Unusual Sex Chromosome Inheritance in Mammals

K. Fredga

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Unusual sex chromosome inheritance in mammals

By K. Fredga
Institute of Genetics, University of Lund, Lund, Sweden

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[Plates 1 to 3]

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INTRODUCTION

The male has proven to be the heterogametic sex in all mammals studied so far. As is well known, the males usually have the sex chromosomes XY and the females XX. In recent years, however, many exceptions from this general pattern have been discovered. With our present knowledge, the different sex chromosome mechanisms in mammals may be divided into five main groups, and the first of them into subgroups, as follows:

- (i) Species with XX/XY sex chromosomes:
  - (*a*) X of original size (see below), Y small;
  - (*b*) X large, Y small;
  - (*c*) X large, Y large:
    - (i) end-to-end association of X and Y at male meiosis,
    - (ii) chiasma between X and Y at male meiosis.
- (ii) Species with XX/XY_1Y_2 sex chromosomes.
- (iii) Species with $X_1X_1X_2X_2/X_1X_2Y$ sex chromosomes.
- (iv) Species with complicated or unknown mechanisms for sex determination.
- (v) Species with mosaicism of the sex chromosomes, but apparently with an XX/XY mechanism for sex determination.

The present contribution will mainly deal with unusual sex chromosome inheritance, that is the groups (ii), (iii) and (iv) above, but the other two groups will also be briefly discussed and examples will be given. Recently Raicu, Kirillova & Hamar (1969) described a new sex chromosome mechanism ($X_1X_1X_2X_2/X_1X_2Y_1Y_2$) in the vole *Microtus arvalis*, but this observation was not confirmed by Schmid (1969), who found an ordinary XX/XY mechanism with both X and Y readily identifiable and of 'normal' size, the X comprising 5.6% of (nA + X) and Y being the smallest chromosome of the complement. Late DNA replication was demonstrated in the allocyclic X and in the Y. Also Wolf (1969) found normal sex chromosomes in this species with no multivalents at male meiosis.

Species with XX/XY sex chromosomes

X *of original size*, Y *small*

As was first shown by Ohno, Beçak & Beçak (1964), there is a constant size ratio between the X chromosome and the autosomes in the great majority of placental mammals. The X comprises about 5 % of the female haploid set and is called the original-type X. In principle, the amount of genetic material is the same in all placental mammals (Mandel, Métais & Cuny 1950; Atkin, Mattinson, Beçak & Ohno 1965), and consequently the size of the chromosomes is inversely proportional to the number of chromosomes. This also means that the size of the X chromosome relative to the other chromosomes of the complement varies. More than $\frac{2}{3}$ of placental mammals have chromosome numbers between 36 and 56 (from Matthey 1968*c*) and among these the original-type X is of intermediate size. The Y chromosome is as a rule the smallest or one of the smallest chromosomes of the complement. No mammalian species has been described with a Y chromosome larger than the X. The grey hamster of Armenia, *Cricetulus migratorius*, has large and equal-sized sex chromosomes (Yerganian & Papoyan 1965), but this is an exception from the rule that the X is larger than the Y.

The location of the centromere of the sex chromosomes varies from m to t (nomenclature according to Levan, Fredga & Sandberg 1964). All chromosomes of the complement, including the sex chromosomes, may be telocentric as in the mouse (Tjio & Levan 1954) or atelocentric as in the ocelot (Hsu, Rearden & Luquette 1963). In the dog (Moore & Lambert 1963; Gustavsson 1964) and in cattle (Melander 1959) all autosomes are t chromosomes, but both sex chromosomes are m – sm. On the contrary, the vole *Microtus montanus* has all autosomes m – sm but both sex chromosomes are t (Schmid 1967*b*). These examples show that there is no general rule for the morphology of the sex chromosomes.

X *large*, Y *small*

Some species have an X chromosome that is markedly larger than the original-type but still the Y chromosome is small. Examples of this group are the hystricomorph rodent *Chinchilla laniger* (Galton, Benirschke & Ohno 1965), the Australian native mouse, *Leggadina hermannsburgensis* (Matthey 1968*b*) and the fin whale, *Balaenoptera physalus* (Arnason 1969). In this whale the X is approximately ten times the size of the Y. At male meiosis the large X chromosome associates end-to-end with the small Y chromosome (figure 1*a*, plate 1).

This group includes the mammals with the greatest amplitude in size between X and Y. Among them should be found favourable materials for experimental separation by weight of X and Y carrying spermatozoa.

X *large*, Y *large*

As indicated above, this group may be further subdivided into two: (i) species with an end-to-end association of the sex chromosomes at male meiosis, and (ii) species with a distinct chiasma between X and Y at male meiosis. Representatives of the first subgroup are the Syrian hamster, *Mesocricetus auratus* (Matthey 1952; Fredga & Santesson 1964) and the reindeer, *Rangifer tarandus* (Fraccaro, Gustavsson, Hultén, Lindsten & Tiepolo 1968). There is no chiasma between the extremely large X and Y chromosomes of the field vole, *Microtus agrestis*, but the true nature of the association is obscure (Matthey 1949*b*; Sachs 1953; Muldal & Williams 1968). At first metaphase the sex chromosomes are completely separated from each other (figure 1*b*, plate 1). The second subgroup includes the Chinese hamster, *Cricetulus griseus* (figure 1*c–e*,

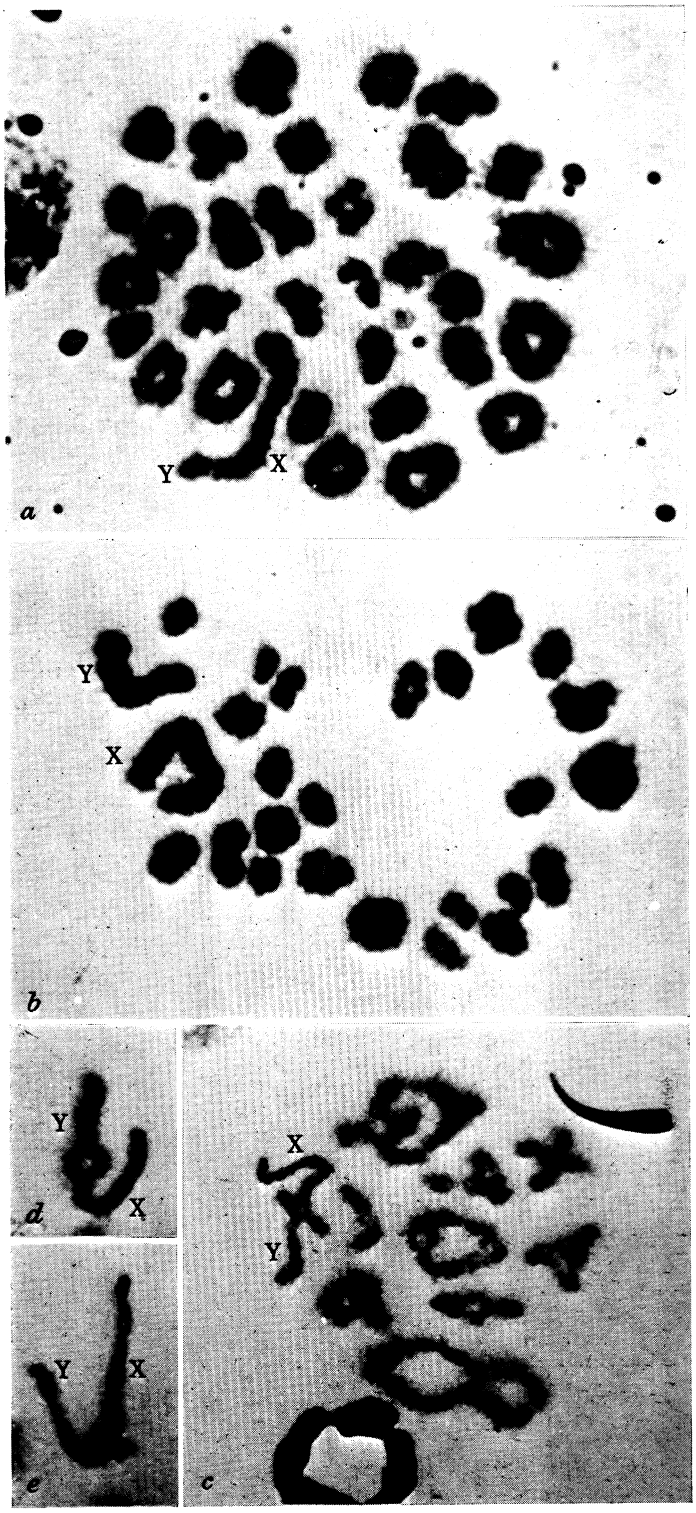

FIGURE 1. Male meiosis of three mammals with large sex chromosomes. (*a*) *Chinchilla laniger*, $2n = 64$, metaphase I, 31 autosomal bivalents, the large X and the small Y are associated end-to-end. (*b*) *Microtus agrestis*, $2n = 50$, metaphase I, 24 autosomal bivalents, the large sex chromosomes are separated from each other. (*c*) *Cricetulus griseus*, $2n = 22$, diakinesis, 10 autosomal bivalents, the large sex chromosomes form a distinct interstitial chiasma. (*d*, *e*) The sex bivalent of *Cricetulus griseus* from two other cells at diakinesis.—Acetic orcein squash (*a*, *b*) and air drying (*c*-*e*) preparations. (Magn. × 2470.)

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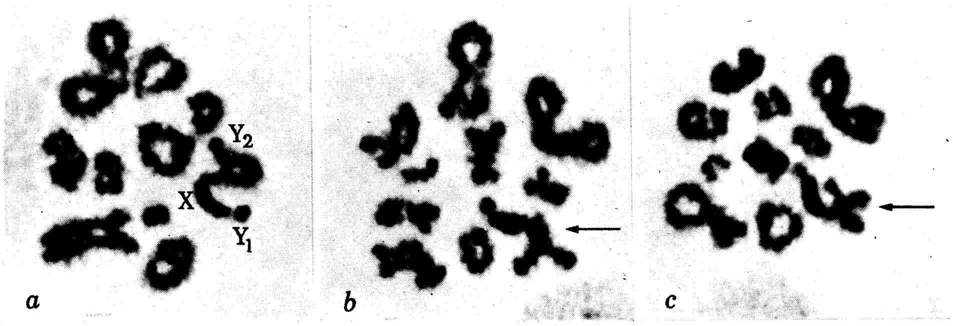

FIGURE 2. (*a* to *c*) Male meiosis of *Sorex araneus*, $2n=21$, three cells at metaphase I, 9 autosomal bivalents and a sex chromosome heterotrivalent (arrows in *b* and *c*). The small Y_1 associates end-to-end with the original (gonosomal) part of X, whereas the bigger Y_2 associates by chiasmata with the autosomal part of X.—Acetic orcein squash preparation. (Magn. × 2750.)

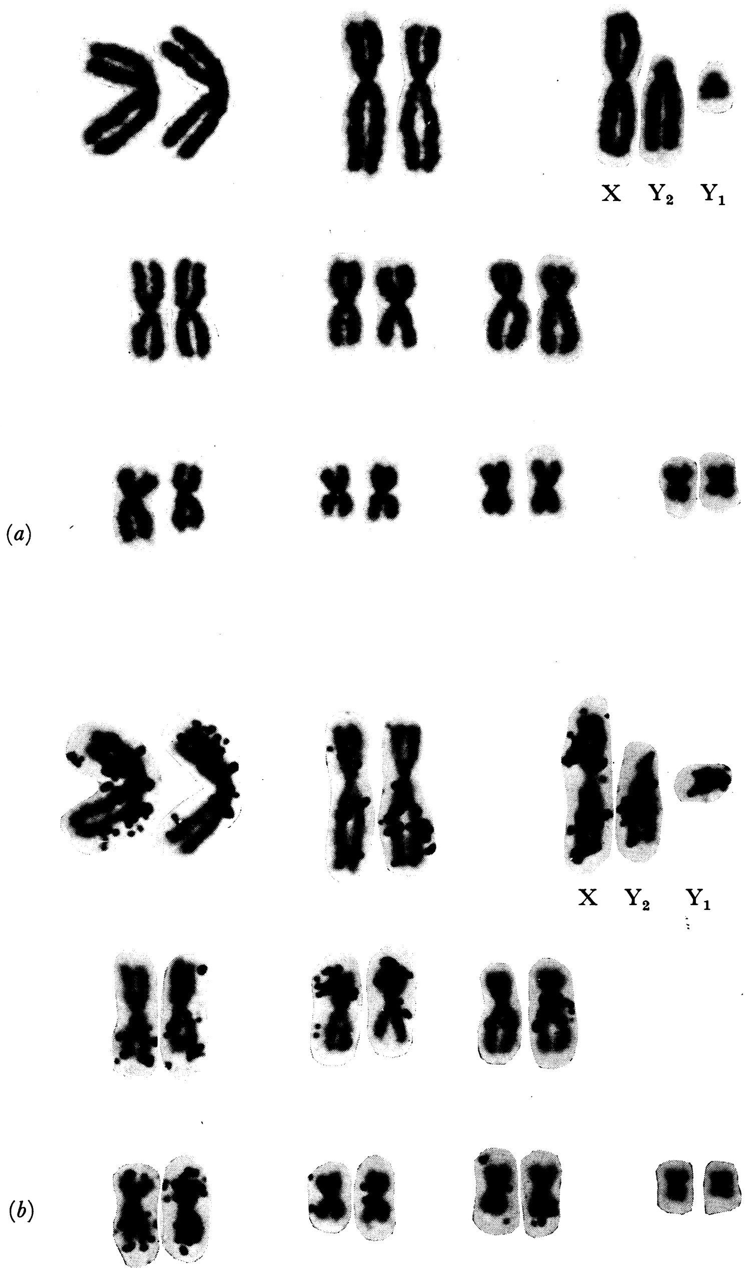

FIGURE 4. Karyotypes of male *Sorex araneus* with $2n=21$. The chromosomes photographed (*a*) before and (*b*) after application of autoradiographic film. See text on p. 19 for comments.—Acetic orcein squash preparations from lung tissue culture. (Magn. × 2500.)

FIGURE 9. Male meiosis of *Herpestes sanguineus*, two cells in diakinesis—metaphase I showing 19 autosomal bivalents and the sex chromosome heterotrivalent (arrows). The true X (X_1) is associated end-to-end with the neo-Y, which forms an interstitial (left cell) or terminal (right cell) chiasma with the X_2. Inserted is the sex chromosome trivalent from another cell in diakinesis, showing two chiasmata between the Y and the X_2, and also showing the orientation of the sex chromosomes on the spindle. The X_1 and X_2 are directed upwards, the Y downwards in the figure.—Acetic orcein squash preparation. (Magn. × 2750.)

FIGURE 10. Male meiosis of *Herpestes sanguineus*, two cells in metaphase I and early anaphase I, side view, showing the orientation of the sex chromosomes on the spindle. Diagrams of the sex trivalents are inserted.—Acetic orcein squash preparations. (Magn. × 2750.)

plate 1), the European hamster, *Cricetus cricetus* (Matthey 1952; Fredga & Santesson 1964) and some pigmy mice from Africa, e.g. *Mus minutoides* from Congo (Matthey 1963). It is also possible that the North American porcupine, *Erethizon dorsatum* (Benirschke 1968) and the African mouse, *Rattus natalensis* (Hamerton 1958; Huang & Strong 1962) should be included in this subgroup, although the chiasma between the large X and Y chromosomes is less distinct than, for instance, in the Chinese hamster. Some species with large sex chromosomes cannot be placed into either of the subgroups since their male meiosis has not been studied. Examples are the sitatunga, *Tragelaphus speki* (Koulischer, Tijskens & Mortelmans 1967; Wurster, Benirschke & Noelke 1968) and the nilgai, *Boselaphus tragocamelus* (Wurster & Benirschke 1967*b*) of the family Bovidae, some species of wood rats belonging to the genus *Neotoma*, e.g. *N. phenax* (Baker & Mascarello 1969), and the vole *Microtus chrotorrhinus* which has giant sex chromosomes, similar to those of *M. agrestis* (Meylan 1967).

The large X chromosomes may have been produced by literal duplication, triplication and quadruplication of the original-type X, or by the addition of autosomal material to the original-type X (Ohno 1965). The last-mentioned hypothesis seems more probable (for discussion see Wurster *et al.* 1968). According to Schmid and collaborators (Schmid, Smith & Theiler 1965; Schmid 1967*a*) the large sex chromosomes of *Microtus agrestis* possibly originated by accumulation of heterochromatin which in other species is scattered among the autosomes. These heterochromatic segments (if homologous) were not necessarily transmitted to the X and Y chromosomes in the same sequence and this may be the reason why no chiasma is formed between the sex chromosomes of this species. In other cases, a complete autosome pair, or a relatively large part of it, may have been translocated on to the end of the original X and Y chromosomes (Matthey 1961), and clear chiasmata may then be formed between the autosomal parts of X and Y, as is the case in the Chinese hamster. These autosomal parts of the sex chromosomes were either heterochromatic from the beginning, or were later converted into heterochromatin by the influence of the sex chromosomes. Schmid & Leppert (1969) have shown that there is a strikingly similar pattern of DNA synthesis in the large X chromosomes of *Microtus agrestis* and *Cricetulus griseus*. It is evident that evolution of the unusually large sex chromosomes may involve several steps and these may not be the same in all species (Wurster *et al.* 1968). Our knowledge in this field is rapidly increasing by detailed studies of the association of X and Y at meiosis, and by autoradiographic studies of the DNA synthesis of the different components of the large sex chromosomes in somatic as well as germ cells.

Species with XX/XY$_1$Y$_2$ sex chromosomes

This sex chromosome mechanism, which equally well could be designated A^XA^X/A^XYA, has arisen by a translocation between the original X chromosome and an autosome. One centromere is lost. The homologue of the autosome is unchanged and is designated Y_2. The original Y chromosome is designated Y_1 and is as a rule much smaller than Y_2. (Some authors designate the largest Y chromosome Y_1 and the smallest Y_2, in accordance with the recommendations of the Denver Conference (1960). The present author prefers to follow the older convention which designates the small original Y chromosome Y_1. In the same way, the original X chromosome of species with multiple X chromosomes, will be referred to as X_1. It should be observed that neither X_2 or Y_2 take any part in sex determination.) At male meiosis the autosomal part of the X forms one or two chiasmata with the Y_2 and the original part of the X associates end-to-end with the small Y_1 (figure 2, plate 2). At the first meiotic division, the heterotrivalent regularly orients on the spindle in such a way that Y_1 and Y_2 are directed to one pole, and the X to the other. Two kinds of spermatozoa are produced, one with Y_1 plus Y_2 and the other with X, in addition to the haploid number of autosomes. It is characteristic of this group of animals that the males have an odd number of chromosomes, and one chromosome more than the females.

At least 12 mammalian species, representing four different orders have the XX/XY_1Y_2 sex chromosome mechanism (table 1), and the sex chromosomes of some of these species are schematically illustrated in figure 3. Three marsupial species belong to this group, including the two well-known species *Protemnodon bicolor*, the black-tailed wallaby, and *Potorous tridactylus*, the

TABLE 1. SPECIES WITH XX/XY_1Y_2 SEX CHROMOSOMES

		2*n*		
order	species	female	male	references
Marsupialia	*Macrotis* (*Thylacomys*) *lagotis*	18	19	Hayman & Martin 1965*a*
	Protemnodon bicolor	10	11	Sharman 1961
	Potorous tridactylus	12	13	Sharman *et al.* 1950
Insectivora	*Echinops telfairi*	40	40, 41†	Borgaonkar 1967*a*, *b*
	Sorex araneus	20–32‡	21–33	Bovey 1948; Sharman 1956
Chiroptera	*Choeroniscus godmani*	(18)§	19	Baker 1967; Hsu *et al.* 1968
	Carollia perspicillata azteca	(20)	21	
	C. subrufa	20	21	
	Artibeus jamaicensis	30	31	
	A. lituratus	30	31	
	A. toltecus	30	31	
Rodentia	*Gerbillus gerbillus*	42	43	Matthey 1954*b*; Wahrman & Zahavi 1955

† Five males studied, three had 40 and two had 41 chromosomes.

‡ Owing to chromosome polymorphism of the centric fusion/fission type, the number of autosomes may vary in different specimens.

§ Parentheses indicate that no females were studied.

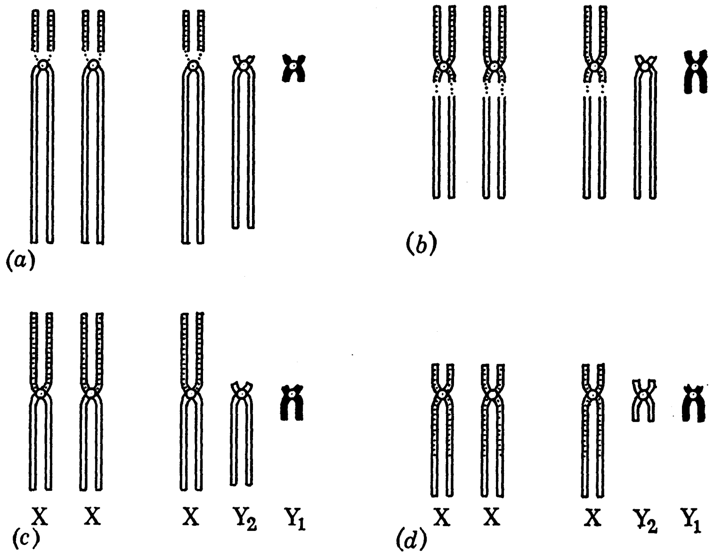

FIGURE 3. Diagrams of the sex chromosome constitution (female left, male right) of (*a*) *Protemnodon bicolor*, (*b*) *Potorous tridactylus*, (*c*) *Sorex araneus* and (*d*) *Artibeus lituratus*. The true X is dotted, the true Y (Y_1) is black and Y_2 and autosomal parts of the X are white. (Based on: *a* and *b*, Hayman & Martin 1965*b*, Moore 1965; *c*, Fredga & Levan 1969; *d*, Hsu *et al.* 1968; Beçak *et al.* 1969).

long-nosed rat-kangaroo. These species have the lowest chromosome numbers known for mammals, $2n = 10$ ♀, 11 ♂ and 12 ♀, 13 ♂, respectively. (The lowest chromosome number among placental mammals is found in the bat *Choeronycteris mexicana* with $2n = 16$ (Baker 1967), and the highest in the black rhinoceros (*Diceros bicornis*) with $2n = 84$ (Hungerford, Chandra & Snyder 1967).)

Two species of insectivores, a tenrec from Madagascar and the common shrew have multiple Y chromosomes. The chromosomes of the tenrec *Echinops telfairi* were briefly described by Borgaonkar (1967*a*, *b*). He studied five males, and three of these had 40 chromosomes and two had 41. He interpreted this deviation in chromosome number as due to the presence of two Y chromosomes in the 41-chromosome males, since the autosomes and the X were similar in all animals studied. The Y chromosome in the 40-chromosome males was small and 'acrocentric', the extra Y chromosome in the 41-chromosome males was still smaller. The occurrence of XY and XY_1Y_2 males in the same species is surprising, particularly as the Y_1 and Y_2 cannot have arisen by a centric fission of the 'acrocentric' Y. More specimens of this species should be studied to clarify this unusual situation. Four closely related species have an ordinary XX/XY mechanism for sex determination.

The common shrew (*Sorex araneus*) is well-known among mammalian cytologists, especially for two reasons: the XX/XY_1Y_2 sex chromosome system and the occurrence of chromosomal polymorphism of the centric fusion/fission type (Ford, Hamerton & Sharman 1957). Six pairs of autosomes are involved in this polymorphic system (Meylan 1964; 1965) and thus the chromosome number may vary between 20 and 32 in females and 21 and 33 in males. The karyotype of a male with 21 chromosomes is shown in figure 4, plate 2, which is from an unpublished study of the DNA synthesis in the chromosomes of *Sorex araneus* (Fredga & Levan 1969). The figure illustrates the incorporation of tritiated thymidine at the end of the synthesis period. It is clear that the small Y_1 chromosome replicates relatively late, as is the rule in mammalian Y chromosomes. The Y_2 and its homologous part of the X do not differ significantly from the autosomes in their DNA synthesis, thus in good agreement with the X–autosome translocation hypothesis.

Six species of bats from central and south America, all belonging to the family Phyllostomatoidae, have the present type of sex chromosome mechanism. Three of them have a relatively large Y_2 chromosome, comparable with the Y_2 of the Marsupials and of *Sorex araneus*. On the other hand, three species of the genus *Artibeus* have a Y_2 chromosome considerably shorter than the long arm of the X. In *A. jamaicensis* the Y_2 is somewhat larger than Y_1 and in the other two species the two Y chromosomes are of similar size. The most likely mode of origin of these sex chromosomes is that a small autosome, approximately the size of Y_2, has fused with the long arm of a metacentric X (Hsu, Baker & Utakoji 1968). This interpretation was supported by a study of male meiosis in one of the species, *A. lituratus* (Beçak, Batistic, Vizotto & Beçak 1969). At diakinesis, the sex chromosomes formed a trivalent with both the Y chromosomes connected end-to-end with the extremities of the X; the original Y (Y_1) with the short arm, and the Y_2 with the long arm of the X. A fourth species of the genus *Artibeus*, *A. turpis*, was found with the classical XX/XY karyotype. Hsu *et al.* (1968) suggested that this apparently normal sex chromosome mechanism had arisen by a more recent fusion between Y_1 and Y_2. This hypothesis is supported by the facts that the Y chromosome of *A. turpis* is metacentric and approximately twice the size of the Y_1 and Y_2 of *A. lituratus* and *A. toltecus*. In addition, the autosomes of all four species are morphologically indistinguishable from one another, indicating a close karyological relationship between them. On the other hand, the observation of Beçak *et al.* (1969)

that the small Y_2 of *A. lituratus* is not an 'acrocentric' but a submetacentric chromosome, makes the centric fusion hypothesis less attractive and indicates a more complicated mechanism.

Finally, the rodent *Gerbillus gerbillus* belongs to this group. A sex chromosome trivalent was discovered at male meiosis (Matthey 1954*b*; Wahrman & Zahavi 1955). The X-chromosome is the largest of the complement and easily distinguished but the Y_1 and Y_2 chromosomes have not been identified.

SPECIES WITH $X_1X_1X_2X_2/X_1X_2Y$ SEX CHROMOSOMES

In the preceding group, the X had been translocated on to an autosome; in the present group there is the same situation with the Y. This sex chromosome mechanism could as well be designated $XXAA/XAA^Y$ or simply XX/XA^Y. If a small Y chromosome has become translocated on to a large autosome, the difference between the Y-carrying autosome and its non-Y-carrying homologue may escape discovery, and such a case may appear as an XX/XO. If, however, the X chromosome does not form a univalent at male meiosis but attaches end-to-end to an autosomal bivalent, there is good reason to assume that the Y chromosome is present and fused to one of these autosomes.

The smooth function of this sex chromosome mechanism at male meiosis is ensured by the orientation on the spindle of the sex trivalent with the Y always moving to one pole and X_1 (the true X) and X_2 (the non-Y-carrying homologue) to the other. In this group of animals it is characteristic that the males have an odd number of chromosomes and one chromosome less than the females.

The $X_1X_1X_2X_2/X_1X_2Y$ sex chromosome mechanism has so far been discovered in 11 species belonging to five mammalian orders (table 2). The sex chromosomes of females and males of some of these species are schematically illustrated in figure 5.

TABLE 2. SPECIES WITH $X_1X_1X_2X_2/X_1X_2Y$ SEX CHROMOSOMES

		2n		
order	species	female	male	references
Marsupialia	*Lagorchestes conspicillatus*	16	15	Martin & Hayman 1966
Edentata	*Choloepus hoffmanni*	49	49	Corin-Frederic 1968
Rodentia	*Mus minutoides* ssp_3	36	35	Matthey 1965*b*
Carnivora	*Herpestes ichneumon*	44	43	Fredga 1969
	H. sanguineus	(42)†	41	Fredga 1969
	H. javanicus(?)	36	35	Todd & Pressman 1966
	H. auropunctatus	36	35	Fredga 1965*a*, *b*
	H. edwardsi	36	35	Ray-Chaudhuri *et al.* 1968
	H. fuscus	36	35	Fredga 1969
	H. brachyurus	36	35	Fredga 1969
	Atilax paludinosus	36	35	Hsu 1966
Artiodactyla	*Tragelaphus angasi*	(56)	55	Wurster & Benirschke 1968*b*
	T. strepsiceros	32	31	Wallace & Fairall 1967

† Parentheses indicate that no females were studied.

The first case, a hare wallaby (*Lagorchestes conspicillatus*) from Australia, is perhaps the most complicated of them all. According to Martin & Hayman (1966), two autosome pairs are involved in translocations with the sex chromosomes. One large autosome pair has fused with the original sex chromosomes, forming the largest part of the long arms of the neo-X (X_1) and neo-Y. Another smaller autosome has also fused with the Y, forming the largest part of the short arm of the neo-Y. The homologue of this autosome is unchanged and is now designated X_2 (see figure 5*a*). The occurrence of autosomal polymorphism of the centric fusion/fission type makes this sex chromosome system particularly hard to interpret.

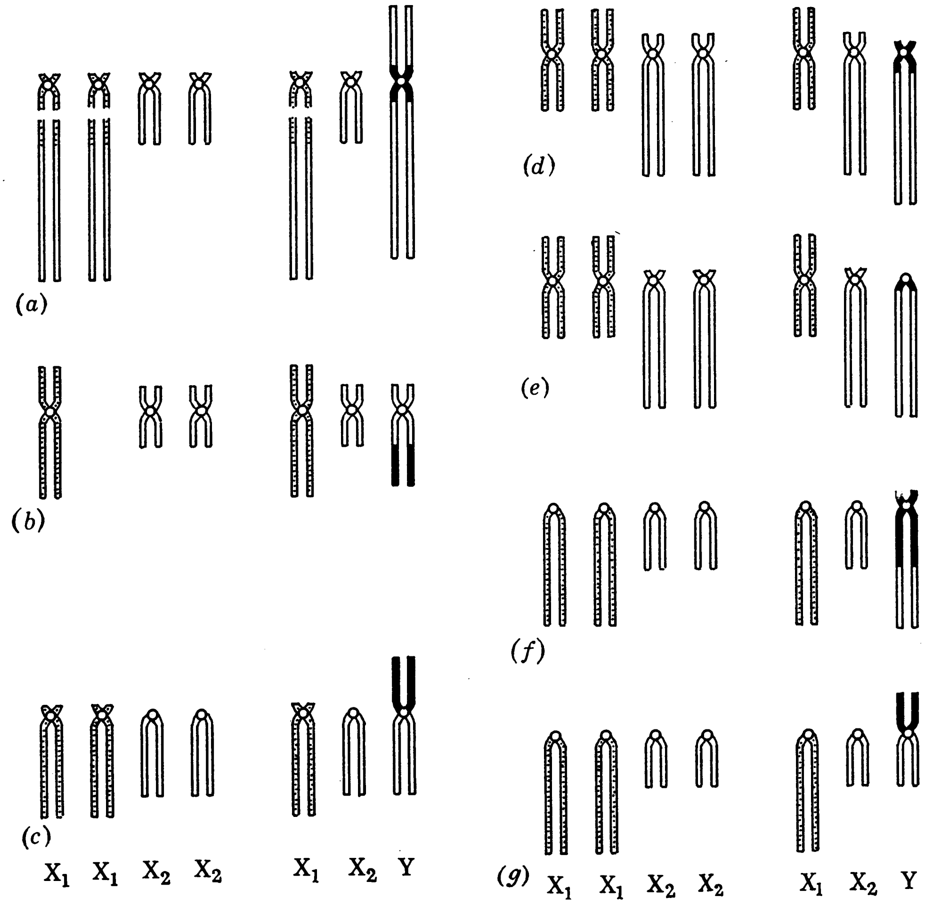

FIGURE 5. Diagrams of the sex chromosome constitution (female left, male right) of (*a*) *Lagorchestes conspicillatus*, (*b*) *Choloepus hoffmanni*, (*c*) *Mus minutoides* ssp_3, (*d*) *Herpestes ichneumon* and *H. sanguineus*, (*e*) *H. auropunctatus*, (*f*) *Tragelaphus angasi* and (*g*) *T. strepsiceros*. The true X (X_1) is dotted, the true Y is black and X_2 and autosomal parts of the Y are white. (Based on: *a*, Martin & Hayman 1966; *b*, Corin-Frederic 1969; *c*, Matthey 1965*b*; *d*, *e*, Fredga 1969; *f*, Wurster & Benirschke 1968*b*; *g*, Wallace & Fairall 1968).

The next case is a sloth (*Choloepus hoffmanni*) from South and Central America recently studied by Corin-Frederic (1969). She examined the somatic chromosomes in tissue cultures from muscles of six females and four males. The chromosome number was 49 in both sexes. In the females one X_1 (the late replicating one) was missing and in the males a translocation was found between the original Y chromosome and one of the smallest autosomes. In this case the neo-Y was easily distinguishable (figure 5*b*). A sex chromosome heterotrivalent found at male meiosis confirmed the A–Y translocation hypothesis. Unfortunately, the female germ line has not yet been investigated, but probably it should have two X_1 chromosomes and produce only one kind of eggs: $X_1 + 24A$. That is, the female embryo starts with 48 autosomes and two X_1 chromosomes but the ordinary inactivation of one X_1 is simply replaced by the elimination of one X_1 with the consequence that all (?) somatic tissues have only one X_1 chromosome in each cell.

A particular subspecies of pigmy mice from South Rhodesia, called *Mus* (*Leggada*) *minutoides* ssp$_3$ by Matthey (1965*b*) seems also to belong to the present group of sex chromosome mechanisms. The males have 35, the females 36 chromosomes. All autosomes and the X:es are t chromosomes but the Y chromosome is a large m – sm chromosome. The simplest explanation of the origin of this Y chromosome is by a centric fusion of the original Y and an autosome, the homologue of which is X$_2$ (figure 5*c*). At male meiosis, a true chiasma is formed between one arm of the Y and the X$_2$. It is remarkable that some figures of diakinesis in the paper by Matthey (1965*b*, figures 24, 25 and 28) show a distinct chiasma also between the other arm of the Y and the X$_1$. If this interpretation is correct, it means that another pair of autosomes has fused with the original sex chromosomes in a way similar to that described above for the hare wallaby.

TABLE 3. SPECIES AND NUMBER OF CHROMOSOMALLY INVESTIGATED MONGOOSES (1969)

species	number of specimens studied				chromosome number		references
	Fredga		others				
	♂	♀	♂	♀	♂	♀	
Herpestes ichneumon	2	1	—	—	43	44	8
H. sanguineus	2	—	—	—	41	(42)	8
H. javanicus (?)	—	—	3	1	35	36	1, 16
H. auropunctatus	4	3	10+	4+	35	36	2–8, 11–15
H. edwardsi	—	—	2	2	35	36	13, 14
H. fuscus	1	1	—	—	35	36	8
H. urva	—	2	—	—	?	36	8
H. brachyurus	1	1	—	—	35	36	8
Atilax paludinosus	—	—	2	3	35	36	10, 17, 19, 20
Helogale parvula	1	1	—	—	36	36	8
Mungos mungo	7	5	—	1	36	36	8, 19, 20
Crossarchus obscurus	1	—	—	—	36	(36)	8
Ichneumia albicauda	—	—	1	—	36	(36)	19, 20
Bdeogale nigripes (?)	—	—	1	—	36	(36)	19, 20
Cynictis penicillata	1	1	2	1	36	36	8, 9, 18
Suricata suricatta	—	—	2	2	36	36	16, 19, 20

1, Benirschke (1969); 2, Bhatnagar (1969); 3, 4, Fredga (1965*a*, *b*); 5, 6, Fredga (1967*a*, *b*); 7, Fredga (1968); 8, Fredga (1969); 9, Gerneke (1967); 10, Hsu (1966); 11, Manna & Talukdar (1965); 12, Ray-Chaudhuri *et al.* (1966); 13, Ray-Chaudhuri *et al.* (1968); 14, Sharma (1967); 15, Talukdar & Manna (1966); 16, Todd & Pressman (1966); 17, Todd & Pressman (1967); 18, Todd *et al.* (1967); 19, Wurster & Benirschke (1967*a*); 20, Wurster & Benirschke (1968*a*).

Several species of mongooses have the present type of sex chromosome mechanism. According to Morris (1965), the subfamily Herpestinae of the family Viverridae comprises 40 species; according to Hinton & Dunn (1967) the number of species is 36 (minimum number 34, maximum number 42). About $\frac{3}{4}$ of the species are native in Africa and $\frac{1}{4}$ in Southern Asia, including Java, Sumatra, Borneo and Phillippines. All the Asian species belong to the genus *Herpestes*, e.g. *H. edwardsi*, Kipling's Rikki-tikki-tavi. One species, *H. ichneumon*, is occasionally found in Europe, in southern Spain and Portugal. The chromosomes have been studied in 16 species of mongooses, females from 12 species and males from 15 (table 3). Among the latter 15, eight have an odd number of chromosomes and seven have an even number including a small Y chromosome. All seven species of the genus *Herpestes*, in which the chromosomes of male individuals have been studied, have the autosome–Y translocation. This is especially interesting considering that this genus is regarded as the most primitive in the entire order of Carnivora. The genus *Herpestes* has been in existence for some 30 million years, or longer than any recent genus of the order (Hinton & Dunn 1967). The genus considered as the second most primitive among the Herpestinae is *Atilax* with just one species, *Atilax paludinosus*, which also exhibits the autosome–Y translocation.

The most common chromosome number among the mongooses is 36 and the karyotypes are very similar. It was thus surprising to find 43 and 44 chromosomes in two males and one female of *Herpestes ichneumon*, respectively (figure 6*a*, *b*) and 41 chromosomes in two males of *H. sanguineus* (figure 7). However, these deviations from the standard karyotype of the mongooses (figure 8*b*) can be accounted for by centric fusion/fission events. In both species, the neo-Y chromosome is identified with relative ease as a large t chromosome with a small but distinct second arm. The X_2 is somewhat smaller with a longer short arm and a shorter long arm (figures 6 and 7).

In *H. auropunctatus*, the identification of Y and X_2 is more difficult. The chromosomes of this species were recently re-examined utilizing cultured cells from four individuals, two males and two females. By this improved technique, a difference between the chromosomes of the two sexes was discovered. The four large t chromosomes all have small but distinct short arms in the female, whereas in the male, one of them lacks short arm (figure 8*a*, *b*). This latter chromosome, designated t(4) by Fredga (1967*a*), is most likely the neo-Y. The size of the four t chromosomes is very similar but detailed studies, also in related species, indicate that there is one larger and one smaller pair and that the larger pair is identical in females and males. This means, that the smallest t chromosome is the X_2 and that the neo-Y, although lacking a distinct short arm, is somewhat larger than X_2. The sex chromosomes of some mongoose species are represented schematically in figure 5*d*, *e*.

Some examples of the behaviour of the sex chromosomes at male meiosis of *H. sanguineus* are shown in the figures 9 and 10, plate 3. The autosomes form 19 bivalents and the X_1, X_2 and Y form a trivalent at diakinesis and metaphase I. The true X (X_1) is elongated and slender and associates end-to-end with the Y. The non-Y-carrying homologue (X_2) forms one or two chiasmata with the autosomal part of the Y (figure 9, plate 3). The sex chromosomes orient on the spindle in the same way as previously described, the Y moving to one pole and X_1 and X_2 to the other (figure 10, plate 3). A detailed description and discussion of the karyotypes of the mongoose species listed in table 3 is in preparation.

Finally, the present type of sex chromosome mechanism has been indicated in two species of spiral-horned antelopes, the nyala (*Tragelaphus angasi*) and the greater kudu (*T. strepsiceros*). The case of the nyala is still a little speculative and based only on mitotic chromosomes of one male (Wurster & Benirschke 1968*b*). The chromosome number was $2n = 55$ and the unpaired element was easily identified as a large st chromosome. Autoradiography revealed that the short arm and proximal half of the long arm were late labelling. This portion would represent the original Y chromosome. The distal half of the long arm was not late replicating and would represent an autosome. The X (X_1) chromosome was not identified, all other chromosomes (except the largest pair of autosomes) forming a continuous series of t chromosomes. In all probability, the X_1 was one of the largest of the t chromosomes and X_2 one of the smaller.

The case of the kudu was better supported by evidence. The somatic chromosomes were studied in bone marrow from three males and two females, and meiosis was studied in one of the males (Wallace & Fairall 1968). The females had 32 and the males 31 chromosomes and the X_1, X_2 and Y formed a trivalent at male meiosis.

The sex chromosomes of the nyala and the kudu are shown schematically in figure 5*f*, *g*.

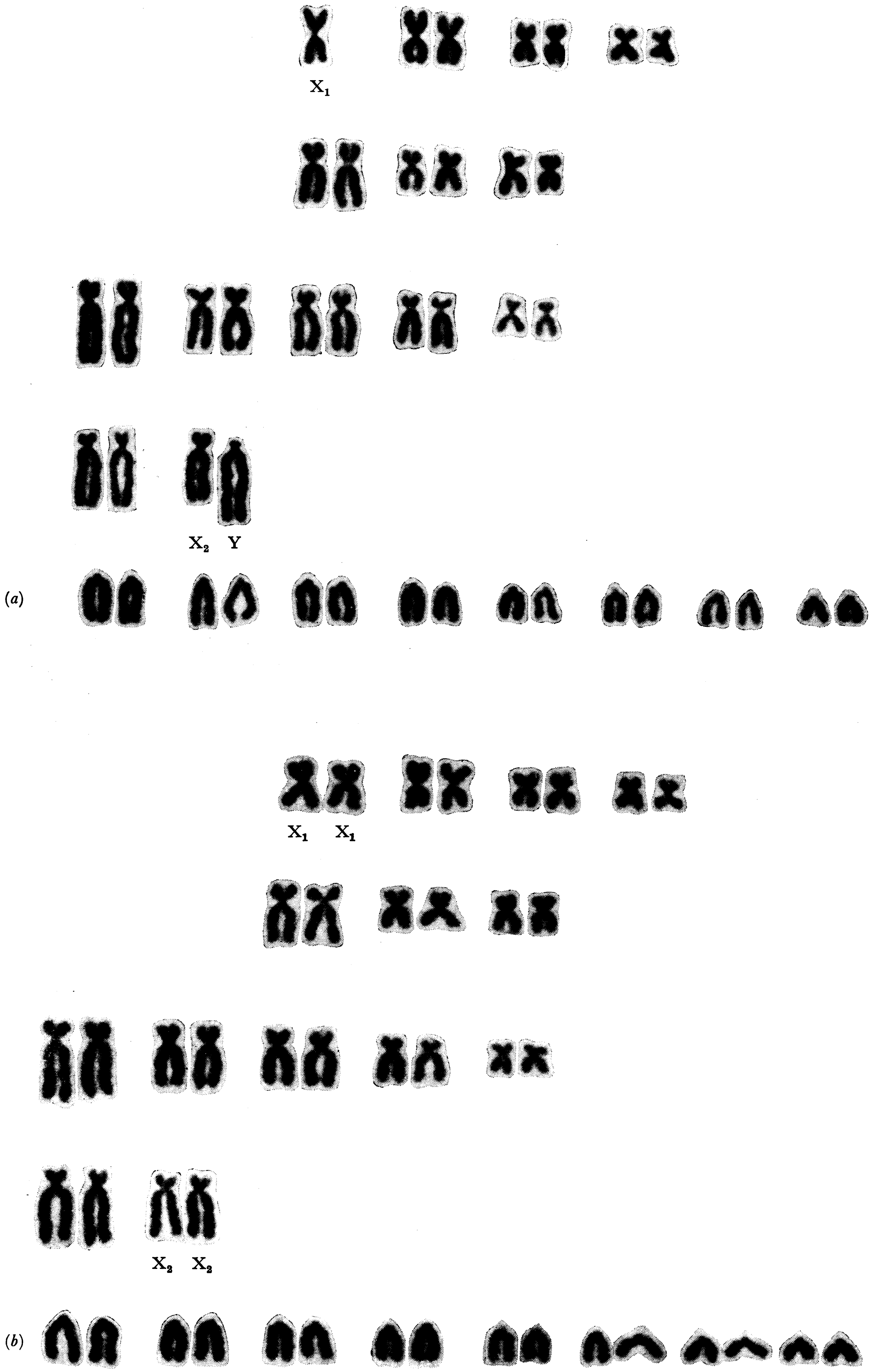

FIGURE 6. Karyotypes of *Herpestes ichneumon*, (*a*) male, $2n = 43$, (*b*) female, $2n = 44$. Note the sex chromosomes and 8 pairs of telocentric autosomes. Acetic orcein squash preparations from skin tissue cultures. (Magn. × 2775).

SPECIES WITH COMPLICATED OR UNKNOWN MECHANISMS FOR SEX DETERMINATION

This group (table 4) is of course no natural unity. As our knowledge increases, some species included under this heading will be transferred to other groups. On the other hand, at least one of the species, *Microtus oregoni*, has been studied thoroughly enough to make it reasonable that even in the future it will keep its position as representative of a group with a complicated mechanism for sex determination.

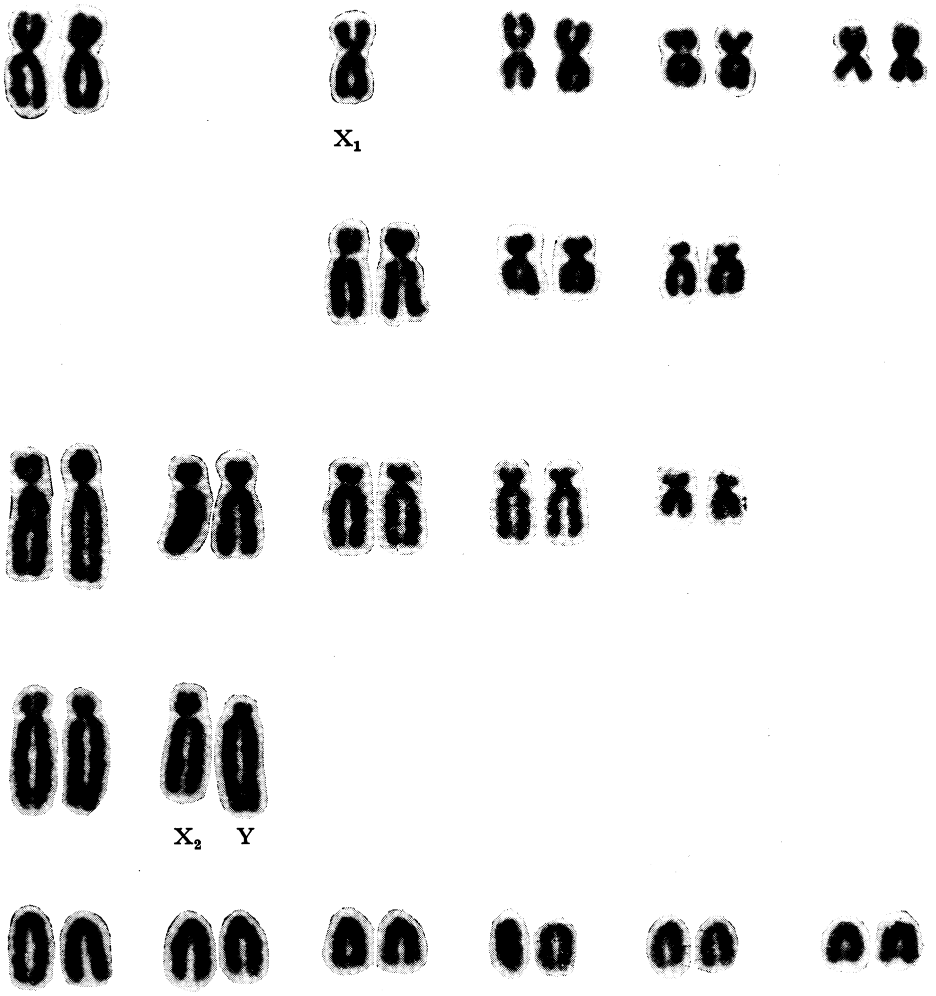

FIGURE 7. Karyotype of a male *Herpestes sanguineus*, $2n = 41$. Note the sex chromosomes and six pairs of telocentric autosomes. Acetic orcein squash preparations from skin tissue culture. (Magn. × 3225.)

The echidna (*Tachyglossus aculeatus*) and the platypus (*Ornithorhynchus anatinus*) of the order Monotremata are highly primitive, egg-laying mammals from Australia. Their chromosomes have been studied by Matthey (1949*a*) and Brink (1959), and more recently by Bick & Jackson (1967*a*, *b*), who found an odd number of chromosomes in males of both species and suggested that the males might be XO and the females XX. No detailed examination of meiosis has been carried out so far and until that has been done, it seems more probable that the sex chromosome mechanism is similar to that found in the mongooses, that is, a small original Y chromosome is translocated on to a relatively large autosome. If this is true, the echidna and the platypus would

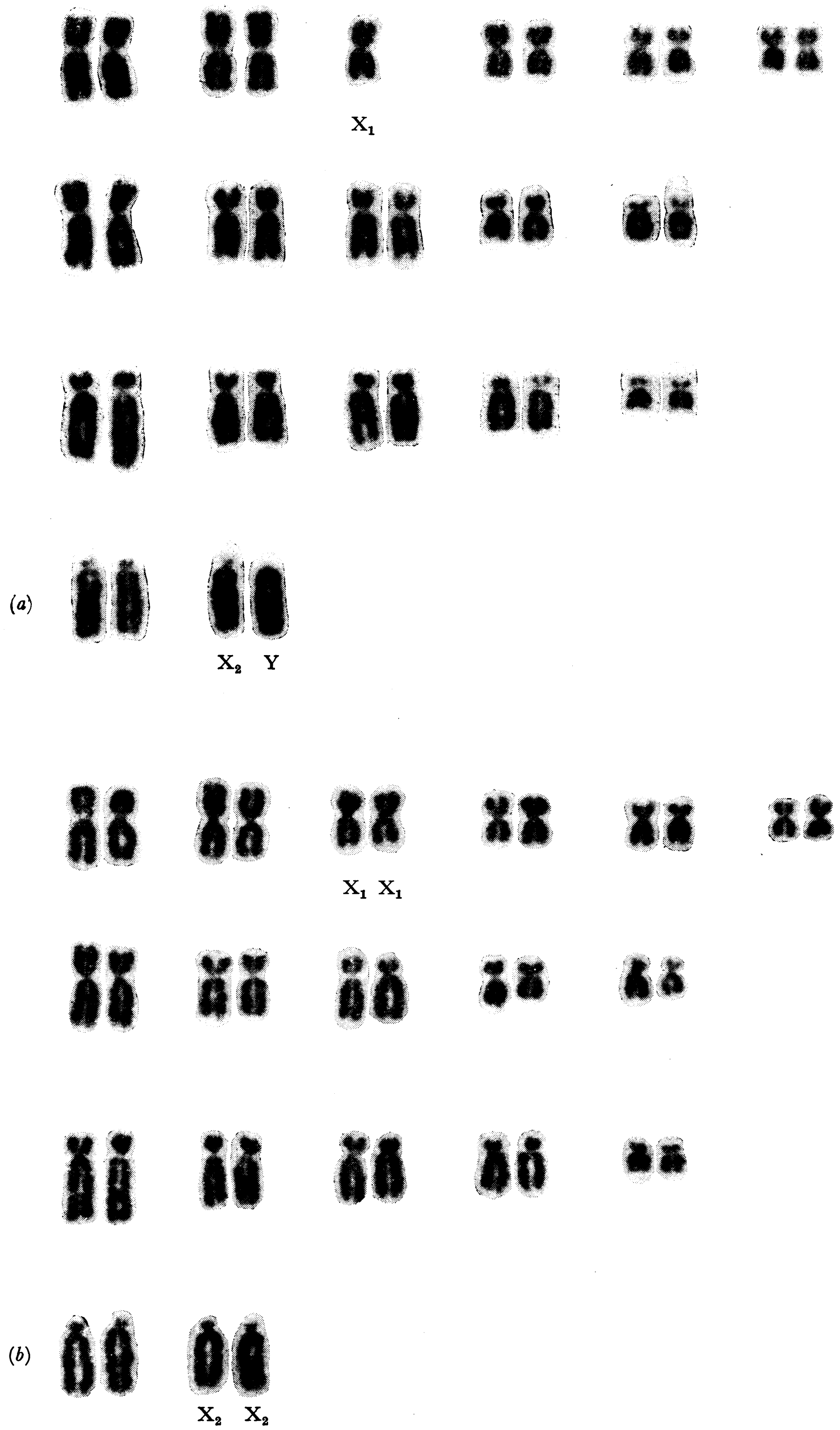

FIGURE 8. Karyotypes of *Herpestes auropunctatus* (*a*) male, $2n=35$, (*b*) female, $2n=36$. Note the small morphological difference between the Y and the X_2. The karyotype of the female may be regarded as representative of all mongooses having 35/36 or 36/36 chromosomes even though small interspecific differences occur. Acetic orcein squash preparations from testis (*a*) and skin (*b*) tissue cultures. (Magn. × 2920.)

belong to group (iii). According to Bick & Jackson (1967*a*) the general chromosome morphology in monotremes may be regarded as an extreme mammalian type strongly resembling that found in the crocodiles and turtles which represent premammalian lineages. It is not known if the male heterogamety of the XY/XX type operates in members of the orders Crocodylia and Chelonia since no heteromorphic sex elements or sex-linked genes have been found in these reptiles (Ohno 1967, p. 37). In the monotremes, however, the male is the heterogametic sex, even though their sex chromosome system is still unknown.

TABLE 4. SPECIES WITH COMPLICATED OR UNKNOWN MECHANISMS FOR SEX DETERMINATION

		$2n$				
		female		male		
order	species	soma	germ	soma	germ	references
Monotremata	*Tachyglossus aculeatus*	64, XX	—	63, X	63, X	Bick & Jackson 1967*a*, *b*
	Ornithorhynchus anatinus	54, XX	—	53, X	—	Bick & Jackson 1967*a*, *b*
Rodentia	*Microtus oregoni*	17, X	18, XX	18, XY	17, Y	Matthey 1956, 1958 Ohno *et al.* 1963, 1966
	Ellobius lutescens	17, X	—	17, X	17, X	Matthey 1953, 1964
	Ctenomys tuconax	—	—	61, X	—	Reig & Kiblisky 1968

The interest in the sex chromosome mechanism of the creeping vole (*Microtus oregoni*) was raised when Matthey (1956) reported the chromosome number 17 in germ cells of the male, and also in somatic cells of the female (Matthey, 1958). Ohno and collaborators, analysing the chromosomes of germ cells and somatic cells in males and females, established that both sexes were gonosomic mosaics, the male with the constitution OY/XY and the female with the constitution XX/XO (Ohno, Jainchill & Stenius 1963; Ohno 1964; Ohno, Stenius & Christian 1966). 'The male has 18 chromosomes and XY in somatic cells but predirected non-disjunction of the X occurs to primordial germ cells in fetal testis. The XXY and OY germ cells are produced. Of these, only the OY's ($2n = 17$) differentiate into definitive spermatogonia. As a result, the male produces two types of spermatozoa, one Y bearing and the other having no sex chromosome at all. Because the spermatozoon which contains no sex chromosome is the female determining gamete, the female of this species starts as the XO ($2n = 17$) and the XO constitution is maintained by the soma. In primordial germ cells of fetal ovaries, however, non-disjunction of the X again takes place. OO germ cells die off and only the XX germ cells differentiate into definitive oögonia. This enables the XO female to produce only one type of egg, each endowed with one X' (cited from Ohno 1967, p. 140). The X chromosome of *Microtus oregoni* is of m type and approximately three times as large as an original type X. The Y is a t chromosome and relatively large.

The chromosomes of the vole *Ellobius lutescens* have been studied comparatively thoroughly, but nevertheless the mechanism for sex determination remains obscure. Somatic cells of both sexes and male germ cells have 17 chromosomes and the karyotypes are identical in the male and the female (Matthey 1953, 1954*a*, 1958, 1962, 1964). The unpaired chromosome (no. 9) is of the m type and the smallest of the complement. Its size amounts to some 5 % of the haploid complement (including this chromosome) and would thus correspond to an original-type X. No sex chromatin is seen in somatic interphase nuclei of male and female. The labelling pattern of the unpaired chromosome is identical in the two sexes and no chromosome of the complement is remarkably late replicating (Castro-Sierra & Wolf 1967; Schmid 1967*a*). All these facts speak in favour of the odd chromosome in *Ellobius* being an isocyclic, functional X chromosome.

The next question is: where is the Y chromosome? Castro-Sierra & Wolf (1967) suggested the possibility that a segment of the presumed ancestral Y chromosome carrying male-determining factors had been translocated to a terminal position on an autosome, that is, a situation similar to that described for the mongoose *Herpestes auropunctatus*. However, Matthey's report (1964) on male meiosis of *Ellobius lutescens* did not support this hypothesis, since he found the odd sex element to be isolated at first meiotic metaphase. Castro-Sierra & Wolf (1968) considered the possibility that the odd chromosome might be associated with an autosome bivalent earlier during meiosis. Unfortunately, their investigation yielded no definitive solution of the problem. At diplotene, diakinesis and metaphase I the chromosome 9 appeared as a univalent and was not joined to any of the other chromosomes, which all formed bivalents. At pachytene the chromosome 9 was positively heteropycnotic and formed a sex vesicle. The sex vesicle was associated to one of the thread-like autosomal bivalents in 25 out of 100 cells studied. According to the authors this indicated the presence of an X autosomal trivalent. This, however, must be regarded as rather weak evidence for the A^Y-translocation hypothesis, since the sex vesicle of many species with ordinary X and Y chromosome often appears associated with heterochromatic parts of one or several autosomal bivalents during pachytene. E.g., in cattle usually one to seven autosomal bivalents are associated with the sex vesicle (Gustavsson 1969). In addition, the remaining 75 cells did not show any association between the sex vesicle and any autosomal bivalents. However, the A^Y-translocation hypothesis is attractive since a Y chromosome (or part of it) would seem to be indispensable for normal male development in mammals. If the A^Y-hypothesis turns out to be correct the sex chromosome mechanism of *Ellobius lutescens* might be similar to that found in the sloth (*Choloepus hoffmanni*) (p. 21). No information is available, however, as to the chromosome constitution in the female germ line of the sloth, and in *Ellobius* our knowledge is restricted to observations in a few cells. Thus, Matthey (1964) presented three figures from female meiosis: one diakinesis with eight bivalents and one univalent, one prophase II with nine chromosomes, and one metaphase II, also with nine chromosomes. The cell in diakinesis is particularly interesting since it indicates that the female germ line has 17 chromosomes and only one X. If this is the case, the sex chromosome mechanism of *Ellobius* is more complicated than that suggested for *Choloepus hoffmanni*. The thought of a fertile female rodent with XO sex chromosomes is not totally absurd. In the mouse, *Mus musculus*, XO individuals are phenotypically normal and fertile females (Russell, Russell & Gower 1959; Welshons & Russell 1959). The average litter size is, however, reduced being 4.46 in XO females as compared with 8.17 in XX siblings (Morris 1968). All OY sons and two-thirds of XO daughters either die pre-natally or are formed in reduced numbers due to an abnormally low segregation of nullo-X gametes from XO females (Cattanach 1962; Morris 1968). It is difficult to see how an XO/XY mechanism might be established in nature.

The first hypothesis concerning the mechanism of sex determination in *Ellobius* was put forward by White (1957, 1960) and was accepted by Matthey (1958, 1964). According to this hypothesis, the odd chromosome of the male represents a fusion of the original X and Y, whereas the odd chromosome of the female is an attached XX. Many facts speak against this hypothesis: the identical morphology of the odd chromosome in males and females, the fact that the odd chromosome comprises 5% of the haploid chromosome set, the absence of sex chromatin in the female, and the autoradiographic pattern. The system would have to operate as a balanced lethal mechanism, zygotes with two sex chromosomes ($2n = 18$, XXXY) and with no sex chromosomes ($2n = 16$) would be regularly produced and eliminated. Castro-Sierra &

Wolf (1968) discuss two alternative interpretations of the sex-determining mechanism of *Ellobius lutescens* and stress the need of further studies of female oogenesis and of the reproductive biology of this species. It is worth mentioning that there are three species of the genus *Ellobius*, *E. fuscocapillus*, *E. lutescens* and *E. talpinus* (Ellerman & Morrison-Scott 1951). The last-mentioned species has $2n = 54$ and apparently a normal XX/XY mechanism, but since all the chromosomes are of the t type, no difference between the male and the female karyotypes could be demonstrated (Ivanov 1967).

The vole *Microtus montebelli* was reported long ago to have 31 chromosomes in the male and the sex chromosomes XX/XO (Oguma 1937), but recently Utakoji (1967) has shown that both sexes have $2n = 30$ and an ordinary XX/XY mechanism for sex determination.

Finally *Ctenomys tuconax*, a hystricomorph rodent from South America, will be mentioned. Only one tissue (bone marrow) from one male individual has been investigated so far (Reig & Kiblisky 1968). All cells studied had 61 chromosomes and the only chromosome lacking a partner was a large metacentric, similar to the X of closely related species. For the time being, *Ctenomys tuconax* must be included in the present group 'species with an unknown mechanism for sex determination'.

Species with mosaicism of the sex chromosomes, but apparently with an XX/XY mechanism for sex determination

In some of the species included in this group, one sex chromosome is missing from one or several somatic tissues, and this may lead to a wrong conclusion as to the mechanism of sex determination. However, it is reasonable to assume that the germ lines of females and males of the species included in table 5 have the normal XX and XY sex chromosomes, respectively, and that the loss of one X chromosome, or part of it, is an unusual expression of dosage compensation. Instead of inactivation of one X chromosome, females of these species eliminate one X, or part of it, from some somatic tissues. The three marsupial species of table 5 are remarkable since not only one X of the females but also the Y of the males are eliminated in cells of the blood, liver and spleen. The germ line of the male is XY and that of the female is most likely XX (Hayman & Martin 1965*a*). This was first interpreted as being a general difference between soma and germ line, but when other somatic tissues of the species *Perameles nasuta* were studied it became obvious that this was not the case. Cells derived from skin of females and males showed the sex chromosome constitutions XX and XY, respectively (Jackson & Ellem 1968), and the same was the case in corneal epithelium cells (Hayman & Martin 1969, reported by Walton 1969). Apparently, one sex chromosome is eliminated from hemopoietic cells and not from somatic tissues in general.

The other species of table 5 are rodents, which all have in common that their 'normal' X chromosome is unusually large, comprising more than 5 to 6% of (nA + X). The X chromosome of *Acomys selousi* comprises no less than 19% (Matthey 1965*a*, 1968*a*). The reason for including species with X chromosome polymorphism in this group is that the same mechanism may be working—it is just a question whether all or only part of one X is eliminated from somatic cells of females. This opinion is supported by observations on the chromosome constitutions of females of *Akodon azarae*, a field mouse from South America (Bianchi & Contreras 1967; Bianchi, Dulout & Contreras 1968). Five different combinations of X chromosomes were found: 38, XX, 38, XXq- (deletion of the long arm of one X), 38, XXp- (deletion of the short arm of one

X), 37, X/38, XXq- (mosaic) and 37, X. The two most frequent types were 38, XX and 38, XXq-. Autoradiographic studies and examination of the sex chromatin showed that the deleted X was always the allocyclic one.

The X chromosomes in all males of the rodent species of table 5 are consistently of the 'normal', undeleted type. Unfortunately, female germ cells have not been studied in any of the rodents, and it would be highly interesting to know if, e.g., two large X chromosomes are present in oögonia of *Acomys selousi*. The great majority of observations on somatic tissues have been carried out on cells from bone marrow or spleen, and thus it would be valuable to study other somatic tissues as well, for example cornea and skin. The elimination-inactivation hypothesis discussed here could explain why Matthey (1967*b*) did not find any Xp-Xp- females or Xp-Y males in his sample of 21 females and 18 males of *Mus triton*. Both in man and the mouse, at least one complete X chromosome is necessary for survival of the individual.

The number of species which might be included in this group will probably increase rapidly as our knowledge of the chromosomes of wild mammalian populations increases.

Finally, it shall be mentioned that individuals with loss of one X chromosome or a deletion of one of the two female X chromosomes may occasionally be found in species with normal sex chromosomes. In man the XO constitution is well known as are different structural alterations of one of the two female X:es (XXpi, XXqi, XXp-, XXq-, XXr) (Lindsten 1963; Jacobs 1969). Also in the European hamster (Schmid 1967*b*) and in the Syrian hamster (Sasaki & Kamada 1969) females with deletions of one X chromosome have been described.

TABLE 5. SPECIES WITH MOSAICISM OF THE SEX CHROMOSOMES, BUT APPARENTLY WITH AN XX/XY MECHANISM FOR SEX DETERMINATION

order and species	female		male		references
	soma	germ	soma	germ	
Marsupialia					
Perameles nasuta	13,X; 14,XX	(14,XX)†	13,X; 14,XY	14,XY	Hayman & Martin 1965*a*
Thylacis (*Isodon*) *obesulus*	13,X	(14,XX)†	13,X	14,XY	
T. (*Isodon*) *macrourus*	13,X	—	13,X	14,XY	
Rodentia					
Akodon azarae	38,XX 38,XXq-, XXp- 37/38,X/XXq- 37,X	—	38,XY	—	Bianchi *et al.* 1967, 1968
Phodopus sungorus campbelli	28,XX?-	—	28,XY	—	Vorontsov *et al.* 1967
Mus triton	32,XX 32,XXp-	—	32,XY	—	Matthey 1967*b*
M. minutoides musculoides	32,XX 32,XXp-	— —	32–34,XY	XY	Matthey 1967*a*
Acomys selousi	60 ± 2,XO?	—	60 ± 2,XY?	XY	Matthey 1965, 1968

† Ovarian tissue, the origin of the dividing cells was not known.

CONCLUSION AND SUMMARY

The mammals have been divided, in the present survey of their sex chromosomes, into five groups. Two main types of deviations from the usual XX/XY type (group (i)) are distinguished, namely those in which either X or Y have become translocated on to an autosome and have thus given rise to an XX/XY$_1$Y$_2$ (group (ii)) or an X$_1$X$_1$X$_2$X$_2$/X$_1$X$_2$Y (group (iii)) mechanism, respectively. So far, 12 species have been described, belonging to group (ii) (table 1) and 13 to group (iii) (table 2). New data on ten species of mongooses, recently studied by the author, are included in a survey of the sex chromosomes of the subfamily Herpestinae (table 3). Mammals in which both members of an autosome pair have fused with the X and the Y and which actually have the XX/XY type are included in group (i).

Translocations between an autosome and a sex chromosome occasionally occur in man, and in recent years a number of such translocations have been recorded. Cases have been described in which the X chromosome has fused with a chromosome no. 3 (Mukherjee & Burdette 1966), a chromosome no. 5 (Mann, Valdmanis, Capps & Puite 1965), a C group chromosome (Neuhäuser & Back 1967) and with a part of an unknown chromosome (Wie Lie, Coenegracht & Stalder 1964; Thorburn, Miller & Dovey 1967; German 1967). The Y chromosome has fused with a chromosome no. 2 (Berghe, Steeno, Verrensen & Moor 1965), a D group chromosome (Federman, Davidoff & Ouellette 1967), and with a D or G group chromosome (Genest, Bouchard & Bouchard 1967). Further, Ferguson-Smith (1966) has suggested that an interchange between an X chromosome and a small part of a Y chromosome could explain the cases of true hermaphroditism and those of Klinefelter's syndrome with an apparently normal female (XX) karyotype. An interchange between X and Y could also explain some unusual inheritance of the Xg blood group in some families (Sanger, Race, Tippett, Gavin, Hardisty & Dubowitz 1964; Ferguson-Smith 1966).

Translocations with a sex chromosome involved have been reported also from other species. Thus, several X–autosome translocations have been described in the mouse (see Ohno 1967, pp. 123–132) and recently an X–autosome translocation was found in a cow (Gustavsson, Fraccaro, Tiepolo & Lindsten 1968).

The strong male-determining effect of the Y chromosome (or a part of it) has been demonstrated above all in man but also in some animals. An XXY-sex chromosome constitution in the mouse (Russell & Chu 1961), and in the cat (Thuline & Norby 1961) gives rise to a sterile male phenotype corresponding to Klinefelter's syndrome in man. It seems likely that at least a part of a Y chromosome is necessary for testicular differentiation in all mammals. There are, however, some mammalian species in which so far no Y chromosome has been demonstrated in the male. In the present paper these have been included in group (iv) together with the vole *Microtus oregoni*, a remarkable gonosomic mosaic (table 4).

Group (v) includes eight species with mosaicism of the sex chromosomes but apparently with an XX/XY mechanism for sex determination. Some somatic tissues have lost all or a part of one X chromosome in the female sex and this may be interpreted as an unusual way of inactivation of one X. Furthermore, the males of three marsupial species have eliminated the Y chromosome from certain somatic tissues. In species of this group the germ line is XY in males and probably XX in females.

Unusual sex chromosome inheritance has been demonstrated in a variety of species belonging to eight mammalian orders. It is likely that unusual sex chromosome mechanisms of similar type have originated independently in different orders. Considering that to date only 15–20 % of all mammals of the world have been studied from a chromosomal point of view, it is reasonable to assume that many more species with sex chromosome mechanisms deviating from the usual XX/XY pattern will be discovered. 'Ultimately, a knowledge of the nature of the more unusual types of sex-chromosome mechanisms will clearly be essential for an understanding of the function of sex chromosomes in general' (Mittwoch 1967, p. 171).

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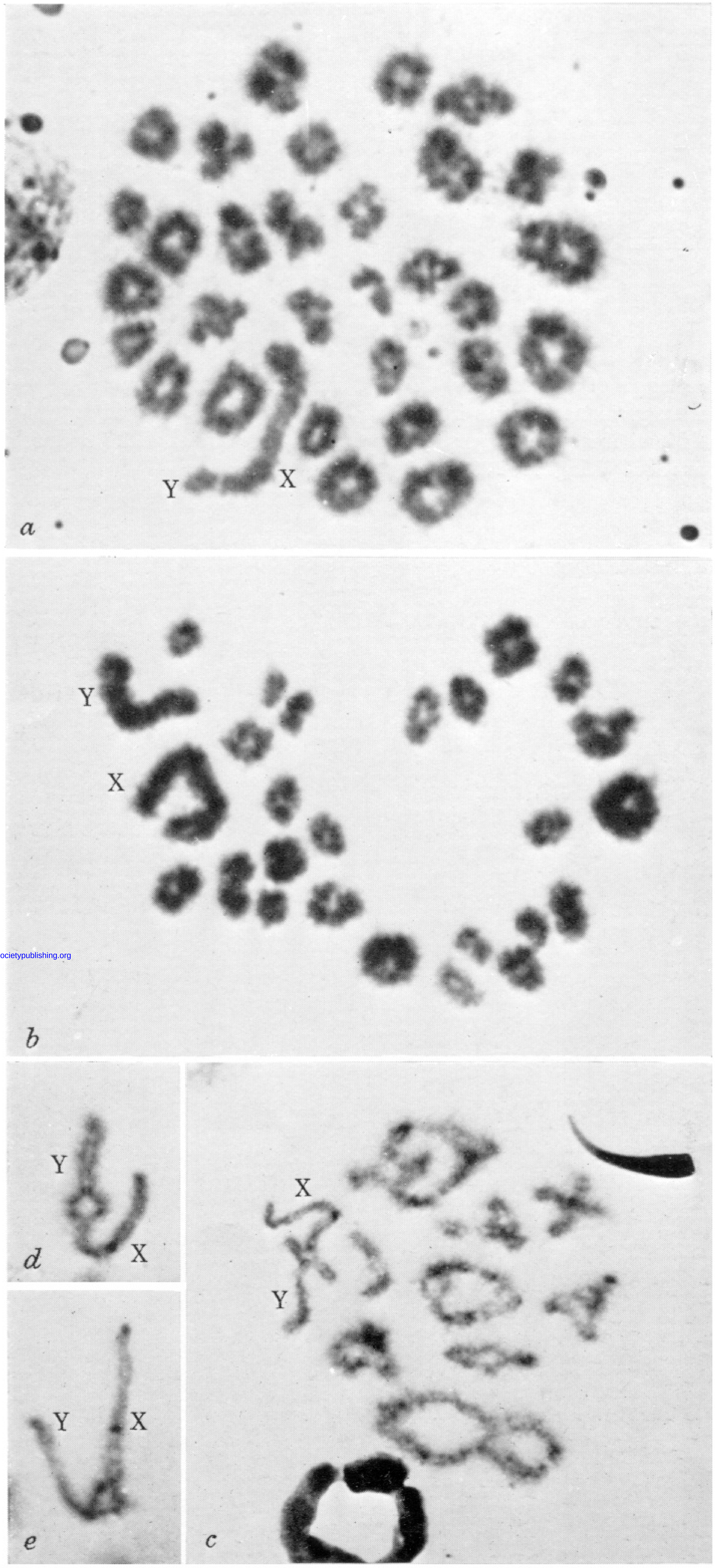
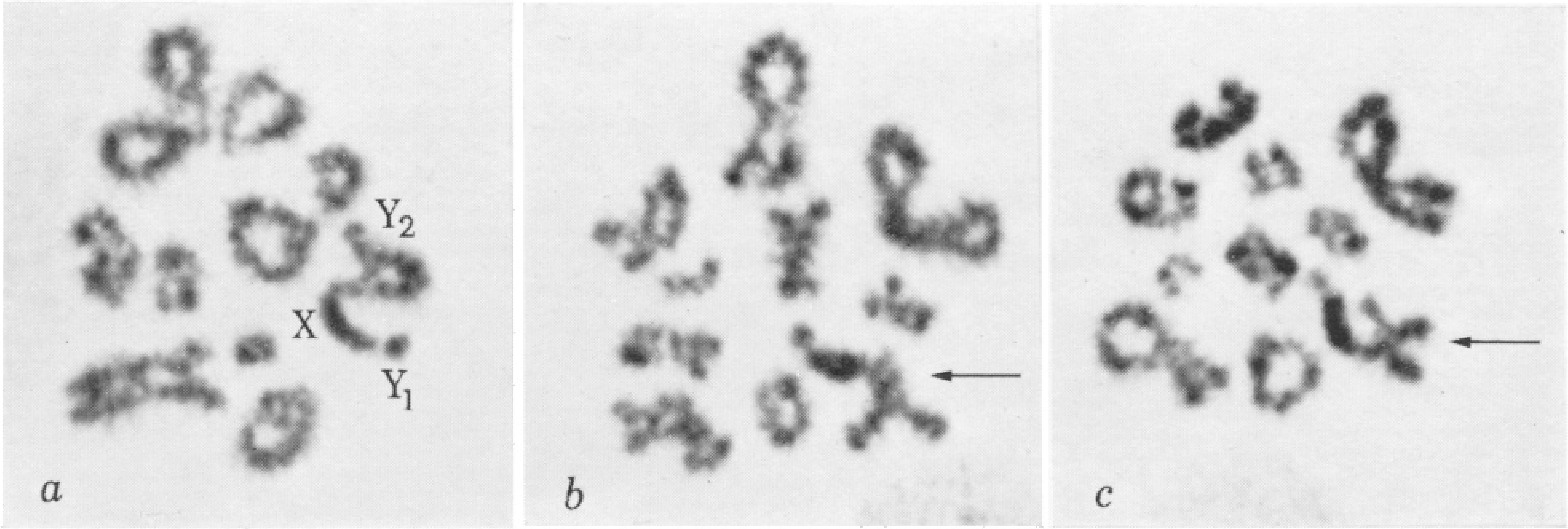


FIGURE 1. Male meiosis of three mammals with large sex chromosomes. (*a*) *Chinchilla laniger*, $2n = 64$, metaphase I, 31 autosomal bivalents, the large X and the small Y are associated end-to-end. (*b*) *Microtus agrestis*, $2n = 50$, metaphase I, 24 autosomal bivalents, the large sex chromosomes are separated from each other. (*c*) *Cricetulus griseus*, $2n = 22$, diakinesis, 10 autosomal bivalents, the large sex chromosomes form a distinct interstitial chiasma. (*d*, *e*) The sex bivalent of *Cricetulus griseus* from two other cells at diakinesis.—Acetic orcein squash (*a*, *b*) and air drying (*c*-*e*) preparations. (Magn. × 2470.)



IGURE 2. (*a* to *c*) Male meiosis of *Sorex araneus*, $2n = 21$, three cells at metaphase I, 9 autosomal bivalents and a sex chromosome heterotrivalent (arrows in *b* and *c*). The small Y_1 associates end-to-end with the original (gonosomal) part of X, whereas the bigger Y_2 associates by chiasmata with the autosomal part of X.—Acetic orcein squash preparation. (Magn. × 2750.)

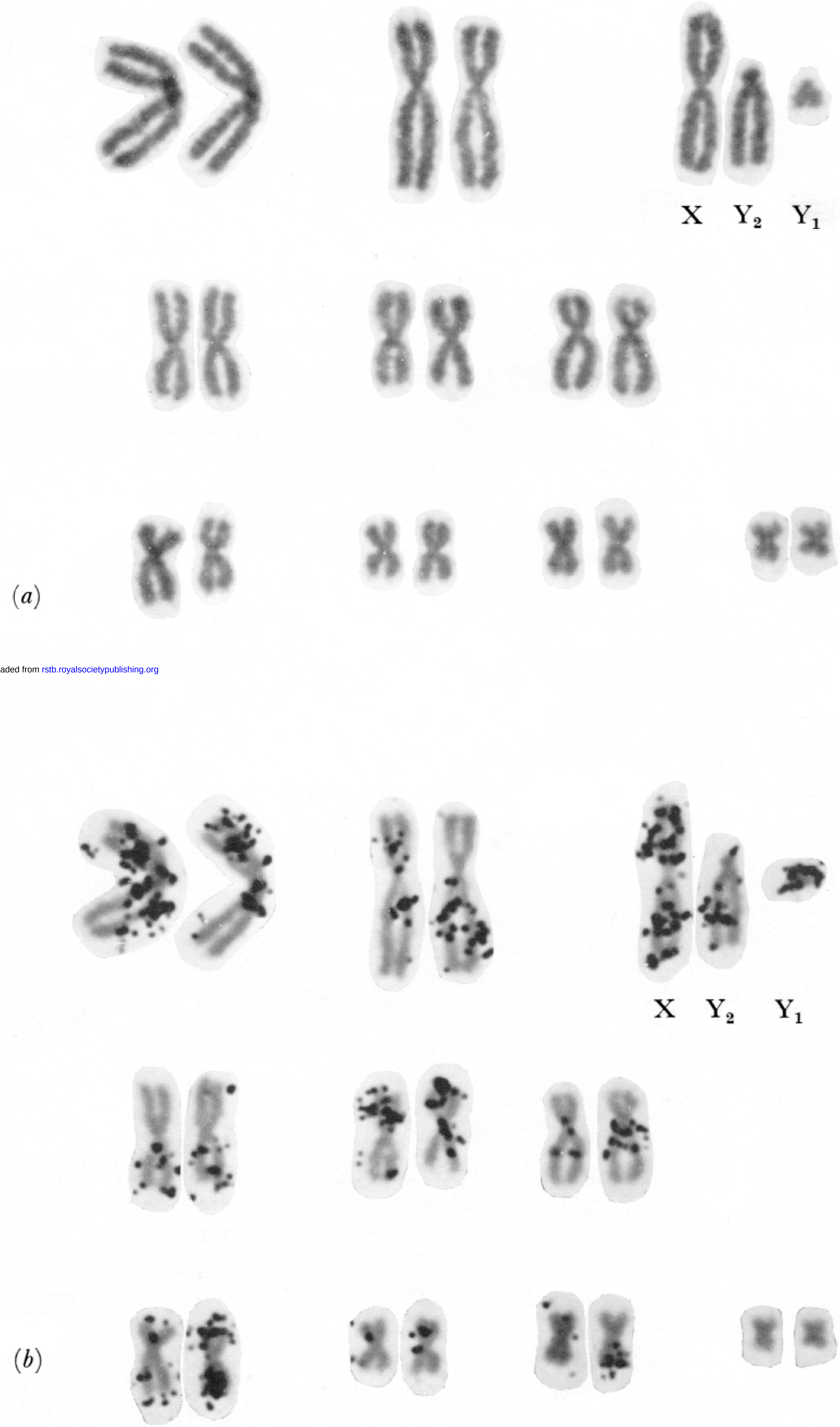


FIGURE 4. Karyotypes of male *Sorex araneus* with $2n = 21$. The chromosomes photographed (*a*) before and (*b*) after application of autoradiographic film. See text on p. 19 for comments.—Acetic orcein squash preparations from lung tissue culture. (Magn. × 2500.)

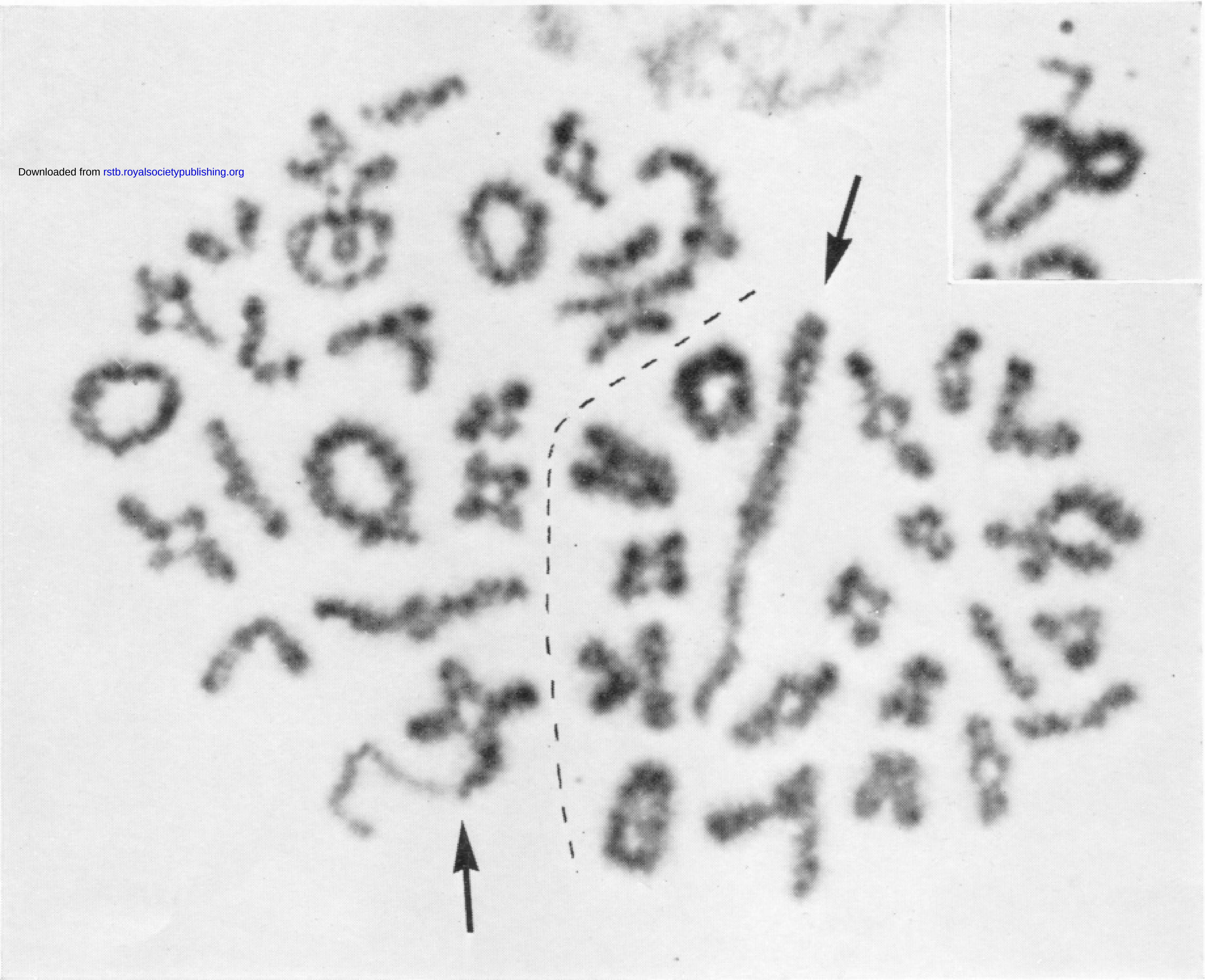


FIGURE 9. Male meiosis of *Herpestes sanguineus*, two cells in diakinesis—metaphase I showing 19 autosomal bivalents and the sex chromosome heterotrivalent (arrows). The true X (X_1) is associated end-to-end with the neo-Y, which forms an interstitial (left cell) or terminal (right cell) chiasma with the X_2. Inserted is the sex chromosome trivalent from another cell in diakinesis, showing two chiasmata between the Y and the X_2, and also showing the orientation of the sex chromosomes on the spindle. The X_1 and X_2 are directed upwards, the Y downwards in the figure.—Acetic orcein squash preparation. (Magn. × 2750.)

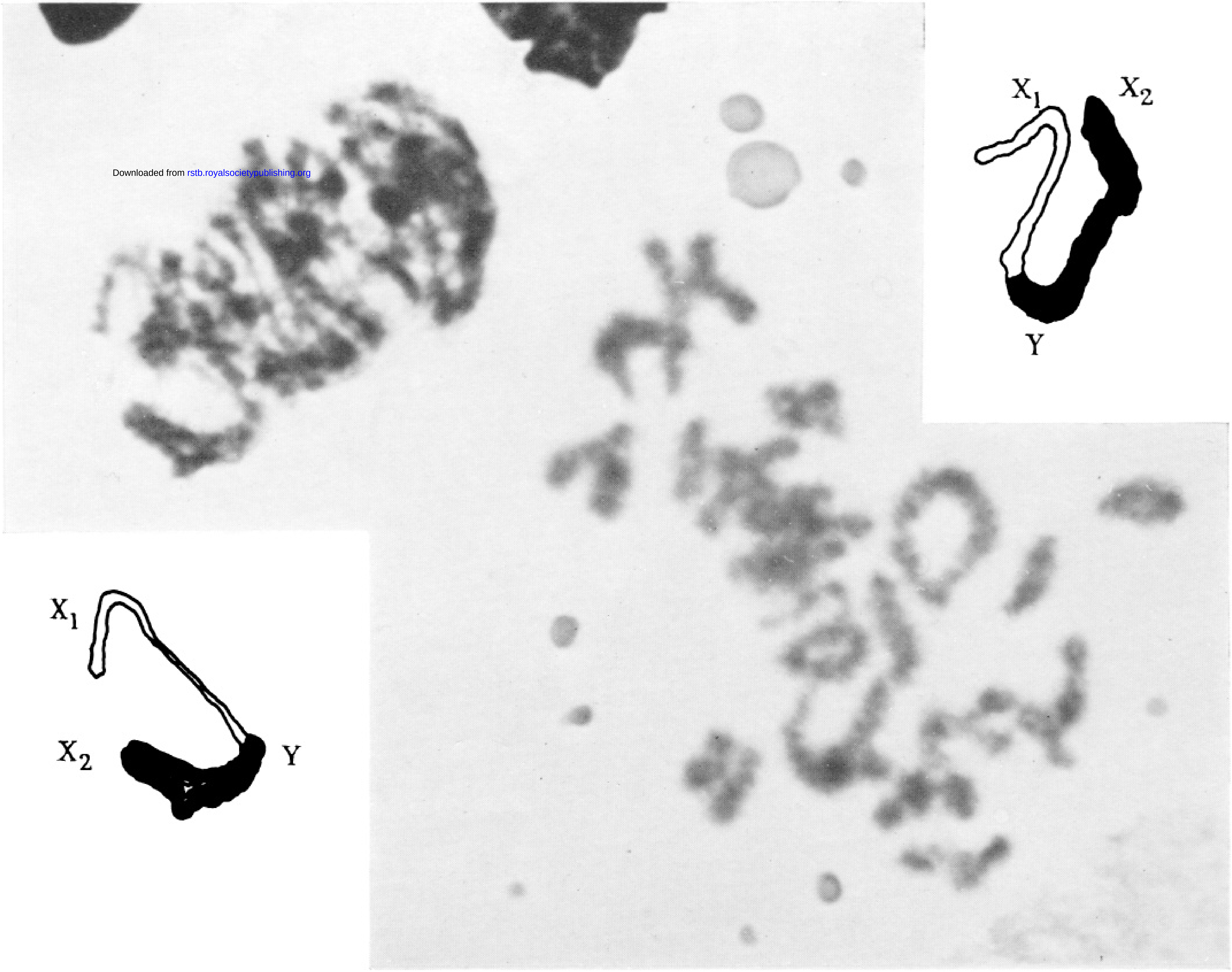


Figure 10. Male meiosis of *Herpestes sanguineus*, two cells in metaphase I and early anaphase I, side view, showing the orientation of the sex chromosomes on the spindle. Diagrams of the sex trivalents are inserted.—Acetic orcein squash preparations. (Magn. × 2750.)

FIGURE 6. Karyotypes of *Herpestes ichneumon*, (*a*) male, $2n = 43$, (*b*) female, $2n = 44$. Note the sex chromosomes and 8 pairs of telocentric autosomes. Acetic orcein squash preparations from skin tissue cultures. (Magn. × 2775).

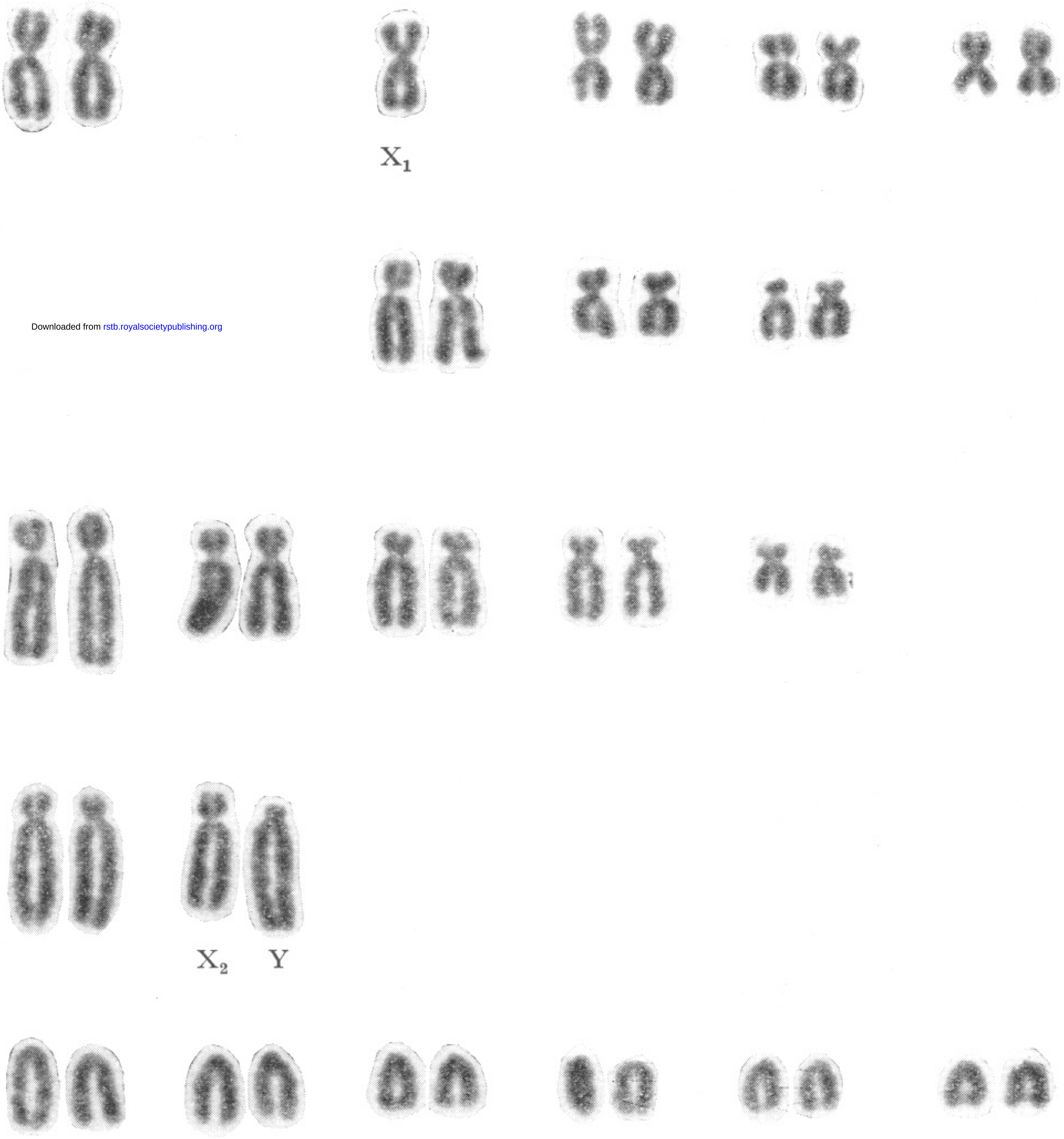


FIGURE 7. Karyotype of a male *Herpestes sanguineus*, $2n = 41$. Note the sex chromosomes and six pairs of telocentric autosomes. Acetic orcein squash preparations from skin tissue culture. (Magn. × 3225.)

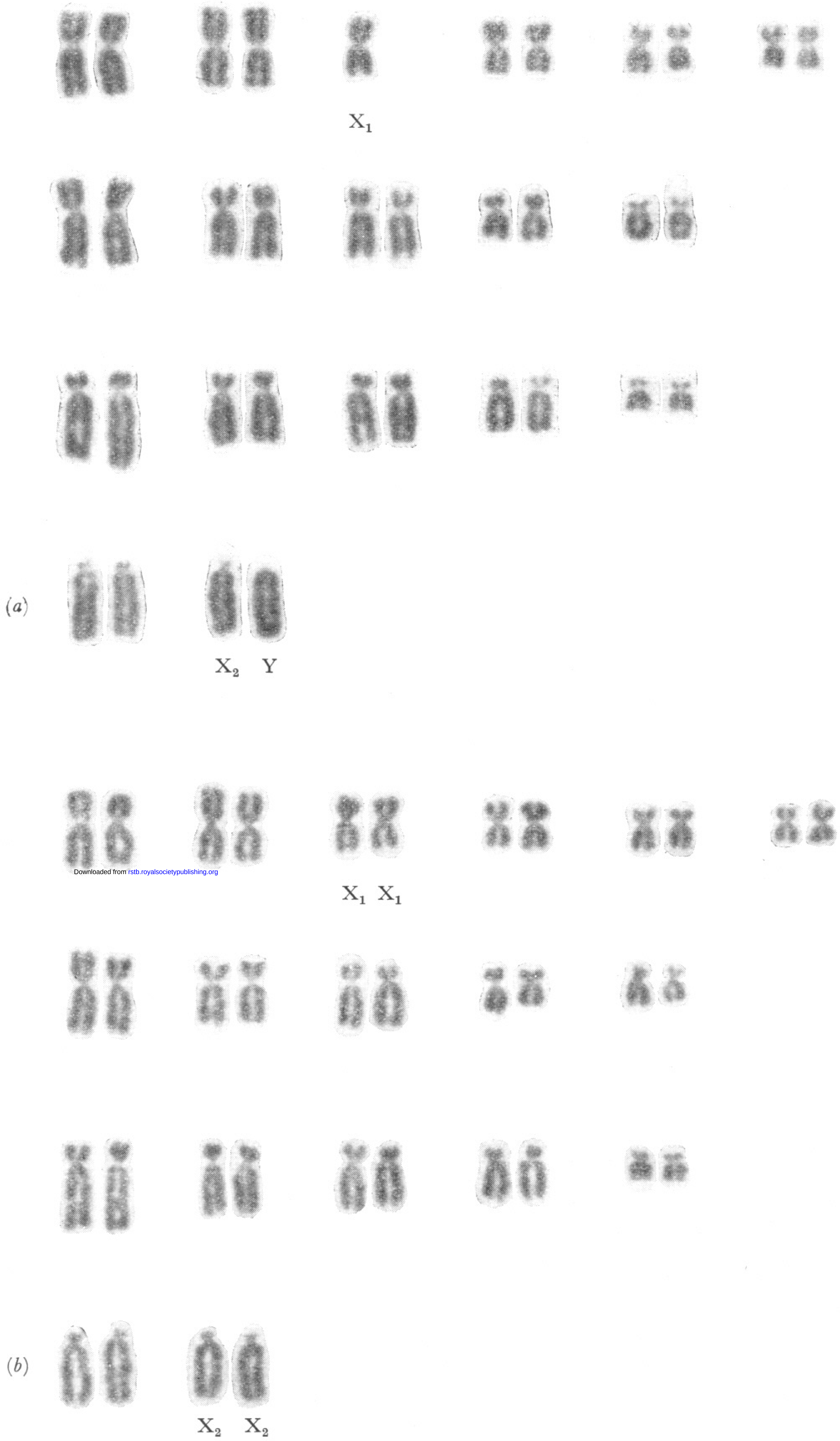


FIGURE 8. Karyotypes of *Herpestes auropunctatus* (*a*) male, $2n = 35$, (*b*) female, $2n = 36$. Note the small morphological difference between the Y and the X_2. The karyotype of the female may be regarded as representative of all mongooses having 35/36 or 36/36 chromosomes even though small interspecific differences occur. Acetic orcein squash preparations from testis (*a*) and skin (*b*) tissue cultures. (Magn. × 2920.)