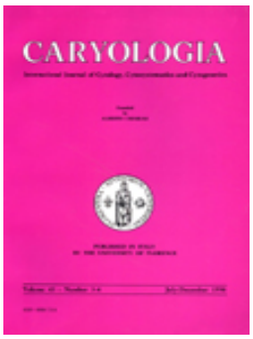

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Canio G. Vosa & Simon T. Bennett

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CHROMOSOME STUDIES IN THE SOUTHERN AFRICAN FLORA. 58-94. CHROMOSOME EVOLUTION IN THE GENUS *GASTERIA* DUVAL

CANIO G. VOSA and SIMON T. BENNETT
Department of Plant Sciences, University of Oxford, Oxford, England.

SUMMARY — A cytological analysis of thirty-seven accessions of *Gasteria* has shown that this genus is very uniform chromosomally. All the species have a bimodal karyotype of eight large and six small chromosomes. Karyotype variability between the species is no more than that found between individuals of a single species showing that *Gasteria* is composed of taxa more closely related than in other genera.

INTRODUCTION

The genus *Gasteria* Duval is closely allied to *Aloe* L. and includes about forty species all found in South Africa. *Gasteria* are small to medium sized, stemless or short stemmed succulent plants. The genus was established by DUVAL (1809) and the name refers to the Greek word γαστηρ (gaster = a belly) from the peculiar swollen base of the flower tube. *Gasteria* has been somewhat neglected by taxonomists and indeed it is a difficult genus to classify owing to the difficulty of obtaining satisfactory herbarium specimens. Any meaningful classification of the genus, except possibly for a few well defined species, must rely on living collections. The comment by BERGER (1908) summarizes the situation in the genus: *Gasteriae e nullo modo satis cognitae genus difficillimum formant.* Apart form the original work by DUVAL (1809), there is a Synopsis by HAWORTH (1812) and other accounts by BAKER (1880) and THISELTON-DYER (1896). The most modern taxonomic works on the genus are those by BERGER (1908) and by VON POELLNITZ (1938).

The present work includes chromosome studies in thirty-seven taxa of which twelve are as yet undetermined. Since the scope of the present account is chromosome evolution in the genus as a whole, it has been considered convenient and meaningful to include the unnamed accessions.

MATERIAL AND METHODS

All the taxa are kept as living specimens in the Department of Plant Sciences of the University of Oxford and as living specimens and herbarium vouchers in the Compton Herbarium of the National Botanic Gardens, Kirstenbosch, South Africa.

For cytological preparations actively growing root-tips were pretreated in an aqueous solution of 0.05% colchicine for 4 hours at room temperature (18°C ± 3°C), fixed in 1:3 acetic alchol overnight and then stained in Feulgen. In the diagrammatic illustrations of haploid karyotypes the nucleolar organizers are represented by solid circles.

RESULTS

58. *Gasteria maculata* Haw.

Chromosome number: $2n = 14$.

Origin of material: Cape - 3325 (Steytlerville): Betheldorp, P.E. (-DC), E.J.v. Jaarsveld 6847A.

Observations: In the chromosome complement of this species it is difficult to distinguish between chromosome pairs L2 and L3, both of which have distally located allocyclic segments in their short arms. Chromosome S2 has an allocyclic segment in the distal half of is long arm.

59. *Gasteria nigricans* Haw.

Chromosome number: $2n = 14$.

Origin of material: Cape - 331 (Ladismith): 24 m.E. of Barrydale (-CC), Mrs Thomas s.n.

Observations: The karyotype of this species is similar to that of *G. maculata*, except that there is a small allocyclic constriction in the short arm of chromosome L1.

60. *Gasteria verrucosa* Duval

Chromosome number: $2n = 14$.

Origin of material: Cape - 3420 (Bredasdorp): De Hoop, Swellendam District (-AD), NBG exp.

Observations: In this species, allocyclic constrictions are visible in the short arms of chromosomes L1 and L2 and in the long arms of S1 and S2. It is difficult to distinguish between chromosomes L3 and L4.

61. *Gasteria ernest-ruschii* Dinter & Poelln.

Chromosome number: $2n = 14$.

Origin of material: Numeis (Nabibia), H. Hall s.n.

Observations: Chromosomes L2 and L3 are very similar with allocyclic constrictions in their short arms. There are no apparent allocyclic segments in the S-chromosomes.

62. ***Gasteria armstrongii*** **Schoenland**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3424 (Humansdorp): Jeffrey Bay (-BB), E.J.v. Jaarsveld 6960.

Observations: There is a small allocyclic constriction in the short arm of chromosome L2.

63. ***Gasteria pulchra*** **Haw.**

Chromosome number: $2n = 14$.

Origin of material: Fraser's Camp, Grahamstown, F. Stayner 1581/60.

Observations: In this species, there are allocyclic constrictions in the short arms of chromosomes L1 and L2 and distally located allocyclic segments in the long arms of chromosomes S2 and S3.

64. ***Gasteria schweikerdtiana*** **Poelln.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3422 (Mosselbaai): Great Brak River (-AA), Stellenbosch University s.n.

Observations: Allocyclic constrictions are found in the short arms of chromosomes L1 and L2 and in the long arms of all S-chromosomes.

65. ***Gasteria croucheri*** **Bak.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3423 (Knysna): The Heads (-AA), E.J.v. Jaarsveld 6891.

Observations: In this species the short arms of the L1 chromosomes have a small allocyclic constriction. Distally located allocyclic segments are found in the short arms of chromosomes L2 and L3 and in the long arms of chromosomes S1 and S3.

66. ***Gasteria batesiana*** **Rowley**

Chromosome number: $2n = 14$.

Origin of material: Cape - 2630 (Stegi): Umbulumipoort (-BD), Swaziland, R.H. Compton 788/59.

Observations: The karyotype of this species resembles that of *G. schweikerdtiana* with only minor differences.

67. ***Gasteria liliputana*** **Poelln.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3326 (Grahamstown): Pluto's Vale (-BA), C.L. Scott s.n.

Observations: The S2-chromosome of this species has a small allocyclic constriction in its long arm.

68. ***Gasteria loeriensis*** **Poelln.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3325 (Steytlerville): Gantoosriver (-CC), E.J.v. Jaarsveld 6861.

Observations: Chromosomes L1 and L2 have allocyclic constrictions in their short arms.

69. ***Gasteria longiana*** **Poelln.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3326 (Grahamstown): Pluto's Vale (-BA), H. Hall s.n.

Observations: The karyotype of this species is well within the range of variation found in the genus.

70. ***Gasteria pillansii*** **Kensit**

Chromosome number : $2n = 14$.

Origin of material: Cape -3218 (Clanwilliam): 6 km S. of Clanwilliam (-BB), E.J. v. Jaarsveld 7011.

Observations: In this species there is a small allocyclic constriction in the short arm of chromosome L1.

71. ***Gasteria translucens*** **Haw.**

Chromosome number: $2n = 14$.

Origin of material: Transvaal -2732: J.G. Strydom Dam (-AC), M. Strydom s.n.

Observations: Distally located allocyclic segments are found in the short arms of chromosomes L2 and L3 and in the long arm of chromosome S3.

72. ***Gasteria decipiens*** **Haw.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3324 (Steytlerville): Loerie (-DD), E.J. v. Jaarsveld 6849.

Observations: The karyotype of this species resembles that of *G. loeriensis*

with small allocyclic constrictions in the short arms of chromosomes L1 and L2. It is very difficult to distinguish between the chromosomes S1 and S2. Chromosome S3 is almost metacentric.

73. ***Gasteria chamaegigas* Poelln.**

Chromosome number: $2n = 14$.

Origin of material: Mekay Bridge (Port Elizabeth), F. Stayner 139/59.

Observations: In the chromosome complement of this species allocyclic segments are found in the terminal regions of the short arms of chromosomes L1, L2 and L3 and in the long arms of S1 and S2.

74. ***Gasteria marmorata* Bak.**

Chromosome number: $2n = 14$.

Origin of material: Cape -3326 (Grahamstown): Kommittees Drift (-BB), E.J.v. Jaarsveld 6820.

Observations: The L1-chromosome has a small allocyclic constriction in its short arm. There are no apparent allocyclic regions in the S-chromosome complement.

75. ***Gasteria acinacifolia* Haw.**

Chromosome number: $2n = 14$.

Origin of material: Cape -3324 (Steytlerville): Hankey (-DD), E.J.v. Jaarsveld 6850.

Observations: In this species there is a distinct allocyclic 'gap' in the short arm of chromosome L1. There is a small allocyclic constriction in the short arm of chromosome L2. Chromosomes S1 and S2 are indistinguishable with distinct allocyclic segment in their long arms.

76. ***Gasteria rowlinsonii* Oberm.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3324 (Steytlerville): Baviaanskloof, G.J. Rossouw 584.

Observations: Chromosome L2 has a small allocyclic constriction in its short arm.

77. ***Gasteria salmodyckiana* Poelln.**

Chromosome number: $2n = 14$.

Origin of material: Cape -3326 (Grahamstown): 30 km S. of Grahamstown (-BC), H. Hall s.n.

Observations: This species is characterized by distally located segments in

the short arm of chromosome L2 and the long arm of S3. Chromosome S2 has a small allocyclic constriction in its long arm.

78. ***Gasteria repens* Haw.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3421 (Caledon): Gouritzriver Mouth (-DA), F. Stayner s.n.

Observations: The L-chromosome complement of this species has no apparent allocyclic regions. All S-chromosomes have distal allocyclic segments on their long arms.

79. ***Gasteria baylissiana* Rauh.**

Chromosome number: $2n = 14$.

Origin of material: Cape -3325 (Port Elizabeth): Oudekraal, Somerset East (-DA), the type plant, N.B.G.

Observations: There are no apparent allocyclic regions in the karyotype of this species.

80. ***Gasteria excelsa* Bak.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3327 (Peddie): Chalumna Police Station (-BA), E.J.v. Jaarsveld 6829.

Observations: The karyotype of this species is well within the range of variation found in the genus.

81. ***Gasteria disticha* Haw.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3319 (Worcester): 2 km from Nuy Station (-DA), leigit F. Stayner (E.J.v. Jaarsveld 4654).

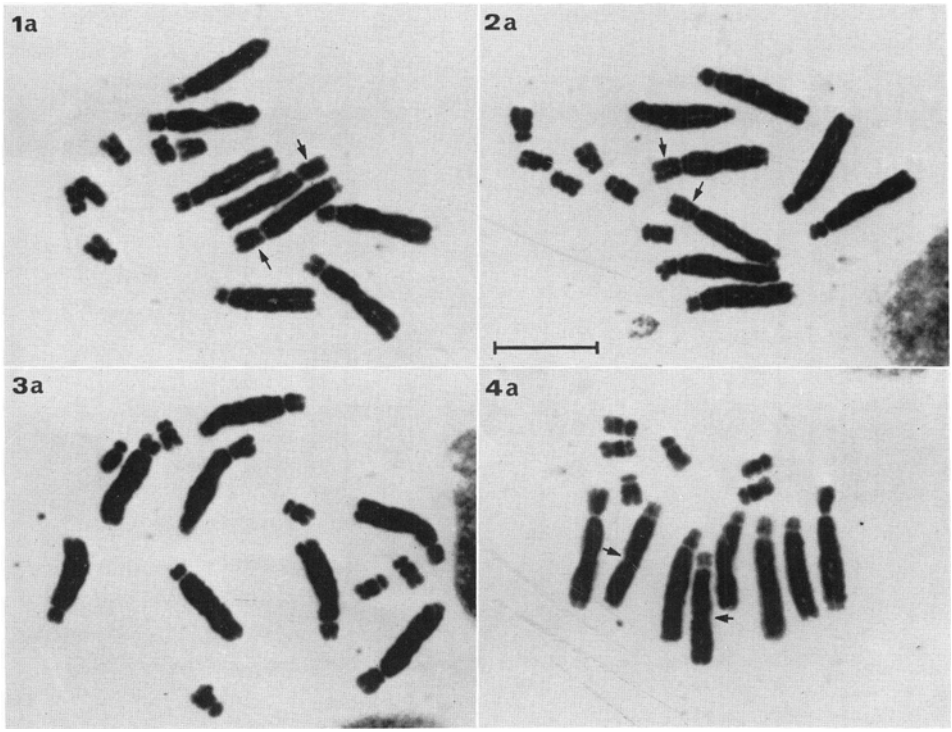
Observations: Chromosome L2 has a small allocyclic contriction in its short arm. Chromosome S2 has a terminal allocyclic segment in its long arm.

82. ***Gasteria fusco-punctata* Bak.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3327 (Peddie): Msenge Ridge, Kingwilliamstown (-CD), D.M. Commins 1710.

Observations: This species has small allocyclic constrictions in the short arm of L1 and the long arm of S1. Larger allocyclic constrictions are found in the short arm of chromosome L2 and the long arm of chromosome S3. Allocyclic segments are found in the distal half of the short arm of chromosome L4 and the long arm of S2 (Figs. 1a, 1b).



Figs. 1a - 4a. — Mitotic metaphases in some *Gasteria* taxa; the bar represents 10 µm. 1a. *G. fusco-punctata* Bak. Note the small allocyclic constrictions in the short arms of L1 (arrows). 2a. *Gasteria* sp. M.B. Bayer 380/76. Note the small allocyclic constrictions in the short arms of L1 (arrows). 3a. *Gasteria* sp. E.J.v. Jaarsveld 4152. 4a. *Gasteria* sp. J. Dekenah s.n.. Note the allcyclic constrictions in the long arms of L3 (arrows).

83. ***Gasteria* sp.**

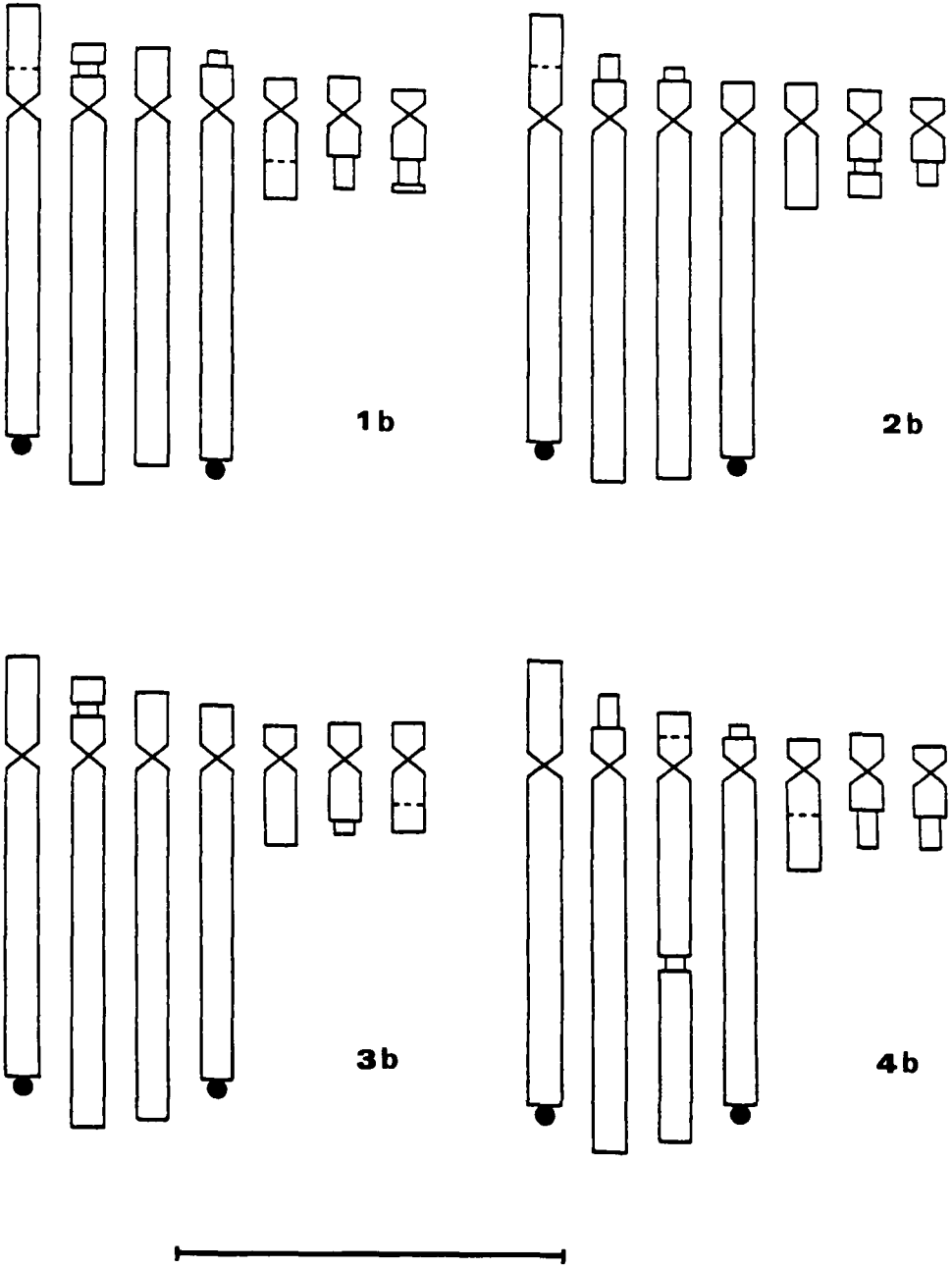
Chromosome number: $2n = 14$.

Origin of material: Swartwater, M.B. Bayer 380/76 (KG).

Observations: This taxon has a small allocyclic constriction in the short arm of chromosome L1. Chromosomes L2 and L3 have small distally located allocyclic segments on their short arms. The S2-chromosome has an allocyclic constriction in its long arm and the distal half of the long arm of chromosome S3 is allocyclic (Figs. 2a, 2b).

84. ***Gasteria* sp.**

Chromosome number; $2n = 14$.



Figs. 1b - 4b. — Diagrams of haploid karyotypes in some *Gasteria* taxa, the bar represents 10 µm. 1b. *G. fusco-punctata* Bak. 2b. *Gasteria* sp. M.B. Bayer 380/76. 3b. *Gasteria* sp. E.J.v. Jaarsveld 4152. 4b. *Gasteria* sp. J. Dekenah s.n.

Origin of material: Cape - 2816 (Oranjemund): Hellskloof (-BB), E.J.v. Jaarsveld 4152.

Observations: The karyotype of this taxon is characterized by the presence of small allocyclic constrictions in the short arm of chromosome L2 and in the long arm of chromosome S3. Chromosome S2 has a small distal allocyclic segment in its long arm (Figs. 3a, 3b).

85. ***Gasteria* sp.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3321 (Ladismith): Huis River Pass (-BC). R.D. Kraty 10/77.

Observations: The karyotype of this taxon is well within the range of variation found in the genus.

86. ***Gasteria* sp.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3319 (Worcester): De Wet (-DA), legit F. Stayner (E.J.v. Jaarsveld 4512).

Observations: Chromosome L2 has an allocyclic constriction in its short arm.

87. ***Gasteria* sp.**

Chromosome number: $2n = 14$.

Origin of material: Duiwehoksrivier (S. Cape), Mrs Thomas s.n.

Observations: In this taxon allocyclic regions are found in the short arms of chromosomes L1, L2 and L3 and in the long arms of chromosomes S1 and S2.

88. ***Gasteria* sp.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3326 (Grahamstown): Naude's Hoek, Alice (-BB), E.J.v. Jaarsveld 6823.

Observations: Small distal allocyclic segments are found in the short arms of chromosomes L2 and L3. The S-chromosomes are characterized by allocyclic regions in their long arms.

89. ***Gasteria* sp.**

Chromosome number: $2n = 14$.

Origin of material: Gemsbokvlei, Richtersveld, F. Kuehnel s.n.

Observations: The karyotype of this taxon is well within the range of variation found in the genus.

90. ***Gasteria* sp.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3420 (Bredasdorp): Melkbos (-AC), E.J.v. Jaarsveld 7024.

Observations: Chromosome S1 has a small allocyclic segment in its long arm.

91. ***Gasteria* sp.**

Chromosome number: $2n = 14$.

Origin of material: Natal - 2930 (Pietermaritzburg): Schogweni Dam (-DC), R.C. Walch s.n.

Observations: Allocyclic regions are found in the short arms of chromosomes L2 and L3 and in the long arms of the chromosomes S2 and S3.

92. ***Gasteria* sp.**

Chromosome number: $2n = 14$.

Origin of material: Cape -3325 (Steytlerville): Southkloof, Addo (-DA), E.J.v. Jaarsveld 6852.

Observations: The L1-chromosome has a small allocyclic constriction in its short arm. Small distal allocyclic segments are found in the short arms of chromosomes L2 and L3. It is difficult to distinguish between the S-chromosomes which all have allocyclic constrictions in their long arms.

93. ***Gasteria* sp.**

Chromosome number: $2n = 14$.

Origin of material: Cape - 3420 (Mosselbaai): Gourily River Mouth, J. Dekenah s.n.

Observations: The karyotype of this taxon is unusual in that chromosome L3 has a prominent allocyclic segment in its long arm (Figs 4a, 4b). The long arms of all the S-chromosomes have allocyclic segments.

94. ***Gasteria* sp.**

Chromosome number: $2n = 14$.

Origin of material: Natal - 3030 (Port Shepstone): Oribi Gorge (-CA), E.J.v. Jaarsveld 3887.

Observations: Characteristically, all chromosomes in this taxon appear to have allocyclic segments. Further investigation is needed.

DISCUSSION

The results show that the genus *Gasteria* is very uniform chromosomally. All the thirty-seven accessions in this study have a bimodal karyotype of $2n = 14$ composed of eight large subterminal chromosomes (L-) and six small submedian chromosomes (S-). The centromeric position nomenclature is that suggested by LEVAN *et al.* (1964). The index of bimodality, calculated as in BRUYNS and VOSA (1987), shows little variability (79.3 to 85.9 with a mean of 82.9), with a variance curve approaching normality but with a tendency to increase in parallel with the total genome length. This is confirmed in Diagram 1 where the relationship between the relative total genome length and the relative length of the L- and S-chromosomes shows that the total length of the

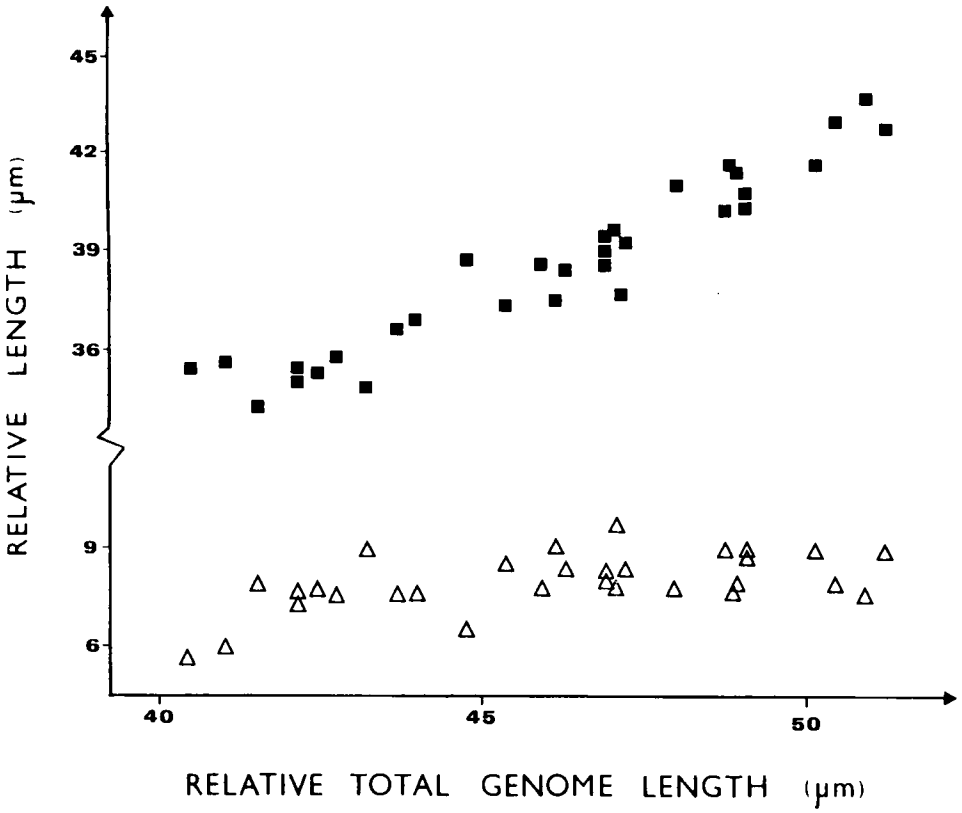


Diagram 1. — Relative total length and its relationship to the relative length of the L- (■) and S-chromosomes (△) in *Gasteria*.

genome increases proportionally to the length of the L-chromosomes. A similar relationship has been described in the related genus *Aloe* by BRANDHAM (1983).

The slight variability is probably not more than that found between the individuals of a normal natural population of a single species. This implies that *Gasteria* is composed of taxa which are rather more closely related than in other genera.

The close relationship is mirrored in the fact that in all the thirty-seven accessions the nucleolar organizers are located distally on the long arms of chromosomes L1 and L4. Further, interspecific hybridization in this genus shows a maximum of pairing with regular bivalent formation and with high fertility (BRANDHAM 1983).

The most noticeable variation between the species are the allocyclic segments found mostly in the short arms of chromosomes L2, L3 and 4 and in most long arms of the S-chromosomes (Figs. 1 - 4). In some of the accessions, there is a small allocyclic segment towards the middle of the short arm of chromosome L1 (e.g. Figs. 1 and 2). In one accession (Dekenah s.n.) there is a prominent allocyclic segments located about the middle of the long arm of chromosome L3 (Figs. 4a, 4b).

The allocyclic segments in *Gasteria* behave as the segments described by DYER (1963) in *Hyacinthus litwinowii* and in *Tulbaghia alliacea* (= *T. verdoornia*) and are under-contracted both at prophase and early to middle colchicine metaphase. At late metaphase/anaphase, they are indistinguishable from normal euchromatin. As in *H. litwinowii* and in *T. alliacea*, they are not connected with classical heterochromatin.

Such segments may provide good diagnostic characters to distinguish the various species, they are usually homozygous and have been found and described in the allied genera *Aloe* (VOSA and MOGFORD 1981; VOSA 1982) and *Haworthia* (VOSA and BAYER 1981, 1986). Their significance and function are not known.

CONCLUSIONS

BERGER (1908) correctly states that *Gasteria* is a very difficult genus taxonomically (see Introduction). The results of the present study confirm this difficulty from the cytological point of view. All the species of *Gasteria* have a uniform bimodal chromosome complement with a constant index of bimodality and only some small but significant indications of chromosome evolution. This uniformity most probably reflects, at least in part, the propagation strategy of the genus. This includes a remarkable and very efficient vegetative reproduction: leaf fragments readily produce offshoots from their broken margin. Sexual reproduction is efficient and, at least in some species, there is no self-incompatibility.

Perenniality and relative hardiness, combined with the climatological stability of Southern Africa over the geological eras, contribute to the morphological and cytological uniformity of the genus *Gasteria*.

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