

Aloioideae—Asphodelaceae And The Genera Thereof

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Reprinted from *Alsterworthia International Special Issue No 4*

My fascination with *Haworthia* has presented me with many problems in the way the genera in the Aloioideae have been discussed, appraised and modified in and subsequent to G. D. Rowley's analysis (1967). Parr (1971) coalesced *Astroloba*, *Haworthia* and *Poellnitzia* and I refuted this in 1972 when I also wrote a rebuttal of Rowley's paper. My remarks did not deter Mrs Obermeyer-Mauve (1973) following and accepting Parr, nor in adding *Chortolirion* to *Haworthia*. Rowley (1976) quite pragmatically discussed the Aloid genera, but in 1980 suggested the incorporation of *Poellnitzia* in *Aloe*. He implemented this proposal in 1981 and promoted it again in 1985. Smith and van Wyk (1991) published a cladistic analysis of the Aloioideae which I felt was unacceptable because of the fallacious character states and sets that were used there. Despite that paper and at least four others (Smith 1991, 1994, 1995; Smith & van Wyk 1992) generally supporting the unispecific status of *Poellnitzia*, Manning and Smith (2000) incorporated the genus in *Astroloba*.

My objection to this manipulation of the genera is that the supporting arguments have been incorrect and that it essentially has not addressed or considered what I perceived to be the stumbling block to arriving at a better delimitation of the genera in the sub-family. This is the relationship within the genus *Haworthia* where it is quite evident to me that it comprises three distinct sets of species (the subgenera of Bayer ex Uitewaal). The floral and morphological differences for those three sets are absolute, and I am sure will need to be seen so in any way in which *Aloe* is configured. This is because the floral similarities within those subgenera are so minimal. I consider these floral differences to be as dramatic for genus delimitation as any of the character states covered in Rowley's (1967) analysis. It would alarm me if the result of a DNA study produced any other result. The sets also appear to me to be "behaviorally" different and with this consideration the genera (even if unispecific) *Poellnitzia*, *Chortolirion*, *Astroloba* are of similar status. This is not to imply that I do not recognise the problems with many other oddities in the Aloioideae which require re-evaluation of the generic arrangement.

Adam Harrower of NBI asked me to identify an *Haworthia* he had collected near the Potberg (cf *H. heidelbergensis*). In view of his interest I asked him to lookout for *H. limifolia* on a trip he was to undertake to the eastern Transvaal. On his return he presented to me a plant he took to be that species. It was in fact *Chortolirion angolense*. However, he produced photographs of another species at which I exclaimed "This is a new genus". Here I recognize the irony of this reaction when the generic arrangement in *Aloe* is so questionable.

The plant that Harrower collected has thin, slender, spineless, hyacinthoid leaves (Figs 1–2) with very pronounced bulbous bases. There seem to be few accumulated dry bulb scales as in *Chortolirion* and the plants have not displayed deciduousness as does that species. The blades of

the older leaves dehisce leaving fleshy bulbous bases and these are spirally arranged in the lowest order of the Fibonacci series viz. 2, 3 or 5 (Fig 2). The roots seem rather sparse and are the yellowish color of Aloe. The flower intrigues me more (figs 3 & 4). The free terminal portions of the flower are not channeled but are flared in the style of the sub-genus *Haworthia*. The midribs of the inner petals remain exposed and the margins of the outer petals adhere close to the mid-rib of the inner. This is the case in the subgenus *Hexangulares* and *Chortolirion*, as well as in this "new genus". The lower petals are more undershot than is the case in either the *Hexangulares* or subgenus *Haworthia*.

The geographical location is the high-lying escarpment between the ranges of the species *H. koelmaniorum* and *H. limifolia* of the *Haworthia* subgenus *Hexangulares*.

Why I have stated so categorically that this is a "new genus" is largely because of the historical (mal) treatment of the genera of Alooideae and the failure of students and commentators of *Haworthia* to exhibit any rational species concept. Such a concept appears to be missing for the genera as well. These shortcomings, coupled with the name changes which would ensue, have discouraged me from ever trying to formalize three distinct genera for *Haworthia*. What has troubled me in recent times is the emerging belief that molecular study will provide the basis for a real and irrefutable phylogenetic classification. We have now a paper published in *Taxon* 52:193 (2003) (see reprint pages 6–21) by Treutlein et al which will enable one to see to what extent these expectations are being met.

What strikes me immediately about the paper is firstly a statement in the abstract, and secondly the unfortunate selection of study material. The abstract summarizes the results of the work done and this is: "The current taxonomic system does not reflect the phylogenetic affinities and relationships among the succulent genera *Aloe*, *Chortolirion*, *Gasteria*, *Haworthia* and *Poellnitzia*." I find this extraordinary as it has never occurred to me that it did, and I would have expected this sentence to be worded in such a way as to form a key question to be answered by the study rather than as a conclusion. Similarly Treutlein's closing paragraphs of his discussion should have been used as key questions to be answered by the study and not have been derived from it. One sentence reads "complete sampling... needed".

The selection of material I take to be somewhat irresponsible given the past history of classification of the group and the literature. I would have expected some kind of predictive approach to the selection of material. The inclusion of unknown hybrids such as *H. ryderiana*, *H. kewensis*, and *H. icosiphylla* can tell us nothing. Ignorance of the actual taxonomic position of *H. geraldii* is similarly curious. The material is virtually entirely ex hortus and given my experience with identification, even voucher specimens are hardly likely give such material much credibility. I do think more thought and consideration should have been given to the species used in relation to the problems they present to their classification.

Putting these considerations aside, I would comment as follows on the results as presented primarily in Treutlein et al's fig 4. It does tell me what I had supposed i.e. subgenus *Haworthia* is very different from the other two subgenera of *Haworthia*. BUT *H. geraldii* (i.e. *retusa*) is grouped with *H. attenuata* and *H. glauca* and close to *Gasteria*! It is a result which does not make sense. The true *H. geraldii* is *H. retusa* and that is arguably an ecotype of *H. turgida* as much as it

is a discrete species. We could indeed just be seeing—in Treutlein's own words—a "gene tree". Of course genes that can be sampled in the different types of DNA analysis are only another data set, and are not necessarily responsible for the morphology that we can see. Nevertheless it is equally true that, say, observed floral morphology may be the product of interplay of far more genetic material than those analyses entertain.

The inclusion of the unknown hybrids just introduces unnecessary tension or clutter or inaccuracies into the cladograms. *H. kewensis* may have female parentage as *H.* subgenus *Hexangulares*, and *H. ryderiana* similarly subgenus *Haworthia*, to explain their position in the cladogram. *Astroworthia bicarinata/skinneri* is the hybrid *H. pumila* X *A. corrugata* (*muricata*!) so it is not surprising that it comes out with that species.

What is significant is that *Chortolirion* comes out with the grass aloes, thus showing that the *Hexangulares* flower may be homoplasious (i.e., having evolved more than once). It would surprise me for a structure as complex as the flower to be so. Please note that Treutlein is wrong in saying *Uitewaal* divided *Haworthia* into two groups and that the "former including the subg. *Haworthia* and subgenus *Robustipedunculares*". *Uitewaal* divided the group *Hexangulares* into *Gracilipedunculatae* and *Robustipedunculatae*. The way this is has been repeated in the closing paragraph of *Uitewaal*'s paper has confounded Treutlein, who goes on to say "This division is strongly supported by...". This is not true. He has no *Robustipedunculares* in his analysis apart from the DNA (cytoplasmic) in the hybrid *Astroworthia*. It is thus not surprising that it comes out in the "heterogenous group" that includes *Aloe aristata*, *Gasteria*, *Poellnitzia*, *Astroloba* and *H. retusa* ("geraldii") and its position here is very dubious.

Dr Manning (personal communication) feels that the results vindicate the treatment he and Smith gave *Poellnitzia*. I must state that he is quite correct on the point of bird pollination and it has been shown that sunbirds do pollinate *Microloma*. But I cannot agree that *Poellnitzia* is unequivocally *Astroloba*. In Treutlein's fig. 3, *Poellnitzia* could be with either *Gasteria* or *Astroloba*, with *Aloe aristata* as a wild card nearer to *Astroloba* than is *Poellnitzia* (one needs to look at distribution and variability of *Aloe aristata* to know that something is not kosher here). In fig. 4 *Poellnitzia* collapses below *Astroloba* as does *Aloe aristata* and the cladogram shows no "bootstrap values" to substantiate an opinion. Would one argue that *Aloe aristata* then also belongs in *Astroloba*?

As there is no member of the *Robustipedunculares* in the analysis and one can only wonder what a better species representation would have done to the cladogram. It is important that *Chortolirion* is seen to group with the "grass" aloes. The flower is definitely *Hexangulareoid* whereas the bulbous structure is replicated in *Aloe buetneri* as well as in a few of the "grass" aloes. My opinion regarding the Harrower "new genus" is that it is in fact discrete and introduces an entirely new dimension to the discussion.

Something should also be said about cladograms. The binomial system is essentially built on the concept of dichotomous branching. The fact of the matter is that in any two-dimensional cladogram which is used to depict relationships, the one axis will represent time and the other two-dimensional space if one considers that species, like any other phenomenon in creation, are spread in space (they change with time). Therefore a two-dimensional diagram is very restricting

and leads, for example, to statements such as "Poellnitzia is nested in Astroloba". To think that a statistical bootstrap value will give a true measure of that distance in a two-dimensional array may be wishful thinking.

After seeing this Treutlein paper I am happier with the way in which the existing classification meets my needs for identification and communication and I do not think the word "merely" used by Treutlein in this connection is appropriate. Whatever high-grounded attitudes now seem to prevail that DNA studies give a new and correct dimension to phylogeny as the intent of classification, my contention is that this has always been the aim even in the most simplistic morphological studies. Classification is a prime function in zoology as well and there has never been any doubt that phylogeny was the prime aim of the classification. The only reason it seems to be obscure in botany is the absence of good archaeological or fossil evidence and the problem of determining homologies in a muscle and nerve free organelle.

Dr Manning kindly made this comment among others which I may not be doing justice to: "Clearly there are just two alternatives IF one wants to define genera in phylogenetic terms: lump everything into Aloe or split Aloe up into several other genera, each corresponding to one of the monophyletic branches that are revealed by the analysis. The latter treatment is confounded by a) incomplete sampling within Aloe and b) probable lack of good characters by which these segregate genera could be recognized". I would have omitted "within Aloe."

Treutlein et al make another statement... "The further the status quo departs from reality, the more difficult it will be to integrate practice and theory". This seems to be a twist of words. I think it should read "The further theory departs from practice the more difficult it will be to integrate the status quo with reality"? Again that is the problem that should have been addressed in the preliminary approach to the study. The status quo by definition cannot depart from anything.

To close, I need to say something about definitions. I have already made several statements about the absence of definition at species level where I still find resistance among students of *Haworthia* (if not wider). It is simply a fact that classification is a process of specifying so that one can generalize about a set of some kind. In dealing with *Haworthia*, I experience the group as three sets, and as stated above, these sets relate to the present classification as I have already described. The current generic classification expresses the experience of collective experience of all previous writers and researchers in the field. It has an historic value and an embedded "truth" of some kind; or, if the classification process has credibility, it should have and it should be respected accordingly. The definition of genus quite obviously has to be linked to that of species-systems of species which can be shown to be related sets in respect of morphology (physiology), genetics and geographical considerations. I contend that this has always been an unspoken aim and intent of classification and it is wrong to suggest now that it is absent from existing classifications. In my experience it is/was always seen to be the ideal that classification should reflect phylogeny. In doing so it would also reflect morphological/physiological, genetic and behavioral characters that lead to understanding. This is what I wrote in *Asklepios* 77:6 (1999) "... understanding of what it really means to be human". If we are pursuing knowledge for any other purpose it may be that we are on an ego-trip. To maintain that floral structure is very limiting in the way it has largely driven classification is correct to a degree. I think it is wrong to

make the implication that floral structure is driven by less characters than, say, those nucleotide sequences of the Treutlein analysis.

Touching on the "behavior" aspect—I think Poellnitzia is unique. The Robustipedunculares and Astroloba possibly could not maintain their integrity in each other's company viz. hybridization between members where they co-occur. They complement each other geographically. Hexangulares maintains integrity wherever and with whatever it grows except with its own members. Subgenus Haworthia similarly always maintains integrity except with own members and presents a degree of plasticity far greater than any complementary set. Poellnitzia maintains its own integrity and is extraordinarily invariable in the close company of Gasteria, Robustipedunculares, and subg. Haworthia. Hexangulares and Robustipedunculares occupy quite different territories and virtually do not meet at all.

Acknowledgements

Dr J. C. Manning, Compton Herbarium, Kirstenbosch responded in very kind manner to my criticisms in Bayer 2003, and was most helpful in obtaining hard-copy of the Treutlein publication, as well as in interpreting the DNA methodology for me for the purposes of this paper. In having written this, I do not dispute his need for a pure phylogenetic model. I am simply trying to put a case based on my practical experience and knowledge of the plants concerned, hoping that the two poles will eventually meet in a functional way. Paul Forster of the Queensland Herbarium and Steve Hammer of California were kind enough to comment on, and edit, drafts of this article.

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