

SOME TRENDS IN THE EVOLUTION OF THE CHROMOSOMES IN THE BOVIDAE

C. WALLACE

*Anatomy Department
Medical School
Witwatersrand University
Johannesburg
2001*

Abstract – A survey of the chromosome status of all members of the family Bovidae (60 species) studied to date is described. A special mention is made of chromosome studies in bovids in the Kruger National Park. A tentative course of chromosomal status is outlined.

Introduction

A continuing survey of the chromosomes of free-roaming wild mammals in the Kruger National Park (KNP), Republic of South Africa, has drawn interest to the chromosomes of members of the family Bovidae in the Park (Wallace & Fairall 1968b, Wallace 1977b). This interest has been extended to other African bovids, and to bovids in general.

It is judged to be beyond the scope of the present communication to undertake a complete and detailed review of the chromosomes of all bovids studied. The present study deals rather with certain relevant findings, with a summary of studies so far reported on. A more detailed review is to be found elsewhere (Wallace 1976). In the present study, chromosome results in the different bovids have been analysed as follows: (1) diploid chromosome number; (2) chromosome arm number or N.F.

Chromosome studies in bovids in general

A summary of chromosome findings to date show a diploid variation of 30–60 and a N.F. variation of 55–60. Most of the studies under review were carried out before the advent of the sophisticated banding techniques.

With an adequate knowledge of the number and morphology of the chromosomes of different species, useful information concerning phylogenetic relationships within a group can be obtained. In addition, the chromosomes of present-day species can point the way towards mechanisms of

chromosome evolution, and the possible means whereby the chromosomes of the present-day species have changed as these species gradually evolved from their primitive, ancestral forms.

In comparing chromosome complements (or karyotypes as they are termed) of different species, it is important to try to explain differences or similarities encountered. A close phylogenetic relationship between species can often be emphasised by similar karyotypes. Thus, in certain cases, similarity of karyotypes of different related species can also suggest a common origin of the karyotypes. Taxonomic divergence can be accompanied by karyotypic changes (Sybenga 1972), although this is not always the case (Tobias 1953). Where the chromosomes of related species are not all that similar, a reconstruction of the possible steps in chromosomal evolution from the common ancestor can often be made, and in certain cases, postulates can even be advanced on the primitive ancestor's chromosome constitution.

Mechanisms of chromosome evolution

The two most common means whereby the chromosomes can evolve (Figs. 1 and 2) are Robertsonian fusion and pericentric inversion. Robert-

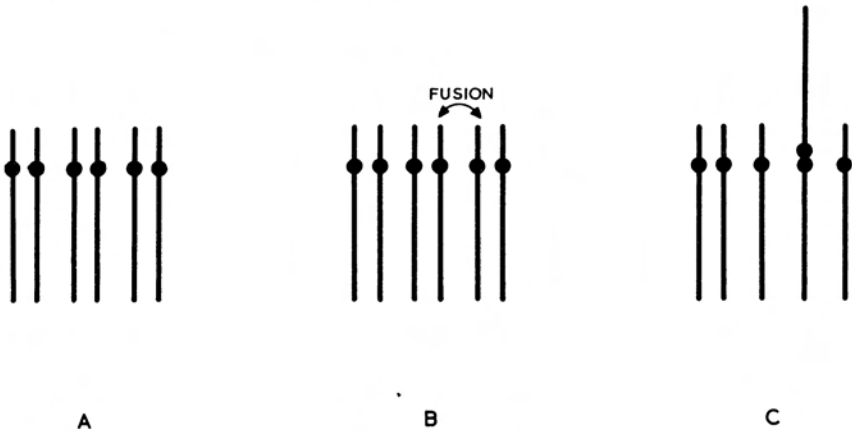


Fig. 1. Diagrammatic representation of a Robertsonian fusion.

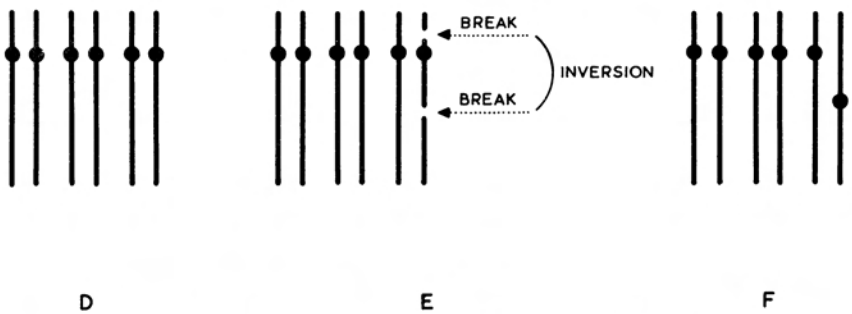


Fig. 2. Diagrammatic representation of a pericentric inversion.

sonian fusion (or variation) consists commonly of fusion between two acrocentric chromosomes (chromosomes with terminal centromeres) to produce a single metacentric chromosome (with a centrally situated centromere). A Robertsonian fusion reduces the diploid number of chromosomes but does not alter the number of chromosome arms, as the new metacentric produced by the fusion of the two acrocentrics still has the same number of arms as the original acrocentrics. Figure 1 illustrates the process of Robertsonian fusion.

A pericentric inversion embodies a change in chromosomal structure whereby a chromosomal segment, which includes the centromere, is rotated and reversed. The reversal takes place after the occurrence of two breaks on the chromosome. Unlike Robertsonian variation, changes associated with pericentric inversion are not attended by alterations of diploid number, but by changes in the number of chromosome arms. The chromosome arm number is reduced when a pericentric inversion converts a metacentric to an acrocentric, and increased when an acrocentric is converted to a metacentric. Figure 2 illustrates an example of a pericentric inversion converting an acrocentric chromosome to a metacentric.

Bovid chromosomes

A consideration of the chromosome results in bovids can be most easily dealt with as follows: (1) diploid number of chromosomes and (2) chromosome arm numbers.

- (1) Diploid chromosome number. The diploid number varies widely in the different species. Certain species (for example steenbok *Raphicerus campestris*, Wallace & Fairall 1967b) have a chromosome count of 30. This is the lowest diploid number of any member of the family. At the other extreme, the highest diploid number is 60 (for example in duikers, Hard 1969). Lower numbers are encountered less commonly than higher numbers. Thus, 35 of 60 species have a diploid number of 54 or more, whilst 25 of 60 have a number between 30 and 52. The commonest diploid number is 60, with 20 of the 60 species having this number of chromosomes.
- (2) Chromosome arm numbers. There is little variation in the chromosome arm numbers. The lowest chromosome arm number is 55 (male kudu *Tragelaphus strepsiceros*, Wallace and Fairall 1968a), and the highest 60 (blue wildebeest *Connochaetes taurinus*, Wallace 1976). Forty two of the 60 species have a chromosome arm number of 58.

The detailed results in the 60 bovid species have been considered in full elsewhere (Wallace 1976), and these show that when relative numbers of acrocentric and metacentric chromosomes are related to diploid number and chromosome arm numbers in different species, a correlation is noted. Species with a high diploid number have a high proportion of acrocentrics and a low proportion of metacentrics; species with a low diploid number

have a higher proportion of metacentrics and fewer acrocentrics. The chromosome arm number remains relatively constant, no matter what the diploid number or relative proportions of acrocentrics and metacentrics. This situation indicates that Robertsonian variation was the major force in the chromosomal evolution of the bovids of the present day. This view is in keeping with that of Wurster & Benirschke (1968) and Taylor, Hungerford & Snyder (1969).

Bovids in the Kruger National Park

The chromosomes of eight species of bovids have been investigated. Chromosomes for study were obtained from bone marrow preparations using a technique especially adapted for use in the Park. Chromosome results in the eight species are summarised in Table 1.

There is wide variation in the diploid number (30–60) and it can be seen that a high diploid number is associated with a high number of acrocentrics, and that a low diploid number is associated with a high number of metacentrics. The chromosome arm number is relatively constant in the different species (55–60).

Four of the eight species studied show interesting chromosome changes. The impala *Aepyceros melampus* exhibits a state of chromosome polymorphism for a Robertsonian fusion (Wallace & Fairall 1967a). Impala heterozygous for the fusion (diploid number 59) are found, as well as impala homozygous for the fusion (diploid number 58) and impala with no fusion (diploid number 60). Tragelaphine antelopes (kudu *Tragelaphus strepsiceros*, Wallace & Fairall 1968a, nyala *Tragelaphus angasi*, Wallace 1976, bushbuck *Tragelaphus scriptus*, Wallace 1977a) all show the presence of a Y-to-autosome fusion in all males studied.

The Bovid Ancestor

Can a postulate be made as to the chromosomal constitution of a common bovid ancestor? In comparing the chromosomes of the different related species of bovids, a reconstruction of the possible paths in chromosomal evolution followed from a common ancestor can be put forward (Wallace 1977b). The chromosome arm number of the different bovids is relatively constant, but the range of diploid numbers shows wide variation. Such a situation is in keeping with Robertsonian variation having taken place during morphological evolution of the different species from a common ancestor.

Several postulates can be made as to the actual chromosomal complement of the ancestral bovid. Firstly, it can be postulated that the ancestral form had an all-acrocentric chromosome complement. Then, chromosome fusion between acrocentrics to produce metacentrics (either associated with morphological divergence or not) would have resulted in the present-

day complements of the different species. Some species have accumulated more metacentrics than others over the years. Such fusions would have occurred to a greater or lesser extent in the different forms as divergence on different paths from common ancestral forms and speciation within separated lineages took place. Secondly, it can be postulated that the ancestral bovid had a diploid number of 60. This, too, fits in with the explanation that the findings in present-day bovids are due to the acceptance of a varying number of Robertsonian fusions by the different evolving species.

Table 1

Summary of chromosome findings in bovids in Kruger National Park

| Species | Sex | Diploid Number | Autosomes | | | X | Y |
|---------------------------------|-----|----------------|--------------|--------------|---|------|------|
| | | | Acrocentrics | Metacentrics | | | |
| Impala | M | 60 | 58 | — | — | 1/a | s/m |
| <i>Aepyceros</i> | F | 60 | 58 | — | — | 1/a | |
| <i>melampus</i> | M | 59 | 56 | 1 | — | 1/a | s/m |
| | F | 59 | 56 | 1 | — | 1/a | |
| | M | 58 | 54 | 2 | — | 1/a | s/m |
| | F | 58 | 54 | 2 | — | 1/a | |
| Kudu | M | 31 | 3 | 26 | — | 1/a | 1/m |
| <i>Tragelaphus strepsiceros</i> | F | 32 | 4 | 26 | — | 1/a | |
| Nyala | M | 55 | 51 | 2 | — | 1/a | 1/sm |
| <i>Tragelaphus angasi</i> | F | 56 | 52 | 2 | — | 1/a | |
| Bushbuck | M | 33 | 7 | 24 | — | 1/a | 1/m |
| <i>Tragelaphus scriptus</i> | F | 34 | 8 | 24 | — | 1/a | |
| Steenbuck | M | 30 | — | 28 | — | 1/a | s/m |
| <i>Raphicerus campestris</i> | F | 30 | — | 28 | — | 1/a | |
| Wildebeest | M | 58 | 56 | 2 | — | 1/a | s/a |
| <i>Connochaetes taurinus</i> | F | 58 | 56 | 2 | — | 1/a | |
| African Buffalo | M | 52 | 42 | 8 | — | 1/a | s/a |
| <i>Syncerus caffer</i> | F | 52 | 42 | 8 | — | 1/a | |
| Waterbuck | M | 50 | 38 | 10 | — | 1/sm | 1/a |
| <i>Kobus ellipsiprymnus</i> | F | 50 | 38 | 10 | — | 1/sm | |

l = large s = small a = acrocentric m = metacentric sm = submetacentric

Acknowledgements

I thank the National Parks Board of Trustees for permission to undertake the study which forms the basis of this paper. The study was aided, in part, by grants from the Witwatersrand University Council Research Fund and the C.S.I.R. I would also like to thank Mr P.M. Faugust for preparing the drawings.

REFERENCES

- HARD, W. L. 1969. The chromosomes of duikers. *Mammalian Chromosomes Newsletter* 10:216–217.
- SYBENGA, J. 1972. *General Cytogenetics*. Amsterdam: North Holland.
- TAYLOR, K. M., D. A. HUNGERFORD and R. L. SNYDERS, 1969. Artiodactyl mammals; their chromosome cytology in relation to patterns of evolution. In: BENIRSCHKE K. (Ed.) *Comparative Mammalian Cytogenetics*. Berlin: Springer-Verlag.
- TOBIAS, P. V. 1953. Trends in the evolution of mammalian chromosomes. *S. Afr. J. Sci.* 50:134–140.
- WALLACE, C. 1976. *Cytogenetic Investigations of Certain Free-roaming Wild Mammals in the Kruger National Park*. Ph.D. Thesis. University of the Witwatersrand, Johannesburg.
- WALLACE, C. 1977a. Chromosome analysis in the Kruger National Park; the chromosomes of the bushbuck (*Tragelaphus scriptus*). *Cytogenet. Cell Genet.* 18:50–56.
- WALLACE, C. 1977b. Chromosome evolution in bovids in the Kruger National Park. *S. Afr. J. Sci.* 73:334–336.
- WALLACE, C. and N. FAIRALL. 1967a. Chromosome polymorphism in the impala. *S. Afr. J. Sci.* 63:482–486.
- WALLACE, C. and N. FAIRALL. 1967b. The chromosomes of the steenbuck. *S. Afr. J. Med. Sci.* 32: 55–57.
- WALLACE, C. and N. FAIRALL. 1968a. Chromosome analysis in the Kruger National Park; a rare translocation chromosome in the kudu. *S. Afr. J. Med. Sci.* 33:113–118.
- WALLACE, C. and N. FAIRALL. 1968b. Chromosome analysis in the Kruger National Park; preliminary results in the Bovidae. *S. Afr. J. Med. Sci.* 33: 119–123.
- WURSTER, D. H. and K. BENIRSCHKE. 1968. Chromosome studies in the super-family Bovoidea. *Chromosoma* 25:152–171.