Chromosome Numbers in Lotononis and Buchenroedera (Fabaceae-Crotalarieae)
Author(s): Ben-Erik Van Wyk and Anne Lise Schutte
Source: *Annals of the Missouri Botanical Garden*, Vol. 75, No. 4 (1988), pp. 1603-1607
Published by: Missouri Botanical Garden Press
Stable URL: http://www.jstor.org/stable/2399303
Accessed: 21/01/2009 08:23

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

[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.*

[2] *Department of Botany, Rand Afrikaans University, P.O. Box 524, Johannesburg 2000, South Africa.*

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 ($2n$)	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*.

Literature Cited

Baker, J. G. 1871. Suborder I. Papilionaceae. *In:* D. Oliver (editor), Flora of Tropical Africa. Volume 2. London.

Byth, D. E. 1964. Breeding system and chromosome number in *Lotononis bainesii* Baker. Nature 202: 830.

Dahlgren, R. 1964. The genus *Euchlora* Eckl. & Zeyh. as distinguished from *Lotononis* Eckl. & Zeyh. Bot. Not. 117: 371–388.

———. 1967. Chromosome numbers in some South African genera of the tribe Genisteae s. lat. (Leguminosae). Bot. Not. 120: 149–160.

Duemmer, R. A. 1913. A synopsis of the species of *Lotononis* Eckl. & Zeyh. and *Pleiospora* Harv. Trans. Roy. Soc. South Africa 3: 275–335.

Frahm-Leliveld, J. A. 1969. Cytotaxonomic notes on African Papilionoideae. Acta Bot. Neerl. 18: 67–73.

Goldblatt, P. 1981a. Cytology and the phylogeny of Leguminosae. *In:* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics. Royal Botanic Gardens, Kew.

———. 1981b. Chromosome numbers in Legumes II. Ann. Missouri Bot. Gard. 68: 551–557.

Harvey, W. H. 1862. Leguminosae. Pp. 47–66 *in* W. H. Harvey & O. W. Sonder (editors), Flora Capensis. Volume 2. Hodges & Smith, Dublin.

Polhill, R. M. 1968. Miscellaneous notes on African species of *Crotalaria* L. Kew Bull. 22: 169–348.

———. 1973. A revision of *Pearsonia* (Leguminosae—Papilionoideae). Kew Bull. 29: 383–410.

———. 1976. Genisteae (Adans.) Benth. and related tribes (Leguminosae). Bot. Syst. 1: 143–348.

———. 1981. Tribe 29. Crotalarieae (Benth.) Hutch. *In:* R. M. Polhill & P. H. Raven (editors), Advances in Legume Systematics. Royal Botanic Gardens, Kew.

Van Wyk, B-E. 1988. *Lotononis caerulescens* (Fabaceae—Crotalarieae): a new combination for *Lebeckia microphylla*, with notes on the distinction between *Buchenroedera*, *Lebeckia* and *Lotononis*. S. African J. Bot. 54: 175–181.

——— & G. H. Verdoorn. 1988. The chemotaxonomic significance of integerrimine in *Buchenroedera* and *Lotononis* section *Krebsia*. Biochem. Syst. Ecol. 16: 287–289.

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*.