A cladistic analysis of *Gasteria* (Aloaceae)

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Gasterioid species were initially treated as belonging to the original wide concept of Aloe *L., until the genus received its present-day circumscription early in the 19th century.* Gasteria *Duval (family Aloaceae), a distinctive but taxonomically controversial genus, was recently monographically revised, and only 16 of the more than 100 names available were upheld. Although the genus is readily recognizable, its infrageneric classification has remained obscure for more than 180 years. Using morphological data and a computerized parsimony programme,* Gasteria, *which is endemic to southern Africa, has been analysed cladistically in order to formulate a hypothesis of its infrageneric phylogenetic relationships. The results indicate that* Gasteria *forms a monophyletic group diagnosed by several synapomorphies. Based on floral and vegetative characters the 16 species of* Gasteria *are placed in two sections,* Longiflorae *Haw. and* Gasteria. *Each section is again subdivided into two series,* Longifoliae *(Haw.) Van Jaarsv. and* Multifariae *(Haw.) van Jaarsv. in the case of section* Longiflorae, *and* Gasteria *and* Namaquana *Van Jaarsv. in the case of section* Gasteria.

The succulent plant genus *Gasteria* Duval (Fig. 1) is endemic to southern Africa and has its main areas of distribution in the dry, karroid and savannah regions of the south-eastern Cape Province (Fig. 2). The genus is more or less restricted to the summer-dry, semi-arid coastal regions below the climatically severe central-southern African inland escarpment, with outliers in the arid river valleys of Natal, Swaziland and the eastern Transvaal.

The family Aloaceae, in which *Gasteria* is classified, includes succulent plants with leaves arranged in a rosette (or in a few cases remaining distichous) and with tubular flowers. An hypothesis of phylogenetic relationships within the Aloaceae (then treated as subfamily Alooideae of the Asphodelaceae), based on morphological data and phytogeographical considerations was recently published.[2] This study showed that *Gasteria* is readily distinguished from related genera by pendulous pedicels and recurved, basally swollen (gasteriform) perianths, which are usually laxly and secundly arranged on spreading racemes.

Previous studies on the genus have been primarily taxonomic in nature and involved descriptive studies of morphology[3,4] and karyology.[5] However, due to a lack of population-based, *in situ* investigations the patterns of variation have not been described. Furthermore, no infrageneric classification of *Gasteria* has been published. Recently the genus was revised monographically[6] and only 16 of the more than 100 available names were upheld at the species level. In this revision, the 16 species of *Gasteria* were placed into two sections, *Longiflorae* Haw. and *Gasteria*. The sections are each subdivided into two series, *Longifoliae* (Haw.) Van Jaarsv. and *Multifariae* (Haw.) Van Jaarsv. in the case of section *Longiflorae*, and *Namaquana* Van Jaarsv. and *Gasteria* in the case of section *Gasteria*. The present cladistic analysis has been conducted to obtain a greater understanding of the phylogenetic relationships of the species.

Materials and methods

The 16 species of *Gasteria* were used as terminal taxa (Table 1; cf. van Jaarsveld[6] for the full nomenclatural treatment of the species). Twenty-one vegetative and reproductive morphological characters (Table 2) were included in the analysis, i.e. those which are informative on relationships among the species (Table 3). Character states were polarized by reference to the genus *Poellnitzia* Uitewaal. Smith and van Wyk[2] demonstrated that *Poellnitzia* and *Gasteria* are sister taxa based on four synapomorphies: vegetative reproduction; a scabrid, asperulous or tuberculate leaf surface; a laxly flowered inflorescence; and the absence of floral fragrance.

We followed the cladistic methodology described by Humphries and Funk[7] and Linder.[8] The data matrix (Table 3) was analysed using the Hennig86 programme, which contains several algorithms for inferring phylogenies under the principle of maximum parsimony. All characters were non-additive.

Results and discussion

The data in Table 3 resulted in a single cladogram (Fig. 3) with a consistency index of 86 and a length of 30 character

Fig. 1. *Gasteria disticha* (arrowed), the type species of the genus, photographed near Ashton in the south-western Cape.

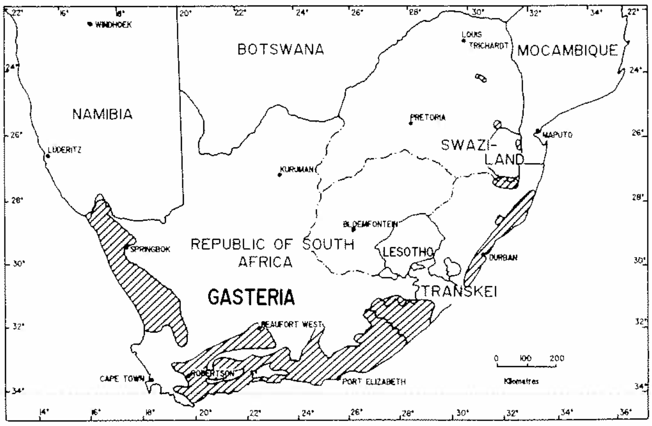

Fig. 2. Geographical distribution of the genus *Gasteria* in southern Africa.

Table 1. Infrageneric classification of *Gasteria* (see ref. 6).

A. *Gasteria* sect. *Longiflorae* Haw.
  I. *G.* ser. *Longifoliae* (Haw.) Van Jaarsv.
    1. *G. batesiana* Rowley
    2. *G. croucheri* (Hook.f.) Bak.
    3. *G. acinacifolia* (Jacq.) Haw.

  II. *G.* ser. *Multifariae* (Haw.) Van Jaarsv.
    4. *G. excelsa* Bak.
    5. *G. pulchra* (Ait.) Haw.
    6. *G. nitida* (Salm-Dyck) Haw.
    7. *G. ellaphieae* Van Jaarsv.
    8. *G. vlokii* Van Jaarsv.
    9. *G. carinata* (Mill.) Duv.
B. *Gasteria* sect. *Gasteria*
  III. *G.* ser. *Namaquana* Van Jaarsv.
    10. *G. pillansii* Kensit
  IV. *G.* ser. *Gasteria*
    11. *G. disticha* (L.) Haw.
    12. *G. brachyphylla* (Salm-Dyck) Van Jaarsv.
    13. *G. bicolor* Haw.
    14. *G. baylissiana* Rauh
    15. *G. glomerata* Van Jaarsv.
    16. *G. rawlinsonii* Obermeyer

Table 2. Characters used in constructing the cladogram in Fig. 3 (autapomorphic characters of the species are described in the caption).

No.	Character	States recognized
1	Regeneration from detached leaves	Absent = 0; present = 1
2	Root shape	Terete = 0; linear-obclavate = 1
3	Leaf arrangement and architecture	Rosulate, leaves indistinctly keeled = 0; rosulate, leaves keeled = 1; more or less distichous, leaves not keeled = 2
4	Leaf shape	Triangular, indistinctly keeled = 0; triangular, distinctly keeled = 1; lorate, not keeled = 2
5	Size of tapering, keeled leaves	200–600 mm = 0; 16–150 mm = 1
6	Leaf margin	Straight = 0; wavy = 1
7	Leaf apex	Pungent-acuminate, triquetrous = 0; acute, keeled = 1; obtuse, not keeled = 2
8	Leaf apex	Straight = 0; incurved = 1
9	Leaf apex	Straight = 0; recurved = 1
10	Leaf maculation	Indistinct = 0; distinct = 1
11	Leaf consistency	Hard = 0; brittle = 1
12	Inner cap of leaf vascular bundle sheath	Sclerenchymatous = 0; parenchymatous = 1
13	Panicle shape	Erect = 0; flat-topped = 1
14	Panicle disposition	Descending = 0; ascending = 1
15	Pedicel at anthesis	Erectly secund = 0; pendulous = 1
16	Perianth symmetry	Weakly zygomorphic = 0; distinctly zygomorphic = 1
17	Perianth shape	Perigon not constricted near the middle (*Poellnitzia*) or if so, then basal portion not narrow elliptical = 0; basal portion narrow elliptical, diameter of basal portion and tube the same, perigon 35–47 mm long = 1; basal portion narrow elliptical, its diameter > that of the tube, perigon 20–33 mm long = 2
18	Perianth shape	Basal portion narrow elliptical = 0; basal portion gasteriform, its diameter approximating that of the tube, perigon 30–45 mm long = 1; basal portion gasteriform, its diameter > that of the tube, perigon 12–30 mm long = 2
19	Perianth shape	Upper half different from lower half = 0; upper half narrow elliptical, approximating lower portion = 1
20	Shape of inner perianth segments	Indistinctly channelled = 0; distinctly channelled = 1
21	Flower colour	Trichromatic = 0; monochromatic = 1

state changes. If generic apomorphies (characters 11, 12, 15, 16 and 20) are excluded, and identical taxa (*G. croucheri*/*G. acinacifolia; G. excelsa*/*G. pulchra; G. ellaphieae*/*G. vlokii; G. disticha*/*G. brachyphylla; G. baylissiana*/*G. glomerata*) are reduced to single entities, the consistency index changes to 90 and the length reduces to 21 character state changes. In presenting our results (Fig. 3), we have included all the taxa and all the characters to show the overall pattern of putative character evolution within *Gasteria*. The genus is clearly distinguished from *Poellnitzia* by eight synapomorphies without reversals and two apomorphies which both reverse only in *G. rawlinsonii*. *Gasteria* is postulated to be monophyletic on the basis of its distinctly maculate, brittle, keeled or lorate leaves, which anatomically have a parenchymatous cap at the leaf vascular bundle. In terms of reproductive morphology all species of *Gasteria* have pendulous pedicels, and the flowers are zygomorphic with distinctly channelled tepals. The two convergences (Table 3, characters 9 and 14) do not appear to be of great consequence. A recurved leaf apex and an ascending inflorescence disposition are known to have evolved independently in a number of the other aloaceous genera.

The phylogenetic analysis of *Gasteria* divided the genus into two major groups, sections *Gasteria* and *Longiflorae*. Each of these two phyletic lines in turn is divided into two groups which are treated here at the series rank. The clade representing section *Longiflorae* (Fig. 3) is rather weakly diagnosed by one character, i.e. narrow elliptical flowers where the diameter of the basal portion and the tube are the same, and the perigon is between 35 and 47 mm long (Fig. 4). Species that are included in section *Longiflorae* occur mainly in the low-altitude subtropical eastern and southern parts of southern Africa and are usually associated with subtropical thicket vegetation. They are only rarely encountered in fynbos and renosterveld. In contrast to section *Longiflorae*, section *Gasteria* is strongly supported by both vegetative and floral characteristics. The species included in this section (Fig. 3) have lorate leaves with obtuse apices, and the leaves are more or less distichously arranged and usually lack a keel. The perianth of section *Gasteria* is usually markedly globose or globose elliptical at the base (Fig. 4). The section is widespread in the arid and semi-arid western, southern and south-eastern Cape, just entering Namibia in the south west. It occurs in succulent Karoo, renosterveld and subtropical thicket.

The subdivision of section *Longiflorae* into the series *Longifoliae* and *Multifariae* is based on perianth characters alone (Fig. 4). Series *Longifoliae*, which consists of three species (Fig. 3), is characterized by narrow elliptical flowers in which the upper half approximates the gasteriform portion. The six species of series *Multifariae* (Fig. 3) have relatively small flowers (20–33 mm long) in which the diameter of the basal portion is greater than that of the tube.

Section *Gasteria* is divided into two series, *Namaquana* and *Gasteria*. They, too, are differentiated mainly by their floral characteristics (Fig. 4). Series *Namaquana* comprises a single species, *G. pillansii*, (Fig. 3) which is clearly separated by its large perianth (30–45 mm), and the gasteriform portion, which is a third or less of the perianth length. Series *Gasteria* (Fig. 3) has flowers of 12–30 mm in length, the gasteriform portion more than half of the perianth length and sometimes abruptly constricted below the gasteriform portion (gasteriform portion rarely narrow-elliptical).

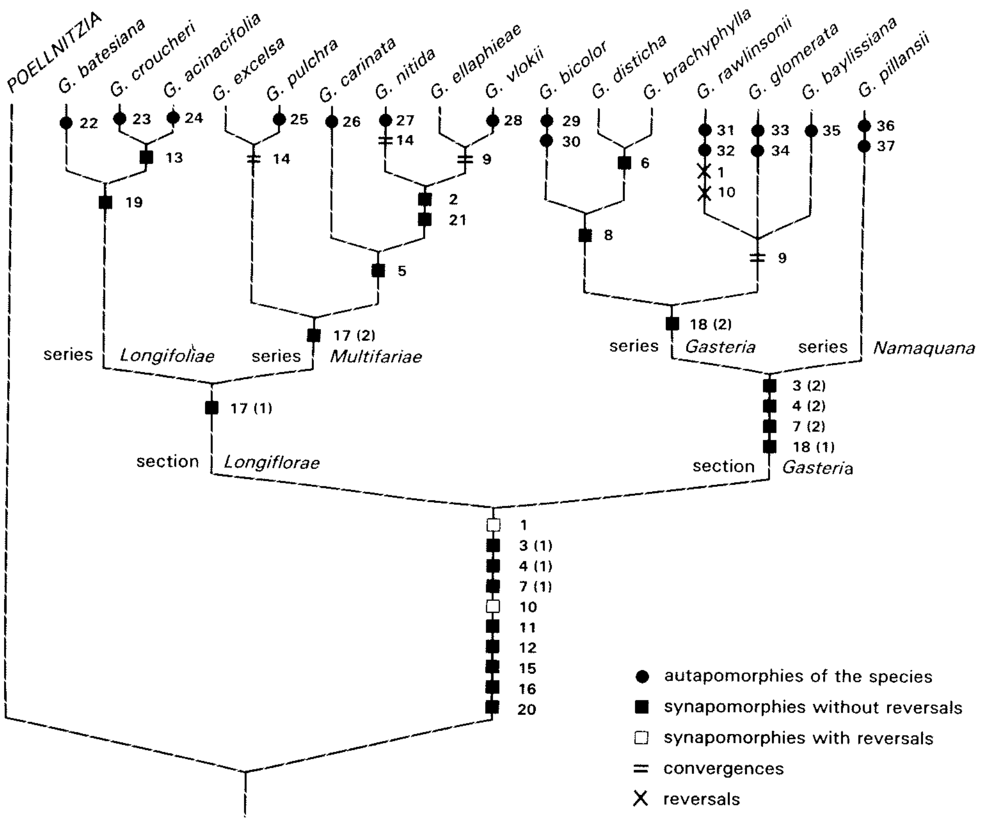

Fig. 3. Cladogram of phylogenetic relationships among the species of *Gasteria*. Numbers 1–21 refer to characters given in Table 3. Autapomorphies of the species are: 22, mature leaves densely rugose-tuberculate, tubercles usually white; 23, leaves glaucescent; 24, seeds large (6–8 mm); 25, leaves linear-triangular or ensiform; 26, leaves smooth with sparingly arranged tubercles; 27, leaf margin entire; 28, leaves falcate; 29, short decumbent stem; 30, leaves twisted sideways; 31, stem pendulous; 32, leaf margin sparingly denticulate; 33, leaf margin entire except for apex; 34, sea-green leaf colour; 35, mature leaves densely rugose-tuberculate, tubercles concolorous; 36, inner perianth segments constricted; 37, capsule large (35–43 mm).

The distinction between sections *Gasteria* and *Longiflorae* is not always clear-cut, especially in the south-western Cape. For example, *G. disticha* in the southern part of its distribution range has flowers which come close to *G. carinata* (series *Multifariae*, section *Longiflorae*). The gasteriform portion of the perianth of *G. disticha* plants from this region is often narrow-elliptical and not unlike those of *G. carinata*, which might be the result of reticulate evolution.

The recommended phylogenetic solution, to recognize

Table 3. Phylogenetic character states of the species of *Gasteria*. *Poellnitzia* was chosen as the outgroup (see Fig. 2 in ref. 2). Characters and their states are numbered as in Table 2. Autapomorphic characters of the species are described in the caption to Fig. 3.

	Character number				
Taxon	1 2 3 4 5	6 7 8 9 10	11 12 13 14 15	16 17 18 19 20	21
Poel	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0 0 0 0 0	0
Bate	1 0 1 1 0	0 1 0 0 1	1 1 0 0 1	1 1 0 1 1	0
Crou	1 0 1 1 0	0 1 0 0 1	1 1 1 0 1	1 1 0 1 1	0
Acin	1 0 1 1 0	0 1 0 0 1	1 1 1 0 1	1 1 0 1 1	0
Exce	1 0 1 1 0	0 1 0 0 1	1 1 0 1 1	1 2 0 0 1	0
Pulc	1 0 1 1 0	0 1 0 0 1	1 1 0 1 1	1 2 0 0 1	0
Niti	1 1 1 1 1	0 1 0 0 1	1 1 0 1 1	1 2 0 0 1	1
Ella	1 1 1 1 1	0 1 0 1 1	1 1 0 0 1	1 2 0 0 1	1
Vlok	1 1 1 1 1	0 1 0 1 1	1 1 0 0 1	1 2 0 0 1	1
Cari	1 0 1 1 1	0 1 0 0 1	1 1 0 0 1	1 2 0 0 1	0
Pill	1 0 2 2 0	0 2 0 0 1	1 1 0 0 1	1 0 1 0 1	0
Dist	1 0 2 2 0	1 2 1 0 1	1 1 0 0 1	1 0 2 0 1	0
Brac	1 0 2 2 0	1 2 1 0 1	1 1 0 0 1	1 0 2 0 1	0
Bico	1 0 2 2 0	0 2 1 0 1	1 1 0 0 1	1 0 2 0 1	0
Bayl	1 0 2 2 0	0 2 0 1 1	1 1 0 0 1	1 0 2 0 1	0
Glom	1 0 2 2 0	0 2 0 1 1	1 1 0 0 1	1 0 2 0 1	0
Rawl	0 0 2 2 0	0 2 0 1 0	1 1 0 0 1	1 0 2 0 1	0

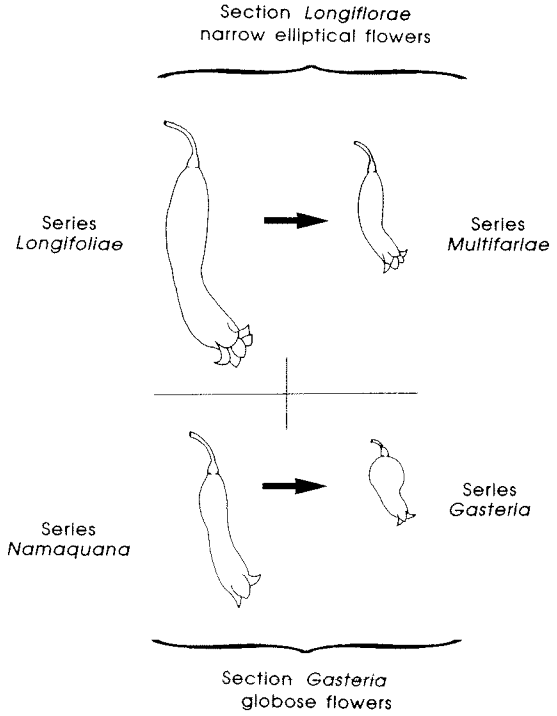

Fig. 4. Postulated phylogenetic transformation series in the flowers of *Gasteria*.

Gasteria as consisting of two sections, each divided into two series, has practical merit, especially on grounds of taxonomic utility. Differentiation within *Gasteria* has occurred in reproductive and vegetative characters; both character sets are to a greater or lesser extent useful in diagnosing clades. Much of the evolution can therefore be related to pollination characters, whilst edaphic factors, palaeoclimate, herbivory and fire seem to be reflected in the large number of vegetative characters, accounting for much of the intrageneric diversity.

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The role of natural history museums in preserving biodiversity in South Africa

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Natural history museums and their collections should be regarded as an important component of the environmental conservation network. South Africa is a signatory of the Rio Convention and has an obligation to develop strategies for the conservation of biodiversity. A survey was carried out to determine the role that South African natural history museums currently play in the conservation of biodiversity. Several important aspects were examined: mission statements and goals; the adequacy of the taxonomic work-force to meet South Africa's present and future requirements; the computerization of collections; the utilization of collections for research; and the transfer of information through scientific publications. The biodiversity crisis offers natural history museums a unique opportunity to prove their value and draw attention to the urgent need for the establishment of a national biodiversity network. The prioritization of goals and focused education and research programmes are essential. The existing taxonomic work-force is inadequate to meet present requirements. This problem must be addressed urgently if we are to inventorize our national biodiversity over the next two decades. Co-ordinated data base development is an essential initial step in mobilizing collections for efficient management and conservation. Currently, zoological collections are under-utilized by the research community. Increased use of the collections must be encouraged. The publication of scientific papers that use museum collection material can help to achieve this, besides benefiting overall scientific knowledge which is the base of education. Change is inevitable and natural history museums will have to adapt.

The biodiversity crisis is rapidly attaining priority status in the environmental community throughout the world, focusing attention on the urgent need to inventorize and describe all living species. It is estimated that the 1.4–1.8 million species of living organisms described by scientists represent less than 15% of those that actually exist.[1] The present rate of biotic extinction threatens the world with the estimated loss of 25% of the present plant and animal species in the next 50 years.[2] The increase in the awareness of the importance of preserving biodiversity has highlighted the crucial role of the backbone of almost every natural history museum — the biological collections. Museum collections provide a physical data base of a nation's biodiversity and offer spatial and temporal perspectives, which are potentially valuable in developing conservation strategies.

Taxonomy, the science of classifying organisms, has a key role to play in the world-wide conservation of biodiversity: providing the documentation of biodiversity, the record of which species exist and which have become extinct. In addition, taxonomy provides a framework for investigating phylogenetic relationship among species. The related science of systematics describes evolutionary relationships and the processes that underlie these observed patterns. Natural history collections are the primary resource for systematics.[3]

Despite the fact that natural history museums hold centuries' worth of biodiversity data in collections, libraries, archives and technical data bases, they may be perceived by some as unaffordable luxuries. Changing economic circumstances, particularly in Third World countries, are making it increasingly necessary for museums to justify their existence and to be seen to play an active and productive role in both public and scientific arenas. South Africa is facing a period of considerable political change and a subsequent alteration of priorities and administration. Scientific institutions, including natural history museums, already have faced substantial reductions in funding and have come to the realization that they too have to 'prove their value' both to the public and scientific communities.

South Africa is a signatory to the international Convention on Biological Diversity, which resulted from the United Nations Conference on Environment and Development (UNCED) held in Rio de Janeiro in June 1992. An important obligation of the signatories to the Convention is the development of national, regional and local strategies for the conservation and sustainable use of biodiversity. In addition, the World Conservation Union's (IUCN) Global Biodiversity Strategy calls for the establishment of strategies in all countries by the year 2000, and a comprehensive world ***in situ*** and ***ex situ*** genetic conservation system to be operational by 2010. Consequently, South African governmental and non-governmental agencies