A TAXONOMIC REVISION OF THE SOUTH AFRICAN ENDEMIC GENUS *ARCTOPUS* (APIACEAE, SANICULOIDEAE)[1]

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Abstract

The genus *Arctopus* L. is revised. It is an anomalous member of the family Apiaceae, with several unusual morphological characters such as the prostrate spiny leaves, thick resinous tuberous roots, sessile female flowers with a homochlamydeous perianth, and pseudanthia formed by distinctive bracteoles. The three species of *Arctopus* were found to differ mainly in their reproductive morphologies, being easily distinguishable by the large involucral bracteoles that surround the female pseudanthia. The anatomy of the petiole as well as the morphology of the inflexed spines and leaf margins were also found to be useful diagnostic characters and are illustrated and discussed. Possible phylogenetic relationships were explored using both morphological and DNA sequence data (ITS). A formal taxonomic treatment is presented, including a key to the species, correct nomenclature, typification, descriptions, illustrations, and distribution maps.

Key words: Apiaceae, *Arctopus*, ITS, IUCN Red List, phylogeny, Saniculoideae, taxonomy.

Arctopus L. is endemic to the Cape Floristic Region (CFR) of South Africa and consists of three dioecious species. They are important medicinal plants with a rich ethnobotanical history (Magee et al., 2007). *Arctopus* was described by Linnaeus (1753) in *Species Plantarum*, from figures by Plukenet (1691–1705: tab. 271, fig. 5) and Burman (1738: tab. 1). The name *Arctopus* is derived from Greek, meaning "bear's foot," due to the broad simple leaves that remain appressed to the ground and are armed with large inflexed spines. The genus was originally thought to be monotypic, consisting only of *A. echinatus* L., whose virtue as an important medicinal plant was well known to the Khoisan people (Pappe, 1857). It also became popular among the early Cape Dutch settlers and became known by the vernacular names "sieketroost" or "platdoring" (Smith, 1966). Two additional species, *A. dregei* Sond. and *A. monacanthus* Carmich. ex Sond., were later described by Sonder (1862) in *Flora Capensis*. Wolff last revised the genus in 1913 but reported male material of *A. monacanthus* as unknown. Because the species circumscriptions were based solely on female material, the identification of male plants has been difficult, resulting in much confusion.

This paper is aimed at presenting a complete revision of the genus, including the circumscription, nomenclature, typification, formal descriptions, and illustrations of diagnostic characters for the three species that are recognized. A key to aid identification of female and, for the first time, male non-flowering material is provided. The known distribution of each species is recorded. Morphological, anatomical, and sequence data (ITS) from *Arctopus* are also evaluated in order to explore possible phylogenetic relationships at both generic and species level.

Taxonomic Position

Arctopus is an anomalous genus of geophytes belonging to the family Apiaceae. There have been differences of opinion as to the correct taxonomic position of the genus within the family. Drude (1897–1898) divided Apiaceae into the three subfamilies Apiodeae, Saniculoideae, and Hydrocotyloideae. He placed *Arctopus* in the subfamily Saniculoideae based on the presence of toothed leaves, surface outgrowths on the mericarps, and intrajugal oil ducts. In Wolff's (1913) treatment, *Arctopus* was also placed in Saniculoideae. However, both Froebe (1964) and Magin (1980), in their studies of the inflorescence structure of the Saniculoideae, found that *Arctopus* shares many characteristics with the Hydrocotyloideae. Pimenov and Leonov (1993) listed it in the

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Table 1. Material of *Arctopus* species used for anatomical studies (all material kept at JRAU). f, flower; ifr, immature fruit; l, lamina; md, midrib; mfr, mature fruit; p, petiole.

Taxon	Voucher specimens	Locality	Plant parts studied
A. dregei	*Magee & Boatwright 2*	Rondeberg	p, l, md, mfr
	Magee & Boatwright 5	Darling	p, md, f, mfr
	Magee & Boatwright 31	Malmesbury	p, mfr
A. echinatus	*Magee & Boatwright 4*	Rondeberg	p, md
	Magee & Boatwright 6	Yzerfontein	p, l, md, mfr
	Van Wyk & Viljoen 3715	Oorlogskloof	p, l, md
	Van Wyk 4128a	Nieuwoudtville	md, f
	Van Wyk s.n., 14 Oct. 1993	Arendskraal	p, mfr
	Winter et al. 170	Du Toitskloof	f
A. monacanthus	*Magee & Boatwright 34*	Pakhuis Pass	p, mfr
	Van Wyk 3594	Piketberg	p, ifr
	Van Wyk 4128b	Nieuwoudtville	md
	Van Wyk 4141a	Elandskloof	p, l, md, f, mfr
	Van Wyk 4161a	Gifberg	p, md
	Van Wyk s.n., 12 July 1997	Jonaskop	p, md
	Van Wyk, Winter & Tilney s.n., 8 Oct. 1993	McGregor Rd.	p

subfamily Hydrocotyloideae but were uncertain about the tribal affinity (listed under incertae sedis). However, recent molecular data (Plunkett & Lowry, 2001; Chandler & Plunkett, 2004; Plunkett et al., 2004) show Hydrocotyloideae to be polyphyletic. A new subdivision of the family into Apioideae, Saniculoideae, Azorelloideae, and Mackinlayoideae has been proposed (Plunkett et al., 2004), in which a close relationship between *Arctopus* and the Saniculoideae is suggested. Liu et al. (2003), in their evaluation of the fruit structure of Saniculoideae, proposed a broader saniculoid concept that includes *Arctopus* and some other anomalous African genera (viz. *Lichtensteinia* Cham. & Schltdl., *Polemanniopsis* B. L. Burtt, and *Steganotaenia* Hochst.). Calviño and Downie (2007), using chloroplast sequence data (*trnQ-trnK* 5′: exon region) to assess the circumscription of the subfamily, proposed two tribes within Saniculoideae, namely a redefined Saniculeae and a newly described Steganotaenieae (comprising *Polemanniopsis* and *Steganotaenia*). In this analysis, *A. echinatus* is placed within Saniculeae as a sister group to *Eryngium* L., *Sanicula* L., *Hacquetia* Neck. ex DC., *Petagnaea* T. Caruel, *Astrantia* L., and *Actinolema* Fenzl, with *Alepidea* D. Delaroche successively sister and the most basally diverging lineage within the tribe.

Materials and Methods

The three species were studied in situ and observed throughout much of their known distributional range. Herbarium material from BM, BOL, JRAU, K, NBG, PRE, S, and SAM was studied (abbreviations follow Holmgren et al., 1990). From this material, together with geographical information from Leistner and Morris (1976), the recorded distributions of all the species were carefully verified and mapped. The conservation status of each species was assessed using IUCN Red List criteria (IUCN, 2001).

For anatomical procedures, leaf (petiole, lamina, and midrib) and fruit material were fixed in formalin, acetic acid, and alcohol (FAA) for at least 24 hr. and then treated according to the method of Feder and O'Brien (1968) for embedding in glycol methacrylate (GMA), but modified so that the material in the first two changes of GMA was infiltrated for a minimum of 24 hr., followed by a final infiltration of five days. Staining was done according to the periodic acid Schiff/toluidine blue (PAS/TB) staining method (Feder & O'Brien, 1968). A list of voucher specimens for the anatomical study is given in Table 1. Drawings, all done by the first author, were made with the aid of a camera lucida attachment on a Zeiss (Göttingen, Germany) compound microscope.

Total DNA was extracted from 0.5–1.0 g of fresh leaf material following the CTAB method of Doyle and Doyle (1987). The extracts were cleaned and concentrated in QIAquick silica columns according to the manufacturer's protocol (Qiagen Inc., Hilden, Germany). Genera of the Saniculoideae belonging to both tribes Saniculeae (*Alepidea*, *Astrantia*, *Erygium*, *Hacquetia*, *Petagnaea*, and *Sanicula*) and Steganotaenieae (*Steganotaenia*) were included in the analysis, together with two representative genera of the Apioideae (*Heteromorpha* Cham. & Schltdl. and *Anginon* Raf.). *Hermas villosa* Thunb. was selected as the outgroup based on the sister relationship

Table 2. Data matrix of character states in the genus *Arctopus*, used to construct the cladogram in Figure 4. For details of the characters and polarization of character states, see Appendix 2.

	Characters and character states														
Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Alepidea amatymbica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Arctopus dregei	0	0	0	0	1	1	0	0	0	1	0	0	1	1	1
Arctopus echinatus	1	1	1	1	1	1	0	0	0	0	1	1	0	0	1
Arctopus monacanthus	1	2	1	0	1	1	1	1	1	1	1	1	0	0	1

between the *Hermas* L. clade and the clade of Apioideae and Saniculoideae found by Calviño et al. (2006). Voucher specimen information (including sources of plant material, GenBank accession numbers, species names, and their author citations) is listed in Appendix 1.

The ITS of nuclear ribosomal DNA was amplified using the Sun et al. (1994) AB101 (5′-ACG AAT TCA TGG TCC GGT GAA GTG TT-3′) and AB102 (5′-TAG AAT TCC CCG GTT CGC TCG CCG TT-3′) primers. Amplified polymerase chain reaction (PCR) products were purified using a QIAquick PCR purification kit (Qiagen Inc.) according to the manufacturer's instructions and directly sequenced on a 3130 *xl* Genetic Analyzer (Applied Biosystems Inc., Foster City, California, U.S.A.) using BigDye Terminator version 3.1 (Applied Biosystems Inc.). Complimentary strands were assembled and edited using Sequencher version 3.1.2 (Gene Codes Corporation, Ann Arbor, Michigan, U.S.A.), and aligned manually in PAUP* version 4.0b1 (Swofford, 2002), with gaps positioned so as to minimize nucleotide mismatches.

Characters and character states used for the cladistic analysis of morphological data are given in Table 2 and Appendix 2. Character states were polarized using the method of outgroup comparison, with *Alepidea amatymbica* Eckl. & Zeyh. as the outgroup. Where both states were found to co-occur in a single taxon, it was coded for the plesiomorphic state. Phylogenetic analyses were conducted using the parsimony algorithm of PAUP* version 4.0b1. Morphological characters were treated as ordered and equally weighted (Wagner parsimony; Farris, 1970), whereas for the molecular data, all character transformations were treated as equally likely (Fitch parsimony; Fitch, 1971). Tree searches were performed using a heuristic search with 1000 random sequence additions, tree bisection-reconnection (TBR) branch swapping, and the MULPARS option in effect. A limit of 10 trees per replicate was set to reduce the time spent on swapping in each replicate. Internal support was assessed with 1000 bootstrap replicates (Felsenstein, 1985) using TBR swapping and holding 10 trees per replicate. Only values greater than 50% are reported, and the following scale was applied for support percentages: 50%–74%, weak; 75%–84%, moderate; and 85%–100%, strong.

Bayesian analysis was performed on the ITS sequence data, using MRBAYES v. 2.01 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). The TrN+G model, indicated to be the best model by MODELTEST v. 3.06 (Posada & Crandall, 1998), was implemented. The analysis was performed with one million generations of Markov chain Monte Carlo and a sampling frequency of 100. The resulting trees were plotted against their likelihoods in order to determine where the likelihoods converge on a maximum value. All the trees before this convergence were discarded as the "burn-in" phase. The remaining trees were imported into PAUP* v. 4.0b1, and a majority rule consensus tree was produced in order to show the posterior probabilities (PP) of all observed bi-partitions (only PPs above 0.5 are reported on the tree in Fig. 4). The following scale was used to evaluate the PPs: 0.50–0.84, low; 0.85–0.94, moderate; 0.95–1.0, strong.

Morphological and Taxonomic Characters

habit

Arctopus is unlike any other genus found within the Apiaceae. The species are summer deciduous geophytes not exceeding 15 cm in height when in flower. Their broad simple leaves, which arise directly from a tuberous rootstock, are spiny and sprawl out in a rosette, remaining appressed to the ground. The plants are distinctly dioecious, and each sex is immediately apparent when in flower or fruit. The three species show no obvious differences in growth form.

leaf shape

The leaves of *Arctopus* species are simple and vary greatly in shape, from ovate to semi-orbicular or rhomboidal (Figs. 5A, B, 7A–F, 9A–C), with only

those coastal populations of *A. echinatus* that occur between Knysna and Hermanus bearing leaves that are pinnatipartite to pinnatifid (Fig. 7D, E). In all the species, the leaves are incised into three segments, each of these being two- or three-lobed. In *A. monacanthus* and *A. echinatus*, the lobes are prominently toothed, giving them a very distinctly dentate appearance (Figs. 7A, C–F, 9A–C), whereas in *A. dregei*, the teeth are inconspicuous and thus the lobes appear crenate (Fig. 5A, B).

LEAF VESTITURE

The teeth on the leaf margin terminate in either flexuose setae (the presumed plesiomorphic state found in *Alepidea*) as in *Arctopus dregei*, or spinose setae as in *A. echinatus* and *A. monacanthus*. Such marginal hairs or setae are a characteristic feature of many genera belonging to the subfamily Saniculoideae (van Wyk & Tilney, 2004). Within *Arctopus*, leaf vestiture was found to be a useful diagnostic character. Vertical spines are usually present in the recesses between the leaf segments. In *A. monacanthus*, these spines are attached to an inflexed laminar tooth (Fig. 9D–I), which is often conspicuously broad with marginal setae almost invariably present. However, in *A. echinatus*, the inflexed laminar tooth is either absent or very narrow and almost always without marginal setae (Fig. 7L–N). Inflexed laminar teeth and vertical spines are very rarely present in *A. dregei* (if present, then small, sparse, and attached to a narrow laminar tooth, without setae). The leaves of *A. monacanthus* are markedly more spinescent than those of *A. echinatus*, with up to six stellate spines in each leaf recess being common. In *A. echinatus*, the spines are often solitary or in threes; however, populations from the Cederberg in the north and around Port Elizabeth in the Eastern Cape have up to four or rarely five stellate spines per recess.

LEAF ANATOMY

While the three species are very similar in their vegetative anatomy, certain characters (as discussed later) have been found to be of diagnostic value, particularly in the field where they are easily observed with a 10× hand lens. This is especially true of *Arctopus echinatus* and *A. monacanthus*, which are often difficult to identify when female flowering or fruiting material is not available. *Arctopus dregei* shows much variability in its vegetative anatomy and often shares similar character states to *A. echinatus* and *A. monacanthus*. Because the macromorphology of this species is relatively distinctive, it is not easily confused, even when flowering or fruiting material is unavailable. The use of anatomical characters to distinguish it is therefore superfluous.

Transverse sections of the lamina were found to be markedly similar in all three species and were therefore of little diagnostic value. The mesophyll is distinctly differentiated into palisade and spongy parenchyma, with the palisade parenchyma comprising about half of the mesophyll thickness in *Arctopus echinatus* and *A. monacanthus*, and less than half in *A. dregei*.

The midrib of the lower third of the leaf, when studied in transverse section, was found to be far more useful (Fig. 1A–F). The extent of sub-epidermal collenchyma and the arrangement of the vascular bundles are diagnostic. Sub-epidermal collenchyma is found on both the adaxial and abaxial surfaces. On the abaxial surface, the collenchyma extends at least halfway along the midrib in *Arctopus monacanthus* (Fig. 1E, F) and, to a lesser extent, in *A. dregei* (Fig. 1A, B) and *A. echinatus* (Fig. 1C, D). At least two large, oppositely arranged vascular bundles can usually be found. Of these, the adaxial bundle is solitary (Fig. 1A–C) or further split dorsiventrally (Fig. 1B–D), that is, into a dorsal and a ventral bundle in *A. echinatus* and in *A. dregei*. In *A. monacanthus*, the adaxial bundle is always collaterally split (Fig. 1E, F), that is, into two lateral bundles, although this has also been found to occur occasionally in *A. dregei* (Fig. 1B). One or two additional smaller adaxial bundles are often found in the midribs of larger leaves in all three species.

The transverse sections of the petiole are similarly diagnostic (Fig. 1G–I). The petioles are adaxially flattened and prominently raised abaxially. They extend laterally into wings, which are always prominently ribbed in *Arctopus dregei* (Fig. 1G). Sub-epidermal collenchyma is present along the abaxial surface in all three species. In *A. echinatus* (Fig. 1H) and *A. monacanthus* (Fig. 1I), collenchyma is also found in the wings, but in *A. monacanthus*, it is continuous, or almost so, with the abaxial collenchyma strand. Large cavities between the vascular bundles can be found in *A. echinatus* (Fig. 1H) and in the late season growth of *A. dregei*, but never in *A. monacanthus*.

FEMALE INFLORESCENCE

The bracteoles of the involucel are of diagnostic value and render a female flowering plant quite unmistakable. They are prominent and accrescent in all three species, giving the umbellule the appearance of a single flower, called a pseudanthium (Figs. 5C–F, 7O–R, 9J–M). This is commonly found in other

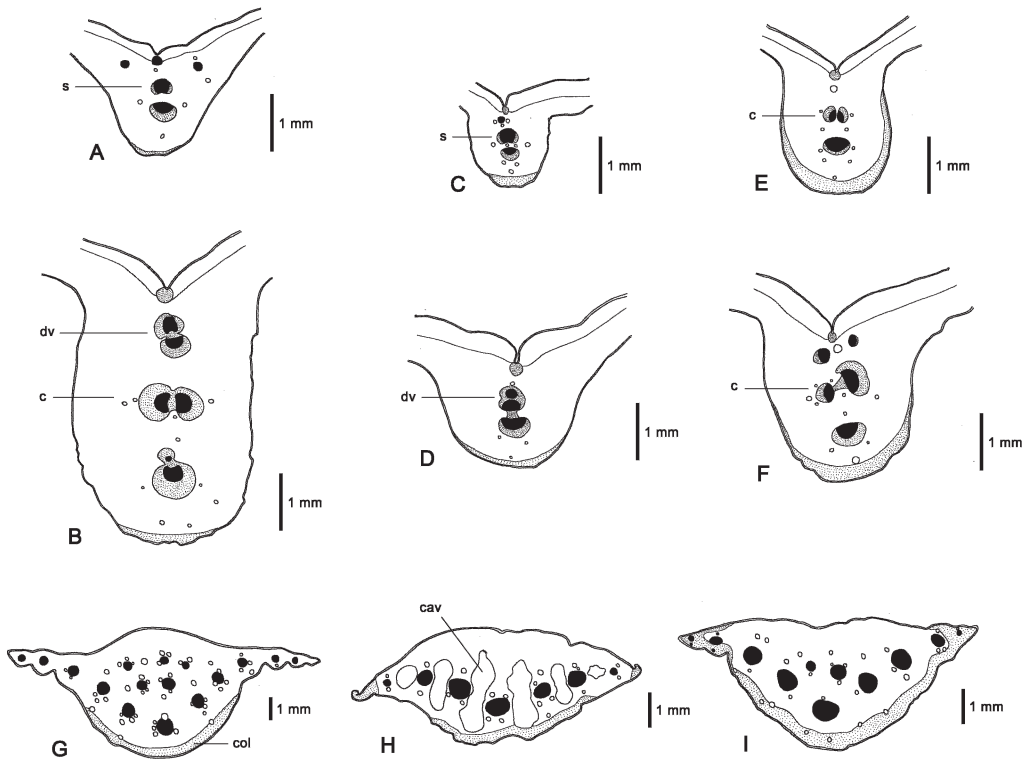

Figure 1. Transverse sections through the midribs (A–F) and petioles (G–I) of *Arctopus* species to illustrate diagnostic anatomical differences. In the midribs, the adaxial vascular bundle can be solitary (C) or dorsiventrally split (D) in *A. echinatus*, collaterally split in *A. monacanthus* (E, F) and a combination of all of these in *A. dregei* (A, B). In the petioles, the presence of collenchyma in the wings of *A. echinatus* (H) and *A. monacanthus* (I), and the markedly ribbed wings in *A. dregei* (G) are characteristic. Cavities between the vascular bundles of healthy, mature leaves are present only in *A. echinatus* (H). —A. *A. dregei* (*Magee & Boatwright 2*, JRAU). —B. *A. dregei* (*Magee & Boatwright 5*, JRAU). —C. *A. echinatus* (*Van Wyk & Viljoen 3715*, JRAU). —D. *A. echinatus* (*Magee & Boatwright 6*, JRAU). —E. *A. monacanthus* (*Van Wyk 4141a*, JRAU). —F. *A. monacanthus* (*Van Wyk s.n., Jonaskop*, JRAU). —G. *A. dregei* (*Magee & Boatwright 2*, JRAU). —H. *A. echinatus* (*Van Wyk s.n., Arendskraal*, JRAU). —I. *A. monacanthus* (*Van Wyk 3594*, JRAU). c, collaterally split adaxial bundle; cav, cavity; col, collenchyma; dv, dorsiventrally split adaxial bundle; s, solitarily adaxial bundle.

members of the Saniculoideae such as *Alepidea*, *Astrantia*, and *Eryngium* (Burtt, 1991).

In *Arctopus*, the pseudanthial bracteoles are fused to the base of the fruit and, as in *Alepidea*, to one another. The bracteoles of *A. dregei* (Fig. 5F) are obovate and involute, with an obtuse spine-tipped apex and one or two inflexed, spinescent hairs along the margin. In *A. monacanthus* (Fig. 9L, M), they become very large, widely obovate and foliose, with an obtuse, spine-tipped apex. Their foliose appearance is enhanced by the prominent reticulate venation. The margin is usually entire, but one to three marginal spines may rarely occur. In *A. echinatus* (Fig. 7R), the bracteoles are ovate, boat-shaped and keeled, with an acute spine-tipped apex plus one or two inflexed and overlapping spines along the margin. They are markedly thickened along the margin and midrib. The pseudanthium of *A. dregei* consists of three to six bracteoles that become white when dry, whereas *A. echinatus* and *A. monacanthus* have either four or five bracteoles that become brown when dry. In *A. monacanthus*, the pseudanthium is brittle and papery at the fruiting stage and tends to break apart easily, so that the bracteoles separate from one another with the ripe fruit still attached to them. In *A. dregei* and *A. echinatus*, the pseudanthium becomes leathery at the fruiting stage and does not break apart easily, so that intact pseudanthia are found with the dying leaves at the end of the growing season (November–December).

FLOWERS

The male flowers are pentamerous with five large petaloid sepals (Figs. 5L, 7H, 9Q) that are linear to oblong and about the same size as the petals. According to Drude (1897–1898), large sepals are commonly found in Saniculoideae (i.e., *Sanicula*, *Hacquetia*, *Actinolema*, and *Eryngium*). There are five oblong to

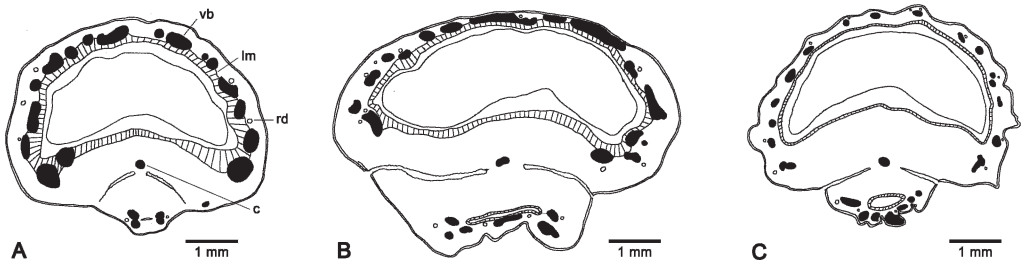

Figure 2. Transverse sections through the pseudo-monocarpellate mature fruit of *Arctopus* species. In all three species, both the single endocarp layer as well as the adjacent mesodermal cells are lignified (a generic synapomorphy). The epidermis remains continuous between both mericarps in *A. dregei* (A), but becomes discontinuous between the two mericarps in *A. echinatus* (B) and *A. monacanthus* (C). —A. *A. dregei* (*Magee & Boatwright 2*, JRAU). —B. *A. echinatus* (*Van Wyk s.n.*, *Arendskraal*, JRAU). —C. *A. monacanthus* (*Van Wyk 4141a*, JRAU). c, carpophore; lm, lignified mesocarp; rd, rib oil duct; vb, vascular bundle.

oblanceolate petals with inflexed tips (Figs. 5M, 7G, 9R, S). On the inner surface, a thin septum joins the basal and apical portions of the inflexed petal, preventing the petals from straightening. The stamens are twice as long as the petals, and the filaments are inflexed at their tips. Although the ovary is absent, a flattened, papillate stylopodium (common to many Saniculoideae) is present along with reduced styles.

The female flowers are sessile (as in *Alepidea*) and tubular (Figs. 5G, 7U, 9O), with a homochlamydeous perianth (a character unique to this genus within the family) consisting of 10 persistent triangular lobes (Figs. 5J, 7V, 9N). Due to the typically pentamerous nature of the male flowers and the almost petaloid sepals, these perianth lobes are here interpreted as five sepals and five sepaloid petals in the female flower, but further ontogenetic studies are required to resolve the homology of these peculiar structures. Stamens are absent and the stylopodium is papillate, cushion-shaped, and swollen so that it almost completely envelops the two style bases. The styles are conical in shape and longer than the sepals. The ovary is bilocular.

FRUIT MORPHOLOGY AND ANATOMY

The fruit of *Arctopus* are unusual in Apiaceae because they become pseudo-monocarpellate with the abortion of one of the two mericarps early in fruit development (Fig. 2). However, in some populations of *A. echinatus* around Vanrhynsdorp and in the Hottentots Holland Mountains, both mericarps may develop. In *A. echinatus* and *A. monacanthus*, the fruit are rostrate (Figs. 7S, 9L, M) and brownish, whereas in *A. dregei* they are white and unbeaked (Fig. 5I). The fruit surface is spinescent in *A. echinatus* and *A. monacanthus*, while in *A. dregei* it has wart-like protuberances. Surface outgrowths on fruit are a common feature in the Saniculoideae (Drude, 1897–1898). In mature fruit, the abortive mericarp separates from the fully developed one in *A. echinatus* and *A. monacanthus*. In *A. dregei*, the developed carpel and the abortive carpel are slightly fused along their margins (Fig. 2A) so that they do not separate at maturity. A detailed study of mature fruit in transverse section (Fig. 2) revealed that the epidermis remains continuous between the two mericarps in *A. dregei* (Fig. 2A) but becomes discontinuous in *A. echinatus* (Fig. 2B) and *A. monacanthus* (Fig. 2C).

Much of the mesocarp becomes lignified in the mature fruit of *Arctopus dregei* (Fig. 2A) and *A. echinatus* (Fig. 2B) but less so in *A. monacanthus* (Fig. 2C). The innermost one or two cell layers of *A. monacanthus* (Fig. 2C) and one to five layers of *A. dregei* (Fig. 2A) and *A. echinatus* (Fig. 2B) are lignified. This was interpreted by Liu et al. (2003) as consisting of a single lignified endocarp layer with adjacent lignified mesodermal cells and therefore different from the multicellular lignified endocarp characteristic of Drude's Hydrocotyloideae (currently treated as Azorelloideae and Mackinlayoideae). In all three species of *Arctopus* (Fig. 2), the small rib oil ducts are always external to and associated with the numerous vascular bundles.

Phylogenetic Relationships

CLADISTIC ANALYSIS OF MORPHOLOGICAL DATA

In order to explore character evolution in *Arctopus*, a cladistic analysis was performed in which 15 characters were polarized (Table 2, Appendix 2). The African endemic saniculoid *Alepidea amatymbica* was selected as the outgroup because both *Alepidea* and *Arctopus* share similar kaurenoic acids (van Wyk et al., 1997), as well as numerous morphological characters (e.g., geophytes with simple leaves, toothed and occasionally inflexed leaf margins ending in setae, fused pseudanthial bracteoles and sessile female flowers). A single, shortest-length tree was produced with a tree

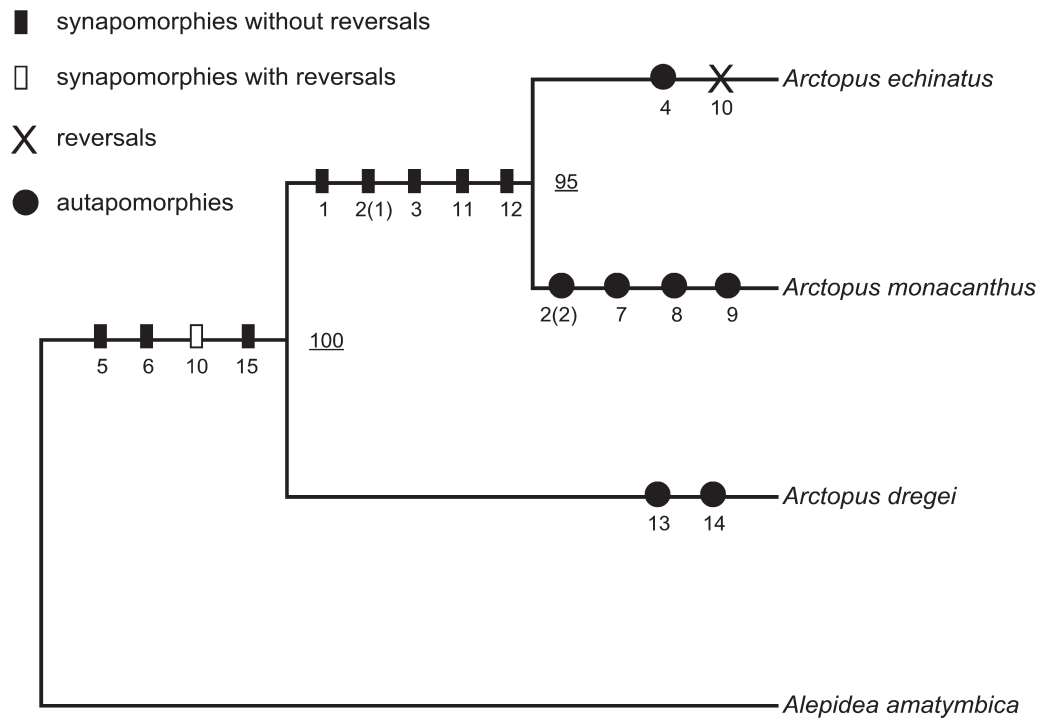

Figure 3. The single shortest-length tree (TL = 17 steps, CI = 0.94, RI = 0.83) obtained by a cladistic analysis of 15 morphological characters (Table 2) to explore possible relationships within the genus *Arctopus*. Characters and character states are numbered as in Appendix 2. Underlined numbers within the branch nodes are bootstrap percentages.

length (TL) of 17 steps, a consistency index (CI) of 0.94, and a retention index (RI) of 0.83 (Fig. 3). The monophyly of *Arctopus* is strongly supported (100 bootstrap percentage [BP]) by four rather convincing and unambiguous generic synapomorphies, namely the dioecious habit, the homochlamydeous perianth in female flowers, the pseudo-monocarpellate fruit, and the lignified endocarp. The pseudo-monocarpellate fruit, a generic synapomorphy, was scored as a reversal in *A. echinatus* because sporadic populations were found with mature fruit in which both mericarps had developed.

Arctopus echinatus and *A. monacanthus* are strongly supported as sister taxa (95 BP) by five synapomorphies. *Arctopus dregei* can be hypothesized to have retained more of the ancestral character states. There also appears to be a trend toward complete monospermy in *A. dregei* (perhaps an autapomorphy), with the carpels not separating from one another when mature and the epidermis remaining continuous between the two mericarps.

CLADISTIC ANALYSES OF ITS SEQUENCE DATA

The total number of characters from ITS-1, ITS-2, and the 5.8S gene was 687, of which 337 were variable (49.05%) and 232 (33.77%) potentially informative. Parsimony analysis produced six shortest-length trees (TL = 715 steps, CI = 0.72, RI = 0.73). The same overall topology was recovered in both the Bayesian (BI) and parsimony (MP) analyses, with the BI differing only in that *Sanicula* is more resolved, with a poorly supported clade (PP 0.75) consisting of *Sanicula arguta* Greene ex J. M. Coult. & Rose and *S. purpurea* H. St. John & Hosaka. A strict consensus of the six trees from MP is shown in Figure 4. It is interesting to note that ITS data produced the same overall topology as was found in a previous analysis (Calviño & Downie, 2007) based on chloroplast data (*trnQ-trnK* 5′: exon region). The tribe Steganotaenieae (represented here by *Steganotaenia araliacea* Hochst.) forms the earliest branching lineage within Saniculoideae (76 BP; PP 0.84) and *Alepidea* (represented here by *Alepidea amatymbica*) forms the earliest branching lineage within Saniculeae (50 BP; PP 0.98). In both analyses, the monophyly of *Arctopus* is strongly supported (100 BP; PP 1.0), but species relationships are unresolved.

TAXONOMIC TREATMENT

Arctopus L., Sp. Pl.: 1058. 1753. TYPE: *Arctopus echinatus* L.

Apradus Adans., Fam. Pl. 2: 102, 519. 1763, nom. illeg.

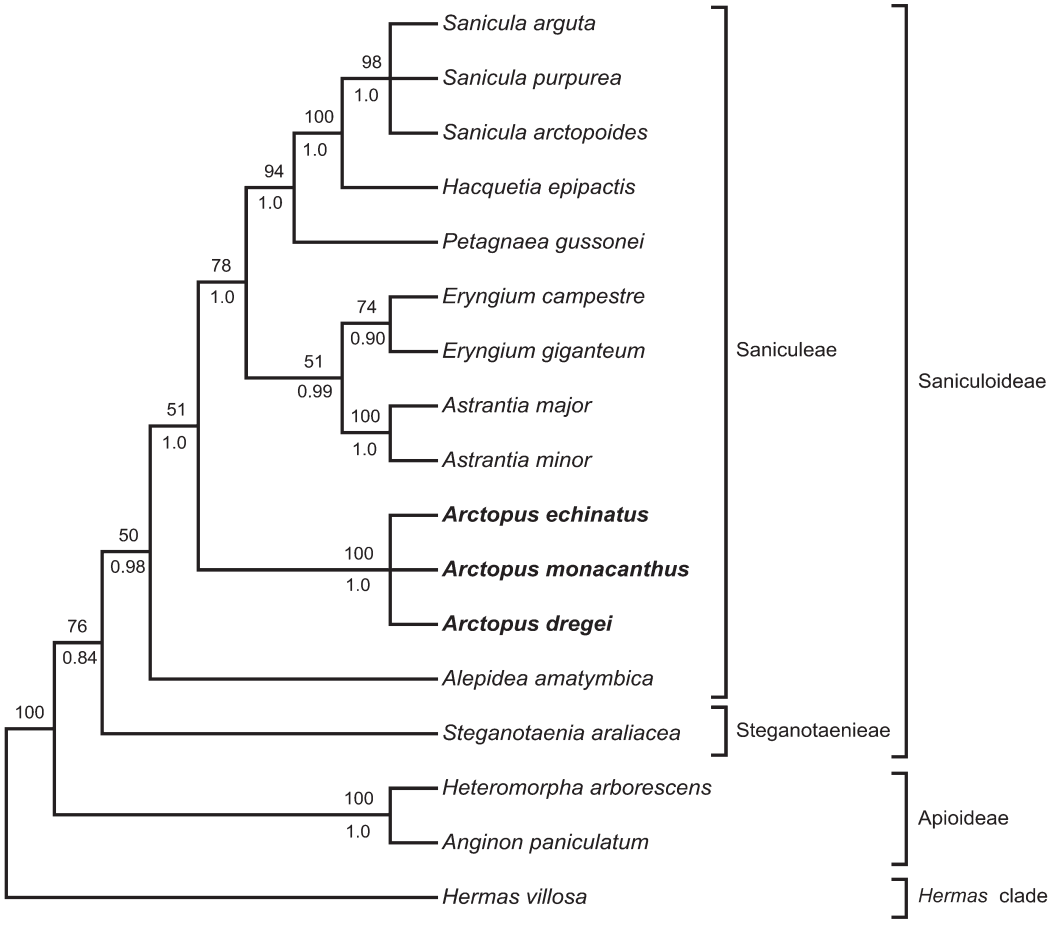

Figure 4. Strict consensus tree of six shortest-length 715-step trees derived from the parsimony analysis of the nrITS region (CI = 0.72, RI = 0.73). Numbers above the branches are bootstrap percentages above 50%, and those indicated below the branches are posterior probabilities obtained by Bayesian inference.

Dioecious, acaulescent, summer-deciduous geophytes; roots long, tuberous, ± 35 mm diam., resinous. Leaves simple, prostrate, spreading in a rosette with the inner smaller; ovate to semi-orbicular or rhomboidal, incised, 3-fid, each segment again 2- or 3-lobed, lobes dentate to crenate; margins toothed, setae spinose-flexuose; leaf base truncate to subtruncate or cuneate; glabrous on both sides; inflexed spine(s) usually present in leaf recesses between segments, often attached to an inflexed laminar tooth; venation palmate, 5- to 7-veined, sunken adaxially but prominently raised abaxially, secondary venation reticulate; petioles adaxially flattened, membrane-winged. Male inflorescence pedunculate, often with up to 5 lateral umbels; involucre spiny, of many linear or occasionally foliose bracts; rays 1 to 8; involucel spiny, of many ovate to lanceolate bracteoles; umbellule with more than 20 flowers. Male flowers pedicellate; sepals 5, linear-oblong, ± same size as petals; petals 5, white, oblong to oblanceolate, with inflexed tips, septum on inner face; stamens 5, twice as long as petals, tips inflexed; stylopodium flat, papillate; styles 2, short; ovary absent. Female inflorescence shortly pedunculate, often with up to 5 compound umbels; involucre as in male; rays 2 to 10; involucel accrescent, of 3 to 6 prominent, ovate or obovate, spiny bracteoles, forming a pseudanthium; bracteoles permanently fused to the fruit. Female flowers sessile, 3 to 5 per pseudanthium, tubular; sepals 5, triangular; petals 5 (the 10 perianth lobes on the female flowers are interpreted here as 5 sepals and 5 sepaloid petals; however, further ontogenetic studies are required), triangular, sepals and petals persistent in fruit; stamens absent; stylopodium cushion-shaped, raised above the style bases, papillate; styles 2, long, conical, longer than the sepals; ovary bilocular. Fruit usually rostrate, base adnate to the bracteoles, usually pseudo-monocarpellate due to abortion of inner mericarp.

Distribution. The genus is endemic to the Cape Floristic Region of South Africa. The rainfall is generally restricted to the winter months (Goldblatt & Manning, 2002) with only *Arctopus echinatus* extending into the almost year-round rainfall in the Eastern Cape Province. The three species share a sympatric distribution (Figs. 6, 8).

Phenology. The plants are dormant in summer and form new leaves in early winter (April). Flowering commences in June through September. Mature fruit are borne around November, at which time the leaves have begun to die back, followed by complete dormancy throughout the dry summer months.

Notes. The numerous unique and unusual characters in this genus make it immediately distinguishable from any other in the family. The species are dioecious geophytes with large, appressed, spiny leaves, female flowers that lack differentiation between sepals and petals, and pseudo-monocarpellate fruit that are surrounded by large, spiny, involucel bracteoles.

Adanson (1763–1764) superfluously described the genus *Apradus* from the same Plukenet (1691–1705: tab. 271, fig. 5) and Burman (1738: tab. 1) figures used earlier by Linnaeus (1753) when he described *Arctopus*. The name *Apradus* is, therefore, considered illegitimate here.

KEY TO THE SPECIES OF *ARCTOPUS*

1a. Female material (flowers sessile, leaves not required).
  2a. Involucel bracteoles flat or keeled.
    3a. Involucel bracteoles ovate, leathery, boat-shaped and keeled, with an acute apex . . . . . *A. echinatus*
    3b. Involucel bracteoles widely obovate, foliose and papery, flat, not keeled, with an obtuse apex . . . . . *A. monacanthus*
  2b. Involucel bracteoles strongly involute, not keeled . . . . . *A. dregei*
1b. Male material (flowers pedicellate) or leaves only.
  4a. Marginal teeth conspicuous so that lobes appear dentate; inflexed spines in leaf recesses typically present (except in a population around Milnerton, which has only sparsely spinescent leaves), involucel bracteoles ± as long as pedicels, 5–10 mm long.
    5a. Laminar tooth of inflexed spine(s) in leaf recesses absent or narrow, 0.5–1.0(–4.0) mm wide, setae almost always absent on tooth margins; petioles with cavities in transverse section . . . . . *A. echinatus*
    5b. Laminar tooth of inflexed spine(s) in leaf recesses usually broad, (2.0–)4.0–10.0 mm wide, setae usually present on tooth margins; petioles without cavities in transverse section . . . . . *A. monacanthus*
  4b. Marginal teeth inconspicuous so that lobes appear crenate; inflexed spines in leaf recesses usually absent, involucel bracteoles usually shorter than pedicels, 1–5 mm long . . . *A. dregei*

1. Arctopus dregei Sond. in Harv. & Sond., Fl. Cap. 2: 565. 1862. TYPE: South Africa. Western Cape Province: Agter de Paarl, sandy hills, s.d., *J. F. Drège 7649* (holotype, S!). Figure 5.

Leaves widely ovate or rhomboidal, blades 40–100 mm long and broad, not thorny; lobes crenate; margins inconspicuously toothed; setae flexuose, 1–5 mm; spine(s) in leaf recesses between segments usually absent, when present then inflexed, attached to an inflexed laminar tooth, inflexed part of lamina absent or narrow, less than 1 mm wide, setae absent, vertical spines 0(to 3), 5 mm; petioles 20–80 × 4–7 mm; wings broad, 1–4 mm wide. Male umbellule with pedicels longer than bracteoles, pedicels 1–10 mm; bracteoles lanceolate, spiny, 1–5 mm. Female inflorescence with rays 4–15 mm; pseudanthial bracteoles relatively small; 3 to 6; obovate, involute; ca. 8 × 4 mm at flowering stage, accrescent, becoming 9–20 × 5–10 mm at fruiting stage; apex obtuse, with a sharp spine, spine ca. 2 mm; margin with 1 or 2 inflexed, spinescent hairs; pseudanthial bracteoles becoming leathery at fruiting stage, reticulate venation not markedly prominent, becoming white when dried, not separating. Fruit not rostrate; 1-seeded; surface pustulate, white; developed mericarp ca. 8 × 5 mm; abortive mericarp small, not separating in mature fruit.

Distribution. Arctopus dregei was originally considered to be endemic to the Lowland Renosterveld of the Western Cape Province, from Paarl to Malmesbury, Yzerfontein, and Darling, and extending north to Hopefield. However, two recent collections of outlying populations around Vredenburg and Koekenaap in 2006 and 2007 have significantly extended the known geographical range for this species (Fig. 6) and shown for the first time that *A. dregei* is not restricted to Renosterveld, but may also occur in both Strandveld and Sandveld fynbos. It thrives in seasonally moist sandy soils and is often found in sparse vegetation dominated by Restionaceae (pers. obs.).

IUCN Red List category. Arctopus dregei is considered Vulnerable (VU B1ab[i,ii,iii,iv,v]) according to IUCN Red List criteria (IUCN, 2001). Lowland Renosterveld (the vegetation to which *A. dregei* is largely restricted) is considered to be one of the most threatened habitats in the Cape Floristic Region, with over 80% of the area completely transformed and currently only a few patches formally protected (Mucina & Rutherford, 2006). It is subject to

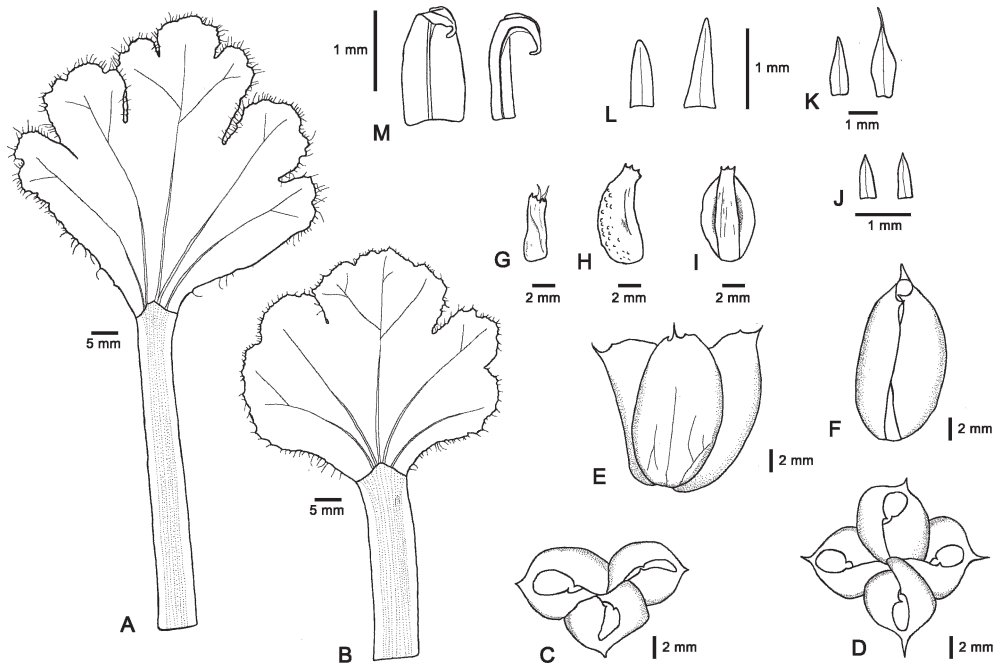

Figure 5. *Arctopus dregei*. —A, B. Leaves, adaxial view (A: *Magee & Boatwright 2*, JRAU; B: *Magee & Boatwright 5*, JRAU). C–J. Female flowers and fruits (*Magee & Boatwright 31*, JRAU). C–F. Pseudanthium. —C, D. Top view. —E. Lateral view. —F. Single pseudanthium bracteole. —G. Female flower. —H. Fruit, lateral view. —I. Fruit, dorsal view. —J. Sepals and petals. K–M. Male flowers (*Boucher & Shepherd 4408*, NBG). —K. Bracteoles. —L. Sepals. —M. Petals.

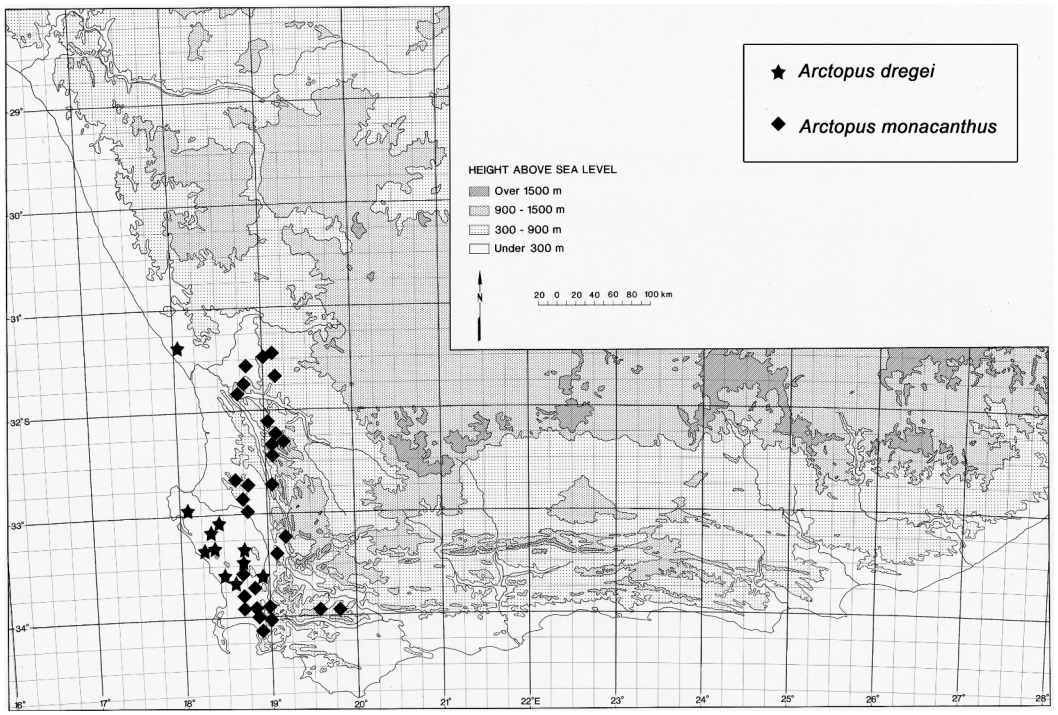

Figure 6. The known geographical distribution of *Arctopus dregei* and *A. monacanthus*.

extensive pressure in the form of agricultural expansion and seepage (drift sprays of herbicides and pesticides, as well as fertilizer runoff), and the spread of alien invasive species and urban encroachment and, as a result, is severely fragmented today. The species has also been recorded outside of Renosterveld; however, only two such populations are known. One of these is known to occur in Strandveld vegetation near Vredenburg and is threatened by proposed industrial expansion (*Helme 4181* [NBG], in schedula). Consequently, Helme and Raimondo (in prep.) have recommended that *A. dregei* be considered Vulnerable (VU) according to IUCN Red List criteria (IUCN, 2001) as it has a severely fragmented distribution and an extent of occurrence estimated to be 12,388 km^2.

Notes. *Arctopus dregei* (Fig. 5) is a distinctive species that can easily be distinguished by the crenate lobes of the leaves due to the inconspicuously toothed margins and the usually absent inflexed spines in the leaf recesses. The female bracteoles are involute. The male flowers have bracteoles that are shorter than the pedicels.

Additional specimens examined. SOUTH AFRICA. **Western Cape Province:** NW of Koekenaap, Farm Graafwater, *Goldblatt & Manning 12875* (NBG); 7 km SE of Vredenburg on Langeberg 187, N of R79, E of Namaqua Sands plant, *Helme 4181* (NBG); betw. Yzerfontein & Darling, *Magee & Boatwright 5* (JRAU); Hopefield, *Bolus 12699* (BOL, K); *Garside 1608* (K); Hopefield, Enkelvlei Farm, *Goldblatt & Manning 11414* (PRE); Yzerfontein, De la Rey Farm, *Louw 2529* (NBG); Malmesbury Allotment area, *Helme 2165* (NBG); Malmesbury, Klipfontein 598, *Helme 2574* (NBG); Malmesbury, *Magee & Boatwright 31* (JRAU); Malmesbury, Pella area, Burgers Post Farm, *Boucher & Shepherd 4408* (NBG); Malmesbury, Rustenburg Farm, *Helme 2719* (NBG); Malmesbury, Rondeberg Farm, *Helme 2763* (NBG); *Magee & Boatwright 1, 2, 3, 4* (JRAU); Paarl, *Acocks 2440* (K, PRE). Precise locality unknown: *Drège s.n.* (BM).

2. Arctopus echinatus L., Sp. Pl.: 1058. 1753. TYPE: South Africa. Western Cape Province: Cape Town, Signal Hill near Kramat, 16 July 2003, *J. Manning & G. Reeves 2845* (proposed conserved type, designated by van Wyk et al., 2006: 541, NBG!). Figure 7.

Leaves widely to very widely ovate, semi-orbicular or rhomboidal, blades 20–80 mm long and broad, thorny (sparsely thorny in the Milnerton population); lobes dentate to doubly dentate, rarely crenate (Milnerton population); margins conspicuously toothed; setae spinose, rarely flexuose, 3–10 mm; spine(s) in leaf recesses between segments inflexed, occasionally attached to an inflexed laminar tooth; inflexed part of lamina absent or narrow, 0.5–1.0 (–4.0) mm wide, setae absent, vertical spines 1 to 3(4), stout, 6–15 mm; petioles 20–200 × 5–7 mm; wings narrow, ca. 1 mm wide. Male umbellules with pedicels ± as long as the bracteoles; bracteoles ovate to lanceolate, spiny, 5–10 mm. Female inflorescence with rays 10–40 mm; pseudanthial bracteoles relatively small, 4 or 5, ovate, boat-shaped and keeled; ca. 6 × 3 mm at flowering stage, accrescent, becoming 10–18 × 5–8 mm at fruiting stage; apex acute, with a sharp spine, spine 2–3 mm; margin with 1 or 2 inflexed and overlapping spines; pseudanthial bracteoles becoming leathery and firm at fruiting stage, prominently thickened along periphery and midrib, becoming brown when dried, not separating. Fruit rostrate; usually 1-seeded, rarely 2-seeded; surface usually spiny, brown; developed mericarp ca. 10 × 5 mm; abortive mericarp small, separating in mature fruit.

Distribution. *Arctopus echinatus* is the most widespread species of the genus, occurring throughout the Western Cape Province and extending both north to Nieuwoudtville in the Northern Cape Province and east along the coast to Port Alfred in the Eastern Cape Province (Fig. 8). Plants are usually found in seasonally moist sandy soils (pers. obs.).

IUCN Red List category. *Arctopus echinatus* is considered Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Notes. *Arctopus echinatus* (Fig. 7) can be distinguished from *A. dregei* by the dentate lobes on the leaves, due to the conspicuously toothed margins, and the presence of inflexed spines in the leaf recesses. More notably, the female bracteoles are ovate, boat-shaped and keeled, with an acute apex. The male flowers have bracteoles that are equal in length to the pedicels. This species differs from *A. monacanthus* by the narrow or absent inflexed laminar tooth of the spine in the leaf recesses, which usually lacks setae. The leaf anatomy also differs from that of *A. monacanthus* in that the petiole in transverse section has cavities and the adaxial vascular bundle of the midrib is either simple or dorsiventrally split.

Burtt (in Jarvis et al., 1993: 20) designated the Burman plate (tab. 1 in J. Burman, Rar. Afric. Pl. 1738) as lectotype of *Arctopus echinatus*. Unfortunately, the plant illustrated in this plate was not identifiable as *A. echinatus* of current usage, but rather as *A. monacanthus*. Van Wyk et al. (2006) therefore proposed the conservation of *A. echinatus* with a conserved type in order to maintain the widespread usage of this name. This proposal has been recommended by the Nomenclature Committee (Brummit, 2007: 1293).

Additional specimens examined. SOUTH AFRICA. **Eastern Cape Province:** Uitenhage, *Drège s.n.* (K), *Zeyher s.n.*

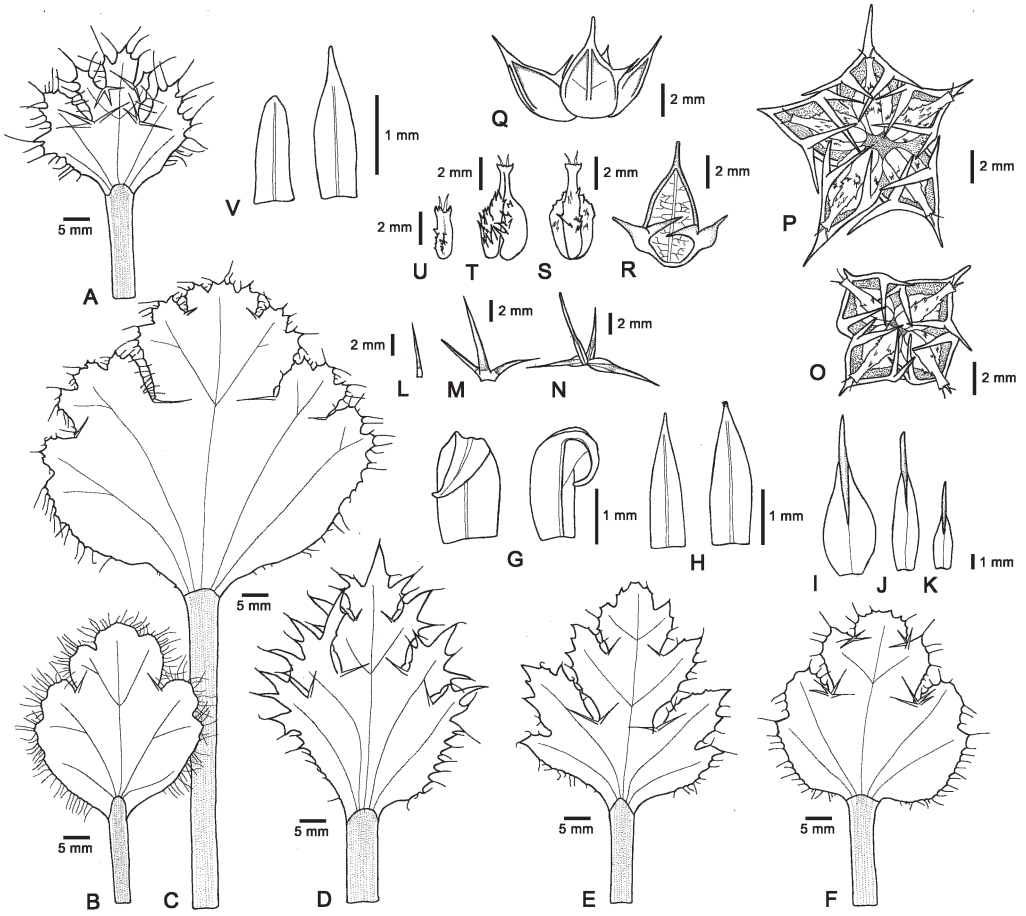

Figure 7. *Arctopus echinatus*. —A–F. Leaves, adaxial view (A: *Esterhuysen 12231*, BOL; B: *Adamson 2517*, BOL; C: *Magee & Boatwright 6*, JRAU; D: *Magee & Boatwright 15*, JRAU; E: *Theron 1764*, PRE; F: *Tilney 257*, JRAU). G–K. Male flowers (G, H: *Van Wyk & Viljoen 3715*, JRAU; I: *Rycroft 1939*, NBG; J: *Bond 1149*, NBG; K: *Adamson 2865*, PRE). —G. Petals. —H. Sepals. —I–K. Bracteoles. —L–N. Inflexed lamina spines (L: *Taylor 5099*, PRE; M: *Magee & Boatwright 15*, JRAU; N: *Brink 767*, PRE). O–V. Female flowers and fruits (*Magee & Boatwright 6*, JRAU). O–R. Pseudanthium. —O, P. Top view. —Q. Lateral view. —R. Single pseudanthium bracteole. —S. Fruit, dorsal view. —T. Fruit, lateral view. —U. Flower. —V. Sepals and petals.

(BM); Paterson, *Retief 471* (PRE); Port Elizabeth, *Bolus 2246* (BOL, K), *Borle 28* (PRE), *Patterson 25755* (PRE); Port Elizabeth, Victoria Park Lands, *Long 618* (K, PRE); Botha's Hill, *Rodgers 4438* (BOL); Alexandria, *Galpin 10762* (K, PRE), *Watt 1445* (PRE); Alexandria, Bushmans River Mouth, *Archibald 3634* (K, PRE), *Marais 409* (K, PRE); Alexandria, Bokness village, *Brink 767* (PRE); Kasouga, *Tilney 257* (JRAU); Kowie, *Britten 2135* (PRE), *Tyson 19229* (PRE); Bathurst, *Henrici 12* (PRE); Port Alfred, *Hutton s.n.* (PRE). **Northern Cape Province:** Van Rhyns Pass top, *Bond 1149* (NBG), *Taylor 2908* (NBG), *Van der Schijff 7179* (PRE); Nieuwoudtville, *Van Wyk 4128a* (JRAU); Aarendskraal, *Van Wyk s.n.* (JRAU); Oorlogskloof, *Van Wyk & Viljoen 3715* (JRAU); Oorlogskloof farm, Tuinlaagte, *Magee et al. 93* (JRAU). **Western Cape Province:** Cederberg, betw. Middelberg hut & Crystal Pool, *Barnes 19284* (BOL); Cederberg, Scorpionspoort, *Esterhuysen 12231* (BOL); Cedarberg, *Thode A2003* (PRE); 11 km from Op-Die-Berg to Cedarberg, *Stirton 9162* (PRE); Rondegat River valley, *Le Maitre 337* (PRE); Sneeuberg, Cedarberg Forest Reserve, *Taylor 5099* (PRE); Langebaan Lagoon, *Axelson 443* (NBG); Darling Flora Reserve, *Rycroft 1939* (NBG); betw. Yzerfontein & Darling, *Magee & Boatwright 6* (JRAU); Sea Point, *MacOwan 1624* (BM, S), *Phillips s.n.* (BM); Clifton, *Acocks 4566* (S), *Barker 1528* (NBG); Rondebosch Common, *Barker 1529* (NBG); Claremont, *Salter 9231* (BM); Wynberg Hill, *Salter 9224* (BM); Wynberg, *Gamble 22123* (K); Table Mtn., *Fries 3133* (S), *Peter 50305* (K); Signal Hill, *Blake s.n.* (NBG); *Marloth 5562* (PRE); Lions Rump, *Thode A105* (NBG, PRE), *Worsdell s.n.* (K); Milnerton, *Adamson 2517* (BOL), *2865* (BOL, PRE), *Hanson 2517* (BOL), *Salter 8199* (BOL); Killarney, *Lussem 17* (NBG); Porterville, Grootwinterhoek Mtn., *Barker 262* (PRE); Stellenbosch, *Garside 1506* (K), *Kerfoot 5842* (PRE) [atypical, possible hybrid with *Arctopus monacanthus*], *Moss 4046* (BM); Gydo Pass, *Johnson 505* (NBG); Ceres, *C. M. Van Wyk 3319* (PRE); Ceres, Skoongesig, *Hanekom 662* & *663* (PRE); Worcester Veld Reserve, *Olivier 61* (PRE); Worcester, *Van Breda 71* (PRE); Worcester, Langerug koppie, *Walters 1991* & *1992* (NBG); Du Tooits Kloof pass, *Winter et al. 170* (JRAU); Botrivier

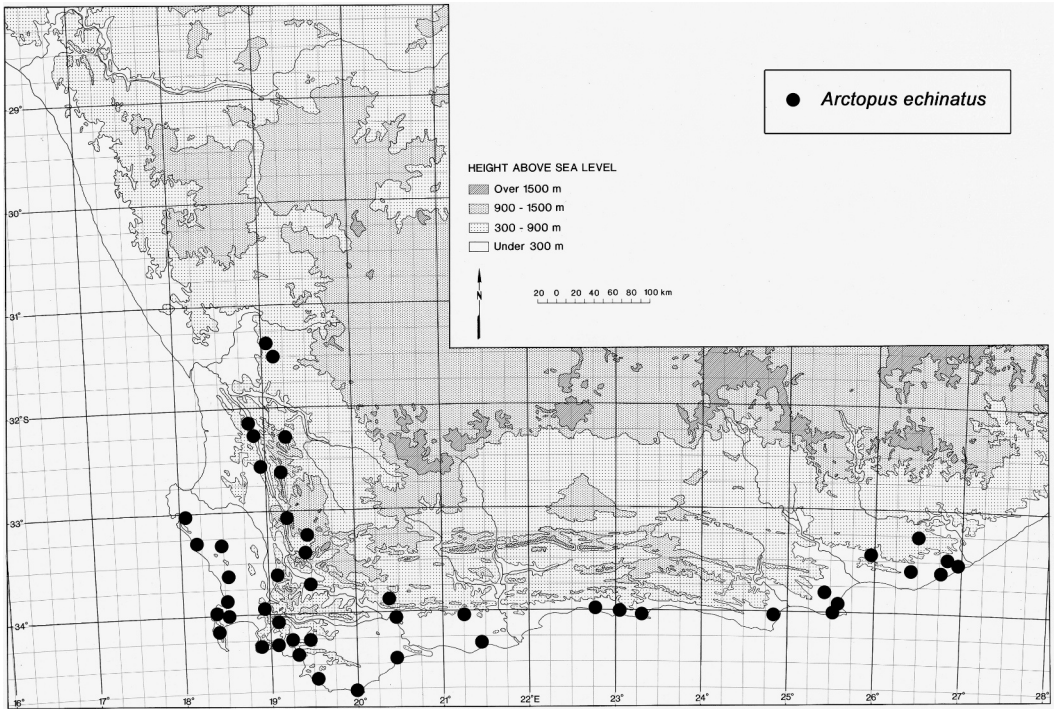

Figure 8. The known geographical distribution of *Arctopus echinatus*.

vlei, *Loubser s.n.* (NBG); Clock Peaks, *Wurts 148* (NBG); Constantianek, *Young 26521* (PRE); Simon's Town, *Alice & Godman 67* (BM); Betty's Bay, Dawidskraal, *Boucher 1379* (NBG); Kleinmond, *Burman 1171* (BOL), *De Vos 607* (NBG); Palmiet, *De Vos 719* (NBG); Hermanus, Fernkloof Nature Reserve, *Orchard 558* (K, NBG, PRE), *Magee & Boatwright 15* (NBG); Hermanus, Westcliff, *Williams 303* (K); Pearly Beach, Kleinhagelkraal, *C. M. Van Wyk 616* (NBG, PRE); Zoetendalsvlei, *Smith 3098* (PRE); De Hoop flats near Die Mond, *Burgers 2576* (NBG); De Hoop, *Van der Merwe 800* (PRE); Soetmelksfontein, *Muir 5204* (PRE); Riversdale, Still Bay, *Bohnen 7540* (NBG, PRE); Riversdale, *Muir 24400* (BOL); Knysna, *Theron 1764* (PRE); Kranshoek lookout point, near Harkerville, *Boatwright, Magee & Van Wyk 4* (JRAU); Humansdorp, Blouleliesbos, *Geldenhuys 99* (PRE). Precise locality unknown: *Sieber 141* (S).

3. Arctopus monacanthus Carmich. ex Sond., Fl. Cap. 2: 565. 1862. TYPE: South Africa. Cape Province: s.d., *Captain Carmichael s.n.* (holotype, S!). Figure 9.

Leaves widely to very widely ovate, semi-orbicular or rhomboidal, blades 25–120 mm long and broad, thorny; lobes dentate to doubly dentate; margins conspicuously toothed; setae spinose, 3–7 mm; spine(s) in leaf recesses between segments inflexed, attached to an inflexed laminar tooth; inflexed part of lamina usually broad, (2.0–)4.0–10.0 mm wide, setae present, vertical spines 1 to 5(6), stout, 2–20 mm; petioles 20–100 × 3–7 mm; wings narrow, ca. 1 mm wide. Male umbellules with pedicels ± as long as bracteoles; bracteoles lanceolate or occasionally ovate, spiny, 5–10 mm. Female inflorescence with rays 10–50 mm; pseudanthial bracteoles large, 4 or 5, widely obovate, foliose, ca. 10 × 3 mm at flowering stage, massively accrescent, becoming 20–40 × 15–50 mm at fruiting stage; apex obtuse, with a sharp spine, spine ca. 4 mm; margin entire, rarely with 1 to 3 spines; pseudanthial bracteoles becoming brittle and papery at fruiting stage, reticulate venation prominent, becoming brown when dried, breaking away (with the ripe fruit attached). Fruit markedly rostrate; 1-seeded; surface occasionally spiny, brown; developed mericarp ca. 15 × 5 mm; abortive mericarp small, separating in mature fruit.

Distribution. *Arctopus monacanthus* has an extreme western distribution occurring from Somerset West in the Western Cape Province, north toward Nieuwoudtville in the Northern Cape Province (Fig. 6). It is an inland species occurring in seasonally moist clay soils or, less often, on sand (pers. obs.).

IUCN Red List category. *Arctopus monacanthus* is considered Least Concern (LC) according to IUCN Red List criteria (IUCN, 2001).

Notes. *Arctopus monacanthus* (Fig. 9) is similar to *A. echinatus*, but differs in having a broad inflexed laminar tooth in each of the leaf recesses with setae usually present on the margins of these teeth. The

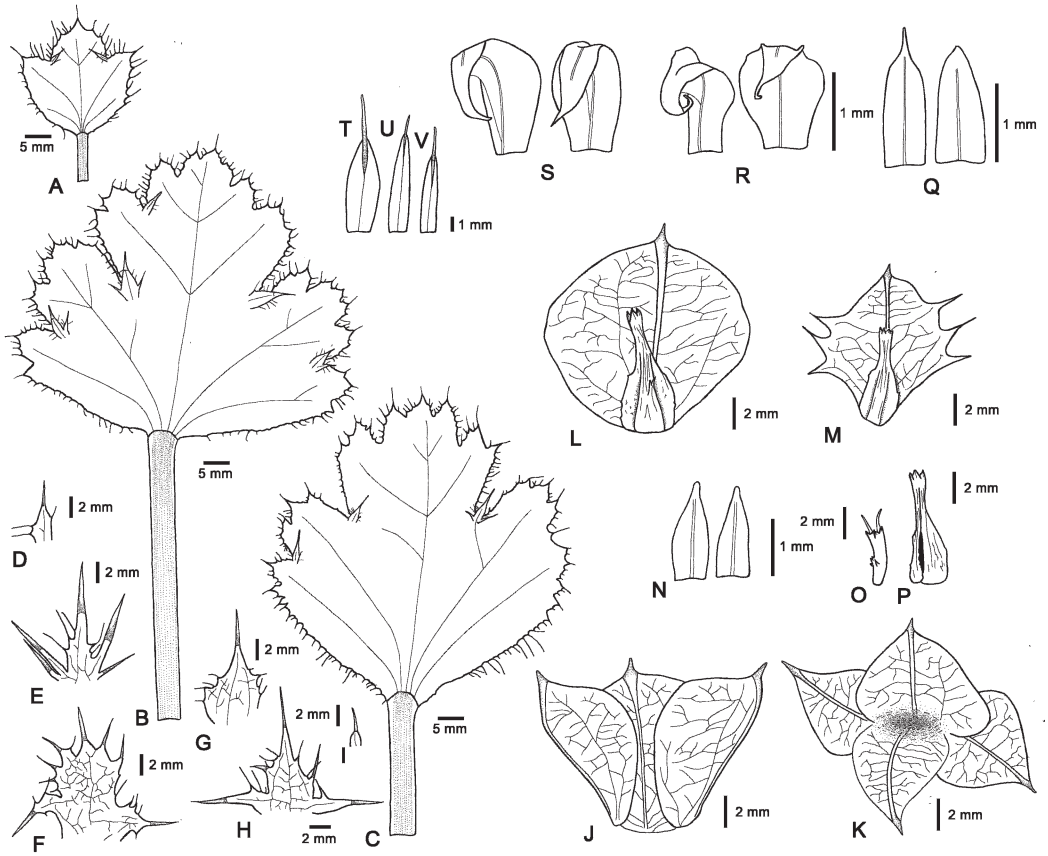

Figure 9. *Arctopus monacanthus*. —A–C. Leaves, adaxial view (A: *Acocks 17286*, PRE; B: *Mauve & Hugo 49*, PRE; C: *Van Wyk 4141a*, JRAU). —D–I. Inflexed lamina spines (D: *Van Wyk 4128b*, JRAU; E: *Barker 9882*, NBG; F: *Loubser 3348*, NBG; G: *Van Zyl 3140a*, NBG; H: *Runnalls 511*, NBG; I: *Van Wyk 3522*, JRAU). J–P. Female flowers and fruits (J, M, P: *Van Wyk 4161a*, JRAU; N, O: *Magee et al. 96*, JRAU). J–M. Pseudanthium. —J. Lateral view. —K. Top view. —L, M. Single pseudanthium bracteoles, with fruit in dorsal view. —N. Sepals. —O. Flower. —P. Fruit, lateral view. Q–V. Male flowers (Q, S, T: *Boucher 4389*, NBG; U: *Runnalls 512*, NBG; R, V: *Parker 3518*, PRE). —Q. Sepals. —R, S. Petals. —T–V. Bracteoles.

female bracteoles are widely obovate and foliose with an obtuse apex. In transverse section, the petiole is without cavities and the adaxial vascular bundle of the midrib is collaterally split.

Additional specimens examined. SOUTH AFRICA. **Northern Cape Province:** Nieuwoudtville, *Van Wyk 4128b* (JRAU); Nieuwoudtville, Oorlogskloof Nature Reserve, *Pretorius 181504* (NBG); Oorlogskloof farm, Tuinlaagte, *Magee et al. 96* (JRAU); Heerenlogement, *Barker 9882* (NBG); Gifberg, *Van Wyk 3522* & *4161a* (JRAU); Lokenburg, *Acocks 17286* (PRE). **Western Cape Province:** Piqueniers Kloof, *Oskolski et al. 35-06* (JRAU), *Schlechter 10756* (BM, BOL, K); Piquetberg, De Hoek, *Steyn 540* (NBG); Piquetberg, *Laers 19629* (BOL), *Stephens & Glover 8710* (BOL, K), *Van Wyk 3594* (JRAU); Pakhuis Pass top, *Wisura 2982* (NBG), *Magee & Boatwright 34* (JRAU); Clanwilliam, 20 km along rd. to Algeria, *Scott 393* (BOL); Wupperthal, *MacOwan 3236* (K); Cedarberg, Middelberg West, *Viviers 514* (PRE); Middleberg pass, *Van Wyk s.n.* (JRAU); Oliphants River Valley, opposite Warm Bath, *Stephens 7246* (K); Durbanville, Klipheuwel Farm, *Van Zyl 3140a* (NBG); Malmesbury, N side of Hercules Pillar, *Adamson 3168* (BM, BOL); Dassenberg, summit of Kanonkop, *Boucher 4389* (NBG); Tygerberg Nature Reserve, *Loubser 3348* (NBG); Langverwacht above Kuils River, *Olivier 4686* (NBG); Bottelaryberg, *Acock 2511* (S); Stellenbosch, *Bos 328* (PRE), *Gillett 583* (NBG); Stellenbosch, Vlottenberg station, *Stegmann 10566* (BOL, PRE); Straatkerk, 3 km W of Tulbagh, *Mauve & Hugo 49* (PRE); Elandskloof pass, *Van Wyk 4141a* (JRAU); Jonaskop, *Van Wyk s.n.* (JRAU); McGregor rd., *Van Wyk*, *Winter & Tilney s.n.* (JRAU); Somerset West, *Boucher & Mauve 4948* (PRE), *Parker 3518* (BOL, K, NBG, PRE); Somerset West, Helderberg Nature Reserve, *Runnalls 511 & 512* (NBG); Somerset in Hottentots Holland Mtn., *Ecklon & Zeyher s.n.* (S). Precise locality unknown: Malmesbury–Clanwilliam rd., *Alice & Godman 514* (BM).

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Appendix 1. List of the voucher specimens of taxa used in the molecular analysis, with GenBank accession numbers.

New Sequence Data

Azorelloideae: *Hermas villosa* Thunb., *A. R. Magee & J. S. Boatwright 24* (JRAU), AM748815. **Saniculoideae:** *Alepidea amatymbica* Eckl. & Zeyh., *A. R. Magee & J. S. Boatwright 45* (JRAU), AM158945; *Arctopus dregei* Sond., *A. R. Magee & J. S. Boatwright 2* (JRAU), AM158942; *Arctopus echinatus* L., *A. R. Magee & J. S. Boatwright 6* (JRAU), AM158943; *Arctopus monacanthus* Carmich. ex Sond., *B.-E. van Wyk 3522* (JRAU), AM158944; *Steganotaenia araliacea* Hochst., *O. Maurin 566* (JRAU), AM748814.

Sequence Data from GenBank

Apioideae: *Anginon paniculatum* (Thunb.) B. L. Burtt, AF467922 (Neves & Watson, 2004); *Heteromorpha arborescens* Cham. & Schltdl., U27578 (Downie & Katz-Downie, 1996). **Saniculoideae:** *Astrantia major* L., AF077876 (Downie & Katz-Downie, 1996); *Astrantia minor* L., AF337183, AF337191 (Valiejo-Roman et al., 2002); *Eryngium campestre* L., AF077887 (Valiejo-Roman et al., 1998); *Eryngium giganteum* Bieberd., AF337182, AF337190 (Valiejo-Roman et al., 2002); *Hacquetia epipactis* DC., AF077892 (Valiejo-Roman et al., 1998); *Petagnaea gussonei* (Spreng.) Rauschert, AM403487, AM403486 (De Castro, unpublished); *Sanicula arctopoides* Hook. & Arn., AF031974 (Vargas et al., 1998); *Sanicula arguta* Greene ex J. M. Coult. & Rose, AF031975 (Vargas et al., 1998); *Sanicula purpurea* H. St. John & Hosaka, AF031971 (Vargas et al., 1998).

Appendix 2. Morphological characters and character states used for cladistic analysis of *Arctopus*.

1. **Setae on leaf margins:** 0 = flexuose; 1 = spinose.
2. **Inflexed laminar teeth in the recesses between the leaf segments:** 0 = absent; 1 = present, narrow (< 2(–4) mm); 2 = present, broad (> 4 mm).
3. **Collenchyma in petiole wings:** 0 = absent; 1 = present.
4. **Petiole cavities:** 0 = absent; 1 = present.
5. **Sexual system:** 0 = monoecious; 1 = dioecious.
6. **Sepals and petals of female flowers:** 0 = distinct sepals and petals; 1 = homochlamydeous perianth.
7. **Size of pseudanthium bracteoles:** 0 = small; 1 = large.
8. **Shape of pseudanthium apex:** 0 = acute; 1 = obtuse.
9. **Texture of pseudanthium:** 0 = leathery; 1 = papery.
10. **Fruits:** 0 = bicarpellate; 1 = pseudo-monocarpellate.
11. **Fruit shape:** 0 = not rostrate; 1 = rostrate.
12. **Fruit surface:** 0 = protuberant; 1 = spinescent.
13. **Mature fruits:** 0 = separating; 1 = not separating.
14. **Fruit epidermis between mericarps of mature fruits:** 0 = discontinuous; 1 = continuous.
15. **Endocarp:** 0 = parenchymatous; 1 = lignified.