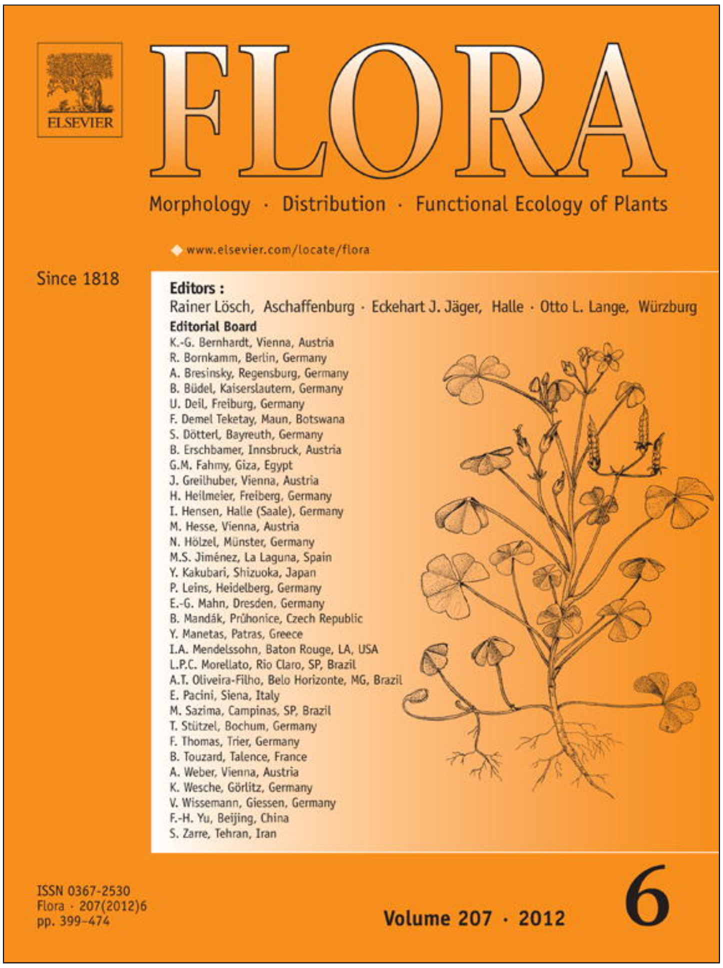
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The systematic value of flower structure in *Crotalaria* and related genera of the tribe Crotalarieae (Fabaceae)

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ABSTRACT

Flowers in the tribe Crotalarieae of the family Fabaceae are generally adapted to bee pollination mechanisms. Molecular systematics have recently provided a major step towards a profound insight into generic relationships, thereby creating the opportunity to re-evaluate the taxonomic and functional significance of flower structure in the tribe, with emphasis on the large genus *Crotalaria*. A representative sample of flowers from 211 species was dissected to record morphological character states. These data were supplemented from the literature to allow for generalizations for the tribe as a whole. Six structural–functional flower types were identified: (1) pump; (2) gullet; (3) hugging; (4) saddle; (5) tunnel and (6) brush (saddle and tunnel types described here for the first time). *Crotalaria* uniquely has the brush type, characterized by a rostrate keel, highly dimorphic anthers, stylar trichomes and elaborate callosities on the standard petal. Remarkably, *Crotalaria* and *Bolusia* are the only genera of the tribe Crotalarieae with callosities present in all of the species. In other genera, callosities are generally absent or infrequent. Trends towards specialization of pollination syndromes are apparent as assemblages of apomorphic states that co-occur in what we refer to here as "specialized flowers"; individual characters are labile or non-homologous (e.g. callosities) and diagnostically less valuable. Unique combinations of flower characters are often useful to support current generic concepts in Crotalarieae.

Introduction

The Crotalarieae (Benth.) Hutch. (Papilionoideae, Fabaceae) is part of the core genistoids (Crisp et al., 2000) and comprises ca. 1204 species (Van Wyk, 2005). Generic delimitations within the tribe have been changed as a result of morphological and chemotaxonomic studies (Van Wyk and Schutte, 1995) and more recently of molecular systematic studies (Boatwright et al., 2008b, 2009, 2011). Three clades and 16 genera are now recognized as shown in Fig. 1.

Specialization of reproductive characters has evolved several times within Crotalarieae which has raised questions about the functionality of the flower structure (Van Wyk, 1991). Flowers from the subfamily Papilionoideae have a zygomorphic symmetry and are mostly adapted to bee pollination (Arroyo, 1981; Etcheverry et al., 2008; Polhill, 1976). The papilionoid flower consists of standard, wing and keel petals, the last-mentioned of which enclose the ovary and style.

In Crotalarieae, the androecial filaments are fused into a tube that is open on the upper side (Polhill, 1976; Van Wyk, 1991). Some genera have special floral features to increase protection of the ovary and to optimize pollen dispersal over a longer period of time (Polhill, 1976). *Bolusia* is exceptional in having a strange, helically coiled keel. *Crotalaria* has numerous specialized flower features (i.e. a combination of apomorphic states). It is also the largest genus within the tribe and includes ca. 700 species (Jianqiang et al., 2010). Polhill (1982) revised the African and Madagascan species and informally recognized two groups: (1) an "unspecialized group" characterized by a rostrate keel with an untwisted beak, callosities present on the standard petal blade and claw and trichomes usually distributed along one side of the style; and (2) a "specialized group" with a highly rostrate keel, usually a twisted beak, callosities present on the standard petal blade only and trichomes distributed along two sides or along a single spiral line on the style (Polhill, 1976, 1982).

Polhill (1976) noted different ways in which pollen is released by various genera of the Crotalarieae. Four basic types of pollen presentation in papilionoid legumes have been described by Delpino (1868/1869): valvular, explosive, brush, and pump types (Delpino, 1868/1869; Etcheverry, 2001a,b; Leppik, 1966; Westerkamp, 1997). Lavin and Delgado (1990) distinguished four variations of the brush type, based on the distribution of the trichomes: (1) the ciliate style, with trichomes present on the ovary extending onto the proximal area of the style (but the function thereof is uncertain); (2) the ciliate- and (3) penicillate stigma, with trichomes present above the anthers on the distal area of the style prior to

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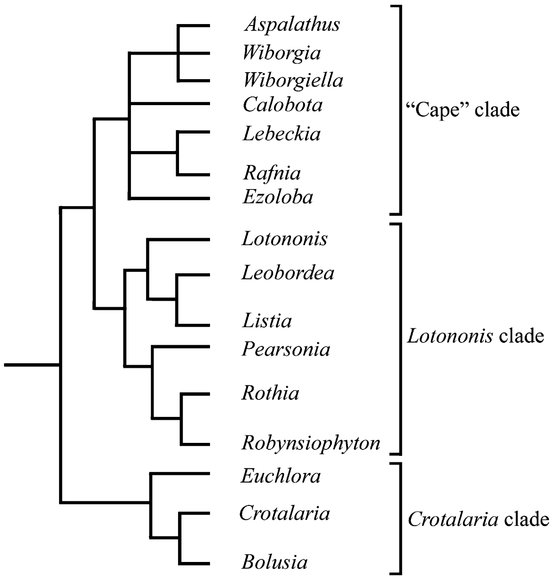

Fig. 1. Cladogram (based on morphological and molecular evidence) of phylogenetic relationships of all the genera of the tribe Crotalarieae, showing the "Cape", *Lotononis* and *Crotalaria* clades, as published by Boatwright et al. (2008b).

anthesis, thus preventing autogamy and (4) the true brush type, with erect trichomes (uniform in shape, density and orientation) that are densely arranged on the distal end of the style at anthesis; these serve to brush the pollen out of the keel beak after anthesis, thereby promoting xenogamy and delayed self-pollination (Etcheverry, 2001a,b,c, 2003). In *Crotalaria* species, pollen is presented through a pollen pump mechanism, with the narrow keel beak serving as a cylinder and the style and anthers acting as a piston; the pollen is pushed or pumped out through a brush action when the flower is tripped (Arroyo, 1981).

With new information and insight available into generic relations within the Crotalarieae, the opportunity has arisen to study the pattern of flower morphological variation amongst the newly circumscribed genera, not only to better understand the flower as a functional unit, but also to evaluate the taxonomic value of the shape of the petals, the presence of callosities, the degree of anther dimorphism and the shape and vestiture of the style. The various pollination syndromes in the tribe are described, with special emphasis on flower structure in the large genus *Crotalaria*.

Materials and methods

Taxon sampling

Flowers of 211 species (226 flower samples in total) representative of all genera in Crotalarieae were obtained from field work and rich herbarium collections from the following herbaria: BOL, C, CEN, GRA, JRAU, K, NBG (including SAM), NU, PRE, STE, UPS and WIND. Voucher information, including author citations of individual species and infrageneric groups are listed in Appendix 1.

Morphology

Herbarium material was rehydrated for a few minutes in boiling water. Rehydrated and FAA-fixed material was dissected under a WILD M3Z stereomicroscope. Anther lengths were recorded using AcQuis v.4.0.1.7 digital image program. Callosities, gynoecia and anthers were studied under an Olympus SZX16 stereomicroscope and photographed with a Color View IIIu digital camera. Various flower morphological characters were recorded for all genera and are listed in Appendix 1.

Results

Reproductive morphology

Three calyx types are apparent in the Crotalarieae (Table 1): (1) the "lebeckioid" type (e.g. Fig. 2B1) with subequal calyx lobes; (2) the bilabiate type (e.g. Fig. 2L7) with the two upper calyx lobes and the three lower ones fused higher up forming an upper and lower lip and (3) the "lotononoid" type (e.g. Fig. 2H3) with the upper and lateral lobes on either side fused higher up and the lower lobe often narrower (Polhill, 1976).

The colour of the corolla in Crotalarieae is usually pale to bright yellow, but variation includes several other colours, for example red (Fig. 2L10 – outer side of standard blade), violet (Fig. 2H1), yellowish-green (Fig. 2L12) and whitish, lilac to purple or rose-coloured (Fig. 2M1, L5 and L11). Colour patterns are present in some species of the tribe, for example the darker coloured beak tip in *C. agatiflora* (Fig. 2L12) or in *Lotononis brachyantha* and *L. pallidirosea* (Fig. 2H2 and H3), but these do not seem to have any diagnostic value at intergeneric or infrageneric level. Flower colour sometimes changes after pollination from yellow to different shades of pink, orange, red or brown leading to reduced pollinator visits (Arroyo, 1981). The visual spectrum of bees is shifted to the shorter wavelengths so they are unable to see true red and will therefore concentrate on the yellow flowers which are not yet pollinated. The shape of the standard petals is variable in the Crotalarieae and not of much diagnostic significance.

The shape of the wing petals (oblong to obovate) and their length relative to the keel (longer or shorter) vary and are of little diagnostic value at generic level. Sculpturing is present in the upper basal area in all genera of the tribe except *Bolusia* (and also not in all species of *Rafnia* section *Colobotropis*). The absence of cavae (Stirton, 1981) is related to the pollination syndromes (see later).

The shape of the keel apex generally varies from obtuse (or blunt) to rostrate (Fig. 2; Table 1). When the keel tip is obtuse, the curve or bend of the keel is typically slightly above the middle. Rostrate keels usually have the curve about the middle or below (Fig. 2L3–L12). The beak of the keel is flat in all genera except *Crotalaria*, *Bolusia* and three species of *Lebeckia* where they are variously twisted.

The anther filaments of all genera of the Crotalarieae are fused into a tube that is open along the upper side. *Crotalaria* species are distinct from all others in having the two upper edges of the staminal tube interlocking with one another, thus forming a "closed" tube. The anthers are usually dimorphic (Fig. 2T). Oblong, basifixed anthers alternate with short, dorsifixed ones and the carinal anther is often intermediate in size and attachment. In Fig. 3, the basifixed, carinal and dorsifixed anthers of selected members of the Crotalarieae are shown (from left to right). Anther configurations for all species studied are listed in Appendix 1. In Fig. 4, the degree of dimorphism (expressed as the ratio of basifixed to dorsifixed anther length) is shown for all the genera studied. The range and mean values (of the species listed in Appendix 1) are indicated for each genus. Dimorphism is most pronounced in *Crotalaria*, followed by *Lotononis*, *Rafnia*, *Bolusia* and *Aspalathus* (Fig. 4). The anthers are monomorphic in *Pearsonia*, *Rothia* and *Robynsiophyton* (Fig. 4).

The pistil is almost invariably up-curved, except in the gullet type flowers (*Pearsonia*, *Robynsiophyton* and *Rothia*) where it is either straight or down-curved (Boatwright and Van Wyk, 2009; Polhill, 1976; Van Wyk and Schutte, 1995). When the keel apex is

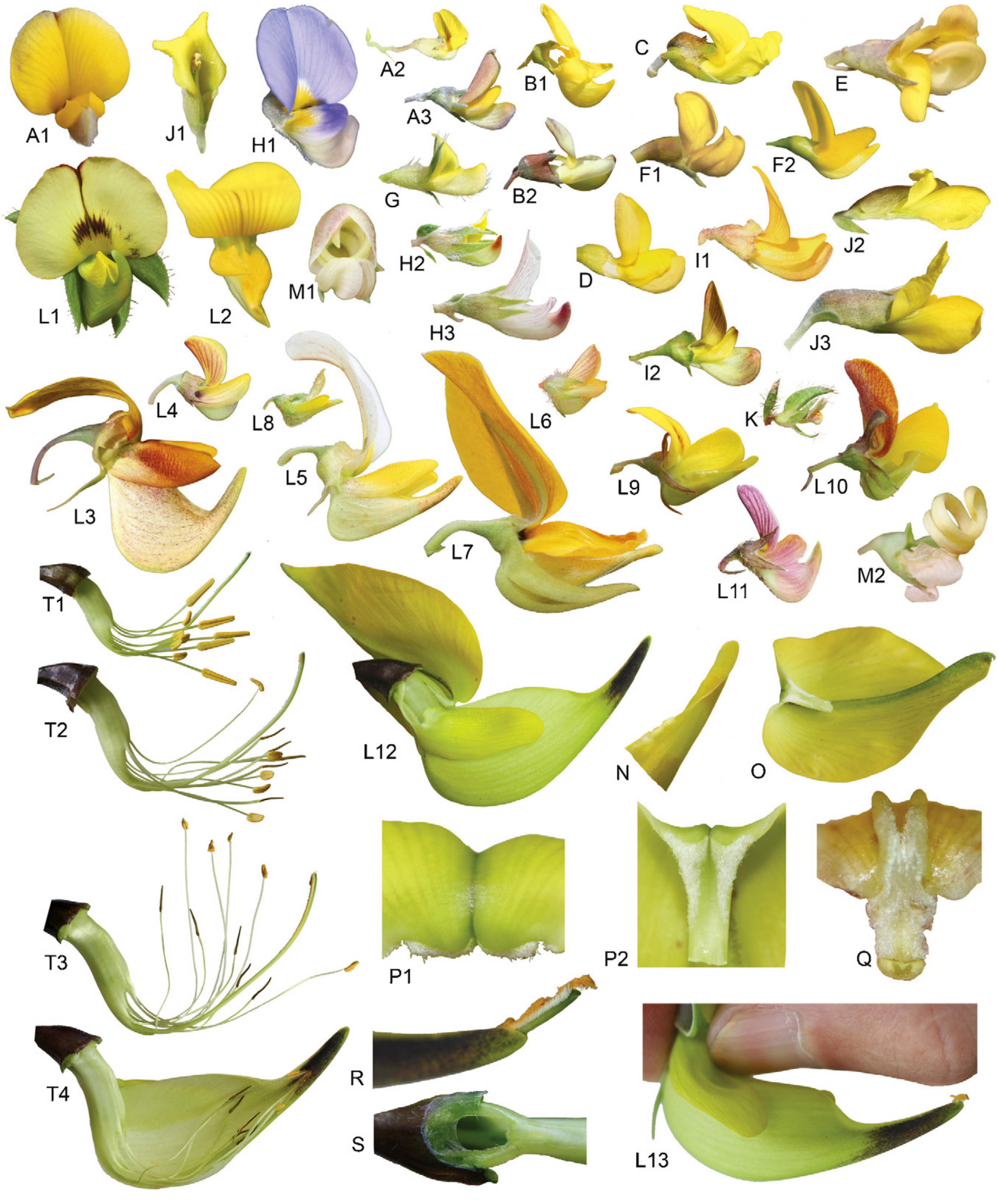

Fig. 2. Flowers of the tribe Crotalarieae (A–M), showing the variation in structure and colour. Note the peculiar violet-blue (H1) and purple (L11) colours, enlarged upper calyx lobes (K), calyx lobes fused at the tips (L7), abruptly contracted calyx tips (L10), coiled keel (E and M2) and twisting of the keel (L7, L9 and N). Details of the flowers of *Crotalaria agatiflora* (L13–P and R–T) and *C. virgultalis* (Q) to illustrate the function of individual flower parts as part of the pollen pump pollination syndrome. Flowers in front and lateral view: (A1) *Aspalathus kougaënsis*; (A2) *A. perforata*; (A3) *A. nivea*; (B1) *Wiborgia fusca*; (B2) *W. mucronata*; (C) *Wiborgiella sessilifolia*; (D) *Calobota pungens*; (E) *Lebeckia pauciflora*; (F1) *Rafnia capensis*; (F2) *R. thunbergii*; (G) *Leobordea platycarpa*; (H1) *Lotononis sericophylla*; (H2) *L. brachyantha*; (H3) *L. pallidirosea*; (I1) *Listia bainesii*; (I2) *L. heterophylla*; (J1 and J3) *Pearsonia sessilifolia*; (J2) *P. aristata*; (K) *Rothia hirsuta*; (L1) *Crotalaria obscura*; (L2) *C. spartioides*; (L3) *C. laburnifolia*; (L4) *C. lanceolata*; (L5) *C. virgultalis*; (L6) *C. pisicarpa*; (L7) *C. juncea*; (L8) *C. sphaerocarpa*; (L9) *C. kurtii*; (L10) *C. platysepala*; (L11) *C. dissitiflora*; (L12 and L13) *C. agatiflora*; (M1 and M2) *Bolusia amboensis*; (N) twisted keel beak; (O) standard petal; (P1) ridge callosities on the standard petal; (P2) ridge callosities on the standard claw; (Q) columnar callosities on the standard petal; (R) style emerging from the keel, showing pollen and trichomes (white) along the upper edge; (S) opening at the bottom of the staminal tube leading to the nectar chamber; (T1) anthers one day before anthesis; (T2) anthers at anthesis; (T3) anthers ± two days after anthesis; (T4) keel opened out to show position of androecium and gynoecium.

Table 1
Summary of the most important diagnostic flower characters in the tribe Crotalarieae.

	Calyx type	Keel apex shape	Keel beak	Anther number and configuration	Callosity	Callosity type	Pollination syndrome
Genus and infrageneric group (where available)	+ "lebeckioid" ++ bilabiate +++ "lotononoid"	– oblong/obtuse + rostrate	– flat + twisted ++ spiral +++ coiled	Monomorphic: – 10, 9 or 5 Dimorphic: + 4 + 6 ++ 4 + 1 + 5 +++ 5 + 5	– absent + single ++ paired	– absent + ridge ++ disc +++ lamelliform ++++ columnar	– pump –– gullet ––– saddle + hugging ++ brush +++ tunnel
Aspalathus	+	–/+	–	++	–/++	+	–
Bolusia	+	+	+++	+++	+	++	+++
Calobota	+	–	–	++	–	–	–
Crotalaria							
Section *Calycinae*	+/++	+	+	+++	++	+++	++
Section *Chrysocalycinae*	+/++	+	–	+++	++	+	++
Section *Crotalaria*	+	+	+	+++	++	+/++/+++	++
Section *Dispermae*	+	+	+	+++	++	++	++
Section *Geniculatae*	+	+	–	+++	++	+/++/++++	++
Section *Grandiflorae*	+/+++	+	–	+++	++	+	++
Section *Hedriocarpae*	+	+	–	+++	++	+	++
Section *Schizostigma*	+	+	+	+++	++	+/++	++
Euchlora	+	+	–	+	–	–	–
Ezoloba	+	+	–	+++	–	–	–
Lebeckia	+	+	–/++	+++	–	–	–/+
Leobordea	+++	–	–	+	–	–	–
Listia	+++	–	–	++	–	–	–
Lotononis							
Section *Aulacinthes*	+++	–	–	++	–	–	–
Section *Buchenroedera*	(+)/+++	–	–	++	–	–	–
Section *Cleistogama*	+	–	–	++	–	–	–
Section *Krebsia*	+++	–	–	++	++	+	–
Section *Lotononis*	+++	+	–	+/++	–	–	–
Section *Monocarpa*	+	+	–	++	–	–	–
Section *Oxydium*	+/+++	+	–	+/++	+	+	–
Section *Polylobium*	+++	–	–	++	–	–	–
Pearsonia	(+)/+++	–	–	–	–	–	––
Rafnia							
Section *Rafnia*	+	+	–	+/++/+++	–/++	–/(+)/++	–
Section *Colobotropis*	++	–/+	–	+/++/+++	–/++	–/(+)	–––
Robynsiophyton	+	–	–	–	–	–	––
Rothia	+	–	–	–	–	–	––
Wiborgia	+	–/+	–	++	–	–	–
Wiborgiella	+	–/+	–	+	–	–	–

rounded or obtuse, the curvature of the style (and keel) is near the middle or above the middle. The style curvature in rostrate keels is in the middle in all genera (Fig. 3O) or below the middle (in several species of *Crotalaria*, Fig. 3R). Those species of *Crotalaria* with angular keels (i.e. with the style curvature below the middle) have geniculate styles (i.e. with a knee-like bend, as shown in Fig. 3R) with the distal part typically straight or only slightly curved. The style is usually glabrous in Crotalarieae with ciliate stigmas (defined by Lavin and Delgado, 1990), but in *Crotalaria* the brush type style is always present with trichomes arranged in an upward direction on the distal part (Polhill, 1976, 1982). Three types of trichome distributions are apparent in *Crotalaria*, namely a single line along the upper edge (Fig. 3Q), two lines along the sides (Fig. 3R) or distributed all around (Fig. 3S) the style. In those flowers where the keel is twisted, the hairs are spirally arranged because the style is also twisted.

Little attention has previously been given to the presence of callosities in Crotalarieae although these structures are known from other genera in the subfamily (Polhill, 1976). Callosities are found at the base of the standard petal as callous swellings or very prominent appendages. These are usually paired and present on the claw, extending onto the blade or it may be restricted to the blade (Fig. 2P2 and Q; Table 1). Only two genera of the tribe invariably have callosities, namely *Bolusia* and *Crotalaria*. Three other genera show a variable occurrence of callosities, namely *Aspalathus* (10 out of 280 species), *Lotononis* (10 out of 89 species) and *Rafnia* (13 out of 19 species). The callosities found in each of these genera are quite distinct and unlikely to be homologous. *Aspalathus* species have raised ridges (mainly on the blade), *Rafnia* species have swollen lamina margins at the point of attachment of the blade or rounded swellings at the base of the blade, *Lotononis* species have paired (section *Krebsia*) or single (section *Oxydium*) callosities pointing downwards (i.e. towards the base of the claw), *Crotalaria* species have paired callosities in the middle of the blade near the base often extending onto the claw and *Bolusia* species have a single, central callosity at the base of the blade. Diagnostic reproductive characters are summarized in Table 1.

Discussion

Systematic value of reproductive characters

Polhill (1976) mentioned in his detailed studies of the tribe Genisteae (Adans.) Benth. *sensu lato* (i.e. including the Crotalarieae) that genera are distinguished by a combination of unique characters rather than single apomorphies. Recent systematic studies in the Crotalarieae (especially of *Lebeckia sensu lato*) have led to new insights into combinations of morphological characters, such as the configuration of anthers (5 + 5, 4 + 6 or 4 + 1 + 5) and the structure of the fruit wall (Boatwright et al., 2008b; Le Roux et al., 2011). Trends towards specialization of flowers are re-evaluated and characters of diagnostic value are briefly discussed here, followed by a short

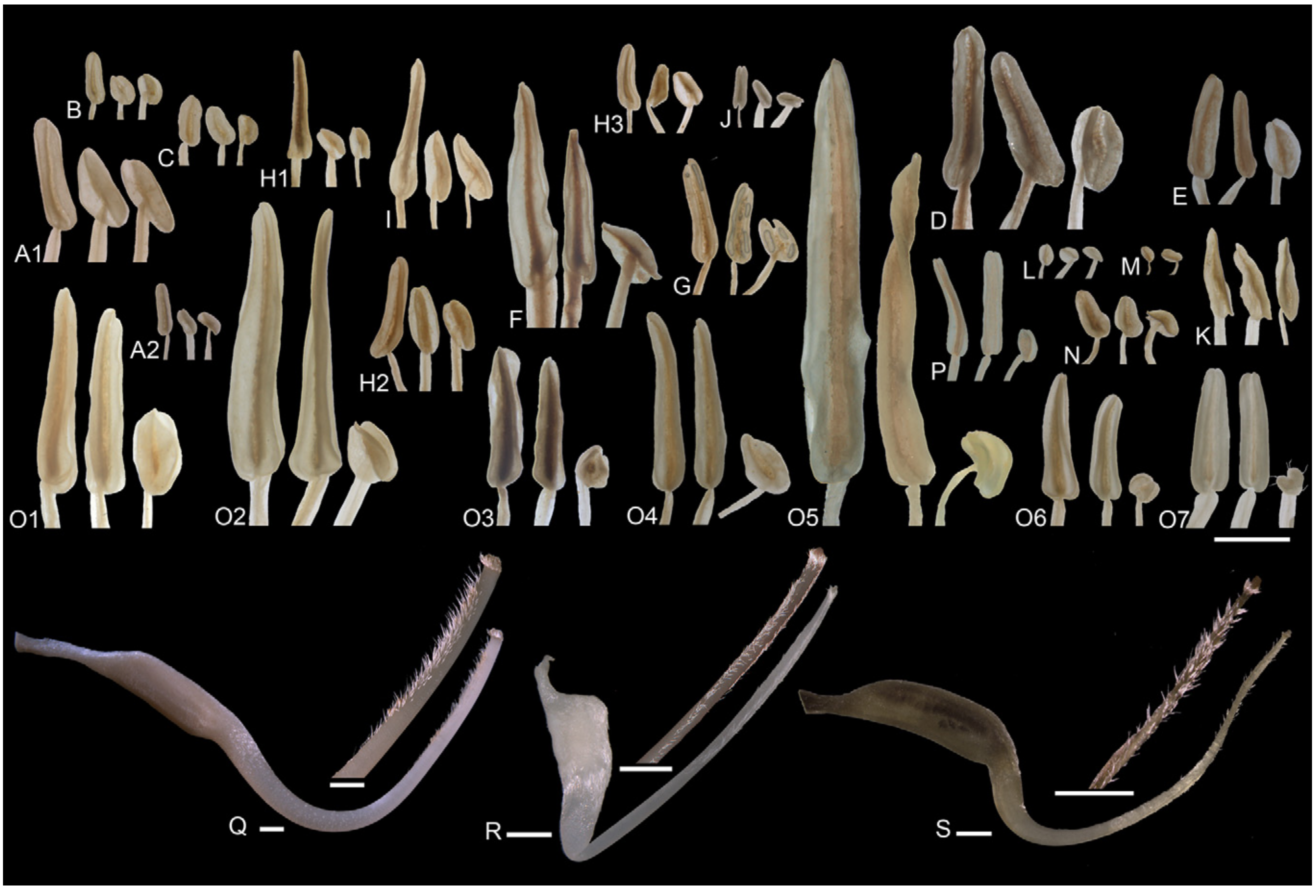

Fig. 3. Variation in the size and configuration of anthers (A–P) in the tribe Crotalarieae (basifixed anther on the left, carinal anther in the middle and dorsifixed anther on the right). The basic configurations are 4 + 1 + 5 (e.g. A1 and A2), 4 + 6 (e.g. C, N, and I), 5 + 5 (e.g. O and P). Note the extreme dimorphism in H1, O and P, and the lack of dimorphism in K and L. The three basic patterns of trichome distributions on the styles of *Crotalaria* species (Q–S): (Q) hairs in a straight line along the upper edge of the style; (R) hairs in two spiral lines along the sides of the style; (S) hairs distributed all around the style. Voucher specimens: (A1) *Aspalathus tridentata* [*Van Wyk 2437* (JRAU)]; (A2) *A. linearis* [*Niemand 3* (JRAU)]; (B) *Wiborgia humilis* [*Boatwright et al. 216* (JRAU)]; (C) *Wiborgiella inflata* [*Barker 204* (JRAU)]; (D) *Calobota cytisoides* [*Pretorius 105* (NBG)]; (E) *Lebeckia sepiaria* [*Baker 6515* (NBG)]; (F) *Rafnia angulata* [*Rycroft 1810* (NBG)]; (G) *Ezoloba macrocarpa* [*Hardy 853* (K)]; (H1) *Lotononis carnea* [*Van Wyk 2411* (JRAU)]; (H2) *L. dissitinodis* [*Acocks 20502* (BOL)]; (H3) *L. dissitinodis* [*Acocks 20502* (BOL)]; (I) *Leobordea longiflora* [*Strauss 135* (NBG)]; (J) *Listia bainesii* [*Van Wyk and Theron 4579* (PRE)]; (K) *Pearsonia bracteata* [*Van Wyk 3103* (JRAU)]; (L) *Rothia hirsuta* [*Boatwright 253* (WIND)]; (M) *Robynsiophyton vanderystii* [*Richards 5309* (K)]; (N) *Euchlora hirsuta* [*Schutte 290* (JRAU)]; (O1 and Q) *Crotalaria monteiroi* [*Le Roux et al. 40* (JRAU)]; (O2) *C. phylloloba* [*Mhoro 868* (UPS)]; (O3) *C. pallida* [*Lautenbach s.n.* (JRAU)]; (O4) *C. flavicarinata* [*Curtis BC1485A* (WIND)]; (O5) *C. juncea* [*Le Roux et al. 36* (JRAU)]; (O6 and R) *C. dinteri* [*Le Roux et al. 57* (WIND)]; (O7) *C. luondeensis* [*Iwarsson 1091* (UPS)]; (P) *Bolusia amboensis* [*Boatwright et al. 248* (WIND)]; (S) *C. pearsonii* [*Dean 664* (JRAU)]. Scale bars = 1 mm.

review and discussion of the four known pollination syndromes and the two new ones that have been revealed by this study.

Calyx

The calyx is traditionally a useful character in the tribe Crotalarieae because it tends to be relatively conservative, so that genera and infrageneric groups can be distinguished by the different types of fusion of the lobes. The calyx appears to be important in supporting the petals and directing their movement during the process of pollination, when the pollinator "opens" the flower to gain access to the nectar. Dorsal lobes are often fused higher up and the sinus between them supports the standard petal and prevents lateral movement; lateral lobes keep the wing petals from moving sideways and the carinal lobe is often narrower and/or shorter to allow free downward movement of the keel. The "lebeckioid" type (Fig. 2A–E, F2, L1–L6 and L8–L11) is present in most genera with a pump pollination syndrome (see below) and allows unimpeded movement of the corolla during pollination. Reflexed calyx lobes further enhance the free movement of the petals. The relatively long and curved claw of the standard petal (e.g. in *Wiborgia*, Fig. 2B) seems to act as a "spring" to ensure that the petal returns to its original position after the insect visit but the role of the very short calyx in this genus is not entirely clear.

Bilabiate calyces (Fig. 2F1 and L7) have the two upper lobes united into an upper lip and the three lower ones fused into a lower lip. The upper lip supports the standard petal and prevents it from bending backwards beyond a certain point; the lower lip similarly supports the keel and regulates its downward movement. This type of calyx is typical of the tribe Genisteae but also occurs in some species of *Crotalaria* (e.g. Fig. 2L7). In a few *Crotalaria* species the lobes of each lip are fused at their tips, thus providing additional support. In *Rafnia* section *Colobotropis* the flower becomes resupinate and the large, upper lip supports the standard petal (which in this case acts as the landing platform for the pollinator).

"Lotononoid" calyces (Fig. 2G–J) have the upper and lateral lobes on either side fused higher up in pairs, thus providing support for the wing petals and/or the strongly reflexed standard petal. The flowers of *Pearsonia* are resupinate and the four upper calyx lobes support the standard petal which is the landing platform during pollination. *Rothia* has a "lebeckioid" calyx type, but the upper two calyx lobes are much enlarged. These flowers are also resupinate and the enlarged calyx lobes serve to support the standard petal during pollination. The few bird-pollinated flowers in *Crotalaria* have "lotononoid" calyces, apparently to restrict lateral movements

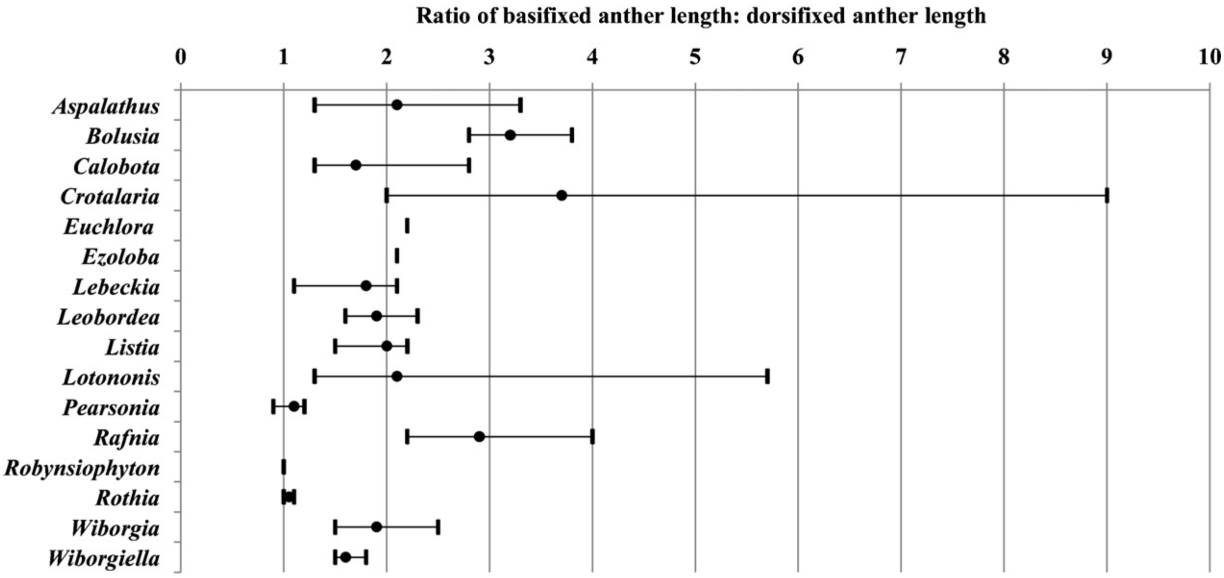

Fig. 4. Variation in anther dimorphism in all genera of the tribe Crotalarieae, expressed as the ratio of basifixed anther length:dorsifixed anther length. For each genus, the mean and range are indicated, based on the samples listed in Appendix 1. Note the extreme dimorphism in species of *Crotalaria*, *Lotononis*, *Rafnia* and *Bolusia* and the lack of dimorphism in *Pearsonia*, *Robynsiophyton* and *Rothia*.

of the petals during pollination and to enhance the lifting of the standard petal and the simultaneous lowering of the keel.

Keel

The shape of the keel petal and its apex are diagnostically important in the Crotalarieae. According to Polhill (1976), "unspecialized flowers" tend to have keels with obtuse apices and the curvature above or about the middle (e.g. Fig. 2B1 and F–I). In contrast, "specialized flowers" have rostrate keels with the curvature mostly in the lower third (Polhill, 1976), as shown in Fig. 2 (L5 and L8–L10). Further modification occurs in the twisting or coiling of the beak (Fig. 2E and M2). In some species of *Crotalaria* section *Chrysocalycinae* subsection *Glaucae* the keel tips are circumflexed (to about 90°), but in a large number of species from various sections within the genus, the flowers are highly modified and the keel tips are completely twisted (Fig. 2N) – a unique character within the tribe. The keel is spirally half turned (less than 180°) in the *Lebeckia pauciflora* group (Fig. 2E) and helically coiled through several turns in *Bolusia* (Fig. 2M2) forming a tunnel (Polhill, 1982; Le Roux and Van Wyk, 2009; Van Wyk et al., 2010). The close relationship between *Bolusia* and *Crotalaria* has been mentioned previously (Boatwright et al., 2008b; Polhill, 1976, 1982). The presence of the coiled keel in *Bolusia* and a strongly incurved keel beak (becoming slightly coiled) in *C. cornu-ammonis* seemed to provide a link between the two genera (Polhill, 1976, 1982) but it has become clear in this study that the keels of the two genera are only superficially similar. The presence of a lanate-pilose to tomentose vestiture on the upper edge of the keel is diagnostic for *Crotalaria* section *Chrysocalycinae* subsections *Incanae* and *Stipulosae* (Polhill, 1982). These interlocking, sometimes curly trichomes serve to bind the two keel petals along their upper edges and ensure that the keel protects the androecium and gynoecium and functions as a single unit during pollination.

Anthers

Members of the tribe Crotalarieae have different anther arrangements (Polhill, 1976) that are informative at generic level (Boatwright et al., 2008a; Boatwright and Van Wyk, 2009). Species with obtuse keel apices tend to have either monomorphic anthers (those genera that invariably have straight or down-curved styles) or dimorphic anthers (rounded or geniculate styles) with an arrangement of four long, basifixed anthers and six, shorter dorsifixed anthers (4 + 6) or four basifixed anthers, the carinal anther intermediate to varying degrees and five, shorter dorsifixed anthers (4 + 1 + 5). Flowers with rostrate keels have anthers markedly differentiated into five long, basifixed anthers and five short, dorsifixed anthers (5 + 5; Polhill, 1976). All three configurations mentioned above are present in different species of *Rafnia*. Anther dimorphism appears to be directly linked to the degree to which the keel tip is rostrate, and is therefore most strongly developed in *Crotalaria* species (Fig. 2T, 3 and 4), followed by *Lotononis*, *Rafnia*, *Bolusia* and *Aspalathus* (Fig. 4).

Callosities

The presence of callosities on the standard petal is often mentioned in literature, but this study has clearly shown that the systematic value of callosities has been under-estimated. Callosities are sporadically present in several genera but consistently present only in *Bolusia* and *Crotalaria*. Details of their structure show that they are not homologous, with each genus having its own unique type or types of callosities. The paired callosities in *Aspalathus* are present in (but not restricted) the *Rostratae* group and do not seem to have diagnostic value at infrageneric level. *Rafnia* has paired ridge or disc-type callosities, but these are not restricted to either of the two sections. The callosities in *Lotononis* are either single (section *Oxydium*) or paired (section *Krebsia*) and have the appearance of very short lobes that point downwards (towards the base of the claw). Contrary to literature reports, *Bolusia* does not have paired callosities but invariably a single, central callosity restricted to the base of the standard petal blade. This character is an additional apomorphy for the genus that separates it from *Crotalaria*, which invariably have paired callosities.

Each of the genera of the tribe Crotalarieae seems to have a unique combination of characters as shown in Table 1.

The flower as a functional unit

The papilionoid flower structure is adapted to melittophily or bee-pollination (Arroyo, 1981; Etcheverry, 2001b; Leppik, 1966; Polhill, 1976; Tewari and Nair, 1978). Observations of *Anthophorini*

(Apidae), *Xylocopini* (Apidae) and *Megachilinae* (Megachilidae) species visiting flowers of Crotalarieae have been reported (Arroyo, 1981; Campbell and Van Wyk, 2001; Etcheverry, 2001a, 2003; Gess and Gess, 2006). The standard petal (sometimes with nectar guides) attracts pollinators while the wing petals and keel form a landing platform. Cavae (sculpturing) on the wing petals creates a rough area to ease gripping and balance of the pollinator while foraging nectar (Arroyo, 1981; Stirton, 1981). Ornithophily is rare in the Crotalarieae, with only a few species of *Crotalaria* reported to be bird-pollinated [*Crotalaria agatiflora*, *C. exaltata*, *C. grevei* and *C. humbertii* (Du Puy and Labat, 2002; Polhill, 1976, 1982)]. These species have large flowers (Fig. 2L12) in which the calyx hypanthium is prominent, calyx lobes sometimes fused laterally to the tips and wing petals relatively smaller than the keel, with less prominent sculpturing.

Six pollination mechanisms, each with a different adaptation in its flower structure, are recognized within the tribe Crotalarieae:

(1) *Pump type* (the general type in Crotalarieae, see Table 1): pollen is released into the apical part of the keel and pumped out when the pollinator lands on the keel and wing petals and forces its proboscis into the nectar well at the base of the standard petal. The pressure created by this action pushes the wings and keel downwards, so that the glabrous style and filaments emerge from the keel tip and in so doing pumps out the pollen from the keel tip in a piston action. Callosities may be present at the pressure point on the standard petal and these are particularly prominent in flowers with strongly reflexed standard petals, where considerable force is required to lift the petal and thus 'open' the flower. A small amount of pollen is usually pumped out with each flower visit (especially in those flowers with strongly beaked keels) so that several pollinators may be dusted with pollen. The pollen is deposited on the ventral side in the centre of the pollinator's body. This pollination mechanism is ubiquitous in papilionoid legumes and was described by Arroyo (1981), Delpino (1868/1869), Leppik (1966), Polhill (1976), Westerkamp (1997) and Etcheverry (2001a,b).

(2) *Gullet type* (*Pearsonia*, *Robynsiophyton* and *Rothia*): the androecium and gynoecium are displaced from their normal position (in the keel) during flower development, in the mature flower ending up in a hollow or channel along the adaxial side of the standard petal (Fig. 2J1). The flowers may become resupinate (Boatwright et al., 2008b; Polhill, 1976) so that the apical part of the standard petal serves as the landing platform. In gullet flowers, the androecium and gynoecium are typically straight (not curved) and the keel and wing petals are usually narrow and closely appressed to the standard petal, thus forming a throat or gullet into which the pollinator has to crawl in order to reach the nectar (Fig. 2J2, J3, K). The pollen will be deposited on the dorsal side of the pollinator (or on the ventral side, in the case of resupinate flowers). The gullet-type pollination syndrome was described by Polhill (1974, 1976).

(3) *Hugging type* (*Lebeckia pauciflora*, *L. wrightii* and *L. uniflora* – see revision by Le Roux and Van Wyk, 2009): the keel is spirally curved sideways (to about 180°), so that it is closely appressed to the standard petal (Fig. 2E). When the pollinator applies pressure to reach the nectar, the shape and position of the keel result in the latter tightening around the insect's body, thus hugging it. This pollination mechanism was first described in *Vigna vexillata* (L.) R.Reich. by Hedström and Thulin (1986). The pollen is deposited off-centre on the dorsal side of the pollinator's body.

(4) *Saddle type* (*Rafnia* section *Colobotropis*): this pollination mechanism was first described by Campbell and Van Wyk (2001) and we here propose the name 'saddle type' for this interesting adaptation (Fig. 2F1). It is easily recognized by the truncate keel tip, which fits nicely onto the dorsal side of the insect's body (like a saddle on the back of a horse). The flowers are resupinate and lack sculpturing on the wings, because the standard petal serves as the landing platform (and not the wings). The flower visitor has to grasp onto the standard petal to force its way to the nectar well and in so doing pushes the dorsal side of its body against the truncate or emarginate keel tip, resulting in the pollen being deposited onto the thorax or abdomen.

(5) *Tunnel type* (*Bolusia* only): this bizarre pollination syndrome is here described for the first time. The keel is highly modified and helically coiled through several turns, forming a tunnel into which the pollinator has to crawl to reach the nectar (Fig. 2M1 and M2). It is not surprising that petal sculpturing is absent, because there is no contact between the wing petals and the insect. The standard petal and wing petals are hooded around the coiled keel, obstructing access to the nectar and forcing the pollinator to move into the tunnel. The insect grips onto the coiled keel and pushes against a single (central) callosity on the standard petal to force entry into the nectar well. Pollen is usually deposited off-centre on the dorsal part of the pollinator's body but this may vary in cases where the flowers are partly or completely resupinate.

(6) *Brush type* (within Crotalarieae, unique to the genus *Crotalaria*, and present in all except one of the 700 species): this is a modification of the pump type, differing only in the more efficient pumping action, which is aided by the presence of trichomes on the apical part of the style. The stylar trichomes serve to brush the pollen out of the keel tip (Fig. 2R). This mechanism occurs sporadically in several unrelated groups of legumes and was described by Arroyo (1981), Delpino (1868/1869), Lavin and Delgado (1990), Leppik (1966), Polhill (1976, 1982), Westerkamp (1997), Etcheverry (2001a,b, 2003) and Etcheverry et al. (2008).

Stylar trichomes should not be confused with ciliate or penicillate stigmas, which are present in most genera of Crotalarieae. These, in their turgid state, probably act to isolate the pollen from the stigma during anthesis to prevent initial autogamy and initiate xenogamy. If pollinators do not visit the flower and cross-pollination fails, delayed selfing occurs when the dorsifixed anthers elongate (see Fig. 2T3), pushing pollen into the keel beak above the stigma, guaranteeing reproduction and seed-set (Etcheverry, 2003).

The brush type mechanism functions as follows: one day prior to anthesis the larger, basifixed anthers [compared to the dorsifixed ones (Fig. 2T1)] release pollen into the keel beak. At anthesis, the pollinator lands on the wing petals and keel and inserts its proboscis along a groove (Fig. 2P1) in the standard petal that guides it to the nectar chamber through an opening (nectar well) at the bottom of the staminal tube (Fig. 2S). On either side of the groove, at the point where the claw meets the blade, two callosities are apparent (Fig. 2P). Trichomes are present on the proximal side of the callosities (Fig. 2L12, O and P2) and these very effectively block any lateral access to the nectar well by illegal pollinators (Polhill, 1976). The callosities act as a lever for the legal pollinator to push against, lifting the standard petal up to reach the nectar through the nectar well. The position of the callosities at or near the point of attachment of the claw results in a very rigid structure that takes considerable effort to lift in order to reach the nectar. While the pollinator is manoeuvring to access the nectar, it depresses the keel with its weight and the pressure exerted against the standard and keel. The associated movement of the keel causes the style, which remains static, to emerge from the tip of the beak in a tripping event (Fig. 2L13 and R). Pollen is pushed out from the keel tip against the body of the pollinator and the stigma also brushes against it (Arroyo, 1981). Approximately one day after anthesis the short, dorsifixed anther filaments elongate and extend past the long, basifixed ones, thus pushing the remaining pollen into the keel beak (Fig. 2T2–T4). These shorter anthers then also release some pollen. This mechanism has also been described for *C. micans* (Etcheverry, 2001a) and *C. stipularia* (Etcheverry, 2001b). It ensures that pollen release is regulated and allows for numerous tripping events, through which small quantities of pollen may repeatedly be pumped out of the keel tip over a longer period.

Rounded styles require more movement from the keel (and hence more effort from the pollinator) in order to emerge than geniculate ones. It is interesting to note that when the keel tip is twisted, the style is also twisted, resulting in the single or double line of hairs being spirally arranged. When the keel is depressed in this type of flower, the pollen is brushed out through a cork-screw action.

Our study has shown the intricate relationships between the structure of the calyx, the shape and configuration of the keel, the presence of callosities on the standard petal, the dimorphism and attachment of the anthers, as well as the curvature and pubescence of the style. Each of these characters and character states individually has diagnostic value and were traditionally used to characterize and circumscribe genera. This study has shown that there may be new and interesting interpretations for some of the "old" characters previously thought to have limited systematic value (e.g. callosities on the standard petal, which are clearly non-homologous and independently derived in the genera in which they occur). However, a more holistic view of how these combine to create functional units comes closer to a complete understanding of the adaptations that have driven the extreme diversification in *Crotalaria* and the tribe Crotalarieae.

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Appendix 1.

Salient morphological characters of the corolla, androecium and gynoecium of 226 flower samples from 16 genera and 211 species of the tribe Crotalarieae, together with voucher specimens and pollination syndromes.

Species	Group/section (if applicable)	Voucher specimen	Callosity shape	Keel apex shape	Anther configuration	Anther ratio (basifixed/dorsifixed lengths)	Style vestiture	Pollination syndrome
Aspalathus acutiflora R.Dahlgren	*Pingues*	*Van Wyk et al. 3420* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.6	Glabrous	Pump
Aspalathus angustifolia (Lam.) R.Dahlgren	*Borboniae*	*Van Wyk 2592* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.3	Glabrous	Pump
Aspalathus astroites L.	*Astroites*	*Schutte 428* (JRAU)	Absent	Rostrate	4 + 1 + 5	2.3	Glabrous	Pump
Aspalathus caledonensis R.Dahlgren	*Sericeae*	*Van Wyk 1364* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.9	Glabrous	Pump
Aspalathus chortophila Eckl. and Zeyh.	*Laterales*	*Van Wyk 1118* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.4	Glabrous	Pump
Aspalathus ciliaris L.	*Adnates*	*Van Wyk 3175* (JRAU)	Disc	Obtuse	4 + 1 + 5	1.4	Glabrous	Pump
Aspalathus cordata (L.) R.Dahlgren	*Borboniae*	*Van Wyk 2294* (JRAU)	Ridge	Obtuse	4 + 1 + 5	2.0	Glabrous	Pump
Aspalathus divaricata Thunb.	*Terminales*	*Niemand 21* (JRAU)	Absent	Rostrate	4 + 1 + 5	2.7	Glabrous	Pump
Aspalathus hirta E.Mey.	*Laterales*	*Van Wyk 2070* (JRAU)	Absent	Obtuse	4 + 1 + 5	2.1	Glabrous	Pump
Aspalathus juniperina Thunb.	*Teretilobae*	*Van Wyk 2756* (JRAU)	Absent	Obtuse	4 + 1 + 5	?	Glabrous	Pump
Aspalathus laeta Bolus	*Aciphyllae*	*Niemand 12* (JRAU)	Absent	Obtuse	4 + 1 + 5	2.5	Glabrous	Pump
Aspalathus latifolia Bolus	*Peduncularis*	*Schutte 704* (JRAU)	Absent	Rostrate	4 + 1 + 5	1.6	Glabrous	Pump
Aspalathus linearis (Burm.f.) R.Dahlgren.	*Lebeckiiformis*	*Niemand 3* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.8	Glabrous	Pump
Aspalathus macrantha Harv.	*Rostratae*	*Barker 195* (JRAU)	Absent	Rostrate	4 + 1 + 5	3.3	Glabrous	Pump
Aspalathus nigra L.	*Purpureae*	*Van Wyk 2233* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.9	Glabrous	Pump
Aspalathus pendula R.Dahlgren	*Lebeckiiformis*	*Van Wyk 2451* (JRAU)	Absent	Rostrate	4 + 1 + 5	2.7	Glabrous	Pump
Aspalathus rugosa Thunb.	*Sericeae*	*Marshall 222* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.9	Glabrous	Pump
Aspalathus sericea Berg.	*Sericeae*	*Schutte 435* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.5	Glabrous	Pump
Aspalathus spinosa L.	*Pingues*	*Schutte 500* (JRAU)	Absent	Obtuse	4 + 1 + 5	2.3	Glabrous	Pump
Aspalathus subulata Thunb.	*Carnosae*	*Maree 4* (JRAU)	Absent	Obtuse	4 + 1 + 5	2.0	Glabrous	Pump
Aspalathus tridentata L.	*Sericeae*	*Van Wyk 3427* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.4	Glabrous	Pump
Aspalathus tylodes Eckl. and Zeyh.	*Callosae*	*Schutte-Vlok s.n.* (JRAU)	Absent	Obtuse	4 + 1 + 5	?	Glabrous	Pump
Bolusia acuminata (DC.) Polhill		*Acocks 12481* (PRE)	Disc	Rostrate	5 + 5	3.3	Glabrous	Tunnel
Bolusia amboensis (Schinz) Harms		*Boatwright et al. 248* (WIND)	Disc	Rostrate	5 + 5	2.8	Glabrous	Tunnel
Bolusia grandis B.-E.van Wyk		*Lawton 1521* (K)	Disc	Rostrate	5 + 5	2.9	Glabrous	Tunnel
Bolusia resupinata Milne-Redh.		*Fanshawe 3428* (K)	Disc	Rostrate	5 + 5	3.8	Glabrous	Tunnel
Calobota acanthoclada (Dinter) Boatwr. and B.-E.van Wyk		*Williams 2594a* (BOL)	Absent	Obtuse	4 + 1 + 5	2.2	Glabrous	Pump
Calobota angustifolia (E.Mey.) Boatwr. and B.-E.van Wyk		*Mannheimer 2020* (WIND)	Absent	Obtuse	4 + 1 + 5	1.6	Glabrous	Pump
Calobota angustifolia		*Watrilaugh 867* (WIND)	Absent	Obtuse	4 + 1 + 5	1.8	Glabrous	Pump
Calobota cinerea (E.Mey.) Boatwr. and B.-E.van Wyk		*Le Roux 2066* (NBG)	Absent	Obtuse	4 + 1 + 5	1.6	Glabrous	Pump
Calobota cuspidosa (Burch.) Boatwr. and B.-E.van Wyk		*Van Wyk 3055* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.6	Glabrous	Pump
Calobota cytisoides (Berg.) Eckl. and Zeyh.		*Pretorius 105* (NBG)	Absent	Obtuse	4 + 1 + 5	1.9	Glabrous	Pump
Calobota elongata (Thunb.) Boatwr. and B.-E.van Wyk		*Van Breda 4486* (PRE)	Absent	Obtuse	4 + 1 + 5	2.0	Glabrous	Pump

Species	Group/section (if applicable)	Voucher specimen	Callosity shape	Keel apex shape	Anther configuration	Anther ratio (basifixed/ dorsifixed lengths)	Style vestiture	Pollination syndrome
Calobota halenbergensis (Merxm. and A.Schreib.) Boatwr. and B.-E.van Wyk		*Van Wyk 2836* (JRAU)	Absent	No	4 + 1 + 5	1.3	Glabrous	Pump
Calobota halenbergensis		*Middlemost 2129* (NBG)	Absent	Slightly rostrate	4 + 1 + 5	1.5	Glabrous	Pump
Calobota linearifolia (E.Mey.) Boatwr. and B.-E.van Wyk		*Mervin et al. 3615* (PRE)	Absent	Obtuse	4 + 1 + 5	1.3	Glabrous	Pump
Calobota lotononoides (Schltr.) Boatwr. and B.-E.van Wyk		*Boatwright 142* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.3	Glabrous	Pump
Calobota obovata (Schinz) Boatwr. and B.-E.van Wyk		*Pearson 8036* (BOL)	Absent	Obtuse	4 + 1 + 5	1.5	Glabrous	Pump
Calobota pungens (Thunb.) Boatwr. and B.-E.van Wyk		*Snijman 353* (NBG)	Absent	Obtuse	4 + 1 + 5	1.4	Glabrous	Pump
Calobota sericea (Thunb.) Boatwr. and B.-E.van Wyk		*Thorns s.n.* (NBG)	Absent	Obtuse	4 + 1 + 5	1.8	Glabrous	Pump
Calobota spinescens (Harv.) Boatwr. and B.-E.van Wyk		*Hilton-Tyalor 1366* (PRE)	Absent	Obtuse	4 + 1 + 5	2.2	Glabrous	Pump
Calobota sp. nov.		*Owen-Smith 117* (WIND)	Absent	Obtuse	4 + 1 + 5	1.5	Glabrous	Pump
Crotalaria anthyllopsis Baker	*Hedriocarpae* Wight and Arn.	*Aleljung 401* (UPS)	Ridge	Rostrate	5 + 5	2.3	One line	Brush
Crotalaria argyraea Baker	*Hedriocarpae*	*Tinley 1150* (WIND)	Ridge	Rostrate	5 + 5	2.4	One line	Brush
Crotalaria aurea Dinter ex Baker f.	*Crotalaria*	*Vlok et al. 1834* (BOL)	Disc	Rostrate	5 + 5	5.0	Two lines	Brush
Crotalaria barkae Schweinf.	*Chrysocalycinae* (Benth.) Baker f.	*De Winter et al. 5538* (PRE)	Ridge	Rostrate	5 + 5	3.0	One line	Brush
Crotalaria barnabassii Baker f.	*Grandiflorae* (Baker f.) Polhill	*Van Wyk 4228* (JRAU)	Ridge	Rostrate	5 + 5	3.3	One line	Brush
Crotalaria brachycarpa (Benth.) Burtt Davy ex I.Verd.	*Crotalaria*	*Bester 4226* (PRE)	Disc	Rostrate	5 + 5	?	Two lines	Brush
Crotalaria burkeana Benth.	*Chrysocalycinae*	*Rogers 13764* (PRE)	Ridge	Rostrate	5 + 5	3.6	One line	Brush
Crotalaria capensis Jacq.	*Grandiflorae*	*Acocks 11394* (PRE)	Ridge	Rostrate	5 + 5	3.6	One line	Brush
Crotalaria colorata Schinz	*Crotalaria*	*Giess 12426* (WIND)	Ridge	Rostrate	5 + 5	3.0	Entire	Brush
Crotalaria damarensis Engl.	*Chrysocalycinae*	*Germishuizen 2741* (PRE)	Ridge	Rostrate	5 + 5	4.4	One line	Brush
Crotalaria dinteri Schinz	*Crotalaria*	*Uiras MU512* (WIND)	Disc	Rostrate	5 + 5	6.3	Two lines	Brush
Crotalaria distans Benth.	*Crotalaria*	*Steyn 496* (PRE)	Disc	Rostrate	5 + 5	?	Two lines	Brush
Crotalaria doidgeae I.Verd.	*Grandiflorae*	*Van Wyk 6771* (PRE)	Ridge	Rostrate	5 + 5	2.8	One line	Brush
Crotalaria dura J.M.Wood and M.S.Evans	*Chrysocalycinae*	*De Castro 11* (JRAU)	Ridge	Rostrate	5 + 5	2.0	One line	Brush
Crotalaria eremicola Baker f.	*Crotalaria*	*Giess et al. 7166* (WIND)	Disc	Rostrate	5 + 5	3.5	Two lines	Brush
Crotalaria excisa (Thunb.) Baker f.	*Crotalaria*	*Bean et al. 1705* (BOL)	Ridge	Rostrate	5 + 5	2.8	Entire	Brush
Crotalaria flavicarinata Baker f.	*Geniculatae* Polhill	*Curtis BC1485A* (WIND)	Column	Rostrate	5 + 5	2.4	Two lines	Brush
Crotalaria gamwelliae Baker f.	*Dispermae* Wight and Arn.	*Bidgood et al. 4596* (UPS)	Disc	Rostrate	5 + 5	9.0	Two lines	Brush
Crotalaria gazensis Baker f.	*Chrysocalycinae*	*Schelpe 519* (BOL)	Ridge	Rostrate	5 + 5	2.3	Two lines	Brush
Crotalaria globifera E.Mey.	*Crotalaria*	*Acocks 13428* (PRE)	Disc	Rostrate	5 + 5	3.8	Two lines	Brush
Crotalaria goodiiformis Vatke	*Chrysocalycinae*	*Bidgood et al. 4172* (UPS)	Ridge	Rostrate	5 + 5	2.3	One line	Brush
Crotalaria graminicola Taub. ex Baker f.	*Dispermae*	*Bidgood et al. 4759* (UPS)	Disc	Rostrate	5 + 5	4.7	Two lines	Brush
Crotalaria griquensis Bolus	*Crotalaria*	*Hafstrom H1053* (PRE)	Disc	Rostrate	5 + 5	3.6	Two lines	Brush
Crotalaria heidmannii Schinz	*Geniculatae*	*Giess 13516* (WIND)	Disc	Rostrate	5 + 5	2.8	Two lines	Brush
Crotalaria humilis Eckl. and Zeyh.	*Crotalaria*	*Le Roux 2658* (BOL)	Ridge	Rostrate	5 + 5	2.7	Entire	Brush
Crotalaria hyssopifolia Klotzsch	*Dispermae*	*Bidgood et al. 3737* (UPS)	Disc	Rostrate	5 + 5	?	Two lines	Brush
Crotalaria incana L.	*Chrysocalycinae*	*Roos 735* (UPS)	Ridge	Rostrate	5 + 5	2.8	One line	Brush
Crotalaria incrassifolia Polhill	*Crotalaria*	*Thulin et al. 10085* (UPS)	Disc	Rostrate	5 + 5	?	Two lines	Brush
Crotalaria inopinata (Harms) Polhill	*Hedriocarpae*	*Mankelow et al. 91080* (UPS)	Ridge	Rostrate	5 + 5	2.7	One line	Brush
Crotalaria juncea L.	*Calycinae* Wight. and Arn.	*Wells 4478* (PRE)	Lamelliform	Rostrate	5 + 5	6.0	One line	Brush
Crotalaria keniensis Baker f.	*Crotalaria*	*Lundgren 205* (UPS)	Disc	Rostrate	5 + 5	3.6	Two lines	Brush
Crotalaria kipandensis Baker f.	*Dispermae*	*Bidgood et al. 4060* (UPS)	Disc	Rostrate	5 + 5	?	Two lines	Brush
Crotalaria kurtii Schinz	*Crotalaria*	*Uiras MU259* (WIND)	Disc	Rostrate	5 + 5	4.0	Two lines	Brush
Crotalaria laburnifolia L.	*Grandiflorae*	*Curson 418* (PRE)	Ridge	Rostrate	5 + 5	2.5	One line	Brush
Crotalaria laburnoides Klotzsch	*Crotalaria*	*Mhoro 513* (UPS)	Disc	Rostrate	5 + 5	4.4	Two lines	Brush
Crotalaria lachnophora A.Rich.	*Chrysocalycinae*	*Gilbert et al. 757* (UPS)	Ridge	Rostrate	5 + 5	3.3	One line	Brush
Crotalaria lanceolata E.Mey.	*Hedriocarpae*	*Van Wyk 1865b* (JRAU)	Ridge	Rostrate	5 + 5	4.0	One line	Brush

Species	Group/section (if applicable)	Voucher specimen	Callosity shape	Keel apex shape	Anther configuration	Anther ratio (basifixed/ dorsifixed lengths)	Style vestiture	Pollination syndrome
Crotalaria lebeckioides Bond.	*Grandiflorae*	*Vlok 2543* (JRAU)	Ridge	Rostrate	5 + 5	2.4	One line	Brush
Crotalaria leubnitziana Schinz	*Crotalaria*	*Muller 1328* (PRE)	Disc	Rostrate	5 + 5	4.4	Two lines	Brush
Crotalaria longidens I.Verd.	*Grandiflorae*	*Onderstall 1427* (PRE)	Ridge	Rostrate	5 + 5	3.7	One line	Brush
Crotalaria lotoides Benth.	*Chrysocalycinae*	*Van Wyk 1875* (JRAU)	Ridge	Rostrate	5 + 5	2.7	One line	Brush
Crotalaria luondeensis R.Wilczek	*Dispermae*	*Iwarsson 1091* (UPS)	Disc	Rostrate	5 + 5	4.8	Two lines	Brush
Crotalaria macrocarpa E.Mey.	*Crotalaria*	*Huntley 1767* (NU)	Disc	Rostrate	5 + 5	3.8	Two lines	Brush
Crotalaria massaiensis Taub.	*Hedriocarpae*	*Jensen 4571* (UPS)	Ridge	Rostrate	5 + 5	3.0	One line	Brush
Crotalaria mauensis Baker f.	*Chrysocalycinae*	*Verdcourt 2301* (UPS)	Ridge	Rostrate	5 + 5	2.2	Two lines	Brush
Crotalaria melanocalyx Polhill	*Dispermae*	*Bidgood et al. 3595* (UPS)	Disc	Rostrate	5 + 5	6.0	Two lines	Brush
Crotalaria meyerana Steud.	*Crotalaria*	*Muller 832* (PRE)	Ridge	Rostrate	5 + 5	3.4	Entire	Brush
Crotalaria microphylla M.Vahl	*Geniculatae*	*Thulin 11016* (UPS)	Disc	Rostrate	5 + 5	4.7	Two lines	Brush
Crotalaria miranda Milne-Redh.	*Crotalaria*	*Bidgood et al. 3970* (UPS)	Disc	Rostrate	5 + 5	5.8	Two lines	Brush
Crotalaria mollii Polhill	*Chrysocalycinae*	*Bolus 11782* (BOL)	Ridge	Rostrate	5 + 5	2.8	Two lines	Brush
Crotalaria monophylla Germish.	*Geniculatae*	*Fabian 1402* (PRE)	Column	Rostrate	5 + 5	3.2	Entire	Brush
Crotalaria monteiroi Baker f.	*Grandiflorae*	*Pienaar 428* (PRE)	Ridge	Rostrate	5 + 5	2.8	One line	Brush
Crotalaria natalensis Baker f.	*Crotalaria*	*Smith 3784* (PRE)	Disc	Rostrate	5 + 5	3.0	Two lines	Brush
Crotalaria natalitia Meisn.	*Chrysocalycinae*	*Breijer 19419* (PRE)	Ridge	Rostrate	5 + 5	3.3	One line	Brush
Crotalaria nigricans Baker	*Chrysocalycinae*	*Bidgood et al. 4508* (UPS)	Ridge	Rostrate	5 + 5	2.4	One line	Brush
Crotalaria obscura DC.	*Chrysocalycinae*	*Le Roux et al. 110* (JRAU)	Ridge	Rostrate	5 + 5	2.5	One line	Brush
Crotalaria ochroleuca G.Don	*Hedriocarpae*	*Clark 556* (PRE)	Ridge	Rostrate	5 + 5	4.6	One line	Brush
Crotalaria oligosperma Polhill	*Crotalaria*	*Thulin et al. 7745* (UPS)	Disc	Rostrate	5 + 5	3.8	Two lines	Brush
Crotalaria ononoides Benth.	*Chrysocalycinae*	*Thulin et al. 2874* (UPS)	Ridge	Rostrate	5 + 5	2.7	One line	Brush
Crotalaria pallida Aiton	*Hedriocarpae*	*Lautenbach s.n.* (JRAU)	Ridge	Rostrate	5 + 5	3.0	One line	Brush
Crotalaria parvula Baker	*Dispermae*	*Bidgood et al. 3775* (UPS)	Disc	Rostrate	5 + 5	?	Two lines	Brush
Crotalaria pearsonii Baker f.	*Crotalaria*	*Marloth 12445* (PRE)	Ridge	Rostrate	5 + 5	2.7	Entire	Brush
Crotalaria phylloloba Harms	*Chrysocalycinae*	*Mhoro 868* (UPS)	Ridge	Rostrate	5 + 5	4.9	One line	Brush
Crotalaria pisicarpa Baker	*Chrysocalycinae*	*Strohbach 1043* (WIND)	Ridge	Rostrate	5 + 5	3.7	One line	Brush
Crotalaria platysepala Harv.	*Crotalaria*	*Hines 641* (WIND)	Disc	Rostrate	5 + 5	6.4	Two lines	Brush
Crotalaria podocarpa DC.	*Chrysocalycinae*	*Giess 10345* (WIND)	Ridge	Rostrate	5 + 5	6.1	One line	Brush
Crotalaria pseudotenuirama Torre	*Dispermae*	*Bidgood et al. 3590* (UPS)	Disc	Rostrate	5 + 5	8.0	Two lines	Brush
Crotalaria pumila Ortega	*Calycinae*	*Pareira-Silva 4700* (CEN)	Disc	Rostrate	5 + 5	5.0	One line	Brush
Crotalaria recta Steud. ex A.Rich.	*Crotalaria*	*Grobberlaar 1057* (PRE)	Lamelliform	Rostrate	5 + 5	3.7	Two lines	Brush
Crotalaria rhodesiae Baker f.	*Chrysocalycinae*	*Teague 61* (BOL)	Ridge	Rostrate	5 + 5	4.1	One line	Brush
Crotalaria schinzii Baker f.	*Hedriocarpae*	*Van Hoepen 1707* (PRE)	Ridge	Rostrate	5 + 5	2.8	One line	Brush
Crotalaria senegalensis (Pers.) Bacle ex DC.	*Crotalaria*	*Eylers 11584* (SAM)	Disc	Rostrate	5 + 5	5.1	Two lines	Brush
Crotalaria sericifolia Harms.	*Chrysocalycinae*	*Maguire 1582* (BOL)	Ridge	Rostrate	5 + 5	2.5	Two lines	Brush
Crotalaria spartea Baker	*Hedriocarpae*	*Germishuizen 5196* (PRE)	Ridge	Rostrate	5 + 5	4.0	One line	Brush
Crotalaria spartioides Torre	*Geniculatae*	*Gubb KM 10709* (PRE)	Column	Rostrate	5 + 5	?	Two lines	Brush
Crotalaria spectabilis Roth	*Crotalaria*	*Le Roux et al. 98* (JRAU)	Lamelliform	Rostrate	5 + 5	3.5	Two lines	Brush
Crotalaria sphaerocarpa DC.	*Geniculatae*	*Le Roux et al. 74* (JRAU)	Disc	Rostrate	5 + 5	2.3	One line	Brush
Crotalaria steudneri Schweinf.	*Hedriocarpae*	*De Winter et al. 4986* (WIND)	Ridge	Rostrate	5 + 5	2.3	One line	Brush
Crotalaria teixeirae Torre	*Crotalaria*	*Burke 95308* (WIND)	Disc	Rostrate	5 + 5	?	Two lines	Brush
Crotalaria ulbrichiana Harms	*Grandiflorae*	*Dinter 7496* (BOL)	Ridge	Rostrate	5 + 5	3.5	One line	Brush
Crotalaria vasculosa Benth.	*Hedriocarpae*	*Vahrmeijer 661* (PRE)	Ridge	Rostrate	5 + 5	2.4	One line	Brush
Crotalaria virgulata Klotzsch	*Crotalaria*	*Retief 408* (PRE)	Disc	Rostrate	5 + 5	7.8	Two lines	Brush
Crotalaria virgultalis DC.	*Geniculatae*	*Van Wyk 3060* (JRAU)	Column	Rostrate	5 + 5	3.2	One line	Brush
Euchlora hirsuta (Thunb.) Druce		*Schutte 257* (JRAU)	Absent	Slightly rostrate	4 + 6	2.2	Glabrous	Pump
Ezoloba macrocarpa (Eckl. and Zeyh.) B.-E.van Wyk and Boatwr.		*Hardy 853* (K)	Absent	Slightly rostrate	5 + 5	2.1	Glabrous	Pump
Lebeckia ambigua E.Mey.		*Barker 9781* (NBG)	Absent	Rostrate	5 + 5	1.7	Glabrous	Pump
Lebeckia contaminata (L.) Thunb.		*Vlok et al. 23* (JRAU)	Absent	Rostrate	5 + 5	2.0	Glabrous	Pump
Lebeckia meyeriana Eckl. and Zeyh. ex Harv.		*Compton 16628* (NBG)	Absent	Rostrate	5 + 5	2.0	Glabrous	Pump
Lebeckia pauciflora Eckl. and Zeyh.		*Van Wyk 2899* (JRAU)	Absent	Rostrate	5 + 5	1.1	Glabrous	Hugging
Lebeckia plukenetiana E.Mey.		*Hall s.n.* (NBG)	Absent	Rostrate	5 + 5	2.1	Glabrous	Pump
Lebeckia sepiaria (L.) Thunb.		*Schutte 261* (JRAU)	Absent	Rostrate	5 + 5	2.0	Glabrous	Pump
Lebeckia wrightii (Harv.) Bolus		*Stokoe 964* (BOL)	Absent	Rostrate	5 + 5	1.7	Glabrous	Hugging
Leobordea anthylloides (Harv.) B.-E.van Wyk and Boatwr.	*Synclistus* (B.-E.van Wyk) B.-E.van Wyk and Boatwr.	*Schlieben 11452* (PRE)	Absent	Obtuse	4 + 6	1.6	Glabrous	Pump

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Leobordea arida (Dümmer) B.-E.van Wyk and Boatwr.	*Leptis* (E.Mey. ex Eckl. and Zeyh.) B.-E.van Wyk and Boatwr.	*Germishuizen 197* (PRE)	Absent	Obtuse	4 + 6	2.0	Glabrous	Pump
Leobordea benthamiana (Dümmer) B.-E.van Wyk and Boatwr.	*Digitata* (B.-E.van Wyk) B.-E.van Wyk and Boatwr.	*Leach et al. 17446* (JRAU)	Absent	Obtuse	4 + 6	1.9	Glabrous	Pump
Leobordea bracteosa (B.-E.van Wyk) B.-E.van Wyk and Boatwr.	*Leobordea*	Van Wyk (1991b)	Absent	Obtuse	4 + 6	2.3	Glabrous	Pump
Leobordea corymbosa (E.Mey.) B.-E.van Wyk and Boatwr.	*Lipozygis* (E.Mey.) B.-E.van Wyk and Boatwr.	Van Wyk (1991b)	Absent	Obtuse	4 + 6	1.6	Glabrous	Pump
Leobordea decumbens (Thunb.) B.-E.van Wyk and Boatwr.	*Leptis*	*Van Wyk 1383* (JRAU)	Absent	Obtuse	4 + 6	2.0	Glabrous	Pump
Leobordea decumbens (Thunb.) B.-E.van Wyk and Boatwr.	*Leptis*	*Scheepers 1799* (PRE)	Absent	Obtuse	4 + 6	2.0	Glabrous	Pump
Leobordea grandis (Dümmer and A.J.Jenn.) B.-E.van Wyk	*Lipozygis*	*Strey 9402* (NH)	Absent	Obtuse	4 + 6	1.8	Glabrous	Pump
Leobordea hirsuta (Schinz) B.-E.van Wyk and Boatwr.	*Leptis*	*Louw 1264* (PRE)	Absent	Obtuse	4 + 6	2.0	Glabrous	Pump
Leobordea longiflora (Bolus) B.-E.van Wyk and Boatwr.	*Digitata*	*Strauss 135* (NBG)	Absent	Rostrate	4 + 6	1.9	Glabrous	Pump
Leobordea mucronata (Conrath) B.-E.van Wyk and Boatwr.	*Leptis*	Van Wyk (1991b)	Absent	Obtuse	4 + 6	1.6	Glabrous	Pump
Leobordea pariflora (N.E.Br.) B.-E.van Wyk and Boatwr.	*Leptis*	*Junod et al. 4374* (PRE)	Absent	Obtuse	4 + 6	2.0	Glabrous	Pump
Leobordea platycarpa (Viv.) B.-E.van Wyk and Boatwr.	*Leobordea*	*Acocks 17597* (PRE)	Absent	Obtuse	4 + 6	2.0	Glabrous	Pump
Leobordea polycephala (E.Mey.) B.-E.van Wyk and Boatwr.	*Synclistus*	Van Wyk (1991b)	Absent	Obtuse	4 + 6	1.9	Glabrous	Pump
Listia angolensis (Welw. ex Baker) B.-E.van Wyk and Boatwr.		*Richards 564* (K)	Absent	Obtuse	4 + 1 + 5	1.8	Glabrous	Pump
Listia bainesii (Baker) B.-E.van Wyk and Boatwr.		*Van Wyk et al. 4579* (PRE)	Absent	Obtuse	4 + 1 + 5	2.0	Glabrous	Pump
Listia heterophylla E.Mey.		*Hankom 608* (PRE)	Absent	Obtuse	4 + 1 + 5	2.2	Glabrous	Pump
Listia marlothii (Engl.) B.-E.van Wyk and Boatwr.		*Krynauw 61* (PRE)	Absent	Obtuse	4 + 1 + 5	1.9	Glabrous	Pump
Listia marlothii		Van Wyk (1991b)	Absent	Obtuse	4 + 1 + 5	2.1	Glabrous	Pump
Listia subulata (B.-E.van Wyk) B.-E.van Wyk and Boatwr.		Van Wyk (1991b)	Absent	Obtuse	4 + 1 + 5	2.0	Glabrous	Pump
Lotononis acocksii B.-E.van Wyk	*Aulacinthes* (E.Mey.) Benth.	*Acocks 20573* (PRE)	Absent	Obtuse	4 + 1 + 5	1.4	Glabrous	Pump
Lotononis acuminata Eckl. and Zeyh.	*Lotononis*	*Vlok 1701* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.8	Glabrous	Pump
Lotononis arenicola Schltr.	*Oxydium* Benth.	Van Wyk (1991b)	Absent	Rostrate	4 + 1 + 5	5.7	Glabrous	Pump
Lotononis azurea (Eckl. and Zey.) Benth.	*Lotononis*	*Acocks 2325* (STE)	Absent	Obtuse	4 + 1 + 5	1.9	Glabrous	Pump
Lotononis azureoides B.-E.van Wyk	*Aulacinthes*	Van Wyk (1991b)	Absent	Obtuse	4 + 1 + 5	1.3	Glabrous	Pump
Lotononis caerulescens (E.Mey.) B.-E.van Wyk	*Krebsia* (Eckl. and Zeyh.) Benth.	*Bayliss 7949* (GRA)	Inverted ridge	Obtuse	4 + 1 + 5	1.6	Glabrous	Pump
Lotononis carnea B.-E.van Wyk	*Oxydium*	*Van Wyk 199*	Absent	Rostrate	4 + 6	4.9	Glabrous	Pump
Lotononis carnosa (Eckl. and Zeyh.) Benth.	*Krebsia*	*Bandert 6* (GRA)	Inverted ridge	Obtuse	4 + 1 + 5	2.2	Glabrous	Pump
Lotononis delicata (Baker f.) Polhill	*Oxydium*	*Teixeira 311* (PRE)	Absent	Obtuse	4 + 1 + 5	2.0	Glabrous	Pump
Lotononis densa (Thunb.) Harv.	*Aulacinthes*	*Acocks 24507* (MO)	Absent	Obtuse	4 + 1 + 5	2.0	Glabrous	Pump
Lotononis densa	*Aulacinthes*	*Stokie 8447* (SAM)	Absent	Obtuse	4 + 1 + 5	1.7	Glabrous	Pump
Lotononis dichiloides Sond.	*Krebsia*	*Guinzius s.n.* (C)	Inverted ridge	Obtuse	4 + 1 + 5	1.5	Glabrous	Pump
Lotononis dissitinodis B.-E.van Wyk	*Aulacinthes*	*Acocks 20502* (PRE)	Absent	Obtuse	4 + 1 + 5	1.9	Glabrous	Pump
Lotononis elongata (Thunb.) D. Dietr.	*Lotononis*	Van Wyk (1991b)	Absent	Rostrate	4 + 1 + 5	1.3	Glabrous	Pump
Lotononis filliformis B.-E.van Wyk	*Lotononis*	*Van Wyk s.n.* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.9	Glabrous	Pump
Lotononis galpinii Dümmer	*Krebsia*	*Killick 4172* (PRE)	Inverted ridge	Obtuse	4 + 1 + 5	1.8	Glabrous	Pump

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Lotononis involucrata (Berg.) Benth.	*Polylobium* (Eckl. and Zeyh.) Benth.	*Acocks 24408* (PRE)	Absent	Obtuse	4 + 1 + 5	1.2	Glabrous	Pump
Lotononis involucrata	*Polylobium*	*Acocks et al. 2323* (PRE)	Absent	Obtuse	4 + 1 + 5	1.2	Glabrous	Pump
Lotononis involucrata	*Polylobium*	*Barker 10793* (NBG)	Absent	Obtuse	4 + 1 + 5	1.5	Glabrous	Pump
Lotononis jacottetii (Schinz) B.-E.van Wyk	*Krebsia*	Van Wyk (1991b)	Absent	Obtuse	4 + 1 + 5	2.0	Glabrous	Pump
Lotononis lotononoides (Scott-Elliot) B.-E.van Wyk	*Buchenroedera* (Eckl. and Zeyh.) B.-E.van Wyk	Van Wyk (1991b)	Absent	Obtuse	4 + 1 + 5	1.9	Glabrous	Pump
Lotononis macrosepala Conrath	*Oxydium*	Van Wyk (1991b)	Inverted ridge	Rostrate	4 + 6	1.9	Glabrous	Pump
Lotononis pallens (Eckl. and Zeyh.) Benth.	*Oxydium*	*Ecklon et al. 1294* (SAM)	Absent	Rostrate	4 + 1 + 5	2.0	Glabrous	Pump
Lotononis prostrata (L.) Benth.	*Lotononis*	*Boucher 3813* (STE)	Absent	Obtuse	4 + 6	1.6	Glabrous	Pump
Lotononis pseudodelicata (Torre) Polhill	*Oxydium*	*Grossweiler 10983* (K)	Absent	Rostrate	4 + 1 + 5	2.5	Glabrous	Pump
Lotononis pungens Eckl. and Zeyh.	*Cleistogama* B.-E.van Wyk	*Barker 7938* (NBG)	Absent	Rostrate	4 + 1 + 5	2.0	Glabrous	Pump
Lotononis racemiflora B.-E.van Wyk	*Polylobium*	Van Wyk (1991b)	Absent	Rostrate	4 + 1 + 5	1.7	Glabrous	Pump
Lotononis rigida (E.Mey.) Benth.	*Aulacinthes*	*Walters 169* (NBG)	Absent	Obtuse	4 + 1 + 5	1.6	Glabrous	Pump
Lotononis schreiberae B.-E.van Wyk	*Oxydium*	*Kers 1586* (WIND)	Ridge	Obtuse	4 + 1 + 5	2.4	Glabrous	Pump
Lotononis stricta (Eckl. and Zeyh.) B.-E.van Wyk	*Krebsia*	*Van Wyk 1711* (JRAU)	Inverted ridge	Obtuse	4 + 1 + 5	1.9	Glabrous	Pump
Lotononis umbellata (L.) Benth.	*Aulacinthes*	*Taylor 3824* (STE)	Absent	Obtuse	4 + 1 + 5	1.6	Glabrous	Pump
Lotononis varia (E.Mey.) Steud.	*Lotononis*	*Roberts et al. 17674* (PRE)	Absent	Obtuse	4 + 1 + 5	1.8	Glabrous	Pump
Lotononis venosa B.-E.van Wyk	*Monocarpa* B.-E.van Wyk	*Oliver 8965* (STE)	Absent	Obtuse	4 + 1 + 5	1.8	Glabrous	Pump
Lotononis villosa (E.Mey.) Steud.	*Lotononis*	*Esterhuysen 16192* (BOL)	Absent	Obtuse	4 + 6	1.4	Glabrous	Pump
Lotononis viminea (E.Mey.) B.-E.van Wyk	*Buchenroedera*	*Tyson 2709* (C)	Absent	Obtuse	4 + 1 + 5	2.3	Glabrous	Pump
Pearsonia aristata (Schinz) Dümmer		*Van Wyk 1995* (JRAU)	Absent	Obtuse	10	1.1	Glabrous	Gullet
Pearsonia bracteata (Benth.) Polhill		*Van Wyk 3010* (JRAU)	Absent	Obtuse	10	1.3	Glabrous	Gullet
Pearsonia cajanifolia (Harv.) Polhill		*Van Wyk 1783* (JRAU)	Absent	Obtuse	10	1.0	Glabrous	Gullet
Pearsonia grandifolia (Bolus) Polhill		*Van Wyk 2705* (JRAU)	Absent	Obtuse	10	1.1	Glabrous	Gullet
Pearsonia obovata (Schinz) Polhill		*Van Wyk 2919* (JRAU)	Absent	Obtuse	10	0.9	Glabrous	Gullet
Pearsonia sessilifolia (Harv.) Dümmer		*Van Wyk 2729* (JRAU)	Absent	Obtuse	10	1.1	Glabrous	Gullet
Rafnia amplexicaulis (L.) Thunb.	*Rafnia*	*Van Wyk s.n.* (JRAU)	Disc	Rostrate	4 + 1 + 5	2.6	Glabrous	Pump
Rafnia angulata Thunb.	*Rafnia*	*Rycroft 1810* (NBG)	Disc	Rostrate	4 + 1 + 5	3.7	Glabrous	Pump
Rafnia angulata	*Rafnia*	*Esterhuysen 28056* (BOL)	Absent	Rostrate	4 + 1 + 5	4.0	Glabrous	Pump
Rafnia angulata	*Rafnia*	*Young s.n. sub TM 27829* (PRE)	Disc	Rostrate	4 + 1 + 5	4.0	Glabrous	Pump
Rafnia angulata	*Rafnia*	*Thorne s.n. sub NBG 14264* (NBG)	Disc	Rostrate	4 + 1 + 5	3.1	Glabrous	Pump
Rafnia angulata	*Rafnia*	*Van Wyk 3679* (JRAU)	Ridge	Rostrate	4 + 1 + 5	2.6	Glabrous	Pump
Rafnia capensis (L.) Schinz	*Colobotropis* E.Mey.	*Schutte et al. 563* (JRAU)	Absent	Truncate	4 + 1 + 5	3.0	Glabrous	Saddle
Rafnia capensis	*Colobotropis*	*Esterhuysen 35798* (BOL)	Absent	Truncate	4 + 1 + 5	2.5	Glabrous	Saddle
Rafnia capensis	*Colobotropis*	*Haynes 686* (STE)	Absent	Truncate	4 + 1 + 5	2.4	Glabrous	Saddle
Rafnia capensis	*Colobotropis*	*Campbell 98* (JRAU)	Absent	Truncate	4 + 1 + 5	2.4	Glabrous	Saddle
Rafnia crassifolia Harv.	*Rafnia*	*Walters 595* (NBG)	Ridge	Rostrate	4 + 1 + 5	3.8	Glabrous	Pump
Rafnia diffusa Thunb.	*Colobotropis*	*Compton 20815* (NBG)	Ridge	Truncate-rostrate	4 + 1 + 5	2.5	Glabrous	Saddle
Rafnia lancea (Thunb.) DC.	*Rafnia*	*Esterhuysen 11936* (BOL)	Absent	Rostrate	4 + 1 + 5	3.0	Glabrous	Pump
Rafnia ovata E.Mey.	*Rafnia*	*Barker 9568* (NBG)	Disc	Rostrate	4 + 1 + 5	2.5	Glabrous	Pump
Rafnia ovata	*Rafnia*	*Campbell et al. 128* (JRAU)	Disc	Rostrate	4 + 1 + 5	2.3	Glabrous	Pump
Rafnia racemosa Eckl. and Zeyh.	*Rafnia*	*Campbell et al. 155* (JRAU)	Absent	Rostrate	4 + 1 + 5	2.2	Glabrous	Pump
Rafnia rostrata G.J.Campb. and B.-E.van Wyk	*Rafnia*	*Esterhuysen 3727* (BOL)	Ridge	Rostrate	4 + 1 + 5	3.0	Glabrous	Pump

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Rafnia schlechteriana Schinz	*Colobotropis*	*Campbell et al. 117* (JRAU)	Disc	Truncate	4 + 1 + 5	2.3	Glabrous	Saddle
Rafnia triflora (L.) Thunb.	*Rafnia*	*Purcell 259* (SAM)	Disc	Rostrate	4 + 1 + 5	3.2	Glabrous	Pump
Robynsiophyton vanderystii R.Wilczek		*Weston 717* (K)	Absent	Obtuse	5	1.0	Glabrous	Gullet
Rothia hirsuta (Guill. and Perr.) Baker		*Akpabla 1982* (K)	Absent	Obtuse	9	1.0	Glabrous	Gullet
Rothia indica (L.) Druce		*Wight 5821* (K)	Absent	Obtuse	9	1.3	Glabrous	Gullet
Wiborgia fusca Thunb.		*Van Wyk et al. 4196* (JRAU)	Absent	Rostrate	4 + 1 + 5	2.5	Glabrous	Pump
Wiborgia humilis (Thunb.) R.Dahlgren		*Boatwright 216* (JRAU)	Absent	Obtuse	4 + 1 + 5	1.5	Glabrous	Pump
Wiborgia monoptera E.Mey.		*Boatwright 152* (JRAU)	Absent	Rostrate	4 + 1 + 5	1.8	Glabrous	Pump
Wiborgiella bowieana (Benth.) Boatwr. and B.-E.van Wyk		*Streicher s.n.* (JRAU)	Absent	Slightly rostrate	4 + 6	1.7	Glabrous	Pump
Wiborgiella dahlgrenii Boatwr. and B.-E.van Wyk		*Barker 10407* (NBG)	Absent	Obtuse	4 + 6	1.5	Glabrous	Pump
Wiborgiella leipoldtiana (Schltr. ex R.Dahlgren) Boatwr. and B.-E.van Wyk		*Schutte 295* (JRAU)	Absent	Obtuse	4 + 6	1.5	Glabrous	Pump
Wiborgiella mucronata (Benth.) Boatwr. and B.-E.van Wyk		*Stirton 11608* (PRE)	Absent	Obtuse	4 + 6	1.7	Glabrous	Pump
Wiborgiella sessilifolia (Eckl. and Zeyh.) Boatwr. and B.-E.van Wyk		*Albertyn 498b* (NBG)	Absent	Obtuse	4 + 6	1.8	Glabrous	Pump
Wiborgiella vlokii Boatwr. and B.-E.van Wyk		*Vlok 2045* (PRE)	Absent	Obtuse	4 + 6	1.5	Glabrous	Pump

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