

Systematic studies in the *Gloriosa superba* complex (Colchicaceae): a re-assessment of species boundaries

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Background and aims – *Gloriosa superba* L. is a highly variable species occurring in a wide range of ecological habitats in South Africa, tropical Africa and Asia. The morphological variation in *G. superba* was found to be complicated and therefore numerical methods were used to re-evaluate morphological variation and species delimitation in the *G. superba* complex.

Methods – This study was based on 79 herbarium specimens from B, BM, BR, C, COI, F, K, L, SRGH, U, UPS and WAG (abbreviations follow Holmgren et al. 1990). Cluster and ordination analyses were used to explore morphological variation within the study group. The morphometric data set based on both qualitative and quantitative characters was entered directly into a computerized matrix and a cluster analysis was computed using NTSYS package. The variability of individual characters was evaluated by box-plots using SPSS.

Key results & conclusions – The morphological study has revealed the existence of four phenetic species in the *G. superba* complex. Recognition of these species is based on habit, inflorescence characters and distribution patterns. It is here proposed that four species should be recognized in the *G. superba* complex: *G. baudii* (Terracc.) Chiov., *G. carsonii* Baker, *G. superba* L. and *G. simplex* L. *Gloriosa superba* is the most widespread taxon, occurring in South Africa, tropical Africa and Asia. *Gloriosa simplex*, *G. carsonii* and *G. baudii* are confined to the African continent, with *G. simplex* widespread in tropical Africa, *G. carsonii* common in south, central to east tropical Africa, and *G. baudii* having the most restricted range, confined to the arid regions of northern Kenya, Ethiopia and Somalia.

Key words – *Gloriosa superba* complex, species boundaries, systematic studies.

INTRODUCTION

Gloriosa superba L. (tribe Colchiceae, family Colchicaceae, Vinnersten & Manning 2007) was first described by Linnaeus in 1737, based on material from southwest India (Malabar) and the name was validated in 1753 (Linnaeus 1753). It is native to South Africa, tropical Africa and Asia. Many authors have discussed the delimitation of the species and many satellite species have been described, which were often rejected by other authors (electronic appendix 1). The whole set of species related to *Gloriosa superba* is here referred to as the *Gloriosa superba* complex.

The *G. superba* complex occupies a wide range of ecological habitats; it is common in forest-savanna boundaries, thickets, hedges, open forests, grasslands and bush lands. It occurs from sea level up to 2530 m a.s.l. (Neuwinger 1996). The major morphological variations in *G. superba* complex

are found in the plant habit, the perianth segment colour and the perianth segment shape. *Gloriosa superba* is found as short, stocky and self-supporting plants, and as tall slender scramblers, clinging to other plants by means of leaf tendrils. According to Baker (1898), *G. abyssinica* A.Rich., *G. carsonii* Baker and *G. minor* Rendle are non-climbing while *G. virescens* (synonym of *G. simplex* L.) and *G. superba* are climbing. *Gloriosa minor* was said to have small and solitary flowers, whereas *G. abyssinica* and *G. carsonii* were said to have several and larger flowers. *Gloriosa abyssinica* is now generally regarded as a synonym of *G. superba* (Sebsebe Demissew 1997, Hoenselaar 2005). *Gloriosa carsonii* was sunk into *G. simplex* by Hepper (1968), and *G. superba* var. *superba* by Hoenselaar (2005). *Gloriosa minor* has been treated as a synonym of *G. superba* by Thulin (1995); of *G. baudii* by Sebsebe Demissew (1997), and of *G. superba* L. var. *graminifolia* (Franch.) Hoenselaar by Hoenselaar (2005).

According to Baker (1898), *G. superba* is distinguished from *G. virescens* (= *G. simplex* L.) by having perianth segments that are narrow and heavily crisped. *Gloriosa virescens* (= *G. simplex*) is confined to South Africa and tropical Africa, whereas *G. superba* has been recorded in South Africa, tropical Africa, India and south-eastern Asia (Baker 1898). Based on Baker's synopsis (1898), it can be concluded that *G. virescens* (= *G. simplex*) is more variable than *G. superba*; hence he described an infraspecific taxon, *G. virescens* var. *grandiflora* Baker from the Niger Delta.

Baker's delimitation (1897, 1898) was adopted by Hepper (1968) and van der Burg (2006) who recognised *G. simplex* and *G. superba* for the Flora of West Tropical Africa and Flora of Benin, respectively. The taxonomic revisions of *Gloriosa* by Sebsebe Demissew (1997) and Hoenselaar (2005) acknowledged the need to separate the more compact form of *G. superba* that has been recorded from arid regions of northern Kenya, Ethiopia and Somalia from the widespread, climbing *G. superba*. Sebsebe Demissew (1997) recognized *G. superba* and *G. baudii* while Hoenselaar (2005) recognized two varieties, *G. superba* var. *superba* and *G. superba* var. *graminifolia*. Plants from western Zambia, the Bulozhi flood plain, though similar to *G. superba* complex in some morphological and floral characteristics, are here recognized as distinct belonging to *G. sessiliflora* (Nordal & Bingham 1998).

Species delimitation in *G. superba* complex is clearly controversial, which is also reflected in the high number of synonyms (electronic appendix 1). It is the result of a poor understanding of the taxonomy and evolutionary relationships within the group. To solve this problem, numerical methods were used to re-evaluate morphological variation and species delimitation in the *G. superba* complex.

MATERIALS AND METHODS

Plant material

The present study is largely based on herbarium material received on loan from B, BM, BR, C, COI, F, K, L, U and UPS and collections kept in the following herbaria: SRGH and WAG (abbreviations follow Holmgren et al. 1990). In addition, herbarium specimens were augmented with field observations and fresh material collected in the field between 2007 and 2011 in several localities of Zimbabwe. Of the 635 specimens examined, 79 were included in this analysis. As far as possible herbarium specimens were selected to represent the entire geographical range of the *G. superba* complex in South Africa, tropical Africa and Asia, and to reflect the morphological variability present within the taxa. As far as possible, herbarium specimens were selected to include specimens matching descriptions of *G. baudii*, *G. carsonii*, *G. superba* and *G. simplex* / *G. virescens* (after Baker 1898, Hepper 1968, Hoenselaar 2005, Sebsebe Demissew 1997, van der Burg 2006). All original descriptions of the taxa were obtained and images of type specimens were obtained from K. Only specimens with fully open flowers were included in the study in order to allow standardized measurements to be made. Sterile and incomplete specimens were excluded from this study. Field studies also clarified character states such

as leaf arrangement, leaf shape, perianth segment shape and colour for the analyses. Published keys and descriptions of species (e.g. Baker 1897, 1898, Berhaut 1967, Dassanayake 2000, Geerinck 2010, Hepper 1968, Hoenselaar 2005, Jessop 1979, Maroyi 2002, Sebsebe Demissew 1997, Thulin 1995, van der Burg 2006) were consulted to establish characters that had previously been considered to be of taxonomic importance.

Each specimen measured was treated as an independent operational taxonomic unit (OTU) for all the statistical tests. Data on all characters were entered in a data matrix (electronic appendix 2). A review of floristic treatments was conducted to produce an initial list of qualitative characters used to distinguish the species. Quantitative characters were counted or measured with a ruler and digital callipers. A total of twenty-one vegetative and floral characters were recorded for each specimen. Sixteen of these characters were measured quantitatively and three qualitatively (table 1). Two ratios were used, and stem diameter and leaf length were excluded from the analysis to avoid weighing of characters. Most of the floral measurements were done on material soaked in tap water with a little detergent overnight or directly on samples in 70% ethanol.

Table 1 – Qualitative and quantitative characters used for multivariate analysis of *G. superba* complex.

Characters used in the final CA and PCA are marked with an asterisk.

Acronym	Character state
PH*	Plant height (mm)
SD	Stem diameter at the widest point (mm)
HS*	Ratio of plant height to stem diameter
ST*	Stem type: 1=simple; 2=branched
SF*	Stem form: 1=erect; 2=climbing
LL	Length of leaf from base to tip (including tendril if present) (mm)
LW*	Width of leaf at widest point (mm)
LWR*	Leaf length to width ratio
DW*	Distance from leaf base to the widest point of the leaf (mm)
PL*	Pedicle length (mm)
TL*	Tepal length (mm)
TW*	Tepal width at the widest point, excluding serrations (mm)
TS*	Tepal shape: 1 = linear and crisped; 2 = oblanceolate / oblong and entire, flat
DL*	Distance from tepal base to the widest point of the tepal (mm)
TT*	Length of tepal tube (mm)
BW*	Basal tepal width (mm)
SL*	Style length (mm)
SLL*	Style lobe length (mm)
FL*	Filament length (mm)
AL*	Anther length (mm)
AW*	Anther width (mm)

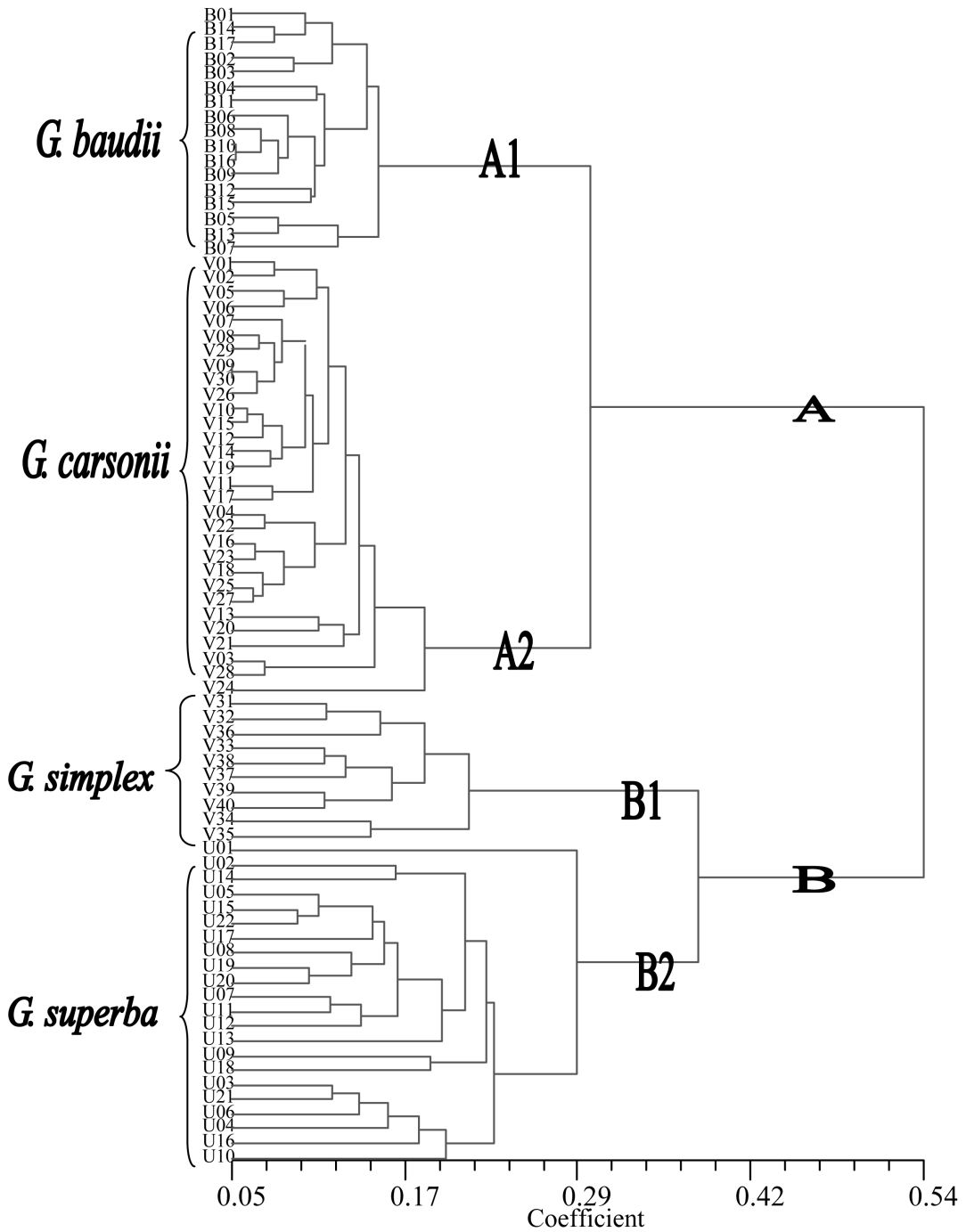


Figure 1 – Phenogram depicting the groups within the *G. superba* complex based on vegetative and floral characters. Four clusters corresponding to: *G. baudii* (A1); *G. carsonii* (A2); *G. simplex* (B1) and *G. superba* (B2) are indicated. OTUs are numbered as in electronic appendix 3.

Multivariate analysis

Data were entered in Excel. Prior to doing Cluster Analysis (CA) and Principal Components Analysis (PCA), the data were standardized to remove the effects of characters with large variances. CA and PCA were performed using NTSYS package version 2.11a (Rohlf 2002) to verify morphological discontinuities among the taxa. PCA was carried out to

examine the pattern of relationships between specimens or OTUs as well as the relative importance of the characters employed. This technique projects samples in multivariate space so that maximum variances that are not correlated are extracted along different axes. CA based on unweighted pair group method using arithmetic averages (UPGMA) was used to generate phenograms.

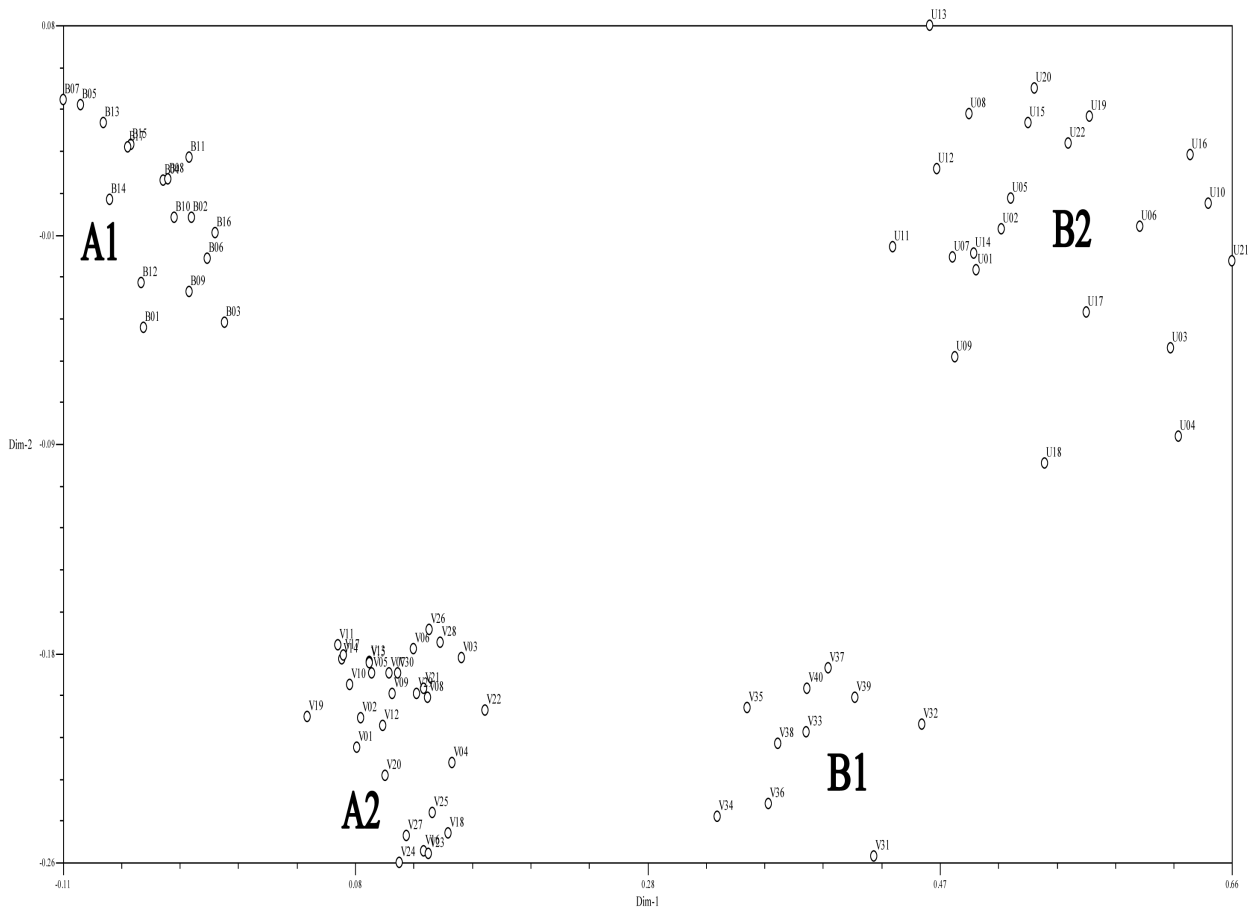


Figure 2 – An ordination of the principal coordinates reveals four discrete groupings: A1 = *G. baudii*; A2 = *G. carsonii*; B1 = *G. simplex* and B2 = *G. superba*. OTUs are numbered as in electronic appendix 3.

Univariate analysis

The variability of quantitative characters (except length of tepal tube and anther width) was evaluated by box-plots using SPSS Statistics 17.0 (Field 2009). Box plots featuring medians, first and third quartiles and range of selected characters were drawn. These plots allowed individual characters to be evaluated to determine the extent of overlap between the specimens detected in the phenetic analysis. The groupings used for box-plots follow the phenetic results of CA and PCA.

RESULTS

Cluster analysis of 79 specimens revealed two main groups A and B (fig. 1). Group A consists of dwarf to short non-climbing plants, rarely exceeding 80 cm in height. Group B has noticeably tall and climbing plants, averaging 250 cm in height. Within both Groups A and B, two subgroups are evident (fig. 1). Each subgroup or cluster was given the name of the type specimen found within it. Subgroup A1 is made up of seventeen specimens matching the description of *G. baudii*. These are the dwarf plants found in the arid regions of northern Kenya, Ethiopia and Somalia, which rarely exceed 40 cm in height. Subgroup A2 matches the description of

G. carsonii. These are short, erect and non-climbing plants, averaging 60 cm in height, widespread in southern and east Africa, extending to West Africa. Specimens of subgroup B1 have wide perianth segments, which are not crisped, but straight or slightly undulate edges or margins corresponding to *G. simplex*. *Gloriosa simplex* occurs in South Africa and tropical Africa. Specimens of subgroup B2 matches the description of *G. superba*, the only species of *Gloriosa* that naturally occurs in tropical Asia. Its perianth segments are narrower than those of *G. simplex* and are crisped to heavily crisped.

Principal components analysis of the data revealed similar groupings as obtained by cluster analysis (fig. 2). Electronic appendix 4 presents an alternative view of the 3-dimensional ordination. The 3D plot confirmed the distinctiveness of the four clusters, with *G. baudii* and *G. superba* on the extremes and *G. carsonii* and *G. simplex* in the middle of the 3D space. In the PCA run using the characters shown in table 1, the first three principal components explain 83.6% of the total character variation, with 60.8%, 16.4% and 6.4% for the respective axes (table 2). In the case of PC1, fourteen characters had loadings with an absolute value greater than 0.6. PC2 had four characters with such an absolute value while PC3 has only TW as the major variable (table 2). These characters with the highest loadings (both quantitative and qualitative

Table 2 – Factor loadings on the first three principal components for quantitative and qualitative characters used in the final PCA. Qualitative characters are marked with an asterisk.

Character	PC1	PC2	PC3
1. PH	0.884	0.084	0.122
2. HS	0.844	0.044	0.09
3. LW	0.548	-0.756	-0.221
4. LWR	-0.533	0.725	0.308
5. DW	0.52	0.712	-0.206
6. PL	0.857	-0.05	-0.149
7. TL	0.872	-0.008	0.057
8. TW	0.056	-0.671	0.658
9. DL	-0.531	-0.511	0.416
10. TT	-0.689	0.52	0.26
11. BW	0.826	0.0004	0.1
12. SL	0.882	0.329	-0.006
13. SLL	0.864	-0.016	-0.043
14. FL	0.877	0.359	-0.022
15. AL	0.908	0.116	0.175
16. AW	0.942	-0.081	0.129
17. SF*	0.878	0.117	0.314
18. ST*	0.905	0.133	0.298
19. TS*	-0.819	-0.477	0.243

characters) can be considered as taxonomically useful for partitioning the *G. superba* complex into subgroups.

Univariate analyses using boxplots (electronic appendix 5) indicate that plant height, ratio of plant height to stem diameter, filament length, anther length and width contribute most to the separation of the two major clusters, Group A and B. The discontinuities obtained in these vegetative and floral characters were used in the key to delineate different species in the complex. Plant height, ratio of plant height to stem diameter, leaf width, distance from leaf base to the widest point of the leaf, ratio of leaf length to width and anther width can be used to separate Group A into *G. baudii* (Group A1) and *G. carsonii* (Group A2). Plants forming the Group B cluster are long, have sarmentose stems, and are collected from both tropical Africa and Asia. Floral characters (electronic appendix 5J, K & O) convincingly separate *G. simplex* (Group B1) from *G. superba* (Group B2). *Gloriosa simplex* has been collected from South Africa and tropical Africa, while *G. superba* has been collected from South Africa, tropical Africa and Asia.

DISCUSSION

In this study CA, PCA and univariate analysis of morphological characters strongly suggest the existence of two assemblages of species in *G. superba* complex: one comprising *G. baudii* and *G. carsonii* and the other *G. superba* and *G. simplex*. CA and PCA were able to discriminate between *G. baudii* and *G. superba* placing them on two extremes. *Gloriosa carsonii* appears to be phenetically closer to *G. baudii*; and *G. simplex* is phenetically closer to *G. superba*. These findings are consistent with the habit and floral charac-

ters used by Baker (1898) to differentiate *Gloriosa* species. Baker (1898) divided *Gloriosa* species into two groups depending on whether they are climbing or erect. Of the two climbing species, *G. superba* and *G. simplex* are separated by the former having crisped perianth segments. These taller species are more or less regularly branched with numerous flowers, climbing on other plants. In addition to these observations, *G. superba* is more widespread than the other *Gloriosa* species. It occurs in South Africa, tropical Africa and Asia, while *G. simplex* is confined to South Africa and tropical Africa. On the other hand, *G. baudii* is a short, erect herb confined to the stony, sandy soils of the arid regions of northern Kenya, Ethiopia and Somalia (Field 1972, Sebsebe Demissew 1997). *Gloriosa carsonii* is another short and erect species widespread in tropical Africa, particularly southeast and east tropical Africa. It is therefore not surprising that in CA and PCA, these species clustered together as a phenetic group. In light of the data presented here, it is evident that the four clusters should probably be treated as separate species. Taxonomic implications of this study are as detailed below.

The *G. baudii* Group A1

Gloriosa baudii was incorrectly placed in the genus *Littonia*. Baker (1898) considered it an imperfectly known species and hinted that it could be a *Gloriosa* species as the perianth segments were reflexed. Chioyenda made the formal combination in 1916. Later workers (e.g. Field 1972, Thulin 1995) hinted at the need to accord some taxonomic recognition of the dwarf plants of the arid regions of northern Kenya, Ethiopia and Somalia based mainly on their short, erect and non-climbing stature. In his treatment of Colchicaceae for the Flora of Ethiopia and Eritrea, Sebsebe Demissew (1997) recognized *G. baudii* as a distinct species. In the most recent taxonomic treatment of Colchicaceae for Flora of Tropical East Africa, Hoenselaar (2005) reduced *G. baudii* to a synonym of *G. superba* var. *graminifolia*. In this study, specimens of *G. baudii* form a distinct cluster within the *G. superba* complex, which is also well supported by geographical distribution. Quantitative characters such as plant height, ratio of plant height to stem diameter, leaf width, distance from the base to widest leaf width, ratio of leaf length to width and anther width support the recognition of *G. baudii* as a distinct species. CA, PCA and univariate analysis agree with the recommendation to separate *G. baudii* from *G. superba* (after Sebsebe Demissew 1997).

The *G. carsonii* Group A2

Baker (1898) considered *G. carsonii* as a distinct species, while Hepper (1968) and Hoenselaar (2005) treated it as a synonym of *G. simplex* and *G. superba* var. *superba* respectively. Baker (1898) recognized it as a short and erect form, characterized by oblong-lanceolate leaves, confined to Mozambique and Malawi. According to CA (fig. 1) and PCA (fig. 2), the *G. carsonii* Group A2 appears to be phenetically closer to the *G. baudii* Group A1 than to the Group B cluster (*G. superba* and *G. simplex*). These findings are consistent with morphological characters used by Baker (1898). Therefore, the morphometric distinctiveness of *G. carsonii* as demonstrated by CA and PCA in this study suggests that

Key to the species of the *Gloriosa superba* complex

- 1a. Stems long, usually higher than 80 cm; branched and climbing; stamens with long filaments, more than 2.2 cm long.....2
 - 1b. Stems erect, short, less than 80 cm high, not branched; stamens with short filaments, less than 2.2 cm long.....3
 - 2a. Perianth segments with much crisped margins, more or less the same width, less than 1.5 cm wide (distribution: electronic appendix 6A).....*G. superba*
 - 2b. Perianth segments not crisped but straight or slightly undulate margins, gradually narrowed at the base, broadening towards the middle and curving inwards in the upper half; usually more than 1.5 cm wide in the middle (distribution: electronic appendix 6B).....*G. simplex*
 - 3a. Short stems, often less than 40 cm high; crowded leaves, leaf blade 0.2–1.5 cm wide, perianth segments fused for 4–5 mm at the base (distribution: Kenya, Ethiopia and Somalia; electronic appendix 6C).....*G. baudii*
 - 3b. Stems often higher than 40 cm, lower leaves alternate, leaf blade more than 2 cm wide, perianth segments fused for less than 3 mm at the base (distribution: electronic appendix 6D).....*G. carsonii*
-

it should probably be treated as a separate species. We therefore here propose its reinstatement at the specific level. But there is also need to revise the concept of *G. carsonii* on account of the type specimen and the distributional range of the species. It is erect and non-climbing; but taller than *G. baudii* and has a wider geographical range in tropical Africa. *G. carsonii* is not specific to one particular habitat, but has been recorded in miombo woodland, wooded grasslands, dry scrubby roadsides and open grasslands.

The *G. simplex* Group B1

Specimens of the *G. simplex* Group B1 do form a cluster distinct from specimens of *G. superba*. The qualitative character of the perianth segments supports the recognition of this cluster as a distinct taxonomic unit. Results of this study are consistent with morphological characters used by Baker (1897, 1898) to differentiate between *G. virescens* (= *G. simplex* L.) and *G. superba*. Baker (1897, 1898) described *G. virescens* (= *G. simplex* L.) as having wider, undulate to non-undulate perianth segments. Several authors studying the flora of East and West Africa adopted this delimitation (e.g. Andrews 1956, Berhaut 1967, Cufodontis 1971, Hepper 1968, Lund & Tallantire 1962, van der Burg 2006, Verdcourt & Trump 1969). Although *G. simplex* L. has been considered a *nomen incertae sedis* by Field (1971, 1972), because no type specimen was designated when the species was described which led to the suggestion to abandon this widely used name. Here, we propose that the name, *G. simplex* L., should be reinstated.

The *G. superba* Group B2

This study has shown that the *G. superba* Group B2 is a well-defined cluster both in the CA and PCA. Baker (1898) described *G. superba* as a climbing perennial, characterized by crisped perianth segments occurring in South Africa, tropical Africa and Asia. Specimens with crisped perianth segments confirming to the description of *G. superba* are widespread, recorded in South Africa, tropical Africa and Asia. Characters that can be considered diagnostic for *G. superba*

are the narrow and crisped perianth segments. We hereby recommend the treatment of *G. superba* in a narrower sense, characterized by narrow, crisped to heavily crisped perianth segments.

SUPPLEMENTARY DATA

Supplementary data are available at *Plant Ecology and Evolution*, Supplementary Data Site (<http://www.ingentaconnect.com/content/botbel/plecevo/supp-data>), and consists of the following: (1) taxonomy of *Gloriosa superba* (pdf format); (2) data matrix of characters measured on OTUs (Excel table); (3) specimens of *Gloriosa superba* complex used in the phenetic study (pdf format); (4) 3-dimensional plot of vegetative and floral characters (pdf format); (5) boxplots of selected vegetative and floral characters (pdf format); (6) distribution maps of species of the *Gloriosa superba* complex, based on georeferenced herbarium specimens (pdf format).

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