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Comparative Cytogenetic Studies in the Order *Carnivora*

D. H. WURSTER and K. BENIRSCHKE
Department of Pathology, Dartmouth Medical School, Hanover, New Hampshire

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Abstract. The chromosome morphology of at least 93 species of carnivores has now been investigated. This information has been summarized and karyotypes of a number of previously unstudied species are presented. Karyotype evolution and interpretation, and the value of cytogenetic information in the study of taxonomy and phylogeny with respect to an understanding of speciation and hybridization are discussed. A complete bibliography is presented for each species.

Introduction

The chromosomes of at least 93 species of the large order *Carnivora* have now been studied, many of them with modern techniques of chromosome preparation. The diploid number, among those species studied, varies from 30 to 78. The nombre fondamental (NF), which is the total number of major chromosome arms in a female complement (MATTHEY, 1945), for the whole order ranges only from 66 to 88, with three individual exceptions of 90 to 100. The NF is relatively constant within each family, except for the *Canidae* and *Mustelidae*. Traditionally, the seven families of the *Fissipedia* or land-adapted carnivores have been defined on the basis of skull features, number and structure of teeth, number of toes and other morphological characteristics. This present study is not meant to be a revision of the classification, but a review and presentation of one of the most recently used parameters in the fields of taxonomy and phylogeny. Chromosome morphology of a number of previously unstudied species will be presented.

Material and Methods

Skin explants were cultured under glass slides in large Leighton tubes and the resultant outgrowth of fibroblasts passed to Carrel flasks before harvesting. The cells were grown in Eagle's basal medium with 10% calf serum added. At the time of harvesting cell division was arrested with 0.04% colchicine (0.1 ml per ml medium) for two hours, the cells were freed with 0.25% trypsin, washed with Earle's solution, treated with 1:5 hypotonic Earle's solution, fixed in 1:3 acetic acid-methanol fixative, and air dried on slides. Preparations were stained with the carbol-fuchsin method of CARR and WALKER (1961).

Results

In the following descriptions only four types of chromosomes are arbitrarily recognized; metacentric, submetacentric, subacrocentric, and acrocentric, with the centromere progressing from the center toward the end, respectively, as for instance in Fig. 17. There are many instances where it is hard, even by measurement, to place a chromosome in one or the other category. In figuring the NF, a metacentric or submetacentric has been counted as 2, and an acrocentric or subacrocentric as 1.

The Table (pp. 356—361) summarizes the carnivores that have been studied, elsewhere or in this laboratory. Of these, karyotypes of species not previously described or those in which there is some discrepancy between authors will be described below.

Canidae

Hoary fox, ♀ (*Dusicyon vetulus* LUND) (Fig. 1). $2n = 74$: $NF = 76$. There are 36 pairs of acrocentric elements and 1 pair of large meta-

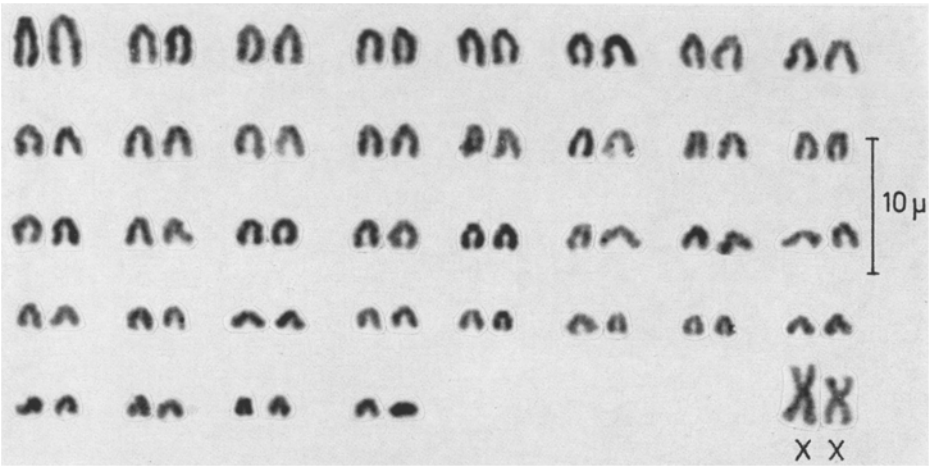


Fig. 1. Karyotype of a female hoary fox, *Dusicyon vetulus*

centrics. The X chromosomes are unknown, but, judging from other members of the *Canidae*, are presumed to be the 2 metacentric chromosomes.

Fennec fox, ♂ (*Fennecus zerda* ZIMMERMAN) (Fig. 2). $2n = 64$: $NF = 70$. The autosomal complement consists of 2 pairs of meta- and submetacentrics and 29 pairs of acrocentrics. Two pairs of medium-sized acrocentrics possess achromatic regions in the long arm next to the centromere. The X chromosome is a large submetacentric and the Y is a very tiny element.

Fig. 2. Karyotype of a male fennec fox, *Fennecus zerda*

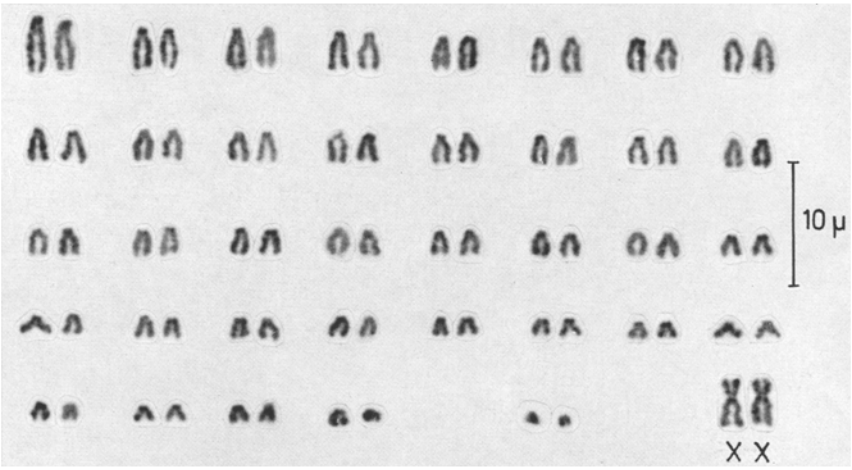


Fig. 3. Karyotype of a female short-eared fox or dog, *Atelocynus microtis*

Short-eared fox or dog, ♀ (*Atelocynus microtis* SCLATER) (Fig. 3). $2n = 74$—76: $NF = 76$. There are 36 pairs of acro- or subacrocentrics and 1 pair of large submetacentrics. The latter are supposed to be the X chromosomes in keeping with the other canids, but this is not known to be so.

Grey fox, ♀ (*Urocyon cinereoargenteus* SCHREBER) (Fig. 4). $2n = 66$: $NF = 70$. The autosomal complement consists of 1 pair of medium-sized metacentric and 31 pairs of size-graded acro- or subacrocentric elements. Two pairs of medium-sized acrocentrics possess achromatic regions in

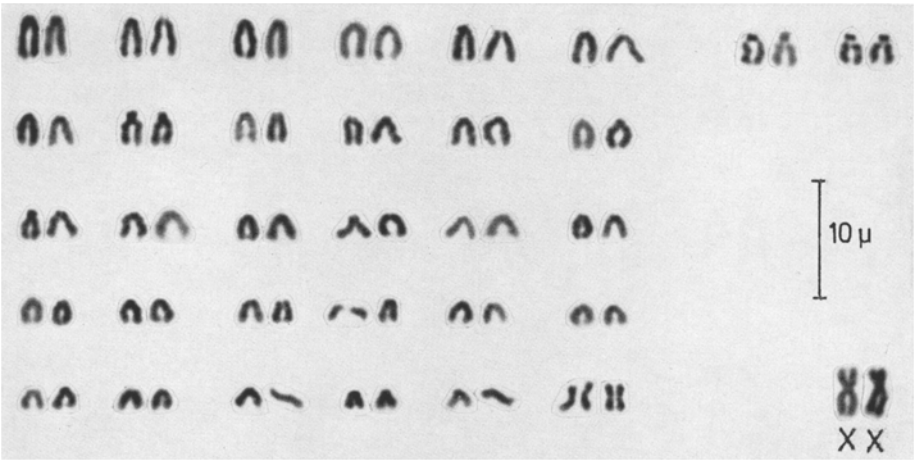


Fig. 4. Karyotype of a female grey fox, *Urocyon cinereoargenteus*

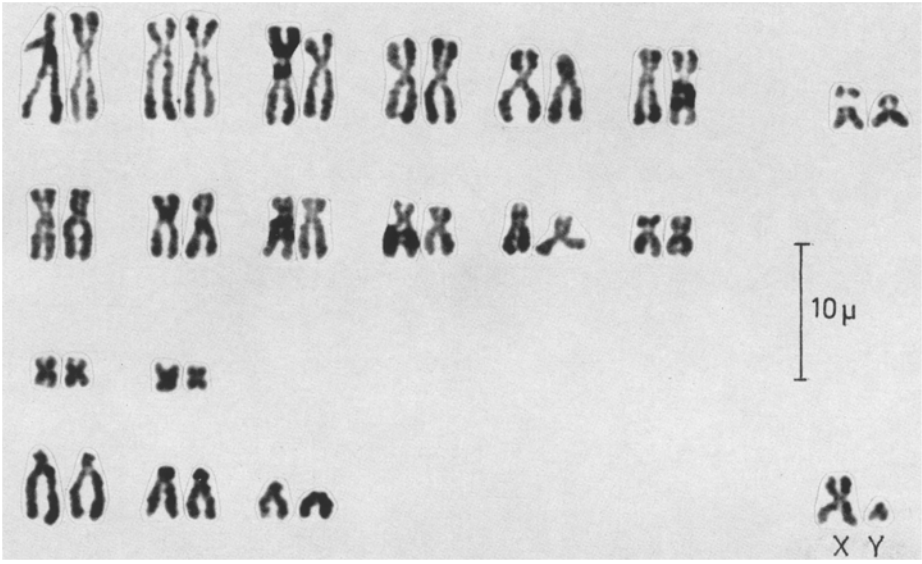


Fig. 5. Karyotype of a male coati, *Nasua nasua*

the long arm next to the centromere. The X chromosome is the largest element and is submetacentric.

Procyonidae

Coati, ♂ (*Nasua nasua* L.) (Fig. 5). $2n = 38$: $NF = 68$. There are 14 pairs of meta- and submetacentric and 4 pairs of acrocentric auto-

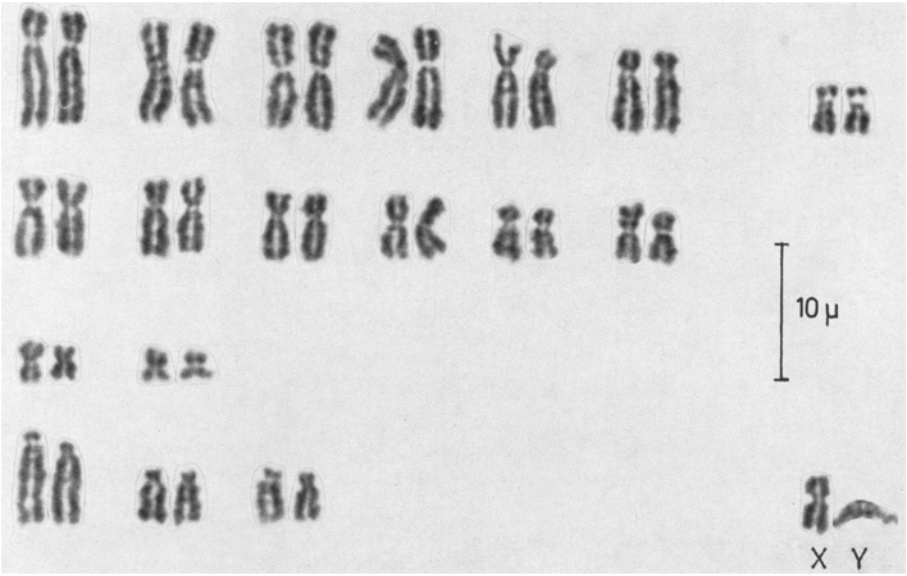


Fig. 6. Karyotype of a bushy-tailed olingo, *Bassaricyon gabbii*

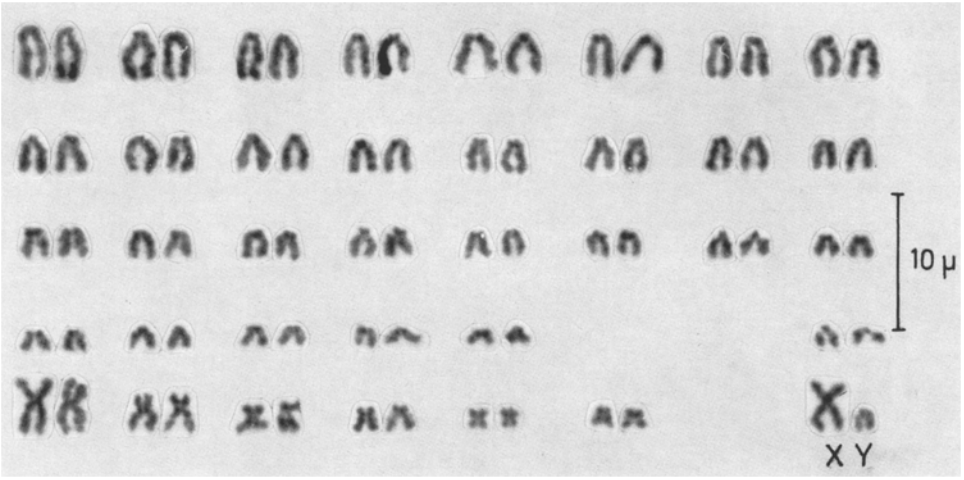


Fig. 7. Karyotype of a male grizzly bear, *Ursus horribilis*

somes. One pair of small acrocentrics has satellites on the short arms. The X chromosome is a medium-sized submetacentric and the Y is a small subacrocentric.

Bushy-tailed olingo, ♂ (*Bassaricyon gabbii* ALLEN) (Fig. 6). $2n = 38$: $NF = 68$. The autosomal complement is composed of 14 pairs of meta-

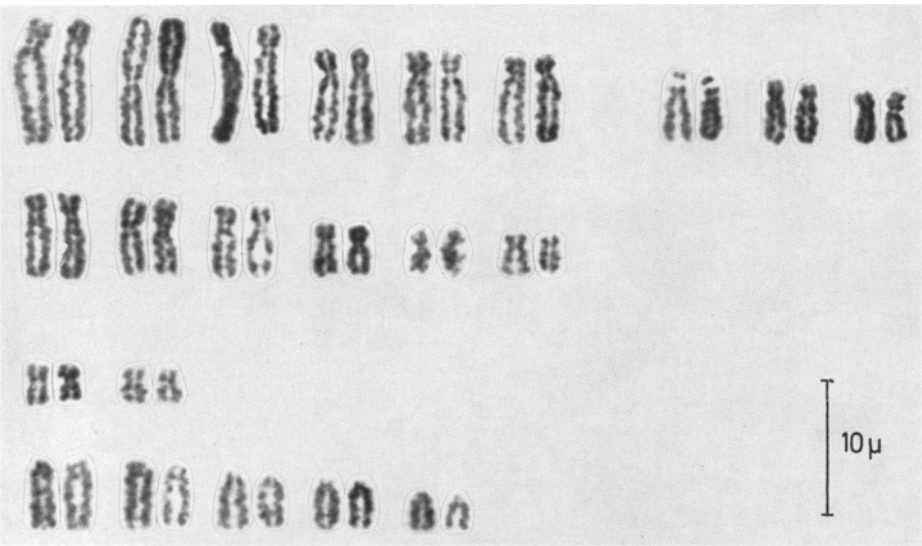


Fig. 8. Karyotype of a female Eurasian badger, *Meles meles*

and submetacentric elements and 4 pairs of acrocentrics. One pair of small acrocentrics has satellites on the short arms. The X chromosome is a medium-sized submetacentric and the Y is the smallest element, a subacrocentric.

Ursidae

Grizzly bear, ♂, ♀ (*Ursus horribilis* ORD) (Fig. 7). $2n = 74$: $NF = 88$. This species has 6 pairs of meta- or submetacentric and 30 pairs of acro- or subacrocentric autosomes. There are 2 pairs of acrocentrics that have achromatic regions in the long arm adjacent to the centromere. The X chromosome is a large submetacentric and the Y a small subacrocentric element. This karyotype is essentially identical to that of the polar bear.

Mustelidae

Eurasian badger, ♀ (*Meles meles* L.) (Fig. 8). $2n = 44$: $NF = 72$. There are 13 pairs of meta- or submetacentric and 8 pairs of acrocentric autosomes. The X chromosome is a medium-sized metacentric chromosome. Three pairs of the acrocentrics bear satellites.

Chinese (golden-bellied) ferret badger, ♂ (*Melogale moschata* GRAY) (Fig. 9). $2n = 38$: $NF = 74$. Thirty-four autosomes of this species are meta- or submetacentric, and 2 are subacrocentric. The largest pair, metacentrics, is satellited, and 2 other pairs of large submetacentrics possess satellites on the long arms. The X chromosome is a medium-sized nearly metacentric element and the Y is a small submetacentric.

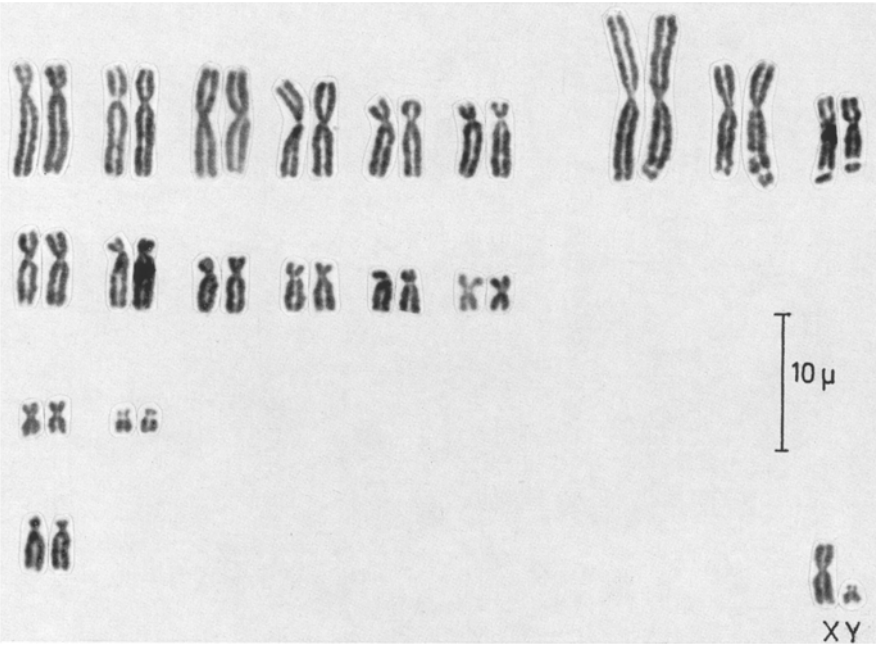


Fig. 9. Karyotype of a male Chinese or golden-bellied ferret badger, *Melogale moschata*

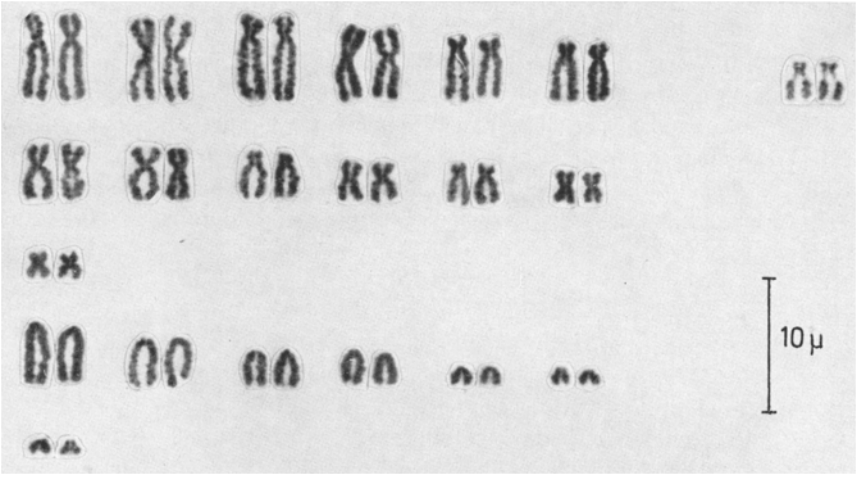


Fig. 10. Karyotype of a female wolverine, *Gulo gulo*

Wolverine, ♀ (*Gulo gulo* L.) (Fig. 10). $2n = 42$: $NF = 70$. This species has 14 pairs of meta- or submetacentrics and 7 pairs of acrocentrics.

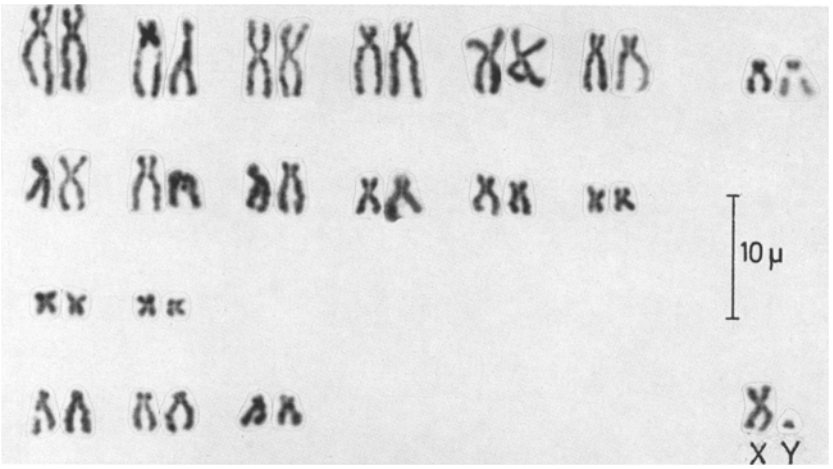


Fig. 11. Karyotype of a male tayra, *Eira barbara*

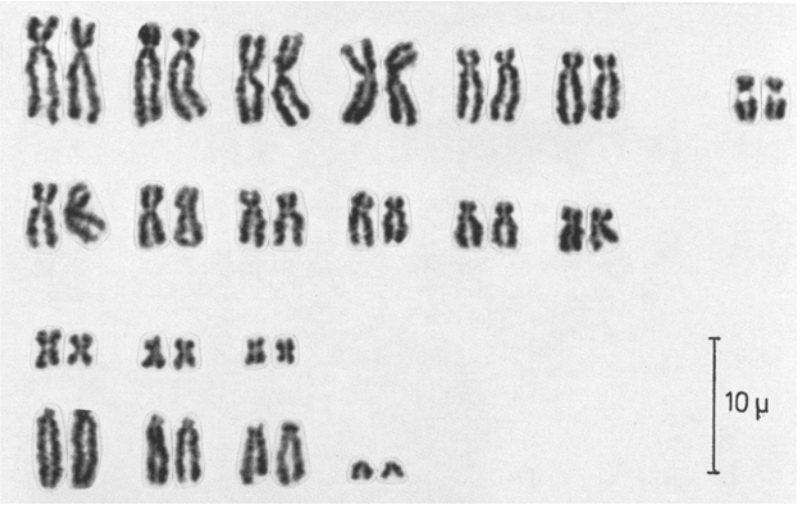


Fig. 12. Karyotype of a female yellow-throated marten, *Martes flavigula*

The sex chromosomes are unknown. The long arms of 1 pair of small submetacentrics possess an achromatic region adjacent to the centromere.

Tayra, ♂ (*Eira barbara* L.) (Fig. 11). $2n = 38$: $NF = 68$. Fourteen pairs of the autosomes in this species are meta- or submetacentric. The other 8 pairs are subacrocentric. The X chromosome is a medium-sized submetacentric and the Y is a minute element. The long arms of 1 pair of subacrocentrics possess an achromatic region adjacent to the centromere.

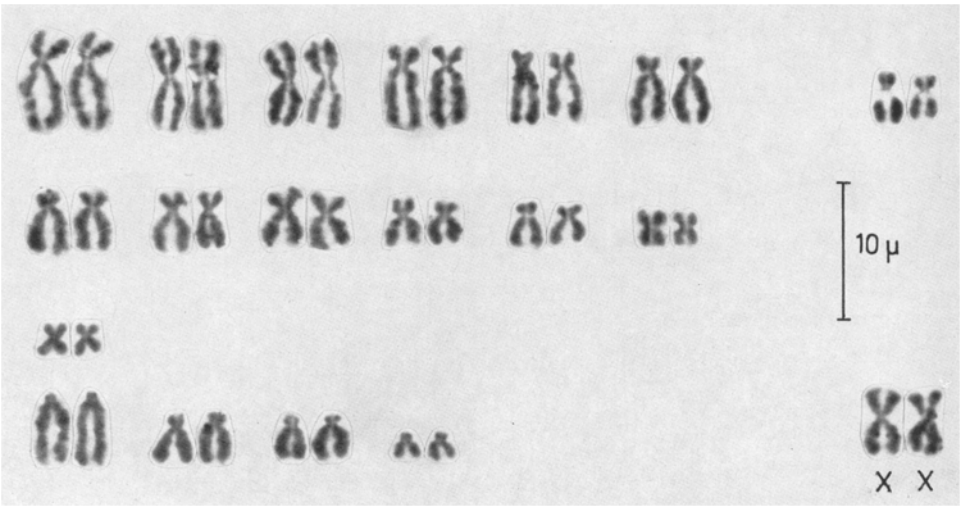


Fig. 13. Karyotype of a male fisher, *Martes pennanti*

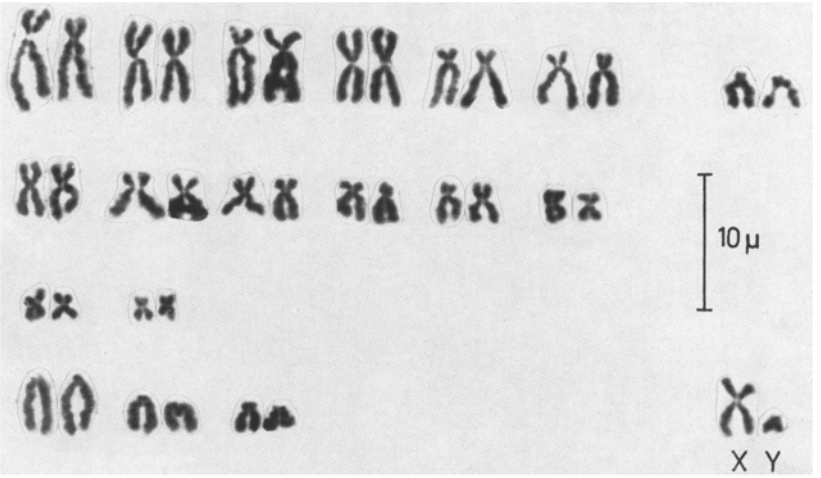


Fig. 14. Karyotype of a male pine marten, *Martes americana*

Yellow-throated marten, ♀ (*Martes flavigula* BODDAERT) (Fig. 12). $2n = 40$: $NF = 72$. Fifteen pairs of the autosomes are meta- or submetacentric and 4 pairs are acrocentric. The X chromosome is a medium-sized submetacentric. The long arms of 1 pair of small submetacentrics possess an achromatic region adjacent to the centromere.

Fisher, ♂, ♀ (*Martes pennanti* MILLER) (Fig. 13). $2n = 38$: $NF = 68$. Of the autosomes 14 pairs are meta- or submetacentric and 4 pairs are

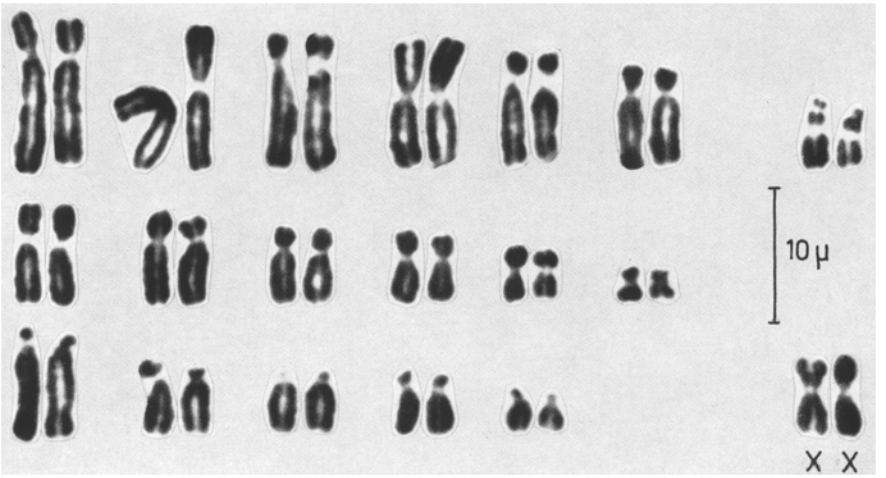


Fig. 15. Karyotype of a female river otter, *Lutra canadensis*

acro- or subacrocentric. The X is a rather large submetacentric and the Y a small metacentric. One pair of small submetacentrics has an achromatic region in the long arm adjacent to the centromere.

Pine marten, ♂ (*Martes americana* MILLER) (Fig. 14). 2n = 38: NF = 68. There are 14 pairs of meta- or submetacentric and 4 pairs of acrocentric autosomes in this species. The X chromosome is a medium-sized submetacentric and the Y is the smallest element and probably a submetacentric. One acrocentric is marked by a constriction or achromatic region in the long arms.

River otter, ♀ (*Lutra canadensis* SABINE) (Fig. 15). 2n = 38: NF = 64. This species has 13 pairs of meta- or submetacentric and 6 pairs of acro- or subacrocentric autosomes. Autoradiographic studies suggest that the X chromosomes are medium-sized nearly metacentric elements. There is a constriction or achromatic region in the long arm of 1 pair of acrocentrics.

Viverridae

Small-spotted genet, ♂, ♀ (*Genetta genetta neumanni* MATSCHIE) (Fig. 16). 2n = 52: NF = 100. There are 23 pairs of meta- or submetacentric and 2 pairs of very small acrocentric autosomes. One pair of small submetacentrics bears satellites on the short arms and another pair of small metacentrics may also bear satellites. The X chromosome is a large meta- or submetacentric and the Y is a medium-sized acrocentric element.

Small Indian civet (Formosan spotted civet or lesser oriental civet), ♂, ♀ (*Viverricula indica* DESMAREST) (Fig. 17). 2n = 36: NF = 64.

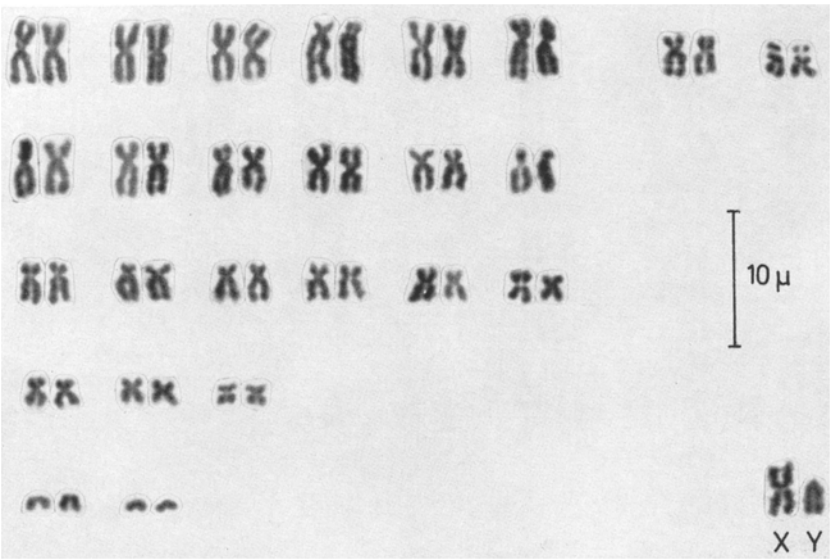


Fig. 16. Karyotype of a male small-spotted genet, *Genetta genetta*

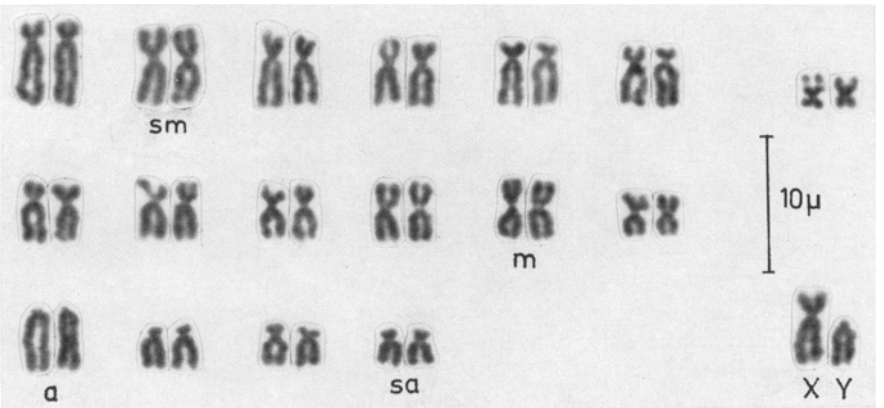


Fig. 17. Karyotype of a male small Indian civet, *Viverricula indica*. Examples of arbitrarily defined metacentric, submetacentric, acrocentric and subacrocentric chromosomes are marked with appropriate letters

Twenty-six of the autosomes are meta- or submetacentric, and eight are acro- or subacrocentric. The smallest pair of metacentrics bears satellites. The X chromosome is a large submetacentric and the Y is a medium-sized acrocentric.

Banded linsang, ♂, ♀ (*Prionodon linsang* HARDWICKE) (Fig. 18). $2n = 34$: $NF = 66$. There are 15 pairs of meta- and submetacentric and

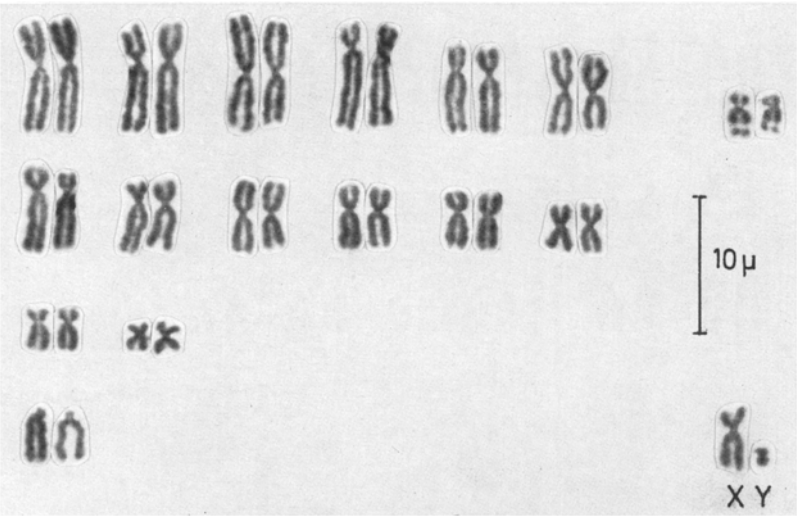


Fig. 18. Karyotype of a male banded linsang, *Prionodon linsang*

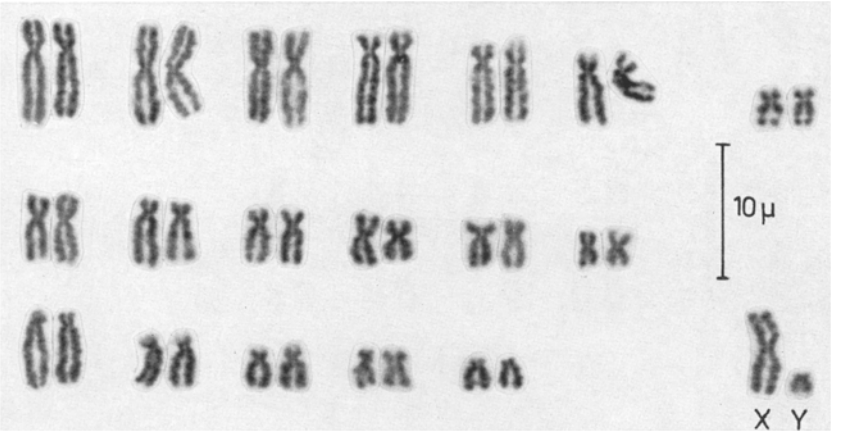


Fig. 19. Karyotype of a male African or two-spotted palm civet, *Nandinia binotata*

only one pair of acrocentric autosomes. The smallest pair, submetacentrics, possesses satellites on the long arms. The X is a medium-sized submetacentric and the Y is a minute metacentric.

African (two-spotted) palm civet, ♂ (*Nandinia binotata* REINWARDT) (Fig. 19). $2n = 38$: $NF = 66$. The autosomal complement is composed of 13 pairs of meta- or submetacentric and 5 pairs of acro- or subacrocentric elements. One pair of small submetacentrics bears satellites on the long arms. The X chromosome is a large metacentric and the Y chromosome is the smallest element, an acro- or subacrocentric.

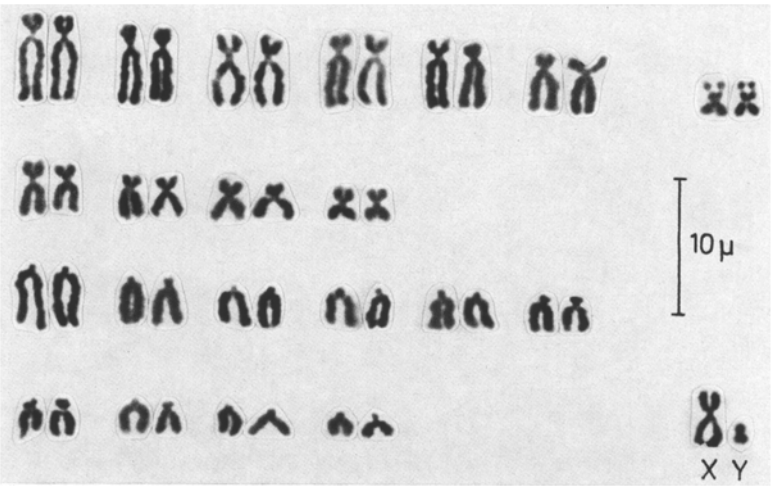


Fig. 20. Karyotype of a male masked palm civet, *Paguma larvata*

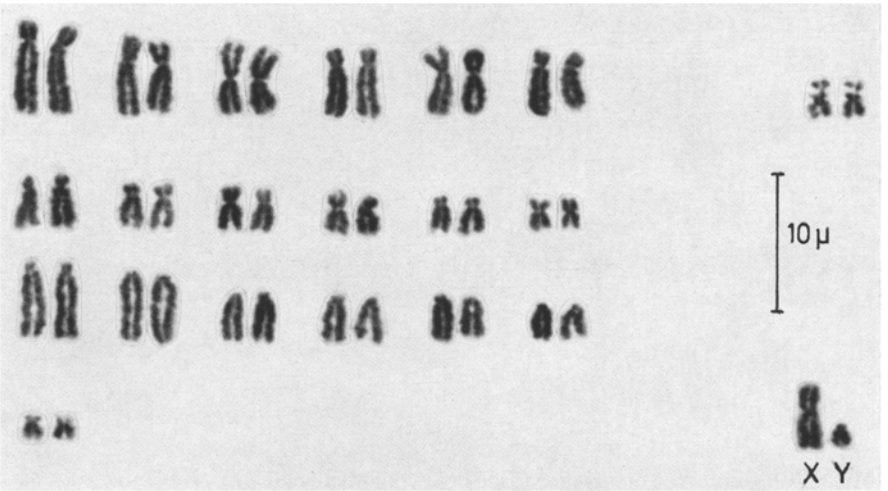


Fig. 21. Karyotype of male fossa, *Cryptoprocta fossa*

Masked palm civet, ♂ (*Paguma larvata* Hamilton-Smith) (Fig. 20). $2n = 44$: $NF = 68$. There are 11 pairs of meta- or submetacentric and 10 pairs of acrocentric autosomes. One pair of small submetacentrics bears satellites on the short arms. The X chromosome is a fairly large metacentric and the Y a small submetacentric.

Fossa, ♂ (*Cryptoprocta fossa* Bennett) (Fig. 21). $2n = 42$: $NF = 70$. This species has 13 meta- or submetacentric and 7 pairs of acro- or subacrocentric autosomes. One pair of small submetacentrics bears satel-

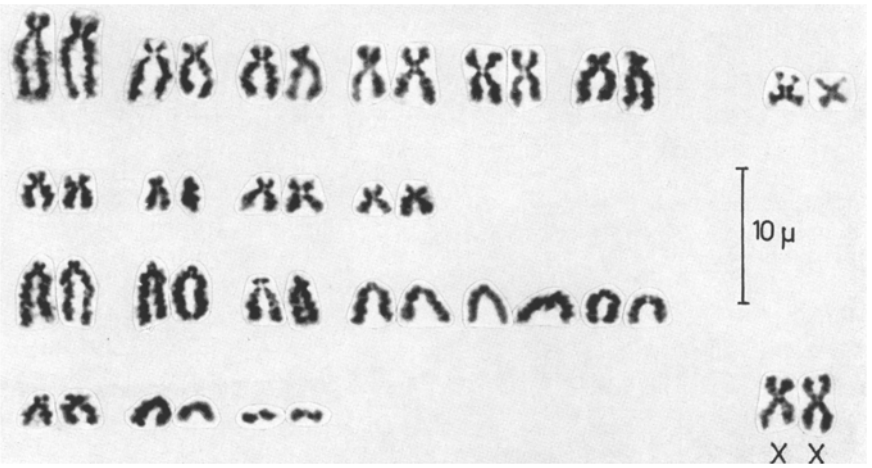


Fig. 22. Karyotype of a female fanaloka or Malagasy civet, *Fossa fossa*

lites on the short arms. The X chromosome is a medium-sized submetacentric and the Y is a small subacrocentric.

Fanaloka or Malagasy civet, ♂, ♀ (*Fossa fossa* SCHREBER) (Fig. 22). 2n = 42: NF = 68. Of the autosomes there are 11 pairs of meta- or submetacentric and 9 pairs of acrocentric elements. One pair of small submetacentrics possesses satellites on the short arms. The X chromosome is a large metacentric and the Y is a small submetacentric, the smallest element of all.

Banded palm civet, ♂ (*Hemigalus derbyanus* GRAY) (Fig. 23). 2n = 42: NF = 70. This species has 13 meta- or submetacentric and 7 pairs of acro- or subacrocentric autosomes. The smallest pair of submetacentrics bears satellites on the short arms. The X chromosome is a medium-sized submetacentric and the Y is a small acrocentric.

Ring-tailed mongoose, ♂ (*Galidia elegans* GEOFFROY) (Fig. 24). 2n = 44: NF = 66. In this species there are 10 pairs of meta- or submetacentric and 11 pairs of acrocentric elements. One pair of small submetacentrics bears satellites on the short arms. The X chromosome is a medium metacentric and the Y is a small submetacentric, the smallest element.

Marsh mongoose, ♂, ♀ (*Atilax paludinosus* G. CUVIER) (Fig. 25). 2n = ♂ 35, ♀ 36: NF = 66. Fourteen pairs of the autosomes are meta- or submetacentric and 3 pairs are acro- or subacrocentric. The X chromosome is a medium metacentric. The male may be XO, may carry the Y translocated to one of the autosomes or may have some other sex chromosome arrangement. The 6th largest pair in the male is generally heteromorphic, suggesting a translocated Y.

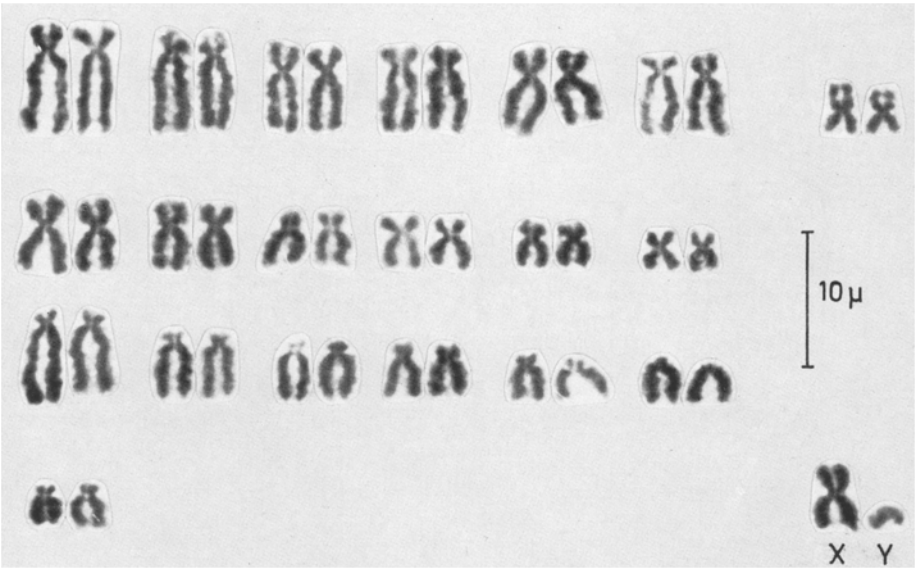


Fig. 23. Karyotype of a male banded palm civet, *Hemigalus derbyanus*

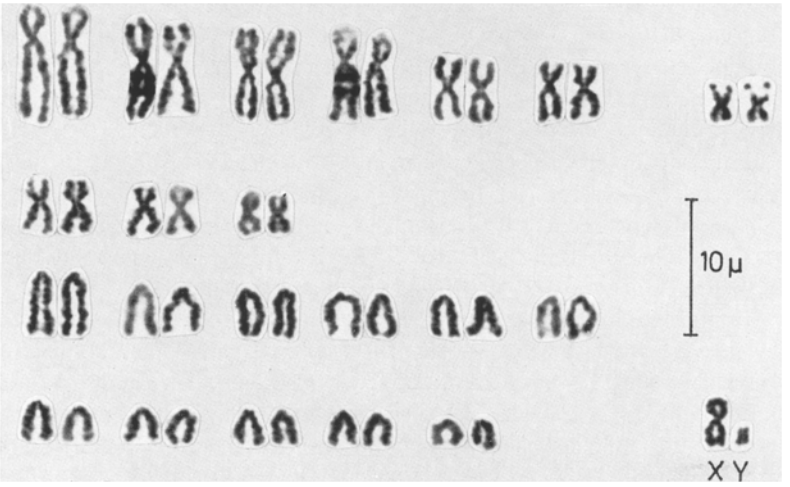


Fig. 24. Karyotype of a male ring-tailed mongoose, *Galidia elegans*

Banded mongoose, ♀ (*Mungos mungo* Gmelin) (Fig. 26). $2n = 36$: $NF = 66$. There are 15 pairs of meta- or submetacentric and 3 pairs of acrocentric chromosomes. The X chromosome is unknown.

White-tailed mongoose, ♂ (*Ichneumia albicauda* Cuvier) (Fig. 27). $2n = 36$: $NF = 66$. The autosomes are composed of 14 pairs of meta- or

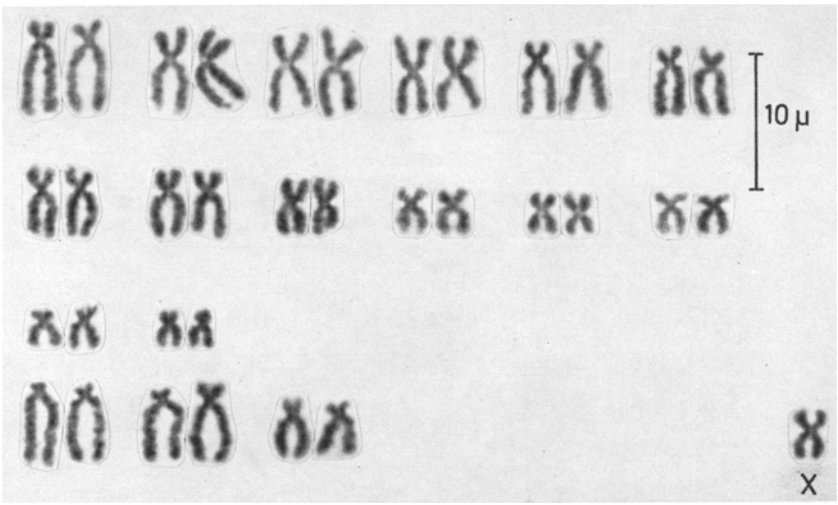


Fig. 25. Karyotype of a male marsh mongoose, *Atilax paludinosus*. 2n = 35; there is no apparent Y chromosome. The second pair of subacrocentrics (bottom row) is heteromorphic

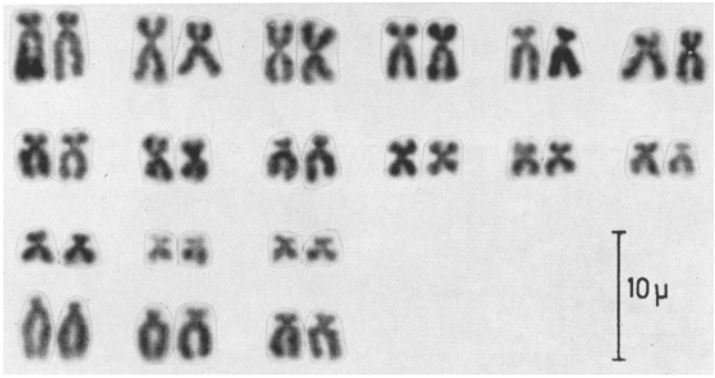


Fig. 26. Karyotype of a female banded mongoose, *Mungos mungo*

submetacentric and 3 pairs of acrocentric elements. The X chromosome is a medium-sized metacentric and the Y is a very small submetacentric, the smallest element.

Black-footed mongoose, ♂, ♀ (*Bdeogale sp.* PETERS) (Fig. 28). 2n = 36: NF = 66. There are 14 pairs of meta- or submetacentric and 3 pairs of acrocentric autosomes. The X chromosome is a medium-sized submetacentric and the Y is a little submetacentric, the smallest element.

Aardwolf, ♂, ♀ (*Proteles cristatus* SPARRMAN) (Fig. 29). 2n = 40: NF = 72. There are 15 pairs of meta- and submetacentrics and 4 pairs

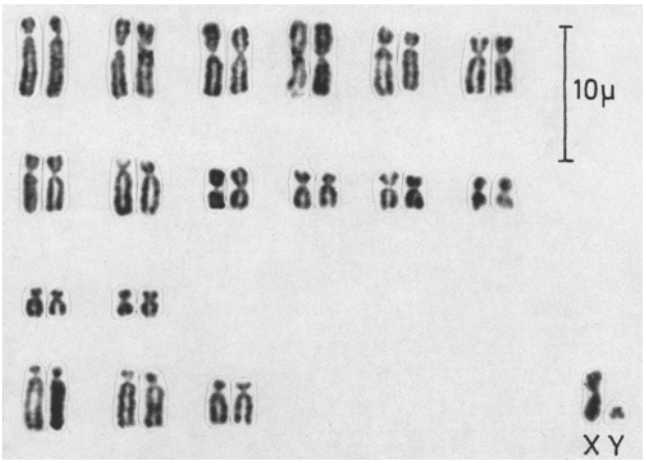


Fig. 27. Karyotype of a male white-tailed mongoose, *Ichneumia albicauda*

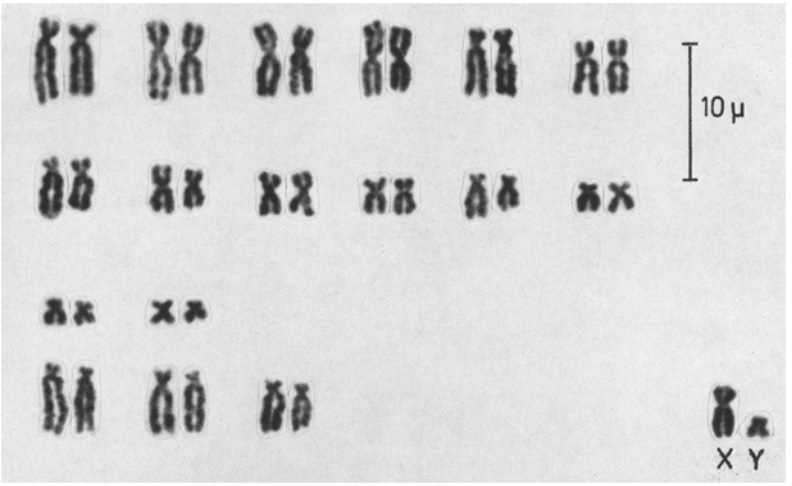


Fig. 28. Karyotype of a black-footed mongoose, *Bdeogale sp.*

of acro- or subacrocentric autosomes. One pair of small submetacentrics bears satellites on the short arms. The X chromosome is a medium-sized metacentric and the Y chromosome is a small submetacentric, the smallest element.

Felidae

Serval, ♀ (*Felis serval* Schreber) (Fig. 30). 2n = 38: NF = 72.

Indian golden cat, ♀ (*Felis temmincki* Vigors et Horsfield). 2n = 38: NF = 72.

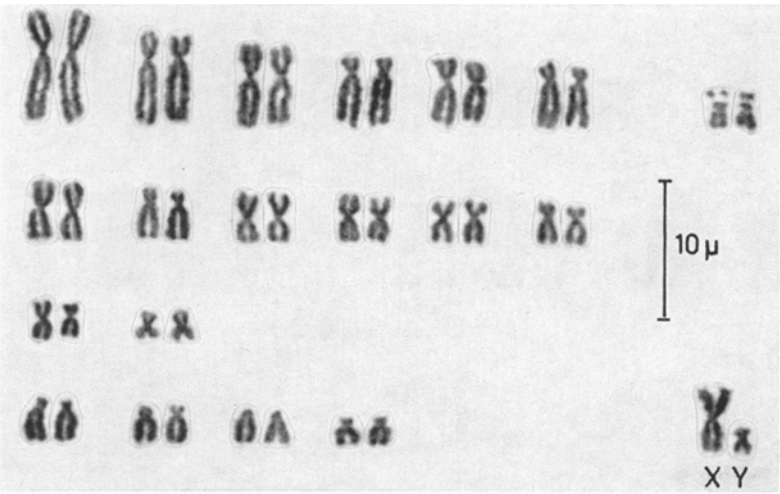


Fig. 29. Karyotype of a male aardwolf, *Proteles cristatus*

Black-footed cat, ♂, ♀ (*Felis nigripes* BURCHELL). 2n = 38: NF = 72.

Canadian lynx, ♂ (*Felis lynx* L.). 2n = 38: NF = 72.

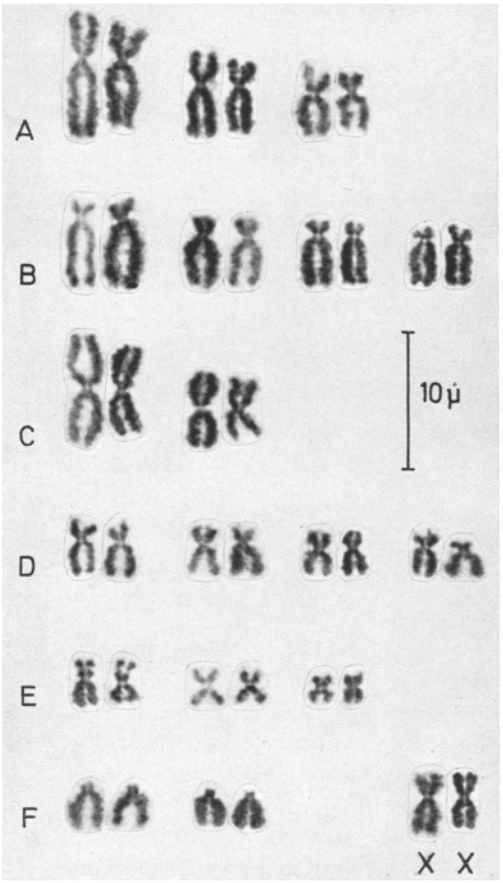
In these 4 species there are 16 pairs of meta- or submetacentric and 2 pairs of acrocentric autosomes. The E_1 pair of small submetacentrics bears satellites on the short arms. The X chromosome is a medium-sized submetacentric and the Y is a small subacrocentric. These karyotypes are indistinguishable from that of the domestic cat as outlined by the San Juan agreement (JONES, 1965), and all 4 species are here represented by the karyotype of the serval. Some variation in the karyotype of the black-footed cat has been reported by other workers (see discussion).

African golden cat, ♀ (*Felis aurata* TEMMINCK). 2n = 38: NF = 72. There are 16 pairs of meta- or submetacentric and 2 pairs of acrocentric autosomes. The X chromosome is a medium-sized submetacentric. The E_1 chromosomes are metacentric and may or may not be satellited; otherwise the karyotype is identical to that of the domestic cat.

Fishing cat, ♂, ♀ (*Felis viverrina* BENNETT) (Fig. 31). 2n = 38: NF = 74.

Leopard cat, ♂, ♀ (*Felis bengalensis* KERR). 2n = 38: NF = 74.

These 2 species have identical karyotypes with 17 pairs of meta- or submetacentric and only 1 pair of acrocentric autosomes. One pair of small submetacentrics bears satellites. The X chromosome is a medium-sized submetacentric and the Y is a small submetacentric. The karyotype is similar to that of the domestic cat, but has only 1 pair of acro-



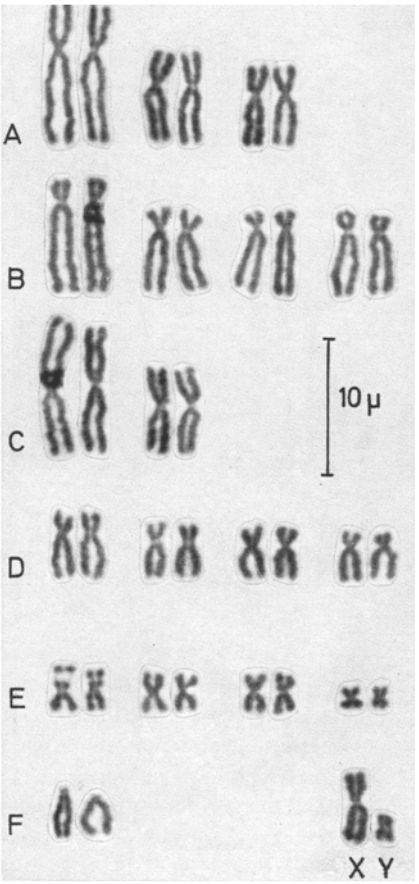


Fig. 30 Fig. 31

Fig. 30. Karyotype of a female serval, *Felis serval*

Fig. 31. Karyotype of a male fishing cat, *Felis viverrina*

centrics in the F group and an additional pair of metacentrics in the E group.

Jaguarondi, ♀ (*Felis yagouaroundi* Desmarest) (Fig. 32). $2n = 38$: $NF = 76$.

This species has 36 meta- or submetacentric and no acrocentric autosomes. One pair of small submetacentrics (E_1) bears satellites on the short arms. The X chromosome is a medium-sized submetacentric. The karyotype differs from that of the domestic cat in having no acrocentrics in the F group, an extra pair of submetacentrics in the B group and an extra pair of metacentrics in the E group.

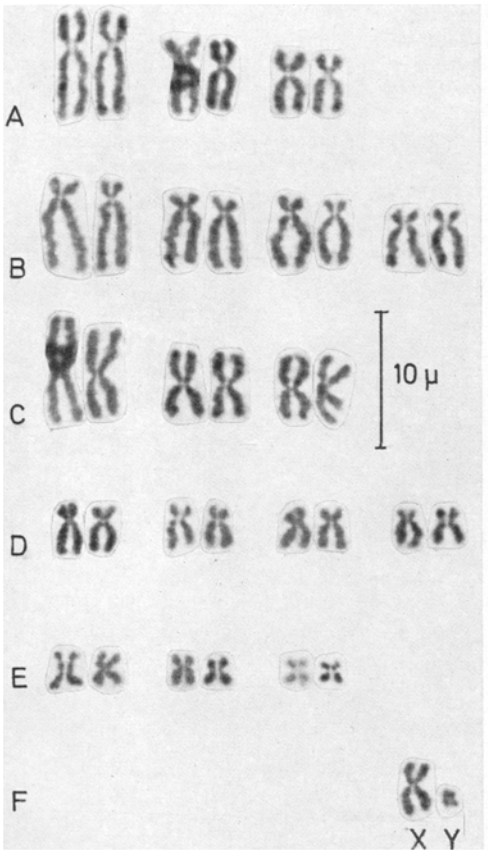


Fig. 32

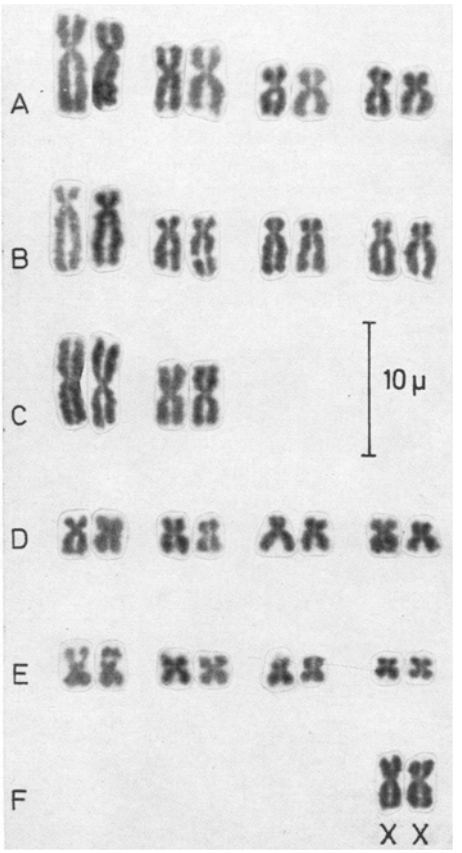


Fig. 33

Fig. 32. Karyotype of a female jaguarondi, *Felis yagouaroundi*. Note absence of F group

Fig. 33. Karyotype of a male Geoffroy's cat, *Felis geoffroyi*. Note absence of F group

Geoffroy's cat, ♂, ♀ (*Felis geoffroyi* D'ORBIGNY) (Fig. 33). $2n = 38$: $NF = 72$.

There are 34 meta- or submetacentric, and no acrocentric, chromosomes in the autosomal complement. The E_1 pair of small submetacentrics is satellited. The X chromosome is a medium-small nearly metacentric element and the Y is a tiny submetacentric. The karyotype differs from that of the domestic cat in having no acrocentrics in the F group and an extra pair of metacentrics in the C group. This karyotype is identical to that of the tiger cat.

Table. *Summarization of all carnivores studied. Species for which there is an entry in column "No. spec." have been studied in this laboratory. All species shown have been judged to have approximately an original type (5%) X chromosome* (OHNO, BEÇAK, and BEÇAK, 1964). *Size of the sex chromosomes, as indicated, is relative to the autosomes, and size and morphology are denoted by the following key: l, large; m, medium-sized; s, small; M, meta- or submetacentric; A, acro- or subacrocentric. Each pair of marker chromosomes in a karyotype is represented by the drawing of one chromosome of the pair, with the exception of the two members of the asymmetrical pair shown for the giant panda. Pinnipedia have not been included in the Table but pertinent references are numbers [17, 20], and [48] in the Taxonomic Bibliography* (pp. 362—367)

	No. spec. ♂:♀	2n	NF	M+ SM	A+ SA	X	Y	Markers	Reference number to Taxonomic Bibliography
Fam. *Canidae*, Subfam. *Caninae*									
Canis familiaris Domestic dog	many	78	80	0	76	1M	sM?		[1, 3, 5, 13, 21, 31, 43, 62, 67, 77, 83, 87, 91, 95, 97, 105]
C. latrans Coyote	1:1	78	80	0	76	1M	s?		[8, 43, 49]
C. dingo Dingo dog		78	80	0	76	1M	sA		[113]
C. aureus Indian jackal		78	80	0	76	1M	sA		[93]
C. lupus European wolf		78	80	0	76	1M	sA		[49]
C. niger Red wolf		78	80	0	76	1M	sA		[42]
Chrysocyon brachyurus Maned wolf		76	78	0	74	1M	sA		[87]
Alopex lagopus Arctic fox	2:1	48—50	94	44	2	1M	sM		[2, 33, 58, 119]
Dusicyon vetulus Hoary fox	1:0	74	76	0	72	1M	?		—
Fennecus zerda Fennec fox	1:0	64	70	4	58	1M	tiny		[74]
Vulpes vulpes Red fox	1:3	34—38	68—76	32	4?	1M	sM	 *	[2, 12, 32, 33, 34, 57, 61, 81, 118, 119, 120]
V. ruppelli Sand fox		40							[74]
V. bengalensis Indian fox		60	72	10	48	mM	sA		[94, 104]

* or microchromosomes.

Table (continued)

	No. spec. ♂:♀	2n	NF	M+ SM	A+ SA	X	Y	Markers	Reference number to Taxonomic Bibliography
Urocyon cinereoargenteus Grey fox	1:1	66	70	2	62	1M	sM		—
Nyctereutes viverrinus Japanese raccoon dog		42	68	26	14	1A?	sA?		[79]
Atelocynus microtis Short-eared dog	0:1	74—76	76	0	72	1M?	?	micro-chromo-somes	—
Fam. *Procyonidae*, Subfam. *Ailurinae*									
Ailuropoda melanoleuca Giant panda		42	78	36	6	?	?		[87]
Fam. *Procyonidae*, Subfam. *Procyoninae*									
Procyon lotor N. American raccoon	1:1	38	70	30	6	mM	sM		[10, 42, 43, 82, 112, 115, 121]
Potos flavus Kinkajou	1:1	38	70	30	6	mM	sA		[15, 25, 44, 112, 121]
Bassariscus astutus N. American cacomistle	1:0	38	68	28	8	mM	sA		[42, 43, 121]
Nasua nasua Coati	1:1	38	68	28	8	mM	sA		[42, 92, 112, 121]
Bassaricyon gabbii Bushy-tailed olingo	1:0	38	68	28	8	mM	sA		[121]
Fam. *Ursidae*									
Selenarctos thibetanus Asiatic black bear	0:1	74	84	8	64	1M	?		[10, 43, 87]
Thalarctos maritimus Polar bear	0:1	74	88	12	60	1M	?		[10, 60]
T.m. × *Ursus middendorfii* Polar × brown bear	0:1	74	88	12	60	1M	?		[60]
Ursus americanus American black bear	1:0	74	84	8	64	1M	sA		[7, 43, 60, 87]
U. arctos syriacus Syrian bear		74	84	8	64	1M	sA		[50]
U. horribilis Grizzly bear	1:1	74	88	12	60	1M	sA		—
Tremarctos ornatus Spectacled bear		52	84	30	20	1M	sA		[88]

Table (continued)

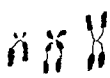
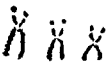
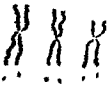
	No. spec. ♂:♀	2n	NF	M+ SM	A+ SA	X	Y	Markers	Reference number to Taxonomic Bibliography
Fam. *Mustelidae*, Subfam. *Mustelinae*									
Mustela erminea Stoat		42 or 44	62	16	26	mM	s?		[26, 44, 76, 103]
M. vison American mink		30	58	26	2	mM	sM		[6, 22, 26, 44, 47, 55, 86, 100, 101]
M. itatsi itatsi Japanese mink		38	68	28	8	mM	sM	?	[61, 65]
M. nivalis Weasel		38 or 42							[26, 84, 90]
M. putorius European polecat	1:1	40	70	28	10	mM	sM		[4, 25, 26, 42, 43, 53, 56, 90, 121]
Martes martes Pine marten		38							[26]
M. americana American marten	1:0	38	68	28	8	mM	sM		[121]
M. foina Stone marten		38							[19]
M. flavigula Yellow-throated marten	0:1	40	72	30	8	mM	?		[25, 26, 121]
M. pennanti Fisher	1:1	38	68	28	8	1M	sM		[9, 121]
Eira barbara Tayra	1:0	38	68	28	8	mM	tiny		[25, 26, 42, 121]
Grison vittatus Grison		38	70	30	6	mM	mM		[25, 26]
Gulo gulo Wolverine	0:1	42	70	28	14	?	?		[26, 121]
Fam. *Mustelidae*, Subfam. *Melinae*									
Meles meles Eurasian badger	0:1	44	72	26	16	mM	sA		[25, 26, 84, 90, 121]
Melogale moschata Chinese ferret badger	1:0	38	74	34	2	mM	sM		[64, 121]
Fam. *Mustelidae*, Subfam. *Mephitinae*									
Mephitis mephitis Striped skunk		50	96	44	4	1M	tiny		[25, 26, 42 43]
Spilogale putorius Spotted skunk		64	74	8	54	1M	tiny		[42, 43]

Table (continued)

	No. spec. ♂:♀	2n	NF	M+ SM	A+ SA	X	Y	Markers	Reference number to Taxonomic Bibliography
Fam. *Mustelidae*, Subfam. *Lutrinae*									
Lutra canadensis N. American otter	0:1	38	64	28	10	mM	?		[10, 121]
L. perspicillata Smooth Indian otter		38	66	28	10	?	?	?	[106]
Aonyx cinerea Oriental small-clawed otter	1:0	38	66	26	10	mM	tiny M		[42, 44, 121]
Fam. *Viverridae*, Subfam. *Viverrinae*									
Genetta genetta neumanni Small-spotted genet	1:1	52	100	46	4	1M	mA	 	[75, 121]
Viverricula indica Small Indian civet	1:1	36	64	26	8	1M	mA		[121]
Civettictis civetta African civet		38	72	32	4	1M	mA		[108]
Prionodon linsang Banded linsang	1:1	34	66	30	2	1M	tiny M		—
Fam. *Viverridae*, Subfam. *Paradoxurinae*									
Nandinia binotata Two-spotted palm civet	1:0	38	66	26	10	1M	sA		[108, 121]
Paradoxurus hermaphroditus Common palm civet		42	66	22	18	mM	s?		[96]
Paguma larvata Masked palm civet	1:0	44	68	22	20	1M	sM		[121]
Arctictis binturong Binturong	1:1	42	66	22	18	mM	sM		[42, 43, 121]
Fam. Viverridae, Subfam. *Cryptoproxinae*									
Cryptoprocta ferox Fossa	1:0	42	70	26	14	mM	sA		[121]
Fam. *Viverridae*, Subfam. *Hemigalinae*									
Fossa fossa Malagasy civet	1:1	42	66	22	18	1M	sM		[121]
Hemigalus derbyanus Banded palm civet	1:0	42	70	26	14	mM	sA		—

Table (continued)

	No. spec. ♂:♀	2n	NF	M+ SM	A+ SA	X	Y	Markers	Reference number to Taxonomic Bibliography
Fam. *Viverridae*, Subfam. *Galidiinae*									
Galidia elegans Ring-tailed mongoose	1:0	44	66	20	22	1M	sM		[121]
Fam. *Viverridae*, Subfam. *Herpestinae*									
Suricata suricatta Slender-tailed meerkat	1:1	36	66	28	6	mM	sM	none	[43, 109, 121]
Herpestes ichneumon Egyptian mongoose		48?					0?	?	[63]
H. auropunctatus (=*H. javanicus*) Small Indian mongoose		♂ 35 ♀ 36	66	28	6	mM	?	none	[23, 24, 27, 28, 70, 106, 109]
Atilax paludinosus Marsh mongoose	1:1	♂ 35 ♀ 36	66	28	6	mM	?	none	[41, 110, 121]
Mungos mungo Banded mongoose	0:1	36	66	30	6	?	?	none	[121]
Ichneumia albicauda White-tailed mongoose	1:0	36	66	28	6	mM	sM	none	[121]
Bdeogale sp. Black-footed mongoose	1:0	36	66	28	6	mM	sM	none	[121]
Cynictis penicillata Yellow mongoose		36	72	34	0	mM	sM	none	[29]
C. sp. Bushy-tailed meerkat		36	70	32	2	mM	s?	none	[111]
Fam. *Hyaenidae*, Subfam. *Hyaeninae*									
Crocuta crocuta Spotted hyaena	1:1	40	72	30	8	mM	sM		[44, 124]
Hyaena hyaena Striped hyaea		40	72	30	8	1M	s?		[42]
Fam. *Hyaenidae*, Subfam. *Protelinae*									
Proteles cristatus Aardwolf	1:1	40	72	30	8	1M	sM		[123]
Fam. *Felidae*									
Felis catus Domestic cat	many	38	72	32	4	mM	sM		*
F. chaus Jungle cat	1:0	38	72	32	4	mM	sM		[70, 106]

* [3, 11, 16, 18, 35, 37, 43, 45, 51, 52, 54, 66, 68, 71, 72, 73, 78, 80, 85, 89, 99, 102, 107, 114, 116, 117].

Table (continued)

	No. spec. ♂:♀	2n	NF	M+ SM	A+ SA	X	Y	Markers	Reference number to Taxonomic Bibliography
F. bengalensis Leopard cat	1:1	38	74	34	2	mM	sM		[44, 66, 107, 121, 122]
F. nigripes Black-footed cat	1:2	38	72	32	4	mM	sM		[30, 42, 44, 121, 122]
F. caracal Caracal lynx		38	72	32	4	mM	sM		[42]
F. lynx Canadian lynx	1:0	38	72	32	4	mM	sM		[10]
F. rufa Bobcat		38	72	32	4	mM	sM		[46]
F. aurata African golden cat	0:1	38	72	32	4	mM	?	?	[69]
F. viverrina Fishing cat	1:1	38	74	34	2	mM	sM		[121]
F. pardalis Ocelot	1:0	36	70	32	2	mM	tiny		[40, 46]
F. wiedi Marguay cat		36	70	32	2	mM	sM		[40, 46, 59, 98]
F. tigrina Tiger cat		36	72	34	0	mM	sM		[59]
F. geoffroyi Geoffroy's cat	1:1	36	72	34	0	mM	tiny M		—
F. yagouaroundi Jaguarondi	0:1	38	76	36	0	mM	?		[46]
F. concolor Puma	1:0	38	74	34	2	mM	sM		[39, 46]
F. serval Serval	0:1	38	72	32	4	mM	?		—
F. temmincki Indian golden cat	0:1	38	72	32	4	mM	?		—
Panthera leo Lion		38	74	34	2	mM	sM		[14, 46, 66, 98]
P. tigris Tiger		38	72	32	4	mM	sM	?	[45]
P. pardus Leopard		38	72	32	4	mM	sM		[38, 39, 44, 46]
P. onca Jaguar		38	72	32	4	mM	sM		[38, 39, 46]
Acinonyx jubatus Cheetah	0:1	38	74	34	2	mM	?		[36, 39, 46]

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[1] The often cited Mammalian Chromosomes Newsletter is an informal publication which may be obtained by writing to Dr. T. C. Hsu, M.D. Anderson Hospital and Tumor Institute, Houston, Texas 77025, U.S.A.

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Discussion

The results that have been presented will be discussed in individual families and the reader will find it helpful to make frequent reference to the table. References concerning individual species are listed by species in the bibliography. The phylogeny of carnivoran families and the marker chromosomes to be found in each family are pictured in Fig. 34. For uniformity and simplicity the nomenclature of MORRIS (1965) has been followed.

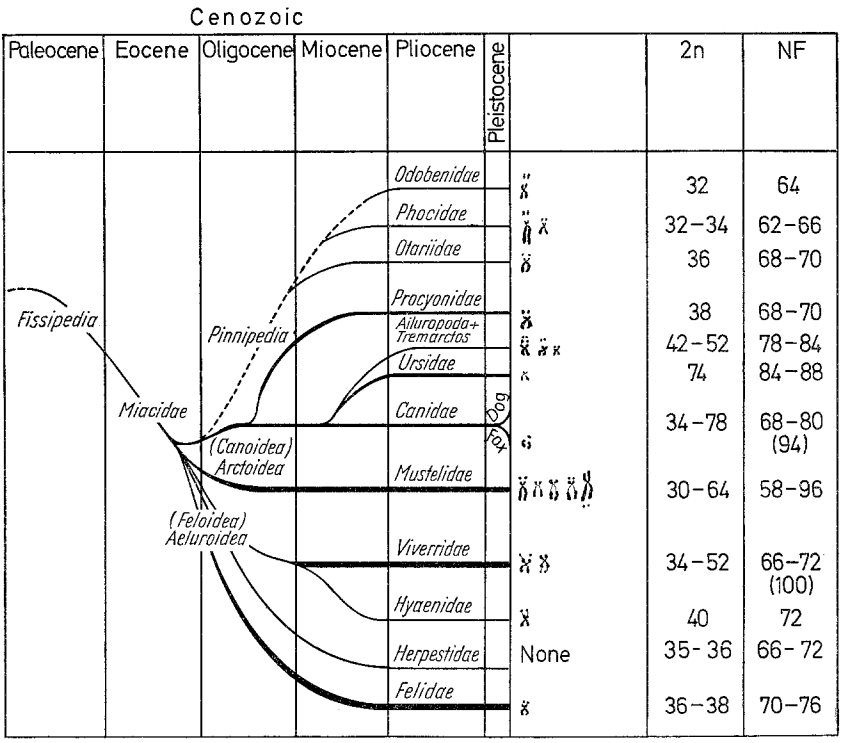

Fig. 34. Depicts the carnivoran phylogeny as modified from ROMER (1966), and THENIUS and HOFER (1960) to accommodate the cytogenetic viewpoint. The marker chromosomes shown for each family occur in one or more species of that family

In the Order *Carnivora* the Suborder *Fissipedia* (land-living carnivores) is divided into two superfamilies, the *Canoidea* (*Arctoidea*) and the *Feloidea* (*Aeluroidea*). The superfamily *Canoidea* is composed of the *Canidae*, *Procyonidae*, *Ursidae*, and *Mustelidae* and these families are thought to be derived from a canid stock which had its origin from the *Miacidae* in the late Eocene. The superfamily *Feloidea* is composed of the *Viverridae*, *Hyaenidae* and *Felidae* and these families arose from the feloid stock which was derived from the *Miacidae* prior to the origin of the canid stock.

Enough species in each of the major carnivore families have now been studied to give us at least an impression of the chromosome constitution in this order. It can be seen from the table that there is a good family karyotypic pattern in the *Procyonidae*, the *Ursidae*, the *Felidae*, and the *Hyaenidae*. The *Mustelidae*, the *Canidae*, and the *Viverridae* are large families which offer a diversity that is best handled in smaller groups. Some of the recognized subfamilies have excellent group patterns, for instance, the *Lutrinae* and the *Herpestinae*. Others, such as the *Caninae* and the *Mustelinae* are too large and too diversified in pattern to be contained within one group when chromosome morphology is used as a taxonomic parameter. The use of chromosome morphology in this capacity may be debated, but it is known for instance that for successful hybridization, *i.e.*, the production of fertile hybrids, two species of mammals must have almost identical karyotypes. Conversely, while we cannot state that two animals with identical karyotypes are necessarily closely related, we can say that known close relatives do have similar karyotypes. Therefore, dissimilar karyotypes probably indicate a relative distance in a relationship.

Chromosomal Polymorphism

Chromosome polymorphism within the species has been revealed in several cases by investigation of more than one specimen. For example, diploid numbers in the following animals may vary as indicated: pronghorn (*Antilocapra americana*), $2n = 56$, 57 and/or 58 (WURSTER and BENIRSCHKE, 1967a, b); red fox $2n = 34$ to 38; arctic fox $2n = 48$ or 50. In other cases chromosome differences have been revealed between isolated populations of single species. For example, the African buffalo (*Syncerus caffer*) from Kenya was found by ULBRICH and FISCHER (1967) to have a diploid number of 52 while the African buffalo (*S. caffer*) from the Congo was reported by HECK, WURSTER and BENIRSCHKE (1968) to have $2n = 54$. The animals of these two isolated populations differ considerably in appearance and habits, and may in actuality represent two distinct species. Similarly, three or more specimens of moose (*Alces alces*) from Scandinavia (AULA and KÄÄRIÄINEN, 1964;

GUSTAVSSON, 1965) had diploid numbers of 68 and three specimens of moose (*A. alces*) from the northern United States and Canada had 2n = 70 (WURSTER and BENIRSCHKE, 1967a). Here again we may have two separate species or we may be seeing two isolated populations of one species engaged in the slow process of becoming separate species.

Intraspecific Karyotype Discrepancies

Occasionally there are discrepancies between the results of different workers, using similar modern methods, concerning a given species, and explanations cannot be offered without further investigation; for example, one specimen of small-spotted genet had 2n = 54 (MATTHEY, 1965) and four other specimens had 2n = 52 (HSU, personal communication, and this laboratory), and two specimens of black-footed cat had one pair of acrocentrics in the F group (HSU and ARRIGHI, 1966; GROPP, GEISLER, and LEYHAUSEN, 1968) while three other specimens had two such pairs in the F group similar to a domestic cat (this laboratory). Further investigation revealed that the crossing of a black-footed cat with one pair of acrocentrics with a mate having two pairs of acrocentrics yielded an offspring with three acrocentrics ($1^1/_2$ pairs). This pedigree has been discussed by GROPP, GEISLER, and LEYHAUSEN (1968). The study of many specimens from different populations of any species will eventually be instructive in the processes of speciation and hybridization.

Karyotype Evolution

Karyotype evolution may proceed along different pathways in various populations of a species leading to a distinction in chromosome morphology that is sufficient to be a reproductive barrier, and therefore a factor in the production of two species where there was formerly one. Since karyotypic changes must occur according to certain rules of chromosome mechanics, it may be possible through the study of chromosome morphology in existing species to deduce something about the phylogeny and taxonomy of a group. The mechanics of chromosome evolution allow for a change in chromosome number and/or a change in form. Any change in form requires at least one break in the chromosome; subsequent rearrangement of chromosomal material accounts for karyotype evolution. If a break occurs in one place only, the broken ends may reunite with the same or another chromosome, or the broken piece may be lost; multiple breaks permit exchange of parts of chromosomes. Some of the important mechanisms are the following: 1) reciprocal translocation, 2) pericentric inversion, 3) centric fusion between two acrocentric elements resulting in a large meta- or submetacentric chromosome: the remaining small fragment functions as a small chromo-

some or is deleted, thus reducing the chromosome number by one, 4) tandem fusion which involves a break near the centromere of one chromosome and near the distal end of the arms of another chromosome with subsequent rearrangement that produces a longer chromosome of any type, plus a very small chromosome that may be lost or retained. If too many of these mechanisms are used in the evolution of a karyotype, its evolutionary pathway will be difficult to decipher. If, on the other hand, a group tends to use one mechanism exclusively, the pattern will be more evident to the observer. An example of the latter is the consistent use of the Robertsonian type of karyotype evolution (ROBERTSON, 1916), *i.e.*, centric fusion, among members of the *Bovoidea* (HECK, WURSTER and BENIRSCHKE, 1968). The NF in the *Bovoidea* ranges only from 58 to 62 with very few exceptions. Almost all variations of the diploid number are readily explicable by centric fusion; as the diploid number decreases, the number of metacentrics increases and the NF remains constant (WURSTER and BENIRSCHKE, 1967b). Within the large order *Carnivora* there is in evidence no single, consistent pathway of karyotype change.

Marker Chromosomes

Remarkably constant throughout this large order, however, is the presence of a satellited marker chromosome. So consistent is this, and so uniform in appearance is it within the *Feloidea*, that it early acquired the name "carnivore chromosome". Characteristically, the "carnivore chromosome" is a small to medium submetacentric element with satellites on the short arms. Among the *Canoidea* its form is quite diverse, but it is equally ubiquitous. It is not known how important this may be in determining the relationship among species; the form of the marker does tend to be uniform within families thus indicating a certain similarity in mechanisms of karyotype evolution used by the species of a family. The family with the most uniform karyotype pattern, the *Felidae*, also has the most uniform type of marker, and the family with the most diversity in its karyotype patterns, the *Mustelidae*, also has the greatest diversity of forms in its marker.

Canidae

The *Canidae* come from an arctoid stock dating back to the very beginning of arctoid history in the Eocene and from which also arose the *Ursidae* and *Procyonidae*. Among the present day *Caninae* we find a number of "dogs", all of the genus *Canis*, with identical karyotypes; these include the domestic dog, the dingo dog, the coyote, the Indian jackal and the European and red wolves. Most of these species hybridize successfully (GRAY, 1954, 1966), which indicates a close relationship. Serologically, the dog falls between the wolf and coyote in similarity

but is somewhat closer to the latter (LEONE and WIENS, 1956). The hoary fox, the small-eared fox (short-eared dog), and the maned wolf, all of South America, represent three different genera, but possess similar karyotypes which differ in only minor respect from that found in the genus *Canis*. The fennec fox of Africa and Asia and the grey fox of North and South America also have nearly identical karyotypes which are similar to that of *Canis* in having nearly all acrocentrics but fewer of them. Each of these foxes possesses two pairs of acrocentric marker chromosomes with achromatic regions in the long arms adjacent to the centromere. The marker chromosome of the *Canidae*, when present, is similar to that found in the *Ursidae* and some members of the *Mustelidae*, but quite different from the typical "carnivore chromosome" found in most members of the other families. Two canids possess apparent microchromosomes; the red fox has 32 metacentric macroautosomes plus anywhere from 0 to 4 microchromosomes, and the short-eared fox (or dog) of South America has 72 acrocentric macroautosomes with 0 to 2 microchromosomes. The reported modal diploid numbers for the red fox have ranged from 34—42, the variation in number being provided by the number of microchromosomes present, and representing, perhaps, a species polymorphism. A pair of satellited chromosomes was described for the red fox by WIPF and SHACKELFORD (1942) but they made no mention of microchromosomes. Apparently, when satellited chromosomes are seen, microchromosomes are not seen, thus raising the question of whether the microchromosomes might be detached satellites. Studies concerning this problem are underway in this laboratory. The fennec, red, grey and Indian foxes and the raccoon dog all differ in their karyotypes but do group together by way of a similar NF. The sex chromosomes of the raccoon dog reportedly differ markedly from the typical and very uniform canid sex chromosomes and its autosome morphology is unlike all others. It is most desirable to study this species with modern methods to obtain a clear-cut karyotype since this single report dates to 1929. The arctic fox has such a distinctive karyotype that it does not fit conveniently anywhere. Having a chromosome complement consisting of 48—50 elements, nearly all of which are metacentric or submetacentric, it may represent the most highly evolved and specialized, and, karyotypically, the most stable of the canids thus far studied. It is reported to cross with the genus *Vulpes* but the hybrids are sterile (WIPF and SHACKELFORD, 1949). The foxes have each achieved a karyotypic distinction from the dogs, *i.e.*, the genus *Canis*, which has a uniform karyotype pattern. This distinction is great enough to suggest the need for one or more subfamilies separate from *Caninae*, to accomodate the foxes. Of all the carnivoran families only the *Canidae* show the inverse relationship between the diploid number and the number of

mediocentric elements that is suggestive of a Robertsonian mechanism of karyotype evolution. However, this relationship is not precise in the way that can be found among members of the *Bovoidea* (HECK, WURSTER, and BENIRSCHKE, 1968).

Procyonidae

The *Procyonidae* presented here are so similar to one another in karyotype that it would be difficult to distinguish among them solely on the basis of chromosome morphology. All of them can be arranged to resemble the standard domestic cat karyotype according to the San Juan agreement with the satellited "carnivore chromosome" fitting into the proper E_1 position. They all have a diploid number of 38 and an NF of 68 or 70. Karyologically, the resemblance of these *Procyonidae* to all of the *Felidae* thus far studied is striking, but there is no evidence that relates the two families closely. Serologically, the *Felidae* and *Procyonidae* are only very distantly related (PAULY and WOLFE, 1957; LEONE and WIENS, 1956). Classically, this is a family considered to be closely related to the canids, having split off from the canid stock in the Oligocene. ROMER (1966) characterizes the members of this family as seeming to be "a series of persistently primitive relics of the arboreal ancestors of the dog"; their dentition, however, reflects their mixed diet and seems to represent a "reversion from the primitive carnivorous canid adaptation back toward an omnivorous diet". The giant panda is a procyonid, placed in an isolated subfamily; it has even better development of the grinding teeth and is almost completely herbivorous. This species will be discussed with the bears, because there is much evidence of its even closer relationship to that family.

Ursidae

Subsequent to the origin of the *Procyonidae*, the *Ursidae* also arose from the canid stock and, presumably, because of this common origin in the primitive dog stock, members of these two families share some similar structural and dietary characteristics. Karyologically, almost all the bears studied so far are very similar to one another ($2n = 74$) and might, with excellent chromosome preparations, even be found to be identical. ROMER (1966) states that most modern bears are so similar structurally that they can be included in a single genus, *Ursus*. Several species of bears that are now placed in separate genera are known to hybridize successfully (GRAY, 1954, 1966; BENIRSCKHE, 1967) suggesting a close relationship that is probably at least intrageneric. An exception to the ursid pattern is the South American spectacled bear with 52 chromosomes, relatives of which existed in both North and South America in the Pleistocene (ROMER, 1966). This bear has the marker

chromosome of the *Procyonidae*, and a karyotype that differs markedly from the other bears although its NF is similar. On the basis of karyotype analysis there is some indication that this species may represent a very early offshoot of the *Ursidae* or an intermediate between the *Ursidae* and *Procyonidae*. It may also be more closely related than heretofore thought to the giant panda ($2n=42$) of the *Procyonidae*, which it resembles in some characteristics. Although the giant panda is classified with the procyonids, anatomically it is indicated to be a primitive offshoot of the early bear stock (ROMER, 1966; DAVIS, 1964). LEONE and WIENS (1956) investigated the serological relationships of the raccoon, the bears and the giant panda and concluded that the giant panda definitely belongs in the family *Ursidae*. The karyotype of the giant panda (NEWNHAM and DAVIDSON, 1966) more closely resembles that of the procyonids than that of the bears. It has an asymmetrical pair of marker chromosomes, one of which is identical to that found in the raccoon, and the other of which is similar but has longer short arms. Neither resembles the type of marker found in bears. Although the diploid number of the panda is closer to that of the procyonids, its NF lies midway between the procyonids and the ursids. One could thus imagine the off-shoot of an ancestor of the spectacled bear and the giant panda at the very origin, or even slightly prior to the origin, of the *Ursidae* carrying with it the apparently primitive and stable marker chromosome found in the *Procyonidae*. The marker that is found commonly in the *Ursidae* and some of the *Canidae* could be the result of pericentric inversion of the presumed primitive marker or "carnivore chromosome" found in the *Procyonidae*, the *Pinnipedia* (FAY, RAUSCH, and FELTZ, 1966; CORFMAN and RICHART, 1964; HUNGERFORD and SNYDER, 1964), and the *Feloidea* all of which arose earlier.

Mustelidae

The *Mustelidae* originated from the miacids or primitive canid stock in the late Eocene and today they compose a diversified group the general form and habits of which are relatively primitive. The applicable primitive characteristics, according to ROMER (1966) are as follows: small size, short stocky limbs, full complement of toes, and the presence of many forest-dwelling arboreal types. The fossil history of the mustelids is not good and classification of the many diverse modern forms is difficult. Karyotypically, the martens, fishers, wolverine, tayra, grison (all belonging to the *Mustelinae*) and otters (*Lutrinae*) are very similar to one another and have the type of marker that is found in some of the canids and ursids. The genus *Mustela* (ferrets, minks, weasels) shows considerable diversity in karyotype pattern and type of marker chromosome with the mink being markedly different, having a lower

diploid number, lower NF and an odd marker. There is no consistent "*Mustela* karyotype pattern" such as one can expect to find within a genus, and, indeed, as we have seen, within a whole family. This is a challenging group, of economic as well as biological interest, that needs more adequate study. Some hybridization is reported among members of the *Mustelinae* (GRAY, 1954, 1966) but it is neither widespread nor very successful. The *Mustelinae* and *Lutrinae* are apparently traceable to the Oligocene while the *Melinae* (badgers) and *Mephitinae* (skunks) are traceable only to the Miocene (ROMER, 1966). The badgers have a somewhat higher NF than the two earlier or older subfamilies, but are remarkable for their quantity and diversity of marker chromosomes. Fig. 34 shows the great diversity of marker chromosome structure found in the *Mustelidae* in general and this is an indication of a tendency toward chromosomal rearrangement in this group. The skunks are remarkably different from the rest of the family and also from each other, each species having a highly individualistic karyotype. Serologically, anti-skunk (striped skunk) serum was shown to be highly specific, and no closer relationship to tayra and ferret was demonstrated than to the *Ursidae* (PAULY and WOLFE, 1957). Investigations on other species of the *Mephitinae* are needed.

Viverridae

The *Viverridae* represent a continuum of the basal stock of the *Feloidea* (*Aeluroidea*). They possess many primitive characteristics, and occupy a position in the *Feloidea* comparable to that of the *Mustelidae* in the *Canoidea* (*Arctoidea*). ROMER (1966) states that in dentition and other respects civets are similar to ancestral miacids from which they are descended. The viverrids are exclusively an Old World family but are widespread through Asia and Africa. As might be expected, a number of catlike characteristics are found among the viverrids since the cats and the viverrids represent two branches of a major split in the primitive feloid stock. Karyotypically, they do not vary as much as the *Mustelidae* but there are some differences between the subfamilies. With the exception of the genet, the NF varies only from 66—72 for the whole family. Every member of the family, with the exception of the *Herpestinae*, bears well defined satellited marker chromosomes. Eight species of the subfamily *Herpestinae* have been studied chromosomally, and these species represent seven different genera which are based on the adaptive trend of their dentition and skulls. Karyotypically, they are all nearly identical to one another and, without exception, they bear no satellited marker chromosome. It has been proposed on the basis of anatomical structures that the subfamily *Herpestinae* (mongooses) be elevated to the rank of family *Herpestidae* (GREGORY and HELLMAN, 1939). Karyologically, the distinguishing features of this group as a whole are the

lack of a marker chromosome, and the uniformity of karyotype among the members studied thus far, and this provides karyological support for GREGORY and HELLMAN'S separate family grouping. Two species, the small Indian mongoose and the marsh mongoose, have an unusual sex determining mechanism which has not yet been deciphered. The other members appear to have a normal XY sex determination. The subfamily *Viverrinae* (genets and some civets) is also notable for some different features, but few species have been studied. The small-spotted genet is the only species of genet that has been studied so far; it is remarkable for its diploid number of 52 (or 54 found by MATTHEY), its NF of 100 and its possession of two types of marker chromosomes. Although it is unlike the other members of its subfamily karyotypically, it shares with two of them a medium-sized acrocentric Y chromosome which is unlike other viverrids. Three members of this subfamily also possess a marker chromosome that is unique among the *Viverridae*; the small Indian civet is an exception to this feature and has the more common type of marker. The two-spotted palm civet of the *Paradoxurinae* has been removed from that subfamily and, on the basis of anatomical structures, it has been elevated to the rank of subfamily, the *Nandiniinae*, by GREGORY and HELLMAN (1939). Karyologically, this species is similar in all respects, including the Y chromosome and marker chromosome, to the members of the *Viverrinae*. Its removal from the *Paradoxurinae* and placement with the *Viverrinae*, rather than a new subfamily, might therefore be considered. The common palm civet, the binturong, the Malagasy civet and the banded palm civet are karyotypically essentially identical. The masked palm civet and the fossa are very similar. If two pairs of acrocentrics in the ring-tailed mongoose were to fuse in a Robertsonian manner it would then be identical to the binturong. These comparisons are meant only to point out how many karyotypic similarities there are among the members of the four subfamilies *Paradoxurinae*, *Hemigalinae*, *Galidiinae* and *Cryptoproctinae*, while the other two subfamilies, *Viverrinae* and *Herpestinae* each have remarkable and distinctive karyotypic features which are not shared with the other subfamilies. Hybridization studies would be very informative in this family. Several species of *Genetta* and two species of *Paguma* have been reported to hybridize (GRAY, 1954) but hybridization information concerning the *Viverridae* is scant. *Cryptoprocta* (fossa) has often been likened to the cats for anatomical reasons, but karyologically these two are not similar.

Hyaenidae

The *Hyaenidae* are a Miocene offshoot from the *Viverridae* apparently representing specialized derivatives of such a typical viverrine as the African civet (*Civettictis*) (GREGORY and HELLMAN, 1939). The family

is composed of two subfamilies and only four species representing three genera. All three genera have been karyologically studied and have nearly identical karyotypes with a diploid number of 40 and the typical "carnivore chromosome".

Felidae

More members of the *Felidae* have been studied chromosomally than of any other family, and the uniformity of the karyotype pattern is remarkable. Of 22 species thus far studied 18 are reported to have a diploid number of 38 and four, all South American species, to have 36. The NF varies only from 70—74 (one exception, the Jaguarondi, with 76) and the structure of the sex chromosomes is uniform. All species have the common type of marker with the possible, but improbable, exception of the African golden cat. There is some variation in the number of acrocentrics present in each species. Cats are structurally and karyotypically similar and most, if not all, (excepting the cheetah for anatomical reasons) are often included in the genus *Felis*, although the genus denomination *Panthera* is still widely used for the lion, tiger, leopard and jaguar. Serologically, there is some evidence that the tiger and mountain lion may belong to a different genus (PAULY and WOLFE, 1957). As a whole the cats are so similar chromosomally that for the purposes of this paper it is reasonable to use the three genera *Felis*, *Panthera* and *Acinonyx* as listed by MORRIS (1965). There are some non-chromosomal reasons to divide this large genus *Felis* into a number of genera, and karyotypically there is some support for placing the fishing cat and leopard cat in the genus *Prionailurus*, the ocelot, tiger cat, marguay cat, and Geoffroy's cat in the genus *Leopardus*, and the jaguarondi in the genus *Herpailurus* as THENIUS and HOFER (1960) have done. The cheetah is karyotypically identical to the fishing and leopard cats but is for anatomical reasons placed in a separate genus. The jaguarondi is karyotypically unique among the cats so far studied in having a diploid number of 38 but no acrocentric chromosomes. There is no karyotypic support for placing the golden cats into the genus *Profelis* (after THENIUS and HOFER, 1960) since their karyotypes are indistinguishable from that of the domestic cat and others of the genus *Felis*. Karyotypically, the cats differ from each other very little, but the overall view offers some support for the above mentioned genera as used by THENIUS and HOFER (1960). From chromosome morphology alone one would judge all the cats to be very closely related; the slight diversification in this very old family probably indicates an explosive and uniform, rather than a slow and nondirectional, type of family evolution. The cat karyotype pattern can be considered a stable one. Fairly wide hybridization reported among cats (GRAY, 1954, 1966),

indicates a very close relationship among some of the species. Serologically, the *Felidae* are more closely related to the *Hyaenidae* than to any other group (PAULY and WOLFE, 1957; LEONE and WIENS, 1956).

Karyotype Interpretation

With respect to diploid number, NF, number of metacentric or submetacentric chromosomes and type of marker chromosome, the carnivores can be divided into two groups, one composed of the *Ursidae* and *Canidae* and the second composed of the remaining five families.

The *Ursidae* have a high diploid number and a low number of metacentrics, and the *Canidae* range in diploid number from 34—78 with the number of metacentrics varying inversely with the diploid number. This group has a characteristic marker chromosome, an acrocentric or subacrocentric element with an achromatic region in the long arm adjacent to the centromere.

The *Mustelidae*, *Viverridae*, *Felidae*, *Procyonidae* and *Hyaenidae* form the second group all having lower diploid numbers and greater numbers of metacentrics. Except for the diversity in the *Mustelidae*, the common marker chromosome is a small submetacentric or subacrocentric element with satellites on the short arms.

The following species are exceptions to the two groupings: 1) The spectacled bear (*Ursidae*) lies between the groups with regard to the diploid number, has an NF in the *Canidae-Ursidae* range, and has a number of metacentrics and a marker chromosome that places it in the second group. 2) The red fox (*Canidae*) has a diploid number, a number of metacentrics, an NF and possibly a marker chromosome all of which place it in the second group. 3) The spotted skunk (*Mustelidae*) lies apart from the second group by virtue of its high diploid number, and low number of metacentrics. Its marker chromosome is consistent with those of the *Mustelidae* (of the second group) by virtue of the diversity in form of the marker that is found in this family. If a Robertsonian fusion of all its acrocentric elements were to occur, this species would be karyotypically similar to the Chinese ferret badger of the *Melinae*. 4) The arctic fox (*Canidae*) fits in neither group: it has an intermediate diploid number and a number of metacentrics and an NF much greater than either group. 5) The small-spotted genet (*Viverridae*) also fits in neither group having an intermediate diploid number, and a number of metacentrics and an NF much greater than either group.

The small-spotted genet, the striped skunk and the arctic fox group together by themselves in having a diploid number range of 50—52, an NF range of 95—100, and a number of meta- or submetacentrics equal to 44 or 46. The small-spotted genet has a karyotype almost identical to the striped skunk except that it has a fairly large acro-

centric Y chromosome instead of a minute element, and it has two pairs of markers that are different in form from the skunk's one pair. The arctic fox karyotype appears identical to that of the striped skunk except that it has one more pair of small metacentrics and one less pair of acrocentrics and appears to lack a marker chromosome. Since these three species represent three different families and two different superfamilies, a close relationship could hardly be implied by these karyotypic similarities. Instead, these findings demonstrate that the use of a cytogenetic parameter to determine relationships between and among species is probably useful only within a defined taxonomic group and its border areas. Each of these three species lies, by these chromosomal parameters, well outside of its own group, and by virtue of their very similar karyotypes they form together an isolated group. This can be considered evidence that there are defined mechanisms of karyotype evolution that may yield similar results karyotypically in completely independent groups (parallelism). This is also shown at the family level by the apparent parallel development of similar karyotypes by the *Procyonidae* and *Felidae*. It is conceivable that the procyonid-felid karyotype pattern is representative of that which existed in the primitive miacids with all other patterns having evolved therefrom. This would have involved a considerable amount of chromosomal fissioning, a mechanism propounded by TODD (1967) and NADLER and HARRIS (1967) and for which we find as yet no clear-cut proof. In every Order studied there is abundant evidence that Robertsonian fusion of chromosomes is a spontaneous and frequent occurrence. As examples of such karyotype evolution from a primitive form with a high diploid number to one with a lower diploid number of the modern form we cite the following: 1) The Przewalski horse has $2n = 66$ while all modern horses have $2n = 64$ (BENIRSCHKE, 1967). 2) The same trend (decreasing number of acrocentric chromosomes with increasing numbers of metacentrics through various types of fusion) can be followed in the remaining members of *Equidae*. Thus, the species geographically farthest removed from the more ancestral Przewalski horse ($2n = 66$), the Hartmann zerba of South Africa, possesses the lowest diploid number of the family ($2n = 32$). 3) Numerous examples of translocational aberrations have been described in man. These balanced translocations are not necessarily in themselves harmful or phenotypically identifiable and it is conceivable that through the chance marriage of translocation carriers there may someday be, or there may now be, human populations with $2n = 44$.

Conversely, we are not aware of a single instance of verifiable fissioning in man or other mammals. This would require the acquisition of new centromeres, an event which should be readily ascertained by cytologic techniques. Of course, the concept excludes polyploidization, as we are

satisfied with the evidence of a nearly constant DNA content in mammals and see no evidence that trisomies, etc. are ever an advantageous event. In this context it is important to make reference to the finding by McFee, Banner, and Rary (1966) of two populations of *Sus scrofa*, those with $2n = 38$ and $2n = 36$, as well as intermediates. All pigs studied to date have been found to possess 38 chromosomes. These authors postulate that *Sus scrofa*, introduced to the USA may have possessed 36 chromosomes and then mixed with domestic pigs to form these three groups of karyotypes. A single translocational event (of 2 acrocentrics of the domestic pig or the wild form) explains the event better than assuming, as one is otherwise forced to, that during domestication the wild pig changed its chromosome number from 36 to 38. This is an important possible example which needs investigation of European wild pigs. Those from Japan (Muramoto, Makino, Ishikawa, and Kanagawa, 1965) had identical karyotypes with the domestic animal.

For the purposes of our own investigation then we are still convinced that fusions and inversions are the commonest events of karyotype evolution and that the original, or primitive karyotypes of mammals must have possessed mostly acrocentric elements. With reference to the carnivores we envisage that the primitive miacids and their ancestors had at least 80 chromosomes from which current species have evolved. In some families, like the *Canidae*, little change has taken place alongside marked phenotypic evolution, while other families, like the *Felidae*, had both marked phenotypic and karyotypic development. It is, of course, the ultimate aim of studies such as these to ascertain whether a correlation exists between the phenotypic and karyotypic evolution. More specifically, the question can be posed whether the reason for a particular offshoot from ancestral stock of what now is a distinct family is related to karyotypic evolution. Further, are there reasons why seemingly specific conservative karyotype patterns are followed for instance in the *Felidae*, but not in *Mustelidae*? These and many other questions cannot be answered as yet since only a few species have been examined critically. Moreover, it is here that taxonomists with a special interest in this Order can point to critical intermediate forms whose cytogenetic examination might be especially helpful to ascertain evolutionary paths. In this connection then it is perhaps no accident that the only *Felidae* with 36 elements (? the most evolved) are of South America, a point which favors Robertsonian mechanisms. Perhaps the spectacled bear with 52 elements, the others having 74, is subject to the same trend. Further, the consistent presence of a marker chromosome throughout the *Carnivora*, with the exception of the *Herpestinae*, attests to its stability regardless of evolutionary changes; the diversity

of its form, especially within the family *Mustelidae*, is evidence of a number of different forces, i.e., translocation, pericentric inversion, fusion, possibly fission, etc. at work on these karyotypes. When more species can be compared critically it may then be possible to use this marker in establishing relationships not currently evident. Similarly, the lack of acrocentrics in the jaguarondi with an otherwise similar felid karyotype strongly suggests pericentric inversion in one or two elements which may eventually be made visible by analysis of meiotic elements in possible hybrids. Meiosis studies are also needed in order to unravel the sex-determining mechanism of the marsh mongoose with its possibly translocated Y and the small Indian mongoose.

All carnivoran families are linked by a complex network of common characteristics, and taxonomic groups will vary according to the parameter(s) used as criterion. Chromosome analysis is a relatively new parameter that, obviously, cannot be used alone but it is useful when combined with others. No single parameter should be the basis for the classification of the complex assemblage of features composing species. Cytogenetic studies are of particular interest when applied to the process of speciation and hybridization; occasionally they are of particular value in settling difficult relationships, as in the aardwolf.

Species and Hybridization Concepts

As a working concept, a species is composed of a breeding population that does not interbreed with other than its own kind, regardless of circumstances. In actuality, a species is a dynamic biologic entity that defies such strict limitations and may reveal its flexibility when either forced or given the opportunity to do so. It may adapt its reproductive compatibility with closely related organisms to fit the circumstances. For instance, two species that live sympatrically in nature and do not interbreed may indeed do so when placed in circumstances that isolate them from their normal mates. There are many examples of separate species, and even separate genera, interbreeding in captivity to form hybrids of various degrees of viability and fertility (Gray, 1954, 1966). These offspring may properly be called interspecific or intergeneric hybrids since the parental species do not naturally, even when given the opportunity provided by sympatric living, form breeding populations. Allopatric species may, however, interbreed freely when placed together. For example, the Eurasian red deer (*Cervus elaphus*) and the North American wapiti (*Cervus canadensis*) have both been introduced into New Zealand recently. These two species mix readily now as a breeding population and produce fertile hybrids (Howard, 1965). Depending on the criteria one adopts, one may then wish to consider these species as one and reserve judgement of other closely related forms until such

critical tests may be used. Clearly, this is impractical and it is for this reason, among others, that the usual species concept pays little attention to reproductive barriers. From an evolutionary view, these barriers are, of course, of great importance and one prominent barrier which might evolve in speciation of sympatric animals is a profound karyotypic change. Pressures of allopatric species to change reproductive modes, behavior, karyotypes, etc. may be considerably less than among sympatric forms. When divergence of karyotype has evolved, this commonly represents an effective barrier, not so much for hybridization as for sterility, and it is from this vantage point that it may be advantageous to examine Families or Orders when complete groups have been studied.

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Dr. Doris H. Wurster, Dr. K. Benirschke
Department of Pathology, Dartmouth Medical School
Hanover, N. H. 03755, U.S.A.