



# A revision of African Velloziaceae based on leaf anatomy characters and *rbcL* nucleotide sequences

H.-DIETMAR BEHNKE<sup>1\*</sup>, ERIC HUMMEL<sup>1†</sup>, STEFAN HILLMER<sup>1</sup>, HEDWIG SAUER-GÜRTH<sup>2</sup>, JAVIER GONZALEZ<sup>2</sup> and MICHAEL WINK<sup>2</sup>

<sup>1</sup>*Pflanzliche Zellbiologie, Centre for Organismal Studies, Ruprecht-Karls-Universität Heidelberg, Im Neuenheimer Feld 230, 69120 Heidelberg, Germany*

<sup>2</sup>*Institut für Pharmazie und Molekulare Biotechnologie, Ruprecht-Karls-Universität Heidelberg, Im Neuenheimer Feld 364, 69120 Heidelberg, Germany*

Received 16 February 2012; revised 29 May 2012; accepted for publication 11 December 2012

The African Velloziaceae is revised mainly using evidence from leaf anatomy and *rbcL* sequence data. *Xerophyta* is the only African genus in the family. Forty-five species are recognized in Africa, 11 of which are described as new and distinct on the basis of morphological, anatomical and/or genetic characters; one species is known to occur on the Arabian Peninsula, and 25 species are presently identified in Madagascar. The leaf anatomy of all *Xerophyta* spp. and the *rbcL* sequences of 44 *Xerophyta* spp. are examined. Four distinct types of leaf anatomy are (re-)defined and, with additional anatomical and morphological features, are used to produce a key to African *Xerophyta*. For each species, the morphology, leaf anatomy, synonymy, distribution, extensive literature sources and specimens used are given. The combined anatomical/genetic evidence allowed the description of the new species and the definition of *X. simulans* as singular in African Velloziaceae with leaf anatomical similarities to the South American *Vellozia plicata* and to Cyclanthaceae. The analysis of the *rbcL* sequence data supports the Chinese genus *Acanthochlamys* as sister to Velloziaceae s.s., the monophyly of the Old World genus *Xerophyta* and its separation from the New World taxa. In *Xerophyta*, a well-supported clade includes all species with radial isolateral mesophyll (*Barbacenia*-type leaf anatomy). The other leaf types do not separate into uniform clades. A Madagascar clade houses species with *Vellozia*- and *Xerophyta*-type leaf anatomy and also contains the pan-African *X. humilis*. © 2013 The Linnean Society of London, *Botanical Journal of the Linnean Society*, 2013, **172**, 22–94.

ADDITIONAL KEYWORDS: *Acanthochlamys* – *Barbacenia* – *Barbaceniopsis* – Cyclanthaceae – Madagascar – morphology – *Vellozia* – *Xerophyta*.

## INTRODUCTION

Velloziaceae is an ancient monocotyledon family with a disjunct distribution, the taxa being mainly confined to South America, Africa and Madagascar. The vast majority of the approximately 300 described species occur in tropical South America; only about 70 species are found in the Old World.

Members of Velloziaceae are adapted to xeric conditions and to specific substrates, such as quartzite or

granite. This combination favours endemism, e.g. on inselberg locations, and accounts for the comparatively many new taxa recently described. As many members of Velloziaceae grow in localities that are difficult to reach and therefore botanically unexploited, it is expected that yet more species will be described in the future.

Each known species is confined to one geographical region and this relative isolation is supported by DNA data, which have been used to estimate the divergence time between South American and African, and African and Madagascan species (Behnke *et al.*, 2000). Therefore, in the absence of a fossil record, it is difficult to ascertain the location of the centre of origin of the family. Ayensu (1973a) used leaf ana-

\*Corresponding author: E-mail: dbehnke@ix.urz.uni-heidelberg.de

†Present address: Geschäftsbereich Biosciences, Carl Zeiss Microscopy GmbH, Kistlerhofer Str. 75, 81379 München, Germany

tomical data, among other characters, to propose that Velloziaceae originated in Madagascar, whereas Menezes (1980) suggested that the wealth of floral characters and the fact that the centre of diversity is in the central Brazilian mountains support South America as the centre of origin. The molecular data exclude Madagascar as the origin of evolution in the family, but cannot rule in favour of Africa or South America (Behnke *et al.*, 2000).

Established in 1841 by Endlicher, the family has received rather divergent treatments, concerning ordinal affinities and infrafamilial classification (see Mello-Silva, 1991; Behnke *et al.*, 2000). With regard to the taxonomy of Old World species, Smith & Ayensu (1974, 1976) recognized two genera, *Xerophyta* Juss. and the monotypic *Talbotia* Balf., whereas Menezes (1980) included all Old World species in *Xerophyta*. Furthermore, Smith & Ayensu (1976) restricted *Xerophyta* to Africa and Madagascar and placed it with *Talbotia* and the South American genera *Barbaceniopsis* L.B.Sm. and *Barbacenia* Vand. into subfamily Barbacenioidae. In the classification of Menezes (1980), the genus *Xerophyta* is, with *Vellozia* (*sensu* Menezes), part of subfamily Vellozioidae and includes not only the African *Talbotia*, but also the South American *Barbaceniopsis* and all those species of *Vellozia* (*sensu* Smith & Ayensu) with six stamens. A subsequent cladistic analysis (Menezes, Mello-Silva & Mayo, 1994), using floral and vegetative characters of virtually all genera and their sections, revealed *Talbotia* as an independent clade, sister to a clade composed of *Xerophyta* and *Barbaceniopsis*, and supported in part *Vellozia* in the circumscription of Smith & Ayensu (1976), but did not suggest a strong subfamilial concept. Consequently, in *The Families and Genera of Vascular Plants*, Kubitzki (1998) separated the monotypic *Talbotia* from *Xerophyta* and restricted the latter to African and Madagascan species, and provided a key to the eight genera recognized, but refrained from dividing the family into subfamilies.

The first molecular analysis of the family, based on *trnL-F* sequences, supported both the separation of *Talbotia* as a monotypic genus and the merging of the South American species of *Xerophyta* (*sensu* Menezes, 1980) with *Vellozia* (Salatino, 1999; Salatino *et al.*, 2001). The study included sequences of *Acanthochlamys* P.C.Kao, *Pandanus* R.Br. and *Cyclanthus* Poit., but *Barbaceniopsis* and Old World *Xerophyta* spp. were included. Therefore, when *rbcL* sequence data for Velloziaceae from the three geographical regions and from seven of the eight genera recognized in Kubitzki (1998) were analysed together with samples from all families that were sometimes discussed as close allies, the result was different: all African species, including *Talbotia*, were found to cluster in the same clade, with

the consequence that *Talbotia* was merged with *Xerophyta*, as the reinstated *Xerophyta elegans* (Balf.) Baker (Behnke *et al.*, 2000). In their molecular and morphological study of Velloziaceae, Mello-Silva *et al.* (2011) reduced the ten described genera to only five with a distinct vicariant pattern of distribution and also transferred *Talbotia* to *Xerophyta*.

The earliest account of the Old World Velloziaceae was the synopsis by Baker (1875a) of African *Xerophyta* spp., with ten from the African continent and two from Madagascar. Towards the end of the 19th century, Durand & Schinz (1895) listed 24 *Xerophyta* spp. in their *Conspectus Florae Africae*. When Greves (1921) undertook the first critical revision of the Old World Velloziaceae, the number of species published had increased to 34. The only other treatment of the entire group was the *Classification of Old World Velloziaceae* by Smith & Ayensu (1974), in which many previously published taxa were downgraded to varietal status or reduced to synonymy, with the result that their key contained only 29 species. At about the same time and since then, Velloziaceae has been treated in several regional studies and/or cladistic analyses (e.g. Coetzee, van der Schijff & Steyn, 1973; Coetzee, 1974; Smith & Ayensu, 1975; Lye & Edwards, 1997; Mello-Silva, 2000, 2005; Gonçalves, 2009), but never again were the Old World species revised *in toto*.

In continuation of our anatomical and molecular study of the family (Behnke *et al.*, 2000; Behnke, Kramer & Hummel, 2002), and taking into account herbarium collections not covered in Smith & Ayensu (1974) and new species described and new material collected, we started this revision of African Velloziaceae.

## MATERIAL AND METHODS

### TAXON SAMPLING

The species included in the present study were selected to cover as many taxa as available of Velloziaceae. Many samples were taken from fresh leaves, either collected in the field or from plants cultivated in botanic gardens, but the great majority came from herbarium sheets from which small leaf pieces were removed with permission. For *rbcL* sequencing, some samples were obtained from dried herbarium material which was revived for 2–5 days in a moist chamber.

### LEAF ANATOMY

For all anatomical studies, transverse sections were taken from the mid-portions of leaf blades. Fresh leaves or herbarium samples were soaked in 5% ammonium hydroxide and, after about 48 h, were

transferred to 70% ethanol and subsequently hand-sectioned. Permanent slides were prepared by mounting the sections in Kaiser's glycerol gelatine and bordering the cover glasses with Eukitt. All sections were viewed with a Zeiss Standard or a Zeiss IM 35 inverted microscope equipped with Zeiss Plan objectives. Photographs were taken with an Olympus camera attached to a Zeiss IM 35 or a Canon Powershop G2 camera (including Canon image software) attached to a Zeiss Axiovert 200 inverted microscope.

#### ANALYSIS OF ANATOMICAL CHARACTERS

The leaf anatomical characters used are listed in Table 1 and the matrix is presented in Table 2. One outgroup (*Acanthochlamys*) was used to establish polarities for Velloziaceae and to root trees. Multi-state characters (22) were treated as ordered and with equal weights. Heuristic searches were performed with the tree bisection–reconnection (TBR) method, stepwise addition with 100 random replicates, MAXTREES of 5000 trees and 'MulTrees' option in effect. These analyses were conducted with PAUP (Swofford, 2002) and the results were summarized by a majority-rule consensus tree.

#### DNA SEQUENCING AND DATA ANALYSIS

DNA isolation and amplification and PCR purification were performed as described previously (Behnke *et al.*, 2000). Sequencing was carried out on an ABI 3730 automated capillary sequencer (Applied Biosystems) with the ABI Prism Big Dye Terminator Cycle Sequencing Ready Reaction Kit 3.1 by STARSEQ GmbH (Mainz, Germany).

The sequences were aligned in WinEdit version 5.3. Molecular phylogenetic trees were constructed using maximum likelihood (ML) in RAxML version 7.0.4 (Stamatakis, 2006), maximum parsimony (MP) in PAUP\* version 4.0b10a (Swofford, 2002) and Bayesian inference (BI) in MrBayes version 3.1.2 (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003). MP heuristic searches were performed with closest stepwise sequence additions, TBR branch swapping and 'MulTrees' option. ML trees were reconstructed using the rapid hill-climbing algorithm implemented in RAxML version 7.0.4 with the random starting tree option and GTR-GAMMA model. In the MP and ML analyses, the robustness of each node was assessed by 1000 bootstrap replicates. For BI analyses, two independent runs of 8 000 000 generations each were performed with four Markov chains. The evolutionary model selected for BI analysis was GTR + G + I. Trees were sampled every 500 generations and the first 4000 samples were discarded as 'burn-in'. *Acorus calamus* L. was used as the outgroup.

**Table 1.** Character analysis and coding

1	Leaf lamina: deciduous (0); persistent (1)
2	Leaf sheath: not distinct (0); scale-like (1); early split into fibres (2)
3	Attachment of leaf sheath: appressed (0); tip exerted/revolute (1)
4	Stomatal distribution in leaf lamina: hypostomatic (0); amphistomatic (1)
5	Leaf trichomes or emergences: absent or only at midrib and margins (0); present on lower and/or upper surface (1)
6	Arrangement of mesophyll: dorsiventral (0); isolateral (1)
7	Hypodermis: present (0); absent (1)
8	Aquiferous parenchyma between bundles: absent (0); present (1)
9	Adaxially extended bundle sheath and/or hypodermis: absent (0); present (1)
10	Furrows in leaf blade: absent (0); on abaxial surface only (1); on both surfaces (2)
11	Leaf epidermis: not elaborate (0); papillate (1); (partly) sclerified (2)
12	Trichomes in furrows: absent or inconspicuous (0); coronulate, finger-like or other (1)
13	Leaf glands: absent (0); deeply sunken (0); patellar or other (1)
14	Crystals in leaf blade: absent (0); present (1)
15	Transcurrent lateral bundles: absent (0); basic <i>Barbacenia</i> type (1); <i>Capillaris</i> group type (2)
16	Nontranscurrent lateral bundles: absent (0); <i>Vellozia</i> type (1); <i>Xerophyta</i> type (2)
17	Minor fibrovascular bundles in mesophyll: absent (0); present (1)
18	Spaces between lateral bundles: narrow (0); double (1); triple or more (2)
19	Sclerenchyma bands underneath lateral bundles: absent (0); present (1)
20	Sclerenchyma strands between lateral bundles: absent (0); present (1)
21	Midvein abaxial girder: crescentiform (0); bulbiform or other (1)
22	Sclerenchyma at marginal bundle: rounded (0); triangular (1)

GenBank accession numbers and vouchers are listed in Table 3.

## RESULTS

### ANATOMY AND MORPHOLOGY

#### *Leaf morphology*

Leaves of African Velloziaceae are xerophytic and have resurrection abilities, the only exception being *X. elegans* with mesophytic leaves. In some species, leaf blades are persistent but, in the majority of

Table 2. Morphological matrix

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	
<i>Xerophyta</i> species																							
<i>acuminata</i>	1	0	0	1	0	0	0	0	0	1	1	1	1	1	0	1	0	2	0	0	1	0	0
<b><i>adendorffii</i></b>	1	0	0	0	0	0	0	0	0	1	1	1	1	1	0	1	0	1	0	0	0	0	0
<i>andringitrensis</i>	0	2	1	1	0	0	0	0	1	1	2	1	1	0	0	1	0	1	1	1	0	0	0
<i>aymoninii</i>	0	0	0	0	0	0	0	0	1	1	2	1	0	0	0	1	0	1	1	1	0	0	0
<i>arabica</i>	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	1	0	0	0	0	0
<i>argentea</i>	0	1	0	1	1	1	1	1	0	2	0	0	0	0	1	0	0	0	1	0	0	0	1
<i>brevifolia</i>	0	1	1	0	0	0	0	0	1	2	2	0	0	0	0	1	0	0	1	0	1	0	0
<i>calvicola</i>	0	2	1	1	0	0	0	0	0	1	2	0	0	1	0	1	0	1	1	1	1	0	0
<i>capillaris</i>	0	1	0	1	0	1	1	0	1	2	0	0	0	0	2	0	0	1	0	1	0	0	0
<b><i>cauliflora</i></b>	0	1	1	1	0	0	0	0	0	1	2	1	1	0	0	1	0	1	1	1	0	0	0
<i>concolor</i>	0	0	0	1	0	1	1	1	0	2	0	0	0	0	1	0	0	1	1	0	0	0	1
<i>connata</i>	0	2	0	0	1	1	1	0	0	1	0	0	0	0	1	0	0	1	1	0	0	0	0
<i>croatii</i>	0	2	0	1	1	0	0	0	0	1	2	0	0	0	0	2	0	1	1	1	1	0	0
<i>dasytiroides</i>	0	2	1	0	0	0	0	0	1	2	2	1	0	0	0	1	0	1	1	1	0	0	0
<i>decaryi</i>	0	0	0	1	0	0	0	0	1	2	2	1	0	0	0	0	1	1	1	1	0	0	0
<i>demeesmaeckeriana</i>	0	2	0	1	1	1	1	1	0	2	0	1	0	0	1	0	0	0	1	0	0	0	1
<i>eglandulosa</i>	0	1	0	1	1	0	0	0	0	2	1	1	0	0	0	1	1	0	1	1	0	0	0
<i>elegans</i>	1	1	0	1	0	0	0	0	0	0	0	-	0	0	0	1	0	2	0	0	0	0	0
<i>equisetoides</i>	0	2	0	1	0	1	1	1	0	2	0	0	0	0	1	0	0	1	1	0	0	0	1
<i>eylesii</i>	0	2	0	1	1	1	1	1	0	2	1	0	0	0	0	0	0	0	1	0	0	0	1
<b><i>glabra</i></b>	0	2	0	1	0	1	1	1	1	1	0	0	0	0	2	0	0	1	1	1	0	0	0
<b><i>glutinosa</i></b>	0	2	0	1	0	1	1	1	1	2	0	0	1	0	2	0	0	1	1	1	0	0	1
<i>goetzei</i>	0	2	0	1	1	1	1	1	0	2	0	0	0	0	0	1	0	2	1	0	0	0	0
<i>hereroensis</i>	1	0	0	0	0	0	0	0	0	1	1	0	1	0	0	1	0	1	0	0	1	0	0
<b><i>hirtiflora</i></b>	0	2	0	1	1	1	1	1	0	2	0	0	0	0	1	0	0	0	1	1	0	0	1
<i>humbertii</i>	0	0	0	1	0	0	0	0	0	2	2	1	0	0	0	2	1	1	1	1	1	?	?
<i>humilis</i>	0	0	0	1	0	0	1	0	0	1	0	0	0	0	0	1	0	2	0	0	1	0	0
<i>isaloensis</i>	0	0	0	1	0	0	0	0	1	2	2	1	0	0	0	1	0	0	1	1	0	0	0
<i>jouyiana</i>	0	0	0	1	1	0	0	0	1	2	2	0	0	1	0	1	0	0	1	1	0	0	0
<b><i>junodii</i></b>	1	2	0	0	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0	0
<i>kirku</i>	0	1	0	1	0	1	1	1	0	2	0	0	1	0	1	0	0	1	1	0	0	0	1
<i>labatii</i>	0	1	0	1	0	0	0	0	1	2	2	1	0	0	0	1	1	0	1	1	0	0	0
<i>leandrii</i>	0	2	0	1	0	0	0	0	1	2	2	1	0	0	0	1	0	0	1	1	0	0	0
<i>lewisiae</i>	0	0	0	1	0	0	0	0	1	2	2	1	0	0	0	1	0	1	1	1	0	0	0
<i>longicaulis</i>	0	1	0	0	0	1	0	0	0	1	1	0	1	0	1	1	0	0	0	0	0	0	0
<i>monroi</i>	0	2	1	1	1	1	1	1	0	2	1	0	0	0	1	0	0	0	0	0	0	0	0
<b><i>naegelebachii</i></b>	0	2	1	1	1	1	1	1	0	2	0	0	0	0	1	0	0	1	1	1	0	0	0



Table 2. Continued

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>nandrasanae</i>	0	2	1	1	1	0	0	0	1	2	2	1	0	0	0	1	0	1	1	1	0	0
<i>nutans</i>	0	2	0	1	1	1	1	1	0	2	0	0	0	0	1	0	0	1	1	1	0	1
<i>parviflora</i>	0	?	?	1	0	0	0	0	1	0	0	0	0	0	0	1	0	2	1	1	1	0
<b><i>pauciramosa</i></b>	0	1	1	1	0	1	1	1	0	2	0	0	0	0	1	0	0	0	1	0	0	1
<i>pectinata</i>	0	2	0	1	1	0	0	0	1	2	2	2	0	0	0	1	0	1	1	1	0	0
<i>pinifolia</i>	0	2	0	1	0	0	0	0	0	2	2	0	0	0	0	2	0	1	1	1	1	0
<b><i>pseudopinifolia</i></b>	0	2	1	1	1	1	1	1	0	2	0	0	0	0	1	0	0	1	1	0	0	0
<b><i>purpurascens</i></b>	0	2	0	1	1	1	1	1	0	2	1	0	0	0	1	0	0	0	1	0	0	1
<b><i>rehmannii</i></b>	1	1	0	1	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	0	0
<i>retinerivis</i>	0	2	0	1	0	1	1	1	0	2	1	0	0	0	1	0	0	0	1	0	0	1
<i>rippsteinii</i>	0	2	0	1	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0
<i>rosea</i>	1	0	0	1	1	0	0	0	0	1	0	1	1	1	0	1	0	1	0	0	0	0
<i>scabrada</i>	0	2	0	1	1	1	1	1	0	2	0	0	0	0	1	0	0	0	1	0	0	1
<i>schatzii</i>	0	2	1	1	1	0	0	0	0	2	2	0	0	0	0	2	0	1	1	0	1	0
<i>schlechteri</i>	1	1	0	1	0	0	0	0	0	1	0	1	1	1	0	1	0	0	0	0	1	0
<i>schmizleinia</i>	0	2	0	1	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	1	0	0
<i>seinei</i>	1	1	0	1	0	0	0	0	0	1	0	0	1	1	0	1	0	1	0	0	0	0
<i>sessiliflora</i>	0	0	0	1	0	0	0	0	0	2	0	0	0	0	0	2	0	0	1	0	1	0
<i>setosa</i>	0	1	0	1	1	0	0	0	0	2	2	0	0	0	0	2	0	0	1	0	1	0
<i>simulans</i>	0	2	0	1	1	0	0	1	0	0	0	-	0	0	0	0	0	-	0	1	1	0
<i>spekei</i>	0	1	0	1	1	1	1	1	0	2	0	0	0	0	1	0	0	1	1	0	0	0
<i>splendens</i>	0	1	0	0	0	1	1	1	0	2	1	0	0	0	1	0	0	0	1	0	0	0
<i>squarrosa</i>	0	2	1	1	1	1	1	1	1	2	0	0	0	0	2	0	0	2	1	0	1	1
<i>suaveolens</i>	0	2	1	1	1	1	1	1	0	2	1	0	0	0	1	0	0	2	1	1	1	1
<i>tabulare</i>	0	0	0	1	0	0	0	0	1	2	2	1	0	0	0	1	0	0	1	1	0	0
<b><i>tanzaniana</i></b>	0	2	0	1	0	1	1	1	1	2	0	0	1	0	2	0	0	1	1	1	0	1
<i>trichophylla</i>	0	2	0	1	1	1	1	1	0	2	0	0	0	0	1	0	0	1	1	0	0	0
<i>tulearensis</i>	0	1	1	1	1	0	0	0	1	2	2	1	0	0	0	1	0	1	1	1	0	0
<b><i>vallispongolana</i></b>	0	2	0	1	1	1	1	1	0	2	0	0	0	0	1	0	0	1	1	1	0	1
<i>velutina</i>	0	1	0	1	1	1	1	1	1	2	0	0	0	0	2	0	0	2	1	1	0	1
<i>villosa</i>	0	2	0	1	1	1	1	1	0	2	0	0	0	0	1	0	0	1	1	0	0	1
<i>viscosa</i>	0	2	1	0	0	1	0	0	0	1	0	1	1	0	1	1	0	1	0	0	0	0
<i>wentzeliana</i>	0	1	0	1	1	1	1	1	0	2	0	0	0	0	1	0	0	2	1	0	0	1
<b><i>zimbabwensis</i></b>	1	0	0	1	0	0	0	0	0	0	0	-	1	0	0	1	0	1	0	0	1	0
<i>Acanthochlamys</i> <i>bracteata</i>	1	?	?	2	0	1	1	0	0	0	0	0	0	0	0	0	0	?	?	?	?	?

?, missing data; -, inapplicable.

**Table 3.** List of plant samples with voucher information, Heidelberg Institute (IPMB) and GenBank numbers

Taxon	Origin of material/literature citation	IPMB No	GenBank No
<i>Acanthochlamys bracteata</i> P.C.Kao	Chase <i>et al.</i> , 1995	–	HQ845619
<i>Acorus calamus</i> L.	Duvall <i>et al.</i> , 1993	–	M91625
<i>Barbacenia grisea</i> L.B.Sm.	cult. Bot. Garden Bonn 9647 (M)	P382	JX032705
<i>Barbacenia purpurea</i> Hook.	cult. Bot. Garden Sao Paulo (M)	P6391	JX032706
<i>Barbacenia stenophylla</i> Goethard & Henrard	cult. Bot. Garden Bonn 12786 (M)	P380	JX032704
<i>Barbaceniopsis boliviensis</i> (Baker) L.B.Sm.	cult. Bot. Garden Bonn 9978 (M)	P384	JX032712
<i>Barbaceniopsis vargasiana</i> (L.B.Sm.) L.B.Sm.	cult. Bot. Garden Heidelberg (M)	P419	JX032713
<i>Carludovica palmata</i> Ruiz & Pav.	cult. Bot. Garden Bonn (M)	P411	JX042582
<i>Cyclanthus bipartitus</i> Poit.	cult. Bot. Garden Heidelberg (M)	P412	JX032702
<i>Dicranopygium polycephalum</i> Harling	cult. Bot. Garden Heidelberg (M)	P408	JX042580
<i>Evodianthus funifera</i> (Poit.) Lindm.	cult. Bot. Garden Heidelberg (M)	P410	JX042581
<i>Freycinetia luzonensis</i> C.Presl.	cult. Bot. Garden Heidelberg (M)	P394	JX032701
<i>Harperocallis flava</i> McDaniel	A. F. Johnson s.n. (M)	P4680	JX032759
<i>Lophiola americana</i> (Pursh) Wood	L. Chafin s.n. (M)	P423	JX032758
<i>Nartheccium ossifragum</i> (L.) Huds.	cult. Bot. Garden Heidelberg (M)	P420	JX032757
<i>Pleea tenuifolia</i> Michx.	B.A. Sorrie s.n. (M)	P421	JX032760
<i>Stichoneuron caudatum</i> Ridl.	cult. Bot. Garden Heidelberg (M)	P409	JX032703
<i>Tofieldia pusilla</i> (Michx.) Pers.	E. & K. Kramer s.n., cult. Bot. Garden Heidelberg (M)	P424	JX032761
<i>Vellozia andina</i> Ibisch, Vasquez & Nowicki	Ibisch & Nowicki 98.133 (M)	P405	JX032709
<i>Vellozia declinans</i> Goethard & Henrard	cult. Bot. Garden Sao Paulo (M)	P374	JX032708
<i>Vellozia plicata</i> Mart.	cult. Bot. Garden Bonn 5655 (M)	P403	JX032711
<i>Vellozia tubiflora</i> (A.Rich.) H.B.K.	cult. Bot. Garden Bonn 4412 (M)	P402	JX032707
<i>Vellozia variegata</i> Goethard & Henrard	cult. Bot. Garden Bonn 9651 (M)	P4688	JX032710
<b><i>Xerophyta adendorffii</i></b> Behnke	Adendorff 1 (M)	P6279	JX032726
<b><i>Xerophyta cauliflora</i></b> Behnke	Eb. Fischer & Höller s.n., cult. Bot. Garden Bonn 15808 (M)	P6568	JX049995
<i>Xerophyta croatii</i> Phillipson & Lowry	Dorr 4190 (MO)	P6668	JX032743
<i>Xerophyta dasyliroides</i> Baker	cult. Bot. Garden Bonn 9649 (M)	P5455	JX032755
<i>Xerophyta decaryi</i> Phillipson & Lowry	Phillipson 5700 (MO)	P6669	JX032750
<i>Xerophyta demesmaekeriana</i> P. A. Duvign. & Dewit	J. E. & S. M. Burrows 6456 (BNRH)	P8621	JX032737
<i>Xerophyta eglandulosa</i> H.Perrier	Guillaumet 3612bis (P)	P6666	JX032754
<i>Xerophyta elegans</i> (Balf.) Baker	cult. Bot. Garden Heidelberg 101408 (M)	P395	JX032717
<i>Xerophyta equisetoides</i> Baker	Seine 1496, cult. Bot. Garden Bonn 17012 (M)	P4670	JX032730
<i>Xerophyta hereroensis</i> (Schinz) M.L. Menezes	Becker s.n. (M)	P6564	JX032716
<b><i>Xerophyta hirtiflora</i></b> Behnke & E.Hummel	Seine s.n., cult. Bot. Garden Bonn 11775 (M)	P4672	JX032727
<i>Xerophyta humilis</i> (Baker) T.Durand & Schinz	Adendorff 16 (M)	P6559	JX032719
<i>Xerophyta isaloensis</i> Phillipson & Lowry	Phillipson 5713 (MO)	P6651	JX032747
<i>Xerophyta labatii</i> Phillipson & Lowry	Phillipson 5722 (MO)	P6667	JX032742
<i>Xerophyta lewisiae</i> Phillipson & Lowry	Phillipson 5677 (MO)	P6652	JX032749
<i>Xerophyta longicaulis</i> Hilliard	Adendorff 39 (M)	P7611	JX032724
<i>Xerophyta monroi</i> (Greves) N.L.Menezes	Seine 767, cult. Bot. Garden Bonn 17016 (M)	P4691	JX042583
<b><i>Xerophyta naegelsbachii</i></b> (Dinter ex M.Holzhammer) Behnke	B. Eichhorn 2003-2 (M)	P5454	JX032731

**Table 3.** *Continued*

Taxon	Origin of material/literature citation	IPMB No	GenBank No
<i>Xerophyta nandrasanae</i> Phillipson & Lowry	Phillipson 5729 (MO)	P6653	JX032751
<i>Xerophyta parviflora</i> Phillipson & Lowry	Phillipson 5711 (MO)	P6654	JX032746
<b><i>Xerophyta pauciramosa</i></b> (L.B.Sm. & Ayensu) Behnke	cult. Bot. Garden Bonn 11776 (M)	P4671	JX032728
<i>Xerophyta pectinata</i> Baker	Phillipson 5720 (M)	P6673	JX032756
<i>Xerophyta pinifolia</i> Lam.	Randriambololana 92 (MO)	P6655	JX032753
<b><i>Xerophyta pseudopinifolia</i></b> Behnke	Patel 878 (BR)	P6648	JX032741
<b><i>Xerophyta purpurascens</i></b> Behnke	J. E. Burrows 6593 (M & BNRH)	P6275	JX032736
<b><i>Xerophyta rehmannii</i></b> Behnke	Adendorff 32 (M)	P6684	JX032722
<i>Xerophyta retinervis</i> Baker	A. E. van Wyk 13300 (PRE & M)	P400	JX032732
<b><i>Xerophyta retinervis</i> var. <i>multiramosa</i></b> Behnke	Adendorff 33 (M)	P6686	JX032733
<i>Xerophyta rosea</i> (Baker) N.L.Menezes	Adendorff 6 (M)	P6412	JX032723
<i>Xerophyta scabrida</i> (Pax) T.Durand & Schinz	de Witte 3311 (BR)	P8085	JX032738
<i>Xerophyta schatzii</i> Phillipson & Lowry	Eb. Fischer 3028, cult. Bot. Garden Bonn 13895 (M)	P5458	JX032744
<i>Xerophyta schlechteri</i> (Baker) N.L.Menezes	Adendorff 29 (M)	P6677	JX032725
<i>Xerophyta seinei</i> Behnke, K.Kramer & E.Hummel	Seine 615 (M)	P381	JX032721
<i>Xerophyta sessiliflora</i> Baker	Phillipson 5717 (MO)	P6657	JX032748
<i>Xerophyta setosa</i> Phillipson & Lowry	Eb. Fischer 3020, cult. Bot. Garden Bonn 725 (M)	P5461	JX032745
<i>Xerophyta simulans</i> L.B.Sm. & Ayensu	Friis & Vollesen 1150 (BR)	P7165	JX032714
<i>Xerophyta spekei</i> Baker	S. & T. Pocs 04034 (M)	P6425	JX032740
<i>Xerophyta splendens</i> (Rendle) N.L.Menezes	Burt 6416, cult. Bot. Garden Edinburgh 19710136 (M)	P8392	JX032739
<b><i>Xerophyta tanzaniana</i></b> Behnke	S. & T. Pocs, A. Sass-Gyarmati & Z. Tuba 04093 (M)	P6660	JX032715
<i>Xerophyta tulearensis</i> (H.Perrier) Phillipson & Lowry	cult. Bot. Garden Bonn 18033 (M)	P6566	JX032752
<b><i>Xerophyta vallispongolana</i></b> J.E.Burrows, S.M.Burrows & Behnke	J. E. & S. M. Burrows 6586 (BNRH)	P6273	JX032734
<i>Xerophyta villosa</i> (Baker) L.B.Sm. & Ayensu	cult. Bot. Garden Edinburgh 19651016 (M)	P393	JX032735
<i>Xerophyta viscosa</i> Baker	Adendorff 7 (M)	P6413	JX032720
<i>Xerophyta wentzeliana</i> (Harms) Sölch	Seine 1292, cult. Bot. Garden Bonn 17015 (M)	P4673	JX032729
<b><i>Xerophyta zimbabwensis</i></b> Behnke & E.Hummel	Seine 1403 (M)	P4689	JX032718

African species, the blades are deciduous but leave enduring leaf sheaths which densely cover the stem and branches. Their shape (tricuspidate, truncate, emarginate or other) contributes diagnostic characters.

Leaf surfaces are either glabrous or have an indumentum composed of any type and arrangement of nonglandular trichomes or emergences. Glutinous secretions may be present, mostly produced by patel-

liform or deeply sunken glands or, rarely, by subepidermal tissue. On the lower or upper surfaces, furrows are common and correspond to the spaces between the veins, but the upper or both surfaces may be undulating and then furrows are absent.

#### *Types of leaf anatomy*

The results of our leaf anatomical studies basically support the three leaf types defined by Ayensu (1969,

1973a, b, 1974) and Smith & Ayensu (1974), based on the arrangement of the mesophyll (dorsiventral or isolateral) and the form, size and arrangement of sclerenchyma associated with lateral vascular bundles. However, in *Xerophyta*, as covered in this article, additional characters are found which: (1) add to the description of Ayensu's types; (2) support the definition of one additional leaf type clearly distinct from those described previously; and (3) identify distinct groups within the types. All of this helps in the circumscription of species and, consequently, the better identification of specimens and assignment to distinct taxa.

*Barbacenia* type: (1) Most species belong to a basic group (BT), which is further characterized by: (a) furrows spaced between lateral vascular bundles on upper and lower surfaces and located opposite; (b) prominent aquiferous cells below most furrows; (c) absence of a hypodermis; and (d) mesophyll radially arranged (cf. Coetzee, 1974: 22) and centred towards the lateral bundles, i.e. large aquiferous cells below the furrows are strictly perpendicular to the leaf surfaces and connected to smaller cells in the middle of the lamina, which, in turn, connect to mesophyll cells oriented parallel to the surfaces, but perpendicular to the bundle sheath. The aquiferous cells are obscured if the leaf is in its unexpanded dry condition (Figs 11A, 16A).

This basic BT leaf anatomy is found in all available samples of *X. argentea* (H.Wild) L.B.Sm. & Ayensu, *X. concolor* L.B.Sm. & Ayensu, *X. demeesmaekeriana* P.A.Duvign. & Dewit, *X. equisetoides* Baker, *X. eylesii* (Greves) N.L.Menezes, *X. goetzei* (Harms) L.B.Sm. & Ayensu, *X. hirtiflora* Behnke & E.Hummel, *X. kirkii* (Hemsl.) L.B.Sm. & Ayensu, *X. monroi* (Greves) N.L.Menezes, *X. nutans* L.B.Sm. & Ayensu, *X. naegelsbachii* (Dinter ex M.Holzhammer) Behnke, *X. pauciramosa* (L.B.Sm. & Ayensu) Behnke, *X. pseudopinifolia* Behnke, *X. purpurascens* Behnke, *X. retinervis* Baker, *X. scabrada* (Pax) T.Durand & Schinz, *X. spekei* Baker, *X. splendens* (Rendle) N.L.Menezes, *X. suaveolens* (Greves) N.L.Menezes, *X. trichophylla* (Baker) N.L.Menezes, *X. villosa* (Baker) L.B.Sm. & Ayensu, *X. vallispongolana* J.E.Burrows, S.M.Burrows & Behnke, *X. wenzeliana* (Harms) Sölch and the Madagascan *X. connata* McPherson & van der Werff.

Within the basic group, the distribution of sclerenchyma strands is another distinct feature. In all of the above species, sclerenchyma bands accompany lateral bundles on both adaxial and abaxial sides, but small sclerenchyma strands (knobs: Fig. 11C–F) are found on top of the aquiferous cells just inside: (a) all adaxial furrows in *X. hirtiflora* and *X. monroi*; or (b)

occasionally the two to four furrows adjacent to the central bundle in *X. spekei*, *X. suaveolens* and *X. villosa*.

(2) The prominent distinguishing leaf anatomical characters of the so-called *Capillaris* group type (CGT) are the lateral vascular bundles with vertically extended adaxial bundle sheath cells that bridge the gap between the adaxial partial girder (Figs 4B–D, F, G and 12) and a subepidermis that is either sclerenchymatic or parenchymatic. Coetzee (1974: 22 and fig. 6) mentioned ‘cells, which interrupt the bundle sheath adaxially . . .’; McPherson, van der Werff & Keating (1997: 391 and table 2) described ‘adaxial sheath extensions’. Additional features include: (a) furrows on both leaf surfaces (two adaxial furrows alternate with one abaxial); (b) abundant adaxial aquiferous cells between lateral bundles; (c) sclerenchyma strands between adaxial furrows; and (d) additional sclerenchyma strands outside and separate from marginal bundles. *Xerophyta capillaris* Baker, *X. glabra* Behnke, *X. glutinosa* Behnke, *X. squarrosa* Baker, *X. tanzaniana* Behnke and *X. velutina* Baker belong to this group.

(3) A mixed *Barbacenia*/*Vellozia*-type leaf anatomy (BVT) is present in *X. longicaulis* Hilliard and *X. viscosa* Baker (Fig. 6A–F) and is distinct from the BT group by: (a) the absence of adaxial furrows; (b) the presence of abaxial furrows surrounded by aquiferous cells which, in basal leaf parts, disintegrate and form lacunae; (c) the presence of a hypodermis; (d) a mesophyll without radial arrangement; (e) the presence of patelliform glands on the upper surface; and (f) the absence of sclerenchyma outside vascular bundles.

*Vellozia* type: (1) The basic *Vellozia* type (VT) has furrows on the abaxial surface only, no sclerenchyma, strands or bands, outside vascular bundles and aquiferous cells restricted to the adaxial groove located above the central bundle (Figs 5, 6G, H). This configuration is present in *X. acuminata* (Baker) N.L.Menezes, *X. adendorffii* Behnke, *X. arabica* (Baker) N.L.Menezes, *X. elegans* (Balf.) Baker, *X. hereroensis* (Schinz) N.L.Menezes, *X. humilis* (Baker) T.Durand & Schinz, *X. junodii* Behnke, *X. rehmannii* Behnke, *X. rippsteinii* L.B.Sm., J.-P.Lebrun & A.L.Stork, *X. rosea* (Baker) N.L.Menezes, *X. schlechteri* (Baker) N.L.Menezes, *X. schnizleinia* (Hochst.) Baker, *X. seinei* Behnke, K.Kramer & E.Hummel and *X. zimbabwensis* Behnke & E.Hummel. However, furrows are absent in *X. elegans* (Fig. 4A), and small abaxial strands are present in *X. schnizleinia* (Fig. 5E) and *X. rippsteinii*.

(2) The characters of the Madagascan *Vellozia* group (MVT) include alternate furrows and lateral bundles with vertically extended bundle sheath cells. However, in contrast with the *Capillaris* group: (a)



the mesophyll is dorsiventral; (b) the extended bundle sheath cells are in contact with one or a few layers of aquiferous mesophyll cells bridging the distance to the epidermis; and (c) broad subepidermal sclerenchyma bands and/or a variety of adaxial strands are present which make the leaves much harder (Figs 18–20).

The MVT leaf anatomy includes *X. andringitrensis* (H.Perrier) Phillipson & Lowry, *X. aymoninii* Phillipson & Lowry, *X. brevifolia* (H.Perrier) Phillipson & Lowry, *X. cauliflora* Behnke, *X. decaryi* Phillipson & Lowry, *X. dasylirioides* Baker, *X. eglandulosa* H.Perrier, *X. humbertii* Phillipson & Lowry, *X. isaloensis* Phillipson & Lowry, *X. jouiana* Phillipson & Lowry, *X. labatii* Phillipson & Lowry, *X. leandrii* Phillipson & Lowry, *X. lewisiae* Phillipson & Lowry, *X. nandrasanae* Phillipson & Lowry, *X. parviflora* Phillipson & Lowry, *X. pectinata* Baker, *X. tabulare* Phillipson & Lowry and *X. tulearensis* (H.Perrier) Phillipson & Lowry.

*Xerophyta* type: The Madagascan species with the *Xerophyta*-type (XT) leaf anatomy (*X. calcicola* Phillipson & Lowry, *X. croatii* Phillipson & Lowry, *X. pinifolia* Lam., *X. schatzii* Phillipson & Lowry, *X. sessiliflora* Baker and *X. setosa* Phillipson & Lowry) differ from those with the *Barbacenia* or *Vellozia* type by a sclerenchymatous epidermis and a much larger number of subepidermal sclerenchyma strands. In addition, they have alternate furrows and, in general, small lateral bundles reside in the middle of the lamina (Figs 18A, C, 20F, H).

*Plicata* type: The dorsiventral leaf anatomy of *Xerophyta simulans* L.B.Sm. & Ayensu (Fig. 9) is characterized by a number of large lateral vascular bundles, confined to the lower points of the lengthwise-folded (plicate) leaf blade, and multiple minor bundles spaced between two major ones, almost equidistant in the ascending and descending parts of the blade and occasionally also found in the 'peaks'. The major bundles have a U-shaped abaxial girder and an inversely Y-shaped adaxial girder, and their bundle sheath is, in most cases, in contact with the epidermis. The minor bundles are circular, surrounded by bundle sheath cells and composed of only a few tracheal elements and little or no phloem. Aquiferous cells are located above the central bundle and on each side of the major bundles. The name chosen for this type (PT) refers to the American species *Vellozia plicata* Mart. [= *Nanuza plicata* (Mart.) L.B.Sm. & Ayensu] which has a similar leaf anatomy (Warming, 1893; Ayensu, 1974; Smith & Ayensu, 1976; McPherson *et al.*, 1997).

#### *Further leaf anatomical characters of diagnostic value*

*Spacing and number of lateral vascular bundles:* In transverse sections of leaves, lateral bundles are equidistant from each other. Compared with the size of lateral bundles, the space between them is narrow (about the single width of a bundle), double, triple or more. The number of bundles present is not fixed, but depends on the position of the transverse section (exact middle portion or somewhat distant to it) and the age and strength of the leaves.

*Central vascular bundles:* These are usually reduced (Figs 4D, 6D, 10D, 11D–F, 16D, 18F), but accompanied by a prominent abaxial sclerenchyma girder which, in most species, is crescentiform (either winged, ascending or other; see Metcalfe & Gregory, 1964).

*Marginal bundles:* These are also small, but associated with large triangular or roundish distal girders (Figs 6F, 14A, F, 19E, F, 20B, H).

*Furrows:* In transverse sections of leaf blades, furrows may be absent, present on the abaxial side only or, if present on both sides, located opposite or alternate; they may be wide or narrow, and shallow (less than one-quarter of the lamina thickness) or deep (one-third or more). The furrow epidermis may be papillate, coronulate or finger-like, or have sclerified uniseriate trichomes.

*Aquiferous cells:* Vertically extended cells that are devoid of chlorophyll and occur in groups below the adaxial (and abaxial) epidermis, preferentially between lateral bundles, but also above central bundles, are thought to store water (Warming, 1893). Their function is related to the unfolding of resurrection leaves when moist conditions replace extreme drought. Under laboratory conditions, desiccation tests have shown that the leaf width is reduced to about one-half of the hydrated state (Hallam & Luff, 1980a, b) and aquiferous cells are compressed considerably.

*Leaf glands:* Unlike capitate glands present in flower organs, leaf glands are either: (a) patelliform with a large opening (Fig. 6A, C); or (b) deeply sunken into and separated from the mesophyll by an endodermis (Fig. 5B). The latter distribute their viscous secretion products over the leaf surface through a central duct and small opening (see Behnke *et al.*, 2002: fig. 5).

*Crystals:* If present in leaves (Fig. 5A–C), rectangular or cubical solitary crystals may occur in cells of either one or several of the following layers: epidermis,

Majority rule



**Figure 1.** Majority rule consensus tree based on anatomical characters and 2100 most-parsimonious trees. Bootstrap percentages are given for each branch.

hypodermis, palisade or bundle sheath. Although several small crystals are occasionally found within one cell, raphides are absent in African Velloziaceae [but see the report by Smith & Ayensu (1976) for American species and the review by Prychid & Rudall (1999)].

*Subepidermal sclerenchyma:* Sclerenchyma strands and/or unicellular or multicellular bands (see defini-

tion by Metcalfe & Gregory, 1964) are often present between and/or adjacent to lateral vascular bundles. Small fibre bundles are present in a few species.

#### *Anatomical analysis*

The consensus tree (Fig. 1) with *Acanthochlamys* as the outgroup included 2100 equally parsimonious trees with 151 steps, a consistency index (CI) of 0.20 and a retention index (RI) of 0.77. *Xerophyta* spp. are divided

into two major clades, with one including all species with the *Barbacenia*-type (BT and CGT) leaf anatomy and the other with non-BT species. In the *Barbacenia*-type clade, the Madagascan *X. connata* is sister to the African species. The non-BT clade is further divided into two clades, one with BVT and VT species and the other almost exclusively with Madagascan species. In the latter, *X. rippsteinii* and *X. schnizleinia* (both VT) are sister to all other taxa and *X. simulans* (PT) and the Madagascan *X. parviflora* are, in turn, sister to all other Madagascan species.

#### *rbcL* analysis

ML and BI analyses recovered congruent topologies (Figs 2, 3). Velloziaceae is monophyletic and sister to Stemonaceae (Pandanales (Cyclanthaceae)) in the Pandanales clade. Within Velloziaceae, the Chinese genus *Acanthochlamys* is sister to the rest of the family. At the infrafamilial level, the African/Madagascan and the South American species form two distinct clades, with the dioecious *Barbaceniopsis* being separated from *Barbacenia* + *Vellozia*.

The Old World *Xerophyta* is monophyletic and divided into several clades, with *X. hereroensis* and *X. zimbabwensis* separated from three distinct clades mainly composed of BT, VT or Madagascan species. One strongly supported clade comprises all species with erect stems, deciduous leaves and basic BT leaf anatomy; a second contains all Madagascan *Xerophyta* (MAD+) and is sister to *X. simulans*, which, in turn, is sister to *X. elegans* and *X. tanzaniana*. The third clade is composed of species with leaf glands, and the BVT species *X. longicaulis* and *X. viscosa* (both with patellar glands) are sister to VT species with sunken glands. The anatomically distinct *Vellozia* and *Xerophyta* types do not separate into uniform clades.

*Xerophyta humilis*, an African species with VT leaf anatomy, is nested in the Madagascan clade. This species is certainly the tiniest and most widespread African species, and may represent a possible link between the continental African Velloziaceae and the Madagascan island species; our previous evolutionary study revealed that the Madagascan species appeared considerably later than those of the African continent (Behnke *et al.*, 2000). However, any evidence of its occurrence in Madagascar is missing. The previously reported presence of the Madagascan species *X. piniifolia* in Malawi and Mozambique (Gonçalves, 2009) was not supported by anatomical or *rbcL* data, and this led to the new species *X. pseudopiniifolia* being described.

The results of the *rbcL* analysis further support: (1) the morphological identification of new species and their separation from established taxa, e.g. *X. tanzaniana* and *X. scabrida*, *X. pseudopiniifolia* and *X. piniifolia*, *X. piniifolia* and *X. setosa*, *X. cauliflora* and

*X. dasyliroides*, and *X. pectinata* and *X. dasyliroides*; and (2) the distinctiveness of the different species with leaf glands.

As, at the species level, *rbcL* sequences are close to each other and often differ by only one or two bases, a strict MP consensus tree (not shown here) only supports the separation of *Acanthochlamys*, but does not further resolve Velloziaceae s.s. The sequences of recognized varieties are not different from those of the respective type varieties of the species, but their morphology and/or anatomy is distinct.

## TAXONOMIC TREATMENT

### DESCRIPTION OF AFRICAN SPECIES OF *XEROPHYTA*

1. *Xerophyta elegans* (Balf.) Baker, J. Bot. 13: 234 (1875a).

*Vellozia talbotii* Balf., Trans. Bot. Soc. Edinb. 9: 190. 1868a; Trauseld, Wild Flow. Drakensb.: 33. 1969. – *Type*: South Africa, KwaZuluNatal, Fox Talbot s.n. (K, holotype).

*Talbotia elegans* Balf., Trans. Bot. Soc. Edinb. 9: 192. 1868b; Ayensu, Biotropica 5(3): 143, 147, 148 + fig. 5. 1973b; Coetzee *et al.*, Dinteria 9: 3–7. 1973; Coetzee, Dinteria 10: 19–26. 1974; Smith & Ayensu, Kew Bull. 29: 183. 1974; Dyer, Gen. Southern Afr. Flow. Pl. 2: 959. 1976; Hallam & Luff, Bot. Gaz. 141: 180. 1980b. – *Type*: South Africa, KwaZuluNatal, Fox Talbot s.n. (K, holotype).

*Vellozia elegans* (Balf.) Oliv. ex Hook.f., Bot. Mag. 95, t. 5803. 1869; Greves, J. Bot. 59: 279, 284. 1921; Ayensu, Kew Bull. 23: 328. 1969; Hilliard & Burtt, Notes Roy. Bot. Gard. Edinb. 31: 2. 1971; Ross, Fl. Natal, 132. 1972.

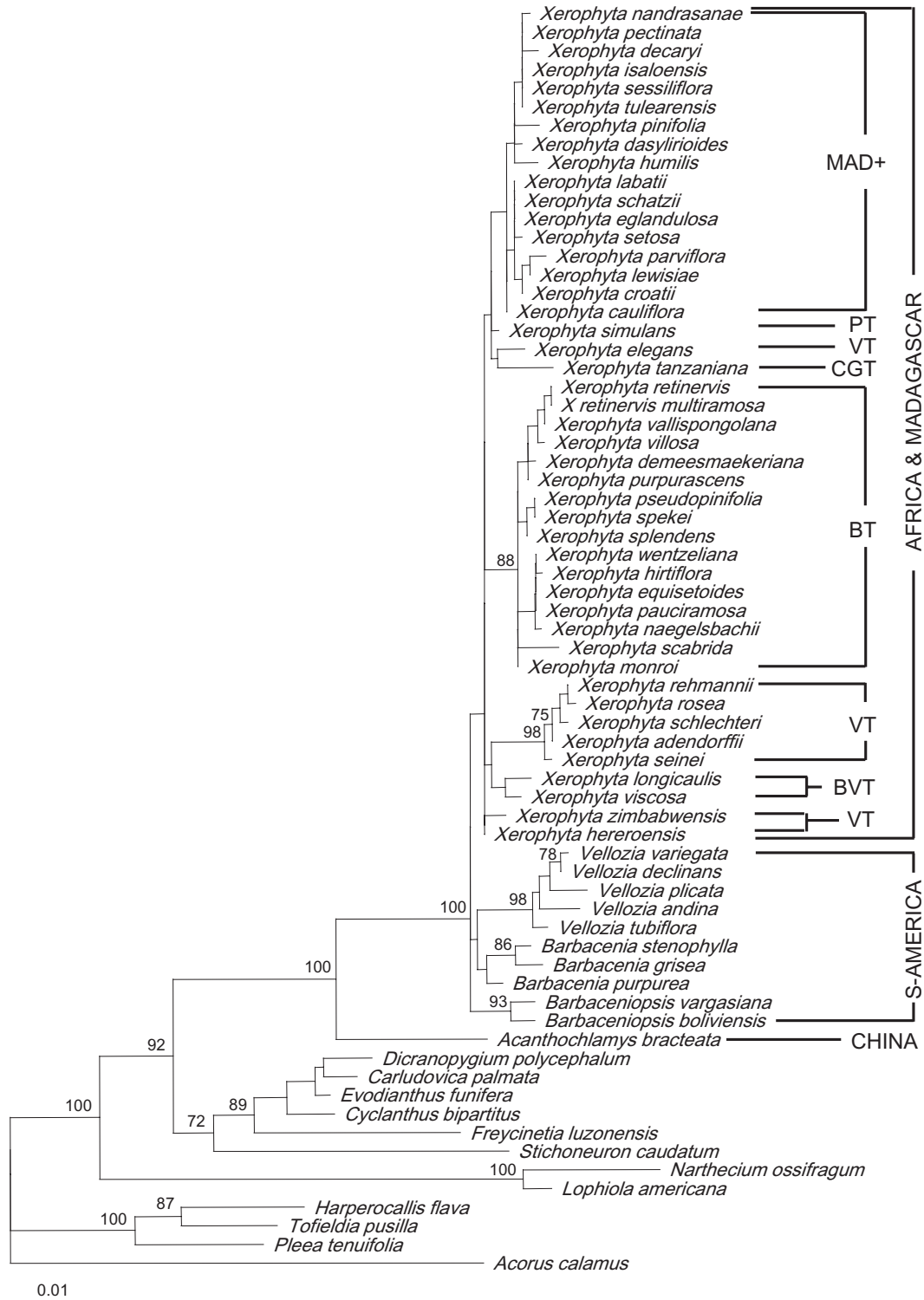
*Hypoxis barbacioides* Harv. ex Baker, l.c. 1875a, listed in synonymy only.

*Xerophyta minuta* Baker, l.c. 1875a. – *Type*: South Africa, KwaZuluNatal, Gueinzius s.n. (K, holotype).

*Xerophyta 'miniata'* T.Durand & Schinz, Consp. Fl. Afr. 5: 271. 1895, in error for *X. minuta* Baker.

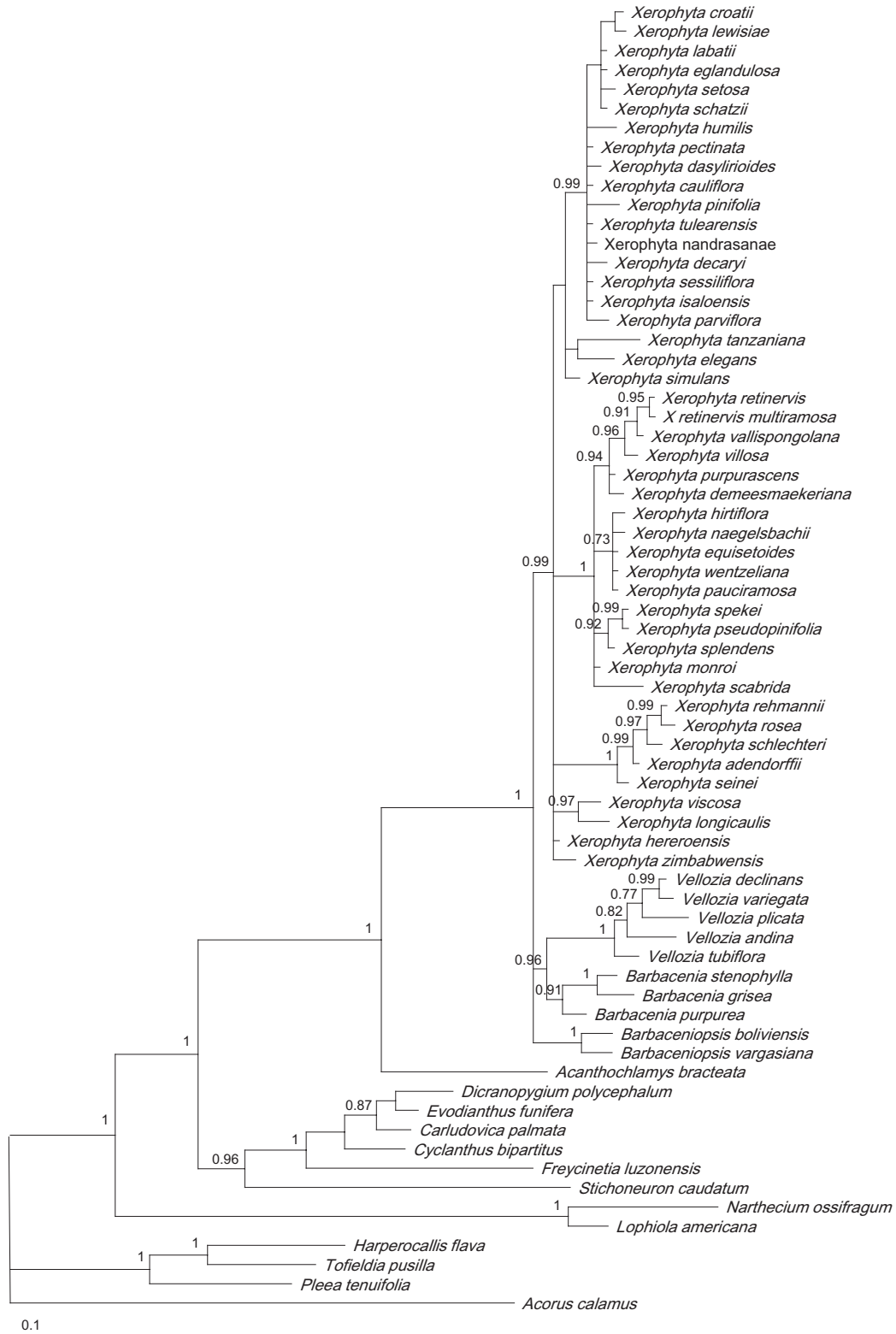
*Vellozia elegans* var. *minor* Baker in Harvey, Fl. Cap. 6: 246. 1896. – *Type*: South Africa, KwaZuluNatal, Gueinzius s.n. (K, holotype).

*Description*: Stem slender, decumbent and, in lower part, covered with disintegrated fibrous remnants of old leaf sheaths. Leaves 10–15(–20) cm long, mesophytic and persistent, tristichous, recurved or falcate, sharply keeled and with many ribs on each side, glabrous but distinctly serrulate in the upper part of the keel and margins. Peduncle terminal, undivided or divided into three to five 5–15-cm-long pedicels, each bearing one flower. Flowers pale lilac in bud, then pure white and turning green after flowering. Stamens six, erect, adnate to and as long as the style.



**Figure 2.** Maximum likelihood phylogram for Velloziaceae based on nucleotide sequences of the complete *rbcL* gene ( $\ln L = -5140.33$ ). The numbers indicate bootstrap values ( $\geq 70$ ). BT, basic *Barbacenia*-type leaf anatomy; BVT, mixed *Barbacenia/Vellozia*-type leaf anatomy; CGT, *Capillaris* group-type leaf anatomy; MAD+, Madagascan *Vellozia* and *Xerophyta*-type leaf anatomy plus *X. humilis*; PT, *Plicata*-type leaf anatomy; VT, *Vellozia*-type leaf anatomy.





**Figure 3.** Bayesian inference phylogram based on nucleotide sequences of the complete *rbcL* gene. The numbers next to the nodes are posterior probability values ( $\geq 0.70$ ).

## KEY TO THE SPECIES IN AFRICA AND THE ARABIAN PENINSULA

(In the key, anatomical distinctions between trichomes and emergences or between different leaf types are disregarded.)

1. Shrubs with 0.2–5.0-m-long erect stem and usually many woody branches, covered with a mantle of closely packed persistent leaf sheaths; leaf blades deciduous .....17
1. Perennial herbs with less than 20-cm-long, erect or to 40-cm-long slender, decumbent stem; leaf blades deciduous or persistent .....2
2. Plants with inconspicuous, about 1-cm-long stem; leaf blades persistent .....13
2. Plants with short, less than 20-cm-long erect or to 40-cm-long slender, decumbent stem; leaf blades deciduous or persistent .....3
3. Ovary glabrous, obovate triangular; three to five flowers on terminal peduncle; leaf blades mesophytic, persistent .....1. *X. elegans*
3. Ovary vestite, spherical, obovate or other, but not triangular; flowers solitary on terminal peduncle; leaf blades xerophytic, and deciduous or persistent .....4
4. Ovary and upper part of peduncle covered with bristle-like eglandular trichomes .....5
4. Ovary, peduncle and part of exterior tepals covered with glandular trichomes .....6
5. Ovary globose; leaf blades glabrous .....2. *X. schnizleinia*
5. Ovary ellipsoid; leaf blades mostly pubescent with soft trichomes present on abaxial surface .....3. *X. rippsteinii*
6. Leaf blades persistent .....10
6. Leaf blades deciduous .....7
7. Leaf blades viscid, with patelliform glands .....9
7. Leaf blades glabrous, not viscid .....8
8. Plants apparently stemless, but leaf sheaths sometimes forming elongate stem-like extensions; leaves up to 8 cm, peduncles to 7 cm long, tepals white, 12–20 mm long, style two to three times longer than stigma .....4. *X. arabica*
8. Plants with short stem, covered with old leaf sheaths split into many fibres; leaves about 5 cm long, peduncles about the same size, but raising the small flowers just above the leaf rosette; tepals 7–15 mm long, the outer aristate; style slightly shorter than stigma .....5. *X. humilis*
9. Stem slender, up to 40 cm long, branched, with leaf sheaths closely appressed, blades rarely viscid; flowers mauve, rarely white, stigma about twice the length of style base .....6. *X. longicaulis*
9. Stem short, only up to 5 cm long; old leaf sheaths split into fibres with recurved tips, blades viscid, especially towards base; flowers purple to violet, stigma three times longer than style base .....7. *X. viscosa*
10. Leaves with many deeply sunken glands, leaf surfaces strongly covered with their viscid secretions .....11
10. Leaves with few glands, leaf surfaces not viscid .....8. *X. rosea*
11. Flowers rose; old leaf sheaths not split into fibres .....9. *X. junodii*
11. Flowers dark violet; old leaf sheaths split into long wiry fibres .....10. *X. seinei*
12. Stem 5–10 cm long; leaves not longer than 10 cm, apical recurved, adaxial surface with dark spots; tepals retuse .....11. *X. rehmannii*
12. Stem up to 20 cm long; leaves 10–20 cm long with long acuminate tip; outer tepals cuspidate .....14
13. Leaves viscid all over, with dark secretions from sunken glands .....12. *X. zimbabwensis*
13. Leaves almost glabrous, somewhat viscid in their lower part and then with white secretions on adaxial surface .....13. *X. hereroensis*
14. Flowers bright blue–lilac or mauve, rarely white; tepals 20–30 mm long; leaf blades slightly flanged V-shaped, margins often revolute .....15
14. Flowers white or cream; tepals 15–25 mm long; leaf blades V-shaped, margins not revolute .....14. *X. adendorffii*
15. Leaves somewhat falcate, dry leaves in upper part often spirally twisted; outer tepals cuspidate .....16
15. Leaves neither falcate nor twisted, outer tepals obtuse or apiculate .....15. *X. acuminata*
16. Outer tepals obtuse .....16. *X. schlechteri*
16. Outer tepals apiculate .....18
17. Leaf blades more or less V-shaped and not plicate; ovary glabrous or with glandular or eglandular trichomes .....17. *X. simulans*
17. Leaf blades almost plane, strongly corrugate, and in transverse sections plicate; ovary with eglandular simple, subulate or forked trichomes

18. Ovary vestite	19
18. Ovary glabrous	18. <i>X. goetzei</i>
19. Trichomes of the ovary eglandular	33
19. Trichomes of the ovary glandular	20
20. Ovary and peduncle covered with capitate glandular trichomes	21
20. Ovary covered with truncate glandular trichomes; peduncle to a large extent eglandular, near ovary with glands	19. <i>X. demeesmaekeriana</i>
21. Leaf blades strongly scabrous; sheaths fan-like, not early disintegrating	20. <i>X. scabrida</i>
21. Leaf blades glabrous or vestite, but not strongly scabrous; sheaths either remaining whole or early disintegrating	22
22. Leaf sheaths scale-like, not early disintegrating	23
22. Leaf sheaths soon splitting after abscission of the blade	29
23. Leaf sheaths truncate, cuspidate or other	25
23. Leaf sheaths emarginate	24
24. Leaf sheaths dark grey, about 2.5 cm long; blades on abaxial side with a dense hair-like cover and shining silver	21. <i>X. argentea</i>
24. Leaf sheaths with marginal teeth, blackish with grey apices, about 1.5 cm wide and 2.0 cm long; blades with mottled surfaces and setose midrib and margins	22. <i>X. kirki</i>
25. Plants to 5 m high; leaf blades glabrous, to 50 cm long; sheaths retuse with strong midvein	23. <i>X. splendens</i>
25. Plants in general less than 2 m high; leaf blades densely vestite, less than 25 cm long; sheaths obtuse, tricuspidate or other	26
26. Leaf sheaths with prominent midvein	27
26. Leaf sheaths obtuse or praemorse	28
27. Leaf sheaths with long cuspidate midvein; blades pubescent with velvet surfaces	24. <i>X. velutina</i>
27. Leaf sheaths almost blunt with prominent midvein; blades resinous dotted, glabrous or with silky trichomes on both sides	25. <i>X. capillaris</i>
28. Leaf sheaths praemorse with strong veins, apically spreading; blades 3–8 cm long terminating into a 2-mm-long strong point, tomentose with soft scales	26. <i>X. pseudopinifolia</i>
28. Leaf sheaths obtuse, sharply tricuspidate, the younger with short trichomes; blades 15–20 cm long, in part densely pilose	27. <i>X. spekei</i>
29. Leaf blades glabrous and without secretions on surfaces	31
29. Leaf blades with finely mottled surfaces and glutinous or resinous secretions	30
30. Leaf blades with fine scabrae above veins (often broken or removed), on lower surface with dark spots and resin particles between veins	28. <i>X. tanzaniana</i>
30. Leaf blades glabrous and glutinous, upper and lower surfaces with secretions above veins	29. <i>X. glutinosa</i>
31. Leaf sheaths projecting outwards; blades serrate at margins and below midvein	30. <i>X. squarrosa</i>
31. Leaf sheaths not projecting outwards, blades glabrous with thickened margins	32
32. Small much branched plants with up to 50-cm-high stems; leaf blades acuminate and 5–10 cm long	31. <i>X. glabra</i>
32. Stem up to 1.5 m high; leaf blades filiform attenuate and up to 50 cm long	32. <i>X. concolor</i>
33. Ovary covered with long soft trichomes	34
33. Ovary covered with bristle-like, stellate or orbicular trichomes	37
34. Leaf sheaths fan-like and glabrous, up to 7.0 cm long and to 6.5 cm wide	35
34. Leaf sheaths inversely fan-like, about 4 cm long, 1 cm wide at top and to 2 cm at base, the younger ones with white plumose tips	33. <i>X. hirtiflora</i>
35. Leaf sheaths about 4.0 cm long and to 6.5 cm wide; blades with dense trichomes underneath or on both sides; ovary densely covered with to 2–5-mm-long spreading trichomes	36
35. Leaf sheaths about 7 cm long, split at the top, the younger ones with revolute tips; blades with silky trichomes at margins; ovary densely covered with 1–2-mm-long appressed trichomes	34. <i>X. monroi</i>
36. Leaf sheaths 6.5 cm wide; blades 30–40 cm long and 1.0–1.5 cm wide with dense trichomes underneath and at margins, upper side almost glabrous	35. <i>X. purpurascens</i>
36. Leaf sheaths 4.5 cm wide; blades 10–20 cm long and 5 mm wide with dense trichomes on both sides	36. <i>X. villosa</i>

37. Leaf sheaths quickly splitting after abscission	39
37. Leaf sheaths scale-like, not early splitting	38
38. Leaf blades glabrous	37. <i>X. pauciramosa</i>
38. Leaf blades softly hairy on both surfaces	38 <i>X. wentzeliana</i>
39. Leaf sheaths spreading on top or distinct by different colour	40
39. Leaf sheaths uniform in colour and not spreading	41
40. Leaf sheaths squarrose, with spreading apices; blades setose above and glabrous beneath; ovary trichomes short and bristle-like	39. <i>X. naegelsbachii</i>
40. Leaf sheaths with grey apices; blades with linear lanceolate or plumose trichomes; ovary with orbicular short-rayed emergences	40. <i>X. nutans</i>
41. Trichomes of the ovary stellate; leaf blades setose above or with long hairy trichomes beneath	41. <i>X. suaveolens</i>
41. Trichomes of the ovary simple, forked or scutate, but not stellate; leaf blades glabrous or vestite	42
42. Ovary covered with scutate trichomes ending in a long apical seta; peduncle with long trichomes	42. <i>X. eylesii</i>
42. Ovary and upper part of peduncle covered with bristle-like trichomes	43
43. Ovary densely covered with flexuous, slightly swollen trichomes; leaf blades densely hairy on both surfaces	43. <i>X. trichophylla</i>
43. Ovary covered with straight bristle-like trichomes; leaf blades glabrous or vestite, but not densely hairy on both surfaces	44
44. Ovary trichomes appressed, less than 1 mm long	44. <i>X. equisetoides</i>
44. Ovary trichomes spreading, 1 mm and longer	45
45. Leaf blades glabrous; ovary trichomes pungent, 1–2 mm long; tepals mauve to rose, 30–40 mm long	45. <i>X. retinervis</i>
45. Leaf blades covered underneath with stiff trichomes; ovary trichomes spreading, 2–3 mm long; tepals white, 50–60 mm long	46. <i>X. vallispongolana</i>

Stigma cylindrical, six-furrowed, smaller than the style and overtopping the anthers. Ovary glabrous, obovate, triangular.

*Distribution:* South Africa: KwaZuluNatal to eastern Mpumalanga.

*VT leaf anatomy:* Blades amphistomatic, only weakly dorsiventral with two layers of small palisade cells (cell length about 1.5 times their width), amphistomatic; lateral vascular bundles with partial abaxial Y- or  $\psi$ -shaped girder (Fig. 4A, see also Behnke *et al.*, 2002: fig. 7C).

*Specimens examined:* SOUTH AFRICA. KwaZuluNatal, Gerrard 1555 (BM); Nolena Forest, Cathkin Peak, Edwards 2691 (M); Fern Cliffs Nature Res., Weigend 2021 (M); near York, Medley Wood *s.n.* (B); Shelter Falls, Blankinon *s.n.* (Herb. Moss 16143 in BM); *H. & S s.n.* (Herb. Th. Bernhardt in B). Mpumalanga, Bridal Veil Falls, Mariepskop Forest Reserve, Weigend 2866 (M); Drakensberg, Mariepskop, Werdermann & Oberdieck 1858 (B). – Cultivated, Bot. Gard. Heidelberg, no. 101408, Rauh 57713 (M); no. 106896, *s.n.* (M).

*Comments:* Ayensu (1969) describes isolateral leaves in *Vellozia elegans*, which, because of the shape of some girders, resemble BT, and dorsiventral leaves in *Vellozia minuta*. Our studies confirmed dorsiventral

leaves in all specimens examined, although, in some collections, e.g. Werdermann & Oberdieck 1858 (B), the palisade cells are difficult to detect. BT lateral vascular bundles are partially (away from the cental and marginal bundles) found in *H. & S.* (Herb. Th. Bernhardt at B).

2. *Xerophyta schnizleinia* (Hochst.) Baker, J. Bot. 13: 235. 1875a, ‘Schnizleinia’; Durand & Schinz, Consp. Fl. Afr. 5: 272. 1895; Cufodontis, Bull. Jard. Bot. Nat. Belge 42, Suppl.: 1580. 1972; Smith & Ayensu, Kew Bull. 29: 189. 1974 (incl. var. *occidentalis*); Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 4. 1975 (including var. *occidentalis*); Thulin, Fl. Somalia 4: 77. 1995; Lye & Edwards in Fl. Ethiopia 6: 311–312 (1997). – *Type:* Ethiopia, Semien, Sabra, Schimper 1365 (BM, holotype; B, BR, E, K, M, Z isotypes).

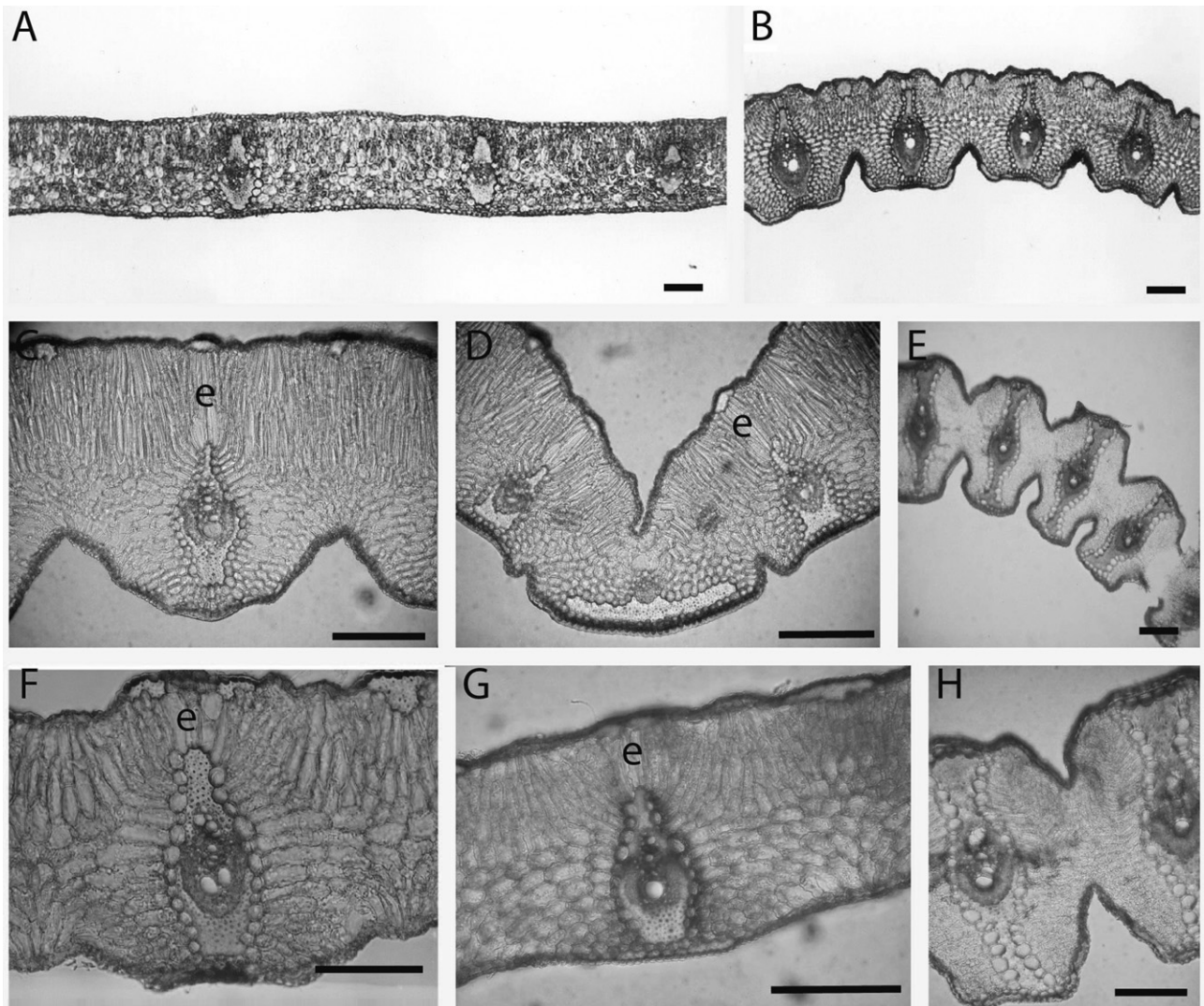
*Schnizleinia amica* Steud. in sched. Schimper iter abyss. no. 1365 (1840), *nomen nudum*.

*Hypoxis schnizleinia* Hochst., Flora 27: 31–32. 1844. *Vellozia schnizleinia* (Hochst.) Martelli, Fl. Bogosensis: 82. 1886 (‘schnizleiniana’); Baker in Oliver, Fl. Trop. Afr. 7: 409. 1898; Greves, J. Bot. 59: 280. 1921.

*Barbacenia schnizleinia* (Hochst.) Pax in Engler, Hochgebirgsfl.: 171. 1892 (‘schnizleiniana’); Pax in Engler, Pflanzenfam., ed. 2, 15a: 433–434. 1930.

*Barbacenia hildebrandtii* Pax *l.c.* 1892. – *Type:* Somalia, Serrut Mountains, Meis, Hildebrandt 1466 (B, holotype).





**Figure 4.** Transverse sections of leaves with *Vellozia*-type (VT) (A), *Capillaris* group-type (CGT) (B–D, F, G) and basic *Barbacenia*-type (BT) (E, H) leaf anatomy. A, *Xerophyta elegans* (from Blankinon – Herb. Moss 16143), dorsiventral leaf part with wide spacing of bundles and absence of furrows. B, F, *Xerophyta glutinosa* (from Gossweiler 12157 resp. Merxmüller 1520), lateral leaf parts with alternate furrows, sclerenchyma strands between bundles and adaxial extended bundle sheath cells (e). C, D, Lateral and median bundles in *Xerophyta tanzaniana* (from S. & T. Pocs, A. Sass-Gyarmati & Z. Tuba 04093): on adaxial side abundant aquiferous cells between lateral bundles; adaxial bundle sheath cells vertically extended (e). E, H, Lateral leaf parts of *Xerophyta scabrada* (from Pogge 423) with opposite furrows and bundles with radial mesophyll. G, *Xerophyta glabra* (from Merxmüller & W. Giess 30477), almost dorsiventral leaf part with wide distance between lateral bundles, adaxial bundle sheath cells vertically extended (e). Scale bars, 100  $\mu\text{m}$ .

*Vellozia schnitzleinia* var. *somalensis* A.Terracc., Bull. Soc. Bot. Ital. 1892: 425. 1892; Baker in Oliver, Fl. Trop. Afr. 7: 410. 1898. – Type: Somalia, Gerar-Amaden, Candeo & Baudi di Vesme s.n. (FT, holotype). *Barbacenia* (*Schnitzleinia*) *amica* Baill., Hist. Pl. 13: 23. 1895, nomen nudum. *Xerophyta hildebrandtii* (Pax) T.Durand & Schinz, Consp. Fl. Afr. 5: 271. 1895; Cufodontis in Bull. Jard. Bot. Nat. Belge 42, Suppl.: 1580. 1972.

*Vellozia hildebrandtii* (Pax) Baker in Oliver, Fl. Trop. Afr. 7: 409. 1898; Greves, J. Bot. 59: 280. 1921.

*Vellozia somalensis* (A.Terracc.) Chiov., Annali Bot. 9: 141–142. 1911; Greves, J. Bot. 59: 281. 1921.

*Vellozia schnitzleinia* var. *brevifolia* Chiov., Fl. Somala: 314. 1929. – Type: Ethiopia. Bur-Cal-Je-Corar near Tigieglò, Stefanini & Puccioni 247 (FT, holotype).

*Xerophyta somalensis* (A.Terracc.) N.L.Menezes, *Ciência e Cultura* 23: 422. 1971; Cufodontis, *Bull. Jard. Bot. Nat. Belge* 42, Suppl.: 1581. 1972.

*Xerophyta schnizleinia* var. *brevifolia* (Chiov.) Cufod., *Bull. Jard. Bot. Nat. Belge* 42, Suppl.: 1581. 1972.

*Xerophyta schnizleinia* var. *somalensis* (A.Terracc.) Lye, *Lidia* 3: 143. 1995; Lye & Edwards in *Fl. Ethiopia* 6: 311–312. 1997.

*Description:* Stem variable, from hardly showing above ground to about 50 cm long, rarely branched, covered with brown leaf sheaths splitting into coarse fibres; leaves five to ten in an apical rosette, up to 40 cm long, blades V-shaped, deciduous, linear, glabrous but scabrous on margin and midrib. Flowers one to three at the apex of stem, each on a separate, up to 30-cm-long, peduncle that in its upper third is covered with eglandular emergences. Tepals 10–40 mm long, white but turning brown or almost black when drying. Stamens six, about 15 mm long with yellow anthers. Style 2–3 mm long, stigma 9–10 mm long. Ovary (sub-)globose, densely covered with yellow to brown eglandular emergences with broad base.

*Distribution:* Nigeria, Ethiopia, Somalia, Uganda, Kenya.

*VT leaf anatomy:* Blades amphistomatic and dorsiventral with three to four distinct layers of palisade cells; abaxial side with shallow furrows. Uncommon for species with VT leaf anatomy, sclerenchyma strands are present outside lateral vascular bundles: below the adaxial epidermis, one large strand alternates with two smaller; inside the abaxial epidermis, a continuous band of one to three fibre layers or two single-layered fibre bands (one on each side of a lateral bundle) underline the ribs (Fig. 5E).

Stem about 10 cm long .....a. var. *schnizleinia*

Stem about 30–50 cm long ....b. var. *occidentalis*

a. var. *schnizleinia*

*Specimens examined:* ETHIOPIA. Sabra, *Schimper* 1365 (M); Tacaze River, *Schimper* 1693 (BR); without location, *Schimper* 253 (BR); Lake Stephanie, *Brown* 30 (K); Latamba, La Keren, *Steudner* 507 (B); Wochny, *Steudner* 509 (B); Abita, Keren, sul Mt. Deban, *Beccari* 142 (B); Haverge, Ogaden, 21 km W of Degeh Bur on track to Degeh Medo, *Gilbert & Gilbert* 3984 and 3984A (K). SOMALIA. Pass between Halin and Hedidera Tug, *Bally* 10882 (K); Serrut Mts., Meid, *Hildebrandt* 1466 (B); Abdullah, *Keller* 169 (Z); Las Anod District, *Glover & Gilliland* 1015 (K); 62 km SE of El Wak, on road from Garba Hare, *Gillet & Hemming* 24831 (K). – Without location, *Donaldson*

*Smith s.n.* (BM). KENYA. Mathews Peak, Ol Doinyo Lengiyu, *Newbold* 3510 (B).

b. var. *occidentalis* (Milne-Redh.) Behnke, *comb. nov.* *Vellozia schnizleinia* (*schnitzeinia*) var. *occidentalis* Milne-Redh., *Kew Bull.* 5: 381. 1951; Hepper in Hutchinson, *Fl. West Trop. Afr.*, ed. 2, 3: 174, fig. 378. 1968; Ayensu, *Kew Bull.* 23: 322. 1969. – *Type:* Nigeria, Zaria Province, Zaria District, Anara Forest Reserve, *Keay* in *F.H.I.* 22903 (K, holotype; BM, BR isotypes).

*Description:* var. *occidentalis* is morphologically distinct by its up to 50-cm-long stems and longer leaves.

*Distribution:* Nigeria.

*VT leaf anatomy:* In transverse sections of leaf blades, the abaxial ribs of the 30 or more lateral bundles are lined by an undivided band of two or three layers of sclerenchyma fibres. An arch-shaped thick subepidermal band of fibres supports the leaf margins.

*Specimens examined:* NIGERIA. Zaria Province: Anara Forest Reserve, *Keay*, *F.H.I.* 22903 (BR and BM); Igabi District, Anara Forest Reserve, 2 ml S of Birnin Yero Quibaba, *Keay*, *F.H.I.* 25758 (B); Anara Forest Reserve, Kangimi, *Olorunfemi*, *F.H.I.* 24356 (K).

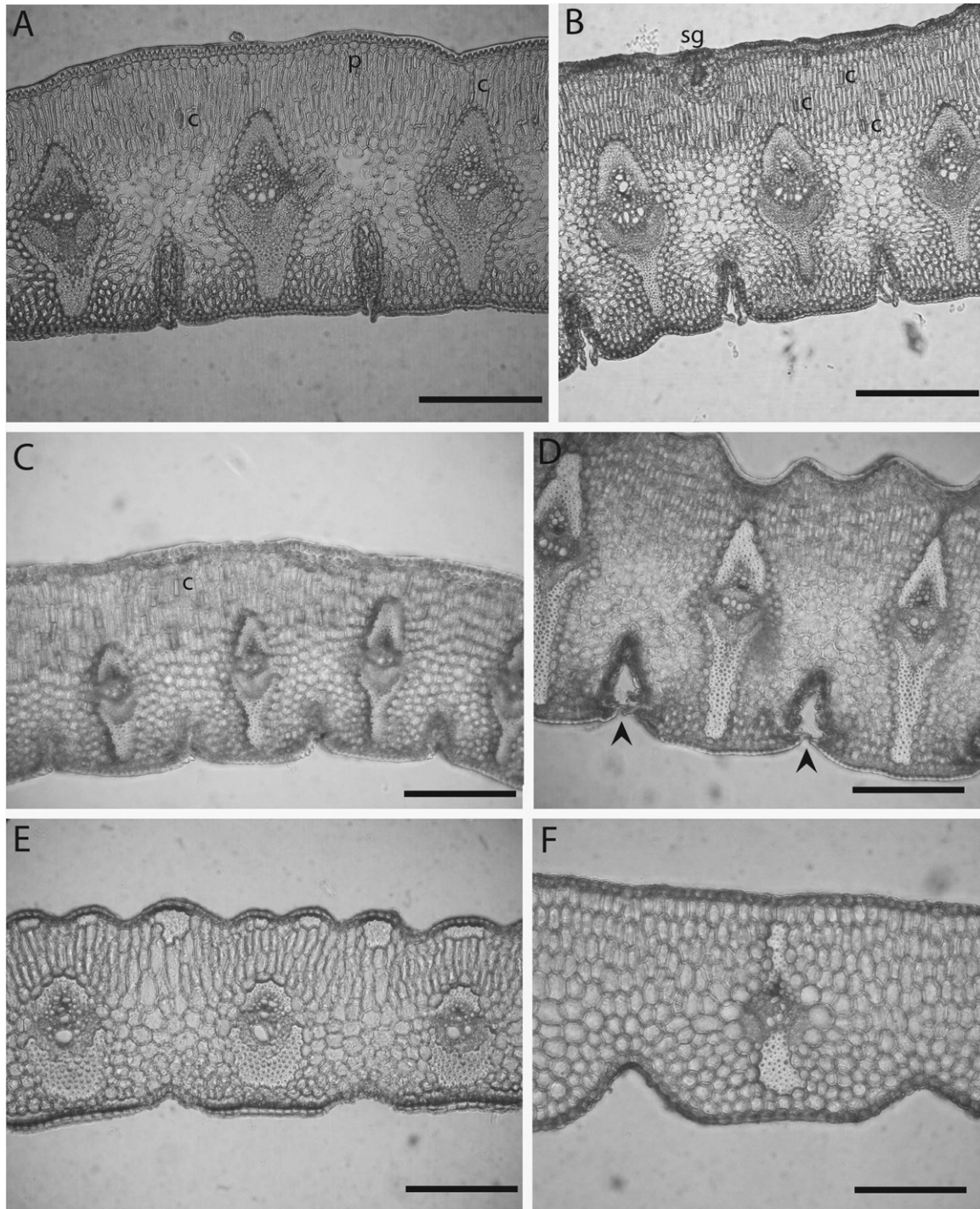
3. *Xerophyta rippsteinii* L.B.Sm., J.-P.Lebrun & A.L.Stork, *Adansonia*: 297. 1986; Lye & Edwards in *Fl. Ethiopia* 6: 312. 1997. – *Type:* Ethiopia, Bale, West of Wachsen, *Rippstein* 1131 (US, holotype; ALF, K isotypes).

*Description:* Small plants, short stem covered with grey leaf sheaths split into fibres. Leaves up to 10 cm long, blades V-shaped, deciduous, linear, recurved, abaxial surface densely covered with long soft trichomes, adaxial surface glabrous. Flowers solitary on up to 5-cm-long peduncle; upper part of peduncle and ovary covered with eglandular emergences. Tepals up to 25 mm long. Stamens six, filaments short, anthers about 12 mm long. Style about 6 mm long, stigma about 6 mm long. Ovary 5 mm long, ellipsoid.

*Distribution:* Ethiopia, Somalia.

*VT leaf anatomy:* Blades amphistomatic; lateral vascular bundles with partial abaxial U-shaped girder; large lacunae between bundles. Extra sclerenchyma outside lateral bundles as in *X. schnizleinia*.





**Figure 5.** Transverse sections of leaves with *Vellozia*-type (VT) leaf anatomy. A, *Xerophyta adendorffii* (from Adendorff 14). B, *Xerophyta rehmannii* (from Adendorff 5). C, *Xerophyta rosea* (from Adendorff 6). A–C, Mesophyll with four layers of palisade (p) and loosely arranged spongy parenchyma, deep abaxial furrows with hairy epidermis outgrowths, palisade cells with crystals (c) and deeply sunken gland (sg). D, *Xerophyta junodii* (from Junod 2768): palisade cells lacking crystals, abaxial furrows nearly closed by a two-horned anvil-like extension of the epidermis (arrowheads), slim lateral bundles with long abaxial prong. E, *Xerophyta schnizleinia* (from Gillett & Hemming 24831): shallow furrows on abaxial surface, adaxial sclerenchyma strands above and between lateral bundles. F, *Xerophyta humilis* (from Adendorff 18): mesophyll almost isolateral, lateral bundles together with their surrounding bundle sheath form an omega shape. Scale bars, 100  $\mu$ m.

*Specimens examined:* SOMALIA. Hiiran Region, Buldo District, 15 km on hwy from Halgan to Beledweyne, then 2 km E on cutline, *Kuchar* 16931 (K).

4. *Xerophyta arabica* (Baker) N.L.Menezes, *Ciência e Cultura* 23: 422. 1971; Smith & Ayensu, *Kew Bull.* 29: 199. 1974; Collenette, *Illustr. Guide Flow. Saudi Arabia*: 494. 1985.

*Vellozia arabica* Baker, *Bull. Misc. Inform. Kew* 93: 342. 1894; Baker, *Hook. Icon. Pl.* 24, t. 2364. 1895a; Greves, *J. Bot.* 59: 284. 1921. – *Type:* South Yemen, Hadramaut Valley, Dobaibah, *Lunt* 205 (K, holotype).

*Barbacenia arabica* (Baker) O.Schwartz, *Mitt. Inst. Bot. Hamburg* 10: 355. 1939.

*Description:* Perennial herb with short, about 2–4-cm-long stem clothed with leaf sheaths. Leaf blades about 3–8 cm long and 3–5 mm wide, V-shaped with prominent keel and adaxial median groove, deciduous, linear, tapering towards the apex, glabrous with short trichomes at margins and against apex. Flowers solitary on about 7-cm-long peduncle. Tepals 12–20 mm long, white. Stamens six, anthers about six times longer than filaments. Style about three times the size of stigma. Capitulate glands present on peduncle, ovary and outer side of exterior tepals.

*Distribution:* Yemen.

*VT leaf anatomy:* Blades amphistomatic with three or four layers of palisade cells which often contain large styloid crystals; abaxial side with furrows; adaxial surface strongly undulating and wart-like as a result of tiny, short multicellular trichomes arranged in rows and with their tips pointing towards the apex. Epidermis cells are thick walled, large respiratory cavities ease the localization of adaxial stomata, abaxial stomata present in furrows (see Behnke *et al.*, 2002: fig. 7G).

*Specimens examined:* YEMEN. Hadramout Valley, Dobaibah, *Lunt* 206 (K); Mahwit, *Ironside Wood* 72/16 (BM); on Naqila path from Suq al Ribat to Al Jabin, *Radcliffe-Smith & Henchie* 4858 (K); Hadja, *Rathjens* 119 (HBG); Djebel Masna'a T[e]âm, *Wissmann* 1672 (HBG); Djebel Dhûrân, *Wissmann* 1828 (HBG); between Usil and 'Attâra, *Wissmann* 2249 (HBG); N of Radá, *E. Bisset* 217 (K); near Bani Khadayr, *E. Bisset* 49 (K); near Al Milah, *Lavranos* 1870 (K).

5. *Xerophyta humilis* (Baker) T.Durand & Schinz, *Consp. Fl. Afr.* 5: 271. 1895; Sölch & Roessler in Merxmüller, *Prodromus Fl. Südwestafr.*, fam. 152: 2. 1969; Coetzee *et al.*, *Dinteria* 9: 4, 8, figs 9, 11. 1973; Coetzee, *Dinteria* 10: 26. 1974; Smith & Ayensu, *Kew Bull.* 29: 203. 1974; Smith & Ayensu in *Fl. Trop. East*

*Afr.*, *Velloziaceae*: 2. 1975; Compton, *Fl. Swaziland in J. of South Afr. Bot.*, *Suppl.* 11: 132. 1976; Tredgold & Biegel, *Rhod. Wild Flow.*: 10 and fig. 6. 1979; Seine, *Veget. Inselb. Zimbabwe*: 117 & 233 1996; Lye & Edwards in *Fl. Ethiopia* 6: 312. 1997; Gonçalves in *Fl. Zambesiaca* 12, 2: 162. 2009.

*Vellozia humilis* Baker, *J. Bot.* 27: 4. 1889; Baker in Harvey, *Fl. Cap.* 6: 246. 1896; Baker in Oliver, *Fl. Trop. Afr.* 7: 409. 1898; Eyles, *Trans. Roy. Soc. South Afr.* 5: 329. 1916; Greves, *J. Bot.* 59: 284. 1921; Letty, *Wild Flow. Transvaal*: 73. 1962; Ayensu, *Kew Bull.* 23: 325. 1969; Jacobsen, *Kirkia* 9: 153. 1973. – *Type:* South Africa, Mpumalanga, bank of Aapges river, *Burke* 122 (K, holotype).

*Vellozia minuta* Baker, *Bull. Herb. Boiss.* II, 3: 667. 1903. – *Type:* Namibia, Hereroland, Epako, *Rautanen s.n.* (Z, holotype).

*Vellozia minuta sensu* Ayensu, *Kew Bull.* 23: 328. 1969, non *V. elegans* Oliver ex Hook.f. var. *minor* Baker.

*Barbacenia humilis* (Baker) Pax ex Burt Davy & Pott-Leendertz, *Ann. Transvaal Mus.* 3: 121 1912.

*Vellozia* spp. of Eyles, *Trans. Roy. Soc. South Afr.* 5: 329. 1916, *quoad Eyles* 517.

*Barbacenia minuta* (Baker) Dinter, *Fedde Repert.* 15: 346 (1918).

*Description:* Small herbaceous plants with short stem and a rosette of leaves about 5 (rarely to 20) cm long; leaf sheaths soon splitting into wiry fibres; blades V-shaped with shallow median adaxial groove, deciduous, glabrous, midvein and margins only towards the tip serrate. Flowers solitary and tiny, peduncle up to 5 (rarely 10) cm. Tepals 5–15 mm long, white, light violet, pink–mauve or (in Namibia) blue, exterior ones aristate. Stamens six, filaments 1–2 mm long, anthers 4 mm long. Style 1.5 mm long, stigma 2.5 mm long. Ovary 1.5–2.0 mm wide and 1.5 mm long. Peduncles, ovary and back of tepals with glands.

*Distribution:* Sudan, Ethiopia, Zambia, Zimbabwe, Mozambique, Botswana, Namibia, South Africa, Swaziland.

*VT leaf anatomy:* Blades amphistomatic, with three to five layers of short palisade cells, spongy parenchyma cells comparatively large; lower surface with shallow furrows; lateral vascular bundles with adaxial/partial adaxial V- to Y-shaped (rarely baculiform) girders and small partial abaxial baculiform girders. Bundle sheath cells are large where they border the two phloem parts and give the entire bundle a shape that looks like the Greek 'phi' (Φ). Marginal bundles circular and almost without any sclerenchyma, but additional sclerenchyma surrounded by a bundle sheath



distal to last bundle. Unusually among species with VT leaf anatomy, a hypodermis is absent (Fig. 5F).

*Specimens examined:* NAMIBIA. District Windhoek, Windhoek-Swakopmund, 26 ml., *Ihlenfeld, de Winter & Hardy* 3002 (M); Avis Mts., *H. Becker s.n.* (M); Avis Mts., *Seydel* 4203 (B); Auas Mts., Lichtenstein, *Dinter* 4459 (B). – Outjo, Otjitambi, *Naegelsbach* 191 (M); GR 552, Farm Kumkauas, *W. Giess* 12468 (M). – Karibib edge of Namib, ‘granite pans’, Naibbank, *Seydel* 150a (M); Altenbronn, Farm Nudis *Seydel* 150 (M); Neuschwaben, Undasbank, *Seydel* 1073 (BREM); Unduas granite bank, *Dinter* 7026 (M and HBG); Unduas granite bank, *Dinter* 6809 (B). – Grootfontein, Otavi, *Dinter* 5516 (B); 2 ml near Grootfontein, *Schoenfelder* 2 (B). – Without location: *Dinter* 776 (B); *Volk* 1326 (M). ZIMBABWE. West, Gwayi River Hotel Crossing, *Seine* 401 and *Seine* 545 (M). – South, Lake Mutirikwi Recreational Park, *Seine* 1495, cult. Bot. Gard. Bonn 17011 and *Seine s.n.*, cult. Bot. Gard. Bonn 11771 (M). SOUTH AFRICA. Limpopo, Rd Potgietersrus-Limburg, 18 km to Limburg, Grasveld, *Ihlenfeld* 2097 (HBG); Pietersburg District, 10 ml S of Limburg, *Schlieben* 9195 (M). Marakele National Park, *Adendorff* 16 and 18 (M). – Without location: *Farrant s.n.*, cult. Cape Town University (M).

*Comments:* The absence of a hypodermis and short palisade cells, often not much longer than spongy cells, are characters that are found in species with BT leaf anatomy, but all other anatomical details agree with VT.

6. *Xerophyta longicaulis* Hilliard, Notes Roy. Bot. Gard. Edinb. 43: 405. 1986; Crouch & Condy, Flow. Pl. Afr. 61: 48. 2009. – *Type:* South Africa, KwaZuluNatal, Royal Natal National Park, Tugela Gorge, *Trauseld* 279 (NU, holotype).

*Vellozia viscosa* Baker, white flowered variety, *Trauseld*, Wild Flow. Drakensb.: 33. 1969.

*Description:* Plants forming close mats with up to 40-cm-long decumbent stem, at the apex divided into two or more branches, densely covered with closely appressed yellow–brown leaf sheaths; blades up to 45 cm long and 8 mm wide and ending in a long attenuate tip, deciduous. Flowers solitary, peduncle 15 cm long, glandular. Tepals 35–40 mm long, mauve or white with faintly violet nerves, the outer with glandular trichomes outside. Stamens six, filaments short (about 1 mm), anthers 13 mm long. Style 4 mm long, stigma 10 mm long. Ovary about 6 mm wide and 6 mm long, turbinate.

*Distribution:* Known from the type locality only.

*BVT leaf anatomy:* Isolateral and hypostomatic with median adaxial groove and abaxial furrows; lateral vascular bundles with narrow spaces and aquiferous cells fusing into lacunae between them. A few patelliform glands are present on the adaxial side (Fig. 6B, D, F).

*Specimens examined:* SOUTH AFRICA. KwaZuluNatal, Bergville district, Royal Natal National Park, (Tugela) Gorge, *Trauseld* 279 (NU); Royal Natal National Park, Tugela Gorge, *Adendorff* 39 (M).

*Comments:* *Xerophyta longicaulis* shares all anatomical characters with *X. viscosa*, but is distinct by its longer decumbent stem, length of stigma relative to style, and its *rbcL* sequence.

7. *Xerophyta viscosa* Baker, J. Bot. 13: 235. 1875.; Smith & Ayensu, Kew Bull. 29: 202. 1974, *pro parte*, excluding *X. hereroensis*. – *Type:* South Africa, Cape Province, Pondoland, Faku Territory, *Sutherland s.n.* (K, holotype).

Non *Xerophyta viscosa sensu* Coetzee *et al.*, *Dinteria* 9: 4, 8, fig. 3, 11E. 1973 and Coetzee, *Dinteria* 10: 26, fig. 12. 1974.

Non *Xerophyta viscosa sensu* Gonçalves in Fl. Zamb. 12, 2: 175. 2009.

*Xerophyta villosa* T.Durand & Schinz, Consp. Fl. Afr. 5: 272. 1895, by mistake for *X. viscosa* Baker.

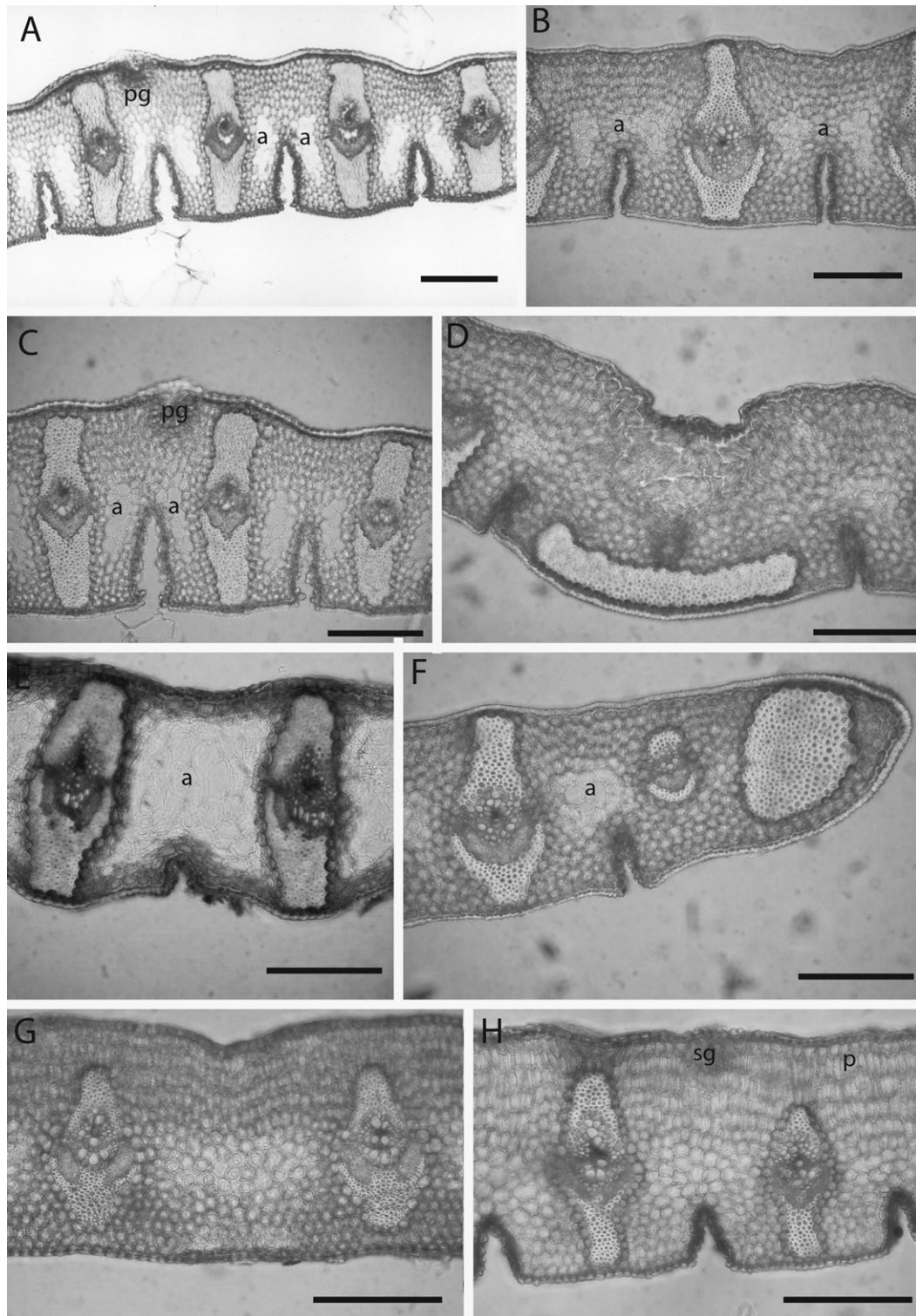
*Vellozia viscosa* Baker in Harvey, Fl. Cap. 6: 245. 1896; Greves, J. Bot. 59: 283, fig. 4.1921; Bullock, Curtis’s Bot. Mag. 76, t. 493. 1966; Ayensu, Kew Bull. 23: 327. 1969, *pro parte quoad* Tyson 896; *Trauseld*, Wild Flow. Drakensb.: 33. 1969; Guillard, Fl. Lesotho: 150. 1971; Ross, Fl. Natal: 133. 1972; Ayensu, Biotropica 5(3): 145–147 + fig. 5e, f. 1973.

Non *Xerophyta viscosa* Baker *sensu* Sölch & Roessler in Merxmüller, Prodromus Fl. Südwestaf., fam. 152: 2. 1969.

*Barbacenia viscosa* (Baker) Burt Davy & Pott-Leendertz, Ann. Transvaal Mus. 3: 121. 1912.

*Description:* Stems short, up to 5 cm long, rarely branched, clothed with leaf sheaths, the tips of which are bent outward. Leaf blades 10–20 cm long and 3–5 mm wide, deciduous, V-shaped with scabrous margins and keel. Flowers solitary, peduncle slightly longer than leaves, covered with black glandular trichomes. Tepals 35–50 mm long, bright rose-red to violet, the outer with glandular trichomes outside. Stamens six, with short filament and up to 12-mm-long anthers. Style 2–3 mm long, stigma 10–12 mm long. Ovary 4 mm wide and 5 mm long, oblong-turbinate.

*Distribution:* Lesotho, Swaziland, South Africa: East Cape, Free State, KwaZuluNatal.



**Figure 6.** Transverse sections of leaves with mixed *Barbacenia/Vellozia*-type (BVT) (A–F) and *Vellozia*-type (VT) (G, H) leaf anatomy. A, C, E, *Xerophyta viscosa* with patelliform glands (pg) and lacuna-like areas (a) on either side of abaxial furrows (A, C from Tyson 896, E from Sutherland s.n.). B, D, F, Lateral, median and marginal bundles of *Xerophyta longicaulis* (from Trauseld 279). G, Aquiferous cells between lateral bundles and absence of furrows in *Xerophyta zimbabweensis* (from Seine 1403). H, *Xerophyta hereroensis* (from Becker s.n.), leaf part with abaxial furrow, palisade cells (p), deeply sunken gland (sg) and lateral bundles of different sizes. Scale bars, 100  $\mu$ m.



*BVT leaf anatomy:* Isolateral and hypostomatic (stomata restricted to furrows) with median adaxial groove and narrow and deep abaxial furrows. Lateral bundles next to central and/or marginal bundles often with partial girders; epidermis with thickened walls, on adaxial side slightly undulated, on abaxial side distinctly papillate, in furrows coronulate; hypodermis with short broad cells; a few patelliform glands without distinct canal on adaxial side; large aquiferous cells on each side of furrows, towards leaf base uniting into large lacuna-like areas (*Sutherland s.n.*) (Fig. 6A, C, E).

*Specimens examined:* SOUTH AFRICA. East Cape, Pondoland, Faku Territory, *Sutherland s.n.* (K); Griqualand East, Mt. Currie, *Tyson* 896 (Z). – Free State, District Bethlehem, NW from Golden Gate's House, *Liebenberg* 6861 (HEID). – KwaZuluNatal, van Reenen, *Wood* 9174 (Z); near Umkomaas, *Wood* 8070 (E); Weza State Forest, Ngeli Mountain, foothills, *A. E. van Wyk* 7451 (M); Polela District, *Rennie* 451 (E); Mpendle District, Kamber area, Storm Heights, *Hilliard & Burt* 11751 (E); Mpendle District, Loteni River Valley, *Hilliard & Burt* 15129 (E); Mpendle District, Mulangane Ridge, above Carter's Neck, *Hilliard & Burt* 16963 (E); Mpendle District, Upper Loteni Valley, vicinity of Ash Cave, *Hilliard & Burt* 18092 (E); Mpendle District, Storm Heights, *Wright* 1337 (E); Drakensberg, cult. Chelsea Physics Gard., *Botfield s.n.* (K, spirit collection); Drakensberg, rocks on top of Mt. 'Rooikop' above Oliver's Hook, *Thode* 85 (B); Drakensberg, Cathkin Park, summit Little Berg, *Galpin* 11716 (K); Bergville District, Cathedral Peak area, *Robinson* 55 (E); Drakensberg, Giant's Castle, *Adendorff* 7 (M and TEX); without location, *Bajjnath s.n.* (TEX). SWAZILAND. Hlatikulu, *Johnston* 749 (E).

*Comments:* *Xerophyta viscosa* is the preferred assignment used by collectors for all South African plants with viscid leaves, and monographers (e.g. Coetzee *et al.*, 1973; Coetzee, 1974) often treat *X. schlechteri* and *X. hereroensis* as synonyms. In his 'Leaf-anatomy and systematics of Old World Velloziaceae', Ayensu (1969) studied three species with viscid leaves, *X. acuminata*, *X. schlechteri* and *X. viscosa*, and for the latter reported on fundamental differences among the samples studied: whereas most specimens (e.g. *de Winter & Hardy* 8075) clearly exhibited VT leaf anatomy with dorsiventral mesophyll and V-shaped adaxial cap in their lateral vascular bundles, some (e.g. *Tyson* 896) had isolateral mesophyll and resembled BT leaf anatomy. This conflict is in part the result of Ayensu's (1969) incorporation of *X. hereroensis*, with VT leaf anatomy, into his *Xerophyta* (*Vellozia*) *viscosa*, a treatment which was later adopted by Smith & Ayensu (1974). According to observations by

Behnke *et al.* (2002, fig. 7E) and in the present article, the leaves of *X. viscosa* are distinct by: (1) patelliform glands in their adaxial surface (Fig. 6C) (most other viscid species have glands deeply sunken into the palisade layers); (2) a total absence of crystals; and (3) the formation of chlorophyll-free aquiferous cells between their lateral vascular bundles.

8. *Xerophyta rosea* (Baker) N.L.Menezes, *Ciência e Cultura* 23: 422 (1971).

*Vellozia rosea* Baker, *Vierteljahrsschr. Nat.forsch. Ges. Zür.* 49, Heft 3, 4: 177. 1904a; Greves, *J. Bot.* 59: 282 (1921); Ayensu, *Kew Bull.* 23: 325 (1969). – *Type:* South Africa, Limpopo, on rocks, Shiluvane, *Junod* 969 (Z, holotype; G, K, isotypes).

*Barbacenia rosea* (Baker) Pax ex Burt Davy & Pott-Leendertz, *Ann. Transvaal Mus.* 3: 121. 1912.

*Xerophyta schlechteri sensu* Smith & Ayensu, *Kew Bull.* 29: 202. 1975; *sensu* Gonçalves in *Fl. Zamb.* 12, 2: 160. 2009.

*Description:* Stem short (< 5 cm long), rarely bifurcated. Leaves about 5–10 cm long and 3–5 mm wide, persistent, V-shaped with prominent midvein, no glandular spots on surfaces. Flowers solitary, peduncle 8–10 cm long, upper part covered with clear (later turning dark purple) capitate glands. Tepals 15–25 mm long, rose to pale purplish pink, the outer with glands outside. Stamens six, filaments short, anthers up to 8 mm long. Style 2–4 mm long, stigma 5–7 mm long. Ovary about 3 mm wide and 5 mm long, obconical to ovate, densely covered with glands.

*Distribution:* South Africa: Limpopo, Mpumalanga.

*VT leaf anatomy:* Amphistomatic and dorsiventral with two to three layers of long palisade cells containing long rectangular crystals, spongy tissue between lateral vascular bundles with thickened walls; adaxial surface slightly undulated, inconspicuous median adaxial groove and narrow abaxial furrows. Epidermis with upright cells, on adaxial side generally with thickened walls, on abaxial side only outer wall thickened, within furrows with coronulate and (towards furrow opening) cylindrical papillae; hypodermis with one layer of slightly thickened prismatic cells; small cells between bundle sheath and sclerenchyma girder with cubical crystals; sunken leaf glands few or absent (Fig. 5C; see also Ayensu, 1969: 325).

*Specimens examined:* SOUTH AFRICA. Limpopo, rocks near Shiluvane, *Junod* 969 (K and G); rocks Marovuni, *Junod* 2574 (G); Letaba District, Lekgalameetse Nature Reserve, Makwens, *K. & J. M. Balkwill, Gesell & Melville* 5603 (E); Potgietersrus District,

Naboomspruit, *Galpin* 133138 (K); Sekhukhuneland District, Abel Erasmus Pass at highest point, *Balkwill & Cadman* 3554 (M); Ohrigstad District, beside rd Ohrigstad to Hoedspruit, Abel Erasmus Pass, highest point, *Balkwill & Manning* 659 (E); Abel Erasmus Pass, *Adendorff* 6 (M); Wolkberg, near Serala (Klipdraai) Forest Station, *Adendorff* 10 and 13 (M); without location, *Barleys s.n.*, cult. G (from samples sent by Junod) (G).

9. *Xerophyta junodii* Behnke, **sp. nov.** – *Type*: South Africa; Limpopo, top of Mt. Mamotswiri, ii.1906, *Junod* 2768 (G, holotype; M, Z isotypes).

*Diagnosis*: Planta suffruticosa erecta, caudice 2–8 cm longo, praeter partes apicales foliis siccis et basin versus basibus foliorum induviis filis metallicis similibus oblecto. Folia 5–10 cm longa, 3–5 mm lata, lamina lineari-lanceolata, apice acuminato. Flores solitarii; pedunculo 6–12 cm longo. Tepala 15–20 mm longa, atroviolacea, exteriora glandibus paucis vestita, interiora glabra. Stamina 6, filamentis brevibus, ad tepala adnatis, antheris 7–8 mm longis. Stylus *c.* 3.5 mm longus; stigma *c.* 4 mm longum. Ovarium oblongum, glandulosum.

*Eponymy*: The specific epithet honours H. A. Junod, missionary at Shiluvane (Limpopo, South Africa) from 1899–1906, who collected the type specimen.

*Distribution*: South Africa: Limpopo.

*Description*: Stem short, up to 8 cm long and about 1 cm in diameter, rarely branched (Fig. 7A). Leaves about 5–10 cm long and 3–5 mm wide; blades V-shaped, persistent over some time with midvein on lower surface prominent, midvein and margins thickened and serrate, some glandular spots on upper surface; leaf sheaths extensively splitting (Fig. 7B) into long fibres (> 1 cm). Flowers solitary on 6–12-cm-long peduncle. Tepals 15–20 mm long, dark violet, the outer with glands outside, the inner glabrous, Stamens six, filaments short, anthers 7–8 mm long. Style and stigma of about equal sizes (3.5–4.0 mm each). Ovary 3–4 mm long and 2–3 mm in diameter, oblong, densely covered with dark glandular trichomes; peduncle and outer tepals almost eglandular.

*VT leaf anatomy*: Hypostomatic, dorsiventral with three or four (five) layers of palisade cells, strongly undulating adaxial surface, narrow median groove and narrow abaxial furrows; slim lateral vascular bundles extending to six-sevenths of leaf thickness and with abaxial Y-shaped girder, the lower arm of which is long; marginal bundles circular without caps or girders but with large distal roundish scleren-

chyma; epidermis with elliptical cells and thick outer walls, abaxial epidermis forming a two-horned anvil-like structure at furrow openings; hypodermis single layered with prismatic cells; adaxial mesophyll with deeply sunken glands and some rectangular crystals; no crystals near bundle sheath cells (Fig. 5D).

*Specimens examined*: SOUTH AFRICA. Limpopo, Summit Mamotswiri, *Junod* 2768 (G, M and Z); Naphuno 2 Distr., Sekororo, near Makhutswi River, *van Dam s.n.* (K).

*Comments*: The dark violet flowering *X. junodii* is distinct from *X. rosea* by its leaf sheaths split into long wiry fibres and blades with some glands deeply sunken into adaxial mesophyll. Leaf blade anatomy is different by its large and slim lateral vascular bundles and its abaxial furrows nearly closed by a two-horned anvil-like extension of the epidermis, among other characters. Junod's 2768 collections are annotated as 'Fleurs violet foncé, certes différent de la rosea'.

10. *Xerophyta seinei* Behnke, K.Kramer & E. Hummel, *Taxon* 51: 55. 2002; Gonçalves in *Fl. Zambes.* 12, 2: 162. 2009, *quoad Philcox & Leppard* 8850 and fig. 12.2.41. – *Type*: Zimbabwe, Rhodes Matopos National Park, View of the World, *Seine* 615 (K, holotype; B, SRGH, TEX, isotypes).

*Description*: Stem up to 10 cm high; branches about 5–10 mm in diameter and, with the exception of the apical leaf rosette, entirely covered by the persistent blades of dry leaves. Leaf blades 4–8 cm long and 4–10 mm wide, glabrous with dark secretions on both surfaces, dry leaves folded adaxial at midrib, coiling outwards. Flowers solitary, arising from the centre of the leaf rosette, peduncles 8–10 cm long, glandular, with the density of prominent capitate glands increasing towards the apex. Tepals 20–22 mm long and up to 5 mm wide, white, retuse, with the apex distinctly notched; outer tepals glandular dotted and slightly smaller than the glabrous inner ones. Stamens six, with 1.5–2.0-mm-long filaments and about 7-mm-long anthers. Style 4–6 mm, stigma about 6 mm long. Ovary about 4 mm long and about 3 mm in diameter, densely covered with dark capitate to sessile glands.

*Distribution*: Known from the type locality only.

*VT leaf anatomy*: Amphistomatic, dorsiventral with three or four layers of palisade cells, slightly undulating adaxial surface, median adaxial groove and wide shallow furrows; lateral vascular bundles comparatively small, extending only to about half of the lamina height; epidermis with thickened walls, within





**Figure 7.** A, B, *Xerophyta junodii* (from Junod 2768 ex G): entire plant (A) and magnified old leaf sheaths (B). C, *Xerophyta zimbabwensis*, cult. Bot. Gard. Bonn (17009, ex *Seine* 1403): waxy secretions on lower leaf surface. D, *Xerophyta pauciramosa*, cult. Bot. Gard. Bonn (11776, ex *Seine* s.n.): young shoot with bicoloured leaf sheaths. E, *Xerophyta equisetoides* (from Leach 11184): upper leaf surface with setae. F, *Xerophyta equisetoides* (from Schmidt, Gereau, Mhoro, Kayombo & Mwangoka 1184): upper leaf surface with many setae over furrows. Scale bars: A, B, D, 1 cm; C, 1 mm; E, F, 100  $\mu$ m.



furrows some cells with small papillae; hypodermis and palisade cells with rectangular crystals (see also Behnke *et al.*, 2002: figs 4 and 5).

*Specimens examined:* ZIMBABWE. West, Rhodes Matopos National Park, View of the World, *Seine* 615, cult. Bot. Gard. Bonn 17008 (K, B, SRGH and TEX).

*Comments:* *Philcox & Leppard* 8850 (K) is collected at the type locality of *X. seinei*, the figure chosen by Gonçalves (2009) to represent *X. schlechteri* shows the same morphology as depicted in Behnke *et al.* (2002) for *Seine* 615 (K).

11. *Xerophyta rehmannii* Behnke, **sp. nov.** – *Type:* South Africa; Mpumalanga: Roossenekal, near Mapoch's Cave, dirt road to mining site, sloping smooth rock faces. 1580 m, 25°12'50.6"S, 29°58'11.9"E, 29.iii.2005, *Adendorff* 31 (M, holotype). – *Paratype:* South Africa; Mpumalanga: Roossenekal, near Mapoch's Cave, 1500 m, 3.i.1999, *J. E. Burrows & S. M. Burrows* 6357 (BNRH, PRE).

*Diagnosis:* Planta suffruticosa erecta, caudice 5–20 cm longo, ramoso, praeter partes apicales foliis siccis obtecto. Folia 15–20 cm longa, 3–9 mm lata, tristicha, lamina non caduca, lineari, glutinosa, costa marginibusque setosis, apice longe acuminato. Flores solitarii; pedunculo 12–15 cm longo, glanduloso. Tepala 20–25 mm longa, candida, exteriora obtusa acumine brevi, extra pallide subrosea et glandibus sessilibus vestita, interiora obtusa, glabra. Stamina 6, filamentis 1–2 mm longis, antheris *c.* 8–10 mm longis. Stylus *c.* 4–6 mm longus; stigma *c.* 6–10 mm longum. Ovarium 4 mm longum, 5 mm diametro, subglobo-sum, multiglandulosum.

*Eponymy:* The specific epithet honours A. Rehmann, who collected in Southern Africa between 1875 and 1880.

*Distribution:* South Africa: Mpumalanga and Limpopo.

*Description:* Plants with distinct stem (Fig. 8D, E), 5–20 cm long, branched. Leaves 15–20 cm long and 3–9 mm wide, persistent, V-shaped with midvein and margins thickened and serrate, glandular spots on upper surface. Flowers solitary (Fig. 8F) on 12–15-cm-long peduncle covered with black capitate glands. Tepals 20–25 mm long, white, the outer externally often pale pink and with glands. Stamens six, filaments 1–2 mm long, anthers 8–10 mm long. Style about 4–6 mm long, stigma 6–10 mm long. Ovary about 4 mm long and 5 mm in diameter, subglobose, densely covered with glands.

*VT leaf anatomy:* Amphistomatic, dorsiventral with three or four layers of palisade cells, undulated upper surface, median adaxial groove, and deep abaxial furrows; lateral vascular bundles with large partial abaxial Ψ-shaped girders (towards midvein and margin Y-shaped), often with slim and long lower arm and narrow spaces between them; marginal bundles circular, without caps or girders, but with large distal roundish sclerenchyma; epidermis with thickened walls, adaxial epidermis partly double, abaxial epidermis forming U-profiles beneath lateral vascular bundles and within furrows clearly papillate; hypodermis cells slightly thickened; many glands deeply sunken into palisade tissue; aquiferous cells restricted to area above central bundle; rectangular crystals in palisade and spongy cells; cubical crystals in hypodermis and inner epidermis cells and in small cells between bundle sheath and sclerenchyma (Fig 5B).

*Specimens examined:* SOUTH AFRICA. Mpumalanga, Roossenekal near Mapoch's Cave, *Adendorff* 31 (M); Roossenekal near Mapoch's Cave, *J. E. & S. M. Burrows* 6357 (BNRH); Roossenekal, 12 km from tar road on Mapoch's Road, *J. E. Burrows & S. M. Burrows* 6355 (BNRH); near tarred road between Steelpoort and Stoffberg, *Adendorff* 5 (M); small dirt road (West) off tarred road towards Jane Furse, *Adendorff* 32 (M); Lydenburg District, Pilgrim's Rest, *Rogers* 18257 (BM). **Limpopo**, inselberg E of Pietersburg, large open sloping rock, *Adendorff* 37 (M); in saxosis pr. Houtbosch, *Schlechter* 4696 (BR and E); Houtbosch, *Rehmann* 5791 (Z); Pietersburg District, Campus U. C. N., 18 miles E of Polokwane, road to Tzaneen, *van Vuuren* 1432 (HEID).

12. *Xerophyta zimbabwensis* Behnke & E. Hummel, **sp. nov.** – *Type:* Zimbabwe, Matabeleland South, Rhodes Matopos National Park, View of the World, 20°32'41"S, 28°30'39"E, 1470 m, 2.iii.1994, *Seine* 1089 (M, holotype; B, SRGH, isotypes). – *Paratypes:* Zimbabwe, Manicaland, near Mt. Dombo, in soil-filled depression, 18°17'08"S, 32°37'50"E, 2005 m, 16.vii.1993, *Seine* 496 (M, SRGH). Zimbabwe, Mashonaland East, Domboshawa, 17°36'31"S, 31°10'32"E, 1640 m, 23.ii.1994, *Seine* 1011 (M, K). – Two plants are cultivated in the Bot. Gard. Bonn, Germany (with vouchers at M): one collected at the holotype location on 14.ii.1997, *Seine* 1497 (M), and the other near Mt. Dombo (paratype location) on 28.iii.1994, *Seine* 1403 (M).

*Diagnosis:* Planta subcaulis. Folia 15–30 cm longa, 3–8 mm lata, lamina non caduca, linearia, basin versus glutinosa, costa marginibusque denticulatis, apice longe setoso. Flores solitarii, perfecti, pedunculo





**Figure 8.** A–C, *Xerophyta adendorffii*: small plants on quartzite, flower with glandular ovary and pedicel, and beetle on flower (photographs by J. D. Adendorff, taken at Magaliesberg summit, North West, South Africa). D–F, *Xerophyta rehmannii*. D, Large mats on sloping smooth rock faces. E, Two plants with elongated stems and dried flowers (photographs by J. D. Adendorff, taken at Woodbush, off tarred road towards Jane Furse, Mpumalanga, South Africa). F, Flowering plant at Roossenekal, Mpumalanga, South Africa (photograph by J. E. Burrows). Scale bars: A–C, E, 1 cm; F, 5 cm.

15–25 cm longo, glanduloso. Tepala 20–30 mm longa, 5–8 mm lata, alba vel pallide lilacina, in circulis duobus, exteriora lanceolata acuta, extra glandibus sessilibus vestita, interiora glabra. Stamina 6, fila-

mentis *c.* 2 mm longis, antheris 8–10 mm longis. Stylus 4–5 mm longus; stigma cylindricum, *c.* 6 mm longum. Ovarium *c.* 4.5 mm longum, *c.* 3 mm diametro, oblate subglobosum, multiglandulosum.



*Distribution:* Zimbabwe.

*Description:* Perennial herbs with short stem (< 1 cm) formed by the bases of the leaf rosettes. Leaves 15–30 cm long and 3–8 mm wide, persistent, V-shaped with prominent keel, linear, somewhat viscous in their lower part and then with white secretions on abaxial surface (Fig. 7C). Leaf tip 2–3 cm long, fine and covered with bristle-like teeth, the same as found on leaf blade margins and below midrib. Flowers solitary, peduncle 15–25 cm long and covered with capitate glands which increase in number towards the apex. Tepals about 20–30 mm long and 5–8 mm wide, white to faintly lilac, in two series, lanceolate, the outer covered with sessile or subsessile glands on the outside, the inner completely glabrous. Stamens six, with about 2-mm-long filaments attached to the tepals, anthers yellow and 8–10 mm long. Style 4–5 mm long, stigma 5–6 mm long. Ovary oblate subglobose, about 4.5 mm long and 3 mm in diameter, on the outside entirely covered with capitate glands.

*VT leaf anatomy:* Amphistomatic and dorsiventral with three or four layers of short palisade cells, undulated surfaces and adaxial median groove; furrows absent; lateral vascular bundles with areas of aquiferous cells between them, partly fusing to lacunae; outer walls of epidermis cells thickened; hypodermis not thickened, patelliform glands are occasionally found and embedded into adaxial epidermis and hypodermis (Fig. 6G).

*Specimens examined:* ZIMBABWE. Central, near Mt. Dombo, *Seine* 496 and *Seine* 1403, cult. Bot. Gard. Bonn 17009 (M); Domboshava, *Seine* 1011 (K, M). – West, Rhodes Matopos National Park, View of the World, *Seine* 1089 and *Seine* 1497, cult. Bot. Gard. Bonn 17013 (M). – East, Mutare District, SW of Chido Peak, Zimunya's reserve, *Corner s.n.* (E); Nyanga District, Mt. Dombo, 19 ml W of Nyanga village, *Crook* 579 (K). – South, Lake Mutirikwi, near km 32–33 of road on S side of Lake to dam wall, *Wilkin* 739 (K). West: Matobo District, Besna Kobilá Farm, *Miller* 2563 (BR).

13. *Xerophyta hereroensis* (Schinz) N.L.Menezes, *Ciência e Cultura* 23: 422. 1971.

*Barbacenia hereroensis* Schinz, *Bull. Herb. Boiss.* 4, App. 3: 49. 1896; *Dinter*, *Fedde Repert.* 15: 346. 1918. – *Type:* Namibia, Hereroland, Tebris Pass, *Fleck* 80 (Z, holotype).

*Vellozia hereroensis* Baker in Oliver, *Fl. Trop. Afr.* 7: 411. 1898; Greves, *J. Bot.* 59: 283. 1921.

*Barbacenia jostiana* *Dinter*, *Deutsch-Südwest-Afrika*, *Fl.*, Forst & landw. *Fragm.*: 51. 1909, *nomen provisorium*.

*Vellozia viscosa* sensu Ayensu, *Kew Bull.* 23: 327. 1969, quoad de Winter & Hardy 8075.

*Xerophyta viscosa* sensu Sölch & Roessler in Merxmüller, *Prodromus Fl. Südwestafr.*, fam. 152: 2. 1969; sensu Smith & Ayensu, *Kew Bull.* 29: 202. 1974; sensu Gonçalves in *Fl. Zambes.* 12, 2: 175. 2009.

*Description:* Plants without distinct stem. Leaves about 20–30 cm long and 3–5 mm wide, persistent, slightly flanged V-shaped, midvein both on upper and lower surface prominent, midvein and margins thickened and serrate otherwise blades glabrous, dark glandular spots on upper surface and occasionally on lower surface near midrib, in dry leaves margins revolute. Flowers solitary on 15–20-cm-long peduncle which is covered in its upper part with capitate glands. Tepals 20–30 mm long, bright blue–lilac (in rare cases white: *Dinter* 6812, *Schlieben* 11318, *Giess* 11302). Stamens six, 10–15 mm long. Style and stigma equal in size (about 4–5 mm long). Ovary 4 mm long and 6 mm in diameter, obovate, densely covered with glands.

*Distribution:* Namibia.

*VT leaf anatomy:* Hypostomatic, dorsiventral with three or four layers of short palisade cells, median adaxial groove and narrow abaxial furrows; lateral vascular bundles with V-shaped cap or partial adaxial Y-shaped girders and abaxial Y- or  $\psi$ -shaped girders; bundles in the highest point of flanges are comparatively large with only the hypodermis bridging between bundle sheath and adaxial epidermis, those next to midvein and margin are small; double space between lateral vascular bundles in part occupied by thin-walled, chlorophyll-free cells (aquiferous cells otherwise restricted to area below median groove); epidermis cells with thick outer walls and stomata restricted to abaxial furrows; deeply sunken glands regularly present (Fig. 6H).

*Specimens examined:* NAMIBIA. Hereroland, Tebris Pass, *Fleck* 80 (Z); mica schist mountains E of Windhoek, *Dinter* 870 (Z). – District Windhoek, Neudam Kuppe, H. Becker *s.n.* (M); Neudam Experimental Farm, 20 km E Windhoek, *de Winter* 2372 (M); WIN 32, Farm Regenstein, on summit Großherzog Friedrichsberg, W. & B. *Giess* 11641 (M); Zassas Mts., Binsenheim, *Leippert* 4578 (M). – Karibib, granite banks at Okonzawa, *Dinter* 6812 (HBG and M); Otjimbingwe, *Fischer* 194 (HBG); massif of rocks Undasbank, *Kinges* 3032 (M); Pontok Mts., *Kinges* 3647 (M); Neuschwaben, Undasbank, *Seydel* 1078 (BREM and B); edge of Namib, Kubas Mts., *Seydel* 2018 (M); Farm Ameib in Erongo Mts., more or less 18 ml W Usakos, *de Winter & Hardy* 8075 (M); Erongo Mts. near Usakos,

*Schlieben* 10318 (HEID); KAR 60, near Phillipsgrotte, W. Giess 11302 (M); Farm Ameib at S-end of Erongo, about 30 km N of Usakos, Greuter 20120 (B); KAR 112, Farm Anschluss, granite mountains N of main road, W. Giess, Volk & Bleissner 5671 (M). – Omaruru, Erongo Mts., R. & F. v. Wettstein 151 (M); Ameib River in Erongo Mts., R. & F. v. Wettstein 254 (M); Erongo, Farm Omandumba, Bleissner 46 (M). – Rehoboth, Farm Weißenfels, H. & E. Walter 1684 (M); Rd Windhoek–Walfish Bay, Farm Gamsberg 23, 75 km W of Rehoboth, Wannorp 171 (K); REM 18, Gamsbergpass, Farm Hopefield, W. Giess & Gaff 10979 (M); Gamsbergpass on the way down, Farm Hopefield, W. Giess 9124 (M); Gamsberg, on the plateau, Meyer 1117 (M and BR); Donkerhoek, Volk 2762 (M); Farm Weenen, Volk 11492a (M). – Maltahöhe, Naukluft Mts., top of mountains, Blesskreuz, McDonald 472 (BM); Naukluft Mts., Blässkreuz, Volk 914 (M).

*Comments:* *Xerophyta hereroensis* was diagnosed by Schinz (1896) and had widely been accepted by botanists collecting in Namibia. However, Sölch & Roessler (1969), in their treatment of Namibian Velloziaceae, included all these collections within the South African *X. viscosa*. During their 1971 herbarium work for the ‘Classification of Old World Velloziaceae’, Smith and Ayensu determined most of the *X. hereroensis* specimens as the South African *X. schlechteri*, but, in their 1974 publication, incorporated *X. hereroensis* into *X. viscosa*. Flower and vegetative morphology, leaf anatomy and genetic analysis presented here clearly confirm Schinz’s (1896) treatment as a distinct species.

14. *Xerophyta adendorffii* Behnke, **sp. nov.** – *Type:* South Africa, North West Province, about 5 km S of Broederstroom, on slopes W of Crocodile River, on either side of Road 512 from Broederstroom to Lanseria, in rocky terrain consisting mainly of dolomite with chert inclusions, about 1300 m, 5.iii.2004, *Adendorff* 1 (M, holotype; B, K, isotypes).

*Diagnosis:* Herba perennis, acaulis. Folia 6–12 cm longa, 2–5 mm lata, lamina non caduca, lineari-lanceolata, subfalcata, glutinosa, costa marginibusque setosis, apice acuminato; folia sicca ad costam adaxialiter plicata et partim torsiva. Flores solitarii; pedunculo 10–15 cm longo, glanduloso. Tepala 15–20 mm longa, candida, exteriora cuspidata, extra glandulosa, interiora obtusa, glabra. Stamina 6, filamentis c. 1 mm longis, antheris 9–10 mm longis. Stylus 3–4 mm longus, stigma 5–6 mm longum. Ovarium 3 mm longum, 4 mm diametro, subglobo-sum, glandulosum.

*Eponymy:* The specific epithet honours Jaco D. Adendorff, who collected the type specimen and made several other collecting trips into the North West, Mpumalanga, Gauteng and KwaZuluNatal provinces of South Africa.

*Distribution:* South Africa: North West, Gauteng.

*Description:* Perennial herbs without distinct stem (Fig. 8A). Leaves 6–12 cm long and 2–5 mm wide, blades persistent, V-shaped with prominent keel, falcate with an acuminate tip, moderately viscid, margins and midrib distinctly setose, dry leaves folded at midvein and partly spirally twisted. Flowers solitary (Fig. 8B, C) on 10–15-cm-long peduncle with dark glands. Tepals 15–20 mm long, white, the outer cuspidate and with glands on the outside, the inner obtuse and glabrous. Stamens six, filaments short (about 1–2 mm), anthers 9–10 mm long. Style 3–4 mm long and clearly shorter than stigma (5–6 mm). Ovary 3 mm long and 4 mm in diameter, almost globose, densely covered with dark glands.

*VT leaf anatomy:* Hypostomatic, small lateral vascular bundles; central bundle with large partial abaxial crescentiform girder and tiny adaxial cap; marginal bundles circular, epidermis with thickened walls, on lower surface with coronulate papillae within furrows, upper surface slightly undulated; hypodermis and small cells between bundle sheath and sclerenchyma with cubical crystals, palisade cells with rectangular crystals; glands regularly present, deeply sunken into palisade tissue (Fig. 5A).

*Specimens examined:* SOUTH AFRICA. North West, about 5 km S of Broederstroom, on slopes W of Crocodile River, on either side of rd from Broederstroom to Lanseria, *Adendorff* 1, 3, and 24 (M); on westside of Lime Hill, *Adendorff* 22 (M); 10 km west of Hartbeespoort, within the main range of the Magaliesberg, *Adendorff* 38 (M); Brits, Magaliesberg, *Adendorff* 14 and 25 (M); Brits, Magaliesberg, summit quartzite, *Adendorff* 15 (M); Brits District, Magaliesberg, Jacksontuin, *Worsdell s.n.* (K); Magaliesberg, *Mogg s.n.* (M). – Gauteng, Hennopsrivier, near crossing with road R 511, *Adendorff* 21, 23 and 27 (M).

15. *Xerophyta acuminata* (Baker) N.L.Menezes, *Ciência e Cultura* 23: 422. 1971; Cufodontis, *Bull. Jard. Bot. Nat. Belge* 42, Suppl.: 1580. 1972; Smith & Ayensu, *Kew Bull.* 29: 199. 1974; Thulin, *Fl. Somalia* 4: 77. 1995.

*Vellozia acuminata* Baker, *Bull. Misc. Inform. Kew* 1895: 228. 1895b; Baker in Oliver, *Fl. Trop. Afr.* 7: 410. 1898; Greves, *J. Bot.* 59: 283. 1921; Ayensu, *Kew*



Bull. 23: 323. 1969. – *Type*: Somalia, Golis range, in rock water courses near Woob, *Cole s.n.* (K, holotype).

*Description*: Stem short. Leaves about 20–30 cm long and 5–8 mm wide; leaf blades V-shaped, persistent, midvein on both upper and lower surfaces prominent, midvein and margins thickened and serrate, on lower surface 10–12 distinct veins between midvein and margin, glandular spots on upper surface and (less frequent) on margins. Flowers solitary; peduncle about 6–12 cm long with glands. Tepals up to 25 mm long, white flushed with purple, obtuse, the outer glandular outside. Stamens six, about 8 mm long. Ovary about 8 mm in diameter and 10 mm long, oblong, covered with dark glands.

*Distribution*: Somalia.

*VT leaf anatomy*: Amphistomatic, dorsiventral with three or four layers of palisade cells, median adaxial groove and deep, narrow abaxial furrows; epidermis with thickened walls, within furrows with coronulate papillae; hypodermis cells slightly thickened; rectangular crystals in palisade cells and cubical crystals in small cells between bundle sheath (see also Ayensu, 1969: 323 + fig. 3, 1a–b and Behnke *et al.*, 2002: fig. 7H).

*Specimens examined*: SOMALIA. Danodleh, *Bally* 11046 (K); Eastern Al Madu Range, *Gillett & Aglener s.n.* (BM).

16. *Xerophyta schlechteri* (Baker) N.L.Menezes, *Ciência e Cultura* 23: 422. 1971; Smith & Ayensu, *Kew Bull.* 29: 202. 1974; Tredgold & Biegel, *Rhod. Wild Flow.*: 10. 1979; Gonçalves in *Fl. Zambes.* 12, 2: 160. 2009, *pro parte*, excluding *Philcox & Leppard* 8850 and excluding *Vellozia rosea*.

*Vellozia schlechteri* Baker, *Bull. Herb. Boiss.* II, 4:1003. 1904b; Greves, *J. Bot.* 59: 283. 1921; Ayensu, *Kew Bull.* 23: 326. 1969. – *Type*: South Africa, Gauteng, Mount Donkerhoek, *Schlechter* 4136 (Z, holotype).

*Barbacenia schlechteri* (Baker) Burt Davy & Pott-Leendertz, *Ann. Transvaal Mus.* 3: 121. 1912.

*Xerophyta viscosa sensu* Coetzee *et al.*, *Dinteria* 9: 4, 8, fig. 3, 11E. 1973; Coetzee, *Dinteria* 10: 26, fig. 12. 1974.

*Description*: Perennial herbs without distinct stem. Leaves about 15 cm long and 3–5 mm wide, blade persistent, V-shaped, slightly flanged, linear with acuminate tip, midvein on both adaxial and abaxial surfaces prominent, midvein and margins thickened and serrate, margins not revolute, glandular spots on adaxial surface. Flowers solitary on 12–15-cm-long peduncle. Tepals 20–25 cm long, white to cream, the

outer apiculate, the inner obtuse. Stamens six, filaments short, anthers about 10 mm long. Style 3–4 mm long, stigma about the same size or slightly longer. Ovary 3–4 mm long and 4–5 mm in diameter, subglobose. Peduncle, ovary and outside of external tepals covered with dark glands.

*Distribution*: Zimbabwe, Botswana, South Africa: Gauteng, Limpopo, Mpumalanga, North West.

*VT leaf anatomy*: Amphistomatic, dorsiventral with (2–)3–(4) layers of palisade cells; upper surface slightly undulated, lower surface with deep and narrow furrows widening into oval area; epidermis with thickened walls, strong beneath lateral vascular bundles, and in furrows with coronulate papillae; stomata mainly restricted to inner parts of furrows, but a few found also on adaxial surface; hypodermis cells small, slightly thickened; rectangular crystals in palisade cells and cubical crystals in small cells next to bundle sheath (see also Ayensu, 1969: 326 + plate 2, 3 and Behnke *et al.*, 2002: fig. 7A, D).

*Specimens examined*: ZIMBABWE. North, Guruve District, Nyamunyeche Estate, *Nyariri* 711 (E); Guruve District, Nyamunyeche Estate, on Great Dyke, *Nyariri* 856 (E); Great Dyke, Caesar's Pass, *Baudesson, Leteinturier & Malaisse* 57 (BR); Great Dyke, Mutorashanga Pass, Umvukwe Range, *Baudesson, Leteinturier & Malaisse* 100 (BR); Great Dyke, 4 km near Red Lichen, *Baudesson, Leteinturier & Malaisse* 641 (BR); Great Dyke, Horseshoe, Nyarasuswi, *Baudesson, Leteinturier & Malaisse* 698 (BR); Guruve District, Horseshoe, Great Dyke, 2 km ESE of Red Lichen, *Baudesson, Leteinturier & Malaisse* 613 (BR). – South, Mberengwa District, Mt. Buhwa, *Pope* 948 (BR); Masvingo, Bikita District, Turwi–Dafana confluence, Dwala W bank, Turwi, *Biegel* 3011 (M and B). BOTSWANA. South East, 10 km N of Lobatse, *Hansen* 3204 (K). SOUTH AFRICA. Gauteng, in saxosis Donkerhoek, *Schlechter* 4136 (Z). – Mpumalanga, NE corner of Buffelskloof Nature Reserve, *J. E. & S. M. Burrows* 4211 (BNRH); Buffelskloof Nature Reserve, *Weigend* 2924 (M). – Limpopo, Marakele National Park, *Adendorff* 17 (M). – North West, near Assen, *Adendorff* 19 and 28 (M); Waterpoort District, Messina, about 56 ml NW of Greefswald, *Pienaar* 327 (K); Thabazimbi District, Waterberg Range, 30 km W of Vaalwater, Farm Sterkstroom, *K. & J. M. Balkwill* 4349 (E); Thabazimbi District, Waterberg Range, 30 km W of Vaalwater, Farm Onvermoeid, *K. & J. M. Balkwill, Gesell & Williamson* 5512 (E); Soutpansberg, Dungola Reserve, Farm Hilda, *Codd* 4057 (K); Subiaco Mission, Molepo Reserve, 20 ml E of Polokwane, *Gerstner* 5579 (K); KwaNdebele Homeland,

Goederede (Diana Ranch), *Retief* 650 (K); Rustenburg Kloof, top of Kloof, *Prosser* 1836 (K).

*Comments:* Figure 3 in Coetzee *et al.* (1973) depicts a plant of *X. schlechteri* from Loskopdam Nature Reserve (Mpumalanga), not *X. viscosa* as mentioned. Coetzee (1974) describes and depicts dorsiventral leaf anatomy, as is characteristic of *X. schlechteri*, in her *X. viscosa* (p. 22 and fig. 12).

17. *Xerophyta simulans* L.B.Sm. & Ayensu, Kew Bull. 29: 189–190, 191, fig. 1. 1974; Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 6. 1975; Gonçalves in Fl. Zambes. 12, 2: 158. 2009. – *Type:* Uganda, Acholi District, Gulu, Kilak, A. S. Thomas 4046 (K, holotype).

*Description:* Stem to 2.4 m high, branches short, terete, to 1 cm in diameter. Leaf sheaths dark brown, about 4 cm long, soon splitting and disintegrating after abscission. Leaf blades up to 30 cm long and 1.2 cm wide, deciduous, linear attenuate, flat with distinct midvein and with lamina on both sides plicate, pubescent at base only with white spreading trichomes. Flowers solitary, peduncle about 5 cm long at apex of branches. Tepals 20–35 mm long, white or pale mauve, almond scented. Stamens with short filaments, anthers about half as long as tepals. Stigma as long as style base, length of style about two-thirds of tepals. Ovary 6–10 mm long, ovate to subcylindrical with eglandular emergences, swollen at base and with fine apex, sometimes two-forked.

*Distribution:* Sudan, Uganda, Tanzania, Zambia, Zimbabwe.

*PT leaf anatomy:* Dorsiventral with two layers of palisade cells and spongy mesophyll, amphistomatic; 10–13 major lateral vascular bundles in the lower ‘turning points’ of the plicate lamina and a multitude of minor bundles in the ascending and descending sides, with five to seven minor bundles between two major ones; major bundles are drop-like or club-shaped with broad U-shaped abaxial girder, three or four large vessels, two phloem parts, and a slim inverted Y-shaped (partial) adaxial girder; minor bundles within chlorenchyma, at the border between palisade and spongy mesophyll, completely circular, surrounded by a bundle sheath, and composed of only 10–15 cells: one to four tracheal elements, some vascular parenchyma and a few (if any) phloem cells; central bundle small with a large abaxial, winged crescentiform girder and a tiny adaxial cap composed of only about five sclerenchyma cells; marginal bundles small and, on their distal side, surrounded by a large ovate sclerenchyma; epidermis cells with thick outer walls; groups of adaxial aquiferous cells on each

side of major bundles; subepidermal sclerenchyma strands are present between major bundles, large ones evenly spaced on the adaxial side and smaller ones irregularly distributed on the abaxial side (Fig. 9; see also Smith & Ayensu, 1974: fig. 1, 5 + 6).

*Specimens examined:* SUDAN. Equatorial Province, Imatong Mts., NE of mountains, N of Molongori, *Friis & Vollesen* 1150 (BR); Torit District, Lomolongori, Itaba Hill, *Jackson* 1807 (K). UGANDA. Chua District, Paimol, *Eggeling* 1765 (K); U1, Moroto District, Watershed Road, *Wilson* 2061 (K); Acholi District, at Omnia Onyemya National Park, *Liebenberg* 409 (K). TANZANIA. Rukwa, Mpanda District, Buyenze, 20–30 ml S of Uvinza, *Procter* 413 (K).

*Comments:* The leaf anatomy of *X. simulans* is singular in the African Velloziaceae and is met in only one American species, *Vellozia plicata*. Moreover, the presence of two types of lateral vascular bundle is a unique feature repeatedly found in the leaves of other members of Pandanales: *Asplundia*, *Sphaeradenia* and other taxa in Cyclanthaceae contain small lateral bundles of second or third order that are similar to the minor bundles in *X. simulans* (Wilder, 1985; Wirsching, 2002).

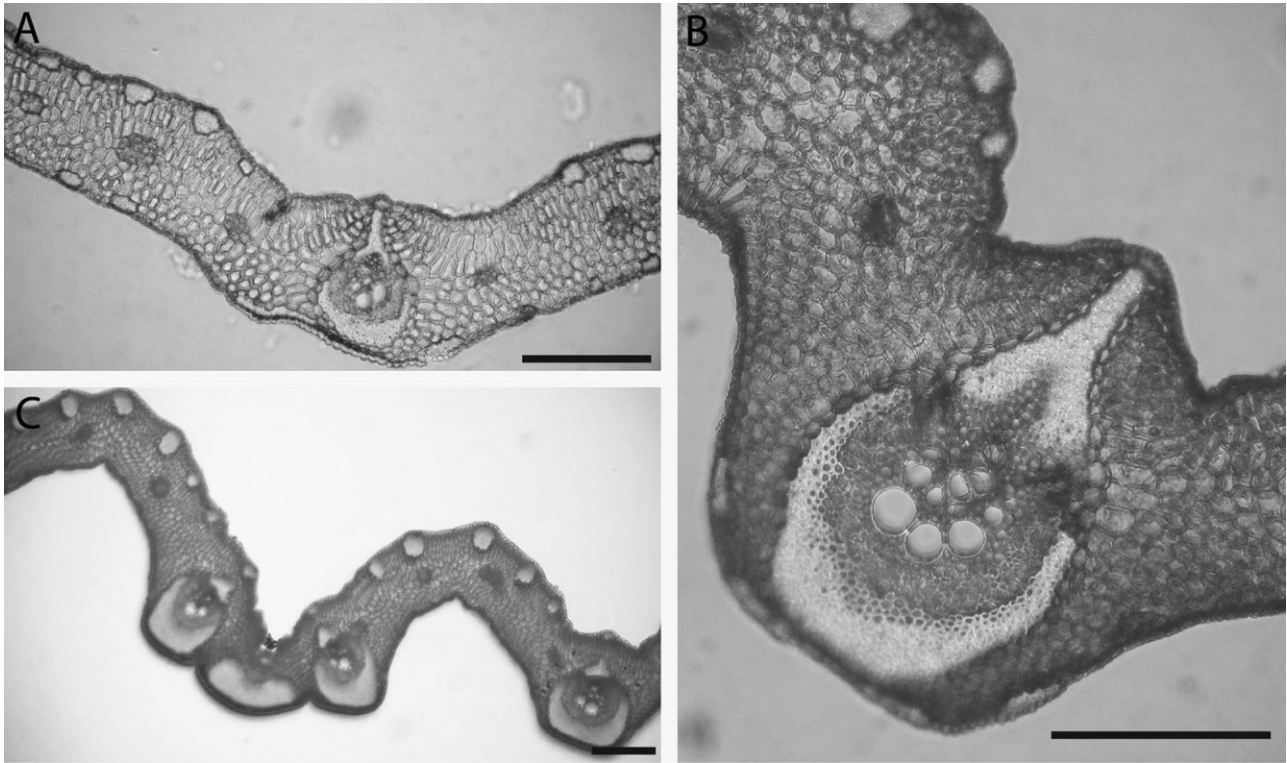
18. *Xerophyta goetzei* (Harms) L.B.Sm. & Ayensu, Kew Bull. 29: 188. 1974; Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 2. 1975.

*Barbacenia goetzei* Harms, Englers Bot. Jahrb. 28: 363. 1900. – *Type:* Tanzania, Iringa District, Little Ruaha River, c. 600 m, 4.i.1899, *Goetze* 426 (B, holotype; K, isotype).

*Description:* Stem 1–2 m high and about 10–15 cm in diameter; branches moderately thick and covered with leaf sheaths that show many parallel nerves and are almost sharply cut. Leaves about 15–25 cm long and 4–8 mm wide, at the top of branches, blades deciduous, V-shaped with prominent midvein, covered on both sides with fine, about 2–3-mm-long, glassy transparent trichomes. Flowers solitary on 4–7-cm-long glabrous peduncle. Tepals 4–5 cm long, pale blue. Ovary 8 mm long, totally glabrous.

*Distribution:* Tanzania.

*BT leaf anatomy:* Amphistomatic and with deep opposite furrows; outer wall of epidermis cells thickened; simple unicellular trichomes in multicellular base (emergence) on adaxial and abaxial sides; aquiferous cells below adaxial furrows; short adaxial and abaxial sclerenchyma bands underline the epidermis on either side of lateral vascular bundles (Fig. 10E).



**Figure 9.** Transverse sections of *Xerophyta simulans* leaves with *Plicata*-type (PT) leaf anatomy. A, Large bundle and small circular second-order bundles, adaxial aquiferous cells on either side of large bundle, small subepidermal sclerenchyma strands in adaxial and abaxial position. B, Median part of plicate leaf: median bundle accompanied by two large lateral bundles, between two large bundles smaller (second-order) bundles are located in the ascending and descending leaf parts. C, Large bundles are drop-shaped with an inversely Y-shaped adaxial girder, a semicircular phloem surrounding the xylem, and a broad cup-shaped abaxial girder. (A from Friis & Vollesen 1150, B, C from Procter 413). Scale bars, 100 µm.

*Specimens examined:* TANZANIA. Iringa, Little Ruaha River, Goetze 426 (B). – Tangea, Kwai, Usambara Mts., Albert *s.n.* (B).

19. *Xerophyta demeesmaekeriana* P.A.Duvign. & Dewit, Bull. Soc. Roy. Bot. Belgique 96: 145. 1963. – *Type:* Democratic Republic of the Congo, Katanga, Kambove–Kamoia, sloping steppe with *Cryptosepalum* on cupriferous soil, 13.xi.1959, Duvigneaud 4095 (BRLU, holotype).

*Xerophyta zambiana* L.B.Sm. & Ayensu, Kew Bull. 29: 198. 1974, excluding *Angus* 886; Gonçalves in Fl. Zambes. 12, 2: 172. 2009, excluding *de Koning* 7563 & *West* 6132. – *Type:* Zambia, *Robson* 898 (BM, holotype; BR, K, isotypes).

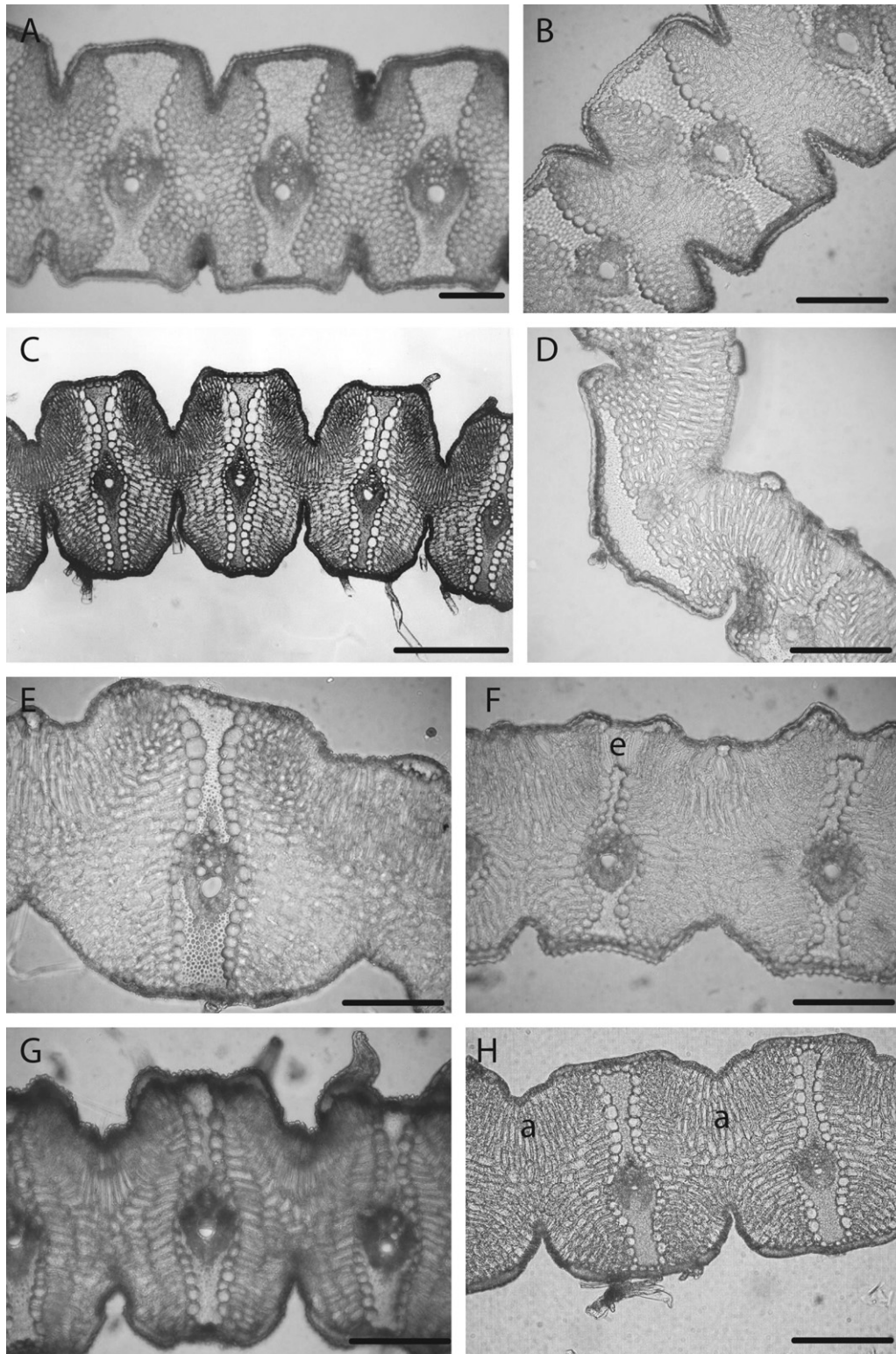
*Xerophyta demeesmaekeriana* Smith & Ayensu, Kew Bull. 29: 189. 1974, by mistake for *X. demeesmaekeriana*.

*Description:* Plants 50–80 cm high with almost undivided, 3–5-cm-wide stems and with branches clustered at base; branches conically tapering and covered with

long (to 7 cm) brownish leaf sheaths split into many parallel fibres that are laterally meshed. Leaves up to 50 cm long and to 1.7 cm wide, in terminal pseudo-rosette, blades deciduous, V-shaped with prominent midvein, linear with filiform attenuate tips, young leaves covered on both sides with 1.0–1.5-mm-long whitish silky and glossy trichomes, spreading at the margins and close appressed on surfaces; older leaves densely covered with long appressed trichomes. Flowers solitary on 10–15-cm-long peduncle, that is covered with woolly trichomes decreasing in density towards the apex and then, near the ovary, being replaced by sessile glands. Tepals 20–45 mm long, pink to mauve inside and greenish outside, with acute tips and few glands on the outside of the outer tepals. Stamens six, with short filaments and about 12-mm-long anthers. Style 3–4 mm, stigma 10 mm long. Ovary ellipsoid, covered with sessile glands that are flattened on top (Fig. 15H).

*Distribution:* Democratic Republic of the Congo, Zambia, Mozambique.





**Figure 10.** Transverse sections of leaves with basic *Barbacenia*-type (BT) leaf anatomy. A, B, *Xerophyta splendens* (from Chapman 8165). C, D, *Xerophyta spekei* (C from Burt 5426, D from Verdcourt & Polhill 2697). E, *Xerophyta goetzei* (from Albert *s.n.*). F, *Xerophyta suaveolens* (from Angus 781) with extended adaxial bundle sheath cells (e). G, *Xerophyta suaveolens* (from Rand 1) with adaxial setae. H, *Xerophyta pseudopinifolia* (from Torre & Paiva 10694) with aquiferous cells (a). Scale bars, 100  $\mu$ m.



*BT leaf anatomy:* Amphistomatic and with narrow, deep opposite furrows; central bundle with small adaxial cap and a large abaxial ascending crescentiform girder, often also embracing the first lateral vascular bundle; outer wall of epidermis cells thickened, slightly papillate, stomata mainly confined to furrows; short sclerenchyma bands underline the epidermis adjacent to lateral bundles, and both on the adaxial and abaxial sides; aquiferous cells below furrows; many simple unicellular trichomes, often occurring in fascicles of two, three or more, are present on both surfaces (Fig. 11A).

*Specimens examined:* DEMOCRATIC REPUBLIC OF THE CONGO. Katanga, Kambove–Kamoia, *Duvigneaud* 4095V2 (BRLU); between Lukuni and Luishia, *Duvigneaud* 4396V (BRLU); Shinkolobwe, *Malaisse* 11804 (BR); Mitwaba District, Tanda (Kundelungu Natl. Park), *Coget* 204 (BR); Luswishi, copper mine, *Malaisse* 12832 (BR); Mine de Luswishi, *Lefebvre, Leteinturier & Malaisse* 13 (BR); Sokoroshe Hill, road Lubumbashi–Likasi, km 50, about 2 km from village, *Lefebvre, Leteinturier & Malaisse* 42 (BR); Ruiss. Kilongo, 100 km on road Jadotville–Kolwezi, *Schmitz* 5942 (BR); District Jadotville, 60 km N of Elizabethville, *de Caters* 42 (BR); Lupoto, 20 km ENE of Elizabethville, *Schmitz* 6043 (BR). ZAMBIA. West, Mine at Luswishi, *Malaisse* 11202 (BR). – North: Nkumbo Hill (Chibuli Hill), *Leteinturier, Malaisse & Matera* 463A (BR). – East: Petauke District, Nyimba–Luembe Road, *Robson* 898 (BR). – South, Victoria Falls District, Hubert Young Drive, *Wild* 3152 (K). – Central, Serenje District, *Fanshawe* 11654 (K); Katondwe, *Fanshawe* 10288 (K); c. 45 km from Kapiri Mposhi on road to Mkushi, *J. E. & S. M. Burrows* 6456 (BNRH).

*Comments:* *Xerophyta demeesmaekeriana* is the only African species with peduncles that are covered with two different trichomes: hair-like in its lower two-thirds and glandular in the upper part connecting to the ovary.

20. *Xerophyta scabrida* (Pax) T. Durand & Schinz, *Consp. Fl. Afr.* 5: 271. 1895; Smith & Ayensu, *Kew Bull.* 29: 202. 1974, *quoad Pogge* 423; Smith & Ayensu in *Fl. Trop. East Afr., Velloziaceae*: 8. 1974, *quoad Pogge* 423; Gonçalves in *Fl. Zambes.* 12, 2: 160. 2009, *quoad Pogge* 423.

*Barbacenia scabrida* Pax, *Englers Bot. Jahrb.* 15: 144. 1893 – *Type:* Angola, Quango, 10.5°S., *Pogge* 423 (B, holotype).

*Vellozia scabrida* (Pax) Baker in Oliver, *Fl. Trop. Afr.* 7: 410. 1898; Greves, *J. Bot.* 59: 283. 1921.

*Description:* Stem short, covered with about 2.5-cm-wide and 3.5-cm-long fan-like leaf sheaths (! de Witte

3511); blades 10–12 cm long and 4–7 mm wide, deciduous, V-shaped with prominent midvein and strong veins on both sides, linear-lanceolate with long tip, midrib and margins with short stiff trichomes pointing to the leaf tip, abaxial surface densely covered with stiff eglandular emergences oriented towards the veins, adaxial surface almost glabrous. Flowers solitary on 10-cm-long peduncles in the upper part covered with glands. Tepals about 3 cm long, white, tinted with violet. Stamens six, filaments short, anthers about 1.3–2.0 cm long. Style 4 mm long, stigma 10 mm long. Ovary 4 mm in diameter and 10 mm long, turbinate, densely covered with glands.

*Distribution:* Angola, Democratic Republic of the Congo.

*BT leaf anatomy:* Amphistomatic and with deep opposite furrows; epidermis cell walls moderately thickened, stomata confined to furrow parts that are not underlined by sclerenchyma; short sclerenchyma bands adjacent to lateral bundles bending into the furrow opening; short stiff eglandular emergences present on furrow corners of adaxial side (Fig. 4E, H).

*Specimens examined:* DEMOCRATIC REPUBLIC OF THE CONGO. Katanga, Parc de l'Upemba, *de Witte* 3311 (BR, K). ANGOLA. At Quango, *Pogge* 423 (B).

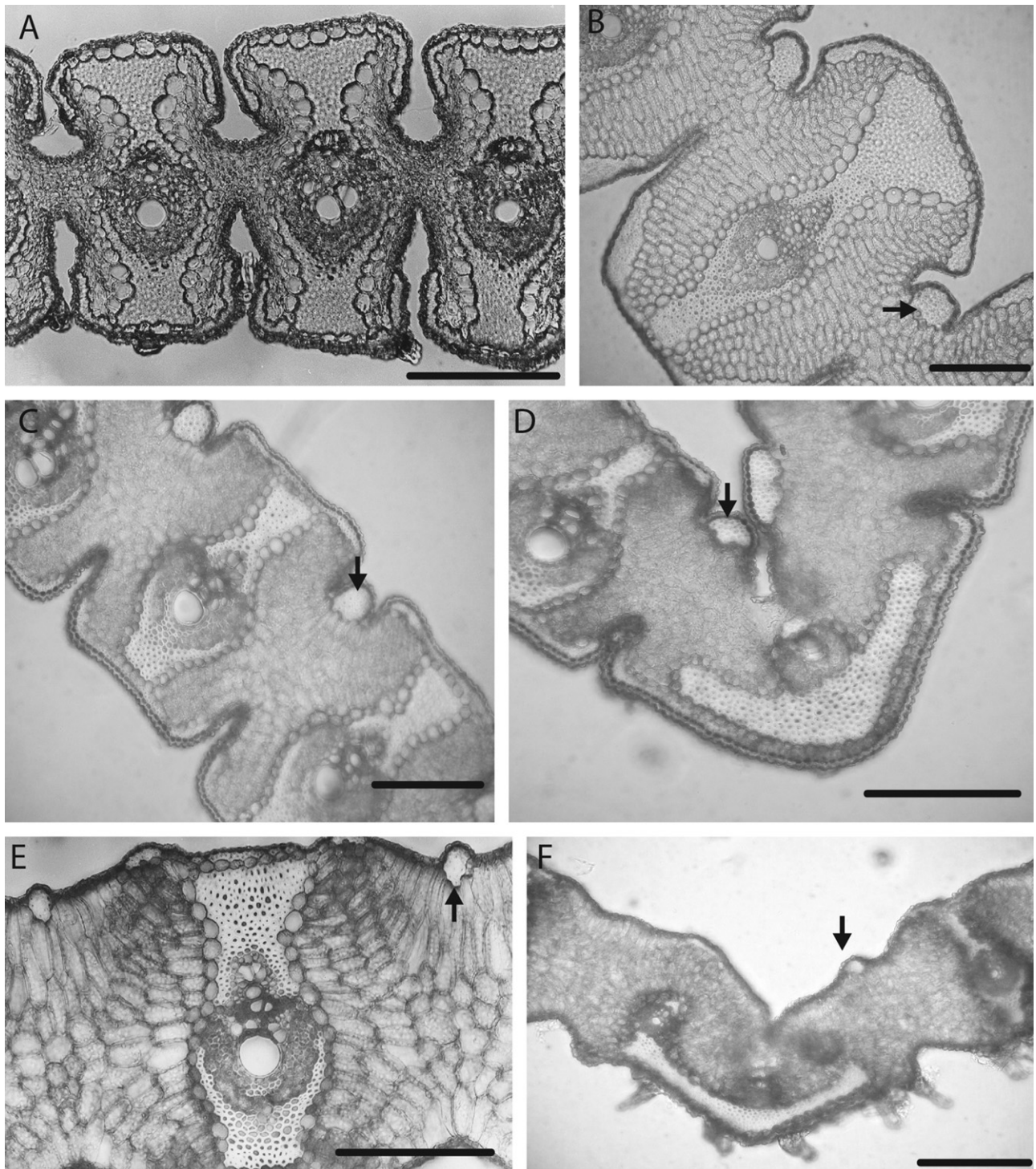
*Comments:* Smith & Ayensu (1974, 1975) described VT anatomy in many specimens identified as *X. scabrida*, mainly from Tanzania. However, the type specimen, collected in Angola (*Pogge* 423), which they did not study, has BT anatomy. A collection from Katanga (*de Witte* 3511) with a sheet in K was annotated by L. B. Smith as 'keys near *scabrida*, but not possible to resolve now; . . . B [= *Barbacenia*]-leaf type; change key or double entry'.

The VT anatomy, combined with other characters in most collections assigned to *X. scabrida*, led us to describe a new species, *X. tanzaniana*.

21. *Xerophyta argentea* (Wild) L.B.Sm. & Ayensu, *Kew Bull.* 29: 198. 1974; Gonçalves in *Fl. Zambes.* 12, 2: 171. 2009.

*Vellozia argentea* Wild, *Kirkia* 4: 135. 1964; Wild, *Kirkia* 6: 215. 1968. – *Type:* Zimbabwe, Chimanimani, among crags on quartzite peak near Mount Peza, 6000 ft, 16.x.1950, *Wild* 3612 (SRGH, holotype; B, BR, K, isotypes).

*Description:* Plants up to 4 m high with erect sparsely branched stem, branches to 1.7 cm in diameter, covered with dark grey leaf sheaths that do not split early, but persist for some years as emarginate, 2.5 cm long and 1.0 cm wide scales; blades about 25 cm long



**Figure 11.** Transverse sections of leaves with basic *Barbacenia*-type (BT) leaf anatomy. A, *Xerophyta demeesmaekeriana* (from *Leteinturier, Malaisse & Matera* 463): unexpanded leaf part with deep opposite furrows. B, Lateral bundle of *Xerophyta villosa* (from *Adendorff* 36). C, D, Lateral and median bundles of *Xerophyta monroi* (from *Seine* 767). E, Lateral bundle of *Xerophyta hirtiflora* (from *Seine s.n.*). F, Midvein of *Xerophyta eylesii* with two bundles (from *Angus* 886). Arrows point to sclerenchyma knobs. Scale bars, 100  $\mu\text{m}$ .



and 5 mm wide, deciduous, V-shaped with prominent midvein, linear, with acuminate tip, their upper surface is glabrous or nearly so with a few trichomes, the lower surface is covered with closely compacted and appressed white trichomes, giving the entire surface a silvery shine. Flowers solitary on 12-cm-long peduncles covered with brown glands. Tepals about  $3.5 \times 1.4 \text{ cm}^2$ , lilac, oblong elliptical, on the outside with purple glands. Stamens with about 1.3-cm-long anthers and short sessile filament. Style filiform, about 2.5 cm long. Ovary turbinate, densely covered with glands.

*Distribution:* Known from the type locality only.

*BT leaf anatomy:* Hypostomatic and with deep opposite furrows; epidermis cells with thickened outer wall, within adaxial furrows fusing to a continuous V-shaped line; short sclerenchyma bands underline the epidermis on the abaxial side of lateral bundles, on the adaxial side the sclerenchyma bands are restricted to areas adjacent to the bundles; directly above adaxial girders the epidermis, subepidermis and bundle sheath are often dark stained (see also Behnke *et al.*, 2002: fig. 7I).

*Specimens examined:* ZIMBABWE. East, Chimanimani: Chimanimani Mts., Mt. Peza, *Wild* 3612 (B and BR); Chimanimani Mts., peak next to Mt. Peza, *Munch* 286 (K); Chimanimani Mts., Martin Forest Res., *Mavi* 606 (M).

22. *Xerophyta kirkii* (Hemsl.) L.B.Sm. & Ayensu, *Kew Bull.* 29: 201. 1974; Gonçalves in *Fl. Zambes.* 12, 2: 174. 2009.

*Vellozia kirkii* Hemsl., *Bot. Mag.* 130: sub t 7962. 1904; Greves, *J. Bot.* 59: 283. 1921. – *Type:* Malawi, Zomba, *Kirk s.n.* (K, holotype).

*Vellozia equisetoides sensu* Baker in Oliver, *Fl. Trop. Afr.* 7: 411. 1898, *quoad Kirk s.n.* & *Scott-Elliot* 8524. *Vellozia splendens sensu* Baker in Oliver, *Fl. Trop. Afr.* 7: 412. 1898, *quoad Whyte s.n.* from Malosa Mt.; *sensu* Greves, *J. Bot.* 59: 283. 1921, *quoad Whyte s.n.*

*Description:* Up to 2-m-high shrub with erect, often forked stem; branches up to 2.5 cm in diameter, clothed with persistent bilobed (abscission of midrib deeper than sides), scale-like leaf sheaths arranged like roof tiles. Leaf blades to 30 cm long and 8 mm wide, deciduous, almost flat with prominent midvein and veins on both sides, linear, gradually tapering into acute tip, margins minutely setose with 0.3–0.5-mm-long trichomes, on both sides with regularly spaced dark resinous spots. Flowers solitary on about 8–10-cm-long peduncles covered with dark glands. Tepals 5.0–6.0 cm long and 1.2 cm wide, white or fading

purple, the outer outside on midrib and at base covered with glands. Stamens six, about 2.5 cm long. Style including stigma 2 cm long. Ovary 4 mm in diameter and 10 mm long, densely covered with dark glands.

*Distribution:* Malawi.

*BT leaf anatomy:* Amphistomatic and with shallow opposite furrows; outer wall of epidermis cells moderately thickened but not papillate; subepidermal sclerenchyma confined to few cells (less than ten) on each side of lateral bundles, near both adaxial and abaxial girders; epidermis, subepidermis and bundle sheath often dark stained.

*Specimens examined:* MALAWI. South, Zomba District, Mt. Malosa, *Whyte s.n.* (E); Zomba Mt, *Robson & Jackson* 1316 (BM); Zomba District, Zomba Plateau, *Brass* 16144 (K); near Blantyre, Midima Mt, *Hilliard & Burt* 4105 (E); Machinga District, Liwonde Forest Reserve, Chikala Mt, *Chapman, Patel & Balaka* 6042 (K).

23. *Xerophyta splendens* (Rendle) N.L.Menezes, *Ciência e Cultura* 23: 422. 1971; Smith & Ayensu, *Kew Bull.* 29: 199. 1974; Porembski, *Flora* 191: 6 + fig. 3. 1996; Gonçalves in *Fl. Zambes.* 12, 2: 174. 2009.

*Vellozia splendens* Rendle, *Trans. Linn. Soc. II*, vol. 4: 49, plate 8. 1894; Baker in Oliver, *Fl. Trop. Afr.* 7: 412 (1898) excluding *Whyte s.n.* from Malosa Mt.; Greves, *J. Bot.* 59: 283 (1921) excluding *Whyte s.n.*; Binns, *Check List Fl. Malawi*, p.103 (1968); Ayensu, *Kew Bull.* 23: 326 (1969); Chapman & White, *Evergr. Forests Malawi*: 170 (1970). – *Type:* Malawi, Mulanje, *Whyte s.n.* (K, holotype).

*Barbacenia splendens* (Rendle) Harms in Engler, *Pflanzenwelt Ost-Afr. C*: 145 (1895).

*Description:* Plants up to 4–5 m high with branched woody stems, up to 30 cm in diameter; branches covered with brown scale-like, about 7-cm-long leaf sheaths with prominent longitudinal ribs. Leaves in apical tufts, blades 30–45 cm long and at base 10–14 mm wide, deciduous, almost flat with midvein and many veins on both sides, gradually tapering to a filiform apex, both sides glabrous, with prominent midvein and minutely setose margins (trichomes from 0.2 to 0.5 mm). Flowers solitary on 15–23-cm-long peduncles. Tepals about 6 cm long and to 2 cm wide, white, ovate-lanceolate, with acuminate and falcate apex, the outer outside at their bases and on midribs with dark glands. Stamens six, filaments short, anthers about 18 mm long. Style including stigma 4.5 cm long. Ovary 1.5 cm long, turbinate. Peduncle, ovary and the outside bases and midribs of outer tepals covered with dark glands.

*Distribution:* Malawi, endemic to Mt. Mulanje.

*BT leaf anatomy:* Hypostomatic with narrow and deep opposite furrows; outer walls of epidermis cells heavily thickened and clearly papillate, stomata confined to abaxial furrow epidermis that is not underlined by sclerenchyma; subepidermal sclerenchyma bands (one layer thick) underline both the adaxial and abaxial sides of lateral bundles and partly merge into furrows (Fig. 10A, B; see also Ayensu, 1969: 326 + fig. 3:4).

*Specimens examined:* MALAWI. South, Mt. Mulanje, Whyte *s.n.* (B); Mt. Mulanje, descent to Knife-edge from Thuchila shelf, *J. D. & E. G. Chapman* 7623 (E); Mt. Mulanje slopes leading to Cilemba Peak, *J. D. & E. G. Chapman* 8165 (E); Mulanje District, Mt. Mulanje, *Burt* 6416, cult. Bot. Gard. Edinburgh 19710136\*A (M).

24. *Xerophyta velutina* Baker, *Trans. Linn. Soc. II*, 1: 265 (1878); Durand & Schinz, *Consp. Fl. Afr.* 5: 272. 1895; Rendle, *Catalogue Afr. Pl. II*, 1: 36. 1899. – *Type:* Angola, Pungo Andongo, at the banks of the Cuanza river, 2400–3800 ft, iii.1857, *Welwitsch* [1556] (BM, holotype; LISU, isotype).

*Vellosia velutina* Welw. ex Baker in *l. c.* 1878, listed in synonymy only.

*Barbacenia velutina* (Baker) Pax, *Englers Bot. Jahrb.* 15: 145. 1892; Fries, *Rhodesia-Kongo-Exped.*, *Bot. I*: 234. 1914

*Vellozia velutina* Welw. ex Baker in Oliver, *Fl. Trop. Afr.* 7: 412. 1898; Greves, *J. Bot.* 59: 283. 1921; Wild, *Kirkia* 6: 215. 1968.

*Description:* Stem upright and up to 75 cm high, branches about 15 mm thick. Leaf sheaths truncate mucronate, closely appressed to stem and not early disintegrated. Leaves: six to eight in a terminal rosette, blades 15–25 cm long and 6–12 mm wide, deciduous, almost flat with prominent midvein and distinct lateral veins, linear or lanceolate, with many veins and prominent midvein, finely hairy on both sides. Flowers solitary, peduncle about 5 cm long and in the upper part covered with black glands. Tepals 25 mm long, blue, acuminate. Stamens six, about 10–12 mm long with linear anthers and short filament. Ovary 6 mm long, club-shaped, covered with glands.

*Distribution:* Angola.

*CGT leaf anatomy:* Amphistomatic with shallow abaxial furrows and strongly undulating adaxial surface, occasionally with shallow furrows alternating to the abaxial ones; rather slim lateral vascular

bundles with double to triple spaces between them; subepidermal sclerenchyma abundant: triangular adaxial strands between lateral bundles, broad bands above and below lateral bundles and merging into the furrows; aquiferous cells in furrows of abaxial side and twice as much between bundles and sclerenchyma strands on the adaxial side; stomata restricted to areas next to aquiferous cells (Fig. 12C, D).

*Specimens examined:* ANGOLA. Pungo Adongo, *Welwitsch* 1556 (BM); Mossamedes, Camucuiu, *Azancot de Menezes* 322 (K); between Mossamedes and Villa Arriaga, *Humbert* 16523 (BM).

25. *Xerophyta capillaris* Baker, *Trans. Linn. Soc. II*, 1: 264, t 36, fig. 1. 1878; Durand & Schinz, *Consp. Fl. Afr.* 5: 271. 1895; Rendle, *Catalogue Afr. Pl. II*, 1: 35. 1899; Smith & Ayensu, *Kew Bull.* 29: 201. 1974. – *Type:* Angola, Huila, Monino, Empalanca Plateau, 3800–5500 ft, ii.1860, *Welwitsch* 1558 (K, holotype; BM, LISU, isotypes).

*Vellosia capillaris* Welw. ex Baker in *l. c.* 1878, listed in synonymy only.

*Barbacenia capillaris* (Baker) Pax in Engler, *Hochgebirgsfl.*: 171. 1892.

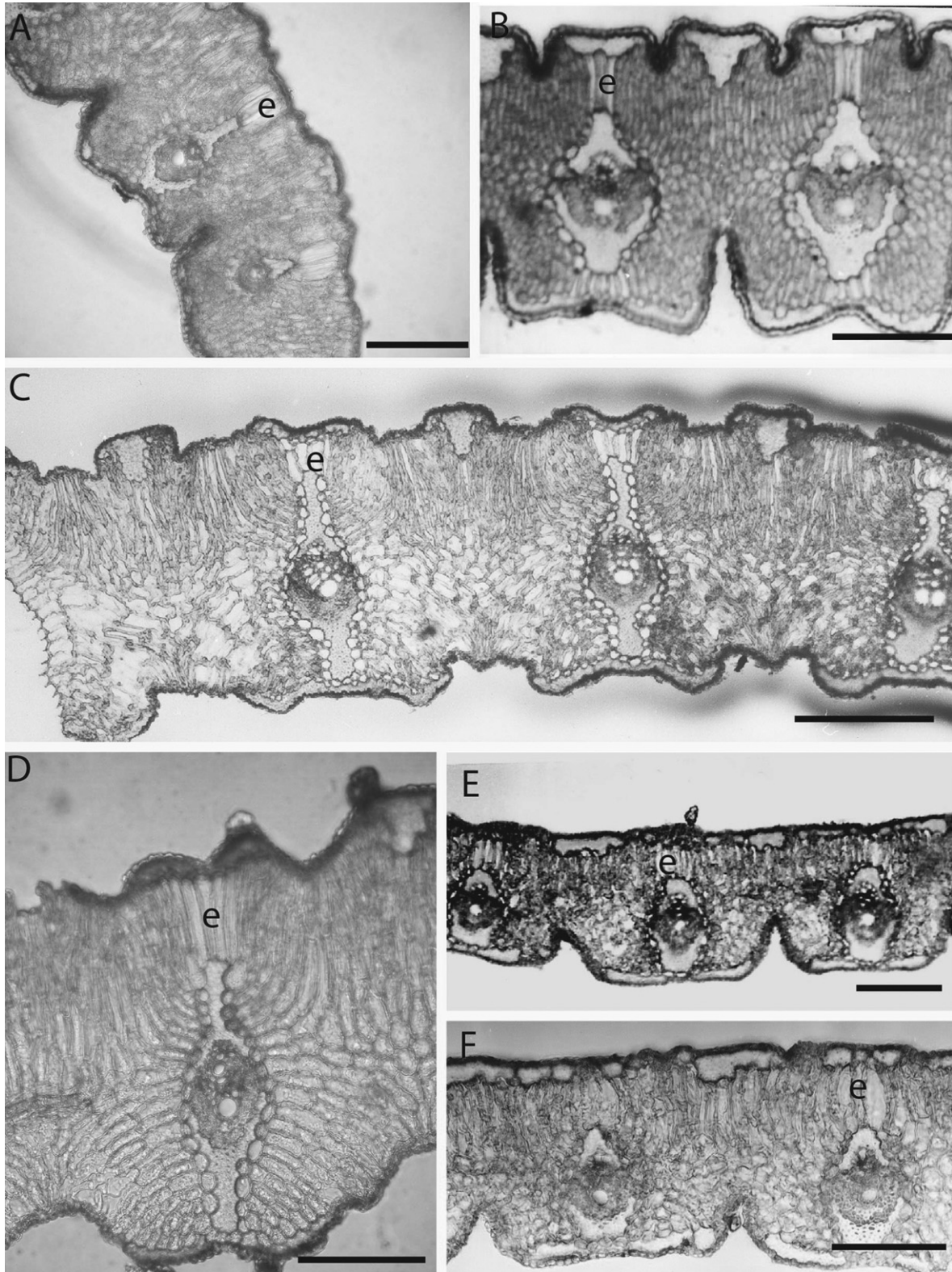
*Vellozia capillaris* (Baker) Baker in Oliver, *Fl. Trop. Afr.* 7: 411. 1898; Greves, *J. Bot.* 59: 282. 1921.

*Description:* Stem about 60 cm high, branches up to 12 mm thick. Leaf sheaths brown, truncate and with many veins. Leaf blades 10–15 cm long and about 6 mm wide, deciduous, V-shaped with prominent midvein and strong veins on both sides, linear and aristate, resinous dotted. Flowers solitary, peduncles 5–8 cm long, two to three in a tuft. Tepals 30–35 mm long and about 10 mm wide at base, white, lanceolate acuminate. Stamens six, anthers 10–12 mm long, filaments short. Ovary 6 mm long, turbinate. Ovary and peduncle densely covered with glands.

*Distribution:* Angola.

*CGT leaf anatomy:* Amphistomatic with shallow adaxial and abaxial furrows, two adaxial alternating with one abaxial; outer wall of epidermis cells moderately thickened, stomata confined to furrow epidermis that is not underlined by sclerenchyma; subepidermal sclerenchyma abundant, with abaxial bands adjacent to lateral bundles and bending into thick adaxial strands on top of the extended bundle sheath cells alternating with triangular strands opposite abaxial furrows; parenchyma cells below lateral bundles resinous-stained (Fig. 12A, B).





**Figure 12.** Transverse sections of leaves with *Capillaris* group-type (CGT) leaf anatomy. A, B, *Xerophyta capillaris* (from Gossweiler 3830 resp. Antunnes s.n.). C, D, *Xerophyta velutina* (from Welwitsch 1556 resp. Azancot de Menezes 322). E, F, *Xerophyta squarrosa* (from Welwitsch 1555). Alternate furrows with associated aquiferous cells, elongated adaxial bundle sheath cells (e) and sclerenchyma strands between lateral bundles are characteristics of CGT. Scale bars, 100  $\mu$ m.

Leaf blades glabrous but with fine regular resinous spots .....a. var. **capillaris**

Leaf blades pubescent, the trichomes largely hiding the resinous spots .....b. var. **occultans**

*a. var. capillaris*

*Specimens examined:* ANGOLA. Huilla, Monino, Empalanca Plateau, *Welwitsch* 1558 (BM). – Benguela, Ganguellas & Ambuellas District, *Gossweiler* 3830 (K); Lépi, *Gossweiler* 12157 (BM). – Ganda, Alto Elende and Alto Catumbela, *Faulkner* A385 (K).

*b. var. occultans*

var. *occultans* L.B.Sm. & Ayensu, *Kew Bull.* 29: 201. 1974; Gonçalves in *Fl. Zambes.* 12, 2: 159. 2009, excl. *Richards* 14966. – *Type:* Angola, Catengue, 500 ft, always found near or on rocks, *Pittard* 109 (BM, holotype).

*Distribution:* Angola.

*Description:* The variety is distinct by its hair-like trichomes on the adaxial and abaxial sides of the leaf blade and on the abaxial side of leaf sheaths.

*CGT leaf anatomy:* Not distinct from the typical variety.

*Specimens examined:* ANGOLA. Benguela, Catengue, *Pittard* 109 (BM). – Cuanza Sul, Amboin, Capir, near river Carloaongo-Cuvo, *Gossweiler* 10001 and 10006 (K). – Cambambe-Dondo, Calarada, near Cuanza River, *Gossweiler* 9251 (K). – Huambo, *Vanderyst* 13295 (BR).

26. *Xerophyta pseudopinifolia* Behnke, **sp. nov.** – *Type:* Mozambique, Marrupa Distr., 9 km from Mahua to Cuamba, c. 600 m, 20.ii.1964, *Torre & Paiva* 10694 (K, holotype; LISC, LMU, WAG, isotypes).

*Xerophyta pinifolia* var. *pinifolia sensu* Gonçalves in *Fl. Zambes.* 12, 2: 158 + fig. 12.2.41. 2009, *quoad* *Torre & Paiva* 10694, *Torre & Correia* 16015, and *Patel* 878.

*Diagnosis:* Planta suffruticosa erecta, caudice 50–75 cm longo, ramoso, foliorum basibus appressis c. 1 cm longis, ad apicem aspere squarrosis velato, extra squamis mollibus tecto. Folia 3–8 cm longa, 1.5–3.5 mm lata, in pseudorosulas terminales aggregata, lamina caduca, lineari-lanceolata, in apicem rigidum 1–3 mm longum attenuata, utrinque squamis mollibus tomentosa. Flores solitarii; pedunculo 1–2 cm longo, glanduloso. Tepala 10–15 mm longa, lanceolata, candida, exteriora extra glandulosa acumine 1–2 mm longo, interiora apice obtuso. Stamina 6, filamentis 1–2 mm longis, antheris c. 5–7 mm longis. Stylus cum stigmatate c. 10 mm longus. Ovarium

1.0–1.2 mm diametro, 2–3 mm longum, obovatum, multiglandulosum.

*Distribution:* Malawi, Mozambique.

*Description:* Plant suffruticose, erect, with stem 50–75 cm long, branched, concealed by the appressed bases of leaves which are about 1 cm long, roughly squarrose at the top and covered on the outside by soft scales. Leaves 3–8 cm long and 1.5–3.5 mm wide, aggregated into terminal pseudorosettes, with the lamina caduceus, linear-lanceolate, tapering to a rigid, 1–3-mm-long apex, tomentose on both sides with soft scales. Flowers solitary, on a glandular 1–2-cm-long peduncle. Tepals 10–15 mm long, white, the outer glandular on the outside, with a 1–2-mm-long point, the inner with obtuse apex. Stamens six, with filaments 1–2 mm long and anthers about 5–7 mm long. Style (including stigma) about 10 mm long. Ovary 1.0–1.2 mm in diameter and 2–3 mm long, obovate, covered with glands.

*BT leaf anatomy:* Amphistomatic with shallow opposite furrows and stomata restricted to furrows; rather slim lateral vascular bundles with double and wider spaces between them; central bundle with large abaxial winged crescentiform girder and small adaxial cap; marginal bundles small, partly surrounded by semispherical sclerenchyma. Below adaxial furrows large aquiferous cells are perpendicular to the leaf surfaces and form a small protrusion which, at least in furrows near the central bundle, is often supported by tiny sclerenchyma knobs; short sclerenchyma bands underline the epidermis on either side of lateral bundles, and on the abaxial side are continuous into the furrow openings (Fig. 10H).

*Specimens examined:* MALAWI. South, Machinga Distr., Mlinda Hill Saddle, *Patel* 878 (BR and K). MOZAMBIQUE. – North, Marrupa Distr., 9 km from Mahua to Cuamba, *Torre & Paiva* 10694 (K).

*Comments:* Gonçalves (2009) included the specimens assigned to the new species in his *X. pinifolia* var. *pinifolia*. Although the morphology of these collections shows some similarities with the Madagascan *X. pinifolia*, anatomical and genetic characters support an affinity with *X. spekei*. The leaves of *X. pinifolia* are glabrous, dorsiventral and with strict XT leaf anatomy (Fig. 20F), whereas those of *Patel* 878 from Malawi and *Torre & Paiva* 10696 from Mozambique are covered with small scales, isolateral and with BT leaf anatomy.

27. *Xerophyta spekei* Baker, *J. Bot.* 13: 234. 1875a; Durand & Schinz, *Consp. Fl. Afr.* 5, 272. 1895; Smith



& Ayensu, *Kew Bull.* 29: 198. 1974; Smith & Ayensu in *Fl. Trop. East Afr., Velloziaceae*: 7. 1975; Lye & Edwards in *Fl. Ethiopia* 6: 312–314. 1997; Gonçalves in *Fl. Zambes.* 12, 2: 171. 2009. – *Type*: Tanzania, Tabora District, Boss Rock, 6°S, *Speke & Grant* 782 (K, holotype).

*Vellozia spekei* (Baker) Baker, *Trans. Linn. Soc.* 29: 156. 1875b; Baker in Oliver, *Fl. Trop. Afr.* 7: 412. 1898; Greves, *J. Bot.* 59: 283. 1921; Dale & Greenway, *Kenya Trees & Shrubs*: 15. 1961.

*Barbacenia tomentosa* Pax, *Englers Bot. Jahrb.* 15:144. 1893; Harms in Engler, *Pflanzenwelt Ost-Afr. C*: 145. 1895. – *Type*: Kenya, Asi River, *Fischer* 585 (B, holotype; K, isotype).

*Vellozia aequatorialis* Rendle, *J. Linn. Soc.* 30: 409. 1895; De Wildeman, *Ann. Mus. Congo, série 4*. 1902–1903; Thonner, *Blütenpfl. Afrikas* 6: 148. 1908; Greves, *J. Bot.* 59: 283–284. 1921; Dale & Greenway, *Kenya Trees & Shrubs*: 14. 1961; Ayensu, *Kew Bull.* 23: 324. 1969. – *Type*: Tanzania, between Zanzibar and Uyui, *W. E. Taylor s.n.* (BM, holotype).

*Xerophyta tomentosa* (Pax) T.Durand & Schinz, *Consp. Fl. Afr.* 5: 272. 1895.

*Barbacenia aequatorialis* (Rendle) Harms in Engler, *Pflanzenwelt Ost-Afr. C*: 145. 1895; Pax in Engler, *Pflanzenfam.*, ed. 2, 15a: 433. 1930.

*Barbacenia spekei* (Baker) Harms in *l.c.* 1895.

*Vellozia tomentosa* (Pax) Baker in Oliver, *Fl. Trop. Afr.* 7: 412. 1898; Greves, *J. Bot.* 59: 283. 1921; Dale & Greenway, *Kenya Trees & Shrubs*: 15. 1961; Ayensu, *Kew Bull.* 23: 327. 1969; Jacobsen, *Kirkia* 9: 153. 1973.

*Barbacenia helenae* Buscaloni & Muschler, *Englers Bot. Jahrb.* 49: 462. 1913; Piscicelli, *Nella Regione dei Laghi Equatoriali*: 464. 1914. – *Type*: Kenya, Masei District, Guasso Nyiro, *Aosta* 1601 (B, holotype).

*Xerophyta aequatorialis* (Rendle) N.L.Menezes, *Ciência e Cultura* 23: 422. 1971.

*Description*: Stem up to 2 (rarely 5) m high with 10–13-cm-thick trunk and 1.5–2.0-cm-thick branches. Leaf sheaths scale-like, convex, dark brown, tricuspidate; in most specimens the younger ones are obtusely carinate with thick midvein apically ending in a rigid point and with the margins provided with a similar but smaller point; the uppermost leaf sheaths bear white to yellow trichomes. Leaves five or six in an apical tuft, blades 10–30 cm long and 6–12 mm wide, deciduous, V-shaped with prominent midvein, linear, densely pilose beneath, less dense above and often nearly glabrous, towards the apex serrulate at margins and beneath midvein. Flowers solitary, peduncles 5–8 cm long and in upper part with glands. Tepals about 20–35 mm long, white to pale blue or mauve, lanceolate, glandular at base. Stamens six,

filaments short, anthers 13–20 mm long. Ovary 5–10 mm long, ellipsoid, covered with glands.

*Distribution*: Kenya, Tanzania, Zambia, Democratic Republic of the Congo.

*BT leaf anatomy*: Amphistomatic with narrow, deep opposite furrows; rather slim lateral vascular bundles. Stomata restricted to furrow epidermis. Below adaxial furrows large aquiferous cells are perpendicular to the leaf surfaces and form a small protrusion which, at least in furrows near the central bundle, is often supported by tiny sclerenchyma knobs; short sclerenchyma bands underline the epidermis on either side of lateral bundles; on the abaxial side they are continuous into the furrow openings (Fig. 10C, D).

*Specimens examined*: KENYA. Athi River, *Fischer* 585 (B). – Southern Province, Machakos District, SE of Mtito Andei, *Perdue & Kibuwa* 10211 (BR); Mile 11, Mtito Andei/Mombasa, *Napper* 1342 (BR); Kitui District (K4), 1 ml S of Tana on Embu–Kangonda Road, *Napper* 1641 (K); Mtito Andei, *Duvigneaud* 73V (BRLU); Machakos District, Nguungi Hill, 2 ml N of Kangonde, *Kimani* 182 (BR); Machakos District, Mile 148 from Mombasa on Nairobi Road, *Verdcourt & Polhill* 2697 (K and BR). – Northern Frontier Province, Dandu: *Gillett* 12635 (BR and B); Kajiado District, Olmaki Hill, c. 6 km NW of Hunter's lodge on Main Mombasa Road, *Gillett* 19386 (BR); Kajiado District, WSW of Chyulu Range in Rift Valley Province, Mbirikani Plains, 10 km SW of Ol Donyo Wuas Lodge, *S. & T. Pocs* 04034 (EGR, voucher at M); Mile 98 Nairobi–Mombasa, *Napper* 1331 (BR); Voi District, *Lynes* 1209 (BM); Kilimandscharo, *von Prittwitz und Gaffron* 133 (B and BM). DEMOCRATIC REPUBLIC OF THE CONGO. Katanga, Surroundings of Parc de l'Upemba, near Lusinga, 10 km from the road Kuibo–Mitwaba, *Malaisse* 9126 (BR). TANZANIA. Tanga, Mlalo, *Holst* 2455 (B); E Usambaras, Longuza Hill, Sigi River Gorge, *Brenan & Greenway* 8345 (BR); E Usambaras, Sigi River Ravine, *Greenway* 7555 (BR); Lushoto District, Zevigambo, 2 ml NW of Malo, W Usambaras, *Drummond & Hemsley* 2961 (B); Usambara, Mombo, *Engler* 3272 (B); Unianemba, *Stuhlmann* 510 (B). – Morogoro, Kilosa District, Berega-Mlali on Mpwapwa Road, *Burt* 5426 (BM and BR); Kilosa District, Mamboya, Massai Steppe, *Stuhlmann* 4300(B); Rubeho Mts. Mamboya Hills, on the N side of Morogoro-Dodomard, just above Pentecostal Church of Magubike village, *S. & T. Pocs*, *A. Sass-Gyarmati & Z. Tuba* 04100 (EGR, voucher at M). – Manyora, Mbulu, Tarangire National Park Boundary, *Richards* 24772 (M). – Arusha, Massai-Steppe,



*Merker s.n.* (B). MALAWI. Central, Sani Hill, *Kaessner* 731 (BR). ZAMBIA. North, Musesha, *Fanshave* 4875 (BR).

*Comments:* Ayensu described the leaf anatomy of *Velozia aequatorialis* with sclerenchyma knobs in adaxial furrows (1969: 324 and fig. 1: 4) and of *V. tomentosa* (1969: 327 and fig. 3: 2). There is no difference from the anatomy of *X. spekei*.

**28. *Xerophyta tanzaniana* Behnke, sp. nov.** – *Type:* Tanzania; T2: Masasi District, 7 km Kibaya–Kondoa, 5°15'S, 36°32'E, 6300 ft, 16.i.1965, *Leippert* 5463 (M, holotype; K isotype).

*Xerophyta scabrida sensu* Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 8. 1975, *quoad* *Leippert* 5463. *Xerophyta scabrida sensu* McPherson et al., Novon 7: 390 and 394. 1997, *quoad* *Balslev* 42.

*Diagnosis:* Planta suffruticosa erecta, caudice 0.5–1.0 m longo, ramoso, foliorum basibus tecto, c. 12 mm longis, 16 mm latis, ad apicem aspere squarrosis. Folia 15–20 cm longa, 5–8 mm lata, in pseudorosulas terminales aggregata, lamina caduca, lineari, apice acuminato, marginibus setosis, supra et subtus secus nervos scabra, subtus inter venas glandulis resiniferis basin versus regulatim punctata. Flores solitarii, pedunculo 10–12 cm longo, glanduloso. Tepala 25–30 mm longa, acuminata, candida, exteriora extra glandibus sessilibus vestita, interiora glabra. Stamina 6, filamentis 1–2 mm longis, antheris c. 15 mm longis. Stylus cum stigmatem c. 16 mm longus. Ovarium 4.5 mm diametro, 9.0 mm longum, turbinatum, multiglandulosum.

*Distribution:* Tanzania, Mozambique.

*Description:* Plants with about 0.5–1.0-m-high branched stem. Leaf sheaths about 12 mm long and 16 mm wide, appressed to stem, with tips splitting and somewhat spreading. Leaf blades 15–20 cm long and 5–8 mm wide, V-shaped with prominent midvein and strong veins on both sides, deciduous, linear, ending in a long attenuate tip, adaxial surface shiny, abaxial surface between veins regularly dotted and with resinous secretions. Flowers solitary on 10–12-cm-long peduncles. Tepals 25–30 mm long, white, the outer on the abaxial side with glands, inner glabrous. Stamens six, filaments 1–2 mm long, anthers about 15 mm long. Style including stigma about 16 mm long. Ovary 4.5 mm in diameter and 9.0 mm long, turbinate, glandular.

*CGT leaf anatomy:* Amphistomatic with deep abaxial furrows and alternating twice as much shallow adaxial ones; aquiferous cells on adaxial side between lateral

bundles and above central one; outer wall of epidermis cells moderately thickened, stomata confined to furrow epidermis that is not underlined by sclerenchyma; a resinous duct formed inside abaxial furrows with stained cells lining the innermost part; short adaxial sclerenchyma bands underline the epidermis on either side of lateral bundles bending into the furrow opening, caps of three or four layers of subepidermal fibres above the adaxial extended bundle sheath cells alternate with triangular to roundish sclerenchyma strands between two furrows, i.e. directly opposite to an abaxial furrow (Fig. 4C); short stiff trichomes present at furrow corners of both sides.

*Specimens examined:* TANZANIA. Mtwara, Masasi District, 7 km Kibaya–Kondoa, *Leippert* 5463 (M); Morogoro District, Uluguru Mts., *Schlieben* 3165 (BR and M); Morogoro District, 7 km SW of Morogoro, at the bottom of E slopes of Mindu Mts., *Bjørnstad* 1227 (K). – Morogoro, 5 ml W of Morogoro at Rianga Rd, *Balslev* 42 (B and MO); Morogoro Region, Rubeho Mts., Mamboya Hills, near Changia village, 30 km WNW of Magole, S. & T. Pocs, A. *Sass-Gyarmati* & Z. *Tuba* 04093 (EGR, voucher at M); Morogoro Kanga Mts, Northern Nguru, *Lovett & Thomas* 2667 (K); N of Livale River, N Ngurus, *Bjørnstad Drummond & Hemsley* 2001 (K); 7 km SW of Morogoro, at the bottom of E slopes of Mindu Mts., *Bjørnstad* 1227 (K); Kilosa District, Mamboya, *Haarer* 1971B (K); N of Mpwapwa, *Hornby* 729 (K). – Dodoma, Kibariani Mts., B. D. *Burt* 3886 (K). MOZAMBIQUE. Tete, Changara District, Zambesi River, Sisitsa Station, *Chase* 2776 (BM).

**29. *Xerophyta glutinosa* Behnke, sp. nov.** – *Type:* Namibia; District Kaokoland: Ejau (W of Epupa Falls, eastern edge of Baynes Mts), 24.ii.1974, *Merxmüller & W. Giess* 30544 (M, holotype; WIND, isotype). *Xerophyta squarrosa* Baker *sensu* Sölch & Roessler in *Merxmüller*, Prodr. Fl. Südwestaf., fam. 152: 2. 1969, *quoad* *Merxmüller* 1444 & 1520.

*Diagnosis:* Planta suffruticosa erecta, caudice 20–50 cm longo, ramoso, foliorum basibus tecto. Folia c. 20–30 cm longa, 6–10 mm lata, lamina caduca, lineari, apice attenuato, supra et subtus secus glandulosa, viscida. Flores solitarii, pedunculo 8–10 cm longo, glanduloso. Tepala 25–30 mm longa, candida, exteriora cuspidata extra glandibus sessilibus vestita, interiora glabra. Stamina 6, filamentis 1–2 mm longis, antheris c. 7 mm longis. Stylus c. 4 mm longus, stigma c. 8 mm longum. Ovarium 12 mm longum, 15 mm diametro, subglobulosum, multiglandulosum.

*Distribution:* Namibia.

*Description:* Plants 20–50 cm high with branched stem. Leaf sheaths appressed to stem and splitting. Leaf blades about 25 cm long and 6–10 mm wide, almost flat with prominent midvein, deciduous, linear, strongly viscid. Flowers solitary on 8–10-cm-long peduncles that are covered with glandular trichomes. Tepals 20–30 mm long, white, lanceolate, the outer with glands on the outside, the inner glabrous. Stamens six, filaments 1–2 mm long, anthers about 7 mm long. Style about 4 mm long, stigma about 10 mm long. Ovary 12 mm long and 15 mm in diameter, subglobose, densely covered with glands.

*CGT leaf anatomy:* Amphistomatic with undulating adaxial surface and shallow abaxial furrows; small, uneven triangular sclerenchyma strands on adaxial side regularly alternating with bundles, short sclerenchyma bands underline the epidermis on either side of lateral bundles, but are absent directly above and below bundles where epidermis and subepidermis cells are dark stained and produce glutinous secretions; aquiferous cells inside abaxial furrows and twice as much between bundles and adaxial sclerenchyma strands; outer wall of epidermis cells heavily thickened, on abaxial surface stomata confined to furrows (Fig. 4B, F).

*Specimens examined:* NAMIBIA. Kaokoland, Ejau (W of Epupa Falls), eastern edge of Baynes Mts., *Merxmüller & W. Giess* 30544 (M); ravine near Otjikondo, *Merxmüller* 1444 (M); 15 ml E of Ohopuko, *Merxmüller* 1520 (M). – Grootfontein, Farm Blyerust, SW dolomite slope, *W. Giess* 11248 (M); Farm Nimitz, *W. Giess & Müller* 11827 (M).

*Comments:* According to Dinter's description in *Fedde Repertorium* 15: 346 (1918), his *Barbacenia spec. fruticosa* fol. *atroviridibus, viscosis (nomen nudum)* collected near Outjo (Namibia) is to be placed here.

30. *Xerophyta squarrosa* Baker, *Trans. Linn. Soc. II*, 1: 264. 1878; Durand & Schinz, *Consp. Fl. Afr.* 5: 272. 1895; Rendle, *Catalogue Afr. Pl. II*, 1: 36. 1899; Coetzee *et al.*, *Dinteria* 9: 4, 8, fig. 7, 11F. 1973; Coetzee, *Dinteria* 10: 26, fig. 1, 6. 1974; Smith & Ayensu, *Kew Bull.* 29: 202. 1974; Gaff, *Oecologia* 31: 97. 1977; Gonçalves in *Fl. Zambes.* 12, 2: 159. 2009. – *Type:* Angola, Pungo Adongo, *Welwitsch* 1555 (BM, holotype; LISU, M, isotypes).

*Vellozia squarrosa* Welw. ex Baker in l. c. 1878, listed in synonymy only.

*Vellozia squarrosa* (Baker) Baker in Oliver, *Fl. Trop. Afr.* 4: 410. 1898; Greves, *J. Bot.* 59: 283. 1921; Ayensu, *Kew Bull.* 23: 327. 1969.

Non *Xerophyta squarrosa sensu* Sölch & Roessler in *Merxmüller, Prodromus Fl. Südwestafr.*, fam. 152: 2. 1969.

*Description:* Stem about 1.0–1.5 m high, at base about 5 cm thick. Leaf sheaths early splitting with tips bending outwards. Leaf blades about 15 cm long and 10 mm wide, moderately V-shaped with prominent midvein and distinct lateral veins, deciduous, linear, acuminate, glabrous, at margins with small teeth. Flowers solitary on 10–13-cm-long peduncles. Tepals 20–25 mm long, white to bluish, lanceolate. Stamens six, about 10 mm long. Ovary 8–9 mm long, club-shaped. Ovary and peduncle densely covered with glands.

*Distribution:* Angola, Namibia.

*CGT leaf anatomy:* Amphistomatic with undulating adaxial surface and deep abaxial furrows; central bundle with small adaxial cap, a small partial abaxial bulbiform girder and a divided subepidermal winged sclerenchyma band not in contact with the partial girder; subepidermal sclerenchyma abundant: many adaxial bands of various lengths between and above lateral bundles and broad abaxial bands below bundles; stomata mainly restricted to furrow epidermis. Aquiferous cells restricted to adaxial side of central bundle, but vertically extended bundle sheath cells may also have water-storing function (Fig. 12E, F; see also Ayensu, 1969: 327 + fig. 5).

*Specimens examined:* ANGOLA. Pungo Adongo, *Welwitsch* 1555 (M).

31. *Xerophyta glabra* Behnke, **sp. nov.** – *Type:* Namibia; District Kaokoland: 5 km S of Swartbootsdrif at Kunene River, 22.iii.1974, *Merxmüller & W. Giess* 30477 (M, holotype; K, WIND, isotypes).

*Xerophyta squarrosa* Baker *sensu* Sölch & Roessler in *Merxmüller, Prodromus Fl. Südwestafr.*, fam. 152: 2. 1969, *quoad de Winter & Giess* 7104.

*Diagnosis:* Planta suffruticosa erecta, caudice 10–50 m longo, 5–15 mm latiore, multi-ramoso, foliorum basibus tecto. Folia 8–10 cm longa, 5–8 mm lata, lamina caduca, lanceolata, apice brevi acuto, omnino glabra. Flores solitarii, pedunculo 5–10 cm longo, glanduloso. Tepala 25–30 mm longa, candida, exteriora obtusa acumine c. 2–3 mm longo, exteriora extra glandibus sessilibus vestita, interiora glabra. Stamina 6, filamentis 1–2 mm longis, antheris c. 8–10 mm longis. Stylus c. 3–4 mm longus, stigma c. 8–10 mm longum. Ovarium 6–9 mm diametro, 15–18 mm longum, turbinatum, multiglandulosum.

*Distribution:* Namibia.

*Description:* Small, between 10 and 50-cm-high plants with multibranched up to 15-mm-thick stem. Leaf sheaths appressed to stem, early splitting. Leaf blades about 8–10 cm long and 5–10 mm wide, V-shaped with prominent midvein and strong veins on both sides, deciduous, lanceolate with short acute tip, completely glabrous. Flowers solitary on 5–10-cm-long peduncle. Tepals 25–30 mm long, cream coloured, the outer with 2–3-mm-long acuminate tip. Stamens six, filaments 1–2 mm long, anthers about 8–10 mm long. Style 3–4 mm long, stigma 8–10 mm long. Ovary about 6–9 mm in diameter and 8–15 mm long, turbinate. Peduncle, outside of outer tepals and ovary covered with glands.

*CGT leaf anatomy:* Amphistomatic with undulating adaxial surface and shallow abaxial furrows; subepidermal sclerenchyma bands (one or two layers) are present on abaxial side below lateral bundles and extend about one bundle width on either side, whereas on the adaxial side broad strands are regularly present both above and between lateral bundles; aquiferous cells inside shallow abaxial furrows and twice as much between adaxial sclerenchyma strands and lateral bundles; outer wall of epidermis cells moderately thickened, stomata confined to areas next to aquiferous cells (Fig. 4G).

*Specimens examined:* NAMIBIA. Kaokoland, 5 km S of Swartbootsdrif at Kunene River, *Merxmüller & W. Giess* 30477 (M); 16 km S of Epembe, *Merxmüller & W. Giess* 30436 (M). – Ovambo, stony mountain slope near Ruacana Falls, Kunene, *de Winter & W. Giess* 7104 (M).

32. *Xerophyta concolor* L.B.Sm. & Ayensu, *Kew Bull.* 29: 201. 1974. – *Type:* Angola, Serra de Candungo, Calenga, *Gossweiler* 12594 (BM, holotype).

*Description:* Stem up to 1.5 m high, terminal branches including leaf sheaths at least 2.5 cm thick. Leaf sheaths blackish brown, quickly splitting after abscission, blades over 50 cm long and about 7 mm wide, V-shaped with prominent midvein and strong veins on both sides, deciduous, linear, filiform-attenuate, glabrous but with thickened ciliate margins. Peduncles three at the apex of a branch, 9.5 cm long, densely covered with glands. Tepals 38 mm long, blue, linear-lanceolate, acuminate; the outer outside glandular, the inner glabrous. Filaments triangular, anthers linear, about half as long as the tepals. Stigma linear, apical, much longer at the style base. Ovary 7 mm long, ellipsoid, covered with dark glands.

*Distribution:* Known from the type locality only.

*BT leaf anatomy:* Amphistomatic with deep opposite furrows; slim lateral vascular bundles with double spaces between them; outer wall of epidermis cells moderately thickened, stomata confined to part of furrow epidermis that is not underlined by sclerenchyma; subepidermal sclerenchyma bands (one or two layers thick) are present on both the adaxial and abaxial sides of lateral bundles.

*Specimens examined:* ANGOLA. Benguela, Serra de Candungo, Calenga, *Gossweiler* 12594 (BM). – Cuanza Sul, Santa Comba-Amboiva (bank of Queve river), *Bamps* 4653bis, cult. Bot. Gard. Bruxelles (BR).

33. *Xerophyta hirtiflora* Behnke & E.Hummel, **sp. nov.** – *Type:* Zimbabwe, Mashonaland East, near Domboshawa, 17°37'0"S, 31°09'0"E, 1220 m, vii.1993, *Seine s.n.* (M, holotype; B isotype).

*Xerophyta equisetoides* Seine, *Vegetation von Inselbergen in Zimbabwe:* 89. 1996.

*Diagnosis:* Frutex erectus; caudice brevi, crasso, ad basin ad 12 cm diametro, furcato; rami primarii duo crassi, c. 15 cm longi, 6 cm diametro; rami secundarii numerosi in caudices apice numerosi, 6–10 cm longi, foliorum basibus brunneis, 3–4 cm longis, dense tecti et apicibus albigriseis plumosis praediti. Folia 40–70 cm longa, 4–6 mm lata, tristicha; lamina caduca, lineari, acuta, supra et subtus dense et longe lanato-tomentosa. Flores solitarii, pedunculo 12–15 cm longo, lanato-tomentoso. Tepala 4.0–4.5 cm longa, pallide malvicoloria, extra viridia et in parte inferiore lanato-tomentosa. Stamina 6, filamentis brevibus, antheris violaceis polline luteo, 1.4–1.7 cm longis. Stylus 3–4 mm longus, stigma 1.0–1.2 cm longum. Ovarium 4 mm diametro, 10 mm longum, turbinatum, dense lanato-tomentosum.

*Distribution:* Zimbabwe.

*Description:* Woody shrub with thick stem (base up to 12 cm in diameter), after 10 or more centimetres divided into two or three thick branches, each about 15 cm long and 6 cm wide, with many new shoots on top (Fig. 13A). Young (secondary) branches covered with about 3–4-cm-long brown leaf sheaths disintegrating into a meshwork of fibrous nerves and with whitish grey feathery tips slightly bent outwards (Fig. 13D). Leaves with deciduous blades, V-shaped with median adaxial groove and opposite furrows, about 40–70 cm long and 4–6 mm wide, covered on both sides with long white, woolly trichomes as part of eglandular emergences (Fig. 13C, E). Flowers soli-





**Figure 13.** *Xerophyta hirtiflora*, cult. Bot. Gard. Bonn (11775 ex *Seine s.n.*) A, Entire plant with bifurcated thick stem, c.  $\frac{1}{4}\times$ . B, Flowers, original size. C, Lower leaf side with trichomes. D, Young shoot with plumose tips of leaf sheaths, c.  $2\times$ . E, Upper leaf side with trichomes, c.  $2\times$ . F, Dried old flowers on long pedicels covered with trichomes, c.  $2\times$ . G, Lower part of ovary with trichomes. Scale bars: A, 5 cm; B, D, F, 1 cm; C, E, G, 1 mm.



tary (Fig. 13B), not scented, on 10–15-cm-long peduncles covered with woolly trichomes (Fig. 13F). Tepals 4.0–4.5 cm long, faintly mauve, on the outside and on basal parts with woolly trichomes. Stamens six, with 1.4–1.7-cm-long mauve to violet anthers and yellow pollen, filament short. Style 3–4 mm long, stigma 1.0–1.2 cm long. Ovary turbinate, size about 4 mm in diameter and 10 mm long, densely covered with long woolly trichomes of eglandular emergences (Fig. 13G).

*BT leaf anatomy:* Amphistomatic with shallow opposite furrows; epidermis not thickened; small adaxial and abaxial sclerenchyma bands underline the epidermis on either side of lateral bundles; a small sclerenchyma strand (knob) below each adaxial furrow; eglandular emergences with terminal, long, unicellular trichomes on both adaxial and abaxial sides (Fig. 11E).

*Specimens examined:* ZIMBABWE. Central, near Domboshawa, *Seine s.n.*, cult. Bot. Gard. Bonn 11775 (M and B); Chivurumuti, near Arcturus, *Seine* 488 (M).

*Comments:* *Xerophyta hirtiflora*, known from Zimbabwe only, is genetically distinct and differs from *X. villosa* by its short thick stem, brown leaf sheaths with plumose tips (Fig. 13D), unicellular trichomes and large bright mauve flowers, and from *X. trichophylla* by its woolly trichomes covering ovary, peduncle and part of the outer tepals.

34. *Xerophyta monroi* (Greves) N.L.Menezes, *Ciência e Cultura* 23: 422. 1971.

*Vellozia monroi* Greves, *J. Bot.* 59: 280. 1921. – *Type:* Zimbabwe, Victoria, *Monro* 2160 (BM, holotype).

*Vellozia* spp. of Eyles in *Trans. Roy. Soc. South Afr.* 5: 329. 1916, *quoad Monro* 800.

*Description:* Plants with short erect straight stem, about 5–10 cm long and including leaf sheaths up to 3 cm in diameter. The sheaths are about 5 cm long, dark brown, and soon splitting into many fibres that are covered with trichomes in their apical part. The leaves are in terminal and subterminal rosettes, blades 40–55 cm long, to 5 mm wide, V-shaped with median adaxial groove and opposite furrows, deciduous, linear with long attenuate tip, towards the base covered with soft trichomes. Flowers are solitary on about 15-cm-long peduncles. Tepals mauve, the inner obtuse, the outer with acute apex. Stamens with short filaments and about 20-mm-long anthers, sometimes partly black and covered with orange pollen. Stigma about 15 mm long, style base about half as long. Ovary 1.0–1.5 cm long, narrowly turbinate and tapering below. Ovary, peduncle and midvein of outer

tepals densely covered with eglandular emergences making up a woolly indumentum.

*Distribution:* Zimbabwe.

*BT leaf anatomy:* Amphistomatic with deep opposite furrows, often widened in their innermost part; below abaxial girder of the central bundle a band of single-layered sclerenchyma is present between bundle sheath and papillate epidermis; outer epidermis cell walls are heavily thickened and papillate, especially on the adaxial surface and in furrows; heavy adaxial and abaxial sclerenchyma bands underline the epidermis on either side of lateral bundles and merge into the furrow opening; aquiferous cells are present below adaxial furrows, topped in most cases by a large sclerenchyma strand (knob) (Fig. 11C, D).

*Specimens examined:* ZIMBABWE. South, Masvingo, *Monro* 2160 (BM); Masvingo, *Rand* 390 (BM); Lake Mutirikwi, hills on S shore, near km 32–33 of road on S side of lake to dam wall, *Wilkin* 740 (K). – Central, Marondera District, *Miller* 5511 (BR). – West, Farm Chesterfield, *Wild* 3323 (M); Rhodes Matopos National Park, *Seine* 537 (M). – North, near Banket, *Seine* 767, cult. Bot. Gard. Bonn 17016 (M).

*Comments:* *Xerophyta monroi*, first described by Greves (1921), but included in *X. villosa* by Norlindh (1948), Smith & Ayensu (1974) and Gonçalves (2009), has less dense leaf trichomes and shorter ovary trichomes; its leaves are with a heavily thickened papillate epidermis and sclerenchyma knobs on top of aquiferous cells (Fig. 11C, D). These anatomical characters complement the morphological distinctions (see Greves, 1921) and the genetic differences (Figs 2, 3).

35. *Xerophyta purpurascens* Behnke, **sp. nov.** –

*Type:* South Africa, Mpumalanga, below Simon's Dam, Buffelskloof Nature Reserve, Lydenburg, *J. E. Burrows* 6593 (holotype: M, isotype: BNRH).

*Diagnosis:* Frutex demissus, caudice *c.* 80 cm longo, raro ramoso, foliorum basibus brunneis, 4 cm longis, 6.5 cm latis, crebre nervatis, tecto. Folia 30–40 cm longa, 1.0–1.5 cm lata, arcuata, lamina caduca, lineari, acuta, margine et infra dense tomentosa. Flores solitarii, pedunculo 10 cm longo, lanato-tomentoso. Tepala 2.5–3.0 cm longa, pallide purpurea, exteriora in inferiore parte lanato-tomentosa. Stamina 6, filamentis brevibus, antheris 1.5 cm longis. Stylus 5 mm longus, stigma 10 mm longum. Ovarium *c.* 10 mm longum, dense lanato-tomentosum.

*Distribution:* South Africa: Limpopo, Mpumalanga.

*Description:* Small erect shrubs, about 80 cm high and scarcely branched. Leaf sheaths brown, fan-like, 4 cm long and about 6.5 cm wide, blades arching, deciduous, 30–40 cm long and 1.0–1.5 cm wide. Flowers solitary, peduncles about 10 cm long, covered with woolly trichomes. Tepals about 2.5–3.0 cm long, pale to deep purplish-mauve. Stamens six, with short filaments and anthers about 1.5 cm long. Style base 5 mm long, stigma about 1 cm long. Ovary 1 cm long. Ovary, peduncle and outside of outer tepals densely covered with a woolly indumentum.

*BT leaf anatomy:* Amphistomatic with deep opposite furrows, often widened in their innermost part; outer epidermis cell walls are thickened and papillate; adaxial and abaxial sclerenchyma bands underline the epidermis on either side of lateral bundles and merge into the furrow opening; aquiferous cells are present below adaxial furrows and above midvein.

*Specimens studied:* SOUTH AFRICA: Mpumalanga, Buffelskloof Nature Reserve, below Simon's Dam, Lydenburg, 22.xi.1999 *J. E. Burrows* 6593 (M, BNRH). – Limpopo, Letaba District, E flank of Piemang Kop, 4300 ft, 25.x.1960, *Scheepers* 1034 (M).

36. *Xerophyta villosa* (Baker) L.B.Sm. & Ayensu, *Kew Bull.* 29: 188. 1974, excluding *X. monroi* and *X. violacea*; Gaff, *Oecologia* 31: 97. 1977; Hallam & Gaff, *New Phytol.* 81: 345. 1978; Hallam & Luff, *Bot. Gaz.* 141: 173. 1980a; Seine *et al.*, *Edinb. J. Bot.* 55: 283. 1998; Gonçalves in *Fl. Zambes.* 12, 2: 163. 2009.

*Vellozia (Vellozia) villosa* Baker, *J. Bot.* 27: 3. 1889; Greves, *J. Bot.* 59: 280. 1921; Norlindh, *Bot. Notiser* 1948: 28. 1948; Letty, *Wild Flow. Transvaal*: 73. 1962; Ayensu, *Kew Bull.* 23: 318. 1969; Ayensu, *Biotropica* 5(3): 145, 147 + fig. 5c, d. 1973. – *Type:* South Africa, Transvaal, Houtbosh, *Rehmann* 5792 (BM, holotype; K, M, Z, isotypes).

*Xerophyta villosa* (Baker) T.Durand & Schinz, *Consp. Fl. Afr.* 5: 272. 1895, mistaken name for *X. viscosa* (referring to Baker 1875a), and this combination erroneously used by Coetzee *et al.*, *Dinteria* 9: 4, 8, fig. 4, 11D. 1973, and by Coetzee, *Dinteria* 10: 26, fig 7. 1974.

*Xerophyta bakeri* T.Durand & Schinz, *Consp. Fl. Afr.* 5: 270. 1895, *nomen nudum* based on *Rehmann* 5792 (Z, an isotype of *X. villosa*).

*Xerophyta mollissima* Schinz in Durand & Schinz, *Consp. Fl. Afr.* 5: 271. 1895, *nomen nudum* based on *Rehmann* 5792 (Z, an isotype of *X. villosa*).

*Barbacia villosa* (Baker) Pax ex Burtt Davy & Pott-Leendertz, *Ann. Transvaal Mus.* 3: 121. 1912.

*Description:* Shrub with irregular thick stem base and woody, rarely branched erect stem that is up to 1.5 m

high and, including a thick coat of leaf sheaths, up to 5 cm in diameter. Leaf sheaths are about 5 cm long and early disintegrating into parallel wiry fibres. Leaves up to 60 cm long and to 1.2 cm wide, in apical or subapical rosettes, blades V-shaped with median adaxial groove and opposite furrows, deciduous, linear with acuminate tip, falcate, on both sides silvery white as a result of dense long and appressed trichomes as terminal cells of eglandular emergences. Flowers solitary on up to 10-cm-long peduncles. Tepals about 30 mm long, mauve to dark magenta, the outer with trichomes on the back. Stamina with short filaments and 15-mm-long anthers. Style base about 5 mm long, stigma 10 mm long. Ovary about 1.5 cm long, turbinate. Ovary and peduncle densely clothed with the long simple spreading end cells of eglandular emergences that are up to 2 mm long with their bases bulged out like a club (inversely claviform).

*Distribution:* Zambia, Zimbabwe, South Africa: Limpopo, Mpumalanga.

*BT leaf anatomy:* Amphistomatic with deep opposite furrows; central bundle with small adaxial cap and large abaxial ascending crescentiform girder, and there is no additional sclerenchyma band between bundle sheath and abaxial epidermis; outer epidermis cell walls are almost not thickened and also not papillate; thin sclerenchyma bands, single layered in general, underline the adaxial and abaxial sides of the epidermis on either side of lateral bundles; aquiferous cells are present below adaxial furrows, topped by a sclerenchyma strand (knob) in only the two or three closest to the central bundle (Fig. 11B; see also Ayensu, 1969: 318 + fig. 3, 3).

*Specimens examined:* ZIMBABWE. East, Mutare District, *Corner s.n.* (E). SOUTH AFRICA. Limpopo, Houtbosch, *Rehmann* 5792 (B and Z); between Haenertsburg and Ebenezer Dam, *Adendorff* 8 (M); Woodbush road crossing, close to bald peaks on edge of escarpment, *Adendorff* 34 (M); near Houtbosdorp, halfway down from high escarpment, *Adendorff* 36 (M); Rocks Marouvogne, *Junod* 2578 (G and M); between Ebenezer Dam and Haenertsburg, *Burtt* 2978, *cult. Bot. Gard. Edinburgh* 19651016\*A (M); Letaba District, E flank of Piemang Kop, *Scheepers* 1034 (M). – Mpumalanga, Barberton District, Queens River Valley, on road from Barberton village to Nelschoogte Forest Reserve, *K. & M. J. Balkwill & Williamson* 6683 (E); Buffelskloof Nature Reserve, Anne's Hoek Stream, N of Woodcutter's Knoll, *J. E. Burrows* 4342 (BNRH).

37. *Xerophyta pauciramosa* (L.B.Sm. & Ayensu) Behnke, **comb. nov.**



*Xerophyta pauciramosa* L. B. Smith in sched. (White 3369, K; Wild 3126, K).

*Xerophyta equisetoides* var. *pauciramosa* L.B.Sm. & Ayensu, Kew Bull. 29: 192 + fig. 2. 1974, excluding *Goetze* 1409, *Naegelsbach s.n.* & *Milne-Redhead* 3001; Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 3. 1975, *pro parte* excluding *Goetze* 1409 & *Naegelsbach s.n.*; Gonçalves in Fl. Zambes. 12, 2: 167. 2009, excluding *Goetze* 1409. – *Type*: Mwinilungu District, near Zambezi River, 4 ml north of Kalene Hill Mission, in cracks of extensive bare granite outcrop, 25.ix.1952, *F. White* 3369 (BM, holotype; BR, K, isotypes).

*Description*: Stem up to 50 cm high with branches about 1 cm in diameter, the young ones with exserted grey–brown leaf sheaths that are distinct by their broad yellow–brown apical parts (Fig. 7D). Leaf blades up to 15 cm long and 8 mm wide, V-shaped with median adaxial groove, deciduous, linear and acute, on both sides glabrous. Flowers solitary, fragrant, often with three pedicels on terminal peduncle, pedicel in upper part covered with eglanular emergences. Tepals about 25 mm long, white or pink to lilac, the outer lanceolate acute. Stamens with 10–12-mm-long yellow anthers and short filament. Style about 2 mm, stigma 5 mm long. Ovary 8 mm long and 4 mm in diameter, densely covered with short emergences.

*Distribution*: Democratic Republic of the Congo, Tanzania, Malawi, Zambia, Zimbabwe, South Africa: Limpopo.

*BT leaf anatomy*: Amphistomatic with deep opposite furrows; outer wall of epidermis cells not thickened, stomata restricted to furrows; aquiferous cells below adaxial and abaxial furrows; small sclerenchyma bands underline the epidermis on the abaxial side of the central bundle and on both the adaxial and abaxial sides of lateral bundles (see also Smith & Ayensu, 1974: fig. 2).

*Specimens examined*: ZAMBIA. West, Mwinilungu District, near Zambesi River, 4 ml N of Kalene Hill Mission, *White* 3369 (BR); Copperbelt Province, Chingola District, Luano Forest Reserve, *Duvigneaud* 4241B (BRLU); Luanshya, *Duvigneaud* 4245 (BRLU); Mwinilungu, Zambezi Rapids, near Kalene Hospital, Ikalenge, *J. E. & S. M. Burrows* 6444 (BNRH); Natumbachusi Falls, Mbereshi, *J. E. & S. M. Burrows* 6469 (BNRH). – South, Victoria Falls District, Hubert Young Drive, *Wild* 3126 (K and BR). ZIMBABWE. – Central, near Domboshawa, *Seine* 470 and *Seine s.n.*, cult. Bot. Gard. Bonn 11776 (M). SOUTH AFRICA. Limpopo, Masisi, on Mutali Road, off Pafuri to Tshipise road, *J. E. & S. M. Burrows* 6644 (BNRH).

38. *Xerophyta wentzeliana* (Harms) Sölch, Mitt. Bot. Staatssamml. München 4: 74. 1961.

*Barbacenia wentzeliana* Harms, Englers Bot. Jahrb. 30: 277. 1902. – *Type*: Tanzania, Mbeya District, Sante on Yamba River, *Goetze* 1409 (B, holotype; BM, isotype).

*Barbacenia wentzeliana* Harms var. *rhodesiana* R.E.Fr., Rhodesia-Kongo-Exped. I, Bot. 1: 234. (1914). – *Type*: north-eastern Zambia, Kalungwisi River, stony slopes, *Fries* 1160 (UPS, holotype).

*Vellozia wentzeliana* (Harms) Greves, J. Bot. 59: 281. 1921; Wild in Clark, Victoria Falls Handbook: 135 & 140. 1952.

Non *Xerophyta wentzeliana* (Harms) *sensu* Sölch & Roessler in Merxmüller, Prodromus Fl. Südwestafri., fam. 152: 2. 1969.

*Xerophyta retinervis* Baker var. *wentzeliana* (Harms) Coetzee in Coetzee *et al.*, Dinteria 9: 4, 8, fig. 6, 11A. 1973; Coetzee, Dinteria 10: 21. 1974.

*Xerophyta equisetoides* var. *pubescens* L.B.Sm. & Ayensu, Kew Bull. 29: 194. 1974; Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 4. 1975; Gonçalves in Fl. Zambes. 12, 2: 167. 2009. – *Type*: Mazoe District, near Tsatsi River, about 14 ml north of Concession, *Leach* 11283 (K, holotype; B, P, isotypes).

*Xerophyta equisetoides* var. *pauciramosa* L.B.Sm. & Ayensu, Kew Bull. 29: 192. 1974, *quoad* *Goetze* 1409 and *Milne-Redhead* 3001; Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 4. 1975, *quoad* *Goetze* 1409; Gonçalves in Fl. Zambes. 12, 2: 167. 2009, *quoad* *Goetze* 1409.

*Xerophyta equisetoides* var. *trichophylla* *sensu* Gonçalves in Fl. Zambes. 12, 2: 166. 2009, *quoad* Chisumpa 115, Fanshave 2609 & Salubeni 1253.

*Xerophyta suaveolens* var. *vestita* *sensu* Gonçalves in Fl. Zambes. 12, 2: 167. 2009, *quoad* *LaCroix* 2424 & *Linder* 3931.

*Xerophyta capillaris* Baker var. *occultans* *sensu* Gonçalves in Fl. Zambes. 12, 2: 159. 2009, *quoad* *Richards* 14966.

*Description*: Small branched shrub, young ones with exserted grey–brown leaf sheaths with small yellow–brown apical bands. Leaf blades up to 15 cm long and 8 mm wide, V-shaped with median adaxial groove, deciduous, linear and acute, on both sides with long trichomes. Flowers solitary, fragrant, often with three pedicels on terminal peduncle, pedicel in upper part covered with eglanular emergences. Tepals about 25 mm long, white or pink to lilac, the outer lanceolate acute. Stamens six, filament short, anthers 10–12 mm long, yellow. Style about 2 mm, stigma 5 mm long. Ovary 8 mm long and 4 mm in diameter, densely covered with short eglanular emergences.

*Distribution:* Democratic Republic of the Congo, Tanzania, Zambia, Zimbabwe, Angola, Namibia.

*BT leaf anatomy:* Amphistomatic with deep opposite furrows; outer wall of epidermis cells slightly thickened, stomata restricted to furrows; small sclerenchyma bands underline the epidermis on the abaxial side of the central bundle and on both the adaxial and abaxial sides of lateral bundles (Fig. 14E, F).

Leaves on both sides with short lanuginose trichomes .....a. var. *wentzeliana*

Leaves on both surfaces with many small protruding warts .....b. var. *verrucosa*

a. var. *wentzeliana*

*Specimens examined:* DEMOCRATIC REPUBLIC OF THE CONGO. Katanga, Luita, *Malaisse* 12153 (BR) and *Duvigneaud* 3617V (BRLU); Farm Sevrancx, *Duvigneaud* 3465V (BRLU); Kambove–Kamoia, *Duvigneaud* 4102V3 (BRLU); Mulungwishi, *Duvigneaud* 4986V1 (BRLU). – Without location: *Duvigneaud* 3087/A (BRLU). TANZANIA. Mbeya District, Sante on Yamba River, Unyika Plateau, *Goetze* 1409 (B). MALAWI. North, Nkhata Bay District, Viphya Plateau, 37 km SW of Mzuzu, *Pawek* 12034 (BR); Karonga District, 19 ml W of Karonga, *Pawek* 12135 (K); Rumphi District, near Nyika Plateau Junction, *Salubeni* 385 (B). – South, Zomba District, Nkhoronje Hill, *La Croix* 2424 (BM). – Central, Chisamba, *Chisumpa* 115 (K); Dedza District, Chongoni Forest Reserve, *Salubeni* 1285 (K). ZAMBIA. East, Chipata Region between Nyimba and Kachalola, *Linder* 3931 (K); Mazabuka to Kafu, *Burt Davy* 20789 (K). – West, Mwinilunga District, Matonchi Farm, *Milne-Redhead* 3001 (BR); Kitwe District, *Fanshove* 2609 (BR). – North, Musesha, *Fanshove* 10027 (K); Chibulula Hill, *Leteinturier, Malaisse & Matera* 71 (BR). – Central: Serenje District, Kundalia Falls, 8 ml from Kanona, *Richards* 14966 (K); Kasanka National Park N, *J. E. & S. M. Burrows* 6470 (BNRH). ZIMBABWE. North, Mazowe District, near Tsatsi River, about 14 ml N of Concession, *Leach* 11283 (B); Mazowe District, College Farm, *Boughey* 11009 (K); near Banket, *Seine* 462 (B); near Banket, *Seine* 464, cult. Bot. Gard. Bonn 17015 (M). – East, near Nyanga, *Seine* 1292 (M). ANGOLA. Huila, Tschivinguiro, descent from Banja, *Barbosa & Moreno* 9734 (BR). MOZAMBIQUE. MS, Tambara District, road between Alfiate and Nhasansugodi, *Lesne s.n.* (BR). – N, Niassa Province, 40 km on road Marrupa–Mukwajaja, near phenological observation field of Mademo, *Jansen & Boane* 7982 (K).

b. var. *verrucosa* Behnke, var. *nov.*

A var. *wentzeliana* foliis non pubescentibus sed multiverrucosis differt. – *Type:* Democratic Republic of

the Congo, Katanga, Kamvali, cobalt-rich rocks with *Vellozia* 19.i.1960, *Duvigneaud* 5124 V (BRLU, holotype).

*Description:* The leaves of this variety are almost glabrous, but have wart-like emergences on the adaxial side (Fig 14E).

*BT leaf anatomy:* Not different from the typical variety.

*Specimens examined:* DEMOCRATIC REPUBLIC OF THE CONGO. Katanga, Kamvali, Forest with *Ficus*, *Duvigneaud* 3938Ve (BRLU); Kamvali, *Duvigneaud* 5124V (BRLU).

39. *Xerophyta naegelsbachii* (Dinter ex M. Holzhammer) Behnke, **comb. nov.**

*Barbacenia naegelsbachii* Dinter ex M. Holzhammer, Mitt. Bot. Staatssamml. München 1: 334. 1953. – *Type:* Namibia, Northern section, Kamanjab, 10°S, 15°E, *Naegelsbach s.n.* (M, holotype).

*Xerophyta wentzeliana* (Harms) Sölch *sensu* Sölch & Roessler in Merxmüller, Prodr. Fl. Südwestaf., fam. 152: 2. 1969.

*Xerophyta equisetoides* var. *pauciramosa sensu* Smith & Ayensu, Kew Bull. 29: 192. 1974; Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 4. 1975, *quoad Naegelsbach s.n.*

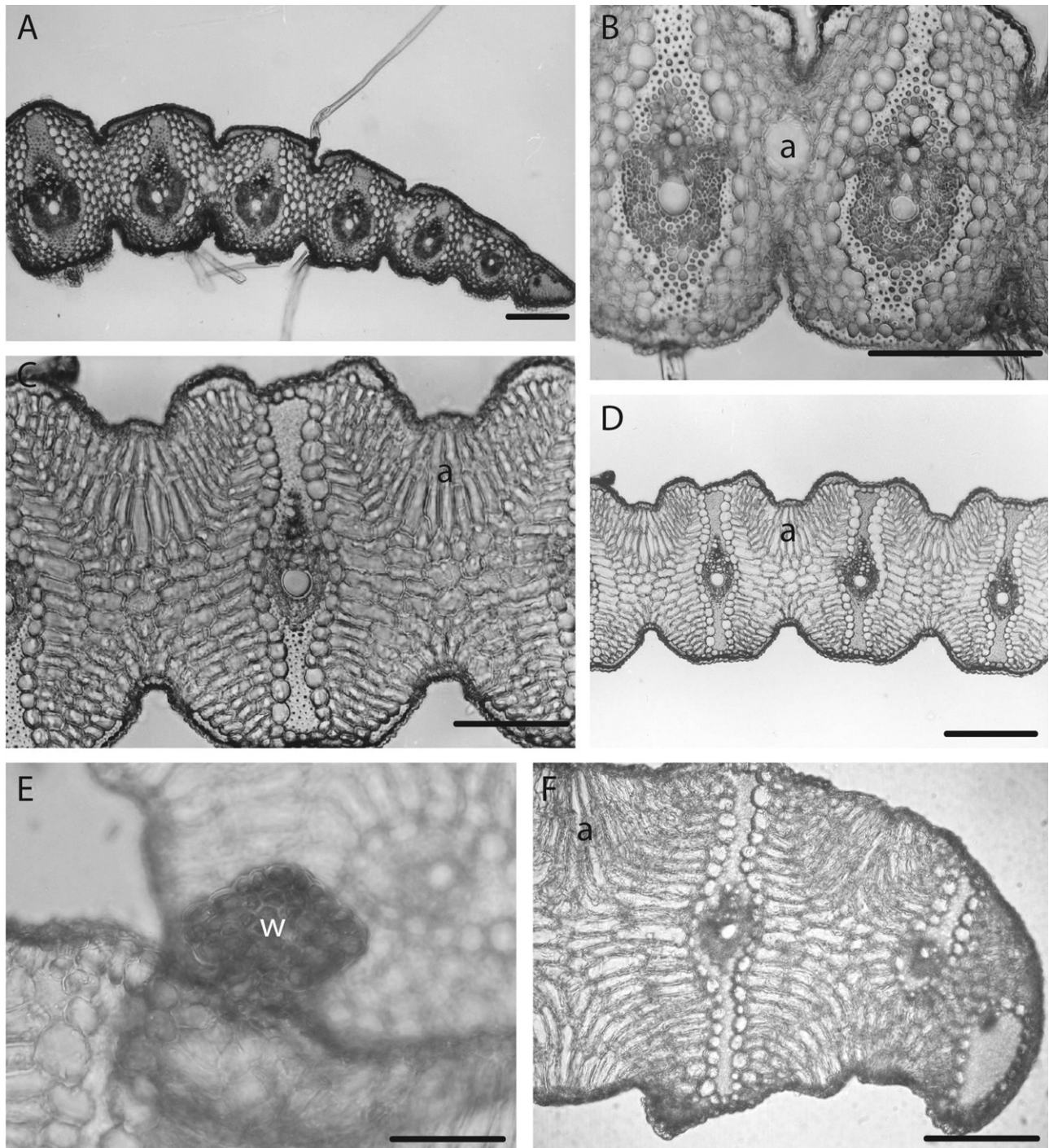
*Description:* Much branched shrub with short woody stem and about 1.0–1.5-cm-thick branches covered with squarrose leaf sheaths about 3 cm long, split into fibres. Leaf blades 15–30 cm long and up to 8 mm wide, V-shaped with median adaxial groove, deciduous, linear and acute, glabrous on outer surface and with short setae on the inner one. Flowers solitary, peduncle about 6.5 cm long. Tepals about 4 cm long. Stamens six, filaments short, anthers 1 cm long. Style including stigma about 1 cm long. Ovary 8 mm long and 4 mm in diameter. Ovary and upper part of peduncle covered with short eglandular emergences.

*Distribution:* Angola, Namibia.

*BT leaf anatomy:* Amphistomatic with shallow to deep opposite furrows; outer wall of epidermis cells only slightly thickened, stomata restricted to furrows; aquiferous cells fill the entire space between lateral bundles; small adaxial and abaxial subepidermal sclerenchyma bands on either side of lateral bundles (Fig. 14C, D).

*Specimens examined:* ANGOLA. Mossamedes-Curoca, Otchifengo, *Teixera* 375 (BM). – Huila, *Antunnes* 305





**Figure 14.** Transverse sections of leaves with basic *Barbacenia*-type (BT) leaf anatomy. A, B, Marginal leaf part (A) and lateral bundles (B) of *Xerophyta trichophylla* (from Buchanan 854). C, D, Lateral bundles of *Xerophyta naegelsbachii* (from Teixeira 735). E, F, Wart-like structure (w) and marginal leaf part of *Xerophyta wentzeliana* var. *verrucosa* (from Dwigneaud 5124). a = aquiferous cells. Scale bars, 100  $\mu$ m.

(B). NAMIBIA. Kaokoland, near Oruvandjai on road DR 3710 from Ombombo to Baadjie, *B. Eichhorn* 2003-2 (M). – Outjo, near Kamanjab, *Naegelsbach s.n.* (M and B); Farm Ondura, at Quarzkopf, *H. u. E.*

*Walter* 1/181 (BR); 8 km N Kamanjab, *Merxmüller & Giess* 30391 (M); on road from Welwitschia to Fransfontein, *Volk in Herb. W. Giess* 6121 (M); 5 km E of Fransfontein, Dolomite mountains, SW slope, *Giess*



11249 (M); 15 km W of Otjiyanyasemo, stone slope, *Giess & van der Walt* 12673 (M).

*Comments:* According to Dinter's description in Fedde Repertorium 15: 346 (1918), his *Barbacenia* spec. *suffruticosa* fol. *glaucis* (*nomen nudum*), collected near Fransfontein (Namibia), is to be included here.

40. *Xerophyta nutans* L.B.Sm. & Ayensu, Kew Bull. 29: 195, fig. 3. 1974; Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 7. 1975; Gonçalves in Fl. Zambes. 12, 2: 170. 2009. – *Type:* Tanzania, Masasi District, *Milne-Redhead & Taylor* 7687 (EA, holotype; BR, K, isotypes).

*Description:* Stem up to 50 cm high with up to 3-cm-thick branches. Leaf sheaths blackish brown with grey apices, quickly splitting after abscission. Leaf blades up to 30 cm long and 4 mm wide, V-shaped with prominent midvein and strong veins on both sides, deciduous, linear, filiform-attenuate, covered beneath with flat linear-lanceolate eglandular emergences, glabrous above. Flowers solitary, nodding. Peduncles three at apex of small branches. Tepals 30 mm long, pale lilac, uniform, linear-lanceolate, acute. Stamens six, filaments short, anthers about 15 mm long. Stigma linear, much longer than style base. Ovary 8–10 mm long, ellipsoid, covered with orbicular short-rayed eglandular emergences.

*Distribution:* Tanzania, Zambia, Mozambique.

*BT leaf anatomy:* Amphistomatic with deep opposite furrows; in adaxial furrows, aquiferous cells generally bulge out and are topped by sclerenchyma knobs; outer wall of epidermis cells moderately thickened, stomata confined to furrows; sclerenchyma bands, often interrupted by parenchymatic cells, underline the epidermis on both the adaxial and abaxial sides of lateral bundles and bend into the furrow openings (see also Smith & Ayensu, 1974: fig. 3).

Leaf blades densely covered with long emergences partly split into three to five short rays .....

.....a. var. ***nutans***

Leaf blades covered at margins or all over with flat feathery emergences having a palm-like base and five to ten glassy fingers .....b. var. ***plumosa***

a. var. *nutans*

*Specimens examined:* TANZANIA. Mtawa, Masasi District: 33.5 km E of R. Lemesule, *Milne-Redhead & Taylor* 7687 (BR). – Kilimanjaro, T3 Pare, 10 km from

Same at Old Mwembe, *Balslev* 225 (B). MOZAMBIQUE. Zambesia, Gurué District, Cascata, *de Koning* 7563 (K & BR).

b. var. ***plumosa*** Behnke, var. **nov.**

A var. *nutanti* foliorum trichomatibus plumosis basi plana lata palmata, 5–10 extensionibus dactyloideis longis et vitreis praeditis, differt. – *Type:* Zambia, Northern Province, Isoka District, Mafinga Mountains, *Robinson* 6296 (K, holotype; B, isotype).

*Distribution:* Zambia.

*Description:* The leaves of this variety are covered on both sides with spreading glassy and brittle feathery eglandular emergences that are distinct from the lanceolate emergences of var. *nutans* (see fig. 3 in Smith & Ayensu, 1974). The emergences of var. *plumosa* have a flat and broad palm-like base and up to ten or more finger-like extensions. In some leaves, they are restricted to the margins.

*BT leaf anatomy:* Transverse sections of the leaf lamina differ by their lateral bundles with less wide spaces between them and by broader adaxial and abaxial Y-shaped girders. The opposite furrows are as deep as in the typical variety, but the adaxial ones do not contain aquiferous cells or sclerenchyma knobs.

*Specimens examined:* ZAMBIA. North, Isoka District, Mafinga Mts., *Robinson* 9296 (B); Kaputa District, Nsama–Mporokoso, *Bullock* 1375 (K). – East, Chama District, Makutu Mts., *Fanshawe* 11542 (K); Nyika National Park, Manjanjere forest, *van der Linden* 357 (BR).

41. *Xerophyta suaveolens* (Greves) N.L.Menezes, *Ciência e Cultura* 23: 422. 1971; Smith & Ayensu, Kew Bull. 29: 194. 1974; Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 6. 1975; Gonçalves in Fl. Zambes. 12, 2: 168. 2009, *pro parte*, excluding *Angus* 866 & *Leach* 11184.

*Vellozia suaveolens* Greves, J. Bot. 59: 282. 1921. – *Type:* Zimbabwe, Eyles 439 (BM, holotype).

*Vellozia equisetoides sensu* Baker in Harvey, Fl. Cap. 6: 245. 1896, *quoad Baines s.n.*; *sensu* Eyles in Trans. Roy. Soc. South Afr. 5: 328. 1916, *quoad Baines s.n.*, Eyles 25, 439, 516, & *Rand* 270; *sensu* Greves, J. Bot. 59: 281. 1921, *quoad Baines s.n.*; *sensu* White, Forest Flora of Northern Rhodesia: 17. 1962, *quoad Angus* 866 & *White* 3680; *sensu* Norlindh, Bot. Notiser 1948: 28. 1948, *quoad Fries, Norlindh & Weimarck* 2211. *Vellozia* spp. of Eyles in Trans. Roy. Soc. South Afr. 5: 329. 1916, *quoad Monro* 801.

**Description:** Shrub up to 2 m high and at the base to 15 cm in diameter. Branches terete, to 1.5 cm thick, covered with fibrous leaf sheaths. Leaf blades about 60 cm long and 1.2 cm wide, V-shaped with prominent midvein and strong veins on both sides, deciduous, linear and tapering to an acute apex, adaxial surface with distinct setae, abaxial surface glabrous or laxly covered with eglandular emergences, margins smooth. Flowers solitary, strongly scented. Peduncles one to four at apex of a branch, 6–13 cm long and covered with flat or swollen stellate eglandular emergences in uppermost part. Tepals up to 60 mm long, white to pale lavender. Stamens six, with short filaments, anthers from 2 cm to about half as long as tepals. Stigma linear, much longer than the style base. Ovary 8–16 mm long, ellipsoid, covered with flat forked or stellate emergences, in young flowers flat and triangular (Fig. 15B), in old ovaries typically swollen, less dense and four-sided (Fig. 15E, G).

**Distribution:** Democratic Republic of the Congo, Tanzania, Malawi, Zambia, Zimbabwe, Botswana, Mozambique.

**BT leaf anatomy:** Amphistomatic with deep opposite furrows; up to four lateral bundles on either side of the central bundle differ from all other lateral bundles by adaxial extended bundle sheath cells; in adaxial furrows, aquiferous cells generally bulge out and, in the three to four furrows adjacent to the central bundle, may be topped by sclerenchyma knobs; outer wall of epidermis cells moderately thickened on the adaxial side, heavily thickened and papillate on the abaxial side, stomata confined to furrows; sclerenchyma bands, occasionally interrupted by parenchymatic cells, underline the epidermis on both the adaxial and abaxial sides of lateral bundles and bend into the furrow openings (Fig. 10F, G).

Leaf blades glabrous beneath, setose to scabrous above .....a. var. *suaveolens*

Leaf blades beneath (and above) laxly vestite with long, glassy emergences .....b. var. *vestita*

*a. var. suaveolens*

**Specimens examined:** DEMOCRATIC REPUBLIC OF THE CONGO. Katanga, Kambove, Cimetière, *Malaisse* 12136 (BR); Luiswishi, *Malaisse* 12159 (BR); 23 km NNW of Kolwezi, road Nzilo–Kyamasmebue, *Schaijes* 1139 (BR); near Kolwezi, *Schaijes* 2411 (BR); Kasompi East, *Duvigneaud & Timperman* 2046 & 2047 (BRLU); Kambove–Kamoia, *Duvigneaud* 4092V1+V4 and 4101Va (all: BRLU); Fungurume, *Duvigneaud* 4106VE and 4108V2+V3, and 4113V3+V6 (all: BRLU); Chabara, *Duvigneaud* 4137V and 4138V (BRLU); Swambo, *Duvigneaud* 4407V2 (BRLU); Kasompi W,

*Duvigneaud* 4424V (BRLU); Kolwezi, *Duvigneaud* 4476X (BRLU); Kakanda, *Duvigneaud* 4819 (BRLU); Lukopu, *Verdick* 238 (BR); Kundelungu Plateau, Kasenga, 7 km off road Elisabethville–Kasenga, *Schmitz* 6256 (BR). TANZANIA. Ruvuma, S of Songea, Matagoro Hills, *Milne-Redhead & Taylor* 8592 (K). – Lindi, Nachingwea District, Kilimmarondo inselberg, *Mogoro & Rose Innes* 454 (K). ZAMBIA. North, track to Kapata village, *Richards* 20674 (K and B); Mbala, *Angus* 781 (BR). ZIMBABWE. West, Semokwe River, *Baines s.n.* (B); Matopos Hills, granite country, on side of kloofs, *Eyles* 25 (BM). – North, Sanyati, Gokwe Distr., F body North Mine, *Wengler* 249 (BR); Makonde District, Molly South Hill, *Wild & Drummond* 6676 (BR). – East, Nyanga District, Nyangombe Falls, *Chase* 3073 (K and BR); Mutare District, 25 km S from Mutare town, *Fries, Norlindh & Weimark* 2211 (BR); Mutare District, E of Mt. Pleasant Road, Commonage, *Chase* 5334 (BM and BR). MOZAMBIQUE. – MS, Moribane, *Dawe* 502 (K). BOTSWANA. North, Francistown, *Rand* 1 (BM). SOUTH AFRICA. Limpopo, Zoutpansberg, Punda Maria, *Dyer* 31068 (BR).

*b. var. vestita*

var. *vestita* L.B.Sm. & Ayensu, *Kew Bull.* 29: 194. 1974; Gonçalves in *Fl. Zambes.* 12, 2: 170. 2009, excluding *LaCroix* 2424 & *Linder* 3931. – *Type:* Zambia, 48 km east of Mbala on Tunduna road, *Napper* 1161 (EA, holotype; K, isotype).

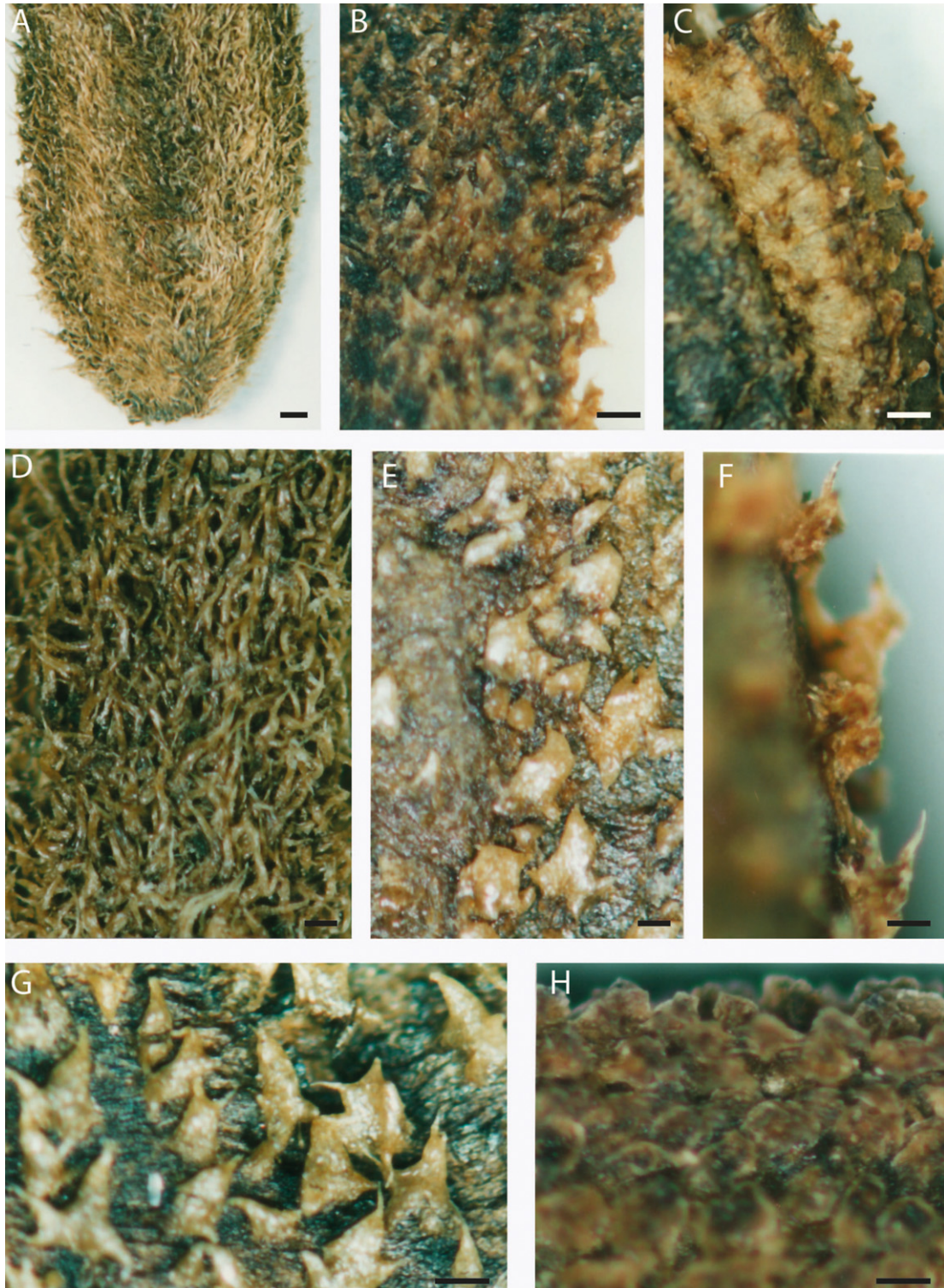
**BT leaf anatomy:** Transverse sections of the leaf blade are distinct from the typical variety by the greater depth of their opposite furrows, more closely spaced lateral vascular bundles without extended bundle sheath cells and almost complete absence of sclerenchyma knobs above aquiferous cells.

**Specimens examined:** DEMOCRATIC REPUBLIC OF THE CONGO. Katanga, Kambove, Cimetière, *Malaisse* 12129 (BR). ZAMBIA. West, Copperbelt Province, Kitwe District, *Fanshave* 10215 (K). ZIMBABWE. North, Mashonaland Central, Mazowe District, Spelonken Farm, *Biegel* 2695 (BR); Urungwe National Park, 20 km from Makuti on road to Kariba, *Philcox, Leppard & Dini* 8729 (K).

42. *Xerophyta eylesii* (Greves) N.L.Menezes, *Ciência e Cultura* 23: 422. 1971; Smith & Ayensu, *Kew Bull.* 29: 189. 1974; Gonçalves in *Fl. Zambes.* 12, 2: 164. 2009. *Vellozia eylesii* Greves, *J. Bot.* 59: 281. 1921. – *Type:* Zimbabwe, Mazoe, ‘Iron Mask Hill’, *Eyles* 400 (BM, lectotype).

*Vellozia* spp. of Eyles in *Trans. Roy. Soc. South Afr.* 5: 329. 1916, *quoad Eyles* 440.





**Figure 15.** Ovary trichomes. A, D, *Xerophyta trichophylla* with long and flexuous, slightly swollen trichomes (from Buchanan 262 and 214, respectively). B, E, *Xerophyta suaveolens* var. *suaveolens* with triangular emergences on young and swollen stellate trichomes on old ovaries (from Schmitz 6256). C, F, *Xerophyta eylesii* with scutate emergences ending in a long tip (from Angus 886). G, *Xerophyta suaveolens* var. *vestita* with swollen stellate emergences (from Biegel 2695). H, *Xerophyta demesmaekeriana* with flattened sessile glandular emergences (from Robson 898). Scale bars: A–C, 500  $\mu\text{m}$ ; D–H, 200  $\mu\text{m}$ .



*Xerophyta zambiana* Smith & Ayensu, Kew Bull. 29: 199. 1974, *quoad* Angus 886 and Gonçalves in Fl. Zambes. 12, 2: 172. 2009, *quoad* West 6132.

*Description:* Stem 15–30 cm long, not branched, but leaves and flowers arising separately from forked apex. Leaf sheaths about 4 cm long, dark brown with strong veins; blades 15–25 cm long and about 1 cm broad, V-shaped with prominent midvein and strong veins on both sides, deciduous, linear with distinct midrib, both sides covered with about 1-mm-long eglandular emergences, spreading at margins. Flowers solitary on 12–15-cm-long peduncles, covered with trichomes over their entire length. Tepals 4.5–5.0 cm long, pale purple. Stamens six, filaments 2–3 mm long, anthers 1.2–1.8 cm long. Style plus stigma about as long as anthers. Ovary turbinate, covered with scutate eglandular emergences with stiff spinulose outgrowths (Fig. 15C, F).

*Distribution:* Zambia, Zimbabwe.

*BT leaf anatomy:* Amphistomatic and with deep opposite furrows; central bundle with small adaxial cap and a large abaxial cap ascending to winged crescentiform girder also embracing an adjacent lateral bundle; outer wall of epidermis cells thickened and papillate, stomata confined to furrows; short adaxial and abaxial sclerenchyma bands underline the epidermis on either side of lateral bundles bending into the furrow opening; many eglandular emergences present on both adaxial and abaxial surfaces (Fig. 11F).

*Specimens examined:* ZAMBIA. Central, District Serenje, woodland at Kanona, Angus 886 (BR). – South: Kalomo District, Siantambo, Kalomo, Mitchell 15/55 (BR). – North, Nkumbo Hill (Chibuli Hill), Leteinturier, Malaisse & Matera 463 (BR). ZIMBABWE. North, Mazowe District, Archie Henderson Research Station on Iron Mask Range, West 6132 (K).

43. *Xerophyta trichophylla* (Baker) N.L.Menezes, Ciência e Cultura 23: 422. 1971; Gaff in Oecologia 31: 97. 1977.

*Vellozia equisetoides* var. *trichophylla* Baker in Oliver, Fl. Trop. Afr. 7: 411. 1898; Binns, Check List Fl. Malawi: 103. 1968. – Syntypes: Malawi, Southern Region: Shire Highlands, xii.1881, Buchanan 162 (K, syntype; E, isosyntype); Malawi, without precise locality, 1891, Buchanan 854 (K, syntype; B, BM, US, isosyntypes); Malawi, Southern Region: Zomba District, Whyte 92 (K, syntype).

*Vellozia equisetoides sensu* W. Watson, Gard. Chron., ser. 3, 34: 425. 1903, *non* Baker.

*Vellozia trichophylla* (Baker) Hemsl., Bot. Mag. 130, t. 7962. 1904; Greves, J. Bot. 59: 281. 1921; Ayensu, Kew Bull. 23: 322. 1969; Jacobsen, Kirkia 9: 153. 1973.

*Vellozia equisetoides* (*pro parte*) in White, Forest Fl. N. Rhod.: 17. 1962.

*Xerophyta barbarae* P.A.Duvign. & Dewit, Bull. Soc. Roy. Bot. Belgique 96: 145. 1963. – *Type:* Democratic Republic of the Congo, Katanga, Kolwezi, Dikuluwe Hill, 14.xi.1959, *Duvigneaud* 4118 (BRLU, holotype). *Xerophyta barbarae* ssp. *cuprophila* P.A.Duvign. & Dewit, Bull. Soc. Roy. Bot. Belgique 96: 147 + fig. 10. 1963. – *Type:* Democratic Republic of the Congo, Katanga, Kolwezi, Dikuluwe Hill, 14.xi.1959, *Duvigneaud* 4124 V<sub>2</sub> (BRLU, holotype).

*Xerophyta equisetoides* var. *trichophylla* (Baker) L.B.Sm. & Ayensu, Kew Bull. 29: 192. 1974; Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 3. 1975; Gonçalves in Fl. Zambes. 12, 2: 166. 2009, *pro parte* excluding *Chisumpa* 115, *Fanshave* 2609 & *Salubeni* 1253.

*Description:* Shrub with short and thick (20 cm or more in diameter) woody stem and a few thick primary branches, both covered with leaf sheaths split into fibres. Leaf blades up to 40 cm long and to 1.2 cm wide, V-shaped with median adaxial groove, deciduous, linear and acute, on both sides with simple long, unicellular trichomes, surrounded by a multicellular base (emergence). Flowers solitary, fragrant, often with three pedicels on terminal peduncle, pedicel in upper part covered with eglandular emergences. Tepals about 25 mm long, pale blue to mauve, the outer lanceolate acute. Stamens six, filaments short, anthers 10–12 mm long, yellow. Style about 2 mm, stigma 5 mm long. Ovary 8 mm long and 4 mm in diameter, densely covered with eglandular emergences that are often swollen and flexuous (Fig. 15A, D).

*Distribution:* Democratic Republic of the Congo, Tanzania, Malawi, Zambia, Zimbabwe.

*BT leaf anatomy:* Amphistomatic with deep opposite furrows; outer wall of epidermis cells moderately thickened, stomata restricted to furrows; prominent aquiferous cells below adaxial and abaxial furrows; subepidermal sclerenchyma present on both the adaxial and abaxial sides of lateral bundles (Fig. 14A, B; see also Ayensu, 1969: 322).

*Specimens examined:* DEMOCRATIC REPUBLIC OF THE CONGO. Katanga, Lukafu, Verdick 147 (BR); Fungurume, Malaisse 9239 (BR); Luita, Malaisse 12183 (BR); Vallée de la Lofoi (Lukafu-Sampwe), Schmitz

2080 (BR); N'Zilo, 60 km from Kolwezi, Schmitz 4255 (BR); Bunkeya, Hoffmann 894 (BR); (BRLU); Dikuluwe, Duvigneaud 3087V, 4119V, 4120V, 4124V+V2, 4125V, 4484V, 4489V and 4490V (all: BRLU); Kolwezi, Duvigneaud 4482V2, 4483V, 4494V and Plancke 99/1338 and 101/1350 (all: BRLU); Kalongwe, Duvigneaud 4620V and Plancke 124/1646 (both: BRLU). MALAWI. – Without location: Buchanan 854 (K and B). – South, Shire Highlands, Buchanan 162 (E); Shire Highlands, hill tops, Buchanan 214 (E); Zomba, Old Naisi Road, 0.75 miles from Mlunguzi Bridge, Chapman 6020 (K); Zomba District, above Monga village, Malosa valley, Patel 966 (BR). ZAMBIA. – North, Mbala District, Plain of Death, Chilongwelo, Richards 2310 (K); Chishimba Falls, left side of Luembe River, near Chilubula, Symoens 9035 (BM). ZIMBABWE. North, Silverside Mine, c. 19 km from Mhangura, Baudesson, Leteinturier & Malaisse 332 (BR).

44. *Xerophyta equisetoides* Baker, J. Bot. 13: 233. 1875; Durand & Schinz, Consp. Fl. Afr. 5: 271. 1895; Duvigneaud & Denaeyer de Smet, Bull. Soc. Roy. Bot. Belg. 96: 145. 1963; Smith & Ayensu, Kew Bull. 29: 190. 1974; Smith & Ayensu in Fl. Trop. East Afr., Velloziaceae: 3. 1975; Compton, Fl. Swaziland in J. South Afr. Bot., Suppl. 11: 132. 1976; Gaff, Oecologia 31: 97. 1977; Tredgold & Biegel, Rhod. Wild Flow.: 10 and Plate 6. 1979; Seine, Veget. Inselberg. Zimbabwe: 101, 134, 233. 1996; Seine *et al.* in Edinb. J. Bot. 55: 283. 1998; Gonçalves in Fl. Zambes. 12, 2: 165. 2009. – *Type*: Malawi, Zomba and East end of Lake Chilwa, *Meller s.n.* (K, holotype).

*Xerophyta melleri* Baker, J. Bot. 13: 234. 1875. – *Type*: Malawi, Manganja Hills, *Meller s.n.* (K, holotype).

*Vellozia equisetoides* (Baker) Baker in Harvey, Fl. Cap. 6: 245. 1896, excluding *Baines s.n.*; Baker in Oliver, Fl. Trop. Afr. 7: 411. 1898, excluding *Baines s.n.*, *Kirk s.n.* & *Scott-Elliot* 8524; Eyles in Trans. Roy. Soc. South Afr. 5: 328. 1916, *quoad Teague* 236; Greves, J. Bot. 59: 281. 1921, excluding *Baines s.n.*; Norlindh, Bot. Notiser 1948: 28. 1948, excluding Fries, Norlindh & Weimarck 2211; White, Forest Fl. N. Rhod.: 17. 1962, excluding *Angus* 866 & *White* 3680; Ayensu, Kew Bull. 23: 320. 1969; Jacobsen, *Kirkia* 9: 153. 1973.

*Barbacenia equisetoides* (Baker) R.E.Fr., Rhodesia-Kongo-Exped. I, Bot., 1, 233. 1914.

*Xerophyta retinervis* Baker var. *equisetoides* (Baker) Coetzee in Coetzee *et al.*, Dinteria 9: 4, 8, fig. 2 + 11B. 1973; Coetzee, Dinteria 10: 26. 1974.

*Xerophyta equisetoides* Baker var. *setosa* L.B.Sm. & Ayensu, Kew Bull. 29: 194. 1974, excluding *Chase* 3073; Gonçalves in Fl. Zambes. 12, 2: 167. 2009. – *Type*: Zimbabwe, Eastern Province, Umtali District, Commonage, *Chase* 1866 (K, holotype; BM isotype).

*Description*: Shrub with short and thick (20 cm or more in diameter) woody stem and a few thick primary branches, both covered with leaf sheaths split into fibres. Leaf blades 10–30 cm long and up to 1.2 cm wide, V-shaped with median adaxial groove, deciduous, linear and acute, on both sides glabrous or covered with short stiff setae (Fig. 7E, F). Flowers solitary, fragrant, often with three pedicels on terminal peduncle, pedicel in upper part covered with eglandular emergences. Tepals about 25 mm long, white or pink to lilac, the outer lanceolate acute. Stamens six, filaments short, anthers 10–12 mm long. Style about 2 mm, stigma 5 mm long. Ovary 8 mm long and 4 mm in diameter, densely covered with short fine to long slender yellowish or brownish eglandular emergences.

*Distribution*: Democratic Republic of the Congo, Tanzania, Zambia, Zimbabwe, Mozambique, Angola, Namibia, South Africa: Limpopo, Swaziland.

*BT leaf anatomy*: Amphistomatic with deep opposite furrows; outer wall of epidermis cells somewhat thickened, stomata restricted to furrows; small sclerenchyma bands underline the epidermis on the abaxial side of the central bundle and on both the adaxial and abaxial sides of lateral bundles (see also Ayensu, 1969: 320 + plate 3: 1).

*Specimens examined*: DEMOCRATIC REPUBLIC OF THE CONGO. Katanga, Menda, *Duvigneaud* 4440 and 4441T/V2+V (all: BRLU); Luiswishi, *Duvigneaud* 2812V and 4874V (BRLU); Kambove–Kamoia, *Duvigneaud* 4094, *Duvigneaud* 4705V2, 4716V and 4718V (all: BRLU); Kasekalesa, *Duvigneaud* 5231V (BRLU); 100 km from Jadotville to Kolwezi, *Schmitz* 6278 (BR); Kolwezi, *Plancke* 101/1350 and 106/1451 (BRLU); 8 km NE of Likasi, *Malaisse* 6690 (BR); Parc Natl. de l'Upemba, *Kimilimbo de Witte* 2879 (BR); Tilwizembe, 30 km ESE of Kolwezi, *Empain, Malaisse & Robbrecht* 2399 (BR); Fungurume, *Duvigneaud* 4729V and 5494X (BRLU); Fungurume, *Malaisse* 9238 (BR); Fungurume, copper-rich hill, *Malaisse & Gregoire* 73 (BR); Plateau de Kundelungu, Chute Kaloba, Gorge of Lofoi, *Malaisse* 6524 (BR). TANZANIA. Rukwa, Sumbawanga District, road to Safa, 2 km SW of Junction Sumbawanga–Mbala (Zambia) road, *H. H. Schmidt, Gereau, Mhoro, Kayombo & Mwangoka* 1184 (K and MO). ZAMBIA. North, Mbala District, Mbala–Sumbawanga Road, 8 ml from Mbala, *Kuhni* 17 (BM); Mbala, *Glover in Bredo* 6167 (BR); Mpika District, 30 km S of Shiwa Ngandu on road to Mpika, *Angus* 866, (BR). – South, Mazabuka, Ridge-way Rd, *Trapnell s.n.* (K); M'Tulunga, *van Meel* 1405 (BR); Kabwe, rocks at right bank of river Tshilongo, *Malaisse* 11428 (BR). ZIMBABWE. East, Nyanga Dis-

trict, 8 km NE of Nyanga, Lindi waterfalls, *Bamps, Symoens & van den Berghen* 475 (BR); Mutare District, Commonage, Nenen River, *Chase* 1866 (K); Mutare District, NE boundary, Murakwa's Hill, *Chase* 8510 (M); Mutare District, Honde Valley, *Chase* 1361 (K). – Central, Mashonaland East, Arcturus, Gilnockie Farm, *Seine* 1167, cult. Bot. Gard. Bonn 17010 (M); Kwekwe District, Sabe Park, 8 km NE Kwekwe (K). – North, Gokwe Distr., Sanyati, Copper Queen Mine, *Wengler* 220 (BR); Gokwe District, Sanyati, Copper Beacon Mine, *Wengler* 209 (BR); Gokwe District, Sanyati, Copper King North Mine, Sanyati Mining Company, *Wengler* 276 (BR); Mashonaland Central, near Mt. Darwin, *Seine* 485 (M). – South, Masvingo, 2 ml S of Runde River Bridge, Fort Victoria–Beitbridge Rd, *Leach* 11184 (K and BR); Masvingo, Mushandike, at lake, *Malaisse* 12260 (BR); Masvingo, Lake Mutirikwi Recreational Park, *Seine* 523 and *Seine* 1496, cult. Bot. Gard. Bonn 17012 (M). MOZAMBIQUE. MS, Manica Province, Manica District, Mavita, Serra Mocuta, *Pereira & Marques* 1074 (BR).

45. *Xerophyta retinervis* Baker, J. Bot. 13: 233. 1875; Durand & Schinz, Consp. Fl. Afr. 5: 272. 1895; Coetzee *et al.*, Dinteria 9: 4, 8, figs 1, 10A, E–F. 1973; Coetzee, Dinteria 10: 26, figs 2, 5, 11. 1974; L. B. Smith & Ayensu, Kew Bull. 29: 190. 1974; Compton, Fl. Swaziland in J. South Afr. Bot., Suppl. 11: 132. 1976; Gonçalves in Fl. Zambes. 12, 2: 164. 2009. – Type: South Africa, Transvaal, Magaliesberg, *Burke s.n.* (K, holotype).

*Xerophyta clavata* Baker in *l.c.* 1875; Coetzee *et al.*, Dinteria 9: 4, 8, figs 8, 11C. 1973; Coetzee, Dinteria 10: 26, figs 8, 9. 1974. – Type: South Africa, Natal, Gerrard 1824 (K, holotype).

*Hypoxis vellosioides* Harv. ex Baker in *l.c.* 1875, listed in synonymy only.

*Vellozia retinervis* (Baker) Baker in Harvey, Fl. Cap. 6: 244. 1896; Eyles in Trans. Roy. Soc. South Afr. 5: 329. 1916; Greves, J. Bot. 59: 280. 1921; Letty, Wild Flow. Transvaal: 72 and Plate 35. 1962; Ayensu, Kew Bull. 23: 321–322. 1969; Ross, Fl. Natal: 133. 1972.

*Vellozia clavata* (Baker) Baker in Harvey, Fl. Cap. 6: 244–245. 1896; Greves, J. Bot. 59: 280. 1921.

*Barbacenia retinervis* (Baker) Pax ex Burt Davy & Pott-Leendertz, Ann. Transvaal Mus. 3: 121. 1912; Marloth, Fl. South Afr. 4, fig. 37. 1915.

**Description:** Woody shrubs with stems up to 1.5 (rarely 2.5) m high and 4–5 cm in diameter, branched at base only, but with several tufts of three to six leaves proceeding near the top from beneath the leaf sheaths, or extensively branched at a height of about 1 m. Leaf sheaths brown, fan-like, about 5–6 cm long, soon splitting; blades to 50 cm long and 2–8 mm wide,

deciduous, V-shaped with median adaxial groove, linear, sizes variable, glabrous on both sides but often serrulate at margins and on keel. Flowers solitary on 10–15-cm-long peduncles that are covered in the upper part with dark coloured eglandular emergences. Tepals about 50 mm long and 10 mm wide, light blue to light mauve, glabrous on the outside but with a few trichomes on basal part of midrib. Stamens six, filaments short, anthers about 20 mm long. Style including stigma 25 mm long. Ovary oblong about 12 mm long and 6 mm in diameter, densely covered with ascending brown, about 2-mm-long eglandular emergences.

**Distribution:** Botswana, Swaziland, South Africa: Gauteng, Limpopo, Mpumalanga, North West.

**BT leaf anatomy:** Amphistomatic with deep opposite furrows; outer walls of epidermis cells thickened and slightly papillate, distinctly papillate within furrows, stomata restricted to the innermost part of furrows; aquiferous cells below furrows on both sides and often double the space between lateral bundles, make adaxial furrows broader and less deep, and occasionally produce small protrusions; heavy adaxial and abaxial sclerenchyma bands underline the epidermis on either side of lateral bundles and merge into furrows (Fig. 16A–D; see also Ayensu 1969: 321 + plate 4, 2).

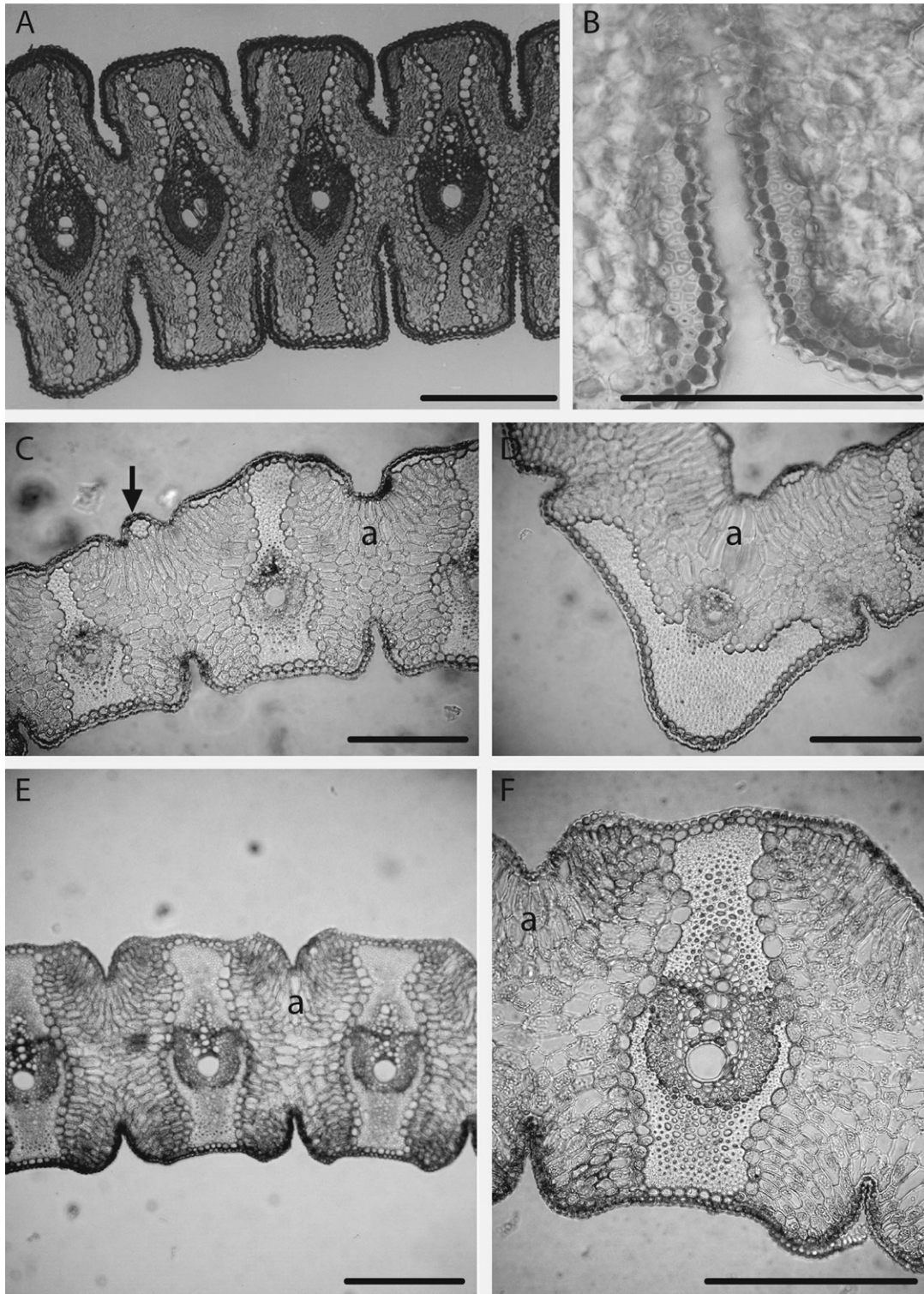
Stem 0.5–1.5 m high and not branched .....a. var. **retinervis**

Stem up to 2.5 m high and, after about 1 m, divided into five to ten branches .....b. var. **multiramosa**

a. var. *retinervis*

**Specimens examined:** SOUTH AFRICA. Gauteng, Pretoria–Rietfontein, Magaliesberg, *Merxmüller* 137 (M); District Pretoria, Meintjes Kop, *Schlieben* 10555 (HEID) and *Schlieben* 7928 (BR); Pretoria, rocky quartzitic ridge in BG-PRE, about 3 km SW of Magaliesberg, *A.E. van Wyk* 13300 (PRE); Hills North Pretoria, *Scott Elliot* 1385 (E); Pretoria, Brummeria Nat. Bot. Gard., *Balsinhas* 3411 (BR); 20–30 miles NO Pretoria, *Werdermann & Oberdieck* 1321 (B). – North West, about 5 km S of Broederstroom, *Adendorff* 2 (M); near Assen, *Adendorff* 20 (M). – Mpumalanga, rocky ridge N of Stoffberg on way to Roosenekal, *Adendorff* 30 (M); Piet Retief, *Devenish* 1055 (HEID); 4 km N of Havelock, *Malaisse* 4650 (BR); between Luneburg and Dirkiesdorp, *Schwabe s.n.* (B); Sekhukhuneland, entrance road to Thorncliffe Mine, *Burrows* 6592 (BNRH); Barberton, Agnes Mine, *Weigend* 2261 (M). – Limpopo, Wolkberg, above waterfall, near Serala (Klipdraai) Forest Station, *Adendorff* 9 (M). SWAZILAND. Dabriach High Veld, near Mbabane, *Bolus* 12368 (BR).





**Figure 16.** Transverse sections of leaves with basic *Barbacenia*-type (BT) leaf anatomy: *Xerophyta retinervis* (A–D) and *Xerophyta vallispongolana* (E–F). A, Unexpanded leaf with opposite furrows. B, Abaxial furrow with papillate epidermis and subepidermal sclerenchyma. C, Expanded leaf with aquiferous cells (a) and sclerenchyma knobs (arrow). D, Midvein with large winged crescentiform abaxial girder and aquiferous cells (a). E, F, Expanded leaf with radial arrangement and aquiferous cells (a). (A, B from Scott Elliot 1385, C, D from Adendorff 9, E, F from J. E. & S. M. Burrows 6586). Scale bars: A, C–F, 100  $\mu$ m; B, 50  $\mu$ m.





**Figure 17.** A, B, *Xerophyta vallispongolana* at type location in KwaZuluNatal, South Africa (photographs by J. E. Burrows). C, D, *Xerophyta retinervis* var. *multiramosa* in Woodbush resp. Roossenekal, Mpumalanga, South Africa (photographs by J. D. Adendorff). E, F, *Xerophyta cauliflora*. E, Branched plant in Tulear, Madagascar (photograph by Eberhard Fischer). F, Dried flower and seed capsule hanging down from stem of cultivated plant at Bot. Gard. Bonn (11428). Scale bars: A, 5 cm; B, D, F, 1 cm.

*b. var. multiramosa* Behnke, *var. nov.*

A var. *retinervi* caule alto (ad 2.5 m) multiramoso, foliisque laterioribus differt (Fig. 17C, D). – *Type*: South Africa, Limpopo, small dirt road off tarred road towards Jane Furse, 1193 m, 24°48'30.4"S, 29°58'22.3"E, 30.iii. 2005, Adendorff 33 (M, holotype).

*Specimens examined*: SOUTH AFRICA. **Limpopo**, small dirt road off tarred road towards Jane Furse, Adendorff 33 (M).

46. *Xerophyta vallispongolana* J.E.Burrows, S.M.Burrows & Behnke, *sp. nov.* – *Type*: South Africa, KwaZuluNatal, 7.6 km from Commondale on

road to Piet Retief, on rocky outcrop in grassland, 8.xi.1999, *J. E. Burrows & S. M. Burrows* 6586 (J, holotype; BNRH, PRE, isotypes).

*Diagnosis:* Frutex ramosus ad 1.5 m altus, ramis c. 4–5 cm diametro, basibus foliorum brunneis c. 6 cm longis lente fatiscantibus vestitis. Folia 5–7, ad 60 cm longa, 1.3 cm lata, in ramorum apicibus disposita, lamina caduca, rigida, lineari, apicem versus attenuata, margine integro, supra et subtus pilis mollibus dense vestita, ad apicem sparsius pilosa. Flores solitarii, pedunculo ad 25 cm longo, in parte inferiore sparsim piloso, in parte superiore dense piloso. Tepala c. 6.0 cm longa, 1.5 cm lata, albida, lanceolata, apice acuminato, exteriora in costa et basin versus pilosa. Stamina 6, c. 2 cm longa, filamentis brevibus (2–3 mm), antheris polline luteo. Stylus 3–4 cm longus; stigma c. 1.2 cm longum. Ovarium c. 7 mm diametro, 10 mm longum, obovatum, pilis unicellularibus, c. 2.0–2.5 mm longis, magis minusve appressis dense vestitum.

*Eponymy:* The specific epithet refers to the valley in which the type specimens were found.

*Distribution:* Known from the type locality only.

*Description:* Branched shrub up to 1.5 m high, with branches about 4–5 cm in diameter (Fig. 17A), clothed in the brown leaf sheaths about 6 cm long, slowly disintegrating and laxly beset with grey trichomes. Leaves five to seven, up to 60 cm long and 1.3 cm wide, arranged at the tip of the branches, with the lamina deciduous, rigid, linear, tapering towards the apex, with an entire margin, densely clothed above and below with soft trichomes (about 1.5 mm long), more sparsely hairy on the midrib and in lower part, densely hairy in the upper part. Flowers solitary (Fig. 17B), with a peduncle up to 25 cm long which is sparsely hairy in the lower part and densely hairy in the upper part. Tepals about 6.0 cm long and 1.5 cm wide, white, lanceolate with an acuminate apex, the outer hairy on the midrib and towards the base. Stamens six, about 2 cm long with short (2–3 mm) filaments, anthers with yellow pollen. Style 3–4 mm long, stigma about 1.2 cm long. Ovary about 7 mm in diameter and 10 mm long, obovate, densely clothed with unicellular hairs which are about 2.0–2.5 mm long and more or less appressed.

*BT leaf anatomy:* Amphistomatic with opposite shallow to deep furrows; outer wall of epidermis cells moderately thickened, stomata restricted to furrows; on adaxial and abaxial sclerenchyma bands underline the epidermis on either side of lateral bundles and merge into the furrows (Fig. 16E, F).

*Specimens examined:* SOUTH AFRICA. KwaZulu Natal, 7.6 km from Comondale on road to Piet Retief, near Pongola River, *J. E. & S. M. Burrows* 6586 (BNRH).

#### ANATOMICAL DESCRIPTION OF THE MADAGASCAN SPECIES OF *XEROPHYTA*

47. *Xerophyta andringitrensis* (H.Perrier) Phillipson & Lowry, *Tropicos* (2009). – Syntypes: Madagascar, Fianarantsoa, Andringitra, *Perrier* 12100, 13624, 14368 (P, holotype; K, TAN, isotypes).

*Vellozia dasyliroides* (Baker) Poisson, *Récherch. Fl. Mérid. Madagascar*: 98. 1912, *pro parte*.

*Xerophyta dasyliroides* var. *andringitrensis* H.Perrier, *Arch. Bot. Bull. Men.* 4: 69. 1930; Perrier in Humbert, *Fl. Madagascar*, fam. 42: 9. 1950; Smith & Ayensu, *Kew Bull.* 29: 197. 1974.

*Vellozia dasyliroides* (Baker) Poisson var. *andringitrensis* Ayensu, *Kew Bull.* 23: 324. 1969, *nomen nudum*.

*Vellozia dasyliroides* (Baker) Poisson var. *dasyliroides*, *pro parte*, Ayensu, *Kew Bull.* 23: 324. 1969, *quoad* fig. 2: 2, *nomen nudum*.

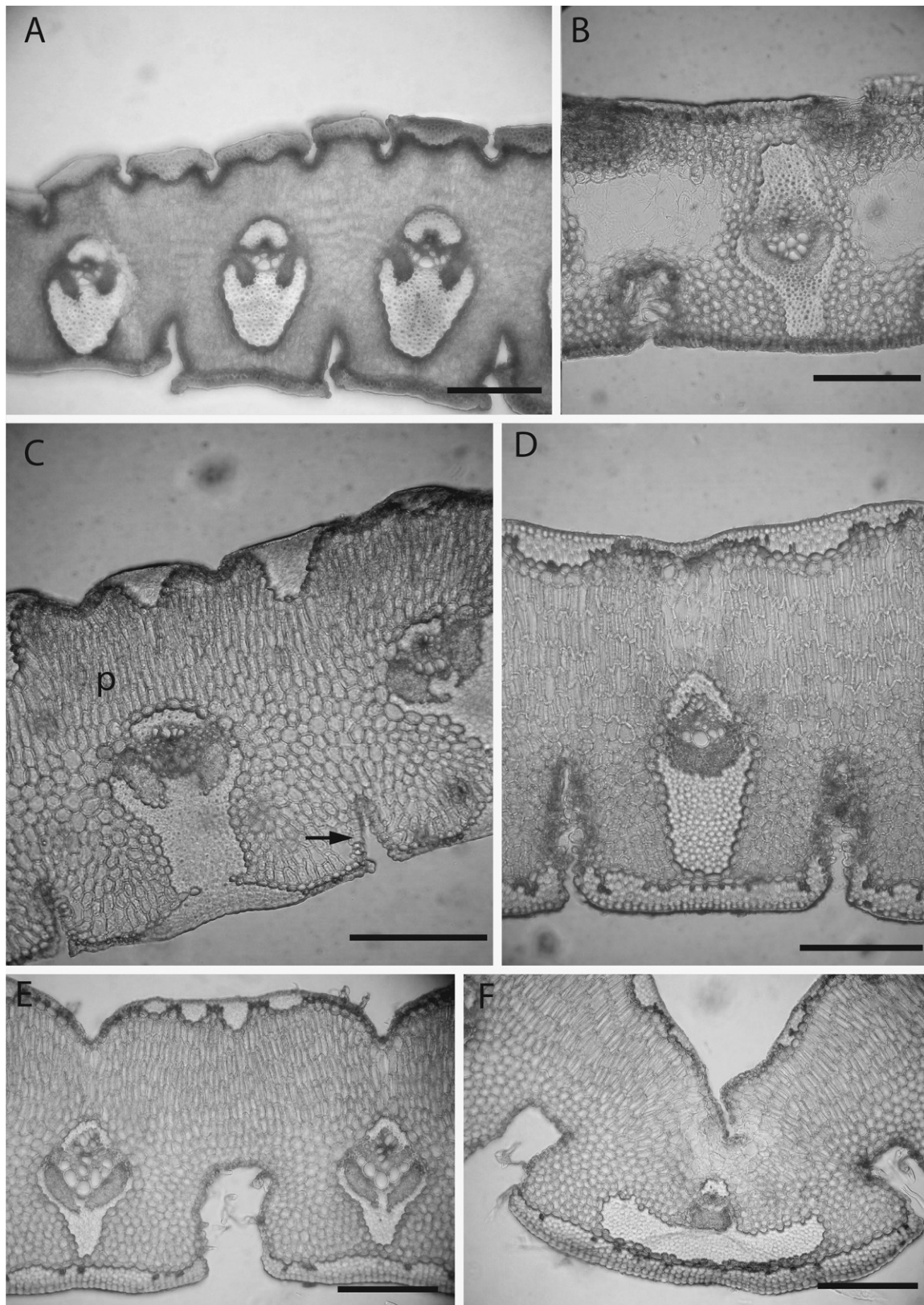
*MVT leaf anatomy:* Amphistomatic, stomata also in abaxial furrows and adaxial middle groove; furrows deep and narrow with many bulged unicellular hairs; lateral bundles with partial abaxial W- to  $\psi$ -shaped girder and U-shaped adaxial partial girder; central bundle with small abaxial crescentiform girder; marginal bundle with ovate distal girder. Epidermis generally fibrous except for stomata locations, adaxial cells much heavier thickened and only on either side of lateral bundles supported by a few cells of subepidermal sclerenchyma (Fig. 18B).

*Specimens examined:* MADAGASCAR. Fianarantsoa, Andringitra AP, *Perrier* 12100 (K); Andringitra RN, *Perrier* 13624 (K); Andringitra AP, *Phillipson* 5682 (MO).

48. *Xerophyta aymoninii* Phillipson & Lowry, *Tropicos*. 2009.

*MVT leaf anatomy:* Hypostomatic with stomata restricted to furrows; alternating furrows on adaxial and abaxial sides, deep abaxial furrows between bundles, narrow and shallow adaxial furrows opposite bundles. Lateral bundles with heavy abaxial Y- to  $\psi$ -shaped girder and small adaxial cap, with a complete bundle size of about half leaf thickness. A band of about three aquiferous cells bridges lateral bundles to the adaxial hypodermis. Epidermis cells sclerenchymatic and heavy subepidermal sclerenchyma bands (three to four cells thick) surround the entire





**Figure 18.** See caption on next page.

**Figure 18.** Transverse sections of leaves with *Xerophyta*-type (XT) (A, C) and Madagascan *Vellozia* group-type (MVT) (B, D, E) leaf anatomy. A, *Xerophyta sessiliflora* (from Baron 13) with alternate furrows and heavy sclerenchyma bands between both adaxial and abaxial furrows. B, *Xerophyta andringitrensis* (from P. B. Phillipson, H. H. Schmidt & S. Rakotonandrasana 5682): lacuna-like area between lateral bundles, deeply sunken glands and abaxial furrows with wide trichomes. C, *Xerophyta calcicola* (from P. B. Phillipson & S. Rakotonandrasana 5707): dorsiventral leaf with palisade (p) and spongy parenchyma, abaxial furrows and triangular adaxial sclerenchyma above and between bundles; the section is taken from a more basal part of the leaf where the abaxial sclerenchyma is in contact with the lower prong of the bundles; stomata are preferentially located in furrows (arrow). D, *Xerophyta aymoninii* (from Guillaumet 3612): dorsiventral leaf with palisade and spongy parenchyma, abaxial furrows with small epidermis outgrowths, and adaxial and abaxial sclerenchyma bands. E, F, *Xerophyta decaryi* (from P. B. Phillipson, H. H. Schmidt & S. Rakotonandrasana 5700): lateral and median bundles embedded in dorsiventral leaf.

lamina with thin-walled epidermis cells within abaxial furrows only (Fig. 18D).

*Specimens examined:* MADAGASCAR. Antananarivo, Mt Ibity, 25 m S of Antsiabo Lewis & Razafimandimbison 740 (BR); Mt. Ibity Rauh 22510 (HEID); – Fianarantsoa, Col d'Iremo Appert 916 (Z); Andringitra AP, Guillaumet 3612 (P).

49. *Xerophyta brevifolia* (H.Perrier) Phillipson & Lowry, *Tropicos*. 2009.

*Xerophyta dasyliroides* var. *brevifolia* H.Perrier, *Arch. Bot. Bull. Men.* 4 (6): 71. 1930; Perrier in Humbert, *Fl. Madagascar*, fam. 42: 9. 1950; Smith & Ayensu, *Kew Bull.* 29: 197. 1974. – *Type:* Madagascar, Centre, between Mania and l'Ivato, West of Ambositra, Perrier 12385 (P, holotype).

*Vellozia dasyliroides* (Baker) Poisson var. *brevifolia* Ayensu, *Kew Bull.* 23: 324. 1969, *nomen nudum*.

*MVT leaf anatomy:* Hypostomatic, stomata restricted to furrows. Abaxial furrows deep (about two-thirds of lamina thickness) and with abundant bulged and forked unicellular hairs, adaxial furrows almost absent, near central bundle a few small canals between heavy sclerenchyma. Lateral vascular bundles with small partial abaxial long Y-shaped girder and extending from two-thirds to seven-eighths of leaf thickness, central bundle with small partial abaxial crescentiform girder and tiny cap, marginal bundles with distal triangular partial girder. Epidermis fibrous, subepidermal sclerenchyma heavy below the entire surface, except for abaxial furrows and adaxial median groove, interrupted only by small canals; adaxial sclerenchyma twice as much as abaxial one (Fig. 19F).

*Specimens examined:* MADAGASCAR. Fianarantsoa, Ambatofinandrahana, Decary 12960 (K). – Toliara, afft du Mandrare Decary 9450 (BR).

*Comments:* The anatomy of Decary 9450 is identical to that of Decary 12960 as reported here and earlier

documented by Ayensu (1969: 319 and fig. 2: 3 + 8); it is distinct and different from that of *X. aymoninii* and *X. leandrii*.

50. *Xerophyta calcicola* Phillipson & Lowry, *Tropicos*. 2009.

*XT leaf anatomy:* Amphistomatic; deep abaxial furrows, adaxial surface undulated. Lateral bundles with partial abaxial W-shaped girder and small adaxial cap extending to about one-third of the leaf thickness; central bundle small with partial abaxial U-shaped girder and almost no adaxial cap; marginal bundles with large ovate distal girder that is connected to a marginal subepidermal sclerenchyma band. Palisade tissue with three or four layers of long cells, some with long crystals, occupies the upper one-third of the transverse sectioned leaf lamina. Epidermis cells with slightly thickened outer walls, but fibrous above subepidermal sclerenchyma; on the adaxial side large triangular sclerenchyma strands between bundles alternate with smaller ones above bundles, broad abaxial bands present between furrows and below central bundle (Fig. 18C).

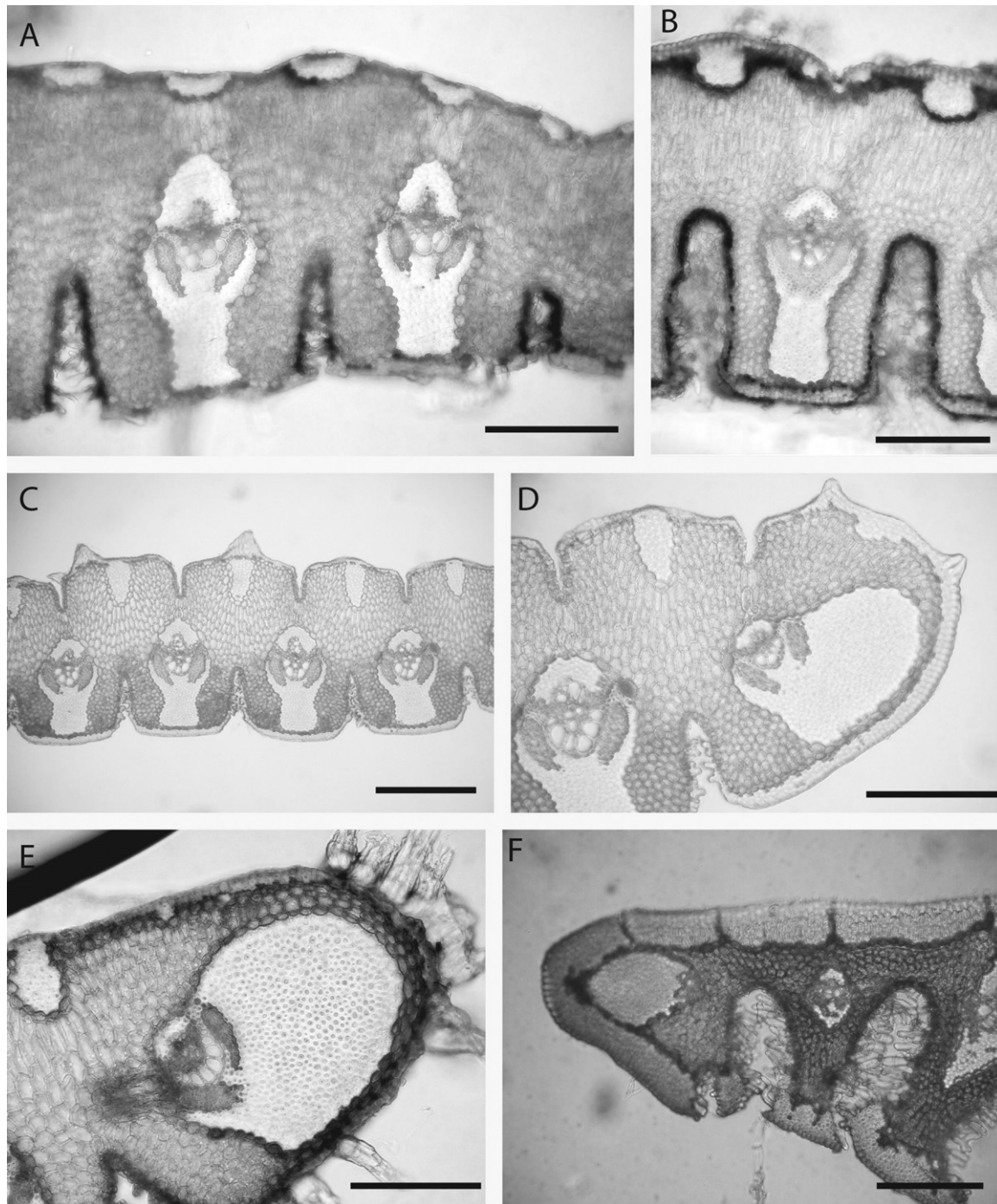
*Specimens examined:* MADAGASCAR. Toliara, La Table, Phillipson & Rakotonandrasana 5707 (MO).

51. *Xerophyta cauliflora* Behnke, **sp. nov.** – *Type:* Madagascar, Fianarantsoa, 25 km SW of Ambalavao, *Eb. Fischer & Höller s.n.*, cult. Bot. Gard. Bonn 15808 (M, holotype).

*Diagnosis:* *Xerophyta dasyliroides* Baker valde simulans sed pedunculis brevibus inter bases foliorum paene omnino obtectis et foliorum laminis glandulosus differt.

*Description:* This species is distinct by flowers with about 5-cm-long pedicels (Fig. 17F) almost completely hidden between the sheaths of old leaves. The stem is multibranched in its upper part (Fig. 17E) and covered with old leaf sheaths ending in revolute tips.





**Figure 19.** Transverse sections of leaves with Madagascan *Vellozia* group-type (MVT) leaf anatomy. A, *Xerophyta leandri* (from *Leandri* 4271): abaxial furrows with long unicellular trichomes, adaxial sclerenchyma strands above and between lateral bundles. B, *Xerophyta lewisiae* (from P. B. Phillipson, H. H. Schmidt & S. Rakotonandrasana 5677): deep abaxial furrows completely filled with long trichomes, alternate adaxial furrows shallow and line with small sclerenchyma strands. C, D, *Xerophyta tabulare* (from P. B. Phillipson & S. Rakotonandrasana 5699): lateral and marginal bundles; dorsiventral leaves with short palisade cells and alternate furrows, abaxial ones with sclerified trichomes; prominent baculiform adaxial sclerenchyma strands between bundles. E, *Xerophyta nandrasanae* (from P. B. Phillipson & S. Rakotonandrasana 5729): marginal bundle with large globular distal sclerenchyma; wide abaxial furrow with sclerified trichomes, baculiform adaxial sclerenchyma strands between bundles. F, *Xerophyta brevifolia* (from *Decary* 12960): leaves almost isolateral with heavy adaxial and abaxial sclerenchyma and with deep abaxial furrows filled with long unicellular trichomes.



Leaves are about 30 cm long, the lamina deciduous, with some sunken glands and gradually ending in an attenuate tip. Petals are about 20 mm long. Ovary 2 mm in diameter and 4 mm long. Peduncle, ovary and the outside of the external tepals are covered with glandular emergences.

*MVT leaf anatomy:* Amphistomatic with wide and deep abaxial furrows. Lateral bundles large with partial abaxial Ψ-shaped girder, adaxial V-shaped cap and aquiferous extended adaxial bundle sheath cells vertically duplicated towards epidermis. Central bundle with large partial abaxial crescentiform girder and adaxial cap composed of a few cells only. Broad abaxial subepidermal sclerenchyma bands between furrows and around margins. Adaxial strands many: two small ones above lateral bundles alternate with one or two broader ones between the bundles. Abaxial furrows with large unicellular trichomes. Abaxial surface with a few sunken glands (Fig. 20E).

*Specimens examined:* MADAGASCAR. Toliara, La Table, *Eb. Fischer & Höller s.n.*, cult. Bot. Gard. Bonn 11428 (M). – Fianarantsoa, 25 km SW of Ambalavao, *Eb. Fischer & Höller s.n.*, cult. Bot. Gard. Bonn 15808 (M).

52. *Xerophyta connata* McPherson & van der Werff, *Novon* 7: 387, figs 1, 2A–C. 1997. – *Type:* Madagascar, Antsiranana, Manongarivo RS, E of Ankaramy, 14°05'S, 48°20'E, 16.x.1994, *McPherson & van der Werff* 16374 (MO, holotype; P, TAN, isotypes).

*BT leaf anatomy:* Hypostomatic with shallow to deep opposite furrows; lateral bundles with double spaces between them; central bundle small with abaxial winged crescentiform girder and adaxial aquiferous tissue; marginal bundle surrounded by distal globular sclerenchyma. Subepidermal sclerenchyma restricted to single-layered adaxial and abaxial bands on each side of lateral bundles.

*Specimens examined:* MADAGASCAR. Antsiranana, Manongarivo RS, *Malcomber & Rakotomalala* 2601 (MO).

53. *Xerophyta croatii* Phillipson & Lowry, *Tropicos*. 2009.

*XT leaf anatomy:* Amphistomatic with stomata restricted to furrows. Abaxial furrows narrow and one-quarter of laminar thickness, adaxial furrows less than one-eighth of lamina. Lateral bundles between one-third and one-half of lamina with partial abaxial W-shaped girder and adaxial cap, bundle sheath cells not extended; central bundle with small partial

abaxial U-shaped girder and tiny adaxial cap; marginal bundle with globular distal girder. Epidermis cells fibrous, with the exception of the inner parts of furrows. Broad subepidermal sclerenchyma bands all over, interrupted only by furrows, but going halfway into abaxial furrows; adaxial bands with triangular extensions.

*Specimens examined:* MADAGASCAR. Fianarantsoa, Mahaso, *Dorr, Barnett, Rakootozafy, Cheek & Razafimala* 4190 (MO); Ranohira, Isalo Mts, *Eb. Fischer* 3028, cult. Bot. Gard. Bonn 13895 (M); Inselberg c. 25 km SW of Ambalavao, *Eb. Fischer & Höller s.n.*, cult. Bot. Gard. Bonn 11422 (M).

54. *Xerophyta dasyliroides* Baker, *J. Bot.* 13: 235. 1875a. – *Type:* Madagascar, Antananarivo, Antongona, (*Hils. & Bojer s.n.* (K, holotype; P, isotype).

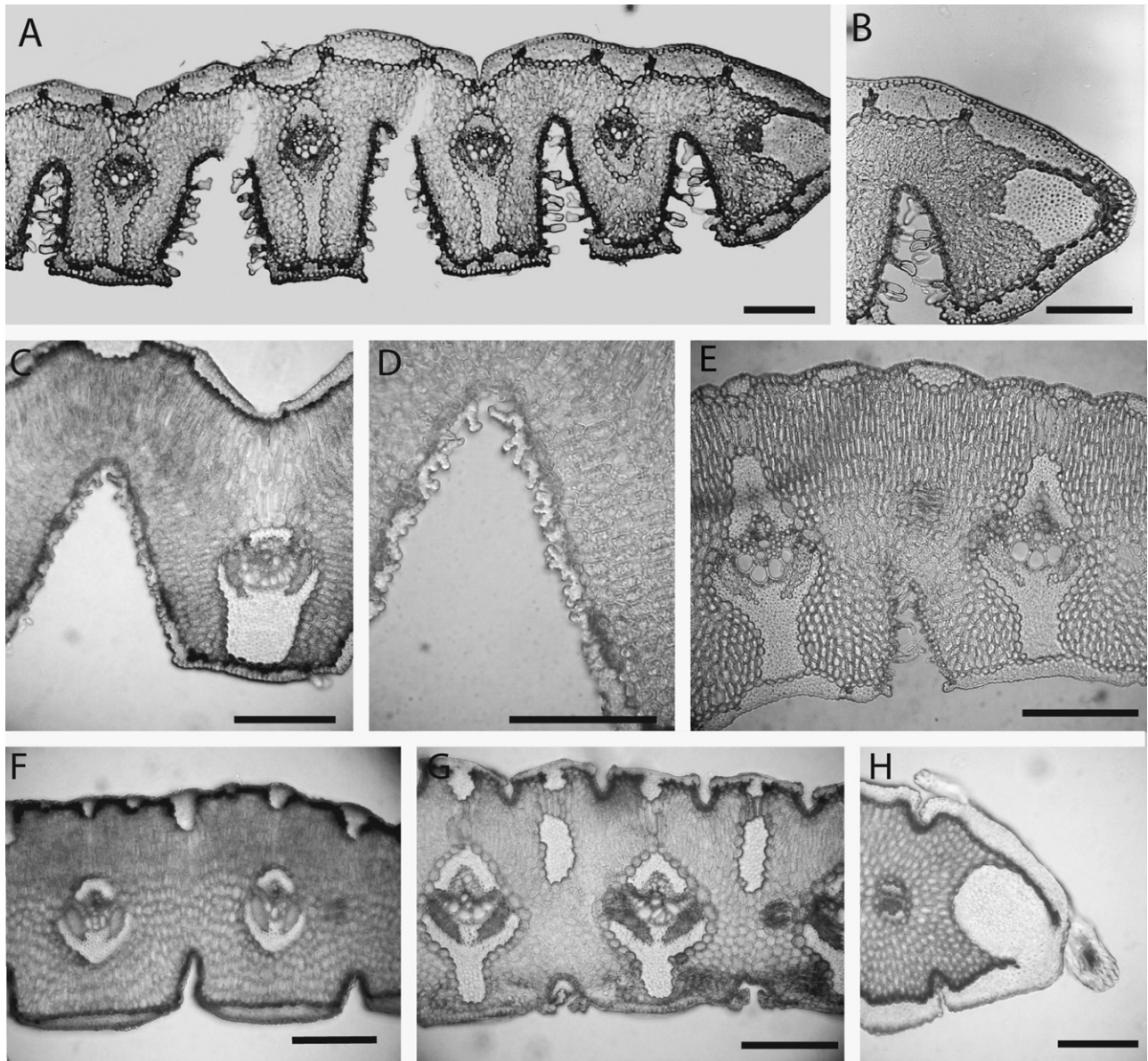
*Vellozia dasyliroides* (Baker) Poisson, *Récherch. Fl. Mérid. Madagascar*: 98. 1912.

*Xerophyta dasyliroides* var. *dasyliroides* (= var. *typica*) H. Perrier, *Arch. Bot. Bull. Mens.* 4 (6): 67–68. 1930; Perrier in Humbert, *Fl. Madagascar*, fam. 42: 7–8. 1950, excl. *Decary* 12960 & 14991; Smith & Ayensu, *Kew Bull.* 29: 197. 1974.

*Vellozia dasyliroides* (Baker) Poisson var. *dasyliroides*, *pro parte*, Ayensu, *Kew Bull.* 23: 324. 1969, *nomen nudum*.

*MVT leaf anatomy:* Hypostomatic with stomata confined to abaxial furrows. Abaxial furrows narrow and deep (one-half to two-thirds of leaf lamina thickness), adaxial surface slightly undulated, rarely with shallow furrows. Lateral bundles large, about two-thirds or more of leaf lamina thickness with partial abaxial Y-shaped girder, V-shaped adaxial cap and adaxial extended aquiferous bundle sheath cells vertically duplicated towards epidermis and laterally continued by a single or double translucent hypodermis; central bundle with partial abaxial winged crescentiform girder, tiny adaxial cap and adaxial aquiferous cells. Epidermis fibrous; subepidermal sclerenchyma forming broad abaxial bands between furrows and at margins, and heavy bulbiform adaxial strands of different sizes above and between bundles (Fig. 20A, B).

*Specimens examined:* MADAGASCAR. Antananarivo, Antongona, in *rupibus humilis collibusque sylvaticis*, *Bojer s.n.* (M); mountain sides near L. Itasy, *Scott Elliot* 1943 (B); Ambatondrapeto, *Bosser* 2399 (P); direction Tamatave, Mantasoa, *Barthlott* 10305, cult. Bot. Gard. Bonn 9649 (M); 45 km N Tananarivo, inselberg Luhavuhitra near Andranovelona, *Fischer & Höller s.n.*, cult. Bot. Gard. Bonn 11404 (M). **Toliara**, Central Madagascar, *Baron* 974 (BM); *Baron*



**Figure 20.** Transverse sections of leaves with Madagascan *Vellozia* group-type (MVT) (A–E, G) and *Xerophyta*-type (XT) (F, H) leaf anatomy. A, B, *Xerophyta dasyliroides* (from Baron 974): marginal and lateral bundles in dorsiventral leaves; abaxial furrows deep and with unicellular trichomes, adaxial sclerenchyma heavy. C, D, *Xerophyta pectinata* (from P. B. Phillipson & S. Rakotonandrasana 5720): leaves almost plicate because of wide and deep abaxial furrows, abaxial furrows with multicellular sclerified trichomes. E, *Xerophyta cauliflora* (from Eb. Fischer & Höller s.n.): dorsiventral leaf with abaxial furrows. F, *Xerophyta pinifolia* (from Randriambololana 92) with strict *Xerophyta*-type leaf anatomy. G, *Xerophyta eglandulosa* (from Guillaumet 3612 bis): large baculate adaxial fibre bundles between lateral bundles; openings of adaxial and abaxial furrows narrowed down by extensions of sclerenchyma bands. H, *Xerophyta setosa* (from Eb. Fischer 3020): marginal bundle and large distal sclerenchyma, the latter connected to adaxial and abaxial sclerenchyma bands Scale bars: A–C, E–H, 100 µm; D, 50 µm.

3134 (B). – Without location, cult. Bot. Gard. Bonn 13690 (M); *Rauh* M78 (HEID).

55. *Xerophyta decaryi* Phillipson & Lowry, *Tropicos*. 2009.

*MVT leaf anatomy:* Amphistomatic, stomata restricted to furrows; alternate furrows: on abaxial side wide and deep (up to one-half of leaf thickness) between bundles, shallow ones opposite bundles on adaxial side. Lateral bundles about one-half of leaf



thickness, with small partial abaxial Y-shaped girder and adaxial cap, central bundle small with partial abaxial winged crescentiform girder, marginal bundle with ovate partial girder. Palisade tissue composed of four of five layers of long cells with inconspicuous small bands of aquiferous cells above bundles. Epidermis cells with thickened outer walls and in contact with subepidermal sclerenchyma fibrous. Broad sclerenchyma bands between abaxial furrows and at margins, four strands of slightly different sizes between adaxial furrows. Abaxial furrows with long unicellular hairs (Fig. 18E, F).

*Specimens examined:* MADAGASCAR. Toliara, La Table, Phillipson 5700 (MO).

56. *Xerophyta eglandulosa* H.Perrier in Arch. Bot. Bull. Mens. 4: 71–72. 1930; Perrier in Humbert, Fl. Madagascar, fam. 42: 14. 1950; Smith & Ayensu, Kew Bull. 29: 188. 1974. – *Type:* Madagascar, Fianarantsoa, Betsiléo, Perrier 13146 (P, holotype; K, isotype). *Xerophyta eglandulosa* var. *hirtocarpa* H.Perrier in Arch. Bot. Bull. Mens. 4: 72. 1930; Smith & Ayensu, Kew Bull. 29: 188. 1974. – *Type:* Madagascar, Fianarantsoa, Ambotofinandrahana, Perrier 12565 (P, holotype).

*Xerophyta eglandulosa* var. *trichocarpa* H.Perrier in Humbert, Fl. Madagascar, fam. 42: 15. 1950. non *Xerophyta eglandulosa* H.Perrier *sensu* Ayensu, Kew Bull. 23: 323. 1969.

*MVT leaf anatomy:* Amphistomatic, with stomata restricted to furrows. Abaxial and adaxial furrows only about one-sixth of lamina thickness deep, adaxial furrows alternating and twice as much as abaxial ones. Lateral bundles broad and large, about three-quarters of lamina thickness with partial abaxial  $\psi$ -shaped girder and adaxial cap, adaxial bundle sheath cells extended and duplicated towards surface; baculate fibre bundles with adaxial extended bundle sheath alternate with the lateral ones. Epidermis fibrous except in furrows. Broad subepidermal sclerenchyma bands below bundles and at margins, small bulbiform adaxial strands above lateral bundles and fibre bundles (Fig. 20G).

*Specimens examined:* MADAGASCAR. Fianarantsoa, Ambatofinandrahana, Perrier 12569 (P); Itremo, Guillaumet 3612bis (P).

*Comments:* Ayensu (1969: 323 & fig. 1: 2) described the leaf anatomy of *X. eglandulosa* as being similar to that of *X. pinifolia*. However, the specimens studied by him belong to either *X. humbertii* (Humbert 6964) or *X. schatzii* (Decary 9372), and both account

for the presence of hairs and of adaxial furrows mentioned.

57. *Xerophyta humbertii* Phillipson & Lowry, Tropicos. 2009.

*Xerophyta eglandulosa sensu* Ayensu (non H.Perrier), Kew Bull. 23: 323. 1969, *pro parte, quoad* Humbert 6964 (K).

*MVT leaf anatomy:* Leaves V-shaped with median adaxial groove and alternate narrow furrows, the abaxial ones about one-third of lamina thickness, the adaxial double as much but less deep; stomata restricted to furrows (amphistomatic). Lateral bundles almost elliptical and about one-half of lamina thickness with large partial abaxial W-shaped girder and U-shaped adaxial cap, small fibre bundles are located within the palisade tissue, above abaxial furrows. Epidermis cells are sclerenchymatic and, together with several layers of subepidermal sclerenchyma, form distinct strands: on both abaxial and adaxial sides they are bi-arched with strong middle knobs, extend between the furrows and narrow down the furrow openings.

*Specimens examined:* MADAGASCAR. Fianarantsoa, Ihorombe, Humbert 6964 (P).

58. *Xerophyta isaloensis* Phillipson & Lowry, Tropicos. 2009.

*MVT leaf anatomy:* Amphistomatic, on abaxial surface stomata restricted to furrows. Abaxial furrows narrow and about one-half lamina thickness, adaxial furrows wide and shallow (less than one-eighth of lamina thickness). Lateral bundles about one-half of lamina thickness with broad partial abaxial Y-shaped girder and adaxial cap, adaxial bundle sheath cells aquiferous and extended; central bundle with broad partial abaxial crescentiform girder and adaxial cap; marginal bundles with globular distal girder. Epidermis cells partly fibrous. Broad subepidermal sclerenchyma bands between abaxial furrows with thicker parts near furrow openings; adaxial bulbiform strands above abaxial furrows.

*Specimens examined:* MADAGASCAR. Fianarantsoa, Ihorombe, Phillipson 5713 (MO).

59. *Xerophyta jouyiana* Phillipson & Lowry, Tropicos. 2009.

*MVT leaf anatomy:* Amphistomatic with narrow furrows on both surfaces, the adaxial ones shorter and alternating with the abaxial ones; lateral bundles with partial abaxial Y-shaped girder, U-shaped



adaxial cap and aquiferous cells bridging between bundle sheath and epidermis on both adaxial and abaxial sides; central bundle with small partial abaxial crescentiform girder and adaxial aquiferous tissue, marginal bundle distally surrounded by globular sclerenchyma. Heavy subepidermal sclerenchyma all over: on the adaxial side triangular strands above and between lateral bundles, on the abaxial side broad and thick bands between furrows with small extensions narrowing down the furrow openings, and a semicircular band outside marginal bundles. The epidermis cells are heavily thickened and occasionally contain cubical crystals.

*Specimens examined:* MADAGASCAR. Fianarantsoa, S of Ranotsara Atsimo, *Humbert* 19330 (P).

60. *Xerophyta labatii* Phillipson & Lowry, *Tropicos* 2009.

*MVT leaf anatomy:* Amphistomatic, with stomata restricted to adaxial and abaxial furrows which are only about one-eighth of lamina thickness deep, adaxial furrows alternating and double as much as abaxial ones. Lateral bundles broad and about two-thirds of lamina thickness with large partial abaxial  $\psi$ -shaped girder and prominent V-shaped adaxial cap, both adaxial and abaxial bundle sheath cells extended towards surface; central bundle small, with abaxial winged crescentiform girder and tiny adaxial cap; marginal bundles with large ovate distal girder. Epidermis fibrous, except in furrows. Triangular to bulbiform subepidermal sclerenchyma strands above, below and between lateral bundles, the abaxial strands smaller than the adaxial ones.

*Specimens examined:* MADAGASCAR. Fianarantsoa, Ihosy, *Phillipson* 5722 (MO); Madagascar, Fianarantsoa, W of Ihosy, *Bernardi* 11251 (BR); S of Ambalavao, *Eb. Fischer* 3021, cult. Bot. Gard. Bonn 5919 (M); rock plateau 25 km SW Ambalavao, *Eb. Fischer & Höller s.n.*, cult. Bot. Gard. Bonn 11423 (M). – Without location, *W. Rösli s.n.*, cult. Bot. Gard. Bonn 16802 ex cult. HEID 105989 (M); *W. Rösli s.n.*, cult. Bot. Gard. Bonn 18034 (M).

61. *Xerophyta leandrii* Phillipson & Lowry, *Tropicos* 2009.

*MVT leaf anatomy:* Amphistomatic, with stomata mainly restricted to abaxial furrows. Abaxial furrows narrow and about one-third of lamina thickness, adaxial surface slightly undulated. Lateral bundles about three-quarters of lamina thickness with broad partial abaxial  $\psi$ -shaped girder and large V-shaped adaxial girder, adaxial bundle sheath cells aquiferous

and extended; central bundle with partial abaxial winged crescentiform girder and small adaxial cap; marginal bundles with globular distal girder. Epidermis cells partly fibrous, otherwise with thick outer wall. Single- to double-layered subepidermal sclerenchyma bands between abaxial furrows and below central bundle; adaxial semicircular strands above and between bundles (Fig. 19A).

*Specimens examined:* MADAGASCAR. Toliara, Andohahela RN, *Leandri & Sabouraux* 4271 (P).

62. *Xerophyta lewisiae* Phillipson & Lowry, *Tropicos* 2009.

*Xerophyta dasyliroides* var. *spinulosa* Ridley *sensu* H.Perrier in *Humbert*, Fl. Madagascar, fam. 42: 8. 1950, *pro parte*, *quoad Perrier* 14615.

*MVT leaf anatomy:* Amphistomatic, with stomata mainly restricted to abaxial furrows and median adaxial groove. Abaxial furrows narrow and about one-half of lamina thickness, adaxial furrows alternating and short. Lateral bundles about one-half of lamina thickness with broad partial abaxial Y-shaped girder and adaxial cap, adaxial bundle sheath cells extended, aquiferous and with thickened walls; central bundle with partial abaxial winged crescentiform partial girder and small adaxial cap; marginal bundles with large globular distal girder. Epidermis cells mostly fibrous, otherwise with thick outer wall. Single- to double-layered subepidermal sclerenchyma bands between abaxial furrows, below central bundle and at margins; adaxial bulbiform strands between bundles and tiny strands on each side of adaxial furrows (Fig. 19B).

*Specimens examined:* MADAGASCAR. Fianarantsoa, Andringitra PA, *Phillipson, Schmidt & Rakotonandrasana* 5677 (MO); Massif d'Andringitra, Iratsy, vallées de la Riambara et de l'Antsifotra et montagnes environnantes, (*Viguiet & Humbert* 3920a (B, M).

63. *Xerophyta nandrasanae* Phillipson & Lowry in *Tropicos* (2009).

*MVT leaf anatomy:* Amphistomatic with stomata restricted to nonfibrous areas of adaxial epidermis and abaxial furrows. Abaxial furrows wide and deep (less than one-half of leaf lamina thickness). Lateral bundles about one-half of leaf lamina thickness with broad partial abaxial girder, small adaxial cap and aquiferous, adaxial extended bundle sheath cells vertically duplicated towards adaxial epidermis; central bundle with partial abaxial winged crescentiform girder, tiny adaxial cap and adaxial aquiferous tissue;

marginal bundles with large globular distal girder. Epidermis thickened and partly fibrous; subepidermal sclerenchyma forming broad abaxial bands between furrows and bulbi- to baculiform adaxial strands above bundles; additional tiny strands (composed of less than ten cells) may pair near aquiferous bundle sheath ends (Fig. 19E).

*Specimens examined:* MADAGASCAR. Fianarantsoa, between Antsirabe and Ambositra, *Phillipson & Rakotonandrasana* 5729 (MO); 5 km SSE Sandrandahy along rd Antanarivo–Fianarantsoa, S Ilaka-Afovoany village, 30 km N Ambositra, *S. & T. Pocs & Z. Tuba* 04112 (EGR, voucher at M); N of Abositra, *Rauh* M731 (HEID).

64. *Xerophyta parviflora* Phillipson & Lowry, *Tropicos*. 2009.

*MVT leaf anatomy:* Amphistomatic, on abaxial surface stomata restricted to furrows. Abaxial furrows wide and shallow, adaxial surface slightly undulated, almost even. Lateral bundles about one-half of lamina thickness with broad partial abaxial  $\psi$ -shaped girder and adaxial cap, adaxial bundle sheath cells not extended; central bundle with abaxial horizontal to deeply crescentiform girder and adaxial cap; marginal bundles with globular distal girder. Epidermis partly fibrous: below lateral and central bundles and distal to marginal ones. Broad subepidermal sclerenchyma bands around margins, small adaxial strands between and above lateral bundles.

*Specimens examined:* MADAGASCAR. Toliara, Sept Lacs, *Phillipson & Rakotonandrasana* 5711 (MO).

65. *Xerophyta pectinata* Baker, *J. Bot.* 20: 270. 1882. – *Type:* Madagascar, Fianarantsoa, Betsiléo, *Baron* 15 (BM, holotype; P, K, isotypes).

*Xerophyta spinulosa* Ridl., *J. Linn. Soc.* 20: 333. 1883. – *Type:* Madagascar, Fianarantsoa, Ankafina, *Deans Cowan s.n.* (BM, holotype).

*Vellozia pectinata* (Baker) Poisson, *Récherch. Fl. Mérid. Madagascar*: 98. 1912; Greves, *J. Bot.* 59: 284. 1921.

*Vellozia spinulosa* (Ridl.) Poisson, *Récherch. Fl. Mérid. Madagascar*: 98. 1912; Greves, *J. Bot.* 59: 284. 1921.

*Xerophyta dasylirioides* var. *pectinata* H. Perrier, *Arch. Bot. Bull. Mens.* 4 (6): 69. 1930; Perrier in Humbert, *Fl. Madagascar*, fam. 42: 8–9. 1950; Smith & Ayensu, *Kew Bull.* 29: 197. 1974.

*Xerophyta dasylirioides* var. *spinulosa* H. Perrier, *l.c.* 1930; Perrier in Humbert, *Fl. Madagascar*, fam. 42: 8. 1950, excl. *Perrier* 14615; Smith & Ayensu, *l.c.* 1974.

*Vellozia dasylirioides* (Baker) Poisson var. *pectinata* Ayensu, *Kew Bull.* 23: 324. 1969, *nomen nudum*.

*Vellozia dasylirioides* (Baker) Poisson var. *spinulosa* Ayensu in *l.c.* 1969, *nomen nudum*.

*MVT-type leaf anatomy:* Amphistomatic with stomata mainly confined to abaxial furrows. Wide and deep (one-half to two-thirds of leaf lamina thickness) abaxial furrows between vascular bundles alternate with shallow adaxial furrows above bundles. Lateral bundles about one-half of leaf lamina thickness with broad partial abaxial girder, small adaxial cap and aquiferous, adaxial extended bundle sheath cells vertically duplicated towards adaxial epidermis; central bundle with partial abaxial winged crescentiform girder, tiny adaxial cap and adaxial aquiferous cells. Epidermis thickened and fibrous, except for areas with stomata; subepidermal sclerenchyma forming broad abaxial bands between furrows and triangular adaxial strands above bundles; additional adaxial bands occur on each side of adaxial furrows (Fig. 20C, D; see also Ayensu, 1969: 324 + figs 2, 4, 5, 10).

*Specimens examined:* MADAGASCAR. Fianarantsoa, Ihoay, *Phillipson & Rakotonandrasana* 5720 (MO); S of Ambavalao, Iandranbaky, *Bernardi* 11177 (K); Betsiléo, *Hildebrandt* 3894 (M); along NE side of Ambositra–Antsirabé rd, at Tsarasatra village, 18 km NNE Ambositra, *S. & T. Pocs, R. Ranaivojaona & Z. Tuba* 04131 (M); Plateaux de l’Horombe, W of the valley d’Ihoay, *Humbert* 2951 (B); rock plateau 25 km SW of Ambalavao, *Eb. Fischer & Höller s.n.*, cult. Bot. Gard. Bonn 11421 (M); *NN*, Madagascar, cult. Bot. Gard. Bonn 5919A (M). Without location, *Rauh* M650 (HEID); *NN*, cult. Bot. Gard. Bonn 13691 (M); *NN*, cult. Bot. Gard. Bonn 15815 (M); *Röösli s.n.*, Bot. Gard. Bonn 18032 (M).

66. *Xerophyta pinifolia* Lam., *Illustr. Genres* 1, t. 225. 1791; Willdenow, *Spec. Plant.* 2 (1): 15. 1799; Persoon, *Syn. Plant.* 1: 346. 1805; Poirer, *Encycl.* 8: 804. 1808; Perrier in Humbert, *Fl. Madagascar*, fam. 42: 11. 1950. – *Type:* Madagascar, *Commerson* (P, holotype; B, isotype).

*Xerophyta madagascariensis* J. F. Gmel., *Syst.* 1: 530 (1796).

*Xerophyta neglecta* Roem. & Schult., *Syst.* 7, 1: 289–290. 1829.

*Vellozia neglecta* (Roem & Schult.) Poisson, *Récherch. Fl. Mérid. Madagascar*: 98. 1912; Greves, *J. Bot.* 59: 284. 1921.

*Vellozia pinifolia* (Lam.) Poisson, *l.c.* 1912.

*Vellozia pinifolia* Poisson ex Greves, *J. Bot.* 59: 284. 1921.

*Xerophyta pinifolia* var. *pinifolia* sensu Smith & Ayensu, Kew Bull. 29: 187. 1974, *pro parte*. non *Xerophyta pinifolia* var. *pinifolia* sensu Gonçalves in Fl. Zambes. 12, 2: 158 + fig. 12.2.41. 2009, *quoad* Torre & Paiva 10694, Torre & Coreia 16015, and Patel 878.

*XT leaf anatomy*: Amphistomatic with stomata restricted to nonfibrous epidermis, deep abaxial furrows, adaxial surface undulated; lateral bundles almost circular and about one-third of lamina thickness with partial abaxial W-shaped girder and U-shaped adaxial cap; central bundle small with partial abaxial U-shaped girder and almost without adaxial cap, marginal bundle with large distal oval partial girder. A multilayered subepidermal sclerenchyma plus thickened epidermis form broad abaxial bands between furrows and below central bundle, a marginal semicircle, and large triangular adaxial strands opposite furrows alternating with about three smaller ones in between (Fig. 20F; see also Ayensu, 1969: 321 and Fig 1:1).

*Specimens examined*: MADAGASCAR. Toliara, Tsiaripiky, *Randriambololona et al.* 92 (MO); Antanimora, Decary 4309 (MO); SW of Ifotaka, *Lam & Meeuse* 5463 (K); Fort Dauphin, *Scott Elliot* 2550 (B); Sainte Luce, *Scott Elliot* 3030a (B); *Rauh* M1479 (HEID).

67. *Xerophyta schatzii* Phillipson & Lowry, *Tropicos* 2009.

*Xerophyta eglandulosa* sensu Ayensu (non H.Perrier), Kew Bull. 23: 323. 1969, *pro parte, quoad* Decary 9372 (K).

*XT leaf anatomy*: Amphistomatic with stomata restricted to furrows. Abaxial furrows narrow and one-quarter of laminar thickness, adaxial furrows about one-eighth of lamina thickness. Lateral bundles between one-third and one-half of lamina thickness with partial abaxial W-shaped girder and adaxial cap, bundle sheath cells not extended; central bundle with thick partial abaxial U-shaped and tiny adaxial cap; marginal bundle with globular distal girder. Epidermis cells fibrous, with the exception of the inner parts of furrows. Broad subepidermal sclerenchyma bands all over, interrupted only by inner parts of furrows, but going halfway into them; some adaxial bands with baculate extensions.

*Specimens examined*: MADAGASCAR. Toliara, Andohahela RN, Schatz 1280 (K, BR); Andohahela RN, Andrianarisata, Lewis, Rakotomalaza, *Randriambololona, Ramisamiantanirina, McDonagh & Randriamampionona* 58 (MO); Andohahela RN, Phillipson

2849 (BR). – Fianarantsoa, Ampilira, Decary 9372 (K); Ranohira, Isalo Mts, SW Ranohira, Eb. Fischer 3028, cult. Bot. Gard. Bonn 13895 (M).

68. *Xerophyta sessiliflora* Baker, J. Bot. 20: 271 (1882); Perrier, Arch. Bot. Bull. Mens. 4 (6): 73–74. 1930. – *Type*: Madagascar, Fianarantsoa, Betsiléo, *Baron* 13 (K, holotype).

*Vellozia sessiliflora* (Baker) Poisson, *Récherch. Fl. Mérid. Madagascar*: 98. 1912.

*Vellozia pinifolia* sensu Greves (non Lam.), J. Bot. 59: 279, 284. 1921, *pro parte, quoad* Deans Cowan s.n. (BM).

*Xerophyta sessiliflora* var. *scabra* H.Perrier, Arch. Bot. Bull. Mens. 4 (6): 74. 1930. – *Type*: Madagascar, Fianarantsoa, Betsiléo, *Baron* 13 (K, holotype) [this is the typical variety].

*Xerophyta sessiliflora* var. *villosa* H.Perrier in l.c. 1930, *pro parte, quoad* Perrier 13128. (P).

*XT leaf anatomy*: Amphistomatic with stomata restricted to furrows. Abaxial furrows narrow and from one-quarter to one-third of laminar thickness, twice as much adaxial furrows narrow but less deep (about one-eighth of lamina). Lateral bundles with partial abaxial W-shaped girder and adaxial cap with sizes of about one-half of lamina (in type specimen larger), bundle sheath cells not extended; central bundle with small partial abaxial U-shaped girder and tiny adaxial cap; marginal bundles with globular distal girder. Epidermis cells fibrous, with the exception of the inner parts of furrows. Broad subepidermal sclerenchyma bands all over, interrupted only by furrows, but narrowing down their openings (Fig. 18A).

*Specimens examined*: MADAGASCAR. Fianarantsoa, Betsiléo, *Baron* 13 (K); Horombe Plateau, *Phillipson & Rakotonandrasana* 5717 (MO). – Antananarivo, Imerina, *Deans Cowan* s.n. (BM).

*Comments*: Perrier 13126 differs from all other collections: the adaxial surface has no furrows and less subepidermal sclerenchyma.

69. *Xerophyta setosa* Phillipson & Lowry in *Tropicos* (2009).

*Xerophyta sessiliflora* var. *villosa* H.Perrier in Arch. Bot. Bull. Mens. 4 (6): 74. 1930, *pro parte, quoad* Perrier 12095 (P).

*Xerophyta pinifolia* var. *villosa* (H.Perrier) H.Perrier in Humbert, Fl. Madagascar, fam. 42: 12. 1950; Smith & Ayensu, Kew Bull. 29: 187. 1974.

*XT leaf anatomy*: Amphistomatic with stomata restricted to furrows; furrows alternate and on adaxial side twice as much as on abaxial side, narrow



but not deep, entry narrowed down by flanges of sclerenchyma band; lateral bundles small (occupying about one-third of leaf thickness) and almost circular with partial abaxial W-shaped girder and U-shaped cap; central bundle tiny with partial abaxial U-shaped girder and small adaxial cap, marginal bundle with large distal globular girder which is in contact with a semicircular subepidermal sclerenchyma. Epidermis heavily thickened and continuous with subepidermal bands composed of four to six fibre layers which extend between furrows and to some extent bend into them. A clear single-layered hypodermis separates the sclerenchyma bands from the dorsiventral mesophyll (Fig. 20H).

*Specimens examined:* MADAGASCAR. Fianarantsoa, Ilakaka, Phillipson & Rakotonandrasana 5712 (MO); Isalo PA, Phillipson & Rakotonandrasana 5714 (MO); Isalo NP, Du Puy, Menezes & Ranjamalala 170 (K); Isalo Mts, Schlieben 8227 (M); Ambalavao, Eb. Fischer 3019, cult. Bot. Gard. Bonn 5923 (voucher at TEX); Ambalavao, Eb. Fischer 3020, cult. Bot. Gard. Bonn 725 (M).

70. *Xerophyta tabulare* Phillipson & Lowry, *Tropicos*. 2009.

*Xerophyta dasyliroides* Baker var. *subteretifolia* H.Perrier in Humbert, Fl. Madagascar, fam. 42: 9. 1950, *pro parte, quoad Poisson* 220.

*MVT leaf anatomy:* Amphistomatic with stomata restricted to nonfibrous epidermis of adaxial and abaxial furrows. Abaxial furrows wide and deep (about one-third of leaf lamina thickness), adaxial furrows alternating and above bundles, about one-quarter of lamina. Lateral bundles one-half to two-thirds of lamina thickness with broad partial abaxial girder, small adaxial cap and a few thickened and extended adaxial bundle sheath cells; central bundle with partial abaxial winged crescentiform girder, tiny adaxial cap and adaxial aquiferous tissue; marginal bundles with large globular distal girder. Epidermis thickened and partly fibrous; subepidermal sclerenchyma forming broad abaxial bands between furrows and baculiform adaxial strands above bundles; additional adaxial bands extend from the strands into the furrow openings and bear setose extensions (Fig. 19C, D).

*Specimens examined:* MADAGASCAR. Toliara, La Table, Phillipson & Rakotonandrasana 5699 (MO); La Table, Lorence 1946 (K).

71. *Xerophyta tulearensis* (H.Perrier) Phillipson & Lowry, *Tropicos*. 2009.

*Xerophyta dasyliroides* var. *tulearensis* H.Perrier, Arch. Bot. Bull. Mens. 4 (6): 70. 1930; Perrier in Humbert, Fl. Madagascar, fam. 42: 10; Smith & Ayensu, Kew Bull. 29: 198. 1974. – *Type:* Madagascar, Toliara, La Table, Perrier 18002 (P, holotype).

*MVT leaf anatomy:* Amphistomatic, on abaxial surface stomata restricted to furrows. Abaxial furrows wide and about one-half of lamina thickness, adaxial furrows alternating, wide and shallow (less than one-eighth of lamina thickness). Lateral bundles about one-half of lamina thickness with broad partial abaxial Y-shaped girder and adaxial cap, adaxial bundle sheath cells aquiferous and extended; central bundle with broad partial abaxial crescentiform girder and adaxial cap; marginal bundles with globular distal girder. Epidermis cells partly fibrous. Even subepidermal bands of two or three fibre layers are between abaxial furrows; adaxial triangular strands above abaxial furrows with occasional smaller strands in between.

*Specimens examined:* MADAGASCAR. Toliara, Sarofana, Phillipson & Rakotonandrasana 5703 (MO); Beza Mahafaly RS, Phillipson 2459 (BR). – Without location, W. Rössli s.n., cult. Bot. Gard. Bonn 18033 (M).

#### *Species incertae sedis*

*Xerophyta stenophylla* Baker, Trans. Linn. Soc. II, 1: 162. 1878; Rendle, Rendle, Catalogue Afr. Pl. II, 1: 36. 1899; T.Durand & Schinz, Consp. Fl. Afr. 5: 272. 1895. – *Type:* Angola, Mossamedes, Welwitsch 1557 (K, holotype; BM, LISU, isotypes). Flowers unknown.

*Vellozia stenophylla* (Baker) Baker in Oliver, Fl. Trop. Afr. 7: 410. 1898; Greves, J. Bot. 59: 284. 1921.

*Xerophyta violacea* (Baker) N.L.Menezes, Ciência e Cultura 23: 422. 1971.

*Vellozia violacea* Baker, Bull. Herba. Boiss. II, 4: 1003. 1904; Greves, J. Bot. 59: 280. 1921. – *Type:* South Africa, Transvaal, Haenertsburg, Junod s.n. (Z, holotype). – *Type specimen* not found in Z; there are two *Junod* specimens without number in G (where most of *Junod's* collections are located); neither matches the description given by Baker in l.c. 1904.

#### ACKNOWLEDGEMENTS

We would like to thank the directors of the cited herbaria and botanic gardens for loan of material and their kind permission to use specimens and to remove small samples for our research. In particular, thanks are due to all those who have, over the years, generously supported our study and without

whose help this work would have been far less complete: Jaco D. Adendorff (Johannesburg, South Africa), Himansu Bajinath (Botany, School of Life and Environmental Sciences, University of Durban-Westville, South Africa), Hildegard Becker (Windhoek, Namibia), John E. Burrows (Buffelskloof Nature Reserve and Herbarium, Lydenburg, South Africa), Barbara Eichhorn (Institut für Ur- und Frühgeschichte, Universität Köln, Germany), Brigitte Hamman and Jill Farrant (Department of Molecular and Cell Biology, University of Cape Town, South Africa), Pócs Tamás (Botany Department, Teachers' College, Eger, Hungary), Zoltán Tuba (Department of Botany and Plant Physiology, Szent István University, Gödöllő, Hungary) and Abraham E. van Wyk (Department of Botany, University of Pretoria, South Africa) collected specimens in the field; Roselle Andrews (Royal Botanic Garden, Kew, UK), Philip Ashby and John Main (Royal Botanic Garden, Edinburgh, UK), Josef Bogner (Botanic Garden, Munich, Germany), Ulrich Hecker (Botanic Garden, Mainz, Germany) and Clinton Morse (Conservation and Garden, University of Connecticut, Storrs, CT, USA) helped to select and/or sent samples of the living collections housed in their institutions; Dee Snijman Paterson-Jones (Compton Herbarium, South Africa) and M. C. Proctor (School of Biological Sciences, University of Exeter, UK) made contact with people collecting in the field; Brian L. Burt (Edinburgh, UK) contributed detailed information on his collections of two *Xerophyta* species cultivated in the Royal Botanic Garden, Edinburgh, UK; David Harris and Helen Hoy (E), Mats Hjertson (UPS), Tassilo Feuerer and Hans-Helmut Poppendieck (HGB), Ferdinand Jacquemoud (G), W. J. Kress (MO), Jean Lejoly (BRLU), Porter P. Lowry II and Peter B. Phillipson (MO and P), Christina Potgieter and Trevor Edwards (NU), Elmar Robbrecht and Piet Stoffelen (BR), Monika Steinhoff (BREM), Hans-Jürgen Tillich (M), Edwin Urmi (Z), Roy Vickory (BM), Robert Vogt (B), Paul Wilkin (K) and Odile Weber (K) prepared loans of or assisted in removal of leaf samples or provided digital close-ups from herbarium sheets; Werner Höller and Otto Kriesten maintained the large collection of living Velloziaceae at the Botanic Garden, Bonn (Germany) and provided useful information and continued support during the frequent visits of the senior author. The original research documented in this article incorporates some results obtained by the senior author's graduate students, Veronika Partl, Ute Schreiber and Anne Wirsching, and was conducted with the skilful technical help of Mrs Steffi Gold (Heidelberg, Germany). We thank Philip Oswald for the correction of the Latin diagnoses.

## REFERENCES

- Ayensu ES. 1969.** Leaf-anatomy and systematics of old world Velloziaceae. *Kew Bulletin* **23**: 315–335.
- Ayensu ES. 1973a.** Phytogeography and evolution of the Velloziaceae. In: Meggers BJ, Ayensu ES, Duckworth WD, eds. *Tropical forest ecosystems in Africa and South America: a comparative review*. Washington DC: Smithsonian Institution Press, 105–119.
- Ayensu ES. 1973b.** Biological and morphological aspects of the Velloziaceae. *Biotropica* **5**: 135–149.
- Ayensu ES. 1974.** Leaf-anatomy and systematics of New World Velloziaceae. *Smithsonian Contributions to Botany* **15**: 1–125.
- Baillon H. 1895.** *Histoire des plantes, Vol. 13*. Paris: Hachette.
- Baker JG. 1875a.** Synopsis of the African species of *Xerophyta*. *Journal of Botany* **13**: 231–236.
- Baker JG. 1875b.** Monocotyledones Petaloideae. The botany of the Speke and Grant Expedition. *Transactions of the Linnean Society* **29**: 151–163.
- Baker JG. 1878.** Report on the Liliaceae, Iridaceae, Hypoxidaceae, and Haemodoraceae of Welwitsch's Angolan Herbarium. *Transactions of the Linnean Society, 2nd series, Botany* **1**: 245–273.
- Baker JG. 1882.** Contributions to the flora of central Madagascar. *Journal of Botany* **20**: 266–271.
- Baker JG. 1889.** New petaloid monocotyledons from Cape Colony. *Journal of Botany* **27**: 1–4.
- Baker JG. 1894.** Botany of the Hadramaut Expedition. *Bulletin of Miscellaneous Information Kew* **1894**: 328–343.
- Baker JG. 1895a.** *Vellozia arabica* Baker. *Hooker's Icones Plantarum* **24**: t. 2364.
- Baker JG. 1895b.** Diagnoses Africanæ VII. *Bulletin of Miscellaneous Information Kew* **1895**: 211–230.
- Baker JG. 1896.** Amaryllideae. In: Thiselton-Dyer WT, ed. *Flora Capensis* **6**. London: Reeve, 171–246.
- Baker JG. 1898.** Amaryllideae. In: Thiselton-Dyer WT, ed. *D. Oliver's Flora of Tropical Africa* **7**. London: Reeve, 376–413.
- Baker JG. 1903.** Velloziaceae. In: Schinz H, ed. *Beiträge zur Kenntnis der afrikanischen Flora XV. Bulletin Herbarier Boissier Sér. II, 3*, 667–668.
- Baker JG. 1904a.** Velloziaceae. In: Schinz H, ed. *Beiträge zur Kenntnis der afrikanischen Flora XVIII. Vierteljahresschrift der Naturforschenden Gesellschaft Zürich*, **49**: 177–178.
- Baker JG. 1904b.** Velloziaceae p. 1003. In: Schinz H, ed. *Beiträge zur Kenntnis der afrikanischen Flora XVI. Bulletin Herbarier Boissier Sér. II, 4*, 995–1025.
- Balfour JH. 1868a.** On a supposed new species of *Vellozia*, or probably a new genus in the order Haemodorea. *Transactions of the Botanical Society Edinburgh* **9**: 189–190.
- Balfour JH. 1868b.** *Talbotia*. *Transactions of the Botanical Society Edinburgh* **9**: 192.
- Behnke H-D, Kramer K, Hummel E. 2002.** *Xerophyta seinei* (Velloziaceae), a distinctive new species from Zimbabwe. *Taxon* **51**: 55–67.

- Behnke H-D, Treutlein J, Wink M, Kramer K, Schneider C, Kao PC. 2000.** Systematics and evolution of Velloziaceae, with special reference to sieve-element plastids and *rbcL* sequence data. *Botanical Journal of the Linnean Society* **134**: 93–129.
- Binns B. 1968.** *A first check list of the herbaceous flora of Malawi*. Zomba: The Government Printer.
- Bullock AA. 1966.** *Vellozia viscosa*. *Curtis's Botanical Magazine* **76**: t. 493.
- Burt Davy J, Pott-Leendertz R. 1912.** A first check-list of the flowering plants and ferns of the Transvaal and Swaziland. *Annals of the Transvaal Museum* **3**: 119–182.
- Buscaloni L, Muschler R. 1913.** Beschreibung der von Ihrer Königlichen Hoheit der Herzogin Helena von Aosta in Zentral-Africa gesammelten neuen Arten. *Englers Botanische Jahrbücher* **49**: 457–515.
- Chapman JD, White F. 1970.** *The evergreen forests of Malawi*. Oxford: Commonwealth Forestry Institute.
- Chase MW, Duvall MR, Hills HG, Conran JG, Cox AV, Eguiarte LE, Hartwell J, Fay MF, Caddick LR, Cameron KM, Hoot S. 1995.** Molecular phylogenetics of Liliaceae. In: Rudall PJ, Cribb PJ, Cutler DF, Humphries CJ, eds. *Monocotyledons: systematics and evolution*. Kew: Royal Botanic Gardens, 109–137.
- Chiovenda E. 1911.** Plantae novae vel minus notae e regione aethiopica. *Annali Botanica* **9**: 135–152.
- Chiovenda E. 1929.** *Flora Somalia*. Rome: Sindacio Italiano Arti Grafiche.
- Coetzee H. 1974.** Anatomy of the leaves of the Velloziaceae in South Africa and South West Africa and a key based on leaf anatomy. *Dinteria* **10**: 19–33.
- Coetzee H, van der Schijff HP, Steyn E. 1973.** External morphology of the species of the South African Velloziaceae including a key based on external morphological characteristics. *Dinteria* **9**: 3–21.
- Collenette S. 1985.** *An illustrated guide to the flowers of Saudi Arabia*. London: Scorpion Publishing.
- Compton RH. 1976.** Velloziaceae. In: Compton RH, ed. *The Flora of Swaziland*. *Journal of South African Botany* **11**: Supplementary: 132.
- Crouch NR, Condy G. 2009.** *Xerophyta longicaulis*. *Flowering Plants of Africa* **61**: 42–49.
- Cufodontis G. 1972.** Enumeratio plantarum Africanum Aethiopiae Spermatophyta. *Bulletin du Jardin Botanique National de Belge* **42**: **Supplement**: 1579–1657.
- Dale IR, Greenway PJ. 1961.** *Kenya trees & shrubs*. Nairobi: Buchanan.
- De Wildeman EAJ. 1902–1903.** Étude sur la Flore de Katanga. *Annales du Musée du Congo – Botanique, Sér. 4*. Bruxelles.
- Dinter MK. 1909.** *Deutsch-Südwest-Afrika: flora, forst- und landwirtschaftliche Fragmente*. Leipzig: Weigel.
- Dinter MK. 1918.** Index der aus Deutsch-Südwestafrika bis zum Jahr 1917 bekannt gewordenen Pflanzenarten II. *Fedde Repertorium* **15**: 340–433.
- Durand T, Schinz H. 1895.** *Xerophyta. Conspectus Florae Africae ou Énumération des plantes d'Afrique*. Berlin, 5: 270–272.
- Duvall MR, Clegg MT, Chase MT, Clark WD, Kress WJ, Hills HG, Eguiarte LE, Smith JF, Gant BF, Zimmer E. 1993.** Phylogenetic hypotheses for the monocotyledons constructed from *rbcL* sequence data. *Annals of the Missouri Botanical Garden* **80**: 607–619.
- Duvigneaud P, Denaeyer-de Smet S. 1963.** Études sur la végétation du Katanga et de ses sols métallifères 7: Cuivre et végétation au Katanga. *Bulletin de la Société royale de Botanique de Belgique* **96**: 93–231.
- Dyer RA. 1976.** *The genera of Southern African flowering plants, 2: gymnosperms and monocotyledons*. Pretoria: Department Agricultural Technical Services.
- Endlicher S. 1841.** *Enchiridion Botanicum*. Leipzig & Vienna: Engelmann.
- Eyles F. 1916.** A record of plants collected in Southern Rhodesia. *Transactions of the Royal Society of South Africa* **5**: 273–564.
- Fries RE. 1914.** Velloziaceae. In: *Wissenschaftliche Ergebnisse der Schwedischen Rhodesia-Kongo-Expedition 1911–1912. Band I, Botanische Untersuchungen*. Stockholm: Aftonbladets Druckerei, 233–234.
- Gaff DF. 1977.** Desiccation tolerant vascular plants of Southern Africa. *Oecologia* **31**: 95–109.
- Gmelin JF. 1796.** *Caroli a Linné Systema Naturae*. Lyon: Delamolliere.
- Gonçalves AE. 2009.** Velloziaceae. In: Timberlake JR, Martins ES, eds. *Flora Zambesiaca 12*. Kew: Royal Botanic Gardens, 153–175.
- Greves S. 1921.** A revision of the Old World species of *Vellozia*. *Journal of Botany* **59**: 273–284.
- Guillarmod AJ. 1971.** *Flora of Lesotho (Basutoland)*. Lehre: Cramer.
- Hallam ND, Gaff DF. 1978.** Re-organization of fine structure during rehydration of desiccated leaves of *Xerophyta villosa*. *New Phytologist* **81**: 349–355.
- Hallam ND, Luff SE. 1980a.** Fine structural changes in the mesophyll tissue of the leaves of *Xerophyta villosa* during desiccation. *Botanical Gazette* **141**: 173–179.
- Hallam ND, Luff SE. 1980b.** Fine structural changes in the leaves of the desiccation-tolerant plant *Talbotia elegans* during extreme water stress. *Botanical Gazette* **141**: 181–187.
- Harms H. 1895.** Velloziaceae. In: Engler A, ed. *Die Pflanzenwelt Ost-Afrikas und der Nachbargebiete*. Berlin: Reimer, 145–146.
- Harms H. 1900.** Velloziaceae. In: Engler A, ed. *Berichte über die botanischen Ergebnisse der Nyassa-See und Kinga-Gebirgs-Expedition, III. Die von W. Goetze und Dr. Stuhlmann im Urugurugebirge, sowie die von W. Goetze in der Kisaki- und Khutu-Steppe und in Uehe gesammelten Pflanzen*. *Englers Botanische Jahrbücher*, **28**, 332–510.
- Harms H. 1902.** Velloziaceae. In: Engler A, ed. *Berichte über die botanischen Ergebnisse der Nyassa-See und Kinga-Gebirgs-Expedition, IV. Die von W. Goetze und Dr. Stuhlmann im Urugurugebirge, sowie die von W. Goetze in der Kisaki- und Khutu-Steppe und in Uehe gesammelten Pflanzen – nebst einigen Nachträgen zu Bericht III*. *Englers Botanische Jahrbücher*, **30**, 239–445.



- Hemsley WB. 1904.** *Vellozia trichophylla*. Native of eastern tropical Africa. *Curtis's Botanical Magazine* 130: Tab. 7962.
- Hepper FN. 1968.** Velloziaceae. In: Hepper FN FN, ed. *Flora of West Tropical Africa 2nd ed., 3 pt. 1*. Kew: Crown Agents for Oversea Governments and Administrations, 174–175.
- Hilliard OM, Burt BL. 1971.** Notes on some plants of southern Africa chiefly from Natal II. *Notes from the Royal Botanic Garden Edinburgh* 31: 1–3.
- Hilliard OM, Burt BL. 1986.** Notes on some plants of Southern Africa: XIII. *Notes from the Royal Botanic Garden Edinburgh* 43: 345–405.
- Hochstetter CF. 1841–1844.** Nova genera plantarum Africae proposit et describit. *Flora* 24: 657–672; 25: 225–240; 26: 69–83; 27: 17–32.
- Holzhammer M. 1953.** *Barbacenia naegelsbachii*: 334. In: Suessenguth K, ed. *Neue Taxa, Kombinationen und Vorkommen in Süd-Afrika. Mitteilungen der Botanischen Staatssammlungen München* 1: 333–345.
- Hooker JD. 1869.** *Vellozia elegans*. Natal *Vellozia*. *Botanical Magazine* 95: t. 5803.
- Huelsenbeck JP, Ronquist F. 2001.** Mr. Bayes: bayesian inference of phylogenetic trees. *Bioinformatics Applications Note* 17: 754–755.
- Jacobsen WBG. 1973.** A checklist and discussion of the flora of a portion of the Lomagundi District, Rhodesia. *Kirkia* 9: 139–207.
- Kubitzki K. 1998.** Velloziaceae. In: Kubitzki K, ed. *The families and genera of vascular plants*. Berlin: Springer, 3: 459–467.
- Lamarck M. 1791.** *Illustrations des genres, ou expositions des caractères de tous les genres de plantes établis par les botanistes (Encyclopédie méthodique), vol. I*. Paris: Panckoucke.
- Letty C. 1962.** *Wild flowers of the Transvaal*. Pretoria: Trustees of the Wild Flowers of the Transvaal Fund.
- Lye KA. 1995.** A new combination in Velloziaceae. *Lidia* 3: 143.
- Lye KA, Edwards S. 1997.** 202A. Velloziaceae. In: Edwards S, Demissew S, Hedberg I, eds. *Flora of Ethiopia and Erithrea*. Addis Ababa & Uppsala: Uppsala University, 6: 311–314.
- Marloth R. 1915.** *The Flora of South Africa. With synoptical tables of the genera of the higher plants, Vol. 4*. Capetown and London: Darter & Wesley.
- Martelli U. 1886.** *Florula Bogosensis*. Florence: Ricci.
- McPherson G, van der Werff H, Keating RC. 1997.** A new species of *Xerophyta* (Velloziaceae) from Madagascar. *Novon* 7: 387–394.
- Mello-Silva R. 1991.** The infra-familial taxonomic circumscription of the Velloziaceae: a historical and critical analysis. *Taxon* 40: 45–51.
- Mello-Silva R. 2000.** Partial cladistic analysis of *Vellozia* and characters for the phylogeny of the Velloziaceae. In: Wilson KL, Morrison DA, eds. *Monocots. Systematics and evolution*. Collingwood, Vic.: CSIRO, 505–522.
- Mello-Silva R. 2005.** Morphological analysis, phylogenies and classification in Velloziaceae. *Botanical Journal of the Linnean Society* 148: 157–173.
- Mello-Silva R, Santos DYAC, Salatino MLF, Motta LB, Cattai MB, Sasaki D, Lovo J, Pita PB, Rocini C, Rodrigues CDN, Zarrei M, Chase MW. 2011.** Five vicariant genera from Gondwana: the Velloziaceae as shown by molecules and morphology. *Annals of Botany* 108: 87–102.
- Menezes NL. 1971.** New taxa and new combinations in Velloziaceae. *Ciência e Cultura* 23: 421–422.
- Menezes NL. 1980.** Evolution in Velloziaceae, with special reference to androecial characters. In: Brickell CD, Cutler DF, Gregory M, eds. *Petaloid monocotyledons. Linnean Society Symposium Series* 8, London: Linnean Society of London & Academic Press, 117–138.
- Menezes NL, Mello-Silva R, Mayo SJ. 1994.** A cladistic analysis of the Velloziaceae. *Kew Bulletin* 49: 71–92.
- Metcalf CR, Gregory M. 1964.** Comparative anatomy of monocotyledons. Some new descriptive terms for Cyperaceae with a discussion of variations in leaf form noted in the family. *Notes from the Jodrell Laboratory Royal Botanic Gardens, Kew* 1: 1–11.
- Milne-Redhead EWBH. 1951.** Velloziaceae pp. 381–382. In: Tropical African plants XX. *Kew Bulletin* 5: 335–384.
- Norlindh T. 1948.** Velloziaceae. In: Norlindh T, Weimarck H, eds. *Beiträge zur Kenntnis der Flora von Süd-Rhodesia VIII. Botaniska Notiser*, 1948, 27–30.
- Pax F. 1892.** *B. hildebrandtii*. In: Engler A, ed. *Über die Hochgebirgsflora des tropischen Africa*. Berlin: Königliche Akademie der Wissenschaften, 171.
- Pax F. 1893.** Velloziaceae africanæ. In: Engler A, ed. *Beiträge zur Flora von Afrika II. Englers Botanische Jahrbücher*, 15, 95–160.
- Pax F. 1930.** Velloziaceae. In: Engler A, ed. *Die natürlichen Pflanzenfamilien, 2nd edn, 3*. Leipzig: Engelmann, 459–467.
- Perrier H. 1930.** Les *Xerophyta* de Madagascar. *Archives de Botanique. Bulletin Mensuel* 4: 65–75.
- Perrier H. 1950.** Velloziacées. In: Humbert H, ed. *Flore de Madagascar et des Comores*. Paris: Firmin-Didot, fam. 42, 1–15.
- Persoon CH. 1805.** *Synopsis Plantarum, seu Enrichidium Botanicum*. Tübingen: Cramer.
- Piscicelli M. 1914.** *Nella regione dei Laghi Equatoriali*. Napoli: Pierro.
- Poiret JLM. 1808.** *Encyclopédie méthodique. Botanique, vol 8*. Paris: Agasse.
- Poisson H. 1912.** *Recherches sur la Flore Méridionale de Madagascar*. Paris: Challamel.
- Poremski S. 1996.** Notes on the vegetation of inselbergs in Malawi. *Flora* 191: 1–8.
- Prychid CJ, Rudall PJ. 1999.** Calcium oxalate crystals in monocotyledons: a review of their structure and systematics. *Annals of Botany* 84: 725–739.
- Rendle AB. 1894.** The plants of Milanji, Nyassa-land, collected by Mr. Alexander Whyte, F.L.S., and described by Messrs. Britten, E. G. Baker, Rendle, Gepp and others; with an introduction by William Carruthers, F.R.S., F.L.S. *Transactions of the Linnean Society II* 4: 1–67.
- Rendle AB. 1895.** A contribution to the Flora of Eastern tropical Africa. *Journal of the Linnean Society – Botany* 30: 373–435.

- Rendle AB. 1899.** *Catalogue of the African plants collected by Dr. Friedrich Welwitsch in 1853–61, Vol. 2, pt. I, monocotyledons and gymnosperms.* London: By the order of the Trustees.
- Ridley HN. 1883.** Description and notes on new or rare monocotyledonous plants from Madagascar, with one from Angola. *Journal of the Linnean Society* **20**: 329–338.
- Roemer JJ, Schultes JA. 1829.** *Caroli a Linné Systema Vegetabilium*, ed. 16, 7 (1). Stuttgart: Cotta.
- Ronquist F, Huelsenbeck JP. 2003.** MrBayes 3: bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.
- Ross JH. 1972.** *The flora of Natal.* Pretoria: Department of Agricultural Technical Services.
- Salatino A. 1999.** Main results from *trnL-F* sequencing of Velloziaceae and allied taxa. *Anais da Academia Brasileira de Ciencias* **71**: 202–206.
- Salatino A, Salatino MLF, Mello-Silva R, van Sluys M-A, Giannisi DE, Price RA. 2001.** Phylogenetic inference in Velloziaceae using chloroplast *trnL-F* sequences. *Systematic Botany* **26**: 92–103.
- Schinz H. 1896.** Die Pflanzenwelt Deutsch-Südwest-Afrikas. *Bulletin Herbar Boissier* **4**, Appendix **3**: 1–57.
- Schwartz O. 1939.** Flora des tropischen Arabien. *Mitteilungen aus dem Institut für allgemeine Botanik in Hamburg* **10**: 1–393.
- Seine R. 1996.** *Vegetation von Inselbergen in Zimbabwe.* Wiehl: Martina Galunder Verlag.
- Seine R, Becker U, Porembski S, Follmann G, Barthlott W. 1998.** Vegetation of Inselbergs in Zimbabwe. *Edinburgh Journal of Botany* **55**: 267–293.
- Smith LB, Ayensu ES. 1974.** Classification of Old World Velloziaceae. *Kew Bulletin* **29**: 181–205.
- Smith LB, Ayensu ES. 1975.** Velloziaceae. In: Polhill RM, ed. *Flora of Tropical East Africa.* Kew: Royal Botanic Gardens, 1–9.
- Smith LB, Ayensu ES. 1976.** A revision of American Velloziaceae. *Smithsonian Contributions to Botany* **30**: 1–172.
- Smith LB, Lebrun J-P, Stork AL, Wüest J. 1986.** Un *Xerophyta* (Velloziaceae) nouveau d’Ethiopie méridionale. *Bulletin Muséum national d’Histoire naturelle, Paris, 4<sup>e</sup> série, 8, section B, Adansonia* **3**, 297–300.
- Sölch A. 1961.** *Xerophyta wenzeliana*: 74 in *Miscellanea. Mitteilungen der Botanischen Staatssammlungen München* **4**: 73–74.
- Sölch A, Roessler H. 1969.** Velloziaceae. In: Merxmüller H, ed. *Prodromus einer Flora von Südwestafrika.* Lehre: Cramer, 152.
- Stamatakis A. 2006.** RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics* **22**: 2688–2690.
- Swofford DL. 2002.** *PAUP\*, Phylogenetic analysis using parsimony (and other methods). Version 4.0b10a.* Sunderland, MA: Sinauer Associates.
- Terracciano A. 1892.** Contribuzione alla flora del paese dei Somali. *Bolletino della Società Botanica Italiana* **1892**: 421–426.
- Thonner F. 1908.** *Die Blütenpflanzen Afrikas – eine Anleitung zum Bestimmen der Gattungen der afrikanischen Siphonogamen.* Berlin: Friedlaender & Sohn.
- Thulin M. 1995.** 158. Velloziaceae. In: Thulin M, ed. *Flora of Somalia.* Kew: Royal Botanic Gardens, 4: 76–77.
- Trauseld WR, Biegel HM. 1969.** *Wild flowers of the Natal Drakensberg.* Cape Town: Purnell.
- Tredgold MH. 1979.** *Rhodesian wild flowers. Thomas Meikle Series Number 4.* Salisbury: The National Museums and Monuments of Rhodesia.
- Tropicos. 2009.** Botanical information system at the Missouri Botanical Garden – <http://www.tropicos.org>. (accessed 5 February 2012).
- Warming E. 1893.** Note sur la biologie et l’anatomie de la feuille des Velloziacées. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandling og dets Medlemmers Arbejder* **2**: 57–100.
- Watson W. 1903.** *Vellozia equisetoides.* *The Gardener’s Chronicle III*, 34: 425 + fig. 167.
- White F. 1962.** *Forest flora of Northern Rhodesia.* Oxford: Oxford University Press.
- Wild H. 1952.** A guide to the flora of the Victoria Falls. In: Clark JD, ed. *The Victoria Falls.* Lusaka: Commission for the Preservation of Natural and Historical Monuments and Relics, 121–145.
- Wild H. 1964.** The endemic species of the Chimanimani Mountains and their significance. *Kirkia* **4**: 125–156.
- Wild H. 1968.** Phytogeography in south central Africa. *Kirkia* **6**: 197–222.
- Wilder GJ. 1985.** Anatomy of noncostal portions of lamina in the Cyclanthaceae (Monocotyledoneae). IV. Veins of inter-ridge areas, expansion tissue, and adaxial and abaxial ridges. *Botanical Gazette* **146**: 545–563.
- Willdenow CL. 1799.** *Caroli a Linné Species plantarum ed. 4.* Berlin: Nauk.
- Wirsching A. 2002.** *Vergleichende Blattanatomie bei Cyclanthaceae, Pandanaceae und Stemonaceae.* Thesis (Diplomarbeit), Fakultät für Biologie, Universität Heidelberg.

INDEX TO SPECIFIC AND INFRASPECIFIC EPITHETS OF *XEROPHYTA*

*acuminata*, Baker, 15  
*adendorffii*, Behnke, 14  
*aequatorialis*, Rendle, 27  
*andringitrensis*, H.Perrier, 47  
*amica*, Steud., 2

*arabica*, Baker, 4  
*argentea*, Wild, 21  
*aymoninii*, Phillipson & Lowry, 48  
*bakeri*, T.Durand & Schinz, 36  
*barbacenioides*, Harv. ex Baker, 1

- barbarae*, P.A.Duvign. & Dewit, 43  
*brevifolia*, H.Perrier, 49  
*brevifolia*, Chiov., 2  
*calcicola*, Phillipson & Lowry, 50  
*capillaris*, Baker, 25  
***cauliflora***, Behnke, 51  
*clavata*, Baker, 45  
*concolor*, L.B.Sm. & Ayensu, 32  
*connata*, McPherson & van der Werff, 52  
*croatii*, Phillipson & Lowry, 53  
*cuprophila*, P.A.Duvign. & Dewit, 43  
*dasyliroides*, Baker, 54  
*decaryi*, Phillipson & Lowry, 55  
*demeesmaeckeriana*, P.A.Duvign. & Dewit, 19  
*eglandulosa*, H.Perrier, 56  
*elegans*, Balf., 1  
*equisetoides*, Baker, 44  
*eylesii*, Greves, 42  
***glabra***, Behnke, 31  
***glutinosa***, Behnke, 29  
*goetzei*, Harms, 18  
*helenae*, Buscaloni & Muschler, 27  
*hereroensis*, Schinz, 13  
*hildebrandtii*, Pax, 2  
***hirtiflora***, Behnke & E.Hummel, 33  
*hirtocarpa*, H. Perrier, 56  
*humbertii*, Phillipson & Lowry, 57  
*humilis*, Baker, 5  
*isaloensis*, Phillipson & Lowry, 58  
*jostiana*, Dinter, 13  
*jouyiana*, Phillipson & Lowry, 59  
***junodii***, Behnke, 9  
*kirkii*, Hemsl., 22  
*labatii*, Phillipson & Lowry, 60  
*leandrii*, Phillipson & Lowry, 61  
*lewisiae*, Phillipson & Lowry, 62  
*longicaulis*, Hilliard, 6  
*madagascariensis*, J.F.Gmel., 66  
*melleri*, Baker, 44  
*miniata*, T.Durand & Schinz, 1  
*minor*, Baker, 1  
*minuta*, Baker (sub *Vellozia*), 4  
*minuta*, Baker (sub *Xerophyta*), 1  
*mollissima*, Schinz, 36  
*monroi*, Greves, 34  
***multiramosa***, Behnke, 45  
***naegelsbachii***, Dinter ex M.Holzhammer, 39  
*nandrasanae*, Phillipson & Lowry, 63  
*neglecta*, Roem. & Schult., 66  
*nutans*, L.B.Sm. & Ayensu, 40  
***occidentalis***, Milne-Redh., 2  
*occultans*, L.B.Sm. & Ayensu, 25  
*parviflora*, Phillipson & Lowry, 64  
***pauciramosa***, L.B.Sm. & Ayensu, 37  
*pectinata*, Baker, 65  
*pinifolia*, Lam., 66  
***plumosa***, Behnke, 40  
***pseudopinifolia***, Behnke, 26  
*pubescens*, L.B.Sm. & Ayensu, 38  
***purpurascens***, Behnke, 35  
***rehmannii***, Behnke, 11  
*retinervis*, Baker, 45  
*rhodesiana*, R.E.Fr., 38  
*rippsteinii*, L.B.Sm., J.-P.Lebrun & A.L.Stork, 3  
*rosea*, Baker, 8  
*scabra*, H.Perrier, 68  
*scabrida*, Pax, 20  
*schatzii*, Phillipson & Lowry, 67  
*schlechteri*, Baker, 16  
*schizleinia*, Hochst., 2  
*seinei*, Behnke, K.Kramer & E.Hummel, 10  
*sessiliflora*, Baker, 68  
*setosa*, L.B.Sm. & Ayensu, 69  
*setosa*, Phillipson & Lowry, 44  
*simulans*, L.B.Sm. & Ayensu, 17  
*somalensis*, A.Terracc., 2  
*spekei*, Baker, 27  
*spinulosa*, Ridl., 65  
*splendens*, Rendle, 23  
*squarrosa*, Baker, 30  
*stenophylla*, Baker, *incertae sedis*  
*suaveolens*, Greves, 41  
*tabulare*, Phillipson & Lowry, 70  
*talbotii*, Balf., 1  
***tanzaniana***, Behnke, 28  
*tomentosa*, Pax, 27  
*trichocarpa*, H.Perrier, 56  
*trichophylla*, Baker, 43  
*tulearensis*, H.Perrier, 71  
***vallispongolana***, J.E.Burrows, S.M.Burrows & Behnke, 46  
*vellosioides*, Harv. ex Baker, 45  
*velutina*, Baker, 24  
***verrucosa*** Behnke, 38  
*vestita*, L.B.Sm. & Ayensu, 41  
*villosa*, Baker, 36  
*villosa*, H.Perrier, 68  
*villosa*, T.Durand & Schinz, 7  
*viscosa*, Baker, 7  
*violacea*, Baker, *incertae sedis*  
*wentzeliana*, Harms, 38  
*zambiana*, L.B.Sm. & Ayensu, 19  
***zimbabwensis***, Behnke & E.Hummel, 12