

# INTERRELATIONSHIPS AND EVOLUTION OF THE TRIBE ALOINEAE AS REFLECTED IN ITS CYTOLOGY

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## INTRODUCTION

The two families Liliaceae and Amaryllidaceae have undergone considerable changes in systematic position as proposed by different taxonomists. The principal controversies involve the basic criteria for the identification of the different genera under the two families. The original contention regarding the character of the ovary—superior and inferior ovary as the delimiting characteristic of the two families (Engler & Prantl, 1930)—has been questioned by Hutchinson (1959). He has regarded the character of the inflorescence as the diagnostic feature and consequently the systematic position of the different genera has been changed considerably. Several genera have been transferred from one family to the other irrespective of the nature of the ovary. Several others have been taken out from both the families and new families have been constituted out of them. With regard to these families, Hutchinson's system differs from that of Engler and Prantl in the position of the different constituent genera as well as in the scope and delimitation of the families. The creation of a new family, such as Agavaceae by Hutchinson, has been fully justified on cytological grounds.

In spite of the difference in outlook of the different taxonomists with regard to these two families, the position of the Aloineae, constituted principally of three genera, namely, *Gasteria*, *Haworthia* and *Aloë*, has undergone little change in taxonomy. These taxa have been included by all the authors under one tribe, viz. the Aloineae (Hutchinson, 1959) or Aloeae (Engler & Prantl, 1930). In the two principal systems, this tribe has been assigned a position near Kniphofeae and Hemerocallideae of Liliaceae. A distinct family Aloeaceae was proposed by Nakai in 1936 (cf. Aloinaceae). In Engler's system the origin of Aloineae has been traced from the Asphodeloideae of the Liliaceae. Hutchinson too has considered Asphodeloideae as a very successful tribe of the Liliaceae giving rise to different taxa including the Aloineae, which represents an advanced level though maintaining the primitive rhizomatous character (Hutchinson, 1959, p. 592). However, he has also admitted that to trace the phylogeny of the various groups of the Liliaceae (on taxonomic grounds) at present would be premature. Even though the Aloineae represents undoubtedly a natural assemblage, a critical and exhaustive monograph is still lacking. Only the South African representatives, which grow wild, have been critically studied by Reynolds (1950).

These three genera resemble each other in their external morphology as well as in ecology. They can be identified mainly by the nature of the perianth. They are all succulents occurring in the tropical and subtemperate zones and are cultivated for ornamental purposes throughout the world.

All three genera are characterised by chromosome numbers with a basic set of 7. The deep seated number is  $2n=14$ . Riley's analysis shows that the genus *Gasteria* is characterised by almost universally diploid species, *Aloe* by mostly diploid and a few polyploid, and *Haworthia* by diploid with a considerable frequency of polyploids. In spite of the presence of a large number of species (Riley, 1945, 1947, 1948a, b, 1950, 1958a, b, 1959a, b, c, 1960a, b) not a single case of aneuploidy has been reported. The striking uniformity in cytology makes the Aloineae a natural assemblage.

The chromosome morphology is also very distinct. All genera show marked asymmetry in the karyotype. The chromosome complement shows an abrupt size difference, being represented by eight very long and six very short chromosomes. Most chromosomes possess submedian to subterminal primary constrictions. This unequal arm ratio, though varying to a certain extent, is maintained in all three genera. If evolution should involve a change from symmetry to asymmetry, as postulated by Levitsky (1931a, b), Navaschin (1932) and others, the advanced level of the Aloineae is unquestionable. Intergeneric hybrids have been reported in a number of cases showing that the assemblage is a natural one. Hybrids are formed out of such crosses, and chromosome pairing too has been observed. Formation of seven bivalents by crossing species of two genera with  $n=7$  chromosomes in each is an index of their homology. All these factors, taken together, emphasize the relationships between the major taxa of the tribe.

In spite of the success in hybridization at an intergeneric level, data from this aspect is rather meagre because hybridization is limited by the production of nonviable gametes in the two parents. Most species reproduce principally by vegetative means and continued cultivation under horticulture has possibly eliminated their capacity for sexual reproduction. Meiosis is abnormal for nearly all the species where it could be studied and seed formation is scarce.

The purpose of undertaking the present investigation has been manifold. Due to the similarity in the karyotypes of the different taxa, in the absence of any numerical variation, the mechanism of speciation of these successful genera is problematic. Gene mutation has been considered to be the principal means of speciation in this tribe. The importance of this process in the origin of new species of plants is unequivocally accepted. But even so it has been thought desirable to find out the extent to which this process alone is affecting the mechanism of speciation.

In recent years a considerable amount of evidence has accumulated showing that structural changes in chromosomes have played a significant role in evolution. A review of the recent data shows that the importance of this process was not properly assessed in the past though its scope in the origin of species was already known. Lately, the invention of a number of pretreatment schedules has been helpful in a detailed study of the karyotype, and the clarification of the minute differences in the chromosome morphology is at present quite possible. Not only between species, but even between varieties and strains of the same species, detectable chromosomal differences have been established. The tribe Aloineae, with a uniform chromosome number in different taxa, provides ideal material for investigations on differences in chromosomal

structure. Though apparently identical to a significant extent, it was thought possible that the application of pre-treatment methods may reveal minute differences between the chromosome complements. In order to study the detailed karyotype and meiosis for a proper assessment of their mechanism of speciation and the taxonomic status of these genera, the present work was undertaken.

Methods of propagation of the three genera are interesting. Under conditions of cultivation, sexual reproduction is nearly obsolete, vegetative means of propagation being obligatory. Numerous publications from this laboratory have shown that plants reproducing through vegetative means harbour altered chromosome complements within the somatic tissue which effectively help in the origin of new genotypes through vegetative propagation. The members of the Aloineae, with a similar method of propagation, evidently require investigation from this aspect to assess the scope of vegetative reproduction in their evolution.

#### MATERIAL AND METHODS

The present investigation includes forty species and varieties of *Aloe*, *Haworthia* and *Gasteria*. The species worked out here have been properly identified and verified from the Indian Botanical Gardens at Shibpur. Most of them are succulents and some of them are horticultural. The genera reproduce both by vegetative and sexual means, though seed formation is lacking in most cases.

The materials were collected from Imperial Nursery, Calcutta, Chandra Nursery, Kalimpong and Ghosh's Nursery, Darjeeling, and also from private gardens. The plants were grown in earthenware pots containing loam and sand. A sufficient quantity of gravel was put under the pot to provide good drainage.

For the study of somatic chromosomes healthy root tips were obtained. The peak period of mitotic division has been found to be between 12 noon and 2 p.m. For temporary preparations, trials were made with various pretreating chemicals such as aesculine, oxyquinoline, para-dichlorobenzene, etc. with different concentrations and varying periods of time (Sharma and Bal, 1953; Tjio and Levan, 1950; Sharma and Mookerjea, 1955), of which para-dichlorobenzene gave the best results.

Healthy root-tips were treated with saturated para-dichlorobenzene solution for 10 mins. at 2-4°C, then for 3 hours at a temperature of 18-20°C. The root-tips were then fixed in acetic-alcohol (1:2) for half an hour and heated gently in a mixture of 2% aceto-orcein and (N)HCl in the proportion 9:1 for 5-6 seconds and kept in that mixture for 1 hour or more. Subsequently they were squashed in 1% aceto-orcein solution, sealed and observed. Permanent preparations of these temporary squashes were made by inverting the slides in normal butyl alcohol after 1 or 2 days when the squash preparation became dry. When the coverslip was detached, both the cover-slip and the slide were mounted separately in euparal.

For permanent preparations, the root-tips were fixed in Levitsky's fixative—1% chromic acid and 10% formalin (1:1). Better results were obtained, however, if oxyquinoline (0.002 M) was added (fixative 3 parts: oxyquinoline 1 part) and if the

preparations were cooled (18-20°C) for an hour before overnight fixation at room temperature (Sharma and Ghosh, 1950).

Meiosis was studied both from temporary and permanent preparations. The peak period of division of meiotic chromosomes was found to be between 12 noon and 2 p.m.

For temporary preparations, buds of suitable size were smeared in 1% aceto-carmine solution. For permanent preparations, the buds were smeared and fixed in Navashin's A and B solutions (1:1) for 3-4 hours, washed in running water and stained according to Newton's crystal violet method.

For both root-tips and flower buds paraffin sections were cut at a thickness of 14 $\mu$ . The slides were stained following the usual schedule of Newton's crystal violet technique.

The mitotic figures were drawn at a table magnification of approximately  $\times 1950$  using a Zeiss microscope with a compensating eye-piece of 12.5, an apochromatic objective of 1.3 N.A. and an aplanatic condenser of 1.2 N.A. Photomicrographs were taken at a magnification of  $\times 1200$  (approx.). The meiotic figures have been drawn at a magnification of  $\times 900$ .

In the drawings, chromosomes bearing secondary constrictions or satellites and with heterochromatic gaps have only been drawn in outline and non-homologous chromosomes have been distinguished by stripes.

#### OBSERVATIONS

The different species and varieties of the three genera so far investigated show a uniform chromosome number of  $2n=14$  with a high degree of structural heterogeneity, except for a few cases where polyploidy has been noted. In some cases inconstancy in the chromosome complements within the same species have been frequently met with. The normal number in such cases is held to be the one present in the highest frequency. A detailed karyotype analysis of the different species and varieties reveals a gross similarity in the chromosome complement. 8 chromosomes are distinctly large and 6 are distinctly small, though in a few cases duplication of large chromosomes, of small chromosomes, or of both, has taken place.

Karyotypes of all the species and varieties investigated in the present paper reveal that on the basis of gross morphological features, a number of chromosomal types is common to all of them. A critical analysis, however, shows that the different species and varieties differ in different combinations of these types as well as in the finer morphological details. So it will be convenient to describe the general types separately at the beginning and their finer differences in the individual karyotype description for each species and variety. In certain species of the genera investigated here, a particular type of faintly stained area simulating a gap, the stainability of which shows its heterochromatic nature, has been noted in some of both long and short chromosomes in addition to the primary and secondary constrictions (vide microphotographs, Figs. 103-108).

A general description of the different types, depending on the locations of primary

and secondary constrictions, faintly stained gaps of heterochromatin, and size is given below:

Type *A*: Long chromosomes, each with two distinct constrictions, primary and secondary, one submedian in position and the other a satellite at the distal end of the long arm. In addition to these, a faintly stained area, simulating a gap, is situated nearly in the middle of the short arm.

Type *B*: Long chromosomes, each with a nearly submedian primary constriction and a satellite at the distal end of the long arm. The short arm is comparatively longer than the other long types.

Type *B'*: Long chromosomes, each with a nearly submedian primary constriction and a satellite at the distal end of the long arm. The short arm is comparatively shorter than that of the *B* type.

Type *C*: Long chromosomes, each with one distinct constriction, nearly submedian in position, and another faintly stained area simulating a gap situated at the middle of the short arm.

Type *D*: Long chromosomes, each with one nearly submedian primary constriction only. The short arm is comparatively longer than those of the other long types.

Type *D'*: Long chromosomes, each with a nearly submedian primary constriction. The short arm is comparatively shorter than that of the *D* type.

Type *E*: Medium sized chromosomes with median primary constrictions.

Type *F*: Short chromosomes, each with two distinct constrictions, primary and secondary, one nearly submedian in position, and the other located at the distal end of the short arm. In addition to these, a faintly stained area simulating a gap is situated nearly in the middle of the long arm.

Type *G*: Short chromosomes, each with a nearly submedian primary constriction and a satellite at the end of the short arm.

Type *H*: Short chromosomes, each with one distinct submedian constriction and another faintly stained area simulating a gap situated nearly at the middle of the long arm.

Type *I*: Short chromosomes, each with a nearly submedian primary constriction.

Type *J*: A very short chromosome with a median primary constriction.

#### Genus: *Aloë*

The chromosome complements of the thirty five species and varieties of this genus so far investigated show extreme size variations.

1. *Aloë begunii* Radl. L.c. ( $2n=14=B'_2+D_2+D'_4+G_1+I_5=5.1\mu$  to  $17.9\mu$ ). (Figs. 1 and 1a.) The *G* type and one of the *I* type chromosomes do not show any homologues. A variation number of  $2n=13$  has also been found ( $2n=B'_2+D_2+D'_4+G_1+I_4$ ). (Fig. 2.)
2. *A. strausii* Berger ( $2n=14=A_1+B'_1+D_2+D'_4+G_1+I_5=5.1\mu$  to  $20.5\mu$ ). (Figs. 3 and 3a.) One *A*, one *B'*, one *G*, and one of the *I* type chromosomes have no homologues.

3. *A. pringeli* Jacobsen ( $2n=14=B'_2+D_2+D'_4+E_1+G_2+I_2+J_1=3.1\mu$  to  $18.0\mu$ ). (Figs. 4 and 4a.) Both *E* and *J* type chromosomes possess median constrictions and are non-homologous. This species is possibly a structural hybrid. A segmental translocation has probably taken place between the two short chromosome types. The portion from the long arm of an *I* type chromosome has been translocated to the short arm of the *I* type, thus giving rise to the '*E*' and '*J*' type of chromosomes, which are strictly non-homologous.

4. *A. commutata* Tod. ( $2n=14=A_2+C_1+D_2+D'_3+G_1+I_5=5.0\mu$  to  $20.5\mu$ ). (Figs. 5 and 5a.) The *C*, one of the *D'*, the *G* and one of the *I* type chromosomes are without any homologues. Variation nuclei with thirteen ( $2n=A_1+B'_1+C_1+D_2+D'_3+G_1+I_4$ ) and fourteen ( $2n=B'_1+D_2+D'_5+G_1+I_5$ ) chromosomes with an altered karyotype have also been observed (Figs. 6 and 7).

5. *A. striata* Haw. ( $2n=14=A_1+B'_1+D_2+D'_4+G_1+H_2+I_3=5.0\mu$  to  $20.0\mu$ ). (Figs. 8 and 8a.) The *A* type, *B'* type, *G* type, and one of the *I* type do not have homologues. A variant nucleus with fifteen chromosomes ( $2n=B'_2+D_1+D'_5+G_1+H_2+I_4$ ) has been recorded (Fig. 9).

6. *A. dyeri* Schonl. ( $2n=14=A_2+D_2+D'_4+G_2+I_4=5.0\mu$  to  $19.5\mu$ ). (Figs. 10 and 10a.) The *A* pair is characterized by the presence of satellites on the long arms and median supernumerary constrictions on the short arm, and the *G* pair has satellites at the short arm. One *D* pair is longer than the other long types. Variation metaphase plates with thirteen chromosomes ( $2n=A_2+D_2+D'_4+G_1+I_4$ ) and fourteen chromosomes ( $2n=A_2+D_2+D'_4+G_1+I_5$ ) with a different combination in the same tissue have been found (Figs. 11 and 12).

7. *A. spuria* Berger ( $2n=14=A_2+C_2+D_2+D'_2+F_1+H_3+I_2=5.7\mu$  to  $22.0\mu$ ). (Figs. 13 and 13a.) The *F* and one of the *H* types do not have homologues.

A variation nucleus with thirteen chromosomes ( $2n=A_2+D_2+D'_4+F_1+H_2+I_2$ ) has also been observed (Fig. 17). The meiotic stages are more or less regular showing seven bivalents, four large and three small, in the first, and seven chromosomes in second metaphase. An occasional laggard and early or late separation have been seen (Figs. 14—16, Plate 11).

8. *A. pseudopicta* Berger ( $2n=14=B'_2+D_2+D'_4+G_1+I_5=4.6\mu$  to  $16.5\mu$ ). (Figs. 18 and 18a.) The *G* type and one of the *I* type chromosomes have no homologues. Variation nuclei with thirteen chromosomes ( $2n=B_1+D_2+D'_5+G_1+I_4$ ) have also been recorded (Fig. 19).

9. *A. longistyla* Baker ( $2n=14=B'_4+D_2+D'_2+H_2+I_4=4.1\mu$  to  $16.5\mu$ ). (Figs. 20 and 20a.) The *B'* type chromosomes are characterised by the presence of a satellite at the end of the long arm and one pair of the *B'* type is smaller than the other long types. A variation nucleus has been recorded with thirteen chromosomes. In it, two pairs of *B'* of a variant size, one pair of *D*, one pair of *D'*, one pair of *H* and three *I* type chromosomes are present (Fig. 21).

10. *A. cryptopoda* Baker ( $2n=14=B'_2+C_2+D_2+D'_2+H_2+I_4=5.1\mu$  to  $20.5\mu$ ). (Figs. 22 and 22a.) The pair of *B'* chromosomes is characterised by the presence of satellites at the ends of the long arms.

11. *A. saponaria* (Ait.) Haw. ( $2n=14=B'_2+C_1+D_2+D'_3+H_2+I_4=4.1\mu$  to  $15.9\mu$ ). (Figs. 23 and 23a.) The *C* and one of the *D'* type chromosomes are non-homologous. The *D'* type chromosomes are longer than the other long types. Variation nuclei bearing twenty-eight chromosomes ( $2n=B'_2+C_2+D_2+D'_{10}+H_2+I_{10}$ ) and twenty-five chromosomes ( $2n=B'_2+C_2+D_2+D'_9+H_2+I_8$ ) have also been seen (Figs. 24 and 25).

12. *A. brunthalieri* Berger ( $2n=14=A_2+B'_1+C_1+D_2+D'_2+H_4+I_2=4.6\mu$  to  $17.0\mu$ ). (Figs. 26 and 26a.) The *B'* type and *C* type chromosomes have no homologues. The long chromosomes show a slight variation in size.

13. *A. ekloisii* ( $2n=14=B'_2+D_2+D'_4+I_6=4.1\mu$  to  $16.4\mu$ ). (Figs. 27 and 27a.) The long chromosomes show a slight variation in size.

14. *A. globosa* ( $2n=14=B'_2+D_2+D'_4+H_2+I_4=4.1\mu$  to  $14.5\mu$ ). (Figs. 28 and 28a.)

15. *A. globuligemma* Pole Evans ( $2n=14=B'_2+D_2+D'_4+I_6=4.1\mu$  to  $15.9\mu$ ). (Figs. 29 and 29a.) The *B'* type chromosomes are characterised by the presence of satellites on the long arms and are smaller, whereas the *D* type chromosomes are longer than the other long types.

16. *A. ciliaris* Haw. ( $2n=42=B'_6+D_6+D'_{12}+G_2+H_4+I_{12}=3.6\mu$  to  $14.8\mu$ ). (Figs. 30 and 30a.) The long types show a slight variation in size. The species is a hexaploid one. Nuclei with thirtyone, thirtythree, twentytwo, fortytwo, thirtyfive and twenty-eight chromosomes are also on record (Figs. 31 to 36).

17. *A. rubrolutea* Schinz. ( $2n=14=B'_2+C_2+D_2+D'_2+H_2+I_4=4.1\mu$  to  $17.4\mu$ ). (Figs. 37 and 37a.) The *B'* pair possesses satellites at the ends of long arms, the *C* pair possesses median heterochromatic gaps at the short arms and the *H* pair shows median heterochromatic gaps at the long arms. The *C* type here is smaller than the other long types.

18. *A. microstigma* Salm. Dyck. ( $2n=14=A_2+C_2+D_2+D'_2+F_2+I_4=5.1\mu$  to  $20.0\mu$ ). (Figs. 38 and 38a.) The type *A* chromosomes possess satellites on the long arms and median constrictions on the short arms, the *C* type has a median constriction on the short arm, the *F* types possess satellites on the short arms and median constrictions on the long arms. Nuclei with thirteen ( $2n=B'_1+C_2+D_1+D'_3+F_1+I_5$ ) and twenty-eight chromosomes ( $2n=B'_2+C_4+D_4+D'_6+F_2+H_2+I_8$ ) have also been observed (Figs. 42 and 43).

Meiotic behaviour is more or less normal, showing seven bivalents in first metaphase, four long and three short. Irregularities, such as early or late separation, non-disjunction, lagging, etc., are also on record. Segregation in second anaphase, is normal showing seven chromosomes in a majority of cases (Figs. 39 and 40, Plate 11). Pollen division is normal showing seven chromosomes, four long and three short. Occasionally six chromosomes, three long and three short, are also noted in certain metaphase plates (Fig. 41, Plate 11).

19. *A. brevifolia* Miller ( $2n=14=A_2+B'_1+C_1+D_2+D'_2+G_1+H_2+I_3=4.1\mu$  to  $15.4\mu$ ). (Figs. 44 and 44a.) The *A* type chromosomes have satellites on the long arms and median heterochromatic gaps on the short arms, the *B'* type a satellite on the long arm, the *C* a median heterochromatic gap on the short arm, the *G* type a satellite on the short arm and the *H* type median heterochromatic gap on the long arm. The *B'*

type, *C* type, *G* type and one of the *I* type chromosomes do not have homologues. A slight variation in size in the long chromosome types has also been observed. Variant nuclei with fourteen ( $2n = A_2 + C_1 + D_2 + D'_3 + H_2 + I_4$ ) and fifteen ( $2n = A_2 + D_2 + D'_4 + G_1 + H_2 + I_4$ ) chromosomes have also been observed (Figs. 45 and 46).

20. *A. aristata* Haw. ( $2n = 14 = A_1 + B'_{1+2} + C_1 + D_1 + D'_2 + H_2 + I_4 = 4.1 \mu$  to  $16.9 \mu$ ). (Figs. 47 and 47a.) The *A* type, one of the *B'* type, the *C* type and the *D* type in these cases do not possess any homologue. One pair of the *B'* type is comparatively smaller than the others. A variation nucleus with thirteen chromosomes ( $2n = A_1 + B'_3 + C_1 + D'_2 + H_2 + I_4$ ) has also been found (Fig. 48).

21. *A. verdoorniae* Reynolds ( $2n = 14 = B'_2 + C_2 + D_2 + D'_2 + H_2 + I_4 = 5.1 \mu$  to  $20.9 \mu$ ) (Figs. 49 and 49a). The *B'* type, *C* type and *H* type chromosomes are characterised by the presence of a satellite on the long arm, a median heterochromatic gap on the short arm and a median heterochromatic gap on the long arm of short chromosomes respectively. The *D* type chromosomes are comparatively longer than the others. A variation metaphase plate with thirteen chromosomes ( $2n = B'_2 + D_2 + D'_3 + H_2 + I_4$ ) has also been observed (Fig. 50).

22. *A. winteri* Berger ( $2n = 14 = A_2 + D_2 + D'_4 + F_1 + H_1 + I_4 = 5.6 \mu$  to  $21.0 \mu$ ). (Figs. 51 and 51a.) The *F* type and *H* type chromosomes are non-homologous.

23. *A. davtyana* Schonl. ( $2n = 14 = B'_2 + C_2 + D_2 + D'_2 + H_2 + I_4 = 4.6 \mu$  to  $16.4 \mu$ ). (Figs. 52 and 52a.) The *B'*, *C* and *H* type chromosomes are characterised by the presence of satellites on the long arms, median heterochromatic gaps on the short arms of the long chromosomes and on the long arms of the short chromosomes respectively. Variant nuclei with twentyeight ( $2n = A_2 + B'_2 + D_2 + D'_{10} + H_4 + I_8$ ) and twentyseven chromosomes ( $2n = B'_2 + C_2 + D_4 + D'_7 + H_4 + I_8$ ) are also on record (Figs. 53 and 54).

24. *A. ferox* Miller ( $2n = 14 = A_2 + B'_1 + D_2 + D'_3 + H_2 + I_4 = 4.1 \mu$  to  $15.4 \mu$ ). (Figs. 55 and 55a.) The *A* type chromosomes possess satellites on the long arms and median supernumerary constrictions on the short arms, the *B'* type satellites on the long arms, and the *H* type a median heterochromatic gap on the long arm. One *B'* type and one *D'* type are non-homologous.

25. *A. humiliis* (L.) Miller ( $2n = 21 = B'_{1+2} + C_2 + D_2 + D'_5 + H_5 + I_4 = 4.1 \mu$  to  $14.8 \mu$ ). (Figs. 56 and 56a.) One each of the *B'* type, *D'* type and *H* type chromosomes do not possess homologues. A variation nucleus with twenty chromosomes ( $2n = B'_2 + C_2 + D_3 + D'_5 + H_4 + I_4$ ) has been observed (Fig. 57).

26. *A. runcinata* Berger ( $2n = 14 = A_2 + D_2 + D'_4 + G_1 + I_5 = 5.6 \mu$  to  $21.5 \mu$ ). (Figs. 58 and 58a.) The *G* type and one of the *I* type chromosomes are non-homologous. Abnormal nuclei with twentyeight ( $2n = A_2 + B'_2 + D_4 + D'_8 + G_2 + I_{10}$ ) and thirteen ( $2n = A_2 + D_2 + D'_3 + G_1 + I_5$ ) chromosomes are also found (Figs. 59 and 60).

27. *A. marlothi* Berger ( $2n = 14 = A_2 + B'_1 + D_2 + D'_3 + H_2 + I_4 = 5.1 \mu$  to  $20.5 \mu$ ). (Figs. 61 and 61a.) One *B'* and one *D'* have no homologues. A variation nucleus with twelve chromosomes ( $2n = A_2 + B'_1 + D_2 + D'_3 + H_2 + I_2$ ) has also been found (Fig. 62).

28. *A. greatheadii* Schonl. ( $2n = 14 = A_2 + B'_1 + C_2 + D_2 + D'_1 + H_4 + I_2 = 5.1 \mu$  to  $16.4 \mu$ ). (Figs. 63 and 63a.) The *B'* type and *D'* type chromosomes do not have homo-

logues. A variation nucleus with thirteen chromosomes ( $2n = A_2 + B'_1 + D_2 + D'_2 + H_3 + I_3$ ) has also been observed (Fig. 64).

29. *A. variegata* L. ( $2n = 14 = A_2 + B'_2 + D_2 + D'_2 + H_2 + I_4 = 5.1 \mu$  to  $18.4 \mu$ ). (Figs. 65 and 65a.)

In most cases, meiosis is found to be normal. The normal number of bivalents is seven, but cases of irregularity, such as lagging, non-disjunction, early and late separation, etc., in first anaphase are also seen. Pollen division clearly shows 7 chromosomes in metaphase, 4 long and 3 short (Figs. 66-68, Plate 11).

30. *A. arborescens* var. *milleri* Berger ( $2n = 14 = A_2 + C_2 + D_2 + D'_2 + H_2 + I_4 = 4.6 \mu$  to  $17.4 \mu$ ). (Figs 69 and 69a.) Variation nuclei with  $2n = 13$  chromosomes ( $2n = A_2 + C_2 + D_2 + D'_2 + H_2 + I_3$ ) have also been found (Fig. 70).

31. *A. arborescens* var. *natalensis* Berger ( $2n = 14 = A_2 + D_2 + D'_4 + H_1 + I_5 = 4.6 \mu$  to  $20.0 \mu$ ). (Figs. 71 and 71a.) The *H* type and one of the *I* type chromosomes have no homologues.

32. *A. wickensii* Pole Evans ( $2n = 14 = A_2 + D_2 + D'_4 + H_2 + I_4 = 5.1 \mu$  to  $19.0 \mu$ ). (Figs. 72 and 72a.) Variant nuclei with thirteen ( $2n = A_2 + D_2 + D'_4 + I_5$ ) and twenty-four ( $2n = A_2 + D_2 + D'_{10} + H_2 + I_8$ ) chromosomes are also on record (Fig. 73).

33. *A. malesticum* ( $2n = 14 = B'_3 + D_2 + D'_3 + H_2 + I_4 = 4.6 \mu$  to  $20.5 \mu$ ). (Figs. 74 and 74a.) One chromosome each of the *B'* and *D'* types has no homologue.

#### Genera: *Haworthia* and *Gasteria*

Four species of *Gasteria* and three species of *Haworthia* were studied.

1. *H. papillosa* Haw. ( $2n = 14 = A_1 + B_2 + C_1 + D'_4 + H_4 + I_2 = 4.1 \mu$  to  $16.4 \mu$ ). (Figs. 75 and 75a.) *A* type and *C* type chromosomes do not possess any homologues. A variation nucleus with thirteen chromosomes ( $2n = B_2 + C_2 + D'_4 + H_4 + I_1$ ) has been observed. The complement shows a slight alteration in the karyotype. It has obviously originated from the normal set through numerical alterations and minor structural changes.

2. *H. fasciata* Haw. ( $2n = 14 = B_2 + C_2 + D'_4 + H_2 + I_4 = 4.0 \mu$  to  $15.3 \mu$ ). (Figs. 76 and 76a.)

Meiotic behaviour is mostly normal with seven bivalents. But irregularities such as early and late separation, non-disjunction and lagging have also been observed in first anaphase. Pollen divisions show seven chromosomes but occasionally 6 chromosomes (3 long and 3 short) have also been noted (Figs. 77 to 82, Plate 00).

3. *H. planifolia* Haw. ( $2n = 14 = B_2 + C_2 + D'_4 + H_2 + I_4 = 3.6 \mu$  to  $15.9 \mu$ ). (Figs 83 and 83a.) A variant nucleus with thirteen chromosomes ( $2n = B_2 + C_2 + D'_4 + H_2 + I_3$ ) has also been found (Fig. 89).

In meiosis, seven bivalents have been observed. Irregularities such as early separation, non-disjunction of bivalents and occasional laggards are also seen (Figs. 84-87, Plate 00). Pollen metaphase shows 7 chromosomes, 4 large and 3 small (Fig. 88, Plate 00).

4. *Gasteria minima* v. *Poelln.* ( $2n = 14 = B_2 + B'_1 + C_2 + D'_3 + H_4 + I_2 = 3.6 \mu$  to  $18.4 \mu$ ).

(Figs. 90 and 90a.) The  $B'$  type and one smaller  $D'$  type do not have homologues. Variation nuclei bearing twelve ( $2n=B_2+C_2+D'_4+H_2+I_2$ ) and eleven ( $2n=B_2+B'_1+C_2+D'_3+I_3$ ) chromosomes have also been observed (Figs. 95 and 96).

Meiotic behaviour is normal showing seven bivalents in metaphase I. A few P.M.C.s show early separation. Laggards are also on record in anaphase (Figs. 91-93, Plate 00). Pollen metaphase shows 7 chromosomes, 4 long and 3 short (Fig. 94, Plate 00).

5. *G. liliiflora* v. *Poelln.* ( $2n=14=B_2+C_2+D'_4+H_2+I_4=3.6\ \mu$  to  $17.9\ \mu$ ). (Figs. 97 and 97a.) A variation nucleus bearing thirteen ( $2n=B_2+C_2+D'_4+H_2+I_3$ ) chromosomes has also been observed (Fig. 98).

6. *G. maculata* Haw. ( $2n=14=B_2+B'_2+C_2+D'_2+H_2+I_4=4.1\ \mu$  to  $21.9\ \mu$ ). (Figs. 99 and 99a.) A variation nucleus with thirteen chromosomes ( $2n=B_2+B'_2+C_2+D'_2+H_2+I_3$ ) has been noted (Fig. 101).

7. *G. croucheri* (Hook.f.) Bak. ( $2n=14=B_2+C_1+D'_5+H_{45}+I_2=3.6\ \mu$  to  $20.0\ \mu$ ). (Figs. 100 and 100a.) The  $C$  type and one of the  $D'$  type do not possess homologues.

## DISCUSSION

### 1. Assessment of the chromosome number in previous and present investigations:

Of the 40 species and varieties of Aloineae studied during the present investigations, 33 belong to the genus *Aloe*. This genus is characterised by a uniform chromosome number of  $2n=14$  in all the species and varieties except *A. humilis* and *A. ciliaris*. In *A. ciliaris*, 42 chromosomes have been observed, confirming the previous reports of Müller (1945), Snoad (1951) and Riley (1959c). Riley prepared a detailed review of chromosome studies so far carried out in Aloineae. In *A. humilis*, 21 chromosomes have been found in the body cells. The material investigated by Sato (1942) revealed  $2n=14$  chromosomes in the same species. The number  $2n=21$ , as reported here, is new for this species as well as for the genus *Aloe* as a whole.

In addition to this uniformity in chromosome number, all species included in the present scheme show remarkable homogeneity in gross morphology of their chromosomes. The uniformity in number and karyotypes noted in *Aloe* holds good also for *Gasteria* and *Haworthia*. Polyploid species are however not uncommon in the genus *Haworthia* as is specially evident from the works of Riley (1959b). The cytological data provide additional support to the taxonomical consideration of the interrelationships of the three genera which have been put under a common assemblage.

### 2. Structural alterations of chromosomes in the evolution of species:

In spite of the gross similarity in the chromosome complements of the different genera represented with regard to number, the general karyotype as well as the total amount of chromatin matter (vide histograms), certain differences are noticeable which distinguish one species from another. Whatever may be the karyotype for each species, the total chromatin material remains nearly identical indicating that structural alterations merely involve rearrangement of chromosome parts. The only intergeneric difference observed is the absence of chromosomes of type *B* in *Aloe*

and *D*, *E*, *F*, *G*, and  $\mathcal{J}$  in *Gasteria* and *Haworthia*. The type *B* is replaced by *B'* in *Aloë* and *D* by *D'* in *Gasteria* and *Haworthia*. In both of these, a portion of the short arm appears to be deleted. In this respect, *Gasteria* and *Haworthia* are closely related karyotypically, and are different from *Aloë* (Fig. 101). Except for this difference, no marked dissimilarity was noted between them. Taylor (1925) indicated the possibility of the use of satellite chromosomes as markers of different taxa, a contention which however was strongly criticised by Resende (1937a, b).

The karyotype difference between species indicates clearly that an analysis of the karyotype may be considered essential for the identification of different species. Long chromosomes however show more alterations than shorter ones. The evidence of structural changes has been brought out in *Aloë pringeli* where chromosomal types were obtained which could not be homologised with others. The two types are represented by one medium sized *E* chromosome with a median constriction and a small  $\mathcal{J}$  chromosome with a similar type of constriction. It is likely that in meiosis they would form heteromorphic bivalents or remain as univalents. The presence of such a non-homologous pair is a clear indication of the chromosomal changes that the species has undergone during evolution.

In view of its hybridity, at least three different types of progeny are expected in this species—two representing homozygous levels and one heterozygous, depending on the random union of the different types of gametes. However, in view of the absence of the regular methods of sexual reproduction, this issue cannot be investigated. At least under local conditions, no flowering of *A. pringeli* is observed. Moreover, of the forty species studied here, as the idiograms show, twenty species have an odd number of two or more chromosome types. The presence of such odd numbers of chromosomes immediately points to their heterozygous constitution.

All species investigated here were grown in the University compound, after being initially collected from their sources. Though a large number of individuals of each species were studied, all of them evidently belonged to a single clone. Intensive studies with the techniques adopted here on different clones of the same species are expected to yield significant results.

Such wide occurrence of structural hybridity in the Aloineae is however very remarkable. In all the literature published so far, the uniformity in karyotype has throughout been emphasized. The minute variations in karyotype presented here for the first time could only be studied because of the special technique adopted during the present investigation. The application of such refined methods is therefore extremely necessary to find out the importance of minute structural alterations, if any, in widely different taxa.

### 3. Factors responsible for evolution:

Whenever the different cytological factors in evolution are mentioned, it is always implied that chromosomal or gene changes produce merely the raw materials for evolution. Selection of desirable combinations, effected later on by isolation and other factors, ultimately brings about the evolution of the species.

With regard to the cytological factors operating in the Aloineae, polyploidy seems to be of little significance in the genus *Aloe*. Of the large number of species so far studied, only two cases of polyploids have been observed.

Riley (1959b) suggested that gene mutation might have been a significant factor in the evolution of species within the Aloineae. The importance of gene mutation in the origin of species cannot be overrated. The present investigation, however, shows that in addition to gene mutation, structural changes involving, principally, rearrangements of chromosome parts have played a very important role in evolution.

The importance of structural alteration in evolution was realised a long time ago (Delauney, 1926; Levitsky, 1931a, b; Navaschin, 1932). Only chromosome segments were seen to be able to undergo fragmentation and translocation, but at the same time, certain parts may be deleted from the complement, specially due to the elimination of acentric fragments. Diminution in chromatin matter may easily follow. Moreover, such changes may cause a symmetrical karyotype to become asymmetrical. In several members of the Liliaceae and Amaryllidaceae, as well as in several other genera, evidences of karyotypic alteration in evolution are clear.

How far these structural changes are responsible for the phenotypic differences from species to species is not possible to ascertain at present. The difficulty of ascertaining this may largely be attributed to the fact that gene mutation, which has undoubtedly played a significant role in the evolution of the species, is also associated with structural alterations of chromosomes. In fact, gene changes, occurring at the molecular level, are potentially capable of bringing about a large number of variations compared to the scope of structural alterations which are very few specially in a complement with such a low number of chromosomes as in the Aloineae. Even so, as an individual species is characterised by its own karyotype, the significance of these changes, in addition to mutation, in evolution cannot be denied. Lately evidence has also accumulated to show that not only different species but even strains of the same species may differ with respect to very minute details of the karyotype (Lima-de-Faria, 1949; Bhaduri and Ghosh, 1954; Bose, 1956; Sharma and Bhattacharjee, 1957; Nilan et al., 1958). The differences may not necessarily involve the primary and secondary regions but may also be manifested in the pattern of the chromosomes or heterochromatic segments. These data simply emphasize that though the importance of structural alterations had earlier been recognised, its dynamic role in evolution has been demonstrated only recently. Therefore, in the Aloineae, where an identical karyotype predominates the entire tribe, the importance of structural changes of chromosomes is very conspicuous.

Several species of the Aloineae (vide idiogram table) are characterised by minute heterochromatic segments which cannot be strictly referred to as secondary constrictions. Their heterochromatic nature is exhibited by faint stainability in metaphase. It will be worthwhile to see the behaviour of the chromosomes when the plants are kept under cold conditions for a prolonged period. Darlington and LaCour (1940) observed the exaggeration of heterochromatic segments. The existence of hetero-

chromatic segments which often show a susceptibility to breakage (Levan and Lofty, 1950; Kihlman and Levan, 1957), might have facilitated the process of structural changes in chromosomes (Bhattacharjya, 1958).

#### 4. Ecological and distributional aspect:

From Müller's account (Müller, 1941, 1945; vide Riley, 1959a), *Gasteria* and *Haworthia* are principally natives of South Africa whereas the distribution of *Aloe* extends upto the Mediterranean Coast and Asia Minor. In general, none of the taxa go beyond the subtropical and tropical zones but there may be exceptions due to cultivation. This restricted distribution in a tribe otherwise so successful is quite interesting. The large number of species, totalling about 276, according to Riley, provides the presence of innumerable genotypes in nature. With the existence of such a diversity in genotypes, a distribution covering a wide range of climate would have been expected. But none of the species can withstand extreme climatic conditions, which is possibly the principal reason for their limited distribution. This lack of tolerance of extreme climatic conditions may be attributed to the low incidence of polyploidy in the Aloineae in general and *Aloe* in particular (vide Löve and Löve, 1943, 1949).

But why does *Haworthia*, with quite a lot of polyploids, have a restricted distribution? This may be explained on the basis of the fact that only a few species of *Haworthia* have so far been recorded. Polyploidy can impart tolerance to extreme climatic conditions to suitable gene combinations already existing at the diploid level. So if at the diploid level the choice of gene combinations is restricted, as in genera with a few species, polyploidy may not necessarily impart tolerance. Further investigations on the cytoecology of the Aloineae may throw light on this aspect.

Being forced to remain under an equable climatic condition, species of the Aloineae seem therefore to have extended their area of distribution within tropical and subtropical regions which provide a variety of environmental conditions. This process may have been accelerated by the diverse genotypic combinations brought about by gene mutation and structural changes in the chromosomes. The distributional pattern, mechanism of speciation, and non-adaptability to extreme climatic conditions of the Aloineae, finds a parallel, to some extent, in some members of the Aroideae such as *Caladium*. However *Caladium* differs in that in addition to structural alterations, aneuploid numerical changes too have operated in this genus (Sharma and Das, 1954).

#### 5. Taxonomic status of the different species:

The taxonomy of the Aloineae is complex. Except Jacobsen (1954) and Reynolds' (1950) monograph on the South African Aloineae, no comprehensive account is available. The complexity in taxonomy has arisen because the species have been created principally from a few cultivated plants or inadequate herbarium sheets. The problems of mutation as well as extensive hybridisation, changes under environmental conditions, etc., have been overlooked. A thorough systematic survey coupled with cytogenetic analysis may reduce a number of species to synonymy. According

to Riley (1959c) the problem of evolution in the Aloineae in general and *Gasteria* in particular will be almost unsolvable until the taxonomy is cleared up.

Jacobsen (1954) grouped the different species of the genera of the Aloineae under different sections. In the present work an attempt was also made to find out whether any correlation can be obtained between the grouping of the different species and their different karyotypes. No such correlation has been found and species differ from each other in minute karyotypic details even within a section. Therefore these groupings, which are undoubtedly of taxonomic value in aiding identification, should be considered as composed of an assemblage of different genotypes which have certain major factors in common responsible for their grouping together. The assemblage has been given the rank of a tribe, the Aloineae (Engler and Prantl, 1930) or the Aloeae (Nakai, 1936) by the former two authors whereas Nakai separated it into a new family Aloeaceae. Its similarity with Kniphofiae and Hemerocallideae has been emphasized by taxonomists who further consider it as an offshoot from the Asphodeleae.

The chromosome complement with its abrupt size difference and distinctive karyotype is a character which marks out the Aloineae from the rest. The origin of such a distinctive karyotype may be traced in two alternative ways: (1) through continued deletion of certain chromosome parts resulting in marked asymmetry, or (2) through hybridisation between two species with very long and very short chromosomes respectively.

It is not possible to state at present as to which particular mechanism has operated in the initial origin of the different genera of the Aloineae. The remarkable similarity of the chromosomes of the three genera suggests that instead of evolving in parallel lines, they must have diversified from a common taxon in which the characteristic karyotype was already attained. Further differentiation both at the genetic and morphological levels associated with different mechanisms of isolation led to the establishment of the three genera in the course of evolution.

In this connection the chromosomes of *Kniphofia* and *Hemerocallis* may be recalled. The former is characterised by very long and the latter by rather short chromosomes. Though the affinities of these two tribes with the Aloineae have been emphasized on taxonomic grounds, cytological similarities are yet to be obtained. Duplication of chromosomes resulting from  $x=6$  to 7 followed by asymmetry of the complement in some of its members may have led to the Aloineae from the Kniphofiae. On the other hand both the tribes may have contributed to the ancestry of the Aloineae through their hybridisation but the chromosome number and the absence of any such record do not point to the latter possibility. In any case it is not possible to state how far the tribes, in spite of their taxonomic affinities, are related genotypically to the Aloineae until direct evidence is available.

That the Aloineae may represent an offshoot from the Asphodeleae of Hutchinson is also borne out on cytological grounds. The Asphodeleae of Hutchinson represent the main stock of the family, from which the various lines of evolution can easily diverge. This tribe includes genera which are characterised by long as well as short chromosomes and have potentialities of giving rise to diverse genotypic combinations. The Kniphof-

fiae, the Hemerocallideae and the Aloineae are all supposed to originate from the Asphodeleae. This offshoot is taxonomically more remarkable in the family as it maintains a perennial habit though retaining the rhizomatous portion and in some cases the plants even attain an unusual height.

The chromosome characteristics and the general taxonomy, taken in conjunction with the wide distribution of the three genera, indicate clearly the advanced status of this assemblage. Taxonomists regard these succulents as a blind line in evolution. From a cytological standpoint, the potentiality of this assemblage for further evolution seems limited. The great differentiation in chromosome morphology already attained in a complement with a very low number of chromosomes which, further, do not differentiate markedly through polyploidy, shows that the potentiality of its evolution towards broader variation is also rather limited. Therefore cytological data provide full confirmation to the taxonomists' view of the evolutionary potentiality of the Aloineae.

How far this assemblage is to be considered as a tribe or a family is debatable. In view of its distinct and stable cytological characters, succulent and perennial habit, and morphological differences from other tribes, it appears more reasonable to place the three genera under a distinct family as an offshoot from the Asphodeleae of the Liliaceae.

#### 7. Inconstancy in the chromosome complement of somatic tissue:

One of the characteristic features of the somatic tissue of all three genera is the regular occurrence of altered complements in the somatic tissue in association with the normal ones. From such a mosaic of normal and abnormal karyotypes, the normal karyotypes had to be worked out by a study of the frequencies of occurrence of different complements and those occurring with the highest frequencies have been considered as the normal ones. Such an alteration not only involves structure but in certain cases numerical differences as well. This type of inconstancy has been observed to be a constant feature in plants reproducing by vegetative means, where they play a significant role in speciation (Sharma, 1956; Sharma and Sharma, 1959).

In species of the Aloineae too, the significance of this variation seems immense. Under cultivated conditions, in a large number of species, specially in India, seed formation is scarcely noticed, and as such, structural alterations may take part in the formation of the daughter shoots and help in the origin of individuals with new genotypes through vegetative propagation.

#### SUMMARY

The present investigation deals with the study of karyotypes of forty species and varieties of the tribe Aloineae belonging to the three genera *Aloë*, *Haworthia* and *Gasteria*. The propagation of all these species is mainly by vegetative means. For the study of the detailed structure of chromosomes, pretreatment in paradichlorobenzene has been effective. All the species studied show  $2n=14$  chromosomes, except *Aloë ciliaris* ( $2n=42$ ) and *A. humilis* ( $2n=21$ ).

The karyotype studies show a gross homogeneity in the chromosome complement represented by the presence of eight long chromosomes and six very short chromosomes. But the special technique adopted here has revealed minor karyotypic differences between different taxa. Moreover, in one species of *Aloe*, *A. pringeli*, a distinct case of structural heterozygosity has been observed and in twenty species evidences of structural heterozygosity have been seen. Gene mutation accompanied by minor structural changes has been assumed to have played a significant role in the evolution of the species.

The three genera have probably evolved from a common taxon in different directions. Cytological considerations and restricted distribution make further evolution in this tribe seem limited. So this distinctive tribe with a uniform chromosome complement and striking morphological similarity should be considered as a separate family having three genera. The inconstancy of the chromosome complement and the vegetative means of propagation have been suggested as the principal factors in evolution.

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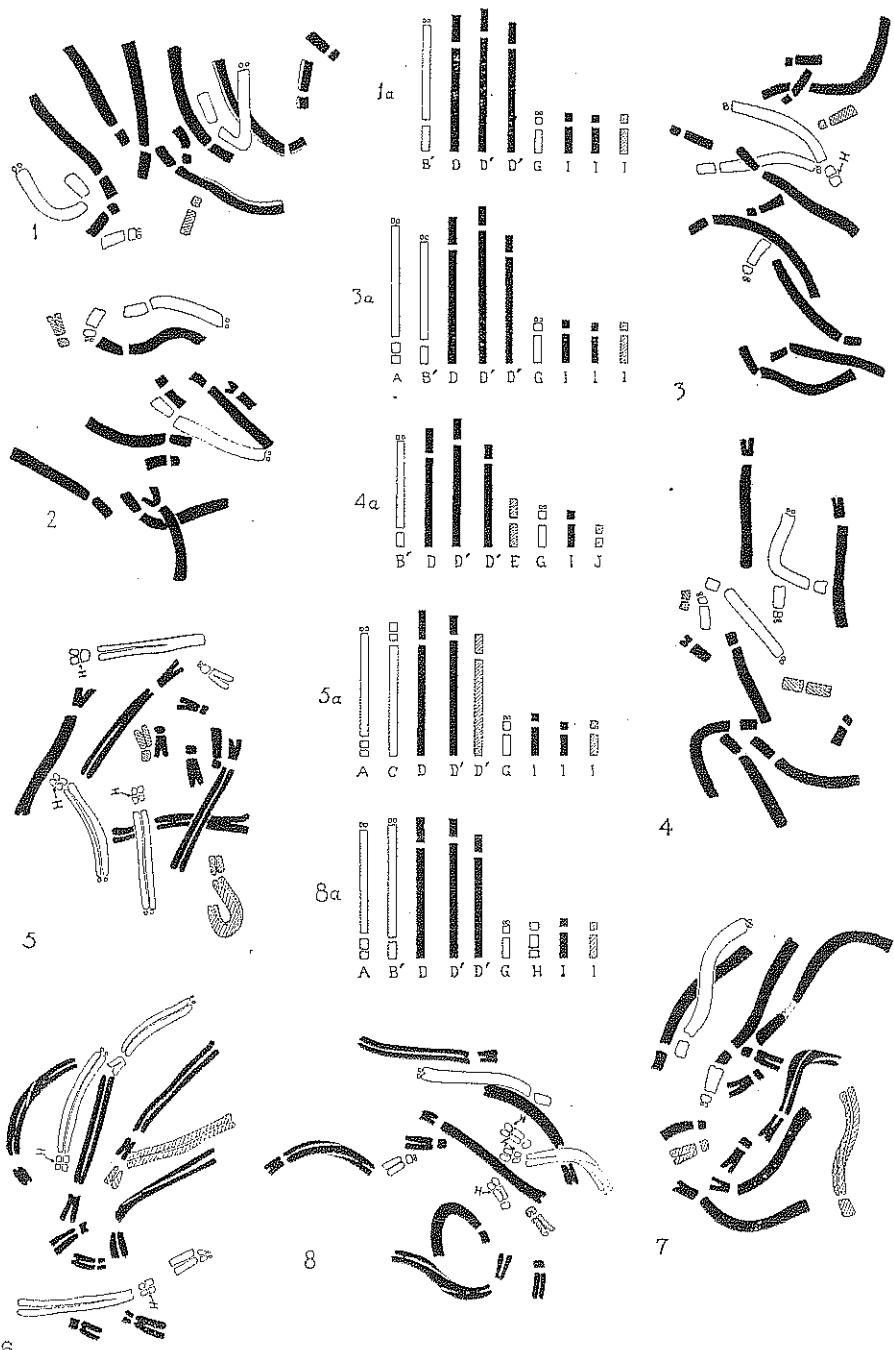


PLATE 3

Figs. 1-2. *Aloë begunii*. Figs. 1 & 1a. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Fig. 2. Variation metaphase with  $2n=13$  chromosomes. Figs. 3 & 3a. *A. strausii*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 4 & 4a. *A. pringeli*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 5-7. *A. commutata*. Figs. 5 & 5a. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Fig. 6. Variation metaphase with  $2n=13$  chromosomes. Fig. 7. Variation metaphase with  $2n=14$  chromosomes showing altered karyotype. Figs. 8-9. *A. striata*. Figs. 8 & 8a. Somatic metaphase with  $2n=14$  chromosomes and its idiogram.

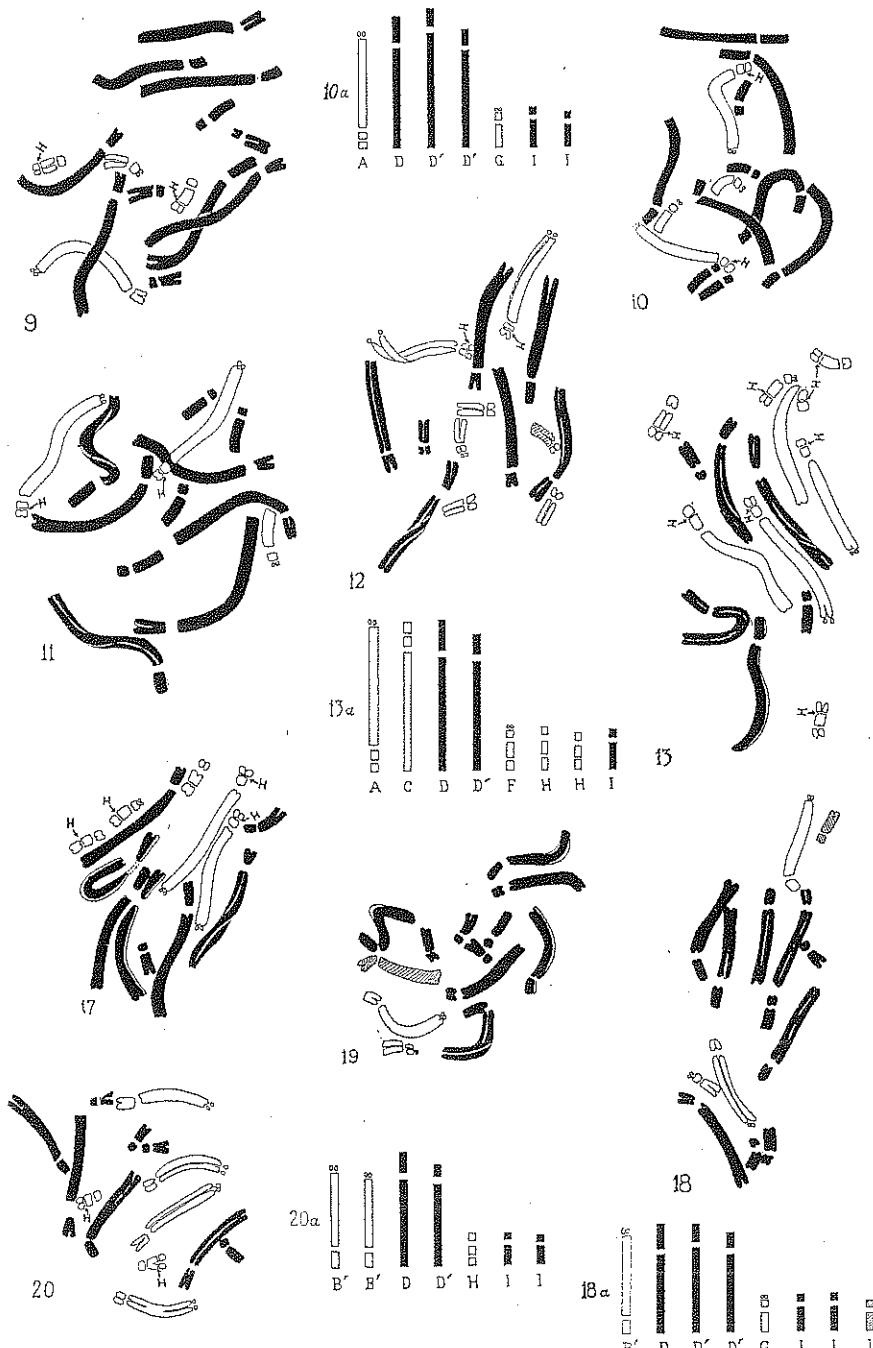


PLATE 4

Fig. 9. *A. striata*. Variation metaphase with  $2n=15$  chromosomes. Figs. 10-12. *A. ayeri*. Figs. 10 & 10a. Somatic metaphase with  $2n=14$  chromosomes and its idiomorph. Fig. 11. Variation metaphase with  $2n=13$  chromosomes. Fig. 12. Variation metaphase with  $2n=14$  chromosomes showing altered karyotype. Figs. 13, 13a, 17. *A. spuria*, Figs. 13 & 13a. Somatic metaphase showing  $2n=14$  chromosomes and its idiomorph. Fig. 17. Variation metaphase with  $2n=13$  chromosomes. Figs. 18-19. *A. pseudopicta*. Figs. 18 & 18a. Somatic metaphase with  $2n=14$  chromosomes and its idiomorph. Fig. 19. Variant metaphase with  $2n=13$  chromosomes. Figs. 20-21. *A. longistyla*. Figs. 20 & 20a. Somatic metaphase with  $2n=14$  chromosomes and its idiomorph.

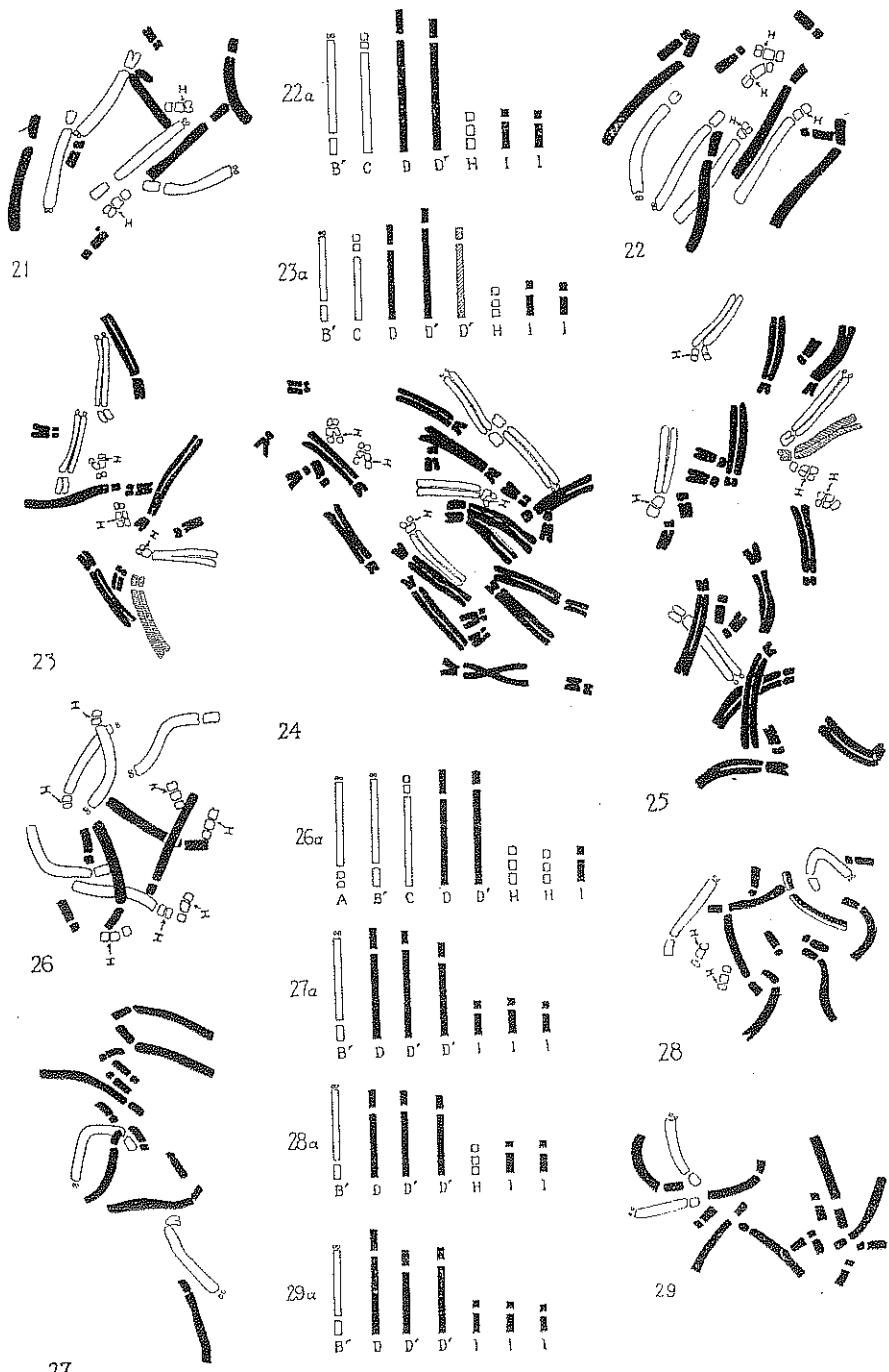


PLATE 5

Fig. 21. *A. longistyla*. Variation metaphase with  $2n=13$  chromosomes. Figs. 22 & 22a. *A. cryptopoda*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 23-25. *A. saponaria*. Figs. 23 & 23a. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 24 & 25. Variation nuclei with  $2n=28$  and 25 chromosomes respectively. Figs. 26 & 26a. *A. brunthaleri*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 27 & 27a. *A. ekloisii*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 28 & 28a. *A. globosa*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 29 & 29a. *A. globuligemma*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram.



PLATE 6

Figs. 30-36. *A. ciliaris*. Figs. 30 & 30a. Somatic metaphase with  $2n=42$  chromosomes and its idiogram. Figs. 31-36. Variant nuclei with  $2n=31$ ,  $33$ ,  $22$ ,  $42$ ,  $35$  and  $28$  chromosomes respectively. Figs. 37-38. *A. microstigma*. Figs. 38 & 38a. Somatic metaphase with  $2n=14$  chromosomes and its idiogram.

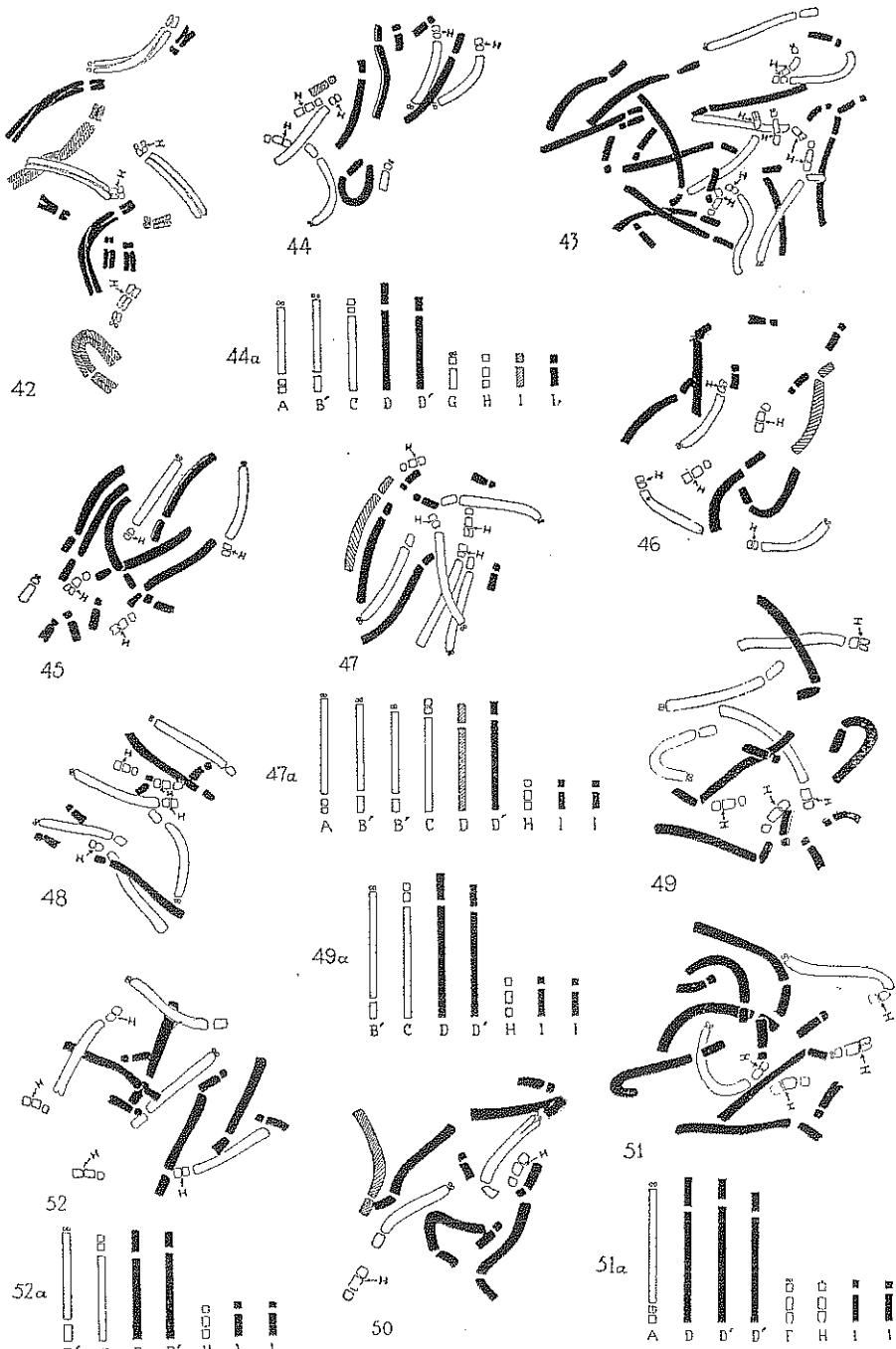


PLATE 7

Figs. 42-43. *A. microstigma*. Variation metaphase with  $2n=13$  and 28 chromosomes respectively, Figs. 44-46. *A. brevifolia*. Figs. 44 & 44a. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 45-46. Variation metaphase with  $2n=15$  and 14 chromosomes respectively. Figs. 47-48. *A. aristata*. Figs. 47 & 47a. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Fig. 48. Variation metaphase with  $2n=13$  chromosomes. Figs. 49-50. *A. verdorniae*. Figs. 49 & 49a. Somatic metaphase showing  $2n=14$  chromosomes and its idiogram. Fig. 50. Variation metaphase with  $2n=13$  chromosomes. Figs. 51 & 51a. *A. winteri*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 52-54. *A. davayana*. Figs. 52 & 52a. Somatic metaphase with  $2n=14$  chromosomes and its idiogram.

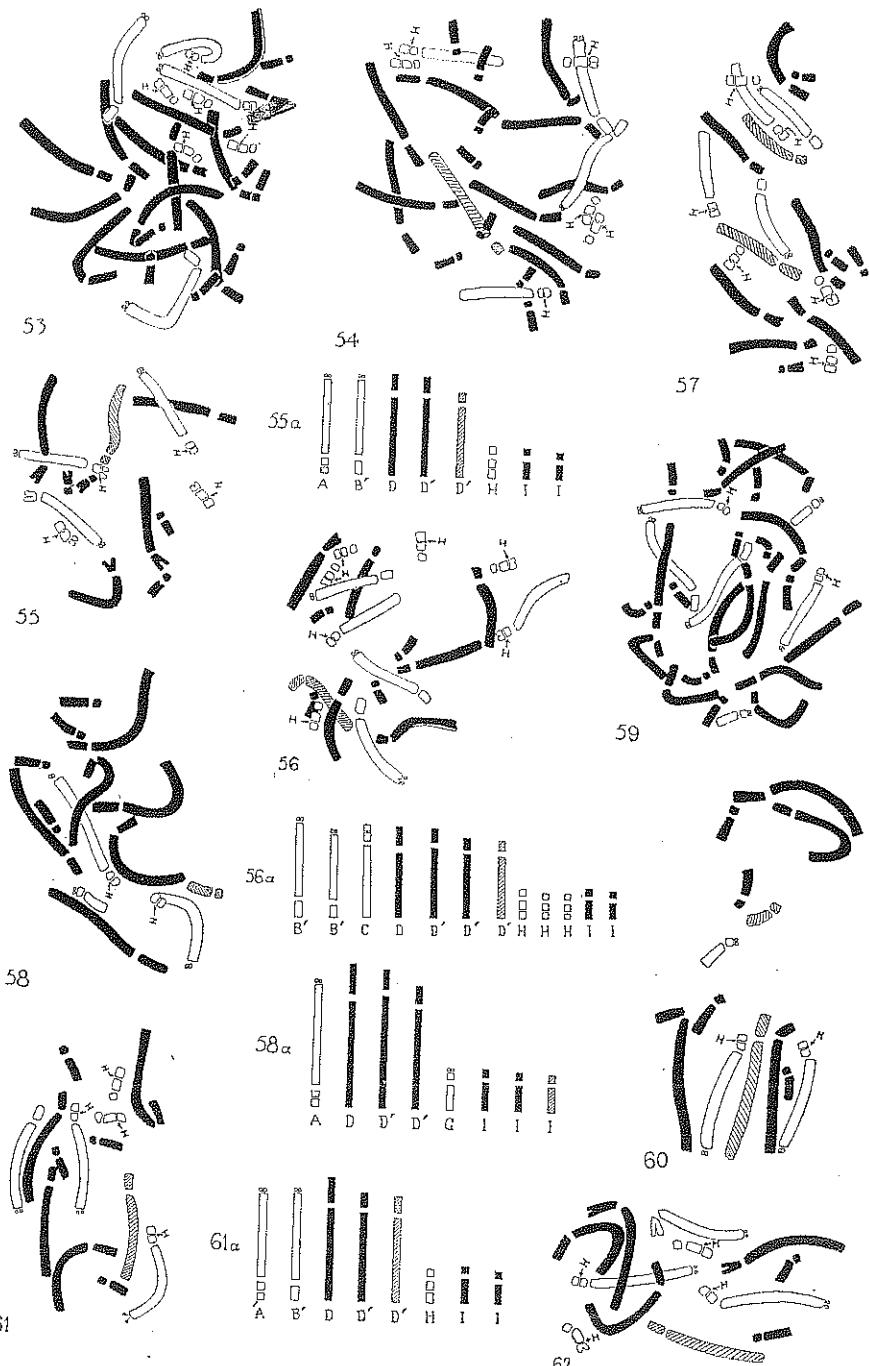


PLATE 8

Figs. 53-54. *A. daviana*. Variation metaphase with  $2n=28$  and  $27$  chromosomes respectively. Figs. 55 & 55a. *A. ferox*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 56-57. *A. humilis*. Figs. 56 & 56a. Somatic metaphase with  $2n=21$  chromosomes and its idiogram. Fig. 57. Variation metaphase with  $2n=20$  chromosomes. Figs. 58-60. *A. runcinata*. 58 & 58a. Somatic metaphase with  $2n=28$  and  $26$  chromosomes and its idiogram. Figs. 59-60. Variation metaphase with  $2n=13$  chromosomes respectively. Figs. 61-62. *A. marlothi*. Figs. 61 & 61a. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Fig. 62. Variation metaphase with  $2n=12$  chromosomes.



PLATE 9

Figs. 63-64. *A. greatheadii*. Figs. 63 & 63a. Somatic metaphase with  $2n=14$  chromosomes and its idiomogram. Fig. 64. Variation metaphase with  $2n=13$  chromosomes. Figs. 65 & 65a. *A. variegata*. Somatic metaphase with  $2n=14$  chromosomes and its idiomogram. Figs. 69-70. *A. arborescens* var. *milleri*. Figs. 69 & 69a. Somatic metaphase with  $2n=14$  chromosomes and its idiomogram. Fig. 70. Variation metaphase with  $2n=13$  chromosomes. Figs. 71 & 71a. *A. arborescens* var. *natalensis*. Somatic metaphase with  $2n=14$  chromosomes and its idiomogram. Figs. 72-73. *A. wickensii*. Figs. 72 & 72a. Somatic metaphase with  $2n=14$  chromosomes and its idiomogram. Fig. 73. Variation metaphase with  $2n=24$  chromosomes and its idiomogram. Figs. 74 & 74a. *A. malesticum*. Somatic metaphase with  $2n=14$  chromosomes and its idiomogram. Figs. 75 & 75a. *Haworthia papillosa*. Somatic metaphase with  $2n=14$  chromosomes and its idiomogram.

## Cytology of the Aloineae

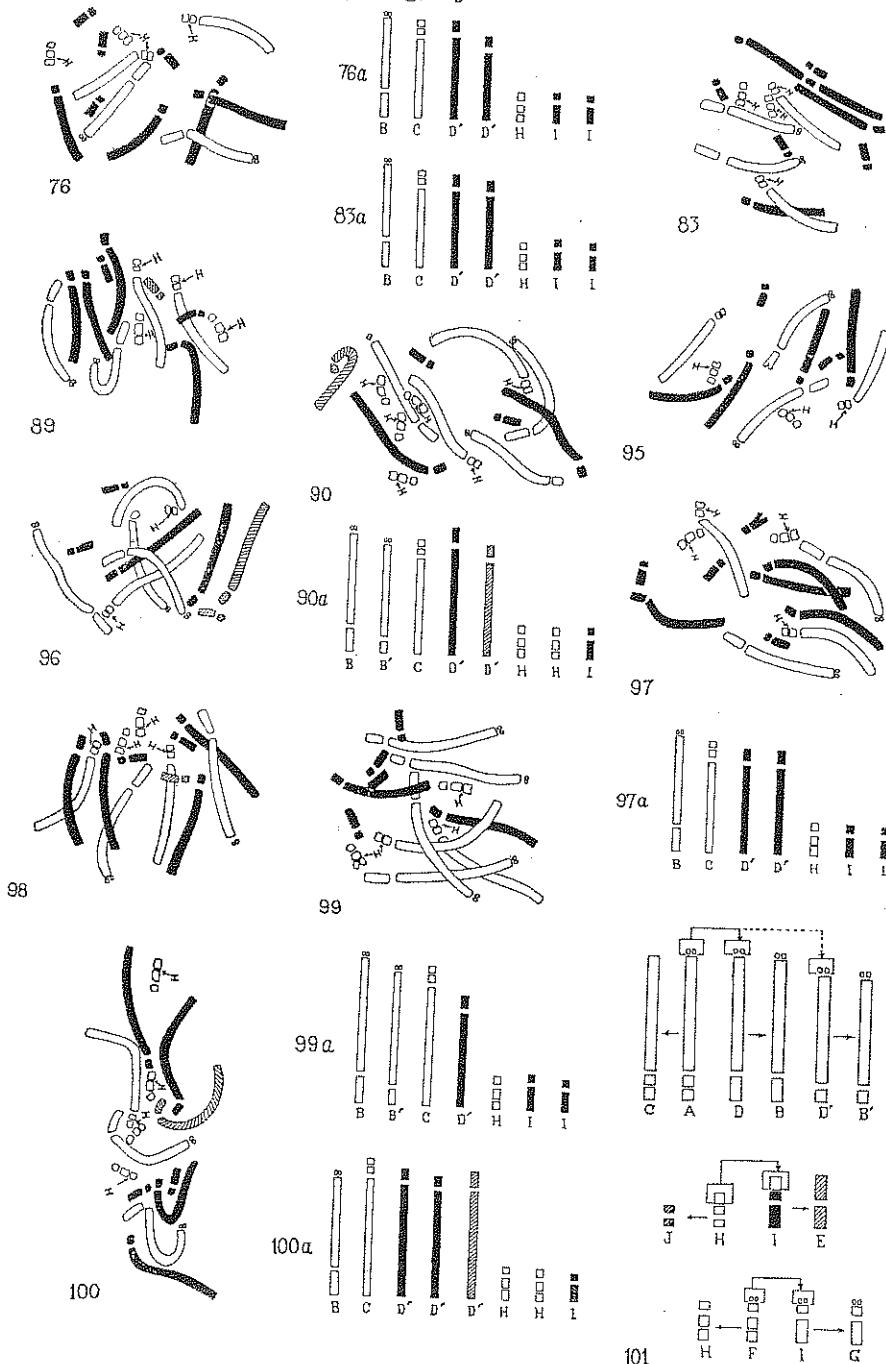


PLATE 10

Figs. 76 & 76a. *H. fasciata*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 83 & 89. *H. planifolia*. 83 & 83a. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Fig. 89. Variation metaphase with  $2n=13$  chromosomes. Figs. 90, 95, 96. *Gasteria minima*. Figs. 90 & 90a. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 95-96. Variant nuclei showing  $2n=12$  and 11 chromosomes respectively. Figs. 97-98. *G. lithopetala*. Figs. 97 & 97a. Somatic metaphase with  $2n=13$  chromosomes and its idiogram. Fig. 98. Variation metaphase with  $2n=14$  chromosomes and its idiogram. Fig. 99. *G. maculata*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Figs. 100 & 100a. *G. croucheri*. Somatic metaphase with  $2n=14$  chromosomes and its idiogram. Fig. 101. Possible types of structural alteration of chromosomes in the tribe Aloineae.

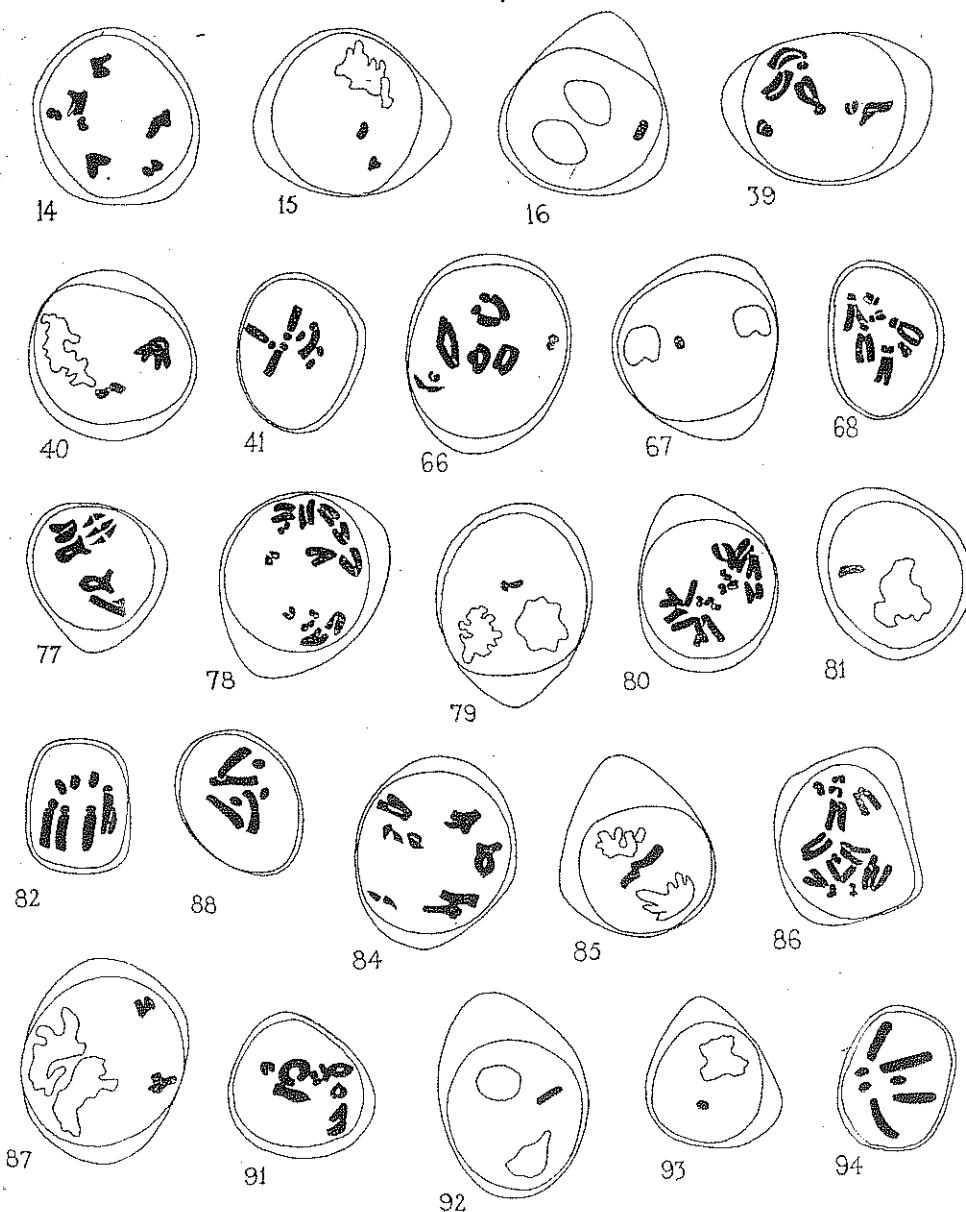
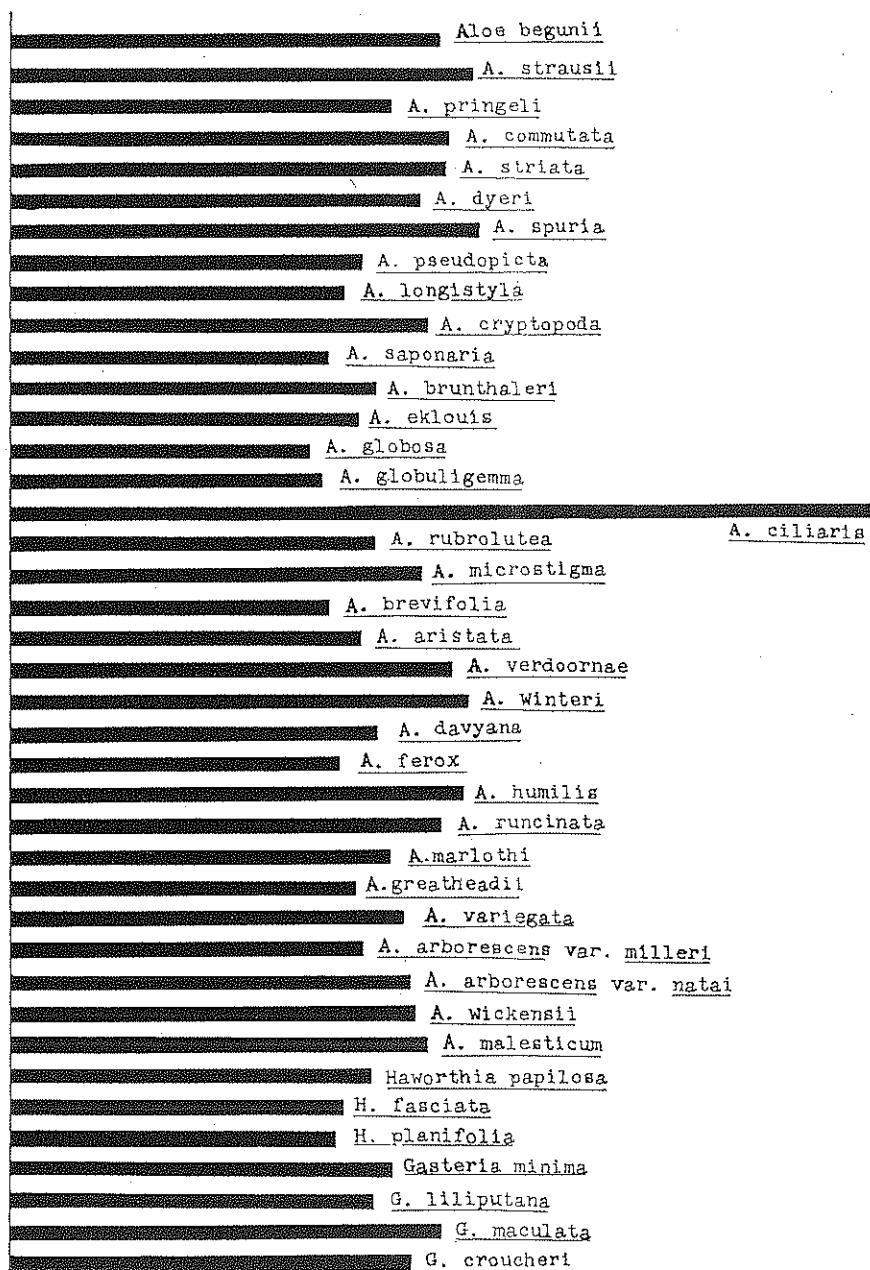


PLATE 11

Figs. 14-16. *Aloë spuria*, showing different meiotic stages. Figs. 39-41. *A. microstigma*. Figs. 39 & 40. Meiotic stages. Fig. 41. Pollen metaphase showing 7 chromosomes. Figs. 66-63. *A. variegata*. Figs. 66 & 67. Meiotic stages. Fig. 68. Pollen metaphase showing 7 chromosomes. Figs. 77-82. *Haworthia fasciata*. Figs. 77-81. Different meiotic stages. Fig. 82. Pollen metaphase with 7 chromosomes. Fig. 84-88. *H. planifolia*. Figs. 84-87. Different meiotic stages. Fig. 88. Pollen metaphase with 7 chromosomes. Figs. 91-93. *Gasteria minima*. Figs. 91-93. Different meiotic stages. Fig. 94. Pollen metaphase showing 7 chromosomes.



0 5 10  
Scale in  $\mu$

PLATE 12

Fig. 102. Histogram showing the total amount of chromatin matter in length of the haploid complements of the different species of *Aloë*, *Haworthia*, and *Gasteria*.

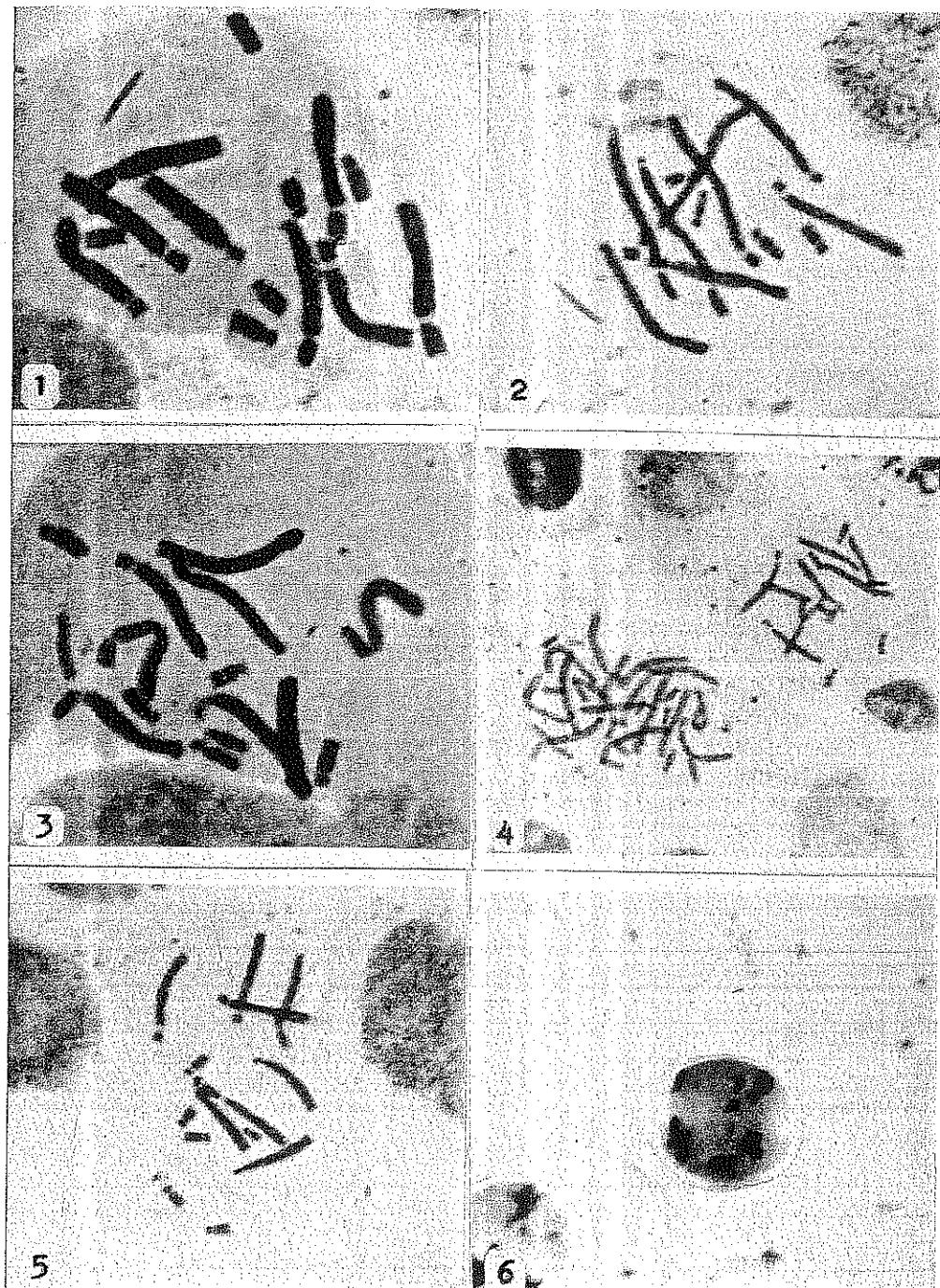


PLATE 13

Photomicrographs:

Fig. 103. *Aloë cryptopoda*. Somatic metaphase showing  $2n=14$  chromosomes.  
 Fig. 104. *Gasteria minima*. Variation metaphase showing  $2n=12$  chromosomes.  
 Fig. 105. *Aloë verdoorniae*. Somatic metaphase showing  $2n=14$  chromosomes.  
 Fig. 106. *Aloë davyana*. Variant nuclei showing  $2n=14$  and  $28$  chromosomes side by side.  
 Fig. 107. *Haworthia fasciata*. Somatic metaphase showing  $2n=14$  chromosomes.  
 Fig. 108. *Haworthia planifolia*. P.M.C. showing 7 nucleoli.