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CYTOGENETIC DATA ON THE RODENT FAMILY
GERBILLIDAE

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Gerbils and jirds comprise 16 genera with between 86 and 90 species (Nowak and Paradiso, 1983; Carleton and Musser, 1984). The group is unique and probably represents a separate family of rodents—the Gerbillidae (Heptner, 1933; Chaline *et al.*, 1977; Carleton and Musser, 1984; Qumsiyeh, 1986a). Recent morphologic, karyotypic, and electrophoretic studies have documented an accelerated rate of evolution and diversification in several lineages within this economically and medically important group of rodents (Benazzou *et al.*, 1982a, 1982b, 1984; Pavlinov, 1982; Qumsiyeh, 1986b; 1989; Qumsiyeh *et al.*, 1987; Qumsiyeh and Chesser, 1988).

Jotterand-Bellomo (1984) summarized diploid and fundamental numbers for rodents including 42 species of Gerbillidae. Herein, we provide a more complete and detailed account and updated information on chromosomes of gerbils and jirds. This includes a review of 1) known diploid numbers and autosome and sex chromosome morphology, 2) heterochromatin evolution, 3) individual and geographic variation, and 4) meiotic studies. We hope this review will serve as a resource and thereby stimulate additional research on the evolutionary relationships of gerbils.

Interspecific chromosomal variation.—Karyotypic data from nondifferentially stained chromosomes are known for 64 species of gerbils (Appendix 1). These data illustrate a range in diploid number ($2N$) from 18 in *Ammodillus imbellis* and females of *Taterillus petteri* to 74 in *Gerbillus dunnii* and *G. latastei*. The distribution of diploid numbers in the species of gerbils that have been reported is plotted in Figure 1. In that

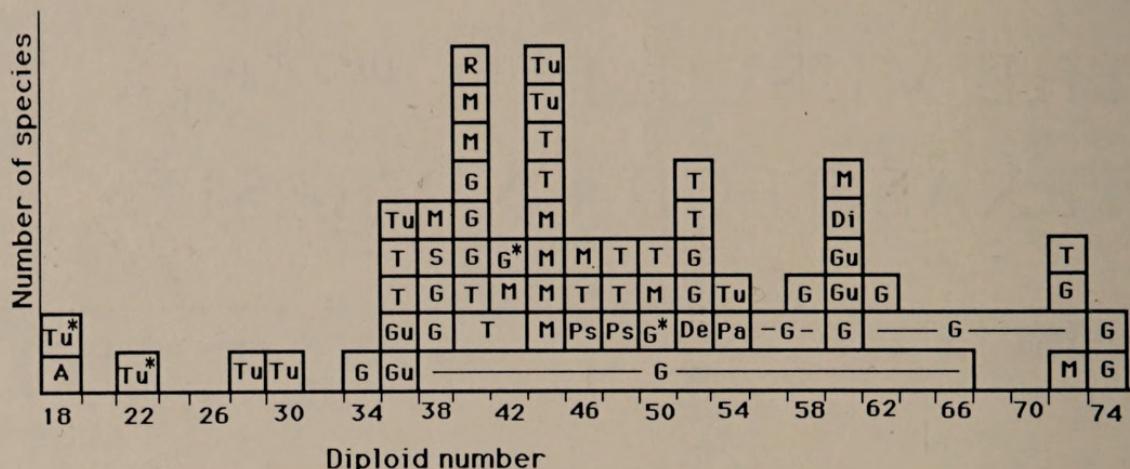


FIG. 1.—Distribution of diploid numbers in species of the family Gerbillidae. Intraspecific variability in diploid numbers is indicated by thin horizontal lines. Asterisks indicate species with sex chromosome-autosome translocations (males have an odd diploid number). Abbreviations: A, *Ammodillus*; De, *Desmodillus*; Di, *Dipodillus*; G, *Gerbillus*; Gu, *Gerbillurus*; M, *Meriones*; Pa, *Pachyuromys*; Ps, *Psammomy*; S, *Sekeetamys*; T, *Tatera*; Tu, *Taterillus*.

figure, we show the number of species of each genus with particular diploid numbers. The genera *Tatera*, *Meriones*, and *Gerbillus* show extensive variability and include species with the highest recorded diploid numbers. These are also the genera with the greatest number of species (Lay, 1983; Carleton and Musser, 1984). Mean and median diploid numbers for gerbils coincide at 44. Species with a range in diploid number resulting from chromosome fusions or fissions, or both, do not affect these central values. This is observed by taking calculations using the highest and lowest diploid numbers possible. This mean or median diploid number of 44 is close to the proposed primitive karyotype ($2N = 52$) based on G-band analysis (Qumsiyeh, 1986b; Qumsiyeh and Chesser, 1988; and see below). From the evidence available it is quite likely that a species with a diploid number of 44 to 52 was the ancestor for all modern species of gerbillids. Higher and lower diploid numbers must have originated by chromosome fissions and fusions, which, on average, raised or lowered the diploid numbers of the effected taxa. However, fusions and fissions were not restricted to certain lineages as clearly some genera show both processes.

Unique insights into relationships and evolution in gerbils became possible with the advent of chromosomal banding techniques. Gamperl and Vistorin (1980) recorded homology of 11 chromosomal arms of *Meriones unguiculatus* with those of *Gerbillus campestris*, providing evidence for the feasibility of a phylogenetic study of gerbil chromosomes. In France, C- and R-banding techniques were used to assess homology among several species of gerbillids (Benazzou *et al.*, 1982a,

1982b, 1984). These papers documented some of the large amount of variation observed and suggested some basic homologies and relationships between certain groups. Other investigations in which differentially stained chromosomes have been utilized include the studies by Wassif (1981). That work was the first in which G- banded sex chromosomes in gerbils were examined and comments were made on the evolution of a sex chromosome complex (see below). The study was limited to eight species of the *Dipodillus-Gerbillus* complex including *Gerbillus calurus* (= *Sekeetamys calurus*). However, based on chromosomal, electrophoretic, and morphological data, the latter species is not a member of that group but is more closely related to species of the genus *Meriones* (Qumsiyeh and Chesser, 1988). Outgroups were not used in any of these earlier studies of chromosomal evolution in gerbils. When characters were used as synapomorphies (shared derived conditions), the most common condition was assumed to be primitive. However, this is not necessarily true and was shown to produce limited information in the case of the gerbillids (Qumsiyeh and Baker, 1988; Qumsiyeh, 1989). In our own studies of chromosomal evolution in this family, the outgroup method for determining primitive as opposed to derived character states was used and independent data sets (morphology and allozyme electrophoresis) were employed to test these relationships. The results of these studies can be summarized as follows.

1. It is possible to compare and find homologies for most or all euchromatic segments from all examined species of gerbils utilizing a standard numbering system for gerbil chromosomes (Qumsiyeh, 1986b, 1989; Qumsiyeh and Chesser, 1988; Qumsiyeh *et al.*, 1991).

2. Using this numbering system and including outgroup taxa (murids and sigmodontids), the primitive karyotype for the family Gerbillidae probably had a $2N = 52$ and $FN = 68$ condition. This reconstructed karyotype was composed of acrocentric or telocentric autosomes 1, 2, 4d, 5, 6, 7, 8, 9, 10, 13, 14, 29, 30, 31, 32, and 33, and biarmed autosomes 3/4p, 11/12, 15/16, 17/18, 19/20, 21/22, 23/24, 25/26, and possibly 27/28 (Qumsiyeh, 1986b; Qumsiyeh and Chesser, 1988).

3. From this proposed primitive karyotype, chromosomal evolution in gerbils proceeded with centric fissions, centric fusions, paracentric and pericentric inversions, tandem fusions, translocations, and heterochromatic additions (Qumsiyeh, 1986b, 1989; Qumsiyeh and Chesser, 1988; Qumsiyeh *et al.*, 1991).

4. These chromosomal rearrangements provide reliable phylogenetic information on gerbils (as shown by concordance with results of studies

using electrophoresis and morphology) except in two situations. First, phylogenetic relationships of taxa with extensive Robertsonian rearrangements (centric fusions and fissions) can be obscured if one follows strict parsimony and no other data set is examined (Qumsiyeh et al., 1987; Qumsiyeh, 1989). Second, heterochromatin on some chromosomes provides no phylogenetic information in gerbils (Qumsiyeh, 1988).

Individual and geographic variation.—Geographic variation in number and morphology of chromosomes is common among rodents. Geographic variation in diploid numbers has been reported for several species of gerbils (for example, *Gerbillus campestris*, *G. pyramidum*, and *Tatera indica*). In well studied examples, variation in 2N is usually the result of Robertsonian translocations (for example, in *Gerbillus pyramidum* and *G. nigeriae*). Other types of geographic variation in gerbil chromosomes are additions and deletions of heterochromatin (Korobitsyna and Korablev, 1980; Qumsiyeh, 1986b; Qumsiyeh and Chesser, 1988) and euchromatin (Qumsiyeh, 1986b; Qumsiyeh et al., 1987). An interesting variation recently discovered is the presence of interstitial C-banded regions in *Gerbillurus paeba* (Qumsiyeh et al., 1991). Similar regions found in wild populations of *Mus musculus* were shown to represent homogeneously staining regions carrying amplified DNA (Traut et al., 1984; Weith et al., 1987).

Heterochromatin.—Patterns of heterochromatic distribution and variation in some species of gerbils have been reviewed by Qumsiyeh (1988). Heterochromatic additions in gerbils are extensive. In some taxa as much as one-third of the chromosomal material is C-band positive (Viegas-Péuignot et al., 1984). As in other rodents, heterochromatic variations appear to provide little phylogenetic information. However, there are certain features of the heterochromatic distribution that are not easily explained. In many of the species of gerbils that have been studied, a pair of autosomes, corresponding to no. 33 of the standard numbering system for gerbils (Qumsiyeh, 1986b), appears to be completely heterochromatic. These species include members of diverse genera of gerbils (for example, *Meriones unguiculatus*, *Tatera leucogaster*, and *Gerbillurus paeba*). The function and significance of this observation remains to be elucidated.

Sex-determining mechanism.—Four of the 64 karyotypically characterized species of gerbils show autosome to sex chromosomes translocations, which result in a non-XX/XY sex-determining system (Appendix). These four species are *Gerbillus gerbillus*, *G. gleadowi*, *Taterillus gracilis*, and *T. petteri*. Detailed studies implicated both

X- and Y-autosome translocations in these species (Wassif, 1977, 1981; Wahrman *et al.*, 1983; Viegas-Péquignot *et al.*, 1984).

Meiotic studies.—Synaptonemal complex analyses in gerbils have contributed to understanding the behavior and origin of sex chromosomes (Wahrman *et al.*, 1983). Our understanding of the behavior of synaptonemal complexes in general has also been advanced by studies on gerbils. The classical studies on XY synapsis (Solari and Ashley, 1977) and the synapsis in inversion loops (Ashley and Moses, 1980; Ashley *et al.*, 1981) in *Psammomys obesus* provided the impetus for further development of this field of cytogenetic investigation.

CONCLUSIONS

The extensive karyotypic diversity in the family Gerbillidae contrasts sharply with the limited morphological evolution found in the family and provides an example of accelerated karyotypic evolution. Chromosomal rearrangements reported in gerbils include centric fusions, centric fissions, tandem fusions, pericentric and paracentric inversions, translocations, euchromatic additions and deletions, and heterochromatic additions and deletions. Intraspecific geographic variation in chromosomal rearrangements also appears to be common in gerbils.

Studies of the rich chromosomal evolution in gerbils combined with recent new studies of variation in morphology and proteins should continue to provide empirical data needed to test the many hypotheses concerning chromosomal evolution and speciation. The feasibility of collecting samples and establishing laboratory colonies in gerbils adds to the benefits of using them as models for studying chromosomal evolution in mammals.

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APPENDIX—*Karyotypic data for gerbils.*

The diploid number is given for each species followed by the number of metacentric and submetacentric autosomes (B), the numbers of acrocentric and telocentric autosomes (A), the size (small letters) and shape (capital letters) of the X and Y chromosomes, general locality or country of origin of samples, and recent references. Some authors include sex chromosomal arms in counts of fundamental numbers, others only autosomal arms. Because of this, we give the number of biarmed autosomes (B) and numbers of acrocentric autosomes (A) rather than the fundamental number (unless this information is not obtainable from these references). In cases where the authors did not separate the sex chromosomes, we indicate this condition with an asterisk under column "B."

Species	2N	B	A	X	Y	Locality	Banding	Reference
<i>Ammodillus imbellis</i>	18	18*	0	—	—	Somalia	—	(Capanna and Merani, 1981)
<i>Brachionus przewalskii</i>	No data							
<i>Desmodillus auricularis baueri</i>	No data							
<i>Desmodillus auricularis</i>	52	—	—	—	—	S. Africa	—	(Matthey, 1954b)
	52	28	22	IM	mM	S. Africa	G,C	(Qumsiyeh, 1986b)
<i>Dipodillus magharebi</i>	No data							
<i>Dipodillus simoni</i>	60	8-10	48-50	—	—	Egypt	—	(Wassif <i>et al.</i> , 1969)
	60	0	58	IM	sSM	Egypt	G,C	(Wassif, 1977; Wassif, 1981)
	60	8-10	48-50	—	—	Tunisia	—	(Cockrum <i>et al.</i> , 1976a)
<i>Gerbillurus paeba</i>	36	—	—	—	—	S. Africa	—	(Matthey, 1958)
	36	34	0	mSM	sA	S. Africa,	—	(Schlitter <i>et al.</i> , 1984)
	36	34	0	mSM	sA/sB	Namibia	G,C	(Qumsiyeh, 1986b; Qumsiyeh <i>et al.</i> , 1991)
<i>Gerbillurus setzeri</i>	60	18	40	ISM	sA	Namibia	—	(Schlitter <i>et al.</i> , 1984)
	60	20	38	ISM	sA	Namibia	G,C	(Qumsiyeh <i>et al.</i> , 1991)
<i>Gerbillurus tytonis</i>	36	34	0	SM	—	Namibia	R	(Benazzou <i>et al.</i> , 1982b)
	36	34	0	mSM	sA	Namibia	—	(Schlitter <i>et al.</i> , 1984)
	36	34	0	ISM	sA	Namibia	G,C	(Qumsiyeh <i>et al.</i> , 1991)

Species	2N	B	A	X	Y	Locality	Banding	Reference
<i>Gerbillurus vallinus</i>	60	22	36	1M	sA	S. Africa, Namibia	—	(Schlitter <i>et al.</i> , 1984)
	60	12-20	38-46	1SM	sA	S. Africa, Namibia	G,C	(Qumsiyeh, 1986b; Qumsiyeh <i>et al.</i> , 1991)
<i>Gerbillus agag</i>	No data							
<i>Gerbillus andersoni</i> (= allenbyi)	40	38	0	1SM	sSM	Egypt	—	(Wassif <i>et al.</i> , 1969)
	40	38	0	1SM	mSM	Egypt	—	(Lay, 1975)
	40	38	0	1SM	SM	Israel	—	(Wahrman <i>et al.</i> , 1988)
	40	38	0	1SM	sSM	Egypt	G,C	(Wassif, 1977; Wassif, 1981)
	40	38	0	—	—	Tunisia	—	(Cockrum <i>et al.</i> , 1976b)
	40	38	0	—	—	Israel	—	(Wahrman and Zahavi, 1955)
<i>Gerbillus aquilus</i>	38	36	0	1SM	sM	Pakistan, Iran	—	(Lay, 1975)
								(Lay and Nadler, 1975)
<i>Gerbillus bottai</i>	No data							
	56	—	—	SM	SM	Algeria	—	(Matthey, 1953)
	56	13-15	41-43	—	—	Egypt	—	(Wassif <i>et al.</i> , 1969)
	58	8	48	1M	mM	Egypt	G,C	(Wassif, 1977; Wassif, 1981)
	56, 57, 58	10-12	44-48	mM	sA	Morocco	—	(Lay, 1975)
	56	14	40	1Ms	SM	Morocco	G,C	(Vistorin and Gamperl, 1978; Gamperl and Vistorin, 1980)
	56	14	40	1SM	sSM	Tunisia	—	(Jordan <i>et al.</i> , 1974)
	38	34	2	mM	sM	Iran	—	(Lay, 1975; Lay and Nadler, 1975)
<i>Gerbillus campestris</i>								(Hsu and Benirschke, 1967-1971)
	38	34	2	mSM	sM	Iran	—	(Ratompomirina <i>et al.</i> , 1986)
	38	—	—	SM	SM	Saudi Arabia	C	(Viegas-Péquignot <i>et al.</i> , 1986)
	38	36	—	M	—	—	R	

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
<i>Gerbillus dasyurus</i>	60	6-8*	52-54	—	—	Sinai	—	(Wahrman and Zahavi, 1955)
	60	6	52	IM	—	Sinai	—	(Lay <i>et al.</i> , 1975; Lay and Nadler, 1975)
	60	9-10	50-51	—	—	Egypt	—	(Wassif <i>et al.</i> , 1969)
	60	8-12	46-50	IM	sA	Jordan, Palestine	G,C	(Qumsiyeh, 1986b)
<i>Gerbillus dunnii</i>	74	24	48	ISM	mM	Somalia	—	(Capanna and Merani, 1981)
<i>Gerbillus famulus</i>	No data	—	—	—	—	—	—	(Matthey, 1953; Matthey, 1954a)
<i>Gerbillus gerbillus</i>	42,43	—	—	—	Y1, Y2	Algeria	—	(Wahrman and Zahavi, 1955)
	42,43	38-40*	—	ISM	Y1,Y2	Israel	—	(Lay <i>et al.</i> , 1975)
	42	32	8	ISM	—	Morocco	—	(Lay <i>et al.</i> , 1975; Lay and Nadler, 1975)
	42,43	32	8	ISM	Y1=sM	Egypt	—	(Wassif, 1977; Wassif, 1981)
	42,43	34	6	ISM	Y1=SM	Egypt	G,C	(Wassif <i>et al.</i> , 1969)
	42,43	34-36	—	ISM	Y2=SM	Egypt	—	(Jordan <i>et al.</i> , 1974)
	42,43	36	6	ISM	Y1=A	Egypt	—	(Hsu and Benirschke, 1967-1971)
	42,43	32	8	ISM	Y2=A	Tunisia	—	(Wahrman <i>et al.</i> , 1983)
	42,43	36	6	ISM	—	Egypt	G,C	(Hsu and Benirschke, 1967-1971; Lay <i>et al.</i> , 1975; Lay and Nadler, 1975)
<i>Gerbillus gleadowi</i>	50,51	20	28	ISM	mA,mM	Pakistan	—	(Wassif <i>et al.</i> , 1969)
<i>Gerbillus henleyi</i>	52	11-13	39-48	—	—	Egypt	—	(Lay <i>et al.</i> , 1975)
	52	8	42	ISM	sA	Morocco	—	(Lay <i>et al.</i> , 1975)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
<i>Gerbilus hesperinus</i>	58	22	34	ISM	M	Morocco	—	(Lay <i>et al.</i> , 1975)
	58	20	36	IM	mM	Morocco	—	(Lay, 1975)
	58	22	34	ISM	M	Morocco	—	(Benazzou and Genest-Villard, 1980)
	58	22	34	ISM	M	Morocco	R,C,Q	(Viegas-Péquignot <i>et al.</i> , 1984)
<i>Gerbilus hoogstraali</i>	72	6	64	ISM	mM	Morocco	—	(Lay, 1975)
	72	6	64	ISM	IM	Morocco	—	(Lay <i>et al.</i> , 1975)
	72	—	—	ISM	M	Morocco	R	(Ratomponirina <i>et al.</i> , 1986; Viegas-Péquignot <i>et al.</i> , 1986)
<i>Gerbilus jamesi</i>	No data					Tunisia	—	(Jordan <i>et al.</i> , 1974; Cockrum <i>et al.</i> , 1976)
<i>Gerbilus latastei</i> (as <i>G. aureus</i>)	74	20-28	44-52	ISM	A			
<i>Gerbilus mackillini</i>	No data							
<i>Gerbilus mauritaniae</i>	No data							
<i>Gerbilus mesopotamiae</i>	No data							
<i>Gerbilus muriculus</i>	No data							
<i>Gerbilus nancilus</i>	No data							
<i>Gerbilus nanus</i>	54	—	—	ISM	ISM	Algeria	—	(Matthey, 1954a)
	52	10-14*	36-40	—	—	Israel	—	(Wahrman and Zahavi, 1955)
	52	8	42	IM	sA	Morocco	—	(Lay <i>et al.</i> , 1975; Lay and Nadler, 1975)
	52	8	42	IM	sA	Tunisia	—	(Jordan <i>et al.</i> , 1974)
	52	9-10*	42-43	—	—	Egypt	—	(Wassif <i>et al.</i> , 1969)
	52	8	44	ISM	sA	Egypt	G,C	(Wassif, 1977; Wassif, 1981)
	52	10	40	ISM	sA	Jordan	G,C	(Qumsiyeh <i>et al.</i> , 1986)

Species	2N	B	A	X	Y	Locality	Banding	Reference
<i>Gerbilus nigeriae</i>	68-72	(variable)		ISM	mM	Burkina Faso	—	(Volobouev <i>et al.</i> , 1988)
	62-68	>30	—	IA	—	Niger	—	(Tranier, 1975)
	72	—	—	IA	M	Niger	R,C,Q	(Viegas-Péquignot <i>et al.</i> , 1984)
	72	—	—	A	M	Burkina Faso	R	(Ratomponirina <i>et al.</i> , 1986)
	67-68	—	—	—	—	Burkina Faso	—	(Gautun <i>et al.</i> , 1985)
<i>Gerbilus occiduus</i>	40	38	0	mM	mM	Morocco	—	(Lay, 1975)
<i>Gerbilus perpallidus</i>	40	34	4	ISM	sM	Egypt	—	(Lay <i>et al.</i> , 1975)
	40	34	4	ISM	sM	Egypt	G	(Wassif, 1977, 1981)
<i>Gerbilus poecilops</i>	No data							
	62	20	40	M?	M?	Ethiopia	—	(Hubert, 1978)
	34	18	14	mA	sM	Somalia	—	(Capanna and Merani, 1981)
<i>Gerbilus pulvinatus</i>				—	—	Algeria	—	(Matthey, 1952; Matthey, 1953)
<i>Gerbilus pusillus</i>				ISM	sM	Egypt	—	(Wassif <i>et al.</i> , 1969; Lay <i>et al.</i> , 1975; Wassif, 1977, 1981)
<i>Gerbilus pyramidum</i>	40	36	2	—	—	Tunisia	—	(Jordan <i>et al.</i> , 1974)
	38	36	0	ISM	IM	Senegal	—	(Hubert and Bohme, 1978)
	40	36	2	IM	IM	Sinai, Israel	—	(Wahrman and Zahavi, 1955; Zahavi and Wahrman, 1957)
	40	—	—	—	—			
40-66 variable			—	—	—			
	50-52	26-24	24-28	SM	M	Israel/Coast	C,B	(Wahrman <i>et al.</i> , 1983)
	64-66	12-10	52-56	SM	M	Negev/Sinai	C,B	(Wahrman <i>et al.</i> , 1983)
<i>Gerbilus riggenbachi</i>	No data							
<i>Gerbilus rosalinda</i>	No data							
<i>Gerbilus ruberrimus</i>	No data							
<i>Gerbilus syrticus</i>	No data							
<i>Gerbilus watersi</i>	No data							
<i>Meriones changi</i>	No data							

Species	2N	B	A	X	Y	Locality	Banding	Reference
<i>Meriones crassus</i>	60	—	—	—	—	Israel	—	(Zahavi and Wahrman, 1957)
	60	10	48	ISM	mSM	Egypt, Iran	—	(Nadler and Lay, 1968)
	60	12	46	ISM	—	Iran	R	(Benazzou <i>et al.</i> , 1982b)
	60	12	48	ISM	mM	Jordan	G,C	(Qumsiyeh <i>et al.</i> , 1986)
<i>Meriones hurrianae</i>	40	36	2	ISM	SM	Iran	—	(Nadler and Lay, 1968)
<i>Meriones libycus</i> (incl. <i>erythrourus</i>)	44	—	—	—	—	—	—	(Matthey, 1953)
	44	30	12	IA	sSM	USSR	—	(Vorontsov and Korobitsyna, 1969)
	44	30	12	IA	mSM	Iran	—	(Nadler and Lay, 1968)
	44	30	12	IA	mSM	Iran	R	(Benazzou <i>et al.</i> , 1982b)
	44	30	12	—	—	Jordan	G	(Qumsiyeh, 1986b as <i>shawii</i>)
<i>Meriones meridianus</i>	50	26	22	IM	sA	USSR	—	(Korobitsyna, 1969; Orlov, 1969; Vorontsov and Korobitsyna, 1969, 1970)
	50	26	22	IM	sSM	Mongolia	—	(Nadler <i>et al.</i> , 1969; Orlov <i>et al.</i> , 1978)
<i>Meriones persicus</i>	42	34	6	ISM	mSM	Iran	—	(Matthey, 1957)
	42	34	6	ISM	—	Iran	R	(Benazzou <i>et al.</i> , 1982b)
	42	34	6	ISM	mSM	USSR	—	(Vorontsov and Korobitsyna, 1969, 1970)
<i>Meriones rex</i>	38	34	2	mM	sM	Saudi Arabia	—	(Al-Saleh and Khan, 1987)
<i>Meriones sacramenti</i>	46	—	—	—	—	Israel	—	(Zahavi and Wahrman, 1957)
<i>Meriones shawi</i>	44	32	10	—	—	—	—	(Matthey, 1957)
	44	30	12	ISM	mSM	Egypt	—	(Hsu and Benirschke, 1967– 1971)
	44	30	12	ISM	mSM	Morocco	R	(Benazzou <i>et al.</i> , 1982b)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
<i>Meriones tamariscinus</i>	40	36	2	IM	—	USSR	—	(Vorontsov and Korobitsyna, 1969, 1970)
	40	36	2	IM	sSM	USSR	—	(Orlov <i>et al.</i> , 1978)
<i>Meriones tristrami</i>	72	0	70	—	—	Iran	R	(Matthey, 1957)
	72	0	70	ISM	—	Iran	R	(Benazzou <i>et al.</i> , 1982a, 1982b)
	72	6-19	51-64	ISM	sSM	USSR	C	(Olov, 1969; Vorontsov and Korobitsyna, 1969; Korobitsyna and Korablev, 1980)
	72	4	66	—	—	Israel	—	(Zahavi and Wahrman, 1957)
	72	0-6	64-70	—	—	Jordan	R	(Qumsiyeh, 1986b, 1988)
<i>Meriones unguiculatus</i>	44	32	10	ISM	mSM	Domestic	—	(Nadler and Lay, 1968)
	44	32	10	ISM	mSM	Domestic	G,C	(Gampel and Vistorin, 1978; Qumsiyeh and Chesser, 1988)
	44	32	10	ISM	sSM	Mongolia	—	(Korobitsyna, 1969; Vorontsov and Korobitsyna, 1969)
	44	32	10	ISM	sSM	Domestic	G	(Gampel and Vistorin, 1980)
<i>Meriones vinogradovi</i>	44	32	10	—	—	—	—	(Matthey, 1954b)
	44	32	10	—	—	Iran	—	(Nadler and Lay, 1968)
	44	32	10	IM	sM	USSR	—	(Orlov, 1969; Vorontsov and Korobitsyna, 1969, 1970; Orlov <i>et al.</i> , 1978)
<i>Meriones zarudnyi</i>	No data							
<i>Microdillus peeli</i>	No data							
<i>Pachyuromys duprasi</i>	54	10	42	SM	—	Morocco	R	(Benazzou <i>et al.</i> , 1984)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
<i>Psammomys obesus</i>	48	24	22	IM	sM	Captive	—	(Smith <i>et al.</i> , 1966)
	48	28	18	ISM	sSM	Captive	—	(Hsu and Benirschke, 1967–1971)
							C	(Solari and Ashley, 1977)
							G,C	(Qumsiyeh, 1986b, 1988)
							—	(Cockrum <i>et al.</i> , 1977)
							—	(Cockrum <i>et al.</i> , 1977)
<i>Psammomys vexillaris</i>	48	28	18	IM	mM	Jordan	—	(Voronitsov and Korobitsyna, 1969)
	48	28	18	IM	mM	Tunisia	—	(Wahrman and Zahavi, 1955)
	48	28	18	IM	M	Tunisia	—	(Wassif <i>et al.</i> , 1969; Wassif, 1977, 1981)
	46	30	14	IM	—	Tunisia	—	(Qumsiyeh and Chesser, 1988)
<i>Rhombomys opimus</i>	40	36	2	ISM	sM	Mongolia	—	(Matthey, 1954b)
				—	—	Sinai	—	(Qumsiyeh, 1986b)
<i>Sekeetamys calurus</i>	38	32-36*	—	IM	sA	Egypt	—	(Matthey, 1954b)
	38	34	2	IM	—	Sinai	G	(Qumsiyeh, 1988)
	38	34	2	ISM	—	S. Africa	—	(Matthey, 1954b)
	38	34	2	ISM	—	S. Africa	G	(Qumsiyeh, 1986b)
<i>Tatera afra</i>	44	NF=70-76	—	—	—	S. Africa	—	(Matthey, 1954b)
	44	24	30	ISM	mM	S. Africa	G	(Qumsiyeh, 1986b)
<i>Tatera boehmi</i>	No data							
<i>Tatera brantsii</i>	44	NF=70-76	M	M	S. Africa	—	(Matthey, 1954b)	
	44	24	20	ISM	mM	S. Africa	G,C	(Qumsiyeh, 1986b)
<i>Tatera gambiana</i>	52	—	—	—	—	Senegal	—	(Hubert <i>et al.</i> , 1973)
<i>Tatera guineae</i>	50	16	32	ISM	A	Burkina Faso	—	(Matthey and Petter, 1970)
	50	16	32	ISM	A	Burkina Faso	R	(Benazzou <i>et al.</i> , 1984; Gautun <i>et al.</i> , 1985)
<i>Tatera hopkinsoni</i>	48	16	30	IA	A	Burkina Faso	—	(Matthey and Petter, 1970; Gautun <i>et al.</i> , 1985)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
<i>Tatera inclusa</i>	No data							
<i>Tatera indica</i>	72	NF=80	—	—	—	India	—	(Matthey, 1953) (Yosida, 1981)
<i>Tatera kempfi</i>	68	16	50	IM	sA	C. African Republic	—	(Matthey and Petter, 1970—prob. <i>T. robusta</i> , Qumsiyeh et al., 1987)
<i>Tatera leucogaster</i>	36	28	6	ISM	mSM			
	42	NF=72	—	M	—	S. Africa	—	(Matthey, 1954b; Matthey, 1958)
	40	28	10	mSM	ISM	S. Africa	—	(Gordon and Rattenbach, 1980)
	40	28	10	ISM	sSM	S. Africa, Namibia	—	(Qumsiyeh, 1986b)
<i>Tatera nigricauda</i>	40	32	6	ISM	mSM	Ethiopia	—	(Matthey, 1969)
	40	32	6	ISM	—	Kenya	G,C	(Qumsiyeh et al., 1987)
<i>Tatera nigrita</i>	48	16	30	ISM	A	Burkina Faso	—	(Matthey and Petter, 1970)
	48	16	30	ISM	A	C. African Republic, Chad	—	(Tranier, 1974a— X polymorphic)
	48	16	30	ISM	A	C. African Republic	R	(Benazzou et al., 1984)
<i>Tatera philippi</i>	46	20	24	ISM	mSM	C. African Republic	—	(Matthey and Petter, 1970; Qumsiyeh et al., 1987)
<i>Tatera robusta</i>	36	34	0	ISM	sSM	Kenya	G,C	(Qumsiyeh et al., 1987)
<i>Tatera valida</i>	52	14	36	ISM	—	Senegal	—	(Matthey, 1969)
<i>Taterillus angelus</i>	No data							
<i>Taterillus arenarius</i>	30	8	20	IM	—	Mauritania	—	(Matthey, 1969—as <i>T. nigritae</i> , see Robbins, 1974)

APPENDIX—Continued.

Species	2N	B	A	X	Y	Locality	Banding	Reference
<i>Taterillus congicus</i>	54	12	40	ISM	—	C. African Republic	—	(Matthey and Petter, 1970)
	54	—	—	—	—	Chad	—	(Tranier <i>et al.</i> , 1974a)
	54	—	—	ISM	sSM	C. African Republic	—	(Genest and Petter, 1973)
	54	12	40	ISM	—	C. African Republic	R	(Benazzou <i>et al.</i> , 1984)
<i>Taterillus emini</i>	44	22	20	ISM	—	Ethiopia	—	(Matthey, 1969)
	44	—	—	—	—	C. African Republic	—	(Genest and Petter, 1973)
<i>Taterillus gracilis</i>	36,37	10	24	IM	SM,M	Senegal	—	(Matthey and Jotterand, 1972— Autosomal polymorphism in addition to XY1Y2 system)
	36,37	8	26	IM	mSM,M	Burkina Faso	—	(Matthey and Petter, 1970)
	36	—	—	r	ISM	Senegal	—	(Viegas-Pequignot <i>et al.</i> , 1982)
					ISM	Kenya	—	
					mSM	Cameroon	—	
					mSM	—		
					—			
<i>Taterillus harringtoni</i>	44	20	22	ISM	—	Burkina Faso	—	(Gautun <i>et al.</i> , 1985)
<i>Taterillus lacustris</i>	28	18	8	ISM	—	Niger	—	(Tranier, 1974)
<i>Taterillus nigeriae</i>	No data (see <i>T. arenarius</i>)			—	—	Burkina Faso	R	(Benazzou <i>et al.</i> , 1984; Sicard <i>et al.</i> , 1988)
<i>Taterillus petteri</i>	18,19	—	—	—	—	—	—	(Matthey, 1969; Matthey and Jotterand, 1972)
	18,19	16	0	—	—	—	—	
	18,19	16	0	—	—	—	—	
<i>Taterillus pygargus</i>	22,23	20	0	ISM	M,SM	Senegal	—	(Ratomponirina <i>et al.</i> , 1986)
	22,23	20	0	SM	SM	Senegal	R	



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