

Monarchs in the veld:

The *Arctotis* Annual Clade provides insight into recent floristic diversification in a semi-arid region of southern Africa

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ABSTRACT

A revision of the main clade of annual species of *Arctotis* L. recognises eight species. All but one taxa are distributed in the winter and/or year-round rainfall regions of southern Africa, with the highest species diversity in semi-arid areas. Altitude and several temperature and precipitation parameters best explain latitudinal and longitudinal gradients in the distribution of taxa. Cypselae and pappus morphology suggest adaptation for reduced dispersibility in a semi-arid environment during diversification. Phylogenetic analyses of ITS and noncoding cpDNA sequence data resolve strongly supported basal nodes and a haplotype network suggests a degree of taxonomic structure to cpDNA diversity. Further research to resolve a genetically diverse “*A. fastuosa* species complex” is required. Diversification of the clade is not explainable solely by a simple vicariance model with parapatric speciation. A biogeographic hypothesis for diversification of the clade is formulated for future testing.

Keywords: biogeography, Namaqualand, Namibia, South Africa, taxonomy

South Africa hosts a rich temperate vascular plant flora (Raimondo et al., 2013), of which the Asteraceae constitutes almost one-tenth (~250 genera and 2250 species; Koekemoer, 1996). Endemism in the Greater Cape Floristic Region, which roughly corresponds to the winter rainfall region of South Africa, is estimated to be 77.9% of the ~11,000 seed plant species (Snijman, 2013). The northern part of this region is a mild, semi-arid area, colloquially known as Namaqualand, which is a magnet for wildflower enthusiasts and photographers. The Namaqualand flora is renowned in part for spectacular flowering displays by annual species in winter and spring.

A conspicuous component of the Namaqualand annuals flora is a clade of showy annual species of the genus *Arctotis* L. (tribe Arctotideae Cass.),

informally designated the ‘*Arctotis* Annual Clade’ (McKenzie & Barker, 2008). Several clade members are common in cultivation, of which *A. fastuosa* Jacq. is often sold under the name ‘Monarch of the Veld’ by commercial seed companies. Although a popular ornamental, *Arctotis* has long been synonymous with taxonomic chaos. An ongoing revision of the genus aims to instill taxonomic order. A revised taxonomy for the *Arctotis* Annual Clade (McKenzie & Barker in press) recognises eight species (Figure 1 and Figure 2) primarily distinguishable by cypselae and pappus morphology (Table 1). The updated taxonomy includes two previously unrecognised species (*A. “chrysantha”* and *A. “namibiensis”*). A putative cline between *A. fastuosa* and *A. “namibiensis”*, to which the name *A. macrocephala* (DC.) Beauverd is applicable and is treated as a nothospecies. The taxa are distributed in western and central southern



Figure 1. Species in the *Arctotis* Annual Clade. **A-B.** *Arctotis venusta* Norl. **C.** *Arctotis* "chrysantha". **D.** *Arctotis leiocarpa* Harv. **E-F.** *Arctotis flaccida* Jacq. Photos: R.J. McKenzie.



Figure 2. Species in the *Arctotis* Annual Clade. **A-B.** *Arctotis hirsuta* (Harv.) Beauverd. **C-D.** *Arctotis fastuosa* Jacq. **E.** *Arctotis* "namibiensis". **F.** *Arctotis subacaulis* (DC.) Beauverd. Photos: A, D, Gwynne-Evans; B-D, F, R.J. McKenzie; E, C.A. Mannheimer.

Table 1. Character states useful to discriminate taxa in the *Arctotis* Annual Clade.

TAXA	CHARACTERS														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
<i>A. sp. nov. "chrysantha"</i>	a	a	a	b	a	b	a,b	b	a	d	a	c	a	a,b	b
<i>A. fastuosa</i>	a,b	a,b	a	a	a	a	b	a	b	b	NA	a	NA	NA	NA
<i>A. flaccida</i>	b	b	b	b	a	b	b	b	b	b,c	NA	b	b	b	a
<i>A. hirsuta</i>	b	b	b	b	a	b	a	b	b	b	NA	b	b	b	a
<i>A. leiocarpa</i>	a,b	a,b	a	b	b	b	a,b	b	a	a,d	b	c	a	c	c
<i>A. "macrocephala"</i>	b	b	b	b	a,b	a	a,b	a	b	b,c	NA	a,b	b	b	a
<i>A. sp. nov. "namibiensis"</i>	b	b	b	b	b	a	b	a	b	c	NA	b	b	b	a
<i>A. subacaulis</i>	b	b	b	b	a	a	b	a	a,b	a,b	NA	a,b	b	b	a
<i>A. venusta</i>	a	a	b	b	a	b	a,b	b	a	d	b	c	a	a,b	c

Characters: **1.** Leaf pubescence: a, lanate; b, pilose. **2.** Outer involucral bract pubescence: a, lanate; b, pilose. **3.** Cypselas shape: a, obconical; b, obovoid. **4.** Cypselas symmetry: a, bilaterally flattened in tangential plane; b, not bilaterally flattened. **5.** Shape of cypselas base: a, subtruncate to tapering; b, abruptly narrowed above base. **6.** Number of abaxial wings on cypselas: a, two; b, three. **7.** Margin of cypselas wings: a, entire; b, undulate to dentate. **8.** Number of abaxial 'cavities' on cypselas: a, one; b, two. **9.** Cypselas surface: a, smooth; b, rugose. **10.** Pubescence on cypselas surface: a, glabrous; b, papillate to clavate; c, pilose; d, lanate. **11.** Length of basal whorl of twin hairs relative to cypselas length: a, shorter to \pm equal length; b, distinctly longer. **12.** Number of whorls of pappus scales: a, zero; b, uniseriate; c, biseriate. **13.** Shape of pappus scales in inner whorl: a, obovate; b, suborbicular. **14.** Apex of pappus scales in inner whorl: a, obtuse; b, rounded; c, subtruncate. **15.** Length of pappus scales of inner whorl relative to cypselas length: a, shorter; b, \pm equal length; c, distinctly longer. NA, Not applicable.

Africa (Figure 3). Dissection of relationships within this clade is providing fascinating insights into factors that contributed to recent floristic diversification in semi-arid southern Africa.

The only molecular data currently available for phylogenetic reconstruction of the clade are nucleotide sequences for non-coding nrDNA (ITS) and cpDNA (*trnT-trnF* and *trnH-psbA*) regions (McKenzie & Barker, 2008). Bayesian inference consistently resolves a previously unrecognised species, *A. "chrysantha"*, restricted to coastal red aeolian sediments of the Kalahari Group, as an early divergence (Figure 4). The monophyly of *A. venusta* Norl. and *A. leiocarpa* Harv., from the year-round and summer rainfall regions (Figure 3), is supported but the sequence of divergence events varies depending on the dataset. The remaining taxa form a poorly resolved "*A. fastuosa* species complex".

A cpDNA haplotype network, constructed using the TCS statistical parsimony algorithm (Templeton et al., 1992), suggests there is a degree of taxonomic

structure to cpDNA haplotype diversity (Figure 5). *Arctotis venusta* and *A. "chrysantha"* harbour taxon-specific haplotype lineages, and a group of haplotypes is predominantly detected in *A. subacaulis* (DC.) Beauverd (group D, Figure 5). Notably, *A. fastuosa* includes haplotypes from at least four independent lineages and harbours the greatest haplotype diversity. Resolution of an "*A. fastuosa* species complex" is not supported.

The species exhibit limited vegetative diversification: initially rosulate, caulescent upon flowering, and usually lyrate-pinnatisect or pinnatisect, relatively thin to fleshy, glandular leaves with thin woolly or pilose pubescence (Figure 1 and Figure 2). The involucre exhibits subtle differences among the taxa, with the outer involucral bracts bearing a leafy apical appendage that varies in length, width and shape, and clothed with cobwebby or pilose pubescence (Figure 6). In contrast, the cypselas and pappus have undergone notable evolution (Figure 4, Table 1), putatively concomitant with geographic expansion and taxonomic diversification.

Land of extremes

The Desert biome is the most arid region of South Africa, hugging the lower Gariep River to the Atlantic coast. This is a region of extremes: the lowest amount and highest variability in rainfall, among the highest temperatures recorded, and the highest incidence of coastal fog.



Near the eastern limit of the Desert biome, north of Pofadder; Northern Cape
Photo by Robert McKenzie

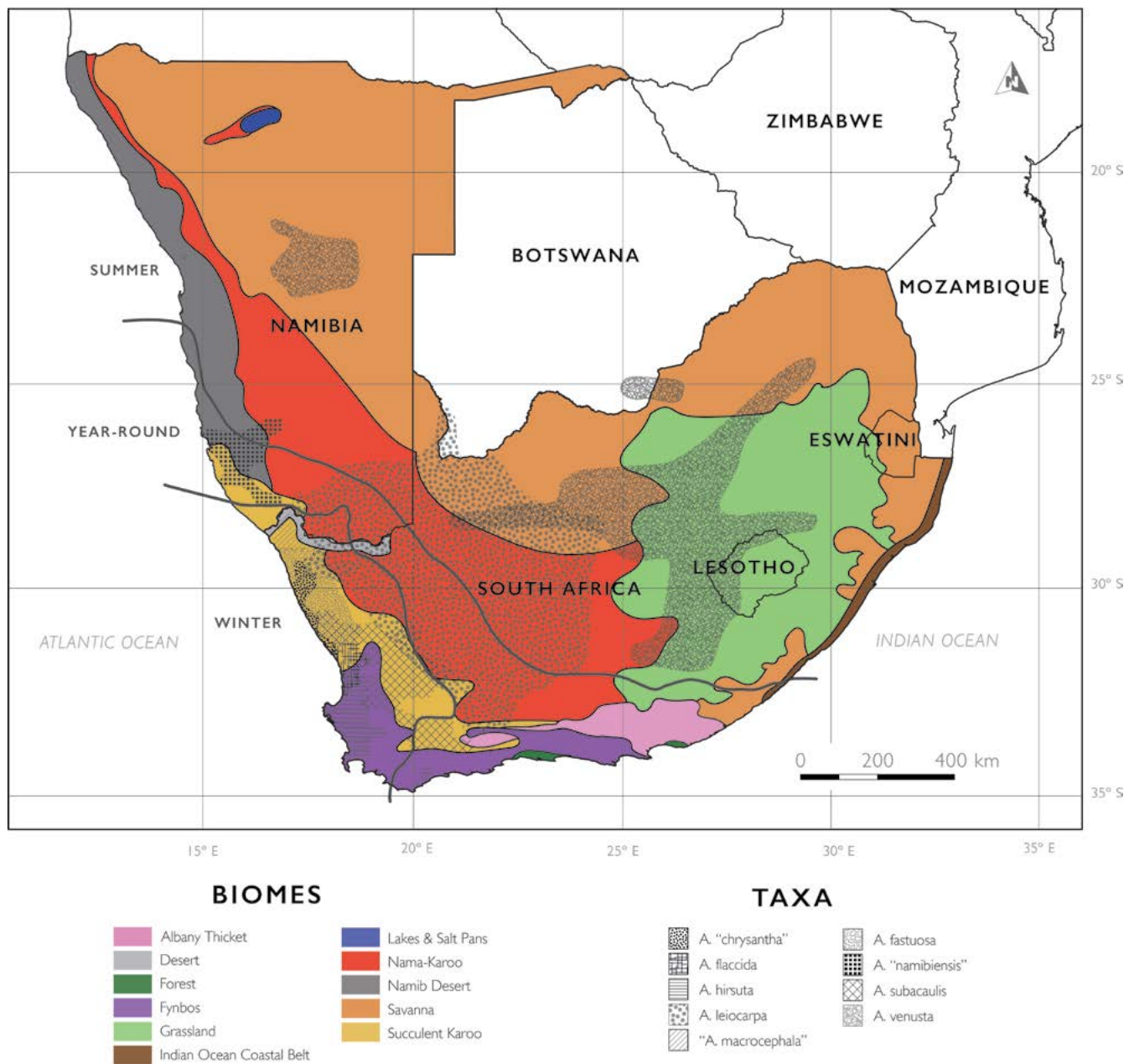


Figure 3. Known distribution in southern Africa of the taxa recognised in the *Arctotis* Annual Clade by McKenzie & Barker (in press) in relation to recognised biomes. The biomes for Namibia and South Africa are as delineated by Mendelsohn et al. (2002) and SANBI (2018), respectively. The boundaries of the regions in which greater than 66% of the annual precipitation falls in either the winter or summer months, with a transitional region that receives rainfall all year round (based on Chase & Meadows, 2007), are indicated. Biome areas have been simplified and Azonal Vegetation is not shown.

Although incompletely resolved, the phylogenies enable formulation of a hypothesis of cypselae and pappus evolution in the clade. *Arctotis* is characterised by cypselae with three woody, abaxial wings that are fused at each end to create two 'cavities' (McKenzie et al., 2005). The earliest-diverging extant lineages in the Annual Clade (*A. "chrysantha"*, *A. venusta* and *A. leiocarpa*) have relatively large cypselae with three well-developed abaxial wings, forming two 'cavities',

and a biseriate pappus of scales with the inner whorl longer than the cypselae (Figure 4). The *A. fastuosa* complex exhibits reduction in size of the cypselae, abaxial wings and pappus scales, with loss of the medial abaxial wing and pappus in *A. fastuosa* and *A. subacaulis*. These taxa are distributed in the most arid areas (average annual rainfall as low as ~50 mm). The latter cypselae phenotypes are consistent with adaptation for reduced dispersibility in a semi-arid, desert-like environment.

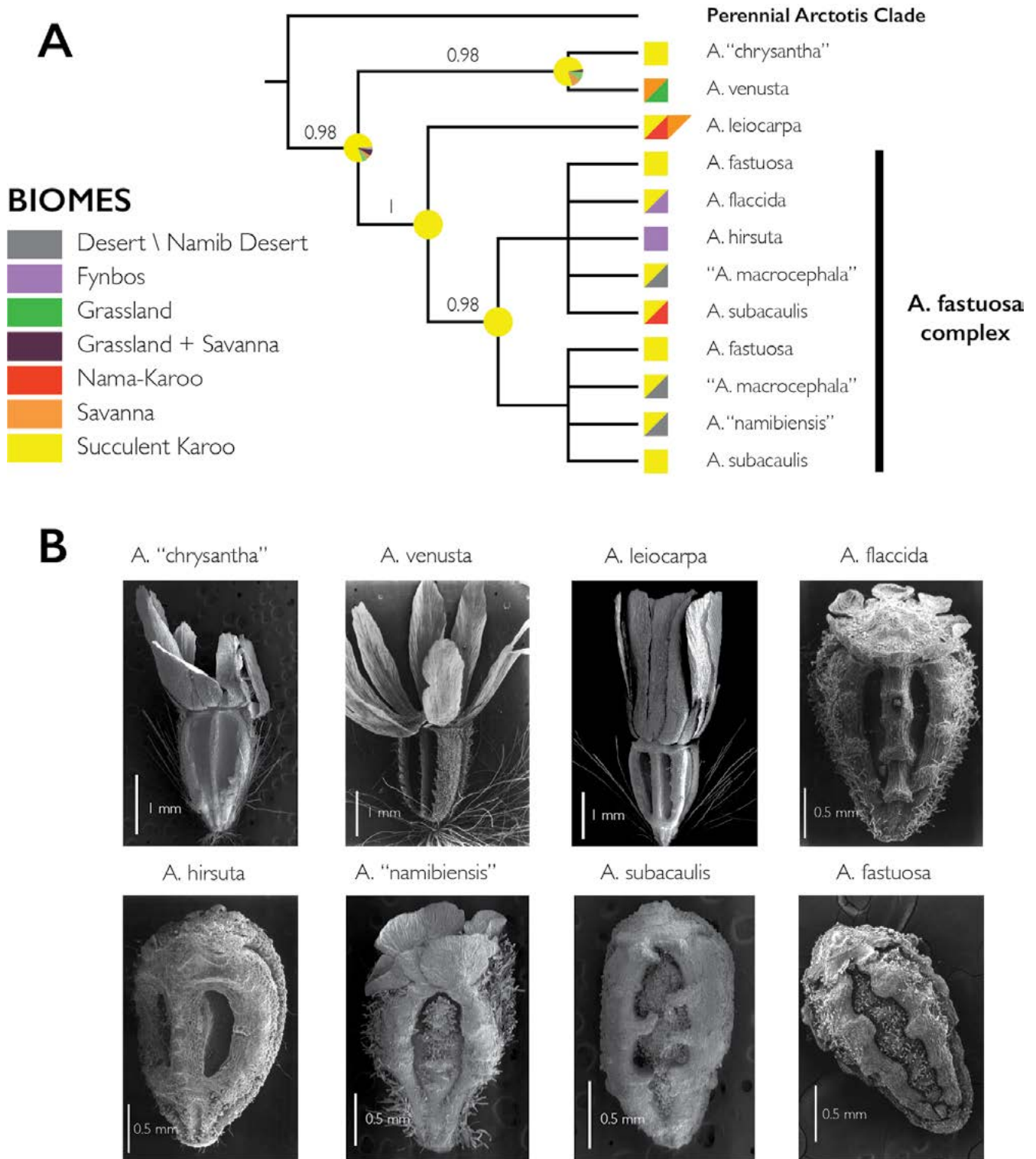


Figure 4. A. Simplified Bayesian inference phylogeny of the *Arctotis* Annual Clade reconstructed from nrDNA ITS sequences and cypsels of the recognised taxa. Support values at nodes are posterior probabilities. Pie charts at nodes indicate ancestral ranges estimated using the dispersal–extinction–cladogenesis model, including the j parameter to allow for founder-event speciation, maximum of six areas, and conservative root date of 9.1 Mya, as implemented in BioGeoBEARS (Matzke, 2018). Boxes beside species names indicate present-day biome distributions. **B.** SEM photos of *Arctotis* annual clade. The fruit of *A. "chrysantha"*, *A. leiocarpa* and *A. venusta* are typical for *Arctotis* as a whole: the abaxial vascular ribs of the cypselae are elaborated into either three woody wings, which create two abaxial 'cavities'; the pappus comprises two unequal whorls of papery scales; and a persistent whorl of long twin trichomes is attached to the cypselae base (mostly removed in the depicted fruit). The *A. fastuosa* complex exhibits reduction of these structures to varying degrees and loss of the whorl of twin trichomes.

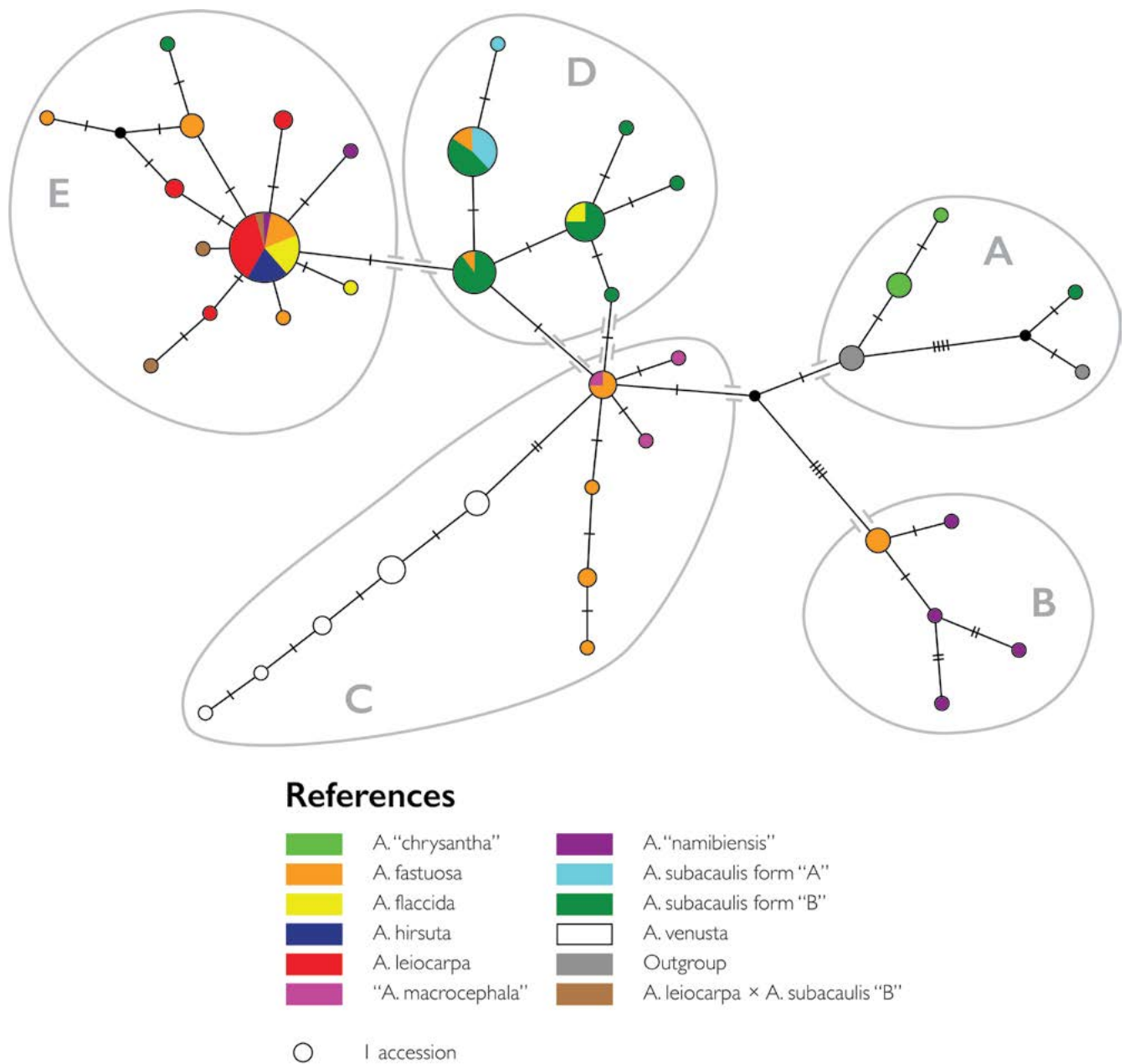


Figure 5. Chloroplast DNA haplotype network constructed from concatenated sequences for the *trnT-trnF* and *trnH-psbA* regions using the TCS statistical parsimony method.

An early attempt at estimating the timing of divergence of the *Arctotis* Annual Clade, using published ITS mutation rates for other Asteraceae groups and a relaxed molecular clock with branch substitution rates drawn from a lognormal distribution (McKenzie & Barker, 2008), yielded 95% highest posterior density intervals ranging from 1.5 to 9.1 Mya (Late Miocene to Early Pleistocene). While imprecise, this range coincides with the trend for increasing seasonal aridity in the northwestern

Cape, especially during the past ~3.2 My (Marlow et al., 2000). A possible Late Pliocene/Early Pleistocene origin of the clade is comparable with estimates for development of annualness in southern African *Nemesia* (Datson et al., 2008).

Here, we present results from preliminary bioclimatic and historical biogeographic analyses of the clade. An exploratory DIVA-GIS analysis of the relationships of altitude and 19 bioclimatic variables (WorldClim

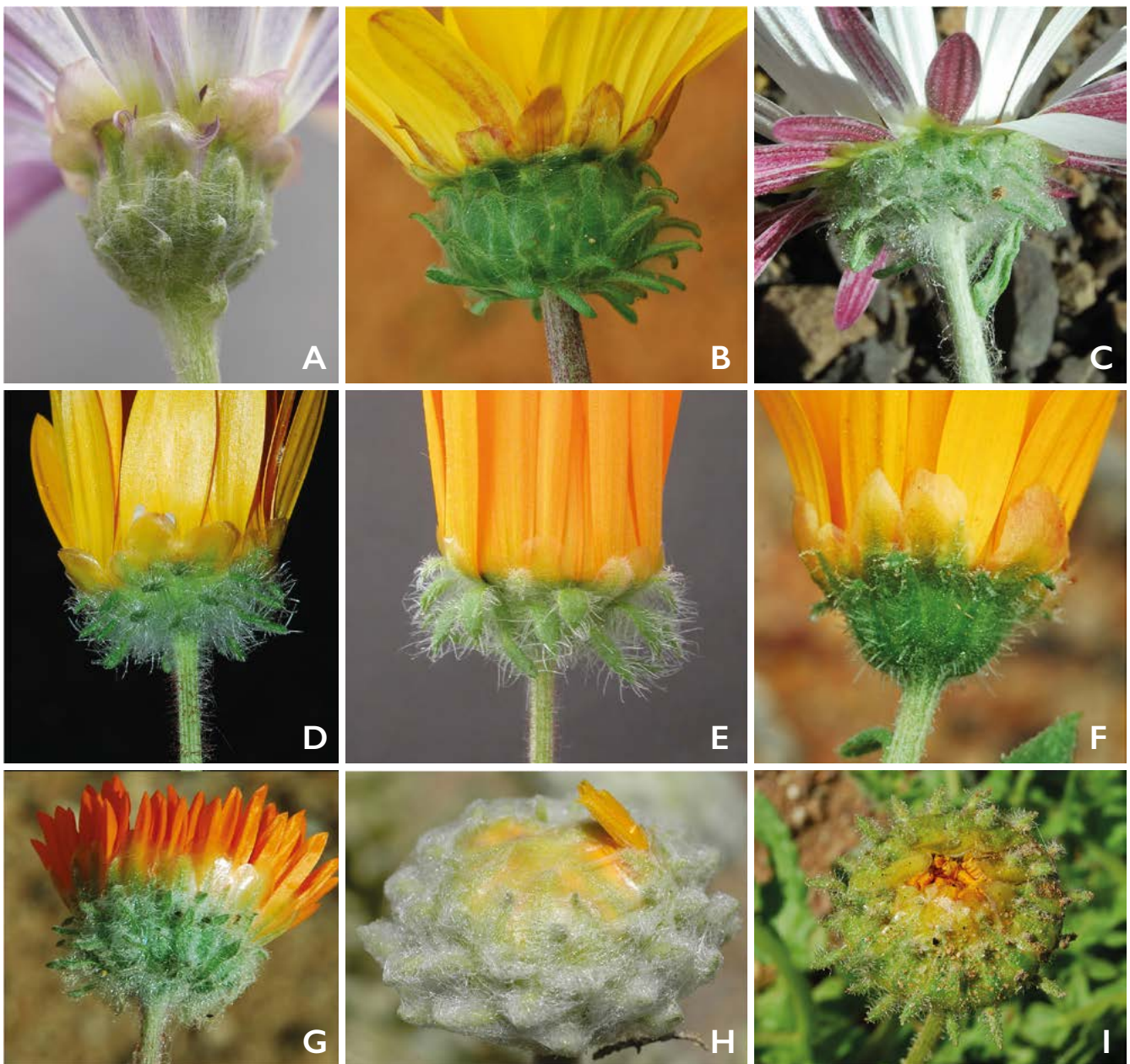


Figure 6. Involucre of species in the *Arctotis* Annual Clade. **A.** *Arctotis venusta* Norl. **B.** *Arctotis* “*chrysantha*”. **C.** *Arctotis leiocarpa* Harv. **D.** *Arctotis flaccida* Jacq. **E.** *Arctotis hirsuta* (Harv.) Beauverd. **F.** *Arctotis subacaulis* (DC.) Beauverd. **G-H.** *Arctotis fastuosa* Jacq. **I.** *Arctotis macrocephala* (DC.) Beauverd. Photos: A–G, I, R.J. McKenzie; H, D. Gwynne-Evans.

database; <https://www.worldclim.org/data/bioclim.html>) and the provenance of the 118 sequenced accessions suggests that altitude and several temperature and precipitation parameters may have contributed to the adaptive radiation (Figure 7). Further analysis to eliminate autocorrelated variables and incorporate geomorphic (e.g., edaphic) factors with an expanded dataset incorporating authenticated herbarium accessions will be undertaken.

The extant species distributions suggest a relationship with biomes in Namibia and South Africa (Figure 3). Model-building methods and statistical testing in historical biogeography continue to evolve and various technical challenges remain. Methods in current use each have advantages and drawbacks (Ree & Sanmartín, 2018; Schram, 2019). We acknowledge that resolution of relationships within the *A. fastuosa* complex is crucial to enable

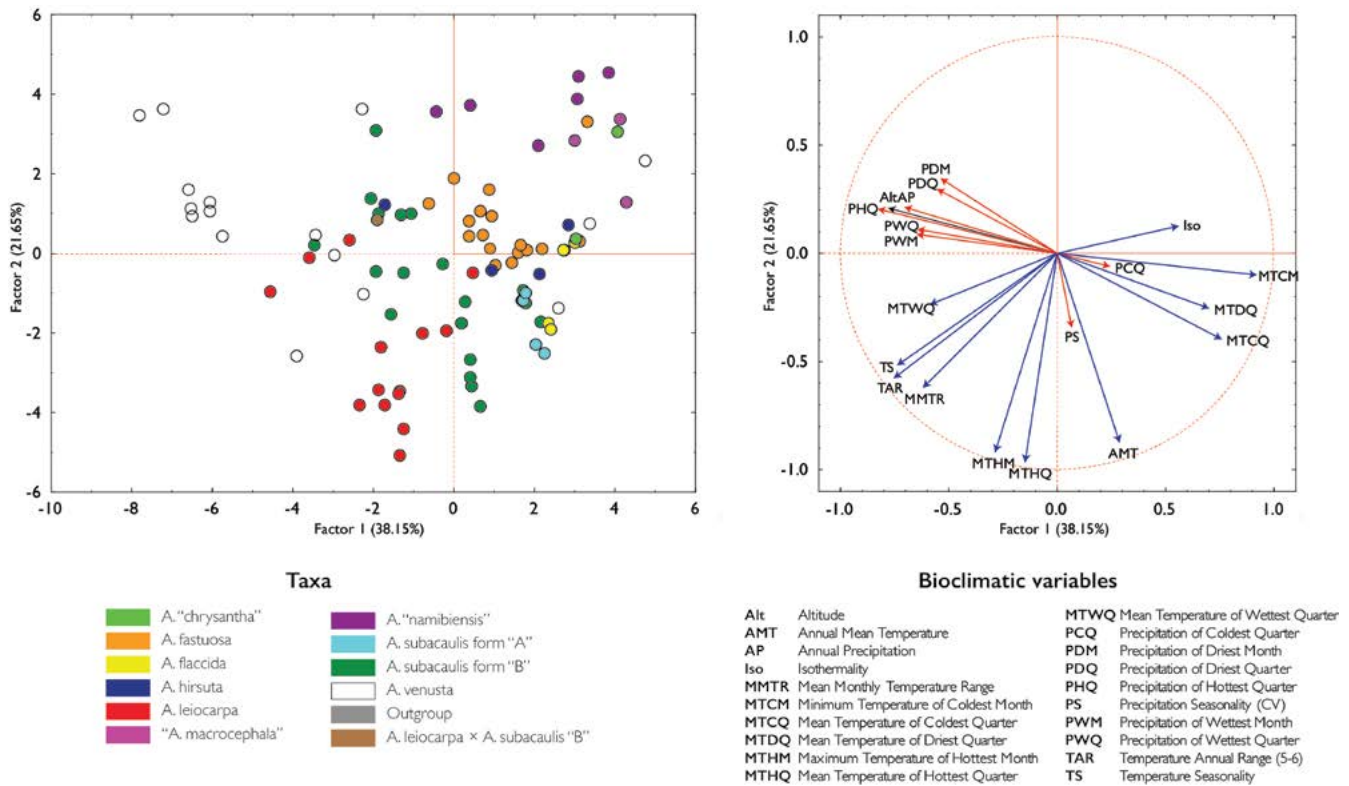


Figure 7. DIVA-GIS analysis of the geographic distribution of the 115 sequenced accessions and 20 bioclimatic variables. The loadings of precipitation- and temperature-related variables to the first two factors are represented by red and blue vectors, respectively.

rigorous testing of biogeographic hypotheses. Keeping this limitation in mind, we conducted an exploratory estimation of biome-scale ancestral ranges with the R package 'BioGeoBEARS' (Matzke, 2018). A chronogram was generated from the majority-rule consensus Bayesian inference tree, using a relaxed molecular clock and the aforementioned minimum and maximum posterior densities from McKenzie and Barker (2008) to date the root, with the function 'chronos' in the R package 'ape' (Paradis et al., 2021). Six models were compared: dispersal–extinction–cladogenesis (DEC; Ree & Smith, 2008), dispersal–vicariance analysis-like (DIVA-LIKE; Yu et al., 2010) and BAYAREA-LIKE (Landis et al., 2013), each with or without the 'jump dispersal' (*j*; founder event) parameter. The DEC + *j* model showed the best fit in all analyses based on corrected Akaike information criterion values. Ancestral range estimations with all models that included the *j* parameter were highly consistent. Maximum range size (4 or 6 areas) and pruning of terminals (28%

of the total number, removing multiple accessions from the same biome of a taxon within a clade) had negligible impact on range and parameter estimates but the latter improved model fit. The analyses suggested that diversification within the clade is not explainable solely by a simple vicariance model with parapatric speciation.

Formulation of a biogeographic hypothesis for future testing, with emphasis on the basal nodes, is feasible. The clade ancestor likely diverged in a region of low, erratic or aseasonal rainfall, possibly in present-day southwestern Namibia or northwestern South Africa (Figure 8). Southwestern Africa has a long history of aridity dating to the Middle Miocene (~16–17 Mya; Senut et al., 2009). Populations of annual *Arctotis* species in southwestern Namibia and northern Namaqualand harbour the highest present-day cpDNA haplotype diversity. Populations in this region harbour derivatives of hypothetically early-evolving cpDNA haplotypes.

Fynbos

Arguably the most distinctive South African biome, comprising an evergreen, sclerophyllous shrubland that grows on nutrient-poor soils predominantly derived from quartzitic sandstones. The various types of fynbos are characterised by members of certain families, especially Proteaceae, Restionaceae, and Ericaceae, but asteraceous-dominated fynbos types are also common. Fynbos generally requires a more mesic climate (mean annual rainfall ~500 mm, but may be as high as 3000 mm).

Fire is a vital part of Fynbos ecology. The plants are fire-prone and fire-adapted (resprouting or reseeded after fire), and regular burning is essential to promote vigour and maintain diversity.

Putative *Protea* hybrid in the Proteoid Fynbos on the Riviersonderendberge, Western Cape.
Photo by Robert McKenzie

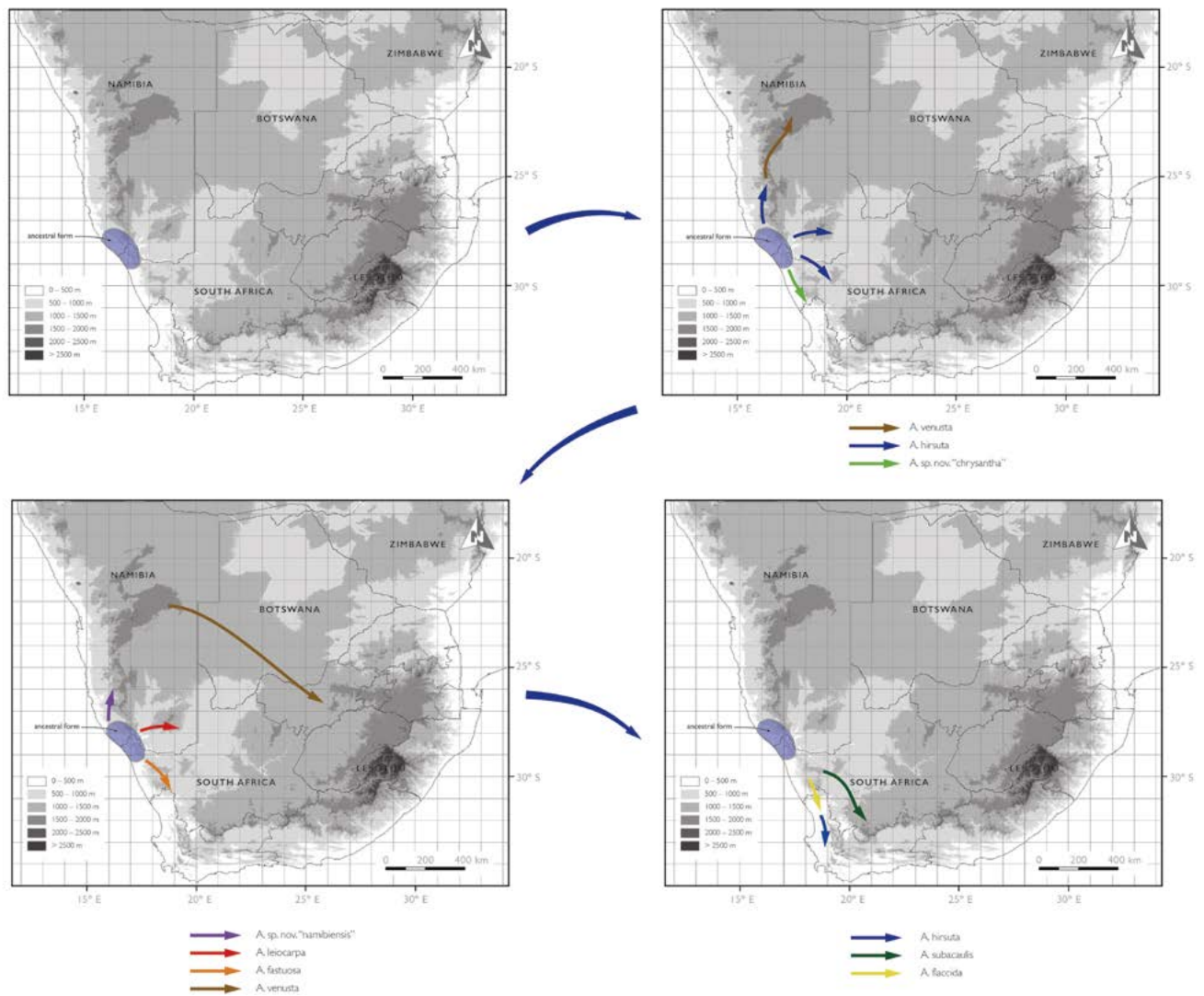


Figure 8. Biogeographic hypothesis of the possible ancestral area and taxonomic diversification of the *Arctotis* Annual Clade.

Strong climatic and edaphic gradients and habitat heterogeneity are likely to have been important drivers of diversification. *Arctotis* “*chrysantha*” may have arisen as an early adaptation to southwestern redistribution of Kalahari Group red aeolian sediments. The oldest Kalahari sand deposits are of Pliocene to Pleistocene age (Vainer et al., 2018), but the deposits on the Namaqualand coastal plain are of more recent origin (e.g., Philander & Rozendaal, 2015). Current molecular data provide conflicting signals on the timing of divergence of *A. venusta*, the only summer-rainfall endemic species. Namibian cpDNA haplotypes of *A. venusta* are indicated to be ancestral to South African haplotypes (Figure 5), suggesting *A. venusta* adapted to a summer-rainfall regime in central or southern Namibia. Eastward

expansion through the summer-rainfall savanna and grassland of Botswana is more plausible than through the semi-arid, erratic-rainfall Nama-Karoo, which undoubtedly poses a severe biogeographic barrier to eastward migration of Namaqualand species. Nevertheless, *A. leiocarpa* adapted to the erratic, year-round transitional rainfall zone in eastern Karas and the Nama-Karoo and may have secondarily dispersed into the Succulent Karoo.

Diversification of the *A. fastuosa* complex in the winter-rainfall region may have coincided with reduction in cypselae size and dispersibility. Southward and eastward range expansion and parapatric speciation may account for the divergence of *A. flaccida* Jacq. and *A. hirsuta* (Harv.) Beauverd on the coastal plain,

and *A. subacaulis* in drier inland regions. Expansion and contraction of the winter-rainfall zone in wetter glacial and drier interglacial periods, respectively, during the Pleistocene is implicated (Tankard & Rogers, 1978; Chase & Meadows, 2007). Such oscillations may have promoted allopatric speciation in refugia, while also contributing to introgression and genetic blurring between contiguous taxa in the *A. fastuosa* complex. Biogeographic exploration of the adaptation to extreme aridity by *A. "namibiensis"* requires resolution of the taxon's paraphyly in phylogenetic reconstructions.

Alternative data, such as polymorphic molecular markers or next-generation sequencing data, are needed to improve resolution of the *A. fastuosa* complex to test this biogeographic hypothesis. A target-enrichment sequencing methodology for Compositae (Mandel et al., 2014) has shown potential for resolving relationships within traditionally recalcitrant groups (Susanna, 2021), and offers a promising tool to resolve relationships within the Arctotidinae. Phylogenetic dating using additional recent fossil records for the family (see Mandel et al., 2019) may refine divergence and diversification estimates for the clade, and improve correlation with past geoclimatic changes.

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