

# CHROMOSOMES OF RATS AND MICE OF THAILAND

by

Amara Markvong, Joe Marshall, and Alfred Gropp

We report here the gross morphology of the chromosomes of the species of Thai rats and mice that we have been able to capture. Unexpected individual variations are revealed—enough to discourage using minor karyologic differences to distinguish species from each other. Some species are readily separable from their closest relatives by karyotype, as is *Rattus niviventer* with its three pairs of large submetacentric autosomes. On the other hand, identical karyotypes can be found in separate species, such as *Rattus losea* and *R. argentiventer*. We rely on the classical work of YONG (1968, 1969a, 1969b) both for rare Thai rodents that we were unable to capture and for comparisons with Thai populations of species common to Thailand and Malaysia, as summarized diagrammatically in figures 1 and 2. From the evidence in these figures we conclude that there is a distinctive karyotype for each natural group of species, which we will call a subgenus.

## MATERIALS AND METHODS

Rats were trapped in screen rat traps baited with banana, mice in Sherman traps using peanut butter. Karyograms were prepared by the accustomed procedure of *in vivo* colchicine injection, extraction of bone marrow into a hypotonic solution, fixation, staining in orcein, and photomicrography.\* From a large photograph, chromosomes were cut out and pasted in rows according to position of centromere (revealed by where the two unseparated chromatids are joined) and size as follows: telocentric with centromere (holding the two chromatids together) so close to the end that bifurcation of the small limbs cannot be discerned, subtelocentric with separate limbs plainly distinguishable at the small

\* In conducting the research described in this report, the investigators adhered to the "Guide for Laboratory Animal Facilities and Care," as promulgated by the Committee on the Guide for Laboratory Animal Facilities and Care of the Institute of Laboratory Animal Resources, National Academy of Sciences-National Research Council.

end in the photographs, metacentric with centromere in the middle such that the two conjoined chromatids form an x shape, and submetacentric comprising only those large chromosomes with centromere nearer the center than the end of the chromatids. Rodents, identified by Marshall, were prepared as museum skins with skull cleaned by dermestid beetles and were deposited at the Centre for National Reference Collections at the Applied Scientific Research Corporation of Thailand. In the following accounts of species, a few diagnostic morphologic characters are mentioned parenthetically as evidence that the taxa we studied are truly different species.

I. **Arboreal Rats and Mice** (hallux with flat nail).

A. *Vandeleuria oleracea*, **Long-tailed Cane Mouse**. (The fifth digits also have a nail.) The diploid number is 46. There are two pairs of large metacentric chromosomes, five pairs of large submetacentrics, and five pairs of small telocentrics. The X-chromosome is a medium telocentric; the Y is a subtelocentric of size equal to the X. Our specimens are the subject of a separate paper (Gropp et al. in press) that contains the photographic and specimen evidence as well as a discussion of the 48 chromosome karyotype found in Nakhorn Phanom.

II. **Terrestrial Rats and Mice** (hallux with sharp claw).

A. **Genus *Bandicota*** (molar lamellae straight crosswise), **Bandicoots**.

1. *Bandicota savilei*, **Lesser Bandicoot** (molar row less than 9.2 mm). The diploid number is 44. The autosomes consist of 13 pairs of large to small telocentrics and 8 pairs of medium to small metacentrics. The X-chromosome is one of the larger, but not the largest, telocentric; the Y is the smallest telocentric. (Hereinafter the sex chromosomes will be described only if they are *not* as above, namely the X about the fifth largest telocentric and the Y the smallest telocentric.) Two males and one female were examined, from tall grass, Saraburi Province, numbers V183, A185, A186.

2. *Bandicota indica*, **Great Bandicoot** (feet and back black, molar row more than 10 mm). The diploid number is 46. Yosida et al. (1969) report 44 from Taiwan. The autosomes consist of one large subtelocen-



tric pair, one small pair of subtelocentrics, one pair of large submetacentric, ten pairs of medium to small telocentrics, and nine pairs of medium to small metacentrics. The X is a medium subtelocentric. Three males and two females were examined from tall grass, Bangkok, numbers V115, V116, V177, V178, 6870.

B. **Genus *Mus*** (first molar longer than half the tooth row), **Mice.**

1. **Subgenus *Leggadilla*, Spiny Mice** (with skull ridges).

a. ***Mus shortridgei*, Shortridge's Mouse** (3+2 mammae and grey bases of ventral fur). Except for one pair of medium-sized metacentric chromosomes, all are telocentric, with diploid number of 46. This is the basic karyotype. Individual variation gives additional telocentrics, often minute, up to 49. This is discussed in a separate paper (GROPP et al. ms) together with the evidence from specimens and photographs.

2. **Subgenus *Coelomys*, Shrew-mice** (with broad frontals and small eye).

a. ***Mus pahari*, Sikkim Mouse** (spiny, in Thailand). There are 48 telocentric chromosomes in the diploid set, described in the paper by GROPP et al. (ms), together with the evidence from specimens preserved.

3. **Subgenus *Mus*, House Mouse and Commensal Allies** (long incisive foramina, no spines).

a. ***Mus caroli*, Ryukyu Mouse** (long tail, very short nasals, dark brown incisors). There are 40 telocentric chromosomes as in the house mouse. Six specimens were examined: a female (no. 17, Museum Alexander Koenig) and her litter of two males and one female from a pasture at Chiang Mai, male V404 the offspring of a female from Rayong x male from Saraburi, and male 357575 in the Smithsonian Institution, from the colony at the National Institutes of Health, originally caught by us at Chon Buri Province in a grass field, with karyogram kindly supplied by J. Fred Duncan.

b. ***Mus cervicolor*, Fawn-colored Mouse** (short tail, proodont). There are 40 telocentric chromosomes as in the house mouse. Two subspecies are represented by our ten specimens examined. Male 6744, male 6751, and female 6750 from teak forest at Tak belong to the large race, *Mus cervicolor popaeus*, as does male V678 of parents from deciduous



forest of the Khorat Plateau. Smithsonian specimen number 357576 from NIH colony originally captured by us in a grass field at Chon Buri yielded a karyogram prepared by and kindly supplied to us by J. Fred Duncan; it belongs to the race *Mus cervicolor cervicolor* that is of small size and usually found along with *Mus caroli* in rice paddies. The remaining specimens from our laboratory colony are all F1 of crosses between *popaeus* of the Khorat Plateau and *cervicolor* of Chon Buri: females V394, V395, and males V401, V402, V403.

c. *Mus cookii*, **Cook's Mouse** (recurved incisors, molar row 4 mm or more). There are 40 telocentric diploid chromosomes as in *Mus musculus*. Two males, 6722 and 6723, were trapped at the forest edge at the east base of Doi Luang Chiangdao, Chiangmai Province. Female 6749 comes from pine savanna at the summit of Phu Kradueng National Park, Loei Province.

d. *Mus musculus castaneus*, **Asian House Mouse** (flat skull, short rostrum, small teeth, dark belly concolorous with back). There are 40 telocentric chromosomes. A male and a female were examined, V157 and V158 respectively, now at Museum Alexander Koenig, Bonn. These siblings are offspring of a female (690904-5) captured in a grain warehouse at Thon Buri. An additional karyogram was kindly sent by Dr. Yosida, from a male specimen caught by us at the same warehouse.

C. **Genus Rattus** (molar lamellae bent in a chevron shape, postero-internal cusp missing), **Rats**.

1. **Subgenus Berylmys**, **White-toothed Rats** (incisors white, back iron-grey).

a. *Rattus berdmorei*, **Lesser White-toothed Rat** (proodont, large bullae, 3+2 mammae). The diploid number is 40. The autosomes consist of 5 pairs of large subtelocentrics, one large pair of submetacentrics, 6 pairs of medium to small telocentrics, and 7 medium to small metacentric pairs. Four specimens were examined as follows: female V154 now in Museum Alexander Koenig from lakeside grass, Phetchaburi; male V194 from secondary forest, Nakhon Nayok; and males V156 and V207 from farm plantation, Khorat Province.

b. *Rattus bowersi*, **Giant White-toothed Rat** (recurved incisors, small bullae, 2+2 mammae). The karyogram is exactly similar to that of



*berdmorei* unless it should be pointed out that our one specimen shows the fifth pair of subtelocentric chromosomes to be smaller than their counterparts in *berdmorei*. Male V197 is from oak-chestnut forest at the summit of Doi Pui, Chiang Mai.

2. **Subgenus *Rajah* Rats** (short, broad incisive foramina; small bullae).

a. *Rattus aurifer*, **Yellow Rajah Rat** (yellowish fur, mixed with black piles; nasals do not project posteriorly past the level of the premaxillo-frontal suture). The diploid number is 52. The autosomes consist of one pair of medium subtelocentric, 19 pairs of large to small telocentrics, and 5 pairs of large to medium-sized metacentric chromosomes. The X chromosome is a large metacentric; the Y is a rather small subtelocentric. DUNCAN et al. (1970) and YONG (1969b) both find a difference from the above in one less pair of metacentrics, a small subtelocentric pair instead. The two males examined, V168 and A188, were from mixed deciduous forest in limestone hills east of Saraburi.

3. **Subgenus *Niviventer* Group** (small forest rats with very long tail and rather short palate that is only half or less than half the total length of the skull). We have completed a study of this subgenus that is being reported elsewhere together with karyograms and specimen data (MARSHALL et al. ms). The basic karyotype of all the species in this group that occur in Hong Kong, Thailand, and Malaysia is a diploid number of 46 of which the three smallest pairs are metacentric, all the rest telocentric except for the next to largest pair, which is subtelocentric. Only exceptions to this plan will be mentioned below.

a. *Rattus niviventer*, **White-bellied Rat** (dark fuscous; elongated, narrow skull; narrow frontals). Three among the largest pairs of autosomes, instead of being telocentric as in the other members of the subgenus, are submetacentric. This woolly-furred rat from the summit of Doi Inthanon, Chiang Mai Province, is according to Dr. G.G. Musser the true *Rattus niviventer* of China and Nepal. The rat which in most of the literature goes under the name of *niviventer* should, we feel, be correctly called *Rattus fulvescens bukit*. *Rattus fulvescens* occurs in deciduous forest on Doi Inthanon whereas true *R. niviventer* (bullae larger) is in the summit moss forest of the same mountain.



b. *Rattus rapit orbus*, **Long-tailed Rat** (interorbital breadth greater than in the other species, dark rufous color, small bullae). The usual karyotype.

c. *Rattus fulvescens*, **Chestnut Rat, Bonhote's Rat** (brighter buff or rufous colors). The subspecies *Rattus fulvescens bukit* ranges over most of Thailand, where it has the normal karyotype. But in the mountains of the north it intergrades with *R. f. huang*. These intergrading populations vary in color from the buff of *bukit* to the bright rufous of *huang* and some of them, including individuals from both extremes of coloration, have several subtelocentric chromosomes.

4. **Subgenus *Rattus*, Roof Rat and Allies** (nasals and premaxillae do not extend far in front of incisors, palate prolonged conspicuously to the rear of the third molar, tail uniformly dark in all Thai species except the introduced Norway). In this subgenus we shall adhere to the terminology and analysis of Yosida et al. (1971b). The characteristic karyotype is of 42 chromosomes including seven pairs of medium to small metacentrics. These are grouped to the right of Yosida's ideograms. The remaining 13 autosomal pairs are usually telocentric and they are numbered in order of decreasing size from 1-13. Numbers 1, 4, 6, 7, 9, 11 and 13 become subtelocentric in various taxa within the subgenus that we find includes full species as well as subspecies, whereas Dr. Yosida thinks they are all subspecies of "*Rattus rattus*." In most of the taxa that have subtelocentric chromosomes, numbers 1, 9, and 13 are involved. Number 1 is often heteromorphic, and in Japan there is individual variation as well as geographic variation in whether number 1 is heteromorphic, homomorphic telocentric, or homomorphic subtelocentric. In the following accounts only differences from the basic karyotype will be mentioned.

a. *Rattus norvegicus*, **Norway Rat** (fairly straight and parallel parietal ridges). Autosomes 1, 9, 11, and 13 are all subtelocentric. Females V164, V175, 6902, and a male, 6904, were all caught at Marshall's house in Bangkok.

b. *Rattus nitidus*, **Himalayan Rat** (long nasals, small bullae, soft fur, pearly white feet). Autosomal pairs numbers 1 and 5 are subtelocentric, whereas number 13 is a metacentric pair. The six specimens



examined all came from inside houses of mountain villages in Chiang Mai Province : males 1470 and 1477 (the latter apparently with only 15 instead of 16 metacentrics), females V176, 1469, 1471, and 1476.

c. *Rattus losea*, **Lesser Ricefield Rat** (small, dark, short-tailed, with short rostrum and skull ridges high above rear zygomatic root). Numbers 1 and 9 are subtelocentric. Three specimens from rice fields were examined : a male, 6945 from Chiang Mai and a male and female, 6952 and 6953 from Pakthongchai District, Khorat Province.

d. *Rattus argentiventer*, **Ricefield Rat** (large bullae, deep skull, silver underparts, variegated buff x black dorsal fur). Autosomal pairs 1 and 9 are subtelocentric. Our specimens thus differ somewhat from those at Kuala Lumpur (YONG, 1969a). Three males, numbers 6868, 6869, and 6911 were captured in a rice field at Bangkok.

e. *Rattus remotus*, **Island Rat** (large size, long tail, small bullae—contra *annandalei*—and teeth and palate as in the subgenus *Rattus*—contra *mülleri*). Autosomal pairs 1, 4, 9, and 13 are subtelocentric. Autosomal pair number 11 is heteromorphic. Three males were examined from evergreen forest on Samui Island, numbers 6875, 6893, and 6909.

f. *Rattus sladeni*, **Sladen's Rat** (long tail, small bullae, broad rostrum, pure white underparts, molars usually black-rimmed). This species has the full complement of non-telocentric pairs. Our specimens are essentially the same as those pictured by YONG (1969b) and Yosida et al. (1971b) except that in our best karyograms the subtelocentric pairs seem to have a different size sequence : pairs 1, 2, 5, 7, 9, and 11 are subtelocentric; 13 is a metacentric pair. Thus *Rattus sladeni*, like *Rattus nitidus*, characteristically shows 8 metacentric pairs of autosomes. Our five specimens came from mountain evergreen forests in Chiang Mai Province : males 1497, 6898, 6899, and females 6719 and 6900.

g. *Rattus exulans*, **Polynesian Rat** (small size, 2+2 mammae). Autosomal pairs 1 and 11 are subtelocentric. However, the best of Mrs. Bückig's slides, shown in the figure number 19, suggests that two additional pairs of subtelocentrics might be discerned. The two males, 1464 and 1472, and one female, 1482, were caught inside houses of a mountain village in Chiang Mai Province.



h. *Rattus rattus*, Roof Rat (large bullae, slender rostrum, 2+3 mammae with tendency for twinning of the postaxial nipples). Our colleagues from Kuala Lumpur unanimously agree that their wild, pale-bellied, smallish rat, *jalorensis*, is a different species from *Rattus rattus*. However we are compelled temporarily at least to include all the Thai examples in the one species *R. rattus* because we have not yet been able to recognize the skull differences in Thai material nor to find the break between *jalorensis* (type locality at Pattani, Thailand) and *Rattus rattus thai* of the north, if there is such a break. Figure 2 contains a hint in the north to south line-up of ideograms. Between the central plains population and that of Chiang Mai is a change-over from subtelocentric pair number 9 (characteristic of *jalorensis*) to telocentric 9 (characteristic of *thai* and populations northward to China and Japan).

Normal *R.r. thai* karyograms have been pictured in GROPP et al. (1970), wherein the specimen evidence is also given. There are no subtelocentric chromosomes. We add here an additional normal specimen from Chiang Mai, female 6940.

The population of the Central Plains is similar to the above except for the largest autosomal pair, which is heteromorphic or homomorphic subtelocentric. Furthermore, two specimens, shown in figure 2, have an additional single or pair of subtelocentrics, suggesting *jalorensis*. The five specimens are from houses, farms, and tall grass at Bangkok, Saraburi, and Khorat: males V138, A184, V171, 6951, and female V151.

Two specimens of *Rattus rattus robinsoni* from woodland on Samui Island appear to have heteromorphic pairs 1 and 9. They are females V119 and 6910.

Our only two examples of *jalorensis* of the peninsula are from beach woodland, Ranong Province. Pair number 1 is telocentric; 9 is subtelocentric. Karyograms are diagrammed in figure 2. Number 2090 is a female. The male, number 2088, is extremely odd both in coloration and karyotype and is undoubtedly not representative.

For better or for worse karyology has gotten far ahead of morphology-taxonomy in the species "*Rattus rattus*." Cytology is pointing out the places to look for those skull differences that are so needed, if the



group is to be split. And the discovery of only 38 chromosomes in the true *Rattus rattus*, the black rat of Europe, by CAPANNA and CIVITELLI (1969) together with its very long tail and its polychromatism requires that we justify anatomically or ecologically our continued union of it and the eastern Asian forms.

5. **Subgenus *Leopoldamys*, Giant Rats** (very long, bicolored tail, small bullae).

a. *Rattus sabanus*, **Long-tailed Giant Rat** (color brighter, pattern more contrasting, and tail longer than with *R. edwardsi*). The diploid number is 42, mostly telocentric chromosomes. Four among the largest pairs are subtelocentric; two of the smallest are metacentric pairs. A male, V149, and female, A187, are from evergreen forest of limestone ravines near Saraburi. Female V176 is from dry evergreen forest at Khorat Province.

#### ACKNOWLEDGEMENTS

We thank Mr. Vandee Nongngork for trapping the animals, extracting the femora, and preparing the voucher museum specimens. Mr. Prasert Vitayadiloke and Mrs. Margarete Bückig made the photomicrographs. Mr. Inkam Inlao and Dr. Harold E. Stark collected some of the rats. Several workers on karyotypes of rodents have been most generous in sending us manuscripts, reprints, photomicrographs, and suggestions, namely Dr. Toshihide H. Yosida, Dr. T. C. Hsu, J. Fred Duncan, and Dr. Yong Hoi Sen.

#### LITERATURE CITED

- CAPANNA, E., and M.V. CIVITELLI. 1969. An endemic population of *Rattus rattus* (L) with a 38 chromosome complement. *Mammalian Chromosomes Newsletter* 10 : 220-222.
- DUNCAN, J.F., P.F.D. VAN PEENEN, and P.F. RYAN. 1970. Somatic chromosomes of eight mammals from Con Son Island, South Vietnam. *Caryologia* 23 : 173-181.
- DUNCAN, J.F., and P.F.D. VAN PEENEN. 1971. Karyotypes of ten rats (Rodentia: Muridae) from southeast Asia. *Caryologia* 24 : 331-346.
- GROPP, A., J. MARSHALL, G. FLATZ, M. OLBRICH, K. MANYANONDHA, and A. SANTADUSIT. 1970. Chromosomenpolymorphismus durch überzählige Autosomen, Beobachtungen an der Hausratte (*Rattus rattus*). *Zeitschrift für Säugetierkunde* 35 : 363-371.



- GROPP, A., A. MARKVONG, J. MARSHALL, and Y.J. KIM. Robertsonian chromosomal variation in the long-tailed tree mouse (*Vandeleuria*). *Zeitschrift für Zoologische Systematik und Evolutionsforschung*. In press.
- GROPP, A., J. MARSHALL, and A. MARKVONG. Chromosomal findings in the spiny mice of Thailand (Genus *Mus*) and occurrence of a complex intraspecific variation in *M. shortridgei*. *Zeitschrift für Säugetierkunde*. ms submitted.
- MARSHALL, J. T., A. GROPP, and A. MARKVONG. Chromosomes and the taxonomy of the *Rattus niviventer* group. ms.
- YONG, H.S. 1968. Karyotype of four Malayan rats (Rodentia-Muridae, genus *Rattus* Fischer). *Cytologia* 33 : 174-180.
- 1969a. Karyotypes of Malayan rats (Rodentia-Muridae, genus *Rattus* Fischer). *Chromosoma* 27 : 245-267.
- 1969b. Karyotypes of three species of rats from Hong Kong and Thailand (Muridae, genus *Rattus* Fischer). *Cytologia* 34 : 394-398.
- YONG, H.S. and S.S. DHALIWAL. Heteromorphism in the longest autosome of the Malayan house rat, *Rattus rattus diardii* (Rodentia-Muridae). ms.
- YOSIDA, T.H., K. MORIWAKI, H.T. IMAI, K. TSUCHIYA, and H. SAKATA. 1969. Scientific expedition for the study of rodents to southeast Asia and Oceania. I-VI. Annual Rep. Nat. Inst. Genetics, Japan no. 19 (1968) : 9-14, 40-41.
- YOSIDA, T.H., K. TSUCHIYA, and K. MORIWAKI. 1971a. Frequency of chromosome polymorphism in *Rattus rattus* collected in Japan. *Chromosoma* 33 : 30-40.
- 1971b. Karyotypic differences of black rats, *Rattus rattus*, collected in various localities of east and southeast Asia and Oceania. *Chromosoma* 33 : 252-267.
- N.B. The author has just examined the types of "*Mus sladeni*" and found them to be *Rattus rattus*. The rat listed here as *Rattus sladeni* is therefore to be called *Rattus koratensis*, Sladen's Rat.



Figure 1. Chromosomes of Muridae of Thailand.

GENUS	Pairs of Autosomes																									Authority		
Subgenus	Y	X	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
Species																												
Vandeleuria oleracea	π	π	X	X	X	X	X	π	π	π	π	π	π	X	X													gropp et al. in press
BANDICOTA																												
B. savilei	π	π	π	π	π	π	π	π	π	π	π	π	π	π	X	X	X	X	X	X	X	X	X	X	X	X	X	present paper
B. indica	π	X	X	X	π	π	π	π	π	π	π	π	π	π	X	X	X	X	X	X	X	X	X	X	X	X	X	" "
MUS																												
Leggadilla																												
M. shortridgei	π	π	π	π	π	π	π	π	π	π	π	X	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	gropp et al. ms
Coelomys																												
M. pahari	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	" " "
Mus																												
M. caroli	}	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	present paper
M. cervicolor		π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	" "
M. cookii		π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	" "
M. m. castaneus		π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	" "
RATTUS																												
Berylmys																												
R. berdmorei	π	X	X	X	X	X	X	π	π	π	π	π	π	X	X	X	X	X	X	X	X	X	X	X	X	X	X	" "
" "	π	X	X	X	X	X	X	π	π	π	π	π	π	X	X	X	X	X	X	X	X	X	X	X	X	X	X	Duncan et al. 1970
R. bowersi	π	X	X	X	X	X	X	π	π	π	π	π	π	X	X	X	X	X	X	X	X	X	X	X	X	X	X	present paper
Rajah Rats																												
R. whiteheadi	π	X	X	X	X	X	X	π	π	π	π	π	π	X	X	X	X											Yong 1969 a
R. rajah	π	X	X	X	X	X	X	π	π	π	π	π	π	X	X	X	X	X										" "
R. surifer	π	X	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	X	X	X	present paper
" "	π	X	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	X	X	X	Duncan et al. 1971
Niviventer Group																												
R. cremoriventer	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	Yong 1969 a
R. niviventer	π	π	X	X	X	X	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	Marshall et al. ms
R. rapit orbus	}	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	" "
R. fulvescens		π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	" "
R. bukit		π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	" "
Stenomys																												
R. mülleri	π	X	X	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	Yong 1968
Leopoldamys																												
R. edwardsi	π	π	X	X	X	X	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	" "
R. sabanus	π	π	X	X	X	X	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	π	present paper

▲ Essentially the same as originally published by Yong Hoi Sen 1968, 1969a, 1969 b.



Figure 2. Chromosomes of the Subgenus Rattus

(compared with published karyograms, reely interpreted)

Species	Pairs of Autosomes, System of Yosida 1972																				Authority
	1	2	3	4	X*	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
<i>R. norvegicus</i>	X	U	U	U	U	U	U	U	U	X	U	X	U	X	X	X	X	X	X	X	present paper <sup>▲</sup>
<i>R. nitidus</i>	X	U	U	U	U	X	U	U	U	U	U	U	U	X	X	X	X	X	X	X	" "
<i>R. losea</i>	X	U	U	U	U	U	U	U	U	X	U	U	U	U	X	X	X	X	X	X	" "
<i>R. argentiventer</i>	X	U	U	U	U	U	U	U	U	X	U	U	U	U	X	X	X	X	X	X	" "
" " "	X	U	U	U	U	U	U	U	U	X/	U	U	U	X	X	X	X	X	X	X	Yong 1969 a
<i>R. remotus</i>	X	U	U	X	U	U	U	U	U	X	U	X/	U	X	X	X	X	X	X	X	present paper
<i>R. sladeni</i>	X	X	U	U	U	U	U	U	U	X	U	U	U	X	X	X	X	X	X	X	" "
" "	X	U	U	X	U	U	U	U	U	X	U	U	U	X	X	X	X	X	X	X	Yong 1969 b
" "	X	U	U	X	U	U	U	U	U	X	U	U	U	X/	X	X	X	X	X	X	Yosida et al. 1971 b
<i>R. exulans</i>	X	U	U	U	U	U	U	U	U	X	U	U	U	U	X	X	X	X	X	X	present paper <sup>▲</sup>

Subspecies of Rattus "rattus," north to south:

<i>R. r. tanezumi</i>	•	U	U	U	U	U	U	U	U	•	U	U	U	•	U	X	X	X	X	X	Yosida et al. 1971a
<i>R. r. flavipectus</i>	U	U	U	U	U	U	U	U	U	U	U	U	U	U	X	X	X	X	X	X	" " " " b
<i>R. r. thai</i>	U	U	U	U	U	U	U	U	U	U	U	U	U	U	X	X	X	X	X	X	Gropp et al. 1970
<i>R. r. Saraburi</i>	X/	U	U	U	U	U	U	U	U	U	U	U	U	X/	X	X	X	X	X	X	A184 present paper
<i>R. r. Bangkok</i>	X/	U	U	U	U	U	U	U	U	X	U	U	U	U	X	X	X	X	X	X	V138 " "
<i>R. r. robinsoni</i>	X/	U	U	U	U	U	U	U	U	X/	U	U	U	U	X	X	X	X	X	X	" "
<i>R. r. jalorensis</i>	U	U	U	U	U	U	U	U	U	X	U	U	U	X/	U	X	X	X	X	X	2088 " "
" " "	U	U	U	U	U	U	U	U	U	X	U	U	U	U	X	X	X	X	X	X	2090 " "
" " "	X	U	U	U	U	U	U	U	U	X	U	U	U	U	X	X	X	X	X	X	Yong 1969 a
" " "	X	U	U	U	U	U	U	U	U	X?	U	U	U	U	X	X	X	X	X	X	Yosida et al. 1971 b
<i>R. r. diardii</i>	•	X	U	U	U	U	U	U	U	X	U	U	U	U	X	X	X	X	X	X	Yong et al. ms
" " "	•	X	U	U	U	U	U	U	U	X	U	U	U	X/	X	X	X	X	X	X	Yosida et al. 1971 b
<i>R. r. germani</i>	X	U	U	U	U	U	U	U	U	X	U	U	U	U	X	X	X	X	X	X	Duncan et al. 1970

\* Y is the smallest telocentric.

• Polymorphic

X/n X/X n/n

▲ Essentially the same as published by Yong Hoi Sen 1969 a.



## CORRECTIONS

Plate	V	should read	Plate	I
	VI	”		II
	VII	”		III
	VIII	”		IV
	IX	”		V
	X	”		VI







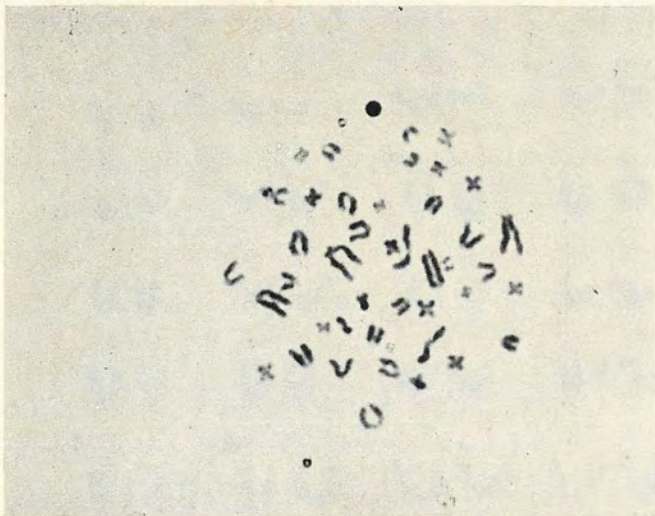


Fig. 3. Typical metaphase, *Rattus nitidus* male 1477

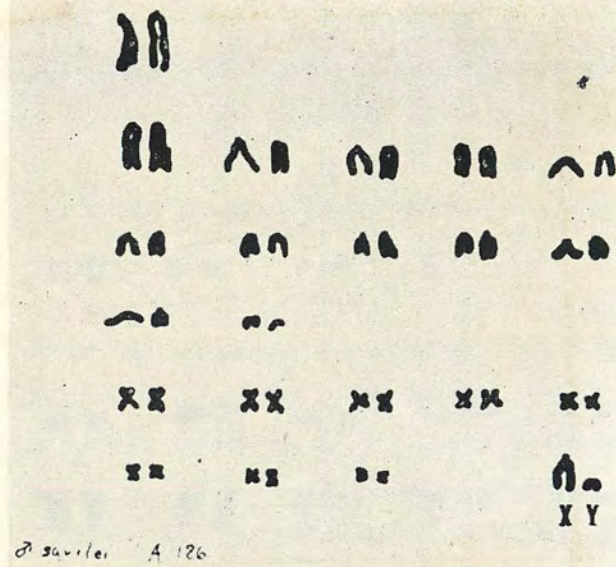


Fig. 4. *Bandicota savilei* male A186

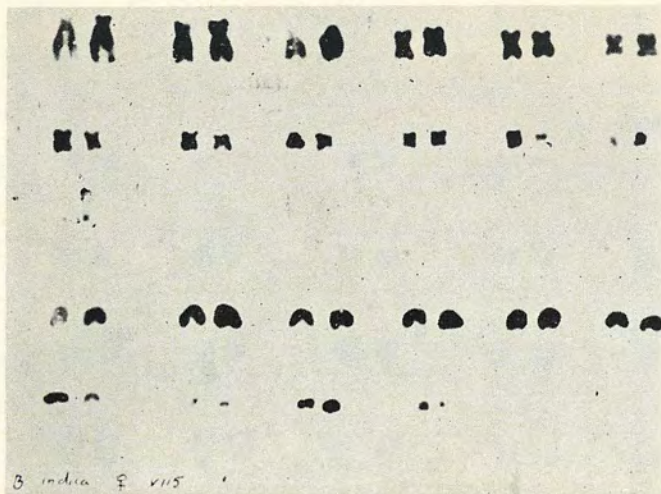


Fig. 5. *Bandicota indica* female V115 courtesy of Mr. J. Fred Duncan

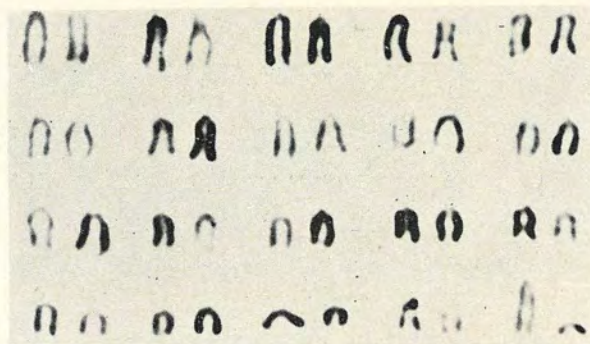


Fig. 6. *Mus caroli* male of litter from Museum Alexander Koenig number 17



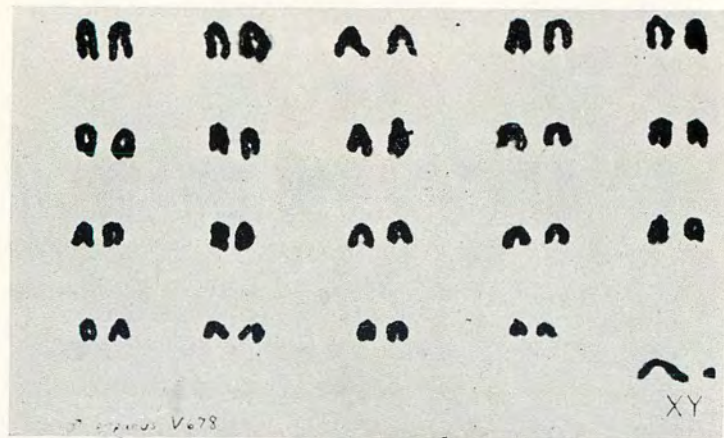


Fig. 7. *Mus cervicolor popaeus* male V678  
courtesy of Miss Prisna Chariyavidhayawat

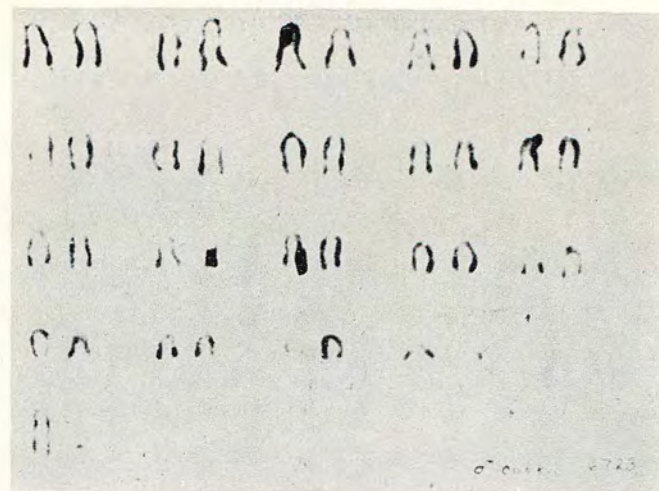


Fig. 8. *Mus cookii* male 6723

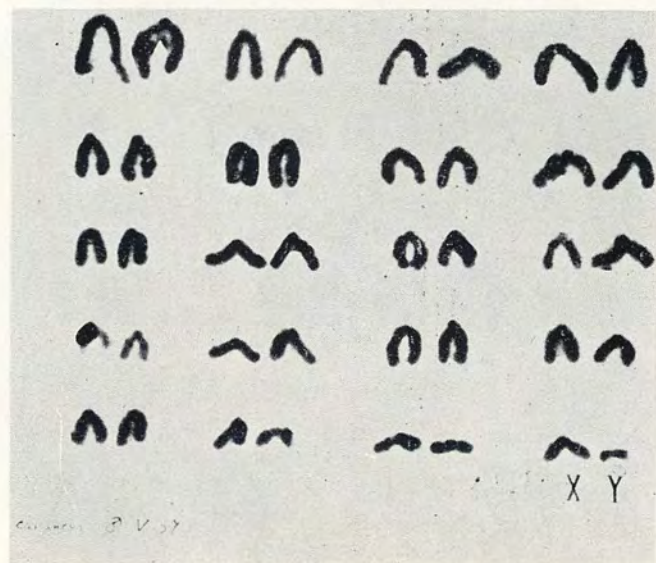


Fig. 9. *Mus musculus cantonensis* male V167

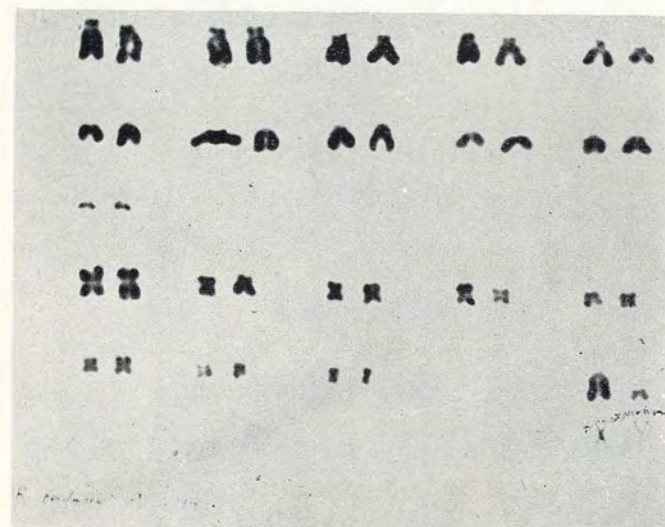


Fig. 10. *Mus musculus cantonensis* male V167



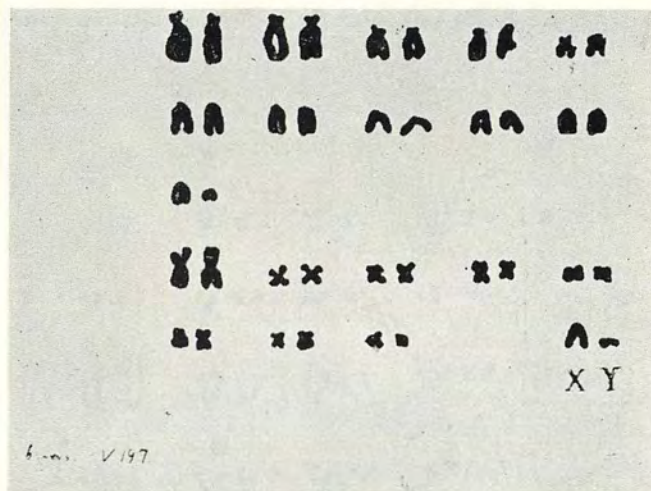


Fig. 11. *Rattus bowersi* male V197

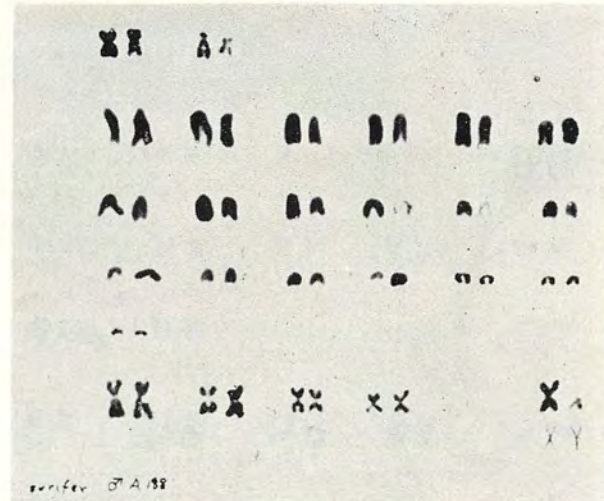


Fig. 12. *Rattus surifer* male A188

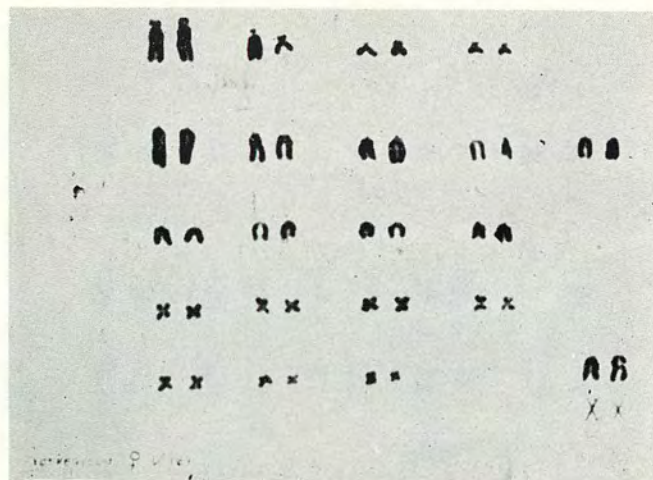


Fig. 13. *Rattus norvegicus* female V164

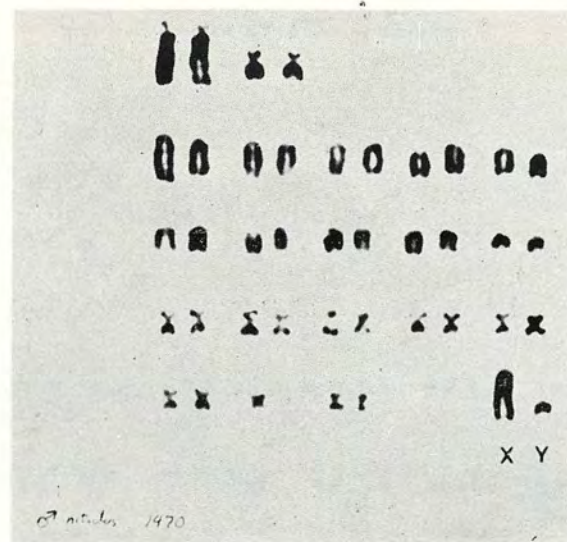


Fig. 14. *Rattus nitidus* male 1470



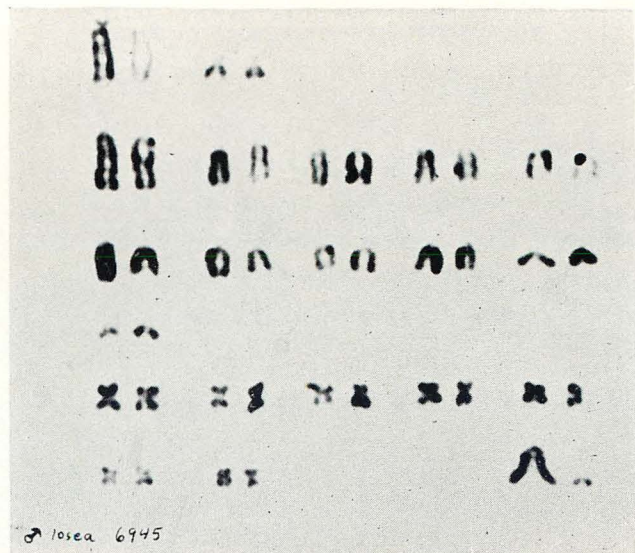


Fig. 15. *Rattus losea* male 6945

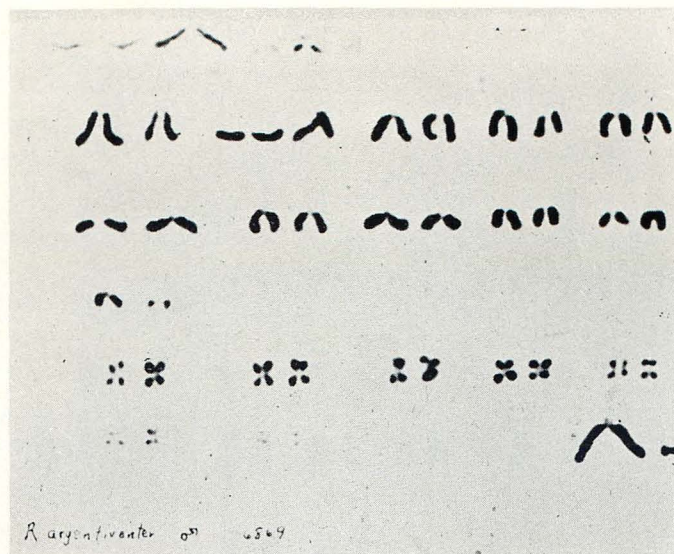


Fig. 16. *Rattus argentiventer* male 6869

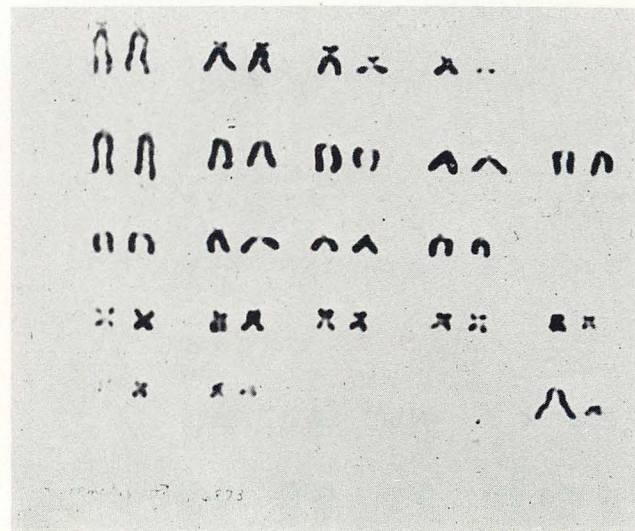


Fig. 17. *Rattus remotus* male 6873

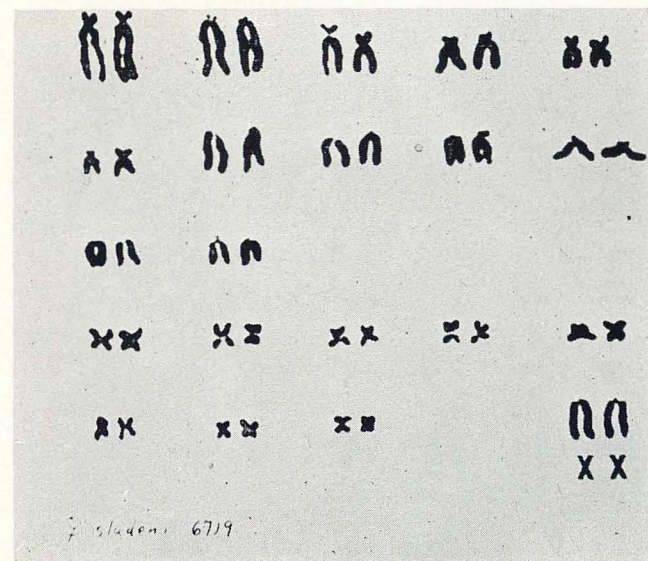


Fig. 18. *Rattus cladoni* female 6719



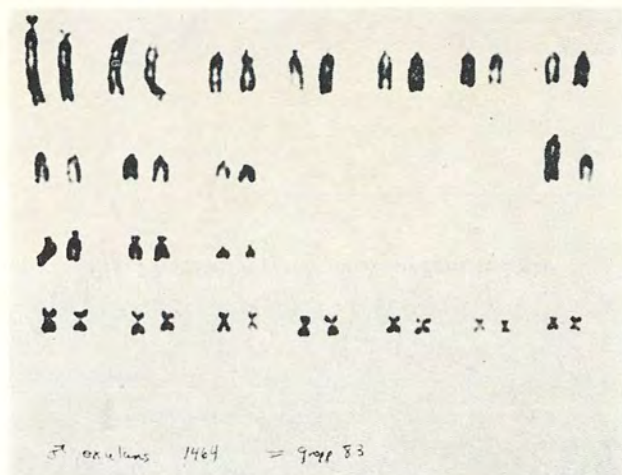


Fig. 19. *Rattus exulans* male 1464

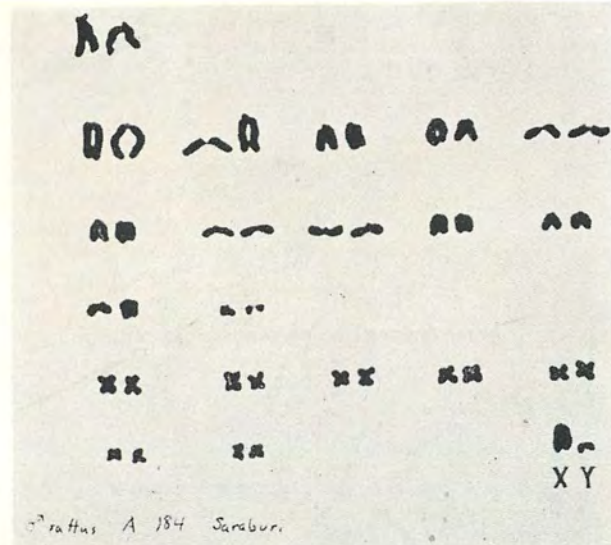


Fig. 20. *Rattus rattus* male A184

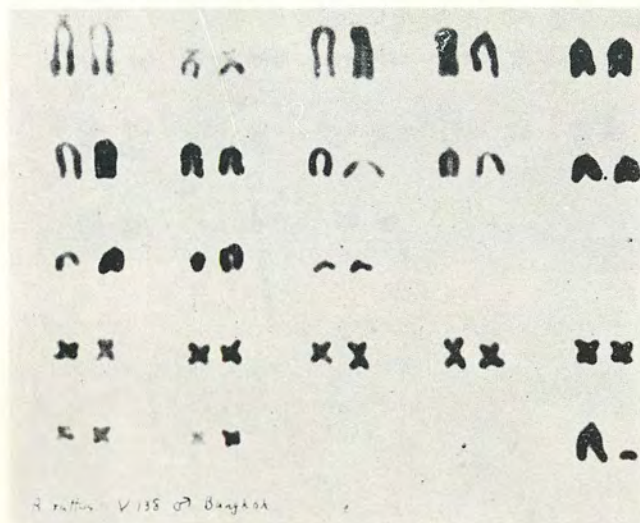


Fig. 21. *Rattus rattus* male V138

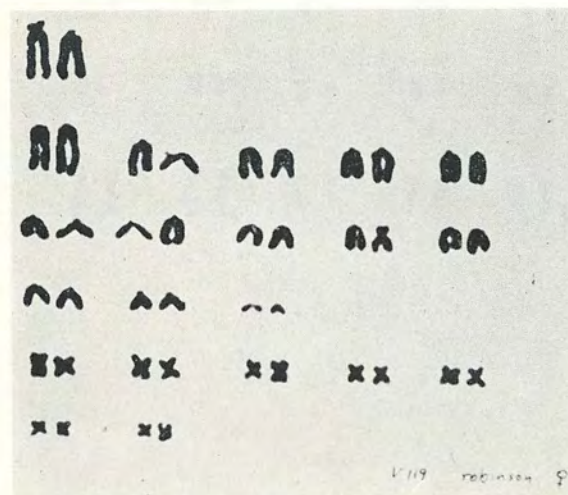


Fig. 22. *Rattus rattus robinsoni* female V119

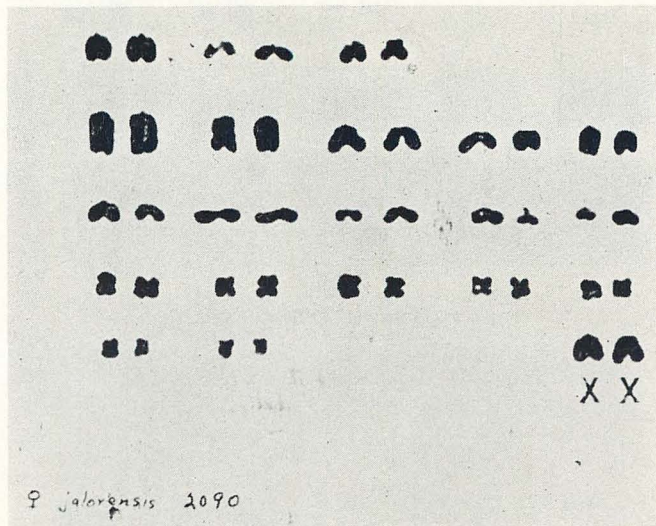


Fig. 23. *Rattus rattus jalorensis* female 2090

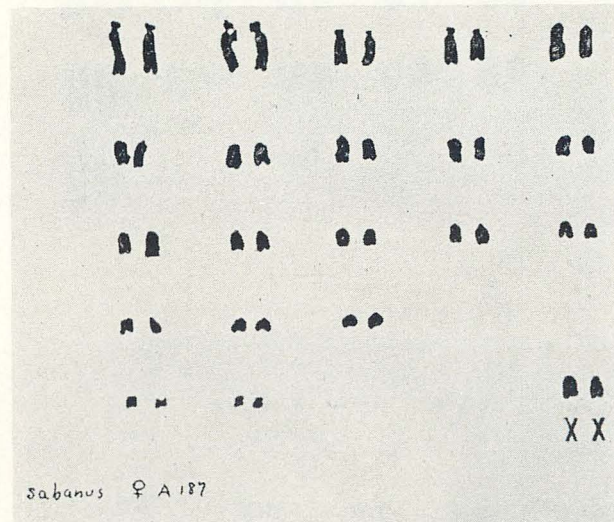


Fig. 24. *Rattus sabanus* female A187