

Studies in the genus *Lotononis* (Crotalariaeae, Fabaceae). 13. Two new species and notes on the occurrence of cleistogamy in the section *Leptis*

B-E. VAN WYK*

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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.

UITTREKSEL

Die voorkoms van blomdimorfisme in die genus *Lotononis* (DC.) Eckl. & Zeyh. word vir die eerste keer gerapporteer. Kleistogame blomme is by 12 spesies van vier verskillende groepe van die seksies *Leptis* (Eckl. & Zeyh.) Benth. en *Oxydium* Benth. waargeneem. Morfologiese verskille tussen chasmogame en kleistogame blomme word bespreek en geïllustreer. Die verskynsel van blomdimorfisme is klaarblyklik 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 reported here for the first time. Morphological differentiation 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 would be much better placed in *Oxydium* (Van Wyk 1990). 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; Arroyo 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 Crotalariaeae than was previously recognized. 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 Crotalariaeae 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 recognize (by the remains of the style) those pods which were formed from cleistogamous flowers. The size and shape of the pods and

TABLE 1.—Flower dimorphism in various groups of the sections *Leptis* and *Oxydium*. The occurrence, observed frequency and degree of differentiation are indicated

Group and species	Frequency	Degree of differentiation
Section <i>Oxydium</i> Benth.:		
<i>Lotononis</i>		
<i>sparisiflora</i> (E. Mey.) B-E. van Wyk	rare	slight
<i>micrantha</i> Eckl. & Zeyh.	rare	slight
Section <i>Leptis</i> (Eckl. & Zeyh.) Benth.:		
<i>Lotononis</i>		
<i>L. calycina</i> group:		
<i>acuticarpa</i> B-E. van Wyk	rare	slight
<i>L. leptoloba</i> group:		
<i>leptoloba</i> H. Bol.	common	distinct
<i>maximiliani</i> Schltr.	common	distinct
<i>L. tenella</i> group:		
<i>tenella</i> (E. Mey.) Eckl. & Zeyh.	very common	distinct
<i>pungens</i> Eckl. & Zeyh.	very common	distinct
<i>L. laxa</i> group:		
<i>laxa</i> Eckl. & Zeyh.	common	distinct
<i>macrosepala</i> Conr.	very common	distinct
<i>crumanina</i> Burch. ex Benth.	very common	slight
<i>burchellii</i> Benth.	very common	slight
<i>maculata</i> Dümmer	very common	slight

* Department of Botany, Rand Afrikaans University, P. O. Box 524, Johannesburg 2000.
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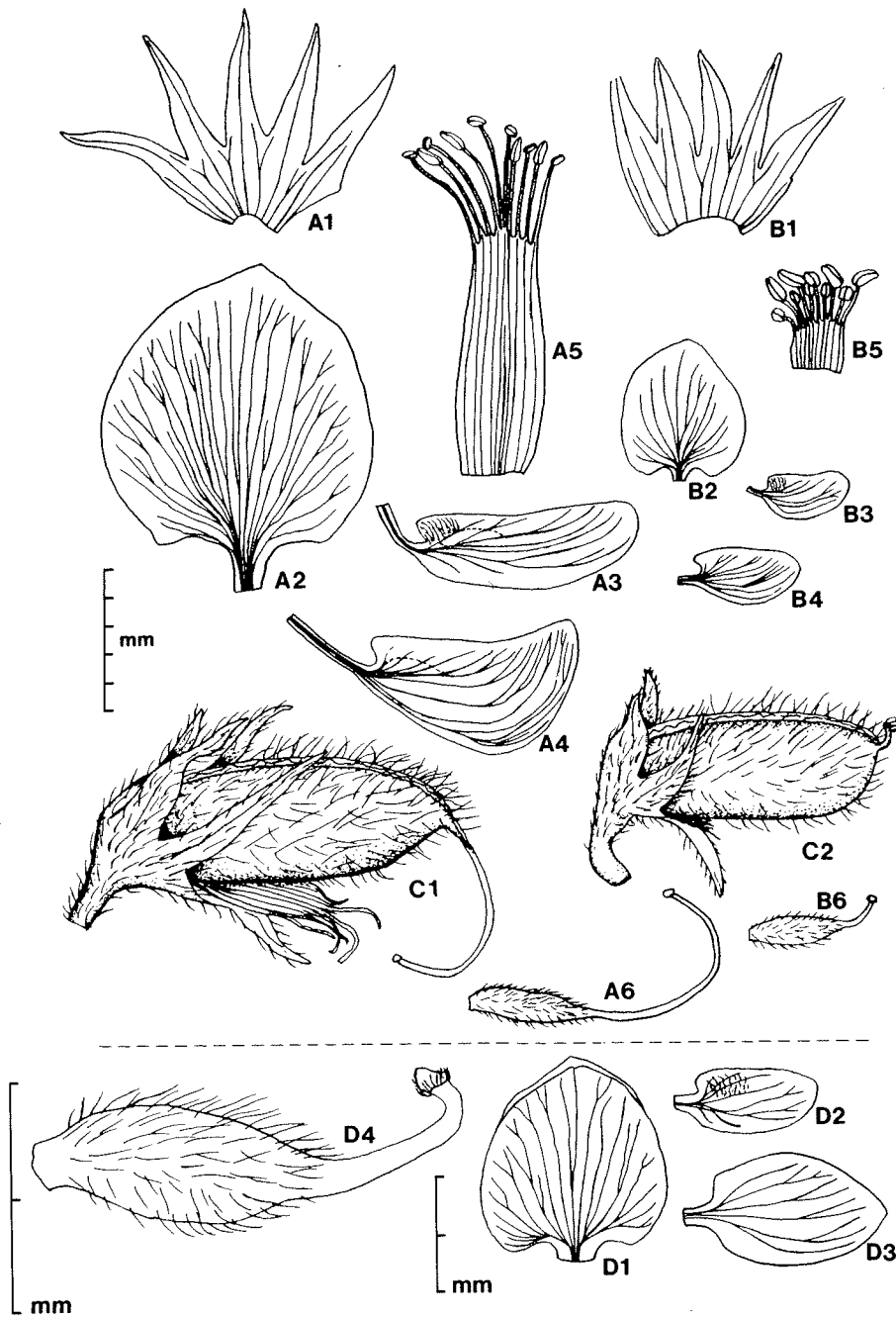


FIGURE 1.—Flower and fruit dimorphism in *Lotononis pungens*. Morphological differences between flowers and pods taken from the same individual (Van Wyk 1626b, JRAU) are shown above, and details of a cleistogamous flower from Schutte 215 (JRAU) below. A1–A6, chasmogamous flower: A1, calyx opened out with upper lobes to the left; A2, standard petal; A3, wing petal; A4, keel petal; A5, androecium; A6, pistil. B1–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–D4, cleistogamous flower: D1, standard petal; D2, wing petal (note sculpturing); D3, keel petal; D4, pistil.

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 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 likelihood 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-cleistogamy (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 1990). 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 illustrate that cleistogamy has limited value as a taxonomic character. *L. venosa* B-E. van Wyk is apparently not cleistogamic but is here placed in the *L. leptoloba* group, 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 (see Table 1).

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) × (0,5–)1–2(–2,5) mm, 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) × (0,5–)1,5–2,5(–3,5) mm. 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 venation; 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 × 13–16 mm, 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 2× 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 × 5 mm, ± 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 are very similar to that of *L. leptoloba*. It differs, however, from this species in its smaller, leafier habit, its narrowly oblong to linear leaves (obovate in *L. leptoloba*), stipules which may be paired (in *L. leptoloba* always single), and in the much larger flowers and pods. 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.

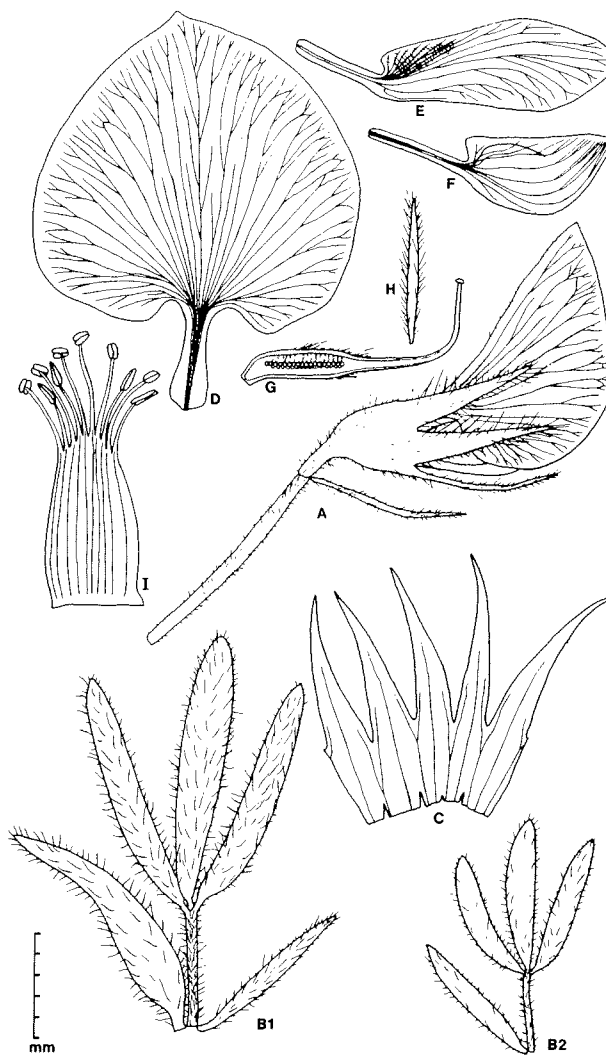


FIGURE 2. —*Lotononis venosa*. A, flower in lateral view showing the long peduncle and the vestiture of the calyx and standard petal; B1 & B2, leaves in adaxial view, showing paired stipules (B1) and a single stipule (B2); C, calyx opened out, upper lobes to the left (vestiture not shown); D, standard petal; E, wing petal; F, keel petal; G, pistil; H, bract; I, androecium. All from *Oliver 8965*.

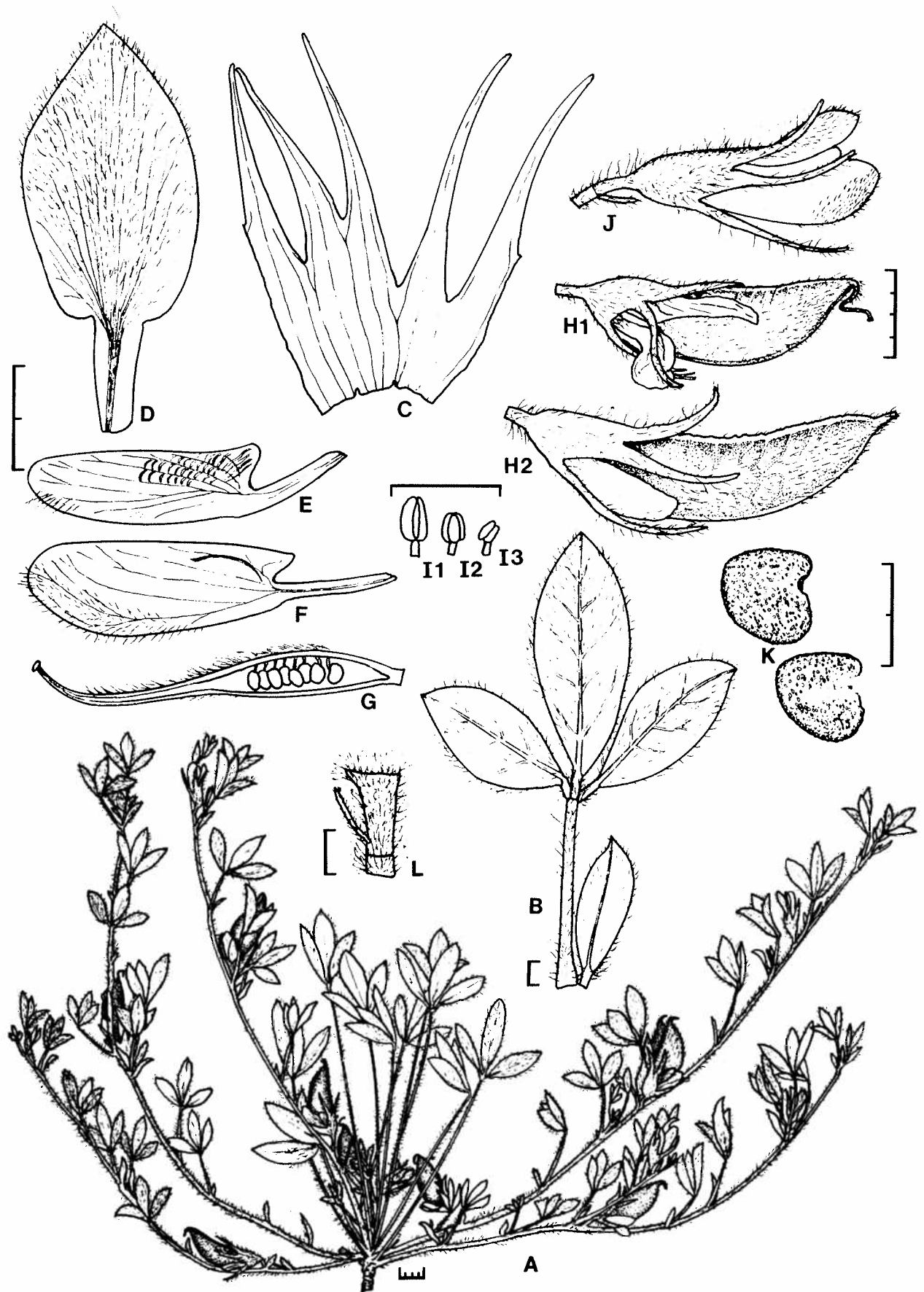


FIGURE 3.—*Lotononis acuticarpa*. A, habit; B, leaf in abaxial view; C, calyx opened out, upper lobes to the left showing the fusion of the lateral lobes (vestiture not shown); D, standard petal; E, wing petal; F, keel petal; G, pistil; H1 & H2, mature fruit in lateral view (note the size, shape and also the pointed, tapering apices). I1–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.

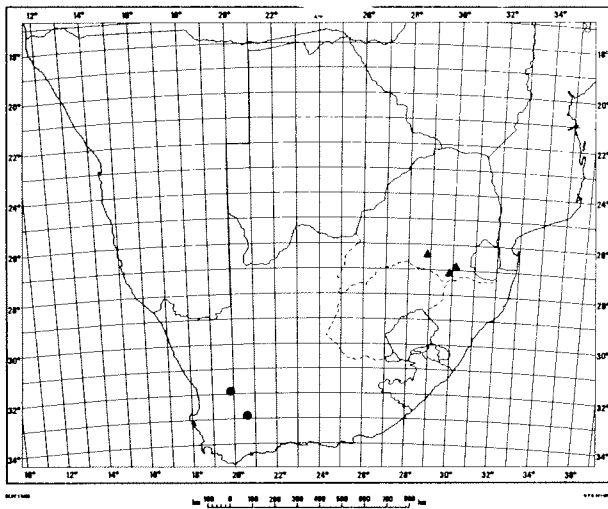


FIGURE 4.—The known geographical distribution of *Lotononis venosa*, ●; and *L. acuticarpa*, ▲.

CAPE.—3119 (Calvinia): ± 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, holo.; STE, iso.).

***Lotononis acuticarpa* B-E. van Wyk, sp. nov.**, *L. calycinae* similis sed habitu foliisque minore, floribus valde minoribus angustioribus, praesertim forma magnitudine fructus differt. Fructus calycem valde superantia (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 annuo, superficie adaxiali glabro foliolorum 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.). Figure 3.

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) × (1–)2–2,5(–3) mm, 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 2× 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 × 2–3,5 mm, 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. adpressae* 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, holo.; JRAU, K, MO, NBG, iso.), 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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REFERENCES

- ARROYO, M.T.K. 1981. Breeding systems and pollination biology in Leguminosae. In R.M. Polhill & P.H. Raven, *Advances in legume systematics* 2: 723–769. Royal Botanic Gardens, Kew.
- BENTHAM, G. 1843. Enumeration of Leguminosae, indigenous to southern Asia, and central and southern Africa. *Hooker's London Journal of Botany* 2: 594–613.
- BYTH, D.E. 1964. Breeding system and chromosome number in *Lotononis bainesii* Baker. *Nature* 202: 830.
- DÜMMER, R.A. 1913. A synopsis of the species of *Lotononis*, Eckl. & Zeyh., and *Pleiospora* Harv. *Transactions of the Royal Society of South Africa* 3: 275–335.
- ERICKSON, E.H. 1975. Variability of floral characteristics influences honey bee visitation to soybean blossoms. *Crop Science* 15: 767–771.

- HANSON, C.H. & COPE, W.A. 1955. Reproduction in the cleistogamous flowers of ten perennial species of *Lespedeza*. *American Journal of Botany* 42: 624–627.
- HARMS, H. 1909. Über Kleistogamie bei der Gattung *Argyrolobium*. *Berichte der Deutschen Botanischen Gesellschaft* 27: 85–96.
- HARMS, H. 1917. Weitere Beobachtungen über Kleistogamie bei afrikanischen Arten der Gattung *Argyrolobium*. *Berichte der Deutschen Botanischen Gesellschaft* 35: 175–186.
- HARVEY, W.H. 1862. Leguminosae. In W.H. Harvey & O.W. Sonder, *Flora capensis* 2: 47–66. Hodges & Smith, Dublin.
- SCHUTTE, A.L. 1988. 'n Taksonomiese studie van die genus *Dichilus* DC. (*Fabaceae*–*Crotalariaeae*). M.Sc. thesis, Rand Afrikaans University, Johannesburg.
- UPHOF, J.C.Th. 1938. Cleistogamic flowers. *The Botanical Review* 4: 21–49.
- VAN WYK, B-E. 1990. Studies in the genus *Lotononis*. 12. Four new species of the *L. falcata* group, section *Leptis*. *Bothalia* 20: 9–16.
- WOJCIECHOWSKA, B. 1972. Pollination and fertilization in *Ornithopus* sp. *Genetica Polonica* 13: 37–52.