

THE X CHROMOSOMES OF MAMMALS: KARYOLOGICAL HOMOLOGY AS REVEALED BY BANDING TECHNIQUES¹

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ABSTRACT

A comparison of the Giemsa-banding patterns of the *X* chromosomes in various mammalian species including man indicates that two major bands (A and B), which are resistant to trypsin and urea-treatments, are always present irrespective of the gross morphology of the *X* chromosomes. This is true in all mammalian species with the "original or standard type" *X* chromosomes (5–6% of the haploid genome) thus far analyzed. In the unusually large-sized *X* chromosomes the extra chromosomal material may be due either to the addition of genetically inert constitutive heterochromatin or to an *X*-autosome translocation. In these *X* chromosomes two major bands are present in the actual *X*-chromosome segment. Our data on C and G band patterns also support OHNO's hypothesis that the mammalian *X* chromosome is extremely conservative in its genetic content, in spite of its cytogenetic variability.

THE mammalian sex chromosomes vary considerably from species to species, in size as well as in morphology. The *X* chromosome, for example, may be the smallest or the largest element of the complement depending on the number and size of the autosomes present in a species. If many autosomes fused to form a small number of very large elements, as in the case of many species of bats, the *X* chromosome becomes the smallest element. On the other hand, if the autosomes are numerous and small, as in the case of the domestic *Bos* and the domestic dog, the *X* becomes the largest chromosome in the genome. It may be metacentric, submetacentric, or acrocentric. The *Y* chromosome is also extremely variable in size, ranging from a barely-discernible minute chromosome to second in size only to the *X* chromosome.

OHNO (1967) hypothesized that the mammalian *X* chromosome is extremely conservative in its genetic content, in spite of its cytological variability. This hypothesis is based on several facts: (a) many sex-linked genes, e.g., glucose-6-phosphate dehydrogenase (G-6-PD), are found to be sex-linked throughout the class, whenever genetic data are available; (b) the "dosage compensation" phenomenon prevail in placental mammals so far studied; (c) the functional *X* chromosome of mammals is similar in size relative to the entire complement, i.e.,

¹ This paper is dedicated to PROF. T. C. Hsu for his untiring dedication and generous contributions toward the progress of mammalian cytogenetics throughout the world.

it comprises approximately 5–6% of the haploid female genome (OHNO, BECAK and BECAK 1964).

The variability of the size of the *X* chromosome in mammals is, therefore, determined by two major factors: the number and size of the autosomes as mentioned earlier and the amount of extra chromosomal material attached to the *X* chromosome. Actually there are two systems whereby this ratio may change. The first, and probably the more common one, is the addition of the genetically inert constitutive heterochromatin material to the *X* chromosome, thus increasing the size of the *X* but not the genetic information. Many such examples have been described (SHARMA, PATHAK and RAY-CHAUDHURI 1970; WURSTER, SNAPPER and BENIRSCHKE 1971; PATHAK *et al.* 1973). The second category is the *X*-autosome translocation. When an autosome is translocated *in toto* or in part onto an *X*, the size of the *X* is naturally increased. Such cases are not common (FREDGA 1970), and usually these can be identified by the presence of the homolog of the translocated autosome which becomes an unpaired element, giving the males an odd diploid number.

The situation with the *Y* chromosome variation is very similar. The variation in size of the mammalian *Y* is due principally to the addition of constitutive heterochromatin. However, *Y*/autosome translocation has also been reported (MATHEY 1966).

The chromosome banding procedures have significantly increased the resolution of cytological preparations. Comparison between the *X* chromosomes of related species by means of the fluorescence banding (Q bands), the Giemsa banding (G bands), and the reverse banding (R bands) revealed similar patterns, indicating a crude homology in terms of the arrangement of genetic material within the mammalian *X* chromosome (PEARSON *et al.* 1971; YOSIDA and SAGAI 1973; BORROW and MADAN 1973; PATHAK, HSU and ARRIGHI 1973; EVANS, BUCKLAND and SUMNER 1973; GROUCHEY *et al.* 1972; TURLEAU, GROUCHY and KLEIN 1972; LEJEUNE *et al.* 1973). However, in most of these studies, comparisons were made with a limited number of closely related species. Since we have in our laboratory a variety of frozen animal cells, we considered it worthwhile to compare the sex chromosomes of as many representative taxa as feasible by means of the G and C banding techniques. Table 1 contains a list of the mammalian species whose sex chromosomes have been studied by others using Giemsa-banding.

MATERIALS AND METHODS

With a few exceptions in which primary cultures were used for cytological preparations, all others were recovered cultures frozen during the past decade in this laboratory. All cultures were grown in McCoy's 5a medium supplemented with 20% fetal bovine serum.

Harvest was made with a 1-hr Colcemid (0.05 $\mu\text{g}/\text{ml}$) treatment to arrest mitoses. Air-dried slides were made and the trypsin procedure (SEABRIGHT 1971) or the Urea procedure (SHIRAIISHI and YOSIDA 1972) was used for G-banding. The slides were stained in 2% Giemsa mixture diluted in phosphate buffer.

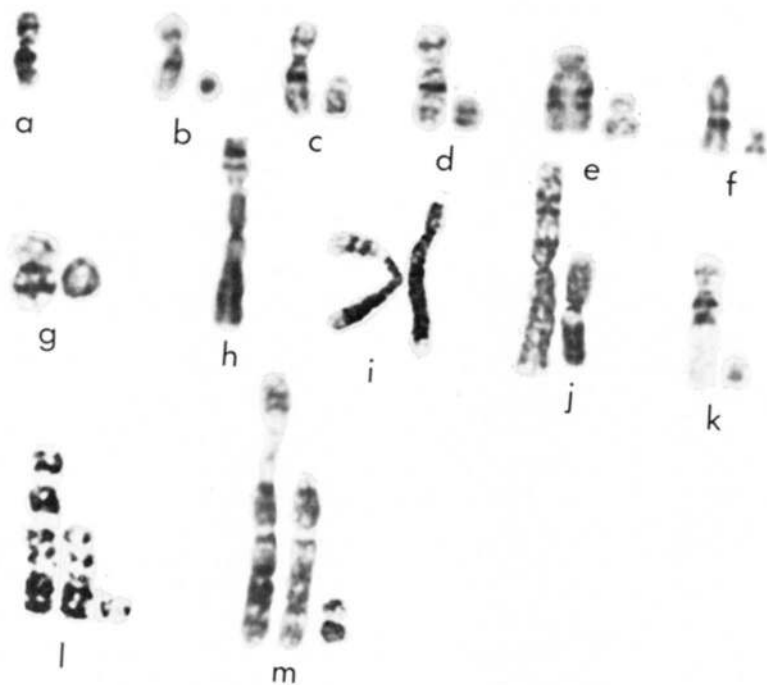
In many species the cells were available from only one sex, either from a male or from a female individual. Since two *X* chromosomes of a female exhibit similar Giemsa-banding patterns, only one *X* has been reproduced in the figures.

RESULTS

The X Chromosome

Table 1 lists the species of the mammals, with their taxonomic positions, whose sex chromosomes have been analyzed by G banding thus far. Although the bulk of the material came from the present investigation, the table also includes data obtained by other investigators. Figure 1 presents photomicrographs of the sex chromosomes of several representative types in respect to the X chromosome constitution. Figures 1a-f show the "standard type", (the "original type" of OHNO, BECAK and BECAK 1964), viz., the type with the X chromosome representing approximately 5-6% of the haploid genome. Figures 1g-k exemplify those containing additional heterochromatin; and Figures 1l-m, those with autosomal translocation. In Figure 2, a number of diagrammatic representations are shown for comparison of the G bands patterns.

Generally, in the "standard type," the X chromosome exhibits two major bands and several minor bands when the preparations are treated with trypsin properly.



FIGURES 1a-m.—Giemsa-banding patterns of X chromosomes in various mammalian species. First row: "Original or standard type" metacentric, submetacentric, subtelocentric, and acrocentric X chromosomes, a. *Atilax paludinosus* (X), b. *Ursus americanus* (XY), c. *Homo sapiens* (XY), d. *Xerus rutilus* (XY), e. *Sigmodon hispidus* (XY), f. *Clethrionomys rutilus* (XY). Second row: Unusually large-sized X chromosomes where constitutive heterochromatin is added, g. *Didelphis virginiana* (XY), h. *Microtus agrestis* (X), i. *Tylomys panamensis* (XY), j. *T. nudicaudus* (XY), k. *Balaenoptera acutorostrata* (XY). Third row: Large-sized X chromosomes due to X-autosome translocation, l. *Carollia perspicillata* (XY₁Y₂), m. *Muntiacus muntjak* (XY₁Y₂).

TABLE 1

A list of mammalian species whose sex chromosomes have been analyzed by Giemsa (G) banding

Species	References
Marsupialia	
Didelphidae	
<i>Didelphis virginiana</i> (Opossum)	This paper
Macropodidae	
<i>Potorous tridactylus</i> (Rat kangaroo)	This paper
Primates	
Tupaiaidae	
<i>Tupaia montana</i> (Mountain tree shrew)	This paper
<i>Urogale everetti</i> (Mindanao tree shrew)	This paper
Cercopithecidae	
<i>Macaca mulatta</i> (Rhesus macaque)	STOCK and HSU 1973
<i>Cercopithecus aethiops</i> (African green monkey)	STOCK and HSU 1973
Pongidae	
<i>Pan troglodytes</i> (Chimpanzee)	BOBROW and MADAN 1973; EGOZCUE, CABALLIN and GODAY 1973
<i>Gorilla gorilla gorilla</i> (Gorilla)	EGOZCUE <i>et al.</i> 1973; SPERLING, Pers. comm.
<i>Pongo pygmaeus</i> (Orangutan)	EGOZCUE <i>et al.</i> 1973; SPERLING, Pers. comm.
Homonidae	
<i>Homo sapiens</i> (Man)	SEABRIGHT 1972; This paper
Chiroptera	
Pteropidae	
<i>Syconycteris australis</i>	This paper
Phyllostomidae	
<i>Artibeus lituratus</i> (Big fruit-eating bat)	This paper
<i>Carollia perspicillata</i> (Seba's fruit bat)	PATHAK, HSU and UTAKOJI 1973
<i>C. brevicauda</i>	This paper
<i>C. castanea</i> (Allen's fruit bat)	This paper
<i>Chiroderma villosum</i>	This paper
<i>Sturnira</i> spp.	This paper
<i>Anoura geoffroyi</i> (Geoffroy's tailless bat)	This paper
<i>Choeroniscus intermedius</i> (Long-tailed bat)	This paper
Rodentia	
Heteromyidae	
<i>Dipodomys microps</i> (Kangaroo rat)	This paper
<i>D. merriami</i>	This paper
Cricetidae	
<i>Gerbillus gerbillus</i> (Gerbil)	This paper
<i>Cricetulus griseus</i> (Chinese hamster)	KATO and YOSIDA 1972; KAKATI and SINHA 1972; This paper
<i>Mesocricetus auratus</i> (Syrian or "golden" hamster)	POPESCU and DI PAOLO 1972
<i>M. newtoni</i> (Romanian hamster)	VOICULESCU, VOGEL and WOLF 1972
<i>Microtus agrestis</i> (Field vole)	COOPER and HSU 1972; This paper
<i>Clethrionomys rutilus</i> (Alaskan red-backed vole)	This paper
<i>Peromyscus crinitus</i> (Canyon mouse)	PATHAK, HSU and ARRIGHI 1973
<i>P. eremicus</i> (Cactus mouse)	PATHAK, HSU and ARRIGHI 1973
<i>Neotoma albigula</i> (White-throated wood rat)	MASCARELLO, STOCK and PATHAK 1974

- N. lepida* MASCARELLO, STOCK and PATHAK 1974
N. micropus (Plains woodrat) MASCARELLO, WARNER and BAKER 1974
N. phenax MASCARELLO, WARNER and BAKER 1974
Tylomys panamensis (Climbing rat) PATHAK *et al.* 1973
T. nudicaudus PATHAK *et al.* 1973
Baiomys taylori (Pygmy mouse) This paper
Sigmodon arizonae (Arizona cotton rat) ZIMMERMAN and SIHVONEN 1973;
This paper
S. hispidus (Eastern cotton rat) This paper
- Muridae
- Mus musculus* (House mouse) SCHNEDEL 1971; BUCKLAND, EVANS and
SUMNER 1971; NESBITT and
FRANCKE 1973; This paper
M. poschiavinus (Tobacco mouse) ZECH *et al.* 1972
Rattus norvegicus (Norway rat) SCHNEDEL and SCHNEDEL 1972; UNAKUL
and HSU 1972
R. rattus (Black rat) YOSIDA and SAGAI 1973
R. exulans YOSIDA and SAGAI 1973
R. muelleri YOSIDA and SAGAI 1973
R. fuscipes YOSIDA and SAGAI 1973
R. conatus YOSIDA and SAGAI 1973
R. sabanus YOSIDA and SAGAI 1973
Apodemus flavicollis WOLF *et al.* 1972
- Sciuridae
- Spermophilus columbianus* (Ground squirrel) This paper
Xerus rutilus (African ground squirrel) This paper
- Caviidae
- Cavia porcellus* (Guinea pig) This paper
- Lagomorpha
- Leporidae
- Lepus americanus* (Snowshoe hare) This paper
Oryctolagus cuniculus (Domestic rabbit) This paper
Sylvilagus bachmanni (Brush rabbit) This paper
- Carnivora
- Mustelidae
- Mustela putorius furo* (Ferret) FREDGA and MANDAHL 1973
M. rozosa (Least weasel) This paper
- Procyonidae
- Bassariscus astutus* (Ring-tailed cat) This paper
- Canidae
- Vulpes velox* (Plains kit fox) This paper
V. macrotis (Desert kit fox) This paper
Canis familiaris (Dog) This paper
- Ursidae
- Ursus americanus* (American black bear) This paper
U. arctos (Grizzly bear) This paper
- Viverridae
- Atilax paludinosus* (Marsh mongoose) This paper
Herpestes edwardsi (Indian mongoose) FREDGA and MANDAHL 1973
- Cetacea
- Balaenopteridae
- Balaenoptera acutorostrata* (Minke whale) This paper
B. physalus (Fin whale) This paper

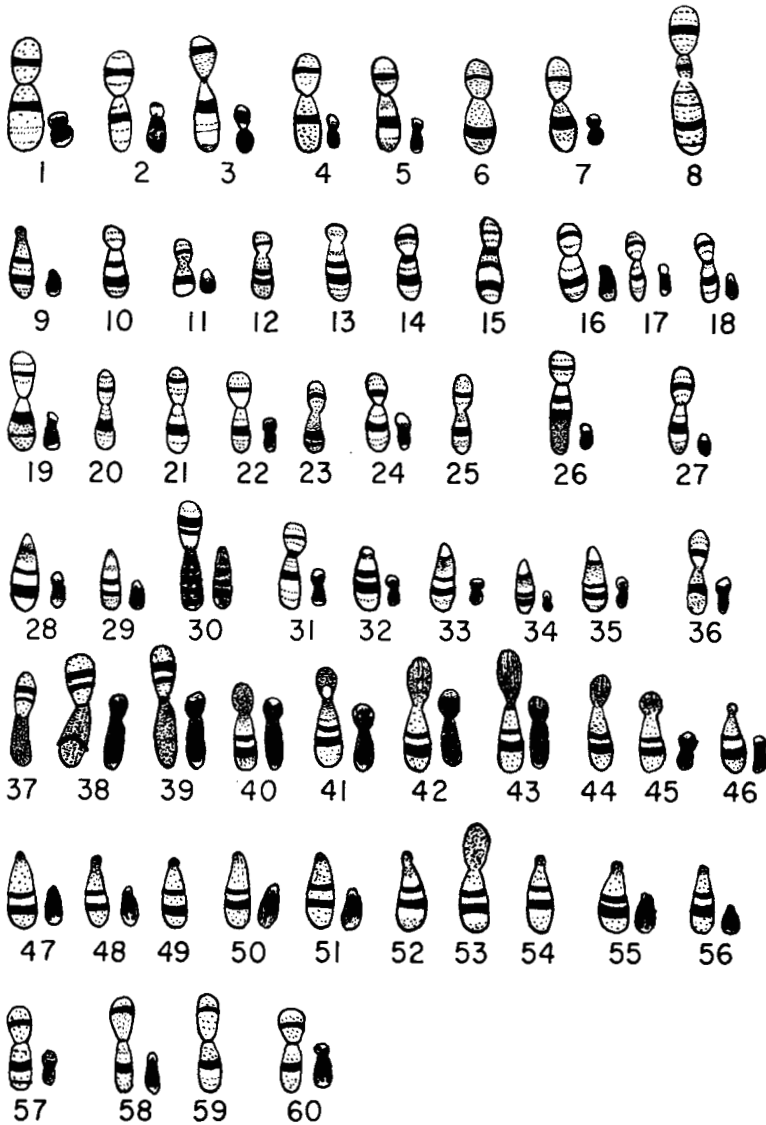


FIGURE 2.—Diagrammatic figures of X chromosome Giemsa banding patterns in 1. *Pan troglodytes*, 2. *Gorilla gorilla*, 3. *Pongo pygmaeus*, 4. *Cercopithecus aethiops*, 5. *Macaca mulatta*, 6. *Urogale everetti*, 7. *Tupaia montana*, 8. *Potorous tridactylus*, 9. *Syconycteris australis*, 10. *Artibeus lituratus*, 11. *Carollia castanea*, 12. *Chiroderma villosum*, 13. *Sturnira* spp., 14. *Anoura geoffroyi*, 15. *Choeroniscus intermedius*, 16. *Lepus americanus*, 17. *Oryctolagus cuniculus*, 18. *Sylvilagus bachmanni*, 19. *Mustela putorius*, 20. *M. rososa*, 21. *Bassariscus astutus*, 22. *Vulpes velox*, 23. *V. macrotis*, 24. *Canis familiaris*, 25. *Herpestes edwardsi*, 26. *Balaenoptera physalus*, 27. *Tapirus terrestris*, 28. *Cervus elaphus*, 29. *Muntiacus reevesi*, 30. *Rangifer tarandus*, 31. *Bos taurus*, 32. *Capra hircus*, 33. *Ovis canadensis*, 34. *O. aries*, 35. *Ammotragus lervia*, 36. *Sus scrofa*, 37. *Gerbillus gerbillus*, 38. *Cricetulus griseus*, 39. *Mesocricetus auratus*, 40. *M. neotoni*, 41. *Peromyscus crinitus*, 42. *P. eremicus*, 43. *Neotoma albigula*, 44. *N. phenax*, 45. *Baiomys taylori*, 46. *Sigmodon arizonae*, 47. *Mus musculus*, 48. *M. poschiavinus*, 49. *Apodemus flavicollis*, 50. *Rattus*

TABLE 1—Continued

Species	References
Artiodactyla	
Cervidae	
<i>Cervus elaphus</i> (Red deer)	This paper
<i>Muntiacus muntjak</i> (Indian muntjac)	PATTERSON and PETRICCIANI 1973
<i>M. reevesi</i> (Reeves' muntjac)	This paper
<i>Rangifer tarandus</i> (Caribou)	This paper
Bovidae	
<i>Bos taurus</i> (Cattle)	SCHNEIDL 1972; EVANS, BUCKLAND and SUMNER 1973; This paper
<i>Capra hircus</i> (Goat)	EVANS, BUCKLAND and SUMNER 1973
<i>Ovis canadensis</i> (Wild sheep)	NADLER, HOFFMANN and WOLF 1973
<i>O. aries</i> (Domestic sheep)	EVANS, BUCKLAND and SUMNER 1973
<i>Ammotragus lervia</i> (Barbary sheep)	This paper
Suidae	
<i>Sus scrofa</i> (Wild pig)	SCHNEIDL 1973
Perissodactyla	
Tapiridae	
<i>Tapirus terrestris</i> (Brazilian tapir)	This paper

When the preparations are over-treated, the minor bands are no longer noticeable, but the two major bands usually persist. One of the major bands, hereafter referred to as Band A, is apparently composed of two dark sub-bands spaced closely to each other. This differentiation can be observed only in favorable cells. In most cases, these two sub-bands merge, forming a single broad band. The second band, referred to as Band B, is narrower than Band A but is always intensely stained with Giemsa.

Using the human X chromosome as a convenient example, Band A is located at the proximal portion of the long arm, straddling the zones Xq1 and Xq2, whereas Band B is located in the middle of the short arm, crossing zones Xp1 and Xp2 (PARIS CONFERENCE 1972). An additional broad band (Xq2.5) is found to locate at the distal portion of the human X chromosome. However, this particular band, like minor bands, is susceptible to trypsin overtreatment. In the SEABRIGHT paper (1972), her Figure 1 shows the major bands as well as the additional bands, but her Figure 5 shows only the two major bands.

In all mammalian species with the "standard type" X chromosomes thus far analyzed, the two major bands are present irrespective of the gross morphology of the chromosomes. However, the locations of these two major bands may vary. In acrocentric chromosomes, they are of course together in the same arm, with Band A more distal than Band B. In metacentric and submetacentric chromosomes, the two bands may be separated, one on each arm (Figure 2).

norvegicus, 51. *R. rattus*, 52. *R. exulans*, 53. *R. muelleri*, 54. *R. fuscipes*, 55. *R. conatus*, 56. *R. sabanus*, 57. *Spermophilus columbianus*, 58. *Dipodomys microps*, 59. *D. merriami*, 60. *Cavia porcellus*.

It is now very easy to demonstrate constitutive heterochromatin. The C band staining procedure (ARRIGHI and HSU 1971) can positively identify heterochromatic segments. In many species with large X chromosomes—e.g., the Chinese hamster, the Syrian hamster, *Microtus agrestis*, *Tylomys panamensis*, etc.—the long arm is invariably totally C band positive. In opossum X chromosome the heterochromatin is present in both arms (SINHA, KAKATI and PATHAK 1972). In *M. agrestis* and *T. nudicaudus*, a portion of the short arm (the proximal 1/4) is also heterochromatic. G band staining shows two distinct bands in the euchromatic segment of the giant X chromosome. A similar situation is found in other species possessing large X chromosomes. Thus, when the large amount of heterochromatin is disregarded, the euchromatic segments of these chromosomes are similar in G band patterns to those of the standard type (Figures 1a–f). Since in most of these cases heterochromatin is added, as one total chromosome arm, to the original acrocentric X , the two major G bands are invariably together in the same arm. An exceptional case is found in the Minke whale, *Balaenoptera acutorostrata* whose original X is a submetacentric and heterochromatin was added as an extension of the euchromatic long arm; the two major G bands are found in separate arms.

When an autosome is translocated onto an X chromosome, as in the cases of the Seba's fruit bat (*Carollia perspicillata*), and the Indian Muntjac (*Muntiacus muntjak*), the banding pattern of this translocated segment is expected to be the same as the free homolog or Y_1 . This was found to be true (Figures 1l–m). The real X chromosome is, therefore, represented by the short arm and the proximal segment of the long arm. The two typical G bands are both located in the short arm of the Muntjac, but are separated, one on each arm, in *Carollia*. FREDGA (1971) and COMINGS (1971) failed to demonstrate these two bands on the X chromosomes of the same Muntjac using the QM banding technique.

The Y Chromosome

In C band preparations, the mammalian Y chromosome usually appears heterochromatic except when the Y is a tiny element. However, the intensity of staining of the Y chromosome varies from species to species and in some cases even from segment to segment within the same Y . The best example is probably the Caribou *Rangifer tarandus* (Figure 3). The Y chromosome contains distinct C banding pattern.

In G band preparations, longer Y chromosomes frequently show light and dark bands instead of being heavily stained throughout the lengths (Figures 1 and 2). Of particular interest is the Y of *Microtus agrestis*. COOPER and HSU (1972) reported that in G band preparations the centromeric area, including the very short second arm, is lightly stained while the rest of the long arm is heavily stained. This staining characteristic of the Y chromosome has also been reported in several species of *Tylomys* (PATHAK *et al.* 1973). Whether this lightly stained area represents the functional portion of the Y remains to be confirmed. In C band preparations this tiny fragment is not always observed.

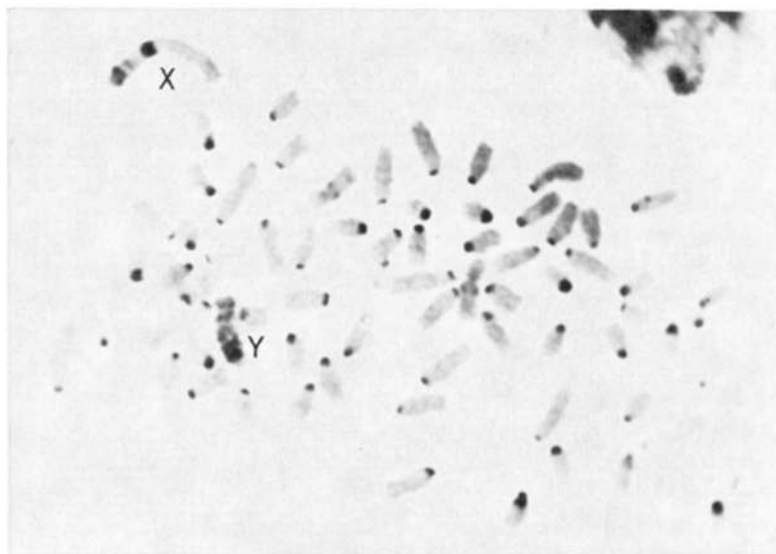


FIGURE 3.—A metaphase spread C band pattern of *Rangifer tarandus* chromosomes. Sex chromosomes (X-Y) showing segmental staining patterns.

DISCUSSION

Although G band patterns of metaphases are not as precise as the banding patterns of the polytene chromosomes where the chromosomes are not only greatly stretched but also pair between the homologs, the G bands (or other banding techniques) are at least great improvements from conventional karyotyping. When closely related species are compared, or when a limited number of rearrangements occur within a karyotype, banding pattern analyses provide excellent information for determining homology. When phylogenetic relationships are remote and when the chromosome morphology changes a great deal as in the present report, comparing G bands for homology is unfortunately not as precise as one would like. There is no assurance that a band found in the X chromosome of one species is strictly homologous to a similar band found in the X chromosome of another species belonging to an entirely different order. Nevertheless, when a large sample of specimens is analyzed, and the similarity persists, the value of the data may be increased. The two trypsin-resistant bands of all X chromosomes are always present, strongly suggesting that they are more or less the same. The banding patterns of the X chromosomes of various mammals add further credence to the hypothesis arrived at from genetic data that the evolution of the mammalian X has been conservative in terms of the retention of its genetic material. When the field of molecular cytogenetics advances to such a stage that the DNA composition of each band can be identified, the problem should be re-examined.

If the foregoing assumption is a reasonable one, then the basic mammalian X chromosome simply underwent a number of inversions, pericentric and para-

centric. Our data on C banding and G banding also support OHNO's contention that the basic X chromosome comprises of approximately 5–6% of the haploid mammalian genome. Larger X chromosomes contain either additional heterochromatic material or an autosomal segment translocated onto the X. Our only objection is to his terms "duplicate," "triplicate," etc., which at least imply that the genetic material is doubled, tripled, etc. Since constitutive heterochromatin is not known to carry genetic messages, addition of heterochromatin would mean only the addition of inert chromatin material. Furthermore, the addition of heterochromatin can be of various proportions, not necessarily in the exact doubling or tripling the length of the original X.

The Y chromosome may be a very small, microscopically barely perceptible body, in a number of mammals, notably in the opossum *Didelphus albiventris*, in many bats, and in many marmosets (HSU and BENIRSCHKE 1967–1973). Since these species perpetuate without difficulty, it must be assumed that the tiny Y chromosomes of these species carry the necessary genetic information.

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LITERATURE CITED

- ARRIGHI, F. E. and T. C. HSU, 1971 Localization of heterochromatin in human chromosomes. *Cytogenetics* **10**: 81–86.
- BOBROW, M. and K. MADAN, 1973 A comparison of chimpanzee and human chromosomes using the Giemsa-11 and other chromosome banding techniques. *Cytogenet. Cell Genet.* **12**: 107–116.
- BUCKLAND, R. A., H. J. EVANS and A. T. SUMNER, 1971 Identifying mouse chromosomes with the ASG technique. *Exptl. Cell Res.* **69**: 231–236.
- COMINGS, D. E., 1971 Heterochromatin of the Indian muntjac replication, condensation, DNA ultracentrifugation, fluorescent and heterochromatin staining. *Exptl. Cell Res.* **69**: 441–460.
- COOPER, J. E. K. and T. C. HSU, 1972 The C-band and G-band patterns of *Microtus agrestis* chromosomes. *Cytogenetics* **11**: 295–304.
- EGOZCUE, J., M. R. CABALLIN and C. GODAY, 1973 Banding patterns of the chromosomes of man and the chimpanzee. *Humangenetik* **18**: 77–80.
- EGOZCUE, J., J. ARAGONÉS, M. R. CABALLIN and C. GODAY, 1973 Banding patterns of the chromosomes of man and Gorilla. *Ann. Génét.* **16**: 207–210.
- EVANS, H. J., R. A. BUCKLAND and A. T. SUMNER, 1973 Chromosome homology and heterochromatin in goat, sheep and ox studied by banding techniques. *Chromosoma* **42**: 383–402.
- FREDGA, K., 1970 Unusual sex chromosome inheritance in mammals. *Philos. Trans. Roy. Soc B* **259**: 15–36. —, 1971 Idiogram and fluorescence pattern of the chromosomes of the Indian muntjac. *Hereditas* **68**: 332–337.
- FREDGA, K. and N. MANDAHL, 1973 Autosomal heterochromatin in some carnivores. In: "Chromosome Identification: Techniques and applications in biology and medicine." Edited by T. CASPERSSON and L. ZECH. *Nobel Symposium* **23**: 104–117.
- GROUCHY, J. DE, C. TURLEAU, M. ROUBIN and M. KLEIN, 1972 Évolutions caryotypiques de l'homme et du chimpanzé. Etude comparative des topographies de bandes après denaturation ménagée. *Ann. Génét.* **15**: 79–84.

- HSU, T. C. and K. BENIRSCHKE, 1967-73 An Atlas of Mammalian Chromosomes, Vols. 1-7. Springer-Verlag, New York.
- KAKATI, S. and A. K. SINHA, 1972 Banding patterns of Chinese hamster chromosomes. *Genetics* **72**: 357-362.
- KATO, H. and T. H. YOSIDA, 1972 Banding patterns of Chinese hamster chromosomes revealed by new techniques. *Chromosoma* **36**: 272-280.
- LEJEUNE, J., B. DUTRILLAUX, M. O. RETHORE and M. PRIEUR, 1973 Comparison de la structure fine des chromatides d'*Homo sapiens* et de *Pan troglodytes*. *Chromosoma* **43**: 423-444.
- MASCARELLO, J. T., J. W. WARNER and R. J. BAKER, 1974 A chromosome banding analysis of the mechanisms involved in the karyological divergence of *Neotoma phenax* (Merriam) and *Neotoma micropus* Baird. *J. Mamm.* (In press.)
- MASCARELLO, J. T., A. D. STOCK and S. PATHAK, 1974 Conservatism in the arrangement of genetic material in rodents (Submitted for publication.)
- MATTHEY, R., 1966 Le polymorphisme chromosomique des *Mus* africains due sous-genre *Leggada*. Révision générale portant sur l'analyse de 213 individus. *Rev. suisse Zool.* **73**: 585-607.
- NADLER, C. F., R. S. HOFFMANN and A. WOOLF, 1973 G-band patterns as chromosomal markers, and the interpretation of chromosomal evolution in wild sheep (*Ovis*). *Experientia* **29**: 117-119.
- NESBITT, M. N. and V. FRANCKE, 1973 A system of nomenclature for band patterns of mouse chromosomes. *Chromosoma* **41**: 145-158.
- OHNO, S., 1967 *Sex Chromosomes and Sex-linked Genes*. Springer-Verlag, Berlin/Heidelberg/New York.
- OHNO, S., W. BECAK and M. L. BECAK, 1964 X-autosome ratio and the behavior pattern of individual X-chromosomes in placental mammals. *Chromosoma* **15**: 14-30.
- PARIS CONFERENCE, 1972 Standardization in human cytogenetics. Birth defects: Original art ser. VIII, No. 7. The National Foundation, New York.
- PATHAK, S., T. C. HSU, L. SHIRLEY and J. D. HELM, 1973 Chromosome homology in the climbing rats, genus *Tylomys* (Rodentia: Cricetidae). *Chromosoma* **42**: 215-228.
- PATHAK, S., T. C. HSU and T. UTAKOJI, 1973 Relationships between patterns of chromosome banding and DNA synthetic sequences: A study on the chromosomes of the Seba's fruit bat, *Carollia perspicillata*. *Cytogenet. Cell Genet.* **12**: 157-164.
- PATHAK, S., T. C. HSU and F. E. ARRIGHI, 1973 Chromosomes of *Peromyscus* (Rodentia: Cricetidae). IV. The role of heterochromatin in karyotypic evolution. *Cytogenet. Cell Genet.* **12**: 315-326.
- PATTERSON, R. M. and J. C. PETRICCIANI, 1973 A comparison of prophase and metaphase G-bands in the muntjak. *J. Heredity* **64**: 80-82.
- PEARSON, P. L., M. BOBROW, C. G. VOSA and P. W. BARLOW, 1971 Quinacrine fluorescence in mammalian chromosomes. *Nature* **231**: 326-329.
- POPESCU, N. C. and J. A. DI PAOLO, 1972 Identification of Syrian hamster chromosomes by Acetic-Saline-Giemsa (ASG) and trypsin techniques. *Cytogenetics* **11**: 500-507.
- SCHNEDL, W., 1971 The karyotype of the mouse. *Chromosoma* **35**: 111-116. —, 1972 Giemsa banding, quinacrine fluorescence and DNA replication in chromosomes of cattle (*Bos taurus*). *Chromosoma* **38**: 319-328. —, 1973 Giemsa banding techniques. In: "Chromosome Identification: Techniques and applications in biology and medicine." Edited by T. CASPERSSON and L. ZECH. *Nobel Symposium* **23**: 34-37.
- SCHNEDL, W. M. SCHNEDL, 1972 Banding patterns in rat chromosomes (*Rattus norvegicus*). *Cytogenetics* **11**: 188-196.

- SEABRIGHT, M., 1971 A rapid banding technique for human chromosomes. *Lancet* **ii**: 971-972.
 1972 The use of proteolytic enzymes for the mapping of structural rearrangements in the chromosomes of man. *Chromosoma* **36**: 204-210.
- SHARMA, T., S. PATHAK and S. P. RAY-CHAUDHURI, 1970 Large sex chromosomes of Indian house shrew. *The Nucleus* **13**: 62-69.
- SHIRAIISHI, Y. and T. H. YOSIDA, 1972 Banding pattern analysis of human chromosomes by use of a urea treatment technique. *Chromosoma* **37**: 75-83.
- SINHA, A. K., S. KAKATI and S. PATHAK, 1972 Exclusive localization of C-bands within opossum sex chromosomes. *Exptl. Cell Res.* **75**: 265-268.
- STOCK, A. D. and T. C. HSU, 1973 Evolutionary conservatism in arrangement of genetic material: A comparative analysis of chromosome banding between the rhesus macaque ($2n=42$, 84 arms) and the African green monkey ($2n=60$, 120 arms). *Chromosoma* **43**: 211-224.
- TURLEAU, C., DE J. GROUCHY and M. KLEIN, 1972 Phylogénie chromosomique de l'homme et des primates hominiens (*Pan troglodytes*, *Gorilla gorilla* et *Pongo pygmaeus*). Essai de reconstitution du caryotype de l'ancêtre commun. *Ann. Génét.* **15**: 225-238.
- UNAKUL, W. and T. C. HSU, 1972 The C- and G-banding patterns of *Rattus norvegicus* chromosomes. *J. Natl. Cancer Inst.* **49**: 1425-1431.
- VOICULESCU, I., W. VOGEL and U. WOLF, 1972 Karyotyp und heterochromatinmuster des rumänischen Hamsters (*Mesocricetus newtoni*). *Chromosoma* **39**: 215-224.
- WOLF, U., I. VOICULESCU, M. T. ZENZES, W. VOGEL and W. ENGEL, 1972 Chromosome polymorphism in *Apodemus flavicollis* possibly due to creation of a new centromere. In: *Symposia Medica Hoechst 6, Modern Aspects of Cytogenetics: Constitutive heterochromatin in man*. Edited by R. A. PFEIFFER. F. K. Schattauer Verlag. Stuttgart and New York.
- WURSTER, D. H., J. R. SNAPPER and K. BENIRSCHKE, 1971 Unusually large sex chromosomes: New methods of measuring and description of karyotypes of six rodents (Myomorpha and Hystricomorpha) and one Lagomorpha (Ochotonidae). *Cytogenetics* **10**: 153-176.
- YOSIDA, T. H. and T. SAGAI, 1973 Similarity of Giemsa banding patterns of chromosomes in several species of the genus *Rattus*. *Chromosoma* **41**: 93-101.
- ZECH, L., E. P. EVANS, C. E. FORD and A. GROPP, 1972 Banding patterns in mitotic chromosomes of tobacco mouse. *Exptl. Cell Res.* **70**: 263-268.
- ZIMMERMAN, E. G. and D. A. SIHVONEN, 1973 Chromosome banding pattern and idiogram of the cotton rat, *Sigmodon arizonae* (Rodentia, Muridae). *Chromosoma* **41**: 85-91.

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