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Morphology and taxonomic reclassification of *Gorteria* (Asteraceae)

Abstract

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A phylogeny of the South African and Namibian genus *Gorteria* was recently elucidated by analysis of DNA sequence data, which indicated that the prevailing taxonomic concepts of generic circumscription and species delimitations do not reflect the evolutionary history of the group. In the present paper a reclassification of the genus is presented. The treatment includes an overview of morphological variation, an identification key, descriptions and a distribution map for all of the eight species recognized, including three new combinations (*G. alienata*, *G. parviligulata* and *G. piloselloides*) and one new species (*G. warmbadica*). Two lectotypes are designated (*G. affinis* and *Oedera* (*Gorteria*) *alienata*).

Additional key words: *Arctotideae*, *Compositae*, *Gorteriinae*, *Hirpicium*, Namibia, South Africa

Introduction

Arctotideae is a small tribe of *Asteraceae* more or less restricted to sub-Saharan Africa. It is divided into two subtribes, *Arctotidinae* and *Gorteriinae* (Karis & al. 2009). During the last ten years the tribe has been subjected to several phylogenetic studies at the tribal, subtribal and generic levels (Funk & al. 2004; Karis 2006; Funk & Chan 2008; McKenzie & al. 2006; Howis & al. 2009; Stångberg & al. 2013). Studies based on molecular, morphological, and palynological data have shown that *Gorteriinae* is comprised of two clades, one containing *Berkheya* Ehrh., *Cullumia* R. Br., *Cuspidia* Gaertn., *Didelta* L'Hér. and *Heterorhachis* Sch. Bip. ex Walp., and the other clade comprising *Gazania* Gaertn., *Gorteria* L. and *Hirpicium* Cass. (Leins & Thyret 1971; Funk & al. 2004; Karis 2006; Funk & Chan 2008; Wortley & al. 2008).

Gorteria is a small genus of the subtribe *Gorteriinae* distributed mainly in the Western Cape and Northern Cape provinces in South Africa and the most southern part of the !Karas region in Namibia in the winter and year-round rainfall zones (Chase & Meadows 2007). It has been considered easily recognizable as annual herbs with a few hermaphroditic disc florets among otherwise functionally male disc florets in capitula that fall off at maturity, and subsequently with seedlings sprouting in situ from within the capitulum (Goldblatt & Manning 2000; Leistner 2000; Karis 2007).

All genera that presently constitute *Arctotideae* – *Gorteriinae* were originally referred to *Gorteria* by Linnaeus (1759, 1760, 1763, 1771). Thunberg monographed *Gorteria* and recognized 12 species (Thunberg 1798), of which ten were herbaceous and two were shrubby. He described seven new species, including *G. diffusa* Thunb.

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and the fruticose *G. integrifolia* Thunb. (\equiv *Hirpicium integrifolium* (Thunb.) Less.). Thunberg emphasized the connate phyllaries as the most important characteristic of the genus, but this feature is now known to be diagnostic of the entire subtribe *Gorteriinae*. Cassini (1818) described the monotypic genus *Ictinus* Cass. (*I. piloselloides* Cass.) but later (Cassini 1824) merged it with *Gorteria*. Cassini also described the genus *Hirpicium* (Cassini 1820) with *H. echinulatum* Cass. (nom. illeg. \equiv *Oedera alienata* Thunb. \equiv *H. alienatum* (Thunb.) Druce) as its type. In *Tableau encyclopédique et méthodique Lamarck* (1797) described the genus *Personaria*, but in *Encyclopédie méthodique Poiret* (1816) referred *P. personata* to Linnaeus's *G. personata* L., and therefore *P. personata* "Poir." should be considered a new combination, viz. *P. personata* (L.) Poir. Lessing (1832) excluded many taxa from *Gorteria* as it had been circumscribed by earlier workers, and his classification is similar to the one used today. Candolle (1838) added three new species (*G. affinis* DC., *G. calendulacea* DC. and *G. corymbosa* DC.) based on material collected by Drège and by Ecklon.

The present-day concept of the taxonomy of *Gorteria* is based on the most recent revision of the genus (Roessler 1959; 1973). This was an extensive work involving examination of a large number of specimens. Roessler considered *Gorteria* to comprise three variable species: *G. corymbosa*, *G. diffusa* and *G. personata*. Roessler subdivided *G. personata* into two subspecies, *G. personata* subsp. *personata* and *G. personata* subsp. *gracilis* Roessler, and *G. diffusa* was subdivided into three subspecies, *G. diffusa* subsp. *diffusa*, *G. diffusa* subsp. *calendulacea* (DC.) Roessler, and *G. diffusa* subsp. *parviligulata* Roessler (Table 1). Based on all the specimens investigated, Roessler (1959, 1973) also presented distribution maps for all taxa. The distribution of *G. diffusa* comprised four geographically disjunct areas (designated "Namibia", "Northern", "Middle", and "Southern" by Stångberg & al. 2013) and their allopatric distributions were corroborated by Ellis & Johnson

(2009; plants from Namibia were, however, not included in their study). In Roessler's treatment the four areas of distribution of *G. diffusa* do not correspond to the distribution of the subspecies he recognized, with the exception of *G. diffusa* subsp. *parviligulata*, which is the only subspecies restricted to the area "Namibia". Populations of *G. diffusa* from the "Northern" and "Middle" areas show a remarkable variation in colour and spot pattern of the ray florets. In the "Northern" part of the distribution, also shrubby specimens of *G. diffusa* have been collected close to the Atlantic coast, which Ellis & Johnson (2009) referred to as "Kz" (Kleinzee).

Before Roessler's (1959) treatment, *Hirpicium* contained only two species, i.e. *H. alienatum* and *H. integrifolium*, but he dramatically changed the circumscription of the genus by adding ten species formerly classified in *Berkheya*, *Berkheyopsis* O. Hoffm., *Crocodylodes* Adans., *Gazania* and *Meridiana* Hill based on pappus morphology, but he also considered *H. alienatum* and *H. integrifolium* to be the closest relatives of *Gorteria*.

The recently published phylogenetic analysis of Stångberg & al. (2013), based on nrDNA (ETS and ITS) and cpDNA (*trnL-F*) data, showed that *Gorteria* as presently circumscribed is not monophyletic because two species of *Hirpicium* (*H. alienatum* and *H. integrifolium*) are embedded within *Gorteria*. This is interesting considering Roessler's earlier statement mentioned above. Furthermore, Stångberg & al. (2013) demonstrated that *G. diffusa* is not monophyletic, but that it represents three different evolutionary lineages that correspond to different distribution areas recognized by Roessler:

(1) *Gorteria diffusa* from the "Southern" part of the distribution was grouped with *G. personata* subsp. *gracilis* and together they constitute the sister group of all other taxa of *Gorteria*, including *Hirpicium alienatum* and *H. integrifolium*. Roessler (1959) described the new subspecies *G. personata* subsp. *gracilis* from material formerly classified as *G. diffusa* with the argument that the phyllaries of these plants were more similar to the phyllaries of *G. personata*.

Table 1. *Gorteria* taxa recognized by Roessler (1959, 1973) and by Stångberg & Anderberg (present study).

<i>Gorteria</i> taxa sensu Roessler (1959, 1973)	<i>Gorteria</i> taxa sensu Stångberg & Anderberg (present study)
<i>Gorteria personata</i> L. subsp. <i>personata</i>	<i>Gorteria personata</i> L.
<i>Gorteria personata</i> subsp. <i>gracilis</i> Roessler	<i>Gorteria piloselloides</i> (Cass.) Stångb. & Anderb.
<i>Gorteria diffusa</i> Thunb. subsp. <i>diffusa</i> ("Middle" area)	<i>Gorteria diffusa</i> Thunb.
<i>Gorteria diffusa</i> Thunb. subsp. <i>diffusa</i> ("Northern" area)	<i>Gorteria diffusa</i> Thunb.
<i>Gorteria diffusa</i> Thunb. subsp. <i>diffusa</i> ("Southern" area)	<i>Gorteria piloselloides</i> (Cass.) Stångb. & Anderb.
<i>Gorteria diffusa</i> subsp. <i>calendulacea</i> (DC.) Roessler	<i>Gorteria diffusa</i> Thunb.
<i>Gorteria diffusa</i> subsp. <i>parviligulata</i> Roessler ("Namibia" area)	<i>Gorteria parviligulata</i> (Roessler) Stångb. & Anderb.
<i>Gorteria corymbosa</i> DC. (8 ray florets)	<i>Gorteria corymbosa</i> DC.
<i>Gorteria corymbosa</i> DC. (13 ray florets)	<i>Gorteria warmbadica</i> Stångb. & Anderb.
<i>Hirpicium alienatum</i> (Thunb.) Druce	<i>Gorteria alienata</i> (Thunb.) Stångb. & Anderb.
<i>Hirpicium integrifolium</i> (Thunb.) Less.	<i>Gorteria integrifolia</i> Thunb.

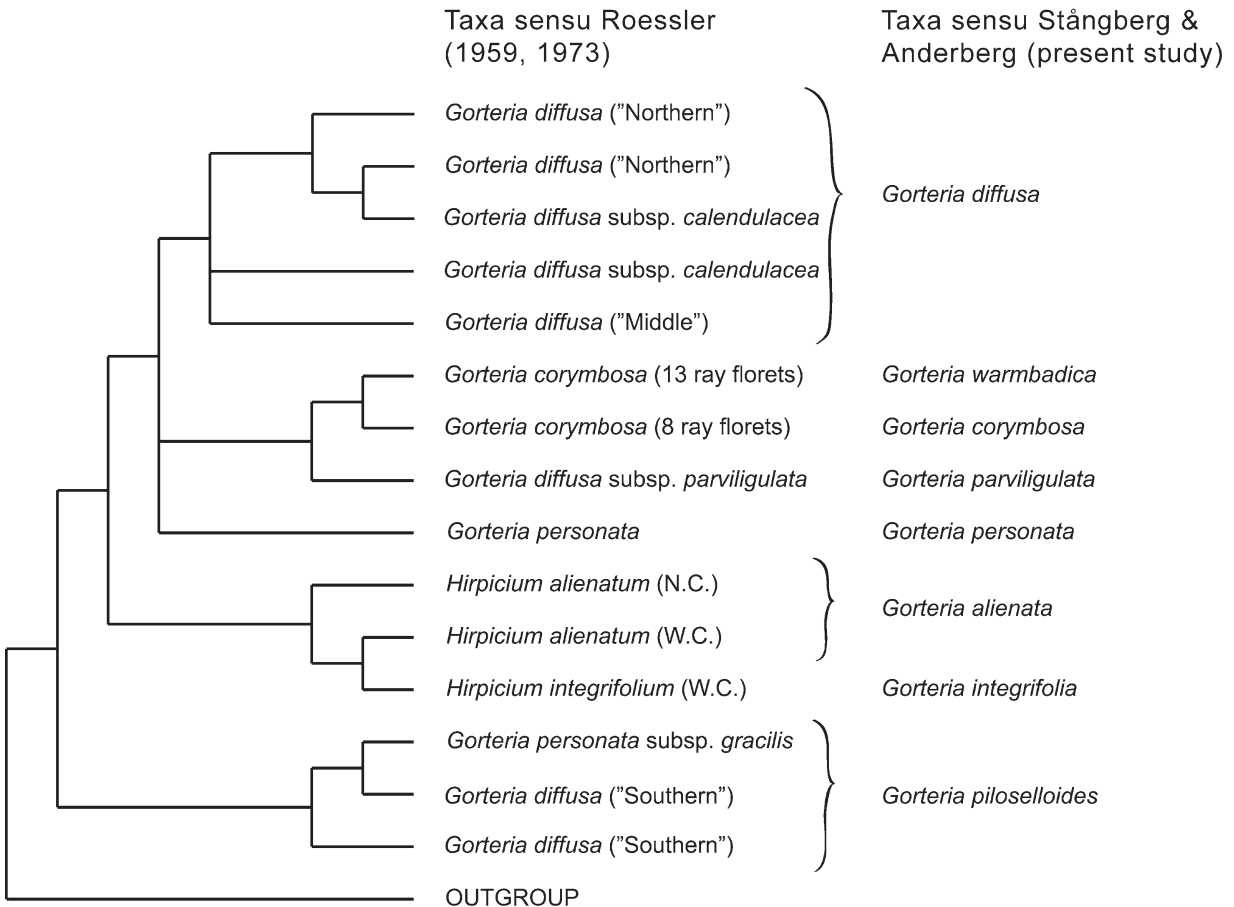


Fig. 1. Simplified phylogeny of *Gorteria* based on Stångberg & al. (2013: fig. 4) with taxa sensu Roessler (1959, 1973) in the left column and taxa sensu Stångberg & Anderberg (present study) in the right column. All included nodes have posterior probability (pp) value = 1. "Northern", "Middle" and "Southern" indicate from which part of the distribution the *G. diffusa* samples were collected. N.C.= Northern Cape province, W.C.= Western Cape province.

(2) *Gorteria diffusa* subsp. *parviligulata* is closely related to *G. corymbosa*, which on the other hand consisted of two subclades diagnosed by capitula with eight or 13 rays, respectively.

(3) All *Gorteria diffusa* representatives in the analysis from the "Northern" part of the distribution, including *G. diffusa* subsp. *calendulacea*, all the different ray floret varieties, as well as the shrubby coastal form, formed a polytomy with *G. diffusa* from the "Middle" distribution area as their sister group.

The phylogenetic analysis of *Gorteria* has shed new light on the evolutionary relationships in the genus, not only because two species of *Hirpicium* have been shown to be an integrated part of *Gorteria*, but also because the morphological characterization of the genus must be redefined and the current species delimitation based on Roessler's treatment must be revised. In this context, we believe it is useful to discuss the morphology of the genus, to present a key, and in the light of the new results to present descriptions of the different clades that have been identified. A revised species taxonomy is also proposed.

Material and methods

Fieldwork was undertaken in the Northern Cape and Western Cape provinces of South Africa, and in the !Karas region in Namibia, during which all recognized taxa of *Gorteria* (except *G. warmbadica* Stångb. & Anderb. sp. nov.) were studied and collected. Vouchers were deposited in the Swedish Museum of Natural History (S). In addition, herbarium material from the herbaria BM, BOL, G, K, LINN, NBG, PRE, S, UPS and WIND was studied (herbarium codes following Thiers 2008+). A scanned image of a type specimen (*Ictinus piloselloides* Cass.) from P was also examined. The herbarium specimens examined are listed in Appendix 1.

Morphological characters were examined on herbarium material using a stereo microscope. Dried material was softened in hot water with detergent added. Floral parts were dissected and mounted in Hoyer's solution (Anderson 1954) on microscope slides for examination with a light microscope. Softened capitula were stored in 70% ethanol. Phyllaries, floral parts and cypselas were drawn with a camera lucida attached to the stereo mi-

croscope. Morphological details of florets and cypselas were also examined by means of scanning electron microscopy. Dry material was sputter-coated with gold and examined with a Stereoscan 260 scanning electron microscope (Cambridge Instruments Ltd, Cambridge, England).

In the following section, the morphological descriptions refer to groups identified in the phylogenetic analysis of Stångberg & al. (2013) and the taxon names are those formally published in the Taxonomy section below. As *Hirpicium alienatum* (the type of *Hirpicium*) and *H. integrifolium* are formally transferred to *Gorteria* in the revised taxonomy, the term “*Hirpicium*” (in quotation marks) will be used for the remaining, as yet unclassified species of that genus.

Morphology

Habit — Most *Gorteria* species are annual herbs (Fig. 2A–C, F, H–L), but two of the species are compact ericoid shrublets (*G. alienata* and *G. integrifolia*; Fig. 2G, D). It has been reported (Roessler 1959; Karis 2006; Ellis & Johnson 2009) and observed on herbarium material that in Namaqualand, close to the coast, populations of *G. diffusa*, which are normally annuals, are perennating and develop into small shrublets (Fig. 2E). All *Gorteria* have attached at their base (in annuals) or at the base of seedlings (frutescent species and shrubby *G. diffusa* (i.e. “Kz”) the previous year’s capitulum from which the plant has sprouted (Fig. 3A). Occasionally, several cypselas germinate concurrently from the same capitulum resulting in a group of sibling individuals growing in almost exactly the same site. Examined herbarium specimens of *G. alienata* and *G. integrifolia* do not include seedlings, so the fact that their seedlings also sprout from cypselas enclosed in the previous year’s capitulum has previously been observed only in the field (Stångberg 2009; collected, dried seedlings from that study have been deposited in S). *Gorteria alienata* also spreads vegetatively by means of rhizomes.

The herbaceous species of *Gorteria* all have a decumbent or sometimes erect growth habit. Whether they are erect or not depends on their age and the impact of surrounding vegetation. Young individuals without well-developed branches tend to be more upright, whereas older, heavily branched individuals are prostrate, especially when growing on bare ground. When growing in grassy vegetation or among shrubs, herbaceous *Gorteria* attain a more erect habit. Some populations of *G. corymbosa* even attain a cushion-like habit (Fig. 2J). The decumbent specimens can cover an area up to 1 m², but in such cases, or when forming cushions, more than one plant might have contributed to what seems to be only one individual, because of the presence of siblings sprouting from within the same capitulum (Fig. 2C). All branches terminate with a single capitulum.

In *Arctotideae* – *Gorteriinae*, the most common life form is perennial herbs and this is also the case with most representatives of the *Gazania* – *Gorteria* – “*Hirpicium*” clade. As the heavily lignified involucre evolved in the ancestor of *Gorteria*, the dormant seeds became more effectively protected and seeds probably germinated to a higher degree, which could have favoured an annual life form. In the shrubby *Gorteria* the extremely hard, protective involucre was lost. Shrubs are the most common and perhaps most advantageous life forms in the Cape Floristic Region (CFR) (Goldblatt & Manning 2000). Annual herbs are, compared to other life forms, rare in the CFR, possibly because they are competitively excluded in fynbos vegetation because of the longer disturbance (fire) cycles; therefore specialization in seed protection is more necessary for survival between flowering seasons. Furthermore, Duncan & Ellis (2011) observed, during cultivation of *G. diffusa*, that not all seeds in one diaspore (i.e. capitulum) germinate in the same season, but all except one or a few remain as a reservoir of dormant seeds and can survive years of drought.

Trichomes — The longitudinally striate hairs found in *Gazania*, *Gorteria* and “*Hirpicium*” are unique in the family (Karis 2006) (Fig. 3B–C). In *Gorteria* these hairs are found on stems, leaves, involucres and corollas. The hairs have a multicellular base and on leaves and stems the bases are most often slightly raised. The margins of these hairs are scabrous in most species but smooth in *G. alienata*, *G. integrifolia* and *G. personata*. The hairs, although of varying length, are always present on the abaxial surface of the disc floret corolla lobes in *Gorteria* (Fig. 3L), which is a diagnostic character for the genus. Longitudinally striate hairs are also found scattered abaxially on the ray floret corollas, sometimes also distally in some populations of *G. diffusa*.

The leaves and phyllaries are referred to as being hispid or, in cases when the hairs are longer and denser, as white silky. On the stems the hairs are patent with the exception of one population (the woody “Kz” morphotype) in which they are tightly and erectly adpressed (strigose).

Woolly hairs in *Gorteria* are found on stems, on the abaxial side of the leaves (Fig. 3K) and on the involucres, and in the descriptions below this kind of pubescence is referred to as tomentose. Glandular hairs are always found on disc floret corollas and rarely on ray floret corollas. They have a biseriate stalk leading to one distal mucilaginous cell (Fig. 3F). Glandular hairs are sometimes found also on phyllaries (*G. parviligulata*). Globose glandular hairs are arranged in indistinct rows on the cypselas of *Gazania* and of “*Hirpicium*” (i.e. Roessler’s concept of that genus minus *H. alienatum* and *H. integrifolium*), whereas in *Gorteria* glands of the same type are more or less sparsely scattered on the cypselas (Fig. 3O). The glands consist of a sessile spherical mucilaginous cell (Fig. 3E). *Gorteria corymbosa* was the only species included in the cypselas study of Reese (1989), who



Fig. 2. Habit of *Gorteria* – A: *G. personata*; B, C: *G. diffusa*; D: *G. integrifolia*; E, F: *G. diffusa*; G: *G. alienata*; H, I: *G. piloselloides*; J: *G. corymbosa*; K: *G. warmbadica*; L: *G. parviligulata*. – Photographs by F. Stångberg (A–D, F, I, J, L), M. Arnerup (E), A. Bengtson (G, H) and S. Rügheimer (K).

concluded that *Gorteria* lacks globose cypselas glands. However, such glands are actually present in *G. corymbosa* and all other *Gorteria* taxa except *G. integrifolia*, which was stated by Reese (1989) and Karis (2006) to have this kind of glands in rows. Twin hairs, which are a common hair-type on cypselas within *Asteraceae* (Hess

1938; Bremer 1994), are also found on the cypselas of *Gorteria* (Fig. 3D, O). The twin hairs are twisted but the degree of twisting varies between specimens within one and the same species.

Presence of woolly hairs, glandular hairs and twin hairs must be considered as plesiomorphic features in *Gorteria*.

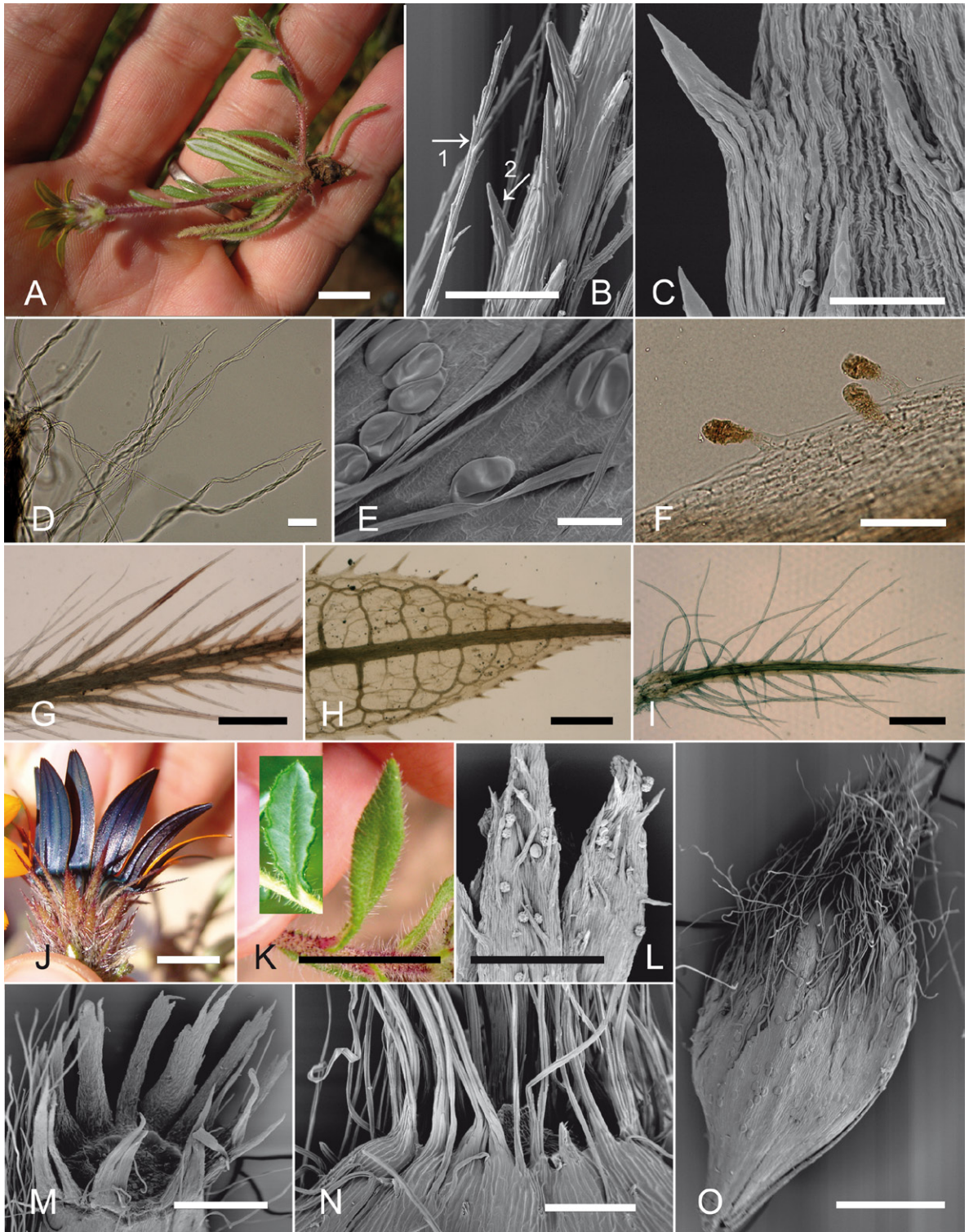


Fig. 3. Morphological characters of *Gorteria*. – A: plant germinating from inside previous year's lignified involucre; B: longitudinally striate hair with scabrous margin (arrow 1), longitudinally striate hairs with smooth margin on phyllary (arrow 2); C: longitudinally striate hairs with smooth margin on disc corolla; D: twisted twin hairs on cypsel; E: globose glandular hairs on cypsel; F: glandular hairs on disc corolla; G: phyllary with lobed margin (note the veins); H: phyllary with hispid margin; I: phyllary with villous margins; J: bent ray florets (which give the spots a raised appearance); K: leaves hispid on adaxial surface, densely tomentose on abaxial surface (inset); L: ray florets with longitudinally striate hairs (the round structures are pollen grains); M: pappus scales, inner series somewhat narrower; N: pappus with a fringed crown; O: cypsel bilaterally flattened, pubescent only distally, with scattered globose glands. – Scale bars: A = c. 1 cm; B = 200 μ m; C = 60 μ m; D = 100 μ m; E = 100 μ m; F = 100 μ m; G = 1000 μ m; H = 1000 μ m; I = 1000 μ m; J = c. 1 cm; K = c. 1 cm; L = 400 μ m; M = 600 μ m; N = 200 μ m; O = 800 μ m. – Photographs by F. Stångberg from *Stångberg 152* (S), *Giess 14631* (WIND), *Meyer 251* (PRE), *Pillans 10839* (S), *Örtendahl 221* (UPS), *Stångberg 65* (S), *Stångberg 82* (S), *Karis 1040* (S), *Stångberg 122* (S), *Stångberg 140* (S) and *Stångberg 60* (S).

In other *Asteraceae* taxa where the cypselas themselves are diaspores, the twin hairs might be of importance in dispersal (anemochory) and may also have a water-absorbing function associated with germination. In the herbaceous *Gorteria* taxa the twin hairs are reduced both in number and appearance and are unlikely to have the same function. The characters of the twin hairs (density, degree of twisting, and curling) are possibly correlated to the degree of lignification of the involucre because the shrubby *Gorteria* taxa show the same twin-hair features as *Gazania* and “*Hirpicium*”, even though they are slightly twisted.

The globose glandular hairs found on the cypselas may also have a more important role in *Gazania* and “*Hirpicium*”, where they are arranged in regular rows, whereas in *Gorteria* (incl. *G. alienata*) this kind of hair is a plesiomorphy and entirely lost in *G. integrifolia* perhaps because their cypselas have also lost their function as diaspores.

The presence of longitudinally striate hairs on the corolla is a synapomorphy for *Gorteria*. The spiny-looking hairs might have a role in protecting the floral buds from pollen thieves as well as seed predators at least during anthesis. Since the twin hairs on the cypselas have lost their function in *Gorteria*, perhaps the longitudinally striate hairs on the phyllaries have taken over the role as a water-absorbing organ. The amount of longitudinally striate hairs on the involucre seems to be correlated to geographical distribution. The *Gorteria* most dependent on efficient water uptake are taxa found in the driest region, i.e. *G. corymbosa*, *G. parviligulata* and *G. warmbadica*, which also have the most hairy involucre.

Leaves — The leaves in *Gorteria* are alternate, more or less revolute and all have the same type of pubescence. The leaves are hispid on the adaxial surface and on the abaxial midvein, but densely tomentose on the abaxial surface except for the midvein (Fig. 3K). In *G. alienata* the longitudinally striate hairs sometimes seem to consist only of the raised bases, which give these leaves an almost glabrous appearance. In herbaceous *Gorteria* both size and shape of leaves vary within a single individual. The oldest leaves on the plant, i.e. the most basal ones, are always noticeably larger than the cauline leaves, which become smaller distally. Both the basal and cauline leaves may comprise a combination of entire and pinnatifid leaves in most herbaceous species. There are species with only entire leaves, but it is very uncommon that pinnatifid leaves are the only kind of leaves on the plant.

In woody *Gorteria* the leaves are strongly revolute and on older branches are congregated on brachyblasts, which is an apomorphic character not found in any other taxon in the *Gazania* – *Gorteria* – “*Hirpicium*” clade. Sometimes it is not possible to see the woolly hairs on the abaxial side because of the revolute margin. The most distal longitudinally striate hair is rigid and renders the apex mucronate. The hairs on the proximal portion of the

leaves of the woody *Gorteria* are noticeably longer than those occurring on other parts of the surface.

Capitulum — All species have radiate capitula (Fig. 2), which are found in the majority of the *Gorteriinae* species. The ray florets are neuter, and most disc florets are functionally male, so disc florets are responsible for both pollen and seed production. In *Gorteria parviligulata* and *G. personata* the ray florets are short and do not extend beyond the involucre. As mentioned above, the capitula act as diaspores in all *Gorteria*.

Involucre and phyllaries — All species of *Arctotideae* – *Gorteriinae*, except for *Didelta*, have at least to some degree fused phyllaries (Roessler 1959; Karis 2006). There is a clear distinction between the portions of the involucre consisting of the fused and free parts of the phyllaries. The fused, cup-like part is here referred to as the involucre and only the free portions are referred to as phyllaries. In most species, the phyllaries are equally scattered on the entire surface of the involucre, but in most *Gorteria diffusa* populations the phyllaries are found only on the upper two-thirds of the involucre, which gives them a characteristic “naked” involucre base. All *Gorteria* taxa except *G. alienata* and *G. integrifolia* have strongly lignified mature involucre. The seeds, which never leave the involucre, sprout from within it and the root always penetrates the strongly lignified involucre through its base (abscission zone) where it is somewhat softer. In the less lignified mature involucre of *G. alienata* and *G. integrifolia* the root is able to penetrate the involucre wall anywhere (Stångberg 2009). If there are many phyllaries and hairs the shape of the involucre may be concealed. The involucre is campanulate or urceolate, but in *G. parviligulata* and in some populations of *G. diffusa* the involucre becomes more spherical (globose) after anthesis as it becomes lignified.

The phyllaries provide many taxonomically important characters in *Gorteria*. Their shape, pubescence and direction vary among the species, but sometimes the character states are dependent on the position of the phyllaries on the involucre. The shape of the phyllaries is generally linear-triangular but narrower and almost setiform in *G. corymbosa*, *G. integrifolia*, *G. parviligulata* and *G. warmbadica*. In general, the phyllaries become longer towards the inner phyllaries but in some cases (*G. piloselloides* and some populations of *G. diffusa*) the innermost phyllaries instead become wider. In *G. diffusa* different populations show differences in phyllary morphology, but it is common that the middle phyllaries are the widest and that they also are slightly declinate after anthesis (Fig. 4A), whereas in some *G. diffusa* (from the “Middle” area), *G. integrifolia*, *G. parviligulata* and *G. piloselloides*, instead the innermost phyllaries are declinate after anthesis. In some populations of *G. diffusa* the margins on the innermost phyllaries are provided with narrowly thorn-like acute lateral lobes (Fig. 3G). It is easy to mistake these

lobes for rigid longitudinally striate hairs, which also occur on the phyllaries, but the lobes have veins and are sometimes hairy and/or provided with minute secondary lobes. The other taxa are very different in the degree of pubescence on the phyllaries, varying from hispid (Fig. 3H) to villous (Fig. 3I). In *G. alienata* the margins of the phyllaries, at least the innermost phyllaries, have membranous serrulate margins, as in most *Gazania* species.

It is interesting to note that, because the entire capitulum functions as a diaspore in *Gorteria*, this has also been subject to selection leading to differentiation in size, shape and possibly function in different lineages. This is normally not the case in other groups of the *Asteraceae*, where involucre remains attached and merely act as a platform for the dispersing cypselas.

Receptacle — As with all members of *Gorteriinae*, *Gorteria* has alveolate receptacles that in all species become lignified after anthesis. In most other *Gorteriinae* genera (*Berkheya*, *Cullumia*, *Cuspidia*, *Didelta* and *Heterorhachis*) the cypselas are totally enclosed in the alveoles (Roessler 1959), whereas in *Gazania*, *Gorteria* and “*Hirpicium*” only the most basal part of the cypselas is enclosed in the 0.5–2 mm-deep alveole, (1–2 mm deep in *Gorteria*). In the herbaceous *Gorteria* taxa the central alveoles are inconspicuous. Reduced alveoles are plesiomorphic in *Gorteria* and the heavy lignification of the involucre may be a response to the loss of seed protection that other taxa receive from the alveoles.

Ray florets — The ray florets are neuter with inconspicuous staminodes. No other organ in *Gorteria* is subject to a larger variation in shape, colour, spot pattern etc. (Ellis & Johnson 2009; Stångberg & al. 2013). Even though the number of ray florets varies to some extent between individuals in a population, it is more or less constantly 5 (Fig. 2H), 8 (Fig. 2A, C, F, I, J, L) or 13 (Fig. 2B, D, E, G, K). The subtribe *Gorteriinae* is unique in having a 4-lobed ray floret lamina, or “*Gorteriinae*-rays” (Bremer 1988; 1994; Karis & al. 1992). In this character *Gorteria* is no exception, but in *G. personata*, with its small ray florets, the number of lobes is reduced to 3. Most species have a narrowly elliptic ray floret lamina, but the short lamina of *G. personata* is narrowly obovate and in *G. diffusa* the lamina shape varies from obovate to narrowly elliptic and obtuse to acute, respectively. All species except for *G. diffusa* have yellow ray florets but populations and individuals with orange-coloured rays can also be found in *G. piloselloides*. There is significant variation in colour in *G. diffusa*, from sulphur yellow to bright orange to brownish orange, and in eight-rayed populations of *G. diffusa* the range is between white and yellow. In the species with orange ray florets, their lamina may have a basal brown to blackish spot, or merely more or less equally two-coloured. A spot pattern on petals is found in several angiosperm families (e.g. *Ericaceae*, *Geraniaceae* and *Iridaceae*) (Thomas & al. 2009). Presence of dark

spots basally on ray florets occurs in several South African *Asteraceae* genera representing different tribes, e.g. *Ursinia* Gaertn. (*Anthemideae*), *Dimorphotheca* Moench and *Osteospermum* L. (*Calenduleae*) and *Arctotis* L., *Gazania* and *Gorteria* (*Arctotideae*) (le Roux 2005). Exceptional among these species are some populations of *Gorteria diffusa* in which only a subset of the ray florets (1–5 out of 8 or 13 florets) is provided with dark spots. Another peculiar feature of these spots is their anatomy: differently shaped epidermal cells generate their characteristic three-dimensional form, which yields the raised spots. The spot morphology and development was investigated by Thomas & al. (2009). There are also populations of “Northern” *G. diffusa* in which the dimorphism in ray florets is even more complex; the ray florets with spots are also significantly smaller, erect and sometimes lighter coloured than the other ray florets. Diversity in spot pattern in *Gorteria* was discussed in Ellis & Johnson (2009) regarding possible pollinator-driven evolution of the many different colour and spot morphotypes. Some populations of “Northern” *G. diffusa*, in which all ray florets are spotted, have raised spots, but not necessarily because of complexity in the epidermal cells, but rather because the ray floret lamina is bent and gives the spot area a raised appearance.

In *Gorteria parvilligulata*, *G. personata* and *G. piloselloides*, on the other hand, the dark spots are present on all ray florets exactly as in the other *Asteraceae* genera mentioned above (there is also *G. piloselloides* without any spots, in same populations as spotted individuals). The dark spots, raised or not, are provided with white dots with variation in number between populations, which were described by Johnson & Midgley (1997) as UV-reflective. The ray florets are only rarely provided with glandular hairs, but all *Gorteria* have some longitudinally striate hairs on the abaxial side of the ray florets. These hairs are inconspicuous and sparsely scattered on the surface, but in some populations of *G. diffusa* the hairs, which congregate more densely distally, are characteristic.

Disc florets — The number of disc florets varies between 10 and 50 per capitulum among the species in *Gorteria*. The disc florets in subtribe *Gorteriinae* are, in contrast to the *Arctotideae*, deeply lobed. The lobes are slightly differently sized, which makes the corolla somewhat zygomorphic. The disc floret corollas are always provided with longitudinally striate hairs, on the lobes and also further down on the tube, but the difference in size and quantity makes them more or less conspicuous (Fig. 3C, L). Among the longitudinally striate hairs, there are also glandular hairs (Fig. 3F).

Anthers and pollen — Anthers in *Gorteria* are calcarate, ecaudate, with a triangular sterile apex with fringed margins, and the endothelial tissue exhibits cell-thickening without a plate (cf. endothelial cells containing plates in the *Berkheya* clade, Karis 2006). The pollen morphology

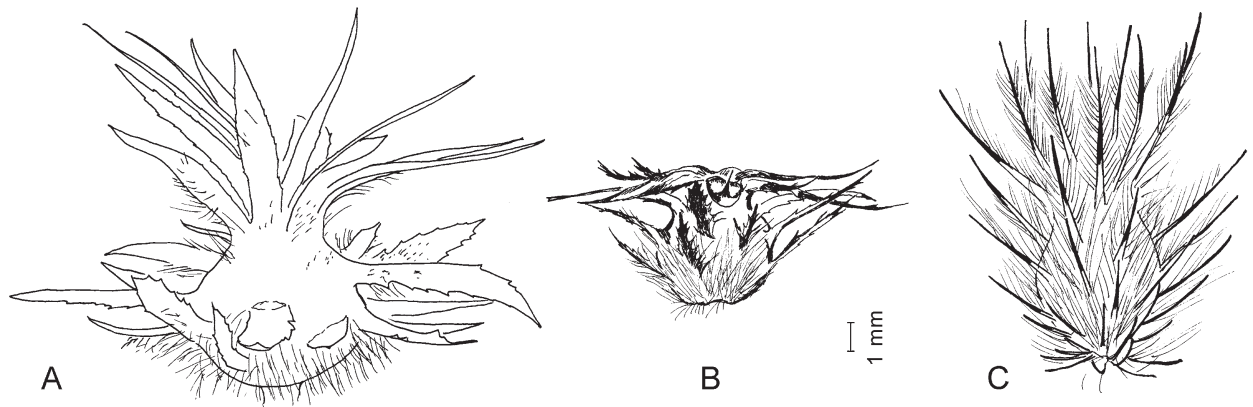


Fig. 4. Direction of phyllaries on mature involucres of *Gorteria*. – A: middle phyllaries become slightly declinate after anthesis (*G. diffusa*); B: innermost phyllaries become slightly declinate after anthesis (*G. diffusa*); C: all phyllaries remain erecto-patent after anthesis (*G. warmbadica*). – Scale bar = 1 mm. – Drawn by F. Stångberg from Stångberg 126 (S), Stångberg 93 (S) and Bartsch 1879 (WIND).

in *Gorteriinae* was investigated by Leins & Thyret (1971) and Wortley & al. (2008), and both studies showed that *Gazania*, *Gorteria* and “*Hirpicium*” have the same type of lophate pollen grains.

Styles — *Gazania*, *Gorteria* and “*Hirpicium*” have styles with the same type of subulate-ensiform sweeping hairs and style branches tapering towards the apex, as in other *Gorteriinae* (Karis 2006). In herbaceous *Gorteria* taxa the style is almost undivided in the central-most disc florets and is gradually more deeply cleft, to c. 1/3 of the style length, towards the periphery. In woody *Gorteria* taxa the degree of bifurcation seems to be constant within one capitulum but never deeper than c. 1/10. In these species only one or few cypselas develop; therefore it is possible that there is variation in style function. The evolution of functionally male florets is of great importance in that it allows one involucre to contain only one or a few mature cypselas, thereby reducing potential competition among seedlings that germinate from the same diaspore, especially in the woody species.

Cypselas — In the herbaceous *Gorteria* taxa only the most peripheral ovaries develop into mature cypselas because the central disc florets are functionally male. The cypselas are pear-shaped with the base strongly constricted and curved towards the centre of the capitulum. The fact that the cypselas are tightly packed makes the sides facing the neighbouring cypselas slightly flattened, similar to garlic cloves (Fig. 3O).

In capitula of *Gorteria alienata* and *G. integrifolia* only 1 or 2 cypselas reach maturity, and because the cypselas are not pressed against each other they have all sides more or less convex making the cypselas turbinate, but the cypselas shape is obscured by the many twin hairs that cover the surface.

Ovaries in the central disc florets, which never develop into cypselas, are tube-shaped in all species. Both ovaries and ripening cypselas in all species are villous

with twin hairs to some extent but both the degree of coverage and density varies. In *Gorteria alienata* and *G. integrifolia*, the entire cypselas surface is densely covered with twin hairs. In the other species, the twin hairs cover only the distal part of the cypselas, occasionally more, and only sparsely so (Fig. 3O). In addition, the twin hairs are twisted to varying extents in different individuals.

In *Gazania* and “*Hirpicium*”, the cypselas have large globose glands, arranged in longitudinal rows (Reese 1989). In *Gorteria* the glands are irregularly scattered on the cypselas surface. In most *Asteraceae* species the cypselas function as a diaspore. As this is not the case in *Gorteria*, the plesiomorphic characters associated with the cypselas (twin hairs, glands and pappus) have lost their function and have become more or less reduced.

Pappus — In all herbaceous species the pappus is either absent or varies from absent to forming a small fringed crown (Fig. 3N). In *Gorteria alienata* and *G. integrifolia* the pappus consists of two series of distinct scales (Fig. 3M).

Taxonomy

Gorteria L., Syst. Nat., ed. 10, 2: 1229. 1759 = *Personaria* Lam., Tabl. Encycl. 2: t. 716. 1797. – Type: *Gorteria personata* L.

= *Ictinus* Cass. in Bull. Sci. Soc. Philom. Paris 1818: 142. 1818. – Type: *Ictinus piloselloides* Cass. (= *Gorteria piloselloides* (Cass.) Stångb. & Anderb.).

= *Hirpicium* Cass. in Bull. Sci. Soc. Philom. Paris 1820: 27. 1820. – Type: *Hirpicium alienatum* (Thunb.) Druce (= *Oedera alienata* Thunb. = *Gorteria alienata* (Thunb.) Stångb. & Anderb.).

Description — Annual herbs or shrublets. Young stems terete, ± hispid, sparsely tomentose with whitish woolly hairs; hairs whitish, rarely with reddish or black base,

longitudinally striate, 1–2 mm long. *Leaves* alternate, sessile, margins revolute, upper surface and midvein abaxially densely or rarely sparsely hispid; hairs whitish, longitudinally striate, 0.5–2 mm long; abaxial surface (except for midvein) densely tomentose with whitish woolly hairs. *Capitula* solitary, terminal, heterogamous, radiate. *Involucre* tomentose and ± hispid to white silky, with longitudinally striate hairs, ± lignified with age, enclosing cypselas, falling off and functioning as diaspore, lignified capitulum with 1(–5) seedlings sprouting from within. *Receptacle* epaleate, with 1–2 mm-deep alveoles. *Phyllaries* pluriseriate, basally connate, sparsely whitish tomentose. *Ray florets* neuter with inconspicuous staminodes, pale yellow-orange, with or without dark spots adaxially, abaxially with scattered short longitudinally striate hairs. *Disc floret corolla* deeply 5-lobed, somewhat zygomorphic, ± covered with both longitudinally striate hairs and glandular hairs. *Anthers* ecaudate, with triangular sterile apex with fringed margins; endothelial tissue without wall thickenings. *Cypselas* enclosed in involucre, most basal parts enclosed in alveoles, ± pubescent with twisted twin hairs. *Pappus* biseriate with scales, a uniseriate fringed crown, or absent, concealed by cypselas hairs.

Phenology — According to the specimens found during field studies and the examined herbarium material, flowering specimens of all species of *Gorteria* have been collected from August to October, mainly in September, except for *G. warmbadica*, which has been collected from March to September but mainly in May and June. Herbarium specimens not in flower are extremely rare.

Distribution — The genus contains eight species in South Africa distributed in the Western Cape and Northern Cape provinces (a few specimens have been collected in the Eastern Cape province), and in Namibia in the !Karas region, in the winter and year-round rainfall zones (Fig. 5). For a more extensive treatment of the distribution of *Gorteria alienata*, including localities from Roessler’s (1959) study, see Appendix 2.

Remarks — The inclusion of *Hirpicium alienatum*, the type of *Hirpicium*, in *Gorteria*, renders *Hirpicium* a synonym of *Gorteria* and leaves the remaining *Hirpicium* species unassigned to a genus. These species are the subject of an ongoing study that will be the topic of a forthcoming paper. When Cassini described the genus *Hirpicium* he also described the species *H. echinulatum*, in the synonymy of which he cited Thunberg’s earlier name *Oedera alienata*, thereby rendering the name *H. echinulatum* illegitimate.

Key to the species of *Gorteria*

- 1. Woody shrublets 2
- Annual herbs 4

- 2. Ray florets adaxially with dark spots *G. diffusa* p.p.
- Ray florets adaxially without dark spots 3
- 3. Phyllaries setiform, densely hispid 3. *G. integrifolia*
- Phyllaries narrowly triangular, sparsely hispid 4. *G. alienata*
- 4. Ray florets 5(or 6) 5. *G. piloselloides* p.p.
- Ray florets generally either (7 or)8(or 9) or (12 or)13(or 14) 5
- 5. Ray florets generally (12 or)13(or 14) 6
- Ray florets generally (7 or)8(or 9) 7
- 6. Outermost phyllaries setiform, ray florets adaxially without spots 8. *G. warmbadica*
- Phyllaries, triangular to narrowly triangular, 1 to all ray florets adaxially with dark spots 2. *G. diffusa* p.p.
- 7. Ray florets shorter than or equalling phyllaries 8
- Ray florets distinctly longer than phyllaries 9
- 8. Phyllaries hard, pungent 1. *G. personata*
- Phyllaries flexible, soft 7. *G. parviligulata*
- 9. Phyllaries setiform 6. *G. corymbosa*
- Phyllaries triangular or narrowly triangular, not setiform 10
- 10. Phyllaries < 25, innermost narrowly triangular, acute 2. *G. diffusa* p.p.
- Phyllaries > 35, innermost triangular, acuminate 5. *G. piloselloides* p.p.

1. *Gorteria personata* L., Syst. Nat., ed. 10, 2: 1229. 1759 ≡ *Personaria personata* (L.) Poir., Encycl. Suppl. 4: 369. 1816. – Lectotype (designated by Roessler 1959: 321): Herb. Linn No. 1027.1 (LINN!).

Description — *Herbs* annual, erect or rarely decumbent, (3–)9–15(–35) cm tall, basally branched, rarely branched also in distal part of shoots or unbranched. *Stems* green or reddish, densely patently hispid. *Basal leaves* 32–90 × 2–13 mm; *cauline leaves* (5–)10–50 × (1–)2–7(–10) mm, gradually smaller distally, narrowly obovate, entire or pinnatifid and incised to c. ¼ of width, adaxially densely hispid. *Capitula* (10–)15(–18) mm in diam. *Involucre* urceolate, ± lignified already at anthesis, free parts of phyllaries covering entire involucre. *Phyllaries* c. 40, pungent, midvein rigid, lignified already during anthesis, green or reddish with dark apices; *outermost phyllaries* c. 3.5 × 1 mm, narrowly triangular, with whitish hispid margins, somewhat subulate, erecto-patent, gradually longer towards inner phyllaries, less hispid, erect; *innermost phyllaries* c. 8 × 1.5 mm, narrowly triangular, acuminate. *Ray florets* (7–)8(–9), (7–)9(–10) × 1–2 mm, shorter than phyllaries, narrowly obovate, 3-lobed, adaxially yellow with black spot at base, black spot sometimes with white dot (spot not raised), abaxially brownish. *Disc florets* 9–15, yellow, peripheral florets hermaphroditic, central florets functionally male.

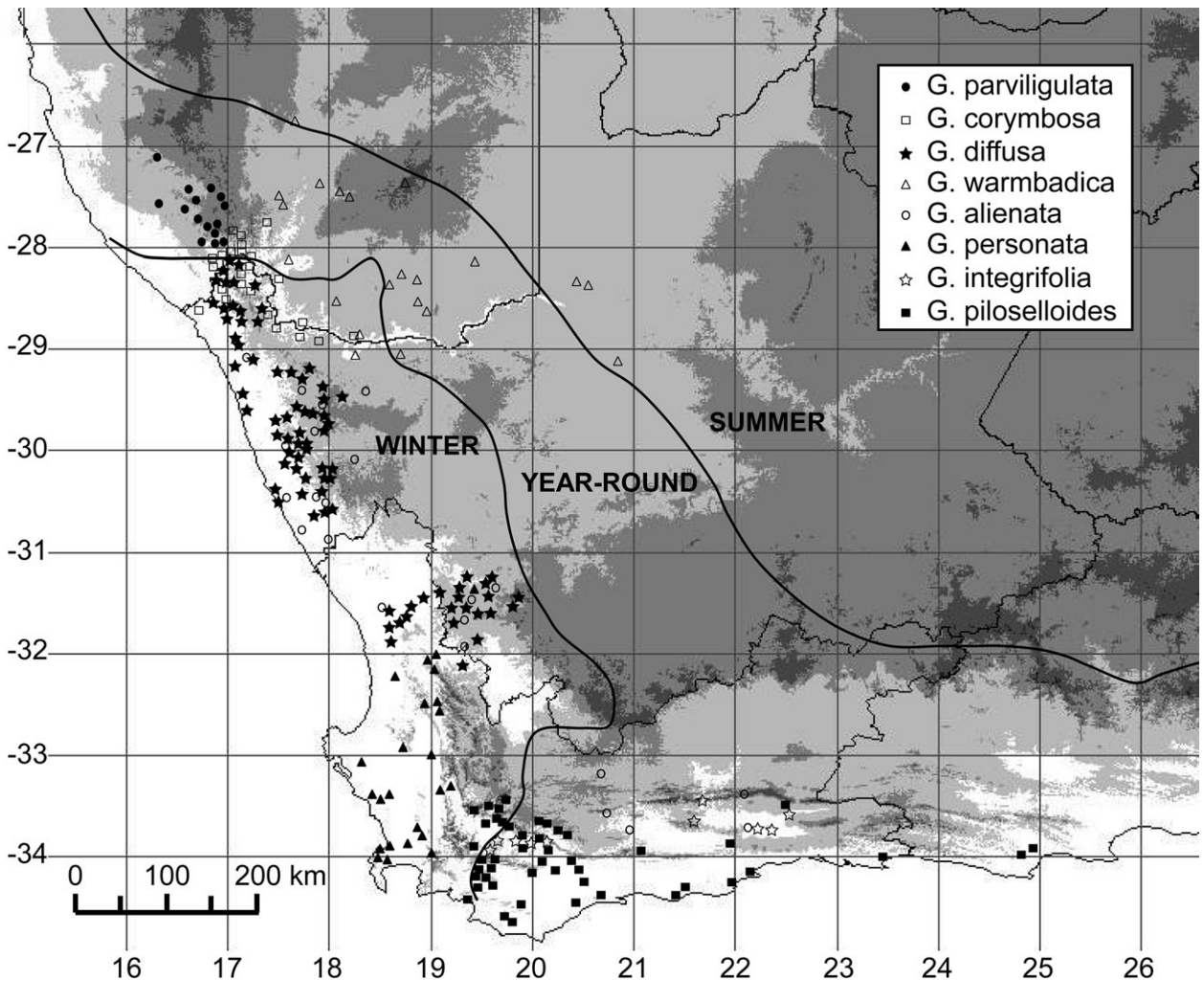


Fig. 5. Distributions of the species of *Gorteria*. Approximate boundaries of the different rainfall zones are indicated (based on Chase & Meadows 2007).

Style ± bifurcate (less so towards centre of disc). *Cypsel*a 4–6 mm long, asymmetrically pyriform, adaxially flattened, not ribbed, basally glabrous, distal ½ villous, occasionally with few small globose glands, twin hairs twisted. *Pappus* a minute fringed crown.

Diagnostic features — *Gorteria personata* is characterized by 8 ray florets with a basal dark spot; the phyllaries are hard and pungent already at anthesis and extend beyond the ray florets.

Distribution — South Africa: Western Cape province, in the winter rainfall zone, from Cape Flats to Clanwilliam.

2. *Gorteria diffusa* Thunb. in Skr. Naturhist.-Selsk. 4(2): 2, t. 2. 1798 ≡ *Gazania diffusa* (Thunb.) Spreng., Syst. Veg. 3: 606. 1826. – Holotype: *Thunberg s.n.* (UPS-THUNB 20512!).
= *Gorteria affinis* DC., Prodr. 6: 501. 1838 ≡ *Gorteria diffusa* var. *intermedia* Harv., Fl. Cap. 3: 470. 1865. – **Lecto-**

type (designated here): Klein Namaqualand, *Drège 494* (G-DC G00203749!).

= *Gorteria calendulacea* DC., Prodr. 6: 501. 1838 ≡ *Gorteria diffusa* var. *calendulacea* (DC.) Roessler in Mitt. Bot. Staatssamml. München 3: 327. 1959 ≡ *Gorteria diffusa* subsp. *calendulacea* (DC.) Roessler in Mitt. Bot. Staatssamml. München 11: 93. 1973. – Holotype: Cap Bonæ-Spei ad Leeuweberg, *Drège 494* (G-DC G00202219!).
– “*Chrysostemma calendulacea* E. Mey.” in Candolle, Prodr. 6: 501. 1838, nom. inval., pro syn. sub *Gorteria calendulacea*.

Description — *Herbs* annual, decumbent or rarely erect, rarely *shrublets*, 2–20 cm tall, basally branched, and often branched also in distal part of shoots, rarely unbranched. *Stems* reddish or green, densely patently hispid or strigose, hairs whitish, rarely reddish. *Basal leaves* 25–90 × 2–10 mm; *cauline leaves* (4–)12–42(–50) × (1–)2–7(–10) mm, gradually smaller distally, narrowly obovate, entire or sometimes pinnatifid and incised to c. ¼ of width, adaxially densely hispid. *Capitula* (20–)30–55 mm in diam. *Involucre* urceolate, becom-

ing lignified and sometimes globose with age, free part of phyllaries covering entire or c. $\frac{2}{3}$ of distal part of involucre. *Phyllaries* (18–)20–32, flexible, green or reddish with reddish or black apices, erecto-patent to erect, sometimes becoming patent or declinate after anthesis; *outermost phyllaries* 3–6(–8) \times 0.5–1.3 mm, narrowly triangular or linear-triangular, hispid to villous, with whitish to black hairs, sometimes becoming patent after anthesis, gradually longer, narrower and less pubescent towards inner phyllaries; *middlemost phyllaries* 4–8(–9) \times 0.5–1.8 mm, linear or narrowly triangular, elliptic or narrowly obovate and rarely truncate, becoming patent or slightly declinate-patent or staying erecto-patent after anthesis, sometimes with narrowly thorn-like pungent acute lobes; *innermost phyllaries* 4–10(–13) \times 0.4–1.3 mm, triangular to linear-triangular, sometimes becoming declinate after anthesis, hispid and sometimes with narrowly thorn-like acute lateral lobes, lobes basally hispid. *Ray florets* (7–)8(–9) or (12–)13(–14), 10–23 \times (2–)3–6 mm, longer than phyllaries, rarely equal in length; lamina elliptic, narrowly elliptic or obovate, base flat or curved in one series but with some overlapping, or in two series, apex obtuse or acute, 4-lobed; *ray floret colour* very variable, adaxially yellowish white, bright yellow, sulphur yellow, bright orange, or reddish orange, rarely two-coloured yellowish white and bright yellow, or bright orange and brown; lamina base adaxially with or without bright yellow markings, with or without dark spots; dark lamina spots flat or sometimes raised, on 1 to all ray florets (spotted ray florets sometimes significantly smaller, sometimes brighter in colour and more erect); black raised spots with 1–4 white dots, abaxially green, brown, purple or black, striped, completely coloured or spotted, corolla hairs sometimes dense abaxially. *Disc florets* 30–40, yellow, lobes sometimes orange, peripheral florets hermaphroditic, central florets functionally male, corolla hairs sometimes longer and more dense distally, glandular hairs few to many. *Style* \pm bifurcate (less so towards centre of disc). *Cypsela* c. 4 mm long, asymmetrically pyriform, adaxially flattened, not ribbed, basally glabrous, distal $\frac{1}{3}$ villous, sometimes upper $\frac{1}{6}$ glabrous, \pm covered with small globose glands, twin hairs twisted. *Pappus* absent or a minute fringed crown.

Diagnostic features — *Gorteria diffusa* with 13 ray florets is distinguished from *G. corymbosa* (8 ray florets), *G. parviligulata* (8 ray florets), *G. personata* (8 ray florets) and *G. piloselloides* (8 or 5 ray florets) by the number of ray florets and from *G. alienata*, *G. integrifolia* and *G. warmbadica* by the spots on the ray florets (*G. diffusa* with 13 ray florets always has spots, whereas *G. alienata*, *G. integrifolia* and *G. warmbadica* never have spots). *Gorteria diffusa* with 8 ray florets (always from Richtersveld) is distinguished from *G. alienata* (13 ray florets), *G. integrifolia* (13 ray florets) and *G. warmbadica* (13 ray florets) by the number of ray florets, and by the length of the ray florets compared to the involucre from *G. parvi-*

ligulata and *G. personata* (ray florets do not extend beyond the involucre). *Gorteria diffusa* with 8 ray florets is distinguished from *G. corymbosa* and *G. piloselloides* by the shapes of the innermost phyllaries, which are triangular with narrowly thorn-like acute lobes, linear-triangular and triangular-acuminate, respectively. The area where the type was collected (see Remarks) corresponds to the area we refer to as “Middle”. Plants from this area can be recognized by always having 13 ray florets with an orange lamina, always 1–4 dark raised spots per capitulum and the spots always display only one white dot. *Gorteria diffusa* from further north in Namaqualand has 13 ray florets with a dark orange, orange, yellow or sulphur yellow lamina always with some kind of spot pattern, but in the Richtersveld, close to the Namibian border, *G. diffusa* has only 8 ray florets with a yellow or yellowish white lamina with or without spots.

Distribution — South Africa: Western Cape and Northern Cape provinces, in the winter rainfall zone, from Clanwilliam to Gariep (Orange) River.

Remarks — Of Thunberg’s specimens the one that constitutes the type of *Gorteria diffusa* is illustrated in Thunberg (1798: t. 2) and therefore this particular specimen (*Thunberg s.n.*, UPS-THUNB 20512!) can be considered the holotype as it was selected by the author. This is a 13-rayed specimen without any locality information on the label. It was collected by Thunberg himself and since his travelling routes are known (Karsten 1939) this specimen must originate from somewhere between Clanwilliam in the Western Cape (no 13-rayed *G. diffusa* has been collected further south) to Hantamsberg in the Northern Cape (Thunberg did not travel further north). The type material cited in the protologue of *G. affinis* is not cited exactly as on the labels on the herbarium sheet in G-DC. The protologue states “in Africa Capensi ad Olifant-rivier et Klein Namaqualand (Drege, Eckl.!)”, whereas the labels provide the following information: “N. 8Z1. 73 Namaqualand, m Eklon 1835” (G-DC G00202221!), “494. Klein Namaqualand. R. II III. m Drege 1835” (G-DC G00203749!) and “494. Olifant-rivier m Drege R.I. 1835” (G-DC G00202222!). Morphologically, the specimen from Olifant-rivier is similar to Thunberg’s holotype of *G. diffusa* (UPS-THUNB 20512!). The specimen best preserved is chosen here as the lectotype. The number “494” is apparently not a unique identification number. It is also important to note that the only material cited by Candolle (1838) (“Eckl.!”) as representing *G. diffusa* is the holotype of *G. personata* subsp. *gracilis*.

3. *Gorteria integrifolia* Thunb. in Skr. Naturhist.-Selsk. 4(2): 9, t. 2. 1798 \equiv *Hirpicium integrifolium* (Thunb.) Less., Syn. Gen. Compos.: 53. 1832 \equiv *Gazania integrifolia* (Thunb.) Spreng., Syst. Veg. 3: 606. 1826 – Holotype: *Thunberg s.n.* (UPS-THUNB 20513!).

Description — *Shrublets* 25–60 cm tall. *Young stems* reddish, ± densely patently hispid. *Leaves* (7–)10–20(–25) × 1–3 mm, oblong, entire, mucronate, on older branches leaves congregated on brachyblasts, adaxially hispid, leaf base always with a few longer hairs c. 1.5 mm long. *Capitula* c. 30 mm in diam. *Involucre* narrowly campanulate to cylindrical, somewhat lignified with age, free parts of phyllaries covering entire involucre. *Phyllaries* (30–)40–45(–65), flexible, densely whitish hispid, erect to erecto-patent, linear-triangular, gradually longer towards inner phyllaries; *outermost phyllaries* c. 5 × 0.25 mm; *innermost phyllaries* 8–12 × 0.25–0.7 mm, setiform. *Ray florets* 13(–18), c. 20 × 4 mm, longer than phyllaries, narrowly elliptic, 4-lobed, adaxially yellow to orange, abaxially with a median brownish stripe. *Disc florets* c. 15, yellow, 1 or 2 florets hermaphroditic, other florets functionally male. *Style* ± bifurcate (less so towards centre of disc). *Cypsela* c. 5 mm long, turbinate to asymmetrically pyriform, adaxially flattened, slightly ribbed, densely villous, without globose glands, twin hairs not twisted. *Pappus* of scales, biseriate, 10+10, 0.5–1 mm long, somewhat shorter towards centre of capitulum, scales triangular to narrowly triangular, sometimes irregularly dentate, innermost somewhat narrower than outer.

Diagnostic features — *Gorteria integrifolia* is characterized by its shrubby life form in combination with hairy, setiform (bristle-like) phyllaries.

Distribution — South Africa: Western Cape province, in the year-round rainfall zone, from Langeberg to Oudtshoorn.

Remarks — Of the specimens in Thunberg's herbarium the one that constitutes the type of *Gorteria integrifolia* is illustrated in Thunberg (1798: t. 2) and therefore this particular specimen (*Thunberg s.n.*, UPS-THUNB 20513!) can be considered the holotype as it was selected by the author.

4. *Gorteria alienata* (Thunb.) Stångb. & Anderb., **comb. nov.** ≡ *Oedera alienata* Thunb., Prodr. Pl. Cap.: 169. 1800. ≡ *Hirpicium echinulatum* Cass. in Bull. Sci. Soc. Philom. Paris 1820: 27. 1820, nom. illeg. ≡ *Hirpicium alienatum* (Thunb.) Druce in Rep. Bot. Soc. Exch. Club Brit. Isles 1916: 628. 1917 – **Lectotype (designated here):** *Thunberg s.n.* (UPS-THUNB 20929!).

Description — *Shrublets* 25–60 cm tall. *Young stems* reddish, sparsely patently hispid, rarely glabrous. *Leaves* 4–15 × 1–2 mm, oblong, entire, mucronate, on older parts leaves congregated on brachyblasts, margins strongly revolute (woolly hairs abaxially often hidden by revolute margins), adaxially hispid to almost glabrous with only scattered hairs c. 1 mm long, leaf base always with

a few longer hairs c. 1.5 mm long. *Capitula* c. 40 mm in diam. *Involucre* campanulate, becoming somewhat lignified with age, free parts of phyllaries covering entire involucre. *Phyllaries* 25–35(–40), midveins becoming strongly lignified, sparsely hispid, hispid to serrulate on margins, erecto-patent to patent, narrowly triangular, gradually longer towards inner phyllaries; *outermost phyllaries* 2.5–5 × c. 0.7 mm; *innermost phyllaries* 5–11 × 1–1.7 mm, narrowly triangular to linear-triangular, sometimes acuminate, margins membranous, serrulate. *Ray florets* (12–)13(–14), 20–30 × 3–7 mm, longer than phyllaries, narrowly elliptic, 4-lobed, adaxially yellow, base adaxially with or without bright yellow markings, abaxially with a median blackish or brownish stripe, occasionally glandular hairs. *Disc florets* 20–30(–40), yellow, 1 or 2 florets hermaphroditic, other florets functionally male. *Anther endothecium* sometimes with a rectangular crystal in each cell. *Styles* equally bifurcate. *Cypsela* c. 3 mm long, turbinate, not ribbed, densely villous, concealed by twin hairs, scattered with globose glands, twin hairs not twisted. *Pappus* of scales, biseriate, 10+10, outermost 3–8 mm long, narrowly triangular, irregularly lobed, acuminate, with serrulate margins, innermost much smaller than outer, c. 0.4 mm long, subulate.

Diagnostic features — *Gorteria alienata* is characterized by its shrubby life form and triangular phyllaries, the innermost ones with membranous margins.

Distribution — South Africa: Western Cape and Northern Cape provinces, in the winter and year-round rainfall zones. One record is from Eastern Cape province (see Appendix 2).

Remarks — In the molecular phylogeny of Stångb. & al. (2013) *Gorteria alienata* was shown to be paraphyletic with the samples collected in the year-round rainfall zone of the Western Cape more closely related to *G. integrifolia*, from the same area, than to *G. alienata* from the winter rainfall zone. While we do not advocate recognition of paraphyletic taxa, resolution of the problem requires a detailed study of the relationships within this complex group before changes in species delimitation are contemplated. As these two species were not part of our original focus, as *Hirpicium* species, we are content, for now, with transferring them to *Gorteria*.

5. *Gorteria piloselloides* (Cass.) Stångb. & Anderb., **comb. nov.** ≡ *Ictinus piloselloides* Cass. in Bull. Sci. Soc. Philom. Paris 1818: 142. 1818 ≡ *Gorteria ictinus* Cass. in Cuvier, Dict. Sci. Nat. 33: 455. 1824, nom. illeg. ≡ *Ictinus gorterioides* Cass. ex Steud., Nomencl. Bot., ed. 2, 1: 801. 1840. – Holotype: Cap de Bonne-Espérance, *Sonnerat s.n.* (P-JU P00307455 image!). = *Gorteria personata* subsp. *gracilis* Roessler in Mitt.

Bot. Staatssamml. München 3: 323. 1959. – Holotype: Caledon, Ecklon & Zeyher 51.8 sub. nom. *Gorteria diffusa* Thunb. (G-DC G00023609!; isotypes: S S-G-9769!, S S07-9442!, S S07-9443!).

Description — *Herbs* annual, decumbent or rarely erect, 3–25 cm tall, basally branched, sometimes branched also in distal part of shoots, rarely unbranched. *Stems* reddish, densely patently hispid. *Basal leaves* 20–105(–120) × (1–)3–10 mm; *cauline leaves* (5–)8–32 × (0.5–)2–11 mm, gradually smaller distally, narrowly obovate to obovate, entire or pinnatifid, lobes incised to c. 1/3 of width, adaxially densely hispid. *Capitula* 10–20 or 30–45 mm in diam. *Involucre* at first campanulate, becoming lignified and urceolate with age, free parts of phyllaries covering entire involucre. *Phyllaries* (15–)20 or 35–45, flexible, green or green and reddish, whitish hispid, erecto-patent; *outermost phyllaries* 3–6 × 0.5–0.8 mm, narrowly triangular, gradually broader triangular towards inner phyllaries; *innermost phyllaries* 4–10 × 1.3–2 mm, triangular, acuminate, sometimes becoming patent after anthesis. *Ray florets* 5(–6) or (7–)8(–9), (6–)8–18(–20) × (1.5–)2–4(–5) mm, longer than phyllaries, narrowly elliptic, 4-lobed, adaxially yellow or rarely orange, rarely with black base (not a raised spot), abaxially completely green or rarely yellow, or with a median green stripe, occasionally with longitudinally striate hairs and glandular hairs abaxially. *Disc florets* 8–10 or 15–25, yellow, rarely orange, peripheral florets hermaphroditic, central florets functionally male, corolla occasionally with longitudinally striate hairs and glandular hairs. *Style* ± bifurcate (less so towards centre of disc). *Cypselas* 2–4 mm long, asymmetrically pyriform, adaxially flattened, not ribbed, basally glabrous, distal 3/4 villous, occasionally with a few small globose glands, twin hairs twisted. *Pappus* c. 0.5 mm long, a fringed crown.

Diagnostic features — *Gorteria piloselloides* is characterized by 5 or 8 ray florets that extend beyond the phyllaries. The 8-rayed form could possibly be confused with 8-rayed *G. diffusa* from Richtersveld. In addition to the geographical separation they are morphologically distinguished i.a. by the innermost phyllaries, which are acuminate and triangular with lobes, respectively.

Distribution — South Africa: Western Cape province, mainly the year-round rainfall zone, from Paarl to Bitou and Overberg to Ceres. Two collections are from Humansdorp in Eastern Cape province.

Remarks — Populations of *Gorteria piloselloides* with 5 ray florets (former *G. personata* subsp. *gracilis*) are restricted to the Overberg and the S coast of Western Cape province, geographically separated from *G. piloselloides* with 8 ray florets (formerly *G. diffusa* from the “Southern” area) by the Rivieronderend Mountains.

6. *Gorteria corymbosa* DC., Prodr., 6: 501. 1838 – Holotype: Africa Capensis Regione Gariepina, Drège 2724 (G-DC G00202026!; possible isotypes: BM BM000924694-0, HAL HAL113457, HBG HBG504561, K K000307420, K K000307419, SAM SAM0017178, P P00153617, P P00153618, P P00153619, PRE PRE0217826-0, S! [s.n.], TUB TUB005886 [images of these possible isotypes seen]).

Description — *Herbs* annual, erect or decumbent, sometimes cushion-forming, 2–40 cm tall, basally branched, and often also in distal part of shoots, rarely unbranched. *Stems* green or rarely reddish, patently hispid. *Basal leaves* (35–)49(–75) × (3–)6(–10) mm; *cauline leaves* (4–)8–22(–52) × 1–3(–8) mm, gradually smaller distally, narrowly obovate, entire, adaxially densely hispid. *Capitula* (10–)15–20 mm in diam. *Involucre* narrowly urceolate, villous, becoming lignified with age, free parts of phyllaries covering entire involucre. *Phyllaries* 35–45(–50), flexible, reddish or green with reddish apices; *outermost phyllaries* setiform, 2–3 mm long, less than 0.5 mm wide (± formed by midvein only), erecto-patent, densely villous, hairs white, gradually longer and more erect towards inner phyllaries; *innermost phyllaries* 6–9 × c. 1 mm, linear-triangular, erecto-patent, hispid. *Ray florets* (7–)8(–9), c. 12 × 2 mm, longer than phyllaries, narrowly elliptic, 4-lobed, adaxially yellow, without darker basal spots, abaxially green, brown or rarely black, entirely or in stripes, corolla hairs more dense distally. *Disc florets* 20–30, yellow, peripheral florets hermaphroditic, central florets functionally male. *Style* ± bifurcate (less so towards centre of disc). *Cypselas* c. 4 mm long, asymmetrically pyriform, adaxially flattened, not ribbed, basally glabrous, distal 2/3 villous, scattered with small globose glands, twin hairs twisted. *Pappus* a minute fringed crown.

Diagnostic features — *Gorteria corymbosa* is recognized by 8 yellow ray florets without spots in combination with setiform (bristle-like) phyllaries.

Distribution — South Africa: Northern Cape province, and Namibia: !IKaras region, mainly in the winter rainfall zone, on both sides of the Gariep (Orange) River from Alexander Bay to Vioolsdrif.

Remarks — In the protologue Candolle stated “in Africa Capensis Regione Gariepina legit cl Drege!” as the type material. The herbarium label states “2724, Felsige Orte an Garip. RI m Drege 1835”. Drège’s (1843: 93) locality is more precise “Garip, auf stenigen und felsigen Höhen bei Verleptpram, unter 1000 Fuss, September”. Drège collected this plant in only one place (Drège 1843: 188), and material is present in several herbaria and may be isotypes. For taxa restricted to the lower Gariep River Nordenstam (1966, 1969) coined the term “Gariep elements”.

7. *Gorteria parviligulata* (Roessler) Stångb. & Anderb., **comb. & stat. nov.** ≡ *Gorteria diffusa* subsp. *parviligulata* Roessler in Mitt. Bot. Staatssamml. München 11: 92. 1973. – Holotype: Namibia, Zebrafontein, unten am Berghang des westlichen Bakenberges auf Witpütz-Süd, *Merxmüller & Giess 28763* (M; isotypes: PRE!, WIND!).

Description — *Herbs* annual, erect or decumbent, 5–11 cm tall, basally branched, rarely unbranched. *Stems* dark purple or rarely green, sparsely patently hispid, hairs whitish with dark bases. *Basal leaves* 30–60 × 2–9 mm; *cauline leaves* (5–)11–24 × (0.5–)1–5 mm, gradually smaller distally, entire, narrowly obovate, margins revolute (rarely flat), adaxially densely hispid. *Capitula* (8–)10(–15) mm in diam. *Involucre* urceolate, becoming lignified and globose with age, free parts of phyllaries covering entire involucre. *Phyllaries* c. 30, flexible, green, free parts blackish or rarely green, sometimes scattered with glandular hairs; *outermost phyllaries* c. 4 × 0.3 mm, linear-triangular, erecto-patent, whitish villous, hairs basally on margins c. 10 mm long, phyllaries gradually longer and less villous towards inner phyllaries; *innermost phyllaries* c. 8 × 0.8 mm, linear-triangular, at anthesis erecto-patent, becoming patent with age. *Ray florets* (7–)8(–9), 7(–8) × c. 2 mm, shorter than or equaling phyllaries, elliptic to narrowly obovate, 4-lobed, adaxially yellow with black basal spot (not raised), rarely also with small white dots, abaxially with a median brownish stripe, corolla hairs denser distally. *Disc florets* c. 10, yellow, peripheral florets hermaphroditic, central florets functionally male. *Anther endothecium* sometimes with a rectangular crystal in each cell. *Style* ± bifurcate (less so towards centre of disc). *Cypselas* c. 3 mm long, asymmetrically pyriform, adaxially flattened, not ribbed, basally glabrous, distal ½ villous, ± densely covered with small globose glands. *Pappus* a minute fringed crown.

Diagnostic features — *Gorteria parviligulata* is characterized by 8 yellow ray florets, all with a dark spot, phyllaries extending beyond the ray florets, and the involucre becoming globose after anthesis.

Distribution — Namibia: ||Karas region, in the year-round rainfall zone, from Rosh Pinah midway to Aus.

8. *Gorteria warmbadica* Stångb. & Anderb., **sp. nov.** – Holotype: Namibia, ||Karas region, between Karasburg and Warmbad, along main road, 28°42'55"S, 18°55'52"E, 872 m, 14 Jun 2005, *S. Bartsch, S. Loots & G. L. Maggs-Kölling 1879* sub. nom. *Gorteria corymbosa* DC. (WIND 87529.0!). – Fig. 6.

Description — *Herbs* annual, erect or decumbent, sometimes cushion-forming, 2–40 cm tall, branched basally and often also in distal part of shoots, rarely unbranched. *Stems* green or rarely reddish, patently

hispid. *Basal leaves* (30–)45–55(–75) × (2–)4(–8) mm; *cauline leaves* (7–)14–35(–55) × 1–4(–6) mm, gradually smaller distally, narrowly obovate, entire, adaxially densely hispid. *Capitula* (15–)20–25 mm in diam. *Involucre* urceolate (shape concealed by long white hairs), densely villous, becoming lignified with age, free parts of phyllaries covering entire involucre. *Phyllaries* (50–)60(–65), flexible, reddish black; *outermost phyllaries* setiform, 3–5 mm long, less than 0.5 mm wide (± formed by midvein only), erecto-patent, densely white villous, gradually longer and more erect towards inner phyllaries; *innermost phyllaries* 8–12 × c. 1 mm, linear-triangular, erecto-patent, hispid. *Ray florets* (12–)13(–14), c. 16 × 3 mm, longer than phyllaries, narrowly elliptic, 4-lobed, adaxially yellow, without darker basal spots, abaxially green, brown or rarely black, entirely or in stripes, corolla hairs more dense distally. *Disc florets* 20–30, yellow, peripheral florets hermaphroditic, central florets functionally male. *Style* ± bifurcate (less so towards centre of disc). *Cypselas* c. 4 mm long, asymmetrically pyriform, adaxially flattened, not ribbed, basally glabrous, distal ⅔ villous, scattered with small globose glands, twin hairs twisted. *Pappus* a minute fringed crown.

Diagnostic features — *Gorteria warmbadica* is distinguished from *G. corymbosa* by the number of ray florets, i.e. 13 versus 8, respectively, the shape of the involucre, geographical distribution, and flowering period (*G. warmbadica* flowers from March to September but mainly in May and June, whereas *G. corymbosa* flowers from July to November but mainly in September). The absence of dark spots on the ray florets distinguishes *G. warmbadica* from *G. diffusa*.

Distribution — Namibia: ||Karas region, and South Africa: Northern Cape province, mainly in the year-round rainfall zone. The collections in South Africa have been made close to the Namibian border from Goodhouse to Lutzputs.

Etymology — The specific epithet is derived from Warmbad, a locality in S Namibia, where several specimens of this plant, the type specimen included, have been collected.

Remarks — The description is based on material formerly classified as *Gorteria corymbosa*.

Excluded taxa

Gorteria acaulis hort. (1883) = *Haplocarpha leichtlinii* N. E. Br.

Gorteria arachnoidea hort. angl. ex Steud. (1840) = ? (planta dubia fide Steudel).

Gorteria araneosa Meerb. (1775/1782) = *Cuspidia ceruina* (L. f.) B. L. Burt

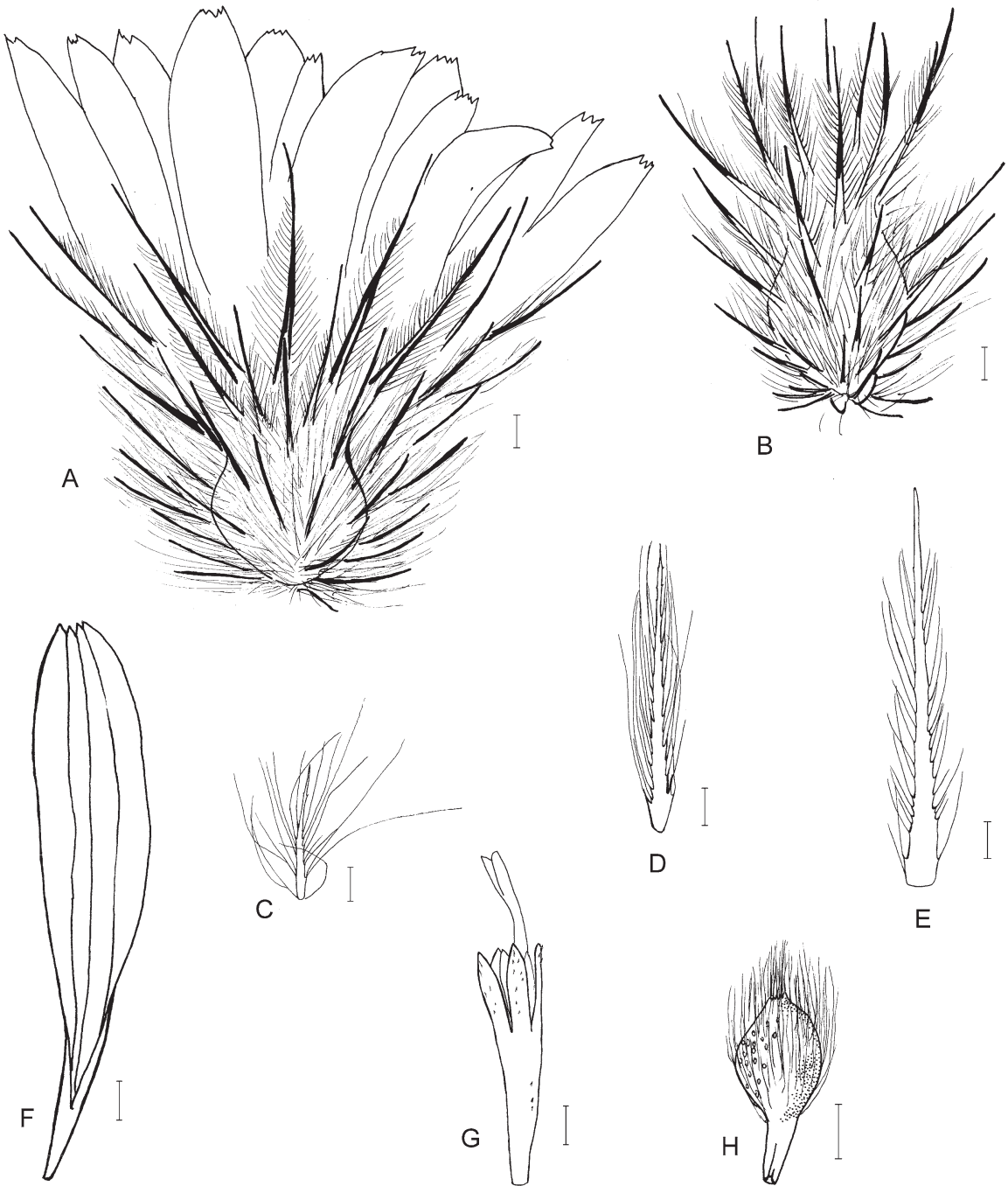


Fig. 6. *Gorteria warmbadica* – A: flowering capitulum; B: mature involucre; C: outermost phyllary; D: middlemost phyllary; E: innermost phyllary; F: ray floret; G: disc floret; H: cypselum. – Scale bars = 1 mm. – Drawn by F. Stångberg from *Bartsch 1879* (WIND) (A, F, G), *Middlemost 1959* (NBG) (B, H) and *Örtendahl 221* (UPS) (C, D, E).

Gorteria asteroides L. f. (1782) = *Berkheya fruticosa* (L.) Ehrh.

Gorteria asteroites Jacq. ex Steud. (1840) = *Berkheya fruticosa* (L.) Ehrh.

Gorteria barbata L. f. (1782) = *Berkheya barbata* (L. f.) Hutch.

Gorteria carthamoides Lam. (1789) = *Berkheya barbata* (L. f.) Hutch.

Gorteria cernua L. f. (1782) = *Cuspidia cernua* (L. f.) B. L. Burtt

Gorteria ciliaris (L.) L. (1763) = *Cullumia ciliaris* (L.) R. Br.

Gorteria ciliata Thunb. (1798) = *Cullumia patula* (Thunb.) Less.

Gorteria cruciata Houtt. (1779) = *Berkheya cruciata* (Houtt.) Willd.

Gorteria echinata Aiton (1789) = *Cuspidia cernua* (L. f.) B. L. Burtt

Gorteria fruticosa (L.) L. (1763) = *Berkheya fruticosa* (L.) Ehrh.

- Gorteria herbacea* L. f. (1782) ≡ *Berkheya herbacea* (L. f.) Druce
- Gorteria heterophylla* Willd. (1812) = *Gazania* sp., fide Roessler
- Gorteria hispida* L. f. (1781) = *Cullumia aculeata* (Houtt.) Roessler
- Gorteria ilicifolia* Lam. (1789) = *Berkheya fruticosa* (L.) Ehrh.
- Gorteria incisa* Thunb. (1798) = *Gazania* sp., fide Roessler
- Gorteria linearis* Thunb. (1798) ≡ *Gazania linearis* (Thunb.) Druce
- Gorteria loureiroana* DC. (1838) = ? (the description in Candolle (1838) does not match a *Gorteria* and Candolle himself placed the taxon under “doubtful species and probably excluded”).
- Gorteria lyratopinnatifida* Poir. (1811) = *Gazania pinnata* (Thunb.) Less.
- Gorteria mitis* Burm. f. (1768) = *Heterolepis mitis* (Burm. f.) DC.
- Gorteria oppositifolia* Lam. (1789) = *Berkheya angustifolia* (Houtt.) Merril
- Gorteria othonnites* Thunb. (1798) ≡ *Gazania othonnites* (Thunb.) Less.
- Gorteria ovata* Vahl ex Less. (1832) = *Relhania rotundifolia* Less.
- Gorteria pavonia* Andrews (1808) = *Gazania pavonia* (Andr.) R. Br.
- Gorteria pectinata* Thunb. (1798) ≡ *Gazania pectinata* (Thunb.) Spreng.
- Gorteria pinnata* Lam. (1789) = *Gazania* sp. (the type specimen in P is a *Gazania* but the name *G. pinnata* Lam. was never mentioned by Thunberg (1798, 1800), Lessing (1832), Candolle (1838) or Roessler (1959) in their treatments of *Gorteria pinnata*/*Gazania pinnata*).
- Gorteria pinnata* Thunb. (1798), nom. illeg. ≡ *Gazania pinnata* (Thunb.) Less.
- Gorteria rigens* (L.) L. (1763) = *Gazania rigens* (L.) Gaertn.
- Gorteria rigida* Banks ex Gaertn. (1791) = *Stobaea gaertneri* DC.; *Berkheya* sp. fide Roessler (Gaertner referred to a herbarium sheet marked “*Gorteria rigida*” by Banks, not a description).
- Gorteria setosa* L. (1771) ≡ *Cullumia setosa* (L.) R. Br.
- Gorteria speciosa* (Willd.) Poir. (1811) = *Gazania pectinata* (Thunb.) Spreng.
- Gorteria spectabilis* Salisb. (1796) = *Gazania rigens* (L.) Gaertn.
- Gorteria spinosa* L. f. (1782) ≡ *Berkheya spinosa* (L. f.) Druce
- Gorteria spinosa* auct. non. L. f. (Jacq. 1798) = *Cullumia bisulca* (Thunb.) Less.
- Gorteria squarrosa* L. (1760) ≡ *Cullumia squarrosa* (L.) R. Br.
- Gorteria uniflora* L. f. (1782) ≡ *Gazania rigens* var. *uniflora* (L. f.) Roessler

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Appendix 1 – Specimens examined

1. *Gorteria personata*

SOUTH AFRICA:

Herb. Linn. 1027.1 (LINN [lectotype of *Gorteria personata*]); Sandy flats 1–2 miles N of Koelenhof, 23 Sep 1935, *Acocks 5096* (S); Habitat in Cape, *Forster s.n.* (K); Afr. Austr., Cap of B. Sp., *Osbeck & Sparrman s.n.* (S); Fl. Cap., 1875, *DeVylder s.n.* (S); Cap. B. Spei., 1773, *Thunberg s.n.* (S).

WESTERN CAPE PROVINCE: Stellenbosch, very local on sandy flats Strand, 18 Sep 1950, *Parker 4513* (BOL); Stellenbosch, College Grounds Stellenbosch, 27 Sep 1919, *Garside 1279* (K); Stellenbosch, Apr 1903, *Alexander Prior s.n.* (K); “Stellenbosch, Umgegend des Dorfes Sommerset, in Hottentottsholland, August”, Aug 1837, *Ecklon & Zeyher s.n.* (S); Durbanville and Wellington, 27 Oct 1928, *Hutchinson 1003* (BOL); Cape Town, Stony bank beside Victoria Drive, near van Breda’s, 11 Sep 1935, *Acocks 4849* (S); Cape Town, Signal Hill, 5 Sep 1896, *Wolley Dod 1578* (BOL, K); Cape Town, Eastern side of Lions Rump, 6 Dec 1810, *Burchell 135* (K); Cape Town, Lions Head over Sea Point, 5 Sep 1896, *Wolley Dod 1591* (BOL); Cape Town, Lions Head, 13 Sep 1938, *Wall s.n.* (S); Cape Town, in clivis montis Leonis, 66 m, 27 Aug 1892, *Schlechter 1335* (S); Twentyfourrivermountains, 22 Aug 1894, *Penther 1330* (S); Citrusdal, Bergriver, Piquenierskloof, 25 Sep 1938, *Wall s.n.* (S); Citrusdal, Die kloof, Modderfontein, 27 Aug 1968, *Hanekom 1161* (NBG, K); Tulbagh Road, 600', 13 Sep 1896, *Schlechter 9001* (S, K); Tulbagh, Nuwekloof, near Tulbagh, 900', Sep 1886, *MacOwan 826* (K); Ceres, Tulbagh Road, 600', 13 Sep 1958, *Acocks 19690* (K); Porterville, 20 Aug 1894, *Schlechter 4905* (BOL); Piketberg, 1 Sep 1930, *Barnes 26402* (BOL); Clanwilliam, Olifants River Valley, at road to Klawer, 31°58'30.0"S, 18°54'17.8"E, 16 Aug 2007, *Mucina 160807/34* (S); Clanwilliam, Olifants River Valley, Clanwilliam Dam, E bank, 31°17'53.3"S, 18°56'36.4"E, 16 Aug 2007, *Mucina 160807/8* (S); Malmesbury, roadside between Preekstol and Rondevlei, 33°24.321'S, 18°18.718'E, 194 m, 16 Sep 2007, *Stångberg & al. 140* (S); Clanwilliam, Ramskop wild flower garden, 28 Aug 1979, *leRoux 2464* (BOL); Clanwilliam, Klipfontein, N of Pakhuis, 29 Aug 1941, *Esterhuisen 5987* (BOL); Clanwilliam, Foot of Oliphant’s River Mountains near Warm Baths, 22 Sep 1911, *Stephens 6991* (BOL); Clanwilliam, 32°53'S, 19°01'E, 6 Sep 2006, *Karis & Arnerup 1027* (S); Clanwilliam, roadside between Graafwater and Clanwilliam, 32°10.193'S,

18°48.225'E, 359 m, 1 Sep 2006, *Stångberg & Karis 4* (S); Clanwilliam, just NE of Citrusdal, 32°35'S, 19°01'E, 200 m, 31 Aug 1993, *Strid & Strid 37349* (S).

NORTHERN CAPE PROVINCE: Nieuwoudtville, 1 Sep 1930, *Lavis s.n.* (BOL); Calvinia, Bokkeveld Mountains, along road to Perdekraal, near turnoff to Loeriefontein, 31°20.760'S, 19°05.539'E, 17 Oct 2001, *Karis & Johansson 788* (S); Calvinia, Mountains, Grasberg, 31°18.283'S, 19°03.536'E, 17 Oct 2001, *Karis & Johansson 790* (S).

2. *Gorteria diffusa*

SOUTH AFRICA:

Thunberg s.n. (S); *Thunberg s.n.* (UPS [holotype of *Gorteria diffusa*]); Leeuweberg, *Drège 494* (G [holotype of *Gorteria calendulacea*]).

WESTERN CAPE PROVINCE: Vanrhynsdorp, Farm Troetoe, at gate, 3 km from Vanrhynsdorp on Nieuwoudtville road, 3 Aug 1977, *leRoux 2008* (NBG); Vanrhynsdorp, 6 miles N of Klawer, 22 Aug 1950, *Maguire 141* (NBG); Vanrhynsdorp, 2 km W Aties, 31°41'S, 18°38'E, 50 m, 30 Sep 1972, *Bremer 243* (S); Vanrhynsdorp, road between Vanrhynspass and Vanrhynsdorp, at padstal, 31°26'06.3"S, 18°59'07.8"E, 30 Jul 2006, *Mucina 300706/01* (S); Vanrhynsdorp, picnic site beside road R27, NE of Vanrhynsdorp, 31°32.089'S, 18°51.360'E, 376 m, 12 Sep 2007, *Stångberg & Karis 134* (S); Vanrhynsdorp, rest place on N7 near turn off to Aties, 31°40'14.5"S, 18°42'14.5"E, 29 Jul 2006, *Mucina 290706/50* (S); Vanrhynsdorp, Zandkraal, 400', 13 Sep 1948, *Acocks 14730* (K); Klawer, at turn off to Ratelsfontein from Clanwilliam-Klawer road, 16 Aug 1970, *Wisura 1720* (NBG); Klawer, Nov 1917, *Roberts & Adendorff 17683* (PRE); Clanwilliam, E end of Biedou Valley, between Mierkraal and Bultfontein, 245 m, 25 Aug 1983, *Koutnik 1200* (BOL); Clanwilliam, Doorn Bridge, 18 Sep 1931, *Salter 1378* (K); Clanwilliam, between Pakhuis and Doom Rivier, Sep 1935, *Leyvin 5059* (BOL).

NORTHERN CAPE PROVINCE: Nieuwoudtville, Nieuwoudtville Nature Reserve, 31°22'14"S, 19°08'19"E, 740 m, 15 Sep 2000, *Koekemoer & Funk 1945* (PRE); Nieuwoudtville, Nieuwoudtville Flower Reserve, 31°22'00.1"S, 19°08'51.2"E, 30 Jul 2006, *Mucina 300706/09* (S); Nieuwoudtville, Nieuwoudtville Reserve, 26 Jul 1983, *Perry & Snijman 2194* (NBG); Calvinia, Hantam, Saaihoek, ± 100 from riparian zone. 31°16'46"S, 19°47'09"E, 7 Sep 2002, *Rosch 120* (NBG); Nieuwoudtville, ± 15 km S of Nieuwoudtville, 7 Sep 1979, *Plowes s.n.* (NBG); Calvinia, Akkerdam Nature reserve,

- below Hantam Peak, 19 Aug 1975, *Thompson 2413* (NBG); Calvinia, 17 miles N of Botterkloof, 24 Sep 1952, *Johnson 563* (NBG); Calvinia, close to Grootdrif along R27, below Vanrhyns Pass, 3 Sep 2005, *Karis & Arnerup 1003* (S); Calvinia, Kareeboomfontein, (W of Rebonie), 5 Sep 1974, *Hanekom 2391* (K); Calvinia, E of the Aloe forest at Gannabos, NE of Nieuwoudtville, 31°13.912'S, 19°17.902'E, 428 m, 12 Sep 2007, *Stångberg & Karis 137* (S); Calvinia, at the Waterfall c. 5 km N of Nieuwoudtville, 31°19.109'S, 19°07.162'E, 12 Sep 2007, *Stångberg & Karis 136* (S); Calvinia, 20 km, from Calvinia towards Loeriesfontein, Little Tower, hills north of the Hantams Mountains, 27 Sep 1983, *Coetzer 813* (PRE); Calvinia, 38 miles from Clanwilliam to Calvinia, c. 750', 24 Aug 1967, *Thompson 359* (PRE); Calvinia, NW side of Hantamsberg, 31 Aug 1986, *Plowes 7212* (PRE); "Groenrivier, karrooartige höhe, 1000–2000 Fuss (auf dieser höhe Kweekrivier genannt)", Aug 1843, *Drège s.n.* (S); Namaqualand, Top of Wildeperdehoek pass, 29°56'32.6"S, 17°37'58.7"E, 3 Sep 2006, *Stångberg & al. 29* (S); Namaqualand, Farm Kykokeis, 29°57'15.0"S, 17°38'37.1"E, 3 Sep 2006, *Stångberg & al. 30* (S); Namaqualand, Soebatsfontein, 30°06'01.0"S, 17°35'05.3"E, 3 Sep 2006, *Stångberg & al. 24* (S); Namaqualand, Namaqua National Park, 29°01'04.7"S, 17°35'02.0"E, 3 Sep 2006, *Stångberg & al. 25* (S); Namaqualand, "Namaqualand, Reise nach Kamiesberg, Boschmanland, bis zur Mündung des gariep, October", Oct 1837 *Ecklon & Zeyher 73* (S); Namaqualand, 24 km from Springbok along road to Kleinsee, 29°42'S, 17°42'E, 600 m, 10 Sep 1993, *Strid & Strid 37708* (S); Namaqualand, Brakdam, 24 Aug 1941, *Esterhuysen 5690* (BOL); Namaqualand, 11 km from Garies along road to Springbok, 30°31'S, 17°27'E, 500 m, 10 Sep 1993, *Strid & Strid 37644* (S); Namaqualand, Springbok, Spektakel Mountains. Farm Naries 24 km west of Springbok on road to Kleinsee, 29 Aug 1980, *leRoux 2739* (BOL); Namaqualand, Komaggas, 9 Sep 1950, *Barker 6697* (NBG); Namaqualand, Namaqua National Park, 29°58'46.2"S, 17°33'00.2"E, 3 Sep 2006, *Stångberg & al. 26* (S); Namaqualand, near Kookfontein, c. 3000', Aug 1883, *Bolus 397* (BOL, K); Namaqualand, beside the road between Komaggas and Namaqua National Park, 29°55.365'S, 17°28.545'E, 234 m, 10 Sep 2007, *Stångberg & Karis 126* (S); Namaqualand, 5 km W of Komaggas, 29°49.317'S, 17°25.778'E, 270 m, 10 Sep 2007, *Stångberg & Karis 124* (S); Namaqualand, beside road 355, Spektakel Pass, 29°41.815'S, 17°39.414'E, 886 m, 10 Sep 2007, *Stångberg & Karis 122* (S); Namaqualand, Kanariefontein, c. 2800', 22 Aug 1957, *Acocks 19396* (PRE, K); Namaqualand, Spektakel, 25 Aug 1941, *Esterhuysen 5729* (BOL, PRE); Namaqualand, McDougall Bay, 8 Sep 1982, *Mauve 5420* (PRE, K); Namaqualand, Steyerkraal, 26 Sep 1974, *Rosch & leRoux 802* (PRE); Namaqualand, between Steinkopf and Springbok, 15 Aug 1967, *van der Schijff 8235* (PRE); Namaqualand, 20 km from Wallekraal on road to Kamieskroon, 25 Aug 1976, *Rosch & leRoux 1432* (PRE); Namaqualand, Spektakel, W of Springbok, 21 Jul 1967, *van der Schijff 6962* (PRE); Namaqualand, Springbok, *Eliovson s.n.* (PRE); Namaqualand, 1 km S of Springbok towards Kamieskroon, 23 Aug 1976, *van Jaarsveld 1370* (PRE); Namaqualand, Springbok area, 21 Aug 1983, *Venter 8821* (PRE); Namaqualand, in begin of Wildeperdehoek Pass on road to Soebatsfontein, 4 Sep 1982, *Botha 2945* (PRE); Namaqualand, Springbok, Spektakel Pass c. 20 km W of town, 23 Aug 1975, *de Winter 9521* (PRE); Namaqualand, Steinkopf, Anenous pass, 23 Aug 1983, *van Wyk 6249* (PRE); Namaqualand, Steinkopf, 20 km from Steinkopf on road to Port Nolloth, 22 Aug 1995, *Rodriguez-Oubina & Cruces 2014* (PRE); Namaqualand, 10 km S Springbok, 7 Sep 1986, *Plowes 7257* (PRE); Namaqualand, Soebatsfontein, top of Wildeperdepass, 29°56'32.1"S, 17°39'33.5"E, 3 Sep 2006 *Mucina 030906/15* (S); Namaqualand, Spektakelberg pass, W slopes of the pass towards Komaggas, 9 Sep 2005, *Mucina 090905/22* (S); Namaqualand, near the top of Spektakelpas west of Springbok, 29°42'11.2"S, 17°40'38.0"E, 737 m, 10 Sep 1996, *Bayer & Puttock SAF-96168* (S); Namaqualand, near Ookiep, Nov 1878, *Morris 5770* (BOL); Namaqualand, Ookiep, 30 Sep 1911, *Dümmer s.n.* (K); Namaqualand, Port Nolloth, Anenous Pass, 2 km from the bottom of the pass on the Port Nolloth side, 10 Oct 1992, *Burgoyne 1333* (PRE); Namaqualand, Springbok, Eselsfontein (W of Springbok), 1000 m, 15 Sep 1969, *Schlieben 11433* (K, PRE); Steinkopf, Klipfontein, 15 Oct 1928, *Hutchinson 901* (BOL); Steinkopf, Oct 1931, *Mathews s.n.* (BOL); N of Steinkopf, 29°11.848'S, 17°48.580'E, 999 m, 2 Sep 2006, *Stångberg & Karis 15* (S); 29 miles ENE of Springbok, 26 May 1961, *Leistner 2532* (K); between Springbok and Steinkopf, 1000 m, 11 Oct 58, *Werdemann & Oberdieck 539* (K); Steinkopf, Klipfontein, 21 Sep 1930, *Herre STE12445* (PRE); Springbok, 5 miles N from Okiep, 18 Jul 1961, *van der Schijff & Schweickerdt 5741* (K); along road 3 km E of Springbok, 1000 m, 13 Sep 1985, *Zietsman & Zietsman 656* (PRE); Namaqualand, dry water courses between hills, SE of Sendling's Drift, Sep–Oct 1926, *Pillans 5099* (BOL); Namaqualand, Platte Klip, coast south of Hondeklip Bay, 1 Oct 1924, *Pillans 18118* (BOL); Namaqualand, Kleinsee, granite rocks and cliffs facing stream 29°40.279'S, 17°04.552'E, 5 Sep 2006, *Karis & Arnerup 1020* (S); Namaqualand, Hondeklip Bay, 1 Oct 1924, *Pillans 18117* (NBG); Namaqualand, 20 miles S of Port Nolloth, 23 Sep 1953, *Hall 830* (NBG); Namaqualand, between Springbok and Steinkopf, 21 Sep 1931, *Salter 1426* (BOL); Namaqualand, about 10 km North of Kleinsee on the road to Port Nolloth, 29°33'45"S, 17°05'58"E, 261 m, 23 Aug 1998, *Koekemoer 1176* (PRE); Namaqualand, SE of Port Nolloth before turnoff to Kleinsee, 28 Sep 1981, *Hugo2843* (K, PRE); Namaqualand, Klein Namaqualand, *Drège 494* (G [lectotype of *Gorteria affinis*]); Namaqualand, 5 km NNW Kamieskroon, close to Blyderus, 30°09.846'S, 17°53.752'E, 650 m, 4 Sep 2005,

Karis & Arnerup 1009 (S); Namaqualand, along dirt road near N7, Soebatsfontein, 30°14.009'S, 17°53.194'E, 759 m, 31 Aug 2006, *Stångberg & Karis 9* (S); Namaqualand, 13 km from Kamieskroon along road to Soebatsfontein, 30°13'S, 17°49'E, 700 m, 12 Sep 1993, *Strid & Strid 37804* (S); Namaqualand, along road Kamieskroon-Kamiesberg, close to Kamieskroon, 30°12.36'S, 17°56.33'E, 780 m, 3 Sep 2006, *Karis 1081* (S); Namaqualand, Kamieskroon, 30°00'S, 17°59'E, 600 m, 6 Sep 2001, *Venter 9595* (S); "Leeuwenberg, steinige trockne Anhöhen, unter 1000 Fuss", Oct 1839, *Drège s.n.* (S); Namaqualand, Brackdamm, 9 Sep 1897, *Schlechter 11153* (S); Namaqualand, Namaqualand, between Rietkloof and Darter's Grave, Oct 1931, *Mathews 26403* (BOL); Namaqualand, Namaqualand, Darter's Grave, Oct 1932, *Mathews 1925/31* (BOL); Namaqualand, Kamieskroon, 24 Aug 1941, *Esterhuysen 5698* (BOL); Namaqualand, Groot vallei, near Kamieskroon, Oct 1930, *Mathews 2166/30* (BOL); Namaqualand, between Kamieskroon and Springbok, 20 Sep 31, *Salter 1423* (BOL); Namaqualand, Kamieskroon, at road to Skilpad, 30°08'38.2"S, 17°49'54.8"E, 4 Sep 2005 *Mucina 040905/11* (S); Namaqualand, Kamieskroon, 30°13'12.3"S, 17°54'13.1"E, 713 m, 21 Sep 2006, *Ellis 1* (S); Richtersveld, Holgat, 1 Sep 1926, *Pillans 5167* (BOL); Richtersveld, Khubus, Bloedrif, 19 Aug 1982, *Metelkamp 383* (BOL); Richtersveld, Richtersveld National Park, 40 km SE Sendelingsdrift, 1 Sep 1994, *Williamson 5515* (NBG); Richtersveld, Numees, 10 Aug 1983, *leRoux 3038* (NBG); Richtersveld, Koeroegab area alongside road between De Hoop and Die Kooi, 9 Jul 1987, *McDonald 1326* (NBG); Richtersveld, Numees camping site, 26 Sep 1981, *Hugo 2804* (K, NBG); Richtersveld, hills E of Lekkersing, 27 Aug 1977, *Thompson & leRoux 63* (K); Richtersveld, SW of Kodas prek, 1 Sep 1977, *Thompson & leRoux 243* (K); Richtersveld, Doornpoort dist., Sep 1953, *Munro s.n.* (PRE, K); Richtersveld, at Numees mine, 27 Aug 1987, *Germishuizen 4537* (PRE); Richtersveld, kloof by Doornpoort, 25 Sep 1930, *Herre STE12440* (PRE); Richtersveld, top of Hells Kloof, 10 Oct 1974, *Watmough 862* (PRE); Richtersveld, at Numees copper mine, 27 Aug 1987, *Nicholas 2495* (PRE); Richtersveld, Noemees, 6 Oct 1991, *Koekemoer 928* (PRE); Richtersveld, on top of Hellsberg, 8 Sep 1961, *van Breda 1294* (PRE); Richtersveld, Hills E of Lekkersing, 27 Aug 1977, *Thompson & leRoux 63* (PRE); Richtersveld, Kookrivier, 7 Aug 1991, *van Jaarsveld 11752* (PRE); Richtersveld, Helskloof, 6 Oct 1991, *Dreyer 65* (PRE); Richtersveld, Kouams River bed, 8 Oct 1991, *Koekemoer 961* (PRE, S); Richtersveld, Helskloof, 29 Aug 1980, *Venter 8085* (PRE); Richtersveld, at Numees copper mine, 5 Oct 1991, *Germishuizen 5433* (PRE); Richtersveld, Klein Helskloofmond Sandbedding, 30 Aug 1980, *Venter 8108* (PRE); Richtersveld National Park, between Sendelingsdrif and Potjiespram, 10 Jul 1993, *van Rooyen 2265* (PRE); Richtersveld, c. 5 km from Eksteensfontein-Cornellsberg road on the way to

Mount Stewart, 600 m, 30 Aug 1987, *Nicholas 2573* (PRE); Richtersveld, Helskloof, 15 Sep 1977, *van Jaarsveld 2523* (PRE); Richtersveld, Numees camping site, 26 Sep 1981, *Hugo 2804* (PRE); Richtersveld, Lekkersing, 230 m, 24 Aug 1925, *Marloth 12281* (PRE); Richtersveld, c. 26 km from Eksteensfontein on road to Stewart's Mine, 30 Aug 1987, *Pienaar 1024* (PRE, BOL); Richtersveld, NW of Eekstensfontein, 28°42.669'S, 17°03.372'E, 1 Sep 2007, *Stångberg & Karis 94* (S); Richtersveld, NW of Eksteensfontein, 28°43.537'S, 17°07.616'E, 1 Sep 2007, *Stångberg & Karis 96* (S); Richtersveld National Park 28°8.356'S, 16°58.956'E, 31 Aug 2007, *Stångberg & Karis 84* (S); Richtersveld National Park, 28°9.824'S, 17°1.09'E, 31 Aug 2007, *Stångberg & Karis 89* (S); Richtersveld, road side South of Richtersveld National Park, 28°36.884'S, 16°57.245'E, 30 Aug 2007, *Stångberg & Karis 82* (S); Richtersveld, Camp south of Doornpoort, sandy flat, 250 m, 25 Aug 1926, *Marloth 12306* (PRE); Richtersveld, 2 km S of Ploegberg, between Khubus and Lekkersing, 15 Sep 1985, *Zeitsman & Zeitsman 758* (PRE); Richtersveld, S of Richtersveld National park, 28°33.637'S, 16°55.959'E, 1 Sep 2007, *Stångberg & Karis 93* (S); Richtersveld National park, 28°8.795'S, 17°00.993'E, 31 Aug 2007, *Stångberg & Karis 87* (S); Richtersveld, Zebrakloof, 9 Oct 1991, *Dreyer 155* (PRE); Richtersveld, NW of Eksteensfontein, near Skouerfontein, 28°46'32.9"S, 17°11'16.9"E, 29 Aug 2006, *Mucina 290806/21* (S); Richtersveld, Koeboes, pass south of Wallekraal, 28°18'57.6"S, 16°55'31.6"E, 27 Aug 2006, *Mucina 270806/03* (S); Richtersveld, NW of Eksteensfontein, 28°42'44.3"S, 17°07'48.8"E, 415 m, 17 Sep 2006, *Ellis 9* (S); Richtersveld, S of Kubous, 28°32'11.0"S, 16°55'04.8"E, 398 m, 16 Sep 2006, *Ellis 8* (S).

3. *Gorteria integrifolia*

SOUTH AFRICA:

Thunberg s.n. (UPS [holotype of *Gorteria integrifolia*]). WESTERN CAPE PROVINCE: Oudtshoorn, along road from Dysseldorp to N9, c. 15 km SE of Oudtshoorn, 33°37.1'S, 22°24.4'E, c. 400 m, 8 Sep 2005, *Karis & al. 1029* (S); Oudtshoorn, roadside S of Oudtshoorn, road towards Mossel Bay, Remhoog, 33°43.2'S, 22°07.019'E, 380 m, 11 Sep 2006 *Stångberg & Karis 55*(S); Oudtshoorn, roadside between Calitzdorp and vanWyksdorp, Rooiberg, 33°38.238'S, 21°39.514'E, 281 m, 11 Sep 2006, *Stångberg & Karis 60* (S); Oudtshoorn, along N12 c. 10 km SSE of Oudtshoorn, Oskloof, c. 375–400 m, 33°41.04'S, 22°16.07'E, 9 Sep 2005, *Karis & Arnerup 1040* (S); Worcester, Dept. Of Agriculture Veld Reserve, 33°37'15.6"S, 19°28' 06.9"E, 30 Aug 2005 *Mucina 300805/78D* (S); Worcester, Along Villiersdorp-Worcester road just N of Villiersdorp, 316 m, 4 Sep 1996, *Bayer & Puttock SAF-96094* (S); Robertson, between Robertson and Worcester, Oct 1952, *Pillans 10794* (UPS); Bonnievale, Shaley hills on lower bank of Breede River, Sep 1933, *Acocks 1578* (S); Calitzdorp, Matjesvlei,

33°26.82'S, 21°38.72'E, 320 m, 28 Sep 2011, *Karis & Stångberg s.n.* (S).

4. *Gorteria alienata*

SOUTH AFRICA:

Thunberg s.n. (UPS [lectotype of *Oederia alienata*]).

WESTERN CAPE PROVINCE: Prince Albert, Foot of Swartberg Pass (N side) c. 2000', 13 Sep 1955, *Leistner 213* (K); Prince Albert, Foot of Swartberg Pass (N side) c. 2000', 13 Sep 1955, *Leistner 212* (K); Prince Albert, Boschuis-kloof Pass, 3500', 14 Nov 1938, *Wall s.n.* (S); Laingsburg, Anysberg Nature Reserve, plain north of Anysberg, between Vrede and Goede Hoop farmhouses, 12 Aug 1993, *Meyer 251* (PRE); Swellendam, along R62 just E of Warmwaterberg, 22 km NE Barrydale, 33°47.75'S, 20°55.305'E, c. 400 m, 9 Sep 2005, *Karis & Arnerup 1044* (S); Vanrhynsdorp, 2 km W Aites, 31°41'S, 18°38'E, 50 m, 30 Sep 1972, *Bremer 242* (S); Lainsburg, 3 miles North of Matjiesfontein, 914 m 20 Sep 1953, *Acocks 17162* (S); Oudtshoorn, 33°43.200'S, 22°07.019'E, 11 Sep 2006, *Stångberg & Karis 54* (S); Clanwilliam, South of Nieuwoudtville on the road to Clanwilliam, 31°55'43"S, 19°14'30"E, 284 m, 27 Aug 1998, *Koekemoer 1386* (PRE).

NORTHERN CAPE PROVINCE: Nieuwoudtville, Nieuwoudtville Nature Reserve, 31°22'14"S, 19°08'19"E, 740 m, 15 Sep 2000, *Funk & Koekemoer 1950* (PRE); Calvinia, W slope of Hantamsberg on road to Groot Toring, 23 Jul 1981, *Goldblatt 6059* (PRE); Namaqualand, 9 km West of Nariëp, Farm Roodeheuwel, 134 m, 28 Sep 1987, *Perold 1677* (PRE); Namaqualand, WNW of Wallekraal, c. 400', 21 Aug 1963, *Acocks 23321* (PRE); Namaqualand, Plaas Anenas between Droëdap and Kamiesberg pass, 25 Aug 1983, *van Wyk 6439* (PRE); Namaqualand, Kotzesrus, 33km from Garies to Kotzerus (12 km from Kotzesrus), 20 Nov 1995, *Koekemoer 1102* (PRE); Namaqualand, Bulletrap (N of Springbok) c. 5 km on road to Nigramoep, 29°27'47.6"S, 17°42'33.1"E, 2 Sep 2006, *Mucina 020906/04* (S); Namaqualand, Near Carolusberg, c. 7 km ENE of Springbok, 29°38'S, 17°57'E, 950 m, 11 Sep 1993, *Strid & Strid 37756* (S); Namaqualand, 1 km S of Mesklip, c. 22 km from Springbok along road to Garies, 29°50'S, 17°52'E, 750 m, 10 Sep 1993, *Strid & Strid 37696* (S); Namaqualand, 11 km from Garies along road to Springbok, 30°31'S, 17°27'E, 500 m, 10 Sep 1993, *Strid & Strid 37653* (S); Namaqualand, Naip se Berg (between Springbok and Aggeneys), mountain, 29°21'14.3"S, 18°17'24"E, 8 Sep 2005, *Mucina 080905/13* (S); Garies, below Studers pass, 30°26'35.5"S, 18°03'47.6"E, 740 m, 6 Sep 2005 *Mucina 060905/74* (S); Calvinia, along road to Clanwilliam, at turn-off to Nieuwoudtville, flats E of Stinkfonteinberge 31°45.186'S, 19°17.921'E, 18 Oct 2001, *Karis 800* (S); Namaqualand, Namaqua National Park, 29°56.275'S, 17°37.543'E, 596 m, 11 Sep 2007, *Stångberg & Karis 132* (S); Richtersveld, S of Lekkersing, 29°05.799'S, 17°05.069'E, 340 m, 30 Aug 2007, *Stångberg & Karis 78* (S).

5. *Gorteria piloselloides*

SOUTH AFRICA:

WESTERN CAPE PROVINCE: Worcester, 33°37'41.3"S, 19°32'46.1"E, 321 m, 25 Sep 2006, *Ellis 11* (S); Worcester, 33°44'40.0"S, 19°44' 58.4"E, 284 m, 25 Sep 2006, *Ellis 10* (S); Worcester, Hexrivervalley, Klipheuwel, 33°32'S, 19°30'E, 350 m, 15 Sep 1972, *Bremer 178* (S); Worcester, hills between Brandvleidam and Breede River, 33°42'S, 19°27'E, 200 m, 8 Sep 1972, *Bremer 139* (S); Worcester, beside the small road connecting R60 and R43 between Over-Hex and Aan de Doorns, 33°41.806'S, 19°29.607'E, 214 m, 13 Sep 2007, *Stångberg & Karis 139* (S); Worcester, in convalle Hex River near De Doorns, 1700', Apr 1907, *Bolus s.n.* (PRE); Worcester, 775 m, 2 Nov 1965, *van Breda 2060* (PRE); Worcester, Dept. Of Agriculture Veld Reserv, 33°39'20.5"S, 19°28'04.8"E, 30 Aug 2005, *Mucina 300805/#78C* (S); Bonnievale, shaley hills on L. bank of Breede River at Bonnievale, 26 Sep 1933, *Acocks 1468* (S); Bonnievale, 1 Sep 1933, *Acocks s.n.* (S); Bonnievale, kloof between Storms Vlei and Bonnievale, 27 Sep 1933, *Acocks 1733* (S); Bonnievale, Oct 1952, *Pillans 10839* (BOL, NBG, S); Swellendam, Bontebok park, 23 Aug 1965, *Grobler 436* (NBG); Swellendam, Bontebok park, 23 Aug 1965, *Grobler 438* (NBG, PRE); Swellendam, Farm Sandkraal, 23 km S of Swellendam, 6 Aug 2003, *Manning 2866* (NBG); Swellendam, 25 Sep 1930, *Fries, Nordlindh & Weimarck 1405* (BOL); Swellendam, Reisebaan, 1 Sep 1959, *Barnard 598* (PRE); Swellendam, Fonteineieskloof, 5 Sep 1959, *Barnard 637* (PRE); Swellendam, Sep 1962, *Liebenberg 6411* (PRE); Swellendam, 21 m from Swellendam, Caledon Rd, 6 Sep 1947, *Story 3083* (PRE); Montagu nature garden, 33°47'S, 20°07'E, 230 m, 14 Sep 2006, *Stångberg & Karis 69* (S); Montagu, 5 km E of Montagu towards Barrydale, 33°49'S, 20°11'E, 321 m, 14 Sep 2006, *Stångberg & Karis 73* (S); Montagu, Roadside in Ashton, 33°50.260'S, 20°02.186'E, 193 m, 14 Sep 2006, *Stångberg & Karis 74* (S); Montagu, roadbank close to Montagu nature garden, 33°47.334'S, 20°08.013'E, 231 m, 14 Sep 2006, *Stångberg & Karis 72* (S); Montagu, between Montagu and Barrydale, 33°50'14"S, 20°12'11"E, 395 m, 30 Aug 1998, *Koekemoer 1418* (PRE); Robertson, Middelstekloof in Farm Middelburg. 14 km NW of Robertson, 2 Sep 1987, *Hilton-Taylor 2288* (NBG); Robertson, 1 Sep 1934, *Nel 19444* (NBG); Robertson, 2 miles E of Robertson, 10 Sep 1951, *Dyer 5347* (PRE); Mossel Bay, Attakwaskloof, *Gill s.n.* (K); Robertson dist., Vrolijkheid Nat. Res., 27 Sep 1974, *van der Merwe 2527* (K, PRE); Near Villiamsdorp, Worcester road, just after turning off to Hammanshof, 25 Sep 1980, *Hilliard & Burt 13061* (K); Ceres, Karooport, Farm Vrede, at road to Touwsrivier Sof Saalberg, 33°18' 06.7"S, 19°46' 40.6"E, 21 Sep 2006, *Mucina 210906/34* (S); *Ecklon & Zeyher 51.8* Caledon, Swartberg und Umgegend des bades, 1000–2000' (G-DC [holotype of *Gorteria personata* subsp. *gracilis*]); Caledon, road between Greyton and Genadendal, 10 Nov 1936, *Hafström & Lindeberg s.n.* (S); Caledon,

Roadside near Uitkyk, 34°04'S, 19°24'E, 18 Sep 1972, *Bremer 190* (S); Caledon, 1 Sep 1943, *Wasserfall 387* (NBG); Caledon, Hermanus rocky coast, 30 Sep 1928, *Gillett 31* (NBG); Caledon, 34°13'S, 19°25'E, *Stångberg & Karis 75* (S); Caledon, 1 Apr 1903, *Alexander Prior s.n.* (K); Caledon, 34°21.906'S, 19°38.246'E, 71 m, 20 Sep 2007, *Stångberg & al. 148* (S); Caledon, beside the dirt road between Caledon and Doomkraal, 34°21.943'S, 19°37.344'E, 83 m, 20 Sep 2007, *Stångberg & al. 147* (S); Riversdale, near Albertinia, 24 Sep 1930, *Fries, Nordlindh & Weimarck 1359* (BOL); Riversdale, Still Bay, De Jager street, 8 Sep 1980, *Bohnen 7649* (NBG); Riversdale, Still Bay, 34°21.346'S, 21°25.359'E, 13 Sep 2006, *Stångberg & Karis 65* (S); Riversdale Nature Reserve, c. 1 mile south of town near dam, c. 152 m, 1 Nov 1970, *Taylor 7828* (PRE); Bredsdorp, Elim Hills, 5 Aug 1940, *Compton 9131* (NBG); Bredasdorp, Bosch Kloof (west side) south side of the Potberg, 14 Oct 1940, *Pillans 9443* (BOL, PRE); Bredasdorp, Nachtwacht, in the Bontebok camp, Sep 1926, *Smith 3051* (K); Bredasdorp, in wheel track in De Hoop Nature Reserve 34°45.629'S, 20°01.791'E, 7 m, 21 Sep 2007, *Stångberg & al. 152* (S); “Zwelendam, am Berge bei Puspasvalei, Voormansbosch, Duivelbosch, und am Fluss Keureboomsrivier, 1000–4000', October”, *Ecklon & Zeyher s.n.* (S); Swellendam, 25 Sep 1930, *Fries, Nordlindh & Weimarck 1405* (PRE); Mossel Bay, Dry hills on eastern side of Gouritz river, Nov 1810, *Burchell 6440* (K); Mossel Bay, Klein Berg, 800', 25 Sep 1897, *Galpin 4259* (PRE); Mossel Bay, Sandy hills near the landing place, 18 Oct 1814, *Burchell 6236* (K); George, Keurboouis river, long kloof, 1800ft, Oct 1933, *Fourcade 5057* (K); Mountains above Korente river, 1000', Nov 1908, *Muir 253* (PRE); Bassonsrus, upper cango valley at campsite, 4 Nov 1974, *Moffett 396* (PRE, NBG); Cape Town, Nov 1921, *Fries & Fries 3757* (UPS); Riviersonderend, *Zeyher 3018* (S).

EASTERN CAPE PROVINCE: Hankey, 1 Sep 1915, *Paterson 3193* (BOL); Humansdorp, Zuurbron, Oct 1927, *Fourcade 3333* (BOL)

6. *Gorteria corymbosa*

NAMIBIA:

||KARAS REGION: Boomrivier, in Nuobrivier, 2 km N of Orange, 23 Sep 1974, *Giess 13651* (WIND); Chamaites, Mara-Letter Klip area in bed of Konkiep River, 9 Jul 1986, *Craven 2630* (WIND); Viooldrif, Nuob River, 3 km N junction with the Orange, 2 Oct 1975, *Giess 13842* (WIND, PRE); Rosh Pinah, abandoned mine at Lorelei, just north of Orange River, 28°03'20"S, 16°52'39"E, 120 m, 14 Oct 2005, *Kolberg & Tholkes 1714* (WIND); Rosh Pinah, on flood area at the ferry at Orange river E of Sendlingsdrift, 21 Sep 1972, *Merxmüller & Giess 28684* (K, WIND); Chamaites, area W of Nuobrivier, 2 Oct 1977, *Merxmüller & Giess 32428* (WIND); Rosh Pinah, Loreleifelsen and copper mine area, 2 Oct 1977, *Merxmüller & Giess 32475* (WIND); Oranjemund, Orange, N of Sendlingsdrift, 8 Oct 1970, *Mittendorf 67*

(PRE); Chamgab, hills near Orange River, about 4 miles down from Chamgab, Sep 1931, *Pillans 6542* (BOL); Ai-Ais park, 28°04.166'S, 16°59.642'E, 81 m, 9 Sep 2007, *Stångberg & Karis 116* (S); Ai-Ais park, 28°04.803'S, 17°07.887'E, 73 m, 9 Sep 2007, *Stångberg & Karis 117* (S); Goodhouse poort, 29 Aug 1989, *van Wyk 8704* (WIND); Ai-Ais park, 28°10.985'S, 17°14.536'E, 73 m, 9 Sep 2007, *Stångberg & Karis 119* (S).

SOUTH AFRICA:

NORTHERN CAPE PROVINCE: Richtersveld, “Garip auf steinigen und felsigen Höhen bei Verleptpram, unter 1000 Fuss, September”, *Drège s.n.* (G [holotype of *Gorteria corymbosa*], S, K); Richtersveld, 26 km from Eksteenfontein on road to mount Stewart, 30 Aug 1987, *Germishuizen 4602* (PRE); Richtersveld, Richtersveld National Park, Maerpoort, 28°15'23"S, 17°08'10"E, 19 Sep 2001, *Jürgens 122556* (NBG); Richtersveld, Khubus, Bloeddrijf mt., 17 Aug 1982, *Metelerkamp 321* (BOL); Richtersveld, Richtersveld national park, 28°20'04.9"S, 17°10'08.6"E, 28 Aug 2006, *Mucina 280806/23* (S); Richtersveld, dry bed of Oerlap river, near Anisfontein, Oct 1926, *Pillans 5046* (K); Richtersveld, Groot Derm, Sep 1926, *Pillans 5253* (BOL); Richtersveld, dry sandy course of Dorlap River, west of Anis, Sep 1926, *Pillans 5076* (BOL); Richtersveld, 4 km from Vioolsdrif on road N7 to Steinkopf, 23 Aug 1995, *Rodrigues-Oubina & Cruces 2035* (PRE); Richtersveld, near Orange river, 1600', 28 Sep 1897, *Schlechter 11445* (BOL); Richtersveld, Richtersveld National Park, bank of Gannakouriep river, 1 Nov 1995, *Williamson 5857* (NBG); Richtersveld, 20 km W of Vioolsdrif, 28°48.928'S, 17°26.149'E, 528 m, 1 Sep 2007, *Stångberg & Karis 98* (S); Namaqualand, Swartberg mine between Steinkopf and Vioolsdrif, 27 Aug 1983, *van Wyk 6525* (PRE).

7. *Gorteria parviligulata*

NAMIBIA:

||KARAS REGION: Zebrafontein, unten am Berghang des westlichen Bakenberges auf Witpütz-Süd, *Merxmüller & Giess 28763* (PRE, WIND [isotypes of *Gorteria diffusa* subsp. *parviligulata*]); Shale hills north of Rooival, near Orange river, Kalahari Region, Sep 1931, *Pillans 6421* (BOL); Witpütz, Namuskluft (LUS 88), at Berghang (17.5 km E of Rosh Pinah), between Gestein and Westhang, 18 Sep 1972, *Merxmüller & Giess 28548* (WIND); Witpütz, Farm Spitskop: LU 111, SW Berghang, 14 Aug 1976, *Giess 14631* (WIND); Lüderitz, 35 km N of Rosh Pinah (road towards Aus), 2–4 km W of the road, 29 Oct 1983, *Leuenberger & al. 3245* (WIND); Witputz, Farm Zebrafontein LUS 87, 22 Sep 1981, *Müller & Horn 1511* (WIND); Namuskluft, Mc-Millanspas. Bo-op berg, 1800 m, 31 Aug, *Zietsman 5814* (WIND); Aurus fountain, 27°37'33"S, 16°16'15"E, 9 Aug 2001, *Mannheimer 1547* (WIND); Witputz, Namuskluft 88, 10 Oct 1970, *Mittendorf 88* (WIND); Farm Pockenbank, 26 Aug 1963, *Merxmüller & Giess 3143* (PRE).

8. *Gorteria warmbadica*

Except for the holotype, all cited specimens are paratypes of *Gorteria warmbadica*.

NAMIBIA:

||KARAS REGION: Karasburg, between Karasburg and Warmbad, along main road 28°42'55"S, 18°55'52"E, 872 m, 14 Jun 2005, *Bartsch & al. 1879* (WIND [holotype of *Gorteria warmbadica*]); Gordonia, North of Orange River, Kakamas, 26 Sep 1938, *Middlemost 1959* (NBG); Kenhardt, 12 m SE of Kakamas, 15 Jun 1958, *Acocks 14380* (K); Keetmanshoop, 30 m from Ariamsvlei on road to Ham River Station, 16 May 1955, *deWinter 3561* (WIND); Klein Karas, 13 Aug 1923, *Dinter 4896* (BOL, UPS); Warmbad, Farm Kanabeam: WAR 331, 8 Aug 1976, *Giess 14551* (WIND); Warmbad, Farm Eendoorn: WAR 106, 26 May 1972, *Giess & Müller 12230* (WIND); Warmbad, Farm Iris, part of Farm Ortman'sbaum: WAR 120, 22 May 1972, *Giess & Müller 12107* (WIND); Chamaites, Farm Holoog: KEE 106, 17 Jun 1976, *Giess & Müller 14441* (WIND); Warmbad, Farm Witpütz: WAR 258, 15 May 1963, *Giess &*

al. 6955 (WIND); Warmbad, 12 miles E of Karasburg, 31 Jul 1965, *Leach & Bayliss 13082* (WIND, K); Warmbad, Fish River Canyon National Park, Plateau at the end of the canyon, c. 16 miles downriver, 13 May 1965, *Meyer 18* (WIND); Mountains just NW of Seeheim & west of Fish River, 6 May 1976, *Oliver & al. 6336* (K); Karasburg, Warmbad, Farm. Umeis: 110, 24 Mar 1979, *Owen-Smith 1248* (WIND); Great Karasberg, dry banks of riverine gravels in Dassiefontein, 23 Jan 1913, *Pearson 7938* (BOL); Warmbad, Fish river canyon, 29 Mar 1953, *Walter 2283* (WIND); Goodhouse Poort, 29 Aug 1989 *van Wyk 8748* (WIND); Klein Karas, 800 m, 11 May 1931, *Örterndahl 221* (S, UPS).

SOUTH AFRICA:

NORTHERN CAPE PROVINCE: Pofadder-Aughrabie, 30 Sep 1938, *Wall s.n.* (S); Namaqualand, 8 miles S W of Goodhouse, 31 May 1961, *Leistner 2593* (K); Namaqualand, Aggeneys, Black mountain Area, 29°14'0"S, 18°43'0"E, 1 Feb 2000, *Netnou 52* (PRE); Kakamas, 70 km NW from Upington on road to Karasburg, 4 May 1976, *Oliver & Steenkamp 6245* (K).

Appendix 2

Distribution map of *Gorteria alienata* including localities from specimens examined for this study and localities taken from Roessler (1959). Those taken from Roessler (1959), given by him in more or less precise geographical positions, are as follows: SOUTH AFRICA: NORTHERN CAPE PROVINCE: Kenhardt, Pofadder, *Lewis 4667* (NBG); Calvinia, Loeriesfontein, *Pearson 4862* (K); Calvinia, Nieuwoudtville, *Lavis s.n.* (BOL); Calvinia, between Nieuwoudtville and Oorlogs Kloof, *Leipoldt 3623* (BOL); Williston, *Hutchinson 972* (BOL, K, PRE); Williston, *Acocks 18253* (K, PRE); Sutherland, between Sutherland and Middlepost, *Hutchinson 720* (BOL, K). – WESTERN CAPE PROVINCE: Vanrhynsdorp, Karee Bergen, *Schlechter 8177* (BM, BOL, G, K, Z); Clanwilliam, Graafwater, *Zinn s.n.* (NBG); Laingsburg, from Touws Rivier on Laingsburg Road, *Story 3615* (PRE); Laingsburg, Matjesfontein, *Foley 84* (PRE); Laingsburg, Karroo Garden, Whitehill, *Compton 2830* (BOL); Laingsburg, between Seven Weeks Port and Rooinek Pass, *Zinn s.n.* (NBG); Prince Albert, *Bolus 11570* (BOL); Uniondale, *Bolus 2368* (BOL, NBG). – EASTERN CAPE PROVINCE: Graaff-Reinet, Stegman's farm, Kruidfontein, *Pole-Evans 2557* (K, PRE).

