

Available online at www.sciencedirect.com ScienceDirect

South African Journal of Botany 75 (2009) 600–605

SOUTH AFRICAN
JOURNAL OF BOTANYwww.elsevier.com/locate/sajb

Short communication

Diaspore capitula in *Hirpicium* supports close evolutionary relationship to *Gorteria* (Asteraceae–Arctotideae)

F.K. Stångberg

Department of Botany, Stockholm University, SE-106 91 Stockholm, Sweden

Received 13 January 2009; received in revised form 9 March 2009; accepted 13 March 2009

Abstract

Among the 17 genera in the southern African tribe Arctotideae (Asteraceae), only the three genera of subtribe Gorteriinae (*Cuspidia*, *Gorteria* and *Didelta*) have capitula that function as diaspores. The feature is reported here also in the genus *Hirpicium* for the first time. The discovery supports recent phylogenetic studies of the group that *Hirpicium integrifolium* and *H. alienatum* are more closely related to *Gorteria* than to the rest of the *Hirpicium* species.

© 2009 SAAB. Published by Elsevier B.V. All rights reserved.

Keywords: Asteraceae; Diaspore; *Gorteria*; Gorteriinae; *Hirpicium*; South Africa

1. Introduction

Arctotideae is a small tribe of the Asteraceae–Cichorioideae with 17 genera and 215 species. The tribe is predominantly restricted to sub-Saharan Africa, and particularly South Africa, with the exception of the Australian endemic genus *Cymbonotus* Cass. (Karis, 2007). Although the tribe Arctotideae in itself is weakly supported, the two presently recognised subtribes Arctotidinae and Gorteriinae are clearly monophyletic, as evidenced from both morphological and molecular data (Funk et al., 2004; Karis, 2006; Karis et al., 2009). Recent studies of molecular, palynological and morphological data show that the subtribe Gorteriinae is comprised of two well supported clades, the first comprising the genera *Gazania* Gaertn., *Gorteria* L. and *Hirpicium* Cass., and the second comprising the genera *Berkheya* Ehrh., *Cullumia* R. Br., *Cuspidia* Gaertn., *Didelta* L'Hér. and *Heterorhachis* Sch. Bip. ex Walp. (Leins and Thyret, 1971; Funk et al., 2004; Karis, 2006, 2007; Funk and Chan 2008; Wortley et al., 2008).

One of the characters diagnosing the subtribe Gorteriinae is the presence of partially connate involucre bracts. In the

Gazania–*Gorteria*–*Hirpicium*-clade the involucre bracts are fused to form a cylindrical, campanulate, broadly obconical or urceolate cup (Fig. 1) (Roessler, 1959; Karis, 2006, 2007; Karis et al., 2009). The extent of fusion and the pubescence of the involucre bracts are important characters that are used to diagnose the genera of Gorteriinae. Additional generic characters are the pappus structures and the shape and arrangement of the cypselae on the more or less alveolate receptacle. The cypselae of *Gorteria* are entirely enclosed by the more or less woody receptacle and through the protection this provides, the pericarp has been reduced to a thin membrane; in *Hirpicium* the receptacle encloses the cypselae only to some extent; and whereas in *Gazania* they are not enclosed at all (Karis, 2006, 2007; Karis et al., 2009).

Roessler (1959) revised the subtribe Gorteriinae and in the key separated *Gorteria* from *Hirpicium* and *Gazania* the combination of the annual life form (versus perennial herbs or shrubs) and by the fact that last year's capitulum remains attached to the base of the plant, as one or more of the fruits germinate *in situ* with their root penetrating the base of the capitulum (Fig. 2). This phenomenon was not known from the *Hirpicium* or *Gazania*. Roessler even used the Latin word “numquam” meaning “never” (Stearn, 1966) to emphasize that this conspicuous mode of sprouting was unique to *Gorteria*. The character is used in determination

E-mail address: stangberg@botan.su.se.

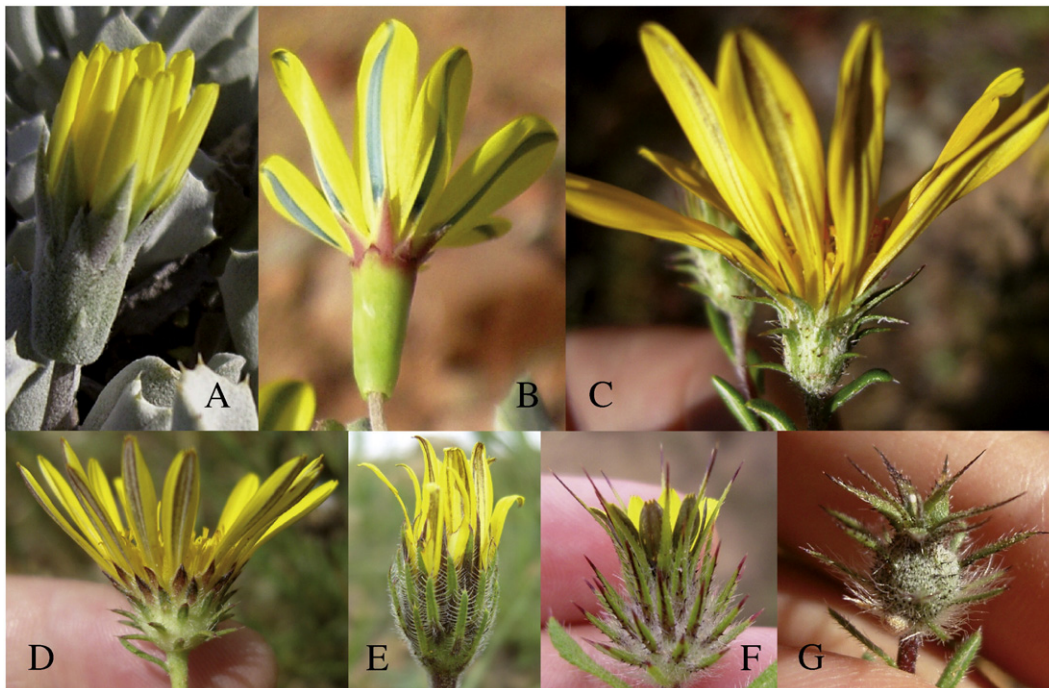


Fig. 1. Capitula in species of *Gazania*, *Hirpicium* and *Gorteria*. (A) *Gazania schenkii* O.Hoffm. Capitulum cylindrical and tomentose. (B) *Gazania lichtensteinii* Less. Capitulum cylindrical and glabrous. (C) *Hirpicium alienatum* (Thunb.) Druce. Capitulum bell-shaped (campanulate). (D) *Hirpicium bechuanense* (S.Moore) Roessler. Capitulum broadly obconical. (E) *Hirpicium linearifolium* (Bolus) Roessler. Capitulum broadly obconical. (F) *Gorteria personata* L. Capitulum urn shaped (urceolate). (G) *Gorteria diffusa* Thunb. Capitulum urceolate, mature and lignified. Photos: F. Stångberg.

keys, not only in Roessler's revision (1959) but also in other scientific documents and floras (Dyer, 1975; Goldblatt and Manning, 2000; Leistner, 2000; Karis, 2007) (however, not in Harvey, 1864–1866; Hoffmann, 1890; Trinder-Smith, 2003).

2. Results

During a field work in South Africa, in September 2006, to study species of *Gorteria* and *Hirpicium*, I noted how easily the old capitula of *Hirpicium integrifolium* (Thunb.) Less. were falling off when touched. When I started to look for seedlings close by, I noted that seedling emerged from the centre of the old capitula, and that the cypsela apparently germinated within the fallen capitulum of the mother plant (Fig. 3). The entire capitulum had apparently been functioning as a diaspore, and although it was not as lignified as in *Gorteria* it had basically the same function. The aspect of the hairy involucre bracts in the somewhat withered post-anthesis capitula of *Hirpicium integrifolium* gave the impression of a cypselae with hairy pappus awns adapted to anemochory.

The two species *Hirpicium integrifolium* and *Hirpicium alienatum* (Thunb.) Druce are similar in several respects and difficult to tell apart when not in flower. They are both small shrubs of the same size and they have a similar leaf shape. The flowers in the two species are almost the same colour but the involucre bracts of *H. integrifolium* are much longer, more narrow and covered with long hairs, while in *H. alienatum* they

are shorter, more or less glabrous, tomentose or provided with some short hairs. The distribution of these two succulent Karoo species overlaps although *H. alienatum* is found in both the Western and Northern Cape provinces of South Africa, north to the Namibian border, while *H. integrifolium* is restricted to the Western Cape province.

Following the surprising discovery of diaspore capitula in *Hirpicium integrifolium*, I investigated the situation in *H. alienatum*. In this species the young plants seemed to be connected to the mother plant and to each other with rhizomes, something I have never seen mentioned in the literature (Fig. 4). The following year (September 2007), during the next season of field work in Namaqualand in the Northern Cape province (South Africa) I found seedlings of *Hirpicium alienatum* sprouting from inside an old capitulum (Fig. 5). Just as in *H. integrifolium*, the fallen capitula of *H. alienatum* are not as hard and lignified as in *Gorteria*, but showed the same adaptation.

The fact that the two *Hirpicium* species, *H. integrifolium* and *H. alienatum*, have been shown to have entire capitula acting as diaspores just like all 3 species of *Gorteria* has never been observed before.

In the tribe Arctotideae, capitula acting as diaspores, were previously known to occur only in a few genera of the subtribe Gorteriinae namely *Cuspidia*, *Didelta* and *Gorteria* (Roessler, 1959; Bremer, 1994; Karis, 2007). The capitula in *Didelta* act as a diaspore in a different way than in the other genera; parts of the receptacle is becoming lignified with age, enclosing the cypselae, subsequently breaking up into 3–5 parts, while the involucre



Fig. 2. *Gorteria personata* L. The arrow points out the previous year's lignified capitulum. South Africa, Western Cape, Clanwilliam Div., F. Stångberg and P. O. Karis 4 (S). Photo: F. Stångberg.

bracts become membranous. In *Cuspidia* and *Gorteria* the entire involucre becomes lignified at maturity, falls off the plant, thus enclosing and protecting the cypselae until they germinate.

Gorteria is characterized by its annual life form in combination with the way the seedlings sprout from within the previous year's fallen capitulum (Fig. 2). After flowering the involucre gets lignified and encloses the cypselae completely. The entire capitulum falls off at maturity and is probably adapted to anemochory or zoochory depending on the extent of lignification and amount of hairs on the involucral bracts, which vary between the species. Since all *Gorteria* species are annuals it is always possible to find the previous year's lignified capitulum at the base of the plants, more or less buried in the ground with one to several new plants sprouting from within

it. The lignified capitula are most likely to have a protective function, insulating the fruit against extreme temperature or resting predation.

3. Discussion

Roessler (1959) considered that the closest relatives to the genus *Gorteria* were the small shrubs *Hirpicium integrifolium* and *H. alienatum*.

In contrast to Roessler's taxonomic work (Roessler, 1959), more recent studies have used a cladistic approach (Funk et al., 2004; Karis, 2006; Funk and Chan, 2008), and show that *Hirpicium* is paraphyletic, with one or two species being closer to *Gorteria* than to the remaining species of that genus.



Fig. 3. *Hirpicium integrifolium* (Thunb.) Less. Seedlings sprouting from within old diaspore capitula. South Africa, Western Cape, Oudtshoorn Div., F. Stångberg and P.O. Karis 55 (S). Photo: F. Stångberg.

In the analysis of morphological characters by Karis (2006) *Hirpicium integrifolium* and *H. alienatum* are retrieved as a sister group to a monophyletic *Gorteria*, which is in turn sister to the part of *Hirpicium* formerly known as *Berkheyopsis* O. Hoffm. (included in this study are *Hirpicium bechuanense* (S. Moore) Roessler, *H. gorterioides* (Oliv. & Hiern) Roessler and *H. diffusum* (O. Hoffm.) Roessler). Spine-like hairs on disc and ray-floret corollas, involucre bracts connate only at the bases and the presence of subepidermal crystal cells in the testa are synapomorphies diagnosing the *Gorteria*-*H. integrifolium*-*H. alienatum* clade.

The preliminary analysis of Funk et al. (2004) also indicates that *Hirpicium* is paraphyletic, and that at least *Hirpicium integrifolium* is closer to *Gorteria* than to the other *Hirpicium* species in the study. In Funk and Chan (2008) phylogenetic trees are based on nuclear (ITS), chloroplast (*trnL-F* and *ndhF*) data and also those markers combined. All data show the same

pattern regarding the paraphyletic nature of *Hirpicium*, with *Hirpicium integrifolium* as sister to a monophyletic *Gorteria*. *Hirpicium bechuanense*, *H. gorterioides* and *H. gazanioides* (Harv.) Roessler are always retrieved as a monophyletic group but the positions of *Hirpicium echinus* Less. and *H. diffusum* are different with different data sets.

In the molecular studies of Funk et al. (2004) and Funk and Chan (2008) *H. alienatum* was not included. In Funk et al. (2004) the sequence of *Hirpicium integrifolium* is from the specimen Koekemoer & Funk 1956 (PRE). A photograph of the specimen was reproduced in Karis et al. (2009) under the name *Hirpicium alienatum* and the fact that it was collected in the Northern Cape Province, South Africa, strongly suggests that the specimen was misidentified, and is in fact *Hirpicium alienatum*.

Cladistic analyses have pointed to a close evolutionary relationships between *Hirpicium integrifolium*, *H. alienatum*



Fig. 4. *Hirpicium alienatum* (Thunb.) Druce. Small plants connected with rhizome. South Africa, Western Cape, Uniondale Div., F. Stångberg and P.O. Karis 56 (S). Photo: F. Stångberg.

and *Gorteria*. It is therefore very interesting that capitula acting as diaspores have been found in both these species, but not in any of the other *Hirpicium* species I have seen in the field. The fact that the salient diagnostic feature of *Gorteria* is shared with their alleged closest relatives in *Hirpicium* corroborates the

hypothesis that the taxa are immediately related and sheds light on the possible evolutionary transformation of the capitula into a diaspore.

Acknowledgements

I am grateful to Cape Nature, South African National Parks and Northern Cape Department of Nature and Environmental Conservation for issuing collecting permits (to P. O. Karis and F. Stångberg). Grants have been obtained from Swedish International Development Cooperation-Swedish Research Links (to P.O. Karis) for field work. Thanks to P.O. Karis, Jan Vlok and AnneLise Vlok for company and assistance in the field and for sharing your knowledge about the South African flora. Thanks also to Jürg Schönenberger for help with translation from German and to Arne Anderberg for constructive criticism and valuable comments on the manuscript.

References

- Bremer, K., 1994. Tribe Arctoteae. Asteraceae, Cladistics, and Classification. Timber Press, Portland, Oregon, pp. 246–262.
- Dyer, R.A., 1975. The Genera of Southern African Plants 1. Botanical Research Institute, Pretoria, pp. 1–756.
- Funk, V.A., Chan, R., 2008. Phylogeny of the spiny African daisies (Compositae, tribe Arctotideae, subtribe Gorteriinae) based on *trnL-F*, *ndhF*, and ITS sequence data. *Molecular Phylogenetics and Evolution* 48, 47–60.
- Funk, V.A., Chan, R., Keeley, S.C., 2004. Insights into the evolution of the tribe Arctoteae (Compositae: subfamily Cichorioideae s.s.) using *trnL*, *ndhF*, and ITS. *Taxon* 53, 637–655.



Fig. 5. *Hirpicium alienatum* (Thunb.) Druce. Seedlings sprouting from within old diaspore capitula. South Africa, Northern Cape, Namaqualand Div., F. Stångberg and P.O. Karis 132 (S). Photo: F. Stångberg.

- Goldblatt, P., Manning, J.C., 2000. Cape Plants. A Conspectus of the Cape flora of South Africa. *Strelitzia*, vol. 9. National Botanical Institute, Pretoria, pp. 1–743.
- Harvey, W.H., 1864–1866. Compositae. In: Harvey, W.H., Sonder, O.W. (Eds.), *Flora Capensis*, Being a Systematic Description of the Plants of the Cape Colony, Caffraria and Port Natal, Vol. 3. L. Reeve, London, pp. 44–530.
- Hoffmann, O., 1890. Compositae. In: Engler, A., Prantl, K. (Eds.), *Die Natürlichen Pflanzenfamilien* 4(5). Verlag von Wilhelm Engelmann, Leipzig, pp. 87–391.
- Karis, P.O., 2006. Morphological data indicates two major clades of the subtribe Gorteriinae (Asteraceae–Arctotideae). *Cladistics* 22, 199–221.
- Karis, P.O., 2007. Tribe Arctotideae Cass. In: Kadereit, J.W., Jeffrey, C. (Eds.), *The Families and Genera of Vascular Plants. Flowering Plants. Eudicots. Asterales*, vol. 8. Springer-Verlag, Berlin, pp. 200–207.
- Karis, P.O., Funk, V.A., McKenzie, R.J., Barker, N.P., Chan, R., 2009. Arctotideae. In: Funk, V.A., Susanna, A., Stuessy, T., Bayer, R. (Eds.), *Proceedings of the International Compositae Alliance*, Barcelona, 2006. In *Systematics, Evolution and Biogeography of Compositae*. IAPT, Vienna, Austria, pp. 285–310.
- Leins, P., Thyret, G., 1971. Pollen phylogeny and taxonomy exemplified by an African Asteraceae group. *Mitteilungen der Botanischen Staatssammlung München* 10, 280–286.
- Leistner, O.A., 2000. Seed plants of southern Africa: families and genera. *Strelitzia*, vol. 10. National Botanical Institute, Pretoria, pp. 1–775.
- Roessler, H., 1959. Revision der Arctotideae–Gorteriinae (Compositae). *Mitteilungen der Botanischen Staatssammlung München* 3, 71–500.
- Stearn, W.T., 1966. *Botanical Latin*. Nelson, London, pp. 1–546.
- Trinder-Smith, T.H., 2003. The Levyns guide to the plant genera of the southwestern Cape. *Contributions from the Bolus Herbarium number*, vol. 21. University of Cape Town, pp. 1–355.
- Wortley, A.H., Funk, V.A., Skvarla, J.J., 2008. Pollen and the evolution of Arctotideae (Compositae). *Botanical Review* 74, 438–466.