

Notes on the pollen morphology and taxonomy of *Aloe bowiea* (Asphodelaceae: Alooideae)

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ABSTRACT

The comparative macromorphology and palynology of the monotypic genus *Chamaealoe* Berger was studied as part of an on-going investigation of generic relationships in the subfamily Alooideae (Asphodelaceae). Pollen morphology was examined using scanning electron microscopy. Pollen grains are free, monosulcate, bilaterally symmetrical, medium in size and have a perforated tectum. Pollen of *Chamaealoe* is typically aloecoid and the lack of differences in pollen morphology offers additional evidence for the inclusion of the genus in *Aloe*. Furthermore, no single macromorphological character or combination of characters could be found to be diagnostic at the generic level. Neither vegetative nor reproductive morphology supports the recognition of *Chamaealoe* as a genus, thereby confirming that *C. africana* (Haworth) Berger should best be included in the synonymy of *Aloe bowiea* Schult. & J.H. Schult. An amplified description and the full nomenclatural treatment of *A. bowiea* are given.

INTRODUCTION

Taxonomic work on *Aloe* L. commenced shortly after Linnaeus (1753) established the genus in his *Species Plantarum* (see for example Miller 1768). The taxonomy of the group was at first conservatively a single genus with nine species and a number of varieties. By 1804 Haworth had recognized the infrageneric heterogeneity of *Aloe sensu* L. and shortly afterwards Duval (1809) proposed the splitting of the genus into more coherent, natural genera. This process continued for about a century and a half, with the latest additions being *Poellnitzia* Uitewaal (1940), *Astroloba* Uitewaal (1947) and *Guillauminia* Bertrand (1956). This resulted in the unsatisfactory situation we have today where 27 generic names are available for some 450 species which could easily be accommodated in seven genera.

In recent years taxonomic and biosystematic interest in the subfamily Alooideae (Asphodelaceae), (Dahlgren *et al.* 1985), in which *Aloe* and allied genera are classified, has been renewed. Working on cytogenetics and leaf anatomy, respectively, Drs P.E. Brandham and D.F. Cutler, both of the Royal Botanic Gardens, Kew, have, amongst others, played an important part in elucidating patterns of variation within the subfamily. Currently a multidisciplinary project on the systematics of the smaller aloecoid genera is in progress at the Potchefstroom University for Christian Higher Education, South Africa.

The Alooideae is a fairly large, generally easily recogniz-

able and apparently natural subfamily. Unifying subfamilial characters include the widespread occurrence of secondary thickening, leaf succulence, usually tubular petaline flowers, fusion of the perianth segments and a basic diploid karyotype ($2n = 14$) with four pairs of long chromosomes, and three much shorter pairs. Although being a genetically simple group, the Alooideae displays unusual patterns of variation among populations and inconsistent intergradations among species, *Haworthia* Duval being especially notorious (Bayer 1970, 1971, 1972, 1974, 1982). Furthermore, in most cases the range of variation in individual phenetic traits overlaps. Generic delimitation and species concepts have thus been the subject of much discussion.

Among the uncertainties regarding characters of potential diagnostic value, several stand out as warranting additional research. Among these are studies relating to palynology and reproductive biology (Smith 1988, 1991). In this contribution scanning electron microscopy (SEM) provided quantitative and qualitative data on the pollen of *Aloe bowiea* Schult. & J.H. Schult. - a species sometimes treated as a monotypic genus, *Chamaealoe* Berger (Smith 1990a, b). The principle aim of the study was to examine the taxonomic significance of pollen morphology in a taxonomically controversial unit of the subfamily. Although Smith (1988, 1991) suggested that it is unlikely that palynology should solve classificatory problems in the subfamily, it is unwise to infer this for a taxon, until a detailed study has been made.

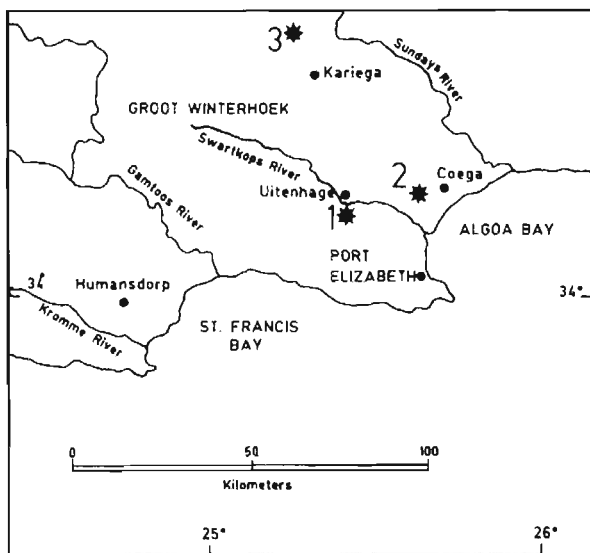


FIGURE 1: Location of populations of *Aloe bowiea* (*) investigated in this study. The three localities shown are the only ones known for the species.

A comparative macromorphological study of *Aloe bowiea* was conducted in parallel to complement the pollen morphological evidence. The former supplements an earlier contribution on the infrageneric affinities of *A. bowiea* (Smith 1990a) and was carried out to gain a clearer understanding of its intraspecific variation. Conclusive evidence is presented, showing that those characters previously used for the recognition of *Chamaealoe* can all be accommodated in the circumscription of *Aloe sensu* Duval (1809).

Aloe bowiea is endemic to arid parts of the eastern Cape Province (Figure 1). It has a very restricted distribution, and is known from only two localities at present, one in the vicinity of Coega and the other near Kariega. Extensive field work has shown that the species is now extinct at the type locality near Uitenhage. Plants from the type locality probably survive in cultivation only. *Aloe bowiea* is ecologically specialized, growing in open areas in the fairly closed canopy layer of Valley Bushveld vegetation *sensu* Acocks (1988).

MATERIALS AND METHODS

Owing to its restricted geographical distribution, small and inconspicuous stature and scarcity, only a small number of herbarium accessions are known for *Aloe bowiea*. Hence measurements of vegetative and reproductive structures based on herbarium specimens were supplemented by measurements taken from plants in the field, as well as cultivated plants of known origin grown under uniform conditions in the greenhouse of the Botanical Garden of the Potchefstroom University for Christian Higher Education. The sample sites were selected to reflect the entire geographical range of *A. bowiea*. These sites were visited regularly over a period of eight years (1983-1990) and measurements were taken from a large number of individuals.

For SEM anthers were taken from post-anthesis flowers of material collected in natural habitat and prepared

according to the filter technique of Bredenkamp & Hamilton-Attwell (1988) (for details of pollen grain surface) and the osmium tetroxide technique of Smith & Tiedt (1991) (for dimensions, shape, symmetry and aperture features of pollen). Prepared pollen samples were attached to electron microscope stubs using two-sided sticky tape and were subsequently carbon flash evaporated and sputter-coated in an argon atmosphere with gold/palladium (60:40) to a thickness of 3 nm. The samples were studied with a Cambridge Stereoscan 250 S scanning electron microscope operating at about 10 kV, the voltage being adjusted for each preparation. Pollen dimensions were measured from scaled SE micrographs. The descriptive terminology follows mainly Erdtman (1966, 1969) and the attempts at standardization offered by Reitsma (1970) and Nilsson & Muller (1978). *Smith 1, 4, 160 and 173* are the voucher specimens. For comparison, pollen grains of species of *Chortolirion* Berger, *Haworthia* and *Poellnitzia*, are illustrated.

RESULTS AND DISCUSSION

GENERAL

It has been clearly illustrated that there is no consensus among previous authors on the validity of the generic status of *Chamaealoe* (Smith 1990a,b). This has led to the publication of a number of synonyms for this entity, which provides a misleading reflection of its comparatively uniform, typically aloecoid macromorphology. It appears that the synonyms were created by botanists who worked on a single plant or herbarium specimen. In the Alooideae in general scant regard was paid to natural variation and genera were often based on characters which later proved to be insufficient for segregating taxa at any level in a hierarchical classification system. An evaluation of a wide range of morphological characters was carried out with reference to *Aloe bowiea* (= *Chamaealoe*).

The decision of Berger (1905, 1908) to afford *Aloe bowiea* separate generic status as *Chamaealoe* relied heavily upon certain vegetative and reproductive morphological characters which he regarded as irreconcilable with *Aloe sensu* Duval (1809). The present study shows that *Aloe* is polymorphic with respect to the features used by Berger to distinguish *A. bowiea* as a monotypic genus. These characters are listed in Table 1 and it is shown that none of them is unique to the species, thereby refuting its elevation to generic rank by Berger (1905). In the interests of consistency, many more *Aloe* segregates would need to be upheld as genera, if Berger's point of view on the classification of *A. bowiea* were to be accepted. This would lead to a large inflation in the number of genera included in the Alooideae and would not be in the best interest of aloecoid taxonomy.

Morphological characters of the leaves (number, arrangement), racemes (shape, density) and flowers (pedicel length, exertion of anthers and stigma) of *Aloe bowiea* have been found to be useful at the infrageneric level and

TABLE 1: Morphological features used by Berger (1905, 1908) to establish the monotypic genus, *Chamaeculoe*. A selection of taxa of *Aloe* which share the respective characters are listed in the second column.

Characters used as diagnostic for <i>Chamaeculoe</i> (Berger 1905, 1908)	Species and infrageneric taxa of <i>Aloe</i> sharing the characters
Dense, grass-like rosettes	Section <i>Leptoaloe</i> Berger
Small, narrowly linear leaves (Figure 2)	Section <i>Graminialoe</i> ; dwarf Madagascan species
Slender, lax inflorescence	Dwarf Madagascan species
Small, greenish-white flowers	<i>A. inconspicua</i> Plowes
Subsessile flowers	<i>A. modesta</i> Reynolds
Free perianth segments	<i>A. pictifolia</i> Hardy
Exserted filaments (Figure 3)	Widespread in <i>Aloe</i> , but usually not as prominent as in <i>A. bowiea</i>

can be used to discriminate between the species and other members of *Aloe* sect. *Graminialoe* Reynolds (Figures 2 and 3). This investigation therefore confirms Smith's (1990a) earlier reinstatement of *Bowiea* at subsectional level in *Aloe* sect. *Graminialoe*.



FIGURE 2: Growth form of *Aloe bowiea* showing rosette of small, linear leaves. Photograph taken in habitat near Kariega. Diameter of lens cover = 50 mm.

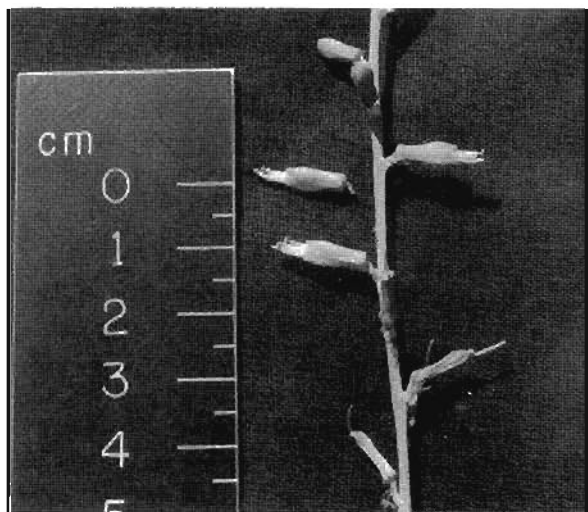


FIGURE 3: *Aloe bowiea* bears a laxly-flowered raceme with small, subsessile flowers. The anthers and style are much exserted. Specimen from Coega.

POLLEN MORPHOLOGY

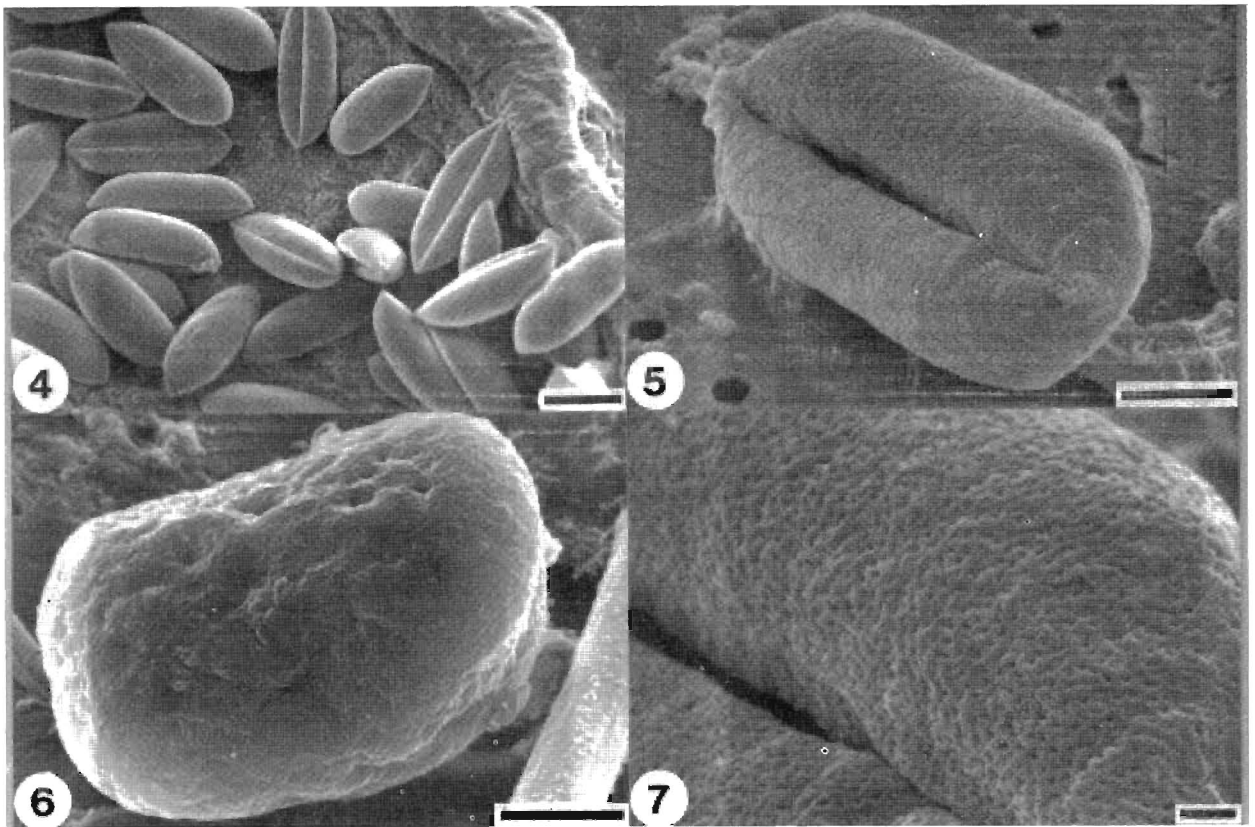
The morphology of pollen grains of *Aloe bowiea* was found to be consistent for all the specimens examined (Figures 4—7) and are in most respects morphologically similar to the pollen of other genera of the Alooideae, viz. *Chortolirion*, *Haworthia* and *Poellnitzia* (Figures 8-11).

Pollen shed as monads. Grains bilaterally symmetrical. Ambelliptical (occasionally pyriform). Grains heteropolar with an inaperturate proximal wall (Figures 4, 6) and a distal, monosulcate aperture (Figure 5). Sulcus well-defined and equal to the dominant equatorial axis. Grain size (dominant axis) varying within fairly narrow limits (35 (41,4) 46 μm) within and between samples. Pollen grain surface perforated by numerous minute micropores (Figures 5-7). Sexine discontinuous and subtectate. Lumina in general circular and less than 0.1 μm in diameter. Muri ca. 0.3 μm wide, smooth. The proximal surface of some grains prepared for SEM by means of the filtering technique displayed a degree of sculpturing superimposed on the perforated sexine (Figure 6). Due to its inconsistent occurrence this feature is not thought to have any taxonomic significance.

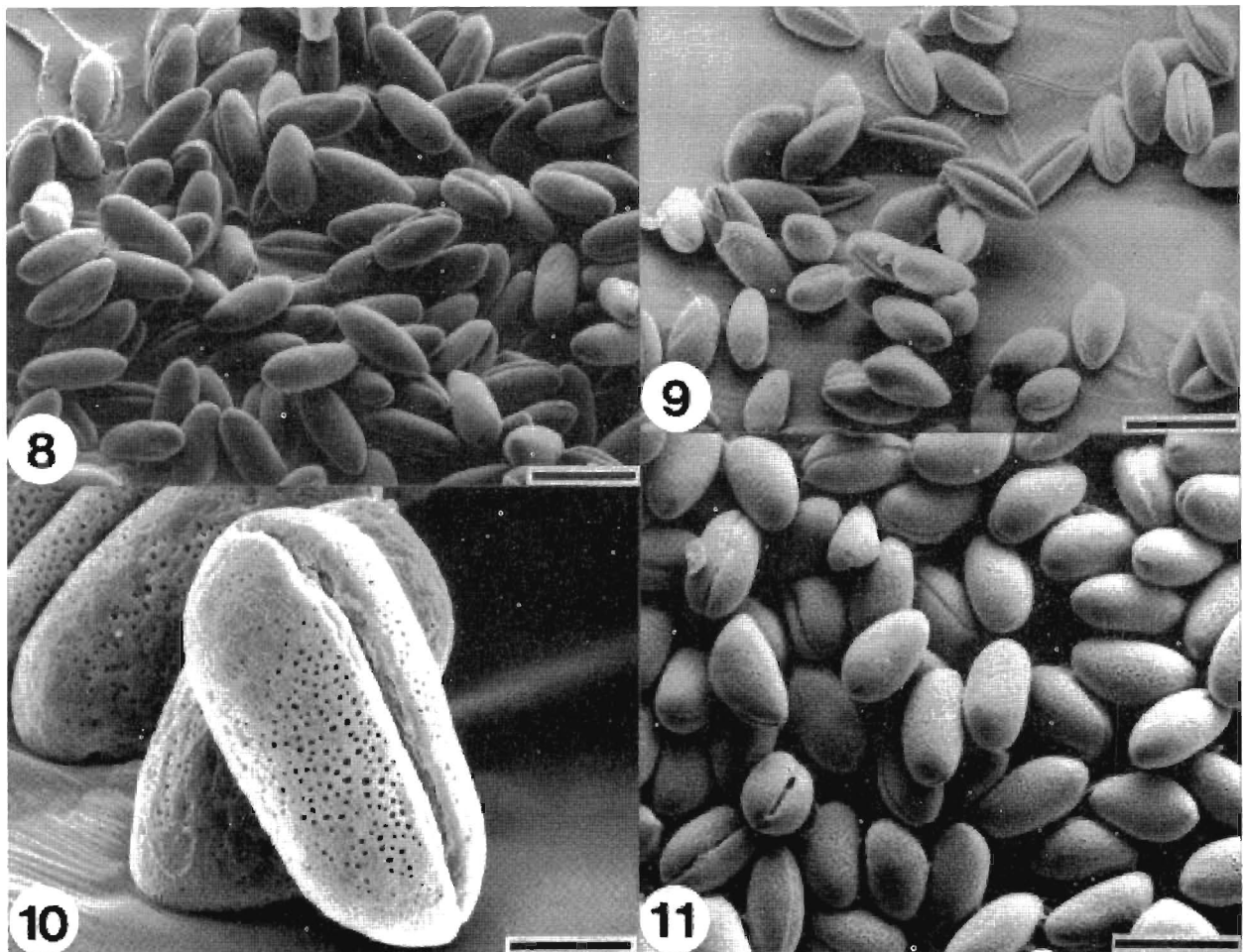
No narrow, unsculptured zone bordering the sulcus was observed. The existence of such a zone had previously been reported for pollen of *Haworthia* (Yuhl & Majumdar 1981). The micropores which occur in the pollen grain surface of *Aloe bowiea* are in general smaller than those of pollen grains of related genera (Smith 1988, 1991). This feature is taxonomically insignificant since pollen of especially *Chortolirion* often displays extremely small perforations in the pollen grain surface. The mean pollen grain size of *A. bowiea* is slightly greater than that of related genera. However, the range of grain size of *A. bowiea* overlaps with that of pollen of *Haworthia* and *Poellnitzia* (Erdtman 1966). It is therefore clear that no single pollen morphological character or combination of characters are diagnostic at the specific or generic level.

NOMENCLATURE AND AMPLIFIED DESCRIPTION OF *ALOE BOWIEA*

Aloe bowiea Schult. & J.H. Schult. in *Systema Vegetabilium* 7, 1: 704 (1829); Salm-Dyck: 14, 313 (1834); Endlicher: 143 (1836); Salm-Dyck: Fasc. 1, t. 24 [Sect. 14, t. 1] (1836); Kunth: 515 (1843); Baker: 158 (1880); Bentham & Hooker: 776 (1883); Baker: 309 (1896); Obermeyer: 119 (1973); Jeppe: 134 (1977); Hardy: 518 (1982); Smith: 10 (1983). As *A. bourea* Schult. & J.H. Schult. Orthographic variant. Berger: 120 (1908); Jacobsen: 348 (1954); Jacobsen: 270 (1974); Jacobsen: 144 (1977); Jacobsen: 259 (1986). As *A. bowieae* Schult. & J.H. Schult. Orthographic variant. Bond & Goldblatt: 28 (1984). Type: SOUTH AFRICA (Cape of Good Hope), without precise locality [probably vicinity of Uitenhage and Algoa Bay (Port Elizabeth), cf. Smith and Van Wyk (1989)], 30 December 1821—26 February 1822, typotype collected by James Bowie s.n., no material preserved; unpublished drawing by Thomas Duncanson, neotype [iconotype] (K!); Figure 1 (Smith 1990c).



FIGURES 4—7: Scanning electron micrographs of pollen of *Aloe howiea*. (4) Group of pollen grains showing uniform symmetry and aperture shape and length within a sample. (5) Distal face showing elongated aperture (sulcus). (6) Proximal surface displaying some degree of sculpturing. (7) Detail of tectum surface in the apertural region showing minute perforations and smooth muri. Figure 4 from Smith 173, prepared for SEM using the osmium tetroxide technique; Figures 5 and 7 from Smith 4 and Figure 6 from Smith 160, all prepared for SEM using the filtering technique. Scale bar = 20 μm in Figure 4; 5 μm in Figures 5 & 6 and 1 μm in Figure 7.



FIGURES 8—11: Scanning electron micrographs of groups of pollen grains showing uniform symmetry, tectal ornamentation and aperture shape/length in the Alooideae. (8) *Haworthia attenuata* (Haworth) Haworth f. *attenuata* (Smith 170, farm "Ntshutsha", King William's, Town); (9) *H. glabrata* (Salm-Dyck) Baker (*Greyling 1*, ex hort. Botanical Garden of the Potchefstroom University for Christian Higher Education); (10) *Chortolirion angolense* (Baker) A. Berger (Smith 14, Potchefstroom); (11) *Poellnitzia rubriflora* (H.M.L. Bolus) Uitewaai (Smith 174, farm "Langverwacht", Robertson). Scale bar = 40 μm in Figures 8, 9 & 11 and 10 μm in Figure 10. All specimens are deposited in PUC.

Bowiea africana Haw.: 299 (1824); Haworth: 123 (1827), nom. rej. Type: as for *A. bowiea*.

Chamaealoe africana (Haw.) Berger: 43 (1905); Berger: 120 (1908); Jacobsen: 348 (1954); Ginns: 57 (1974); Jacobsen: 270 (1974); Rauh: 129 (1979); Court: 174 (1981); Jacobsen: 259 (1986); Innes: 93 (1988), nom. illeg. Type: as for *A. bowiea*.

Icons: Salm-Dyck: Fasc. 1, t. 24 [Sect. 14, t. 1] (1836); Berger: t. 41 (1908); Jacobsen: t. 230, 231 (1954); Lamb: 42 (1960); Jacobsen: t. 257, 258 (1974); Jacobsen: t. 34 (1 & 2) (1977); Jeppe: back of p. 135 (1977); Lamb & Lamb: 802 (1977); Barkhuizen: t. 164 (1978); Rauh: t. 65 (4) (1979); Smith: t. 4 (1983); Jacobsen: t. 257, 258 (1986).

SPECIES EXCLUDED

Aloe bowieana Salm-Dyck: Fasc. 5, t. 9 [Sect. 29, t. 3] (1849). A species of *Gasteria* [*G. picta* Haw. *sensu* Stearn (1938); *G. bicolor* Haw. var. *bicolor sensu* Van Jaarsveld (1989)] which Jacobsen (1954, 1974, 1977, 1986) inexplicably placed in the synonymy of *A. bowiea*.

Herbaceous perennial; acaulescent, with leaves in a basal rosette ± 150 mm in diameter; proliferous from the base and forming closely packed clusters; roots fusiform, up to 10 mm in diameter. *Leaves* rosulate-multifarious, flaccid, ± 25 , dull green to glaucous green, spreading to recurved, the young erect, the old spreading, subulate, narrowly linear, ± 140 mm long, diameter ± 4 mm, dilating and becoming amplexicaul at or below ground level, thickness ± 2 mm; *upper surface* green with 1—2 centrally positioned white to light green nerves, canaliculate, immaculate or with very few white spots near base; *lower surface* convex, green with white spots, more copiously spotted near base, the spots tuberculate-subspinulose; *margins* armed with firm, white, deltoid or recurved teeth, ± 1 mm long, larger low down, smaller and becoming obsolescent upwards, 4—5 mm distant throughout. Inflorescence up to 410 mm tall; *peduncle* simple, diameter ± 2 mm, up to 280 mm long, sterile bracteate in upper two-thirds, sterile bracts membranous, caudate, abruptly long acuminate, ± 6 mm long, erect, keeled with a yellowish vein; *raceme* elongate, lax, up to 130 mm long, 20 mm wide, ± 20 spirally arranged flowers and buds, 3—4 open simultaneously; *floral bracts* membranous, 5 mm long, cuspidate, keeled, clasping the pedicels, longer than the pedicels; *pedicels* erect to slightly recurved, persistent, dull green, 1—2 mm long throughout, diameter 1 mm. *Flowers* sub-erect, slightly zygomorphic, greenish-white, basally substipitate; *perianth* cylindrical-trigonal, ventricose, narrowing slightly at the mouth, the mouth trigonal upturned, tube slightly constricted 3 mm from the base, 8—15 mm long, ± 5 mm across; *outer segments* free to base, with sub-acute apices, greenish-white, 1 broad, green nerve from base to apex; *inner segments* free, broader than the outer, greenish-white, 1 narrow green nerve from base to apex, apices more obtuse, tips very slightly flared; *bud* narrow, straight, slightly up-curved at tip; *stamens* 6 usually of unequal length; *filaments* white, filiform-flattened, longer than perianth; *anthers* bright yellow, exserted 2—4 mm; *ovary* olive

green, 3 mm long, diameter 2 mm, finely 6-grooved; *style* light green, straight, capitate, up to 13 mm long, much exserted. *Fruit* trilocular capsule, cylindrical, apically retuse, dull glaucous green, up to 12 mm long, diameter 4 mm. *Seed* light brownish-grey, angled, shortly winged, 3 mm long. *Chromosome number*: $2n = 14$ (Brandham 1969, 1971). Figure 12.

Flowering asynchronous throughout the year with a peak during the summer months, December to March (southern hemisphere).

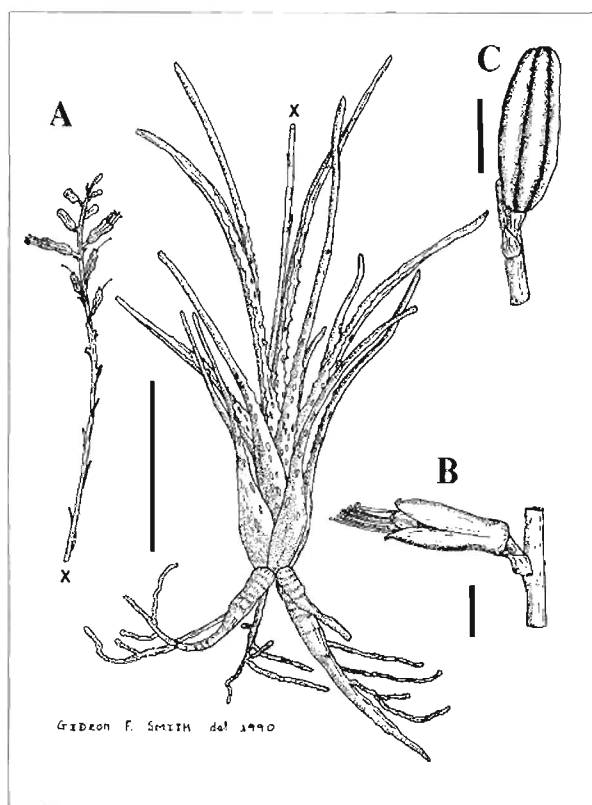


FIGURE 12: *Aloe bowiea* Schult. & J.H. Schult. A. Habit; B. Single flower in lateral view, showing the position of the peduncle and bract; C. Fruit, trilocular capsule. All drawings were made from live material of *Smith 4*. Scale bar = 50 mm in Figure 8A and 5 mm in Figures 8B & 8C.

SPECIMENS EXAMINED

The localities of the collections are listed according to the grid reference system of Leistner & Morris (1976). The abbreviations of herbarium names are according to Holmgren *et al.* (1981).

SOUTH AFRICA, CAPE PROVINCE. — 3325 (Port Elizabeth): 5 km from Uitenhage (-CD), *Reynolds 1206* (PRE); the farm "Jachtvlakte" between Uitenhage and Despatch, 4 km from Uitenhage, *Smith 1* (PEU, PUC); Despatch railway station, *Hardy 2184* (PRE); the farm "Zwartkoppes" near Coega (-DC), *Smith 160* (PUC); Maasward Private Nature Reserve near Coega, *Smith 4*, *Smith 173* (PUC).

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