

On the classification of some species of the genus *Haworthia*, subgenus *Haworthia* (Asphodelaceae)

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In memory of the late Prof. R.B.Rycroft, former Director of the Kirstenbosch Botanic Garden and a very good and knowledgeable friend over many years.

Abstract — Morphological and cytological observations have been made *in situ* as well as in cultivation and on herbarium specimens on more than two hundred accessions of the genus *Haworthia* subgenus *Haworthia*. The evidence has provided ample support for the hypothesis of superspecies for two groups of taxa and to the selection of two species as representative of their respective groups.

Keywords: classification, cytology, *Haworthia* subgenus, *Haworthia* superspecies.

INTRODUCTION

The following notes on the genus *Haworthia* subgenus *Haworthia* are the results of more than twenty-five years of familiarity with the genus, both in cultivation and in the wild and of several field collecting trips in South Africa. They represent an explanatory account of some of our ideas on its classification.

One of the foremost authority on the genus *Haworthia* is Bruce BAYER, former Curator of the Karoo Garden at Worcester (South Africa). Over many years, he has written several books and a large number of articles and notes on the genus. His main accounts (1976, 1982 and 1999a and b) including especially his latest, volume 1 of *Haworthia Update: Essays on Haworthia* (2002), are very comprehensive regarding species morphological descriptions and their habitat preferences. However, the content of *Haworthia Update* (vol. 1, 2002) with its very many excellent photographic illustrations, maps and explanations, seems to us to provide well documented evidence for introducing tentatively the concept of "superspecies".

In fact, the morphological characters, as used for species definition of the taxa in question, do not give a clear indication of true discontinuity over their geographical range which in some case is rather restricted. Thus, a classification system based on the classic dichotomous keys, cannot be used successfully

in our subgenus in view of its observed natural variation which appears to be bewildering and endless.

In our opinion, it is perhaps useful to consider at least part of the subgenus *Haworthia* as forming a single highly polymorphic assembly of species which can be subdivided, albeit with some difficulty in some cases, into two groups.

A taxonomic **type** (**holotype**, **isotype**, etc.) must refer to something tangible and for most plant species, this is a dry specimen kept in an herbarium.

In the case of *Haworthia*, however, the very nature of the plant material, which is usually very fleshy, in the dry state becomes totally disfigured and very difficult to assess with certainty. In any case, owing to the already mentioned variability of the plants even within a single population, to cover representatively a given population it would be necessary to have a very large number of specimens with the consequent difficulties of handling and storage. We think that it is far better to bring into service photographs and/or detailed drawings or paintings (i.e. **iconotypes**) which, together with accurate descriptions, can give a satisfactory and, above all, readily usable representation of the living plant.

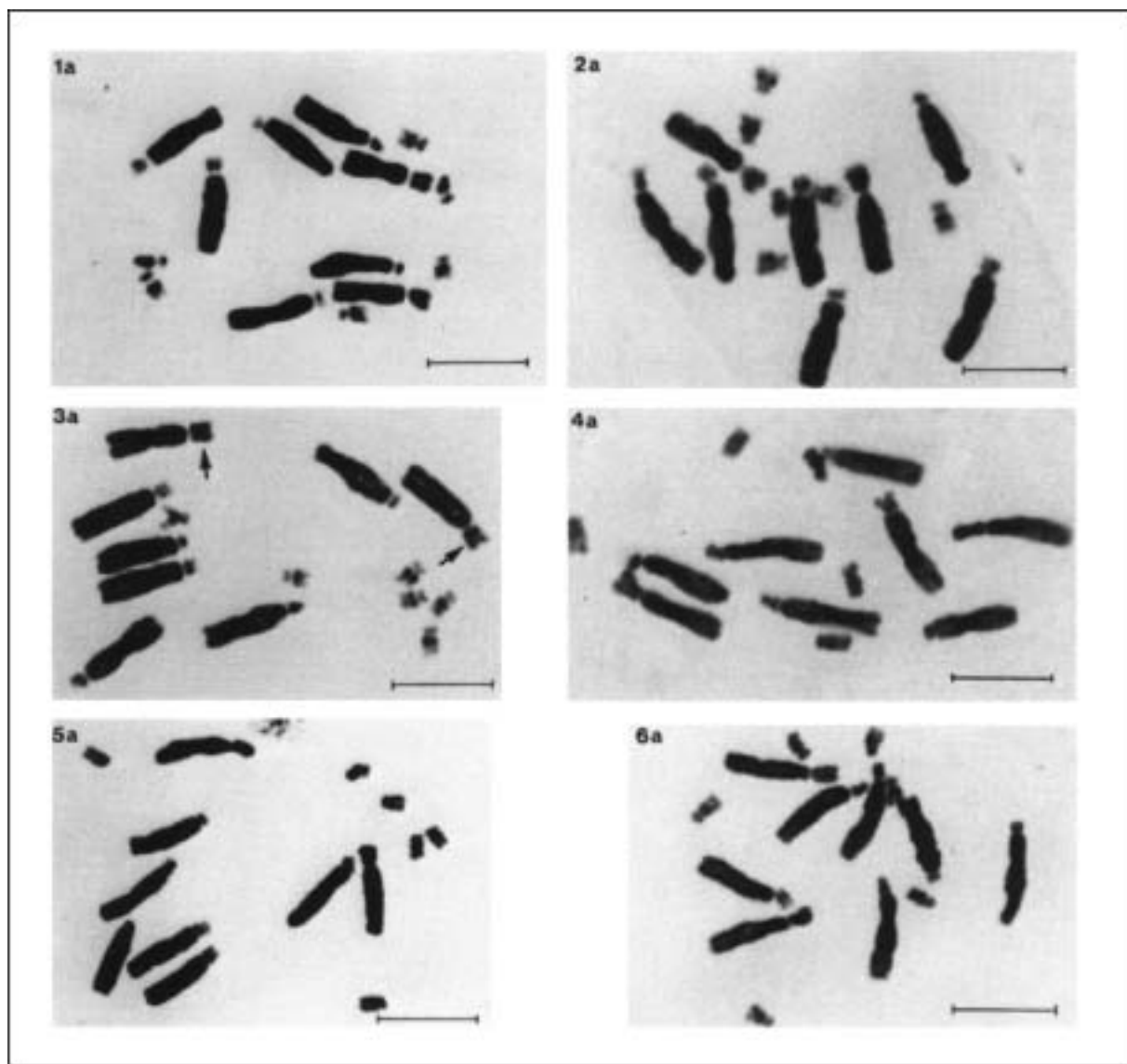
CYTOLOGY

The evidence of our cytological investigations on more than one hundred collections, of which chromosome counts and morphology for more than thirty has been published (VOSA and BAYER 1981, 1986), shows a high degree of similarity between the karyotypes. All the investigated material shows a diploid bimodal chromosome complement com-

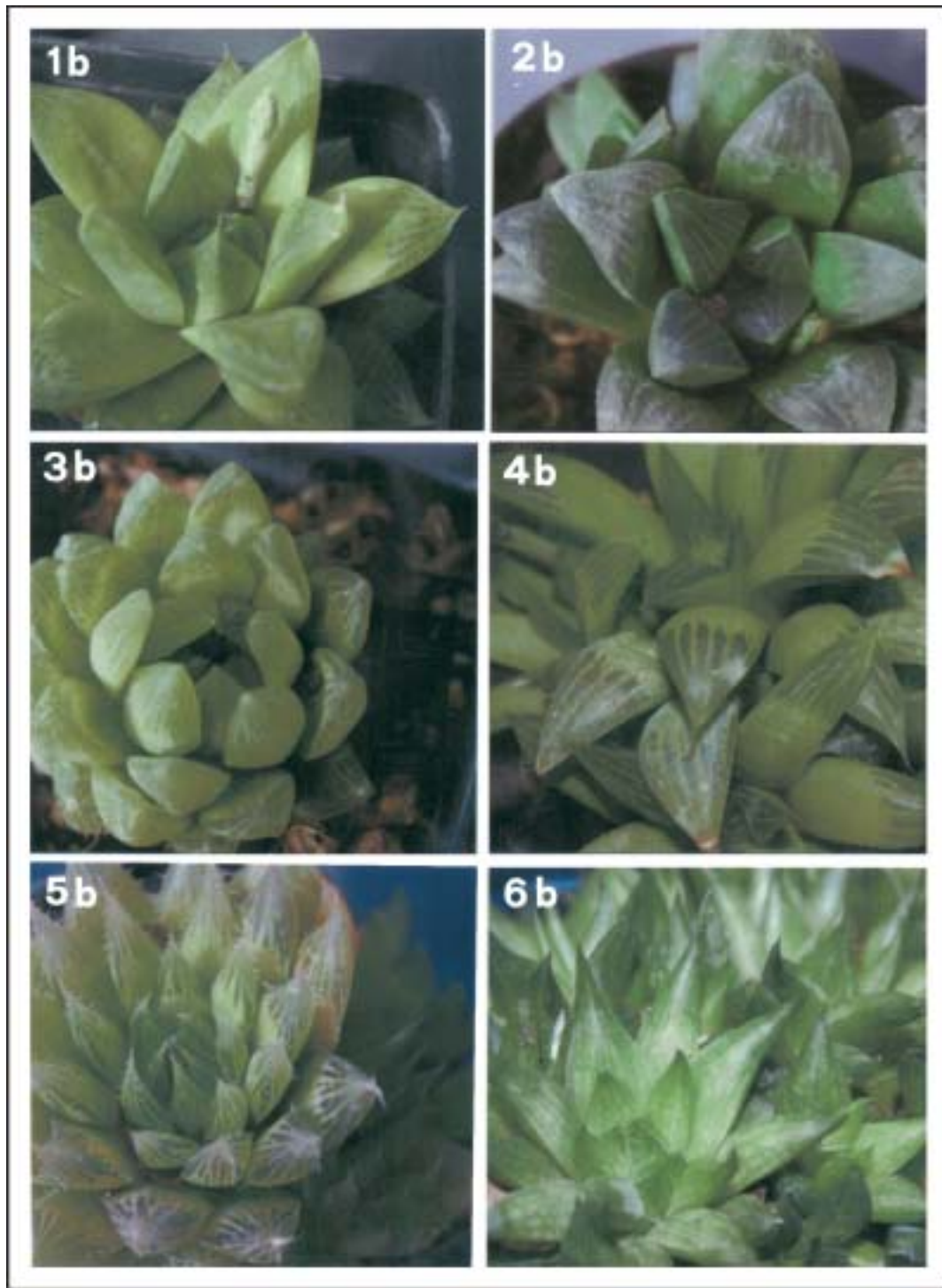
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posed of eight large (L-) and six small (S-) chromosomes, as generally found in the Aloineae. The allocyclic differential segments (DYER 1963; VOSA and BAYER 1981; 1986; VOSA and COLASANTE 1995; COLASANTE and VOSA 2001), present in all karyotypes, show a fair degree of variability but, so far, do not seem to supply usable means of discrimination (figs. 1a to 6a). Our own experience also in other genera of

the Aloineae, such as a several species of *Aloe* and of *Gasteria* (VOSA and MOGFORD 1981, VOSA 1982; VOSA and BENNETT 1990), seem to indicate that, at least in some groups of related taxa, the small variabilities found, whether morphological or cytological, are probably no more than those existing between plants of the same species in a single population of some size.



Figs. 1a. to 6a. — Mitotic metaphases in *Haworthia* (the bar represents 10 micra): 1a. *H. arachnoidea* (L.) Duval var. *aranea* (A. Berger) M.B.Bayer; 2a. *H. chloracantha* Haw. var. *denticulifera* (V. Poelln.) M.B.Bayer.; 3a. *H. decipiens* V. Poelln.; 4a. *H. monticola* Fourc. var. *monticola* M.B.Bayer; 5a. *H. floribunda* V.Poelln. var. *dentata* M.B.Bayer; 6a. *H. maraisii* V.Poelln. var. *maraisii* M.B.Bayer;.) Fearn. Note that all S-chromosomes possess allocyclic segments (AC-segments) distally in their long arm and that most of the L-chromosomes, except the longest, possess AC-segments distally in their short arm. The arrows in fig. 3a. (*H. decipiens* V. Poelln.) indicate the presence of small intercalary AC-segments in the short arm of the longest chromosomes. The occurrence of AC-segments is quite variable. The results of our continuing studies, so far, seem to indicate that in *Haworthia* the AC-segments may be considered population specific rather than species specific. Nomenclature as from Bayer (1999).
Herbarium specimens: *H. arachnoidea* var. *aranea* MBB 2071 (NBG); *H. chloracantha* var. *denticulifera* KG 209/70; *H. monticola* var. *monticola* KG 349/70; *H. floribunda* var. *dentata* KG 197/70; *H. decipiens* var. *decipiens* KG 140/72; *H. maraisii* var. *maraisii* KG 400/61.



Figs. 1b. - 6b. — Photographic illustrations of *Haworthia* subgenus *Haworthia*. Fig. 1b. *H. cymbiformis* (Haw.) Duval, var. *cymbiformis* M.B.Bayer; 2b. *H. magnifica* V.Poelln. var. *magnifica* M.B.Bayer; 3b. *H. cymbiformis* (Haw.) Duval var. *transiens* (V.Poelln.) M.B.Bayer; 4b. *H. turgida* Haw. var. *turgida* M.B.Bayer; 5b. *H. cooperi* Baker var. *gordoniana* (V.Poelln.) M.B.Bayer; 6b. *H. marumiana* Uitewal var. *batesiana* (Uitewal) M.B.Bayer. Nomenclature as from Bayer (1999).
Herbarium specimens and/or living material: *H. cymbiformis* var. *cymbiformis* KG 409/70; *H. magnifica* var. *magnifica* KG 94/72; *H. cooperi* var. *gordoniana* CGV 2271/79; *H. cymbiformis* var. *transiens* KG 34/70; *H. turgida* var. *turgida* CGV 2044/79; *H. marumiana* var. *batesiana* KG 534/77.

CONCLUSIONS

The above findings, as well as the photographic illustrations in Bayer's accounts and his comments, together with our own morphological observations in the field and on plants in cultivation over a very long period, seem to provide ample support for the "superspecies" hypothesis.

Careful observations in the field as well as on cultivated and on herbarium specimens show that it is very difficult to discriminate reasonably at the species level between the *Haworthias* found in a rather wide area of the Southern and Eastern Cape. In this area there coexist a virtually endless number of "types" somewhat intermingled and gradually fading one into the other with no true solution of continuity. We are referring especially to the two groups of species listed in Table 1.

According to the *International Code of Botanical Nomenclature*, the first described and published specific epithet must be used in any instance in which the question of priority may arise. Therefore, it is suggested that the representative species of group 1 should be *Haworthia cymbiformis* described and published by Duval in 1809. The iconotype (neotype according to BAYER, 1999), of *H. cymbiformis* can be found in Table 802 of the *Botanical Magazine* (London). The representative species of group 2 should be *H. retusa*, again described and published by DUVAL in 1809. Its iconotype can be found in Commelin's *Hort. Amstel.* Table 6, fig. 2 (1701).

We consider iconotypes as more reliable and more easily understood and consulted than formal descriptions. These are usually in Latin, a language of great prestige and precision but nowadays sadly neglected.

Our researches, as well as those of BAYER (2002), on *Haworthia* suggest that the widely accepted principle where one given specimen represents an entire species might be somewhat outdated and not always true. This was one of the ideas on the then state of art in taxonomy, expressed by the late Prof. C. D. DARLINGTON in his inaugural address on taking over the Directorship of the Botany School of the University of Oxford in 1953. He was referring in particular to his experiences on some species of *Fritillaria* and *Tulipa* from the Middle East, which he collected and studied morphologically and cytologically over a long period of time. In his altogether provocative speech, he went as far as to propose the abolition of herbaria which he thought, at least in part, obsolete apart from their historical value.

The synopsis of the species included in group 1 and in group 2 is indicated in Table 1. All the evidence points to the conclusion that *H. cymbiformis*

Table 1 — The documented nomenclature of the species listed is to be regarded as useful in the issue of species definition. It may provide good reference points in the absence of clear geographical discontinuities which represent the more untractable problem in the classification of some species of *Haworthia* subgenus *Haworthia*.

Group 1

Typical species: *Haworthia cymbiformis* (Haw.) Duval in *Plantae Succulentae in Hort. Alenconia*, 7 (1809).

iconotype (neotype according to Bayer, 1999): t. 802 in *Botanical Magazine* (London).

Representative species:

H. arachnoidea Duval in *Pl. Succ. Hort. Alenc.* 7 (1809).

H. reticulata Haworth in *Syn. Pl. Succ.* 94 (1812).

H. mucronata Haworth in *Syn. Pl. Succ.* 50 (1819)

H. aristata Haworth in *Suppl. Pl. Succ.* 51 (1819).

H. chloracantha Haworth in *Revis.* 57 (1821).

H. cooperii Baker in *Saund. Ref. Bot.* 4: t. 233 (1870).

H. bolusii Baker in *J. Linn. Soc.* 18: 215 (1880)

H. gracilis V. Poellnitz in *Feddes Repert. Sp. Nov.* 27 (1929).

H. decipiens V. Poellnitz in *Feddes Repert. Sp. Nov.* 23: 103 (1930).

H. nortieri G.G. Smith in *J. S. Afr. Bot.* 12: 13 (1946).

Group 2

Typical species: *Haworthia retusa* (L.) Duval in *Plantae Succulentae in Hort. Alenconia*, 7 (1809).

iconotype: Commelin in *Hort. Amstel.*, t. 6: fig. 2 (1701).

Representative species:

H. mirabilis Haworth in *Syn. Pl. Succ.* 95 (1812).

H. turgida Haworth in *Suppl. Pl. Succ.* 52 (1819).

H. mutica Haworth in *Revis.* 55 (1821).

H. pygmaea V. Poellnitz in *Feddes Repert. Sp. Nov.* 27: 132 (1930).

H. magnifica V. Poellnitz in *Feddes Repert. Sp. Nov.* 33: 239 (1933).

H. maraisi V. Poellnitz in *Feddes Repert. Sp. Nov.* 38: 194 (1935).

H. springbokvlakensis C.L.Scott in *J. S. Afr. Bot.* 36: 287 (1970).

H. bayeri Venter & Hammer in *Cact. Succ. J. (U.S.)* 69: 75 (1997).

N.B. *H. turgida* Haworth in *Suppl. Pl. Succ.* 52 (1819) appears intermediate between *H. cymbiformis* and *H. retusa*.

(Haw.) Duval and *H. retusa* (L.) Duval may be usefully referred as "superspecies" and representative of their groups.

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