

Heterolepis: an unplaced genus

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HISTORICAL OVERVIEW AND MORPHOLOGY

The three species of *Heterolepis* Cass. are found in southern South Africa and especially in parts of the Succulent Karoo and almost throughout the Cape Floristic Region (CFR; Linder 2003). One of the species, *H. aliena* (L. f.) Druce, forms a small shrub covered with large yellow heads and is often cultivated. The genus has been moved from tribe to tribe. Cassini (1816, 1821) described *Heterolepis* and placed it in the tribe Arctotideae. Lessing (1832) treated the whole tribe Arctotideae along with Calenduleae and some Senecioneae, as part of a large Cynaroideae. Bentham (1873) reestablished Arctotideae but he placed *Heterolepis* in Inuleae; Hoffmann (1890–1894) followed Bentham. Robinson and Brettell (1973a) returned *Heterolepis* to Arctotideae, and Norlindh (1977) placed it in the subtribe Gorteriinae. Merxmüller et al. (1977) in his treatment of Inuleae agreed that *Heterolepis* did not belong in that tribe and suggested a placement in Mutisieae, but nearly everyone has left it in Arctotideae.

In truth, *Heterolepis* never fit very well in Arctotideae, and Bremer (1994) pointed out that it did not have all the diagnostic characters of the subtribe Gorteriinae, where it was placed by Norlindh (1977). In comparison to both subtribes of Arctotideae, there is little reason to include it. It has none of the putative synapomorphies of Gorteriinae, for instance, it lacks latex, the involucre bracts are only slightly connate, the receptacle is not deeply alveolate, it has female ray florets where the lamina is 3-toothed and 4-veined, and finally it has a pappus of bristle-like scales. In the subtribe Arctotidinae the anthers are without exception ecaudate, while in

Heterolepis the anthers are caudate with barely branched tails (somewhat similar to those of the *Berkheya* clade of Gorteriinae). The anther apical appendages of *Heterolepis* are soft but longer and quite unlike the shorter but likewise soft ones of Arctotidinae. Also *Heterolepis* has anthers with a polarized endothecium, or many cells have a plate but no polarized pattern, which is similar to the endothecium in some species of the *Berkheya* clade of Gorteriinae. In contrast, Arctotidinae have a consistently radial endothecium.

Bremer's (1994) morphological cladistic analysis placed *Heterolepis* as the sister group to the *Platycarpha*-Arctotidinae clade or in a trichotomy with the two main subtribes depending on the outgroup used. Based on this analysis Bremer decided to list *Heterolepis* as belonging to Arctotideae but unassigned to subtribe, and the same approach was followed by Karis (2007). In Funk et al. (2004) and Funk and Chan (2008) *Heterolepis* was sometimes linked with the base of Gorteriinae but with very weak support.

It is interesting to note that Ahlstrand (1992) studied the embryology of species from both subtribes as well as *Heterolepis aliena* and *H. peduncularis*. He found that while representatives of Arctotidinae and Gorteriinae all shared a possibly plesiomorphic monosporic *Polygonum* type of embryosac development, *Heterolepis* species displayed a bisporic embryosac development. All other examples of bisporic embryo sac development are confined to the subfamily Asteroideae (Asplund 1978; Ahlstrand 1992). However, *Heterolepis* has other symplesiomorphic morphological characters that demonstrate its affinity to groups outside of Asteroideae, such as deeply lobed disc

corollas, an entire stigmatic surface, and a style with a ring of longer sweeping hairs below the bifurcation. In addition, *Heterolepis* also lacks the apomorphic length mutation of the *rbcL* gene (Karis, pers. obs., sequence from Forest et al. 2007), and which is found in all Asteroideae (Bremer 1994).

PHYLOGENY

The subtribes Arctotidinae and Gorteriinae as currently defined are monophyletic. In order to accomplish this, three taxa (nine species) had to be removed: *Heterolepis* and the tribes Eremothamneae, and Platycarpeae. The most recent analysis has not resolved the placement of *Heterolepis* within the subfamily (Chapter 23).

TAXONOMY

Heterolepis Cass. in Bull. Sci. Soc. Philom. Paris 1820: 26. 1820, nom. cons. [information taken from Karis 2007; Hermann et al. 2000, and pers. obs.] (Fig. 31.1)

Small, rounded, sometimes sprawling, densely leafy sub-shrubs to ca. 0.5 m tall with woody rootstocks; sometimes scented. Leaves linear-oblong, 15–40 mm long, ericoid; apex linear to acute, base tapering, margins entire or apically dentate, abaxial surface densely woolly, adaxial surface glabrous. Heads pedunculate, radiate, up to 6 cm in diameter. Involucral bracts in 2–3 rows, somewhat connate at base, outer lanceolate, foliaceous, acute; inner bracts rounded-truncate, apically scarious and lacinate; receptacle areolate. Florets yellow; ray florets female, fertile, generally with staminoides, with a filiform lobe ventrally in the sinus of the tube, lamina apically 3-lobed; disc florets bisexual, fertile, corolla deeply 5-lobed; anthers calcarate, shortly caudate, with a long collar of reinforced cells, apical appendages soft, oblong; styles slender, style branches short; slightly thickened below the style branches, sweeping hairs acute, somewhat longer in a ring below the bifurcation. Achenes small, ca. 3 mm long, oblong-obovoid, densely sericeous with twin hairs and without ribs. Pappus of 1–10 yellow-brown, stout, subulate, bristle-like, marginally barbellate or subplumose scales of varying length up to 10 mm, usually in two rows (Fig. 31.1).

Heterolepis is a well-defined genus confined to South Africa. *Heterolepis aliena* is easily recognizable from a distance by the large number of flowering heads that almost completely cover the plant (Fig. 31.1B), and the pom-pom like shape of the older heads is typical for all three species (Fig. 31.1A). On a more detailed scale it can be identified by its ray florets, which generally have staminodes and a filiform lobe ventrally in the sinus of the tube (Fig.

31.1D), its pappus of 1–10 irregular length bristle-like scales (Fig. 31.1A insert), and its small achenes covered with dense white twin hairs (Fig. 31.1A insert).

The genus name *Heterolepis* is derived from the Greek *hetero* meaning dissimilar and *lepis* a scale.

POLLEN

Spherical, ca. 30–35 μm in diameter (dry), tricolporate, echinate with spines evenly and deeply separated, tips of spines solid, sides with distinct microperforations; internally nearly totally cavate, with sparse slender, sometimes branched columellae under sides of spines, outer exine with well-developed layer of columellae with distinct underlying inner tectum. Spines fistulose under apex, fistula bordered by a few enlarged columellae (Fig. 31.1E, F. Additional photos and comments on the pollen can be found in Wortley et al. (2008).

CHROMOSOME NUMBERS

The only count reported is $x = 6$ (Strother et al. 1996), probably $2n = 12$. The TROPICOS database reports this number and reference as does the Compositae chromosome website maintained by Watanabe (<http://www.lib.kobe-u.ac.jp/products/asteraceae/index.html>). There is a report of $x = 10$ in Hermann (2000), but that appears to be an error as we have searched all of the listed references and can find only the Strother et al. count.

CHEMISTRY

We found no information on the chemistry of *Heterolepis*.

BIOGEOGRAPHY

Heterolepis aliena occurs on rocky sandstone slopes, in crevices and on outcrops from the Cedarberg Mountains to the Witteberg and Hermanus (pers. obs.; Goldblatt and Manning 2000). It is most often found on steep, sunny, north or northeast-facing slopes or well-drained, rocky outcrops on shallow soils, in dry fynbos as well as in areas that receive high rainfall, such as Franschoek. *Heterolepis peduncularis* DC. grows on plains near rocky slopes, has smaller heads on longer peduncles than *H. aliena*, and it is scented. It has a wider distribution, but it is less common. The third species, *H. mitis* DC. occurs in the Eastern Cape, but it has not been collected for a considerable time.



Fig. 31.1. *Heterolepis aliena* (L.f.) Druce. **A** head in late flower/early fruit, note “pom-pom” like appearance of head; **insert** achene, note small size, white pubescence, and irregular bristle-like pappus; **B** plant in full flower; **C** lateral view of heads and narrow leaves; **D** close-up of flowering head; **E** internal view of pollen, note that it is nearly totally cavate, with sparse slender, sometimes branched columellae under sides of spines; **F** external view of pollen. [Photographs: A–D, A. Notlen; E, F, from Wortley et al. 2008.]

ECOLOGY, CONSERVATION, HORTICULTURE

Along with members of both subtribes of Arctotideae, *Heterolepis* grows in the succulent karoo and CFR. It is xeromorphic with rather narrow leaves (Fig. 31.1A, C), a situation paralleled in many plant groups inhabiting vegetation in regions with Mediterranean climate.

Victor and Dold (2003) list *Heterolepis mitis* DC. as a plant that is “Near Threatened (NT)” in that it does not meet the criteria for being listed as threatened with extinction but could qualify in the future.

Heterolepis aliena (Rock Daisy or Rotsgousblom) makes a very attractive garden plant and if one can mimic the

hot, dry, sunny, well-drained habitat it normally inhabits, it will thrive almost anywhere although standing water should be avoided. It will propagate from seed and from cuttings (Notten 2007).

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