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Resurrection of *Talbotia* as a monotypic genus in Velloziaceae

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ABSTRACT

The recognition of *Talbotia* as a separate genus has been controversial for over 150 years. We have consolidated information available in the literature and added much information that we have gained in the field and from examination of many cultivated specimens. We have compiled a list of 32 characters from the literature and our observations that clearly differentiate *Talbotia* from *Xerophyta* and another six characters where there is a small amount of overlap between *Talbotia* and a minority of species of *Xerophyta*. Although there are molecular-based phylogenies available for African Velloziaceae, they either include few species or are based on only a single gene region. In the first case, *Talbotia* is sister to all five included taxa of *Xerophyta* and in the second case, *Talbotia* appears to be related to the shrubby species of *Xerophyta* rather than the herbaceous ones. This may indicate that further investigation based on more species and more gene regions may reveal that additional genera should be recognised to appropriately reflect the relationships between Old World Velloziaceae. In the meanwhile, we are resurrecting *Talbotia* as this would not render *Xerophyta* poly- or paraphyletic and so that the large number of differences between *Talbotia* and *Xerophyta* are not obscured by its combination with *Xerophyta*.

1. Introduction

In 1866, H. Fox Talbot brought a specimen pronounced by Oliver to be a species of *Vellozia* and identical to the taxon known by Harvey's manuscript designation, *Hypoxis barbacenioides*, to the Kew Herbarium and the name *Vellozia elegans* (Balf.) Oliv. ex Hook.f. was proposed, but not published (Hooker, 1869). In January 1867, Balfour presented the plant to the Botanical Society of Edinburgh as *Vellozia elegans*, and then in June 1867 as *Vellozia talboti* Balf. with the provisothat should it be found to be a new genus, he would call it *Talbotia elegans* Balf. (Hooker, 1869). In July 1867, he presented the same plant as *Talbotia elegans*, but did not state how this proposed genus differed from *Vellozia* Vand., described in 1788, nor *Xerophyta* Juss., which had been described in 1789 (Hooker, 1869) to accommodate African species of the family (Hooker, 1869). Hooker (1869) appears surprised that Balfour did not include the species in *Xerophyta* or at least compare the new species to that genus, but, at that time, *Xerophyta* was only known from three taxa based on Commerson specimens all collected on Madagascar and housed in Muséum National d'Histoire Naturelle, Paris, France (P), Staatliche Naturwissenschaftliche Sammlungen Bayerns (SNSB), München, Germany (M) and an unspecified herbarium, but presumably on the European continent as it was seen by J.F. Gmelin when he described *Xerophyta madagascariensis* J.F. Gmel. in the 15th edition of Linnaeus' *Systema vegetabilium* (Gmelin, 1796). Thus, Balfour may not have seen any specimens assigned to *Xerophyta* and/or he may have assumed that *Xerophyta* was confined to Madagascar.

The first species of the Velloziaceae to be described from the African mainland was *Xerophyta schnizleiniana* (Hochst.) Baker, which was described in the genus *Hypoxis* L. (Hochstetter, 1844). This was followed by *Talbotia elegans* in 1868 and then Baker (1875) made the *Xerophyta schnizleiniana* combination and described at least six new species in 1875 (in his synopsis of the African species of the genus). Hooker (1869) treated *T. elegans* as a species of *Vellozia* and Baker (1875) as a species of *Xerophyta* and the controversy has persisted since then. Ayensu (1973), Coetzee et al. (1973 & 1974), Smith & Ayensu (1974), Dyer (1976), Hallam & Gaff (1978), Goldblatt & Poston (1988), Williams et al. (1991), Menezes et al. (1994), Kubitzki (1998), Archer (2000), Salatino et al. (2001), Behnke et al. (2002), Mello-Silva (2005), Crouch and Condy (2009), Furness (2013), Sousa-Baena (2014) and Zdravchev et al. (2023) all treated or accepted *Talbotia* Balf. as a distinct genus, but Greves (1921), Fahn (1954) and Ayensu (1969) treated *T. elegans* as a species of *Vellozia*, whereas Durand & Schinz (1895), Menezes (1988), Melo et al. (1997), Behnke et al. (2000), Mello-Silva et al. (2011), Behnke et al. (2013) and Koekemoer

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et al. (2023) all treat *T. elegans* as a species of *Xerophyta.* In their global appraisal of the family based on morphology and DNA, Mello-Silva et al. (2011) concluded that five genera should be recognised in the family — *Acanthochlamys* P.C.Kao, with one species confined to China, *Xerophyta,* now confined to Africa and Madagascar, and three genera in the Americas. *Barbaceniopsis* L.B. Smith has four species in western South America, *Barbacenia* Vand. has about 100 species in eastern South America and *Vellozia* has about 100 species in Panama and north-eastern South America. *Vellozia* differs from *Xerophyta* by the expanded, horizontal stigma lobes and is no longer considered to occur in Africa. None of the foregoing authors had the opportunity to examine the full range of published information that is currently available on the differences between *Talbotia* and *Xerophyta*, nor a large number of living plants of many African species in the family and we intend to do that in this paper.

2. Material and methods

Our team has been actively working on the South African species of *Xerophyta* for 25 years. As part of that process, relevant literature has been gathered. To augment those publications to facilitate a sufficiently complete literature review, we used Google Scholar and searched for Talbotia and then for Velloziaceae together with elegans. This yielded some additional references. We then worked through the reference lists of all the publications we had, to see whether there were additional publications that may be relevant. Literature was sourced online, via the library of the University of the Witwatersrand, from the Biodiversity Heritage Library and from the Mary Gunn Library at the National Herbarium (PRE). When we managed to obtain searchable pdf's of documents, we searched for Talbotia and / or elegans to find what was said about the species. We manually scanned unsearchable documents to find where the publication referred to the species of interest.

We mainly work at HSMC (abbreviations according to Herbarium acronyms follow index Herbariorum, 2025 [continually updated]), where amongst the 12 000 herbarium specimens there is a targeted collection of 249 accessions of herbarium sheets of *Xerophyta* and *Talbotia*. Specimens are augmented with floral material when cultivated plants flower. We have borrowed herbarium material from J and BNRH and have visited BOL, GRA, NH, NU, PRE, PRU and SRGH and have taken digital images of specimens and have made A3 prints of full sheets from these herbaria, which we then use as herbarium specimens. We have undertaken many field trips throughout the distribution range of *Xerophyta sensu lato* in South Africa and have made observations and taken many detailed photographs in the field. Live material has been taken to Whyte Thorne Botanical Garden near Mbombela in Mpumalanga, where it is documented and cultivated and this has facilitated observations of plants grown and flowerd under similar environmental conditions. Two hundred and eighty-six live plant accessions, of which 60 are duplicated in additional pots, represent 17 described and many as yet undescribed South African species. Fourteen extra-limital live collections represent 3 extra-limital species. Voucher numbers preceded by W represent the reference number for the labels on pots and the entry in the Whyte Thorne register. Photographs of fresh flowers, including dissections, were taken using an OM System TG-7 camera with Focus Stacking by K. Balkwill, except Fig. 9A, which was taken with the same model of camera by D. Oosthuizen.

3. Results

Differences between *Talbotia* and species of *Xerophyta* are described in the order in which structures appear in descriptions in taxonomic treatments and then aspects of physiology and caryology are considered (Table 1).

- More clearcut differences include that in *Talbotia*, adventitious roots penetrate the base of the soft leaf sheath, whereas in *Xerophyta*, they grow between the stem and the hardened leaf sheaths, that is within the leaf sheaths (Coetzee, 1973).
- In *Talbotia*, groups of bract-like foliage leaves with triangular blades alternate with groups of normal foliage leaves along the same shoot (Fig. 1 and Dyer, 1976) rendering the leaves dimorphic, whereas in *Xerophyta* the leaves on a single shoot are all similar (monomorphic), although in the shrubby species the leaves of the apical shoot may be broader and longer than those on lateral shoots.
- In *Talbotia*, the leaf sheaths are split to the base (Fig. 2A), whereas in *Xerophyta*, the leaf sheaths are united to well above the base (Fig. 2B).
- The leaf sheaths of *Talbotia* are not hardened, whereas those of *Xerophyta* are thickened, presumably with sclerenchyma (Fig. 2B).
- In *Talbotia*, the leaf epidermis is thin, whereas it is thicker in species of *Xerophyta* (Coetzee, 1974).
- There is no abscission line between sheath and lamina in *Talbotia* (Mello-Silva et al., 2011), but there is an abscission zone at the point where the leaf blade meets the leaf sheath in *Xerophyta*.
- Consequently, the leaf blades are persistent in *Talbotia* and deciduous in *Xerophyta* (Smith and Ayensu, 1974).
- Leaves of all species of *Xerophyta* have longitudinal furrows at least on the bottom surface (Coetzee, 1974), but the leaves of *Talbotia* lack longitudinal furrows on either surface (Coetzee, 1974).
- In *Talbotia*, the area of mesophyll between the vascular bundles is at least 4 times the width of the vascular bundles (Fig. 3A), contrasted with the area of mesophyll between the vascular bundles being up to twice the width of the vascular bundles (Fig. 3B) in all species of *Xerophyta*.
- The xylem in leaves of *Talbotia* comprises mainly tracheids, whereas the xylem in the leaves of *Xerophyta* comprises mainly vessels (Ayensu, 1969).
- No conduction tissues are present in the marginal bundles of *Talbotia*, but conduction tissues occur in the marginal bundles of *Xerophyta* (Mello-Silva et al., 2011).
- The foliar stomata are hypoamphistomatic in *Talbotia*, but amphistomatic in *Xerophyta* (Mello-Silva et al., 2011).
- There are strands of fibres present near the abaxial surface of the leaves in *Xerophyta* (Mello-Silva et al., 2011), but not in *Talbotia* (Mello-Silva et al., 2011).
- In *Talbotia*, the filaments are adnate to roof of ovary (Fig. 4A), but they are adnate to the tepals in *Xerophyta* (Fig. 4B).
- All filaments are slenderly cylindric in *Talbotia*, whereas the filaments broad and flattened in *Xerophyta* (Smith and Ayensu, 1974).
- The anthers are monomorphic in *Talbotia* (Fig. 5A), but usually dimorphic in *Xerophyta* (Fig. 5B). An exception is *X. connata* McPherson & van der Werff, where they are monomorphic (McPherson et al., 1997).
- All six anthers are extrorse in *Talbotia* (Fig. 5A), whereas three are usually latrorse and three introrse in *Xerophyta* (Fig. 5B). Although the anthers are said to be introrse in *X. connata* (McPherson et al., 1997), that is unexpected as it is then difficult to understand how the pollen is deposited onto pollinators.
- The filaments are basally attached to the connective of the anthers (basifixed) in *Talbotia*, but attached to the dorsal side of the connective (i.e. dorsifixed or subdorsifixed) in *Xerophyta* (Coetzee, 1973).
- In *Talbotia*, the anthers are slightly arcuate (Fig. 5A), and straight in *Xerophyta* (Fig. 5B).

Table 1
Summary of differences between *Talbotia* and *Xerophyta*.

		Talbotia	*Xerophyta*
Clearcut differences			
1	Adventitious roots	penetrate base of leaf sheath (Coetzee 1973)	produced between stem and base of leaf sheaths (Coetzee 1973)
2	Leaves mono- or dimorphic	dimorphic (Fig. 1& Dyer, 1976)	monomorphic
3	Leaf sheaths split	split to the base (Fig. 2A)	united to well above the base (Fig. 2B)
4	Leaf sheath texture	not hardened (Fig. 2A)	thickened with sclerenchyma (Fig. 2B)
5	Leaf cuticle	thin (Coetzee 1974)	thicker (Coetzee 1974)
6	Abscission zone in leaf	absent (Mello-Silva et al., 2011)	present between sheath and lamina (Mello-Silva et al., 2011)
7	Leaf blade persistence	persistent (Smith and Ayensu 1974)	deciduous (Smith and Ayensu 1974)
8	Leaf furrows	longitudinal furrows absent (Coetzee 1974)	longitudinal furrows present (Coetzee 1974)
9	Mesophyll between vascular bundles	At least 4 times the width of vascular bundles (Fig. 3A)	Up to twice the width of vascular bundles (Fig. 3B)
10	Composition of leaf xylem	mainly tracheids (Ayensu 1969)	mainly vessels (Ayensu 1969)
11	Conduction tissue in marginal bundle	absent (Mello-Silva et al., 2011)	present (Mello-Silva et al., 2011)
12	Distribution of stomata in leaves	hypoamphistomatic (Mello-Silva et al., 2011)	amphistomatic (Mello-Silva et al., 2011)
13	Abaxial strands of fibres in leaves	absent (Mello-Silva et al., 2011)	present (Mello-Silva et al., 2011)
14	Filament attachment	adnate to roof of ovary (Figs. 4A & B)	adnate to tepals (Fig. 4C)
15	Filament shape	slenderly cylindric (Smith and Ayensu 1974)	broad and flattened (Smith and Ayensu 1974)
16	Anthers mono- or dimorphic	monomorphic (Fig. 5A)	usually dimorphic (Fig. 5B) (monomorphic in *X. connata*)
17	Direction in which anthers shed pollen	extrorse (Fig. 5A)	usually latrorse and introrse (Fig. 5B) and said to be introrse in *X. connata*
18	Attachment of anthers	filaments basally attached to connective (basifixed) (Coetzee 1973)	filaments attached on dorsal side of connective (dorsifixed or subdorsifixed) (Coetzee 1973)
19	Orientation of anthers	slightly arcuate (Fig. 5A)	straight (Fig. 5B)
20	Dehiscence of microsporangia	each pair by a separated slit (Mello-Silva et al., 2011)	each pair by a single common slit (Mello-Silva et al., 2011)
21	Process on connective	no apical appendage (Fig. 6A)	usually with apical appendage (Fig. 6C)
22	Shape of base and tip of thecae	both rounded (Figs. 6A & B)	both usually pointed (Figs. 6C & D)
23	Operculum on pollen	operculate (Furness and Rudall 2006)	not operculate (Maguire 1969)
24	Pollen surface	finely reticulate (Furness and Rudall 2006)	coarsely reticulate (Maguire 1969)
25	Length of style	longer than stamens (Fig. 7A & Mello-Silva et al., 2011)	shorter than stamens (Fig. 7B) i.e. stigma at same level or below anthers (Mello-Silva et al., 2011) or very rarely longer than stamens (*X. connata*)
26	Relative length of stigma	stigma much shorter than style (Mello-Silva et al., 2011); up to a tenth of the style length (Fig. 7A)	style similar length or much shorter than stigma (Mello-Silva et al., 2011); up to 5 times as long as stigma (Fig. 7B)
27	Relative length of stigma	up to twice as long as broad (Fig. 8A & B)	more than twice as long as broad (Fig. 8C & D)
28	Shape of roof of ovary	broad, flat and with a rim, possibly a rudimentary corona (Fig. 9A)	narrow, with three depressions between three style buttresses (Fig. 9B)
29	Microhooks on seed surface	present (Ayensu 1973)	absent in sampled species (Ayensu 1973)
30	Shape of seeds	rod-shaped (Coetzee 1973)	conical (Coetzee 1973)
31	Chlorophyll in dehydrated leaves	present (Hallam and Gaff 1978)	absent (Hallam and Gaff 1978)
32	Resurrection strategy	homoiochlorophyllous (Marks et al., 2021)	poikilochlorophyllous (Farrant et al., 2015)
Less clearcut differences			
33	Habitat	usually shady, sometimes on cliffs	usually exposed
34	Moisture regime	habitat usually moist	habitat usually dry, rarely moist (e.g. *X. longicaulis*)
35	Shape of pedicels in cross-section	triangular (Mello-Silva et al., 2011)	circular or circular near base and triangular with rounded angles near the apex (e.g. *X. retinervis*) (Mello-Silva et al., 2011 & *pers. obs.*)
36	Shape of ovary in cross-section	3-angled to 3-winged	with rounded angles
37	Indumentum on ovary	glabrous or with minute sessile glands	usually glandular or with excrescences, very rarely glabrous or with minute sessile glands (e.g. *X. burrowsiorum* and *X. goetzii*)
38	Colour of roof of ovary	green (Fig. 9A)	often white, lilac or purple, as inside of tepals, sometimes green.

- Each pair of microsporangia dehisces by a separated slit in *Talbotia*, but by a single common slit in *Xerophyta* (Mello-Silva et al., 2011).
- The connective is not produced into a process (apical appendage) in *Talbotia* (Fig. 6A), whereas the connective usually has a terminal process (apical appendage) in *Xerophyta* (Fig. 6C).
- The tips and bases of the anther thecae are rounded in *Talbotia* (Fig. A & B), but they are usually pointed in *Xerophyta* (Fig. 6C & D).
- The pollen of *Talbotia* is operculate (Furness and Rudall, 2006) and not so in *Xerophyta* (Maguire 1969).
- The pollen grains are finely reticulate in *Talbotia* (Furness and Rudall, 2006), but coarsely so in *Xerophyta* (Maguire, 1969).
- In *Talbotia*, the style is longer than anthers (Fig. 7A) so that the stigma is held above stamens, whereas in *Xerophyta* the styles are shorter than the anthers (Fig. 7B) so that the stigma is at the same level or below the stamens (Mello-Silva et al., 2011), except in *X. connata* where the style is longer than the stamens (McPherson et al., 1997).
- The style is much longer than the stigma in *Talbotia* [ten times or more (pers. obs)], but more or less of the same length or much shorter than stigma in *Xerophyta* (Mello-Silva et al., 2011) [up to six times as long (pers. obs)].
- In *Talbotia*, the stigma is up to twice as long as broad (Fig. 8A), but it is more than twice as long as broad in *Xerophyta* (Fig. 8B).
- In *Talbotia*, the top of the ovary is green, flattened and has a slight rim (possibly a rudimentary corona, Fig. 9A), whereas in *Xerophyta,* the roof of the ovary is narrow, often the same colour as the inner surface of the tepals and includes three pits between the bases of three style buttresses (Fig. 9B).

Fig. 1. Alternating bract-like (b) and normal (a) foliage leaves of *Talbotia*. Voucher: W8772, *McMurtry 16299a* (HSMC).

- The seeds of *Talbotia* have microhooks on the surface, but microhooks are absent from the seeds of all sampled species in *Xerophyta* (Ayensu, 1973).
- In *Talbotia, the* seeds are rod-shaped, whereas they are conical in *Xerophyta* (Coetzee, 1973).
- Dehydrated leaves of *Talbotia* contain chlorophyll, whereas there is no chlorophyll in the dehydrated leaves of *Xerophyta* (Hallam and Gaff, 1978). Thus *Talbotia* is said to be homoiochlorophyllous (Marks et al., 2021), but *Xerophyta* is poikilochlorophyllous (Farrant et al., 2015).

Less clearcut differences include the habitat of *Talbotia* usually being shady, but some subpopulations occur on south-facing cliffs, whereas the habitat of *Xerophyta* is usually exposed and sunny. *Talbotia* occurs in moist places and *Xerophyta* in drier places, but *X. longicaulis* grows in damp areas very close to some *Talbotia* subpopulations. The pedicels of *Talbotia* are triangular in cross-section, whereas those of *Xerophyta* are circular in cross-section or circular near base and triangular with rounded angles near the apex (e.g. *X. retinervis*) (Mello-Silva et al., 2011 and pers. obs.). In *Talbotia* the ovary is 3-angled to 3-winged, but in *Xerophyta* the ovary has rounded angles. In*Talbotia*, the ovary is glabrous or has minute sessile glands, but in *Xerophyta* the ovary is almost always glandular or with excrescences although very rarely glabrous or with minute sessile glands (e.g. *X. burrowsiorum* and *X. goetzii*).

4. Discussion

Coetzee (1973) credits Perrier (1946) as the first author to clearly circumscribe genera in the Velloziaceae, specifically *Xerophyta, Barbacenia* and *Vellozia*. Perrier recognised *Xerophyta* as a separate genus, which at the time had three species in Madagascar (Perrier, 1946) and defined the genus on the basis of the flowers having a short perianth tube on which six stamens are inserted, the stamens being linked by a membrane, the anthers having auricles but not linear appendages, the style being undivided and at least its upper half being covered with stigmatoid bands. All the shrubby species of Velloziaceae in South Africa possess these character states, but the herbaceous species lack the membrane linking the stamens. *Talbotia elegans* has none of the characters that Perrier (1946) used to define *Xerophyta* (Coetzee, 1973). Our investigations have found 32 character states by which *T. elegans* is clearly differentiated from all the South African species of *Xerophyta* and a further six character states where there is a small amount of overlap between *T. elegans* and some species of *Xerophyta* (Table 1). These character states are diverse in their nature and include vegetative morphology, floral morphology, micromorphology, leaf anatomy, and physiology (Table 1).

Some of the arguments that mitigate against recognising *Talbotia* as a separate genus include that the chromosome numbers are the same (i.e. n = 24) in the two genera (Goldblatt and Poston, 1988). Although we have noticed considerable variation in a number of characters (see Taxonomic Notes below) and there appears to be geographical disjunction in *Talbotia* (Fig. 10), we cannot find patterns in the variation that allow us to recognise more than one taxon. There is reluctance to recognise monotypic groups (Backlund and Bremer, 1998) and so the recognition of *Talbotia* is controversial from that perspective. Behnke (2000) states that genetic distances between *Talbotia* and *Xerophyta* are very small (Table 3 in Behnke, 2000) and sees this as a further reason to combine the genera, but these distances are based on a single gene sequence. *Xerophyta connata* from Madagascar (McPherson et al., 1997) is intermediate between *Talbotia* and *Xerophyta* in several features and this does detract from the motivation for recognising *Talbotia* as a separate genus. The desiccation tolerance strategy of *X. connata* is still unknown and it shares important floral characters with *Talbotia* like possession of a corona, filaments being attached to the roof of the ovary rather than being epipetalous, anthers appressed to the style, a style longer than the anthers, a short stigma and a naked ovary, but the leaf anatomy is consistent with *Xerophyta.* When a comprehensive molecular-based phylogeny is produced with sufficient African and Madagascan species, it may be found that *X. connata* may be best treated as another separate genus.

The first phylogenetic analyses of Velloziaceae based on molecular markers were those of Salatino (1999) and Salatino et al. (2001), which used *trnL-F* sequences from the chloroplast. Although the latter publication included *Talbotia*, the two species of *Xerophyta* that were included are Brazilian species that have subsequently been transferred to *Vellozia*, so this analysis is not informative in terms of the relationship between *Talbotia* and *Xerophyta.* The next molecular analysis was that of Behnke et al. (2000) and was also based on *trnL-F* sequences from the chloroplast. In the neighbour joining analysis (Fig. 13 of Behnke et al., 2000), the branch that included *Talbotia* as well as species of *Xerophyta, Barbaceniopsis, Pleurostima* Raf., *Barbacenia, Vellozia* and *Nanuza* L.B.Sm. & Ayensu is unresolved and so it is unwise to draw phylogenetic conclusions from this analysis. In the analysis using maximum parsimony (Fig. 14 of Behnke et al., 2000), *Talbotia* is sister to two shrubby African species of *Xerophyta* and that clade is in turn sister to herbaceous African species. Although this mitigates for the inclusion of *Talbotia* in *Xerophyta*, the phylogeny is

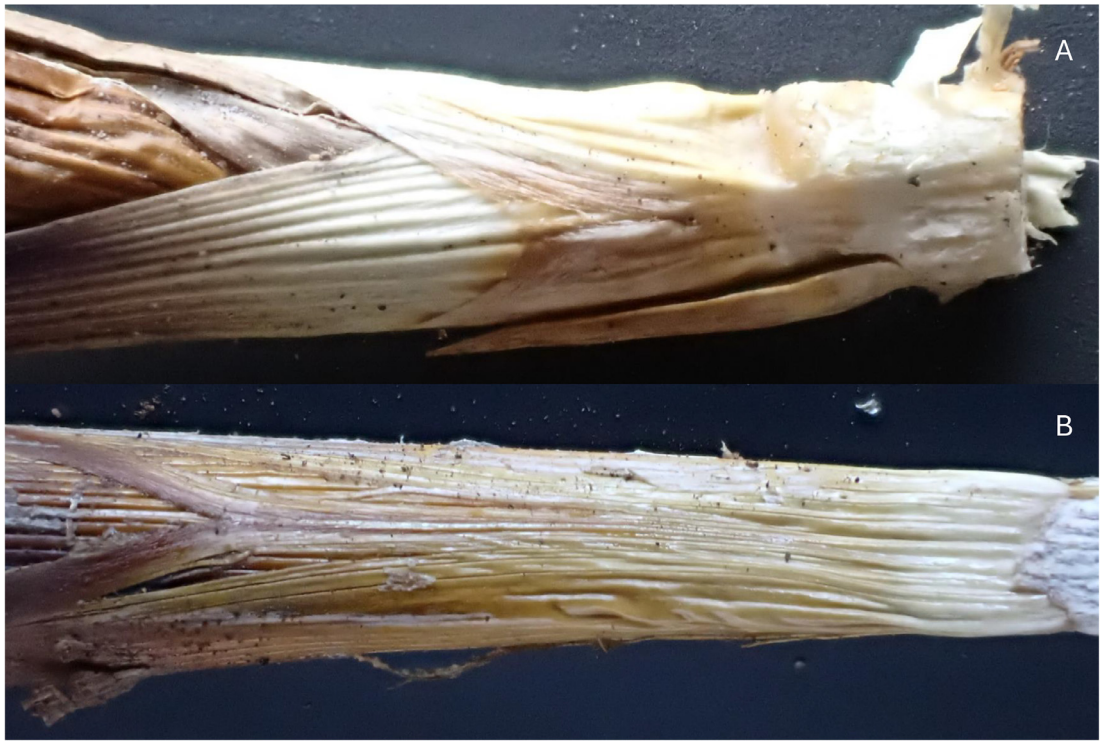

Fig. 2. Leaf bases of A. *Talbotia* split to the base and B. *Xerophyta* sp. near *X. rehmannii* Behnke united for the length of the sheath and hardened. Vouchers: A. Cultivated, from Hebronberg, Mpumalanga. B. W10797, *Fourie 2198* (HSMC).

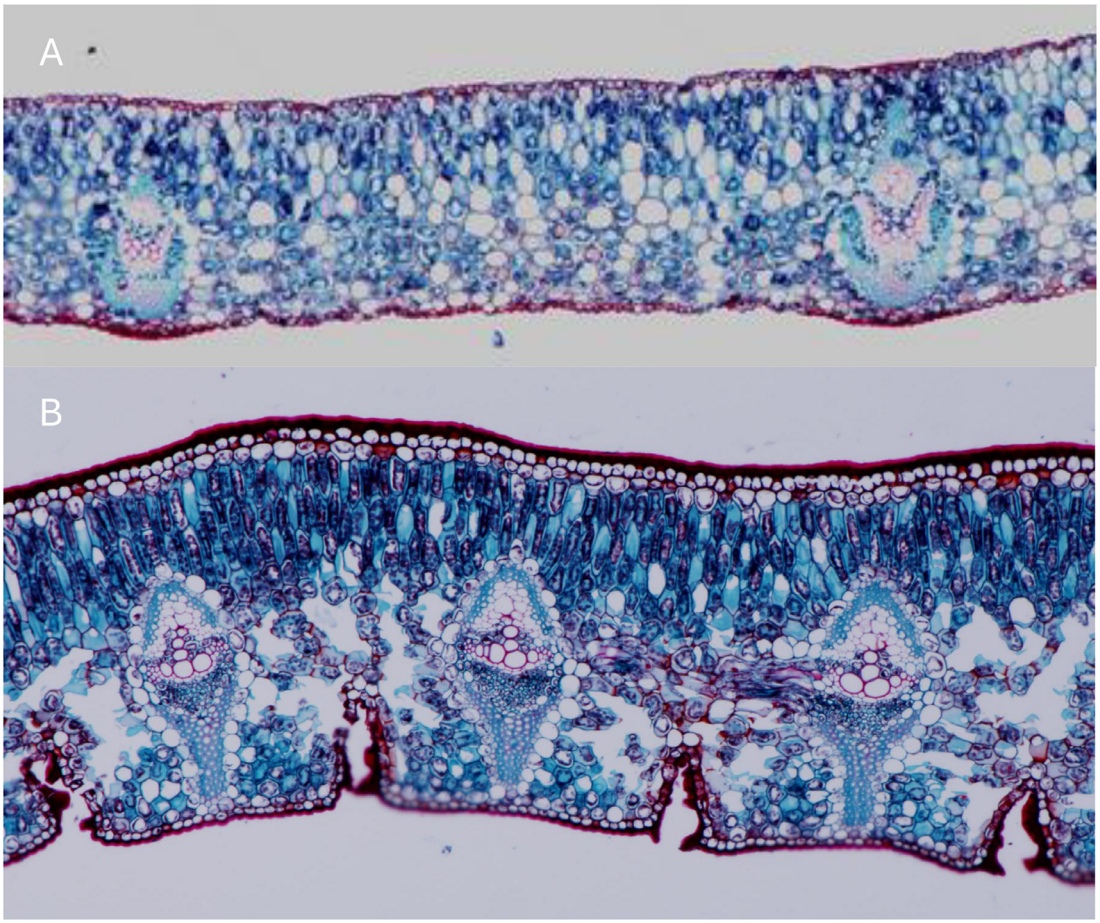

Fig. 3. Cross-sections of leaves of A. *Talbotia*, with mesophyll between veins at least 4 times the width of the veins, and B. *Xerophyta rehmannii*, with mesophyll between veins less than twice the width of the veins. Vouchers: A. W4350 †, from Waterval Boven. B. W4338, *McMurtry 10,236* (HSMC).

Fig. 4. Filaments of A & B. *Talbotia*, adnate to the roof of the ovary, and C. *Xerophyta rehmannii*, adnate to the tepals. Vouchers: A & B. W8772, *McMurtry 16299a* (HSMC). C. W10343, *McMurtry 18,117* (HSMC).

Fig. 5. Anthers of A. *Talbotia*, extrorse and slightly arcuate, and B. *Xerophyta rehmannii*, latrorse and introrse and straight. Vouchers: A. W8772, *McMurtry 16299a* (HSMC). B. W10031, *Balkwill 14,642* (J).

Fig. 6. Anther of A & B. *Talbotia*, without an appendage and rounded at base, and C & D. *Xerophyta rehmannii*, with an apical appendage and pointed at the base. Vouchers: A & B. W7912, *McMurtry 18,580* (HSMC). C. W10343, *McMurtry 18,117* (HSMC). D. W8347, *McMurtry 15,062* (HSMC).

based on only a single gene sequence and there are many floral and anatomical differences between the shrubby and herbaceous African species, which might suggest that they are polyphyletic, so that the inclusion of *Talbotia* does not necessarily justify subsuming it into *Xerophyta*. In 2011, Mello-Silva et al. published phylogenies based separately on morphological data, five gene sequences and a single tree as well as a strict consensus tree based on data combined. In the morphological analysis (Fig. 1A in Mello-Silva et al., 2011), *Talbotia* is sister to *Xerophyta, Barbaceniopsis, Burlemarxia* N.L.Menezes & Semir, *Barbacenia, Aylthonia* N.L.Menezes, *Pleurostima, Nanuza* and *Vellozia*, with *Acanthochlamys* being the only member of the Velloziaceae that is basal to *Talbotia*. In the molecular analyses (Fig. 1B in Mello-Silva et al., 2011), *Talbotia* is sister to the five *Xerophyta* species and the *Talbotia-Xerophyta* clade is sister to all other members of Velloziaceae

Fig. 7. Longitudinal section of flowers of A. *Talbotia*, with style longer than anthers, and B. *Xerophyta rehmannii*, with style shorter than anthers. Vouchers: A. W9935, *McMurtry 17,663* (HSMC). B. W10343, *McMurtry 18,117* (HSMC).

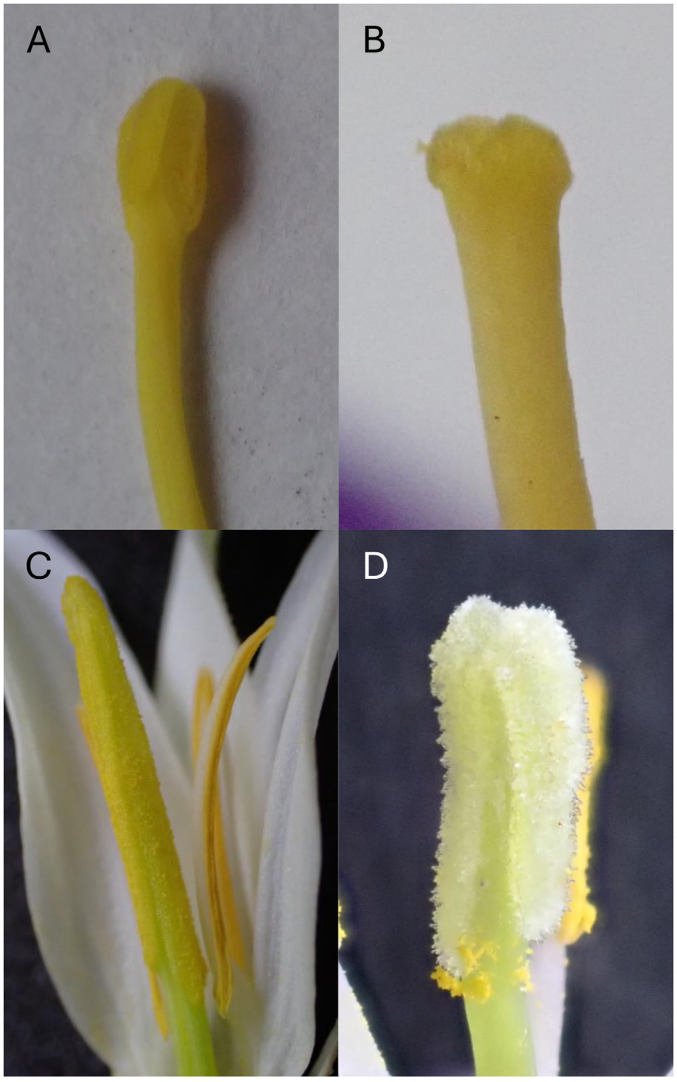

Fig. 8. Stigma of A & B. *Talbotia*, up to twice as long as broad, C. *Xerophyta rehmannii*, much longer than broad, and D. *Xerophyta humilis*, more than twice as long as broad. Vouchers: A. W8772, *McMurtry 16299a* (HSMC). B. W9935, *McMurtry 17,663* (HSMC). C. W8347, *McMurtry 18,578* (HSMC). D. W9897, *Balkwill & Froneman 14,573* (J).

except *Acanthochlamys* and in this clade, the shrubby species are in one subclade and the herbaceous species in another. This same pattern is repeated in both combined analyses (Figs. 2& 3 in Mello-Silva et al., 2011). A further molecular analysis based on the complete *rbcL* gene and including 45 African and Madagascan species is provided by Behnke et al. (2013). In both the maximum likelihood and Bayesian analyses (Figs. 2& 3 in Behnke et al., 2013), *Talbotia* is nested within *Xerophyta* but there is lack of resolution in these phylograms and so caution must be exercised when interpreting them. A majority rule consensus tree based on anatomical characters is also provided (Fig. 1 in Behnke et al., 2013) — it is fully resolved and *Talbotia* is nested within *Xerophyta*, but multistate characters were coded as ordered without any justification that they represent evolutionary sequences, so this result must be treated with caution.

Backlund and Bremer (1998) provide guidance on whether or not to recognise monotypic taxa: the primary principle is monophyly and secondary principles include maximising stability, maximising phylogenetic information or minimising redundancy, maximising support for monophyly and maximising ease of identification. In their justification for subsuming *Talbotia* and other genera in the Vellozioceae, Mello-Silva et al. (2011) state that whether or not *Talbotia* is recognised does not affect monophyly and continue to state that "for reasons of maximizing phylogenetic information and ease of identification" *Talbotia* should be subsumed into *Xerophyta* and *Nanuzia* into *Vellozia*. Following the principles of Backlund and Bremer (1998), we assert that: i. recognising *Talbotia* as a separate genus does not violate the principle of monophyly, ii. the recognition of *Talbotia* has been controversial since its description in 1868 and neither recognising it or not doing so would better promote stability, iii. subsuming *Talbotia* into *Xerophyta* will obscure the 32 clearcut and six less clearcut differences between the genera, and iv. that many of the characters that separate *Talbotia* from *Xerophyta* are readily observable and easily understood so that the separation of *Talbotia* makes its identification easier. We are thus convinced that *Talbotia* should be recognized as a separate genus.

The study of Mello-Silva et al. (2011) includes 5 gene sequences, but only six African and Madagascan taxa of Velloziaceae, whereas that of Behnke et al. (2013) includes 45 African and Madagascan taxa, but only one gene sequence. A study that includes sufficient gene sequences and many African and Madagascan taxa will be helpful in assessing relationships between the taxa as well as in assessing whether additional genera should be recognised to reflect those relationships.

5. Conclusion

Recognition of *Talbotia* as a separate genus has been controversial for over 150 years. We have consolidated information available in the literature and added much information that we have gained in the field and from examination of many cultivated specimens. We have compiled a list of 32 characters from the literature and our observations that clearly differentiate *Talbotia* from *Xerophyta* and another six characters where there is a small amount of overlap between *Talbotia* and a minority of species of *Xerophyta.* Although there are molecular-based phylogenies available for African Velloziaceae, they either include few species (six in the case of Mello-Siva et al., 2011) or are based on only a single gene region (Behnke et al., 2013). In the first case, *Talbotia* is sister to all the included taxa of *Xerophyta* and in the second case, *Talbotia* appears to be related to the shrubby species of *Xerophyta* rather than the herbaceous ones. This may indicate that further investigation based on more species and more gene regions may reveal that additional genera should be recognised to appropriately reflect the relationships between Old World Velloziaceae. In the meanwhile, we are resurrecting *Talbotia* as this would not render *Xerophyta* poly- or paraphyletic and so that the large number of differences between *Talbotia* and *Xerophyta* are not obscured by its combination with *Xerophyta*.

6. Taxonomy

Talbotia Balf., Trans. Bot. Soc., Edinb. 9: 190. (1868a); Smith & Ayensu, Kew Bull. 29: 183 (1974); Dyer, Gen. Southern Afr. Flow. Pl. 2: 959 (1976); Archer, Strelitzia 10: 737 (2000). Type species: *Talbotia elegans* Balf.

Talbotia elegans Balf., Trans. Bot. Soc., Edinb. 9: 192. (1868b); Smith & Ayensu, Kew Bull. 29: 183 (1974); Dyer, Gen. Southern Afr. Flow. Pl. 2: 959 (1976); Archer, Strelitzia 10: 737 (2000). *Xerophyta elegans* (Balf.) Baker, J. Bot. 13: 234 (1875); Durand & Schinz, Consp. Fl. Afr. 5: 271 (1895); Koekemoer et al., Strelitzia 46: 188–191 (2023). *Vellozia elegans* (Balf.) Oliv. ex Hook.f., Bot. Mag. 95, t. 5803 (1869); Baker, Fl. Cap. 6, 245 (1896); Greves, J. Bot. 59: 284 (1921); Ayensu, Kew Bull. 23: 328 (1969); Hilliard & Burtt, Notes Roy. Bot. Gard. Edinb. 31: 2 (1971); Ross, Fl. Natal 132 (1972). *Vellozia talbotii* Balf. (as *V. talboti*), Trans. Bot. Soc. Edinb. 9: 190 (1868a); Trauseld, Wild Flow. Drakensb. 33. (1969). – Type: South Africa, KwaZulu-Natal, *Fox Talbot s.n.* (K000523776, holotype, seen on Global Plants).

Xerophyta minuta Baker, J. Bot. 13: 234 (1875); Durand & Schinz, Consp. Fl. Afr. 5: 271, as *X. miniata* (1895). *Vellozia minuta* Baker in

Fig. 9. Top of the ovary of A. *Talbotia*, flat and with rudimentary corona, and B. *Xerophyta humilis* (Baker) T.Durand & Schinz, with pits between style buttresses and no corona. Photographer of A: D. Oosthuizen. Vouchers: A. *Balkwill* et al. *15,010* (J). B. W10582, *McMurtry 18,581* (HSMC).

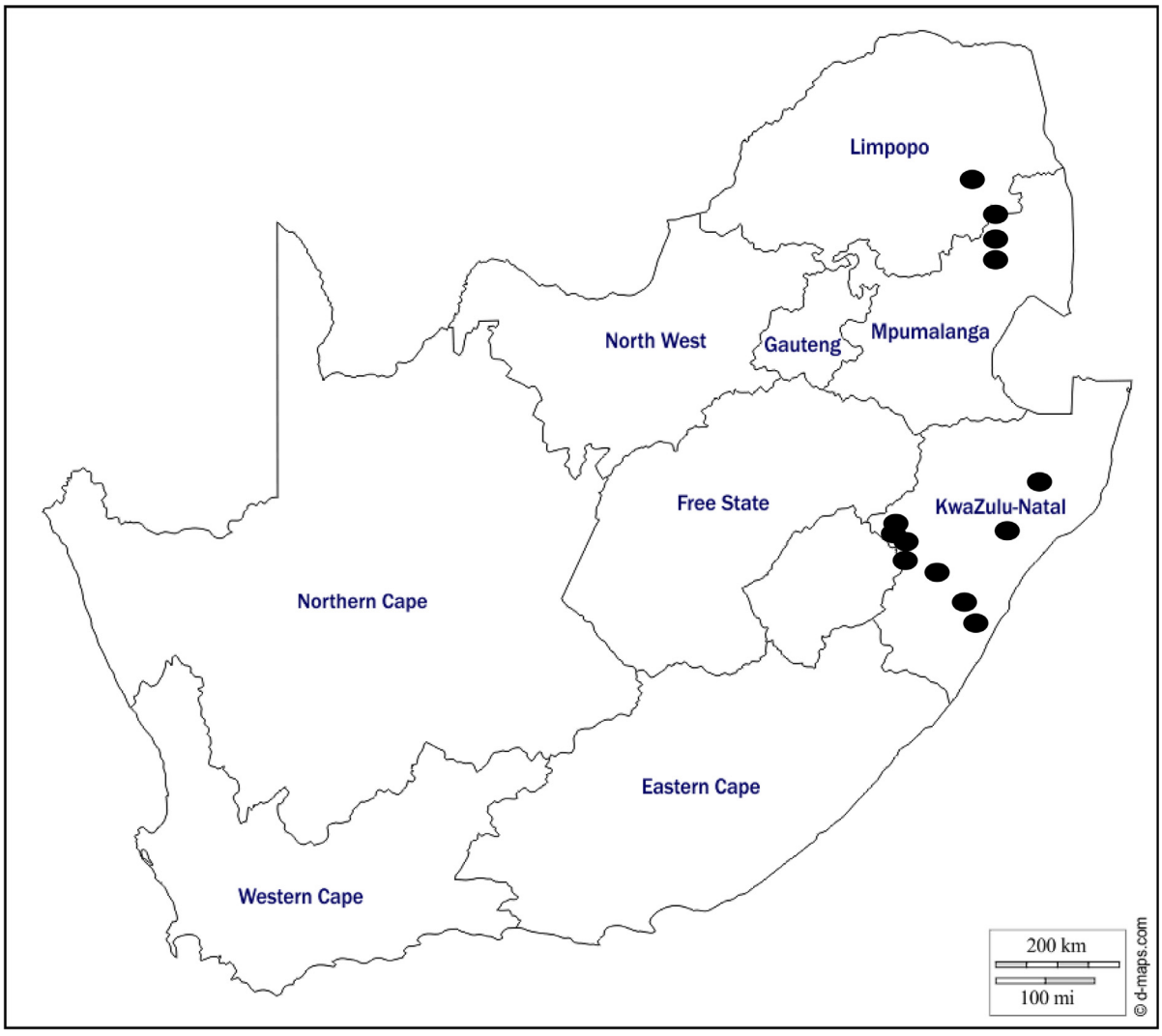

Fig. 10. Distribution map of *Talbotia*, based on herbarium specimens.

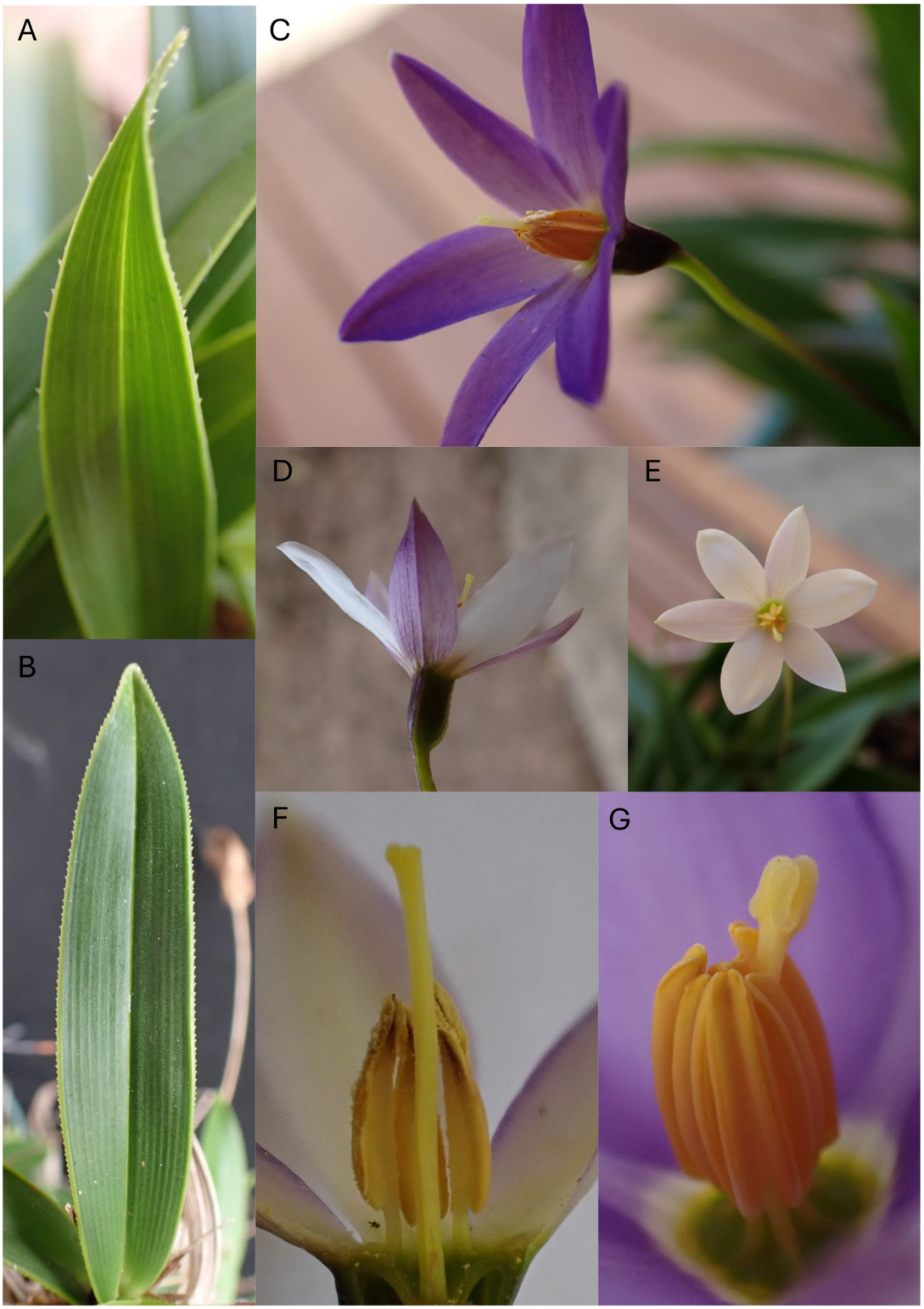

Fig. 11. Variation in *Talbotia elegans*: teeth on leaf margin A. mainly near apex, B. over full length; tepal colour C. purple, D. mauve, E. white; and length of style F. much longer than stamens, G. very slightly longer than stamens. Vouchers: A & E. W10120, *Fourie 2308* (HSMC). B & G. W7912, *McMurtry 18,580* (HSMC). C. W9935, *McMurtry 17,663* (HSMC). D. W10213, *Balkwill* et al. *14,787* (J). F. W9991, *McMurtry 17,762* (HSMC).

Bull. Herb. Boiss. Ser. 2, 3: 667 (1903). *Vellozia elegans* var. *minor* Baker, Fl. Cap. 6: 246 (1896); Greves, J. Bot. 59: 284 (1921). — Type: South Africa, KwaZulu-Natal, *Gueinzius s.n.* (K000523779, holotype, seen on Global Plants).

Multistemmed, lithophytic, occasionally epiphytic or terrestrial, homoiochlorophyllus perennial; stems branched, bifurcating, often decumbent 150–300 (–680) mm long x 5–7 mm in diameter, covered in dry, slowly disintegrating leaves. *Leaves* numerous, in growth spurts of 3–5 foliage leaves occasionally more, interspersed with sheathing bract-like leaves, tristichous, persistent for more than a year, without abscission zone, mesophytic, glabrous, patent, mid to dark green, becoming purple on dessication; base clasping, c. 3–

5 mm long, white; blade linear-lanceolate, shortly attenuate, 70–150 (–200) mm long x 10–16 mm wide, distinctly keeled below, shallowly grooved above, keel and margins serrulate, sometimes along entire length, with teeth pointing toward apex; margins hyaline; veins longitudinal, parallel, visible, 7–8 on each side of mid-vein bract-like leaves narrow, c. 20 mm long; old dried leaves conduplicate, often falcate, greyish. *Inflorescence* (1–) 3 (–5) pedicels from truncate, bracteate peduncle, pedicels 1–3 bracteate, eglandular, triangular in cross-section, 5–150 mm long x 1 mm diameter. *Bracts* papyraceous, green aging brown, serrulate apically. *Flowers* bisexual, regular, to 25 mm diameter when open, broadly campanulate to saucer-shaped when fully open, closing partially at night; tepals petaloid, free, persistent, 3 + 3, whorls subsimilar, broadly elliptic, outer 8–14 mm long x 4–7 mm wide and inner 1–2 mm smaller, eglandular, white, bluish-mauve, or purple, turning green post-pollination with veins becoming markedly ribbed externally and finally tan-brown and slightly withered with prominent veins once capsule matures. *Stamens* 3 + 3, held adjacent to style; filaments cylindrical, white, 0.5–0.75 (–1) mm long; anthers convergent, basifixed, introrse with 2 lateral longitudinal slits, slightly arcuate, 4–5 mm long, yellow; pollen golden-yellow. *Ovary* inferior, 3-locular with axile placentation, trigonous, winged, 5–7 mm x 2–4 mm, green to purple, eglandular; ovules many per locule. *Style* 5–7 mm long. *Stigma* knob-like to very shortly cylindric, 3-lobed, 0.5–1 (–1.5) mm long. *Capsule* erect, 5–10 mm x 4–7 mm, greenish purple drying brown, glabrous or with very small, sparse sessile glands, crowned with dried remains of perianth, basally loculicidal, opening with 3 slits. *Seeds* rod-shaped; testa with scattered white dots and micro-hooks.

Diagnostic characters: Talbotia elegans can be distinguished from all other South African members of the Velloziaceae by its ovary and pedicels being triangular in cross-section, its style that is longer than (or almost as long as) the stamens, its capitate stigma, its basifixed anthers that are slightly arcuate and its persistent leaves that are interspersed with bract-like leaves along the stem. *Talbotia elegans* has a glabrous ovary (sometimes with minute sessile glands) that distinguishes it from most species of *Xerophyta* that have stalked glands or bristly excrescences on the ovary (*X. burrowsiorum* D.McMurtry & S.Burns and some as yet to be described species are rare exceptions).

Taxonomic notes: Talbotia elegans shows considerable variation in a number of features. The largest specimen is *Doidge sub PRE 38,458* (PRE), from Mount Tintwa in KwaZulu-Natal and the smallest is *Kluge 1786* (PRE) from MacMac in Mpumalanga and they compare as follows: stem girth 9.3 mm vs 3.3 mm; leaf size 280 × 15 mm vs 58 × 3.5 mm; tepal 30 × 5.6 mm vs 8 × 3.5 mm and ovary 11.2 × 5.6 mm vs 3.3 × 2.6 mm. Other features that vary include the dentition on the margins of the leaves (Figs. 11A & B), tepal colour from purple to white (Figs. 11C – E) and which may also vary with the age of the flower, becoming green in the fruit, the length of the style (Figs. 11F & G), the length of the stigma (Figs. 8A & B) and the indumentum on the ovary (Figs. 12A & B). We have tried to find patterns in these and other features that would mitigate for the recognition of more than one species, but have been unsuccessful in doing so.

Etymology: The genus *Talbotia* was named by John Hutton Balfour (1808–1884), a botanist at Edinburgh Botanic Garden, for William Henry Fox Talbot (1800–1877). The specific epithet means elegant and refers to the aesthetic nature of the plant and its flowers.

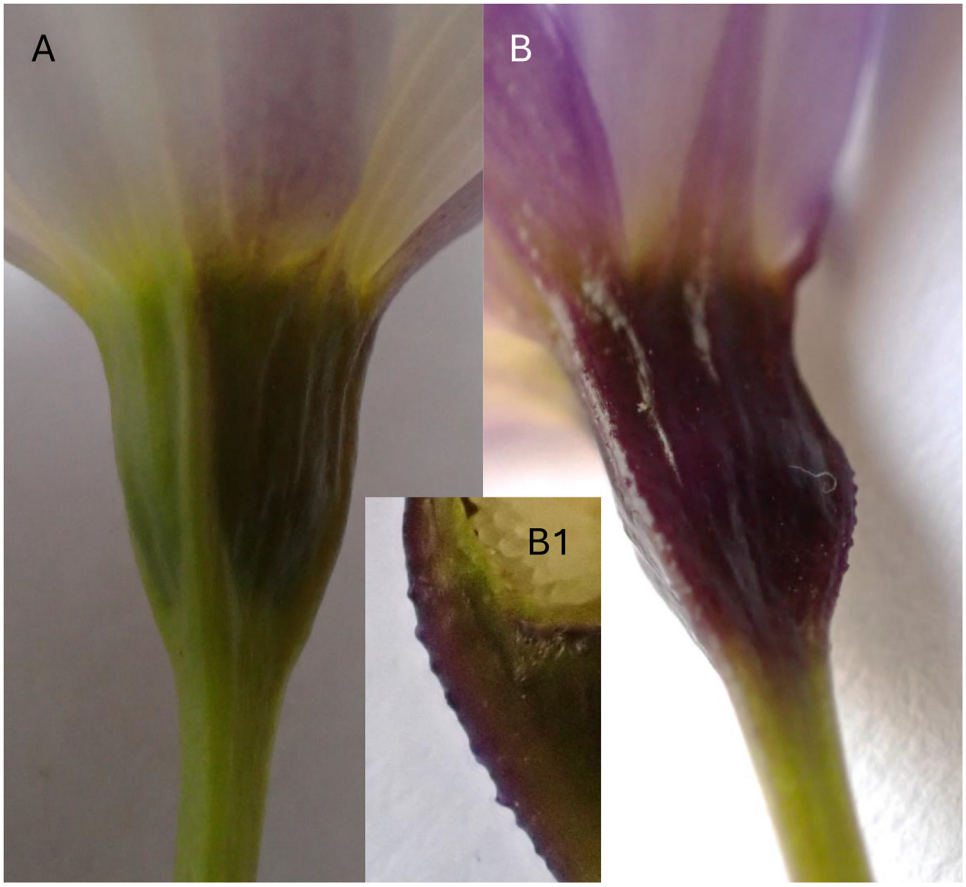

Fig. 12. Variation in indumentum on ovary of *Talbotia elegans*: A. ovary glabrous, B. ovary with minute sessile glands. Vouchers: A. W8772, *McMurtry 16299a* (HSMC). B. W9935, *McMurtry 17,663* (HSMC).

Distribution and ecology: The species is endemic to South Africa, occurring in the provinces of Limpopo, Mpumalanga and KwaZulu-Natal (Fig. 10). It occurs on mesic cliffs and boulders along river and stream valleys, usually shaded by forest trees, at elevations between 1500 and 2000 m. Occasionally, it occurs on the shaded south-faces of exposed cliffs.

Phenology: Flowering occurs year-round, with a peak from December to February.

Conservation Notes: Talbotia elegans is a widespread species that can be quite common in the areas where it occurs. Many localities are in nature reserves and are thus formally protected. The habitat types in which the species occurs are not suitable for agriculture or urbanisation, which reduces threat outside of reserves. Although invasion by alien trees endangers many species, the shade tolerance of *T. elegans* makes it less vulnerable to this threat. The ability of *T. elegans* to thrive in unusually wet periods, but survive extensive dry periods through desiccation will provide some resilience to climate change. Thus, we agree with the Threat Status of Least Concern that was assigned by von Staden (2014).

Additional Specimens seen

LIMPOPO — 2430 (Pilgrim's Rest): Legalameetse Nature Reserve, In stream about 1 km south-south-west of Makhutsi Camp, 922 m (–AB), 27 Nov 2022, *McMurtry 17,762* (HSMC). MPUMALANGA —2430 (Pilgrim's Rest): Mariepskop Forestry Station, Klaserie Falls (–DB), 30 May 1975, *van Jaarsveld 520* (NBG); Klaserie Waterfall, 1350 m (–DB), 16 Nov 1987, *Venter 12,634* (PRE); Mariepskop, about 1700 m (–DB), 10 Apr 1958, *van der Schijff 4363* (PRE); Mariepskop, forest near Klaserie Waterfall, about 1500 m (–DB), 16 Jan 1959, *van der Schijff 4505* (PRE); Mariepskop, Klaseriedrif (–DB), 9 Dec 1963, *van der Schijff 6303* (PRE); Mariepskop, about 1500 m (–DB), 10 Jul 1935, *Taylor 579* (PRE); Mariepskop (–DB), *Fitz Simmons & van Dam sub Transvaal Museum 26,261* (PRE); Mariepskop, about 1400 m (–DB), 11 Jan 1964, *Bos 1063* (PRE); Mariepskop (–DB), 15 Jan 1959, *Wedermann & Oberdieck 1858* (PRE); Graskop, Farm Erasmushoop 457 KT, north of Treur River (–DB), 21 May 2011, McMurtry 14,020 (HSMC); Welgevonden Forestry Station, along forest stream (–DB), 29 Jun 2003, *McMurtry 11,304* (HSMC); Welgevonden Plantations, Welgevonden Falls (top of Sand River), 960 m (–DB), 26 Apr 2008, *Burrows & Burrows 10,394* (J); Graskop (–DB), 17 Dec 1956, *Prosser 2055* (PRE); Graskop district, Farm Wilgerboom, below Fairyland, 1077 m (–DD), 15 Sep 2013, *Turpin* et al. *731* (J). 2530 (Mashishing [Lydenburg]): Mac Nature Reserve, gallery forest (–BB), 7 Mar 1979, *Kluge 1786* (PRE); North of Graskop, on the farm Erasmushoop 457 KT, 1519 m (–DB), 21 Feb 2025, *Balkwill* et al. *15,010* (J); Mac Pools, just inside forest edge (–BB), 17 May 2023, *Balkwill* et al. *14,787* (HSMC, J). KWAZULU-NATAL — 2731 (Louwsburg): Near Ngome police station, Ngome Forest (–CD), *Fourie 2308* (HSMC). 2829 (Harrismith): Klip River, Strydhoek, Tintwa Mountains (–CB), 9 Jan 1920, *Doidge sub PRE 38,458* (PRE); Cathedral Peak (–CC), Feb 1971, *Admiraal & Drijfhout sub PRE 57,460* (PRE); Weenen County, Draycott Hill, about 1300 m (–DC), 19 Apr 1945, *Acocks 11,442* (PRE); Estcourt district, at foot of Cathedral Peak, Little Berg, Loskop (–DC), 7 Feb 1932, *Galpin sub PRE 11,318* (PRE). 2831 (Nkandla): Nkandhla, Entumeni, about 1850 m (–CA), 3 March 1935, *Gerstner 592* (PRE). 2929 (Underberg): Giants Castle, Njesuthi (–AB), 7 Aug 2012, *McMurtry 14,579* (HSMC); Cathkin Peak, moist forests on Little Berg, about 1400 to 1550 m (–AB), *Galpin sub PRE 11,852* (PRE); Cathkin Peak Hostel, in kloof near waterfall, about 1550 m (–AB), 27 Dec 1936, *West 3* (PRE); Between Champagne Castle Hostel and Cathkin Peak, about 1500 – 1850 m (–AB), 9 Jan 1947, *Story 1745* (PRE); Champagne Castle, about 1660 m (–AB), Jan 1942, *Bayer 4751* (NU); Loskop area, Cathkin Park, on way to Grotto (–AB), 2 Dec 1946, *Howlett & Howlett 23* (PRE); Estcourt district, Giants Castle Game Reserve, Lower Injasuti (–AB), *Trauseld 339* (PRE). 2930 (Pietermaritzburg): Howick, Shelter Falls (–AC), 21 Jan 1928, *Blenkinson sub Moss 16,143* (J); Lions River district, Farm Ehlatini, Karkloof (–AC), 17 Feb 1967, *Moll 3480* (PRE); Pietermaritzburg district, Table Mountain, about 900 m (–DA), 13 Jan 1949, *Killick 243* (PRE); Krantzkloof (–DD), Nov 1921, *Haygarth sub Transvaal Museum 22,739* (PRE).

Declaration of competing interest

The authors declare that they have no conflict of interest.

CRediT authorship contribution statement

K. Balkwill: Writing – review & editing, Writing – original draft, Resources, Methodology, Investigation, Conceptualization. **D. McMurtry:** Writing – review & editing, Writing – original draft, Resources, Investigation, Conceptualization. **S. Burns:** Writing – review & editing, Writing – original draft, Resources, Investigation, Data curation, Conceptualization.

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