

The generic concept of *Lotononis* (Crotalariaeae, Fabaceae): Reinstatement of the genera *Euchlora*, *Leobordea* and *Listia* and the new genus *Ezoloba*

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

Keywords Crotalariaeae; *Euchlora*; *Ezoloba*; Fabaceae; *Listia*; *Leobordea*; *Lotononis*; southern Africa; taxonomy

Supplementary Material Figures S1–S2 and Table S1 are available in the free Electronic Supplement to the online version of this article (<http://www.ingentaconnect.com/content/iapt/tax>).

■ INTRODUCTION

Lotononis (DC.) Eckl. & Zeyh. (tribe Crotalariaeae) is a large and complex genus of 151 species (one recently described from Namibia by Van Wyk & Kolberg, 2008), ca. 144 of which occur in southern Africa (Van Wyk, 1991a). The classification system of the genus has been somewhat volatile since the original concept was established by Candolle in 1825, published as *Ononis* sect. *Lotononis* DC. This section was thereafter raised to generic level by Ecklon & Zeyher (1836) who, along with Meyer (1836), proposed numerous other genera to accommodate the species of what is today *Lotononis*. The genus *Euchlora* Eckl. & Zeyh. was described by Ecklon & Zeyher (1836) to accommodate an anomalous plant that was placed in the genus *Ononis* L. by Thunberg (1800) and in *Crotalaria* L. and later *Microtropis* E. Mey. by Meyer (1832, 1836). Bentham (1843) expanded the concept of *Lotononis* to include the genera described by Ecklon & Zeyher (1836) and Meyer (1836), with the exception of *Euchlora*, and a sectional classification was proposed which Harvey (1862) also followed in the treatment of the genus in the *Flora capensis*. Dahlgren (1964) discussed the taxonomic history and synonymy of *Euchlora* and mentioned the similarities between it and *Lotononis*, such as trifoliolate, stipulate leaves (in some forms of *Lotononis hirsuta* (Thunb.) D. Dietr.), a similar hair type and the warty upper suture of

the pod. *Euchlora serpens* (E. Mey.) Eckl. & Zeyh. was subsequently transferred to *Lotononis* (as *L. serpens*) by Dahlgren (1964). The most recent revision of *Lotononis* by Van Wyk (1991a) follows Bentham (1843) to some extent but expanded the generic concept to include *Buchenroedera* Eckl. & Zeyh. Based on cladistic analyses of morphological, cytological and chemical data, a detailed infrageneric classification system was proposed, comprising 15 sections (Van Wyk, 1991a). This study, published as a series of papers and as a synopsis in 1991, represents the most rigorous treatment of the genus to date, and provided a framework for future studies on *Lotononis*.

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

Data presented by Boatwright & al. (2008a) showed that *Lotononis* is polyphyletic, through the analysis of nrITS and plastid *rbcL* sequence data which included 52 species of *Lotononis* representing all the currently recognized sections of the genus. However, the analysis of morphological characters in combination with the sequence data indicated that *Lotononis* was in fact weakly supported to be monophyletic if *L. hirsuta* (L. sect. *Euchlora* (Eckl. & Zeyh.) B.-E. van Wyk) was excluded. However, an anomalous species, *Lotononis macrocarpa* Eckl. & Zeyh.,

could not be included in this study seeing that it is extremely rare and several attempts to recollect the plant have failed. *Lotononis macrocarpa* possesses a unique combination of characters: paired stipules that are equal in size, a 5+5 anther arrangement, minutely serrate bracts, presence of bracteoles and large fruit. Subsequent to the study of Boatwright & al. (2008a) material of the species was obtained from a herbarium specimen of the only recent collection. The new sequence data, in combination with available data from Boatwright & al. (2008a) has allowed for a re-evaluation of the generic circumscription of *Lotononis*.

This paper is aimed at presenting a new generic classification system for *Lotononis* s.l. based on molecular and morphological evidence. A discussion of critical characters is presented along with systematic data on the placement of the anomalous *Lotononis macrocarpa*. The necessary new name combinations are made for 54 species. A key to the genera of Crotalariaeae is also presented in which the changes at generic level formalised in this paper are incorporated.

■ MATERIALS AND METHODS

DNA sequencing and phylogenetic analyses. — Subsequent to a phylogenetic study of tribe Crotalariaeae by Boatwright & al. (2008a), material of the rare and unusual *Lotononis macrocarpa*, a species which is pivotal in studying relationships within the genus *Lotononis*, was obtained from the Compton Herbarium, South Africa (voucher specimen: *Helme* 2076, NBG). The combined *rbcL*/ITS/morphology dataset of Boatwright & al. (2008a), with and without the morphological data, was used to evaluate relationships within *Lotononis* and assess the position of *L. macrocarpa*. DNA of this anomalous species was extracted using a DNeasy Plant Minikit (Qiagen Inc., Hilden, Germany) and sequenced following the procedures outlined in Boatwright & al. (2008a). These sequences of ITS (GenBank accessions FM875935 and FM875936) and *rbcL* (GenBank accession FM875934) were added to the matrices of Boatwright & al. (2008a; available on TreeBASE, study number S2070), which required minimal adjustments to the original alignment and the 31 morphological characters included in the latter study were also polarized for *L. macrocarpa* for inclusion in the morphological matrix. Parsimony (MP) analyses were conducted in PAUP* using a heuristic search with 1000 random sequence additions, tree-bisection-reconnection (TBR) branch swapping and the MULTREES option in effect, keeping only 10 trees per replicate. Character transformations were treated as unordered and with equal weighting (Fitch parsimony, Fitch, 1971). Trees collected in the 1000 replicates were used as starting trees for another similar search, but without a tree limit, to test whether the shortest trees were obtained in the first search. Delayed transformation character optimization (DELTRAN) was used to calculate branch lengths. Internal support was estimated with 1000 bootstrap replicates (Felsenstein, 1985)

using TBR and holding 10 trees per replicate. The following scale was used to evaluate bootstrap support percentages (BP): 50%–74%, low; 75%–84%, moderate; 85%–100%, strong. Congruence of the separate datasets was evaluated through visual inspection of the individual bootstrap consensus trees as well as incongruence length difference tests (ILD) as described in Boatwright & al. (2008a). Although this test indicated significant difference between the datasets ($P = 0.001$ for the combined molecular dataset and $P = 0.002$ for the combined *rbcL*/ITS/morphology dataset) visual inspection indicated no ‘hard’ incongruence. Following suggestions of Seelanan & al. (1997) and Wiens (1998), together with indications of the possible unreliability of the ILD test (Reeves & al., 2001; Yoder & al., 2001), the datasets were combined directly. Bayesian MCMC analysis (BI; Yang & Rannala, 1997; Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; MrBayes v.3.1.2.) was performed using the GTR+I+G model for the molecular data as selected by Modeltest v.3.06 (Posada & Crandall, 1998) using the corrected Akaike information criterion (Akaike, 1974) and a total of three million generations with a sampling frequency of 100. The ‘standard’ model (default parameters) was used for the morphological data (Lewis, 2001). The analysis was terminated after the standard deviation of split frequencies fell below 0.01. One fourth of the resulting trees were discarded as the burn-in and a majority-rule consensus tree produced from the remaining trees to illustrate the posterior probabilities (PP) of all observed bipartitions. The following scale was used to evaluate the PPs: 0.50–0.84, low; 0.85–0.94, moderate; 0.95–1.0, strong. The GenBank accession numbers for all the taxa of Crotalariaeae used are listed in Boatwright & al. (2008a).

Evolution of morphological characters. — The patterns of evolution of eight morphological, cytological and chemical characters (Appendix 1; polarisations included as Supplementary Appendix S1) traditionally regarded as apomorphies for *Lotononis* s.l. were examined by reconstructing these onto the majority rule consensus tree produced by BI for both the combined molecular and combined *rbcL*/ITS/morphology datasets. The character reconstructions were done using parsimony in Mesquite v.2.5 (Maddison & Maddison, 2008).

■ RESULTS

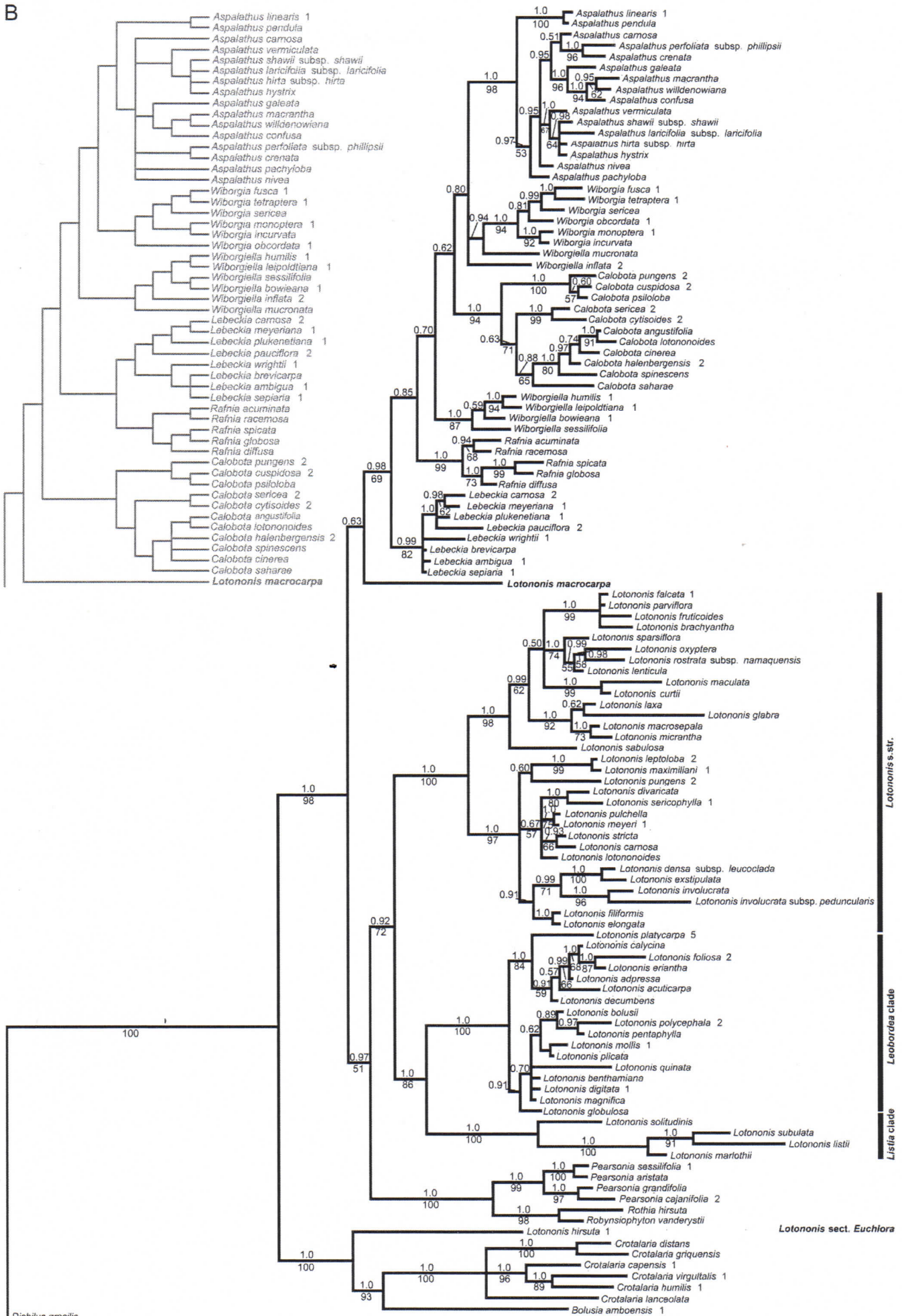
Combined ITS/*rbcL* dataset. — The combined molecular dataset consisted of 1854 included characters, 1401 of which were constant, 453 variable and 276 parsimony-informative. A total of 560 trees were retrieved using MP with a tree length (TL) of 1056, consistency index (CI) of 0.55 and a retention index (RI) of 0.82. The MP and BI analyses produced similar topologies, except for some differences in the ‘Cape’ group (Fig. 1A). The topology of the BI phylogram is similar to that retrieved by Boatwright & al. (2008a), with the exception that *Lebeckia* was monophyletic, albeit with weak support (PP 0.50). The

Fig. 1. Majority-rule consensus phylograms for **A** the combined molecular analysis, and **B** (overleaf) the combined molecular/morphological analysis. Numbers above the branches are posterior probabilities >0.5 and below the branches bootstrap percentages >50%. Topological differences in the parsimony strict consensus trees are indicated alongside in grey.

A



B



‘Cape’ group, including *Lotononis macrocarpa*, was strongly supported (PP 0.98). In the MP analysis *Rafnia* was sister to the *Aspalathus-Wiborgia* clade followed subsequently by *Lebeckia* and *Calobota* with *Lotononis macrocarpa* in a position outside the ‘Cape’ group, but without support. In this analysis *Lebeckia* was not monophyletic as in Boatwright & al. (2008a) with *L. pauciflora* not included in the main *Lebeckia* clade. In both MP and BI analyses *Lotononis* was polyphyletic with *Lotononis* s.str. (*L.* sect. *Lotononis* and allies) sister to *Pearsonia*, *Robynsiophyton* R. Wilczek and *Rothia*, i.e., the *Pearsonia* clade (51 BP; PP 0.97). *Lotononis* s.str. was strongly supported to be monophyletic (100 BP; PP 1.0). The *Leobordea* Del. clade (*Lotononis* sect. *Leobordea* (Del.) Benth. and allies) was sister to the *Listia* E. Mey. clade (*Lotononis* sect. *Listia* (E. Mey.) B.-E. van Wyk excluding *L. macrocarpa*) with a BP of 75 and PP of 1.0, and both these groups were strongly supported as monophyletic (99 BP; PP 1.0 and 100 BP; PP 1.0, respectively). *Lotononis hirsuta* (sect. *Euchlora*) was strongly supported as sister to *Bolusia* Benth. and *Crotalaria* (100 BP; PP 1.0).

Combined ITS/*rbcL*/morphological dataset. — The analysis of the combined molecular and morphological matrix included 1885 characters, 1401 of which were constant, 484 variable and 404 parsimony informative. The resulting 370 trees from the MP analysis were 1185 steps long, had a CI of 0.52 and a RI of 0.84. The MP and BI analyses produced similar topologies with some differences in the ‘Cape’ group (Fig. 1B). The topology differed slightly from that obtained by Boatwright & al. (2008a), largely within the ‘Cape’ group. *Aspalathus* L. and *Wiborgia* Thunb. were sister to each other and both monophyletic (98 BP; PP 1.0 and 94 BP; PP 1.0, respectively). *Wiborgiella inflata* and *W. mucronata* were not included in the main *Wiborgiella* Boatwr. & B.-E. van Wyk clade in the BI tree, although in the MP consensus tree these are included in *Wiborgiella*. Sister to the *Aspalathus-Wiborgia* clade in the BI tree is *Calobota* followed by *Wiborgiella*, *Rafnia* and *Lebeckia*. In the MP consensus tree *Wiborgiella* was sister to the *Aspalathus-Wiborgia* clade followed by *Lebeckia* and *Rafnia* which were sister without support and finally *Calobota*. The ‘Cape’ group was weakly supported (69 BP; PP 0.98) and *Lotononis macrocarpa* placed in a position sister to this group, but without bootstrap support and weak PP of 0.63. With the exclusion of *Lotononis hirsuta* and *L. macrocarpa*, the rest of *Lotononis* s.l. was weakly or moderately supported as monophyletic, as opposed to being polyphyletic in the combined molecular analysis (72 BP; PP 0.92). *Lotononis* s.str. (100 BP; PP 1.0), the *Leobordea* clade (100 BP; PP 1.0) and the *Listia* clade (100 BP; PP 1.0) were strongly supported, with the *Leobordea* and *Listia* clades strongly supported to be sister (86 BP; PP 1.0). *Lotononis hirsuta* (sect. *Euchlora*) was strongly supported as sister to *Bolusia* and *Crotalaria* (100 BP; PP 1.0).

Evolution of morphological characters. — The reconstructions of the eight morphological, cytological and chemical characters onto the BI trees from the combined molecular analysis are indicated in Figs. 2 and 3 and as supplementary data (Figs. S1–S2) for the combined molecular/morphological data.

Stipules are largely absent from the ‘Cape’ group and only some taxa of the *Lotononis* and *Crotalaria* clades (character 1;

Fig. 2; Fig. S1). Asymmetrical stipules are found mostly in *Lotononis* s.l. and reconstructed as an apomorphy for this group on the combined *rbcL*/ITS/morphology tree (Fig. S1), while on the tree from the combined molecular data the character is convergent between *Lotononis* s.str. and the *Leobordea* and *Listia* clades, with a reversal in *Lotononis* sect. *Aulacanthus* (E. Mey.) Benth. and sect. *Polylobium* (Eckl. & Zeyh.) Benth. in both analyses. Only one species of *Rothia*, *R. hirsuta* Baker, has single stipules. Loss of bracteoles (character 2; Fig. 2; Fig. S1) is convergent between *Lotononis hirsuta* and the other *Lotononis* clades, while the *Listia* clade is unique in having bracteoles. A zygomorphic calyx (character 3; Fig. 2; Fig. S1) is present in the *Lotononis* clades and *Pearsonia* with a reversal to an equal or subequal calyx in *Robynsiophyton* and *Rothia*. An anther arrangement (character 4; Fig. 2; Fig. S1) of 4+1+5 is most frequent in the ‘Cape’ group with *Lebeckia* and *Wiborgiella* species distinct in having 5+5 and 4+6 arrangements, respectively. This character is variable within *Lotononis* s.l. with only the *Listia* clade having an exclusively 4+1+5 arrangement. A verrucose upper suture of the pod (character 5; Fig. 3; Fig. S2) shows multiple convergences within the tribe and is present in species of all the *Lotononis* clades, except the *Listia* clade. The presence of long funicles (character 6; Fig. 3; Fig. S2) was reconstructed as an apomorphy for *Lotononis* s.l. in the combined *rbcL*/ITS/morphology analysis, but is also present in *Lotononis macrocarpa*. A chromosome base number (character 7; Fig. 3; Fig. S2) of $x = 9$ appears to be the plesiomorphic state in the Crotalariaeae with a reduction to $x = 8$ in *Crotalaria*, *Rafnia* and some *Aspalathus* species, while $x = 7$ is found in *Lotononis* s.str. and *Pearsonia*. Cyanogenesis (character 8; Fig. 3; Fig. S2) is unique to *Lotononis* s.str. with a reversal in *L.* sect. *Cleistogama* B.-E. van Wyk

DISCUSSION

Evolution of characters. — Polhill (1976) and Van Wyk & Schutte (1995) discussed the distribution of characters within Crotalariaeae and related tribes, but given the high incidence of convergence, some doubt has remained about the circumscription of certain genera, e.g., *Lebeckia* and *Lotononis*. The new insights into generic delimitations and relationships from this study and those of Boatwright & al. (2008a, 2009) allow for a re-evaluation of diagnostic characters and apomorphic states.

Stipules. — A loss of stipules is autapomorphic for some species of the *Leobordea* clade, *Pearsonia* and *Crotalaria* where stipules are largely present. Asymmetrical stipules are unique to the lotononoid groups, i.e., *Lotononis* s.str., together with the *Leobordea* and *Listia* clades (Fig. 2; Fig. S1) and *Rothia hirsuta*, while *Lotononis hirsuta* and *Lotononis macrocarpa* are conspicuously different in having symmetrical stipules (when present in the former). In *Rothia hirsuta*, the stipules are single as opposed to being paired in *R. indica* (L.) Druce (Boatwright & al., 2008b). Asymmetrical stipules were reconstructed as an apomorphy for *Lotononis* s.l. in the combined molecular/morphological analysis, with a reversal in species from *Lotononis* sect. *Aulacanthus* and sect. *Polylobium*, but as a convergent character in the combined molecular analysis.

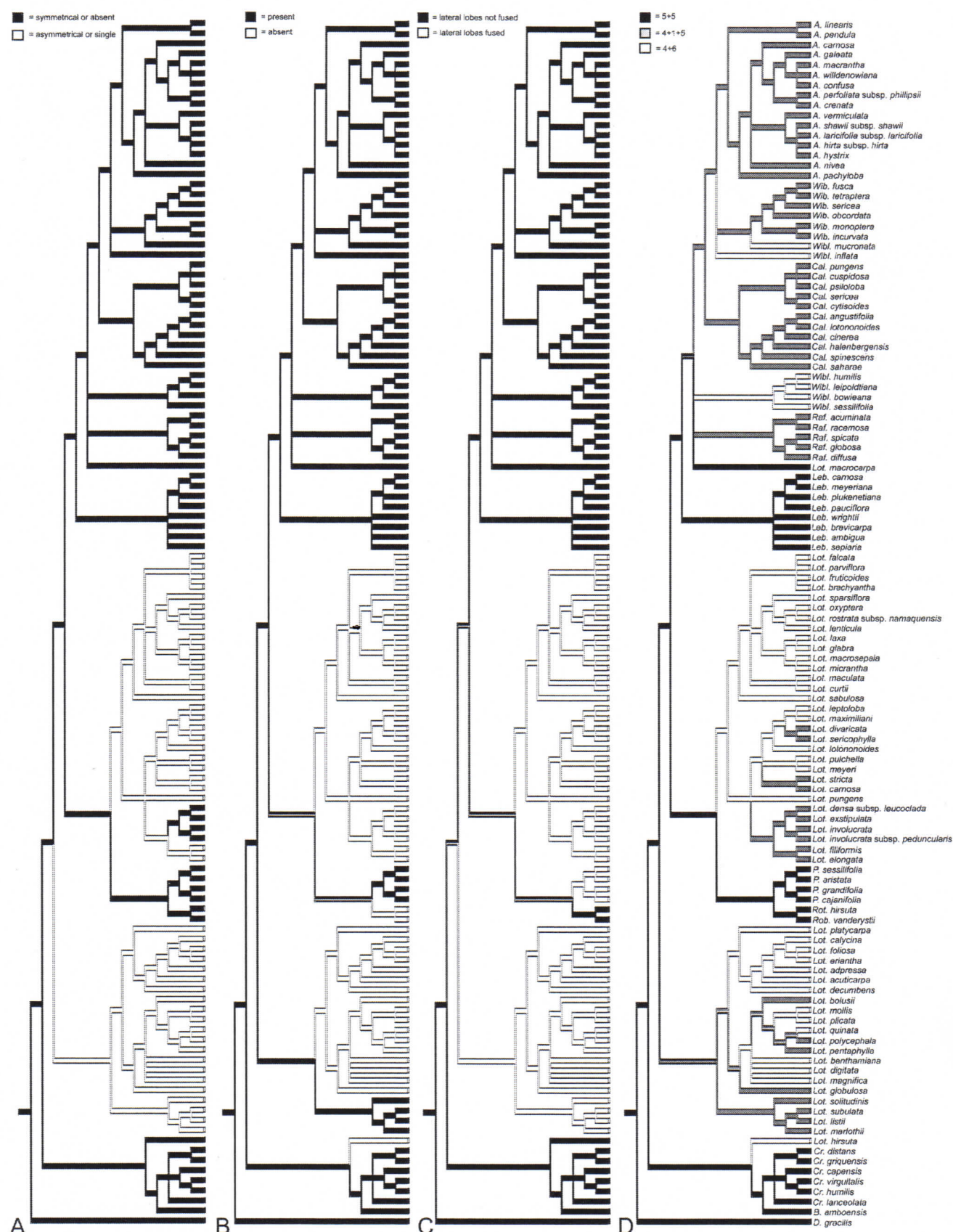


Fig. 2. Parsimony-based reconstructions of **A** stipule symmetry (character 1), **B** bracteole presence or absence (character 2), **C** calyx symmetry (character 3), and **D** anther arrangement (character 4) on the majority-rule consensus tree from the combined molecular analysis.

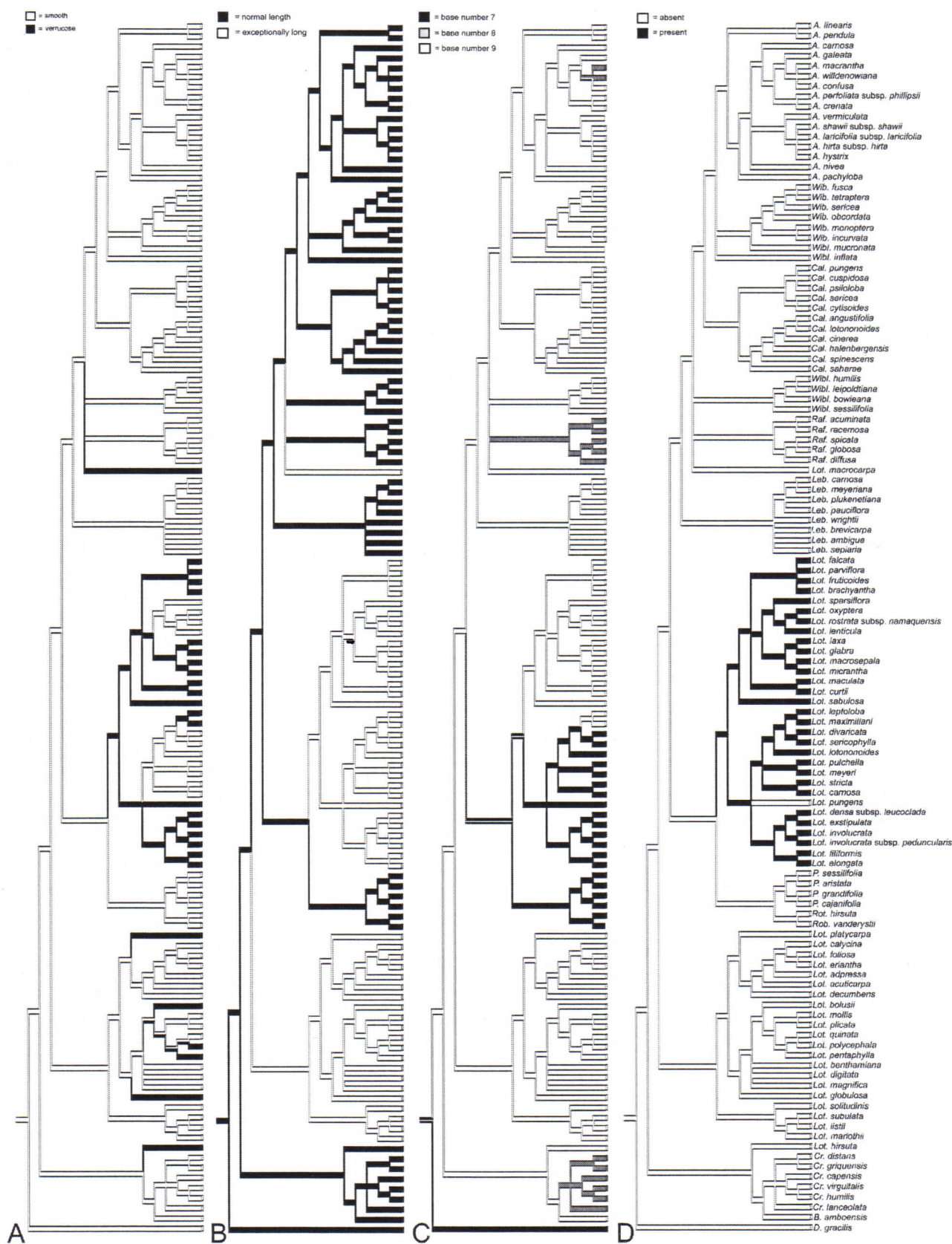


Fig. 3. Parsimony-based reconstructions of **A** verrucose upper suture presence or absence (character 5), **B** funicle length (character 6), **C** chromosome base number (character 7), and **D** presence or absence of cyanogenenic glucosides (character 8) on the majority-rule consensus tree from the combined molecular analysis.

Bracteole presence. — Bracteoles are present in all genera of the ‘Cape’ group, the *Listia* group, *Lotononis macrocarpa*, *Pearsonia*, *Bolusia* and *Crotalaria*. The loss of bracteoles appears to be a largely convergent character within the tribe and not unique to *Lotononis* s.l. Bracteoles are absent in *Lotononis* sect. *Euchlora*, the *Leobordea* clade and *Lotononis* s.str., as well as *Rothia* and *Robynsiophyton* (Van Wyk, 1991a; Boatwright & al., 2008b; Boatwright & Van Wyk, 2009) and this was reconstructed as convergences between these groups in the combined molecular and combined molecular/morphological analysis (Fig. 3). Only four species of the *Leobordea* clade have bracteoles present (large in two species of *Lotononis* sect. *Lipozygis*; very small or vestigial in two species of *Lotononis* sect. *Leptis* (E. Mey. ex Eckl. & Zeyh.)).

Calyx type. — Two calyx types are found within the Crotalariaeae; the lebeckioid calyx type (equally or sub-equally lobed) and the lotononoid calyx type (upper and/or lateral lobes on either side fused higher up than the lower lobe to varying degrees). *Lotononis* s.str., the *Leobordea* clade, the *Listia* clade and *Pearsonia* all have calyces of the lotononoid type, while the remaining genera have the lebeckioid calyx type. The distinction of *Lotononis hirsuta* and *L. macrocarpa* from *Lotononis* s.l. based on this character is notable.

Anther arrangement. — Anther dimorphism and arrangement are important within Crotalariaeae and informative at the generic level (Boatwright & al., 2008a, 2009). *Pearsonia*, *Rothia* and *Robynsiophyton* are unique within the tribe in having uniform anthers that are all similar in shape and size. The rest of the tribe have dimorphic anthers with alternating dorsifixed and basifixed anthers. The size, shape and attachment of the carinal anther is important and three arrangements are found: 5+5 (carinal anther resembles the long, basifixed anthers) present in *Bolusia*, *Crotalaria*, *Lebeckia* and *Lotononis macrocarpa*; 4+1+5 (the carinal anther intermediate between the dorsifixed and basifixed ones) present in *Aspalathus*, *Calobota*, *Lotononis* s.str., the *Listia* clade, *Rafnia* and *Wiborgia*; 6+4 (carinal anther resembling the dorsifixed anthers) present in *Lotononis hirsuta*, the *Leobordea* clade, *Lotononis* s.str. and *Wiborgiella*. Anther arrangement is fairly diagnostic for the genera within the ‘Cape’ group, but the distinction within *Lotononis* s.l. is not as clear (Fig. 2; Fig. S1).

Fruit. — A verrucose upper suture of the pod was thought to be unique to *Lotononis* s.l., but this character is convergent between the *Leobordea* clade, *Lotononis* s.str., *L. hirsuta* (sect. *Euchlora*) and *L. macrocarpa* (Fig. 3; Fig. S2).

Exceptionally long funicles are only found in species of *Lotononis* s.l. In the combined molecular/morphological analysis it is reconstructed as an apomorphy for *Lotononis* s.l., but it is also present in *L. macrocarpa* (Fig. 3; Fig. S2).

Chromosome base number. — Goldblatt (1981) suggested a base number of $x = 9$ for the tribe Crotalariaeae, which seems to be likely from the reconstructions presented here, showing a reduction to $x = 8$ and $x = 7$ in some lineages (Fig. 3; Fig. S2). *Crotalaria*, *Rafnia* and some *Aspalathus* species have a number of $x = 8$, while some species of *Lotononis* s.str., *Pearsonia* and *Rothia* have a base number of $x = 7$. It is possible that this pattern may become more complex as more counts become

available if, for example, living material of *L. macrocarpa* (*Ezoloba*) can be found.

Chemistry. — Chemical data are of important systematic value in the Crotalariaeae (Van Wyk, 2003) and provide additional insight into generic relationships. Cyanogenesis was reconstructed as an apomorphy for *Lotononis* s.str. and is absent from the *Leobordea* and *Listia* clades, *Lotononis hirsuta* and *L. macrocarpa* (Fig. 3; Fig. S2). The superficially similar genera *Pearsonia*, *Rothia* and *Robynsiophyton* are acyanogenic. The presence of prunasin and related cyanogenic glycosides therefore strongly supports the exclusion of the non-cyanogenic groups from *Lotononis*.

Quinolizidine alkaloids are present in most genera of the tribe, but absent from *Lotononis* s.str. and *Crotalaria*, where they are seemingly replaced by macrocyclic pyrrolizidine alkaloids. The presence of pyrrolizidine alkaloids in some sections of *Lotononis* s.l. was thought to suggest a sister relationship with *Crotalaria* that also produces such alkaloids (Van Wyk, 1991a). The presence of these alkaloids appears to be a convergence between *Lotononis* s.str. and *Crotalaria*.

***Lotononis hirsuta*.** — *Lotononis* sect. *Euchlora* is only distantly related to the rest of *Lotononis*. It is placed within a clade comprising *Crotalaria* and *Bolusia* (100 BP; PP 1.0) and this clade represents the earliest diverging lineage within the tribe. The placement of *Lotononis hirsuta* in this clade is supported by the strongly inflated pods and trifoliolate leaves (if present) with paired stipules that are equal in size found in these genera. Dahlgren (1964) transferred the species to *Lotononis* where it was treated as a section by Van Wyk (1991a). This anomalous plant differs markedly from species of *Lotononis* s.str., the *Leobordea* clade and the *Listia* clade by the large underground tuber (geophytic habit), simple, sessile leaves (in some forms), large pods and the subequally lobed calyx. The enormous underground tuber may be an adaptation possibly to survive periods of aridity or unfavourable weather conditions. Species of *Lotononis* sect. *Polylobium* and sect. *Lipozygis* (E. Mey.) Benth. are also somewhat tuberous with annual shoots produced from a fleshy, carrot-like root, but the extensive underground system of *Lotononis hirsuta* is not found in any of these sections. In *Lipozygis* the tuberous habit could be an adaptation to recurrent fires in the grassland habitat where these plants occur (Van Wyk, 1991a). The position of *Lotononis hirsuta* renders two important generic apomorphies for *Lotononis* s.l., to be the result of convergence, namely the loss of bracteoles and the verrucose upper suture of the pod (Van Wyk, 1991a).

***Lotononis* s.str.** — With the exception of *Lotononis* sect. *Oxydium*, *Lotononis* s.str. is endemic to southern Africa. Two sections are mainly found in the eastern parts of southern Africa, *L. sect. Krebsia* and sect. *Buchenroedera*, while all the remaining sections are restricted to the Cape and Namaqualand. *Lotononis* sect. *Monocarpa* occurs in the north-western Cape, while sect. *Lotononis*, sect. *Aulacanthus* and sect. *Polylobium* are more or less restricted to the Western Cape Province. *Lotononis* sect. *Cleistogama* has a more eastern distribution in the Cape region (Van Wyk, 1991a). *Lotononis* s.str. is chemically distinct from the *Leobordea* and *Listia* clades in that its members are cyanogenic (except for *L. sect. Cleistogama*) and

accumulate macrocyclic pyrrolizidine alkaloids, the first of which is a synapomorphy for this group.

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

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

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

Generic circumscription. — The close agreement of the relationships within *Lotononis* s.str. found by Boatwright & al. (2008a) and this study with those proposed by Van Wyk (1991a) is notable. The only difference is the inclusion of *L. sect. Euchlora* in *Lotononis* s.l. and the sister relationship proposed between *L. sect. Oxydium* and sects. *Cleistogama* and *Monocarpa* (Van Wyk, 1991a). Cladograms from Van Wyk's (1991a) study,

based on vegetative and reproductive morphology, cytology and chemical characters, also show *Lotononis* sect. *Listia* (the *Listia* clade) as sister to *L. sects. Digitata, Leobordea, Leptis, Lipozygis*, and *Synclistus*, i.e., the *Leobordea* clade. This clade is sister to *L. sects. Aulacanthus, Buchenroedera, Cleistogama, Euchlora, Krebsia, Lotononis, Monocarpa, Oxydium* and *Polylobium*, i.e., *Lotononis* s.str. (excluding sect. *Euchlora*).

Dahlgren (1970) discussed some examples of convergence and parallelisms in the tribe, but the results presented in this study have uncovered that the relationships within the *Crotalariaeae* are even more complex (Boatwright & al., 2008a, 2009) and revealed more examples of convergent evolution of morphological and chemical characters. Characters thought to be unique to certain groups, especially *Lotononis* s.l., have proven to be shared by distantly related groups. Due to the extreme overlap of character states in the genera of the *Crotalariaeae*, unique generic apomorphies are frequently not available and a combination of characters is necessary for generic circumscription. The original generic concept of *Lotononis* s.l. was shown to be polyphyletic (Boatwright & al., 2008a), largely due to the positions of *L. macrocarpa* and *L. hirsuta* and also the polyphyly of *Lotononis* s.l. shown by combined molecular evidence. Despite weak support for the monophyly of *Lotononis* s.l. in the combined molecular/morphological analysis, a narrower concept of *Lotononis* can be better circumscribed in light of the lack of generic apomorphies for *Lotononis* s.l. The recognition of smaller, monophyletic groups is now more practical and therefore the reinstatement of *Euchlora*, *Leobordea* and *Listia* is proposed and '*Ezoloba*' described as a new genus to accommodate *Lotononis macrocarpa*. Unique combinations of characters are available to circumscribe these genera that are strongly supported as monophyletic in the phylogenetic analyses presented here.

■ TAXONOMIC TREATMENT

Key to the genera of the *Crotalariaeae*

1. Stipules absent (if stipules rarely present then leaves acicular and keel spirally twisted) 2
1. Stipules present. 11
2. Calyx zygomorphic (upper and lateral lobes on either side fused higher up in pairs). *Lotononis* (partly)
2. Calyx subequally lobed 3
3. Style with 1–2 lines of hairs *Crotalaria*
3. Style glabrous 4
4. Bracteoles absent, leaves (at least the basal ones) simple, flat and sessile; geophyte with large underground tuber. *Euchlora*
4. Bracteoles present, leaves (simple and flat) not sessile; annuals, suffrutices or shrubs 5
5. Leaves acicular, terete 6
5. Leaves digitate, unifoliolate or simple (flat, never terete) . 7
6. Ovary 2 to 4 ovulate, pods 1- to ±2-seeded . . *Aspalathus*
6. Ovary with more than 6 ovules, pods many-seeded *Lebeckia*

7. Upper suture of pod asymmetrically convex 8
7. Upper suture of pod symmetrically convex 9
8. Plants glabrous except occasionally on bracts and bracteoles, usually turning black when dried *Rafnia*
8. Plants usually pubescent on all parts, if leaves glabrous then standard petal hairy and inner surface of calyx glabrous *Aspalathus*
9. Petals pubescent, if glabrous then plants strongly spinescent shrubs; twigs green (bark formation late); leaves isobilateral *Calobota*
9. Petals glabrous; twigs brown (bark formation early), if twigs rarely green then plant an annual fireweed; leaves dorsiventral 10
10. Fruits winged, indehiscent; carinal anther intermediate (anthers 4+1+5) *Wiborgia*
10. Fruits without wings, dehiscent (if rarely indehiscent then ovary and fruit distinctly stalked); carinal anther resembles short anthers (anthers 4+6) *Wiborgiella*
11. Style straight or rarely down-curved, anthers all similar in size and shape 12
11. Style curved upwards, anthers dimorphic 14
12. Stamens nine (five fertile and four lacking anthers) *Robynsiophyton*
12. Stamens 10 (all fertile) 13
13. Anthers monomorphic, prostrate annuals *Rothia*
13. Anthers slightly dimorphic, four basifixed, six attached slightly higher up, all elongate, perennial herbs or shrubs *Pearsonia*
14. Bracteoles absent 15
14. Bracteoles present 19
15. Geophyte with woody tuber; leaves (at least the basal ones) flat, simple and sessile *Euchlora*
15. Annuals, suffrutices, shrubs; if leaves flat and simple then not sessile 16
16. Stipules paired or absent 17
16. Stipules dimorphic or single 18
17. Keel obtuse, hairy *Leobordea*
17. Keel beaked, glabrous *Lotononis*
18. Keel obtuse, hairy *Leobordea*
18. Keel beaked, glabrous *Lotononis*
19. Keel obtuse 20
19. Keel beaked or helically coiled 22
20. Stipules single at each node; keel (and standard petal) densely hairy over most of the surface of the lamina *Leobordea*
20. Stipules paired at each node (sometimes dimorphic); keel and standard petal glabrous or with a few hairs only . . 21
21. Calyx subequally lobed; fruit more than 20 mm long; stems without adventitious roots; seeds $\pm$ 4 mm long; anthers 5+5 *Ezoloba*
21. Calyx zygomorphic (upper and lateral lobes on either side fused higher up in pairs); fruit less than 20 mm long; stems often with adventitious roots; seeds $\pm$ 1 mm long; anthers 4+1+5 *Listia*
22. Keel and style helically coiled through several turns *Bolusia*
22. Keel and style not helically coiled *Crotalaria*

Taxonomy

I. *Ezoloba* B.-E. van Wyk & Boatwr., **gen. nov.** – Type: *Ezoloba macrocarpa* (Eckl. & Zeyh.) B.-E. van Wyk & Boatwr.

Listiae E. Mey. similis, sed stipulis aequimagnis, calyce subpariter lobato, 5+5 dispositione antherarum, leguminibus magnis (longioribus 20 mm) et seminibus (longioribus 4 mm) et habitu non stoliferenti differt.

The generic concept proposed here is based on a unique combination of characters, namely the stipules that are equal in size, the sub-equally lobed calyx, presence of bracteoles, 5+5 anther arrangement, the very large fruit with a warty upper suture and the large seeds (Fig. 4). The bracts are often minutely toothed along the margins (Fig. 4C1, C2), a character not yet found in any other genera of the tribe. The molecular and morphological evidence presented here indicates that this species is more closely related to the ‘Cape’ group of *Crotalariaeae* than to *Lotononis* s.l. The single species is known from only a few localities in the Western Cape Province of South Africa. The generic name commemorates Ecklon and Zeyher who first described this species.

1. *Ezoloba macrocarpa* (Eckl. & Zeyh.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis macrocarpa* Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 176. Jan. 1836 – Type: South Africa, Cape Province, Brackfontein, Clanwilliam, *Ecklon & Zeyher 1271* (S!, lectotype, designated by Van Wyk, 1991a; C!, S!, SAM!, isoelectotypes).

II. *Euchlora* Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 171. Jan. 1836 = *Microtropis* E. Mey., Comm. Pl. Afr. Austr. 1(1): 65. Feb. 1836 = *Lotononis* sect. *Euchlora* (Eckl. & Zeyh.) B.-E. van Wyk in Contr. Bolus Herb. 14: 213. 1991 – Type: *Euchlora serpens* (E. Mey.) Eckl. & Zeyh.

The genus is easily recognisable by the large underground tuber, simple, sessile leaves (in some forms) and the large, inflated pods (illustrations are provided by Dahlgren, 1964). The results presented by Boatwright & al. (2008a) and in this study indicate that this genus forms part of the early diverging elements of *Crotalariaeae* and that it is closely related to *Bolusia* and *Crotalaria*. The single species occurs in the Northern and Western Cape Provinces of South Africa.

1. *Euchlora hirsuta* (Thunb.) Druce in Rep. Bot. Exch. Cl. Brit. Isles 1916: 622. 1917 = *Ononis hirsuta* Thunb., Prodr. Pl. Cap.: 129. 1800 = *Microtropis hirsuta* (Thunb.) E. Mey., Comm. Pl. Afr. Austr. 1(1): 65. Feb. 1836 = *Lotononis hirsuta* (Thunb.) D. Dietr., Syn. Pl. 4: 960. 1847 – Type: South Africa, Cape Province, ‘prope Cap juxta Leuwestaart’, *Thunberg s.n. sub THUNB-UPS 16614* (UPS!, lectotype, designated by Dahlgren, 1964).

= *Crotalaria serpens* E. Mey. in Linnaea 7: 153. 1832 = *Euchlora serpens* (E. Mey.) Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 171. Jan. 1836 = *Lotononis serpens* (E. Mey.) Dahlgren in Bot. Not. 117: 373. 1964 – Type: South Africa, Cape Province, ‘Sandige Stellen unweit Salzwivier’, *Ecklon s.n.* (S!, lectotype, designated by Dahlgren, 1964).

III. *Listia* E. Mey., Comm. Pl. Afr. Austr. 1(1): 80. Feb. 1836 $\equiv$ *Lotononis* sect. *Listia* (E. Mey.) B.-E. van Wyk in Contr. Bolus Herb. 14: 99. 1991 – Type: *Listia heterophylla* E. Mey.

The concept of *Listia* proposed here conforms to that of *Lotononis* sect. *Listia* subsect. *Listia* as described by Van Wyk (1991a), which includes seven species. The genus can be distinguished from especially *Ezoloba*, *Lotononis* s.str. and *Leobordea* by a unique combination of characters: stoloniferous habit, paired, dimorphic stipules, presence of bracteoles, 4+5+1 anther arrangement, largely glabrous petals and pods, the latter often folded like a concertina. The root nodules differ from all other members of Crotalariaeae in being lupinoid (sleeve-like). The species mainly occur in the interior of southern Africa, but *L. angolensis* and *L. heterophylla* extend into central Africa.

1. *Listia angolensis* (Welw. ex Bak.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis angolensis* Welw. ex. Bak. in Oliver, Fl. Trop. Afr. 2: 6. 1871 – Type: Angola, Huilla District, Welwitsch 1896 (BM!, lectotype, designated by Van Wyk, 1991a; BM!, C!, K!, isoelectotypes); Angola, Pungo Andongo District, Welwitsch 1895 (BM!).

2. *Listia bainesii* (Bak.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis bainesii* Bak. in Oliver, Fl. Trop. Afr. 2: 6. 1871 – Type: In the interior near the Tropic of Capricorn, Chapman & Baines s.n. (holotype: K!).

3. *Listia heterophylla* E. Mey., Comm. Pl. Afr. Austr. 1(1): 81. Feb. 1836 $\equiv$ *Lotononis listii* Polhill in Bot. Syst. 1: 324. 1976 – Type: South Africa, Cape Province, Gaatje, Drège s.n. a (K!, herb. Benth., lectotype, designated by

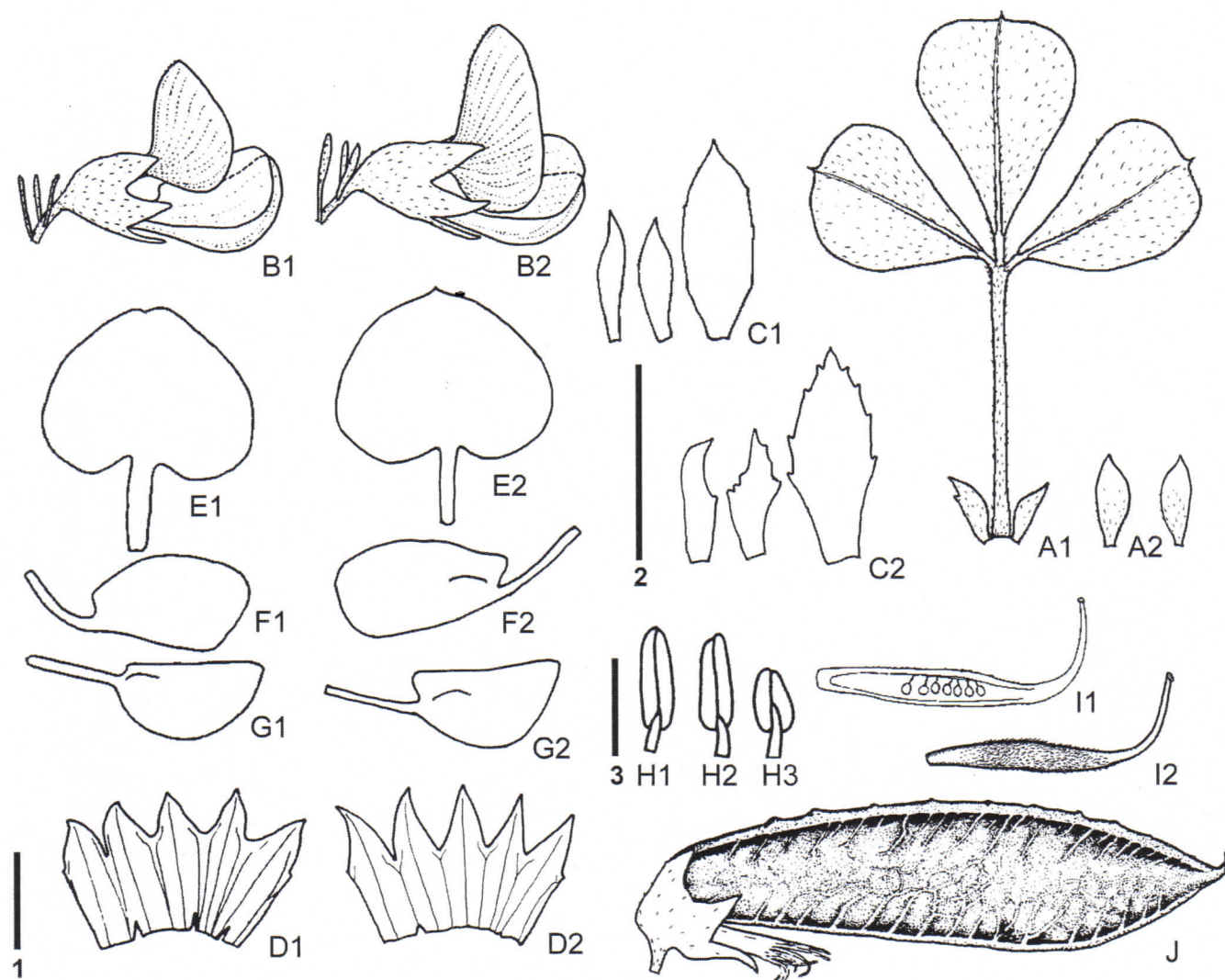


Fig. 4. *Ezoloba macrocarpa* [J. Burrows 5 (NBG), Voëlvlei Dam, Gouda, South Africa – A1, A2, D2, E2, F2, G2, I2: Ecklon & Zeyher 1271 (SAM), Clanwilliam, South Africa – B1, B2, D1, E1, F1, G1, H, I1, J]. **A**, Leaf with stipules; **B**, flowers in side view; **C**, bracts and bracteoles; **D**, calyces (opened out with the upper lobes to the left); **E**, standard petals; **F**, wing petals; **G**, keel petals; **H**, anthers (H1 = long basifixed anther, H2 = carinal anther, H3 = short dorsifixed anther); **I**, gynoeceum; **J**, fruit. Scale bars: 1 = 5 mm; 2 = 3 mm (bracts and bracteoles only); 3 = 1 mm (anthers only).

Van Wyk, 1991a; BM!, K!, herb. Hook., SI, TCD!, isolecotypes); Cape Province, 'prope Wildschutshoek', *Drège s.n. b* (BM!, K!, SI!).

4. *Listia marlothii* (Engl.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis marlothii* Engl. in Bot. Jahrb. Syst. 10: 26. 1888 – Type: South Africa, Cape Province, Griqualand West, Kimberley, *Marloth 765* (K!, herb. Engl., lectotype, designated by Van Wyk, 1991a; BOL!, K!, PRE!, isolecotypes).

5. *Listia minima* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis minima* B.-E. van Wyk in S. African J. Bot. 54(6): 628. 1988 – Type: South Africa, Cape Province, Kenhardt Div., Jagbult, floor of Uilpan, *Acocks 12664* (PRE!, holotype; K!, isotype).

6. *Listia solitudinis* (Dümmer) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis solitudinis* Dümmer in Trans. Roy. Soc. South Africa 3(2): 297. 1913 – Type: South Africa, Vaal River, *Wilms 400* (BM!, holotype).

7. *Listia subulata* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis subulata* B.-E. van Wyk in Bothalia 20(1): 79. 1990 – Type: South Africa, Gauteng, Parys, near bridge over Vaal River on Potchefstroom Road, *B.-E. van Wyk 2884* (PRE!, holotype; JRAU!, K!, MO!, SI!, isotypes).

IV. *Leobordea* Del. in Laborde, Voy. Arabie Pétrée ("Delile, Fl. Arabie Pétrée"): 82, 86. 1830 *emend.* B.-E. van Wyk & Boatwr., *emend. nov.* – Type: *Leobordea lotoidea* Del. (= *Leobordea platycarpa* (Viv.) B.-E. van Wyk & Boatwr.).

Note. – *Leobordea* is here reinstated and its concept greatly broadened to include *Lotononis* sects. *Digitata*, *Lep-tis*, *Leobordea*, *Lipozygis* and *Synclistus*. We were unable to determine which of the two species names were published first in 1830 and provisionally follow previous authors in accepting *Lotus platycarpus* Viv. as the oldest available name. Of the names available for the generic concept proposed here, *Amphinomia* DC. is the oldest. This genus was described by Candolle (1825) based on a plate of *Connarus decumbens* Thunb. in Arch. Bot. 1(1): 1. 1796. The identity of this species has until now been unclear. Gillet & Bullock (1957) mentioned that *Connarus decumbens* might not even be a legume and that *Amphinomia* is possibly not a synonym of *Lotononis*. A reinvestigation of the type specimen of *Connarus decumbens* in UPS has provided clarity regarding the identity of this plant. The unusual vestiture of the calyx (hairs in rows along the veins) and the short, few-seeded pods of the specimen are diagnostic characters of *Lotononis pallens* (Eckl. & Zeyh.) Benth. The epithet *decumbens* has already been used in *Lotononis*, so that the nomenclature at species level is not affected. In light of this discovery, *Amphinomia* in actual fact represents a synonym of *Lotononis* s.str. *Amphinomia* has already been rejected in favour of *Lotononis* (Rickett, 1960; Lanjouw & al., 1966). *Leobordea* is the oldest available name that can here be considered for reinstatement.

The genus *Leobordea* now includes 51 species that occur mostly in the eastern parts of South Africa and extend into tropical Africa and the Mediterranean region. They can be distinguished from especially *Listia* by the habit that is never stoloniferous, the single stipules that are sometimes similar to the leaflets, pubescent vegetative and reproductive parts, absence of bracteoles (except in four species) and the 4+6 anther arrangement (very rarely 4+5+1). After *Lotononis* s.str. which now comprises 91 species, this is the largest of the genera proposed here. The species have been classified into distinct sections by Van Wyk (1991a) based on cladistic analyses of morphological, chemical and cytological data. The number of species sampled for the molecular studies does not allow for a re-evaluation of the infrageneric classification system and the sectional classification of Van Wyk (1991a) is followed here. See Van Wyk (1991a) for complete species synonymies as well as keys to the sections and species. Fortunately, the nomenclature of the 91 species remaining in *Lotononis* s.str. are not affected (see Van Wyk, 1991a).

1. *Leobordea* sect. *Digitata* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis* sect. *Digitata* B.-E. van Wyk, Contr. Bolus Herb. 14: 107. 1991 – Type: *Leobordea digitata* (Harv.) B.-E. van Wyk & Boatwr. (= *Lotononis digitata* Harv.)

This section can be distinguished by the following combination of characters: prostrate shrubs or shrublets with the basal parts of the branches woody, leaves mostly 5-foliolate with long, slender petioles, stipules single at each node, bracteoles absent, calyx zygomorphic, keel petals obtuse and glabrous pods that are stipitate to long-stipitate and flat, linear or falcate and sometimes plicate (Van Wyk, 1991a). The section includes six species.

1.1. *Leobordea digitata* (Harv.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis digitata* Harv. in Harvey & Sonder, Fl. Cap. 2: 52. 1862 – Type: South Africa, in some part of the eastern provinces, *Capt. Carmichael s.n.* (TCD!, holotype).

1.2. *Leobordea benthamiana* (Dümmer) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis benthamiana* Dümmer in Trans. Roy. Soc. South Africa 3(2): 294. 1913 – Type: South Africa, Cape Province, Little Namaqualand: Near Ookiep, *Scully s.n. sub Herb. Norm. Austr. Afr. 1127* (K!, lectotype, designated by Van Wyk, 1991a; BOL!, K!, isolecotypes), *Scully 150* (BM!, isosyntype), *Morris s.n. sub BOL 5622* (BOL!, K!, isosyntypes); *Steinkopf, Schlechter 39* (BM!, BOL!, GRA!, MO!, isosyntypes).

1.3. *Leobordea longiflora* (H. Bolus) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis longiflora* H. Bolus in J. Linn. Soc. 25: 159. 1889 – Type: South Africa, Cape Province, Namaqualand, *Dowdle s.n. sub BOL 6568* (BOL!, holotype; K!, isotype).

1.4. *Leobordea magnifica* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis magnifica* B.-E. van

Wyk in S. African J. Bot. 55(6): 647. 1989 – Type: South Africa, Cape Province, summit of Kamiesberg, 3 km south of radio tower, *B.-E. van Wyk 2421* (PRE!, holotype; K!, MO!, NBG!, isotypes).

1.5. *Leobordea plicata* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis plicata* B.-E. van Wyk in S. African J. Bot. 55(6): 649. 1989 – Type: South Africa, Cape Province, near Bitterfontein, between Vanrhynsdorp and Bitterfontein, *Salter 1601* (K!, holotype; BOL!, isotype).

1.6. *Leobordea quinata* (Thunb.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Ononis quinata* Thunb., Prodr. Pl. Cap.: 130. 1800 = *Lotononis quinata* (Thunb.) Benth. in London J. Bot. 2: 608. 1843 – Type: South Africa, 'e Cap. B. Spei', *Thunberg s.n. sub THUNB-UPS 16636* (UPS!, lectotype, designated by Van Wyk, 1991a).

2. *Leobordea* sect. *Leobordea* = *Lotononis* sect. *Leobordea* (Del.) Benth. in London J. Bot. 2: 607. 1843.

The most useful character to distinguish species of sect. *Leobordea* from other sections are the leaves that are opposite on the flowering nodes and not alternate as in all the other sections (Van Wyk, 1991a). The section includes six species.

2.1. *Leobordea bracteosa* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis bracteosa* B.-E. van Wyk in Bothalia 20: 73. 1990 – Type: Namibia, Outjo district, mountains 14 miles [22.4 km] east of Torra Bay, *Giess, Vlok & Bleissner 6198* (PRE!, holotype; M!, PRE!, WIND!, isotypes).

2.2. *Leobordea furcata* (Merxmüller & Schreiber) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis furcata* (Merxmüller & Schreiber) Schreiber in Mitt. Bot. Staats-samml. München 3: 613. 1960 – Type: Namibia, Rehoboth district, Buellspoor, *Strey 2614* (M!, holotype; K!, M!, PRE!, SAM!, isotypes).

2.3. *Leobordea newtonii* (Dümmer) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis newtonii* Dümmer in Trans. Roy. Soc. South Africa 3(2): 303. 1913 – Type: Angola, Mossamedes, Moullino, *Newton 95* (K!, lectotype, designated by Van Wyk, 1991a; Z., isolectotype).

2.4. *Leobordea platycarpa* (Viv.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotus platycarpus* Viv., Pl. Aegypt., Dec IV: 14, t. 2, fig. 9. 1830 = *Lotononis platycarpa* (Viv.) Pic-Serm. in Webbia 7: 331. 1950 – Type: Egypt, 'in desertis prope Kahirum' [near Cairo], *Figari s.n.* (G, holotype).

Note. – As noted under the generic citation, the relative priority of *Leobordea lotoidea* Del. in relation to *Lotus platycarpus* Viv. is in need of further investigation.

2.5. *Leobordea schoenfelderi* (Dinter ex Merxmüller & Schreiber) B.-E. van Wyk & Boatwr., **comb. nov.** = *Amphinomia schoenfelderi* Dinter ex Merxmüller & Schreiber

in Bull. Jard. Bot. État Bruxelles 27: 273. 1957 = *Lotononis schoenfelderi* (Dinter ex Merxmüller & Schreiber) Schreiber in Mitt. Bot. Staatssamml. München 3: 613. 1960 – Type: Namibia, Grootfontein district, 'Gross Huis', *Dinter 7383* (M!, holotype; BM!, BOL!, K!, M!, PRE!, S!, WIND!, isotypes).

2.6. *Leobordea stipulosa* (Bak. f.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis stipulosa* Bak. f., Leg. Trop. Afr. 1: 18. 1926 – Type: Zimbabwe, Macheke, *Eyles 2020* (K!, holotype; K!, SAM!, isotypes).

3. *Leobordea* sect. *Leptis* (E. Mey. ex Eckl. & Zeyh.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Leptis* E. Mey. ex Eckl. & Zeyh., Enum. Pl. Afr. Austr. 2: 174. Jan. 1836 = *Lotononis* sect. *Leptis* (E. Mey. ex Eckl. & Zeyh.) Benth. *emend.* B.-E. van Wyk in Contr. Bolus Herb. 14: 124. 1991 – Lectotype: *Leptis debilis* Eckl. & Zeyh. (*Lotononis prolifera* (E. Mey.) B.-E. van Wyk).

The species of this section are mostly distributed in central and southern Africa and extend into the Mediterranean region. They are perennial suffrutescent herbs, shrublets or annuals with the stipules single at each node, leaves predominantly 3-foliate, the inflorescences few-flowered, bracteoles absent and the keel petals obtuse and hairy. The section includes 20 species.

3.1. *Leobordea acuticarpa* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis acuticarpa* B.-E. van Wyk in Bothalia 20: 21. 1990 – Type: South Africa, Gauteng, Springs district, 5 km from Devon radar station to Leandra, *Van Wyk 1815* (PRE!, holotype; JRAU!, K!, MO!, NBG!, isotypes).

3.2. *Leobordea adpressa* (N.E. Br.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis adpressa* N.E. Br. in Kew. Bull. 1906: 18. 1906 – Type South Africa, Natal, Stony hill near Charlestown, *Wood 5712* (K!, holotype). Two subspecies are recognised:

3.2.1. *Leobordea adpressa* (N.E. Br.) B.-E. van Wyk & Boatwr. subsp. *adpressa* = *Lotononis adpressa* N.E. Br. subsp. *adpressa*.

3.2.2. *Leobordea adpressa* (N.E. Br.) B.-E. van Wyk & Boatwr. subsp. *leptantha* (B.-E. van Wyk) B.-E. van Wyk, **comb. nov.** = *Lotononis adpressa* N.E. Br. subsp. *leptantha* B.-E. van Wyk in Contr. Bolus Herb. 14: 141. 1991 – Type: South Africa, Gauteng, Farm Waterval, 2 miles [3.2 km] WNW of Krugersdorp, *Mogg 22844* (PRE!, holotype; PRE!, 2 sheets, isotypes).

3.3. *Leobordea arida* (Dümmer) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis arida* Dümmer in Trans. Roy. Soc. South Africa 3(2): 324. 1913 – Type South Africa, Cape Province, mountain tops, Eland's Hoek near Aliwal North, *F. Bolus 31 sub BOL 10559* (K!, lectotype, designated by Van Wyk, 1991a; BOL!, isolectotype).

- 3.4. *Leobordea bullonii* (Emberger & Maire) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis bullonii* Emberger & Maire, Pl. Maroc. Nov. (Arch. Sc. Maroc.) Fasc. 1: 1. 1929 – Type: not seen.
- 3.5. *Leobordea carinata* (E. Mey.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lipozygis carinata* E. Mey., Comm. Pl. Afr. Austr. 1(1): 80. Feb. 1836 = *Lotononis carinata* (E. Mey.) Benth. in London J. Bot. 2: 609. 1843 – Type: South Africa, North-eastern Transkei, between ‘Omsamculo’ and ‘Umcomas’, Drège s.n. (K!, lectotype, designated by Van Wyk, 1991a; MO!, S!, isoelectotypes).
- 3.6. *Leobordea decumbens* (Thunb.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Ononis decumbens* Thunb., Prodr. Pl. Cap.: 129. 1800 – Type: South Africa, ‘Roggeveld’, Thunberg s.n. sub THUNB-UPS 16604 (UPS!, lectotype, designated by Van Wyk, 1991a).
Two subspecies are recognised:
- 3.6.1. *Leobordea decumbens* (Thunb.) B.-E. van Wyk & Boatwr. subsp. *decumbens*.
- 3.6.2. *Leobordea decumbens* (Thunb.) B.-E. van Wyk & Boatwr. subsp. *rehmannii* (Dümmer) B.-E. van Wyk, **comb. nov.** = *Lotononis rehmannii* Dümmer in Trans. Roy. Soc. South Africa 3(2): 326. 1913 = *Lotononis decumbens* subsp. *rehmannii* (Dümmer) B.-E. van Wyk in Contr. Bolus Herb. 14: 139. 1991 – Type: South Africa, Gauteng, ‘Hogge Veld, Perekopberg’, Rehmann 6831 (K!, lectotype, designated by Van Wyk, 1991a; BM!, Z, isoelectotypes).
- 3.7. *Leobordea divaricata* Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 175. Jan. 1836 – Type: South Africa, Cape Province, side of Bothasberg, not far from ‘Vischrivier’, Ecklon & Zeyher 1266 (S!, lectotype, designated by Van Wyk, 1991a; C!, M!, S!, SAM!, isoelectotypes).
= *Lipozygis calycina* E. Mey., Comm. Pl. Afr. Austr. 1(1): 78. Feb. 1836 = *Lotononis calycina* (E. Mey.) Benth. in London J. Bot. 2: 611. 1843 – Type: South Africa, Cape Province, Katberg, Drège s.n. a (K!, Herb. Benth., lectotype, designated by Van Wyk, 1991a; BM!, K!, Herb. Hook., TCD, isoelectotypes); Klipplaatrivier, Drège s.n. c (P!, S!, syntypes); Bothasberg, Drège s.n. d (P!, syntype).
- 3.8. *Leobordea esterhuyseana* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis esterhuyseana* B.-E. van Wyk in Bothalia 20: 70. 1990 – Type: South Africa, Cape Province, Ceres District, Stompiesvlei, Swartruggens, Esterhuysen 29341 (BOL!, holotype; C!, K!, MO!, isotypes).
- 3.9. *Leobordea genistoides* Fenzl, Pug. Pl. Nov. Syr.: 6. 1842 = *Lotononis genistoides* (Fenzl) Benth. in London J. Bot. 2: 607. 1843 – Type: Turkey, ‘in monte Tauro prope Gulek’, Kotschy 159 (K!, syntype, 2 sheets).
- 3.10. *Leobordea hirsuta* (Schinz) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis hirsuta* Schinz in Bull. Herb. Boiss. 7: 33. 1899 – Type: South Africa, Limpopo Province, Houtbosch, Rehmann 6265 (Z, holotype; K!, isotype).
= *Lotononis wilmsii* Dümmer in Trans. Roy. Soc. South Africa 3(2): 307. 1913 – Type: South Africa, Gauteng, between Middelburg and Crocodile River, Wilms 277 (K!, holotype).
- 3.11. *Leobordea lupinifolia* Boiss. in Biblioth. Universelle Genève, n.s. 13: 408. 1838 = *Lotononis lupinifolia* (Boiss.) Benth. in London J. Bot. 2: 607. 1843 – Type: Spain, Malaga Province, ‘in arenis torrentium Malaga, Motril’, Boissier El. 61 (G, holotype; K! 2 sheets, M! 2 sheets, TCD, isotypes).
- 3.12. *Leobordea maroccana* (Ball) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis maroccana* Ball in J. Bot. 11: 302. 1873 – Type: ‘Ourika’, Ball s.n. (K!, upper specimen on sheet with illustration, lectotype, designated by Van Wyk, 1991a; BM!, K!, bottom of second sheet, isoelectotypes), Hooker s.n. (K!, isosyntype); Morocco, ‘in regione inferiori Atlantis Majoris: prope Tasseremout’ Ball s.n. (K!, isosyntype); ‘Ait Mesan’, Ball s.n. (K!, 2 sheets, isosyntypes); ‘Amsmiz’, Ball s.n. (K!, 2 sheets, isosyntypes), Hooker s.n. (K!, isosyntype).
- 3.13. *Leobordea mirabilis* (Dinter) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis mirabilis* Dinter in Feddes Repert. 30: 200. 1932 – Type: Namibia, ‘Granitflachberge von Aus und Gubub’, Dinter 3597 (SAM!, lectotype, designated by Van Wyk, 1991a; BOL!, K!, PRE!, isoelectotypes); ‘Granitberge von Zwartaus (6 km nordl. Aus)’, Dinter 6098 (BM!, BOL!, K!, M!, PRE!, S!, SAM!, syntypes).
- 3.14. *Leobordea mollis* (E. Mey.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lipozygis mollis* E. Mey., Comm. Pl. Afr. Austr. 1(1): 79. Feb. 1836 = *Lotononis mollis* (E. Mey.) Benth. in London J. Bot. 2: 609. 1843 – Type: South Africa, Cape Province, Leliefontein, Drège s.n. (K!, lectotype, designated by Van Wyk, 1991a; MO!, S!, isoelectotypes).
- 3.15. *Leobordea mucronata* (Conrath) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis mucronata* Conrath in Kew Bull. 1908: 222. 1908 – Type: South Africa, Gauteng, Modderfontein, Conrath 124 (K!, holotype).
- 3.16. *Leobordea pariflora* (N.E. Br.) B.-E. van Wyk & Boatwr., **comb. nov.** = *Lotononis pariflora* N.E. Br. in Burtt Davy, Man. Pl. Transvaal: 388. 1932 – Type: South Africa, Gauteng, Pietersburg District, The Downs, Rogers 21994 (K!, lectotype, designated by Van Wyk, 1991a; PRE!, isoelectotype); Rogers 22017 (PRE!, syntype).
- 3.17. *Leobordea prolifera* (E. Mey.) Eckl. & Zeyh., Enum. Pl. Afr. Austr.: 175. Jan. 1836 = *Crotalaria prolifera* E. Mey. in Linnaea 7: 152. 1832 = *Lotononis prolifera* (E. Mey.) B.-E. van Wyk in Contr. Bolus Herb. 14: 135. 1991 – Type: South

Africa, Cape Province, 'Nieuwe veld', Distr. Beaufort, *Drège s.n.* (S!, lectotype, designated by Van Wyk, 1991a).

- 3.18. *Leobordea pusilla* (Dümmer) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis pusilla* Dümmer in Trans. Roy. Soc. South Africa 3(2): 324. 1913 – Type: South Africa, Cape Province, slopes of mountains, Eland's hoek near Aliwal North, *F. Bolus 122 sub BOL 10535* (K!, lectotype, designated by Van Wyk, 1991a); *F. Bolus 122 sub BOL 8141* (BOL!, isoelectotype), *F. Bolus 122* (PRE!, isoelectotype).

- 3.19. *Leobordea stolzii* (Harms) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis stolzii* Harms in Bot. Jahrb. Syst. 54: 379. 1917 – Type: Tanzania (North of Lake Nyasa, Kyimbila District), Western Njombe District, Madehani, *Stolz 2602* (B†; K!, lectotype, designated by Van Wyk, 1991a; BM!, BOL!, C!, K!, MO!, PRE!, isoelectotypes).

- 3.20. *Leobordea tapetiformis* (Emberger & Maire) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis tapetiformis* Emberger & Maire in Bull. Soc. Hist. Nat. Afrique Nord 28(6): 349. 1937 – Type: Morocco, 'Atlantis Majoris orientalis ad radices australes montis Masker, inter Tagoudimt et Anemzi, ad alt. 2200–2400 m', *Emberger & Maire s.n. 1936* (not seen).

4. *Leobordea* sect. *Lipozygis* (E. Mey.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lipozygis* E. Mey., Comm. Pl. Afr. Austr. 1(1): 80. Feb. 1836 $\equiv$ *Lotononis* sect. *Lipozygis* (E. Mey.) Benth. *emend.* B.-E. van Wyk in Contr. Bolus Herb. 14: 114. 1991 – Type: *Leobordea corymbosa* (E. Mey.) B.-E. van Wyk & Boatwr. ($\equiv$ *Lipozygis corymbosa* E. Mey.).

The species of this section are suffrutescent, pyrophytic herbs. The bracts are inserted near the middle of the pedicel rather than at the base as in the other sections (Van Wyk, 1991a). The section includes two subsections and ten species.

- 4A. *Leobordea* subsect. *Bracteolata* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis* sect. *Lipozygis* subsect. *Bracteolata* B.-E. van Wyk in Contr. Bolus Herb. 14: 117–118. 1991 – Type: *Leobordea difformis* (B.-E. van Wyk) B.-E. van Wyk & Boatwr. ($\equiv$ *Lotononis difformis* B.-E. van Wyk).

Leobordea subsect. *Bracteolata* can be distinguished from *L.* subsect. *Lipozygis* by the broadly ovate bracts and presence of conspicuous paired bracteoles (Van Wyk, 1991a). Two species are included in this subsection.

- 4.1. *Leobordea difformis* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis difformis* B.-E. van Wyk in S. African J. Bot. 55: 529. 1989 – Type: South Africa, Gauteng, Piet Retief District, Iswepe, *Sidey 1609* (PRE!, holotype; S!, isotype).

- 4.2. *Leobordea procumbens* (H. Bolus) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis procumbens* H. Bolus

in J. Bot. 1896: 18. 1896 – Type: South Africa, Free State, Harrismith district, plateau and mountains at Bester's Vlei, *Bolus 8139* (BOL!, holotype; NBG!, isotype).

- 4B. *Leobordea* subsect. *Lipozygis* (E. Mey.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis* sect. *Lipozygis* subsect. *Lipozygis* (E. Mey.) B.-E. van Wyk in Contr. Bolus Herb. 14: 118. 1991.

In this subsection the bracts are linear to narrowly lanceolate and bracteoles absent or vestigial (Van Wyk, 1991a). This subsection includes eight species.

- 4.3. *Leobordea corymbosa* (E. Mey.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lipozygis corymbosa* E. Mey., Comm. Pl. Afr. Austr. 1(1): 80. Feb. 1836 $\equiv$ *Lotononis corymbosa* (E. Mey.) Benth. in London J. Bot. 2: 605. 1843 – Type: South Africa, Transkei, 'prope Omtata', *Drège s.n.* (S!, lectotype, designated by Van Wyk, 1991a; BM!, K!, 2 sheets, M!, S!, isoelectotypes).

- 4.4. *Leobordea eriantha* (Benth.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis eriantha* Benth. in London J. Bot. 2: 605. 1843 – Type: South Africa, 'Macalisberg', *Burke 383* (K!, Herb. Benth. specimen, holotype; K!, Herb. Hook. specimen, PRE!, isotypes).

- 4.5. *Leobordea foliosa* (H. Bolus) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis foliosa* H. Bolus in J. Linn. Soc. (Bot.) 24: 173. 1887 – Type: South Africa, Gauteng, 'prope Pretoria', *Maclea s.n. sub BOL 5620* (BOL!, holotype; K!, isotype).

- 4.6. *Leobordea grandis* (Dümmer & Jennings) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis grandis* Dümmer & Jennings in Trans. Roy. Soc. South Africa 3(2): 310. 1913 – Type: South Africa, KwaZulu Natal, at the Umzinyati River, *Wylie s.n. sub Wood 11525* (K!, holotype).

- 4.7. *Leobordea lanceolata* (E. Mey.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Aspalathus lanceolatus* E. Mey., Comm. Pl. Afr. Austr. 1(1): 37. Feb. 1836 $\equiv$ *Lotononis lanceolata* (E. Mey.) Benth. in London J. Bot. 2: 606. 1843 – Type: South Africa, Cape Province, 'Witbergen ... prope Leeuwenspruit', *Drège s.n.* (K!, lectotype, designated by Van Wyk, 1991a; BM!, K!, MO!, PRE!, S!, SAM!, isoelectotypes).

- 4.8. *Leobordea pulchra* (Dümmer) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis pulchra* Dümmer in Trans. Roy. Soc. South Africa 3(2): 308. 1913 – Type: South Africa, Gauteng, Lydenburg, *Wilms 280* (K!, lectotype, designated by Van Wyk, 1991a; BM!, isoelectotype), *Wilms 279a p.p.* (BM!), *Atherstone s.n.* (not seen).

- 4.9. *Leobordea spicata* (Compton) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis spicata* Compton in J. S. African Bot. 41(1): 48. 1975 – Type: Swaziland, Mpaleni, *Compton 32111* (NBG!, holotype; K!, 2 sheets, PRE!, isotypes).

4.10. *Leobordea sutherlandii* (Dümmer) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis sutherlandii* Dümmer in Trans. Roy. Soc. South Africa 3(2): 307. 1913 – Type: South Africa, KwaZulu Natal, without precise locality, *Sutherland s.n.* (K!, holotype).

5. *Leobordea* sect. *Synclistus* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis* sect. *Synclistus* B.-E. van Wyk in Contr. Bolus Herb. 14: 157. 1991 – Type: B.-E. van Wyk & Boatwr. (*Lotononis longicephala* B.-E. van Wyk). *Leobordea* sect. *Synclistus* differs from the other sections of the genus in the dense heads of sessile flowers and the small, few-seeded and indehiscent pods that remain enclosed in the persistent calyx. The section includes nine species.

5.1. *Leobordea anthylloides* (Harv.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis anthylloides* Harv. in Harvey & Sonder, Fl. Cap. 2: 59. 1862 $\equiv$ *Lotononis anthyllopsis* B.-E. van Wyk in Contr. Bolus Herb. 14: 164. 1991 – Type: South Africa, Cape Province, Namaqualand, *Wyley s.n.* (TCD, holotype; K!, S!, isotypes).

5.2. *Leobordea diffusa* (Thunb.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Trifolium diffusum* Thunb., Prodr. Pl. Cap.: 136. 1800 – Type: Cape Province, ‘e Cap. B. Spei’, *Thunberg s.n. sub THUNB-UPS 17620* (UPS!, lectotype, designated here).
 $\equiv$ *Lotononis rosea* Dümmer in Trans. Roy. Soc. S. Africa 3(2): 305. 1913, **syn. nov.** – Type: South Africa, Cape Province, Clanwilliam, *Mader 207* (K!, lectotype, designated by Van Wyk, 1991a; GRA!, isoelectotype).

Note. – Thunberg described the broad bracts and flower colour as red, so that the identity of his plant as that later described as *L. rosea* is beyond doubt. The only Thunberg specimen in UPS is chosen as lectotype.

5.3. *Leobordea globulosa* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis globulosa* B.-E. van Wyk in Bothalia 20: 2. 1990 – Type: South Africa, Cape Province, 29.5 km from Touws River to Laingsburg, near Tweedside, *B.-E. van Wyk 2210* (PRE!, holotype).

5.4. *Leobordea lanata* (Thunb.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Trifolium lanatum* Thunb., Prodr. Pl. Cap.: 136. 1800 – Type: South Africa, Cape Province, Heerenlogement, *Thunberg s.n. sub THUNB-UPS 17648* (UPS!, lectotype, designated here).
 $\equiv$ *Lotononis bolusii* Dümmer in Trans. Roy. Soc. South Africa 3(2): 306. 1913, **syn. nov.** – Type: South Africa, Cape Province, near Piquetberg, *Bolus 8431* (K!, lectotype, designated by Van Wyk, 1991a; Z, isoelectotype).

Note. – Thunberg described the flowers of this species as white which confirms the identity of his plant as the species generally known as *Lotononis bolusii* that has cream-coloured and not yellow flowers. The only Thunberg specimen in UPS is chosen as lectotype.

5.5. *Leobordea laticeps* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis laticeps* B.-E. van Wyk in Bothalia 20: 3. 1990 – Type: South Africa, Cape Province, Ceres District, Stompiesvlei, Swartruggens, *Esterhuysen 29334* (BOL!, holotype; C!, K!, M!, MO!, S!, isotypes).

5.6. *Leobordea longicephala* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis longicephala* B.-E. van Wyk in Bothalia 20: 5. 1990 – Type: South Africa, Cape Province, flats east of Prince Alfred’s Hamlet, *Oliver 5063* (PRE!, holotype; K!, MO!, STE!, isotypes).

5.7. *Leobordea oligocephala* (B.-E. van Wyk) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lotononis oligocephala* B.-E. van Wyk in Bothalia 20: 1. 1990 – Type: South Africa, Cape Province, Areb, $\pm$ 27 miles [43.2 km] NE of Springbok, *Van der Westhuizen 276* (PRE!, holotype; K!, MO!, isotypes).

5.8. *Leobordea pentaphylla* (E. Mey.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lipozygis pentaphylla* E. Mey., Comm. Pl. Afr. Austr. 1(1): 79. Feb. 1836 $\equiv$ *Lotononis pentaphylla* (E. Mey.) Benth. in London J. Bot. 2: 605. 1843 – Type: South Africa, Cape Province, ‘Karakuus’, *Drège s.n.* (K!, lectotype, designated by Van Wyk, 1991a; MO!, S!, isoelectotypes).

5.9. *Leobordea polycephala* (E. Mey.) B.-E. van Wyk & Boatwr., **comb. nov.** $\equiv$ *Lipozygis polycephala* E. Mey., Comm. Pl. Afr. Austr. 1(1): 79. Feb. 1836 $\equiv$ *Lotononis polycephala* (E. Mey.) Benth. in London J. Bot. 2: 605. 1843 – Type: South Africa, Cape Province, ‘Khamiesbergen’, *Drège s.n.* (K!, lectotype, designated by Van Wyk, 1991a; BM!, MO!, S!, isoelectotypes).

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Appendix 1. List of characters and character states for eight morphological, cytological and chemical characters scored for the accessions included in the combined molecular and molecular/morphological analysis. Characters were assessed from personal observations or the following literature sources (Polhill, 1974, 1976, 1982; Dahlgren, 1975, 1988; Schutte & Van Wyk, 1988; Van Wyk 1991a; Campbell & Van Wyk, 2001; Boatwright & al., 2008b, 2009, 2010; Boatwright & Van Wyk, 2009; Van Wyk & al., 2010).

(1) **Stipule symmetry:** symmetrical or absent = 0, asymmetrical or single = 1. (2) **Bracteoles:** present = 0, vestigial or absent = 1. (3) **Calyx symmetry:** lateral lobes not fused higher up = 0, lateral lobes fused higher up = 1. (4) **Anther arrangement:** 5+5 = 0, 4+1+5 = 1, 4+6 = 2. (5) **Verrucose upper suture of fruit:** absent = 0, present = 1. (6) **Funicle length:** normal = 0, exceptionally long = 1. (7) **Chromosome base number:** $x = 7 = 0$, $x = 8 = 1$, $x = 9 = 2$. (8) **Cyanogenic glucosides:** absent = 0, present = 1.