Infrageneric classification of *Haworthia* (Aloaceae): perspectives from nectar sugar analysis

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Abstract. — Species and genus concepts and infrafamilial delimitations in the Aloaceae (subfamily Alooidae of the Asphodelaceae) have often been controversial. Arguments are mostly based on evidence obtained from vegetative and floral morphology, but data from other fields have also been used for speculating on taxonomic affinities within the Aloaceae. For the present study, nectar sugar composition (glucose, fructose, sucrose) was determined for representatives of Astroloba, Chortolirion, the three subgenera of Haworthia and for interspecific haworthioid hybrids and miscellaneous taxa. Two nectar types were distinguished in Haworthia and the two related genera: a Haworthia type (subg. Haworthia only, usually less than 50% sucrose) and a Hexangulares type (subg. Hexangulares, subg. Robustipedunculares, Chortolirion and Astroloba, usually more than 60% sucrose). Results support Uitewaal’s subdivision of Haworthia in two main groups, but reveal little substantiation for infrasubgeneric groupings.

Key words: Aloaceae, Astroloba, Chortolirion, Haworthia, nectar sugars, chemotaxonomy.

Introduction

The Aloaceae, often regarded as subfamily Alooidae of the Asphodelaceae (Dahlgren & al. 1985; Smith & Van Wyk 1991, 1998), is a medium-sized family comprising five to seven genera and about 510 species (Smith & Van Wyk 1998) of succulent-leaved, petaloid monocotyledons. Most researchers recognise the family as a taxonomically difficult unit and species and genus concepts have often been controversial. The basic integrity of the three principal genera, Aloe L., Gasteria Duval and Haworthia Duval is usually accepted, but infrageneric classification in Haworthia and the legitimacy and intergeneric relationships of the remaining genera (Astroloba Uitewaal, Chortolirion A.Berger, Lomatophyllum Willd. and Poellnitzia Uitewaal) have frequently been debated (Uitewaal 1947; Rowley 1967, 1996; Parr 1971; Bayer 1972; Obermeyer 1973; Manning & Smith 2000). Arguments are mostly based on evidence obtained from vegetative and floral morphology, but data from other fields, e.g. in vitro callus growth (Hayashi 1987), cytogenetics (Rollins 1953; Brandham 1971; Riley & Majumbar 1979) and phytochemistry (Reynolds 1985; Viljoen & Van Wyk 1996), have also been used for speculating on taxonomic affinities within the Aloaceae.

The haworthioid genera of the Aloaceae

Three of the genera of the Aloaceae are included in the so-called haworthioid group. These are, chronologically and in descending order in terms of number of species, Haworthia, Astroloba and Chortolirion. On morphological grounds these genera are united by their small stature and dull-whitish, more or less or distinctly two-lipped or at least obsolescently zygomorphic flowers (Bayer & al. 1997). Geographically Haworthia is near-endemic to South Africa, with only one species, H. venosa (Lam.) Haw. entering Namibia in the west, and another, H. limifolia Marloth, extending into Mozambique in the east. Astroloba is restricted to the southern parts of South Africa while Chortolirion has a very wide distribution in the southern African grasslands, extending from Angola in the west, through Namibia, Botswana and Zimbabwe to the northern, central and eastern provinces of South Africa.

Data from nectar sugar analysis of Aloaceae

In a cladistic study of Aloe and related genera, Smith & Van Wyk (1991) used nectar sugars (glucose, fructose and sucrose) as one of an array of phylogenetically informative characters to investigate generic relationships in the Aloaceae. The data on which the character polarities were based were presented in a later paper (Van Wyk & al. 1993). During the latter study, high performance liquid chromatography (HPLC) analyses of nectar samples had shown distinct generic and suprageneric discontinuities in the family and three distinct nectar types could be distinguished. These comprised (a) an alooid type (Aloe, Kniphofia, Lomatophyllum and Poellnitzia) with less than 5% sucrose and more or less equal proportions of fructose and glucose; (b) a gasterioid type (Gasteria only) with sucrose dominant and about equal proportions of fructose and glucose; (c) a haworthioid type (Astroloba, Chortolirion and Haworthia) with sucrose dominant, but with much more glucose than fructose.

According to Smith & Van Wyk (1991) and Van Wyk & al. (1993), nectar sugar composition is remarkably consistent within each of genera of the Aloaceae. However, subsequent scrutiny of results obtained during the 1993 study showed that the nectar of a few haworthias did not conform to the haworthioid type: the dominant sugar in the nectar of Haworthia arachnoidea (L.) Duval, H. comptoniae G.G.Sm. and H. herbacea (Mill.) Stearn was not sucrose, but glucose; the sucrose content for these species was in fact unusually low at 36%, 42% and 35 %, respectively (tab.1 in Van Wyk & al. 1993). Since all three aberrant species belong to H. subg. Haworthia, it seemed possible that nectar sugar analyses might reveal infrageneric groups in this genus and help to elucidate intergeneric relationships in the family. To test this hypothesis, a rigorous comparison of nectar sugars was made for species...
of all three subgenera of *Haworthia* as well as for representatives of *Chortolirion* and *Astroloba*. The results of our investigation are reported in the present communication.

**Material and methods**

Nectar was sampled from newly opened flowers on cultivated plants in private collections and various botanical gardens (see tab. 1). Collecting voucher specimens was therefore not only unpractical, but also unnecessary (most of the co-authors of this paper are taxonomic experts on the various genera of the family). A total of 65 samples, representing 49 taxa as listed in tab. 1, were analysed. Nectar samples were applied as spots to Whatman no.1 filter paper with a micropipette, air-dried and stored at -18 °C. For analysis, the sugars were recovered from the filter paper by repeated rinsing with distilled water, followed by centrifugation (usually 3x with 25 to 50 ml, depending on the size of the spot). Analyses were done with a refractive index detector coupled to a isocratic HPLC system operating at 2.5 ml per minute, with a “Waters Sugarpack” column and acetonitrile-water (87:13) as eluent. The percentages of the sugars were calculated on a weight basis from peak area, using 2, 4, 6, and 8 mg per ml of fructose, glucose and sucrose as external standards.


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<th>Nectar composition (%)</th>
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<td><em>H. glauca</em> Baker</td>
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**II. Subgenus Hexangulares**

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**III. Subgenus Robustipedunculares**

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**Interspecific hybrids and miscellaneous taxa**

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**Astroloba**

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**Chortolirion**

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Figure 1.
Composition of nectar sugars in 65 samples taken from 49 taxa of Haworthia, Astroloba and Chortolirion.
Samples and species are numbered as in tab. 1.
Results and discussion

In the list of taxa studied (tab. 1), the composition of nectar sugars present in the samples are given. The results of the analysis are also depicted graphically (fig. 1) to ease comparison of species. The outcome of the study clearly shows that the composition of nectar sugars varies considerably among species of *Haworthia* and *Astroloba* and, especially, among those representing *H.* subg. *Haworthia*. Moreover, samples taken from plants belonging to the same species but from different localities, i.e. botanical gardens or private collections, vary in their ratio of sucrose to hexose, i.e. glucose plus fructose (compare Nos. 3 & 4; 10 & 11; 13 & 14; 34, 35 & 36). In samples of *Chortolirion* taken from plants of the same locality, the variation is negligible (compare Nos. 63, 64 & 65). Hence, results on *Haworthia* and *Astroloba* do not support the findings of Van Wyk & al. (1993) that “...the sugar composition of the nectar is remarkably invariable within each of the genera (of Aloeaceae)”.

The various nectar samples were selected so as to cover most of the sections and subsections or series within the subgenera of *Haworthia* as recognised by Pilbeam (1983) and by Breuer (1998), who both based their infrageneric subdivisions on leaf and rosette characters. Where our study provided data on the nectar of more than one representative of a subsection or series, it shows that some species, grouped together on account of morphological similarities such as *H.* *bolusii* Baker, *H.* *cooperi* Baker and *H.* *habdomadis* Poelln. var. *morrisiae* (Poelln.) M.B.Bayer, are remarkably uniform in sugar composition (compare Nos. 6, 8 & 15). Nevertheless, other species belonging to the same series (Limpidae), namely *H.* *decipiens* Poelln. and *H.* *semiviva* (Poelln.) M.B.Bayer (Nos. 10 & 27), differ notably.

According to Van Wyk & al. (1993) the fructose/glucose ratio in intergeneric hybrids of Aloeaceae is inherited from the pod parent. Our results on interspecific hybrids and *H.* *tortuosa*, a possible hybrid of *H.* *viscosa* (Pilbeam 1983), are inconclusive (compare Nos. 53, 54 & 56 with Nos. 46–48). The nectar composition of a new, undescribed species (No. 55) supports its placement under *H.* subg. *Haworthia*. Nectar of *H.* *mcmurthyi* (No. 57), regarded by Scott (1985) as allied to *H.* *koelmaniorum* (No. 32), is very similar to that of the latter species.

Despite the variation in nectar composition within the subgenera of *Haworthia* and in *Astroloba*, for example the deviation shown by *Astroloba* *bullulata* (No. 58), our results show a general trend. On the basis of the ratio of sucrose to hexose (fructose plus glucose) the 49 investigated taxa can be divided into two groups, namely those with sucrose-rich nectar (usually more than 60% sucrose) and those with nectar that is low in sucrose (usually less than 50% sucrose). Both nectar types have a relative higher proportion of glucose than fructose. The results of the present investigation suggest that sucrose-low nectar is generally characteristic of representatives of the largest subgenus within *Haworthia*, namely *H.* subg. *Haworthia*. This subgenus includes 93 of the 132 taxa recognised by Breuer (1998). Consequently, the characteristic nectar type is here referred to as the Haworthia type. On account of its lower proportion of sucrose, the Haworthia type is quite unlike the ‘haworthioid’ type of Van Wyk & al. (1993).

Sucrose-rich nectar, comparable to the ‘haworthioid’ type of Van Wyk & al. (1993) is produced by a second, smaller group of taxa within *Haworthia*. This nectar type is here referred to as the Hexangurales type, since it characterises the nectar of representatives within the second largest subgenus, namely *H.* subg. *Hexangulares*. The investigated species of *H.* subg. *Robustipedunculares*, *Chortolirion* and *Astroloba* also belong to this group. The correlation of nectar in *Astroloba* and members of *H.* subg. *Robustipedunculares* with the sucrose-rich Hexangulares type is surprising. Because of floral and other morphological features it was expected that the sugar composition of species belonging to these two units would be nearer to the sucrose-low *Aloe* type nectar of Van Wyk & al. (1993).
Conclusions

- Two nectar types occur in *Haworthia*, namely a sucrose-low *Haworthia* type (generally less than 50% sucrose and more glucose than fructose) and a Hexangulares type (generally more than 60% sucrose and more glucose than fructose).
- Evidence from nectar sugar analyses knits *Haworthia* to *Astroloba* and *Chortolirion*, and also suggests that *Chortolirion* and *Astroloba* may not be closely linked to species within *H*. subg. *Haworthia*.
- Our findings support Uitewaaal’s (1947) subdivision of *Haworthia* in two main groups, but reveal little substantiation for infra-subgeneric groupings.

References


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