

On chromosome uniformity, bimodality and evolution in the tribe Aloineae (Asphodelaceae)

CANIO GIUSEPPE VOSA*

Linacre College, Oxford, U.K.

Abstract — Variable AC-segments (allocyclic chromosome segments) are present in all the species of the tribe Aloineae and are an indication of karyotype evolution and speciation in progress. In all species, the karyotype is very uniform and this uniformity may be the consequence of climatic stability and of similarity of habitat. All the species in the tribe possess a bimodal chromosome complement, a special character of ancient origin present in many organisms both vegetable and animal with a bearing on gene recombination and on evolution.

Key words: AC-segments, Aloineae, chromosome bimodality, crossing-over, speciation.

INTRODUCTION

The chromosome complement of all the species belonging to the genera *Aloe*, *Haworthia*, *Gasteria* and *Poellnitzia*, (family Asphodelaceae, tribe Aloineae) is very uniform and generally bimodal composed of eight large (L-) and of six small (S-) chromosomes. Apart from a few species of *Aloe* and of *Haworthia* which are known to have various degrees of polyploidy, all the species in the tribe are diploid with $2n=2x=14$.

VOSA and BENNETT (1990), in their cytological survey of 37 wild collected accessions of *Gasteria*, have reported some important findings in relation to the index of chromosome bimodality calculated as in BRUYNS and VOSA (1987). In their chromosome analysis, VOSA and BENNETT (1990) found that in the relationship between genome length and the relative length of the L- and S-chromosome, the total length of the genome increases proportionally to the length of the L-chromosomes. A result that is very similar to that illustrated by BRANDHAM (1983) in the related genus *Aloe* and is to be considered as evidence of chromosome evolution in the tribe. The tendency seems to be a reduction in the relative size of the S-chromosomes probably leading to the translocation of certain groups of genes to the L-chromosomes. Eventually, this new gene distribution and packaging would have an effect on genetic recom-

ination and, of course, on speciation. This process, at least in some groups of species in *Haworthia*, subgenus *Haworthia*, seems to be in progress so much so that they are very difficult to classify with certainty (BAYER 2002; VOSA 2004). For these species, a case could be made for considering them as infraspecific taxa of one variable species, i.e. a *superspecies* (VOSA, 2004).

THE SIGNIFICANCE OF THE AC-SEGMENTS

In all genera of the Aloineae, the L- and S-chromosomes possess AC-segments (allocyclic segments) that is chromosome regions of various length which, during the mitotic cycle, show a spiralization/condensation cycle different from that of the rest of the chromosome (DYER 1963; VOSA & COLASANTE 1995; COLASANTE & VOSA 2001). These segments of various sizes and position generally appear as regions of reduced stainability and are readily visible especially at the late mitotic metaphase stages. They are not to be confused with heterochromatin which, in the classical definition by HERTZ (1929), consists of chromosome segments which maintain the mitotic anaphase spiralization during interphase. At this stage they are visible as chromocentres and are considered to be made up of constitutive heterochromatin (C-heterochromatin) which can be made visible in the somatic chromosomes as differentially stained segments with special techniques such as C-banding or Q-banding, etc.

(*) Address for correspondance: Dipartimento di Scienze Botniche, Università di Pisa, Italy; e-mail: caniovosa@tin.it.

At the moment, the occurrence of AC-segments, at least in the genera *Gasteria* and *Haworthia*, seems to be population specific rather than species specific. However, we think that more extensive investigations, with chromosome analysis of large number of plants from many different populations in a variety of habitats over a wide area, are likely to give some interesting results. In any case, the significance of the AC-segments, especially regarding speciation and/or ecological adaptation, is so far unknown but, together with chromosome bimodality, may affect genetic recombination.

ON THE ORIGIN OF CHROMOSOME BIMODALITY

Chromosome bimodality occurs in a very wide range of organisms both vegetable and animal and may have had different origin. As first pointed out by MCKELVEY and SAX (1933), in these organisms the chromosome complement has a unique character and there is an almost complete absence of median or sub-median chromosomes.

As far as the origin of bimodality, in the case of the tribe Aloineae, BRANDHAM (1983) ascribed its origin to ancient allopolyploidy involving a cross between $x=4$ species with large chromosomes and $x=3$ species with small chromosomes perhaps followed by a differential increase in the size of $x=4$ genome. According to BRANDHAM hypothesis, subsequent structural rearrangements may have led to the stabilization of the chromosome complement.

A different hypothesis, at least for some South African species of the genus *Ornithogalum*, subgenus *Urophyllum*, has been put forward by VOSA (1983). This author made several crosses between species with $2n=6$ and related species with a bimodal complement of six L-chromosomes and a varying number of S-chromosomes. In the analysis of the meiotic pairing behaviour of his F1 crosses, Vosa found that the S-chromosomes seem to be derived from a somewhat complicated chromosome rearrangements. These involve primarily the breakage of the proximal region of the L-chromosomes, the loss of most the long arm and reunion with the remaining distal segment.

BRANDHAM's and VOSA's hypotheses may be not mutually exclusive and might be two of some of the processes leading to the establishment of bimodality.

Chromosome bimodality clearly shows that one of the directions of evolutionary change may

be an increase in the basic chromosome number with perhaps the creation of a kind of cryptic polyploidy.

It is to be noted that the changes in meiotic recombination between the L- and the S-chromosomes, due to their significant disparity in size, may have led to the establishment of a virtual two-track differential heredity for the genes carried in the two types of chromosomes.

The evidence of several studies, and a perusal of the literature on the subject, show that bimodal chromosome complements have a very ancient origin and are one of the most successful line of chromosome evolution. In the animal kingdom they are found generally in *all* birds and in fishes, snakes and other reptiles and probably in many other organisms. In the plant kingdom, bimodal chromosome complements are found in many monocotyledonous genera some of which are listed in Table 1.

Table 1 — Bimodal chromosome complements in some monocotyledonous plant genera (**L**- = long chromosomes; **S**- = short chromosomes)

$x = 30: 5 L- + 25 S-$

Agave
Fourcroya
Yucca
Hosta

$x = 15: 4 L- + 11 S-$

Eucomis

$x = 14: 5 L- + 9 S-$

Brimeura

$x = 10: 4 L- + 6 S-$

Bowiea
Rhadamanthus
Litbanthus (extreme bimodality!)

$x = 9: 3 L- + 6 S-$

Albuca
Ornithogalum (all South African species of the subgenus *Osmyne*)

$x = 9: 4 L- + 5 S-$

Drimia
Schizobasis

$x = 9: 2 L- + 7 S-$

Leopoldia

$x = 7: 4 L- + 3 S-$

Aloe
Gasteria
Haworthia
Poellnitzia

$x = 4, 5, 6...: 3 L- + 1,2,3... S-$

Ornithogalum (some South African species of the subgenus *Urophyllum*)

It is likely that these very different animal and plant organisms may have remained stable in regard to the bimodality of the chromosome complement perhaps since the Paleozoic period. Further, they must have been derived from groups of organisms distinct in this respect since that time.

CONCLUSIONS

1) Chromosome studies point not only to the past but also to the future and are paramount to unravel the process of evolution.

2) Variable AC-segments are found in the chromosomes of all the species of the tribe Aloineae. Although so far considered to be typical of a given population, rather than species specific, further studies might show that they are indicative of karyotype evolution in progress and of speciation.

3) Climatic stability and similarity of habitat, over most of the area of distribution of the tribe, may have been very important in creating and maintaining karyotype uniformity. It is evident that these prevailing conditions have probably influenced the great power of selection which has been directed, not to producing change, but indeed to maintaining the *status quo*.

4) Chromosome bimodality is a special karyotypic character which parcels the genes into two different recombining units: one with relatively few large chromosomes and the other with a varying number of small chromosomes.

Overall, bimodal karyotype ubiquity, ancient origin and importance is testified by its occurrence in many plant genera (see Table 1) as well as in *all* birds and a large number of reptiles in the animal kingdom.

Acknowledgement — I am very grateful to all people in Africa for their help during many collecting trips in the continent. My sincere thanks also go to the Royal Society and to the British Council for their unstinting support through the years.

Lastly, I would like to thank my colleagues, Prof. Emilio Battaglia and Dr. Andrea Costa for useful discussions and for critical comments on the manuscript.

REFERENCES

- BAYER M.B., 2002 — *Haworthia update: Essays on Haworthia*. Vol. 1, edit. Undau Press, Hatfield, South Africa.
- BRANDHAM P.E. 1983 — *Evolution in a stable chromosome system*. Kew Chrom.Conference, 2: 251-260.
- BRUYNS P.V. & VOSA C.G. 1987 — *Taxonomic and cytological notes on Bowiea and allied genera (Liliaceae)*. Caryologia, 40: 287-297.
- COLASANTE M.A. & VOSA C.G. 2001 — *Iris allocyclic segments as chromosome markers*. Ann. Bot. N.S. (Rome), 58: 127-134.
- DYER A.F. 1963 — *Allocyclic segments of chromosomes and the structural heterozygosity they reveal*. Chromosoma (Berl.), 13: 545-576.
- HEITZ E., 1929 — *Heterochromatin, Chromocentren, Chromomeren*. Ber.Deuts.Bot.Ges., 47: 274-284.
- MACKELVEY S.D. & SAX K. 1933 — *Taxonomic and cytological relationship of Yucca and Agave*. J. Arnold Arbor. 14: 756-81.
- VOSA C.G., 1983 — *Chromosome evolution in Ornithogalum*. Kew Chrom. Conference, 2: 370.
- VOSA C.G., 2004 — *On the classification of some species of the genus Haworthia, subgenus Haworthia (Asphodelaceae)*. Caryologia, 57(4): 395-399.
- VOSA C.G. & BENNETT S. 1990 — *Chromosome studies in the Southern African Flora. 95-102: Chromosome evolution in the genus Gasteria Duval*. Caryologia, 43: 235-247.
- VOSA C.G. & COLASANTE M.A. 1995 — *I segmenti allociclici nelle Liliiflore*. Inform. Bot. Ital. 27: 307-308.