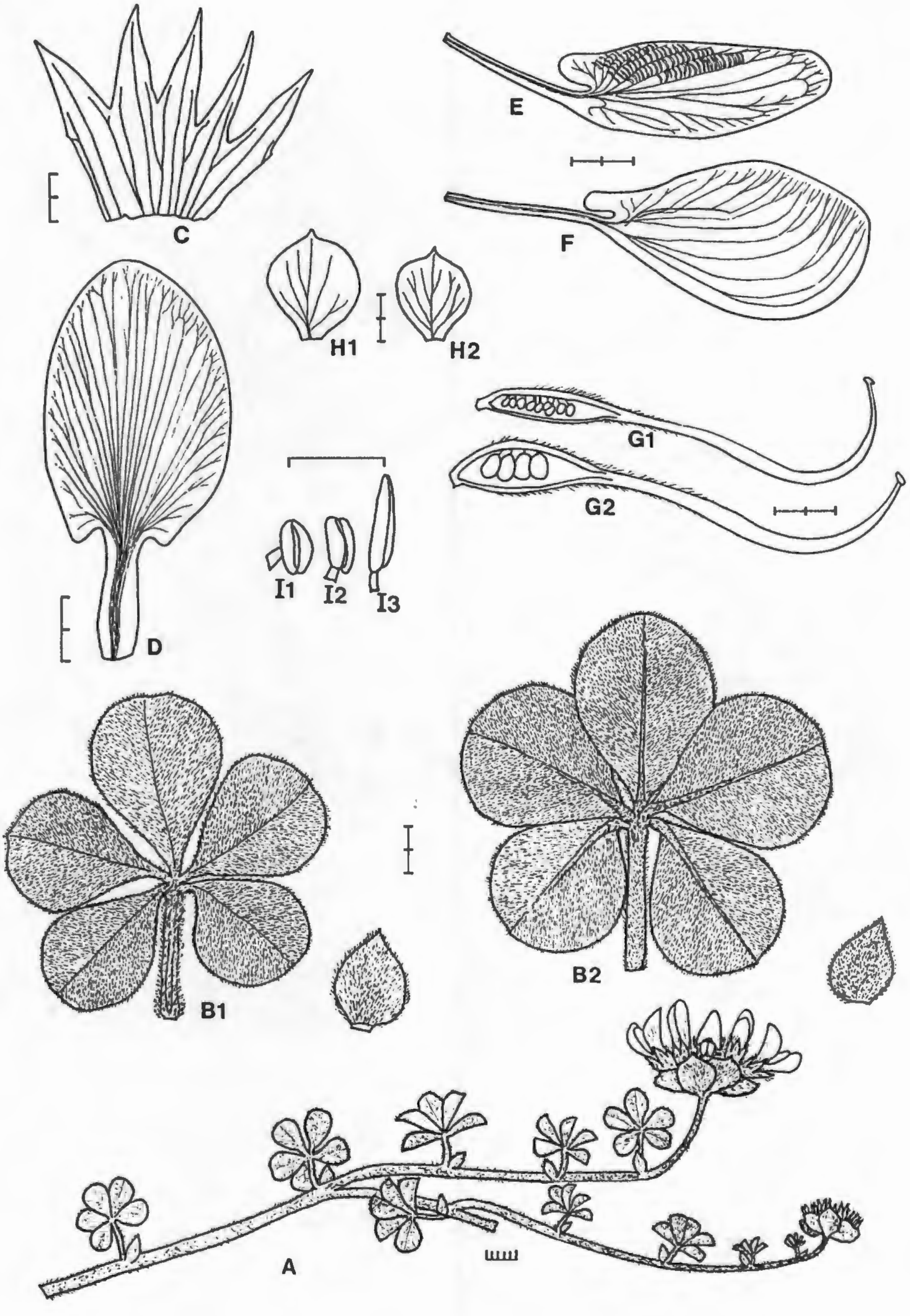

Figure 1. Lotononis oligocephala. A, flowering twig; B1 & B2, leaves and stipules: B1, adaxial view, B2, abaxial view; C, calyx opened out with the upper lobes to the left (vestiture not shown); D, standard petal; E, wing petal; F, keel petal; G1 & G2, pistils: G1, from young flower, G2 from older flower; H1 & H2, bracts; I1, I2 & I3, anthers: I1, dorsifixed anther, I2, carinal anther, I3, long basifixed anther. All from Van der Westhuizen 276. Scales in mm.

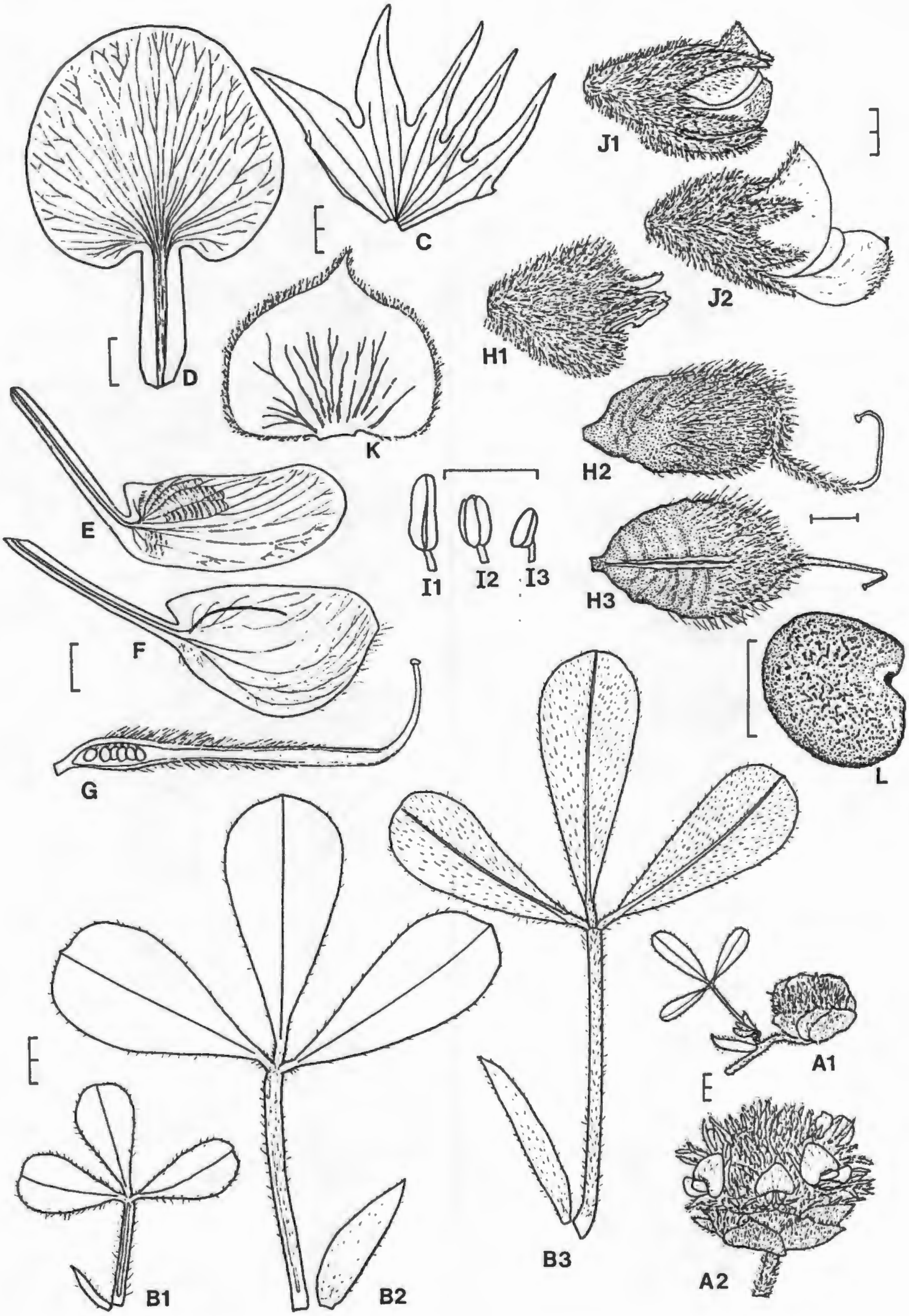

Figure 2. *Lotononis globulosa*. A1 & A2, inflorescences: A1, young inflorescence, A2, mature inflorescence showing the globose shape and large bracts; B1, B2 & B3, leaves and stipules: B1 & B2, adaxial view, B3, abaxial view; C, calyx opened out with the upper lobes to the left (vestiture not shown); D, standard petal; E, wing petal; F, keel petal; G, pistil; H1, mature fruit (dispersal unit or diaspore), showing the persistent inflated calyx which totally encloses the pod; H2 & H3, pods with the calyx removed: H2, lateral view, H3, top view; I1, I2 & I3, anthers: I1, long basifixed anther, I2, carinal anther, I3, dorsifixed anther; J1 & J2, flowers in lateral view; K, bract; L, seed in lateral view. All from *Van Wyk 2210* except J1 from *Van Wyk 2211*, J2 from *Leipoldt 3123*. Scales in mm.

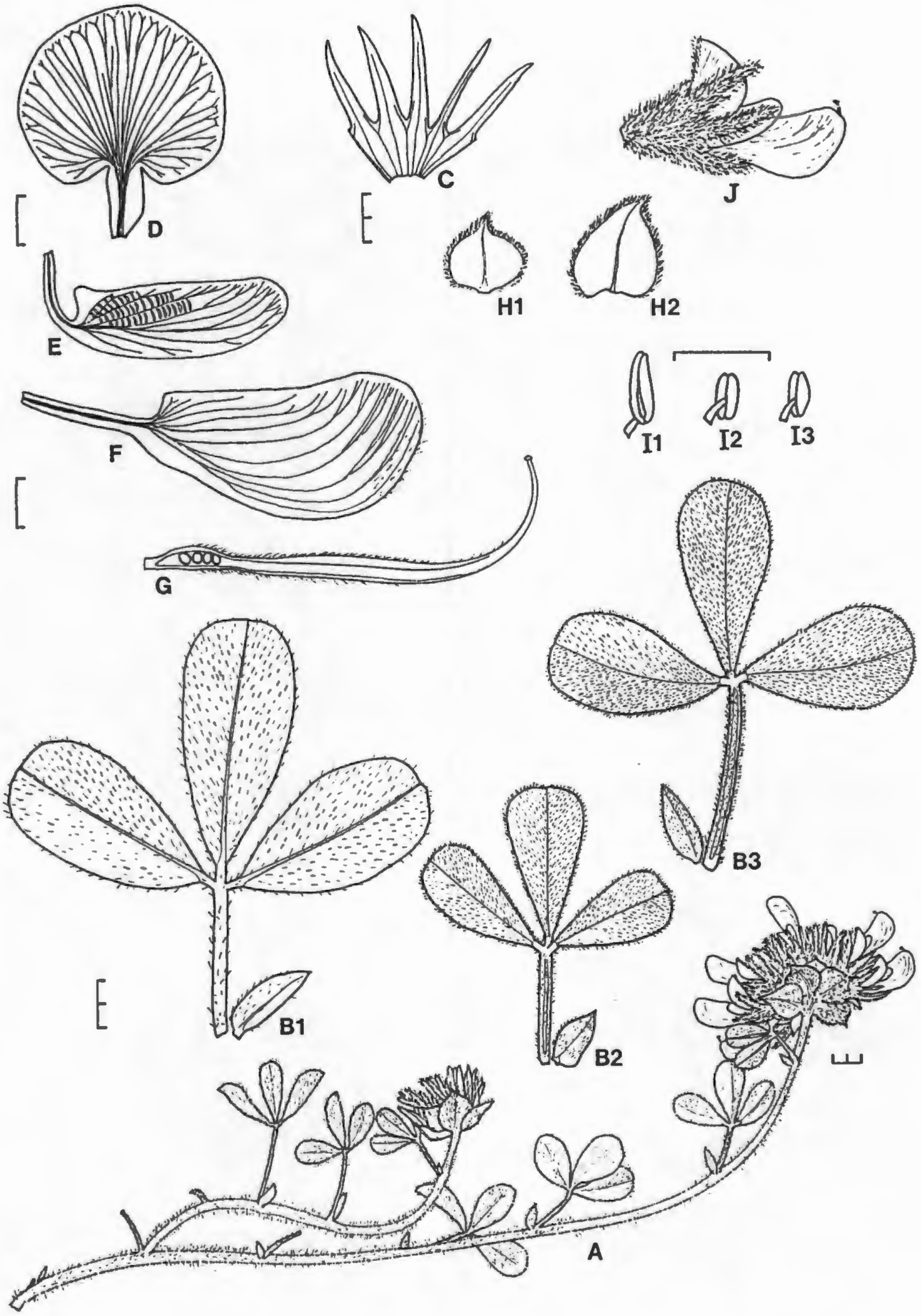

Figure 3. Lotononis laticeps. A, flowering twig; B1, B2 & B3, leaves and stipules: B1, abaxial view, B2 & B3, adaxial view; C, calyx opened out with the upper lobes to the left (vestiture not shown); D, standard petal; E, wing petal; F, keel petal; G, pistil; H1 & H2, bracts; I1, I2 & I3, anthers: I1, basifixed anther, I2, carinal anther, I3, dorsifixed anther; J, flower in lateral view showing the short standard petal. All from Esterhuysen 29334. Scales in mm.

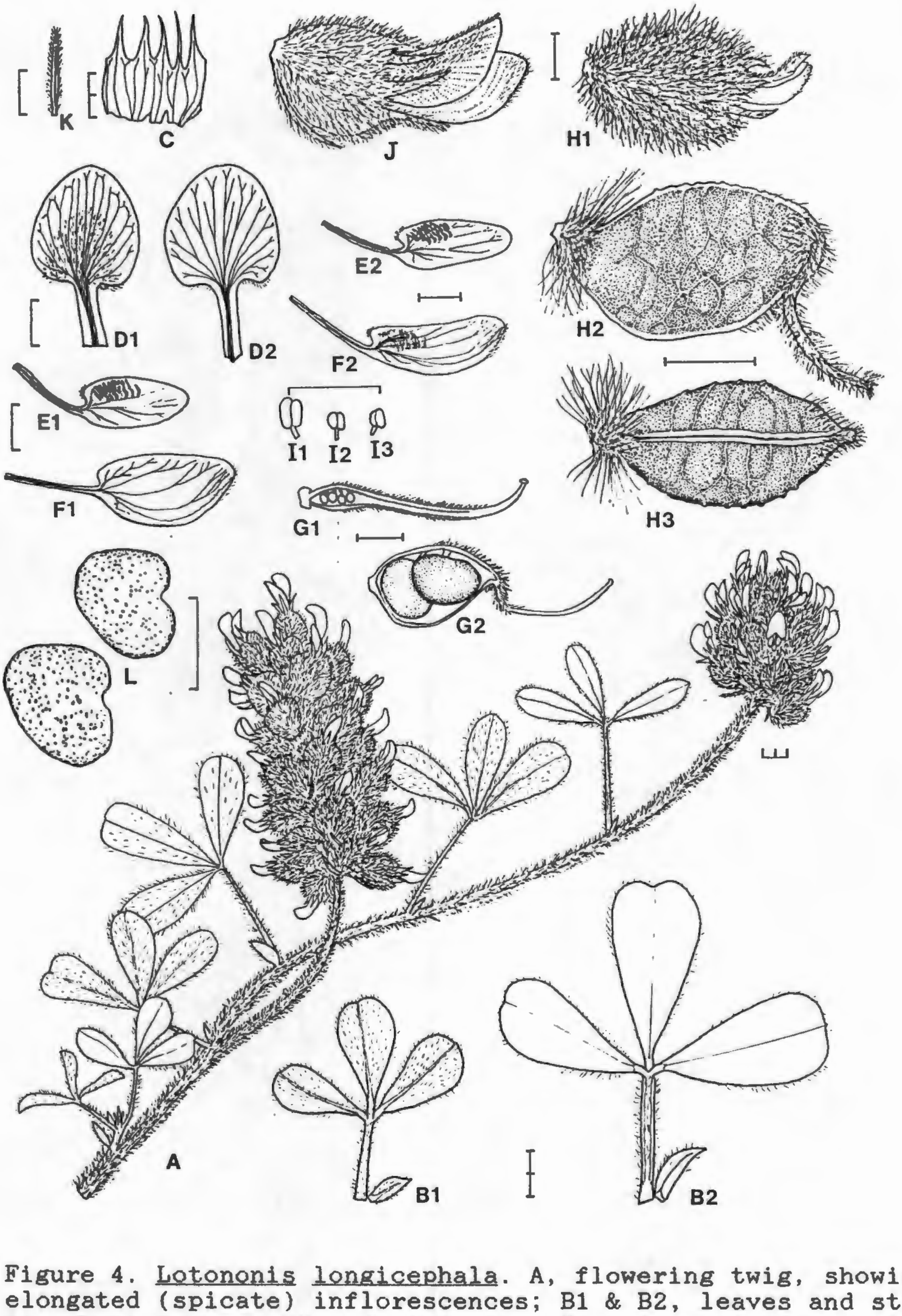

Figure 4. Lotononis longicephala. A, flowering twig, showing the elongated (spicate) inflorescences; B1 & B2, leaves and stipules: B1, abaxial view, B2, adaxial view; C, calyx opened out with the upper lobes to the left (vestiture not shown); D1 & D2, standard petals: D1, abaxial view, D2, adaxial view; E1 & E2, wing petals; F1 & F2, keel petals (note sculpturing on F2); G1, pistil; G2, young pod; H1, mature fruit (dispersal unit or diaspore), showing the persistent inflated calyx which totally encloses the pod; H2 & H3, pods with the calyx removed: H2, lateral view, H3, top view; I1, I2 & I3, anthers: I1, long basifixed anther, I2, carinal anther, I3, dorsifixed anther; J, flower in lateral view; K, bract; L, seeds in lateral view, showing the sparsely tuberculate surface. All from Van Wyk 2200 except C, D1, E2, F2, G2 & K from Esterhuysen 29299. Scales in mm.

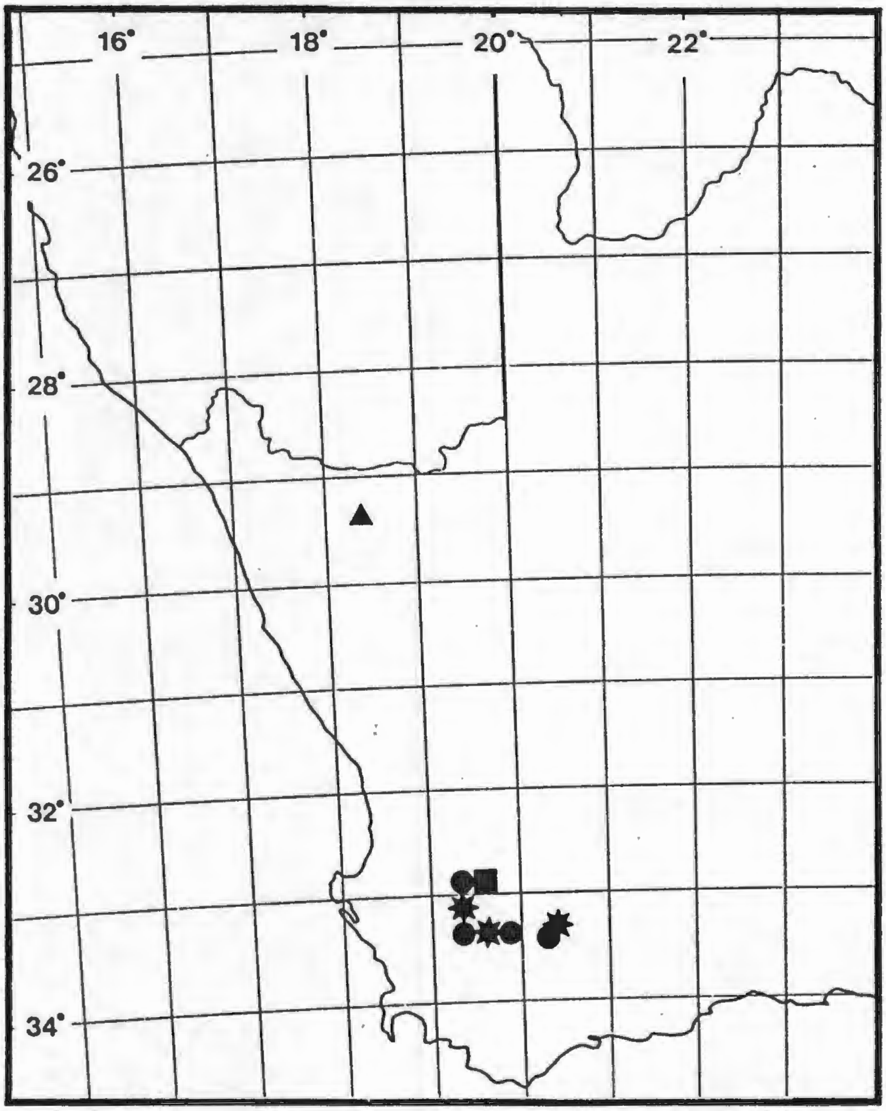

Figure 5. The known geographical distribution of Lotononis oligocephala (▲), L. globulosa (✱), L. laticeps (■) and L. longicephala (●).

APPENDIX 29

Studies in the genus *Lotononis* (Crotalarieae, Fabaceae). X. *L. esterhuyseana*, a new species from the south-western Cape Province

B-E. VAN WYK*

Keywords: Fabaceae, *Lotononis* sectional limits, new species

ABSTRACT

An unusual new species, *L. esterhuyseana* B-E. van Wyk, is described. The affinities of this species are uncertain and it does not fit readily into any of the existing section of *Lotononis* (DC.) Eckl. & Zeyh. The calyx and corolla suggest a position in the section *Leobordea* (Del.) Benth., but the leaf arrangement and pods agree more with those of the *L. pentaphylla* group of section *Lipozygis* (E. Mey.) Benth. A new monotypic section seems the most practical way in which to accommodate the new species in *Lotononis*.

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UITTREKSEL

'n Ongewone nuwe spesie, L. esterhuyseana B-E. van Wyk, word beskryf. Die verwantskappe van hierdie spesie is onseker en dit pas nie geredelik in enige van die bestaande seksies van Lotononis (DC.) Eckl. & Zeyh. nie. Die kelk en kroon dui op 'n posisie in die seksie Leobordea (Del.) Benth., maar die blaarrangskikking en peule stem meer ooreen met dié in die L. pentaphylla-groep van die seksie Lipozygis (E. Mey.) Benth. 'n Nuwe monotipiese seksie lyk na die mees praktiese wyse om die nuwe spesie by Lotononis in te sluit.

Introduction

The taxonomic position of an undescribed species with a superficial similarity to species of the section Leobordea (Del.) Benth. is considered in this paper. At first, the morphology did not seem unusual, but on closer examination it became clear that the species did not fit readily into any of the existing sections of Lotononis (DC.) Eckl. & Zeyh. The significance of the new species described below is that it indicates a direct relationship between the L. pentaphylla group [presently part of the section Lipozygis (E. Mey.) Benth., see Van Wyk 1989) and the section Leobordea. In terms of appearance however, it is rather insignificant.

A summary of similarities and differences between the new species and various groups of Lotononis is given in Table 1. The comparison shows that it has more in common with the sections Leobordea and Lipozygis than with Leptis (Eckl. & Zeyh.) Benth. It differs from Leobordea mainly in the alternate leaf arrangement and the smaller number of ovules and seeds. The character states also agree well with those of Lipozygis (L. pentaphylla group) except for the structure of the calyx and inflorescence. The only way to retain the present diagnostic value of the opposite leaf arrangement (for Leobordea) and the capitate inflorescence (for the L. pentaphylla group) would be to exclude the new species from these two groups. The very small number of ovules and the unusual combination of other characters are of sufficient diagnostic value to form a new monotypic section. This seems the most practical solution.

Lotononis esterhuyseana B-E. van Wyk sp. nov. distincta cum affinitatibus nullis manifestis. Similis est L. leobordeae (Viv.) Pic.-Serm. aliisque speciebus sectionis Leobordeae, sed ab illis foliis alternatis in ramis floriferis atque ovulis valde paucioribus (1 vel 2, non 5 vel ultra ut in Leobordea) differt. Etiam similis est L. laticipi B-E. van Wyk aliisque speciebus gregis L. pentaphyllae (sectionis Lipozygis), ab illis inflorescentia racemosa (non capitata), lobo carinale calycis parvo, leguminibus maioribus compressis atque calyce non inflato non legumen ubi maturo includente, differt. Etiam similis est L. microphyllae Harv. (sectionis Leptidis), sed ab illa habitu annuale, fabrica calycis, forma longitudineque vexillae et numero parvo ovulorum differt.

TYPE --- Cape Province, 3219 (Wuppertal): Ceres District, Stompiesvlei, Swartruggens (in sand near pan, 4000 ft.), 19/11/1961, Esterhuysen 29341 (BOL, holo.; C, K, MO, iso.).

The species is named after Miss Elsie Esterhuysen of the Bolus Herbarium, who collected and distributed the only material known so far. Through her numerous collections of rare and unusual species, Miss Esterhuysen has made a very significant contribution to the phytogeography and taxonomy of Lotononis.

Prostrate annual up to 0,4 m wide. Branches sparsely leafy, minutely hirsute. Leaves invariably 3-foliolate, (5--) 8--12 (--15) mm long; petiole as long or longer than the terminal leaflet; leaflets relatively small, obovate, (2--) 5--7 (--9) mm long, (1--) 2--4 (--5) mm wide, base cuneate, apex rounded to truncate, minutely but densely pubescent on both surfaces. Stipules single at each node, small, lanceolate to ovate, up to 3 mm long, ± 1,5 mm wide, minutely pubescent on both surfaces. Inflorescences in terminal and leaf-opposed racemes, (3--) 6--12 (--15)-flowered; peduncle short, (2--) 3--6 (--12) mm long; bracts small and inconspicuous, lanceolate, ± 1 mm long; bracteoles absent. Flowers small, 7--8 mm long, yellow; pedicel up to 2 mm long. Calyx subequally lobed but with the lower lobe much narrower and slightly shorter than the upper four lobes; lateral sinuses a little shallower than the upper and lower ones; lobes narrowly triangular, acute. Standard suborbicular, much shorter than the keel; claw short, ± 1,5 mm long; lamina ± 4 mm long, 3--4 mm wide, without lobes or callosities, adaxially pubescent along the apex. Wing petals oblong, much shorter than the keel, distinctly auriculate; pubescent along the apex; sculpturing in ± 4 rows of intercostal lunae, fading into transcostal lamellae towards the auricle. Keel petals broadly oblong, wider towards the obtuse apex, only slightly auriculate; claw ± 3 mm long; lamina 5--6 mm long, ± 3 mm wide, pubescent on most of the upper half. Androecium long and narrow; anthers dimorphic; basifixed anthers oblong, almost twice as long as the small ovoid dorsifixed anthers; carinal anther similar to dorsifixed anthers. Gynoecium shortly stipitate; pistil very small, ovoid-oblong, pubescent, with 1 or 2 ovules; style with the basal part straight, broad and pubescent, the upper part short, slender, glabrous. Pods very small, ovoid, ± as long as the calyx, 3--3,5 mm long, 2--2,5 mm wide, shortly stipitate, compressed (not inflated), densely pubescent, indehiscent (?); upper suture minutely verrucose, 1 or 2-seeded. Seeds suborbicular, ± 1,2 mm in diameter, testa pale orange-brown, sparsely and minutely tuberculate (Figure 1).

L. esterhuyseana is a distinct species with no obvious affinities. It is similar L. leobordea (Viv.) Pic.-Serm. and other species of the section Leobordea but differs from these in the alternate arrangement of the leaves on flowering twigs and also in the much smaller number of ovules (more than 5 in section Leobordea). It is also similar to L. laticeps B-E. van Wyk and other species of the L. pentaphylla group (section Lipozygis), but differs from these in the racemose inflorescence (not capitate), the small carinal lobe of the calyx, the larger and compressed pods and in the calyx, which is not inflated and which does not enclose the pod at maturity. It also resembles L. microphylla Harv. (section Leptis) but differs from this species in the annual habit, the calyx structure, the shape and length of the standard petal and the small number of ovules.

The geographical distribution of *L. esterhuyseana* supports the suggested affinity with the *L. pentaphylla* group (presently section *Lipozygis*) and the section *Leobordea* rather than with the section *Leptis*. The single known locality is shown in Figure 2.

---3219 (Wuppertal): Ceres District, Stompiesvlei, Swartruggens (--DC), *Esterhuysen 29341* (BOL, holotype; C, K, MO, isotypes).

Acknowledgements

I thank Dr H. F. Glen (Botanical Research Institute, Pretoria) for the Latin translation and the Directors and staff of the cited herbaria for the loan of specimens. The taxonomic study of *Lotononis* is a registered Ph. D. project at the University of Cape Town.

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VAN WYK, B-E., 1989. Studies in the genus *Lotononis* (Crotalarieae, Fabaceae). VIII. A new species of the *L. corymbosa* group and notes on the taxonomy of the section *Lipozygis*. *S. Afr. J. Bot*. (submitted).

Table 1. Similarities and differences between *L. esterhuyseana* and various other groups of the genus *Lotononis*.

	L. esterhuyseana	section *Lipozygis* *L. pentaphylla* group	section *Leobordea*	section *Leptis* *L. mucronata* group
Habit	annual	annual	annual	perennial
Inflorescence	racemose	capitate	racemose to 1-flowered	racemose to 1-flowered
Pedicel	present	absent	present or when rarely absent, then the inflorescence 1-flowered	present
Leaf type	invariably 3-digitate	often 5-digitate	invariably 3-digitate	invariably 3-digitate
Leaf arrangement of flowering twigs	alternate	alternate	opposite	alternate
Pod - size	± as long as the calyx	very small, included within the calyx	as long or longer than the calyx	as long or longer than the calyx
- shape	compressed	turgid	slightly turgid	slightly turgid
- dehiscence	indehiscent?	indehiscent	dehiscent or tardily dehiscent	dehiscent or tardily dehiscent

- TABLE 1 CONTINUED -

Ovule number	1 or 2	2 to 12	6 to 15	4 to 18
Seed number	1 or 2	2 to 5	4 to 9	2 to 16
Calyx - shape	not inflated	inflated	rarely inflated	not inflated
- carinal lobe	shorter than upper four lobes	not shorter	shorter than upper upper four lobes	not shorter
Standard - shape	suborbicular	oblong or suborbicular	oblong	oblong
- length	much shorter than the keel	as long as the keel, rarely much shorter	usually much shorter than the keel	as long as the keel
Distribution	south-western Cape	western coastal areas of the Cape Province	Karoo, Namibia and northwards to Pakistan	eastern parts of southern Africa

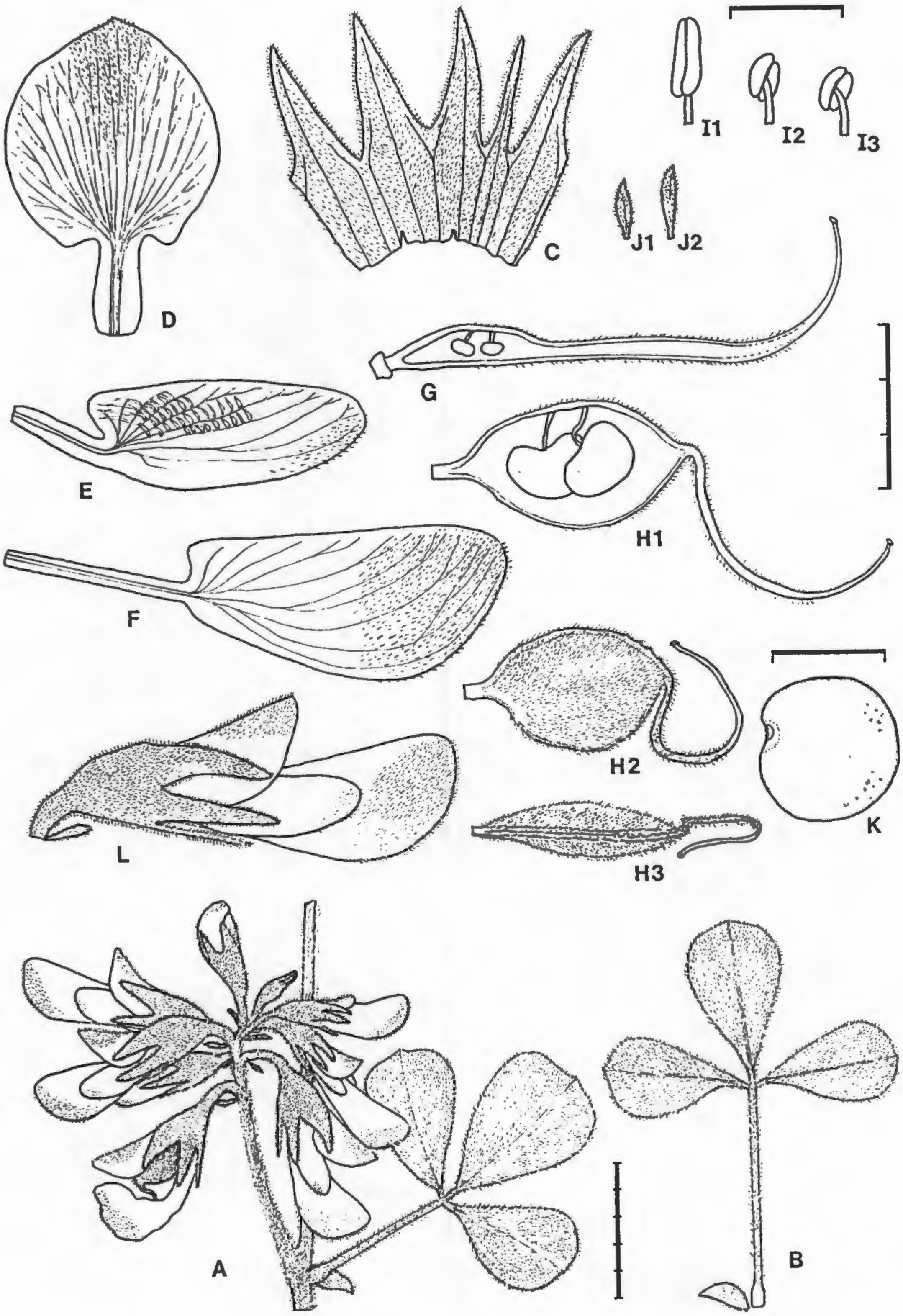

Figure 1. *Lotononis esterhuyseana*. A, flowering twig, showing the racemose inflorescence and a leaf in adaxial view; B, leaf and stipule in abaxial view; C, calyx opened out with the upper lobes to the left; D, standard petal; E, wing petal; F, keel petal; G, pistil; H1, H2 & H3, pods: H1, in longitudinal section, showing the seeds, H2, in lateral view, H3, in top view; I1, I2 & I3, anthers: I1, long basifixed anther, I2, carinal anther, I3, dorsifixed anther; J1 & J2, bracts; K, seed, showing the almost smooth surface, L, flower in lateral view. All from *Esterhuysen 29341*. Scales in mm.

APPENDIX 30

Studies in the genus Lotononis (Crotalarieae, Fabaceae). XI. A new species of the section Leobordea from north-western Namibia

B-E. VAN WYK*

Keywords: Fabaceae, Lotononis section Leobordea, new species

ABSTRACT

Diagnostic characters of the section Leobordea (Del.) Benth. are discussed. The opposite arrangement of leaves on flowering branches appears to be the most reliable character to distinguish Leobordea from all other sections of Lotononis (DC.) Eckl. & Zeyh. A new species from north-western Namibia, L. bracteosa B-E. van Wyk, is described. This species was previously confused with L. stipulosa Bak. f. but it is shown that the latter does not occur in Namibia. In the new species, the involucrate appearance of the inflorescences is due to enlarged bracts and not to enlarged stipules as in L. stipulosa.

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UITTREKSEL

Diagnostiese kenmerke van die seksie *Leobordea* (Del.) Benth. word bespreek. Die teenoorstaande blaarrangskikking van blommende takke lyk na die mees betroubare kenmerk om *Leobordea* te onderskei van alle ander seksies van *Lotononis* (DC.) Eckl. & Zeyh. 'n Nuwe spesie van noord-westelike Namibië, *L*. *bracteosa* B-E. van Wyk, word beskryf. Hierdie spesie is voorheen verwar met *L*. *stipulosa* Bak. f. maar daar word aangetoon dat laasgenoemde nie in Namibië voorkom nie. By die nuwe spesie is die omwindselagtige voorkoms van die bloeiwyses te wyte aan vergrote skutblare en nie vergrote steunblare soos by *L*. *stipulosa* nie.

Introduction

The section Leobordea (Del.) Benth. is geographically the most widespread section of Lotononis (DC.) Eckl. & Zeyh. L. platycarpa (Viv.) Pich.-Serm. occurs throughout Africa and eastwards to Pakistan but the other species of the section are all restricted to southern Africa.

Bentham (1843) listed the small subsessile flowers, the subsessile leaf-opposed inflorescences and the small carinal lobe of the calyx as diagnostic characters for the section, but also mentions the dichotomous branches. Detailed studies of the genus as a whole have shown that the length of the pedicels, the inflorescence structure and the calyx structure are rather variable, and that most of the diagnostic characters of Leobordea also occur sporadically in other sections. It is here suggested that the opposite arrangement of leaves on flowering branches is the only reliable character to distinguish Leobordea from other sections of Lotononis. In the section Leptis (Eckl. & Zeyh.) Benth., some leaves may occasionally be subopposite, but the leaves are never invariably opposite as in Leobordea. It is important to note that the distinction only applies to flowering nodes. Basal leaves that are formed during the vegetative phase are alternate (also in Leobordea). This is true for all species of Lotononis except L. lenticula (E. Mey.) Benth. (section Oxydium Benth.) where the basal nodes (but not the flowering nodes) have opposite leaves.

The new species described below provides an interesting example of non-homologous similarity in Leobordea. Schreiber (1970) confused the species with the superficially similar L. stipulosa Bak. f. The many-flowered fascicles of the two species are remarkably similar in appearance due to the presence of large leaflike structures around the base of the inflorescences. In the new species, these are enlarged bracts and not enlarged stipules as in L. stipulosa.

Lotononis bracteosa B-E. van Wyk sp. nov.
L. stipulosa Bak. f. sensu Schreib.: 85 (1970).

L stipulosae Bak. f. valde affinis sed habitu minori, foliis basalibus oppositis (L. stipulosa foliis basalibus alternis), foliolis minoribus, stipularum magnitudine formaque, quae oblongae vel ovatae ad 5 X 3 mm sunt, inflorescentiam non tegentes (in L. stipulosa late cordatae, plerumque valde maiores quam 5 X 3 mm, inflorescentiam tegentes), differt. Stipulae inflorescentiam subtendentes costam unicam, dum illae L. stipulosae venas plures e basi habent. Etiam bracteis 2--4 mm latis, late ellipticis vel obovatis (in L. stipulosa infra 2 mm latis, lanceolatis).

TYPE---Namibia, Outjo district, mountains 14 miles [22,4 km] east of Torra Bay, Giess, Volk & Bleissner 6198 (PRE, holo.; M, PRE, WIND, iso.).

Prostrate or procumbent herbaceous annual, often small and short-lived. All mature parts densely pubescent. Leaves trifoliolate, densely pubescent on both surfaces. Leaflets relatively short, elliptic to oblanceolate, (4--) 6--11 (--16) mm long, (1,5--) 2--4 (--5) mm wide; base cuneate; apex acute. Stipules broadly oblong to ovate, up to 5 mm long and 3 mm wide. Inflorescences sessile, umbellately (2--) 5--8 (--12) -flowered; bracts conspicuous, broadly elliptic to broadly obovate, 3--4 mm long, 2--4 mm wide; apex acute to obtuse, mucronate; base cuneate to cordate. Flowers subsessile, 6--8 mm long. Calyx not inflated, densely pubescent, with the upper and lateral lobe on either side fused higher up in pairs, the lower lobe slightly narrower and shorter; lobes usually broadly acuminate. Standard ovate to oblong, usually shorter than the keel, densely pubescent. Wing petals oblong, not much shorter than the keel, pubescent along the lower edge of the lamina; apex obtuse to acute; sculpturing upper basal and upper left central, in 4 rows of intercostal lunae, fading into thin transcostal lamellae towards the auricle. Keel petals half oblong-elliptic to oblong, densely pubescent; apex obtuse. Pods sessile, scarsely longer than the persistent calyx, broadly obovoid to broadly oblong, only slightly inflated, upper suture ± smooth, ± 8-seeded. Seeds suborbicular, testa minutely and densely tuberculate (Figure 1).

Closely related to *L. stipulosa* Bak. f. but differs in the smaller habit, the smaller leaflets and in the size and shape of the stipules, which are oblong to ovate, up to 5 X 3 mm and not covering the inflorescence (broadly cordate, usually much more than 5 X 3 mm and covering the inflorescences in L. stipulosa). The stipules subtending the inflorescences have a single midrib, while those of L. stipulosa have several veins from the base (Figure 1). It also differs in the 2--4 mm wide, broadly elliptic to obovate bracts (less than 2 mm wide and lanceolate in L. stipulosa). The bracts are visible and conspicuous, not hidden by the large and foliaceous stipules as in L. stipulosa (Figure 1). There is no vegetative phase as in L. stipulosa, where the basal parts of the branches are without inflorescences and the basal leaves alternate. In L. bracteosa, inflorescences are formed at the first nodes (the basal leaves opposite).

L. bracteosa is known only from the north-western parts of Namibia, where it appears to be quite common. Figure 2 shows that L. bracteosa and L. stipulosa are geographically isolated and that the latter does not occur in Namibia.

---1812 (Sanitatas): Kaokoveld, river course 6 miles [9,6 km] south of Orupembe (--BA), Giess & Leippert 7524 (M, NBG, PRE, WIND).

---2013 (Unjab Mouth): Outjo district, mountain 14 miles [22,4 km] east of Torra Bay (--AD), Giess, Volk & Bleissner 6198 (PRE, holotype; M, PRE, WIND, isotypes); 23 km south-east of Torra Bay (--AD), Giess 8020A (WIND); c. 13 miles [20,8 km] east of Torra Bay (--AD), Ihlenfeldt, de Winter & Hardy 3229 (M, PRE); 27 miles [43,2 km] south-east of Torra Bay, at Koichab River (--AD), Nordenstam 3795 (S); Farm Wêreld-End, c. 5 miles [8 km] west of house (--BB), Giess, Volk & Bleissner 6208 (M, WIND); Farm Wêrelds-End, on Petrified Forest to Torra Bay Road, at the coast (--BB), Kers 1513 (WIND); Middle-Huab (--DB), Müller & Loutit 1153 (WIND).

---2014 (Welwitschia): Damaraland, just south of Twyfelfontein (--CA), Craven 989 (WIND); Welwitschia, Gai-as (--CC), Müller & Loutit 1248 (WIND).

---2214 (Swakopmund): Swakopmund district, 22 miles [35,2 km] east of Hentiesbay (--BA), Giess, Volk & Bleissner 5772 (M, WIND).

---2215 (Trekkopje): Swakop River, Welwitschia flat, along the track from Farm Nordenberg to Swakop River at Tsavischab (--CA), Kers 8 (WIND).

---2315 (Rostock): Walvis Bay district, Walvis Bay to Kuisab River to Gamberg Road, 20 miles [32 km] before the Gorob Mine track (--BA), Kers 1287 (WIND); Namib Desert Park, Hotsas (--BA), Müller 224 (M, WIND).

Acknowledgements

Thanks are due to Dr H. F. Glen (Botanical Research Institute, Pretoria) for the Latin translation and the Directors and staff of the cited herbaria for the loan of specimens. The taxonomic study of Lotononis is a registered Ph. D. project at the University of Cape Town.

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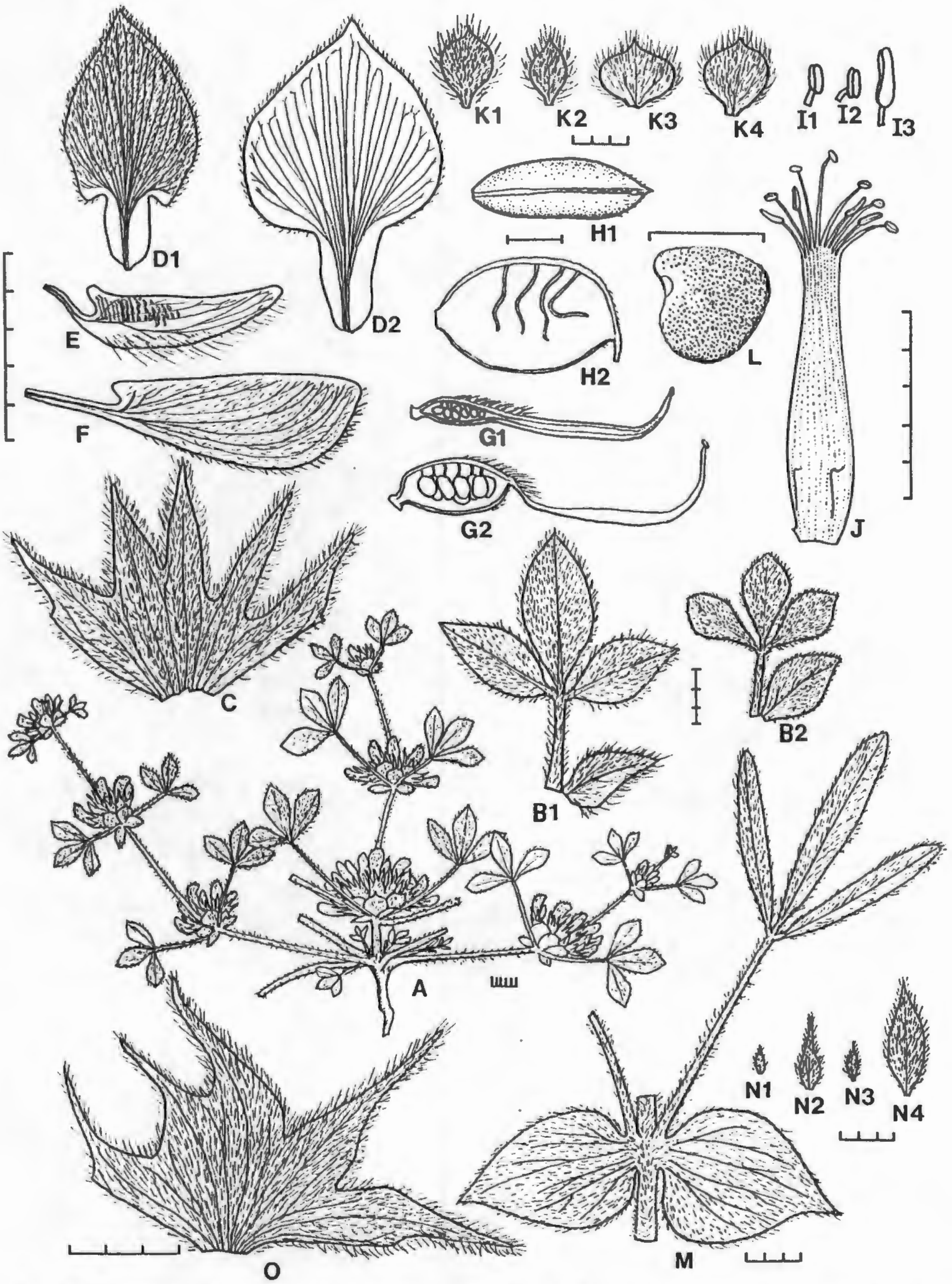

Figure 1. *Lotononis bracteosa*. A, habit; B1 & B2, leaves: B1, abaxial view, B2, adaxial view; C , calyx opened out with the upper lobes to the left; D1 & D2, standard petals: D1, abaxial view showing vestiture, D2, adaxial view; E, wing petal; F, keel petal; G1 & G2, pistils: G1, from young flower, G2, from older flower; H1 & H2, pods: H1, top view, H2, pod after dehiscence as viewed from inside, showing funicles; I1, I2 & I3, anthers: I1, small dorsifixed anther, I2, carinal anther, I3, long basifixed anther; J, androecium; K1 to K4, bracts, showing the broadly ovate shape; L, seed in lateral view showing the densely tuberculate surface. *Lotononis stipulosa*. M, leaf from flowering node showing the foliaceous stipules; N1 to N4, bracts, showing the lanceolate shape; O, calyx opened out with the upper lobes to the left. All from *Giess*, *Volk* & *Bleissner* *5772* except A from *Giess*, *Volk* & *Bleissner* *6198*; B1, D2, G1, G2, T1 & T2 from *Kers* *1513*; M, N4 & O from *Miller* *7748*; N1 from *Davies* *715*; N2 from *Eyles* *2020*; N3 from *Biegel* *2923*. Scales in mm.

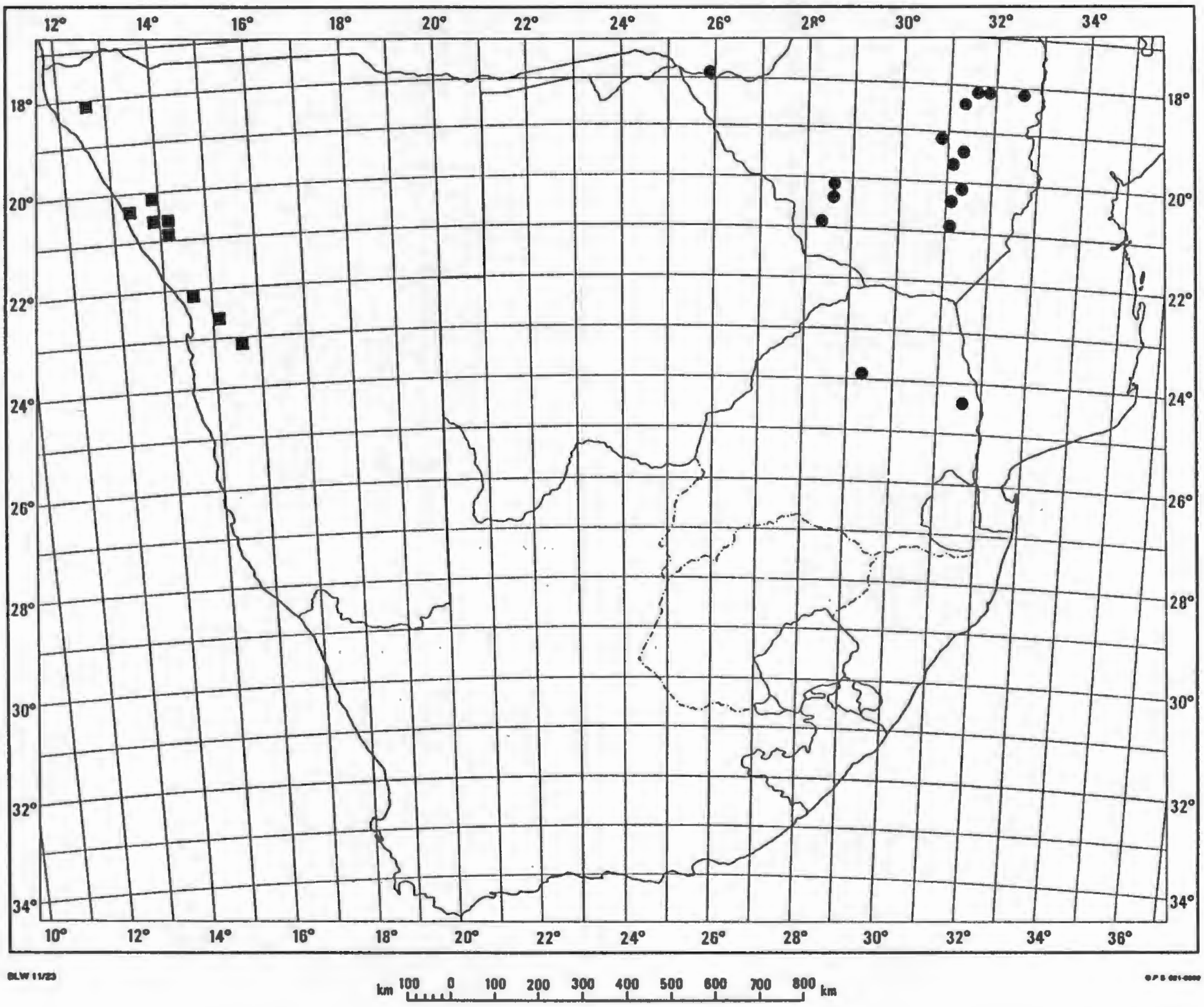

Figure 2. The known geographical distribution of Lotononis bracteosa (■) and L. stipulosa (●).

APPENDIX 31

Studies in the genus *Lotononis* (Crotalarieae, Fabaceae). XII. Four new species of the *L. falcata* group (section *Leptis*)

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Keywords: southern Africa, Fabaceae, *Lotononis* section *Leptis*, new species

ABSTRACT

The taxonomic position of *Lotononis falcata* (E. Mey.) Benth. and related species is briefly discussed. These species were previously included in the section *Leptis* (Eckl. & Zeyh.) Benth. but new information indicates an affinity with the section *Oxydium* Benth. Four new species of this group are described: *L. fruticoides* B-E. van Wyk, *L. pachycarpa* Dinter ex B-E. van Wyk, *L. linearifolia* B-E. van Wyk and *L. schreiberi* B-E. van Wyk. The known geographical distribution and diagnostic characters of the new species are given.

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UITTREKSEL

Die taksonomiese posisie van *Lotononis falcata* (E. Mey.) Benth. en verwante spesies word kortliks bespreek. Hierdie spesies is voorheen ingesluit in die seksie *Leptis* (Eckl. & Zeyh.) Benth. maar nuwe inligting dui op ´n verwantskap met die seksie *Oxydium* Benth. Vier nuwe spesies van hierdie groep word beskryf: *L. fruticoides* B-E. van Wyk, *L. pachycarpa* Dinter ex B-E. van Wyk, *L. linearifolia* B-E. van Wyk en *L. schreiberi* B-E. van Wyk. Die bekende geografiese verspreiding en diagnostiese kenmerke van die nuwe spesies word aangegee.

INTRODUCTION

A study of Lotononis falcata (E. Mey.) Benth. and its allies [previously included in the section Leptis (Eckl. & Zeyh.) Benth.] has shown the presence of four undescribed species. The purpose of this paper is to describe the new species and to show that the L. falcata group is better placed in the section Oxydium Benth. than in Leptis.

The original concept and limits of the genus Leptis Eckl. & Zeyh. were considerably broadened by Bentham (1843) when he included it as a section within Lotononis (DC.) Eckl. & Zeyh. As presently circumscribed (Dümmer 1913), Leptis is undoubtedly an artificial group. It appears to have been used as a convenient position for species that did not seem to fit comfortably elsewhere.

Similarities and differences between the section Oxydium and various groups of the section Leptis are given in Table 1. The L. laxa and L. falcata groups clearly have more in common with Oxydium than with Leptis sensu stricto. This is indicated by chemical similarities as well as the subequally lobed calyx, the basally dilated standard petal, the strongly dimorphic anthers and the keel petals, which are often beaked. In the L. falcata group however, the keel petals are usually not distinctly beaked but all the other characters are typical for Oxydium. The panduriform shape of the standard petal (see Figures 1 to 4) is a useful diagnostic character for the L. falcata group and the annual habit also distinguishes this group from L. laxa and related species.

Lotononis fruticoides B-E. van Wyk sp. nov., L. falcatae valde affinis sed habitu valde robustiore (planta annua fruticiformis 0,3 -- 0,6 m alta), pedunculis longis (L. falcata pedunculis ± absentibus), inflorescentiis plerumque 3-floratis (plerumque 1- vel rarius 2-floratis in L. falcata), foliolis angustioribus acutis, leguminis valde brevioribus, distributione plus orientali differt.

TYPE.---Cape Province, 3224 (Graaff-Reinet): Naudesberg Pass, 39 km from Graaff-Reinet, 31/08/1986, Van Wyk 2020 (PRE, holo.; K, MO, NBG, SAAS, iso.).

Robust annual up to 0,6 m high and wide. Branches divaricate, rigid, sparsely leafy, glabrescent. All mature parts (except the corolla) sparsely and minutely strigillose. Leaves trifoliolate, (6--) 12--25 (--36) mm long; petiole ± half as long as the terminal leaflet; leaflets very narrowly elliptic to linear, (4--) 10--20 (--30) mm long, (0,5--) 1--2 mm wide, sparsely and inconspicuously strigillose on both surfaces. Stipules absent or when very rarely present then single at each node, linear, 1 mm long. Inflorescences leaf-opposed, distinctly pedunculate, umbellately (1--) 3 (--5)-flowered; peduncle short, (3--) 5--10 (--27) mm long; bracts minute, linear, ± 0,5 mm long; bracteoles absent. Flowers 8--10 mm long, yellow; pedicel short, 1--1,5 mm long. Calyx subequally lobed but with the lower lobe narrower than the upper four, the sinuses of equal depth; lobes narrowly triangular, acute. Standard panduriform, as long as the keel; claw much dilated at the base, 2,5--3 mm long, 1--1,5 mm wide at the base, with a small central callosity; lamina 5--7 mm long, 4--5 mm wide, without lobes or callosities, glabrous but with a few minute hairs dorsally along the middle, often with a reddish-brown line along the midrib. Wing petals oblong, slightly shorter than the keel, folded into a long shallow pocket near the base, glabrous; apex rounded; sculpturing indistinct or absent. Keel petals half oblong-elliptic, auriculate, glabrous; apex acute but not beaked. Androecium with the anthers markedly dimorphic; basifixed anthers linear, more than 2x longer than the small ovoid dorsifixed anthers; carinal anther intermediate in size and shape. Gynoecium subsessile; pistil ovoid-oblong, sparsely pubescent; style only slightly curved. Pods subsessile, shortly oblong, 10--14 mm long, 2,5--3,5 mm wide, compressed, glabrous, apex somewhat cuspidate, upper suture ± smooth, ± 6-seeded, the seeds on 1,5--2 mm long funicles. Seeds subtriangular, ± 1,5 mm in diameter; testa pale yellow, often with dark purple marks, densely but minutely tuberculate (Figure 1).

L. fruticoides is closely related to L. falcata, but differs in the much more robust habit (a shrub-like annual of 0,3 -- 0,6 m high), the long peduncles (peduncles ± absent in L. falcata), the predominantly 3-flowered inflorescences (usually 1- or rarely 2-flowered in L. falcata), the narrower and acute leaflets, the much shorter pods and in the more eastern distribution. A form of L. falcata from the Calvinia-Sutherland area is rather similar to L. fruticoides and may be confused with it, but in this form the leaflets are broadly obovate to oblanceolate and the habit totally different. L. fruticoides has been recorded only from the south-eastern regions of the Cape Province, where it appears to be very common (Figure 5). It is highly cyanogenic (Van Wyk 1989), and stock losses reported from the Beaufort West area (Burtt Davy 1912) may be due to this species rather than Dichilus gracilis Eckl. & Zeyh., with which it is often confused. The chromosome number of L. fruticoides (2n = 18) has been reported by Van Wyk & Schutte (1988) and the presence of pyrrolizidine alkaloids by Van Wyk & Verdoorn (1989).

---3125 (Steynsburg): Middelburg division, Bangor Farm (--AC), Bolus s.n. sub BOL 14075 (BOL).

---3222 (Beaufort West): ca. 80 km west of Beaufort West, back of the mountain on farm Ezels Kom, adjoining the farm Layton (--AB), Shearing 1272 (JRAU); Karoo National Park, rocky plateau just above Wagenpad Dam (--AD), Bengis 474 (PRE); Molteno Pass near Beaufort West (--BA), Van Wyk 2137 (JRAU, NBG, PRE); Start of Molteno Pass (--BC), Schutte 219 (GRA, JRAU, K, MO, NBG, PRE),

220 (BOL, GRA, JRAU, PRE, SAAS, STE).

---3223 (Rietbron): Courlands Kloof, Nelspoort (--AA), Pearson 832 (NBG).

---3224 (Graaff-Reinet): Naudesberg Pass, 39 km from Graaff-Reinet (--BA), Van Wyk 2020 (PRE, holotype; JRAU, K, MO, NBG, isotypes), 2021 (GRA, JRAU, PRE, S, SAAS), 2022 (JRAU, NBG, PRE), 2023 (BOL, BLFU, JRAU, STE), 2024 (JRAU, KMG, PRE, STE), 2025 (JRAU, M, NH, WIND), 2026 (JRAU); C. M. van Wyk s.n. (JRAU).

L. pachycarpa Dinter ex B-E. van Wyk sp. nov.

L. pachycarpa Dinter in sched.
Amphinomia curtii (Harms) Schreiber sensu Schreiber: 286 (1957), pro parte.
L. leptoloba H. Bol. sensu Schreiber: 82 (1970).

L. linearifoliae valde affinis sed foliolis oblanceolatis vel obovatis (non linearibus), stipulis valde maioribus, pube patentiore, leguminis ovoideis turgidibus. A L. curtii forma magnitudineque florium, vexilla panduriformi, pedicellis longioribus atque forma leguminum differt. Etiam cum L. leptoloba confusa est, sed species altera pedicellos brevissimos in pedunculis longis (pedicellum longum, pedunculo ± deficiente in L. pachycarpa) et flores omnino dissimiles magnitudine et forma habet. L. leptoloba habet alas valde longiores, vexillam valde maiorem omnino forma dissimilem, legumines oblongos (non ovoideos), et distributionem geographicam dissimilem.

TYPE.---Namibia, 2615 (Lüderitz): Halenberg, 29/08/1929, Dinter 6648 (PRE, holo.; BM, BOL, K, M, SAM, STE, iso.).

Small annual up to 0,1 m high and up to 0,3 m wide. Branches divaricate, slender, sparsely leafy. All mature parts (except the corolla) densely but minutely silky-strigillose. Leaves trifoliolate, (6--) 8--16 (--26) mm long; petiole long or longer than the terminal leaflet; leaflets oblanceolate to obovate, (2--) 4--8 (--14) mm long, (1--) 2--3 mm wide, sparsely silky-strigillose on both surfaces. Stipules single at each node, small, lanceolate, 1--3 (--4) mm long. Inflorescences leaf-opposed, invariably single-flowered; peduncle ± absent, up to 0,5 mm long; bracts very small, linear, up to 1,5 mm long; bracteoles absent. Flowers small, 4,5--7 mm long, yellow; pedicel long and slender, as long or longer than the calyx, up to 10 mm long. Calyx subequally lobed but with the lower lobe a little narrower than the upper four and the lateral sinuses slightly shallower than the upper and lower ones; lobes triangular, acute. Standard broadly panduriform, as long as the keel; claw very short, slightly dilated at the base, 1--2 mm long, ± 1 mm wide, without callosities; lamina 4--5 mm long, 3--4 mm wide, without lobes or callosities, glabrous but with a few hairs dorsally along the middle. Wing petals oblong, slightly shorter than the keel; apex rounded; sculpturing in ± 3 rows of intercostal lunae fading into a few transcostal lamellae towards the auricle. *Keel petals* subtriangular, auriculate, glabrous; apex acute but not beaked. *Androecium* with the anthers markedly dimorphic; basifixed anthers oblong, more than 3x longer than the small ovoid dorsifixed anthers; carinal anther slightly larger than the dorsifixed anthers. *Gynoecium* subsessile; pistil ovoid-oblong, pubescent; style only slightly curved. *Pods* subsessile, small, ovoid, 6--10 mm long, 3--4 mm wide, much inflated laterally, minutely silky-strigillose, apex obtuse, upper suture minutely but distinctly verrucose, 8--15-seeded, the seeds on up to 2 mm long funicles. *Seeds* suborbicular, ± 1,5 mm in diameter; testa brown, densely but minutely tuberculate (Figure 2).

L. pachycarpa is closely related to *L. linearifolia*, but differs in the oblanceolate (not linear) leaflets, the much larger stipules, the more spreading vestiture and the ovoid, turgid pods (Figure 2). From *L. curtii* it differs in the shape and size of the flowers, the panduriform standard petal, the longer pedicels and also in the shape of the pods. It has also been confused with *L. leptoloba* (Schreiber 1970) but the inflorescence structure is only superficially similar (a long pedicel with the peduncle ± absent in *L. pachycarpa*; a short pedicel on a long peduncle in *L. leptoloba*). The flowers are also totally different in size and structure. *L. leptoloba* has much longer wing petals, a much larger and differently shaped standard petal, oblong (not ovoid) pods, and a different geographical distribution. *L. pachycarpa* occurs in southern Namibia (Figure 5), while *L. leptoloba* has been recorded only from the western and north-western parts of the Cape Province.

---2615 (Lüderitz): Halenberg (--DA), *Dinter 4070* (BOL, PRE, SAM), *6648* (PRE, holotype; BM, BOL, K, M, SAM, STE, isotypes).
---2616 (Aus): 12 miles [19,2 km] west of Aus on the way to Lüderitz (--CA), *Giess*, *Volk* & *Bleissner 5462* (PRE, M, MO, WIND).
---2716 (Witputz): 9 km N of Rosh Pinah (--DC), *Merxmüller* & *Giess 28505* (M, WIND).
---2816 (Oranjemund): Namib, west of Obibberge, 14 km S of Obib Wasser (--BA), *Merxmüller* & *Giess 32363* (M).

L. linearifolia B-E. van Wyk sp. nov., *L. pachycarpae* similis sed foliolis gracilibus linearibus, stipulis inconspicuis, pube breviori plus arcte appressa ac leguminis oblongo-linearibus tantum parum inflatis differt. Etiam similis est *L. falcatae*, sed ab illa speciebusque affinibus differt pedicello longo gracili (calyce longiore) ac foliolis anguste linearibus, plus dense sericeo-strigillosis.

TYPE.---Cape Province, 2822 (Glen Lyon): Hay 0.303 [see map in Wilman 1946], 09/07/1936, *Acocks 506* (PRE, holo.; BOL, KMG, PRE, iso.).

Very small annual up to 0,1 m high and 0,25 m wide. Branches procumbent, slender, sparsely leafy. All mature parts (except the corolla) densely but minutely strigillose. Leaves trifoliolate, slender, (12--) 18--28 (--42) mm long; petiole usually very much longer than the terminal leaflet; leaflets very narrowly oblanceolate or usually linear, (4--) 6--14 (--18) mm long, (0,5--) 1--1,2 (--2) mm wide, densely but minutely strigillose on both surfaces. Stipules single at each node, inconspicuous, linear, up to 1 mm long. Inflorescences leaf-opposed, invariably single-flowered; peduncle ± absent, up to 0,5 mm long; bracts very small, linear, up to 1 mm long; bracteoles absent. Flowers small, 4,5--7 mm long, yellow; pedicel long and slender, as long or much longer than the calyx, up to 8 mm long. Calyx subequally lobed but with the lower lobe a little narrower than the upper four and the lateral sinuses slightly shallower than the upper and lower ones; lobes triangular, acute. Standard broadly panduriform, as long as the keel; claw short, slightly dilated at the base, ± 1,5 mm long, ± 1 mm wide, with a central callosity; lamina ± 4,5 mm long, ± 3 mm wide, without lobes or callosities, glabrous but with a few hairs dorsally along the middle. Wing petals oblong, slightly shorter than the keel; apex rounded; sculpturing in ± 3 rows of intercostal lunae fading into a few transcostal lamellae towards the auricle. Keel petals shortly oblong, auriculate, glabrous; apex acute but not beaked. Androecium with the anthers markedly dimorphic; basifixed anthers oblong, more than 3x longer than the small ovoid dorsifixed anthers; carinal anther slightly larger than the dorsifixed anthers. Gynoecium subsessile; pistil oblong, pubescent; style curved upwards. Pods subsessile, oblong to linear, (8--) 10--14 mm long, 2,5--3 mm wide, not inflated laterally, minutely strigillose, apex obtuse, upper suture distinctly and evenly verrucose, 10--15-seeded, the seeds on up to 1,5 mm long funicles. Seeds suborbicular, ± 1,2 mm in diameter; testa brown, densely but minutely tuberculate (Figure 3).

A distinct species, similar to L. pachycarpa but differs in the slender, linear leaflets, the inconspicuous stipules, the shorter and more closely appressed vestiture and the oblong-linear and only slightly inflated pods. It is also similar to L. falcata, but differs from this and related species in the long slender pedicel (much longer than the calyx) and the linear, densely silky-strigillose leaflets (Figure 3).

L. linearifolia was listed as an unidentified species by Wilman (1946, p.52) and the two specimens from Namibia was cited by Schreiber (1970, p.82) as perhaps belonging to L. leptoloba sensu Schreiber (= L. pachycarpa). It is highly cyanogenic (Van Wyk 1989) and, according to notes on the Kinges specimen in M, is said to have caused sheep losses. The only known localities (southern Namibia and the northern Cape) is given in Figure 5, but the species is probably not as rare as the scanty herbarium record would suggest.

---2616 (Aus): Lüderitz district, Farm Weissenborn (--AB), *Kinges 2433* (M); Namib plain between Neisip and Eureka (--AD), *Merxmüller* & *Giess 2876* (M).

---2822 (Glen Lyon): Hay 0.303 [near the Orange River W of Groblershoop, see map in Wilman 1946] (--CD), *Acocks 506* (PRE, holotype; BOL, KMG, PRE, isotypes).

L. schreiberi B-E. van Wyk sp. nov. Species distincta sine affinitatibus manifestis. *L. leptolobae* est superficialiter similis, sed stipulis perpusillis inconspicuis, pedunculo subnullo, vexillo panduriformi (non late cordato) conspicue striato pubescenti, apice acuto (non obtuso) basi dilatato, antheris plus valde dimorphis, leguminis breviter ellipticis (non oblongis) cum ± 12 -- 15 seminibus (non ± 30 seminibus) differt. Etiam *L. falcatae* speciebusque affinibus est similis; sed ab illis speciebus omnibusque sectionis *Oxydii* alis carinisque pubescentibus differt.

TYPE.---Namibia, 2113 (Cape Cross): Cape Cross, about 0,5 km from the coast, 29/04/1965, *Giess 8707* (PRE, holo.; K, M, WIND, iso.).

Small annual up to 0,1 m high and 0,3 m wide. Branches prostrate, divaricate, often densely leafy. All mature parts densely to sparsely pubescent. *Leaves* trifoliolate, variable in size, (7--) 10--20 (--28) mm long; petiole as long or often much longer than the terminal leaflet; leaflets oblanceolate to obovate, (3--)

5--10 (--14) mm long, (2--) 3--5 (--7) mm wide; vestiture very variable, densely to sparsely pubescent on both surfaces, adaxial surface glabrescent and often totally glabrous at maturity. *Stipules* single at each node, minute and inconspicuous, linear, up to 2 mm long. *Inflorescences* leaf-opposed, single-flowered, very rarely with some 2-flowered; peduncle ± absent, up to 0,5 mm long; bracts very small and inconspicuous, linear, up to 1 mm long; bracteoles absent. *Flowers* 9--11 mm long, yellow; pedicel short, 2--3 mm long. *Calyx* subequally lobed; lobes long, very narrowly triangular, acute. *Standard* broadly panduriform, as long as the keel; claw short, slightly dilated at the base, ± 2 mm long, ± 1,5 mm wide, often with an inconspicuous central callosity; lamina 7--9 mm long, 4--5 mm wide, without lobes or callosities, strongly striated, dorsal surface densely pubescent; apex tapering to an acuminate tip. *Wing petals* narrowly oblong, slightly shorter than the keel, distinctly auriculate, pubescent along the lower margin; apex rounded; sculpturing in ± 5 rows of intercostal lunae. *Keel petals* oblong, distinctly auriculate, pubescent along the lower half, strongly striated; apex obtuse. *Androecium* with the anthers markedly dimorphic; basifixed anthers oblong, more than 2x longer than the ovoid dorsifixed anthers; carinal anther slightly larger than the dorsifixed anthers. *Gynoecium* subsessile; pistil oblong, densely pubescent; style long and slender, upper part curved upwards. *Pods* subsessile, shortly oblong, 8--10 mm long, 3--3,5 mm wide, only slightly inflated laterally, pubescent, apex obtuse, upper suture distinctly verrucose, 12--15-seeded, the seeds on up to 1,5 mm long funicles. *Seeds* suborbicular, ± 1,2 mm in diameter; testa brown, densely tuberculate (Figure 4).

This species (named after Dr Annelis Schreiber of the Botanischen Staatssammlung München) was listed as *L. spec.* (no. 18) in the Prodromus einer Flora von Südwestafrika (Schreiber 1970). *L. schreiberi* is a very distinct new species and has no obvious affinities. The relatively large flowers, pubescent and striated petals and single-flowered inflorescences are useful diagnostic characters (Figure 4). It is superficially similar to *L. leptoloba*, but differs in the very small, inconspicuous stipules, the panduriform (not broadly cordate) and conspicuously striated, pubescent standard petal, with an acute (not obtuse) apex and a dilated base, the more markedly dimorphic anthers, the shortly elliptic (not oblong) pods that are ± 12--15-seeded (not ± 30-seeded). It is also superficially similar to *L. falcata* and related species, but differs from these and all other species of the section *Oxydium* in the pubescent wing and keel petals (*L. arenicola* Schltr. is the only species of *Oxydium* with pubescent wing and keel petals but the morphology of this species is totally different). Several collections of *L. schreiberi* have been made in the north-western parts of Namibia, where it appears to be quite common (Figure 5).

---2013 (Unjab Mouth): Skedelkuspark (--AC), Venter 9025 (BLFU); 23 km SE of Torra Bay (--AD), Giess 8020 (M, PRE, WIND); 14 miles [22,4 km] E of Torra Bay (--AD), Giess, Volk & Bleissner 6277 (M, PRE, WIND); 15 miles [24 km] SE of Torra Bay (--AD), Nordenstam 3789 (M).

---2014 (Welwitschia): Welwitsch, Damaraland (--BD), Galpin & Pearson sub Galpin 7547 (PRE, SAM); Koppies S of Ugab River Station (--DD), Müller & Loutit 1096 (M, WIND).

---2113 (Cape Cross): flats a few miles inland on road to Brandberg West Mine (--BD), Oliver & Müller 6660 (PRE, partly); Cape Cross, about 0,5 km from the coast (--DD), Giess 8707 (PRE, holotype; K, M, WIND, isotypes).

---2114 (Uis): S of the Messumberge ca. 12 miles [19,2 km] E of the coast (--BA), Giess 3576 (PRE, WIND).

---2214 (Swakopmund): track from Goanicontes to Rossing Mountain (--DB), Kers 1311 (WIND).

---2215 (Trekkopje): Farm Nordenberg, Swakop River at Tsavischab (--CA), Kers 4 (WIND); Swakop River, along the track from Swakop at Tsavischab to Farm Nordenberg and Karibib (--CA), Kers 1532 (WIND).

---2315 (Rostock): Kuiseb River, SE of Hope Mine, on the Namib plain between Hope Mine and Garob Mine (--CB), Kers 1580, 1586 (WIND).

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APPENDIX 32

Studies in the genus *Lotononis* (Crotalarieae, Fabaceae). XIII. Two new species and notes on the occurrence of cleistogamy in the section *Leptis*

B-E. VAN WYK*

Keywords: cleistogamy, Fabaceae, flower dimorphism, *Lotononis* section *Leptis*, new species

ABSTRACT

The occurrence of flower dimorphism in the genus *Lotononis* (DC.) Eckl. & Zeyh. is reported for the first time. Cleistogamous flowers have been observed in 12 species from four different groups of the sections *Leptis* (Eckl. & Zeyh.) Benth. and *Oxydium* Benth. Morphological differences between chasmogamous and cleistogamous flowers are discussed and illustrated. The phenomenon of flower dimorphism appears to be of limited taxonomic value but nevertheless supports the idea of an affinity between the *L. laxa*, *L. pungens* and *L. leptoloba* groups. Two recently discovered new species of the *L. leptoloba* and *L. calycina* groups, *L. venosa* B-E. van Wyk and *L. acuticarpa* B-E. van Wyk, are described.

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UITTREKSEL

Die voorkoms van blomdimorfisme in die genus *Lotononis* (DC.) Eckl. & Zeyh. word vir die eerste keer gerapporteer. Kleistogame blomme is waargeneem by 12 spesies van vier verskillende groepe van die seksies *Leptis* (Eckl. & Zeyh.) Benth. en *Oxydium* Benth. Morfologiese verskille tussen chasmogame en kleistogame blomme word bespreek en geïllustreer. Die verskynsel van blomdimorfisme is skynbaar van beperkte taksonomiese waarde maar ondersteun nietemin die idee van ´n verwantskap tussen die *L. laxa*-, *L. pungens*- en *L. leptoloba*-groepe. Twee nuwe spesies van die *L. leptoloba*- en *L. calycina*-groepe wat onlangs ontdek is, *L. venosa* B-E. van Wyk en *L. acuticarpa* B-E. van Wyk, word beskryf.

INTRODUCTION

The occurrence of flower dimorphism in the genus *Lotononis* (DC.) Eckl. & Zeyh. is here reported for the first time. Morphological diffentiation between chasmogamous and cleistogamous flowers appears to be restricted to the sections *Leptis* (Eckl. & Zeyh.) Benth. and *Oxydium* Benth. As presently circumscribed (Bentham 1843, Dümmer 1913), *Leptis* was recently shown to be an artificial group and it was suggested that some species will be much better placed in *Oxydium* (Van Wyk 1989). The taxonomic value of cleistogamy is briefly discussed and two recently discovered new species of *Leptis sensu lato* are described below.

Cleistogamy has been reported from several genera of the Fabaceae (Uphof 1938, Arroya 1981). Precocious bud pollination, with little or no effect on flower morphology, is known to occur in *Lotononis bainesii* Bak.f. (Byth 1964) and in the genus *Dichilus* DC. (Schutte 1988) and may be more common in the Crotalarieae than was previously recognised. Morphological differentiation between cleistogamous and non-cleistogamous flowers of the same species however, is less common (Arroyo 1981). Flower dimorphism in the genus *Argyrolobium* Eckl. & Zeyh. was discussed in detail by Harms (1909, 1917) but no reports for other genera of the tribe Crotalarieae could be found.

FLOWER DIMORPHISM IN *LOTONONIS*

Dimorphic flowers were observed in 12 species of the sections *Leptis* and *Oxydium* (Table 1). Unlike precocious bud-pollination, which is difficult to observe (and which probably occurs in many species of *Lotononis*), flower dimorphism is readily detected in herbarium material.

Bud-cleistogamy in the species listed in Table 1 results in a marked reduction in the size of the corolla, androecium and style but has only a slight effect on the calyx. The corolla does not open but is usually pushed out of the calyx by the developing ovary. Figure 1 shows a typical example of flower dimorphism in *Lotononis* - the two flowers illustrated are from different branches of a single plant. It is also possible to recognise (by the remains of the style) those pods which were formed from cleistogamous flowers. The size and shape of the pods and the number of seeds are apparently not affected, but the old stylar tissue is short and hooked, often with one or more anthers adhering to the stigma. Scanning electron microscope studies have shown that pollen tubes grow right through the anther wall and into the stigma, thereby firmly attaching the anther to the stigma. Cleistogamy in *Lotononis* seems identical to that described in species of *Lespedeza* Mich. (Hanson & Cope 1955) and in *Ornithopus* L. (Wojciechowska 1972).

It is obvious that the 12 species listed in Table 1 are only facultatively cleistogamic and that they show no particular adaptation towards cleistogamy. The presence of petal sculpturing for example, indicates that the normal development of the flower bud is arrested at a relatively late stage of development. Furthermore, the co-occurrence of both flower forms at the same locality (and even on a single specimen) shows that cleistogamy is not a permanent condition. It is nevertheless significant that there is a clear difference between cleistogamous and non-cleistogamous flowers -- intermediate stages are rare or absent. Many factors are known to cause cleistogamy (Uphof 1938, Erickson 1975) and it may be worthwhile to gain experimental evidence for the mechanisms that influence cleistogamy in Lotononis. Personal observations have indicated that it is a seasonal phenomenon (at least in L. laxa) and that it may be induced by unfavourable climatic conditions.

Cleistogamy is generally considered to have limited value as a taxonomic character because of its variability and the likelyhood of convergence (Uphof 1938). In the genus Lotononis, it has indeed led to taxonomic errors, such as a confusion between L. calycina (E. Mey.) Benth. and cleistogamous forms of L. tenella (Harvey 1862). The former is not cleistogamous but the very short corolla results in a superficial similarity with L. tenella. Early bud-cleis=

togamy (i.e. that which leads to dimorphic flowers) does not appear to be randomly distributed in *Lotononis*. A direct relationship between the section *Oxydium* and some groups of the section *Leptis* is indicated, and other characters were shown to support this idea (Van Wyk, 1989). Paradoxically, most of the species with dimorphic flowers have acute or beaked keel petals, a character that is more readily associated with outcrossing because it promotes an increased efficiency in the transfer of pollen. This remarkable versatility may partly explain why *L. laxa* and *L. tenella* have a wider geographical distribution than most other perennial species of *Lotononis*.

The two new species described below clearly illustrates that cleistogamy has limited value as a taxonomic character. *L. venosa* B-E. van Wyk is apparantly not cleistogamic but is here placed in the *L. leptoloba* group (see Table 1), while *L. acuticarpa* B-E. van Wyk is the only species of the *L. calycina* group known to display at least some degree of flower dimorphism.

Lotononis venosa B-E. van Wyk sp. nov., *L. leptolobae* H. Bol. affinis sed habitu minore foliosiore, foliis anguste oblongis vel linearibus (in *L. leptoloba* obovatis) stipulis geminis disperse dispositis (in *L. leptoloba* semper singularis), floribus leguminibusque valde maioribus differt.

TYPE.--- Cape Province, 3220 (Sutherland): De Hoop in Klein Roggeveld, 06/09/1986, Oliver 8965 (PRE, holo.; STE, iso.).

Small prostrate annual up to 0,2 m wide. Branches densely leafy; twigs sparsely pilose with long spreading hairs. Leaves digitately trifoliolate, very variable in size, sparsely pilose with long spreading hairs; petioles slightly winged, ± as long as the terminal leaflet or longer, (2--) 3--7 (--16) mm long; leaflets narrowly oblong to linear, (2--) 5--12 (--14) mm long, (0,5--) 1--2 (--2,5) mm wide, abaxially sparsely pilose, adaxially glabrescent. Stipules large, consistently present, single at each node or rarely paired at some nodes, oblong to narrowly oblong and often slightly falcate, similar to the leaflets or much larger, (2--) 6--12 (--14) mm long, (0,5--) 1,5--2,5 (--3,5) mm wide. Inflorescences subterminal and leaf-opposed towards the branch ends, invariably single-flowered; peduncle usually ± as long as the calyx, (3--) 6--8 (--12) mm long; bracts relatively large, narrowly linear, 5--8 mm long; bracteoles absent. Flowers large, 16--20 mm long, pale yellow with grey veination; pedicel short, ± 2 mm long. Calyx almost as long as the corolla, equally lobed, sparsely pilose; lobes very long and slender. Standard very large, broadly ovate; claw 4--5 mm long, very slightly dilated at the base, dilated part up to 1,8 mm wide; lamina acute, cordate at the base, 13--15 mm long, 13--16 mm wide, glabrous but with a line of hairs dorsally along the middle. Wing petals oblong, much longer than the keel, glabrous, apex obliquely truncate; sculpturing in 4--5 rows of thin transcostal lunae and lamellae. Keel petals small, semi-circular, acute but not beaked, auriculate and pocketed near the base, glabrous. Anthers dimorphic, basifixed anthers ± 2x longer than the dorsifixed anthers, carinal anther similar to dorsifixed anthers. Pistil 11--13 mm long; ovary oblong, ± 6 mm long, densely pubescent; style sharply curved. Immature pods oblong, slightly turgid, longer than the calyx, up to 18 mm long, ± 5 mm wide, ± 30-seeded, upper suture distinctly verrucose, sparsely pilose; funicles up to 2 mm long. Seed unknown (Figure 2).

L. venosa is a distinct species known only from two recent collections in the Roggeveld area (Figure 4). The annual habit, general morphology, inflorescence structure and flower morphology is very similar to that of L. leptoloba. Although there is no evidence of cleistogamy in this species and mature pods are unknown, it is placed in the affinity of L. leptoloba with some confidence. The flowers turn from yellow to a bluish colour when dried and the species may therefore be mistaken for L. maximiliani Schltr., but the shape of the leaflets and the very large flowers (Figure 2) are quite distinct.

---3119 (Calvinia): c. 3,6 km from the farm Blomfontein to De Hoop (--DD), 13/09/1986, Schutte 259 (JRAU).

---3220 (Sutherland): De Hoop in Klein Roggeveld (--DC), 06/09/1986, *Oliver 8965* (PRE, holotype; STE, isotype).

Lotononis acuticarpa B-E. van Wyk sp. nov., *L. calycinae* similis sed habitu foliisque minore, floribus valde minoribus angustioribus, praesertim forma magnitudineque fructus differt. Fructus valde longiores sunt calyce (calycem aequantes in *L. calycina*), plani (non turgidi ut in *L. calycina*) et apices sunt acuti sursum curvati (non obtusi deorsum curvati ut in *L. calycina*). Etiam similis est *L.* adpressae N.E. Br. sed ab illa specie habitu minori annuale, superficie adaxiali glabro foliolum et fructu valde longiori acutiori subfalcato differt.

TYPE.---Transvaal, 2628 (Johannesburg): Springs district, 5 km from Devon radar station to Leandra (--BD), 20/02/1986, *Van Wyk 1815* (PRE, holo.; JRAU, K, MO, NBG, iso.).

Small procumbent annual up to 0,1 m high and 0,2 m wide. *Branches* slender, spreading from a very short main axis; twigs sparsely pilose. *Leaves* digitately trifoliolate, sparsely pubescent, variable in size, those on the main axis with long and slender petioles, those of lateral twigs with the petiole 3--6 (--8) mm long; leaflets oblanceolate to elliptic, (3--) 5--10 (--14) mm long, (1--) 2--2,5 (--3) mm wide, abaxially sparsely pubescent, adaxially glabrous.

Stipules consistently present, single at each node, oblanceolate to elliptic, 2--4 mm long. Inflorescences leaf-opposed at each node, fasciculate, 1--3-flowered; peduncle very short or absent; bracts small, up to 2,5 mm long, often inserted slightly above the pedicel base; bracteoles absent. Flowers very small, narrow, 6--7 mm long, yellow; pedicel short, up to 2 mm long. Calyx almost as long as the corolla, with the lateral lobes on either side fused much higher up in pairs, sparsely pubescent; lobes long and slender. Standard oblong-ovate, 6--7 mm long; claw 1,5--2 mm long; lamina acute, densely pubescent on the dorsal surface. Wing petals narrowly oblong, slightly shorter than the keel, pubescent towards the rounded apex; sculpturing in 3--4 rows of transcostal lunae fading into a few transcostal lamellae towards the auricle. Keel petals oblong, obtuse, auriculate and pocketed near the base, pubescent along the lower edge of the lamina. Anthers dimorphic, basifixed anthers more than 2x longer than the dorsifixed anthers, carinal anther intermediate in size. Pistil 5--6 mm long; ovary oblong, ± 3 mm long, densely pubescent; style short, almost straight. Pods oblong, compressed, slightly falcate, ± twice as long as the calyx, 8--12 mm long, 2--3,5 mm wide, gradually tapering to the acute apex, ± 6-seeded, upper suture ± smooth, indehiscent or tardily dehiscent, inconspicuously pubescent. Seed suborbicular in side view, up to 1,8 mm long; funicles up to 2 mm long; testa brown, often yellowish brown mottled with black, distinctly tuberculate (Figure 3). Chromosome number: 2n = 18!

L. acuticarpa is similar to L. calycina (E. Mey.) Benth. but differs in the smaller habit and leaves, the much smaller and narrower flowers and particularly in the shape and size of the fruit. The fruit are much longer than the calyx (as long as the calyx in L. calycina), flat (not turgid as in L. calycina) and the apices are acute and curved upwards (not obtuse and curved downwards as in L. calycina). It is also similar to L. adpressa N. E. Br. but differs from this species in the smaller and annual habit, the glabrous adaxial surface of the leaflets and in the much longer, more acute and slightly falcate fruit.

It is remarkable that this distinct species has escaped the notice of plant collectors for so long. L. acuticarpa was only recently collected for the first time and is now known from three different localities in the south-eastern Transvaal (Figure 4). It appears to be restricted to well-drained stony soils and is locally abundant, at least at the type locality.

TRANSVAAL.---2628 (Johannesburg): Springs district, 5 km from Devon radar station to Leandra (--BD), 20/02/1986, Van Wyk 1815 (PRE, holotype; JRAU, K, MO, NBG, isotypes), 22/02/1987, Van Wyk 2625 (M, NH, S, STE).

---2630 (Carolina): Mbabane, Kalkoenkranz, Goedemoed farm (--CC), 15/03/1987, Turner 1468 (PRE).

---2729 (Volksrust): Frankfort, Amersfoort, Bergvliet farm (--BB), 01/04/1987, Turner 1624 (PRE).

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Table 1. Flower dimorphism in various groups of the sections *Leptis* and *Oxydium*. The occurrence, observed frequency and degree of differentiation is indicated.

GROUPS AND SPECIES	FREQUENCY	DEGREE OF DIFFERENTIATION
section *Oxydium* Benth.		
L. sparsiflora (E. Mey.) B-E. van Wyk	rare	slight
L. micrantha Eckl. & Zeyh.	rare	slight
section *Leptis* (Eckl. & Zeyh.) Benth.		
L. calycina group		
L. acuticarpa B-E. van Wyk	rare	slight
L. leptoloba group		
L. leptoloba H. Bol.	common	distinct
L. maximiliani Schltr.	common	distinct
L. tenella group		
L. tenella (E. Mey.) Eckl. & Zeyh.	very common	distinct
L. pungens Eckl. & Zeyh.	very common	distinct
L. laxa group		
L. laxa Eckl. & Zeyh.	common	distinct
L. macrosepala Conr.	very common	distinct
L. crumanina Burch. ex Benth.	very common	slight
L. burchellii Benth.	very common	slight
L. maculata Dummer	very common	slight

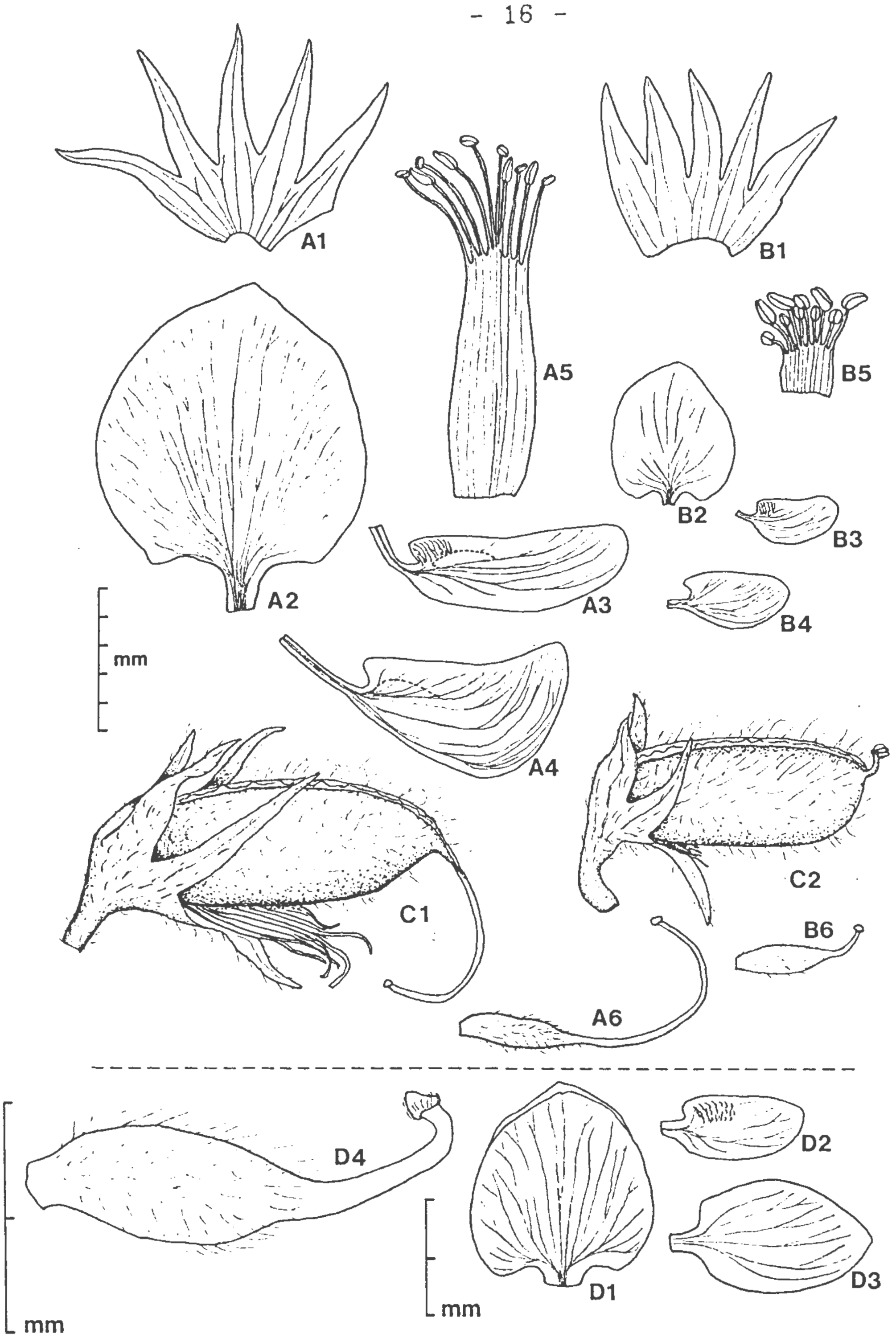

Figure 1. Flower and fruit dimorphism in *Lotononis pungens*. Morphological differences between flowers and pods taken from the same individual (*Van Wyk 1626b*, JRAU)) are shown above, and details of a cleistogamous flower from *Schutte 215* (JRAU) below. A1 to A6, chasmogamous flower: A1, calyx opened out with upper lobes to the left; A2, standard petal; A3, wing petal; A4, keel petal; A5, androecium; A6, pistil. B1 to B6, cleistogamous flower: B1, calyx; B2, standard petal; B3, wing petal; B4, keel petal; B5, androecium; B6, pistil. C1 & C2, pods: C1, pod formed from a chasmogamous flower, C2, pod formed from a cleistogamous flower (note the small hooked stylar tissue and the anthers adhering to the stigma). D1 to D4, cleistogamous flower: D1, standard petal; D2, wing petal (note sculpturing); D3, keel petal; D4, pistil.

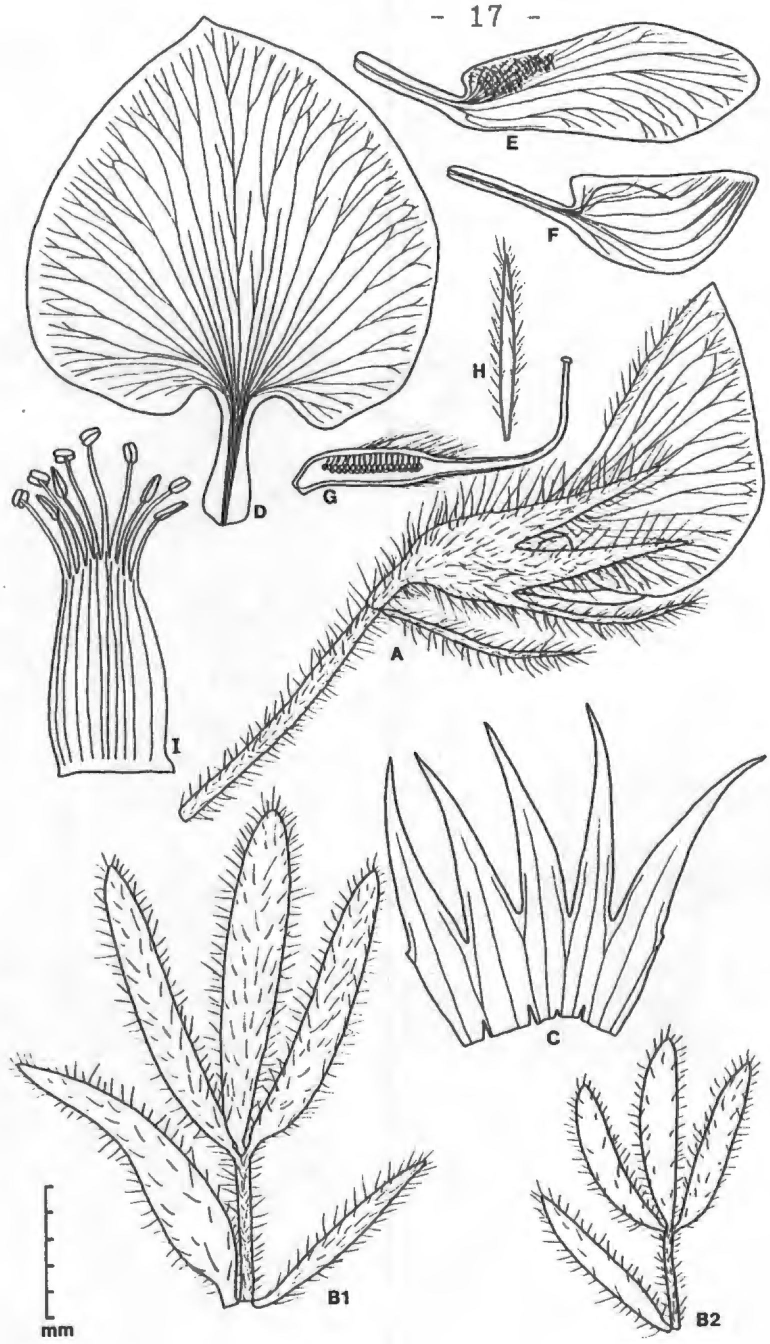

Figure 2. Lotononis venosa. A, flower in lateral view showing the long peduncle and the vestiture of the calyx and standard petal; B1 & B2, leaves in adaxial view, showing paired stipules (B1) and a single stipule (B2); C, calyx opened out, upper lobes to the left (vestiture not shown); D, standard petal; E, wing petal; F, keel petal; G, pistil; H, bract; I, androecium. (All from Oliver 8965).

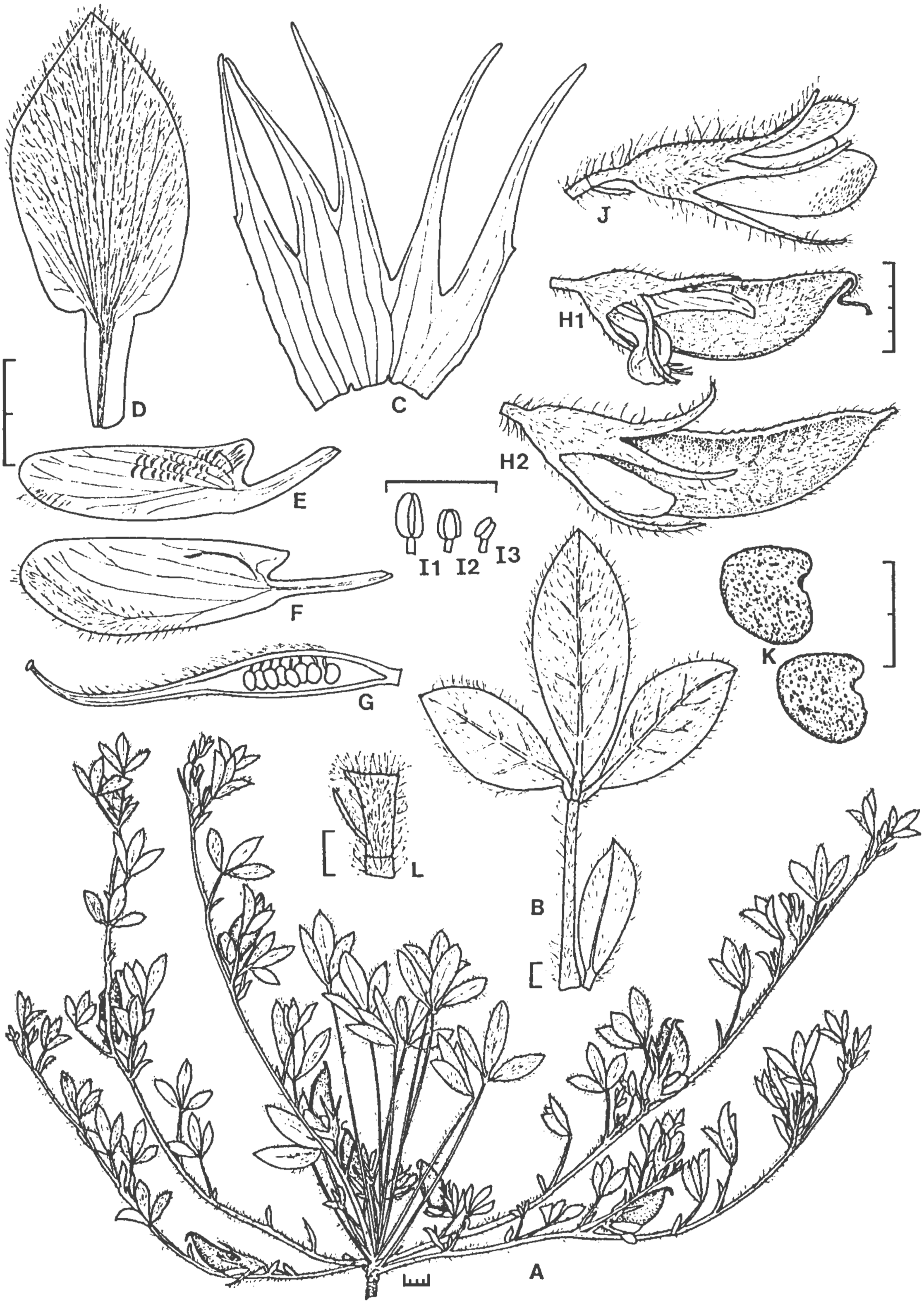

Figure 3. Lotononis acuticarpa. A, habit; B, leaf in abaxial view; C, calyx opened out, upper lobes to the left, showing the fusion of the lateral lobes (vestiture not shown); D, standard petal; E, wing petal; F, keel petal; G, pistil; H1 & H2, mature fruit in lateral view (note the size, shape and also the pointed, tapering apices); I1, I2 & I3, anthers: I1, basifixed anther, I2, carinal anther, I3, dorsifixed anther; J, flower in lateral view; K, seeds in lateral view, showing tuberculate surfaces; L, peduncle with pedicel and bract. (All from Van Wyk 1815). Scales in mm.

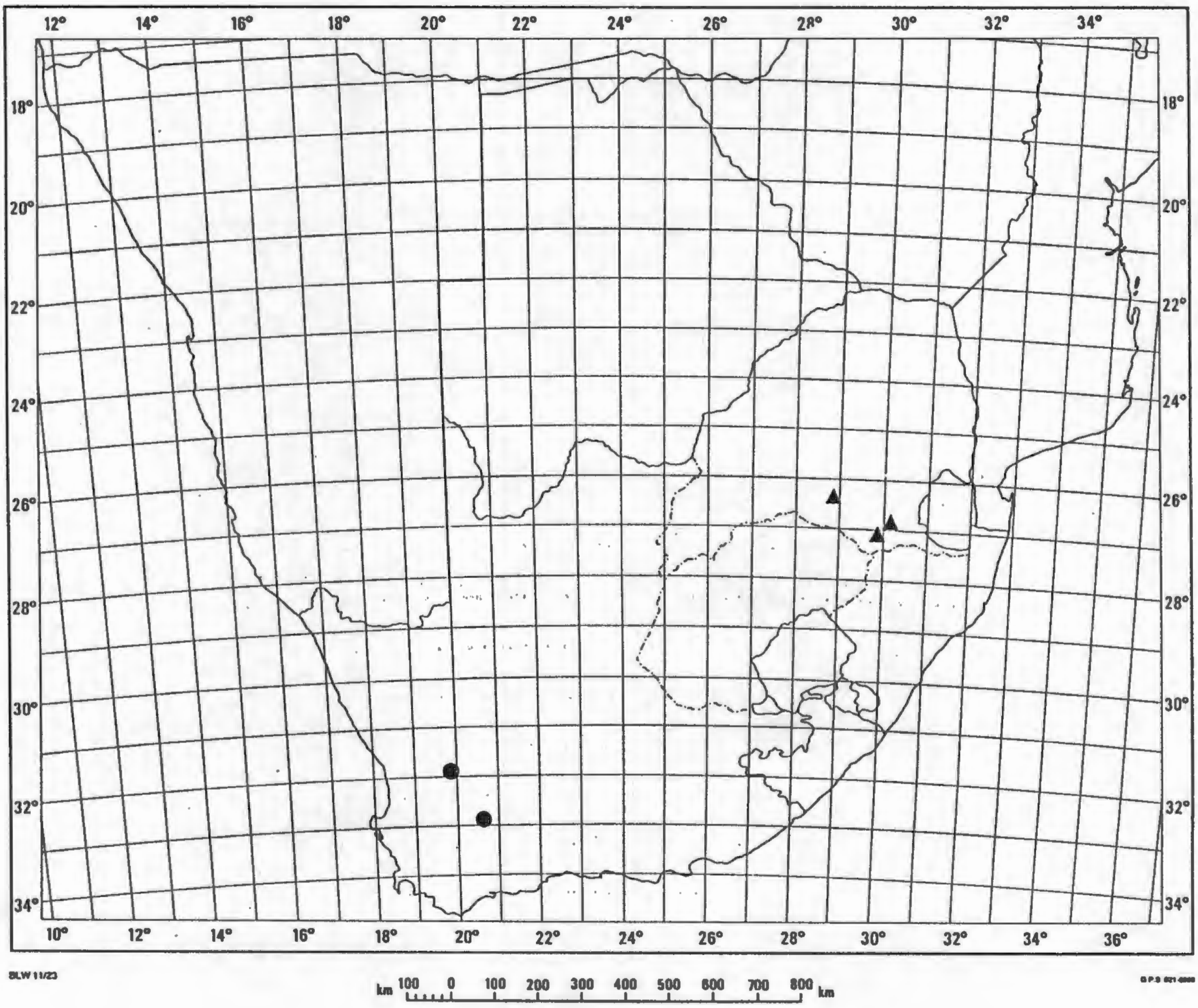

Figure 4. The known geographical distribution of Lotononis venosa (●) and L. acuticarpa (▲).

APPENDIX 33

Studies in the genus Lotononis (Crotalarieae, Fabaceae). XIV. Three new species of the sections Telina and Polylobium

B-E. VAN WYK*

Keywords: southern Africa, Lotononis, Fabaceae, new taxa

ABSTRACT

As part of final preparations for a synoptic revision of the genus Lotononis (DC.) Eckl. & Zeyh., another three new species are described: L. filiformis B-E. van Wyk and L. complanata B-E. van Wyk of the section Telina (E. Mey.) Benth. and L. subulata B-E. van Wyk of the section Polylobium (Eckl. & Zeyh.) Benth.

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UITTREKSEL

As deel van finale voorbereidings vir ´n sinoptiese hersiening van die genus *Lotononis* (DC.) Eckl. & Zeyh. word nog drie nuwe spesies beskryf: *L. filiformis* B-E. van Wyk en *L. complanata* B-E. van Wyk van die seksie *Telina* (E. Mey.) Benth. en *L. subulata* B-E. van Wyk van die seksie *Polylobium* (Eckl. & Zeyh.) Benth.

INTRODUCTION

As part of preparatory studies for a synoptic revision of *Lotononis* (DC.) Eckl. & Zeyh., several new species have been described in previous parts of this series. The section *Telina* (E. Mey.) Benth. and the *L. angolensis* group of the section *Polylobium* (Eckl. & Zeyh.) Benth. were treated in parts 2 and 3 respectively (Van Wyk 1988, 1989). Recent studies however, have shown the presence of another two new species of *Telina* and one new species of the *L. angolensis* group. These are described below.

Section *Telina* (E. Mey.) Benth.

Lotononis filiformis B-E. van Wyk sp. nov. *L. azureae* Eckl. & Zeyh. valde affinis sed habitu longissimo gracili sparsim ramoso, foliolis gracilibus linearibus, lobis calycis oblongis (non triangularibus), fructu minore angustiori et praesertim pube minute strigillosa ramulorum foliorum calycis fructusque (sparsim pilosa in *L. azurea*) differt.

TYPE.---Cape, 3321 (Ladismith): Northern slopes of Outeniqua mountains, between farms Bonniedale and Woeska (--DD), 14/10/1988, *Vlok 2030* (PRE, holo.; JRAU, K, MO, NBG, SAAS, STE, iso.).

Very sparse perennial herb, up to 1 m wide. *Branches* long, slender, sparsely leafy, glabrescent, reddish-brown; twigs minutely strigillose. *Leaves* digitately trifoliolate; petiole (4--) 7--14 (--22) mm long; leaflets linear, thick in texture, (4--) 8--22 (--26) mm long, (0,5--) 1--1,5 (--2) mm wide, inconspicuously strigillose on both surfaces. *Stipules* consistently present, single or paired at each node, narrowly lanceolate, (2--) 4--8 (--10) mm long. *Inflorescences* leaf-opposed, slender, long-pedunculate, 25--120 mm long, invariably single-flowered; bracts small, up to 1,5 mm long; bracteoles absent. *Flowers* relatively large, 8--12 mm long, blue; pedicel 3--8 mm long. *Calyx* 8--10 mm long, subequally lobed, minutely strigillose; lobes narrowly oblong. *Standard* broadly ovate to suborbicular, 7--12 mm long, minutely pubescent on the middle part of the dorsal surface, deep blue with yellow at the base. *Wing petals* oblong, longer that the keel; apex rounded; sculpturing in 2--3 rows of mostly transcostal lunae and lamellae. *Keel petals* semicircular, obtuse, auriculate and pocketed near the base. *Anthers* dimorphic. *Pistil* 9--11 mm long; ovary linear, 6--9 mm long, pubescent; style erect. *Pods* narrowly oblong, 14--20 mm long, 3--4 mm wide, laterally much inflated, ± 5--8-seeded, minutely strigillose, lower suture sunken, upper suture verrucose, dehiscent. *Seed* suborbicular, ± 2 mm in diameter; testa reddish brown, dark brown or almost black, densely tuberculate; funicles up to 1,2 mm long (Figure 1).

L. filiformis is very closely related to *L. azurea* Eckl. & Zeyh. but differs in the very long, slender and sparsely branched habit, the slender linear leaflets, the oblong (not triangular) calyx lobes, the smaller narrower fruit and particularly in the minutely strigillose vestiture of the twigs, leaves, calyx and fruit (not sparsely pilose as in *L. azurea*). It is also geographically isolated from the latter and has a more western distribution, known only from the northern slopes of the Outeniqua Mountains (Figure 4). The narrow calyx lobes are very similar to those of *L. azurea* var. *lanceolata* Harv. (based on *Ononis villosa* Thunb.), with which *L. filiformis* has previously been confused (Figure 1). I have examined the Thunberg type specimen of *Ononis villosa*, but the long, sparse and spreading hairs of the latter is very different from the dense and minutely strigillose vestiture of *L. filiformis*.

I am much indebted to Mr J. H. J. Vlok of Saasveld, George for the opportunity to study the species *in situ*. The almost climbing habit is quite unlike that of any other species of *Lotononis* - the long, slender branches are supported by the surrounding vegetation and when not in flower, the plants are almost invisible.

CAPE.---3321 (Ladismith): Mossel Bay Division, Vryers Berg (--DC), *Muir 2042* (BOL); Northern slopes of Outeniqua mountains, between farms Bonniedale and Woeska (--DD), *Vlok 2030* (PRE, holotype; JRAU, K, MO, NBG, SAAS, STE, isotypes). ---3322 (Oudtshoorn): Oudtshoorn district, Moeras River between Oudtshoorn and Robinson´s Pass (--CC), *Bolus 11767* (BOL, GRA); lower northern slopes of the Outeniqua mountains, near Zebrafontein in Doornrivier Wilderness area (--CC), *Van Wyk 2857* (JRAU, K, MO, NBG, PRE, STE); 4,2 miles [6,72 km] WNW of Camfer Station (--CD), *Acocks 23250* (STE).

Lotononis complanata B-E. van Wyk, sp. nov., *L. variae* (E. Mey.) Benth. similis sed habitu foliisque minore, apicibus foliolum recurvatis, stipulis singularibus (plerumque geminis in quoque nodo in *L. varia*), pube foliorum plus dense strigillosa (foliis ± glabris in *L. varia*), inflorescentiis semper unifloratis (saepe 2- vel pluri-floratis in *L. varia*), floribus minoris et praesertim fructu breve oblongo compresso indehiscenti (longiore valde inflato dehiscenti in *L. varia* et speciebus omniis aliis sectionis *Telinae*). Fructus sunt etiam multiseminatis, cum ad 30 seminis per legumen (± 6 -- 12 -seminatis in speciebus aliis), et funiculi sunt usque ad 4 mm longi (usque ad 2 mm in speciebus aliis).

TYPE.---Cape, 3319 (Worcester): Riebeeck-Wes, on Elandsberg nature reserve (--AC), 15/06/1988, Vlok 1941 (PRE, holo.; K, NBG, iso.).

Dwarf suffrutescent perennial up to 0,1 m high and 0,2 m wide. Branches slender, procumbent from a thick central rootstock; young twigs densely strigillose. Leaves digitately trifoliolate, relatively small, sparsely pubescent, variable in size, those on the main axis with long and slender petioles, those of lateral twigs with the petiole (4--) 6--15 (--22) mm long; leaflets narrowly to broadly oblanceolate, variable in length, (2--) 4--10 (--15) mm long, (1--) 2--3 (--3,5) mm wide, adaxial surface glabrous, abaxial surface minutely pubescent; apex acute, recurved. Stipules invariably single at each node, small, narrowly lanceolate, up to 3 mm long. Inflorescences subterminal or leaf-opposed on short lateral branches, invariably single-flowered; peduncle slender, variable in length, (16--45) mm long; bract small, oblong, up to 1 mm long; bracteoles absent. Flowers relatively small, 8--12 mm long, blue; pedicel short, 1--2 mm long. Calyx 5--7 mm long, subequally lobed, minutely pubescent; lobes narrowly triangular. Standard large, suborbicular, 7--11 mm long, with a line of minute hairs dorsally along the middle. Wing petals longer than the keel, oblanceolate; apex obliquely obtuse; sculpturing in 3--4 rows of mostly intercostal lunae and lamellae. Keel petals semicircular, somewhat acute, auriculate and pocketed near base. *Anthers* dimorphic. *Pistil* short; ovary oblong, ca. 7 mm long, minutely pubescent; style short, erect. *Pods* very broadly oblong, 10--21 mm long, 5--7 (--8) mm wide, compressed, indehiscent, minutely pubescent, apex broad and rounded, ± 6--30-seeded, upper suture very conspicuously verrucose. *Seed* kidney-shaped, ± 1,5 mm in diameter, on very long funicles; funicles up to 4 mm long; testa brown, densely tuberculate (Figure 2).

This species is similar to *L. varia* (E. Mey.) Benth. but differs in the smaller habit and leaves, the recurved leaflet apices, the single stipules (usually paired at each node in *L. varia*), the more densely strigillose vestiture of the leaves (± glabrous in *L. varia*), the invariably single-flowered inflorescences (often 2- or more-flowered in *L. varia*), the smaller flowers and particularly in the shortly oblong, compressed and indehiscent fruit (longer, laterally much inflated and dehiscent in *L. varia* and in all other species of the section *Telina*). Differences between the two species are shown in Figure 2. The shape of the pods ["complanatus" = flattened out] is very unusual for the section *Telina* and the tooth-like projections along the upper suture is more strongly developed than in most if not all other species of *Lotononis*. The large number of seeds per pod and the very long funicles are also unique features not found in other species of the section *Telina*.

Only a single collection (without precise locality details) was known prior to the discovery of the species on the Elandsberg nature reserve (Figure 4). This discovery is another example of the valuable contributions Mr J. H. J. Vlok has made to the phytogeography of rare Cape legumes. *L. complanata* is known only from one population and it may be worthwhile to assess the population structure from time to time.

CAPE.---3319 (Worcester): Riebeeck-Wes, on Elandsberg nature reserve (--AC), 15/06/1988, *Vlok 1941* (PRE, holotype; K, NBG, SAAS, isotypes), 07/10/1988, *Van Wyk 2879* (BOL, GRA, JRAU, K, MO, NBG, PRE, S, SAAS, STE).
---Without precise locality, *Bowie s.n.* (BM, K).

Section *Polylobium* (Eckl. & Zeyh.) Benth. (*L. angolensis* group)

Lotononis subulata B-E. van Wyk sp. nov. *L. bainesii* Bak. f., *L. listii* Polhill et *L. marlothii* Engl. valde affinis. A *L. bainesii* lobis calycis longis angustis (non late triangularibus), racemis sparsim paucifloris (non subumbellate multifloris) et fructu semper plicato (rare tantum plicato in *L. bainesii*) differt. A *L. listii* lobis calycis longis angustis (late triangularibus in *L. listii*, inflorescentiis usque ad 4-floratis (rare minus quam

6-floratis in *L. listii*) et ramulis foliis calyce fructuque distincte pubescentibus (ramulis foliis calyce fructuque ± glabris in *L. listii*) differt. A *L. marlothii* habitu floresque valde maiore, et fructu valde maiore plicato pubescente (fructu parvo recto glabrescenti in *L. marlothii*) differt.

TYPE.---Transvaal, 2627 (Potchefstroom): Parys, near bridge over Vaal River on Potchefstroom Road (--CD), 01/05/1989, *B-E. van Wyk 2884* (PRE, holo.; JRAU, K, MO, S, iso.).

Prostrate herbaceous perennial, up to 1 m in diameter. *Branches* slender, prostrate, spreading from a woody caudex, often rooting at the nodes to form dense mats, thinly and minutely pubescent. *Leaves* digitately trifoliolate, very variable in size and shape, adaxially glabrous, abaxially thinly and minutely pubescent, at length glabrescent, somewhat fleshy; petiole slender, (5--) 7--24 (--60) mm long; leaflets variable in size and shape, linear, narrowly elliptic to oblanceolate, the terminal one (4--) 10--28 (--36) mm long, (1--) 2--5 (--7) mm wide, the lateral ones similar but smaller. *Stipules* up to 5 mm long and 3 mm wide, dimorphic (the one large and foliaceous, the other similar or more often much smaller), ovate to narrowly lanceolate; base cordate; apex acute; minutely pubescent. *Inflorescences* leaf-opposed or subterminal on lateral branches, slender, 20--120 mm long, sparsely 1--4 -flowered; bract linear to narrowly oblanceolate, 2--3 mm long; bracteoles linear, ± 1 mm long. *Flowers* 8--10 mm long, yellow. *Calyx* 4--6 mm long, with the upper and lateral lobe on either side fused higher up in pairs, minutely but distinctly pubescent; lobes very long and narrow, the free part up to 3 mm long. *Standard* orbicular, ± as long as the keel. *Wing petals* oblong, only slightly shorter than the keel. *Keel petals* elliptic; apex obtuse. *Anthers* dimorphic. *Pistil* 12--14 mm long; ovary oblong-linear, 8--10 mm long, pubescent; style short. *Pods* 10--15 mm long, 2--4 mm wide, invariably folded like a concertina, ± 12-seeded, upper suture ± smooth, indehiscent, distinctly pubescent at maturity. *Seeds* small, ± 1 mm in diameter, testa nearly smooth (Figure 3).

L. subulata is closely related to *L. bainesii* Bak. f. , *L. listii* Polhill and *L. marlothii* Engl. and may be confused with these species, particularly when mature fruit are not available. As shown in Figure 3, however, it can easily be distinguished from these species by the shape and size of the calyx alone. The long and narrow calyx lobes have suggested the specific epithet. The inflorescence structure and the shape and vestiture of the fruit are also useful diagnostic characters. *L. subulata* differs from *L. bainesii* in the shape of the calyx lobes (not broadly triangular), the sparsely few-flowered racemes (not subumbellately many-flowered) and in the consistently plicate fruit (only rarely plicate in *L. bainesii*). It can be distinguished from *L. listii* also by the shape of the calyx lobes, the fewer (up to 4) flowers per inflorescence (rarely less than 6-flowered in L. listii) and in the distinctly pubescent twigs, leaves, calyx and fruit (twigs, leaves, calyx and fruit ± glabrous in L. listii. From L. marlothii it differs in the much larger habit and flowers and in the much larger, plicate and pubescent fruit (fruit small, straight and glabrescent in L. marlothii).

Compared to its close relatives, L. subulata has a much more restricted distributed and has been recorded only from the banks of the Vaal River (south-western Transvaal, eastern Orange Free State and the northern Cape Province, Figure 4). The robust habit and obvious similarities with L. bainesii suggest that it may be worthwhile to investigate the agronomic potential of the new species. Despite the similarity between L. subulata and L. listii and the co-occurrence of the two species at some localities, Wilman (1946, p.52) recognised L. subulata as a distinct species.

TRANSVAAL.---2627 (Potchefstroom): Potchefstroom district, Scandinavia Drift, bank of Vaal River (--CC), 06/03/1948, Louw 1691 (PRE), 25/04/1979, Krynauw 61 (PRE); Schoemansdrift road, near turn-off to Venterskroon (--CD), 20/02/1979, Ubbink 865 (PRE); Parys (--CD), 04/1907, Potts 553 (BLFU); Parys, near bridge over Vaal River on Potchefstroom Road (--CD), 01/05/1989, B-E. van Wyk 2884 (PRE, holotype; JRAU, K, MO, S, isotypes).

---2724 (Taung): Internieurungslager Andalusia (--DD), 28/12/1941, *Giess 103* (M), 05/1942, *Volk 228* (WIND).

CAPE.---2824 (Kimberley): bank of Vaal River at Warrenton (--BB), 13/10/1936, *Acocks* & *Hafstrom 1279* (KMG, PRE); Schmidt´s Drift, bank of Vaal River (--CA), 03/1935, *Wilman s.n. sub KMG 3294* (BOL, KMG); Riverton (--DA), 10/1917, *Wilman s.n. sub BOL 15660* (BOL).

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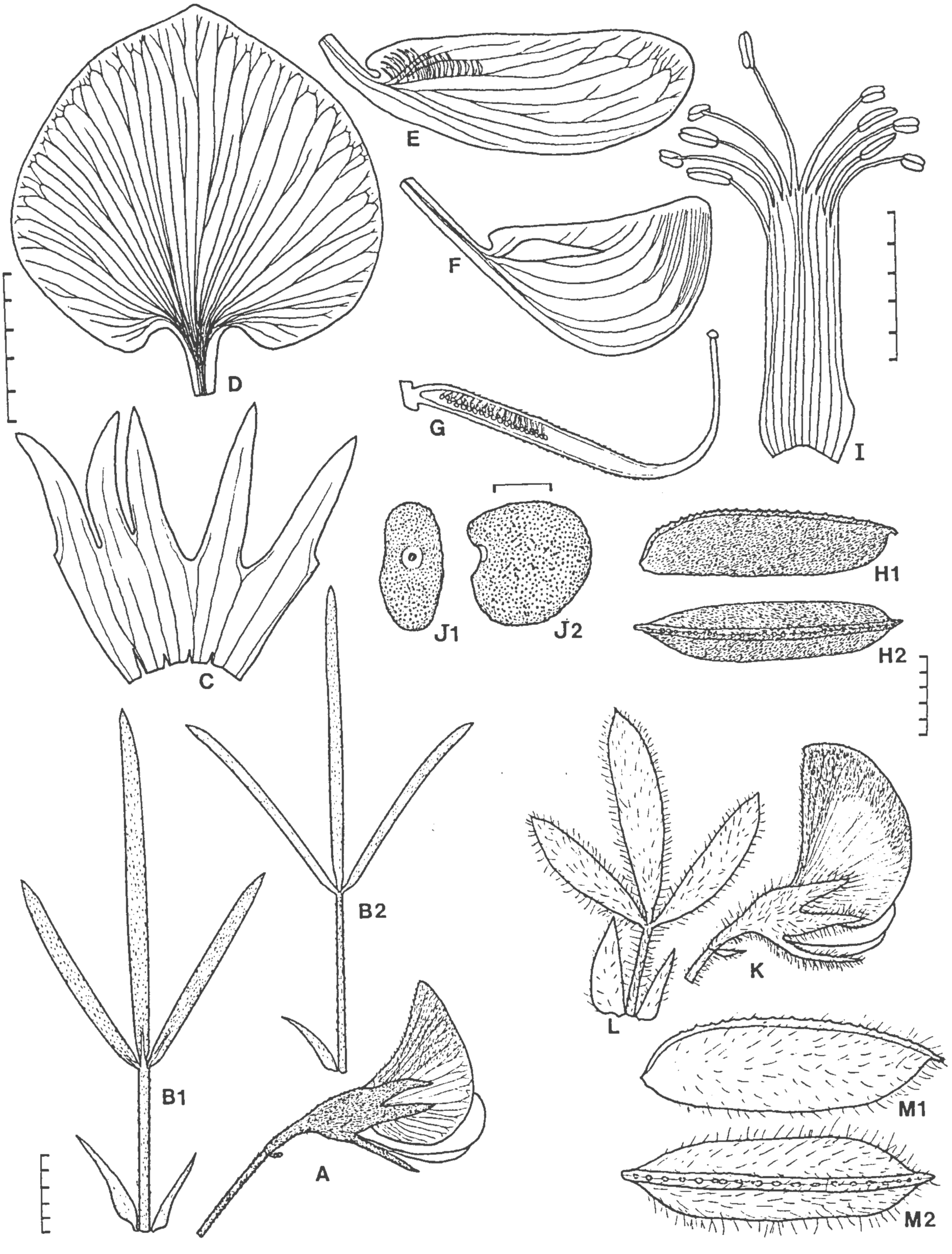

Figure 1. Lotononis filiformis. A, flower in lateral view; B1 & B2, leaves, showing the stipules and strigillose vestiture: B1, abaxial view, B2, adaxial view; C, calyx opened out, with the upper lobes to the left, vestiture not shown; D, standard petal; E, wing petal; F, keel petal; G, pistil; H1 & H2, fruit, showing the densely strigillose vestiture and verrucose upper suture: H1, lateral view, H2, top view; I, androecium; J1 & J2, seeds: J1, hilar view, J2, lateral view. Lotononis azurea var. lanceolata. K, flower in lateral view; L, leaf in adaxial view; M1 & M2, fruit in lateral and top view. (all from Van Wyk 2857 except H1, H2, J1 & J2 from Vlok 2030 and K, L, and M from Acocks 13713). Scales in mm.

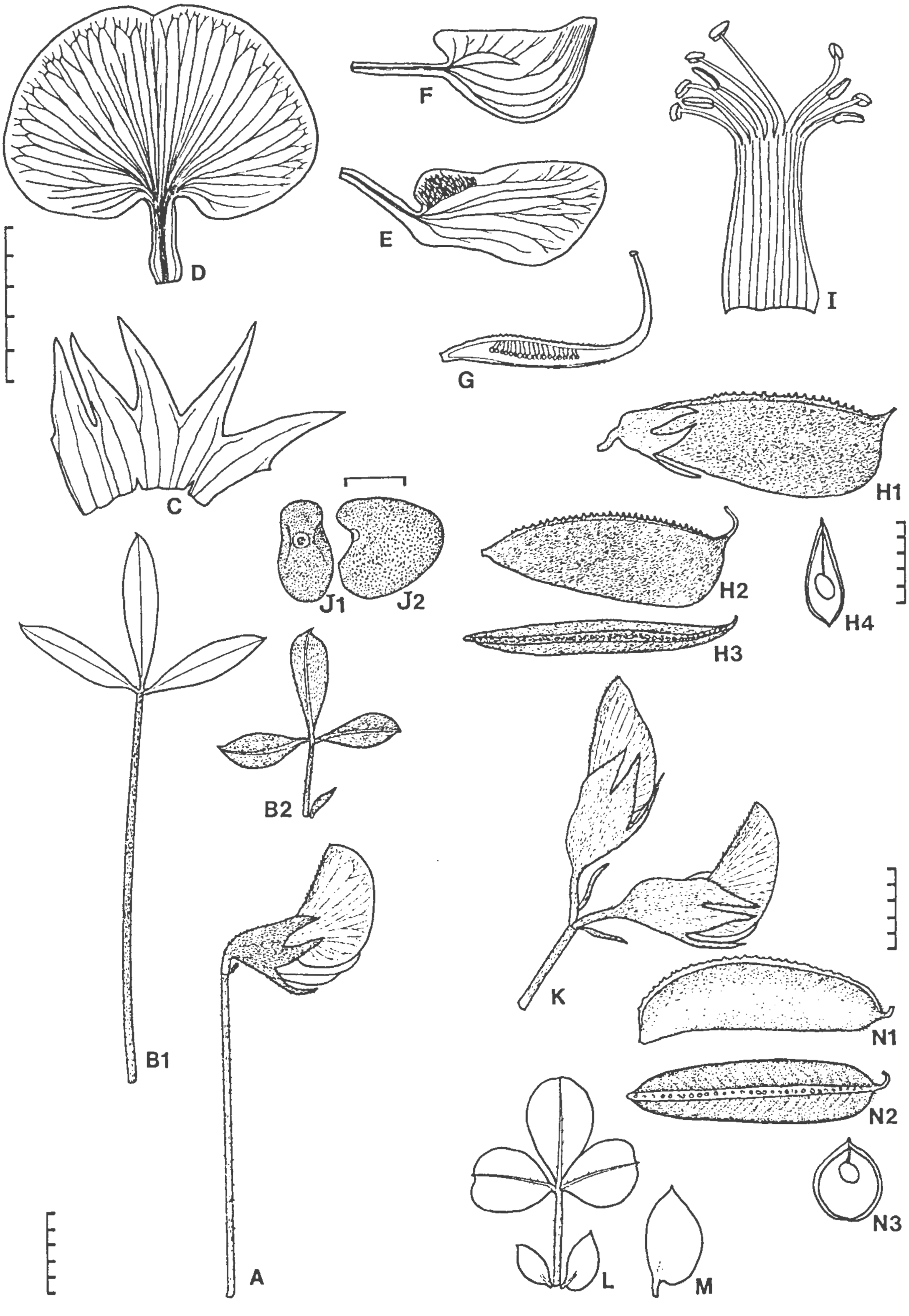

Figure 2. Lotononis complanata. A, flower in lateral view; B1 & B2, leaves, showing the slightly recurved leaflet apices and strigillose vestiture: B1, leaf from central branch in adaxial view, B2, leaf from lateral branch in abaxial view; C, calyx opened out, with the upper lobes to the left, vestiture not shown; D, standard petal; E, wing petal; F, keel petal; G, pistil; H1, H2, H3 & H4, fruit, showing the distinctive shape, densely strigillose vestiture and verrucose upper suture: H1 & H2, lateral view, H3, top view, H4, transverse section; I, androecium; J1 & J2, seeds: J1, hilar view, J2, lateral view. Lotononis varia. K, flowers in lateral view; L, leaf in abaxial view; M, stipule; N1, N2 & N3, fruit: N1, lateral view, N2, top view, N3, transverse section. (all from Vlok 1941 except H1, H2, H3 H4, J1 & J2 from Van Wyk 2879, K from Esterhuysen 35558, L, M, N1, N2 & N3 from Barker 7164). Scales in mm.

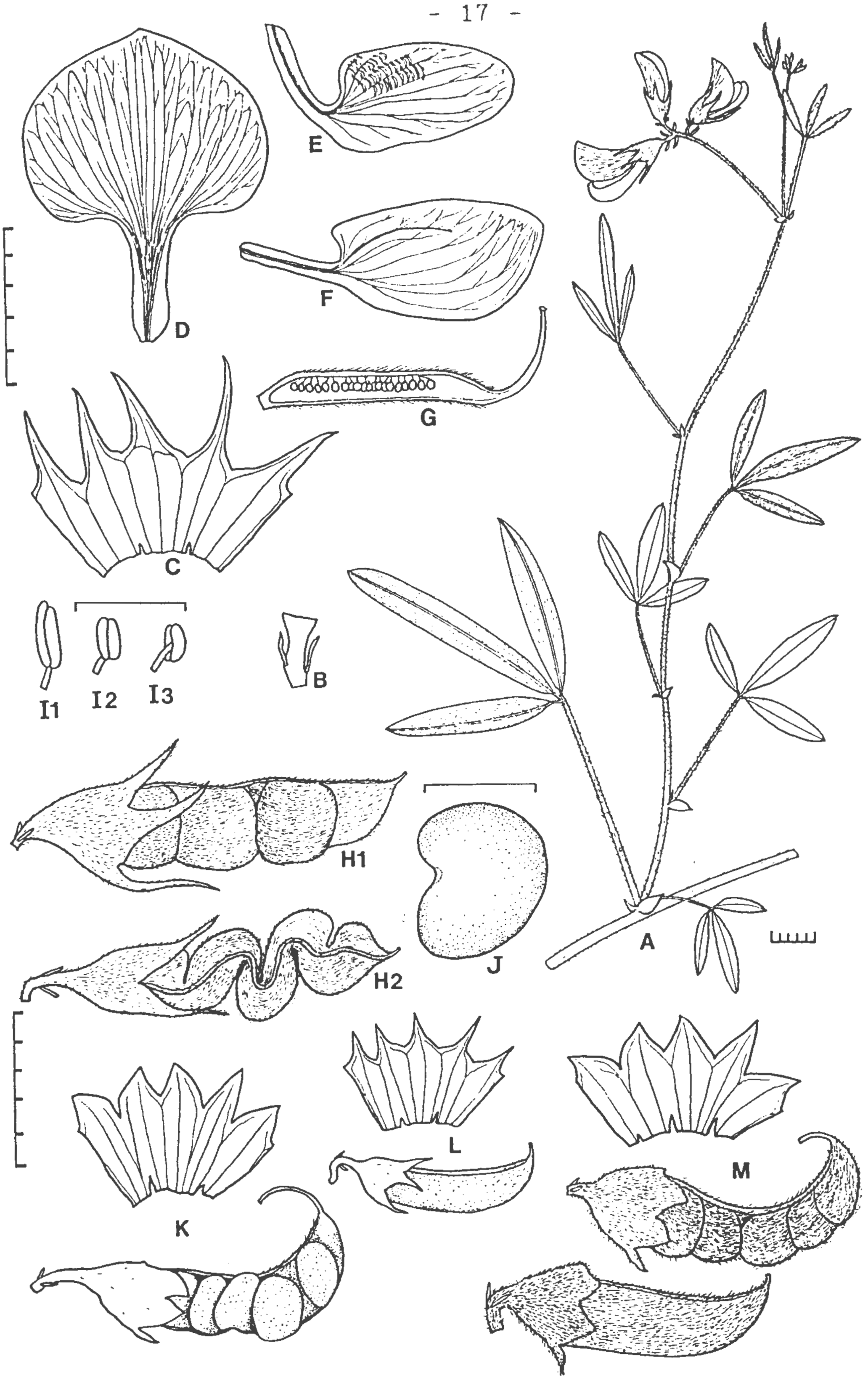

Figure 3. Lotononis subulata. A, flowering branch, showing the inflorescence structure, leaves and paired stipules; B, pedicel with bracteoles; C, calyx opened out, with the upper lobes to the left, vestiture not shown; D, standard petal; E, wing petal; F, keel petal; G, pistil; H1 & H2, fruit, showing the distinctive shape and vestiture: H1, lateral view, H2, top view; I1, I2 & I3, anthers: I1, basifixed anther, I2, carinal anther, I3, dorsifixed anther; J, seed in lateral view (slightly immature). K, L & M, calyces and fruit of related species (note differences in the shape of the calyx lobes and fruit): K, Lotononis listii; L, Lotononis marlothii; M, Lotononis bainesii. (A, B, C, D, E, F, G, I1, I2 & I3 from Krynauw 61; H1, H2 & J from Louw 1691) Scales in mm.

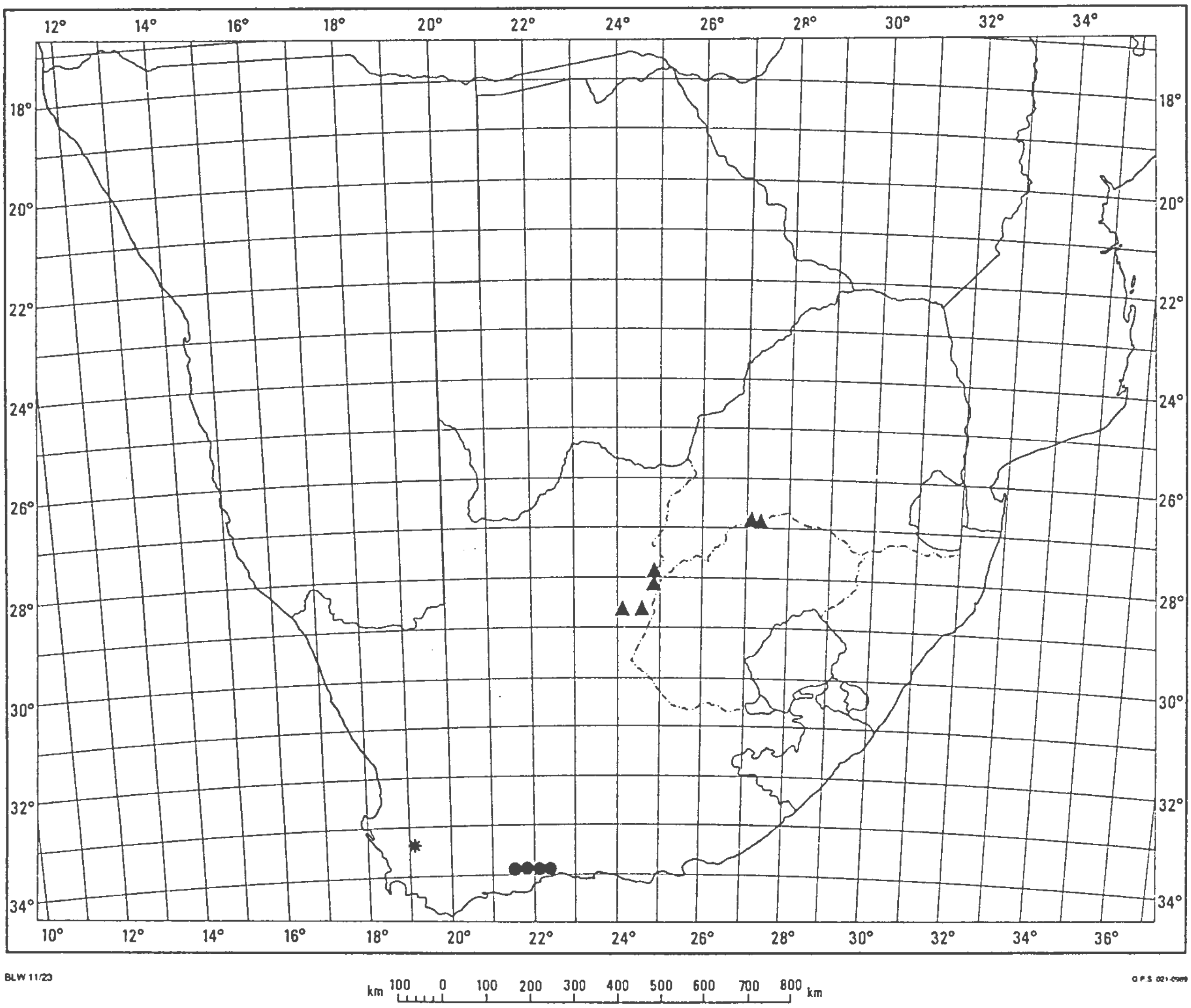

Figure 4. The known geographical distribution of Lotononis filiformis (●), L. complanata (✱) and L. subulata (▲).