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The generic concept of *Lebeckia* (Crotalarieae, Fabaceae): Reinstatement of the genus *Calobota* and the new genus *Wiborgiella*

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Abstract

Evidence from the internal transcribed spacer (ITS) of nuclear ribosomal DNA and plastid *rbcL* data revealed that the genus *Lebeckia* Thunb. as currently circumscribed may not be monophyletic. These analyses, combined with morphological and anatomical data, showed that the genus could be divided into three genera: (1) *Lebeckia* sensu stricto (*L.* section *Lebeckia*); (2) *Calobota* [*L.* section *Calobota* (Eckl. and Zeyh.) Benth. and *L.* section *Stiza* (E.Mey.) Benth.] including the monotypic, North African genus *Spartidium* Pomel; (3) a new genus, *Wiborgiella* [*L.* section *Viborgioides* Benth., together with *L. inflata* Bolus, *L. mucronata* Benth. and *Wiborgia humilis* (Thunb.) Dahlgr.]. The reinstatement of the genus *Calobota* Eckl. and Zeyh. is proposed and *Wiborgiella* Boatwr. and B.-E. Van Wyk described as new. Synopses of the genera *Calobota* and *Wiborgiella*, including nomenclature, synonymy, descriptions and diagnostic characters are presented.

Keywords: *Calobota*; Crotalarieae; Fabaceae; *Lebeckia*; Taxonomy; *Wiborgiella*

1. Introduction

The current broad generic concept of *Lebeckia* Thunb. dates back to Bentham (1844) and Harvey (1862) and refers to a group of ca. 36 species of papilionoid legumes that occur mainly in the southern and western parts of South Africa, with some extending into Namibia. The group is particularly common in the Cape Floristic Region (CFR). Bentham (1844) reduced several genera described by Meyer (1836) and Ecklon and Zeyher (1836) to the synonymy of an expanded *Lebeckia*. This broadened concept included Meyer's *Stiza* and *Sarcophyllum*, together with Ecklon and Zeyher's *Acanthobotrya* and *Calobota*. A new sectional classification was proposed, based mainly on the shape of the keel and the morphology of the fruit. This comprised five sections, viz. section *Calobota* (Eckl. and Zeyh.) Benth., section *Eulebeckia* Benth., section *Phyllodiastrum* Benth., section *Stiza* (E.Mey.) Benth., and section *Viborgioides* Benth. Harvey (1862) followed this sectional classification of *Lebeckia* for his treatment in the Flora Capensis. For nearly 150 years, the generic concept and relationships between the morphologically rather diverse species were never studied in depth. A revision of *Lebeckia* sensu stricto (sections *Eulebeckia* and *Phyllodiastrum*) was recently completed by Le Roux and Van Wyk (2007, 2008, 2009). Their results show that the 14 species of *Lebeckia* s.s. can easily be distinguished by their acicular leaves and 5 + 5 anther arrangement, not only from all other species of the so-called "Cape group" of the tribe Crotalarieae (i.e. *Aspalathus* L., *Rafnia* Thunb. and *Wiborgia* Thunb.) but also from all other species hitherto included in *Lebeckia*.

Spartidium Pomel is a monotypic genus that occurs in North Africa. The affinities of the genus within the genistoid legumes have been unclear for some time and possible alliances have been suggested with both *Retama* Raf. and *Lebeckia* (Polhill, 1976). The genus is currently placed within the Crotalarieae based on the open androecial sheath, but an evaluation of its systematic position is clearly desirable. Polhill (1981) considered *Spartidium* to be "virtually indistinguishable from *Lebeckia*". He used the orientation of the seeds in the fruit and the North African distribution as the only key characters to distinguish *Spartidium*.

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In a broad study of molecular (ITS, *rbcL*) and morphological data of 117 species representing all the genera of the Crotalarieae, Boatwright et al. (2008a) discovered that *Lebeckia* is polyphyletic (Fig. 1a, b). This study revealed important new relationships within the Crotalarieae as well as *Lebeckia* and showed the need for new generic circumscriptions. The species can be readily accommodated in three easily recognizable morphological groups (genera): (1) *Lebeckia* s.s. (*L.* section *Lebeckia,* including sections *Phyllodiastrum* and *Eulebeckia*); (2) *Calobota* Eckl. and Zeyh. [*L.* section *Calobota* (Eckl. and Zeyh.) Benth. and *L.* section *Stiza* (E.Mey.) Benth., together with the monotypic North African *Spartidium* Pomel] and (3) "*Wiborgiella*" [*L.* section *Viborgioides* Benth., together with *L. inflata* Bolus, *L. mucronata* Benth. and *Wiborgia humilis* (Thunb.) Dahlgr.].

In this paper, new evidence is presented to show that Bentham's (1844) broad concept of *Lebeckia* is polyphyletic. We propose a new generic classification system to reflect new insights into morphological discontinuities within the tribe which are also supported by molecular systematic evidence (Boatwright et al., 2008a).

2. Materials and methods

2.1. Morphology

Morphological data were obtained from herbarium specimens as well as from fresh material collected. Specimens of *Lebeckia* from the following herbaria were studied: BM, BOL, GRA, J, JRAU, K, NBG (including SAM and STE), P, PRE, S, SBT, UPS and WIND (abbreviations according to Holmgren et al. (1990)). Online photographs of the collections of B, M and Z were studied. Drawings of reproductive structures (all by JSB) were done using a stereoscope (WILD M3Z) with a *camera lucida* attachment.

2.2. Anatomy

For anatomical studies, fresh material was fixed directly in FAA (formaldehyde:acetic acid:96% alcohol:water; 10:5:50:35); dried material was rehydrated and then fixed in FAA for 24 h. A modification of the method of Feder and O'Brien (1968) was used for embedding in glycol methacrylate (GMA). A minimum of five days was used for the third infiltration in GMA. Sections were stained according to the periodic acid Schiff/toluidine blue (PAS/TB) staining method (Feder and O'Brien, 1968).

3. Morphological and anatomical evidence for the polyphyly of *Lebeckia*

3.1. Habit and branches

Most genera of the Crotalarieae have a shrubby habit (Polhill, 1976), but variation in habit is quite pronounced within *Lebeckia*. Species of *Lebeckia* section *Lebeckia* are predominantly suffrutescent plants that branch mainly at ground level, whereas the species of the remaining sections are almost invariably woody shrubs. A strongly spinescent habit is characteristic of *Lebeckia* section *Stiza* but also of two species of section *Calobota*, viz. *L. acanthoclada* Dinter and *L. spinescens* Harv. Both sections *Calobota* and *Stiza* have green young branches (except *L. acanthoclada*), as opposed to the woody, rigid, ramified brown to greyish branches of section *Viborgioides* (similar to the genus *Wiborgia* Thunb.). In species with green stems [sections *Calobota*, *Lebeckia* and *Stiza*, and *Spartidium saharae* (Coss. and Dur.) Pomel] a large part of the cortex is composed of chlorenchyma which serves a photosynthetic function (Metcalfe and Chalk, 1950). This layer is absent in species of section *Viborgioides* and also *L. mucronata*.

3.2. Leaves

Leaves are extremely variable, ranging from trifoliolate and petiolate (sections *Calobota* and *Viborgioides*), to unifoliolate (section *Stiza*) or simple (section *Calobota* and *Spartidium*) and completely phyllodinous (and acicular) in section *Lebeckia*. Cultivated plants of the section *Stiza* showed that the juvenile leaves are petiolate and trifoliolate, but a loss of the lateral leaflets and shortening of the petioles result in unifoliolate leaves on the older branches, as was also mentioned by Polhill (1976) and Dahlgren (1970). This transition is also seen in *L. obovata* Schinz. Stipules are absent in all but two species of *Lebeckia* s.l.: *L. wrightii* (Harv.) Bolus and *L. uniflora* M.M. Le Roux and B-E.Van Wyk (Le Roux and Van Wyk, 2009).

Transverse sections through the leaves of *Lebeckia* species (Fig. 2) revealed a remarkable difference between the species of *Calobota*/*Stiza*/*Spartidium* on the one hand (hereafter called the *Calobota* group) and *Viborgioides*/*L. inflata*/*L. mucronata*/*Wiborgia humilis* on the other hand (hereafter called the *Viborgioides* group), namely that the former group has isobilateral leaves, while the latter has dorsiventral leaves. This difference was unexpected, as anatomical characters are generally regarded as conservative. Even more remarkable was the exact congruence between the anther arrangements of the two groups (respectively 4+1+5 and 4+6 — see later). Leaves of *Lebeckia* s.s. are completely different from the species mentioned above, as they are phyllodinous, acicular and terete in transverse section.

Another interesting difference between the *Calobota* group and the *Viborgioides* group is the presence of mucilage cells in the latter but not the former (Fig. 2). In this character, the *Viborgioides* group agrees with other Cape genera (*Aspalathus*, *Rafnia* and *Wiborgia*, as well as the predominantly Cape *Lebeckia* s.s.). In contrast, the *Calobota* group, which extends into arid regions (Northern Cape and Namibia), does not have mucilage cells in mature leaves. The North African *Spartidium*, however, has mucilage cells in the epidermis, as do immature leaves of *L. pungens*, suggesting that there is a loss of these cells as the leaves mature (Boatwright, pers. obs.). Mucilage cells are widely distributed among flowering plants and several authors have speculated about their function (Gregory and Baas, 1989). Although experimental evidence is lacking, mucilage

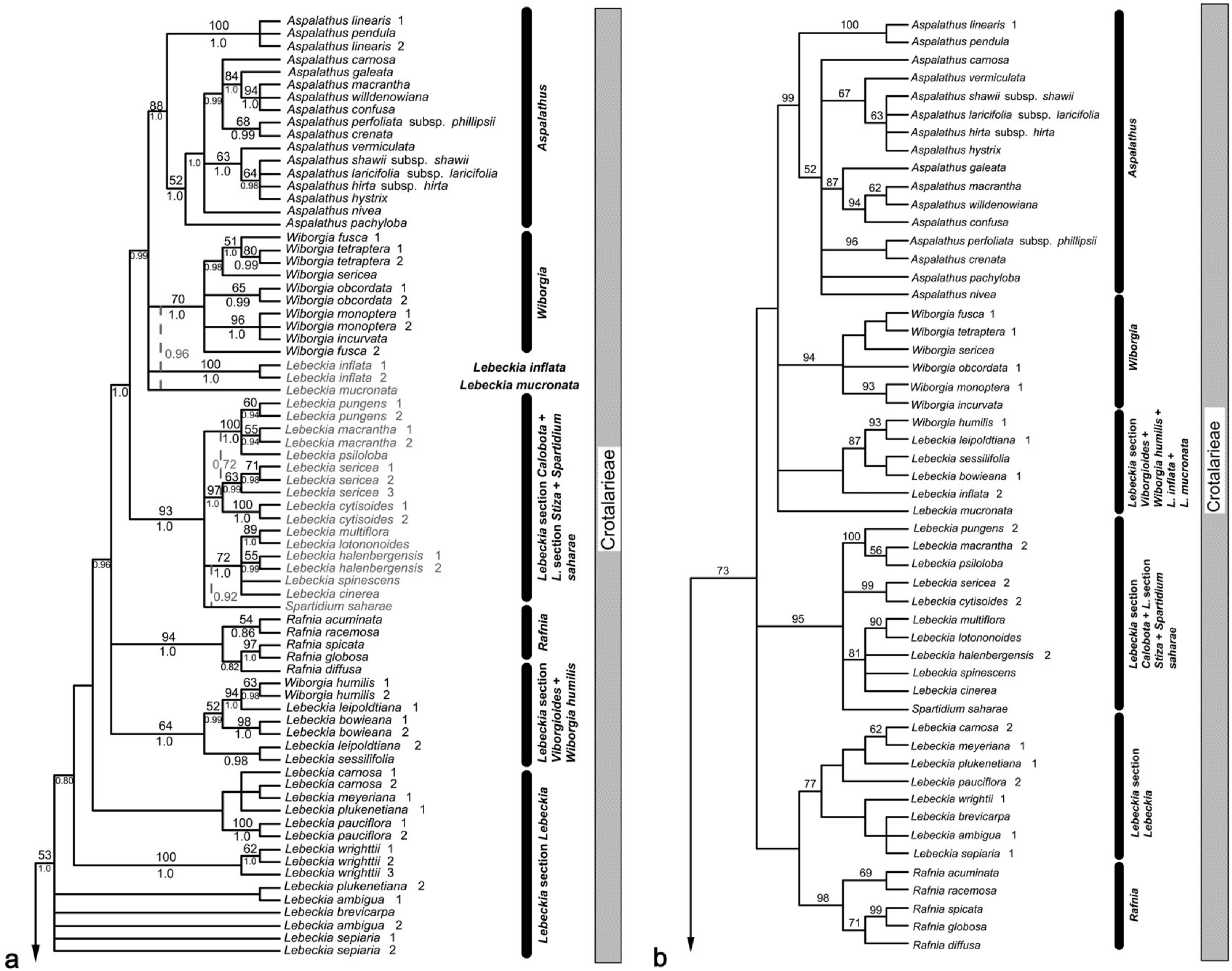

Fig. 1. The "Cape group" taken from (a) a strict consensus tree of the combined analysis of ITS and *rbcL* data (no. trees = 560; tree length = 1473 steps; consistency index = 0.50; retention index = 0.86); and (b) a strict consensus tree of the combined analysis of molecular (ITS and *rbcL*) and morphological data for the tribe Crotalarieae from Boatwright et al. (2008a; no. trees = 370; tree length = 1166 steps; consistency index = 0.53; retention index = 0.84). Bootstrap percentages are given above the branches and Bayesian posterior probabilities below the branches. Grey dotted lines indicate alternative topologies in the Bayesian analysis.

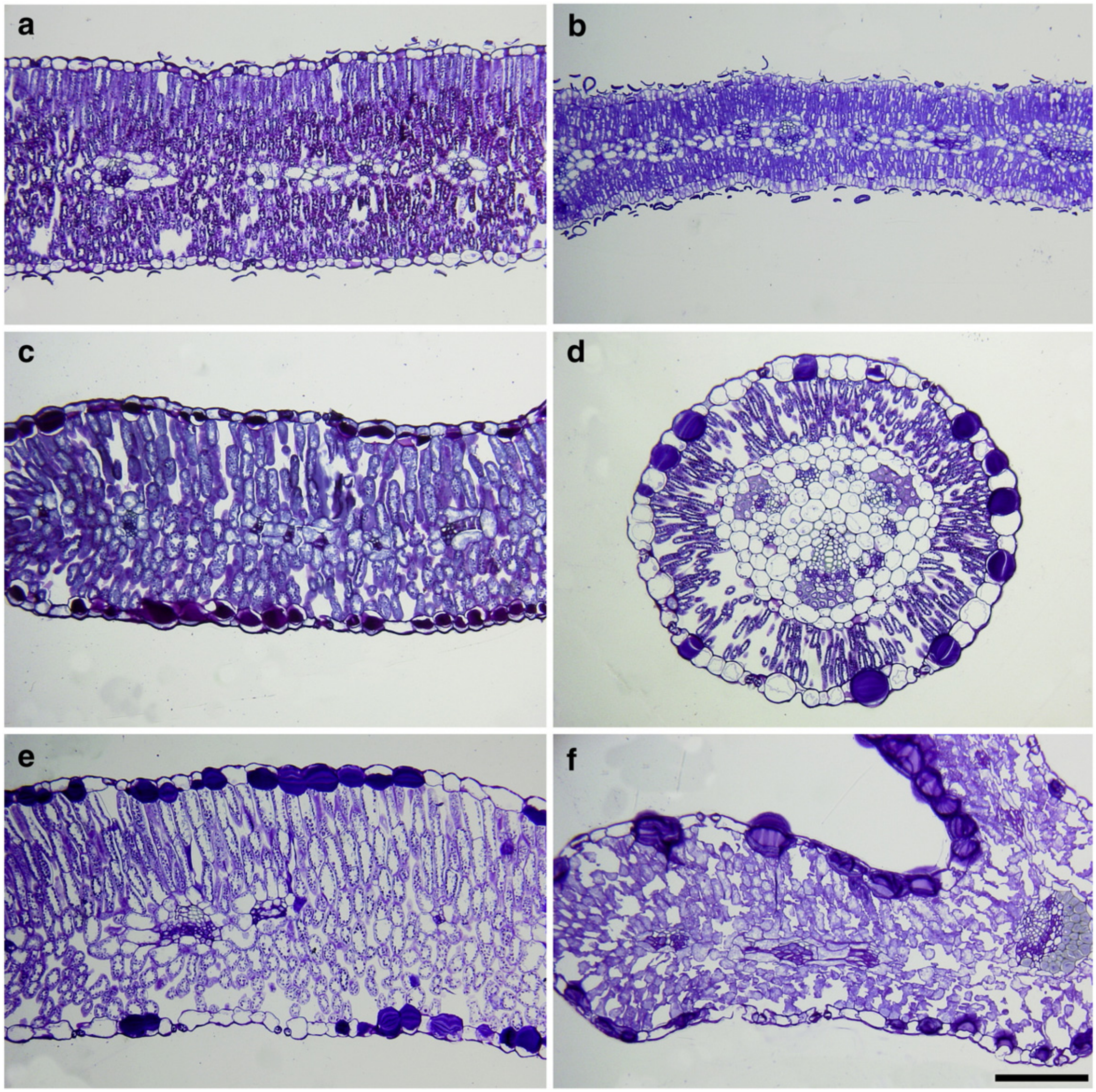

Fig. 2. Transverse sections through the leaves of *Lebeckia* species, showing isobilateral (a, b, *Calobota* group) and dorsiventral (c, e, f, *Viborgioides* group) leaflet laminas and an acicular, terete, phyllode with a circular arrangement of palisade cells (d, *Lebeckia* s.s.). Note the presence of mucilage cells in the epidermis. (a) *L. cytisoides*; (b) *L. pungens*; (c) *L. sessilifolia*; (d) *L. sepiaria*; (e) *L. inflata*; (f) *L. mucronata*. Voucher specimens: (a) *Boatwright et al. 107* (JRAU); (b) *Boatwright et al. 106* (JRAU); (c) *Van Wyk 2120* (JRAU); (d) *Le Roux et al. 10* (JRAU); (e) *Johns 162* (JRAU); (f) *Vlok 1726* (JRAU). Scale bar = 0.2 mm.

cells are postulated to aid in water storage and reduction of transpiration, protection against intensive radiation and also against herbivory (Gregory and Baas, 1989). Mucilage cells are often associated with plants that occur in Mediterranean climates (Van der Merwe et al., 1994). Bredenkamp and Van Wyk (1999) speculated that in *Passerina* L. (Thymelaeaceae) the mucilage serves as a regulator of hydration in the leaves, protecting them against water loss, but also helping to accumulate reserve water. *Lebeckia* s.s. and the *Viborgioides* group are restricted to the CFR and the presence of the mucilage cells in these taxa could be linked to diversification in a Mediterranean climate. It is interesting to note the presence of mucilage cells in *Spartidium saharae*, which also occurs in a Mediterranean climate. The *Calobota* group (excluding *Spartidium*) extends out of the CFR into summer rainfall, more arid regions and shows a different adaptation to drought, viz. isobilateral leaves (Fig. 2a, b; also in *Spartidium*). Van der Merwe et al. (1994) mention that the presence of more layers of palisade parenchyma improves the transport of water through the leaves and also offers increased protection to the chloroplasts. In contrast, the leaves of species within the *Viborgioides* group are dorsiventral (Fig. 2c, e, f). In *Lebeckia* s.s., the acicular leaves have a complete circular zone of palisade cells, with no spongy parenchyma (Fig. 2d).

The petioles are always shorter than the leaflets in the *Viborgioides* group and are persistent, becoming hard and woody when the leaflets are shed producing rigid and somewhat thorny branches. These characters are also found in some species of *Wiborgia* s.s. (Dahlgren, 1975). In the *Calobota* group, the petioles are either longer or shorter than the leaflets and are sometimes persistent, but are never rigid and spinescent. The acicular leaves of some species of *Lebeckia* s.s. are articulated or "jointed" near the middle or reduced to petioles in species with unarticulated leaves, i.e. the leaves are phyllodinous (Dahlgren, 1970), which serves as a synapomorphy for this group.

3.3. Inflorescences

As in most Crotalarieae, the inflorescences in *Lebeckia* are terminal racemes, varying in length and number of flowers. In *Lebeckia* s.s., the inflorescences may be relatively long and are often densely flowered with up to 93 flowers per raceme, for example in *L. brevicarpa* M.M. Le Roux and B-E.Van Wyk (Le Roux and Van Wyk, 2007). Species of section *Calobota* generally have fewer flowers per inflorescence, except in *L. melilotoides* Dahlgr., where more than 100 flowers are found on the elongated racemes (Dahlgren, 1967). The racemes of the three species of section *Stiza* are characteristically spine-tipped. Very short and few-flowered inflorescences are found in *L.* section *Viborgioides*, with the flowers often solitary in *L. bowieana* Benth.

3.4. Flowers

Calyx structure is often an important generic character in the Crotalarieae. *Lebeckia* species normally have equally lobed or "lebeckioid" calyces (Polhill, 1976), as opposed to the zygomorphic calyx ("lotononoid") in *Lotononis* (DC.) Eckl. and Zeyh. and *Pearsonia* Dümmer or the bilabiate calyx typical of all members of the tribe Genisteae (Van Wyk, 1991a; Van Wyk and Schutte, 1995). In the *Calobota* and *Viborgioides* groups, the carinal lobe is slightly narrower than the upper and lateral lobes, whereas in *Lebeckia* s.s. it is equal to the other lobes (Fig. 3). In the former two groups, the calyces are pubescent or at least glabrescent as opposed to the usually glabrous calyces found in section *Lebeckia* (*L. wrightii* is an exception in having a sparsely pubescent calyx).

The pubescence of the petals, the shape of the keel petal and the arrangement of the anthers closely follow the three major groups within *Lebeckia* s.l. Glabrous petals are found in *Lebeckia* s.s. and the *Viborgioides* group, whereas species of the *Calobota* group generally have pubescent petals (or at least pilose along the dorsal midrib of the standard petal). *Lebeckia macrantha* Harv. and *L. psiloloba* (E.Mey.) Walp. are the only

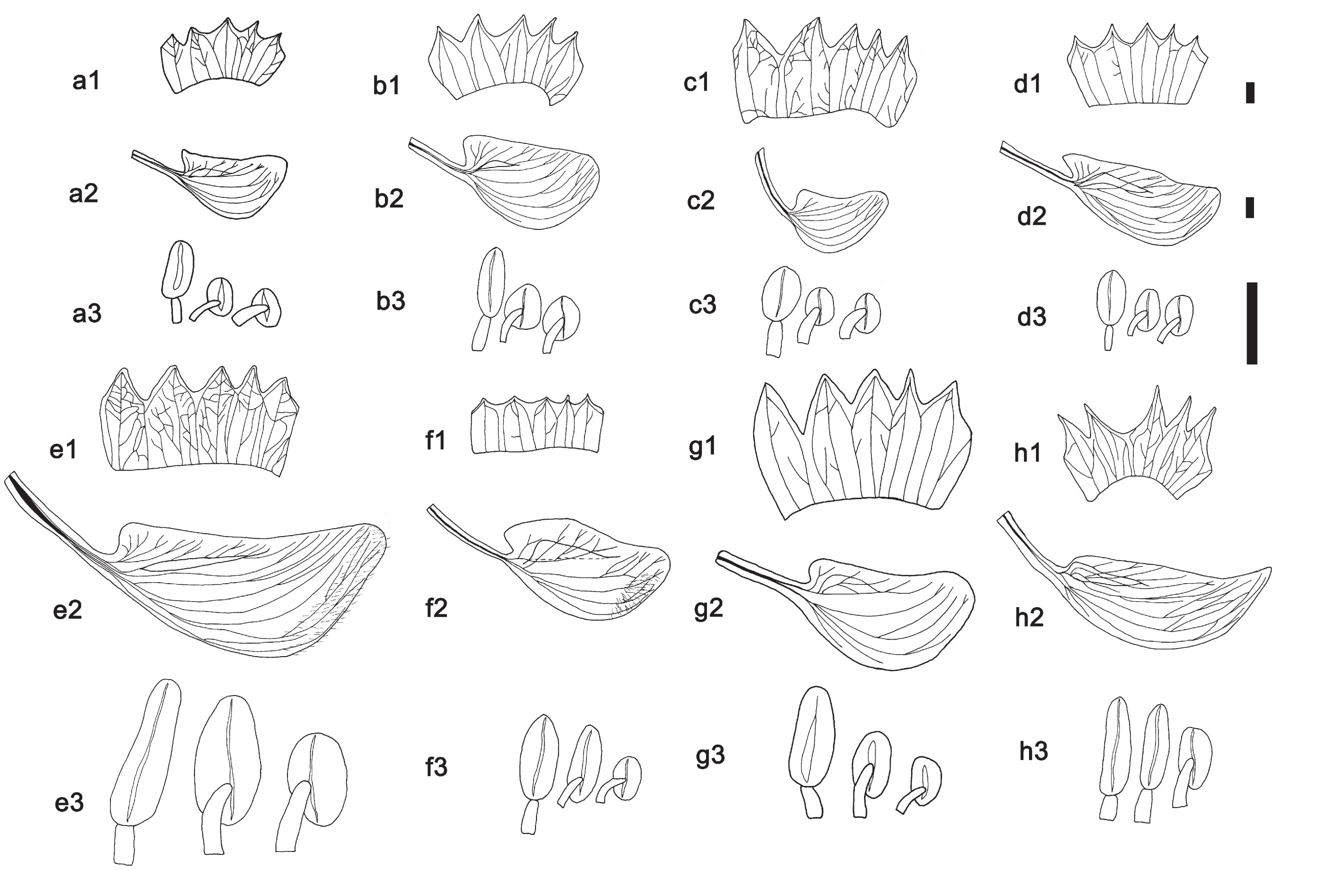

Fig. 3. Calyces (vestiture not shown), keel petals and anthers (carinal anthers in the centre) of selected species of *Lebeckia* s.l., *Spartidium saharae* and *Wiborgia humilis*. Note the relative size of the carinal lobe of the calyx, the apex and vestiture of the keel petal and the relative size of the carinal anther. (a1–a3) *W. humilis*; (b1–b3) *L. mucronata*; (c1–c3) *L. inflata*; (d1–d3) *L. leipoldtiana*; (e1–e3) *L. cytisoides*; (f1–f3) *L. pungens*; (g1–g3) *S. saharae*; (h1–h3) *L. sepiaria*. Voucher specimens: (a1, a3) *Van Wyk 3530* (JRAU); (a2) *Boatwright et al. 216* (JRAU); (b1–b3) *Stirton 10880* (JRAU); (c1–c3) *Vlok et al. 2* (JRAU); (d1–d3) *Boatwright et al. 123* (JRAU); (e1–e3) *Boatwright et al. 107* (JRAU); (f1) *Taylor 9386* (NBG); (f2) *Boatwright et al. 106* (JRAU); (f3) *Van Wyk 3252* (JRAU); (g1–g3) *Hill 1910* (K); (h1, h3) *Barker 6515* (NBG); (h2) *Le Roux et al. 24* (JRAU). Scale bars = 1.0 mm.

exceptions and have totally glabrous petals. The keel petals in *Lebeckia* s.s. are characteristically rostrate as opposed to the obtuse keel petals found in the other groups (Fig. 3).

3.5. Anthers

Surprisingly, it was found that the size and shape of the carinal anthers are diagnostic for each of the three groups in *Lebeckia* s.l. In *Lebeckia* s.s., the carinal anther resembles the long, basifixed anthers (Fig. 3h3) resulting in a 5+5 arrangement. In the *Calobota* group (including *Spartidium saharae*), the carinal anther is intermediate between the dorsifixed and basifixed anthers (Fig. 3e3, f3, g3), resulting in a 4+1+5 anther configuration (i.e., four long basifixed anthers, an intermediate carinal anther and five short dorsifixed anthers). The carinal anther is usually attached a little higher up. In the *Viborgioides* group, the carinal anthers resemble the short, dorsifixed anthers (Fig. 3a3, b3, c3, d3), resulting in a 4+6 anther arrangement (i.e., four long anthers and six short anthers). The anther arrangement therefore correlates to the leaf anatomy of the three groups.

3.6. Fruit and seeds

Pods in the Crotalarieae are an important source of systematic information, as specializations for seed protection and dispersal may result in structural differences. *Lebeckia* s.l. displays a great diversity of fruit structure, including dehiscent and indehiscent fruits that are either inflated or laterally compressed, and with or without wings (Polhill, 1976). Fruits of *Lebeckia* s.s. are terete to semi-terete and thick- or thin-walled, with wings on the upper suture in some species, e.g. *L. meyeriana* Eckl. and Zeyh. ex Harv. Species of the *Calobota* group generally have terete or semi-terete pods that are thick-walled and spongy or the fruits are thin-walled (membranous), laterally compressed and pubescent or glabrous, as is also found in *Spartidium saharae*. In contrast, the fruits of section *Viborgioides* (and *L. inflata*) are inflated and always glabrous, with highly sclerified, thin walls. The placement of *Wiborgia humilis* within the *Viborgioides* group is supported by fruit structure. *Wiborgia humilis* has inflated pods that lack wings on the upper suture and do not have highly sclerified fruit walls. In contrast, the winged samaras of the rest of *Wiborgia* are laterally compressed and have highly sclerified fruit walls in most species (Dahlgren, 1975).

Polhill (1976, 1981) used the orientation of the seed in *Spartidium* as the only diagnostic character to separate this genus from *Lebeckia* s.l. A study of most of the species showed that at least three species of the *Calobota* group (*L. macrantha*, *L. psiloloba* and *L. pungens* Thunb.) have the seed oriented at right angles to the placenta, exactly as in *Spartidium saharae*.

The seed surface of species in *Lebeckia* s.s. is invariably rugose, while the seeds of only one species in the *Calobota* group (*L. lotononoides* Schltr.) and one species in the *Viborgioides* group (*L. inflata*) have rugose seeds (Le Roux and Van Wyk, 2007, 2008, 2009; Boatwright and Van Wyk, 2007).

4. Molecular evidence for the polyphyly of *Lebeckia*

4.1. Combined molecular analyses

In the combined molecular analyses (Parsimony and Bayesian analyses; Fig. 1a) of Boatwright et al. (2008a), the *Calobota* group is clearly monophyletic with very strong support. In the Bayesian analysis, *Spartidium* groups with the *Lebeckia multiflora* group with strong support (Fig. 1a). The *Viborgioides* group is partly monophyletic with weak to strong support, but the positions of *L. inflata* and *L. mucronata* are unresolved. It is interesting to note that molecular evidence strongly supports the exclusion of *Wiborgia humilis* from *Wiborgia* and the transfer of this species to the *Viborgioides* group. Surprisingly, *Lebeckia* s.s. is unresolved in the molecular analyses. Morphologically this group is very distinct from the other groups of *Lebeckia* s.l. and all other Cape Crotalarieae.

4.2. Combined molecular and morphological analysis

When the molecular data were combined with morphological data (Fig. 1b), the resolution within the “Cape group” and among the three groups of *Lebeckia* s.l. was much improved. The *Calobota* group is again strongly supported as monophyletic. *Lebeckia* section *Viborgioides* (including *Wiborgia humilis*) is monophyletic with strong support and *L. inflata* is sister to this group, albeit without support. The position of *L. mucronata*, however, remains unresolved in this analysis, although abundant morphological and anatomical evidence suggests its placement within this group. The inclusion of *W. humilis* in the *Viborgioides* group again receives strong support. With the addition of morphological data *Lebeckia* s.s. is moderately supported as monophyletic as opposed to being unresolved in the molecular analyses (Boatwright et al., 2008a).

5. Taxonomic treatment

Major continuities and discontinuities in morphological characters amongst the three groups discussed above closely agree with the three main clades revealed by genetic analysis (Fig. 1a, b). The new system proposed here is based on a wider consideration of the intricate relationships amongst all genera of the tribe Crotalarieae, all of which have been revised in recent years (*Pearsonia* — Polhill, 1974; *Wiborgia* — Dahlgren, 1975; *Crotalaria* — Polhill, 1982; *Aspalathus* — Dahlgren, 1988; *Lotononis* — Van Wyk, 1991b; *Rafnia* — Campbell and Van Wyk, 2001; *Bolusia* — Van Wyk, 2003, Van Wyk et al., submitted; *Lebeckia* s.s. — Le Roux and Van Wyk, 2007, 2008, 2009; *Robynsiophyton* — Boatwright and Van Wyk, 2009; *Rothia* — Boatwright et al., 2008b). Dahlgren (1970) and Polhill (1976) both discussed the high incidence of convergence in the tribe Crotalarieae and the complex relationships between the genera. The difficulty in determining generic limits within the Crotalarieae is discussed by Polhill (1976), who emphasized that it would be unwise to propose modifications to the system without a clear understanding of the patterns of character state distributions. Furthermore, alterations to the system should result in a more predictive and useful system without running the risk of instability of circumscriptions and nomenclature. In existing keys to the genera of the Crotalarieae (Polhill, 1981; Van Wyk and Schutte, 1995), the lack of uniformity and clearcut diagnostic characters for *Lebeckia* s.l. is clearly reflected in the fact that the genus keys out no less than three times (in both keys). Unique combinations of morphological characters have now been identified for the three main groups that we are convinced should be given generic status. The improvement in generic delimitations is also reflected in the following key.

5.1. Key to the genera of the Crotalarieae

1a Leaves acicular, terete:

2a Ovary 2- to 4-ovulate, pods 1- to 8-seeded.......................... **Aspalathus**

2b Ovary with more than 6 ovules, pods many-seeded................. **Lebeckia**

1b Leaves digitate, unifoliolate or simple (flat, never terete):

3a Stipules present:

4a Style curved upwards; anthers dimorphic:

5a Stipules asymmetrical or single; style glabrous and not helically coiled; keel obtuse or rostrate; anther arrangement 4+6, 4+1+5 or very rarely 5+5.. **Lotononis**

5b Stipules symmetrical; style with 1 or 2 lines of hairs or glabrous and helically coiled; keel strongly rostrate (often at right angles) or helically coiled; anther arrangement 5+5:

6a Stipules dentate; beak of keel and style helically coiled, style glabrous... **Bolusia**

6b Stipules entire; beak of keel and style not helically coiled, style with 1 or 2 lines of hairs... **Crotalaria**

4b Style straight or rarely down-curved; anthers similar in size and shape

7a Stamens 9 (5 fertile and 4 lacking anthers)...................... **Robynsiophyton**

7b Stamens 10 (all fertile):

8a Anthers all rounded and sub-basifixed; prostrate annuals................ **Rothia**

8b Anthers all elongate, 4 anthers basifixed, 6 attached slightly higher up; perennial herbs or shrubs... **Pearsonia**

3b Stipules absent:

9a Calyx with upper and lateral lobes fused.................................... **Lotononis**

9b Calyx lobes sub-equal (upper and lateral lobes not fused):

10a Leaves sessile; upper suture of pod asymmetrically convex:

11a Plants glabrous except occasionally on bracts and bracteoles, minutely pubescent on inner surface of calyx lobes; usually turning black when dried.. **Rafnia**

11b Plants usually pubescent on all parts, if leaves glabrous then standard petal hairy and inner surface of calyx glabrous; not turning black when dried... **Aspalathus**

10b Leaves usually petiolate, if leaves sessile then plants with many-seeded pods and at least some hairs on the leaves or stems; upper suture of pod symmetrically convex:

12a Petals pubescent; at least on the dorsal midrib of the standard petal (if glabrous then plants strongly spinescent, woody, practically leafless shrubs); twigs green (bark formation late, chlorenchyma present); leaves isobilateral.. **Calobota**

12b Petals glabrous; twigs brown (bark formation early, chlorenchyma absent; if twigs rarely green then plant a short-lived fireweed); leaves dorsiventral:

13a Fruits winged, indehiscent; carinal anther intermediate (anthers 4+1+5)... **Wiborgia**

13b Fruits without wings, dehiscent (if rarely indehiscent then ovary and fruit distinctly stalked); carinal anther resembles short anthers (anthers 4+6).. **Wiborgiella**

5.2. Calobota

Calobota Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 192 (Jan. 1836) *emend.* Boatwr. and B-E.Van Wyk, emend. nov., *Lebeckia* section *Calobota* (Eckl. and Zeyh.) Benth. in Hook., Lond. J. Bot. 3: 358–361 (1844) *pro parte majore*. Lectotype species (here designated): *Calobota cytisoides* (Berg.) Eckl. and Zeyh. [Note: This species is chosen as lectotype as it is the only species included in Ecklon and Zeyher's original concept of *Calobota*].

Acanthobotrya Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 192 (Jan 1836) *pro parte*. Lectotype species (here designated): *A. pungens sensu* Eckl. and Zeyh. [now *Calobota psiloloba* (E.Mey.) Boatwr. and B-E.Van Wyk]. [Note: As mentioned by Bentham (1844), *Acanthobotrya* is a mixed concept representing at least four different genera. However, the diagnosis agrees with the concept of *Stiza* E.Mey. (e.g. linear-oblong, compressed fruits). Furthermore, *C. psiloloba* (= *A. pungens*) has all the diagnostic characters mentioned in the diagnosis and is listed first, directly after the diagnosis].

Stiza E.Mey., Comm. Pl. Afr. Austr. 1: 31 (Feb. 1836), syn. nov. *Lebeckia* section *Stiza* (E.Mey.) Benth. in Hook., Lond. J. Bot. 3: 355–356 (1844). Lectotype species (here designated): *Stiza erioloba* E.Mey. [now *Calobota pungens* (Thunb.) Boatwr. and B-E.Van Wyk]. [Note: Meyer (1836) included *Stiza erioloba* and *S. psiloloba* E.Mey. (now *Calobota psiloloba*) in *Stiza*. The original description of *Stiza* is too general to allow for a considered choice of lectotype, so we here choose *C. pungens* simply as it is the first-mentioned species.].

Spartidium Pomel, Nouv. Mat. Fl. Atl.: 173 (1874), syn. nov. Type species: *Spartidium saharae* (Coss. and Dur.) Pomel. [Note: *Spartidium* is monotypic].

[Note: The concept of *Calobota* is here expanded to include the genus *Stiza* and also the monotypic North African *Spartidium* (but excluding *Lebeckia mucronata*)].

Spinescent shrubs or shrublets. *Branches* thick and woody; young branches green, lacking bark (except in *C. acanthoclada*), pubescent, often sericeous. *Leaves* unifoliolate, digitately trifoliolate (rarely 4- or 5-foliolate) or simple; leaflets flat, oblanceolate to suborbicular, less often spathulate, pubescent; petioles shorter or longer than leaflets. *Stipules* absent. *Inflorescence* terminal, few- to many-flowered racemes. *Bracts* linear to obovate, pubescent. *Bracteoles* linear, pubescent. *Calyx* subequally lobed, upper sinus often deeper than the lateral or lower sinuses, carinal lobe narrower than the others, pubescent or at least glabrescent. *Corolla* yellow, usually pubescent or at least pilose along the median section of the standard petal (except in *C. cuspidosa* and *C. psiloloba*). *Standard* linear to broadly ovate, with basal callosities in *C. cytisoides*. *Wing petals* narrowly oblong to oblong or slightly ovate, longer or shorter than the keel, sometimes pubescent distally; apex obtuse. *Keel petals* oblong, pockets present, sometimes pubescent distally; apex obtuse. *Anthers* dimorphic, four long, basifixed anthers alternating with five ovate, dorsifixed anthers, carinal anther intermediate in size and shape (4+1+5 configuration). *Pistil* subsessile to very shortly stipitate; ovary linear to slightly elliptic, with four to many ovules, pubescent or glabrous; style shorter than the ovary, curved upwards, glabrous. *Pods* laterally compressed, semi-terete or terete, linear to oblong, few- to many-seeded, glabrous or pubescent, dehiscent or indehiscent. *Seeds* reniform to oblong-reniform, or less often suborbicular; colour variable, light pink to pink, sometimes mottled with brown; hilum round, brown or black; surface smooth [rugose in *C. lotononoides*; seeds of *C. obovata* and *C. saharae* not seen].

5.2.1. Diagnostic characters Bark formation is late, so that the twigs remain green and photosynthetic, whereas it is early in most species of *Wiborgiella*, so that even the young twigs are not green but covered in brown bark (as in *Wiborgia* species). The green twigs are a useful diagnostic character, visible even in sterile herbarium specimens. *Calobota* also differs from *Wiborgiella* in the hairy petals (*C. cupidosa* and *C. psiloloba* are exceptions). The most reliable diagnostic character distinguishing *Calobota* from *Wiborgiella* is the anther configuration of 4+1+5 (4+6 in the latter). The pods are never inflated in *Calobota* and are usually pubescent (pods are inflated in most species of *Wiborgiella* and are always glabrous).

5.2.2. Notes on distribution The species of *Calobota* occur in southern and south-western South Africa and in Namibia, with the exception of *Calobota saharae*, which is endemic to North Africa, where it occurs on sand dunes from Libya to Algeria and Morocco (Polhill, 1976).

5.3. The species of Calobota

5.3.1. Calobota acanthoclada (Dinter) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia acanthoclada* Dinter, Feddes Repert. 30: 196 (1932). Type—Namibia, Kleinfonteiner Fläche, *Dinter 6269* (B, photo!); Kovisberge, *Dinter 6293* (B, photo!, BM!); Buchuberge, *Dinter 6574* (B, photo!, BM!); Granietberge, *Dinter 6694* (B, photo!).

Lebeckia spathulifolia Dinter, Feddes Repert. 30: 197 (1932). Type—Namibia, Kleinfonteiner Fläche, *Dinter 3735* (B, photo!, BM!, SAM!, Z, photo! 2 sheets).

Lebeckia candicans Dinter, Feddes Repert. 30: 198 (1932), syn. nov. Type—Namibia, Kleinfonteiner Fläche, *Dinter 3737* (B, photo!, BM!, BOL!, NBG!, PRE!, S!, Z, photo!).

5.3.2. Calobota angustifolia (E.Mey.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia angustifolia* E.Mey. in Linnaea 7: 155 (1832). Type—South Africa, without locality, *Ecklon s.n.* (S!) [Note: Although *Spartium sericeum* Ait. is the oldest name for this taxon, the epithet is occupied by *Calobota sericea* (Thunb.) Boatwr. and B-E.Van Wyk and therefore the next available name is used].

Spartium sericeum Ait. in Hort. Kew. 3: 12 (1789). Type—South Africa, without precise locality, Cape of Good Hope, *Masson s.n. sub BM000794145* (BM, photo!). [Note: According to Stafleu and Cowan (1976), most of the Aiton types are in the Banks collection in BM)].

Lebeckia multiflora E.Mey., Comm. Pl. Afr. Austr. 1: 34 (Feb. 1836). Type—South Africa, Western Cape, near Heerenlogement, *Drège s.n.* (P!); Olifantsrivier, *Drège s.n.* (P!); between Holrivier and Mierenkasteel, *Drège 6474* (P!, S!).

5.3.3. Calobota cinerea (E.Mey.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia cinerea* E.Mey., Comm. Pl. Afr. Austr. 1: 35 (Feb. 1836). Type—South Africa, Northern Cape, hills near Noagas and near Aris on the Gariep, *Drège s.n.* (BM!, K!, P!).

5.3.4. Calobota cuspidosa (Burch.) Boatwr. and B-E.Van Wyk, comb. nov. *Spartium cuspidosum* Burch., Trav. S. Africa 1: 348 (1822). Type—South Africa, Northern Cape, between ‘Gatikamma’ and ‘Klaarwater’ [now Griquatown], *Burchell 1697* (K!).

Lebeckia macrantha Harv. in Harv. and Sond., Fl. Cap. 2: 83–84 (1862), syn. nov. Type—South Africa, without precise locality, ‘Zooloo country’, *Miss Owen s.n.* (TCD, photo!).

5.3.5. Calobota cytisoides (Berg.) Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 191 (Jan. 1836). *Spartium cytisoides* Berg., Descr. Pl.: 199. 1767; L.f., Suppl. Pl. 320 (1781). *Lebeckia cytisoides* (L.f.) Thunb., Nov. Gen.: 143 (1800); Prodr. Pl. Cap.: 122 (1800). Type—South Africa, without precise locality, ‘e Cap. b. Spei’, *Grubb s.n. sub Bergius 236.57* (SBT!).

Ebenus capensis L., Mant II: 264 (1771) *nom. illegit*.

5.3.6. Calobota elongata (Thunb.) Boatwr. and B-E.Van Wyk, comb. nov. *Crotalaria elongata* Thunb., Fl. Cap.: 571 (1823). Type—South Africa, Western Cape, ‘Carro prope Bockeveld’, *Thunberg s.n. sub THUNB-UPS 16544* (UPS!).

Lebeckia melilotoides Dahlgr., Bot. Notiser 120: 268–271 (1967). Type—South Africa, Western Cape, Platfontein, east of Hottentots Holland Kloof, *H. Hall 177* (NBG!, 2 sheets, PRE!, S!).

5.3.7. Calobota halenbergensis (Merxm. and Schreib.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia halenbergensis* Merxm. and Schreib., Bull. Jard. Bot. Bruxelles 27: 276 (1957). Type—Namibia, Lüderitz South, Halenberg, *Dinter 6632* (M, photo!; K!, NBG!, PRE!, S!, Z, photo!).

5.3.8. Calobota linearifolia (E.Mey.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia linearifolia* E.Mey., Comm. Pl. Afr. Austr. 1: 33 (Feb. 1836). Type—South Africa, Northern Cape, on the Gariep, near Verleptpraam, *Drège s.n.* (P!, S!).

Lebeckia dinteri Harms, Feddes. Repert. 16: 360 (1920), syn. nov. Type—Namibia, Garub, *Dinter 1057* (NBG!).

5.3.9. Calobota lotononoides (Schltr.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia lotononoides* Schltr. in Engler Bot. Jahr. 27: 143 (1900). Type—South Africa, Western Cape, ‘In regione namaquensi: In sabulosis montium Karree-Bergen, alt. C. 4500 ped.’, *Schlechter 8214* (BM!, BOL!, K!, PRE!, S!, Z, photo!).

5.3.10. Calobota obovata (Schinz) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia obovata* Schinz, Mem. Herb. Boiss. 1: 126 (1900). Type—Namibia, Gansberg, *Fleck 75* (Z, 2 sheets, photo!).

5.3.11. Calobota psiloloba (E.Mey.) Boatwr. and B-E.Van Wyk, comb. nov. *Stiza psiloloba* E.Mey. Comm. Pl. Afr. Austr. 1: 31 (Feb. 1836). *Lebeckia psiloloba* (E.Mey.) Walp., Linnaea 13: 478 (1839). Type—South Africa, without locality, *Drège 6470* (P!, K!, S!).

5.3.12. Calobota pungens (Thunb.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia pungens* Thunb., Nov. Gen.: 141 (1800). Type—South Africa, Eastern Cape, near Olifant's River [close to Oudtshoorn] at Cannaland [now Little Karoo], *Thunberg s.n. sub THUNB-UPS 16417* (UPS!).

5.3.13. Calobota saharae (Coss. and Dur.) Boatwr. and B-E. Van Wyk, comb. nov. *Genista saharae* Coss. and Dur., B. Soc. Bot. France 2: 247 (1855). *Spartidium saharae* (Coss. and Dur.) Pomel, Nouv. Mat. Fl. Atl.: 173 (1874). Type—Algeria, D'Oran Province, *Cosson s.n.* (K!, P).

5.3.14. Calobota sericea (Thunb.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia sericea* Thunb., Nov. Gen.: 143 (1800); Prodr. Pl. Cap.: 122 (1800). Type—South Africa, without precise locality, 'e Cap. b. Spei', *Thunberg s.n. sub THUNB-UPS 16423* (UPS!).

5.3.15. Calobota spinescens (Harv.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia spinescens* Harv. in Harv. and Sond., Fl. Cap. 2: 88 (1862). Type—South Africa, Western Cape, Rocks of Driekoppe, *Drège s.n.* (K, P!), without precise locality, Dwaka River, *Burke s.n.* (K!), Northern Cape, Great Fish River and Zout River, Beaufort, *Zeyher 397* (K).

5.3.16. Calobota sp. 1. *De Winter and Hardy 7919* (WIND!, K!, PRE!).

5.4. Wiborgiella

Wiborgiella Boatwr. and B-E.Van Wyk, gen. nov., *Wiborgiae* Thunb. *similis sed fructibus oblongis non alatis valde inflatis*, *anthera carinali breve* (*aliis in eodem flore brevibus dorsifixis simile*) *differt*; *Calobotae* Eckl. and Zeyh. *similis sed petalis ubique glabris*, *antheris ut supra et foliis dorsiventralibus differt*; *Lebeckiae* Thunb. sensu stricto *similis sed foliolis planis non acicularibus valde differt*. Type species: *Wiborgiella leipoldtiana* (Dahlgr. ex Schltr.) Boatwr. and B-E.Van Wyk.

Lebeckia section *Viborgioides* Benth. in Hook., Lond. J. Bot. 3: 361 (1844). Lectotype species (here designated): *Wiborgiella fasciculata* (Benth.) Boatwr. and B-E.Van Wyk [Note: As there is no indication as to which species would be a better choice of lectotype, we here choose the first listed species].

[Note: the new genus proposed here conforms to Bentham's (1844) concept of *Lebeckia* section *Viborgioides*, a taxon for which no name is available at generic level. The name *Wiborgiella* reflects the vegetative similarity and close relationship to the genus *Wiborgia*].

Rigid, resprouting, woody shrubs (rarely lignotuberous shrublets or short-lived fireweeds). *Branches* thick and woody (except in two short-lived species where they are green and herbaceous); young branches brown, covered with bark (green in *W. inflata* and *Wiborgiella* sp. 1), pubescent. *Leaves* digitately trifoliolate; leaflets flat, linear to obovate, pubescent; petioles shorter than leaflets, usually persistent and becoming woody after leaflets are shed, often tuberculate. *Stipules* absent. *Inflorescence* terminal, multi-flowered racemes or rarely single-flowered. *Bracts* linear to lanceolate or elliptic, at least slightly pubescent. *Bracteoles* linear to lanceolate, at least slightly pubescent. *Calyx* lobes subequal, upper sinus often deeper than the lateral or lower sinuses, carinal lobe narrower than the others, pubescent or glabrous. *Corolla* yellow, glabrous or very rarely a few hairs along the dorsal midrib. *Standard* ovate to broadly ovate to oblong. *Wing petals* oblong, ovate or rarely obovate, shorter, to longer than the keel petals, glabrous; apex obtuse. *Keel petals* oblong or lunate, pockets present or absent, glabrous; apex obtuse. *Anthers* dimorphic, four long, basifixed anthers alternating with five ovate, dorsifixed anthers, carinal anther ovate, resembling the dorsifixed anthers (4+6 configuration). *Pistil* subsessile to stipitate; ovary linear to slightly elliptic, with four to many ovules, glabrous, very rarely slightly pubescent on the upper basal parts; style shorter or rarely longer than the ovary, curved upwards, glabrous. *Pods* terete or semi-terete, without wings, inflated or turgid (laterally compressed only in *Wiborgiella* sp. 1), oblong to oblanceolate or lanceolate or elliptic, few- to many-seeded, glabrous, dehiscent (rarely indehiscent). *Seeds* reniform, light pink (*W. leipoldtiana*) or black with white or light brown spots (*W. inflata* and *Wiborgiella* sp. 1), surface smooth or rugose [seeds of *W. bowieana*, *W. fasciculata*, *W. humilis*, *W. mucronata* and *W. sessilifolia* not seen].

5.4.1. Diagnostic characters The genus is similar to *Wiborgia*, but differs in the oblong, wingless, much inflated fruits (ovate to orbicular, markedly winged, samara-like and laterally compressed in *Wiborgia*). It also differs in that the carinal anther resembles the short, dorsifixed anthers (carinal anther intermediate in both *Wiborgia* and *Calobota*). It further differs from *Calobota* in the glabrous petals (in *Calobota*, at least the standard petal has a few apical hairs) and in the dorsiventral leaves (isobilateral in *Calobota*). It differs markedly from *Lebeckia* s.s. in the flat leaflets (invariably acicular in *Lebeckia*). Bark formation is early and the young twigs are brown and covered with bark as opposed to the green twigs of *Calobota* (the short-lived *W. inflata* and *Wiborgiella* sp. 1 have green stems).

5.4.2. Notes on distribution The genus is endemic to the Greater Cape Floristic Region.

5.5. The species of Wiborgiella

5.5.1. Wiborgiella bowieana (Benth.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia bowieana* Benth. in Hook., Lond. J. Bot. 3: 362–363 (1844). Type—South Africa, without precise locality, 'Cape', *Bowie s.n.* [K!, lectotype, designated by Dahlgren (1975)].

5.5.2. Wiborgiella fasciculata (Benth.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia fasciculata* Benth. in Hook., Lond. J. Bot. 3: 361 (1844). Type—South Africa, without precise locality, 'Cape', *Bowie s.n.* [K!, lectotype, designated by Dahlgren (1975)].

5.5.3. Wiborgiella humilis (Thunb.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia humilis* Thunb., Nov. Gen.: 143 (1800). *Wiborgia humilis* (Thunb.) Dahlgr., Op. Bot. 38: 31 (1975). Type—South Africa, without precise locality, 'e Cap. b. Spei', *Thunberg s.n. sub THUNB-UPS 16416* [UPS!, lectotype, designated by Dahlgren (1975)].

Wiborgia apterophora Dahlgr., Bot. Notiser 123: 112 (1970). Type—South Africa, Western Cape, Gifberg, sand at edge of lands, *Esterhuysen 22042* (BOL!).

5.5.4. Wiborgiella inflata (Bolus) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia inflata* Bolus in Hook. Icones Pl. 16: pl. 1576 (1887). Type—South Africa, Western Cape, eastern slopes of Devil's Peak, *Bolus 4826* (BOL!, K!, NBG!).

5.5.5. Wiborgiella leipoldtiana (Schltr. ex Dahlgr.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia leipoldtiana* Schltr. ex Dahlgr., Op. Bot. 38: 72 (1975). Type—South Africa, Western Cape, Calvinia Div.: 'Inter Grasberg et Nieuwoudtville', *Lewis 5839* (NBG!).

5.5.6. Wiborgiella mucronata (Benth.) Boatwr. and B-E.Van Wyk, comb. nov. *Lebeckia mucronata* Benth. in Hook., Lond. J. Bot. 3: 359 (1844). Type—South Africa, Eastern Cape, Uitenhage, *Zeyher 344* (K!, TCD, photo!); Van Stadensberg, *Zeyher 2318* (S!, SAM!).

Lebeckia leptophylla Benth. in Hook., Lond. J. Bot. 3: 359 (1844), syn. nov. Type—South Africa, Western Cape, 'Grassy subalpine situations near Swellendam', *Mundt 87* (K!, S!).

5.5.7. Wiborgiella sessilifolia (Eckl. and Zeyh.) Boatwr. and B-E.Van Wyk, comb. nov. *Acanthobotrya sessilifolia* Eckl. and Zeyh., Enum. Pl. Afr. Austr. 2: 193 (Jan. 1836). *Lebeckia sessilifolia* (Eckl. and Zeyh.) Benth. in Hook., Lond. J. Bot. 3: 362 (1844). Type—South Africa, Western Cape, 'between Breede River and Duyvelshoek', *Ecklon and Zeyher 1344* [S!, lecto.; K!, SAM!, isolecto., designated by Dahlgren (1975)].

5.5.8. Wiborgiella sp. 1. *Vlok 2045* (PRE!, 2 sheets).

5.5.9. Wiborgiella sp. 2. *Baker 10407* (NBG!).

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