



A revision of *Heterolepis* Cass. (Asteraceae: Cichorioideae)



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ABSTRACT

The small Cape genus *Heterolepis* (Asteraceae: Cichorioideae) containing four species, is poorly known and its tribal affinities within the subfamily are enigmatic. The genus has not been taxonomically treated since the 1865 publication of Harvey and Sonder's *Flora Capensis*, and a new species was recently described. Here, we collate information from the more than 200 collected specimens, combined with a detailed morphological investigation of each species, and present a full revision of the genus. A review of previous work, the taxonomic history, intrafamilial phylogenetic affinities, and morphological characteristics of *Heterolepis* are presented, together with a key to the species and detailed images of floral features. For each species a nomenclatural review, detailed description and observations, illustrations of selected features, distribution map and list of examined specimens is provided, as well as a full list of all relevant literature and a database of existing specimens.

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1. Introduction

The Asteraceae subfamily Cichorioideae is diverse in southern Africa, housing several large genera such as *Berkheya* Ehrh. and *Arctotis* L., as well as a number of small, morphologically unusual genera such as *Eremothamnus* O.Hoffm., *Hoplophyllum* DC. and *Platycaurpha* Less. *Heterolepis* Cass. is one of these small and curious genera, comprising four species, all distributed in the winter-rainfall Cape Floristic Region (CFR) of South Africa. All species of *Heterolepis* are small shrublets with narrow leaves and solitary, usually radiate yellow capitula. They possess an unusual combination of micromorphological characters that has led to conflicting phylogenetic placements by different authors, sometimes in different subfamilies of the Asteraceae.

Three species of *Heterolepis* are poorly-known, but one, the large-flowered *Heterolepis aliena* (L.f.) Druce, is not uncommon throughout the drier parts of the western CFR (Fig. 1) where it is well-collected, and known by the name 'rotsgousblom' ("rock daisy"). The remaining three taxa are *Heterolepis peduncularis* DC., a species with smaller capitula and much longer peduncles, which is found predominantly on shale

soils on the southern Cape coastal forelands; *H. anomala* J.C.Manning & Goldblatt, a recently-described species with discoid capitula; and the distinctive *H. mitis* (Burm.f.) DC., a small radiate rock-crevice specialist that occurs only in a range of mountains in the Eastern Cape.

Heterolepis has not been revised since Harvey and Sonder (1865) and there has been no modern compilation of taxon descriptions, nomenclatural history, distribution maps or illustrations. Although *H. aliena* is well-represented in herbaria, the remaining three species, including the recently described *H. anomala* (Manning and Goldblatt, 2011), are narrowly-distributed, poorly known, and likely to be of conservation interest. A compilation of all known information on the genus, together with a comprehensive investigation of morphology and the publication of illustrations and distribution maps, is an important step towards increased knowledge of this anomalous and poorly-known genus.

2. Materials and methods

Herbarium specimens were examined at NBC, BOL and PRE, and additional loan material was obtained from GRA; all sheets were photographed using a standard digital camera. Type material not available in these herbaria was examined, where possible, using digital images from the JStor Global Plants website (<https://plants.jstor.org/>) or provided by the curators of UPS-THUNB, G-DC, C and LINN. The specimen database was supplemented by field collections of all species except *Heterolepis anomala*. Information from specimens not yet

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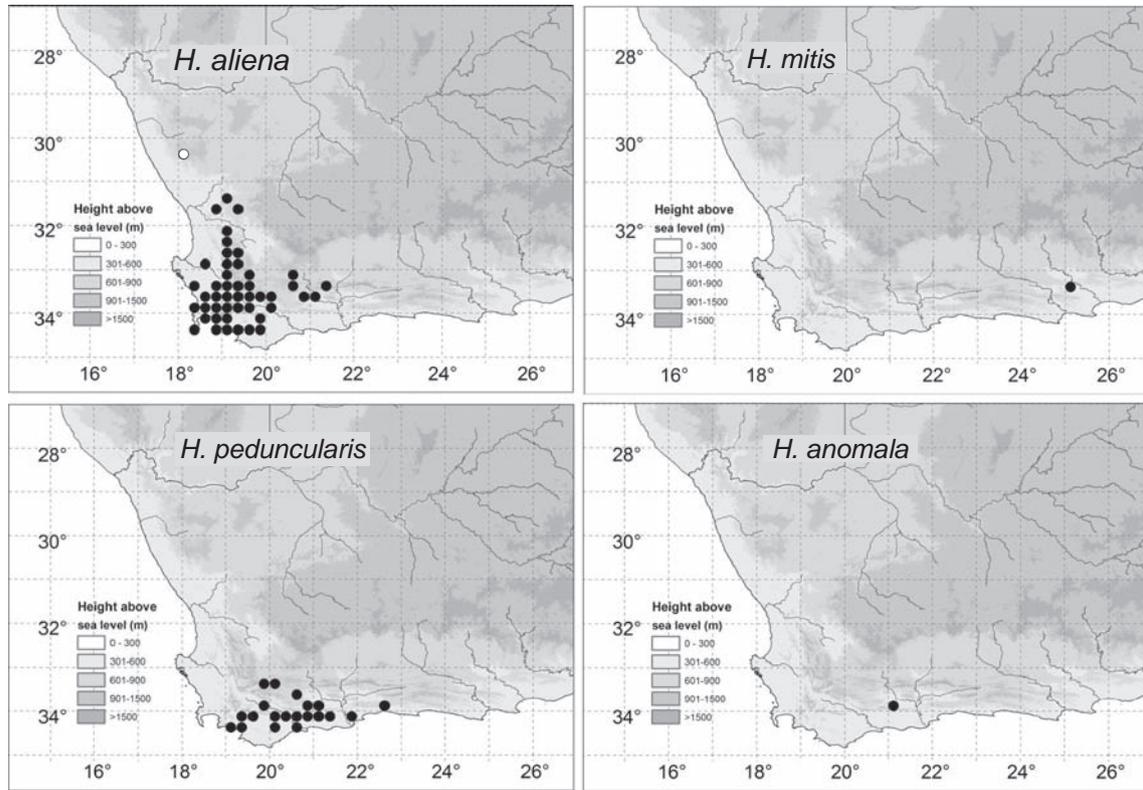


Fig. 1. Geographic distributions of *Heterolepis* species, based on specimens from BOL, NBC, GRA and PRE. Each dot represents the centroid of a quarter-degree grid square from which the species has been collected at least once. The white dot for *H. aliena* indicates a doubtful locality from a collection by T.P. Stokoe apparently from 'Little Namaqualand, Kamiesbergen'. Snijman (2013) reports that there is a series of Stokoe collections with this locality label, all of CFR-restricted species that are otherwise unknown from as far north as the Kamiesberg. Some of the specimens have duplicates in BOL that are instead labelled 'Castle Rock, Ceres', a far more likely origin (Snijman, 2013).

captured on the SANBI specimen database were encoded from the photographs of herbarium specimens, and the data on already-captured specimens was checked and corrected, if necessary, in the same way. All specimens were databased and those with sufficiently precise locality information were georeferenced to quarter-degree grid square (QDS). Georeferenced localities were used to produce species distribution maps (mapped to QDS centroid) in Arcview. Morphological measurements were taken with precision calipers off at least ten specimens per species unless otherwise indicated. Heads from at least three specimens of each species were rehydrated in boiling water and dissected under a stereomicroscope to obtain counts of floret number; where fewer specimens were available, this is indicated in the text. Micromorphological features were examined in dried material rehydrated in boiling water under a dissecting microscope, the images being captured with a digital imaging system. Measurements were taken on the captured images using a calibrated digital imaging software, or by calibrated drawings produced via a drawing tube attached to a dissecting stereoscope. Cypselae hairs were investigated by mounting rehydrated hairs in a fuchsin-stained glycerine jelly melted under a coverslip using gentle heat; the hairs were examined in a stereomicroscope under 100× magnification.

A full list of all names associated with *Heterolepis* is provided in Appendix A, while the history of relevant taxonomic work is outlined in Appendix B.

3. Species concepts

The species concept followed here corresponds to the theoretical precepts of the evolutionary species concept, in which a basic unit in evolution corresponds to an ancestor–descendant sequence of interbreeding populations with its own separate and unitary evolutionary role and tendencies (Simpson, 1951, 1961; Wiley, 1978). Fixed

morphological differences as observed on herbarium specimens were used as evidence for evolutionary independence; thus the species defined here will correspond with those defined on purely morphological grounds.

4. Morphology

4.1. Habit

All *Heterolepis* species are shrublets. They vary in height (from 20 cm to over 100 cm high) and degree of branching, from well-branched and rounded to sparsely branched and erect. Two species are strongly associated with rocky habitats or root in rock crevices, while the remaining two grow in soil in open shrubland. Some species have a degree of development of a woody rootstock and resprout after fire or disturbance. Apical growth is terminated by the flowerhead, with growth in subsequent years initiating from well below the point of attachment of the old head.

4.2. Trichomes

Heterolepis species possess multicellular, biseriate trichomes on the peduncles, involucre bracts, corolla tube and corolla lobes. There appear to be at least three, possibly up to four or five, different types of trichomes, although a detailed ultrastructural investigation would be required to determine differences in trichome structure, and the apparent differences may be due to variations in the volumes of cells in different parts of the trichome. All the trichome types comprise a distinct, usually biseriate stalk, and a separate head structure. We have distinguished the types based on both their position and shape.

4.2.1. Trichome type A

This is the largest type of trichome and occurs on the peduncles and involucre bracts (Figs. 2b,e; 4c,e; 6a). The base has a conical shape with a broad, somewhat sprawling multicellular basal section narrowing to a slender stalk which is made up of a double row of cells. The head is relatively small and may be spherical or oblong and appears to comprise many small stacked cells, also in a double row, and often with darkened portions that may be pigmented cell contents or thickened cell walls. These trichomes attain their greatest size in the central portion of the involucre bracts, where the bases can be especially large; the trichomes on the bracts and peduncle are, however, quite variable in size so that any portion of the peduncle or central part of the involucre bract comprises a mix of differently-sized trichomes. The cells of these structures are generally filled with a dark red-purple pigment. On the involucre

bracts these glands are bent and directed upwards (towards the bract apex), while on the peduncle they are straight, being directed outwards. On the margins of the bract, the trichomes contain less pigment and are often more slender, and lack the broad sprawling base.

4.2.2. Trichome type B

This trichome type appears to have a very similar basic structure to type A. It occurs on the corolla tubes of both rays and discs nearly in all species (Fig. 4g,h,k). It differs from type A in being more slender, with a narrower base, so the overall shape is hair-like or elongate-clavate. It also lacks the red pigment. Slender, segmented, headless trichomes on the corolla lobes of *H. anomala* (Fig. 6d,g) may be a variation of this type, or may be a different type of trichome entirely.

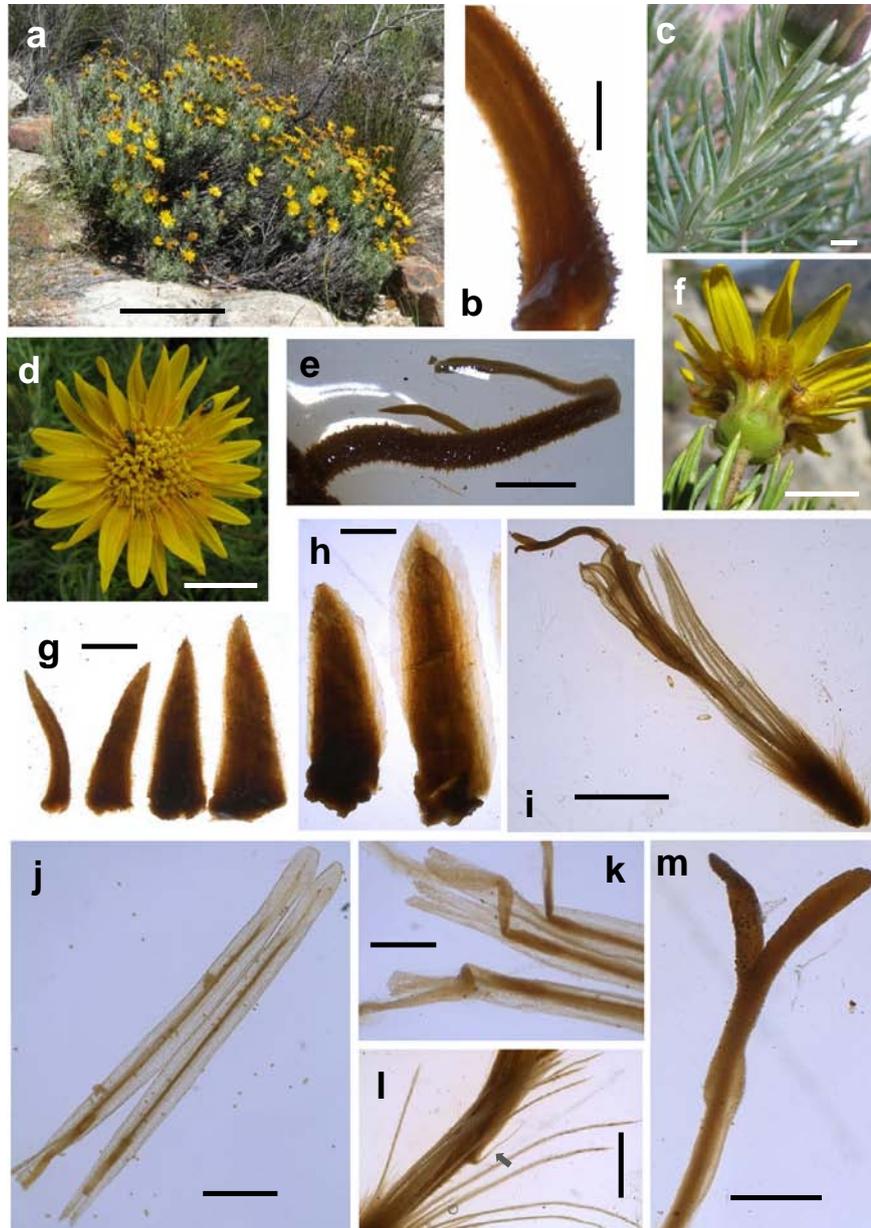


Fig. 2. *Heterolepis aliena*. a – habit (scale bar = 250 mm); b – middle involucre bract showing glands (scale bar = 0.6 mm); c – leaves below immature capitulum (scale bar = 9.0 mm); d – mature capitulum (photo by Jon Richfield, Wikipedia; scale bar ≈ 20 mm); e – densely glandular peduncle (scale bar = 40 mm); f – involucre, showing the basal fusion of the bracts, the fleshy, herbaceous texture and glandular indumentum of the outer bracts and peduncle, and the membranous apices and margins of the inner bracts (scale bar = 30 mm); g – involucre bract series with outermost at left and middle at right (scale bar = 2.2 mm); h – involucre bract series with inner at left and innermost at right (scale bar = 2.2 mm); i – disc floret, post-anthesis (scale bar = 3.4 mm); j – anthers of disc floret showing obtuse, flat apices and tailed, calcarate bases (scale bar = 0.93 mm); k – anther tails (scale bar = 0.7 mm); l – ray floret corolla showing the filiform lobe (arrow) in the tube sinus (scale bar = 2.0 mm); m – style branches of disc floret (scale = 0.8 mm). All photos by N. Bergh unless otherwise indicated. Images b, e, f, g, h, i, k, l and m taken from rehydrated material of *Compton 21178* (NBG).

4.2.3. Trichome type C

Apart from the elongate types A and B, there is at least one type of sessile, clavate trichome occurring on various parts of the plants. Sessile trichomes appear to be scattered amongst the longer A-type glands on the involucre of *H. anomala*, but these may just be short variants of the A-type. The young stems of *Heterolepis mitis* bear oblong trichomes that may be responsible for a resiniferous covering sometimes visible in this species. However, the corolla lobes of *Heterolepis mitis* bear on their abaxial surfaces very short stalked globular-headed glands (Fig. 3c) that appear to have a much simpler cellular structure than any of the glands mentioned thus far. These we have called gland type C.

4.3. Stems

At least one species (*H. aliena*) possesses white milky sap in the young branches, but this character is not observable in dried specimens

and has not been investigated in the other species. The lower parts of the stems are frequently bare, with leaves borne towards the ends of the branches. The stems are thin-barked and glabrous, or alternatively white-woolly, and are sometimes glandular.

4.4. Leaves

Leaves are alternate and erect to spreading, straight or slightly incurved. Most species have leaves that are leathery in texture, ericoid, sclerophyllous and narrow (Figs. 2c; 4e; 5). In three of the species, the leaves are linear-oblong to narrowly oblanceolate, sessile, with a somewhat thickened and leathery texture, an acute to rounded and shortly mucronate leaf apex and leaf margins that are entire or obscurely minutely and sparsely toothed. The margins are also revolute. The adaxial surface is glabrous or sparsely white-woolly becoming glabrescent, while the abaxial surface is densely to sparsely white-woolly except



Fig. 3. *Heterolepis mitis*. a – habit (photo: R. McKenzie; scale bar \approx 250 mm); b – flowering shoot (photo: Nick Helme; scale bar \approx 7 mm); c – disc floret corolla lobes with sessile trichomes (scale bar = 0.6 mm); d – immature ray floret (scale bar = 1.8 mm); e – disc floret with pappus (scale bar = 1.5 mm); f – side view of ray floret showing filiform corolla lobe (scale bar = 1.3 mm); g – disc style apex showing papillate region (scale bar = 1.2 mm); h – disc floret anthers (scale bar = 1.2 mm); i – mature ray floret showing relatively short 3-lobed lamina with 4 veins, filiform corolla lobe in the tube sinus, and staminodes (scale bar = 1.7 mm); j – dissected receptacle showing alveole margin projections (scale bar = 25 mm); k – disc floret anther tails and filaments (scale bar = 0.5 mm); l – dissected ray floret to show staminodes (scale bar = 0.08 mm). All images are of McKenzie 3147, except b which is of Helme 8036 (both NBG). Images c–l are of dried, rehydrated material. All photos by N. Bergh unless otherwise indicated.

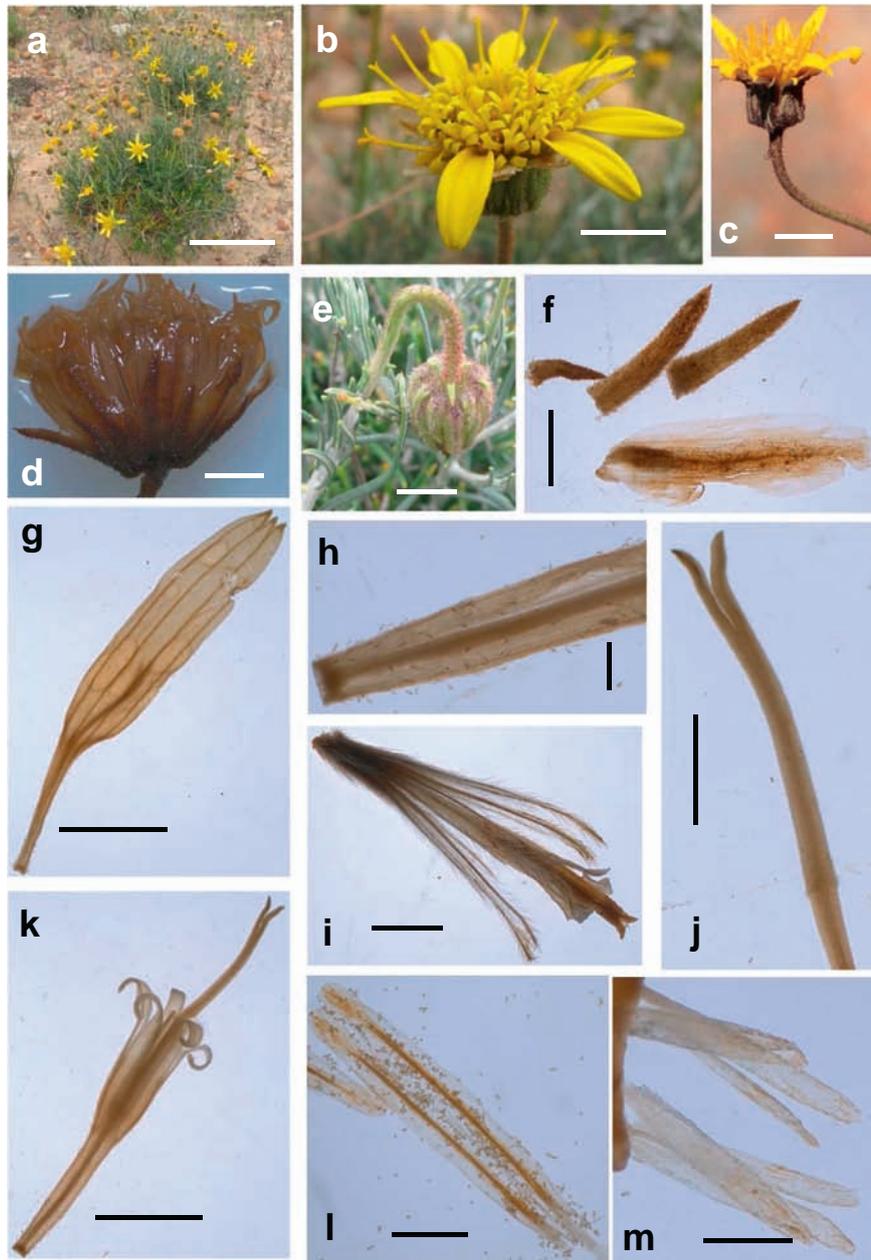


Fig. 4. *Heterolepis peduncularis*. a – habit (photo: D. Euston-Brown, iSpot; scale bar \approx 110 mm); b – capitulum (photo: D. Euston-Brown, iSpot; scale bar \approx 8.0 mm); c – involucre and upper part of peduncle (scale bar = 9 mm); d – capitulum, showing arrangement of the involucre bracts (scale bar = 4.0 mm); e – immature capitulum (photo: D. Euston-Brown, iSpot; scale bar \approx 6 mm); f – involucre bract series from outermost at upper left to innermost at lower right (scale bar = 2.0 mm); g – ray floret corolla (scale bar = 2.8 mm); h – disc floret corolla showing trichomes of type 'B' (scale bar = 0.55 mm); i – disc floret immediately post-anthesis, before style elongation (scale bar = 2.0 mm); j – disc style apex showing inconspicuous 'tuft' at base of pappillose region (scale bar = 0.9 mm); k – disc floret corolla (scale bar = 2.2 mm); l – dissected disc anthers releasing pollen (scale bar = 1.0 mm); m – ray staminodes (scale bar = 0.5 mm). Images d and f – m from rehydrated material of Bohnen 9046 or Helme 5368 (NBG). All photos by N. Bergh unless otherwise indicated.

on the somewhat enlarged abaxial midrib. The leaves of *Heterolepis mitis* (Fig. 3b) differ from those of the other species in being glabrous, thin and shiny, and in frequently having a short petiole-like narrowed base.

4.5. Peduncles

The peduncle comprises the apical portion of the shoot (Fig. 5) and is unbranched and leafless, although it may bear a few bracts. Peduncle length is one of the characters that distinguishes species in *Heterolepis*, varying from very short in *Heterolepis mitis* (Fig. 3b) to more than 20 cm long in *H. peduncularis* (Fig. 5a). Peduncles are often longitudinally striate and may be densely glandular, particularly near the capitulum (Figs. 2e,f; 4c,e); peduncular bracts bear the same glandular covering as

the peduncle. In species with distinct peduncles, the vestiture of the peduncle is markedly different to that of the stem.

4.6. Capitula and receptacle

Capitula are always solitary in *Heterolepis*, and are generally radiate, with only *H. anomala* being consistently discoid. The rays, when present, are borne in a peripheral whorl and are female fertile, while the discs are always hermaphrodite. Capitula are smallest in *H. mitis*, and largest in *H. aliena*. Paleae are absent. The receptacle is alveolate, and the alveole margins have short, irregular projections (Fig. 3j). The receptacle becomes somewhat woody with age.



Fig. 5. Pressed specimens of *Heterolepis peduncularis* (a) and *H. anomala* (b) to illustrate the longer peduncles bearing fewer bracteoles in *H. peduncularis*, as well as its more slender leaves that are more sparsely-arranged on the stems, and decrease in length acropetally.

4.7. Involucre

The involucre in *Heterolepis* comprises 2–4 indistinct series of imbricate bracts, fused at the base to form a cup with a flattish, rounded or concave base (Figs. 2f; 3b; 4c,d). The outer bracts are the smallest and narrowest, and are entirely fleshy, subulate, herbaceous and green with an acute apex and a dense covering of stout glandular trichomes of type A (Figs. 2g; 4f; 6a). Bract structure undergoes a transition from the outermost to the innermost, the transition involving an increase in size and a decrease in the proportion of the bract that is fleshy, this being confined to an increasingly smaller basal portion. In contrast, increasing proportions of the bract apex and margins become membranous, thin, glabrous, brown and translucent (Figs. 2f,h; 4f; 6a). The membranous margin is often serrate and drawn into fine points. The bracts become dark brown with age.

4.8. Corolla

Ray and disc corollas in *Heterolepis* are the same colour, usually bright yellow (Figs. 2a,d,f; 3a,b; 4a–c) but much paler (almost whitish) in *H. anomala* (Fig. 6b,d,g). The corolla tubes are sparsely covered with slender, multicellular trichomes of type 'B'. The rays have a shallowly three-lobed, strap-shaped lamina (Figs. 3d,i; 4g) and a long, filiform lobe in the sinus of the tube (Figs. 2l; 3f,i), giving a very unusual 3 + 1 corolla lobe structure. Disc corollas are narrowly campanulate (Figs. 3e; 4k; 6d), actinomorphic, deeply five-lobed (Figs. 3c,e; 4b,k; 6b,g) and the corolla lobes are narrow, apically rounded and recurved at maturity, with slightly thickened margins (Figs. 3c; 6g) and sometimes bearing globular trichomes of type 'C' on their abaxial surfaces. Five conspicuous veins are situated alternatively with the lobes (Figs. 3c; 6d,g).

4.9. Anthers

Fertile anthers are present only in the disc florets, while the rays possess staminodes. The fertile anthers are calcarate and shortly caudate with obtuse, un- or barely-branched and slightly curled tails (Figs. 2j,k; 3h,k; 6g). The filament collar is oblong and conspicuous. The apical appendages are obtuse, truncate or bifid and are thin, soft and flat (Figs. 2j; 3h; 4l; 6g,h). The staminodes are smaller than the

fertile anthers, but otherwise similar in structure, and protrude slightly from the ray floret corolla tube (Figs. 3l; 4m).

4.10. Style

Styles do not vary between the ray and disc florets; they are terete, slender and glabrous with a swollen base, and protrude at length from the corolla tubes (Figs. 2d; 3b; 4b,c,k; 6b,d). The apical ends of the style branches are rounded to acute, obtuse or truncate with the stigmatic region covering the entire adaxial surface of the branches. Style branches are densely covered in very short, acute papillae that extend down the style to below the point of bifurcation, where they end abruptly, with or without a ring of longer sweeping hairs on a slightly thickened portion (Figs. 2m; 3g; 4j; 6e,f).

4.11. Cypsela

Both ray and disc cypselas are small, up to 4 mm long, oblong-ovoid and densely covered with long, slender upwardly-directed twin-hairs (Figs. 2i; 4i; 6b,c). The twin-hairs are shorter at the base of the cypsela, very long towards the top, and each twin-hair comprises a double set of extremely slender cells whose apices may be slightly divergent forming a Y-shape, or one of the cells in the pair may be shorter and pressed against the side of the longer cell, making the hair single-celled at its very apex. The twin-hairs are straight, brittle and shiny, and can be reddish-brown, straw-coloured or almost pure white, depending on the species. The upper hairs extend above the top of the cypsela, over the base of the pappus, giving the appearance of an additional and structurally different pappus whorl. The fruits are longitudinally ribbed, but this is obscured by the twin hairs (Fig. 6c). The cypsela does not appreciably increase in size with maturity.

4.12. Pappus

An identical pappus is present on ray and disc florets. The pappus consists of two alternating series, each of ca. 10 stout, elongate-subulate, marginally and especially apically barbellate or subplumose elongate bristle-like scales that are up to 10 mm long (Figs. 3d,e; 4i; 6b,c). The pappus bristles are flattened and widest at the base, narrowing towards the apex. The marginal barbs are directed upwards at ca. 45 degrees to the bristle axis, and the barbs are stout; the barbs increase in density and length towards the bristle apex. The pappus

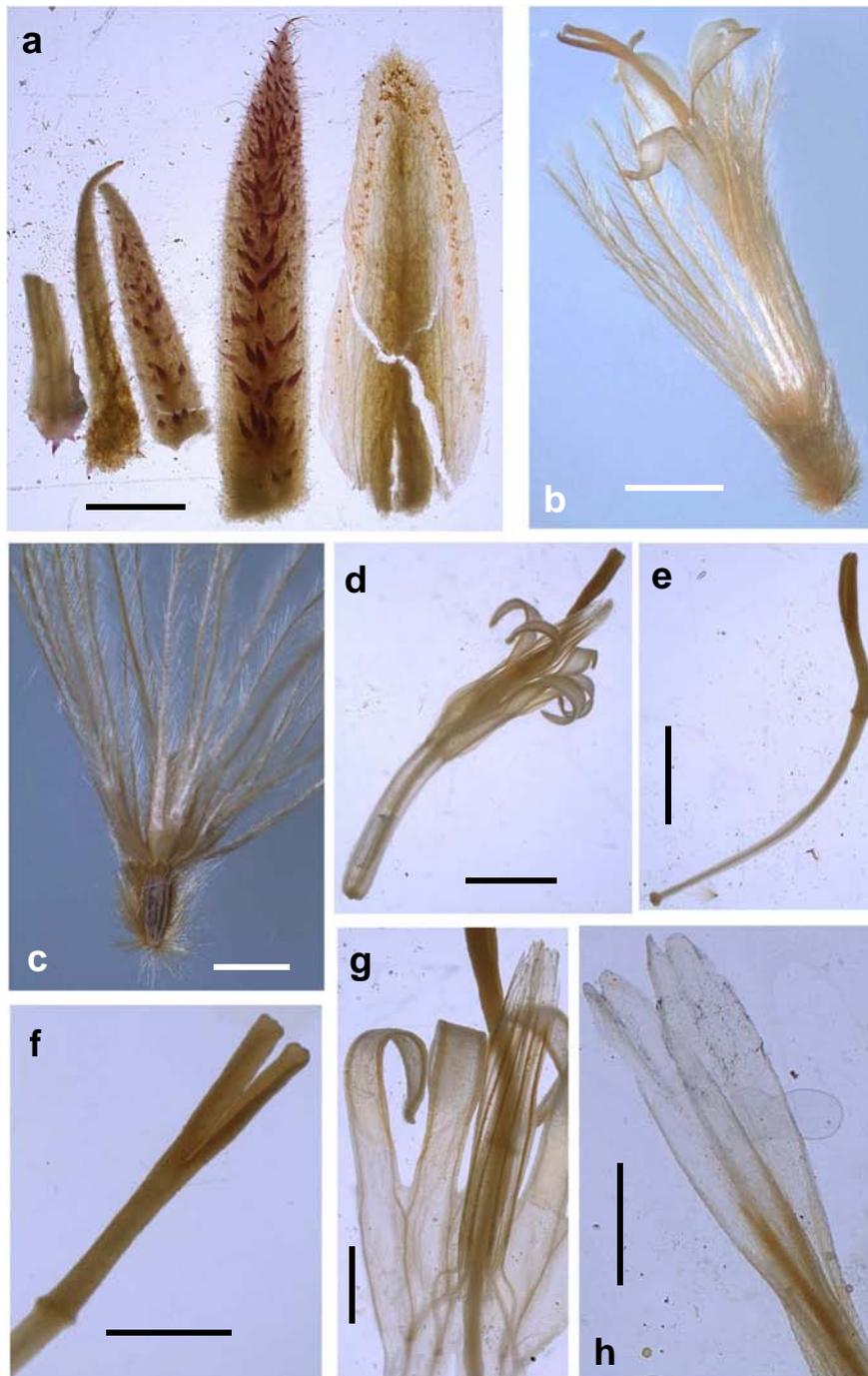


Fig. 6. *Heterolepis anomala*, Bohnen 9129. a – involucre bract series, from outermost at left to innermost at right (scale bar = 2.5 mm); b – disc floret showing pale corolla and pappus (scale bar = 1.6 mm); c – disc pappus and cypsela, the latter with the twin-hairs scraped off the front surface to show the ribbed wall (scale bar = 1.9 mm); d – disc floret (scale bar = 2.0 mm); e – disc style (scale bar = 2.2 mm); f – disc style apex showing truncate style branches and conspicuous hair tuft (scale bar = 1.2 mm); g – dissected disc corolla to show anthers (scale bar = 2.0 mm); h – disc anther apical appendages (scale bar = 0.65 mm).

bristles are shiny and pale straw-coloured, although in most species they are tinged an inky blue-black towards the tips (Fig. 3d,e), although this blue-black colour may not be present in all individuals. One of the series of bristles is shorter and narrower and with smaller, sparser barbs. This smaller whorl can be the inner or the outer (e.g. outer in *H. mitis*; inner in *H. peduncularis*).

4.13. Embryo sac development

Heterolepis has unusual bisporic embryo sac development, which was described by Ahlstrand (1992) after examination of *H. aliena* and

H. peduncularis. The other genera of tribe Arctotideae have the usual *Polygonum*-type of embryo sac development (Ahlstrand, 1979a, 1979b). Bisporic development is rare in the Asteraceae, apart from *Heterolepis* being documented only in a few members of the distantly-related sub-family Asteroideae (Ahlstrand, 1992).

4.14. Pollen

Pollen is a distinctive bright orange colour in fresh specimens (Fig. 2d). The structure of pollen grains of *H. aliena* was investigated by Wortley et al. (2008) and the following description comes from

their publication. In *H. aliena*, and presumably in other members of the genus, the pollen grains are oblate-spheroidal (round in equatorial view and round or sub-triangular in polar view), 25–30 µm in diameter and echinate. Pollen is echinate and tricolporate, the colpi being narrow with acute ends. The infratectum is 1.2–1.5 µm thick and comprises two distinct columellae layers separated by a single or multiple, spongy internal tectum. The outer layer is 0.8–1 µm thick and the inner 0.4–0.5 µm. The columellae of the inner layer are evenly distributed and not swollen at the base. The inside of the endexine is smooth. The grains are partially cavate, the cavea is of medium depth, spanned by thread-like columellae. The grains have about 70 unevenly-distributed spines that are 3–4 µm high and 4.5–5 µm in diameter at the base, with perforations throughout, including at the apex, a slightly swollen basal region, and with pendant columellae inside. The pollen surface is reticulate and slightly raised between the spines.

4.15. Chromosome numbers

Strother et al. (1996) investigated the karyology of *H. aliena* and reported a count of $x = 6$ (probably $2n = 12$). A count of $2n = 20$ is mentioned in Karis (2007) and $x = 10$ in the flora of Herman et al. (2000), but Funk and Karis (2009) consider these erroneous as they were unable to find any published study other than that of Strother et al. (1996). No authenticated records for other species have been traced.

5. Systematic position

The unique combination of morphological features characterising *Heterolepis*, and not found in any other Asteraceae taxon, comprises the following: deeply-lobed disc floret corollas, the 3 + 1 – lobed, female-fertile ray florets (true bilabiate rays have a 3 + 2 structure and are found with elongated ligules only in the Mutisioideae, while pseudobilabiate rays have a 4 + 1 lobe arrangement and occur only in the Barnadesioideae); the possession of staminodes in the rays; caudate anthers with relatively short, un-branched or barely-branched tails and a thin, soft, obtuse apical appendage; a biseriate pappus of barbellate or subplumose bristle-like scales; and the unusual stylar morphology. *Heterolepis*-type styles are found only in the tribe Arctotideae, but there are similarities with the styles of some members of Cichorioideae, Mutisioideae and Cardueae.

As a consequence of its unusual morphology, the systematic position of the genus has been subject to marked divergence of opinion. Linnaeus the younger, who published the first description in 1781, placed the type species in *Oedera* L. (currently in subfamily Asteroideae, tribe Gnaphalieae). Vahl (1791) considered the same taxon to be a member of *Arnica* L. (currently subfamily Asteroideae, Heliantheae alliance of tribes). Cassini (1821) was the first to note the morphological affinities between *Heterolepis* and Arctotideae. Lessing (1832) incorporated *Heterolepis*, together with all other Arctotideae, into an enlarged concept of Cynaroideae (the thistles; currently subfamily Carduoideae). Bentham (1873) re-established Arctotideae but placed *Heterolepis* in Inuleae; he was followed by Hoffmann (1894). De Candolle (1838b) placed his genus *Minurothamnus* DC. (based on *H. peduncularis*) within what today would be considered tribe Inuleae, despite having treated *Heterolepis* in an earlier volume published the same year (De Candolle, 1838a) in which he followed Lessing (1832) and placed it within Cynareae. Merxmüller et al. (1977), in his treatment of Inuleae, considered that *Heterolepis* did not belong in that tribe, suggested instead that it be placed in Mutisieae.

The constantly-shifting phylogenetic position of *Heterolepis* has contributed to its taxonomic complexity, with the same species being placed unwittingly by different authors in what today would be recognised as different subfamilies. Currently, however, there is broad consensus, supported by molecular phylogenetic analysis (Funk and Chan, 2008), that the genus is related to tribe Arctotideae (subfamily

Cichorioideae), confirming Cassini's (1821) assignment. However, the position of *Heterolepis* within Arctotideae has never been convincingly established: different morphological features appear to indicate an alliance with different subtribes, and some features are anomalous within Arctotideae, such as the bisporic embryo-sac development, the 3 + 1 lobed ray florets, and the pappus comprising robust capillary bristle-like scales.

Affinities with Arctotideae subtribe Arctotidinae are indicated by some aspects of the stylar morphology, the soft apical anther appendages, a very similar pollen shape and ultrastructure, and the fact that the plants are non-spiny. Also, the stems, peduncles and involucre in Arctotideae-Arctotidinae often bear unusual trichomes, similar to those in *Heterolepis*. Another shared feature is the dimorphic involucral bracts, with the outer bracts in both taxa being smaller, herbaceous and often glandular, while the inner bracts are larger with membranous margins and obtuse, papery apices (this giving rise to Cassini's name *Heterolepis*). However, in Arctotidinae the outer bracts are entirely herbaceous and the inner bracts entirely papery; the transition between the different types of bract series is relatively abrupt. In *Heterolepis* there is, instead, a gradual transition in structure from herbaceous outermost to membranous innermost bracts, with the middle bracts being morphologically intermediate.

Affinities with Arctotideae subtribe Gorteriinae (the spiny daisies) are indicated by the following: basal fusion of the involucral bracts (although the degree of fusion is much less in *Heterolepis*); by an alveolate receptacle (although the alveole margin projections are much shorter in *Heterolepis*); possession of milky sap (a feature not previously noted in *Heterolepis* but apparent at least in the type species, *H. aliena* [L.f.] Druce); caudate, barely-branched anther tails; the pattern of anther endothelial cell-wall thickening (which is similar to some members of the *Berkheya* Ehrh. clade of Gorteriinae, but markedly different from Arctotidinae, in which the endothelial thickenings are consistently radial; Funk and Karis, 2009). In addition, *Heterolepis* shares with many members of the Gorteriinae (including both species of *Didelta* L'Hér., but also species from other genera) the feature of ray florets bearing staminodes. Although *Didelta* in the Gorteriinae was reported by Robinson and Bretell (1973) to possess pappus bristles, *Didelta* pappus elements are spinescent and quite unlike those of *Heterolepis*. The chromosome number of $x = 6$ (for *H. aliena*; Strother et al. 1996) has been recorded within both Gorteriinae and Arctotidinae, although counts in the tribe vary. Gorteriinae has records of $2n = 10, 12, 14$ and 16 while most Arctotidinae have $2n = 18$ with variation in this subtribe (of $2n = 10, 12, 18$ and even higher) found only within the genus *Haplocarpha* Less (Karis, 2007). The ancestral number for the tribe is postulated to be $x = 9$, making *Heterolepis* unusual within the tribe (Funk and Karis, 2009).

Within Arctotideae, Cassini (1821) considered *Heterolepis* to be closer to subtribe Arctotidinae, due to style characteristics, but the possession of staminodes in the ray florets led Norlindh (1977) to place *Heterolepis* in subtribe Gorteriinae. DNA-based studies have been unable to resolve the issue, possibly due to a lack of comprehensive taxon sampling but also due to lack of sufficient information in the molecular markers sampled. As a result, Funk and Chan (2009) and Funk and Karis (2009) left *Heterolepis* unassigned to a tribe within the subfamily Cichorioideae in the most recent treatment of the family (Funk et al., 2009).

6. Taxonomic treatment

***Heterolepis* Cass.** in Bull. Sci. Soc. Philom. 1820: 26 (1820), nom. cons. –Type: *Arnica inuloides* Vahl. = *Heterolepis aliena* (L.f.) Druce.

***Heteromorpha* Cass.** in Bull. Sci. Soc. Philom. 1817: 12 (1817), nom. rej. –Type: *Arnica inuloides* Vahl. = *Heterolepis aliena* (L.f.) Druce.

***Minurothamnus* DC.**, Prodr. 7(1): 286 (1838). –Type: *Minurothamnus phagnaloides* DC. = *Heterolepis peduncularis* DC.

Nomenclatural notes:

Heterolepis Cass. (Cassini, 1820) was formally conserved over *Heteromorpha* Cass. (Cassini, 1817) by Rickett and Stafleu (1960). See further taxonomic notes under *H. aliena*, below.

Key to the species of *Heterolepis*:

- 1a Fully elongated peduncles >25 mm.....2
 1b Fully elongated peduncles <25 mm.....3
 2a At least some leaves >20 mm long; capitula usually radiate.....4
 2b All leaves <20 mm long; capitula discoid.....**4. *H. anomala***
 3a Capitula >35 mm in diameter including expanded rays; leaves linear-lanceolate, not narrowing towards base, greyish, densely tomentose abaxially with toothed margins; peduncle and involucre densely glandular.....**1. *H. aliena***
 3b Capitula <35 mm in diameter including expanded rays; leaves linear-oblongate, narrowing towards base, dark green, almost glabrous abaxially with entire margins; peduncle (when present) and involucre sparsely glandular or glabrous.....**2. *H. mitis***
 4a Leaves >20 mm long at the base of the stem, but noticeably decreasing in length acropetally; uppermost leaves <10 mm long.....**3. *H. peduncularis***
 4b All leaves 15–50 mm long; not noticeably decreasing in length up the stems.....**1. *H. aliena***

1. *Heterolepis aliena* (L.f.) Druce in Rep. Bot. Exch. Cl. Brit. Isles 1916: 628 (1917).

Oedera aliena L.f. in Suppl. Pl.: 390 (1781). *Heterolepis decipiens* Cass., in Dict. Sc. Nat. 21: 120 (1821) [incorrectly cited there as Bull Sci., 1820], nom. illeg. superfl. –Type: South Africa, ‘Cap. Bonae spei’, P.J. Bladh s.n. (LINN 1047-3-image!, holo)

Arnica inuloides Vahl. in Symb. Bot. 2: 91 (1791). –Type: South Africa, ‘Capite b. Spei’. C.A.W. Bulow s.n. (C-image!, holo).

Leysera arctotooides Thunb. in Prodr. Pl. Cap. 2: 160. 1800. –Type: Cap. b. Spei, in Roggeveld, C.P. Thunberg s.n., (UPS-THUNB 20073-image!, lecto, designated here).

Illustration: Fig. 2.

Habit: compact, sparsely- to well-branched shrublet forming a low, broad bush, to about 1.2 m (but usually 0.30–0.70 m) high. **Stems:** young stems soft, herbaceous, longitudinally striate, white-tomentose but not glandular; white-woolly tomentum of young stems continuous onto leaf buds and abaxial surfaces of mature leaves. Older stems woody, to about 1.0 cm in diameter, leafless, with smooth greyish-brown bark marked with leaf-scars. **Leaves:** densely or sparsely arranged around stem at branch ends, imbricate, erect, linear-lanceolate, 15–50 × 1.5–3.0 mm, ± equal in length along stem, sessile, not narrowing towards base, apically acute with a small mucro, leaf lamina somewhat thickened and leathery; margins strongly revolute, folded back over the abaxial surface which is thus largely obscured except for a small central portion, margins entire or with small, widely-spaced, acute mucro-like teeth; leaf adaxial surface dark green, glabrescent with slightly indented midvein; abaxial surface densely white-tomentose with midvein thickened, prominent, green and glabrescent in contrast to the white-tomentose abaxial leaf surface. **Peduncle:** 10–40 mm or rarely up to 70 mm long, increasing in length at floral maturity, sometimes bearing one or two small leaflike bracteoles; reddish-brown, faintly striate, not woolly or only sparsely so, and bearing a covering of trichomes (type A) that is most densely spaced at top of the peduncle.

Capitula: radiate, 40–70 mm in diameter including the expanded rays; containing ± 75–85 disc florets and (12–)20–30 rays. Old heads not retained on plant. **Involucre:** 10–25 mm across, fleshy portions of bracts densely glandular with trichome type A, or glabrous or sparsely white-woolly. Outer bracts narrowly deltoid-lanceolate, free portion 6–9 × 1.5–2.5 mm, inner bracts longer and wider, free portion

15–20 × 3–7 mm. All bracts becoming dark brown with age. **Receptacle:** alveole margins with shallow, irregular projections <1 mm long. **Ray florets:** golden yellow, tube sparsely covered with slender trichomes (type B), lamina 3–4 × 8–12 mm, ± glabrous; style apex thickened below the bifurcation but without a tuft of longer sweeping-hairs. Style branch apices rounded. **Staminodes** white, thin, basally with short, rounded tails, apically rounded, filaments present. **Pappus** and **cypselas** as in disc florets. **Disc florets:** golden yellow, 10 mm long, tube sparsely hairy with slender, multicellular hairs (trichome type B), corolla lobes broadly acute, 2–3 mm in length, slightly recurved at maturity, bearing glandular hairs (trichome type C) on abaxial surfaces. Style much-exserted, extending ± 6 mm beyond corolla tube, with a slight, abrupt thickening below the bifurcation, papillae slightly larger on thickening. Style branches ± 1 mm long, apically rounded. **Anther tails** extending ± 1 mm below the point of filament attachment, obliquely truncate. **Apical anther appendages** short, rounded, thin and flat. **Cypselas:** hair-covering straw-coloured or reddish-brown. **Pappus:** inner pappus series about the same length as the corolla, outer series about half this length, all the individual pappus elements possessing a thickened main shaft, frequently tinged blue-black towards tip.

Diagnostic characters: *Heterolepis aliena* is the commonest and most widespread member of the genus, and also the most variable. It is generally distinguishable from all other species by its much larger and showier heads, with a greater number of florets. The usual *H. aliena* head bears roughly double the number of both rays and discs of *H. mitis* and *H. peduncularis*; however, some plants have smaller heads with fewer rays. The leaves are generally stouter than those of the other species, and the peduncles of *H. aliena* are almost always much shorter than those of either *H. peduncularis* or *H. anomala*. The presence of milky-white sap has been noted in *H. aliena*, but this feature, observable only in fresh specimens, has not been investigated in the other species.

Flowering time: recorded in flower mostly between October and February, with peak flowering in November, December and January (Fig. S1). Most of the specimens flowering in other months come from localities growing very close to the sea in the Hangklip–Betty’s Bay region of the south-western Cape.

Distribution: *Heterolepis aliena* is restricted to the western half of the CFR (Fig. 1), where it is found mainly in mountainous regions. There are several outlying populations further to the east in the sandstone mountains of the Little Karoo (Anysberg and Groot Swartberg ranges near Ladismith, and Witteberg near Matjiesfontein). The single record from the Kamiesberg in the Northern Cape is doubtful (see Fig. 1).

Habitat and ecology: *Heterolepis aliena* is recorded from rocky sites on Table Mountain Sandstone, usually in fire-protected sites, rooting amongst rocks or on cliff faces. We would classify the vegetation type to which it is endemic as Arid Fynbos, since the plant occurs in the more arid microsites (e.g. north-facing slopes) and at the arid margins of the fynbos on sandstone rocks. Although some collectors record cliff sites as being in shade for part of the day, this species generally grows in full sun. The following notes have been made about fire ecology: “Nine months after burning” (Kruger 139); “In 20 year-old vegetation” (Taylor 4629); “Sprouting in firebreak” (Kruger 1138); “A reseeding shrublet, in 6-yr old restioid veld” (Viviers 738); “Fynbos vegetation burnt 19 months ago” (Kruger 879); “Spruit na brand, groei in elk geval in plekke wat moeilik brand” (van der Merwe 24–37); and “In rock crevices, resprouting after fire (of one year previously)” (Williams 3398). From these comments, and from the flowering-time distribution with particular peaks in the midsummer months it can be concluded that, although the species may resprout after some fire damage, it does not necessarily have a resprouting fire-survival strategy. Instead, it grows in rocky, fire-protected sites. There is no strong evidence of resprouting on any of the specimens except for the fact that the living stems are generally small, perhaps indicating only a single year’s growth; one specimen, *Snijman 1338* (NBG) includes a portion of a woody rootstock attached to the above-ground stem. Quite possibly the main stems are protected from fire in rock crevices, while the

shorter-lived flowering stems grow out from this protection to bear the flowers.

Etymology: the species epithet 'aliena' was provided by Linnaeus filius for the basionym, *Oedera aliena*, perhaps referring to the incongruity of this species in the genus *Oedera*.

Red-List status: Least Concern (Foden and Potter, 2005a).

Nomenclatural notes: The name *Heterolepis decipiens* is not linked to any known specimen, but appears to represent a new combination, although neither of the two basionyms listed by Cassini (1821) and Lessing (1832) is reflected in the name. Confusion starts with Cassini (1817), who published a new genus, *Heteromorpha*, for the taxon described by Vahl (1791) as *Arnica inuloides*. Cassini recognised that this species did not belong in *Arnica* and considered it to have greater affinity with the tribe Arctotideae. However, he did not formalise the new combination in *Heteromorpha*. A few years later (Cassini, 1820), Cassini decided to change the name *Heteromorpha* to *Heterolepis* because he considered the former too adjectival. In this publication, he considered the names *Arnica inuloides* Vahl and *Oedera aliena* L.f. to apply to a single species, which he classified in *Heterolepis*, but again he did not make the new combination for either name. The species epithet 'decipiens' is mentioned first in Cassini's (1821) treatment of *Heterolepis*, where he wrote (pp. 120–121) "Hétérolèpe trompeur: *Heterolepis decipiens*, H. Cass., Bulletin des sciences, Février 1820; *Heteromorpha*, H. Cass., Bulletin des sciences, Janvier 1817" and then listed *Arnica inuloides* Vahl and *Oedera aliena* L.f., seemingly as synonyms. Thus he appears to be citing an earlier publication (Bulletin des sciences, February 1820) for the name *Heterolepis decipiens*. However, we have not been able to discover any publication referring to the name prior to the 1821 publication cited above. In particular, Cassini (1820), which is presumed to be the article referenced by "Bulletin des sciences, Février 1820", makes no mention of the binomial "*Heterolepis decipiens*". In his writings between 1817 and 1821, Cassini refers all mention of *Heterolepis* and *Heteromorpha* to *Arnica inuloides* Vahl. and/or *Oedera aliena* L.f., merely placing those taxa in his new genus. Cassini's (1821: p. 123) statement "L'épithète de trompeur, *decipiens*, que nous donnons à l'hétérolèpe, est bien justifiée par toutes les remarques qu'on vient de lire", suggests his intention to publish a new binomial. If this interpretation is accepted, the name *Heterolepis decipiens* is nomenclaturally both illegitimate and superfluous, because Cassini (1821) simultaneously cited two validly published earlier names, *Arnica inuloides* Vahl and *Oedera aliena* L.f. The valid basionym for the species would therefore be the earliest published name, i.e. *Oedera aliena*.

Lessing (1832) accepted *Heterolepis decipiens* as a validly published binomial, citing both *Oedera aliena* L.f. and *Arnica inuloides* Vahl. as synonyms, as well as Thunberg's *Leysera arctotoides*. The combination of the earliest available name, *Oedera aliena*, in *Heterolepis* was formally published by Druce (1917). Rickett and Stafleu (1960) noted that the combination of *Arnica inuloides* under the generic name *Heterolepis* was never made, but stated that in their view, proposing this combination was not necessary "because it would be superfluous in view of the generally accepted taxonomic synonymy with *Heterolepis aliena*" (i.e., the basionym *Oedera aliena* has nomenclatural priority over *Arnica inuloides*). As noted previously by Flann et al. (2010), in Appendix IIIA of the *International Code of Nomenclature for algae, plants and fungi* (McNeill et al., 2012), the type for *Heterolepis* is incorrectly listed as *Heterolepis decipiens* Cass. As noted above, Cassini (1821) cited both *Arnica inuloides* Vahl and *Oedera aliena* L.f. in conjunction with the name *H. decipiens*, therefore the generitype is *Heterolepis aliena* (L.f.) Druce, based on the earliest available name, *Oedera aliena* L.f.

Minurothamnus phagnaloides DC. was mistakenly synonymised with *H. aliena* by Merxmüller (1950). Examination of a scan of the type specimen from G-DC indicates that this specimen is in fact *H. peduncularis* DC., so this name is treated under this species.

Leysera arctotoides Thunb. is a name originally published in 1800. There are two sheets named '*Leysera arctotoides*' in Thunberg's collection housed at Uppsala. The sheet '*Leysera arctotoides*. 1.' (UPS-THUNB

20073) has been annotated with subsequent names (*Oedera aliena* L.f. nec Thunberg; *Arnica inuloides* Vahl! and *Heterolepis decipiens* Cass.) and is a specimen of *Heterolepis aliena*. The sheet '*Leysera arctotoides*. 2.' (UPS-THUNB 20074) has no further annotations and comprises two twigs. That on the right and an additional capitulum are of *Heterolepis aliena*, but the leftmost twig has extremely long peduncles and the leaves are thin, weak and decrease in length up the shoot, so it is more likely to be a specimen of *H. peduncularis*. Unlike the 20073 sheet, ray florets are not easily discernable in the second sheet. The unmix collection, sheet UPS-THUNB 20073, is here designated the lectotype.

Additional specimens examined: 176 specimens from BOL, NBG, PRE, GRA.

South Africa, NORTHERN CAPE. **3018 (Kamiesberg):** Little Namaqualand, Kamiesbergen (-AC), Oct 1929, *Stokoe 2051* (PRE); note that this is a doubtful locality (see Fig. 1).

WESTERN CAPE. **3318 (Paarl):** Paarlberg (-DB), Jan 1904, *Marloth 3479* (NBG); Paarl Mountain (-DB), Nov, Dec, *Drege s.n.* (HBG 504802, K 415224).

3119 (Calvinia): Wupperthal, on rd. to Eselbank (-AC), 27 Oct 1977, *Gouws 163* (PRE).

3218 (Clanwilliam): Grey's Pass (-DB), Oct. 1925, *Rennie 2616* (BOL); slopes above Piekener's Pass (-DB), 24 Nov 1910, *Pillans 5188* (BOL); Clanwilliam Div., Cederberg–Klein Valley (-AA), 9 Nov 1956, *Taylor 1840* (NBG); near Wupperthal on road to Eselbank (-AC), 27 Oct 1977, *Emdon 163* (NBG, PRE).

3219 (Ceres): top of Middelburg pass (-CA), c. 3500 ft. [1070 m], 19 Oct 1958, *Acocks 19845* (PRE); Cold Bokkeveld, Elands Kloof (-CA), 3000 ft. [914 m], 14 Dec 1936, *Levyns 5102* (BOL); Ceres Division, Elands Kloof (-CA), 3000 ft. [914 m], 15 Aug 1946, *Levyns 8126* (BOL); Ceres Division, Elands Kloof (-CA), 3000 ft. [914 m], Dec 1948, *Levyns 9359* (BOL); Ceres Dist. (-CB), 1500 ft. [457 m], Jan 1892, *Guthrie 2175* (NBG); Wuppertal Division, Cederberg Mtns, on Uitkykpas (Cederbergpas), 1.5 km from top of pass on Algeria Station side (-AC), 19 Nov. 1994, *Watson 94-49* (NBG); Koue Bokkeveldberge, naby Agtuurkop (-CC), 28 Jan 1972, *Hanekom 1773* (PRE); Uitkykpas (-AC), ca. 1000 m, 19 Nov 1985, *Taylor 11437* (NBG, PRE); Kouebokkeveld, Skoongesig, klipkop teen berg (-CC), 29 Dec 1978, *Hanekom 2576* (PRE).

3318 (Stellenbosch): Malmesbury Division, North slopes of Riebeeck's Kasteel (-BD), 2000 ft. [610 m], Jan 1928, *Pillans 6132* (BOL); Swartboskloof (-DD), 1600–1800 ft. [488–549 m], 23 Nov 1960, *van der Merwe 24-37* (PRE); Jonkershoek, Langrivier (-DD), 3000 ft. [914 m], Feb 1965, *Kerfoot 5101* (NBG, PRE); Kirstenbosch near Cape Town (-CD), 14 Nov 1929, *Grant 5007* (PRE); Jonkershoek State Forest, The Valley (-CD), 1200 ft. [366 m], 7 Jan 1976, *Kruger 139* (NBG, PRE); Jonkershoek (-CD), 2500 ft. [762 m], 30 Jan 1963, *Taylor 4629* (NBG); Gordon's Bay on mountain slopes (-CD), 25 November 1955, *van der Merwe s.n.* (NBG); Stellenbosch, Duthie-reservaat (-CD), 11 Oct 1960, *van Rensburg 1990* (NBG, PRE); Jonkershoek Nature Reserve, Panorama trail (-DA), 766 m, 13 Feb 2008, *Brandon 121* (NBG); Paarl Mountain (-DB), Nov 1846, *Alexander-Prior PRE 42920* (PRE); Paarl Mountain (-DB), *Drége PRE 12753* (PRE); Paarl Mountain (-DB), Jan 1904, *Marloth 3479* (PRE); Franschhoek Pass, top of pass (-DB), 4 Dec 1935, *Taylor 1500* (PRE); Worcester Dist. Sanddriftvalley, 12 miles N of Worcester (-DC), 5 Nov 1963, *Schlieben 9919* (NBG); Jonkershoek, Beacon (-DD), Jan 1936, *Borchardt (135)1580* (PRE); Jonkershoek (-DD), 7 Nov 1943, *Compton 15318* (NBG); Stellenbosch Division, Jonkershoek Twins (-DD), 3000–4000 ft. [914–1219 m], 14 Feb 1945, *Esterhuysen 11482* (BOL, PRE); Stellenboschberg, summit (-DD), 10 Feb 1931, *Galpin 10602* (PRE); Stellenbosch, near Steenbras reservoir (-DD), 14 Dec 1933, *Galpin 12447* (PRE); Jonkershoek State Forest, Stellenboschberg (-DD), 2600 ft. [792 m], 8 Dec 1975, *Haynes 1137* (NBG, PRE); in saxosis Jonkershoek prope Stellenbosch (-DD), 1400 m, Jan 1888, *Marloth 1836 (=1649)*, (PRE); Jonkershoek, Sosyskloof (Swartboschkloof) (-DD), 27 Oct 1982, *McDonald 851* (NBG, PRE); Jonkershoek, slopes below Ridge Peaks, S aspect along contour path

(-DD), c. 2500 ft. [762 m], 30 Jan 1963, *Taylor 4629* (NBG, PRE); Jonkershoek, Swartboskloof (-DD), 2500 ft. [762 m], 20 Jan 1960, *van der Merwe 2061* (NBG, PRE); C.B.S., Stellenbosch Mountain, *Harvey TCD 3212* (TCD).

3319 (Ceres): Winterhoek mountains (-AA), 1200 ft. [366 m], Jan 1887, *Marloth 1649* (PRE); Tulbagh div. (-AC), 300 ft. [91 m], 12 Oct 1890, *Guthrie 2175* (NBG); Tulbagh: Nuwekloof Pass (-AC), 160 m, 21 Oct 2000, *Koekemoer 2028* (PRE); Tulbagh, at the top of the waterfall (-AC), Nov, *Zeyher 977* (NBG, PRE); Ceres Division, Castle Rocks (-AD), 3000–3500 ft. [914–1067 m], 9 Nov 1952, *Esterhuysen 20703* (BOL); Michells Pass, rocky slopes above railway line (-AD), 16 Nov 1952, *Esterhuysen 20725a* (BOL, PRE); Ceres Dist; eastern slopes of Witzenbergen above January's Kraal (-AD), 700 m, Dec 1919, *Andreae 180* (PRE); kloof to Ceres Dorpsdam (-AD), 2000 ft. [610 m], 5 Feb 1980, *Hugo 2322* (NBG, PRE); Ceres (-AD), *Rogers 17659* (PRE); Ceres (-AD), Dec 1929, *Thode A2254* (PRE); Mitchells Pass (-AD), Jan 1918, *Thode 2914* (NBG); Mitchells Pass Ceres (-AD), 1 Nov 1962, *Walters 926* (NBG); Worcester Dist., Waaihoek (-AD), 4500 ft. [1372 m], 10 Jan 1944, *Wasserfall 817* (NBG); Michells Pass, 3 km from the Ceres town centre, junction R 303 and R 46 (-AD), 20 Nov 1994, *Watson 94-63* (NBG); hillside at Leeufontein (-BA), 28 Nov 1908, *Pearson 3208* (NBG); in convalle Hex River prope De Doorns (-BC), Jan 1908, *Bolus PRE 42912* (PRE); Ceres District, Conical Peak (-BC), Dec 1940, *Stokoe 8193* (NBG, PRE); De Doorns, Orchard, Worcester (-BC), 500 m, 21 Oct 1975, *Walters 590* (NBG); Bainskloof, in berg (-CA), 9 Oct 1955, *Balkema s.n.* (NBG); Worcester, Du Toits Kloof (-CA), 15 Oct 1949, *Barker 5968* (NBG); Du Toitskloof Pass, near old tunnel on Worcester side (-CA), 9 Nov 1988, *Beyers 121* (NBG, PRE); in mont. Drakensteenbergen, prope "The Neck" - Bains Kloof (-CA), 1500 ft. [457 m], Mar 1877, *Bolus 4038* (BOL); Wellington Distr., Bains Kloof (-CA), 27 Nov 1939, *Bond 6* (NBG); Bainskloof, 25 km from Wellington on road to Ceres, steep rocky mountain slope (-CA), 1 Dec 1986, *Germishuizen 4067* (PRE); Worcester Dist., centre of Baines Kloof, N side (-CA), 14 Sep 1928, *Gillett, 213* (NBG); Bains kloof summit (-CA), c. 2000 ft. [610 m], 18 Feb 1933, *Gillett 785* (NBG); Bain's Kloof, lower cliffs near the road (-CA), 28 Oct 1928, *Hutchinson 1066* (BOL); Wellington Dist., Bainskloof (-CA), Oct 1936, *Kok STEU 26503* (NBG); Worcester Dist., Du Toits Kloof Tunnel, east end (-CA), 28 Oct 1951, *Maguire 1145* (NBG); Du Toit's Kloof (-CA), Jan 1922, *Marloth B.7 (PRE 42916)* (PRE); Paarl Division, near west entrance to Du Toits Kloof (-CA), about 1500 ft. [457 m], Nov 1937, *Pillans 8490* (BOL); Du Toit's Kloof Pass, lower Krom River off Du Toit's Pass (-CA), 6 Nov 1969, *Thompson 987* (NBG, PRE); Worcester, Du Toits Kloof (-CA), 10 Jun 1962, *Walters 307* (NBG); Paarl Division, Wemmershoek Valley, rocks above river (-CA/CC), 1 Jan 1945, *Esterhuysen 11353* (BOL, PRE); Karoo Garden, Worcester (-CB), 11 Sep 1968, *Tarr s.n.* (NBG); Worcester Div., Brandwagt, slopes of mountains (-CB), 14 Mar 1949, *van Breda 360* (PRE); Worcester Division, Waaihoek, (-CB), 4500 ft. [1372 m], 10 Jan 1944, *Wasserfall 817* (PRE); Paarl Division, Franschoek (-CC), 18 Oct 1846, *Alexander-Prior PRE 42911* (PRE); Franschoek Pass, just at entrance to Mount Rochelle Nature Reserve (-CC), 752 m, 19 Dec 2001, *Bayer SAF-01124* (PRE); Paarl District, French Hoek Pass (-CC), 2500 ft. [762 m], 26 Nov 1939, *Compton 8153* (NBG); Franschoek - La Motte SAFCOL plantation (-CC), 357 m, 7 Feb 2006, *Cowell MSBP3014* (NBG); French Hoek (-CC), Dec 1896, *Guthrie 2175* (NBG); Paarl, Wemmershoek Mountains, north of dam, in Veilingskloof, SW slopes of Winterberg (-CC), 1000 m, 21 Dec 2004, *Helme 3158* (NBG); Palmiet Valley-Theewaterskloof area (-CC), c. 1100 ft. [335 m], 7 Dec 1979, *Hugo 2164* (NBG, PRE); Elandsloof Pass, near Villiersdorp (-CC), 27 Mar 1988, *Joffe 509* (PRE); Klein Drakenstein Mtns., upper Bakkerskloof Catchment (-CC), c. 2600 ft. [792 m], 1 Mar 1971, *Kruger 1138* (NBG, PRE); French Hoek, western aspect (-CC), 16 Dec 1938, *Louw 119* (NBG); Paarl Division, Franschoek Pass (-CC), 5 Jan 1948, *Rodin 3086* (BOL); Zachariashoek Experimental catchment, Kasteelkloof catchment (-CC), c. 2000 ft. [610 m], 14 Dec 1972, *Smith 80* (NBG); Zachariashoek Experimental catchment, Kasteelkloof catchment (-CC), c. 1800 ft. [550 m], 10 Jan 1974, *Smit*

183 (NBG, PRE); Paarl Div., Franschoek Pass (-CC), Dec 1929, *Thode A2208* (PRE); Paarl, Drostersberg, farm of Mnr. W.A. De Klerk (-CC), 16 Dec 1976, *van Wyk, 1933* (PRE); La Motte Forest Station: Zachariashoek, Kasteelkloof (-CC), 1600 ft. [488 m], 21 Oct 2982, *Viviers 738* (NBG, PRE); Paarl Dist., Groot Drakenstein Mtns., Devils Tooth (-CC), 2500–3000 ft. [762–914 m], 12 Dec 143, *Wasserfall 728* (NBG); Villiersdorp Wild Flower Reserve (-CD), 554 m, 15 Jan 2004, *Botha (4)036* (NBG); Franschoek Pass (-CD), 5 Jan 1948, *Rodin 3086* (PRE); Worcester Division, Boschjesveld Mountains (-CD), 4000 ft. [1219 m], Feb 1940, *Stokoe 8081* (BOL); Montagu Dist., lower slopes of Naudesberg, Koo (-DA), 24 Nov 1959, *Lewis 5703* (NBG); Sanddrift valley, 12 miles N of Worcester (-DA/CB), 5 Nov 1963/83, *Schlieben 9919* (PRE); Farm Doringkloof, on Voetpads Berg, above firebreak (-DB), 2600–3000 ft. [792–914 m], 22 Nov 1985, *Morley 500* (NBG); Riviersonderend mountains, Jonaskop (-DC), 1524 m, 14 Jan 1979, *Boucher 4251* (NBG); Onklaarberg, 20 mi. S of Worcester (-DC), Dec 1924, *Marloth 112* (PRE); Worcester Div.; Karoo Bot. Garden, cultivated (-BA), 9 Oct 1960, *Gentry 18621* (PRE); Worcester, waterfall, *Ecklon & Zeyher s.n.* (HBG 504803).

3320 (Laingsburg): Laingsburg Division, foot of Witteberg (-BC), 4000 ft. [1219 m], 14 Nov, *Adamson s.n.* (BOL); Matjiesfontein; SW of Witteberg, SE end of Witterivierpoort (-BC), c. 950 m, 3 Nov 2008, *Bergh 1794* (NBG); Laingsburg Division, Witteberg (-BC), 3500 ft. [1067 m], 30 Nov 1924, *Compton 2818* (BOL, NBG); Laingsburg Dist., Keurkloof, Witteberg (-BC), 3500 ft. [1067 m], 8 Nov 1948, *Compton 21178* (NBG); Anysberg Nature Reserve, on eastern slopes of Land-Se-Kloof (-BC), 1097 m, 10 Dec 1991, *Vlok 2542* (PRE); Worcester Dist. Karoo Garden (-CA), 21 Oct 1946, *Barker 4276* (NBG); Robertson Division, Langeberg, Cogmans Kloof (-CC), 28 Oct 1954, *Esterhuysen 23863* (BOL, PRE); Montagu, Kogmans Kloof in saxosis (-CC), Oct 1903, *Marloth 3235* (BOL, NBG, PRE); Plathuis District, lower northern slopes of Touwsberg, Rietkloof (-DB), 550 m, 6 Oct 1993, *Bean 2944* (BOL, PRE); Montagu, Touwsberg, N slopes in deep kloof at Miskraal (-DB), 17 Sep 1993, *Snijman 1338* (NBG, PRE).

3321 (Ladismith): Ladismith, Waterkloof (-AD), 2000 ft., 1 Nov 1928, *Hutchinson 1111* (BOL, PRE); NW side of Touwsberg; Farm Rietfontein 139, 1500 m, 6 Oct 1993, *Bredenkamp 860* (PRE).

3418 (Cape Town): Sir Lowrey's Pass in the Hottentots Hollandsberge (-AD), 450 m, 19 Dec 2001, *Bayer SAF-01111* (PRE); Caledon Dist., Kogelberg Forest Reserve, 2200 ft., 19 Nov 1952, *Rycroft 1423* (NBG); Caledon Dist., Aries Kraal (-BB), 18 Nov 1944, *Barker 3340* (NBG); Caledon Dist., Shaw's Pass (-BB), 24 Jan 1951, *Barker 7202* (NBG); In montibus prope Sir Lowry's Pass (-BB), 400 ft. [122 m], Jan, *Bolus 4038* (PRE); Stellenbosch Division, Lourensford (-BB), Dec 1939, *Esterhuysen 4370* (BOL); Clarence Drive, below Boskloof Peak, at Clarence Drive 'monument' pull-off (-BB), 8 Dec 1998, *Forrester 1293* (PRE); between Gordons Bay and Kogelbaai (-BB), 24 Nov 1961, *Ihlenfeldt 1690* (PRE); Stellenbosch Div., in rupibus mts. S of Gordonsbay (-BB), 100 m, Nov 1919, *Marloth 1015* (PRE); Caledon Dist., Steenbras River Mouth (-BB), 23 Nov 1945, *Parker 4021* (NBG);

Elgin Basin, Arieskraal Farm (portion Arieskraal) (-BB), 210 m, 27 Jan 1996, *Rode 621* (NBG); Caledon Division, mountain slopes North of Kogelberg, 2200 ft., (-BB), 19 Nov 1952, *Rycroft 1423* (BOL); Sir Lowry's Pass (-BB), 2000 ft. [610 m], 17 Jan 1896, *Schlechter 7279/386* (PRE); above Gordons Bay (-BB), c. 100 ft. [30 m], 6 Nov 1927, *Smith 4798* (PRE); other side Gordon's Bay (-BB), 25 Nov 1955, *van der Merwe s.n.* (NBG); Kogel Bay (-BD), 28 Aug 1971, *Bohlman 4* (NBG); Kogelberg Forest Reserve, Louw/Palmiet River junction (-BD), 300 ft. [91 m], 21 Nov 1969, *Boucher 898* (NBG, PRE); Cape Hangklip area (-BD), 20 m, 14 Nov 1982, *Burman 1058* (BOL); Caledon Dist., Betty's Bay (-BD), 11 Oct 1963, *Codd 10138* (PRE); Betty's Bay, Disa Kloof, Klooffront in rigting van see [valley front in the direction of the sea] (-BD), 4 Apr 1972, *Eicker 40* (PRE); Cape Hangklip between Rooi-Els and Bot River (-BD), 15 Mar 1985, *Ekokonsult 34-27* (PRE); Palmietriver mouth, Paardebeg (-BD), 250 ft. [76 m], 21 Dec 1961, *Grobler 238* (NBG); Kogelberg State Forest, across Palmiet River, left of Fairy Glen road, in line with Oudebosch

dwellings which are on the eastern slope (-BD), 50 m, 15 Nov. 1991, Kruger 60 (NBG); Kogelberg State Forest, ± 0.75 km from 2nd house at Oudebos, E of 2nd koppie at northern road, ± 60 m from Palmiet River (-BD), 40 m, 4 Nov 1992, Kruger 897 (NBG); Palmiet River Mouth (-BD), 16 Feb 1936, Levyns 5348 (BOL); Caledon Dist., Hangklip Estates (-BD), Nov 1947, Stokoe PRE 42914 (PRE); Caledon Dist., Cascades, Betty's Bay (-BD), Taylor 4398 (NBG); Betty's Bay (-BD), Jan 1970, van der Schijff 7425 (PRE).

3419 (Caledon): Villiersdorp road from Elgin Mountain (-AA), 2000 ft. [610 m], 4 Nov 1973, Bayliss BRI B 708 (PRE); in collibus prope Grabouw, Palmiet R. (-AA), c. 1200 ft. [366 m], Dec 1877, Bolus 4038 (BOL); in collibus saxosis prope Houw Hoek (-AA), 1400 ft. [427 m], Dec 1894, Bolus 6945 (BOL, PRE); Caledon Dist., Elgin (-AA), Dec 1917, Elbrecht TRV 22127 (PRE); Houwhoek, Elgin (-AA), Feb 1926, Gillett s.n. (NBG); Elgin, Rooskraal Nature Reserve (-AA), 10 Jun 1937, Hubbard 427 (NBG); Caledon Dist., Houwhoek (-AA), 18 Nov 1951, Maguire 1233 (NBG); Viljoen's Pass (-AA), Dec 1924, Rogers 25895 (29244) (PRE); Caledon Dist., Nuberg, top of Viljoen's Pass (-AA), 6 Dec 1954, Stokoe SAM68549 (PRE); Grabouw Dist., Viljoen's Pass (-AA), 20 Dec 1956, Strey 2920 (PRE); Caledon Dist., Grabouw (-AA), Taylor 4423 (NBG); Caledon Dist., Hawston Mtn (-AC), 30 Dec 1940, Bond 750 (NBG); Caledon Division, Hermanus (-AC), Jan 1920, Burt-Davy Sub-BH18719 (BOL); Caledon Dist., Kleinmond dorpsrwe (-AC), 23 Nov 1946, de Vos 314 (NBG); Caledon Dist., Hermanus (-AC), 11 Feb 1950, Martin 312 (NBG); Hermanus (-AC), 9 Nov 1921, Rogers 26450 (PRE); Mossel River (-AD), Jan 1920, Guthrie PRE 42913 (PRE); Fernkloof Nature Reserve Hermanus (-AD), 125 m, 4 Dec 1975, Orchard 340 (NBG); Caledon Dist., Mossel River, at foot of mountain (-AD), ± 100 ft. [30 m], Jan 1929, Pont 1171 (PRE); Vogelgat, Caledon Div. (-AD), 150–500 ft. [46–152 m], 6 Dec 1978, Williams 2659 (NBG, PRE); Caledon Division, Vogelgat, near Lookout (-AD), 170 m, 19 Dec 1982, Williams 3398 (NBG); Ceres Dist., Bokkerivier Farms, ridge SE of camping site (-BB), 9 Nov 1963, Horrocks 111 (NBG); Paarl Dist., by Paarlberg, brandperseel (-BC), 17 Jan 1963, Guthrie M170 (NBG); Caledon Dist., Kogelberg Reserve, Paardeberg, seaward side (-BD), 250 ft. [76 m], 21 Dec 1961, Grobler 238 (PRE).

Without precise locality: Zeyher 3017 (NBG); Zeyher 977 (K 415223).

2. *Heterolepis mitis* (Burm.) DC. in Prodr. 6: 497 (1838).

Gorteria mitis Burm. f. in Prodr. Fl. Cap.: 28 (1768). -Type: 'Carlina folius simplicibus flore aureo' in Burm., Rar. Afr. Pl. t.54 f.2.: 151 (1738). (-image!, icono). Epitype: South Africa, Eastern Cape, Kirkwood, Kabouga, 260 m, 24 Aug. 2014, R.J. McKenzie 3142 (NBG! epi., designated here; BOL!, GRA!, PRE!, SI, iso.).

Illustration: Fig. 3.

Habit: small, slender, sparsely- to well-branched shrublet, 0.15–0.3 m high. **Stems:** young stems green, sparsely glandular. Older stems twiggy, to 4.0 mm diameter, bark thick relative to stem diameter, stems marked with old leaf scars. **Leaves:** borne only towards the ends of the branches, loosely imbricate, uppermost leaves more densely-spaced, at least partially overlapping the capitulum; erect to spreading; linear-oblongate, 8–24 \times 0.3–1.5 mm, not becoming smaller acropetally; narrowed towards base, sessile to very shortly petiolate, apex acute with a distinct mucro, thin and smooth-textured, margins narrowly revolute, entire, both leaf surfaces dark green, glabrous and sparsely to densely obscurely glandular, glands sunken into leaf surface to give a slightly pitted (foveolate) appearance, resinous, pitted and wrinkled on drying, mid-rib slightly raised on abaxial surface.

Peduncle: capitula sessile, or peduncle 1–2 mm long, glandular with trichome type A, trichomes on peduncle larger than those on the adjacent stem. **Capitula:** radiate, in peduncled specimens 22–30 mm in diameter including expanded rays, with ~ 44 disc and ~ 2 –16 ray florets (note: this number based on only two dissected specimens). **Involucre:**

7–12 mm wide, fleshy portion sparsely dotted with very small pale glands; outermost bracts only slightly smaller than middle or inner, narrowly deltoid-lanceolate, free portion 5–7 \times 0.8–1.0 mm, apically acute; inner bracts with free portion 8–10 \times 2.0–4.0 mm. Involucre becoming dark brown when old. **Receptacle:** alveoles pentamerous, margins with short toothlike projections 0.5 mm long, a tooth at each of the five corners of each alveole. **Ray florets:** corolla deep yellow, corolla tube glabrous or with a few scattered glands, ± 4.5 mm long; ray lamina 3.0–4.0 \times 7.5–9.0 mm, abaxial surface of lamina lobes apically gland-dotted with small, rounded trichomes. **Staminodes** with filaments; staminode tails rounded and incurved, apical appendages obtuse. **Cypselas** and pappus as in disc florets. **Disc florets:** deep yellow, tube 6.0 mm long; corolla lobes 2.5–3.0 mm long, becoming strongly recurved after anthesis, apically dotted with globose multicellular trichomes. **Style** extending ± 5 mm beyond corolla tube at maturity, becoming densely papillate at a slight thickening ~ 2.0 –3.0 mm below apex, thickening without a longer tuft of sweeping hairs. **Stigmatic branches** short, narrowing slightly to rounded apices. **Apical anther appendages** about 1.0 mm long, obtuse with short mucro-like structure, central vein with dark yellow pigment near apex. **Anther tails** about 0.07 mm long, broadly acute, slightly curved inwards. **Pappus:** of approximately 20 robust, brittle, strap-shaped cartilaginous bristle-like scales, apically tinged strongly blue-black, colour fading to base which is straw-coloured and shiny; flattened and widened near base (to about 0.13 mm wide), tapering towards apex. **Inner series** of ± 10 bristles, 8–9 mm long, slightly longer than the full length of the corolla, narrowing towards the apex where the barbs become longer and increasingly dense. **Outer series** of ± 10 bristles, slightly narrower and much shorter than inner series, ± 3 mm long, apically more sparsely barbellate than inner bristles. **Pappus elements** free. **Cypselas:** twin-hairs bright white, providing a strong colour contrast to the pappus bristles.

Diagnostic characters: *Heterolepis mitis* is the most morphologically distinct member of the genus, due to its small size, dark green, glabrous and slender leaves, small, sessile capitula partly enveloped by the upper leaves, and habit of growing in the crevices of sandstone rocks. The leaves, stems and involucral bracts are markedly less glandular-scabrid than all other species in the genus, although small, somewhat sunken glands are present. Probably the most distinctive feature of *Heterolepis mitis* is its glabrous foliage, giving the plant a dark-green appearance in contrast to the grey-green or whitish appearance of the other species. *Heterolepis mitis* also has the easternmost distribution. Several collections note the fact that the plants are 'aromatic', and rehydrated material is exceptionally pungent-smelling. The stems and leaves frequently become viscid on drying, as if covered with a clear varnish layer, a feature which has not been observed on other species of *Heterolepis*.

Flowering time: recorded in flower in January, April, August, October and December (Fig. S1), despite the small number of records. Possibly the plant flowers continuously throughout the year, or sporadically, depending on rainfall, and plants may bear only a few capitula at any one time.

Distribution: (Fig. 1). This species is known from only a few collections, all in the same quarter-degree grid square, in the southern and western foothills of the Suurberg and Klein Winterhoek ranges near Kirkwood in the Eastern Cape.

Habitat and ecology: *Heterolepis mitis* grows only on rock faces, rooting in crevices in rocks of the Witteberg Group sandstones. The rock-crevice habit is otherwise found only in some individuals of *H. aliena*.

Etymology: the species epithet 'mitis' means "mild, mellow, innoxious, soft" (Stearn, 1967). Burman (1768) placed the species in the genus *Gorteria* which at the time contained several of the spiny, thorny daisies currently placed in *Berkheya*. By comparison, *H. mitis* is indeed 'innocuous'.

Red-List status: Rare (Herman and Victor, 2007).

Nomenclatural notes: The basionym, *Gorteria mitis*, was published by N.L. Burman (1768) in an addendum, *Flora Capensis Prodrum*, to his *Flora Indica*. The species was based solely on an engraved illustration published in *Rariorum Africanum Plantarum* by his father, J. Burman, in 1739 that was labelled with the descriptive polynomial ‘*Carlina foliis simplicibus flore aureo*’ and was accompanied by a description. De Candolle (1838a) published the new combination *Heterolepis mitis*, citing the basionym published by N.L. Burman (1768), the illustration in J. Burman (1739) on which the basionym was based, and a collection by J.F. Drège from ‘in Africa Capensi ad Zontagrivier et Zneurobergen’. A specimen presumed to be of this gathering (Drège 3699), collected in 1835, is housed in the G-DC herbarium, where it is annotated ‘Typus’. This has mistakenly been digitised as the holotype of *H. mitis*. An earlier (unnumbered) Drège gathering, collected ‘between Zoutpansnek and Enon in (rich?) bushy places under 1000 ft, in March’ in 1829, is lodged in K. Both of these sheets (seen only as high-resolution digital images) are clearly of *H. mitis*. However, neither the illustration on which the name is based, nor the description, can be unambiguously matched with the taxon currently known as *Heterolepis mitis*. Although the leaf arrangement is somewhat similar, the leaves in the illustration are linear with acuminate tips that appear to be recurved or laxly bent. Leaves in *H. mitis* are slightly but definitely oblanceolate with rounded or blunt tips. The capitulum in the Burman illustration is broad and very shallow, with no detail of the florets. If it is interpreted as an empty receptacle lacking florets, the capitulum is indicated to be much too broad to represent that of *H. mitis*. If the illustration depicts flowering material, there is only a single whorl of radiating structures surrounding the capitulum; these could be interpreted as either rays or involucre bracts. If the structures represent rays, there are too many and the involucre is too shallow to be consistent with *H. mitis*. If involucre bracts, these structures are far too long, apically acute rather than rounded with no suggestion of the apex being papery or semi-translucent, and the involucre is too shallow to represent those of *H. mitis*. The accompanying short description of “*Carlina foliis simplicibus flore aureo*” by Burman (1739) fails to provide any additional clues to clarify the identity of the species. Although the illustration cannot be matched to *H. mitis*, it similarly cannot be matched unambiguously to any other known species of Asteraceae (or another family) from the Cape region.

Several Cape plant collectors (mostly associated with the Dutch East India Company’s Gardens in Cape Town) could have contributed the specimen on which the illustration in Burman (1739) was based (Wijnands, 1992). However, the first half of the 1700s are very early for Cape plant collecting, and most collections from this time are from the Cape colony close to Cape Town. Hendrik Oldenland, who resided at the Cape from 1688 until his death in 1697, is documented by Glen and Germishuizen (2010) to have participated in one expedition that in 1689 reached a region of the Karoo in the Eastern Cape only a few hundred kilometres from the presently-known range of *H. mitis*. Oldenland’s collections are known to have been used by Burman, but there are to our knowledge no other documented plant collecting expeditions in the Eastern Cape region before the mid 1700s. In the absence of any further information about the illustration in Burman (1739), we can only speculate as to whether any plant specimens were actually collected from the Suurberg region prior to the publication of *Rariorum Africanum Plantarum*.

De Candolle (1838a) did not state his reasons for considering the Drège 3699 collection to be conspecific with the illustration and description on which *Gorteria mitis* was based. No specimen of *H. mitis*, or one that can be linked to the illustration of “*Carlina foliis simplicibus flore aureo*”, has been seen in the Burman Herbarium or in G, although the authors have not personally visited the collection in Geneva. Perhaps De Candolle had access to original material, not available to us, that provided additional information. We are unaware of any gathering of *H. mitis* that could be dated to the late-seventeenth or early-eighteenth centuries. The illustrations in J. Burman’s *Rariorum*

Africanum Plantarum were based on several sources, including the personal herbarium of Nicolaas Witsen and the ‘Witsen Codex’, a collection of paintings and manuscripts currently known from several incomplete and scattered volumes (Macnae and Davidson, 1969). Burman (1739), in the description accompanying the illustration of *Carlina foliis simplicibus flore aureo*, does mention the Witsen Codex: “Semina in Cod. Wits. non sunt delineata, ubi haec planta vocatur Scolymus Chrysanthemum flore luteo, & annotatur, quod juxta montes locis saxosis crescat, florens Septembri” [Seeds in Cod. Wits. not drawn, where the plant is called Scolymus Chrysanthemum flore luteo, and annotated, that it grows near mountains in rocky places, flowering in September]. We have been unable to match any illustration in presently accessible ‘Codex’ volumes to the figure in Burman (1739). The illustration is taxonomically ambiguous and its features, even with a large degree of artistic licence, do not match those of the species currently known as *H. mitis*. One option is to propose formal rejection of the name *Gorteria mitis* Burm.f., due to the fact that the original material cannot be unambiguously linked to any known species. However, this solution is nomenclaturally disruptive as it would require publication of a new name for the species. We are continuing to search for an original illustration or specimen on which the figure in Burman (1739) was based, which might clarify application of the name *Gorteria mitis*. In the interim, with nomenclatural stability in mind, we have opted to epitypify the name *Gorteria mitis* based on a recent, well-preserved gathering of the species to which De Candolle applied the name.

Additional specimens examined (8 collections from BOL, GRA, HAL, K, NGB and PRE):

South Africa–EASTERN CAPE: **3325 (Uitenhage):** Uitenhage, Claassen’s (nr/r) Paarde Poort, rocky hillsides (–AC), Jan 1867, *Bolus s.n.* (Sub-BH1650) (BOL); 12 km NW of Kirkwood, Suurberge, ridge 300 m NE of Kabouga cottage (–AD), 250 m, 13 Dec 2013, *Helme 8036* (NBG); Kirkwood, Addo Elephant National Park, Kabouga section, near Kabouga Cottage (–AD), 24 August 2014, *McKenzie 3147* (NBG, BOL, GRA, PRE); Kirkwood, north of Sapkamma Siding, Soutkloof (–AC), 340 m, 29 Oct 2013, *McKenzie 3135/1* (NBG, GRA); One km N of Sapkamma Station (–AC), 14 Apr 1989, *van Jaarsveld 10835* (PRE); In rupestribus pr. Uitenhage, 1000 ft. [305 m], Jan 1867, *Bolus 1650* (GRA); In Africa Capensi ad Zontagrivier sond Zuurebergen, Feb 1835, *J.F. Drège 3699* (G-DC, K, GRA); Cape, Klein Winterhoek, in rich bushy places between Zoutpansnek and Enon, below 1000’ [305 m], Mar 1826–1834, *J.F. Drège s.n.* (HAL, K).

3. *Heterolepis peduncularis* DC. in Prodr. 6:497 (1838). –Type: South Africa, ‘Cap. Bonae-Spei [Cape of Good Hope] ad Orientem urbis, 1814, *W.J. Burchell 6828* (G-DC-image!, lecto, designated here; P-image!, isolecto.). Syntype: South Africa, ‘Zwillingdam’, *C.F. Ecklon/C.L. Zeyher 3300* (K-image!, syn., here designated; NBG!, PRE!, isosyn.);

Minurothamnus phagnaloides DC. in Prodr.7(1): 286 (1838), *syn. nov.* –Type: South Africa, ‘Cap. Bonae Spei in distr. Caledon’, *C.F. Ecklon 274*. (G-DC-image!, holo).

Illustration: Fig. 4 (specimen in Fig. 5).

Habit: sparsely-branched, twiggy shrublet 0.20–1.0 m high. **Stems:** younger stems slender and pale with a dense white-woolly indumentum; older stems with thin dark bark; longitudinally striate, eglandular. **Leaves:** borne mainly on the lower stems, loosely imbricate, erect or erect-spreading, linear, lower leaves 20–60 × 1.5–2.0 mm, leaves decreasing in length acropetally, upper leaves < 10 mm long; sessile, obscurely auricled at base, apex bluntly acute, somewhat thickened and leathery, margins strongly revolute and covering the edges of the abaxial surface, with small sparse marginal teeth or sometimes entire, adaxial surface grey-green, glabrous to glabrescent, abaxial surface densely white-tomentose except on midrib which is prominent and green. **Peduncle:** 40–190 mm long when mature, elongating rapidly on

floral maturation, bearing one or two minute leaflike bracteoles; not woolly or only sparsely so; reddish-brown, faintly striate and densely invested with very fine to stout stalked trichomes (type A). *Capitula*: radiate, occasionally discoid, in pressed specimens mature heads are 12–35 mm in diameter including expanded rays, containing ± 25 –42 discs and ± 6 –12 rays (based on dissection of heads from two specimens). *Involucre*: 8–15 mm across, green, fleshy portion of bracts glabrous or sparsely white-woolly, as well as densely glandular with trichomes of type A. Outermost bracts narrowly deltoid-lanceolate, free portion 4–6 \times 1.0–1.2 mm, innermost bracts with free portion 14–18 \times 2.5–5 mm.

Receptacle: alveole margin projections irregular and slightly thickened. *Ray florets*: corolla golden yellow, tube with stalked trichomes of type B, lamina 3–4 \times 8–12 mm. Point at which style sweeping-hair covering begins is unmarked by any swelling or hair tuft. Style branches short, broadly acute. Sterile anthers reduced, with no or very short filaments. Cypselas and pappus as in disc florets. *Disc florets*: golden yellow, 10 mm long, tube sparsely covered in elongate, multicellular clavate-tipped trichomes (type B); corolla lobes broadly acute, 2–3 mm in length, strongly recurved after anthesis, abaxially invested with blunt-ended multicellular trichomes (type C) near apex. Style exerted ± 6 mm beyond corolla tube; point at which sweeping-hair covering begins marked by a ring of longer hairs. Style branches short, broadly acute. Anther tube narrow, apical anther appendages thin, flat, short, obtuse, with a central patch of pigmented cells; anther bases sagittate with elongate, rounded tails.

Pappus: of approximately 25–35 straw-coloured or black-tinged bristle-like scales, inner series coming to about halfway up the corolla lobes, outer series shorter than this, to between half and three-quarters of the length of the inner. Pappus scales fused at base, individual bristles conspicuously widened near base (to about 0.5 mm wide), tapering towards apex. Bristle margins and apex plumose, plumes upwardly-directed. *Cypselas*: twin-hairs straw-coloured or reddish-brown.

Diagnostic characters: *Heterolepis peduncularis* is most easily confused with the discoid-headed *H. anomala*. However, *H. anomala* has thicker leaves that do not noticeably decrease in length upwards on the stem (Fig. 5), and also has a very narrow distribution range only on the northern slopes of the Langeberg in the Garcia's Pass area. *Heterolepis peduncularis* is distinguished from the remaining members of the genus by its long peduncles, usually 100 mm or longer, and by its lax, slender leaves that decrease in length moving acropetally up the stem (Fig. 5). It is a plant with a very 'straggly' appearance, which is probably exacerbated by grazing. Several collectors noted an aromatic or sharp odour associated with this species, with one collector classifying the odour as lanolin, and another as apples. One specimen of (*le Roux 1452*, collected between Worcester and Robertson) has discoid heads. However, in all other characteristics, this is clearly *H. peduncularis*. One mutant specimen, *Bohnen 9046* from Springfontein near Elim, has true bilabiate ray florets and a trifid style. Three-lobed style branches are commonly observed in *Dymondia* Compton (Arctotideae subtribe Arctotidinae).

Flowering time: *Heterolepis peduncularis* flowers mainly in early summer (Fig. S1), with the peak flowering period in October and November, tailing off in December. However, flowering specimens have been collected in several other months (January, February, June, July and September).

Distribution: the species occurs almost entirely on the Southern Cape coastal platform south of the east–west trending Cape Fold ranges (Langeberg and Riviersonderend mountains), but there are collections from between Worcester and Touwsriver, and from the Warmwaterberg area in the Little Karoo (Fig. 1). The species has not been collected west of the 19 degree line of longitude. The easternmost collection is from the Mossel Bay region, just east of the Gouritz River bridge.

Habitat and ecology: *Heterolepis peduncularis* grows in soil in open scrubland in South Coast renosterveld vegetation, or possibly in the renosterveld–fynbos transition. Recorded substrates are frequently a mixture of shales and sandstone, for example, collectors note the

substrate type to be shale overlain by Table Mountain Sandstone gravel, or silcrete. Renosterveld vegetation is frequently noted on herbarium labels, as is rocky, loamy soil and occurrence on flats or flat areas. In terms of its fire ecology, the following collector notes are relevant: "Veld 7 years old" (*Helme 5368*); "Burnt areas on slopes: frequent" (*Levyns 6196*); "Resprouting shrub in veld burnt recently—approx. several months to one year previously?" (*Bergh 2043*); "200 ha patch of >20-year old (renoster)veld" (*Helme 1898*); "resprouts after fires (?)" (*Burgers 1641A*). From these notes it seems that post-fire resprouting may be present in *H. peduncularis*, although it is not known to what extent this is obligatory.

Etymology: the species epithet 'peduncularis' likely refers to the long peduncle which, together with the smaller capitula containing fewer florets, distinguishes this species from *H. aliena*.

Red-List status: Least Concern (*Foden and Potter, 2005b*)

Nomenclatural notes: In the protologue for *Heterolepis peduncularis*, De Candolle cites two specimens: Burchell 6828 and Ecklon 'in Zwellendam' (this is probably Ecklon 3300, also ticketed 'Zeyher 3300' in some herbaria). Both specimens are in Geneva. The Burchell specimen is here designated the lectotype.

The name *Minurothamnus phagnaloides* DC. was published by De Candolle (1838b) in a supplement (Mantissa Compositarum) to his treatment of the Asteraceae in the *Prodromus systematis naturalis regni vegetabilis*. De Candolle clearly considered his new genus to be a member of the tribe Inuleae (as it is defined today), because he listed it between *Pegolettia* and *Geigeria*, and also stated '*Videtur Inulea. Affinis Cypselodontiæ et Pegolettia*'. Possibly for this reason, De Candolle (and subsequent authors) did not recognise that *Minurothamnus phagnaloides* is actually a species of *Heterolepis*. Only in the 20th Century did Merxmüller (1950) synonymise the name with *Heterolepis aliena* (L.f.) Druce. However, Merxmüller based this only on the description as he was unable to examine the original material in G-DC. One of us examined a digital image (on microfiche at BOL) of the specimen Ecklon 274, which is the sole sheet in G-DC annotated by De Candolle with the name *Minurothamnus phagnaloides*. The specimen is clearly conspecific with *H. peduncularis* and not *H. aliena*. The name *Heterolepis peduncularis* has nomenclatural priority and therefore *Minurothamnus phagnaloides* is here placed in synonymy with that name.

Additional specimens examined (41 collections from BOL, G, GRA, K, NBG and PRE):

South Africa—WESTERN CAPE. **3319 (Worcester)**: Worcester, Bonteberg (-BD), 3000 ft. [914 m], 3 Nov 1940, *Compton 9901* (NBG), Worcester Division, Gouronna (-BD/3320AC), 3 Nov 1940, *Esterhuysen 3739* (BOL, PRE); Worcester, Droogeriviersberg (-DC), 487 m, Dec 2015, *le Roux 1452* (NBG); Karroid places South of Robertson (-DD), 800 ft. [244 m], Oct 1929, *Levyns 2801* (BOL); Vrolikheid Nature Reserve (-DD), 27 Sep 1974, *van der Merwe 2506* (PRE).

3320 (Swellendam): Klein Karoo, Dobbelaar's Kloof, slopes of kopje near "Cape" junction (-DA), 2000 ft. [610 m], 15 Dec 1950, *Levyns 9540* (BOL); Swellendam, in montibus pr. Buffeljagts River (-DC/3420 BA), 1871, *Kennedy 1475* (BOL, GRA); Broken Hill 88, south slopes of Langeberg east of Grootvadersbos. Lat: 33°59'40.5"S; Long: 20°54'42.6"E (-DD), 290 m, 1 Jun 2012, *Helme 7391* (NBG); Little Karoo, Warmwaterberg, burnt areas on slopes (-DD), 3000 ft. [914 m], 16 Jul 1939, *Levyns 6196* (BOL).

3321 (Elim): Springfontein; Brandrivier op klipkop—(T.B.S.) noord front [Brandrivier on rockyhill – Table Mountain Sandstone] (-CC), 430 m, 10 Oct 1989, *Bohnen 9046* (NBG, PRE).

3419 (Caledon): Caledon District, east of Grabouw (-AB), 18 Nov 1951, *Maguire 1230* (NBG); Caledon division, Dassiesfontein Farm area, Transect 2 area (-AB), 274 m, 28 Oct 2006, *Walton DA2/530* (NBG); Caledon, E shore of Botrivervlei on Afdakrivier 575 (-AC), 20 m, 10 Nov 2002, *Helme 2600* (NBG); Caledon District, near Hermanus Road on pass over Shaw's Mountain (-AD), 19 Dec 1934, *Salter 5157* (BOL, NBG); Caledon District; Genadendal (-BA), 10 Oct 1846, *Alexander-Prior PRE 42925* (PRE).

3420 (Swellendam): Swellendam (-AA), 9 Nov 1835, *Ecklon 905* (alternatively: 1082) (Geneva, only photograph seen at PRE); Swellendam-Bonnievale (-AA), 5 Dec 1950, *Maguire 786* (NBG); Caledon District, Volmoed, farm near Proteem (-AA), 19 Oct 1983, *van Breda 4539* (PRE); Bontebok National Park, BB12 plot (-AB), 139 m, 2 Sept 2003, *Kraaij 34750* (PRE); Bredasdorp, about 14 km NNE Caledon, farm Brakfontein 123, known as Ongegund, slopes of Tuinkop north of Noordekloof, (-AC), 360–500 m, 27 October 2000, *Helme 1898* (NBG); Swellendam, in collibus prope Zuurbraak (-BA), 1000 ft. [305 m], 17 Jan 1893, *Schlechter 2124* (GRA, NBG); Heidelberg, hill N of Verkykerskop road between Malgas and Heidelberg (-BA), 29 December 1991, *Schutte 759 B* (PRE); Swellendam div., Buffeljagsdam (-BA), Oct 1975, *van der Merwe 2650* (PRE); Bontebok National Park, western edge of plateau overlooking N2 (-BB), 116 m, 25 Feb 2008, *Helme 5368* (NBG); De Hoop, Potberg Nature Reserve, Potberg; 1.2 km west of residence (-BC), 165 m, 3 Dec 1980, *Burgers 2608* (NBG, PRE); Potberg, northern side above Diepkloof (-BC), 150 m, 30 Nov 1976, *Burgers 1641A* (NBG, PRE); Swellendam Div., Malgas (-BC), 27 Oct 1940, *Esterhuysen 4848* (BOL, PRE).

3421 (Riversdale): Langeberg, S of Garcia's Pass; Farm Vetrivier (-AA), 207 m, 2 Oct 2009, *Bergh 2043* (NBG); Riversdale, 2 km onto Kweekkraal (-AA), 12 Oct 1981, *Mauve 196* (NBG, PRE); Riversdale meent (-AB), 315 m, 29 June 1985, *Bohnen 8557* (PRE); hills near Riversdale (-AB), 200–600 ft. [61–183 m], Oct 1923, *Muir 2802* (BOL, PRE); near Riversdale (-AB), 150 ft. [46 m], October 1924, *Muir 3472* (PRE); Mossel Bay district, 1 m. E of Gouritz R. Bridge (-BB), c. 500 ft. [152 m], 4 Dec 1960, *Acocks 21745* (PRE).

Without precise locality: In collibus prope Caledon, Nov 1893, *Bolus 7883* (NBG); ?Caledon, *Guthrie s.n.* (BOL); Caledon Distr., East of Grabouw, 18 Nov 1951, *Maguire 1230* (BOL); Bot River; in montibus, 500 ft. [152 m], 27 Nov 1896, *Schlechter 1649/9457* (BOL, GRA, PRE); *Guthrie No. 27670* (NBG); Swellendam Distr., Bushman's River, 24 Sept 1941, *Walgate 347a* (NBG); near Caledon, in collibus, 900 ft. [274 m], Nov 1893, *Bolus 7883* (BOL); Cape, *Mundt s.n.* (K000415227) (K—photo); C.B.S., *Zeyher 3017* (K); Zwellendam, 9 Nov 1835, *Ecklon 1082* (and/or 1085) (G, —photo).

4. ***Heterolepis anomala*** J.C. Manning & Goldblatt in Pl. Greater Cape Floristic Region 1: 795 (2012).—Type: South Africa, Western Cape, 'Muiskraal, voetheuwels van Langeberg', 370 m, 4 Oct 1990, *Bohnen 9129* (NBG!, holotype).

Illustration: Figs. 5 & 6.

Habit: sparsely-branched, compact shrublet generally to about 0.3 m high. **Stems:** young stems densely white-woolly, older stems sparsely white-woolly with thin dark bark; longitudinally striate, eglandular. **Leaves:** most dense at the lower ends of the branches, densely imbricate, erect, linear, terete, 8–18 × 0.9–1.5 mm, not becoming shorter acropetally, sessile, apex shortly mucronate, thickened and leathery, margins strongly revolute and very sparsely dentate with only (0–) 1–3 tubercle-like teeth per leaf, adaxially sparsely white-woolly when young, becoming glabrous, mid-rib visible on adaxial surface, abaxial leaf surface densely white-tomentose except on green midrib, but this surface mostly obscured by the revolute margins. **Peduncle:** 25–110 mm long when mature, elongating rapidly on floral maturation, bearing one or two leaflike bracteoles, not woolly or only sparsely so, reddish-brown, faintly striate and densely invested with very fine to stout trichomes of type A.

Capitula: discoid, in pressed specimens mature heads are 20–25 mm in diameter, containing about 20 florets (21 in *Bohnen 9129*). **Involucre:** 8–15 mm across, fleshy portion of bract covered with large, conical, reddish-brown or pale trichomes (type A), outermost bracts narrowly deltoid-lanceolate, free portion 6–9 × 1.0–1.2 mm, densely glandular-scarid; innermost bracts lacking trichomes, with free portion 10–13 × 2.0–4.0 mm. **Receptacle:** alveole margins with irregular, very

shallow projections. **Disc florets:** pale yellow, 9–10 mm long, tube sparsely glandular with type B trichomes, corolla lobes broadly acute, 3 mm in length, margins with a dark outline. Style apex slightly thickened at tuft of sweeping-hairs; stigmatic branches short, apices truncate to very slightly cleft. Apical anther appendages short, deltoid; anther bases with acute tails about 0.8 mm long. **Pappus:** of approximately 18–22 robust, brittle, cartilaginous straw-coloured bristle-like scales, free; inner series ± 8 mm long, slightly shorter than the corolla (coming to about halfway up the corolla lobes), outer series ± 6 mm long. Individual pappus bristles of both series widened near base (to about 0.4 mm wide), tapering towards apex. Bristle margins plumose, plumes golden-straw coloured, upwardly-directed. **Cypselae:** twin-hairs straw-coloured or reddish-brown.

Diagnostic characters: *Heterolepis anomala* is distinguished from all other species by its discoid heads. It is, however, most similar to *H. peduncularis*, and specimens in herbaria may be filed with the latter species. The black colour characteristic of the pappus bristles in *H. aliena* and *H. mitis*, and some specimens of *H. peduncularis*, was not observed in any specimens of *H. anomala*, which has instead distinctly pale pappus bristles and corolla lobes. The style-branch apices are unique in *H. anomala*, being truncate and slightly cleft, whereas in all other species the style-branch apices are rounded to broadly acute.

Flowering time: the five collections of this species are mostly from different months: three in late summer / early winter (March and April) and two in early to mid-summer (October and December); Fig. S1.

Distribution: *Heterolepis anomala* is currently known only from the farms Muiskraal and Fisantefontein, on the northern foothills of the Langeberg near Garcia's Pass (Fig. 1).

Habitat and ecology: Collectors note *Heterolepis anomala* growing in arid fynbos on well-drained, often rocky Table Mountain Sandstone-derived soil. In one instance (*Vlok 2780*) the collector noted 'resprouting after fire' but for another collection (*McDonald 2091*) it was noted that the plant was 'growing in undisturbed, old veld'.

Etymology: the species epithet 'anomala' denotes the discoid heads which are unique in the genus.

Red-List status: Vulnerable, due to potential threats from alien invasive plants and habitat degradation linked to heavy livestock grazing after burning (von Staden and Raimondo, 2014).

List of specimens examined: 4 specimens from NBG, SAM and PRE.

South Africa—WESTERN CAPE. **3321 (Riversdale):** Plaas Muiskraal, noordelike voetheuwels van Langeberg, op T.B.S. [Farm Muiskraal, northern foothills of Langeberg, on Table Mountain Sandstone] (-CC), 370 m, 7 March 1987, *Bohnen 8769* (NBG); Langeberg, North end of Garcia's Pass (-CC), 8 December 1938, *Håfstrom 2285* (PRE); Langeberg, Farm Phesantefontein, lower N slopes of Langeberg west of Garcias Pass, bordering Little Karoo (-CC), 470 m, *McDonald 2091* (NBG); Riversdale, on Fisantefontein Farm, on lower Northern slopes of Langeberg (-CC), 1800 ft. [549 m], 7 April 2000, *Vlok 2780* (PRE).

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.sajb.2015.12.004>.

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specimens; in particular the Biodiversity Heritage Library (BHL), Botanicus, JSTOR Plant Science, the Global Plants Initiative, and staff at G-DC Phanerogams, especially Laurence Loze. The authors wish to thank T. Trinder-Smith for the digital specimen information from BOL, and the curators of GRA and PRE for sending material to the first author on loan.

Appendix A. List of scientific names

Names in bold are currently accepted:

- *Arnica inuloides* Vahl. Synonym of *Heterolepis aliena* (L.f.) Druce.
- *Gorteria mitis* Burm.f. Synonym of *Heterolepis mitis* (Burm.) DC.
- *Heteromorpha* Cass. Synonym of *Heterolepis* Cass.
- ***Heterolepis*** Cass.
- ***Heterolepis aliena*** (L.f.) Druce.
- ***Heterolepis anomala*** J.C. Manning & Goldblatt.
- *Heterolepis decipiens* Cass. Illegitimate and superfluous synonym of *Heterolepis aliena* (L.f.) Druce.
- ***Heterolepis mitis*** (Burm.) DC.
- ***Heterolepis peduncularis*** DC.
- *Leysera arctotoides* Thunb. Synonym of *Heterolepis aliena* (L.f.) Druce.
- *Oedera aliena* L.f. Synonym of *Heterolepis aliena* (L.f.) Druce.
- *Minurothamnus phagnaloides* DC. Synonym of *Heterolepis peduncularis* DC.

Appendix B. Historical outline

1738: J. Burman publishes an illustration (p. 151, Fig. 2) and accompanying description (p. 153) in *Rariorum Africanarum Plantarum*. He refers to this plant as “*Carlina foliis simplicibus, flores aureo*”.

1768: N.L. Burman (son of J. Burman), publishes ‘*Flora Indica: cui accedit series Zoophytorum Indicorum, nec non Prodrumus Florae Capensis*’. This is a flora of India but includes the *Prodrumus* at the end. There is a note in the book at the Bolus library: “The ‘*Prodrumus Florae Capensis*’ was based on Oldenland’s collections and comprises pp. 32 at end (pp. 29–32 are misprinted 25–28).” On the first p. 28, N. Burman writes:

FRUSTRANEA

GORTERIA (personata) etc.—4 species entered here.
 ----- (mitis) Burm. afr. t. 54. f.2
 ----- (3 more spp.)

This, the first valid publication of *Gorteria mitis*, cites only the illustration in the J. Burman publication, which is thus the type for this name.

1782: Linnaeus the younger publishes the species *Oedera aliena* L.f. in *Supplementum Plantarum* p. 390, citing a specimen collected by “Bladh”, which is housed in LINN.

1791: Vahl publishes the species *Arnica inuloides* Vahl. in *Symbolae Botanicae* vol. 2: 91. 1791, citing a specimen, Bulow s.n. Capite b. Spei., which is housed in C.

1797: Jacquin publishes the second volume of *Plantarum Rariorum Horti Caesarei Schoenbrunnensis* in which is illustrated and described, *Oedera aliena* L.f. The synonym *Arnica inuloides* Vahl. is also cited.

1800: Thunberg publishes *Leysera arctotoides* in *Prodrumus Pl. Cap.* 2: 160, but mentions no specimens on which the name is based. Only later (Thunberg, 1823) are specimens associated with the name.

1817: In January, Cassini describes a genus, *Heteromorpha*, in *Bulletin des Sciences par la Societe Philomatique de Paris*, erecting this genus to house the species *Arnica inuloides* Vahl., although he doesn’t make the new combination.

1820: In February, in the same journal, Cassini substitutes the name *Heterolepis* for *Heteromorpha*, stating “I had first proposed this genus under the name of *Heteromorpha*...but this name can be considered as

an adjective, I thought I should change it to that of *Heterolepis*, which expresses that the scales of the pericline (involucre) are dissimilar”. Again, he does not actually publish a binomial, only the genus name.

1821: In September is published Cassini’s treatment of *Heterolepis* for the *Dictionnaire des Sciences Naturelles*, second (Octavo) edition. *Heteromorpha* is referred to *Heterolepis* and under *Heterolepis*, after the introduction and description, Cassini writes “*Heterolepis trompeur*: *Heterolepis decipiens*, H.Cass., *Bulletin des sciences*, Fevrier 1820; *Heteromorpha*, H. Cass., *Bulletin des sciences*, Janvier 1817;” and proceeds to list *Arnica inuloides* Vahl and *Oedera aliena* L.f. as synonyms. It may be that “*Heterolepis decipiens*” was never intended as a binomial, since both ‘*trompeur*’ and ‘*decipiens*’ translate roughly as ‘deceptive/deceiving/misleading’. Thus the binomial ‘*Heterolepis decipiens*’ may be the result of mis-interpretation of Cassini’s statement that the name is confusing. Certainly no specimens are mentioned, and during his writings between 1817 and 1821, Cassini refers all mention of *Heterolepis/Heteromorpha* to *Arnica inuloides* or *Oedera aliena*, merely placing those taxa in his new genus. So if *H. decipiens* Cass. were considered a binomial, it would be illegitimate because the 1817 combination would correctly be “*Heteromorpha inuloides* (Vahl) Cass “and the 1820 one would be “*Heterolepis aliena* (L.f.) Cass.”, although Cassini makes none of these combinations himself.

1823: Thunberg, in his *Flora Capensis* (2nd ed., published by J.G. Cotta of Stuttgart) on page 691 lists *Leysera arctotoides*, ‘*crescit in Carro*’. Thunberg’s herbarium has two corresponding specimens, both from ‘Cap. b. Spei’. One sheet is clearly *Heterolepis aliena*, the other a mixed collection of *H. aliena* and *H. peduncularis*.

1832: Lessing treats *Heterolepis* in *Synopsis Generum Compositarum* on p. 58–59, listing the species *Heterolepis decipiens* and citing Cassini for the name.

1838a: De Candolle, in his *Prodrum Systematis Naturalis Regni Vegetabilis* (pars VI, p. 496), gives a description of *Heterolepis*, listing *H. decipiens* (attributing the name to both Cassini and Lessing) and adding two new species: *H. peduncularis* and *H. mitis*, providing descriptions and citing specimens. For *H. mitis*, he cites a Drége specimen from ‘Zondagrivier et Zuurebergen’ (Sunday’s River and Suurberg) as well as the N. Burman *Gorteria mitis* description from 1739. He clearly indicates *Gorteria mitis* as the basionym.

1838b: De Candolle, in *Prodrum Systematis Naturalis Regni Vegetabilis* 7(1) describes a new genus, *Minurothamnus* with one species, *M. phagnaloides* based on an Ecklon specimen from the Caledon district. (Note: an image of this specimen (microfiche of G-DC specimens at BOL) has been examined and it clearly corresponds to *Heterolepis peduncularis* DC.)

1865: Harvey & Sonder in their *Flora Capensis* present a treatment of *Heterolepis* with *H. decipiens* Cass., *H. peduncularis* DC. and *H. mitis* DC. (p. 469, with Arctotideae). On p. 124 of the same volume, with *Inuleae*, they also present *Minurothamnus*, represented by *M. phagnaloides* DC.

1917: Druce, in the 2nd Supplement to the Botanical Society & Exchange Club Report for 1916, formally makes the new combination *Heterolepis aliena* based on L.f.’s *Oedera aliena*. He notes, “*Vice H. decipiens* Cass in Dict. Sc. Nat. xxi., 120. Cited I.K. and Fl. Cap. iii., 469, 1864–5”.

1950: Merxmüller, in *Mitt. Bot. Staats. Munch.* vol. 1: 38–39, synonymises *Minurothamnus phagnaloides* with *Heterolepis aliena*, although stating that the specimen in De Candolle’s herbarium cannot be found. He bases the synonymy only on the descriptions.

1960: Rickett and Stafleu formally conserve the name *Heterolepis* Cass. (published in 1820) over *Heteromorpha* Cass. (published in 1817) and state that the type of the name is *Arnica inuloides* Vahl, even though the combination has never been made. They also state that there is no need to make the combination because it would be superfluous in view of the “generally accepted taxonomic synonymy with *H. aliena*”.

2011: Manning and Goldblatt publish a new species, *H. anomala*, in *Cape Plants*, 2nd edition.

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