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**Summary.** The beetle daisy, *Gorteria diffusa* Thunb., is a South African and Namibian spring-flowering annual with a very interesting pollination strategy involving insect-mimicking petal spots, details of which are given here, in addition to notes on its history, habitat and cultivation, accompanied by a watercolour painting of the subsp. *diffusa* and a habitat photograph.

*Gorteria* is one of about eight genera and 130 species within the tribe Arctotideae, in the subtribe Gorteriinae. Along with other members of this subtribe, it is set apart from genera in subtribe Arctotidinae (which includes *Arctotheca* Vaill., *Arctotis* L. and *Dymondia* Compton, amongst others) in that it possesses latex (Karis *et al*., 2009). In an investigation into the monophyly of the genera within the Arctotideae and their relationship to one another, using three phylogenetic markers, two from chloroplast DNA (*trnL*-F and *ndhF*) and one from the nuclear genome (ITS), *Gorteria* fell within one of the three monophyletic groups that comprise the Gorteriinae, in the *Gazania-Hirpicium-Gorteria* group; the other groups identified were the *Didelta* group and the *Berkheya-Callumia* group (Funk & Chan, 2008). *Gorteria* is easily distinguished from *Gazania* in having sessile capitula; the receptacles become woody and enclose the fruit after anthesis, and its achenes germinate within the closed receptacle. Unlike most members of the Compositae, in which the achenes act as diaspores, in *Gorteria* the entire lignified receptacle drops off and acts as diaspore (Karis *et al*., 2009). This is also the case in *Hirpicium alienatum* (Thunb.) Druce and *H. integrifolium* (Thunb.) Less. which are closely related to *Gorteria* (Funk & Chan, 2008; Stångberg, 2009).

*Gorteria* L. has three species and commemorates the Dutch father and son Johannes and David de Gorter, both botanists and physicists. The first described species was *G. personata* L., an erect, low-growing bushy plant from the Northern and Western Cape that has small spiny flowerheads with short yellow ray florets and dark petal bases (Linnaeus, 1759). The most striking species, *G. diffusa*, was described by the Swede C.P. Thunberg in the late 18th century from an unrecorded locality at the Cape, and his type specimen is preserved in...
his Herbarium at Uppsala University (Thunberg, 1798). The specific name *diffusa* refers to the diffuse or spread-out growth habit of subsp. *diffusa*. A third species, *G. corymbosa* DC. from southern Namibia and the western part of the Northern Cape forms a low spreading bush and has corymbose, yellow flower heads with very hairy involucres; it was described in the early 19th century (De Candolle, 1837).


Most recently the work of Ellis & Johnson (2009) demonstrates that *Gorteria diffusa* in fact consists of many allopatric variants (referred to as floral morphotypes) which differ substantially in floral and capitulum traits (some of these are illustrated in Fig. 18 on p. 375). Ellis & Johnson (2009) describe 14 discrete morphotypes (named according to the localities at which they occur) and two additional morphotypes were recently discovered in the Richtersveld (Allan Ellis, unpubl.). The morphotypes are allopatrically distributed and never co-occur, except in very narrow contact zones along distribution margins where individuals of intermediate phenotype (hybrids) are also often present. *G. diffusa* has a wide distribution across the winter rainfall zone of southern Africa, occurring from southern Namibia to the Richtersveld, Namaqualand and Western Karoo to the western, southwestern and southern parts of the Western Cape, in South Africa (Roessler, 1959). The subsp. *parviligulata* (probably the Khubus morphotype of Ellis & Johnson, 2009) is only found on the coastal plain of southern Namibia, and subsp. *calendulacea* (the Cal morphotype of Ellis & Johnson, 2009) is endemic to the higher areas of the Kamiesberg in central Namaqualand. The additional 12 described morphotypes of subsp. *diffusa* have equally narrow distributions in Namaqualand and the Little Karoo (Ellis & Johnson, 2009).
The most striking feature of *Gorteria diffusa* capitula are the insect-like ornaments present on some or all of the ray florets. These complex structures, comprising numerous cell types which combine to produce intricate visual, tactile and perhaps olfactory signals, vary dramatically between morphotypes (Johnson & Midgley, 1997; Ellis & Johnson, 2009; Thomas et al., 2009). In some morphotypes they are absent and in others their resemblance to insects is uncanny. Johnson & Midgley (1996) demonstrated that the ray floret spots of the Nieuw morphotype are important for attracting bee-fly pollinators (*Megapalpus capensis* Wiedeman). *Megapalpus* flies are the most abundant visitors to all the *G. diffusa* morphotypes that have been studied, suggesting that the diversity of floral form (and spot structure) does not arise from selection imposed by different pollinator types (Ellis & Johnson, 2009). Instead Ellis & Johnson (2010) showed that spot complexity in some morphotypes is linked to exploitation of mating behaviour of male flies. These spots elicit copulatory attempts from male flies, the first incidence of pollination by sexual deception reported in non-orchid flowers. Thus in *G. diffusa* the petal surface structure and the resulting visual effect depends on which insect behavioural modality (feeding or sex) the plants are exploiting for pollination.

*Gorteria diffusa* subsp. *diffusa* grows in large colonies on flats and lower rocky hill slopes in gravelly sand or clay, in full sun, and has a long flowering period from late July to early October. This taxon is common in Namaqualand, transforming large tracts into sheets of orange in spring (Fig. 1).

It usually occurs in arid environments with erratic rainfall cycles, and its achenes, enclosed within the receptacle, are long-lived and capable of surviving years of drought. Judging from the erratic germination results obtained in cultivation, viable seeds appear to have an in-built mechanism preventing them all germinating during the same season, irrespective of whether favourable conditions exist for them to do so, thus ensuring a continuous reservoir of viable seeds in the soil as an insurance against detrimental climatic conditions, such as periods of drought that may occur during the active growing season.

**Cultivation.** All three *Gorteria* species are winter-growing annuals and have more or less the same cultivation requirements. Despite the striking beauty of *G. diffusa* subsp. *diffusa*, it is seldom cultivated as
the plants are highly sensitive to soil moisture and air humidity, the seedlings and mature plants rapidly succumbing to fungal infection. The plants require full sun and a dry atmosphere, and in suitable climates are suited to mass planting in rock garden pockets and to troughs or window boxes, in gritty media. Mature plants and seedlings should be allowed to dry off almost to the point of wilting before the next drench is applied.

The receptacles containing the achenes are ‘sown’ just below soil level in autumn in a well drained sandy-gritty medium, in a protected position, in bright light. Germination is erratic in that only one or two achenes may germinate, the others remaining dormant for one or more seasons. In ideal conditions, seedlings reach flowering stage in three to four months.

In temperate climates it should be noted that *Gorteria personata* has become naturalised along roadsides in Western Australia, where it is considered a noxious weed (Hussey *et al*., 1997) and the same potential may exist with *G. diffusa*. 

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Fig. 1. *Gorteria diffusa* subsp. *diffusa* in habitat near Bitterfontein, southern Namaqualand. Photograph: Graham Duncan.


*Gorteria affinis* DC., Prodromus systematis naturalis 6: 501 (1837). Type: South Africa, Northern Cape, Groenrivier, Drège 494 (G-DC.) (syntype); Kamiesberg, Ecklon & Zeyher 73 (G-DC.) (syntype).

**Description.** Winter-growing annual, 5–30 cm high. **Plant** sprawling, branching from base, with slender taproot and numerous fibrous lateral roots. **Stems** cylindrical, diffuse, hairy, light green. **Leaves** linear, lanceolate or oblanceolate, alternate, 20–50 × 5–8 mm, light green, upper surface hairy, lower surface woolly, entire, toothed or pinnatifid, mostly sessile, lower leaves tapering into a short petiole, margins revolute. **Capitula** radiate, solitary, sessile, terminal, 20–35 mm in diam. **Involucre** ovoid; bracts acuminate, hairy to tips, united towards base into a more or less urceolate cup, pungent, enclosing fruit after anthesis. **Receptacle** basin-shaped. **Ray florets** ligulate, 12–20 × 4–6 mm, sterile, narrowed at base into long claw, orange above, purplish dorsal stripe below, with dark basal, glossy spot on 1, (usually two or 3) or rarely 4 florets, each with a small white reflective dot. **Disc florets** orange, outer florets mostly female-sterile, inner florets male, corolla with five linear or lanceolate lobes. **Anthers** shortly sagittate at base, apical appendage ovate. **Style** linear, subglobose at base, branches linear-lanceolate. **Cypselas** obovoid, apically sericeous. **Pappus** of minute scales, hidden between cypsela hairs; achenes germinating within the closed receptacle. **Chromosome number:** unknown.

**Distribution.** Southern Namibia and in South Africa from the northern Richtersveld, Namaqualand and western Karoo to the western, southwestern and southern Western Cape.

**Habitat.** Flats and lower rocky hill slopes in gravelly sand or clay, in full sun.

**Flowering time.** July to October, with a peak in August and September.

**REFERENCES**


