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A taxonomic revision of *Aloe* sect. *Purpurascentes* (Asphodelaceae subfam. Alooideae)

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Abstract

Aloe sect. *Purpurascentes*, or the speckled aloes (not to be confused with the maculate aloes, which are members of *A.* sect. *Pictae*), occurs in southern and western South Africa and southern Namibia. This section is here revised using macro-morphology, seed morphology, palynology, chemistry, and molecular evidence. Seed morphology, palynology, chemistry, and to a greater extent molecular markers, are shown to be inconclusive for demarcation at species level in *A.* sect. *Purpurascentes*. Nonetheless, evidence from these sources does provide support for the general coherence of the group. Although some species can be clearly differentiated from most other members of *A.* sect. *Purpurascentes*, the results are not consistent among the different character sets investigated. No changes are thus proposed here in terms of the placement of taxa within the section. Two species suspected to be members of the section under study (*A. pictifolia* and *A. chlorantha*), although being chemically related, do not cluster with the rest of the members of *A.* sect. *Purpurascentes* in the morphological analysis, and evidence on the sectional placement of these taxa from molecular analyses is inconclusive. Hence, these two aloes are here excluded from *A.* sect. *Purpurascentes*. The most useful evidence to distinguish among taxa in *A.* sect. *Purpurascentes* were those from comparative morphology. In this revision five species are retained: *A. framesii*, *A. gariepensis*, *A. khamiesensis*, *A. microstigma*, and *A. succotrina*. The following taxonomic changes are proposed: *A. knersvlakensis* becomes a subspecies of *A. khamiesensis*; aberrant populations of the latter species from the Hantam region are described as *A. khamiesensis* subsp. *hantamensis*; *A. juttae* is reinstated at subspecific level under *A. microstigma*; *A. amoena* is reinstated at subspecific level under *A. framesii*, and a third subspecies, *A. framesii* subsp. *maraisii*, is described for the southern populations of this aloe. Lectotypes are designated for five names and epitypes for three names. The notion that DNA barcodes should not be seen as a replacement technique for comprehensive taxonomic analysis is clearly illustrated in this revision of *A.* sect. *Purpurascentes*. Since traditional barcodes are insufficient to distinguish samples at species level, alpha taxonomic techniques are essential to delimit species in this group of aloes, and likely for all other aloes.

Key words: *ITS*, *matK*, morphological characters, Namibia, South Africa, speckled aloes, taxonomy, typification

Introduction

The genus *Aloe* Linnaeus (1753: 319) in its more restricted definition (sensu Grace *et al*. 2013a, Manning *et al*. 2014) comprises around 610 taxa (including subspecies and varieties) of which at least 158 species (173 taxa, including subspecies and varieties) occur in the Flora of Southern Africa region [FSA = Botswana, Lesotho, Namibia, South Africa, and Eswatini (previously Swaziland)]. Several genera, which all occur in the FSA-region, were segregated from *Aloe* s.str. (Grace *et al*. 2013a, Manning *et al*. 2014). These are *Aloiampelos* Klopper & Gideon F.Sm. in Grace *et al*. (2013a: 10) with seven species and 10 taxa, *Aloidendron* (Berger 1905: 56) Klopper & Gideon F.Sm. in Grace *et al*. (2013a: 9) with five species, *Aristaloe* Boatwr. & J.C.Manning in Manning *et al*. (2014: 69) with a single species, *Gonialoe* Boatwr. & J.C.Manning in Manning *et al*. (2014: 69) with three species [a fourth species has recently been described from southern Angola, thus from outside the FSA-region (Hanáček *et al*. 2023)], and *Kumara* Medikus (1786: 69) with two species. The total number of aloes (in the broad sense) in the FSA-region thus amounts to around 176 species (194 taxa). South Africa has an exceptionally diverse aloe flora (leaf succulents classified in the genera mentioned above), and harbours the largest number of aloes of any country in the world (159 species or 177 taxa; of which 141 species or 156 taxa are in the genus *Aloe* s.str.). Aloes tend to be morphologically variable and often geographically restricted. Although a few species are widespread, most aloes have localised distribution ranges. This makes them exceptionally vulnerable to threats such as habitat destruction and illegal collecting. Around 50% of all aloes are considered to be taxa of conservation concern (IUCN Red List of Threatened Species 2023, Raimondo *et al*. 2009, Rakotoarisoa *et al*. 2014) and all species of aloe [except for *A. vera* (Linnaeus 1753: 320) Burman (1768: 83)] appear on CITES (Convention on the International Trade in Endangered Species of Wild Fauna and Flora) Appendices (CITES 2023) [Finished products of *A. ferox* Miller (1768: 22) are also exempt from CITES regulations]. As a result of multiple risks, such as those mentioned above, the conservation of aloes and their habitats, especially aloe diversity hot spots, is critical. A robust taxonomic classification is also required if conservation efforts are to adequately deal with the observed diversity.

The genus *Aloe* s.str. is fraught with taxonomic anomalies and several species complexes are known (see for example Smith *et al*. 2012a on the summer-flowering species of maculate aloe). This makes a clear distinction of the individual species, subspecies, and varieties challenging at some localities (Reynolds 1950). Furthermore, at infrageneric ranks different authors often treat the same group of aloes differently (further discussed below under 'Historical review and problem statement'). Species complexes include taxa that grade into each other: some populations are easy to assign to a single species within the complex, but others show characters of related neighbouring taxa and individual plants are difficult or even impossible to identify with certainty (see for example Smith *et al*. 2020, 2021, Smith 2022). Such a species complex can either be lumped under one broad concept (an easy but very unsatisfactory solution), or split into two or more segregate species that often may be difficult to distinguish in certain parts of their natural distribution ranges (Smith *et al*. 2008, Smith *et al*. 2012a, b). Differing treatments of aloe groups in the historically influential literature on the genus, such as Berger (1905, 1908), Schönland (1907), and Reynolds (1950), is a recurring problem and present in several aloe taxa at infrageneric ranks. Specifically problematic groups that contain species complexes include *A.* sect. *Purpurascentes* Salm-Reifferscheid-Dyck (1842: 22), *A.* sect. *Pictae* Salm-Reifferscheid-Dyck (1837: 23), and *A.* sect. *Leptoaloe* Berger (1908: 164). These are, however, not the only sections of *Aloe* where the existence of species complexes results in different opinions on the demarcation of infrageneric taxa amongst aloe taxonomists and enthusiasts.

Aloe sect. *Purpurascentes*, or the speckled aloes (Van Wyk & Smith 1996, 2014; not to be confused with the maculate aloes, which are members of *A.* sect. *Pictae*), are characterised by somewhat ensiform leaves that are more or less white-spotted on both surfaces. The spots on the leaves are sometimes lost with age. In the case of *A. gariepensis* Pillans (1933b: 213), for instance, spots are often absent in mature plants, but the leaves are then distinctly lineate. Rosettes can be solitary or clustered in dense groups, and range from acaulescent to plants with stems of up to 2 m tall. Inflorescences are usually simple or few-branched, but can be up to 8-branched in *A. khamiesensis* Pillans (1934: 25). Racemes are elongated-cylindric to -conical with cylindric to cylindric-trigonous flowers that lack a basal swelling (Reynolds 1950, Van Wyk & Smith 1996, 2014, Glen & Hardy 2000).

Most members of *A.* sect. *Purpurascentes* are viewed as belonging to a species complex and have been treated differently in various publications (Reynolds 1950, Van Wyk & Smith 1996, 2014, Glen & Hardy 2000, Carter *et al*. 2011). Considerable uncertainty exists as to the taxonomic status and exact distribution ranges of the various infrageneric entities, especially since several previously unrecorded (and often unplaced) populations of aloes that clearly belong to this section were recently found.

This paper presents the results of a taxonomic revision of *A.* sect. *Purpurascentes* that incorporates, inter alia, macro-morphological characters, and a synthesis of evidence from phytogeography, chemotaxonomy, palynology, and seed morphology.

Very few infrageneric groups in *Aloe* have been recently revised (Lavranos 2004, Van Jaarsveld 2010). Surprisingly, molecular evidence has only once before been utilised in the taxonomic revision of a group of aloes (see Ellis 2013). *Aloe* sect. *Purpurascentes* thus presents a good test case for assessing the taxonomic value of DNA barcodes for the recognition of species and infraspecific taxa in aloes.

Historical review and problem statement

The genus *Aloe* was described by Linnaeus (1753: 319) and then comprised several taxa that are now included in other genera of Asphodelaceae subfam. Alooideae, as well as in *Kniphofia* Moench (1794: 631, Asphodelaceae subfam. Asphodeloideae). Attempts have been made in the past to describe segregate genera for certain groups of aloes—over two dozen generic names are available for taxa included in *Aloe* (see for example Smith *et al*. 1994 and Klopper *et al*. 2010)—but these were generally not upheld, mostly because many were deemed to be artificial assemblages. In recent decades, molecular tools were used to build a phylogenetic classification for the aloes, and resulted in more changes being proposed at generic rank (Grace *et al*. 2013a, Manning *et al*. 2014). These changes did not affect the placement of *A.* sect. *Purpurascentes* within a more narrowly defined genus *Aloe*.

The section name, *Aloe* sect. *Purpurascentes*, was first published by Salm-Reifferscheid-Dyck (1842) and probably refers to the fact that leaves are often tinged with purple when fresh (Glen & Hardy 2000), or to the exudate of *A. succotrina* Weston (1770: 5), the oldest species name in the section, that dries a deep purple.

In some of the most recent literature, *A.* sect. *Purpurascentes* has been treated as comprising six recognised species, namely *A. framesii* Bolus (1933: 140), *A. gariepensis*, *A. khamiesensis*, *A. knersvlakensis* Marais (2010: 96), *A. microstigma* Salm-Reifferscheid-Dyck (1854: §26 f.4), and *A. succotrina* (Carter *et al*. 2011, Grace *et al.* 2011). Other authors recognise fewer species, some with infraspecific taxa (e.g., Glen & Hardy 2000). Two further aloes have been debatably associated with this section, namely *A. pictifolia* Hardy (1976: 62) (Van Wyk & Smith 1996, 2014, Carter *et al*. 2011) and *A. chlorantha* Lavranos (1973: 87) (Carter *et al.* 2011). Members of *A.* sect. *Purpurascentes* all occur in southern and western South Africa, with two of the currently recognised species entering southern Namibia

(Fig. 1) (Reynolds 1950). At present, there is no published molecular evidence to support the coherence of the section. In the phylogeny presented by Grace *et al*. (2015), *Aloe succotrina* is recovered on a single taxon branch, far removed from *Aloe pictifolia*. However, no other members of core *A*. sect. *Purpurascentes* were included in that study.

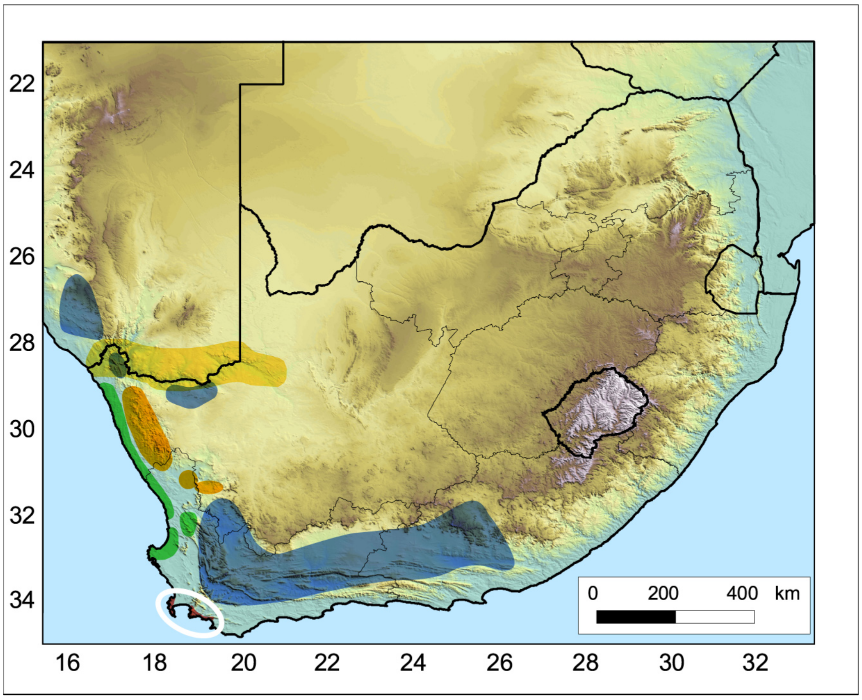


FIGURE 1. Known distribution of the members of *A.* sect. *Purpurascentes* (green—*A. framesii*; yellow—*A. gariepensis*; orange—*A. khamiesensis*; blue—*A. microstigma*; red in white circle—*A. succotrina*).

Aloe succotrina

Aloe succotrina was described by Richard Weston (1770: 5) based on an illustration in Commelin (1697). It is restricted to mountain slopes on the Cape Peninsula with a disjunction to the Steenbras River mouth, Kleinmond, and Hermanus in the Western Cape, South Africa. It grows in mountain fynbos on steep cliffs and rocky slopes comprised of Table Mountain Sandstone, in a high winter-rainfall region with a Mediterranean-type climate, and always generally close to the sea (Klopper 2014).

The placement of *A. succotrina* in *A.* sect. *Purpurascentes* has been questioned (Kemble 2011). It is argued that *A. succotrina* might have closer affinities with *A. arborescens* Miller (1768: 3) from *A.* sect. *Arborescentes* Salm-Reifferscheid-Dyck (1849: 26) than it has to other members of *A.* sect. *Purpurascentes*. Reasons for this include a strong resemblance to *A. arborescens* in terms of the size and shape of the floral bracts, the overall appearance of the racemes, the white marginal teeth on the leaves, and the appearance of the seed (S.J. Marais, pers. comm.). Furthermore, *A. succotrina* has a confused history and wrong synonymy that is probably rivalled by no other aloe (Guiglielmone *et al*. 2009, Walker *et al*. 2015). This is mostly due to early authors incorrectly assuming that this plant is from the Indian Ocean island of Socotra (Reynolds 1950, Guglielmone *et al*. 2009).

Historically, disjunct distributions of the species that also exhibit morphological differences, were considered to be separate species: plants growing on the Cape Peninsula were regarded as *A. succotrina*, while plants from Hermanus, Kleinmond, and other mainland localities were treated as *A. purpurascens* (Aiton 1789: 466) Haworth (1804: 20). Haworth (1804) gives the differences as follows: *A. succotrina*—leaves ensiform, virescent with tips subincurved, marginal teeth numerous, small, white; *A. purpurascens*—leaves ensiform, glaucous with tips recurved, marginal teeth white. Haworth (1804) also remarked under both names that the stems of these aloes become dichotomous with age, but lacks the radical offsets present in other members of *A.* sect. *Grandiflorae* Haworth (1804: 14), in which he included them. Reynolds (1950) concluded that these are merely geographical variants in growth forms and do not warrant distinction at either specific or varietal level.

Aloe microstigma

Aloe microstigma was described and illustrated by Prince Salm-Reifferscheid-Dyck (1854: §26 f. 4). It is the most widespread of the aloes in the section and has a disjunct distribution: it is widespread in the western parts of the Eastern Cape, the central areas of the Western Cape, and just into the Northern Cape in the Tankwa Karoo, and disjunctly in the far Northern Cape just south of the Orange River, South Africa, as well as in southwestern Namibia. It grows on rocky outcrops, sometimes on steep slopes, in karroid, desert, semidesert, and Namaqua Broken Veld vegetation (Klopper 2014).

Aloe microstigma is closely related to *A. khamiesensis* from western South Africa (Van Wyk & Smith 1996, 2014) and *A. gariepensis* from the Orange River Valley in the Northern Cape, South Africa, and southern Namibia (Glen & Hardy 2000, Carter *et al*. 2011). *Aloe khamiesensis* is in fact treated as conspecific with *A. microstigma* by certain authors (e.g., Glen & Hardy 2000), while plants attributed to the eastern form of *A. gariepensis* (between Keimoes, Northern Cape, South Africa, and Warmbad, Namibia) are considered by some to be a possible variant of *A. microstigma* (e.g., Carter *et al*. 2011). *Aloe pictifolia* a cliff-dweller from the Eastern Cape, South Africa, is also at times considered to be a close ally (Carter *et al*. 2011).

Aloe brunnthaleri A.Berger ex Cammerloher (1933: 131) is regarded to be a yellow-flowering form of *A. microstigma* (Reynolds 1950). *Aloe brunnthaleri* was used as a provisional name by Alwin Berger for a plant collected in the early 1900s by Joseph Brunnthaler near Matjiesfontein in the Western Cape, South Africa. The name appeared in a catalogue, *Collection des Plantes Grasses du Jardin Botanique de Monaco*, in 1921. It was, however, never formally published by Berger and thus remained a *nomen nudum*, until Herman Cammerloher validated the name based on the description of a plant that flowered in the botanical garden of the University of Vienna in January of 1930 and 1933 (Cammerloher 1933). This yellow-flowered form is known from several localities north of the Swartberg in the Western Cape (e.g., at Matjiesfontein, Laingsburg, and Beaufort West) and the Northern Cape (e.g., at Sutherland and Fraserburg), South Africa, and more recently also reported from the Gannaga Pass in the Tankwa Karoo National Park, Northern Cape, South Africa (Bester *et al*. 2012).

Namibian plants currently assigned to *A. microstigma* were previously described as *A. juttae* Dinter (1923: 159), but for a long time this name has been treated as a synonym of *A. microstigma* (Reynolds 1950). Because of morphological differences between *A. juttae* and *A. microstigma*, as well as the outlier distribution range of the Namibian plants, certain people feel strongly that these Namibian plants should be recognised at specific or subspecific level (J.J. Lavranos, pers. comm.). Indeed, the disjunction in the distribution ranges of these populations of *A. microstigma* has long been a source of uncertainty (Kemble 2011). Suggestions have even been made that the Namibian populations of *A. microstigma* might have closer affinities to *A. framesii*, because of their geographical proximity and the fact that both entities often form large groups (according to W.J. Jankowitz and B. Kemble, pers. comms.).

However, the gap in the distribution has recently been reduced: plants believed to be *A. microstigma* were recently found on the Hunsberg (Namibia), in the Richtersveld, and on several inselbergs in Bushmanland, Northern Cape, South Africa (Kemble 2011; E.J. van Jaarsveld and P. Desmet, pers. comms.). Plants resembling *A. microstigma* occur on several inselbergs in the Bushmanland region of the far Northern Cape, South Africa; these include Achab, Aggeneys, Gamsberg, Namies, Witberg (P. Desmet, pers. comm.), and the Slangberg (J.C. Kruger, pers. comm.). Plants are confined to the crests of south-facing aspects and occur as scattered individuals and do not form discrete populations (P. Desmet, pers. comm.). These plants apparently do not differ from *A. microstigma* in any significant way, although they do form clumps (J.J. Lavranos, pers. comm.), suggesting a close affinity with the Namibian form (i.e., *A. juttae*). In some localities plants occur as solitary rosettes, and are believed to mix with *A. gariepensis* that is present on the north facing slopes of these inselbergs (P. Desmet, pers. comm.).

Williamson (2000) reported the occurrence of *A. microstigma* in the Richtersveld, Northern Cape, South Africa, stating that 'the aloe is restricted to high ridges along the summit of the Stinkfonteinberge and the high eastern mountains overlooking the Orange River'. This aloe is not common in the Richtersveld and only two colonies are known from this region: one on the eastern aspect towards the summit of Cornellsberg, where plants grow on fairly rocky terrain of the Stinkfontein Subgroup amongst Richtersveld montane vegetation; and the second about halfway down the Klein Hellskloof, where plants grow among rocks of the Richtersveld Suite (G. Williamson, pers. comm.). There are also two known populations in the Sperrgebiet of southwestern Namibia: in a population towards the summit of the Heiob Mountain, plants grow on the eastern aspect; the population from the Rooiberg, just east of the Aurusberge, grows on the southern aspect (G. Williamson, pers. comm.). Plants resembling *A. microstigma* were also recently found at the eastern end of the Hunsberg in southern Namibia (E.J. van Jaarsveld, pers. comm.).

A specimen at Herb. NBG (*A. Jooste 46*, collected 7 August 1993) from the Akkerendam Nature Reserve just north of Calvinia in the Northern Cape, South Africa, was identified as '*Aloe* cf. *khamiesensis* (description inadequate)'. However, this locality is outside the generally accepted distribution range of this aloe (even though aberrant forms of *A. khamiesensis* have been reported from near Calvinia). The Akkerendam Nature Reserve was visited in July 2010 to search for this population. Despite the NBG specimen label information describing the occurrence as 'locally common', only one plant was found, with the remains of a second dead plant close-by. No fruit were formed in the 2010 season, suggesting isolation from other plants (aloes are generally self-incompatible). Although the NBG specimen label indicates that no fruit were present, there are three capsules on one of the inflorescences that form part of this specimen, which suggests that the second plant was probably still alive and also flowering in 1993. The plant grows on a low rocky ridge on the plain (not on the footslopes of the Hantamsberg) in dwarf karroid shrubland. It is geographically relatively close to populations related to *A. khamiesensis* near Loeriesfontein to the northwest and populations of *A. microstigma* on the Bloukrans Pass just south of Calvinia. Morphologically the Akkerendam (Calvinia) plants more closely resemble *A. microstigma* and not *A. khamiesensis*, as was suggested by the determination on the NBG specimen.

Similar plants occur elsewhere in the Calvinia area, where huge numbers of plants are dying in some of the populations (F. van der Merwe, pers. comm.). Reasons for the mass die off could possibly be attributed to damage caused by aloe snout beetle activity, but more likely due to herbivory by porcupines (A.J. Urban, pers. comm.).

Plants in full flower resembling either *A. framesii* or *A. microstigma* were found near Kagga Kamma Nature Reserve in the Swartruggens Mountains (Cederberg region) in the Western Cape, South Africa, in early August 2012 (M. Koekemoer, pers. comm.).

It has been suggested by Mottram (2013) that the correct name for *A. microstigma* is *A. perfoliata* Linnaeus (1753: 319). According to the *Index Nominum Genericorum* (Farr & Zijlstra 1996+), the latter name was also designated as the type of the genus name *Aloe* by Britton & Millspaugh (1920). Given the confused history and uncertainty of the application of the name *A. perfoliata*, the proposal of Mottram (2013) should perhaps be treated with circumspection. *Aloe perfoliata* has been recorded as an imperfectly known taxon by Reynolds (1950), even though there is a supposed type specimen annotated by Linneaus. Reynolds (1950) specifically referred to the Linneaus specimen (LINN 442.1) as 'type' material, thus effectively designating it as the lectotype of the name *A. perfoliata* (Art. 7.11, Turland *et al*. 2018). Glen & Hardy (2000) applied this name to a broad concept in which they included material today treated as (at least) three species, namely *A. mitriformis* Miller (1768: ALO, nr. 1), *A. comptonii* Reynolds (1950: 382), and *A. distans* Haworth (1812: 78), without a clear explanation for the reason behind this decision and superfluously lectotypified the name with plate 17 of Dillenius in *Hortus Elthamensis* 1: 21, t.17, fig.19 (1732). Mottram (2013) erroneously regarded another Dillenius plate in *Hortus Elthamensis* 1: 18–19, t.15, fig.16 (1732) as the lectotype for *A. perfoliata*. This view is based on citation of plate 15 by Scopoli (1783). However, since Scopoli (1783) did not specifically refer to the illustration as 'type' or an equivalent term, this is not a valid lectotypification (Art. 7.11, Turland *et al*. 2018) (for more details see Klopper *et al*. 2016). According to his interpretation of the lectotype of the name *A. perfoliata*, Mottram (2013) attempted to illustrate that plate 15 of Dillenius (1732) represents what we now call *A. microstigma*. The arguments provided by Mottram (2013) are not entirely convincing and the name *A. microstigma* is preferred for the purposes of this present study, until further clarity on the taxonomic identity of *A. perfoliata* can be obtained.

Aloe framesii

Aloe framesii was described by Louisa Bolus (1933: 140) from a specimen collected at a population to the north of Port Nolloth in 1929 by Percy Ross Frames. It occurs from Port Nolloth in the Northern Cape, south to Saldanha in the Western Cape, South Africa. It has not yet been recorded from bordering southern Namibia. A form of *A. framesii* (see *A. amoena* further on) also occurs in the Cederberg near Clanwilliam, Western Cape, South Africa. *Aloe framesii* grows on sandy coastal flats and on sandstone outcrops (Klopper 2014).

Its closest relatives are thought to be *A. khamiesensis*, from western South Africa (Reynolds 1950, Carter *et al*. 2011) or *A. microstigma* from southern and western South Africa (Glen & Hardy 2000). It is treated by some authors as a subspecies of the latter, namely *A. microstigma* subsp. *framesii* (L.Bolus) Glen & Hardy (2000: 107).

Aloe amoena Pillans (1933a: 168) from the Clanwilliam area, Western Cape, South Africa, is generally regarded as a southern and more inland form of *A. framesii* (Reynolds 1950). This species was decribed as being allied to *A. microstigma*, but differs in having branched stems, larger more attenuate leaves (30–40 × 5.5–7.0 cm) and larger flowers (35–40 mm long) (Pillans 1933a). The Clanwilliam, Agter Pakhuis, and Cederberg populations of *A. framesii* represent this form.

Aloe gariepensis

Aloe gariepensis was described by Neville S. Pillans (1933b: 213) from a population near Warmbad, Namibia that he visited in 1931. This aloe is restricted to both sides of the Orange River Valley from Grootderm to around Keimoes in the Northern Cape, South Africa, and as far north as Warmbad in Namibia. It grows in rock cracks on steep rocky slopes, often facing the Orange River in the driest part of its course (Klopper 2014). Its closest relative is *A. microstigma* from south-central and western South Africa. It is sometimes regarded as possibly only a robust form of *A. microstigma* (Carter *et al*. 2011).

The form with consistently greenish yellow flowers and stemless rosettes of strongly incurved, heavily striated leaves from the extreme western reaches of the Orange River are thought by some to constitute a separate species or subspecies (Carter *et al.* 2011; J.J. Lavranos, pers. comm.). Others are of the opinion that the harsher environmental conditions in the lower reaches of the Orange River Valley are responsible for this variation and that it does not warrant taxonomic recognition (Reynolds 1950; E.J. van Jaarsveld, pers. comm.).

The designation '*Aloe gariusana*' is mentioned by Dinter (1928) in the account of his journeys in Namibia (then South West Africa). He had found this aloe with coppery red rosettes of striped leaves near Warmbad and near Garius. However, this 'name' was never validly published and it remains a *nomen nudum* that was taken up in the synonymy of *Aloe gariepensis* by Reynolds (1950).

Aloe khamiesensis and *Aloe knersvlakensis*

Aloe khamiesensis was described by Neville S. Pillans (1934: 25) from a specimen he collected at Kamieskroon in 1922. It occurs from Steinkopf south to the Kamiesberg (its type locality), Northern Cape, South Africa. It is also present in the Bokkeveld Mountains north of Nieuwoudtville and the Hantamsberg near Calvinia in the Northern Cape, South Africa, but is absent from Namibia. This aloe grows in mountainous country on rocky slopes and outcrops, almost exclusively on granitoid rocks (Klopper 2014). It is closely allied to *A. microstigma* from south-central and western South Africa and *A. framesii* from western South Africa (Reynolds 1950, Carter *et al*. 2011). Some authors consider it to be conspecific with *A. microstigma* (Glen & Hardy 2000), while others recognise it as distinct (Carter *et al*. 2011, Grace *et al*. 2011).

Disjunct populations between Loeriesfontein and Calvinia, Northern Cape, South Africa, were reported on by Van Wyk & Smith (1996, 2014) as an isolated form of *A. khamiesensis*. Reynolds (1950) also refers to unconfirmed reports of this species occurring in the Hantamsberg, Calvinia Division. One population on the plains near the farm Holrivier was visited in July 2010, but several extensive populations were witnessed on the crests of ridges further north towards Loeriesfontein. Another population is known from the Hantam National Botanical Garden near Nieuwoudtville, Northern Cape, South Africa, and specimens from Meulsteenvlei west of Nieuwoudtville are lodged at Herb. PRE (*Watermeyer in Marloth 6829 & 12937*). The Calvinia–Loeriesfontein plants also show close affinities to *A. knersvlakensis* and may be closer to the latter taxon in terms of morphology, flowering time, and geographical distribution range.

Aloe knersvlakensis was discovered and described by Sarel J. Marais (2010: 96) from the Knersvlakte. It is currently only known from its type locality near Kliprand in the Knersvlakte, Western Cape, South Africa, where it grows on north-facing quartzitic sandstone ridges and medium slopes (Klopper 2014). This aloe clearly belongs in *A.* sect. *Purpurascentes* (Marais 2010, Carter *et al*. 2011). However, doubts have been raised as to its recognition at specific level. One view is that it is an outlying population and form of *A. framesii* (J.J. Lavranos, pers. comm.), while B. Kemble (pers. comm.) regards it as intermediate between *A. microstigma* and *A. khamiesensis*.

Species doubtfully included in *Aloe* sect. *Purpurascentes*

Aloe chlorantha was described from the Fraserburg district by John J. Lavranos (1973: 87). It is confined to an area around Fraserburg in the Northern Cape, South Africa. It commonly grows wedged among dolerite boulders on the summits and north-facing aspects of a few ridges in the upper Groot Karoo (Klopper 2014). This aloe shows morphological affinities with *A. broomii* Schönland (1907: 137) from central South Africa and with *A. comosa* Marloth & A.Berger in Berger (1905: 86) from the Western Cape, South Africa (Lavranos 1973). It is, however, considered by some to be most closely related to *A. microstigma* from south-central and western South Africa (Carter *et al*. 2011; J.J. Lavranos, pers. comm.). Chemistry of the leaf compounds also show affinities with both *A. broomii* and members of *A.* sect. *Purpurascentes* (Van Wyk & Smith 1996, 2014, Viljoen 1999). This intermediate position in terms of both morphology and chemistry could indicate that *A. chlorantha* may have arisen as a hybrid between *A. broomii* and *A. microstigma*.

Aloe pictifolia was described by David S. Hardy (1976: 62) from a specimen collected by G.X. Marais from near Patensie. It is endemic to Cape sourveld vegetation in the Humansdorp area of the Eastern Cape, South Africa, where it grows on steep rocky quartzitic sandstone cliffs (Klopper 2014). The taxonomic affinities of this aloe are uncertain. Glen & Hardy (2000) includes it in *Aloe* sect. *Echinatae* Salm-Reifferscheid-Dyck (1837: 15) with its closest relative being *A. krapohliana* Marloth (1910: 408) from western South Africa (Hardy 1976). On the other hand, Van Wyk & Smith (1996, 2014) and Carter *et al*. (2011) consider it to be closest to *A. microstigma* from southern and western South Africa, and other members of *A.* sect. *Purpurascentes*. Associated with this latter view, some consider it to be a form of *A. microstigma* that is adapted to a cremnophytic habit.

Materials

An effort was made to obtain morphological and molecular information from as many populations of each member of *A.* sect. *Purpurascentes* as possible. Material for molecular study was collected in the field. At least two individuals from each population were sampled. Voucher specimens were deposited at the National Herbarium, Pretoria (PRE), with duplicates sent to a representative herbarium of the province or country in which it was collected according to collecting permit conditions. Herbarium codes follow Thiers (2023 [continuously updated]).

For the macro-morphological study, measurements were taken from both existing herbarium specimens at Herbs PRE and NBG, and from additional specimens collected by the authors. In most cases measurements from the additional specimens obtained from sampled populations were also taken in the field. Measurements obtained from preserved and living specimens are included in the range of dimensions provided in the taxon descriptions in the taxonomic revision.

Additional specimens from Herbs BLFU, BOL, GRA, K, NMB, SAM, and WIND, were also evaluated against the taxon concepts adopted in this study to determine the variation and complete distribution ranges of the taxa.

For the molecular study, multiple accessions of taxa in *A.* sect. *Purpurascentes*, as well as taxa with affinities to the group, were included in the analyses. In the phylogenetic analyses, taxa from neighbouring sections within *Aloe* were also included to assess monophyly in *A.* sect. *Purpurascentes*. *Kniphofia* was used as the outgroup in all these analyses. Internal Transcribed Spacers (*ITS*) 1 and 2, and the region coding for Maturase Kinase (*matK*), a plant barcoding region, were selected as markers representing the nuclear ribosomal and plastid plant genomes, respectively. Both regions are widely used to infer phylogenies due to the ease with which they are sequenced, and the presence of phylogenetically informative polymorphisms (Lahaye *et al*. 2008, China Plant BOL Group 2011). Sequence data for *A. ferox* and *Aristaloe aristata* (Haworth 1825: 280) Boatwr. & J.C.Manning in Manning *et al*. (2014: 69) [=*Aloe aristata* Haworth (1825: 280)] were obtained from the National Center for Biotechnology Information (NCBI) nucleotide database (http://www.ncbi.nlm.nih.gov/).

Only *matK* was used to draw the Minimum Spanning Network due to the large number of ambiguous bases in the *ITS* sequences, and only the ingroup-*Purpurascentes* taxa were included in these results to infer affinities among the taxa.

Herbarium vouchers that were included in the macro-morphological, molecular, and combined analyses, as well as other specimens examined are listed under the relevant taxa. Here the respective uses of the specimens in the various analyses are indicated by a superscript letter following the herbarium code: macro-morphological (^{m}), molecular (^{g}), and combined analyses (^{c}).

Methods

Macro-morphology

Measurements were taken to represent characters that historically have been used to delimit taxa within *A.* sect. *Purpurascentes*, namely branching of the inflorescence, relative length of the floral bracts and pedicels, and flower length. Additional characters that are regularly used to delimit groups within *Aloe* were also included, namely leaf marginal teeth length and spacing, as well as leaf width. Accurate measurements of leaf length are not possible from herbarium vouchers.

Other characters that would be useful to include in these analyses are: stem characters (presence and length), rosette characters (solitary or suckering), and further flower characters (e.g., colour). However, as with leaf length mentioned above, the latter characters can not be reliably obtained from most herbarium specimens. Therefore, to keep the dataset as representative as possible, these characters were excluded from the macro-morphological analyses. Nonetheless, where available, these characters were considered in the delimitation of taxa, together with information obtained from collaborators regarding populations that were not visited or that could not be located.

Measurements were recorded in an Excel spreadsheet. A Principal Component Analysis (PCA) was carried out on the data in Excel using an add-in function designed by Prof. Wagner A. Kamakura, Rice University, Houston, Texas, United States of America (available for free download from http://wak2.web.rice.edu/bio/WagnerKamakuraDownloads.htm). Three components were analysed and the components were rotated as recommended. Since *A. gariepensis* and *A. microstigma* consistently have unbranched inflorescences, this character was excluded from the PCA analyses for these species. Scores for each specimen along the extracted components were plotted on a scatterplot diagram. The PCA analysis was run for the entire dataset, and also for each species group separately (see Figs 2 & 3).

Note that for the sake of brevity representatives of *A.* sect. *Purpurascentes* are often referred to as “speckled aloes” in this paper, to so also distinguish them from representatives of *A.* sect. *Pictae*, the ‘true’ spotted aloes.

Seed morphology

Seeds can have potential diagnostic value in certain groups of aloes, but this character is likely more useful at infrageneric level and not at species level (Kamstra 1968, 1971). For this reason, the seed characters of *A.* sect. *Purpurascentes* were not investigated further in detail in the present study. Information related to the appearance of seeds presented in the section on seed morphology under ‘Characters and states’ below is thus sourced mostly from the literature.

Palynology

Steyn *et al*. (1998) demonstrated that pollen morphology in *Aloe* is of limited use at infrageneric level and likely not taxonomically significant at species level. Nonetheless, palynological information drawn from the literature is presented under ‘Characters and states’ below.

Chemistry

General information on the leaf chemistry of members of *A.* sect. *Purpurascentes* and other related taxa was obtained from a detailed literature study.

Molecular data

For DNA extraction, sequencing and alignment, methods followed protocols previously described by Grace *et al*. (2013b, 2015). Total genomic DNA was extracted and purified from ± 0.03 g silica-dried leaf material using a Qiagen TissueLyser and Qiagen DNeasy Plant Mini Kit (250) (Qiagen, Copenhagen, Denmark).

The *ITS* region (402 base pairs) was amplified using the ITS-4 (forward; TCCTCCGCTTATTGATATGC) and ITS-5 (reverse; GGAAGTAAAAGTCGTAACAAGG) primers (White *et al*. 1990). DNA solutions for polymerase chain reaction (PCR) were prepared in 25 µl volumes. This was achieved by combining 5 µl DNA template with 6 µl Promega 5x Green GoTaq Flexi Buffer, 1 µl of 0.04% bovine serum albumin (BSA), 1 µl dimethyl sulfoxide (DMSO), 1.5 µl of 25 mM magnesium chloride ($MgCl_2$), 0.5 µl deoxynucleotide triphosphates (Promega DNTP mix), 0.1 µl Promega GoTaq Flexi polymerase, 1 µl of each primer (forward and reverse, 25% v/v), and 7.9 µl double distilled water (dd H_20).

The *matK* region (836 base pairs) was optimised by trials of primer pairs, including matK-XF (forward; TAATTTACGATCAATTCATTC) and matK-5R (reverse; GTTCTAGCACAAGAAAGTCG) primers (Ford *et al*. 2009). Hereafter, primers matK-19F (forward; CGTTCTCATATTGCACTATG; Mike *et al*. 1999) and matK-5R were chosen as the optimal pair for amplifying the DNA from members of *A*. sect. *Purpurascentes*. DNA solutions for polymerase chain reaction (PCR) were prepared in 25 µl volumes. This was achieved by combining 2 µl DNA template with 12.5 µl Promega 5x Green GoTaq Flexi Buffer, 0.25 µl Promega GoTaq Flexi polymerase, 0.5 µl of each primer (forward and reverse, 25% v/v), and 9.25 µl dd H_20.

Thermal cycling was done with a Veriti 96 Well Thermal Cycler (Applied Biosystematics). For *ITS* initial denaturation was done at 94°C for four minutes. This was followed by 33 cycles of denaturation at 94°C for one minute, annealing at 50°C for one minute, elongation at 72°C for one minute and final extension at 72°C for two minutes. For *matK* initial denaturation was done at 94°C for four minutes, followed by 32 cycles of denaturation at 94°C for one minute, annealing at 50°C for one minute, elongation at 72°C for 2.5 minutes, and final extension at 72°C for seven minutes.

PCR products were purified using a Qiagen QIAquick PCR Purification Kit (250) (Qiagen, Copenhagen, Denmark). Cleaned PCR products were sequenced by Eurofins MWG Operon, Germany. The resulting electropherograms were edited and assembled using Sequencher 4.8^{TM} (Gene Codes Corporation, Ann Arbor, USA) and aligned using MUSCLE (Edgar 2004) in Geneious V7.1.7 (Biomatters, Auckland, New Zealand), with minor manual adjustments.

For gene trees a rapid maximum likelihood approach implemented in RAxML V8 (Stamatakis 2014) was used to reconstruct tree topologies for each data partition (*ITS* and *matK*). The tree search was conducted under standard settings for the recommended GTR model with 1000 bootstrap replicates. The Cyber Infrastructure for Phylogenetic Research (CIPRES) computation facility was used for all analyses (www.phylo.org; Miller *et al*. 2010). No supported conflicts were observed in the resulting gene tree topologies, and a tree search using the combined dataset (1238 base pairs) was conducted using the same parameters in RAxML.

The phylogenetic tree was evaluated by comparing clusters of populations to current species concepts within *A*. sect. *Purpurascentes*, as well as to the revised classification presented in this paper. This approach is somewhat similar to that used by Fazekas *et al*. (2008) to investigate the value of multilocus barcodes in plants. It is based on the notion that there should be a high degree of correlation between the support for species monophyly and the ability of barcode markers to distinguish species. The distinction of a species from closely related ones is determined by the robustness of the branch subtending a monophyletic cluster of populations that represents a single species (Fazekas *et al*. 2008).

The results were also visualised with a distance-based minimum spanning network generated in ARLEQUIN 2.0 (Schneider *et al*. 2000). Minimum Spanning Networks for haplotypes (Excoffier *et al*. 1992) were constructed to visualise genealogical relationships, based on pairwise differences obtained from ARLEQUIN 2.0. Number of nucleotide differences between the haplotypes is indicated, as well as the minimum number of possible mutations that can account for these differences. The number of mutations was calculated based on the assumption that differences in adjacent nucleotides most likely represents a single mutation, rather than multiple mutations at the same site. This is especially so for deletions leading to the removal of aminoacids from the resulting protein.

Combined molecular and macro-morphological analysis

A combined analysis of morphological characters and molecular data was conducted. For this purpose, a total of three morphological characters (habit, inflorescence branching, and floral bract:pedicel length) were coded for the relevant specimens (64 accessions representing seven species in the core *Purpurascentes* clade) in a data matrix based on their discrete character states. The characters and character states used in this analysis is explained in the legend of Fig. 6. Nine taxa outside *A*. sect. *Purpurascentes* and five taxa for which morphological data were missing, were pruned from the best-scoring maximum likelihood tree in Mesquite (Maddison & Maddison 2015) while 10 additional accessions of core *Purpurascentes* taxa were added to each of the respective clades. Each of the three characters were mapped on the resulting tree and the ancestral character states at internal nodes reconstructed under the parsimony optimisation using default settings in Mesquite.

Taxonomy and nomenclature

Citation of authors of taxon names follows IPNI (2023+), but in the notation required by *Phytotaxa*. Nomenclatural matters accord with the Shenzhen Code (Turland *et al*. 2018).

Macro-morphology results

Members of *Aloe* sect. *Pupurascentes* are often referred to as speckled aloes (Van Wyk & Smith 1996, 2014). They differ from the maculate or spotted aloes (*Aloe* sect. *Pictae*) by having tubular flowers without a distinct basal swelling, as well as leaves that are longer and narrower than those of the spotted/maculate aloes. Furthermore, leaves of the speckled aloes often turn a distinct reddish brown, even under favourable conditions (Van Wyk & Smith 1996, 2014).

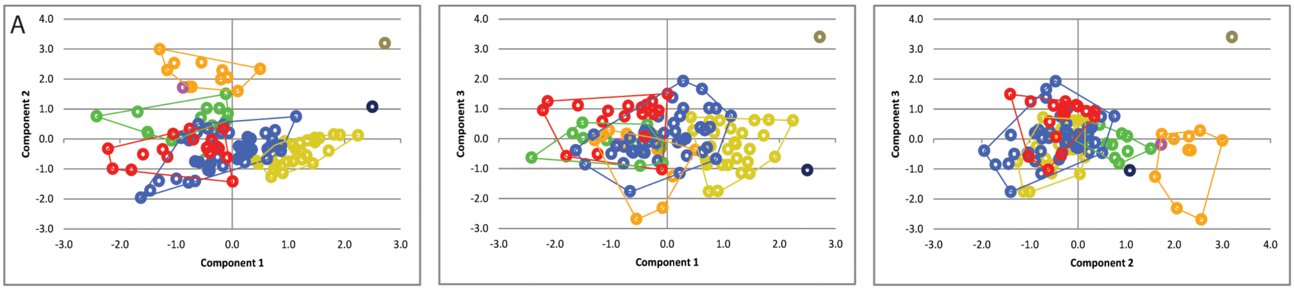
Morphological characters that historically have been used to delimit taxa within *A.* sect. *Purpurascentes* are branching of the inflorescence, relative length of the floral bracts and pedicels, flower colour and length, and to a lesser extent the growth form (Reynolds 1950, Glen & Hardy 2000). Other characters that are regularly used to delimit groups within *Aloe* include leaf dimensions and proportions, marginal teeth length and spacing, and the length of the sterile bracts. As many aloes are range-restricted, geography and habitat also play an important role in the delineation of several taxa within the genus.

The characters of an aloe can vary considerably throughout its distribution range, owing to, for example, habitat influences. In this regard, certain characters are more flexible than others. Species delimitation is also challenging when sympatric taxa grade into each other, likely due to hybridisation (Reynolds 1950, see also Smith & Figueiredo 2015, 2019, Smith & Klopper 2021a). Owing to this variability, a species cannot be defined by a single or small number of characters; rather, a suite of characters and dimensions, including certain tendencies in the expression of characters, are usually required to adequately circumscribe aloe species. The extent to which variation (in itself a character) is accepted within a taxon will have an influence on the delimitation of taxa.

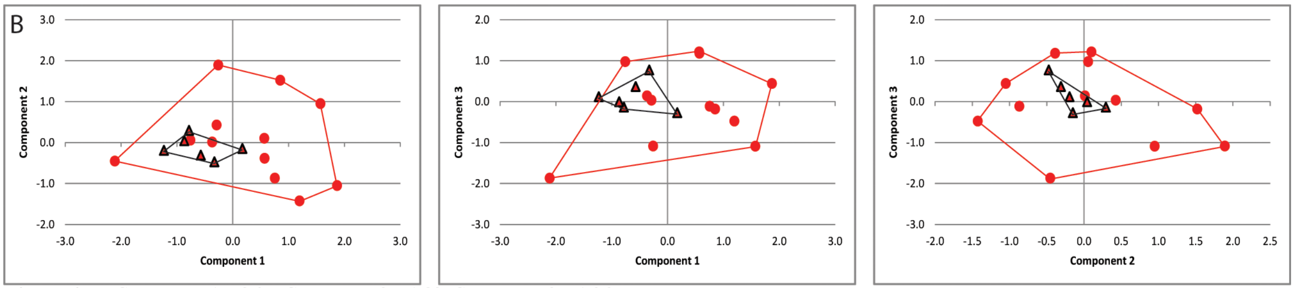
Results from the macro-morphological analysis provide insights into the taxonomic status of, and relationships among the taxa investigated. The results from the PCA analyses on *A.* sect. *Purpurascentes* together with the two putative members of the section (*A. chlorantha* and *A. pictifolia*) show that the latter two species do not cluster with the other members of the section (Fig. 2A). *Aloe pictifolia*, in particular, differs from the other taxa, primarily in terms of leaf width. *Aloe chlorantha* appears to have closer affinities to members of *A.* sect. *Purpurascentes*, but differs primarily in the spacing of its marginal teeth. Removal of *A. pictifolia* and *A. chlorantha* from the analysis did not significantly alter the topology of the ordination plots for the remaining species, apart from inverting the axes for Components 2 and 3. Based on these results, *A. chlorantha* and *A. pictifolia* are not strongly associated with the rest of the species in *Aloe* sect. *Purpurascentes*. Their putative placement within this section is thus not supported.

In general, *A. succotrina* forms a loose cluster that is not clearly separated from other members of the section. Mainland and Cape Peninsula populations of *A. succotrina* are recovered together in the ordination plots for this species (Fig. 2B). Therefore, separate taxonomic status for the mainland and Peninsula forms of *A. succotrina* is refuted by the results of this study. Although the ordination plots do not clearly separate *A. succotrina*, its status as a good species is not in dispute. The inconclusive clustering of *A. succotrina* specimens among those of other taxa highlights the problematic nature of morphological characters in this group of aloes—a well-defined species is not necessarily recovered as separate from the rest of the taxa by morphological analyses.

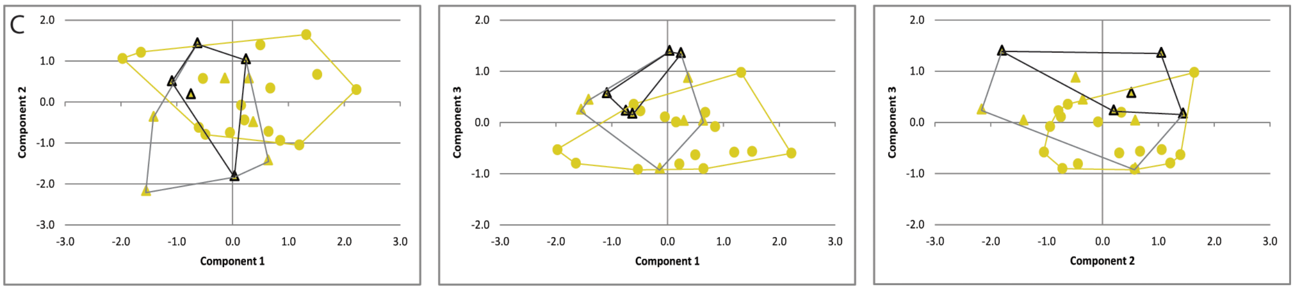
Specimens of *A. gariepensis* consistently cluster together in all plots. Component 1 separates it from other members of *A.* sect. *Purpurascentes*, although some overlap with *A. microstigma* is present (Fig. 2A). Even though this species has the longest bracts in the section, especially in relation to its pedicel length, important characters for its separation from other taxa are indicated as flower length and pedicel length. Eastern and western populations are not clearly defined in their clustering in the ordination plots for this species (Fig. 2C). The notion that *A. gariepensis* might constitute two taxa is thus not supported, with the general clustering of samples underlining its species status.



Eigen values: Component 1 = 1.84; Component 2 = 1.68; Component 3 = 1.40



Eigen values: Component 1 = 2.07; Component 2 = 1.82; Component 3 = 1.36



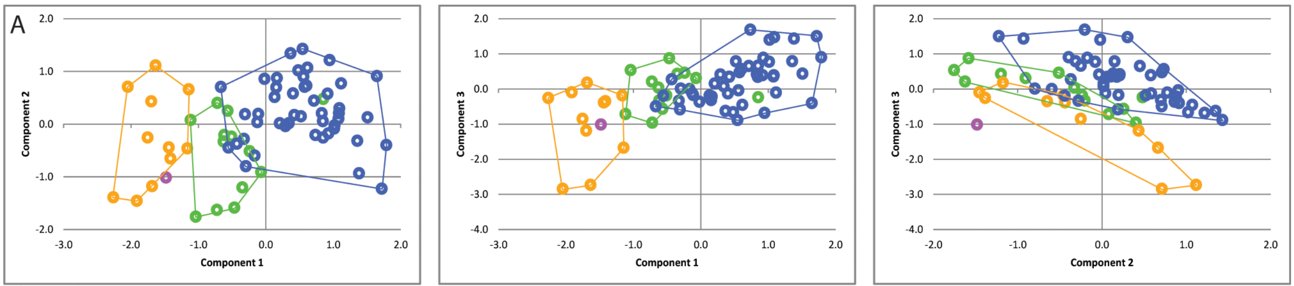
Eigen values: Component 1 = 2.43; Component 2 = 1.82; Component 3 = 0.71

FIGURE 2. Ordination plots. **A.** All members of *A.* sect. *Purpurascentes* and two putative members of the section (green—*A. framesii*; yellow—*A. gariepensis*; orange—*A. khamiesensis*; purple—*A. knersvlakensis*; blue—*A. microstigma*; red—*A. succotrina*; black—*A. chlorantha*; brown—*A. pictifolia*). **B.** *Aloe succotrina* (circles—mainland populations; triangles—peninsula populations). **C.** *Aloe gariepensis* (circles—eastern populations; triangles—western populations; framed triangles—populations next to the Orange River). New classification: *Aloe knersvlakensis* = *A. khamiesensis* subsp. *knersvlakensis*.

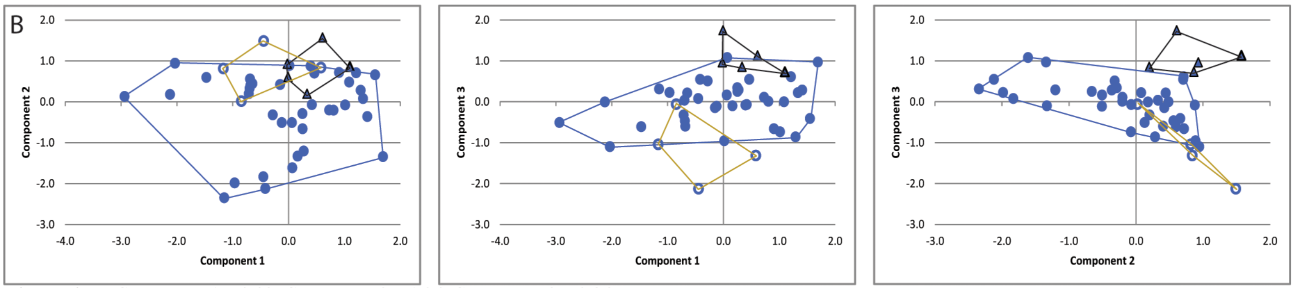
Since the status of *A. gariepensis* and *A. succotrina* has not been questioned (and is also supported by other results of this study), the PCA analysis was repeated on only the remaining problematic taxa within the section (namely *A. framesii*, *A. khamiesensis*, *A. knersvlakensis*, and *A. microstigma*).

Three main taxon clusters were obtained in the ordination plots for that analysis (Fig. 3A). These clusters are separated by Component 1 where inflorescence branching, leaf width, and floral bract length are the main distinguishing characters. *Aloe microstigma*, *A. framesii*, and *A. khamiesensis* are morphologically very similar. *Aloe framesii* occupies a median position and is nearer to *A. microstigma*. The separate status of these three species, but especially of *A. khamiesensis*, is strongly supported by these results.

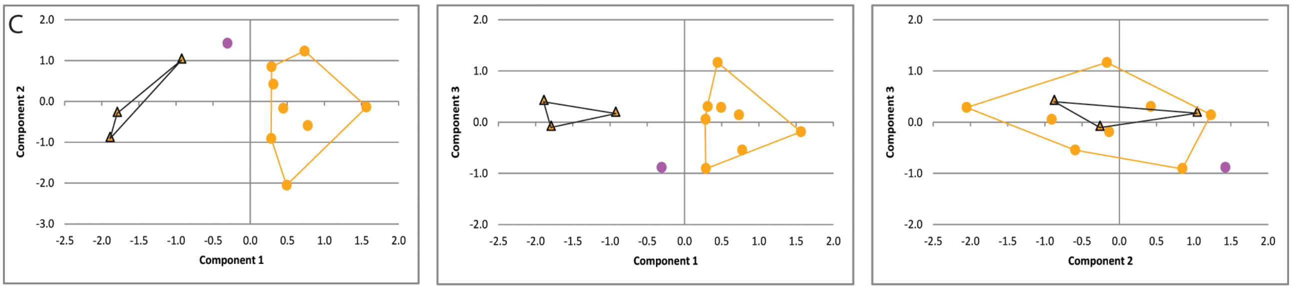
The first cluster contains all specimens of *A. microstigma* (blue circles in Fig. 3A). The Kagga Kamma specimen (*M. Koekemoer 4308*, tentatively identified as *A. framesii*) consistently group with the *A. microstigma* samples, as does the Akkerendam *A. microstigma/khamiesensis* specimen (*A. Jooste 46*). The identity of all specimens with tentative identifications was thus elucidated. In this regard both the Akkerendam and Kagga Kamma specimens consistently cluster with *A. microstigma*. Given the intermediate position of the *Koekemoer 4308* specimen between *A. microstigma* and *A. framesii*, both in terms of morphology and geography, the possibility of it being of hybrid origin cannot be excluded. Both the Namibian and the yellow-flowering form of *A. microstigma* grouped together with other samples (Fig. 3B). The Namibian specimens do tend to be grouped to the outer perimeter of the main *A. microstigma* cluster, especially in terms of Components 2 and 3. Leaf width, and teeth length and spacing are indicated as important characters for separating the Namibian samples. Grouping of the yellow-flowering form was less conclusive (Fig. 3B). Clustering of the *A. microstigma* samples does not support reinstatement of *A. brunnthaleri* for the yellow-flowering form of this species. Although separate grouping of the Namibian specimens is not entirely convincing, there is sufficient evidence to confirm the differences in these populations and support a possible segregation of these samples at subspecific level.



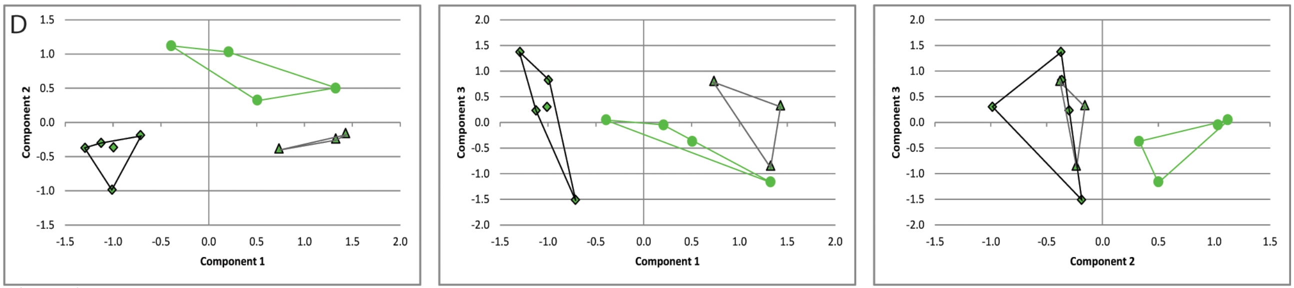
Eigen values: Component 1 = 2.35; Component 2 = 2.02; Component 3 = 1.10



Eigen values: Component 1 = 2.82; Component 2 = 1.26; Component 3 = 0.86



Eigen values: Component 1 = 2.52; Component 2 = 1.67; Component 3 = 1.46



Eigen values: Component 1 = 2.73; Component 2 = 1.86; Component 3 = 0.92

FIGURE 3. Ordination plots. **A.** *Aloe framesii* (green), *A. khamiesensis* (orange), *A. knersvlakensis* (purple) and *A. microstigma* (blue). **B.** *Aloe microstigma* (circles—southern populations; triangles—Namibian populations; open circles—yellow-flowering populations). **C.** *Aloe khamiesensis* (orange circles—Namaqualand populations; framed orange triangles—Hantam populations) and *A. knersvlakensis* (purple circles). **D.** *Aloe framesii* (circles—northern populations; framed diamonds—southern populations; framed triangles—eastern populations).

New classification: Southern populations of *A. microstigma* = *A. microstigma* subsp. *microstigma*; Namibia populations of *A. microstigma* = *A. microstigma* subsp. *juttae*; Namaqualand populations of *A. khamiesensis* = *A. khamiesensis* subsp. *khamiesensis*; Hantam populations of *A. khamiesensis* = *A. khamiesensis* subsp. *hantamensis*; *A. knersvlakensis* = *A. khamiesensis* subsp. *knersvlakensis*; Northern populations of *A. framesii* = *A. framesii* subsp. *framesii*; Southern populations of *A. framesii* = *A. framesii* subsp. *maraisii*; Eastern populations of *A. framesii* = *A. framesii* subsp. *amoena*.

A second cluster comprises samples of *A. khamiesensis* and *A. knersvlakensis* (orange and purple circles in Fig. 3A). In the ordination plots for all members of the section (Fig. 2A) this group is clearly separated from other taxa by Component 2, where inflorescence branching and floral bract length are shown to be important distinguishing characters. Three subgroups are formed by Component 1 in the ordination plots for this group (Fig. 3C), with teeth length and spacing, leaf width, and inflorescence branching indicated as the main characters for their distinction. Although *A. knersvlakensis* is closely associated with the main *A. khamiesensis* cluster, it does not overlap with it in the ordination plot for this species group (Fig. 3C). The three Hantam specimens tend to be removed from the main cluster and only loosely associated with it (Fig. 3C). The placement of these populations in relation to *A. khamiesensis* supports recognition of the three subgroups at subspecific level.

A third cluster contains specimens of *A. framesii* (green circles in Fig. 3A). This group occupies a median position between the *A. microstigma* and *A. khamiesensis* assemblages. There is some overlap between the *A. framesii* and *A. microstigma* clusters. Furthermore, there is a geographic pattern in the grouping of this cluster and three subgroups are formed in the ordination plot for this species (Fig. 3D). The samples from the southwestern populations form a group, which is clearly separated from a second group containing specimens from around Clanwilliam (eastern populations) by Component 1. Flower length, leaf width, pedicel length, and inflorescence branching are important characters to differentiate between these forms. Thirdly, the Port Nolloth specimens consistently group together and are separated from the other populations by Component 2. Floral bract length, pedicel length, leaf width, and teeth spacing are indicated as useful characters to distinguish it from the two other forms of *A. framesii* (Fig. 3D). The geographic grouping of *A. framesii* specimens suggest a solution to clarify the morphological diversity within this species and how it can best be delimited. Separation of the northern (Port Nolloth) and southern (Elands Bay, St Helena Bay, Stompneus Bay) populations, and reinstatement of *A. amoena* for the inland populations (Clanwilliam) at subspecific level are warranted.

Characters and character states

This section briefly discusses the most important characters of this group of aloes. It also comments on the distribution of character states and their taxonomic significance.

Habit:—In *Aloe framesii* plants are either acaulescent or have a slender usually procumbent stem. Rosettes generally sucker or branch freely to form dense groups. This is an extremely variable taxon that differs considerably in growth form among different populations. At St Helena Bay rosettes grow in groups. These aloes grow amongst large granite boulders in Strandveld vegetation. At Elands Bay rosettes occur in dense groups among boulders on lower slopes of a ridge overlooking the Verlore Vlei. Plants at Leipoldtville (S.J. Marais, pers. comm.) and Doringbaai also have their rosettes in groups. Around Papendorp, rosettes form dense clusters with longer, more erect stems, giving plants a more robust appearance. South of the Cederberg Wilderness Area the plants occur in small clusters or sometimes solitary and usually with a short, erect stem. At Clanwilliam plants form fairly large groups among sandstone formations and rosettes have short, erect to slightly decumbent stems. At the type locality of *A. framesii*, ± 25 km north of Port Nolloth, rosettes form very large groups with decumbent to erect stems. This impressive population in Southern Richtersveld Yellow Duneveld (Mucina & Rutherford 2006) spreads over a very large area and some rosette clusters are evidently very old.

Plants of *Aloe gariepensis* are also extremely variable at different localities. Plants are sub-acaulescent or with erect to procumbent stems of up to 1 m tall. Rosettes are usually solitary. At Grootderm in the west of its distribution range, plants are smaller and mostly acaulescent. At Grootderm and at the De Hoop Campsite in the Richtersveld National Park (B. Hölscher, pers. comm.), plants grow amongst boulders or on cliffs overlooking the Orange [Gariep] River. Throughout Bushmanland, *A. gariepensis* is often found on the northern slopes of inselbergs (P. Desmet, pers. comm.). Around Pofadder and Pella, in the centre of its range, plants are robust and often with a short stem. Robust plants with unicoloured yellow racemes also occur south of Pofadder (J.C. Kruger, pers. comm.). At Keimoes, in the east of its range, plants are considerably more robust with stems of up to 1 m tall that are densely covered in persistent dried leaves. Although Reynolds (1950) reports caulescent plants to predominate, all populations visited in this area had an approximately equal mixture of acaulescent rosettes and shortly caulescent plants, with acaulescent plants sometimes outnumbering those with stems. Near the type locality at Warmbad in the south of Namibia, plants are also very robust, usually with an erect stem.

Aloe khamiesensis is characterised by tall, erect stems of up to 2 m tall that are usually simple, but sometimes branched. In the Hantam populations plants are multistemmed with erect to slanting stems of up to ± 1.5 m long. *Aloe knersvlakensis* is closely related to *A. khamiesensis* and plants of this taxon are usually short caulescent with stems of up to 1.5 m tall, which sucker freely, and the short stems are covered in numerous rosettes in older plants. The usually tall stems separate this group of aloes from others in the section.

Plants of *Aloe microstigma* are usually acaulescent or with erect to procumbent stems of up to 0.5 m long. Rosettes are usually single or sometimes in small groups. Populations of yellow-flowering plants exhibit considerable variation in vegetative features, e.g., at Verlatekloof near Sutherland (J.J. Lavranos and S.J. Marais, pers. comm.) and on the Gannaga Pass, plants form dense clusters of many-branched rosettes; in a population near Fraserburg, plants form dense multi-headed clusters (Kemble 2011); whereas a population near Barrydale tends to have solitary rosettes (S.J. Marias, pers. comm). Plants at Akkerendam (Calvinia) have clustered acaulescent rosettes. At Kagga Kamma Nature Reserve (Cederberg region), stems vary from very short to long and can be erect, decumbent or leaning against rocks forming an upright, often multi-headed plant. Rosettes are solitary or in clusters with the stems seemingly branching from low down.

In some localities of *A. microstigma* in Bushmanland, plants occur as solitary rosettes, and are believed to grow sympatrically with *A. gariepensis* on the north facing slopes of these inselbergs (P. Desmet, pers. comm.). Namibian plants usually form small clusters of many smaller rosettes in the form of a disorderly shrub (Rothmann 2004, Kemble 2011). Rosettes of plants in the Richtersveld are always solitary and plants flower mainly in late spring (G. Williamson, pers. comm.). In the Sperrgebiet population towards the summit of the Heiob Mountain, plants grow on the eastern aspect and form dense clustered colonies of narrow-leaved plants. The population from the Rooiberg, just east of the Aurusberge, grows on the southern aspect and consists of small, miniaturised plants (G. Williamson, pers. comm.).

In *Aloe succotrina* plants can be acaulescent, but usually have erect or procumbent stems of up to 2 m long that are simple or branched. This is a variable species, but nonetheless in all its forms quite recognisable. In certain localities rosettes are solitary with short, simple or branched, erect stems. Where conditions are favourable, rosettes occur in large dense groups. The largest forms have stems of 1–2 m long that are dichotomously branched and form a large canopy of many rosettes (Reynolds 1950).

Leaves:—Leaves of *Aloe framesii* usually have copious white spots on both surfaces, but plants without spots or with only a few spots are sometimes encountered. This is an extremely variable taxon that differs considerably in leaf characters. In the most southern populations at Saldanha, the leaves have few spots (S.J. Marais, pers. comm.). At St Helena Bay the blue-green leaves vary from completely immaculate to spotted. At Elands Bay leaves are blue-green with few to numerous scattered spots on both surfaces. Rosettes of plants at Leipoldtville have the most clearly spotted leaves of all populations (S.J. Marais, pers. comm.). At Papendorp leaves are blue-green with a strong reddish tinge and have a few scattered spots especially towards the base of leaves. South of the Cederberg Wilderness Area leaves are a light greyish green with few to several spots and obscure to fairly prominent lines. At Clanwilliam leaves are rather broad with few spots and obscure lines. In December 2012 a population was observed at Traveller's Rest in the Agter Pakhuis area, east of Clanwilliam. Since it was the hot dry season, leaves were an intense red. At the type locality of *A. framesii*, ± 25 km north of Port Nolloth, leaves are reddish blue-green, with very few, if any, spots.

Leaves of *Aloe gariepensis* are also extremely variable at its different localities. The distinctly lineate leaves are copiously spotted on both surfaces in young plants and usually turn pink or bright reddish brown during dry periods. At Grootderm in the west of its distribution range, leaves are usually reddish with prominent longitudinally aligned lines. Around Pofadder and Pella (in the centre of its range), leaves are mostly yellowish green, often turning reddish during drought, and heavily striped with dark green to brownish lines. In populations at Keimoes, in the east of its range, leaves are larger and more glaucous-green, and inflorescences taller than elsewhere (Reynolds 1950). Leaves are always lineate, but can be entirely without spots to copiously spotted at various localities (Reynolds 1950). The strongly lineate leaves separate this aloe from others in the section.

In *Aloe khamiesensis* leaves are usually spotted on both surfaces, but spots are more numerous on the lower surface; lower surfaces are additionally obscurely lineate. Leaves of the Hantam populations are yellowish green with few spots in large plants, but copiously spotted on both surfaces in young plants. In *Aloe knersvlakensis* the usually incurved leaves have distinct longitudinal lines and spots on both surfaces.

Leaves of *Aloe microstigma* are usually copiously white-spotted on both surfaces and obscurely lineate. *Aloe microstigma* is quite variable in leaf colour and markings (Reynolds 1950, Kemble 2011). Leaves vary from entirely without spots, to copiously spotted on both surfaces (Reynolds 1950). For instance, plants from the area between Steytlerville and Grahamstown are very heavily spotted (S.J. Marais, pers. comm.), while adult plants from a population ± 20 km southeast of Fraserburg are entirely without spots (Kemble 2011). Young plants grown from seed collected at the Fraserburg population do, however, have spots on their leaves (B. Kemble, pers. comm.). Plants in this population also form dense multi-headed clusters (Kemble 2011) of blue-green leaves that are strongly tinged with pinks and purples towards the tips (B. Kemble, pers. comm.). In another population, ± 50 km south of Fraserburg, plants grow as solitary rosettes with spotted leaves that are reddish tinged (completely lacking the lavender hues of the other population nearby) (B. Kemble, pers. comm.). At Akkerendam Nature Reserve (Calvinia) leaves were long and narrow with some spots. The most variable leaves are found in the populations north of the Swartberg, where plants with unicoloured, yellow racemes seem to be the more common form; plants from near Beaufort West have very narrow leaves (B. Kemble, pers. comm.); near Matjiesfontein leaves are variously coloured and often markedly striped (Kemble 2011); southeast of Laingsburg leaves can be an intense fiery red-orange and only somewhat striated (Kemble 2011); populations closer to Fraserburg have unspotted leaves (S.J. Marais, pers. comm.). Leaf colouring is especially intense during dry periods (Kemble 2011). Leaves of plants at Calvinia are fairly heavily spotted on the lower surface, but sparingly spotted on the upper surface with a distinct line of white spots present in the median line of the upper surface. At Kagga Kamma Nature Reserve (Cederberg region), leaves are incurved, yellowish to reddish green, with few to numerous white spots and fairly distinct striations on both surfaces.

In populations of *A. microstigma* in Bushmanland, leaves are narrow and usually reddish. However, the same plant was observed after good rains when the leaves had a deep green colour and after prolonged drought when the leaves were distinctly reddish. Namibian plants have smaller rosettes of narrow, red, ascending, flexible leaves. A published image taken in the Richtersveld (Williamson 2000, bottom right on page 113) shows a plant with very red, narrow leaves (which in the text is said to have white spots). In a population in the Sperrgebiet, towards the summit of the Heiob Mountain, plants form dense clustered colonies of narrow-leaved plants. Another Sperrgebiet population from the Rooiberg, just east of the Aurusberge, consists of small, miniaturised plants (G. Williamson, pers. comm.).

Leaves of *Aloe succotrina* are obscurely lineate and sometimes with a few spots. It is the only member of the section with white teeth on the leaf margins (all other taxa have reddish brown marginal teeth). Other important distinguishing characters include the leaf exudate that dries purple (as opposed to yellow or brownish in other species of the section). These characters clearly separate *A. succotrina* from other members of the section.

Red colour in leaves are most probably due to the presence of anthocyanins, a type of flavonoid. All colour pigments, but especially anthocyanins, have antioxidant properties that can help to prevent cellular damage and is responsible for stress mitigation in plants, e.g., herbivory, pathogens, drought, frost, and UV radiation (Narbona *et al.* 2021, Sapir *et al.* 2021). Leaves of many of the aloes studied here often turn red during dry periods. This increase of red pigments in the leaf tissue is hypothesised to be a protective measure to minimise potential damage to the leaves associated with increased drought and radiation.

Inflorescence:—Inflorescences of *Aloe framesii* are simple or 2- or 3-branched with conical to cylindric-acuminate mostly unicoloured or slightly bi-coloured racemes of orange-red, greenish yellow tipped flowers (25–30 mm long). In the most southerly populations at Saldanha, inflorescences are simple with unicoloured racemes (S.J. Marais, pers. comm.). At St Helena Bay, inflorescences are sometimes forked with mostly unicoloured red racemes, although flower colour varies and bicoloured racemes are not uncommon. Plants near Elands Bay have the largest and most striking inflorescences of all populations of this aloe (S.J. Marais, pers. comm.). Here, inflorescences are simple or forked low down with elongated-conical bicoloured or unicoloured racemes. At Leipoldtville inflorescences are mostly simple and short, with bicoloured racemes (S.J. Marais, pers. comm.). At Doringbaai inflorescences are either simple or forked with fairly unicoloured racemes (S.J. Marais, pers. comm.). At Papendorp inflorescences are simple or usually forked. South of the Cederberg Wilderness Area inflorescences are simple with mostly unicoloured reddish racemes, although bicoloured racemes with reddish buds and orange-yellow flowers were also observed. In terms of inflorescence orientation and raceme shape, these plants are probably closer to those at Kagga Kamma (Cederberg region). At Clanwilliam branched inflorescences are more common than simple ones and the long racemes are mostly unicoloured (S.J. Marais, pers. comm.), although 3-branched inflorescences are not uncommon (N.R. Crouch, pers. comm.). At Traveller's Rest in the Agter Pakhuis area, east of Clanwilliam, remains of simple inflorescences were found amongst the rosettes in December 2012. At the type locality of *A. framesii*, ± 25 km north of Port Nolloth, inflorescences are mostly forked with bicoloured racemes.

In *Aloe gariepensis* inflorescences are unbranched with long narrow cylindric-acuminate bicoloured or unicoloured racemes. At Grootderm in the west of its distribution range, plants produce unicoloured yellow racemes. Around Pofadder and Pella (in the centre of its range) inflorescences are usually tall and bicoloured with orange-red buds and yellow flowers, although a yellow-flowered population from south of Pofadder is known (J.C. Kruger, pers. comm.). At Keimoes, in the east of its range, inflorescences can be unicoloured yellow, but bicoloured racemes with red buds and very pale yellow to greenish white flowers predominate (B. Kemble, pers. comm.). At Warmbad plants usually have tall, unicoloured or bicoloured inflorescences.

Inflorescences of *Aloe khamiesensis* are repeatedly branched with up to eight long conical unicoloured racemes of orange-red, greenish yellow-tipped flowers (30–35 mm long). Inflorescences of Hantam populations are generally 3- or 4-branched with long bicoloured racemes of red buds and yellow flowers. Inflorescences of *Aloe knersvlakensis* are 3- or 4-branched with long conical bicoloured racemes. The much-branched inflorescences separate this group of aloes from others in the section.

In *Aloe microstigma* inflorescences are normally unbranched with conical to cylindric-acuminate, usually bicoloured racemes. In the east of its distribution range, plants usually have bicoloured racemes, while in the west plants with unicoloured yellow racemes occur together with the more regularly encountered bicoloured forms. Near Robertson plants with unicoloured red racemes have been recorded (Reynolds 1950). In the populations north of the Swartberg unicoloured yellow racemes seem to be the more common form. Inflorescences of plants on the Gannaga Pass are sometimes very lightly bicoloured, but predominantly yellow. Populations of yellow-flowering plants exhibit considerable variation in vegetative features, e.g., at Verlatekloof near Sutherland (J.J. Lavranos and S.J. Marais, pers. comm.) and on the Gannaga Pass, plants have simple ascending inflorescences; in populations with unspotted leaves closer to Fraserburg, the inflorescences are very compact and relatively short (S.J. Marais, pers. comm.); a population near Barrydale tends to have simple, erect, very robust inflorescences (S.J. Marias, pers. comm.). Inflorescences of plants in the Kagga Kamma Nature Reserve (Cederberg region) are simple, relatively short and compact, with unicoloured red to slightly bicoloured conical racemes.

Inflorescences of *A. microstigma* in Bushmanland can be up to 3-branched and racemes seem to be either unicoloured red, or bicoloured, with orange buds and yellow flowers. In Namibian plants, inflorescences are simple and racemes usually bicoloured (S.J. Marais, pers. comm.). The image in Williamson (2000, bottom right on page 113) from the Richtersveld shows a plant with 2- or 3-branched inflorescences with bicoloured racemes (rather light orange buds and yellowish flowers). The population from the Rooiberg, just east of the Aurusberge, consists of small, miniaturised plants with unbranched inflorescences (G. Williamson, pers. comm.).

Inflorescences of *Aloe succotrina* are mostly unbranched with cylindric-acuminate racemes of red flowers (25–40 mm long).

The primary purpose of flower colour is to act as a visual signal advertising the presence of pollen and nectar rewards to potential pollinators. Even though many pollinators have an innate colour preference, their behaviour is influenced by flower colour since they can learn to associate certain colours with floral rewards. Pollinator behaviour directly affects pollination success and thus the fitness of the plant (Weiss 1991, Weiss & Lamont 1997, Sapir *et al*. 2021).

The visual systems of different pollinators vary considerably, resulting in differences in the colours they can perceive and in their ability to detect colours against a background, as well as the distance at which they can do this (Weiss & Lamont 1997, Sapir *et al*. 2021). Aloes are mainly pollinated by birds and insects, such as honeybees (Botes *et al*. 2009). Yellow flowers are said to be more attractive to insects than red flowers (Linau 1995, Weiss & Lamont 1997), whereas birds apparently tend to prefer orange or red flowers (Linau 1995, Botes *et al*. 2009). Furthermore, long-distance detection of objects by honeybees seemingly depends on "green contrast", while they only perceive the chromatic characteristics of a flower at short distances (Weiss & Lamont 1997).

A large number of flowers in a floral display or inflorescence (as in the tall racemes of aloes) acts to make the flowers more visible and attractive to pollinators over long distances, whereas flower colour differences offer signals to pollinators at close range (Weiss & Lamont 1997). Display size of inflorescences and learning behaviour by pollinators, linked to changes in flower colour as flowers mature (i.e., differently coloured buds, receptive and/or old flowers in an inflorescence), can greatly increase pollination success (Weiss 1991, Weiss & Lamont 1997, Makino & Ohashi 2017). Position of flowers in the inflorescence of aloes might be a better indicator of rewarding flowers than the colour of the open flowers (Makino & Ohashi 2017), especially in species and populations where floral buds and open flowers are the same colour. In cases with bicoloured inflorescences the position and colour of flowers might act in combination to direct pollinators to rewarding flowers.

Potential pollinators for flowers of *Aloe* sect. *Purpurascentes* include birds (especially sunbirds) and insects such as honeybees. There is a considerable need for more research on aspects of pollination, especially the association between floral morphology and function, not only in *Aloe* sect. *Purpurascentes*, but aloes in general.

Pedicels and floral bracts:—*Aloe gariepensis* is the only species where pedicels (15–20 mm long) are shorter than the floral bracts (± 25 mm long). In all other members of the section the pedicels are longer than the floral bracts. In *A. framesii*, *A. khamiesensis*, and *A. succotrina* floral bracts are about a third of the length of the pedicels, while in *A. knersvlakensis* and *A. microstigma* the pedicels are almost twice as long as the floral bracts.

Aloe succotrina is distinguished by its fairly large, broad, purplish floral bracts. Other taxa in the section all have narrower ovate-acute to lanceolate-acute floral bracts.

Perianth:—*Aloe succotrina* consistently has red flowers (25–40 mm long) and *A. framesii* orange-red, greenish yellow-tipped flowers (25–30 mm long). In other taxa the bud and/or mature flower colour varies. *Aloe khamiesensis* usually has orange-red, greenish yellow-tipped flowers (30–35 mm long) that are similar to those of *A. framesii*. However, the Hantam plants have red buds and yellow flowers, and in *A. knersvlakensis* the floral buds are orange-red while the open flowers are yellow and greenish-tipped (± 28 mm long). In *A. gariepensis* floral buds are yellow to greenish or sometimes red, while mature flowers are yellow to greenish yellow (23–27 mm long).

Aloe microstigma is quite variable in the colour of the perianth (Reynolds 1950, Kemble 2011). Floral buds are usually red, while open flowers are normally greenish yellow (25–30 mm long). Colour variations are found in populations to the north of the Swartberg where floral buds are often greenish yellow; in Bushmanland, the Richtersveld and Akkerendam (Calvinia) orange to light orange floral buds have been recorded; while mature flowers of populations near Robertson are red. In the west of its distribution range flowers are more glossy, whereas they are more dull and with a pale waxy bloom in the east (Reynolds 1950).

Flower colour is a result of four types of pigments that are present in plants: chlorophylls, carotenoids, flavonoids, and betalains (Weiss & Lamont 1997, Narbona *et al*. 2021, Sapir *et al*. 2021). With their yellow to red flowers and buds, flower colour in the members of *Aloe* sect. *Purpurascentes* is most probably due to the presence of carotenoids and flavonoids. Yellow to orange flowers are mostly due to carotenoids, while anthocyanins (a type of flavonoid) are responsible for, amongst others, red to pink flower colours (Weiss & Lamont 1997, Narbona *et al*. 2021, Sapir *et al*. 2021). Other flavonoids can also produce yellow flowers (Narbona *et al*. 2021). Anthocyanins are responsible for the widest range of flower colours and are the most common pigment involved in colour variation (Weiss & Lamont 1997, Narbona *et al*. 2021, Sapir *et al*. 2021). Chromatic traits of flower colour (e.g., hue and intensity), can further be influenced by structural differences in cells and by environmental factors, such as soil and cell pH, water availability, etc. (Weiss & Lamont 1997, Narbona *et al*. 2021, Sapir *et al*. 2021). Flower colour can thus be influenced by a combination of anatomical, molecular, ecological, and physiological factors (Sapir *et al*. 2021).

Variation in the colour of open flowers within a population are not common among the aloes studied here, with the exception of the *Aloe microstigma* populations north of the Swartberg. The occurrence of different flower colours in a population can be the result of selection by multiple agents that act in different directions: such as multiple pollinators with different preferences for flower colour; or where biotic agents and abiotic factors exert selection in opposite directions. On the other hand, monochromatic flowers may be due to a single agent or multiple agents acting in the same direction (Sapir *et al*. 2021). Where there is a geographical difference in the frequency of floral colour variation within populations, this is presumably driven by changes in selection agents (Sapir *et al*. 2021). It is not just ecological factors that affect flower colour variation within and between populations, there could also be genetic factors involved (such as genetic drift, mutations, and gene flow), but this requires further research (Sapir *et al*. 2021).

Flowering time:—Most members of *A.* sect. *Purpurascentes* flower during the southern hemisphere winter months, but variation throughout the distribution range of some species is known. *Aloe framesii* plants normally flower in June and July (Klopper 2014). However, at Papendorp, the population of *A. framesii* next to the Olifant River Estuary flowers earlier than other coastal populations. For instance, in July 2010 the Papendorp plants were all in fruit, while those at St Helena Bay, Elands Bay, and Port Nolloth were mostly still in full flower. Just south of the Cederberg Wilderness Area a population of plants was seen in flower in August 2007, which is much later than most other populations of *A. framesii*.

Aloe khamiesensis, similarly, usually flowers in June and July (Klopper 2014). However, plants in the Hantam populations seem to flower slightly earlier (April–June) than in the Kamiesberg. In July 2010, the flowering event of the Loeriesfontein population had been almost completed with only some inflorescences still bearing a few flowers and most plants being in fruit. Three days later, plants of *A. khamiesensis* near Kamiesberg were still found to be in full flower with fruit not yet formed. Plants at Nieuwoudtville developed inflorescences during late April in 2014 and were in flower in mid-May in 2015. *Aloe knersvlakensis* is unusual in that it flowers much earlier than other members of the section, i.e., from March to April (Klopper 2014).

Aloe gariepensis flowers between July (in the west) and September (in the east). *Aloe succotrina* similarly flowers slightly later, between July and August. *Aloe microstigma* has the longest flowering period and flowers between May and August (Klopper 2014).

Seed morphology:—Seed classification studies of some 100, mainly South African, *Aloe* species (Kamstra 1968, 1971), showed that several types of seed are present in the genus. Minor variations within certain species were reported. Most of the infrageneric groups used by Reynolds (1950) were supported by seed morphology. There were, however, several exceptions where a species had a completely different type of seed than the other members of the same section or series investigated (Kamstra 1968, 1971).

Kamstra (1968, 1971) classified members of *A.* sect. *Purpurascentes* into a subset of a group containing 'seeds with no wings at all, or very rudimentary wings'. He only investigated *A. framesii*, *A. gariepensis*, *A. khamiesensis*, and *A. microstigma*, stating that no seed of *A. succotrina* was available. Seeds of these aloes were described as being dark brown to black, distinctly triangular, with a smooth surface and with rudimentary wings that are slightly larger than those of the subgroup containing members of *Aloe* sect. *Arborescentes* [namely *A. arborescens*, *A. mutabilis* Pillans (1933a: 167), *A. pluridens* Haworth (1824: 299), and *A. vanbalenii* Pillans (1934: 25)] (Kamstra 1968). Kamstra (1968, 1971) was of the opinion that, based only on seed morphology, *A. framesii* did not fit into this group, as it had small wings and not rudimentary wings as the rest of the species.

Based on seed morphology *A.* sect. *Purpurascentes* forms a coherent group, with the small wings of *A. framesii* being slightly larger than the very rudimentary wings of other species (Kamstra 1968, 1971). However, this type of seed is very common in *Aloe*, as the seed type group of which *A.* sect. *Purpurascentes* forms a subset also contains several other subsets representing various sections within the genus, amongst others *Aloe* sect. *Arborescentes* (Kamstra 1968, 1971). Since the seed of members of *Aloe* sect. *Arborescentes* also have very rudimentary wings, the notion that seed morphology points to a possible closer relationship of *A. succotrina* with *A. arborescens* (S.J. Marais, pers. comm.) is not supported by the seed morphology results of Kamstra (1968, 1971).

Palynology:—Palynological data in *Aloe* have not been used extensively in treatments of this genus. A palynological study of 36 South African *Aloe* species, covering several of the categories in the classification system used by Reynolds (1950), has shown this character to be of limited use, although further investigation was called for (Steyn *et al*. 1998). Since the species investigated in certain groups (including *A.* sect. *Purpurascentes*) all displayed the same pollen type, some taxonomic significance is present at infrageneric level. However, certain infrageneric groups contained more than one pollen type (Steyn *et al*. 1998). The only two species from *A.* sect. *Purpurascentes* included in the study of Steyn *et al*. (1998) were *A. microstigma* and *A. succotrina*.

Both *A. microstigma* and *A. succotrina* display the so-called *Dinteri*-type pollen (Steyn *et al*. 1998). This pollen type has a smooth and even surface, with the tectum being microreticulate and heterobrochate. The lumina are irregular in shape and the muri is as wide as or narrower than the dominant lumina diameter. Pollen grains in *A. microstigma* are 45–55 µm in size, and those of *A. succotrina* 45–50 µm (Steyn *et al.* 1998).

The fact that both members of *A.* sect. *Purpurascentes* investigated by Steyn *et al*. (1998) display the same pollen type, points to possible coherence in the section. Palynology, at least, supports inclusion of *A. succotrina* in *A.* sect. *Purpurascentes* and does not support its supposed alliance with *A. arborescens* from *Aloe* sect. *Arborescentes*, where both species investigated (*A. arborescens* and *A. pluridens*) display the *Albida*-type pollen (Steyn *et al.* 1998).

Chemistry:—The chemistry of aloes has received considerable research attention (e.g., Herbin & Robins 1968, Reynolds 1985, Van Wyk *et al*. 1995, Dagne *et al.* 1997, Viljoen *et al*. 1998, Viljoen 1999, Grace *et al*. 2013b). As *Aloe* is a large and taxonomically complex genus on which extensive and varied botanical studies have been conducted, it is regarded as ideal for chemotaxonomic investigation (Herbin & Robins 1968). Therefore, several chemotaxonomic studies on *Aloe* species or groups have been conducted (e.g., Van Wyk *et al*. 1995, Viljoen 1999, Viljoen & Van Wyk 1999, Grace *et al*. 2010). These studies have shown that chemical characters in aloes can be of taxonomic value, even though chemical fluctuations and seasonal variation within a plant (Beaumont *et al*. 1984, Chauser-Volfson & Gutterman 1996), as well as within and between populations (Viljoen 1999) have been illustrated.

Variations in chemistry can be either, or both, quantitative or qualitative, depending on the species. However, such chemical fluctuations and seasonal variation within a plant have been shown to be of minor importance (Beaumont *et al.* 1984, Chauser-Volfson & Gutterman 1996). A classification of chemotypes, proposed by Viljoen (1999), is mostly based on anthrones, which are less variable than chromones. Viljoen (1999) provides a long list of aloe taxa that do not fit into any of his chemotypes. This large number of unplaced taxa points to a possible limitation on the use of chemical characters in aloe taxonomy and that further research is needed. Related species can lack a diagnostic compound or profile because of a secondary loss of such a compound. Furthermore, incorrect identification of material used in a chemotaxonomic study or unknown chemical variation within the species can result in it not fitting into the expected chemotype (Viljoen 1999).

In general, hybridisation is one of many factors that can obscure taxonomic relationships. The notion that hybridisation within *Aloe* is very common, has been supported by the results from chemotaxonomic studies. Chemistry has even helped to elucidate the hybrid origin of some taxa. For this reason, chemotaxonomic evidence could be an important character to include in a multidisciplinary revision of the infrageneric relationships within *Aloe* (Viljoen 1999). In fact, numerous examples show where chemotaxonomic data support the alpha taxonomic treatment of aloes at infrageneric level, as it was proposed by Berger (1908) and further expanded by Reynolds (1950, 1966).

The chemistry of the leaf exudate of aloes belonging to *A.* sect. *Purpurascentes* is complex. During a survey of the leaf exudate chemistry of *Aloe* species, it was found that most members of this section contain the chemotaxonomic marker microstigmin (Viljoen 1999). Microstigmin is a 6'-O-caffeoyl-5-hydroxyaloin that was isolated for the first time from leaf exudate of *A. microstigma* (Dagne *et al*. 1997). Microstigmin has thus far only been found in leaf exudate of members of this section and other putative relatives. This compound was present in samples of *A. microstigma*, *A. framesii*, and *A. khamiesensis*, as well as in *A. pictifolia*. However, it was absent from samples of *A. gariepensis* and *A. succotrina* (Dagne *et al*. 1997, Viljoen 1999). These two taxa also differ from other members of the section in their general morphology and their inclusion in *A.* sect. *Purpurascentes*, especially in the case of *A. succotrina*, has been questioned (Kemble 2011). The only other species examined that also contained microstigmin in the leaf exudate profile of some of its samples was *A. broomii* from *Aloe* sect. *Anguialoe* Reynolds (1940: 111). In samples containing microstigmin, the anthrone isomers aloin A and B were always absent. *Aloe pictifolia* and the three members of *A.* sect. *Purpurascentes* that contain microstigmin also contain 5-hydroxyaloin A as a chemotaxonomic marker compound (Viljoen 1999). The compounds microstigmin and 5-hydroxyaloin A have thus been identified as chemotaxonomic markers for *A.* sect. *Purpurascentes*.

The chemical profile of the leaf exudate of *A. framesii* contains several unidentified compounds. The UV spectrum of these compounds does not correspond to any of the known classes of compound that have been identified in aloes. It is the only member of the section to contain such unidentified compounds (Viljoen 1999).

The leaf exudate of *A. succotrina* is very different to that of the other members of *A.* sect. *Purpurascentes*. It contains 7-hydroxyaloin derivatives and this combination of exudate anthrones was not observed in any of the other species included in the study (Viljoen 1999). The leaf mesophyll exhibits the typical glucose-mannose-xylose profile that is present in most aloes. In *A. succotrina*, glucose and mannose are present in almost equal quantities (glucose occurs in a slightly higher percentage), with very little xylose (Grace *et al*. 2013b). It is noteworthy that in the phylogeny presented by Grace *et al*. (2013b), *A. succotrina* is recovered on a single-taxon branch. The leaf exudate of *A. succotrina* being so markedly different from those of the other members of *A.* sect. *Purpurascentes* supports the view that this aloe perhaps does not belong in this section. It has been shown that 7-hydroxyaloin and its derivatives are indicative of hybridisation between an aloin- and homonataloin-containing species. The presence of this compound in *A. succotrina* therefore suggests a putative hybrid origin for this aloe, with the parent species being unknown (Viljoen 1999). This is not surprising, given the observed hybridisation of *A. succotrina* with other garden aloes at Hermanus [where one of the samples used by Viljoen (1999) was taken]. Nonetheless, it severely complicates the taxonomic placement of *A. succotrina*.

The chemistry of the leaf exudate of *A. gariepensis* is also very different to that of the other members of *A.* sect. *Purpurascentes*. It contains the anthrone isomers homonataloin A and B, as well as cinnamoyl chromones. Other species all contain the anthrone aloin or derivatives thereof in the presence of cinnamoyl chromones (Viljoen 1999). Cinnamoyl chromones are not common in the genus *Aloe* and were only found in ± 10% of the species included in the chemotaxonomic study by Viljoen (1999). The presence of this compound in *A. gariepensis* has therefore been interpreted as indicating a hybrid origin for this aloe, again complicating its proper placement in both phylogenetic and taxonomic contexts. A possible hybrid origin is also supported by the aberrant morphology of *A. gariepensis* within the section, especially in terms of its floral bract:pedicel ratio. *Aloe comosa*, a species containing the leaf exudate anthrone homonataloin and a similar inflorescence morphology to *A. gariepensis*, has been suggested as a possible parent (Viljoen 1999), although the present-day distribution ranges of these aloes do not overlap.

The leaf exudate of *A. chlorantha* contains unidentified anthrone derivatives that resemble 5-hydroxyaloin A in its UV absorbance (Viljoen 1999). The presence of 5-hydroxyaloin derivatives is characteristic of *A.* sect. *Purpurascentes*, and their presence in *A. chlorantha* supports the probable alliance of this aloe to other members of the section. On the other hand, its postulated relationship with *A. broomii* is likewise supported by leaf exudate chemistry, as some populations of the latter species also contain 5-hydroxyaloin A and microstigmin. Since *A. broomii* contains chemical compounds characteristic of both *Aloe* sect. *Anguialoe* (the anthrone aloin A and B, as well as various caffeoyl, cinnamoyl, and coumaroyl chromones) and *A.* sect. *Purpurascentes* (5-hydroxyaloin A and microstigmin), it has been suggested that it is of ancient hybrid origin, with the parents belonging to these sections (Viljoen 1999).

Although currently available evidence on the leaf exudate chemistry of members of *A.* sect. *Purpurascentes* sheds some light on relationships within the section, and also with other aloes, the picture is not complete. A larger sampling over the full distribution range of the section needs to be conducted before any significant taxonomic changes can be made based on chemotaxonomic markers.

Molecular results

DNA is thought to hold the most useful information about the phylogenetic history of an organism (Grace & Rønsted 2013). Molecular information is increasingly used in studying the evolution, relationships, and identity of plants

(Hajibabaei *et al*. 2007, Lahaye *et al*. 2008), including the aloes and their relatives (Adams *et al*. 2000, Chase *et al*. 2000, Treutlein *et al*. 2003a, b, Ramdhani *et al*. 2011, Daru *et al*. 2013, Ellis 2013, Grace & Rønsted 2013, Grace *et al*. 2015). The present study, however, represents only the second time (see Ellis 2013) that molecular data is included in the taxonomic revision of a group of aloes, and the first time at infrageneric rank.

Gene trees

ITS sequences were obtained for 74 specimens and *matK* sequences for 76 specimens, with a total dataset including at least one sequence for 82 specimens. Samples with missing data were excluded from the final combined gene tree, which represents a total of 68 samples.

The combined maximum likelihood tree (Fig. 4) is not well resolved and very few branches have good support. Short branches and weakly supported tree topologies are consistent with the divergence patterns of recent, rapid radiations shown in previous studies of *Aloe* (e.g., Grace *et al*. 2015). In the present study, node supports are problematic for all except *A. succotrina* and, while this limits the taxonomic interpretation of the data, some consistent relationships recovered during analyses warrant discussion.

Aloe succotrina specimens were recovered in a clade that is sister to the rest of the *A.* sect. *Purpurascentes* and other taxa (with strong bootstrap support; BP=99). The two specimens of *A. succotrina* (318 & 317) from the same locality in Hermanus, which are recovered outside the main *A. succotrina* clade, may represent hybrid plants. The broad *Purpurascentes* clade includes various non-*Purpurascentes* outgroup taxa, namely *A. arborescens*, *A. broomii*, and *A. krapohliana*, as well as *A. pictifolia*. This might support the affinity of *A. pictifolia* with *A. microstigma*. However, none of these nodes were well supported. *Aloe chlorantha* is sister to its putative parent, *A. broomii*, in the *matK* tree. Unfortunately, an *ITS* sequence for *A. chlorantha* could not be obtained to investigate its nuclear genome association to further test its assumed hybrid origin and relationship with *A.* sect. *Purpurascentes*.

Although not statistically supported, geographical trends are evident in the clustering patterns observed among the species traditionally included in the *A.* sect. *Purpurascentes*. Several geographically defined clades were recovered: a Karoo clade (mainly comprising *A. microstigma*), a northwestern clade (mainly Namaqualand and Namibia populations), an Eastern Cape clade (*A. microstigma*), a southwestern clade (southern populations of *A. framesii*), and a clade comprising populations in the Hantam (Calvinia and Nieuwoudtville) region.

Notably, two specimens (*A. microstigma* 388 & 396) representing the Namibian form of *A. microstigma* (=*A. juttae*) were recovered in the northwestern clade of *Purpurascentes* rather than in the main *A. microstigma* clade. *Aloe pictifolia* was recovered in the Karoo clade.

Most specimens of *A. framesii* do not show any patterns in its grouping within the molecular trees. Two Port Nolloth specimens (*A. framesii* 374 & 375) did consistently cluster more closely with other northwestern samples (representing other species) than with the very weakly clustered *A. framesii* specimens from more southern populations.

All specimens of *A. gariepensis* cluster together. Similarly, all specimens of true *A. khamiesensis* cluster in the northwestern *Purpurascentes* clade. Two specimens from the aberrant form of *A. khamiesensis* (342 & 343) in the Hantam region are recovered in the Hantam clade. *Aloe knersvlakensis* does not cluster with any of the other *Purpurascentes* taxa.

Minimum Spanning Networks

Eleven alleles or haplotypes were identified in the *matK* minimum spanning network (Fig. 5). The grouping of these alleles mirrors and more clearly illustrates the geographic pattern seen in the phylogenetic tree. Allele 1 contains samples from the southern populations of *A. framesii*, the eastern populations of *A. gariepensis*, the Hantam populations of *A. khamiesensis*, and the Tankwa Karoo and Calvinia populations of *A. microstigma*. The western samples of *A. gariepensis* are isolated in Allele 7, while Allele 8 is only present in the sample of *A. knersvlakensis*.

Allele 2 contains samples from the northern populations of *A. framesii*, all samples from the core distribution of *A. khamiesensis*, and the northern populations of *A. microstigma*. The other samples of *A. microstigma* is divided geographically between Alleles 3 and 4 (Karoo samples), and Alleles 5 and 6 (Eastern Cape samples). Allele 5 also contains two specimens of *A. succotrina* (318 & 317) from Hermanus. The rest of the *A. succotrina* samples are represented by Alleles 9, 10, and 11.

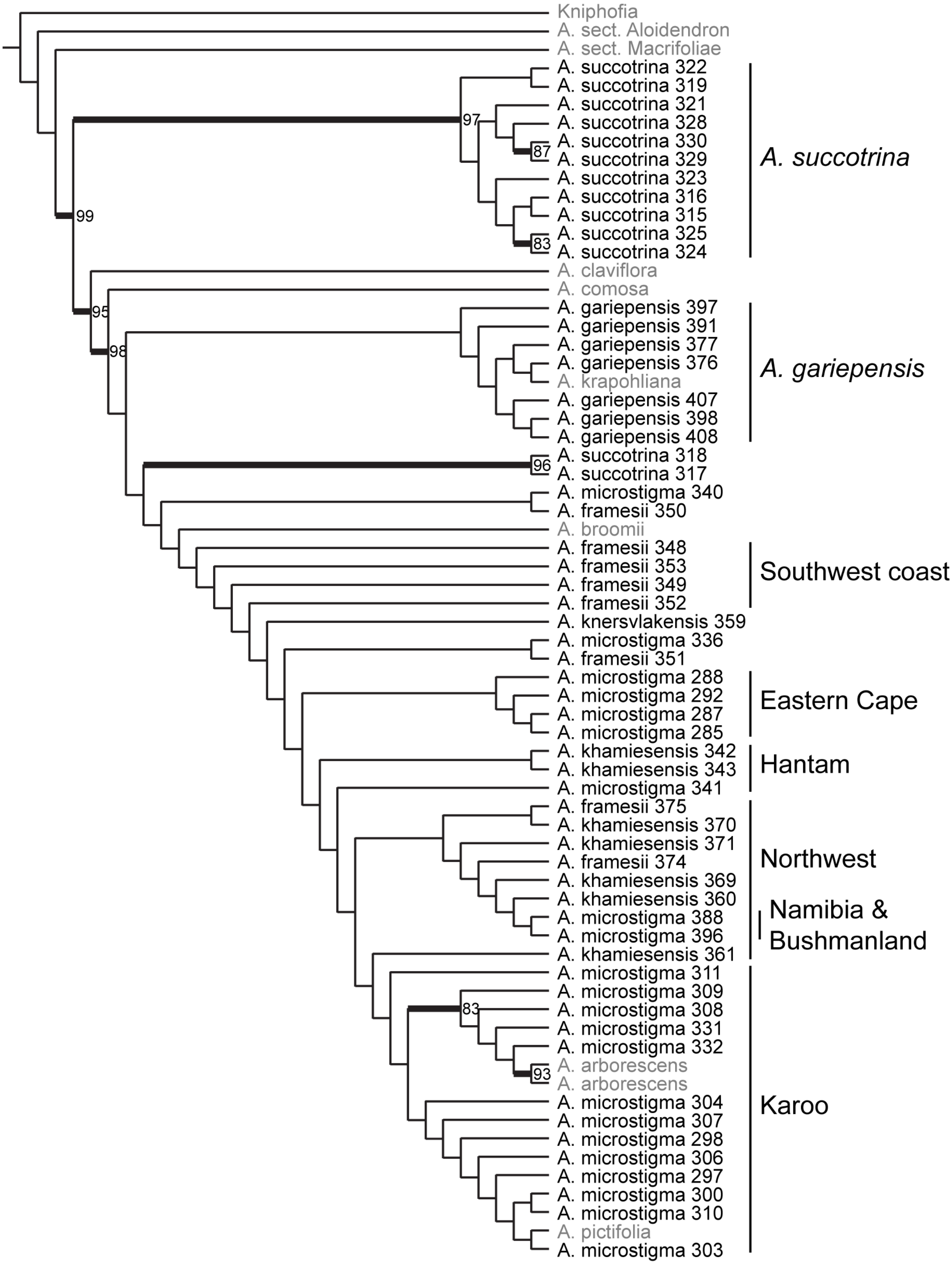


FIGURE 4. Combined *matK* and *ITS* tree. Bootstrap Percentage is shown for well supported nodes. Specimens with only one of the gene sequences are not included in this tree. Taxa in grey represent species that are not members of *A.* sect. *Purpurascentes*.
New classification: Eastern Cape, Karoo, and unnamed populations of *A. microstigma* = *A. microstigma* subsp. *microstigma*; Namibia and Bushmanland populations of *A. microstigma* = *A. microstigma* subsp. *juttae*; Northwestern populations of *A. khamiesensis* = *A. khamiesensis* subsp. *khamiesensis*; Hantam populations of *A. khamiesensis* = *A. khamiesensis* subsp. *hantamensis*; *A. knersvlakensis* = *A. khamiesensis* subsp. *knersvlakensis*; Northwestern and unnamed populations of *A. framesii* = *A. framesii* subsp. *framesii*; Southwest coast populations of *A. framesii* = *A. framesii* subsp. *maraisii*.

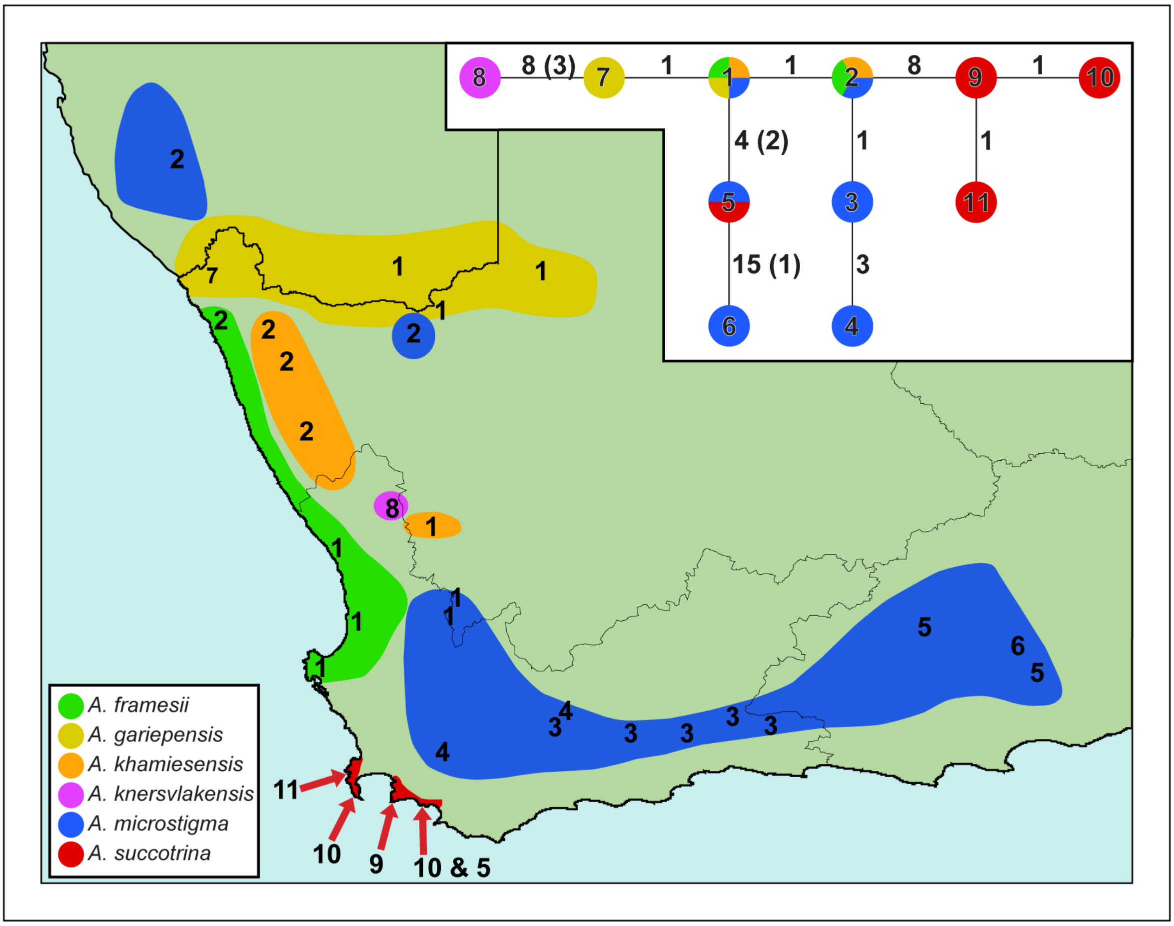


FIGURE 5. Minimum spanning network for members of *A.* sect. *Purpurascentes*. Allele numbers for specimens are indicated on the map at the collecting locality. Number of nucleotide differences between the alleles are shown adjacent to the connection lines. If the minimum number of possible mutations to obtain these differences are less than the number of nucleotide differences, then the number of mutational steps are indicated in brackets.
New classification: *Aloe knersvlakensis* = *A. khamiesensis* subsp. *knersvlakensis*.

Discussion of molecular evidence

In the most comprehensive molecular phylogeny available for the aloes (Grace *et al*. 2015), members of *A.* sect. *Purpurascentes* were not recovered in a single clade, but interspersed with other *Aloe* species (including some used as outgroups in the present study). The weak node supports and clustering of taxa from other sections among the members of *A.* sect. *Purpurascentes* in the molecular tree, prevents any conclusions regarding the coherence of the section based on the current molecular results. However, it highlights the complexity of evolutionary relationships among aloes. Despite its convincing morphological cohesion, *A.* sect. *Purpurascentes* as currently circumscribed, could be paraphyletic.

The recovery of *A. succotrina* as sister to the remaining members of *A.* sect. *Purpurascentes* and other sampled taxa, validates its status as a good species, whereas nodes for other *Purpurascentes* species were generally not supported. The notion that *A. succotrina* might not belong to *A.* sect. *Purpurascentes* is reinforced by its placement in the gene trees. This is further supported by the large number of mutational steps (eight) separating the alleles of *A. succotrina* from those of the rest of the *A.* sect. *Purpurascentes* species as observed in the minimum spanning network. The taxonomic interpretation of these results is limited due to the absence of good node supports for most of the taxa in the gene trees.

Two forms of *A. succotrina* that have historically been recognised [namely a Cape Peninsula/Table Mountain (*A. succotrina*) and a Hermanus/Kleinmond form (*A. purpurascens*)] are not distinguishable on the tree topology and there is little evidence to support their segregation into taxonomic units. These two forms are also not clearly separated in the minimum spanning network, as Allele 10 occurs in both mainland and Peninsula populations. Further sampling and better node supports will be necessary to interrogate the possibility that *A. succotrina* is more closely affiliated to *Aloe* sect. *Arborescentes*. Given that *A. succotrina* is the type species for *A.* sect. *Purpurascentes*, nomenclatural adjustments at this point would be premature.

The status of *A. gariepensis* as a robust taxon is supported by the clustering of specimens from this species. The suggestion that *A. gariepensis* may constitute multiple taxa is not upheld here, as the data from the present study do not support recognition of ecotypes as such. However, this might require further investigation owing to the fact that the western and eastern populations are represented by two different alleles (Alleles 1 and 7) in the minimum spanning network.

Conversely, the inconsistent recovery of specimens of *A. framesii* in the trees reflects the morphological variation within this taxon. In the minimum spanning network the northern and southern populations of this aloe are represented by two different alleles (Alleles 1 and 2), both of which are also found in other taxa. These results highlight the need for detailed investigation before the affinities and variation of the various populations will be fully understood.

The two specimens of *A. microstigma* (388 & 396) that were recovered in the northwestern clade of *Purpurascentes*, rather than in the main *A. microstigma* clades, represent the Namibian form of this species. It was described as *A. juttae* by M.K. Dinter in 1923, but regarded by Reynolds (1950) as conspecific with *A. microstigma*. Its clustering in the phylogenetic trees away from *A. microstigma* suggests that it should be reinstated, especially given its distinct morphological characters. This notion is further supported by the fact that it is represented by a different allele (Allele 2) in the minimum spanning networks than the southern populations of *A. microstigma*. On the other hand, specimens (*A. microstigma* 306, 307, 308 & 311) representing *A. brunnthaleri* (a yellow-flowering form of *A. microstigma* from north of the Swartberg) are not recovered in a clade in the gene trees. This form is represented by Alleles 3 and 4, which are also found in other Karoo samples. Providing taxonomic status to this colour variation is therefore not supported by the current results.

The consistent clustering of all specimens of true *A. khamiesensis* in the northwestern *Purpurascentes* clade (usually together with the Namibian and Bushmanland specimens of *A. microstigma* and the Port Nolloth specimens of *A. framesii*), highlights the pronounced geographical affinities of these very closely related species. This observation is strongly mirrored by the results from the minimum spanning network. The separate recovery of the Hantam form of *A. khamiesensis* (342 & 343) in the gene trees, as well as the morphological differences between these populations and those from Namaqualand, suggest that the Hantam form of *A. khamiesensis* warrants separate taxonomic status. This notion is further supported by the fact that this form is represented by a different allele (Allele 1) in the minimum spanning network than the specimens from the core distribution of *A. khamiesensis* (Allele 2). Similarly, *A. knersvlakensis* does not cluster with either *A. microstigma* or *A. khamiesensis* in the gene trees. It is also the sole taxon represented by Allele 8 in the minimum spanning network. All the results support the recognition of this aloe as a separate entity.

The molecular data of *A.* sect. *Purpurascentes* contains a much stronger geographic signal than a taxon level signal. Geographically isolated taxa (e.g., *A. knersvlakensis* and *A. succotrina*) tend to also be isolated in their evolutionary relationships. However, where the distribution ranges of taxa converge, this is reflected in the molecular results in a sharing of haplotypes. This is likely the result of interspecific hybridisation and resultant introgression of such haplotypes in these populations. These taxa likely represent a swarm that has descended from a common ancestor. They are still in the process of becoming more genetically and taxonomically distinct, and this development is slowed by ongoing introgression due to their geographic proximity.

The lack of resolution yielded by the *matK* barcode could be a result of the fact that this marker is apparently remarkably conserved with limited phylogenetic signal in many monocotyledon groups (Chase & Fay 2009). Resolution for *ITS* was negatively influenced by the presence of numerous ambiguous bases owing to the presence of multiple alleles at the same locus or multiple loci of this marker amplified within individuals, which prevent the attainment of readable sequences (Hollingsworth *et al*. 2011). The addition of further molecular markers might increase the resolution of the combined gene tree. The use of low-copy nuclear genes or microsatellites should be considered as an additional tool in future studies, as they have been reported to be useful in resolving close interspecific relationships in some plants (Powel *et al*. 1995, Sang 2002). At present, we caution against the use of molecular data alone for taxonomic changes in aloes, given the general low level of branch support and lack of resolution in some clusters.

Combined morphological-molecular results

The importance of combining molecular data with more traditional morphological character analyses has been debated extensively (Hillis 1987, Wheeler 2008, Ronse De Craene & Wanntorp 2011, De Almeida *et al*. 2023). Morphological characters may reflect information that is lacking in a purely molecular dataset. Morphology and molecular data are complementary and results from studies based on both sources are more informative than those where only one dataset was used (Hillis 1987, De Almeida *et al*. 2023). Therefore, morphological characters for the *A*. sect. *Purpurascentes* were mapped onto a pruned best-scoring maximum likelihood tree.

Species relationships among members of *A*. sect. *Purpurascentes* are elucidated on the basis of the three morphological characters: habit, inflorescence branching, and floral bract:pedicel length. The reconstructions indicated that ancestral states for the three characters analysed were likely to be a branched stem, simple inflorescence, and flowers with floral bracts shorter than the pedicels (Fig. 6).

Whereas *A. succotrina* is phylogenetically distinct, it is less morphologically distinctive on the basis of the three analysed characters. *Aloe gariepensis* is very distinct from the other species on the basis of floral bract:pedicel length ratio, providing additional support for the recovered clade containing all specimens of this species. None of the morphological characters support the proposed splitting of eastern and western populations of *A. gariepensis*. *Aloe khamiesensis*, and to a lesser extent *A. knersvlakensis*, are distinguishable from the other species on the basis of inflorescence branching. More importantly, both differ markedly from *A. microstigma* on the basis of habit. This supports their status as separate entities, i.e., not being conspecific with *A. microstigma*. *Aloe microstigma* is very constant in the branching of its inflorescence and floral bract:pedicel length, but is variable in terms of its habit. The recognition of *A. brunnthaleri* is not supported by these results. The Namibian form of *A. microstigma* is supported to some degree by habit. As with the variable habit of *A. microstigma*, no geographical pattern was observed in the results for any of the characters that can be used for infraspecific delimitation of *A. framesii* populations.

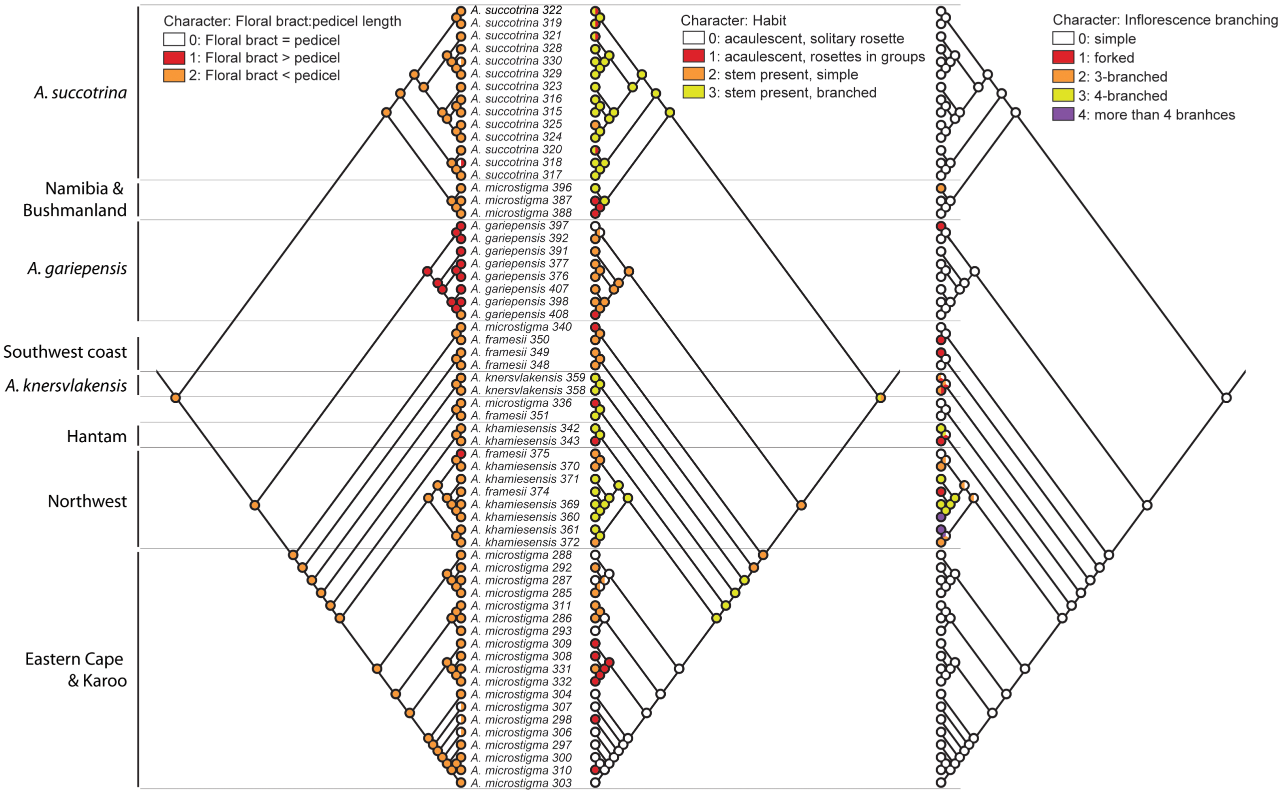


FIGURE 6. Morphological features mapped on the best-scoring maximum likelihood tree for *ITS* and *matK* combined.

New classification: Eastern Cape, Karoo, and unnamed populations of *A. microstigma* = *A. microstigma* subsp. *microstigma*; Namibia and Bushmanland populations of *A. microstigma* = *A. microstigma* subsp. *juttae*; Northwestern populations of *A. khamiesensis* = *A. khamiesensis* subsp. *khamiesensis*; Hantam populations of *A. khamiesensis* = *A. khamiesensis* subsp. *hantamensis*; *A. knersvlakensis* = *A. khamiesensis* subsp. *knersvlakensis*; Northwestern and unnamed populations of *A. framesii* = *A. framesii* subsp. *framesii*; Southwest coast populations of *A. framesii* = *A. framesii* subsp. *maraisii*.

Usefulness of DNA barcodes in *Aloe*

The application of DNA barcodes is based on the principle that a short standardised sequence can differentiate among individuals of distinct species, because the genetic variation among species is larger than that within species (Hajibabaei *et al*. 2007). Therefore, DNA barcodes only work if sequence variation between species is high enough to discriminate the species. Yet, it must also be low enough within a species to be able to define a clear threshold between intra- and interspecific genetic variation (Lahaye *et al*. 2008).

Discrimination ability of DNA barcodes at species level varies considerably amongst different plant groups. In certain taxa barcodes can only identify species groups (usually a local group of close relatives) rather than individual species (Hollingsworth *et al*. 2011). The likelihood of identifying species through DNA barcodes is significantly lowered by factors such as very narrowly defined species, frequent hybridisation especially where hybrids are fertile, frequent polyploidy, recent radiation, continuously large historical population sizes where ancestral polymorphisms are maintained, long lifespans, slow mutation rates, and limited seed dispersal (Hollingsworth *et al*. 2011).

It was anticipated that the largest contribution of DNA barcodes would be to species-level plant taxonomy in terms of defining and delimiting species, and furthermore, that such barcodes might assist in the discovery of new taxa in some plant groups (Hollingsworth *et al*. 2011). A further application of DNA barcodes that has recently emerged is to identify protected plant species in trade. This is especially important for distinguishing species listed on the appendices of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES; http://www.cites.org/eng/app/index.php) and/or on the list of South African Threatened or Protected Species [TOPS; as regulated by the National Environmental Management: Biodiversity Act (NEMBA), No. 10 of 2004 (Chapter 4, Part 2)], from related or morphologically similar species that are not listed. For most plants included on CITES appendices, the entire genus or family is listed, rather than individual species. Therefore, even with its current limitations, DNA barcoding can be useful in this regard, since identification to a higher taxonomic group (for example a genus or family) is all that is required (Hollingsworth *et al*. 2011).

Aloes are highly sought after by collectors worldwide and illegal trade of especially seedlings and juvenile plants, which are difficult to accurately identify based on morphology, is not uncommon. Barcodes are potentially useful to identify plant material, but the effectiveness of these molecular tools on species level identification in aloes has not been widely tested. Since all species of aloe (except *Aloe vera*) are listed on the appendices of CITES (CITES 2023, see also Grace & Klopper 2014), identification to genus level will be sufficient. However, not all South African aloes are listed on TOPS (M. Pfab, pers. comm.) and DNA barcodes will thus need to discriminate at species level for it to be of any use in identifying TOPS species. *Aloe* sect. *Purpurascentes* was chosen as a test case to see if DNA barcodes can provide additional distinguishing evidence at species level. This is only the second time (see Ellis 2013) that molecular data is included in the taxonomic revision of a group of aloes.

The earliest study on *Aloe* making use of molecular data (Adams *et al*. 2000) showed that geography plays an important role in defining relationships among aloes (Grace & Rønsted 2013). It was illustrated that species within the same geographical area seem to be more closely related to each other, than to morphologically similar species from other areas, possibly due to factors such as interspecific hybridisation. This notion is also strongly supported by the results from the present study.

Within *A.* sect. *Purpurascentes*, DNA barcodes are able to identify certain species (*A. succotrina*), but the majority cluster in a group of closely related species (namely *A. framesii*, *A. gariepensis*, *A. khamiesensis*, and *A. microstigma*). Ellis (2013) obtained similar results for *rbcL+matK* during a phylogenetic analysis of the rambling aloes in genus *Aloiampelos* Klopper & Gideon F.Sm. in Grace *et al.* (2013a: 10) [=*Aloe* sect. *Macrifoliae* (Haworth 1825: 280) Glen & Hardy (2000: 92)]. The results from the present study and those by Ellis (2013) support the notion by Fazekas *et al.* (2008) that there will always be certain plant groups that are better resolved by a region other than the chosen DNA plant barcode.

In the results from the present study there is limited branch support and the majority of species (apart from *A. succotrina*) do not form monophyletic groups. There is thus no correlation between the support for species monophyly and the ability of barcode markers to distinguish species. This is the main point on which species-level resolution of DNA is tested (Fazekas *et al*. 2008).

DNA barcodes can only be applied successfully for the identification of species if there has been sufficient time since speciation to allow for mutations and/or drift to become fixed in the genetic characters of the conspecific populations, so that they can be distinguished from other species. Barcodes may be shared between related species if the speciation in the group has been very recent or if mutation rates are very slow (Hollingsworth *et al*. 2011). In groups, such as the aloes, where evidence suggests recent and rapid radiation (Grace *et al*. 2015), DNA barcodes will likely not provide adequate information at species level (Hollingsworth *et al*. 2011).

Furthermore, the often narrowly defined species within taxonomically complex groups are unlikely to be identified to species level by barcodes. Such complex groups are often the result of speciation through processes such as recurrent ploidy transitions, apomixes, recent hybrid speciation, as well as recurrent ecotypic taxon origins (Hollingsworth *et al*. 2011). The latter two, especially, are very prevalent amongst the aloes and are probably some of the main speciation processes within the group. Hybridisation results in the sharing of plastid haplotypes among species, which prevents species identification with barcodes even in groups where species limits are clear morphologically (Hollingsworth *et al*. 2011). *Aloe* sect. *Purpurascentes*, and probably aloes in general, are often good examples of this.

Therefore, probably the most important of the three criteria for the selection of DNA barcodes (CBOL Plant Working Group 2009), i.e., discrimination power at species level, were not met in the present study on *A.* sect. *Purpurascentes*, nor in the study of Ellis (2013) on *Aloiampelos* (=*Aloe* sect. *Macrifoliae*). Based on these separate investigations, the results could well be extrapolated to the genus *Aloe* as a whole, as well as the other alooid genera. Several of the factors mentioned by Hollingsworth *et al*. (2011) that lower the likelihood of DNA barcodes to be able to identify species are very much prevalent in *A.* sect. *Purpurascentes* in particular and aloes in general. These factors include narrowly defined species, frequent hybridisation, recent radiation, retention of ancestral alleles, limited seed dispersal, and a comparatively long lifespan, including clonal proliferation.

The present study provides a revised classification of *A.* sect. *Purpurascentes* based on morphological and other characters. Such a robust classification is essential to form a basis for applied molecular studies. At this stage the popular *ITS* region and *matK* barcode do not seem to be a suitable method for identification of aloes to species level. Nonetheless, it is sufficient to identify species groups and adequate to assist with genus level identification of material in terms of CITES regulations. However, since barcodes do not distinguish species of aloes at this point, it will not be useful for the identification of traded material that might potentially be obtained of Threatened or Protected Species of aloes (TOPS listed species).

Even though DNA barcodes can facilitate the taxonomic process, the identification and description of new species will likely continue to be done through comprehensive taxonomic work (Hajibabaei *et al*. 2007). Taxonomic changes implemented here in the revision of *A.* sect. *Purpurascentes* and recently in several other aloes (Klopper & Smith 2009, 2010, Castillon & Castillon 2010, Klopper *et al*. 2011, 2014, Smith *et al*. 2012a, 2016, 2020, 2021, 2022, Smith & Lautenschlaeger 2021, Smith & Klopper 2021b, 2022a, 2022b, Smith & Figueiredo 2022), were based mainly on morphological studies of herbarium specimens and extensive fieldwork to investigate the characters of living plants and their population dynamics. These characters were sufficient to elucidate the relationships and status of these taxa. Since traditional barcoding approaches have limited resolution in recently-evolved lineages, such as we hypothesise is the case with *A.* sect. *Purpurascentes*, morphology remains the most powerful tool with which to evaluate species relationships.

Phytogeography

Recent phylogeographic studies (Grace *et al*. 2015) have shown that ancestral aloes most probably originated in southern Africa some 19 million years ago (Ma) during the early Miocene. It was suggested that vicariance and peripheral isolation played a significant role in the speciation of aloes (Grace *et al*. 2015).

In a phylogeny for the aloes (Grace *et al*. 2015), members of *A.* sect. *Purpurascentes* are recovered in a clade with other South African aloes. Although the existence of an arid corridor between southern and northeastern Africa is not refuted (see Van Wyk & Smith 2001), the affinities of *A.* sect. *Purpurascentes* clearly lies within South Africa. The restricted geographical distribution of most taxa in *A.* sect. *Purpurascentes* and the huge molecular and morphological similarity between the taxa, indicate that these taxa form a natural group of closely related taxa.

The majority of species in *A.* sect. *Purpurascentes* can be viewed as a taxon complex, with *A. succotrina* as an outlying species. *Aloe microstigma* is the core species with the largest distribution range and greatest abundance. Peripheral to it are *A. framesii*, *A. gariepensis*, and *A. khamiesensis* (including *A. knersvlakensis*). All members of this complex are extremely conservative in the morphology of the flowers. The main character distinguishing *A. gariepensis* is the relative length of the floral bracts and pedicels, while *A. khamiesensis* is characterised by its often caulescent habit and the degree of branching of the inflorescence. It is, however, not always easy to draw distinct boundaries around these taxa. For instance, *A. knersvlakensis* can be seen as an intermediate between *A. khamiesensis* and *A. microstigma* (B. Kemble, pers. comm.). Such transitional populations can well be the result of introgression (in the case of *A. knersvlakensis*: possible introgression between *A. khamiesensis* and *A. microstigma*). The variable nature of members in this group could likely be explained through introgression following hybridisation with other aloes occurring in close proximity. In this light, the glaucous colour of the leaves in *A. gariepensis* plants from around Keimoes, could perhaps be explained by introgression with *A. hereroensis* Engler (1888: 2) (B. Kemble, pers. comm.).

Between the Pliocene and Pleistocene ice ages (2 million to 150 000 years ago), the Cape Peninsula was periodically isolated from the mainland by shallow marine transgressions for long periods of time (Compton 2004). This may have led to the isolation of *A. succotrina* populations on the Peninsula from those in mainland populations, leading to morphological differences between plants of the two areas. *Aloe succotrina* is restricted to sandstone formations and thus has a limited distribution. Furthermore, pollinators of flora on mountainous areas do not move over the flat, lowlying areas surrounding the Cape Mountains. This, together with its limited seed dispersal abilities, further restricts gene flow between populations, thus effectively isolating it from the rest of the members of *A.* sect. *Purpurascentes*. It is thus not surprising that chemically, morphologically, and genetically, *A. succotrina* is significantly different to the rest of the species in the section.

Aloe gariepensis occurs along the Orange River in the Gariep Centre of Endemism. This local centre of endemism has affinities with arid areas in northeastern Africa owing to the existence of a suggested arid corridor during arid periods of the Pleistocene (Van Wyk & Smith 2001). Furthermore, it also has floristic links (often disjunct) to areas where other members of *A.* sect. *Purpurascentes* occur, namely the Knersvlakte and Klein Karoo (Van Wyk & Smith 2001). Although the general climate of the area is harsh, the influence of the cold Benguela Current and the influx to the interior of winter rain along the Orange River Valley has buffered the region against huge fluctuations. It is thus a stable refuge and an area where several succulent groups seem to be in a state of active speciation (Van Wyk & Smith 2001). Even though there are definite morphological differences between eastern and western populations of *A. gariepensis*, none of the results from this study support their recognition as separate entities. These forms may be mere ecotypes, or the onset of active speciation has been too recent to infer any taxonomic status to the forms.

Aloe microstigma has the widest distribution of the members of *A.* sect. *Purpurascentes*. It is morphologically very variable throughout its range. No clear geographical or morphological distinctions could be made in the results of this study. The regional variation present in *A. microstigma* is thus masked by continued gene flow, especially among the southern populations of this aloe. Although there were no clear distinctions based on morphology, the molecular results do suggest some geographic separation. The molecular results recognise the geographical clustering of northern and southern populations of *A. microstigma*. However, the observed morphological differences between these disjunct populations are not adequately reflected in the result from the present study. If habit and relative leaf length:width could be added to the analyses, more support might be gained for recognising the northern populations as a distinct entity.

Aloe microstigma occurs in several local centres of endemism (sensu Van Wyk & Smith 2001), most notably the Albany, Klein Karoo, Worcester-Robertson Karoo, and Hantam-Roggeveld Centres in the south, and the Gariep Centre in the north. The Albany and Klein Karoo Centres are especially strongly linked from a floristic perspective with clear migration corridors along the mountains and valleys connecting these regions. The Worcester-Robertson Karoo Centre has stronger affinities with the Cape Floristic Region, and also with the Hantam-Roggeveld Centre, than with the Klein Karoo (Van Wyk & Smith 2001). It is noteworthy that some of the most striking morphological variations of *A. microstigma* occur in the Worcester-Robertson Karoo (e.g., caulescent plants, unicoloured red inflorescences). The Klein Karoo, Groot Karoo, and Albany regions have well-developed migration routes between them, whereas the Worcester-Roberston area is somewhat isolated from these by the mountains surrounding the Breede River Valley. The connections between the southern populations of *A. microstigma* are still fairly recent. There has probably not been sufficient time to develop gene flow barriers and marked morphological differences beyond the relatively heterogeneous concept for this species.

The northernmost populations of *Aloe microstigma* are restricted to the Gariep Centre of Endemism. However, unlike *A. gariepensis,* this aloe is not known from the Orange River Valley, but occurs on isolated mountains to the north and south of the river. There are strong floristic links between arid northwestern South Africa including bordering southern Namibia and the Albany and Klein Karoo Centres of Endemism with numerous taxa that are shared between these areas (Van Wyk & Smith 2001, Steyn *et al*. 2019). The disjunct distribution of *A. microstigma* further supports the floristic affinities of these areas. Vicariance events that gave rise to these disjunctions probably occurred a long time ago, as many of the taxa with such a distribution pattern can already be separated at infraspecific or even species level, e.g., members of the *Aloe striata*-complex (Van Wyk & Smith 2001). The northern populations of *A. microstigma* have thus undoubtedly been isolated from the southern populations for a sufficient amount of time to permit the establishment of gene flow barriers. This is reflected in the results from the molecular analyses of this study and supports recognition of the northern populations as separate from the southern populations.

Convincing evidence was obtained to recognise *A. khamiesensis* as a good species. Both molecular and morphological results suggest a very close affinity of this aloe with *A. knersvlakensis*, while the Hantam populations are sufficiently different to be recognised as a separate entity. The geology of the Kamiesberg predominantly consists of gneiss and granite that supports an outlier of Fynbos vegetation (and a core Cape floristic element) in a Succulent Karoo matrix. The Kamiesberg is likely a buffer of stability within a more variable environment and thus supports a unique flora. A presumed corridor existed between the Cape Fold Mountains and the Kamiesberg, along the Roggeveld and Bokkeveld Escarpment, as well as the highlands of the Calvinia (Hantam)-Loeriesfontein-Kliprand region (Van Wyk & Smith 2001). *Aloe khamiesensis* is strongly centred around the Kamiesberg, while the distribution of the Hantam populations and *A. knersvlakensis* falls within this corridor. These aloes thus provide further support for the supposed dispersal route for Cape taxa and the affinities of the Kamiesberg and Hantam-Roggeveld Centres of Endemism.

Aloe framesii mostly occurs in an ecotonal zone between Fynbos or Succulent Karoo and azonal coastal vegetation. The environment in which this aloe grows is thus not stable. Populations constantly need to adapt to different environmental factors and pressures, adding to the bewildering variation in morphology seen between populations. Most populations of *A. framesii* are usually sufficiently geographically isolated, as a result of both natural and anthropogenic influences, to limit possible gene flow among them. The distance between the northern and southern populations arguably is greater than the foraging capabilities of most pollinators. It is therefore not surprising to find the extreme morphological variation exhibited between different populations of this aloe, which is to some extent also reflected in the molecular results of this study. Southern and inland populations of *A. framesii* are invariably found on rocky outcrops of Sandstone Fynbos and Strandveld Fynbos vegetation, where they are to some degree protected from frequent fires. Northern populations (Papendorp, Kleinzee, and Port Nolloth) more often grow on sandy flats in Succulent Karoo Strandveld and Duneveld, where they form long stems and huge clumps of very old plants in the absence of fire. There is reason to recognise three distinct entities (northern, southern, and inland or eastern) in this species, based on both the molecular and morphological evidence presented here.

General discussion

The same level of morphological variation as encountered in, for instance, certain members of *A.* sect. *Purpurascentes* (for example *A. gariepensis*, *A. microstigma*, and especially *A. framesii*) is frequently found in other aloes. It is, however, not always well understood and is therefore often treated variously in different groups of aloes. Since aloes are charismatic plants and commonly found in succulent plant collections, there is a trend towards the recognition of micro- or pseudo-species that are based on small morphological differences, sometimes for the benefit of collectors. Although this inclination should not drive the taxonomy of the genus, it is still important to classify and formally label the existing variation within taxa. In this regard, one way of dealing with the observed variation is to make use of infraspecific categories (subspecies, variety, subvariety, forma, and subforma), or informal labels.

A general expectation is that clines of characters will grade into each other in a single direction from one part of the distribution range to the next. However, this transitional geographic pattern variation is not found in *A. microstigma*, where the morphological variation, in especially the characters of the leaves, is quite random. Plasticity in morphological characters is often influenced by the environment. For example, extreme red colouration in the leaves of some populations of this species is induced by the very harsh arid climate of the area in which the plants grow. This is especially evident when such a character is lost in cultivated material (B. Kemble, pers. comm.). Several other factors might also influence the absence of variational clines. The most obvious of these in the case of aloes could be hybridisation. In nature, the inevitable incorporation of hybrids back into a breeding population can lead to a convergence of characters, especially if the process has been ongoing for a long period of time. The possibility of hybridisation in the aberrant populations of *A. microstigma* near Fraserburg for instance (B. Kemble, pers. comm.) could not be excluded, especially given the close proximity of *A. chlorantha*, itself reputed to be of hybrid origin (Viljoen 1999), with *A. broomii* and *A. microstigma* (or a relative) its putative parents.

Hybridisation is an important evolutionary stimulus that results in reticulate evolution. For this reason many aloes are likely of polyphyletic origin, often due to successive introgression. This is clearly supported by chemical studies on aloes (Viljoen 1999). In large species complexes, morphological and genetic characters can evolve at different rates. Speciation in *Aloe* likely follows a similar pattern, where the impact of breeding isolation and selection pressure on the formation of discontinuities have not been sufficient to create the discontinuities that are found in groups with highly divergent character states (Viljoen 1999).

Hybridisation is very widespread throughout the genus. For example: the numerous granite-gneiss outcrops near Tolañaro, southeastern Madagascar, harbour a multitude of crosses between mainly *A. bakeri* Scott-Elliot (1891: 60), *A. werneri* Castillon (2007: 23), and *A.* cf. *ruffingiana* Rauh & Petignat (1999: 271). Several of these hybrids produce fertile seed, which results in a confusing array of second-generation crosses. However, in certain cases the hybrids seemed to have stabilised and produce uniform offspring. *Aloe bruynsii* Forster (2003: 53) resembles a well delimited species, but might likely be an example of such a stabilised hybrid (Castillon & Castillon 2010, Carter *et al*. 2011). Another example is the complex containing *A. versicolor* Guillaumin (1950: 723), *A. versicolor* var. *steffanieana* (Rauh 2000: 73) Castillon & Castillon (2010: 28), *A. bernadettae* Castillon (2000: 136), *A. buchlohii* Rauh (1966a: 2), *A. schomeri* Rauh (1966b: 22), and *A. werneri* from southeastern Madagascar. In this group Castillon & Castillon (2010) similarly concluded that 'geographic proximity is in accordance with the morphological proximity of plants'. There are also several intermediate forms present in certain localities, making it difficult to delimit clear boundaries between these taxa. Furthermore, it is virtually impossible to ascertain if these plants have the same origin, or whether the intermediate forms encountered are the result of hybridisation between the extreme forms (Castillon & Castillon 2010).

The immense popularity of aloes in horticulture and the general ease with which interspecific hybrids are formed further increases the possibility of introgression of foreign alleles in natural populations (see for example Smith & Klopper 2021a). The two aberrant samples of *A. succotrina* (317 & 318) from Hermanus are good examples of this. The population where these samples were collected is in very close proximity to several urban gardens where a range of aloes are cultivated. The Hermanus *A. succotrina* plants contain an allele that is present in *A. microstigma* from the Eastern Cape. This is likely the result of a recent hybridisation event, where *A. succotrina* in the natural population around Hermanus came into contact with possibly one or more *A. microstigma* plants of Eastern Cape origin (or another Eastern Cape aloe that shares the same allele) that were cultivated in a nearby garden. The Eastern Cape allele was thereafter spread through the natural population through introgression, even though the expression of phenotypic characters of *A. succotrina* was largely retained. Introgression between naturally occurring and cultivated aloes may lead to large scale genetic 'contamination' of natural populations. This results in reticulate evolution and obscures the affinities and origin of aloes in general. Such events will decrease the value of molecular markers in elucidating the evolutionary history of these plants.

It is important to note that aloes are rarely self-fertile. In general, outbreeding is therefore necessary for sexual reproduction. Even though numerous natural hybrids are known among the aloes (Reynolds 1950, Smith & Figueiredo 2019, Smith 2020), there are several examples of different aloes that grow in close proximity, but that do not cross because of reproductive barriers, such as differences in, for instance, flowering time (Castillon 2011).

The taxa currently recognised in *A.* sect. *Purpurascentes* do not form monophyletic groups in the results obtained from the molecular analysis done as part of the taxonomic revision of this group of aloes. Results from a molecular study on another genus in Asphodelaceae subfam. Asphodeloideae, namely *Kniphofia*, has resulted in similar 'rampant non-monophyly' (Ramdhani *et al*. 2009). The reasons postulated for this rather unexpected phenomenon in *Kniphofia*, could well be extrapolated and applied to the genus *Aloe* as well. It has been shown by several studies (see Ramdhani *et al*. 2009 and references therein) that 'low sequence divergence has been implicated in recent radiations', resulting in morphologically distinguishable species appearing as non-monophyletic in molecular studies. In recently radiated species there may not have been sufficient time for the development of reproductive barriers, and in particular not enough accumulated DNA base pair mutations to serve as reliable molecular markers. This also leads to a high degree of hybridisation between related species and a mixing of haplotypes (Ramdhani *et al.* 2009). It has been suggested that recent speciation and simultaneous ongoing hybridisation in *Haworthia* Duval (1809: 7) *s.l.* accounts for the high degree of non-monophyly that is seen in this close relative of *Aloe*. This also explains the complex taxonomy of the group and the large amount of range-restricted taxa found among the haworthioids (Ramdhani *et al.* 2011), and probably the alooids in general. Furthermore, incomplete lineage sorting can lead to differences between morphologically delimited species and plastid genotypes (Avise *et al*. 1990, Ramdhani *et al*. 2009). Due to patterns of maternal lineage survival and extinction during the process of speciation, it is entirely possible that certain individuals of a species may be genetically more closely related to another species than to other members of their own species (Avise *et al*. 1987, Ramdhani *et al*. 2009). As a result these species will appear to be non-monophyletic.

This latter notion is especially well illustrated by the results from the molecular analyses, and especially those from the population genetics methods, done on *A.* sect. *Purpurascentes* as part of the present study. The DNA of these aloes has a much stronger geographic signal than a taxon-level signal. This may be the result of incomplete lineage sorting, as well as factors such as recent radiation, poor gene flow between isolated populations of the same species and hybridisation (especially where hybrids are fertile, which is often the case in aloes) with related species in close geographical proximity. The latter two processes may also explain the huge morphological variation seen in different populations of the same species, like *Aloe framesii* for instance. Poor gene flow (through pollen and seed dispersal) among populations of *A.* sect. *Purpurascentes* in particular, and aloes in general, is likely very prevalent. It has been shown that seed dispersal distance in tall-stemmed aloes [*Aloe marlothii* Berger (1905: 87) and *Aloe ferox*] is on average 30 m, but can be up to 50 m in strong winds (Symes 2012). None of the members of *A.* sect. *Purpurascentes* are as tall as the often 3–5 m plants found in *Aloe marlothii* and *Aloe ferox*, with *Aloe khamiesensis* reaching heights of 2 m, but rarely more. It can therefore be expected that the wingless seeds of these short-stemmed or acaulescent aloes will be dispersed over much shorter distances. Pollinators of these aloes (like sunbirds and insects, such as nectar- and/or pollen-collecting bees) will not necessarily travel between fragmented and distant populations of a species, thus eliminating the flow of genes between isolated populations. The lack of genetic exchange between populations results in morphological changes developing between populations over time, for example in the different populations of *Aloe framesii*. This can be seen as a possible start of the speciation process and pollinators could possibly have an effect on aloe diversification and speciation by limiting gene flow between populations.

Vicariance and genetic drift undoubtedly play important roles in the speciation process in aloes. As explained above, gene flow in aloes probably occurs only over short distances. This leads to vicariance due to physical barriers to gene flow. Isolated populations are formed, which in turn increases the influence of genetic drift. The latter process is especially important in small populations, as mutations will largely become either fixed or eliminated, irrespective of the selective value of such mutations (Runemark 1970). In this respect *A. khamiesensis* subsp. *knersvlakensis* is a very good example.

Taxonomic treatment

Key to the taxa

It is important to note that the identification key provided here for the members of *A.* sect. *Purpurascentes* will likely only be fully valuable for natural populations or where the provenance of a plant is known. In some cases it might not be possible to accurately identify cultivated plants of this section, especially where the precise origin of the parent plants are uncertain, for reasons discussed above.

1a Leaves with pale or white marginal teeth; floral bracts turning purple with age; occurring from the Cape Peninsula to Hermanus, Western Cape .... **5. *A. succotrina***
1b Leaves with reddish brown marginal teeth; floral bracts not turning purple with age; not occurring from the Cape Peninsula to Hermanus, Western Cape 2
2a Racemes with floral bracts longer than pedicels .... **2. *A. gariepensis***
2b Racemes with floral bracts shorter than pedicels or sometimes of almost equal length 3
3a Arborescent plants with tall erect stems of up to 2 m; inflorescences branched 4
3b Acaulescent or shortly caulescent plants with stems shorter than 0.5 m; if stems longer than 0.5 m, then stems are decumbent 6
4a Leaves yellowish green, with marginal teeth 3–5 mm long; flowers 21–33 mm long; occurring in the Hantam region .... **3b. *A. khamiesensis* subsp. *hantamensis***
4b Leaves dull green to reddish brown, with marginal teeth 1–3 mm long; flowers 28–35 mm long; not occurring in the Hantam region 5
5a Leaves with marginal teeth 2–3 mm long; inflorescence 4- to 8-branched; buds and flowers at anthesis orange-red, 30–35 mm long .... **3a. *A. khamiesensis* subsp. *khamiesensis***
5b Leaves with marginal teeth 1–2 mm long; inflorescence 2- to 4-branched; buds orange-red, flowers at anthesis yellow, ± 28 mm long .... **3c. *A. khamiesensis* subsp. *knersvlakensis***
6a Occurs from the Eastern Cape, through the Karoo to the Tankwa Karoo and Hantam regions, Bushmanland, Richtersveld and southern Namibia 7
6b Occurs along the West Coast and in the Cederberg area 8
7a Rosettes usually solitary, sometimes in groups; leaves 6–8 cm wide; marginal teeth 2–4 mm long; inflorescence always simple; pedicels 25–30 mm long and longer than floral bracts (10–25 mm) .... **4a. *A. microstigma* subsp. *microstigma***
7b Rosettes always in groups; leaves 2.5–4.5 cm wide; marginal teeth 0.5–2.0 mm long; inflorescence sometimes simple, often up to

3-branched; pedicels 20–28 mm long and about as long as floral bracts (12–20 mm) .... **4b.** ***A. microstigma*** **subsp.** ***juttae***

8a Leaves grey-green, often obscurely lineate; racemes 30–40 cm long; inland distribution, occurs on sandstone in Fynbos .... **1b.** ***A. framesii*** **subsp.** ***amoena***

8b Leaves bluish green, not often obscurely lineate; racemes 20–30 cm long; coastal distribution, occurring in Strandveld Fynbos and Succulent Karoo Duneveld and Strandveld **9**

9a Plants with short or more often long semi-erect to decumbent stems; floral bracts 11–16 mm long; pedicels usually 16–20 mm long; flowers 25–35 mm long; occurs in Succulent Karoo vegetation .... **1a.** ***A. framesii*** **subsp.** ***framesii***

9b Plants sometimes acaulescent or usually with short, often decumbent stems; floral bracts 14–20 mm long; pedicels usually 20–30 mm long; flowers 40–45 mm long; occurs in Fynbos .... **1c.** ***A. framesii*** **subsp.** ***maraisii***

Aloe **sect.** ***Purpurascentes*** Salm-Reifferscheid-Dyck (1842: 22)

Homotypic synonym:—Aloe ser. *Purpurascentes* (Salm-Dyck) Berger (1908: 282). Type:—*Aloe succotrina* Weston (1770: 5).

The species and infraspecific taxa are arranged in numerical sequence following the numbering preceding taxon names in the key. Herbarium vouchers that were included in the macro-morphological, molecular, and combined analyses, as well as other specimens examined are listed under the relevant taxa. Here the use of the specimens in the various analyses are indicated by a superscript letter following the herbarium code: macro-morphological (^{m}), molecular (^{g}), and combined analyses (^{c}).

1. ***Aloe framesii*** Bolus (1933: 140)

Homotypic synonym:—Aloe microstigma subsp. *framesii* (L.Bolus) Glen & Hardy (2000: 107). Lectotype (designated here):—SOUTH AFRICA. Northern Cape: Coastal belt north of Port Nolloth, August 1929, fl. hort. Frames July–August 1930, *P. Ross Frames BOL19186* (lectotype BOL BOL140202! [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.bol140202]).

Epitype (designated here):—SOUTH AFRICA. Northern Cape: Coastal belt north of Port Nolloth, fl. hort Frames, no date, *P. Ross Frames BOL19186* (epitype BOL BOL140201! [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.bol140201]).

Note regarding type:—There are two specimens at Herb. BOL labelled '*fld. hort. Frames BOL19186*' (BOL140201 and BOL140202). Both sheets are annotated with a red 'Type' label. Sheet BOL140201 consists of an inflorescence, two leaves, and an envelope with pressed perianth segments and dissected flowers. The specimen labels of this sheet does not contain a date or collector, but merely states 'Coastal belt north of Port Nolloth, fld. hort. Frames', followed by 'June 29' that is struck through. Sheet BOL140202 consists of a single inflorescence, and envelopes containing mounted floral bracts and perianth segments. The label of this sheet indicates that it was collected by P. Ross Frames in August 1929 and flowered in his garden in July–August 1930 (initially written as '1929', but struck through with '1930' written above it) when the specimen was evidently made. A hand-written note is attached to the sheet, containing descriptive information that was based on a plant collected at the type locality by M. Schlechter and that flowered in the Kennilworth, Cape Town, garden of Mr Frames in August 1933 (a specimen collected in 1932 by Schlechter from Port Nolloth, 'ex hort. Frames, Aug. 1933', is present in Herb. BOL). In the protologue Bolus (1933: 140) states that the description of *A. framesii* is based on a plant collected in Namaqualand in August 1929 and that flowered in the garden of Mr Frames in June 1930. The sheet BOL140202 most closely matches the information provided in the protologue and is here designated as lectotype. Since the lectotype only consists of an inflorescence, sheet BOL140201 (also containing leaves) is here designated as epitype to compliment the lecotype.

1a. ***Aloe framesii*** **subsp.** ***framesii*** (Fig. 7)

Type:—As for *A. framesii*.

Description:—Shortly caulescent plants. *Stem* 0.5–1.0 m long, erect to decumbent, freely branching from base to form dense groups, with persistent dried leaves. *Leaves* densely rosulate, incurved or erectly spreading, bluish green, often with a reddish tinge, usually with only a few white spots on both surfaces, often towards the base of the leaf, lanceolate-attenuate, 30–35 cm long, 6–7 cm wide at base; margin with pungent, deltoid, reddish brown teeth, 3–4 mm long, 7–10(–13) mm apart; exudate honey-coloured, drying to purplish tinged. *Inflorescence* usually single, up to 0.7 m high, erect, simple or 2-branched, only rarely up to 3-branched from middle or lower, branches ascending. *Peduncle* ± 1.4–1.7 cm wide and plano-convex below, terete upwards, reddish green; with several sterile bracts when simple, ovate-acute, ± 17 mm long, (11–)18–23 mm wide, pale brownish, thin scarious, many-nerved. *Racemes* conical to cylindric-acuminate, 21–30 cm long, ± 10 cm wide, erect, dense; buds erect to spreading, flowers nodding to pendent when open. *Floral bracts* ovate-acute, amplexicaul below, 11–16 mm long, 5–6 mm wide, pinkish, rather fleshy to thin and scarious, many-nerved. *Pedicels* 16–20(–25) mm long, pinkish. *Flowers: perianth* orange-red with greenish yellow tips, 25–35 mm long, 5–6 mm across ovary, not narrowed above ovary, slightly widening to 6–7 mm towards middle, slightly narrowing to ± 5 mm at mouth, cylindric-trigonous; outer segments free to base, tips straight to slightly spreading; *stamens* with yellow filiform-flattened filaments, exserted portion turning brown, exserted to 5 mm; *ovary* 6.0 × 3.5 mm, green; *style* yellow, exserted to 6 mm.

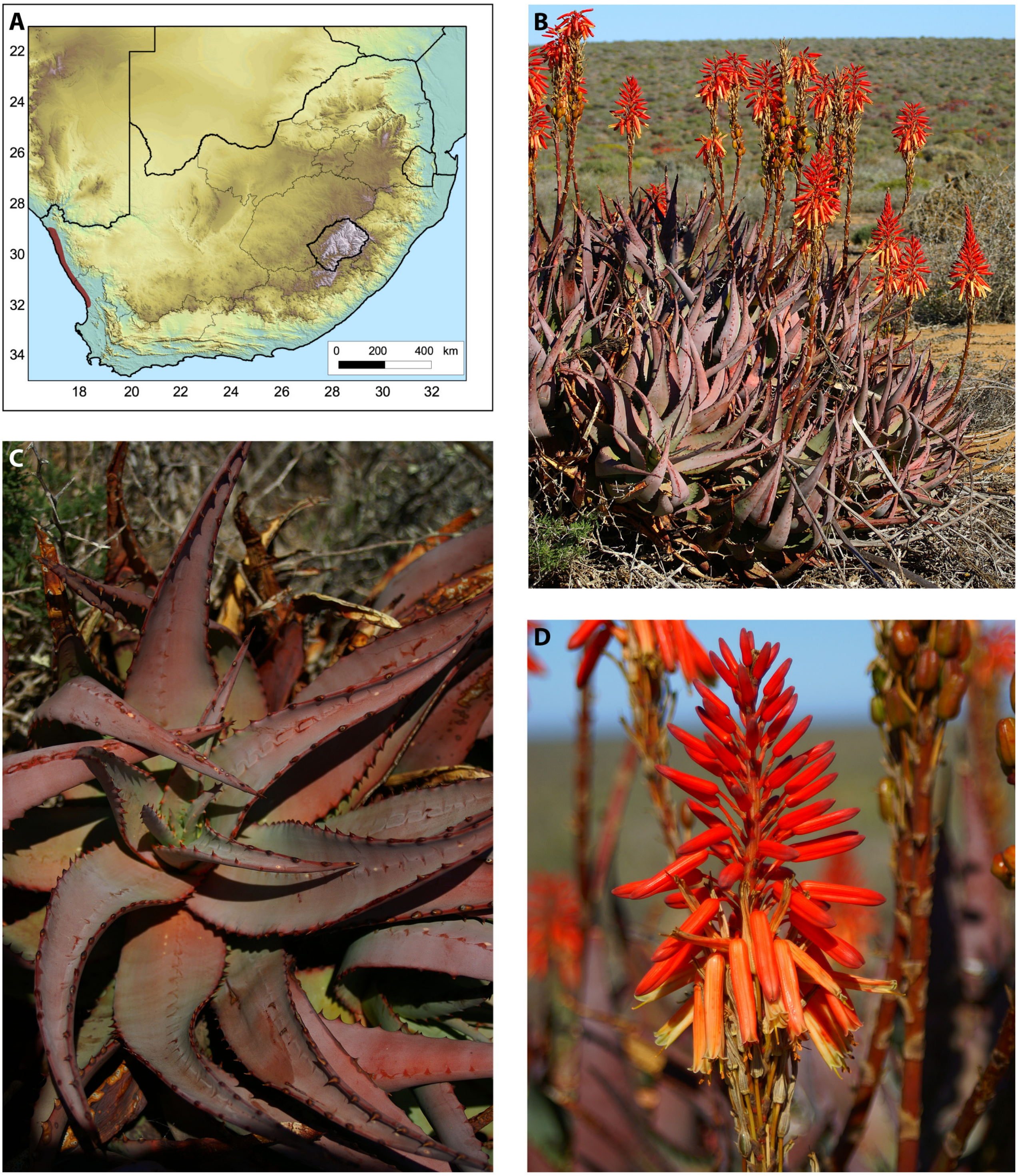


FIGURE 7. *Aloe framesii* subsp. *framesii*. **A.** Known distribution (red shading). **B.** Very large group of clustered rosettes with decumbent to erect stems. **C.** Rosette of bluish-green, red-tinged leaves with very few white spots. **D.** Raceme with orange-red, greenish-tipped flowers. Photographs: Arrie W. Klopper (Port Nolloth, Northern Cape, South Africa, July 2010).

Diagnostic characters:—*Aloe framesii* subsp. *framesii* is distinguished by its semi-erect to procumbent stems and rosettes that form dense groups. Leaves have a few white spots on both surfaces, usually towards the base, and reddish brown marginal teeth that are 3–4 mm long. Inflorescences are sometimes simple or usually 2-branched, with racemes 21–30 cm long. Pedicels are usually 16–20 mm long. Flowers are 25–35 mm long. Leaf exudate dries brownish yellow, often with a slight purple tinge.

Distribution:—Confined to the coastal sandveld on the West Coast from Port Nolloth and Kleinsee, Northern Cape, southwards to possibly to Papendorp, Western Cape, South Africa. Endemic to the Succulent Karoo.

Habitat:—Sandy coastal flats on sandstone in Succulent Karoo Strandveld and Duneveld.

Elevation:—0–100 m

Flowering time:—June–July

Etymology:—Commemorates Mr Percival ('Percy') Ross Frames (1863–1947), South African solicitor, collector, and grower of succulents, who collected the type specimen in Namaqualand.

General notes:—Populations from the Olifants River Estuary around Papendorp, Western Cape, South Africa, are tentatively included in this subspecies. The affinities and placement of these plants require further study.

Additional specimens examined:—SOUTH AFRICA. Western Cape: Papendorp, near Olifants River Estuary, 12 July 2010, *R.R. Klopper & A.W. Klopper 352 & 353* (NBG^{g}, PRE^{g}). Van Rhynsdorp Div., Strandfontein, ex hort. Stellenbosch University, May 1940, *H. Herre SUGardens 7136* (BOL). **Northern Cape:** N of Port Nolloth, 1932, fl. ex hort August 1933, *M. Schlechter s.n.* (BOL); 6 July 1949, *G.W. Reynolds 5412* (K, PRE^{m}, SAM); 27 May 1985, *R.L. Verhoeven & G.J. Beukes 179* (BLFU); 30 August 1985, *H.F. Glen 1491* (PRE); 16 July 2010, *R.R. Klopper & A.W. Klopper 374* (KMG^{gmc}, PRE^{gmc}) *& 375* (NBG^{gmc}, PRE^{gmc}). Namaqualand, between Port Nolloth and Holgat, 25 July 1937, *G.W. Reynolds 2558* (BOL, PRE^{m}). Kleinzee, Molyneux Reserve, 20 July 2005, *P. Kruger 1066* (K, PRE). Van Rhynsdorp/Vredendal Distr., Brandsebaai, March 1993, *A.J. de Villiers 62* (PRE, WIND).

1b. ***Aloe framesii* subsp. *amoena*** (Pillans) Klopper *comb. et stat. nov*. (Fig. 8)

Basionym:—*Aloe amoena* Pillans (1933a: 168). Lectotype (designated here):—SOUTH AFRICA. Western Cape: 4 miles north of Van Rhynsdorp, January 1928, fl. hort. Pillans, Rosebank May 1933, *N.S. Pillans BOL16024* (lectotype BOL BOL140199!; isolectotype K K000256678! [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.k000256678]).

Note regarding type:—There are two sheets in Herb. BOL labelled as *N.S. Pillans BOL16024* (BOL140199 and BOL140200). The label of sheet BOL140199 states that it was collected by Pillans in January 1928, four miles north of Van Rhynsdorp, and that the plant flowered in his garden at Rosebank in May 1933, when the specimen was evidently made. The label contains the text '*Aloe amoena* Pillans Type'. This sheet consists of a leaf and unbranched inflorescence. The sheet BOL140200 [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.bol140200] consists of a leaf and unbranched inflorescence, an envelope containing a painting of a flower and floral bract, and another envelope with descriptive notes that contains some loose flowers. The label of this sheet states the following 'Four miles N of Van Rhynsdorp on Rd to Namaqualand. Flowered in N.S. Pillans's garden, Rosebank. June 1919'. There is no species name written on the label. The protologue of *A. amoena* indicates as type a specimen collected by Pillans near Van Rhynsdorp ('Bolus Herb. no. 16024 — typus') that flowered in the garden of Pillans at Rosebank, Cape Town, in June 1933 (Pillans 1933a: 168). Sheet BOL140199 is here chosen as lectotype as the information on the label most closely matches that provided in the protologue. A duplicate of this specimen is housed at Herb. K.

Description:—Shortly caulescent plants. *Stem* 0.1–0.2 m long, erect to slightly decumbent, simple or usually 2- or 3-branched, with persistent dried leaves. *Leaves* densely rosulate, erectly spreading to spreading, grey-green, turning an intense red in dry conditions, with sparse white spots on both surfaces, often obscurely striated, lanceolate-acuminate, 30–40 cm long, 5.5–7.0 cm wide, margin with pungent, deltoid, red-brown teeth, 2–3 mm long, 7–10 mm apart; exudate honey-coloured, drying orange-brownish. *Inflorescence* usually single, sometimes 2 simultaneously, 0.7–0.9 m high, erect, usually simple or sometimes up to 3-branched. *Peduncle* up to 2 cm wide and plano-convex below, terete upwards, reddish green; with numerous sterile bracts, ovate-deltoid, 10–17 mm long, 10–12 mm wide, brownish, scarious, many-nerved. *Racemes* elongate-conical, attenuate, 30–40 cm long, ± 9 cm wide, erect, rather lax; buds erect to spreading, flowers nodding to pendent when open. *Floral bracts* ovate-acute, 15–18 mm long, 5–6 mm wide, red to brown, fleshy to scarious, many-nerved. *Pedicels* 20–22 mm long, red. *Flowers: perianth* red, 25–28 mm long, ± 8 mm across ovary, slightly narrowed towards mouth, cylindric-trigonous; outer segments free to base, tips slightly spreading; *stamens* with yellow filiform flattened filaments, exserted portion turning dark brown, exserted 3–5 mm; *ovary* 6 mm long, 3 mm diameter, pale green; *style* yellow, exserted 3–5 mm.

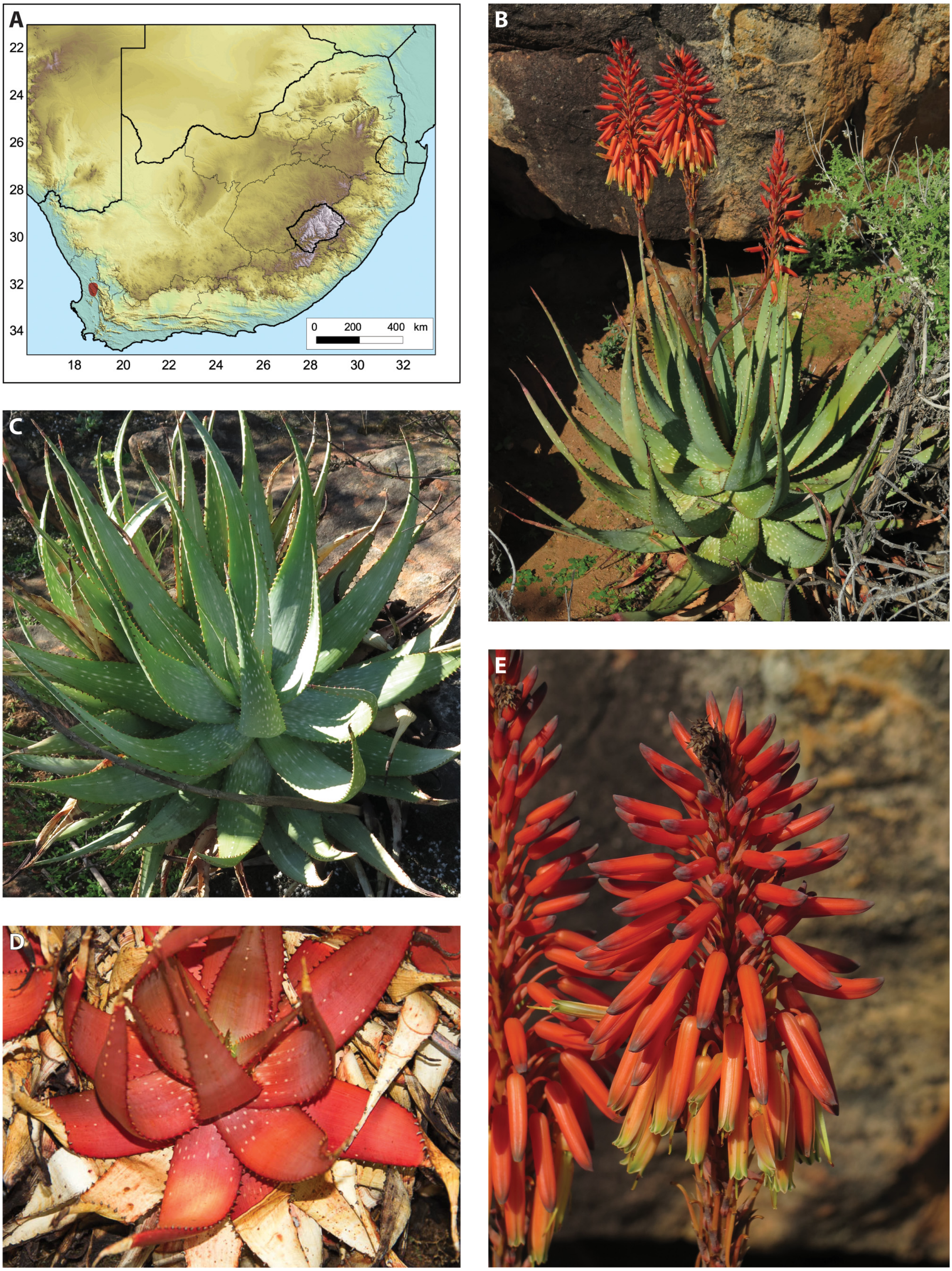


FIGURE 8. *Aloe framesii* subsp. *amoena*. **A.** Known distribution (red shading). **B.** Single rosette with 3-branched inflorescence. **C.** Rosette of grey-green leaves with obscure striations and sparse white spots on both surfaces. **D.** Rosette of intense red leaves during very dry conditions. **E.** Raceme with red, greenish yellow-tipped flowers. Photographs: B, C, E. Neil R. Crouch (Clanwilliam, Western Cape, South Africa, July 2015); D. Arrie W. Klopper (Agter Pakhuis, Cederberg, Western Cape, South Africa, December 2012).

Diagnostic characters:—*Aloe framesii* subsp. *amoena* is distinguished by its semi-erect to slightly decumbent stem with rosettes that are either solitary or forming small groups. Leaves have a few white spots on both surfaces and are often obscurely lineate, with reddish brown marginal teeth 2–3 mm long. Inflorescences are usually simple or sometimes up to 3-branched, with unicoloured red racemes of 30–40 cm long. Pedicels are 20–22 mm long. Flowers are 25–28 mm long. Leaf exudate does usually not dry purple (dries orange-brownish).

Distribution:—Known only from the area around and between Graafwater, Clanwilliam and Van Rhynsdorp, Western Cape, South Africa. Endemic to the Fynbos Biome.

Habitat:—Rocky outcrops of Sandstone Fynbos.

Elevation:—170–600 m

Flowering time:—June–August

Etymology:—From Latin 'amoena' (beautiful); refers to the beauty of the plant.

General notes:—Originally described as *Aloe amoena*, but long treated as a synonym and southern form of *Aloe framesii* (Reynolds 1950). It was first collected on the main road between Graafwater and Lambert's Bay (by Miss Lavis), near Clanwilliam and north of Van Rhynsdorp (Pillans 1933a).

Dimensions of the flowers suggest a close affinity to *Aloe microstigma* (S.J. Marais, pers. comm.). This should be investigated, especially in the light of the geographic proximity of populations of *Aloe* cf. *microstigma* at Kagga Kamma Nature Reserve (Cederberg region).

Additional specimens examined:—SOUTH AFRICA. Western Cape: Near Olifants River Bridge, W of Clanwilliam, fl. Johannesburg 11 June 1936, *G.W. Reynolds 931* (PRE^{m}); 30 July 1937, *G.W. Reynolds 2595* (BOL, K, PRE^{m}); Fl. Pretoria June 1938, *G.W. Reynolds 2592* (PRE^{m}). Olifants River Valley near Clanwilliam, May 1907, *N.S. Pillans 959* (GRA); fl. Rosebank, August 1907, *N.S. Pillans 6799* (BOL). Clanwilliam, Steenrug farms, Kleinvlei, 14 August 1980, *A. le Roux 2615* (BOL). Warmhoek-Platberg, SE of Clanwilliam, 15 June 1984, *H.C. Taylor 10948* (PRE). Between Graafwater and Lambert's Bay, June 1932, *M. Lavis 20453* (BOL). N of Van Rhynsdorp, June 1919, fl. Rosebank, *N.S. Pillans BOL16024* (BOL).

1c. *Aloe framesii* subsp. *maraisii* Klopper *subsp. nov*. (Fig. 9)

Diagnosis:—*Aloe framesii* subsp. *maraisii* is distinguished from other subspecies of *A. framesii* by its short procumbent stem (not semi-erect) and rosettes that form dense groups (not solitary or in small groups). Inflorescences in this subspecies are usually simple or 2-branched (as opposed to usually 2-branched or sometimes up to 3-branched). Racemes are 23–30 cm long (not up to 40 cm). Pedicels are 20–30 mm long (not 16–22 mm). Flowers are 40–45 mm long (not 25–35 mm). Although leaves usually have copious white spots on both surfaces, it can sometimes have only a few spots as in the other subspecies, or can even be without spots, but are never lineate.

Type:—SOUTH AFRICA. Western Cape: Stompneus Bay, in St Helena Bay, 28 May 1952, *A. Hertzog NBG 390/52* (holotype NBG! [2 sheets])

Description:—Acaulescent plants or with short *stem* procumbent, freely branching from base to form dense groups; with persistent dried leaves. *Leaves* densely rosulate, erectly spreading, bluish green, sometimes without spots or with only a few spots, but usually copiously white-spotted on both surfaces, lanceolate-attenuate, up to 35 cm long, 6–7 cm wide at base; margin with pungent, deltoid, reddish brown teeth, 2–4 mm long, 4–11 mm apart; exudate honey-coloured, sometimes drying with slight purple tinge. *Inflorescence* usually single, up to 0.85 m high, erect, simple or 2-branched from low down, branches ascending. *Peduncle* ± 1.1–2.0 cm wide and plano-convex below, terete upwards, reddish green; with several sterile bracts when simple, ovate-acute, 19–24(–30) mm long, 10–13(–27) mm wide, pale brownish, thin scarious, many-nerved. *Racemes* conical to cylindric-acuminate, 23–30 cm long, ± 10 cm wide, erect, dense; buds erect to spreading, flowers nodding to pendulous when open. *Floral bracts* ovate-acute, amplexicaul below, 14–20 mm long, 5–6 mm wide, pale pinkish, thin, sub-scarious, many-nerved. *Pedicels* 20–30 mm long, pink to pinkish orange. *Flowers: perianth* dark pink in bud, dark pinkish to usually orange-red with greenish yellow tips when mature, 40–45 mm long, 6–7 mm across ovary, not narrowed above ovary, slightly widening to 7–9 mm in middle, slightly narrowing to 5–6 mm towards wide-open mouth, cylindric-trigonous; outer segments free to base, tips spreading; *stamens* with yellow filiform-flattened filaments, exserted to 5(–9) mm; *ovary* 7 × 3 mm, yellow; *style* yellow, exserted 4–6 mm.

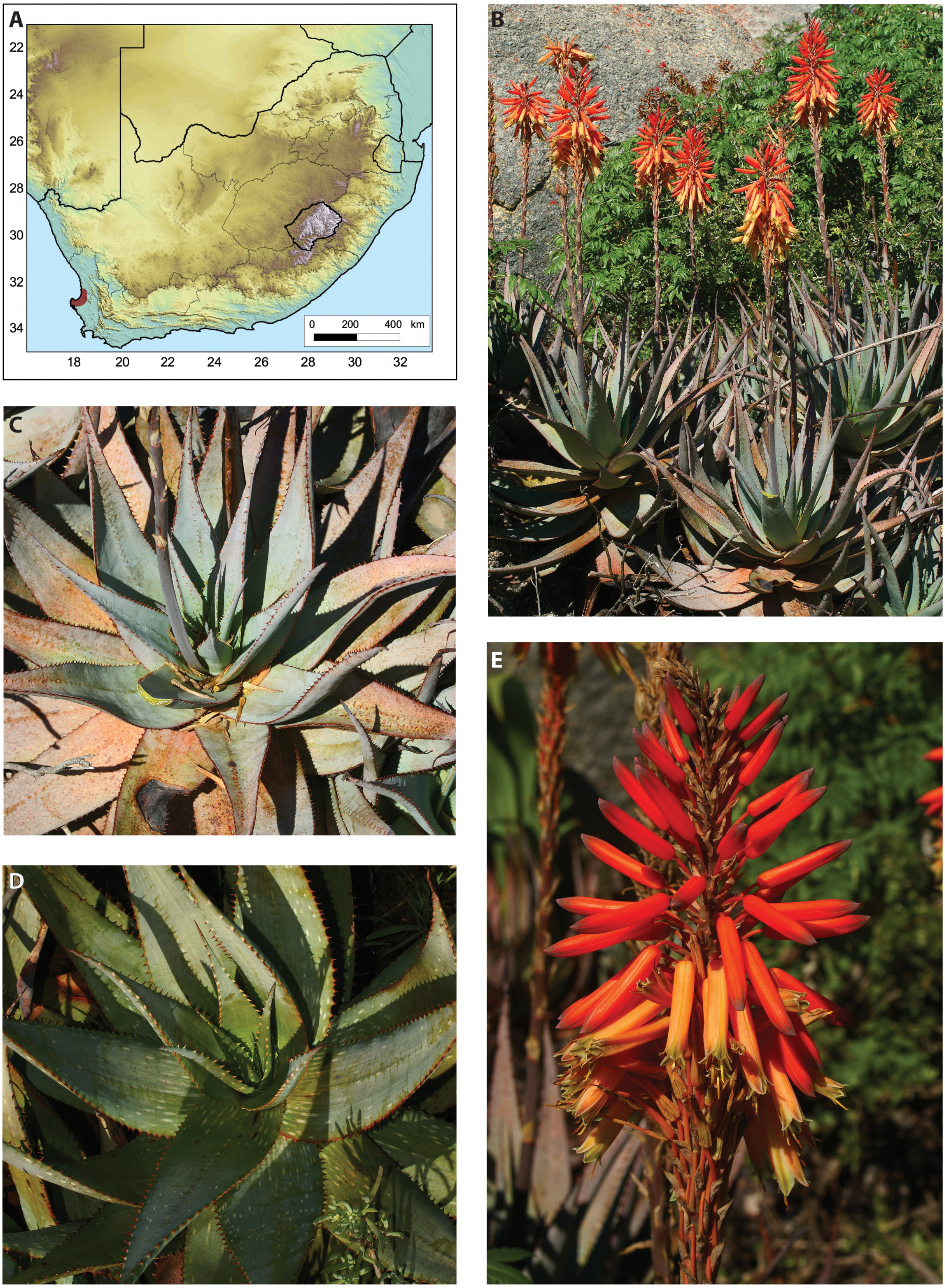


FIGURE 9. *Aloe framesii* subsp. *maraisii*. **A.** Known distribution (red shading). **B.** Dense group of rosettes with simple or 2-branched inflorescences. **C.** Rosette of bluish green leaves with very few white spots. **D.** Rosette of more greenish leaves with several spots. **E.** Raceme with orange-red, greenish yellow-tipped flowers. Photographs: Arrie W. Klopper (B, C, E. St Helena Bay, Western Cape, South Africa; D. Elands Bay, Western Cape, South Africa; July 2010).

Diagnostic characters:—*Aloe framesii* subsp. *maraisii* is distinguished by its short procumbent stem and rosettes that form dense groups. Leaves usually have copious white spots on both surfaces, but sometimes have only a few or are even without spots, with reddish brown marginal teeth 2–4 mm long. Inflorescences are usually simple or 2-branched, with racemes 23–30 cm long. Pedicels are 20–30 mm long. Flowers are 40–45 mm long. Leaf exudate dries brownish yellow, sometimes with a slight purple tinge.

Distribution:—Confined to the coastal strandveld on the West Coast from around Elands Bay to Saldanha, Western Cape, South Africa. Endemic to the Fynbos Biome.

Habitat:—Rocky sandstone outcrops and ridges in Strandveld Fynbos.

Elevation:—0–50 m

Flowering time:—May–July

Etymology:—Commemorates Mr Sarel J. Marais (1943–), aloe enthusiast and owner of the Weskus Aloe Nursery, Moorreesburg, Western Cape, South Africa, who is extremely knowledgeable regarding the aloes that occur along South Africa's West Coast and in Namaqualand.

General notes:—This is an exceptionally variable subspecies that differs considerably in growth form and leaf characters among the different populations.

Additional specimens examined (paratypes):—SOUTH AFRICA. Western Cape: Stompneus Bay, in St Helena Bay, 28 May 1952, *A. Hertzog NBG 390/52* (holotype NBG^{m}). St Helena Bay, 12 July 2010, *R.R. Klopper & A.W. Klopper 348 & 349* (NBG^{gmc}, PRE^{gmc}). Elands Bay, 12 July 2010, *R.R. Klopper & A.W. Klopper 350 & 351* (NBG^{gmc}, PRE^{gmc}). Vredenburg Dist., from St. Helena Bay to Slipper Bay, 14 June 1967, *J.A. Marsh 186* (NBG, PRE). Malmesbury Div., Saldanha Bay, Paternoster, *H.W.R. Marloth PRE38429* (PRE); Saldanha Bay, 1921, fl. ex hort. June–July 1924, *H.W.R. Marloth 10996* (PRE). Near Danger Bay, Saldanha Bay, 13 July 1946, *F.M. Leighton s.n.* (BOL). Near Saldanha Bay, 30 January 1921, *I.B. Pole-Evans s.n.* (K); May 1952, *H. Hall 731* (NBG).

2. *Aloe gariepensis* Pillans (1933b: 213) (Fig. 10)

Type:—NAMIBIA: Near Warmbad, hills near Marinka's Spring, September 1931, *N.S. Pillans 6557* (holotype BOL BOL140197! [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.bol140197])

Designation not validly published:—'*Aloe gariusana* Dinter' (1928: 31), *nom. nud.* Type not cited (Types are for names not designations).

Description:—Sub-acaulescent plants; rosettes usually solitary. *Stem* absent to short, up to 1 m, usually unbranched or sometimes branched, procumbent to erect; with persistent dried leaves. *Leaves* densely rosulate, erect to slightly incurved, dull green to reddish brown, clearly lineate, copiously white-spotted on both surfaces in young plants, some spots on upper surface in mature plants, lanceolate-attenuate, 30–40 cm long, 5–8 cm wide at base; margin with small, sharp, deltoid, reddish brown teeth, 2–4 mm long, 5–15 mm apart; exudate pale yellow, drying yellow to amber. *Inflorescences* 2 to 5 simultaneously, 0.8–1.5 m high, erect, simple. *Peduncle* 15–22 mm wide and plano-convex below, terete upwards, reddish green to pale brown; with many ovate, long-acuminate sterile bracts, 25–35(–45) mm long, 12–25 mm wide at base, scarious, pale, yellowish, many-nerved. *Raceme* narrowly cylindric-acuminate, 35–50 cm long, ± 7 cm wide, erect, dense; buds erect to spreading, flowers nodding to pendulous when open; youngest buds obscured by imbricate bracts. *Floral bracts* lanceolate, 17–25 mm long, 5–10 mm wide, pale, thin, sub-scarious, 5- to 7-nerved. *Pedicels* (7–)15–23 mm long, greenish yellow. *Flowers: perianth* red or yellow in bud, yellow to greenish yellow at maturity, (15–)20–27 mm long, 4–5 mm across ovary, slightly widening to 6–8 mm towards middle, slightly narrowing to 4–5 mm towards slightly upturned mouth, cylindric-trigonous; outer segments free almost to base, tips slightly spreading; *stamens* with filiform-flattened filaments, included portion lemon, exserted portion turning deep brown, exserted 4–7 mm; *ovary* 4–5 mm long, 1.5–2.5 mm diameter, green to greenish yellow; *style* light greenish yellow, exserted 4–9 mm.

Diagnostic characters:—*Aloe gariepensis* is easily distinguished by its long narrow unbranched raceme and long floral bracts. Leaves are striate and usually turn pink or bright reddish brown during dry periods. Racemes are long cylindric-acuminate and 35–50 cm long. Pedicels are only 15–23 mm long. Floral bracts (17–25 mm) are much longer than the pedicels. Leaf exudate does usually not dry purple (dries yellow to amber).

Distribution:—Along both sides of the Orange River Valley from Grootderm to Keimoes in the Northern Cape of South Africa and as far north as Warmbad in Namibia. Endemic to the lower Orange River Valley and the Gariep Centre of Endemism (Van Wyk & Smith 2001).

Habitat:—Rock cracks on steep rocky slopes, often facing the Orange River in the driest part of its course.

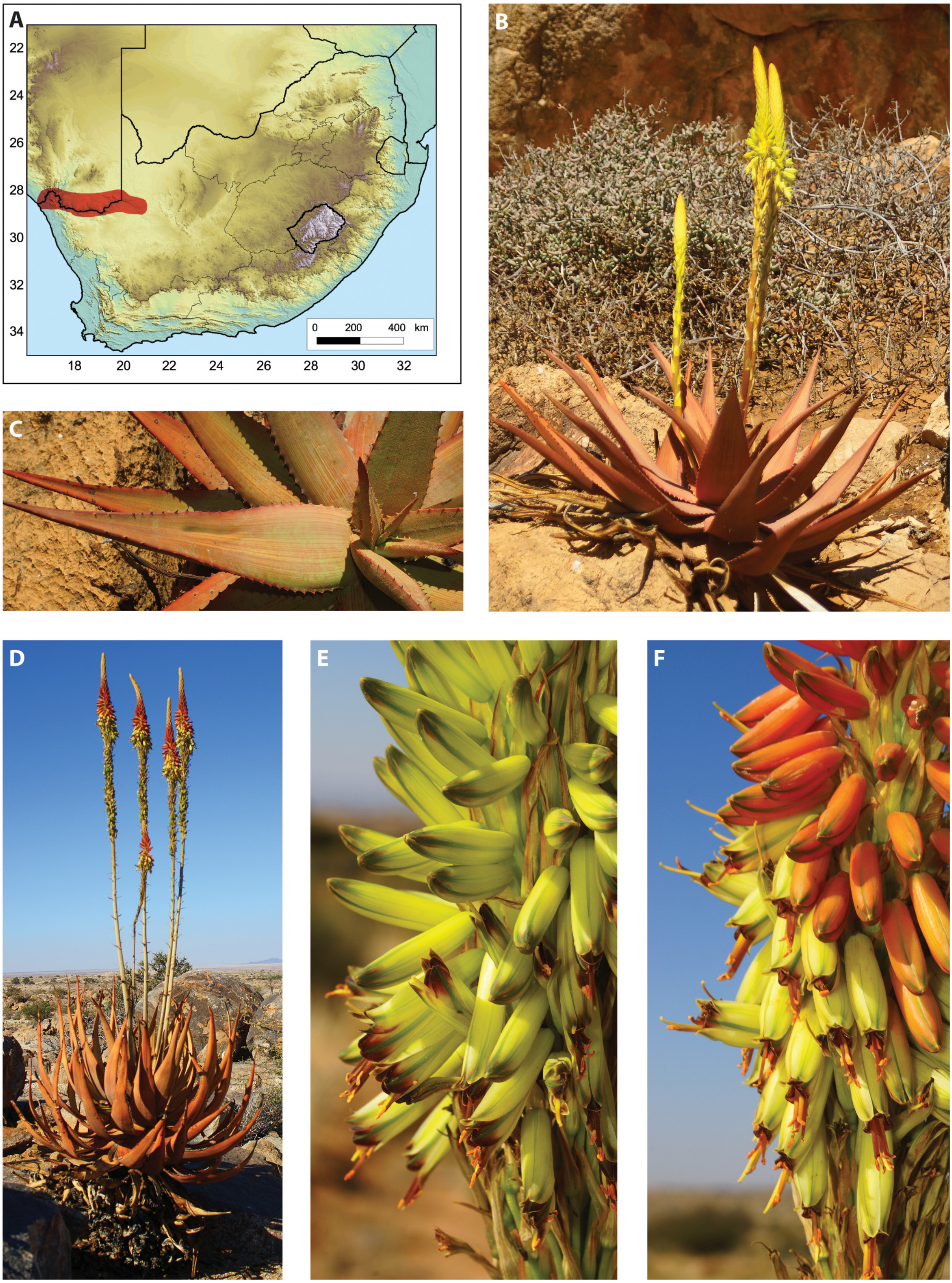


FIGURE 10. *Aloe gariepensis*. **A.** Known distribution (red shading). **B.** Small, single, acaulescent rosette with short, uniform yellow inflorescences. **C.** Rosette of reddish brown, clearly lineate leaves with no white spots. **D.** Big, caulescent rosette with tall, bicoloured inflorescences. **E.** Yellow buds and flowers on a unicoloured raceme. **F.** Red buds and yellow open flowers on a bicoloured raceme. Photographs: Arrie W. Klopper (B, C. Grootderm, near Orange River, Northern Cape, South Africa; D–F. Warmbad, Namibia; July 2010).

Elevation:—20–1 020 m

Flowering time:—July–September

Etymology:—From the Khoikoigowab (Nama) name Gariep (*!garib* = large river) for the Orange River in South Africa; refers to its occurrence along the Orange/Gariep River.

General notes:—*Aloe gariepensis* is extremely variable across different localities. At Grootderm in the west of its distribution range, plants are smaller, mostly acaulescent, with red leaves and unicoloured yellow racemes. At Keimoes, in the east of its range, plants are considerably more robust with stems of up to 1 m that are densely covered in dried persistent leaves, leaves are larger and more green, and inflorescences taller. Leaves are always lineate, but can be entirely without spots to copiously white-spotted at various localities. Inflorescences can be unicoloured yellow or bicoloured with red buds and yellow flowers (Reynolds 1950).

Additional specimens examined:—SOUTH AFRICA. Northern Cape: Alexander Bay Dist., Beauvallon, 30 August 1985, *H.F. Glen 1495* (PRE); Farm Grootderm, 25 July 1937, *G.W. Reynolds 2555* (K, PRE^{m}); *s. coll. s.n.* (NBG); July 1967, *J. Admiraal & D.S. Hardy 1151* (PRE); 16 July 2010, *R.R. Klopper & A.W. Klopper 376 & 377* (KMG^{gmc}, PRE^{gmc}). Richtersveld, De Hoop, 1 September 1977, *E.G.H. Oliver, H.R. Tölken & S. Venter 382* (PRE^{m}). Namaqualand Distr., Richtersveld, Rooiberg Concervancy area, NNE of Eksteensfontein, 8 August 2011, *S.P. Bester 10676* (PRE^{m}). Bushmanland, Abbassaberg, 16 August 2011, *E.J. van Jaarsveld 23822* (PRE). Aggeneys, 26 March 1985, *E.J. van Jaarsveld & J.D. Kritzinger 8046* (NBG). Gordonia, Lutzputs, Molopo N of Kakamas*, J. van der Vyver PRE38430 & PRE38436* (PRE^{m}). Augrabies Waterval Nasionale Park [Augrabies Falls National Park], 9 September 1996, *P.C. Zietsman 3464B* (NMB, PRE); Great Bushmanland, Kakamas, August 1931, *N.S. Pillans 6794* (BOL). Gordonia, NW of Kakamas, 30 August 1961, *O.A. Leistner & V.P. Joynt 2855* (K, PRE^{m}). Gordonia Division, Keimoes, September 1927, *F.C. Kolbe 20503* (BOL). Upington, Keimoes, August 1929, *H.W.R. Marloth 14031* (PRE); 12 August 1964, *H. Hall 1680* (NBG^{m}). Keimoes, W of Upington, 10 September 1949, *G.W. Reynolds 5503* (K, PRE^{m}). Keimoes, on road to Upington, just outside Keimoes opposite De Werf, 23 July 2010, *R.R. Klopper & A.W. Klopper 407* (KMG^{gc}, PRE^{gc}) *& 408* (NBG^{gc}, PRE^{gc}). Gordonia Div., Kakamas, 23 August 1954, *G.J. Lewis 4385 / SAM 68247* (PRE^{m}, SAM). Upington Dist., N of Kakamas, 24 August 1954, *A.J. Middlemost 1878* (NBG^{m}). Great Namaqualand, Pofadder, 3 October 1956, *Kirstenbosch Expedition NBG 732/54* (NBG). Pofadder, farm Boomrivier, 29 September 2006, *R.R. Klopper & A.W. Klopper 235* (KMG, PRE^{m}); Boomrivier, on Slangberg, 21 July 2010, *R.R. Klopper & A.W. Klopper 397* (KMG^{gc}, PRE^{gc}) *& 398* (NBG^{gc}, PRE^{gc}). Namaqualand Dist., N of Steinkopf, 7 July 1952, *H. Hall N.B.G. 485/52* (BOL, NBG). Pellaberg, 27 March 1985, *E.J. van Jaarsveld & J.D. Kritzinger 8063* (NBG). **NAMIBIA.** Luderitz District, Geelperahoek, 15 July 1970, *W. Jankowitz 225/562* (WIND). Namuskluft, 17 August 2012, *M. Koekemoer 4317* (PRE^{m}). Ai-ais Reserve, 30 June 1986, *E.J. van Jaarsveld 8705* (NBG). Luderitz, Lorelei Copper Mine, 14 September 1958, *B. de Winter & J.W.H. Giess 6368* (BOL, K, PRE, WIND); 16 September 1966, *D.S. Hardy 2314* (PRE^{m}). Kahanstal, Lorelei, 15 September 1973, *J.W.H. Giess 12973* (PRE^{m}, WIND). Luderitz-Sud, Spitzkop LUS111, 24 September 1972, *H. Merxmueller & W. Giess 28817* (WIND). Namaqualand, Skilpadberg, NE of Oranjemund, October 1994, *G.F. Williamson 5508* (NBG^{m}). Karasburg District, Haib River mouth, N from Noordoewer, 19 October 2005, *H. Kolberg & T. Tholkes HK1729* (K, WIND). Warmbad, 30 July 1924, *M.K. Dinter 5211* (BOL, K, PRE^{m}, SAM); 20 July 1937, *G.W. Reynolds 2528* (K, PRE^{m}); *G.W. Reynolds 2529* (BOL, PRE^{m}); 13 September 1959, *D.S. Hardy 198* (PRE^{m}). Warmbad, on D206 just outside Warmbad, 20 July 2010, *R.R. Klopper & A.W. Klopper 391 & 392* (PRE^{gmc}, WIND^{gmc}). Warmbad Dist., Namib near Goodhouse Drift, June 1926, *H.W.R. Marloth 13249* (PRE^{m}). Sperlingputs Farm, SW of Warmbad, 20 July 1937, *G.W. Reynolds 2531* (K, PRE^{m}). Sandfontein WAR 148, 05 August 1976, *J.W.H. Giess 14510* (PRE, WIND). Between Goodhouse Poort and Geidip, 29 August 1989, *A.E. van Wyk 8747* (PRE, WIND). Nakop, E of Nakop, 23 August 1938, *J. van der Vyver PRE38422* (K, PRE^{m}).

3. ***Aloe khamiesensis*** Pillans (1934: 25)

Lectotype (designated here):—SOUTH AFRICA, Northern Cape: Namaqualand, Kamieskroon, ex hort. June 1933, *N.S. Pillans 6665* (lectotype BOL BOL140205! [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.bol140205]; isolectotype NBG NBG0067768-0!).

Note regarding type:—There are three sheets of *N.S. Pillans 6665* at Herb. BOL (BOL140203, BOL140204, and BOL140205). All three carry a ‘Type’ label. The date on BOL140203 and BOL140204 is June 1932, and the name on the specimen labels is ‘*Aloe sp. nov.*’. These two sheets are indicated in pencil as ‘Sheet I’ and ‘Sheet II’ respectively, and can thus be seen as part of a single collecting event. BOL140203 [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.bol140203] consists of three racemes and a leaf, while BOL140204 [https://plants.jstor.org/stable/

viewer/10.5555/al.ap.specimen.bol140204] consists of a leaf and the lower portion of the inflorescence (peduncle and base of first branches), and a hand written note (presumably by Pillans) with descriptive information, as well as envelopes containing a coloured drawing of a flower and bract, loose plant material, and a mounted dissected flower and bracts. The leaf material on these two sheets represents the abaxial and adaxial surface of the same leaf, thus confirming that they represent two sheets of a single collection. The date on BOL140205 is June 1933, there is no sheet number on this specimen, and the species name on the original label is '*Aloe khamiesensis*, Pillans'. This sheet consists of the separated abaxial and adaxial surfaces of a leaf, and a single raceme. The protologue of *A. khamiesensis* (Pillans 1934: 25) states that *Pillans 6665* was collected at Khamieskroon in August 1929, and that it flowered in May 1933 ('Maio–Sept 1933' in the diagnosis). Sheet BOL140205 is here chosen as lectotype as the information on the label most closely matches that provided in the protologue. A duplicate of this specimen is housed at Herb. NBG.

3a. *Aloe khamiesensis* subsp. *khamiesensis* (Fig. 11)

Type:—As for *A. khamiesensis*.

Description:—Usually solitary, arborescent plant up to 2 m high, sometimes forming groups. *Stem* usually single with only one rosette, sometimes branched from base or about middle, erect, 0.5–2.0 m high, with persistent dried leaves. *Leaves* densely rosulate, erectly spreading to slightly incurved, dull green, usually with small white spots, more numerous on lower surface, slightly and obscurely lineate, lanceolate-attenuate, ± 40 cm long, 6–8 cm wide at base; margin with pungent, deltoid, reddish brown teeth, 2–3 mm long, 5–10(–14) mm apart; exudate honey-coloured, drying bright yellow. *Inflorescence* single, 0.6–0.9 m high, erect, 4- to 8-branched from about middle, branches often rebranching and ascending. *Peduncle* 2–5 cm wide and plano-convex basally; terete upward, reddish brown; without sterile bracts below lowest branch, several ovate-acute sterile bracts below racemes, 20–25 mm long, 20–33(–40) mm wide at base, pale brown, thin, scarious, many-nerved. *Racemes* long-conical, acuminate, 25–30(–35) cm long, ± 9 cm wide, erect, rather dense; buds erect to spreading, flowers pendulous when open. *Floral bracts* ovate-acute, sub-amplexicaul, 7–14 mm long, 4–8 mm wide, pinkish brown, thin, scarious, many-nerved. *Pedicels* (15–)20–25 mm long, reddish to light orange. *Flowers: perianth* orange-red with greenish yellow tips, (20–)30–35 mm long, 6–7 mm across ovary, not or only very slightly narrowed above ovary, slightly widening to 7–8 mm towards middle, slightly narrowing to 4–5 mm towards mouth, cylindric-trigonous; outer segments free to base, tips slightly spreading; *stamens* with yellow filiform-flattened filaments, exserted 4–9 mm; *ovary* 6–8 mm long, 3.0–3.5 mm diameter, green; *style* yellow, exserted 3–6(–10) mm.

Diagnostic characters:—*Aloe khamiesensis* subsp. *khamiesensis* is easily distinguished by its tall, erect stem and repeatedly branched inflorescence. Leaves are dull green and have a few spots particularly on the under surface and is often obscurely lineate, with reddish brown marginal teeth 2–3 mm long. Inflorescences are 4- to 8-branched with buds and flowers orange-red. Flowers are 30–35 mm long. Leaf exudate does not dry purple (dries bright yellow).

Distribution:—Steinkopf to Kamiesberg, Northern Cape, South Africa. Endemic to the Succulent Karoo.

Habitat:—Mountainous country, rocky slopes and outcrops. Almost exclusively on granitoid rocks.

Elevation:—500–1 400 m

Flowering time:—June–July(–August)

Etymology:—Refers to the Kamiesberg in South Africa, where specimens of the species was first collected.

Additional specimens examined:—SOUTH AFRICA. Northern Cape: Steinkopf, W of Steinkopf towards Anenous Pass, 16 July 2010, *R.R. Klopper & A.W. Klopper 371* (KMG^{gmc}, PRE^{gmc}) *& 372* (NBG^{gc}, PRE^{gc}). Steinkopf Area; W of Steinkopf on Port Nolloth Rd., 30 August 1985, *H.F. Glen 1490* (PRE). O van Anenouspas [E of Anenous Pass], 21 August 1983, *H.J.T. Venter 8842* (BFLU). Kosies, NW of Steinkopf, 24 July 1937, *G.W. Reynolds 2545* (K, PRE^{m}). Steinkopf Dist., Klipfontein, June 1929, *H.W.R. Marloth 13262* (PRE). Namaqualand, Steinkopf, 16 June 1941, *J. Jackson NBG 2061/34* (NBG). W van [W of] Steinkopf-Port Nolloth, 27 May 1985, *R.L. Verhoeven & G.J. Beukes 178* (BFLU). Little Namaqualand; Springbok Dist., 5 June 1926, *G. Meyer 6857* (PRE). Springbok, just S of Springbok on Fonteintjie road, 15 July 2010, *R.R. Klopper & A.W. Klopper 369* (KMG^{gmc}, PRE^{gmc}) *& 370* (NBG^{gmc}, PRE^{gmc}). Springbok Distr., Okiep, 16 August 1925, *H.W.R. Marloth 12205* (PRE). Namaqualand, Kamieskroon, ex hort. June 1932, *N.S. Pillans 6665* (BOL); S of Khamieskroon, 29 July 1937, *G.W. Reynolds 2579* (K, PRE^{m}); 14 July 2010, *R.R. Klopper & A.W. Klopper 360* (KMG^{gmc}, PRE^{gmc}) *& 361* (NBG^{gmc}, PRE^{gmc}). Klipfontein, ex hort. Kirstenbosch, July 1933, *J.W. Mathews BOL20491, NBG2215/29* (BOL).

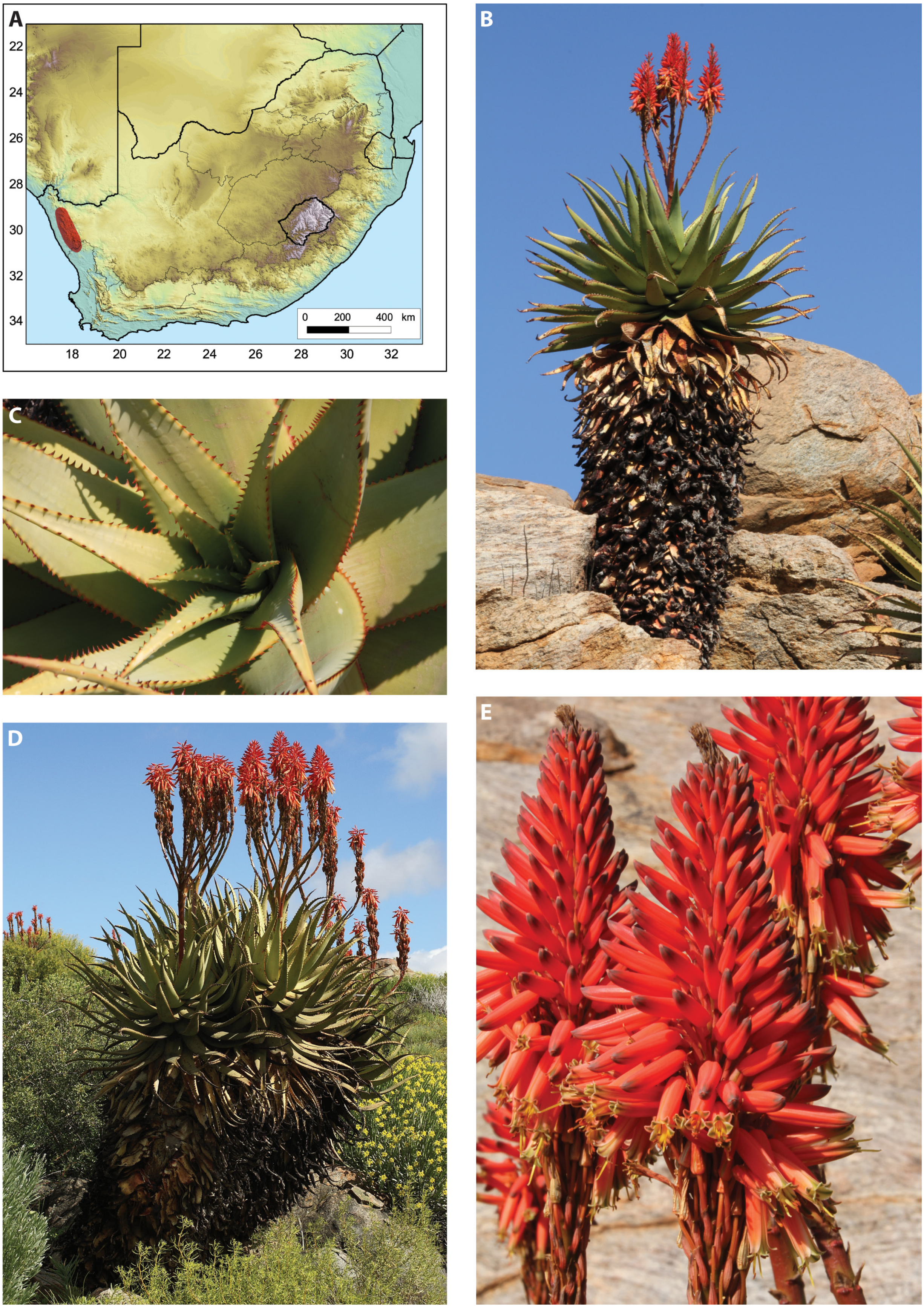


FIGURE 11. *Aloe khamiesensis* subsp. *khamiesensis*. **A.** Known distribution (red shading). **B.** Tall plant with unbranched stem. **C.** Rosette of dull green leaves with a few white spots. **D.** Plant with branched stem and numerous rosettes. **E.** Raceme with orange-red, greenish yellow-tipped flowers. Photographs: B, C, E. Marinda Koekemoer (Concordia, Northern Cape, South Africa, July 2013); D. Arrie W. Klopper (Kamieskroon, Northern Cape, South Africa, August 2007).

3b. *Aloe khamiesensis* subsp. *hantamensis* Klopper *subsp. nov*. (Fig. 12)

Diagnosis:—*Aloe khamiesensis* subsp. *hantamensis* is easily distinguished from the other two subspecies of *A. khamiesensis* by its yellowish green leaves (not dull green to reddish brown) with 3–5 mm long marginal teeth (not 1–3 mm). Inflorescences are 3- or 4-branched (not up to 8-branched). It flowers in April–June (not March–April or June–July).

Type:—SOUTH AFRICA, Northern Cape: Calvinia Division, Bokkeveld Mountains, on top of the hills between Meulsteinvlei and Zwart Doorn River, 15 May 1926, *E.B. Watermeyer in H.W.R. Marloth 6829* (holotype PRE!)

Description:—Usually solitary, arborescent plant, sometimes forming groups. *Stem* usually single with only one rosette, sometimes branched from base, erect, up to 1 m high, with persistent dried leaves. *Leaves* densely rosulate, erectly spreading to sometimes slightly incurved, light yellowish green, usually with few white spots, more numerous on juvenile plants, very slightly and obscurely lineate, lanceolate-attenuate, ± 40 cm long, ± 8 cm wide at base; margin with pungent, deltoid, reddish brown teeth, 3–5 mm long, 8–18 mm apart; exudate bright yellow, drying dark bright yellow. *Inflorescence* single or often 2 simultaneously, ± 1 m high, erect, 3- or 4-branched from below middle, branches ascending. *Peduncle* 2.4–3.0 cm wide and plano-convex below, terete above, green; with several sterile bracts below racemes, ovate-acute, (30–)38–40 mm long, (27–)36–37 mm wide at base, pale brown, thin, scarious, many-nerved. *Racemes* long-conical, acuminate, ± 35 cm long, ± 9 cm wide, erect, rather dense; buds erect to spreading, flowers pendulous when open. *Floral bracts* ovate-acute, sub-amplexicaul, 10–13 mm long, 4–5 mm wide, brown, thin, scarious, 3-nerved. *Pedicels* 19–22 mm long, yellowish green. *Flowers: perianth* red in bud, orangey yellow to yellow when mature, with greenish tips, 21–33 mm long, 6–7 mm across ovary, not narrowed above ovary, slightly widening to ± 8 mm towards middle, slightly narrowing to 5–6 mm towards mouth, cylindric-trigonous; outer segments free to base, tips slightly spreading; *stamens* with yellow filiform flattened filaments, exserted 5–6 mm; *ovary* 5 mm long, 2 mm diameter, green; *style* yellow, exserted to ± 7 mm.

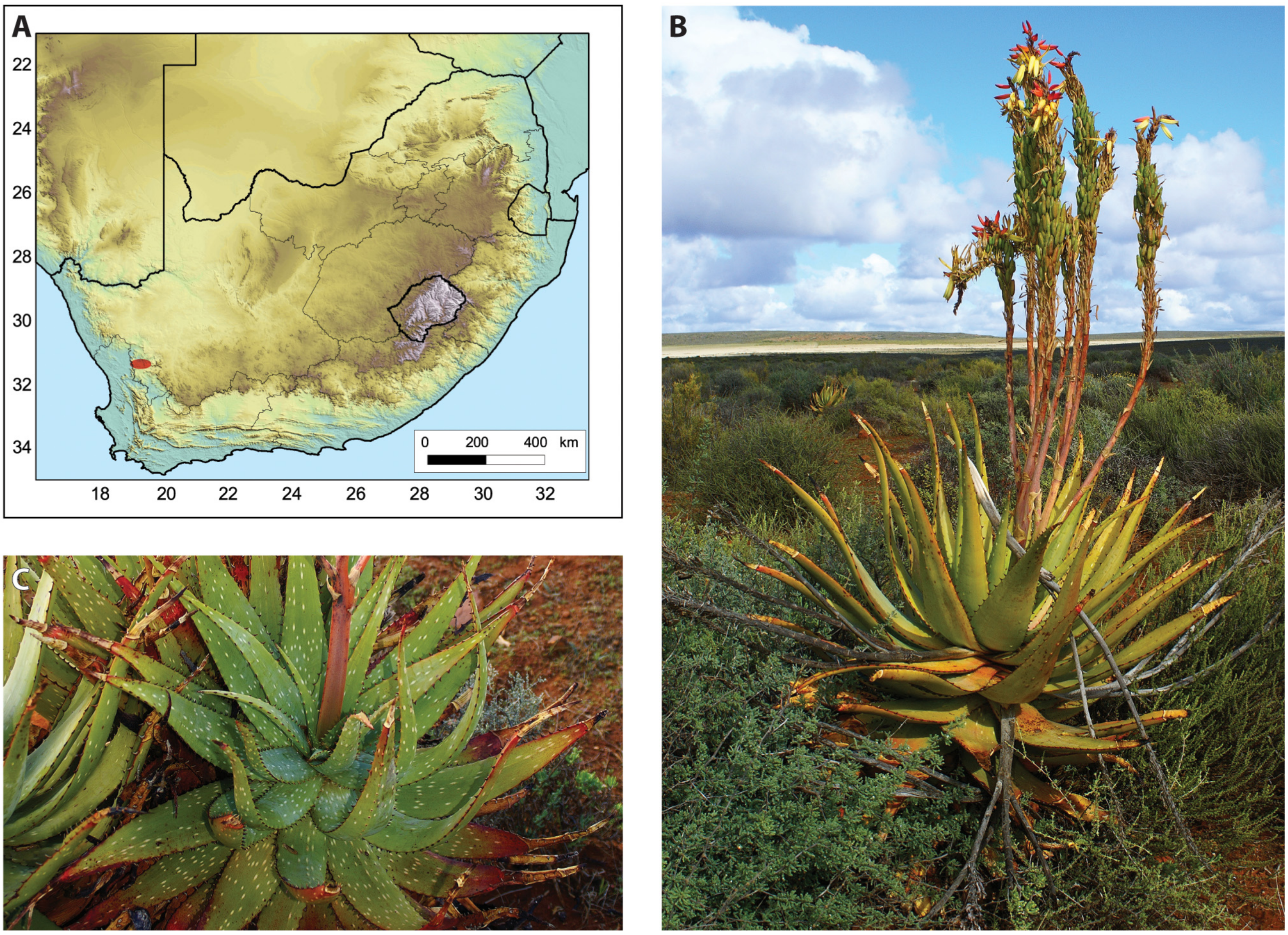


FIGURE 12. *Aloe khamiesensis* subsp. *hantamensis*. **A.** Known distribution (red shading). **B.** Shortly caulescent plant with greenish yellow leaves, as well as bicoloured inflorescences (with red buds and yellow open flowers) and developing fruit. **C.** Rosette of young plant with green leaves and numerous white spots. Photographs: Arrie W. Klopper (Hantam region, Northern Cape, South Africa, July 2010)

Diagnostic characters:—*Aloe khamiesensis* subsp. *hantamensis* is easily distinguished by its tall, erect stem and branched inflorescence. Leaves are yellowish green and have a few white spots in adult plants (usually more in juvenile plants), with reddish brown marginal teeth 3–5 mm long. Inflorescences are 3- or 4-branched with orange-red buds and yellow flowers. Flowers are 21–33 mm long. Leaf exudate does not dry purple (dries dark bright yellow).

Distribution:—Only known from around Nieuwoudtville and between Calvinia and Loeriesfontein, Northern Cape, South Africa. Endemic to the Hantam-Roggeveld Centre of Endemism (Van Wyk & Smith 2001).

Habitat:—Kloofs and rocky slopes in Fynbos and Renosterveld. Endemic to the Fynbos Biome.

Elevation:—600–1 000 m

Flowering time:—April–June

Etymology:—Refers to its occurrence in the Hantam region of South Africa.

General notes:—This taxon represents the isolated populations of *Aloe khamiesensis* from near Loeriesfontein and Calvinia reported on by Van Wyk & Smith (1996, 2014).

Additional specimens examined (paratypes):—SOUTH AFRICA. Northern Cape: Calvinia Div., Bokkeveld Mountains, between Meulsteinvlei and Zwart Doorn River, 15 May 1926, *E.B. Watermeyer in H.W.R. Marloth 6829* (holotype PRE^{m}); September 1926, *E.B. Watermeyer in H.W.R. Marloth 12937* (PRE). N of Nieuwoudtville, 16 June 1938, *T.M. Salter 7330* (BOL). Nieuwoudtville, Hantam National Botanical Garden, Maayerskloof, 4 May 2015, *E. Marinus EMHNBG104* (PRE). Hantam mountains, Tierhoek nek, 29 July 1948, *D.K. Davis 64480* (SAM). Calvinia-Loeriesfontein road, near Beeswater, 11 July 2010, *R.R. Klopper & A.W. Klopper 342* (KMG^{gmc}, PRE^{gmc}) *& 343* (NBG^{gmc}, PRE^{gmc}).

3c. ***Aloe khamiesensis* subsp. *knersvlakensis*** (S.J.Marais) Klopper *comb. et stat. nov*. (Fig. 13)

Basionym:—*Aloe knersvlakensis* Marais (2010: 96). Type:—SOUTH AFRICA, Western Cape: Knersvlakte, Namaqualand (between Vanrhynsdorp and Nuwerus), Jakkalsdraai, no date, *S.J. Marais s.n.* (holotype NBG! NBG0207177-1 to NBG0207177-9 [9 sheets]).

Description:—Shortly caulescent plants. *Stem* simple or usually densely branched, up to ± 1.5 m, erect to decumbent, with persistent dried leaves; rosettes solitary or densely clustered around main stem. *Leaves* densely rosulate, usually incurved, dull green to reddish brown, with clear longitudinal lines, sometimes without spots, usually with few to many white spots on both surfaces, lower surface often with fewer spots, lanceolate-attenuate, 30–40 cm long, 5–8 cm wide; margin with deltoid, pungent, reddish brown teeth, 1–2 mm long, 7–14 mm apart; exudate yellowish green, drying dark brownish yellow. *Inflorescences* 2 or 3 simultaneously, up to 0.73 m high, erect, 2- to 4-branched from below middle, branches arcuate-erect. *Peduncle* 1.6–2.7 cm and somewhat plano-convex below, terete upwards, yellow-green; with many sterile bracts below racemes, ovate, long acuminate, 22–25(–31) mm long, 22–25 mm wide, pale brown, scarious, many-nerved. *Racemes* long conical, (22–)33–43 cm long, 7–9 cm wide, erect, dense; flower buds erect to spreading, flowers nodding to pendent when open. *Floral bracts* ovate-acute, basally amplexicaul, 11–13 mm long, 4–5 mm wide at base, pale, scarious. *Pedicels* up to 27 mm long, yellow. *Flowers: perianth* orange-red in bud, yellow, greenish tipped when mature, ± 28 mm long, ± 5 mm across ovary, slightly widening towards middle, slightly narrowing towards mouth, cylindric-trigonous; outer segment tips slightly spreading; *stamens* with filiform flattened filaments, included portion lemon, excluded portion turning deep brown, exserted to 5 mm; *ovary* 8 mm long, 3 mm diameter, green; *style* yellow, exserted 5–6 mm.

Diagnostic characters:—*Aloe khamiesensis* subsp. *knersvlakensis* is easily distinguished by its relatively short erect stem that is covered in numerous rosettes in older plants, and its branched inflorescence. Leaves usually have few to many spots on both surfaces and are often clearly lineate, with reddish brown marginal teeth 1–2 mm long. Inflorescences are 2- to 4-branched with buds orange-red and yellow flowers. Flowers are on average 28 mm long. Leaf exudate does not dry purple (dries dark brownish yellow).

Distribution:—Only known from one locality near Kliprand, Western Cape, South Africa. Endemic to the Knersvlakte Centre of Endemism (Van Wyk & Smith 2001).

Habitat:—North-facing quartzitic sandstone ridges and medium slopes.

Elevation:—± 270 m

Flowering time:—March–April

Etymology:—Refers to its occurrence in the Knersvlakte of South Africa.

General notes:—This taxon was originally described as *Aloe knersvlakensis*. Together with *Aloe gariepensis* it has the longest racemes and smallest flowers in *A.* sect. *Purpurascentes* (Marais 2010).

Additional specimens examined:—SOUTH AFRICA. Western Cape: Van Rhynsdorp, Jakkalsdraai farm, *S.J. Marais s.n.* (holotype NBG^{m}); 14 July 2010, *R.R. Klopper & A.W. Klopper 358 & 359* (PRE^{gc}).

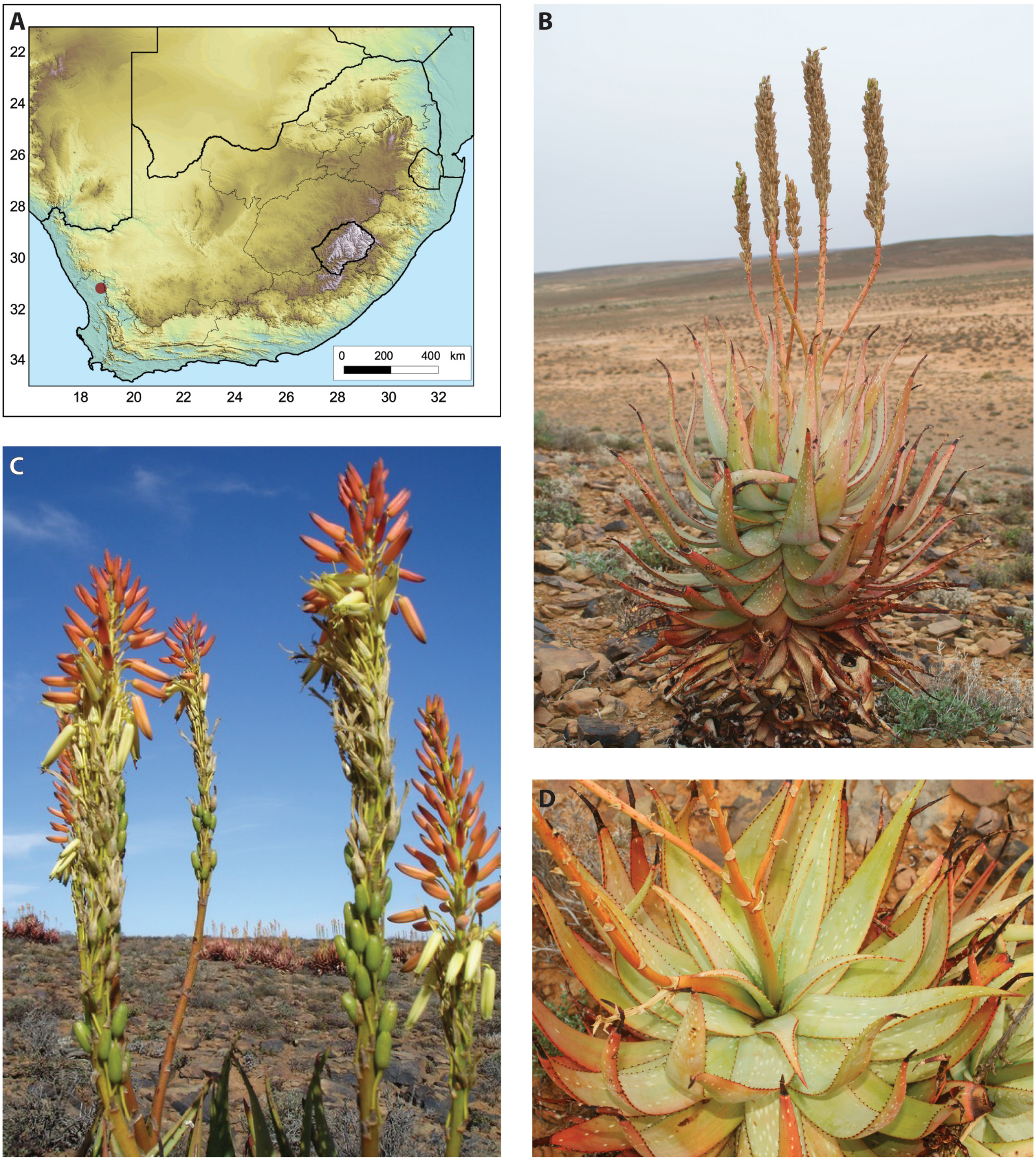


FIGURE 13. *Aloe khamiesensis* subsp. *knersvlakensis*. **A.** Known distribution (red shading). **B.** Caulescent, unbranched plant with developing fruit. **C.** Inflorescences with orange-red buds and yellow, greenish-tipped open flowers. **D.** Rosette of dull green leaves with numerous white spots. Photographs: B, D. Arrie W. Klopper (Kliprand, Western Cape, South Africa, July 2010); C. Sarel J. Marais (Kliprand, Western Cape, South Africa, April 2006).

4. *Aloe microstigma* Salm-Reifferscheid-Dyck (1854: §26, t.4)

Type:—Salm-Dyck, Monographia generum Aloes et Mesembryanthemi 6: sec. 26, t. 4 (1854) (lectotype, designated by Glen & Hardy 2000: 106, as ‘iconotype’, here corrected to lectotype).

Epitype (designated here):—SOUTH AFRICA, Western Cape: 2 miles north of Worcester, 12 July 1949, *G.W. Reynolds 5429* (epitype PRE PRE0090543!).

Note regarding type:—Glen & Hardy (2000: 106) designated the plate Salm-Reifferscheid-Dyck (1854: §26, t.4) as 'iconotype', which is a term not defined in Turland *et al*. (2018); 'iconotype' is here corrected to lectotype. The lectotype (a plate available at https://www.biodiversitylibrary.org/item/257287#page/60/mode/1up) is an illustration by Joseph Franz Maria Anton Hubert Ignatz Fürst zu Salm-Reifferscheid-Dyck (1773–1861), prepared from a plant grown at the Schönbrunn Gardens in Vienna, Austria. In the protologue Salm-Reifferscheid-Dyck (1854) mentions that he had seen an adult plant there in 1816. This plant was sent from the Cape of Good Hope by a Mr. Boose and successfully grown in the famous gardens of the Schönbrunn Palace. Salm-Reifferscheid-Dyck later received seeds of this species from Christian Friedrich Ecklon (1795–1868) and germinated them with success in his own garden near Düsseldorf, Germany. Not surprisingly, the growth form of the plant in the illustration is not typical of plants grown in its natural environment. Leaves on the illustration is very long, narrow, recurved and almost pendent in old leaves, unlike the erectly spreading leaves of plants found in its natural distribution range. The small white spots on the leaves, as well as the inflorescence and flowers are accurately illustrated.

A specimen from the Worcester region in the Western Cape, South Africa (*G.W. Reynolds 5429*), held at Herb. PRE is here chosen as epitype to complement the illustration that serves as lectotype. This specimen consists of a single inflorescence that is split lengthwise and the ab- and adaxial surfaces of a single leaf. The specimen shows the diagnostic characters of the species, even though the leaf surfaces are only slightly white-spotted, consistent with older plants from that region. *Aloe microstigma* is abundant in the Worcester area and this was likely the first significant population of this species that early explorers would have encountered on their expeditions from the Cape into the interior.

Synonyms:—*Aloe arabica* Salm-Reifferscheid-Dyck (1817: 27, 60), *nom. illegit*. Type not cited.

Aloe brunnthaleri A.Berger ex Cammerloher (1933: 131). Type:—SOUTH AFRICA, Western Cape: Matjiesfontein, 1910, *J. Brunnthaler* s.n. (holotype B†). [It was confirmed that this specimen is no longer extant at Herb. B (J. Paule, pers. comm., July 2023)]. Lectotype (designated here):—Unnumbered figure (photograph) of vegetative material of *Aloe brunnthaleri* at the bottom of page 131 of Cammerloher (1933). Epitype (designated here):—SOUTH AFRICA. Western Cape: Laingsburg, Anysberg road, between Rooikop and Rondekop, 6 July 2010, *R.R. Klopper & A.W. Klopper 308* (epitype PRE!; isoepitype NBG!).

Other designation:—'*Aloe perfoliata* sensu Mottram' (2013: 11). Representative material:—Aloe africana maculata spinosa minor, Dillenius, *Hortus elthamensis* 1: t. 15, fig.16, (1732). Mottram (2013) erroneously accepted the lectotype as having been designated by Scopoli (1783: 128) (see Klopper *et al*. 2016 for more information).

Note regarding type of *A. brunnthaleri*:—The only specimen referred to in the protologue of *A. brunnthaleri* (Camerloher 1933) is "Südafrika: Matjesfontein, leg. Brunnthaler 1910". It is here presumed that "1910" is the date of the collection and not the collecting number of Brunnthaler (see Cammerloher 1933: 131, last line on page). This specimen, later cited as being deposited at Herb. B (e.g., Glen & Hardy 2000: 106), is here interpreted as the holotype. It was confirmed that this specimen is no longer extant at Herb. B and that, if it was deposited there, was likely destroyed during World War II (J. Paule, pers. comm., July 2023). Josef Brunnthaler (1871–1914) collected the plant in South Africa and Hermann Josef Cammerloher (1885–1940) later validly published the name *Aloe brunnthaleri* and provided a description based on a plant that flowered in the botanical garden of the University of Vienna, Austria. Both Cammerloher and Brunnthaler were staff of the University of Vienna at the time. Further enquiries to the Herbaria W and WU did not reveal any other material of *A. brunnthaleri* (H. Voglmayer, Herb. W, and A. Berger, Herb. WU, pers. comm., October 2023). Since the type specimen is no longer extant, the only other original material is the images in the protologue. One of the two figures included on p. 131 of Cammerloher (1933) is here designated as lectotype. This black and white photograph of vegetative material of a plant grown under glasshouse conditions in Europe for more than 20 years, is not typical of the plant in its natural environment. Therefore, a specimen collected in the Laingsburg area just east of Matjiesfontein (the type locality) in July 2010 (*R.R. Klopper & A.W. Klopper 308*) is here designated as epitype to support the lectotype. This specimen is deposited at Herb. PRE with a duplicate at Herb. NBG. Both duplicates consist of an inflorescence that is split lengthwise (each specimen with one of the halves), ad- and abaxial surfaces of a leaf, and an envelope with loose flowers. In addition the epitype at Herb. PRE also has a cross-section through a leaf and a flower sequence (which is not present on the isolectotype at Herb. NBG).

4a. ***Aloe microstigma*** **subsp.** ***microstigma*** (Fig. 14)

Type:—As for *A. microstigma*.

Description:—Acaulescent plants or *stem* short, up to 0.5 m high, up to 10 cm diameter, simple or branched, sometimes procumbent, usually erect, with persistent dried leaves; rosettes usually single, sometimes in small groups. *Leaves* densely rosulate, erectly spreading, usually reddish green (colour can vary considerably), both surfaces usually copiously white-spotted, obscurely lineate, lanceolate-deltoid, 30–50 cm long, (4–)6–8 cm wide at base, without spines or prickles; margin with pungent, deltoid, reddish brown teeth, 2–4 mm long, 5–10 mm apart; exudate yellow, drying dark yellow. *Inflorescences* usually 2 or 3 simultaneously, 0.6–0.8 m high, erect or slightly arcuate-erect, simple. *Peduncle* 1.1–2.3 cm wide and plano-convex below, terete above, greenish to brownish; with several sterile bracts, broadly deltoid, acute, (15–)20–30(–37) mm long, 10–20(–27) mm wide, brownish, thin, scarious, many-nerved. *Raceme* conical to cylindric-acuminate, 20–40 cm long, bicoloured, subdense; buds erect to spreading, hidden by densely imbricate bracts, flowers nodding to pendulous when open. *Floral bracts* lanceolate-acute, ± 10–25 mm long, 4–8 mm wide, deep brown, thin, dry, many-nerved. *Pedicels* (16–)25–30(–37) mm long, yellowish to pinkish green. *Flowers: perianth* dull red in bud, sometimes greenish yellow, yellowing with age, sometimes uniformly yellow or red, 25–35 mm long, 4–6 mm across ovary, enlarging slightly to 6–9 mm towards middle, narrowing to 4–5 mm towards mouth, cylindric to ventricose; outer segments free to base, tips slightly spreading; *stamens* with pale lemon, filiform-flattened filaments, exserted 2–5(–7) mm; *ovary* 6–8 mm long, 3 mm diameter, green; *style* yellow, exserted 4–6 (–10) mm.

Diagnostic characters:—*Aloe microstigma* subsp. *microstigma* is distinguished by its usually copiously white-spotted leaves in solitary rosettes or with rosettes sometimes in groups. Leaves are 6–8 cm wide, with reddish brown marginal teeth of 2–4 mm long. Inflorescences are simple, 0.6–0.8 m high, and usually with bicoloured racemes of 20–40 cm long. Floral buds are red or yellow and mature flowers greenish yellow and 25–35 mm long. Pedicels are 25–30 mm long. Floral bracts (10–25 mm) are usually half as long as pedicels. Leaf exudate does not dry purple (dries dark yellow).

Distribution:—It occurs fairly widespread in the western parts of the Eastern Cape, the central areas of the Western Cape and just into the Northern Cape in the Tankwa Karoo and Calvinia area, South Africa.

Habitat:—Rocky outcrops in Karoo and Namaqua Broken Veld. In hot, dry flat country, sometimes on steep slopes.

Elevation:—50–1 200 m

Flowering time:—May–August

Etymology:—From Greek 'mikros' (small), 'stigma' (spot, stigma); refers to the small white spots on the leaves.

General notes:—*Aloe microstigma* is very variable in leaf colour and markings, and colour of the flowers. Leaves vary from entirely without spots, to copiously spotted on both surfaces. In the west of its distribution range flowers are more glossy, whereas they are more dull and with a bloom in the east. In the west plants with unicoloured yellow racemes occur together with the normal bicoloured forms. Near Robertson plants with unicoloured red racemes have been recorded (Reynolds 1950).

Aloe brunnthaleri A.Berger ex Cammerl. from near Matjiesfontein and Laingsburg is only a yellow-flowering form of *Aloe microstigma* (Reynolds 1950).

Aloe microstigma was grown in Schönbrunn Gardens, Vienna, Austria in 1816, where Salm-Dyck reportedly saw it (Reynolds 1950).

Additional specimens examined:—SOUTH AFRICA. Eastern Cape: Middelburg, 20 July 1948, *J. Theron 501* (PRE^{m}); Conway farm, September 1899, *D.F. Gilfillan 5575* (PRE^{m}). Graaff-Reinet Distr., Karoo Nature Reserve, 25 July 1981, *M.T. Linger 2119* (PRE^{m}). Graaff-Reinet, May 1867, *H. Bolus 598* (BOL, K); *Miss Auret Nat.Bot.Gardens 170* (BOL); Fl. at Botany Laboratory, 20 May 1916, *P.J. Pienaar 150* (K, PRE^{m}); Fl. at Kirstenbosch, July 1915, *J.C. Auret NBG 1710/14* (BOL). Jansenville area, on Klipplaat road, 4 July 2010, *R.R. Klopper & A.W. Klopper 292 & 293* (GRA^{gmc}, PRE^{gmc}). Baviaanskloof/Makedaad, 30 January 2003, *G. Middelberg 168* (PRE). Steytlerville Golf course, 10 November 2004, *G.J. Bredenkamp & M. Watson 63* (PRE); *L.P. Steenkamp 183* (GRA, PRE). Addo bush, June 1904, *Curator Pretoria Bot. Garden 2493* (PRE); 13 August 1915, *S. Schönland 112* (PRE^{m}, SAM); Fl. ex hort., *S. Schönland SAM22682* (SAM); Fl. ex hort Schönland, June–July 1899, *S. Schönland 1502* (GRA, SAM); Fl. in Grahamstown, July 1907, *s. coll. BOL No. 24294* (BOL). Near Fort Brown, August 1934, *G.W. Reynolds 872* (BOL). Grahamstown-Bedford road, at Carlisle's Bridge turnoff, 4 July 2010, *R.R. Klopper & A.W. Klopper 287 & 288* (GRA^{gmc}, PRE^{gmc}).

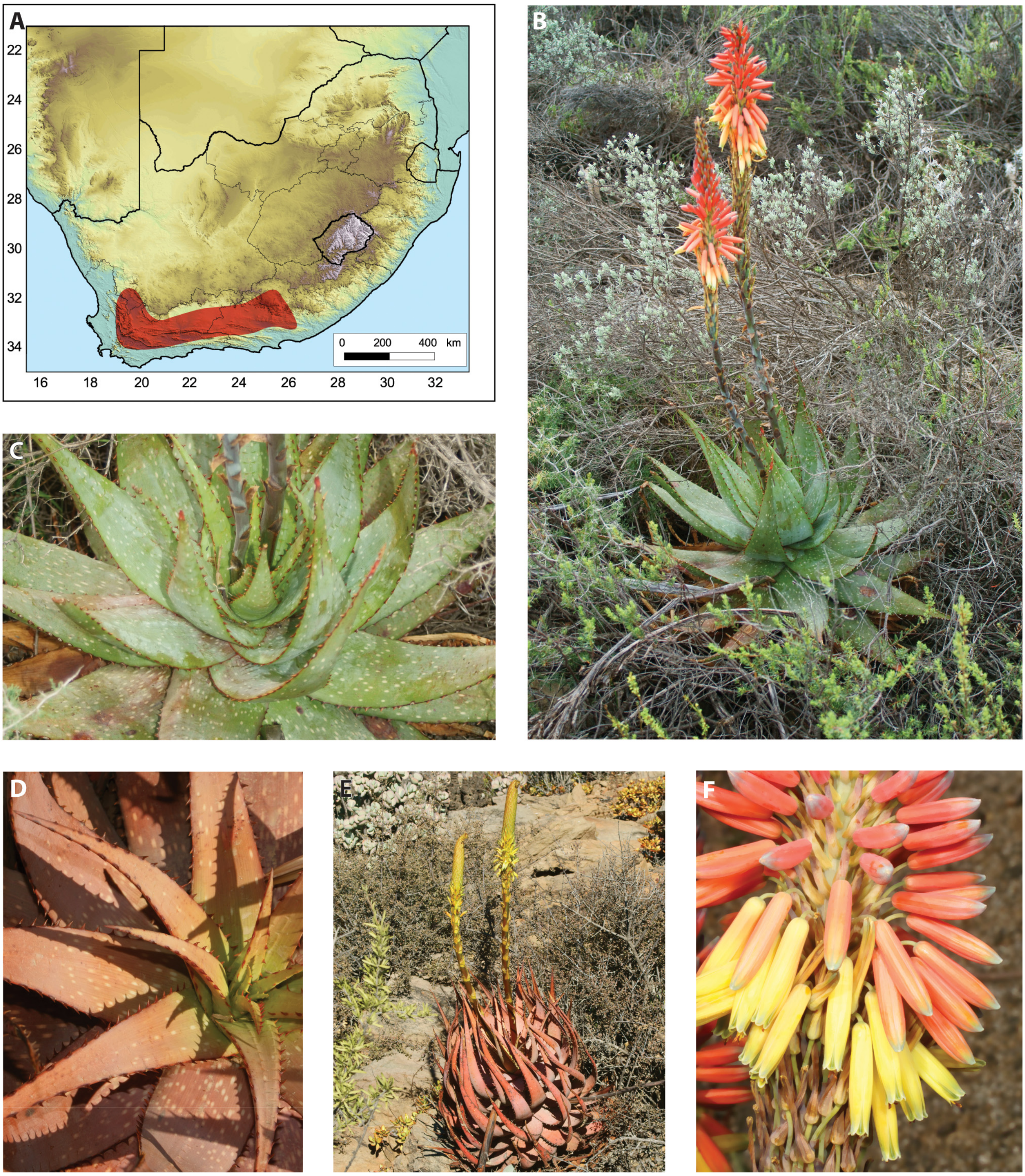


FIGURE 14. *Aloe microstigma* subsp. *microstigma*. **A.** Known distribution (red shading). **B.** Single rosette with simple, bicoloured inflorescences. **C.** Rosette of grey-green leaves with copious white spots on both surfaces. **D.** Rosette of reddish leaves with copious white spots. **E.** Single rosette with reddish leaves and simple, unicoloured, yellow inflorescences. **F.** Raceme with red buds and yellow, green-tipped open flowers. Photographs: Arrie W. Klopper (B, C. Uniondale, Western Cape, South Africa; D, E. Anysberg, Western Cape, South Africa; F. Carlisle Bridge, Eastern Cape, South Africa; July 2010).

Grahamstown-Bedford road, near Carlisle's Bridge at Fort Beaufort turnoff, 4 July 2010, *R.R. Klopper & A.W. Klopper 285 & 286* (PRE^{gmc}). Albany, S of Carlisle Bridge, 28 June 1935, *G.W. Reynolds 1421* (BOL, K, PRE^{m}); 15 July 1949, *G.W. Reynolds 5440* (GRA, PRE^{m}, SAM); Fish River Valley, near Carlisle Bridge, 23 June 1938, *G.W. Reynolds 2405* (PRE^{m}). Between Grahamstown and Carlisle Bridge, August 1927, *R.A. Dyer 985* (GRA). Grahamstown, on Cradock Road, near Carlisle Bridge, July 1925, *R.A. Dyer 1578* (GRA). Albany Dist., beyond Hellspoort on road to Bedford, June 1936, *G.G. Smith 347* (PRE). Grahamstown, on Cradock Road, July 1929, *R.A. Dyer 2000* (GRA). Albany Dist., Grahamstown, 17 June 1941, *L.A. Bolus NBG 1423/32* (NBG); Ex hort. H.H. Bolus, July 1929, *H.H. Bolus 88* (BOL). Cradock, 22 July 1932, *Immelman s.n.* (K). Midlands of Cape Province, fl. ex hort. East London, July 1933, *G.G. Smith 182* (BOL). **Western Cape:** Matjesfontein, fl. at Kirstenbosch, July 1915, *L. Bolus NBG 2264/14* (BOL); *Dr Beattie NBG 2532/14* (BOL). Wuppertal, Matjiesrivier Nature Reserve, Sandleegte and Zuurfontein Farmstead, 14 September 2002, *A.B. Low 7829* (NBG^{m}). Kagga Kamma Nature Reserve, near Bobbejaankrans camp, 12 August 2012, *M. Koekemoer 4308* (PRE^{m}). Worcester, De Doorns, June 1921, *H.W.R. Marloth 10141* (PRE^{m}). Worcester, July 1912, *H.W.R. Marloth 5157* (NBG, PRE); August 1919, *H.W.R. Marloth 8768* (PRE); N of Worcester, 12 July 1949, *G.W. Reynolds 5429* (epitype PRE^{m}); Worcester Dist. Field Reserve, July 1963, *M.C. Olivier 95* (NBG); Karoo Desert National Botanical Garden, 3 November 2008, *O.M. Grace, E. van Wyk, et al. 127* (K); 9 July 2010, *R.R. Klopper & A.W. Klopper 331 & 332* (NBG^{gmc}, PRE^{gmc}). Between Goudini and Worcester, 12 May 1928, *N.S. Pillans 6797* (BOL). Between Worcester and Robertson, fl. Grahamstown, August 1907, *s. coll.* (GRA). Robertson, W of Robertson, 12 July 1949, *G.W. Reynolds 5430* (PRE^{m}). Touwsrivier, 12 March 1904, *I.B. Pole-Evans 16* (PRE); 28 May 1919, *I.B. Pole Evans 213* (PRE^{m}, SAM). Laingsburg area, near Anysberg, 6 July 2010, *R.R. Klopper & A.W. Klopper 310 & 311* (NBG^{gmc}, PRE^{gmc}); Anysberg road, between Rooinek and Rondekop, 6 July 2010, *R.R. Klopper & A.W. Klopper 308 & 309* (NBG^{gmc}, PRE^{gmc}). Laingsburg, fl. Grahamstown July 1905, *S. Schonland GRA No. A7260* (GRA). Between Ladismith and Laingsburg, fl. hort. H.H. Bolus, Kennilworth, July 1928, *H.H. Bolus 92* (BOL). Montagu, Nougas Hills, 11 July 1954, *A.J.M. Middlemast 1872* (NBG^{m}). Heidelberg Distr., Grootvadersbosch State Forest, Duiwenhoksrivier ravine, 31 July 1974, *R.A. Haynes 967* (PRE^{m}). Laingsburg area, road to Seweweekspoort, near Nietvoorby, 6 July 2010, *R.R. Klopper & A.W. Klopper 306 & 307* (NBG^{gmc}, PRE^{gmc}). Little Karoo, Farm Die Eike, Five Oaks, 20 August 1982, *D.F. Laidler 317* (NBG, PRE). Klein Karoo, near Muiskraal, 29 July 1983, *P. Bohnen 8223* (NBG). Riversdale, Phesantefontein, June 1925, *J. Muir 3619* (PRE^{m}). Oudtshoorn area, R62 near Calitzdorp, 6 July 2010, *R.R. Klopper & A.W. Klopper 303 & 304* (NBG^{gmc}, PRE^{gmc}). Klaarstroom area, on Prince Albert road, 5 July 2010, *R.R. Klopper & A.W. Klopper 299* (NBG^{m}, PRE^{m}) *& 300* (NBG^{gmc}, PRE^{gmc}). Oudtshoorn, De Rust, 2 August 1958, *S. Burger PRE38403* (PRE). Oudtshoorn, fl. in Grahamstown, August 1908, *A. Taylor s.n.* (GRA, K); Ex hort. Kirstenbosch, 3 August 1943, *M.R. Henderson 1749* (NBG); Oudtshoorn Dist., Cango Valley, 8 August 1949, *W.F. Barker 5481* (NBG). Prince Albert, Swartberg, between Prince Albert and Meiringspoort, 2 August 1958, S. *Burger PRE38402* (PRE^{m}). Uniondale, on Willowmore road, close to first De Rust turnoff from Willowmore, 5 July 2010, *R.R. Klopper & A.W. Klopper 297 & 298* (GRA^{gmc}, PRE^{gmc}). Willowmore, ex hort. Stellenbosch University, August 1932, *H. Herre SUGardens 5053* (BOL). **Northern Cape:** Calvinia, Akkerendam Nature Reserve, 7 August 1993, *A.M. Jooste 46* (NBG); *R.R. Klopper & A.W. Klopper 341* (KMG^{g}, PRE^{g}); Bloukranz Pass, 11 July 2010, *R.R. Klopper & A.W. Klopper 340* (KMG^{gmc}, PRE). Tankwa Karoo National Park, Farm Kleinfontein 1027, top of Gannaga Pass, 8 May 2006, *R.R. Klopper 321* (PRE^{m}); 10 July 2010, *R.R. Klopper & A.W. Klopper 336* (KMG^{gc}, PRE^{gc}) *& 337* (NBG, PRE).

4b. ***Aloe microstigma*** **subsp.** ***juttae*** (Dinter) Klopper *comb. et stat. nov*. (Fig. 15)

Basionym:—*Aloe juttae* Dinter (1923: 159). Type:—NAMIBIA: Gubub, 7 June 1922, *M.K. Dinter 3601* (lectotype [designated here] B B 10 1244036!, as ‘holotype’ [http://herbarium.bgbm.org/object/B101244036]; isolectotypes B B 10 1244034! & B 10 1244035! [2 sheets] as ‘holotype’ [http://herbarium.bgbm.org/object/B101244034; http://herbarium.bgbm.org/object/B101244035], BOL BOL140198! as ‘isotype’ [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.bol140198], DR DR081354! [https://dr.jacq.org/DR081354], PRE! PRE0090536-1 & -2 [2 sheets] as ‘isotype’ [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.pre0090536-1; https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.pre0090536-2], SAM SAM0073732-0! as ‘isotype’ [https://plants.jstor.org/stable/viewer/10.5555/al.ap.specimen.sam0073732-0]).

Note regarding type:—The protologue of *A. juttae* (Dinter 1923) states that the holotype of this name is in Herb. B and that isotypes are at Herbs. BOL, PRE, and SAM. During this study, a further, previously uncited, duplicate was traced at Herb. DR.

Two duplicates of *Dinter 3601* could be traced at Herb. B. One duplicate consists of two sheets (B 10 1244034 & B 10 1244035) and shows signs of insect damage; sheet I contains two inflorescences and an envelope with the remains of flowering and fruiting material, while sheet II consists of two leaves. The second duplicate (B 10 1244036) consists of a leaf, an inflorescence, and an envelope with a flower and what appears to be a bract. The duplicate with barcode B 10 1244036 is here designated as lectotype as it shows all the diagnostic characters of the species and is in a better state of preservation than the other duplicate at Herb. B that consists of two sheets (B 10 1244034 & B 10 1244035).

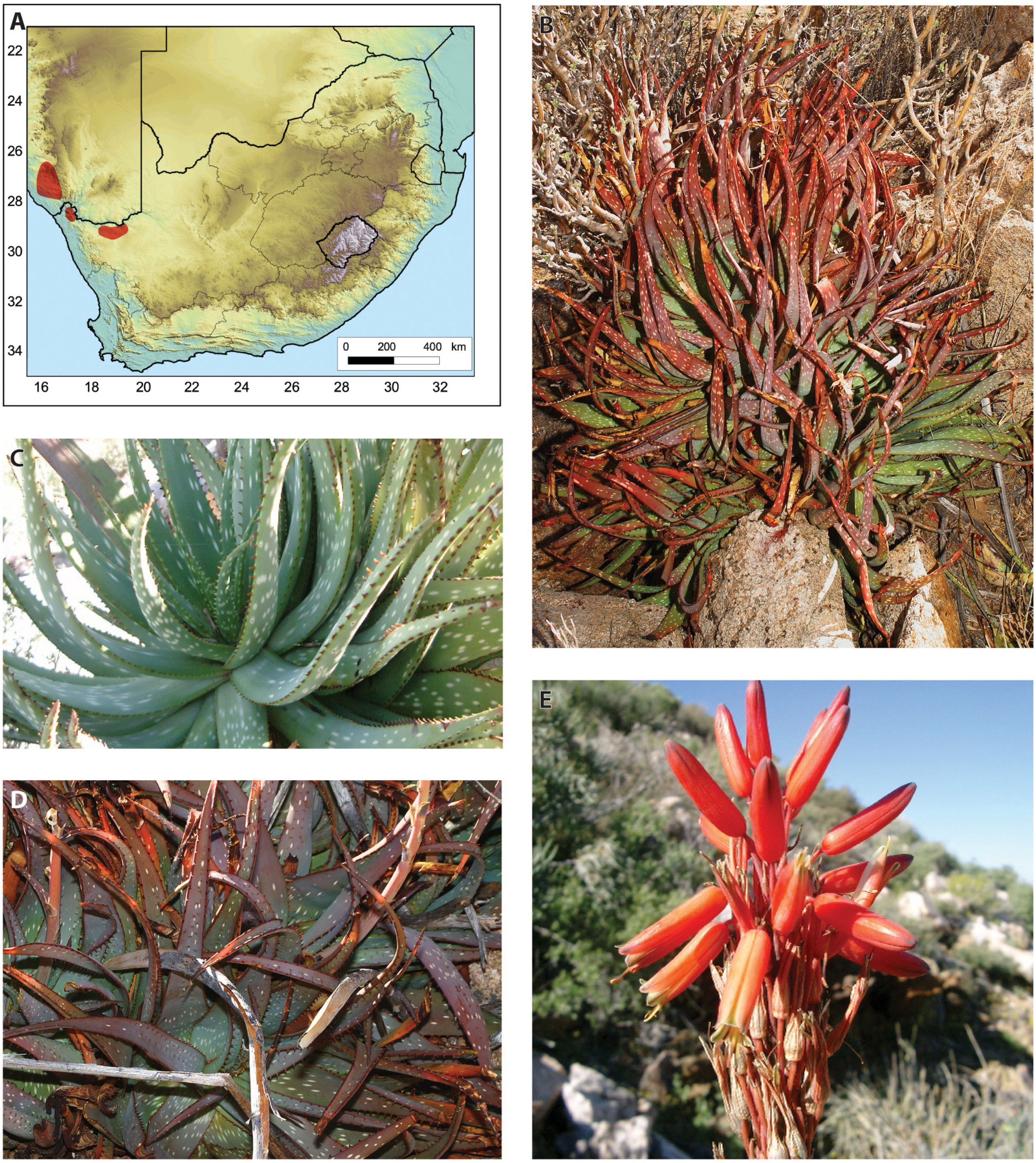


FIGURE 15. *Aloe microstigma* subsp. *juttae*. **A.** Known distribution (red shading). **B.** Dense, multi-headed cluster of rosettes. **C.** Rosette of thin, blue-green leaves with white spots during a period of above-average rainfall. **D.** Rosettes of reddish leaves during a dry season. **E.** Raceme with orange-red flowers. Photographs: B, D. Arrie W. Klopper (Aus, Namibia, July 2010); C, E. Japie C. Kruger (Pofadder, Northern Cape, South Africa, June 2006).

Description:—Acaulescent to shortly caulescent plants; rosettes in dense groups. *Leaves* densely rosulate, erectly spreading, blue-green, often reddish, with few elongated white spots on both surfaces, narrowly lanceolate, gradually attenuate, ± 30 cm long, 2.5–4.5 cm wide; margin with pungent, deltoid, reddish brown teeth, 0.5–2.0(–3.0) mm long, 4–8 mm apart; leaf exudate yellow, drying yellow. *Inflorescence* single or up to 3 per rosette simultaneously, ± 0.6 m high, erect, simple or often 2- or 3-branched from below middle. *Peduncle* 1.1–1.4 cm wide and plano-convex below, terete upwards, reddish green to brown; with sterile bracts, acute, 20–25(–32) mm long, 10–14(–18) mm wide, pale, scarious, 8-nerved. *Racemes* cylindrical, (25–)30–40 cm long, erect, dense; buds erect to spreading, flowers nodding when open. *Floral bracts* broadly lanceolate, acute, amplexicaul, 12–20 mm long, 4–6 mm wide, reddish brown, rather scarious, 5- to 7-nerved. *Pedicels* 15–20 mm long, red. *Flowers: perianth* bright orange-yellow to orange-red, green-tipped, (18–)20–28(–30) mm long, 7 mm across ovary, not narrowed above ovary, cylindrical; outer segments free to base, tips slightly spreading; *stamens* with filiform flattened filaments, yellow with exserted portion turning purplish brown, shortly exserted or included; *ovary* 5 mm long, 2.0–2.5 mm diameter, green; *style* bright yellow, exserted 4–5 mm.

Diagnostic characters:—*Aloe microstigma* subsp. *juttae* is distinguished by its dense rosette clusters forming a disorderly shrub. Leaves are usually copiously white-spotted and narrow (2.5–4.5 mm wide), with reddish brown marginal teeth of 0.5–2.0 mm long. Inflorescences are simple or often 2- or 3-branched, ± 0.6 m high, and usually with unicoloured to only very slightly bicoloured racemes of 30–40 cm long. Floral buds are orange-red and mature flowers orange-yellow to orange-red and 20–28 mm long. Pedicels are 15–20 mm long. Floral bracts (12–20 mm) are about as long as the pedicels. Leaf exudate does usually not dry purple (dries yellow).

Distribution:—Only known from southwestern Namibia, isolated mountains in Bushmanland, and the Richtersveld, Northern Cape, South Africa. Endemic to the Gariep Centre of Endemism.

Habitat:—Granite ridges with large scattered boulders.

Elevation:—1 000–1 600 m

Flowering time:—May–June

Etymology:—Commemorates Mrs Jutta Dinter (fl. 1906–1935), wife of Namibian botanist M.K. Dinter (author of the basionym).

General notes:—This taxon was originally described as *Aloe juttae*, but has long been treated as a synonym of *Aloe microstigma* (Reynolds 1950).

Additional specimens examined:—SOUTH AFRICA. Northern Cape: Pofadder, farm Boomrivier, on Slangberg, 21 July 2010, *R.R. Klopper & A.W. Klopper 396* (KMG, PRE). **NAMIBIA.** Luderitz, Klein Aus Farm LU8, 24 June 1974, *J.W.H. Giess 13368* (PRE^{m}). Between Gubub and Aus, 7 June 1922, *M.K. Dinter 3601* (isotypes BOL, PRE^{m}, SAM). Farm Kubub LU15, 9 September 1973, *J.W.H. Giess 12864* (WIND); no date, *J.W.H. Giess & D. van Vuuren 793* (WIND); Farm Kubub, just S of Aus, 18 July 2010, *R.R. Klopper & A.W. Klopper 387 & 388* (NBG^{gc}, PRE^{gc}, WIND^{gc}). Klinghardtberge, 20 September 1977, *H. Merxmüller & J.W.H. Giess 32202* (WIND). Heiob Mountains, 15 February 1984, *M.B. Bayer 3885* (NBG). Witputz, Aurus Mountains, Rooiberg, *D.S. Hardy 5056* (PRE^{m}). Luderitz, Witputz-Sud LU31 Farm, 26 June 1975, *M.A.N. Müller & W.J. Jankowitz 294* (PRE^{m}, WIND); 16 June 1976, *J.W.H. Giess & M.A.N. Müller 14424* (PRE^{m}, WIND); S of Witputs, fl. hort. Stellenbosch University, *H. Herre SUGardens 7119* (BOL). Rosh Pinah, Numeis, 2 September 2000, *P.V. Bruyns 8835* (NBG); S of Farm Zebrafontein 87, 28 August 2003, *P.V. Bruyns 9479a* (WIND). Namibia, ex Triebner, fl. in hort. Frames, Kenilworth, July 1935, *P. Ross Frames s.n.* (BOL).

5. ***Aloe succotrina*** Weston (1770: 5) (Fig. 16)

Homotypic synonyms:—*Aloe succotrina* Allioni (1773: 65), *nom. superfl.*; *Aloe succotrina* Lamarck (1783: 85), *nom. illegit.*; *Aloe perfoliata* var. *succotrina* (Lam.) Aiton (1789: 466). Type:—*A. succotrina, angustifolia spinosa, flore purpureo*, J. Commelin, Horti medici Amstelaedamensis 1: 91, t. 48 (1697) (Lectotype!, designated by Wijnands 1983: 126).

Epitype (designated by Guglielmone *et al.* 2009: 180):—SOUTH AFRICA, Western Cape: Boulder field near Window Gorge, above Newlands, July 1905; *R. Marloth 3967* (epitype PRE!).

Synonyms:—*Aloe perfoliata* var. *ξ* Linnaeus (1753: 320). Type:—not cited.

Aloe soccotrina Garsault (1764: pl. 102), *nom. inval*. Type:—not cited.

Aloe vera Miller (1768: 15), non (Linnaeus 1753: 320) Burman (1768: 83), *nom. illegit*. Type:—not cited.

Aloe perfoliata var. *purpurascens* Aiton (1789: 466); *A. socotrina β purpurascens* (Aiton) Ker Gawler (1812: t.1474), *nom. inval.*; *Aloe purpurascens* (Aiton) Haworth (1804: 20). Type:—not cited.

Aloe sinuata Thunberg (1794: 61). Type:—not cited.

Aloe soccotrina De Candolle (1801: t.85). Type:—not cited.

Aloe soccotorina Schult. & Schult.f. in Roemer & Schultes (1829: 701), *nom. inval*. Type:—not cited.

Aloe succotrina var. *saxigena* Berger (1908: 283). Type:—SOUTH AFRICA. Western Cape: Steenbras River Mouth, *H.W.R. Marloth 4357* (holotype B†) [It was confirmed that this specimen is no longer extant at Herb. B (J. Paule, pers. comm., July 2023)].

Description:—Caulescent or sometimes acaulescent plants, forming dense groups. *Stem* short or up to 2 m long, 10–15 cm diameter, simple or dichotomously branched, erect or procumbent, with persistent dried leaves; rosettes solitary or usually in dense large groups. *Leaves* densely rosulate, erectly spreading, dull green to grey-green, obscurely lineate, sometimes with few white spots, lanceolate-attenuate, 25–50 cm long, 5.5–10.0 cm wide at base; margin with firm, deltoid, white teeth, 2–4 mm long, 5–10 mm apart; exudate honey-coloured, drying purple. *Inflorescence* single or sometimes 2 simultaneously or consecutively, 0.75–1.00 m high, arcuate-erect, mostly simple, rarely 2-branched from around middle or below. *Peduncle* 1.0–1.5 cm wide and plano-convex below, terete upwards, reddish green to brown; with many sterile bracts, ovate-acute, 17–25(–33) mm long, 8–15(–23) mm wide, thin, rather scarious, purplish, many-nerved. *Raceme* cylindric-acuminate, 21–37 cm long, erect, rather dense; buds erect to spreading, flowers nodding to pendent when open, buds partly obscured by large imbricate bracts. *Floral bracts* broadly lanceolate, 16–22(–29) mm long, 6–10 mm wide, pinkish green, turning purplish, thin, scarious, many-nerved. *Pedicels* 20–33(–38) mm long, yellowish green to pinkish or purplish green. *Flowers: perianth* glossy red to reddish salmon, green-tipped, (25–)30–40 mm long, 6–8 mm across ovary, not narrowed above ovary, slightly widening to 7–9 mm toward middle, slightly narrowing to 6–7 mm towards wide-open mouth, cylindric-trigonous; outer segments free to base, tips slightly spreading; *stamens* with pale lemon, filiform flattened filaments, exserted 4–8 mm; *ovary* 7–8 mm long, 2–3 mm diameter, green; *style* yellow, exserted 4–8 mm.

Diagnostic characters:—*Aloe succotrina* is distinguished by its erect, dull grey-green leaves with white marginal teeth and leaf exudate that dries purple. Inflorescences are up to 1 m long, with fairly large purplish bracts. Flowers are red and 30–40 mm long.

Distribution:—Restricted to mountain slopes from the Cape Peninsula to Hermanus, Western Cape, South Africa. Confined to mountain Fynbos on Table Mountain Sandstone.

Habitat:—Mountain Fynbos on Table Mountain Sandstone on steep cliffs and rocky slopes. High winter rainfall, generally close to the sea.

Elevation:—up to 600 m

Flowering time:—July–August

Etymology:—Refers to either the plant being thought to be the source of the drug socotrine aloes and originating from Socotra, however, it grows wild only in the extreme southwestern part of the Western Cape province of South Africa, or to the compound word meaning ‘succus’ (sap), ‘citrinus’ (lemon-yellow). Even though the latter suggests that the leaf exudate turns yellow when it dries (Reynolds 1950), the juice that dries purple is characteristic of *A. succotrina*.

General notes:—This is a very variable species. Plants are either solitary with short, simple or branched erect stems, or where conditions are favourable, plants form large dense groups. The largest forms have stems of 1–2 m long that are dichotomously branched and form a large canopy of many rosettes (Reynolds 1950, Smith & Van Wyk 1996).

Aloe succotrina have a confused history and wrong synonymy that is rivalled by no other aloe. This is mostly due to early authors wrongly assuming that this plant is from the Island of Socotra (Reynolds 1950).

Plants received by Commelin flowered in 1689 and 1690 in Amsterdam and it was the first South African aloe to be grown in Europe. It is thus surprising that *Aloe succotrina* is not among the aloes grown at the Dutch East India Company’s Garden in Cape Town when Oldenland was Superintendent there in 1695 (Reynolds 1950).

Additional specimens examined:—SOUTH AFRICA. Western Cape: Cape Town, 30 September 1921, *J. Elffers PRE 38405* (PRE); From the Camps Bay Road, Unknown s.n. (NBG). Table Mountain, 28 August 1905, *s. coll.* (GRA); Between Devil’s Peak and Kirstenbosch, 17 September 1928, *J.B. Gillett 501* (NBG). Kirstenbosch National Botanical Garden, on contour path on Table Mountain, 9 July 2010, *R.R. Klopper & A.W. Klopper 328, 329 & 330* (NBG^{gmc}, PRE^{gmc}). Kirstenbosch, Fernwood Buttress, 10 June 1943, *E. Wasserfall s.n.* (NBG). Table Mt., Kirstenbosch, 15 May 1955, *J.P. Stokoe s.n.* (SAM); June 1913, *L. Bolus 24298* (BOL); 6 June 1967, *D. McMurtry 202* (PRE). E slopes of Table Mountain, Kirstenbosch, October 1917, *M.M. Page n.s.* (BOL). Newlands, May 1907, *N.S. Pillans s.n.* (GRA); Slopes of Table Mountain above Newlands, August 1905, *N. Pillans BOL10595* (BOL). Table Mountain National Park, 8 July 2010, *R.R. Klopper, A.W. Klopper & E.J. van Jaarsveld 323, 324 & 325* (NBG^{gmc}, PRE^{gmc}). Cape Peninsula, Karbonkelberg, 18 July 1926, *H.W.R. Marloth 5133B* (PRE); 5 July 1942, *R.H. Compton 13291* (NBG^{m}); *E.S.C. Dyke 5133* (PRE). Cape of Good Hope Nature Reserve, Boer ridge S of Batsata Nek, 1 August 1983, *H.C. Taylor 10551* (NBG). Cape Point Nature Reserve, between Smitswinkel Bay and Paulsberg, 17 July 1979, *E.J. van Jaarsveld 5956* (NBG^{m}). Fish Hoek Mountains, Cape Peninsula, 15 September 1942, *Dr Gonlimis BOL24296* (BOL). On Steenberg, December 1904, *C.B. Fair BOL24295* (BOL). Steenbras Riv. Mouth, near Palmiet River Mouth, 4 May 1924, *H.W.R. Marloth 5132* (PRE^{m}). Groot Hangklip, 11 September 1969, *C. Boucher 582* (NBG, PRE). Hermanus, 1 January 1915, *H.W.R. Marloth 97A* (PRE); 8 January 1915, *H.W.R. Marloth 97B* (PRE); 6 June 1935, *J.C. van Balen 951* (PRE^{m}); Komma beach, 7 July 2010, *R.R. Klopper & A.W. Klopper 315 & 316* (NBG^{gmc}, PRE^{gmc}); Kraal rock, 7

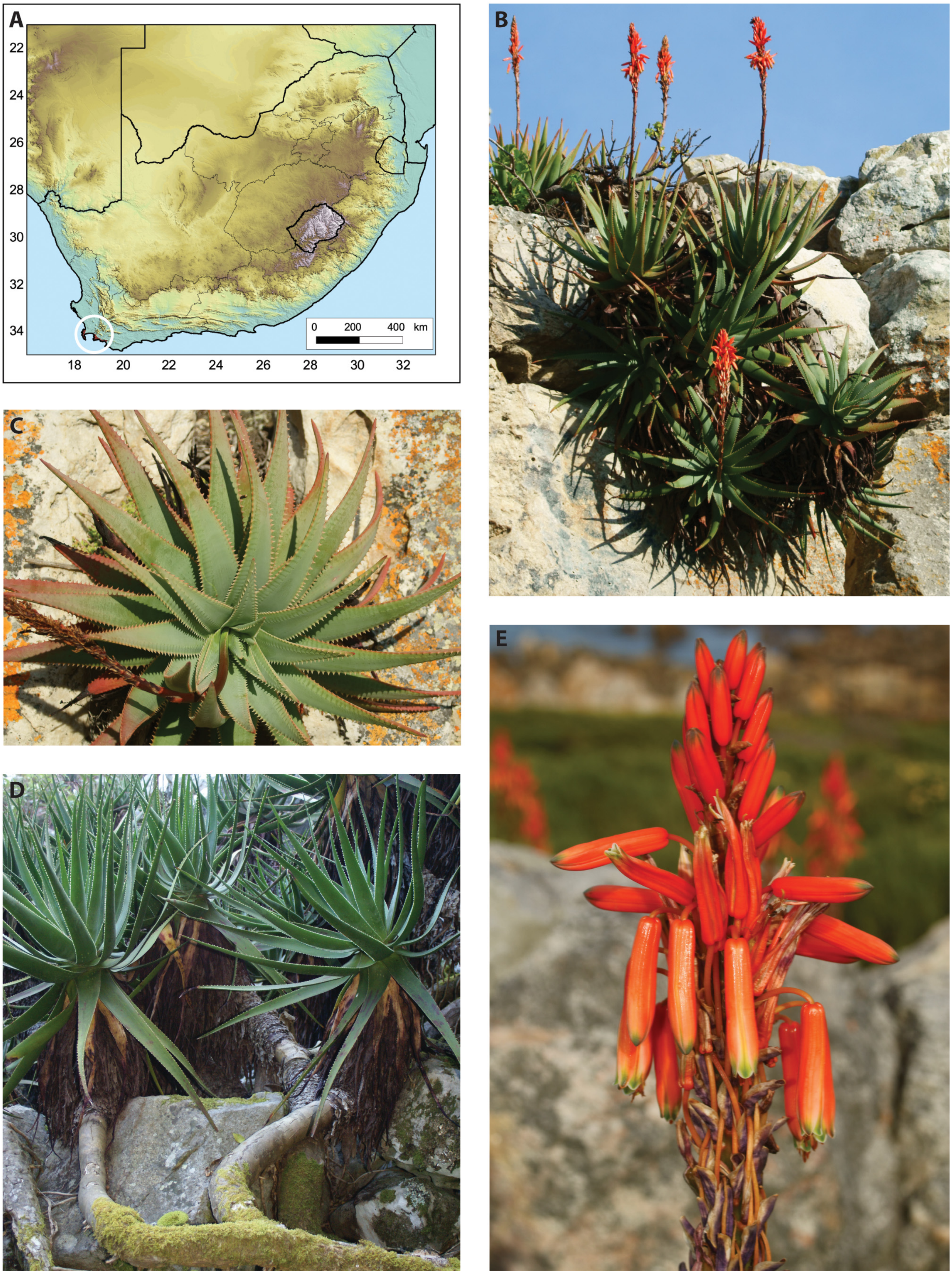


FIGURE 16. *Aloe succotrina*. **A.** Known distribution (red shading in white circle). **B.** Plants froming dense groups. **C.** Rosette of dull green leaves with few to no white spots. **D.** Plants with long trailing stems growing over boulders. **E.** Raceme with glossy red, green-tipped flowers and diagnostic broad purple bracts. Photographs: Arrie W. Klopper (B, C. Cape Peninsula, Western Cape, South Africa; D. Kirstenbosch National Botanical Garden, Western Cape, South Africa; E. Kleinmond, Western Cape, South Africa; July 2010).

July 2010, *R.R. Klopper & A.W. Klopper 317 & 318* (NBG^{gmc}, PRE^{gmc}). Caledon Dist., Klein River Mouth, *H.W.R. Marloth 5149* (NBG, PRE^{m}); September 1940, *J.P. Stokoe 7821* (BOL); December 1920, *H.W.R. Marloth 10033* (PRE). Kleinmond, 7 July 2010, *R.R. Klopper & A.W. Klopper 319 & 320* (NBG^{gmc}, PRE^{gmc}); At old harbour, 7 July 2010, *R.R. Klopper & A.W. Klopper 321 & 322* (NBG^{gmc}, PRE^{gmc}).

Specimens from other species

***Aloe arborescens*:—**Copenhagen Botanic Garden, Accession no. P2012-5002 (ex hort.^{g}); South Africa, Mpumalanga, Mariepskop, *R.R. Klopper & A.W. Klopper 416* (PRE^{g}). ***Aloe arenicola*:—**South Africa, Northern Cape, Koingnaas, on road to Soebatsfontein, *R.R. Klopper & A.W. Klopper 363* (PRE^{g}). ***Aloe broomii*:—**Copenhagen Botanic Garden, Accession no. P2012-5002 (ex hort.^{g}). ***Aloe burgersfortensis*:—**Copenhagen Botanic Garden, Accession no. P2012-5006 (ex hort.^{g}). ***Aloe chlorantha*:—**South Africa, Northern Cape, Farm Tafelberg, *E.J. van Jaarsveld 22666* (PRE^{g}); South Africa, Northern Cape, Williston, *J.P.H. Acocks 16431* (PRE^{m}). ***Aloe claviflora*:—**South Africa, Northern Cape, Pofadder, Farm Boomrivier, *R.R. Klopper & A.W. Klopper 400* (PRE^{g}). ***Aloe comosa*:—**South Africa, Western Cape, Skitterykloof picnic cite, *R.R. Klopper & A.W. Klopper 335* (PRE^{g}). ***Aloe ferox*:—**Published DNA sequence (Adams *et al*. 2000), GenBank accession no. AF234338^{g}. ***Aloe krapohliana*:—**South Africa, Western Cape, near Vredendal, *R.R. Klopper & A.W. Klopper 354* (PRE^{g}). ***Aloe marlothii*:—**Published DNA sequence (Yessoufou 2012), GenBank accession no. JF270641^{g}. ***Aloe pictifolia*:—**Copenhagen Botanic Garden, Accession no. S1997-0760 (ex hort.^{g}); South Africa, Eastern Cape, Kouga District, Paul Sauer Dam, *G.X. Marais s.n.* (PRE^{m}). ***Aloiampelos striatula*:—**South Africa, Eastern Cape, Tarkastad area, *R.R. Klopper & A.W. Klopper 284* (PRE^{g}). ***Aloidendron dichotomum*:—**South Africa, Northern Cape, Nieuwoudtville, Gannabos quiver tree forest, *R.R. Klopper & A.W. Klopper 356* (PRE^{g}). ***Aristaloe aristata*:—**Published DNA sequence (Treutlein *et al*. 2003b), GenBank accession no. AY323713^{g}. ***Kniphofia*:—**Copenhagen Botanic Garden, DNA bank accession no. C559 (ex hort.^{g}).

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References

Adams, S.P., Leitch, I.J., Bennett, M.D., Chase, M.W. & Leitch, A.R. (2000) Ribosomal DNA evolution and phylogeny in *Aloe*

(Asphodelaceae). *American Journal of Botany* 87(11): 1578–1583. https://doi.org/10.2307/2656733

Aiton, W. (1789) *Hortus Kewensis* 1. George Nicol, London, 496 pp. https://doi.org/10.5962/bhl.title.4504

Allioni, C. (1773) Auctarium ad synopsim methodicam stirpium horti regii taurinensis. *Melanges de Philosophie et de Mathematique de la Societé Royale de Turin pour les années 1770–1773*, 5: 53–96. [https://www.biodiversitylibrary.org/item/32648#page/73/mode/1up]

Avise, J.C., Ankney, C.D. & Nelson, W.S. (1990) Mitochondrial gene trees and the evolutionary relationships of Mallard and Black ducks. *Evolution* 44 (4): 1109–1119. https://doi.org/10.2307/2409570

Avise, J.C., Arnold, J., Ball, R.M., Bermingham, E., Lamb, T., Neigel, J.E., Reeb, C.A. & Saunders, N.C. (1987) Intraspecific phylogeography: the bridge between population genetics and systematics. *Annual Review of Ecology & Systematics* 18: 489–522. https://doi.org/10.1146/annurev.es.18.110187.002421

Beaumont, J., Reynolds, T. & Vaughan, J.G. (1984) Homonataloin in *Aloe* species. *Planta Medica* 50 (6): 505–508. https://doi.org./10.1055/s-2007-969784

Berger, A. (1905) Liliaceae–Aloïneae africanae. *Botanische Jahrbücher für Systematik, Pflanzengeschichte und Pflanzengeographie* 38: 84–87. [https://www.biodiversitylibrary.org/item/700#page/94/mode/1up]

Berger, A. (1908) Liliaceae-Asphodeloideae-Aloineae. *In:* Engler, A. & Prantl, K. (Eds.) *Das Pflanzenreich IV. 38 (Heft 33).* Engelmann, Leipzig, 347 pp. [https://www.biodiversitylibrary.org/item/68230#page/5/mode/1up]

Bester, S.P., Klopper, R.R. & Steyn, H.M. (2012) New plant records for Tankwa Karoo National Park, South Africa. *Koedoe* 54: Art. #1066, 9 pages. http://doi.org/10.4102/koedoe.v54i1.1066

Bolus, L. (1933) Plants, new or noteworthy. *South African Gardening and Country Life* 23: 140.

Botes, C., Wragg, P.D. & Johnson, S.D. (2009) New evidence for bee-pollination systems in *Aloe* (Asphodelaceae: Alooideae), a predominantly bird-pollinated genus. *South African Journal of Botany* 75 (4): 675–681. https://doi.org/10.1016/j.sajb.2009.07.010

Britton, N.L. & Millspaugh, C.F. (1920) *The Bahama flora*. Privately published, New York, 695 pp. https://doi.org/10.5962/bhl.title.1494

Burman, N.L. (1768) *Flora Indica, Prodromus Florae Capensis*. Leiden, Amsterdam, 34 pp. [https://www.biodiversitylibrary.org/item/123275#page/201/mode/1up]

Cammerloher, H. (1933) *Aloe brunnthaleri* Berger. *Kakteenkunde* 1933 (7): 131–132.

Carter, S., Lavranos, J.J., Newton, L.E. & Walker, C.C. (2011) *Aloes, the definitive guide*. Royal Botanic Gardens, Kew, 719 pp.

Castillon, J.-B. (2000) Deux nouvelles espèces d'*Aloe* (Liliaceae) de Madagascar. *Adansonia*, ser.3, 22: 135–138. [https://sciencepress.mnhn.fr/fr/periodiques/adansonia/22/1/deux-nouvelles-especes-d-aloe-liliaceae-de-madagascar]

Castillon, J.-B. (2007) *Aloe werneri* and *Aloe ampefyana*, two new *Aloe* (Asphodelaceae) species from Madagascar. *Haseltonia* 13: 23–28. https://doi.org/10.2985/1070-0048(2007)13[23:AWAAAT]2.0.CO;2

Castillon, J.-B. (2011) Two new *Aloe* taxa (Asphodelaceae) from the vicinity of the town of Ambatofinandrahana, Madagascar. *CactusWorld* 29 (1): 51–55. [https://www.jstor.org/stable/42795205]

Castillon, J.-B. & Castillon, J.-P. (2010) *Les aloe de Madagascar / The aloe of Madagascar*. J.-B. & J.-P. Castillon, Reunion, 399 pp.

CBOL Plant Working Group. (2009) A DNA barcode for land plants. *Proceedings of the National Academy of Sciences of the United States of America* 106 (31): 12794–12797. https://doi.org/10.1073/pnas.0905845106

Chase, M.W. & Fay, M.F. (2009) Barcoding of plants and fungi. *Science* 325 (5941: 682–683). https://doi.org/10.1126/science.1176906

Chase, M.W., De Bruijn, A.Y., Cox, A.V., Reeves, G., Rudall, P.J., Johnson, M.A.T. & Eguiarte, L.E. (2000) Phylogenetics of Asphodelaceae (Asparagales): an analysis of plastid rbcL and trnL-F DNA sequences. *Annals of Botany* 86 (5): 935–951. https://doi.org/10.1006/anbo.2000.1262

Chauser-Volfson, E. & Gutterman, Y. (1996) The barbaloin content and distribution in *Aloe arborescens* leaves according to the leaf part, age, position and season. *Israel Journal of Plant Sciences* 44 (4): 289–296. https://doi.org/10.1080/07929978.1996.10676652

China Plant BOL Group. (2011) Comparative analysis of a large dataset indicates that internal transcribed spacer (*ITS*) should be incorporated into the core barcode for seed plants. *Proceedings of the National Academy of Sciences of the United States of America* 108 (49): 19641–19646.

https://doi.org/10.1073/pnas.1104551108

CITES. (2023) *CITES Appendices I, II and III*. Available online at http://www.cites.org/eng/app/appendices.php (accessed July 2023)

Compton, J.S. (2004) *The rocks & mountains of Cape Town*. Double Story, Cape Town, 112 pp.

Commelin, J. (1697) *Horti medici Amstelodamensis rariorum tam orientalis quam occidentalis Indiae, aliarumque perergrinarum plantarum magno studio ac labore, sumptibus civitatis Amstelodamensis longa annorum serie collectarum: descriptio et icons ad vivum aeri incisae*. Pars prima. Blaeu, Amsterdam, 220 pp.
https://doi.org/10.5962/bhl.title.820

Dagne, E., Bisrat, D., Van Wyk, B-E., Viljoen, A., Hellwig, V. & Steglich, W. (1997) Anthrones from *Aloe microstigma*. *Phytochemistry* 44 (7): 1271–1274.
https://doi.org/10.1016/S0031-9422(96)00710-8

Daru, B.H., Manning, J.C., Boatwright, J.S., Maurin, O., Maclean, N., Schaefer, H., Kuzmina, M. & Van der Bank, M. (2013) Molecular and morphological analysis of subfamily Alooideae (Asphodelaceae) and the inclusion of *Chortolirion* in *Aloe*. *Taxon* 62 (1): 62–76.
https://doi.org/10.1002/tax.621006

De Almeida, R.F., Pellegrini, M.O.O., De Morais, I.L., Simão-Bianchini, R., Rattanakrajang, P., Cheek, M. & Simões, A.R.G. (2023) Barking up the wrong tree: the dangers of taxonomic misidentification in molecular phylogenetic studies. *Plant Ecology and Evolution* 156 (2): 146–159.
https://doi.org/10.5091/plecevo.101135

De Candolle, A.P. (1801) *Historia plantarum succulentarum. Histoire des plantes grasses* 2. A.J. Dugour et Durand, Paris, 51 tab.
https://doi.org/10.5962/bhl.title.503

Dillenius, J.J. (1732) *Hortus Elthamensis*, Vol. 1. Sumptibus Auctris, London, 204 pp., 166 Tab.
https://bibdigital.rjb.csic.es/idurl/1/10700

Dinter, M.K. (1923) Beiträge zur Flora von Südwestafrika 1. *Feddes Repertorium Specierum Novarum Regni Vegetabilis* 19 (8–10): 122–160.
https://doi.org/10.1002/fedr.19230190807

Dinter, M.K. (1928) Sukkulentenforschung in Südwestafrika 2. Erlebnisse und Ergebnisse meiner Reise in den Jahren 1923 bis 1925. *Repertorium Specierum Novarum Regni Vegetabilis* Beihefte 53: 1–145.

Duval, H.A. (1809) *Plantae Succulentae in Horto Alenconio*. Gabon, Paris, 18 pp.

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research* 32 (5): 1792–1797.
https://doi.org/10.1093/nar/gkh340

Ellis, K. (2013) Revision of *Aloiampelos* Klopper & Gideon F.Sm. (Xanthorrhoeaceae subfam. Asphodeloideae). Unpublished M.Sc. thesis, Nelson Mandela Metropolitan University, Port Elizabeth, 126 pp.
https://doi.org/10.13140/2.1.3206.4804

Engler, H.G.A. (1888) Plantae Marlothianae. Ein Beitrag zur Kenntnis der Flora Südafrikas. *Botanische Jahrbücher fur Systematik* 10: 1–50. [https://www.biodiversitylibrary.org/item/684#page/10/mode/1up]

Excoffier, L., Smouse, P.E. & Quattro, J.M. (1992) Analysis of molecular variance inferred from metric distances among DNA haplotypes: application to human mitochondrial DNA restriction data. *Genetics* 131 (2): 479–491.
https://doi.org/10.1093/genetics/131.2.479

Farr, E.R. & Zijlstra, G. (Eds.) (1996+) *Index Nominum Genericorum (Plantarum)*. Available from: http://botany.si.edu/ing (accessed July 2021).

Fazekas, A.J., Burgess, K.S., Kesanakurti, P.R., Graham, S.W., Newmaster, S.G., Husband, B.C., Percy, D.M., Hajibabaei, M. & Barrett, C.H. (2008) Multiple multilocus DNA barcodes from the plastid genome discriminate plant species equally well. *PLoS ONE* 3 (7): e2802, 12 pp.
https://doi.org/10.1371/journal.pone.0002802

Ford, C.S., Ayres, K.L., Toomey, N., Hai, N., Van Alphen Stahl, J., Kelly, L.J., Wikström, N., Hollingsworth, P., Duff, R.J., Hoot, S.B., Cowan, R.S., Chase, M.W. & Wilkinson, M.L. (2009) Selection of candidate DNA barcoding regions for use on land plants. *Botanical Journal of the Linnean Society* 159 (1): 1–11.
https://doi.org/10.1111/j.1095-8339.2008.00938.x

Forster, P.I. (2003) *Aloe bruynsii* (Asphodelaceae: Alooideae), a new species from Madagascar. *Bradleya* 21: 53–56.
https://doi.org/10.25223/brad.n21.2003.a11

Garsault, F.A. de (1764) Les figures des plantes et animaux d’usage en medecine, décrits dans la Matiere Medicale de Geoffroy Medecin 1. Desprez, Paris, 118 tab.
https://doi.org/10.5962/bhl.title.49481

Glen, H.F. & Hardy, D.S. (2000) Aloaceae (First part): *Aloe*. *In*: Germishuizen, G. (Ed.) *Flora of Southern Africa* 5, Part 1, Fascicle 1. National Botanical Institute, South Africa, 167 pp. [https://www.biodiversitylibrary.org/item/209564#page/3/mode/1up]

Grace, O.M. & Klopper, R.R. (2014) *Recommendation to the CITES Plants Committee: name changes affecting* Aloe *and related genera*. 21st meeting of the CITES Plants Committee, PC21 Doc. 20.2. Available online at: http://cites.org/sites/default/files/eng/com/pc/21/E-PC21-20-2.pdf (accessed July 2022).

Grace, O.M. & Rønsted, N. (2013) Unlocking the secrets of DNA in the classification of aloes. *Aloe* 50: 22–23.

Grace, O.M., Buerki, S., Symonds, M.R.E., Forest, F., Van Wyk, A.E., Smith, G.F., Klopper, R.R., Bjorå, C.S., Neale, S., Sebsebe Demissew, Simmonds, M.S.J. & Rønsted, N. (2015) Evolutionary history and leaf succulence as explanations of medicinal use in aloes and the global popularity of *Aloe vera*. *BMC Evolutionary Biology* 15: a29, 12 pp.
https://doi.org/10.1186/s12862-015-0291-7

Grace, O.M., Dzajic, A., Jäger, A.K., Nyberg, N.T., Önder, A. & Rønsted, N. (2013b) Monosaccharide analysis of succulent leaf tissue in *Aloe*. *Phytochemistry* 93: 79–87.
https://doi.org/10.1016/j.phytochem.2013.03.015

Grace, O.M., Klopper, R.R., Figueiredo, E. & Smith, G.F. (2011) *The Aloe Names Book*. Strelitzia 28. South African National Biodiversity Institute, Pretoria; Royal Botanic Gardens, Kew, 232 pp. [http://hdl.handle.net/20.500.12143/270]

Grace, O.M., Klopper, R.R., Smith, G.F., Crouch, N.R., Figueiredo, E., Rønsted, N. & Van Wyk, A.E. (2013a) A revised generic classification for *Aloe* (Xanthorrhoeaceaea subfam. Asphodeloideae). *Phytotaxa* 76 (1): 7–14.
https://doi.org/10.11646/phytotaxa.76.1.2

Grace, O.M., Simmonds, M.S.J., Smith, G.F. & Van Wyk, A.E. (2010) Chemosystematic evaluation of *Aloe* section *Pictae* (Asphodelaceae). *Biochemical Systematics & Ecology* 38 (1): 57–62.
https://doi.org/10.1016/j.bse.2009.10.009

Guglielmone, L., Gallo, L., Meregalli, M., Smith, G.F. & Figueiredo, E. (2009) Allioni's *Aloe* names (Asphodelaceae): nomenclature and typification. *Bothalia* 39 (2): 177–183.
https://doi.org/10.4102/abc.v39i2.243

Guillaumin, A. (1950) Plantes nouvelles, rares ou critiques des serres du Muséum. *Bulletin du Muséum National d'Histoire Naturelle* sér. 2, 21: 722–724. [https://www.biodiversitylibrary.org/page/54382861#page/754/mode/1up]

Hajibabaei, M., Singer, G.A.C., Hebert, P.D.N. & Hickey, D.A. (2007) DNA barcoding: how it complements taxonomy, molecular phylogenetics and population genetics. *Trends in Genetics* 23 (4): 167–172.
https://doi.org/10.1016/j.tig.2007.02.001

Hanáček, P., Klak, C. & Bruyns, P.V. (2023) A new species of *Gonialoe* from southern Angola. *South African Journal of Botany* 159: 653–657.
https://doi.org/10.1016/j.sajb.2023.06.040

Hardy, D.S. (1976) A new species of *Aloe* from the Humansdorp district. *Bothalia* 12 (1): 62–64.
https://doi.org/10.4102/abc.v12i1.1378

Haworth, A.H. (1804) A new arrangement of the genus *Aloe*. *Transactions of the Linnean Society of London* 7: 1–28. [https://www.biodiversitylibrary.org/item/13717#page/45/mode/1up]

Haworth, A.H. (1812) *Synopsis Plantarum Succulentarum*. Taylor, London, 207 pp.
https://doi.org/10.5962/bhl.title.9462

Haworth, A.H. (1824) Decas Secunda Novarum Plantarum Novarum Succulentarum. *Philosophical Magazine & Journal* 64: 298–302. [https://www.biodiversitylibrary.org/item/53102#page/324/mode/1up]

Haworth, A.H. (1825) Decas Quinta Novarum Plantarum Succulentarum. *Philosophical Magazine & Journal* 66: 279–283. [https://www.biodiversitylibrary.org/item/53098#page/301/mode/1up]

Herbin, G.A. & Robins, P.A. (1968) Studies on plant cuticular waxes – I. The chemotaxonomy of alkanes and alkenes of the genus *Aloe* L. (Liliaceae). *Phytochemistry* 7 (2): 239–255.
https://doi.org/10.1016/S0031-9422(00)86322-0

Hillis, D.M. (1987) Molecular versus morphological approaches to systematics. *Annual Review of Ecology & Systematics* 18: 23–42.
https://doi.org/10.1146/annurev.es.18.110187.000323

Hollingsworth, P.M., Graham, S.W. & Little, D.P. (2011) Choosing and using a plant DNA barcode. *PLoS ONE* 6: e19254, 13 pp.
https://doi.org/10.1371/journal.pone.0019254

IPNI. (2023+) *The International Plant Names Index*. Available from: https://www.ipni.org/ (continuously updated; accessed July 2023).

IUCN Red List of Threatened Species. (2023) Version 2021.3. Available online at www.iucnredlist.org (accessed July 2023).

Kamstra, M.W. (1968) Aloe seeds. *Aloe* 6: 8–10, 23–27.

Kamstra, M.W. (1971) Aloe seeds. *Excelsa* 1: 19–26.

Kemble, B. (2011) The speckled aloes. *Cactus and Succulent Journal (U.S.)* 83: 27–30.

https://doi.org/10.2985/0007-9367-83.1.39

Ker Gawler, J.B. (1812) *Aloe soccotrina* (β) *purpurascens*. Largest Soccotrine aloe. *Curtis's Botanical Magazine* 36: t.1474. [https://www.biodiversitylibrary.org/item/14321#page/159/mode/1up]

Klopper, R.R. (2014) *Contributions to the systematic of the genus* Aloe *L. (Asphodelaceae: Alooideae) in southern Africa*. PhD thesis, University of Pretoria, Pretoria.

Klopper, R.R. & Smith, G.F. (2009) Asphodelaceae: *Aloe hahnii*, a new species in the Section Pictae, in the Soutpansberg Centre of Endemism, Limpopo Province, South Africa. *Bothalia* 39 (1): 98–100.
https://doi.org/10.4102/abc.v39i1.233

Klopper, R.R. & Smith, G.F. (2010) Asphodelaceae: Reinstatement of *Aloe spectabilis* Reynolds. *Bothalia* 40 (1): 91–93.
https://doi.org/10.4102/abc.v40i1.197

Klopper, R.R., Grace, O.M., Smith, G.F. & Figueiredo, E. (2011) Reinstatement of *Aloe graciliflora* Groenew. (Asphodelaceae: Alooideae), a maculate aloe from north-east South Africa. *Bradleya* 29: 125–130.
https://doi.org/10.25223/brad.n29.2011.a15

Klopper, R.R., Smith, G.F., Grace, O.M. & Crouch, N.R. (2014) Reinstatement of *Aloe barbertoniae* (Asphodelaceae: Alooideae) from northeastern South Africa. *Bradleya* 32: 70–75.
https://doi.org/10.25223/brad.n32.2014.a21

Klopper, R.R., Smith, G.F., Figueiredo, E. & Van Wyk, A.E. (2016) (2469–2472) Proposals to reject the names *Aloe perfoliata*, *A. obscura*, *A. picta*, and *A. perfoliata* var. *saponaria* (*A. saponaria*) (Asphodelaceae: Alooideae). *Taxon* 65 (5): 1173–1175.
https://doi.org/10.12705/655.22

Klopper, R.R., Van Wyk, A.E. & Smith, G.F. (2010) Phylogenetic relationships in the family Asphodelaceae (Asparagales). *Schumannia* 6 / *Biodiversity & Ecology* 3: 1–36.

Lahaye, R., Van Der Bank, M., Bogarin, D., Warner, J., Pupulin, F., Gigot, G., Maurin, O., Duthoit, S. Barraclough, T.G. & Savolainen, V. (2008) DNA barcoding the floras of biodiversity hotspots. *Proceedings of the National Academy of Sciences* 105 (8): 2923–2928.
https://doi.org/10.1073/pnas.0709936105

Lamarck, J.B.A.P.M. de (1783) *Encyclopédie Méthodique, Botanique* 1. Panckoucke, Paris, 748 pp.
https://doi.org/10.5962/bhl.title.824

Lavranos, J.J. (1973) *Aloe chlorantha*: a new species from the southwestern Karoo (South Africa). *Journal of South African Botany* 39 (1): 85–90. [https://archive.org/details/journalofsouthaf39unse/page/84/mode/2up]

Lavranos, J.J. (2004) *Aloe striata* Haw. and its associates: reflections on consistency in taxonomic treatment. *Aloe* 42: 50–51.

Linnaeus, C. (1753) *Species Plantarum* 1. Impensis Laurentii Salvii, Stockholm, 560 pp.
https://doi.org/10.5962/bhl.title.37656

Lunau, K. (1995) Innate colour preferences of flowers visitors. *Journal of Comparative Physiology A* 177: 1–19.

Maddison, W.P. & Maddison, D.R. (2015) Mesquite: a modular system for evolutionary analysis. Version 3.02. Available from: https://mesquiteproject.org (accessed February 2015).

Makino, T.T. & Ohashi, K. (2017) Honest signals to maintain a long-lasting relationship: floral colour change prevents plant-level avoidance by experienced pollinators. *Functional Ecology* 31: 831–837.
https://doi.org/10.1111/1365-2435.12802

Manning, J.C., Boatwright, J.S., Daru, B.H., Maurin, O. & Van der Bank, M. (2014) A molecular phylogeny and genetic classification of Asphodelaceae subfamily Alooideae: A final resolution of the prickly issue of polyphyly in the alooids? *Systematic Botany* 39 (1): 55–74.
https://doi.org/10.1600/036364414X678044

Marais, S.J. (2010) *Aloe knersvlakensis*, a new aloe from the north-eastern Knersvlakte. *Aloe* 47: 96–99.

Marloth, H.W.R. (1910) Some new South African succulents. Part II. *Transactions of the Royal Society of South Africa* 1 (2): 403–409.
https://doi.org/10.1080/00359191009520051

Medikus, F.K. (1786) *Theodora Speciosa: Ein Neues Pflanzen Geschlecht*. Hof- und Akademische Buchhandlung, Mannheim, 116 pp. [https://gallica.bnf.fr/ark:/12148/bpt6k98082x/f1.item]

Mike, T., Lena, S. & Joachim, W.K. (1999) The phylogenetic relationships and evolution of the Canarian laurel forest endemic *Ixanthus viscosus* (Aiton) Griseb. (Gentianaceae): evidence from matK and ITS sequences, and floral morphology and anatomy. *Plant Systematics & Evolution* 218: 299–317.
https://doi.org/10.1007/BF01089233

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. *In: Proceedings of the Gateway Computing Environments Workshop (GCE).* 14 November 2010, New Orleans, pp. 1–8.
https://doi.org/10.1109/GCE.2010.5676129

Miller, P. (1768) *The Gardener's Dictionary,* ed. 8. Rivington *et al.*, London, 228 pp.

https://doi.org/10.5962/bhl.title.541

Moench, C. (1794) *Methodus plantas horti botanici et agri Marburgensis: a staminum situ describendi* 2. Officina Nova Libraria Academiae, Marburgi Cattorum, 411 pp. https://doi.org/10.5962/bhl.title.304

Mottram, R. (2013) Typification and the application of the name *Aloe perfoliata* L. *The Cactician* 1: 1–15. [https://www.crassulaceae.ch/docs/43ab8f4f61de6cf2c3b32ec36701b9e5_Cactician%201%20HQ.pdf]

Mucina, L. & Rutherford, M.C. (Eds.) (2006) *The vegetation of South Africa, Lesotho and Swaziland*. Strelitzia 19. South African National Biodiversity Institute, Pretoria, 807 pp.

Narbona, E., Del Ville, J.C. & Whittall, J.B. (2021) Painting the green canvas: how pigments produce flower colours. *The Biochemist* 43 (3): 6–12.
https://doi.org/10.1042/bio_2021_137

Pillans, N.S. (1933a) Plants, new or noteworthy. *South African Gardening and Country Life* 23: 167–168.

Pillans, N.S. (1933b) Plants, new or noteworthy. *South African Gardening and Country Life* 23: 213.

Pillans, N.S. (1934) Plants, new or noteworthy. *South African Gardening and Country Life* 24: 24–25, 28.

Powell, W., Morgantet, M., Andre, C., McNicol, J.W., Machray, G.C., Doyle, J.J., Tingeyt, S.V. & Rafalski, J.A. (1995) Hypervariable microsatellites provide a general source of polymorphic DNA markers for the chloroplast genome. *Current Biology* 5 (9): 1023–1029.
https://doi.org/10.1016/s0960-9822(95)00206-5

Raimondo, D., Von Staden, L., Foden, W., Victor, J.E., Helme, N.A., Turner, R.C., Kamundi, D.A. & Manyama, P.A. (2009) *Red List of South African plants*. Strelitzia 25. South African National Biodiversity Institute, Pretoria, 668 pp. [http://hdl.handle.net/20.500.12143/260]

Rakotoarisoa, S.E., Klopper, R.R. & Smith, G.F. (2014) A preliminary assessment of the conservation status of the genus *Aloe* L. in Madagascar. *Bradleya* 32: 81–91.
https://doi.org/10.25223/brad.n32.2014.a1

Ramdhani, S., Barker, N.P. & Baijnath, H. (2009) Rampant non-monophyly of species in *Kniphofia* Moench (Asphodelaceae) suggests a recent Afromontane radiation. *Taxon* 58 (1): 1141–1152.
https://doi.org/10.1002/tax.584008

Ramdhani, S., Barker, N.P. & Cowling, R.M. (2011) Revisiting monophyly in *Haworthia* Duval (Asphodelaceae): incongruence, hybridization and contemporary speciation. *Taxon* 60: 1001–1014.
https://doi.org/10.1002/tax.604005

Rauh, W. (1966a) Bemerkenswerte Sukkulenten aus Madagaskar, 19. Neue Aloe-Arten aus Madagaskar. *Kakteen und andere Sukkulenten* 17: 2–4.

Rauh, W. (1966b) Bemerkenswerte Sukkulenten aus Madagaskar, 19. Neue Aloe-Arten aus Madagaskar. *Kakteen und andere Sukkulenten* 17: 22–24.

Rauh, W. (2000) *Aloe steffaniana* Rauh spec. nov., eine neue Art aus Madagascar. *Kakteen und andere Sukkulenten* 51: 71–74.

Rauh, W. & Petignat, H. (1999) Eine neue *Aloe* aus Madagascar: *Aloe ruggingiana* spec. nov. *Kakteen und andere Sukkulenten* 50: 269–272.

Reynolds, G.W. (1940) Genus *Aloe*: a new section and a new series. *Journal of South African Botany* 6: 111–116. [https://archive.org/details/journalofsouthaf06unse/page/110/mode/2up]

Reynolds, G.W. (1950) *The Aloes of South Africa.* Aloes of South Africa Book Fund, Johannesburg, 520 pp.

Reynolds, G.W. (1966) *The Aloes of Tropical Africa and Madagascar.* Aloes Book Fund, Mbabane, 537 pp.

Reynolds, T. (1985) The compounds in *Aloe* leaf exudate: a review. *Botanical Journal of the Linnean Society* 90 (3): 157–177.
https://doi.org/10.1111/j.1095-8339.1985.tb00377.x

Roemer, J.J. & Schultes, J.A. (1829) *Systema Vegetabilum* 7. Sumtibus J.G. Cottae, Stuttgardt, pp. 631–715. [https://bibdigital.rjb.csic.es/idurl/1/10985]

Ronse De Craene, L.P. & Wanntorp, L. (2011) Chapter 1: Introduction: Establishing the state of the art–the role of morphology in plant systematics. *In*: Wanntorp, L. & Ronse De Craene, L.P. (Eds.) *Flowers on the Tree of Life*. Cambridge University Press, Cambridge, pp. 1–7.

Rothmann, S. (2004) *Aloes, aristocrats of the Namibian flora*. ST Promotions, Swakopmund, pp. 96.

Runemark, H. (1970) The role of small populations for the differentiation in plants. *Taxon* 19: 196–201.
https://doi.org/10.2307/1217954

Salm-Reifferscheid-Dyck, Prince J.F.M.A.H.I. von (1817) *Catalogue raisoné des Espèces d'Aloes*. Düsseldorf, 72 pp.
https://doi.org/10.5962/bhl.title.149682

Salm-Reifferscheid-Dyck, Prince J.F.M.A.H.I. von (1837) *Monographia generum Aloes et Mesembryanthemi* 2. Henry & Cohen, Düsseldorf & Bonn, 58 tab.

https://doi.org/10.5962/bhl.title.153143

Salm-Reifferscheid-Dyck, Prince J.F.M.A.H.I. von (1842) *Monographia generum Aloes et Mesembryanthemi* 4. Henry & Cohen, Düsseldorf & Bonn, 56 tab.
https://doi.org/10.5962/bhl.title.153143

Salm-Reifferscheid-Dyck, Prince J.F.M.A.H.I. von (1849) *Monographia generum Aloes et Mesembryanthemi* 5. Henry & Cohen, Düsseldorf & Bonn, 54 tab.
https://doi.org/10.5962/bhl.title.153143

Salm-Reifferscheid-Dyck, Prince J.F.M.A.H.I. von (1854) *Monographia generum Aloes et Mesembryanthemi* 6. Henry & Cohen, Düsseldorf & Bonn, 50 tab.
https://doi.org/10.5962/bhl.title.153143

Sang, T. (2002) Utility of low-copy nuclear gene sequences in plant phylogenetics. *Critical Reviews in Biochemistry & Molecular Biology* 37 (3): 121–147.
https://doi.org/10.1080/10409230290771474

Sapir, Y., Gallagher, M.K. & Senden, E. (2021) What maintains flower colour variation within populations? *Trends in Ecology* 36 (6): 507–519.
https://doi.org/10.1016/j.tree.2021.01.011

Schneider, S., Roessli, D. & Excoffier, L. (2000) *ARLEQUIN ver 2.000: a software for population genetic data analysis*. Genetic and Biometry Laboratory, University of Geneva, Switzerland.

Schönland, S. (1907) On some new and some little known species of South African plants belonging to the genera *Aloe*, *Gasteria*, *Crassula*, *Cotyledon* and *Kalanchoe*. *Records of the Albany Museum* 2: 137–155.

Scopoli, J.A. (1783) *Fundamenta botanica praelectionibus publicis accommodate*. Horto Botanico Ticinensis, Paiva, 192 pp. [https://wellcomecollection.org/works/jctrpg83/items]

Scott Elliot, G.F. (1891) New and little-known Madagascan plants. *Journal of the Linnean Society, Botany* 29: 1–67. [https://www.biodiversitylibrary.org/item/8386#page/9/mode/1up]

Smith, G.F. (2020) *Aloe ×retiefii* (Asphodelaceae subfam. Alooideae), a new nothospecies from northeastern South Africa, with *A. globuligemma* and *A. marlothii* as parents. *Phytotaxa* 468 (1): 150–154.
https://doi.org/10.11646/phytotaxa.468.1.12

Smith, G.F. (2022) *Aloe davyana* var. *magdae* (Asphodelaceae subfam. Alooideae), a distinctive new variety from central-northeastern South Africa. *Phytotaxa* 536 (3): 261–269.
https://doi.org/10.11646/phytotaxa.536.3.6

Smith, G.F. & Figueiredo, E. (2015) *Garden aloes. Growing and breeding cultivars and hybrids*. Jacana Media (Pty) Ltd, Auckland Park, Johannesburg, 193 pp.

Smith, G.F. & Figueiredo, E. (2019) *Aloe ×gemmelliae* (Asphodelaceae subfam. Alooideae), a new natural hybrid between *A. broomii* and *A. grandidentata* from the southwestern Free State province, South Africa. *Phytotaxa* 423 (3): 182–186.
https://doi.org/10.11646/phytotaxa.423.3.6

Smith, G.F. & Figueiredo, E. (2022) *Aloe hankeyi* (Asphodelaceae subfam. Alooideae; Aloe sect. Leptoaloe), a new species from northern South Africa. *Phytotaxa* 549 (1): 122–126.
https://doi.org/10.11646/phytotaxa.549.1.12

Smith, G.F. & Klopper, R.R. (2021a) *Aloe ×selmarii* (Asphodelaceae subfam. Alooideae), a new nothospecies from South Africa, with *A. davyana* var. *davyana* and *A. parvibracteata* as parents. *Phytotaxa* 521 (4): 289–300.
https://doi.org/10.11646/phytotaxa.521.4.4

Smith, G.F. & Klopper, R.R. (2021b) Reinstatement of *Aloe labiaflava* (Asphodelaceae subfam. Alooideae), a distinctive species of maculate aloe endemic to the western Mpumalanga province of South Africa. *Phytotaxa* 512 (3): 179–189.
https://doi.org/10.11646/phytotaxa.512.3.5

Smith, G.F. & Klopper, R.R. (2022a) Reinstatement of *Aloe longibracteata* (Asphodelaceae subfam. Alooideae), a maculate aloe from northeastern South Africa. *Phytotaxa* 568 (2): 291–300.
https://doi.org/10.11646/phytotaxa.568.2.4

Smith, G.F. & Klopper, R.R. (2022b) *Aloe immaculata* and *A. affinis* (Asphodelaceae subfam. Alooideae), two endemics from northern and eastern South Africa, are different maculate aloe species. *Phytotaxa* 571 (3): 291–300.
https://doi.org/10.11646/phytotaxa.571.3.3

Smith, G.F. & Lautenschlaeger, T. (2021) *Aloe uigensis* (Asphodelaceae subfam. Alooideae), a new species from northwestern Angola. *Phytotaxa* 521 (3): 227–231.
https://doi.org/10.11646/phytotaxa.521.3.8

Smith, G.F. & Van Wyk, B-E. (1996) *Aloe succotrina* and Reynolds' book on the aloes of South Africa. *Aloe* 33: 57–58.

Smith, G.F., Klopper, R.R. & Crouch, N.R. (2008) *Aloe arborescens* (Asphodelaceae: Alooideae) and CITES. *Haseltonia* 14: 189–198. https://doi.org/10.2985/1070-0048-14.1.189

Smith, G.F., Meyer, N.L. & Glen, H.F. (1994) Little-known generic names in the family Aloaceae. *South African Journal of Science* 90 (8 & 9): 489–490.

Smith, G.F., Figueiredo, E., Klopper, R.R., Campbell, E.E. & Martin, K. (2022) *Aloiampelos tenuior* var. *ernstii*, a new orange-flowered variety of rambling aloe (Asphodelaceae subfam. Alooideae). *Phytotaxa* 571 (1): 91–96. https://doi.org/10.11646/phytotaxa.571.1.8

Smith, G.F., Figueiredo, E., Klopper, R.R. & Crouch, N.R. (2012a) Summer-flowering species of maculate *Aloe* L. (Asphodelaceae: Alooideae) in the *Aloe zebrina*-complex from South Africa: reinstatement of four names, and description of *A. braamvanwykii* Gideon F.Sm. & Figueiredo. *Bradleya* 30: 155–166. https://doi.org/10.25223/brad.n30.2012.a19

Smith, G.F., Klopper, R.R., Figueiredo, E. & Crouch, N.R. (2012b) Aspects of the taxonomy of *Aloe arborescens* Mill. (Asphodelaceae: Alooideae). *Bradleya* 30: 127–137. https://doi.org/10.25223/brad.n30.2012.a15

Smith, G.F., Klopper, R.R., Crouch, N.R. & Figueiredo, E. (2016) Reinstatement of *Aloe candelabrum* A.Berger (Asphodelaceae: Alooideae), a tree-like aloe of KwaZulu-Natal province, South Africa. *Bradleya* 34: 59–69. https://doi.org/10.25223/brad.n34.2016.a21

Smith, G.F., Klopper, R.R., Crouch, N.R. & Figueiredo, E. (2020) Reinstatement of *Aloe davyana* (Asphodelaceae subfam. Alooideae), a winter-flowering species endemic to central-northeastern South African aloe. *Phytotaxa* 475 (3): 201–208. https://doi.org/10.11646/phytotaxa.475.3.4

Smith, G.F., Klopper, R.R., Crouch, N.R. & Figueiredo, E. (2021) Reinstatement of *Aloe davyana* var. *subolifera* (Asphodelaceae subfam. Alooideae), a distinctive variety of an endemic South African aloe. *Phytotaxa* 482 (2): 208–212. https://doi.org/10.11646/phytotaxa.482.2.9

Stamatakis, A. (2014) RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033

Steyn, E.M.A., Smith, G.F., Nilsson, S. & Grafström, E. (1998) Pollen morphology in *Aloe* (Aloaceae). *Grana* 37 (1): 23–27. https://doi.org/10.1080/00173139809362635

Symes, C.T. (2012) Seed dispersal and seed banks in *Aloe marlothii* (Asphodelaceae). *South African Journal of Botany* 78: 276–280. https://doi.org/10.1016/j.sajb.2011.06.008

Thiers, B. (2023+ [continuously updated]) *Index herbariorum, a global directory of public herbaria and associated staff*. New York Botanical Garden's Virtual Herbarium. Available from: http://sweetgum.nybg.org/ih (accessed July 2023).

Thunberg, C. (1794) *Prodromus Plantarum Capensium: quas in promontorio Bonæ Spei Africes, annis 1772–1775*, Vol. 1. J. Edman, Upsala, p. 60. https://doi.org/10.5962/bhl.title.84

Treutlein, J., Smith, G.F., Van Wyk, B-E. & Wink, M. (2003a) Phylogenetic relationships in Asphodelaceae (subfamily Alooideae) inferred from chloroplast DNA sequences (*rbcL*, *matK*) and from genomic fingerprinting (ISSR). *Taxon* 52 (2): 193–207. https://doi.org/10.2307/3647487

Treutlein, J., Smith, G.F., Van Wyk, B-E. & Wink, M. (2003b) Evidence for the polyphyly of *Haworthia* (Asphodelaceae subfamily Alooideae; Asparagales) inferred from nucleotide sequences of *rbc*L, *matK*, ITS1 and genomic fingerprinting with ISSR-PCR. *Plant Biology* 5 (5): 513–521. https://doi.org/10.1055/s-2003-44793

Turland, N.J., Wiersema, J.H., Barrie, F.R., Greuter, W., Hawksworth, D.L., Herendeen, P.S., Knapp, S., Kusber, W.-H., Li, D.-Z., Marhold, K., May, T.W., McNeill, J., Monro, A.M., Prado, J., Price, M.J. & Smith, G.F. (2018) *International Code of Nomenclature for algae, fungi, and plants (Shenzhen Code)* adopted by the Nineteenth International Botanical Congress Shenzhen, China, July 2017. Koeltz Botanical Books, Glashütten. [Regnum Vegetabile 159: 1–254]. https://doi.org/10.12705/Code.2018

Van Jaarsveld, E.J. (2010) *Aloe tongaensis*, a new species from Tongaland, KwaZulu-Natal (South Africa), and a new sectional arrangement of the tree aloes. *Aloe* 47: 64–71.

Van Wyk, A.E. & Smith, G.F. (2001) *Regions of floristic endemism in southern Africa. A review with emphasis on succulents*. Umdaus Press, Hatfield, 199 pp.

Van Wyk, B-E. & Smith, G.F. (1996) *Guide to the aloes of South Africa*. Briza, Pretoria, 302 pp.

Van Wyk, B-E. & Smith, G.F. (2014) *Guide to the aloes of South Africa*, 3rd edn. Briza, Pretoria, 376 pp.

Van Wyk, B-E., Yenesew, A. & Dagne, E. (1995) Chemotaxonomic survey of anthraquinones and pre-anthraquinones in roots of *Aloe*

species. *Biochemical Systematics & Evolution* 23 (3): 267–275.
https://doi.org/10.1016/0305-1978(94)00095-X

Viljoen, A. (1999) *A chemotaxonomic study of the phenolic leaf compounds in the genus* Aloe. Ph.D. thesis, Rand Afrikaans University, Johannesburg, 634 pp. [http://hdl.handle.net/10210/6612]

Viljoen, A.M. & Van Wyk, B-E. (1999) The chemotaxonomic value of two cinnamoyl chromones, aloeresin E and F, in *Aloe* (Aloaceae). *Taxon* 48 (4): 747–754.
https://doi.org/10.2307/1223645

Viljoen, A.M., Van Wyk, B-E. & Van Heerden, F.R. (1998) Distribution and chemotaxonomic significance of flavonoids in *Aloe* (Asphodelaceae). *Plant Systematics & Evolution* 211: 31–42.
https://doi.org/10.1007/BF00984910

Walker, C.C., Klopper, R.R., Smith, G.F. & Condy, G. (2015) *Aloe succotrina*. *Flowering Plants of Africa* 64: 26–40, t.2304.

Weiss, M.R. (1991) Floral colour changes as cues for pollinators. *Nature* 354: 227–229.

Weiss, M.R. & Lamont, B.B. (1997) Floral color change and insect pollination: a dynamic relationship. *Israel Journal of Plant Sciences* 45 (2–3): 185–199.
http://dx.doi.org/10.1080/07929978.1997.10676683

Weston, R. (1770) *Botanicus universalis et hortulanus*, Vol. 1. Wheble & Etherington, Bell, Riley, 384 pp.

Wheeler, Q.D. (2008) Chapter 1: Introductory – toward the new taxonomy. *In*: Wheeler, Q.D. (Ed.) *The new taxonomy*, The Systematics Association Special Volume Series 76. CRC Press, New York, pp. 1–17.

White, T.J., Bruns, T., Lee, S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *In*: Innis, M., Gelfand, D., Sninsky, J. & White, T. (Eds.) *PCR protocols: a guide to methods and applications*. Academic Press, San Diego, pp. 315–322.

Wijnands, D.O. (1983) *The botany of the Commelins*. A.A. Balkema, Rotterdam, 232 pp.

Williamson, G. (2000) *Richtersveld. The enchanted wilderness*. Umdaus Press, Hatfield, 258 pp.