

THE
ANNALS OF ZOOLOGY

EDITED BY

Professor B. C. Mahendra, F. A. Z.

VOLUME XXIII

(1985)

PART 2

April, 1985

(pp. 53-70)

**CHROMOSOME VARIATION IN THE ASIAN MOUNTAIN
VOLE, *ALTICOLA MACROTIS* Radde, 1861
(RODENTIA, CRICETIDAE)**

By

V. N. Bolshakov, F. A. Z., E. A. Gileva, and G. V. Bykova



Published by

**THE ACADEMY OF ZOOLOGY
KHANDARI CROSS-ROAD,
AGRA-2 (India)**

THE ANNALS OF ZOOLOGY

Published by

THE ACADEMY OF ZOOLOGY

Vol. XXIII

April, 1985

Part 2

**CHROMOSOME VARIATION IN THE ASIAN MOUNTAIN
VOLE, *ALTICOLA MACROTIS* Radde, 1861
(RODENTIA, CRICETIDAE)**

By

V. N. Bolshakov, F. A. Z., E. A. Gileva, and G. V. Bykova
Institute of Plant and Animal Ecology, Urals Scientific Centre,
Academy of Sciences of USSR, Sverdlovsk (USSR)

(With Two Text-figures and Five Plates)

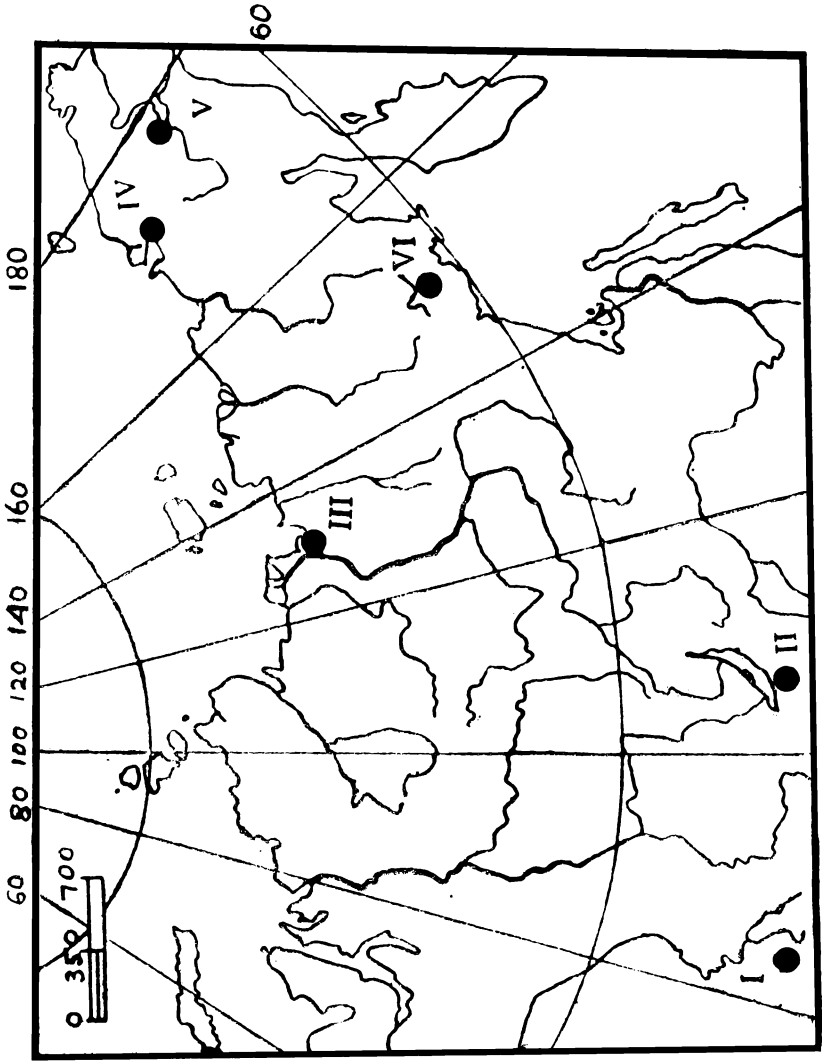
ABSTRACT

Karyotypes of the rodent *Alticola macrotis* Radde from six East-Asian populations were investigated by G- and C-staining methods and an extensive intra- and interpopulational chromosome variability was found. The variability was due mainly to changes in the quantity of C-heterochromatin in the sex chromosomes and probably the ninth autosome. The cytogenetic grouping is congruent with the taxonomic relationships within the species.

INTRODUCTION

The role of karyotype changes in speciation and evolution is a matter of intense discussion. Some authors consider the karyotype changes to be a primary factor in speciation and organismal evolution (Wilson *et al.*, 1974; White, 1978; Templeton, 1981); others regard evolutionary transformation of chromosome complements as a result of a general divergence of species (Mayr, 1978; Charlesworth *et al.*, 1982). It is important, therefore, to investigate the relationship between chromosomal and phenotypic diversity at the early stages of the evolutionary process.

We have studied this relationship in the Asian mountain vole of the genus *Alticola* Blanford, 1881 for a long time. At present taxonomists



Text-fig. 1

include in this genus five species, which are distributed in the mountains of Central and North-Eastern Asia from Western Tibet and Southern Himalayas to North-Eastern Siberia. *A. roylei* Gray, 1842 possesses the largest area. *A. stoliczkanus* Blanford, 1875 inhabits the southern part of the genus *Alticola* area (India: Kashmir). *A. macrotis* Radde, 1861 is distributed in the northern region (mountains of Southern and Eastern Siberia); apparently, this group of typical mountain species is at the stage of an active form-making process. *Alticola macrotis* is of interest from the cytogenetic point of view, as its interpopulation cranio-dental variability has been thoroughly studied (Bolshakov *et al.*, 1980; Vasilyeva *et al.*, 1983; Vasilyeva and Vasilyev, 1984; Gileva *et al.*, 1984). We have investigated the karyotypes of *A. macrotis* from six populations, which were analyzed earlier morphologically. In the present paper we describe the intra- and interpopulation variability of the chromosomes of this species.

MATERIAL AND METHODS

A. macrotis inhabits stony patches and rock exposures wherever it occurs. Most taxonomists recognize three subspecies: *A. m. macrotis* (south of Eastern Siberia), *A. m. vinogradovi* (Altai mountains), and *A. m. lemminus* (North-Eastern Siberia and Chukotka peninsula). We have studied the karyotypes of 104 specimens of *A. macrotis* from six populations. The localities from which they were taken (Text-fig. 1) are as follows: I—the Altai mountains (*A. m. vinogradovi*); II—Baikal Reserve (*A. m. macrotis*); III—the Laptev Sea coast (*A. m. lemminus*); IV—the Chaun inlet coast (*A. m. lemminus*); V—the Anadyr inlet coast (*A. m. lemminus*); and VI—the Kolyma upland (*A. m. lemminus*). These localities will be referred to henceforth by the numbers assigned to them in the figure.

Chromosome preparations of bone marrow were made in a standard way. C-bands were induced according to Sumner (1972). G-banding was performed by the method of Radjabli and Kryukova (1973). The length of routinely stained and G- and C-banded chromosomes were measured on photographs of 282 cells. The nomenclature for centromeric position on chromosomes is given according to Levan *et al.* (1964). The significance of differences of the means was estimated by a one-way analysis of variance. To get relative sizes of the short and long arms of the X and the Y, the arm lengths were normalized by the combined length of both homologues of pairs 9 and 27.

RESULTS AND DISCUSSION

In all the voles karyotyped the diploid number was 56, the same as in the other species of *Alticola* (Bolshakov *et al.*, 1972; Yatsenko, 1980),

The 26 autosome pairs were identical in the animals from all the 6 populations; they include 25 acrocentric pairs (Nos. 1-8 and 10-26) and a pair of small metacentrics (No. 27). These chromosomes do not display any interpopulation variability of G- or C- banding pattern. At the same time *A. macrotis* from various populations is distinguished by the shape of chromosome No. 9 and by the size and shape of the X and Y chromosomes.

In *A. m. vinogradovi* (Population I), the chromosome 9 is telocentric with an arm ratio of 10·98 (obtained from the measured G-banded chromosomes). The telocentric X chromosome is one of the largest in the set, and displays three G-positive bands (Plate I, Fig. 1 A and B). The Y chromosome is the smallest in the complement and consists entirely of C-heterochromatin.

On the whole, the karyotype of *A. m. macrotis* (Population II) is similar to that of *A. m. vinogradovi* (Plate II, Fig. 2 A and B). The autosome No. 9 is telocentric. The X chromosome has a discernible C-heterochromatic short arm; its mean arm ratio is 7·80. Although small in size, the Y chromosome is not the smallest. Its relative length is significantly higher than that in the voles of Population I.

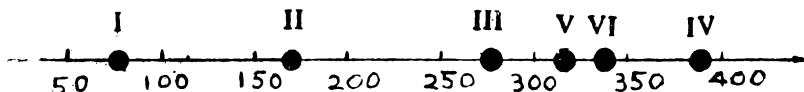
In *A. m. lemminus* (Population III) an intrapopulation variability of shape of the autosome No. 9 is observed (Plate III, Fig. 3 A and B). Its arm ratio, obtained from G-banded chromosomes, varied significantly from 3·95 to 10·98 ($p < 0\cdot001$). The mechanisms responsible for this variation and the interpopulation differences in shape of autosome No. 9 are not completely clear. There is no certainty as to whether its short arm consists entirely of heterochromatin. The intensity of C-staining of the arm is very different in various cells. It can be as dark as the pericentromeric heterochromatin, or as light as the euchromatic chromosomal regions. This discrepancy results probably from the specific molecular properties of the chromatin that the short arm is composed of. The X chromosome of *A. m. lemminus* (III) possesses a distinctive C-positive short arm. The arm ratio ranged from 3·19 to 10·98 with an average value of 4·74 (significant variation, $p < 0\cdot001$). The G-banding pattern of the long arm of the X is identical to that of the voles in Populations I and II. The Y chromosome, composed of C-heterochromatin, is a middle-sized subtelocentric, with a mean arm ratio of 3·52. After G-staining, it exhibits a positive band near the centromere (Plate III, Fig. 3 A and B).

A. m. lemminus (Population IV) displays a most extensive sex chromosome variability in the species investigated (Plate IV, Figs. 4 and 5). The G-banding pattern and the length of the long arm of the X are the same as in other forms, but the arm ratio varies continuously from

1.95 to 3.32, due to significant changes ($P < 0.001$) in the length of the C-heterochromatic short arm. Three discrete morphological variants of the Y chromosome were found in Population IV: a subtelocentric (3 males), a submetacentric (4 males), and a metacentric (1 male), with mean arm ratios 6.09, 2.30 and 1.39 respectively. The size of the long arm of the Y is constant, while the size of the C-positive short arm varies largely. The G-banding pattern of the long arm of the Y is similar to that of the Y of *A. m. lemminus* (III); the short arm is stained dully and homogeneously after G-banding. Autosome No. 9 is submetacentric, its mean arm ratio being 2.71.

The karyotypes of *A. m. lemminus* from Populations V and VI are alike (Plate V, Fig. 6). Autosome No. 9 is nearly submetacentric with arm ratio 2.68-3.09. Two discrete structural types of the X chromosome were observed: telocentric (mean arm ratio 9.34) and subtelocentric (mean arm ratio 3.18), their long arms being equal and identical with respect to G-banding pattern (with the three positive bands) and their short C-heterochromatic arms varying in length ($P < 0.001$). Among 11 X chromosomes studied in Population V, 7 were subtelocentric and 4 were submetacentric. In Population VI, we observed 3 subtelocentric and 4 submetacentric X's. The Y chromosome in both the populations resembles that of the voles from Population III in size, shape, heterochromatic nature, and G-banding pattern.

Thus, *A. macrotis* exhibits a considerable chromosomal diversity, primarily because of changes in the quantity of C-heterochromatin. Generalized estimates of geographical variation of chromosome complements were obtained by canonical variate analysis (Anderson, 1958). Cytogenetic characters used here were arm ratios and relative lengths of autosome No. 9 and short and long arms of sex chromosomes. This first canonical axis accounted for 97.6% of the variance; Text-fig. 2 shows the positions of 6 populations investigated on this axis. As seen from this figure, the cytogenetic grouping of populations is on the whole congruent with the taxonomic relationships within the species. All three subspecies are well separated; furthermore, *A. m. lemminus* exhibits a recognizable geographical



Text-fig. 2

Projection of canonical variables for 6 populations of *A. macrotis* on to the first canonical axis obtained from 6 cytogenetic characters. The numbers here denote the same populations as in Figure 1.

differentiation of karyotypes. It should be noted that the cytogenetic distance between populations III and IV in *A. m. lemminus* is greater than between the pair *A. m. vinogradovi* (I) and *A. m. macrotis* (II), or the pair *A. m. macrotis* (II) and *A. m. lemminus* (III). This is in agreement with the findings of a considerable craniodental divergence within *A. m. lemminus*. In this respect Populations III and IV are also the most remote (Bykova *et al.*, 1978; Vasilyeva *et al.*, 1983).

In other words, *A. macrotis* demonstrates a good concordance between the cytogenetic and morphological differentiation. This is not the case for many other mammals. Recently, some authors have denied the possibility of any causal relationship between chromosomal and phenotypic evolution (Patton and Sherwood, 1983). The problem seems far from being clear. Quite a number of species of mammals is known to display an evident parallelism between karyotypic and exophenotypic differentiation (c. g., Fashing, 1973; Nadler *et al.*, 1973; Davis and Baker, 1974; Mascarello and Hsu, 1976; Pembleton and Baker, 1978; Bohlin and Zimmerman, 1982). This parallelism may be the result of a simple coincidence, but probably in some cases karyotypic changes of a certain type could produce a noticeable phenotypic effect due to the reorganization of nuclear architectonics (Bennet, 1982; Jones, 1979). Such a variation of heterochromatin as that observed in *A. macrotis* may cause the very effect.

Probably, a better understanding of the evolutionary role of chromosomal changes can be attained by performing a comparative study of cytogenetical and morphological diversification in a much broader range of species than it has been done so far.

SUMMARY

In *Alticola macrotis* an extensive variation of the chromosome complement due to changes of C-heterochromatin has been found. *A. macrotis* exhibits a good concordance between the geographic variation of karyotypes and the morphological differentiation.

REFERENCES

- ANDERSON, T. W. (1958) An introduction to multivariate statistical analysis. *New York: Wiley*, 374 p.
- BENNET, M. D. (1982) Nucleotypic basis of the spatial ordering of chromosomes in eukaryotes and the implications of the order for genome evolution and phenotypic variation. *In: Genome evolution*, ed. G. A. Dover and R. B. Flavell. *New York, London: Academic Press*, 239-261.
- BOHLIN, P. G. and ZIMMERMAN, E. G. (1982) Genic differentiation of two chromosome races of the *Geomys bursarius* complex. *Journal of Mammalogy*, 63, N. 2, 218-228.

- BOLSHAKOV, V. N., GILEVA, E. A., MIHALEV, M. V., and POKROVSKY, A. V. (1972) An experimental study of biological specificity of the Gobi-Altai vole. *Proceedings of Academy of Sciences of USSR*, 202, N. 5, 1216-1218 (In Russian).
- BOLSHAKOV, V. N., VASILYEVA, I. A., and MALEEVA, A. G. (1980) Morphotypic variability of the vole teeth. *Moscow : Nauka*, 137 p. (In Russian).
- BYKOVA, G. V., VASILYEVA, I. A., and GILEVA, E. A. (1978) Chromosomal and morphological diversity in two populations of Asian mountain vole, *Alticola lemminus* Miller (Rodentia, Cricetidae). *Experientia*, 34, N. 9, 1146-1148.
- CHARLESWORTH, B., LANDE, R., and SLATKIN, M. (1982) A neo-Darwinian commentary on macroevolution. *Evolution*, 36, N. 3, 474-498.
- DAVIS, B. L. and BAKER, R. J. (1974) Morphometrics, evolution and cytotaxonomy of mainland bats of the genus *Macrotus* (Chiroptera : Phyllostomatidae). *Systematic Zoology*, 23, N. 1, 26-39.
- FASHING, N. J. (1973) Implications of karyotypic variation in kangaroo rat, *Dipodomys heermanni*. *Journal of Mammalogy*, 54, N. 4, 1018-1020.
- GILEVA, E. A., VASILYEVA, I. A., and VASILYEV, A. G. (1984) Variability of skull traits in cytotypes of the lemming vole. In : Research in genetics and selection in the Urals. *Sverdlovsk*, 14-16. (In Russian).
- JONES, R. W. (1979) Speculations on the function of satellite DNA in evolution. *Zeitschrift für Morphologie und Anthropologie*, 69, N. 2, 143-171.
- LEVAN, A., FREDGA, K., and SANDERSON, A. A. (1964) Nomenclature for centromeric position on chromosomes. *Hereditas*, 60, N. 2, 269-271.
- MASCARELLO, J. T. and HSU, T. C. (1976) Chromosome evolution in woodrats, genus *Neotoma* (Rodentia : Cricetidae). *Evolution*, 30, N. 1, 152-169.
- MAYR, E. (1978) Modes of animal speciation. *Systematic Zoology*, 27, N. 4, 478-482.
- NADLER, C. F., KOROBITSYNA, K. V., HOFFMAN, R. S., and VORONTSOV, N. N. (1973) Cytogenetic differentiation, geographic distribution, and domestication in palaeartic sheep (*Ovis*). *Zeitschrift für Säugetierkunde*, 38, N. 2, 109-125.
- PATTON, J. L. and SHERWOOD, S. W. (1983) Chromosome evolution and speciation in rodents. *Annual review of ecology and systematics*, 14 : 139-158.
- PEMBLETON, E. F. and BAKIR, R. J. (1978) Studies of a contact zone between chromosomally characterized populations of *Geomys bursarius*. *Journal of Mammalogy*, 59, N. 2, 233-242.

- RADJABLI, S. I. and KRYUKOVA, E. P.** (1973) A comparative analysis of the chromosome banding pattern in two hamster species. *Tsitologiya*, 15, N. 12, 1527-1531 (In Russian).
- SUMNER, A. T.** (1972) A simple technique for demonstrating centromeric heterochromatin. *Experimental Cell Research*, 75, N. 1, 304-306.
- TEMPLETON, A. R.** (1981) Mechanisms of speciation—a population genetic approach. In: *Annual review of ecology and systematics*, 12, 23-48.
- VASILYEVA, I. A., VASILYEV, A. G., and GILEVA, E. A.** (1983) Morphometrics of M^3 in two populations of the lemming vole and chromosome differentiation. In: *Actual problems in theriology. Sverdlovsk*, 22-25 (In Russian).
- VASILYEVA, I. A. and VASILYEV, A. G.** (1984) A phenetic investigation of systematic relationship in two subspecies of *Alticola macrotis* Radde, 1861. In: *Research in genetics and selection in the Urals. Sverdlovsk*, 53-70 (In Russian).
- WHITE, M. J. D.** (1978) Modes in speciation. *San Francisco: Freeman*, 455 p.
- WILSON, A. C., SARICH, V. M., and MAXSON, L. R.** (1974) The importance of gene rearrangement in evolution: evidence from studies on rates of chromosomal, protein and anatomical evolution. *Proceedings of National Academy of Sciences of USA*, 71, N. 8, 3028-3030.
- YATSENKO, V. N.** (1980) C-heterochromatin and chromosome polymorphism in the Gobi-Altai vole, *Alticola stoliczkanus barakschin* Bannikov, 1948 (*Rodentia, Cricetidae*). *Proceedings of Academy of Sciences of USSR*, 254, N. 4, 1009-1010 (In Russian).

EXPLANATION OF PLATES

PLATE I

- Fig. 1** Karyotype of a male *A. m. vinogradovi* (Population I): (A) routine staining (autosome 9 is marked arbitrarily); (B) G-banding.

PLATE II

- Fig. 2** Karyotype of a male *A. m. macrotis* (Population II): (A) routine staining; (B) C-banding (autosome 9 is marked arbitrarily).

PLATE III

- Fig. 3** Karyotype of a male *A. m. lemminus* (Population III): (A) G-banding; (B) C-banding.

PLATE IV

- Fig. 4** Karyotype of a male *A. m. lemminus* (Population IV): routine staining.
- Fig. 5** Various morphological variants of sex chromosomes of *A. m. lemminus* (Population IV): (A) G-banding; (B) C-banding.

PLATE V

- Fig. 6** Karyotype of a male *A. m. lemminus* (Population V): C-staining.

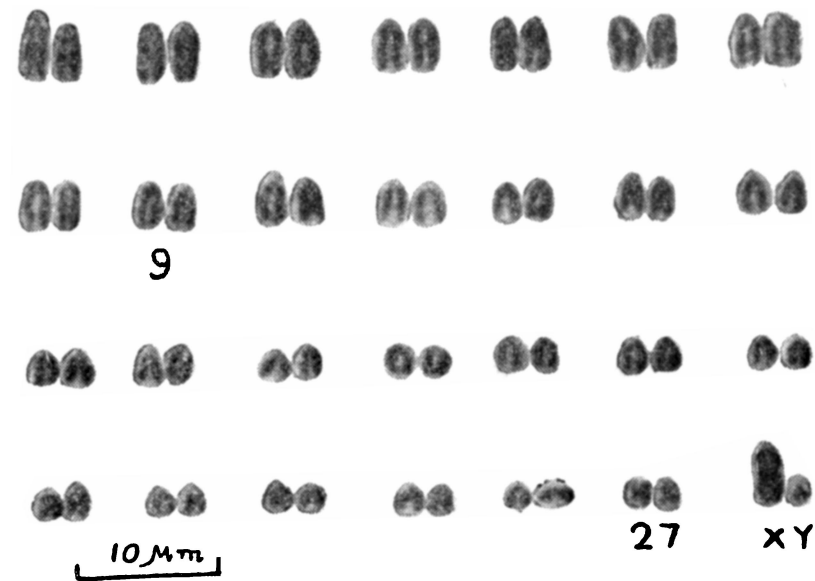


Fig. 1, A

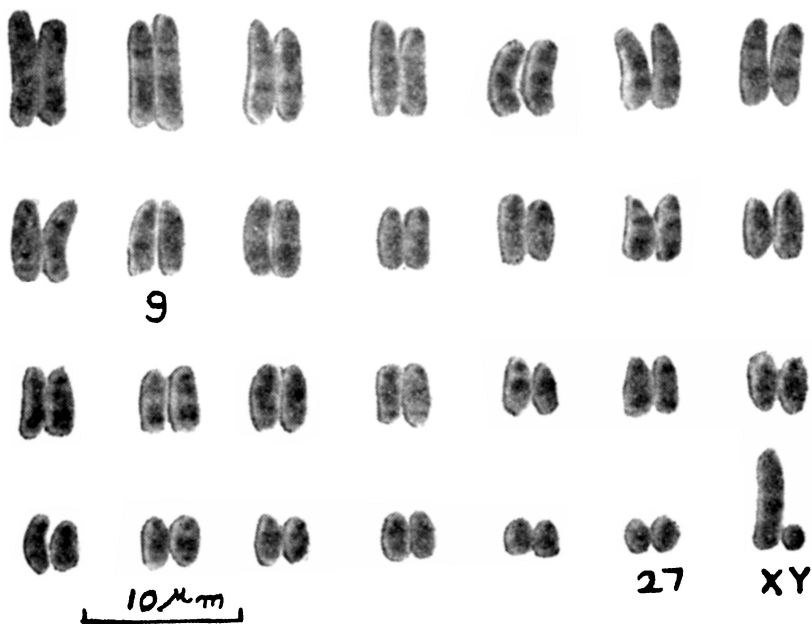


Fig. 1, B

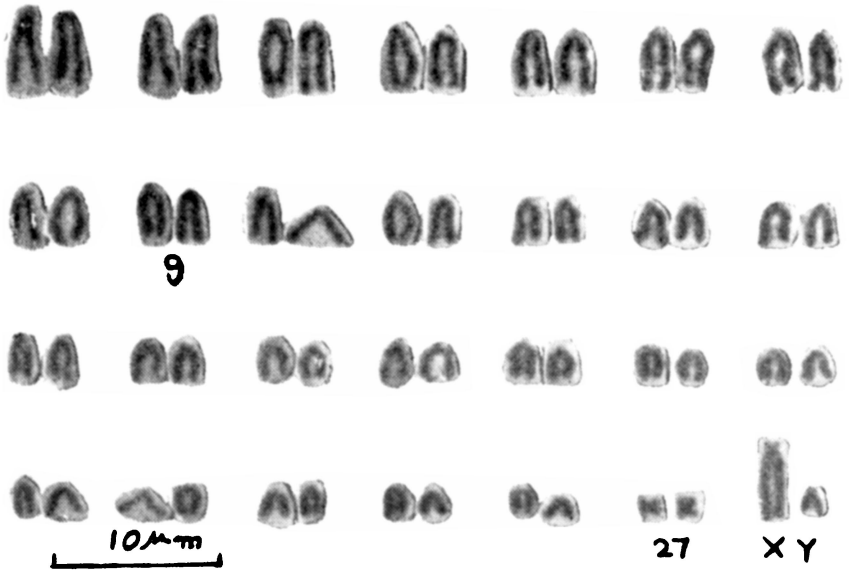


Fig. 2, A

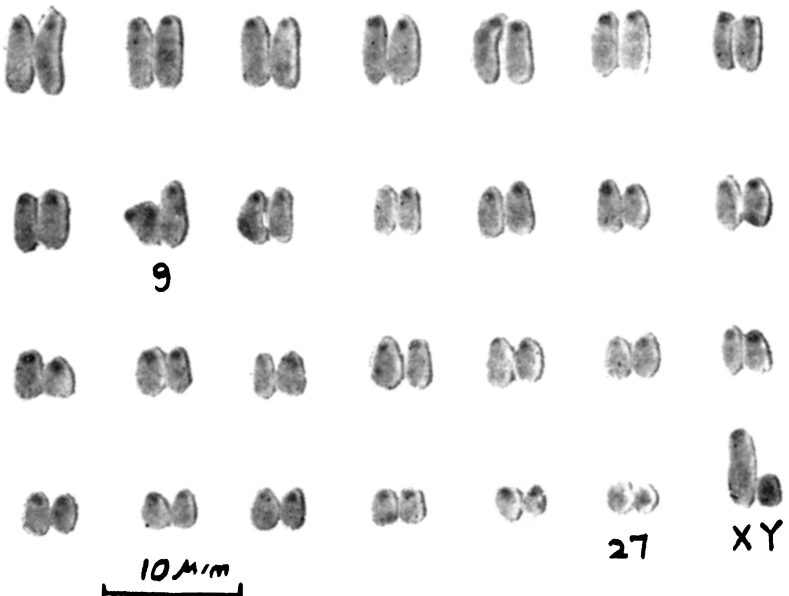


Fig. 2, B

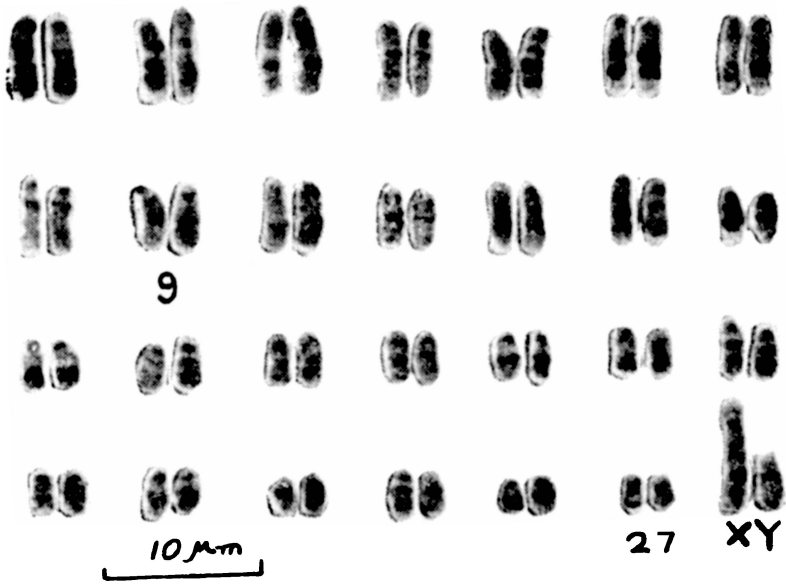


Fig. 3, A

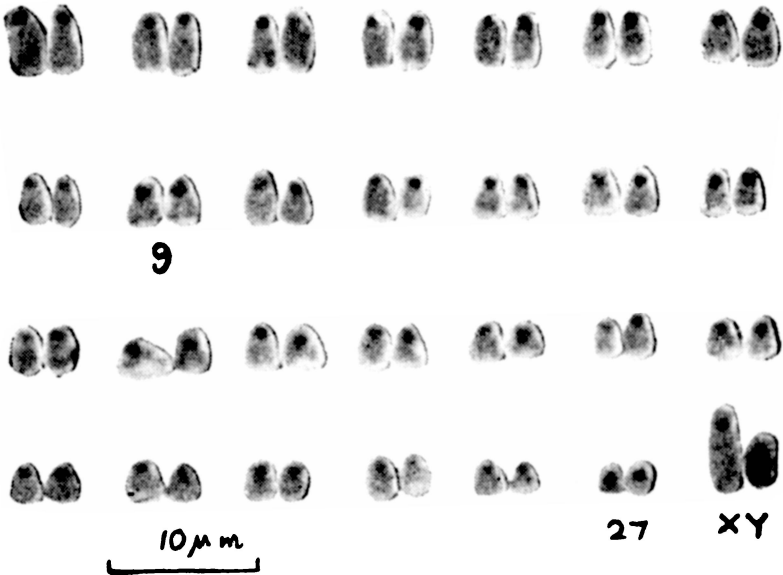


Fig. 3, B

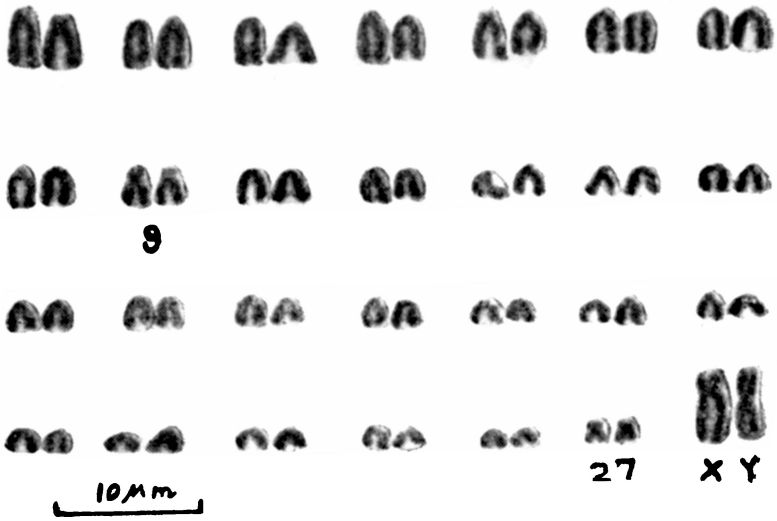


Fig. 4

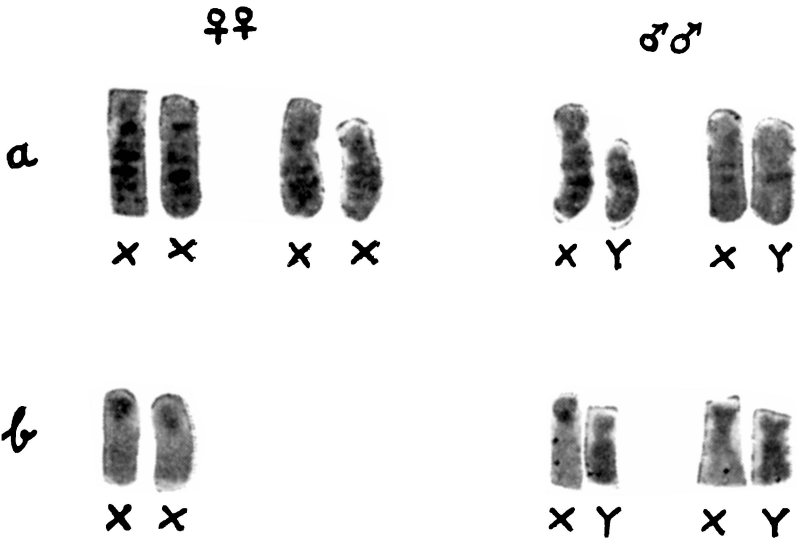


Fig. 5

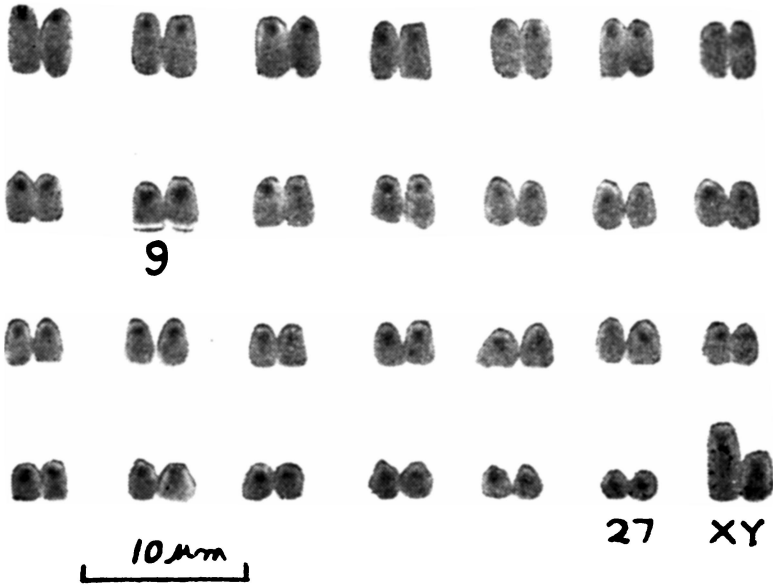


Fig. 6
PLATE V