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Comparative chromosome studies in mongooses (Carnivora, Viverridae)

I. Idiograms of 12 species and karyotype evolution in Herpestinae

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The chromosomes of 45 mongooses (Herpestinae) representing 5 genera and 12 species were studied mainly in tissue cultures of skin biopsies. Karyotypes and idiograms were constructed for the different species, and every chromosome was compared through all the species.

All species of the genus *Herpestes* have the functional Y chromosome translocated on to an autosome, and consequently the males have one chromosome less than the females. This "pseudo-XO/XX" or $X_1X_2Y/X_1X_1X_2X_2$ sex chromosome mechanism is unique among the Carnivora. All species of the other genera studied have the usual XY/XX mechanism.

The most frequent chromosome number in the Herpestinae is 2n = 36, but some species have different numbers. *Herpestes ichneumon* has 2n = 43/44, *H. sanguineus* 2n = 41/42 and *H. pulverulentus* 2n = 39/40; the remaining *Herpestes* species have 2n = 35/36. *Helogale parvula*, *Mungos mungo*, *Crossarchus obscurus* and *Cynictis penicillata* all have 2n = 36/36. The karyotypes of the different species show great similarities; the deviations in chromosome number in *Herpestes ichneumon*, *sanguineus* and *pulverulentus* can be accounted for by centric fusion/fission events, in the last-mentioned species in combination with pericentric inversions. In six species of *Herpestes* the neo-Y chromosome was identified as one relatively large t chromosome, showing intraspecific morphologic variation in two of the species. The Y of *Helogale*, *Mungos* and *Crossarchus* is a very small m chromosome, that of *Cynictis* is somewhat larger. The true X chromosome (X_1 of *Herpestes*) is most likely identical in all species: it is a medium-sized m chromosome comprising 5 per cent of the female haploid set.

Two alternatives of karyotype evolution in Herpestinae are discussed. Five species, not studied by the present author, are included in the discussion. Their karyotypes fit well into the general pattern with the exception of *Atilax paludinosus* (2n = 35/36), which for cytogenetic reasons should be included in the genus *Herpestes*. Some features of the karyotypes of the mongooses are unique among the Carnivora and the karyological data support the view of elevating the subfamily Herpestinae to the rank of family Herpestidae.

In 1964 it was discovered that the small Indian mongoose (*Herpestes auropunctatus*) had a deviating sex chromosome mechanism (FREDGA 1965). The female studied had 36 chromosomes, including two X chromosomes, whereas two males both had 35 chromosomes including one X chromosome but no Y. The study of male meiosis revealed that the X chromosome did not behave as a univalent at diakinesis and metaphase I, but attached end-to-end to one autosomal bivalent. The conclusion was that the original Y chromosome – or part of it – had been translocated on to an autosome, but due to the small size of the Y segment relative to the autosome, this

chromosome could not be recognized in somatic cells with the technique used (direct preparations from bone marrow). The sex-chromosome mechanism was apparently XX female, XA^y male, where A stands for an unidentified autosome and y for a deleted and translocated Y chromosome. This type of sex chromosome mechanism might also be called "pseudo-XO/XX" (PECCININI et al. 1971).

In 1965 MATTHEY described a similar type of deviating sex-chromosome mechanism in another mammal, *Mus minutoides* ssp_3, but in this case the A-Y chromosome was immediately recognizable. When this is the case, it is convenient to use the nomenclature $X_1X_1X_2X_2$ female, X_1X_2Y male, where X_1 is the true X chromosome, Y is the Y-autosome-translocation chromosome and X_2 is its non-Y-carrying homologue.

The unexpected finding in the mongoose was brought in doubt when TALUKDAR and MANNA (1966) reported 36 chromosomes and a small Y chromosome in a male of *Herpestes auropunctatus*. Again, when TODD and PRESSMAN (1966) found 35 chromosomes in another male of the same species, the question was raised as to mosaicism (TALUKDAR and MANNA 1966) or intraspecific polymorphism (MATTHEY 1967). The present author decided to elucidate these problems and started by analyzing the chromosomes in different tissues of a male, and in 1967 he published the results from a study of the chromosomes in 654 cells from six different tissues of a third male of *H. auropunctatus*. The somatic chromosomes were analyzed in direct preparations from bone marrow and in tissue cultures from kidney, heart, lung, skin and testis. Since all cells of the tissues examined contained 35 chromosomes, the conclusion was that *H. auropunctatus* is not a sex-chromosome mosaic. Due to the tissue culture technique, better chromosome preparations were obtained this time, and one heteromorphic chromosome pair was discovered, even though its implications on sex determination had to be left open until more material, from both male and female specimens, could be examined.

Up to now the present author has studied altogether 7 males and 4 females of *H. auropunctatus* and others have studied at least 11 males and 5 females of this species (cf. Table 18) without finding a single case of a male having 36 chromosomes and a small Y chromosome. Hence, the above-mentioned report by TALUKDAR and MANNA (1966) remains a mystery (see discusssion by FREDGA 1967b). So far the presence of a heteromorphic chromosome pair, as described by FREDGA (1967a), has not been confirmed by other authors. As will be shown in the present paper, this chromosome pair represents the X_2 and the Y chromosomes and is a feature characteristic of males of many species of the genus *Herpestes*.

The report of a deviating sex-chromosome mechanism in *H. auropunctatus* – the first species of the family Viverridae to be studied chromosomally – initiated studies of other species of the Viverridae in general and of the Herpestinae in particular. Now the chromosomes of at least one representative of all the six subfamilies of the Viverridae have been studied, and the results indicate that the deviating sex-chromosome mechanism is restricted to the Herpestinae. Rather soon, however, it became evident that not all species of the Herpestinae had the XX/XA^y or $X_1X_1X_2X_2/X_1X_2Y$ sex-chromosome mechanism. In 1966 TODD and PRESSMAN reported $2n = 36$ and a small individual Y chromosome in a male *Suricata suricatta* and later similar findings were reported in *Cynictis penicillata* (GERNEKE 1967; TODD et al. 1967), *Bdeogale nigripes* and *Ichneumia albicauda* (WURSTER and BENIRSCHKE 1968). Only one or two males of each species were studied and still no systematic chromosome investigation of the Herpestinae exists. To fill this gap the present study was undertaken and the aim was primarily to answer the following questions:

(1) Which species have the deviating sex-chromosome mechanism and how and when did this mechanism originate?
(2) How is the normal sex ratio maintained in species with XX/XA^y sex chromosomes?
(3) Which autosome is involved in the Y translocation?
(4) Is there a definite trend in karyotype evolution in this group of mammals?

The present paper is the first in a planned series of 3 papers with the common title: Comparative chromosome studies in mongooses (Carnivora, Viverridae). Questions (1), (3) and (4) will be dealt with in the present paper and in a forthcoming paper: "II. Autoradiographic studies." Question (2), although answered in prin-

ciple in FREDGA (1970), will be treated in detail in "III. Male meiosis". It is expected that a better understanding of question (4) will result from the application of the new staining techniques, QM fluorescence and various Giemsa procedures.

Animal material

In all, 45 mongooses of 12 species and five genera were investigated. The intention was to study at least one specimen of each sex of as many species as possible from genera of different specialisation within the subfamily Herpestinae. However, sometimes only one specimen of a species was available (*Crossarchus obscurus*) or the "pair" obtained turned out to be two males (*Herpestes sanguineus*) or two females (*Herpestes urva*). The animals were obtained alive from different sources in the years of 1964–1970. Fig. 1 and 2 show the appearance of the different species studied and the entire material is surveyed in Table 1. The taxonomic identity of the animals was based mainly on the following literature: POCOCK 1916, 1941, SCHWARZ 1947, ROBERTS 1951, HINTON and DUNN 1967, and DORST and DANDELOT 1970. For a control of the determinations a personal visit was paid to the British Museum (Natural history) in November 1969, on which occasion the mongoose collection of the Museum was examined. In 1966, the skulls of specimens *H. a.* 1–3 were sent to the British Museum for identification and Dr. R. W. Hayman kindly replied: "The three skulls agree very well with *Herpestes auropunctatus* HODGSON, the small Indian mongoose." All attempts to determine the animals studied as to subspecies were postponed until the publication of measurements and other descriptive data.

The nomenclature of HINTON and DUNN (1967) seems to be best in agreement with that generally accepted today and will be followed in the present work. The sequence of the genera is the same as in HINTON and DUNN and the sequence of the species within the *Herpestes* conforms with MORRIS (1965). As will be clear from the present study, this sequence is also applicable on the basis of karyological data.

The majority of the animals were bought from Ravensden Zoological Company Ltd., Bedford, England, viz. the following: *Herpestes ichneumon* 1–3, *H. sanguineus* 1–2, *H. auropunctatus* 1–7, *H. fuscus* 1–2, *H. urva* 1–2, *H. brachyurus* 1–2, *Mungos mungo* 1–2, *Crossarchus obscurus* 1 and *Cynictis penicillata* 1–2. The following animals were obtained from Bureau d'Exportation, Karachi, West Pakistan: *Herpestes auropunctatus* 8–11, and *H. edwardsi* 1–4. The two specimens of *H. pulverulentus* were a gift from Dr. T. D. GLOVER, Unit of Reproductive Biology, University of Liverpool, England, and sent to Lund by the Animal Travel Service, Cape Town, South Africa. Offspring was obtained from only one pair, viz. the *Mungos mungo*, the *M. m.* 3–12 representing their first three litters born in Lund.

Some of the mongooses are still alive and the dead ones are preserved at the Zoological Museum of the University of Lund and included in their collection of mammals.

Comments to Table 1. All mongooses studied by the author are included in the table. The specimens *H. a.* 1–3 and *H. a.* 4 are those studied by FREDGA (1965, 1967a). The majority of animals listed in the table are included in Table 3 in FREDGA (1970). The following specimens, lacking in that table, had not been investigated at that time *H. p.* 1–2, *H. a.* 8–11 and *H. e.* 1–4.

In the text and in some figures abbreviations are used for the species or animal under discussion. The initials of the scientific name are generally used and each individual of a species is given a number (column "Animal" in the table). The next column gives the author's code number, successive numbers being used regardless of species, starting with 01 for each year (the last two figures). The sex is indicated in the next column (M = male, F = female). Braces indicate either that the animals were obtained together or that they belong to the same litter (*H. a.* 5–7, *M. m.* 3–5, 6–8, 9–12). That the animals were obtained together might mean that they were from the same geographical area or locality, and might also indicate that they were related, although this was never confirmed. In the column "Origin" all available information about the locality or area where the animals originally were trapped or bred is gathered according to the information required from the dealers. Unfortunately, this information is incomplete in many cases. The table also includes information about the tissues and passages utilized for the chromosome studies in the individual cases (only

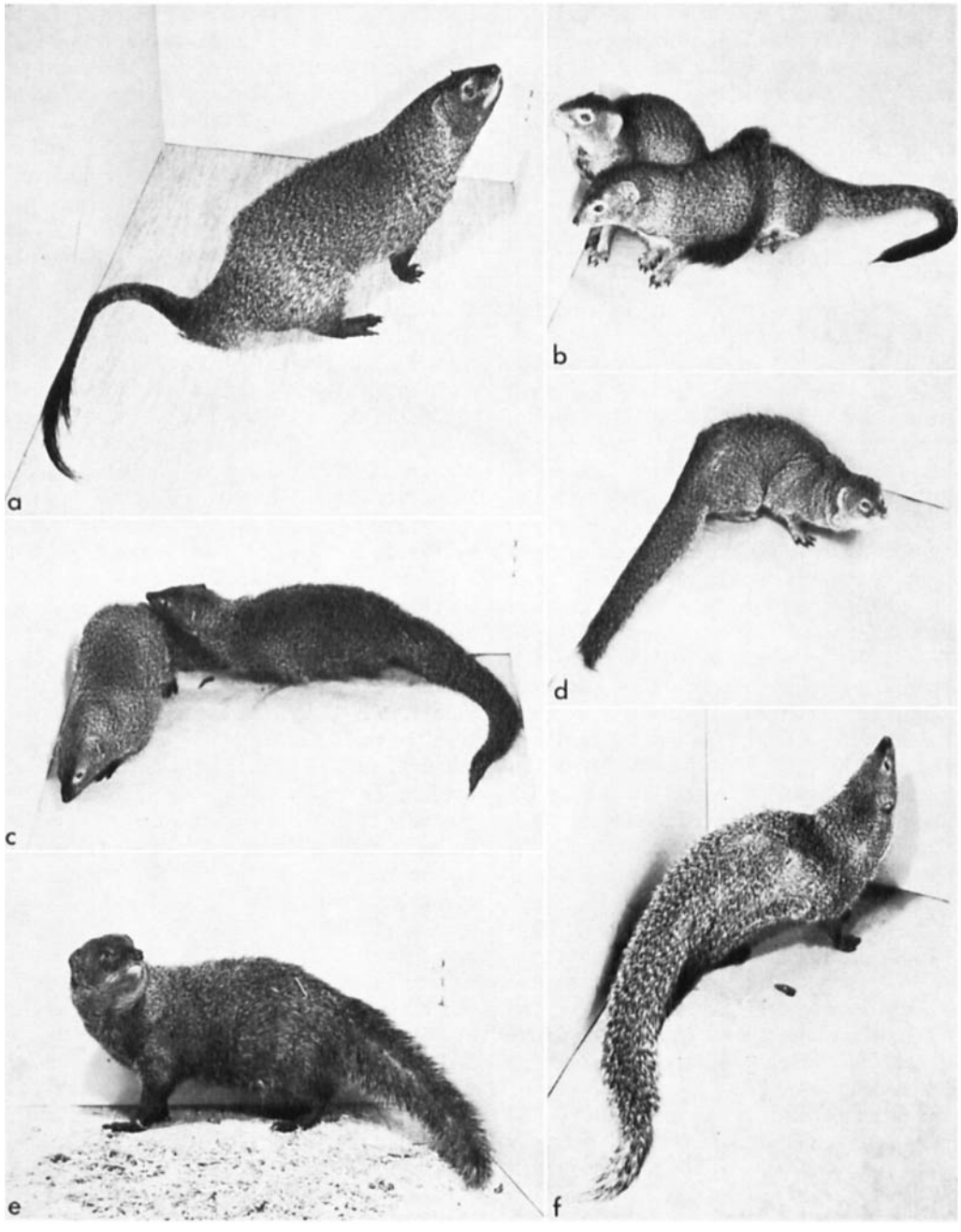


Fig. 1. The mongooses studied, a: *Herpestes ichneumon*; b: *Herpestes sanguineus*; c: *Herpestes pulverulentus*; d: *Herpestes auropunctatus*; e: *Herpestes fuscus*; f: *Herpestes edwardsi*.

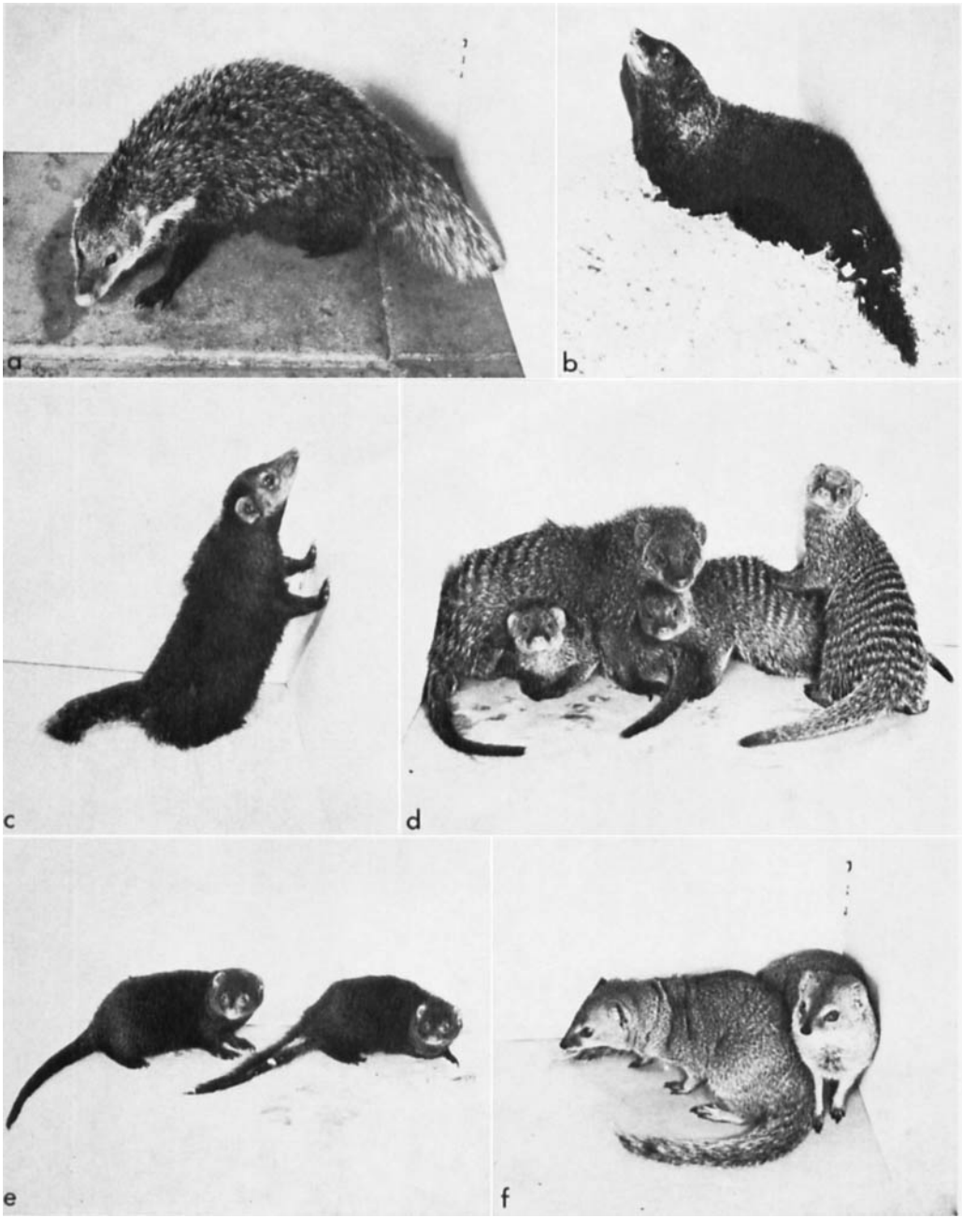


Fig. 2. The mongooses studied, a: *Herpestes urva*; b: *Herpestes brachyurus*; c: *Crossarchus obscurus*; d: *Mungos mungo*; e: *Helogale parvula*; f: *Cynictis penicillata*. The photos in Fig. 1 and 2 give an idea of the relative sizes of the species.

Table 1. Survey of the material

Species	Animal		Code No.	Sex	Origin	Tissues and passages (P) studied				
						Heart	Lung	Skin	Testis	Bone marrow (BM), kidney (K) or muscle (M)
Herpestes ichneumon	*H.i.*	1	55–68	M	Unknown			P2–P3		
		2	56–68	F		P2	P4	P2–P3		
		3	38–69	M	Unknown			P1–P11		
Herpestes sanguineus	*H.s.*	1	52–68	M	Botswana			P2–P5		
		2	53–68	M				P2–P5	P1	
Herpestes pulverulentus	*H.p.*	1	65–70	M	Robertson (?),			P1–P2		
		2	66–70	F	S. Africa			P1–P2 (P34)		
Herpestes auropunctatus	*H.a.*	1	13–64	F						BM
		2	15–64	M	Calcutta (?),					BM
		3	18–64	M	India					BM
		4	48–65	M		P0	P0	P0–P1	P1	BM, K: P0
		5	25–67	F		P1	P0–P27	P0–P25		BM
		6	08–68	M	Born in England			P0–P6 (P99)		
		7	47–68	F				P0–P8		
		8	15–70	M				P1		
		9	16–70	M	West Pakistan			P1		
		10	17–70	M				P1		
		11	18–70	F				P1		
Herpestes edwardsi	*H.e.*	1	14–70	M	West Pakistan			P1		
		2	62–70	F	Thatta distr.,			P1–P38		
		3	63–70	M	Sind prov.,			P1–P23		
		4	64–70	M	West Pakistan			P1–P22		
Herpestes fuscus	*H.f.*	1	26–67	F	Ceylon	P1–P3	P2–P23	P1 (P26)		
		2	36–69	M				P1–P3	P1–P17	
Herpestes urva	*H.u.*	1	44–68	F	Thailand	P1–P5	P0	P2		K: P0–P1
		2	54–68	F		P2	P4	P1		
Herpestes brachyurus	*H.b.*	1	40–69	M	Singapore	P3–P13	P6	P1–P8	P3–P14	
		2	41–69	F				P2–P8		
Helogale parvula	*Hel.p.*	1	48–68	F	Botswana			P2–P3		
		2	49–68	M				P2–P4		

Mungos mungo	*M.m.*	1	10–69	M	Botswana				P2
		2	35–69	F					P1
		3	45–68	F	Born in Lund,				P0–P2
		4	46–68	M	Sweden. *M.m.* 1				P0–P2
		5	57–68	M	and *M.m.* 2 parents				P2
		6	07–69	F				P1–P3	P2
		7	08–69	F	– ” –				P1
		8	09–69	M					P2
		9	32–69	F					P1–P2
		10	33–69	M	– ” –				P1
		11	34–69	M					P1–P4
		12	14–69	M					P1 (P29)
								M: P4–P29	
Crossarchus obscurus	*Cr.o.*	1	37–69	M	Sierra Leone	P1–P2			P1–P2
Cynictis penicillata	*Cy.p.*	1	50–68	M	Botswana	P3	P0		P0–P8
		2	51–68	F					P0–P3

See p. 3 for comments

the bone-marrow preparations were direct preparations). Thus, P1–P38 means that the chromosomes were studied at different passages between 1 and 38. Chromosome preparations were sometimes made from different cultures of the same passage number. P0–P6 (P99) means that preparations were made from passages 0 (primary culture) to 6 as described above, and also from passage 99, but not between passages 6 and 99.

Methods

1. Chromosome preparations

For the present comparative study it was necessary to obtain chromosome preparations of high quality and for that reason the tissue-culture technique was chosen and used throughout the investigation. Cell cultures were initiated from biopsies of different origin, primarily from skin but also from heart, lung and testis and exceptionally from kidney and muscle (Table 1). The biopsies were taken aseptically, the skin and testis under ether anaesthesia and the others after the death of the animal. The piece of skin, about 2×10 mm in size, was taken from the inside of a thigh after the hair was shaved off and the skin cleaned with pHiseHex (Winthrop). The piece was immediately transferred to a tube with 5 ml of tissue-culture medium and processed further in the tissue-culture laboratory in the following way: The biopsy was minced with scissors and planted in 2–3 milk dilution bottles (bottom area approx. 45×130 mm) with screw caps. In order to have the tissue fragments attached to the glass, the bottles were placed upside down for some hours, 10 ml medium being added to the "ceiling" of the bottles. The cells were usually grown in basal medium Eagle with Hank's salts with 20% calf serum and containing 100 IU of penicillin and 0.2 mg streptomycin per ml, pH = 7.2. The bottles were incubated at 36–37°C; usually after 2–3 weeks the cells had grown out sufficiently to be transferred to 2–3 new bottles (P1). The biopsies from the other tissues were handled in a similar way. Usually explants from lung and testis grew faster and were transferable after 1–2 weeks. After the first transfer, the cultures were usually subcultured once or twice a week. Chromosome preparations were made from as early passages as

possible, in some cases even from the primary culture (P0) but usually from the first subculture (P1) (cf. Table 1). The cells were refed 24 to 48 hours prior to harvesting, and before trypsinization the cultures were treated for one hour with 0.1 µg Colcemid (Ciba) per ml medium. The cells were loosened by replacing the medium with 2 ml of 0.25% trypsin solution at 37°C (Difco 1:250, pH 7.6), which was left on for 5–10 minutes. Hypotonic treatment was performed by addition of 4 ml of distilled water and after 10–15 minutes the cells were centrifuged for 5 minutes at 500–1000 rpm. The cell button was fixed for 10–20 minutes in a mixture of 9 parts 60% acetic acid and 1 part 1N HCl. After the fixative was poured off, the cells were resuspended in a few drops of stain (2% orcein in 60% acetic acid) and a drop of the cell/stain suspension was placed on a slide and squashed under a coverslip in the usual way. The preparations were sealed with Krönig cement. By using siliconized coverslips the squashing could be improved and the cells remain on the slide, when the coverslip was removed by the quick-freeze method of CONGER and FAIRCHILD (1953). This is valuable for making the semipermanent preparations permanent and for processing the preparations for autoradiography.

2. Chromosome measurements

Favourable cells were photographed under oil immersion (Apochromat HI 100/1.32 or Planachromat HI 100/1.25) at a magnification of 940× on the film. Copex Ortho film was used, developed 8 minutes in Rodinal 1:50 at 20°C. The measurements of the chromosomes were performed on photographic enlargements at a magnification of 5000×. A large number of cells from each specimen were arranged into karyotypes and the best of them selected for the measurements. As a rule the chromosomes of 5 cells from each sex were measured (Table 2), but in the case of *H. sanguineus* 5 cells from each of the two males were used, from *H. urva* 5 female cells and from *Crossarchus obscurus* 5 male cells. From *H. edwardsi* 5 female and 10 male cells were selected for measurements; the male cells were from the same individual but from two different passages, P1 and P8. This was done to find out whether the karyotype had undergone any changes during the time in culture and whether the addition of

Table 2. Survey of material used for chromosome measurements

Species	Female					Male					
	Animal	Tissue	Passage	No. of cells		Animal	Tissue	Passage	No. of cells		
Herpestes ichneumon	*H.i.* 2	Skin	P2	4	Skin P3	1*	*H.i.* 1	Skin	P2	4	Skin P3	1*
Herpestes sanguineus	—	—	—	—	— —	—	*H.s.* 1	Skin	P2	3	Skin P5	2*
Herpestes sanguineus	—	—	—	—	— —	—	*H.s.* 2	Skin	P2	1	Skin P5	4*
Herpestes pulverulenius	*H.p.* 2	Skin	P1	4	Skin P2	1*	*H.p.* 1	Skin	P1	2	Skin P2	3*
Herpestes auropunctatus	*H.a.* 5	Skin	P2	5*	— —	—	*H.a.* 4	Testis	P1	2	Lung P0	3
Herpestes edwardsi	*H.e.* 2	Skin	P2	5	— —	—	*H.e.* 4	Skin	P1	5	Skin P8	5*
Herpestes fuscus	*H.f.* 1	Skin	P2	3*	Heart P3	2*	*H.f.* 2	Skin	P1	2	Skin P3	3*
Herpestes urva	*H.u.* 1	Heart	P4	4*	Heart P5	1*	—	—	—	—	— —	—
Herpestes brachyurus	*H.b.* 2	Skin	P2	5	— —	—	*H.b.* 1	Testis	P14	5*	— —	—
Helogale parvula	*Hel.p.* 1	Skin	P3	5*	— —	—	*Hel.p.* 2	Skin	P4	5*	— —	—
Mungos mungo	*M.m.* 3	Skin	P2	5*	— —	—	*M.m.* 4	Skin	P2	5*	— —	—
Crossarchus obscurus	—	—	—	—	— —	—	*Cr.o.* 1	Heart	P1	5	— —	—
Cynictis penicillata	*Cy.p.* 2	Skin	P3	5*	— —	—	*Cy.p.* 1	Skin	P0	2	Skin P7	3*

* Autoradiography

tritiated thymidine to the culture medium had affected the karyotype. Since this was not the case (Table 23) many of the measurements were actually made on labelled cells, later on used for autoradiography (indicated with * in Table 2). Even though autoradiography was valuable for the identification of certain chromosomes, particularly the X, labelled cells were not exclusively used for the measurements, the main principle being to choose cells most favourable for measurements, namely well-fixed cells with the chromosomes in one plane, at an optimal degree of contraction and with a minimum of overlapping. In order to avoid individual errors, all photographic enlargements and measurements were performed by one and the same person, the author.

The chromosome measurements were carried out by placing one arm of a bipointed compass in the middle of the centromere and the other at the end of each arm. If the two chromatids were of different lengths, it was first decided whether one of them was overcontracted or overelongated. If that was the case the abnormal chromatid was discarded; if none of the chromatids appeared abnormal the mean value of the two chromatids was used. However, problems of this kind were rare, since the two chromatids were usually of equal length. As will be discussed later, some chromosomes had vague satellites but due to their small size and irregular occurrence they were neither included in the measurements nor indicated in the idiograms. The length of the chromosome arms was scored with an accuracy of 0.5 mm. Absolute length, relative length and centromeric index were calculated for each chromosome.

Chromosome nomenclature

There are two main principles in the nomenclature of chromosomes, one based on the total length of the chromosome, the other based on the centromeric position. Both systems have advantages and disadvantages. In the former system the chromosomes are numbered consecutively from the longest to the shortest chromosome, which has the advantages that a number is easier to remember than a combination of letters and numbers, and that the number of the smallest chromosome indicates the haploid chromosome number minus 1 (this is not the case in species in which the sex chromosomes are included in the numbering, as in some nomenclatures of the Chinese hamster chromosomes). In the latter system, the chromosomes are first divided into classes on the basis of centromeric index, and then numbered within each class according to decreasing length. This system has the advantages that the combination of letters and figures will give some idea about the morphology of each chromosome, and also that in many species the chromosomes become divided into more natural groups. The criteria for the groups should be defined for each individual material with the sole purpose of making the subdivision of the karyotype as natural and convenient as possible. The nomenclature recommended by LEVAN et al. (1964), making use both of total chromosome length and location of the centromere, seems to have been accepted generally and has been applied in the present study. The chromosomes were included in any of the four classes m, sm, st and t with centromeric indices as follows:

m	50 – 37.5
sm	37.5 – 25.0
st	25.0 – 12.5
t	12.5 – 0.0

In the individual idiograms of the species the chromosomes were strictly distributed into these classes. In the karyotypes, on the other hand, the chromosomes were arranged in a somewhat different way, in order to clarify the similarities among the different species. Because many chromosomes turned out to be borderline cases in the m-sm-st-t system, the demand for another grouping with slightly changed class limits was felt very strongly when comparisons were undertaken with the individual chromosomes among the species. This resulted in a modified division of the chromosomes, viz. into four groups called A, B, C, and D, within each of which the chromosomes were numbered essentially according to decreasing length. The boundaries for the centromeric indices were chosen as follows:

A	50 – 40
B	40 – 30
C	30 – 20
D	20 – 0

As is evident from Table 17, this modified subdivision is natural and convenient in the great majority of chromosomes in all of the species dealt with in the present work. There are 6, 6, 4 and 2 chromosome pairs in the groups A, B, C and D, respectively. The X (X_1) chromosome is included in group A, the X_2 and Y chromosomes in group D. In the karyotypes group A occupies the first row, group B the second and groups C and D the third.

In two species, *H. ichneumon* and *H. sanguineus*, 4 and 3 pairs of m-sm chromosomes in the "standard" mongoose karyotype were substituted by 8 and 6 pairs of t chromosomes and in *H. pulverulentus* 2 large pairs of sm chromosomes were missing and 4 "new" sm-st chromosomes were present. In the karyotypes of these three species, gaps were left open in the first and/or second rows and the "new" chromosomes were placed in a fourth row.

In brief, the idiograms show the dissimilarities among the species, the karyotypes the similarities. When the karyotype of a species is described, the nomenclature generally accepted is used (m, sm, st, t); when the karyotypes of the different species are compared, the modified nomenclature adapted to the chromosomes of the subfamily Herpestinae is used (A, B, C, D).

Usually mammals have XX/XY sex chromosomes. In many mongooses, the functional Y has been translocated on to an autosome giving rise to a difference in chromosome number between female and male, the males having one chromosome less than the females. In the present study, the autosome-Y-translocation chromosome is designated Y, the non-Y-carrying homologue is designated X_2, and the true X is designated X_1. Some mongooses, like a few other species (survey in FREDGA 1970), thus have $X_1X_1X_2X_2$/X_1X_2Y sex chromosomes. It must be stressed, however, that X_2 is an autosome and has nothing to do with sex determination.

Results

1. General remarks

A large number of cells were analysed microscopically from each individual. The chromosome number was determined for each cell and special attention was paid to the morphology and appearance of the D chromosomes (viz. the st1 or st2, X_2 and the Y). Cells with deviating chromosome numbers were found regularly but in low frequencies (cf. FREDGA 1967a), and in no single specimen were found indications of mosaicism either within or between tissues. No intraspecific differences in chromosome number and morphology could be verified apart from the following exceptions in regard to chromosome morphology: The Y chromosomes differed in the two males studied of both *H. ichneumon* and *H. sanguineus*, and two autosomes were abnormal in one specimen of *Mungos mungo*. This individual, born in captivity in Lund, turned out to be heterozygous for a balanced reciprocal translocation.

The results of the chromosome measurements are presented in Tables 3–6, 8–15 and 19–28. In the tables, as in the idiograms, all chromosomes are placed in any of the classes m, sm, st and t, and arranged within each class in order of decreasing length. For each chromosome, total absolute length is given in μ, total relative length in parts per hundred of female haploid set, and the centromeric index (c.i.) is calculated from the formula $\text{c.i.} = \frac{100}{p+q}$ (p = short arm, q = long arm of chromosome). Standard errors (S.e.) for absolute length, relative length and centromeric index are also included in the tables. Tables 3–6 and 8–15 give the mean values for each species, Tables 19–28 (appendix) give the measurement data for each individual (for *Herpestes urva* and *Crossarchus obscurus* the values for the only individuals measured are given in Tables 10 and 14). In the Tables 3–6 and 8–15 the relative lengths for each chromosome arm, calculated from the formula $p = \frac{\text{c.i.}\,(p+q)}{100}$, are also given. The values of X_1 and X_2 are weighted means of the male and female values.

Idiograms and karyotypes, printed at the same magnification, are presented for each species.

2. Karyotypes and idiograms

A. Ichneumon, *Herpestes ichneumon* (LINNAEUS) (1758)

Two males and one female were studied, 2n = 43 male, 44 female. The karyotype is shown in Fig. 3 and the idiogram in Fig. 4. The results

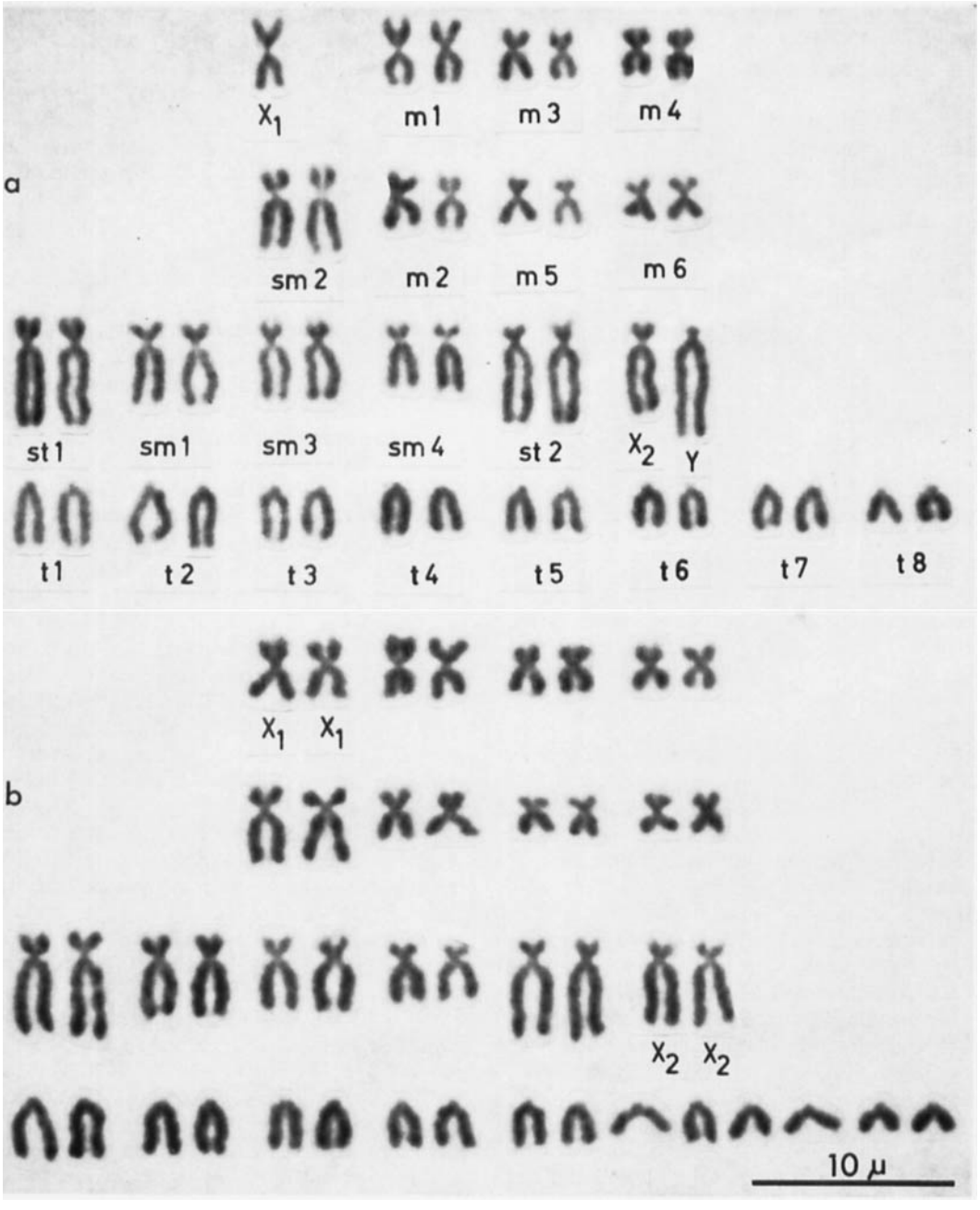


Fig. 3. Karyotypes of *Herpestes ichneumon*, a: male, 2n = 43 (*H.i.* 1); b: female, 2n = 44. — × 2,880.
This magnification of the chromosomes, is used throughout the article unless otherwise stated.

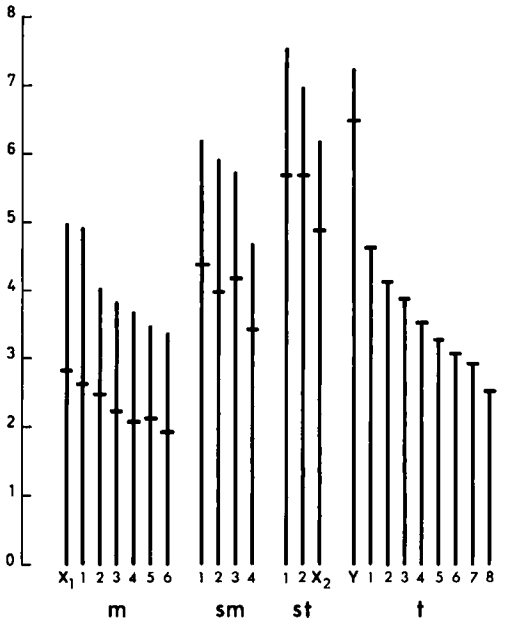


Fig. 4. Idiogram of *Herpestes ichneumon*; unit of the ordinate, per cent of total haploid female chromosome length.

of the chromosome measurements are given in Tables 3 and 19.

The karyotype consists of 6 m, 4 sm, 2 st and 8 t autosome pairs. The X_1 chromosome is an m, the X_2 an st and the Y a t or st chromosome (see below). The largest chromosome of the complement is st1 and the smallest t8.

Chromosome m1 is very similar to X_1, which is slightly larger and has a somewhat lower centromeric index. The m2–m6 pairs are similar but may be distinguished individually in good preparations on the basis of relative length and centromeric index; m2 and m5 have a centromeric index of 38 as compared with 41–43 in the other three pairs. Among the sm chromosomes, sm4 is easily identified, whereas the other three pairs form a group of relatively large chromosomes with a centromeric index of 27–33; sm2 is intermediate in size and has the highest centromeric index of the three pairs. The st1 and st2 pairs are easily identified on the basis of length and centromeric index. As to their length, the t autosomes form a continuous series making individual identification dubious even though probably the largest and the smallest pairs are recognizable. Small "heads", occasionally seen in some members of this group, were of none or little help in the identification of individual pairs; they were neglected at the measurements, at which all chromosomes of this group were regarded as lacking a short arm.

The X_1 is the largest of the m chromosomes and constitutes 5.0 per cent of the length of the female haploid set (A+X). The X_2 is considerably smaller than the Y and may be confused with the pairs sm1 and sm3. The Y turned out to be different in the two males studied (Fig. 10). The Y of *H. i.* 1 which is shown in the karyotype and in the idiogram is smaller than that of *H. i.* 3 due to a smaller short arm. The Y of *H. i.* 1 is the second largest chromosome and easily recognized due to its small short arm (c.i. = 10.4). The Y of *H. i.* 3 is of the same size as the largest autosome (st1) and not so easily recognized, but its centromeric index (18.3) is clearly different from that of st1 (24.3). Measurements were performed on chromosomes st1, st2, X_2 and the Y of 5 cells from *H. i.* 3 and the size of the long arm of the Y was calculated relative to the total length of st1. It was shown that the ratio obtained in *H. i.* 3 was similar to that in *H. i.* 1 (1.22 and 1.17, respectively). The centromeric index of st1 from *H. i.* 3 was in good agreement with that of *H. i.* 2 and *H. i.* 1 (24.1, 23.5 and 25.4, respectively).

Vague satellites were observed more or less regularly on the short arms of one m chromosome, most likely m4, and on the short arms of sm3, st2 and X_2 (Fig. 5).

Previous chromosome studies on this species do not exist. An old reference needs to be clarified, however. In MAKINO's chromosome number atlas (1951) the following information is listed: "*Mungos ichneumon* ('Mongoose'), n ca 24 ♂, prob. X-0 ♂, JORDAN 14" (l.c., p. 282). This has been cited even quite recently (e.g. WURSTER and BENIRSCHKE 1968). In the paper by JORDAN, the mongoose studied was not referred to by its scientific name. Since *Herpestes ichneumon* is neither a member of the native fauna of the West Indies, nor has ever been introduced there, it seems most likely that the species studied by JORDAN, the material of which emanated from Jamaica, was actually *Herpestes auropunctatus*. This species is common in Jamaica since 1872 when it was introduced and successfully estab-

Table 3. Chromosome measurements of *Herpestes ichneumon*
Mean of 5 female and 5 male cells

Chromosome	Absolute length in μ		Relative length, % of female haploid set				Centromeric index	
			p	q	p+q			
	Mean	S.e.	Mean	Mean	Mean	S.e.	Mean	S.e.
X_1	3.19	0.08	2.14	2.84	4.98	0.05	43.0	0.6
m1	3.19	0.08	2.29	2.65	4.94	0.05	46.4	0.4
m2	2.61	0.05	1.55	2.50	4.05	0.03	38.3	0.3
m3	2.49	0.05	1.61	2.24	3.85	0.04	41.0	0.4
m4	2.38	0.05	1.57	2.12	3.69	0.03	43.2	0.5
m5	2.24	0.04	1.33	2.17	3.50	0.05	37.9	0.5
m6	2.18	0.03	1.46	1.93	3.39	0.04	43.1	0.5
sm1	4.01	0.08	1.79	4.42	6.21	0.04	28.8	0.3
sm2	3.83	0.07	1.95	3.98	5.93	0.04	32.8	0.4
sm3	3.70	0.08	1.53	4.20	5.73	0.05	26.7	0.5
sm4	3.04	0.05	1.27	3.44	4.71	0.04	26.9	0.5
st1	4.88	0.10	1.84	5.71	7.55	0.06	24.4	0.4
st2	4.52	0.08	1.32	5.69	7.01	0.06	18.8	0.3
X_2	3.97	0.11	1.29	4.91	6.20	0.06	20.8	0.5
Y	4.80	0.21	0.75	6.48	7.23	0.12	10.4	0.4
t1	3.02	0.07	—	4.67	4.67	0.06	—	—
t2	2.68	0.06	—	4.15	4.15	0.03	—	—
t3	2.54	0.05	—	3.92	3.92	0.02	—	—
t4	2.30	0.05	—	3.56	3.56	0.04	—	—
t5	2.14	0.05	—	3.31	3.31	0.04	—	—
t6	2.02	0.04	—	3.12	3.12	0.03	—	—
t7	1.91	0.05	—	2.96	2.96	0.04	—	—
t8	1.65	0.04	—	2.55	2.55	0.03	—	—

lished there (HINTON and DUNN 1967); it has 2n = 35 male, 36 female (FREDGA 1965). JORDAN writes that "at metaphase ....., no chromosome seems marked by peculiar behaviour or uncommon size. An accurate count seems impossible ....., the number of chromosomes is somewhere around 24". Although this statement indicates that 2n = ca 24, it seems clear from the entire background of the paper that JORDAN means the number of bivalents at metaphase of the first meiotic division. The statement "prob. X-0" is interesting in the light of our present knowledge, viz. that some mongoose species have a "pseudo-XO/XX" mechanism for sex determination. However, in addition to the mongoose, JORDAN includes the cat, squirrel, pig and rabbit into the group of animals with heterochromosomes lacking in the male, as contrary to the white mouse, sheep, horse, mule, bull and dog. Considering that now the last-mentioned ten species are all known to possess a normal sex-chromosome mechanism with X and Y chromosomes of different size in the male, it is sensible not to strain the details of JORDAN's observations too much.

B. Slender mongoose, *Herpestes sanguineus* RÜPPELL (1836)

Two males were studied, 2n = 41 male, (42 female). The karyotypes is shown in Fig. 6 and the idiogram in Fig. 7. The results of the chromosome measurements are given in Tables 4 and 20.

The karyotype consists of 4 m, 6 sm, 3 st and 6 t autosome pairs. The X_1 chromosome is an m, the X_2 an st and the Y a t chromosome. The largest chromosome of the complement is st1 and the smallest t6.

Chromosome m1 is easily distinguishable.

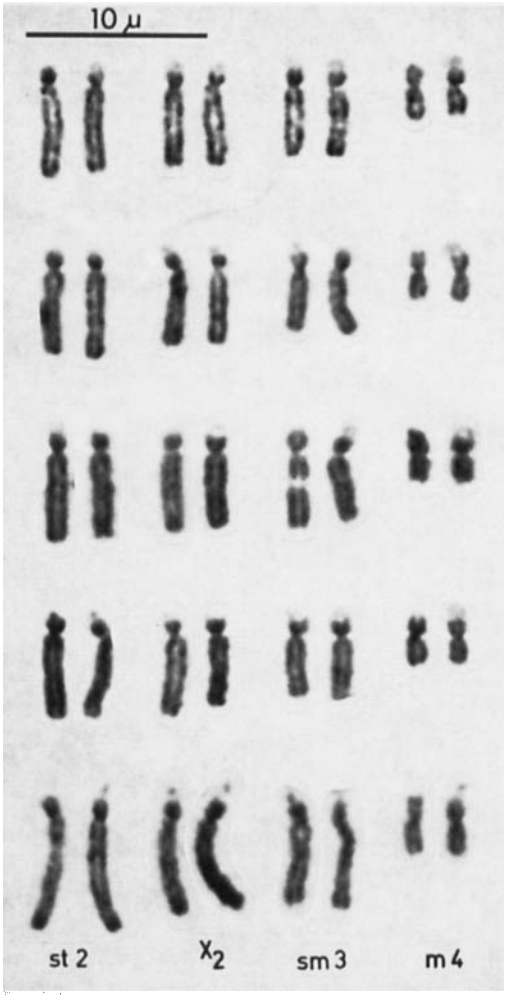


Fig. 5. *Herpestes ichneumon*, female; chromosomes st2, X_2, sm3 and m4 from five cells at early metaphase showing vague satellites on the short arms. The satellites of the two chromatids of each chromosome sometimes appear separate, and sometimes fused. — × 2,420.

Chromosome m2 is very similar to X_1, which is slightly larger and has a somewhat lower centromeric index. The m3–m4 pairs may be distinguished individually on the basis of length and centromeric index, m4 being shorter and with a more median position of the centromere. The sm chromosomes fall into two size groups, each with three pairs; the larger group consists of the sm1–sm3 pairs with centromeric indices of 25–31; sm2 is intermediate in size and has the highest centromeric index of the three pairs. The sm4–sm6 pairs are distinguishable individually on the basis of length and centromeric index; sm5 has the lowest centromeric index and sm6 is the smallest of these three pairs. The sm4 pair is most easily confused with m3. The st1, st2 and st3 pairs are readily distinguished individually, the greatest problem is to recognize st2 from X_2 which also is an st chromosome, but X_2 is smaller and has a higher centromeric index than st2. As to their length, the t autosomes form a rather continuous series making individual identification of at least the four smallest pairs dubious. No distinct short arms were observed on any of the t autosomes.

The X_1 chromosome constitutes 5.2 per cent of (A + X). The X_2 is smaller than the Y which is the second largest chromosome of the complement. Also in this species, the Y turned out to be different in the two males studied (Fig. 10). The centromeric indices of the Y's of *H. s.* 1 and *H. s.* 2 are similar (11.2 and 10.6, respectively) but the total relative lengths are different (7.20 and 7.70, respectively). This difference is statistically significant; $t = 3.75$, $df = 8$, $0.002 < P < 0.01$. The mean value of the Y chromosomes of the two males is used in the idiogram.

Previous chromosome studies on this species do not exist.

C. Cape grey mongoose, *Herpestes pulverulentus* WAGNER (1839)

One male and one female were studied, $2n = 39$ male, 40 female. The karyotype is shown in Fig. 8 and the idiogram in Fig. 9. The results of the chromosome measurements are given in Tables 5 and 21.

The karyotype consists of 4 m, 8 sm and 6 st autosome pairs; no t autosomes are present. The X_1 chromosome is an m, the X_2 an st and the Y a t chromosome. The largest chromosome of the complement is st1 and the smallest sm8.

Chromosome m1 is one of the largest chromosomes and immediately recognizable by its high centromeric index. The m2 pair is very similar to X_1 which is slightly larger and has a somewhat lower centromeric index. The smallest chromosomes of the m group, m3 and m4, are distinguishable individually on the basis of relative length. The sm4 pair divides the sm class into two groups, one with large (sm1–3) and one with

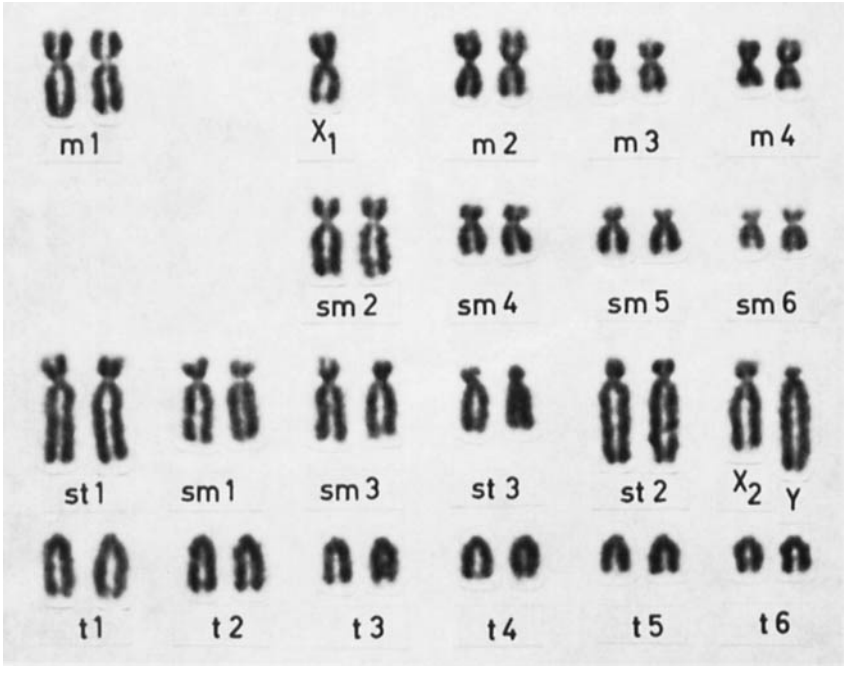


Fig. 6. Karyotype of *Herpestes sanguineus*, male, 2n = 41, (*H.s.* 1). (No female was available of this species).

small (sm5–8) chromosomes. The sm1 chromosome has a centromeric index of 37.4 and is thus very close to the borderline to the m class (37.5). The sm2 has a lower centromeric index than sm3. Of the sm5–8 chromosomes, sm5 and sm8 are readily distinguished within the group; sm5, however, is easily confused with m3; sm8 is distinguished from other sm chromosomes by its small size and from m4 by its lower centromeric index. The sm6 and sm7 chromosomes are difficult to distinguish individually and also from st6; sm7, however, is smaller than sm6, and st6 has the lowest centromeric index of the three pairs. Among the two longest st pairs, the st1 is identified easily, whereas the st2 resembles X_2, which also is a large st chromosome; st1 is larger, however, and has a lower centromeric index. The three medium-sized pairs, st3–5, are very similar, but may be distinguished by the length of the short arm, which is longest in st3 and shortest in st5.

The X_1 chromosome constitutes 4.9 per cent of (A + X). The X_2 is only slightly smaller than

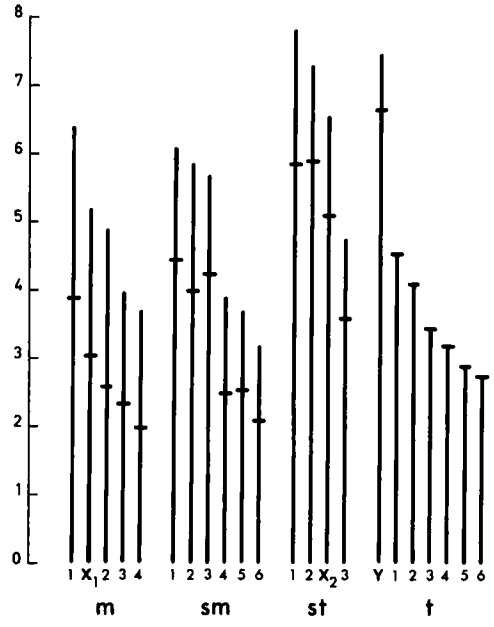


Fig. 7. Idiogram of *Herpestes sanguineus*.

Table 4. Chromosome measurements of *Herpestes sanguineus*
Mean of 10 cells, 5 from each of two males

Chromosome	Absolute length in μ		Relative length, % of female haploid set				Centromeric index	
			p	q	p+q			
	Mean	S.e.	Mean	Mean	Mean	S.e.	Mean	S.e.
m1	4.27	0.08	2.50	3.92	6.42	0.08	38.9	0.4
X_1	3.45	0.07	2.17	3.03	5.20	0.05	41.7	0.5
m2	3.26	0.05	2.33	2.58	4.91	0.04	47.4	0.2
m3	2.65	0.05	1.63	2.36	3.99	0.04	40.8	0.5
m4	2.47	0.04	1.70	2.01	3.71	0.05	45.8	0.6
sm1	4.04	00.6	1.64	4.44	6.08	0.04	26.9	0.3
sm2	3.87	0.05	1.83	4.00	5.83	0.03	31.4	0.3
sm3	3.78	0.06	1.43	4.26	5.69	0.05	25.1	0.3
sm4	2.60	0.05	1.43	2.48	3.91	00.4	36.7	0.5
sm5	2.45	0.05	1.15	2.53	3.68	0.05	31.2	0.6
sm6	2.14	0.04	1.13	2.08	3.21	0.04	35.1	0.6
st1	5.20	0.08	1.96	5.86	7.82	0.06	25.0	0.3
st2	4.85	0.05	1.40	5.91	7.31	0.05	19.2	0.3
X_2	4.34	0.11	1.45	5.08	6.53	0.10	22.2	0.5
st3	3.15	0.05	1.15	3.59	4.74	0.04	24.2	0.5
Y	4.95	0.13	0.81	6.64	7.45	0.10	10.9	0.5
t1	3.04	0.05	—	4.57	4.57	0.04	—	—
t2	2.73	0.05	—	4.11	4.11	0.04	—	—
t3	2.28	0.03	—	3.43	3.43	0.03	—	—
t4	2.11	0.03	—	3.18	3.18	0.03	—	—
t5	1.93	0.03	—	2.91	2.91	0.03	—	—
t6	1.83	0.03	—	2.76	2.76	0.03	—	—

the Y, which (in the only male studied) is the fourth largest chromosome of the complement, slightly shorter than m1 and st2. The Y is the only t chromosome and thus relatively easy to recognize also in this species (Fig. 10).

Previous chromosome studies on this species do not exist.

D. Small Indian mongoose, *Herpestes auropunctatus* (Hodgson) (1836)

Altogether 7 males and 4 females were studied, 2n = 35 male, 36 female. The karyotype is shown in Fig. 11 and the idiogram in Fig. 12. The results of the chromosome measurements are given in Tables 6 and 22.

The karyotype consists of 5 m, 7 sm and 4 st autosome pairs. The X_1 chromosome is an m, the X_2 and the Y are t chromosomes. The largest chromosome of the complement is st1 and the smallest sm7.

Chromosome m1 is the third largest chromosome and may be confused only with sm1, which, however, is larger and has a lower centromeric index. The m2 pair is easily distinguished by its size and its high centromeric index. Chromosome m3 is very similar to X_1, which is slightly larger and has a somewhat lower centromeric index. Of the five smallest pairs of the complement, m4, m5, sm5, sm6 and sm7, only m4 and sm5 may be confused. Their size is the same and their centromeric indices are similar, 40.7 and 36.8. The m5 is the second smallest chromosome of the complement and has a high centromeric index in comparison with sm6 and sm7, which are distinguished among themselves on the basis of total length. The chromosomes sm2–sm4 and st3 form a group of similar chromosomes of

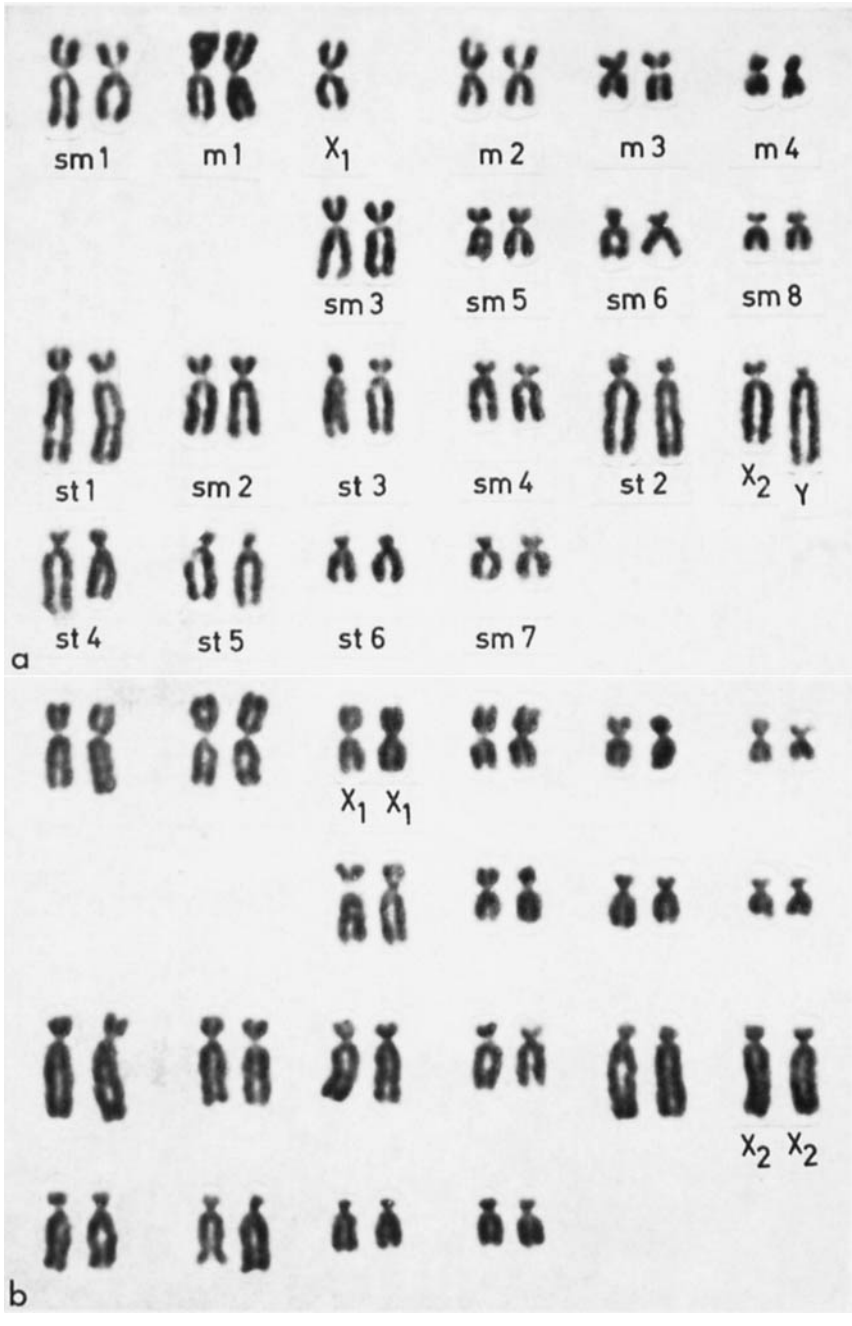


Fig. 8. Karyotypes of *Herpestes pulverulentus*, a: male, 2n = 39; b: female, 2n = 40.

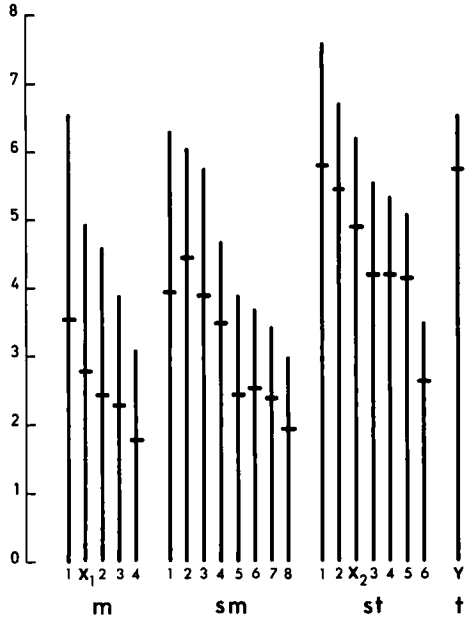


Fig. 9. Idiogram of *Herpestes pulverulentus*.

Table 5. Chromosome measurements of *Herpestes pulverulentus*
Mean of 5 female and 5 male cells

Chromosome	Absolute length in μ		Relative length, % of female haploid set				Centromeric index	
			p	q	p+q			
	Mean	S.e.	Mean	Mean	Mean	S.e.	Mean	S.e.
m1	4.15	0.07	3.02	3.55	6.57	0.04	46.0	0.3
X_1	3.14	0.05	2.12	2.82	4.94	0.04	42.9	0.5
m2	2.91	0.04	2.16	2.45	4.61	0.04	46.8	0.4
m3	2.46	0.03	1.60	2.30	3.90	0.03	41.0	0.4
m4	1.96	0.02	1.30	1.81	3.11	0.04	41.8	0.5
sm1	3.97	0.07	2.35	3.94	6.29	0.05	37.4	0.3
sm2	3.83	0.07	1.62	4.44	6.06	0.04	26.8	0.4
sm3	3.63	0.05	1.85	3.89	5.74	0.04	32.3	0.3
sm4	2.97	0.05	1.21	3.48	4.69	0.04	25.9	0.4
sm5	2.46	0.03	1.45	2.45	3.90	0.04	37.2	0.4
sm6	2.35	0.04	1.15	2.56	3.71	0.03	31.0	0.5
sm7	2.18	0.03	1.05	2.40	3.45	0.03	30.5	0.6
sm8	1.90	0.02	1.05	1.97	3.02	0.04	34.8	0.6
st1	4.80	0.09	1.82	5.78	7.60	0.08	24.0	0.3
st2	4.23	0.06	1.22	5.47	6.69	0.05	18.3	0.5
X_2	3.94	0.07	1.29	4.91	6.20	0.05	20.8	0.4
st3	3.51	0.08	1.35	4.19	5.54	0.06	24.3	0.4
st4	3.38	0.06	1.15	4.21	5.36	0.06	21.4	0.5
st5	3.23	0.05	0.98	4.13	5.11	0.05	19.1	0.5
st6	2.21	0.04	0.84	2.66	3.50	0.04	24.0	0.5
Y	4.06	0.21	0.80	5.74	6.54	0.14	12.3	0.6

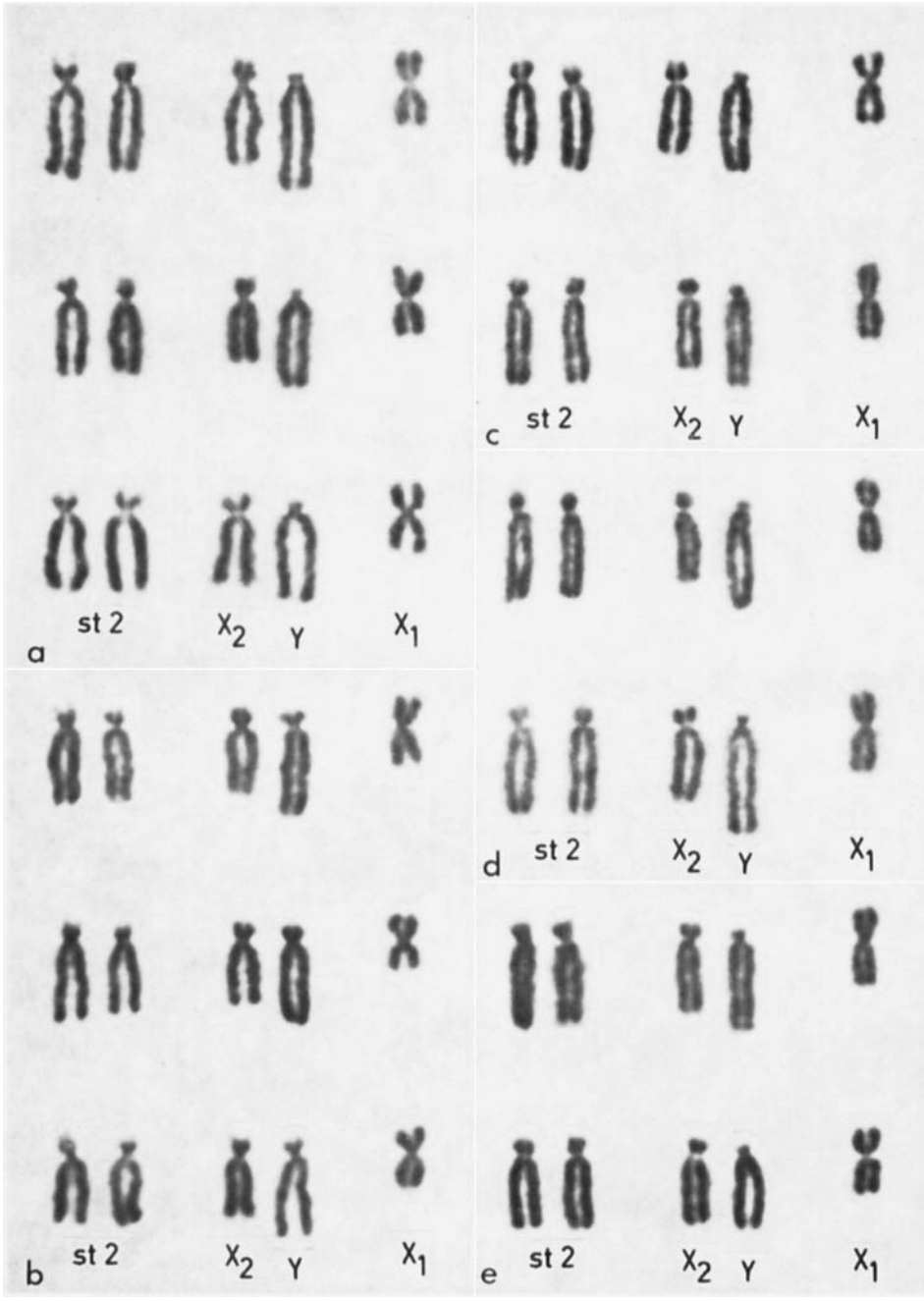


Fig. 10. Chromosomes st2, X_2, Y and X_1 from three species of the "*ichneumon*-group"; a and b: *Herpestes ichneumon* (*H.i.* 1 and *H.i.* 3); c and d: *Herpestes sanguineus* (*H.s.* 1 and *H.s.* 2); e: *Herpestes pulverulentus* (*H.p.* 1). Note intraspecific differences of the Y chromosome: the short arm of the Y chromosome is larger in *H.i.* 3 (b) than in *H.i.* 1 (a), and the total relative length of the Y chromosome is larger in *H.s.* 2 (d) than in *H.s.* 1 (c).

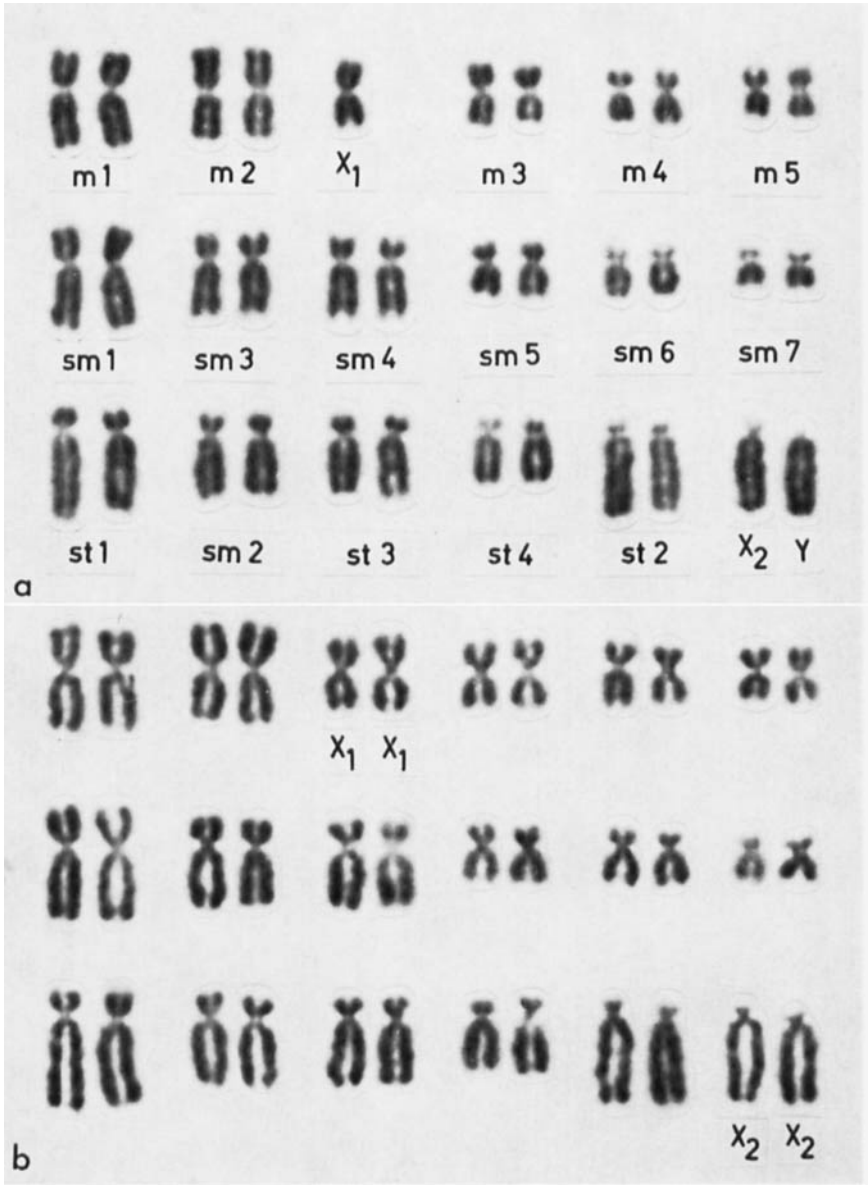


Fig. 11. Karyotypes of *Herpestes auropunctatus*, a: male, 2n = 35; b: female, 2n = 36. Note the diminutive short arm of the Y chromosome.

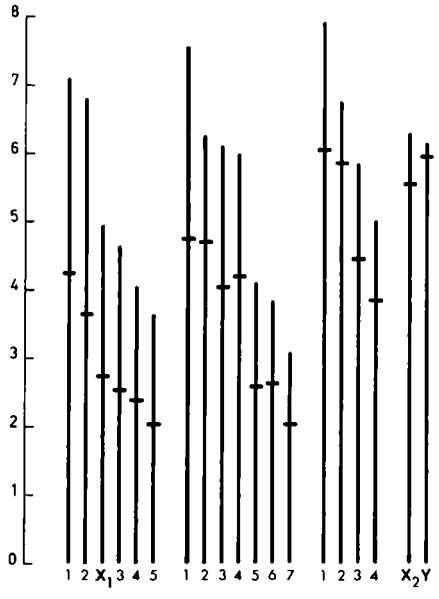


Fig. 12. Idiogram of *Herpestes auropunctatus*.

Table 6. Chromosome measurements of *Herpestes auropunctatus*
Mean of 5 female and 5 male cells

Chromosome	Absolute length, in μ		Relative length, % of female haploid set				Centromeric index	
	Mean	S.e.	p	q	p+q			
			Mean	Mean	Mean	S.e.	Mean	S.e.
m1	4.51	0.15	2.86	4.26	7.12	0.06	40.1	0.4
m2	4.30	0.14	3.16	3.64	6.80	0.06	46.5	0.3
X_1	3.24	0.09	2.22	2.74	4.96	0.04	44.8	0.4
m3	2.92	0.08	2.10	2.53	4.63	0.04	45.4	0.4
m4	2.57	0.09	1.65	2.41	4.06	0.05	40.7	0.5
m5	2.32	0.08	1.61	2.05	3.66	0.06	43.9	0.6
sm1	4.77	0.14	2.77	4.77	7.54	0.06	36.8	0.3
sm2	3.96	0.11	1.57	4.70	6.27	0.06	25.1	0.4
sm3	3.84	0.11	2.01	4.07	6.08	0.04	33.1	0.3
sm4	3.78	0.11	1.80	4.18	5.98	0.03	30.1	0.4
sm5	2.58	0.06	1.51	2.58	4.09	0.04	36.8	0.4
sm6	2.43	0.06	1.22	2.63	3.85	0.04	31.8	0.5
sm7	1.97	0.05	1.07	2.05	3.12	0.03	34.2	0.6
st1	5.01	0.15	1.85	6.07	7.92	0.06	23.3	0.4
st2	4.26	0.12	0.89	5.84	6.73	0.05	13.2	0.4
st3	3.71	0.11	1.39	4.47	5.86	0.05	23.7	0.4
st4	3.16	0.11	1.16	3.83	4.99	0.05	23.3	0.5
X_2	4.10	0.12	0.73	5.55	6.28	0.05	11.7	0.5
Y	3.48	0.14	0.18	5.97	6.15	0.06	2.9	0.05

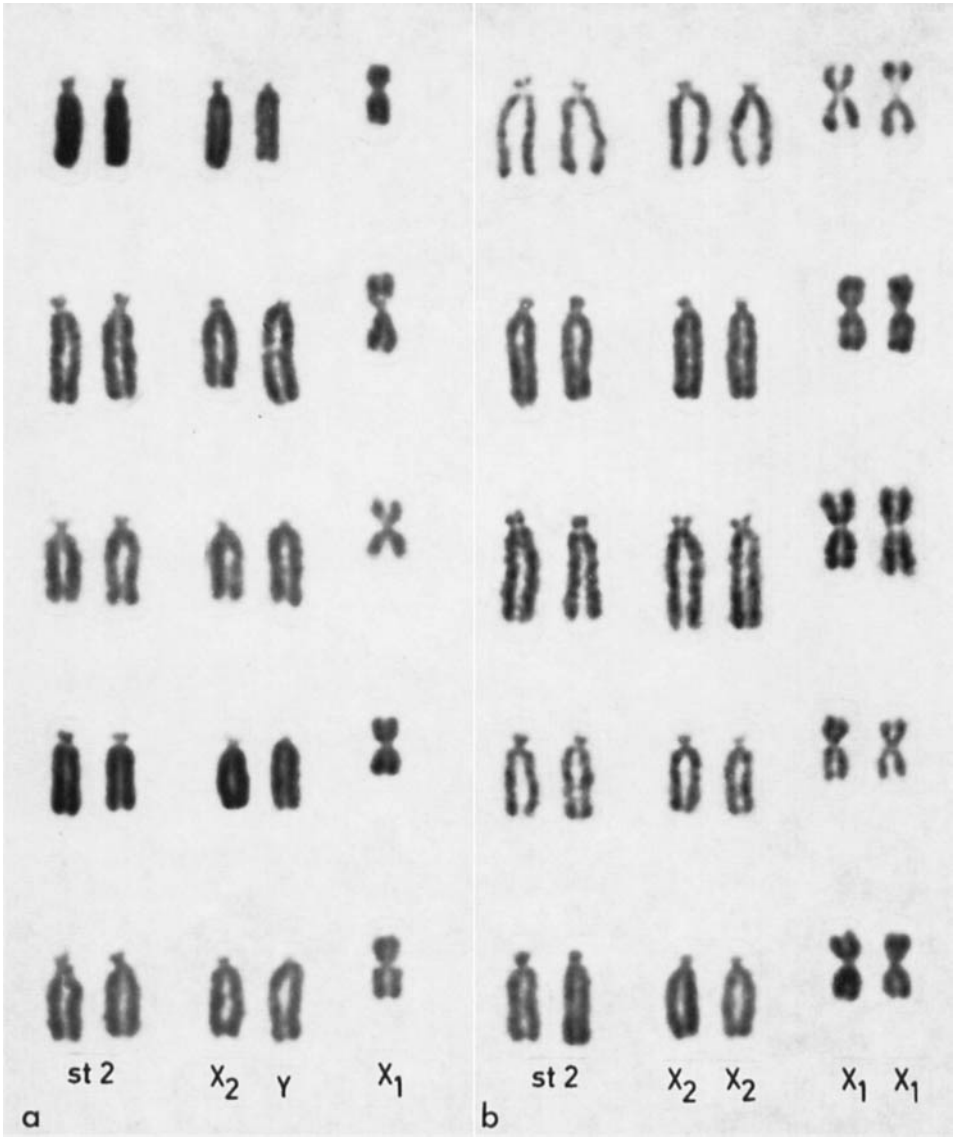


Fig. 13. *Herpestes auropunctatus*, a: males; b: females. Representative chromosomes st2, X_2, Y and X_1 from different specimens, tissues and passages. From above a: *H.a.* 4 lung P0, *H.a.* 4 heart P0, *H.a.* 8 skin P1, *H.a.* 9 skin P1, *H.a.* 10 skin P1; b: *H.a.* 5 skin P0, *H.a.* 5 skin P2, *H.a.* 5 lung P1, *H.a.* 7 skin P8, *H.a.* 11 skin P1. Note the small differences between the st2, X_2 and Y chromosomes.

Table 7. Herpestes auropunctatus. Comparison of two sets of measurements (AL drawings; KF photographs), the AL values from FREDGA 1967, the KF values from the present study

Chromosome		Chromosome designation		Relative length			Centromeric index		
		AL	KF	AL	KF	$\frac{KF}{AL} \cdot 100$*	AL	KF	$\frac{KF}{AL} \cdot 100$*
A	1	m1	m1	7.3	7.1	97	39	40	103
	2	m2	m2	7.1	6.8	96	48	46	96
	3	X	X_1	5.1	5.0	98	46	45	98
	4	m3	m3	4.7	4.6	98	47	45	97
	5	m4	m4	3.9	4.1	103	39	41	105
	6	m5	m5	3.4	3.7	107	49	44	90
B	1	sm1	sm1	7.7	7.5	98	36	37	103
	2	sm2	sm3	6.2	6.1	98	30	33	110
	3	sm3	sm4	5.9	6.0	101	29	30	105
	4	sm4	sm5	3.9	4.1	105	36	37	102
	5	sm5	sm6	3.4	3.8	112	26	32	121
	6	st5	sm7	2.6	3.1	121	25	34	137
C	1	st1	st1	8.2	7.9	97	21	23	112
	2	st2	sm2	6.3	6.3	100	22	25	115
	3	st3	st3	5.9	5.9	99	21	24	113
	4	st4	st4	4.8	5.0	103	20	23	118
D	1	t(1)+t(2)	st2	7.0	6.7	96	10	13	138
	2	t(3)	X_2	6.5	6.3	97	8	12	143
	3	t(4)	Y	6.8	6.2	91	2	3	121

* Calculated from unabbreviated data

intermediate size. The sm2 has a centromeric index of 25.1 and is consequently close to the st class and this pair is also most easily confused with st3 which has a centromeric index of 23.7; sm2 is slightly larger than st3. The pairs st3, sm3 and sm4 are similar in size, but the latter two sm chromosomes have higher centromeric indices, 33.1 and 30.1, respectively. It is practically impossible to distinguish these two pairs with certainty and the centromeric index is the prime criterion in matching the four chromosome into pairs. The st1 pair is immediately recognized by its large size and its centromeric index and also st4 is a "marker" chromosome. The st2 is easily confused with X_2, but st2 is the larger one and its short arm is more prominent.

The X_1 chromosome constitutes 5.0 per cent of (A + X). The X_2 and the Y are very similar in size and general appearance, but the Y is distinguished in good preparations by its diminutive short arm. In all the males studied with the cell-culture technique, one of the t chromosomes can be recognized as the Y by this criterion, whereas in the females both t chromosomes have small 'heads' of similar size (Fig. 13). As pointed out by FREDGA (1967a), it is doubtful whether the Y of this species really has a second arm. The chromatic material occasionally seen at the proximal end may represent centromeric components.

Previous chromosome studies: *Herpestes auropunctatus* is the 'classical' mongoose from the chromosomal point of view, since the deviating sex-chromosome mechanism was first discovered in this species (FREDGA 1965). An idiogram was constructed by FREDGA (1967a) on the basis of measurements by Dr. A. Levan on camera-lucida drawings of 10 male cells. New measurements on photographs were undertaken in five male and five female cells. The two sets of measurements designated A L and K F are compared in Table 7 in which the values from 1967 are adapted to the general arrangement of the present

paper. The arm ratios (r) in Table 2 in FREDGA (1967a) are converted into centromeric indices (c.i.) by the following formula: $c.i. = \frac{100}{r+1}$. The four chromosomes with the highest arm ratios were treated separately in 1967, but now we know that t(1) and t(2) make one pair, t(3) corresponds to the X_2 and t(4) to the Y. At the calculation of (A + X) for the relative length in 1967, $\frac{t(1)+t(2)+t(3)+t(4)}{2}$ was used, but since t(3) and t(4) are similar in size very small differences are obtained if $\frac{t(1)+t(2)}{2} + t(3)$ is used instead. However, in Table 7 the recalculated values are used. Since certain chromosomes have centromeric indices close to the borderline between two classes, it is not surprising that some chromosomes fall into different classes in the two sets of measurements. The chromosomes involved are chromosome C2, which in 1967 was an st chromosome (c.i. = 21.8) but now became an sm (c.i. = 25.1), chromosome B6 which in 1967 was placed in the st group (c.i. = = 25.0) but now became a clear sm chromosome (c.i. = 34.2) and chromosome D1 which in 1967 was a t chromosome (c.i. = 9.6) but now became an st (c.i. = 13.2).

The agreement between the two sets of measurements is good but there is a general tendency to obtain higher centromeric indices for the sm, st and t chromosomes when measurements were undertaken on photographs. In addition, the relative lengths of the chromosomes vary in a specific way: The KF values are consistently lower than the AL values for long chromosomes, but higher for short ones. The $\frac{KF}{AL} \cdot 100$ ratios were calculated for relative length and centromeric index, and Table 7 shows that these ratios increase both with decreasing chromosome length and decreasing centromeric index. It is striking that the same tendencies were obtained by ÁRNASON (1969), in centromeric index (arm ratio) and relative length, in a similar comparison of measurements from drawn and photographed chromosomes. He discusses the factors underlying the discrepancies, and his conclusions are valid also in the present observations. It seems that more of the halo, always present at the outer boundaries of the chromosome ends, was included in the measurements on photos than in those on drawings.

The chromosome numbers of 2n = 35 in the male and 36 in the female *Herpestes auropunctatus* have been confirmed by several Indian authors (BHATNAGAR pers. comm. 1969; RAY-CHAUDHURI et al. 1966; RAY-CHAUDHURI et al. 1968). MANNA and TALUKDAR (1965) reported 36 chromosomes in a female specimen and TALUKDAR and MANNA (1966) 36 chromosomes, including a small Y chromosome, in a male. As pointed out by FREDGA (1967b) this observation is puzzling, particularly in the light of our present knowledge that all males of the genus *Herpestes* studied so far (8 species) have one chromosome less than the females, because the functional Y is translocated on to an autosome. The karyotype presented by TALUKDAR and MANNA differs in several other respects from the karyotype of *H. auropunctatus* as well as from the karyotypes of all other mongoose species (17) studied. The present author has studied 7 males of *H. auropunctatus* from at least two different geografic localities, and found identical karyotypes in all of them. In one of the males six different tissues were studied (FREDGA 1967a). RAY-CHAUDHURI et al. (1968) have investigated 10 males and BHATNAGAR (1969) at least one male without finding any evidence for the presence of 36 chromosomes and a small individual Y chromosome. TODD and PRESSMAN (1966) studied one male and one female of this species (under the name of *Herpestes javanicus* GEOFFROY) and confirmed the chromosome number of 2n = 35 in the male and 2n = 36 in the female (see p. 58 for commments on the taxonomic identity of the specimens studied by these authors).

COHEN and CHANDRA (1970) have made an autoradiographic study of the chromosomes of "*Herpestes auropunctatus*". As will be discussed further in connection with *H. edwardsi*, it is extremely likely that their material actually belonged to *edwardsi* and not to *auropunctatus*.

E. Indian mongoose, *Herpestes edwardsi* (GEOFFROY) (1812)

Three males and one female were studied, 2n = 35 male, 36 female. The karyotype is shown in Fig. 14 and 15 and the idiogram in Fig. 16. The results of the chromosome measurements are given in Tables 8 and 23.

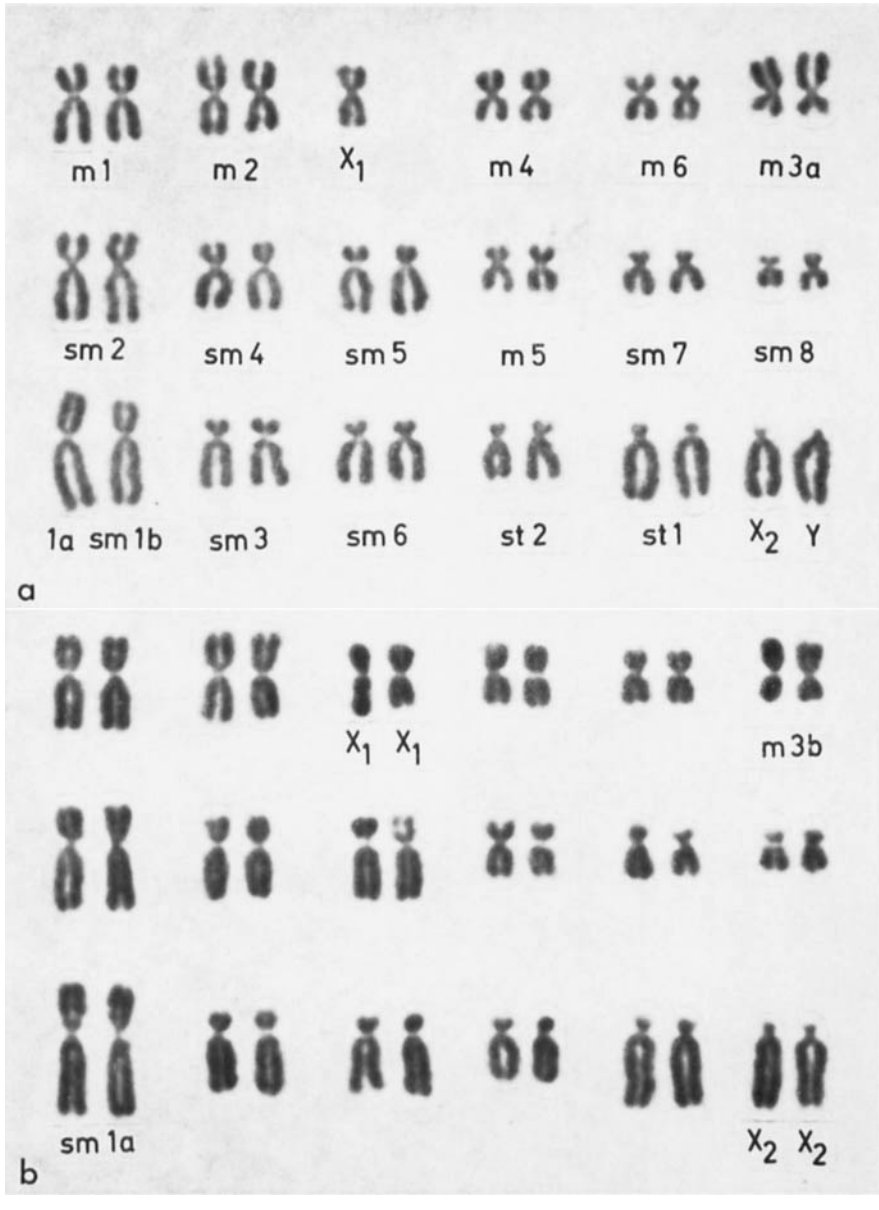


Fig. 14. Karyotypes of *Herpestes edwardsi*, a: male, 2n = 35 (*H.e.* 4); b: female, 2n = 36 (*H.e.* 2). Note heteromorphism in the short arm of pair sm1 in Fig. a but not in Fig. b. The difference between m3a and m3b is not distinct; in comparison with the long arm of m4, however, the long arm of m3a is longer, that of m3b equal in length (the long arm of m3 is directed upwards in the karyotypes). Note minute short arm of the Y chromosome.

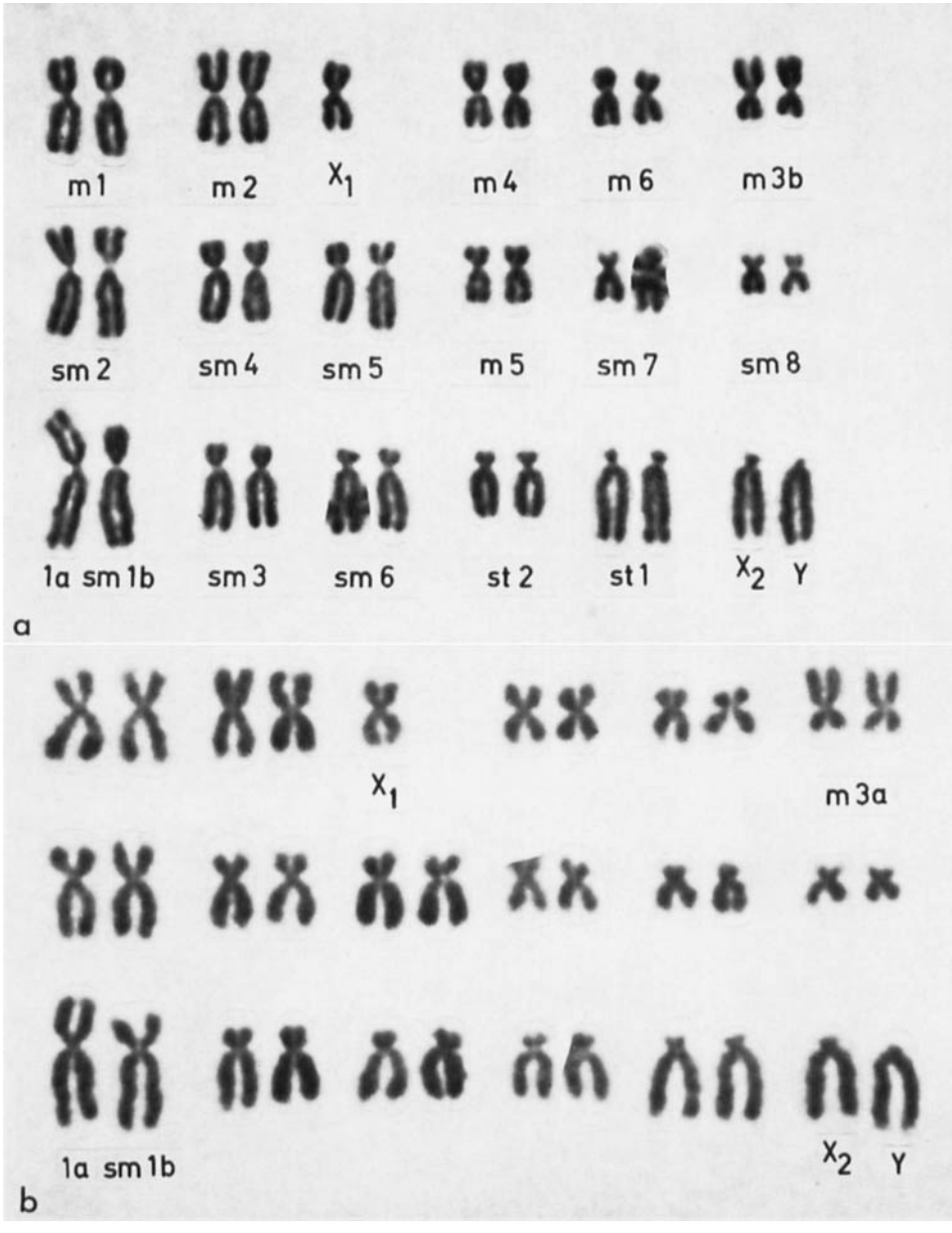


Fig. 15. Karyotypes of *Herpestes edwardsi*, a: male (*H.e.* 3); b: male (*H.e.* 1). These males were homozygous for m3b and m3a, respectively, and heterozygous for sm1.

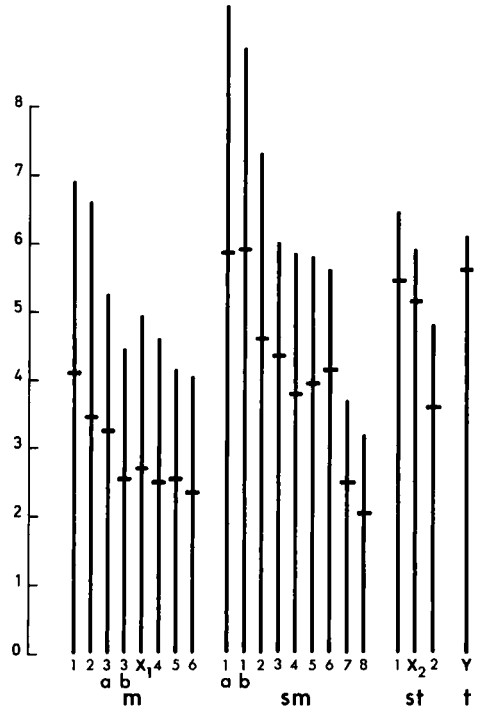


Fig. 16. Idiogram of *Herpestes edwardsi*. The two different morphologic types of m3 and sm1 chromosomes are designated a and b.

Table 8. Chromosome measurements of *Herpestes edwardsi*
Mean of 5 female and 10 male cells

Chromosome	Absolute length in μ		Relative length, % of female haploid set				Centromeric index	
			p	q	p+q			
	Mean	S.e.	Mean	Mean	Mean	S.e.	Mean	S.e.
m1	4.07	0.08	2.79	4.09	6.88	0.06	40.5	0.3
m2	3.88	0.07	3.12	3.46	6.58	0.04	47.4	0.3
m3a	3.01	0.05	2.00	3.23	5.23	0.06	38.2	0.5
m3b	2.76	0.06	1.89	2.58	4.47	0.08	42.3	0.8
X_1	2.95	0.06	2.22	2.72	4.94	0.04	44.9	0.4
m4	2.71	0.04	2.11	2.49	4.60	0.03	45.9	0.6
m5	2.45	0.04	1.62	2.53	4.15	0.02	39.1	0.4
m6	2.38	0.03	1.69	2.35	4.04	0.04	41.8	0.3
sm1a	5.65	0.11	3.59	5.87	9.46	0.08	37.9	0.3
sm1b	5.09	0.15	2.95	5.90	8.85	0.14	33.3	0.6
sm2	4.31	0.09	2.70	4.60	7.30	0.06	37.0	0.3
sm3	3.55	0.07	1.65	4.36	6.01	0.04	27.4	0.3
sm4	3.44	0.06	2.01	3.82	5.83	0.04	34.4	0.3
sm5	3.42	0.06	1.82	3.97	5.79	0.05	31.4	0.2
sm6	3.29	0.05	1.44	4.14	5.58	0.03	25.8	0.3
sm7	2.17	0.04	1.18	2.51	3.69	0.03	32.1	0.4
sm8	1.90	0.03	1.18	2.04	3.22	0.03	36.5	0.5
st1	3.80	0.07	0.98	5.45	6.43	0.04	15.3	0.3
X_2	3.53	0.08	0.77	5.13	5.90	0.06	13.1	0.4
st2	2.83	0.04	1.20	3.60	4.80	0.04	24.9	0.3
Y	3.51	0.13	0.51	5.58	6.09	0.10	8.3	0.7

The karyotype of this species is particularly interesting because two pairs of chromosomes show dimorphism and both morphological types are larger than the corresponding pairs in other species. One of these pairs (sm1) is the largest chromosome of the complement and its comparatively high centromeric index makes the karyotype of *H. edwardsi* characteristic and immediately distinguishable from other mongoose species. The karyotype consists of 6 m, 8 sm and 2 st autosome pairs. The X_1 chromosome is an m, the X_2 an st and the Y a t chromosome. The smallest chromosome of the complement is sm8.

Chromosome m1 is the third largest chromosome and may be confused only with sm2, which, however, is larger and has a lower centromeric index. The m2 pair is easily distinguished by its size and its high centromeric index. The chromosomes m3 and m4 are similar to X_1, and because m3 appears in two different morphological types (a and b) it is very difficult to identify these chromosomes and to combine them into correct pairs. The following general description is based on experiences from autoradiographic studies, which will be presented in detail elsewhere (FREDGA, in prep.). The long arm of m3 is strikingly late replicating, and this is the segment which shows varying length. The short arm of m3, which for reasons which will be discussed later, is directed downwards in the karyotypes, shows no dimorphism. The larger of the two m3 types, m3a, is longer than X_1 and m4 and has a lower centromeric index (38.2); the smaller one, m3b, is shorter than X_1 and m4 and has an only slightly lower centromeric index (42.3; the indices of X_1 and m4 being 44.9 and 45.9, respectively). None of the animals studied were heterozygous for chromosome m3, two were homozygous for m3a and two for m3b. The m6 pair is similar to m5 but somewhat smaller and has a higher centromeric index. As mentioned before, the second pair to show dimorphism is sm1, and in this pair it is the short arm that is strikingly late replicating and varies in length. This pair is easily recognized by its large size in both types, sm1a with longer short arm than sm1b. The latter chromosome, however, has a longer short arm than the corresponding chromosome (C1) in other species. The female specimen studied was homozygous for sm1a, the three males were heterozygous. The four animals studied had the following combinations of chromosomes in the two dimorphous pairs:

H. e. 1: sm1a, sm1b, m3a, m3a (Fig. 15 b)
H. e. 2: sm1a, sm1a, m3b, m3b (Fig. 14 b)
H. e. 3: sm1a, sm1b, m3b, m3b (Fig. 15 a)
H. e. 4: sm1a, sm1b, m3a, m3a (Fig. 14 a)

The chromosomes sm3–6 form a group of similar chromosomes of intermediate size. The largest and the smallest pairs of this group, sm3 and sm6, have lower centromeric indices (27.4 and 25.8) than sm4 and sm5 (34.4 and 31.4). The two smallest pairs of the complement, sm7 and sm8, differ from the small m chromosomes by lower centromeric indices and are distinguished individually by difference in size. Chromosome st2 is easily recognized on the basis of relative length and centromeric index. The st1 pair may be confused with X_2 but is larger and has a longer short arm. The Y chromosome is slightly longer than X_2 and is also in this species characterized by its minute short arm.

The X_1 constitutes 4.9 per cent of (A + X).

Previous chromosome studies. RAY-CHAUDHURI et al. (1968) studied two males and two females of *H. edwardsi* and found 35/36 chromosomes and sex chromosomes of the XA^{y}/XX type, but gave no further comments on the karyotype. As mentioned above, COHEN and CHANDRA (1970) studied the chromosomes of one male and one female mongoose under the name of *H. auropunctatus*. Their published karyotypes agree well with the karyotypes of *H. edwardsi* presented here. The characteristic sm1 chromosome is immediately distinguished, and also their autoradiographic findings indicate that the species studied by them was *H. edwardsi* and not *H. auropunctatus*.

F. Indian brown mongoose, *Herpestes fuscus* WATERHOUSE (1838)

One male and one female were studied, 2n = 35 male, 36 female. The karyotype is shown in Fig. 17 and the idiogram in Fig. 18. The results of the chromosome measurements are given in Tables 9 and 24.

The karyotype consists of 5 m, 8 sm and 3 st autosome pairs. The X_1 chromosome is an m, the X_2 and the Y are t chromosomes. The largest chromosome of the complement is sm1 and the smallest sm8.

The karyotype of *H. fuscus* cannot be distinguished from that of *H. auropunctatus*. The only

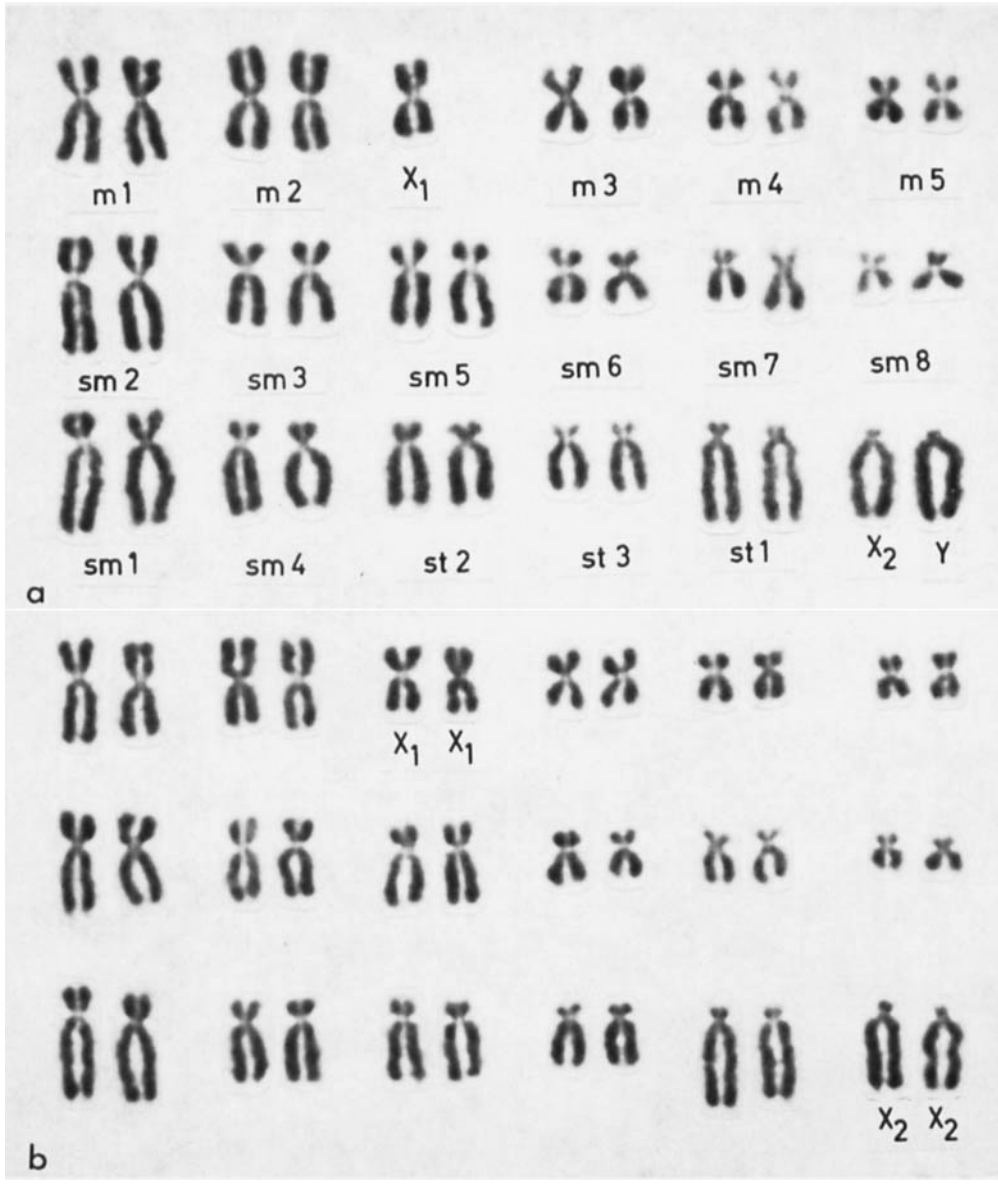


Fig. 17. Karyotypes of *Herpestes fuscus*, a: male 2n = 35; b: female 2n = 36. Note minute short arm of the Y chromosome.

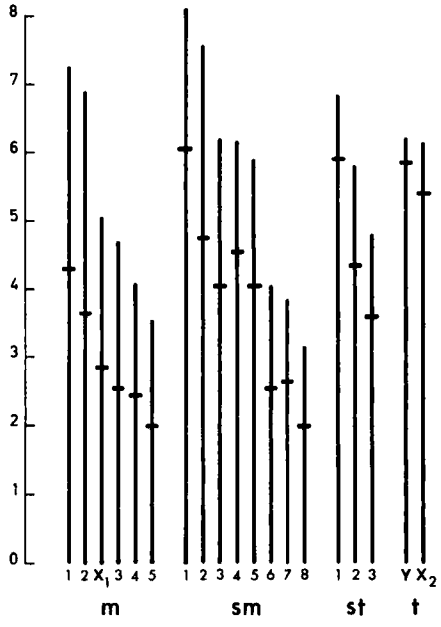


Fig. 18. Idiogram of *Herpestes fuscus*.

Table 9. Chromosome measurements of *Herpestes fuscus*
Mean of 5 female and 5 male cells

Chromosome	Absolute length in μ		Relative length, % of female haploid set				Centromeric index	
			p	q	p+q			
	Mean	S.e.	Mean	Mean	Mean	S.e.	Mean	S.e.
m1	4.56	0.09	2.95	4.32	7.27	0.05	40.6	0.4
m2	4.31	0.09	3.21	3.67	6.88	0.07	46.6	0.4
X_1	3.15	0.07	2.22	2.84	5.06	0.04	43.8	0.4
m3	2.95	0.07	2.15	2.55	4.70	0.04	45.7	0.3
m4	2.56	0.06	1.64	2.44	4.08	0.06	40.3	0.3
m5	2.22	0.04	1.55	1.99	3.54	0.05	43.8	0.5
sm1	5.06	0.10	2.04	6.05	8.09	0.06	25.2	0.4
sm2	4.75	0.11	2.82	4.75	7.57	0.07	37.3	0.3
sm3	3.88	0.07	2.14	4.05	6.19	0.05	34.5	0.3
sm4	3.87	0.08	1.63	4.54	6.17	0.05	26.4	0.3
sm5	3.70	0.06	1.83	4.07	5.90	0.04	31.0	0.4
sm6	2.54	0.04	1.48	2.57	4.05	0.05	36.5	0.4
sm7	2.41	0.05	1.24	2.61	3.85	0.04	32.1	0.5
sm8	1.97	0.04	1.15	1.99	3.14	0.04	36.5	0.4
st1	4.29	0.08	0.94	5.91	6.85	0.05	13.7	0.3
st2	3.64	0.08	1.43	4.37	5.80	0.06	24.7	0.4
st3	2.99	0.05	1.19	3.59	4.78	0.04	24.8	0.4
Y	3.94	0.15	0.37	5.83	6.20	0.15	6.0	0.9
X_2	3.83	0.10	0.75	5.38	6.13	0.06	12.2	0.4

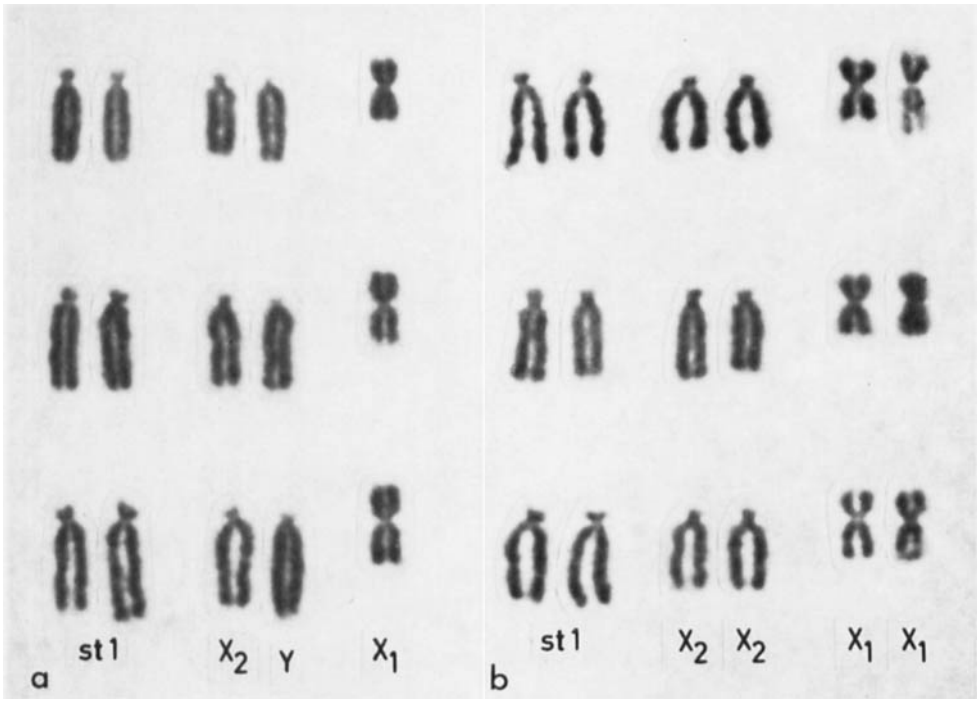


Fig. 19. *Herpestes fuscus*, a: male; b: female. Chromosomes st1, X_2, Y and X_1 from six cells. Note the difference between X_2 and Y, characteristic for species of the "*edwardsi*-group".

distinction between the idiograms of the two species (Fig. 12 and 18) was that in *H. fuscus* the centromeric index of the largest chromosome (C1) was determined to 25.2 thus making C1 an sm chromosome, whereas in *H. auropunctatus*, as in the majority of other species, the centromeric index of the C1 was below the borderline of the sm chromosomes. Neither this difference, nor the fact that the short arm of the Y chromosome may be slightly longer in *H. fuscus* than in *auropunctatus*, is of any practical help for distinguishing these two karyotypes.

The X_1 chromosome constitutes 5.1 per cent of (A + X). The X_2 and they Y are very similar in size and general appearance but the Y may be distinguished by its short arm, still smaller than in X_2 (Fig. 19).

Previous chromosome studies on this species do not exist.

G. Crab-eating mongoose, *Herpestes urva* (HODGSON) (1836)

Two females were studied, 2n = 36 female. The karyotype is shown in Fig. 20 and the idiogram in Fig. 21. The results of the chromosome measurements are given in Table 10.

The karyotype consists of 5 m, 6 sm, 5 st and 1 t autosome pairs. The X_1 chromosome is an m; since so far no male has been available, the X_2 and the Y are unknown, but it seems likely that this species, like all others of the genus *Herpestes*, has $X_1X_1X_2X_2/X_1X_2Y$ sex chromosomes and that the t1 pair is the X_2. The largest chromosome of the complement is st1 and the smallest sm6.

The general appearance of the karyotype of *H. urva* is similar to that of *H. auropunctatus*, and the differences in chromosome designation are caused by the fact that the sm2 chromosomes

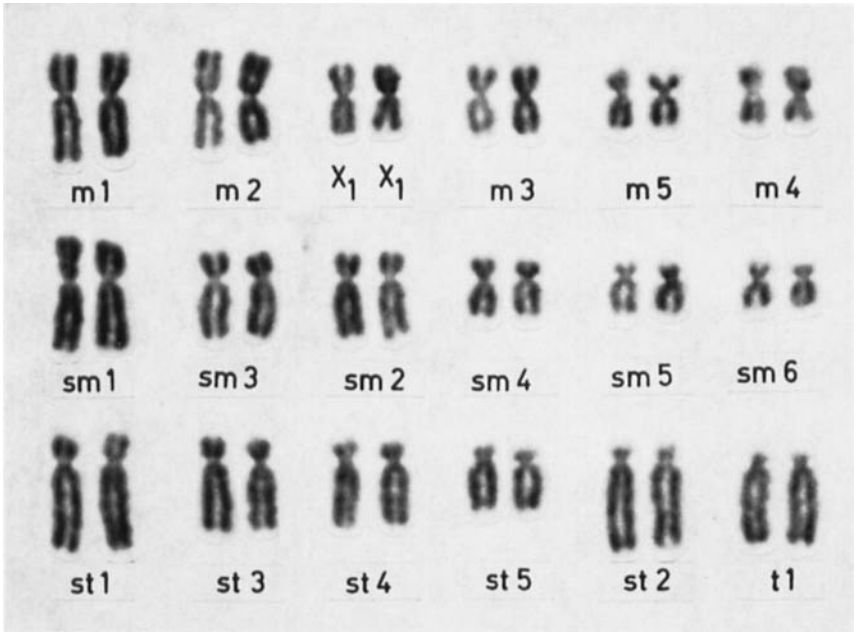


Fig. 20. Karyotype of *Herpestes urva*, female, 2n = 36. (No male was available of this species).

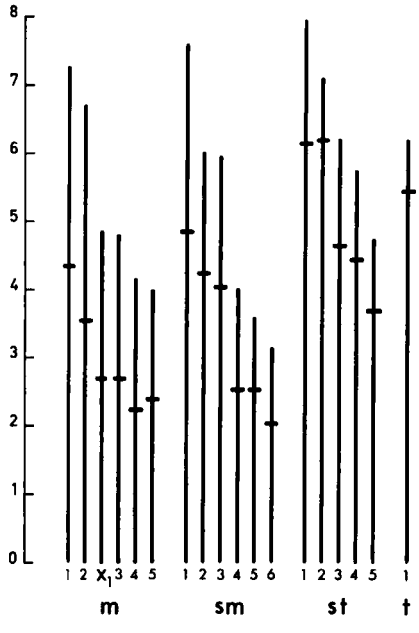


Fig. 21. Idiogram of *Herpestes urva*.

of *auropunctatus* (c.i. = 25.1) fall into the st class in *H. urva* (st3, c.i. = 24.8). The comparison of the idiograms of *urva* and *auropunctatus* shows that the difference between X_1 and m3 is still smaller in *urva*, that m5 of *urva* corresponds to m4 of *auropunctatus*, and that m4 of *urva* is larger than m5 of *auropunctatus*.

The X_1 chromosome constitutes 4.9 per cent of (A + X).

Previous chromosome studies on this species do not exist.

H. Malay short-tailed mongoose, *Herpestes brachyurus* GRAY (1936)

One male and one female were studied, 2n = 35 male, 36 female. The karyotype is shown in Fig. 22 and the idiogram in Fig. 23. The results of the chromosome measurements are given in Tables 11 and 25.

The karyotype consists of 6 m, 7 sm and 4 st autosome pairs. The X_1 is an m chromosome; the X_2 and Y chromosomes could not be identi-

Table 10. Chromosome measurements of *Herpestes urva*
Mean of 5 female cells

Chromosome	Absolute length in μ		Relative length, % of female haploid set				Centromeric index	
			p	q	p+q			
	Mean	S.e.	Mean	Mean	Mean	S.e.	Mean	S.e.
m1	4.90	0.10	2.87	4.38	7.25	0.09	39.6	0.5
m2	4.52	0.10	3.12	3.56	6.68	0.10	46.7	0.4
X_1	3.29	0.06	2.16	2.71	4.87	0.08	44.4	0.8
m3	3.23	0.04	2.06	2.72	4.78	0.05	43.0	0.3
m4	2.80	0.04	1.90	2.24	4.14	0.05	45.8	0.9
m5	2.71	0.04	1.60	2.41	4.01	0.04	39.9	0.5
sm1	5.15	0.08	2.75	4.87	7.62	0.09	36.1	0.5
sm2	4.07	0.08	1.76	4.26	6.02	0.07	29.3	0.4
sm3	4.01	0.05	1.89	4.05	5.94	0.05	31.9	0.3
sm4	2.71	0.04	1.45	2.56	4.01	0.05	36.2	0.5
sm5	2.42	0.04	1.04	2.54	3.58	0.04	29.0	0.9
sm6	2.13	0.04	1.12	2.03	3.15	0.05	35.7	0.7
st1	5.36	0.11	1.78	6.15	7.93	0.09	22.5	0.3
st2	4.80	0.10	0.90	6.20	7.10	0.05	12.7	0.4
st3	4.20	0.08	1.54	4.67	6.21	0.06	24.8	0.4
st4	3.90	0.07	1.32	4.45	5.77	0.06	22.9	0.5
st5	3.22	0.09	1.08	3.68	4.76	0.07	22.7	0.6
t1	4.19	0.08	0.74	5.46	6.20	0.06	11.9	0.3

fied individually although a male was available and studied in detail. The st2, st3 and X_1 chromosomes from tissue cultures of different origin (skin, testis, lung and heart) are shown in Fig. 24. Evidently, there was no clear morphological difference between the X_2 and the Y chromosomes in the single male studied of this species, and the small variations in appearance of the st2 and st3 chromosomes, noticed in the male, were present also in the female. *H. brachyurus* thus has a "pseudo-XO/XX" sex-chromosome mechanism.

The general appearance of the karyotype of *H. brachyurus* is rather similar to that of *H. auropunctatus*, and the differences in chromosome designation may be interpreted as follows: Chromosome m5 of *brachyurus* (c.i. = 39.1) corresponds to sm7 of *auropunctatus* (c.i. = 34.2); chromosome sm5 of *brachyurus* (c.i. = 26.4) corresponds to st4 of *auropunctatus* (c.i. = 23.3) and chromosome st3 of *brachyurus* (c.i. = 15.8) corresponds to X_2 of *auropunctatus* (c.i. = 11.7). Many of the *brachyurus* chromosomes have slightly higher centromeric indices than the corresponding chromosomes of *auropunctatus*. In *auropunctatus* there is a marked size difference between the smallest (sm7) and the second smallest (m5) chromosomes; this is contrary to *brachyurus*, in which the two smallest chromosomes (m5 and m6) are very similar in size. Also the two largest pairs of *brachyurus* show less size difference than the two largest pairs of *auropunctatus*. The most interesting difference, however, is the absence of an individually distinguishable Y chromosome in *brachyurus*.

The X_1 chromosome constitutes 5.0 per cent of (A + X).

Previous chromosome studies on this species do not exist.

I. Dwarf mongoose, *Helogale parvula* (SUNDEVALL) (1846)

One male and one female were studied, 2n = 36 male and female. The karyotype is shown in Fig. 25 and the idiogram in Fig. 26. The results

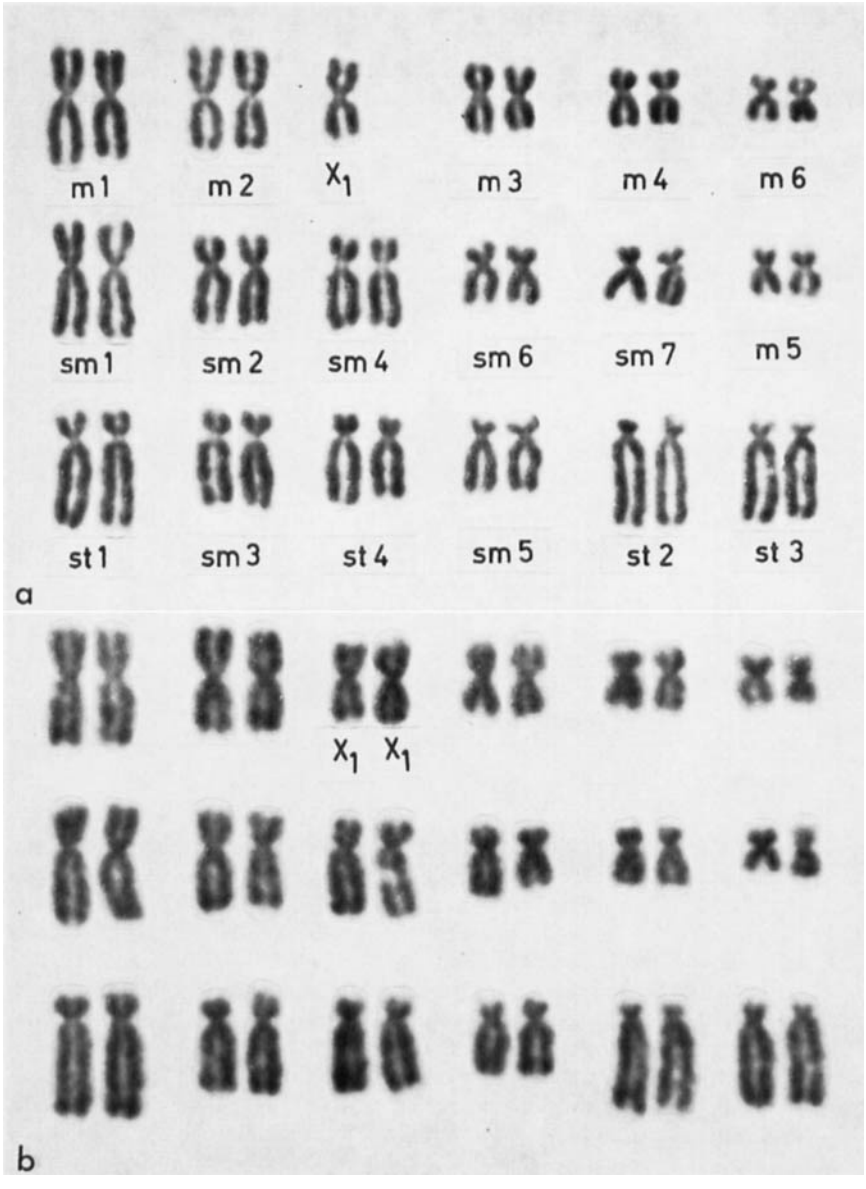


Fig. 22. Karyotypes of *Herpestes brachyurus*, a: male, 2n = 35; b: female, 2n = 36. No Y chromosome could be identified in the male of this species.

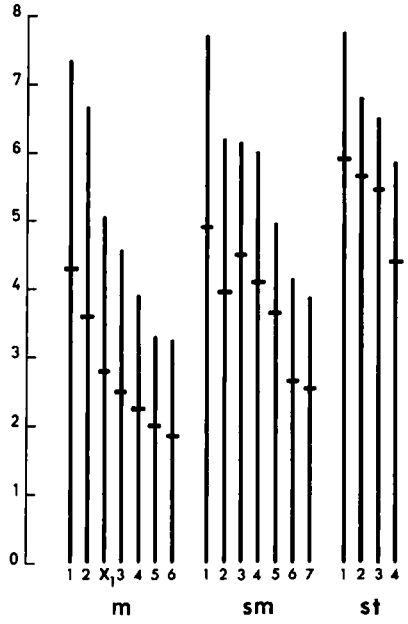


Fig. 23. Idiogram of *Herpestes brachyurus*.

Table 11. Chromosome measurements of *Herpestes brachyurus*
Mean of 5 female and 5 male cells

Chromosome	Absolute length in μ		Relative length, % of female haploid set				Centromeric index	
			p	q	p+q			
	Mean	S.e.	Mean	Mean	Mean	S.e.	Mean	S.e.
m1	5.18	0.09	3.05	4.31	7.36	0.07	41.4	0.3
m2	4.69	0.07	3.08	3.58	6.66	0.05	46.2	0.3
X_1	3.59	0.07	2.24	2.80	5.04	0.06	44.5	0.5
m3	3.21	0.05	2.06	2.49	4.55	0.04	45.3	0.5
m4	2.75	0.06	1.63	2.27	3.90	0.06	41.9	0.6
m5	2.33	0.04	1.29	2.02	3.31	0.04	39.1	0.4
m6	2.28	0.04	1.39	1.85	3.24	0.03	43.0	0.5
sm1	5.41	0.10	2.80	4.88	7.68	0.06	36.4	0.4
sm2	4.37	0.10	2.24	3.95	6.19	0.07	36.2	0.5
sm3	4.34	0.08	1.66	4.49	6.15	0.05	27.0	0.4
sm4	4.21	0.06	1.88	4.10	5.98	0.04	31.4	0.4
sm5	3.49	0.05	1.31	3.65	4.96	0.05	26.4	0.4
sm6	2.93	0.07	1.49	2.67	4.16	0.04	35.8	0.5
sm7	2.73	0.05	1.32	2.56	3.88	0.04	34.1	0.5
st1	5.46	0.09	1.87	5.89	7.76	0.05	24.1	0.4
st2	4.80	0.07	1.16	5.66	6.82	0.05	17.0	0.5
st3	4.58	0.07	1.03	5.47	6.50	0.05	15.8	0.3
st4	4.12	0.07	1.46	4.39	5.85	0.04	24.9	0.3

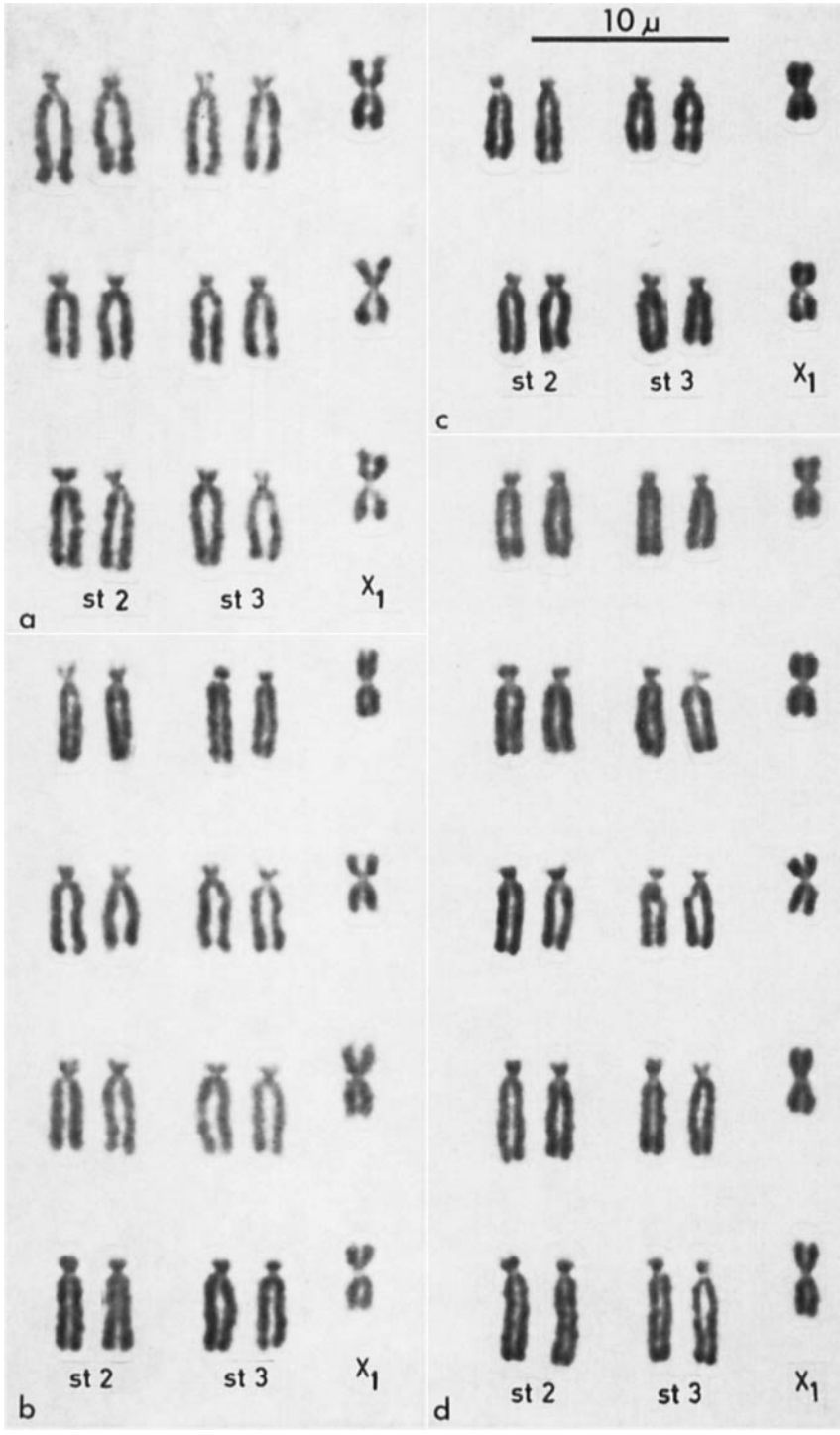


Fig. 24. *Herpestes brachyurus*, male. Representative chromosomes st2, st3 and X_1 from different tissues showing the difficulty of identifying the Y in this species; a "pseudo-XO/XX" sex chromosome mechanism. a: skin; b: testis; c: lung; d: heart. — ×2,630.

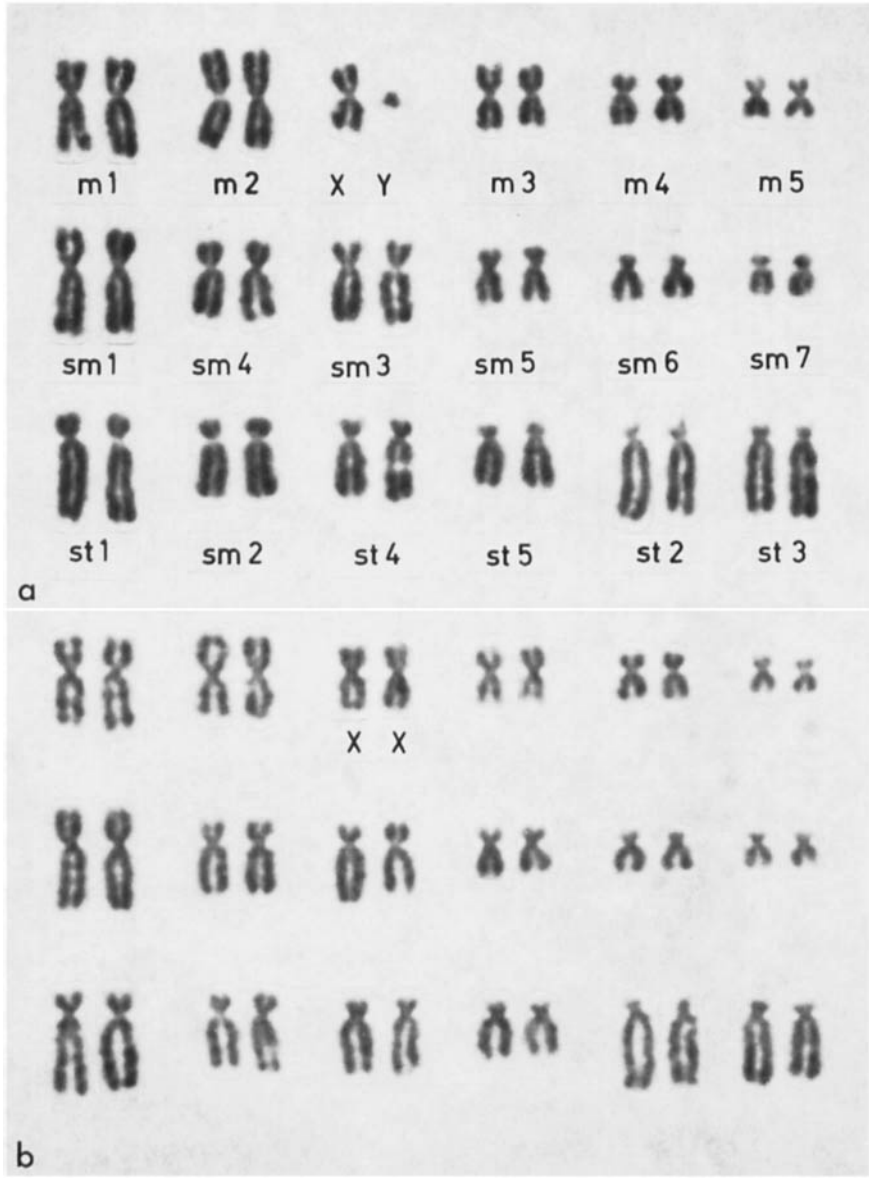


Fig. 25. Karyotypes of *Helogale parvula*, 2n = 36, a: male; b: female. Note the small Y chromosome and 36 chromosomes in the male.

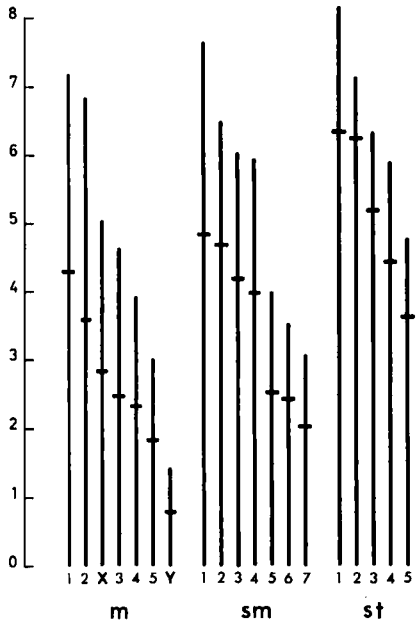


Fig. 26. Idiogram of *Helogale parvula*.

Table 12. Chromosome measurements of *Helogale parvula*
Mean of 5 female and 5 male cells

Chromosome	Absolute length in μ		Relative length, % of female haploid set				Centromeric index	
			p	q	p+q			
	Mean	S.e.	Mean	Mean	Mean	S.e.	Mean	S.e.
m1	4.87	0.07	2.87	4.35	7.22	0.06	39.7	0.4
m2	4.64	0.07	3.28	3.60	6.88	0.05	47.7	0.3
X	3.43	0.04	2.23	2.79	5.02	0.05	44.4	0.6
m3	3.19	0.05	2.14	2.58	4.72	0.04	45.4	0.5
m4	2.79	0.05	1.67	2.47	4.14	0.05	40.3	0.5
m5	2.16	0.03	1.32	1.88	3.20	0.04	41.3	0.6
Y	0.94	0.02	0.65	0.80	1.45	0.06	44.7	1.6
sm1	5.17	0.10	2.77	4.89	7.66	0.07	36.1	0.2
sm2	4.29	0.07	1.71	4.65	6.36	0.05	26.9	0.3
sm3	4.09	0.07	1.89	4.17	6.06	0.06	31.2	0.4
sm4	4.00	0.06	2.02	3.91	5.93	0.05	34.0	0.3
sm5	2.78	0.04	1.50	2.62	4.12	0.04	36.4	0.6
sm6	2.49	0.04	1.13	2.56	3.69	0.03	30.6	0.4
sm7	2.12	0.03	1.07	2.07	3.14	0.03	34.0	0.5
st1	5.40	0.10	1.91	6.09	8.00	0.07	23.9	0.3
st2	4.55	0.07	0.90	5.84	6.74	0.05	13.4	0.3
st3	4.31	0.06	1.13	5.26	6.39	0.06	17.7	0.4
st4	3.98	0.07	1.41	4.48	5.89	0.04	23.9	0.3
st5	3.26	0.05	1.16	3.67	4.83	0.05	24.1	0.4

of the chromosome measurements are given in Tables 12 and 25.

The karyotype consists of 5 m, 7 sm and 5 st autosome pairs. The X and Y are m chromosomes with similar centromeric indices (44.4 and 44.7, respectively). The largest chromosome of the complement is st1 and the smallest the Y.

Chromosome m1 is the third largest chromosome and may be confused with sm1 which, however, is larger and has a lower centromeric index. The m2 pair is easily recognized by its size and its high centromeric index. Chromosome m3 is slightly smaller and has a somewhat higher centromeric index than the X. The five smallest autosome pairs are m4–5 and sm5–7, and among them m4 and sm5 are similar in total length, and so are m5 and sm7, but they may all be distinguished individually on the basis of centromeric index. The sm6 is intermediate in size and has the lowest centromeric index of these chromosomes. The chromosomes sm2–4 and st4 form a group of similar chromosomes of intermediate size; among them the largest, sm2 and the smallest, st4, have lower centromeric indices (26.9 and 23.9) than the others, of which sm3 has lower centromeric index than sm4. The st1 and st5 pairs are immediately recognized by their relative lengths and centromeric indices. The pairs st2 and st3 may be confused, but st2 is larger and its short arm somewhat smaller.

It must be stressed that the functional Y chromosome is not translocated on to an autosome in this and the following species, which have an "ordinary" Y, immediately identified in good preparations by its very small size. The X chromosome, which constitutes 5.0 per cent of (A + X) corresponds well with the X_1 of the *Herpestes* species.

Previous chromosome studies on this species do not exist.

J. Banded mongoose, *Mungos mungo* (GMELIN) (1788)

Seven males and five females were studied, 2n = 36. The karyotype is shown in Fig. 27 and the idiogram in Fig. 28. The results of the chromosome measurements are given in Tables 13 and 27.

The karyotype consists of 5 m, 7 sm and 5 st autosome pairs. The X and Y are m chromosomes with centromeric indices of 43.7 and 45.8, respectively. The largest chromosome of the complement is st1 and the smallest the Y. The X constitutes 5.0 per cent of (A + X).

The karyotype of *M. mungo* is identical to that of *Helogale parvula* with the exception that st2 is larger in *Mungos* than in *Helogale*, the relative lengths being 7.17 and 6.74, respectively. In all other chromosomes there is a strikingly good agreement between the two species, both in chromosome length and in centromeric index (cf. Table 17).

It is worthy of mention that the animals *M. m.* 3–12 were all offspring of *M. m.* 1 and *M. m.* 2 and, as expected, no intraspecific difference was found among the males in the morphology of the Y. The reason for investigating so many individuals was that one of the first individuals studied, *M. m.* 5, turned out to be heterozygous for a balanced reciprocal translocation. Measurements indicated that the chromosomes involved were sm3 and sm7; this unique case will be described in more detail in a subsequent article. All other offspring had the same karyotype as the parents, viz. the karyotype described here.

Previous chromosome studies: One female specimen was studied by WURSTER and BENIRSCHKE (1968) and their published karyotype is in good agreement with the female karyotype presented here, although the individual chromosome pairs are arranged differently.

K. Kusimanse, *Crossarchus obscurus* F. CUVIER (1825)

One male was studied, 2n = 36. The karyotype is shown in Fig. 29 and the idiogram in Fig. 30. The results of the chromosome measurements are given in Table 14.

The karyotype consists of 5 m, 6 sm and 6 st autosome pairs. The X and Y are m chromosomes with centromeric indices of 43.3 and 42.1, respectively. The largest chromosome of the complement is st1 and the smallest the Y. The X constitutes 5.1 per cent of (A + X).

The karyotype of *C. obscurus* is very similar to those just described for *Helogale parvula* and *Mungos mungo*. The main difference is that the C2 chromosome in *Helogale* and *Mungos* is an sm chromosome (sm2) but in *Crossarchus* an st (st4, c.i. = 24.6), most likely due to a small reduction in length of the short arm of this

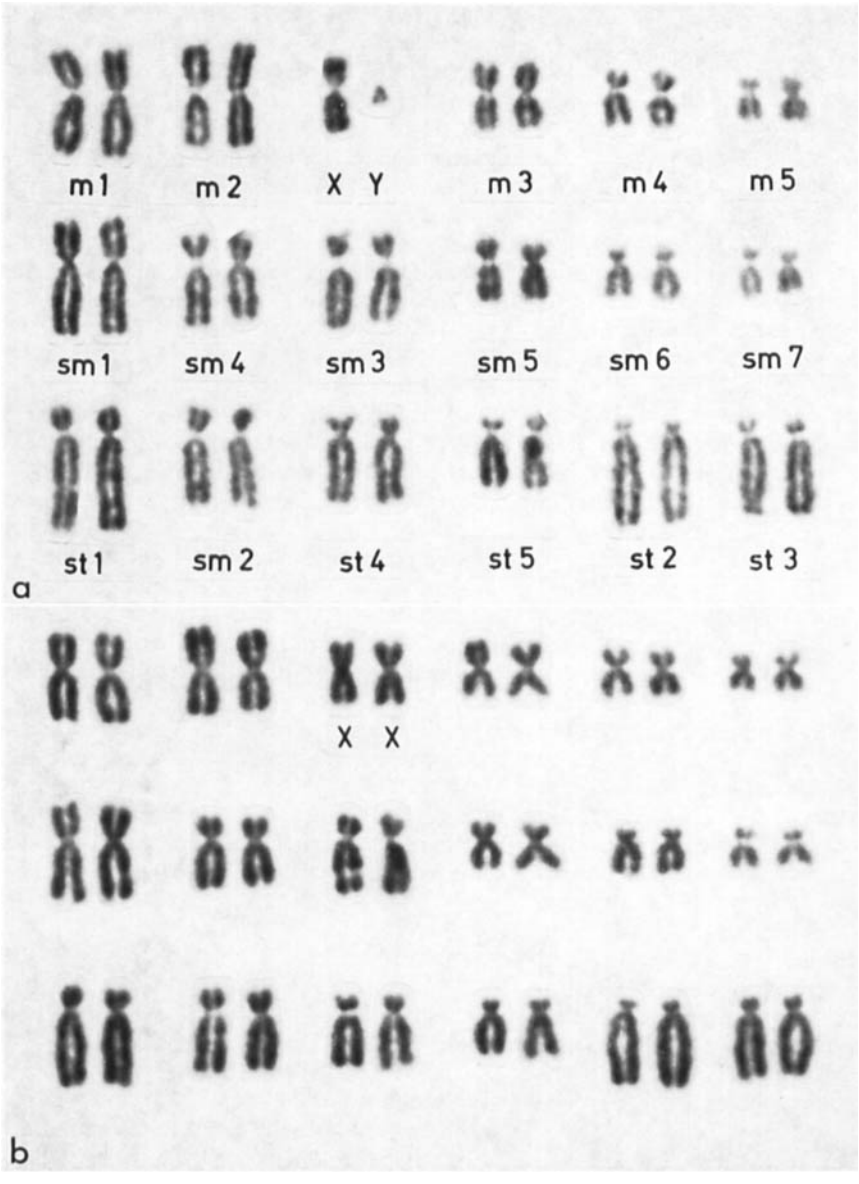


Fig. 27. Karyotypes of *Mungos mungo*, 2n = 36, a: male; b: female.

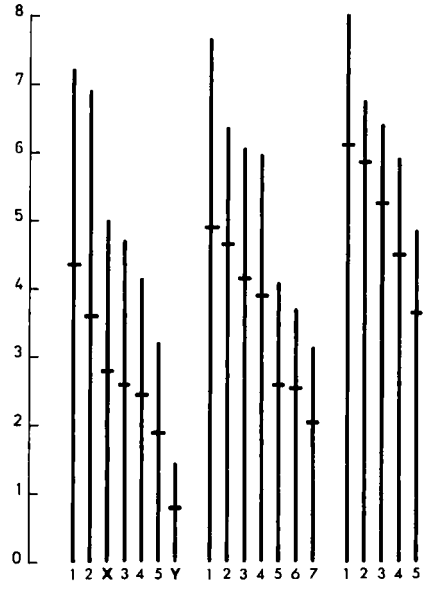


Fig. 28. Idiogram of *Mungos mungo*.

Table 13. Chromosome measurements of *Mungos mungo*
Mean of 5 female and 5 male cells

Chromosome	Absolute length in μ		Relative length, % of female haploid set				Centromeric index	
			p	q	p+q			
	Mean	S.e.	Mean	Mean	Mean	S.e.	Mean	S.e.
m1	4.58	0.11	2.92	4.30	7.22	0.04	40.5	0.3
m2	4.34	0.11	3.24	3.60	6.84	0.04	47.4	0.3
X	3.17	0.06	2.20	2.83	5.03	0.05	43.7	0.6
m3	2.97	0.08	2.14	2.53	4.67	0.04	45.9	0.5
m4	2.51	0.06	1.61	2.34	3.95	0.03	40.8	0.4
m5	1.95	0.05	1.23	1.84	3.07	0.04	40.1	0.6
Y	0.96	0.04	0.67	0.79	1.46	0.04	45.8	1.1
sm1	4.84	0.11	2.79	4.85	7.64	0.05	36.5	0.5
sm2	4.12	0.10	1.80	4.69	6.49	0.05	27.8	0.3
sm3	3.84	0.10	1.84	4.20	6.04	0.05	30.4	0.3
sm4	3.79	0.10	1.95	4.02	5.97	0.06	32.7	0.3
sm5	2.55	0.07	1.46	2.56	4.02	0.05	36.4	0.6
sm6	2.26	0.05	1.12	2.45	3.57	0.03	31.5	0.5
sm7	1.98	0.04	1.09	2.03	3.12	0.05	34.9	0.4
st1	5.18	0.13	1.80	6.36	8.16	0.06	22.1	0.3
st2	4.55	0.12	0.94	6.23	7.17	0.05	13.1	0.1
st3	4.03	0.10	1.13	5.22	6.35	0.04	17.8	0.3
st4	3.73	0.08	1.42	4.46	5.88	0.04	24.1	0.3
st5	3.06	0.07	1.17	3.65	4.82	0.04	24.2	0.3

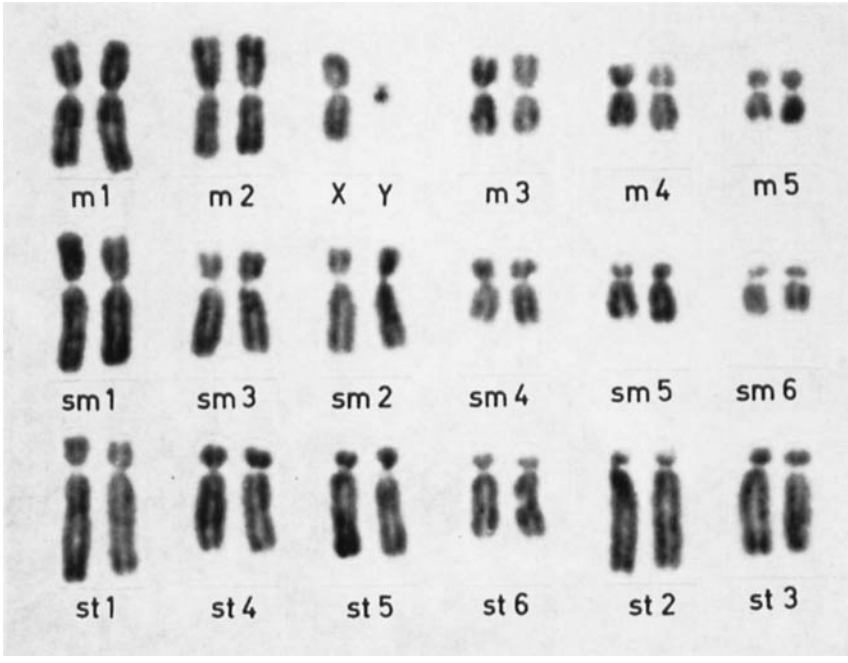


Fig. 29. Karyotype of *Crossarchus obscurus*, 2n = 36, male. (No female was available of this species).

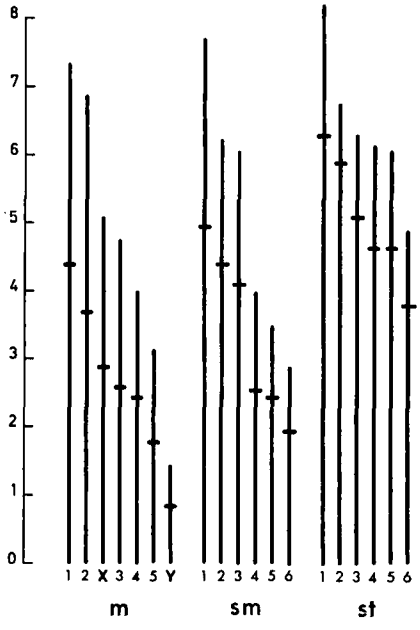


Fig. 30. Idiogram of *Crossarchus obscurus*.

Table 14. Chromosome measurements of *Crossarchus obscurus*
Mean of 5 male cells

Chromosome	Absolute length in μ		Relative length, % of female haploid set				Centromeric index	
			p	q	p+q			
	Mean	S.e.	Mean	Mean	Mean	S.e.	Mean	S.e.
m1	5.13	0.15	2.96	4.41	7.37	0.08	40.2	0.5
m2	4.79	0.14	3.20	3.68	6.88	0.08	46.5	0.5
X	3.56	0.14	2.22	2.90	5.12	0.09	43.3	1.1
m3	3.31	0.10	2.17	2.58	4.75	0.05	45.6	0.7
m4	2.78	0.07	1.57	2.43	4.00	0.04	39.3	0.6
m5	2.18	0.07	1.31	1.82	3.13	0.06	41.8	0.9
Y	1.00	0.04	0.61	0.83	1.44	0.03	42.1	1.7
sm1	5.36	0.14	2.78	4.93	7.71	0.07	36.1	0.8
sm2	4.32	0.09	1.82	4.40	6.22	0.06	29.2	0.4
sm3	4.22	0.10	1.98	4.09	6.07	0.07	32.7	0.5
sm4	2.79	0.09	1.46	2.55	4.01	0.06	36.3	0.6
sm5	2.45	0.08	1.05	2.47	3.52	0.07	29.8	0.6
sm6	2.02	0.07	0.93	1.97	2.90	0.06	32.1	0.5
st1	5.69	0.12	1.88	6.31	8.19	0.09	22.9	0.6
st2	4.70	0.12	0.87	5.89	6.76	0.08	12.8	0.5
st3	4.36	0.08	1.18	5.10	6.28	0.09	18.8	0.4
st4	4.28	0.12	1.51	4.64	6.15	0.08	24.6	0.5
st5	4.20	0.14	1.36	4.67	6.03	0.08	22.5	0.6
st6	3.41	0.09	1.09	3.82	4.91	0.04	22.1	0.6

chromosome in *Crossarchus*. The st2 chromosome of *Crossarchus* is of the same size as that of *Helogale* (relative lengths 6.76 and 6.74).

The Y chromosome of *Crossarchus* has a somewhat lower centromeric index than the Y's of *Helogale* and *Mungos*, a feature hardly clear from the photographs. This conclusion is based not only on the measurement data (which in such a small chromosome are always impaired by large errors of measurement), but mainly on direct observation in the microscope and drawings of individual favourable Y chromosomes. Due to their small size, the Y chromosomes of *Helogale*, *Mungos* and *Crossarchus* often have a "dot-like" appearance making the position of the centromere obscure.

Previous chromosome studies on this species do not exist.

L. Yellow mongoose, *Cynictis penicillata* (G. CUVIER) (1829)

One male and one female were studied, 2n = 36. The karyotype is shown in Fig. 31 and the idiogram in Fig. 32. The results of the chromosome measurements are given in Tables 15 and 28.

The karyotype consists of 9 m, 7 sm and 1 st autosome pairs. The X and Y are m chromosomes with centromeric indices of 43.2 and 46.9, respectively. The large number of m chromosomes is characteristic of this species. The largest chromosome of the complement is sm1 and the smallest the Y.

Chromosome m1 may be confused with sm2 and m3 but is intermediate in size. Chromosome m2 is easily distinguished by its size and high centromeric index. The m4 is smaller than X and has a higher centromeric index. The m5–7 pairs are similar in size and morphology and thus difficult to distinguish individually. Satellites are often present on the short arms of m6, and usually the satellites are more distinct in one member of the pair (Fig. 33). The m8–9 pairs are smaller and have higher centromeric indices than the m5–7 pairs. Satellites have been observed on the short arm of m8. Among the sm chromosomes, the following are relatively easy to distinguish: sm1 by its large size, sm3 by its

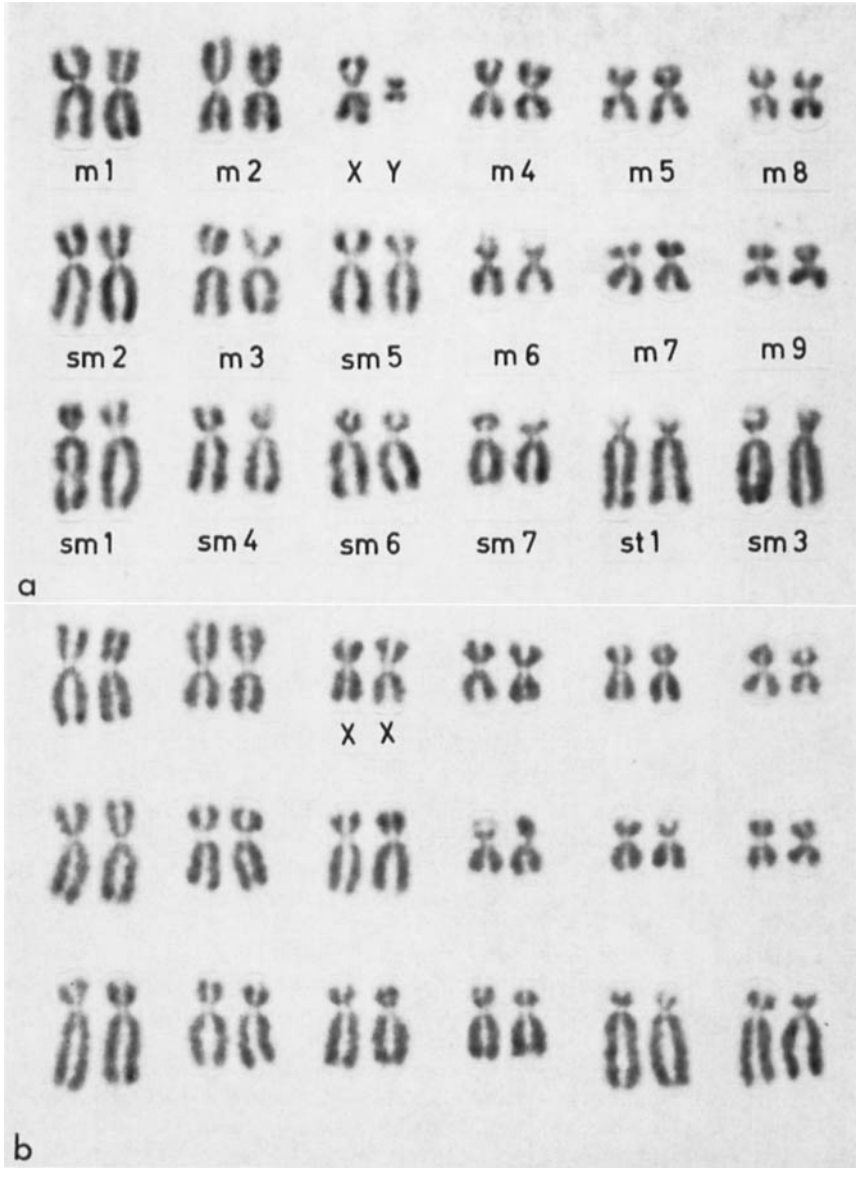


Fig. 31. Karyotype of *Cynictis penicillata*, 2n = 36, a: male; b: female.

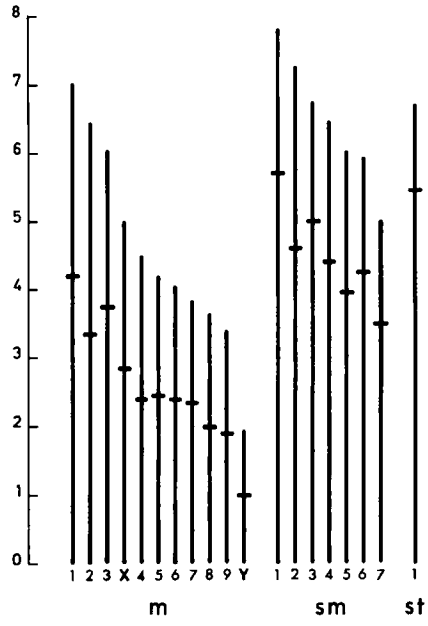


Fig. 32. Idiogram of *Cynictis penicillata*. Note the high number of m chromosomes.

Table 15. Chromosome measurements of *Cynictis penicillata*
Mean of 5 female and 5 male cells

Chromosome	Absolute length in μ		Relative length, % of female haploid set				Centromeric index	
			p	q	p+q			
	Mean	S.e.	Mean	Mean	Mean	S.e.	Mean	S.e.
m1	4.67	0.11	2.83	4.18	7.01	0.06	40.3	0.3
m2	4.28	0.09	3.08	3.36	6.44	0.05	47.8	0.2
m3	4.02	0.08	2.29	3.76	6.05	0.07	37.8	0.4
X	3.29	0.06	2.15	2.83	4.98	0.07	43.2	0.5
m4	2.99	0.06	2.09	2.41	4.50	0.05	46.4	0.3
m5	2.79	0.05	1.79	2.43	4.22	0.03	42.4	0.5
m6	2.69	0.06	1.65	2.40	4.05	0.06	40.7	0.7
m7	2.57	0.04	1.54	2.33	3.87	0.04	39.8	0.6
m8	2.42	0.05	1.65	1.99	3.64	0.05	45.3	0.4
m9	2.24	0.04	1.47	1.91	3.38	0.05	43.5	0.6
Y	1.28	0.02	0.91	1.02	1.93	0.07	46.9	0.8
sm1	5.20	0.13	2.13	5.68	7.81	0.08	27.3	0.4
sm2	4.84	0.12	2.66	4.61	7.27	0.07	36.6	0.4
sm3	4.48	0.12	1.74	4.99	6.73	0.07	25.8	0.5
sm4	4.29	0.11	2.05	4.39	6.44	0.07	31.9	0.5
sm5	3.99	0.08	2.03	3.97	6.00	0.04	33.8	0.4
sm6	3.95	0.08	1.70	4.24	5.94	0.04	28.6	0.4
sm7	3.33	0.06	1.49	3.52	5.01	0.05	29.8	0.5
st1	4.46	0.11	1.25	5.45	6.70	0.08	18.7	0.8

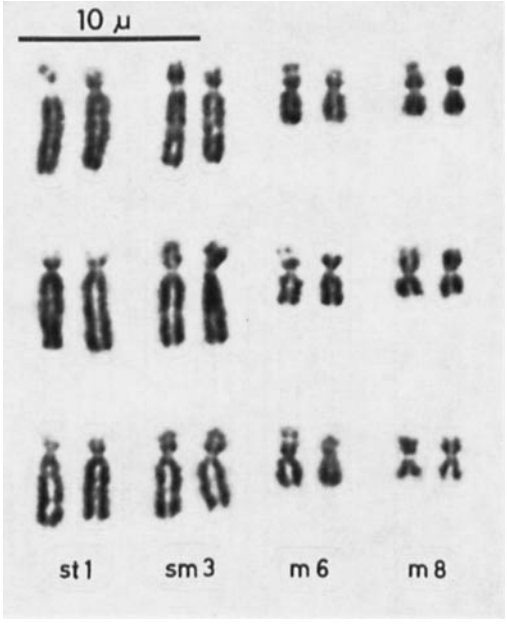


Fig. 33. *Cynictis penicillata*: chromosomes st1, sm3, m6 and m8 from three cells showing satellites on the short arms. The satellites on chromosome m6 are exceptionally distinct in these cells. — ×2,420.

low centromeric index (25.8f and sm7 by its small size compared with the other sm chromosomes. The sm4–6 pairs may be confused but sm5 has a higher centromeric index than the other two pairs and is actually more easily confused with m3. The sm4 has a larger short arm than the sm6 pair. There is only one st pair, and this pair, like sm3, occasionally has vague satellites on the short arm.

The X chromosome constitutes 5.0 per cent of (A + X). The Y chromosome is larger in *Cynictis* than in *Helogale*, *Mungos* and *Crossarchus* (Fig. 34), and its relative length is 1.9 as compared with 1.4–1.5 in the other three species.

Previous chromosome studies: One male and one female specimen were studied by GERNEKE (1967) who found 2n = 36 in bone marrow preparations from both sexes. Two karyotypes from camera lucida drawings were published and are generally compatible with the present findings, in that they show a high number of m and sm chromosomes. The detailed comparison of the karyotypes of GERNEKE with the present ones reveals, however, many small discrepancies, of which only one will be mentioned: GERNEKE claimed that "the X is a submetacentric fitting in between chromosomes 14 and 15" (in size). Actually, the X is an m chromosome fitting in between chromosomes 11 and 12 in size (verified by autoradiography). TODD et al. (1967) described the karyotype of the "bushy-tailed mierkat (*Cynictis* sp.)". One male was studied and the karyotype presented agrees reasonably well with the present observations. Even though satellites are faintly visible in one chromosome in the paper of TODD et al., neither these authors nor GERNEKE mention any satellites.

3. Satellites and chromosome associations

In the previous section the presence of satellites on the short arms of certain chromosomes were mentioned for *Herpestes ichneumon* (A6, C3, D1 and D2) and for *Cynictis penicillata* (A6, B4, D1 and D2). These two species have comparatively distinct satellites rather regularly in one or both homologues in up to four chromosome pairs. Actually, vague satellites on the short arms of the D1 and D2 chromosomes are present in all species. These chromosomes often take part in associations, probably in connection with nucleolar formation, and often members of one or two small sm pairs (usually B5 and B6) also take part. It is the short arms of these chromosomes which associate but occasionally the centromeric region of other chromosomes also are involved (Fig. 35 f, 36 e, f, g); the preferred centromere seems to be A2. Up to three associations were observed in one cell (Fig. 35 b) and occasionally 6 chromosomes were involved in one association (Fig. 35 f). Chromosome associations were observed in all 12 species, examples being given in Fig. 35 (*H. edwardsi*, *H. fuscus* and *H. urva*) and in Fig. 36 (*Helogale parvula*, *Mungos mungo* and *Crossarchus obscurus*). Examples of chromosome associations in *H. auropunctatus* were given by FREDGA (1967 a). It is of particular interest that the Y chromosome of *Mungos mungo* also takes part in associations with the D1 and D2 chromosomes (Fig. 36 j–m), since this gives an idea of the original formation of the translocation chromosome in the *Herpestes* species. The parallel with the well-known D–G translocations in man is obvious.

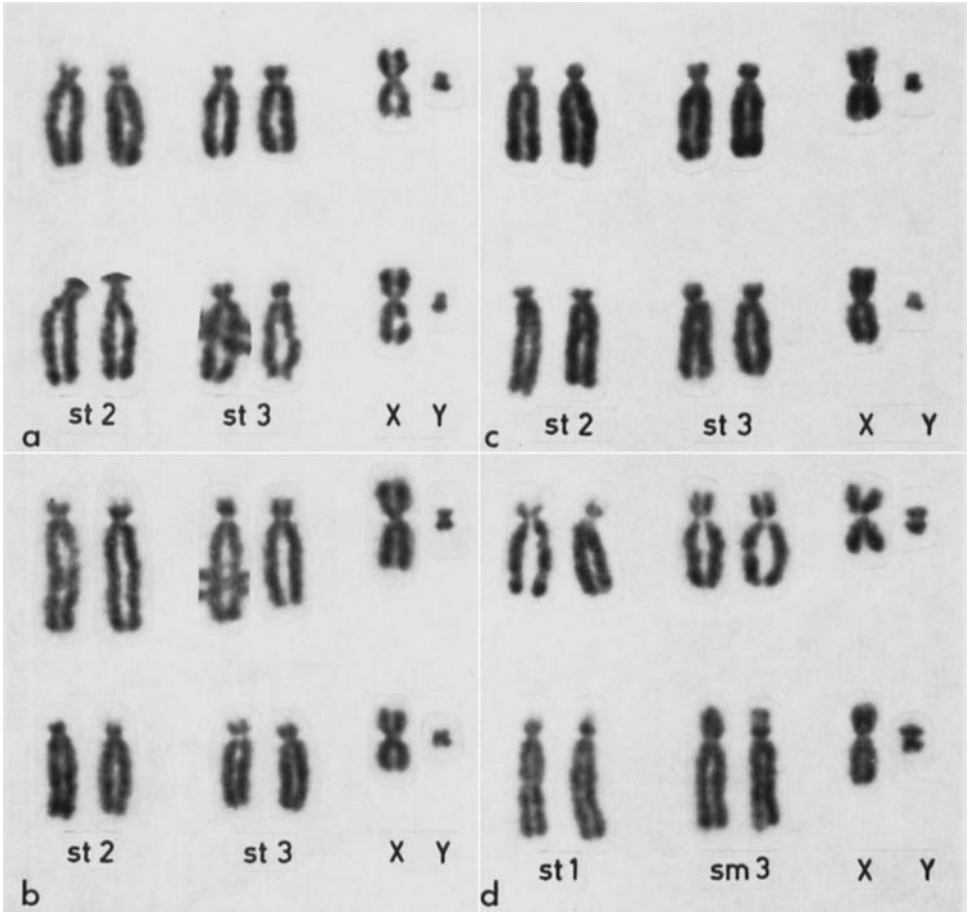


Fig. 34. Chromosomes st2, st3, X and Y from two cells of *Helogale parvula* (a); *Mungos mungo* (b); *Crossarchus obscurus* (c) and chromosomes st1, sm3, X and Y of *Cynictis penicillata* (d). Note the relatively larger size of the Y of *Cynictis penicillata* in comparison with the other three species.

4. Comparisons of the karyotypes

The karyotypes of the mongoose species studied have many features in common and the similarities are great enough to warrant a detailed comparison of each individual chromosome through the different species. For such a comparison it is desirable to use chromosomes with a similar degree of contraction. Relative length and centromeric index for individual chromosomes may vary due to the technique used. SASAKI (1961) showed in mammalian material that long chromosomes usually are more contracted by colchicine treatment than short ones. This applies also to chromosome arms, which means that the centromeric index can be modified by the colchicine treatment.

In the present study all preparations were made by the author using the same technique and efforts were made to select cells with chromosomes of a similar degree of contraction. Since the amount of genetic material is the same, in principle, in all placental mammals (MANDEL et al. 1950; ATKIN et al. 1965), the absolute length of the chromosomes should be the same at least in related species provided chromosomes of the same

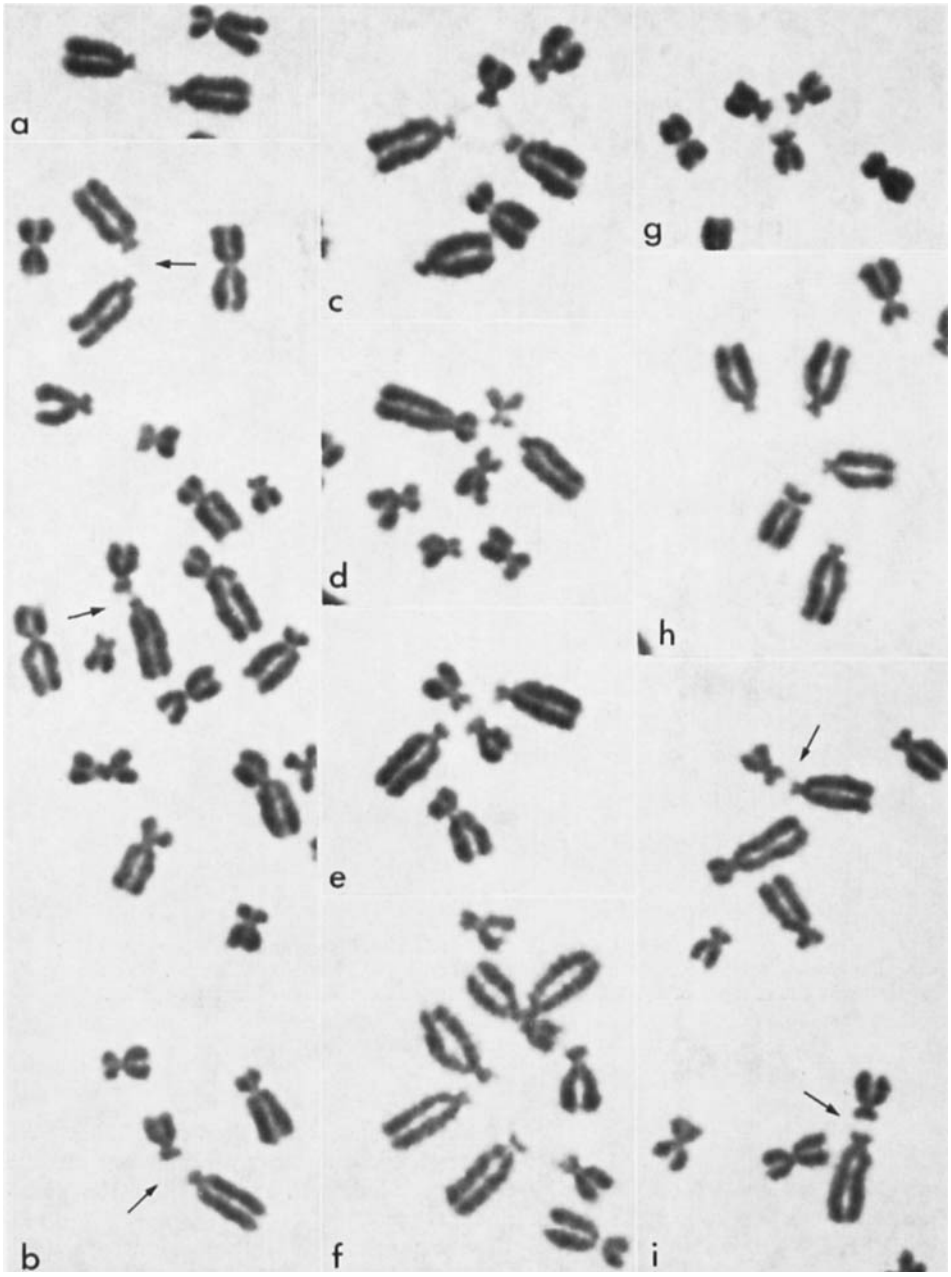


Fig. 35. Examples of chromosome associations in *Herpestes edwardsi* (a); *H. fuscus* (b—f) and *H. urva* (g—i). a: D2—D1; b: three associations in the same cell, D1—D2, B5—D2 and B5—D1; c: D1—B5—D1; d: C1—B6—D2—A5; e: B5—D1—B5—D1; f: centromere B1—D2—(C4—) B5—D1—D2—D1; g: B6—B6—B5; h: D2—D1—D2—D1—D2; i: two associations in the same cell, B6—D2 and B5—D1. Note chromatic material connecting the ends of the short arms of the associating chromosomes in (a) and (c).

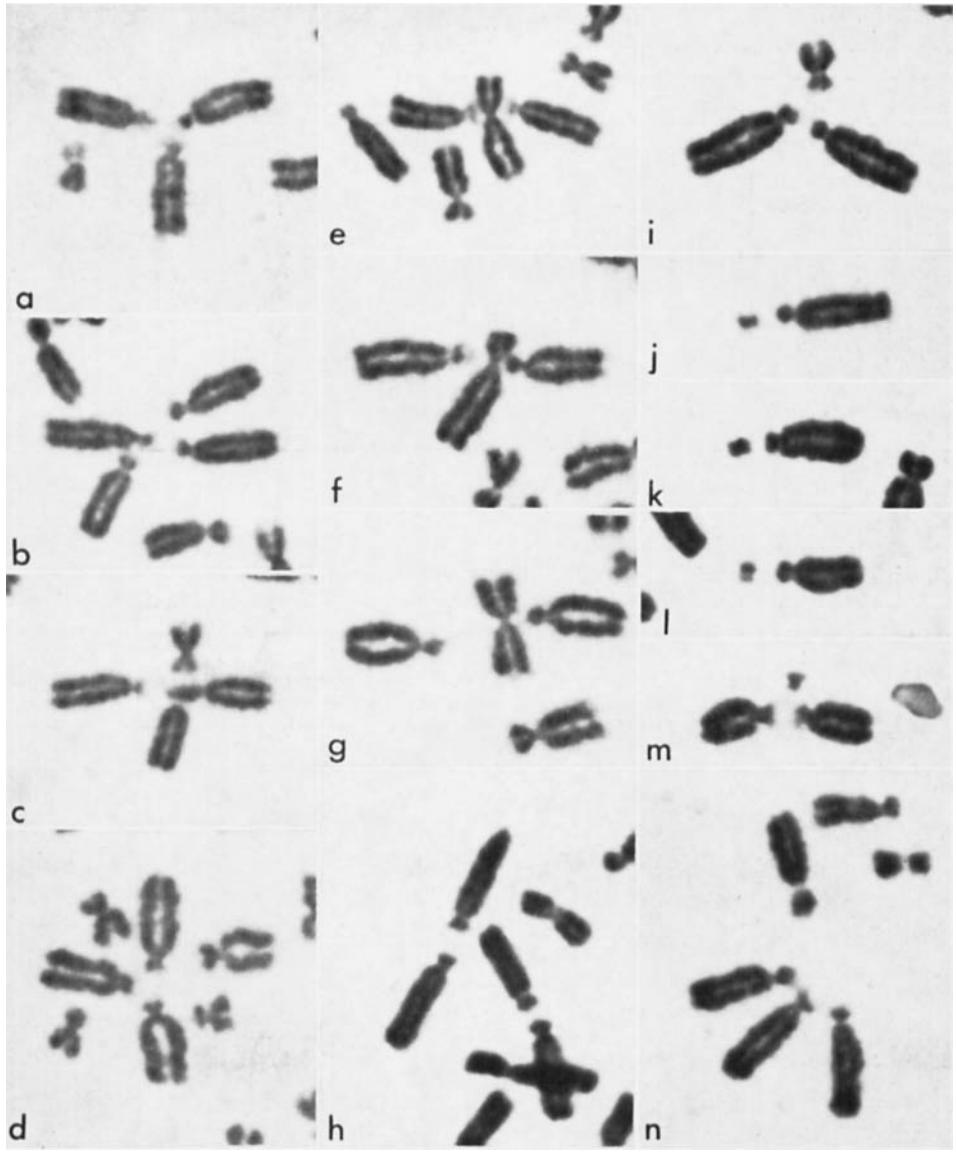


Fig. 36. Examples of chromosome associations in *Helogale parvula* (a—f), *Mungos mungo* (g—m) and *Crossarchus obscurus* (n). a: D2—D1—D1; b: D1—D2—D1—D2; c: B4—D2—D2—D1; d: D1—(C3—) (B6—) D2—D1; e: D2—centromere B1—D1; f: D1—centromere C1—D2; g: D2—centromere A2—D2; D1—D1 and D2—D2; i: B6—D1—D1; j: Y—D1; k: Y—D1; l: Y—D2; m: Y—D1—D2; n: (C2—) D1—D1—D2. The four examples of Y—D1 or D2 associations represent three different males (*M.m.* 5, *M.m.* 10 and *M.m.* 11).

Table 16. Absolute length in μ of the female haploid set in the different mongooses (mean of 5 cells from each individual)

Species	Female	S.e.	Male	S.e.	Mean	S.e.
Herpestes ichneumon	62.8	2.5	66.4	2.4	64.6	1.7
sanguineus 1	—		64.5	1.8	66.4	1.2
sanguineus 2	—		68.3	1.4		
pulverulentus	64.3	0.9	62.0	2.3	63.1	1.2
auropunctatus	69.7	2.0	56.7	2.3	63.2	2.6
edwardsi	61.9	2.2	57.5*	1.5	59.7	1.7
fuscus	61.8	2.9	63.5	1.7	62.6	1.6
urva	67.6	1.4	—		67.6	1.4
brachyurus	73.4	2.3	67.4	0.8	70.4	1.5
Helogale parvula	70.0	1.3	64.9	1.6	67.4	1.3
Mungos mungo	60.6	1.6	66.2	3.6	63.4	2.1
Crossarchus obscurus	—		69.6	2.5	69.6	2.5
Cynictis penicillata	66.2	3.3	66.7	2.1	66.5	1.8

* Mean of P1 and P8, max. and min. (cf. Table 23)

Table 17. Chromosomal synopsis of 12 species of mongooses

Each horizontal line through all species lists chromosomes with best correspondence in size and centromeric location. Within

Group	No.	1 *Herpestes ichneumon* a	b	c	2 *Herpestes sanguineus* a	b	c	3 *Herpestes pulverulent.* a	b	c	4 *Herpestes auropunctat.* a	b	c	5 *Herpestes edwardsi* a	b	c	6 *Herpestes fuscus* a	b	c	7 *Herpestes urva* a	b	c
		t8	2.6	—																		
A	1	t3	3.9	—	m1	6.4	39	sm1	6.3	37	m1	7.1	40	m1	6.9	41	m1	7.3	41	m1	7.3	40
		t5	3.3	—	t4	3.2	—															
	2	t4	3.6	—	t3	3.4	—	m1	6.6	46	m2	6.8	46	m2	6.6	47	m2	6.9	47	m2	6.7	47
	3	X_1	5.0	43	X_1	5.2	42	X_1	4.9	43	X_1	5.0	45	X_1	4.9	45	X_1	5.1	44	X_1	4.9	44
	4	m1	4.9	46	m2	4.9	47	m2	4.6	47	m3	4.6	45	m4	4.6	46	m3	4.7	46	m3	4.8	43
	5	m3	3.9	41	m3	4.0	41	m3	3.9	41	m4	4.1	41	m6	4.0	42	m4	4.1	40	m5	4.0	40
														m3a	5.2	38						
	6	m4	3.7	43	m4	3.7	46	m4	3.1	42	m5	3.7	44	m3b	4.5	42	m5	3.5	44	m4	4.1	46
		t6	3.1	—	t5	2.9	—	st6	3.5	24												
B	1	t1	4.7	—	t1	4.6	—	st4	5.4	21	sm1	7.5	37	sm2	7.3	37	sm2	7.6	37	sm1	7.6	36
		t7	3.0	—	t6	2.8	—	sm7	3.4	30												
	2	t2	4.2	—	t2	4.1	—	st5	5.1	19	sm3	6.1	33	sm4	5.8	34	sm3	6.2	35	sm3	5.9	32
	3	sm2	5.9	33	sm2	5.8	31	sm3	5.7	32	sm4	6.0	30	sm5	5.8	31	sm5	5.9	31	sm2	6.0	29
	4	m2	4.1	38	sm4	3.9	37	sm5	3.9	37	sm5	4.1	37	m5	4.2	39	sm6	4.1	37	sm4	4.0	36
	5	m5	3.5	38	sm5	3.7	31	sm6	3.7	31	sm6	3.8	32	sm7	3.7	32	sm7	3.8	32	sm5	3.6	29
	6	m6	3.4	43	sm6	3.2	35	sm8	3.0	35	sm7	3.1	34	sm8	3.2	36	sm8	3.1	36	sm6	3.2	36
														sm1a	9.5	38						
C	1	st1	7.6	24	st1	7.8	25	st1	7.6	24	st1	7.9	23	sm1b	8.9	33	sm1	8.1	25	st1	7.9	23
	2	sm1	6.2	29	sm1	6.1	27	sm2	6.1	27	sm2	6.3	25	sm3	6.0	27	sm4	6.2	26	st3	6.2	25
	3	sm3	5.7	27	sm3	5.7	25	st3	5.5	24	st3	5.9	24	sm6	5.6	26	st2	5.8	25	st4	5.8	23
	4	sm4	4.7	27	st3	4.7	24	sm4	4.7	26	st4	5.0	23	st2	4.8	25	st3	4.8	25	st5	4.8	23
D	1	st2	7.0	19	st2	7.3	19	st2	6.7	18	st2	6.7	13	st1	6.4	15	st1	6.9	14	st2	7.1	13
	2	X_2	6.2	21	X_2	6.5	22	X_2	6.2	21	X_2	6.3	12	X_2	5.9	13	X_2	6.1	12	t1	6.2	12
	3	Y	7.2	10	Y	7.5	11	Y	6.5	12	Y	6.2	3	Y	6.1	8	Y	6.2	6	—		

[1] Species no. 1 excluded [2] Species nos. 1—2 excluded [3] Species no. 5 excluded [4] Species nos. 1—3 excluded

degree of contraction are measured. The absolute lengths of the female haploid set for the different mongooses are compiled in Table 16. The values are gathered around a mean of 65.4 μ. A t test of the values from the two individuals within each species showed significant differences only for *Herpestes brachyurus* and *Helogale parvula* at the 95% level and for *Herpestes auropunctatus* at the 99% level. Variance analysis of the entire material, however, revealed a highly significant variation between individuals within species, but not between species or between the two groups *Herpestes* versus all other genera. If *Herpestes* is subdivided into three groups, (1) *H. i.* + *H.s.* + + *H. p.*; (2) *H. a.* + *H. e.* + *H. f.*; (3) *H. u.* + *H. b.*, there is a difference in absolute length at the 95% level between the groups. The reason for the unexpected difference between individuals within species is probably a statistical effect due to the fact that cells with chromosomes of similar contraction were chosen within a preparation (or series of preparations from one individual) but, in spite of all precautions taken, the degree of contraction varied in different series of preparations (cf. BENDER and KASTENBAUM 1969). The differences are not of such an amplitude, however, that they invalidate a meaningful comparison, particularly when based on relative lengths.

Table 17 is a synopsis of all chromosomes in the 12 species studied and each horizontal line in the table lists chromosomes with best correspondence in size and centromeric location. In Fig. 37–41 the chromosomes are represented by vertical lines, 0 being the location of the centro-

each species the columns a, b and c refer to chromosome designation, relative length and centromeric index, respectively

8 *Herpestes brachyurus*			9 *Helogale parvula*			10 *Mungos mungo*			11 *Crossarchus obscurus*			12 *Cynictis penicillata*			Average for species 4—11		Average for species 1—12	
a	b	c	a	b	c	a	b	c	a	b	c	a	b	c	b	c	b	c
m1	7.4	41	m1	7.2	40	m1	7.2	40	m1	7.4	40	m1	7.0	40	7.21	40.3	7.04[1]	39.9[1]
m2	6.7	46	m2	6.9	48	m2	6.8	47	m2	6.9	47	m2	6.4	48	6.78	46.9	6.72[2]	46.9[2]
X_1	5.0	45	X	5.0	44	X	5.0	44	X	5.1	43	X	5.0	43	5.01	44.2	5.01	43.7
m3	4.6	45	m3	4.7	45	m3	4.7	46	m3	4.8	46	m4	4.5	46	4.68	45.3	4.70	45.8
m4	3.9	42	m4	4.1	40	m4	4.0	41	m4	4.0	39	m5	4.2	42	4.02	40.6	4.01	40.9
m6	3.2	43	m5	3.2	41	m5	3.1	40	m5	3.1	42	m8	3.6	45	3.43[3]	42.8[3]	3.47[3]	43.2[3]
sm1	7.7	36	sm1	7.7	36	sm1	7.6	36	sm1	7.7	36	sm2	7.3	37	7.59	36.5	7.55[4]	36.5[4]
sm2	6.2	36	sm4	5.9	34	sm4	6.0	33	sm3	6.1	33	m3	6.1	38	6.03	33.7	6.03[4]	34.1[4]
sm4	6.0	31	sm3	6.1	31	sm3	6.0	30	sm2	6.2	29	sm5	6.0	34	6.00	30.5	5.96	31.2
sm6	4.2	36	sm5	4.1	36	sm5	4.0	36	sm4	4.0	36	m6	4.1	41	4.08	36.7	4.04	37.2
sm7	3.9	34	sm6	3.7	31	sm6	3.6	32	sm5	3.5	30	m7	3.9	40	3.70	31.4	3.70	32.6
m5	3.3	39	sm7	3.1	34	sm7	3.1	35	sm6	2.9	32	m9	3.4	43	3.14	35.4	3.18	36.6
st1	7.8	24	st1	8.0	24	st1	8.2	22	st1	8.2	23	sm1	7.8	27	8.01[3]	23.4[3]	7.89[3]	24.1[3]
sm3	6.2	27	sm2	6.4	27	sm2	6.5	28	st4	6.2	25	sm4	6.4	32	6.23	26.3	6.22	27.0
st4	5.9	25	st4	5.9	24	st4	5.9	24	st5	6.0	23	sm6	5.9	29	5.83	24.1	5.80	24.8
sm5	5.0	26	st5	4.8	24	st5	4.8	24	st6	4.9	22	sm7	5.0	30	4.86	24.1	4.83	24.9
st2	6.8	17	st2	6.7	13	st2	7.2	13	st2	6.8	13	st1	6.7	19	6.83	13.9	6.86	15.5
st3	6.5	16	st3	6.4	18	st3	6.4	18	st3	6.3	19	sm3	6.7	26	6.25	14.9	6.31	17.4
?			Y	1.5	45	Y	1.5	46	Y	1.4	42	Y	1.9	47				

mere, and chromosomes which best correspond to each other are selected and coordinated into 19 basic chromosome types, A1–6, B1–6, C1–4 and D1–3. All species but three have 17 autosome pairs; *Herpestes pulverulentus* has 19, *H. sanguineus* has 20 and *H. ichneumon* has 21 autosome pairs. This variation in autosome number can be accounted for by centric fusion/fission events in *sanguineus* and *ichneumon*, but in *pulverulentus* rearrangement mechanisms such as pericentric inversions must also be involved.

The chromosomes responsible for differences in chromosome number will first be dealt with. The 8 t chromosomes of *ichneumon* are regarded as the two arms of chromosomes A1, A2, B1 and B2, and the 6 t chromosomes of *sanguineus* are regarded as the two arms of A2, B1 and B2. The 4 "new" chromosomes of *pulverulentus* are placed as B1 and B2, the two types remaining after all other chromosomes are distributed. The total lengths of these *pulverulentus* chromosomes, however, are too long in comparison with the other chromosomes in their respective group. This distribution of the t chromosomes gives as good an agreement as possible on the basis of the centric fusion/fission hypothesis. As is clear from Fig. 37 and 38 reasonably good agreement is obtained in A2 and B1, whereas the short arm component in A1 (t8) is too short and the short arm components in B2 (t7 and t6) are too long in comparison with the average of the types concerned. The reason for the present arrangement is that t8 and t3 of *ichneumon* correspond well with the short and long arms of the A1 chromosomes of *sanguineus* and *pulverulentus*. However, these chromosomes are somewhat shorter than the other A1 chromosomes, and may alternatively be regarded as B2 chromosomes although in the following features they differ from typical B2 chromosomes: they are too long (relative lengths 6.4 and 6.3 as compared with 6.0) and their centromeric indices are too high (39 and 37 as compared with 34). On the other hand, they resemble the B2 chromosome of *Cynictis* (relative length 6.1, c.i. = 38). Experiments with the new staining techniques may reveal whether the present arrangement of the A1 and B2 chromosomes of *ichneumon*, *sanguineus* and *pulverulentus* is satisfactory.

The most striking feature of Table 17 and Fig. 37–41 is the good agreement in chromosome morphology in the majority of chromosome types. For instance, the chromosomes of type A3, the X (X_1) chromosome, varies in relative length between 4.9 and 5.2 (mean 5.01 ± 0.03) and the centromeric index varies between 42 and 45 (mean 43.7 ± 0.3). Chromosomes, deviating in a group, are as a rule those of the extreme species, that is *Herpestes ichneumon* and *Cynictis penicillata*; particularly the *Cynictis* chromosomes often deviate by a more median position of the centromere. Therefore, average values for relative lengths and centromeric indices are given in Table 17 both for all 12 species and for species 4–11, in the latter case excluding *H. ichneumon*, *H. sanguineus*, *H. pulverulentus* and *Cynictis*.

Of the A-type chromosomes only pair A6 shows comparatively large variation among the species and it may be significant that m3a and m3b of *Herpestes edwardsi* most likely belong to this type. The short arms of these chromosomes correspond relatively well with the long arms of the other chromosomes of this type and therefore the long arm of m3, which varies in length, is turned upwards here (Fig. 38) and in the karyotypes (Fig. 14 and 15).

There are chromosome pairs in all species which are difficult to distinguish from each other, e.g. A5 and B4, and B2 and B3. When these chromosomes were paired off, the centromeric index was used as the primary criterion. A5 has an average centromeric index of 41 and B4 of 37, their average length being the same (A5 is the longest in 2 species, B4 is the longest in 3 species and the two pairs are of equal length in 7 species). In the same manner, B2 has an average centromeric index of 34 and B3 of 31, their average length also being the same (B2 is the longest in 4 species, B3 is the longest in 3 species and in 2 species the two pairs are of equal length; B2 is substituted by other chromosomes in species 1–3 which are therefore excluded from this comparison). The risk of creating nonexistent morphologic differences is obvious when the pairing-off method is used for very similar chromosomes. If the length had been chosen as the primary criterion, perhaps no differences in centromeric indices would have occurred.

In all species the C1 chromosome is the longest one having a centromeric index of 22–27 in 11 species. In *Herpestes edwardsi* this marker chromosome has an altered morphology due to extra chromatin material in its short arm, and as discussed before two different types (a and b) of

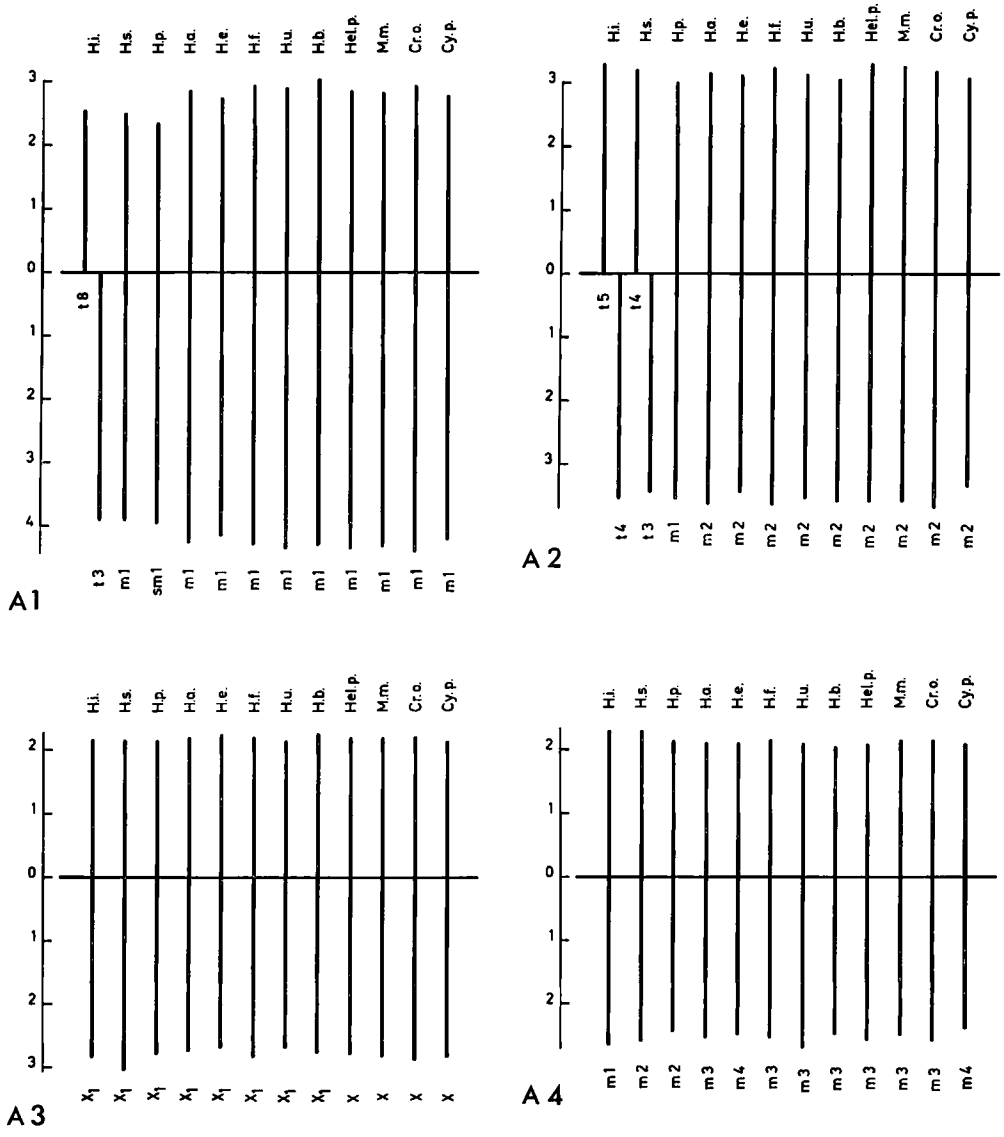


Fig. 37.

Fig. 37—41. Synopsis of the chromosomes through all 12 species; chromosomes which best correspond to each other in relative length and centromeric index are selected and coordinated into 19 basic chromosome types called A1—6, B1—6, C1–4 and D1—3 (cf. Table 17). Scale graduated into per cent of female haploid set, 0 being the location of the centromere. Above: abbreviated designations of the 12 species; below: chromosomal designations according to the m—sm—st—t nomenclature.

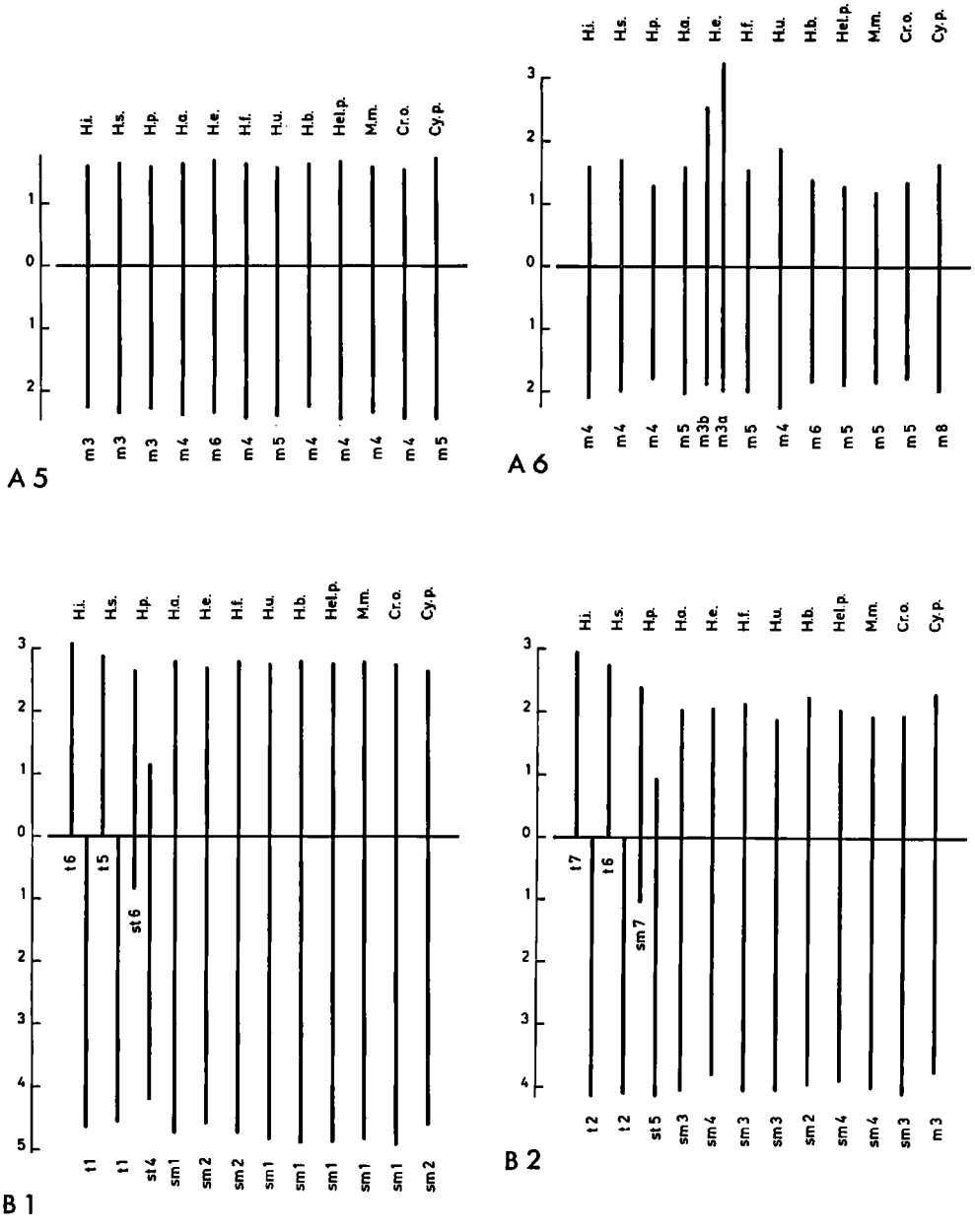

Hi.
Hs.
Hp.
Ha.
He.
Hf.
Hu.
Hb.
Hel.p.
M.m.
Cr.o.
Cy.p.
m3
m3
m3
m4
m6
m4
m5
m4
m4
m4
m4
m5
A5
m4
m4
m4
m5
m3b
m3a
m5
m4
m6
m5
m5
m5
m8
A6
t6
t5
st6
st4
sm1
sm2
sm2
sm1
sm1
sm1
sm1
sm1
sm2
B1
t7
t6
sm7
st5
sm3
sm4
sm3
sm3
sm2
sm4
sm4
sm3
m3
B2

Fig. 38.

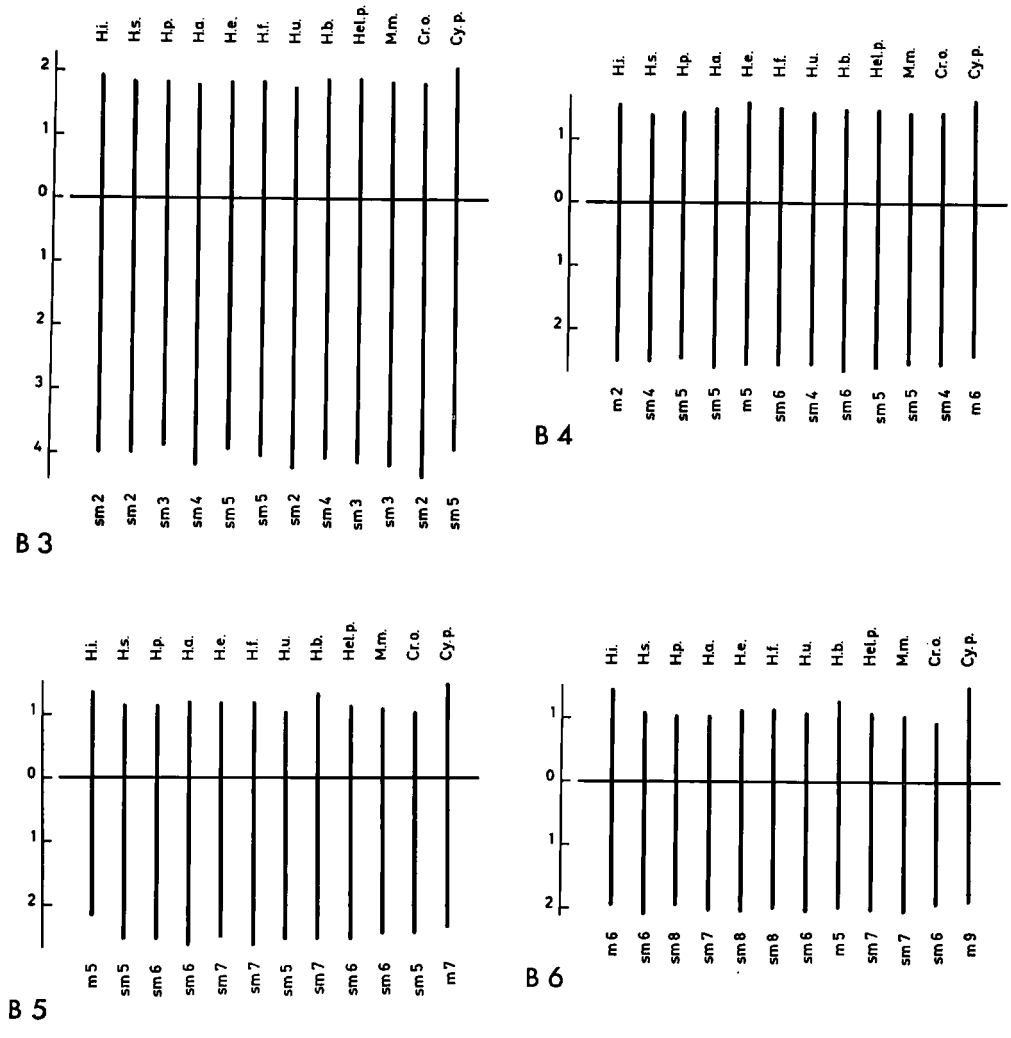


Fig. 39.

this chromosome were present among the four specimens studied. C2 and C3 might be difficult to distinguish from each other. However, C2 is always longer than C3 and has a somewhat higher centromeric index; the length of the short arm is the best criterion for identification.

The D type chromosomes are interesting and will be dealt with in more detail. Some of the species may be arranged into the following groups:

The *ichneumon* group: *Herpestes ichneumon*, *H. sanguineus* and *H. pulverulentus*.

The *edwardsi* group: *Herpestes auropunctatus*, *H. edwardsi*, and *H. fuscus*.

The *mungo* group: *Helogale parvula*, *Mungos mungo* and *Crossarchus obscurus*.

The original Y chromosome is translocated on to an autosome in all *Herpestes* species.

There seem to be some features common to each group (Fig. 41). The short arms of D1 are longer in the *ichneumon* group and in *Cynictis* than in the other species, which, with the exception of *Herpestes brachyurus*, have short arms of similar length. Concerning the long arm of D1

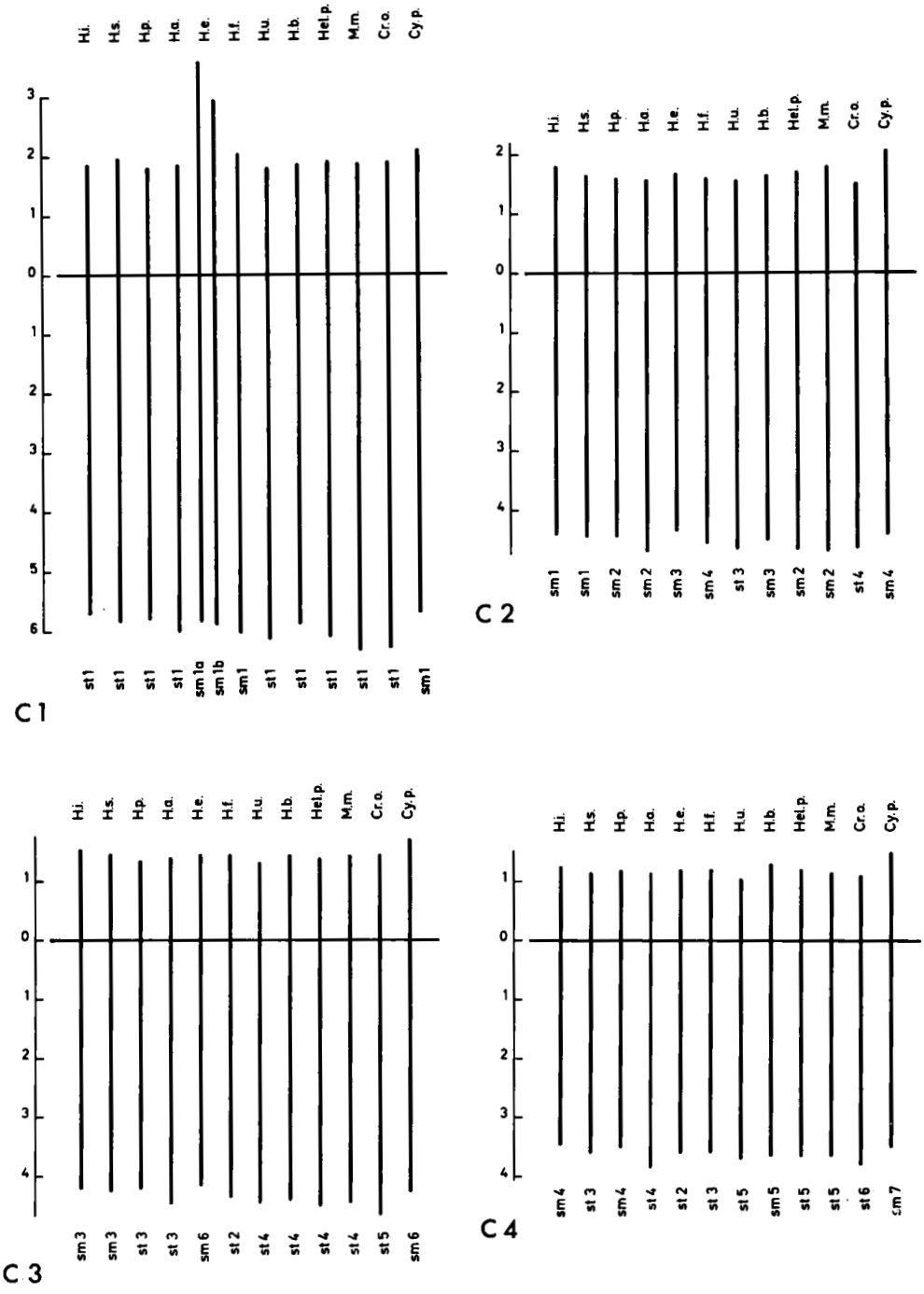
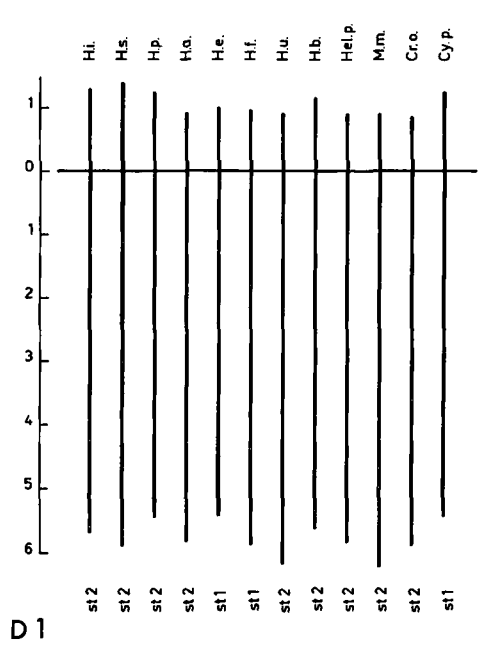
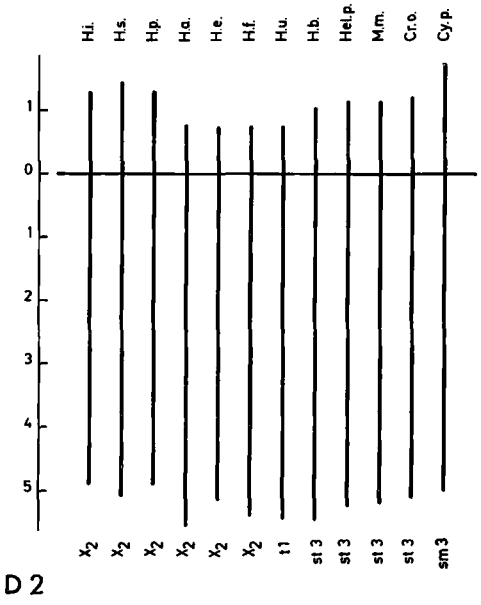

Hi.
Hs.
Hp.
Ha.
He.
Hf.
Hu.
Hb.
Hel.p.
M.m.
Cr.a.
Cy.p.
3
2
1
0
1
2
3
4
5
6
st1
st1
st1
st1
sm1a
sm1b
sm1
st1
st1
st1
st1
st1
sm1
C1
Hi.
Hs.
Hp.
Ha.
He.
Hf.
Hu.
Hb.
Hel.p.
M.m.
Cr.a.
Cy.p.
2
1
0
1
2
3
4
sm1
sm1
sm2
sm2
sm3
sm4
st3
sm3
sm2
sm2
st4
sm4
C2
Hi.
Hs.
Hp.
Ha.
He.
Hf.
Hu.
Hb.
Hel.p.
M.m.
Cr.a.
Cy.p.
1
0
1
2
3
4
sm3
sm3
st3
st3
sm6
st2
st4
st4
st4
st4
st5
sm6
C3
Hi.
Hs.
Hp.
Ha.
He.
Hf.
Hu.
Hb.
Hel.p.
M.m.
Cr.a.
Cy.p.
1
0
1
2
3
4
sm4
st3
sm4
st4
st2
st3
st5
sm5
st5
st5
st6
sm7
C4

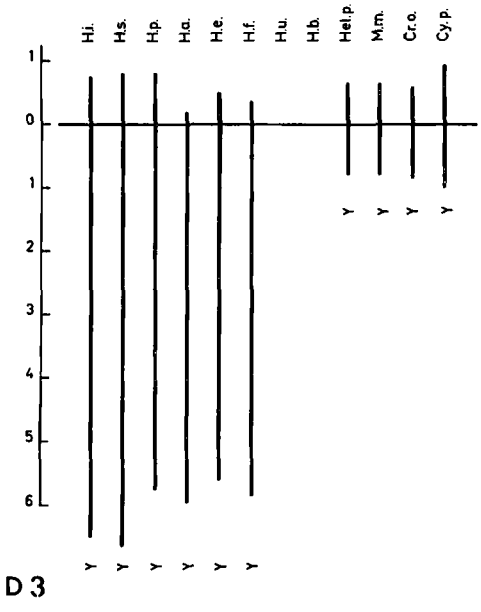
Fig. 40.



D 1



D 2



D 3

Fig. 41.

there is no definite tendency. The length of the short arms of D2 fall into three groups, one formed by the *ichneumon* group and *Cynictis*, one by the *edwardsi* group and one by the *mungo* group. *Herpestes urva* is included in the same group as *edwardsi*, *H. brachyurus* in the same as *mungo*. The lengths of the long arms do not show any clear-cut grouping, although the long arms of the *ichneumon* group and of *Cynictis* are the shortest. In the *ichneumon* group the short arms of D1 and D2 are of equal length, in the *edwardsi* group and in *urva* and *brachyurus* the short arms of D1 are longer than D2 and in the *mungo* group and *Cynictis* the short arms of D2 are longer than D1. Even though the Y chromosomes vary in size and appearance within the species of the *ichneumon* group, some general tendencies become evident from the analysis of type D3. The short arms of the *ichneumon* group are longer than those of the *edwardsi* group and correspond in size with one arm of the Y chromosomes of the *mungo* group. No male was available from *H. urva*, and in the only male of *H. brachyurus* studied no Y chromosome was distinguished among the D chromosomes, indicating that the Y of this species must have a relatively large short arm comparable in size to those of the Y chromosomes of the *ichneumon* group. The Y chromosomes of *H. ichneumon* and *H. sanguineus* have longer long arms than those of the *edwardsi* group, and in this respect *H. pulverulentus* agrees with the *edwardsi* group.

Discussion

1. Chromosomes of other mongoose species

Until now chromosome studies have been performed on 17 species of mongooses, and these are listed in Table 18. Five of these species were not investigated by the present author and their karyotypes will be commented on below:

A. Javan mongoose, *Herpestes javanicus* (Geoffroy) (1812)

There is some uncertainty whether the chromosomes of this species have been studied or not and this is mainly due to the diversity of taxonomical opinions. Some authors regard *javanicus* as synonymous with *auropunctatus* (Pocock 1941; Todd and Pressman 1966), while others follow Chasen (1940) who states "two species of this group, distinguished chiefly by size, occur in the Malay Peninsula: only one can be the local representative of *javanicus* and it appears to be the larger form. *H. auropunctatus* is the earliest name for the other association". The present author, like Ellerman and Morrison-Scott (1951), Morris (1965) and Hinton and Dunn (1967), prefers to regard *javanicus* and *auropunctatus* as separate species.

Todd and Pressman (1966) reported 2n = 35/36 in *H. javanicus*, but there seems to be no doubt that the two specimens studied belonged to the species *H. auropunctatus*, as understood here. This conclusion is supported by the fact that the specimens in question came from Gujarat in north-west India (Todd pers. comm. 1967), an area outside the distribution range of *H. javanicus*.

Benirschke (pers. comm. 1969), studying the chromosomes of two males of *H. javanicus*, found 35 chromosomes in both. His specimens came from South Vietnam, which is within the distribution range of *javanicus* but outside the range of *auropunctatus* (Hinton and Dunn 1967). It thus seems likely that the specimens studied by Benirschke were *H. javanicus*, but to cite his letter "we are not sure whether these are, as some believe, the same as *H. auropunctatus*".

B. Water mongoose, *Atilax paludinosus* (G. Cuvier) (1829)

Five individuals have been studied; one male and one female by Hsu (pers. comm. 1966), one female by Todd and Pressman (1967) and one male and one female by Wurster and Benirschke (1968). The findings are in good agreement, 2n = 35 male, 36 female. A beautiful male karyotype showing a characteristic mongoose karyotype was published by Wurster and Benirschke (1968, p. 351). The four D chromosomes (bottom row, left) are of special interest and are in my opinion, from left to right, Y, st2, st2, and X_2 (with the nomenclature used in the present study). If this interpretation is correct it means that these chromosomes of *Atilax* are most similar to those of the *ichneumon* group, viz. a large Y chromosome with a small but distinct short arm and an X_2 chromosome with a comparatively large short arm. Good support for this opinion comes from the female karyo-

Table 18. Survey of chromosomally investigated mongooses (1972)
Table 3 in FREDGA 1970 revised and brought up to date

Species	Number of specimens studied		Chromosome number		References
	Male	Female	Male	Female	
Herpestes ichneumon	2	1	43	44	7, 8
sanguineus	2	—	41	(42)*	7, 8
pulverulentus	1	1	39	40	8
javanicus (?)	2	—	35	(36)*	1
auropunctatus	18 +	9 +	35	36	2, 3, 8, 14—17
edwardsi	5	3	35	36	8, 16
fuscus	1	1	35	36	7, 8
urva	—	2	?	36	7, 8
brachyurus	1	1	35	36	7, 8
Atilax paludinosus	2	3	35	36	10, 12, 18, 20
Helogale parvula	1	1	36	36	7, 8
Mungos mungo	7	6	36	36	7, 8, 20
Crossarchus obscurus	1	—	36	(36)*	7, 8
Ichneumia albicauda	1	—	36	(36)*	20
Bdeogale nigripes	1	1	36	36	13, 20
Cynictis penicillata	3	2	36	36	7, 8, 9, 19
Suricata suricatta	2	2	36	36	11, 17, 20

* No females were studied

1. BENIRSCHKE (1969 pers. comm.)
2. BHATNAGAR (1969 pers. comm.)
3. FREDGA (1965)
4. FREDGA (1967a)
5. FREDGA (1967b)
6. FREDGA (1968)
7. FREDGA (1970)
8. FREDGA (present paper)
9. GERNEKE (1967)
10. HSU (1966 pers. comm.)
11. HSU and BENIRSCHKE (1967)
12. HSU and BENIRSCHKE (1969)
13. HSU and BENIRSCHKE (1971)
14. MANNA and TALUKDAR (1965)
15. RAY-CHAUDHURI et al. (1966)
16. RAY-CHAUDHURI et al. (1968)
17. TODD and PRESSMAN (1966)
18. TODD and PRESSMAN (1967)
19. TODD et al. (1967)
20. WURSTER and BENIRSCHKE (1968)

type published by HSU and BENIRSCHKE (1969). As would be expected from the chromosome number, however, the other chromosomes show greater similarities with those of other *Herpestes* species having 35/36 chromosomes.

C. White-tailed mongoose, *Ichneumia albicauda* (G. CUVIER) (1829)

One male was studied by WURSTER and BENIRSCHKE (1968) who found 2n = 36, and judging from the figure published, the karyotype of this species is indistinguishable from those of *Helogale*, *Mungos* and *Crossarchus*. Apparently, the Y chromosome of *Ichneumia* is as small as in these three species; the centromeric index, however, appears to be lower than in *Helogale* and *Mungos*.

D. Black-footed mongoose, *Bdeogale nigripes* PUCHERAN (1855)

One male and one female were studied by WURSTER and BENIRSCHKE (1968) who found 2n = 36, and although the matching of some chromosomes in the published karyotype appears incorrect, it is clear that the karyotype of *Bdeogale* very much resembles those of *Helogale*, *Mungos*, *Crossarchus* and *Ichneumia*, with one interesting exception however: The Y chromosome, although the smallest chromosomes of the complement, is larger than the Y of the four other species and seems to be comparable in size to that of *Cynictis*. Recently, karyotypes of one male and one female of *Bdeogale nigripes* were published in the Atlas of Mammalian Chromosomes (HSU and BENIRSCHKE 1971), and al-

though the arrangement of the individual chromosomes differs from that earlier published (WURSTER and BENIRSCHKE 1968), there are still most likely some errors; thus, the chromosome selected as X is certainly not the X.

E. Meerkat, *Suricata suricatta* (SCHREBER) (1776)

Four individuals have been studied, one male and one female by TODD and PRESSMAN (1966) and one male and one female by WURSTER and BENIRSCHKE (1968; karyotype in HSU and BENIRSCHKE 1967), 2n = 36. The karyotype, as judged from the published figures, seems to correspond well with the karyotypes of *Helogale*, *Mungos*, *Crossarchus* and *Ichneumia*, and the size of the Y is in better agreement with Y of these species than with that of *Bdeogale* and *Cynictis*. The location of the centromere is obscure on the karyotypes published, but according to HSU and BENIRSCHKE (1967) the Y is telocentric. It is worthy of mention that the karyotype of *Suricata* does not particularly resemble that of *Cynictis*.

2. Karyotype evolution in Herpestinae

The question as to the role of chromosomal rearrangements in animal speciation is a controversial one. Some authors (e.g., MAYR 1963, 1970) relegate structural rearrangements to a minor role, while others (e.g., WHITE 1968, 1969) regard structural rearrangements as an important factor in speciation under certain circumstances. Recently ÁRNASON (1972) discussed the role of chromosomal rearrangements in mammalian speciation and concluded that in some orders, such as Cetacea and Pinnipedia, this role is insignificant whereas in other orders, such as Insectivora and Rodentia, it is highly important. Ecological and reproductive factors were considered to be responsible for these discrepancies between the different orders.

The great majority of chromosomal rearrangements (inversions and translocations) result from two chromosome breaks, followed by reunion of the broken ends in a way different from the original one. One specific type of chromosomal rearrangement prevalent in karyotype evolution in animals is by Robertsonian changes. The mechanisms by which a metacentric chromosome splits into two telocentrics and two telocentrics (or "acrocentrics") join to form a metacentric are controversial (HSU and MEAD 1969; WHITE 1969; JOHN and HEWITT 1966, 1968), and will not be discussed in detail here. The present author favours the idea that true telocentric chromosomes (viz. without a second short arm) do exist in nature both in plants and in animals, and that a metacentric chromosome can give rise to two telocentric chromosomes with functional centromeres in spite of the fact that these centromeres are only half as complex as the original bipartite one. Similarly, two telocentric chromosomes may fuse and form one metacentric, and consequently it is adequate to speak about centric fission and fusion in such cases. "Fusion" may also occur between chromosomes with a small but distinct short arm (e.g. the human D and G group chromosomes) giving rise to a large metacentric and a small centric fragment, which usually is lost. In such cases it is impossible to decide whether the points of breakage are in the centromeres or in the proximal ends of the chromosome arms. Strong evidence exists for both possibilities occurring in mammals. Concerning centric fusions and fissions (sensu stricto) it is usually difficult or impossible to tell in what direction chromosome evolution has taken place, and this is also true for the Herpestinae. Centric fusions, however, seem to be commoner among mammals than centric fissions and, as a matter of fact, only one convincing example of centric fission "in vivo" has been described (FREDGA and BERGSTRÖM 1970).

In the present descriptions of the karyotypes as well as in Table 18, the genera are listed in order from the relatively primitive to the relatively specialized as far as this can be done in a linear series (HINTON and DUNN 1967). Within the genus *Herpestes* the species are ordered as in MORRIS (1965). The present study shows that this order corresponds to a reduction in chromosome number within the genus *Herpestes: H. ichneumon* has 2n = 43/44, *H. sanguineus* 2n = 41/42, *H. pulverulentus* 2n = 39/40 and all the other species have 2n = 35/36. The genera *Herpestes* and *Atilax* are the only ones having the deviating sex-chromosome mechanism, all other genera have an ordinary sex-chromosome mechanism and 36 chromosomes in both sexes.

Two alternatives of chromosome evolution in Herpestinae will be discussed (Fig. 42). In alternative 1 we start with a karyotype similar to that of *Cynictis*, viz. 17 pairs of atelocentric auto-

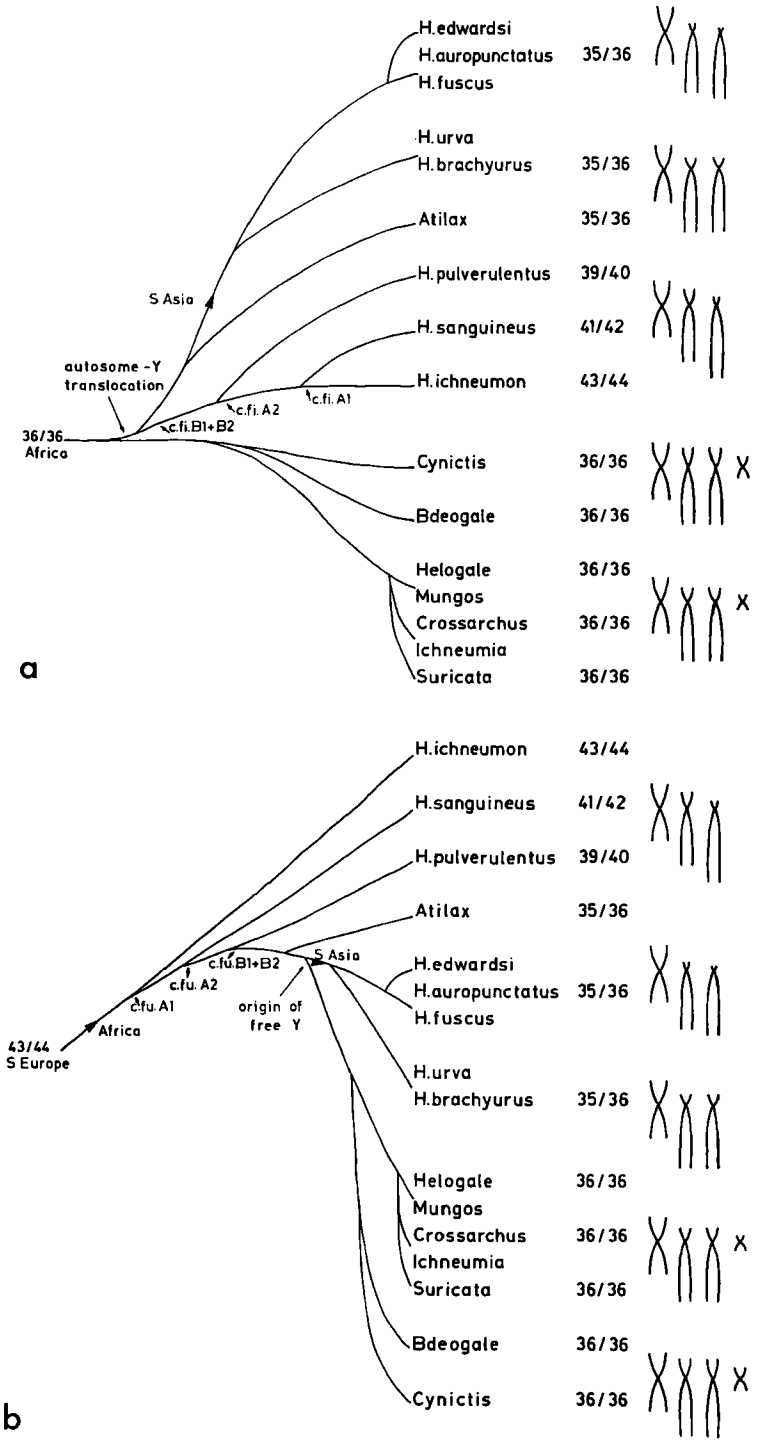


Fig. 42. Phylograms of the Herpestinae constructed on the basis of chromosomal evolution; a: alternative 1, b: alternative 2. Chromosome numbers in male/female are indicated as well as diagrams of the chromosomes, characteristic of the different groups of species. The chromosomes are from left to right: X_1, X_2, "neo-Y", or X, D2, D2, and Y. c.fi. = centric fission, c.fu. = centric fusion.

somes, one X of original type (OHNO et al. 1964) and one comparatively large Y. Translocation between an autosome (D2) and the Y divides the stock into two main branches, one with the genera *Herpestes* and *Atilax*, and one with the remaining genera. Of the present genus *Herpestes*, one branch developed in Asia and the other in Africa. The African *Herpestes* species are characterized by a comparatively large short arm of the neo-Y and of X_2 and it is reasonable from a chromosomal point of view to regard *Atilax* as an early offshoot of this branch. After *Atilax* had branched off, centric fission occurred in two large autosome pairs, B1 and B2 (or, alternatively A1). The karyotype of *H. pulverulentus* was obtained by pericentric inversions of these fission products. The karyotype of *H. sanguineus* was obtained by another centric fission, of A2, and by still another centric fission, of A1 (or alternatively B2), the present karyotype of *H. ichneumon* originated.

Of the Asian species of *Herpestes*, all have 35/36 chromosomes and the *edwardsi* group is characterized by a reduction in size of the neo-Y chromosome, particularly striking in the short arm. The size of the short arm of X_2 is also reduced. The karyotype of *H. edwardsi* is outstanding among all mongooses by the presence of additional chromatin on two autosome pairs, A6 and C1. The evolutionary significance of this heterochromatin is obscure, but it seems reasonable to regard it as a secondary phenomenon.

Looking at the other main branch, the only notable change in chromosome morphology from the "primitive" karyotype is a reduction in size of the Y in the genera *Helogale*, *Mungos*, *Crossarchus*, *Ichneumia* and *Suricata*, and also a slight change in chromosome morphology, viz. that the location of the centromere became less median in many chromosomes. A similar tendency is also evident in the *Herpestes* branch.

In the present dendrogram (alternative 1) the different species are arranged in good agreement with their present karyotypes, but the position of the genera within the dendrogram does not show ideal correlation with morphological specialization in general. The least specialized species show the greatest chromosomal rearrangements, but since there is no general rule about chromosome number and morphology, on the one hand, and specialization, on the other, this does not invalidate alternative 1. Thus, EGOZCUE (1969) concludes in relation to karyotypic evolution in primates "that the 'primitiveness' of a species has no correlation with the morphology of its chromosomes, and it is evident that species regarded as primitive have undergone more chromosomal rearrangements than other more specialized forms. In summary, there is no reason to support the contention that a high diploid number and a predominance of acrocentric chromosomes represent a primitive feature".

One fact speaking in favour of this alternative is that we start with a stock having "normal" mammalian sex chromosomes, and assuming that the X and Y were originally a homologous pair of ordinary chromosomes (OHNO 1967), it seems reasonable to start out with an X and a Y of similar size, and regard the reduction in size of the Y as an evolutionary trend. Another fact speaking in favour of this alternative is that the only species within the Herpestinae which has a satellited chromosome resembling the "carnivore chromosome", viz. a small sm chromosome with satellites on the short arms, is *Cynictis* (chromosome m6, Fig. 33).

In alternative 2 we start with a karyotype similar to that of *H. ichneumon*, viz. 8 pairs of telocentric and 13 pairs of atelocentric autosomes (including X_2) and one X (X_1) of original type and a translocated Y. Thus, we postulate that the unique autosome-Y translocation is of an ancient origin and that the present karyotype of *H. ichneumon* is primitive. By successive centric fusions of the telocentric elements the present karyotypes of *H. sanguineus*, *H. pulverulentus* and the "standard" 36-chromosome karyotype of the Herpestinae originated. In the case of *H. pulverulentus*, pericentric inversions and perhaps other chromosomal rearrangements occurred in 4 telocentric pairs. *Atilax* branched off before some species, all with 35/36 chromosomes, developed further in Asia, of which the *edwardsi* group is characterized by a reduction in size of the Y (see above). The critical point in this dendrogram is the origin of a small individual Y chromosome from the A-Y chromosome of *Herpestes* by some kind of dissociation. During further processes of speciation the very small Y chromosome increased in size and obtained the present size of the Y in *Cynictis* and *Bdeogale*. Within the *mungo* group a shift in centromeric location in the small Y took place, from an m

chromosome in *Helogale* and *Mungos* to a t chromosome in *Suricata*.

In the present dendrogram (alternative 2) we start with the most primitive genus and end with the most specialized genus within the tribe Herpestini (*Suricata suricatta* belongs to the tribe Suricatini, see below, p. 64). It may be logical to start with *Herpestes* because this genus has been in existence for about 30 million years or longer than any other recent genus in the order Carnivora. *Herpestes lemanensis* POMEL is known from the Upper Oligocene of France and other species of *Herpestes* are known from the Miocene of Spain. Species of *Mungos*, *Crossarchus* and *Cynictis* have been described from the Pleistocene of Africa (HINTON and DUNN 1967). It may be reasonable to conclude that the Herpestinae originated in southern Europe and spread into southern Asia and into Africa, where now all recent species but the 8 Oriental ones occur. Only one species, *Herpestes ichneumon*, still remains in southern Europe. The present chromosome study includes species inhabiting the extreme ranges of distribution of the genus *Herpestes*, viz. *H. pulverulentus* in South Africa, *H. ichneumon* in southern Europe and *H. brachyurus* in the Malay Peninsula, Sumatra, Java and Borneo. The widespread distribution of *Herpestes* indicates an ancient origin of the autosome-Y translocation, and in this connection it may be relevant to quote WHITE (1969, p. 95): "It is logical to assume that the translocation which led to the establishment of an X_1X_2Y sex chromosome mechanism in at least 16 genera of Mantids was a single event which occurred in the common ancestor of these genera (with a total of perhaps 500 species) as long ago as the Miocene or Oligocene."

The true X chromosome of the 12 species of mongooses studied in detail comprises 5 per cent of the female haploid genome and is thus of the original-type X (OHNO et al. 1964). This kind of metacentric X chromosome must be of an ancient origin, because it is present in all Carnivora thus far studied, with the single exception of the raccoon dog (*Nyctereutes procyonides*) which has an acrocentric X (WURSTER 1969).

3. Taxonomic remarks

The order Carnivora is usually subdivided into two superfamilies, Canoidea with the four families Canidae, Ursidae, Procyonidae and Mustelidae, and Feloidea with the three families Viverridae, Hyaenidae and Felidae (SIMPSON 1945). Some of the classically recognized families (especially Viverridae, Procyonidae and Mustelidae) have more than average internal divergence and it has been proposed that they be split into a greater number of families. SIMPSON (1961), however, regards it as fairly certain that the classical families are "good" taxa, and thinks it more convenient to continue to rank them as families. ROMER (1966) divides the Carnivora into the same seven families. On the other hand, POCOCK (1916, 1919, 1941) and GREGORY and HELLMAN (1939) rank the mongooses as a family, Herpestidae, and THENIUS and HOFER (1960) and THENIUS (1969) divide the Viverridae of SIMPSON into Viverridae, Herpestidae and Cryptoproctidae.

The chromosomes, their number and morphology, are an important taxonomic parameter, because the karyotype does not respond to selective pressure in the same way as anatomical and physiological characteristics. Thus, chromosome analysis can solve at least some systematic problems. Comparative chromosome studies in the Carnivora were undertaken by WURSTER and BENIRSCHKE (1968), who paid special attention to the satellited marker chromosomes, which are often characteristic for each family. Every member of the family Viverridae with the exception of the Herpestinae bears well defined satellited marker chromosomes. WURSTER and BENIRSCHKE concluded that the lack of a marker chromosome and the uniformity of karyotype among the members thus far studied (8 species), provided karyological support for a separate family grouping of the Herpestinae. The present study deals with 17 species of mongooses, and it is not surprising that the chromosome situation now is somewhat more complicated. Three species have not 35/36 or 36/36 chromosomes, but still there is relatively good uniformity among the species. Only one species, *Cynictis penicillata*, had a satellited marker chromosome comparable with the "carnivore chromosome", but the secondary constriction (or satellite fibre) was not regularly present and usually not as distinct as in the cat (*Felis catus*), for instance. It seems likely that the majority of carnivores have only one but distinct nucleolar-organizing region, whereas the mongooses have 3–4 less

distinct regions. However, the evolutionary implications of this are obscure.

There is no doubt that the Viverridae is one of the most puzzling of all mammalian groups, and systematics of the genet and mongoose is still in its infancy (DORST and DANDELOT 1970). An example of our incomplete knowledge about mongooses is that *Liberiictis kuhni* is known only from eight skulls from forested areas in north-eastern Liberia, which were named and described in 1958 by HAYMAN. The external characters of this mongoose are still not known (WALKER 1964; DORST and DANDELOT 1970).

The number of living mongoose species varies according to the source consulted, there being a general tendency among modern taxonomists to reduce the number of previously described species. MORRIS (1964) lists 40 species, HINTON and DUNN (1967) list 36, with the reservation that a thorough revision of the genus *Helogale* will almost certainly result in a reduction in the number of species now recognized. HINTON and DUNN give 8, MORRIS 6 *Helogale* species, and this number was provisionally reduced to 2 by COETZEE (1967) and finally to 1, *Helogale parvula*, by DORST and DANDELOT (1970, advised by COETZEE?). HINTON and DUNN give *Herpestes ochracea* as a species, DORST and DANDELOT include it in *H. sanguineus*. In respect to other African species, there is full agreement between HINTON and DUNN, on the one hand, and DORST and DANDELOT, on the other, and this means that the number of valid species recognized today is 28, subdivided into the following 13 genera (number of species in parenthesis): *Herpestes* (12), *Atilax* (1), *Helogale* (1), *Mungos* (2), *Crossarchus* (3), *Liberiictis* (1), *Dologale* (1), *Ichneumia* (1), *Rhynchogale* (1), *Bdeogale* (2), *Paracynictis* (1), *Cynictis* (1), and *Suricata* (1). Of *Herpestes*, which is by far the largest genus, 8 species occur in the Oriental region and 4 in Africa. The Oriental species are usually divided into two subgenera, *Herpestes* (5) and *Urva* (3), and the African species are also divided into two subgenera, *Herpestes* (2, *H. ichneumon* and *H. naso*) and *Galerella* (2, *H. sanguineus* and *H. pulverulentus*).

All *Herpestes* species studied thus far have the deviating sex-chromosome mechanism, and all other Herpestinae species excepting *Atilax paludinosus* have an ordinary XY/XX sex-chromosome mechanism. Consequently, from a karyological point of view, *Atilax* should be included in *Herpestes* or, alternatively, the African *Herpestes* species should be split and ranked into one or several new genera. To solve this problem, it would be of the greatest value to investigate the chromosomes of *H. naso*, which like *H. ichneumon* is now included in the subgenus *Herpestes*, but was included in the genus *Atilax* by ALLEN (1939). It should also be valuable to examine the chromosomes of *H. sanguineus* from different areas. This species is represented by a large number of forms (HINTON and DUNN 1967 list not less than 41) distributed over most of Africa south of the Sahara, many of which have even recently been recorded as separate species (e.g. H. *ochracea*, *H. dentifer* and *H. granti*, MORRIS 1965). From a chromosomal point of view there is greater similarity between *H. sanguineus* and *H. ichneumon* than between *H. sanguineus* and *H. pulverulentus*.

The karyological similarities of *Suricata suricatta* and the *mungos* group are interesting. POCOCK (1919) considers it a tenable hypothesis that *Suricata* is a highly specialized offshoot of the *Mungos* + *Crossarchus* stock because there is one significant similarity in the skull (namely the situation of the *foramen rotundum* alongside the anterior orifice of the alisphenoid canal and close to the sphenoidal fissure), a character restricted to *Mungos*, *Crossarchus*, ?*Rhynchogale*, and *Suricata*. ROBERTS (1951) also points to the similarities between *Suricata* and *Mungos*: *Suricata* "is probably more closely related to *Mungos* than any other, indications remaining of the crossbands on the lower back, the claws being long, the tail short, tapering and not bushy, and the first premolar being absent above and below, while the animals are diurnal, gregarious and not of vicious temperament;". However, *Suricata suricatta* has always been admitted to hold an isolated position among the mongooses and is placed in a tribe of its own, Suricatini, mainly due to differences in the skull characters and in the structure of the ear. *Suricata*, like *Bdeogale* and *Paracynictis*, have only four toes on both front and hind feet; *Cynictis* has five toes on the front feet and four on the hind feet, but all other mongooses have five toes on both front and hind feet.

General conclusions

The species of mongooses may be divided into two main groups, those with a deviating sex chromosome mechanism ($X_1X_1X_2X_2/X_1X_2Y$ and those with a normal sex chromosome mechanism (XX/XY). Of the species studied so far, 9 belong to the first category and 7 to the second (of *Herpestes urva* only two females have been studied). The deviating sex-chromosome mechanism is characteristic of the genus *Herpestes*.

The mongooses show a relatively uniform karyotypic pattern with a predominant chromosome number of 36. Three species, *Herpestes ichneumon*, *sanguineus* and *pulverulentus* deviate with the chromosome numbers, 43/44, 41/42 and 39/40, respectively; the remaining *Herpestes* species have 2n = 35/36. *Herpestes auropunctatus* and *fuscus* have identical karyotypes. The karyotype of *H. edwardsi* is remarkable because two pairs of chromosomes show dimorphism, both types of each pair being larger than corresponding pairs in all other species. One of these pairs (C1) is the largest chromosome, and its comparatively high centromeric index makes the karyotype of *edwardsi* immediately distinguishable. The karyotypes of *H. urva* and *brachyurus* show only minor differences from each other and from the karyotype of *auropunctatus*; the D group chromosomes of *brachyurus* have comparatively large short arms and this was the only species in which the neo-Y chromosome could not be identified. The karyotypes of *Helogale parvula*, *Mungos mungo* and *Crossarchus obscurus* are practically indistinguishable: they all have 36 chromosomes in males and females and the Y is a very small m chromosome. The karyotype of *Cynictis penicillata* is striking with its large number of m and sm chromosomes and only one st chromosome; a small change in the centromeric position of certain chromosomes accounts, however, for this. The Y chromosome of *Cynictis* is larger than that of *Helogale*, *Mungos* and *Crossarchus*. The morphology of the D group chromosomes (Fig. 41) shows small but characteristic differences between groups of species. Thus, the African *Herpestes* species differ from the Asian ones by having longer short arms on the D1, X_2 and neo-Y chromosomes. The three species of *Helogale*, *Mungos* and *Crossarchus* also form a homogeneous group in regard to the morphology of the D group chromosomes. The true X chromosome, which apparently is identical through all the species, constitutes 5 per cent of the female haploid set and is thus of the original type.

Up to now the chromosomes have been studied in altogether 17 of the 28 species of living mongooses permitting some conclusions to be drawn in relation to karyotype evolution. Although centric fusion/fission events have been demonstrated in the autosomes, as well as pericentric inversions, it is difficult to visualize the direction taken by the centric fusion/fission changes, whether from telocentric towards metacentric chromosomes or the opposite. Provided that the autosome-Y translocation occurred only once during evolution, it must be of ancient origin, since the genus *Herpestes* is represented in southern Europe, all over Africa and in the Oriental region as far away as Sumatra, Java and Borneo. This conclusion is also supported by the fact that the genus *Herpestes* has been in existence for about 30 million years, or longer than any recent genus in the order Carnivora (HINTON and DUNN 1967).

In the mongooses, up to 4 pairs of chromosomes have vague satellites on their short arms and these chromosomes often take part in associations, probably in connection with nucleolar formation. Carnivores in general have only one pair of chromosomes with satellites, but these are usually distinct (e.g. Felidae, Hyaenidae and Viverridae except Herpestinae), or one pair with a prominent secondary constriction in the long arm close to the centromere (e.g. Mustelidae). Most cytogenetic data, including the deviating sex-chromosome mechanism in *Herpestes* and the relative uniformity of the karyotypes within the Herpestinae, support the opinion of elevating this subfamily to the rank of the family Herpestidae.

From the karyological point of view there is no reason to separate *Suricata suricatta* into a special tribe of the Herpestinae.

Atilax paludinosus is the only species of its genus and has the deviating sex-chromosome mechanism characteristic of the genus *Herpestes*. Since this species resembles *Herpestes* also in morphologic respects it seems sensible to include it in *Herpestes*.

For the eventual revision of the taxonomy of this insufficiently known group of mammals it will be necessary to consider the karyological parameter as well as the morphological, ana-

tomical, paleontological, biochemical and ethological parameters. Since the chromosomes are the vehicle of the genetic constitution, which in its turn is the material for the evolution, the karyologic aspects are of paramount interest for the understanding of these problems.

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Literature cited

ALLEN, G. M. 1939. A checklist of African mammals. — *Bull. Mus. Comp. Zool. Harvard 83*, 763 p.

ÁRNASON, U. 1969. The karyotype of the fin whale. — *Hereditas 62*: 273—284.

—— 1972. The role of chromosomal rearrangement in mammalian speciation with special reference to Cetacea and Pinnipedia. — *Ibid. 70*: 113—118.

ATKIN, N. B., MATTINSON, G., BEÇAK, W. and OHNO, S. 1965. The comparative DNA content of 19 species of placental mammals, reptiles, and birds. — *Chromosoma 17*: 1—10.

BENDER, M. A. and KASTENBAUM, M. A. 1969. Statistical analysis of the normal human karyotype. — *Am. J. Hum. Genet. 21*: 322—351.

CHASEN, F. N. 1940. A handlist of Malaysian mammals. — *Bull. Raffles Museum, Singapore, 15*, 209 p.

COETZEE, C. G. 1967. Carnivora (excluding the family Felidae). — *In Preliminary identification manual for African mammals 7 (Ed. J. MEESTER) Smithsonian Institution, United States National Museum, Washington.*

COHEN, M. M. and CHANDRA, H. S. 1970. The somatic chromosomes of the small Indian mongoose: autoradiographic analysis of an unbalanced translocation heterozygote. — *Cytogenetics 9*: 173—185.

CONGER, A. D. and FAIRCHILD, L. M. 1953. A quick-freeze method for making smear slides permanent. — *Stain Technol. 28*: 281—283.

DORST, J. and DANDELOT, P. 1970. A field guide to the larger mammals of Africa. — *Collins, London*, 287 p.

EGOZCUE, J. 1969. Primates. — *In Comparative mammalian cytogenetics (Ed. K. BENIRSCHKE) Springer-Verlag, Berlin, Heidelberg, New York*, p. 357—389.

ELLERMAN, J. R. and MORRISON-SCOTT, T. C. S. 1951. Checklist of Palaearctic and Indian mammals 1758 to 1946. — *London*, 810 p.

FREDGA, K. 1965. A new sex determining mechanism in a mammal. Chromosomes of Indian mongoose (*Herpestes auropunctatus*). — *Hereditas 52*: 411—420.

—— 1967a. Chromosome studies in six different tissues of a male Small Indian mongoose (*Herpestes auropunctatus*). — *Ibid. 57*: 421—431.

—— 1967b. Chromosome studies in six different tissues of a male Indian mongoose (*Herpestes auropunctatus*), and comments on the nomenclature of the species. — *Mammal. Chromos. Newslett. 8*: 19—21.

—— 1968. Könsbestämningsmekanismen hos mungos. — *Forskning och Framsteg* No. *5*: 5—8.

—— 1970. Unusual sex chromosome inheritance in mammals. — *Phil. Trans. Roy. Soc. Lond. Ser. B. 259*: 15—36.

FREDGA, K. and BERGSTRÖM, U. 1970. Chromosome polymorphism in the root vole (*Microtus oeconomus*). — *Hereditas 66*: 145—152.

GERNEKE, W. H. 1967. Cytogenetic investigations on normal and malformed animals, with special reference to intersexes. — *Onderstepoort J. Vet. Res. 34*: 219—299.

GREGORY, W. K. and HELLMAN, M. 1939. On the evolution and major classification on the Civets (Viverridae) and allied fossil and recent Carnivora: A phylogenetic study of the skull and dentition. — *Proc. Am. Phil. Soc. 81*: 309—392.

HAYMAN, R. W. 1958. A new genus and species of West African mongoose. — *Ann. Mag. Nat. Hist. 13*: 448—452.

HINTON, H. E. and DUNN, A. M. S. 1967. Mongooses. Their natural history and behaviour. — *Oliver and Boyd, Edinburgh, London*, 144 p.

HSU, T. C. and BENIRSCHKE, K. 1967. Folio 30. — *In An atlas of mammalian chromosomes. Vol. 1. Springer-Verlag, Berlin, Heidelberg, New York.*

— 1969. Folio 124. — *In An atlas of mammalian chromosomes. Vol. 3. Springer-Verlag, Berlin, Heidelberg, New York.*

— 1971. Folio 232. — *In An atlas of mammalian chromosomes. Vol. 5. Springer-Verlag, Berlin, Heidelberg, New York.*

HSU, T. C. and MEAD, R. A. 1969. Mechanisms of chromosomal changes in mammalian speciation. — *In Comparative mammalian cytogenetics (Ed. K. BENIRSCHKE) Springer-Verlag, Berlin, Heidelberg, New York.*

JOHN, B. and HEWITT, G. M. 1966. Karyotype stability and DNA variability in the Acrididae. — *Chromosoma 20*: 155—172.

— 1968. Patterns and pathways of chromosome evolution within the Orthoptera. — *Ibid. 25*: 40—74.

JORDAN, H. E. 1914. The spermatogenesis of the mongoose; and a further comparative study of mammalian spermatogenesis, with special reference to sex chromosomes. — *Carnegie Inst. Wash. Publ. 5*: 165—180.

LEVAN, A., FREDGA, K. and SANDBERG, A. A. 1964. Nomenclature for centromeric position on chromosomes. — *Hereditas 52*: 201—220.

MAKINO, S. 1951. An atlas of the chromosome numbers in animals. — *The Iowa State College Press, Ames, Iowa*, 290 p.

MANDEL, P., MÉTAIS, P. and CUNY, S. 1950. Les quantités d'acide désoxypentose-nucléique par leucocyte chez diverses espèces de mammifères. — *C. R. Acad. Sci. (Paris) 231*: 1172—1174.

MANNA, G. K. and TALUKDAR, M. 1965. Somatic chromosome number in twenty species of mammals from India. — *Mammal. Chromos. Newslett.* No. 17: 77—78.

MATTHEY, R. 1965. Un type nouveau de chromosomes sexuels multiples chez une souris africaine du groupe *Mus (Leggada) minutoides* (Mammalia-Rodentia). Male: X_1X_2/Y. Female: X_1X_2/X_1X_2. — *Chromosoma 16*: 351—364.

— 1967. Introduction to the fifth supplement of the list of chromosome numbers by eutherian mammalians. — *Mammal. Chromos. Newslett. 8*: 82—86.

MAYR, E. 1963. Animal species and evolution. — *The Belknap Press of Harward Univ. Press, Cambridge, Mass.*, 797 p.

— 1970. Population, species and evolution. — *Ibid.*, 453 p.

MORRIS, D. 1965. The mammals. A guide to the living species. — *Hodder and Stoughton, London*, 448 p.

OHNO, S. 1967. Sex chromosomes and sex-linked genes. — *Springer-Verlag, Berlin, Heidelberg, New York*, 192 p.

OHNO, S., BEÇAK, W. and BEÇAK, M. L. 1964. X-autosome ratio and the behavior pattern of individual X-chromosomes in placental mammals. — *Chromosoma 15*: 14—30.

PECCININI, D., FROTA-PESSOA, O. and FERRARI, I. 1971. Sex determination of the "pseudo-XO/XX" type in the Brazilian lizard *Polychrus sp.* (Sauria, Iguanidae). — *Caryologia 24*: 129—139.

POCOCK, R. I. 1916. On the external characters of the mongooses (Mungotidae). — *Proc. Zool. Soc. Lond.*, p. 349—374.

— 1919. Classification of the mongooses (Mungotidae). — *Ann. Mag. Nat. Hist. 3*: 515—524.

— 1941. Mammalia *2*: 1—61. — *In The fauna of British India, including Ceylon and Burma. Taylor and Francis, London.*

RAY-CHAUDHURI, S. P., RANJINI, P. V. and SHARMA, T. 1966. Somatic chromosomes of the common palm civet, *Paradoxurus hermaphroditus* (Viverridae-Carnivora). — *Experientia 22*: 740.

— 1968. Karyological studies of 16 species of Indian mammals. — *Mammal. Chromos. Newslett. 9*: 82—84.

ROBERTS, A. 1951. The mammals of South Africa. — *[Johannesb.]* 700 p.

ROMER, A. S. 1966. Vertebrate paleontology 3. ed. — *Univ. Chicago Press, Chicago, London* 468 p.

SASAKI, M. 1960. Observations on the modification in size and shape of chromosomes due to techniqual procedure. — *Chromosoma 11*: 514—522.

SCHWARZ, E. 1947. Colour mutants of the Malay short-tailed mongoose, *Herpestes brachyurus* GRAY. — *Proc. Zool. Soc. Lond. 117*: 79—80.

SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. — *Bull. Am. Mus. Natur. Hist. 85*, 350 p.

— 1961. Principles of animal taxonomy. — *Columbia Univ. Press, New York*, 247 p.

TALUKDAR, M. and MANNA, G. K. 1966. Caryotypes of five carnivoran species from India. — *Mammal. Chromos. Newslett.* No. 21: 151—153.

THENIUS, E. 1969. Stammesgeschichte der Säugetiere (einschliesslich der Hominiden). — *Handb. Zool. Band 8, Lfg. 47, 48. Walter de Gruyter and Co., Berlin*, 722 p.

THENIUS, E. and HOFER, H. 1960. Stammesgeschichte der Säugetiere. — *Springer-Verlag, Berlin, Göttingen, Heidelberg, 322* p.

TODD, N. B. and PRESSMAN, S. R. 1966. The karyotype of the lesser Indian mongoose (*Herpestes javanicus* GEOFFROY), the mierkat (*Suricatta suricatta* DESMAREST) and comments on the taxonomy and karyology of the Viverridae. — *Mammal. Chromos. Newslett.* No. 21: 154—155.

— 1967. The karyotype of the marsh mongoose (*Atilax paludinosus*) and remarks on the phylogeny of the mongooses (Herpestidae). — *Mammal. Chromos. Newslett. 8*: 21—22.

TODD, N. B., YORK, R. M. and COOPER, L. A. 1967. The karyotype of the bushy-tailed mierkat (*Cynictis sp.*). — *Carnivore Genet. Newslett. 2*: 31.

WALKER, E. P. 1964. Mammals of the world. II. — *Johns Hopkins Press, Baltimore*, 1500 p.

WHITE, M. J. D. 1968. Models of speciation. — *Science 159*: 1065—1070.

— 1969. Chromosomal rearrangements and speciation in animals. — *Ann. Rev. Genet. 3*: 75—98.

WURSTER, D. H. 1969. Cytogenetic and phylogenetic studies in Carnivora. — *In Comparative mammalian chromosomes (Ed. K. BENIRSCHKE) Berlin, Heidelberg, New York*, p. 310—329.

WURSTER, D. H. and BENIRSCHKE, K. 1968. Comparative cytogenetic studies in the order Carnivora. — *Chromosoma 24*: 336—382.

Appendix

Table 19. Chromosome measurements of 5 female and 5 male cells of *Herpestes ichneumon*

Chromosome	Absolute length				Relative length				Centromeric index			
	Female		Male		Female		Male		Female		Male	
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.
X_1	3.08	0.09	3.40	0.11	4.90	0.05	5.13	0.09	41.8	0.6	45.3	0.2
m1	3.05	0.10	3.33	0.10	4.86	0.06	5.01	0.07	46.9	0.4	45.9	0.6
m2	2.55	0.06	2.67	0.06	4.07	0.04	4.03	0.05	38.0	0.5	38.6	0.4
m3	2.41	0.06	2.56	0.07	3.85	0.06	3.86	0.06	40.6	0.6	41.4	0.3
m4	2.28	0.06	2.48	0.07	3.63	0.03	3.74	0.06	44.1	0.7	42.4	0.6
m5	2.16	0.03	2.32	0.06	3.46	0.08	3.50	0.07	37.5	0.8	38.4	0.6
m6	2.11	0.04	2.25	0.03	3.37	0.06	3.40	0.05	44.1	0.6	42.2	0.6
sm1	3.93	0.12	4.09	0.10	6.26	0.06	6.16	0.06	28.0	0.3	29.6	0.5
sm2	3.75	0.11	3.91	0.10	5.97	0.05	5.89	0.07	32.6	0.7	33.0	0.2
sm3	3.56	0.11	3.84	0.11	5.67	0.07	5.78	0.06	25.6	0.7	27.7	0.6
sm4	2.95	0.06	3.12	0.08	4.71	0.07	4.70	0.05	26.2	0.8	27.6	0.6
st1	4.79	0.17	4.96	0.12	7.62	0.10	7.48	0.06	23.5	0.4	25.4	0.4
st2	4.50	0.13	4.54	0.10	7.17	0.09	6.85	0.06	18.9	0.4	18.8	0.6
X_2	3.87	0.11	4.16	0.24	6.17	0.06	6.25	0.15	19.9	0.6	22.5	0.7
Y	—	—	4.80	0.21	—	—	7.23	0.12	—	—	10.4	0.4
t1	3.03	0.13	3.00	0.07	4.81	0.09	4.53	0.06	—	—	—	—
t2	2.60	0.09	2.76	0.08	4.14	0.05	4.16	0.05	—	—	—	—
t3	2.46	0.08	2.61	0.07	3.92	0.04	3.93	0.02	—	—	—	—
t4	2.27	0.07	2.33	0.07	3.62	0.03	3.51	0.06	—	—	—	—
t5	2.13	0.06	2.15	0.07	3.39	0.04	3.24	0.05	—	—	—	—
t6	1.94	0.05	2.09	0.06	3.09	0.04	3.15	0.02	—	—	—	—
t7	1.78	0.06	2.04	0.05	2.83	0.04	3.08	0.03	—	—	—	—
t8	1.56	0.05	1.74	0.05	2.49	0.02	2.62	0.05	—	—	—	—
A+X	62.76		66.35									

Table 20. Chromosome measurements of 5 cells from each of two males of *Herpestes sanguineus*

Chromosome	Absolute length				Relative length				Centromeric index			
	H.s. 1		H.s. 2		H.s. 1		H.s. 2		H.s. 1		H.s. 2	
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.
m1	4.22	0.15	4.31	0.04	6.53	0.13	6.31	0.07	39.5	0.5	38.3	0.5
X_1	3.30	0.08	3.60	0.07	5.12	0.05	5.27	0.09	41.2	0.4	42.2	0.9
m2	3.19	0.08	3.33	0.06	4.94	0.05	4.87	0.07	47.3	0.4	47.5	0.3
m3	2.51	0.05	2.79	0.06	3.90	0.06	4.08	0.04	40.2	0.6	41.3	0.7
m4	2.37	0.04	2.56	0.07	3.68	0.05	3.75	0.08	46.4	0.3	45.2	1.1
sm1	3.91	0.08	4.17	0.07	6.06	0.05	6.10	0.06	26.6	0.3	27.3	0.4
sm2	3.76	0.06	3.98	0.05	5.83	0.04	5.83	0.03	30.9	0.3	31.9	0.5
sm3	3.63	0.08	3.93	0.07	5.63	0.07	5.75	0.07	24.8	0.6	25.4	0.4
sm4	2.54	0.07	2.66	0.06	3.94	0.06	3.89	0.05	36.5	0.8	36.9	0.5
sm5	2.33	0.06	2.56	0.05	3.61	0.07	3.75	0.07	29.9	0.8	32.4	0.8
sm6	2.04	0.05	2.23	0.05	3.16	0.06	3.26	0.05	34.3	1.0	35.9	0.7
st1	5.04	0.12	5.35	0.09	7.81	0.09	7.83	0.08	24.4	0.3	25.6	0.5
st2	4.80	0.09	4.90	0.06	7.45	0.05	7.18	0.08	19.4	0.4	19.0	0.5
X_2	4.26	0.12	4.42	0.20	6.61	0.04	6.46	0.19	23.0	0.5	21.4	0.6
st3	3.07	0.06	3.23	0.06	4.76	0.05	4.73	0.05	24.3	0.9	24.1	0.6
Y	4.64	0.12	5.26	0.13	7.20	0.07	7.70	0.11	11.2	0.1	10.6	1.0
t1	2.94	0.06	3.13	0.06	4.56	0.06	4.58	0.05	—	—	—	—
t2	2.65	0.07	2.81	0.05	4.11	0.05	4.11	0.06	—	—	—	—
t3	2.20	0.05	2.36	0.03	3.41	0.04	3.45	0.03	—	—	—	—
t4	2.05	0.04	2.17	0.04	3.18	0.03	3.18	0.04	—	—	—	—
t5	1.89	0.03	1.97	0.04	2.93	0.04	2.88	0.04	—	—	—	—
t6	1.78	0.04	1.88	0.05	2.76	0.04	2.75	0.05	—	—	—	—
A + X	64.48		68.34									

Table 21. Chromosome measurements of 5 female and 5 male cells of *Herpestes pulverulentus*

Chromosome	Absolute length				Relative length				Centromeric index			
	Female		Male		Female		Male		Female		Male	
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e	Mean	S.e.	Mean	S.e.
m1	4.23	0.04	4.07	0.13	6.58	0.05	6.56	0.07	46.1	0.5	46.0	0.4
X_1	3.16	0.06	3.10	0.11	4.92	0.05	5.00	0.05	43.0	0.7	42.7	0.9
m2	2.96	0.05	2.85	0.06	4.61	0.08	4.60	0.04	46.6	0.4	47.0	0.6
m3	2.48	0.02	2.44	0.05	3.86	0.02	3.94	0.07	40.7	0.5	41.4	0.5
m4	1.98	0.03	1.94	0.04	3.08	0.04	3.14	0.07	42.9	0.5	40.7	0.7
sm1	4.04	0.06	3.90	0.12	6.29	0.05	6.29	0.10	37.1	0.5	37.7	0.4
sm2	3.94	0.05	3.72	0.12	6.13	0.03	5.99	0.06	26.4	0.5	27.3	0.5
sm3	3.67	0.04	3.58	0.10	5.71	0.04	5.77	0.07	32.2	0.4	32.4	0.5
sm4	3.06	0.05	2.87	0.08	4.76	0.04	4.63	0.05	25.8	0.5	25.9	0.8
sm5	2.47	0.02	2.45	0.05	3.85	0.05	3.96	0.06	37.7	0.6	36.8	0.6
sm6	2.42	0.04	2.27	0.07	3.77	0.04	3.66	0.04	31.0	0.8	31.0	0.6
sm7	2.23	0.03	2.12	0.05	3.47	0.04	3.42	0.05	28.7	0.8	32.2	0.5
sm8	1.97	0.03	1.83	0.02	3.07	0.05	2.96	0.07	34.5	0.6	35.0	1.0
st1	4.87	0.08	4.73	0.17	7.58	0.11	7.62	0.12	24.0	0.5	24.0	0.4
st2	4.28	0.06	4.17	0.11	6.66	0.07	6.73	0.08	16.8	0.4	19.7	0.7
X_2	4.01	0.08	3.80	0.11	6.24	0.08	6.14	0.05	21.0	0.5	20.6	0.8
st3	3.56	0.06	3.45	0.14	5.54	0.08	5.55	0.09	23.9	0.3	24.8	0.7
st4	3.37	0.06	3.39	0.10	5.25	0.09	5.47	0.08	21.7	0.7	21.1	0.8
st5	3.36	0.04	3.09	0.08	5.23	0.04	4.99	0.08	18.1	0.6	20.1	0.6
st6	2.19	0.04	2.23	0.07	3.41	0.06	3.59	0.04	22.8	0.6	25.2	0.6
Y	—	—	4.06	0.21	—	—	6.54	0.14	—	—	12.3	0.6
A + X	64.25		62.00									

Table 22. Chromosome measurements of 5 female and 5 male cells of *Herpestes auropunctatus*

Chromosome	Absolute length				Relative length				Centromeric index			
	Female		Male		Female		Male		Female		Male	
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.
m1	5.04	0.15	3.98	0.12	7.22	0.10	7.02	0.06	40.2	0.6	39.9	0.4
m2	4.78	0.11	3.82	0.13	6.86	0.06	6.73	0.10	46.0	0.5	47.0	0.4
X_1	3.43	0.07	2.86	0.13	4.92	0.05	5.04	0.03	44.8	0.5	44.7	0.6
m3	3.21	0.05	2.63	0.08	4.61	0.04	4.64	0.08	45.5	0.7	45.2	0.4
m4	2.85	0.08	2.29	0.08	4.09	0.07	4.03	0.07	40.3	0.4	41.1	1.0
m5	2.62	0.05	2.02	0.08	3.76	0.05	3.56	0.09	45.4	0.6	42.4	0.9
sm1	5.25	0.12	4.28	0.11	7.53	0.10	7.55	0.08	36.8	0.3	36.7	0.5
sm2	4.38	0.07	3.54	0.09	6.29	0.07	6.25	0.09	25.3	0.5	24.8	0.5
sm3	4.19	0.10	3.49	0.11	6.01	0.05	6.15	0.06	32.9	0.4	33.2	0.6
sm4	4.13	0.09	3.42	0.11	5.93	0.05	6.03	0.05	30.7	0.3	29.5	0.7
sm5	2.77	0.04	2.38	0.07	3.98	0.04	4.20	0.05	36.5	0.7	37.0	0.4
sm6	2.66	0.04	2.19	0.06	3.82	0.04	3.87	0.06	33.1	0.5	30.5	0.6
sm7	2.16	0.04	1.78	0.05	3.10	0.05	3.14	0.05	34.7	0.7	33.7	0.9
st1	5.53	0.15	4.48	0.12	7.93	0.09	7.91	0.10	24.2	0.4	22.4	0.4
st2	4.70	0.09	3.81	0.11	6.75	0.09	6.72	0.06	13.8	0.6	12.6	0.5
st3	4.10	0.07	3.31	0.10	5.89	0.07	5.84	0.07	24.1	0.5	23.3	0.6
st4	3.55	0.11	2.77	0.08	5.09	0.09	4.89	0.05	23.9	0.6	22.7	0.7
X_2	4.33	0.09	3.64	0.17	6.21	0.06	6.42	0.09	11.8	0.5	11.7	1.3
Y	—	—	3.48	0.14	—	—	6.15	0.14	—	—	2.9	0.1
A+X	69.68		56.69									

Table 23. Chromosome measurements of 5 female and 10 male cells of *Herpestes edwardsi*

Chromosome	Absolute length						Relative length						Centromeric index					
	Female		Male P_1		Male P_8		Female		Male P_1		Male P_8		Female		Male P_1		Male P_8	
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.
m1	4.38	0.14	3.88	0.16	3.94	0.06	7.07	0.11	6.78	0.08	6.80	0.07	40.7	0.6	39.7	0.3	41.1	0.5
m2	4.04	0.09	3.77	0.17	3.83	0.03	6.53	0.06	6.58	0.07	6.62	0.06	48.0	0.4	46.6	0.3	47.5	0.6
m3a	—	—	2.96	0.09	3.05	0.04	—	—	5.20	0.09	5.27	0.06	—	—	38.5	0.8	38.0	0.6
m3b	2.76	0.06	—	—	—	—	4.47	0.08	—	—	—	—	42.3	0.8	—	—	—	—
X_1	3.03	0.08	2.86	0.17	2.88	0.06	4.89	0.06	5.00	0.08	4.97	0.06	44.6	0.4	44.7	0.6	45.8	1.2
m4	2.86	0.08	2.66	0.09	2.62	0.03	4.62	0.05	4.67	0.07	4.53	0.04	45.8	0.3	45.9	0.3	45.8	0.4
m5	2.58	0.06	2.39	0.09	2.38	0.03	4.17	0.04	4.18	0.03	4.11	0.05	38.7	0.6	39.3	0.7	39.5	0.7
m6	2.43	0.07	2.30	0.05	2.41	0.04	3.93	0.07	4.05	0.08	4.16	0.05	41.6	0.7	41.4	0.5	42.3	0.6
sm1a	5.80	0.15	5.52	0.31	5.46	0.12	9.37	0.13	9.66	0.13	9.43	0.18	37.5	0.3	38.6	0.9	38.1	0.4
sm1b	—	—	5.02	0.28	5.16	0.14	—	—	8.79	0.05	8.92	0.28	—	—	33.2	1.1	33.3	0.8
sm2	4.57	0.16	4.13	0.18	4.23	0.04	7.37	0.13	7.22	0.11	7.31	0.07	63.1	0.5	36.8	0.5	38.1	0.4
sm3	3.79	0.11	3.45	0.15	3.41	0.03	6.12	0.07	6.03	0.06	5.89	0.04	28.0	0.4	27.5	0.8	26.7	0.5
sm4	3.67	0.09	3.25	0.13	3.41	0.05	5.93	0.06	5.69	0.06	5.89	0.06	34.1	0.4	34.3	0.6	34.9	0.4
sm5	3.59	0.09	3.32	0.15	3.35	0.07	5.80	0.08	5.80	0.09	5.79	0.09	32.0	0.3	30.8	0.5	31.4	0.4
sm6	3.47	0.07	3.20	0.12	3.19	0.03	5.61	0.05	5.60	0.06	5.51	0.06	25.7	0.5	25.1	0.6	26.7	0.5
sm7	2.29	0.07	2.12	0.07	2.11	0.03	3.70	0.06	3.72	0.05	3.65	0.05	31.9	0.6	31.7	0.6	32.8	0.8
sm8	2.00	0.05	1.83	0.06	1.86	0.03	3.23	0.06	3.21	0.04	3.21	0.05	35.1	0.7	36.7	0.9	37.6	0.9
st1	3.99	0.11	3.66	0.15	3.74	0.03	6.44	0.07	6.40	0.06	6.46	0.08	16.0	0.5	15.4	0.6	14.5	0.6
X_2	3.68	0.12	3.32	0.20	3.42	0.09	5.94	0.10	5.81	0.08	5.91	0.10	13.9	0.6	11.6	0.8	12.8	0.5
st2	2.99	0.08	2.76	0.08	2.74	0.04	4.83	0.07	4.84	0.07	4.74	0.08	24.1	0.6	24.6	0.6	25.9	0.3
Y	—	—	3.40	0.23	3.62	0.11	—	—	5.94	0.10	6.25	0.14	—	—	7.1	0.7	9.5	0.9
A + X	61.92	max.	57.38	max.	58.03													
		min.	56.88	min.	57.73													

Table 24. Chromosome measurements of 5 female and 5 male cells of *Herpestes fuscus*

Chromosome	Absolute length				Relative length				Centromeric index			
	Female		Male		Female		Male		Female		Male	
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.
m1	4.54	0.16	4.57	0.08	7.35	0.10	7.20	0.05	41.2	0.6	40.0	0.4
m2	4.20	0.14	4.42	0.10	6.80	0.08	6.96	0.12	46.8	0.8	46.4	0.4
X_1	3.14	0.09	3.18	0.10	5.09	0.04	5.01	0.10	43.3	0.4	44.6	0.7
m3	2.87	0.12	3.02	0.06	4.64	0.06	4.76	0.05	45.7	0.5	45.7	0.4
m4	2.53	0.09	2.58	0.07	4.09	0.06	4.06	0.10	40.3	0.5	40.3	0.4
m5	2.20	0.08	2.23	0.04	3.56	0.07	3.52	0.07	44.6	0.6	43.0	0.7
sm1	4.98	0.16	5.14	0.11	8.07	0.07	8.09	0.11	24.7	0.3	25.6	0.6
sm2	4.62	0.14	4.87	0.16	7.49	0.07	7.65	0.12	37.9	0.4	36.7	0.5
sm3	3.80	0.13	3.95	0.06	6.15	0.07	6.22	0.07	34.5	0.4	34.5	0.4
sm4	3.77	0.13	3.96	0.07	6.10	0.08	6.24	0.05	26.2	0.5	26.5	0.4
sm5	3.69	0.11	3.70	0.07	5.98	0.05	5.83	0.06	31.8	0.4	30.3	0.6
sm6	2.53	0.08	2.54	0.03	4.10	0.05	4.01	0.08	36.8	0.5	36.2	0.6
sm7	2.34	0.07	2.48	0.07	3.79	0.04	3.90	0.07	31.6	0.9	32.7	0.7
sm8	1.91	0.06	2.02	0.04	3.10	0.06	3.18	0.05	37.2	0.4	35.7	0.7
st1	4.26	0.12	4.32	0.11	6.91	0.06	6.79	0.07	13.8	0.2	13.5	0.5
st2	3.63	0.13	3.64	0.09	5.87	0.06	5.73	0.09	25.4	0.5	23.9	0.5
st3	2.94	0.08	3.04	0.05	4.77	0.06	4.79	0.05	24.9	0.6	24.7	0.5
Y	—	—	3.94	0.15	—	—	6.20	0.15	—	—	6.0	0.9
X_2	3.81	0.14	3.86	0.16	6.16	0.08	6.07	0.10	12.9	0.4	11.0	0.7
A+X	61.76		63.52									

Table 25. Chromosome measurements of 5 female and 5 male cells of *Herpestes brachyurus*

Chromosome	Absolute length				Relative length				Centromeric index			
	Female		Male		Female		Male		Female		Male	
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.
m1	5.45	0.12	4.91	0.06	7.44	0.11	7.28	0.09	41.5	0.3	41.3	0.5
m2	4.88	0.11	4.49	0.05	6.66	0.08	6.66	0.05	45.7	0.4	46.8	0.4
X_1	3.68	0.08	3.42	0.10	5.02	0.08	5.07	0.09	44.2	0.7	45.0	0.9
m3	3.33	0.08	3.08	0.03	4.54	0.06	4.57	0.04	45.4	0.6	45.2	0.8
m4	2.84	0.12	2.65	0.03	3.87	0.12	3.93	0.04	43.1	1.1	40.7	0.5
m5	2.44	0.07	2.22	0.02	3.33	0.07	3.29	0.05	38.9	0.8	39.2	0.5
m6	2.38	0.07	2.18	0.02	3.24	0.05	3.23	0.04	43.8	0.5	42.3	0.9
sm1	5.63	0.16	5.19	0.08	7.67	0.10	7.69	0.07	36.2	0.7	36.6	0.4
sm2	4.68	0.12	4.05	0.05	6.38	0.11	6.01	0.06	37.8	0.7	34.6	0.4
sm3	4.54	0.13	4.13	0.06	6.18	0.07	6.12	0.06	26.6	0.8	27.4	0.3
sm4	4.34	0.11	4.07	0.04	5.92	0.07	6.04	0.05	31.8	0.7	31.0	0.5
sm5	3.59	0.09	3.39	0.03	4.90	0.07	5.03	0.05	26.2	0.6	26.5	0.6
sm6	3.10	0.11	2.76	0.04	4.22	0.07	4.09	0.04	35.3	0.7	36.2	0.6
sm7	2.85	0.07	2.61	0.03	3.89	0.08	3.87	0.04	34.0	0.6	34.1	0.8
st1	5.66	0.13	5.26	0.08	7.72	0.05	7.80	0.09	23.7	0.5	24.5	0.6
st2	4.92	0.12	4.68	0.06	6.70	0.07	6.94	0.07	16.6	0.6	17.5	0.8
st3	4.74	0.12	4.41	0.05	6.46	0.05	6.54	0.08	15.6	0.4	15.9	0.5
st4	4.30	0.10	3.94	0.05	5.86	0.06	5.84	0.06	24.0	0.3	25.9	0.4
A+X	73.35		67.44									

Table 26. Chromosome measurements of 5 female and 5 male cells of *Helogale parvula*

Chromosome	Absolute length				Relative length				Centromeric index			
	Female		Male		Female		Male		Female		Male	
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e	Mean	S.e.	Mean	S.e.
m1	5.01	0.08	4.72	0.10	7.16	0.09	7.27	0.07	39.0	0.4	40.5	0.6
m2	4.73	0.08	4.54	0.10	6.76	0.07	6.99	0.06	48.0	0.4	47.3	0.4
X	3.49	0.04	3.30	0.08	4.99	0.06	5.09	0.05	44.4	0.8	44.3	0.8
m3	3.34	0.06	3.03	0.06	4.77	0.05	4.67	0.07	45.8	0.6	44.9	0.9
m4	2.90	0.04	2.68	0.07	4.15	0.05	4.13	0.08	40.3	0.8	40.3	0.5
m5	2.27	0.04	2.05	0.03	3.25	0.04	3.16	0.06	39.7	0.9	42.9	0.7
Y	—	—	0.94	0.02	—	—	1.45	0.06	—	—	44.7	1.6
sm1	5.43	0.12	4.91	0.09	7.75	0.09	7.57	0.09	36.1	0.3	36.0	0.3
sm2	4.42	0.07	4.16	0.11	6.32	0.06	6.40	0.08	27.2	0.4	26.7	0.4
sm3	4.28	0.09	3.90	0.09	6.12	0.10	6.00	0.07	31.5	0.4	30.8	0.7
sm4	4.10	0.07	3.89	0.08	5.86	0.07	5.99	0.06	34.1	0.3	34.0	0.4
sm5	2.85	0.06	2.70	0.03	4.07	0.06	4.16	0.04	35.8	0.7	37.0	0.9
sm6	2.60	0.04	2.37	0.03	3.72	0.04	3.65	0.04	30.4	0.5	30.8	0.6
sm7	2.22	0.03	2.01	0.04	3.18	0.05	3.10	0.05	34.7	0.6	33.3	0.8
st1	5.57	0.12	5.22	0.13	7.96	0.10	8.04	0.10	23.9	0.4	23.9	0.5
st2	4.70	0.09	4.39	0.08	6.72	0.09	6.76	0.04	14.3	0.5	12.5	0.3
st3	4.52	0.07	4.10	0.05	6.46	0.08	6.33	0.07	18.6	0.4	16.8	0.6
st4	4.16	0.08	3.79	0.08	5.94	0.06	5.84	0.05	24.8	0.3	23.0	0.4
st5	3.37	0.05	3.14	0.05	4.82	0.08	4.84	0.06	24.7	0.5	23.6	0.5
A+X	69.96		64.90									

Table 27. Chromosome measurements of 5 female and 5 male cells of *Mungos mungo*

Chromosome	Absolute length				Relative length				Centromeric index			
	Female		Male		Female		Male		Female		Male	
	Mean	S.e.	Mean	S.e.	Mean	S.e	Mean	S.e	Mean	S.e.	Mean	S.e.
m1	4.37	0.11	4.79	0.17	7.20	0.06	7.24	0.06	40.3	0.5	40.6	0.3
m2	4.16	0.09	4.52	0.19	6.86	0.07	6.82	0.06	47.4	0.4	47.4	0.5
X	3.07	0.05	3.26	0.13	5.07	0.06	4.94	0.11	43.4	0.7	44.3	1.0
m3	2.85	0.05	3.08	0.14	4.70	0.04	4.64	0.06	46.0	0.5	45.9	0.9
m4	2.41	0.05	2.60	0.10	3.98	0.04	3.93	0.04	41.1	0.6	40.5	0.5
m5	1.89	0.03	2.00	0.08	3.13	0.06	3.02	0.05	39.6	0.8	40.5	0.8
Y	—	—	0.96	0.04	—	—	1.46	0.04	—	—	45.8	1.1
sm1	4.58	0.09	5.10	0.17	7.56	0.06	7.72	0.07	36.5	1.0	36.4	0.4
sm2	3.92	0.08	4.31	0.16	6.47	0.08	6.51	0.07	28.4	0.5	27.1	0.4
sm3	3.65	0.07	4.02	0.18	6.03	0.06	6.06	0.09	30.4	0.4	30.4	0.3
sm4	3.61	0.10	3.97	0.17	5.95	0.09	5.99	0.09	32.7	0.3	32.6	0.6
sm5	2.43	0.04	2.67	0.12	4.01	0.06	4.03	0.08	36.6	0.7	36.1	1.0
sm6	2.19	0.04	2.33	0.10	3.62	0.04	3.52	0.04	31.1	0.6	31.9	0.7
sm7	1.90	0.03	2.05	0.07	3.14	0.05	3.11	0.08	34.7	0.5	35.0	0.5
st1	4.91	0.13	5.44	0.21	8.10	0.12	8.22	0.05	22.4	0.5	21.7	0.4
st2	4.37	0.10	4.73	0.20	7.21	0.08	7.14	0.07	13.3	0.9	12.9	0.3
st3	3.85	0.07	4.20	0.16	6.36	0.07	6.34	0.06	18.7	0.2	16.9	0.4
st4	3.54	0.06	3.91	0.12	5.84	0.04	5.92	0.06	24.6	0.4	23.5	0.4
st5	2.90	0.07	3.21	0.10	4.78	0.05	4.86	0.05	24.5	0.5	24.0	0.4
A+X	60.60		66.19									

Table 28. Chromosome measurements of 5 female and 5 male cells of *Cynictis penicillata*

Chromosome	Absolute length				Relative length				Centromeric index			
	Female		Male		Female		Male		Female		Male	
	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.	Mean	S.e.
m1	4.66	0.17	4.67	0.14	7.03	0.08	7.00	0.09	40.2	0.5	40.5	0.5
m2	4.25	0.15	4.31	0.12	6.42	0.09	6.46	0.06	48.0	0.4	47.6	0.3
m3	3.91	0.13	4.13	0.08	5.91	0.09	6.20	0.08	36.9	0.5	38.8	0.6
X	3.30	0.07	3.28	0.14	5.01	0.09	4.92	0.12	42.7	0.4	44.0	1.0
m4	2.98	0.11	2.99	0.05	4.50	0.05	4.49	0.08	46.3	0.5	46.5	0.4
m5	2.79	0.09	2.79	0.05	4.22	0.03	4.22	0.07	42.4	0.8	42.3	0.6
m6	2.70	0.10	2.67	0.05	4.08	0.06	4.02	0.11	40.7	0.6	40.7	1.3
m7	2.55	0.06	2.58	0.07	3.86	0.06	3.87	0.06	40.5	0.8	39.0	0.9
m8	2.42	0.07	2.41	0.06	3.66	0.06	3.62	0.08	45.8	0.7	44.8	0.5
m9	2.29	0.05	2.19	0.05	3.47	0.06	3.29	0.06	44.5	0.5	42.4	1.0
Y	—	—	1.28	0.02	—	—	1.93	0.07	—	—	46.9	0.8
sm1	5.10	0.19	5.29	0.18	7.70	0.08	7.92	0.14	27.4	0.6	27.1	0.6
sm2	4.86	0.22	4.81	0.12	7.32	0.11	7.21	0.09	36.9	0.5	36.2	0.6
sm3	4.43	0.20	4.53	0.12	6.67	0.14	6.79	0.06	24.6	0.8	27.0	0.5
sm4	4.38	0.18	4.19	0.12	6.60	0.11	6.27	0.06	31.7	0.7	32.1	0.7
sm5	3.97	0.13	4.00	0.08	6.00	0.06	6.00	0.06	33.1	0.5	34.6	0.6
sm6	3.85	0.14	4.05	0.09	5.81	0.05	6.07	0.04	28.9	0.5	28.2	0.6
sm7	3.35	0.09	3.30	0.07	5.07	0.08	4.95	0.06	30.2	0.8	29.4	0.8
st1	4.43	0.19	4.49	0.12	6.68	0.12	6.73	0.09	20.0	1.0	17.3	1.0
A + X	66.22		66.68									

Contents

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