Chapter 3
Morphology

The vegetative and reproductive morphology of the tribe Crotalarieae have been studied by Dahlgren (1963, 1967, 1970, 1975), Polhill (1976, 1981) and Van Wyk and Schutte (1989, 1995). Progress in determining the natural delimitations of a group can be made with the application of empirical methods to higher order systematics and comparing critical characters (Van Wyk and Schutte, 1995). The aim of this chapter was a rigorous comparison of several morphological characters to determine their value in species delimitations within the type section of Lebeckia.

Vegetative morphology

3.1 Habit

The shrubby habit predominates in the Crotalarieae (Polhill, 1976), but modifications of a shrubby habit are diverse and an adaptive response of two sorts can be distinguished: (1) woody – aerial parts that can resist unfavourable conditions and (2) suffrutescent – the development of extensive rootstocks that can produce new stems in favourable growing conditions (Polhill, 1976). The genus Lebeckia is generally characterised by a woody or suffrutescent habit (Van Wyk, 1991).
Two aspects of the habit in section *Lebeckia* were included in the cladistic analysis: (1) the type of habit and (2) the branching pattern. The species of section *Lebeckia* are suffrutices with the exception of *L. uniflora* and *L. wrightii* that are annual (or at least short-lived) fireweeds. Six species (*L. ambigua*, *L. brevicarpa*, *L. gracilis*, *L. grandiflora*, *L. pauciflora* and *L. sepiaria*) are virgate and have multiple stems spreading from the base of the plant, reaching heights of up to 0.8 m. The Bredasdorp form (OTU2) of *L. gracilis* is characteristically smaller (up to 0.3 m); *L. grandiflora* is also smaller in habit, growing up to a height of 0.35 m; the Vanrhynsdorp or typical form (OTU1) of *L. pauciflora* grows up to heights of 1.0 m, but the Langkloof form (OTU3) is somewhat smaller (up to 0.6 m). The other species in section *Lebeckia* (*L. brevipes*, *L. contaminata*, *L. longipes*, *L. meyeriana*, *L. plukenetiana*, *L. uniflora*, *L. wrightii* and *L. zeyheri*) are decumbent or trailing in habit and can reach heights of up to 0.5 m, but is generally smaller (0.3 m). Fig. 3.1 illustrates the growth forms found in the species of *L.* section *Lebeckia* and Table 3.1 lists a combination of vegetative characters.

The species of section *Lebeckia* are often found in disturbed areas such as roadsides, river beds or burnt areas. Plants usually flower profusely after fire but the inflorescences often become sparse and few-flowered in the years following a fire (as observed in *L. sepiaria* - Elandskloof population and *L. pauciflora* – Oorlogskloof population). The fireweeds or annuals only occur immediately after fire and disappear after ± a year.
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1. *L. ambigua* (Clanwilliam)  
2. *L. brevicarpa* (Pakhuis Pass)  
3. *L. contaminata* (Gordon’s Bay)  
4. *L. gracilis* (Stil Bay)  
5. *L. meyeriana* (Cape Point)  
6. *L. pauciflora* (Algeria, Cedarberg)  
7. *L. plukenetiana* (Lion’s Head, Cape Town)  
8. *L. sepiaria* (Elandskloof, Citrusdal)

Fig. 3.1. Photographs showing the habit of various species in *Lebeckia* section *Lebeckia* [photographs taken by J.S. Boatwright (1, 4, 6, 7) and B-E. van Wyk (2, 3, 5, 8)].
### Table 3.1 Vegetative characters of the 14 species in *Lebeckia* section *Lebeckia*.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habit</th>
<th>Growth form</th>
<th>Stipules</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>L. ambiguа</em></td>
<td>suffrutex</td>
<td>virgate</td>
<td>absent</td>
</tr>
<tr>
<td><em>L. brevicarpa</em></td>
<td>suffrutex</td>
<td>virgate</td>
<td>absent</td>
</tr>
<tr>
<td><em>L. brevipes</em></td>
<td>suffrutex</td>
<td>decumbent</td>
<td>absent</td>
</tr>
<tr>
<td><em>L. contaminata</em></td>
<td>suffrutex</td>
<td>virgate</td>
<td>absent</td>
</tr>
<tr>
<td><em>L. gracilis</em></td>
<td>suffrutex</td>
<td>decumbent</td>
<td>absent</td>
</tr>
<tr>
<td><em>L. grandiflora</em></td>
<td>suffrutex</td>
<td>virgate</td>
<td>absent</td>
</tr>
<tr>
<td><em>L. longipes</em></td>
<td>suffrutex</td>
<td>decumbent</td>
<td>absent</td>
</tr>
<tr>
<td><em>L. meyeriana</em></td>
<td>suffrutex</td>
<td>decumbent</td>
<td>absent</td>
</tr>
<tr>
<td><em>L. pauciflora</em></td>
<td>suffrutex</td>
<td>virgate</td>
<td>absent</td>
</tr>
<tr>
<td><em>L. plukenetiana</em></td>
<td>suffrutex</td>
<td>decumbent</td>
<td>absent</td>
</tr>
<tr>
<td><em>L. sepiaria</em></td>
<td>suffrutex</td>
<td>virgate</td>
<td>absent</td>
</tr>
<tr>
<td><em>L. uniflora</em></td>
<td>annual (fire-weed)</td>
<td>decumbent</td>
<td>present</td>
</tr>
<tr>
<td><em>L. wrightii</em></td>
<td>annual (fire-weed)</td>
<td>decumbent</td>
<td>present</td>
</tr>
<tr>
<td><em>L. zeyheri</em></td>
<td>suffrutex</td>
<td>decumbent</td>
<td>absent</td>
</tr>
</tbody>
</table>

### 3.2 Leaves

*Lebeckia* is one of the most diverse genera in the Crotalarieae in terms of leaf structure (Dahlgren, 1963; Polhill, 1976). Leaves vary from petiolate and trifoliolate to unifoliolate, simple (without a petiole) or phyllodinous (Dahlgren, 1975; Polhill, 1976). Extreme reduction in stipule size is common in the Crotalarieae (Van Wyk, 1988; Le Roux and Van Wyk, 2007) and it is completely absent in *Wiborgia* and in all except two species of *Lebeckia* – *L. uniflora* and *L. wrightii* – (Van Wyk and Schutte, 1989).

The leaf structure of section *Lebeckia* resembles that of the subgenera *Nortiera* and *Rafnioides* of *Aspalathus* in being phyllodinous, but the origin of the leaf might be different (Dahlgren, 1963).
Three leaf characters were used in the cladistic analysis: (1) the acicular (needle-shaped) leaves as a synapomorphy for the section, (2) the absence or presence of a leaf articulation and (3) the presence or absence of stipules.

Section *Lebeckia* differs from the other sections in the genus in the acicular (needle-shaped and terete) leaves that are often articulated near the middle. In section *Lebeckia*, stipules are absent and the leaves are glabrous, except in *L. uniflora* and *L. wrightii* which have pubescent leaves with stipules.

Leaf length and density have been studied in detail and were found to be variable and not of good diagnostic value. Fig. 3.2 and Fig. 3.3 illustrate the variation in leaf lengths between different forms of each species and the variation in leaf density, respectively. *L. pauciflora* has the longest leaves of all the species in the section (62–134 mm long) and *L. zeyheri* has the shortest leaves (13–14 mm long). The Darling form (OTU1) of *L. plukenetiana* also has very short leaves (13–23 mm long), similar to the leaf lengths in *L. zeyheri*. Both *L. zeyheri* and *L. plukenetiana* are distributed in the same area and could very easily be confused with one another if flowers and fruit are absent.

Some species in section *Lebeckia* have a "joint" or articulation near the middle of the leaf and its presence or absence was found to be diagnostically important. The leaf is reduced to a petiole (phyllode) in the species with the articulation absent (Dahlgren, 1970). The following species have the articulation

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invariably present: *L. ambigua*, *L. brevicarpa*, *L. contaminata*, *L. gracilis*, *L. grandiflora*, *L. meyeriana* and *L. sepiaria*. All the other species have the articulation invariably absent, except *L. pauciflora*. Northern populations (Vanrhynsdorp or typical form – OTU1 and Montagu form – OTU2) of *L. pauciflora* have the articulation invariably present and the eastern regional population (Langkloof form – OTU3) have the articulation invariably absent. The populations between Worcester and Langkloof have the articulation present or absent. If the articulation is absent, the leaves are slightly shorter in length than the articulated forms, but this is not diagnostically different at species level (Fig. 3.2).

The position of the articulation was expressed as a ratio of petiole length : total leaf length and compared for all species with articulated leaves. This ratio overlaps for all the species and is of no diagnostic value (Fig. 3.4).
Fig. 3.2. Variation in leaf length of the 14 species in *Lebeckia* section *Lebeckia*. The average of three measurements from three specimens (where possible) per OTU and the range (longest and shortest leaves) of each OTU are given. The longest leaves are found in *L. pauciflora* and the shortest leaves in *L. zeyheri*.
Fig. 3.3. Variation in leaf density of the 14 species in *Lebeckia* section *Lebeckia*. The average of three counts from three specimens (where possible) per OTU and range (lowest and highest density values) of each OTU are given. Counts were taken in the middle of the stem. The most densely leafy stems are found in *L. sepiaria* and the least densely leafy stems in *L. uniflora* and *L. wrightii*. 
Fig. 3.4. Variation in the leaf articulation position (expressed as a ratio of petiole length: total leaf length) of the eight species of *Lebeckia* section *Lebeckia* with articulated leaves. The average of three measurements from three specimens (where possible) per OTU and the range (lowest and highest values) of each OTU are given. The area where the articulations occur is variable and is overlapping for all species.
The petiole structure is variable in the subfamily Papilionoideae, although some correlation between petiole structure and growth form has been observed (Solereder, 1908). According to Dahlgren (1970), the petiole of species in section Lebeckia did not show any significant anatomical differences. The petiole structure of six species (Table 2.3) in section Lebeckia was studied. The widths of the petioles differ as well as the size and shape of the epidermal cells. These characters may therefore be of diagnostic value. Mucilage cells and stomata are present in the epidermis. There are two to three layers of palisade cells. The vascular bundles are arranged in a ring with the larger primary bundle situated abaxially. In L. ambigua, L. brevicarpa, L. contaminata, L. gracilis and L. sepiaria there are three primary bundles alternating with smaller, secondary bundles (Fig. 3.5. a–e) and in L. pauciflora there are four primary bundles alternating with smaller, secondary bundles (Fig. 3.5. f). Longitudinal sections through the articulations in all six species are similar and there seem to be no diagnostic differences.
Fig. 3.5. Sections of the petiole and leaf articulation of species in *Lebeckia* section *Lebeckia*. (1) Transverse section of the petiole; (2) longitudinal section of the articulation; (a) *L. ambiguа*; (b) *L. brevicarpa*; (c) *L. contaminа*; (d) *L. gracilis*; (e) *L. sepiaria*; (f) *L. pauciflora*. Note the mucilagе cells indicated by arrows. Vouchers: (a) from *Le Roux et al. 6* (JRAU); (b) from *Le Roux et al. 4* (JRAU); (c) from *Le Roux et al. 16* (JRAU); (d) from *Le Roux et al. 17* (JRAU); (e) from *Le Roux et al. 10* (JRAU); (f) from *Le Roux et al. 12* (JRAU). Scale bar: 0.4 mm.
Reproductive morphology

3.3 Inflorescence structure

The inflorescences of the Crotalarieae are commonly terminal racemes or they may become leaf-opposed (sometimes contracted to varying degrees) with continued growth, but the inflorescence structure is rather labile (Polhill, 1976).

A distinctive feature of many of the species of *L. section Lebeckia* is their densely flowered, terminal racemes, with large numbers of flowers (up to 95 flowers per raceme! – Fig. 3.6). Total inflorescence length (Fig. 3.7) and the flower density (number of flowers per 10 mm length of raceme – Fig. 3.8) were measured or counted and are included in the species description but they showed no strong discontinuities and could therefore not be used in the cladistic analysis. The total number of flowers per raceme, however, was quite useful to help define the *L. sepiaria* group (more than 40 flowers per raceme). The species in section *Lebeckia* usually have many-flowered racemes but in *L. wrightii* the racemes are reduced to five (at most) flowers per inflorescence and *L. uniflora* is characterised by having only one flower per inflorescence. Subtle differences occur between the species of section *Lebeckia* (number of racemes formed, number of flowers per raceme and the size of the flowers) as shown diagrammatically in Fig. 3.9. Some of these differences can be used to distinguish between species. In *L. ambigua* (Fig. 3.9a) for example, the stems are invariably branched, resulting in a few lateral branches that also bear
Fig. 3.6. Variation in number of flowers per raceme of the 14 species of *Lebeckia* section *Lebeckia*. The average from three specimens (where possible) per OTU and range (lowest and highest values) of each OTU are given. *L. ambigua*, *L. brevicarpa*, *L. gracilis* and *L. sepiaria* have the most flowers per raceme and *L. uniflora* the least (only one).
Fig. 3.7. Variation in inflorescence length of the 14 species of *Lebeckia* section *Lebeckia*. The average of one measurement from three specimens (where possible) per OTU and range (lowest and highest values) of each OTU are given. The longest inflorescences are found in *L. ambigua* and *L. longipes* and the shortest inflorescences are found in *L. uniflora*.
Fig. 3.8. Variation in flower density in 13 species of *Lebeckia* section *Lebeckia*. The average of one count from three specimens (where possible) per OTU and range (lowest and highest values) of each OTU are given. Counts were made in the middle of the rachis. The most densely arranged inflorescences are found in *L. ambigua*, *L. brevicarpa*, *L. gracilis* and *L. sepiaria* and the least densely arranged inflorescences in *L. uniflora* (with only one flower per raceme, not shown in the figure) and *L. wrightii*. 