

Chapter 4

A multivariate analysis of variation in *Cineraria lobata* L'Hér. and *C. ngwenyensis* Cron.

Abstract

Cineraria lobata is a highly variable species centred in the Western and Eastern Cape Provinces, South Africa, with disjunct populations in Mpumalanga and Limpopo Provinces. Morphological variation was examined in order to delimit the species and to determine whether recognition at infraspecific levels was warranted. Plants from the Ngwenya Hills, Swaziland, similar to *C. lobata* in leaf shape and size, but with glabrous cypselae and a distinct type of trichome, are recognized as a distinct, but closely related species, *C. ngwenyensis*. Cluster Analysis and Principal Coordinates Analysis support the recognition of four subspecies in *C. lobata*: from the Western Cape (ssp. *lobata*), Karoo (ssp. *lasiocaulis*), Soutpansberg (ssp. *soutpansbergensis*) and Eastern Cape (ssp. *platyptera*) regions. A dichotomous key to the subspecies of *C. lobata* is presented. Several recognisable forms from the Western Cape are also delimited.

Introduction

Cineraria L. comprises mainly perennial herbs and subshrubs, with a few annuals or short-lived perennials. It is distinguished by its palmately-veined, 5 – 7-lobed, usually auriculate leaves and radiate yellow capitula. The laterally compressed, obovate cypselae with distinct margins or wings are diagnostic of the genus. It is a senecioid member of the Senecioneae, Asteraceae, with balusterform filament collars and a chromosome number of $x = 10$ (Nordenstam, 1978; Bremer, 1994). The style apex is obtuse with sweeping hairs.

The genus *Cineraria* comprises 35 species, the majority of which occur in South Africa. The most wide-ranging species is *C. deltoidea* Sond., which occurs from the Eastern Cape in South Africa to the highlands of Ethiopia. Only two species occur outside of Africa: *C. abyssinica* Sch.Bip. ex A.Rich. (Ethiopia, Yemen and Saudi-Arabia) and *C. anampoza* (Baker) Baker, endemic to Madagascar. *Cineraria* is essentially an afro-montane genus, with its centre of diversity in KwaZulu-Natal, followed closely by the Eastern Cape, but extends down to sea-level in the Western Cape in the form of *C. geifolia* (L.) L., *C. humifusa* L'Hér. and *C. lobata* L'Hér.

Cineraria lobata is widespread in the Western and Eastern Cape with some disjunct populations in the northern regions of South Africa. The species was initially characterised by distinctly-lobed reniform leaves, glabrous stem and leaves and 5-rayed capitula. However, the species exhibits much variation in size and number of capitula, presence, degree and type

of indumentum on the leaves and stem, robustness of stems, size and shape of auricles, as well as shape, colour and indumentum of the cypselae. This study was undertaken to investigate whether all the specimens considered to be *C. lobata* were in fact a part of this species and whether any infraspecific categories should be recognised. Research into the locality of the types was undertaken to assist with identifying the populations most closely associated with the original description and the epithet ‘*lobata*’.

Taxonomic history of Cineraria lobata

Cineraria lobata was first described by L’Héritier in *Sertum Anglicum* (1788) as having subcorymbose, calyculate capitula, semi-rounded, many-lobed glabrous leaves, petioles auricled at base, and woody stems, and was illustrated by Redouté (t.34, L’Héritier, 1788). The description was based on Banks & Solander and Masson specimens from “Prom. Bonae Spei”. The Banks & Solander specimen, housed at BM and selected as the lectotype (Chapter 6), was collected at the Cape of Good Hope on the first voyage of Captain Cook (HMS Endeavour) during the period 14 March to 14 April 1771. No record of the exact locality for this type specimen has been found, although it seems unlikely that it would have been collected very far inland from Cape Town. Solander was ill for much of the time he was in Cape Town and Banks comments on “...not having had an opportunity of making even one excursion owing in great measure to Dr. Solander’s illness” (Beaglehole, 1962: 255). Cook’s journal also mentions no places other than Cape Town (M. Beasley, *pers. com.*) and no localities are mentioned in the Solander slips (N. Chambers, *pers. com.*). The type specimen nevertheless best matches specimens slightly inland from Cape Town (e.g. Malmesbury) and from the Worcester areas, being glabrous, more slender with fewer capitula than the more robust, sparsely hairy specimens of *C. lobata* known from the Cape Peninsula.

Two varieties have been previously recognised for *Cineraria lobata*: *C. lobata* var. *gracillima* DC. and *C. lobata* var. *pappei* Harv. *Cineraria lobata* var. *gracillima*, from the Uitenhage District in the Eastern Cape, is described as being simple, erect and slender with a weak fibrous root system, but it is most likely that it is simply in its first year of flowering, a possibility noted by De Candolle (1838: 308). *Cineraria lobata* var. *pappei* has very many small heads, lacks auricles and is based on a specimen collected by Dr Pappé from the Winterhoek mountains, Tulbagh (Harvey, 1865).

Cineraria lobata has been distinguished from *C. geifolia* by being glabrous in all parts, with many more, but smaller capitula, with 6 or 7 involucre bracts (not 12 or 13) and a more branching synflorescence (De Candolle, 1838; Harvey, 1865). As noted above, many of these features are however quite variable in *C. lobata*, especially the presence and type of indumentum on the leaves and stem. *Cineraria lobata* also resembles *C. saxifraga* DC. from the Eastern Cape, which is distinguished from it by being slightly succulent (*pers. obs.*) and having smaller and less lobed and reniform leaves (Harvey, 1865).

Cineraria lobata also shows some affinity to *C. alchemilloides*, from the Western and Northern Cape and Namibia. There is also some relationship with *C. geraniifolia*, as shown by molecular studies, but it is distinguished from that species by its ciliate and hairy cypselae and more numerous capitula on shorter peduncles. DNA studies also indicate reticulate evolution between the cobwebby form of *C. lobata* ssp. *soutpansbergensis* Cron from the Soutpansberg and Blouberg in Limpopo Province and *C. cyanomontana* (a Blouberg Mountain endemic), which share a cobwebby indumentum (Chapter 2).

Variation in *Cineraria lobata*

Cineraria lobata occurs mainly in the more southerly regions of South Africa, where it extends from the Saldanha Bay area in the Western Cape to the Uitenhage and Albany Divisions in the Eastern Cape, but has not been recorded from KwaZulu-Natal (Figure 1). Other forms from the hills of Mpumalanga and as far north as the slopes of the Soutpansberg were also (preliminarily) identified as part of *C. lobata*. In addition, *C. ngwenyensis* Cron, a species morphologically similar to *C. lobata* (but with glabrous cypselae), occurs in the Ngwenya Hills in Swaziland (Figure 1). As noted above, *C. lobata* appears to vary in a number of vegetative and reproductive characters. We identified a number of morphological variants associated with geographic regions, although some overlap does occur. The distinguishing features of these forms of *C. lobata* are summarised in Table 1 and discussed below; their distribution is shown in Figure 1.

Figure 1. Distribution of *Cineraria lobata* and *C. ngwenyensis*, showing the variation recognised: *C. lobata* ssp. *lobata*: ● Western Cape form (WC), ○ Worcester form (WO), △ Hairy form (WH), ▲ Montagu Hairy form (MON), ◇ Robust form (WCR), □ Small-leaved, jointed stem form from near Uniondale: narrow-winged (UN), ▲(grey) broad-winged (UNB), ◆ polycapitula form (PY), ▼ *C. lobata* ssp. *lobata* var. *platyptera* from the Eastern Cape (EC), ★ *C. lobata* ssp. *lasiocaulis* from near Layton/Laingsburg (LA), ■ *C. lobata* ssp. *soutpansbergensis* (SP), ▽ cobwebby form (SPCW), ▼(grey) Middleburg specimens cf. *C. lobata* (MB); ☆ *C. ngwenyensis*.

Table 1. Summary of variation in geographical forms of *Cineraria lobata* and *C. ngwenyensis*, with distinguishing features highlighted.

Form/Location (Symbol used)	Distinguishing Features
Western Cape (WC) (Figure 2a)	Deltoid-reniform to reniform leaves, usually distinctly lobed, glabrous or sparsely hairy; slender stems. Many small capitula (3 – 5 rays) on fairly short peduncles. Cypselae ciliate and hairy, usually margined (Figure 5a).
Worcester group (WO) (Figure 2b)	Matching above specimens but with fewer small capitula on slightly longer peduncles, 5 rays, 8 involucre bracts.
Hairy group (WH) (Figure 2c)	Very hairy stems and leaves , involucre bracts hairy or glabrous. 5 rays, 8 involucre bracts.
Montagu group (MON) (Figure 2d)	Stems and leaves hairy . Ray cypselae distinctly winged , ciliate, hairy on outer faces, glabrous or almost so on inner faces (Figure 5b).
Robust Group (WCR) (Figure 3a)	Stems more robust , stems and leaves glabrous or sparsely hairy (mainly on ventral surface of leaves), some with generally larger capitula : 5 – 8 rays, 8 or 9 involucre bracts, rarely 13. Cypselae commonly margined (Figure 5c).
Layton/Laingsburg (LA) (Figure 3b)	Tufted growth form with contracted internodes, leaves glabrous with a few cobwebby hairs at base, petioles cobwebby glabrescent. Few, relatively large capitula on longer peduncles. Cypselae narrowly obovate, black, outer surfaces hairy (short white hairs), inner glabrous (rays) to sparsely hairy (disc), margined (Figure 5e).
Uniondale (UN, UNB) (Figure 3c, d)	Small shrublets with jointed stems, small leaves, glabrous . Few capitula in lax panicle. Ray cypselae distinctly narrow- or broad-winged , disc cypselae margined (rarely narrow-winged).
Polycapitula (PY) (Figure 4a)	Sprawling growth form . Stems fairly robust; leaves large, shallowly-lobed or occasionally deeply-lobed, glabrous or sparsely hairy. Many small capitula, compact, on short peduncles . Cypselae narrow-winged to margined, ciliate with hairy to sparsely hairy outer faces, inner faces sparsely hairy to glabrous (Figure 5d).
Eastern Cape (EC) (Figure 4b)	Stems fairly slender; leaves reniform with distinct (to shallow) lobing, glabrous, occasionally sparsely hairy below, glandular hairs in angles of lobes, usually conspicuous auricles . Broad-winged ray cypselae, disc cypselae distinctly winged , ciliate wings, faces sparsely hairy or glabrous (Figure 5f).
Soutpansberg Region (SP), some cobwebby (SPCW) (Figure 4c)	Slender stems, deltoid to reniform leaves, lanceolate auricles, with or without a cobwebby indumentum , few capitula, with 5 or 6 rays, 8 – 12 involucre bracts. Cypselae margined, ciliate and hairy (Figure 5g, h).
Middleburg, Mpumalanga (MB) (Figure 4d)	Slender stems (unbranched?), upper and lower leaves with lateral pinnae, glabrous, auricles bifid, few capitula on fairly long peduncles (16 – 60 mm), 8 rays, 10 – 13 involucre bracts. Cypselae margined to narrow-winged, ciliate, hairy on outer faces, sparsely hairy on inner.
Ngwenya, Swaziland (NGWEN) Figure 6c	Stems and leaves densely hairy , branching from the base, leaves deeply lobed. Few capitula, with 7 or 8 rays, 12 – 13 involucre bracts, glabrous. Glabrous cypselae. Trichomes eglandular, without long wisp.

The form of *Cineraria lobata* from the **Western Cape (WC)** (Figure 2a) includes Harvey's "var. *pappei*" and has many small capitula and essentially glabrous leaves and stems except for a concentration of cobwebby hairs in the axils of the leaves and a few eglandular hairs at the base of the lamina on the ventral surface of the leaf on some specimens. The **Worcester form (WO)** (Figure 2b) best matches the type specimens and those grown from seed at Kew from the original collections. The **Hairy forms (WH and MON)** (Figures 2c, 2d) from the Hex River Valley, Swellendam and Montagu regions can be extremely hairy all over, a contradiction of the original description of *C. lobata* as a glabrous plant. The cypselae of most of these forms are margined (Figure 5a), with the exception of the plants from Montagu that have distinctly winged cypselae (Figure 5b).

The **Robust form (WCR)** from the Cape Peninsula and Langebaan and Saldanha regions of the Western Cape (Figure 3a) appears to be a more coastal form of the species. Although *Cineraria lobata* generally occurs in the mountains, in the Cape Peninsula and the Saldanha Bay regions, it grows amongst the rocks on the slopes or cliffs near sea level. In these areas, *C. lobata* is more robust than usual and may have slightly larger capitula (7 or 8 rays instead of 5), and occasionally more than 8 involucre bracts (9–12). The stems of these plants are glabrous, but the leaves vary from glabrous to sparsely hairy, rarely being very hairy below and on the petiole. The robust nature of these specimens and the slightly larger capitula make them difficult to distinguish from *C. geifolia* which also occurs on the Cape Peninsula. *C. geifolia* is generally distinguished from *C. lobata* by having more rounded reniform leaves with very shallow lobing and larger capitula. It has larger, more spreading trichomes (without an apical wisp, commonly seen in *C. lobata*) and is generally more robust. The mature capitula of *C. geifolia* have a very "fluffy" pappus, a useful diagnostic feature of the species. The leaves of *C. lobata* are usually more distinctly and acutely lobed than those of *C. geifolia*.

The populations growing in the vicinity of **Layton and Laingsburg in the Karoo (LA)** (Figure 3b) are characterised by a tufted growth form (especially evident on older specimens) due to shortened internodes and a thick woody base to the stem. Thick tufts of woolly hairs in the axils make the stem floccose. The leaves are almost glabrous, but with a few cobwebby hairs remaining towards the base of the lamina. The petioles are cobwebby, glabrescent with small (to medium) auricles and the woolly axils are very conspicuous. These populations are also distinctive due to relatively large capitula with 7, 8 or 9 rays and 12 or 13 involucre bracts, and few capitula, laxly arranged on longish peduncles. Their cypselae are very distinctive as they are longer and more narrowly obovate and only slightly margined (Figure 5e). They are black (or very dark brown) when mature with the outer face densely covered with short white hairs, while the inner faces of the ray cypselae are commonly glabrous (or sparsely hairy), and the inner faces of the disc floret cypselae vary from being slightly to much less hairy than the outer surface. An inner median rib is evident on some mature cypselae.

Figure 2. (Opposite) Specimens showing variation in *Cineraria lobata* ssp. *lobata*. (a, b) Small-headed form from: (a) the Piquetberg, Western Cape (WC2), *Compton 14993* (NBG). Scale bar = 35 mm. (b) near Worcester (WO2), *Compton 21201* (NBG). Scale bar = 33 mm. (c, d) Hairy form from: (c) Prospect Peak, Hex River Mountains (WH4), *Esterhuysen 15889* (BOL). Scale bar = 35 mm. (d) Montagu (MON3), *Levy's 8054* (BOL). Scale bar = 33 mm.

Figure 3. (Overpage) Specimens showing variation in *Cineraria lobata*: (a) ssp. *lobata*, Robust form from Saldanah (WCR1), *Goldblatt 4107* (WAG). Scale bar = 32.5 mm. (b) ssp. *lasiocaulis* from Laingsburg (LA5), *Compton 3601* (BOL). Scale bar = 31 mm. Inset: woolly stem of *Hall 172* NBG (LA4). Scale bar = 3.1 mm. (c) ssp. *lobata*, small leaved form with jointed stems from the Uniondale region: *Cron & Goodman 569* (J, sheet 1), growing in sun. Scale bar = 33 mm. (d) *Cron & Goodman 569* (J, sheet 2), growing in shade of bush. Scale bar = 31 mm.

Specimens of *Cineraria lobata* growing in the Uniondale area of the Western and Eastern Cape (**UN and UNB**) typically have very small leaves and very jointed (abruptly branched) stems (Figure 3c). Some of the specimens from the Uniondale Division have broad-winged ray cypselae (UNB), but most have ray and disc cypselae with distinct narrow wings (UN).

Many-headed forms from the coastal regions of the southern Cape (**PY**) have a scrambling habit, growing profusely near the sea shore in the southern Cape. The many small capitula on short peduncles are compactly arranged (Figure 4a). Some have deeply-lobed leaves, whereas others have leaves resembling the more rounded shallowly-lobed leaves of *Cineraria geifolia* (as seen in Figure 4a), either glabrous or hairy. However, because they have small capitula and lack the indumentum typical of *C. geifolia*, they are considered to be part of the variation in *C. lobata*. These plants are also similar to plants previously identified as *C. polycephala* DC. (known only from the type collection from Gouritz River Mouth and Visbaai) due to the large number of compactly arranged capitula. However they do NOT match it in a number of important features, notably the larger capitula and presence of a cobwebby indumentum in *C. polycephala*, which is now considered to form part of the variation in *C. erodioides* DC (Chapter 6).

Another form of *Cineraria lobata* occurring in the **Eastern Cape (EC)** is distinguishable by its broad-winged ray cypselae which are fringed with hairs and sparsely hairy or glabrous on the faces (Figure 5f). These plants generally have larger leaves with more conspicuous auricles (Figure 4b) than the Uniondale ones. Their broad-winged ray cypselae resemble those found in some populations of *C. platycarpa* DC., but that is a much smaller annual plant, predominantly occurring in the Little Karoo and Namaqualand areas, although some specimens are known from the vicinity of Redhouse in the Eastern Cape. *Cineraria erodioides*, a widespread species also occurring in the Eastern Cape, also has broad-winged ray cypselae but has a cobwebby indumentum not seen in these specimens.

Plants from the **Soutpansberg region** in Limpopo Province (**SP**) resemble *Cineraria lobata* in their growth form and reniform lower leaves but differ in having lanceolate auricles (Figure 6b) compared to the more auriculate, toothed auricles of the Western and Eastern Cape populations (Figure 6c). They are also characterised by a very thick tuft of white-woolly hairs in the axils of the leaves (Figure 4c inset, 6a). Some of these northern specimens have leaves tending more to deltoid than reniform in shape (Figure 4c, specimen on left), and hence also resemble *C. decipiens* from KwaZulu-Natal. Some specimens collected from altitudes of 900 m and higher from both the Soutpansberg and the Blouberg (**SPCW**) are greyish due to fine, cobwebby hairs (Figure 6a).

The population of densely hairy plants (Figure 6d) from the **Ngwenya Hills** in Swaziland (**NGWEN**) shows an affinity to *Cineraria lobata* due to their reniform and deeply lobed leaves

Figure 4. (Opposite) Specimens showing variation in *Cineraria lobata*: (a) Many-headed form from Eersterivier (PY5), *Cron & Goodman 568* (J). Scale bar = 35 mm. (b) ssp. *platyptera* from the Eastern Cape (EC7), *Booi 43* (GRA). Scale bar = 30 mm. (c) ssp. *soutpansbergensis* (SP3), *Cron et al. 282* (J) (on LHS), and (SP2) *Cron et al. 285* (J) on RHS. Scale bar = 29 mm. Inset: thick woolly axils of *Fourie 2768* (K) (SP1). Scale bar = 2 mm. (d) cf. *C. lobata* from near Middleburg (MB1), *Codd 10103* (NBG). Scale bar = 32 mm. Inset: bifid auricles of *Codd & Dyer 2871* (PRE) MB2. Scale bar = 1.2 mm.

Figure 5. (Overpage) Cypselae of *Cineraria lobata*: (a – d) ssp. *lobata*: (a) Margined ray and disc cypselae of *Compton 14993* (NBG)(WC2). Scale bar = 440 μm . (b) Distinctly winged ray and disc cypselae of *Compton 18464* (NBG) from Montagu (MON2). Scale bar = 580 μm . (c) Robust form from Saldanha: *Hugo 2927* (WAG) (WCR2). Scale bar = 560 μm . (d) *Cron & Goodman 568* (J) (PY5). Scale bar = 400 μm . (e) ssp. *lasiocaulis*, from left: Ray cypselae hairy outer surface and almost glabrous inner surface, inner surface of disc cypselae, *Shearing 1332* (PRE) (LA2). Scale bar = 430 μm . (f) ssp. *platyptera*: Broad-winged ray cypselae and distinctly winged disc cypselae of *Bayliss BS 8878* (WAG) from the Albany District, Eastern Cape (EC2). Scale bar = 400 μm . (g) ssp. *soutpansbergensis*: *Fourie 2768* (K) (SP1). Scale bar = 340 μm . (h) ssp. *soutpansbergensis*, cobwebby form, *Cron et al. 344* (J) (SPCW3). Scale bar = 370 μm .

Figure 6. (Overpage) (a) Woolly axil with young leaf of *Cineraria lobata* ssp. *soutpansbergensis* (cobwebby form) *Cron et al. 363* (J) (SPCW1), lanceolate auricle visible. Scale bar = 1.1 mm. (b) Lanceolate auricle of *Fourie 2768* (K) (SP1). Scale bar = 420 μm . (c) Sharply dentate, auriform auricle of ssp. *lobata*, *Pillans 9130* (NBG), (WC3). Scale bar = 770 μm . (d) Hairy stem with lanceolate auricle at base of petiole of *C. ngwenyensis*, *Cron et al. 308* (J) (NGWEN4). Scale bar = 1 mm. (e) Habit of *C. ngwenyensis*, *Cron et al. 308* (J). Scale bar = 30 mm. (f) Glabrous cypselae of *C. ngwenyensis*, *Cron et al. 308* (J). Scale bar = 450 μm .

(Figure 6e). However they have larger capitula than usual for *C. lobata*, and entirely glabrous cypselae (Figure 6f) and are recognised as a putative new species, *C. ngwenyensis*. Their auricles are lanceolate to ovate in shape (Figure 6d), fairly similar to the northerly populations of *C. lobata* in the Soutpansberg.

Aim of study

The aim of this study is therefore to document and analyse the variation in *Cineraria lobata*, to investigate whether recognition of any infraspecific groups is warranted, and to determine if the northern-most specimens are indeed part of the variation in *C. lobata*. The status of the putative new species *C. ngwenyensis* in the Ngwenya Hills, Swaziland is also investigated. The numerical techniques of cluster analysis and principal coordinates analysis are used to assist in the analysis of the *C. lobata* complex.

Multivariate techniques

Two main approaches have been used in numerical taxonomy based on morphological data, ordination and cluster analysis. Ordination techniques summarise large amounts of information in only a few dimensions and have been much used in taxonomic studies (Pimentel, 1981; Chandler & Crisp, 1998). In ordination, the operational taxonomic units (OTUs) are represented as points in some (optimally) low-dimensional space, in which Euclidean distances between points reflect the relationships between the OTUs as indicated in the proximity matrix (Dunn & Everitt, 1982). Cluster analysis is useful in separating organisms into groups that may be used in a classification.

Principal Coordinates Analysis (PCO) is recommended for data sets combining quantitative and qualitative characters (Legendre & Legendre, 2003) as Principal Components Analysis (PCA) assumes normality of data and is essentially intended for use with measurements made on a continuous scale. It is therefore not useful for qualitative characters nor for skewed data sets, and although it may be used with binary data Gower (1966), a “horseshoe effect” can result (Dunn & Everitt, 1982). PCO is a form of multidimensional scaling, concerned with “the construction of a configuration of points in Euclidean space which reflects, in some sense, the relationships between a set of OTUs as implied by their observed proximities *whether these are Euclidean or not*” (Dunn & Everitt, 1982). The aim of PCO is therefore to produce a Euclidean representation of the observed distances between OTUs that minimizes the distortion in two-dimensional representation; that is, “to produce a pattern of points that best represents the pattern in the original multidimensional character space” (Dunn & Everitt, 1982). The method has been used to good effect in a number of taxonomic studies (e.g. Brysting & Elven, 2000; Olvera, 2003).

Cluster analysis has been widely used to examine geographical patterns of variation and imposes a hierarchical structure on the data (Thorpe, 1983). A disadvantage of this is that the

analysis may show distinct clusters even if the variation is clinal, as may be seen using ordination techniques (Thorpe, 1983). Therefore both techniques were used in this study.

Of the numerous techniques available for cluster analysis, the Unweighted Pair-Group Method using Arithmetic Averages (UPGMA) is mostly preferred as it is more space-conservative and shows the highest cophenetic correlation, regardless of the structure of the data (Sokal & Rohlf, 1962; Sneath & Sokal, 1973). The cophenetic correlation is comparable to stress on an ordination (Sneath & Sokal, 1973), however Farris (1969) warns that the cophenetic correlation coefficient is not a direct measure of the degree to which the classification describes the distribution of character states.

Equal weight should be assigned to all characters (Sneath & Sokal, 1973), although it is recognised that the conversion of multistate characters into numerous binary characters can weight certain characters. The inclusion of many characters in the data set can even out the effective weight that each character contributes to the similarity or distance coefficient (Sneath & Sokal, 1973). Multistate ordered characters may be treated like continuous quantitative characters in order that “comparisons should reflect the degree of disagreement rather than simply state it as a match or mismatch” (Sneath & Sokal, 1973: 133).

A phenetic approach in taxonomy is an attempt to use numerical methods as a tool to assist with a more objective classification. However, it is recognised that the many decisions of what characters to include and the character states/units of measurement are often subjective (Gower, 1988). In addition, the decision of where to place the phenon line that delimits the recognised groups is not always objective (Michener, 1970). The application of rank to these “phenons” is also to some extent a matter of subjective decision and influenced by knowledge of the group. The same criterion for rank should be applied to all parts of the analysis. There are two objections to the use of phenon lines: Hill (1980) emphasised that without prior knowledge of the taxonomy of the OTUs, there is no way to predict where the phenon lines should be placed. Clifford & Williams (1973) and Clifford (1976) have shown that the drawing of phenon lines is invalid due to group-size dependence, unless the fusion strategy in use is strictly space-conserving, ie. a centroid one - rarely used (Hill, 1980).

Michener (1970) and Dunn & Everitt (1982) conclude that numerical taxonomic methods are best seen as tools for data exploration, rather than for the production of a formal classification. It is in that sense that the approach is used here.

The species concept applied here is essentially a phenetic one equivalent to the traditional morphological species concept, based on morphological similarity between organisms. Although the phylogenetic species concept of Nelsen & Platnick (1981) and the composite species concept of Kornet & McAllister (1993) are more satisfactory and intuitive, with

species being mutually exclusive groups of organisms, morphologically distinguishable by combinations of diagnostic characters and (in the latter concept) existing over time (Kornet & McAllister, 1993), the method for applying these concepts to very variable and wide-ranging species/species complexes is unclear. Certain taxonomists have admitted to adopting a pluralistic approach (e.g. Sidwell, 1999), making use of phenetic practice to investigate variation in widespread and variable species, while adhering to a phylogenetic concept for other species in a group. Other taxonomists probably do the same, however many do not clearly state the species concepts being applied (Luckow, 1995; McDade, 1995).

Method

Taxa and characters

A total of 68 specimens across the entire geographic and altitudinal range of *Cineraria lobata* and 5 specimens of *C. ngwenyensis* were examined for this study (Appendix 1). In addition, six specimens of *Cineraria longipes* S. Moore, a distinct endemic species from Gauteng, were initially included as a “standard taxon” to ensure that the characters included were sufficient/able to group together specimens of a known species. Multiple sheets were available for 19 of these 79 specimens (Appendix 1), and all the material was examined and used for recording measurements. Specimens were assigned to the groups listed in Table 1 *a priori* to facilitate analysis of the morphometric variation, but without prejudice to the final interpretation.

Characters were chosen according to differences observed in the various forms of *Cineraria lobata* (Table 1), as well as those characters known to be generally useful in distinguishing species of *Cineraria* (Cron, 1991). Forty-nine characters were initially measured or investigated (Table 2), but a number of these were excluded from the final analysis. Cypselae length was excluded as not all specimens had mature cypselae, resulting in missing data. Cypselae colour proved difficult to accurately assess (i.e. dark brown vs. black), and was dependant on age, so was also excluded. Ratios indicating leaf and apical lobe shapes (length to width ratios) and apical lobe depth (lobe length to leaf length), leaf to petiole length and ray limb length to width were used. Therefore leaf width, lobe length, petiole length and ray width were excluded to avoid repetition of character information. Certain leaf shape characters (Table 2) were assessed separately for upper and lower leaves, as these sometimes vary in *Cineraria*. Figure 7 shows how leaf dimensions were measured.

The type of indumentum present (i.e. hairy vs. cobwebby) was expressed in terms of the types of trichomes present or absent (characters 17 – 20). The occurrence of the indumentum on particular organs and the degree of pubescence was coded as binary for stems (character 2, Table 2) and as multistate ordered characters for leaves (characters 15, 16 and 27; Table 2). This coding does not distinguish between a cobwebby and a hairy tomentum and tends to

weight the presence or absence of a tomentum. The data set comprising quantitative and qualitative characters was therefore analysed in two ways: (i) including characters denoting presence and degree of pubescence on stem, leaves and petioles (characters 2, 15, 16 and 27), and (ii) excluding them. Presence of pubescence on the involucre bracts and the peduncles was used as a binary character in both analyses, although this resulted in loss of information regarding type of indumentum in two northern specimens with cobwebby peduncles.

Table 2. List of characters examined for phenetic analysis of *Cineraria lobata* and *C. ngwenyensis*. *Characters excluded from the final analyses. **Pubescence characters included in one set of analyses, excluded from a second set of analyses.

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1. Stem diameter (at widest point at the base; mm).
 - **2. Stem pubescence: (1) glabrous (2) pubescent.
 3. Cobwebby axils: (1) absent (2) present
 4. Upper Leaf Shape (outline): (1) deltoid-reniform (2) reniform.
 5. Lower Leaf Shape (outline): (1) deltoid-reniform (2) reniform.
 6. Pinnae below leaf lamina (upper): (1) absent (2) present.
 7. Pinnae below leaf lamina (lower): (1) absent (2) present.
 8. Leaf length (average of three measurements; mm).
 - *9. Leaf width (average of three measurements; mm).
 10. Leaf l:w ratio (average of three measurements).
 11. Apical lobe width (average of three measurements; mm).
 - *12. Apical lobe length (average of three measurements; mm).
 13. Apical lobe length: leaf length ratio (average of three measurements).
 14. Apical lobe length: width ratio (average of three measurements).
 - **15. Leaf pubescence, dorsal surface: (1) glabrous (2) sparsely pubescent, glabrescent (3) densely and persistently pubescent.
 - **16. Leaf pubescence, ventral surface: (1) glabrous (2) sparsely pubescent, glabrescent (3) densely and persistently pubescent.
 17. Trichome type 1: eglandular multi-celled (no wisp) (Figures 8, 9a, c, d): (0) absent (1) present.
 18. Trichome type 2: multi-celled, tapering base with long apical wisp (Figure 8, 9b): (0) absent (1) present.
 19. Trichome type 3: 2–4 (–6) narrow basal cells, with long apical wisp (Figure 8, 9e, f): (0) absent, (1) present.
 20. Trichome type 4: glandular (Figure 8): (0) absent (1) present (in angles of lobes).
 21. Leaf apex (upper): (1) acuminate (2) acute (3) obtuse (4) rounded.
 22. Leaf base (upper): (1) cordate (2) slightly cordate (3) truncate (4) cuneate.
 23. Leaf apex (lower): (1) acuminate (2) acute (3) obtuse (4) rounded.
 24. Leaf base (lower): (1) cordate (2) slightly cordate (3) truncate (4) cuneate.
 - *25. Petiole length (average of three measurements; mm).
 26. Ratio of leaf length to petiole length (average of three measurements).
 - **27. Petiole pubescence: (1) glabrous (2) sparsely pubescent, glabrescent (3) densely and persistently pubescent.

28. Presence of auricles and shape: (1) absent (2) petiole widens at base (3) present and auriform (4) present and lanceolate.
 29. Number of capitula per stem branch: (1) solitary (2) few (2 – 4) (3) 4 – 8 (4) many (10 – 35) (5) very many (> 40).
 30. Peduncle length (maximum, nearest capitulum; mm).
 31. Peduncle indumentum: (1) glabrous (2) hairy or cobwebby.
 32. Bract length (at middle of peduncle; average of three measurements; mm).
 33. Number of involucral bracts (average of three measurements).
 34. Length of involucral bracts (average of three measurements; mm).
 35. Indumentum of involucral bracts: (1) glabrous (2) hairy.
 36. Number of rays (average of three measurements).
 37. Ray total length (average of three measurements; mm).
 38. Ray limb length (average of three measurements; mm).
 - *9. Ray limb width (average of three measurements; mm).
 40. Ratio limb length:width (average of three measurements).
 41. Number of disc florets (average of three measurements).
 42. Length of disc corolla (average of three measurements; mm).
 43. Cypsela shape: (1) obovate (ca. 2 times as long as wide) (2) narrowly obovate (ca. 3 times as long as wide).
 44. Ray cypsela indumentum: (1) glabrous (2) ciliate on margins only (3) ciliate & hairy on outer face only/mainly (4) ciliate margins & both faces hairy.
 45. Disc cypsela indumentum: (1) glabrous (2) ciliate on margins only (3) ciliate & hairy on outer face only/mainly (4) ciliate margins & both faces hairy.
 46. Ray cypsela extension: (1) margined (2) narrow-winged (3) broad-winged.
 47. Disc cypsela extension: (1) margined (2) narrow-winged (3) broad-winged.
 - *48. Cypsela colour: (1) brown (2) black (3) brown with pale wings (4) black with pale wings.
 - *49. Cypsela length: maximum length (mature) (mm).
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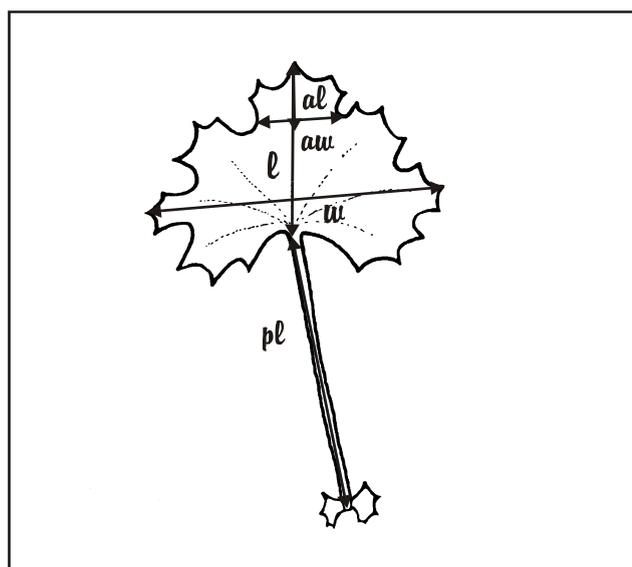


Figure 7. Diagram showing measurement of leaf dimensions: al = apical lobe length, aw = apical lobe width, l = lamina length, w = lamina width, pl = petiole length.

A total of 43 characters was therefore used in the analysis including presence and degree of pubescence: 17 quantitative, 12 binary and 14 multistate ordered. Thirty-nine characters were used in the analysis excluding the four characters denoting presence and degree of pubescence: 17 quantitative, 11 binary and 11 multistate ordered.

In addition, a data set comprising only qualitative characters (11 binary and 15 multistate) was analysed by using the simple matching coefficient, then clustered using the UPGMA algorithm. Indumentum characters (2, 15, 16 and 27) were here coded in multistate unordered form: (1) glabrous, (2) cobwebby, glabrescent, (3) persistently cobwebby, (4) hairy, glabrescent, (5) persistently hairy. This allows for description of the type of indumentum and its persistence in a single character. Peduncle indumentum (character 31) was also coded as a multistate unordered character: glabrous (1) cobwebby (2) or hairy (3). (Data matrices are available on website <http://www.wits.ac.za/apes/ggoodman/cineraria>.)

All measurements were made on dried herbarium specimens housed at J or borrowed from the following herbaria: BOL, GRA, K, MO, PRE, NBG, NU, WAG, Z. A minimum of three measurements was averaged for the quantitative characters, but five measurements were used if a character appeared highly variable on a specimen. Leaf trichomes were examined with a dissecting microscope (at a magnification of 400 X), and a representative specimen from each geographic region was examined using a compound microscope or a JEOL JSM 800 scanning electron microscope. Leaves examined under the compound microscope were cleared and autoclaved according to the procedure of O'Brien & von Teichman (1974). Preparation of leaves for scanning electron microscopy involved dehydration in an alcohol series, critical point drying and coating with a mixture of gold palladium and carbon. Four main types of trichomes were identified (Table 2, Figures 8 and 9) and trichome types were scored as present even if found only in angles of leaf lobes, but not on leaf surfaces, petioles or stems.

Cluster and multivariate analyses

All analyses were performed using NTSYS-PC version 2.0 (Rohlf, 1998). In the cluster analysis, the characters were standardised by dividing the difference between the mean and the actual measurement by the standard deviation (default standardization option in NTSYS), then a dissimilarity matrix based on average taxonomic distance was calculated and the UPGMA clustering method used to hierarchically cluster the OTUs. The cophenetic correlation coefficient (r) for each tree and its distance matrix was calculated as an indication of the goodness of fit of the tree to the data set.

Cluster analysis of the qualitative data set was performed using the simple matching coefficient to create a correlation/similarity matrix, then clustered using the UPGMA algorithm. The simple matching coefficient recognises shared absences of characters (eg. types of trichomes) as significant, however there is no recognisance of a match between two states of a multistate character being less likely than a binary character (Dunn & Everitt, 1982).

Principal Coordinates Analysis was also performed on the two versions of the data set comprising qualitative and quantitative characters (i.e. including and excluding indumentum characters), by standardising the matrix by variables and computing and double-centring a matrix of distances between the OTUs, factoring the double-centred matrix and using the eigen vectors to project the OTUs in 2-dimensional and 3-dimensional space (Rohlf, 1998).

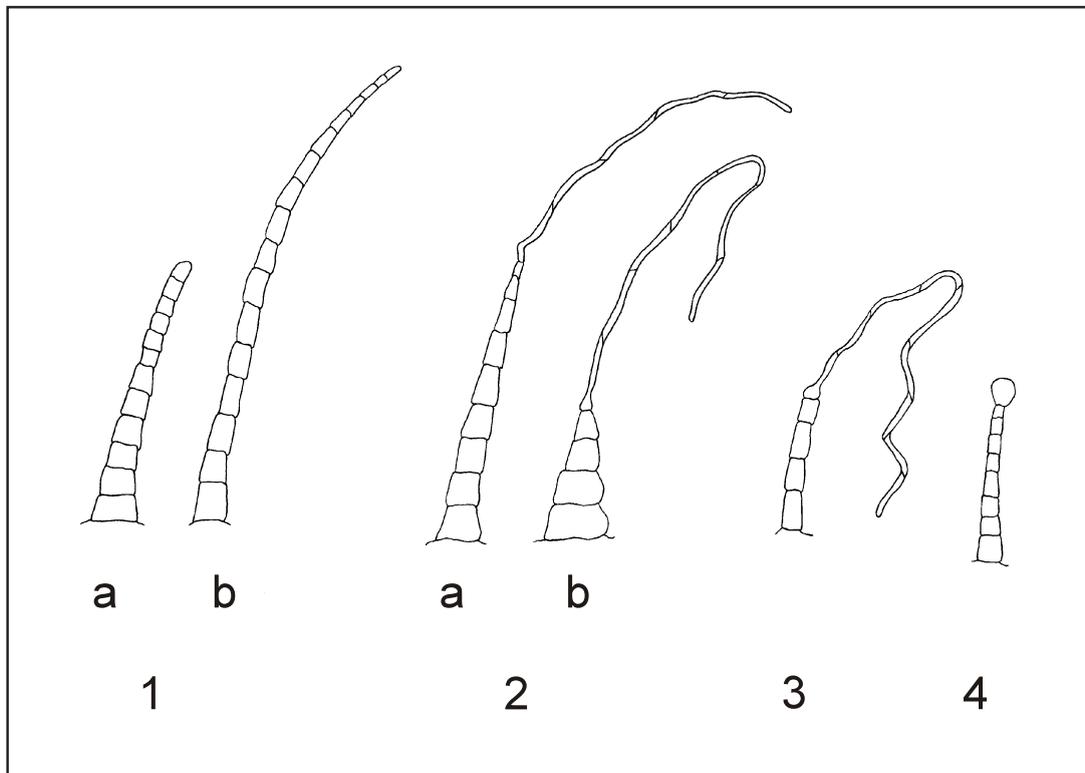


Figure 8. Trichome types 1 – 4: Type 1: Eglandular tapering trichome, (a) 10 – 12 subisodiametric cells or (b) 14 – 18 elongate cells; Type 2: Tapering base consisting of 4 – 8 cells (gradually tapering) or (b) more sharply tapering, with a long multi-celled apical wisp; Type 3: Narrow 4 – 6-celled base with a long multi-celled apical wisp; Type 4: Glandular hairs comprising 8 – 10 cells with a swollen glandular tip (in angles of lobes only).

Figure 9. (Opposite) Trichomes of *Cineraria lobata* and *C. ngwenyensis*: (a) Ventral surface of leaf of hairy form of ssp. *lobata*, (WH1) eglandular hairs with ca. 12 tapering basal cells and long apical wisp. Scale bar = 250 μm . (b) Leaf and petiole of *Cron & Perret 333* (J) (MON1): eglandular hairs with multi-celled tapering base and long apical wisp. Scale bar = 230 μm . (c) Leaf of *C. ngwenyensis* (NGWEN4) with eglandular hairs. Scale bar = 110 μm . (d) SEM showing detail of eglandular trichome of *C. ngwenyensis*. Scale bar = 15 μm . (e) Cobwebby hairs on dorsal surface of leaf of *C. lobata* ssp. *soutpansbergensis* [*Cron et al 373* (J)]. Scale bar = 100 μm . (f) SEM, detail of trichome on ventral surface of leaf of *C. lobata* ssp. *soutpansbergensis* [*Cron et al 373* (J)]: 6-celled base with long multi-celled apical wisp. Scale bar = 10 μm .

Results

Interpretation of phenograms and scattergrams

Cluster analysis of the data set including characters denoting presence and degree of pubescence on stems and leaves) results in a phenogram (Figure 10) in which *Cineraria ngwenyensis* and the Layton/Laingsburg specimens (LA) separate from the rest of *C. lobata* at a distance coefficient of 1.59 and then from each other at 1.55. Within the rest of *C. lobata*, two main groups emerge: the specimens with a dense and persistent tomentum and those glabrous or sparsely hairy or cobwebby and glabrescent. Within the larger cluster of glabrous or less hairy specimens, the specimens from the Eastern Cape form a group (with the exception of EC5 which does not have broad-winged ray cypselae), and those from the Western Cape (WC) and Worcester region (WO) cluster together. The robust form (WCR) also forms a distinct cluster within this larger group. The form with many compact capitula (PY) forms a distinct cluster amongst the group of densely hairy specimens, but a few specimens are interspersed amongst other forms of glabrous/less pubescent specimens. The northern specimens (SP and SPCW) are grouped together, but the Middleburg specimens (MB) are linked to the small-leaved, jointed form from the Uniondale region (UN). The correlation coefficient (r) is 0.75, which is a fair, but not good fit of the data to the phenogram.

In the 3D plot resulting from the Principal Coordinates Analysis of the same data set (Figure 11), specimens of *Cineraria ngwenyensis* separate out very clearly, and specimens of *C. lobata* from the Laingsburg/Layton region (LA) also form a distinct but more diffuse cluster at the extreme right of the 3D space. The various forms of *C. lobata* are generally more closely associated with others of the same form. The Eastern Cape group forms a fairly distinct cluster in the extreme bottom left of the 3D space, while the soutpansberg group is diffusely grouped toward the positive end of the third axis. Specimens with many smaller capitula on shorter peduncles are distributed towards the left of the first principal coordinate, those with fewer and larger capitula on longer peduncles towards the right. Character 28 (number of capitula) and those reflecting size of capitula such as number and length of involucre bracts, ray florets and disc florets most strongly influence distribution along this first principal coordinate (Table 3). Also of importance along this axis are trichomes 2 and 3 and apical lobe width (Table 3). Presence and degree of pubescence of stems, leaves and petiole (characters 2, 15, 16 and 27) strongly influence the distribution of specimens along the second principal coordinate. Specimens with a dense, persistent tomentum (as well as hairy peduncles and involucre bracts) are therefore distributed towards the negative end of this axis. The presence of cobwebby axils and lateral pinnae on the leaves and the shape of the base of the upper leaves influence distribution towards the positive end of the axis (Table 3). Along the third principal coordinate, the extensions of ray and disc cypselae, shape of upper leaf apices, ratios of leaf length to width and lamina length to petiole length, peduncle length and shape of auricles are influential (Table 3). Only 43.3% of the variation in the data set is represented by the first three principal coordinates/axes.

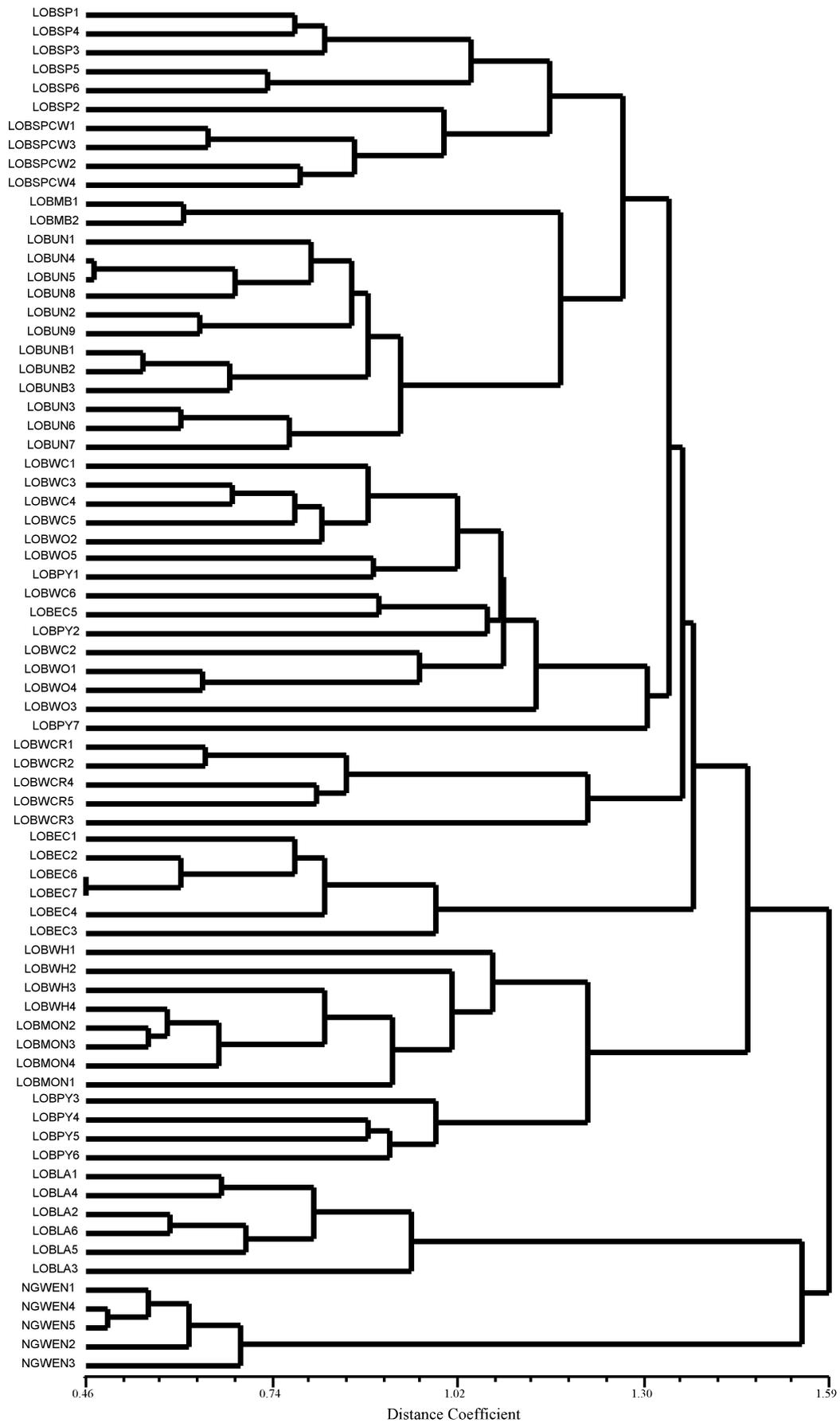


Figure 10. Phenogram resulting from UPGMA cluster analysis of average taxonomic distance of specimens of *C. lobata* and *C. ngwenyensis* based on 43 characters (including stem and leaf pubescence characters; $r = 0.75$). (Abbreviations as in Appendix 1.)

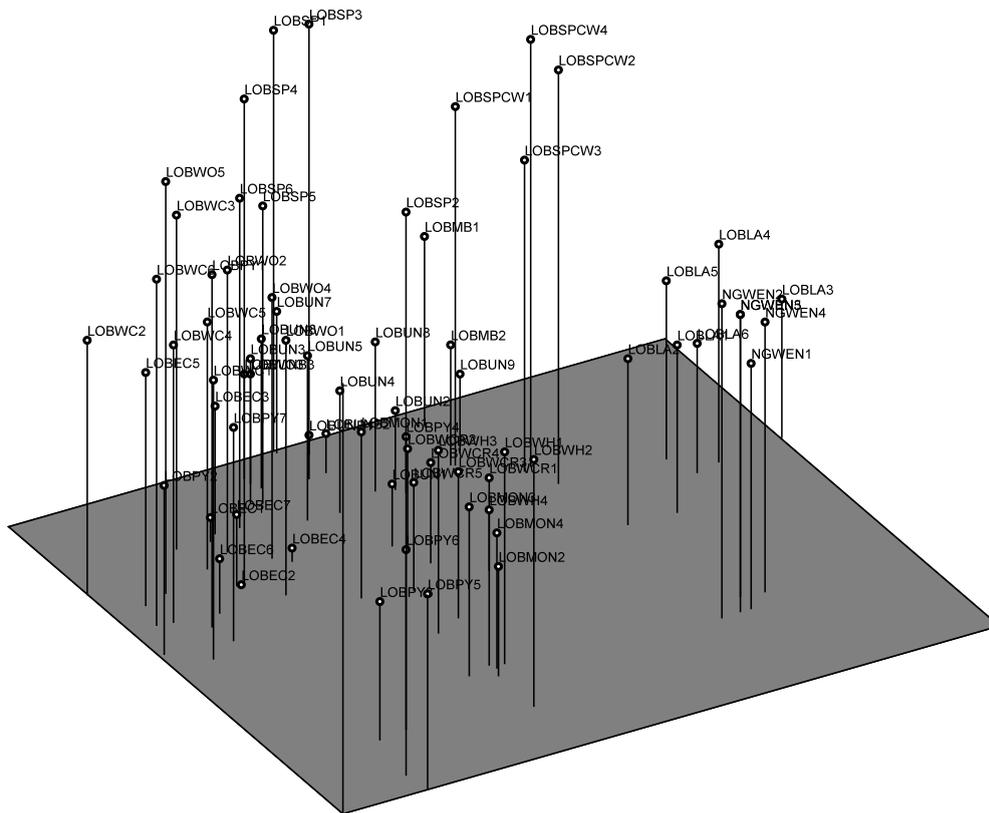


Figure 11. 3D plot of first three principal coordinates in a PCO analysis of *Cineraria lobata* and *C. ngwenyensis* based on 43 characters (including stem and leaf pubescence characters).

Excluding the characters denoting presence and degree of pubescence results in a phenogram (Figure 12; $r = 0.72$) in which the specimens of *Cineraria lobata* from the Layton/Laingsburg region (LA) and *C. ngwenyensis* (NGWEN) again separate out from the rest of *C. lobata*, followed by the specimens from the Soutpansberg region (SP and SPCW) and the Middleburg region (MB), and then the specimens from the Eastern Cape (EC) with broad-winged ray cypselae. The remaining cluster includes all the specimens from the Western Cape with the majority of specimens of the recognisable forms clustering together (exceptions being EC5 and PY1). (PY1 differs from the other compactly many-headed specimens in that it is entirely glabrous.)

In the 3D plot (Figure 13) resulting from the PCO analysis of the data excluding presence and degree of pubescence, size and number of capitula are again the main determinants for the distribution of the specimens along the first PC axis, with specimens possessing many, small capitula and trichome 2 distributed towards the left, and those with larger, fewer capitula and trichome 3 towards the right. Shape of the upper and lower leaf bases and apical lobe length to width ratio most strongly influence distribution along the second axis, while specimens with broad wings on their ray cypselae (i.e. mainly from the Eastern Cape) are separated out towards the base of the third axis (Table 3). This third PC also further separates specimens of *Cineraria ngwenyensis* and those of *C. lobata* from the Layton/Laingsburg region (LA). The specimens from the Soutpansberg loosely occupy the top right area of the 3D space, while the MB specimens are most closely associated with the robust form of *C. lobata* from the Western Cape.

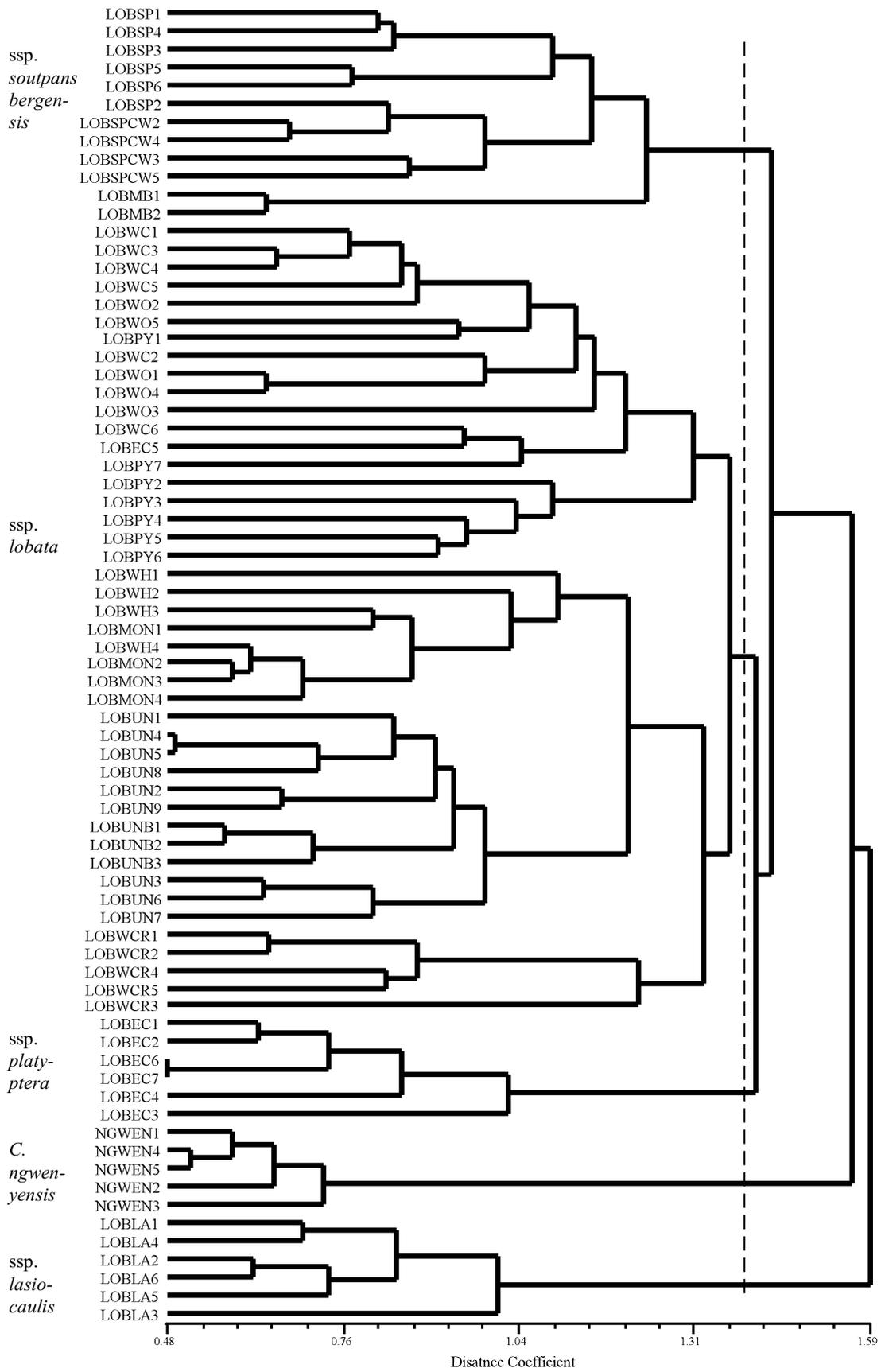


Figure 12. Phenogram resulting from UPGMA cluster analysis of average taxonomic distance of specimens of *C. lobata* and *C. ngwenyensis* based on 39 characters (excluding stem and leaf pubescence characters; $r = 0.72$). (Dotted line = phenon line; abbreviations as in Appendix 1.)

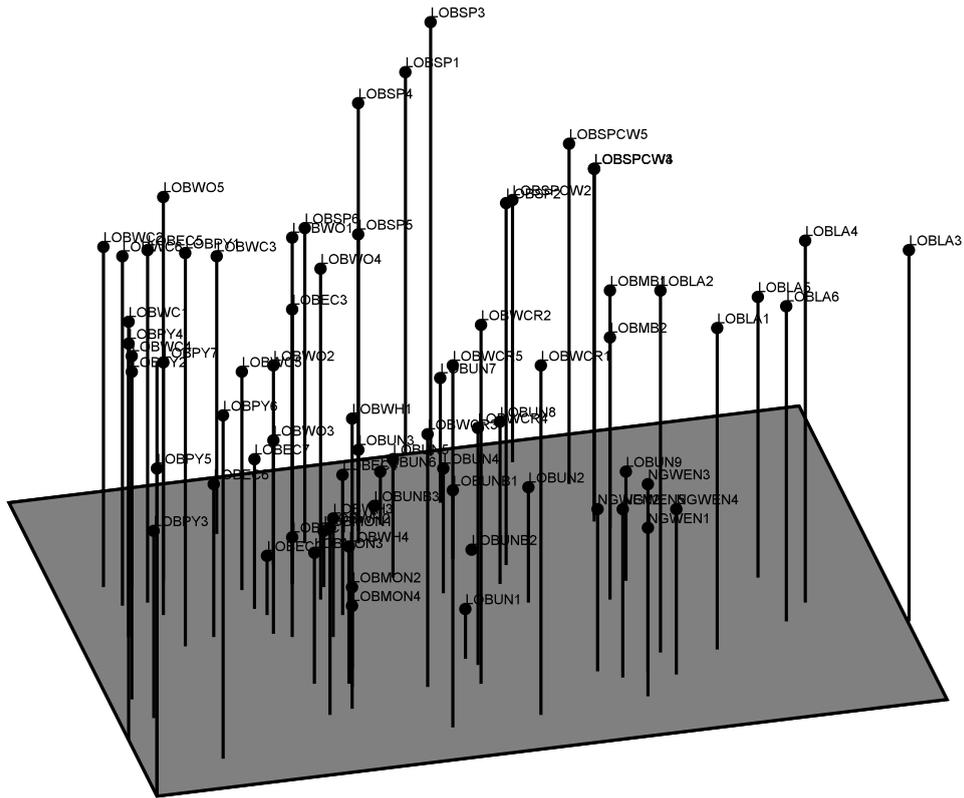


Figure 13. 3D plot of first three Principal Coordinates in a PCO analysis of *Cineraria lobata* and *C. ngwenyensis* based on 39 characters (excluding stem and leaf pubescence characters).

Table 3. Eigen vectors influencing distribution of specimens in 2D and 3D space along the 1st, 2nd and 3rd Principal Coordinates (PC1, PC 2, PC3) for analyses (a) including characters denoting presence and degree of pubescence on stems and leaves and (b) excluding them. Percentage variation represented by each axis shown.

Character	(a) Analysis including pubescence characters			(b) Analysis excluding indumentum characters		
	PC 1 (18.5 %)	PC 2 (15.8 %)	PC 3 (9.0 %)	PC 1 (19.8%)	PC 2 (11.7%)	PC 3 (9.8%)
1. Stem diameter	0.208	0.216	0.271	0.202	0.030	0.420
2. Stem pubescence	-0.260	-0.710	0.167	N/A	N/A	N/A
3. Cobwebby axils	0.134	0.696	-0.199	0.115	0.471	-0.171
4. Upper leaf shape	-0.075	-0.256	-0.339	-0.072	-0.431	-0.218
5. Lower leaf shape	-0.038	-0.206	-0.385	-0.036	-0.370	-0.342
6. Upper pinnae	-0.343	0.552	0.053	-0.356	0.449	-0.022
7. Lower pinnae	-0.250	0.494	0.058	-0.257	0.489	-0.079
8. Leaf length	0.560	-0.081	0.351	0.565	-0.246	0.544
10. Leaf length: width	0.292	0.382	-0.568	0.293	0.547	0.310

11. Apical lobe width	0.601	-0.241	0.210	0.608	-0.466	0.484
13. Apical lobe length: leaf length	-0.285	0.144	0.355	-0.282	0.338	0.153
14. Apical lobe length: lobe width	-0.261	0.463	0.442	-0.256	0.694	0.110
15. Leaf pubescence d/s	-0.104	-0.802	0.188	N/A	N/A	N/A
16. Leaf pubescence v/s	0.085	-0.807	0.035	N/A	N/A	N/A
17. Trichome 1	0.001	-0.331	0.157	-0.001	-0.304	0.118
18. Trichome 2	0.665	-0.306	-0.225	0.659	-0.340	-0.160
19. Trichome 3	-0.430	0.082	0.330	-0.422	0.118	0.375
20. Trichome 4	0.390	0.225	-0.386	0.374	0.047	-0.379
21. Upper leaf apex	0.003	-0.148	-0.612	-0.013	-0.335	-0.601
22. Upper leaf base	0.298	0.526	-0.008	0.287	0.618	-0.321
23. Lower leaf apex	0.478	-0.118	-0.498	0.467	-0.377	-0.378
24. Lower leaf base	0.191	0.621	-0.004	0.179	0.696	-0.271
26. Leaf length: petiole length	0.609	-0.036	0.552	0.619	0.060	0.480
27. Petiole pubescence	0.160	-0.828	0.009	N/A	N/A	N/A
28. Auricles (presence & shape)	-0.155	0.060	0.467	-0.133	0.133	0.341
29. Number of capitula	0.828	0.102	0.302	0.827	-0.032	0.406
30. Peduncle length	-0.495	-0.078	-0.453	-0.502	-0.221	-0.419
31. Peduncle indumentum	0.087	-0.715	0.091	0.105	-0.429	-0.093
32. Peduncle bract length	-0.269	-0.228	-0.082	-0.272	-0.471	0.139
33. Involucral bract number	-0.553	-0.118	-0.114	-0.558	-0.268	0.005
34. Involucral bract length	-0.711	0.132	-0.167	-0.714	0.028	-0.162
35. Invol. bract indumentum	0.416	-0.545	-0.103	0.429	-0.390	-0.181
36. Number of rays	-0.657	-0.155	0.028	-0.659	-0.259	0.121
37. Ray length (total)	-0.514	0.240	-0.054	-0.524	0.009	0.063
38. Ray limb length	-0.450	0.216	-0.128	-0.463	-0.050	0.027
40. Ray limb length:width	-0.295	0.026	0.130	-0.298	-0.020	0.117
41. Number of disc florets	-0.627	0.006	-0.112	-0.635	-0.195	0.035
42. Length of disc corolla	-0.420	0.145	0.214	-0.422	-0.004	0.314
43. Cypsela shape	-0.429	-0.067	0.004	-0.424	-0.230	0.197
44. Ray cypsela indumentum	0.365	0.353	0.096	0.361	0.191	0.216
45. Disc cypsela indumentum	0.371	0.407	-0.118	0.363	0.206	-0.004
46. Ray cypsela extension	0.422	0.386	-0.658	0.402	0.179	-0.717
47. Disc cypsela extension	0.456	0.302	-0.428	0.443	0.134	-0.455

In the phenogram (Figure 14) resulting from the initial cluster analysis based on the data set including the “standard taxon” *Cineraria longipes* (but excluding presence and degree of pubescence), specimens of *C. longipes* form a distinct cluster as do those of *C. ngwenyensis*. These two species separate out from the *C. lobata* cluster at a distance coefficient of 1.64, and then from each other. These species both have glabrous cypselae, as opposed to the ciliate and variously hairy cypselae of *C. lobata*. The pattern of separation and clustering within the *C. lobata* group is essentially the same as in Figure 12, with the recognisable groups all forming distinct clusters, except for EC05, PY01 and PY07, which cluster with the Worcester specimens. Within the large cluster of *C. lobata*, The Layton/Laingsburg group (LA) separate first from the rest, followed by the Eastern Cape specimens (EC, with broad-winged ray cypselae).

PCO of the data set including *Cineraria longipes* results in a scattergram (not shown here) with *C. longipes* and the Ngwenya specimens forming distinct clusters to the right of the first axis, with *C. longipes* most detached from the rest. The various forms of *C. lobata* cluster together with the LA and Eastern Cape groups forming more distinct clusters in the 3D space than in the 2D space (not shown here).

The phenogram (not presented here) resulting from UPGMA analysis of the qualitative data only (with leaf and stem indumentum characters as multistate unordered) has more or less distinct clusters of most of the *C. lobata* forms, with the Ngwenya specimens and the hairy forms of *Cineraria lobata* (WH, MON and PY3–6) separating out first at a level of similarity of 0.46. The correlation coefficient (r) is relatively high at 0.81, however *C. longipes* does not separate out from *C. lobata*, but is nested within the lobata group adjacent to the specimens from the Soutpansberg (SP) and Uniondale (UN) regions.

Placing a phenon line at a distance coefficient of 1.40 on the phenogram excluding the pubescence characters (Figure 12) creates five distinct clusters of specimens: from the Karoo (LA), *Cineraria ngwenyensis* (NGWEN), the Eastern Cape form (EC), the various forms from the Western and southern Cape (WC, WO, WCR, PY, WH, MON) and the northern specimens from the Soutpansberg region (SP/SPCW). This supports recognition of each of these as a distinct taxon, although the level of recognition is open to debate/discussion (which follows) and should also be informed by the scattergrams and by knowledge of the taxa and their geographical distribution.

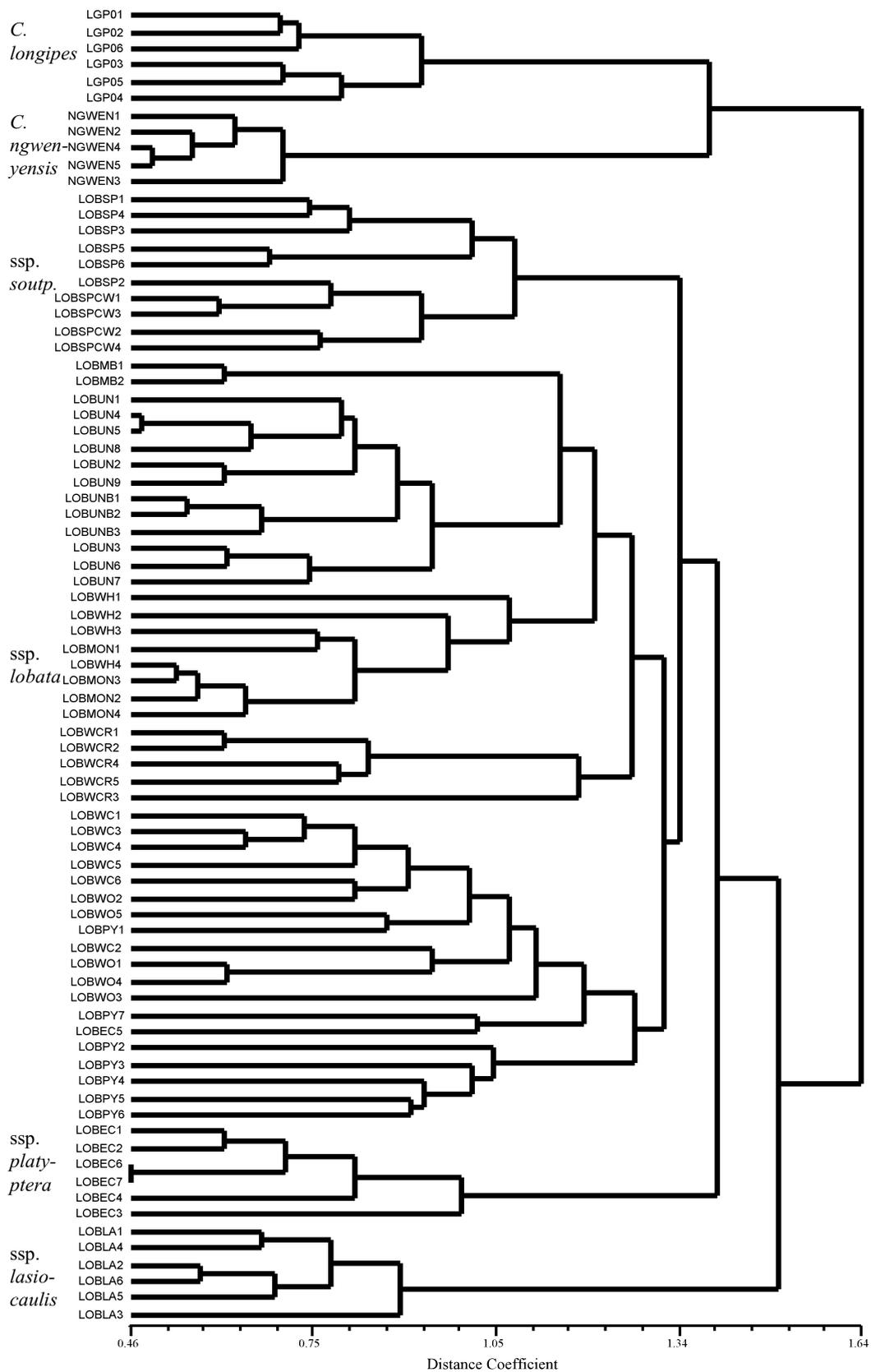


Figure 14. Phenogram resulting from UPGMA cluster analysis of average taxonomic distance between specimens of *Cineraria lobata*, *C. ngwenyensis* and *C. longipes* based on 39 characters (excluding stem and leaf indumentum characters) ($r = 0.73$). (Abbreviations as in Appendix 1.)

Discussion

Recognition of infraspecific variation

Cineraria lobata occupies a wide variety of ecological niches in the Western and Eastern Cape, from mountains to rocks near sea level to arid Karoo. Disjunct populations also occur in the northern mountain ranges of South Africa with related taxa apparently in between (e.g. Swaziland). The northern and southern populations exhibit different flowering times (Appendix 1), linked to their different rainfall regimes. These factors all promote genetic isolation and speciation and recognition of the variation resulting from the geographic isolation and ecological specialization is warranted. Numerous and diverse studies have shown that infraspecific variation is usually continuous rather than discrete, and usually involves many attributes, morphological, physiological and biochemical (Snaydon 1984). Only morphological variation has been studied in this investigation, but cognisance has been taken of the ecological and geographical factors involved.

The application of infraspecific rank in taxonomy is valuable in terms of recognising genetic variation and has considerable significance for conservation practices. A name attracts attention and facilitates reference to a plant (Stace, 1976), whereas variation which is not named tends not to be recognised (Snaydon, 1984). In addition, the incorporation of subspecific categories in modern Floras promotes the gathering of more information on them, and thereby aids conservation decision-makers by providing information on genetic diversity within a species (Stace, 1976). The recognition of subspecies and/or varieties within *C. lobata* will thus be a valuable contribution to the taxonomy and conservation of this variable species. The rank of subspecies is commonly used when there is geographical or ecological distinction and is usually defined as groups of individuals within a species that have some morphological distinctness as well as distributional or ecological integrity (Hamilton & Reichard, 1992), while the rank of variety is used when there is more overlap in one or more of these aspects.

Ranking of groups within Cineraria lobata

The geographically disjunct and morphologically distinct groups (the Soutpansberg, Karoo and the Western Cape clusters) are best recognised at the subspecies level in *Cineraria lobata*. The Eastern Cape population (with a broad wing on the ray cypsela and auricles that often run up the petiole) is not as geographically disjunct, as there is some overlap with the Uniondale populations in the Humansdorp region. However, it is at the edge of the range of the southerly forms and is morphologically quite distinct with its broad-winged ray cypselae, and may therefore also be recognised as a subspecies.

The populations of *Cineraria lobata* in the Western Cape are recognised as a single subspecies (ssp. *lobata*), yet exhibit a fair amount of variation within the subspecies. Much of the variation is environmentally induced (e.g. robustness and leaf size) and there are also distinct clines from west to east, such as decreasing number of capitula and increasing width of cypselae

extensions. The smallest capitula occur in plants from the Western Cape mountains around Tulbagh, Ceres and Piquetberg, while in the southern and Eastern Cape the capitula are somewhat larger. Correlated with this trend of increasing size of the capitula is a tendency for the cypsela wing to be more pronounced. The cypselae of the small headed Western Cape forms are margined, whereas most other forms have a distinct wing, paler than the rest of the cypsela. In the Eastern Cape most plants have broad-winged ray cypselae, although a few, mainly in the Humansdorp region, are only distinctly winged. This may represent an area of transition. This trend is also evident in the southern Cape around Uniondale where the majority of plants have ray cypselae that are narrow-winged, but a few have a broader winged ray cypselae. The variation within this Western Cape region is therefore best recognised informally (outlined below).

The populations growing in the very dry regions of the Little and Great Karoo may well be a distinct species, morphologically distinguishable from *Cineraria lobata* by their larger capitula, very elongate cypselae with characteristic indumentum (Figure 5e), tufted growth form and floccose stems (Figure 3b). (The manuscript name *C. flocculenta* Taylor was found on one of the specimens, but has no validity.) The recognition of this group as a distinct species is supported to some extent by the multivariate and cluster analyses performed here. However we propose to be conservative at this stage and describe it as a subspecies of *C. lobata* (ssp. *lasiocaulis*). Further work using molecular data may indicate a greater distinction justifying species level recognition for this group.

Main distinguishing characteristics of *Cineraria lobata* ssp. *soutpansbergensis* from the Soutpansberg region are their deltoid to deltoid-reniform upper leaves with lanceolate auricles (Figures 4c, 6a, 6b). Also highly characteristic are the thick white cobwebby hairs in the axils of the leaves (Figures 4c, 6a). The cobwebby form occurring at high altitude on the Soutpansberg and Blouberg may be informally recognised. The Middleburg specimens (MB) group with the Soutpansberg group or the Uniondale group or with the robust form from the Western Cape, and their affinity remains uncertain as they also resemble *C. geraniifolia* in growth form, habit and size of capitula. The Middleburg (MB) specimens are therefore tentatively affiliated to *C. lobata* at this stage, as further investigation into their true affinity is required.

Cineraria ngwenyensis

The results of the cluster analysis and PCO support the recognition of *C. ngwenyensis* from the Ngwenya Hills, Swaziland as a species distinct from *Cineraria lobata*. Cypsela indumentum has traditionally been a useful character in distinguishing species of *Cineraria* (De Candolle, 1838; Harvey, 1865; Hilliard, 1977; Cron, 1991) and a major difference between *C. lobata* and *C. ngwenyensis* is the possession of glabrous cypselae by the latter species.

The extreme hairiness of *Cineraria ngwenyensis* is matched by a few populations of *C. lobata* in the Worcester and Montagu regions of the Western Cape, but the trichome differs from that found in these hairy forms of *C. lobata*. The trichome present in *C. ngwenyensis* is a gradually tapering eglandular trichome consisting of about 10 – 12 cells (Figure 8: Trichome 1a, Figure 9d), without the long apical wisp seen in most of the hairy forms of *C. lobata* (Figure 8, Trichome 2, Figure 9b). Eglandular trichomes (Figure 8: Trichome 1b) do occur in *Compton 11858* (NBG) (WH2) from near Swellendam and also in some WC and WCR specimens. On close examination, however, it is evident that these type 1b trichomes are longer with more elongate cells than the type 1a trichomes in *C. ngwenyensis*.

The growth form of *Cineraria ngwenyensis*, with most of the branching occurring from the base of the stem, also distinguishes it from some of the forms of *Cineraria lobata*. Their capitula are generally larger than in *C. lobata*, except in *C. lobata* ssp. *lasiocaulis* from the Karoo, which may itself be a distinct species. Their auricles are lanceolate (to ovate) rather than auriform (Figure 6d), which is similar to the northern populations of *C. lobata* (ssp. *soutpansbergensis*), but very different from the Western and Eastern Cape populations. Its involucre bracts are glabrous compared to hairy bracts in the hairy form of *C. lobata* ssp. *lobata*, which also usually has only 5 rays in contrast to the 8 or 9 rays present in *C. ngwenyensis*. Therefore, based on these differences and the separation of the clusters in the multivariate analyses performed, we have described a new species, *C. ngwenyensis*, endemic to the rocky crevices in the high altitude grasslands of the Ngwenya Hills of Swaziland (Chapter 6).

Variation in *Cineraria lobata*

Environmental influence on size and habit of *Cineraria* has been demonstrated for a number of species, including *C. deltoidea*, *C. aspera*, *C. erodioides* (Chapter 6). Environmental factors playing a role in influencing variation in *C. lobata* include altitude, light intensity, and proximity to the sea. For example, the Uniondale Division is a very arid region due to the rain shadow created by the Outeniqua and Langkloof mountains and this is reflected in the habit of these populations. The effect of light intensity (and associated heat) on *C. lobata* is clearly seen in *Cron & Goodman 569* (J) from near Joubertina (in the Uniondale region), where most plants have the very small leaves and much branched stems typical of this area (Figure 3c), yet a specimen growing in the shade shows much larger leaves and more growth before branching (Figure 3d). Plants in their first year of growth (also growing in the shade) show a similar size and shape of leaf, but are unbranched.

While some of the variation in *Cineraria lobata* is environmentally induced (e.g. size of leaves, pattern of branching, distribution of indumentum), much of it is genetically determined. This is evidenced by the clear clusters of specimens from the geographic regions. Characters such as size and number of capitula, types of trichomes, indumentum of the cypselae and

breadth of extensions of the cypsela are certainly some of the genetically determined features. It is important to distinguish genetically determined variation and environmentally induced, phenotypic variation in the study of infraspecific variation (Snaydon, 1973).

Centres of endemism

It is not surprising that recognisable geographic forms have arisen across the range of *Cineraria lobata* as most of the western and southern forms fall within the Cape Floristic Region (CFR) (Van Wyk & Smith, 2001). This region is dominated by the Cape Fold Belt mountains, characterised by high levels of plant diversity and endemism, with at least 70% of the flora endemic to the region (Van Wyk & Smith, 2001). Geologically the Cape Floristic Region is dominated by rocks of the Cape Supergroup: Table Mountain sandstones forming the main constituent of the Cape Fold Belt mountains; the Witteberg Group (siltstones and sandstones capped by conspicuous white quartzite) mainly associated with some of the inland mountains; and the Bokkeveld shales in the intermontane valleys and lower slopes of the mountains (Visser, 1989). *C. lobata* occurs mainly on the nutrient-poor sandstones and outcrops of quartzite in the region, similar to most species in the genus.

In addition, many of the groups recognised in *Cineraria lobata* correspond with the centres of endemism recognised by Van Wyk & Smith (2001): the Worcester-Robertson Karoo Centre (many-headed form from Worcester [WO]), the Little Karoo Centre of Endemism (the small-leaved form from near Uniondale [UN, UNB]), and the Albany Centre of endemism in the Eastern Cape (subsp. *platyptera* [EC]). Although much of the endemism in these centres is associated with the succulent karoo biome, some level of isolation and specialization is also apparent in *C. lobata*, which occurs at lower altitudes on the mountains, which average from 1000 to 1500 m in elevation.

The trend towards a broader wing in the ray cypselae in some of the forms from the Uniondale division and the Little Karoo is fixed in *Cineraria lobata* ssp. *platyptera* from the Albany area further east in the Eastern Cape. The Little Karoo Centre of Endemism, which extends from Montagu in the west to Uniondale in the east, bounded by the Langeberg and Outeniqua Mountains in the south and by the Waboomsberge, Witberg and Little & Great Swartberg Mountains to the north, shows strong links with the Albany Centre due to east-west trending mountain ranges and intermontane valleys that provide migration links between the two regions (Van Wyk & Smith, 2001). In addition there is a trend towards increasing summer rainfall in the east.

Cineraria lobata ssp. *soutpansbergensis* (SP; SPCW) is also associated with a centre of endemism, the Soutpansberg Centre of Endemism, which includes the Soutpansberg Mountain, the Blouberg Massif to the west and Lake Fundudzi to the north-east (Van Wyk & Smith, 2001); all localities for this northern subspecies of *Cineraria lobata*. The southern

slopes of the Soutpansberg Mountain are much wetter than the northern slopes, contributing to some of the variation in growth form seen in *C. lobata* subsp. *soutpansbergensis*. The wetter parts of the Soutpansberg Centre form part of the Afromontane Region with floristic links to the Wolkberg, the north-eastern Drakensberg and the Chimanimani-Nyanga Centre. Nearly all the endemics of the Soutpansberg Centre are confined to the grassland, fynbos (e.g. *C. cyanomontana*) or bushveld. *C. lobata* occurs in the fynbos at high altitude on Letjuma (highest peak in the Soutpansberg) and on the Blouberg, in open woodland on the lower south-facing slopes and occasionally as a pioneer on disturbed soil on east-facing slopes of the mountain passes.

The Ngwenya Hills on which *Cineraria ngwenyensis* occurs in Swaziland fall into the Barberton Centre of Endemism, characterised by a complex and unique succession of deformed volcanic and sedimentary strata (the Barberton Supergroup). Most of the endemics are grassland endemics, though not many in the Asteraceae (Van Wyk & Smith, 2001). The Ngwenya mountain massif extends for about 10 km along the western border of the Malolotja Nature Reserve on the western border of Swaziland. Ironstones and quartzites are common, giving rise to the rugged relief of the region. *Cineraria ngwenyensis* occurs amongst the quartzite outcrops at altitudes of 1500 to 1700 m in the montane grassland of the high plateau, which also has clear links with the Afromontane Region, but also with the Cape fynbos as six species of *Protea* and a number of heaths are reported to occur in the reserve (SNTC).

Taxonomic conclusions, treatment and key

Three geographically and/or ecologically isolated, morphologically distinct subspecies of *Cineraria lobata* are recognised: *C. lobata* ssp. *lobata* (from the Western and Eastern Cape), *C. lobata* ssp. *lasiocaulis* from the Karoo and *C. lobata* ssp. *soutpansbergensis* from the Soutpansberg region. A fourth subspecies *C. lobata* ssp. *platyptera* from the Eastern Cape with the distinctive broad-winged, ciliate ray cypsela is also recognised and five forms within the Western Cape are informally recognised. *Cineraria ngwenyensis* and the four subspecies of *C. lobata* are described formally in the monograph of *Cineraria* (Chapter 6). A key to the subspecies and a brief outline of their diagnostic characters and those of the informal forms is provided here.

Key to the subspecies in *Cineraria lobata*

- 1a. Auricles lanceolate, small, upper leaves deltoid to deltoid-reniform 4. *C. lobata* ssp. *soutpansbergensis*
- 1b. Auricles auriform, small to large, upper leaves deltoid-reniform or reniform 2
- 2a. Mature cypsela obovate (twice as long as broad), dark or pale brown, margined or distinctly to broadly winged, with densely or sparsely hairy faces, capitula with 3–5

- (rarely 6) rays and 8 (–13) involucre bracts, leaves and stem glabrous or hairy (not cobwebby) 3
- 2b. Mature cypselae narrowly obovate (three times as long as broad), black or dark brown with white hairs densely covering outer faces, glabrous or sparsely hairy inner faces, capitula with 8 or more rays, 12 or 13 involucre bracts, base of leaves and petioles cobwebby, glabrescent, thick woolly tufts in nodes extending to cover stem
 **3. *C. lobata* ssp. *lasiocaulis***
- 3a. Cypselae margined or distinctly winged, auricles small or conspicuous, not running up petiole **1. *C. lobata* ssp. *lobata***
- 3b. Ray cypselae broadly winged, fringed with hairs, disc cypselae distinctly winged, auricles usually conspicuous, often running up petiole
 **2. *C. lobata* ssp. *platyptera***

1. *C. lobata* L'Hér. ssp. *lobata*

Stems glabrous, sparsely hairy, occasionally densely hairy (not cobwebby), usually slender, occasionally more robust, 2 – 4.5 mm in diameter, rigid, lined. *Leaves* reniform, distinctly (to rarely shallowly) lobed, infrequently with lateral pinnae, 8 – 48 × 11 – 67 mm, glabrous above (rarely hairy), glabrous or sparsely or rarely densely hairy below, especially on veins and at base of lamina, trichomes multi-celled with tapering base and apical wisp; petiole 6 – 72 mm long, glabrous or sparsely hairy, thickly cobwebby axils and buds, auricles vary from tiny (or absent) to large, auriform. *Capitula* small to medium, few (4 – 12) to many (ca. 100) on fairly short peduncles (2 – 28 mm long). *Involucre bracts* (5 –) 8 (rarely 10 – 13), 3 – 4 (– 5) mm long, glabrous (rarely hairy), 3 – 4 mm long, glabrous (rarely hairy). *Rays* (3 –) 5 (– 8), 5 – 10.5 mm long. *Disc florets* 7 – 26, corolla 3 – 5 mm long. *Cypselae* obovate, ciliate and hairy or sparsely hairy on faces, brown, margined or narrow winged, 2.0 – 3.2 mm long when mature.

PHENOLOGY. Flowering August to January in the winter rainfall areas, May to July in the Eastern Cape region.

DISTRIBUTION. Western Cape, extending into the Eastern Cape in the Humansdorp region.

(i) Small-headed form from the Western Cape. Stems glabrous, slender, rigid, lined. Leaves distinctly lobed. **Few to many small capitula**, fairly laxly arranged on glabrous peduncles. Involucre bracts 5 – 8, rays 3 – 5, disc florets 8 – 18. Cypselae margined, ciliate and hairy.

(ii) Hairy form mainly from the Worcester and Montagu regions in the Western Cape, also from the Cederberg. **Stems and leaves very hairy**, otherwise similar to above form. Trichomes comprise a tapering multi-celled base with long apical wisp. Few capitula, peduncles hairy. Cypselae margined or distinctly winged.

(iii) **Robust form** from Saldanha Bay to the Cape Peninsula in the Western Cape. A more **robust growth form**, stems 4–5 mm in diameter, glabrous. Leaves reniform, auricles usually conspicuous. Capitula many, larger than in other forms. Involucral bracts 8–13, rays 5–8, disc florets 26–36. Cypselae margined.

(iv) **Small-leaved, jointed stem form** from the vicinity of Uniondale and Humansdorp in the Western Cape, extending slightly into the Eastern Cape. Characteristically **small shrublets with branching woody stems, short internodes** creating a jointed appearance. **Leaves small**, some with lateral pinnae, glabrous. Capitula few, in a lax panicle. Involucral bracts 8 (–10), rays 5 (rarely 8). **Cypselae distinctly winged** (ray cypselae occasionally fairly broad-winged).

(v) **Compactly many-headed form** from the southern region of the Western Cape. **Spreading suffrutex**. Stems robust. Leaves reniform to deltoid-reniform or rounded-reniform, mostly shallowly lobed, glabrous to sparsely hairy or hairy above, sparsely to densely hairy below, trichomes multi-celled, eglandular, usually with an apical wisp; petioles relatively long. **Capitula small, very many 38–90 (–120), compactly arranged on short peduncles**, 2–8 (–12) mm long. Involucral bracts 8, rays 3–6, disc florets 12–14.

2. *Cineraria lobata* L'Hér. subsp. *platyptera* Cron. (Cron 2005: Chapter 6). Type: South Africa, Eastern Cape, Kommadagga, [1500'], Aug. 1963, *Bayliss BS1606* (holotype PRE!; isotypes GRA!, K!, MO!, NBG!, Z!).

Stems glabrous, slender, branching mainly from the base. *Leaves* reniform, distinctly or shallowly lobed, rarely with 1 or 2 pairs of lateral pinnae; auricles conspicuous and may run up petiole. *Capitula* small to medium, involucral bracts 8–13, 3–4 mm long, glabrous; rays commonly 5 (rarely 4 or 6), disc florets 26–28. *Cypselae* ciliate, hairy to sparsely hairy on outer faces, sparsely hairy on inner faces, **ray cypselae broad-winged, disc cypselae narrowly (to broadly) winged**.

PHENOLOGY. Flowering mainly August to January, also in May, June and July.

DISTRIBUTION. Eastern Cape: in the Districts of Albany, Uitenhage and Port Elizabeth.

3. *Cineraria lobata* L'Hér. ssp. *lasiocaulis* Cron (Cron 2005: Chapter 6). Type: South Africa, Western Cape, Laingsburg Division, Whitehill Ridge, south side. Oct. 1929, *Compton 3601* (holotype BOL!; isotype K).

Tufted growth form. *Stems* cobwebby, glabrescent with woolly axils, short internodes. Capitula few (2–6 per stem branch), laxly arranged; peduncles 20–75 mm long. *Involucral bracts* 12 or 13. *Rays* 7, 8 or 9. *Cypselae* narrowly obovate, slightly margined, black (or dark brown), outer face densely covered with short white hairs, inner faces of ray cypselae almost

glabrous, inner faces of the disc floret cypselae less hairy than outer surface, inner median rib sometimes evident on mature cypselae.

PHENOLOGY. Flowering August to October.

DISTRIBUTION. South Africa: In the Laingsburg area of the Little Karoo (Western Cape) and in the vicinity of Layton in the Great Karoo (Northern Cape).

4. *Cineraria lobata* L'Hér. ssp. *soutpansbergensis* Cron (Cron 2005: Chapter 6). Type: South Africa, Limpopo Province, Soutpansberg, roadside on Farm Punchbowl, 1140 m, May 1994, Cron, Balkwill & Balkwill 282 (holotype J!; isotypes B!, K!, MO!, PRE!, S!).

Stems glabrous or cobwebby, glabrescent, slender (2 – 4 mm in diam. at base), woody and branching near the base. *Upper leaves* **deltoid to deltoid-reniform**, distinctly and sharply 5-lobed, sometimes with one or two lateral pinnae, lower leaves deltoid-reniform to reniform, thinly cobwebby to glabrous above and cobwebby to glabrous below, young leaves sometimes thickly cobwebby, fine trichomes, thick cobwebby axils and buds; auricles small, **lanceolate**, caducous. *Capitula* small to medium, few (4 – 8) to many (12 – 42) per stem, on short peduncles (4 – 32 mm long). *Involucral bracts* 8 – 12 (– 13), 3.5 – 5 mm long, glabrous; rays 5 – 8 (rarely 9), 6 – 11.5 mm long, limb 3.5 – 9 mm long; (18 –) 22 – 30 disc florets, corolla 4 – 5 mm long. *Cypselae* dark brown, margined, ciliate and hairy to sparsely hairy (rarely with glabrous faces), 2.2 – 3.0 mm long when mature.

PHENOLOGY. Flowering March to early July, but mainly in May, rarely in October (*Codd & Dyer 18049* from Lake Fundudzi). The cobwebby form also flowers in November and December near mountain summits.

DISTRIBUTION. Mainly in the Soutpansberg Centre of Endemism: Soutpansberg and Blouberg Mountains, near Lake Fundudzi, Limpopo Province. Also near Lobyana in the Drakensberg range between Strydom Tunnel and the Downs, and a collection from the Kransberg near Thabazimbi is a fair match.

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Appendix 1. Specimens of *Cineraria lobata*, *C. ngwenyensis* and *C. longipes* used in phenetic study, identifying codes, locality information and time of flowering.

Code	Specimen	Grid ref.	Locality	Altitude (m)	Flowering time
Western Cape group					
LOBWC1	<i>Watson & Panero 94-30</i> (NBG)	3218DC	Piquetberg, Versveld Pass		November
LOBWC2	<i>Compton 14993</i> (NBG)	3218DD	Piquetberg, De Hoek		September
LOBWC3	<i>Pillans 9130</i> (NBG)	3219AC	Clanwilliam Division, Hex River Valley		October
LOBWC4	<i>Van Zyl 3305</i> (BOL)	3318BA	Oshoekkop, north of Moorreesberg		September
LOBWC5	<i>Compton 12048</i> (NBG)	3319AC	Tulbagh, New Kloof		October
LOBWC6	<i>Pillans 9158</i> (BOL)	3218BD	Between Witelskloof and Lambertshoek		October
Worcester group					
LOBWO1	<i>Esterhuysen 15075</i> (BOL, GRA, PRE, NBG)	3319AD	Du Toit's Kloof, Waaihoek Mountains.	950	January
LOBWO2	<i>Compton 21201</i> (NBG)	3319CB	Karoo Botanic Garden		December
LOBWO3	<i>Bayer 226</i> (NBG)	3319CB	Karoo National Garden	415	August
LOBWO4	<i>Esterhuysen 8440</i> (BOL)	3319CB/	Hex River Mountains, Mount Brodie		December
LOBWO5	<i>Bachman 2223</i> (Z)	3318AB	Malmesbury Division, near Hopefield		October
Hairy group					
LOBWH1	<i>Esterhuysen 1808</i> (BOL)	3218AB	Cederberg, Wolfberg		December
LOBWH2	<i>Compton 11858</i> (NBG)	3420AA	Swellendam district, Storms Vlei Kloof		September
LOBWH3	<i>Esterhuysen 9946</i> (BOL)	3319AC	Hex River Mountains, Kleinberg		November
LOBWH4	<i>Esterhuysen 15889</i> (BOL, PRE)		Prospect Peak, Hex River Mountains	635	October
Montagu (hairy)					
LOBMON1	<i>Cron & Perrett 333</i> (B, J, LISC, MO)	3320CC	Montagu, Donkerkloof	500	February
LOBMON2	<i>Compton 18464</i> (NBG)	3320CC	Montagu, Donkerkloof	480	September
LOBMON3	<i>Levy's 8054</i> (BOL)	3320CC	Montagu, Donkerkloof	540	September
LOBMON4	<i>Cron & Perrett 331</i> (CM, J)	3320CC	Montagu, Badenkloof	470	February (end of

Robust group					
LOBWCR1	<i>Goldblatt 4107</i> (MO, PRE, WAG)	3217DD	Limestone hilltops above Saldanah		September
LOBWCR2	<i>Hugo 2927</i> (PRE, WAG)	3317BB	Saldanah (under geifolia in locs list)	150	October
LOBWCR3	<i>Boucher 4005</i> (PRE, WAG)	3318AC	Malmesbury District, Yzerfontein, Dokter se klip	10	October
LOBWCR4	<i>Cron & Hodgkiss 317</i> (J)	3418AD	Cape Point	50	January
LOBWCR5	<i>Drége s.n. sub PRE 12804</i>	3318CB	Malmesbury between Groenkloof & Saldanha		September
Layton/Laingsburg					
LOBLA1	<i>Shearing 57</i> (PRE)	3121DC	Fraserburg, Layton, Rooiwal Mill	1270	August
LOBLA2	<i>Shearing 1332</i> (PRE)	3221BB	Beaufort West District, Layton, Hoendervoet	914	September
LOBLA3	<i>Compton 14913</i> (NBG, PRE)	3320BA	Laingsburg District, Whitehill Ridge		September
LOBLA4	<i>Hall 172</i> (NBG)	3320BA	North-west of Matjiesfontein		October
LOBLA5	<i>Compton 3601</i> (K, BOL)	3320BA	Laingsburg District, Whitehill Ridge		October
LOBLA6	<i>Compton 9280</i> (BOL, K)	3320BB	Ngaap Kop, Laingsburg	1110	September
Compactly many-headed form					
LOBPY1	<i>Prior s.n.</i> (K)	3322CD	George, Kainan's Gat		October
LOBPY2	<i>Marsh 592</i> (K, PRE)	3422AB	Herolds Bay	9.5	September
LOBPY3	<i>Compton 7558</i> (NBG)	3422BB	Knysna district, Goukama		October
LOBPY4	<i>Fourcade 6521</i> (BOL)	3422BB	Goukamma Pass		November
LOBPY5	<i>Cron & Goodman 568</i> (E, J, K, MO)	3424AA	Eersterivier	10	December
LOBPY6	<i>Fourcade 955</i> (BOL, GRA)	3424AA	Witelsbos		October
LOBPY7	<i>Fourcade 4064</i> (BOL, K)	3422AA	George Division, near Groot Brak River		November

Uniondale: Narrow-winged (UN) and broad-winged UNB)					
LOBUN1	<i>Esterhuysen 6497</i> (PRE)	3322DB	Mannetjeberg	c.1750	November
LOBUN2	<i>Salter 6728</i> (K)	3323CA	3 miles south of Uniondale		July
LOBUN3	<i>Rourke 392</i> (NBG)	3323CB	Hoopsberg	1430	March
LOBUN4	<i>Compton 23880</i> (NBG)	3323DC	Louterwater		January
LOBUN5	<i>Compton 5215</i> (BOL)	3323DC	Louterwater	635	April
LOBUN6	<i>Esterhuysen 10675</i> (BOL)	3323DD	De Hoek, near Joubertina		November
LOBUN7	<i>Story 2446</i> (PRE)	3324DA	Willowmoore-Patentie Pass		April
LOBUN8	<i>de Lange s.n. sub PRE 9406/11</i>	3323DC	Nature's Valley, Formosa Peak		August
LOBUN9	<i>Fourcade 1302</i> (BOL, GRA)	3323CA	South of Avontuur	114–1270	May
LOBUNB1	<i>Compton 10516</i> (NBG)	3323DC	Uniondale Division, Helpmekaar	1270	January
LOBUNB2	<i>Esterhuysen 16860</i> (NBG, PRE)	3323DD	Tsitsikamma Mountains near Joubertina		March
LOBUNB3	<i>Fourcade 2677</i> (BOL)	3323DD	Rocky hill north of Joubertina	635	August
Eastern Cape (broad-winged ray cypselae)					
LOBEC1	<i>Olivier 1985</i> (GRA, WAG)	3325CD	Uitenhage, Springs Reserve		January
LOBEC2	<i>Bayliss BS 8878</i> (WAG)	3326BA	Albany, Pluto's Vale	380	October
LOBEC3	<i>Phillipson 1506</i> (GRA, K, MO, NBG)	3326BA	Fish River Valley, c.40 km north of	300	October
LOBEC4	<i>Bayliss BS 1606</i> (PRE, Z)		Kommadagga	476	August
LOBEC5	<i>Britten 763</i> (GRA, PRE)	3326BC	Bathurst district, Kowie East, near		September
LOBEC6	<i>Liebenberg 6248</i> (PRE)	3325BD	Alexandria, Addo National Park	320	July
LOBEC7	<i>Booi 43</i> (GRA, K, PRE)	3326AB	7.7 miles from Grahamstown on Cradock Road		May
Soutpansberg Region					
LOBSP1	<i>Fourie 2768</i> (K)	2229DC	Soutpansberg, Farm Surprise		
LOBSP2	<i>Cron, Balkwill & Balkwill 285</i> (J)	2229DD	Soutpansberg, Farm Zwarthoek	1300	May
LOBSP3	<i>Cron, Balkwill & Balkwill 282</i> (J)	2229DD	Soutpansberg, Farm Punchbowl	1140	May

LOBSP4	<i>Galpin s.n.</i> (BOL)	2229DD	Soutpansberg, Franzhoek Peak	1460–1555	July
LOBSP5	<i>Codd & Dyer 4505</i> (PRE)	2230CD	Lake Fundudzi	1080	October
LOBSP6	<i>van Graan & Hardy 550</i> (PRE)	2230CD	Lake Fundudzi		May
Soutpansberg Region (Cobwebby)					
LOBSPCW1	<i>Cron, Knox & Winter 363</i> (J)	2329AB	Lejuma, Soutpansberg	1425	December
LOBSPCW2	<i>Esterhuysen 21519</i> (BOL)	22328BB	Blouberg	1430	May
LOBSPCW3	<i>Cron, Knox & Winter 344</i> (J)	2328BB	Blouberg	1600	December
LOBSPCW4	<i>Moss 11365b</i> (J)	2527DD	*Pretoria district, Hartebeespoort Dam (dubious)	1050	November
Middleburg					
LOBMB1	<i>Codd 10103</i> (NBG)	2529CD	Farm Langkloof, 15 miles NW of Middleburg	1492	May
LOBMB2	<i>Codd & Dyer 2871</i> (PRE)	2529CD	Botshabelo Mission, 9 miles N of Middelburg	1525	April
C. ngwenyensis (Ngwenya Hills, Swaziland)					
NGWEN1	<i>Compton 28822</i> (NBG, PRE)	2631AA	Swaziland, Mbabane District, Bomvu Ridge	1746	April
NGWEN2	<i>Maguire 7626/80</i> (J)	2631AA	Swaziland, Ngwenya Hills, Castle Lion	1500	April
NGWEN3	<i>Maguire 7590</i> (J)	2631AA	Swaziland, Ngwenya Hills, Castle Peak	1500	April
NGWEN4	<i>Cron, Balkwill & Balkwill 308</i> (J, K, MO, PRE)	2631AA	Swaziland, Ngwenya Hills, west of Lion Cavern	1650	June
NGWEN5	<i>Cron, Balkwill & Balkwill 311</i> (J)	2631AA	Swaziland, Ngwenya Plateau	1746	June
C. longipes (Standard taxon)					
LGP01	<i>Cron & Brits 336</i> (J)	2627BD	Naturena, south of Johannesburg	1500	May
LGP02	<i>Cron & Balkwill 306</i> (J)	2628BD	Mondeor, south of Johannesburg	1600	June
LGP03	<i>Bryant D94</i> (PRE)	2628AA	Turfontein (Johannesburg)	1500	April
LGP04	<i>Mogg et al. 19562</i> (J)	2628CA	Brakfontein 13, 7 miles east of Meyerton	1600	May
LGP05	<i>Moss 17834</i> (J)	2628AC	Thorntree Kloof, south of Johannesburg		April
LGP06	<i>Cron, Pfab & Mills 485</i> (J)	2628CA	Suikerbosrand Nature Reserve	1830	May

* Locality information not very reliable.