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# The occurrence and taxonomic distribution of the anthrones aloin, aloinoside and microdontin in *Aloe*

Alvaro M. Viljoen[a,*], Ben-Erik Van Wyk[a], Leonard E. Newton[b]

[a]*Department of Botany, Rand Afrikaans University, P.O. Box 524, Auckland Park 2006, South Africa*
[b]*Department of Botany, Kenyatta University, P.O. Box 43844, Nairobi, Kenya*

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**Abstract**

A chemotaxonomic survey of 380 species of *Aloe* indicated the presence of the anthrone isomers aloin A and B together with the aloinoside isomers and microdontin A and B in 36 (10%) species of *Aloe*. This group, referred to as the microdontin chemotype, is thus characterised by a combination of exudate compounds and not merely a single phytochemical marker, implying taxonomic significance of leaf exudate compounds. The 36 representatives of the group occupy disparate taxonomic positions in the largely artificial hierarchy of the present classification system. Although many of the species have previously been considered as related (based on macromorphology only), a large number of species have not been associated with one another before. The chemical profiles and leaf exudate compositions of the species are presented, followed by a brief summary of the morphological diversity. Whilst conceding the possibility of convergent evolution, the geographical distribution of the species and thoughts on possible relationships between the taxa are discussed. 

*Keywords:* *Aloe*; Aloaceae; Aloin; Microdontin; Aloinoside; Chemotaxonomy

## 1. Introduction

Chromatographic patterns in the genus *Aloe* have been investigated by several workers (e.g. Reynolds, 1985, 1986, 1990; Cutler et al., 1980) but the possible

* Corresponding author. Present address: The Department of Pharmacy, University of the Witwatersrand, Faculty of Health Sciences, 7 York Road, Parktown 2193, South Africa. Tel.: + 27-11-647-2169; fax: + 27-11-642-4355.

*E-mail address:* viljoena@chiron.wits.ac.za (A.M. Viljoen).

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taxonomic value of chemical characters in infrageneric classification has yet to be fully explored. A recent chemotaxonomic study of the genus has revealed various chemical groups at the infrageneric level (Viljoen, 1999; Viljoen et al., 1995, 1998, 1999, 2000). The largely artificial nature of the present classification system for the genus *Aloe*, as presented in the two major works of Reynolds (1950, 1966), is in need of revision with the aid of additional characters. Leaf exudate chemistry provides additional evidence in a multidisciplinary approach to assessing possible natural relationships.

Microdontin was isolated by Farah et al. (1992) from *Aloe microdonta*, a species used in Somali traditional medicine to treat jaundice and skin diseases. Groom and Reynolds (1987) indicated the presence of aloin in this species but no mention was made of the chemotaxonomic potential of this anthrone in co-occurrence with other compounds, such as aloinoside and microdontin. The compounds discussed in this paper have been isolated from the following species by Dagne (1996): *A. camperi*, *A. elegans*, *A. gilbertii*, *A. megalacantha*, *A. rivae* and *A. secundiflora*.

## 2. Materials and methods

Leaf exudate samples from a total of 380 *Aloe* taxa were investigated. The exudate was collected in situ and at the National Botanical Institute, Pretoria (NBI), and Royal Botanic Gardens, Kew (RBG). Samples from east Africa were from the aloe collections of L. E. Newton and other succulent plant specialists. Sources of species included in the discussion are listed in Table 1.

The exudate samples, collected by applying slips of filter paper to a cut leaf, were investigated by HPLC. Samples were dissolved in methanol and passed through $C_{18}$ cartridges to remove substances of high retention time. These purified samples were dissolved in methanol–water (1 : 1) and injected into the HPLC system. Operating conditions were as follows: A Phenomenex IB-Sil column was used ($C_{18}$ reverse phase, 5 μm particle size, 250 mm × 4.6 mm internal diameter; flow rate 1 ml min$^{-1}$; 20 μl sample loop). The solvent system comprised a 30–60% linear gradient of methanol in water over 25 min, 3 min isocratic, 100% in 2 min, 4 min isocratic. Detection was by diode array detector, using two channels (A set at 275 ± 70 nm; B set at 365 ± 40 nm). Compounds were identified by comparison of the retention times and UV/VIS spectra with reference samples. Authentic reference samples were made available by previous workers. Aloesin, aloeresin A and D were supplied by Prof. G. Speranza (isolated from Cape aloes), 7-*O*-methylaloesin (from *A. rupestris*) was supplied by Prof. E. Dagne, aloin A and B, aloinoside A and B, microdontin A and B and 8-*O*-methyl-7-hydroxyaloin were isolated from *A. schelpei* and compared with standards of the same compounds received from Prof. E. Dagne isolated from *A. megalacantha*. *Aloe hildebrandtii* leaf exudate was used as a reference standard for dihydroisocoumaringlucoside (Veitch et al., 1994).

Table 1
Species producing aloin/aloinoside/microdontin, with the corresponding voucher and distribution details (NBI = National Botanical Institute, Pretoria, South Africa; RBG = Royal Botanic Gardens, Kew, UK, BSM = Botanische Staatssammlung München, S = Arboretum at the Chemistry Department, Addis Ababa University, Ethiopia)

| Species | Source/voucher | Distribution |
|---|---|---|
| *A. aageodonta* L.E. Newton | Newton 3543 (clonotype, EA, K) | Kenya |
| *A. africana* Miller | Aloes, Fort Brown, Ann's Villa | South Africa |
| *A. boscawenii* Christian | ex hort P. Favell | Tanzania |
| *A. brunneostriata* Lavranos and S. Carter | ex hort NBI | Somalia |
| *A. buchlohii* Rauh | ex hort D. Hardy and NBI 14645 | Madagascar |
| *A. calidophila* Reynolds | RBG 1974-4199 | Ethiopia, Kenya |
| *A. cameronii* Hemsley | NBI 15231 and Ellert 79 | Malawi, Mozambique, Zambia, Zimbabwe |
| *A. camperi* Schweinfurth | S 208, ex hort NBI | Ethiopia |
| *A. canarina* S. Carter | RBG 1977-3888 | Sudan, Uganda |
| *A. chrysostachys* Lavranos and L.E. Newton | Newton 4040 (topotype, EA, K) and Newton 4246 (topotype of *A. merunana*, EA, K) | Kenya |
| *A. diolii* L.E. Newton | Powys and Dioli 824 (clonotype, EA, K) | Sudan |
| *A. elegans* Tod. | Ex hort NBI | Ethiopia |
| *A. ferox* Miller | 24 localities | South Africa |
| *A. fleurentiniorum* Lavranos and L.E. Newton | RBG 1977-3317 | Yemen |
| *A. flexilifolia* Christian | RBG 258-90-01811 | Tanzania |
| *A. gilbertii* T. Reynolds ex Sebsebe and Brandham | RBG 1990-1301 and S 226 | Ethiopia |
| *A. guillaumetii* Cremers | Lavranos 28738 | Madagascar |
| *A. harlana* Reynolds | Ex hort BSM | Ethiopia |
| *A. hemmingii* Reynolds | NBI 11170 and RBG 0848-01059 | Somalia |
| *A. lensayuensis* Lavranos and L.E. Newton | RBG 242-63 24204 and Newton 5571 | Kenya |
| *A. mcloughlinii* Christian | RBG 4858404966 and 5955959502 | Ethiopia |
| *A. megalacantha* Baker | S 325 and RBG 144-93-01240 | Ethiopia, Somalia |
| *A. microdonta* Chiovenda | NBI 13501 and RBG 1966-12803 | Kenya, Somalia |
| *A. ngongensis* Christian | Newton 3531 | Kenya, Tanzania |
| *A. peckii* P.R.O. Bally and I. Verdoorn | RBG 084-81011-40 | Somalia |
| *A. penduliflora* Baker | Newton 3543 (EA, K) and RBG 34963-34907 | Kenya |
| *A. rabaiensis* Rendle | RBG 1975-903 | Kenya, Tanzania |
| *A. rivae* Baker | S 321 | Ethiopia, Kenya |
| *A. scabrifolia* L.E. Newton and Lavranos | Newton 3272 | Kenya |
| *A. schelpei* Reynolds | RBG 427-64-42705 | Ethiopia |
| *A. scobonifolia* Reynolds and P.R.O. Bally | ex BSM and RBG 084-81-01110 | Somalia |
| *A. sinkatana* Reynolds | ex hort BSM | Sudan |
| *A. somaliensis* W. Watson | NBI 11169 and RBG 084-81-01055 | Somalia |
| *A. steudneri* Schweinfurth | ex BSM and RBG 1987-4090 | Ethiopia |
| *A. tewoldei* M.G. Gilbert and Sebsebe | ex Sebsebe (topotype) | Ethiopia |
| *A. tweediae* Christian | RBG 1970-1752 | Kenya, Sudan, Uganda |

## 3. Results and discussion

### 3.1. Leaf exudate chemistry

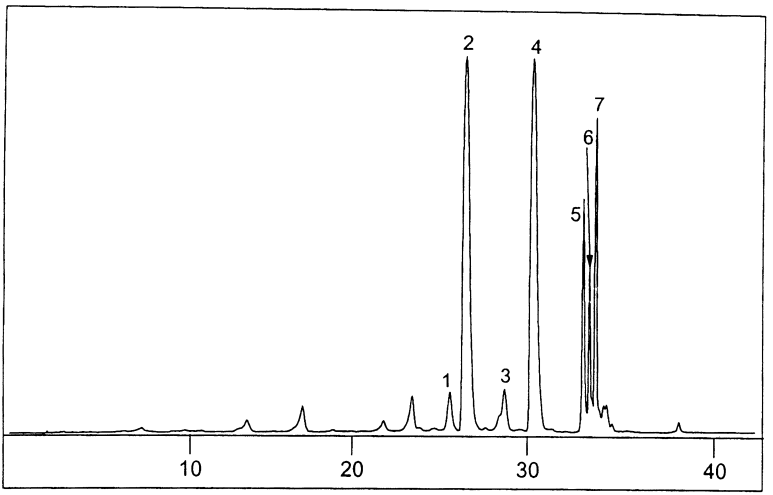
Of the species investigated, 36 were found to contain the compounds whose occurrence forms the subject of this paper (Table 1). Inspection of a typical HPLC chromatogram of a representative of this group (Fig. 1) shows a distinct pattern. Most of the chemical groups that have been defined in a comprehensive chemotaxonomic study of the genus (Viljoen, 1999) are based on a single compound (e.g. plicataloside, Viljoen et al., 1999) or a specific class of compound (e.g. flavanones, Viljoen et al., 1998). Here, the chemical group (hereafter referred to as the 'microdontin chemotype') is defined by the presence of a combination of compounds, usually six biogenetically related compounds (chemical characters).

The characteristic pattern for this group is shown in Fig. 1. Aloin B (1) and aloin A (2) are always present. It is interesting to note that in the case of this group of aloes the two aloin isomers are usually in a quantitative imbalance, i.e. less aloin B than aloin A is produced. The second set of isomers present consists of aloinoside B and A. These two isomers are also quantitatively unequal. Only three species did not produce the aloinosides in the presence of aloin A and B, viz. *A. buchlohii*, *A. schelpei* and *A. steudneri* (see Table 2). In the case of *A. ferox* only one of two chemotypes produce the aloinosides (Van Wyk et al., 1995). The third set of anthrones characteristic of this group comprises microdontin B (5) and microdontin A (6).

In most species these compounds were present as clearly defined peaks on the chromatogram, while in others an irregular baseline in the retention region of the microdontins shows their presence in trace amounts. Evaluation of the UV spectra in this region could usually confirm the presence of microdontin. The authors believe that the microdontin compounds could be unstable, as a microdontin-containing sample has been re-analysed after a storage period of two years. The observation was made that the aloin and aloinoside isomers remained unchanged while the level of microdontin diminished drastically. It is further interesting to note that although only microdontin A and B have been isolated as natural products, a third compound is usually associated with the two isomers. The third unidentified compound (peak 7 in Fig. 1) displays the same UV absorbance spectrum as for the microdontin isomers.

Table 2 shows the total leaf exudate compositions for all the species in the microdontin chemotype, while Fig. 2 displays examples of some specific chromatograms. It is of interest that the chromones (a group of compounds generally detected in *Aloe*) are absent in a large number of these species, while others usually produce the chromones aloesin, aloeresin A and aloeresin D.

In this study these compounds have been identified in the first five of the species listed by Dagne (1996), i.e. all except *A. secundiflora*. Reynolds (1996) compared the chemistry of *A. scabrifolia* and *A. turkanensis* and mentioned a series of compounds ($R_t = 29.1–36.5$) as unidentified compounds. The first two in this range are most probably microdontin B and A as these compounds were positively identified in our study by direct comparison with authentic standards obtained from Dagne.



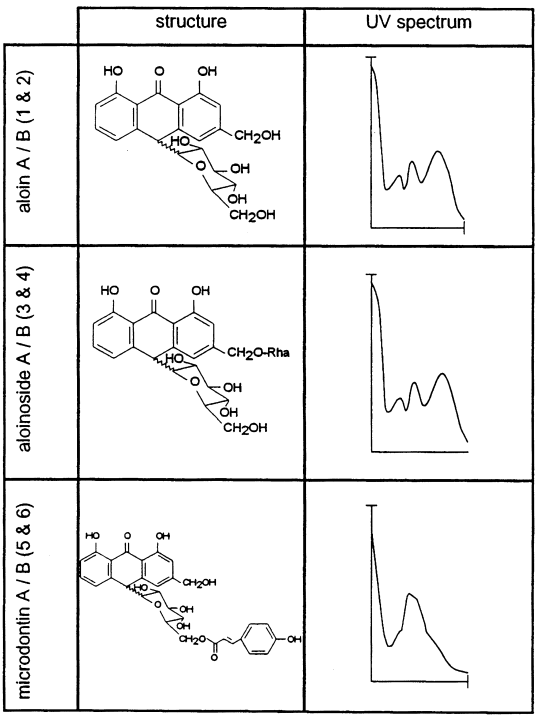




Fig. 1. A typical HPLC chromatogram of a species containing aloin B (1), aloin A (2), aloinoside B (3), aloinoside A (4), microdontin B (5), microdontin A (6) and unidentified anthrone (7). Note the quantitative imbalance between the anthrone isomers and the absence of chromones. Structures and UV spectra of compounds are illustrated below.

Table 2
Presence of the major leaf exudate compounds in the aloin/aloinoside/microdontin group. 1 = aloesin, 2 = 7-*O*-methylaloesin, 3 = aloeresin A, 4 = dihydroisocoumaringlucoside, 5 = 8-*O*-methyl-7-hydroxyaloin, 6 = aloeresin D, 7 = aloin B, 8 = aloin A, 9 = aloinoside B, 10 = aloinoside A, 11 = microdontin B, 12 = microdontin A, 13 = unidentified anthrone

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| $R_t$ (min) | 5.4 | 8.2 | 14.7 | 15.7 | 16.7 | 20 | 23.6 | 24 | 28.9 | 30.9 | 32.3 | 32.9 | 33.8 |
| *A. aageodonta* | | ■ | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| *A. africana* | ■ | | | | | | ■ | ■ | ■ | ■ | | | |
| *A. boscawenii* | | | | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. brunneostriata* | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | |
| *A. buchlohii* | | | | | | | ■ | ■ | | | ■ | ■ | |
| *A. calidophila* | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | |
| *A. cameronii* | ■ | | ■ | | | ■ | ■ | ■ | ■ | ■ | | | |
| *A. camperi* | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. canarina* | ■ | | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. chrysostachys* | | ■ | | | | ■ | ■ | ■ | ■ | ■ | | | |
| *A. diolii* | | | | | | | ■ | ■ | ■ | ■ | ■ | ■ | |
| *A. elegans* | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. ferox* | ■ | | ■ | | | | ■ | ■ | ■ | ■ | | | |
| *A. fleurentiniorum* | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. flexilifolia* | ■ | ■ | | | | ■ | ■ | ■ | ■ | ■ | | | |
| *A. gilberti* | ■ | ■ | | | | | ■ | ■ | ■ | ■ | ■ | ■ | |
| *A. guillaumetii* | | ■ | | | | | ■ | ■ | ■ | ■ | | | |
| *A. harlana* | | | | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. hemmingii* | ■ | | | | ■ | | ■ | ■ | ■ | ■ | | | |
| *A. lensayuensis* | | | | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. mcloughlinii* | ■ | | | ■ | | ■ | ■ | ■ | ■ | ■ | | | |
| *A. megalacantha* | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. microdonta* | | | | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. ngongensis* | | | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. peckii* | ■ | | | ■ | | ■ | ■ | ■ | ■ | ■ | | | |
| *A. penduliflora* | | ■ | | ■ | | | ■ | ■ | ■ | ■ | | | |
| *A. rabaiensis* | | | | | | ■ | ■ | ■ | ■ | ■ | | | |
| *A. rivae* | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. scabrifolia* | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. schelpei* | | | | | ■ | | ■ | ■ | | | ■ | ■ | |
| *A.scobinifolia* | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. sinkatana* | | | | | ■ | | ■ | ■ | ■ | ■ | | | |
| *A. somaliensis* | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. steudneri* | | | | ■ | ■ | | ■ | ■ | | | ■ | ■ | |
| *A. tewoldei* | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | ■ | |
| *A. tweediae* | | | | ■ | | ■ | ■ | ■ | ■ | ■ | | | |

### 3.2. Morphological characters

The group of species that has been chemically delineated above shows great morphological diversity. This is demonstrated below by discussing conspicuous morphological characters as summarised from literature.

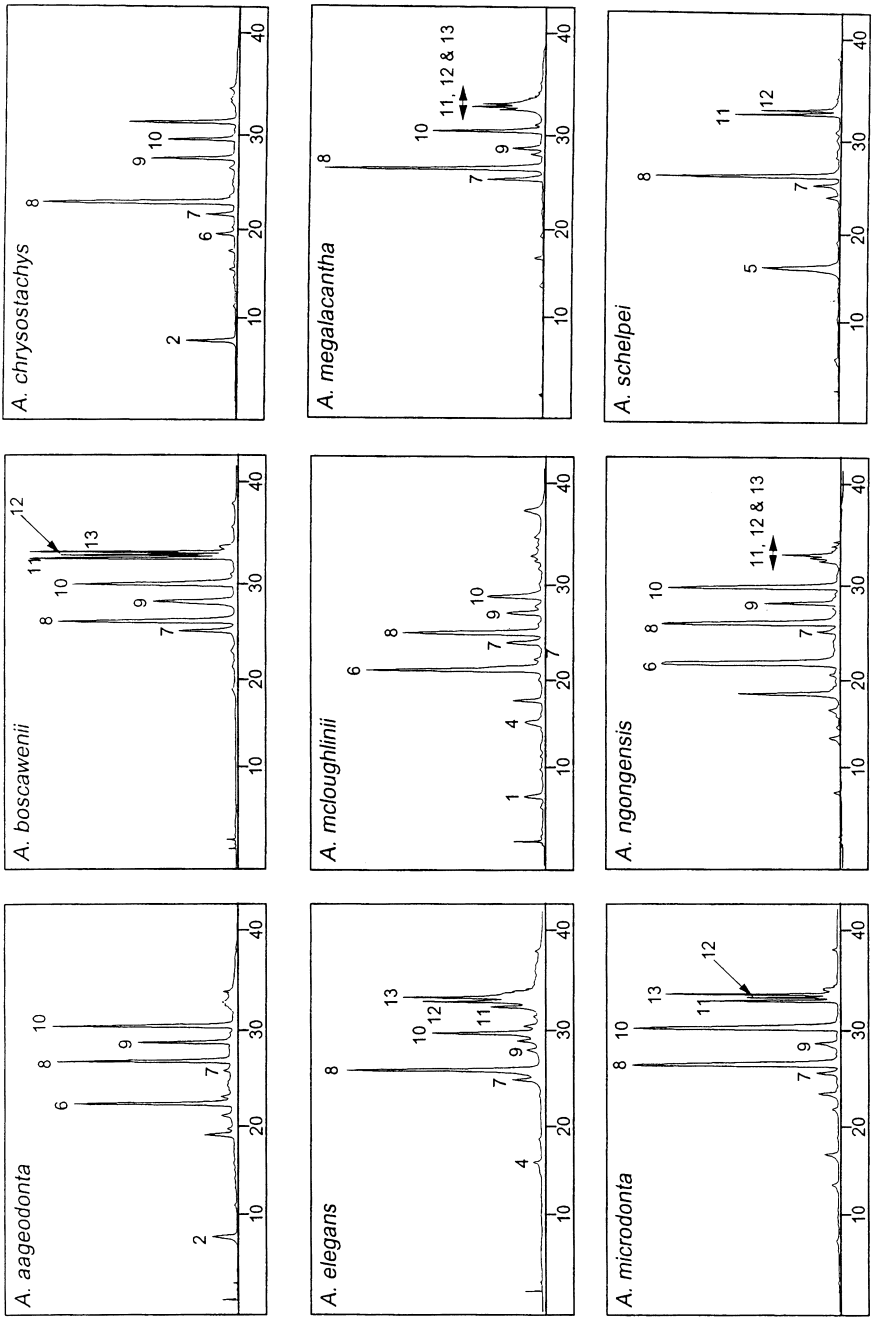



Fig. 2. HPLC chromatograms of nine species containing aloin/aloinoside/microdontin. Numbers of peaks correspond to compounds in Table 2.

*3.2.1. Growth habit characters* (*caulescence*, *branching and orientation*)

Based on habit characters the species of the microdontin chemotype could be divided into two main groups: those that are caulescent (distinctly or shortly so) and those that are acaulescent. Some caulescent species are erect and branching (not suckering) to form dense groups (*A. aageodonta*, *A. cameronii*, *A. flexilifolia*, *A. gilbertii*, *A. megalacantha*, *A. microdonta*, *A. ngongensis* and *A. penduliflora*.). The two South African species *A. africana* and *A. ferox* are the only two species in this group with unbranched erect trunks. In *A. calidophila* stems are erect but basally decumbent. Five species are caulescent but with a procumbent stem (*A. boscawenii*, *A. camperi*, *A. lensayuensis* and *A. scabrifolia*). *Aloe schelpei* is not as distinctly caulescent as the species listed above but it also produces a short procumbent stem and grows in dense groups. *Aloe brunneostriata* and *A. canarina* are two suckering species that are shortly caulescent (the general pattern in *Aloe* is that suckering species are usually acaulescent). *Aloe rivae* and *A. tewoldei* are also shortly caulescent but *A. rivae* is extremely variable in habit characters as individuals are either stemless, shortly caulescent, tightly clustered in groups or solitary rosettes with a procumbent or erect stem. *Aloe tewoldei* is the only species in this group that is pendent.

Most of the acaulescent species usually consist of solitary rosettes. Species in this category are *A. buchlohii*, *A. fleurentiniorum*, *A. somaliensis*, *A. scobinifolia*, *A. sinkatana*, *A. harlana*, *A. peckii* and *A. hemmingii*. *Aloe chrysostachys* rarely produces a stem and branches to form groups only with age.

In summary, species in this group are acaulescent, shortly caulescent, or distinctly caulescent. In the case of the last category the stem may be erect, slender and supported by surrounding vegetation, or procumbent.

*3.2.2. Leaf characters* (*leaf orientation*, *surface*, *marginal teeth and maculation*)

Most species in this group have leaves that are spreading to recurved. In some only the leaf apex is turned outwards but in most cases almost half the leaf is recurved. Eight species produce leaves spreading to recurved, with smooth surface, pungent teeth on the leaf margin and a spotted upper and/or lower surface. These species are *A. buchlohii*, *A. mcloughlinii*, *A. tweediae*, *A. schelpei*, *A. sinkatana*, *A. somaliensis*. *A. hemmingii* and *A. peckii.* The last three species are more similar to one another in leaf characters than the other species mentioned above. Species sharing the same characters as those of the five species above, with the exception that the leaves are completely unspotted include *A. cameronii*, *A. canarina*, *A. ferox*, *A. rabaiensis*, *A. gilbertii*, *A. harlana*, *A. ngongensis* and *A. meruana* ( = *A. chrysostachys* — see below under Section 3.3). Two species bear their leaves in an incurved way (*A. chrysostachys*, and *A. steudneri*). In the case of *A. africana*, *A. camperi* and *A. megalacantha* the leaves are strongly recurved, smooth, immaculate and bear pungent marginal teeth. *Aloe brunneostriata* deviates from the broader pattern as the leaves are distinctly striate and have small cartilaginous teeth. *Aloe fleurentiniorum* and *A. scobinifolia* have an entire leaf margin. In all the species the leaves are smooth, except for *A. scobinifolia*, *A. lensayuensis*, *A. scabrifolia* and *A. fleurentiniorum*, in which the leaf surfaces are distinctly rough.

*3.2.3. Inflorescence and flower characters* (*inflorescence structure*, *perianth shape*, *perianth markings*, *flower orientation*)

Based on the characters in parentheses above the species could be placed into six categories:

1. Species in which the inflorescence is a much-branched panicle with secund flowers that are cylindrical–trigonous in shape with no markings on the perianth. Seven species are included in this group: *A. aageodonta*, *A. brunneostriata*, *A. canarina*, *A. chrysostachys* (including *A. meruana*), *A. lensayuensis*, *A. scabrifolia* and *A. microdonta*.
2. Species in which the inflorescence is 1– 3 (– 6) branched with the flowers cylindrical–trigonous without markings and arranged symmetrically around the floral axis. Species in this group are *A. boscawenii*, *A. diolii*, *A.* flexilifolia, *A. guillaumetii*, *A. harlana*, *A. megalacantha*, *A. ngongensis*, *A. penduliflora*, *A. rabaiensis*, *A. rivae* and *A. tweediae*. Most of the species listed were placed by Reynolds (1966) in his group 19.
3. Species in which the inflorescence is a much-branched panicle with clavate, unmarked flowers arranged symmetrically around the floral axis. Eight species fit the description of this group: *A. calidophila*, *A. camperi*, *A. elegans*, *A. ferox*, *A. fleurentiniorum*, *A. gilbertii*, *A. scobinifolia* and *A. sinkatana*. Most of these species are placed in Group 13 of Reynolds (1966).
4. Species in which the perianth is striped or spotted. Four species are included in this category, which corresponds to group 4 of Reynolds (1966). This group comprises *A. hemmingii*, *A. mcloughlinii*, *A. peckii* and *A. somaliensis*.
5. Species in which the inflorescence is simple (unbranched), with the flowers cylindrical-trigonous, immaculate and symmetrically arranged around the floral axis. *Aloe buchlohii*, *A. schelpei*, *A. steudneri* and *A. tewoldei* are members of this group.
6. The last group consists of only two species, *A. africana* and *A. cameronii*. These two species bear an inflorescence that is 1– 3 branched, the flowers are strongly curved and positioned symmetrically around the axis.

Considering the extreme morphological diversity summarised above it becomes evident that *Aloe* presents a range of variable and perplexing morphological characters that can be interpreted in different ways. This chemical group is characterised by immense morphological diversity, almost representative of the entire range of characters encountered in the genus as a whole. There seems to be no correlation between the morphological characters and a mosaic pattern of variation is evident. The microdontin chemotype illustrates the desperate need to find additional characters as possible taxonomic markers at the infrageneric level.

### *3.3. Relationships within the aloin/aloinoside/microdontin group as represented in the literature*

Previously suggested affinities between species included in the microdontin chemotype are shown schematically in Fig. 3. The classification system of Reynolds (1950, 1966) has been used. Post-Reynolds species have been attached

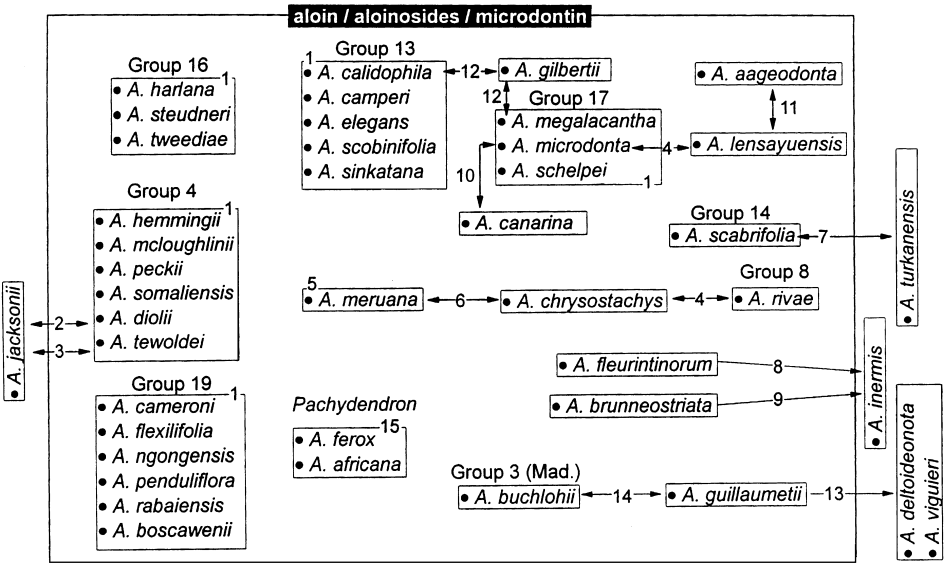



Fig. 3. A. taxonomic 'affinity-diagram' showing possible relationships between the taxa as suggested in literature, based on infrageneric groups used by Reynolds (1950, 1966). Numbers correspond to literature references where these relationships between the taxa have been discussed. 1. Reynolds (1966), 2. Newton (1995), 3. Gilbert & Sebsebe (1997), 4. Lavranos & Newton (1976), 5. Lavranos (1980), 6. Newton (1996), 7. Newton & Lavranos (1990), 8. Larvanos & Newton (1977), 9. Lavranos (1992), 10. Carter (1994), 11. Newton (1993b), 12. Sebsebe & Brandham (1992), 13. Cremers (1976), 14. Glen et al. (1992), 15. Reynolds (1950).

to the groups containing the species to which the authors suggested their new species to be related.

Reynolds created Group 4 for species with striped flowers. The plants in this group are also characterised by fairly small rosettes. The first four species were included in the group by Reynolds (1966) while *A. diolii* and *tewoldei* were added later. *Aloe diolii* was described by Newton (1995) from south-east Sudan and on the basis of gross morphology Newton suggested that the new species is related to *A. jacksonii*. *Aloe tewoldei* was described by Gilbert and Sebsebe (1997) with suggestions that this Ethiopian species too is related to *Aloe jacksonii*. *Aloe jacksonii* produces a unique combination of leaf exudate compounds not found in any other species studied (Viljoen, 1999). The characteristic chemical identity of *A. jacksonii* is also emphasised through the work of Conner et al. (1990), who isolated a series of interesting compounds. It should be noted that the obscurely striped flowers place *A. jacksonii* in Group 4 (Reynolds, 1966), while Gilbert and Sebsebe (1997) suggested that *A. jacksonii* should rather be placed in Group 10 (Reynolds, 1966) together with the other pendent/semi-pendent species and *A. tewoldei*. It is further interesting to note that the two authors emphasise the morphological anomaly of *A. jacksonii*, an observation that is also reflected at the chemical level. In a multidisciplinary study of the *Aloe somaliensis* complex, Carter et al. (1984) describe the immense morphological

variation of *A. somaliensis* and discuss the taxonomic relationships in this species complex.

Several of the infrageneric groups created by Reynolds (1966) were based on perianth characters, as seen above in the case of his Group 4. Another such group is his Group 13, consisting of 10 species containing aloes with clavate perianths. In some instances (e.g. *A. camperi*), the perianth is distinctly clavate, while in others a measure of imagination is required to visualise the inflated perianth. Five of the 10 species in Group 13 produce the same exudate profile as the 36 species in Fig. 3.

Lavranos and Newton (1976) suggested that *Aloe chrysostachys* is related to *A. rivae* in the Reynolds Group 8 (series *Aethiopicae*). A species later described by Lavranos (1980) as *A. meruana* was reduced to synonymy under *A. chrysostachys* (Newton, 1996). However, as samples were available from plants collected at type localities of both *A. chrysostachys* and *A. meruana* the latter name also appears in the discussion. Both taxa produced identical exudate profiles, supporting the view that they are conspecific.

*Aloe scabrifolia* has the mature flowers secund, hence its placement by Newton and Lavranos (1990) in the Reynolds Group 14 (subsection *Orthlophae*), alongside *A. turkanensis*, with which it had been confused by Reynolds (1966). The latter species, however, together with other species producing their flowers in a secund orientation, does not produce the exudate compounds characterising this chemotype. The subsection *Orthlophae* is a morphologically and chemically heterogeneous collection of species. Newton (1993a) suggested that secund flowers, the defining character for subsection *Orthlophae*, probably evolved independently two or more times in *Aloe* and that uniting all aloes with secund flowers creates an artificial group. Reynolds (1996) reported a comprehensive chromatographic comparison between *A. scabrifolia* and *A. turkanensis*. These results showed the two species to be different in leaf exudate composition, thus supporting their separation by Newton and Lavranos but suggesting that they might not be closely related. The results presented here fully support the conclusions reported by Reynolds (1996).

*Aloe fleurentiniorum* was thought by Lavranos and Newton (1977) to be taxonomically related to *A. inermis*, an affinity suggested by the shape of the perianth and the entire leaf margin. As was the case for *A. jacksonii*, mentioned above, *A. inermis* produces a characteristic leaf exudate profile comprising a series of unidentified compounds not correlating to any other species chemically. Lavranos (1992) described *Aloe brunneostriata* as a new species, also suggesting a taxonomic affinity with *A. inermis*. *Aloe brunneostriata* is included in the microdontin chemotype. The entire leaf margin, which partly inspired Lavranos and Newton (1977) to suggest an affinity between *A. fleurentiniorum* and *A. inermis*, is also prominent in *A. brunneostriata*. The leaf exudate of *A. inermis* did not contain any chromones and anthrone *C*-glycosides.

Group 17 of Reynolds (1966) has 13 species, of which three contain the diagnostic compounds discussed in this paper. Group 17 is defined by the leaves of the plants, which are deeply canaliculate and recurved, a character also prominent in other species included in the microdontin chemotype (e.g. *A. camperi*, *A. calidophila* and *A. africana*). Since the time of Reynolds, four species have been described and associated with this group. *Aloe canarina* (Carter, 1994) and *A. lensayuensis* (Lavranos and Newton, 1976) have been suggested by the respective authors to be allied to

*A. microdonta*, while Newton (1993b) suggested *A. aageodonta* to show a taxonomic affinity to *A. lensayuensis*. In their species description of *A. gilbertii*, Sebsebe and Brandham (1992) draw a taxonomic correlation between this species and *A. megalacantha* and *A. calidophila.* The last two species are also represented in the microdontin chemotype. Six species in Group 19 produce the characteristic range of anthrones of the microdontin chemotype and fall within Reynolds' concept of 'plants with shrubby growth'. These species are characterised by prolongate stems. Group 19 is a very large and complex group with each species displaying degrees of variation throughout the geographical distribution. This is another large group created by Reynolds-containing species that are chemically divergent.

The only two Malagasy endemics included in the microdontin chemotype are *A. guillaumettii* and *A. buchlohii*. In his species description of *A. guillaumettii*, Cremers (1976) suggested an affinity between this species and *A. deltoideodonta* and *A. viguieri*. This similarity was dismissed by Lavranos (1994) as a "matter of convergence". In a separate article by Glen et al. (1992), the authors (of which J. Lavranos was one unknowingly, and he later distanced him from the content of the article) suggested a taxonomic affinity between *A. guillaumetii* and five other Malagasy endemics, of which *A. buchlohii* was one. This last species is the other Malagasy aloe to fall within the microdontin chemotype. Lavranos (1994) described a new species, *A. fragilis* from the NE coast of Madagascar, with suggestions that this new species could be related to *A. guillaumetii*. The exudate sample of *A. fragilis* produced an exudate profile unmatched by any other species of *Aloe*.

## 4. Conclusions

No single morphological character, or a combination of them, unifies all the species of the microdontin chemotype into a monophyletic group. It would be premature to suggest that the leaf exudate chemistry (also in combination with the morphology) is a reliable apomorphy to draw all species into a natural group. Convergent evolution cannot be ruled out as a possible explanation for the chemical similarity between these morphologically diverse and geographically distant species. In particular, Madagascan species were treated by Reynolds (1966) as so different from African species that they were classified separately.

However, it is interesting to speculate on possible chemogeographical patterns displayed by the group if we allow the possibility of a phylogenetic relationship. The highest number of species (95%) in this group have a distribution in north-east Africa (Fig. 4). This would suggest that this species-complex would have its origin in this area, whence where further speciation took place in a southerly direction. The only species to occur on the Arabian Peninsula is *Aloe fleurentiniorum*. It might be possible that the species in north Somalia, *A. brunneostriata* (also containing aloinoside), could provide a 'link' between this single species in south Yemen and its chemical counterparts on the African continent. These results parallel a previously published chemogeographical pattern (Viljoen et al., 1998) in which Malagasy endemics were found to be chemically similar to aloes on the African continent.

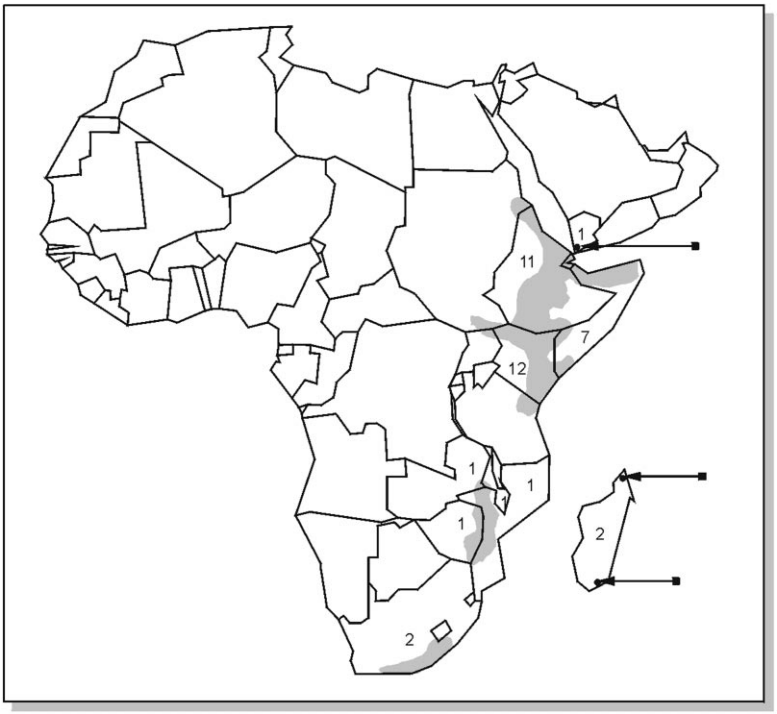



Fig. 4. The geographical distribution of species containing aloin/aloinoside/microdontin as major anthrones. The number in each country represents the total number of species with the characteristic chemical profile.

With reference to the present-day distribution of the species shown in Fig. 4, a possible route of migration to the present distribution patterns could be hypothesized as follows. Although the level of morphological diversity in this group is so vast, salient morphological features that are rare in *Aloe* could possibly provide some answers on relationships. Considering the curved perianth characteristic of *A. cameronii* and *A. africana*, which is a feature not very widespread in the genus, then it is taxonomically noteworthy that the very widespread and variable *A. cameronii*, with an extensive distribution in Malawi, Zimbabwe, Zambia and Mozambique, could be considered a taxonomic intermediate between the southern and northern taxa in this group. This resemblance forces one to consider other species with a similar character, e.g. *A. reitzii*. Close scrutiny of the chromatograms (Viljoen, 1999) shows that two late eluting anthrones are present. The quantities are extremely low and the UV spectrum could not confirm whether these are the aloinosides. The same profile has been recorded for *A. aculeata*, *A. petricola* and *A. gerstneri*. Reynolds (1997) did, however, report the aloinoside isomers to be present in *A. aculeata, A. petricola, A. reitzii*. It is here postulated that this group is of tropical origin, from where speciation took place through the variable and widespread *A. cameronii* to *A. ferox* and *A. africana* in the far

south. *Aloe reitzii* and its three close relatives have a very distant connection with the microdontin chemotype, which is indicated by the very low quantities of what seem to be aloinosides, not found (even in trace amounts) in any other species of *Aloe* in South Africa.

To suggest possible trends amongst the aloes of tropical east Africa would verge on mere guesswork at this stage. The reticulate distribution of chemical and morphological characters in this group indicates the possible influence of hybridisation events. It was demonstrated by Viljoen (1999) that hybrids could obscure the pattern where species are obviously related as various chemical profiles can result from an intermediate species. The value of the microdontin chemotype profile lies in the remarkable similarity in leaf exudate composition for these 36 morphologically diverse species. Unless there has been convergent evolution in the chemistry, these results indicate a measure of taxonomic coherence, however, distant it may be, between a large group of species not previously associated with one another.

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## References

Carter, S., 1994. Aloaceae. In: Polhill, R.M. (Ed.), Flora of Tropical East Africa. Balkema, Rotterdam.

Carter, S., Cutler, D.F., Reynolds, T., Brandham, P.E., 1984. A multidisciplinary approach to a revision of the *Aloe somaliensis* complex. Kew Bull. 39, 611–633.

Conner, J., Gray, A.I., Reynolds, T., Waterman, P.G., 1990. Anthrone and chromone components of *Aloe cremnophila* and *A. jacksonii* leaf exudates. Phytochemistry 29, 941–944.

Cremers, G., 1976. *Aloe* nouveaux du nord de Madagascar. Adansonia, Ser. 2 15, 497–503.

Cutler, D.F., Brandham, P.E., Carter, S., Harris, S.J., 1980. Morphological anatomical cytological and biochemical aspects of evolution in East African shrubby species of *Aloe* L. (Liliaceae). Bot. J. Linn. Soc. 80, 293–317.

Dagne, E., 1996. Review of the chemistry of aloes of Africa. Bull. Chem. Soc. Ethiopia 10, 89–103.

Farah, M.H., Andersson, R., Samuelsson, G., 1992. Microdontin A and B: two new aloin derivatives from *Aloe microdonta*. Planta Med. 58, 88-93.

Gilbert, M.G., Sebsebe, Demissew, 1997. Further notes on the genus *Aloe* in Ethiopia and Eritrea. Kew Bull. 52, 139–152.

Glen, H.F., Hardy, D.S., Lavranos, J., 1992. *Aloe guillaumetii*. Flow. Pl. Afr. 52, 2046.

Groom, Q.J., Reynolds, T., 1987. Barbaloin in *Aloe* species. Planta Med. 53, 345–348.

Lavranos, J.J., 1980. A new species of *Aloe* from Kenya. Cact. Succ. J. (US) 52, 242–243.

Lavranos, J.J., 1992. *Aloe inermis* Forsk, and its relatives with description of a new species. Cact. Succ. J. (US) 64, 206–208.
Lavranos, J.J., 1994. Note on *Aloe guillaumetii* Cremers from Madagascar, with description of a new species. Cact. Succ. J. (US) 66, 3–6.
Lavranos, J.J., Newton, L.E., 1976. Three new aloes from East Africa and an amplified description of a fourth. Cact. Succ. J. (US) 48, 273–280.
Lavranos, J.J., Newton, L.E., 1977. Two new species of *Aloe* from Arabia. Cact. Succ. J. (US) 49, 113–116.
Newton, L.E., 1993a. Comments on aloes with secund flowers. Excelsa 16, 7–10.
Newton, L.E., 1993b. A new Kenyan species of *Aloe* with two colour variants. Cact. Succ. J. (US) 65, 138–140.
Newton, L.E., 1995. A new dwarf *Aloe* in southern Sudan. Cact. Succ. J. (US) 67, 277–279.
Newton, L.E., 1996. *Aloe chrysostachys* and *Aloe meruana* (Aloaceae). Cact. Succ. J. (US) 68, 126–129.
Newton, L.E., Lavranos, J.J., 1990. Two new aloes from Kenya, with notes on the identity of *Aloe turkanensis*. Cact. Succ. J. (US) 62, 215–221.
Reynolds, G.W., 1950. The Aloes of South Africa. Aloes of South Africa Book Fund, Johannesburg.
Reynolds, G.W., 1966. The Aloes of Tropical Africa and Madagascar. The Aloes Book Fund, Mbabane.
Reynolds, T., 1985. The compounds in *Aloe* leaf exudates: a: review. Bot. J. Linn. Soc. 90, 157–177.
Reynolds, T., 1986. A contribution to the phytochemistry of the East African tetraploid shrubby aloes and their diploid allies. Bot. J. Linn. Soc. 92, 383–392.
Reynolds, T., 1990. Comparative chromatographic patterns of leaf exudate compounds from shrubby aloes. Bot. J. Linn. Soc. 102, 273–285.
Reynolds, T., 1996. Chemotaxonomy of *Aloe turkanensis* and *Aloe scabrifolia* from Kenya. Biochem. Syst. Ecol. 24, 347–352.
Reynolds, T., 1997. Comparative chromatographic patterns of leaf exudate components from *Aloe* section *Pachydendron* Haw. Bot. J. Linn. Soc. 125, 45–70.
Sebsebe, Demissew, Brandham, P.E., 1992. A new species of *Aloe* from the Ethiopian Rift Valley. Taxon 47, 509–512.
Van Wyk, B.-E., Van Rheede van Outshoorn, M.C.B., Smith, G.F., 1995. Geographical variation in the major compounds of *Aloe ferox* leaf exudate. Planta Med. 61, 250–253.
Veitch, N.C., Simmonds, M.J., Blaney, W.M., Reynolds, T., 1994. Dihydroisocoumarin glucoside from *Aloe hildebrandtii*. Phytochemistry 35, 163–166.
Viljoen, A.M., 1999. A chemotaxonomic study of phenolic leaf compounds in the genus *Aloe*. Ph.D. Thesis. Rand Afrikaans University, Johannesburg.
Viljoen, A.M., Van Wyk, B.-E., 2000. The chemotaxonomic significance of the phenyl pyrone aloenin in the genus *Aloe*. Biochem. Syst. Ecol., in press.
Viljoen, A.M., Van Wyk, B.-E., Dagne, E., 1995. The chemotaxonomic value of 10-Hydroxyaloin B and its derivatives in *Aloe* series *Asperifoliae* Berger. Kew Bull. 51, 159–168.
Viljoen, A.M., Van Wyk, B.-E., Newton, L.E., 1999. Plicataloside in *Aloe* — a chemotaxonomic appraisal. Biochem. Syst. Ecol. 27, 507–517.
Viljoen, A.M., Van Wyk, B.-E., Van Heerden, F.R., 1998. Distribution and chemotaxonomic significance of flavonoids in the genus *Aloe*. Pl. Syst. Evol. 211, 31–42.